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Challenges in Fish Conservation in Hydropower Affected Rivers in Europe

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Preface

The present dissertation consists of four manuscripts which, respectively, represent the four chapters in this work. All four manuscripts have been published in peer reviewed journals (Chapter I - IV) with permission by the journal sustainability (mdpi) and Fisheries Management & Ecology (Wiley).

The thesis sheds light on the current challenges in freshwater fish conservation in hydropower affected rivers in Europe in terms of the data basis for identifying, assessing and mitigating the impacts of hydropower. An overview of the present data situation on selected life history traits, ecological parameters and habitat requirements related to the most critical life stages of rheophilic fish species is given, highlighting still existing knowledge gaps in species' autecology. Furthermore, a comprehensive literature review focusing on existing and emerging environmental threats to freshwater fishes is presented, using Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta fario*) as model species. In particular, threats affecting critical life stages (i.e. spawning, egg development and emergence) are examined and it is discussed to which extend it may be permissible to draw analogies between the sister species. Moreover, the role of fish behaviour during stow-net fish-monitoring at hydropower plants is investigated, revealing that more consideration should be drawn to fish behaviour in future monitoring, to account for a potential bias of recapture rates. Finally, a comprehensive overview of available recurring and non-recurring costs of fish passage mitigation is given, presenting lifetime costs and possible trade-offs between hydropower use and fish passage mitigation due to water abstraction. The new findings of this work are used to eventually discuss consequences for fish conservation and management, as well as to suggest implications for future research.

Summary

Hydropower plants are one of the main causes for the decline of numerous fish species in Europe, yet hydropower production is of high relevance for reaching the renewable energy targets beyond 2020. This conflicting situation stresses the need for an integrative assessment and mitigation of the impacts of hydropower on fish. In turn, impact assessment and the implementation of suitable mitigation measures require a sound data basis on ecological as well as economic aspects to derive relevant thresholds and decision-support.

In the present thesis a combination of meta-analyses, extensive literature searches and real-world studies is used to (i) present the current knowledge, (ii) add new knowledge and (iii) to reveal existent knowledge gaps on ecological and economic subjects related to hydropower impact assessment and mitigation. Chapter I gives an overview of the present data from grey and peer-reviewed literature on selected life history traits, ecological parameters and habitat requirements related to the most critical life stages of representative riverine fish species, which are considered target species of conservation. Furthermore, the data availability, accessibility and differences between grey and peer-reviewed information is discussed. Chapter II provides a comprehensive review on past, existing and emerging environmental threats to freshwater fish. In detail, it is examined how these threats affect critical life stages (i.e., spawning, egg development and emergence) of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta fario*), which serve as model species. Furthermore, it is discussed which analogies can be drawn between the two sister species. In Chapter III the role of fish behaviour during stow-net fish-monitoring at hydropower plants is examined. A combination of controlled- and real world behavioural experiments is used to film fish behaviour, understand potential trigger mechanisms for certain behavioural patterns and estimate its influence on recapture rates. Chapter IV provides a detailed overview of recurring and non-recurring costs associated with fish passage mitigation. It further presents unit costs and reveals which factors influence capital costs. Eventually, the life time costs for some downstream measures are presented. The results of the thesis highlight that there are still severe knowledge gaps concerning species' autecology. However, grey literature was found to be a valuable complement with the potential to fill some of these gaps. Furthermore, comparisons of life history traits between rheophilic and sister species indicated that analogies between species can be drawn only to a limited extent, clearly emphasizing the need for more basic (field) research on individual fish species ecology. Furthermore, the studies on fish behaviour revealed that fish display specific behavioural patterns which can bias recapture results in net-based monitoring irrespective of their size. Hence, it was concluded that there is an urgent need to further investigate the extent of the bias to be able to account for it in future net-based fish-monitoring investigations at hydropower plants. Finally, the cost analysis on fish passage solutions revealed that there is a need for cost trade-offs between hydropower use and fish passage mitigation, as fish passage solutions can cause power losses. Thereby nature-like bypass systems cause fewer power-losses compared to conventional technical fish passage measures. Furthermore, it was found that construction costs account for the highest share of fish passage lifetime costs. Hence, it was concluded that precise cost figures can simplify the selection process of a mitigation solution.

All in all, the studies herein highlighted that the successful detection of stressor impacts on fish species, their monitoring and the selection of suitable mitigation measures is still hampered by existing knowledge gaps on fish ecology and economic factors. Hence, long-term effective and successful fish conservation and management in hydropower affected rivers relies on solving these identified problems first.

Zusammenfassung

Wasserkraftwerke sind mit für den Rückgang zahlreicher Süßwasser-Fischarten in Europa verantwortlich. Dennoch ist die Wasserkraftnutzung von hoher Relevanz, um den Anteil erneuerbarer Energien weiter zu steigern. Diese Pattsituation unterstreicht die Notwendigkeit einer integrativen Bewertung und Minderung der Auswirkungen von Wasserkraft auf Fische. Die Abschätzung der Auswirkungen und die Umsetzung geeigneter Minderungsmaßnahmen erfordern wiederum eine solide Datenbasis sowohl zu ökologischen als auch zu ökonomischen Aspekten, um relevante Schwellenwerte und Entscheidungshilfen ableiten zu können.

In der vorliegenden Arbeit wird eine Kombination aus Meta-Analysen, umfangreichen Literaturrecherchen und Feldstudien verwendet, um (i) den aktuellen Wissensstand darzustellen, (ii) neues Wissen hinzuzufügen und (iii) bestehende Wissenslücken zu ökologischen und ökonomischen Themen im Zusammenhang mit der Wirkungsabschätzung und -minderung von Wasserkraftwerken aufzuzeigen. Kapitel I gibt einen Überblick über die vorhandenen Daten aus der grauen und peer-reviewed Literatur zu ausgewählten lebensgeschichtlichen Merkmalen, ökologischen Parametern und Habitatanforderungen repräsentativer Fischarten. Ein besonderes Augenmerk liegt dabei auf den kritischen Lebensstadien rheophiler Fischarten. Darüber hinaus werden die Datenverfügbarkeit, die Zugänglichkeit und die Unterschiede zwischen grauen und begutachteten Informationen diskutiert. Kapitel II bietet einen umfassenden Überblick über vergangene, bestehende und aufkommende Umweltbedrohungen für Süßwasserfische. Im Detail wird untersucht, wie sich diese Bedrohungen auf kritische Lebensstadien (d.h. Laichen, Eientwicklung und Emergenz) der Modellarten Atlantischer Lachs (*Salmo salar*) und Bachforelle (*Salmo trutta fario*) auswirken. Weiterhin wird diskutiert, welche Analogien zwischen den beiden Schwesterarten gezogen werden können. In Kapitel III wird die Rolle des Fischverhaltens in Hamennetzen beim Fischmonitoring an Wasserkraftwerken untersucht. Eine Kombination aus kontrollierten und realen Verhaltensexperimenten wird verwendet, um das Fischverhalten zu filmen, mögliche Auslösemechanismen für

bestimmte Verhaltensmuster zu verstehen und deren Einfluss auf die Wiederfangraten abzuschätzen. In Kapitel IV wird eine detaillierte Kostenübersicht über die einmaligen und laufenden Kosten von Fisch-Wanderhilfen präsentiert. Außerdem werden die Preise pro Maßeinheit berechnet und zwischen verschiedenen Wanderhilfen verglichen. Ferner wird aufgezeigt, welche Faktoren die Kapitalkosten maßgeblich mitbeeinflussen. Schließlich werden die Lebenserhaltungskosten für einige Fischwanderhilfen exemplarisch dargestellt. Die Ergebnisse der Arbeit verdeutlichen, dass es immer noch große Wissenslücken bezüglich der Autökologie der Arten gibt. Es wurde jedoch festgestellt, dass graue Literatur eine wertvolle Ergänzung darstellen kann, die das Potenzial hat, einige dieser Lücken zu schließen. Darüber hinaus zeigten Vergleiche von lebensgeschichtlichen Merkmalen zwischen rheophilen und Schwesterarten, dass Analogien zwischen den Arten nur in begrenztem Umfang gezogen werden können. Somit bleibt die Grundlagenforschung (Feldforschung) zur Ökologie einzelner Fischarten für den gezielten Fischschutz von immenser Bedeutung. Weitere Untersuchungen zum Fischverhalten ergaben, dass Fische unabhängig von ihrer Größe spezifische Verhaltensmuster aufweisen, die die Wiederfangergebnisse beim netzbasierten Monitoring verfälschen können. Daraus wurde gefolgert, dass es dringend notwendig ist, das Ausmaß der Ergebnisseverfälschung weiter zu untersuchen, um diese bei zukünftigen netzbasierten Fischmonitoring-Untersuchungen an Wasserkraftwerken berücksichtigen zu können. Schließlich ergab die Kostenanalyse zu Fischwanderhilfen, dass es eine Kostenabwägung zwischen der Wasserkraftnutzung und dem Betrieb von Wanderhilfen gibt, da Fischpasslösungen Stromverluste verursachen können. Dabei verursachen naturnahe Bypass-Systeme im Vergleich zu konventionellen Fischpassmaßnahmen weniger Leistungsverluste. Darüber hinaus wurde festgestellt, dass die Baukosten den größten Anteil an den Lebenserhaltungskosten von Fischwanderhilfen ausmachen. Daraus wurde gefolgert, dass genaue Kostenangaben den Auswahlprozess einer Minderungslösung vereinfachen können.

Alles in allem haben die vorliegenden Studien gezeigt, dass eine Beurteilung der Fischsensitivität gegenüber Stressoren wie der Wasserkraft, sowie die Auswahl geeigneter Minderungsmaßnahmen durch die immer noch vorhandenen Wissenslücken in Bezug auf fischökologische Aspekte und wirtschaftliche Faktoren erschwert wird. Erst, wenn diese Probleme adressiert werden, ist ein effektiver und langfristig erfolgreicher Fischschutz in von Wasserkraft geprägten Flüssen möglich.

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> “*Fischen ist die einzige Art von Philosophie, von der man satt werden kann.*
>
> *Peter Bamm*

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Publication list

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1. General Introduction

Freshwater fish at risk

NICOLE SMIALEK

1.1. Why care about freshwater fish? – Understanding the conservation need

According to global estimates 25,000 – 40,000 fish species account for 30 – 50% of total vertebrate species diversity (Moyle & Cech 2004, Kottelat & Freyhof 2007). Of all known fish species, 40 – 50% inhabit freshwater ecosystems (Moyle & Cech 2004, Hughes et al. 2021). Today, at least 200 million people rely on freshwater fish as their major source of protein and 60 million people depend on it for their livelihoods (Hughes et al. 2021). Fish are valued for the tremendous set of services they provide to support human well-being including ecological, economic and social aspects (Figure 1; Holmlund & Hammer 1999, Geist 2011).

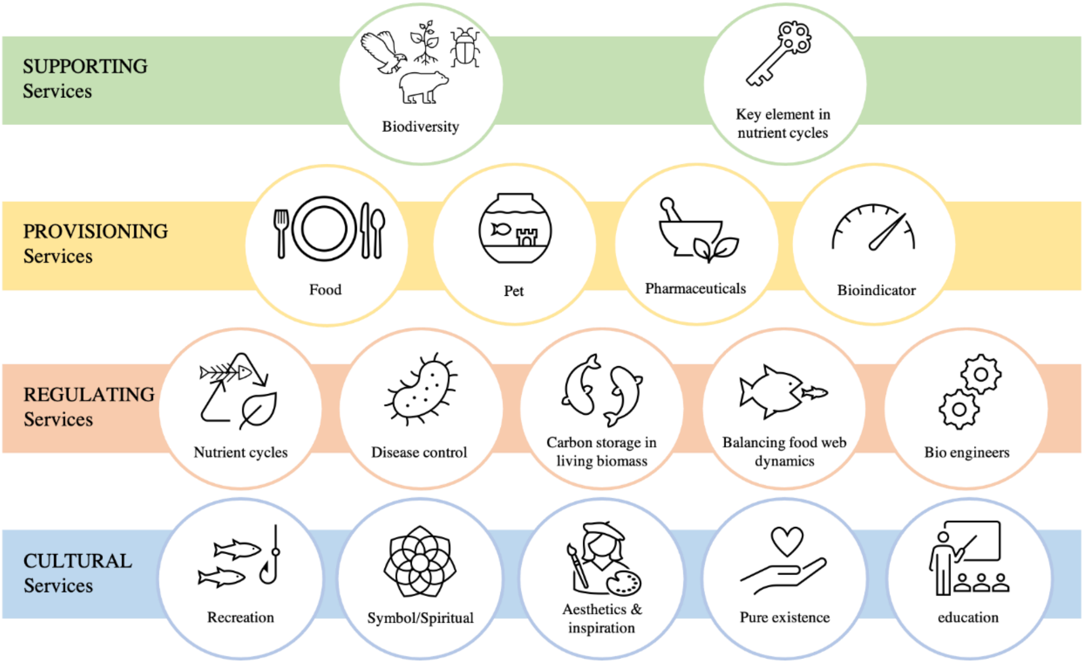

Figure 1. Fish services
Conceptual framework adapted from MEA (2005).

However, freshwater fish are in rapid decline locally and globally (Mueller et al. 2018, Hughes et al. 2021). In 2011, more than 37% of freshwater fish in Europe were already classified as threatened (Freyhof & Brooks 2011). Habitats of freshwater fish are experiencing a biodiversity crisis which appears to be more intense than that of their terrestrial or marine counterparts (Jenkins 2003, Dudgeon et al. 2006) with rivers being most heavily affected (Stein & Flack 1997, Gleick 2003, Dudgeon et al. 2006). Between 1970 and 2016, the biodiversity of freshwater species declined globally about 84% (range 77% – 89%) with most declines seen in fish, amphibians and reptiles (Almond et al. 2020). Considering freshwater fish, the most rapid decline can be seen in migratory fish species. Within 46 years (1970 – 2016) their number has decreased globally by 76% (Almond et al. 2020). Considering only Europe, populations of migratory fish have fallen even more drastically by 93% (Deinet et al. 2020). The reasons for the critical decline in freshwater fish are diverse, with the majority being inextricably linked to human activities (Dudgeon et al. 2006, Mueller et al. 2011, Mueller et al. 2018, Bierschenk et al. 2019, Reid et al. 2019, Mueller et al. 2020c). Common threats include overexploitation, water pollution, climate change, the introduction of invasive species and diseases and the disruption of river ecologies (Figure 2). A challenge for the conservation of freshwater fish is the fact that species are usually exposed to multiple threats simultaneously, which can act additively or synergistically, making their management and mitigation very complex (Groom et al. 2006, Olden et al. 2010, Dudgeon 2019, Reid et al. 2019). The current approach to multiple stressors is to examine one stressor at a time. However, holistic approaches are gaining more and more support (Geist 2011, Ramulifho et al. 2018, Bierschenk et al. 2019, Mueller et al. 2020c).

In Europe, hydropower production causes strong conflicts with conservation needs of freshwater fish species, particular of riverine and migratory species (Aarts et al. 2004, Darwall & Freyhof 2015). However, it is also a threat which can be well studied and offers several opportunities to mitigate its negative impacts (Trussart et al. 2002). Hence, this thesis will focus on the freshwater fish conservation challenges associated with the operation of run-of-the-river power plants in European rivers.

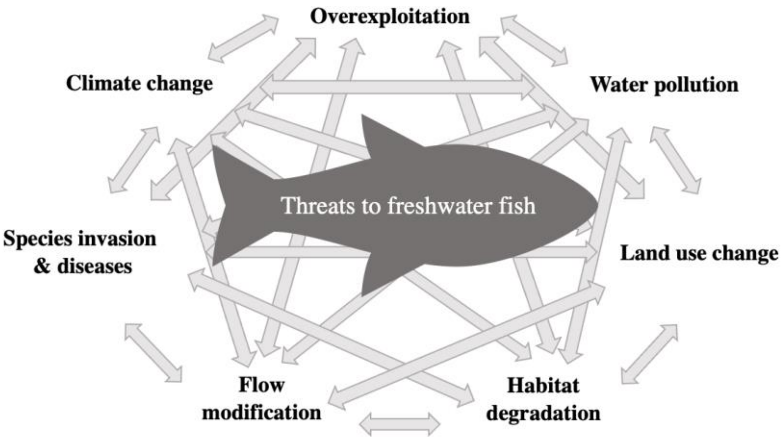

Figure 2. The most prominent threats to freshwater fish
Illustration changed from Dudgeon et al. (2016).

1.2. Hydropower – A prominent example stressor

In 2020, the share of renewable energy production (hydro, wind, solar and bioenergy) in Europe (EU-27s) reached 40% exceeding fossil generation for the first time (Jones & Moore 2020). After wind and solar (21%), hydropower is the largest source of renewable energy (13%) with a total generation of > 348 TWh per year (Agora Energiewende & Sandberg 2020, Jones & Moore 2020). The important contribution of hydropower to the reduction of CO_2 emissions, its low carbon footprint, high resource-efficiency, longevity (up to 80 years) and wide range of ancillary services (e.g., security of supply and grid stability) is often emphasized by hydropower advocates (Eurelectric 2018). Further reported advantages include the ability to generate electricity 24/7 and to offer back-up supply (for bottleneck situations and longer imbalances). This makes them a good complement to solar and wind sources, as these are often only available intermittently (Eurelectric 2018). As such, hydropower today plays a key role in the implementation of the Renewable Energy Directive (2018/2001/EU; European Parliament & Council of the European Union 2018) and in the contribution to the EU energy targets for 2020 – 2030 following the European Green Deal strategy (European Commission 2019).

Despite these benefits to society, hydropower, irrespective of its size, adversely affects river systems and biota with substantial impacts on fish (Santos et al. 2006, Premalatha et al. 2014, Benejam et al. 2016, Mueller et al. 2017, Kuriqi et al. 2021, Mueller et al. 2020d). The percentage of large river systems affected by dams is already over proportionally high in Europe (88%, Nilsson et al. 2005, Amber Consortium 2021) compared to the situation worldwide (77%, Dynesius & Nilsson 1994). It is estimated that there are already 0.74 barriers per kilometre of river (Belletti et al. 2020). Currently, 8,700 additional hydropower plants are planned or under construction with small run-of-the-river power plants being the subject of most criticism (Schwarz 2019, Kuriqi et al. 2021). Compared to their significant impact on river ecosystems (Kuriqi et al. 2021) including potential synergistic effects with other stressors (Ormerod et al. 2010, Mueller et al. 2020c, van der Lee & Verdonshot 2020), they contribute little (13%) to the total electricity production from hydropower and even less towards green energy transition (Arcadis & Ingenieurbüro Floecksmühle 2011, European Union 2018) but account for the majority of hydropower installations in Europe (91%, status 2011). Hydropower effects on the ecosystem are not restricted to operation times but occur at any stage of its life cycle, including construction and retrofitting (European Union 2018). However, the impact can be highly site-specific, depending on various factors such as onsite conditions, type of power plant and the vulnerability of habitats and species affected. Fish, especially riverine and migratory species, are very prone to impacts by hydropower (Larinier 2001, Santos et al. 2006, Benejam et al. 2016, European Union 2018), which can essentially be divided into three main categories: (i) fish get harmed or killed by hydropower structures, (ii) hydropower structures impair fish movements and (iii) hydropower installations cause habitat changes. These can act on individual, population and community level.

Direct fish damage

When fish enter hydropower structures during downstream movement (turbine, spillways etc.), various physical mechanisms can lead to severe harm of the fish (Figure 3; Mueller et al. 2017, Knott et al. 2019a). Occurring strikes and collisions, shear stress, barotrauma and cavitation forces can lead to a broad scale of injuries (e.g., descaling, amputations of body parts or internal injuries; Dedual 2007, Ebel 2013, Mueller et al. 2020d) sometimes resulting in immediate or delayed mortality (Dedual 2007, Ferguson et al. 2006, Killgore et al. 2001, Skalski et al. 2002, Čada et al. 2007, Brown et al. 2012a, Brown 2012b). Moreover, fish can get disorientated after passage and become easy targets for waiting predators e.g., piscivorous birds or fish (Ruggerone 1986, Blackwell & Juanes 1998, Agostinho et al. 2012). The degree of impact depends on the species and size of the fish, with cycloid scaled (e.g., common nase (*Chondrostoma nasus*), common barbel (*Barbus barbus*), European grayling (*Thymallus thymallus*)) and larger fish (e.g., Atlantic salmon (*Salmo salar*), Danube salmon (*Hucho hucho*), European sturgeon (*Acipenser sturio*)) having a higher risk getting injured (descaling, collision with structures; Mueller et al. 2017).

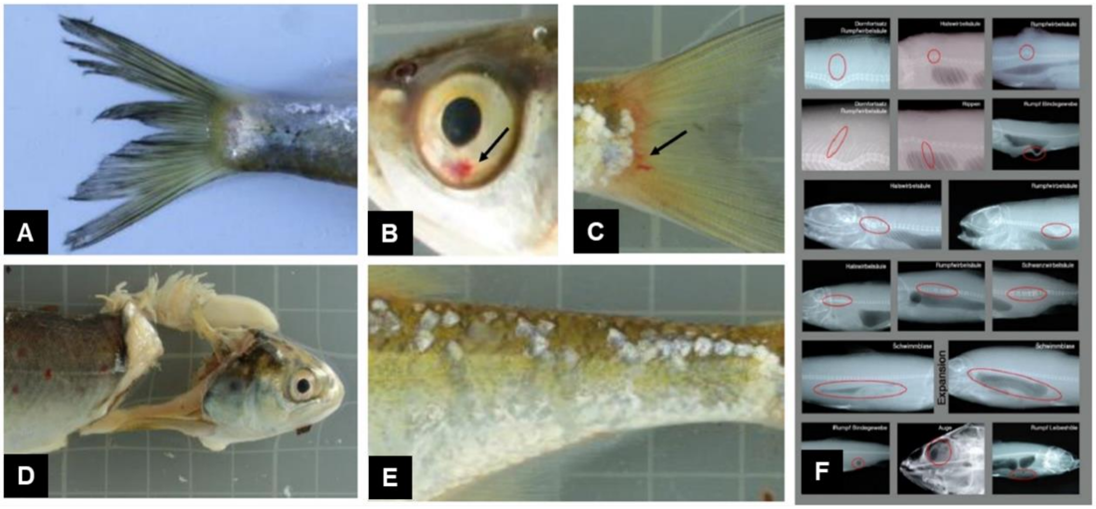

Figure 3. Hydropower induced injuries in fish
External and internal injuries occurring during fish downstream passage at hydropower plants. Pictures taken from Mueller et al. (2017). A: fin tears, B & C: haemorrhages, D: decapitation, E: descaling, F: internal injuries including vertebral fractures and internal haemorrhages.

Impaired fish movement

Up- and downstream movements of fish are impaired or prevented by hydropower facilities and other river impoundments. These are limiting the species' ability to reach important habitats in order to fulfil their life cycle (Lucas & Frear 1997, Kruk & Penczak 2003, Caudill et al. 2007, Wolter et al. 2016). Especially diadromous fish such as Atlantic salmon (*Salmo salar*), Sea trout (*Salmo trutta trutta*), European eel (*Anguilla anguilla*) or European sturgeon (*Acipenser sturio*) suffer from river fragmentation through hydropower plants (Larinier 2001). On long migration routes between freshwater and marine environments, they often have to overcome not only one but several impoundments. This can lead to a delay in migration with detrimental consequences for their reproductive success e.g., mismatch situations or exhaustion

(Larinier 2001, Norrgård et al. 2013). Barriers also block potamodromous fish movements such as of European nase (*Chondrostoma nasus*) or chub (*Leucicus cephalus*), which can cover significant distances between habitats on a diurnal, seasonal or annual basis for e.g., feeding, spawning or overwintering (Larinier 2001, Knott et al. 2019b, Benitez et al. 2015).

Habitat change and loss

Construction and operation of a run-of-the-river hydropower plant is often accompanied by physical modification of the water body (Anderson et al. 2015). Straightening and deepening of river sections (canalisation) as well as bank reinforcement increase homogeneity of structures and correspondingly of associated habitats (Nilsson & Jansson 1995, Poff et al. 2007). The loss of diverse river habitat structures (riparian zones, riffle and pool structures, floodplains etc.) is often linked to a loss in overall biodiversity. Fish species may compete for the remaining limited resources or vanish (Welcomme 1985, Power et al. 1996, Bunn & Arthington 2002, Hoffman & Dunham 2007). Furthermore, the barrier function of a hydropower facility impairs river dynamic processes and matter fluxes e.g., sediment, nutrients, debris (Kuriqi et al. 2021, Poff et al. 2007). The disruption of continuous downstream transport of sediments, for example, can result in a heavy accumulation of sediments upstream of hydropower plants and an increased erosion of the river beds and banks downstream. Both processes can result in the siltation and even colmation of fish spawning grounds. This can have detrimental consequences for the reproductive success of lithophilic (i.e., gravel spawning) species such as European nase (*Chondrostoma nasus*), brown trout (*Salmo trutta fario*) or Atlantic salmon (*Salmo salar*) (Berkman & Rabeni 1987, Chapman 1988, Milan et al. 2000, Ovidio & Philippart 2008, Sternecker & Geist 2010), which highly depend on well flowed and oxygenated gravel banks. Besides the disruption of matter fluxes, dams can suppress natural seasonal flood cycles which connect and support associated habitats (e.g., alluvial forests, temporary ponds and oxbow lakes) and species (Pander et al. 2015, Latrubesse et al. 2021). Furthermore, changes in river temperature (winter warming and summer cooling), chemical quality (especially oxygen and nitrate concentration), mineral composition and pH up- and downstream of dams has been reported. However, these effects are more pronounced in reservoir hydropower plants than in run-of-the-river plants (Olden & Naiman 2010, Fantin-Cruz et al. 2016, European Union 2018, Heggenes et al. 2021).

Those impacts of hydropower on riverine fish species cause strong conflicts with freshwater fish conservation needs which are also laid down in the EU environmental law. Legal requirements to directly or indirectly protect Europe’s fish fauna and their habitats are embedded in the Water Framework Directive (2000/60/EC; Council of the European Communities 2000), the Birds and Habitats Directives (92/43/EEC; Council of the European Communities 1992), the Eel Regulation (1100/2007/EC; Council of the European Union 2007) and the European Union’s Biodiversity strategy for 2030 (European Commission 2020). Therefore, it is important to identify, evaluate, monitor and mitigate hydropower impacts on freshwater fish to find a reasonable trade-off between “green” energy production and the conservation of freshwater fish and the services that they provide to human society (Geist 2021).

1.3. From problem to solution

In order to conserve fish populations, an integrative assessment and mitigation of threats is necessary. This often requires considering multiple scales raging from considering the different modes of action of the stressor on different species levels (indiviual, population, community) as well as the effectiveness of different mitigation options on the respective species levels and its associated costs as illustrated in Figure 4. The first prerequisite to assess and mitigate the impacts of threats such as hydropower includes a sound knowledge on the species' autecology under consideration of the life cycle. Knowledge about species-specific requirements, environmental tolerances and life history traits helps, for example, to identify the sensitivity of species to specific modes of action of hydropower operation. More precisely, it can help to identify population bottlenecks and the sensitivity of critical life stages (e.g., spawning, early development).

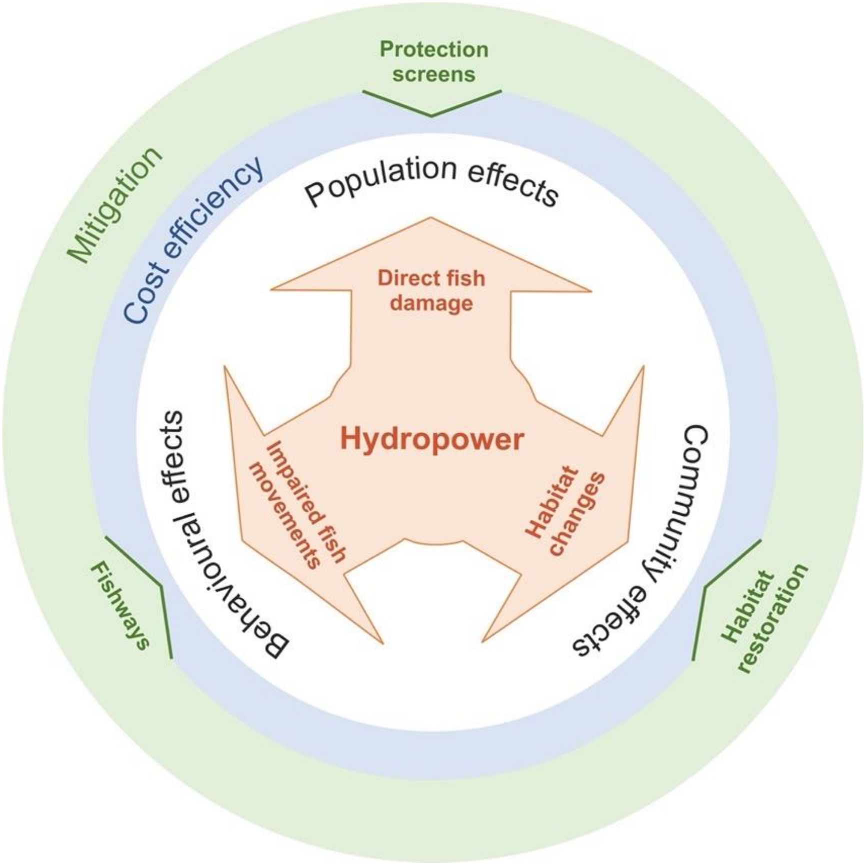

Figure 4. Integrative approach to hydropower mitigation
The illustration is simplified, the terms listed are examples. Hydropower impacts and mitigation options point to the fish aspects/scales, which they effect the most. However, each impact also influences the other components of fish ecology, which is symbolized by the united white open circle in which the fish ecological terms are located.

A very characteristic example for differences in sensitivity to certain stressors is the increasing siltation of spawning grounds of lithophilic fish species. While siltation has no direct lethal effect on adults, it can lead to high mortality rates of eggs and larvae and thus pose a significant threat to the successful reproduction of the population (O’Connor & Andrew 1998, Acornley & Sear 1999, Greig et al. 2005, Sternecker & Geist 2010, Mueller et al. 2018, Nagel et al. 2020). Such data on species-specific requirements, environmental tolerances and life history is increasingly finding its way into hydropower impact assessments (Mueller et al. 2011, van Treeck et al. 2021), ecological modelling (e.g., to predict fish distribution affected by flow dynamics) and habitat suitability modelling (e.g., to determine the effect of siltation on spawning grounds; Hatten et al. 2009, Garcia et al. 2011, Zhang et al. 2018, Bierschenk et al.

2019). The most common types of data used in such model studies are physical-chemical quality parameters (e.g., flow velocity, oxygen content, substrate composition) of adult, mostly economic valuable fish species. In contrast, autecological data on less extensively studied fish species seem scarce and information can differ greatly between sources (Frimpong & Angermeier 2009, Teletchea et al. 2009, Schmidt-Kloiber & Hering 2015). There is data on many species in grey literature such as in technical reports prepared by local expert offices on behalf of local authorities in the respective national language. However, it is unclear how reliable this information is due to a lack of a peer-review process. Autecological data is also highly relevant to implement appropriate and successful management and mitigation measures, especially when management measures should not only include individual species (i.e., single species management) but the ecological community such as in ecosystem-based management (Langhans et al. 2019). This can concern the fish community or even further organisms (e.g., macrozoobentos). Considering only the fish community, the question arises as to whether analogies can be drawn, at least within close relatives, when one species is data deficient or if it is necessary to know the autecology of each species. Transferability of knowledge could be of high advantage when time for action is pressing, especially for species threatened with extinction.

In addition to the understanding of autecological habitat requirements of individual species and a comparative analysis of the life cycles of multiple species, behavioural aspects also play a crucial role in finding suitable mitigation strategies (Figure 4). This is already evident comparing different life histories among closely related species such as anadromous Atlantic salmon and resident brown trout. Both species have similar autecological requirements and are thus known to occur in the same habitats (Klemetsen et al. 2003, Heggberget et al. 1988). However, in contrast to brown trout, Atlantic salmon show a pronounced migratory behaviour at a certain point in their life cycle. Passability of hydropower structures is thus immensely important for Atlantic salmon to fulfil its life-cycle. In this context, the general movement behaviour of a species and its response to external triggers (e.g., discharge) may considerably influence their corridor choice when they try to pass a hydropower structure (Coutant & Whitney 2000, Egg et al. 2017). Furthermore, movement and behaviour can also be triggered by the time of the day or season (Knott et al. 2019b). Fish behaviour may also play an important role during monitoring. For example, during net-based monitoring for hydropower impact assessments, individual fish were observed to display a diverse set of behaviours that lead to them not being caught in the catch unit of the net (Mueller et al. 2020a, Mueller et al. 2020b). This behaviour has not yet been studied in detail and has therefore remained unconsidered in monitoring practice at hydropower plants. Fish behaviour can be investigated using cameras, sonar-systems (Egg et al. 2018) or telemetry methods (Thorstad et al. 2013), depending on the research question.

In addition to understanding the autecology of species, comparing community life histories and integrating behaviour, it is also important to know what kind of mitigation measures can be implemented (Figure 4). This goes beyond the scientific aspect, as it also raises the question of the costs of the solutions and their acceptance. The most common solution in connection with hydropower are fish ways, which can be either technical (e.g., fish ladders, fish lifts, lorries) or nature-like (e.g, bypass channels). Most upstream migration devices are constructed to serve primarly popular game-fish or commercially important fish species such as Atlantic salmon (Mallen-Cooper & Brand 2007, Birnie-Gauvin 2019). However, since each fish species has different preferences regarding for example, flow conditions, slope and water depth depending on their size, swimming abilities and preferred orientation in water, it has been criticized that such “customized” fish ladders may not serve each fish species in the river system equally well (Silva et al. 2018, Birnie-Gauvin 2019). While fish ladders are generally a good solution for upstream fish movements, downstream migrants often do not use these facilities for passage in appreciable numbers (Agostinho et al. 2011). Downstream migrants tend to follow the main flow in the river, hence, typical downstream routes of fish include direct passage through turbines or spillways (Clay 1995, Arnekleiv et al. 2007, Larinier 2008). Thus, solutions mainly focus on preventing fish from entering these structures (e.g., light or electrical installations, fish protection racks). For up- and donwstream fish passage measures, there are various costs including expenses for planning, construction, operation, maintenance and efficency monitoring. Furthermore, water flow modifications through such facilities (e.g., water held back by racks, abstracted water for maintaining constant flow in a fish ladder) can reduce power production. In the European Union, costs for mitigation measures need to be carried by the hydropower operators ("polluter pays principle"; Köhler & Ruud 2019). Support schemes, feed-in tariffs and green power labels can compensate for some of the costs. In other countries, such as Switzerland, mitigation is financed by state authorities using taxes ("Swiss Grid Fund"; Köhler & Ruud 2019). As sustainable management of hydropower must balance mitigation measures for fish with renewable energy production, decision makers require information about cost trade-offs. However, cost overviews are scarce and little is known about how high the lifetime costs of such mitigation measures are.

1.4. Objectives

For successful management and conservation of freshwater fish in hydropower affected rivers, a solid data basis on multiple scales is essential. Knowledge about autecological requirements, the comparison of community life histories and the consideration of behavioural aspects are a prerequisite to both, better assess the impact of threats such as hydropower as well as to implement suitable management and mitigation measures. Moreover, data transparency with respect to the implementation of mitigation measures from both an ecological and economic perspective are important to promote future projects to be more ecologically and economically efficient. In this context the present thesis addresses the following questions:

(1) What is the general accessibility of relevant ecological and economic data for fish conservation in hydropower-affected rivers? (Chapters I & IV)

   a. Can data from grey literature be a valid complement to peer-reviewed data? (Chapter I)

(2) How much do we actually know about basic ecological requirements of European riverine fish species? (Chapter I & Chapter II)

(3) Which analogies and differences do exist within lithophilic species or close relatives concerning their autecological requirements? (Chapter I & Chapter II)

(4) Which conservation implications can be derived for critical life stages (spawning, egg development, emerging larvae) to fish species living in hydropower impacted rivers? (Chapter II)

(5) Which role does fish behaviour play in standardised sampling methods estimating hydropower impacts on fish? (Chapter III)

(6) How much does the construction, operation and maintenance of mitigation measures cost the hydropower operator? (Chapter IV)

1.5. References

Aarts, B.G., Van Den Brink, F.W., & Nienhuis, P.H. (2004). Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: the transversal floodplain gradient. *River research and Applications*, 20(1), 3–23.

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.

Agora Energiewende & Sandbag (2020). The European Power Sector in 2019: Up-to-Date Analysis on the Electricity Transition. *Agora Energiewende*. Retrieved June 26th, 2021 from https://www.agora-energiewende.de/en/publications/the-european-power-sector-in-2019/

Agostinho, C.S., Pelicice, F.M., Marques, E.E., Soares, A.B., & de Almeida, D.A.A. (2011). All that goes up must come down? Absence of downstream passage through a fish ladder in a large Amazonian river. *Hydrobiologia*, 675(1), 1–12.

Agostinho, A.A., Agostinho, C.S., Pelicice, F.M., & Marques, E.E. (2012). Fish ladders: safe fish passage or hotspot for predation?. *Neotropical Ichthyology*, 10(4), 687–696.

Almond, R.E.A., Grooten, M. & Petersen, T. (2020). *Living planet report 2020 - Bending the curve of biodiversity loss*. Gland, Switzerland, WWF International, 83pp.

AMBER Consortium (2020). The AMBER Barrier Atlas. A Pan-European database of artificial instream barriers. Version 1.0 June 29th 2020. Retrieved June 26th, 2021 from: https://amber.international/european-barrier-atlas/

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(2), 268–276.

Arcadis & Ingenieurbüro Floecksmühle, (2011). Hydropower Generation in the context of the EU WFD Contract N ° 070307/2010/574390 EC DG Environment Project number 11418, Version 5. Brussels, Belgium, ARCADIS, 168pp.

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*. Dordrecht, Netherlands, Springer. pp. 5–15.

Belletti, B., de Leaniz, C.G., Jones, J., Bizzi, S., Börger, L., Segura, G., & Castelletti, A., (2020). More than one million barriers fragment Europe's rivers. *Nature*, 588(7838), 436–441.

Benejam, L., Saura-Mas, S., Bardina, M., Solà, C., Munné, A., & García-Berthou, E. (2016). Ecological impacts of small hydropower plants on headwater stream fish: from individual to community effects. *Ecology of Freshwater Fish*, 25(2), 295–306.

Benitez, J.P., Matondo, B.N., Dierckx, A., & Ovidio, M. (2015). An overview of potamodromous fish upstream movements in medium-sized rivers, by means of fish passes monitoring. *Aquatic Ecology*, 49(4), 481–497.

Berkman, H.E., & Rabeni, C.F. (1987). Effect of siltation on stream fish communities. *Environmental Biology of Fishes*, 18, 285–294.

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.

Birnie-Gauvin, K., Franklin, P., Wilkes, M., & Aarestrup, K. (2019). Moving beyond fitting fish into equations: Progressing the fish passage debate in the Anthropocene. *Aquatic conservation: Marine and freshwater ecosystems*, 29(7), 1095–1105.

Blackwell, B.F., & Juanes, F. (1998). Predation on Atlantic salmon smolts by striped bass after dam passage. *North American Journal of Fisheries Management*, 18(4), 936–939.

Brown, R.S., Carlson, T.J., Gingerich, A.J., Stephenson, J.R., Pflugrath, B.D., & Welch, A.E. (2012a). Quantifying mortal injury of juvenile Chinook salmon exposed to simulated hydro-turbine passage. *Transactions of the American Fisheries Society*, 141(1), 147–157.

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

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

Čada, G.F., Garrison, L., & Fisher, R. (2007). Determining the effect of shear stress on fish mortality during turbine passage. *Hydro Review*, 26(7), 52–59.

Caudill, C. C., Daigle, W. R., Keefer, M. L., Boggs, C. T., Jepson, M. A., Burke, B. J., Zabel. R. W., et al. (2007). Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? *Canadian Journal of Fisheries and Aquatic Sciences*, 64(7), 979–995.

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), 1–21.

Clay, C.H. (1995). *Design of Fishways and Other Fish Facilities*. Boca Raton, United States, Lewis Publishers. 256pp.

Council of the European Communities. (1992). Directive 92/43/EEC. On the conservation of natural habitats and of wild fauna and flora. Official Journal of the European Communities, 206, 7–50.

Council of the European Communities. (2000). Directive 2000/60/EC. Establishing a framework for the community action in the field of water policy. Official Journal of the European Communities, 327, 1–73.

Council of the European Union. (2007). Regulation 1100/2007/EC. Establishing measures for the recovery of the stock of European eel. Official Journal of the European Union, 248, 17–23.

Coutant, C.C. & Whitney, R.R. (2000). Fish behavior in relation to passage through hydropower turbines: A review. *Transactions of the American Fisheries Society*, 129, 351–380.

Darwall, W.R. & Freyhof, J. (2015). Lost fishes, who is counting? The extent of the threat to freshwater fish biodiversity. In G.P. Closs, M. Krkosek & J.D. Olden

(Eds.), *Conservation of Freshwater Fishes.* Cambridge, Cambridge University Press. pp. 1–35.

Dedual, M. (2007). Survival of juvenile rainbow trout passing through a Francis turbine. *North American Journal of Fisheries Management*, 27(1), 181–186.

Deinet, S., Scott-Gatty, K., Rotton, H., Twardek, W.M., Marconi, V., McRae, L., Baumgartner, L., et al. (2020). The Living planet index (LPI) for migratory freshwater fish. Technical report. Groningen, Netherlands, World Fish Migration Foundation. 30pp.

Dudgeon, D. (2019). Multiple threats imperil freshwater biodiversity in the Anthropocene. *Current Biology*, 29(19), 960– 967.

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

Dynesius, M., & Nilsson, C. (1994). Fragmentation and flow regulation of river systems in the northern third of the world. *Science*, 266(5186), 753–762.

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

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. (2018). Comparison of sonar-, camera-and net-based methods in detecting riverine fish-movement patterns. *Marine and Freshwater Research*, 69(12), 1905–1912.

Eurelectric, 2018. Water Framework Directive: Experiences & Recommendations from the Hydropower Sector - A Eurelectric position paper, 1–17.

European Commission (2019). The European Green Deal. Communication from the Commission to the European Parliament, the Council, the European Economic and

Social Committee and the Committee of the Regions. Brussels, Belgium COM/2019/640, pp. 24.

European Commission (2020). EU Biodiversity Strategy for 2030 – Bringing nature back into our lives. Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions. Brussels, Belgium. COM/2020/380, pp. 23.

European Parliament & Council of the European Union (2018). Directive 2018/2001/EU. On the promotion of the use of energy from renewable sources. *Official Journal of the European Union*, 328, 1–128.

European Union (2018). *Guidance on the requirements for hydropower in relation to EU Nature legislation*. Luxembourg, Luxembourg, European Union. pp. 87

Fantin-Cruz, I., Pedrollo, O., Girard, P., Zeilhofer, P., & Hamilton, S.K. (2016). Changes in river water quality caused by a diversion hydropower dam bordering the Pantanal floodplain. *Hydrobiologia*, 768(1), 223–238.

Ferguson, J.W., Absolon, R.F., Carlson, T.J., & Sandford, B.P. (2006). Evidence of delayed mortality on juvenile Pacific salmon passing through turbines at Columbia River dams. *Transactions of the American Fisheries Society*, 135(1), 139–150.

Freyhof, J. & Brooks, E. (2011). European Red List of Freshwater Fishes. Luxembourg, Belgium, Publication Office of the European Union. 70pp.

Frimpong, E.A., & Angermeier, P.L. (2009). Fish traits: a database of ecological and life-history traits of freshwater fishes of the United States. *Fisheries*, 34(10), 487–495.

Garcia, A., Jorde, K., Habit, E., Caamano, D., & Parra, O. (2011). Downstream Environmental Effects of Dam Operations: Changes in Habitat Quality for Native Fish Species. *River Research and Application*, 27, 312–327.

Geist, J. (2011). Integrative freshwater ecology and biodiversity conservation. *Ecological Indicators*, 11(6), 1507–1516.

Geist, J. (2021). Editorial: Green or red: Challenges for fish and freshwater biodiversity conservation related to hydropower. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 1–8.

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

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.

Groom, M.J., Meffe, G.K., Carroll, C.R., & Andelman, S.J. (2006) *Principles of Conservation Biology* (3rd ed). Sunderland, UK: Sinnauer Associates. 779pp.

Hatten, J.R., Tiffan, K.F., Anglin, D.R., Haeseker, S.L., Skalicky, J.J., & Schaller, H. (2009). A spatial model to assess the effects of hydropower operations on Columbia River fall Chinook salmon spawning habitat. *North American Journal of Fisheries Management*, 29(5), 1379–1405.

Heggberget, T.G., Haukebø, T., Mork, J., & Ståhl, G. (1988). Temporal and spatial segregation of spawning in sympatric populations of Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L. *Journal of Fish Biology*, 33(3), 347–356.

Heggenes, J., Stickler, M., Alfredsen, K., Brittain, J.E., Bustos, A.A., & Huusko, A. (2021) changes, biological responses and mitigating measures in northern river systems. *River Research and Applications,* 37, 743–765.

Hoffman, R., & Dunham, J. (2007). Fish-movement ecology in high-gradient headwater streams: its relevance to fish passage restoration through stream culvert barriers. Virginia, USA, US Geological Survey, Open File Report 2007–1140, 37pp.

Holmlund, C.M., & Hammer, M. (1999). Ecosystem services generated by fish populations. *Ecological economics*, 29(2), 253–268.

Hughes, K., Harrison, I., Darwall, W., Lee, R., Muruven, D., Revenga, C., Claussen, J., et al. (2021). *The World's Forgotten Fishes*. Gland, Switzerland, WWF International. Retrieved June 26th, 2021 from: https://wwfint.awsassets.panda.org /downloads/world_s_forgotten_fishes__final_april9_.pdf

Jenkins, M. (2003). Prospects for biodiversity. *Science*, 302(5648), 1175–1177.

Jones, D., & Moore, C. (2020). Renewables beat fossil fuels - A half-yearly analysis of Europe’s electricity transition. EMBER. 12pp.

Killgore, K.J., Maynord, S.T., Chan, M.D., & Morgan, R.P. (2001). Evaluation of propeller-induced mortality on early life stages of selected fish species. *North American Journal of Fisheries Management*, 21(4), 947–955.

Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'connell, M.F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of freshwater fish*, 12(1), 1–59.

Knott, J., Mueller, M., Pander, J., & Geist, J. (2019a). Fish passage and injury risk at a surface bypass of a small-scale hydropower plant. *Sustainability*, 11(21), 6037.

Knott, J., Mueller, M., Pander, J., & Geist, J. (2019b). Seasonal and diurnal variation of downstream fish movement at four small-scale hydropower plants. *Ecology of Freshwater Fish*, 29(1), 74–88.

Kottelat, M., & Freyhof, J. (2007). *Handbook of European Freshwater Fishes*. Cornol, Switzerland/Berlin, Germany, Kottelat/Freyhof, 646pp.

Köhler, B., & Ruud, A. (2019). How are environmental measures realized in European hydropower? - A case-study of Austria, Sweden and Switzerland. HydroCen Report No. 9, Trondheim, Norway, Norwegian Institute for Nature Research (NINA). 81pp.

Kruk, A., & Penczak, T. (2003). Impoundment impact on populations of facultative riverine fish. *Annales de Limnologie-International Journal of Limnology*, 39(3), 197–210.

Kuriqi, A., Pinheiro, A.N., Sordo-Ward, A., Bejarano, M.D., & Garrote, L. (2021). Ecological impacts of run-of-river hydropower plants—Current status and future prospects on the brink of energy transition. *Renewable and Sustainable Energy Reviews*, 110833.

Langhans, S.D., Domisch, S., Balbi, S., Delacámara, G., Hermoso, V., Kuemmerlen, M., Martin, R., et al. (2019). Combining eight research areas to foster the uptake of ecosystem-based management in fresh waters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29(7), 1161–1173.

Larinier, M. (2001). Environmental issues, dams and fish migration. *FAO Fisheries Technical Paper*, 419, 45–90.

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

Latrubesse, E.M., d'Horta, F.M., Ribas, C.C., Wittmann, F., Zuanon, J., Park, E., Dunne, T. (2021). Vulnerability of the biota in riverine and seasonally flooded habitats to damming of Amazonian rivers. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(5), 1136–1149.

Lucas, M. C., & Frear, P. A. (1997). Effects of a flow-gauging weir on the migratory behaviour of adult barbel, a riverine cyprinid. *Journal of Fish Biology*, 50(2), 382–396.

Mallen-Cooper, M. & Brand, D.A. (2007). Non-salmonids in a salmonid fishway: what do 50 years of data tell us about past and future fish passage? *Fisheries Management and Ecology*, 14, 319–332.

Milan, D.J., Petts, G.E., & Sambrook, H. (2000). Regional variations in the sediment structure of trout streams in southern England: benchmark data for siltation assessment and restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 10(6), 407–420.

Moyle, P.B. & Cech, J. (2004). *Fishes- An Introduction to Ichtyology* (5th Edition). San Francisco, USA, Pearson Benjamin Cummings. 752pp.

Mueller, M., Knott, J., Egg, L., Bierschenk, B., Pander, J., & Geist, J. (2020a). *Fischökologisches Monitoring an Innovativen Wasserkraftanlagen: Band 1 Hintergrund und Methoden; Technical Report for Bayerisches Landesamt für Umwelt*. Freising, Germany, Technical University Munich.

Mueller, M., Knott, J., Pander, J., & Geist, J. (2020b). *Fischökologisches Monitoring an Innovativen Wasserkraftanlagen: Band 7 Eixendorf an der Schwarzach*; Technical Report for Bayerisches Landesamt für Umwelt. Freising, Germany, Technical University Munich.

Mueller, M., Pander, J., & Geist, J. (2011). The effects of weirs on structural stream habitat and biological communities. *Journal of Applied Ecology*, 48(6), 1450–1461.

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(3), 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. (2020c). 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. (2020d). Assessing turbine passage effects on internal fish injury and delayed mortality using X-ray imaging. *PeerJ,* 8, e9977.

Nagel, C., Pander, J., Mueller, M., & Geist, J. (2020). Substrate composition determines emergence success and development of European nase larvae (*Chondrostoma nasus* L.). *Ecology of Freshwater Fish*, 29(1), 121–131.

Nilsson, C., & Jansson, R. (1995). Floristic differences between riparian corridors of regulated and free-flowing boreal rivers. *Regulated Rivers: Research & Management*, 11, 55–66.

Nilsson, C., Reidy, C. A., Dynesius, M., & Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. *Science*, 308(5720), 405–408.

Norrgård, J. R., Greenberg, L. A., Piccolo, J. J., Schmitz, M., & Bergman, E. (2013). Multiplicative loss of landlocked Atlantic salmon *Salmo salar* L. smolts during downstream migration through multiple dams. *River Research and Applications*, *29*(10), 1306–1317.

O'Conner, W. C. K., & Andrew, T. E. (1998). The effects of siltation on Atlantic salmon, *Salmo salar* L., embryos in the River Bush. *Fisheries Management and Ecology*, 5(5), 393–401.

Olden, J.D., Kennard, M.J., Leprieur, F., Tedesco, P., Winemiller, K.O., García-Berthou, E. (2010). Conservation biogeography of freshwater fishes: recent progress and future challenges. *Divers Distribution* 16, 496–513.

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*(1), 86–107.

Ormerod, S.J., Dobson, M., Hildrew, A.G. & Townsend, C. (2010). Multiple stressors in freshwater ecosystems. *Freshwater Biology*, 55(s1), 1–4.

Ovidio, M., & Philippart, J. C. (2008). Movement patterns and spawning activity of individual nase *Chondrostoma nasus*(L.) inflow-regulated and weir-fragmented rivers. Journal of *Applied Ichthyology*, 24, 256–262.

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

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

Power, M.E., Dietrich, W.E., & Finlay, J.C. (1996). Dams and downstream aquatic biodiversity: potential food web consequences of hydrologic and geomorphic change. *Environmental Management*, 20, 887–895

Premalatha, M., Abbasi, T., & Abbasi, S.A. (2014). A critical view on the eco-friendliness of small hydroelectric installations. *Science of the Total Environment*, 481, 638–643.

Ramulifho, P.A., Rivers-Moore, N.A., Dallas, H.F., & Foord, S.H. (2018). A conceptual framework towards more holistic freshwater conservation planning through incorporation of stream connectivity and thermal vulnerability. *Journal of Hydrology*, 556, 173–181.

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., et al. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94(3), 849–873.

Ruggerone, G.T. (1986). Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. *Transactions of the American Fisheries Society*, 115(5), 736–742.

Santos, J.M., Ferreira, M.T., Pinheiro, A.N., & Bochechas, J.H. (2006). Effects of small hydropower plants on fish assemblages in medium-sized streams in central and northern Portugal. *Aquatic conservation: marine and freshwater ecosystems*, 16(4), 373–388.

Schmidt-Kloiber, A., & Hering, D. (2015). www.freshwaterecology.info–An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, 53, 271–282.

Schwarz, U. (2019). Hydropower Pressure on European Rivers: The Story in Numbers; FLUVIUS. WWF, RiverWatch, EuroNatur, GEOTA Technical Report. Luxembourg, Luexembourg, EU Publications. Retrieved June 26th, 2021 from: https://balkanrivers.net/sites/default/files/European%20Hydropower%20report%202019_w.pdf

Silva, A.T., Lucas, M.C., Castro-Santos, T., Katopodis, C., Baumgartner, L.J., Thiem, J.D., Aarestrup, K., et al. (2018). The future of fish passage science, engineering, and practice. *Fish and Fisheries*, 19(2), 340–362.

Skalski, J.R., Mathur, D., & Heisey, P.G. (2002). Effects of turbine operating efficiency on smolt passage survival. *North American Journal of Fisheries Management*, 22(4), 1193–1200.

Sternecker, K., & Geist, J. (2010). The effects of stream substratum composition on the emergence of salmonid fry. *Ecology of Freshwater Fish*, 19(4), 537–544.

Stein, B.A., & Flack, S.R. (1997). 1997 species report card: the state of U.S. plants and animals. Arlington, Virginia, USA, The Nature Conservancy.

Teletchea, F., Fostier, A., Kamler, E., Gardeur, J.N., Le Bail, P.Y., Jalabert, B., & Fontaine, P. (2009). Comparative analysis of reproductive traits in 65 freshwater fish species: application to the domestication of new fish species. *Reviews in Fish Biology and Fisheries*, 19(4), 403–430.

Thorstad, E.B., Rikardsen, A.H., Alp, A., & Økland, F. (2013). The use of electronic tags in fish research–an overview of fish telemetry methods. *Turkish Journal of Fisheries and Aquatic Sciences*, 13(5), 881–896.

Trussart, S., Messier, D., Roquet, V., & Aki, S. (2002). Hydropower projects: a review of most effective mitigation measures. *Energy Policy*, 30(14), 1251–1259.

van der Lee, G.H. & Verdonschot, P.F.M. (2020). Perspectives on the functional assessment of multi-stressed stream ecosystems. *Freshwater Science*, 39(4), 605–620.

van Treeck, R., Radinger, J., Noble, R. A., Geiger, F., & Wolter, C. (2021). The European Fish Hazard Index–An assessment tool for screening hazard of hydropower plants for fish. *Sustainable Energy Technologies and Assessments*, 43, 100903.

Welcomme, R.L. (1985). River fisheries. *FAO Fisheries Technical Paper*, 262, 339pp.

Wolter, C., Buijse, A.D., & Parasiewicz, P. (2016). Temporal and spatial patterns of fish response to hydromorphological processes. *River Research and Applications*, 32(2), 190–201.

Zhang, P., Cai, L., Yang, Z., Chen, X., Qiao, Y., & Chang, J. (2018). Evaluation of fish habitat suitability using a coupled ecohydraulic model: Habitat model selection and prediction. *River Research and Applications*, 34(8), 937–947.

2. General Material & Methods

Data basis assessment

NICOLE SMIALEK

In order to address the complex and partly interdisciplinary questions of this thesis, a set of various materials and methods was applied. A general overview of the thesis' objectives and its contribution to fish conservation in hydropower affected rivers is provided in Figure 5. A systematic review on the autecological requirements of rheophilic fish species was conducted to examine what kind of data is currently available and which knowledge gaps still exist. A theoretical case study was chosen to investigate the similarities and dissimilarities in autecological requirements and tolerances against stressors between two sister species. Findings from this review should clarify whether in case of poor data situations it would be permissible to transfer knowledge from one species to another. To understand which role individual fish behaviour plays during fish monitoring at hydropower plants, a combination of a controlled and a real-world experiment was conducted. Finally, to evaluate possible cost trade-offs between mitigation measures and hydropower operation, economic modelling was performed. A detailed description on the materials and methods used for each of the studies is provided in the following sub-chapters.

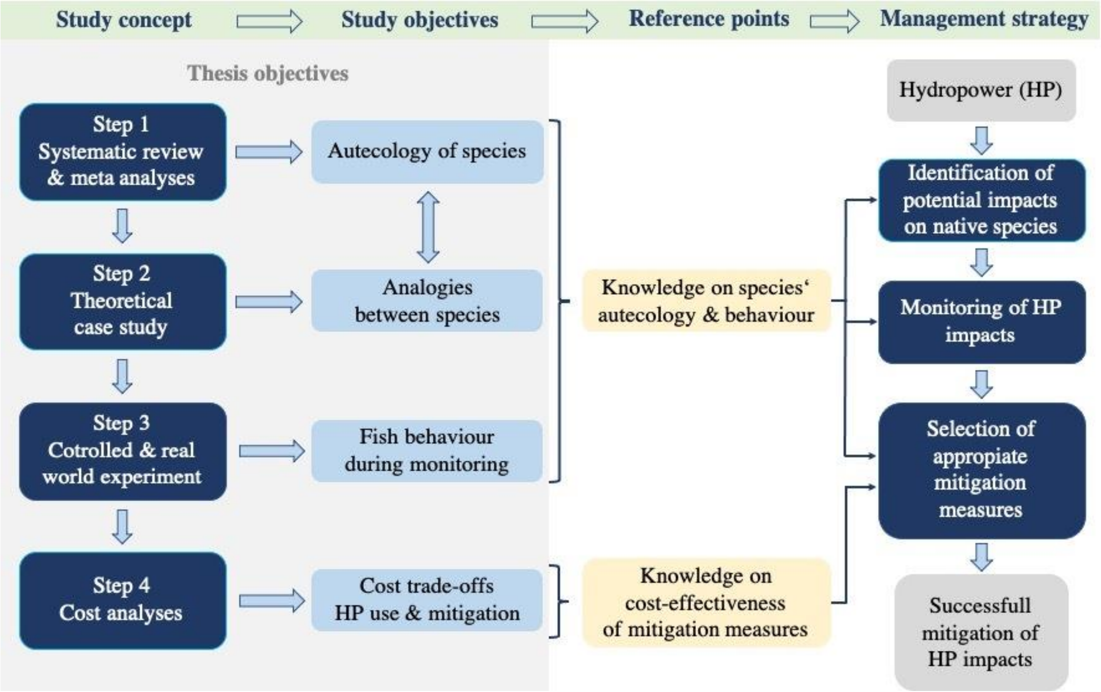

Figure 5. Overview of the thesis' contribution to fish protection from hydropower
General overview of the thesis' objectives and its contribution to fish conservation in hydropower affected rivers. The workflow demonstrates how study results of the thesis can be used to complement the knowledge necessary to provide valuable reference points (and thresholds). These are used to evaluate a stressor's impact and to provide the basis for a suitable mitigation measure selection.

2.1. Systematic review and meta-analysis on autecological requirements

The autecological requirements of riverine fish species can function as a reference point to investigate hydropower impacts on riverine fish. It was assumed that many data on basic autecological traits of most European fish species already exist. To map this knowledge, a systematic review was performed to explore what is already known, what is unknown and where uncertainties exist around findings. The focal point was set on ten rheophilic fish species typically living in hydropower affected rivers covering the most common fish families (cyprinids, salmonids, cottids) in riverine systems in Europe. The systematic review focused on relevant autecological traits covering diverse physiological, chemical and physical aspects on the three critical life-stages of riverine fish (spawning, egg development, emergence). The search was conducted using common search engines (web of science, google scholar, google), scientific data bases (fish base, university library of the Technical University Munich) and scientific literature at hand. The search of scientific literature included both peer-reviewed and grey literature (e.g., academic papers, dissertations, research-, committee-, and government reports provided by governmental agencies) to explore the contribution of comprehensive data. The meta-analysis was then performed using univariate (boxplots, heatmap) and multivariate (nMDS) statistics to evaluate inter- and intraspecific differences in autecological requirements of the species, as well as to compare the data consistency between peer-reviewed and grey literature and how much data was contributed by each.

2.2. Theoretical study on analogies between Atlantic salmon and brown trout

Atlantic salmon (*Salmo salar L.*) and brown trout (*Salmo trutta fario L.*) are species of high socio-economic and ecological value. Declining populations make them target species of fisheries management. The in-depth review was meant to give a holistic view on past, present and possible future environmental threats affecting populations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta fario*) besides or in concert with hydropower impacts. The emphasize was set on the freshwater phase of their life cycles providing a wide-ranging summary on the latest knowledge about environmental threats and autecological requirements of Atlantic salmon and brown trout. Specifically, direct effects of deficient longitudinal connectivity, changes in discharge, high water temperatures, oxygen depletion, changes in water chemistry and increasing loads of fine sediment on the critical life stages spawning, egg incubation and emergence were reviewed. The previously gathered knowledge on physical habitat characteristics (current speed, water depth, water temperature, substrate) from the systematic review (see 2.1) on basic autecological requirements of Atlantic salmon and brown trout was further complemented by data on pH, aluminium and ammonium to give a comprehensive overview of important thresholds of physico-chemical tolerances. Based on the gathered information, implications for conservation and management for salmonid species are proposed with regards to future threats (e.g., chemical pollution, climate change, diseases). The comprehensive data basis on both species was further used to discuss which analogies can be drawn between those closely related species and how this can have an influence on the proposed management implications. For this review, the data was collected from peer-reviewed and grey literature accessed through search engines online (e.g., google, google scholar, research gate, Web of Science) or the Technical University Munich's library. Data was taken from peer-reviewed articles as well as from interactive maps, international governmental and scientific reports, national and international guideline principles, doctoral theses, and scientific books.

2.3. Controlled and real-world experiment on fish behaviour during monitoring

Besides autecological requirements, understanding fish behaviour plays a central role in fish conservation in hydropower impacted rivers. Different behavioural patterns can be observed especially during fish passage of hydropower structures. An understanding of how different species chose the different pathways to pass a hydropower facility can provide valuable information for the development of suitable mitigation measures (see Knott et al. 2019, 2020). Stow-fyke-nets are a common method in these investigations. However, it has been observed that fish caught in the stow-fyke-nets may escape through meshes, commute between the net opening and the fyke-net or dwell at a certain spot in the net (Mueller et al. 2020 a,b). All of which may not get caught in the catch-unit after the standard exposure time of one hour (Pander et. al 2018). Hence, fish behaviour may also play a role in monitoring with the potential to bias the data obtained from it.

Since to the knowledge of the author this behaviour has not been described nor investigated in detail before, the aim was to record these patterns, estimate their influence on the recapture rates and test how fish actually percept nets and which factors might play a role in triggering net-interactions. For this purpose, three experiments were conducted: i) a fall-through experiment to test the mesh sizes, which the test fish would physically be able to pass, ii) a net-perception experiment to investigate the interaction of the fish with nets of different meh sizes under current and lure conditions, and iii) a stow-fyke-net experiment to observe the behaviour of the test fish in a typical stow net used for monitoring at a hydropower plant (real world condition). The experiments are explained in more detail in the sections 2.3.1 to 2.3.3. Brown trout was chosen as model species as it is a target species of conservation, does naturally occur in hydropower affected rivers and thus is standardly used in hydropower monitoring. To test for size differences, hatchery-reared brown trout of three different age classes (0+, 1+ and 2+) were chosen for the experiments. Each fish was used just once to avoid learning behaviour.

All experimental setups and fish handling in this study followed national standards (Adam et al. 2013) and laws as well as European guidelines (European Parliament 2010) for the use of aquatic animals for experimental purposes and were carried out under the official animal care permit number 55.2-1-54-2532-24-2015 (permit agency: Bavarian government/Regierung von Oberbayern).

2.3.1. Fall-through experiment

First, a simple fall-through experiment (based on Herrmann et al. 2009) was conducted to create net selectivity curves of the different mesh sizes of the standard, knotless stow-fyke-net used for fish monitoring at hydropower plants. A net of each mesh size (10, 15, 20 and 30 mm) was stretched on a 40 x 30 cm frame with a mesh opening of 50 % according to the prevailing conditions during standard fish monitoring in the field (Figure 6).

Anaesthetised fish of the different age classes (0+, 1+ and 2+) were then, one after another, dropped head-down onto the mesh to test whether they fit or not fit through. In sum 50 fish per age class and template were tested (total of 600 fish). The collected data on fish size and fell through/did not fell through was used to create selection curves for each net and to calculate the L_{50} value (length of fish at which the probability to fit through the mesh is 50%) with the following formula:

$$L_r = \frac{\exp^{(\alpha + \beta L)}}{1 + \exp^{(\alpha + \beta L)}}, \tag{1}$$

where L_r is the probability that a fish of length L does fit ($L_r > 0.5$) or does not fit through ($L_r < 0.5$) a mesh size. The α (intercept) and β (slope) are estimated coefficients after a logit transformation. The formula for calculating L_{50}:

$$L_{50} = -\frac{\alpha}{\beta}. \tag{2}$$

A logistic regression curve was created, and the model was validated by using deviance residuals, classification matrix, ROC curve and pseudo R^2.

Figure 6. Fall-through experiment setup
Setup of the fall-through experiment showing a framed test net of 20 mm placed above a bucket with water. The fish to be tested is first measured before dropped head down onto the net.

2.3.2. Net-perception experiment

The second experiment investigated the general net perception of fish. Fish were filmed while swimming in a controlled arena set up in a concrete channel (1100 cm x 160 cm x 40 cm), with constant water level and even flow pattern. The area of the arena in the channel was set by nets of fine mesh of 4 mm to allow water flow but not fish to pass. The camera (GoPro Hero 7 Black, GoPro Inc., San Mateo, CA, USA; settings: 1080 resolution, 30 frames per second, wide angle and active stabilizer) for recording the fish’s behaviour was placed on a wooden construction two meters above the arena. A pavilion (3 x 3 m, white folding pavilion with side parts) was placed above the setup to minimize external disturbances during the experiment. (Figure 7).

The arena was divided diagonally to simulate the angle the fish would encounter a stow-net wall in the field during regular fish monitoring. The mesh size of the net was chosen based on the results of the fall-through experiment so that the fish could fit through. Hence, age 0+ brown trout was tested with three mesh sizes (15, 20 and 30 mm), 1+ brown trout encountered two mesh sizes (20 and 30 mm) and 2+ were exposed only to the net with 30 mm mesh size, respectively. (Figure 7). To explore how mesh size, flow conditions, lure factors or a scare effect can affect a fish's willingness to interact or even to pass the net, the test fish were exposed to different treatments.

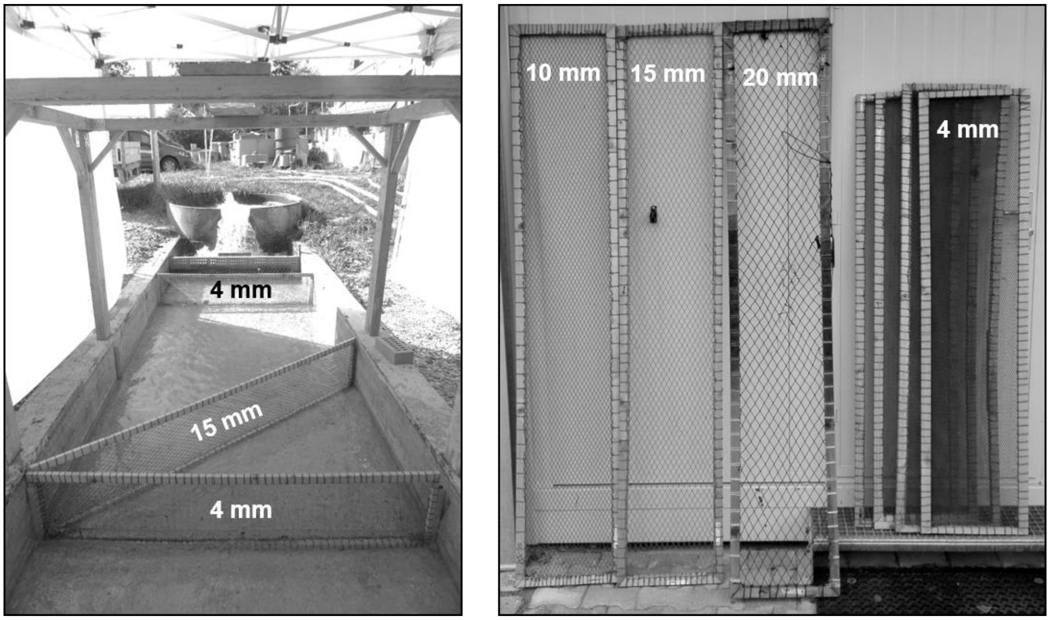

Figure 7. Arena set-up and net frames used
On the left: arena setup with the 4 mm nets defining the area, the wooden construction for the camera and the pavilion to minimize external disturbance. The area is divided by the diagonally placed test net. On the right: test nets of different mesh size (50% net opening) and boundary nets of 4 mm mesh size stretched on frames.

The treatments were set up as follows: for treatment one, 15 fish were exposed to a given mesh size under stagnant water conditions (reference, flow velocity <1 cm s^{-1}). In the second treatment, 15 fish were exposed to a given mesh size at a flow velocity of 9 cm s^{-1}. During the third treatment, 10 fish were exposed to a given mesh size at a flow velocity of 9 cm s^{-1} and a lure factor. The lure consisted of five conspecifics, which were placed on the other side of the test net. Each combination of fish size, mesh size and treatment was replicated three times. After the fish have been exposed to 1 hour to a treatment a landing net was gently wiped from one side to the other to scare the fish. The fish were filmed (GoPro Hero 7 Black, GoPro Inc., San Mateo, CA, USA; settings: 1080 resolution, 30 frames per second, wide angle and active stabilizer) during the exposure. Evaluation of the recordings was done by one person using standard video player (VLC media player x64 version 3.0.11). Based on the data from the video recordings it was examined by univariate statistics how often and for how long the fish performed the following behaviours: (i) fish swims through the net (Figure 8 A), (ii) fish unsuccessfully attempts to swim through the net i.e., the fish puts its snout/head through the net (Figure 8 B); and (iii) fish swims through the net after scare effect.

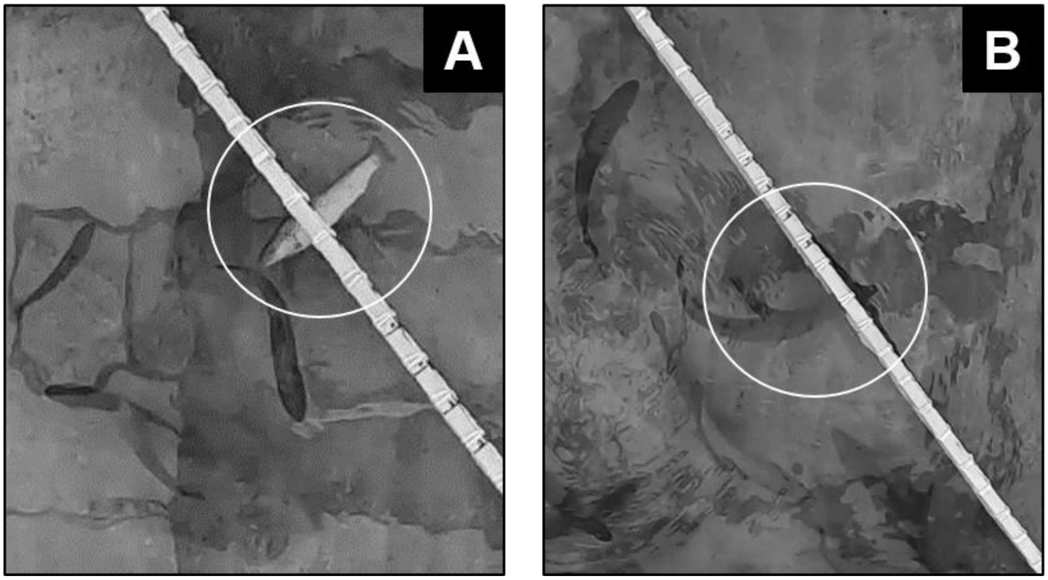

Figure 8. Fish-net interaction
A: Brown trout swimming through the test net by slanting its body to fit through the mesh; B: Attempt of a brown trout to swim through the test net by putting its snout through the mesh.

2.3.3. Stow-fyke-net experiment

In the third experiment (real world experiment), the behaviour of brown trout in a stow-fyke net were recorded during regular fish monitoring at a hydropower plant (Höllthalmühle, river Alz, Germany) to investigate fish behavioural patterns and its potential influence on the recapture rates after one hour of exposure (Figure 9). For this purpose, 50 brown trout of each age class (0+, 1+, 2+; see 2.3.2) were released in front of the opening of the stow-fyke net (inner group) and another 50 fish per age class on the left outer side of the stow net (outer group). The outer group was released to test if fish also enter the net from the outside. To be able to distinguish both groups, the test fish of the outer group were marked with a fin clip at their upper lobe of the tail fin.

In a second part of the real-world-experiment, 50 fish of age class 2+ were released through a zipper into the cod end of the fyke net to investigate if fish also escape back into the stow net (fyke-net-throat experiment).

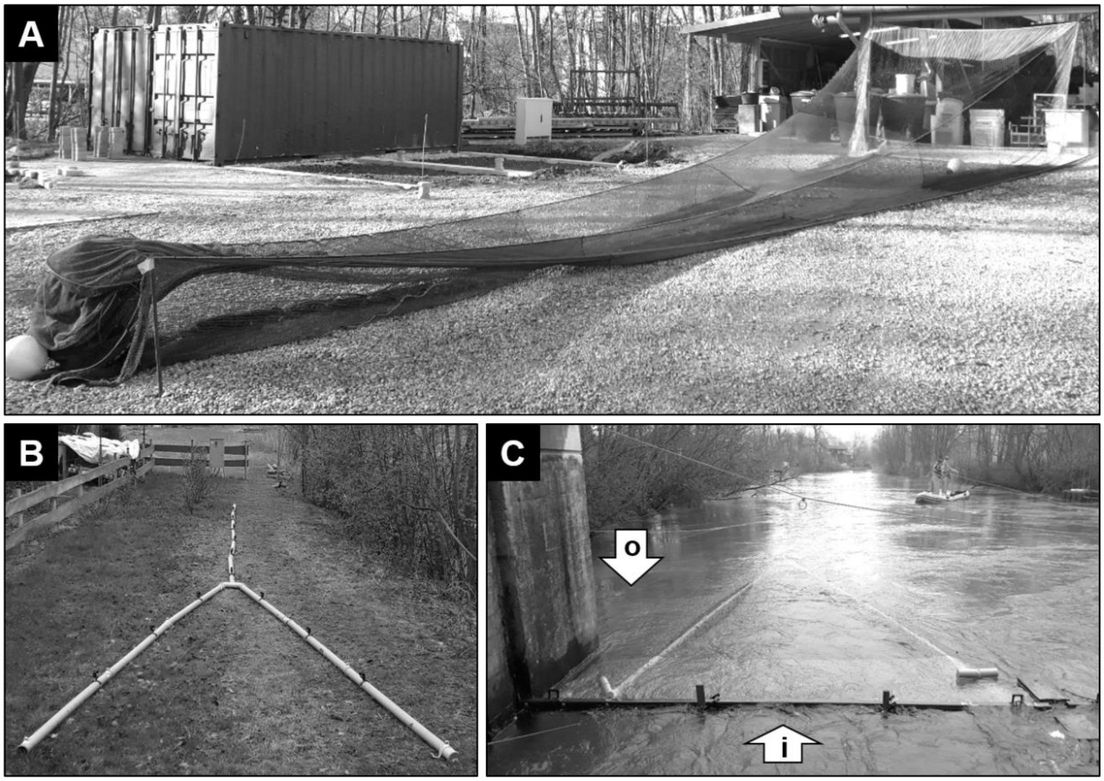

Figure 9. Stow-fyke net setup
A: Typical stow-fyke net used for fish monitoring at hydropower plants. B: Y-shaped scaffold build from PVC tubes with mounted cameras C: Setup of the real-world experiment with the submerged scaffold in the stow-fyke net at a turbine outlet. The letters indicate the position of fish release; o = fish released outside of the net, i = fish released in front of the net.

In order to film most of the relevant net surface in the first part of the experiment, twenty cameras (GoPro Hero 7 Black, GoPro Inc., San Mateo, CA, USA; settings: 1080 resolution, 30 frames per second, wide angle and active stabilizer) were mounted on a Y-shaped scaffold (commercially available drainage pipes of Ø 75 mm filled with floating foam). The scaffold was placed in the net during the experiment with 16 cameras recording the lateral net walls, two cameras at the front opening of the net recording straight into the net and one camera at the end of the scaffold filming the entrance to the fyke-net throat. After one hour of exposure, the scaffold with the cameras was retrieved to save the recordings on hard drives, and the cod end of the net was emptied to count the number of fish caught. Recapture rates and kind of fish (marked, not marked, size class) were noted.

In the second part of the experiment, one camera was installed 30 cm in front of the connection between stow net and fyke net to record the entrance of the fyke-net throat (Figure 10). The fifty fish of age class 2+ were released via a zipper directly into the fyke net. After one hour of exposure, the film material was saved and the number of fish remaining in the cod end were counted.

After the experiments, all video recordings were evaluated by 10 previously trained persons (13% observer effect) using standard video player (VLC media player x64 version 3.0.11). The observers noted each fish sighting including information on time, duration of occurrence within the visual range, position of sighting (number of camera) and striking fish behaviour. The latter could include individual fish swimming through the meshes of the net ("sneaker fish"), dwelling at a certain spot of the stow net for >5 min ("dwellers") or commuting (drift with the flow or/and swim against it) in the stow net or between the fyke net and the stow net ("commuter"). Fish that were filmed in the process of just being released were not counted. For the recordings of the fyke-net throat experiment, additional notes were taken on fyke-net escaping attempts (fish left the fyke net and swam actively upstream into the stow net leaving the visual range of the camera) and "revenants" (fish drifting from the stow net back into the fyke net) and the duration of the observed behaviour. To illustrate the differences in the behaviour of the three size classes in the stow and fyke net, descriptive statistics were used.

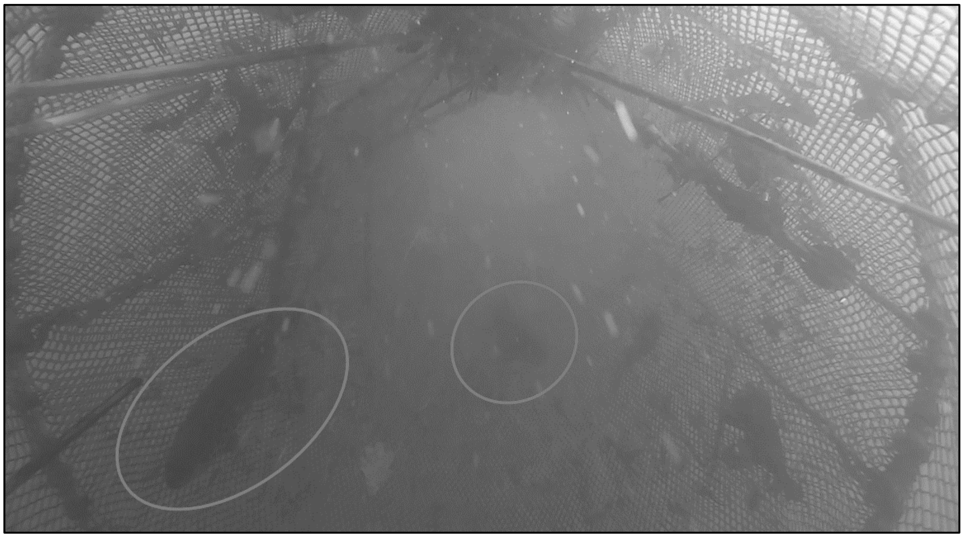

Figure 10. Brown trout escaping the catch unit
Two brown trout (highlighted by circles) filmed in the fyke-net throat.

2.4. Cost analysis on costs associated with fish passage mitigation

Fish passage measures can be considered one of the most common mitigation strategies to minimize hydropower impacts on fish. There is a variety of possible implementation of fish passage solutions as they can be applied for upstream or downstream, can be technical or nature-like. However, implementation is always associated with costs. For the decision making process to find the most cost-effective solution, it is thus important to know how the costs of the individual measures are composed.

Data on costs of building, maintaining and monitoring fish passage measures were collected through a questionnaire sent to European hydropower operators, from available reports and from online sources. It was possible to obtain data on 327 case studies from across Europe, not representing all countries but covering a variety of geographic areas (alpine and low-land region), plant sizes (3.5 kW to 5.88 GW) and technologies (reservoir and run-of-the-river). Types of cost included financial and economic costs associated with upstream and downstream passage facilities. Since the data came from different sources and included different measures, it is important to note that some observations have not been reported or are not relevant for specific measures, which has been documented at each stage of the analysis. For the analysis cost data was deflated to the year 2019 and converted to Euros using the average 2019 exchange rate where necessary.

2.4.1. Analysis of non-recurring costs

Capital costs on planning and construction of passage measures are non-recurring costs. To understand how plant and passage facility characteristics affect the capital costs for upstream passes, a linear mixed model fit by restricted maximum likelihood (REML) was used. Observations were limited to those with complete information for the variables ($n = 127$). Three models were created. The first model controlled for the specific type of measures:

$$\begin{gathered}\log_e Costs_i = \beta_0 + \beta_1 \log_e Height_i + \beta_2 \log_e Length_i + \\ \beta_3 \log_e PlantCapacity_i + \delta_i + \gamma_i + \varepsilon_i.\end{gathered} \tag{3}$$

$log_e\,Costs_i$ is the total capital (construction) cost associated with upstream fish passes. $log_eHeight_i$ and $\log_e Length_i$ are the height of the obstacle to be passed and length of the pass, both in meters. $log_ePlantCapacity$ is the capacity of the plant in kW, which controls for the size of the hydropower plant. By including the logarithmic transformation of cost, we assumed that capital costs would increase exponentially, which we confirmed through visual inspection of the data. We also included measure type (γ_i) controls as we expected differences across types of measures. Random effects for the country (δ_i) are included and ε_i is the error term.

As estimated costs or planned costs can vary from actual implementation costs, the second model compared how big the discrepancy between planned and realized project costs (*Implemented*) is using the unit costs.

$$\begin{aligned}\log_{\mathrm{e}} Costs_i = {} & \beta_0 + \beta_1 \log_e Height_i + \beta_2 \log_e Length_i \\ & + \beta_3 \log_e PlantCapacity_i + \beta_4 Implemented_i + \delta_i + \gamma_i + \varepsilon_i. \end{aligned} \tag{4}$$

In the third model, the cost differences between three categories of measures were tested: technical, nature-like and combined as they considerably differ in their structural characteristic. To account for the quantity of material needed for each of the measures the height, length and plant capacity was also included:

$$\begin{aligned}\log_{\mathrm{e}} Costs_i = {} & \beta_0 + \beta_1 \log_e Height_i + \beta_2 \log_{\mathrm{e}} Length_i \\ & + \beta_3 \log_{\mathrm{e}} PlantCapacity_i + \beta_4 NatureLike_i + \beta_5 Combined_i \\ & + \beta_6 \log_e Height_i * NatureLike_i \\ & + \beta_7 \log_{\mathrm{e}} Length_i * NatureLike_i + \beta_8 \log_e Height_i * Combined_i \\ & + \beta_9 \log_{\mathrm{e}} Length_i * Combined_i + \delta_i + \varepsilon_i. \end{aligned} \tag{5}$$

To further understand how structural characteristics, affect the capital costs for downstream measures, a model using generalized least squares fit by REML was used. The costs of downstream mitigation measures (i.e., screen and bypass) were estimated as a function of screen/rack area (log_eArea_i) and a binary variable for rack configuration ($Vertical_i$) of vertical (1) or horizontal (0). ε_i is the error term. Due to missing information, other factors, such as the angle of the screen/rack were not included.

$$\log_e Costs_i = \beta_0 + \beta_1 \log_e Area_i + \beta_2 Vertical_i + \varepsilon_i. \qquad (6)$$

However, it was tested if there are significant differences in costs between horizontal (n = 27) and vertical (n = 13) racks.

2.4.2. Analysis of recurring costs

Descriptive statistics were used to give an overview of the recurring costs upstream and downstream passage measures. One overview is given about the annual maintenance costs and monitoring costs for upstream measures in Euro (no data available for downstream measures) and for annual power losses related to up- and downstream fish passage measures in GWh.

2.4.3. Analysis of life-time costs

Furthermore, the lifetime costs of different upstream passage measures were evaluated. For this purpose, the mean levelized cost of the capital, operational and power losses of different mitigation were compared. The comparison also included a high and a low electricity price scenario. To calculate the levelized costs of mitigation (LCOM) the following formula was used:

$$\text{LCOM} = \frac{Sum\ of\ costs\ over\ lifetime}{Plant\ capacity} = \frac{I + \sum_{t=1}^{n} \frac{M_t + L_t}{(1+r)^t}}{C}. \qquad (7)$$

I represents the investments (construction) expenditures of the mitigation measure, M_t represents the maintenance expenditures in the year t, L_t represents the power production losses (EUR) in the year t, C represents the plant capacity (kW), r represents the discount rate, and n represents the expected lifetime of the measure. A discount rate of 4% was used as recommended by the European Commission (Satori et al. 2014). As most hydropower concessions in Europe cannot be granted beyond 30 years, this was set as the lifetime period (Glachant et al. 2015). Prices representing the low (0.055 EUR/kWh) and the high (0.125 EUR/kWh) price scenario were chosen based on the feed-in tariffs for retrofitted (including ecological measures) German hydropower plants under the German Renewable Energy Act in 2014.

2.5. References

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.

Herrmann, B., Krag, L.A., Frandsen, R.P., Madsen, N., Lundgren, B., & Stæhr, K.J. (2009). Prediction of selectivity from morphological conditions: methodology and a case study on cod (*Gadus morhua*). *Fisheries Research*, 97(1–2), 59–71.

Glachant, J.M., Saguan, M., Rious, V., & Douguet, S. (2015). *Regimes for Granting the Right to Use Hydropower in Europe. Fiesole*. Italy, European University Institute. 121pp.

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.

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*(21), 6037.

Mueller, M., Knott, J., Egg, L., Bierschenk, B., Pander, J., & Geist, J. (2020a). *Fischökologisches Monitoring an Innovativen Wasserkraftanlagen: Band 1 Hintergrund und Methoden*. *Technical Report for Bayerisches Landesamt für Umwelt*. Freising, Germany. Technical University Munich.

Mueller, M., Knott, J., Pander, J., & Geist, J. (2020b). *Fischökologisches Monitoring an Innovativen Wasserkraftanlagen: Band 7 Eixendorf an der Schwarzach; Technical Report for Bayerisches Landesamt für Umwelt*. Freising, Germany, Technical University.

Pander, J., Mueller, M., Knott, J., & Geist, J. (2017). 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(1), 31–43.

Sartori, D., Catalano, G., Genco, M., Pancotti, C., Sirtori, E., Vignetti, S., & Del Bo, C. (2014). *Guide to Cost-Benefit Analysis of Investment Projects -Economic Appraisal Tool for Cohesion Policy 2014–2020*; Luxembourg, Belgium, European Union. 241pp.

3. Chapter I

Do we know enough to manage European riverine fish?

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3.1. Abstract

Sound knowledge on species-specific autecological requirements of all vulnerable life stages of rheophilic fish species is an important starting point for successful river rehabilitation, species conservation, fish population modeling and management in hydropower-affected environments. We compiled and examined the current data availability in peer-reviewed and grey literature on autecological requirements of ten rheophilic fish species, belonging to the salmonid, cyprinid, and cottid families. In total, 1725 data points from 223 sources were included. Fisheries- important salmonids and the common nase were most studied with highest data availability from both grey and peer-reviewed literature. Overall, grey and peer-reviewed data showed similar dispersion and variance and contributed nearly equally to the species-specific data pool. An in-depth analysis of seven ecological parameters revealed no significant differences between both sources in terms of data availability and concordance. However, substantial data deficits were found for about one quarter of the ecological parameters reviewed. In particular, data were missing on individual densities in specific habitats, egg development and juvenile life stages, despite the necessity of such data

for more advanced population analyses. To protect fish populations in the long-term and especially in hydropower affected environments, more data on basic autecological parameters such as spawning habitat and physiological requirements, fish fertility, densities and survival is needed and grey literature might add valuable information, particularly if it relies on standardised methodologies.

3.2. Introduction

Multiple stressors, including environmental and anthropogenic impacts such as climate change, pollution, habitat fragmentation and degradation, contributed to a massive decline in aquatic biodiversity in the last century (Aarts et al. 2004, Dudgeon et al. 2006, Ormerod et al. 2010, Arthington et al. 2016, Bierschenk et al. 2018). In this context, especially riverine fish species experience the greatest threat by river regulation and fragmentation due to barriers including weirs, dams and hydroelectric plants (Auerswald et al. 2019, Grill et al. 2019). The latter can have detrimental consequences for fish populations such as preventing migratory species from moving between key habitats during their life cycles (Lucas & Frear 1997, Caudill et al. 2007, Wolter et al. 2016). Further, e.g., water abstraction and the loss of shallow littoral areas cause large-scale change, homogenization and loss of fish habitats (Mueller et al. 2011) resulting in reduced abundance, loss of genetic diversity, population decline and change in community structure in the long run (Santucci et al. 2005, Catalano et al. 2007, Spens et al. 2007, Slawski et al. 2008, Nislow et al. 2011). The situation becomes even more severe when multiple stressors act in concert (Arthington et al. 2016).

Successful mitigation of these impacts depends not only on basic and applied research but also on mechanistically understanding the effects of these stressors on freshwater communities and ecosystems. Moreover, targeted research is needed to implement successful river rehabilitation measures including measure design, strategic planning and prioritization tools (Langhans et al. 2016, Geist 2015, Pander & Geist 2013, Geist & Hawkins 2016). In conjunction with improved planning tools there is an urgent need for data about species-specific habitat requirements to streamline rehabilitation efforts. Accurate data on life history traits fostering recovery are considered most important to derive rehabilitation targets, to run realistic model scenarios, to identify possible population bottlenecks and to implement suitable mitigation methods (Van Looy et al. 2019). These traits include for instance reproductive traits as well as habitat requirements of early life-stages for spawning and nursery. Basic autecological knowledge is therefore not only crucial for long-term population conservation and enhancement, but its systematic analysis also provides new insights (Casas-Mulet et al. 2015, Radinger et al. 2017, Duerregger et al. 2018), e.g., on setting research priorities for the future. Usual sources of autecological data are—among others—peer-reviewed articles and grey literature. In the context of river restoration measures and fish conservation, the latter is becoming more and more important today (Morandi et al. 2017). In particular, the implementation of rehabilitation measures commissioned by local authorities is often based on the findings of investigation reports from local expert offices alone or in combination with peer-reviewed data (Morandi et al. 2017, Silva et al. 2018).

Here, we apply a systematical meta-analysis approach to summarize data from grey and peer-reviewed literature on selected life history traits, ecological parameters and habitat requirements related to the most critical life stages of representative riverine fish species, which are considered target species of conservation (Geist 2011). We aimed at (i) determining data availability for each parameter and species using a defined systematic search, (ii) identifying existing knowledge gaps and (iii) examining whether the grey literature has the potential to provide valuable additional data that will help close existing knowledge gaps and provide a more balanced picture of available evidence. With this, we provide a defendable information basis drawn on all relevant and scientifically sound research to be used in evidence-based population conservation actions.

3.3. Materials and methods

3.3.1. Literature review

In this paper, we examined the scope of the literature and available data on the autecology of ten European riverine fish species: *Barbus barbus* (common barbel), *Chondrostoma nasus* (common nase), *Cottus gobio* (European bullhead), *Hucho hucho* (Danube salmon), *Leuciscus leuciscus* (European dace), *Phoxinus phoxinus* (European minnow), *Salmo salar* (Atlantic salmon), *Salmo trutta* (brown trout), *Squalius cephalus* (European chub), and *Thymallus thymallus* (European grayling). According to recent findings in stream fish population trends (Mueller et al. 2018) these species were found to be strongly decreasing over the last decades and deserve high conservation priority. We provide the current national and international conservation status and the affiliation to the main ecological guilds of these species in the Supplementary material, Table S1. Twenty-six ecological parameters comprising critical life phases such as reproductive and early life stage conditions, habitat space requirements, life history traits, and environmental tolerances in respect to the species-specific ecological niche were included, as detailed in Table 1.

Note: Supplementary materials of Chapter I are available electronically only. Please access via: https://www.mdpi.com/2071-1050/11/18/5011

Table 1. Traits overview
Overview table on the 26 ecological parameters considered to evaluate the autecological requirements of the 10 rheophilic species at risk.

Selected Ecological Parameter	**Acronym**	**Description**
Population		
population density (individuals m^2, individuals m^{-1}, kg ha^{-1}, individuals per fish school)	pop dens	reported density of individuals in a population
areal size (m^2, km)	areal size	reported areal size used by a population
Spawner		
spawner density (individuals m^{-2})	sp dens sps	spawner density on spawning ground during spawning
spawning events per female (events $female^{-1}$)	spaw events	spawning events per female per year
Spawning site		
spawning site size (m^2)	sps size	size of spawning site used by fish population
current speed spawning site (m s^{-1})	cur speed sps	measured current speed at spawning ground during spawning
substrate spawning site (cm, %, term)	subs sps	substrate at spawning site
water depth spawning site (m)	w depth sps	water depth at spawning ground during spawning
water temperature spawning (°C)	w temp spaw	water temperature measured during spawning
Redd / nest		
redds at spawning site (redds m^{-1}, redds m^{-2}, redds spawning $site^{-1}$)	redds sps	total number of redds/nests per spawning site
redd size (m^2)	redd size	size of a redd/nest

Table 1. Continued.

Selected Ecological Parameter	**Acronym**	**Description**
Egg and larvae		
egg depth (cm)	egg depth	depth of eggs in interstitial zone
eggs (eggs m^{-2})	eggs per m^2	eggs density found at spawning ground
eggs per female (eggs $female^{-1}$)	eggs per f	number of eggs per female
eggs per redd (eggs $redd^{-1}$)	eggs per redd	number of eggs in a redd/nest
eggs at spawning site (eggs sps^{-1})	eggs sps	total number of eggs counted for a spawning site
days till hatch (days)	days till hatch	days till hatch of fish larvae
degree days (days)	degree days	degree days till hatch of fish larvae
hatch rate/success (%)	hatch rate	hatching rates of eggs
larval survival (%)	larv surv	percentage of larvae surviving till yolk sack depletion
larvae density (individuals m^{-2})	larv dens	larvae density in larval habitats
Juvenile		
* juvenile survival (%)	juv surv	percentage of juvenile surviving first year post hatching
juveniles per m^2 (juveniles m^{-2})	juv per m^2	juvenile density in juvenile habitat
current speed juvenile (m s^{-1})	cur speed juv	measured current speed in juvenile habitat
substrate juvenile (cm, term)	subs juv	substrate in juvenile habitat
water depth juvenile (m)	w depth juv	water depth in juvenile habitat

The abbreviations of the ecological variables are used in the text and figures. The names of the selected variables in the first column are identical with the search terms used to find relevant literature. The units in the brackets indicate the reported units found in the publications. * Term was searched but no data was found.

These parameters are considered fundamental to relate fish populations to habitat availability and quality, to predict fishes’ response to habitat changes, degradation, and rehabilitation and to secure a self-sustaining fish population (Van Looy et al. 2019). For the database screening, we used a combination of the species’ common or scientific names and the ecological parameter (e.g., “Barbus barbus *degree days”) as a search string, both in English and German language. All used search strings are summarized in Appendix 1, Table A1. The search was conducted on the Web of Knowledge, Google Scholar, FishBase, in the Technical University Munich library data base, and in the references lists of the literature already found. In total, we obtained 223 publications originating from peer-reviewed articles and grey literature (e.g., academic papers, dissertations, research-, committee-, and government reports; Supplementary material Table S2) providing data on at least one of the parameters listed in Table 1. For publications providing more than one data point per ecological parameter and species we only considered the minimum and maximum value (Supplementary material Table S3), which then were counted as two observations. Two or more values from the same publication but from independent sampling periods, sites, and populations were treated as individual observations. We exclusively used primary data and omitted data cited from another source ("secondary data") where the original source could not be found. All observations and values used in this review will further be referred to as "data points".

3.3.2. Data analyses

To get an overview of the available data on the autecological parameters for each species we visualized the data using a heatmap with a colour gradient indicating the amount of data points found. An in-depth analysis focused on those seven ecological parameters for which the most data points and at least one data point per species were available including "current speed spawning site", "current speed juvenile habitat", "water depth spawning site", "water depth juvenile habitat", "water temperature spawning site", "degree days" and "substrate spawning site". We tested data differences and variability depending on the literature source using descriptive statistics and unpaired two-sample Wilcoxon tests (Wilcoxon rank sum test). Significance levels are indicated as follows: $0.01 < p \leq 0.05$ *, $0.001 < p \leq 0.01$ **, and $p \leq 0.001$ ***. Following the recommendations of McDonald (2014), we excluded species with less than five data points per ecological parameter from the analysis.

To consider for a bias towards broader data ranges, means and standard deviations driven by a higher amount of publications, we conducted a linear regression on the available data points and the normalized span of range, as well as the normalized mean and the normalized standard deviation (Figure A1). Univariate analyses and graphs for data visualization were computed using the statistical and graphical opensource software R (R Core Team 2020) including the following packages: car (Fox & Weisberg 2011), dplyr (Wickham et al. 2018), extrafont (Chang 2014), ggalt (Rudis et al. 2017), ggplot2 (Wickham 2009), gplots (Warnes et al. 2009), grid (RC Team 2017), plyr (Wickham 2011), RColorBrewer (Neuwirth 2014), and tidyr (Wickham et al. 2018).

To test how the inclusion of grey literature would influence the overall data picture, we used multivariate analysis tools provided by the statistical software PRIMER v7 (PRIMER-e, Massey University, Auckland, NZ). For this purpose, we created four new data sets. The first and second set included the z-transformed median values of each ecological parameter for all species, from grey and peer-reviewed literature, respectively. We created a resemblance matrix using Euclidian distance. To test similarity of the gathered data from the two different literature sources, we used the RELATE function of PRIMER v7. The third data set was created to see if there would be a benefit if grey and peer-reviewed data were combined. Thus, the set included combined median values of the environmental parameter measures from both sources and median values coming only from peer-review. After normalization and creating the Euclidian distance matrix, we conducted nonmetric multi-dimensional scaling (nMDS) to obtain graphical ordination of the samples (McCune & Grace 2002). Additionally, we included the number of data points reviewed per species and data sources using the bubble function. The fourth data set was of the same structure as the third but included the number of data points per species and parameters instead. We added this data as a correlation vector layer to the nMDS.

3.4. Results

3.4.1. Data availability

Overall, we compiled 1725 data points from 223 sources reviewed, of which 33% were identified as grey literature (31 reports, 31 books, 10 dissertations, one personal communication, and one web source from experts) and 67% being peer-reviewed studies. Peer-reviewed articles were accessible over Google Scholar and the university's library, whereas grey literature was mainly found using the Google search or by inquiring with responsible authorities. We provide a list of all literature sources used in the supplementary material (Supplementary material Table S2).

As expected, the success of the data search varied according to species (Figures 11 and 12). The literature reviewed on common nase yielded the highest number of 300 data points (57% peer-reviewed, 43% grey), followed by Atlantic salmon (238; 53% peer-reviewed, 47% grey) and brown trout (124; 50% peer-reviewed, 50% grey). We found the fewest data points for European bullhead and European dace (both 99; both 50% peer-reviewed, 50% grey). For six of the ten species both literature sources provided nearly equal amounts of data points (Figure 11).

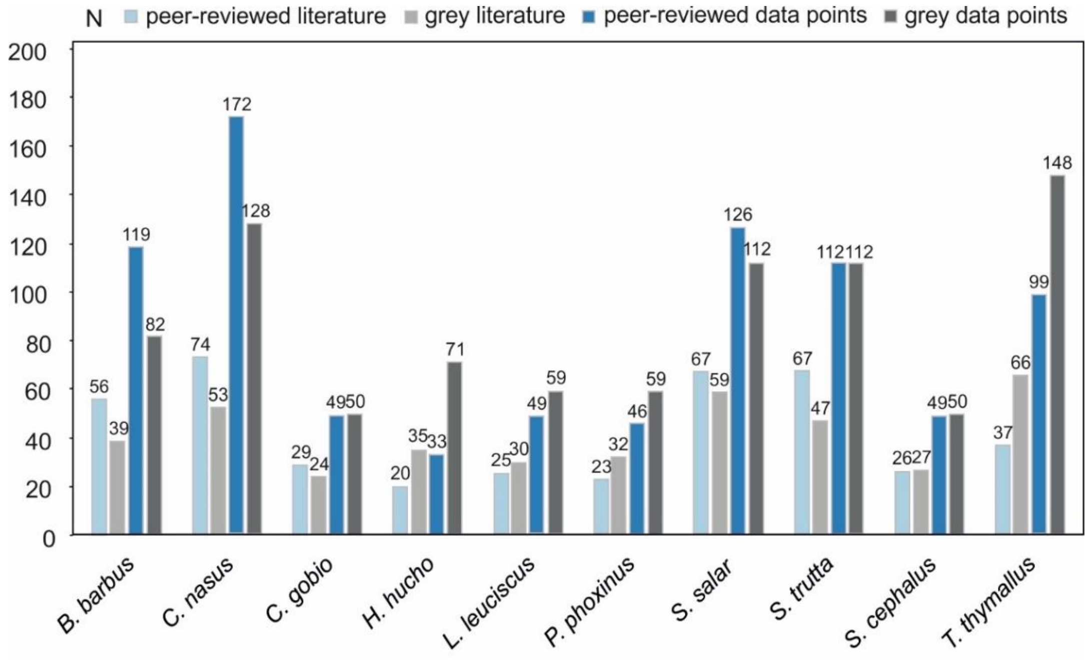
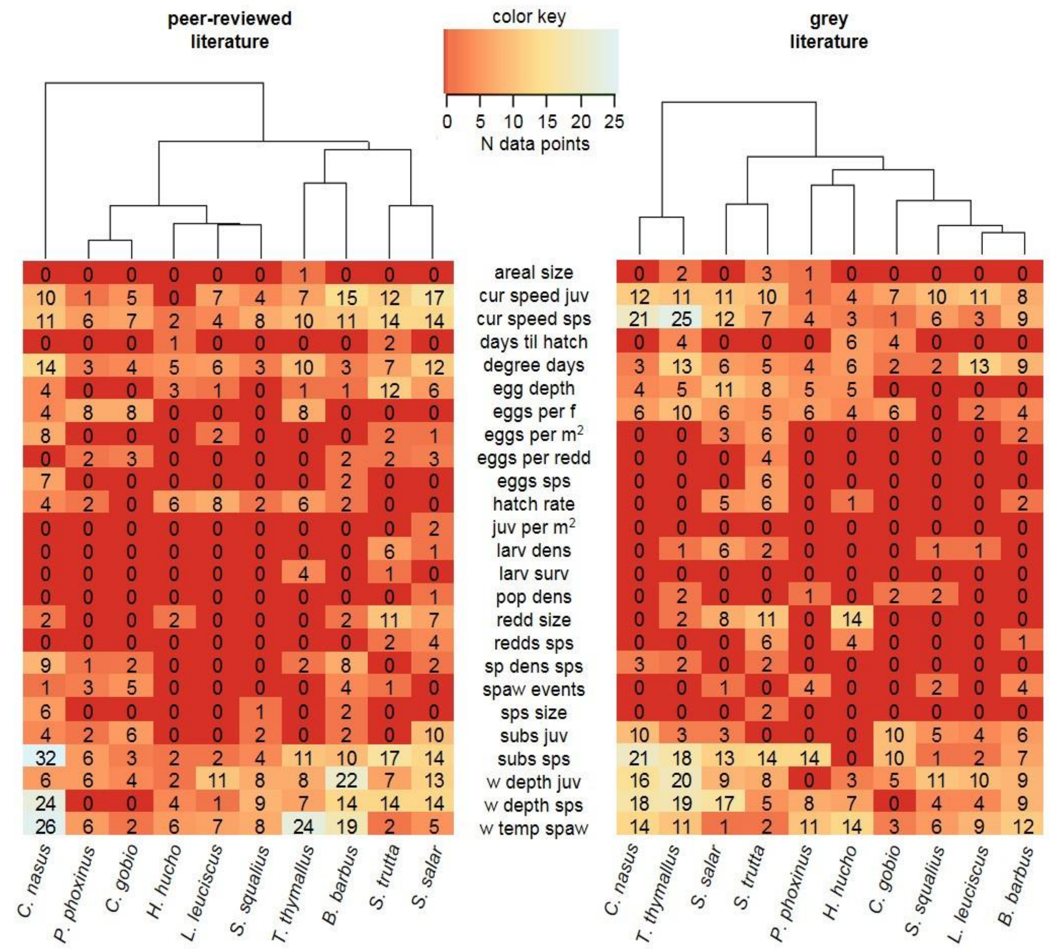


Figure 11. Number of literature per fish species
Bar plot representing the number and type of literature sources and the resulting data points per species compiled for this review.

Data on physical habitat characteristics, e.g., current speed, water depth, and water temperature, were better represented than data on the areal needs and characterizations, e.g., population density, spawning site size, and early-life stages, considering both literature sources. “water temperature during spawning” yielded 83 data points from grey sources (derived from 45 publications) and 105 data points form peer-reviewed literature (out of 54 publications) whereas there was only one search hit for “juveniles per square meter” (Figure 12).



peer-reviewed literature

	C. nasus	P. phoxinus	C. gobio	H. hucho	L. leuciscus	S. squalius	T. thymallus	B. barbus	S. trutta	S. salar
areal size	0	0	0	0	0	0	1	0	0	0
cur speed juv	10	1	5	0	7	4	7	15	12	17
cur speed sps	11	6	7	2	4	8	10	11	14	14
days til hatch	0	0	0	1	0	0	0	0	2	0
degree days	14	3	4	5	6	3	10	3	7	12
egg depth	4	0	0	3	1	0	1	1	12	6
eggs per f	4	8	8	0	0	0	8	0	0	0
eggs per m^2	8	0	0	0	2	0	0	0	2	1
eggs per redd	0	2	3	0	0	0	0	2	2	3
eggs sps	7	0	0	0	0	0	0	2	0	0
hatch rate	4	2	0	6	8	2	6	2	0	0
juv per m^2	0	0	0	0	0	0	0	0	0	2
larv dens	0	0	0	0	0	0	0	0	6	1
larv surv	0	0	0	0	0	0	4	0	1	0
pop dens	0	0	0	0	0	0	0	0	0	1
redd size	2	0	0	2	0	0	0	2	11	7
redds sps	0	0	0	0	0	0	0	0	2	4
sp dens sps	9	1	2	0	0	0	2	8	0	2
spaw events	1	3	5	0	0	0	0	4	1	0
sps size	6	0	0	0	0	1	0	2	0	0
subs juv	4	2	6	0	0	2	0	2	0	10
subs sps	32	6	3	2	2	4	11	10	17	14
w depth juv	6	6	4	2	11	8	8	22	7	13
w depth sps	24	0	0	4	1	9	7	14	14	14
w temp spaw	26	6	2	6	7	8	24	19	2	5

grey literature

	C. nasus	T. thymallus	S. salar	S. trutta	P. phoxinus	H. hucho	C. gobio	S. squalius	L. leuciscus	B. barbus
areal size	0	2	0	3	1	0	0	0	0	0
cur speed juv	12	11	11	10	1	4	7	10	11	8
cur speed sps	21	25	12	7	4	3	1	6	3	9
days til hatch	0	4	0	0	0	6	4	0	0	0
degree days	3	13	6	5	4	6	2	2	13	9
egg depth	4	5	11	8	5	5	0	0	0	0
eggs per f	6	10	6	5	6	4	6	0	2	4
eggs per m^2	0	0	3	6	0	0	0	0	0	2
eggs per redd	0	0	0	4	0	0	0	0	0	0
eggs sps	0	0	0	6	0	0	0	0	0	0
hatch rate	0	0	5	6	0	1	0	0	0	2
juv per m^2	0	0	0	0	0	0	0	0	0	0
larv dens	0	1	6	2	0	0	0	1	1	0
larv surv	0	0	0	0	0	0	0	0	0	0
pop dens	0	2	0	0	1	0	2	2	0	0
redd size	0	2	8	11	0	14	0	0	0	0
redds sps	0	0	0	6	0	4	0	0	0	1
sp dens sps	3	2	0	2	0	0	0	0	0	0
spaw events	0	0	1	0	4	0	0	2	0	4
sps size	0	0	0	2	0	0	0	0	0	0
subs juv	10	3	3	0	0	0	10	5	4	6
subs sps	21	18	13	14	14	0	10	1	2	7
w depth juv	16	20	9	8	0	3	5	11	10	9
w depth sps	18	19	17	5	8	7	0	4	4	9
w temp spaw	14	11	1	2	11	14	3	6	9	12

Figure 12. Heatmaps illustrating current data availability on species traits
Heatmaps representing the number of data points found for all environmental variables and fish species. The colour-gradient is picturing high (light blue) to low (red) data availability. The species were clustered according to data availability using the Euclidian distance. Abbreviations are defined in Table 1.

3.4.2. Data comparability and variability from different sources

Besides quantifying the differences in data availability, we also analysed data comparability and variability depending on the source and species (Figure 13). In both, grey and peer-reviewed data, scatter occurred. However, except for “water temperature during spawning” at the spawning ground for European minnow (Wilcoxon rank sum test; $p < 0.05$ *) and “degree days” for Atlantic salmon (Wilcoxon rank sum test; $p <$

0.01 **) we found no significant difference in the number of data points between grey and peer-reviewed data for a specific parameter and fish species.

Furthermore, we found no linear relationship for the number of publications and the normalized data range ($r^2 = 0.101$; Appendix 1, Figure A1a), normalized mean ($r^2 = 0.013$; Appendix 1, Figure A1b), and normalized standard deviation ($r^2 = 0.002$; Appendix 1, Figure A1c), i.e., the assumption that a larger number of data points from different studies would increase the scatter, was not confirmed. For example, for the European grayling more data was available compared to the other species (seven to 25 values per parameter and source compared to the group mean of all species of 11 values). Variability of grey and peer-reviewed data was very similar where again for the Atlantic salmon, significant differences between both sources occurred. On the other hand, European chub and European dace showed a low variability within the data despite poor data availability.

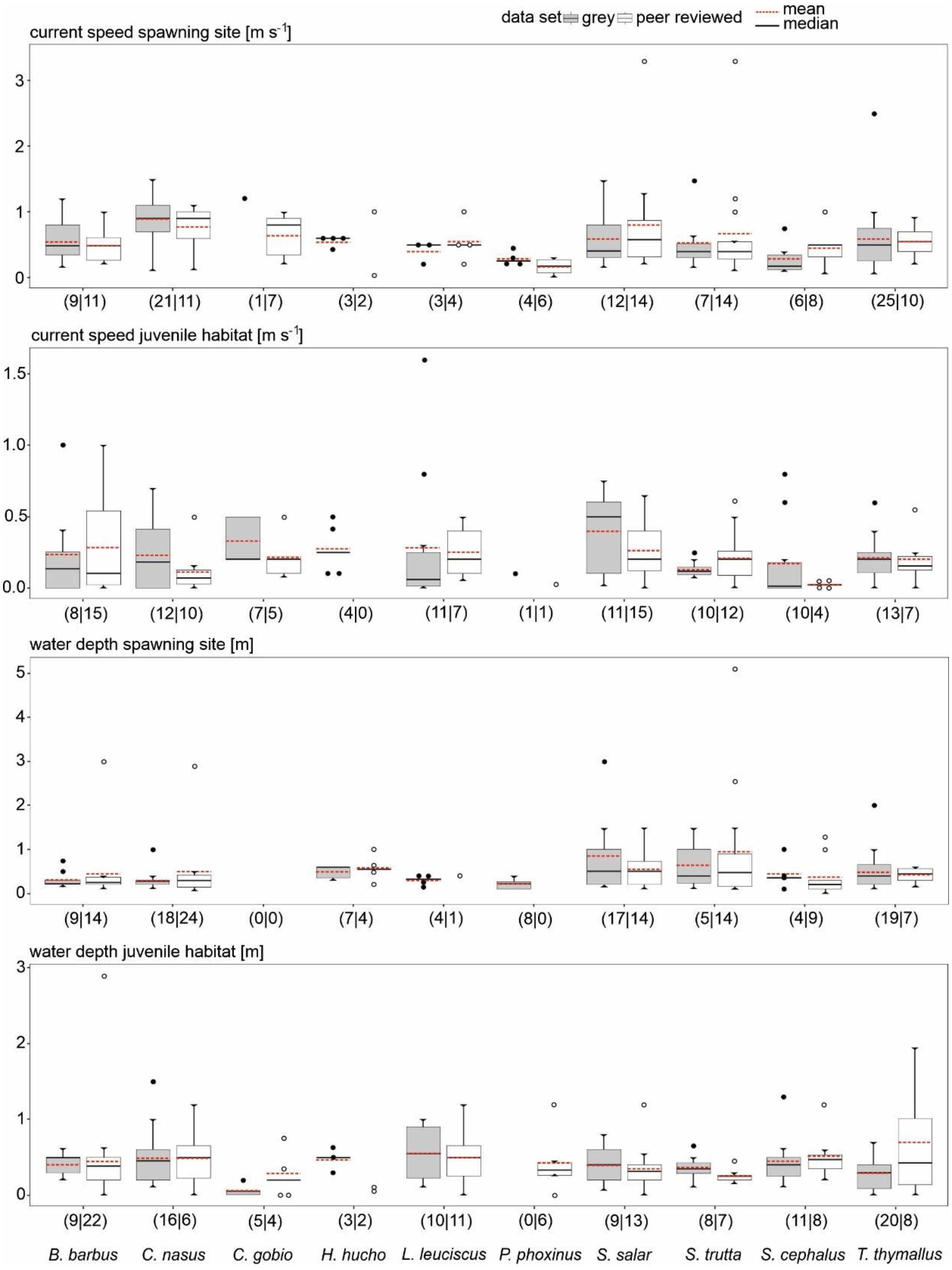


Figure 13. Continues on next page.

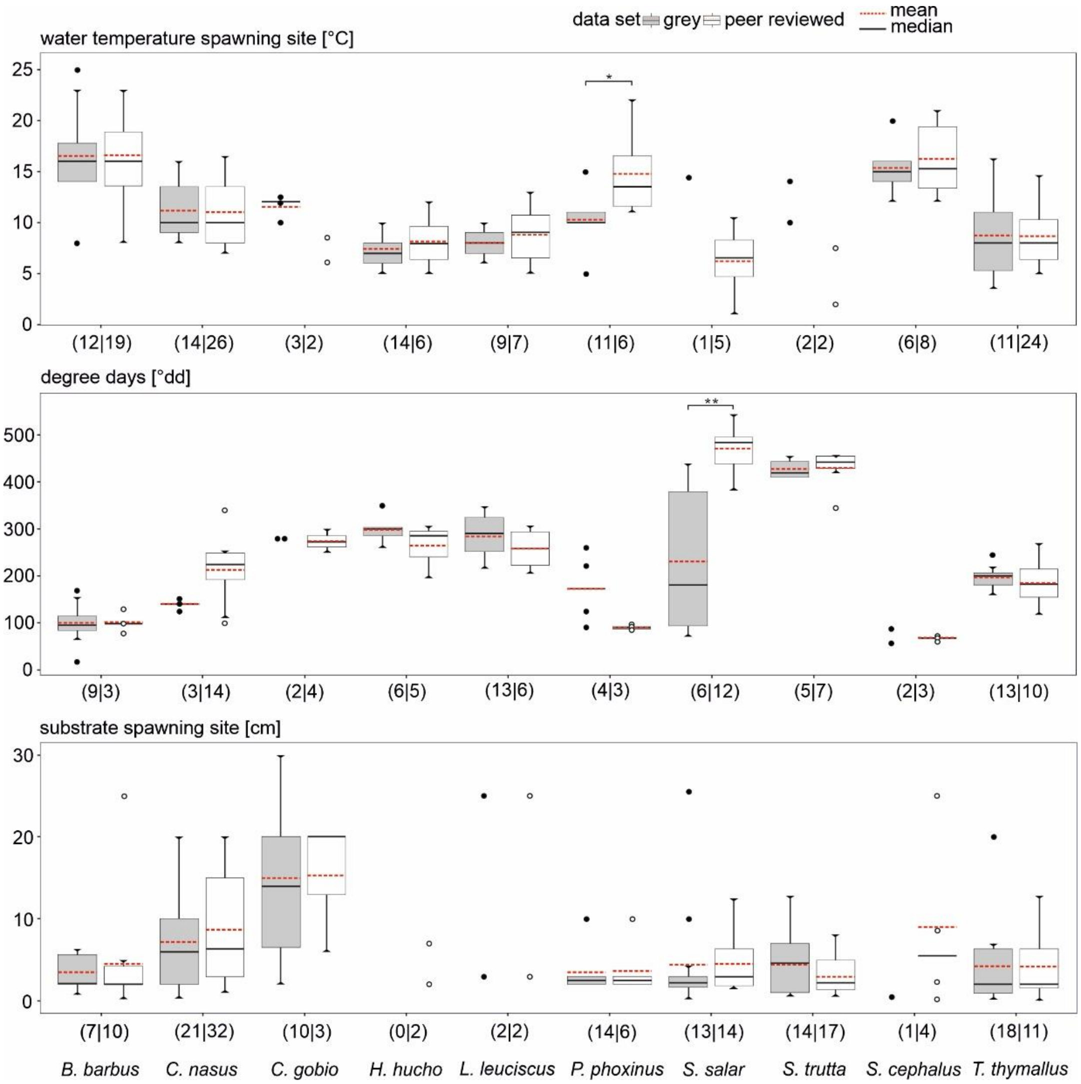


Figure 13. Box plots representing compiled species data
Box plots representing the compiled peer-review (white boxes) and grey (grey boxes) literature data on seven variables for each of the ten fish species. The numbers in brackets reflect the available data points. The dashed red line indicates the mean, the black line the median per species. Box: 25% quantile, 75% quantile; whiskers: minimum, maximum values; outliers refer to data points that are more than 1.5 IQR above the third quartile or below the first quartile; square brackets between boxes show significant differences between grey and peer-reviewed data sets. Significance levels are indicated as follows: $0.01 < p \leq 0.05$ *, $0.001 < p \leq 0.01$ **, and $p \leq 0.001$ ***.

3.4.3. Data quality differences among species

Grey and peer-reviewed data showed an overall similarity between matrices (RELATE, Spearman’s rank correlation coefficient (Rho): 0.8, significance level 0.1%, 999 permutations). The nMDS on the basis of the ecological parameters (comparison of median values) led to a segregation of the fish species (Figure 14).

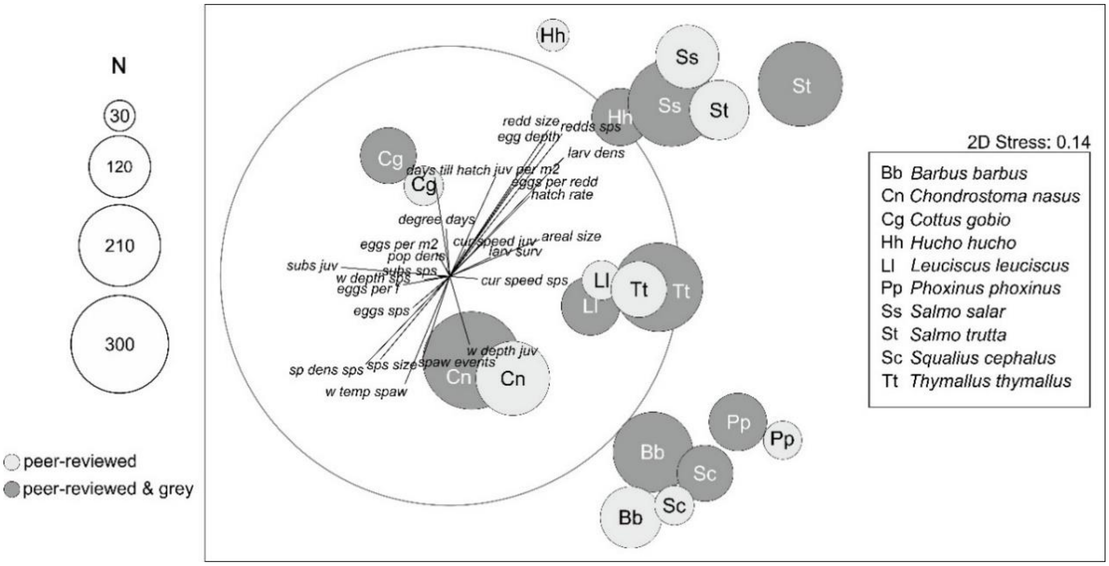


Figure 14. nMDS plot representing the compiled data on species traits
Non-metric multidimensional scaling (nMDS) plot showing the number of studies compiled for ten fish species including all reviewed environmental variables. The distance between the circles resembles the (dis-) similarity of their environmental needs (increasing distance = increasing dissimilarity). The circle size indicates the number of data points (N) found for each species differentiated in data derived from peer-reviewed sources (light grey) or combined with data from grey sources (dark grey). Included as a vector layer are the data on environmental parameters. The vector length represents the strength of correlation with the species arrangement (100% = outer circle line).

Except for European grayling, the salmonids aggregated close to each other, as well as common barbel, European chub, and European minnow. We also found some shifts in preferences when comparing the positions of the combined and peer-reviewed data sets per species. The distance between the bubbles indicates a higher dissimilarity in the data while overlaps point to more similar data. Thus, considerable differences were visible for Danube salmon and brown trout, whereas for European grayling the inclusion of grey literature just added more values in accordance to the peer-reviewed data base. The size of the bubbles also clearly showed the overall differences in the data availability of the species depending on the source. The vector overlay of the data points per species and all ecological parameters indicated which of the species had the most data points on a specific parameter. For species aligned on or close to a line more data was available on that specific trait than for species further away. Accordingly, all salmonids but European grayling held the majority of the data (e.g., for “larval density” and “number of redds on spawning site”). We found most data on the parameters “days till hatch" and "water depth at juvenile habitats" for European bullhead and common nase.

3.5. Discussion

In this study, we applied a systematically meta-analysis approach to summarize data from grey and peer-reviewed literature on selected life history traits, ecological parameters, and habitat requirements related to the most critical life stages of ten riverine fish species. We found substantial deficits in the data for about a quarter of the reviewed ecological parameters across all species. In particular, data on individual densities in the habitats, egg development and information about juvenile stages was scarce. This is very surprising since such data is particularly crucial for any population modelling and management (Anders 1998, Schiemer et al. 2002, Rhodes et al. 2011) as well as for evidence-based conservation (Geist 2015) and restoration (Pander & Geist 2013, Geist & Hawkins 2016). Searching for grey and peer-reviewed data yielded the same amount of data points, and also revealed their similarity in dispersion and variance. The poor data availability for different species corresponds very well to previous works reporting that common species of high economic importance are usually better studied and overrepresented in publications as e.g., evident for brown trout and Atlantic salmon (e.g., Denic & Geist 2010, Mertens et al. 2011). Both species are of high economic value in Europe (Butler et al. 2009, ICES 2018). Further, the common nase, once a very common species, became a target fish for conservation and restoration of European rivers since its rapid decline in the last century (Mueller et al. 2018). Common barbel and European grayling are both character species of specific river zones and are considered indicators for the ecological integrity of a riverine fish region (Huet 1959, Lasne et al. 2007). In contrast, the mainly small-bodied endemic species of low societal and economic interest have been rarely investigated. Consequently, data is scarce and analyses are often based on a rather low number of sources (e.g., we found only 23 peer-reviewed studies for European minnow searching for 26 ecological parameters). As a result, practical applications, e.g., in the context of conservation or management, are often prioritized for species with high data availability and appreciation both in economical or conservation terms. However, the rehabilitation of fish stocks is not only dependent on abiotic factors such as habitat quality (Sternecker et al. 2013). It is also dependent on biotic interactions among the entire fish community, as observed for many novel communities that are severely affected by invasive species (Brandner et al. 2013a, Brandner et al. 2013b, Cerwenka et al. 2018), or by predator–prey relationships (Decker et al. 2017), involving apex predators like the Danube salmon (Schmutz et al. 2002). Therefore, it is advantageous to ground conservation applications of fish populations on a broader basis. This can help to enhance restoration success (Silva et al. 2018, Lewis et al. 1996) and to achieve a sustainable ecosystem based fisheries management (EBFM) as suggested by Fletcher et al. (2010). Although this concept has developed more recently in marine environments, it should be equally considered in freshwater ecosystems.

Another reason for limited data availability is the accessibility of literature. The first studies on critical life stage-specific ecological parameters of the species covered in this review were conducted before the 1960s (e.g., common barbel 1949, European bullhead 1957, and common nase 1958), and sometimes even reach back as far as the 1940s (Danube salmon 1910, brown trout 1932, and European grayling 1937). Old publications like that are harder to access, especially via the common online search engines like Google Scholar and Web of Knowledge. We found the original articles to be often solely accessible through university libraries and research institutes, and copies were not always available or very costly to get. However, old studies can be very beneficial to evaluate the species conservation status and may furthermore present insights on how autecological preferences of fish species change over time.

Additionally, a severe problem is the highly random accessibility of grey literature. In this review, grey literature displayed a hidden value on autecological data that was found to be within the quality range of peer-reviewed literature. Numerous autecology-related data on fish species presented in methodological studies and monitoring reports are generated by governmental or industrial projects for the assessment and management of the ecological integrity of freshwaters as well as by monitoring to implement national legislation such as Environmental impact assessments (Pander & Geist 2013, Silva et al. 2018). However, most of these reports are written in the language of the country in which they were commissioned making them difficult to find via English key words. If found, their content is restricted to readers that know the language. In addition, as Silva et al. (2018) state in their paper on fish passage science, the current practice of decentralized collection by different institutions, based on individual measures, dramatically restricts causal research. This, in turn, can result in decision making based on anecdotal rather than scientific evidence. Since many of these reports are not openly accessible for the general public it contradicts the principles of "Open Data" and the FAIR criteria according to which data should be searchable, accessible, interoperable, and reusable as suggested by Pander & Geist (2013) and Silva et al. (2018).

An ongoing problem, which contributes to the difficulties in comparing autecological studies, is the missing standardisation of methods and materials used in ecological field studies (Burgman et al. 2001, Bonar & Hubert 2002). To date, a great variety of methods, materials, and ways of data presentations exist, making it difficult to compare even simple traits within one species. During the search process of this review, we dismissed many sources, including peer-reviewed articles, because the authors did not use a measurement standard or the procedure of data collection was insufficiently described, hampering their use. This was particularly apparent for spatially referenced data. It is not surprising that most literature was available for physical parameters like current speed or water depth, since those are often well defined and based on a standardised sampling procedure (e.g., Trudgill et al. 2005). However, during our search, we found substrate size mostly described by using either notations of standardised classification systems (e.g., resulting from sieving the material, Blott & Pye 2012) or expressed after visual estimations in the field. We found 29 different descriptions of preferred substrate during spawning (e.g., gravel, sand, cobble, pebble or boulders, sand and silt, blocks, big stones, coarse gravel, crushed rock, etc.). None of them referred to a common standard, e.g., the European Standard (EN 933-1, 1997) or the Udden-Wentworth grain size classification (EN933-1 2012, Udden 1914, Wentworth 1922, Udenn 1898), making systematic analyses very difficult to compare.

Biotic data, such as the number of individuals in a designated habitat, can be measured in multiple ways depending on the situation, which creates multiple data sets that are hardly comparable. For example, species abundance would be described either as individuals per 100 m river length or by individuals per m^2. Certainly, there are good reasons why one is sometimes favoured over the other. For large datasets in well-studied species, this is likely to be less problematic than in understudied species where a small data basis gets further reduced applying strict standards.

To mitigate these issues, a classification and standardisation system for streams and stream habitats was already developed in 1986 by Frissell et al. (1986). However, today for many fish species, space requirements for self-sustaining populations are largely unknown. Factors like the high habitat complexity required by many species, as well as the ongoing, highly controversial discussion about the definition of a population and the concept of a minimum viable population (Flather et al. 2011, Brook et al. 2011, Jamieson & Allendorf 2012, Frankham et al. 2013) hinder the measures associated with them.

Besides the substantial deficits in the data, our review revealed that grey and peer-reviewed data could be used to complement each other. The underrated input of knowledge from grey sources has been lately discussed in the scientific community (e.g., Conn et al. 2003, Haddaway & Bayliss 2015, Paez 2017) and the authors concluded, that by including grey literature publication bias could be reduced and comprehensiveness and timeliness raised. Grey literature may therefore provide a more balanced picture of available data and knowledge. Of course, when including grey literature, the same standard as for using peer-reviewed literature should be applied. Further, there might be a publication error in a way that many ecological data reported in the grey literature will not be accepted into peer-reviewed journals because the latter have shifted their scope away from basic data compilation. This potential bias might selectively comprise especially high quality grey literature such as theses, which include disproportionately high quality ecological data without publishing them beyond the thesis.

Nonetheless, in the general overview of the nMDS we found some exceptions were grey and peer-reviewed literature was not fully in accordance with each other. That observation was found for Danube salmon and brown trout, as the distance between the two data sets indicated some differences. For Danube salmon grey literature dominated the data availability and the addition of these data to the peer-reviewed pool led to a shift as there was now more data on all ecological parameters available that were not examined in the peer-reviewed literature. For brown trout we found an equal amount of grey and peer-reviewed data. However, the distribution of the data points per ecological parameter, besides the physical variables, varied depending on the literature source. Hence, for “areal size”, “redds per spawning site”, and “eggs per square meter” all or the majority of data were derived from grey literature sources. In contrast, data for “larval density”, “spawning events” and “days till hatch” were predominantly based on peer-reviewed sources. Another exception to the high coherence between grey and peer-reviewed literature was found for “degree days” of Atlantic salmon and “water temperature spawning” for European minnow. While the four peer-reviewed sources had been quite consistent, the values of the four grey literature sources varied considerably. Again, reasons for these deviations include the lack of standardised measuring and reporting, some as basic as whether the data were derived from a natural or laboratory observations (e.g., Gerstmeier & Romig 1998, Kottelat & Freyhof 2007).

3.6. Conclusions

Ideally, population conservation actions and strategies should be evidence-based with underlying rich and reliable data. Four aspects appear particularly crucial: (1) closing existing autecological knowledge gaps, (2) better standardisation during data generation and reporting, (3) accessibility, and (4) inclusion of additional data sources that complement peer-reviewed literature.

Closing existing autecological knowledge gaps primarily relates to the need of further research into currently understudied species of low socioeconomic appreciation, but also in spatial requirements and early-life stage ecology for prominent and understudied species (e.g., spawning site size, juveniles per m^2). Establishing standards in data generation and reporting refer to the need to clearly distinguish well-defined laboratory experiments from field studies as well as to include a minimum set of directly comparable physicochemical parameters (e.g., water temperature, current speed, water depth, following international texture definitions for substrate, etc.) and strict biological endpoint definitions (hatching stages, size of a minimum viable population, etc.). Data accessibility can be improved if “Open Data” policies are applied. This can be achieved if funding entities oblige researchers to disseminate their data (including a link to the original study) on international open online data bases such as FishBase (fishbase.se). This process could be similar to that for the National Center for Biotechnology Information (NCBI), which provides open access to biomedical and genomic information and offers a checklist of minimum standards that need to be met before uploading material to ensure high comparability of data. In times of striking headlines, the findability of literature via conventional keywords can be hindered (e.g., substrate preference of *Barbus barbus*) since some of these wordings may appear unattractive. However, using standard keywords is still the most effective way to notably improve the findability of sources. Further, the use of the English language is highly recommended to allow access to knowledge and data for people beyond the own country. The last aspect is the recommendation to consider grey literature such as academic theses and dissertations, research-, committee- and government reports as potential data source to improve comprehensiveness and timeliness of the data, which will then provide a more balanced picture of available knowledge.

3.7. References

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

Anders, P.J. (1998). Conservation aquaculture and endangered species. *Fisheries*, 23, 28–31.

Arthington, A.H., Dulvy, N.K., Gladstone, W., & Winfield, I.J. (2016). Fish conservation in freshwater and marine realms: Status, threats and management. *Aquatic conservations Marine and Freshwater Ecosystems*, 26, 838–857.

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.

Bierschenk, B.M., Pander, J., Mueller, M., & Geist, J. (2018). Fish injury and mortality at pumping stations: A comparison of conventional and fish-friendly pumps. *Marine and Freshwater Research*, 70, 449–458.

Blott, S.J., & Pye, K. (2012). Particle size scales and classification of sediment types based on particle size distributions: Review and recommended procedures. *Sedimentology*, 59, 2071–2096.

Bonar, S.A., & Hubert, W.A. (2002). Standard sampling of inland fish: Benefits, challenges, and a call for action. *Fisheries*, 27, 10–16.

Brandner, J., Auerswald, K., Cerwenka, A.F., Schliewen, U.K., & Geist, J. (2013). Comparative feeding ecology of invasive Ponto-Caspian gobies. *Hydrobiologia*, 703, 113–131.

Brandner, J., Cerwenka, A.F., Schliewen, U.K., & Geist, J. (2013). Bigger is better: Characteristics of round gobies forming an invasion front in the Danube River. *PLoS ONE*, 8, e73036.

Brook, B.W., Bradshaw, C.J., Traill, L.W., & Frankham, R. (2001). Minimum viable population size: Not magic, but necessary. *Trends in Ecology & Evolution*, 26, 619–620.

Burgman, M.A., Breininger, D.R., Duncan, B.W., & Ferson, S. (2001). Setting reliability bounds on habitat suitability indices. *Ecological Applications*, 11, 70–78.

Butler, J.R., Radford, A., Riddington, G., & Laughton, R. (2009). Evaluating an ecosystem service provided by Atlantic salmon, sea trout and other fish species in the River Spey, Scotland: The economic impact of recreational rod fisheries. *Fisheries Research*, 96, 259–266.

Casas-Mulet, R., Saltveit, S.J., & Alfredsen, K. (2015). The survival of Atlantic salmon (*Salmo salar*) eggs during dewatering in a river subjected to hydropeaking. *River Research and Applications*, 31, 433–446.

Catalano, M.J., Bozek, M.A., & Pellett, T.D. (2007). Effects of dam removal on fish assemblage structure and spatial distributions in the Baraboo River, Wisconsin. *North American Journal of Fisheries Management*, 27, 519–530.

Caudill, C.C., Daigle, W.R., Keefer, M.L., Boggs, C.T., Jepson, M.A., Burke, B.J., Zabel, et al. (2007). Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: Delayed negative effects of passage obstacles or condition-dependent mortality? *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 979–995.

Cerwenka, A., Brandner, J., Schliewen, U., & Geist, J. (2018). Population trends of invasive alien gobies in the upper Danube River: 10 years after first detection of the globally invasive round goby (*Neogobius melanostomus*). *Aquatic Invasions*, 13, 525–535.

Chang, W. (2014). Extrafont: Tools for Using Fonts. R Package Version 0.17. Retrieved February 20th, 2018 from: https://CRAN.R-project.org/package=extrafont

Conn, V.S., Valentine, J.C., Cooper, H.M., & Rantz, M.J. (2003). Grey literature in meta-analyses. *Nursing Research*, 52, 256–261.

Decker, E., Linke, S., Hermoso, V., & Geist, J. (2017). Incorporating ecological functions in conservation decision making. *Ecology and Evolution*, 7, 8273–8281.

Denic, M., & Geist, J. (2010). Habitat suitability analysis for lacustrine brown trout (*Salmo trutta*) in Lake Walchensee, Germany: Implications for the conservation of an endangered flagship species. *Aquatic Conservation*, 20, 9–17.

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

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.

EN933-1. (2012). European Standard. Tests for Geometrical Properties of Aggregates—Part 1: Determination of Particle Size Distribution—Sieving Methods, 1st ed.; The Office for Standards, Metrology and testing (ÚNMZ): Prague, Czech Republic, 10pp.

Flather, C.H., Hayward, G.D., Beissinger, S.R., & Stephens, P.A. (2011). Minimum viable populations: Is there a 'magic number' for conservation practitioners? *Trends in Ecology & Evolution*, 26, 307–316.

Fletcher, W.J., Shaw, J., Metcalf, S.J., & Gaughan, D.J. (2010) .An ecosystem based fisheries management framework: The efficient, regional-level planning tool for management agencies. *Marine Policy,* 34, 1226–1238.

Fox, J., & Weisberg, S. (2011). An {R} Companion to Applied Regression, 2nd ed.; Sage: Thousand Oaks, CA, USA. Retrieved February 20th, 2018 from: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Frankham, R., Brook, B.W., Bradshaw, C.J., Traill, L.W., & Spielman, D. (2013). 50/500 rule and minimum viable populations: Response to Jamieson and Allendorf. *Trends in Ecology & Evolution*, 28, 187–188.

Frissell, C.A., Liss, W.J., Warren, C.E., & Hurley, M.D. (1986). A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management*, 10, 199–214.

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.

Gerstmeier, R., & Romig, T. (1998). *Die Süßwasserfische Europas*. Stuttgart, Germany, Franckh-Kosmos Verlags-GmbH und Co. 367pp.

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., et al. (2019). Mapping the world’s free-flowing rivers. *Nature*, 569, 215.

Haddaway, N.R., & Bayliss, H.R. (2015). Shades of grey: Two forms of grey literature important for reviews in conservation. *Biological. Conservation*, 191, 827–829.

Huet, M. (1959). Profiles and biology of western European streams as related to fish management. *Transactions of the American Fisheries Society*, 88, 155–163.

ICES. (2018). Baltic Sea Ecoregion—Fisheries overview. Report of the ICES Advisory Committee, Section 4.2., 23.

Jamieson, I.G., & Allendorf, F.W. (2012). How does the 50/500 rule apply to MVPs? *Trends in Ecology & Evolution,* 27, 578–584.

Kottelat, M., & Freyhof, J. (2007). *Handbook of European Freshwater Fishes*. Cornol, Switzerland, Publications Kottelat. 646pp.

Langhans, S., Gessner, J., Hermoso, V., & Wolter, C. (2016). Coupling systematic planning and expert judgement enhances the efficiency of river restoration. *Science of the Total Environment*, 560, 266–273.

Lasne, E., Bergerot, B., Lek, S., & Laffaille, P. (2007). Fish zonation and indicator species for the evaluation of the ecological status of rivers: Example of the Loire basin (France). *River Research and Applications*, 23, 877–890.

Lewis, C.A., Lester, N.P., Bradshaw, A.D., Fitzgibbon, J.E., Fuller, K., Hakanson, L., & Richards, C. (1996). Considerations of scale in habitat conservation and restoration. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 440–445.

Lucas, M.C., & Frear, P.A. (1997). Effects of a flow-gauging weir on the migratory behaviour of adult barbel, a riverine cyprinid. *Journal of Fish Biology*, 50, 382–396.

McCune, B. & Grace, J.B. (2002). *Analysis of Ecological Communities*. Gleneden Beach, OR, USA, MjM Software Design. 300pp.

McDonald, J.H. (2014). *Handbook of Biological Statistics*. Baltimore, MD, USA, Sparky House Publishing. p157–164.

Mertens, M., Bösiger, R., Imhof, P., Knutti, A., Küry, D., & Staub, E. (2011). *Der Lachs—Ein Fisch kehrt zurück*. Bern, Switzerland, Haupt Verlag. 264pp.

Morandi, B., Kail, J., Toedter, A., Wolter, C., & Piégay, H. (2017). Diverse approaches to implement and monitor river restoration: A comparative perspective in France and Germany. *Environmental Management*, 60, 931–946.

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., & 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.

Neuwirth, E. (2014). RColorBrewer: ColorBrewer Palettes. R Package Version 1.1-2. Retrieved February 20th, 2018: from: https://CRAN.R-project.org/package=RColorBrewer

Nislow, K.H., Hudy, M., Letcher, B.H., & Smith, E.P. (2011). Variation in local abundance and species richness of stream fishes in relation to dispersal barriers: Implications for management and conservation. *Freshwater Biology*, 56, 2135–2144.

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

Paez, A. (2017). Gray literature: An important resource in systematic reviews. *Journal of Evidence-Based Medicine*, 10, 233–240.

Pander, J., & Geist, J. (2013). Ecological indicators for stream restoration success. *Ecological Indicators*, 30, 106–118.

Radinger, J., Kail, J., & Wolter, C. (2017). Differences among expert judgments of fish habitat suitability and implications for river management. *River Research and Applications*, 33, 538–547.

RC Team. (2017). R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria, 2017. Retrieved February 20th, 2018 from: http://www.R-project.org

Rhodes, J.R., Ng, C.F., de Villiers, D.L., Preece, H.J., McAlpine, C.A., & Possingham, H.P. (2011). Using integrated population modelling to quantify the implications of multiple threatening processes for a rapidly declining population. *Biological Conservation*, 144, 1081–1088.

Rudis, B., Bolker, B., Schulz, J., Kothari, A., Sidi, J. (2017). ggalt: Extra Coordinate Systems, ‘Geoms’, Statistical Transformations, Scales and Fonts for ‘ggplot2’. R Package Version 0.6.0. Retrieved July 6th, 2018 from: https://github.com/hrbrmstr/ggalt

Santucci, V.J., Jr., Gephard, S.R., & Pescitelli, S.M. (2005). Effects of multiple low-head dams on fish, macroinvertebrates, habitat, and water quality in the Fox River, Illinois. *North American Journal of Fisheries Management*, 25, 975–992.

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

Schmutz, S.; Zitek, A.; Zobl, S.; Jungwirth, M.; Knopf, N.; Kraus, E.; Bauer, T., et al. (2002). Integrated approach to the conservation and restoration of Danube salmon, *Hucho hucho*, populations in Austria. In I.G. Cowx, Collares-Pereira, M.J., & Coelho, M.M. (Eds.), *Conservation of Freshwater Fishes: Options for the Future*, Oxford, UK, Fishing News Books. p157–173.

Silva, A.T., Lucas, M.C., Castro-Santos, T., Katopodis, C., Baumgartner, L.J., Thiem, J.D., Aarestrup, K., et al. (2018). The future of fish passage science, engineering, and practice. *Fish and Fisheries*,19, 340–362.

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.

Spens, J.; Englund, G.; Lundqvist, H. Network connectivity and dispersal barriers: Using geographical information system (GIS) tools to predict landscape scale distribution of a key predator (*Esox lucius*) among lakes. J. Appl. Ecol. 2007, 44, 1127–1137.

Sternecker, K.; Wild, R.; Geist, J. Effects of substratum restoration on salmonid habitat quality in a subalpine stream. Environ. Biol. Fish. 2013, 96, 1341–1351.

Trudgill, D.L.; Honek, A.; Li, D.; Van Straalen, N.M. Thermal time–concepts and utility. Ann. Appl. Biol. 2005, 146, 1–14.

Udden, J.A. (1898). *The Mechanical Composition of Wind Deposits*;: Rock Island, IL, USA, Augustana Library Publications No 1. 69pp.

Udden, J.A. (1914). Mechanical composition of clastic sediments. *Bulletin of the Geological Society of America*, 25, 655–744.

Van Looy, K., Tonkin, J.D., Floury, M., Leigh, C., Soininen, J., Larsen, S., Heino, J., et al. (2019). The three Rs of river ecosystem resilience: Resources, Recruitment and Refugia. *River Research and Applications*, 35, 107–120.

Warnes, G.R., Bolker, B., Bonebakker, L., Gentleman, R., Liaw, W.H.A., Lumley, T., Maechler, M., et al. (2016). gplots: Various R Programming Tools for Plotting Data. R Package Version 3.0.1. Retrieved July 6th, 2018 from: https://CRAN.R-project.org/package=gplots

Wentworth, C.K. (1922). A scale of grade and class terms for clastic sediments. *The Journal of Geology*, 30, 377–392.

Wickham, H. (2009). *ggplot2: Elegant Graphics for Data Analysis*. New York, NY, USA, Springer-Verlag, 213pp.

Wickham, H. (2011). The Split-Apply-Combine Strategy for Data Analysis. *Journal of Statistical Software*, 40, 1–29.

Wickham, H., François, R., Henry, L., & Müller, K. (2018). dplyr: A Grammar of Data Manipulation. R Package Version 0.7.5. Retrieved July 6th, 2018 from: https://CRAN.R-project.org/package=dplyr

Wickham, H., & Henry, L. (2018). Tidyr: Easily Tidy Data with 'spread()' and 'gather()' Functions. R package version 0.8.1. Retrieved July 6th, 2018 from: https://CRAN.R-project.org/package=tidyr

Wolter, C., Buijse, A.D., & Parasiewicz, P. (2016). Temporal and spatial patterns of fish response to hydromorphological processes. *River Research and Applications*, 32, 190–201.

3.8. Appendix 1

Table A1. Search strings

Species Name					Environmental Parameter
German		**English**		**Latin**	
Barbe	or	common barbel	or	*Barbus barbus*	+ areal size
Nase	or	common nase	or	*Chondrostoma nasus*	+ current speed juvenile
Mühlkoppe or Groppe	or	European bullhead	or	*Cottus gobio*	+ current speed spawning site
Huchen	or	Danube salmon	or	*Hucho hucho*	+ days till hatch
Hasel	or	European dace	or	*Leuciscus leuciscus*	+ degree days
Elritze	or	European minnow	or	*Phoxinus phoxinus*	+ egg depth
Atlantischer Lachs	or	Atlantic salmon	or	*Salmo salar*	+ eggs per female
Bachforelle	or	brown trout	or	*Salmo trutta*	+ eggs per m^2
Döbel or Aitel *	or	European chub	or	*Squalius cephalus*	+ eggs per redd
Äsche	or	European grayling	or	*Thymallus thymallus*	+ eggs spawning site
					+ hatch rate
					+ juvenile per m^2
					+ larval density
					+ larval survival
					+ population density
					+ nest size
					+ redd size
					+ redds spawning site
					+ spawner density spawning site
					+ spawning events
					+ spawning site size
					+ substrate juvenile
					+ substrate spawning site
					+ water depth juvenile
					+ water depth spawning site
					+ water temperature spawning
					+ habitat
					+ spawning
					+ eggs
					+ individual density
					+ hatch success
					+ substrate
					+substrate quality
					+ juvenile
					+ fecundity
					+ autecology

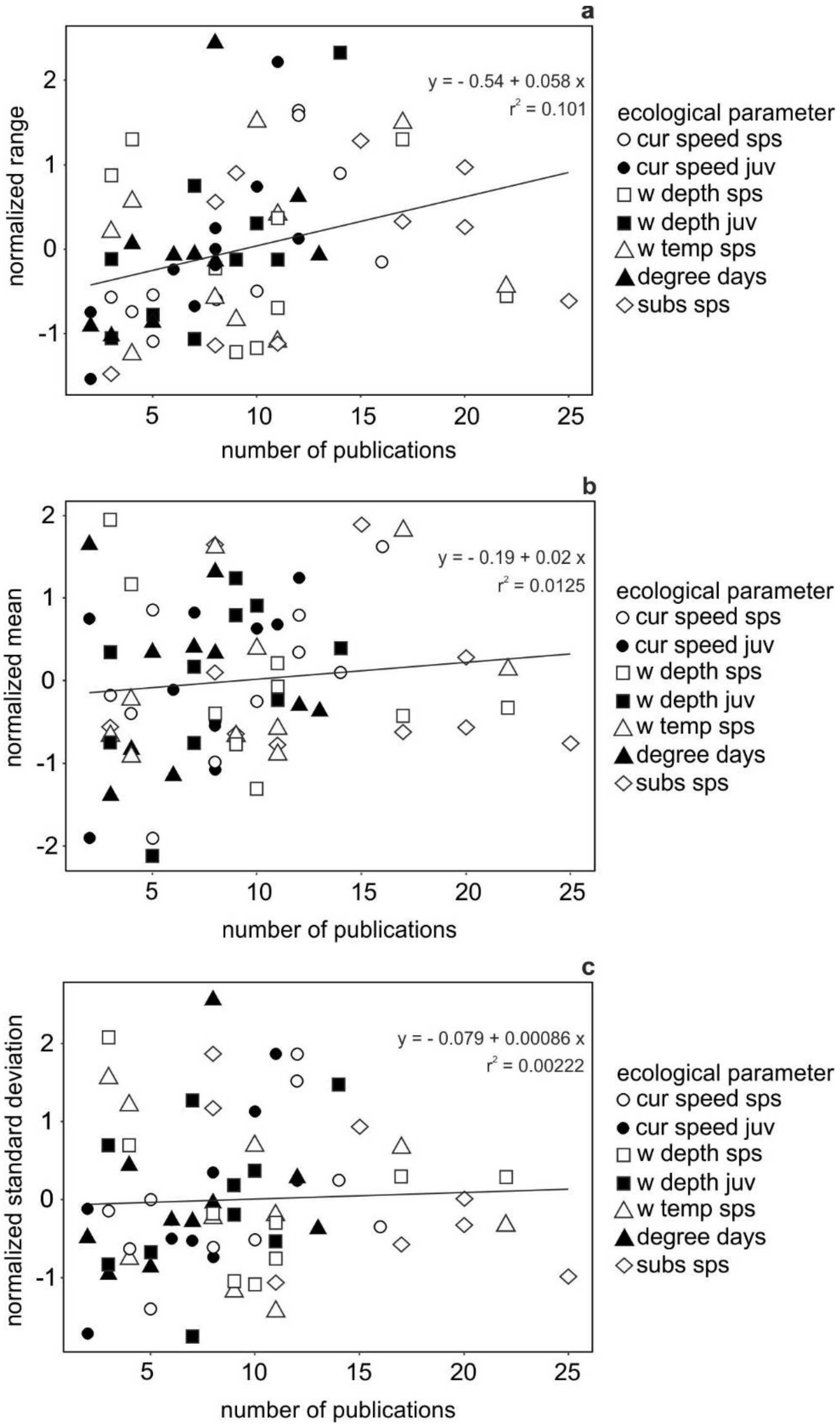


Figure A1. Test for linear relationship between the number of publications and the normalized range (a), normalized mean (b), and normalized standard deviation (c) of the seven selected ecological parameters as specified in Table 1.

4. Chapter II

Atlantic salmon and brown trout in freshwater: conservation implications

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4.1. Abstract

Atlantic salmon (*Salmo salar L.*) and brown trout (*Salmo trutta fario L.*) are species of high socio-economic and ecological value. Declining populations make them target species of fisheries management. This paper reviews the direct effects of deficient longitudinal connectivity, changes in discharge, high water temperatures, oxygen depletion, changes in water chemistry and increasing loads of fine sediment on the critical life stages of spawning, egg incubation and emergence. It further provides an overview about the basic autecological requirements of Atlantic salmon and brown trout and summarises important thresholds of physico-chemical tolerances. This collection of information provides important baselines for assessing historical, ongoing and new threats relevant for the management of both species in fresh waters. Critical early life stages of both species are almost identical, creating synergies in conservation and restoration. Seaward migrating forms are exposed to further stressors, but improving starting conditions can also greatly improve their resilience.

4.2. Introduction

Atlantic salmon (*Salmo salar L.*) and brown trout (*Salmo trutta fario L.*) are species of high socio-economic value related to human consumption and recreational fisheries (Elliott, 1989, Butler et al. 2009, Lobón-Cerviá 2017, Pokki et al. 2018, EUMOFA 2019). They also play important ecological roles in the functioning of freshwater and marine ecosystems (Willson & Halupka 1995, Hastie & Cosgrove 2001, Taeubert & Geist 2017, Reimchen 2018), and are considered indicator species in watercourse quality assessments and restoration (Soulsby et al. 2001, Pander et al. 2009, Pander & Geist 2010, Vehanen et al. 2010a). Thus, the conservation and maintenance of sustainable populations of these species is of important economic and political interest.

Atlantic salmon and brown trout are representatives of the genus *Salmo* (Webb et al. 2007). Atlantic salmon is native to the North Atlantic area and its indigenous distribution range in Europe extends from Iceland eastwards to the Baltic Sea and the Pechora river in the northwest of Russia, and southwards to the British Isles and the Douro river in northern Portugal (Figure 15, MacCrimmon & Grots 1979). The species exhibits differing life-strategies throughout its range in the North Atlantic.

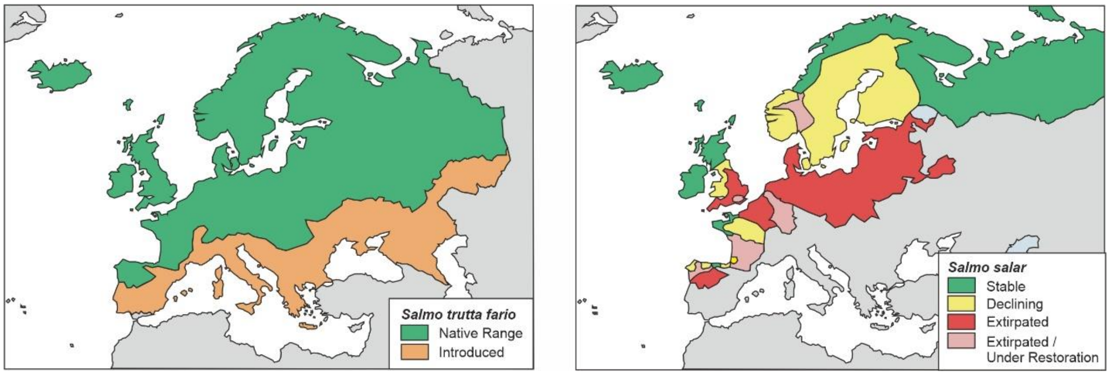

Figure 15. Distribution maps of Atlantic salmon and brown trout
Distribution range of brown trout (*Salmo trutta fario*) and Atlantic salmon (*Salmo salar*) in Europe.

Depending on the degree of sea-ward migration life-strategies can be roughly classified as complete anadromous (Figure 15), incomplete anadromous and non-anadromous (also referred to as landlocked), but uncertainties and variations with regard to aspects of the life cycle remain (Verspoor 2007). The ‘classical’ *Salmo salar*, which is the focus of this review, is the anadromous form, living in the sea and migrating to its natal rivers to spawn. Juveniles spend up to five years in fresh water before migrating to sea to mature (Hutching & Jones 1998). The time of spawning migration can vary between sexes and geographically with fish spending several winters at sea (multi-sea-winter fish) versus the so called grilse that only spend one winter at sea (Porter et al. 1986).

Brown trout is native to Europe with a distribution range that extends from Iceland eastwards to northern Scandinavia and Russia and southwards to the Atlas Mountains, the Ural Mountains and the Aral Sea basin (Figure 15, Williams & Aladin 1991, Jonsson & Jonsson 2011). *Salmo trutta* can be divided into several subspecies, morphotypes, or ecophenotypes that can exhibit distinctive life histories, particularly when it comes to migration directions and habitat preferences of adults. Most commonly, the species is subdivided into *Salmo trutta trutta* (adults living in the sea and migrating to rivers for spawning), *Salmo trutta lacustris* (living in lakes and migrating to lake tributaries for spawning) and *Salmo trutta fario* (a resident form spending its whole life cycle in rivers with migrations to spawning grounds within the river system), which is the most common form and the focus of this review (Figure 16 and 17, Kottelat & Freyhof 2007).

Atlantic salmon has experienced widespread population declines and extirpations over the last century (Parrish et al. 2011). Throughout its range (stocks in 2359 rivers), 43 % of *Salmo salar* populations are at risk, threatened or heavily declining (NASCO 2019). Only 14 % of rivers have sustainable stocks and notably, 36 % of rivers have no available data to assess stock status, some of which (particularly in Southern Europe) may be near extinction (NASCO 2019). While the global IUCN conservation status of Atlantic salmon (least concern; last assessed 1996) is in need of an update (World Conservation Monitoring Centre, 1996), more recent assessments in Europe have classifies Atlantic salmon as vulnerable (Freyhof 2014). Atlantic salmon is already considered extinct in Belgium, Netherlands, Germany, Czech Republic, Poland, Slovakia, and Switzerland, and many populations have been lost from Ireland, Wales, Scotland, England, Iberian Peninsula, France, Denmark, Sweden, Norway, and European Russia. Most recovery plans for Atlantic salmon have been running for more than 20 years and are still characterised by frequent stocking (Monnerjahn 2011, ICES 2017a, ICES 2019c).

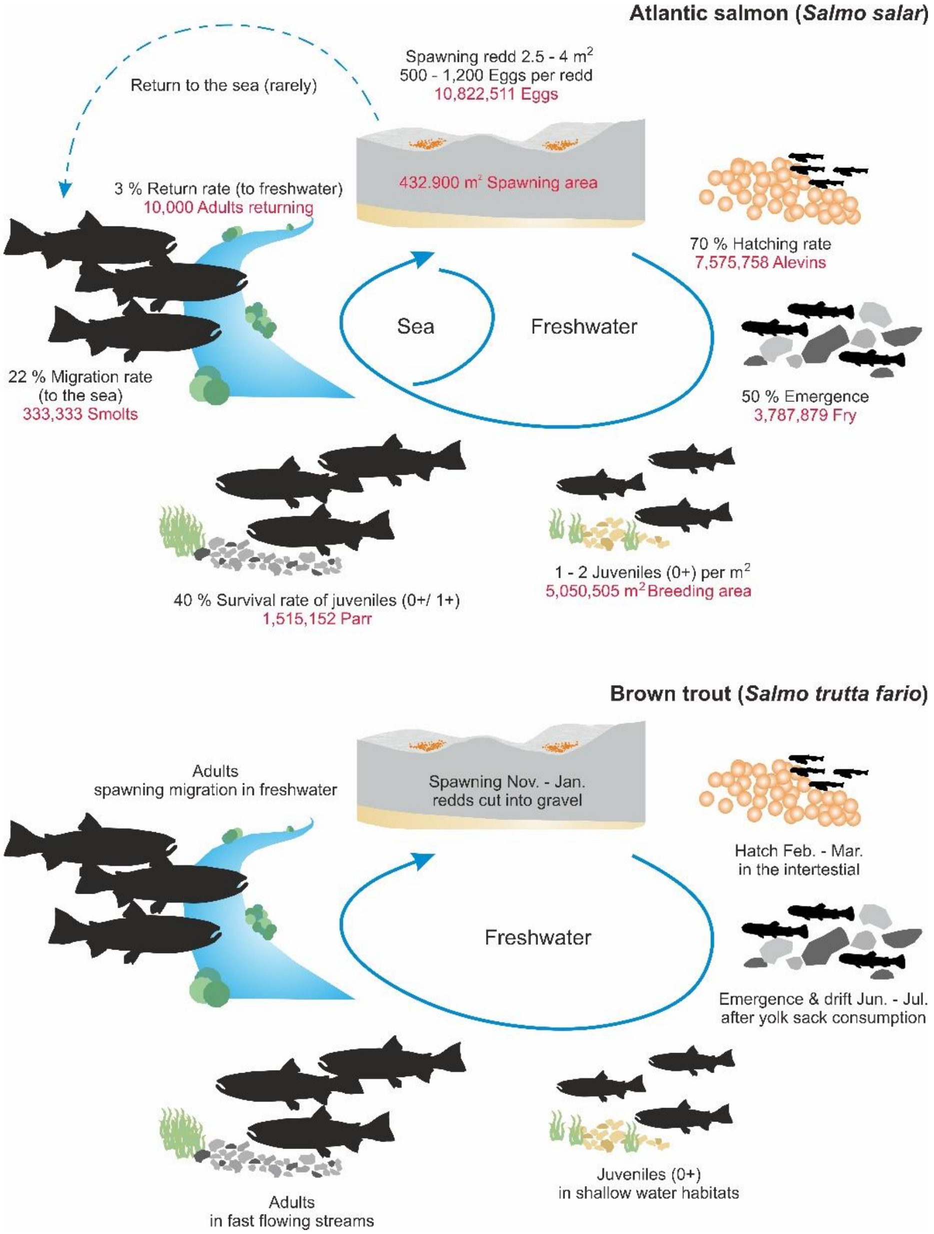

Figure 16. Common life cycles of Atlantic salmon and brown trout
Atlantic salmon life cycle includes the survival rates at different development stages and details on the required area during spawning and juvenile phase (numbers pers. comm. Wolter, 2020).

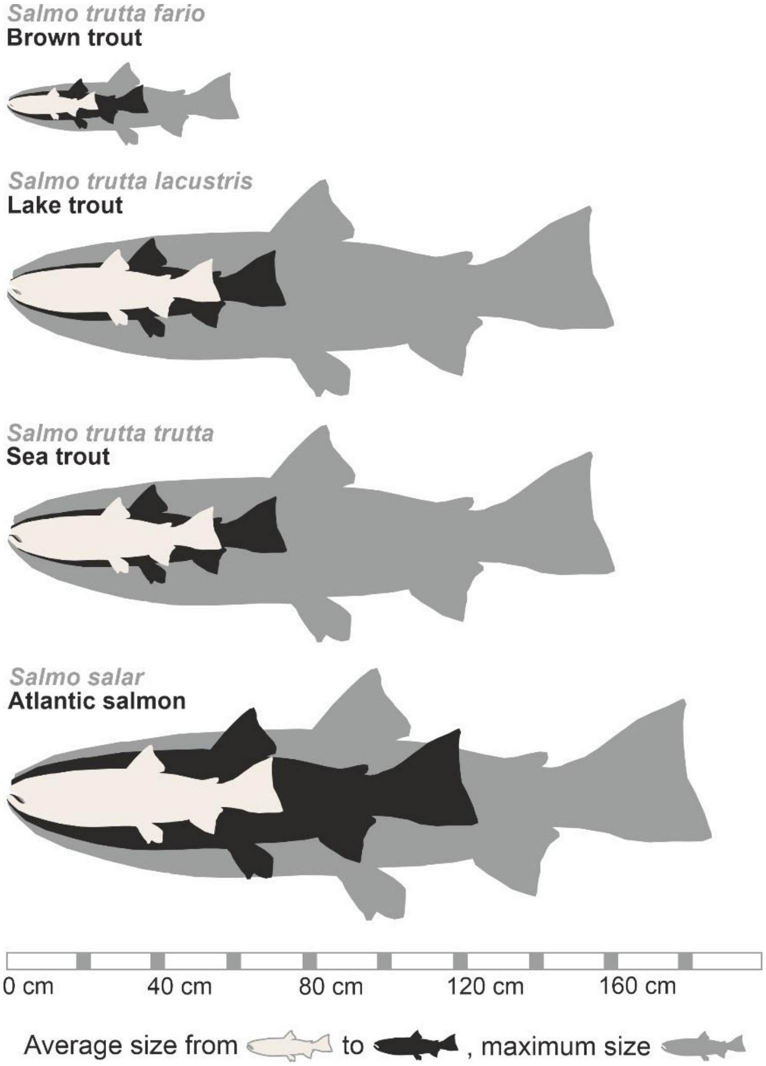

Figure 17. Sizes of different salmonid species
Size variation and overlap between and within different mature salmonid species which can co-occur in the same spawning habitat. Brown trout: 20[1] – 30[1] cm, 50[2] cm; lake and sea trout: 45[1] – 60[1] cm, 130[2] cm; Atlantic salmon: 60[2] – 100[2] cm, 150[2] cm. All sizes provided as standard length (SL). Sources: [1]Kottelat and Freyhof, 2007; [2]Gerstmeier and Romig, 2003.

Brown trout (*Salmo trutta fario*) is classified least concern on the IUCN Red List in Europe (Freyhof 2011). Decreasing population trends for *Salmo trutta fario* are reported from its southern distribution range, e.g. Spain: as vulnerable (Doadrio 2001) and Andalusia as endangered (Ruíz & Rodríguez de los Santos 2001), mostly due to climatic changes. However, the intense and routine stocking of brown trout practised throughout Europe since the beginning of the 20th Century may potentially be masking the real status of natural populations (Bernaś & Wąs-Barcz 2020).

As a result of their variable life-history strategies, the threats affecting the population status of Atlantic salmon and brown trout can also be diverse (Dudgeon et al. 2019), making selection of the most appropiate management and conservation measures complex. The basis for healthy, resilient and sustainable populations of brown trout and Atlantic salmon is already set during their critical early life stages (egg incubation, early development) in fresh water. The conditions for egg and larval development can strongly influence subsequent growth, survival and reproductive fitness (Russell et al. 2012). This is a critical bottleneck for both resident freshwater and sea-migrating populations, since only healthy smolts are sufficiently robust to withstand the manifold threats that they encounter on their way to the sea, in estuaries and intertidal areas (Lauridsen et al. 2017) and within the marine environment. In these habitats, it is known that fish can be easily infected with fish diseases (e.g. complex gill diseases) and parasites (e.g., sea lice, *Gyrodacytlus salaris*) originating from salmon farming (Rosenberg 2008) or escaped farmed salmon (Rozas-Serri 2019). For more information on marine threats on salmon see Parrish et al. (1998) and Forseth et al. (2017). Identifying the threats affecting the critical life stages of brown trout and Atlantic salmon during their early freshwater life stages can be hence seen as prerequisite to sustain healthy populations. In fresh water, local factors such as interruption of migration routes, habitat degradation and pollution are known to impair sustainability of stocks or even cause local extinctions (Hoffmann 1996, Jonsson & Jonsson 2009, Wolter 2014, Lenders et al. 2016, Forseth et al. 2017). Whilst most of these threats act systemically, their mitigation mostly needs to be addressed locally (e.g. in relation to barriers to migration, water quality or habitat availability). This includes restoration measures such as the creation of spawning grounds, and juvenile habitats, or facilitating connectivity (Geist & Hawkins 2016).

To address these threats effectively, it is important to understand the mechanisms of how single factors and their interactions affect the respective life stages and which mitigation measures are most effective (Geist 2015). Due to their cultural and economic importance the number of research programmes on the biology of Atlantic salmon and brown trout, and thus scientific papers, have advanced dramatically over the years, calling for a systematic update on current knowledge and an assessment of past, present and emerging challenges related to the conservation of both species.

This paper aims to provide a comprehensive overview of the latest knowledge on i) the general autecological requirements of the critical life stages of Atlantic salmon and brown trout, namely spawning, egg incubation and emergence; ii) the effects of deficient longitudinal connectivity, changes in discharge, high water temperatures, oxygen depletion, changes in water chemistry and increasing loads of fine materials on those life-stages; and iii) important thresholds of their physico-chemical tolerances. Based on the results of this review, historical, ongoing and new threats in freshwater are discussed and implications for future conservation and management actions of both species in freshwater are proposed.

4.3. General habitat requirements

4.3.1. Water body connectivity

Biological connectivity relates to four dimensions in riverine ecosystems: longitudinal, lateral, vertical and temporal (Ward, 1989). The linear connectivity or linear continuity of watercourses is particularly important for diadromous species like Atlantic salmon and sea trout (Aarestrup & Koed, 2003; Finstad et al., 2005). Migration between spawning areas/sites of hatching, juvenile habitats and the sea is crucial for the survival of these species and must be unhindered. The ability to overcome an obstacle depends on the body length of the fish and the tailwater depth. Ideally, the tailwater depth should be 1.25 times the height of the fish to allow passage (Stuart, 1962). Atlantic salmon can jump up to 1.5 m and overcome higher obstacles than brown trout due to their larger size (Gerlier & Roche, 1998). In steep riffles, water depths of twice to three times the body height are regarded as a minimum for successful passage for both species. Shorter distances (< 2 m) can also be passed in water depths at body height (LfU, 2005; DWA, 2014).

Lateral connectivity, in turn, ensures a network between rivers and laterally located aquatic habitats such as nutrient-rich floodplains or backwaters, generally increasing the overall productivity of the riverine ecosystem (Opperman et al., 2017;

Pander et al., 2018). This also increases the food availability for different fish species such as salmonids.

Vertical connection should exist between the interstitial spaces, the riverbed, the groundwater and the open water. The hyporheic zone is a key habitat for successful egg and larval development of salmonids (Malcolm et al., 2003a,b; Sternecker et al., 2013a,b; Mueller et al., 2014). Eggs and yolk sac larvae find suitable hydraulic conditions in the interstitial space, which offer them not only protection against predators and external influences, but also enables optimal oxygen supply and the disposal of toxic metabolites such as ammonium (Chapman, 1988; Crisp, 1993; Brunke, 1999; Greig et al., 2007; Kondolf et al., 2008).

The temporal dimension represents the varying connectivity with time, for example high or low flow events during different seasons (Ward, 1989). Atlantic salmon and brown trout, as with many other species, have developed and diversified species-specific life-history strategies to adapt to these temporal changes, for example spawning in autumn or spring, migratory or resident species (Sternecker et al., 2014).

The required water body size between riverine ecosystems for a successful development of a fish population is difficult to measure. In general, the distance between essential habitats that need to be accessible during specific life stages, seasons or daytime as well as prey availability are seen as main factors in determining the home range and total distance covered by a species and can be highly variable. During their spawning period, most salmonid species migrate upstream into their natal rivers.

The anadromous form of Atlantic salmon is considered a long-distance migrator of up to 700 km (Cuinat & Bomassi, 1987). Migration distance generally depends on the life stage and season (e.g. rearing, feeding, overwintering, spawning migration). By contrast, non-anadromous freshwater resident populations (mostly landlocked) or male parr can also mature in the absence of a seaward migration (Hutchings et al., 2019). Such forms occur throughout the distributional range of Atlantic salmon in North America (Power, 1958; MacCrimmon & Gots, 1979) and northern Europe (MacCrimmon & Gots, 1979; Berg, 1985; Kazakov, 1992; Davidsen et al., 2020). Some of these resident freshwater populations show deviant spawning behaviour such as spawning in lakes (Verspoor & Cole, 2005) or in lake inlets and outlets (Gibbins et al., 2002).

Brown trout can spawn in the main stems of a river system like Atlantic salmon, but generally prefer smaller streams (Crisp, 2000), often leading to spatial segregation of the two species (Geist et al., 2006). The water bodies used by brown trout for spawning are usually about 3 – 5 m wide and about 50 cm deep, with a gradient of up to 5 % (Crisp, 2000; Jonsson & Jonsson, 2011). Brown trout has also been observed in small tributaries with a width of less than 1 m and an average annual discharge of 30 – 40 $l \cdot s^{-1}$ during spawning (Jonsson et al., 2001; Geist et al., 2006). Landergren (2004) even found spawning sites in waters that periodically dry out, but only when juveniles could migrate to the main stem. Resident brown trout do not need a connection to the sea to fulfil their life cycle, in contrast to its ecophenotype, the sea trout (*Salmo trutta trutta* L.). Sea trout spend their growth phase in the coastal waters of the sea until they return to spawn in their natal river (Klemetsen et al., 2003; ICES, 2013; Thorstad et al., 2016). Another ecophenotype, the lake trout (*Salmo trutta lacustris* L.), typically migrates from pre-Alpine lakes into tributaries for spawning (Klemetsen et al., 2003; Denic & Geist, 2010). Both types have similar requirements for water body size and freshwater passability as the anadromous Atlantic salmon (Aarestrup & Koed, 2003; Klemetsen et al., 2003; Finstad et al., 2005). They can undertake extensive spawning migrations, which can exceed 100 km, or occasionally even > 500 km, the same as recorded for sea trout (Klemetsen et al., 2003; Thorstad et al., 2016). Resident brown trout usually undertake smaller spawning migrations within a river or stream system, but if suitable spawning sites are missing in the immediate vicinity, spawning migrations can also reach up to 100 km (Jungwirth et al., 2003; Olsson et al., 2006).

4.3.2. Discharge and water depth

Discharge and its dynamics are crucial for the reproduction of brown trout and Atlantic salmon in rivers and streams. For Atlantic salmon and sea trout, flow events have been described to stimulate the entry into their natal rivers, often coupled with other environmental factors (Banks 1969, Clarke et al. 1991, Jonsson 1991, Smith et al. 1994, Thorstad et al. 1998, Erkinaro et al. 1999, Svendsen et al. 2004, Jonsson et al. 2018). A rare exception to this observation is the study from Davidsen et al. (2013) conducted in Norway, which could not confirm that river entry of Atlantic salmon was facilitated by increased water discharge and/or ebb tide.

Atlantic salmon prefer to spawn in the main stream of rivers and large tributaries with an average annual discharge of > 1 $m^3 \cdot s^{-1}$ and a gradient of > 3 % (Mills 1989, Bergheim & Hesthagen 1990). Literature on the average runoff rates at spawning grounds of Atlantic salmon and brown trout was reviewed by Louhi et al. (2008). Discharge data from brown trout streams vary between < 1.0 – 350 $m^3 \cdot s^{-1}$, and data on salmon streams between 0.5 – 300 $m^3 \cdot s^{-1}$ depending on whether the fish spawn in small tributaries or in the main stream.

Water depth is crucial during migration and spawning, where the fish alternate between active swimming at various depths, spawning at rather shallow riffle stretches and resting in sheltered pools. Resting in a given pool can last up to 2 – 3 months (Webb 1989). Low discharge may decrease the quantity and quality of important habitat features. Spawning of Atlantic salmon and brown trout mainly occurs at water depths between 0.5 m – 1 m (reviewed by Smialek et al. 2019), and resting pools should have a minimum depth of > 0.9 m (Moreau & Moring 1993).

4.4. Spawning and rearing habitat requirements

The spawning and rearing habitat requirements of Atlantic salmon and brown trout overlap to a large extent (see reviews by Heggberget et al. 1988, Klemetsen et al. 2003, Smialek et al. 2019), so that spawning sites can overlap wherever both species occur together and a suitable habitat exists.

Spawning of both species in central European latitudes takes place between November and January and local spawning events extend over two to three weeks (Crisp 1993; Armstrong et al. 2003). According to Heggberget et al. (1988), spawning in streams with sympatric populations is partly separated by timing. There, spawning season of brown trout starts earlier, with peak spawning occurring two weeks before that of Atlantic salmon (Heggberget et al., 1988, Crisp 1993). Nevertheless, spawning time can vary locally to a large extend and may overlap as evident from regular appearance of hybrids (Youngson et al. 1992, Hartley 1996, Matthews et al. 2000, Westley et al. 2011).

Salmonids in general require spawning habitats with a gravel bottom and a high exchange between the open water and the interstitial zone for successful reproduction (Kondolf 2000, Malcolm et al. 2003a, Malcolm et al. 2003b, Sternecker et al. 2013a, Sternecker et al. 2013b). Thus, the spawning habitats of Atlantic salmon and brown trout are typically characterized by a pool riffle sequence (Figure 18).

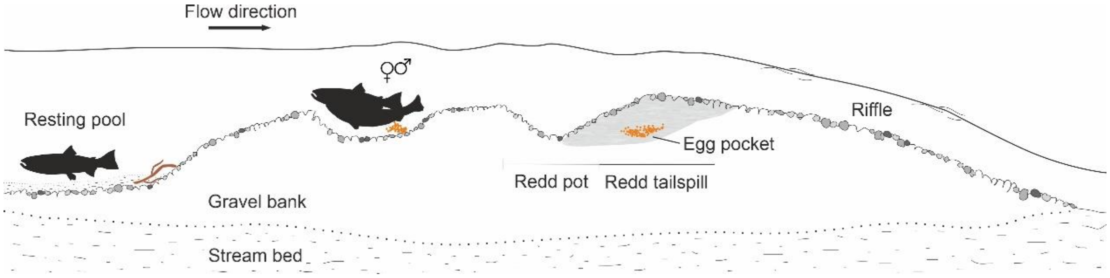

Figure 18. Features of *S. salar* and *S. trutta fario* spawning grounds.

At the transition to shallow overflowing gravel riffle stretches, the females cut spawning redds into the riverbed (Figure 18). Before placing their eggs, females first use their anal fin to examine whether the current conditions are suitable (Crisp 1993). Laying eggs and insemination by males occur at the same time. Thereby, successive fertilization by several males in both species is common (Thompson et al. 1998, Serbezov et al. 2010). Genetic found that alternative mating strategies play a major role in Atlantic salmon populations but not in brown trout (Garcia-Vazques et al. 2001). In Atlantic salmon, small, sexually mature males (precocious freshwater parr) can fertilize up to 40 % of eggs with increasing success rate at decreasing abundance of competitors (Thomaz et al. 1997). This alternative mating strategy in Atlantic salmon ensures that even if spawning occurs simultaneously with brown trout in sympatry, the offspring will predominantly be Atlantic salmon (Garcia-Vazques et al. 2001).

After insemination, eggs are covered with gravel (gravel spawners, e.g., Ottaway et al. 1981, Crisp & Carling 1989, Klemetsen et al. 2003, Louhi et al. 2008). Salmonids are stage spawners, cutting several spawning redds one after the other. On average redds are 1 – 5 m^2 in size (Barlaup et al. 2008, Pulg 2009). Although a relationship exists between female length and redd size, with larger females preparing larger redds (Ottaway et al. 1981, Heggberget et al. 1988), attribution of individual redds to species directly in the field is difficult (Dirksmeyer 2008). The main reason is that the size ranges of Atlantic salmon and brown trout can overlap, that is smaller Atlantic salmon overlap in size with large brown trout (Figure 18). In this case, they may share spawning sites and create same redd sizes. This is further complicated when the spawning ground is also used by the other ecomorphs of *Salmo trutta* as they can become even larger and overlap even more with Atlantic salmon in size (Figure 18). In addition, factors like flow velocity, sediment density and redd superimposition can also influence the size of the redds (Dirksmeyer 2008). Therefore, only the direct identification of spawners, a genetic analysis of deposited eggs, or hatched larvae allow a clear species assignment in case of sympatric occurrence (Gross et al. 1996).

Brown trout lay their eggs at depths of approx. 8 – 25 cm, whereas Atlantic salmon tend to lay their eggs deeper at 15 – 30 cm (Crisp 2000). In contrast to the large quantity of small eggs released by gravel-spawning cyprinids (e.g., *Chondrostoma nasus*, Duerregger et al. 2018, Nagel et al. 2020), salmonids release small quantities (on average 1600 – 1800 kg female $^{-1}$) of large eggs (brown trout approx. Ø 5 mm; Atlantic salmon approx. Ø 6 – 9 mm) (Aulstad & Gjedrem 1973, Thorpe et al. 1984, Bardonnet & Baglinière 2000, Randak et al. 2006).

On average, salmon eggs need more time to hatch than brown trout under the same conditions (Crisp 1993). The development of brown trout and salmon from egg to hatching depends on the average ambient temperature. Brown trout eggs hatch after 1.5 – 5 months or 410 –456 degree days, and Atlantic salmon eggs after 383 – 545 degree days (Kottelat & Freyhof 2007, Smialek et al. 2019).

The larvae stay in the interstitial spaces until their yolk sac is nearly absorbed. This process is dependent on the ambient water temperature and the size of the individual (Einum & Fleming, 2000, Ojanguren & Braña 2003). Afterwards they emerge simultaneously at night from the gravel and drift into shallower water areas with moderate current velocities where they spend their juvenile phase and change to exogenous feeding (Bardonnet et al. 1993, McCormick et al. 1998).

4.4.1. Water temperature

For cold-stenothermic species such as salmonids, the temperature not only determines the spawning time (Klemetsen et al. 2003, Sternecker et al. 2014), but also has a direct effect on the survival and development of eggs, juveniles and adults (Crisp 1993, Crisp 1996). The metabolic rate, growth or oxygen supply, as well as many other vital physiological processes, depend on the ambient temperature. Temperature and the ionic environment, among other factors, are particularly important for the duration and quality of egg maturation and thus, for the reproductive success of salmonids (Jobling 1997, Atse et al. 2002). In addition, sexual maturity and fertility are also influenced by temperature (Jonsson & Jonsson 2009). A general literature overview on thermal limits for salmon and brown trout during their critical life stages is given in Table 2. The optimum temperature range for Atlantic salmon spans from 7 – 20 °C, within which maximal growth occurs at 6 – 17 °C (Jensen et al. 1989). The optimum range for brown trout is 4 – 19 °C (Table 2).

The development of eggs and larvae in brown trout and Atlantic salmon occurs in winter. Low temperatures ensure a high solubility of oxygen in the water and thus, an optimal supply for the brood (Crisp 1993). The early-life stages are more sensitive to temperature fluctuations and high temperatures than emergent larvae and adult fish as temperature tolerance increases with fish age (Hayes 1949, Rombough 1988, Elliott & Elliott 2010). During winter, temperature in the redds is often several degrees higher than in the open water (Witzel & MacCrimmon 1983). However, this can be strongly dependent on interstitial exchange or possible groundwater upwelling at the spawning site (Kondolf & Wolman 1993, Malcolm et al. 2003a). For example, Clark (1998) found a vertical temperature gradient of $-3.7\ °C \cdot m^{-1}$ in the river bottom. For brown trout, temperatures between 0 and 10 °C are considered ideal for egg and larval development at a survival rate of 95 % (Crisp 1993). According to Crisp (1993), the optimal temperature range for salmon is very similar, but slightly higher at 4 – 12 °C (> 95 % survival rate) (Jensen et al. 1989, Crisp 1993, Smialek et al. 2019).

Table 2. Literature overview of temperature tolerances
Literature overview on the optimum, lower critical range (LCR), upper critical range (UCR) and lethal limit of temperature for three critical life stages of Atlantic salmon (AS) and brown trout (BT). Optimum for spawners divides into 'preferred' temperature when moving within a thermal gradient, and temperature range at spawning, marked with a '*'. eggs$_{\text{inc}}$ = eggs incubating.

		Temperature (°C)				
Stage	**Species**	**Optimum**	**LCR**	**UCR**	**Lethal limit**	**Reference**
spawners	AS	6 - 8*				Vernidub (1963) cited in EIFAC (1969)
spawners	AS			> 21		EIFAC (1969)
spawners	AS	1 - 6*				reviewed by Alabaster and Lloyd (1982)
spawners	AS	6 - 10*				Piper et al. (1982)
spawners	AS	10 - 17				Piper et al. (1982)
spawners	AS		0 - 7	22 - 33	< 0 or > 27.8	reviewed by Elliott (1994)
spawners	AS				27 - 28	Garside (1973)
spawners	AS	9 - 17				Mantelman (1958) cited by EIFAC (1969)
spawners	AS	6 - 20		20 - 34		Elliott (1981)
spawners	AS	0 - 8*				Elliott (1981)
spawners	AS	13 - 15				Nikiforov (1953) cited in EIFAC (1969)
spawners	AS	16 - 17	< 7	22	25 - 28	Crisp (1993)
spawners	BT	1 - 2*				Vernidub (1963) cited in EIFAC (1969)
spawners	BT			> 21		EIFAC (1969)
spawners	BT	4 - 19	0 - 4	19 - 25	23 - 30	Elliott (1981)
spawners	BT	1 - 10*				Elliott (1981)
spawners	BT	2 - 6*				reviewed by Alabaster and Lloyd (1982)
spawners	BT	9 - 13*				Piper et al. (1982)
spawners	BT	9 - 16				Piper et al. (1982)
spawners	BT	7 - 9*				Mansell (1966) cited in Raleigh et al. (1986)
spawners	BT	7 - 13*		25		Hunter (1973)
spawners	BT		0 - 4	19 - 30	< 0 or > 24.7	reviewed by Elliott (1994)
spawners	BT	13 - 14	< 4	19	21 - 25	Crisp (1993)
eggs	AS				< 0 or > 16	Elliott (1981)
eggs$_{inc}$	AS	4 - 11		< 12		Poxton (1991)
eggs	AS	4 - 12				Crisp (1993)
eggs$_{inc}$	AS			16		Ojanguren et al. (1999)
eggs	BT				< 0 or > 13	Elliott (1981)
eggs	BT	7			12 - 13	Jungwirth and Winkler (1984)
eggs	BT	0 - 10				Crisp (1993)
eggs$_{inc}$	BT			12	15.5	Crisp (1993)
eggs$_{inc}$	BT	2 - 13	< 0	> 15		Raleigh et al. (1986)
eggs$_{inc}$	BT	8 - 10		14 - 16	16 - 18	Ojanguren and Braña (2003)

		Temperature (°C)				
Stage	**Species**	**Optimum**	**LCR**	**UCR**	**Lethal limit**	**Reference**
larvae	AS	4 - 12				Crisp (1993)
larvae	AS			22		Ojanguren et al. (1999)
larvae	BT				> 22	Hunter (1973)
larave	BT	0 - 10				Crisp (1993)
fry	BT				> 25.46	Spaas (1960) cited in Raleigh et al. (1984)
fry	BT	6.7 - 12.8			< 4.5	Markus (1962) cited in Raleigh et al. (1984)
fry	BT	7 - 15				Brown (1973) cited in Raleigh et al. (1984)

Table 2. Continued.

4.4.2. Oxygen saturation

Salmonids are highly dependent on a sufficient oxygen supply for successful egg and larval development (Chapman 1988, Eklöv et al. 1999). Minimum required oxygen demands of the early-life stages can vary widely, depending on which endpoint is considered. According to Rubin & Glimsäter (1996) a minimum of 10 mg·l^{-1} should be available to achieve > 50 % egg-to-fry survival. However, most authors agree that the eggs of brown trout and salmon can tolerate oxygen concentrations as low as 5 mg·l^{-1}, at least for a short time (Crisp 1993, Niepagenkemper et al. 2003). Generally, 7.0 mg·l^{-1} oxygen at an incubation temperature of 12.5 °C and a flow velocity of >°100 cm·h^{-1} (Crisp 1996, Ingendahl 2001, Sternecker et al. 2013a) are recommended for a successful development. The oxygen demand during egg development depends on the development stage, size, carotene content and blood vessel density of the embryo (Hayes et al. 1951, Rubin & Glimsäter 1996, Ingendahl 1999). An overview of the different literature values on oxygen demands during different stages of development is presented in Table 3. In general, the oxygen demand is highest shortly before hatching (Crisp 1993).

Table 3. Literature overview of oxygen concentration tolerances
Literature overview on the optimum, lower critical limit (LCL) and lethal limit of oxygen levels for three critical life stages of Atlantic salmon (AS), brown trout (BT) and reported for both species (both). eggs$_{inc}$ = eggs incubating.

		Oxygen (mg·l^{-1})				
Stage	**Species**	**Optimum**	**LCL**	**Lethal limit**	**Additional information**	**Reference**
spawners	AS		< 6.5			Johansson et al. (2006)
spawners	BT	≥ 9		< 3	≥ 10 °C	Raleigh et al. (1986)
spawners	BT		< 4.5		20 °C	Hunter (1973)
spawners	both	> 9	7			EU (1976)
eggs$_{inc}$	AS		< 5			Gibson (1993)
eggs$_{inc}$	BT	10	< 10	< 9	egg-to-fry survival	Rubin and Glimsäter (1996)
eggs$_{inc}$	BT		< 2.7		at 5 cm depth; 43 % hatching success	Sternecker et al. (2013a)
eggs$_{inc}$	BT	> 6.9				Ingendahl (2001)
eggs$_{inc}$	both		< 5			Everest et al. (1987)
eggs$_{inc}$	both	> 7				Crisp (1996)
eggs$_{inc}$	both	> 7			< 12.5 °C	Crisp (2000)
eggs$_{inc}$	both		< 5			Crisp (1993)
eggs$_{inc}$	AS			< 6		Lacroix (1985a)
embryos	AS			< 3.7	5 °C, 77 days, LC$_{50}$	Hamor & Garside (1976)
embryos	AS			< 3.9	10 °C, 43 days, LC$_{50}$	Hamor & Garside (1976)
fry	AS	> 8			80 to 100 % saturation	Liao & Mayo (1972)
embryos	BT	7 - 10			at hatching	Louhi et al. (2008)
fry	BT	> 7	< 3		< 15 °C	Raleigh et al. (1984)
fry	BT	> 9	< 5		> 15 °C	Raleigh et al. (1984)
fry	both		< 3		15 °C	Bishai 1962

4.4.3. pH effects

Brown trout and Atlantic salmon occur in silicate and carbonate waters with pH values varying between 7 and 8.5. Maximum fish productivity is expected at pH values between 6.5 and 8.5, and the safe range of 6 – 9 proposed by ORSANCO (1955) has found worldwide acceptance in the national recommended water quality criteria for aquatic life (EU 2006, EPA 2019). The pH furthermore determines the solubility of ammonia or aluminium, which in high concentrations can be toxic to aquatic organisms (Crisp 1993, Gensemer & Playle 1999, Wauer et al. 2004, Finn 2007). An overview of pH, aluminium and ammonium tolerances is presented in Table 4.

Table 4. Literature overview on pH, Al, and NH_4 tolernces
The optimum, critical and lethal concentrations of pH, aluminium, ammonium and ammonia for critical life stages of Atlantic salmon (AS), brown trout (BT) and reported for both species (both). $eggs_{inc}$ = eggs incubating, $eggs_{eye}$ = eggs eyed stage, Al_{tot} = total aluminium, Al_i = inorganic monomeric aluminium, LC_{50} = lethal concentration with 50% mortality, LL_{50} = lethal loading causing 50 % mortality. Opt. = Optimum.

Stage	Species	Opt.		Additional information	References
			Lethal limits		
spawners	AS		NH_4^+ 0.2 - 0.5 $mg \cdot l^{-1}$	LC_{50} after 24 h	Alabaster et al. (1979)
spawners	BT		NH_4^+ 0.6 - 0.7 $mg \cdot l^{-1}$	LC_{50} after 96 h	Env. Canada (2001)
spawners	BT		pH < 5 and Al_{tot} > 100 $\mu g \cdot l^{-1}$	field	Barlaup and Åtland (1996)
$eggs_{eye}$	AS		pH = 4.0 - 4.5	mortality 50 %; > 30 days	Peterson et al. (1980)
$eggs_{inc}$	AS		pH = 4.7	LL_{50}; field	Lacroix (1985a)
$eggs_{inc}$	AS		pH = 3.9	LL_{50}; lab	Daye and Garside (1979)
eggs	AS		pH < 4.8 - 5.6 and Al_i > 20 - 310 $\mu g \cdot l^{-1}$	egg-to-alevin mortality > 93 %; lab	Skogheim and Rosseland (1984)
$eggs_{inc}$	AS		pH = 3.5	mortality 100 %; lab	Carrick (1979)
$eggs_{inc}$	BT		pH = 3.5	mortality 100 %; lab	Carrick (1979)
eggs	BT		pH < 4.8 - 5.6 and Al_i > 20 – 310 $\mu g \cdot l^{-1}$	egg-to-alevin mortality > 86 %; lab	Skogheim and Rosseland (1984)
$eggs_{eye}$	BT		pH < 4.5	mortality > 90 %; lab	Brown and Lynam (1981)
$eggs_{inc}$	both		pH < 4.5 and pH > 9	die before hatching	Crisp (1993)
alevins	AS		pH = 4.3	LL_{50}; lab	Daye and Garside (1979)
alevins	BT		< 20 Al_{tot} $\mu g \cdot l^{-1}$	LC_{50}; field	Weatherley et al. (1990)
fry	AS		pH < 5	sublethal effects; lab	Daye and Garside (1979)
fry	AS		pH < 5	mortality > 70 %; field	Lacroix et al. (1985a)
fry	BT		Al_{tot} = 15 $\mu g \cdot l^{-1}$	LC_{50}; 42 days; field	Weatherley et al. (1990)
fry	BT		pH = 4.5 and Al_i = 323 $\mu g \cdot l^{-1}$	mortality > 50 %; > 108 days; lab	Reader et al. (1991)
fry	BT		pH = 4.5 and Al_i = 324 $\mu g \cdot l^{-1}$	mortality > 50 %; lab	Çalta (2002)
fry	BT		pH = 4.5 and Al_i = 600 $nmol \cdot l^{-1}$ and Ca = 20 $\mu mol \cdot l^{-1}$	mortality > 90 %; lab	Sayer et al. (1991)

Table 4. Continued.

Stage	Species	Opt.		Additional information	References
			Critical limits		
spawners	BT	4.5 - 9.2			Crisp (1993)
spawners	BT	6.8 - 7.8			Heacox (1974) cited in Raleigh et al. (1986)
spawners	both	6 - 9			EU (1978)
spawners	both		$NH_4^+ < 0.03$ mg·l^{-1} and $NH_3 < 0.005$ mg·l^{-1}		EU (1978)
eggs$_{eye}$	BT		pH < 4.0, no Al_i correlation observed	mortality > 40 %; field	Serrano et al. (2008)
eggs$_{inc}$	BT		$NH_4^+ < 1.5$ mg·l^{-1}	mortality > 40 %; field	Sternecker et al. (2013a)
fry	BT		pH < 4.0, no Al_i correlation observed	mortality > 40 %; field	Serrano et al. (2008)
juvenile	BT	6.7 - 7.8	pH < 5.0 or > 9.5		Raleigh et al. (1984)

Ammonium (NH_4^+) in aqueous solution is in equilibrium with free ammonia (NH_3). Rising pH values and temperatures shift the equilibrium towards ammonia. For salmonids, a general guide value of < 0.03 mg·l^{-1} for ammonium and < 0.004 mg·l^{-1} for ammonia (EU 1978; Directive 78/659/EEC) applies. Various other references place the recommended threshold values for ammonia between 0.015 and 0.001 mg·l^{-1} (IWB & IDUS 2012).

Aluminium can be dissolved and mobilized from terrestrial soils, river sediments or mining at pH values below 4.5 (Eriksson 1981, Forseth et al. 2017). High concentrations of aluminium in freshwater often occur after heavy rainfall or during snow melting (Henriksen et al. 1984). A pH value < 6 and total aluminium concentration of > 0.1 mg·l^{-1} is mentioned as critical for the vitality and reproduction of fish in weakly mineralized waters (Lenhart & Steinberg 1984).

4.4.4. Substrate composition

Brown trout and Atlantic salmon favour similar substrate compositions for spawning, egg and larval development (Ottaway et al. 1981, Walker & Bayliss 2007, Louhi et al. 2008). The average grain size at the spawning grounds of brown trout and salmon is about 10 % of body length (Kondolf & Wolman 1993). The formula provided by Crisp

(1993) can be used to determine the maximum average grain size in which a female can still spawn, where P is the median grain size in mm and L the fish length in cm:

$$P = L \times 0.5 + 4.6. \tag{1}$$

Crisp (1993) generally referred to a high tolerance to different substrate compositions and reported 20 – 30 mm average grain size as particularly suitable for brown trout and Atlantic salmon. In contrast, Louhi et al. (2008) report an average use of grain sizes of 16 – 64 mm taking most available literature values into account. The values are understood to apply equally to both species, but with a distinction between large (> 10 $m^3 \cdot s^{-1}$) and small rivers (< 10 $m^3 \cdot s^{-1}$) where in the latter the salmon show a slight preference for larger substrates of 32 – 128 mm.

Another important characteristic determined by substrate composition is the storage density. In order to enable successful egg development, the pore spaces in the interstitial must be large enough to provide sufficient space for the eggs and later the hatched larvae to be supplied with fresh water. On the other hand, the spaces should be small enough to fix the eggs for undisturbed incubation. Optimum storage densities for successful egg and larval development are achieved with grain size fractions of 16 – 32 mm (Sternecker & Geist 2010, Pulg et al. 2013) with less than 5 % fines (particles < 4 mm in diameter; Raleigh et al. 1986).

4.5. Threats to Atlantic salmon and brown trout

4.5.1. Lack of longitudinal connectivity

To date, many efforts have been made to restore river connectivity, for example in the context of the targets set by the EU Water Framework Directive (WFD, EU 2000). However, Grill et al. (2019) demonstrated that out of 29,688 European rivers, 60 % are still considered non free flowing (considering rivers > 10 km). Further, considering only rivers connected to the sea (n = 3726), 15 % are considered non free flowing. Grill et al. (2019) argued that the percentage of disconnected rivers may be even higher as small dams are often not reported in the global river impoundment datasets. This would be in line with the study from Belletti et al. (2020) which described that more than one billion barriers fragment European rivers.

The interruption of longitudinal connectivity through transverse structures (e.g., weirs, power plants and culverts) or consumptive water use can cause (i) interruption or prevention of movement and migration of aquatic organisms and (ii) habitat change or degradation.

The consequences are manifold (Benejam et al. 2016). The lack of access to adequate spawning grounds can have a negative impact on the reproductive success and the stability of populations (Gosset et al. 2006, Johnsen et al. 2011). Lack of genetic exchange due to spatial separation may lead to genetic impoverishment of populations and limited adaptability to environmental stress (Bijlsma & Loeschcke 2012, Klütsch et al. 2019). A high risk of being injured or dying is present during downstream passage as fish enter turbines, bypass devises, trash racks, spill or trash gates or after passage of overflowed weirs (e.g., Rytwinski et al. 2017 for review; Mueller et al. 2017, Bierschenk et al. 2018, Knott et al. 2019, Pflugrath et al. 2019, Geist 2021).

In addition, there can be cumulative effects in waters with a number of transverse structures that need to be passed (Peter 1998, Gowans et al. 2003). Further, obstacles, interrupted flow patterns in rivers or turbine passage may disorient migrating fish, and thereby delay migration and increase the risk of predation (Poe et al. 1991, Jepsen et al. 1998, Baisez et al. 2011). A delay in migration is often associated with exhaustion due to prolonged search times for suitable migration routes, which could negatively affect reproductive success (Hinch & Bratty 2000, Caudill et al. 2007, McLaughlin et al. 2013). Furthermore, temporal mismatch situations can occur in the time of larval development, where suitable habitat conditions do not match the time of larval occurrence (Cushing 1975, Cushing 1990). Hence, interrupted migration routes can lead to a severe thinning of the migrating populations in the long term (Aarestrup & Koed 2003, Lundqvist et al. 2008) with the risk of depressing them below the minimum viable size (Courchamp et al. 2008). However, it has to be noted that not all migration barriers are of anthropogenic origin. The reintroduction of, for example, Canadian and European beavers, which are known to build wooden dams into small to medium sized rivers, cause local conflicts with management actions to restore fish migration and habitat, particularly spawning grounds (Gaywood 2018). Negative effects of river fragmentation on movements of fish were already recognized in the mid-18th century when the first fish pass in northern Europe were built (Johnsen et al. 2011, Birnie-Gauvin et al. 2019). Today it is well-known that mitigation measures need to be adjusted to site-specific conditions and species-specific requirements to be functional. Practically, most equations on how to build suitable fish passes exist for salmonids (Noonan et al., 2012; Birnie-Gauvin et al. 2019). Fish passage efficiency reviewed from articles from 1960 to 2011 by Noonan et al. (2012) revealed that on average salmonid passage success was 61.7 % for upstream and 74.6 % for downstream movement. Best predictors for passage efficiency included type of fish pass and its length. Birnie-Gauvin et al. (2019) argue that low efficiencies result from trying to ‘fit fish into equations’ whereby essential factors such as natural variations on species and ecosystem level are not considered. Further, effective monitoring is seldom standard procedure, and thus, restrictions in connectivity are often overlooked.

van Puijenbroek et al. (2019) found that viable populations of Atlantic salmon occurred mainly in rivers that were at least 85 % accessible. In rivers where the population was extinct or restocking of juvenile salmon was practised, accessibility averaged only 25 %. Restocking of Atlantic salmon in European rivers often occurs in high numbers and repeatedly over several years (HELCOM 2011, Wolter 2014, ICPR 2015). However, van Puijenbroek et al. (2019) pointed out that some reintroduction of the species happened in inaccessible rivers and thus was insufficient as a measure on its own to re-establish a viable population. Indeed, facilitating longitudinal connectivity will not have any long-term effects, unless all essential requirements for the different life stages are taken into account, for example appropriate habitats for spawning, rearing and foraging (Dynesius & Nilsson 1994, Poff et al. 1997, Ward & Wiens 2001, Bond & Lake 2003, Pander & Geist 2013).

Habitat degradation can lead to increased competition for the limited resources, for example high-quality spawning sites (Essington et al. 1998, Gortázar et al. 2012). Possible consequence of a competition for spawning ground are overlapping redds, washed out or destroyed eggs by overcutting of redds by other conspecifics or competitors from the sister species, which can result in high reproductive losses (Rubin & Glimsäter 1996, Bardonnet & Baglinière 2000).

At which point spawning site capacity is reached depends on different factors such as number of females ready to spawn and the quality of the location. However, it is possible to outline the approximate space or habitat capacity required using the following formula:

$$A_{sp} = \frac{N_t}{N_n} \times A_{nest} \times \alpha. \qquad (2)$$

A_{sp} is the required spawning site space, N_t is the number of eggs to reach the desired target of returning spawners, N_n is the number of eggs per nest, A_{nest} is the area of one nest and α is a factor considering the distance between nests, and nests and shore.

If, for example, 10,000 returnees from an Atlantic salmon population are considered as the desired target, the number of eggs originally laid at the spawning site would be approximately 10,822,511 (N_t) (see Figure 17). Taking a conservative approach by assuming a redd size of 4 m^2 (A_{nest}) and 500 eggs (N_n) per redd and a space factor $=$ 5, the resulting nest area would be 432,900 m^2 containing 10,822,511 eggs (Wolter 2020, pers. comm.).

4.5.2. Discharge change

The increase in managed flows and water levels in freshwater systems (e.g., to optimize hydropower production) can impair the highly adapted strategies of fish species to the natural occurring flow regimes. A threat from changes in runoff dynamics usually prevails wherever most of the natural runoff is used for hydropower, industry, irrigation or fish hatcheries (Bunn & Arthington 2002, Nilsson et al. 2005, Haag et al. 2010; Forseth et al. 2017). The runoff in a diversion channel of hydropower plants can be greatly reduced, especially during dry periods, as a higher proportion of water is guided to the turbine. Limited water in the diversion channel can negatively affect certain key habitats such as overwintering habitats and spawning grounds and, in addition, reduce the ability to migrate through the channel (Crisp 1993, Webb et al. 2001, LfU 2005). Both, rapid increasing or decreasing water discharge, for example in response to the power demand (hydropeaking), can have detrimental consequences for fish populations and communities, especially if the river shows a low level of heterogeneity where transition into alternative habitats is not possible (Lobón-Cerviá & Rincón 2004, Harby & Noack 2013, Boavida et al. 2015, Schmutz et al. 2015). For less mobile life stages, such as eggs and larvae, a rapid decrease in water poses the risk of stranding (Saltveit et al. 2001, Casas-Mulet et al. 2015).

Successful spawning migration and spawning can be impaired if water levels are lower than the fish body height and if flow or hydraulic conditions over barriers (natural or artificial) are not optimal. Flow events, which are considered to trigger migration behaviour of Atlantic salmon (Clarke et al. 1991), may not take place during low discharge. Without this initiation, river entry will be delayed or even prevented (Solomon & Sambrook, 2004, Tetzlaff et al. 2008). The migration itself may lead to a faster exhaustion or higher risk of predation (Quinn & Buck 2001) as shallow areas need to be overcome and access to resting pools may be strongly limited. At the spawning site, the fish are very unlikely to spawn if the water depth and flow velocity are insufficient (Webb et al. 2001, Louhi et al. 2008). In addition, the washing out of fine material during redd cutting and the successful insemination of the eggs and their deposition into the interstitial zone can be impaired if the water levels and flow velocities are too low. There is furthermore a higher risk of desiccation of the spawning sites during the period of egg incubation, which can result in recruitment failure (Saltveit & Brabrand 2013, Casas-Mulet et al. 2015). Other risks posed on eggs and larvae include the insufficient vertical exchange between the hyporheic zone and open water, which may lead to lower oxygen contents and accumulation of toxic metabolites. Parry et al. (2018) investigated the impact of flow on the overall distribution and densitiy of redds along a river and found that under low flow conditions redds tended to be more aggregated in the middle river reaches. On the one hand, this may minimize the risk of desiccation or insufficient oxygen supply, but on the other hand, it can result in a highly competitive environment for the emerging fry (Jonsson & Jonsson 1998). Wedekind & Mueller (2005) found that brown trout hatched earlier when there was an increased risk of desiccation. This behaviour could be beneficial as the larvae can move away from the risk of drying out, freezing, predation or being damaged by UV radiation (Crisp 1993, Kouwenberg et al. 1999, Battini et al. 2000). Flow dynamics can also affect the timing and success of emergence, with potential consequences for population dynamics of 0+ juveniles (Bergerot & Cattanéo 2017), if, for example emerged, fry do not reach suitable rearing habitats or are predated on.

Conversely, strong runoff peaks (flooding or reservoir flushing) may expose spawning sites to increased erosion (Crisp 1989, Barlaup et al. 2008). Discharge peaks can lead to the seasonal unavailability of these habitats, particularly in isolated spawning grounds. If, in addition, these areas have only very limited fish passability sucgh as spawning sites in the headwaters of dams, which can naturally be affected by reservoir flushing and short-term strong runoff fluctuations, entire generations may be absent from the population structure. This may ultimately contribute to the instability of the overall population. Such runoff fluctuations also pose a high risk to incubated eggs such as redd stranding. Barlaup et al. (1994) reviewed a 100-year data series on stranded Atlantic salmon and brown trout redds and found a relationship between the high proportions of stranded redds (23 %) and the random occurrence of low water discharge rates at high frequencies (27 % of the year). Further, strong runoff peaks can lead to a destabilization and mobilization of substrate and thus flush eggs or larvae out of the interstitial zone or mechanically damage them by moving material between them (Mills 1971, Eliott 1976, Crisp 1989, Crisp 1993). Immediately after deposition, the eggs of brown trout and Atlantic salmon are very sensitive to physical shock: drifting over a distance of 10 m can lead to a mortality rate of 50 % (Crisp 1990). Sensitivity gradually decreases after the eyed stage. When, eggs and larvae are washed out, they can either become easy prey for predators or may reach unsuitable sites for further development (Crisp 1990).

4.5.3. High water temperatures

In small and medium-sized watercourses, increased or critical water temperatures may occur due to discharges such as domestic and industrial waste waters (Cairns 1970, Kinouchi et al. 2007). Another factor that leads to higher water temperatures is global warming. Rising water temperatures can affect fish at all levels of biological organisation through either direct or indirect changes in physiological and ecological processes (Graham & Haarod 2009). In view of the ongoing climate change, Jonsson

& Jonsson (2009) expect that the thermal niche of cold adapted species, such as brown trout and Atlantic salmon, will result in a shift of distribution further to the north and that species in the southern part of their distributional areas are likely to go extinct (Ellender et al. 2016). In Europe, this mean the disappearance of these species from Portugal and Spain and their spread north and east along the north coast of the Russian continent (Jonsson & Jonsson 2009). However, a growth model scenario for brown trout under possible future climate conditions by Elliott & Elliott (2010) revealed negative effects on trout growth would not be experienced until a water temperature increase of 4 °C in winter/spring and 3 °C in summer/autumn is reached. This study further suggests that small increases of temperatures in winter and spring can lead to an increase in mean-mass of pre-smolts and be beneficial for smolt growth. Larger smolts are considered more resilient, and according to Gregory et al. (2019), have a higher chance to return to their natal rivers after maturation at sea. By contrast, a faster growth can also result in seaward-migrating younger and thus smaller smolts, as has been observed over recent decades, which is expected to result in higher marine mortality (Russell et al. 2012).

Since both species are winter spawners, an increase in water temperature can lead to a delayed spawning migration. Further, more extreme weather events are expected which will cause large fluctuations in runoff rates, making river accessibility and spawning migration more difficult (Jonsson & Jonsson 2009, Harrod et al. 2009). In addition, sexual maturity and fertility of Atlantic salmon and brown trout decrease with rising temperatures (Jonsson & Jonsson 2009). Significant reduced fertility (< 70 % and 45 %, respectively) and survival (40 % and 13 %, respectively) of ova was observed from fish exposed to 22 °C for 4 and 12 weeks (King et al. 2003, King et al. 2007, Pankhurst et al. 2011).

Crisp (1993) reported that during egg incubation at temperatures above 12 °C, 50 % of the eggs die and that no egg survive at temperatures above 15.5 °C. Similar findings are reported by Ojanguren et al. (1999) where 16 °C was established as the thermal limit for pre-hatching stages and 22 °C for hatched larvae. Moreover, high water temperatures can lead to premature consumption of the yolk sac (Ojanguren et al. 1999). Further, the transition of the larvae from endogenous to exogenous food intake may not coincide with the time of occurrence of the prey (mismatch), and the larvae would not find suitable food after emergence and could starve (Cushing 1990, Arevalo et al. 2018).

In addition, temperature, together with salinity, determines the physical properties of water, the amount of dissolved oxygen, the crystalline structure of various substances and the solubility properties of water. This in turn can influence the biochemical and toxicological effects of dissolved gases, solids, antibiotics and xenobiotics with probably negative consequences for the development of salmonids (Oppen-Berntsen et al. 1990, Cousins & Jensen 1994, Honkanen et al. 2001, Arias et al. 2002).

4.5.4. Lack of oxygen

Oxygen deficiency can be caused by various factors, including oxygen-depleting microbial processes and algae blooms as a result of eutrophication and excessive temperatures, low discharge, and clogged pores in the hyporheic zone. As the solubility of oxygen is directly related to the ambient water temperature, the concentration decreases when the temperature rises. At an air saturation in water of 80 % and a water temperature of 5 °C, approx. 10 $mg\cdot l^{-1}$ of oxygen is present dissolved in water. At 20 °C there is only 7 $mg\cdot l^{-1}$ oxygen (Crisp 1993). Hypoxic conditions ($<$ 7 $mg\cdot l^{-1}$ dissolved oxygen) can cause die-off events of spawning salmonid species if high fish densities and low stream flows occur simultaneously, even in rivers with cold thermal regimes (Sergeant et al. 2017 Tillotson & Quinn 2017).

The oxygen concentration in the hyporheic interstitial depends strongly on the temperature, the flow velocity, the permeability of the sediment and consumption by organic processes. Embryo mortality can also occur by dominant ascending hypoxic groundwater (Malcolm et al. 2008). Long-term hypoxia ($<$ 3.7 $mg\cdot l^{-1}$ oxygen) can lead to egg death or significant delays in development and thus to malformations and metabolic disorders (Hamor & Garside 1976). Larvae are less prone to oxygen deficiency compared to eggs, as they are mobile and able to relocate to oxygen-rich areas (Crisp 1993) or adjust their breathing frequency (Quinn 2005). However, premature hatching of larvae may occur (Czerkies et al. 2001).

4.5.5. Extreme values in pH, aluminium and ammonium

Aquatic ecosystems can become acidified through natural processes in the bio- and geosphere (e.g., volcanism or natural pyrite oxidation) as well as through anthropogenic sources (atmospheric deposition of acidity 'acid rain' or pyrite oxidation from mining, agriculture and forestry) (Cresser & Edwards 1987, Geller & Schultze 2009). Spring floods, heavy rainfall events or snow melting can further promote acid discharges into water bodies (Serrano et al. 2008). Areas that are prone to water acidification due to their low buffer capacity include siliceous, low calcareous aquatic systems, which are often populated by Atlantic salmon and brown trout.

Extreme pH values below 6 or above 9 are particularly harmful as they can mobilise or activate other toxic substances (Crisp 1993, Gensemer & Playle 1999, Wauer et al. 2004 Finn 2007). Both, ammonia in combination with high pH values and dissolved aluminium in combination with low pH values are particularly toxic to salmonids and other fish (Henriksen et al., 1984; Wood & McDonald 1987, Parkhurst et al. 1990, Havas & Rosseland 1995, Gensemer & Playle 1999). An overview about critical limits and lethal limits from the literature is given in Table 3.

Eggs, fry, and alevins of Atlantic salmon and brown trout are considered more susceptible to the negative effects of low pH than adult fish (Jensen & Snekvik 1972). The uptake of high H^+ levels disturb the ion-regulation in transcellular processes with its key toxic mechanisms occurring on the gills. It hinders the active uptake of sodium and stimulates efflux leading to an excessive production of mucus (Leivestad & Muniz 1976), and net losses of important electrolytes such as Na^+ and Cl^- through the gills (Booth et at. 1988, Weatherley et al. 1989). The intracellular accumulation of aluminium affects transcellular processes, alters the carrier properties of the gill epithelium and reduces gill diffusion capacity causing respiratory distress (Exley et al. 1991, Havas & Rosseland 1995). Increased aluminium uptake can thus lead to an imbalance in the body's metabolism (water-mineral and acid-base balance) and/or to suffocation (Wauer et al. 2004).

Both field and laboratory studies show that a change in pH, especially in the early-life stages of salmonids, lead to high mortality rates (Schofield 1976, Grande et al. 1978, Sternecker et al. 2013a, Sternecker et al. 2013b). At pH values above 9, the egg stages of salmonids die before hatching (Crisp 1993). The lower limit is 4.5 for Atlantic salmon and brown trout (Jensen & Snekvik 1972, Crisp 1993). Peterson et al. (1980) found that salmon eggs in the ocular stage, which were kept at pH values between 4.0 and 5.5, hatched later or not at all because the low pH value probably inhibited the important hatching enzyme chorionase. Similar results were obtained earlier by Lacroix (1985a,b), who found the LL_{50} to be reached at pH of 4.7 (lethal loading causing 50 % mortality = LL_{50}) in the interstitial water. Daye & Garside (1979) report that LL_{50} for embryos is reached at pH 3.9, and for alevins at pH 4.3. They further claimed that long-term exposure of Atlantic salmon to pH < 4.5 will lead to a substantial decrease of populations or even extinction in freshwater habitats.

Exposure to low pH leads to sublethal effects in vital organs such as the skin, liver, spleen and damage to the blood vessel system, gills, brain, and retina (Daye & Garside 1980). In general, at chronically low pH values of 4.7 – 5.4 in the water, annual juvenile fish productivity of Atlantic salmon is significantly lower than in waters with pH values above 5.6 – 6.3 (Daye & Garside 1979). The critical threshold for first-year juvenile brown trout is 4.8 – 5.4 in streams rich in dissolved organic carbon (Serrano et al. 2008).

Recently hatched salmonids are regarded as particularly sensitive to ammonium (Table 4). A growth depression occurs at sublethal concentrations of 0.35 – 10 µM, while a long-term exposure of 1.4 – 5.3 µM can lead to a reduction of the number of erythrocytes and leukocytes as well as hematocrit and hemoglobin concentrations (Vosylinie & Kazlauskiene 2004). A mortality rate of 50 % (LC_{50}) was observed in adult brown trout at a concentration of 0.6 – 0.7 $mg \cdot l^{-1}$ after 96 h (Env. Canada 2001) and in Atlantic salmon at 0.2 – 0.5 $mg \cdot l^{-1}$ after 24 h (Alabaster et al. 1979). Effects on growth were observed in Atlantic salmon at a concentration of 0.037 – 0.065 $mg \cdot l^{-1}$ NH_3 (28 days, NOEC) (Fivelstad et al. 1993).

Even though acidification continues to be a problem, e.g., in parts of Scandinavia, recognition of the problem, measures of source control (e.g., flue gas desulfurization) and targeted mitigation measures (e.g., liming), has resulted in a slow recovery today (Geller & Schultze 2009).

4.5.6. Increased inputs of fine materials

The type, size and composition of the substrate determine whether the female can cut a suitable redd, how deep and large it becomes, and how stable it remains for the period of egg ripening and larval development.

Anthropogenic influences, such as catchment landuse with erosion-prone crops, forestry practices or overgrazing, can cause significantly increased levels of fine material inputs and the associated sedimentation rates of substances. In general, the introduction of anthropogenic fine material into freshwater systems are mainly caused by agriculture, logging and discharges from urban areas (Hendry et al. 2003, Greig et al. 2005a, Zimmermann & Lapointe 2005, Mueller et al. 2020). Also, climate change and the change in cultivation to ‘energy crops’ such as maize particularly promote soil erosion in agriculture and can cause fine sediment input into water bodies (Bierschenk et al. 2019). Net inputs from agriculture can be as high as 35 – 46.5 $kg \cdot m^{-2}$ (Denic et al. 2014, Pander et al. 2015). In addition, changes of flow regimes can facilitate deposition of fines and degradation of spawning grounds (Auerswald & Geist 2018).

Accumulating fine material causes compaction and colmation of the river bed at spawning sites. Consequently, fish need more effort in relocating the strongly solidified substrate during redd cutting, which, under certain circumstances, may no longer be possible. Consequences include interrupted or completely lost spawning processes or superficially laid eggs, with a higher risk to drift away or being preyed (Crisp 1990).

In evolutionary terms, Atlantic salmon and brown trout have adapted their spawning behaviour to natural deposition of fines by cutting a redd into the gravel, which cleans the substrate naturally from fines (Kondolf & Wolman 1993). After egg deposition new arriving fine material ideally continues to be removed by the current as the loosely backfilled gravel is permeable to a certain extent. However, in case of high fine material loads, the substrate can quickly colmate again. Since winter spawning salmonids have a long egg development time (up to five months) (Acornley & Sear 1999, Soulsby et al. 2001, Mueller et al. 2014, Sternecker et al. 2014) it can happen that the gravel cleaned by the female prior to egg deposition does not remain so through the development time of the eggs. Eggs of other salmonids, such as grayling or Danube salmon, which are laid in spring (Northcote 1995, Sternecker et al. 2014), develop faster due to the higher ambient water temperature and thus have a shorter exposure time (Sternecker et al. 2014).

Embryonic growth can be influenced both directly and indirectly by the complex interaction of interstitial permeability, oxygen availability, temperature and rising groundwater (Greig et al. 2007) by fine materials. Due to these complex interactions, most studies do not distinguish between the exact physical and chemical effects of fine materials on the success of egg development and emergence (Witzel & MacCrimmon 1983, Rubin 1998, Malcolm et al. 2003a, Malcolm et al. 2003b, Heywood & Walling 2007, Pander et al. 2009), but rather represent the overall survival rates in different fine material fractions (Mueller et al. 2014). However, there are two main processes which need to be considered. Sand fractions can lead to a superficial sealing of the river bed (Beschta & Jackson 1979; Sternecker & Geist 2010) and thus build a physical barrier at the boundary layer between open water and hyporheic zone (Everest et al. 1987). The colmation of this upper most layer is most important in determining exchange of water and matter between the two compartments of open water and interstitial habitat (Geist & Auerswald 2007). Additionally, colmation can change the chemical composition of the interstitial water and foster oxygen depletion with negative effects on hatching and emergence success (Everest et al. 1987, Sternecker & Geist 2010, Sternecker et al. 2013a). Other indirect, sublethal or lethal effects can be evoked by toxic chemicals (e.g., heavy metals, pesticides, pharmaceuticals) or nutrients potentially bound to the fines (Kemp et al. 2011). Fine material falling through the upper, coarser gravel layers, fills the redd from the bottom up (Einstein 1968, Turnpenny & Williams 1980, Acornley & Sear 1999, Pander et al. 2015). In such a case, shallower redds can replenish faster, which was often observed after gravel bed restoration (e.g., gravel addition) (Mueller et al. 2014, Pander et al.

2015). Eggs laid near the surface laying in deeper redds would have a buffer, and thus, the eggs and larvae would be less prone to suffocate (Everest et al. 1987).

Mortality rates for eggs caused by high loads of fine material in the hyporheic zone can reach 86 % (Soulsby et al. 2001) and more (Mueller et al. 2014). Greig et al. (2005b) found that particles $D < 4$ µm can block the micro pores of the egg membrane and thus strongly impair the oxygen supply, which led to a weaker growth rate of the embryos. Larvae of brown trout and Atlantic salmon exposed to a high fine material rate had larger yolk sacs compared to the control group that was not exposed to fine material. Larvae with larger yolk sacs are poorer swimmers and therefore more susceptible to predators or drifting, because, due to their size, they are mostly located in larger-pored areas of the interstitial zone and thus mostly near the gravel surface (Louhi et al. 2011).

The larvae emerge from the sediment after absorption of their yolk sac and drift to shallow near-bank habitats. This necessary process is only possible if the larvae are able to ascend through the gravel gaps. Hence, sand-sized particles often hinder the emergence of larvae (Crisp 1993, Kondolf 2000, Hartman & Hakala 2006, Sternecker & Geist 2010). Furthermore, high loads of fine sediment may exert size-selective effects (Sternecker et al. 2013). In a laboratory experiment, Beschta & Jackson (1979) found that sand ($D_{50} = 0.5$ mm) tends to settle in the upper 10 cm of a stable gravel bed and forms a physical barrier. Sternecker & Geist (2010) also found the same effect in their emergence experiment with brown trout at substrate sizes of 5 – 8 mm.

4.6. Present perspective on the discussed threats

In addition to the already well-characterized threats in the marine environment, such as exploitation (ICES 2019 a, ICES 2019b, NASCO 2019), disease and introduced parasites (e.g., *Gyrodactylus salaris* [Johnsen & Jensen 1991] and salmon lice *Lepeophtheirus salmonis* [Thorstad et al. 2015]), as well as genetical mixing with escaped farmed salmon (Karlsson et al. 2016), this review highlights the importance of considering the early-life stages in fresh water for sustainable management of the populations of both *Salmo salar* and *Salmo trutta fario*. The intensity and interaction of the different environmental variables affecting the critical life stages of both species is visualised in Figure 19.

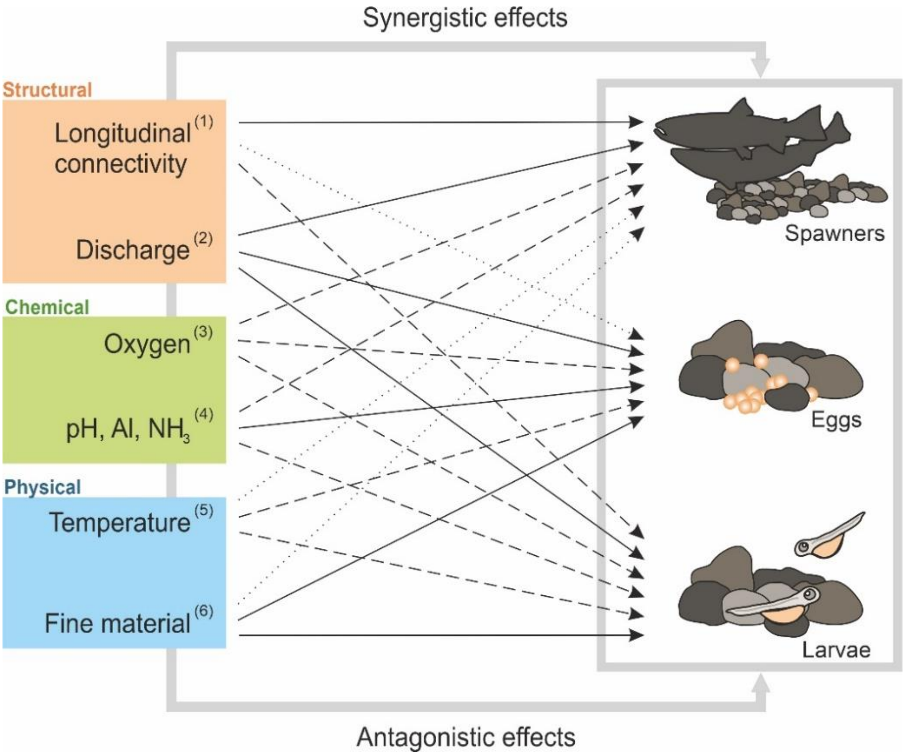

Figure 19. Risk effects on critical life stages of salmonids
Risk scheme presenting levels of impact by six predominant environmental risks representing impacts acting on the structural, chemical and physical level in freshwater on the three critical life stages spawning, egg development and emergence of Atlantic salmon and brown trout. Displayed by arrows are also the individual effects of each risk on the three life stages: straight line = high negative impact, dashed line = medium negative impact, dotted line = low negative impact. Further, these risks can also act additive, synergistic and anatogonist.

Based on this review, the environmental threats for Atlantic salmon and brown trout can be classified into three categories: (i) prominent threats from the past against which actions have been taken; (ii) long-known threats that have further accelerated and lack action; and (iii) emerging threats holding unknown consequences for the future.

Prominent threats from the past

In the 1970s and 80s, freshwater acidification was one of the major environmental threats to aquatic biota, especially in northern Europe and eastern North America in calcium-poor rivers where the buffering capacity of the ecosystems naturally is rather low (Overrein et al. 1980). Through the application of suitable mitigation measures (e.g., liming, Hultberg & Andersson 1982) and introduction of new laws and regulations affecting the sources of acidifying gases (e.g., Convention on Long-range Transboundary Air Pollution in 1979, UN/ECE 1999), freshwater systems across Europe are now slowly recovering (Stoddard et al. 1999, Evans et al. 2001, Skjelkvåle et al. 2001, Geller & Schultze 2009). In the course of this recovery, it was also possible to re-establish lost Atlantic salmon and brown trout populations in previously acidified rivers (Degerman & Appelberg 1992, Howells et al. 1992, Hesthagen et al. 2017). However, chemical and especially biological recovery can be costly and slow, and other threats may negatively affect the recovery process (Skjelkvåle et al. 2003, Austnes et al. 2018). Climate change for instance, may bring back acidification through increased dissolution of carbonic acid in fresh water (Weiss et al. 2018).

Long-known threats further accelerating

The negative impacts of missing longitudinal connectivity and habitat functionality due to structural deficits on riverine fish are well documented and continue to be the major challenge for the future of freshwater conservation (Geist 2011, 2015). Analogously to other cold-water adapted species, access to cold-water patches during extended hot periods becomes a crucial factor of population resilience in the light of global warming (Kuhn et al., 2021). For Atlantic salmon and brown trout both factors are considered key management objectives to re-establish self-sustainable populations in fresh water (Birnie-Gauvin et al. 2017, ICES 2019 a, ICES 2019b, ICES 2019c). On the one hand, the difficulty is finding a compromise between river ecosystem conservation and human demands for green energy, flood protection, shipping routes and land use (Poff et al. 2003, Jackson 2011). On the other hand, there is a lack of action for already existing solutions. While the implementation of the EU Water Framework Directive (WFD, 2000/60/EC) was meant to force action on the member states of Europe to improve the state of river ecosystems including connectivity, only 41% of all rivers in the European Union match the formulated goal of a good ecological status (Kristensen et al. 2018). It is widely considered that the implementation of the respective management plans as basis for the restoration of surface waters cannot catch up with the deadlines set by the EU to reach the goals of the WFD. More than two decades after implementation of the WFD, many experts claimed that these goals were ‘over-ambitious’ resulting in several extensions of deadlines to match the good ecological status of surface waters (Hering et al. 2010).

Another remaining problem is the re-establishment of habitat functionality. Of key importance for the early-life stages of salmonids is the quality of the spawning ground, particularly the well-characterised problem of siltation and colmation of salmonid spawning sites through land use (agriculture, forestry, urban and industrial wastewater) resulting in egg and larval die offs. Now, this knowledge has been complemented by the observation that the problem of colmation can only be solved if combined with approaches of re-establishing flow regimes and mitigation of in-stream modifications of geomorphic structure through carbonate precipitation and internal biomass production (Geist & Hawkins 2016, Auerswald & Geist 2018). Some measures such as local, small-scale in-stream spawning site restorations (e.g., gravel supplementation or loosening by rakig, power hosing or excavation) seem quick, cheap and effective, but their effects often persist for less than one year, especially in catchments with intense agricultural and forest land use (Sternecker et al. 2013, Mueller et al. 2014, Pander et al. 2015). Hence, despite the economic investment, long history, and volumes of literature, considerable uncertainties and controversial debates about the biological effectiveness of such measures remain (Vehanen et al. 2010b, Mueller et al. 2014, Roni et al. 2015, Louhi et al. 2016, Szałkiewicz et al. 2018, Birnie-Gauvin et al. 2019), causing delays in their implementation.

New emerging threats

It should be acknowledged that many European countries made great progress in reducing chemical pollution and nutrient inputs to freshwater ecosystems in the past 30 years. The implementation of a tertiary phase in sewage water treatment as well as the replacement or reduction in chemicals and nutrients in industrial production, land use and household disposal significantly decreased loads of nitrate, phosphate and airborne acidification (Geist and Hawkins 2016). In addition, laws and regulations have been implemented to further improve the ecological status of surface waters in all European countries, including threshold limits for specific priority substances and nutrient loads

(WFD, 2000/60/EC). While the overall chemical and nutrient status of European surface waters is slowly recovering, some countries (e.g., England, Germany, Sweden) are currently failing to meet the limits, largely due to agricultural inputs (e.g., pesticides, fertilizers; Kristensen et al. 2018).

There are many chemicals of which the effects on the life stages of Atlantic salmon and brown trout are not well understood so far. There are arguably three main reasons. The first is that most research on the effects of chemicals on biologic systems is conducted on one specific chemical of interest at a time, while in the real-world most organisms are exposed to mixtures of multiple chemicals at the same time. There can be additive or non-additive, synergistic or antagonistic effects, sometimes also referred to as ‘cocktail effects’ (Connon et al. 2012). The second reason is that most studies tend to exclusively focus on acute (i.e., short-term) effects, whereas more realistic chronic exposure scenarios can have cumulative detrimental consequences for the organism (Spromberg & Meador 2005). The third reason is that the bioavailability of substances in reality may differ from test results of standard toxicity testing (Beggel et al. 2010). Generally, the young life stages tend to be more susceptible to negative effects than to adult fish, but chronic exposure and potential cumulative effects of especially persistent chemicals can also affect reproductive output (Mohammed 2013). An effect assessment is further complicated by the effects of these chemicals on the entire food web (Malaj et al. 2014). Insecticides may be particularly harmful to non-target species, including terrestrial and freshwater insects, which both can make an important contribution to the diet of brown trout and Atlantic salmon during their freshwater life stages.

Another threat becoming increasingly prominent in scientific publications during the last decade is climate change (for review see Harrod et al. 2009, Jonsson & Jonsson 2009). Most likely scenarios for the main distribution areas of Atlantic salmon and brown trout include higher temperatures, wetter winters, dryer summers and more extreme events of flooding and drought (IPCC 2007, IPCC 2014, ICES, 2017b) affecting all components of the freshwater ecosystem (Wilby et al. 2006). Models and predictions of the consequences of climate change have focussed on the adaptability of Atlantic salmon and brown trout to rising temperatures during different life stages

(Sternecker et al. 2014, Casas-Mulet et al. 2020). The likelihood for future losses of salmonid populations is considered high, especially in their lower distribution ranges. However, there is still a lack of knowledge on the extent of climate change impacts (Skjelkvåle et al. 2003, Jonsson & Jonsson 2009) and the possible interaction with existing or emerging stressors. For example, extreme climatic events (drought followed by extreme rainfall) in combination with changed flow regimes (e.g., hydropower) and erosion-prone land use can lead to higher loads of fine material and nutrients being washed into the waterbody. The combination of all or some of these factors will most likely result in unfavourable conditions for egg development and subsequent recruitment. Gregory et al. (2020) found that the 2016 salmon recruitment crash in Wales was most likely caused by the unfavourable combination of warm spawning temperatures, which can inhibit spawning, and higher flood frequencies during egg incubation and emergence, resulting in washouts of eggs and alevins. Such inclement conditions could become more common under future climate change. The predicted increase in the average temperature in the next years is suspected to facilitate the spread of parasites (Bruneaux et al. 2017), invasive species (Bean 2020) and increase the toxic effects of pollutants (Dar et al. 2020) with negative consequences for all life stages of Atlantic salmon or brown trout. From the perspective of research and management, it is thus particularly important to (i) understand and predict the effects of climate change on habitat suitability for both species; (ii) identify and ensure access to cold-water refugia as a key to improving population resilience (Kuhn et al. 2021); and (iii) understand and manage the interactions with other stressors, especially those that are also temperature dependent.

Cumulative effects

Although all threats have been described individually in their effects on the critical life stages of Atlantic salmon and brown trout (Figure 19), it is important to highlight that it is their diversity and complexity combined with the fact that these stressors often act in concert and in a non-linear way, which complicates a mechanistic understanding of their exact modes of action as well as a translation into effective mitigation measures (Armstrong et al. 1998, Ormerod et al. 2010, Mueller et al. 2017, Bierschenk et al.

2019, Mueller et al. 2020). The complex interactions between the stressors are not yet fully understood but are increasingly being addressed (e.g., Brook et al 2008, Jackson et al. 2015, Bouraï et al. 2020).

There is also increasing evidence of negative indirect effects of stressors on fish. For example, when pollutants exert direct effects on keystone species or induce changes in nutrient and oxygen dynamics, they may alter ecosystem functions essential for the critical life stages of Atlantic salmon and brown trout (Fleeger et al. 2003). Nutrient enrichment (eutrophication) and rise in water temperature act additively and can influence fish community dynamics (Jackson et al. 2015, Bouraï et al. 2020). A meta-analysis conducted on net effects of cumulative impacts of multiple stressors (novel and extreme environmental changes) in freshwater ecosystems by Jackson et al. (2015) revealed that the net effects of stressor pairs were frequently more antagonistic (41%) than synergistic (28%), additive (16%) or reversed (15%). Furthermore, they suggested that "a possible explanation for the more antagonistic responses of freshwater biota to stressors is that the inherently greater environmental variability of smaller aquatic ecosystems promotes a greater potential for acclimatisation and co-adaptation to multiple stressors".

4.7. Implications for research and management

Despite some uncertainties related to the newly emerging threats, the current knowledge of Atlantic salmon and brown trout is considered sufficient to significantly mitigate current environmental risks in a way that populations could quickly recover their strength (Lobón-Cerviá 2009) and to increase their general resilience against stressors. For long-lasting solutions, a 'stopping at the source' strategy is considered most promising. This includes in particular river restoration measures to re-establishing connectivity and improve habitat quality as these threats have the greatest impact on all life stages today (Dudgeon et al. 2019, Figure 19), and as they are particularly crucial in the light of climate change increasing the relevance of access to cold-water patches and minimising combined effects of temperature and fines on interstitial habitats important for egg development. There is strong evidence that with approximately one barrier every two kilometres of river, Europe has the most fragmented rivers in the world (Grill et al. 2019, AMBER 2020). Yet, 13 % of these barriers are obsolete obstacles (approx. 156,000) which do not serve any purpose and could be removed. Dam removals can have an extremely positive influence on the abundance of salmonid species (Birnie-Gauvin et al. 2017). Where obstacle removal is not possible, measures to restore fish migration by considering the individual requirements of species (e.g., water depth, discharge, behaviour) should be obligatory (Silva et al. 2018).

Further, there is no way around an appropriate adjustment of land use in terms of a selection of low erosion cultivation methods, crop rotation and suitable cultivation strategies in consideration of the catchment scale. In addition, buffer strips and field wetlands can be a promising mitigation measure not only preventing diffuse input of sediments and associated pollutants into freshwater directly affecting processes relevant for early-life stages of salmonids (Ockenden et al. 2012, Knott et al. 2019), but also enhancing biodiversity and aesthetics (Barling & Moore 1994, Cole et al. 2020). Up to now, fine sediment input in surface waters as key factor affecting trout and salmon from spawning to emergence is barely considered in the WFD monitoring, which should implement a new standard for the monitoring of fine sediment input in surface waters as soon as possible.

The WFD has already set limits for nutrient and chemical inputs into fresh waters, but most European countries have not complied with these standards (Brack et al. 2019). More regular controls and stricter penalties for non-compliance could improve the situation. In addition, scientist from the EU-funded project “SOLUTIONS for present and future emerging pollutants in land and water resources management” call for an improvement of the WFD and current water laws by a more holistic approach of protection from and monitoring of chemical pollution. The status assessments should not only address the selected priority pollutants (currently set by the WFD), but all chemicals that pose a risk also assessing mixture effects and considering mitigation options already at an early stage of the assessment (Brack et al. 2019).

In addition to ‘stopping at the source’, some preventive actions can be taken to minimise the impact of some current and emerging threats. For example, Switzerland upgraded existing wastewater treatment plants to reduce micro pollutants and toxicities from wastewater effluents (Eggen et al. 2015). Further, the reintroduction of more structures in habitats, shading vegetation as well as natural groundwater inflows would offer valuable thermal refugia for salmonid fish, which may help to counteract some of the negative effects of climate change (Kuhn et al. 2021).

Already established measures such as stocking can, properly applied, stabilise depressed populations. However, long-term stocking has often been associated with stocking different genetic backgrounds (Finnegan et al. 2008, Aas et al. 2018, Bernaś & Wąs-Barcz 2020) and this can lead to negative genetic effects on extant populations when stocked and wild fish interbreed (e.g., Machordom et al. 1999, Nielsen et al. 2001, Marzano et al. 2003, McGinnity et al. 2003, Ferguson 2006). This relates to both *Salmo salar* and *Salmo trutta fario* as well. Interbreeding of distant genetic lines can result in outbreeding depression or lowered survival in subsequent generations, as non-local stocks tend to have reduced survival rates compared with natural populations (McGinnity et al. 2003, Araki et al. 2008, Ågren et al. 2019). In addition, genetic mixing can result in the reduction of local adaptations (McGinnity et al. 1997, Wang et al. 2002, Bourret et al. 2011). Particularly *Salmo salar* is known to exhibit distinctive adaptions to single rivers or catchments (Verspoor 1997, Ozerov et al. 2012, Ikediashi et al. 2018) and is therefore particularly prone to loss of genetic diversity at the metapopulational level (Griffiths et al. 2010). Due to its popularity as game fish, *Salmo trutta fario* has been introduced to rivers for fishing, for example, in New Zealand, India and South Africa (Aass 1982). Stocked fish usually originate from hatcheries that are able to produce large numbers of juvenile Atlantic salmon and brown trout. Hence, hatcheries are in the responsibility of developing stocks that more closely resemble wild stocks in their genetics and behaviour to use only appropriate stocks in rebuilding Atlantic salmon and brown trout populations. This way unique stocks can be better conserved and protected. Before stocking, however, river restoration (improving water quality, river access and structure) should be prioritised (Ikediashi et al. 2012).

When mitigating freshwater threats, it is further necessary to take a holistic approach considering all environmental stressors connected to the health of the critical life stages of Atlantic salmon and brown trout (Calles & Greenberg 2009, Pander & Geist 2013, Tummers et al. 2016). Stocking of fish, for example, cannot support a local population if the migration rate or mortality rate due to unsuitable habitat conditions, turbine mortality, predation or disease exceed stock recruitment (Cowx 1994, Aarts et al. 2004). Further, habitat restoration should consider the catchment scale and should include a functional perspective on hydrogeomorphic, biogeochemical and ecological processes that may significantly improve the understanding of in-stream processes and how threats affect habitats (Pander & Geist 2016).

Despite a long research history on Atlantic salmon and brown trout, knowledge gaps on some autecological requirements and population development still exist, which should be addressed. This includes knowledge on minimum viable population size in different habitat types, general spatial requirements of all life stages, synergetic effects between environmental factors and physiological response, and short-term and long-term adaptability to rapid changing environmental conditions (Jonsson & Jonsson 2011, Smialek et al. 2019). In contrast to physical habitat characteristics (e.g., current speed, sediment composition, water depth, and oxygen levels), this information is difficult to obtain and depends on complex synergistic effects or sometimes unpredictable factors. In cases where data are missing for one species, it might be permissible to attribute findings from another well-studied species to its less studied related species to have a starting point for action. For Atlantic salmon and brown trout, the habitat requirements and their sensitivities to the environmental risks during the three critical life stages spawning, egg development and emergence discussed are almost identical, creating synergies in conservation and restoration. This is mainly due to similarities in their spawning behavior (e.g., gravel spawners) and morphology (e.g., body shape, overlapping range in size spectrum). This is also underlined by the fact that both species are found together in key habitats, such as spawning grounds with the same hydromorphological characteristics, and may hybridize with each other (Youngson et al. 1992, Matthews et al. 2000). Differences in the choice of habitat between Atlantic salmon and brown trout are only found to a limited extent and can essentially be attributed to two factors: (i) the overall size spectrum of both species; and (ii) the different life strategy after the juvenile stage. Hence, mitigation measures undertaken for Atlantic salmon will most likely be profitable also for brown trout and vice versa.

4.8. Conclusion

It is important to emphasize that improving freshwater conditions for the early life stages of both species is essential in securing population resilience yet can only contribute in part to their conservation. As mentioned earlier, especially seaward-migrating forms are exposed to further stressors at sea (e.g., overfishing, sea lice infestation, interbreeding with escaped farmed salmon) at a later stage of their life cycle. However, improving the starting conditions for these individuals (i.e., good conditions for early-life stages in freshwater) can also greatly improve their resilience in the later life stages (e.g., sending the healthiest smolts to sea) and their chance to face future risks with fewer losses. Furthermore, Atlantic salmon and brown trout inherit an admirable degree of adaptation themselves. The great plasticity in their life strategies is one key factor to their survival, and thus it is important to protect this plasticity by conserving the genetical diversity between stocks.

4.9. References

Aarestrup, K., & Koed, A. (2003). Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater Fish*, 12, 169–176.

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

Aas, Ø., Cucherousset, J., Fleming, I. A., Wolter, C., Höjesjö, J., Buoro, M., Santoul, F., Johnsson, J. I., Hindar, K., & Arlinghaus, R. (2018). Salmonid stocking in five North Atlantic jurisdictions: Identifying drivers and barriers to policy change. *Aquatic Conservation*, 28, 1451–1464.

Aass, P. (1982). Brown trout stocking in Norway. Proceedings of the Symposium on Stock Enhancement in the Management of Freshwater Fisheries, held in conjunction with the Twelfth Session of EIFAC (Budapest, Hungary, 31 May – 2 June 1982). *EIFAC Technical Paper*, 42 (1). Retrieved Dec. 12, 2020 from: http://www.fao.org/3/ae996b/AE996B12.htm#ch11.

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.

Ågren, A., Vainikka, A., Janhunen, M., Hyvärinen, P., Piironen, J., & Kortet, R. (2019). Experimental crossbreeding reveals strain-specific variation in mortality, growth and personality in the brown trout (*Salmo trutta*). *Scientific Reports*, 9, 1–11.

Alabaster, J. S., & Lloyd, R. (1982). Water quality for freshwater fish (2nd ed.). Butterworths, London.

Alabaster J. S., Shurben D. G., & Knowles G. (1979). The effect of dissolved oxygen and salinity on the toxicity of ammonia to smolts of salmon, *Salmo salar* L. *Journal of Fish Biology*, 15, 705–712.

AMBER (2020, July 2020). *European Barrier Atlas*. [Interactive map] Retrieved from https://amber.international/european-barrier-atlas/

Araki, H., Berejikian, B. A., Ford, M. J., & Blouin, M. S. (2008). Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications*, 1, 342–355.

Arevalo, E., Panserat, S., Seiliez, I., Larrañaga, A., & Bardonnet, A. (2018). Effect of food shortage and temperature on age 0+ salmonids: a contribution to predict the effects of climate change. *Journal of Fish Biology*, 92, 642–652.

Arias, P., Pinochet, L. F., & Disi, A. (2002). Study of the nervous tissue development in rainbow trout (*Oncorhynchus mykiss*) embryos treated with oxytetracycline. *Anatomia, Histologia, Embryologia*, 31, 144–147

Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M., & Milner, N. J. (2003). Habitat requirement of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research*, 62, 143–170.

Armstrong, J. D., Grant, J. W. A., Forsgren, H. L., Fausch, K. D., DeGraaf, R. M., Fleming, I. A., Prowse, T. D., & Schlosser, I. J. (1998). The application of science to the management of Atlantic salmon (*Salmo salar*): integration across scales. *Canadian Journal of Fisheries and Aquatic Science*s, 55, 303–311.

Atse, C. B., Audet, C., & De La Noüe, J. (2002). Effects of temperature and salinity on the reproductive success of Arctic charr, *Salvelinus alpinus* (L.): egg composition, milt characteristics and fry survival. *Aquaculture Research*, 33, 299–309.

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 & Development*, 29, 737–748.

Aulstad, D., & Gjedrem, T. (1973). The egg size of salmon (*Salmo salar*) in Norwegian rivers. *Aquaculture*, 2, 337–341.

Austnes, K., Aherne, J., Arle, J., Čičendajeva, M., Couture, S., Fölster, J., Garmo, Ø., Hruška, J., Monteith, D., Posch, M., Rogora, M., Sample, J., Skjelkvåle, B. L., Steingruber, S., Stoddard, J. L., Ulańczyk, R., van Dam, H., Velasco, M. T., Vuorenmaa, J., Wright, R. F., & de Wit, H. (2018). Regional assessment of the current extent of acidification of surface waters in Europe and North America. Report for the. ICP Waters Report, Prepared at the ICP Waters Programme Centre Norwegian Institute for Water Research, Oslo, Norway, 136 pp. Retrieved on Dec. 12, 2020 from: http://pure.iiasa.ac.at/id/eprint/15542/1/ICPW_Report_135-2018.pdf.

Baisez, A., Bach, J. M., Leon, C., Parouty, T., Terrade, R., Hoffmann, M., & Laffaille, P. (2011). Migration delays and mortality of adult Atlantic salmon *Salmo salar* en route to spawning grounds on the River Allier, France. *Endangered Species Research*, 15, 265–270.

Banks, J. W. (1969). A review of the literature on the upstream migration of adult salmonids. *Journal of Fish Biology*, 1, 85–136.

Bardonnet, A., & Baglinière, J. L. (2000). Freshwater habitat of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 497–506.

Bardonnet, A., Gaudin, P., & Thorpe, J. E. (1993). Diel rhythm of emergence and of first displacement downstream in trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*) and grayling (*Thymallus thymallus*). *Journal of Fish Biology*, 43, 755–762.

Barlaup, B. T., & Åtland, Å. (1996). Episodic mortality of brown trout (Salmo trutta L.) caused by sea-salt-induced acidification in western Norway: effects on different life stages within three populations. Canadian Journal of Fisheries and Aquatic Sciences, 53, 1835–1843.

Barlaup, B. T., Lura, H., Sægrov, H., & Sundt, R. C. (1994). Inter-and intra-specific variability in female salmonid spawning behaviour. *Canadian Journal of Zoology*, 72, 636–642.

Barlaup, B. T., Gabrielsen, S. E., Skoglund, H., & Wiers, T. (2008). Addition of spawning gravel—a means to restore spawning habitat of Atlantic salmon (*Salmo salar* L.), and anadromous and resident brown trout (*Salmo trutta* L.) in regulated rivers. *River Research and Applications*, 24, 543–550.

Barling, R. D., & Moore, I. D. (1994). Role of buffer strips in management of waterway pollution: a review. *Journal of Environmental Management*, 18, 543–558.

Battini, M., Rocco, V., Lozada, M., Tartarotti, B., Zagarese, H. E. (2000). Effects of ultraviolet radiation on the eggs of landlocked *Galaxias maculatus* (Galaxiidae, Pisces) in northwestern Patagonia. *Freshwater Biology*, 44, 547–552.

Bean, C. W. (2020). Atlantic salmon and non-native species: is there an issue? In E. B. Thorstad, D. Bliss, K. Damon-Randall, H. Hanson, G. Horsburgh, N. Ó Maoiléidigh, S. G. Sutton, V. Newton, E. M. C. Hatfield (Eds.), *Managing the Atlantic Salmon in a Rapidly Changing Environment – Management Challenges and Possible Responses* (pp. 105–116). Tromsø: NASCO IYS Symposium.

Benejam, L., Saura-Mas, S., Bardina, M., Solà, C., Munné, A., & García-Berthou, E. (2016). Ecological impacts of small hydropower plants on headwater stream fish: from individual to community effects. *Ecology of Freshwater Fish*, 25, 295–306.

Berg, O. K. (1985). The formation of non-anadromous populations of Atlantic salmon, *Salmon salar* L., in Europe. *Journal of Fish Biology*, 27, 805–815.

Bergerot, B., & Cattanéo, F. (2017). Hydrological drivers of brown trout population dynamics in France. *Ecohydrology*, 10, e1765.

Bergheim, A., & Hesthagen, T. (1990). Production of juvenile Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., within different sections of a small enriched Norwegian river. *Journal of Fish Biology*, 36, 545–562.

Bernaś, R., & Wąs-Barcz, A. (2020). Genetic structure of important resident brown trout breeding lines in Poland. *Journal of Applied Genetics*, 61, 239–247.

Beschta, R. L., & Jackson, W. L. (1979). The intrusion of fine sediments into a stable gravel bed. *Journal of the Fisheries Research Board Canada*. 36, 204–210.

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.

Bierschenk, B. M., Pander, J., Mueller, M., & Geist, J. (2018). Fish injury and mortality at pumping stations: a comparison of conventional and fish-friendly pumps. *Marine and Freshwater Research*, 70, 449–458.

Bijlsma, R., & Loeschcke, V. (2012). Genetic erosion impedes adaptive responses to stressful environments. *Evolutionary Applications*, 5, 117–29.

Birnie-Gauvin, K., Larsen, M. H., Nielsen, J., & Aarestrup, K. (2017). 30 years of data reveal dramatic increase in abundance of brown trout following the removal of a small hydrodam. *Journal of Environmental Management*, 204, 467–471.

Birnie-Gauvin, K., Franklin, P., Wilkes, M., & Aarestrup, K. (2019). Moving beyond fitting fish into equations: Progressing the fish passage debate in the Anthropocene. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29, 1095–1105.

Boavida, I., Santos, J. M., Ferreira, T., & Pinheiro, A. (2015). Barbel habitat alterations due to hydropeaking. *Journal of Hydro-environment Research*, 9, 237–247.

Bishai, H. M. (1962). Reactions of larval and young salmonids to water of low oxygen concentration. *ICES Journal of Marine Science*, 27, 167–180.

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

Booth, C. E., McDonald, D. G., Simons, B. P., & Wood, C. M. (1988). Effects of aluminium and low pH on net ion fluxes and ion balance in the brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences, 45, 1563–1574.

Brown, D. J. A., & Lynam, S. (1981). The effect of sodium and calcium concentrations on the hatching of eggs and the survival of the yolk sac fry of brown trout, *Salmo trutta* L. at low pH. *Journal of Fish Biology*, 19, 205–211.

Bruneaux, M., Visse, M., Gross, R., Pukk, L., Saks, L., & Vasemägi, A. (2017). Parasite infection and decreased thermal tolerance: impact of proliferative kidney disease on a wild salmonid fish in the context of climate change. *Functional Ecology*, 31, 216–226.

Brunke, M. (1999). Colmation and depth filtration within streambeds: retention of particles in hyporheic interstices. *International Review of Hydrobiology*, 84, 99–117.

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

Butler, J. R., Radford, A., Riddington, G., & Laughton, R. (2009.) Evaluating an ecosystem service provided by Atlantic salmon, sea trout and other fish species in the River Spey, Scotland: The economic impact of recreational rod fisheries. *Fisheries Research*, 96, 259–266.

Cairns, J. Jr. (1970). Ecological management problems caused by heated waste water discharge into the aquatic environment. *Journal of the American Water Resources Association*, 6, 868–878.

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.

Çalta, M. (2002). Does brown trout (*Salmo trutta* L.) larval development retardation caused by short-term exposure to low pH and elevated aluminium concentration affect a second episode of toxicity? *Journal of Applied Ichthyology*, 18, 210–215.

Carrick, T. R. (1979). The effect of acid water on the hatching of salmonid eggs. *Journal of Fish Biology*, 14, 165–172.

Casas-Mulet, R., Saltveit, S. J., & Alfredsen, K. (2015). The survival of Atlantic salmon (*Salmo salar*) eggs during dewatering in a river subjected to hydropeaking. *River Research and Applications*, 31, 433–446.

Casas-Mulet, R., Pander, J., Ryu, D., Stewardson, M. J., & Geist, J. (2020). Unmanned Aerial Vehicle (UAV)-based Thermal Infra-Red (TIR) and optical imagery reveals multi-spatial scale controls of cold-water areas over a groundwater-dominated riverscape. *Frontiers in Environmental Science*, 8, 64.

Caudill, C. C., Daigle, W. R., Keefer, M. L., Boggs, C. T., Jepson, M. A., Burke, B. J., Zabel, R. W., Bjornn, T. C., & Peery, C. A. (2007). Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 979–995.

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.

Clark, E. (1998). *Microthermal habitats in British rivers*. Doctoral thesis, Exeter: University of Exeter.

Clarke, D., Purvis, W. K., & Mee, D. (1991). Use of telemetric tracking to examine environmental influences on catch/effort indices. A case study of Atlantic salmon (*Salmo salar* L.) in the R. Tywi, S. Wales. In I.G. Cowx (Eds.), *Catch effort sampling strategies: their application in freshwater fisheries management* (pp. 33–48). London: Blackwell.

Cole, L. J., Stockan, J., & Helliwell, R. (2020). Managing riparian buffer strips to optimise ecosystem services: A review. *Agriculture, Ecosystems & Environment*, 106891.

Courchamp, F., Berec, L., & Gascoigne, J. (2008). *Allee effects in ecology and conservation.* Oxford, Oxford University Press.

Cousins, K. L., & Jensen, J. O. (1994). The effects of temperature on external egg membranes in coho salmon (*Oncorhynchus kisutch*) and the occurrence of soft-shell disease. *Canadian Journal of Zoology*, 72, 1854–1857.

Cowx, I. (1994). Stocking strategies. *Fisheries Management and Ecology*, 1, 15–30.

Cresser, M., & Edwards, A. (1987). *Acidification of freshwaters*. Cambridge, Cambridge University Press.

Crisp, D. T. (1989). Some impacts of human activities on trout, *Salmo trutta*, populations. *Freshwater Biology*, 21, 21–33.

Crisp, D. T. (1990). Some effects of application of mechanical shock at varying stages of development upon the survival and hatching time of British salmonid eggs. *Hydrobiologia*, 194, 57–65.

Crisp, D. T. (1993). The environmental requirements of salmon and trout in fresh water. *Freshwater Forum*, 3, 176–202.

Crisp, D. T. (1996). Environmental requirements of common riverine European salmonid fish species in fresh water with particular reference to physical and chemical aspects. *Hydrobiologia*, 323, 201–221.

Crisp, D. T. (2000). *Trout and salmon: ecology, conservation and rehabilitation.* Oxford, Wiley-Blackwell.

Crisp, D. T., & Carling, P. A. (1989). Observations on siting, dimensions and structure of salmonid redds. *Journal of Fish Biology*, 34, 119–134.

Cuinat, R., & Bomassi, P. (1987). Evolution de la situation pour le saumon du bassin Loire-Allier, de 1979 à 1985. In M. Thibault, & R. Billard (Eds.), *La restauration des rivières à saumons* (pp. 39–51). Paris, INRA.

Cushing, D. H. (1975). *Marine Ecology and Fisheries*. London, Cambridge University Press.

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology*, 26, 249–293.

Czerkies, P., Brzuzan, P., Kordalski, K., & Luczynski, M. (2001). Critical partial pressures of oxygen causing precocious hatching in *Coregonus lavaretus* and *C. albula* embryos. *Aquaculture*, 196, 151–158.

Dar, G. H., Bhat, R. A., Kamili, A. N., Chishti, M. Z., Qadri, H., Dar, R., & Mehmood, M. A. (2020). Correlation between pollution trends of freshwater bodies and bacterial disease of fish fauna. In H. Qadri, R.A. Bhat, M. A. Mehmood, & G. H. Dar (Eds.), *Fresh Water Pollution Dynamics and Remediation* (pp. 51–67). Singapore, Springer.

Davidsen, J. G., Rikardsen, A. H., Thorstad, E. B., Halttunen, E., Mitamura, H., Præbel, K., Skarðhamar, J., & Næsje, T. F. (2013). Homing behaviour of Atlantic salmon (*Salmo salar*) during final phase of marine migration and river entry. *Canadian Journal of Fisheries and Aquatic Sciences*, 70, 794–802.

Davidsen, J. G., Eikås, L., Hedger, R. D., Thorstad, E. B., Rønning, L., Sjursen, A. D., Berg, O. K., Bremset, G., Karlsson, S., & Sundt-Hansen, L. E. (2020). Migration and habitat use of the landlocked riverine Atlantic salmon *Salmo salar* småblank. *Hydrobiologia*, 847, 2295–2306.

Daye, P. G., & Garside, E. T. (1979). Development and survival of embryos and alevins of the Atlantic salmon, *Salmo salar* L., continuously exposed to acidic levels of pH, from fertilization. *Canadian Journal of Zoology*, 57, 1713–1718.

Daye, P. G., & Garside, E. T. (1980). Structural alterations in embryos and alevins of the Atlantic salmon, *Salmo salar* L., induced by continuous or short-term exposure to acidic levels of pH. *Canadian Journal of Zoology*, 58, 27–43.

Degerman, E., & Appelberg, M. (1992). The response of stream-dwelling fish to liming. *Environmental Pollution*, 78, 149–155.

Denic, M., & Geist, J. (2010). Habitat suitability analysis for lacustrine brown trout (*Salmo trutta*) in Lake Walchensee, Germany: implications for the conservation of an endangered flagship species. *Aquatic Conservation*, 20, 9–17

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.

Dirksmeyer, J. (2008). *Untersuchungen zur Ökomorphologie der Laichhabitate von Lachsen und Meerforellen in Deutschland*. Doctoral thesis, Solingen: University Cologne.

Doadrio, I. (2001). *Atlas y libro rojo de los peces continentales de España* (376 pp). Madrid: Ministerio de Medio Ambiente.

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.). *Ecolgy of Freshwater Fish*, 27, 920–932.

DWA (2014). *Merkblatt DWA-M 509 Fischaufstiegsanlagen und fischpassierbare Bauwerke–Gestaltung, Bemessung, Qualitätssicherung*. Hennef: Deutsche Vereinigung für Wasserwirtschaft, Abwasser und Abfall e.V.

Dynesius, M., & Nilsson, C. (1994). Fragmentation and flow regulation of river systems in the northern 3rd of the world. *Science*, 266, 753–762.

EIFAC (1969). Water quality criteria for European freshwater fish—water temperature and inland fisheries. Water Research, 3, 645–662.

Einstein, H. A. (1968). Deposition of suspended particles in a gravel bed. *Journal of Hydraulic Engineering*, 94, 1197–1205.

Einum, S., & Fleming, I. A. (2000). Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution*, 54, 628–639.

Eklöv, A. G., Greenberg, L. A., Brönmark, C., Larsson, P., & Berglund, O. (1999). Influence of water quality, habitat and species richness on brown trout populations. *Journal of Fish Biology*, 54, 33–43

Ellender, B. R., Rivers-Moore, N. A., Coppinger, C. R., Bellingan, T. A., & Weyl, O. L. F. (2016). Towards using thermal stress thresholds to predict salmonid invasion potential. *Biological Invasions*, 18, 3513–3525.

Elliott, J. M. (1976). The downstream drifting of eggs of brown trout (*Salmo trutta* L.). *Journal of Fish Biology*, 9, 45–50.

Elliott, J. M. (1981). Some aspects of thermal stress on fresh-water teleosts. In A. D. Pickering (Ed.), *Stress and Fish* (pp. 43-50). London: Academic Press.

Elliott, J. M. (1989). Wild brown trout *Salmo trutta*: an important national and international resource. *Freshwater Biology*, 21, 1–5.

Elliott, J. M. (1994). *Quantitative Ecology and the Brown Trout*. Oxford: Oxford University Press.

Elliott, J., & Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. *Journal of Fish Biology*, 77, 1793–1817.

Env. Canada (Environment Canada and Health Canada). (2001). Canadian Environmental Protection Act CEPA 1999 - Priority Substances List Assessment Report - Ammonia in the Aquatic Environment. Report for the Minister of Public Works and Government Services, Canada, 96 pp. Retrieved on July 10, 2020 from: https://www.canada.ca/en/health-canada/services/environmental-workplace-health/reports-publications/environmental-contaminants/canadian-environmental-protection-act-1999-priority-substances-list-assessment-report-ammonia-aquatic-environment.html.

EPA (United States Environmental Protection Agency). (2019). National Recommended Water Quality Cirteria - Aquatic Life Criteria Table. Retrieved on 18 June, 2020 from: https://www.epa.gov/wqc/national-recommended-water-quality-criteria-aquatic-life-criteria-table.

Eriksson, E. (1981). Aluminium in groundwater possible solution equilibria. *Hydrology Research*, 12, 43–50.

Erkinaro, J., Økland, F., Moen, K., Niemelä, E., & Rahiala, M. (1999). Return migration of Atlantic salmon in the River Tana: the role of environmental factors. *Journal of Fish Biology*, 55, 506–516.

Essington, T. E., Sorensen, P. W., Paron, D. G. (1998). High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 2310–2316.

EU (European Union). (1978). Directive 78/659/EEC of the European Parliament and of the Council of 18 July 1978 on the quality of fresh waters needing protection or improvement in order to support fish life. *Official Journal of the European Communities*, L222, 1–10.

EU (European Union). (2000). Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for community action in the field of water policy. *Official Journal of the European Communities*, L327, 1–84.

EU (European Union). (2006). Directive 2006/44/EC of the European Parliament and of the Council of 6 September 2006 on the quality of fresh waters needing protection or improvement in order to support fish life. *Official Journal of the European Union*, L264, 1–12.

EUMOFA (2019). *The EU fish market* (107 pp.). Luxembourg: Publications Office of the European Union.

Evans, C. D., Cullen, J. M., Alewell, C., Kopácek, J., Marchetto, A., Moldan, F., Prechtel, A., Rogora, M., Veselý, J., & Wright, R. (2001). Recovery from acidification in European surface waters. *Hydrology and Earth System Sciences*, 5, 283–297.

Everest, F. H., Beschta, R. L., Scrivener, J. C., Koski, K. V., Sedell, J. R., & Cederholm, C. J. (1987). Fine sediment and salmonid production: a paradox. In E. O. Salo & T. W. Cundy T.W. (Eds.), *Streamside Management and Forestry and Fishery Interactions* (pp. 89–142). Washington: College of Forest Resources University of Washington.

Exley, C. A., Chappell, J .S., & Birchall, J. D. (1991). A mechanism for acute aluminium toxicty in fish. *Journal of Theoretical Biology*, 151, 417–427.

Ferguson, A. (2006). *Genetic impacts of stocking on indigenous brown trout populations* (96 pp.). Environment Agency Science Report SC040071/SR. Bristol: Environment Agency.

Finn, R. N. (2007). The physiology and toxicology of salmonid eggs and larvae in relation to water quality criteria. *Aquatic Toxicology*, 81, 337–354.

Finstad, A. G., Økland, F., Thorstad, E. B., & Heggberget, T. G. (2005). Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *Journal of Fish Biology*, 67, 919–930.

Fivelstad S., Kallevik H., & Iversen, H. (1993). Sublethal effects of ammonia in soft water on Atlantic salmon smolts at a low temperature. *Aquaculture International*, 1, 157–169.

Forseth, T., Barlaup, B. T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., Hindar, A., Mo, T. A., Rikardsen, A. H., Thorstad, E. B., Vøllestad, L. A., & Wennevik, V. (2017). The major threats to Atlantic salmon in Norway. *ICES Journal of Marine Science*, 74, 1496–1513.

Freyhof, J. (2011). *Salmo trutta*. The IUCN Red List of Threatened Species 2011: e.T19861A9050312. Retrieved Dec. 6, 2020 from: https://www.iucnredlist.org/species/19861/9050312.

Freyhof, J. (2014). *Salmo salar*. The IUCN Red List of Threatened Species 2014: e.T19855A2532398. Retrieved Dec. 6, 2020 from: https://www.iucnredlist.org/species/19855/9026693.

Garside, E. T. (1973). Ultimate upper lethal temperature of Atlantic salmon *Salmo salar* L. *Canadian Journal of Zoology*, 51, 898–900

Garcia-Vazquez, E., Moran, P., Martinez, J. L., Perez, J., De Gaudemar, B., & Beall, E. (2001). Alternative mating strategies in Atlantic salmon and brown trout. Journal of Heredity, 92, 146–149

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

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

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

Geist, J., Porkka, M., & Kuehn, R. (2006). The status of host fish populations and fish species richness in European freshwater pearl mussel (*Margaritifera margaritifera* L.) streams. *Aquatic Conservation*, 16, 251–266.

Geller, W., & Schultze, M. (2009). Acidification. In G. E. Likens (Ed.), *Encyclopedia of inland waters* (pp. 1–12). Oxford: Elsevier.

Gensemer, R. W., & Playle, R. C. (1999). The bioavailability and toxicity of aluminium in aquatic environments. *Critical Reviews in Environmental Science and Technology*, 29, 315–450.

Gerlier, M., & Roche, P. (1998). A radio telemetry study of the migration of Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta trutta* L.) in the upper Rhine. *Hydrobiologia*, 371, 283–293.

Gerstmeier, R., & Romig, T. (2003). *Die Süßwasserfische Europas* (2nd ed.). Stuttgart, Franckh-Kosmos Verlag GmbH & Co.

Gibbins, C. N., Moir, H. J., Webb, J. H., & Soulsby, C. (2002). Assessing discharge use by spawning Atlantic salmon: a comparison of discharge electivity indices and PHABSIM simulations. *River Research and Applications*, 18, 383–395.

Gibson, R. J. (1993). The Atlantic salmon in fresh water: spawning, rearing and production. *Reviews in Fish Biology and Fisheries*, 3, 39–73.

Gortázar, J., Alonso, C., & García de Jalón, D. (2012). Brown trout redd superimposition in relation to spawning habitat availability. *Ecology of Freshwater Fish*, 21, 283–292.

Gosset, C., Rives, J., & Labonne, J. (2006). Effect of habitat fragmentation on spawning migration of brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish*, 15, 247–254.

Gowans, A. R. D., Armstrong, J. D., Priede, I. G., & Mckelvey, S. (2003). Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland. *Ecology of Freshwater Fish*, 12, 177–189.

Graham, C. T., & Harrod, C. (2009). Implications of climate change for the fishes of the British Isles. *Journal of Fish Biology*, 74, 1143–1205.

Grande, M., Muniz, I. P., & Andersen, S. (1978). Relative tolerance of some salmonids to acid waters. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 20, 2076–2084.

Greig, S. M., Sear, D. A., & Carling, P. A. (2005a). 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.

Greig, S. M., Sear, D. A., & Carling, P. A. (2007). A review of factors influencing the availability of dissolved oxygen to incubating salmonid embryos. *Hydrological Processes*, 21, 323–334.

Greig, S. M., Sear, D. A., Smallman, D., & Carling, P. A. (2005b). Impact of clay particles on the cutaneous exchange of oxygen across the chorion of Atlantic salmon eggs. *Journal of Fish Biology*, 66, 1681–1691.

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

Gross, R., Nilsson, J., & Schmitz, M. (1996). A new species-specific nuclear DNA marker for identification of hybrids between Atlantic salmon and brown trout. *Journal of Fish Biology*, 49, 537–540.

Haag, J. J., White, J. S., & Logan, M. (2010). 2009 fish survey in recently dewatered western irrigation district canals. Prepared for: Western Irrigation District. Edmonton: Aquality Environmental Consulting Ltd.

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.

Harby, A., & Noack, M. (2013). Rapid flow fluctuations and impacts on fish and the aquatic ecosystem. In I. Maddock, A. Harby, P. Kemp & P. Wood (Eds.), *Ecohydraulics: an integrated approach* (323 pp.). Chichester: John Wiley & Sons, Ltd.

Harrod, C., Graham, C., & Mallela, J. (2009). Climate change and the fishes of Britain and Ireland. *Journal of Fish Biology*, 74, 1143–1205.

Hartley, S. E. (1996). High incidence of Atlantic salmon x brown trout hybrids in a lake district stream. *Journal of Fish Biology*, 48, 151–154.

Hartman, K. J., & Hakala, J. P. (2006). Relationships between fine sediment and brook trout recruitment in forested headwater streams. *Journal of Freshwater Ecology*, 21, 215–230.

Hastie, L., & Cosgrove, P. (2001). The decline of migratory salmonid stocks: a new threat to pearl mussels in Scotland. *Freshwater Forum*, 15, 85–96.

Havas, M., & Rosseland, B. O. (1995). Response of zooplankton, benthos, and fish to acidification: An overview. *Water, Air, & Soil Pollution*, 85, 51–62. doi: 10.1007/BF00483688

Hayes, F. R. (1949). The growth, general chemistry, and temperature relations of salmonid eggs. *Quarterly Review of Biology*, 24, 281–308. doi: 10.1086/397213

Hayes, F. R., Wilmot, I. B., & Livingstone, D. A. (1951). The oxygen consumption of the salmon egg in relation to development and activity. *Journal of Experimental Zoology*, 116, 377–395. doi: 10.1002/jez.1401160302

Heggberget, T. G., Haukebø, T., Mork, J., & Ståhl, G. (1988). Temporal and spatial segregation of spawning in sympatric populations of Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L.. *Journal of Fish Biology*, 33, 347–356. doi: 10.1111/j.1095-8649.1988.tb05477.x

HELCOM (2011). *Salmon and Sea Trout Populations and Rivers in the Baltic Sea—HELCOM assessment of salmon (Salmo salar) and sea trout (Salmo trutta) populations and habitats in rivers flowing to the Baltic Sea* (82 pp.). Helsinki: Helsinki Commission, Baltic Marine Environment Protection Commission. Retrieved Dec. 6, 2020 from: https://www.cbd.int/doc/meetings/mar/soiom-2016-01/other/soiom-2016-01-helcom-09-en.pdf.

Hendry, K., Cragg-Hine, D., O'Grady, M., Sambrook, H., & Stephen, A. (2003). Management of habitat for rehabilitation and enhancement of salmonid stocks. *Fisheries Research*. 62, 171–192. doi: 10.1016/S0165-7836(02)00161-3

Henriksen, A., Skogheim, O. K., & Rosseland, B. O. (1984). Episodic changes in pH and aluminium-speciation kill fish in a Norwegian salmon river. *Vatten*, 40, 255–260.

Hering, D., Borja, A., Carstensen, J., Carvalho, L., Elliott, M., Feld, C. K., Heiskanen, A.- S., Johnson, E. K., Moe, J., Pont, D., Solheim, A. L., & van de Bund, W. (2010). The European Water Framework Directive at the age of 10: a critical review of the achievements with recommendations for the future. *Science of the Total Environment*, 408, 4007–4019. doi: 10.1016/j.scitotenv.2010.05.031

Hesthagen, T., Larsen, B. M., Bolstad, G., Fiske, P., & Jonsson, B. (2017). Mitigation of acidified salmon rivers–effects of liming on young brown trout *Salmo trutta*. *Journal of Fish Biology*, 91, 1350–1364. doi: 10.1111/jfb.13454

Heywood, M. J. T., & Walling, D. E. (2007). The sedimentation of salmonid spawning gravels in the Hampshire Avon catchment, UK: implications for the dissolved oxygen content of intragravel water and embryo survival. *Hydrological Processes*, 21, 770–788. doi: 10.1002/hyp.6266

Hinch, S. G., & Bratty, J. (2000). Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. *Transactions* *of the American Fisheries Society*, 129, 598–606. doi: 10.1577/1548-8659(2000)129<0598:EOSSAA>2.0.CO;2

Hoffmann, R. C. (1996). Economic development and aquatic ecosystems in medieval Europe. *American Historical Review*, 101, 631–669. doi: 10.1007/s10152-004-0203-5

Honkanen, J. O., Heinonen, J., & Kukkonen, J. V. (2001(. Toxicokinetics of waterborne bisphenol A in landlocked salmon (*Salmo salar* m. *Sebago*) eggs at various temperatures. *Environmental Toxicology and Chemistry*, 20, 2296–2302. doi: 10.1002/etc.5620201023

Howells, G., Dalziel, T. R. K., & Turnpenny, A. W. H. (1992). Loch Fleet: liming to restore a brown trout fishery. *Environmental Pollution*, 78, 131–139. doi: 10.1016/0269-7491(92)90021-2

Hultberg, H., & Andersson, I. B. (1982). Liming of acidified lakes: induced long-term changes. Water, Air, & Soil Pollution, 18, 311–331. doi: 10.1007/BF02419420

Hunter, J. W. (1973). *A discussion of game fish in the State of Washington as related to water requirements*. Olympia WA, Washington State Dept. Game.

Hutchings, J. A., Ardren, W. R., Barlaup, B. T., Bergman, E., Clarke, K. D., Greenberg, L. A., Lake, C., Piironen, J., Sirois, P., Sundt-Hansen, L. E., & Fraser, D. J. (2019). Life-history variability and conservation status of landlocked Atlantic salmon: an overview. *Canadian Journal of Fisheries and Aquatic Sciences*, 76, 1697–1708. doi: 10.1139/cjfas-2018-0413

ICES (2013). Report of the Workshop on Sea Trout (WKTRUTTA), 12–14 November 2013 (243 pp.). Copenhagen: ICES. ICES CM 2013/SSGEF:15.

ICES (2017a). Report of the Working Group on Effectiveness of Recovery Actions for Atlantic Salmon (WGERAAS), 9–13 November 2015 (115 pp.). Copenhagen: ICES. ICES CM 2015/SSGEPD:03.

ICES (2017b). Report of the Workshop on Potential Impacts of Climate Change on Atlantic Salmon Stock Dynamics (WKCCISA). (ACOM:39). Copenhagen: ICES Advisory Committee. Retrieved Aug. 10, 2020 from: http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2017/WKCCISAL/wkccisal_2017.pdf.

ICES (2019a). North Atlantic Salmon Stocks. In Report of the ICES Advisory Committee, 2019. ICES Advice 2019, sal.oth.nasco. doi: 10.17895/ices.advice.5230

ICES (2019b). Salmon (*Salmo salar*) in subdivisions 22–31 (Baltic Sea, excluding the Gulf of Finland). In Report of the ICES Advisory Committee, 2019. ICES Advice 2019, sal.27.22–31. doi: 10.17895/ices.advice.4742

ICES (2019c). Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports* 1, 1–368. doi: 10.17895/ices.pub.4978

ICPR (2015). Monitoring Rhine fish fauna 2012/2013 (228). Koblenz: International Commission for the Protection of the Rhine (IKSR, CIPR, ICBR). Retrieved July 11, 2020 from: https://www.iksr.org/fileadmin/user_upload/DKDM/Dokumente/Fachberichte/DE/rp_De_0228.pdf.

ICPR (2018). Masterplan Wanderfische Rhein 2018 - eine Aktualisierung des Masterplans 2009 (247). Koblenz: International Commission for the Protection of the Rhine (IKSR, CIPR, ICBR). Retrieved July 11, 2020 from: https://www.iksr.org/fileadmin/user_upload/DKDM/Dokumente/Fachberichte/DE/rp_De_0247.pdf.

Ingendahl, D. (1999). *Der Reproduktionserfolg von Meerforelle und Lachs in Korrelation zu den Milieubedingungen des hyporheischen Interstitials*. Doctoral thesis, Cologne: University Cologne Hundt Druck GmbH.

Ingendahl, D. (2001). Dissolved oxygen concentration and emergence of sea trout fry from natural redds in tributaries of the River Rhine. *Journal of Fish Biology*, 58, 325–341. doi: 10.1111/j.1095-8649.2001.tb02256.x

IPCC (2007). Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (112 pp.). Geneva: IPCC. Retrieved July 6, 2020 from: https://www.ipcc.ch/site/assets/uploads/2018/02/ar4_syr_full_report.pdf.

IPCC (2014). Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (696 pp.). Cambridge:

Cambridge University Press. Retrieved July 6, 2020 from: https://www.ipcc.ch/site/assets/uploads/2018/02/WGIIAR5-PartB_FINAL.pdf.

IWB & IDUS (Institut für Wasser und Boden Dr. Uhlmann & IDUS Biologische Analytisches Umweltlabor). (2012). Untersuchungen zu Ammonium in ostsächsischen Bergbaufolgeseen (234 pp.). Prepared for Sächsiches Landesamt für Umwelt, Landwirtschaft und Geologie. Retrieved Aug. 9, 2020 from: https://www.umwelt.sachsen.de/umwelt/download/Abschlussbericht_TP_05_online.pdf.

Jackson, A. L. (2011). Renewable energy vs. biodiversity: policy conflicts and the future of nature conservation. *Global Environmental Change*, 21, 1195–1208. doi: 10.1016/j.gloenvcha.2011.07.001

Jensen, K. W., & Snekvik, E. (1972). Low pH levels wipe out salmon and trout populations in southernmost Norway. *Ambio*, 1, 223–225.

Jensen, A. J., Johnsen, B. O., & Saksgård, L. (1989). Temperature requirements in Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic char (*Salvelinus alpinus*) from hatching to initial feeding compared with geographic distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, 46, 786–789. doi: 10.1139/f89-097

Jepsen, N., Aarestrup, K., Økland, F., & Rasmussen, G. (1998). Survival of radiotagged Atlantic salmon (*Salmo salar* L.)—and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. *Hydrobiologia*, 371, 347. doi: 10.1023/A:1017047527478

Jobling, M. (1997). Temperature and growth: modulation of growth rate via temperature change. In C. M. Wood & D. G. McDonald (Eds.), *Global Warming: Implications for Freshwater and Marine Fish* (pp. 225-254). Cambridge: Press Cambridge.

Johansson, D., Ruohonen, K., Kiessling, A., Oppedal, F., Stiansen, J. E., Kelly, M., & Juell, J. E. (2006). Effect of environmental factors on swimming depth preferences of Atlantic salmon (*Salmo salar* L.) and temporal and spatial variations in oxygen levels in sea cages at a fjord site. *Aquaculture*, 254, 594–605. doi: 10.1016/j.aquaculture.2005.10.029

Johnsen, B. O., Arnekleiv, J. V., Asplin, L., Barlaup, B. T., Næsje, T. F., Rosseland, B. O., Saltveit, S. J., & Tvede, A. (2011). Hydropower development–Ecological effects. In Ø. Aas, S. Einum, A. Klemetsen & J. Skurdal (Eds.), *Atlantic Salmon Ecology* (pp. 351–386), Chichester: John Wiley & Sons Ltd.

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

Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, 75, 2381–2447. doi: 10.1111/j.1095-8649.2009.02380.x

Jonsson, B., & Jonsson, N. (2011). *Ecology of Atlantic salmon and brown trout: habitat as a template for life history*. Dordrecht, Springer. doi: 10.1007/978-94-007-1189-1

Jonsson, B., Jonsson, N., & Jonsson, M. (2018). Water level influences migratory patterns of anadromous brown trout in small streams. *Ecology of Freshwater Fish*, 27, 1066–1075. doi: 10.1111/eff.12415

Jonsson, B., Jonsson, N., Brodtkorb, E., & Ingebrigtsen, P. J. (2001). Life-history traits of brown trout vary with the size of small streams. *Functional Ecology,* 15, 310–317.

Jungwirth, M., & Winkler, H. (1984). The temperature dependence of embryonic development of grayling (*Thymallus thymallus*), Danube salmon (*Hucho hucho*), Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta fario*). *Aquaculture*, 38, 315–327. doi: 10.1016/0044-8486(84)90336-3

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

Kazakov, R. V. (1992). Distribution of Atlantic salmon, *Salmo salar* L., in freshwater bodies of Europe. *Aquaculture Research*, 23, 461–475. doi: 10.1111/j.1365-2109.1992.tb00790.x

King, H. R., Pankhurst, N. W., & Watts, M. (2007). Reproductive sensitivity to elevated water temperatures in female Atlantic salmon is heightened at certain stages of vitellogenesis. *Journal of Fish Biology*, 70, 190–205. doi: 10.1111/j.1095-8649.2006.01295.x

King, H. R., Pankhurst, N. W., Watts, M., & Pankhurst, P. M. (2003). Effect of elevated summer temperatures on gonadal steroid production, vitellogenesis and egg quality in female Atlantic salmon. *Journal of Fish Biology*, 63, 153–167. doi: 10.1046/j.1095-8649.2003.00137.x

Kinouchi, T., Yagi, H., & Miyamoto, M. (2007). Increase in stream temperature related to anthropogenic heat input from urban wastewater. *Journal of Hydrology*, 335, 78–88. doi: 10.1016/j.jhydrol.2006.11.002

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'connell, M. F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, 12, 1–59. doi: 10.1034/j.1600-0633.2003.00010.x

Klütsch, C. F. C., Maduna, S. N., Polikarpova, N., Forfang, K., Aspholm, P. E., Nyman, T., Eiken, H. G., Amundsen, P.- A., & Hagen, S. B. (2019). Genetic changes caused by restocking and hydroelectric dams in demographically bottlenecked brown trout in a transnational subarctic riverine system. *Ecology and Evolution*, 9, 6068– 6081. doi: 10.1002/ece3.5191

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. doi: 10.3390/su11216037

Kondolf, G. M. (2000). Assessing salmonid spawning gravel quality. *Transactions of the American Fisheries Society*, 129, 262–281. doi: 10.1577/1548-8659(2000)129<0262:ASSGQ>2.0.CO;2

Kondolf, G. M., & Wolman, M. G. (1993). The sizes of salmonid spawning gravels. *Water Resource Research*, 29, 2275–2285. doi: 10.1029/93WR00402

Kondolf, G. M., Williams, J. G., Horner, T. C., & Milan, D. (2008). Assessing physical quality of spawning habitat. *American Fisheries Society Symposium*, 65, 26.

Kottelat, M., & Freyhof, J. (2007). *Handbook of European freshwater fishes*. Berlin, Kottelat, Cornol and Freyhof.

Kouwenberg, J. H. M., Browman, H. I., Cullen, J. J., Davis, R. F., St-Pierre, J. F., & Runge, J. A. (1999). Biological weighting of ultraviolet (280–400 nm) induced mortality in marine zooplankton and fish. I. Atlantic cod (*Gadus morhua*) eggs. *Marine Biology*, 134, 269–284. doi: 10.1007/s002270050545

Lacroix, G. L. (1985a). Survival of eggs and alevins of Atlantic salmon (*Salmo salar*) in relation to the chemistry of interstitial water in redds in some acidic streams of Atlantic Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 42, 292–299. doi: 10.1139/f85-037

Lacroix, G. L., Gordon, D J., & Johnston, D. J. (1985b). Effects of low environmental pH on the survival, growth, and ionic composition of postemergent Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 42, 768–775. doi: 10.1139/f85-098

Landergren, P. (2004). Factors affecting early migration of sea trout *Salmo trutta* parr to brackish water. *Fisheries Research*, 67, 283–294. doi: 10.1016/j.fishres.2003.10.005

Leivestad, H., & Muniz, I. P. (1976). Fish kills at low pH in a Norwegian river. *Nature* 259, 391–392. doi: 10.1038/259391a0

Lenders, H. J. R., Chamuleau, T. P. M., Hendriks, A. J., Lauwerier, R. C. G. M., Leuven, R. S. E. W., & Verberk, W. C. E. P. (2016). Historical rise of waterpower initiated the collapse of salmon stocks. *Scientific Reports*, 6, 29269. doi: 10.1038/srep29269

Lenhart, B., & Steinberg, C. (1984). *Limnochemische und limnobiologische Auswirkungen der Versauerung von kalkarmen Oberflächengewässern - Eine Literaturstudie*. München, Informationsberichte Bayerisches Landesamtes für Wasserwirtschaft 4.

LfU (2005). Mindestabflüsse in Ausleitungsstrecken (30 pp.). Fischereiforschungsstelle Baden-Württemberg. Retrieved Oct. 22, 2020 from: http://www.marcosander.de/pdf/anforderungsprofile_indikatorfischarten.pdf.

Lobón-Cerviá, J. (2009). Why, when and how do fish populations decline, collapse and recover? The example of brown trout (*Salmo trutta*) in Rio Chaballos (northwestern

Spain). *Freshwater Biology*, 54, 1149–1162. doi: 10.1111/j.1365-2427.2008.02159.x

Lobón-Cerviá, J. (2017). Introduction: Princess of the Streams: The Brown Trout *Salmo trutta* L. as Aquatic Royalty. In J. Lobón-Cerviá & N. Sanz (Eds.), *Brown Trout: Biology, Ecology and Management* (pp. 1–13). Hoboken: John Wiley & Sons Ltd. doi: 10.1002/9781119268352.ch1

Lobón-Cerviá, J., & Rincón, P.A. (2004). Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout *Salmo trutta*. *Oikos*, 105, 641–646. doi: 10.1111/j.0030-1299.2004.12989.x

Louhi, P., Mäki-Petäys, A., & Erkinaro, J. (2008). Spawning habitat of Atlantic salmon and brown trout: general criteria and intragravel factors. *River Research and Applications*, 24, 330–339. doi: 10.1002/rra.1072

Louhi, P., Ovaska, M., Mäki-Petäys, A., Erkinaro, J., & Muotka, T. (2011). Does fine sediment constrain salmonid alevin development and survival?. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 1819-1826. doi: 10.1139/f2011-106

Louhi, P., Vehanen, T., Huusko, A., Mäki-Petäys, A., & Muotka, T. (2016). Long-term monitoring reveals the success of salmonid habitat restoration. *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 1733–1741. doi: 10.1139/cjfas-2015-0546

Lundqvist, H., Rivinoja, P., Leonardsson, K., & McKinnell, S. (2008). Upstream passage problems for wild Atlantic salmon (*Salmo salar* L.) in a regulated river and its effect on the population. In S. Dufour, E. Prévost, E. Rochard & P. Williot (Eds.), *Fish and Diadromy in Europe (ecology, management, conservation)* (pp. 111–127). Dordrecht: Springer. doi: 10.1007/978-1-4020-8548-2_9

MacCrimmon, H. R., & Gots, B. L. (1979). World distribution of Atlantic salmon, *Salmo salar*. *Journal of the Fisheries Board of Canada*, 36, 422–457. doi: 10.1139/f79-062

Machordom, A., Garcia-Marin, J. L., Sanz, N., Almodovar, A., & Pla, C. (1999). Allozyme diversity in brown trout (*Salmo trutta*) from Central Spain: genetic consequences of restocking. *Freshwater Biology*, 41, 707–717. doi: 10.1046/j.1365-2427.1999.00418.x

Malcolm, I. A., Youngson, A. F., & Soulsby, C. (2003b). Survival of salmonid eggs in a degraded gravel-bed stream: effects of groundwater–surface water interactions. *River Research and Applications*, 19, 303–316. doi: 10.1002/rra.706

Malcolm I., Youngson A. F., Greig S., & Soulsby C. (2008). Hyporheic influences on spawning success. In D. Sear & P. DeVries (Eds.), *Salmon Spawning Habitat in Rivers: Physical Controls, Biological Responses and Approaches to Remediation* (pp. 225–248). Bethesda: American Fisheries Society.

Malcolm, I. A., Soulsby, C., Youngson, A. F., & Petry, J. (2003a). Heterogeneity in ground water–surface water interactions in the hyporheic zone of a salmonid spawning stream. *Hydrological Processes*, 17, 601–617. doi: 10.1002/hyp.1156

Marzano, F. N., Corradi, N., Papa, R., Tagliavini, J., & Gandolfi, G. (2003). Molecular evidence for introgression and loss of genetic variability in Salmo (*trutta*) macrostigma as a result of massive restocking of Apennine populations (Northern and Central Italy). *Environmental Biology of Fishes*, 68, 349–356. doi: 10.1023/B:EBFI.0000005762.81631.fa

Matthews, M. A., Poole, W. R., Thompson, C. E., McKillen, J., Ferguson, A., Hindar, K., & Wheelan, K. F. (2000). Incidence of hybridization between Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in Ireland. *Fisheries Management and Ecology*, 7, 337–347. doi: 10.1046/j.1365-2400.2000.00208.x

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. doi: 10.1139/d98-011

McLaughlin, R. L., Smyth, E. R., Castro-Santos, T., Jones, M. L., Koops, M. A., Pratt, T. C., & Vélez-Espino, L. A. (2013). Unintended consequences and trade-offs of fish passage. *Fish and Fisheries*, 14, 580–604. doi: 10.1111/faf.12003

Mills, D. (1971). *Salmon and Trout*. Edinburgh, Oliver & Boyd.

Mills, D. (1989). *Ecology and management of Atlantic salmon*. London, Chapman & Hall.

Mueller, M., Pander, J., & Geist, J. (2014). The ecological value of stream restoration measures: an evaluation on ecosystem and target species scales. *Ecological Engineering*, 62, 129–139. doi: 10.1016/j.ecoleng.2013.10.030

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. doi: 10.1111/fme.12229

Mueller, M., Bierschenk, A. M., Bierschenk, B. M., Pander, J., & Geist, J. (2020). 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. doi: 10.1016/j.scitotenv.2019.134523

Monnerjahn, U. (2011). Atlantic salmon (*Salmo salar* L.) re-introduction in Germany: a status report on national programmes and activities. *Journal of Applied Ichthyology*, 27, 33–40. doi: 10.1111/j.1439-0426.2011.01849.x

Moreau, D. A., & Moring, J. R. (1993). Refinement and testing of the habitat suitability index model for Atlantic salmon. Technical report prepared for US Fish and Wildlife Service. Orono: Maine Cooperative Research Unit.

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

NASCO (2018). North Atlantic Salmon stocks. In: Report of the ICES Advisory Committee. ICES Advice 2019, sal.oth.nasco. doi: 10.17895/ices.pub.4335.

NASCO (2019). STATE OF NORTH ALTLANTIC SALMON. Retrieved June 7, 2020 from: http://www.nasco.int/pdf/iys/SoS-final-online.pdf.

Nevoux, M., Finstad, B., Davidsen, J. G., Finlay, R., Josset, Q., Poole, R., Höjesjö, J., Aarestrup, K., Persson, L., Tolvanen, O., Jonsson, B. (2019). Environmental influences on life history strategies in partially anadromous brown trout (*Salmo trutta*, Salmonidae). *Fish and Fisheries*, 20, 1051–1082. doi: 10.1111/faf.12396

Niepagenkemper, O., Schulte, U., Meyer, E., Bode, H., Nusch, E., & Weyand, M. (2003). *Pilotmassnahmen zur Verbesserung der Beschaffenheit von Geschiebebaenken in Laichgewaessern von Salmoniden im Ruhrsystem*. Muenster, Ruhrverband Muenster.

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

Noonan, M. J., Grant, J. W., & Jackson, C. D. (2012). A quantitative assessment of fish passage efficiency. *Fish and Fisheries*, 13, 450–464. doi: 10.1111/j.1467-2979.2011.00445.x

Northcote, T. G. (1995). Comparative biology and management of Arctic and European grayling (Salmonidae, *Thymallus*). *Reviews in Fish Biology and Fisheries*, 5, 141–194. doi: 10.1007/BF00179755

Ojanguren, A. F., & Braña, F. (2003). Thermal dependence of embryonic growth and development in brown trout. *Journal of Fish Biology*, 62, 580–590. doi: 10.1046/j.0022-1112.2003.00049.x

Ojanguren, A. F., Reyes-Gavilán, F. G., & Muñoz, R. R. (1999). Effects of temperature on growth and efficiency of yolk utilisation in eggs and pre-feeding larval stages of Atlantic salmon. *Aquaculture Intnational*, 7, 81–87. doi: 10.1023/A:1009214804949

Olsson, I. C., Greenberg, L. A., Bergman, E., & Wysujack, K. (2006). Environmentally induced migration: the importance of food. *Ecology Letters*, 9, 645–651. doi: 10.1111/j.1461-0248.2006.00909.x

Oppen-Berntsen, D. O., Bogsnes, A., & Walther, B. T. (1990). The effects of hypoxia, alkalinity and neurochemicals on hatching of Atlantic salmon (*Salmo salar*) eggs. *Aquaculture*, 86, 417–430. doi: 10.1016/0044-8486(90)90330-P

Opperman, J. J., Moyle, P. B., Larsen, E. W., Florsheim, J. L., & Manfree, A. D. (2017). *Floodplains: Processes and management for ecosystem services*. Oakland, University of California Press.

Ormerod, S. J., Dobson, M., Hildrew, A. G., & Townsend, C. (2010). Multiple stressors in freshwater ecosystems. *Freshwater Biology*, 55, 1–4. doi: 10.1111/j.1365-2427.2009.02395.x

ORSANCO (1955). Aquatic life water quality criteria. *Sewage ind. Wastes*, 27, 321–313.

Ottaway, E. M., Carling, P. A., Clarke, A., & Reader, N. A. (1981). Observations on the structure of brown trout, *Salmo trutta* Linnaeus, redds. *Journal of Fish Biology*, 19, 593–607. doi: 10.1111/j.1095-8649.1981.tb03825.x

Overrein, L., Seip, H. M., & Tollan, A. (1980). *Acid precipitation-Effects on forest and fish* (175 pp.). Oslo-As: Final report of the SNSF-project 1972-1980.

Pander, J., & Geist, J. (2010). Salmonid-egg floating boxes as bioindication for riverine water quality and stocking success. *Journal of Fish Biology*, 76, 2584–2590. doi: 10.1111/j.1095-8649.2010.02645.x

Pander, J., & Geist, J. (2013). Ecological indicators for stream restoration success. *Ecological Indicators*, 30, 106–118. doi: 10.1016/j.ecolind.2013.01.039

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. doi: 10.1016/j.ecoleng.2015.12.006

Pander, J., Mueller, M., & Geist, J. (2015). A comparison of four stream substratum restoration techniques concerning interstitial conditions and downstream effects. *River Research and Apllications*, 31, 239–255. doi: 10.1002/rra.2732

Pander, J., Mueller, M., & Geist, J. (2018). Habitat diversity and connectivity govern the conservation value of restored aquatic floodplain habitats. *Biological Conservation*, 217, 1–10. doi: 10.1016/j.biocon.2017.10.024

Pander, J., Schnell, J., Sternecker, K., & Geist, J. (2009). The ‘egg sandwich’: a method for linking spatially resolved salmonid hatching rates with habitat variables in stream ecosystems. *Journal of Fish Biology*, 74, 683–690. doi: 10.1111/j.1095-8649.2008.02145.x

Parkhurst, B. R., Bergman, H. L., Fernandez, J., Gulley, D. D., Hockett, J. R., & Sanchez, D. A. (1990). Inorganic monomeric aluminium and pH as predictors of acidic water toxicity to brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, 47, 1631–1640. doi: 10.1139/f90-185

Pankhurst, N. W., King, H. R., Anderson, K., Elizur, A., Pankhurst, P. M., & Ruff, N. (2011). Thermal impairment of reproduction is differentially expressed in maiden and repeat spawning Atlantic salmon. *Aquaculture*, 316, 77–87. doi: 10.1016/j.aquaculture.2011.03.009

Peter, A. (1998). Interruption of the river continuum by barriers and the consequences for migratory fish. In M. Jungwirth, S. Schmutz & S. Weiss (Eds.), *Fish migration and fish bypasses*. Oxford: Fishing New Books.

Peterson, R. H., Daye, P. G., & Metcalfe, J. L. (1980). Inhibition of Atlantic salmon (*Salmo salar*) hatching at low pH. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 770–774. doi: 10.1139/f80-103

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. doi: 10.1016/j.ecoleng.2019.03.010

Piper, R. G., McElwain, I. B., Orme, L. E., McCraren, J. P., Fowler, L. G., & Leonard, J. R. (1982). *Fish hatchery management*. Washington, U.S. Fish Wildlife Service.

Poe, T. P., Hansel, H. C., Vigg, S., Palmer, D. E., & Prendergast, L. A. (1991). Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society*, 120, 405–420. doi: 10.1577/1548-8659(1991)120<0405:FOPFOO>2.3.CO;2

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., Sparks, R. E., & Stromberg, J. C. (1997). The natural flow regime. *Bioscience*, 47, 769–784. doi: 10.2307/1313099

Poff, N. L., Allan, J. D., Palmer, M. A., Hart, D. D., Richter, B. D., Arthington, A. H., Rogers, K. H., Meyer, J. L., & Stanford, J. A. (2003). River flows and water wars: emerging science for environmental decision making. *Frontiers in Ecology and the Environment*, 1, 298–306. doi: 10.1890/1540-9295(2003)001[0298:RFAWWE]2.0.CO;2

Pokki, H., Artell, J., Mikkola, J., Orell, P., & Ovaskainen, V. (2018). Valuing recreational salmon fishing at a remote site in Finland: A travel cost analysis. *Fisheries Research*, 208, 145–156. doi: 10.1016/j.fishres.2018.07.013

Power, G. (1958). The evolution of the freshwater races of the Atlantic salmon (*Salmo salar* L.) in eastern North America. *Arctic*, 11, 86–92.

Poxton, M. G. (1991). Incubation of salmon eggs and rearing of alevins: natural temperature fluctuations and their influence on hatchery requirements. *Aquacultural Engineering*, 10, 31–53. doi: 10.1016/0144-8609(91)90009-9

Pulg, U. (2009). *Laichplätze der Bachforelle (Salmo trutta) in der Moosach-die Bewertung ihrer Funktionsfähigkeit, ihre Degradierung und ihre Restaurierung*. Doctoral thesis. Freising: Technical University Munich.

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. doi: 10.1002/rra.1594

Quinn, T. P. (2005). *The behavior and ecology of Pacific salmon and trout*. Seattle, University of Washington Press.

Quinn, T. P., & Buck, G. B. (2001). Size-and sex-selective mortality of adult sockeye salmon: bears, gulls, and fish out of water. *Transactions of the American Fisheries Society*, 130, 995–1005. doi: 10.1577/1548-8659(2001)130<0995:SASSMO>2.0.CO;2

Raleigh, R. F., Zuckerman, L. D., & Nelson, P. C. (1984). *Habitat suitability index models and instream flow suitability curves: brown trout*. Washington, D.C.: U.S. Fish and Wildlife Sevice Biological Report 82.

Raleigh, R. F., Zuckerman, L. D., Nelson, P. C. (1986). *Habitat suitability index models and instream flow suitability curves: brown trout.* Washington, D.C.: U.S. Fish and Wildlife Service Biological Report 82.

Randak, T., Kocour, M., Žlábek, V., Policar, T., Jarkovský, J. (2006). Effect of culture conditions on reproductive traits of brown trout *Salmo trutta* L. *Bulletin Français De La Pêche Et De La Pisciculture*. 383, 1–12. doi: 10.1051/kmae:2006001

Reader, J. P., Dalziel, T. R. K., Morris, R., Sayer, M. D. J., & Dempsey, C. H. (1991). Episodic exposure to acid and aluminium in soft water: survival and recovery of brown trout, *Salmo trutta* L. *Journal of Fish Biology*, 39, 181–196. doi: 10.1111/j.1095-8649.1991.tb04355.x

Reimchen, T. E. (2018). Diverse ecological pathways of salmon nutrients through an intact marine-terrestrial interface. *The Canadian Field-Naturalist*, 131, 350–368. doi: 10.22621/cfn.v131i4.1965

Rombough, P. J. (1988). Respiratory gas exchange, aerobic metabolism, and effects of hypoxia during early life. *Fish Physiology*, 11, 59–161. doi: 10.1016/S1546-5098(08)60199-5

Roni, P., Beechie, T., Pess, G., & Hanson, K. (2015). Wood placement in river restoration: fact, fiction, and future direction. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 466–478. doi: 10.1139/cjfas-2014-0344.

Rozas-Serri, M. (2019). Gill diseases in marine salmon aquaculture with an emphasis on amoebic gill disease. *Atlantic*, 32, 34–35. doi: 10.1079/PAVSNNR201914032

Rubin, J. F. (1998). Survival and emergence pattern of sea trout fry in substrata of different compositions. Journal of Fish Biology, 53, 84–92. doi: 10.1111/j.1095-8649.1998.tb00111.x

Rubin, J.- F., & Glimsäter, C. (1996). Egg-to-fry survival of the sea trout in some streams of Gotland. *Journal of Fish Biology*, 48, 585–606. doi: 10.1111/j.1095-8649.1996.tb01454.x

Ruíz, A. F., & Rodríguez de los Santos, M. (2001). *Libro rojo de los vertebrados amenazados de Andalucía* (321 pp.). Sevilla: Consejería de Medio Ambiente Junta de Andalucía.

Rytwinski, T., Algera, D. A., Taylor, J. J. Smokorowski, K. E., Bennett, J. R., Harrsion, P. M., & Cooke, S. J. (2017). What are the consequences of fish entrainment and impingement associated with hydroelectric dams on fish productivity? A systematic review protocol. *Environmental Evidence*, 6, 8. doi: 10.1186/s13750-017-0087-x

Saltveit, S. J., & Brabrand, Å. (2013). Incubation, hatching and survival of eggs of Atlantic salmon (*Salmo salar*) in spawning redds influenced by groundwater. *Limnologica*, 43, 325–331. doi: 10.1016/j.limno.2013.05.009

Saltveit, S. J., Halleraker, J. H., Arnekleiv, J. V., & Harby, A. (2001). Field experiments on stranding in juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) during rapid flow decreases caused by hydropeaking. *Regulated Rivers: Research & Management*, 17, 609–622. doi: 10.1002/rrr.652

Sayer, M. D. J., Reader, J. P., & Morris, R. (1991). Embryonic and larval development of brown trout, *Salmo trutta* L.: exposure to aluminium, copper, lead or zinc in soft, acid water. *Journal of Fish Biology*, 38, 431–455. doi: 10.1111/j.1095-8649.1991.tb03132.x

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

Schofield, C. L. (1976). Acid precipitation: effects on fish. *Ambio*, 5, 228–230.

Serbezov, D., Bernatchez, L., Olsen, E. M., & Vøllestad, L. A. (2010). Mating patterns and determinants of individual reproductive success in brown trout (*Salmo trutta*) revealed by parentage analysis of an entire stream living population. Molecular Ecology, 19, 3193–3205. doi: 10.1111/j.1365-294X.2010.04744.x

Sergeant, C. J., Bellmore, J. R., McConnell, C., & Moore, J. W. (2017). High salmon density and low discharge create periodic hypoxia in coastal rivers. *Ecosphere*, 8, e01846. doi: 10.1002/ecs2.1846

Serrano, I., Buffam, I., Palm, D., Brännäs, E., & Laudon, H. (2008). Thresholds for survival of brown trout during the spring flood acid pulse in streams high in dissolved organic carbon. *Transactions of the American Fisheries Society*, 137, 1363–1377. doi: 10.1577/T07-069.1

Skjelkvåle, B. L., Evans, C., Larssen, T., Hindar, A., & Raddum, G. G. (2003). Recovery from acidification in European surface waters: a view to the future. *Ambio*, 32, 170–175. doi: 10.1579/0044-7447-32.3.170

Skjelkvåle, B. L., Stoddard, J. L., & Andersen, T. (2001). Trends in surface waters acidification in Europe and North America (1989-1998). *Water, Air, & Soil Pollution*, 130, 787–792. doi: 10.1023/A:1013806223310

Skogheim, O. K., & Rosseland, B. O. (1984). A comparative study on salmonid fish species in acid aluminium-rich water, 1: Mortality of eggs and alevins. *Report - Institute of Freshwater Research*, 61, 177–185.

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. doi: 10.3390/su11185011

Smith, G. W., Smith, I. P., & Armstrong, S. M. (1994). The relationship between river flow and entry to the Aberdeenshire Dee by returning adult Atlantic salmon. *Journal of Fish Biology,* 45, 953–960. doi: 10.1111/j.1095-8649.1994.tb01065.x

Solomon, D. J., & Sambrook, H. T. (2004). Effects of hot dry summers on the loss of Atlantic salmon, *Salmo salar*, from estuaries in South West England. *Fisheries Management and Ecology,* 11, 353–363. doi: 10.1111/j.1365-2400.2004.00403.x

Soulsby, C., Youngson, A. F., Moir, H. J., & Malcolm, I. A. (2001). Fine sediment influence on salmonid spawning habitat in a lowland agricultural stream: a preliminary assessment. *Science of the Total Environment*, 265, 295–307. doi: 10.1016/S0048-9697(00)00672-0

Sternecker, K., & Geist, J. (2010). The effects of stream substratum composition on the emergence of salmonid fry. *Ecology of Freshwater Fish*, 19, 537–544. doi: 10.1111/j.1600-0633.2010.00432.x

Sternecker, K., Cowley, D. E., & Geist, J. (2013a). Factors influencing the success of salmonid egg development in river substratum. *Ecology of Freshwater Fish*, 22, 322–333. doi: 10.1111/eff.12020

Sternecker, K., Wild, R., & Geist, J. (2013b). Effects of substratum restoration on salmonid habitat quality in a subalpine stream. *Environmental Biology of Fishes*, 96, 1341–1351. doi: 10.1007/s10641-013-0111-0

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. doi: 10.1002/ece3.1128

Stoddard, J. L., Jeffries, D. S., Liikewille, A., Clair, T. A., Dillon, P. J., Driscoll, C. T., Forsius, M., Johannessen, M., Kahl, J. S., Kellogg, J. H., Kemp, A., Mannio, J., Monteith, D., Murdoch, P. S., Patrick, S., Rebsdorf, A., Skjelkvale, B. L., Stainton, M. P., Traaen, T. S., van Dam, H., Webster, K. E., Wieting, J., & Wilander, A. (1999). Regional trends in aquatic recovery from acidification in North America and Europe 1980-95. *Nature*, 401, 575–578. doi: 10.1038/44114

Stuart, T. A. (1962). The leaping behaviour of salmon and trout at falls and obstructions. *Freshwater and Salmon Fisheries Research*, 28, 1–46.

Svendsen, J. C., Koed, A., & Aarestrup, K. (2004). Factors influencing the spawning migration of female anadromous brown trout. Journal of Fish Biology, 64, 528–540. doi: 10.1111/j.0022-1112.2004.00319.x

Szałkiewicz, E., Jusik, S., & Grygoruk, M. (2018). Status of and perspectives on river restoration in Europe: 310,000 Euros per hectare of restored river. *Sustainability*, 10, 129. doi: 10.3390/su10010129

Taeubert, J. E., & Geist, J. (2017). The relationship between the freshwater pearl mussel (*Margaritifera margaritifera*) and its hosts. *Biology Bulletin*, 44, 67–73. doi: 10.1134/S1062359017010149

Tetzlaff, D., Gibbins, C., Bacon, P. J., Youngson, A. F., & Soulsby, C. (2008). Influence of hydrological regimes on the pre-spawning entry of Atlantic salmon (*Salmo salar* L.) into an upland river. *River Research and Applications*, 24, 528–542. doi: 10.1002/rra.1144

Thomaz, D. M. P. F., Beall, E., & Burke, T. (1997). Alternative reproductive tactics in Atlantic salmon: factors affecting mature parr success. *Proceedings of the Royal Society B: Biological Sciences*, 264, 219–226. doi: 10.1098/rspb.1997.0031

Thompson, C. E., Poole, W. R., Matthews, M. A., & Ferguson, A. (1998). Comparison, using minisatellite DNA profiling, of secondary male contribution in the fertilisation of wild and ranched Atlantic salmon (*Salmo salar*) ova. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 2011–2018. doi: 10.1139/cjfas-55-9-2011. https://doi.org/10.1139/f98-076

Thorpe, J. E., Miles, M. S., & Keay, D. S. (1984). Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. *Aquaculture*, 43, 289–305. doi: 10.1016/0044-8486(84)90030-9

Thorstad, E. B., Heggberget, T. G., & Økland, F. (1998). Migratory behaviour of adult wild and escaped farmed Atlantic salmon, *Salmo salar* L., before, during and after spawning in a Norwegian river. *Aquaculture Research*, 29, 419–428. doi: 10.1046/j.1365-2109.1998.00218.x

Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., Kålås, S., Berg, M., & Finstad, B. (2016). Marine life of the sea trout. *Marine Biology*, 163, 47. doi: 10.1007/s00227-016-2820-3

Tillotson, M. D., & Quinn, T. P. (2017). Climate and conspecific density trigger pre-spawning mortality in sockeye salmon (*Oncorhynchus nerka*). *Fisheries Research*, 188, 138–148. doi: 10.1016/j.fishres.2016.12.013

Tummers, J. S., Hudson, S., & Lucas, M. C. (2016). Evaluating the effectiveness of restoring longitudinal connectivity for stream fish communities: towards a more holistic approach. *Science of the Total Environment*, 569, 850–860. doi: 10.1016/j.scitotenv.2016.06.207

Turnpenny, A. W. H., & Williams, R. (1980). Effects of sedimentation on the gravels of an industrial river system. *Journal of Fish Biology*, 17, 681–693. doi: 10.1111/j.1095-8649.1980.tb02802.x

UN/ECE (1999). *Protocol to the 1979 Convention on Long-range Transboundary Air Pollution to Abate Acidification, Eutrophication, and Ground-level Ozone.* Geneva: United Nations Economic Commission for Europe. Retrieved De. 12, 2020 from: http://www.unece.org/env/lrtap/protocol/.

van Puijenbroek, P. J., Buijse, A. D., Kraak, M. H., & Verdonschot, P. F. (2019). Species and river specific effects of river fragmentation on European anadromous fish species. *River Research and Applications*, 35, 68-77. doi: 10.1002/rra.3386

Vehanen, T., Sutela, T., & Korhonen, H. (2010a). Environmental assessment of boreal rivers using fish data–a contribution to the Water Framework Directive. *Fisheries Management and Ecology*, 17, 165–175. doi: 10.1111/j.1365-2400.2009.00716.x

Vehanen, T., Huusko, A., Mäki-Petäys, A., Louhi, P., Mykrä, H., & Muotka, T. (2010b.). APPLIED ISSUES: Effects of habitat rehabilitation on brown trout (*Salmo trutta*) in boreal forest streams. *Freshwater Biology*, 55, 2200–2214. doi: 10.1111/j.1365-2427.2010.02467.x

Verspoor, E., & Cole, L. J. (2005). Genetic evidence for lacustrine spawning of the non-anadromous Atlantic salmon population of Little Gull Lake, Newfoundland. *Journal of Fish Biology*, 67, 200–205. doi: 10.1111/j.0022-1112.2005.00848.x

Vosylienė, M. Z., & Kazlauskienė, N. (2004). Comparative studies of sublethal effects of ammonia on rainbow trout (*Oncorhynchus mykiss*) at different stages of its development. *Acta zoologica Lituanica*, 14, 13–18. doi: 10.1080/13921657.2004.10512568

Walker, A. M., & Bayliss, B. D. (2007). The spawning habitat requirements of sea trout: a multi-scale approach. In G. Harris & N. Milner (Eds.), *Sea Trout Biology, Conservation & Management*. Oxford: Blackwell Publishing Ltd

Wang, S., Hard, J. J., & Utter, F. (2002). Salmonid inbreeding: a review. *Reviews in Fish Biology and Fisheries*, 11, 301–319. doi: 10.1023/A:1021330500365

Ward, J. V. (1989). The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society*, 8, 2–8. doi: 10.2307/1467397

Ward, J. V., & Wiens, J. A. (2001). Ecotones of riverine ecosystems: Role and typology, spatio-temporal dynamics, and river regulation. *Ecohydrology & Hydrobiology*, 1, 25–36.

Wauer, G., Heckemann, H. J., & Koschel, R. (2004). Analysis of toxic aluminium species in natural waters. *Microchimica Acta*, 146, 149–154. doi: 10.1007/s00604-004-0198-2

Weatherley, N. S., Thomas, S. P., & Ormerod, S. J. (1989). Chemical and biological effects of acid, aluminium, and lime additions to a Welsh hillstream. *Environmental Pollution*, 56, 283–297. doi: 10.1016/0269-7491(89)90074-2

Weatherley, N. S., Rogers, A. P., Goenaga, X., & Ormerod, S. J. (1990). The survival of early life stages of brown trout (*Salmo trutta* L.) in relation to aluminium speciation in upland Welsh streams. *Aquatic Toxicology*, 17, 213–230. doi: 10.1016/0166-445X(90)90064-V

Webb, J., (1989). The movements of adult Atlantic salmon in the River Tay. *Scottish Fisheries Research Report*, 44. 1–32.

Webb, J. H., Gibbins, C. N., Moir, H., & Soulsby, C. (2001). Flow requirements of spawning Atlantic salmon in an upland stream: Implications for water-resource management. *Water and Environment Journal*, 15, 1–8. doi: 10.1111/j.1747-6593.2001.tb00296.x

Wedekind, C., & Mueller, R. (2005). Risk-induced early hatching in salmonids. *Ecology*, 86, 2525–2529. doi: 10.1890/04-1738

Weiss, L. C., Pötter, L., Steiger, A., Kruppert, S., Frost, U., & Tollrian, R. (2018). Rising pCO2 in freshwater ecosystems has the potential to negatively affect predator-induced defenses in Daphnia. *Current Biology*, 28, 327–332. doi: 10.1016/j.cub.2017.12.022

Westley, P. A. H., Ings, D. W., & Fleming, I. A. (2011). A review and annotated bibliography of the impacts of invasive brown trout (*Salmo trutta*) on native salmonids, with an emphasis on Newfoundland waters. *Canadian Technical Reports on Fisheries and Aquatic Sciences*, 2924, 81.

Wilby, R. L., Orr, H. G., Hedger, M., Forrow, D., & Blackmore, M. (2006). Risks posed by climate change to the delivery of Water Framework Directive objectives in the UK. *Environmental International*, 32, 1043–1055. doi: 10.1016/j.envint.2006.06.017

Willson, M. F., & Halupka, K. C. (1995). Anadromous fish as keystone species in vertebrate communities. *Conservation Biology*, 9, 489–497. doi: 10.1046/j.1523-1739.1995.09030489.x

Witzel, L. D., & MacCrimmon, H. R. (1983). Embryo survival and alevin emergence of brook charr, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, relative to redd gravel composition. *Canadian Journal of Zoology*, 61, 1783–1792. doi: 10.1139/z83-230

Wolter, C. (2014). Historic catches, abundance, and decline of Atlantic salmon *Salmo salar* in the River Elbe. *Aquatic Sciences*, 77, 367–380. doi: 10.1007/s00027-014-0372-5

Wood, C. M., & McDonald, D. G. (1987). The physiology of acid aluminium stress in trout. *Annales de la Société Royale Zoologique de Belgique*, 117, 399–410.

Youngson, A. F., Knox, D., & Johnstone, R. (1992). Wild adult hybrids of *Salmo salar* L. and *Salmo trutta* L. *Journal of Fish Biology*, 40, 817–820. doi: 10.1111/j.1095-8649.1992.tb02628.x

Zahn, S., Thiel, R., Kohlmann, K., Wolf, R., & Stäblein, S. (2017). *Wiederansiedlung von Lachs und Meerforelle in Brandenburg*. Potsdam-Sacrow, Schriften des Instituts für Binnenfischerei e.V.

Zimmermann, A. E., & Lapointe, M. (2005). Intergranular flow velocity through salmonid redds: sensitivity to fines infiltration from low intensity sediment transport events. *River Research and Applications*, 21, 865–881. doi: 10.1002/rra.856

5. Chapter III

Sneaker, dweller and commuter:
Fish behavior in net-based monitoring at hydropower plants

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5.1. Abstract

Monitoring of fish passage at hydropower plants largely relies on stow-fyke-net captures installed downstream of turbine outlets, yet little is known about which fish behaviour contributes to reduced catch efficiency. We studied fish-net interactions as well as biological and physical factors potentially influencing behaviour in three experiments: (i) fall-through experiment, to measure the general physical ability of a fish to fit through a certain mesh size; (ii) net-perception experiment, where fish were filmed while being exposed to different mesh sizes, flow and lure conditions in a controlled arena setup; and (iii) stow-fyke-net experiment, where fish behaviour was recorded using 20 cameras simultaneously inside a stow net during regular hydropower fish monitoring. In total, we analysed 382 h of video recordings. The material revealed that fish interacted with the net on a high rate, independent of flow conditions, and tried to swim through the mesh regardless of whether their body fits through. Under field conditions, the fish showed three specific behavioural patterns, “sneaking,” “dwelling”

and “commuting,” which led to a reduced recapture rate in the catch unit of the stow-fyke net. This study highlights the importance of considering fish behaviour in future fish monitoring programs to improve the accuracy of turbine-effect assessments on fish.

5.2. Introduction

In light of the controversy about the pros and cons of hydropower, a variety of monitoring programs have been initiated to examine the effects of conventional and innovative hydropower technologies on fish passage. Examinations of seasonal and diurnal patterns of fish passage (Knott et al. 2020), assessments of the acceptance of different corridors for downstream passage (Pander et al. 2013, Knott et al. 2019) as well as analyses of external and internal injury patterns after passage (Mueller et al. 2017, Bierschenk et al. 2019, Mueller et al. 2020c) all depend on stow-net catches of fish at hydropower facilities. Stow-net-based monitoring at hydropower turbine outlets in small- to medium-sized rivers is considered a gold standard to investigate turbine-related fish injury and bypass efficiency compared to camera or sonar-based technologies (Cramer & Donaldson 1964, Dubois & Gloss 1993, Dedual 2007, Egg et al. 2018).

A well-established approach for fish monitoring at hydropower plants includes the use of a full stow net, which forms the guiding unit, in combination with a fyke net, which is the catch unit. Emptying intervals vary widely, but recent studies point at the necessity of retrieving fish from these nets after rather short (i.e., hourly) intervals to avoid increased mortality and additional injuries (Pander et al. 2017.

Information on catch efficiency in stow-fyke nets used for hydropower monitoring are scarce (Egg et al. 2018, Pander et al. 2017). Besides the extreme hydraulic conditions at turbine outlets, which challenge the technical installation of stow-fyke nets, the catch efficiency of those can be highly dependent on unique onsite conditions, which determine the technical constraints for installation of the net. Additionally, fish behaviour may play a major role in catch efficiency. Both fish behaviour as well as net performance are most likely influenced by size, shape and material of the catch device, the amount and composition of floating debris, fish biomass, fish species and size, as well as exposure time (Holst et al. 1998, Pander et al. 2017). Pander et al. 2017 studied catch efficiency and fish damage in stow nets combined with different catch units. This study revealed that some stow-fyke nets had a catch efficiency of only 73%. More specifically, catch efficiency of the species Salmo trutta was 55.2% after 1 h and 26.2% after 12 h exposure time. Understanding the reasons of lower than expected catch rates in relation to fish behaviour is an important prerequisite in interpreting data from such monitoring, yet remains largely unconsidered.

Most scientific studies on catch efficiency focus on commercial fish catching methods and include analyses of mesh size selectivity of cod ends in trawl gear, and in gillnets. These studies usually use size selection models (mostly logit models) to predict at which body size and shape a fish will be retained by the gear (Jensen 1995, Wileman et al. 1996, Holst et al. 1998, Madsen 2007, Stepputtis et al. 2016). Thus, morphological features of diverse fish species (dead condition) and the change in mesh shape and size during fishing have been investigated to understand under which conditions a fish would fit through the mesh (Carol & García-Berthou 2007, Herrmann et al. 2009). Studies focusing on cod end selectivity are more common in marine science (Wileman et al. 1996, Stepputtis et al. 2016), while most studies from freshwater focus on gillnets and are conducted in lentic waters (Jensen 1995, Carol & García-Berthou 2007).

It is important to differentiate between the selectivity of the guiding unit and the actual catch unit in a stow-fyke net. Although small mesh sizes provide a higher catch efficiency, they increase the risk of net damage during high loads of debris or under unfavourable hydraulic conditions. Hence, the net is separated into different sections with different mesh sizes. The largest mesh sizes are located at the entrance, i.e., the front of the stow net and then gradually become smaller towards the tail, with the fyke net having the smallest mesh size. Hence, one would assume that fish would more likely escape or enter the net in the guiding unit, which is characterized by visible fibre and larger mesh sizes compared to the catch unit and thus easier to access by the fish. However, the risk of fish swimming through the meshes is typically ignored in studies on fish passage monitoring. The fish are thought to be disorientated after turbine passage and get quickly carried away by the current to net zones with smaller mesh sizes where they no longer fit through (Ebel 2013).

While selection models only allow conclusions on the probability of fish swimming through the net mesh, different kinds of fish behaviour have been observed during several stow-net experiments (e.g., Mueller et al. 2020a, Mueller et al. 2020b). These provide evidence that fish display a diverse set of behaviours that lead to them not being caught. For example, individual fish were observed escaping but also entering through the larger meshes of the net ("sneaker fish") or dwelling at a certain spot of the net that is not the catch unit ("dwellers"). This behaviour remained unconsidered in fish-monitoring practices at hydropower plants to date. Yet, if such behaviour frequently occurs, it is possible that it results in a bias towards underrepresentation of fish in the catch that passed the turbine with no or little injuries that are in turn more likely to escape from the net. The opposite, an underestimation of turbine effects in the total catch, can occur in the case of healthy fish entering the net from outside. These examples illustrate the importance of understanding fish behaviour in stow nets and its role in catch efficiency and turbine related fish injury estimations.

In this study, the fish behaviour and catch efficiency of stow-fyke nets were examined in relation to a fish's natural morphology ("fall-through experiment"), its willingness to approach and swim through fish nets ("net-perception experiment") and its overall movement profile in stow nets during standardised sampling conditions at a hydropower facility ("stow-fyke-net experiment"). Brown trout of different sizes were used as model species. It was hypothesized that: (i) brown trout interact with the net on a voluntarily basis by trying to swim through; (ii) larger brown trout differ in their behaviour from smaller brown trout corresponding to their greater ability for sustained and burst swimming; and (iii) catch efficiency is reduced when individuals show specific behavioural patterns, which prevent the fish from getting trapped in the fyke net (e.g., sneaking).

5.3. Materials and methods

Note: Supplementary materials of Chapter III are available electronically only. Please access via: https://www.mdpi.com/2071-1050/13/2/669

All experimental setups and fish handling in this study followed national standards (Adam et al. 2013) and laws as well as European guidelines (European Parliament 2010) for the use of aquatic animals for experimental purposes and were carried out under the official animal care permit number 55.2-1-54-2532-24-2015 (permit agency: Bavarian government/Regierung von Oberbayern).

The study involved a stepwise approach comprising three separate experiments. In the first experiment, we tested how physical features determine the ability of a fish to swim through a certain mesh size ("fall-through experiment" adopted from Herrmann et al. 2009). In the second experiment, we tested the net perception of fish and the influence of abiotic (flow velocity) and biotic factors (lure effect through conspecifics) on the frequency of brown trout swimming through the net ("net-perception experiment"). Finally, the third experiment investigated brown trout behaviour in stow nets under realistic field conditions during fish monitoring at hydropower plants ("stow-net and fyke-net experiment").

5.3.1. Study sites and model fish tested

The experiments were conducted between April and August 2019 at the Aquatic Systems Biology Unit of the Technical University Munich (48°23’39.7’’ N 11°43’25.4’’ E) and at the hydropower facility Höllthal Mühle, river Alz (47°58’40.9’’ N 12°30’09.9’’ E) in Germany.

Brown trout was selected as test species due to its wide distribution range, its ecological relevance as a target species for restoration in European streams and foremost for its role as model species in regular fish monitoring at hydropower plants (Birnie-Gauvin et al. 2018, Johnsson & Näslund 2018, Pander et al. 2017). Therein the species represents rheophilic fish with streamlined fusiform body shapes (Pander et al. 2017). We used hatchery-reared brown trout (*Salmo trutta fario* L.; Fisheries

Association Hatchery Mauka, Neufahrn, Germany) of three age classes 0+ (TL: 3–10 cm, mean 4.7 cm), 1+ (TL: 11–20 cm, mean 15.8 cm) and 2+ (TL: 21–30 cm, mean 25.6 cm) originating from the same batch. Each individual participated only once in an experiment to avoid bias by possible learning behaviour. The brown trout were held in ponds and not fed three days prior to and during experiments to reduce stress levels and to standardise the motivational state of the fish (Johnsson & Näslund 2018).

5.3.2. Experimental setups

5.3.2.1. Fall-through experiment

The fall-through experiment uses gravity to test whether or not a fish is physically able to fit through a mesh template in air (Herrmann et al. 2009, ICES 2011). This way, a selection curve can be generated to assess the physical probability of fish fitting through a net of specific mesh size. Prior to the test, all fish were anaesthetized by dissolved tricaine mesylate (MS-222) following the official directive on the protection of animals used for scientific purposes (European Parliament 2010). We tested 600 hatchery-reared brown trout of three age classes (50 fish per template) on four different templates of 10 mm, 15 mm, 20 mm and 30 mm mesh size. The number of fish used were calculated following the international recommendations NC3R (European Parliament 2010) to reduce the number of fish deemed necessary, still obtaining scientifically valid results. The templates were made of stretched net (green knotless nylon, diamond shaped, Engel-Netze GmbH & Co.KG, Bremerhaven, Germany) on a frame (40 x 30 cm) with a setting factor of 50% mesh opening (Table 5).

Table 5. Test-net properties
Net properties used in the fall-through experiment. All nets were of green knotless nylon, diamond shaped, and set to 50% mesh opening.

Template	**Mesh Size**	**Cord Diameter**
Template A	30 mm	1.3 mm
Template B	15 mm	0.8 mm
Template C	10 mm	0.5 mm
Template D	8 mm	0.8 mm

The properties (net type, cord diameter and mesh size) of the nets used were the same as those during the net-perception experiment and the stow-fyke-net experiment to allow direct comparability. The net template was positioned horizontally over a bucket filled with water. The fish were dropped head down from a distance of ca. 3 cm onto the net templates in air. The outcome of each tested fish was documented as either “successful” (the fish fell through the net into the bucket) or “unsuccessful” (the fish did not fall through the net).

5.3.2.2. Net-perception experiment

The arena for studying net perception and the number of fish voluntarily swimming through the net under controlled conditions was set up in a concrete channel (1100 cm x 160 cm x 40 cm) at the Aquatic Systems Biology Unit (Figure 20A). An overflow basin supplied the channel with fresh water from the nearby river Moosach. The water level in the channel was held constant at 38 cm and an even flow pattern was maintained by using perforated bricks. Flow velocity was adjusted by providing additional water into the overflow basin using Easy-Mix pumps (Heide Pumpen GmbH, Easy-mix U20W/F32T8). A camera (GoPro Hero 7 Black, GoPro Inc., San Mateo, CA, USA; settings: 1080 resolution, 30 frames per second, wide angle and active stabilizer) was placed on a wooden construction two meters above the arena. A pavilion (3 x 3 m, white folding pavilion with side parts) was placed above the setup to minimize external disturbances during the experiment. The arena and the acclimatization area were bounded by nets with 4 mm mesh size to maintain flow while making it physically impossible for fish to escape. The size of the arena was adjusted according to the three age classes of fish to avoid crowding and stress (Johnsson et al. 2014). The detailed calculations and dimension of the arena are provided in the Appendix 2, Figure A2. All nets (green knotless nylon, diamond shaped, Engel-Netze GmbH & Co. KG, Bremerhaven, Germany) used in this setup were attached to wooden frames (boundary nets = 160 x 30 cm; test nets = 200 x 30 cm) with a setting factor of 50% mesh opening. The respective net to test fish perception and fish-net interaction was placed diagonally in the middle of the arena, according to the angle the fish would encounter a stow-net wall in the field during fish monitoring (Figure 20A). We used the results of the fall-through experiment to only test mesh sizes on fish that can physically fit through the net to effectively reduce the amount of test fish needed. Hence, size 0+ brown trout were tested with three mesh sizes (15, 20 and 30 mm), 1+ brown trout encountered two mesh sizes (20 and 30 mm) and 2+ were exposed to the net with 30 mm mesh size. Further, we used three treatments to test if different environmental conditions had an influence on net perception and net interaction of fish. For treatment one, 15 fish were exposed to a given mesh size under stagnant water conditions (reference, flow velocity <1 cm s^{-1}). In the second treatment, 15 fish were exposed to a given mesh size at a flow velocity of 9 cm s^{-1}. During the third treatment, 10 fish were exposed to a given mesh size at a flow velocity of 9 cm s^{-1} and a lure factor. For the lure, we used five conspecifics, which were placed on the other side of the test net. Each combination of fish size, mesh size and treatment was replicated three times. Table 6 gives an overview of the combination of age class, mesh size and how many fish were used per treatment.

Before each round, brown trout of one age class (for treatment 1/treatment 2 = 15 individuals, treatment 3 = 10 individuals) were placed in the acclimatization area (Figure 1A) and left for 10 min. Afterwards, the camera recording was started and the net separating the fish from the arena was carefully removed. For treatment 3, five brown trout were additionally placed in the upper part of the arena to act as lure for their conspecifics. After 1 h, which is recommended for emptying intervals of nets in hydropower monitoring (Pander et al. 2017), exposure was terminated. At the end of each run, the remaining fish in the tailwater were given a stimulus to encourage swimming through the net. For this, a landing net was swiped gently from the right to the left corner at the lower border of the arena for30 sec. Afterwards, the recording was stopped and all fish were retrieved and measured to the nearest mm. Recordings were saved on hard drives in MP4 format. The experiment was repeated three times per mesh size and age class always using new fish with nonet-exposure experience. Abiotic factors (oxygen, pH, temperature, conductivity and flow velocity) were measured before each run at nine reference points within the arena. Measures were taken in the water column 10 cm above the channel bottom (Appendix 2, Figure A3).

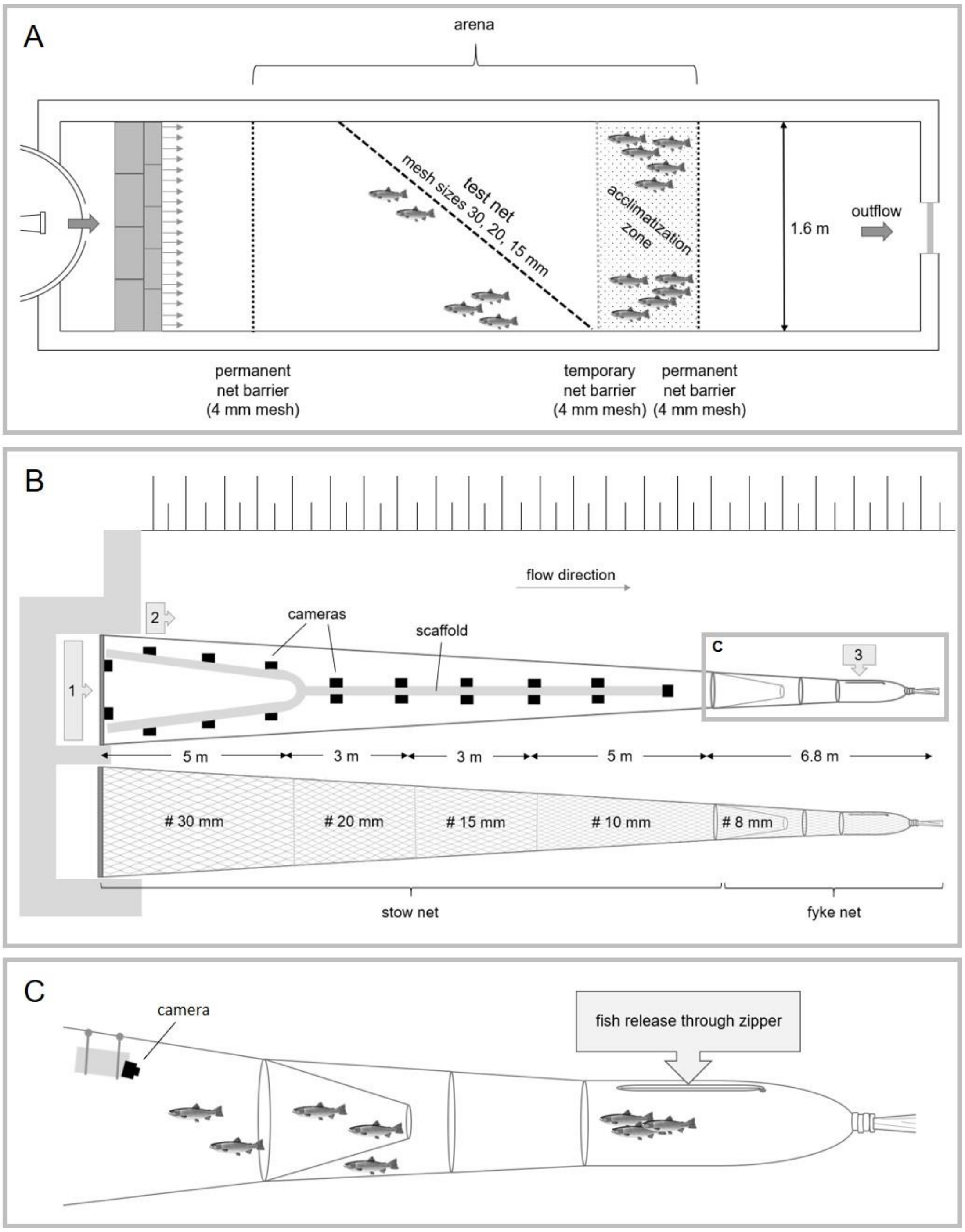

Figure 20. Illustrations of the three experimental setups for behavioural study
Setup (A) shows the concrete channel with the arena to test the willingness of fish through the test net. Setup (B) represents the Y-shaped scaffold with mounted cameras on position while recording fish movements inside the stow net, while 1 and 2 represent positions of fish release. Setup (C) shows the position of the camera and the point of fish release (3 in setup B) for the fyke-net experiment.

Table 6. Experimental details on the net-perception experiment
Details on the net-perception experiment including an overview of material and fish used. Information on the size per age class include the size range, the arithmetic mean and standard deviation (AM ± SD).

	Runs					
Mesh Sizes (mm)	**T1**	**T2**	**T3**	**n Fish (15 per run)**	**Age Class**	**Fish Total Length (cm)**
15, 20, 30	9	9	9	405	0+	3–10 (4.7 ± 0.5)
20, 30	6	6	6	270	1+	11–20 (15.8 ± 1.83)
30	3	3	3	135	2+	21–30 (25.6 ± 2)
	total runs 54			total fish 810		

5.3.2.3. Stow-fyke-net experiment

To investigate brown trout behaviour in stow nets under realistic field conditions, we filmed the inside of a stow-fyke net during fish monitoring at the hydropower plant Höllthal Mühle (river Alz, 47°58’40.9” N 12°30’09.9” E) in Germany. For this, two identical stow-fyke nets (green knotless nylon, diamond shaped, Engel-Netze GmbH & Co. KG, Bremerhaven, Germany; for gear specification see Pander et al. 2017) were attached to metal frames and installed in front of the turbine outlet covering 100% of the turbine outflow. The stow nets had a rectangular opening of 403 x 351 cm becoming narrower over a length of 16 m. The net ended at a metal ring of 65 cm diameter, to which the fyke net was subsequently attached. The mesh size distribution is illustrated in Figure 20B. The attached fyke net was 6.8 m long and had a mesh size of 8 mm. It had a funnel-shaped throat at the entrance and, could be closed with a rope at its end (cod end). In addition, the cod end had an integrated zipper, which can be used to remove floating debris. The experiment was conducted during regular plant operation. Electrofishing and pre-test catches with the stow-fyke net prior to the experiment revealed that only few brown trout were present in the sampled river section. Furthermore, these could be distinguished from the hatchery-reared test fish based on differences in body and fin shape as well as coloration. Influence of naturally occurring brown trout on the experiment was thus considered negligible.

For the first part of the experiment, 19 cameras (GoPro Hero 7 Black, GoPro Inc., San Mateo, CA, USA; 1080 resolution, 30 frames per second, wide angle and active stabilizer) were submerged in 20 cm water depth and evenly distributed in the orthographic left stow-fyke net. The cameras were placed two meters apart (to avoid image overlap) on a Y-shaped scaffold of commercially available drainage pipes (Ø 75 mm) filled with floating foam (Figure 20B). The device could be placed and retrieved from the net by hand. Each camera was assigned to a specific position indicated by a unique number. The view direction of 16 cameras was set towards the lateral net wall. The distance between camera and net ranged from 50 to 150 cm. Two additional cameras were placed at the front opening of the stow net at the metal frame. Both cameras were set to film straight into the net. Another camera was placed at the end of the scaffold to film the entrance to the fyke-net throat. Prior to the experiment, all cameras were synchronized.

Fish were released in front of the stow net (position 1, Figure 20B) and on the left outer side of the stow net (position 2, Figure 20B). For the latter, fish were marked with a fin clip at their upper lobe of the tail fin to be able to distinguish the fish released at the different positions later in the catch and possibly on the video recordings. The fish released at position 2 were used to test if fish also enter the net from the outside. The number of fish corresponds to the standards of fish tests at hydropower plants (Pander et al. 2017). For each of the three age classes, 50 specimens were released at each of the two positions (Figure 20B, pos. 1 and 2). The experiment was carried out 10 times, four times in the evening and three times in the morning and at noon, respectively. In total, 3000 fish (1500 per position) were tested. Prior to their release, fish were randomly selected and held in separate oxygenated tanks for ten minutes to acclimate.

After starting all cameras and placing the gear (camera scaffold) in the net, fifty unmarked fish of each age class were released at position A into the net and fifty marked fish were released at position B, outside the net. Time of camera start, the time the gear being on position in the net, time of fish release as well as river and weather conditions were recorded during each run. After one hour of exposure time, fish were retrieved from the cod end and we measured their total length to the nearest mm. The gear was retrieved and recorded material saved on hard drives in MP4 format. For each run, new fish with no net-exposure experience were used.

In the second part of the experiment, the behaviour of fish in the fyke net was observed to evaluate if the fish are able to escape the catch mechanism of the fyke-net throat. For this purpose, one action camera (GoPro Hero 7 Black, GoPro Inc., San Mateo, CA, USA; settings: 1080 resolution, 30 frames per second, wide angle and active stabilizer) was installed 30 cm in front of the connection ring between the stow- and fyke net, where the funnel-shaped throat starts. The camera was attached to a plastic pipe with view direction towards the fyke net as shown in Figure 20C. Ring diameter of the fyke net decreases from 65 cm to 60 and 55 cm over a length of 608 cm. The funnel-shaped throat of the fyke net was 105 cm long and starts at the first ring (diameter: 65 cm). It had a diameter of 40 cm at its entrance to the cod end. The visual range of the camera reached 150 cm and covered the full range of the throat. After the camera recording was started, 50 brown trout of age class 2+ were directly released into the cod end of the fyke net through the zipper opening (position C, Figure 20B). After an exposure time of an hour fish were retrieved from the cod end and total length of each specimen was measured to the nearest mm. The generated videos were saved on hard drives in MP4 format. The experiment was repeated 10 times always using new fish with no previous net-exposure experience. To prevent occurrence of escaped fish from one run in the subsequent one, the cod end remained open for at least 30 min between the experiments to allow any remaining fish to escape. We additionally checked the net for remaining fish before each run.

5.3.3. Data analysis

5.3.3.1. Fall-through experiment

The results of the fall-through experiment were used to model a logistic size selectivity curve including the parameters L_{50} (the length of fish at which 50% swam through the mesh size) and $L_{75} - L_{25}$ (the selection range, SR) (Wileman et al. 1996, Millar & Fryer 1999). The logistic regression model was computed using the generalized linear model (GLM) function in R. The selection curves provide the basis for determining the catch efficiency in the following experiments.

To predict if a fish of a certain size will fit through a mesh size, the following formula was used

$$L_r = \frac{\exp^{(\alpha + \beta L)}}{1 + \exp^{(\alpha + \beta L)}}, \tag{1}$$

where L_r is the probability that a fish of length L does fit ($L_r > 0.5$) or does not fit through ($L_r < 0.5$) a mesh size. The α (intercept) and β (slope) are estimated coefficients after a logit transformation. The tipping point L_{50} (the length of fish at which the probability to fit through the mesh is 50%) and the selection range $L_{75} - L_{25}$ (the length of fish at which the probability to fit through the mesh is 75% and 25%, respectively) are described by the following formulas (Wileman et al 1996):

$$L_{50} = -\alpha/\beta, \tag{2}$$

$$SR = L_{75} - L_{25}. \tag{3}$$

The logistic regression curve and model validation (deviance residuals, classification matrix, ROC curve, pseudo R^2) were computed using the statistical and graphical opensource software R (version 4.0.3, R Core Team 2020) including the following packages: extrafont (Chang 2014), ggplot2 (Wickham 2016), viridis (Garnier 2018), DescTools (Signorell et al 2018), boot (Davison & Hinkley 1997, Canty & Ripley 2020), caret (Kuhn 2020) and plotROC (Sachs 2017).

5.3.3.2. Net-perception experiment

Video recordings were examined using a standard video player (VLC media player x64 version 3.0.11). The video recordings were evaluated by one person. The time of occurrence and frequency with which the fish performed the following behaviours were noted: (i) fish swims through the net, (ii) fish unsuccessfully attempts to swim through the net i.e., the fish puts its snout/head through the net; and (iii) fish swims through the net after scare effect. We tested for behavioural differences depending on different abiotic and biotic factors using descriptive statistics. To test more generally if the age class or the treatment had a significant influence on the amount of net-interaction behaviour, we used non-parametric Kruskal-Wallis test as data was not normally distributed (Shapiro-Wilk test $p < 0.05$) and had heterogeneous variances (Levene's test $p < 0.05$). To identify which groups differed from each other, we used the Dunn's post-hoc test with Bonferroni correction. All analyses were computed using the statistical and graphical open-source software R (version 4.0.3, R Core Team 2020) including the following packages: extrafont (Chang 2014), ggplot2 (Wickham 2016), viridis (Garnier 2018), dunn.test (Dinno 2017), car (Fox & Weisberg 2019), dplyr (Wickham et al. 2020) and plyr (Wickham 2011).

5.3.3.3. Stow-fyke-net experiment

The recordings of the stow-fyke-net experiment were watched by multiple persons. All persons were previously trained by an expert in this field to recognize the fish in the video and to reduce potential observer effects. For the present study, the observer effect equalled 13% (average difference between the reported sightings of the expert and the trained observer after watching the same videos).

For video evaluation, the standard video player (VLC media player x64 version 3.0.11) was used. Each fish sighting was documented using a time stamp for the duration of occurrence within the visual range of the camera and by noting the position of a sighting (number of camera). Fish that were filmed in the process of just being released were not counted. On the video recordings, individual fish were observed escaping or entering through the meshes of the net (“sneaker fish”), dwelling at a certain spot of the stow net for >5 min (“dwellers”) or commuting (drift with the flow or/and swim against it) in the stow net or between the fyke net and the stow net (“commuter”).

For the recordings of the fyke-net experiment, additional notes were taken on fyke-net escaping attempts (fish left the fyke net and swam actively upstream into the stow net leaving the visual range of the camera) and “revenants” (fish drifting from the stow net back into the fyke net) and the duration of the observed behaviour.

5.4. Results

5.4.1. Fall-through experiment

The predicted selectivity curves computed from the results of the fall-through experiment are presented in Figure 21. GLMs correctly predicted whether the fish passed through the net at least 97% of the time (Table 7). For mesh size 30 mm, fish up to a total length of 23 cm were predicted to swim through the net; for mesh size 20 mm, fish up to a total length of 18 cm should fit through. Fish smaller than 8.6 cm were predicted to fit through meshes of 15 mm and fish smaller than 7 cm to fit through 10 mm meshes. The selection ranges and model validation values are summarized in Table 7.

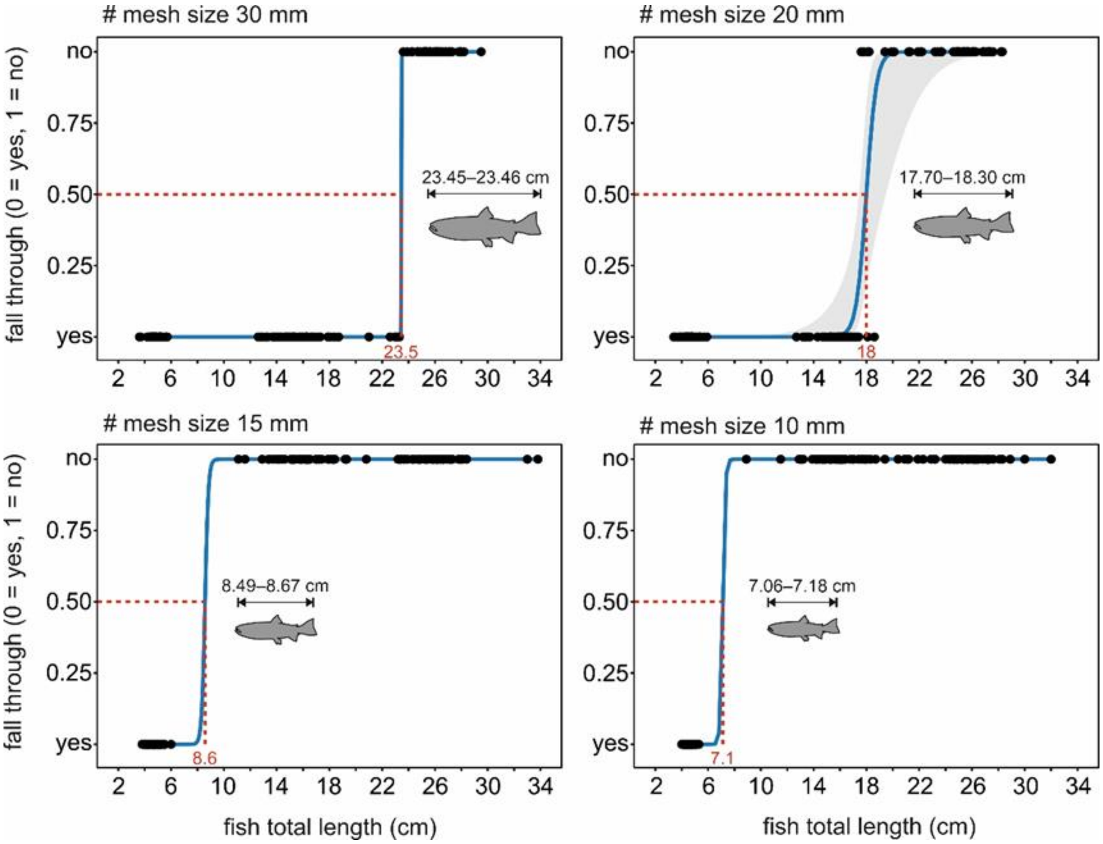

Figure 21. Logistic regression predicting fit-through by fish size
Logistic regression prediction plots showing which fish sizes (total length) fit through each of the four tested mesh sizes of 30 mm, 20 mm, 15 mm and 10 mm. Red dashed lines and numbers indicate the L_{50} values; the selection range $L_{75} - L_{25}$ is listed above the fish symbols. Grey area indicates the likelihood-based 95% confidence interval. Note that L_{50} values are based on model estimates. Due to the restricted availability of specimens in the size range of 6.0–11.1 cm for mesh size 15 mm (bottom left panel) and 5.3–8.9 cm for mesh size 10 mm (bottom right panel), the actual thresholds between fish fitting through and not fitting through the meshes are between 6.0–11.1 cm and 5.3–8.9 cm, respectively.

Table 7. Fall-through model validation summary and fit through thresholds

	# 30 mm	# 20 mm	# 15 mm	# 10 mm
L_{50}	23.45	18.00	8.58	7.12
$L_{25} - L_{75}$	23.45–23.46	17.70–18.30	8.49–8.67	7.06–7.18
pred. accuracy	1.00	0.97	1.00	1.00
α (intercept)	-2494.10	-47.53	-67.33	-77.26
β (slope)	106.30	2.64	7.85	10.85
explained deviance D^2	1.00	0.93	1.00	1.00
pseudo R^2				
McFadden	1.00	0.93	1.00	1.00
Nagelkerke	1.00	0.97	1.00	1.00
Cox & Snell	0.70	0.71	0.72	0.72

5.4.2. Net-perception experiment

Brown trout interacted with the net and it was possible to film several individuals of all age classes voluntarily swimming through the net from both sites (Supplementary Material Video S1–S3). Besides the voluntary passage, we observed fish, mainly of age class 2+, which were actually too large to swim through the present mesh size, yet trying by pressing their snout repeatedly against the net. Water chemistry remained constant throughout the experiments (Appendix 2, Table A2).

Based on 54 h of video recordings, an effect of mesh size and fish size, but not of treatments (flow velocity, lure effect) was detected. A summary of observed fish-net interactions in relation to the above mentioned factors is displayed in Figure 22. The scare effect mainly resulted in the smaller sized fish of age class 0+ and 1+ to escape through the meshes and had only little or no effect on 2+ brown trout (Dunn-Bonferroni $p > 0.05$). Neither the number of fish swimming through the net nor that of attempts to swim through the net differed among the three treatments (Kruskal-Wallis test, $p > 0.05$). Additionally, we compared the size distribution of fish that voluntarily swam through the experimental nets of mesh size 30 mm, 20 mm and 15 mm and the fish that did not swim through the net with the L_{50} value derived from the fall-through experiment (Figure 23).

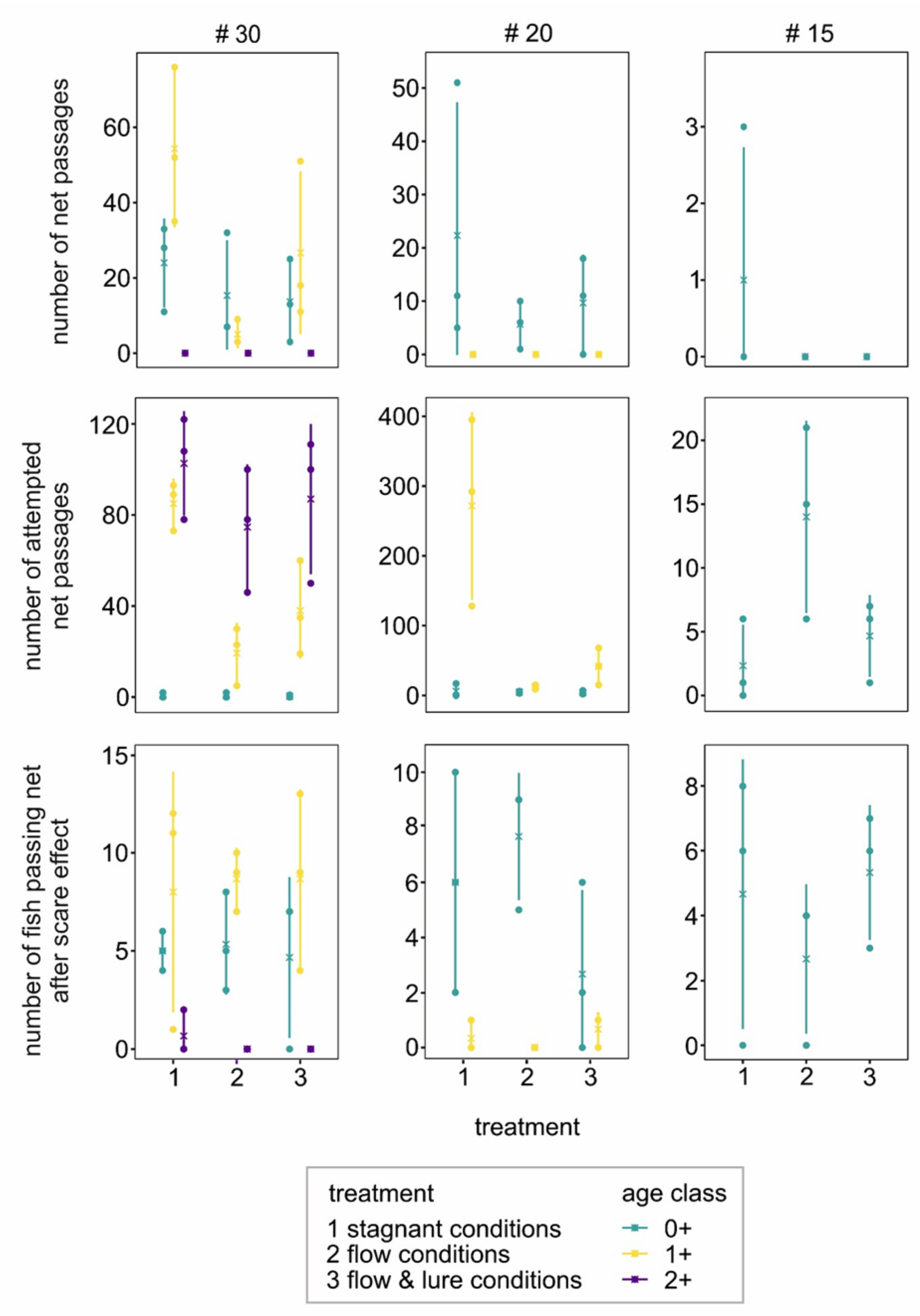

Figure 22. Fish-net interaction and swim-through events of brown trout

Fish-net interaction and swim-through events in relation to mesh size (#) 30 mm, 20 mm, 15 mm, treatment and fish age class. Displayed are the data points ($n = 3$ per treatment) with their corresponding mean and standard deviation. The size range of fish in each age class equalled: 0+ = 3–10 cm, 1+ = 11–20 cm, and 2+ = 21–30 cm.

Surprisingly also larger fish than expected from the L_{50} swam through the net. The prediction accuracy of which fish would fit through the net varied depending on the mesh size. For mesh size 30 mm, 6% of 267 fish that swam through the net should not have fit through according to L_{50}. For mesh size 20 mm, all fish that swam through the mesh were predicted to fit through. For mesh size 15 mm, however, 84% of the fish that swam through the net were above the L_{50} threshold and therefore should not have fit through the net. Probably, some of the 0+ and 1+ fish used their body flexibility to fit through the net. As expected, the majority of the fish (77%) that did not swim through the net were also classified to not fit through according to the L_{50} value. In turn, 33% of the fish that did not swim through the net may have fit through but simply refused to try.

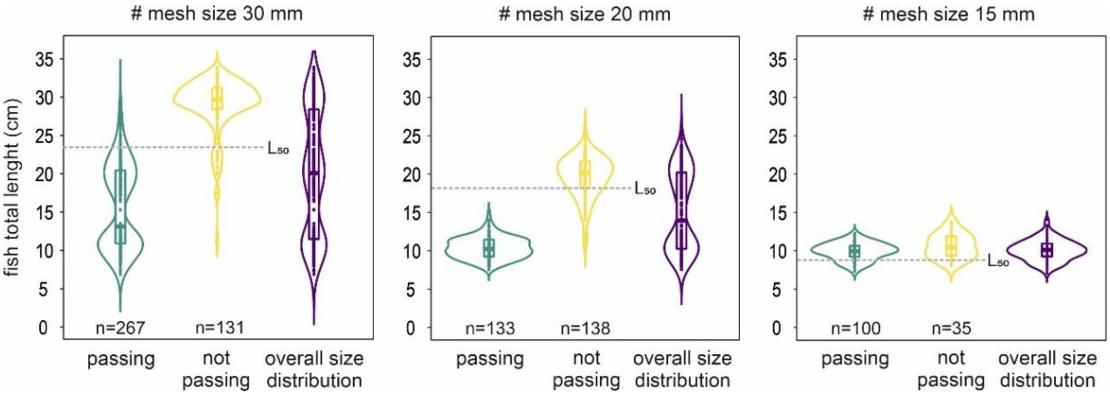

Figure 23. Size distribution of fish that voluntarily swam through the test nets
Size distribution of fish that voluntarily swam through the test nets (mesh size 30 mm, 20 mm, 15 mm), compared to the L_{50} value displayed as dashed line (the length of fish at which 50% fit through the mesh size) of the fall-through experiment.

5.4.3. Stow-fyke-net experiment

5.4.3.1. Fish behaviour in the stow net

We observed 940 fish (875 inside and 65 outside the stow net) on the video recordings. We categorized 93% as commuters, which would either drift with the flow or swim against the current and were in 99.5% of cases just visible for a few seconds. Dwellers were recorded on camera in low numbers ($n = 6$). However, they stayed in one place for an average of 17 min, with one fish exceeding the 60-min recording time. One sneaker fish was recorded when it actively entered the net from the outside

(Supplementary Material Video S4). In the cod end of the fyke net, 31 sneaker (marked) fish were caught (Figure 24). Sneaker fish were on average 4.9 ± 0.7 cm (0+ age class) and 14.3 ± 2.2 cm (1+ age class) in size. One fish was caught with a length of 25.7 cm (2+ age class). The total catch efficiency of the fish released directly into the stow net (position A, no fin clip) was 63 ± 14%, suggesting that 37% of them either sneaked out of the net or dwelled into the main net while the fyke net was retrieved (Figure 25).

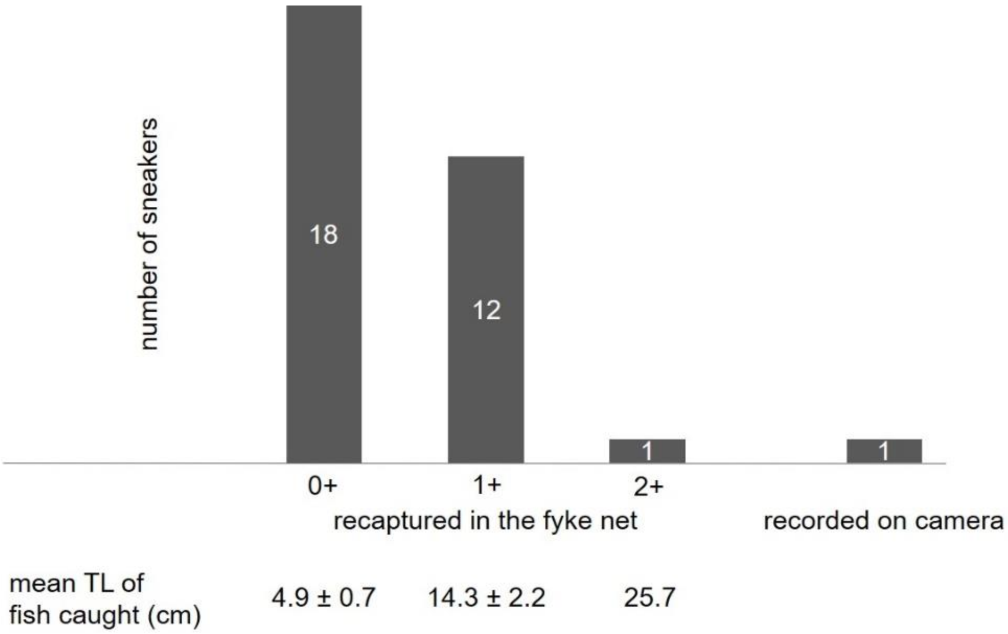

Figure 24. Bar plot representing number of recaptured “sneakers”
Sum of sneaking fish recaptured in the fyke net and visible on camera during the stow-net experiment. For recaptured fish, the average size per age class is provided.

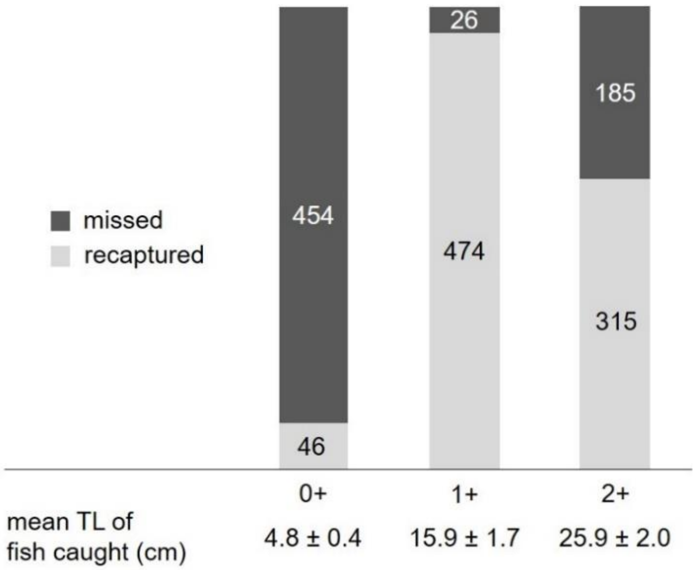

Figure 25. Stacked bar plot representing recaptured and missed brown trout
Stacked bar plot representing the number and size of recaptured brown trout in the fyke net and number of brown trout missed during the stow-net experiment. Originally, 500 fish were released per age class in front of the stow net (see Figure 20B, position 1). Abiotic parameters did not change significantly over the experimental period (Appendix 2, Table A3). Catch efficiency increased over the day from a relative average catch proportion of 50 ± 4% (mean SD) in the morning to, 62 ± 4% at noon and 79 ± 14% in the evening.

5.4.3.2. Fish behaviour in the fyke net

The catch data of the fyke-net experiment revealed that, in 8 of 10 cases, less fish were caught than previously released (Table 8). On average, 6% of fish were missed in the catch. In 7 of the 10 experiments, the entire throat of the fyke net was visible in the video frames and could thus be used for behavioural evaluation. Of the fish released, 16% were sighted escaping through the throat of the net. Successful escapes into the main net area were observed in 12% of the fish.

Table 8. Recapture rates of the stow-fyke-net experiment
Recapture rates and count of fish sighted escaping the fyke-net throat during the fyke-net experiment. Per run, 50 fish have been released. FC = number of fish recaptured after 1 h, FM (%) = percentage of fish missed compared to number of fish released, Esc. = number of fish trying to escape the fyke net, Succ. Esc. = number of successful escapers, Revenants = number of fish returning to the fyke net after the escape, Esc. 1 h = number of escaped fish after one hour (Succ. Esc.–Revenants). Runs, for which video data could not be collected, are indicated by '−'.

Run	FC	FM (%)	Esc.	Succ. Esc.	Revenants	Esc. 1h
1	48	4	-	-	-	-
2	44	12	13	12	8	4
3	45	10	12	7	3	4
4	48	4	6	5	2	3
5	47	6	-	-	-	-
6	49	2	-	-	-	-
7	46	8	3	3	1	2
8	50	0	9	5	1	4
9	45	10	12	10	4	6
10	50	0	3	3	4	−1*
Mean		6	8	6	3	3
SD		4	4	3	2	2

*one successful escaper (Succ. Esc.) in run 10 must have been missed in the video analysis potentially due to two overlapping fish and is here presented as '−1'.

The rate of fish escaping the fyke-net throat increased gradually as the experiment progressed in time and was highest after 50 min. Revenants (i.e., fish drifting back into the fyke net) showed a more dispersed patterns with no clear trend (Figure 26).

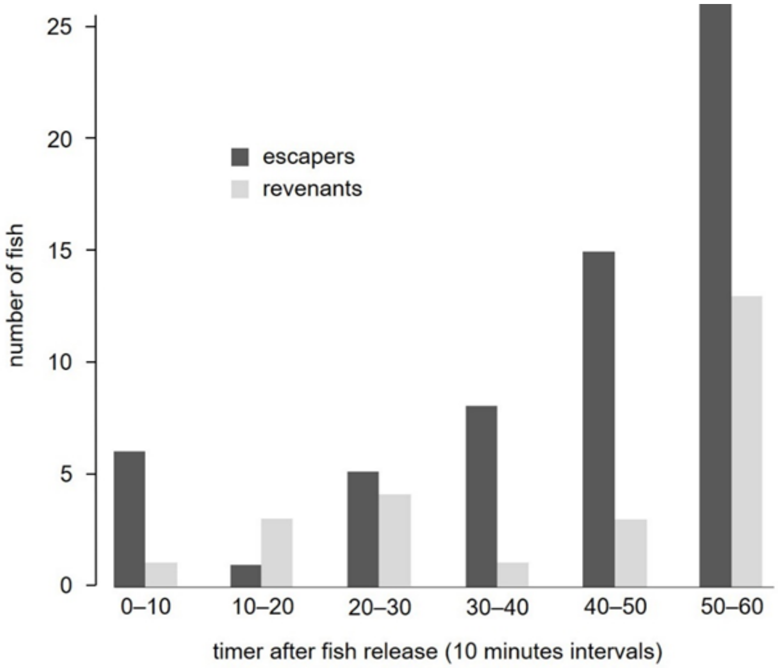

Figure 26. Number of fish escaping and returning over time
Timeline presenting the number of fish escaping the fyke-net throat (escapers) and drifting back into the fyke net (revenants) summed over 10-min intervals.

5.5. Discussion

Findings of this study confirm that fish of a size between 3 and 23 cm swim through the meshes of standardised stow nets to either enter or leave the net during regular fish monitoring of hydropower plants. As expected, the frequency and amount of fish swimming through the net thereby most strongly depend on the fish size as well as the mesh size. In addition, we were able to record other behavioural patterns, namely dwelling and commuting, which can lead to fish not reaching or escaping the catch unit of the fyke net.

The observed behaviour of fish escaping or entering the fishing gear as well as the occurrence of dwellers and commuters can bias the catch outcome and its interpretation. This includes interpretations concerning number and species of fish moving downstream as well as the assessment of fish mortality and injuries resulting from turbines. For example, if the catch includes fish that have entered the net from outside (sneaker), this may lead to an overrepresentation of unaffected fish, resulting in an underestimation of turbine effects. In turn, the presence of dwellers and commuters may lead to an overestimation of turbine effects, as the more agile and potentially less impacted fish are not caught in the catch unit.

Sneakers, fish that fit and swim through the net mesh of the stow net, occurred in the size range of 3–23 cm. While the stow-net mesh width gradually decreases, the net selectivity will naturally increase. Hence, fish < 7 cm (5.3–8.9 cm) fit through all meshes of the stow net. Fish < 18 cm fit through the 30 and 20 mm meshes, which account for ca. 50% of the total net area. Brown trout in the size range of 3–23 cm represent a large proportion or sometimes even 100% of the size distribution of natural brown trout populations (Geist et al. 2006, Birnie-Gauvin et al. 2018), making these findings highly relevant for fish populations in the wild. This holds also true for many other common stream fish not investigated here, e.g., European grayling (*Thymallus thymallus*), European nase (*Chondrostoma nasus*), European minnow (*Phoxinus phoxinus*), common roach (*Rutilus rutilus*), common dace (*Squalius cephalus*) and gudgeon (*Gobio gobio*) (Kottelat & Freyhof 2007). Knott et al. (2020) found that the average total length of downstream-moving fish was 10 ± 6 cm (mean ± SD) based on 39 fish species recorded in central European catchments. The chance that fish of those size ranges are physically able to escape the mesh during regular hydropower fish monitoring is consequently very high.

Sneaking behaviour is not necessarily linked to an escape reflex. In our study, the fish started to actively explore their environment after 10 min of acclimatization time. Some would swim through the meshes of the net or try to (often aggressively and repeatedly) by putting their snout through the mesh or by biting the net. The latter mainly occurred in fish >11 cm, which were too large to actually fit through the distinctive mesh sizes. Some fish were observed to force themselves through the net by turning their body to the side (Supplementary Material Video S4). This behaviour also explains why the logistic regression model of the fall-through experiment, excluding fish behaviour, underestimated the predicted size of fish fitting through the different mesh sizes in the net-perception experiment. In contrast to the fish that were dropped onto the net, free ranging fish can use their body flexibility and take advantage of the net flexibility to some extent. Length is a good indicator for net selectivity, but to obtain a more realistic prediction, it is recommended to use a specific measuring technique where both the largest circumference and the strongest bone structures are considered (Herrmann et al. 2009). However, this procedure is time consuming and requires special equipment.

Adjusting the mesh sizes to smaller meshes seems to be a logic consequence to minimize sneaking behaviour. Unfortunately, the extreme hydraulic conditions at turbine outlets determine the technical constraints for installation and design of stow-fyke nets. Hence, the size, shape and material of the catch device are manufactured to withstand a particular flow rate, pressure and amount of attached and floating debris (Pander et al. 2017). Thus, the possibility for net adjustments such as further decreasing mesh sizes are very limited.

In addition, other behaviour such as dwelling or commuting, which also contribute to a reduced recapture rate, must be considered. The results of the fyke-net experiment demonstrated that commuting behaviour can cause 6% of fish to be missed in the catch after 1 h. The exact effect of dwelling on the catch needs further investigation. Brown trout are strong swimmers that sustain swimming at flow velocities of 0.7 m s^{-1} for at least 200 min (Peake et al. 1997). Hence, brown trout could spend several hours in the stow net where flow velocities were on average 0.4 m s^{-1} (Table A2) without getting exhausted and drifting into the fyke net. Similar to the net perception experiment, fish needed some time to acclimate before they became active. Hence, the longer the fish are exposed to a novel situation, the higher the chance that they start to explore their environment and to show sneaking, dwelling or commuting behaviour. Our experiment also suggests an influence of daytime with an increase in the catch efficiency from morning hours to noon and evening, which may be explained by the diurnal activity patterns of fish that are well-known from other studies on fish passage (Knott et al. 2020 and references therein).

There are indications that personality of fish plays a role in explorative and reactive behaviour (Frase et al 2001, Sneddon 2003, Toms et al. 2010, Shamchuk & Tierney 2012, Näslund et al. 2015, Houslay et al. 2018). We observed that, on average, 16% of the fish actively explored and tried to swim through the mesh (bold individuals), while others would stay motionless at one spot (described as “freezing” in Houslay et al. 2018) or explore cautiously, not attempting to swim through the mesh. This held true for trying to swim though the net (net-perception experiment) as well as for escaping the fyke-net throat (fyke-net experiment). For example, a typical escape in the fyke net was characterized by the fish slowly entering the fyke-net throat, until it had passed the half-way point, to then burst swim upstream into the stow net. Besides these individuals with explorative nature, some fish (mainly in age class 1+ and 2+) in the net-perception experiment became active and tried to swim or swam through the net when a conspecific came to close or attacked them (with snout or flank).

Besides personality, other factors such as adaptation to specific flow conditions and health status can influence fish behaviour as well (Johnsson & Näslund 2018). As rheophilic fish, brown trout belong to the strong swimmers and are adapted to high flow rates. However, critical swimming speeds and the ability to burst swim are species-specific and can further be influenced by health status of the fish (Tudorache et al. 2007, Barber et al. 2017). For example, fish infested by parasites show a significant reduction in their critical swimming speed (Taeubert & Geist 2013, Bui et al. 2016), probably also affecting their behaviour inside of a net. Consequently, the variation in fish behaviour under natural settings is likely to even be greater than the one observed within our standardised experiments with one single species and specimens of the same origin and uniform good health condition.

It is assumed that during fish monitoring at hydropower plants, dead or injured fish will passively drift with the current and are then caught in the fyke net. However, depending on the flow current it is possible that dead fish do not reach the catch unit and are missed. Thus, further investigations on how fish condition influences the catch efficiency are highly recommended.

Certainly, there is a variety of factors that challenge the implementation of strategies to deal with the monitoring of bias caused by fish behaviour. However, great progress has been made in recent years in minimizing influential effects. One example is the standardisation of fish monitoring, where, besides the monitoring of the natural occurring fish fauna, standardised fish releases help to set turbine effects into relation to number of fish passing the hydropower plant. Hereby, selected species representing different body and size classes are released in known numbers (Holzner 2000, Pander et al. 2017, Knott et al. 2019). Further improvements were made by considering the health status of these fish following a standardised protocol including condition, parasite load and injuries (Mueller et al. 2017).

As supported by our findings, innovative technologies like camera- or sonar-based systems could be used to further improve fish monitoring at hydropower plants and set observed behavioural effects and catch efficiency into relation (Egg et al. 2018). However, some specific limitations need to be considered when selecting one of these methods and when interpreting the results. Possible limitations include turbidity conditions, imprecise recording of fish length and underrepresenting fish of size < 100–150 mm (both systems), light conditions (camera-based) or false detection inferences and signal masking (sonar-based) (Egg et al. 2018, Heinrich 2019). Sonar-based systems can be operated day and night and can cover areas of 5–15 m (e.g., ARIS Explorer; Schmidt & Schletterer 2020). However, in highly turbulent waters such as at turbine outlets, the acoustic signal is scattered by the gas bubbles forming in the water column and targets get readily masked behind the acoustic bubble cloud (Shen & Lemmin 1997, Sebastian & Caruthers 2001, Heinrich 2019). Although video cameras are limited to a visual range of 1.5–2 m in clear freshwater, the quality of the recorded objects is very high and species identification is possible. Automated video analysis systems are currently under development (Simon et al. 2020) and could reduce the workload significantly, making it a cheap and fast method for additional monitoring.

5.6. Conclusion

The three behavioural patterns – sneaking, dwelling and commuting – play a central role in fish not being caught in the fyke net and potentially bias fish monitoring results at hydropower plants. Fish can escape through the meshes (sneaking), dwell at a certain spot outside of the catch unit, or commute between the fyke net and the stow net. Whether these behavioural patterns occur is independent of the flow velocity or a lure effect in the case of sneaking behaviour. We assume that the occurrence of this behaviour is individual-specific and thus, relates to the personality of the fish (bold or shy individual). The exact motivation behind the observed behavioural patterns needs further investigation. However, to estimate the effects on the catch result and to improve the accuracy of turbine-effect assessments on fish, automated optical systems are needed in addition to the existing standardised fish monitoring programs to assess potential bias of the catch.

5.7. References

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

Barber, I., Mora, A.B., Payne, E. M., Weinersmith, K. L., & Sih, A. (2017). Parasitism, personality and cognition in fish. *Behavioural processes*, 141, 205–219. doi:10.1016/j.beproc.2016.11.012.

Birnie-Gauvin, K., Candee, M.M., Baktoft, H., Larsen, M.H., Koed, A., & Aarestrup, K. (2018). River connectivity reestablished: E ffects and implications of six weir removals on brown trout smolt migration. *River Research and Applications*, 34(6), 548–554. doi:10.1002/rra.3271.

Bierschenk, B.M., Pander, J., Mueller, M., & Geist, J. (2019). Fish injury and mortality at pumping stations: a comparison of conventional and fish-friendly pumps. *Marine and Freshwater Research*, 70(3), 449–458. doi:10.1071/MF18116.

Bui, S., Dempster, T., Remen, M., & Oppedal, F. (2016). Effect of ectoparasite infestation density and life-history stages on the swimming performance of Atlantic salmon *Salmo salar*. *Aquaculture Environment Interactions*, 8, 387–395. doi:10.3354/aei00184.

Canty, A., & Ripley, B. (2020). Boot: Bootstrap R (S-Plus) Functions; R Package Version 1.3-25. Retrieved October 1st, 2020 from: https://CRAN.R-project.org/package=boot

Carol, J., & García-Berthou, E. (2007). Gillnet selectivity and its relationship with body shape for eight freshwater fish species. *Journal of Applied Ichthyology*, 23(6), 654–660. doi:10.1111/j.1439-0426.2007.00871.x.

Chang, W. (2014). Extrafont: Tools for Using Fonts. R Package Version 0.17. Retrieved October 1st, 2020 from: https://CRAN.R-project.org/package=extrafont

Cramer, F. K., & Donaldson, I. J. (1964). Evolution of recovery nets used in tests on fish passage through hydraulic turbines. *The Progressive Fish-Culturist*, 26(1), 36–41. doi:10.1577/1548-8659.

Davison, A.C.; Hinkley, D.V. (1997) *Bootstrap Methods and Their Applications*. Cambridge, UK, Cambridge University Press. 594pp.

Dedual, M. (2007). Survival of juvenile rainbow trout passing through a Francis turbine. *North American Journal of Fisheries Management*, 27(1), 181–186. doi:10.1577/M05-174.1.

Dinno, A. (2017). dunn.test: Dunn's Test of Multiple Comparisons Using Rank Sums. R Package Version 1.3.5. Retrieved October 1st, 2020 from: https://CRAN.R-project.org/package=dunn.test

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(1), 178–185. doi:10.1577/1548 8675.

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

Egg, L., Pander, J., Mueller, M., & Geist, J. (2018). Comparison of sonar-, camera-and net-based methods in detecting riverine fish-movement patterns. *Marine and Freshwater Research*, 69(12), 1905–1912. doi:10.1071/MF18068.

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.

Fox, J., & Weisberg, S. (2019). An {R} Companion to Applied Regression, 3rd ed.; Sage: Thousand Oaks, CA, USA. Retrieved October 1st, 2020 from: https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N., & Skalski, G.T. (2001). Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *The American Naturalist*, 158(2), 124–135. doi:10.1086/321307.

Garnier, S. (2018). Viridis: Default Color Maps from ‘matplotlib’. R Package Version 0.5.1. Retrieved October 1st, 2020 from: https://CRAN.R-project.org/package=viridis

Geist, J., Porkka, M., & Kuehn, R. (2006). The status of host fish populations and fish species richness in European freshwater pearl mussel (*Margaritifera margaritifera*) streams. *Aquatic Conservation: Marine and freshwater ecosystems,* 16(3), 251–266. doi:10.1002/aqc.721.

Heinrich, A.J. (2019). *How Do Fish Interact with the Net?—First Approaches to Assess Fish-Net-Interactions in the Context of Hydropower Fish Monitoring*. Master Thesis. Freising, Germany, Technical University Munich. 68pp.

Herrmann, B., Krag, L.A., Frandsen, R.P., Madsen, N., Lundgren, B., & Stæhr, K.J. (2009). Prediction of selectivity from morphological conditions: methodology and a case study on cod (*Gadus morhua*). *Fisheries Research*, 97(1–2), 59–71. doi:10.1016/j.fishres.2009.01.002.

Holst, R., Madsen, N., Moth-Poulsen, T., Fonseca, P., Campos, A. (1998). *Manual for Gillnet Selectivity*; Brussels, Belgium, European Commission. 43pp.

Holzner, M. (2000). *Untersuchungen über die Schädigung von Fischen bei der Passage des Mainkraftwerks Dettelbach*. Doctoral Thesis, Freising, Germany, Technical University Munich. 351pp.

Houslay, T.M., Vierbuchen, M., Grimmer, A.J., Young, A.J., & Wilson, A.J. (2018). Testing the stability of behavioural coping style across stress contexts in the Trinidadian guppy. *Functional ecology*, 32(2), 424–438. doi:10.1111/1365-2435.12981.

ICES (2011). *Report of the Study Group on Turned 90° Codend Selectivity, Focusing on Baltic Cod Selectivity* (*SGTCOD), 4–6 May 2011*. Reykjavik, Iceland, IMR. 40pp.

Jensen, J.W. (1995). A direct estimate of gillnet selectivity for brown trout. *Journal of Fish Biology,* 46(5), 857-861. doi:10.1111/j.1095-8649.1995.tb01608.x.

Johnsson, J.I., Brockmark, S., & Näslund, J. (2014). Environmental effects on behavioural development consequences for fitness of captive-reared fishes in the wild. *Journal of Fish Biology*, 85(6), 1946–1971. doi:10.1111/jfb.12547.

Johnsson, J.I., & Näslund, J. (2018). Studying behavioural variation in salmonids from an ecological perspective: observations questions methodological considerations. *Reviews in Fish Biology and Fisheries,* 28(4), 795–823. doi:10.1007/s11160-018-9532-3.

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(21), 6037. doi:10.3390/su11216037.

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. doi:10.1111/eff.12489.

Kottelat, M., & Freyhof, J. (2007). *Handbook of European Freshwater Fishes*. Cornol, Switzerland, Publications Kottelat. 646pp.

Kuhn, M. (2020). Caret: Classification and Regression Training. R Package Version 6.0-86. Retrieved October 1st, 2020 from: https://CRAN.R-project.org/package=caret

Madsen, N. (2007). Selectivity of fishing gears used in the Baltic Sea cod fishery. *Reviews in Fish Biology and Fisheries*, 17(4), 517–544. doi:10.1007/s11160-007-9053-y.

Millar, R.B., & Fryer, R. J. (1999). Estimating the size-selection curves of towed gears, traps, nets and hooks. *Reviews in Fish Biology and Fisheries,* 9(1), 89–116. doi:10.1023/A:1008838220001.

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(3), 240–255. doi:10.1111/fme.12229.

Mueller, M., Knott, J., Egg, L., Bierschenk, B., Pander, J., & Geist, J. (2020a) *Fischökologisches Monitoring an Innovativen Wasserkraftanlagen: Band 1 Hintergrund und Methoden; Technical Report for Bayerisches Landesamt für Umwelt*. Freising, Germany, Technical University Munich.

Mueller, M., Knott, J., Pander, J., & Geist, J. (2020b) *Fischökologisches Monitoring an Innovativen Wasserkraftanlagen: Band 7 Eixendorf an der Schwarzach*;

Technical Report for Bayerisches Landesamt für Umwelt. Freising, Germany, Technical University Munich.

Mueller, M., Sternecker, K., Milz, S., & Geist, J. (2020c). Assessing turbine passage effects on internal fish injury and delayed mortality using X-ray imaging. *PeerJ*, 8, e9977. doi:10.7717/peerj.9977.

Näslund, J., Bererhi, B., & Johnsson, J. I. (2015). Design of emergence test arenas can affect the results of boldness assays. *Ethology*, 121(6), 556–565. doi:10.1111/eth.12368.

Pander, J., Müller, M., & Geist, J. (2013). Ecological functions of fish bypass channels in streams: migration corridor and habitat for rheophilic species. *River Research and Applications*, 29(4), 441–450.

Pander, J., Mueller, M., Knott, J., & Geist, J. (2017). 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(1), 31–43.

Peake, S., McKinley, R.S., & Scruton, D.A. (1997). Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. *Journal of Fish Biolog*y, 51(4), 710–723.

R Core Team (2020). R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria. Retrieved October 1st, 2020 from: https://www.R-project.org/

Sachs, M.C. (2017). plotROC: A tool for plotting roc curves. *Journal of statistical software*, 79, 1–19.

Schmidt, M.B., & Schletterer, M. (2020). Hydroakustik zur Analyse von Fischbeständen und Fischverhalten–Fallstudien aus Österreich. *Österreichische Wasser-und Abfallwirtschaft*, 72(5), 213–222. doi:10.1007/s00506-020-00670-z.

Sebastian, S.M. & Caruthers, J.W. (2001). Effects of Naturally Occurring Bubbles on Multibeam Sonar Operations. *Proceedings of the Conference MTS/IEEE Oceans, 5–8,* 1241–1247

Shamchuk, A.L., & Tierney, K.B. (2012). Phenotyping stimulus evoked responses in larval zebrafish. *Behaviour*, 149(10–12), 1177–1203. doi:10.1163/1568539X-00003016.

Shen, C., & Lemmin, U. (1997). Ultrasonic scattering in highly turbulent clear water flow. *Ultrasonics*, 35(1), 57–64. doi:10.1016/S0041-624X(96)00091-1.

Signorell, A., Aho, K., Alfons, A., Anderegg, N., Aragon, T., Arachchige, C., Arppe, et al. (2018). DescTools: Tools for Descriptive Statistics. R Package Version 0.99.38. Retrieved October 1st, 2020 from: https://CRAN.R-project.org/package=DescTools

Simon, J., Kopp, D., Larnaud, P., Vacherot, J.P., Morandeau, F., Lavialle, G., & Morfin, M. (2020). Using automated video analysis to study fish escapement through escape panels in active fishing gears: Application to the effect of net colour. *Marine Policy*, 103785. doi:10.1016/j.marpol.2019.103785.

Sneddon, L.U. (2003). The bold and the shy: individual differences in rainbow trout. *Journal of Fish Biology*, 62(4), 971–975. doi:10.1046/j.1095-8649.2003.00084.x.

Stepputtis, D., Santos, J., Herrmann, B., & Mieske, B. (2016). Broadening the horizon of size selectivity in trawl gears. *Fisheries Research*, 184, 18–25. doi:10.1016/j.fishres.2015.08.030.

Taeubert, J.E., & Geist, J. (2013). Critical swimming speed of brown trout (*Salmo trutta*) infested with freshwater pearl mussel (*Margaritifera margaritifera*) glochidia and implications for artificial breeding of an endangered mussel species. *Parasitology Research*, 112(4), 1607–1613. doi:10.1007/s00436-013-3314-6.

Toms, C.N., Echevarria, D.J., & Jouandot, D. J. (2010). A methodological review of personality-related studies in fish: focus on the shy-bold axis of behavior. *International Journal of Comparative Psychology*, 23(1), 1–25.

Tudorache, C., Viaene, P., Blust, R., Vereecken, H., & De Boeck, G. (2008). A comparison of swimming capacity and energy use in seven European freshwater fish species. *Ecology of Freshwater Fish*, 17(2), 284–291. doi:10.1111/j.1600-0633.2007.00280.x.

Wickham, H. (2011). The split-apply-combine strategy for data analysis. *Journal of Statistical Software*, 40(1), 1–29.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. New York, NY, USA, Springer. 224pp.

Wickham, H., François, R., Henry, L., & Müller, K. (2020). Dplyr: A Grammar of Data Manipulation. R Package Version 1.0.2. Retrieved October 1st, 2020 from: https://CRAN.R-project.org/package=dplyr (accessed on 1st October 2020)

Wileman, D.A., Ferro, R. S.T., Fonteyne, R., Millar, R.B. (1996). *Manual of Methods of Measuring the Selectivity of Towed Fishing Gears*. ICES Cooperative Research Report, 215. Copenhagen, Denmark, ICES. 132pp.

5.8. Appendix 2

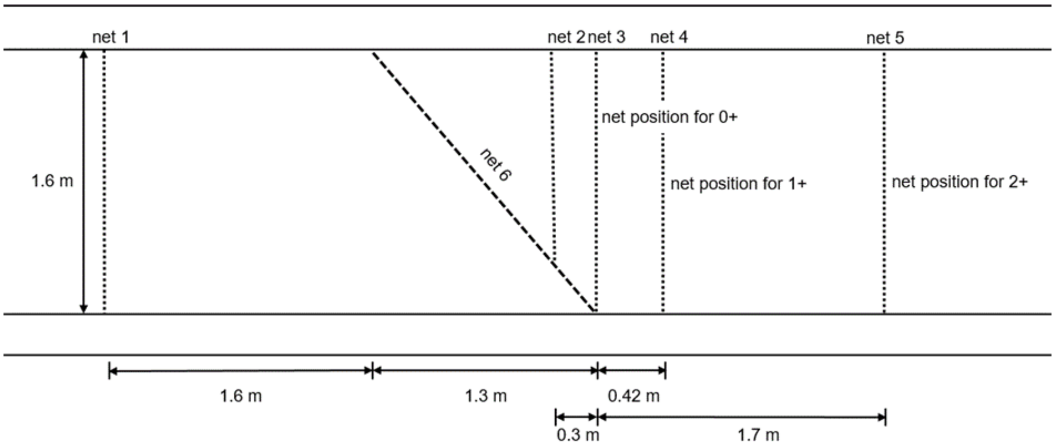

Figure A2. Detailed dimensions of the arena build for the net-perception experiment in a concrete channel. Nets were placed in rails and were therefore flexible in use. Net 1 was permanent and determined the upper boundary of the arena. The lower boundary was set corresponding to which age class of fish was tested. For age class 0+, net 3 defined the lower boundary of the arena, the position of net 4 was used when testing 1 + fish and net 5 was used for 2+ fish. The boundary nets were made of 4 mm mesh size. Net 6 represents the position of the test net, which was changed according to the treatment. The test nets had a mesh size of 30 mm, 20 mm or 15 mm, respectively. Prior to the experiment, the fish were acclimatized for 10 min in a defined area of the arena. Fish of age class 0+ were acclimatized in the area between net 2 and net 3, 1+ fish in the area between net 3 and net 4 and 2+ fish in the area between net 3 and net 5. After the acclimatization time, net 2 or net 3 were removed and fish were able to start exploring the arena.

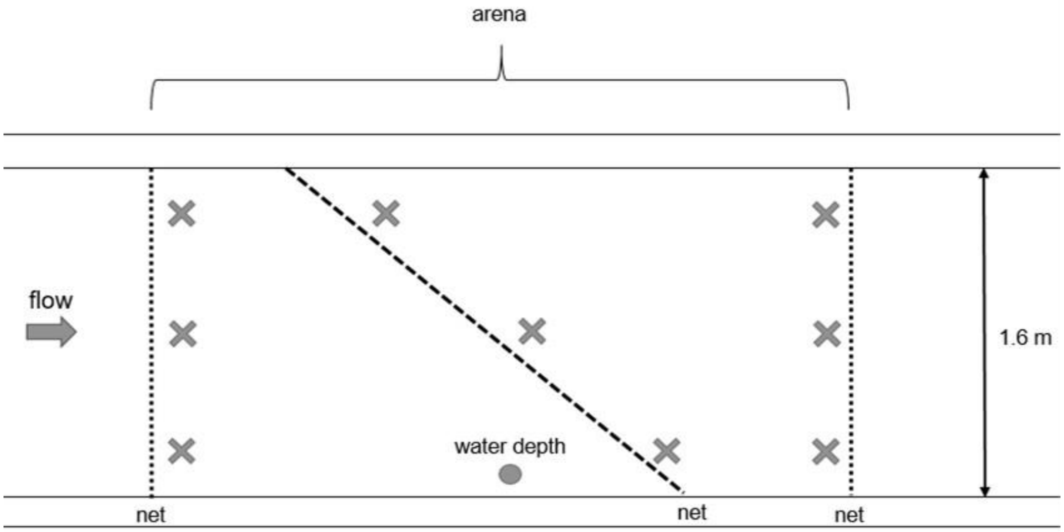

Figure A3. Measurement positions for abiotic factors in the concrete channel during the net perception experiment. The cross symbols indicate the nine measurement positions for oxygen, pH, temperature, electric conductivity and flow velocity. All factors were measured 10 cm above the channel bottom. Water depth was measures at the position of the circle.

Table A2. Arithmetic mean and standard deviation for abiotic parameters measured during the net-perception experiment ($n = 486$ per parameter).

Parameter	Mean ± SD
temperature (C°)	15.6 ± 1.0
dissolved oxygen (mg·l^{-1})	9.3 ± 0.7
electric conductivity (µS·cm^{-1})	780.2 ± 12.3
pH value	8 ± 0
flow velocity (cm·s^{-1}) treatment 1	1.7 ± 2.1
flow velocity (cm·s^{-1}) treatment 2	8.9 ± 3.7
flow velocity (cm·s^{-1}) treatment 3	9.0 ± 1.5

Table A3. Abiotic data measured during the stow-fyke-net experiment.

	Turbidity (NTU)	Oxygen (mg l^{-1})	Temp (°C)	pH	Conductivity (µS cm^{-1})
Day 1	4.89	12.23	7.20	8.41	365
Day 2	6.08	12.15	8.10	8.51	362
Day 3	5.83	11.90	8.00	8.50	362
Day 4	8.35	12.13	8.00	8.54	361

	Discharge (m^3 s^{-1})	Flow velocity stow net (m^3 s^{-1})	Flow velocity fyke net (m^3 s^{-1})
Day 1	91.40	0.46	0.34
Day 2	92.50	0.46	0.07
Day 3	92.50	0.34	0.43
Day 4	92.50	0.20	0.46

6. Chapter IV

Evaluating cost trade-offs between hydropower and fish passage mitigation

TERESE E. VENUS, NICOLE SMIALEK, JOACHIM PANDER,
ATLE HARBY AND JUERGEN GEIST

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6.1. Abstract

To promote the sustainable management of hydropower, decision makers require information about cost trade-offs between the restoration of fish passage and hydropower production. We provide a systematic overview of the construction, operational, monitoring and power loss costs associated with upstream and downstream fish passage measures in the European context. When comparing the costs of upstream measures, nature-like solutions (67 – 88 €/kW) tend to cost less than technical solutions (201 – 287 €/kW) on average. Nature-like fish passes furthermore incur fewer power losses and provide habitat in addition to facilitating fish passage, which strongly argues for supporting their development. When evaluating lifetime costs of fish passage measures, construction (45 – 87 %) accounts for the largest share compared to operation (0 – 1.2 %) and power losses (11 – 54 %). However, under a high electricity price scenario, power losses exceed construction costs for technical fish passes. Finally, there tends to be limited information on operational, power losses and monitoring costs associated with passage measures. Thus, we recommend that

policymakers standardise monitoring and reporting of hydraulic, structural and biological parameters as well as costs in a more detailed manner.

6.2. Introduction

While hydropower represents the largest renewable energy source in Europe, it also poses risks to river ecosystems, an array of animal species, and the downstream transport of sediments (Anderson et al. 2015). To ensure the sustainability of future hydropower development, ecological targets have been established. The primary political instrument is the EU Water Framework Directive (Directive 2000/60/ EC, WFD), which, among other goals, mandates an improvement in the ecological status of waters including the restoration of fish passage and river connectivity of European rivers. While many studies focus on technical advancements and ecological assessments of fish passage technologies (Trussart et al. 2002, Renöfält et al. 2010, Person et al. 2014, Schramm et al, 2016, Beck et al. 2018, Silva et al. 2018), there has been limited research on the costs of these measures in the European context (Nieminen et al. 2017). However, it is important for decision makers to understand the trade-offs between restoring fish passage and hydropower production when they establish and plan cost-effective mitigation measures. Despite worldwide hydropower operation and mitigation programs, overviews of costs related to fish passage measures mainly come from North America (Nieminen et al. 2017). However, it can be problematic to translate costs from one region to another, given differences related to legal and political frameworks, technologies, and input costs (i.e., land, labour, materials).

Across countries, there are differing degrees of environmental regulation related to hydropower. While some countries require mitigation for facilitating fish passage and ensuring flow release, others lack formal rules (Anderson et al. 2015, Couto & Olden 2018). Further, a variety of incentives, including competitive tariffs, private sector investments, rural electrification programs, and simplified licensing processes, have been used to incentivize the development of small hydropower (Couto & Olden 2018). In Europe, there are established guidelines for habitat protection in rivers as well as targets for the expansion of renewable energy under the recast RED II (Directive (EU) 2018/2001) of the Renewable Energy Directive (Wüstenhagen &

Bilharz 2006, EU 2009, Rudberg et al. 2015, Kampa et al. 2017), which have led to incentives for the development of small hydropower. For example, the German Renewable Energy Act facilitated the implementation of small hydropower facilities by providing feed-in tariffs for small hydropower, which were linked to ecological improvements and the restoration of fish passage (Wüstenhagen & Bilharz 2006, Manzano-Agugliaro et al. 2017). In contrast, Brazil and India do not require a full environmental impact assessment for licensing of small hydropower plants, while small plants (less than 10 MW) are exempt from some licensing requirements in the United States (Erlewein 2013, Couto & Olden 2018).

Another difference is related to technology. Many of Europe's hydropower plants are often run-of-the-river (also called diversion) schemes (Manzano-Agugliaro et al. 2017), whereas the United States holds a greater share of large reservoir schemes (Uria-Martinez et al. 2018). In the literature, there are mixed findings as to whether the size and technology of hydropower affect its ecological impact and public acceptance (Bilotta et al. 2016, Venus et al. 2020). However, given the financial incentives to build small hydropower plants across Europe, there is growing concern that cumulative effects can occur (Anderson et al. 2015) in addition to the significant environmental impacts of individual plants.

Construction costs may also differ between the United States and Europe. According to the Power Capital Costs Index, the average cost for building a power plant between 2000 and 2013 increased by 226% in North America compared to 193% in Europe (Sovacool et al. 2014), which implies that trends in construction costs differ. Further, land availability has been noted as one of the key factors for determining how and where river restoration will be conducted (Sudduth et al. 2007). Given the greater availability of land in the United States, it is likely that land acquisition will be more expensive in Europe (Cai et al. 2011).

For fish passage measures, there are various costs. We distinguish between financial and economic costs, which can be non-recurring and recurring. Non-recurring costs refer to costs that occur once and are not expected to be incurred again. Recurring costs refer to ongoing, regular costs incurred usually on an annual basis. Financial costs include capital (pre-construction and construction), operational (management, monitoring, maintenance), and other expenses (compensation of land and habitat, legal work). Most reports focus primarily on planning, construction, and maintenance costs (Nieminen et al. 2017) with no or limited consideration of monitoring, effectiveness, and power losses.

However, economic costs related to reduced power production and system flexibility may represent a significant loss for operators (Pérez-Díaz et al. 2010, Olivares 2008), and are thus likely to influence decision processes related to the construction of hydropower facilities as well as investment in mitigation measures. When measures modify water flow, they can reduce power production (Renöfält et al. 2010). Depending on their design, some measures may not require flow releases, while others may redirect significant amounts of water. These power losses can be highly site-specific, dependent on the head, storage capacity, inflow, season (dry or wet periods), the type of required operation, and the power market (Hirth 2016). The revenue losses associated with reductions or changes in timing of power production are highly dependent on the power market. When revenue losses are calculated based on the hourly energy prices of the day-ahead market, they can vary significantly, based on the hour, day, month, and year (Pérez-Díaz et al. 2010). The timing of lost power production may also reduce overall system flexibility as dispatchable power plants (including hydropower) help to balance variability in renewable energy sources (Hirth 2016). When there is greater demand for water (e.g., dry season, additional water needed for the fish passage facility), some flexibility may be lost. Further, the extent to which flexibility is reduced depends on the type of hydropower plant. As run-of-the-river hydropower plants are not typically used to cover peak demand, we will not quantify the value of lost system flexibility.

Cost-effective fish passage design must balance several objectives: overcoming the fall height and minimizing the length of the fish pass, effects on hydraulic conditions and costs (DWA 2014). There are different approaches to designing fish passage facilities. Traditionally, design is based on species-specific formulas (DWA 2014), which consider fish-specific traits including the duration of migration (long/short), size (small/large), swimming ability (strong/weak), and orientation (pelagic/benthic) (Clay 1995). However, others advocate for the integration of natural variation in fish passage design (Birnie-Gauvin et al. 2019).

Varieties of measures to facilitate fish passage across barriers in rivers exist. We distinguish between upstream and downstream fish passage measures. Upstream measures may also support downstream passage but their design (e.g., placement in the river, position of entrance) is optimized for upstream passage. Following the nomenclature of fish passes proposed by the Food and Agriculture Organization of the United Nations, we distinguish between technical, nature-like, and special designs for upstream fish passages (FAO 2002).

Technical designs for upstream passage include roughened ramps with pool structures, vertical slot passes, and Denil (i.e., baffle) passes. Pool passes are the most common technical design, in which fish move upstream from pool to pool (Birnie-Gauvin et al. 2019). The vertical slot fish pass is another common technical design that enables passage through a vertical, top-to-bottom opening (Linnansaari et al. 2015). Roughened ramps with pool structures are designed similar to slot passes but with natural materials (e.g., pool transitions are formed by more or less strongly dissolved stone bars) (Clay 1995). Denil passes are suitable for low head heights and larger species (i.e., >30 cm in length).

In our case studies, nature-like fish passes include roughened bypass channels with pool structures as well as combined roughened bypass channels with pool structures and vertical slot passes (mostly built at the entrance and the outlet of the fish pass). Such nature-like fish passes use natural materials like boulders and rocks to dissipate energy, provide habitat, facilitate the natural displacement of material (e.g., sediment transport), and support structural changes (e.g., displacement of gravel banks, development of riparian vegetation, and deadwood dynamics). They include three types: rock (bottom) ramps, fish ramps, and bypass channels (DWA 2014). While rock and fish ramps are more suitable for small differences in the height of the head and tailwater, bypass channels can be built to overcome larger obstacles. However, long natural bypass channels may result in high construction and land acquisition costs (Linnansaari et al. 2015).

Fish locks, lifts, screws, pumps, and canons are considered special solutions. As non-volitional passage structures, they transport fish upstream using mechanical means rather than voluntary swimming (Linnansaari et al. 2015).

Compared to upstream passage, measures to support downstream passage tend to be less advanced (Larinier & Travade 2002). This is in part due to downstream moving fish following the main current, the complexity of design, and the view that fish can pass downstream via the turbines (Lundström et al. 2010, Katapodis & Williams 2012). However, passage via the turbines is likely to lead to serious injuries or death (Mueller et al. 2017, Boys et al. 2018). Downstream fish passage can be facilitated either actively (i.e., with screens, louvers, sensory or behavioural barriers, and other guidance structures) by adapting power intake solutions with special design of trash racks, or passively with water release to provide attraction flow and operation of the hydropower infrastructure (Williams et al. 2012).

Our review of downstream measures includes bypasses, fish protection screens/racks, combined screens/racks with bypass systems, and guiding walls/dams. Bypasses refer to systems that funnel fish downstream usually via pipes, gates, or open channels (Linnansaari et al. 2015). The type of passing fish will affect the costs of a bypass facility based on their flow preferences (Enders et al. 2009). Additionally, maintenance costs may be incurred when drifting debris blocks the bypass and must be removed (Larinier & Travade 2002). On the other hand, fish protection screens/racks directly block fish from turbine intakes using physical structures made of plastic, metal, wedge wire, or bars (Larinier & Travade 2002). Combined screen/rack bypass systems use a mixture of both technologies. Guiding walls or dams are used to deflect species that tend to migrate close to the water surface (Dewitte 2018). The walls repel and guide fish to a nearby bypass channel. The success of these downstream measures in fish protection and facilitating the undisturbed passage of fish is controversial and generally considered to be rather low (Fjedstad et al. 2018). Although significant progress has been made in the past decade to improve downstream passage technology, the costs of these measures often fuel debate about their necessity.

Following the categories of fish passage measures described, our study reviews costs of 327 case studies from European hydropower plants. To our knowledge, most studies in the European context have primarily outlined individual case studies. Further, recent literature on the costs of measures to support migratory fish has mainly focused on financial costs associated with passage measures, while potentially significant economic costs were not considered. To shed light on the cost trade-offs associated with sustainable hydropower, we compare the costs of technical and nature-like fish passage measures. Given our limited data about special passes, we cannot draw conclusions about them in this comparison. We investigate the extent to which unit metrics are useful for predicting construction costs and how planning costs differ from actual costs. As they are a common reference point for many operators, we hypothesize that unit metrics can accurately predict costs. Further, we compare how different types of costs (construction, maintenance, power and income losses) contribute to lifetime mitigation costs. To estimate the costs associated with power losses, we compare power losses under low and high electricity price scenarios. We hypothesize that construction and power losses account for the largest shares. Finally, we hypothesize that technical measures for fish passage show lower construction costs than their nature-like counterparts. This is because nature-like measures may require additional land, which can be expensive to acquire (DWA 2014). Further, planners can standardise technical measures across sites, thus incurring fewer costs during the planning stages.

6.3. Materials and methods

6.3.1. Data acquisition

We compared the costs of building, maintaining, and monitoring fish passage measures using 327 case studies (Germany: 151, Austria: 101, Sweden: 58, France: 16, Switzerland: 1). The data were collected from available reports and through a questionnaire sent to European hydropower operators and from a search of online available data. The German data came from the Thüringen State Office for the Environment, Mining and Nature Conservation, which published reports and data on the planned costs of river connectivity measures for various rivers, including the Ilm, Saale, Unstrut, Werra, Gera, Apfelstädt, and Ohra Rivers (Bauerfeind et al. 2011, Anderer et al. 2013, Schmalz 2015, Schmalz & Sauerwein 2015, Reuter & Schmalz 2017). (The data can be accessed on Thüringer State Office for the Environment, Mining and Nature Conservation (Landesamt für Umwelt, Bergbau und Naturschutz)'s website at https://tlubn.thueringen.de/wasser/fluesse-baeche/durchgaengigkeit/) The Austrian data came from the Österreichs Energie (Österreichs Energie 2009) reports about the National Water Management Plan 2009, which reviewed a total of 133 measures for the implementation of the Water Framework Directive. This analysis did not include all Austrian measures as some of them were related to flow and habitat improvements. The Swedish, French, and Swiss data were collected using an online questionnaire with operators (Vattenfall) and the French small hydropower association (France Hydro Electricité). While the data were not representative for all of Europe or the respective countries, they covered a variety of geographic areas (Alpine region, Scandinavia, France), plant sizes (3.5 kW to 5.88 GW), and technologies (reservoir and run-of-the-river). Table A4 in Appendix 3 lists the case studies used in our analysis by country, capacity, and measures type. Because the data came from different sources, it is important to note that some observations are missing variables. Thus, the number of observations is noted at each stage of our analysis.

6.3.2. Types of costs

Financial and economic costs are associated with upstream and downstream passage facilities. Table 9 outlines the specific types of financial and economic costs associated with both. Notably, there were differences for maintenance, legal costs, as well as compensation for land and habitat. Certain downstream measures may not have required any or very little maintenance like passive downstream measures such as guiding walls/dams. On the other hand, downstream measures like screens/racks may have incurred recurrent maintenance costs associated with removing debris and cleaning the screen/rack, unless they were self-cleaning (Larinier & Travade 2002). Further, downstream measures were unlikely to incur legal costs or require compensation for land and habitat as they normally do not require additional space.

Table 9. Financial and economic costs of fish passage measures
Financial and economic costs associated with upstream and downstream fish passage measures. Note: 2 indicates obligatory associated costs; 1 indicates facultative associated cost, and 0 indicates no associated costs.

Category	Sub-Category	Types of Costs	Upstream	Downstream
Financial	Capital	Pre-construction	2	2
		Construction	2	2
	Operational	Management	1	1
		Monitoring	2	2
		Maintenance	2	1
	Other	Legal costs	2	0
		Compensation for land and habitat	2	0
Economic		Lost power production	2	2
		Lost system flexibility	1	0

6.3.3. Data analysis

Before analysis, we deflated our cost data (1992–2017) to 2019 Euro values to adjust for changes in values over time. We first deflated the data to the base year (2019) using average yearly inflation rates based on the Consumer Price Index (CPI) in the respective countries in the year of costing (Turner et al. 2019). We assumed that the start year of the project was the year of costing as planners tend to make decisions based on cost estimates made in the first year of construction. For the Swedish data, we then converted Swedish krona (2019) to Euros using the average 2019 exchange rate after deflating the data. The Swiss data were already reported in Euros. As we indicate which countries the costs come from, we did not correct for purchasing power parity between countries.

6.3.3.1 Analysis of non-recurring costs

First, we discussed the capital costs (construction and planning) of different types of mitigation measures. These are non-recurring costs. In the data, capital costs refer to those associated with constructing the measure. As the data came from different sources, the exact itemization was unavailable. However, it was assumed that the capital costs included the costs of planning, engineering, materials, and labour.

During the planning process, operators often estimate the capital (construction) costs. However, planned costs may differ from actual implementation. To investigate this discrepancy, we visualized the unit costs for planned and actual upstream measures for vertical slot passes (technical) and roughened bypass channels (nature-like). We selected these measures as they tended to be the most common installations for technical and nature-like passes, respectively (DWA 2014), which was also reflected by the greatest number of observations in our data. We only visualized the data from Austria and Germany. As many companies in Austria and Germany plan and build fish passes in both countries, the price difference for planning and construction between Austria and Germany is likely negligent. Furthermore, many regions in Austria (northern Alps) are logical comparison units to the southern part of Germany (Bavarian Alps) from a landscape perspective.

To understand how plant and passage facility characteristics affect the capital costs for upstream passes, we estimated a linear mixed model fit by restricted maximum likelihood (REML). Observations were limited to those with complete information for the variables ($n = 127$). We estimated three models. The first model controlled for the specific type of measures:

$$\begin{gathered}\log_e Costs_i = \beta_0 + \beta_1 \log_e Height_i + \beta_2 \log_e Length_i + \\ \beta_3 \log_e PlantCapacity_i + \delta_i + \gamma_i + \varepsilon_i.\end{gathered} \tag{1}$$

$\log_e Costs_i$ is the total capital (construction) cost associated with upstream fish passes. $\log_e Height_i$ and $\log_e Length_i$ are the height of the obstacle to be passed and length of the pass, both in meters. $\log_e PlantCapacity$ is the capacity of the plant in kW, which controls for the size of the hydropower plant. By including the logarithmic transformation of cost, we assumed that capital costs would increase exponentially, which we confirmed through visual inspection of the data. We also included measure type (γ_i) controls as we expected differences across types of measures. Random effects for the country (δ_i) are included and ε_i is the error term.

We then estimated a second version of the model, which included a binary variable ($Implemented_i$) for whether the costs are based on a planned or implemented project. This tested whether there is a difference between planned and implemented costs while controlling for structural characteristics and the type of measure.

$$\begin{aligned}\log_{\mathrm{e}} Costs_i = {} & \beta_0 + \beta_1 \log_e Height_i + \beta_2 \log_e Length_i \\ & + \beta_3 \log_e PlantCapacity_i + \beta_4 Implemented_i + \delta_i + \gamma_i + \varepsilon_i. \end{aligned} \tag{2}$$

In our third model, we replaced the specific measure variables by grouping them into three categories: technical, nature-like, and combined. The technical design was the baseline and we included interaction terms to investigate how the categories relate to the height of the obstacle and length of the pass. This tested whether generalizations can be made about cost differences between technical, nature-like, and combined fish passes and their structural characteristics. Within the categories, we expected that there would not be significant differences between measure types as technical passes always use concrete and nature-like always use natural materials for construction. Thus, construction costs should be similar but the quantity that is needed might differ. However, we controlled for the quantity by including the height, length, and plant capacity. We therefore estimate the following:

$$\begin{aligned}\log_{\mathrm{e}} Costs_i = {} & \beta_0 + \beta_1 \log_e Height_i + \beta_2 \log_{\mathrm{e}} Length_i \\ & + \beta_3 \log_{\mathrm{e}} PlantCapacity_i + \beta_4 NatureLike_i + \beta_5 Combined_i \\ & + \beta_6 \log_e Height_i * NatureLike_i \\ & + \beta_7 \log_{\mathrm{e}} Length_i * NatureLike_i + \beta_8 \log_e Height_i * Combined_i \\ & + \beta_9 \log_{\mathrm{e}} Length_i * Combined_i + \delta_i + \varepsilon_i. \end{aligned} \tag{3}$$

Similarly, to understand how structural characteristics affect the capital costs for downstream measures, we estimated a model using generalized least squares fit by REML. We estimated the costs of downstream mitigation measures (i.e., screen and bypass) as a function of screen/rack area ($\log_e Area_i$) and a binary variable for rack configuration ($Vertical_i$) of vertical (1) or horizontal (0). ε_i is the error term. Observations were limited to those with complete information for the variables ($n =$ 17). As all observations came from Germany, we did not include country random effects. Due to missing information, we did not include other factors, such as the angle of the screen/rack.

$$\log_e Costs_i = \beta_0 + \beta_1 \log_e Area_i + \beta_2 Vertical_i + \varepsilon_i. \tag{4}$$

For the 40 case studies that reported the configuration of the screen/rack (includes both fish protection screens/racks and combined screen/rack bypass systems), we tested whether there are significant differences in costs between horizontal ($n =$ 27) and vertical ($n =$ 13) racks.

6.3.3.2. Anaylsis of recurring costs

We then presented descriptive statistics for annual maintenance and lost power for both upstream and downstream passage measures and for the monitoring of upstream measures. These are recurring costs. While maintenance and monitoring are expressed in Euros, we presented the lost power production in GWh.

6.3.3.3. Anaylsis of lifetime costs

Finally, we combined capital, maintenance, and lost power costs in a levelized cost of mitigation (LCOM) using the following formula:

$$\text{LCOM} = \frac{Sum\ of\ costs\ over\ lifetime}{Plant\ capacity} = \frac{I + \sum_{t=1}^{n} \frac{M_t + L_t}{(1+r)^t}}{C}. \tag{5}$$

There are a variety of methods for estimating the levelized cost of a technology (Aldersey-Williams & Rubert 2019). In this formula, I represents the investments (construction) expenditures of the mitigation measure, M_t represents the maintenance expenditures in the year t, L_t represents the power production losses (EUR) in the year t, C represents the plant capacity (kW), r represents the discount rate, and n represents the expected lifetime of the measure. Discounting represents the time value of money by expressing the value of future currency in the present. Thus, the discount rate captures how the market and inflation rates change over time. We used a discount rate of 4% as recommended by the European Commission (Satori et al. 2014). We assumed a lifetime of 30 years for the passage measures as most hydropower concessions in Europe cannot be granted beyond this period (Glachant et al. 2015). Although the lifetime of passage measures may be longer than 30 years, the duration of concession is more important for the calculation of levelized costs. This is because when concessions expire, additional modernization may be required, which incurs further costs.

The electricity prices will vary based on the time, country and market in which they operate. However, given that we lacked information about when the power losses occur, detailed assumptions about prices may overpromise precision. Thus, we compared two prices based on the feed-in tariffs for retrofitted (including ecological measures) German hydropower plants under the German Renewable Energy Act in 2014. The 2014 EEG tariffs are based on the size of the plant. We selected these prices as they represent low (0.055 EUR/kWh) and high (0.125 EUR/kWh) remuneration.

Our estimation is similar to the levelized cost of electricity (LCOE) proposed by the United Kingdom's Department for Business, Innovation and Skills, which expresses the average net present cost of generation over a plant's lifetime. Notably, the LCOE is the ratio of total discounted costs over the plant's lifetime divided by the discounted sum of electricity generated. To levelize costs, we used capacity in place of electrical energy generation as information on the annual generation of each plant was missing. It is difficult to make assumptions about annual power generation based on the plant capacity as hydropower operation hours can vary greatly among plants and by season and location. Some power plants are built and used for peaking (with few operating hours), whereas others are built to run almost constantly.

As many of the case studies included only costs for certain categories, we removed observations that did not have information for all three categories of construction, maintenance, and power losses for the calculation of the LCOM. While the maintenance and power losses can plausibly be zero, we removed them unless this was explicitly stated. We also removed two measures with only one observation (guiding dam/wall and fish lift).

6.4. Results

The costs of a large variety of upstream and downstream measures are presented in Table 10. For upstream fish passage, we had most data about technical solutions ($n =$ 160). Geographically, these measures were not evenly distributed. Of the 100 Austrian upstream case studies, the majority (71%) were technical solutions such as vertical slot passes ($n = 68$) and fish lifts ($n = 3$). Combined vertical slot and roughened bypass channels accounted for the next largest share with 20 case studies, while there were only nine nature-like measures. Similarly, of the 86 German case studies, the majority (70%) were technical solutions such as vertical slot passes ($n = 55$) and roughened ramps ($n = 6$). However, nature-like solutions such as roughened bypass channels (n $= 23$) accounted for the next largest share, while there were only two combined solutions. In contrast, of the 52 Swedish case studies, there was an almost equal number of technical ($n = 24$) and nature-like passes ($n = 27$), while there was only one combined measure. Seven of the eight French case studies were technical measures and the Swiss case study was a combined solution.

For downstream measures, operators most frequently reported using a combined screen/rack and bypass, followed by a fish protection screen/rack. Combined screen/rack bypass systems were reported from Germany ($n = 57$) and France ($n = 3$). Fish protection by screens/racks in front of the intake to the power plant included a Coanda effect intake screen ($n = 1$), horizontal rack ($n = 3$), horizontal rack with cleaner ($n = 2$), and trash racks ($n = 3$) and were reported from a variety of countries including France ($n = 3$), Germany ($n = 3$), Sweden ($n = 2$), and Switzerland ($n = 1$). All bypasses were reported from Germany and guiding walls/dams were from Sweden ($n = 4$) and Austria ($n = 1$).

Table 10. Overview of case studies
Overview of case studies by type of fish passage measure and country of origin. AU = Austria, FR = France, GE = Germany, SW = Sweden, SL = Switzerland.

Measure	**AU**	**FR**	**GE**	**SW**	**SL**	**Total**
Upstream						
Technical designs						
Vertical slot pass	68	6	55	21		150
Roughened ramp with pool structures			6			6
Denil pass		1		3		4
Nature-like designs						
Roughened bypass channel with pool structures	9	1	23	27		60
Combined vertical slot and roughened bypass channel with pool structures	20	2	1	1		24
Special designs						
Fish lift	3					3
Downstream						
Combined screen/rack and bypass		3	57			60
Fish protection screen/rack		3	3	2	1	9
Bypass			6			6
Guiding wall/dam	1			4		5
Total						327

6.4.1. Non-recurring costs of passage measures

Capital (construction) costs varied across measures and there were often wide ranges of costs within the same mitigation measure (Figure 27). Among upstream measures, fish lifts and combined vertical slot and vertical slot passes had the greatest total costs. However, between the remaining technical types (roughened ramps, Denil passes) and nature-like solutions (roughened bypass channels), there were no major differences in median costs. Notably, there were many outlier observations for vertical slot passes and roughened bypass channels.

There was less variability for downstream measures. Guiding walls/dams were the most expensive to construct whereas combined screens/racks and bypasses, fish protection screens/racks, and bypasses were relatively similar in costs.

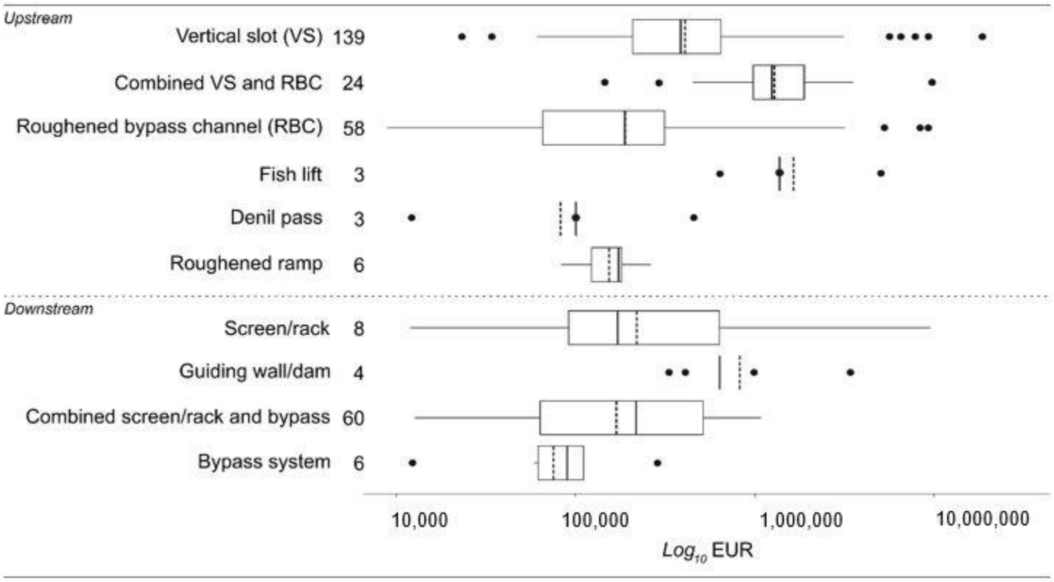

Figure 27. Capital costs of upstream and downstream fish passage measures
Capital costs of upstream and downstream fish passage measures from Austria, Germany, France, Sweden, and Switzerland in Euros.**Note:** The box shows the interquartile range (25%, 50%, 75%). The solid line in the box represents the median while the dotted line represents the mean. The points represent outliers (defined as >1.5 times and <3 times the interquartile range on either side of the box). In cases with fewer than five observations, only points are used.

6.4.2. Seasonal patterns in growth

As hypothesized, there were differences between planned and implemented unit costs (Figure 28). For costs per meter height, planned costs averaged 124,608 EUR/m (SD = 65,187 EUR/m) while implemented costs were 235,408 EUR/m (SD = 310,862 EUR/m). For costs per meter length, planned costs averaged 6156 EUR/m (SD = 5179 EUR/m) while implemented costs were 16,642 EUR/m (SD = 83,352 EUR/m).

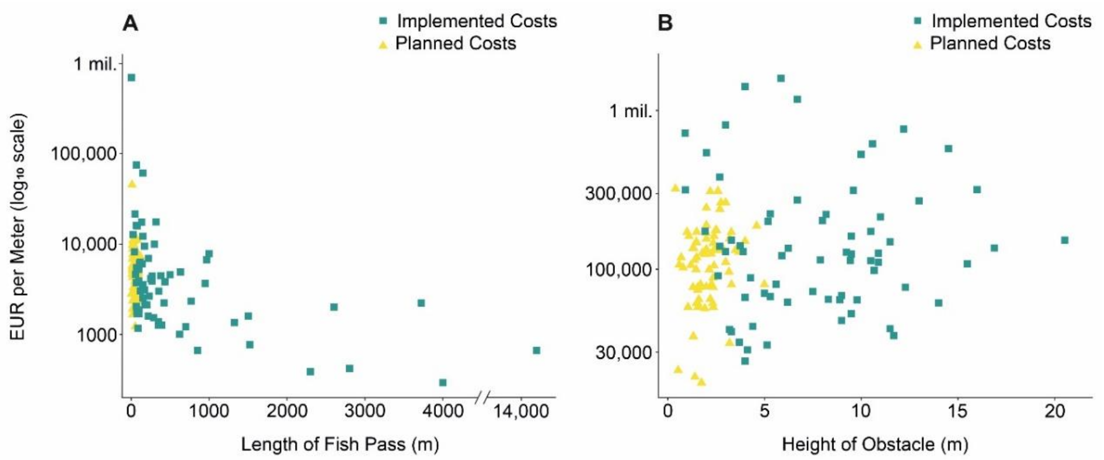

Figure 28. Planned vs. implemented unit costs
Planned (Germany) vs. implemented (Austria) unit costs for upstream fish passage measures ($n = 144$) based on per meter length (**A**) and per meter height of the obstacle (**B**).

Between technical (vertical slot) and nature-like (roughened bypass channels) upstream passes, there were also differences in unit costs (Figure 29), but no clear trends related to increasing length or height of the pass. In terms of fish pass length, the majority of passes were shorter than 250 m. Costs ranged between 194 EUR/m and 61,301 EUR/m (not shown) for vertical slot passes. Comparatively, roughened bypass channels had a narrower range with costs between 125 EUR/m and 7720 EUR/m. The mean cost per meter length of vertical slot passes (6914 EUR/m) and roughened bypass channels (2233 EUR/m) was statistically different ($p < 0.001$). In terms of height, both types of measures overcame heights of around 20 m. There was a weak positive relationship between the height of the pass and cost per meter for vertical slot passes, which implied that as the height increases, the unit cost increases. For vertical slot passes, costs ranged between 9949 EUR and 1,592,769 EUR (not shown) whereas costs ranged between 5866 EUR and 807,920 EUR (not shown) for roughened bypass channels. The mean unit costs of vertical slot passes (6914 EUR/m) and roughened bypass channels (2233 EUR/m) were statistically different ($p < 0.001$). The mean cost per meter height of vertical slot passes (177,788 EUR/m) and roughened bypass channels (122,667 EUR/m) was marginally significant ($p < 0.10$).

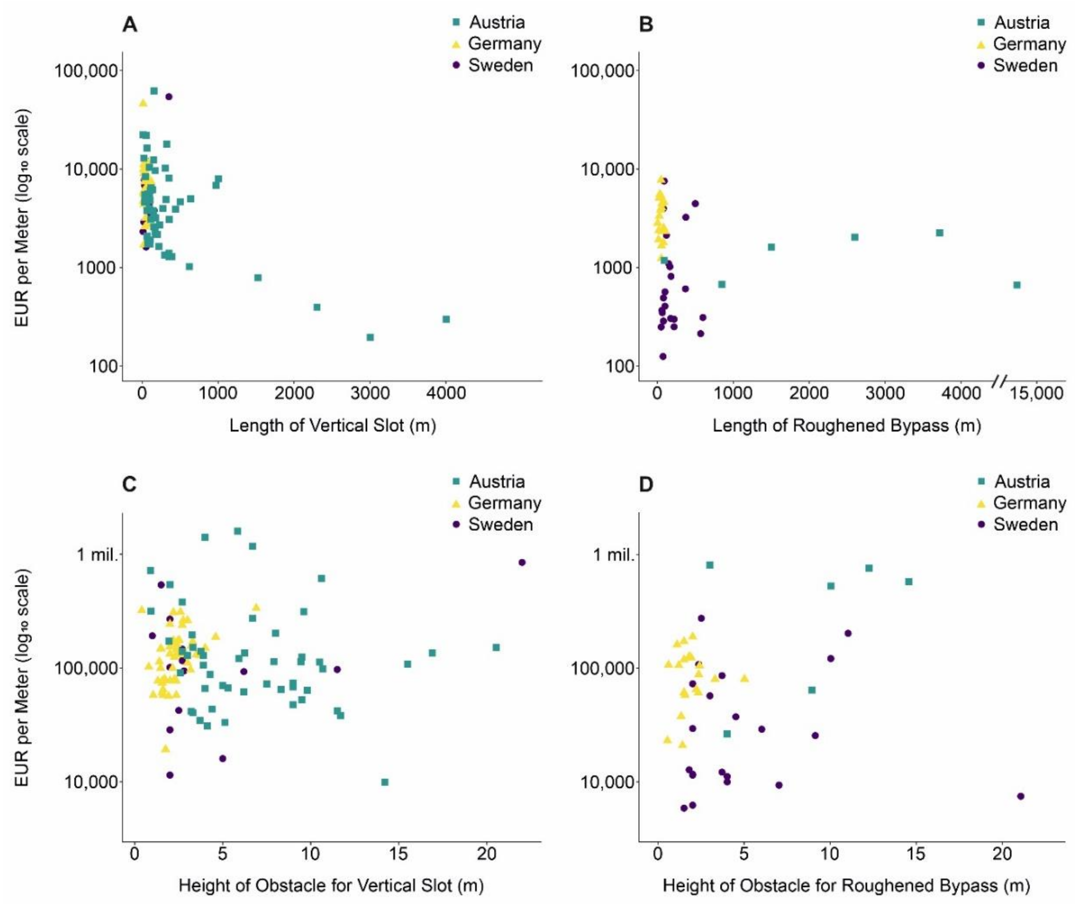

Figure 29. Unit costs for nature-like and conventional fish passes
Cost per meter length for vertical slot passes (**A**, $n = 150$) and roughened bypass channels (**B**, $n = 60$) compared to costs per vertical meter of the obstacle for vertical slot passes (**C**, $n = 150$) and roughened bypass channels (**D**, $n = 60$).

6.4.3. Factors predicting capital costs

Across all three regression models for upstream passage measures, the coefficient estimates were robust (Table 11). Models 1 and 2 compared the inclusion of the implemented binary variable. Both models found positive and statistically significant relationships between length of the pass and construction costs. A 1% increase in length was associated with an increase between 0.54% and 0.55% in capital costs and a 1% increase in the height of the obstacle was associated with an increase between 0.53% and 0.54% for Models 1 and 2, respectively. Also, as expected, capital costs increased with plant capacity. For the type of measures in both models, the variables for fish lift and roughened bypass channels with pool structures were statistically significant. The parameter estimate for fish lift was positive while that of roughened bypass channels was negative, implying that costs are higher for fish lifts than for combined vertical slot and roughened bypass channels (the baseline) while costs are comparatively lower for roughened bypass channels. The variables for roughened ramps and vertical slot passes were not significant. In Model 2, a variable for whether the costs are based on an implemented measure was included. The parameter estimate was negative and significant. This finding implied that costs are lower for implemented measures than planned ones when other structural characteristics are considered. The parameter estimates for Model 3 were slightly different due to the inclusion of the nature-like and combined binary variables (rather than the specific measure types) as well as the interaction terms. Our decision to differentiate between nature-like, technical, and combined passes aligned with the findings of significant differences between measure types in Models 1 and 2. Height, length, and plant capacity were statistically significant and positive. Both binary variables, nature-like and combined, were significant. The parameter for nature-like was negative while that of combined measures was positive. For the interaction terms for nature-like measures, the length of the pass was significant and negative. For the interaction terms for combined measures, the height of the obstacle was significant and negative. The results implied that nature-like passes are less expensive than technical solutions (the baseline), but that this difference diminishes as the pass increases in length. In contrast, combined solutions tend to be more expensive than technical ones, but this difference diminishes as the height of the obstacle increases. When Models 1 and 2 were estimated with Ordinary Least Squares (OLS), the models explained 77% of the total variance observed (R-squared). Model 3 explained 78% of the total variance observed. Appendix 3, Table A5 shows the 95% confidence intervals for the upstream models.

Table 11. Regression estimates for upstream fish passage measures
Regression estimates for the costs of upstream fish passage measures from Austria, Germany, France, and Sweden.

	Log$_e$ of Capital Costs					
	Model 1: Type of Upstream Measure		**Model 2: Implemented vs. Planned Costs**		**Model 3: Nature-Like vs. Technical vs. Combined Passes**	
Fixed Effects	Coeff. (S.E.)	*t*-value	Coeff. (S.E.)	*t*-value	Coeff. (S.E.)	*t*-value
Intercept	9.01 (0.50)	17.89	9.65 (0.37)	26.06	9.76 (0.46)	21.00
Log of length (m)	0.55 (0.08)	6.72	0.54 (0.08)	6.71	0.27 (0.08)	3.32
Log of obstacle height (m)	0.53 (0.13)	3.94	0.54 (0.13)	4.06	0.78 (0.14)	5.42
Log of plant capacity (kW)	0.11 (0.04)	2.87	0.11 (0.04)	2.90	0.12 (0.04)	3.07
Implemented (binary)			−0.97 (0.29)	−3.39		
Nature-like (binary)					−1.64 (0.50)	−3.27
Combined (binary)					3.95 (1.60)	2.46
Nature-like *log of height					−0.28 (0.30)	−0.95
Nature-like *log of length					0.35 (0.15)	2.32
Combined *log of height					−0.85 (0.48)	−1.80
Combined *log of length					−0.31 (0.25)	−1.28
Fish lift	2.89 (0.81)	3.56	2.84 (0.81)	3.51		
Roughened bypass channel	−0.55 (0.25)	−2.18	−0.52 (0.25)	−2.11		
Roughened ramp	0.01 (0.35)	0.02	0.01 (0.35)	0.04		
Vertical slot pass	−0.15 (0.23)	−0.66	−0.14 (0.23)	−0.61		
Random Effects	Var. (S.D.)		Var. (S.D.)		Var. (S.D.)	
Intercept	0.33 (0.58)		0.03 (0.16)		0.27 (0.52)	
Residual	0.40 (0.63)		0.40 (0.63)		0.41 (0.64)	
REML Criterion	261.10		256.90		265.20	
n	127		127		127	

Note: S.E. denotes standard error, S.D. denotes standard deviation, Var. denotes variance, REML is restricted maximum likelihood.* is a multiplication sign.

For downstream measures, one model was estimated with 17 observations of combined screen/rack and bypass systems from Germany (Table 12). The area of the rack was positively and significantly associated with cost. The estimate indicated that, on average, each additional percent of square meter was associated with a 1.18% increase in capital costs. The configuration of the rack (vertical or horizontal) was not significant. When the model was estimated with Ordinary Least Squares, it explained approximately 93% of the variance. When we tested for differences in costs related to the configuration of the rack with a t-test for additional case studies, the difference in mean costs of horizontal (210,671 EUR) and vertical (243,793 EUR) racks was also not statistically significant. Appendix 3, Table A6 shows the 95% confidence intervals for the downstream model.

Table 12. Regression estimates for downstream fish passage measures
Regression estimates for the costs of downstream fish passage measures from Germany.

Variable	**Coeff. (S.E.)**	***t*-Value**
Intercept	8.62 (0.29)	29.49
Log of Area (m^2)	1.18 (0.09)	13.80
Vertical configuration (binary)	−0.09 (0.20)	−0.43
Log-Likelihood	−11.10	
Degrees of freedom	14	
Residual standard error	0.41	
n	17	

6.4.4. Recurring costs of passage measures

For upstream measures, recurring costs such as annual maintenance and monitoring did not account for a large share of lifetime costs (Table 13). For all measures, the annual maintenance costs ranged from 0 EUR/year to 50,220 EUR/year with an overall average of 13,139 EUR per year. Fish lifts had the highest average maintenance costs compared to other measures, but the case study with the highest maintenance costs was a vertical slot pass. In terms of variation, there were large standard deviations across categories, particularly for the roughened bypass channel.

For downstream measures, only two case studies with a guiding dam/wall reported maintenance costs. Between these two case studies, there was large variation.

Table 13. Maintenance costs for upstream fish passage measures
Overview of the annual maintenance costs for upstream fish passage measures from Austria, Germany, France, and Sweden in Euros.

Category	*n*	Median	Mean	S.D.	Min.	Max.
Upstream						
Vertical slot pass	59	10,762	12,206	9143	0	50,220
Combined vertical slot and bypass channel	21	10,944	12,096	4815	6622	32,285
Roughened bypass channel	13	12,946	16,887	15,199	0	39,731
Fish lift	2	23,806	23,806	11,991	15,327	32,285
Downstream						
Guiding dam/wall	2	16,581	16,581	23,449	0	33,162
Total	97	10,762	13,139	9835	0	50,220

Our review of monitoring costs found high variability across case studies and notable differences between the monitoring of simple technical, complex technical, nature-like, and combined upstream measures (Table 14). Monitoring for complex technical (i.e., fish lift) and nature-like measures was most expensive as fish lifts had a mean monitoring cost of 160,456 EUR and roughened bypass channels had a mean cost of 443,503 EUR. Comparatively, vertical slot passes had a mean cost of 92,918 EUR and combined solutions cost of 71,262 EUR on average. However, these values were highly variable as indicated by the large standard deviations.

Beyond costs, additional information about the type of monitoring was limited. Only eight measures specified what kind of monitoring was conducted. This included one-time monitoring of water variables (temperature, quality, discharge, etc.) as well continuous monitoring (over a few months) of habitat availability and fish pass functionality. Fish pass functionality was monitored with fish traps, both alone or combined with video, as well as image-based scanner systems. With the exception of fish traps, the specific types of monitoring tended to be more expensive than the average reported overall. For the three cases of fish traps, the mean cost was 14,215

EUR with a standard deviation of 8740 EUR. Comparatively, monitoring with video in addition to fish traps had a mean cost of 157,223 EUR for three case studies with a standard deviation of 104,405 EUR. Finally, image-based scanner systems cost an average of 142,401 EUR for two case studies. Only five measures reported the time span of monitoring, which ranged from one to 24 months.

Table 14. Monitoring costs of upstream fish passage measures
Overview of monitoring costs related to different upstream fish passage measures from Austria, Germany, France, and Sweden in Euros

Measure	***n***	**Median**	**Mean**	**S.D.**	**Min.**	**Max.**
Vertical slot pass	59 [a)]	22,958	92,918	214,389	0	1,456,388
Combined vertical slot and bypass channel	20 [b)]	62,498	71,262	46,562	10,762	168,956
Roughened bypass channel	7	161,584	443,503	571,168	23,303	1,279,866
Fish lift	3	185,206	160,456	128,550	21,331	274,831
Total	89	39,839	117,902	250,576	0	1,456,388

Note: [a)] Includes 5 fish traps and 1 image-based scanner, [b)] Includes 1 fish trap and 1 image-based scanner.

Annual power losses also represented a recurring cost, which differed sizably across measures (Table 15). For upstream measures, fish lifts and roughened bypass channels incurred the greatest costs on average, although these were highly variable. The majority of observations were vertical slot passes with an average of 149 GWh lost per year and combined vertical slot and bypass channels with an average of 307 GWh lost per year.

For downstream measures, fish protection screens/racks and combined screen and bypass systems reported minimal power losses. For both measures, only three case studies reported power losses, which may be unrepresentative of downstream mitigation measures.

Table 15. Power losses related to fish passage measures
Overview of power losses related to different fish passage measures from Austria, Germany, France, and Sweden in GWh per year.

Category	*n*	Median	Mean	S.D.	Min.	Max.
Upstream						
Vertical slot pass	74	149	859	2481	0	17,950
Denil pass	1	0.438				
Combined vertical slot and bypass channel	22	308	534	768	0	3400
Roughened bypass channel	12	613	2631	4163	0	14,000
Fish lift	3	1500	8098	12,309	495	22,300
Downstream						
Combined screen/rack and bypass system	3	0	0.002	0.003	0	0.006
Fish protection screen/rack	3	0	0.083	0.144	0	0.25
Total	118	1112	199	3136	0	22,300

6.4.5. Levelized costs of upstream passage measures

In total, 55 observations were included from Austria (52) and Germany (3). Our results demonstrated that regardless of the electricity price selected, capital (construction) costs tended to account for the largest share of lifetime costs with the exception of vertical slot passes under the high price scenario (Figure 30). Under the high price scenario for vertical slot passes, capital accounted for 45% while power losses accounted for 54% of lifetime costs. For all other scenarios, capital costs represented between 57–76% of lifetime costs compared to 64–87% under the low price scenario. On average, capital costs were highest for combined measures (415 EUR/kW) compared to technical (130 EUR/kW) or nature-like (50 EUR/kW). However, this was highly variable as combined solutions had a standard deviation of 540 EUR/kW. There was also a high variability of technical (214 EUR/kW) passes, but less variability for nature-like passes (48 EUR/kW).

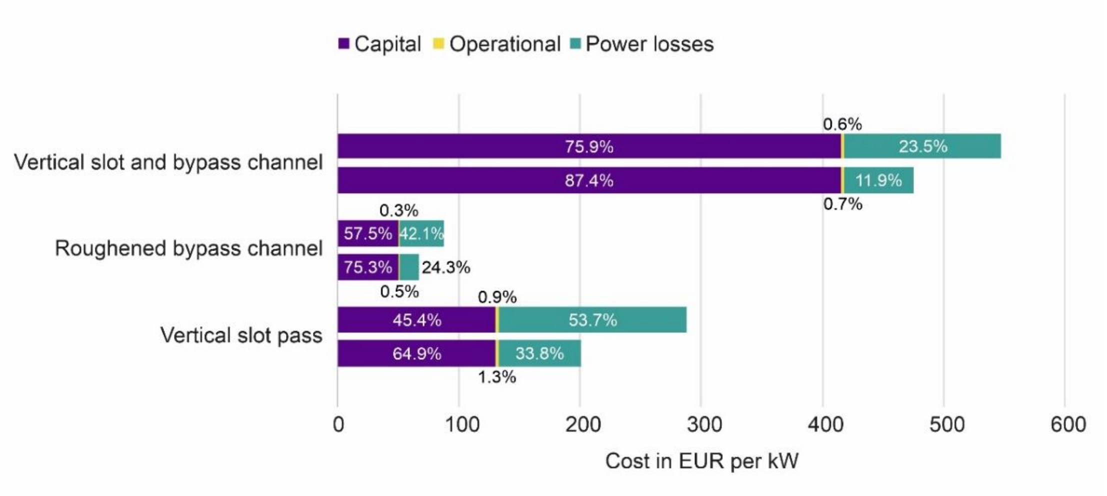

Figure 30. Overview of levelized costs
Comparison of the mean levelized cost of mitigation for different upstream fish passage measures from Austria, Germany, France, and Sweden with high (0.125 EUR/kWh) and low (0.055 EUR/kWh) electricity prices.

Across all measures, maintenance costs accounted for a comparatively small share of levelized lifetime costs. On average, maintenance costs were greatest for combined measures (3 EUR/kW), followed by technical vertical slots (2 EUR/kW). Some missing observations may have represented zero for maintenance costs. Since missing data and zeros cannot be distinguished unless specified, this may have upwardly biased the results. Of the observations included, three reported maintenance costs of zero.

Despite our simplified representation of electricity prices, the comparison of low and high prices revealed that costs associated with power losses can vary greatly. Comparing the low (high) electricity prices, vertical slot passes had the highest mean cost of 68 EUR/kW (154 EUR/kW), compared to 56 EUR/kW (128 EUR/kW) for combined vertical slot/bypass channel and 16 EUR/kW (37 EUR/kW) for roughened bypass channels. The median, however, showed that roughened bypass channels have the greatest costs (16 EUR/kW; 36 EUR/kW) compared to combined (13 EUR/kW; 31 EUR/kW) and vertical slot (8 EUR/kW; 20 EUR/kW). Similar to maintenance costs, power losses could be zero. Since missing data and zeros cannot be distinguished, this may have upwardly biased the average power losses associated with each measure type. Of the observations included, five reported power losses of zero.

6.5. Discussion

To understand the cost trade-offs associated with sustainable hydropower, we established several hypotheses about the costs of fish passage mitigation. We hypothesized that planned costs and unit metrics can accurately predict costs. Further, we posited that construction and power losses account for the largest shares of lifetime mitigation costs. Finally, we hypothesized that technical measures incur lower costs than their nature-like counterparts.

However, we found that planning costs differ substantially from actual costs. This may be because planned costs often cannot account for difficulties that arise throughout the construction process (e.g., shortages and changes in the prices of materials) as well as site-specific factors (e.g., target species, difficulty of site accessibility, ground conditions, and local regulations) (DWA 2014). As many of these complications cannot be foreseen or quantified, we investigated whether other variables can improve predictions about the construction costs of fish passage mitigation.

For upstream passes, we investigated the extent to which the height, length, or type of pass predicts construction costs. Understanding whether height or length is the key driver of upstream passage costs may affect the decision-making process of operators. For example, if an operator is deciding between a fish lift and vertical slot pass, they may find it is cheaper to build the lift if length is the main driver of costs. We found a strong relationship between construction costs and the height of the obstacle and length of the fish pass. A possible exception to the usefulness of height for predicting upstream construction costs are fish lifts, as previous literature suggested that their construction costs are relatively independent of dam height (Larinier & Marmulla 2004).

For downstream passes, we investigated whether the area and configuration of the rack/screen predicts construction costs. Our analysis confirmed that the area can be useful for predicting costs. While a rack/screen is a standard installation for hydropower plants used to repel debris, some can be adapted to function as fish protection and a guiding structure. For this purpose, adaptations in bar spacing (narrowing) or angle as well as inclination are typical but may contribute to higher expenditures (purchase price, reduction in flow during operation, which reduces power production) (Linnansaari et al. 2015). Ideally, other variables about the presence of a cleaning device and inclination (angle) of the rack, and the cost of the bypass structure would have been relevant to potentially explain more variance. As our data did not comprehensively provide information on inclination or other specific characteristics of the racks/screens, only a comparison of the orientation was possible. However, we found no significant difference in construction costs for vertical and horizontal racks/screens.

The first step of our analysis only considered how these factors affect construction costs, but mitigation can also entail maintenance costs and power losses. Power losses can be difficult to quantify. Thus, upfront construction costs may be assumed to account for the largest share, which may lead decision makers to underestimate the total costs of fish passage mitigation if power losses represent a large share of lifetime costs.

For upstream measures, we hypothesized that capital (construction) costs and power losses account for the largest shares of lifetime costs. Under almost all price scenarios, capital costs accounted for the largest share. However, in the high price scenario for vertical slot passes, power losses accounted for a greater share. This means that when electricity prices are high, power losses may represent a significant concern for operators. However, it is difficult to generalize findings about power losses of measures as there may be significant variation in power loss among sites. Fish passage facilities may be designed to operate only during the migration season (Romão et al. 2015). Thus, they do not necessarily operate year-round. Smart management of water release should ideally be adapted to both fish migration and power production needs. This could potentially reduce power and income loss while still maintaining fish passage. Such solutions depend on site-specific conditions, fish species composition, legal requirements, and operational constraints. Our finding is significant because previous cost reports of fish passage measures primarily focused on construction and operation (Nieminen et al. 2017), rather than quantifying the role of power losses. As a result of lack of data, a comparison of lifetime costs for downstream passage measures was not possible. Thus, it represents a potential avenue of future research.

Both of these analyses allow us to compare the costs of different types of upstream passage measures. We hypothesized that technical designs are often favoured since less space is needed, which incurs fewer costs related to land acquisition. This can be most severe in congested urban areas of Europe. Our analysis of construction costs, however, showed that nature-like fish passes were comparatively cheaper, even when controlling for interactions between nature-like builds and the length or height of the pass. We found that nature-like passes are less expensive than technical solutions, but that this difference diminishes as the pass increases in length. In contrast, combined solutions tend to be more expensive than technical ones, but this difference diminishes as the height of the obstacle increases. This finding was consistent with the analysis of lifetime costs.

When considering lifetime costs, nature-like solutions incurred relatively fewer costs, specifically, fewer power losses compared to combined and technical solutions. When comparing combined and technical solutions, combined solutions were more expensive. This may be because combined solutions are often built when the height is too great for the available space. When compared across sites, natural materials may be cheaper for construction, particularly if autochthonous materials with fewer transportation costs are used (BAW 2015). Given that our results showed that nature-like solutions cost less to build and operate, incur fewer power losses, and provide habitat (Katapodis et al. 2001) in addition to facilitating fish passage, there is a strong basis for supporting their development in Europe.

Our study also yielded differences in the monitoring costs of upstream passage measures. The lack of data related to the costs and types of monitoring is evident. Approximately one-third of the case studies reported monitoring costs. However, only eight reported the type and five reported the timeline. While it is unclear whether the case studies simply did not report the costs or whether no monitoring took place, recent studies have noted the dearth of effectiveness monitoring related to fish passage measures (Roscoe & Hinch 2010). In contrast, a study of river restoration measures showed that 80% of the projects are monitored (Szałkiewicz et al. 2018). This may stem from the belief that standardised passage design based on species-specific formulas (Pander & Geist 2013) ensures success. Hence, additional monitoring is often not considered necessary and may result in additional costs if functionality is not proven after all. Recent literature argued that most design criteria are primarily based on salmonids in the Northern Hemisphere, which fails to account for the variation in individuals, populations, and species at individual sites (Birnie-Gauvin et al. 2019).

Our data reveal that when a complex technical solution is built (e.g., fish lift), operators often invest in intensive monitoring. In turn, simpler technical measures (e.g., vertical slot pass) may require less monitoring as proven solutions do not need to be tested. In comparison to vertical slot passes, which can be standardised, nature-like solutions like roughened bypass channels tend to be adapted to local landscape conditions, which may also result in additional monitoring expenses. Nature-like passes may also be more complicated to monitor without standardised and pre-fabricated monitoring gear.

Additionally, there is an array of possible indicators for passage effectiveness. While environmental variables such as temperature, discharge, water depth, and water velocities are regularly used for evaluating passage mechanisms, they are not suitable for cross-site comparisons as they cannot imply a cause and effect (Roscoe & Hinch 2010). However, detailed reporting of hydraulic and structural parameters may make studies more comparable across sites (Roscoe & Hinch 2010). Given the high costs of fish passage restoration, assessing the costs and ecological benefits is important to develop evidence-based solutions in the future (Pander & Geist 2013, Geist & Hawkins 2016). Thus, we recommend that policy makers standardise monitoring and reporting of the hydraulic, structural, and biological parameters as well as costs in a much more detailed manner.

Future analysis of upstream fish passage costs can be strengthened by clear reporting of structural characteristics. For many variables, data were missing, which reduced the observations in a complete case analysis. Further, it was often unclear how the variables were reported. For example, sometimes the reported length was the shortest distance between the entrance and exit of a fish pass, while other times it was the true length of the fish pass. In the analysis, it was not possible to account for such data inconsistencies as it was not always clear how operators reported length. Additional information about the target fish species may also help to account for the variation observed, as technical and nature-like designs may be built for different types of target species. While we did not have information about the target species for all measures, we found that there were no major differences in the target species for technical or nature-like passes (i.e., technical fish passes were not specifically built for stronger swimmers).

For downstream fish passage measures, our analysis was largely limited by missing data, especially related to maintenance and power losses. These costs can be difficult to identify as some downstream measures may be installed at hydropower plants for reasons unrelated to fish (e.g., trash rack to repel debris). However, if they are designed properly, they can serve the dual purpose of protecting fish. Thus, we recommend that future research focus on the costs of downstream passage facilities. Finally, future research can conduct cost-benefit or cost-effectiveness analyses. While we found that nature-like solutions tend to cost less, it will be important to quantify the possible additional ecological benefits (e.g., providing habitat) to assess their value relative to other types of fish passage measures.

Given the costs, the question arises of how the sustainable management of hydropower and fish passage can be financed and how effective solutions can be incentivized. Present financing instruments include support schemes, feed-in tariffs and green power labels (Kampa et al. 2017). While support schemes compensate for the modernization of existing plants through direct financing, grants, or loans, feed-in tariffs guarantee a fixed price for renewable energy fed into the public grid and green power labels set minimum standards related to electricity production (Kampa et al. 2017). Specific to passage restoration, direct financing and loans may cover construction costs, whereas feed-in tariffs may offset the recurring costs associated with power losses.

In some countries, mitigation is financed by state authorities using taxes. In Switzerland, for example, all plants built before 2011 are eligible for financing of upgrades. Ecological improvements are supported by a tax of 0.1 Rappen/kWh on all consumer electricity bills, which amounts to the "Swiss Grid Fund" with a maximum of 50 million CHF/year. To incentivize upgrades, the Swiss Grid Fund is available on a first-come-first-serve basis until the program expires in 2030. After the program's end, operators will be fully responsible for financing, which is in line with the polluter-pays principle (Köhler & Ruud 2019). In contrast, Austria supports approximately 50% through national funding such as the Environmental Aid Act. However, this excludes losses stemming from electricity production (Ruud & Lindström 2018, Köhler & Ruud 2019). In Sweden, green power labels are used to incentivize ecological restoration. For operators to qualify for green power labels, they must make annual contributions to environmental projects (Kampa et al. 2017). The approach of targeted financial contributions may ensure that measures are carried out at sites with the greatest need, which could maximize effectiveness.

In some cases, the amount of funding provided is assessed on a case-by-case basis, which can be time-consuming and costly. On the other hand, arguments can be made for a simpler system based on standard refunds determined by the type, length, and height of the measure or a percentage of costs. While simplification is desirable, the results here do not support a standardisation of costs. Within each category, the standard deviation is often greater than the mean, which indicates a wide range of possible costs.

To offset production losses resulting from fish passage measures, feed-in tariffs may be useful. Feed-in tariffs may be conditional on improvements as in Switzerland, France, and Germany (Kampa et al. 2017). Typically, different rates apply, based on the size of the plant. The larger the plant, the lower the rate. However, given the fluctuations in time of lost power production and market rates, our analysis cannot assess whether feed-in tariff rates are sufficient to offset the losses of power production. When establishing priorities related to financing of fish passage measures for hydropower, decision makers must weigh these factors with societal and political values.

6.6. Conclusion

As sustainable management of hydropower must balance mitigation measures for fish with renewable energy production, decision makers require information about cost trade-offs. This systematic overview detailed non-recurring (construction) and recurring (maintenance, monitoring, power losses) costs of passage measures.

Construction tends to account for the largest share of lifetime costs and while unit metrics (height and length) can be used for estimation of upstream fish passage measures, one should be aware that planning costs often differ substantially from actual costs. In particular, factors such as the target species, site conditions, difficulty of site accessibility, and local regulations contribute to the overall costs of mitigation measures. Comparatively, maintenance accounts for a relatively small share of lifetime costs. As there is limited research on power losses related to fish passage measures, our findings provide a basis for including economic aspects in hydropower decision-making. Under the high price scenario for vertical slot passes, power losses exceed construction as a share of lifetime costs. In most markets, power prices vary significantly over the year, week, and day. Thus, balanced solutions that consider both ecological aspects such as key migration seasons of target species as well as power prices are likely to create win-win situations.

When comparing technical and nature-like upstream passage measures, nature-like measures tend to incur lower costs, even when considering power losses. Given that nature-like solutions cost less to build and operate, incur fewer power losses and provide habitat in addition to facilitating fish passage, there is a strong basis for supporting their development in Europe.

In addition to the limited information on costs, there tends to be limited monitoring of mitigation measures and reporting of their costs, which makes it difficult to explore their efficiency after implementation and enable statements about cost-effectiveness. Thus, we recommend that policy makers standardise monitoring and reporting of hydraulic, structural, and biological parameters as well as costs in a much more systematic and detailed manner.

6.7. References

Aldersey-Williams, J., & Rubert, T. (2019). Levelised cost of energy—A theoretical justification and critical assessment. *Energy Policy*, 124, 169–179.

Anderer, P., Bauerfeind, C., Krischer, S., & Dumont, U. (2013). *Gesamtkonzept zur Herstellung der Durchgängigkeit der Unstrut*; Jena, Germany, Thüringer Landesanstalt für Umwelt und Geologie.

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.

Bauerfeind, C., Ischer, S.K., Keuneke, R., & Dumont, U. (2011). *Modellhafte Erarbeitung einer Gesamtbewertung für die Herstellung der Durchgängigkeit der für Thüringen ausgewiesenen „Schwerpunktgewässer Durchgängigkeit“ am Beispiel der Ilm*. Jena, Germany, Thüringer Landesanstalt für Umwelt und Geologie.

BAW/BfG. (2015). Guideline Upstream Fishways on German Federal Waterways (AH FAA). Version 2. Retrieved April 1st, 2020 from: https://izw.baw.de/publikationen/merkblaetter/1/Guideline_Upstream_Fishways_Version2.pdf

Beck, C., Albayrak, I., & Boes, R.M. (2018). Improved hydraulic performance of fish guidance structures with innovative bar design. *In Proceedings of the 12th International symposium on ecohydraulics (ISE 2018), Tokyo, Japan, 19–24 August 2018*.

Bilotta, G.S., Burnside, N.G., Gray, J.C., & Orr, H.G. (2016). The Effects of Run-of-River Hydroelectric Power Schemes on Fish Community Composition in Temperate Streams and Rivers. *PLoS ONE*, 11, e0154271.

Birnie-Gauvin, K., Franklin, P., Wilkes, M., & Aarestrup, K. (2019). Moving beyond fitting fish into equations: Progressing the fish passage debate in the Anthropocene. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29, 1095–1105.

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

Cai, X., Zhang, X., & Wang, D. (2011). Land Availability for Biofuel Production. *Environmental Science & Technology*, 45, 334–339.

Clay, C.H. (1995). *Design of Fishways and Other Fish Facilities*. Boca Raton, FL, USA, CRC Press.

Couto, T.B., & Olden, J.D. (2018). Global proliferation of small hydropower plants - science and policy. *Frontiers in Ecology and the Environment*, 16, 91–100.

Dewitte, M. (2018). A List of Solutions, Models, Tools and Devices, Their Application Range on a Regional and Overall Level, the Identified Knowledge Gaps and the Recommendations to Fill These. Fishfriendly Innovative Technologies for Hydropower. Retrieved October 1st, 2019 from: https://www.fithydro.eu/wp-content/uploads/2019/08/Deliverable_2.1._executive-summary.pdf

DWA. (2014). *Deutsche Vereinigung für Wasserwirtschaft, A. und A. e. V. Fischaufstiegsanlagen und fischpassierbare Bauwerke—Gestaltung, Bemessung, Qualitätssicherung*. Hennef, Germany, Merkblatt DWA 509, ISBN 978-3-942964-91-3. Retrieved October 1st, 2019 from: https://webshop.dwa.de/de/merkblatt-dwa-m-509-mai-2014.html

Enders, E.C., Gessel, M.H., & Williams, J.G. (2009). Development of successful fish passage structures for downstream migrants requires knowledge of their behavioural response to accelerating flow. *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 2109–2117.

Erlewein, A. (2013). Disappearing rivers—The limits of environmental assessment for hydropower in India. *Environmental Impact Assessment Review,* 43, 135–143.

European Commission. (2009). Directive 2009/28/EC of the European Parliament and of the Council of 23 April 2009 on the Promotion of the Use of Energy from Renewable Sources and Amending and Subsequently Repealing Directives 2001/77/EC and 2003/30/EC; (Text with EEA Relevance). Brussels, Belgium, European Parliament.

FAO/DVWK. (2002). *Fish Passes: Design, Dimensions and Monitoring*. Rome, Italy, Food & Agriculture Organization of the UN. ISBN 3-89554-027-7.

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

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.

Glachant, J.M., Saguan, M., Rious, V., & Douguet, S. (2015). *Regimes for Granting the Right to Use Hydropower in Europe.* Fiesole, Italy, European University Institute. 121pp.

Hirth, L. (2016). The benefits of flexibility: The value of wind energy with hydropower. *Applied Energy*, 181, 210–223.

Kampa, E., Tarpey, J., Rouillard, J., Haakon Bakken, T., Stein, U., Godinho, F., Nunes Eira, A., et al. (2017). Review of policy requirements and financing instruments. Deliverable 5.1 of the FIThydro project funded under the European Union's Horizon, 1–188.

Katopodis, C., Kells, J.A., & Acharya, M. (2001). Nature-Like and Conventional Fishways: Alternative Concepts? *Canadian Water Resource Journal*, 26, 211–232.

Katopodis, C., & Williams, J.G. The development of fish passage research in a historical context. *Ecological Engineering*, 48, 8–18.

Köhler, B. & Ruud, A. (2019). *How Are Environmental Measures Realized in European Hydropower? A Case-Study of Austria, Sweden and Switzerland; HydroCen Report 6*. Trondheim, Norway, Norwegian Research Centre for Hydropower Technology.

Larinier, M., & Marmulla, G. (2003). Fish passes: Types, principles and geographical distribution-an overview. *In Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries, Phnom Penh, Cambodia, 11–14 February 2003; RAP Publication: Bangkok, Thailand*, 183–206.

Larinier, M., & Travade, F. (2002). Downstream Migration: Problems and Facilities. *Bulletin français de la pêche et de la pisciculture*. 364, 181–207.

Linnansaari, T., Wallace, B., Curry, R.A., & Yamazaki, G. (2015). Fish Passage in Large Rivers: A Literature Review. Retrieved October 1st, 2019 from: https://unbscholar.lib.unb.ca/islandora/object/unbscholar%3A7995

Lundström, T.S., Hellström, J.G.I., & Lindmark, E.M. (2010). Flow design of guiding device for downstream fish migration. *River Research and Applications*, 26, 166–1821.

Manzano-Agugliaro, F., Taher, M., Zapata-Sierra, A., Juaidi, A., & Montoya, F.G. (2017). An overview of research and energy evolution for small hydropower in Europe. *Renewable & Sustainable Energy Reviews*, 75, 476–489.

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.

Nieminen, E., Hyytiäinen, K., & Lindroos, M. (2017). Economic and policy considerations regarding hydropower and migratory fish. *Fish and Fisheries*, 18, 54–78.

Österreichs Energie. (2009). Der Nationale Gewässerbewirtschaftungsplan 2009: Umgesetzte Maßnahmen der österreichischen Wasserkraft. Retrieved October 1st, 2019 from: https://oesterreichsenergie.at/der-nationale-gewaesserbewirtschaftungsplan-2009-umgesetzte-massnahmen-der-oesterreichischen-wasserkraft.html

Olivares, M.A. (2008). *Optimal Hydropower Reservoir Operation with Environmental Requirements*. Ph.D. Thesis. Oakland, CA, USA, University of California.

Pander, J., & Geist, J. (2013). Ecological indicators for stream restoration success. *Ecological Indicators*, 30, 106–118.

Pérez-Díaz, J.I., & Wilhelmi, J.R. (2010). Assessment of the economic impact of environmental constraints on short-term hydropower plant operation. *Energy Policy*, 38, 7960–7970.

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.

Renöfält, B., Jansson, R., & Nilsson, C. (2010). Effects of hydropower generation and opportunities for environmental flow management in Swedish riverine ecosystems. *Freshwater Biology*, 55, 49–67.

Reuter, M., & Schmalz, M. (2017). *Gesamtkonzept zur Herstellung der Durchgängigkeit von Gera, Apfelstädt und Ohra*. Jena, Germany, Thüringer Landesanstalt für Umwelt und Geologie.

Romão, F., Santos, J., Katopodis, C., Pinheiro, A., & Branco, P. (2018). How Does Season Affect Passage Performance and Fatigue of Potamodromous Cyprinids? An Experimental Approach in a Vertical Slot Fishway. *Water*, 10, 395.

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.

Rudberg, P., Escobar, M., Gantenbein, J., & Niiro, N. (2015). Mitigating the Adverse Effects of Hydropower Projects: A Comparative Review of River Restoration and Hydropower Regulation in Sweden and the United States. *Georgetown International Environmental Law Review*, 27, 251–274.

Ruud, A., & Lindström, A. (2018). *Hydropower and Water Management in Austria. What Is the Current Status of Implementing the EU Water Framework Directive?* Oslo, Norway, Norwegian Institute for Nature Research, NINA Prosjektnotat 65.

Sartori, D., Catalano, G., Genco, M., Pancotti, C., Sirtori, E., Vignetti, S., & Del Bo, C. (2014). *Guide to Cost-Benefit Analysis of Investment Projects -Economic Appraisal Tool for Cohesion Policy 2014–2020*; Luxembourg, Luxembourg, European Union.

Schmalz, W. (2015). *Gesamtkonzept zur Herstellung der Durchgänigkeit der Saale; Thüringer Landesanstalt für Umwelt und Geologie*. Jena, Germany.

Schmalz, M., & Sauerwein, J. (2015). *Gesamtkonzept zur Herstellung der Durchgängigkeit der Werra*. Jena, Germany, Thüringer Landesanstalt für Umwelt und Geologie.

Schramm, M.P., Bevelhimer, M.S., & DeRolph, C.R. (2016). A synthesis of environmental and recreational mitigation requirements at hydropower projects in the United States. *Environmental Science & Policy*, 61, 87–96.

Silva, A.T., Lucas, M.C., Castro-Santos, T., Katopodis, C., Baumgartner, L.J., Thiem, J.D., Aarestrup, K., et al. (2018). The future of fish passage science, engineering, and practice. *Fish and Fisheries*, 19, 340–362.

Sovacool, B.K., Gilbert, A., & Nugent, D. (2014). An international comparative assessment of construction cost overruns for electricity infrastructure. *Energy Research & Social Science,* 3, 152–160.

Sudduth, E.B., Meyer, J.L., & Bernhardt, E.S. (2007). Stream restoration practices in the southeastern United States. *Restoration Ecology*, 15, 573–583.

Szałkiewicz, E., Jusik, S., & Grygoruk, M. (2018). Status of and Perspectives on River Restoration in Europe: 310,000 Euros per Hectare of Restored River. *Sustainability*, 10, 129.

Trussart, S., Messier, D., Roquet, V., & Aki, S. (2002). Hydropower projects: A review of most effective mitigation measures. *Energy Policy*, 30, 1251–1259.

Turner, H.C., Lauer, J.A., Tran, B.X., Teerawattananon, Y., & Jit, M. (2019). Adjusting for Inflation and Currency Changes Within Health Economic Studies. *Value in Health*, 22, 1026–1032.

Uria-Martinez, R., Johnson, M., O'Connor, P., Samu, N.M., Witt, A.M., Battey, H., & Wagoner, S. (2018). *2017 Hydropower Market Report*. Oak Ridge, TN, USA, U.S. Department of Energy.

Venus, T.E., Hinzmann, M., Bakken, T.H., Gerdes, H., Godinho, F.N., Hansen, B., Pinheiro, A., et al. (2020). The public's perception of run-of-the-river hydropower across Europe. *Energy Policy*, 140, 111422.

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.

Wüstenhagen, R., & Bilharz, M. (2006). Green energy market development in Germany: Effective public policy and emerging customer demand. *Energy Policy*, 34, 1681–1696.

6.8. Appendix 3

Table A4. Overview of all fish passage case studies used in the analysis.

Country	Type of Plant	Plant Capacity (kW)	Measure
Sweden		55	Vertical slot pass
Sweden			Denil fish pass
Sweden	Run-of-the-River	4000	Roughened bypass channel with pool structures
Sweden			Denil fish pass
Sweden			Denil fish pass
Sweden		350	Vertical slot pass
Sweden		40,000	Vertical slot pass
Sweden		599,400	Vertical slot pass
Sweden		90	Vertical slot pass
Sweden			Vertical slot pass
Sweden		5000	Roughened bypass channel with pool structures
Sweden			Vertical slot pass
Sweden			Roughened bypass channel with pool structures
Sweden		1200	Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden		2100	Roughened bypass channel with pool structures
Sweden		600	Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden		3100	Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden		300	Vertical slot pass
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden		40	Roughened bypass channel with pool structures

Country	Type of Plant	Plant Capacity (kW)	Measure
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden			Vertical slot pass
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden			Roughened bypass channel with pool structures
Sweden		1800	Guiding dam or wall
Sweden		5200	Guiding dam or wall
Sweden		29	Combined vertical slot and roughened bypass channel
Sweden		600	Vertical slot pass
Sweden		235	Vertical slot pass
Sweden		9500	Vertical slot pass
Sweden		19	Vertical slot pass
Sweden		300	Vertical slot pass
Sweden		7500	Vertical slot pass
Sweden		2500	Vertical slot pass
Sweden		13,000	Vertical slot pass
Sweden		3100	Screen/rack
Sweden		3300	Screen/rack
Sweden		40,000	Guiding dam or wall
Sweden		5,994,000	Guiding dam or wall
Sweden		7500	Vertical slot pass
Sweden		2500	Vertical slot pass
Sweden		300	Vertical slot pass
Sweden			Vertical slot pass

Country	Type of Plant	Plant Capacity (kW)	Measure
Germany	Run-of-the-River	13,000	Roughened bypass channel with pool structures
Germany	Run-of-the-River	135	Vertical slot pass
Germany	Run-of-the-River	34	Roughened bypass channel with pool structures
Germany	Run-of-the-River	1800	Combined vertical slot and roughened bypass channel
Germany	Run-of-the-River	1300	Combined vertical slot and roughened bypass channel
Germany	Run-of-the-River	6000	Vertical slot pass
Germany	Run-of-the-River	20,000	Vertical slot pass
Germany	Run-of-the-River	5000	Roughened bypass channel with pool structures
Germany			Roughened bypass channel with pool structures
Germany	Run-of-the-River	34	Combined screen/rack and bypass
Germany	Run-of-the-River	34	Vertical slot pass
Germany	Run-of-the-River	30	Roughened ramp with pool structures
Germany	Run-of-the-River	30	Combined screen/rack and bypass
Germany	Run-of-the-River	20	Roughened bypass channel with pool structures
Germany	Run-of-the-River	20	Combined screen/rack and bypass
Germany	Run-of-the-River	5	Roughened ramp with pool structures
Germany	Run-of-the-River	5	Combined screen/rack and bypass
Germany	Run-of-the-River	8	Vertical slot pass
Germany	Run-of-the-River	8	Combined screen/rack and bypass
Germany	Run-of-the-River	4	Roughened ramp with pool structures
Germany	Run-of-the-River	4	Combined screen/rack and bypass
Germany	Run-of-the-River	90	Vertical slot pass
Germany	Run-of-the-River	90	Combined screen/rack and bypass
Germany	Run-of-the-River	7	Roughened bypass channel with pool structures
Germany	Run-of-the-River	7	Combined screen/rack and bypass
Germany	Run-of-the-River	30	Roughened bypass channel with pool structures
Germany	Run-of-the-River	30	Combined screen/rack and bypass
Germany	Run-of-the-River	135	Combined screen/rack and bypass
Germany	Run-of-the-River	60	Vertical slot pass
Germany	Run-of-the-River	69	Roughened ramp with pool structures
Germany	Run-of-the-River	69	Combined screen/rack and bypass
Germany	Run-of-the-River	69	Vertical slot pass
Germany	Run-of-the-River	10	Roughened ramp with pool structures
Germany	Run-of-the-River	10	Combined screen/rack and bypass
Germany	Run-of-the-River	46	Vertical slot pass
Germany	Run-of-the-River	46	Combined screen/rack and bypass
Germany	Run-of-the-River	41	Vertical slot pass

Country	Type of Plant	Plant Capacity (kW)	Measure
Germany	Run-of-the-River	41	Combined screen/rack and bypass
Germany	Run-of-the-River	560	Vertical slot pass
Germany	Run-of-the-River	560	Screen/rack
Germany	Run-of-the-River	560	Vertical slot pass
Germany	Run-of-the-River	560	Combined screen/rack and bypass
Germany	Run-of-the-River	800	Vertical slot pass
Germany	Run-of-the-River	800	Combined screen/rack and bypass
Germany	Run-of-the-River	600	Vertical slot pass
Germany	Run-of-the-River	600	Combined screen/rack and bypass
Germany	Run-of-the-River	540	Vertical slot pass
Germany	Run-of-the-River	496	Vertical slot pass
Germany	Run-of-the-River	496	Combined screen/rack and bypass
Germany	Run-of-the-River	554	Vertical slot pass
Germany	Run-of-the-River	554	Combined screen/rack and bypass
Germany	Run-of-the-River	1300	Vertical slot pass
Germany	Run-of-the-River	1300	Combined screen/rack and bypass
Germany	Run-of-the-River	60	Combined screen/rack and bypass
Germany	Run-of-the-River	80	Vertical slot pass
Germany	Run-of-the-River	300	Vertical slot pass
Germany	Run-of-the-River	300	Combined screen/rack and bypass
Germany	Run-of-the-River	300	Combined screen/rack and bypass
Germany	Run-of-the-River	300	Combined screen/rack and bypass
Germany	Run-of-the-River	300	Combined screen/rack and bypass
Germany			Roughened bypass channel with pool structures
Germany	Run-of-the-River	512	Vertical slot pass
Germany	Run-of-the-River	512	Combined screen/rack and bypass
Germany	Run-of-the-River	960	Vertical slot pass
Germany	Run-of-the-River	960	Screen/rack
Germany	Run-of-the-River	960	Combined screen/rack and bypass
Germany	Run-of-the-River	280	Vertical slot pass
Germany	Run-of-the-River	280	Combined screen/rack and bypass
Germany	Run-of-the-River	290	Roughened bypass channel with pool structures
Germany	Run-of-the-River	290	Combined screen/rack and bypass
Germany	Run-of-the-River	270	Vertical slot pass
Germany	Run-of-the-River	150	Combined screen/rack and bypass
Germany	Run-of-the-River	190	Vertical slot pass
Germany	Run-of-the-River	190	Vertical slot pass
Germany	Run-of-the-River	190	Combined screen/rack and bypass
Germany	Run-of-the-River	190	Roughened bypass channel with pool structures
Germany	Run-of-the-River	190	Bypass system
Germany	Run-of-the-River	30	Vertical slot pass
Germany	Run-of-the-River	29	Vertical slot pass
Germany	Run-of-the-River	80	Combined screen/rack and bypass

Country	Type of Plant	Plant Capacity (kW)	Measure
Germany	Run-of-the-River	55	Vertical slot pass
Germany	Run-of-the-River	55	Bypass system
Germany	Run-of-the-River	40	Vertical slot pass
Germany	Run-of-the-River	40	Bypass system
Germany	Run-of-the-River	33	Vertical slot pass
Germany	Run-of-the-River	33	Bypass system
Germany	Run-of-the-River	33	Roughened bypass channel with pool structures
Germany	Run-of-the-River	33	Bypass system
Germany	Run-of-the-River	50	Combined screen/rack and bypass
Germany	Run-of-the-River	21	Vertical slot pass
Germany	Run-of-the-River	11	Roughened bypass channel with pool structures
Germany	Run-of-the-River	11	Bypass system
Germany	Run-of-the-River	18	Roughened bypass channel with pool structures
Germany	Run-of-the-River	15	Vertical slot pass
Germany	Run-of-the-River	15	Screen/rack
Germany	Run-of-the-River	681	Roughened bypass channel with pool structures
Germany	Run-of-the-River	681	Combined screen/rack and bypass
Germany	Run-of-the-River	681	Vertical slot pass
Germany	Run-of-the-River	681	Combined screen/rack and bypass
Germany	Run-of-the-River	480	Vertical slot pass
Germany	Run-of-the-River	480	Combined screen/rack and bypass
Germany	Run-of-the-River	480	Vertical slot pass
Germany	Run-of-the-River	22	Roughened ramp with pool structures
Germany	Run-of-the-River	520	Roughened bypass channel with pool structures
Germany	Run-of-the-River	520	Combined screen/rack and bypass
Germany	Run-of-the-River	520	Combined screen/rack and bypass
Germany	Run-of-the-River	520	Combined screen/rack and bypass
Germany	Run-of-the-River	520	Combined screen/rack and bypass
Germany	Run-of-the-River	315	Vertical slot pass
Germany	Run-of-the-River	315	Combined screen/rack and bypass
Germany	Run-of-the-River	315	Vertical slot pass
Germany	Run-of-the-River	315	Combined screen/rack and bypass
Germany	Run-of-the-River	400	Roughened bypass channel with pool structures
Germany	Run-of-the-River	400	Combined screen/rack and bypass
Germany	Run-of-the-River	400	Vertical slot pass
Germany	Run-of-the-River	400	Roughened bypass channel with pool structures
Germany	Run-of-the-River	230	Vertical slot pass
Germany	Run-of-the-River	230	Combined screen/rack and bypass
Germany	Run-of-the-River	250	Vertical slot pass

Country	Type of Plant	Plant Capacity (kW)	Measure
Germany	Run-of-the-River	250	Combined screen/rack and bypass
Germany	Run-of-the-River	250	Vertical slot pass
Germany	Run-of-the-River	250	Vertical slot pass
Germany	Run-of-the-River	250	Vertical slot pass
Germany	Run-of-the-River	11	Vertical slot pass
Germany	Run-of-the-River	11	Combined screen/rack and bypass
Germany	Run-of-the-River	13	Roughened bypass channel with pool structures
Germany	Run-of-the-River	13	Combined screen/rack and bypass
Germany	Run-of-the-River	13	Vertical slot pass
Germany	Run-of-the-River	13	Vertical slot pass
Germany	Run-of-the-River	9	Vertical slot pass
Germany	Run-of-the-River	18	Vertical slot pass
Germany	Run-of-the-River	18	Combined screen/rack and bypass
Germany	Run-of-the-River	18	Vertical slot pass
Germany	Run-of-the-River	18	Vertical slot pass
Germany	Run-of-the-River	11	Vertical slot pass
Germany	Run-of-the-River	11	Combined screen/rack and bypass
Germany	Run-of-the-River	35	Roughened bypass channel with pool structures
Germany	Run-of-the-River	21	Roughened bypass channel with pool structures
Germany	Run-of-the-River	21	Combined screen/rack and bypass
Germany	Run-of-the-River	35	Roughened bypass channel with pool structures
Germany	Run-of-the-River	35	Combined screen/rack and bypass
Germany	Run-of-the-River	20	Vertical slot pass
Germany	Run-of-the-River		Combined screen/rack and bypass
Germany	Run-of-the-River	19	Roughened bypass channel with pool structures
Germany	Run-of-the-River	19	Combined screen/rack and bypass
Germany	Run-of-the-River	35	Combined screen/rack and bypass
Germany	Run-of-the-River	40	Roughened bypass channel with pool structures
Germany	Run-of-the-River	40	Combined screen/rack and bypass
Germany	Run-of-the-River	110	Vertical slot pass
Germany	Run-of-the-River	110	Combined screen/rack and bypass
Germany	Run-of-the-River	100	Vertical slot pass
Germany	Run-of-the-River	100	Combined screen/rack and bypass
France	Run-of-the-River	380	Vertical slot pass
France	Run-of-the-River	4381	Combined screen/rack and bypass
France	Run-of-the-River	2610	Screen/rack
France	Run-of-the-River	400	Roughened bypass channel with pool structures
France	Run-of-the-River	400	Vertical slot pass
France	Reservoir	1800	Denil fish pass

Country	Type of Plant	Plant Capacity (kW)	Measure
France	Reservoir	1800	Combined screen/rack and bypass
France	Run-of-the-River	380	Combined screen/rack and bypass
France	Run-of-the-River	1700	Vertical slot pass
France	Run-of-the-River	1700	Screen/rack
France	Run-of-the-River	320	Screen/rack
France	Run-of-the-River	900	Vertical slot pass
France	Run-of-the-River	1600	Vertical slot pass
France	Run-of-the-River	1600	Vertical slot pass
Switzerland	Run-of-the-River	4000	Combined vertical slot and roughened bypass channel
Switzerland	Run-of-the-River	4000	Screen/rack
Austria			Vertical slot pass
Austria			Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	880	Vertical slot pass
Austria	Run-of-the-River	2360	Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	43,200	Vertical slot pass
Austria		24,800	Combined vertical slot and roughened bypass channel
Austria		2900	Combined vertical slot and roughened bypass channel
Austria		900	Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	179,000	Roughened bypass channel with pool structures
Austria	Run-of-the-River	179,000	Vertical slot pass
Austria	Run-of-the-River	168,000	Vertical slot pass
Austria			Vertical slot pass
Austria		3000	Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria	Run-of-the-River	73,000	Roughened bypass channel with pool structures
Austria	Run-of-the-River	187,000	Roughened bypass channel with pool structures
Austria	Run-of-the-River	187,000	Roughened bypass channel with pool structures
Austria			Roughened bypass channel with pool structures
Austria			Vertical slot pass
Austria	Run-of-the-River	328,000	Vertical slot pass
Austria	Run-of-the-River	293,000	Roughened bypass channel with pool structures
Austria			Fish lift
Austria			Vertical slot pass

Country	Type of Plant	Plant Capacity (kW)	Measure
Austria	Run-of-the-River	172,000	Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria	Run-of-the-River	41,000	Guiding dam or wall
Austria	Run-of-the-River	41,000	Vertical slot pass
Austria			Vertical slot pass
Austria			Roughened bypass channel with pool structures
Austria	Run-of-the-River	25,000	Vertical slot pass
Austria	Run-of-the-River	25,000	Vertical slot pass
Austria			Combined vertical slot and roughened bypass channel
Austria			Vertical slot pass
Austria	Run-of-the-River	80,000	Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria		198,000	Vertical slot pass
Austria	Run-of-the-River	79,000	Vertical slot pass
Austria	Run-of-the-River	28,000	Vertical slot pass
Austria	Run-of-the-River	22,000	Vertical slot pass
Austria	Run-of-the-River	10,000	Vertical slot pass
Austria			Roughened bypass channel with pool structures
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria	Run-of-the-River	14,000	Vertical slot pass
Austria			Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	12,000	Vertical slot pass

Country	Type of Plant	Plant Capacity (kW)	Measure
Austria	Run-of-the-River	18,000	Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	19,000	Combined vertical slot and roughened bypass channel
Austria			Fish lift
Austria	Run-of-the-River	19,000	Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	16,000	Vertical slot pass
Austria	Run-of-the-River	15,000	Vertical slot pass
Austria	Run-of-the-River	15,000	Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	13,000	Vertical slot pass
Austria	Run-of-the-River	13,000	Vertical slot pass
Austria	Run-of-the-River	390	Vertical slot pass
Austria			Vertical slot pass
Austria			Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	13,000	Vertical slot pass
Austria	Run-of-the-River	17,000	Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	6400	Vertical slot pass
Austria	Run-of-the-River	1600	Vertical slot pass
Austria	Run-of-the-River	17,000	Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	17,000	Vertical slot pass
Austria	Run-of-the-River	16,000	Vertical slot pass
Austria			Vertical slot pass
Austria	Run-of-the-River	18,000	Roughened bypass channel with pool structures
Austria			Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	16,000	Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	8600	Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	11,700	Vertical slot pass
Austria	Run-of-the-River	2600	Vertical slot pass
Austria	Run-of-the-River	500	Vertical slot pass
Austria			Combined vertical slot and roughened bypass channel
Austria	Run-of-the-River	12,200	Fish lift
Austria	Run-of-the-River	3600	Combined vertical slot and roughened bypass channel
Austria			Vertical slot pass
Austria			Vertical slot pass
Austria			Vertical slot pass

Country	**Type of Plant**	**Plant Capacity (kW)**	**Measure**
Austria			Vertical slot pass
Austria	Run-of-the-River	45,800	Vertical slot pass
Austria	Run-of-the-River	2000	Combined vertical slot and roughened bypass channel

Table A5. Confidence intervals (95%) for the three upstream models presented in Table 3.

	Log$_e$ of Capital Costs					
	Model 1: Type of Upstream Measure		**Model 2: Implemented vs. Planned Costs**		**Model 3: Nature-Like vs. Technical vs. Combined Passes**	
	95% C.I.		**95% C.I.**		**95% C.I.**	
Fixed Effects						
Intercept	8.02	9.95	9.05	10.32	8.84	10.62
Log of length (m)	0.39	0.70	0.38	0.68	0.11	0.43
Log of obstacle height (m)	0.26	0.78	0.29	0.80	0.50	1.05
Log of plant capacity (kW)	0.03	0.18	0.03	0.17	0.04	0.19
Implemented (binary)			−1.31	−0.54		
Nature-like (binary)					−2.59	−0.69
Combined (binary)					0.81	6.94
Nature-like *log of height					−0.85	0.29
Nature-like *log of length					0.06	0.64
Combined *log of height					−1.74	0.08
Combined *log of length					−0.78	0.16
Fish lift	1.31	4.44	1.23	4.30		
Roughened bypass channel with pool structures	−1.02	−0.04	−0.92	−0.01		
Roughened ramp with pool structures	−0.65	0.70	−0.62	0.71		
Vertical slot pass	−0.58	0.32	−0.52	0.33		
Sig01	0.17	1.40	0.00	0.22	0.15	1.26
Sigma	0.55	0.70	0.55	0.70	0.55	0.70

Table A6. Confidence Intervals (95%) for the downstream model presented in Table 4.

Variable	**95% Confidence Interval**	
Intercept	8.04	9.19
Log of Area (m^2)	1.02	1.35
Vertical configuration (binary)	−0.49	0.31

7. General Discussion

Challenges and opportunities for fish conservation in hydropower impacted rivers

NICOLE SMIALEK

The present dissertation highlighted the existing challenges and opportunities in freshwater fish conservation in hydropower affected rivers from a multilevel perspective. It was revealed that there are still considerable data gaps for relevant autecological traits (e.g., minimum viable population size) in rheophilic fish species, which are of great importance for risk assessment and planning of mitigation measures. However, it was also highlighted that the use of grey literature data can add valuable knowledge and complement peer-reviewed data (**Chapter I)**. Furthermore, it has been shown that for closely related species and species sharing a common habitat, it is not readily possible to transfer knowledge from one species to another, but that it is necessary to know the autecological requirements of each individual species (**Chapter II**). New insights were also provided on the role of fish behaviour during net-based fish monitoring at hydropower plants. For the first time, it was revealed which behavioural patterns enable fish to avoid recapture and its relevance for the evaluation of net-based monitoring studies (**Chapter III**). In addition to the biological aspects, this thesis also examined the economic challenges in fish conservation in hydropower affected rivers. Cost-analyses on fish passage mitigation revealed that life-time costs between nature-like and technical solutions vary considerably and that there is a need for a trade-off between mitigating negative impacts and hydropower operation (**Chapter IV**).

7.1. Data accessibility – a short remark

The assessment of the data basis of ecological requirements (e.g., habitat preferences, physical & chemical thresholds) of European riverine fish species **(Chapter I & II)** as well as literature search on fish behaviour during monitoring at hydropower facilities

(**Chapter III**) and cost data on up- and downstream mitigation strategies (**Chapter IV**) revealed considerable data gaps on the respective subjects. While some data gaps exist due to shortcomings in research e.g., data on minimum viable population size of species - **Chapter I**, or cost data on monitoring of mitigation measure efficiency - **Chapter IV**, some of these knowledge gaps are also attributed to a lack in accessibility of data from both, grey and peer-reviewed sources. While most academic articles on these topics are published in English language and easy to find using key words in modern scientific search engines (e.g., Google Scholar, Web of Knowledge), grey literature (dissertations, research-, committee-, and government reports) tends to be written in the respective language of the country of origin and is often poorly indexed, making it harder to find via search engines (e.g., Google, Ecosia). This may be due to the strong local reference of many grey literature studies as “grey” data often originate from small-scale studies with a strong local relevance in support of regulatory requirements (see for example Coeck et al. 2000, Guthruf 2016, Mueller et al. 2020). Accessibility may also be restricted by access rights (e.g., governmental reports) or price (e.g., some articles in peer-review journals). A change towards more open access publishing is currently driven by public research funders and administrations in Europe, which are starting dedicated funds for paying the article publishing charges of authors from the respective countries. Better accessibility of grey literature in terms of language is also becoming better as some countries started to include English abstracts and data table descriptions to their technical reports and most doctoral theses (at least in Europe) are already written in English language. Access to data could also be made easier by comprehensive data bases with high data credibility. Such data bases partly exist for example for general biological traits of freshwater fish species (e.g., FishBase, http://www.fishbase.org; Froese 1990) but not yet for costs on mitigating hydropower impacts. However, maintaining and coordinating such data bases is associated with a high workload for data gathering and review. Hence, Lecocq et al. (2019) criticize the synthesized mixture of data provided on FishBase (http://www.fishbase.org; Froese 1990) and the lack of important contextual information about measurement environmental context or levels of variation and replication for trait data. Lecocq et al. (2019) aim to address these shortcomings in their own newly introduced database

(TOFF database, http://toff-project.univ-lorraine.fr; Lecocq et al. 2019). However, it can be argued that the shortcoming of their TOFF database is that it only focuses on fish species that are important for aquaculture. Hence, the hosting of comprehensive databases which provide valuable information for fish species conversation remains a challenge.

Additionally, some knowledge gaps can be also attributed to a general lack in comparability. Comparability of data was found to be difficult as measures or reporting often lacked standardisation. For example, for data on fish ecology (**Chapter I & II**) and behaviour (**Chapter III**) some studies did not clearly report if their data came from controlled laboratory experiments or from field observations. Standardisation was also lacking for measurements (e.g., reporting of substrate description, **Chapter I**). For future studies, there is especially a need for the inclusion of a minimum set of directly comparable parameters (e.g., water temperature, international substrate categories, recapture rates etc.) and strict biological endpoint definitions (hatching stages, size of a minimum viable population, etc.). For mitigation measures (**Chapter IV**) there tends to be limited monitoring of their effectiveness and reporting of their costs, which makes it difficult to explore their efficiency after implementation and enable statements about cost-effectiveness. A standardisation of monitoring and reporting of hydraulic, structural, and biological parameters as well as costs would help to optimize existent or planned measures according to the knowledge about their efficiency.

7.2. Knowledge on the autecology of species

The current data situation on the autecology of species was examined in **Chapter I** and **Chapter II**. The results illustrate that some but limited knowledge for each of the selected species is present within peer-reviewed as well as grey literature. While the latter is still considered less reliable in the scientific community due to the lack of a scientific review process, this study has demonstrated that grey literature data actually reflects the findings of peer-reviewed literature very well (in cases where both are available on the same topic, **Chapter I**). This is especially true for grey literature that meets high scientific standards (i.e., standardised sampling procedures, statistical validation of results etc.). Following this, grey literature can be highly recommended to be used as a valuable complementation to peer-reviewed sources and to help fill existing data gaps on the autecology of freshwater fish species (**Chapter I**). Whether this applies generally or only to the species examined in our study requires further investigation. At least for the species studied herein grey literature holds a great opportunity to considerably strengthen their general data base and improve and accelerate related processes for their conservation (e.g., species sensitivity analyses and development/ implementation of mitigation measures).

Despite the inclusion of grey literature and the resulting larger amount of data, the general results in **Chapter I** revealed that knowledge regarding environmental tolerances, of many species, particularly during their early development, remains limited. This is particularly true for inconspicuous and little-studied potamodromous and lithophilic fish species such as European minnow (*Phoxinus phoxinus*) and chub (*Squalius cephalus*; **Chapter I**). Although potamodromous fishes are widespread among freshwater fish assemblages, diadromy has received far more attention due to the economic relevance of taxa such as Atlantic salmon (*Salmo salar*) and European eel (*Anguilla anguilla*; Northcote 1998; Lucas & Baras 2001). For example, whilst a body of literature on the influence of fine sediment on the spawning success of some salmonid species exists (**Chapter II**), knowledge of the effects of fines and the variability of other environmental parameters on the spawning of other, typically non-salmonid species, remains limited (but see Kemp et al. 2011, Dueregger et al. 2018, Bašić et al. 2019, Nagel et al. 2020). Nevertheless, potamodromous species are key for river ecosystem functioning by influencing nutrient cycling and energy transfer between ecosystems (Pennuto et al. 2018). For example, a recent study by Gerke et al. (2021) highlighted that top-down effects of European nase (*Chondrostoma nasus*) and chub (*Squalius cephalus*), both potamodromous species, can mitigate the negative effects of eutrophication and increase oxygen availability in the hyporheic zone, typical problems that arise in headwater areas of dams (Geist 2021). This example clearly emphasizes the important role of potamodromous species in river ecosystems, which the limited number of available studies and data on their autecological requirements do not do justice to. Furthermore, this data limitation can also severely hamper the evaluation of fish conversation measures. For example, without the knowledge on tolerances of potamodromous fish early life stages to habitat characteristics (e.g., grain size) and variable abiotic parameters (e.g., current speed), there is currently no easily quantifiable or transferable method to measure the success or failure of conservation actions in relation to species-specific environmental parameters or thresholds. In addition, some fish mitigation actions are limited in their success due to a lack of specific objectives or a sound understanding of underlying ecological processes that provide the context for specific problems (**Chapter II**). However, an encouraging trend towards more research on species of less economic value at least for European nase (*Chondrostoma nasus*) and European barbel (*Barbus barbus*) was already evident in the reviewed data in **Chapter I** (e.g., Bašić et al. 2017, Dueregger et al. 2018, Nagel et al. 2020).

Besides data differences between species there were also data limitations concerning all species (**Chapter I**). Data gaps were pronounced on data that are important for assessing fish population trends (e.g., minimum viable population size, number of individuals per m^2). The potential of such data was presented in **Chapter II**, where the required habitat size for Atlantic salmon and brown trout was estimated using basic information on recruitment factors. What is already possible for these two species still needs to be investigated and verified for other species including lithophilic cyprinids (e.g., nase, barbel). Ultimately, such evidence-based estimates can help to justify (expensive) restoration efforts (Pander et al. 2015). Hence, more research is needed on the recruitment process (e.g., number of eggs, area required for egg deposition, survival rates for different life stages, minimum viable population size) for target species of river restoration. More research is also required to investigate the actual state of fish populations in freshwater systems. In Europe, population trends for 76 % of all freshwater fish species remain unknown because of the lack of reliable data on trends or because no population trend data exist for most European countries (Freyhof & Brooks, 2011). Such knowledge gaps considerably hamper the understanding of the actual impact of stressors on fish populations and equally the assessment of mitigation success on population level.

Since autecological data is of such high relevance for risk assessment and mitigation actions of freshwater fishes, it is also necessary to extend the research to other species and traits of concern. For instance, in the recently published European Fish Hazard Index, van Treeck et al. (2021) use species' life-history traits as basis to assess the sensitivity of European riverine fishes to hydropower impacts. In general, risk assessments and sensitivity analyses have been increasingly used in recent years as a method for assessing ecosystem and species status in aquatic systems, especially in view of increasingly pressing stressors such as climate change (see e.g., Chessman 2013, Moyle et al. 2013, Morrison et al. 2015, Bleckner et al. 2021), which in turn underlines the general importance of a sound knowledge of species autecology. To date, most assessments focus mainly on individual species (mostly of economic relevant species such as Atlantic salmon), however, to ensure thriving populations it may be important to also consider population-level effects as mentioned above.

7.3. Analogies between species

Due to the abundance of fish species and the difficulty to know, monitor and manage every aspect of them, a shortcut could be to transfer knowledge from one species to another. This might be helpful in cases where restoration actions with a long-term perspective are planned, but a typical indicator species (e.g., *Salmo salar*) has disappeared from the river stretch and cannot be expected to return in the medium or short term. Autecological knowledge from a well-studied species could be transferred to a data-poor target species if both share or used to share common habitats. Furthermore, it can be an emergency solution when conservation action is pressing e.g., if a less studied species is facing extinction.

Hence, this thesis explored which analogies can be drawn within lithophilic species or close relatives (i.e., sister species) concerning their autecological requirements (**Chapter I & II**). In **Chapter I**, the traits of nine lithophilic species were reviewed. Due to shortcomings in data on autecological traits for some of the species it was only possible to compare a few traits. However, it was found that the examined autecological requirements "current speed in juvenile habitat", "current speed spawning site", "water depth in juvenile habitat" or "water depth at spawning sites", were very similar between all reviewed species, also between cyprinids and salmonids (**Chapter I**, Fig. 3). Similarity between species was highest among the lithophilic cyprinids European barbel (*Barbus barbus*), European nase (*Chondrostoma nasus*) and common dace (*Leuciscus leuciscus*). This may not seem particularly surprising, as all species share the same habitat in most rivers and must therefore have similar autecological requirements. However, larger differences became evident when comparing the requirements for "substrate spawning site". Although all species are lithophilic they still prefer very different substrate sizes, with some species being very tolerant for a large spectrum of sizes e.g., European nase (*Chondrostoma nasus*), while others tolerate only a narrow range e.g., European minnow (*Phoxinus phoxinus*). Hence, while for some autecological requirements of lithophilic fish species it seems permissible to transfer knowledge between species sharing common habitats, this may not be the case for all life-phases as species may use habitat (e.g., preference for different substrate sizes) and seasonality (e.g., different spawning times) as niche to avoid competition for resources (Sternecker et al. 2014, Wolter et al. 2016). It is therefore recommended to transfer knowledge between lithophilic species only in really urgent cases, but for long-term success, e.g., self-sustainable populations, there is no way around researching each species' individual requirements.

A similar conclusion can be drawn from the in-depth comparison between the two sister species Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta fario*). Since both species are well studied, there is a large body of data which allows for precise comparisons. **Chapter II** highlighted the similarities of both species in terms of body size and shape as well as habitat requirements in freshwater. Nevertheless, both species have a different conservation and population status in Europe (Freyhof 2011, 2014). The comparison revealed that this is mainly due to their habitat changes during their life cycle. While the anadromous Atlantic salmon moves long-distances between freshwater and the sea, brown trout remains in freshwater (Hutching & Jones 1998, Kottelat & Freyhof 2007). In relation to a stressor such as hydropower, this means that the main bottleneck for Atlantic salmon is the safe fish passage and connectivity between relevant habitats. Hence, although the similarity of the two sister species in their critical life stages seems to outweigh the differences, it is the small dissimilarities that determine the risk potential of a species in the presence of a certain stressors. Thus, the results of **Chapter I** and **Chapter II** proof that drawing analogies between species is difficult highlighting the importance of profound research on the ecology of each individual species.

A sound knowledge of the autecology of each species could open up the possibility for another alternative shortcut. These detailed data could be used to identify stressors with the greatest impact on most species. Conservation measures could then be prioritised in terms of mitigating these stressors to achieve maximum positive effect for most species with minimum effort. This would also be in line with Decker et al. (2017) and Geist (2021), which suggest that freshwater fish conservation should shift from considering individual species to a consideration of population-level effects, communities and habitats, ideally focusing more on incorporating ecological function into conservation decision making.

This idea is also embedded in the ecosystem-based approach to management (EBM) which is being promoted by Langhans et al. (2019) for fresh waters and has already been successfully used in the marine realm (Wondolleck & Yaffee 2017). The aim of this integrated management approach is to facilitate ecosystem health and functioning so as to sustain diverse and productive ecosystems and the services they provide while considering the full array of interactions within an ecosystem. However, its implementation is complex as it requires extensive knowledge on a range of different research areas (Langhans et al. 2019). For example, in addition to the proposed expansion of knowledge herein on individual requirements, species history and species movements, the effects of biotic interactions and the effects of genetic differentiation should also be considered (Langhans et al. 2019).

7.4. The role of fish behaviour in net-based fish monitoring

Besides the importance of autecological data of individual species and the consideration of life strategies of multiple species, behavioural aspects have been found to be of major importance for freshwater fish conservation (**Chapter III**). Knowledge about corridor choice or daily and seasonal migration patterns give valuable insights into mitigation options for hydropower operation (Egg et al. 2017, Knott et al. 2019, 2020). The results of **Chapter III** highlight that ignoring the behavioural component can already complicate the evaluation of fish-monitoring at hydropower facilities.

Using brown trout as model organism, it was for the first time possible to record certain behavioural patterns (sneaking, dwelling and commuting), which all have shown to bias recapture rates in standardised stow-net sampling (**Chapter III**). The results further suggest that fish, irrespective of their size will interact with the net and try to pass through (**Chapter III**). This can lead either to an intrusion of fish into the net (e.g., fish enter the net from the outside), or fish escaping the catch unit (e.g., triggered by conspecifics outside the catch unit). Either way would lead to a bias in recapture rates and thus, to an under- or overestimation of fish that are thought of having safely passed the turbine.

For fish-monitoring at hydropower plants net-based sampling is the current state of the art for quantifying downstream fish movement as it offers the needed sharpness of details concerning the number, size and species composition (Pander et al. 2017, Mueller et al. 2020a, Mueller et al. 2020b). This precision is not yet existent in other techniques (Egg et al. 2018) and thus, further studies for a more exact determination of the number of escapers or intruders may be beneficial to minimize the bias. First indications of net-interaction behaviour in other species were already reported for European barbel (*Barbus barbus;* Figure 31) and common bleak (*Alburnus alburnus*; Pander et al. 2017, Mueller et al. 2020a, Mueller et al. 2020b). Thus, the continuation of this research for species other than brown trout also considering different life stages is the next logical step. For example, it is conceivable that in schooling fish such as common bleak (*Alburnus alburnus*), the net interactions could be even more pronounced due to “social effects” (e.g., fish follow their conspecifics). The same may apply for juvenile fish of different species which tend to aggregate as shown for brown trout in **Chapter III**. Recent findings of Kressler et al. (2021) underline the important role of “social effects” and personality in trapping fish, whereby conspecifics can function as lure. Generally, the interest in fish personality has steadily increased over the last years highlighting that explorative and reactive behaviour in individual fish can be highly different even if both individuals belong to the same species or cohort (Fraser 2001, Sneddon 2003, Toms et al. 2010, Castanheira et al. 2013, **Chapter III**). Hence, besides research on behavioural differences between species it might also be of great interest to explore personality in individual fish as this is also a trait possibly affecting adaptive capacity of fish and thus evolutionary responses to stressors (Jacquin et al. 2020).

Figure 31. European barbel trapped in a net
European barbel (*Barbus barbus*) got trapped in a stow-fyke net while trying to swim through the mesh. This net was used during standardised fish passage monitoring at a run-of-the-river hydropower facility. The barbel was photographed after the net had been retrieved after sampling. Source ©AQUASYS.

The consideration of behavioural aspects is not only important to account for the bias caused in net-based fish-monitoring at hydropower plants but can generally better the understanding of fish movement patterns, specific behavioural responses to obstacles and the influential factors behind it. This knowledge can in turn be very useful to improve other aspects of fish conservation such as fish passage (see for example Egg 2020).

7.5. The cost of fish passage mitigation

Mitigating negative impacts of stressors is a key element in freshwater fish conservation. The implementation of measures mitigating hydropower includes the consideration of factors such as engineering (i.e., design), economic, and legal framework (Geist 2021). Engineering considerations will include the assessment of site-specific conditions such as hydrology, available space, selection of construction materials, and aquatic community characteristics. For fish in particular this may include the consideration of general autecological requirements, movement patterns, swimming performance and relevant behaviour (**Chapter I, II, III**). In addition to considering practical and biological components of mitigation, the costs associated with it can contribute to the decision on which measure is ultimately implemented. Economic considerations will include non-recurring (e.g., construction), and recurring costs (e.g., maintenance, operation) which will also factor into the overall engineering design (**Chapter IV**). Furthermore, the societal perception of a project may impact willingness to allow a particular project to proceed e.g., the desire for an ecologically friendly solution (Tabi & Wüstenhagen 2017, Mayeda & Boyd 2020, Venus et al. 2020).

In the European Union the mitigation of hydropower impacts i.e., fish passage must be implemented and paid by the operators following the "polluter-pays principle" (Köhler & Ruud 2019). Hereby, the operators must additionally balance the cost trade-offs between mitigation measures for fish with renewable energy production as fish passage measures usually result in some power production loss (**Chapter IV**). This can be caused for example through water abstraction by fish ladders (upstream solutions) or backlog effects of narrower bar spacings of fish protection screens (downstream solutions) (Francfort et al. 1994, David et al. 2019, Albayrak et al. 2020). These costs can account for > 50 % of the total lifetime costs (i.e., income loss) of a measure (vertical slot pass) under a high electricity price scenario (**Chapter IV**). Therefore, operators have a legitimate interest in selecting measures that cause low income losses and still ensure a functional fish passage to meet the ecological requirement of free fish migration. Aspects of this cost trade-off were investigated in **Chapter IV** using fish passage as case study. A systematic overview was provided on non-recurring costs (construction) and recurring costs (maintenance, monitoring, power losses) for different fish passage solutions, eventually presenting the life-time costs of the measures. Some results have shifted previous perceptions of costs on fish passage solutions such as that nature-like solutions tend to cost less than technical solutions when comparing the total costs of upstream measures across different electricity price scenarios (**Chapter IV**). Furthermore, nature-like fish passes were found to incur fewer power losses. This was surprising, as it was assumed that nature-like fish passes would cause higher overall costs compared to technical solutions due to their larger spatial extent and the associated likely higher costs for land acquisition and water provision e.g., to maintain a certain water level throughout the system. But not only from a financial perspective nature-like fish passes seem an attractive choice. In addition to facilitating fish passage, it can provide valuable habitat for different life stages of freshwater fish (Pander et al. 2013, Meulenbroek et al. 2018, Tamario et al. 2018, Pander et al. 2021) and other organisms (e.g., macrozoobenthos; Gustafsson et al. 2013). In addition, it blends more naturally into the landscape compared to technical solutions, which might also contribute to a higher societal acceptance. Hence, hydropower operators which implemented nature-like bypass systems did not only chose a “fish friendly“ solution but against past perceptions may even pay less for implementation and may experience lower income losses. A higher availability of transparent cost breakdowns would enable more operators to choose such attractive options. In general, cost overviews are of great use for decision makers, not only to compare different cost scenarios, but also to identify the main cost drivers and find the most cost-effective mitigation measure for their own project. Therefore, an open policy should be implemented that allows stakeholders to access such data.

Despite the general scarcity of data on construction, power losses and maintenance costs of fish passage structures (**Chapter IV**), it was possible to compare some upstream fish passage solutions to estimate the share of the different costs during lifetime but not for downstream measures since data on recurring costs was not available. Data was also limited on fish monitoring and related costs. Since cost overviews can be highly valuable for decision makers to compare different cost scenarios, spot the main cost drivers and to help find the most cost-effective mitigation measure for their own project, future research in this area is strongly recommended.

While **Chapter IV** focused mainly on cost figures of mitigation measures, effectiveness studies are equally important, especially when costs and benefits need to be balanced as for hydropower. Comprehensive and ideally long-term effectiveness monitoring of e.g., passage facilities help to understand which factors (natural or technical) may determine the success or failure of a measure. This valuable information can be used to inform design or operational changes to facilitate improvement in future projects to avoid costly retrofits for non-functioning systems. Yet, information on effectiveness-monitoring at fish passage facilities was found to be scarce (**Chapter IV**).

7.6. Conclusion & Outlook

In summary, this thesis highlighted the current challenges in freshwater fish conservation in hydropower affected rivers regarding the data basis to identify, assess and mitigate stressor impacts (Figure 32). It was found that knowledge on species' autecology is still scarce, but grey literature may be a promising complement to peer-reviewed data. The comparison of life history traits between species revealed that analogies can only be drawn to a limited extent, which emphasizes the need for more basic research on individual fish species ecology. It was further shown for the first time that fish behaviour can bias recapture rates in net-based monitoring and thus need more consideration in future investigations. Furthermore, the value of cost figures on fish passage mitigation solutions was evaluated. The results demonstrate that precise cost-figures can not only simplify the selection process of a mitigation solution but can also help to account for possible trade-offs between hydropower operation and mitigation, as power losses may account for a large proportion of the overall life-time costs of mitigation measures. However, to ensure that the selected mitigation measures follow current evidence-based standards, offering the best available trade-off between costs and biological effectiveness, there is a need for more openly available and detailed cost reports as well as long-term data on measure efficiency monitoring.

The studies presented in this thesis reflect only parts of the overall complex research subject. Nevertheless, these results contribute considerably to a progress in fish conservation in hydropower affected rivers, since only if the challenges are recognized and overcome it will be possible to implement long-term effective conservation measures.

Yet, this does not apply for hydropower only, as shown herein, but may be transferrable to other stressors as well, since the general framework of (i) impact identification, (ii) impact assessment and (iii) selection of appropriate mitigation measures can be considered similar among multiple stressors (Figure 32).

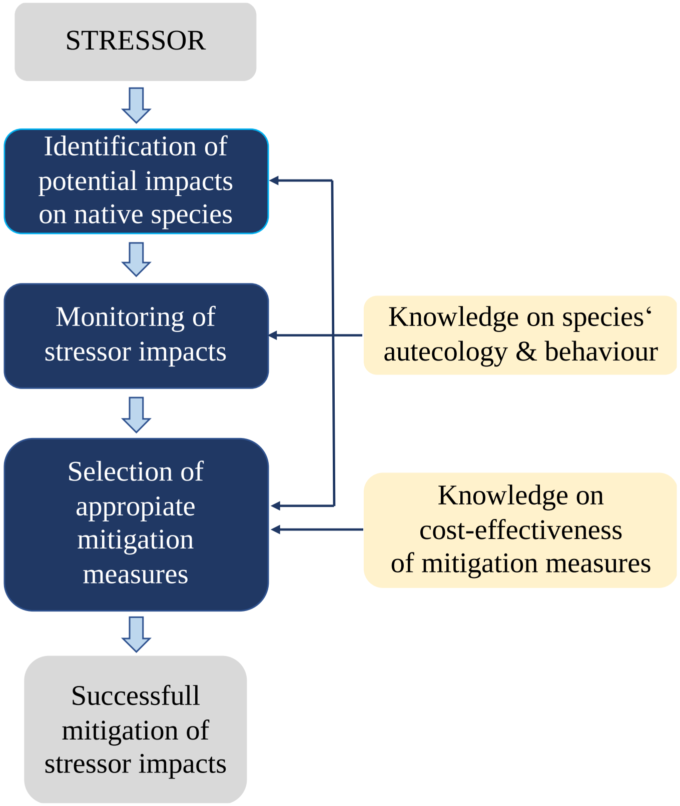

Figure 32. Framework for stressor mitigation
Framework presenting a multi-level approach to reach a successful mitigation of stressors.

7.7. References

Albayrak, I., Beck, C., Kriewitz-Byun, C.R., Doessegger, A., & Boes, R.M. (2019). Downstream fish passage technologies for medium-to-large hydropower plants: Part II. *Proceedings of the SHF Conference* (HydroES ‘19), Grenoble, France, *23*, 1–7.

Bašić, T., (2016). *Applied ecology and management of a European barbel Barbus barbus population of a lowland river*. Doctoral thesis, Bournemouth, U.K., Bournemouth University.

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*(1), 110–122.

Beck, C., Albayrak, I., Meister, J., Peter, A., Selz, O.M., Leuch, C., Vetch, D.F., et al. (2020). Swimming Behavior of Downstream Moving Fish at Innovative Curved-Bar Rack Bypass Systems for Fish Protection at Water Intakes. *Water*, *12*(11), 3244.

Blenckner, T., Möllmann, C., Stewart Lowndes, J., Griffiths, J. R., Campbell, E., De Cervo, A., Belgrano, A., et al. (2021). The Baltic Health Index (BHI): Assessing the social–ecological status of the Baltic Sea. *People and Nature*, *3*(2), 359–375.

Castanheira, M.F., Herrera, M., Costas, B., Conceição, L.E., & Martins, C.I. (2013). Can we predict personality in fish? Searching for consistency over time and across contexts. *PLoS One*, *8*(4), e62037.

Chessman, B.C. (2013). Identifying species at risk from climate change: traits predict the drought vulnerability of freshwater fishes. *Biological Conservation*, *160*, 40–49.

Coeck, J., Colazzo, S., Meire, P., & Verheyen, R.F. (2000). Herintroductie en herstel van kopvoornpopulaties (*Leuciscus cephalus* L.) in het Vlaamse Gewest. Wetenschappelijke opvolging van lopende projecten en onderzoek naar de habitatbinding in laaglandrivieren. Rapport Instituut voor Natuurbehoud, Brussels, Belgium, 176 pp.

David, L., Lemkecher, F., Chatellier, L., Dewitte, M., Courret, D., & Doessegger, A. (2019). Downstream fish passage technologies for small-to-medium hydropower plants: part I. *Proceedings of the SHF Conference,* (HydroES) *2019*, Grenoble, France, 1–6.

Decker, E., Linke, S., Hermoso, V., & Geist, J. (2017). Incorporating ecological functions in conservation decision making. *Ecology and evolution*, *7*(20), 8273–8281.

Drenner, S.M., Clark, T.D., Whitney, C.K., Martins, E.G., Cooke, S.J., & Hinch, S.G. (2012). A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. *PloS ONE*, *7*(3), e31311.

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.

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. (2018). Comparison of sonar-, camera-and net-based methods in detecting riverine fish-movement patterns. *Marine and Freshwater Research*, *69*(12), 1905–1912.

Egg, L. (2020). Fish behavior and movement in front of hydropower plants and hydro engineering installations. Doctoral thesis, Freising, Germany, Technical University Munich.

Francfort, J.E., Čada, G.F., Dauble, D.D., Hunt, R.T., Jones, D.W., Rinehart, B.N., Sommers, G.L. et al. (1994). *Environmental mitigation at hydroelectric projects. Volume 2, Benefits and costs of fish passage and protection*. Idaho Falls, United States, EG & G Idaho Inc. 351pp.

Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N., & Skalski, G.T. (2001). Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. American Naturalist,158, 124–13.

Freyhof, J. (2011). *Salmo trutta*. The IUCN Red List of Threatened Species 2011: e.T19861A9050312. Retrieved December 6th, 2020 from: https://www.iucnredlist.org/species/19861/9050312

Freyhof, J. (2014). *Salmo salar*. The IUCN Red List of Threatened Species 2014: e.T19855A2532398. Retrieved December 6th, 2020 from: https://www.iucnredlist.org/species/19855/9026693.

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

Froese, R. 1990. FishBase: An information system to support fisheries and aquaculture research. *ICLARM Fishbyte*, 8(3), 21–24.

Geist, J. (2021). Editorial: Green or red: Challenges for fish and freshwater biodiversity conservation related to hydropower. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 1–8. https://doi.org/10.1002/aqc.3597

Gerke, M., Hübner, D., Schneider, J. & Winkelmann, C. (2021). Can top-down effects of cypriniform fish be used to mitigate eutrophication effects in medium-sized European rivers? Science of the Total Environment, 755(1), 142547.

Gustafsson, S., Österling, M., Skurdal, J., Schneider, L.D., & Calles, O. (2013). Macroinvertebrate colonization of a nature-like fishway: The effects of adding habitat heterogeneity. *Ecological engineering*, 61, 345–353.

Guthruf, J. (2016). Äschenmonitoring Linthkanal, Fortpflanzungserfolg nach Revitalisierung, Empfehlungen für Schonbestimmungen. Wichtrach, Germany, Aquatica GmbH, 54pp.

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

Hutchings, J.A. & Jones, M.E.B. (1998). Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Science*, 55, 22–47.

Jacquin, L., Petitjean, Q., Côte, J., Laffaille, P., & Jean, S. (2020). Effects of pollution on fish behavior, personality, and cognition: some research perspectives. *Frontiers in Ecology and Evolution*, *8*, 86.

Kemp, P.S., Sear, D., Collins, A., Naden, P., & Jones, I. (2011). The impacts of fine sediment on riverine fish. *Hydrological Processes*, 25(11), 1800–1821.

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*(21), 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*(1), 74–88.

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

Köhler, B., & Ruud, A. (2019). How Are Environmental Measures Realized in European Hydropower? A Case-Study of Austria, Sweden and Switzerland; HydroCen Report 6; Norwegian Research Centre for Hydropower Technology, Trondheim, Norway, 81pp.

Kressler, M.M., Gerlam, A., Spence-Jones, H., & Webster, M.M. (2021). Passive traps and sampling bias: Social effects and personality affect trap entry by sticklebacks. *Ethology*, *127*(6), 446–452.

Langhans, S.D., Domisch, S., Balbi, S., Delacámara, G., Hermoso, V., Kuemmerlen, M., Martin, R., et al. (2019). Combining eight research areas to foster the uptake of ecosystem-based management in fresh waters. *Aquatic Conservation: Marine and Freshwater Ecosystems, 29*(7), 1161–1173.

Lecocq T., Benard A., Pasquet A., Nahon S., Ducret A., Dupont-Marin K., Lang I., et al. (2019). TOFF, a database of traits of fish to promote advances in fish aquaculture. *Scientific Data*, 6, 301.

Lucas, M.C., Baras, E., Thom, T.J., Duncan, A., & Slavík, O. (2001b) Types of Migration. In M.C. Lucas, & E. Baras (Eds.), *Migration of Freshwater Fishes* (pp. 66–84). Oxford, U.K., Blackwell Science Ltd. 420pp.

Mayeda, A.M., & Boyd, A.D. (2020). Factors influencing public perceptions of hydropower projects: A systematic literature review. *Renewable and Sustainable Energy Reviews*, *121*, 109713.

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*(12), 1857–1869.

Morrison, W.E., Nelson, M.W., Griffis, R.B., & Hare, J.A. (2016). Methodology for assessing the vulnerability of marine and anadromous fish stocks in a changing climate. *Fisheries, 41*(7), 407–409.

Moyle PB, Kiernan JD, Crain PK, & Quiñones RM (2013) Climate Change Vulnerability of Native and Alien Freshwater Fishes of California: A Systematic Assessment Approach. *PLoS ONE* 8(5): e63883.

Mueller, M., Knott, J., Egg, L., Bierschenk, B., Pander, J., & Geist, J. (2020a). *Fischökologisches Monitoring an Innovativen Wasserkraftanlagen: Band 1 Hintergrund und Methoden. Technical Report for Bayerisches Landesamt für Umwelt*. Freising, Germany. Technical University Munich.

Mueller, M., Knott, J., Pander, J., & Geist, J. (2020b). *Fischökologisches Monitoring an Innovativen Wasserkraftanlagen: Band 7 Eixendorf an der Schwarzach; Technical Report for Bayerisches Landesamt für Umwelt*. Freising, Germany, Technical University.

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

Nagel, C., Pander, J., Mueller, M., & Geist, J. (2020). Substrate composition determines emergence success and development of European nase larvae (*Chondrostoma nasus* L.). *Ecology of Freshwater Fish*, *29*(1), 121–131.

Pander, J., Nagel, C., & Geist, J. (2021). Integration of Constructed Floodplain Ponds into Nature-Like Fish Passes Supports Fish Diversity in a Heavily Modified Water Body. *Water*, *13*(8), 1018.

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. (2015). Succession of fish diversity after reconnecting a large floodplain to the upper Danube River. *Ecological Engineering, 75*, 41–50.

Pander, J., Mueller, M., Knott, J., Geist, J. (2017) 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.

Pennuto, C.M., Cudney, K.A. & Janik, C.E. (2018). Fish invasion alters ecosystem function in a small heterotrophic stream. *Biol. Invasions*, 20, 1033–1047.

Rillahan, C.B., Alcott, D., Castro-Santos, T., & He, P. (2021). Activity Patterns of Anadromous Fish below a Tide Gate: Observations from High-Resolution Imaging Sonar. *Marine and Coastal Fisheries*, *13*(3), 200–212.

Sneddon, L.U. (2003). The bold and the shy: Individual differences in rainbow trout. Journal of Fish Biology, 62, 971–975.

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*(13), 2749–2758.

Tabi, A., & Wüstenhagen, R. (2017). Keep It Local and Fish-Friendly: Social Acceptance of Hydropower Projects in Switzerland. *Renewable and Sustainable Energy Reviews*, 68, 763–73.

Tamario, C., Degerman, E., Donadi, S., Spjut, D., & Sandin, L. (2018). Nature-like fishways as compensatory lotic habitats. *River Research and Applications*, *34*(3), 253–261.

Thalinger, B., Wolf, E., Traugott, M., & Wanzenböck, J. (2019). Monitoring spawning migrations of potamodromous fish species via eDNA. *Scientific Reports*, 9, 15388.

Thorstad, E.B., Rikardsen, A.H., Alp, A., & Økland, F. (2013). The use of electronic tags in fish research—an overview of fish telemetry methods. *Turkish Journal of Fisheries and Aquatic Sciences*, 13, 881–896.

Toms, C.N., Echevarria, D.J., & Jouandot, D.J. (2010). A methodological review of personality-related studies in fish: Focus on the shy-bold axis of behavior. International Journal of Comparative Psychology, 23, 1–25.

van Treeck, R., Radinger, J., Noble, R.A., Geiger, F., & Wolter, C. (2021). The European Fish Hazard Index–An assessment tool for screening hazard of hydropower plants for fish. *Sustainable Energy Technologies and Assessments*, 43, 100903.

Venus, T.E., Hinzmann, M., Bakken, T.H., Gerdes, H., Godinho, F.N., Hansen, B., Pinheiro, A., et al. (2020). The public's perception of run-of-the-river hydropower across Europe. *Energy Policy*, 140, 111422.

Wolter, C., Buijse, A.D., & Parasiewicz, P. (2016). Temporal and spatial patterns of fish response to hydromorphological processes. *River Research and Applications*, *32*(2), 190–201.

Wondolleck, J.M., & Yaffee, S.L. (2017). *Marine-ecosystem based management in practice: Different pathways, common lessons*. Washington, USA, Island Press. 271pp.

Zydlewski, G.B., Horton, G., Dubreuil, T., Letcher, B., Casey, S., & Zydlewski, J. (2006). Remote monitoring of fish in small streams: a unified approach using PIT tags. *Fisheries*, 31(10), 492–502.