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Restoring flows in modified rivers

Daniel Scott Hayes

Scientific advisors

Doutor Stefan Schmutz
Doutora Maria Teresa Marques Ferreira
Doutor Günther Unfer

THESIS PRESENTED TO OBTAIN THE DOCTOR DEGREE IN
RIVER RESTORATION AND MANAGEMENT

2021

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In loving memory of my grandmother
Sherry K. Hayes,
who kept on checking in
and asking how my studies are going.
† June 23, 2020

Abstract

Free-flowing rivers support diverse, complex and dynamic ecosystems, as well as provide societal and economic services. Globally, however, the water flow of many rivers has been regulated by hydropower or other sources. Flow modification affects crucial ecosystem functions and processes, and organism's capacity to fulfil its life cycle requirements. In light of these widespread effects, it is urgent to mitigate ecological impacts caused by existing water infrastructures. To achieve environmental objectives, as well as to manage water uses in a sustainable way, a thorough understanding of ecological responses to hydrological alterations on different temporal levels (e.g., environmental flow, hydropeaking) is essential. This work aims to establish holistic approaches for restoring flows in modified rivers, and to develop environmental flows able to sufficiently mitigate the ecological effects of short-term and annual flow modifications in fluvial ecosystems.

This thesis disentangles the effects of multiple stressors and shows that flow regulation is a primary predictor of fish populations. Moreover, by assessing flow-ecology relationships on annual, seasonal, and sub-daily levels, this work identifies fundamental principles to implement flow restoration measures in rivers affected by water abstraction and hydropeaking. While more dynamic flows are generally recommended as environmental flows, flow restrictions are needed for hydropeaking mitigation. Regarding the latter, a seasonal framework for hydrological mitigation based on fish life-history stages is established, and thresholds are synthesized.

Overall, this thesis advances the establishment of guidelines for successful flow restoration in river systems affected by competing water uses by establishing holistic flow restoration schemes and by subsuming quantitative and qualitative hydropeaking thresholds. Moreover, this thesis sets the topic of flow restoration into the broader context of hydromorphological river rehabilitation. Hence, this work contributes to a more balanced discussion on trade-offs between societal and environmental water uses.

Keywords: *ecohydrology, water abstraction, hydropower; water for the environment; flow alteration-ecological response relationships.*

Resumo

Os rios sem alterações do seu curso natural sustentam diferentes ecossistemas, complexos e dinâmicos, tal como promovem serviços para a sociedade e economia. No entanto, globalmente o curso de inúmeros rios sofreu algum tipo de regulação, tanto para produção hidroelétrica como outras finalidades. A alteração dos regimes naturais dos rios afeta de forma crucial as funções e processos dos ecossistemas, assim como a capacidade de muitos organismos completarem os seus ciclos de vida. Considerando estes efeitos generalizados, é urgente mitigar os impactes ecológicos originados pelas infraestruturas impactantes. De forma a atingir esses objetivos ambientais, assim como para gerir os recursos aquáticos de forma sustentável, é essencial um entendimento transversal das respostas ecológicas que ocorrem ao longo do tempo (p.e. caudais ambientais, *hydropeaking*). Assim, este trabalho tem como objetivo geral estabelecer uma abordagem holística para o restauro dos caudais de rios impactados, e para desenvolver caudais ambientais capazes de responder aos impactes ecológicos em sistemas fluviais, tanto de curto prazo como anuais, decorrentes da regulação de caudais.

Esta tese pretende clarificar os efeitos de múltiplos impactes em sistemas fluviais, demonstrando que a regulação de caudais é um preditor primário das populações piscícolas. Além disso, através da análise das relações entre componentes fluviais e componentes ecológicos, aos níveis anual, sazonal e infra-diário, este trabalho de investigação identifica os princípios fundamentais para a restauração de caudais em rios impactados por armazenamento de água e *hydropeaking*. No geral, caudais ambientais mais dinâmicos são recomendados, enquanto maiores restrições são necessárias para mitigar os impactes do *hydropeaking*. Relativamente a este, um quadro metodológico sazonal baseado nos vários estágios de vida de salmonídeos é proposto para o estabelecer de medidas de mitigação hidrológicas, e são apresentados também limiares de tolerância hidráulicos.

Em suma, esta tese pretende promover o estabelecimento de diretrizes para a restauração bem-sucedida dos regimes de caudal em rios afetados por múltiplos usos e fins. Para tal, é proposta a implementação de esquemas de restauro holístico de caudais, e a mitigação do *hydropeaking* baseada em limiares de tolerância quantitativos e qualitativos. Além disso, esta tese alarga o tema da restauração de caudais para o contexto da reabilitação fluvial integral, considerando a inclusão da sua hidromorfologia. Portanto, este trabalho de investigação pretende contribuir para uma abordagem mais equilibrada nos trade-offs entre as necessidades humana e ambiental da água dos rios.

Palavras-chave: *eco-hidrologia; captação de água; hidroeletricidade; água para fins ambientais; relação entre alteração de caudais e as respostas ecológicas*

Resumo Alargado

A água é a força motriz de vida na Terra. Nos rios, o fluxo da água ao longo do seu curso tem sido considerado uma “variável principal”, governando os processos e padrões do ambiente físico e biológico. Estes ecossistemas, incluindo os rios de fluxo livre e as zonas húmidas, representam a maior diversidade de espécies no planeta, devido à sua natureza complexa e dinâmica.

Desde o século passado, tem-se vindo a verificar uma diminuição da integridade do ecossistema, a um ritmo sem precedentes. De todos os tipos de ecossistemas, as águas interiores são as mais afetadas, apresentando declínios populacionais de 84% desde 1970, o que equivale a uma redução de 4% ao ano. Essa espiral descendente de integridade das águas interiores é impulsionada por uma série de pressões e respetivas interações. Nesse sentido, uma das maiores ameaças é a modificação do caudal dos rios causada, entre outros motivos, por barragens, desvios de água e transferência de água entre bacias. Considerando que, por si só, as grandes barragens regulam 42% do volume de caudal mundial, o declínio da saúde dos ecossistemas fluviais não é uma surpresa. É por isso urgente implementar uma gestão sustentável do caudal dos rios modificados por barragens.

Mesmo alterações ligeiras do caudal podem causar impactos ecológicos significativos. Portanto, é necessário entender melhor as relações entre alteração do caudal e a resposta ecológica. Sendo um desafio quantificar as relações caudal-ecologia, a investigação deve ter como objetivo a identificação de ligações entre o caudal do rio e as componentes do ecossistema, para uma compreensão mais aprofundada das funções e processos ecológicos. De particular importância são as regras de caudal e limites para as principais fases do ciclo de vida, entre outras razões, para estabelecer soluções de mitigação em rios com hidropicos. Em resposta a esta lacuna de conhecimento, esta tese visa (i) desenvolver abordagens holísticas para restauração de caudal em rios modificados, submetidos à captação de água ou hidropicos, e (ii) definir caudais ambientais, dando resposta ao efeitos ecológicos de curto prazo e modificações de caudal anual.

O primeiro estudo desta tese avaliou o estado populacional de *Thymallus thymallus*, espécie indicadora de uma região de piscícola. Considerando que os rios com *T. thymallus*, também chamados de rios hiporritrais, são ameaçados por múltiplos fatores antrópicos de stress, é difícil desenvolver estratégias de conservação e restauração. É, por isso, urgente adquirir conhecimentos mais detalhados sobre as consequências e interações dos fatores de stress prevalentes nas populações de espécies indicadoras, como *T. thymallus*. Para analisar o estado populacional de *T. thymallus*, foi realizado um estudo, considerando vários sistemas fluviais e diferentes fatores de stress. Usando abordagens exploratórias de árvore de decisão, foi possível separar os efeitos principais e de interação de quatro grupos de fatores de stress: modificação do caudal (hidropicos), canalização, fragmentação e alteração da qualidade da água. Além disso, usando uma variante especial do método de “bootstrapping”, i.e., o “bootstrapping agrupado”, foi possível determinar o número ideal de características que descrevem adequadamente o estado da população de peixes.

No global, os hidropicos tiveram o efeito mais significativo nas populações de *T. thymallus*. A biomassa de *T. thymallus* em locais de referência foi cerca de oito vezes maior do que em locais afetados por hidropicos. Os fatores mais importantes para prever o estado da população foram a amplitude do pico e a taxa da sua redução. Em rios de cabeceira, a morfologia do rio e a conectividade foram os parâmetros principais. Repetir o procedimento com conjuntos de dados

agrupados reforçou a hipótese de que os parâmetros identificados são mais relevantes na previsão do estado da população. O estudo destacou que a mitigação dos hidrópicos, com base em limites ecológicos, é a chave para proteger e restaurar as populações ameaçadas de *T. thymallus*. Em rios de cabeceira, a conectividade e características de habitat heterogêneo podem amortecer os efeitos adversos dos hidropicos, oferecendo abrigo e habitats para todos os estados de desenvolvimento dos peixes. Além disso, a abordagem metodológica apresentada oferece uma estrutura simples para investigadores e gestores analisarem conjuntos de dados multifatoriais e tirarem conclusões de gestão sólidas.

Até ao momento, os regulamentos de fluxo mínimo são a abordagem de gestão mais comum para mitigar os impactos adversos causados pelo desvio e armazenamento do caudal do rio e para proteger os troços do rio afetados pela deterioração ambiental. No entanto, a maioria das avaliações de caudais ambientais considera apenas critérios ecológicos selecionados, negligenciando a planície de inundação como uma parte indispensável do ecossistema fluvial. O segundo estudo expande o foco dos fluxos ambientais para incluir as necessidades de planícies de inundação saudáveis.

Com base em funções e processos essenciais de rios de planície temperada intacta, este estudo identificou princípios fundamentais aos quais devemos aderir para determinar caudais ambientais verdadeiramente relevantes em termos ecológicos. A literatura refere que o regime de caudal natural e seus componentes sazonais são os principais condutores de funções e processos de elementos abióticos e bióticos, como morfologia, qualidade da água, planície de inundação, lençóis freáticos, vegetação ribeirinha, peixes, macroinvertebrados e anfíbios, preservando assim a integridade de ecossistemas fluviais de planície. Com base na relação entre os principais elementos do regime de caudal e os componentes ambientais associados ao rio, foi formulada uma abordagem de caudal de planície de inundação funcional orientada para o processo (ff-flow), que oferece uma estrutura concetual holística para avaliação do caudal ambiental em rios de planície de inundação temperada. A abordagem ff-flow sublinha a importância de emular o regime de fluxo natural com a sua variabilidade sazonal, magnitude do caudal, frequência, duração do evento e rapidez de descida do fluxo hidrograma. Os princípios ecológicos apresentados na abordagem ff-flow devem garantir a proteção dos rios de planície de inundação afetados pela regulação do caudal, estabelecendo caudais ambientais ecologicamente relevantes e definindo medidas de restauração do caudal.

O terceiro e o quarto estudos tratam de modificações de caudal de curto prazo causadas por centrais hidroelétricas. Estas centrais, que são geridas em função das necessidades diárias do mercado de eletricidade, sofrem variações rápidas de descarga da turbina, resultando em flutuações rápidas de caudal a jusante. As alterações hidrológicas que afetam os rios de cabeceira podem ser descritas por cinco variáveis que mudam ao longo do espaço e do tempo (magnitude, taxa de mudança, frequência, duração e tempo), em que cada parâmetro pode estar correlacionado com impactos ambientais distintos. No entanto, o estabelecimento de medidas de mitigação bem-sucedidas requer uma compreensão mais profunda de como os hidropicos afetam os organismos aquáticos e as várias fases do seu ciclo de vida.

Fez-se a revisão da literatura sobre hidrópicos, para estabelecer uma estrutura sazonal de mitigação hidrológica com base nos diferentes estados de desenvolvimento dos peixes salmonídeos e sua relação com os parâmetros-chave do hidrograma: durante a migração e desova, os caudais devem ser mantidos relativamente estáveis, devendo-se implementar um limite de caudal deve para evitar a falta de água nas áreas de desova, no período de reprodução. Embora os ovos possam ser comparativamente tolerantes à desidratação, os estados de desenvolvimento pós-eclosão são muito vulneráveis, o que exige minimizar ou eliminar a duração das situações de rebaixamento e garantir caudais mínimos adequados. Os alevins são particularmente sensíveis às flutuações do caudal, mas à medida que crescem diminuem a sua vulnerabilidade. Portanto, propõe-se a definição de uma "janela de eclosão", com limites rigorosos de definição das taxas de variação de caudal.

O quarto estudo expande o trabalho qualitativo sobre regulamentação sazonal, vinculando a metas as variáveis identificadas de ecologia de caudal e limites para mitigação de hidropicos. O estudo apresenta uma revisão sobre as metas e limites estabelecidos para hidropicos e regulamentação. Os resultados mostraram que, até o momento, apenas alguns países, como a Suíça e a Áustria, possuem regulamentação sobre limites de caudal e hidropicos. Outros países, como Canadá e Estados Unidos, apresentam legislação ambiental que pode forçar medidas de mitigação de hidropicos. A maioria dos limites de mitigação e recomendações de gestão referidos na literatura lidam com a secagem dos leitos nos salmonídeos, bem como caudais mínimos entre hidropicos para evitar a falta de água nas zonas de desova. Em relação a outras espécies de peixes, as informações sobre alvos ou limites de mitigação são mais escassas, ou mesmo inexistentes, bem como sobre estudos de caso sobre mitigação de hidropicos, traduzindo-se numa falta de conhecimento e diretrizes para sua implementação ou regulamentação. No entanto, a literatura disponível indica que múltiplos aspetos devem ser considerados, nessa avaliação. Assim, este estudo propõe que as metas e limites de mitigação devem ser baseados em espécies-chave, incluindo características particulares relacionadas com a estação do ano, o estado de desenvolvimento e os ritmos circadianos, que devem ser combinadas com características morfológicas específicas do local. Portanto, o quadro de mitigação apresentado pode auxiliar a melhoria ambiental dos rios com hidropicos, estabelecendo limites e / ou metas de mitigação de base ecológica.

No geral, esta tese avança no estabelecimento de diretrizes para a restauração bem-sucedida de caudais em sistemas fluviais afetados por usos concorrentes da água, estabelecendo esquemas holísticos de restauração de caudal e incorporando limites quantitativos e qualitativos de hidropicos. Além disso, coloca o tema da restauração de caudais no contexto mais amplo da reabilitação hidromorfológica de rios, contribuindo para uma discussão sobre os trade-offs entre usos da água, pela a sociedade e o ambiente.

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CHAPTER 1

Introduction

1.1 Setting the scene

Water is “the bloodstream of the biosphere” — the thriving force of the life zone on earth (Ripl, 2003). In aquatic ecosystems, the relationship between water and living beings is particularly apparent. So much so that the water flowing down a stream or river has been called the “master variable” (Power et al., 1995), governing processes and patterns of the physical and biological riverine environment (Junk et al., 1989; Poff et al., 1997; Walker et al., 1995).

Unsurprisingly, due to the complex and dynamic nature of free-flowing rivers, these ecosystems, including their wetlands, belong to the most species-diverse places on the planet (Hauer et al., 2016; Tockner and Stanford, 2002). Considering that freshwater ecosystems occupy less than one percent of the world’s surface area, their contribution to total biodiversity is exceptional (Balian et al., 2008).

Since the last century, however, we are witnessing a decrease in ecosystem integrity and global biodiversity of unprecedented speed (FIGURE 1.1). Of all ecosystem types, inland waters are the most heavily impacted, showing population declines of 84% since 1970, which is equivalent to a reduction of four percent per year (WWF, 2020). Regarding extinction, fishes exhibit the highest extinction rate among vertebrates, averaging 7.5 extinct taxa per decade (1950–2006) in North America alone (Burkhead, 2012). But also other freshwater taxa such as turtles, snails, and amphibians are exceptionally imperiled (Tickner et al., 2020). The same holds true for large-bodied animals (He et al., 2019).

This downward spiral of freshwater integrity (FIGURE 1.1) is driven by a number of pressures, as well as interactions between them. The greatest threats are related to habitat loss and degradation, water pollution, overexploitation of resources (e.g., fish catches), invasion by exotic species, and flow modification (Collen et al., 2014; Dudgeon et al., 2006). Especially the topic of river flow alterations has recently been receiving a lot of attention, as the growing demand for (renewable) energies and water resources for increased food production has caused a new global boom in hydropower and reservoir construction, particularly in developing countries and emerging economies (International Energy Agency, 2019; Steffen et al., 2015; Wagner et al., 2019; Zarfl et al., 2015). Hence, the few remaining free-flowing rivers (Dynesius and Nilsson, 1994; Grill et al., 2019; Nilsson et al., 2005) are in danger of becoming degraded – thereby threatening

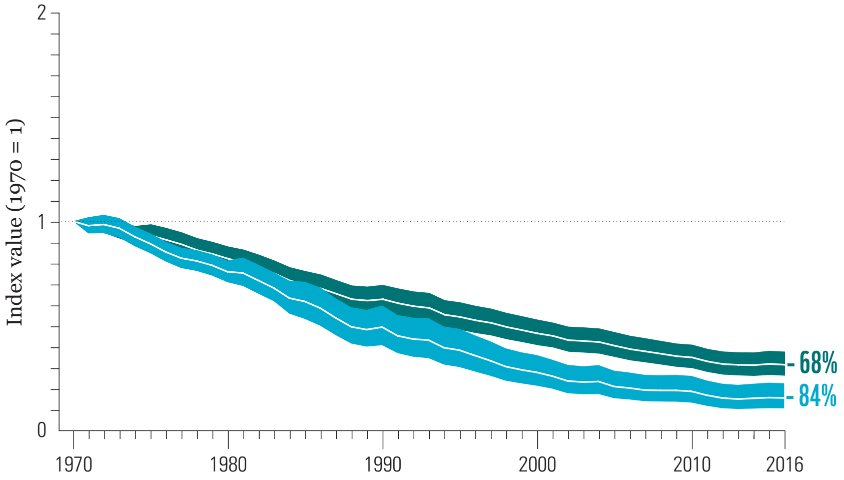

Figure 1.1 The Living Planet Index (1970-2016), a population indicator as a measure of biodiversity and ecosystem health. The dark green line represents the Global Living Planet Index (±95% confidence limits), the blue line the Freshwater Living Planet Index (±95% confidence limits). Modified after WWF (2020).

global and local riverine biodiversity (Schmutz and Moog, 2018; Vörösmarty et al., 2010) as well as socio-economic benefits (Anderson et al., 2019; Auerbach et al., 2014; Jorda-Capdevila and Rodríguez-Labajos, 2017). Considering this threat, it is imperative to protect these remaining jewels from imprudent, non-sustainable water infrastructure development.

In light of the *new* global dam construction boom it should, however, not be overlooked that we are still dealing with the ecological consequences of the *old* construction boom: particularly the time between 1950 and the late 1990s saw a sharp rise in the number of large dams being built (FIGURE 1.2). Today, the number of large dams amounts to around 58,000 (ICOLD, 2019). In addition to that, it has been estimated that there are over 16 million smaller impoundments (>0.01 ha surface area) worldwide (Lehner et al., 2011), including numerous small farm dams which can have a considerable cumulative impact (Stewardson et al., 2017). Considering that large dams alone already regulate 42% of the world's flow volume (Grill et al., 2015), the declining health of river ecosystems as described above comes by no surprise. Instead, it is an urgent call for sustainable flow management of rivers modified by dams and reservoirs.

1.2 Natural processes that govern river flows

As mentioned earlier, river flow is an intrinsic component of fluvial ecosystems. It can be regarded as a river's "hydrological signature" (Rivaes, 2018). In natural systems, river runoff exhibits a seasonal variability as river stage moves to and from low to high flows (Naiman et al., 2008). This happens as river flows are connected to the global water cycle by processes such as precipitation, evapotranspiration, runoff, or groundwater flows (Weingartner et al., 2019). In particular, flow is determined by meteorological and bio-geophysical components. The first includes, for example, type of precipitation, rainfall amount, intensity, duration or distribution in the catchment, as well as conditions that affect evapotranspiration and water infiltration; the latter encompasses aspects such as drainage area, topography, land use, vegetation cover and soil properties (Poff et al., 1997; Zeiringer et al., 2018). These factors lead to different characteristic flow regimes, such as those influenced by rainfall (*pluvial* regime), snow (*nival*) or

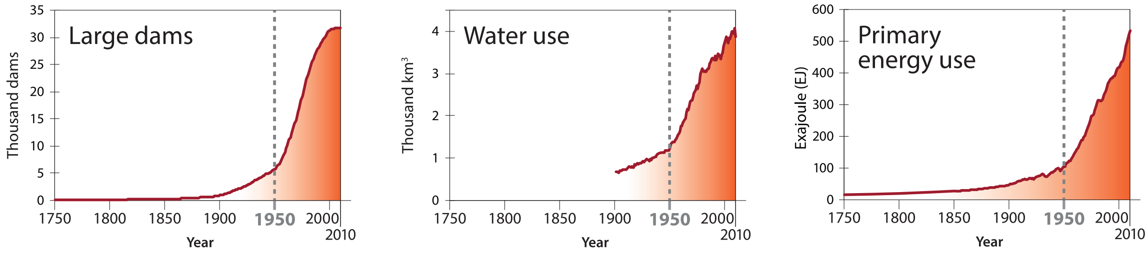

Figure 1.2 Trends from 1750–2010 in globally aggregated socio-economic development indicators: number of large dams (left), water use (middle), primary energy use (right). Modified after Steffen et al. (2015).

glacier melt (*glacial*), or combinations thereof (Baumgartner et al., 1983; Poff, 1996; Rinaldi et al., 2016). Also, floods of various magnitudes can exhibit a spatiotemporal variability (Whipple et al., 2017). Depending on the influence of the factors described above, the contribution of different water sources (e.g., glacier melt or rainfall), as well as the natural flow regime itself, can change within the same river basin. Particularly large rivers can exhibit flow regime changes along their longitudinal pathway. In the headwaters of the Rhine River, for example, glacier-melt determines most of the runoff. In the main stem further downstream, however, most runoff stems from rainfall (Weingartner et al., 2019). Hence, the intra- or inter-annual flow variability (within- and among-year variation) at a given point in the river may be more or less predictable (Poff et al., 1997). Overall, as a basis for understanding and managing flows for ecological sustainability, river discharge can be characterized and described by its five primary elements – magnitude, frequency, duration, timing, and rate of change (BOX 1.1).

Box 1.1 The five flow regime components to characterize river flows.

Five flow regime components, coined by Richter et al. (1996) and Poff et al. (1997), are commonly used today to describe natural as well as modified flow regimes on different temporal scales ranging from sub-daily to seasonal to inter-annual flows (Greimel et al., 2016; Lytle and Poff, 2004):

Magnitude. How much water moves past a fixed location per unit time? What is the river gauge level (e.g., minimum or maximum flows)?

Frequency. How often do flows of a given magnitude occur (i.e., what is their interval)?

Duration. How long do certain flows or water levels last (e.g., number of drought days)?

Timing. When do certain flows or levels occur (e.g., seasonal predictability of flood events)?

Rate of change. How fast do flows or levels change from one condition to another (i.e., flashiness)?

Based on these five components, Richter et al. (1996) developed the 32 indicators of hydrological alteration (IHAs). Through these, it is possible to quantify the hydrological variability of a system in an ecologically-relevant statistic (Richter et al., 1996; Yarnell et al., 2020).

1.3 Flow-ecology relationships

It has been well established that river hydrology is the fundamental driver of fluvial ecosystems (Junk et al., 1989; Poff et al., 1997; Power et al., 1995). Hence, aquatic organisms are not only adapted to cope with floods and droughts inherent to natural flow regimes, but they are actually dependent on the hydrological variability of fluvial systems (Bunn and Arthington, 2002; Lake, 2003; Lytle and Poff, 2004; Naiman et al., 2008; Rood et al., 2007). River flows are responsible for shaping fluvial geomorphology in interaction with riparian vegetation

(Corenblit et al., 2007; Egger et al., 2013; Fryirs and Brierley, 2013; Trush et al., 2000), as well as for transporting and arranging sediments (Trush et al., 2000; Wolman and Miller, 1960), thereby structuring the physical habitat template of freshwater organisms (Bunn and Arthington, 2002; Frissell et al., 1986; Trush et al., 2000). Moreover, flows provide habitat connectivity (Bunn and Arthington, 2002; Opperman et al., 2010; Tockner et al., 2000; Ward, 1989), influence water temperature and oxygen levels (Nilsson and Renöfält, 2008; Olden and Naiman, 2010), frame food-web interactions and productivity through carbon transport and nutrient cycling (Baldwin and Mitchell, 2000; Junk et al., 1989; Thorp and Delong, 1994; Tockner et al., 2000), as well as support requirements of essential life-history stages (Biggs et al., 2008; Bunn and Arthington, 2002; Lucas and Baras, 2001; Unfer et al., 2011; Yarnell et al., 2015). Therefore, in the same way that each river has a distinctive flow regime, it also hosts a peculiar biotic community (Mims and Olden, 2012; Naiman et al., 2002). By governing physical and biological patterns and processes, the master variable *flow* is essentially determining and sustaining the productivity, health, integrity, and resilience of riverine ecosystems.

As the natural flow regime controls the hydraulic array of key habitats, it is fundamental for enabling the completion of vital life-cycle stages of aquatic biota (Greenberg et al., 1996; Humphries et al., 1999; Jungwirth et al., 2000). This can be illustrated by the European grayling (*Thymallus thymallus*, L.), a rheophilic indicator fish species of braided middle courses (Muhar et al., 2000). Grayling spawn between March and June (Ingram et al., 2000). Depending on the river, this can be before, during, or after the snow melt. The length of the spawning time is related to the predictability of the flow regime: the less predictable river flow is, the longer the spawning season will be (e.g., two months at the Austrian Mur River; Unfer, personal communication). Spawning time is furthermore related to the interplay between flow and water temperature (Gönczi, 1989; Ingram et al., 2000; Parkinson et al., 1999). Also, the timing of annual migrations is connected to hydro climatic conditions, whereby decreasing water levels are a crucial factor for initiating fish movement (Ovidio et al., 2004). Migrating grayling are more mobile when water tables fluctuate little (Parkinson et al., 1999). Regarding spawning ground water depths, varying numbers have been reported, for example, ranging from 20–30 cm (Sempeski and Gaudin, 1995a) to 250 cm (Holzer et al., 2002). However, more important than depth is probably flow velocity (0.4–0.7 $\mathrm{m\,s^{-1}}$; Sempeski and Gaudin, 1995a) to ensure delivery of well-oxygenated water. Grayling are gravel bank spawners that require a loose interstitial zone for egg incubation (Jungwirth et al., 2000). Such substrate conditions are made available through bed sediment-redistributing high flows or floods before spawning (Brunke and Gonser, 1997; Hauer et al., 2016; Unfer et al., 2011). However, as grayling lay their eggs in the top layer of the substrate (Fabricius and Gustafson, 1955), their eggs are susceptible to erosion if post-spawning floods should occur (Woolland, 1986, in: Ingram et al., 2000). After an incubation time of few weeks, fish hatch from the eggs and soon emerge from the spawning grounds (Bardonnet and Gaudin, 1991; Jungwirth and Winkler, 1984). From there, they move to shallow bank areas with flow velocities <0.1 $\mathrm{m\,s^{-1}}$ (Ingram et al., 2000; Nykänen and Huusko, 2003). Post-emergent fry soon disperse downstream, particularly during the night (Bardonnet et al., 1991), whereby daily flow increases lead to higher drift densities (Grimardias et al., 2012). Drift distances can be up to >10 km (Meraner et al., 2013). During the summer months, young grayling exhibit significant habitat shifts towards deeper channel habitats as they grow in size (Bardonnet et al., 1991; Sempeski and Gaudin, 1995b, 1995c); again, flow velocity is one of the critical parameters determining habitat use (Nykänen and Huusko, 2003). Summarizing, each life cycle stage – spawning, larvae, juvenile, sub-adult, adult – requires a narrow range of hydrological and hydraulic criteria. The overall range required by this species is, however, broad (Jungwirth et al., 2000; Mallet et al., 2000), underlining the species' need for spatial and temporal habitat heterogeneity created and sustained by river flows.

Similar to grayling, many other aquatic or semi-aquatic biota – including fish, macroinvertebrates or riparian vegetation – also exhibit complex flow-ecology relationships (e.g., Bejarano et al., 2020; Biggs et al., 2008; Bunn and Arthington, 2002; McClain et al., 2014; Rood et al., 2007). Regular or seasonal variations in river flows are, therefore, a prerequisite for the completion of species' life cycles (Poff et al., 1997).

1.4 Flow regulation: why and how

Man-made flow modifications belong to the dominant stressor group in rivers (Nõges et al., 2016), affecting 41% of European running waters (Schinegger et al., 2012). Hydrological stressors can originate from different sources such as dams and reservoirs, hydropower, water diversions and inter-basin water transfers, urbanization and surface sealing, levees and river channelization, or groundwater extraction (de Graaf et al., 2019; Poff et al., 1997; Rosenberg et al., 2000; Shumilova et al., 2018; Stewardson et al., 2017). Of these causes, the effects of dam construction can be especially prevalent. In 2019, for example, the Lower Mekong River Basin exhibited some of its lowest water levels, leading to one of the worst droughts on record. Remote-sensing data revealed that this was caused by more-recently built dams in the Upper Mekong Basin, which held back most of the wet season flows (Basist and Williams, 2020), and thereby could have devastating socio-economic and ecological consequences (Lovgren, 2019). Even though this is one of the more drastic examples, dams in general do have wide-ranging consequences for downstream ecosystems (Schmutz and Moog, 2018).

Since millennia, humans have built dams and associated reservoirs for various purposes, including irrigated agriculture, domestic or industrial water supply, flood control, navigation, recreation, and hydropower generation (ICOLD, 2019; Rosenberg et al., 2000). Nowadays, almost all large river basins are impacted by large dams (Nilsson et al., 2005). Half of the world's large dams were primarily built for crop irrigation; therefore, the World Commission on Dams estimates that these dams directly contribute to 12–16% of the global food production (WCD, 2000). Overall, 30% of the human water consumption is provided from non-sustainable sources – and this number is projected to increase (Wada and Bierkens, 2014). To meet these water demands, reservoirs store 14% percent of the world's surface runoff (Revenga et al., 2000). Moreover, hydropower is the leading renewable energy source: altogether, hydropower dams generate 16% of the world's electricity supply (World Energy Council, 2016). Besides, due to its positive synergies with other electricity generation technologies, hydropower plays a key role in the energy transition towards renewable energy sources (BOX 1.2).

Box 1.2 Hydropower's contribution to a low carbon future.

Pressing issues such as climate change, fossil fuel resource depletion and decommissioning of nuclear power plants call for an "energy transition", which describes a set of policies and structural reforms for decarbonizing the economy (European Commission, 2015a; Gurung et al., 2016). To tackle these issues, the European Union established a road map for a competitive low-carbon economy. This road map calls for an 80% reduction in the EU's greenhouse gas emissions by 2050 (compared to 1990). This goal should be reached by reduced energy consumption and higher energy efficiency but also by expanding renewable energy sources such as wind, solar, biomass, and water (European Commission, 2012).

In comparison to other non-renewable electricity sources such as coal, hydropower is considered a clean energy source (IHA, 2020). Indeed, in 1889, to describe hydropower use, the French electricity pioneer Aristide Bergès even coined the term "*huille blanche*" (white coal) (Matt et al., 2019). Besides, hydropower offers the advantage that potential energy can be stored in reservoirs for later use (World Energy Council, 2016). Moreover, the rapid control capability of (especially storage and pump-storage) hydropower complements other renewables, as hydropower is capable of balancing the increased volatility in the system caused by electricity demand and the unavoidable generation fluctuations of, for example, wind or solar. Hydropower, therefore, can ensure system stability and guarantees security of supply (Greimel et al., 2017; Gurung et al., 2016; IHA, 2020; Matt et al., 2019; World Energy Council, 2016). By supporting the integration of intermittent renewable energies, hydropower plays a crucial role in the energy transition (Greimel et al., 2017; Grilli et al., 2017).

Hydropower, however, also causes severe ecological impacts; among others, by fragmenting and destroying/altering instream and floodplain habitats, or killing or injuring fish through turbine passage (Schmutz and Moog, 2018; Seliger and Zeiringer, 2018), to name a few. Ultimately, these effects reduce ecosystem integrity and diminish biodiversity. Hence, this showcases that not all environmental goals, such as decreasing carbon emissions through hydropower and river restoration (e.g., EU Water Framework Directive; 2000/60/EC) are perfectly aligned (Rees et al., 2020). In this regard, the United Nations 'Brundtland' report correctly highlights that "the exploitation of renewable sources such as […] hydropower also entails ecological problems". In light of sustainability principles, the report urges that any hydropower project must include the local environment as well as the livelihood of the local community into its balance sheets. Therefore, "the abandonment of a hydro project because it will disturb a rare ecological system could be a measure of progress, not a setback to development" (United Nations, 1987).

Irrespective of their usage purpose (as mentioned above), dams serve two main functions: they raise water levels and store water. The first serves, for example, to better divert water and boost hydropower generation through increase of hydraulic head, whereas the latter allows the storage of river flow in order to release water when needed (Poff and Hart, 2002). The way that dams and their associated reservoirs alter river flows (i.e., any anthropogenic change in the five flow regime components; see BOX 1.1) hence depends on different specifications related to these functions, in particular, dam size, diversion structures, and management scheme (McManamay et al., 2016; Poff and Hart, 2002).

Although dam height is often considered a key characteristic for dam classification, the size of a reservoir is a more meaningful metric to describe the extent of hydrological alterations (Poff and Hart, 2002). Depending on the size of the reservoir, the residence time of water can range from less than one day in a small impoundment to several years in a large one (Vörösmarty et al., 1997). The effects of reservoir size on water fluxes are particularly obvious when looking at high flows: reservoirs with a small storage volume, for instance, might only be capable of cutting off the flood peak. Large reservoirs, in contrast, due to their increased storage volume, may completely eliminate both small and large floods downstream – some might even store the equivalent of an entire year of river flow. As a general rule, the larger the storage capacity, the greater the possible hydrological interactions, and the

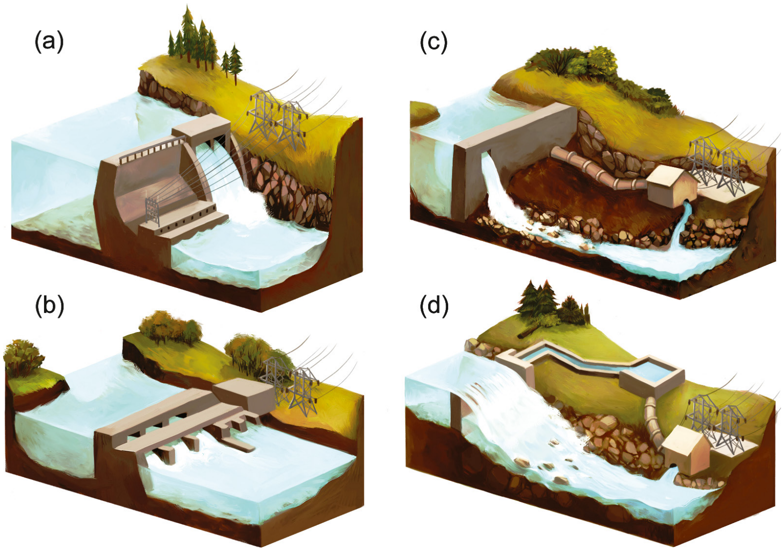

Figure 1.3 Dam classification based on presence or absence of storage and diversion structures: Non-diversion with storage (a) and without storage (b). Diversion with storage (c) and without storage (d) (source: Couto and Olden, 2018).

more severe the ecological feedback (Richter and Thomas, 2007); but more on that later.

In addition to reservoir size, dams can be placed into two broad categories based on the presence or absence of diversion structures (Couto and Olden, 2018) (FIGURE 1.3). In run-of-river schemes, river runoff exits the reservoir at the dam structure, for example, through the hydropower turbines or over the spillway, and continues to flow down the river. Although flow patterns might be altered, the water volume that flows downstream essentially remains the same (Killingtveit, 2019). In diversion schemes, on the other hand, water is directly diverted from the reservoir to off-stream uses (Richter and Thomas, 2007). If water is not consumed by, for example, domestic or industrial uses or crop irrigation, then it is usually returned to the river at a place further downstream. In such cases, the river stretch below the dam – the residual flow stretch – is often characterized by extreme low flows over long periods of time. Often, water levels even fall below natural low-flow levels (Richter and Thomas, 2007). If river water is used up or transferred to another basin, then this quantity it is obviously missing from the respective river system (Stewardson et al., 2017).

Finally, hydrological alterations depend upon the purpose of the reservoir and the operational mode of the dam (McManamay et al., 2016). After dams catch the flood peak (as described above), for example, they are able to release water in a controlled way (Richter and Thomas, 2007). Overall, such releases increase minimum flows and near-bankfull flow duration, as well as reduce seasonal variability through homogenization of flows (McManamay et al., 2012; Poff et al., 2006). Such a pattern is distinctive of many flood control dams but is also found at hydropower dams. Diversion dams would also reduce minimum flow magnitude and near-bankfull flow (Stewardson et al., 2017). Irrigation dams that distribute water through the channel lead to seasonal flow shifts, particularly in regions where irrigation water is needed during the summer months when river flows are naturally low in temperate climates (Magdaleno and Fernández, 2011; Stewardson et al., 2017). Through controlled holding back and releasing of river runoff, dams have increased the global mean age of river water by over one month (Vörösmarty et al., 1997).

A special regulation type are hydropower plants that operate their turbines according to the demands of the energy market: such an operation scheme ("hydropeaking") calls that turbines are quickly turned on and off to maximize generation of electricity. This causes a high sub-daily flow variability. In operation mode, unnatural flood events occur in the downstream river section. During shutdown, no or only little water remains in the river. In between these two extreme flow magnitudes, river levels rise and drop very fast, thereby increasing the rate of change between flows of certain magnitudes (Greimel et al., 2018, 2016; Richter and Thomas, 2007). Also run-of-river hydropower plants may run a hydropeaking scheme, although the peak intensity is typically lower than that of large storage reservoirs (Greimel et al., 2016; McManamay et al., 2016). A special sub-category of peak-operating hydropower plants are pumped-storage facilities that pump water to reservoirs at higher elevations during periods of low energy demand or costs. Once the demand rises again, the pumped water is released and used to run the hydropower turbines (McManamay et al., 2016; Stewardson et al., 2017). In many countries, such as Norway, Switzerland, Sweden and Austria, storage and pumped-storage hydropower constitutes the backbone of the national electricity grid (Greimel et al., 2017). Storing water in reservoirs to use it later for hydropower generation is to date the most efficient way of, essentially, storing energy. Indeed, hydropower constitutes 99% of the global electricity storage capacity (World Energy Council, 2016).

Overall, river regulation caused by reservoirs, water withdrawals and dam operations impact more than 50% of the earth's rivers, whereby the most prevalent hydrological alterations are: discharge reduction of various flow magnitudes, lowered amplitude of seasonal flow variations, as well as extended low flows (Stewardson et al., 2017).

Aside from hydrological alterations, dams also fragment river systems (Barbarossa et al., 2020; Grill et al., 2019, 2015; Nilsson et al., 2005), alter water temperature (Nilsson and Renöfält, 2008; Zolezzi et al., 2011) and river-groundwater exchange (Schmutz and Moog, 2018). Besides, they can change oxygen levels in downstream sections (Pleizier et al., 2020; Pulg et al., 2016). Dams furthermore impede nutrient flows (Maavara et al., 2020), and alter downstream river morphology and sediment composition by trapping sediments in reservoirs (Hauer et al., 2018b; Kondolf, 1997; Kondolf et al., 2014; Schmutz and Moog, 2018).

1.5 Flow regulation: ecological consequences of altered flow regimes

Further above, I illustrated the close linkage between river flows and species' life cycle requirements (CHAPTER 1.3). Based on these ties, it can be expected that alterations of natural flows (CHAPTER 1.4) can negatively impact a species' entire life cycle. Indeed, flow regulation leads to a variety of adverse consequences for many organism groups, including fish, macroinvertebrates and riparian vegetation (e.g., Bejarano et al., 2020, 2018; Lozanovska et al., 2020; Poff and Zimmerman, 2010; Renöfält et al., 2010; Rytwinski et al., 2020; Webb et al., 2013). Repercussions range from reduced recruitment success or lowered population vitality to complete exchange of species assemblages (Poff and Zimmerman, 2010).

In detail, for example, homogenization of flows (i.e., loss of intra-annual flow variability) leads to local extinction of native species adapted to seasonally fluctuating flows and encourages invasion of non-native species (Bunn and Arthington, 2002; Poff et al., 2007, 1997).

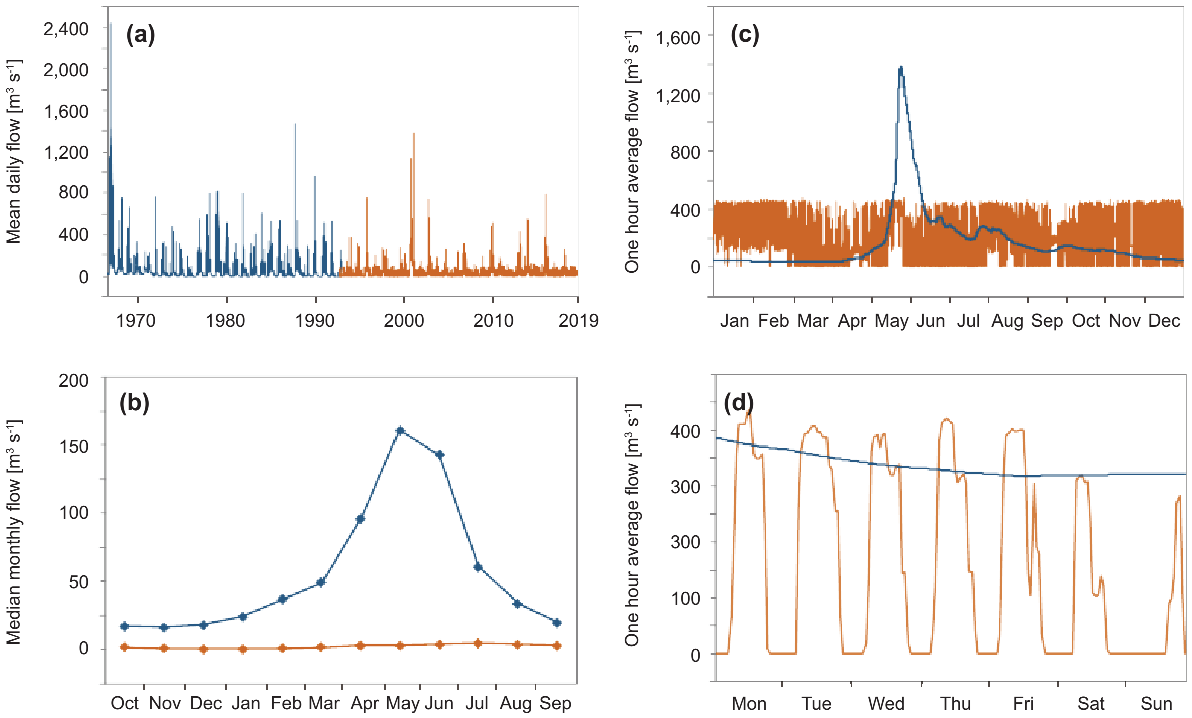

Figure 1.4 Comparison of natural (blue) and modified (red) river flows: (a) Mean daily flows of run-of-river Touvedo dam (start of operation in 1993), Lima River, Portugal (modified after: Rivaes and Aguiar, 2019); (b) median monthly flows in the San Joaquin River in California, USA; the red line shows the alterations caused by an an irrigation supply dam (modified after: Richter and Thomas, 2007); (c) annual and (d) daily short-term flow regime changes in the Ume River, a Swedish hydro-peaking river, in comparison to the free-flowing Vindel River (modified after: Bejarano et al., 2017).

The loss of seasonal flow peaks (FIGURE 1.4A-C), as well as change of their timing, disrupts life cycle cues for fish and other organism groups, for example, regarding spawning, egg hatching, or migration; moreover, missing over bank floods restrict connectivity to the floodplain, which impedes spawning migration, juvenile recruitment and changes species assemblage structure (Poff and Zimmerman, 2010; Poff et al., 1997; Yarnell et al., 2015). Prolonged low flow durations (FIGURE 4B) concentrate aquatic organisms in smaller areas by blocking instream connectivity (Lake, 2003). In combination with increased water temperatures and algae blooms (Zeiringer et al., 2018), this can cause physiological stress, reduce movement or lead to death, for example, due to oxygen depletion (Hayes et al., 2019; Lake, 2003; Nilsson and Renöfält, 2008; Renöfält et al., 2010). Lengthy low flow durations during freezing winters can adversely damage biota by fostering excessive build-up of frazil and anchor ice (Nilsson and Renöfält, 2008). Unsurprisingly, due to reduction of deeper pool habitats, larger fish are often missing in residual flow sections (Zeiringer et al., 2018). Seasonal reversals of flow patterns can lead to changes in fish and macroinvertebrate communities (Rivers-Moore et al., 2007; Ter Morshuizen et al., 1996), and a prolonged inundation alters riparian plant assemblages (Renöfält et al., 2010). Accelerated flood recession hampers the establishment of plant seedlings on the riverbanks, as young shoots fail to reach subsiding water levels (Rood et al., 2005). An increase in sub-daily flow fluctuation caused by hydropeaking (FIGURE 4C-D) diminishes fish and macroinvertebrate populations through stranding and drift (Auer et al., 2017, 2014; Moog, 1993; Schülting et al., 2019, 2016), as well as through reduced spawning and rearing success (Casas-Mulet et al., 2015; Kennedy et al., 2016; McMichael et al., 2005b, 2005a). Moreover, quickly fluctuating flows scour periphyton (Bondar-Kunze et al., 2016), impede ground beetle communities (Van Looy et al., 2007) and constrain riparian vegetation (Bejarano et al., 2018).

Changes in water and sediment flow also indirectly affect biota by changing their physical habitat array (Trush et al., 2000). For example, blocked sediment supply due to river regulation facilitates geomorphic adjustments, for example, reducing bed mobility and natural bed elevation variability or inducing riverbed degradation (Church, 1995; Salant et al., 2006). In addition, lowered flood magnitude and frequency downstream of dams encourages river bank colonization of vegetation, which causes a loss of functional channel area (Corenblit et al., 2007; Gaeuman et al., 2005; Rivaes, 2018; Ryan, 1997). Furthermore, also hydropeaking can lead to sedimentological and morphological changes (Hauer et al., 2018a; Vericat et al., 2020). Also, reservoir flushing operations can negatively impact river biota (e.g., Crosa et al., 2010; Grimardias et al., 2017). Dam-induced changes in delivery of sediments and nutrients can have far-reaching consequences to downstream ecosystems and people communities – even reaching river deltas, which are prone to shrinkage through sediment-starved rivers (Maavara et al., 2020; Syvitski et al., 2009).

Overall, the greater the extent that river flows are altered, the higher the risk of resulting ecological changes (Poff and Zimmerman, 2010). Ultimately, depending on the spatial extent, flow changes can severely reduce biodiversity in a river basin or an entire region (Dudgeon et al., 2006).

1.6 River restoration through flow management

In the mid-twentieth century, when conservationists and scientists realized that damming and diverting of rivers causes broad-scale effects on river ecology and biodiversity, the science and practice of river conservation started to emerge (Petts, 1984; Richter et al., 2016). Since then, much progress has been made on how improved dam design and operation can mitigate negative ecological impacts. But also societal expectations have shifted in the last decades as we better understood the societal value of functioning river ecosystems (Poff and Matthews, 2013).

Until the mid-1990s, river managers only aimed at securing minimum flows for single ecosystem elements (such as valued game fish) downstream of dams and water diversions. It was not until the establishment of conceptual frameworks such as the natural flow paradigm (BOX 1.1) that the scope expanded towards multiple ecological targets as well as entire ecosystems. This enhanced understanding lead to the establishment of the environmental flows (*e-flows*) concept (Hirji and Panella, 2003; Poff and Matthews, 2013).

The science and practice of e-flows aims “to protect and recover aquatic biodiversity, ecosystem integrity and important ecological services by managing freshwater flow regimes” (Arthington et al., 2018) impacted by dams and water diversions. E-flows, therefore, pertain to the water allocation “deliberately left in a river, or released into it to manage river health and the integrity of ecosystems” (Hirji and Panella, 2003). In this regard, e-flows differ from other – often (falsely) interchangeably used – terms such as minimum flow (see BOX 1.3).

Box 1.3 E-flows: multiple terms, same meaning?

Even though different e-flows synonyms have been around for some decades and are still used today (FIGURE 1.5), the emphasis placed on certain terms and their concurrent usage in the scientific literature reflects a change of paradigm.

In the beginning of the dam-construction era, in the mid-nineteenth century, downstream river sections often had *no flow* releases at all as they were left completely dry or contained only dam-seepage flows. It became quickly apparent that river ecosystems require a certain flow quantity and flows began being released – mostly to protect valuable instream resources such as game fish. At that time, however, flow quantity contained only one aspect: *minimum flows* (Petts, 2009; Poff et al., 1997). The term *residual flow* reflects the notion that the environment is served last after all other uses have received their share of water; indeed, the Oxford dictionary defines "residual" as a "(quantity) left after other items have been subtracted." From a practical perspective, minimum flows and residual flows (as well as other synonyms such as such as *minimum acceptable flows*, *minimum allowable flows*, *minimal residual flows*, and *ecological minimum flows*) are probably similar, as only low water quantities with little seasonal variation are released into the river (European Commission, 2015b; Petts, 2009; Renöfält et al., 2010). Such flows, however, are considered inadequate for protecting riverine biodiversity (Arthington et al., 2010).

Nowadays, it has been emphasized that minimum flows are only one part of environmental water allocations (King and Brown, 2018). The concept of *environmental flows* (*e-flows*) includes the notion that multiple flow regime components (see BOX 1.1) are needed to sustain ecological functions and processes. Furthermore, e-flows include a clearly defined aim such as the preservation of aquatic ecosystems through water flows in order to sustain human livelihoods, cultures, economies and general well-being that depend on the functioning of these ecosystems (Arthington et al., 2018; Brisbane Declaration, 2007). Thereby, recent e-flow definitions move beyond *instream flows*, as, for example, floodplains, wetlands or groundwater systems are also included in the term "aquatic ecosystems" as mentioned above (Arthington et al., 2018). Other words such as *environmental water allocations*, the *normative flow regime* or *ecological flows* are often used interchangeably and generally convey the same notions as e-flows (Arthington et al., 2010; Davies et al., 2014). Interestingly, the term *ecological flows* has been selected to describe water releases for the achievement of legal environmental objectives, such as those of the EU Water Framework Directive (European Commission, 2015b).

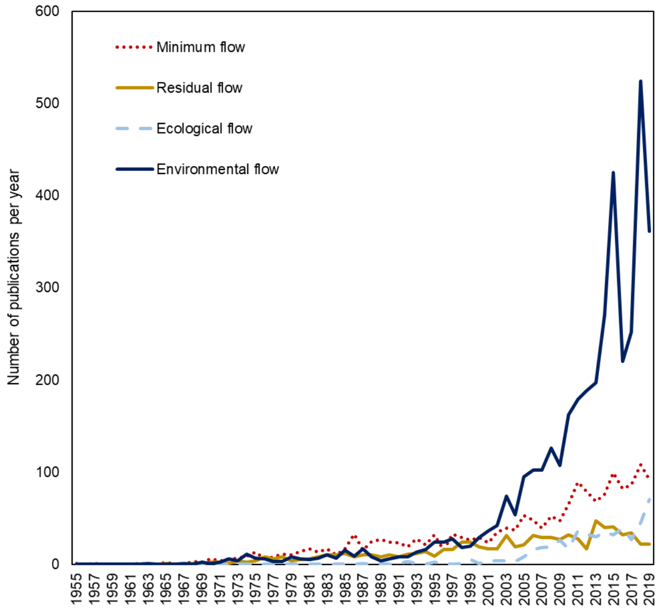

Figure 1.5 Yearly publication output (1955–2019) on selected e-flow keywords: minimum flow, residual flow, ecological flow, and e-flow (SCOPUS literature search on TITLE-ABS-KEY "minimum flow" or "minimal flow*", "residual flow*", "ecological flow*", as well as "environmental flow*" or "e-flow*", on 27 May 2020. Each search was restricted to the subject areas environmental science, engineering, earth and planetary sciences, and agricultural and biological sciences).*

In order to sustain and restore riverine biodiversity, a plethora of e-flow methods has been developed (Tharme, 2003). Based on their purpose, scale, scope, and costs, these assessment approaches can be divided into four broad categories (Acreman and Dunbar, 2004; Linnansaari et al., 2013; Tharme, 2003). Look-up tables or hydrological methods are based on simple flow rules derived from hydrographs – mostly a certain percentage of seasonal or annual low or mean flows, or flow duration (exceedance) curves (Acreman and Dunbar, 2004; Kuriqi et al., 2019; Linnansaari et al., 2013). Such approaches work well to determine first thresholds on the river basin or regional scale in low-risk situations and can assist more complex e-flow assessments. On the spatial scale of the river, however, they are inadequate of providing data required to sustain ecological integrity (Linnansaari et al., 2013; Zeiringer et al., 2018). Hydraulic-based desktop methods examine changes in hydraulic variables such as wetted width as a function of river flow. By using flow-dependent ecological indicators, the change of the channel-flow relationship can be evaluated, and abstraction thresholds recommended (Acreman and Dunbar, 2004; Linnansaari et al., 2013). Building upon this framework, habitat simulation methods combine multiple habitat variables, such as flow velocity, water depth and substrate conditions, and link them to habitat preferences of target species, life stages, or assemblages. Thereby, habitat simulation methods examine the changes in the amount of physical habitat for the target organism(s) as a function of flow (Linnansaari et al., 2013; Tharme, 2003; Zeiringer et al., 2018). Hydraulic and habitat simulation methods are commonly used at the river reach scale but results can also be up-scaled to the basin or regional level (Linnansaari et al., 2013; Parasiewicz et al., 2018). The fourth method group, holistic methods or functional analysis, has contributed greatly to the field of e-flows assessment (Tharme, 2003) and has pushed towards the "e-flows imperative" of the twenty-first century (Petts, 2009; FIGURE 1.5). Holistic methods aim at sustaining various ecosystem elements and societal needs, including cultural and socio-economic aspects, by identifying pivotal flow regime components. Such e-flow assessments can either be done through bottom-up or top-down approaches: while the first builds upon establishing a relevant flow regime, for example, by laying down foundational flow blocks, the latter aims to determine how the system deteriorates according to different flow changes (Tharme, 2003).

Overall, based on mean daily flows, e-flow methods aim to establish intra- or inter-seasonal flows. Restoring flows in hydropeaking rivers, however, also requires the reduction of adverse sub-daily flow fluctuations, which may be masked by mean daily flow values (Zimmerman et al., 2010). In this regard, low and peak flow magnitude, peak frequency, as well as up- and downramping rate (rate of change) are common indicator values used in ecological hydropeaking assessments (Bruder et al., 2016; Greimel et al., 2017; Tonolla et al., 2017a, 2017b). Due to the alternating release of base and peak flows, hydropeaking rivers are essentially "two different rivers in one" (Jones, 2014). Successful mitigation, therefore, requires peak attenuation as well as ecologically-based e-flow releases. The concepts of e-flows and hydropeaking mitigation, however, have to date hardly been merged (Boavida et al., 2020; Holzapfel et al., 2014).

The above section on e-flow methods and hydropeaking mitigation criteria underlines that a thorough understanding of ecological functions and processes is fundamental to establish flow restoration measures (Davies et al., 2014). More generally, knowledge on ecological standards is necessary to guide restoration measures in modified rivers (Palmer et al., 2005).

Even though there has been a rise in flow restoration activities (Muhar et al., 2019; Owusu et al., 2020), and although there have been many successful cases of e-flows implementation around the globe (Harwood et al., 2017), these are, for the most part, still isolated achievements. E-flows are not yet as widely implemented as they should be in order to sustain and restore riverine biodiversity (Poff et al., 2010; Richter et al., 2012; Tickner et al., 2020). This is especially true for hydropeaking rivers: in these cases, flow mitigation has only received little attention so far (Muhar et al., 2019; Owusu et al., 2020).

Considering that even light flow alterations may cause significant ecological drawbacks (Richter et al., 2012), we need a better understanding of flow alteration-ecological response relationships (Arthington et al., 2010). As it can be challenging to quantify flow-ecology relationships, research must target the identification of linkages between river flow and ecosystem components, including an enhanced understanding of ecological functions and processes (Arthington et al., 2010, 2006; Davies et al., 2014). Of particular need are flow rules and thresholds for key life-cycle stages, among other reasons, to establish mitigation solutions in hydropeaking rivers (Costa et al., 2019; Harby and Noack, 2013). Aside from quantitative thresholds, however, also qualitative recommendations are of fundamental importance as they can guide restoration measures in different regions or river types (Yarnell et al., 2015).

> *"There still remains a critical need for greater understanding of flow-ecological response relationships"*
> (Arthington et al., 2010).

1.7 Thesis aim and organization

In light of the above-described effects of dams and flow regulation, it is of utmost importance to thoroughly study the effects of ecological response to hydrological alterations on multiple scales to understand how already existing dams can "go with the flow" (Poff and Schmidt, 2016), that is, be sustainably managed. Nowadays, it is being increasingly understood that rivers ecosystems and their biota are legitimate water users (Naiman et al., 2002), and water managements exhibit an increased willingness to share "their" resources with the environment. Also, environmental flow releases and hydropeaking mitigation measures are more and more mandated through legislation (Acreman and Ferguson, 2010; Tonolla et al., 2017a). However, for this equitable sharing to be effective, we must better understand environmental water demands. Even though much progress has been made, knowledge gaps remain, for example, in regards to flow alteration-ecological response relationships (Arthington et al., 2010; Davies et al., 2014), which are a fundamental basis for ecological flow management.

1.7.1 General objectives

This thesis, therefore, has two main objectives:

- To develop holistic approaches for flow restoration in modified rivers subjected to water abstraction or hydropeaking.
- To develop environmental flows able to sufficiently mitigate the ecological effects of short-term and annual flow modifications.

To pursue and achieve these general objectives, a series of studies were undertaken to respond to four specific objectives.

1.7.2 Specific objectives

- To assess the impacts of flow regulation (hydropeaking), channelization, fragmentation, and water quality alteration on European grayling populations.
- To analyze the interplay between central abiotic and biotic river elements, and to identify the key flow regime components that determine ecological functions and processes in order to advance environmental flow restoration.
- To study the flow-ecology relationships of salmonid fish in order to propose flow regulations as an aid for the environmental enhancement of hydropeaking rivers.
- To provide an extensive review on the so far established hydropeaking thresholds for hydropower impact mitigation.

1.7.3 Thesis structure

This thesis contains six chapters. The first chapter introduced the reader to the general framework of the thesis by presenting the current knowledge on natural and modified river flows, flow-ecology relationships and the need to advance science and practice of flow restoration measures.

CHAPTERS 2–5 contain the studies developed to achieve the thesis' objectives. Each chapter pertains to a scientific question and presents the results and conclusions reached. Each chapter is a stand-alone article that has been published or prepared for journal submission and is, therefore, with the exception of formatting, identical to the published or soon-to-be submitted version.

- CHAPTER 2: Response of grayling to multiple stressors in hydropeaking rivers.
- CHAPTER 3: Advancing towards functional environmental flows for temperate floodplain rivers.
- CHAPTER 4: Life stage-specific hydropeaking flow rules.
- CHAPTER 5: Ecologically-based criteria for hydropeaking mitigation: A review.

Finally, CHAPTER 6 contains a synthesis of the work presented in CHAPTERS 2–5. Besides, it discusses challenges and limitations for practical applicability and offers an outlook on future research needs.

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CHAPTER

2

Response of grayling to multiple stressors in hydropeaking rivers

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2.1 Abstract

Rivers of the large Alpine valleys constitute iconic ecosystems that are highly threatened by multiple anthropogenic stressors. This stressor mix, however, makes it difficult to develop and refine conservation and restoration strategies. It is, therefore, urgent to acquire more detailed knowledge on the consequences and interactions of prevalent stressors on fish populations, in particular, on indicator species such as the European grayling *Thymallus thymallus*. Here, we conducted a multi-river, multi-stressor investigation to analyze the population status of grayling. Using explorative decision-tree approaches, we disentangled the main and interaction effects of four prevalent stressor groups: flow modification (i.e., hydropeaking), channelization, fragmentation, and water quality alteration. Moreover, using a modified variant of the bootstrapping method, pooled bootstrapping, we determined the optimal number of characteristics that adequately describe fish population status. In our dataset, hydropeaking had the strongest single effect on grayling populations. Grayling biomass at hydrological control sites was around eight times higher than at sites affected by hydropeaking. The primary parameters for predicting population status were downramping rate and peak amplitude, with critical ranges of 0.2–0.4 cm min^{-1} and 10–25 cm. In hydropeaking rivers, river morphology and connectivity were the preceding subordinated parameters. Repeating the procedure with pooled bootstrapping datasets strengthened the hypothesis that the identified parameters are most relevant in predicting grayling population status. Hydropeaking mitigation based on ecological thresholds is key to protect and restore already threatened grayling populations. In hydropeaking rivers, high river network connectivity and heterogenous habitat features can dampen the adverse effects of pulsed-flow releases by offering shelter and habitats for all life cycle stages of fish. The presented approach of explorative tree analysis followed by post-hoc tests of identified effects, as well as the pooled bootstrapping method, offers a simple framework for researchers and managers to analyze multi-factorial datasets and draw solid management conclusions.

2.2 Introduction

The European grayling *Thymallus thymallus* is an indicator species for the ecological integrity of an entire fish ecological river region – the grayling zone, which encompasses rivers in wide mountain valleys (Huet, 1959). Unfortunately, grayling stocks in Europe have plummeted in the last decades, underlining the urgency of conservation measures targeted at this species and fish region (e.g., Müller et al., 2018). However, it remains challenging to establish most effective management and restoration strategies as rivers of the grayling zone, also called hyporhithral rivers, are often impacted by multiple anthropogenic stressors (Schinegger et al., 2012). In the European Alps alone, 80% of all larger rivers with a catchment size of >500 km^2 are affected by diverse hydromorphological impacts (Muhar et al., 2019).

Of these, the effects of storage hydropower plants are particularly prevalent in hyporhithral rivers (FIGURE 2.1). Storage hydropower plants are run according to energy demand, thereby causing artificial (sub-daily) flow fluctuations by the discontinuous release of turbined water (Greimel et al., 2016). Such water releases, called hydropeaking, have wide-ranging implications for river ecosystems. Hydropeaking can influence spawning activities and behavior, or cause drift and stranding of juvenile fish as well as of aquatic insects, thereby reducing recruitment rates and food supply (Greimel et al., 2018; Hayes et al., 2019). Unsurprisingly, in Austria, of the almost 900 river kilometers labeled as hydropeaking-impacted, 82% are in risk of failing the objectives of the EU Water Framework Directive (BMLFUW, 2017). However, considering that also run-of-river hydropower schemes can cause hydropeaking (though usually of lower intensity) (Greimel et al., 2016), it is likely that the threat of failing to achieve ecological objectives due to hydropeaking is even higher than initially perceived.

Another common stressor is morphological riverbed degradation caused by river engineering works (Schinegger et al., 2012). As widely known, river straightening and bank stabilization decrease suitable habitats, particularly shallow shoreline areas needed for the rearing of juvenile fish (Jungwirth et al., 2000). Considering that <20% of Austrian grayling rivers still exhibit good habitat quality (Muhar, Schwarz, Schmutz, & Jungwirth, 2000), it can be expected that this trend is reflected in fish population status.

Moreover, river engineering and hydropower development have not only channelized but also fragmented most of the world's rivers (Grill et al., 2015). Instream connectivity, however, plays a fundamental role for life cycle completion of many fish species. The grayling, a medium-distance migratory species, requires an open river corridor for spawning migrations but also for movements between summer and winter habitats, as well as distinctive habitat shifts related to early ontogenetic development (Nykänen, 2004; Sempeski and Gaudin, 1995). Although fish passes are nowadays increasingly retrofitted to dams and weirs, they may still cause delayed or insufficient passage or exhibit other drawbacks (Linløkken, 1993; Silva et al., 2018). Moreover, fish may be injured or killed by turbine passage, which is a common route for downstream migration (Harrison et al., 2019). Also, reservoirs may act "as an ecological barrier to downstream movement" (Silva et al., 2018). Hence, highly fragmented river systems may be restricted in supporting vital fish populations.

Many rivers are also affected by alterations of water quality and nutrient content (Schinegger et al., 2012). Grayling populations can respond negatively to deterioration of water quality, and water quality and nutrient baseline conditions such as saprobity are known to influence fish distribution (Vannote et al., 1980).

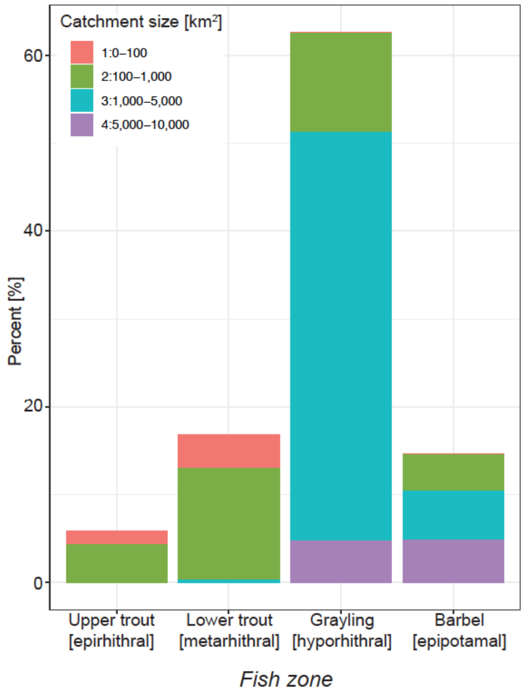

Figure 2.1 Hydropeaking rivers in Austria according to fish region and catchment size (data source: BMLFUW, 2017).

Overall, it is apparent that grayling populations are affected by multiple stressors (Muhar et al., 2007). As stressors can override or interact with each other, it remains a challenge to define best river management approaches. To develop and refine conservation and restoration strategies, it is therefore urgent to acquire more detailed knowledge on the consequences and interactions of prevalent stressors on fish populations.

We hypothesize that hydropeaking intensity is the strongest stressor for grayling, followed by river morphology. To test this assumption, we conducted a multi-river, multi-stressor investigation to analyze the population status of grayling in Austria. Although it is common for such approaches that data are sampled in several rivers and over multiple years, this fact makes it difficult to apply inferential statistics. This raises the question of which methodological approach can deal with these preconditions as well as solve the frequent challenge of a comparably small base sample. In this study, we use explorative methods to identify essential parameters and to elucidate the optimal number of characteristics that adequately describe the status of grayling populations. Thereby, we enhance ecological knowledge to aid river management in establishing the most effective measures for protecting and restoring already threatened grayling populations. Moreover, we offer a simple approach to analyze multi-factorial datasets encompassing sites from different rivers.

2.3 Materials and methods

2.3.1 Study area

Fish samples were collected from Austrian hyporhithral rivers where the grayling, according to the national fish catalogue, is classified as being a dominant (‘Leitart’) or accompanying (sub-dominant) species (BAW, 2007). Regarding flow modifications, our sites ranged from so-called reference sites that are not impacted by hydropower operations (hydrological control

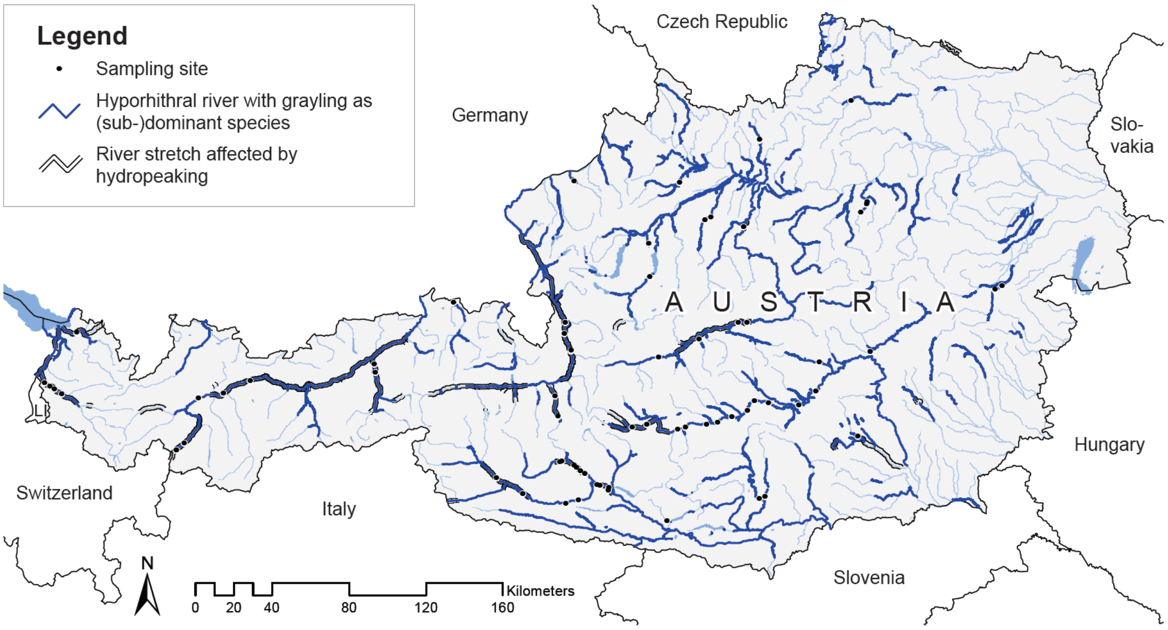

Figure 2.2 Hyporhithral rivers of Austria where grayling is a dominant or subdominant species (BAW, 2007), river stretches affected by hydropeaking (BMLFUW, 2017), and fish sampling locations.

sites) to sites of low-intensity hydropeaking ('hydro-fibrillation') and high-intensity hydropeaking (FIGURE 2.2; Greimel et al., 2016). Similarly, our sites also exhibited a strong stressor gradient regarding other impacts.

2.3.2 Fish stock assessments

Fish data were provided by the Austrian Ministry of Sustainability and Tourism (BMNT), which we complemented by further field samples. The collection of fish data followed the standard protocol of the national sampling guidelines (Haunschmid et al., 2006) under the requirements of the EU Water Framework Directive (2000/60/EC). In short, fish sampling was conducted via electrofishing during low flow conditions in fall. Depending on river size, the fishing campaigns were done by wading, boat, or a mix of both. The reader is referred to Schmutz et al. (2015) for details.

We used grayling biomass per hectare [kg ha^{-1}] to assess the status of grayling populations, as biomass is a robust measure to detect cumulative, multi-annual impacts of a variety of stressors. This target variable (Y_i) is a ratio scaled variable; it follows a non-parametric distribution.

2.3.3 Hydrological features

The Austrian Hydrographic Service provided flow data with a time resolution of 15 min.

To quantify hydropeaking events, we assessed ecologically-relevant event-based parameters (see TABLE 2.1) according to Greimel et al. (2016). The statistical characteristics were calculated out of five years prior to each fish survey to match flow conditions before and during biological assessments (Schmutz et al., 2015). Variables of increase and decrease event types have proven to be highly redundant (Greimel et al., 2016); therefore, we continued working with decrease events only as these are of higher relevance for fish ecological research (Moreira et al., 2019).

We assigned fish sampling stretches to the nearest gauging station that is representative of

Table 2.1 Overview of parameters.

Stressor block[a]	Parameter	Abbreviation	Unit
H	Yearly number of events[b]	CNT	
	Yearly number of daytime events[b]	CNT_D	
	Yearly number of nighttime events[b]	CNT_N	
	Peak amplitude[c]	AMP_dW	cm
	Duration[b]	DUR	s
	Base: peak flow ratio[b]	RATIO	
	Mean downramping rate[b,c]	MEFR_dW	cm min^{-1}
	Maximum downramping rate[b,c]	MAFR_dW	cm min^{-1}
M	Channel width index	CW	
	Standard sinuosity index	SSI	
C	Habitat connectivity index 1[d]	CONN_1	km
	Habitat connectivity index 2[d]	CONN_2	km
Q	Biological assessment: pollutant load	POLL	
	Saprobity baseline status	SAP	

[a] H = hydropeaking, M = morphology, C = river connectivity, Q = water quality.

[b] Event-based flow fluctuation (hydropeaking) parameters following Greimel et al. (2016). To conduct a standardized selection of relevant events out of multiple hydrographs, events of very low intensity regarding ramping rates were excluded (<10% of expected annual natural maximum). All values are means regarding to the selected events.

[c] Parameters describing water level alteration (dW) were transformed into cm or cm min^{-1}. These estimations of mean flow conditions are based on a regression model with the input parameters altitude, mean flow conditions, catchment size, and bankfull river width (Greimel et al., 2017).

[d] Indices are based on grayling jump height: 1 = minimum (0.4 m), and 2 = average (0.75 m) jump height (Baudoin et al., 2015).

the hydrological conditions at the sampling site (average distance: 4.1 km). We removed all sites that did not have relevant gauges and those situated in impoundments or residual flow sections, as well as those with spatial autocorrelation issues with other sites, thereby reducing the number of sites from 197 to 69.

2.3.4 Morphological features

We assessed a gradient from nature-like to channelized rivers to enhance understanding on the effect of habitat conditions on fish populations in hydropeaking rivers (Schmutz et al., 2015); therefore, we tested two morphological indices based on aerial image interpretation.

The first index, the channel width index, reflects the variability of the channel width in hyporhithral rivers (Greimel et al., 2017). It is based on the coefficient of variation of the active channel width, which is calculated by the ratio between standard deviation and mean. Each fishing stretch was divided into as many 500 m sections needed to cover its entire length. For each 500 m section, we measured ten equally-spaced transects from bank to bank and calculated the coefficient of variation. If a fish sampling site encompassed multiple 500 m sections, we averaged the interim results to gain an index for the entire stretch. The resulting coefficient allows a comparison of rivers of different dimensions (Greimel et al., 2017). As a rough guide, sites with a value of <0.1 can be regarded as being heavily channelized. Those with an index between 0.1–0.2 are still considered morphological degraded but may feature small-scale widenings or bay structures. Sections with an index >0.2 constitute structurally diverse, nature-like reaches (Greimel et al., 2017).

The second index, the standard sinuosity index, is based on the idea that sinuosity is an effective functional measure of a rivers' morphological status. It is calculated by dividing the channel index (CI) with the valley index (VI), whereby CI is channel length by aerial length, and VI is valley length by aerial distance. An index <1.05 represents a straight river, from 1.05–1.3 it is a sinuous river, from 1.3–1.5 moderately meandering, and >1.5 meandering (Horacio, 2014).

2.3.5 Connectivity features

Habitat fragmentation is considered a crucial factor in influencing species distribution. However, "the effects of fragmentation depend on the size of the resulting fragments" (Fuller et al., 2015). Taking this into account, we calculated the length of the accessible river network between all barriers for each sampling site, whereby we based this calculation on the grayling's natural core distributional area (see FIGURE 2.1). We defined a barrier based on jump heights of grayling, whereby we calculated two habitat connectivity indices: the first was based on the minimum (0.4 m) and the latter on the average (0.75 m) jump height (Baudoin et al., 2015). In each case, we subtracted the length of reservoirs from the resulting river network if it exceeded one kilometer in length, as these would not support recruitment.

2.3.6 Water quality parameters

To evaluate water quality at the sampling sites, we retrieved a cumulative biological assessment regarding pollutant load from the national monitoring program, as well as a status assessments of national and European priority substances (BMLFUW, 2017). The latter two parameters did not show any variation in the dataset (all sites had the very good or good status, respectively); therefore, we excluded them from analyses. To assess nutrient baseline status, we integrated saprobic basic state classes as determined by bioregion and altitude (Stubauer and Moog, 2003).

2.3.7 Model definition, data treatment, and statistical analyses

In this study, we aimed to find out which parameters (independent variables), as well as which main and interaction effects, make the variation of the biomass level (dependent variable) transparent. Formally, the multi-factorial model can be expressed as:

[1] $Y_i \leftarrow \{ H_{ji} ; M_{ki} ; C_{li} ; Q_{mi} \}$

whereby H, M, C and Q refer to hydrological, morphological, connectivity and water quality parameters, respectively (see TABLE 2.1). As described above, we selected sampling sites of different rivers based on fish ecological criteria. In order to assemble enough sites, they span a period of multiple years (2005–2014). However, this targeted arbitrary site selection has an influence on the sample character of the data, which do not fulfill the criteria of a representative sample (i.e., selection, structure and number of sites), thereby disqualifying approaches based on inferential statistics. Hence, an explorative-statistical data analysis strategy must be implemented.

Here, we used the following two-fold data evaluation strategy. First, we conducted decision tree analysis (CRT) to identify relevant parameters and main and interaction effects (Breiman et al., 1984). Following, we used a two-dimensional frequency analysis, the configuration frequency analysis (CFA) (Von Eye, 2002; Von Eye et al., 2010), to evaluate the statistical significance of the identified effects (global and local). In light of exploratory interpretation, the results of the CFA (e.g., p-value) must not be interpreted strictly; instead, they serve as an orientation aid from a hypothesis-generating point of view.

For step 1, the continuously scaled dependent variable, grayling biomass, was transformed into an ordinally scaled variable to allow the prediction of interaction ranges between situations of low, medium or high biomass. Therefore, we followed two approaches: a statistical and an ecological one. For the first, we trichotomized the target variable (i.e., each category contains 33% of the cases; 1: <3.4 kg ha^{-1}, 2: 3.5–19.9 kg ha^{-1}, and 3: >20 kg ha^{-1}). For the latter, we classified the target variable into three groups according to ecological relevance (1: <10 kg ha^{-1}, 2: 10–39.9 kg ha^{-1}, and 3: >40 kg ha^{-1}).

Before the trees analyses, to minimize multi-collinearity, we removed redundant independent variables by Spearman rank correlation (measure of monotony) ($|\rho| > 0.8$), whereby we selected inter-correlated descriptors according to potential ecological significance. We then ran the analysis with the remaining variables using the classification and regression tree (SPSS: CRT) method (Breiman et al., 1984), which corresponds to a bivariate step-by-step analysis. The CRT method splits the trees based on an internal measure of homogeneity instead of a statistical procedure. Here, we used a standard measure, the Gini-coefficient, as a splitting criterion (IBM Statistics, 2016). We set a minimum number of 10 and 5 cases for the parent and child node, respectively.

In step 2, we performed exploratory analysis in line with the two-dimensional frequency analysis (CFA: tree nodes *versus* biomass categories) to evaluate which end nodes (interaction pathways) contribute to the model explanation. We tested for global significance through chi-square tests and used Cramér's V to describe the strength of the overall effects on the target variable. To determine local significance, we performed Bonferroni-adjusted cell-residual tests.

Up to now, work was carried out at the level of the base sample where, due to the relatively small sample size (n=69), the possibilities of finding interactions are quickly exhausted. To compensate this disadvantage, we used a modified variant of the bootstrapping simulation. Bootstrapping is an internal resampling method that draws random samples from the base dataset (with replacement) to create a new dataset (National Research Council, 1988). Here, we adapted the bootstrapping method by randomly drawing multiple (k=69) single bootstrap samples of the original dataset (each sample containing the same case number as the base dataset). These single samples were then pooled into one dataset (n=69×69=4,761). We hypothesize that such cumulative/pooled bootstrapping simulations increase the number of cases while retaining the overall characteristics of the original dataset, having the advantage that the decision trees can be split deeper, thereby allowing the identification of more and longer interaction chains. To explore this hypothesis, we compared the regular bootstrapping method to the pooled variant: First, using the 69 single bootstrap samples, we tested the stability of the base sample results by assessing which variables consistently reappear in the decision trees and in which level. Following, we ran the CRT models with the pooled bootstrapping dataset.

We used a median test to investigate the hypothesis that hydrological control sites had higher grayling biomass than sites impacted by low- or high-intensity hydropeaking. For pair-wise post-hoc tests, significance values were Bonferroni-adjusted. All analyses were performed with IBM SPSS Statistics 24.

2.4 Results

In total, we analyzed 69 sites from 30 rivers. Among these sites, 12 were classified as hydrological 'reference', 21 as 'hydro-fibrillation' (i.e., low-intensity hydropeaking), and 36 as 'hydropeaking' sites. In the field samples, grayling biomass ranged from 0.0–176.4 kg ha^{-1}. We

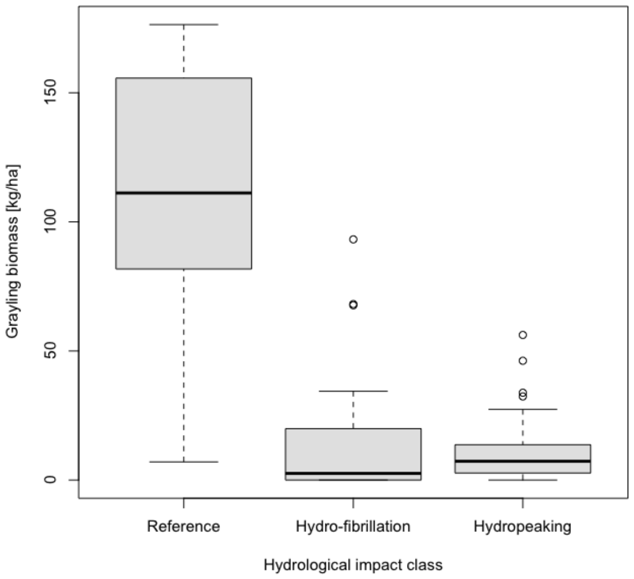

Figure 2.3 Grayling biomass in hydrological control (reference) sites and those affected by hydro-fibrillation or hydropeaking (grand median=8.9 kg ha^{-1}).

found strong evidence that the three hydrological impact types affect biomass of grayling populations ($p=0.004$). In detail, hydrological control sites exhibited a significantly higher biomass (mean=111.6, SD=51.2 kg ha^{-1}) than hydro-fibrillation (mean=16.6, SD=27.1 kg ha^{-1}, $p=0.001$) or hydropeaking sites (mean=11.6, SD=13.5 kg ha^{-1}, $p=0.003$). On average, grayling biomass at hydrological control sites was almost eight times higher than at sites affected by hydro-fibrillation or hydropeaking (FIGURE 2.3).

After removing redundant variables, nine variables were left for tree-based exploration. Out of the nine variables, two variables were retained in each of the decision trees (FIGURE 2.4). The first tree, using the trichotomized target variable, selected mean downramping rate (‘MEFR_dW’) in the first level, and habitat connectivity (‘CONN_2’) in the second level (FIGURE 2.4A). In our dataset, MEFR_dW varies between 0.09 and 1.53 cm min^{-1} (mean=0.31 cm min^{-1}), and CONN_2 between 0.3 and 177.2 km (mean=43.7 km). The model used MEFR_dW to create the first split: sites with highest biomass had a mean downramping rate <0.18 cm min^{-1}, and those with lower biomass exhibited ramping rates >0.18 cm min^{-1}. These latter sites were split again in the second level using CONN_2 at a threshold of 26.3 km. Sites with low biomass tend to be in more fragmented river reaches, whereas sites with higher biomass are situated within sections of higher connectivity. Overall, the model correctly classified 71.0% of the three biomass categories. In detail, the high and low biomass group performed best (82.6% correct for each group), followed by the medium group (47.8%).

The second tree, taking the ecologically classified variable as dependent variable, yielded a branched pattern similar to the first model but selected peak amplitude (‘AMP_dW’) in the first level, and channel width index (‘CW’) in the second one (FIGURE 2.4B). In our dataset, CW varies between 0.05 and 0.33 (mean=0.13), spanning a wide range of morphological conditions, and the amplitude of flow fluctuation events varies between 6.5 and 230.5 cm (mean=32.9). For the first split, the decision tree used AMP_dW at a threshold of 10.9 cm to separate sites of higher and lower biomass, whereby those

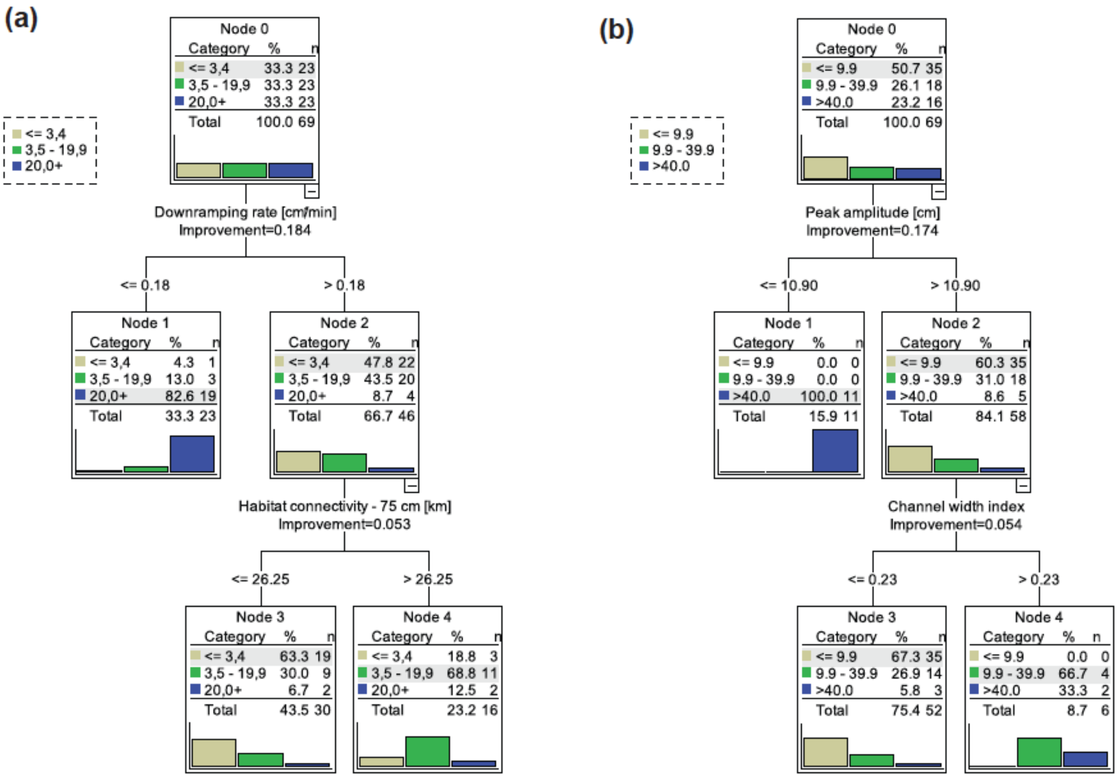

Figure 2.4 Explorative decision trees (CRT). (a) Trichotomized target variable; (b) ecologically-classified target variable. Both trees show two levels.

with highest biomass showed an amplitude <10.9 cm. The other sites (AMP_dW >10.9 cm) were split again in the second level using CW at a threshold of 0.23, indicating that morphologically impacted reaches are characterized by lower grayling biomass, whereas structurally-diverse river reaches feature higher biomass. Overall, the second model correctly classified 72.5% of the three biomass categories. In detail, the low and high biomass group was correctly classified in 100% and 68.8% of the cases, respectively. The medium biomass groups performed least well with 22.2% correct classification.

Following post-hoc tests serve as an orientation aid for the explorative interpretation. Global tests of grayling biomass and the end nodes (interaction pathways) showed a significant influence for both trees (trichotomized: p=0.000; ecologically classified: p=0.000; TABLES 2.2–2.3). In both cases, high effect sizes provide security for the model's strength (trichotomized: Cramér's V=0.597; ecologically classified: Cramér's V=0.621). Extending the test procedure to the performance of local tests highlighted the positioning of the differences. For the first model, five of the nine cells deviated from overall homogeneity (TABLE 2.2). In node 1, low biomass sites were underfrequented and high biomass sites overfrequented, whereas the opposite was the case in node 3. In node 4, medium biomass sites were overfrequented. Regarding the second model, we observed local differences for the low and high biomass sites in node 1 and in node 3 – in both cases, the pattern was the same as in the trichotomized model. In node 4, we found no significant differences, even though the low biomass group approached the threshold of statistical significance (TABLE 2.3).

Following, we conducted tree analyses with the single bootstrapped samples to assess the

Table 2.2 Cross-table (CFA) results for the end nodes (interaction pathways) versus biomass groups: trichotomization. Global test results: χ^2=49.12, df=4, P=0.000; Cramér's V=0.597. Shown here are counts and adjusted residuals (z) to determine typical/overfrequented (T) and atypical/underfrequented (AT) cells. The adjusted level of significance (z) is 2.77.

Node ID and pathway description		Grayling biomass: trichotomized			
		1: <3.4	2: 3.5–19.9	3: >20.0	Total
1: MEFR_dW <0.18 cm min^{-1}	n	1	3	19	23
	z	-3.6 (AT)	-2.5	6.1 (T)	
3: MEFR_dW ≥0.18 cm min^{-1} and CONN_1 ≤26.25 km	n	19	9	2	30
	z	4.6 (T)	-0.5	-4.1 (AT)	
4: MEFR_dW ≥0.18 cm min^{-1} and CONN_1 >26.25 km	n	3	11	2	16
	z	-1.4	3.4 (T)	-2.0	
Total	n	23	23	23	69

Table 2.3 Cross-table (CFA) results for the end nodes versus biomass groups: ecological classification. Global test results: χ^2=53.17, df=4, P=0.000; Cramér's V=0.621. Shown here are counts and adjusted residuals (z) to determine typical/overfrequented (T) and atypical/underfrequented (AT) cells. The adjusted level of significance (z) is 2.77.

Node ID and pathway description		Grayling biomass: ecologically classified			
		1: <10.0	2: 10.0–39.9	3: >40.0	Total
1: AMP_dW <10.9 cm	n	0	0	11	11
	z	-3.7 (AT)	-2.1	6.6 (T)	
3: AMP_dW ≥10.9 cm and CW ≤0.23	n	35	14	3	52
	z	4.8 (T)	0.3	-6.0 (AT)	
4: AMP_dW ≥10.9 cm and CW >0.23	n	0	4	2	6
	z	-2.6	2.4	0.6	
Total	n	35	18	16	69

frequency of variable occurrence and their location in the tree (TABLES 2.4–2.5). In the trichotomized version trees, the variables MEFR_dW and CONN_2 appeared at the same location as in the base sample in 96% and 44% of the cases, respectively. The trees split into a third level in 52 of 69 cases, with duration ('DUR'), yearly number of peak events ('CNT'), and CW being the dominating variables. Only 38% and 13% of all trees had a fourth and fifth level, respectively (TABLE 2.4).

In the ecologically classified trees, the variables AMP_dW and CW appeared at the same location as in the base sample in 61% and 27% of the cases, respectively. MEFR_dW substituted AMP_dW in level one in 36% of the cases but showed a similar split pattern regarding the biomass categories compared to the base sample tree. Variables also frequently occurring in the second level were CNT, AMP_dW, and the standard sinuosity index ('SSI'). In the third level, variable heterogeneity increased, but CNT, CONN_2, and CW were the most frequent parameters. Almost half of the trees did not split beyond the third level, and only 6% reached the fifth level (TABLE 2.5).

The pooled bootstrapping approach revealed that the base sample covered the primary effects of levels 1–2. In comparison to the base sample trees, however, the pooled bootstrapping trees produced wider and deeper branching patterns, thereby yielding more end nodes (13 and 10, respectively; not shown).

Table 2.4 Frequency of variable occurrence (total and per level) in the trees of the 69 single bootstrapping samples. Target variable: trichotomized grayling biomass.

Rank	Variable	Frequency ∑	Frequency per level ∑				
			Level 1	Level 2	Level 3	Level 4	Level 5
1	MEFR_dW: downramping rate	80	65	7	6	2	0
2	CONN_2: habitat connectivity	45	0	35	8	2	0
3	DUR: peak duration	34	0	12	15	4	3
4	CW: channel width index	22	0	6	11	4	1
5	CNT: number of peak events	27	1	6	13	6	1
6	AMP_dW: peak amplitude	19	3	7	3	5	1
7	SSI: standard sinuosity index	11	0	1	5	4	1
8	POLL: pollutant load	4	0	1	2	0	1
9	SAP: saprobity baseline status	1	0	1	0	0	0

Table 2.5 Frequency of variable occurrence (total and per level) in the trees of the 69 single bootstrapping samples. Target variable: ecologically classified grayling biomass.

Rank	Variable	Frequency ∑	Frequency per level ∑				
			Level 1	Level 2	Level 3	Level 4	Level 5
1	AMP_dW: peak amplitude	59	42	12	0	3	2
2	MEFR_dW: downramping rate	39	25	7	6	0	1
3	CNT: number of peak events	39	1	22	14	2	0
4	CW: channel width index	37	1	21	10	4	1
5	SSI: standard sinuosity index	20	0	9	7	4	0
6	CONN_2: habitat connectivity	19	0	1	13	5	0
7	DUR: peak duration	5	0	1	2	2	0

2.5 Discussion

Multi-river studies are an attractive method to assess spatial patterns of ecological impacts. Recently, also in hydropeaking rivers, such approaches are receiving increasing attention. However, so far, such studies only analyzed the interplay between hydropeaking and morphology (Schmutz et al., 2015) or natural environmental variables (Judes et al., 2020). To our knowledge, no study has yet conducted a large-scale comparison to analyze the effects of hydropeaking and further anthropogenic stressors on indicator fish populations of high conservational value, such as European grayling. Here, we filled this knowledge gap by identifying hydropeaking, fragmentation, and river regulation as key stressors in hyporhithral rivers, thereby providing solid groundwork for river management decisions.

2.5.1 Hydropeaking mitigation thresholds

The coherence between the two tree models in the first level (FIGURE 2.4) and the validation by the bootstrapping models strengthens the hypothesis that water level fluctuation is the primary driver in determining grayling population status. To derive operational management recommendations from the models, the end nodes have to be set within the context of other hydropeaking parameters as these are often highly correlated with each other. Based on node analyses with regards to selected hydropeaking parameters (e.g., FIGURE 2.5), it can therefore

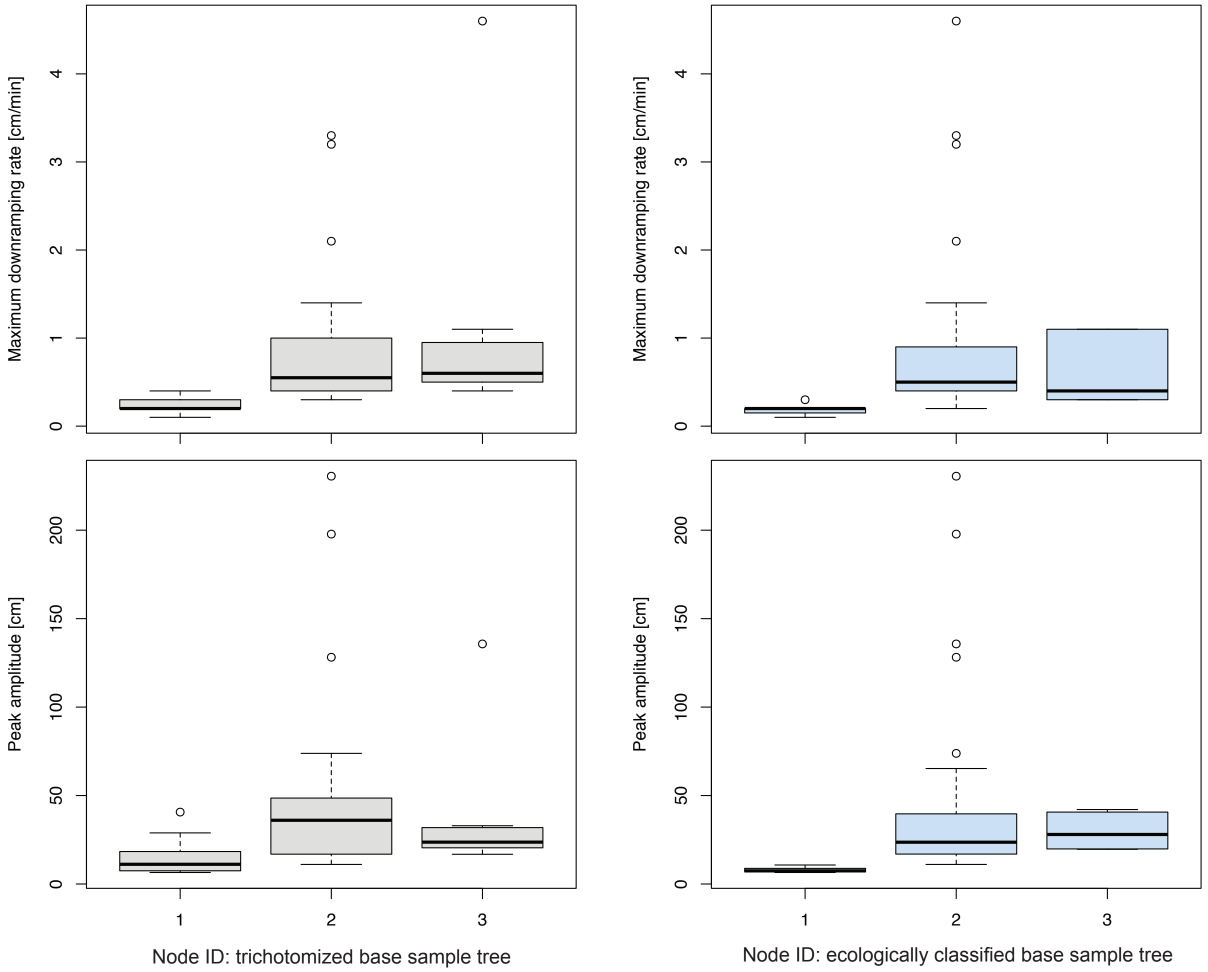

Figure 2.5: Linking the end nodes of the base sample trees (Fig. 2.4) with maximum downramping rate and peak amplitude.

be concluded that the critical peak amplitude range of artificial flow events lies between 10–25 cm, and the critical downramping velocity lies between 0.2–0.4 cm min^{-1}. Interestingly, the critical ramping range matches thresholds established for young-of-year grayling in experimental channels (Auer et al., 2014; Schmutz et al., 2013). Therefore, the fit between modelling and experimental approaches underlines the feasibility of using hydrological thresholds as ecological benchmarks for hydropeaking mitigation, particularly during critical life cycle stages such as fry emergence (Hayes et al., 2019; Moreira et al., 2019).

2.5.2 Hydromorphological criteria

In the second tree level, the models showed that, in hydropeaking rivers, high river network connectivity or heterogeneous habitat features can dampen the adverse effects of pulsed-flow releases (FIGURE 2.4). Regarding connectivity, the first model suggests that once a habitat complex >26 km is available, grayling populations can withstand hydropeaking impacts, at least to a certain degree (as the high biomass category is poorly represented in node 4). Considering that median home ranges are around 8 km (Junge et al., 2014) and migration distances range between 5–15 km (Jungwirth et al., 2000), this threshold seems reasonable from an ecological perspective. However, longer home ranges (>60 km) and migration distances (up to 100 km) have also been documented (Junge et al., 2014; Linløkken, 1993); hence, this threshold must be interpreted with caution as a habitat network of 26 km might still be too small to sustain proper population sizes in many river systems, in particular, if key habitats are missing. In this regard, suitable spawning grounds and juvenile rearing areas are essential, and tributary connectivity probably plays a vital role in mitigating hydropeaking effects (Hauer et al., 2017).

As suggested by the second model, habitat quality is of equal importance to habitat quantity. Indeed, grayling require both, an intact river corridor and a heterogeneous morphology, to complete all life cycle stages (Jungwirth et al., 2000). It is well known that, in hydropeaking rivers, river bank morphology plays a key role in mitigating the impacts of flow regulation (Hauer et al., 2014; Moreira et al., 2019, 2020). Rivers with an array of sediment bars are most resilient to hydropeaking as they offer high habitat diversity in various flow conditions. Braided river reaches with flat and wide gravel bars, however, also exhibit a higher risk of fish stranding (Vanzo et al., 2016). In contrast, point bars show a low stranding risk (Hauer et al., 2014). Hence, based on modelling results, it has been suggested that transitional (i.e., between single-thread and multi-thread) river morphologies may offer best eco-hydraulic trade-offs between habitat diversity and stranding risk (Vanzo et al., 2016); however, field validations of this assumption are still vacant. Overall, at the population level, our results do not support the notion that nature-like hydropeaking rivers exhibit higher stranding risks than channelized ones.

Considering that the effects of morphology and connectivity are interaction effects, our findings also underline that the full benefits of river rehabilitation measures can only become visible if hydropeaking intensity is reduced at the same time. This conclusion is in line with other studies showing that hydropeaking can override the effects of morphological measures (Hellström et al., 2019; Muhar et al., 2007; Schmutz et al., 2015).

Water quality seems to play a negligibly role in Austrian hyporhithral rivers, as most sites exhibited a good status.

2.5.3 Shifting baselines?

Here, we used two approaches to transform the target variable into an ordinally-scaled variable. In an optimal case, with a more balanced distribution of sites, both would have yielded similar class widths. However, as grayling stocks throughout Europe have been in a continuous decline (e.g., Müller et al., 2018), it is increasingly difficult to acquire data from unimpacted sites. It is even likely that we are witnessing a shifting baseline of fish stocks. Hence, it was necessary to conduct analyses with both approaches. Surprisingly, however, both models not only showed a similar correct classification rate but, as discussed above, also yielded comparable results with regards to variable selection and splits.

2.5.4 Bootstrapping validation

The two bootstrapping approaches confirmed that the original base sample sufficiently covers the main effects of levels 1–2. In the trichotomized version of the pooled sample, AMP_dW (≤25.5 cm) further split node 1 to separate higher and lower biomass sites (not shown). This indicates that vital grayling populations depend upon low rates of various hydropeaking parameters.

To further distinguish hydropeaking-impacted sites, the trichotomized tree – as well as some of the single bootstrapped trees – selected DUR and CNT in level 3. Cases with longer peak duration yielded higher fish biomass than those with shorter duration. This pattern is expected as natural flow fluctuation events (e.g., floods) usually have a longer duration and lower mean downramping rate than hydropeaking events (Greimel et al., 2016). Regarding CNT, however, the direction of splits was somewhat unexpected: sites with a greater event frequency exhibited higher biomass than those with lower frequency. This pattern, which was also found in the ecologically classified tree (not shown), can be partially explained by interpreting the bivariate relationship between fish biomass and event counts: once the high biomass sites are cut off in the first tree level, the direction of the relationship seemingly reverses, leading to the presupposition that more hydropeaks produce higher biomass. Nevertheless, the seasonal timing of peaks may explain this pattern, which warrants further studies on the fish ecological effects of peak seasonality.

The ecologically classified tree also showed an unexpected split direction for CONN_2 in level 3, separating high biomass from medium biomass sites. A few high biomass sites are in sections shorter than ca. 10 km. This finding stresses the need to incorporate other measures such as (tributary) spawning grounds into future assessments (Hauer et al., 2017).

Both pooled bootstrapping trees selected river sinuosity (SSI) in some of their end nodes to separate higher biomass sites of more sinuous rivers from lower biomass sites in straight rivers. This pattern again showcases the importance of heterogeneous river channels for ecological integrity.

Summarizing, the pooled bootstrapping approach supported the base sample results and split the tree into deeper levels, thereby indicating which parameters are needed for future stressor assessments in hydropeaking rivers.

2.5.5 Limitations and research needs

A correct classification rate >70% and a high effect measure underline that the two variables chosen in each of the base sample trees were sufficient to predict grayling population status with high accuracy. Nevertheless, this also indicates that further factors may affect grayling, which were not covered in this study. For example, it has been suggested that piscivorous birds and anglers can diminish grayling stocks (Čech and Vejřík, 2011). Also, agricultural land-use may hamper this gravel-spawning species' reproduction if increased fine sediments loads infiltrate and clog gravel layers (Hauer, Unfer, Tritthart, & Habersack, 2011; Müller et al., 2018). Furthermore, increasing water temperatures may not only limit the grayling's future habitat extent (Pletterbauer et al., 2016) but may already have contributed to recent abundance declines (Wedekind and Küng, 2010). Moreover, little is known about the population effects of food web changes, fish diseases, ubiquitous substances, or pharmaceutical products. Aside from multi-river studies on these topics, future research should focus on long-term assessments of case studies describing all ends of the pressure gradient. Such an approach would shed light on natural and anthropogenic effects and fulfill the requirements of an experiment from a statistical point of view.

2.6 Conclusions

Our results highlight the urgency of mitigating hydropeaking impacts to sustain or restore populations of threatened fish species such as European grayling. In this regard, the outcomes support the previously established notion of establishing ecologically-based flow thresholds (Moreira et al., 2019). Here, we identified critical ranges for peak amplitude (10–25 cm) and downramping velocity (0.2–0.4 cm min^{-1}) of artificial flow events. Furthermore, this study underlines the need to maintain or re-establish river connectivity between morphologically diverse habitats to support the requirements of all life cycle stages of fish.

2.7 Author's contributions

DSH, SS and EL conceived the ideas and designed the methodology; DSH, FG and NH assembled the data; DSH and EL analyzed the data; DSH, GU and SS interpreted the results; DSH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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2.9 Data availability statement

Fish data is available from: "Gewässerzustandsüberwachungsverordnung in Österreich gemäß Wasserrechtsgesetz 1959 idgF §§59c-i bzw. Gewässerzustandsüberwachungsverordnung (GZÜV, BGBl II 2006/479 idgF); BMNT, Abteilung I/3." All other data is available from corresponding author upon reasonable request.

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CHAPTER

3

Advancing towards functional environmental flows for temperate floodplain rivers

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3.1 Abstract

Abstraction, diversion, and storage of flow alter rivers worldwide. In this context, minimum flow regulations are applied to mitigate adverse impacts and to protect affected river reaches from environmental deterioration. Mostly, however, only selected instream criteria are considered, neglecting the floodplain as an indispensable part of the fluvial ecosystem. Based on essential functions and processes of unimpaired temperate floodplain rivers, we identify fundamental principles to which we must adhere to determine truly ecologically-relevant environmental flows. Literature reveals that the natural flow regime and its seasonal components are primary drivers for functions and processes of abiotic and biotic elements such as morphology, water quality, floodplain, groundwater, riparian vegetation, fish, macroinvertebrates, and amphibians, thus preserving the integrity of floodplain river ecosystems. Based on the relationship between key flow regime elements and associated environmental components within as well as adjacent to the river, we formulate a process-oriented *functional floodplain flow* (*ff-flow*) approach which offers a holistic conceptual framework for environmental flow assessment in temperate floodplain river systems. The *ff-flow* approach underlines the importance of emulating the natural flow regime with its seasonal variability, flow magnitude, frequency, event duration, and rise and fall of the hydrograph. We conclude that the ecological principles presented in the *ff-flow* approach ensure the protection of floodplain rivers impacted by flow regulation by establishing ecologically relevant environmental flows and guiding flow restoration measures.

3.2 Introduction

The natural hydrological flow regime is referred to as the river's master variable, arranging patterns and processes of the physical and biological environment (Power et al., 1995; Walker et al., 1995). River flows provide adequate habitat quality and quantity for riverine biota which are adapted to seasonally fluctuating flows (Lytle and Poff, 2004; Mims and Olden, 2012). The flow regime influences water quality, water temperature, nutrient cycles, and oxygen levels (Baldwin and Mitchell, 2000; Henriksen et al., 2008; Nilsson and Renöfält, 2008; Tockner et al., 2000), as well as geomorphological processes which shape the river and its floodplain (Egger et al., 2013, Egger et al., 2015; Opperman et al., 2010). The integrity, health, resilience, and productivity of riverine ecosystems depends upon the variability of flow with its constant changes between high and low flows (Naiman et al., 2008).

A river is more than the channel wherein it flows. A healthy river system encompasses diverse habitats along its longitudinal, vertical, and transversal floodplain gradients (Aarts et al., 2004; Ward, 1989; FIGURE 3.1), nurturing diverse species assemblages along its aquatic-terrestrial transition zones (Junk et al., 1989; Ward and Stanford, 1995). Floodplain ecosystems rely on intact connectivity, ensuring the exchange of matter, energy, and biota between the floodplain and the river channel (Tockner et al., 2000; Junk et al., 1989). These landscapes are shaped by recurring cycles of flooding and drying, erosion and sedimentation, as well as complex exchanges between surface- and groundwater (Baldwin and Mitchell, 2000; Tockner et al., 2008).

Floodplains are the naturally accompanying ecosystem of many rivers and thus contribute positively to their ecological status (Grizzetti et al., 2017). They belong to the most productive landscapes worldwide and constitute hotspots of biodiversity (Hauer et al., 2016; Opperman et al., 2010; Ward et al., 1999). In Switzerland, 80% of the fauna are found in riverine floodplains which constitute <1% of the country's surface (Tockner and Stanford, 2002). Regardless, many floodplain rivers are subjected to abstraction and storage of flow. Changes in the hydrological regime and the de-coupling of river channel and floodplain have been identified as the primary reasons for the rapid loss of riverine floodplains (Hughes et al., 2012; Tockner and Stanford, 2002), which now belong to the most threatened ecosystems worldwide (Junk and Wantzen, 2004; Tockner and Stanford, 2002). In Europe, few naturally functioning floodplain rivers remain (Gurnell et al., 2016). Across the pan-Alpine river network, only 8% (4669 km) of rivers are still accompanied by floodplains (Litschauer, 2014). Since 1850, 90% of pristine floodplains in Switzerland have vanished, resulting in the endangerment of 153 vascular plant species (Müller-Wenk et al., 2004). Austria has also lost 85% of its floodplains (Poppe et

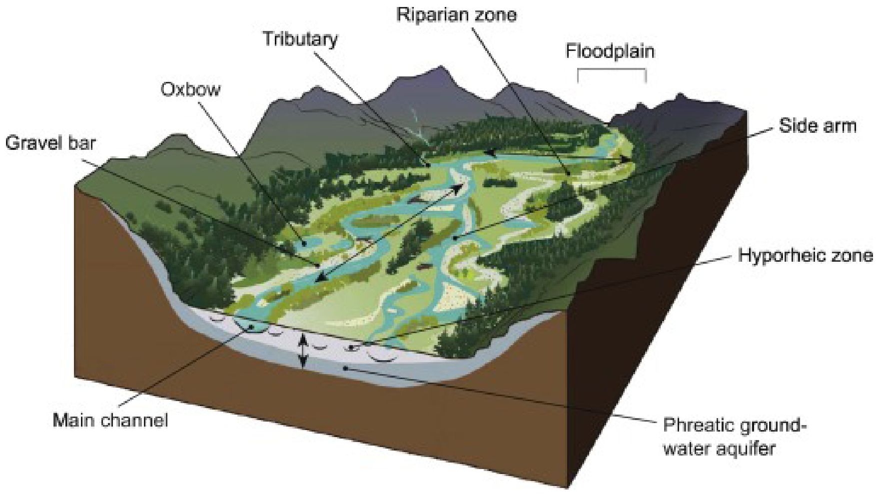

Figure 3.1 A gravel-bed floodplain river with its main elements. The arrows show the river's three-dimensional structure, i.e., its longitudinal, vertical, and transversal floodplain gradients (adapted from Hauer et al., 2016).

al., 2003), which is why >60% of the remaining floodplain areas are protected (Lazowski et al., 2011).

Environmental flow regulations are increasingly implemented to safeguard river reaches downstream of dams from environmental degradation and to maintain a defined ecological condition. However, assessments of environmental flows have mainly focused on determining minimum flows for chosen instream flow criteria (e.g., fish), while the rest of the ecosystem has usually been disregarded (Acreman et al., 2009; Petts, 2009). Although it is commonly known that a functioning floodplain is vital for the health of the entire ecosystem, its requirements have rarely been included in environmental flow assessments (Meitzen et al., 2013; Pusch and Hoffmann, 2000). For this reason, Thoms and Sheldon (2002) argue that environmental flow assessment must go beyond the consideration of only single elements. Instead, it must focus on central ecological processes and functions and their related pivotal hydrological drivers which are needed to sustain the whole ecosystem. While tropical floodplains and (semi-)arid rivers have received much attention in the past (Hughes and Rood, 2003; Junk et al., 1989; Yang et al., 2016), essential functions of temperate floodplains have been neglected in environmental flow assessment to date.

The objectives of this study are, therefore, to analyze the interplay between central abiotic and biotic elements (morphology including sediment transport, water quality, floodplain, groundwater, riparian vegetation, fish, macroinvertebrates, and amphibians) of temperate floodplain rivers and river flow, and to identify the key flow regime elements which determine their ecological functions and processes. We review studies linking ecosystem elements with the aspects of the natural flow regime as well as their responses to regime alterations. Understanding the relationship between flow and ecosystem components will enable us to establish truly ecologically-relevant environmental flows in temperate floodplain rivers. We begin by highlighting elements and targets of environmental flow definitions. We then discuss the relationship between river flow and the studied elements, describing natural and modified fluvial ecosystems. Finally, based on these connections, we formulate a functional floodplain flow (*ff-flow*) approach which offers a holistic conceptual framework for environmental flow restoration in temperate floodplain rivers impacted by flow regulation.

3.3 Environmental flows: objectives and definition

Dams are constructed for multiple purposes, including flood control, irrigation, water supply, recreation, or hydropower generation. Their operation entails a diversion or storage of water, whereby the natural river flow downstream of the facility is fundamentally altered (Poff and Hart, 2002). In response to the degradation of aquatic ecosystems generated by the intensification of water resources infrastructure development and the accompanying overuse of water resources, the ‘environmental flow’ (hereafter e-flow) concept was developed (EC, 2015; Matthews et al., 2014). Although this concept has been in existence for many decades, a coherent definition is lacking (Moore, 2004). Multiple authors have attempted to provide adequate definitions. Nowadays, one of the most widely accepted and best-known is the Brisbane Declaration (2007) describing e-flow as, “the quantity, timing, and quality of water flows required to sustain freshwater and estuarine ecosystems and the human livelihoods and well-being that depend on these ecosystems.” Although e-flow definitions may differ, they generally contain two key aspects: (1.) the flow regime elements to be considered; (2.) the targeted level of ecological protection.

TABLE 3.1 summarizes the key aspects of well-known definitions and lays the foundation for the establishment of a holistic definition for the *functional floodplain flow* (*ff-flow*) approach presented in this paper. Many authors assert that the quantity, timing, and the quality of water flow are key elements of an e-flow regime. Arthington and Pusey (2003) refer to the five central components of the natural flow regime (i.e., magnitude, frequency, duration, timing, rate of change; Poff et al., 1997) and state that these aspects are necessary to "maintain or restore the biophysical components and ecological processes of in-stream and groundwater systems, floodplains and downstream receiving waters." Multiple other authors also explicitly mention habitats beyond the river channel, such as riparian and bank zones, floodplains, wetlands, or groundwater. Most e-flow definitions aim to protect or restore the integrity and health of river ecosystems. Some refer to ecosystem functions and processes as well. Frequent targets are also ecosystem services offered by free-flowing rivers and maintained through e-flow releases (Auerbach et al., 2014; Richter, 2010). An e-flow regime that restores the integrity and health of a river system will also facilitate the provisioning of social and economic services (e.g., Jorda-Capdevila and Rodríguez-Labajos, 2017) and assist in achieving ecological objectives such as those of the EU Water Framework Directive (EC, 2015).

Based on these considerations (TABLE 3.1), we define e-flow as *a river flow capable of maintaining the natural functions and processes regarding quality, quantity, and temporal cycles, to retain the*

Table 3.1 Key flow elements, habitats, and targets contained in environmental flow definitions.

	Source
Flow elements	
Flow regime	1; 2; 3
Dynamic and variable flow	1; 4; (5)
Magnitude/quantity of water flow	1; 2; 5; 6; 7; 8; 9
Frequency	1; 6
Duration	1
Timing/temporal patterns of water flow	1; 4; 5; 6; 7; 8; 9
Rate of change	1
Quality of water flow	5; 7; 8
Habitats (hydrologic systems)	
River channel	1; 2; 3; 5; 10
Riparian zone/bank zone	5; 10
Floodplain/wetlands	1; 2; 3; 5; 10
Groundwater	1; (3); 5
Estuary/coastal zone	1; 3; 5; 7; 10
E-flow targets	
Integrity and health of the river ecosystem	(3); 5; 6; 9; 10; 11; 12
Maintenance of ecosystem functions and processes	1; 2; 8; 9
Ecosystem services (general)	3; 8; 11
Social and economic services (provided by diverse habitats of the ecosystem)	(3); 4; 5; 6; 7; 8
Achievement of legislated ecological objectives	13

1 Arthington and Pusey (2003)
2 Tharme (2003)
3 Dyson et al. (2003)
4 Brown and King (2003)
5 Hirji and Panella (2003)
6 Gupta (2008)
7 Brisbane Declaration (2007)
8 Hirji and Davis (2009)
9 Arthington (2012), in: Meitzen (2016)
10 ISE (2002)
11 IWMI (2004), in: Moore (2004)
12 Meitzen et al. (2013)
13 EC (2015)

integrity and resilience of riverine ecosystems inclusive of all their related components (river, floodplain, groundwater) as well as associated ecosystem services.

3.4 Ecological principles for the functional floodplain flow

3.4.1 Seasonality of hydrological flow regimes

The natural flow regime is the primary conductor of ecological processes in river ecosystems and guarantees the long-term preservation of their functionality, biodiversity, and ecological integrity (Junk et al., 1989; Karr, 1991; Poff et al., 1997; Richter et al., 1997). It can be described by the five flow regime components, as defined by Poff et al. (1997). Multiple hydrological regime types exist, which are differentiated by climatic, geological, and topographic factors (Mader et al., 1996; Rinaldi et al., 2016). Flow regimes of temperate rivers are characterized by spring/summer peak discharge due to melting snowcaps and glaciers. Low flows occur periodically in late summer, fall, or during winter while precipitation events throughout the year lead to quickly fluctuating river flows.

The interaction of river hydrology and morphology shapes riverine populations (Bunn and Arthington, 2002). Plants and animals are adapted to naturally recurring drought and flood events (Lytle and Poff, 2004). Among others, the life cycle of many riparian species, fish, macroinvertebrates or amphibians is synchronized with the occurrence of specific flow events (Lytle and Poff, 2004; Poff et al., 2010; Trush et al., 2000). Intra- and inter-annual flow variability sustains ecological processes in the river and the adjacent floodplain and maintains ecosystems of high abiotic and biotic diversity (Meitzen et al., 2013; Poff et al., 1997; Ward et al., 2002). Flood pulses are a central component of floodplain rivers (Junk et al., 1989) and support diverse ecological functions along the four-dimensional linkages of lotic systems (i.e., lateral, longitudinal, vertical, and temporal connectivity; Ward, 1989).

3.4.2 Effects of flow alteration

Changes in the hydrological regime can be identified depending on location and climatic condition and the type and management of dams. Storage dams homogenize the seasonal flow variability downstream by decreasing peak flow events and increasing minimum flows as well as the duration of near bankfull discharges (Poff et al., 2006). Diversion hydropower plants in temperate rivers drastically reduce the latter two as well (FIGURE 3.2A), whereas peak-load operating facilities also exhibit a high sub-daily flow variability caused by low flow and high peak flow cycles (Greimel et al., 2016). Irrigation dams, especially in Mediterranean regions, create a significant shift in seasonality when irrigation water is distributed via the river channel (FIGURE 3.2B; Magdaleno and Fernández, 2011). The extent of hydrological changes also depends on the reservoir's capacity to store flow (e.g., seasonal, weekly, run-of-river – FIGURE 3.2C) and can result in non-natural flood events (Richter and Thomas, 2007). Diverted water is returned to the river at the tailrace, which is situated either a few meters or up to several kilometers downstream of the intake structure ('non-consumptive use'). Abstracted water used, for example, for irrigation or water supply, may not be returned at all ('consumptive use').

Any modification of the natural hydrology may entail morphological and biological ecosystem transformations (Poff and Zimmerman, 2010), whereby floodplains are especially sensitive to hydrological changes (Fantin-Cruz et al., 2015). Any alteration of the flow regime and its five components (*sensu* Poff et al., 1997) modifies ecological processes and patterns, depending

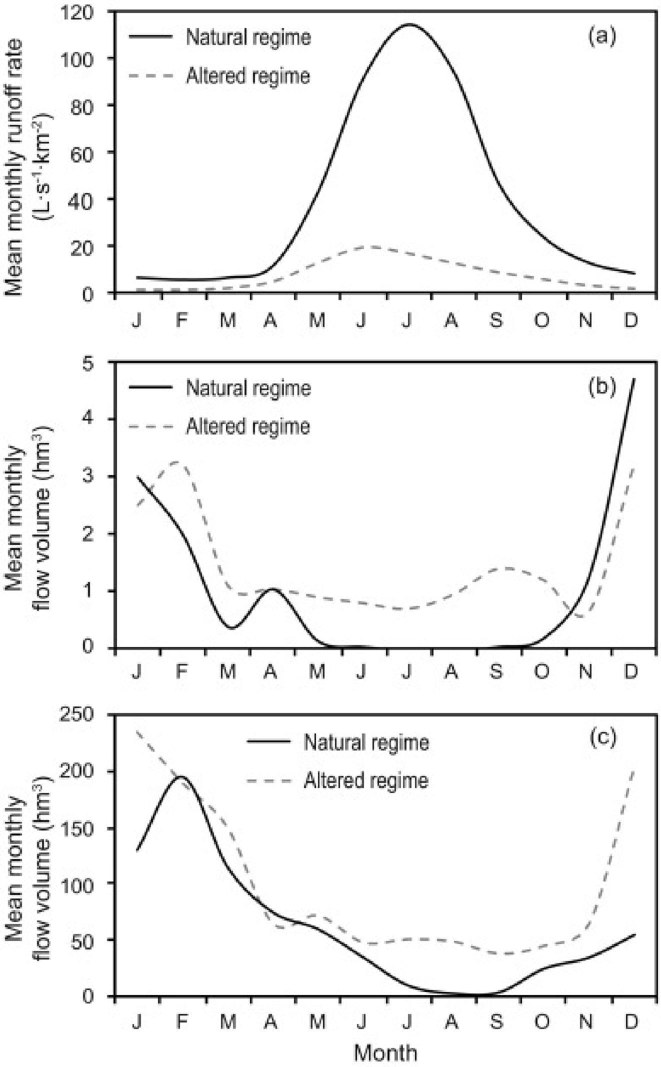

Figure 3.2 Changes in the intra-annual variation of monthly runoff rate/streamflow volume caused by (a) a hydropower derivation dam of high storage capacity in an alpine river, (b) a water storage dam for summer irrigation in a Mediterranean river, and (c) a run-of-river hydropower scheme in a Mediterranean river. The dotted grey line represents the regulated river section where water is abstracted, while the black line represents the corresponding free-flowing river (data source: (a) Hydrographisches Zentralbüro, Austria, (b, c) Portuguese National Water Resources Information Service (http://snirh.apambiente.pt/)).

on the position within the river network (Poff et al., 2006). E-flow assessment targeted at the maintenance of floodplain river functions and processes must, therefore, incorporate flow alteration-ecological and geomorphological response relationships (see e.g., García de Jalón et al., 2017; Poff and Zimmerman, 2010; Webb et al., 2013) so that the main hydrological drivers needed for flow restoration can be determined (Richter and Thomas, 2007). Most e-flow studies that incorporate the water demand of riverine floodplains and wetlands originate from Australia, South Africa, or North America and are primarily based on research in arid or semi-arid rivers (Hughes and Rood, 2003). Nevertheless, it is possible to draw conclusions from these studies that can contribute to the e-flow debate in temperate regions as well.

Based on previous flow classifications (Arthington et al., 1992; Caruso et al., 2013; King et al., 2003; Richter et al., 2006), we describe five different kinds of river flows—low

Table 3.2 Typical flow alterations caused by dams and flow abstraction, and related morphological, floodplain/floral and faunal responses of floodplain river ecosystems. Management options for flow restoration measures are proposed.

Flow characteristic	Alteration	Morphological response	Floodplain/floral response	Faunal response	Flow management recommendation
Magnitude	Flow stabilization (loss of high flow events and reduction of flow variability)	Reduced habitat creation processes via sediment redistribution mechanisms[a], diminished habitat diversity[a]	Reduced water and nutrients directed towards floodplain plant species, leading to altered recruitment and failing of seedling establishment (ineffective seed dispersal, loss of scoured habitat patches needed for plant establishment, seedling desiccation)[b, c], reduced productivity and decomposition rate[a] Lower species richness, altered assemblages[a, c], successful invasion of non-native species[a, c] Vegetation encroachment into channels[b], terrestrialization of flora[c], increased riparian cover[c] Excessive growth of aquatic macrophytes[d]	Competitive species dominate while poor competitors/sensitive species are lost, altered assemblages and dominant taxa[a, c] Invasion and establishment of exotic species, causing local extinction, threat to locally adapted species, altered communities[a, b, c, d] Reduced diversity and abundance[a, c] Reduction in fish populations[d] Increased standing crop and reduced diversity of macroinvertebrates[d]	Increase seasonal variation of flow/ reintroduce aspects of the natural flow regime[a, d, e] Provide flushing flows to clear channels of encroaching vegetation and alien species and to mobilize sediments acting as diversity-enhancing disturbances[a] Promote longer periods of inundation through floods[d] Vary flow during wet season, but with removal of some floods[f] Incorporate interannual flow variability (i.e., wet, normal, and dry years)[e]
	Decreased water level in main channel/reduced mean daily flow	Alteration of size and pattern of the active channel and its geomorphic complexity[g] Deposition of fine sediments in gravel[b] (esp. in pools[i]), increased sedimentation and riparian vegetation encroachment into the active channel may change channel and floodplain morphology, e.g., decreased depth/ width or creation of new floodplain terraces from drying channel sections[h, i, j]	Reduced soil moisture availability for riparian vegetation[g], reduced groundwater depth negatively affects riparian organisms, higher mortality[k] Shifts in density, productivity and species composition[h] Alterations in amount and availability of habitat space and patch size[g]	Changes in amount and availability of habitat space, patch size, amount of water, food and cover available for organisms[g] Smaller refuges for fish, greater mortality in the main channel through competition and predation[l] Increased risk of anoxia[l] (e.g., through rise of summer water temperature and aggravation of water pollution effects[h]) Interruption of migration pathways[l] Changes in fish and macroinvertebrate assemblage structure, abundance, and diversity[k]	Maintain (monthly varying) minimum flows to sustain aquatic habitat (in dry season)[f, m, n] to limit stressful habitat conditions[e], inundate riffle zones[m], provide adequate water levels over in-channel spawning habitats[l] Provide higher minimum flows to ensure connectivity for in-channel migration (to/from feeding, resting or spawning areas)[a, f, l, m], and to keep fish and amphibian eggs suspended[f] Release river flows to maintain water table levels in the floodplain, soil moisture for plants[f], nutrient delivery[m] Maintain adequate water quality[l], e.g., suitable water temperature, dissolved oxygen, and water chemistry[f, m] Support hyporheic organisms (living in saturated sediments)[f]

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Table 3.2 (continued)

Flow characteristic	Alteration	Morphological response	Floodplain/floral response	Faunal response	Flow management recommendation
	Decrease of high flow pulses	Change in spatial range of processes and size of functional surfaces[g], e.g., stabilization and narrowing of river channel[b, j], reduction of active floodplain surface[g] Change in dominant particle size of bed material[g], bed armoring[i], deposition of fine sediments in gravel[b, j]	Floodplain aquifers are not adequately recharged[o], causing long-term dehydration of riparian habitats[g] Terrestrialization of riparian species[c], vegetation encroachment into channel[f]	Changes in amount and types of habitats for aquatic, semiaquatic, and terrestrial biota[b, g] Adverse effects for fish[k], e.g., less space for reproduction, refuge, and feeding of young and adult fish during flood[l], reduction of lateral connectivity[a] Clogging of the riverbed disconnects surface and groundwater and reduces reproductive success of fish and lowers numbers of aquatic species generally[a]	Provide habitat maintenance flows (incl. sediment load) that perform specific functions, e.g., clean spawning gravel[s], enable longitudinal and lateral connectivity or serve as migration cues[e, l], move bed sediments[p], shape physical character of river channel including pools, riffles[f, m], determine substrate composition by transporting and sorting sediments[f, m, q], prevent riparian vegetation from encroaching into channel[f, m], replenish and maintain floodplain water table[p], restore normal water quality conditions after prolonged low flows[f], flush away waste products and pollutants[f], increase water exchange between surface and hyporheic habitats[a] Release wet-season 'initiation flows' to kick-start ecological processes and provide ecological cues[e]
	Decrease of peak flows/ overbank flows	Reduced channel migration and development of secondary channels, point bars, oxbows[b], changes in channel planform (e.g., narrowing, downcutting)[b] Prevention of floodplain deposition and erosion[b], reduction of active floodplain surface[g] Change in available space for river forms, sediments, and processes, floodplain size[g], decrease in river's capability to transport tributary sediment inputs[i] Missing habitats for pioneer vegetation[j]	Failure of flooding of all or part of the floodplain[l], reduced connectivity Alteration of amount and types of patches for riparian organisms[g] Terrestrialization of riparian species[c], vegetation encroachment into channel[f]	Changes in number and types of habitats for aquatic, semiaquatic, and terrestrial biota[b, g] May prevent fish from accessing the floodplain[l], reduced floodplain spawning areas[d] entails abundance decline[b]	Provide flushing flows and continuity of sediment transport to modify/ maintain channel structure[e, l, p] by retaining flood magnitude to scour channel and (encroaching) vegetation and purge alien species from aquatic and riparian communities[a, e, f, m], mobilize sediments acting as diversity-enhancing disturbances[a, m], create sites for recruitment of colonizing plants[f, r], recharge river banks and floodplain water table[f, q, r], disburse seeds and fruits of riparian plants[f] Reconnect floodplain and channel habitats by reintroducing overbank floods[a, q], enable fish to spawn on floodplain, provide nursery area for juvenile fish[f], provide new feeding opportunities for fish and waterfowl[f], deposit nutrients on floodplain[f], flush organic materials (food) and woody debris (habitat structures) into channel[f, m] Enable large floods to shape physical floodplain habitats[f] and to drive lateral movement of river channel[q, r], forming new habitats (secondary channels, oxbow lakes)[f]
Frequency	Decreased variation		Competitive species will dominate while poor competitors might be lost[a]	Competitive species will dominate while weak competitors might be lost[a], negative impacts on fish[k]	Increase seasonal flow variation[a] Match frequency of hydrograph components with life-history requirements[e, q]

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Table 3.2 (continued)

Flow characteristic	Alteration	Morphological response	Floodplain/floral response	Faunal response	Flow management recommendation
	Increased frequency of low flow periods	Increased frequency of in-channel sediment depositiong and stability of channel and banks[g] (i.e., no sediment turnover)	Drought stress[g, s], growth limitations Reduced food web complexity[r]	Greater frequency of limiting hydraulic/habitat conditions[t] Altered availability of floodplain habitats for (semi-)aquatic species[g] Reduced food web complexity[t]	Restrict unnatural frequency of low flow periods by increasing minimum flow[u]
	Decreased frequency of high flow pulses	Alteration of frequency of mobility of channel bed and bank materials, frequency of changes in functional surfaces[g] Reduced flushing of sediments[a]	Long-term dehydration of riparian habitats leads to terrestrialization of riparian biota[c]	Less frequent rejuvenation of riverine and floodplain habitats[v] Adverse effects on fish[k]	Provide regular high flow pulses, preferably every year and correctly timed[e, l, q] Vary flow during wet season, but with removal of some floods[f], to recharge groundwater aquifers[q]
	Decreased frequency of peak flows/overbank flows	Change in spatial range of frequency of functional surfaces[g] Less frequent resetting of the river/pioneer habitat creation	Shift in community composition[c] Reduction in species richness[c] Increase in wood production[c]	Aseasonal/reduced reproduction[c] Decreased abundance or extirpation of native fishes, decreased richness of endemic and sensitive fish[c] Reduced habitat for young fish[c]	Frequently inundate floodplains every 1–3 years[e, q], adjust floods to connect floodplain waterbodies that are further away every 3–5 years[l] Establish large scouring floods[q] to control distribution and abundance of riparian and floodplain plants, and to maintain balance of species in aquatic and riparian communities[f] Reset floodplain vegetation succession every 10–20 years with large magnitude peak flows[e]
	Increased variation (e.g., hydropeaking)	Increased erosion[a]	Impairment of germination, establishment, growth, and reproduction[w] Most riparian species disappear–easily dispersed, flexible, flood-tolerant and amphibious plants are favored[w]	Increased erosion leading to stress and loss of organisms[a, x] Reduced habitat availability[a], diminished spawning and rearing success of fish[x] Lowered species richness and biomass of macroinvertebrates[d]	Reduce frequency of flow variation[a]
Duration	Prolonged low flows	Change in magnitude of in-channel deposition processes[g], limited sediment transport fostering sediment deposition[g], increased siltation[h]	Physiological stress leading to reduced plant growth rate, morphological change, or mortality[b] Reduction or elimination of plant cover[b] Diminished plant species diversity[b]	Limits for aquatic organisms[g] or physiological stress[a] due to reduced river water quality (e.g., oxygen deficits), and temperature variation[a, h], concentration in small areas[b] Long-term alteration in species distribution, abundance[h], and diversity[a]	Prohibit unnatural prolongation of low flows by increasing minimum flow, but maintain natural river characteristics[e] Increase seasonal high flows[a]
	Shortened flood peaks/ interruption of flood	Alterations of magnitude of erosion on banks and in channels, bedload transport, channel sediment texture[g]	Encroachment of terrestrial organisms[a]	Exposure of floodplain spawning substrates, stranding and desiccation of eggs[l], stranding of fish in temporary pools[l] Failure of eggs and larvae to colonize floodplain[l]	Increase duration of seasonal flood peaks[a] to allow ecological processes[e]

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Table 3.2 (continued)

Flow characteristic	Alteration	Morphological response	Floodplain/floral response	Faunal response	Flow management recommendation
	Shortened duration of floodplain inundation		Less time for development of floodplain vegetation[l], reduced growth rate or mortality[c] Altered assemblages, terrestrialization of species composition, increase in abundance of non-natives[c], decline in wetland vegetation[d], reduced area of riparian plant or forest cover[c]	Less time for growth of fish and to remain in floodplain refugia[l] Decreased abundance of young fish, change in juvenile fish assemblage[c] Loss of floodplain specialists in mollusk assemblages[c]	Alternate high short floods with lower but longer ones to favor all groups of species[l] Maintain diversity in floodplain forest types through prolonged inundation[f], e.g., min. of three weeks and periodic connectivity between river and floodplain[e], provide plant seedlings with continued access to soil moisture[f], inundation for vegetation germination, fish recruitment, waterbird breeding[m]
Timing	Loss of seasonal flow or flood peaks/shifts in seasonality	Reduced habitat availability[a], loss of seasonal floodplain waterbodies[q] Change in interactions between erosive flows and stabilizing vegetation[g]	Reduction or elimination of riparian plant recruitment, reduced plant growth rates, increased mortality, and changed succession patterns[a, b, c, k, r] Invasion of exotic riparian plant species[b, c], reduction in species richness and plant cover[c]	Disrupted synchrony of life-cycle cues for fish (spawning, egg hatching, migration)[b, c, d, e, g], reduced growth rate[a] Loss of fish access to floodplain[b], decreased reproduction and recruitment[c] Change in assemblage structure[c], invasion of exotic species[a]	Reintroduce seasonal flow peaks[a, e, p] to trigger flows for migration[a, m, p] and spawning (of floodplain species)[j], and to deposit gravel or cobble in spawning areas[n] Retain spring flushing flow as cue to life cycle[f] Provide well-timed flows which allow delivery of seeds and establishment of seedlings[q, r] Provide adequate recession flows, allowing eggs to emerge[e], fish larvae to develop[l] and to use nursery areas[n]
	Delay in arrival of seasonal flood peaks		Desynchronization of photoperiod, temperature, and hydrology inhibits successful flowering and seed dispersal of cottonwoods[y]	Changes in thermal coupling between flood and temperature influences physical readiness of fish to mature, migrate, and spawn[l], e.g., delayed spawning[d] Desynchronization of fish larvae drift and movement to floodplains and backwaters[l]	Ensure the correct timing of seasonal flood peaks so they can act as triggers for life-cycle cues (e.g., migration, spawning)[e, l]
Rate of change	Overly rapid rise in river stage	Weakening of banks and loss of vegetation[a]	Quick immersion of floodplain[l], failed establishment and recruitment of riparian vegetation[a, j]	Washing-out of organisms[a, b] Submergence of nests and spawning sites at too great depths[l]	Reduce rates of change[a], flood curves should be as smooth as possible[l] Flows shall ensure connectivity to the floodplain and induce lateral migration[l]
	Overly rapid fall in river stage/accelerated flood recession	Weakening of banks and loss of vegetation[a]	Fast drying of floodplain surface[l] Failure of seedling establishment and recruitment of riparian vegetation[a, b]	Increased stranding mortalities (in temporary water bodies)[a, b, l]	Reduce rates of change[a], flood curves should be as smooth as possible[l], esp. spring recession flows[e], do not exceed threshold limits[p] Flows shall ensure connectivity and safe return of fish to the river and floodplain waterbodies[l] Gradual recession of water tables to expose moist sediment for seed germination after floods[m, r]

[a] Renöfält et al. (2010)
[b] Poff et al. (1997)
[c] Poff and Zimmerman (2010)
[d] Bunn and Arthington (2002)
[e] Yarnell et al. (2015)
[f] Postel and Richter (2003)
[g] Graf (2006)
[h] Heicher (1993), in: Smakhtin (2001)
[i] Brandt (2000)
[j] Ryan (1997)
[k] Webb et al. (2013)
[l] Welcomme (2008)
[m] Davies et al. (2014)
[n] Richter and Thomas (2007)
[o] Smakhtin (2001)
[p] Acreman et al. (2009)
[q] Trush et al. (2000)
[r] Hughes et al. (2012)
[s] Rood et al. (2013)
[t] Rolls et al. (2012)
[u] Petts (2009)
[v] Ward and Stanford (1995)
[w] Bejarano et al. (2017)
[x] Young et al. (2011)
[y] Mahoney and Rood (1998).

flow, mean flow, small flood, large flood, and flow variability—and their importance to functions and processes of floodplain river ecosystems. Each component is described separately, yet they are all interrelated (Poff et al., 1997), as depicted by 'flow variability.'

3.4.3 Low flow

Low river flows occur in seasonal periods where there is no rainfall and where only the base flow remains in the river channel. In contrast to quickflows, which contain the direct response of the catchment to precipitation, low-level stream flows originate from either groundwater or delayed sources such as melting glaciers or subsurface storage. Low flows are often defined as flows occurring 70–99% of the time (Smakhtin, 2001). These flow magnitudes govern the availability of minimum aquatic habitat (Postel and Richter, 2003) as they determine the minimal wetted perimeter, available depths, and hydraulic conditions. Hence, they may regulate the carrying capacity of riverine ecosystems as they often present ecological bottlenecks (Behnke, 2007; Jowett et al., 2005; Rolls et al., 2012). Nevertheless, they are a central element of the natural flow regime and are of ecological importance (Humphries and Baldwin, 2003). Monthly low flows vary throughout the season and can be distinguished from extreme low flows (Caruso et al., 2013).

During periodic low flow conditions, the groundwater table in the floodplain sinks as water flows back into the main channel (Smakhtin, 2001; Stanford and Ward, 1988). During winter, low flow conditions exist when vegetation is dormant (Rood et al., 2007). In contrast, summer low flows occur during the growing season. When alluvial groundwater sources can be accessed, these periods promote the regeneration of native riparian and floodplain vegetation (Flanagan et al., 2017) and simultaneously remove invasive species (Postel and Richter, 2003). Plant seedlings can sprout and grow without being washed away (Johnson, 1994; Postel and Richter, 2003). Thus, these periods are essential for the progression of floodplain vegetation (Johnson, 1994), but also in preparation for the next flood pulse (Junk et al., 1989) as the drying of floodplain soils facilitates aerobic processes which increase the availability of nutrients at the next flooding (Baldwin and Mitchell, 2000; Richter and Thomas, 2007). Seasonal floodplain water bodies dry out, guaranteeing that they remain unoccupied by fish. The absence of such predators from ephemeral habitats supports the survival of aquatic life-stages of amphibians (Adams, 1999; Babbitt and Tanner, 2000; Hauer et al., 2016). When the floodplain is dry, amphibians, in their terrestrial life stages can utilize diverse habitats, especially large wood deposits, for resting and foraging (Indermaur et al., 2009a, 2009b).

Low river flows also govern natural changes in the water quality, i.e., extended summer base flows cause an increase in water temperature and a decrease in dissolved oxygen levels (Nilsson and Renöfält, 2008). Native species can cope with such circumstances, especially if habitat diversity is high (Dunbar et al., 2010a). Macroinvertebrates may avoid desiccation by seeking shelter in the hyporheic interstitial (Hynes, 1970; Stubbington, 2012). Stable summer lowflows support rearing of juvenile fish (Freeman et al., 2001). Upwelling of cool, oxygenated hyporheic groundwater sustains aquatic organisms during summer low flows, while hyporheic flow in winter provides suitable, warm instream winter habitats, even though icing can occur (Hauer et al., 2016; Power et al., 1999).

Prolonged or extreme low flows or droughts, however, can have detrimental effects on the ecosystem (TABLE 3.2; Dewson et al., 2007; Humphries and Baldwin, 2003; Poff and Zimmerman, 2010). Such situations can arise if an e-flow assessment is based solely on static minimum flow considerations and does not match natural low flow patterns. Many countries use exceedance percentiles of the flow duration curve in the range of Q_{75}–Q_{95} for minimum flow recommendations (Smakhtin, 2001; Tharme, 2003), however, such artificial extensions of low flow situations may result in the system's loss of resilience (Colloff and Baldwin, 2010). Riparian plants whose roots do not reach lowered groundwater tables will experience drought stress and will likely die if these situations prevail (Egger, 1997; Johnson, 1994; Postel and Richter, 2003; Rood et al., 2013; Stromberg et al., 2007; Webb et al., 2013). If floods are absent for too long, vegetation can follow the water and move into the river channel, giving rise to morphological alterations (e.g., Bejarano and Sordo-Ward, 2011; Ligon et al., 1995; Trush et al., 2000). Flow abstraction generally has an adverse effect on fish abundance, assemblage, composition, and diversity (Webb et al., 2013). Native species may be suppressed by alien species (Caiola et al., 2014). Macroinvertebrates respond through declining species richness, diversity, abundance, and density (Dewson et al., 2007; Webb et al., 2013). Prolonged low flows enhance in-channel deposition processes by limiting sediment transport (Graf, 2006). The shortage of pools and sedimentation thereof create great difficulty for adult trout in residual flow reaches (Petts, 1996), and loss of connectivity restricts escape into more favorable reaches (Welcomme et al., 2006). Evapotranspiration in summer may even exacerbate the minimum flow situation through additional streamflow losses (Smakhtin, 2001). Along with hydraulic changes, extended low flows entail water quality reductions, including oxygen deficits or enhanced water temperature variation due to reduced water volume of residual flow reaches (Dewson et al., 2007; Nilsson and Renöfält, 2008; Smakhtin, 2001; Welcomme, 2008). A temperature model for the braided Hurunui River in New Zealand showed that every 1 $m^3 s^{-1}$ streamflow reduction resulted in a maximum temperature increase of 0.1 °C (Hockey et al., 1982, in: Mosley, 1983). In residual flow reaches summer temperatures can, therefore, exceed critical temperatures, especially for stenothermic coldwater species (Caissie, 2006). Adverse consequences of changed thermal regimes have been documented, for example, with salmonid fish, stoneflies, or mayflies (Caissie, 2006; Cazaubon and Giudicelli, 1999; Webb and Walling, 1993).

Since low flows naturally lead to increased sedimentation rates, the combination of prolonged base flows and missing erosive high flows leads to clogging of the hyporheic interstitial, impeding important ecological functions such as fish spawning (Kemp et al., 2011; Milhous, 1998). It is evident, therefore, that the protection of minimum flows is important but that other aspects of the flow regime are also significant for an ecologically-relevant e-flow allocation.

3.4.4 Mean flow

Discharges ranging from low flows to high flow pulses fulfill a series of ecological functions as they are sustained over extended time periods. According to Leopold et al. (1964), the mean annual flow is reached or exceeded about 25% of the time and fills the main channel to one-third of its bankfull depth. The magnitude is, in most cases, directly related to the size of the drainage area (Leopold, 1994) and is (along with the hydraulic parameters average river depth, width, and flow velocity) one of the key indicators which describe the longitudinal situation of the reach. These components are decisive for characteristic habitat forms and spacing (Leopold et al., 1964).

Discharges in the mean flow range allow for longitudinal connectivity between aquatic habitats, for example diurnal and seasonal habitat

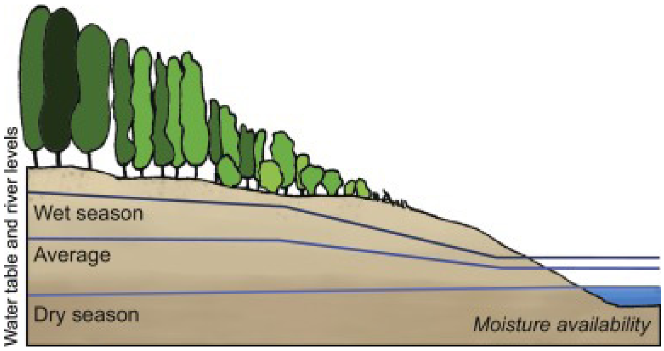

Figure 3.3 A schematic sketch of the usual water table distribution in relation to river stage in a temperate floodplain river in a moist environment (shown here: a reach of the high-energy anabranching and braiding Tagliamento River, Italy, with a perennial flashy flow regime, a partly confined morphology, and cobble-gravel-sand as bed material) during the dry and wet season, and the annual average (adapted from Gurnell et al., 2016).

shifts of fish, including fall or spring spawning migration which can total many kilometers (Jungwirth et al., 2000; Lucas and Baras, 2001). In general, adult fish profit from habitat conditions created by flows higher than low flows, as they predominantly occupy deep runs and pools of depths up to 0.8–2.4 m (Jungwirth et al., 2000; Nykänen et al., 2004). The hydraulic conditions provided during such flows are particularly important for rheophilic fish species. The spawning habitat requirements of the European grayling, *Thymallus thymallus*, include flow velocities between 0.4 and 0.7 $m\,s^{-1}$ (Jungwirth et al., 2000). For the potamodromous nase, *Chondrostoma nasus,* flow velocity requirements are as high as 1.0–1.1 $m\,s^{-1}$ (Melcher and Schmutz, 2010). Many macroinvertebrates, for example, rheophilic species or passive filter feeders such as *Hydropsychidae* or *Rheotanytarsus*, also rely on the presence of areas with stronger flow velocities. Passive filter-feeders aggregate in mean flow range areas as food delivery rates are high, and they exhibit faster feeding rates than in slow-flowing river sections (Dewson et al., 2007; King et al., 2008).

The growth and survival of riparian and floodplain vegetation is primarily determined by the groundwater level and soil moisture availability during non-flood periods (Stromberg et al., 1996). Variable flows within the channel promote plant growth through lateral water seepage into the floodplain (Hughes and Rood, 2003). The level of the hyporheic groundwater table within the floodplain varies seasonally with the river flow (Rood et al., 2013; Stromberg, 1993), whereby the average elevation can be linked with the mean water level in the river channel (FIGURE 3.3). Therefore, mean flow ranges are the primary hydraulic and hydrological regulator of floodplain vegetation, determining where which species will thrive. Water availability is especially important during the recruitment phase and growing season where the water demand for plants is the highest of the year (Egger et al., 2013; Foster and Rood, 2017; Karrenberg et al., 2002; Ye et al., 2010).

Most e-flow determinations are oriented towards the preservation of low flows only (Jager and Smith, 2008), whereby the mean annual flow is often only used as a baseline for minimum flow constraints. Standard hydrological methods allot 2.5–30% of average annual flow as e-flow (Tharme, 2003). Water allocation at this level entails a long-term lowering of the groundwater table within the floodplain and higher areas therein will subsequently dry out (Dister et al., 1990; Pusch and Hoffmann, 2000). Species reliant upon or preferring moist areas, for example, pioneer communities of the softwood floodplain zone, are sensitive indicators for long-term reductions of soil moisture availability (Corenblit et al., 2007; Dister et al., 1990; Egger, 1997; Stromberg et al., 1996). Therefore, it can be expected that minimum flow regulations lead to negative responses of riparian and floodplain vegetation, such as reduced plant growth rate, morphological change, or mortality of recruits, and a decline in native plant species diversity (TABLE 3.2; Merritt et al., 2010; Olivier et al., 2009; Poff et al., 1997; Stromberg et al., 1996; Ward and Stanford, 1995). Water abstraction and lowering of the groundwater table also results in drying and fast disappearing lentic floodplain water bodies, impacting specialized organisms and communities (Egger, 1997).

As the hydraulic parameters associated with discharges in the mean flow range determine the characteristics of instream habitats, flow reduction promotes alterations of size and pattern of the active channel and geomorphic complexity in the river as well as changes in amount and availability of habitat space and patch size (TABLE 3.2; Graf, 2006). For aquatic organisms, food and cover are reduced and there is greater mortality through competition and predation; migration pathways are also often interrupted (Graf, 2006; Welcomme, 2008). Filter-feeding or shredding macroinvertebrates (e.g., stone- and caddisflies) which are dependent on swift flow conditions may be repressed by tolerant species if these habitats disappear (Cortes et al., 2002; Dunbar et al., 2010a, 2010b).

3.4.5 Flow and flood pulses

Regarding high flow events, two types can be distinguished (King and Louw, 1998) in terms of magnitude, frequency, and ecological function. Smaller flow pulses occur multiple times per year (Whipple et al., 2017) and serve as habitat maintenance floods. Larger floods act as channel maintenance or flushing floods. These include bankfull discharges which occur, on average, every 1.5 years (Leopold, 1994), and exceeding (over bank) flows that begin to inundate the floodplain (Richter et al., 2006). In temperate river systems with nival or glacial flow regime components, the timing of seasonal peak discharges are predictable. Floods of a recurrence interval of >5 years can transport major sediment loads and facilitate plant recruitment (Braatne et al., 1996; Wolman and Miller, 1960), whereby a 1-in-10 year or higher flood magnitude is essential for the creation and preservation of complex channel and floodplain morphology (Rood et al., 2005; Trush et al., 2000). It must be noted that flow thresholds, for example, for sediment mobilization or channel movement rates depend on river type and associated characteristics, whereby less frequent and larger events might be necessary for steep gravel-bed mountain rivers, and more frequent but lower discharges might be sufficient for alluvial sand-bed rivers (Beechie et al., 2006; Rood et al., 2007). Overall, floodplains are formed by the combination of frequent flow pulses and less frequent flood pulses (Grove et al., 2012).

3.4.5.1 Habitat maintenance floods

High flow pulses are an essential element in the variability of a discharge regime. By mobilizing and sorting small- and medium-sized sediments, they contribute to habitat heterogeneity within the river (King et al., 2003). Furthermore, they flush out silt and cleanse coarse sediment from periphyton (Biggs et al., 2008). By washing out fines from the riverbed, clogging of the hyporheic interstitial is inhibited (Brunke and Gonser, 1997). A functioning hyporheic zone ensures the exchange of water and nutrients between surface and groundwater layers. This zone is colonized by bacterial and benthic fauna and has a balancing effect on the temperature regime of the river. An intact hyporheal, maintained by high flow pulses, also benefits the reproduction of lithophilic fish species and the river's nutrient and pollutant load (Brunke et al., 2015; Hauer et al., 2016).

High flow pulses not only sustain physical habitat but are also related to the completion of the life-cycle phases that are dependent on and synchronized with flow events (Lytle and Poff, 2004). Such pulses can trigger migration and spawning of fish and enable longitudinal and lateral connectivity (Hauer et al., 2014; King et al., 2003; Welcomme, 2008). Connected off-channel habitats can provide nutrients, serve as refuges of high flow velocities or low temperature in the main channel, and function as spawning areas and juvenile rearing grounds (EC, 2015; Zeug and Winemiller, 2008). The drift of some macroinvertebrate species may increase (Brittain and Eikeland, 1988). Rising water levels lead to seepage of water from the channel into the groundwater aquifer (Stanford and Ward, 1988) and the infiltration of nutrient-rich groundwater into the floodplain results in a phase of high primary production (Tockner et al., 2000). Thereby floodplain ponds can also be recharged and may serve as spawning habitats for amphibians (Babbitt and Tanner, 2000; Dick et al., 2017; Morand and Joly, 1995). High groundwater levels benefit riparian and floodplain vegetation, such as those of the softwood forest (e.g., Salicaceae) (Corenblit et al., 2007). Both, increased groundwater levels and hydraulic forces from floods, prevent riparian encroachment and establishment of terrestrial species (Miller et al., 2013; Poff and Zimmerman, 2010; Postel and Richter, 2003).

Most residual flow reaches experience a substantial decline in flood events of various magnitudes (FIGURE 3.2). A decrease in magnitude and frequency of high flow pulses alters the spatial range of functional surfaces and the frequency of processes which affects, for example, the mobility of channel bed and bank material (TABLE 3.2; Graf, 2006). Reduced hydraulic forces change the dominant particle size and often lead to sedimentation of the riverbed with fines, which creates an almost impermeable layer (Hancock, 2002; Schälchli, 1992). This has negative implications for aquifer exchange, water quality, and aquatic organisms (Brunke and Gonser, 1997; Hancock, 2002). Sedimentation of fines and the absence of flushing flows may constrain the occurrence of macroinvertebrates (Jones et al., 2012; Wood and Armitage, 1999), but also perturb life-history stages of lithophilic or benthic fish (Kemp et al., 2011; Milhous, 1998; Welcomme et al., 2006). A loss of seasonality severely affects flora and fauna adapted to these peaks and may favor invasive species (Bunn and Arthington, 2002). As groundwater layers are not adequately recharged, long-term dehydration of riparian habitats (Graf, 2006) results in a terrestrialization of riparian species (Poff and Zimmerman, 2010).

3.4.5.2 Channel maintenance and overbank floods

Flood pulses evoke similar ecological responses as the smaller flow pulses, however, due to their larger magnitude, they serve further purposes such as mobilizing and transporting larger bed-load fractions or maintaining river channel and floodplain morphology (King et al., 2003; Trush et al., 2000; Opperman et al., 2010). Together with geomorphological characteristics (e.g., slope, grain size, material properties of river bed and banks that determine erosive resistance, and sediment budget), the magnitude and frequency of bed-forming flows determine channel width and geomorphological river type (Ahmari and Da Silva, 2011). Peak discharge events mobilize coarse bed sediments, flush fines and organic material out of the river, and clear the channels from macrophytes, encroaching riparian vegetation, and alien species

(Bejarano and Sordo-Ward, 2011; Biggs et al., 2008; Renöfält et al., 2010; Schälchli, 1992). In this regard, the interrelation between hydrology and vegetation is central in ensuring the geomorphological stability of the river or contributing to its changes (Corenblit et al., 2007; Grabowski et al., 2014; Gurnell et al., 2016). Flow-induced retrogression of vegetation is followed by progression into newly created pioneer sites, which are principal areas for riparian plant establishment (Caruso et al., 2013; Corenblit et al., 2007; Egger et al., 2013; Ward et al., 2001). The recruitment of cottonwood and willow is associated with floods occurring every five or ten years, whereby the flood peak must be aligned with photoperiod and temperature which determine flowering and seed release (Braatne et al., 1996; Mahoney and Rood, 1998). Optimal conditions for plant recruitment comprise a medium to high flood pulse with a rapid rise in river stage, followed by a slow recession. The flood pulse purges and creates river bars and raises the groundwater level (Hughes and Rood, 2003; Mahoney and Rood, 1998; Rood et al., 2007). Seeds are dispersed and germinate underwater to become established on the moist, open gravel bars (Meier, 2008). Recruitment in sand-bed rivers is successful if roots can grow with the slowly receding water levels until the plants can reach base flow groundwater levels (Amlin and Rood, 2002; Mahoney and Rood, 1998; Meier, 2008; Rood et al., 2007). In gravel-bed rivers, the occurrence of a coarse substrate layer over finer material has a rock mulching effect, which provides soil moisture to seedlings even if water input is not significant for some time (Meier, 2008). Furthermore, flushing floods supply dead trees to the river, thereby also shaping the river structure. Washed up dead wood alters streamflow patterns and sedimentation around log jams creates islands or extends bank zones which will be colonized by vegetation (Collins et al., 2012; Gurnell et al., 2012; Karrenberg et al., 2002; Naiman et al., 2008).

In addition to infiltration and subsurface runoff from precipitation, flood pulses recharge the floodplain aquifer until a hydrological equilibrium between the high water level of the channel and floodplain aquifer is reached or river flows start to drop (Stanford and Ward, 1988). Peak discharge events connect floodplain habitats (side channels, oxbows, ephemeral ponds, etc.) with the river channel and provide an influx of fine sediment, nutrient, eggs, and seeds (King et al., 2003). The nutrient input leads to an increase in primary production in the floodplain (Sims and Colloff, 2012). Life cycle stages of many faunal species (e.g., spawning or larval drift) are synchronized with these flood pulses and coinciding rising temperatures (Baumgartner et al., 2014; Junk et al., 1989; Postel and Richter, 2003; Trush et al., 2000). The common toad, *Bufo bufo*, matches spawning with hydrology by utilizing temporary water-filled habitats and exhibiting quick metamorphosis (Tockner et al., 2006). Amphibians require water submersion until the completion of their aquatic life history stage in early summer (Trush et al., 2000). Jager (2014) demonstrated that seasonal, floodplain-inundating flow pulses might benefit salmon production through accelerated fish growth, facilitated by higher water temperature and prey availability (see also Opperman et al., 2010; Sommer et al., 2001, 2005). Although the erosive forces of flood pulses present serious abiotic stressors, native species have adapted to their occurrence (Hering et al., 2004; Marchetti and Moyle, 2001; Valdez et al., 2001; Yarnell et al., 2015). Fish may seek shelter in the bank zone (Biggs et al., 2008) and macroinvertebrates in the pervious hyporheic interstitial (Brunke et al., 2015; Stubbington, 2012), whereas non-native species may be reduced (Marchetti and Moyle, 2001).

The absence of channel forming flows (and natural sediment fluxes) and the application of minimum e-flow rules are often highlighted as some of the reasons for the loss of aquatic and terrestrial habitats as well as geomorphological river transitions (Auble et al., 1994; Tockner et al., 2010; Petts and Gurnell, 2005; Trush et al., 2000). Reductions of flood magnitude and frequency may reduce channel width and promote change of the morphological river type (e.g., from braided to wandering) (Trush et al., 2000; Surian and Rinaldi, 2003; Ahmari and Da Silva, 2011). Gravel-bed rivers adjust mostly via channel degradation and bed armoring, whereby their response time is usually slower than for rivers of finer grain sizes as bed-mobilizing discharges occur less frequently (Grant, 2012). Under such altered flows, fine sediment is deposited along the channel margins, allowing vegetation to encroach into formerly non-vegetated zones. Plants begin to follow low water levels and are no longer uprooted or eroded by regular floods (Aguiar et al., 2016; Grant, 2012; Rivaes et al., 2015, Rivaes et al., 2017). Subsequently, vegetation establishes itself in these areas, stabilizes the location, resists flood erosion and traps further sediments, while narrowing the channel (Corenblit et al., 2007; Petts and Gurnell, 2005; Trush et al., 2000). Hence, a reduction of flood dynamics impedes dynamic morphological processes and formation of river structures (Poff et al., 1997). Through the above-described interactions, vegetation can change the hydraulic structure of instream habitats (Rivaes et al., 2017) and the floodplain can transform from a heterogeneous mosaic towards dryer soil-moisture forest formations, as the connectivity between channel and floodplain diminishes and groundwater resources are lost (Corenblit et al., 2007; Surian and Rinaldi, 2003; Trush et al., 2000).

Adverse implications for floodplain organisms can be detected if hydrological characteristics of peak flows are changed, especially regarding life history cycles such as spawning and rearing (TABLE 3.2). Therefore, reduced peak flows often favor exotic species over native ones, as introduced species can cope better with such hydrological alterations (Gurnell et al., 2016; Marchetti and Moyle, 2001).

3.4.6 Flow variability

Temperate river flow regimes exhibit natural flow fluctuations on multiple scales. The seasonal and yearly flow variability between (the above-described) low, mean and high flows is crucial for ecological functions and processes of floodplain ecosystems (Caruso et al., 2013; Naiman et al., 2008). The rise and fall of river stage from flood pulses facilitates numerous processes, such as the flushing of organic and inorganic matter into and out of the floodplain, the incorporation of terrestrial carbon into the aquatic food web and vice versa, or the exchange between surface water and groundwater aquifers (Junk and Wantzen, 2004). Furthermore, these events maintain the balance of species in aquatic, riparian and floodplain communities (Postel and Richter, 2003). The flooding regime and moisture distribution within the floodplain essentially determine where which species can flourish (Meitzen et al., 2013; Stromberg et al., 1991). Apart from the variation between these two extremes, the flow variability within the channel (i.e., below bankfull discharge) is vital for enhancing floodplain productivity (Tockner et al., 2000).

The life-history requirements of numerous aquatic and semiaquatic species are synchronized with spatially and temporally varying habitat availability caused by fluctuating flows (Tockner et al., 2010). To complete its life cycle, a species relies on qualitatively and quantitatively adequate habitat for each life-history phase (Fisher et al., 2012; Wolter et al., 2016). Thereto related is also the ecologically-significant seasonal

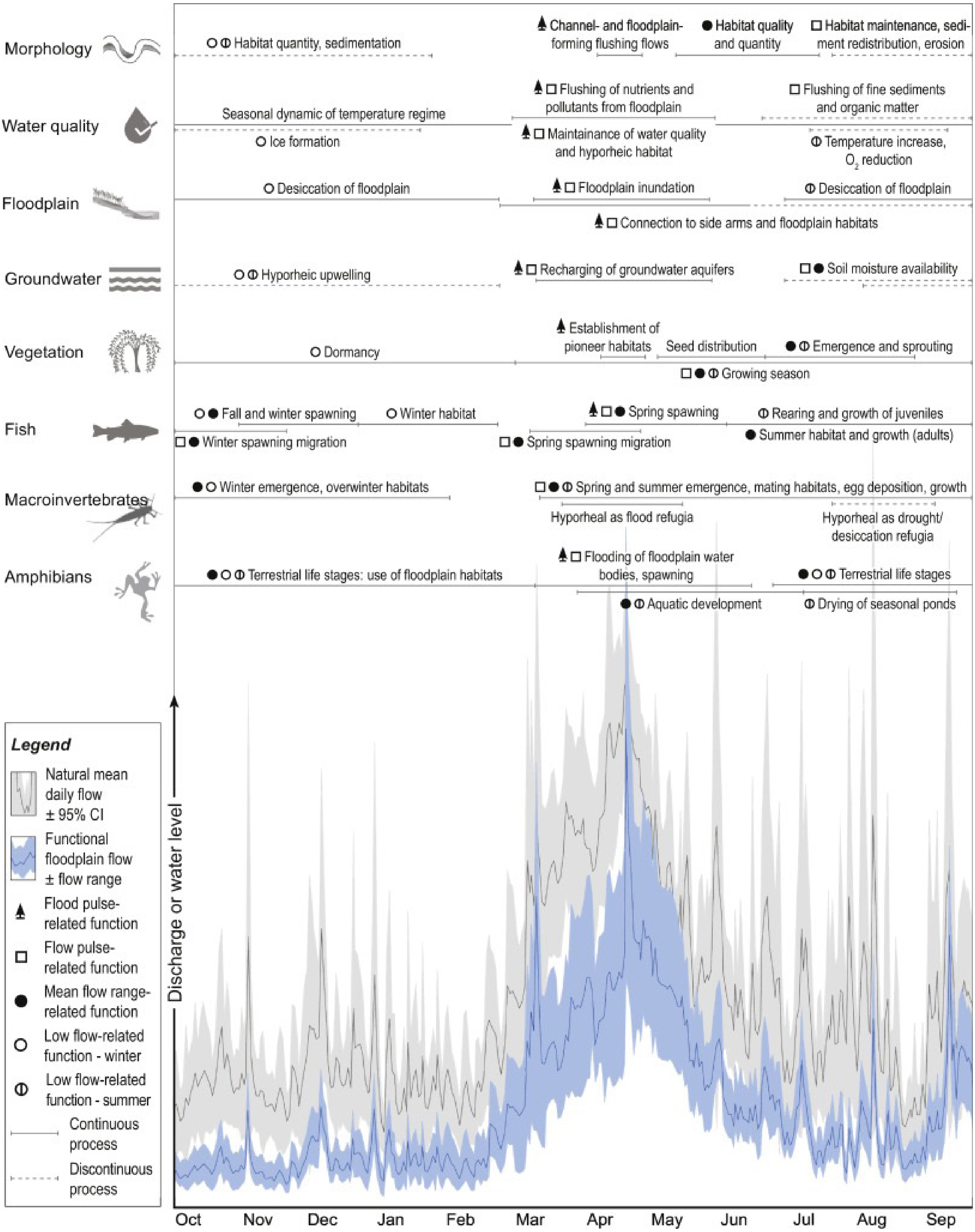

Figure 3.4 The conceptual curve of the functional floodplain flow (ff-flow) approach integrates ecological functions and processes (top) with principal flow regime components and their seasonality (bottom; the natural mean daily flow is depicted in grey). The presented environmental flow hydrograph (depicted in blue) does not establish intra-annual flow thresholds. Instead, it is understood to be a guide towards key aspects of the annual hydrograph and their implications for various elements of floodplain ecosystems.

variability of water temperature (Caissie, 2006; Naiman et al., 2008; Olden and Naiman, 2010; Tockner et al., 2000). For macroinvertebrates, river stage may determine adult emergence, egg-laying, drift, or diapause stage (Hancock and Bunn, 1997; Lytle and Poff, 2004; O'Hop and Wallace, 1983). Amphibians require seasonally inundated water bodies for aquatic life stages and non-inundated, moist areas for terrestrial ones (Indermaur et al., 2009a, 2009b; Tockner et al., 2006; Trush et al., 2000). The aquatic life stages of both, amphibians and macroinvertebrates, are also affected by the thermal regime (King et al., 2008; Tockner et al., 2010). The longitudinal migration of many fish species, their spawning behavior, larval emergence, rearing of juveniles, and lateral movements into the floodplain are interlinked with the natural timing of specific discharge and temperature events (Fenkes et al., 2016; Lobón-Cerviá and Rincón, 2004; Lytle and Poff, 2004; Melcher and Schmutz, 2010; Tockner et al., 2000; Unfer et al., 2011).

Changes in the seasonality or return of flow events may, therefore, influence riverine biota as life-history stages are disconnected from necessary components of the flow or thermal regime (Bunn and Arthington, 2002; Tockner et al., 2010). Mims and Olden (2013) demonstrate that dam-induced flow variability reductions and seasonality shifts transformed fish communities across the United States by favoring equilibrium strategist life-history species over opportunistic ones. Auble et al. (1994) suggest that riparian vegetation can change considerably without alteration of the mean annual flow but through adjustments of minimum and maximum flows. However, responses of distinct guilds can be linked to different components of the flow regime (Merritt et al., 2010). Similarly, temperature regime alterations also affect ecological (Olden and Naiman, 2010) and geomorphological functions and processes (Rood et al., 2007).

3.5 Functional floodplain flow

For a long time, stable minimum flows over an entire year or season were considered adequate to maintain an acceptable ecological status of residual flow reaches. Therefore, constant flow allotments without dynamic components are widespread until today. Recent research, however, shows that multiple elements of the natural annual hydrograph are necessary to maintain the ecological integrity of riverine ecosystems and their related components (river, floodplain, groundwater). To preserve their long-term sustainability, central hydrological aspects can be identified and management criteria derived (see TABLE 3.2). Here, we present a functional floodplain flow (*ff-flow*) approach which aims to establish the basis for an ecologically-relevant e-flow regime for the restoration of temperate floodplain rivers impacted by flow regulation (FIGURE 3.4). The depicted hydrological regime represents all temperate regimes as it contains pluvial, nival, and glacial components. Note that the primary outputs of this conceptual model address ecological benefits but do not reflect social or economic services, though the approach could be adapted to integrate these aspects as well.

The central element determining the structure and functioning of floodplain ecosystems is the shift between dry and wet phases, determined by flood pulses and groundwater dynamic. This entails erosion and sedimentation processes as well as exchanges between surface and groundwater aquifers. Therefore flow stabilization alone is not a viable solution for hydrological restoration of dam-impacted floodplain rivers. Instead, an e-flow regime should emulate the natural distribution of flow events. While the importance of flow variability is well recognized (Acreman et al., 2009), the danger of favoring simplistic, constant e-flow allocations remains (Naiman et al., 2008). As fauna and flora are adapted to intra- and inter-annual flow variability, it can be expected that flows which mimic the natural hydrograph lead to sustainable e-flow rules (Richter et al., 2012; Ritchie et al., 2004).

By establishing the relationship between river morphology and biology with the natural flow regime, the *ff-flow* (FIGURE 3.4) advocates that e-flow regimes must be function- and process-oriented (Yarnell et al., 2015). Above, we demonstrated how different river flows enable these features in natural systems. Mean flows, flow pulses, and floods especially, are most severely affected by diversion or abstraction dams and their restoration, therefore, must be emphasized in modern e-flow assessments. Water management must ensure that all central flow regime components occur correctly timed, with the right frequency as well as duration. In addition, the rate-of-change between flow seasons (Yarnell et al., 2015) must be preserved. Furthermore, the *ff-flow* approach suggests restoring the sediment budget by transporting sediment downstream during high flows (García de Jalón et al., 2017; Kondolf et al., 2014; Wohl et al., 2015). These guidelines ensure that morphological processes are sustained and that native species can fulfill all of their life-history phases (see management recommendations in TABLE 3.2). The conceptual curve of the *ff-flow* (blue band in FIGURE 3.4) is, therefore, a graphical e-flow proposal that aims at maintaining fundamental seasonal flow-dependent functions and processes of floodplain rivers as described in the literature and depicted in the top section of FIGURE 3.4. Following, we accentuate these links by describing the dynamic e-flow hydrograph in its seasonal sequence and its importance for abiotic and biotic elements.

To ensure the maintenance of ecological functions and processes, e-flow allocations need to overlap with natural flow patterns: The beginning of the hydrological year in fall is generally characterized by low to mean flows. The floodplain slowly falls dry, and vegetation becomes dormant. The release of flow pulses, which naturally occur due to precipitation events, promote migration and breeding of winter spawners. During winter low flows, hyporheic upwellings facilitated by earlier high flows add to in-channel flow which safeguards the upkeep of aquatic habitat quantity and provides refugia during cold or even freezing water temperatures.

By raising water levels at the onset of spring, the *ff-flow* approach initiates a series of ecological functions in floodplain rivers. Flushing waste products and pollutants downstream restores water quality. The gravel riverbed is scoured from organic matter and fines, which re-establishes the water exchange between surface and hyporheic habitats, enhancing successful spawning of rheophilic fish and supporting macroinvertebrate gravel and cobble communities. Lateral water seepage replenishes water tables in the river bank and floodplain which stimulates plant growth. Emulating the snow and glacier melt and their corresponding natural sediment load, the e-flow increases in magnitude, and side arms and heterogeneous floodplain habitats become connected to the main channel. Biota such as fish and amphibians receive ecological spawning cues as well as habitats for rearing and feeding. Flushing flows can transport (trapped) sediment downstream (Kondolf et al., 2014) and ensure that the river channel and its floodplain are maintained by redistributing fluvial sediment through erosion and sedimentation, and by resetting successional processes. For safeguarding sediment transport and morphological processes, high flows must exceed the critical shear velocity threshold to mobilize and transport various particle sizes (Meitzen et al., 2013).

Pioneer habitats created by the released flood peaks at a timing and recession rate which emulate the characteristics of the falling hydrograph limb under natural conditions (as flows shift from spring flood pulses to summer low flows) are particularly vital for the establishment of floodplain and riparian plant seedlings. A natural timing and recession rate of these declining flows also allows the safe return of fish into permanent aquatic habitats and amphibians can finish their aquatic development phase before their temporal habitats fall dry.

The *ff-flow* also suggests recreating the typical summer dry-season flow conditions. Though these low flows may produce stressful conditions for native biota, for example, through temperature increase or diminished habitat connectivity, they also incite ecological functions such as rearing and growth of juvenile fish or the desiccation of the floodplain. The drying of seasonal floodplain ponds is a prerequisite for predator-free spawning sites for amphibians. At the same time, the effects of previous flood pulses and occasionally occurring higher flows prevent the potential negative impacts of low flows by providing soil moisture for plants or hyporheic refugia for aquatic biota.

The value of minimum e-flows and regular flooding events is widely recognized (Yang et al., 2016), however, few studies highlight the importance of higher seasonal flows and the role of groundwater to sustain functioning riverine floodplains. During the vegetation period, floodplain flora requires higher flow allocations (Foster and Rood, 2017) and certain biotic guilds (e.g., rheophilic fish) also depend upon hydraulic conditions established by higher flows, especially during spawning (Jungwirth et al., 2000). The capacity of phreatic groundwater layers to contribute to low river flows depends upon seasonal flood pulses that recharge its aquifer (Smakhtin, 2001). Moreover, Miller et al. (2013) predict that the encroachment of terrestrial vegetation into hydrologically altered river channels can be reduced through increased base flows and the release of high flow pulses. Hence, the *ff-flow* approach proposes a dynamic e-flow regime, underlining the importance of emulating the natural flow regime with its seasonal variability, flow magnitude, frequency, event duration, and rise and fall of the hydrograph. By incorporating these flow regime attributes, we hypothesize that the *ff-flow* regime will sustain self-regenerating floodplain forests, as it fulfills their four essential requirements, i.e., regular, correctly timed flows, the establishment of regeneration sites, the provision of water table conditions, and the propagation of needed materials (Hughes et al., 2012).

In summary, the *ff-flow* approach emphasizes the influence of hydrological key factors and their seasonal variation to sustain or restore ecological and morphological components of temperate floodplain rivers by targeting process-form relationships. The presented intra-annual e-flow hydrograph does not, however, establish exact thresholds. Instead, it is understood to be a guide towards functional key aspects of the annual hydrograph and their implications for abiotic and biotic elements of floodplain ecosystems. In modified rivers, the proposed flow management may not be effective if geomorphological impacts on e-flow releases (and vice-versa) are not considered (Meitzen et al., 2013), for example, if levees or riverbed incision prevent floodplain connectivity (Opperman et al., 2010; Richter and Thomas, 2007). In this regard, the combination of hydrological and morphological measures is often considered the most beneficial and cost-effective restoration measure (EC, 2015; García de Jalón et al., 2017; Greimel et al., 2017; Opperman et al., 2010). Moreover, since dams not only alter water flows but also sediment supply and transport, modern e-flow management must administer hydrological and sediment regimes concurrently (García de Jalón et al., 2017; Wohl et al., 2015). If the hydrology (e.g., flood pulses) is restored without considering the restoration of the sediment budget deficit, unanticipated riverbed degradation may occur (Schmidt and Wilcock, 2008). Therefore, especially in floodplain rivers, an e-flow assessment must regard the reciprocal interactions between water flow, sediment, and also vegetation, as these determine physical processes (e.g., erosion and deposition) at different dynamic riparian zones (Corenblit et al., 2007, Corenblit et al., 2009a, Corenblit et al., 2009b; Gurnell et al., 2016; Gurnell and Petts, 2002).

3.6 Conclusion

Research shows that floodplain rivers are dependent upon recurring cycles of hydrological varying river flows which drive ecological and morphological processes and determine the structure and functions of these ecosystems. Due to their dependency on natural flow regimes, floodplain rivers are particularly sensitive to hydrological modifications. There is broad evidence demonstrating that flow abstraction evokes morphological and biological responses (TABLE 3.2). The concept of e-flows is considered a solution to these alterations as it endeavors to prevent ecological deterioration of the impacted reach and to preserve a desired ecological state by allotting the affected reach with a certain flow. As most e-flow assessments are biased towards instream flows based on minimum low flow requirements of selected criteria, it was critical to establish a holistic e-flow framework for temperate floodplain rivers.

Present-day water diversion or abstraction schemes normally exceed modern ecological protection thresholds (e.g., max. flow alteration < 10% or 11–20%; Richter et al., 2012), as only water uses above these limits become economically profitable. The presented *ff-flow* restoration approach (FIGURE 3.4) acknowledges these socio-economic constraints by allowing the utilization of a significant proportion of the natural flow. At the same time, the approach moves away from minimum flow prescriptions by propagating the establishment of an e-flow regime capable of restoring the natural functions and processes of impaired floodplain ecosystems through the release of functional elements of the annual hydrograph. Limitations of the *ff-flow* approach include clear water releases and the associated effects of erosional dynamics caused by interrupted sediment transport, for example, channel incision or bed armoring (Brandt, 2000; Grant, 2012; Kondolf, 1997; Schmidt and Wilcock, 2008), as well as physically modified rivers (García de Jalón et al., 2017; Meitzen et al., 2013). Regarding riparian succession, it shall be noted that once vegetation has established itself in the channel caused by missing floods, even higher flows are necessary to scour these patches (Ryan, 1997; Corenblit et al., 2007). Many studies indicate that native biota benefit from flow restoration (e.g., Caiola et al., 2014; Caruso et al., 2013; Marchetti and Moyle, 2001) yet there still remains the possibility of propagating invasive species through e-flow releases (Stuart and Jones, 2006).

Though e-flow studies conducted in temperate floodplain rivers are scarce (Hughes and Rood, 2003), we conclude that the ecological principles laid out in the presented *ff-flow* approach provide a sound basis for establishing ecologically relevant e-flows and for guiding flow restoration in temperate floodplain rivers (Bunn and Arthington, 2002; Hughes et al., 2012; Tharme et al., 1998, in: Postel and Richter, 2003; Trush et al., 2000), if constraints are considered. The inclusion of inter-annual flows or water management options may improve both ecological and socio-economical outputs, as a dynamic e-flow regime entails, for example, the release of higher flood pulses (‘regeneration flows’) in wet years and ‘maintenance flows’ in dry years (Erfani et al., 2015; Hughes and Rood, 2003; Rood et al., 2003, Rood et al., 2005). Further research is necessary to quantify the amount of flow needed for maintaining specific functions and processes in distinct river types and to provide appropriate e-flow assessment tools.

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CHAPTER 4

Life stage-specific hydropeaking flow rules

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4.1 Abstract

Peak-operating hydropower plants are usually the energy grid's backbone by providing flexible energy production. At the same time, hydropeaking operations are considered one of the most adverse impacts on rivers, whereby aquatic organisms and their life-history stages can be affected in many ways. Therefore, we propose specific seasonal regulations to protect ecologically sensitive life cycle stages. By reviewing hydropeaking literature, we establish a framework for hydrological mitigation based on life-history stages of salmonid fish and their relationship with key parameters of the hydrograph. During migration and spawning, flows should be kept relatively stable, and a flow cap should be implemented to prevent the dewatering of spawning grounds during intragravel life stages. While eggs may be comparably tolerant to dewatering, post-hatch stages are very vulnerable, which calls for minimizing or eliminating the duration of drawdown situations and providing adequate minimum flows. Especially emerging fry are extremely sensitive to flow fluctuations. As fish then grow in size, they become less vulnerable. Therefore, an 'emergence window', where stringent thresholds on ramping rates are enforced, is proposed. Furthermore, time of day, morphology, and temperature changes must be considered as they may interact with hydropeaking. We conclude that the presented mitigation framework can aid the environmental enhancement of hydropeaking rivers while maintaining flexible energy production.

4.2 Introduction

Mountainous rivers are often subjected to sub-daily flow variations caused by peak-operating hydropower plants, which run their turbines according to the demand of the electricity market. These hydropower plants allow high flexibility in energy production, making them an essential part of the current and future electric grid as they can buffer periods of low energy availability of other renewables, such as wind or solar energy [1,2]. At the same time, hydropeaking entails numerous adverse ecological consequences and has therefore been described as “one of the most significant impacts on rivers downstream of dams” [3]. Fish communities, in particular, are severely threatened by hydropeaking [4]. Fish can be affected by changes in various components of the hydrograph, whereby the most common responses—stranding, drift, and dewatering of spawning grounds—are mostly related to up- and down-ramping rates [5,6], peak flow magnitude [5], and baseflow duration [7].

Considering the large capacity of existing storage hydropower plants [8], as well as new ones that are currently being planned and installed [9], it is imperative to develop appropriate and transferable management measures to mitigate these ecological impacts. Many structural (e.g., constructing retention basins) and operational (e.g., reducing flow fluctuation rates) mitigation measures have been proposed [10,11], but implementation remains difficult, among other issues, because of significant reductions in the energy yield when setting ecological thresholds [2,12]. Therefore, well-targeted mitigation measures have to be developed to avoid energy losses and to guarantee ecological efficiency.

Freeman et al. [13] argue that adverse effects can be minimized by either restoring vital features of the natural flow regime or by implementing a flow management scheme which avoids hydropower-induced habitat bottlenecks. Regarding the latter, multiple studies point out the need to identify critical flows, which include seasonal and diel considerations when determining operational mitigation strategies in rivers affected by hydropeaking [5,13,14,15,16]. To maintain self-sustaining fish populations in regulated water bodies, river management must take all life-history stages into account, especially during ecologically sensitive periods, when designing and implementing customized flow regimes [7]. This study aims to establish a framework for hydrological mitigation in rivers affected by hydropeaking, based on life cycle stages of fish and their relationship to key parameters of the hydrograph. We, therefore, describe the impacts of hydropeaking on each life cycle stage and propose critical aspects which must be considered when defining mitigation rules. We focus on salmonid fish as they are the most studied and most affected fish family regarding hydropeaking [17,18]. Nevertheless, many aspects of the presented mitigation concept can potentially be transferred to or adapted to the requirements of other taxa.

4.3 Life cycle stage-specific mitigation approach

Within the life cycle of many salmonids, upstream spawning migrations are followed by the deposition of fertilized eggs in the gravel bed. In the following weeks, the eggs develop within the gravel substrate where, after hatching, the larvae (alevins) also stay until their yolk sack is absorbed. Afterwards, the fry emerge from the riverbed to find nursery habitats, for example, along the shoreline for feeding and growth. As fish increase in size, they use different habitats. Once they reach sexual maturity, their life cycle starts over again [19,20].

The literature indicates that each of these life cycle stages can show a distinct sensitivity to different aspects of the hydropeaking hydrograph, whereby reproduction and early life stages seem to be the most sensitive ones [15]. Thus, the key parameters for flow restoration will vary between the life cycle stages. In the following subchapters, we will therefore discuss the ecological effects of hydropeaking for each sensitive life stage, as well as establish a specific mitigation framework approach for each life cycle stage (FIGURE 4.1).

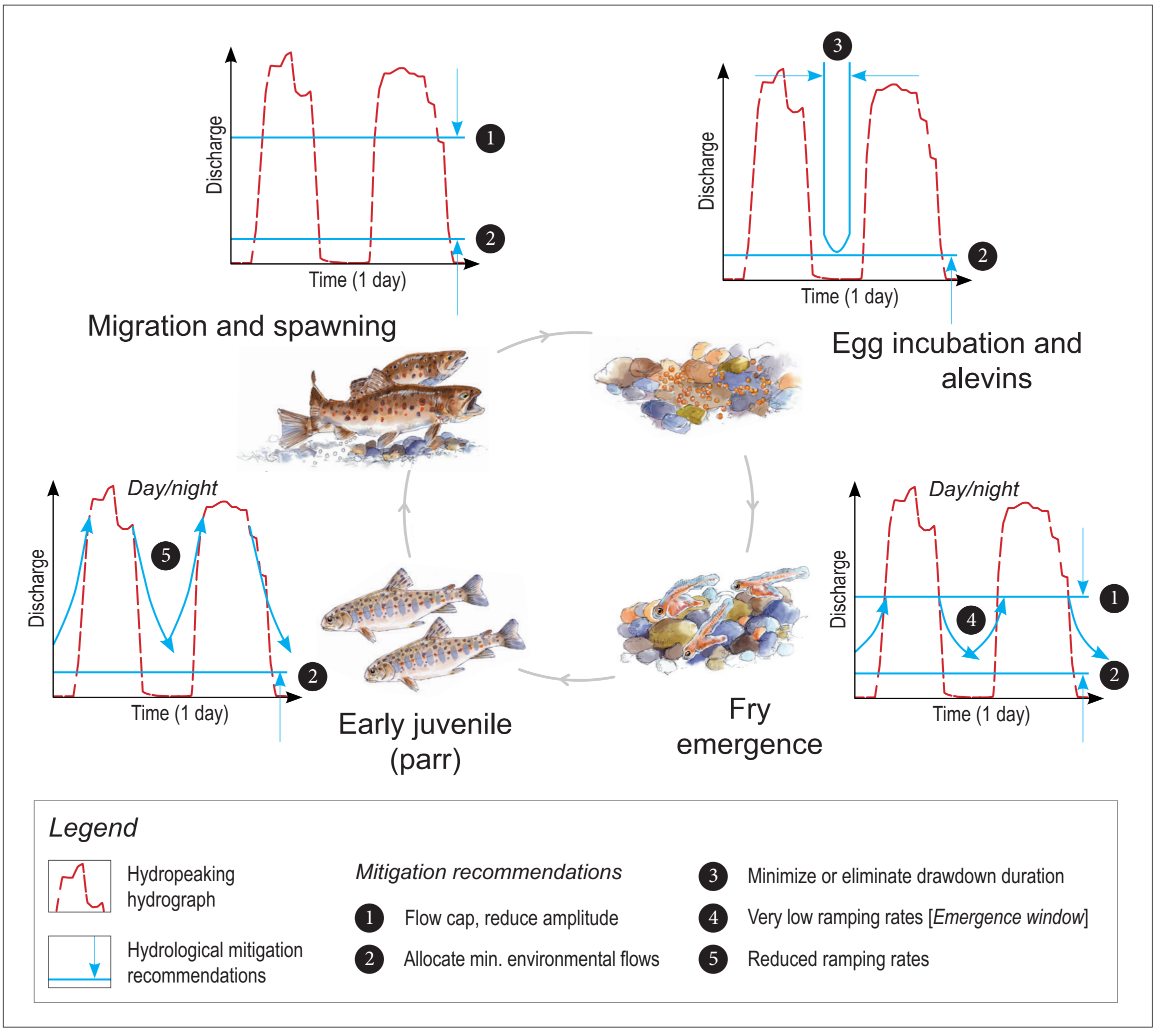

Figure 4.1 Life stage-specific hydropeaking flow rules: Conceptual framework for the sensitive life stage approach to mitigate the adverse impacts of hydropeaking. The dashed red lines represent a schematic daily hydropeaking hydrograph (two peaks and a baseflow phase), whereas the solid blue lines depict recommendations for hydrological restrictions to aid the environmental enhancement of hydropeaking rivers. "Day/night" indicates that restrictions might differ with time of day (salmonid illustrations by DAB graphics, used with permission from The Wild Trout Trust Ltd, Waterlooville, England, www.wildtrout.org).

4.3.1 Migration and spawning

River flow is a crucial factor for spawning-related activities [21]. In hydropeaking rivers, highly variable flows can influence, among other factors, migration, nest digging, and spawning behavior. Studies have shown that migration patterns of lake trout (*Salmo trutta lacustris*), as well as Chinook (*Oncorhynchus tshawytscha*) and pink salmon (*O. gorbuscha*), were correlated with the hydropeaking regime. Fish avoided migrating during changing flow magnitudes and they were able to cover greater distances on the days with peaking operations of lower amplitudes [22,23].

When fish are able to reach suitable reproduction areas, spawning can be interrupted by rapid flow fluctuations [16,24,25,26]. During down-ramping events, brown trout (*S. trutta fario*) stop preparing their redds [24] and brown trout and Atlantic salmon (*S. salar*) leave the spawning area if hydraulic conditions become unsuitable [26]. As soon as flows increase again, Atlantic salmon are highly motivated to continue redd preparation, and resume spawning once flows have returned to more stable conditions [24,25], whereas brown trout take more time to re-engage in spawning-related activities [24].

To mitigate the effects of hydropeaking on migrating fish, it is therefore advantageous to release higher flows during migration periods [21]. Furthermore, during spawning, it is suggested that flows are kept relatively stable [16], at least for a sufficient duration to allow females to complete nest preparation and oviposition [26], which can take multiple hours to days for one spawning bed [27,28], but several weeks for the entire population. The flow magnitude to enable these ecological functions can differ among geomorphic habitat units as it depends on the hydraulic conditions of the reach [21,25] and the species present [26]. By allocating a steady environmental flow release during the peak spawning period (e.g., ca. four weeks for *S. trutta*), the ecological conditions can already be improved [29].

Although some salmonids tend to spawn during discharges greater than the median [30], the release of too high flows is not recommended if these water levels cannot be sustained throughout the incubation period [28]. At that stage, higher discharges could encourage nest-building in areas that will be at a higher risk of being dewatered between the hydropeaks later in the season. Instead, flow caps, i.e., upper peak limits, should be implemented [21,26,31,32,33], as the survival of intragravel life stages is linked to redd site selection during the spawning period.

4.3.2 Intragravel life cycle stages: egg incubation and alevins

In hydropeaking rivers, intragravel life cycle stages can be predominantly influenced through either siltation of sediments [34,35], scouring [21,35], or dewatering of spawning grounds [21,31,32]. In the winter, mountainous rivers are characterized by an extended low baseflow period. During this season, hydropeaking rivers, however, often exhibit relatively high flow fluctuations. This operational scheme leads to higher flow amplitudes in winter compared to summer [36,37].

As salmonids deposit their eggs in the gravel bed, siltation may reduce hatching success by affecting interstitial water flow [38,39]. It has been suggested that hydropeaking is a governing factor regarding fine sediment dynamics in gravel-bed rivers, as hydropeaking can change the fine sediment composition of both surface and subsurface layers [40]. Indeed, a recent study [34] found that ramping zones exhibited significant surface clogging due to a continuous accumulation of fines. In contrast, permanently inundated areas contained little or no fine sediment infiltration into the riverbed's surface layers as fines are subject to transport. Interestingly, the hydropeak magnitude itself, expressed as the peaking ratio, was not related to fine sediment infiltration rates [34]. It seems, therefore, that the spawning ground position in the riverbed can influence hatching success through the effect of sediment sizes.

It is expected that, due to nest-building of female salmonids, spawning ground stability is increased as sediments are sorted and redds, therefore, feature coarser substrate surfaces than unspawned beds through winnowing of fines. Despite this coarsening effect, however, studies [41] have demonstrated that redds are more unstable than unspawned beds. For example, redds exhibited a 12–37% lower grain resistance to motion, as well as a 13–41% higher boundary shear stress for the same flows in comparison to unspawned beds. Also, bed-average shear stress was significantly reduced [41]. Although studies indicate that salmonid spawning usually takes place in locations with less excess shear stress [21], hydropower peak flows may enhance the risk of embryo mortality as redds are more likely to be eroded than the surrounding gravel bed [21,41]. However, although scour has been cited as a potentially adverse effect, no study has yet quantified its impact magnitude. Furthermore, the scouring potential also depends on the peak flow magnitude. Unfer et al. [42] demonstrated that only flow magnitudes larger than half the size of mean annual high flow events were able to substantially erode sediments in the Alpine Ybbs River, Austria. The risk of egg erosion due to hydropeaking may, therefore, be rather case-specific [35] and may only occur in rivers with a high peaking magnitude.

If spawning occurs during peak flow periods, the drawdown to winter baseflows between peaks could lead to the dewatering of spawning grounds, which is a significant concern as it can result in the mortality of eggs and alevins [31,43]. It has been demonstrated that salmonid eggs are generally rather robust to dewatering and can survive extended time frames without inundation, provided that they are kept moist, are not subjected to extreme temperatures (i.e., freezing or heating) exceeding incubation tolerances, and receive sufficient oxygen through the influx of air into the interstitial spaces [31,43,44,45,46]. In contrast, newly hatched alevins (eleutheroembryos) are less tolerant to redd desiccation and may die within 4–12 h of dewatering, whereas pre-emergent alevins are considered the most sensitive intragravel life stage [44,45,46]. Since pre-emergent alevins depend on gills for respiration, dewatering events <1 h lead to very high (>96%) mortality rates [44], which can have profound impacts on fish populations. However, groundwater upwelling might attenuate apparent adverse effects where available [21,43,47].

To prevent the mortality of intragravel life stages, it is recommended that power production is adapted to discourage fish from spawning in shallow water which will later fall dry. Additionally, the duration of hydropower production stops should be minimized. Also, the provision of enhanced minimum flows during this critical development period can help to reduce the difference between incubation and spawning flows [32,43,48,49]. During the egg incubation, limited redd dewatering through the hydropower plant operation might not entail complete losses in some cases [16,32], such as in the presence of local groundwater upwellings and at temperatures above freezing [43]. However, considering that spawning can occur over an extended period and that multiple species can be present in the same river, allowing limited redd dewatering is not recommended since alevins, which require continuous inundation [7], may be present throughout the entire time [16].

4.3.3 Fry emergence and early juvenile development

After alevins have absorbed the major portion of their yolk sack, they emerge as fry from the substrate [19,20]. During this early ontogenetic development, they are very susceptible to pulsed-flow operations as they utilize high-risk habitats in the ramping zone and have little swimming capacities, entailing drift and stranding of individuals [5,6,50,51,52,53]. In the Saltdalselv River, Norway, high flows during the alevin and fry stage significantly increased the mortality of Atlantic salmon and brown trout [54]. Similarly, fry recruitment was negatively related to the number of hydropeaks during the emergence period in the Lez River, France [55].

4.3.3.1 Thresholds for impact mitigation

Rapid flow reductions due to downramping can increase the stranding probability of fish through quickly receding water levels, causing sub-lethal impacts or direct fish mortality [16,18]. Studies have shown that stranding is species- and size-selective, whereby recently emerged fry are the most vulnerable life-history stage [15,52,56,57]. This finding is supported by the analysis of ten-year flow downramping monitoring data of Canadian rivers, showing that the highest stranding probabilities occur from May to August when juveniles inhabit nearshore areas which are likely to be dewatered [50]. Field surveys at the Drava River, Austria, revealed 50–500 stranded larvae of European grayling (*Thymallus thymallus*) per 100 m shoreline after single hydropeaking events [58]. In general, a reduction of ramping rates to <0.17–0.25 cm min^{-1} is related to less stranding and, therefore, a greater probability of attaining a higher fish ecological status [4,59]. On a more detailed level, experimental studies indicate that, during fry emergence, mitigation thresholds on downramping velocity must be rather low to prevent stranding, for example, 0.23–0.31, 0.2, or 0.1 cm min^{-1} for larvae of Atlantic salmon, European grayling, or brown trout, respectively [6,52,56,60].

Early juvenile life stages are also susceptible to downstream displacement [52], especially during nighttime hydropeaking [5]. However, little is known about the long-term population effects caused by drifted fish. Nevertheless, a reduction of drift is advisable. Therefore, a lowered upramping rate and a reduced peak amplitude are recommended [5,29].

4.3.3.2 Emergence window establishment

Generally, it is advisable to stabilize the flow as much as possible in the early growing season [59]. Alfredsen et al. [33] suggest introducing a cap flow and restricting rapid flow changes during swim-up. Since fry are especially vulnerable to sub-daily flow fluctuations and are present only at specific periods of the year [16,52], a feasible management approach is to define temporal 'emergence windows' where stringent thresholds, for example, regarding downramping to prevent stranding, are enforced [8,15,52,61]. These emergence windows should start with the highly sensitive alevin phase [44,45,46] just before fry emerge from the gravel, whereas the length of the window depends on the growth, which is mainly related to temperature. Stranding experiments [52,56] indicate that the temporal duration must be around two weeks for European grayling and four weeks for brown trout, as grayling improves its reactivity to drawdown events quicker than brown trout. Even though these two species spawn at different periods (brown trout in fall/winter and European grayling in late winter/spring), their larvae occur in the same season (mid-April to early August) due to their temperature-dependent egg development [62], underlining the feasibility of the emergence window approach. Approximate start and end dates can be calculated with temperature data if the time of spawning is known [19,33,62]. For example, FIGURE 4.2 depicts a first river-specific assessment of emergence windows for brown trout and European grayling for selected Austrian hydropeaking rivers based on information from anglers. Due to the imprecise data situation, the proposed time frames are still rather long and represent only a rough estimate. It would be possible to confine the time period of the emergence window by assessing the exact emergence time through electrofishing surveys and modeling based on spawning time and day degrees of egg development. The results would allow the deduction of a river-specific period of early fish life cycle development by analyzing the water temperature of the sampling year. This information could then possibly be transferred to the following years. Another feasible approach would be to visually observe (stranding of) larvae from the end of April onwards to determine a river reach-specific emergence window. In rivers with different species of Pacific salmon, the implementation might be more difficult due to varying emergence periods [48].

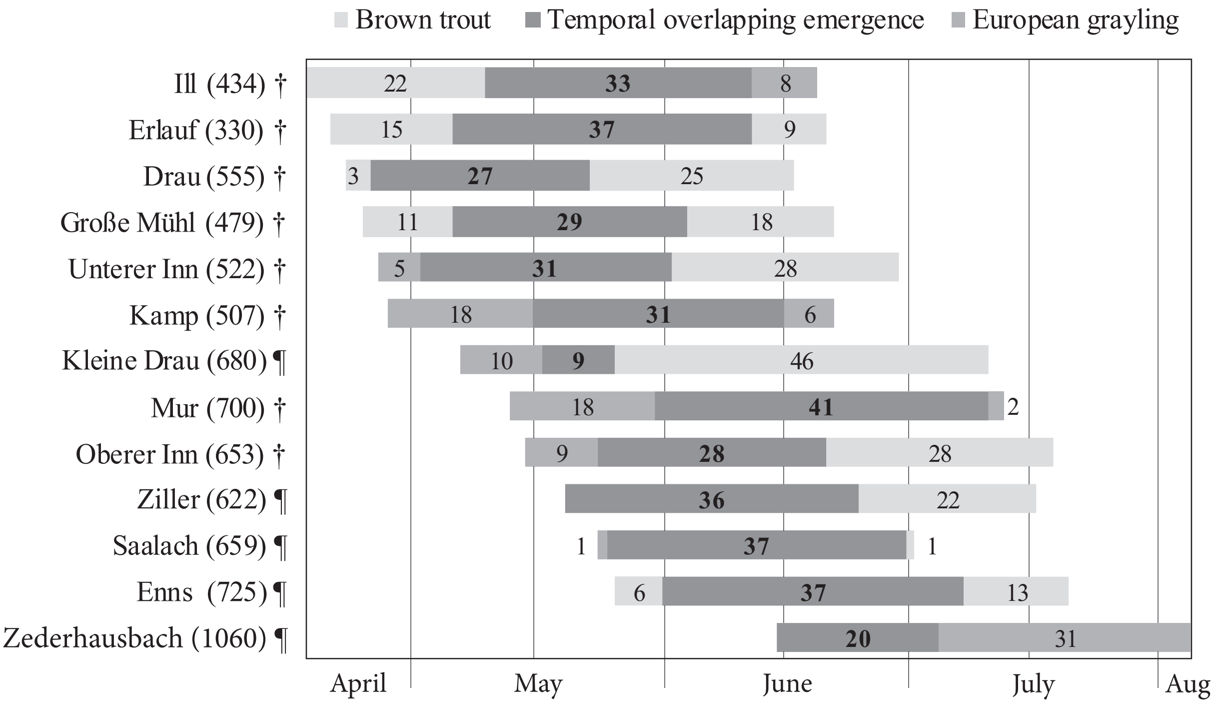

Figure 4.2 Emergence window proposal for brown trout (Salmo trutta) and European grayling (Thymallus thymallus) in selected Austrian hydropeaking rivers. The depicted time frame is based on temperature-dependent models for predicting the time of median hatch as reported in the literature. For the brown trout, we used the formula from Crisp [19], and for the grayling, the one published by Jungwirth & Winkler [62]. The begin and end of the spawning time for each species was reported by anglers and served as the starting point for the calculations, which were then based on daily mean temperature data of ten years (gauging stations of Austrian Hydrographic Service; meters above the Adriatic in brackets; † = metarhithral (i.e., lower trout) fish region; ¶ = hyporhitrhral (i.e., grayling) fish region). Emergence of brown trout and European grayling takes place between mid-April and early August, whereby the emergence windows of both species also partially overlap. The duration of the emergence periods is displayed in the bars as a mean number of days.

4.3.4 Parr to adults

Parr are also vulnerable to stranding and drift, whereby the risk is reduced as they grow in size and increase their swimming performance, and additionally shift to deeper habitats away from the dewatered ramping zone [53]. Therefore, less restrictive ramping rates—in comparison to fry—can be sufficient [5,15,16,52,56,57]. However, since stranding probability is also determined by other factors aside from down-ramping velocity (e.g., wetted history, baseflow conditions, time of day), these must be considered in the establishment of mitigation rules as well [15]. For example, before a large flow reduction, lower reductions are recommended prior to higher ones to shorten the wetted history [50]. Furthermore, the time of day can play a significant role. Some studies report that, during summer, young-of-year brown trout and grayling are less vulnerable during the day and more susceptible to stranding during the night [5,56,60]. In contrast, during colder water temperatures in fall or winter, higher stranding is reported for daytime than for nighttime hours for brown trout, rainbow trout (*O. mykiss*), Atlantic salmon, and Coho salmon (*O. kisutch*) [6,63,64]. Both can be related to diel behavior changes [65] as, for example, in winter, salmonids are passive during the day and active in the night [64,66]. Therefore, ramping rate restrictions should be more stringent during darkness in summer and during daylight hours in winter. It must be noted, however, that Connor and Pflug [48] have reported exactly the opposite as the above cited studies. They recommend limiting downramping to nighttime hours between the emergence and outmigration period. However, this focus on daytime mitigation might be because, in the Skagit River case study, daytime flow reduction represented 89% of all events during the peak stranding period [48]. Differences in stranding or drift might also be triggered by other factors, such as water turbidity or predation. In this regard, more research is necessary. In the meantime, however, case-specific solutions are required.

Regarding fish movement patterns during hydropeaking, Robertson et al. [67] found that, in winter, flow neither affected fish activity or habitat use, nor displaced Atlantic salmon parr. Only in late winter was fish activity reduced during high flows in the night. Similarly, Stickler et al. [68] did not detect differences in fish activity between high and low flows, which was also confirmed by Berland et al. [69], who analyzed parr movement in September related to river flow and ramping rate. Therefore, it can be concluded that, for the most part, hydropeaking does not affect salmonid fish movements in winter. In contrast, in summer, juvenile Atlantic salmon show higher movement rates in hydropeaking channels than in control channels [70], a pattern which was also confirmed for 1+ salmon in a telemetry study during spring [71]. Considering the increase in juvenile fish movement during summer in combination with inhibited feeding during peak flows [72], it is not surprising that, at the end of the growing season, fish that were subjected to fluctuating flows had a lower body fat and body mass than fish subjected to stable flows. Although the effects were small [70] or, in some cases, not detectable [58], the long-term impact on the population can be potentially many times higher. Simulating the effects of stranding on the salmon population in the Dale River, Norway, Sauterleute et al. [73] conclude that the most substantial adverse effect on the population abundance in hydropeaking rivers is related to the stranding of older juvenile fish during winter daylight conditions, suggesting that the stranding of salmon at this life cycle stage is likely to have greater population impacts than that of earlier life cycle stages. Furthermore, the stored energy reserves from the summer may be a critical factor in determining overwinter survival [74,75].

4.4 Discussion

Future sustainable hydropower management relies on the development of well-informed and targeted mitigation strategies [76]. Here, we propose a management framework to mitigate adverse impacts of hydropeaking operations on salmonid fish, whereby we advocate that, in each season, the most sensitive life cycle stage should be the decisive element regarding peaking restrictions. FIGURE 4.1 constitutes a graphical depiction of this mitigation framework approach by illustrating a hydropeaking hydrograph scheme (two peaks and a baseflow phase), as well as the above-described flow restrictions necessary for aiding the environmental enhancement of hydropeaking rivers (i.e., depending on season: implementing flow caps, allocating minimum environmental flows, decreasing the flow ratio, minimizing dewatering durations or prohibiting dewatering, or lowering ramping rates). Alfredsen et al. [33] used a similar approach by defining flow blocks for environmental flow allocation to meet the need of Atlantic salmon life stages in the Daleelva River, Norway. Due to sub-daily flow fluctuations, hydropeaking represents a specific sub-group within environmental flow in rivers where hydrological stress on aquatic ecosystems is intensified. Therefore, there is a need to develop qualitative seasonal flow rules for hydropeaking rivers as well. Here, we focused solely on salmonid species as most available literature deals with this fish family [15,17,18]. Many aspects of the presented framework can potentially be transferred to other taxa as well, but further research must be conducted on other fish families, such as cyprinids, to validate these suggestions.

Literature indicates that different elements of the hydrograph can be tweaked to improve the survival of the respective life stages (FIGURE 4.1), whereby the temporal windows must be adapted to the local river conditions. However, mitigation thresholds (e.g., for baseflow, peak flow, ramping rate) depend not only on the life cycle stage, but also on the respective species present, as well as the time of day. Nevertheless, only a few quantitative thresholds have been proposed so far, highlighting the need for further research [15]. Therefore, for the most part, we were only able to extract qualitative/conceptual mitigation recommendations. Related to that is the question of which life cycle stage is the most sensitive to sub-daily flow fluctuations regarding having the greatest adverse effect for the fish population.

The field of environmental flow has progressed towards advocating function- and process-oriented flows [14,77], thereby moving away from static water allocations and towards dynamic environmental flows to sustain ecological communities [14,78]. Considering that hydropeaking rivers are essentially residual flow stretches—just that, in addition to water abstraction, they are also highly impacted by sub-daily flow fluctuations [79]—mitigation measures for hydropeaking must be incorporated into the seasonal and inter-annual environmental flow requirements. Therefore, scientific advancement must merge the concepts of dynamic environmental flow and hydropeaking mitigation to propose sustainable and holistic management recommendations for flow-altered watercourses.

4.4.1 The effects of river hydromorphology

Many studies indicate that the ecological effects related to hydropeaking, for example, stranding or drift, are also dependent on river morphology, including bank slope, grain size distribution, or cover [5,12,64,80]. Higher stranding, for example, occurs more frequently on lower gradient bars than on steeper banks [64], but steeper banks provide less larval and juvenile habitats. Coarse substrate will trap fish more during dewatering than small grain sizes [80]. Due to water retention, vertical dewatering speed reduces with distance to the hydropower outlet, therefore lowering the stranding risk along the river's course [3,59]. In morphologically unfavorable river sections (e.g., in channelized rivers), spawning, larval, and juvenile habitats are often lacking, whereas in nature-like channels, ramping rate reductions may improve the fish ecological status [4]. Hauer et al. [3,80] highlight that the changes in wetted width between baseflow and peak flow and, thereto related, changes in the lateral ramping velocity depend on the river's channel bar form, as well as the baseflow magnitude (see also [81]). Depending on this combination, a <1:2 peaking ratio can have a greater impact on cross-sectional wetted width than a 1:5 ratio [80]. Therefore, Halleraker et al. [59] recommend different dewatering thresholds for distinct flow ranges in the Surna River, Norway, where more stringent flow limits are needed for lower discharges than for high ones [50,59].

Self-forming gravel bars (e.g., point bars or alternating gravel bars) have been identified as both suitable structures for young-of-year trout, as well as areas of reduced stranding risk due to self-forming backwater habitats [80,82]. These findings underline the need to combine hydrological rehabilitation with morphological restructuring measures to minimize the ecological impact of hydropeaking [8,12,80,83]. Next to river restoration measures, connectivity to tributaries may also play an essential role in supporting fish populations in hydropeaking rivers. Tributaries often exhibit more stable hydrological conditions and less risk of erosion and, therefore, may provide suitable spawning and rearing habitats for fish [3].

4.4.2 The effects of sub-daily temperature changes

Another abiotic factor that can influence the effects of hydropeaking on fish is water temperature, as the release of pulsed flows is often coupled with thermal changes (i.e., thermopeaking) [84]. The ecological effects of long-term thermal alterations below dams have received some attention [85], whereas less is known about the reaction of eggs or fish to sub-daily thermopeaking. Therefore, further analyses have to be performed to study potential effects in detail [4].

Research has shown that both hydropeaking and thermopeaking can influence macroinvertebrate communities [86]. Although we did not integrate macroinvertebrates into our conceptual mitigation framework, this group should be included in more holistic approaches in the future, not only because benthic communities are an essential food source for fish, but also because they are an indispensable aspect of functioning river systems [87]. Also, as benthic dwellers, macroinvertebrates are particularly sensitive to sediment composition and habitat conditions in the river bed [34].

4.4.3 Other hydropeaking-related impacts

Aside from thermopeaking, two other hydropeaking-related impacts have recently been described. 'Saturopeaking' refers to fluctuations of gas saturation which follow the rapid, periodic, and frequent pattern of hydropeaking operations [88], and 'soundpeaking' to hydropeaking-induced changes in river soundscapes, whereby sound pressure levels can be strongly correlated with turbine discharge [89]. Although some guidelines exist for supersaturation (i.e., when total dissolved gases saturation exceeds 100%) [88], possible ecological effects of saturopeaking and soundpeaking in hydropeaking rivers still remain to be studied [15], as well as the combined effects of these pressures.

4.4.4 Achieving hydrological mitigation measures and their economic implications

To achieve mitigation, either structural or operational measures can be utilized [10,12], whereby similar positive hydrological changes in the tailrace can be obtained, for example, by changes in the power plant operation scheme, as well as through the construction of retention basins [2,90]. Considering the economic implications, however, these two approaches show quite different outcomes [2]. Hydropeaking power plants operate competitively according to immediately changing market prices, which means that the quicker their turbines can be turned on and off, the higher the economic benefits are. Therefore, operational restrictions affect the ability to produce highly valuable peak energy [2,12,91], especially if less favorable turbines types are installed [92] or the water availability imposes constraints. In contrast, peak retention basins might initially require significant investment costs, but, according to Person et al. [12], they show high beneficial ecological effects by reducing sub-daily flow fluctuations at reasonable costs. Since retention basins allow ramping rate reductions, they may be especially useful for

Table 4.1 Knowledge matrix on the general fish ecological and hydropeaking research conducted on salmonids. We categorized life-history stages (and their activity) into three classes: "–" = no or hardly any studies conducted; "±" = some research is published, but knowledge gaps remain; "+" = extensive studies have been conducted. Literature examples of each research field are given.

Life-History Stage (and Activity)		Ecological Research	Literature Example(s) [1]	Hydropeaking Research [2]	Literature Example(s)	Particularities on Hydropeaking Studies
Spawning	Migration	+	[20,98,100,101,102]	–	[22,23]	
	Behavior [3]	+	[27,102,103]	–	[24,25,26]	
Intragravel life stages	Egg incubation	+	[19,20,101]	±	[31,43,44,45,46]	Aside from studies on short- or long-term desiccation, information on repeated wetting and drying is largely missing for different species.
	Alevin	+	[19,20,98]	–	[44]	
Young-of-the-year (0+)	Fry	+	[97,98]	±	[52,55,56,57]	Only studies regarding few selected species, topics mostly restricted to stranding and drift.
	Parr	+	[19,20,104]	±	[5,6,70,71]	Only studies regarding few selected species, topics mostly restricted to drift, stranding, movements, habitat use, and growth.
Juvenile	1+ fish (smolt)	+	[19,102,104,105]	–	[61,106]	
Adult	2+ fish	+	[105]	–	[107]	

[1] We focused on reviews or books, as they provide the best overviews of the field of research.

[2] Mostly regarding the impacts of hydropeaking. For a recent review on hydropeaking mitigation, see Moreira et al. [15], who summarized the current status (research and legislation) and presented research needs.

[3] Common conditions contributing to spawning behavior include: Nest selection, building, probing, completion and oviposition, and covering [27].

applying seasonal flow rules during ecologically sensitive periods [90]. Only limited space availability may be the major problem for the construction of such basins. In contrast, instream velocity refuges such as deflectors require less lateral space [93]. In the very critical larval phase, a combination of compensation reservoirs and altered operational management might be most effective by avoiding over-sized reservoirs. Currently, the feasibility of the air cushion underground reservoir (ACUR) technology [94] to mitigate environmental hydropeaking effects is being tested in the European project "HydroFlex" [95].

4.4.5 Limitations of This Study and Research Needs

In recent years, researchers have established a firm knowledge basis regarding general fish ecological topics, such as the response of different salmonid life-history stages to different environmental parameters, including water flow, temperature, or substrate conditions [96,97] (Table 4.1). Of course, there are questions which still remain to be answered [96,98]. In the last years, hydropeaking research has significantly advanced in terms of scientific output [99], and this increasing amount of information has allowed us to formulate the presented mitigation framework (FIGURE 4.1). Nevertheless, although such a life cycle stage approach constitutes the most up-to-date framework on hydropeaking mitigation, it is to be expected that future studies will significantly expand the present knowledge base regarding the effects of hydropeaking on various life cycle stages, and proposed flow management recommendations may have to be adapted. Therefore, TABLE 4.1 presents a knowledge matrix which highlights crucial research areas in the field of hydropeaking impact and mitigation. Future research will, among other goals, have to better quantify the effects of hydropeaking on spawning activities and egg incubation phases (especially with regard to scour or siltation, and sub-daily temperature changes), and investigate impacts on the fish population and community level, including studying the effects of hydropeaking on the food web (e.g., between nutrients, periphyton, macroinvertebrates, and fish).

4.5 Conclusions

Research shows that fish are sensitive to hydrological modifications, especially sub-daily flow fluctuations, which can influence each life cycle stage through various components of the hydropeaking hydrograph. We reviewed the literature to understand how hydropeaking influences each life cycle stage of salmonids. This approach allowed us to conceptualize a qualitative mitigation framework which is based on seasonal flow regulations to protect ecologically sensitive life cycle stages (Figure 1), whereby the following flow rules are recommended: During migration and spawning, flows should be kept relatively stable, and a flow cap should be implemented to prevent the dewatering of spawning grounds during intragravel life stages. While eggs may be comparably tolerant to dewatering, post-hatch stages are very vulnerable, which calls for minimizing or eliminating the duration of drawdown situations. Especially emerging fry are extremely sensitive to sub-daily flow fluctuations. Therefore, a temporally-limited 'emergence window', where stringent thresholds on ramping rates are enforced, is proposed. As fish grow in size, they become less vulnerable. Therefore, less restrictive ramping rates (in comparison to fry) can be acceptable. In all seasons, adequate environmental flows shall be allocated. Furthermore, when setting mitigation thresholds, interacting effects of daytime, river morphology, and water temperature also have to be considered.

The implementation of these seasonal restriction guidelines will not only counter possible hydropower-induced population bottlenecks but has the potential to entail less significant reductions in energy yield compared to all-year round hydrological limits [76]. Nevertheless, further research is necessary to evaluate the ecological effectiveness of the proposed concept and to quantify exact thresholds for different species, life cycle stages, seasons, and time of day in distinct river types [15] while minimizing flexible energy yield reductions in the implementation thereof.

4.6 Author Contributions

Conceptualization, D.S.H.; methodology, D.S.H., M.M., I.B., G.U., and B.Z.; investigation: D.S.H., M.M., and M.H.; writing—original draft preparation, D.S.H.; writing—review and editing, D.S.H., M.M., I.B., M.H., G.U., B.Z., F.G., S.A., T.F., and S.S.; visualization, D.S.H. and M.H.; supervision, S.S. and T.F.; project administration, F.G.; funding acquisition, T.F., F.G., and S.S.

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CHAPTER 5

Ecologically-based criteria for hydropeaking mitigation: a review

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5.1 Abstract

Hydroelectric power plants managed in response to sub-daily changes of the electricity market undergo rapid variations of turbine discharge, entailing quickly fluctuating water levels downstream. This operation regime, called hydropeaking, causes numerous adverse impacts on river ecosystems. The hydrological alterations which affect hydropeaking rivers can be described by five parameters that change over space and time (magnitude, rate of change, frequency, duration, and timing), where each parameter may be correlated with distinct environmental impacts and therefore may be used to define flow thresholds and set targets for operational mitigation strategies. Thus, this study aims to present an extensive review on the so far established hydropeaking targets and thresholds regarding the outputs from the scientific community as well as from national regulations. We found that only few European countries (Switzerland and Austria) have legal regulations regarding hydropeaking flow thresholds. Other countries, such as Canada and the USA, present environmental legislation that can force hydropeaking mitigation measures. Most mitigation thresholds and management recommendations in literature deal with the effect of downramping on the stranding of salmonids, as well as with minimum flows between peak-flows to avoid spawning ground desiccation. Regarding other fish species and parameters, information on mitigation targets or thresholds is scarcer or non-existent, as well as on hydropeaking mitigation case-studies, resulting in a lack of knowledge and guidelines for its implementation or regulation. Nevertheless, the available literature indicates that multiple aspects must be considered when assessing such values. Thus, to aid in that process, we propose that mitigation targets and thresholds must be based on key species, including particular features regarding season, life-stage and time of day, which must be combined with site-specific morphological characteristics. The presented approach may benefit impacted organism groups in hydropeaking reaches through the establishment of ecologically-based relevant mitigation thresholds and/or targets.

5.2 Introduction

Storage and pump-storage hydropower plants offer many advantages to present and future energy systems. Positive aspects include an excellent efficiency, the provision of stability to the energy grid by compensating fluctuations in power production caused by renewable energy sources (e.g., wind, solar), a rapid response to grid demand (flexibility), as well as the possibility to carry over electricity production from high flow to low flow seasons (Tonolla et al., 2017). Turbines are started up and shut down according to the demand of the electricity market, often on daily or sub-daily scales (Bejarano et al., 2017b). Especially this latter operation mode, called 'hydropeaking', leads to quick variations of river discharges which causes a rapid rise and fall of water levels downstream the tailrace (Jones, 2014; Moog, 1993). During non-peaking periods, water is stored in the reservoir, resulting in low river flows (base-flows or environmental flows). The unpredictability and intensity of flow variations are more permanent, frequent and severe than those caused by natural flow events, such as snow melt and intense precipitation (Greimel et al., 2016; Shuster et al., 2008).

Therefore, these anthropogenic induced rapid flow fluctuations may cause different ecological impacts, including periphyton biomass reduction (Bondar-Kunze et al., 2016), drift of macroinvertebrates (Schülting et al., 2016), and physical as well as physiological constraints for riparian vegetation (Bejarano et al., 2017a). Regarding fish biota, hydropeaking can reduce and alter spawning and rearing success (Becker et al., 1982; Casas-Mulet et al., 2014; McMichael et al., 2005), lead to downstream displacement and stranding (Auer et al., 2017; Boavida et al., 2017; Nagrodski et al., 2012), cause metabolic changes (Costa et al., 2018; Flodmark et al., 2002; Taylor et al., 2012) and influence fish growth (Kelly et al., 2017; Korman and Campana, 2009; Puffer et al., 2017). Furthermore, these flow and water level fluctuations can lead to variations in water quality and affect the riverbed morphology (Hauer et al., 2014).

In addition, the turbined discharges often use water from reservoir layers where the water temperature differs significantly from the one found in the river downstream. This phenomenon can thus create temperature peaks called 'thermopeaking', which may amplify the ecological impacts of hydropeaking concerning fish behavior (Zolezzi et al., 2011). Another hydropeaking-related impact is 'saturopeaking', which can be described as an artificial, rapid, periodic and frequent fluctuation of gas saturation that follows the pattern of hydropeaking operations (Pulg et al., 2016). The median saturation of total dissolved gases in natural riverine environments is usually 99–101%. When it reaches values >110%, saturopeaking will likely cause lethal effects on fish due to gas bubble disease, whereas at lower rates (103%–110%) fish may suffer indirect effects such as behavioral changes or increased susceptibility to infections (Pulg et al., 2016; Weitkamp, 2008). Furthermore, hydropeaking also leads to changes in aquatic soundscapes and sound pressure levels by temporal variations in the frequency composition (acoustic signature). This phenomenon has been named 'soundpeaking' and may affect fish physiology or behavior (Lumsdon et al., 2018).

Due to the extensive ecological consequences of hydropeaking on river ecosystems, it is stringent to develop suitable mitigation measures to reduce these adverse impacts. To reach this goal, a variety of measures have been proposed (e.g., Bruder et al., 2016; Moog, 1993; Person et al., 2014; Premstaller et al., 2017), which can be grouped into direct and indirect measures (Greimel et al., 2018a). Direct measures include operational as well as structural measures (e.g., the construction of retention basins or hydropeaking diversion hydropower plants), whereby positive hydrological changes in the downstream river reaches are expected to occur (Premstaller et al., 2017). Indirect measures address river morphological aspects, aiming to compensate the negative impacts of hydropeaking (e.g., through channel restructuring for habitat improvement).

A prerequisite for the establishment of efficient and cost-effective mitigation measures is the identification and establishment of mitigation targets and thresholds. Although hydropeaking has been studied intensively in the last decades (Bejarano et al., 2017a), proposed thresholds for the different parameters, such as magnitude, rate of change, frequency, duration, and timing (cf. Harby and Noack, 2013), have not yet been consolidated, despite the fact that this has been pointed out to be a major further step for hydropeaking research (Costa et al., 2017; Harby and Noack, 2013; Hauer et al., 2017; Young et al., 2011).

In this paper, we provide an overview on the current knowledge and present an extensive review on the so far established hydrological thresholds and targets for mitigating ecological impacts on fish. Based on the outputs from the scientific community as well as indicative values and targets from national regulations and guidelines, we intend to address the following questions: (1) Which are the proposed hydropeaking mitigation thresholds in peer-reviewed literature? (a) Do these thresholds differ among distinct river reaches morphology? (b) Do these thresholds differ among species, their life-stage and time of day? (c) Are there any case studies regarding the successful implementation of operational measures? (2) Which are the established hydropeaking mitigation thresholds and targets in national legislations, regulations and/or guidelines?

5.3 Methods

5.3.1 Literature search and analysis

We firstly obtained data on hydropeaking mitigation thresholds by conducting a search for peer-reviewed literature. We used the Scopus database with the search string TITLE-ABS-KEY (“hydropeaking” OR “hydro peaking” OR “flow fluctuation” OR “pulsed flow” OR “peaking power” OR “flow ramping” OR “hydroelectric peaking” OR “hydro-electric peaking”) which was combined with TITLE-ABS-KEY (“threshold” OR “mitigat*” OR “ramping” OR “dewater*” OR “duration” OR “rate of change” OR “frequency”). We limited the search to the relevant subject areas, i.e., environmental science, agricultural and biological sciences as well as earth and planetary sciences. We did not set a lower date limit and included manuscripts published until September 2018. We initially found 237 peer-reviewed papers, for which we then screened the title, abstract and keywords to exclude articles that did not address the studied topic, reducing that number to 124 papers. Following, we removed papers that did not contain quantitative or qualitative recommendations on hydrological mitigation of peak-flow hydropower operation, reducing the number to 10 articles. We then added additional papers through snowball approaches and available grey literature was also integrated, leading to a final number of 22 publications.

5.3.2 Legislation and guidelines

We assumed that hydropeaking is mostly present in countries which publish on this topic, and that the corresponding pressure extent in the country is related to the research conducted. We, therefore, identified relevant countries by conducting another Scopus literature search using the keywords “hydropeaking” and “hydro peaking” in TITLE-ABS-KEY.

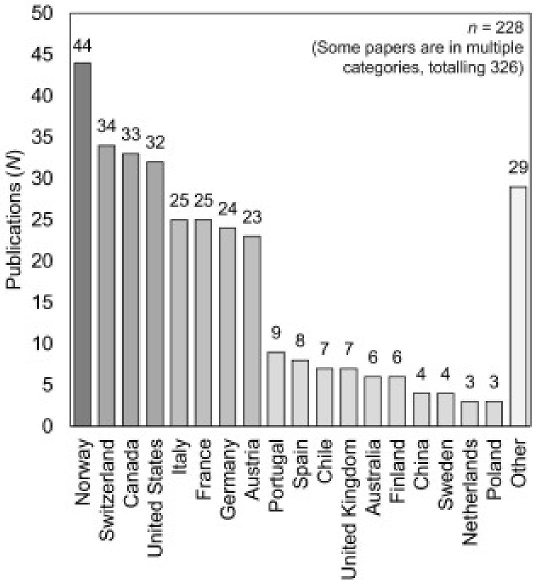

Figure 5.1 Number of papers found in the Scopus database using the keywords "hydropeaking" and "hydro peaking", sorted by country/territory of author affiliation (the literature search includes results until September 2018 based on Title-Abstract-Keywords). "Other" includes: Belgium, Brazil, New Zealand, South Korea, Cyprus, Czech Republic, Denmark, Estonia, Greece, Hong Kong, Iceland, Japan, Croatia, Malaysia, Slovenia, Taiwan, and undefined.

We retrieved 228 documents from 34 distinct countries, where 98 overlapped due to co-authorship, resulting in 326 single country documents (FIGURE 5.1). Based on this list, we assessed the status of national hydropeaking legislation or guidelines in the respective countries by contacting local experts or governmental authorities.

5.4 Results

5.4.1 Database

From the 22 papers which contained thresholds and targets for hydropeaking mitigation, the most commonly used parameters are downramping rate (vertical ramping velocity), baseflow and peak-flow magnitude, peak frequency and time between peaks (TABLE 5.1). The majority of the studies establishing quantitative thresholds assessed the impact of flow reduction on the stranding risk of early salmonid life-stages.

5.4.1.1 Downramping thresholds to mitigate stranding

From a fish ecological point of view, stranding caused by flow downramping can be considered the major pressure related to hydropower operation schemes (Nagrodski et al., 2012; Young et al., 2011). The effects of downramping can be quantified more easily than other ecological responses to hydropeaking through experiments in outdoor or indoor channels. Multiple studies reveal a clear reduction of stranding risk as downramping rates are lowered (FIGURES 5.2–5.4; TABLE 5.1). FIGURES 5.2–5.3 also show that as brown trout, *Salmo trutta*, and European grayling, *Thymallus thymallus*, grow from larvae into early juvenile life-stages, stranding risk is reduced, even if downramping velocity would remain the same, indicating that fish are less susceptible to stranding as they increase in size. Hence, Schmutz et al. (2013) conclude that lowering the downramping rate to <0.2 cm min^{-1} and <0.4 cm min^{-1} significantly reduces the stranding risk of grayling larvae and juvenile, respectively. Therefore, in stretches with hydropeaking, that

Table 5.1 Mitigating adverse ecological impacts of hydropeaking through operational measures – literature recommendations and implemented case studies.

Impact	Species, life-stage	Caused by	Description of operational mitigation measures and hydropeaking thresholds	Type of study	Source
Stranding	Brown trout, *Salmo trutta*, fry and juvenile	Downramping	Decreasing downramping from 1 cm min^{-1} to 0.3 cm min^{-1} reduced the stranding of trout fry by >50% in summer and fall, and almost eliminated stranding of 1+ trout. A further ramping rate reduction to <0.16 cm min^{-1} lead to even less stranding of trout fry.	Lab experiments	Halleraker et al. (2003)
	Brown trout, *S. trutta*, larvae and juvenile (0+)	Downramping	A downramping threshold of ≤0.1 cm min^{-1} during the day and ≤0.05 cm min^{-1} during the night might reduce stranding of larvae, whereas for juvenile (65–70 mm) ≤6.4 cm min^{-1} and ≤3.2 cm min^{-1} are recommended for day and night, respectively.	Outdoor flume experiments (Lunz, Austria)	Auer et al. (2014)
	Atlantic salmon, *Salmo salar*, juvenile (1+)	Downramping	Lowering the downramping rate from 0.9–1.0 cm min^{-1} to 0.23–0.31 cm min^{-1} (4–5 h dewatering time) almost eliminated stranding of wild juvenile salmon on natural substrate during spring daytime trials at low temperatures.	Field study (Nidelva River, Norway)	Saltveit et al. (2001)
	Atlantic salmon, *S. salar*, juvenile	Downramping	Avoiding ramping rates >0.16–0.25 cm min^{-1} can reduce stranding significantly. It is also advised to stabilize flow early in the growing season and restrict dewatering in darkness. Depending on discharge conditions (Q range), more stringent thresholds can be recommended to reduce juvenile stranding from late summer until spring.	Modelling (Surna River, Norway)	Halleraker et al. (2007)
	European grayling, *Thymallus thymallus*, larvae and juvenile (0+)	Downramping	To reduce stranding losses in spring (May–July), maximum downramping rates per minute must be lower than 0.6 or 1 m^3 s^{-1} (equaling 7% or 11% of MQ).	Field study (Drava River, Austria)	Unfer et al. (2011)
	European grayling, *T. thymallus*, larvae and juvenile (0+)	Downramping	Stranding risk of larvae is low if downramping rates are ≤0.2 cm min^{-1} during the day, whereas for juvenile (∅ 35 mm and 53 mm TL) they can be ≤1.2 cm min^{-1} and ≤3 cm min^{-1}, respectively.	Outdoor flume experiments (Lunz, Austria)	Auer et al. (2014)
	European grayling, *T. thymallus*, juvenile (0+)	Downramping	During the night, the daylight threshold of <3 cm min^{-1} is also recommended for larger juveniles (∅ 53 mm TL) on homogeneous gravel bars, where the presence of depressions on heterogeneous gravel bars demands more stringent thresholds of ≤0.5 cm min^{-1}.	Outdoor flume experiments (Lunz, Austria)	Auer et al., (2014, 2017)
	European grayling, *T. thymallus*, larvae and juvenile (0+)	Downramping	Lowering the downramping rate to <0.2 and <0.4 cm min^{-1} significantly reduces the stranding risk of grayling larvae and juvenile, respectively.	Outdoor flume experiments (Lunz, Austria)	Schmutz et al. (2013)
	Coho salmon, *Oncorhynchus kisutch*, rainbow trout, *O. mykiss*, juvenile	Downramping	In winter (water temp. <4 °C), fish losses due to stranding can be reduced if downramping is conducted during the night, as fish are active and do not hide in the substrate (diel shift). A slower downramping rate will furthermore reduce stranding.	Lab experiments	Bradford et al. (1995)
	Pacific salmon and steelhead rainbow trout, *Oncorhynchus* sp., larvae and juvenile (0+)	Downramping	A summer, spring and winter downramping threshold of 0.05 cm min^{-1} and 0.25 cm min^{-1} is necessary to protect salmon and steelhead fry.	Field study (Sultan River, USA)	Olson (1990), in: Schmutz et al. (2015)

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Table 5.1 (continued)

Impact	Species, life-stage	Caused by	Description of operational mitigation measures and hydropeaking thresholds	Type of study	Source
	Pacific salmon and steelhead rainbow trout, *Oncorhynchus* sp.	Downramping	Interim ramping rate criteria, differentiated by three seasons and time of day for each season, are proposed: (1) mid-February–mid-June: no ramping during daylight, and 0.08 cm min^{-1} during the night; (2) mid-June–October: 0.04 cm min^{-1} (day and night); (3) November–mid-February: 0.08 cm min^{-1} (day and night).		Hunter (1992)
	Pink salmon, *Oncorhynchus gorbuscha*, Chum salmon, *O. keta*, and Chinook salmon, *O. tshawytscha*, juvenile (0+)	Downramping	Flow management measures at the Skagit Hydroelectric Project propose that fry stranding can be mitigated by releasing a sufficient minimum flow, by lowering the yearly number of downramping events and by reducing downramping amplitude to 113 m^3 s^{-1} (here: differences between the highest and lowest flow release during any 24 h period due to flow reduction). Also, downramping during the daytime is not allowed during the emergence and outmigration period, when fry are most vulnerable to stranding. The project set a general threshold for downramping flow rate of 85 m^3 s^{-1} h^{-1}.	Field study (Skagit River, USA)	Connor and Pflug (2004)
Entrapment in side channels and potholes	Multiple, mostly juvenile	Downramping	Flow reduction after a forced reservoir spill lead to side channel and pothole entrapment. Downramping rates of >0.08–0.16 cm min^{-1} trapped many fish, in some cases even at receding flows ranging from 0.04–0.08 cm min^{-1}. An alternative strategy to gradual downramping (for cases where stranding risk in substrate depressions and entrapment in off-channel areas is high), is an increase in flow to remove fish from potholes, coupled with a sudden decrease that would allow little time for their return.	Field study (Bridge River, Canada)	Higgins and Bradford (1996)
	Brown trout, *S. trutta*, Atlantic salmon, *S. salar*, juvenile	Peak magnitude	During the swim-up phase (mid-March to mid-June), flows should not exceed 240 m^3 s^{-1} to avoid pool trapping, as fish are not able to reach higher bank areas with many depressions that will fall dry during downramping.	Field study (Dordogne River, France)	Cazeneuve et al. (2009)
Drift	European grayling, *T. thymallus*, juvenile (0+)	Upramping	Lowering the upramping rate from >3 to 0.5 cm min^{-1} can mitigate the risk of drifting for juveniles (∅ 53 mm TL), especially during night experiments.	Outdoor flume experiments (Lunz, Austria)	Auer et al. (2017)
Spawning redd dewatering	Chinook salmon, *O. tshawytscha*, spawning	Peak magnitude and base-flow conditions	It is recommended to discourage fish from spawning in higher elevation areas of the river channel by reducing peak flows to prevent later redd desiccation or provide minimum flows during critical development periods.	Field survey (Columbia River, USA)	McMichael et al. (2005)
Spawning redd dewatering, mortality of intra-gravel life-stages	Pink, Chum and Chinook salmon, *Oncorhynchus gorbuscha*, *O. keta*, and *O. tshawytscha*, egg and embryo	Peak magnitude and base-flow conditions	To protect eggs and embryos from redd dewatering, the Skagit Hydroelectric Project imposed constraints on maximum flows during spawning as well as prescribed higher minimum flows during incubation (70–140 m^3 s^{-1}).	Field study (Skagit River, USA)	Connor and Pflug (2004)
	Chinook salmon, *O. tshawytscha*, egg and alevin	Peak magnitude and base-flow conditions	Redd dewatering can be minimized by providing minimum incubation discharges. The effect is even greater, if these discharge magnitudes are similar to spawning discharges.	Field study and modelling (Columbia River, USA)	Harnish et al. (2014)

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Table 5.1 (continued)

Impact	Species, life-stage	Caused by	Description of operational mitigation measures and hydropeaking thresholds	Type of study	Source
	Chinook salmon, *O. tshawytscha*, egg and alevin	Drawdown to base-flow between peaks	Prevent dewatering of spawning redds after post-hatch life-stages, especially pre-emergence alevins which are very sensitive to redd desiccation (mortality at <1 h dewatering).	Lab experiments	Becker et al. (1982)
	Brown trout, *S. trutta*, Atlantic salmon, *S. salar*, egg and alevin	Drawdown to base-flow between peaks	To prevent dewatering of spawning grounds, minimum flows shall be increased from 10 $m^3 s^{-1}$ to 30 $m^3 s^{-1}$ from mid-November to mid-May, assuring that 90% of the spawning grounds will stay underwater.	Field study (Dordogne River, France)	Cazeneuve et al. (2009)
	Atlantic salmon, *S. salar*, egg	Drawdown to base-flow between peaks	To improve egg survival during cold air temperatures, it is recommended to minimize the duration of hydropower production stops and/or to increase minimum instream flow to prevent exposure of eggs to dry and freezing conditions.	Field study (Lundesokna River, Norway)	Casas-Mulet et al. (2014)
	Robust redhorse, *Moxostoma robustum*, egg and larvae	Drawdown to base-flow between peaks	To reduce dewatering mortality, minimum flows have to maintain the inundation of spawning areas, especially for post-hatched larvae.	Lab experiments	Fisk et al. (2013)
Ecological status	Multimetric index: Fish Index Austria	Ramping rates	Ramping rates of >0.5 cm min^{-1} are associated with a poor or bad fish ecological status, whereas a reduction to <0.25 cm min^{-1} increases the probability of attaining a higher ecological status in nature-like river channels.	Modelling	Schmutz et al. (2015)

TL = total length of fish (mm); MQ = average yearly discharge ($m^3 s^{-1}$).

are suitable for fish spawning and recruitment (potential spawning grounds, habitat availability), a temporal “larval window” is suggested where such stringent thresholds shall be enforced (Greimel et al., 2017). Similarly, other authors proposed different seasonal thresholds to include length-specific distinctions regarding stranding risk (e.g., Auer et al., 2014; Hunter, 1992; Olson, 1990 in: Schmutz et al., 2015).

Aside from these recommendations related to fish length, we detected species-specific differences. Brown trout, for example, is more sensitive to downramping than grayling (FIGURES 5.2–5.3). While the critical rate for grayling larvae is 0.2 cm min^{-1} (Schmutz et al., 2013), stranding of brown trout larvae occurs already at rates >0.1 cm min^{-1} (Auer et al., 2014; Halleraker et al., 2003). For comparison, stranding of juvenile Atlantic salmon, *Salmo salar*, was almost eliminated at rates of 0.23–0.31 cm min^{-1} (Saltveit et al., 2001).

In summer, flow reduction during daytime can reduce stranding rates for European grayling and brown trout in comparison to nighttime downramping (Auer et al., 2014, Auer et al., 2017), whereas in winter the opposite could be detected for brown trout, Atlantic salmon, Coho salmon, *Oncorhynchus kisutch*, and rainbow trout, *O. mykiss*, (Bradford et al., 1995; Saltveit et al., 2001). A further parameter that determines stranding risk is riverbank morphology (Auer et al., 2017; Hauer et al., 2014), as well as the presence of structures and deep areas (Bradford et al., 1995). FIGURE 5.4 shows that the addition of cover and pools in laboratory flume experiments can both increase or decrease

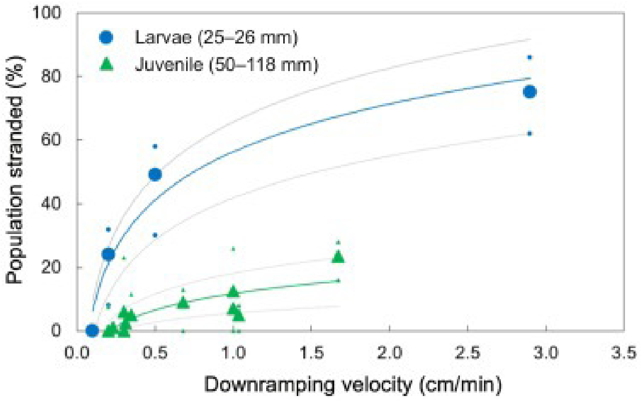

Figure 5.2 Stranding rates of different life-stages of brown trout, Salmo trutta, in relation to downramping velocity during spring and summer daytime experiments on homogeneous gravel bars. The large icons and the dark-colored trendline represent median values, whereas the small icons and the light grey trendline represent the 25th and 75th percentiles reported in the studies. Envelope curves are logarithmic. Four values of juveniles also contain S. salar because Hessevik (2002) did not distinguish between S. trutta and S. salar but grouped them. Data sources: Auer et al. (2014), Halleraker et al. (2003), Hessevik (2002), Saltveit et al. (2001).

stranding rates, depending on species assessed. Furthermore, as described above, FIGURE 5.4 depicts the increased stranding risk during daylight compared to the night in the winter.

Overall, Schmutz et al. (2015) related downramping rates to a multimetric fish index and showed that ramping velocity >0.5 cm min^{-1} is associated with a poor or bad fish ecological status, whereas a reduction to <0.25 cm min^{-1} increases the probability of attaining a higher ecological status in nature-like rivers. These recommendations agree with those from Halleraker et al. (2007), who state that stranding can be significantly reduced if ramping rates >0.17–0.25 cm min^{-1} are avoided.

5.4.1.2 Base- and peak-flow magnitude, peak frequency and time between peaks

Next to downramping velocity, base- and peak-flow magnitude, peak frequency and time between peaks are the most commonly reported parameters regarding hydropeaking, which mostly aim at mitigating the ecological effects related to spawning and intra-gravel life-stages (TABLE 5.1). In this category, however, the majority of papers only suggest qualitative targets. Common impacts include the dewatering of spawning grounds which can lead to mortality of eggs and larvae, whereas the sensitivity of these life-cycle stages can vary: In general, pre-hatch stages are more tolerant to desiccation than post-hatch stages (Becker and Neitzel, 1985), while pre-emergence alevins are especially sensitive and can die if the redd is dewatered for already less than one hour (Becker et al., 1982).

To protect eggs and larvae from redd dewatering during drawdown to base-flow between peaks, it is recommended to discourage fish from spawning during regular peak-flows, as they will spawn in higher elevation areas which can easily fall dry during base-flow. This can be achieved by, for example constraining maximum flows during spawning (Connor and Pflug, 2004). Furthermore, a sufficient base-flow should be provided during critical development periods to always cover spawning redds with water (Casas-Mulet et al., 2014; Connor and Pflug, 2004; Harnish et al., 2014; McMichael et al., 2005).

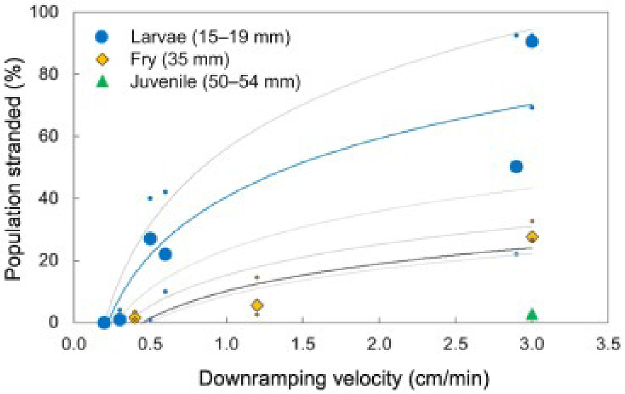

Figure 5.3 Stranding rates of different life-stages of European grayling, Thymallus thymallus, in relation to downramping velocity during spring and summer daytime experiments on homogeneous gravel bars. The large icons and the dark-colored trendline represent median values, whereas the small icons and the light grey trendline represent the 25th and 75th percentiles reported in the studies. Envelope curves are logarithmic. Data sources: Auer et al., 2014, Auer et al., 2017, Schmutz et al. (2013), Zeiringer et al. (2014).

5.4.2 National legislation and guidelines

5.4.2.1 Europe

Based on a literature query, 34 countries that publish on hydropeaking were identified (FIGURE 5.1), where the top three were Norway, Switzerland, and Canada. Nineteen of these 34 countries belong to the European Union and are, therefore, obliged to comply with the goals of the EU Water Framework Directive (2000/60/EC; hereinafter 'WFD'). However, the WFD does not specify methods, targets or thresholds for hydropeaking mitigation, but only refers to the achievement of the good ecological status or good ecological potential in all water bodies by 2027 (cf. Art. 4 WFD). Similar to the environmental flows (EC, 2015), the regulation and implementation of mitigation measures behooves the individual countries. While the assessment of the ecological status follows a standardized approach, the definition of good ecological potential depends on potential effects on use (cf. Art. 4, 3(a) WFD; EC, 2003). Hence, the definition of restoration targets for achieving the good ecological status may follow a more or less standardized approach, while mitigation targets for achieving the good ecological potential may vary depending on potential effects on use (cf. Art. 4 WFD).

A European survey (Halleraker et al., 2016) asked 30 European countries if mitigation of rapidly changing flows (incl. effects of hydropeaking) was included in the national list of mitigation measures. Twelve countries answered "yes", of which we were able to get legal restrictions on hydropeaking for 8 of them (TABLE 5.2). Nine of them said the topic is not relevant, seven did not give a statement and two identified the impact but did not present any measure.

Austria is the only EU Member State that has already established hydropeaking thresholds. On a Federal level, the Autonomous Province of Bolzano, Italy, did it as well. Other countries or regions, like Spain and the German Province of Baden-Württemberg, have recommendations for the mitigation of hydropeaking considered in river basin management plans, while others still work on a case by case basis (e.g., Norway) (TABLE 5.2).

Austria set a base-flow to peak-flow threshold ratio of 1:3 and also demands a maximum

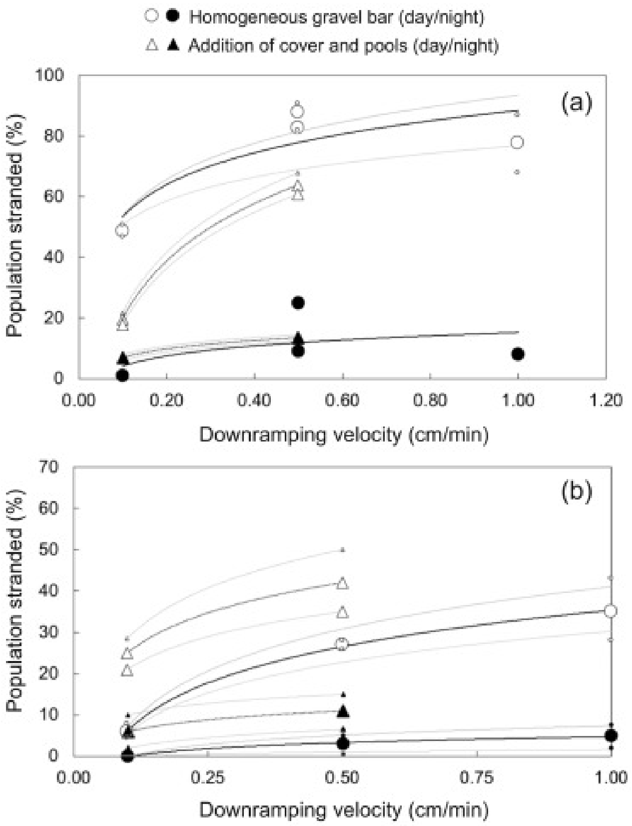

Figure 5.4 Stranding rates of (a) juvenile (53–98 mm) Coho salmon, Oncorhynchus kisutch, and (b) juvenile (79–101 mm) rainbow trout, Oncorhynchus mykiss, in relation to downramping velocity during winter day (white icons) and night (black icons) experiments on homogeneous gravel bars (circles) and with the addition of cover and pools (triangle). The large icons and the black trendline represent median values, whereas the small icons and the light grey trendline represent the standard error reported in the study. Envelope curves are logarithmic. Data source: Bradford et al. (1995).

change of 20% in wetted area for small and medium-sized rivers. In these cases, a ratio of >1:5 automatically leads to the failing of a good ecological status (QZVÖ, 2010). In large rivers, a case by case evaluation is required, as they are more sensitive to this pressure. There, a threshold ratio of 1:3 may already lead to the failing of the good ecological status (QZVÖ, 2010). Already existing hydropeaking reaches are classified as heavily modified water body and, therefore, may not adhere to the above thresholds. Instead they must attain the good ecological potential. Recent R&D projects followed a case specific approach considering additional parameters such as ramping rates, peak frequency, timing, or river morphology. Finally, the ecological potential is defined within an integrative approach including ecological and economic analyses and scenario evaluation to avoid adverse effects on the use sensu WFD (Greimel et al., 2017). On a regional level, the government approved the water management framework plan for Western Tyrol to reach the targets of the WFD, as well as to increase the energy production along the Upper Inn River valley (Reindl et al., 2017). Through the construction of hydropeaking diversion power plants and compensation basins, hydropeaking thresholds of <15 and <12 $\mathrm{cm\,h^{-1}}$ for up- and downramping shall be attained in all affected river reaches. However, when determining thresholds, critical life-stages of fish shall receive special attention (Wasserwirtschaftlicher Rahmenplan Tiroler Oberland, 2014).

Similar to Austria, the Autonomous Province of Bolzano, Italy, set a threshold ratio between base-flow and peak-flow of 1:3 for new facilities.

Table 5.2 Status of hydropeaking legislation thresholds and target values within the studied countries (only countries with information are displayed).

Country	Legislation/guideline	Thresholds and target values (description)	Evaluation
Austria[a]	Qualitätszielverordnung (QZVO), 2010; BMLFUW (2015)	<1:3 and <20% change in wetted area (for small and medium-sized rivers)[b] A ratio >1:5 leads to failing of good ecological status in small and medium-sized rivers	Case by case evaluation in large rivers (as they are more sensitive)[c]
Province of Tyrol: Upper Inn River valley	Wasserwirtschaftlicher Rahmenplan Tiroler Oberland, 2014	After implementation of regional proposed hydropower projects, hydropeaking-induced flow changes should be <15 cm h^{-1} for upramping and <12 cm h^{-1} for downramping in all affected reaches.	Strategic planning instrument, detailed case by case analysis
Canada	Fisheries Act from 1985 – last amended on April 5, 2016 (Canadian Ministry of Justice, 1985)	–	Case by case
Finland[a]	Water Act 2011 (Finnish Ministry of Environment, 2011)	–	Case by case
France[a]	Article L214 – 18 from the Environmental Code (Code de l'Environnement, 2000)	–	Case by case
Germany[a]	–	–	–
Province of Baden-Württemberg	Wassergesetz für Baden-Württemberg (WG), 2013	–	Case by case[d]
Italy[a]	–	–	Case by case
Province of Bolzano	Durchführungsverordnung (6/2008) zum Landesgesetz Nr. 8/2002; Wassernutzungsplan, 2017	<1:3 at new facilities	Case by case evaluation of mitigation measures for impacted rivers
Liechtenstein	Gewässerschutzgesetz (GSchG), 2003	–	Structural or operational measures must prevent ecological impairment
Norway[a]	Water Regulation Act ('Vannforskriften') (Miljøverndepartementet, 2006)	–	Case by case
Spain[a]	Instrucción de Planificación Hidrológica (ARM/2656/2008; 10 Sept. 2008); River Basin Management Plans (Confederaciónes Hidrográficas de España, 2008)	Maximum rate of flow variation – a percentile <90–70% is recommended.	River basin[e]
Switzerland	Gewässerschutzgesetz (GSchG), 1991; Gewässerschutzverordnung (GSchV), 1998; BAFU – Bundesamt für Umwelt, 2012, BAFU – Bundesamt für Umwelt, 2017	Flow ratio <1:1.5 and abundance, composition, or diversity of local biota shall not be adversely changed[f]	Each indicator category has its separate thresholds determining the ecological status classes (e.g., TABLE 5.3)
Sweden[a]	Swedish Environmental Code 1999 (SEPA, 2017)	–	Case by case
United States of America	Clean Water Act (CWA), 2002 – Section 401: Water Quality Certification (WQC); Endangered Species Act (ESA), 1973; Federal Power Act (FPA), 1920	–	Case by case

[a] Mitigation of rapidly changing flows (incl. hydropeaking) is included in the national list of mitigation measures (according to Halleraker et al., 2016).

[b] Threshold for attaining the "good ecological status" with a high probability. The "very good ecological status" can only be reached if anthropogenic river stage fluctuations (hydropeaking) do not occur.

[c] In large rivers, any hydropeaking is considered as significant pressure.

[d] Hydropeaking operations shall be avoided; the water authority remains the right to authorize exceptions (§ 23 (2) WG, 2013).

[e] Each river basin authority is responsible for defining and calculating the maximum rate of change based on mean daily flow values.

[f] Threshold for "non-significant pressure".

According to the regional Water Management Plan (WNP, 2017), it is not possible to derive general threshold criteria to mitigate the impact of existing hydropeaking facilities. In these cases, the necessary measures will be defined and assessed individually within the framework of river protection plans.

In Finland, the Water Act 2011 (Finnish Ministry of Environment, 2011) defines general permit requirements for water resources management projects (ch. 3), but does not set general hydropeaking thresholds. Hydropeaking permits are set after a case-specific impact assessment. Projects with permits issued before 1 May 1991 may undergo an environmental investigation if considerable detrimental impacts on the aquatic environment are detected and the fisheries authority or municipality may apply for a review of the permit regulations or impose new regulations (ch. 19, sec. 7–8).

There are no legal thresholds for hydropeaking in France. Rules are negotiated case by case. Nevertheless, for hydropower plants >4.5 MW, the procedure of concession includes specifications regarding water management issues such as minimum flow, turbine flow or hydropeaking, which are defined in the Environmental Code (Code de l'Environnement, 2000) (L211-1 and L214-1 to L214-6).

All hydropeaking operations in the province of Baden-Württemberg, Germany should be avoided (WG, 2013, §23 (2)), where the water authority is entitled to authorize exceptions. According to §126 (5), it is an administrative offence if non-authorized hydropeaking occurs.

Liechtenstein legislation (GSchG, 2003, Art. 34a §1) states that the operators of hydropower facilities must prevent the impairment of native animals and plants through hydropeaking operations by structural measures. At request of the hydropower plant owner, the government may also allow operational mitigation measures and can determine the type of measures and the deadlines to their implementation (§3). Compensation basins built for hydropeaking mitigation may be used for pump-storage hydropower without the need of amendment to the license (§4).

In Spain, the River Basin Management Plans (Confederaciónes Hidrográficas de España, 2008) recommends maximum rates of discharge variation for each river basin. These values must be estimated based on the analysis of mean annual flows series with, at least, 20 years. The annual rate of change should be calculated from the time series for both up- and downramping rates. The annual series of discharge variation rates, for up- and downramping, shall be computed. It is recommended that the mean rate of change shall not exceed the 90–70% percentile of those time series, for both up- and downramping values. In some particular cases, it may be necessary to consider a refined time scale, which may allow limiting the rate of change at an hourly level.

The Norwegian Water Regulation Act (Miljøverndepartementet, 2006) was adopted in 2006 to include the goals of the EU WFD. A report on setting environmental flows to implement the WFD in Norway (Bakken et al., 2012) devotes a chapter on hydropeaking. However, general operational hydropeaking mitigating measures have not yet been defined. From 2009 to 2016, a national hydropeaking research project was carried out ('EnviPEAK', see Bakken et al., 2016a), where the outcomes were a set of guidelines in how to perform environmental adapted hydropeaking operations in rivers. These guidelines include recommendations on maximum flow ratios, water level reductions, timing of the year/day and frequency, in the context of the considered rivers vulnerability exposed to hydropeaking (Bakken et al., 2016b). Although some of these guidelines have been applied in few hydropeaking rivers during the revision of hydropower licenses, those license requirements are still mostly issued on a case-by-case basis, as each hydropower installation is unique, and historically there are few restrictions on hydropeaking operations (L'Abée-Lund and Otero, 2018).

The Swiss legislation demands that major impairments caused by short-term pulsed flow shall be remedied by 2030, primarily through structural, but also by operational measures (Schweizer et al., 2016; Tonolla et al., 2017). A significant harm is present if the ratio between base-flow and peak-flow exceeds 1:1.5 and if the abundance, composition, or diversity of the local biota is adversely changed. To evaluate the biological aspects, the Federal Office for the Environment (BAFU – Bundesamt für Umwelt, 2012, 2017) developed a list of 15 indicators, divided into four categories (core indicators, hydropeaking-sensitive indicators, broadband indicators, additional indicators) and five ecological status classes (TABLE 5.3). An adverse change is present if most of the core indicators shows a moderate status, or if one core indicator shows an unsatisfactory or bad status (core indicators include: hydrological parameters, stranding of fish, spawning grounds of fish, habitat suitability for fish/macrozoobenthos, water temperature) (TABLE 5.3).

The Swedish Environmental Code was adopted in 1998 to combine 15 other acts, including the Water Act from 1918 (SEPA, 2017). A specific system which was established for the use of water resources, including a permit regime for water operations, and entered into force in 1999. Any hydropower plant or dam must have a permit which coheres with chapters 3–4 of the Code (river protection measures from hydropower exploitation). Regarding hydropeaking, the permit will specify the highest and lowest water levels allowed in the reservoir, as well as the maximum and minimum discharge (and the corresponding rate of change) released from the dam and power station. Thus, hydropeaking is generally allowed as long as the maximum and minimum water levels and discharge values set by the court are not exceeded.

5.4.2.2 North America

Hydropeaking-specific regulations do not exist yet in Canada. However, the Canadian Fisheries Act (Canadian Ministry of Justice, 1985), the national legal instrument for water management and protection, can be used for peak-flow attenuation through, for example the prohibition of works that result in the harmful alteration, or disruption or destruction of fish habitat (Section 35). Furthermore, the governor in council may make regulations for, among others, the conservation and protection of fish, including their spawning grounds (Section 43(1)).

Although the United States of America do not have hydropeaking-specific legislation as well, the Clean Water Act (CWA) (Federal Water Pollution Control Act, 2002), the Endangered Species Act (ESA, 1973) and the Federal Power Act (FPA, 1920) can be used in hydropeaking-power permit negotiations. Any activity that may result in a discharge to U.S. waters must provide a Water Quality Certification (CWA – Section 401), in which the applicant declares that the discharge will comply with the applicable provisions of the act, including water quality standards. If there is sufficient justification and a supporting administrative record, this certification could include restrictions on hydropeaking. If endangered or threatened species are present within the hydropeaking reach, the Endangered Species Act may be used to stipulate conditions on a hydropower project to protect, restore or enhance certain species. If pulsed flow operation is likely to adversely affect a species listed under the Endangered Species Act, the U.S. Fish and Wildlife Service and the National Marine Fisheries Service may issue a biological opinion that contains conditions which require a modification to project operations. The Federal Power Act provides the groundwork for cooperation between the Federal Energy Regulatory

Commission (FERC) and other federal agencies in (re-)licensing hydropower projects. Section 10(j) allows Fish and Wildlife agencies to submit recommendations, for example regarding project operations that the FERC must consider when issuing a license.

5.5 Discussion

5.5.1 National legislation, regulations and recommendations

5.5.1.1 Europe

There is still a lack of quantitative hydrological thresholds for the mitigation of adverse ecological effects of hydropeaking. Unsurprisingly, only a few countries have adopted precise thresholds in national legislation and guidelines. Of these, the Swiss water laws contain the highest level of detail (e.g., TABLE 5.3; BAFU, 2017). By setting these thresholds, Switzerland has established various targets for hydropeaking mitigation until 2030 (Tonolla et al., 2017). Considering that many questions regarding the ecological effects of peak-flow attenuation still have to be more deeply addressed, it is questionable if setting thresholds for the next decades is suitable at this stage. Even now, some of the established thresholds do not necessarily reflect the current state of the art from hydropeaking research. For example, a downramping rate of <0.2 cm min^{-1} is enough to attain the very good ecological status during the larval life-stage of brown trout and grayling (cf. TABLE 5.3). Although this value will probably prevent stranding of grayling, a more stringent threshold of 0.1 cm min^{-1} might be necessary to halt stranding of brown trout larvae (Auer et al., 2014). Furthermore, if multiple events occur in one day, only the greatest and the lowest event are considered. Depending if this daily hydropeaking event is a distinct or a recurring event, the threshold targets of the various indicators must only be attained in 95% or 60% of the days (BAFU, 2017). Considering the high sensitivity of, for example post-hatched gravel life-stages (Becker et al., 1982), spawning ground dewatering can have detrimental effects on a fish population if occurring only 5% of the time.

Austria also adopted rather specific hydropeaking thresholds. Modeling discharge ratios of 1:3, Hauer et al. (2014) found that four out of ten channel bar sites featured a change in the wetted area >20%, which was caused by different river morphologies. Furthermore, Hauer et al. (2016) pointed out that base-flow conditions are entirely different between the seasons and, regarding river morphology, will lead to different extents of the ramping zone, even if the ratio remains the same. Therefore, the authors conclude that such ratios cannot universally be established as a general basis for mitigation thresholds if seasonal aspects of base-flow magnitude, as well as river morphology, are overlooked (Hauer et al., 2016). Additionally, these Austrian thresholds refer only to the good ecological status, whereas most existing hydropeaking rivers have the good ecological potential as a target condition. So far, the good ecological potential has not yet been defined, but feasibility studies have to be carried out by 2021 and then designed and implemented on a river-by-river basis by 2027. Therefore, the integrative assessment approach as developed by Greimel et al. (2017) is being applied in different case studies.

5.5.1.2 North America

In the USA, many hydroelectric dams are subject to relicensing by the Federal Energy Regulatory Commission (FERC) (Young et al., 2011). Although no hydropeaking-specific legislation exists, several laws affect hydropower relicensing and they require consideration or inclusion of conditions for the protection, mitigation, or enhancement of fish resources.

Table 5.3 Swiss legislation core indicator "stranding thresholds" (BAFU, 2017).

Ecological status	Dry falling surface area in relation to wetted area (%)	Downramping rate for larval grayling/ brown trout at daylight (cm min^{-1})	Downramping rate for juvenile grayling at daylight (cm min^{-1})	Downramping rate for juvenile brown trout at daylight (cm min^{-1})
Very good	<10	<0.2	<1	<1.5
Good	10–30	0.2–0.3	1–1.2	1.5–3
Moderate	30–40	0.3–0.4	1.2–2	3–4.5
Unsatisfactory	40–50	0.4–0.5	2–3	4.5–6
Bad	>50	>0.5	>3	>6

One example is the Skagit River Hydroelectric Project, Washington, where eggs and embryos of salmon and steelhead shall be protected from dewatering, and stranding of salmonid fry on gravel bars shall be minimized (Connor and Pflug, 2004). Therefore, the difference between spawning and incubation periods flows was reduced, which decreased the river area subjected to dewatering (see TABLE 5.1). To prevent stranding of fry, downramping was limited to night time hours, whereas also downramping rates and the amplitude of flow fluctuations were lowered. These measures boosted the fish population, which showed a steady yearly increase in spawner numbers of 5.2% (Connor and Pflug, 2004). Similarly, the Vernita Bar Settlement Agreement (Harnish et al., 2014), implemented on the Columbia River in 1984, includes discharge constraints to prevent Chinook salmon of spawning at higher water levels (see TABLE 5.1). During the fall spawning period, redd site selection (which was thought to occur mainly during daylight hours) should be limited to lower elevations by reversing the normal load-following pattern, providing low discharges during the day and higher discharges at night. In 1999, the Hanford Reach Fall Chinook Protection Program Agreement was enacted to protect other life-stages as well. Changes in dam operation led to a 217% increase in salmon productivity in comparison to the period before the Vernita Bar Settlement Agreement, which corresponded with constraints enacted to prevent redd dewatering. An additional increase of 130% coincided with enactment of constraints to limit stranding and entrapment of juveniles during the period of emergence and early rearing (Harnish et al., 2014).

5.5.2 Mitigating direct hydropeaking impacts through thresholds and targets: biological and hydromorphological variables

Hydropeaking events are defined by the magnitude of flows on one hand, and their timing on the other hand. Parameters such as the rapid decrease of flow and stage, daylight conditions and duration of wetted history are of ecological significance in terms of stranding risk (Halleraker et al., 2003; Irvine et al., 2009; Saltveit et al., 2001), as well as for dewatering of spawning grounds (Fisk et al., 2013; Casas-Mulet et al., 2016; McMichael et al., 2005) and rapid within-day flow increases are of major importance concerning downstream displacement of fish (Auer et al., 2017; Boavida et al., 2017; Flodmark et al., 2006; Jensen and Johnsen, 1999;

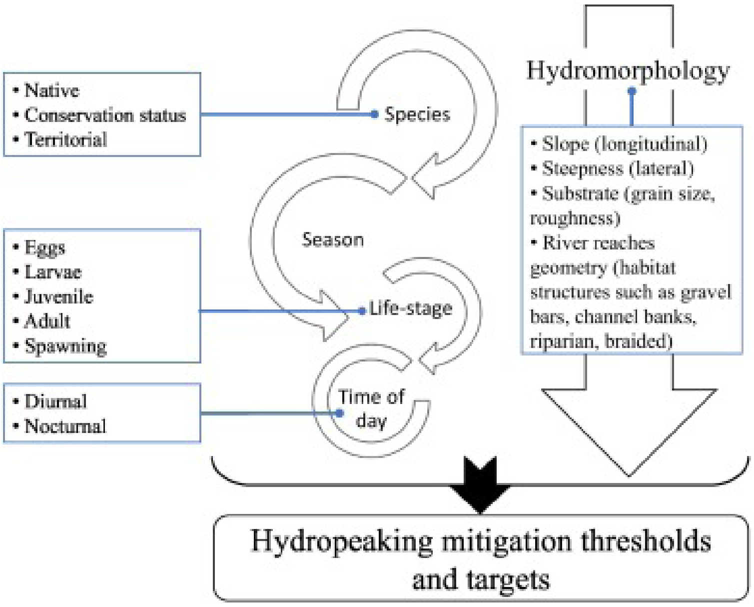

Figure 5.5 Main aspects and corresponding biological and hydromorphological variables for defining hydropeaking mitigation thresholds and targets for fish.

Scruton et al., 2003; Thompson et al., 2011; Zeiringer et al., 2014). Thus, the hydrological parameters (i.e., magnitude, duration, frequency, flow ratio and rate of flow change) which are related with distinct ecological responses may be used to define mitigation thresholds, where its design should consider key species and their ecological requirements (Bruder et al., 2016; Hauer et al., 2017). Furthermore, hydromorphological conditions must be included in the definition of mitigation measures since they are crucial for fish survival as well (Hauer et al., 2014, Hauer et al., 2017). Accordingly, FIGURE 5.5 presents a scheme with the sequence of the main aspects and the corresponding biological and hydromorphological variables that should be considered when designing thresholds and targets for hydropeaking mitigation.

5.5.2.1 Species

Literature indicates that some species are more vulnerable to stranding than others. For example, brown trout are more sensitive than European grayling (FIGURES 5.2–5.3), and Coho salmon has a higher stranding risk than rainbow trout (FIGURE 5.4). Therefore, hydropeaking mitigation designs shall select the species with the highest sensitivity to artificial flow fluctuations, assuming that all other species will be indirectly protected. Endangered species may also be considered of higher priority, although this does not necessarily assure the critical thresholds of the most sensitive species, such as in many Austrian rivers where brown trout and grayling cohabit. Although the grayling has a higher importance in terms of national protection status (Uiblein et al., 2001), brown trout are more sensitive to hydropeaking (cf. FIGURES 5.2–5.3).

Sensitivity among species may also vary depending on life history strategies and behavioral patterns. Highly territorial species such as salmonids may be more vulnerable to stranding as they can be reluctant to abandon spawning territories during receding water levels (Boavida et al., 2017), while cyprinid species, typically of lower swimming performance compared to salmonids, may not have enough resistance to achieve a suitable habitat during downramping (Santos et al., 2014). Some studies also found that hydropeaking may influence fish assemblages in general (e.g., Enders et al., 2017; Hedger et al., 2018; Sauterleute et al., 2016; Scruton et al., 2008), while García et al. (2011) concluded that artificial flow fluctuations may provoke distinct impacts on native and non-native species.

Therefore, hydropeaking mitigation measures should consider, as a first step, the specific requirements (incl. sensitivity and life-history strategy) of the species present in the impacted river reach, as well as their conservation status. Targeting indicator or threatened species will indirectly improve the conditions of other species as well.

5.5.2.2 Life-stage

Literature shows that, in hydropeaking rivers, various life-stages can be influenced by different hydrological parameters. Salmonid eggs can survive dewatering for weeks in dewatered gravel if they are kept moist (at least 4% moisture by weight), do not freeze and are not subject to predation, or if temperatures do not exceed incubation tolerances (e.g., Becker et al., 1983; McMichael et al., 2005). Although salmon eggs are tolerant to dewatering, mortality increases once fish have hatched and larvae are dependent on gills for respiration. Thus, special attention should be given to newly hatched alevins, which are less tolerant and may die within a short time of dewatering (Becker et al., 1982; Fisk et al., 2013). Peak-flows may create temporarily suitable habitat for gravel-spawning fish, which will be subjected to periodic dewatering between the pulsed-flow releases (McMichael et al., 2005; Vocht and Baras, 2005). Therefore, peak flow reductions, combined with minimum flow releases, are a common mitigation recommendation to reduce early life-stages mortality (TABLE 5.1). The sooner and the longer minimum flow release is implemented during the spawning period, the higher is the probability of fish not spawning in high mortality risk areas (Casas-Mulet et al., 2016).

Juvenile fish are more susceptible to hydropeaking events than adults, as juvenile habitat is confined to the shallow banks, where their risk of stranding is enhanced, since they might not reach the central part of the channel during downramping event. In contrast, adults tolerate a wider range of stream conditions (Enders et al., 2017; Pragana et al., 2017; Saltveit et al., 2001). This is in line with our findings from literature, which show that fish are less likely to get stranded as they grown in size (FIGURES 5.2–5.3). Therefore, the establishment of hydropeaking thresholds should consider not only the species present, but also the respective life-stage and the associated season.

Furthermore, intra-annual flow differences have to be considered, especially when determining base-flow magnitudes, as life-cycle phases and their flow requirements are connected to certain periods of the year (Hayes et al., 2018). For example, fish movements are related to discharge alterations (Berland et al., 2004; Boavida et al., 2017; Jones and Petreman, 2015), which can vary according to seasons (Katzman et al., 2010; Scruton et al., 2005), where high flow fluctuations may affect spawning behavior. Under these conditions, different studies found out that both Chinook salmon, *Oncorhynchus tshawytscha*, and common barbel, *Barbus barbus*, repeatedly abandoned spawning redds before completion (Hamilton and Buell, 1976, in: Young et al., 2011; Vocht and Baras, 2005). In such situation, Chinook salmon may decide to move to less desirable and more crowded locations (Hunter, 1992).

5.5.2.3 Time of day

In hydropeaking rivers, seasonal flow thresholds which aim, for instance, at avoiding redd dewatering or stranding and drifting of larvae and juveniles, may attenuate negative effects on fish populations. However, diel variations have to be considered as well. In some cases, the discharge decrease should only be performed after dark to reduce the stranding risk of some salmonid species, especially during winter when fish are less mobile and often hide in the substrate during the daytime (Saltveit et al., 2001; Stickler et al., 2007), suggesting to limit discharge-induced downramping to night time hours (Connor and Pflug, 2004). Similarly, after modeling different operation scenarios in a Portuguese river reach, Pragana et al. (2017) recommend that, in winter, downramping should be performed after 5 or 6 PM, and in the summer after 9 PM, to minimize impacts on juvenile brown trout habitat. In contrast, other studies concluded that, in summer, European grayling (Auer et al., 2017) and brown trout (Auer et al., 2014; Halleraker et al., 2003), as well as Austrian fish communities generally (Schmutz et al., 2015) are less vulnerable during the day than during the night. From the majority of studies, it can be deduced that downramping thresholds should be more stringent during nighttime in summer as well as during daytime in winter, although some recommendations (e.g., Connor and Pflug, 2004; Pragana et al., 2017) do not confirm this generalization. The literature is, therefore, not completely consistent on the issue whether is better to have a peak event during the day or during the night since it may vary according to species-specific characteristics and season. It is clear, however, that the flow reduction rate should be set to give fish sufficient time to leave sheltered habitats near the substrate and to reach the main channel, irrespective of time of day.

5.5.2.4 Hydromorphology

Multiple studies indicate that the impact of hydropeaking is strongly dependent on river reaches morphology (e.g., Boavida et al., 2015; Bradford, 1997; Hauer et al., 2013, Hauer et al., 2014; Parasiewicz et al., 1998; Tuhtan et al., 2012; Vanzo et al., 2015). Person et al. (2014) showed that braided reaches offer the best habitat suitability in terms of quantity and stability for different brown trout life-stages in comparison to other morphological types (e.g., groynes, gravel bars, straight channel). Authors concluded that spawning and young-of-year life-stages depict higher sensitivity to the discharge fluctuations than adults for all morphologies. Due to their wide riverbed, braided reaches are able to retain the rapid fluctuations effects and to produce varying velocity conditions that may be suitable for brow trout and other fish in different life-stages (Person et al., 2014). Nevertheless, stranding risk was not considered is their assessment. Vanzo et al. (2015) also concluded that braided reaches are the most resilient to hydropeaking, offering the highest habitat diversity, and found out that alternate bars are extremely sensitive environments to drift but offer safer regions from stranding.

Furthermore, several studies on salmonid fish demonstrated that stranding risk is positively correlated to the presence of sheltering areas or potholes (e.g., Auer et al., 2017; Saltveit et al., 2001; Scruton et al., 2008). Fish may hide in these spots during peak-flow events to escape from high velocities, but when flow is reduced, fish may get entrapped. Larger juveniles and adults are more likely to inhabit deeper pools, glides, overhanging banks, and mid-channel habitats where they are less vulnerable to stranding and entrapment (Hunter, 1992; Nagrodski et al., 2012). In contrast, early juvenile life-stages prefer shallow habitats along the river margins, which is part of the ramping zone and might get dewatered. In this regard, a river channel with many side channels, potholes, and low gradient bars has a greater stranding potential than a river with a single channel with steep banks (Hunter, 1992). However, steep banks are less favorable for juvenile fish. Controlling ramping rate might be effective in reducing stranding along the river margins but proved to be less effective for pothole and side channel entrapment (Higgins and Bradford, 1996; Hunter, 1992). In the latter cases, flows should be increased before downramping to remove fish from potholes, combined with a low rate decrease that would allow their save return to the channel (Higgins and Bradford, 1996).

Coarse grain sizes on a smooth bank slope are another factor which can increase stranding risk (Boavida et al., 2015; Bradford, 1997; Hauer et al., 2014). Unsurprisingly, Hauer et al. (2014) stress the necessity to consider grain-size distribution of gravel bar surfaces when establishing peak operation thresholds and/or discharge variability in seasonal base-flow targets. In contrast to stranding, the presence of coarse substrate, acting as a velocity shelter, can help fish to avoid downstream displacement in a hydropeaking river (Heggenes, 1988). Multiple studies highlighted the importance of substrate as one of the main parameters structuring fish assemblages in hydropeaking rivers (e.g., Boavida et al., 2015; Chun et al., 2010; Scruton et al., 2008).

Due to river hydromorphology and related retention effects, hydropeaking parameters, such as downramping rate, vary along the course of the river, where the intensity of the impact is mostly directly below the tailrace and is reduced in downstream direction (Hauer et al., 2017; Halleraker et al., 2007). Therefore, the longitudinal variability in hydropeaking reaches must also be considered when defining flow mitigation thresholds.

5.5.3 Indirect impacts: macroinvertebrates

Pulsed flows may also have indirect impacts on fish through effects on food supplies such as benthic macroinvertebrates, which comprise the principal food source of fish populations (Cushman, 1985). As invertebrate populations are diminished, fish growth can be reduced (Bruno et al., 2010; Irvine, 1986; Moog, 1993). Hydropeaking negatively affects density, biomass and species diversity through the catastrophic drift occurring during peak-flow, particularly when combined with high content of suspended solids, and, for some taxa, through the behavioral drift in the base-flow conditions (Bruno et al., 2010; Moog, 1993). Also, the effects of thermopeaking on the drift of benthic invertebrates have been reported (Carolli et al., 2012; Schülting et al., 2016). In Europe, the assessment metrics and benthic habitats regarded in WFD may not reflect the effects of hydropeaking events (Leitner et al., 2017), which may require further research for the development of mitigation strategies regarding the benthic communities.

5.5.4 Economic impacts of mitigation thresholds

Hydrological mitigation thresholds can be achieved either through operational measures, as well as structural measures such as the construction of hydropeaking retention basins or hydropeaking diversion power plants (Greimel et al., 2018a). The latter requires suitable topographic conditions and a significant first-time investment but does not impact the ongoing hydropower operation. In contrast, operational measures entail ongoing restrictions in the power plant's operation mode (Premstaller et al., 2017), reducing the capacity to produce flexible energy according to the current demand and leading to economic losses which are proportional to the intensity of the mitigation thresholds (Greimel et al., 2018b; Hauer et al., 2017). Additionally, some other possible technical constraints such as the start-stop operation and type and number of turbines may limit the application of those measures (Harby and Noack, 2013).

The importance of peak-flow operating hydropower in the energy grid and the adverse ecological impacts need to be balanced. Therefore, operational measures are being evaluated using a cost-benefit approach that assess the trade-offs involved (Niu and Insley, 2013). These include the costs imposed on hydropower operators in terms of lost profits, as well as potential environmental impacts that result from the need to use alternative sources of electricity (Niu and Insley, 2013; Pérez-Díaz and Wilhelmi, 2010).

5.5.5 Research needs

5.5.5.1 Units for defining hydropower mitigation thresholds

Stranding thresholds for the vertical ramping rate variation are reported in different velocity units, mainly cm h^{-1} and, more recently, cm min^{-1}. When designing such flow constraints, it is important to consider not only how post-implementation and monitoring will be addressed. On the one hand, if discharge data is available only with hourly values, it might be more reliable to define thresholds in cm h^{-1}. On the other hand, if a finer scale of discharge is available (e.g., 15 min interval), it may be more feasible to monitor thresholds implementation in cm min^{-1}. From an ecological point of view, however, the units monitored also have to be in accordance with ecological processes to be investigated. Stranding, for example, is a behavioral response taking place within the time scale of minutes, so it might be more coherent to define thresholds in cm min^{-1} instead of cm h^{-1}. However, no research has considered this topic yet, which may be a drawback when defining hydropeaking mitigation thresholds.

5.5.5.2 Lateral ramping velocity

The lateral gradient of river banks will, to a large extent, determine the extent of the ramping zone which can become dewatered. Studies found that stranding is lower on steeper river bars and was reduced when the bank slope was greater than 2% (Bradford et al., 1995; Monk, 1989, in: Schmutz et al., 2015), indicating that there is a trade-off between losing shallow water habitat and reducing stranding risk. Furthermore, it has been suggested that stranding susceptibility seems to be more related to the rate of stream margins dewatering (lateral ramping velocity), than to the vertical downramping rate (Hauer et al., 2017; Tuhtan et al., 2012). Hence, the lateral gradient of the river bar seems to play an important role in wetted history variation, which is a key parameter for stranding risk assessment and, therefore, for mitigation. Nevertheless, no thresholds were found in literature for lateral ramping velocity.

5.5.5.3 Non-salmonid species

Although most of the hydropeaking studies have been focusing on salmonid species (Nagrodski et al., 2012), some attention has been given to non-salmonid species such as cyprinids over the last decade (Alexandre et al., 2015, Alexandre et al., 2016; Boavida et al., 2015; Capra et al., 2017, Capra et al., 2018; Costa et al., 2018). However, in our literature search, we did not find thresholds or mitigation targets for cyprinids, which underlines the research need of this fish family, which is the largest in the world, and other non-salmonid species inhabiting hydropeaking rivers.

5.5.5.4 Thermopeaking, saturopeaking and soundpeaking

The release of hydropeaking discharges can also entail thermal alterations, where their duration is similar to that of the hydropeaks (Zolezzi et al., 2011). However, as most studies only deal with the effects of long-term temperature changes associated with hydropeaking (e.g., Céréghino et al., 2002), there is a lack of information on the short-term ecological effects of thermal alterations (Bruno and Siviglia, 2012; Zolezzi et al., 2011). Observations in fish migration found that the start of migration was linked to an increase in water temperature and a decrease in discharge (Benitez and Ovidio, 2017), which may be affected by (thermo)peaking events. Thus, there is a need to assess the influence of thermopeaking on, for example, migration, spawning, larval growth rates, or on the behavioral drift of fish species (Zolezzi et al., 2011).

Similar to thermopeaking, also gas saturation can follow the pattern of hydropeaking operations (Pulg et al., 2016). Depending on fish species and life-stage, the levels at which supersaturation is harmful may begin at 103–100% of the total dissolved gases (TDG) saturation (Jensen et al., 1986). In natural environments, fish can compensate for supersaturation by moving into deeper water (e.g., 0.3–0.8 m) (Beeman and Maule, 2006), which is why the Canadian guidelines for supersaturation distinguish between deep (>1 m) and shallow water bodies, defining 110% and 103% TDG as the thresholds for deep and shallow rivers, respectively (Canadian Council of Ministers of the Environment, 1999). Nevertheless, so far there are no guidelines for supersaturation in European rivers, as possible ecological effects of saturopeaking in hydropeaking rivers still require more research (Pulg et al., 2016).

Soundscapes affected by hydropeaking are highly homogenized, when compared to unaffected ones, and sound pressure level variations are strongly correlated with turbine discharge, which results in rapid, multiple-fold spikes in low frequency amplitude levels (Lumsdon et al., 2018). As a consequence, fish or macroinvertebrates may be affected physiologically or behaviorally, but further research on this topic is needed to examine the response of biota to changes in soundscapes (Lumsdon et al., 2018).

5.5.5.5 Reporting and monitoring of implemented measures

Most hydropeaking studies report on adverse flow alteration-ecological response relationships and, based on these insights, propose mitigation measures. However, so far there are only a few papers reporting on the outcomes of the implemented measures, where most of these were implemented in the USA (e.g., Connor and Pflug, 2004; Fisk et al., 2013; Harnish et al., 2014) and Cazeneuve et al. (2009) present a French case study. Assessing the success of implemented measures is, therefore, an important step for future hydropeaking mitigation strategies and regulation development.

5.6 Conclusions

Hydropeaking causes severe changes in riverine environments, entailing adverse responses of organisms (e.g., Bejarano et al., 2017b). It is, therefore, stringent to develop ecologically-based criteria for hydropeaking mitigation. In-situ studies, laboratory experiments and numerical modeling are of vital importance to specify terms and conditions that minimize the effects of hydropeaking through the establishment of threshold standards and mitigation targets. These values should be achieved by adapting hydropower plants operation, or by constructing infrastructures to attenuate discharge fluctuations in the river (Charmasson and Zinke, 2011).

Reviewing the literature, we found that, so far, only few studies published quantitative hydropeaking thresholds for operational mitigation measures, most of them established for salmonid fish through stranding trials in experimental channels. Research showed that low downramping rates reduce the stranding risk, whereas exact thresholds are related to species, life-cycle stage, time of day, and river morphology. Other studies recommend management approaches to improve spawning and rearing success, such as restricting peak flows during spawning and raising minimum flows during incubation to prevent redd dewatering. Furthermore, literature indicates that the impact of hydropeaking is strongly dependent on river reaches morphology, especially site-specific characteristics, such as lateral bar angle, grain size distribution, shelters or potholes, which have to be considered when to prescribe mitigation measures. Nevertheless, due to the above-described site-specific characteristics, the intensity of some hydraulic parameters, such as vertical ramping rate, will decrease longitudinally with distance from the turbine outlet, but this is not necessarily true for other parameters, such as lateral ramping velocity, which proved to be highly variable (Hauer et al., 2017).

Due to these factors which have to be considered in hydropeaking rivers, it is not surprising that, so far, only two countries (Austria and Switzerland) have established legal regulations regarding hydropeaking discharges. Other countries established constraints on a regional level (e.g., Germany, Italy). Few countries have recommendations for hydropeaking mitigation (e.g., Spain), while others have regulatory frameworks that may force a case-by-case analysis under specific legal requirements (e.g., Norway, USA). The lack of published literature reporting on the success of implemented measures might thus indicate that few measures have yet been implemented due to the shortage of legal regulations.

Although it might be hard to determine national thresholds due to case-specific effects of hydropeaking impacts, it is urgent to mitigate the ecological impacts caused by flow fluctuations, considering environmental objectives such as demanded by the WFD in Europe. Nevertheless, literature indicates that multiple aspects have to be considered when assessing mitigation targets. To assist in this process, we present a scheme regarding the main aspects and the corresponding biological and hydromorphological variables which should be considered for the design of hydropeaking mitigation measures with a focus on fish. We propose that mitigation targets and thresholds must be based on key species (e.g., hydropeaking-sensitive, protected or territorial species), including particular features regarding season, a parameter that determines life-stage phases (e.g., focusing on vulnerable life-stages, such as larvae) and diel variations, which must be combined with site-specific morphological characteristics (e.g., river geometry or bank gradient, grain size, habitat structures). Furthermore, the potential impacts on uses have to be considered when dealing with the ecological potential as target in river sections of heavily modified water bodies. We, therefore, conclude that the ecologically-based criteria for mitigation measures may benefit the impacted organisms in hydropeaking reaches. Nevertheless, further research is needed to establish thresholds and targets for more species and their life-stages throughout different habitat types and, complementary, the monitoring of hydropeaking mitigation implementation, which is not yet a widespread procedure.

5.7 Acknowledgments

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CHAPTER 6

Synthesis and discussion

Freshwater biodiversity is more threatened than the biodiversity of any other ecosystem type worldwide (Dudgeon et al., 2006; WWF, 2020). One of the driving forces behind this downward spiral of freshwater species (FIGURE 1.1) is the modification of river flows (Collen et al., 2014; Dudgeon et al., 2006). In this regard, dams and their associated reservoirs exert profound and far-reaching pressures on downstream river ecosystems as they alter the natural flow regime components (magnitude, frequency, duration, timing, rate of change; see BOX 1.1) on diverse temporal and spatial levels. However, aquatic organisms depend upon the natural array of river flows for the completion of crucial life-history stages (Bunn and Arthington, 2002; Poff and Zimmerman, 2010). Unsurprisingly, one of the urgent actions to halt this biodiversity loss is flow restoration through the allocation of environmental flows (Arthington et al., 2018a; Tickner et al., 2020). Hence, governments, water managers and stakeholders are called to push e-flows implementation by building on the most recent advances from science and practice (Harwood et al., 2017).

To guide restoration measures in modified rivers, however, a deeper ecological knowledge is needed (Palmer et al., 2005), especially regarding the understanding of flow-ecology relationships. Hence, research efforts must target the identification of linkages between river flow and ecosystem components in order to enhance the comprehension of fundamental ecological functions and processes (Arthington et al., 2010, 2006; Davies et al., 2014). By doing so, science may provide river managers with qualitative or – in the best case – quantitative flow rules, guidelines or thresholds to be applied to modified rivers (Arthington et al., 2010, 2006; Costa et al., 2019; Harby and Noack, 2013).

The purpose of this thesis was, therefore, to develop holistic approaches for flow restoration in modified rivers subjected to water abstraction or hydropeaking, and to develop e-flows able to sufficiently mitigate the ecological effects of short-term and annual flow modifications. The studies pursued here show how flow alterations on multiple temporal scales diminish river integrity, especially pertaining to fish populations, and – based on these insights – how flows can be restored to reduce adverse ecological impacts in modified rivers. Moreover, this thesis sets the topic of flow restoration into the broader context of hydromorphological river rehabilitation, and points towards next steps needed to support the successful implementation of flow restoration measures.

Here, I synthesize the research outputs of CHAPTERS 2–5 by discussing the following questions:

- Is flow regulation a primary parameter that influences aquatic biota?
- How can flows in modified rivers be restored to reduce adverse ecological responses?
- Which steps are needed to accelerate flow restoration in modified rivers?
- Is flow restoration alone sufficient?

6.1 Is flow regulation a primary parameter that influences aquatic biota?

Rivers are often affected by multiple stressors that can act in concert. To answer the question on primary influences, it is, therefore, required to take up the challenge of disentangling the main and interacting factors affecting riverine biota (Birk et al., 2020; Nõges et al., 2016; Schinegger et al., 2016). So, considering the European grayling (*Thymallus thymallus*) introduced in CHAPTER 1 as an indicator species for an entire fish region (Smialek et al., 2019), the first study of this thesis assessed which environmental factors influence this keystone species.

The aim of CHAPTER 2 was to understand the response of grayling populations to four stressor types – hydropeaking, channelization, river fragmentation, and water quality alteration. Through non-linear, exploratory decision-tree approaches, is was possible to detect main and interaction effects. The results showed that downramping rate [cm min^{-1}] and peak amplitude [cm] are the primary predictors of grayling biomass in hyporhithral rivers. The majority of high-biomass sites are situated in river sections without flow regulation or only low hydropeaking intensity. In cases of higher hydropeaking intensity (i.e., after the first split in the tree model, see FIGURE 2.4), a lower morphological state or reduced connectivity within the river network further diminishes fish populations. Interestingly, in bivariate analyses, neither morphology nor connectivity correlated with the target variable, but their effects could only be seen when nested within the hydrological stressors.

Hence, although hydromorphological stressors also affect grayling, hydropeaking is the primary cause of reducing population vitality. A multi-year case study from an Austrian grayling river confirms this conclusion. In the Drava River, grayling stocks plummeted from ~150 to 20 kg ha^{-1} in just 13 years (1989–2002) due to widespread river engineering works and hydropower development (Unfer et al., 2004). To counteract this fish ecological decline, a series of morphological restoration measures was set in place (Muhar et al., 2007). At most sites, as would be expected, these measures led to an increase of fish stocks, particularly of juvenile grayling. At the site that is situated in the hydropeaking stretch, however, age-structure of grayling remained distorted despite morphological rehabilitation measures (Muhar et al., 2007). Similarly, in two Swedish rivers, habitat enhancement by adding boulders, stones and gravel to the stream bed did not improve grayling size nor population abundance – possibly because these rivers are also subject to hydropeaking (Hellström et al., 2019).

Indeed, a large body of literature testifies to the ecological benefits of natural flow regimes and the adverse implications caused by changes thereof. CHAPTERS 3 and 4 present an extensive overview of the literature on the topic of flow-ecology relationships. Although both chapters link the five flow regime components (BOX 1.1) with ecological responses, they do so on different temporal levels. CHAPTER 3 mainly discusses yearly and seasonal flows, and CHAPTER 4 focuses on sub-daily flows.

CHAPTER 3 contains a detailed discussion on the relationship between river flow and central abiotic and biotic elements of temperate rivers: this study identified key flow regime elements which determine essential ecological functions and processes (e.g., FIGURE 3.4), as well as described how typical dam-induced flow alterations impact river morphology, floodplains, as well as plants and animals (TABLE 3.2). The loss of seasonal flow variability, flow magnitude reduction, and extended low flow durations have presumably the greatest adverse consequences for river organisms.

While seasonal flow variability is known to support diverse life cycle functions, the opposite is true for increased daily flow variability through hydropeaking. In this regard, chapter 4 describes how life cycle stages of salmonid fish (migration and spawning, egg incubation and alevins, fry emergence, or early juvenile) can be affected by hydropeaking. To date, it remains difficult to determine the single strongest impact of hydropeaking on fish. However, there is strong evidence that emerging fry as well as early juveniles are particularly sensitive to down-ramping rate (CHAPTERS 4–5) – and these effects can ultimately be measured at the population level (CHAPTER 2).

6.2 How can flows in modified rivers be restored to reduce adverse ecological responses?

From an ecological perspective, one of the best solutions to restore flows may be to disassemble dams and reservoirs and other structures that obstruct or divert the flow of river water. Nowadays, dam removal is more and more considered a viable management option, and the practice of dam removals has significantly accelerated in the last two decades (Bellmore et al., 2017). However, the restoration of flows was hardly the pressing issue as most dam removals constituted run-of-river facilities (Foley et al., 2018). Nevertheless, in consideration of an aging dam infrastructure and many positive ecological and geomorphological responses following dam removals (Foley et al., 2018), these restoration practices will certainly continue. Recently, for example, the European Union, in its Biodiversity Strategy for 2030, has committed itself to restore at least 25,000 river kilometers to a free-flowing state (European Commission, 2020).

In many cases, however, dam removal is no realistically feasible option; for example, regarding large hydropower plants that ensure energy system stability and guarantee security of electricity supply (see BOX 1.2), or irrigation dams that support integral food production (Hayes et al., in prep.). In such instances, it is often a matter of weighing one use against another; for example, economic benefits through hydropower production versus ecological health. In this regard, many mitigation approaches aim at establishing measures along a Pareto-frontier (Kuriqi et al., 2019a, 2019b; Ziv et al., 2012). This balancing of trade-offs is a central focus of achieving the 'good ecological potential' in Europe's 'heavily modified water bodies', as the good ecological potential is determined by the ecological effectiveness and economic implications of measures (Greimel et al., 2018). This approach is particularly relevant in many rivers subjected to cascade reservoir dams or hydropeaking, which have been classified as being 'heavily modified'. All other rivers in Europe must adhere to the 'good ecological status'; in these cases, economic considerations are mostly not considered.

CHAPTERS 2–5 provide evidence that flows can be successfully adapted and managed to provide improved ecological outputs. One of the key recommendations of this thesis is to adapt dam operations according to yearly, seasonal and daily flow requirements of river biota. Most previous studies have usually focused on selected flow components, for example, linking ecological processes to single (e.g., Cruz et al., 2020) or recurring (e.g., Robinson et al., 2018) floods of larger magnitudes, or studying the effects of elevated baseflow discharges (e.g., Adeva-Bustos et al., 2019). Coincidentally, most dam re-operation measures focus on these two topics: minimum or high flow releases (Owusu et al., 2020). However, this thesis underlines that the entire diversity of flow regime components, for example, events of varying frequency and magnitude, are important as they govern different spatial and temporal processes.

CHAPTER 3 recommends managing e-flows as dynamic flows (see FIGURE 3.4). Indeed, this resolution is confirmed by a growing body of ecological evidence (e.g., Kozak et al., 2016). Also, from an economic perspective, there are indications that dynamic e-flow regimes can provide higher energy production than minimum flows, whilst resulting in lesser alterations of river flow (Erfani et al., 2015; Kuriqi et al., 2019a, 2019b; Razurel et al., 2016). Although such results offer promising win-win solution, it is not yet clear from an environmental perspective, how high the magnitude of such dynamic flows must be and to what extent the dynamic bandwidth needs to vary within a year. For example, Kuriqi et al. (2019a) tested two different dynamic flows ('10% of mean daily flow plus annual mean minimum flow' and '30% of mean daily flow'); however, the authors did not quantify ecological responses but only used hydrological indicators to assess the ecological effectiveness of these e-flow regimes. Similarly, Austrian legislation demands a dynamic flow (20% of the actual flow) for the achievement of the 'good hydromorphological state' (QZVÖ, 2010). With this dynamic flow component, the legislation aims to sustain the natural seasonality of bed sediments relocation for a river type-specific sediment composition, sufficient flow during the spawning season, seasonal habitats according to the requirements of life stages of relevant organisms, as well as river type-specific oxygen and water temperature conditions (QZVÖ, 2010). Although this piece of legislation is already quite progressive (Tharme, 2003), its claims need to be verified.

In this regard, CHAPTERS 2–5 highlight that a detailed knowledge on flow-ecology relationships is fundamental to aid the design of flows in regulated rivers in order to enhance environmental sustainability whilst guaranteeing societally acceptable water use. Too often, however, "the life history and ecology of many species […] have yet to be documented" (Harrison et al., 2019). In such cases, if detailed ecological knowledge is lacking, a precautionary approach should be applied; for example, by "restricting hydrologic alterations to within a percentage-based range around natural or historic flow variability" (Richter et al., 2012). In general, the less is known about the ecological functions of a system or the higher the sensitivity of the species, the less flows should be altered to guarantee a sufficient level of ecological protection. For example, Richter et al. (2012) suggest that "protecting 80% of daily flows will maintain ecological integrity in most rivers." Beyond that, more detailed knowledge will help to fine-tune flow recommendations in order to achieve Pareto optimal solutions. Depending on the knowledge level, the relationships between river ecology and flow alterations can be expressed in different forms (Poff et al., 2010). Quantitative expressions might describe the percentage of ecological change *versus* percentage of flow alteration (Poff and Zimmerman, 2010), whereas qualitative relationships might be expressed in form of categorical responses (e.g., low, medium, high) or as trajectory of change (+/-) (Poff et al., 2010).

CHAPTER 3 synthesizes knowledge on ecological functions and processes to formulate the *functional floodplain flow (ff-flow)* restoration approach that propagates "the establishment of an e-flow regime capable of restoring the natural functions and processes of impaired floodplain ecosystems through the release of functional elements of the annual hydrograph". Even though quantitative relationships are largely missing, such understanding of process-based flow-ecology relationships already provide a sound scientific and practical basis for establishing ecologically relevant e-flows and for guiding flow-based river management (Beechie et al., 2010; Poff et al., 2010). Similarly, CHAPTER 4, establishes flow restoration guidelines for hydropeaking rivers by identifying key parameters of the hydropeaking hydrograph relevant for life cycle stages of salmonid fishes (FIGURE 4.1).

The knowledge of quantitative thresholds seems particularly relevant in situations of high public interest, such as hydropeaking mitigation, where operational flow restrictions may affect the stability and flexibility of the energy system, or alter national carbon dioxide emissions (Greimel et al., 2018; Gurung et al., 2016). To address these issues, CHAPTER 5 expands the work of CHAPTER 4 by linking the identified flow-ecology parameters to targets and thresholds for operational hydropeaking mitigation (TABLES 5.1–5.2, FIGURES 5.2–5.4). For example, experimental studies suggest that maximum downramping rate during daytime for brown trout (*Salmo trutta*) larvae is <0.1 cm min^{-1}. For larvae of Atlantic salmon (*Salmo salar*), which are stronger swimmers, a threshold of 0.23–0.31 cm min^{-1} was identified, whereas for grayling larvae the critical rate is 0.2 cm min^{-1} (see CHAPTER 4 and references therein). Surprisingly, the decision tree model presented in CHAPTER 2 (FIGURE 2.3A) validated grayling's critical downramping rates as established in flume experiments (Auer et al., 2014; Zeiringer et al., 2014). Hence, the fit between modeling and experimental approaches showcased in this thesis underlines the feasibility of using such threshold ranges as ecological benchmark for hydropeaking mitigation in grayling rivers, and particularly during the 'emergence window' (Moreira et al., 2020; chapter 4).

Overall, it has been demonstrated that the knowledge on flow-ecology relationships – either through process-based understanding (CHAPTERS 3–4) or quantitative flow thresholds (CHAPTERS 1, 5) – can help to establish flow restoration measures that support riverine biota.

To accelerate flow restoration in modified rivers, however, some challenges and limitations need to be addressed.

6.3 Which steps are needed to accelerate flow restoration in modified rivers?

Flow restoration measures should be implemented as early as possible. However, e-flows are not yet as widely implemented as would be recommended (Poff et al., 2010; Richter et al., 2012; Tickner et al., 2020; Hayes et al., in prep.). This is especially true for hydropeaking rivers as the literature contains only few mitigation case studies, whereby these are mostly from North America (CHAPTER 5). Other examples of implemented measures are known from Switzerland (Hasliaare River; Bieri et al., 2014; Schweizer et al., 2016), France (Doubs and Ain rivers), and Austria (Bregenzerach) (Muhar et al., 2019). Moreover, a large hydropower diversion plant is currently in construction at the Inn River at the Swiss-Austrian border (Moreira et al., 2020). Similar plans exist for the Valsura Torrent in South Tyrol, Italy (Premstaller et al., 2017).

Hence, this status quo underlines the urgency to accelerate flow restoration measures in order to halt the rapid decline in freshwater species populations (Tickner et al., 2020; WWF, 2020). The diversity of rivers and organisms, as well as people cultures and governments, however, stresses that unique solution tailored to each case study are needed (Harwood et al., 2017; Le Quesne et al., 2010; Hayes et al., in prep.). Nevertheless, based on successful case studies worldwide, Harwood et al. (2017) identified seven actions for effective e-flows implementation, which align tightly with the outcomes of a recent e-flows workshop (Hayes et al., in prep.):

1. Engage meaningfully with stakeholders to garner understanding and support. The integration of stakeholders and other actors in decision-making processes is crucial to support co-creation with regards to e-flows design and implementation. Stakeholders need to establish a sense of responsibility in the e-flows process and communicate with one another in order to enhance understanding of trade-offs, for example, by assessing where water comes from, where it is going to, and who or what will be impacted. Through stakeholder engagement processes, target conditions can be defined in a participatory way, including the desired state of the river, conservation and management objectives, and setting of water allocation priorities (Hayes et al., in prep.).

2. Enact clear and effective legislation and regulation, and maintain the political will to implement and enforce. Political will is one of the most important enabling factors for e-flows implementation (Moore, 2004). When governments recognize e-flows as a priority in water resources planning, this will more easily lead to the development of a clear legal basis for securing required e-flow allocations, for example, through rights and licenses, consumption caps, e-flow reserves, or integration into basin-wide water management (Harwood et al., 2017). In situations where many of the existing water infrastructure projects were planned for without having to account for detailed e-flows, the adherence to such new e-flows norms may create tensions. In India, an emerging e-flows nation, for example, e-flows are often not yet allocated because there are no ramifications for failing to comply with legal requirements. With the exception of the Upper Ganga River, mechanisms to enforce e-flow releases are still missing. Therefore, this comparably new situation has often resulted in legal disputes which seem to have caught the legal system and institutional setup as a surprise. Hence, in India, they still need to adapt to these new issues (Hayes et al., in prep.). Regarding hydropeaking mitigation, CHAPTER 5 revealed that to date only few countries have established thresholds and targets in national or federal legislation or guidelines. Unsurprisingly, those with more detailed legislation, such as Switzerland, South Tyrol or Austria, belong to the most prominent countries regarding the implementation of mitigation measures.

3. Secure sufficient resources and capacity for e-flow design (including stakeholder engagement), implementation and monitoring. Sufficient funding from different stakeholders (e.g., government, NGOs, research) is key to effectively manage water resources and to enhance understanding on the outcomes of e-flow allocations (Harwood et al., 2017).

4. Consider how e-flow implementation will affect not just ecological, but also economic and social conditions for different groups of people. Holistic approaches are needed to understand and evaluate how environmental water allocations will affect downstream ecosystems and water-users (Harwood et al., 2017). Nowadays, it is being increasingly emphasized that socio-economic and socio-cultural parameters must be included in e-flow assessments and evaluations (Hayes et al., in prep.). In this regard, the recognition of socio-economic benefits of e-flow releases (e.g., Anderson et al., 2019) will also help to strengthen stakeholder support (see above).

5. Implement some level of protection as early as possible since it is easier to restrict allocation than attempting to re-allocate water. Ideally, e-flows are discussed upfront at the beginning of water resources development to best determine how water should be distributed for ecology and society. By integrating e-flows from the very beginning, it is possible to set precautionary allocation limits in advance, thereby entirely avoiding the need to move from flow protection to the harder task of having to reclaim water through flow restoration. This is particularly important for river systems and countries where a great part of the gross domestic product is based on fisheries (e.g., the Mekong in South-East Asia or the Okavango River Basin in Botswana). Also, the non-deterioration principle of the EU Water Framework Directive could be followed, as it is possible to calculate the legislated e-flows necessary to maintain the ecological status (Hayes et al., in prep.).

6. Keep e-flow prescriptions as scientific as possible according to the level of risk and intensity of water use, and within the available financial and human resource constraints – but balance this with the need to keep science targeted and only as complex as the context allows, and with the need for clear non-technical communication of the issues with stakeholders. The choice of an e-flow assessment method (Tharme, 2003) should be appropriate to the dimension of the problem to be solved (e.g., how complex is the ecosystem? What is the spatial and temporal scale of the impact? Which ecosystem services are affected?). For example, while small-scale and less important uses may be judged based on simple approaches, more elaborate methods are needed for cases of complex spatiotemporal interactions between user demands and ecosystem needs (Schmutz, personal communication). Particularly in the latter situation, the e-flows science must be as detailed as possible. The resulting e-flow prescription, however, needs to be comparably simple to allow for easy implementation, such as a nation-wide applicable formula for environmental flow thresholds (e.g., Parasiewicz et al., 2018)

7. Monitor ecological, social and economic outcomes of e-flow implementation and manage adaptively. The establishment of monitoring mechanisms is crucial to evaluate the outcomes of e-flow releases and to determine if the previously agreed-upon targets have been reached. Post-implementation monitoring will help to quantitatively capture the response of the river system to management actions (Hayes et al., in prep.). Such post-implementation reporting is fundamental, among other reasons, as monitoring results can guide the next course of action, for example through adaptive management processes (Richter et al., 2006; Webb et al., 2018). Thereby, loops of continuous monitoring and fine tuning of e-flows can also facilitate adaptive management for future uncertainty such as climate change (Hayes et al., in prep.).

There is a call to release e-flows in all modified rivers, even if e-flows assessment is an ad-hoc rule-of-thumb at first. As discussed above, such rules should, however, be based on best available science and expertise and should include a sufficient safety margin. This will also promote the application of more sophisticated solutions to optimize flow releases (Hayes et al., in prep.). The continuity of flows should be maintained without altering the natural seasonal variability (CHAPTER 3). It is better to plan and act despite limited knowledge instead of proceeding with freshwater ecosystem degradation. In the best case, the available knowledge on flow-ecology relationships can be used to define reliable e-flows. In any case, the iterative, adaptive nature of e-flows processes needs to be recognized, as initial thresholds should be updated according to new research findings (e.g., regarding less-well researched species and ecosystems).

Aside from direct water releases, improvements in other fields can also lead to higher river flows (in consideration of upper limits and seasonal reversals), thereby assisting in the successful implementation of e-flows. For example, increasing water use efficiency in the agricultural sector, as well as improving wastewater treatment and re-use of water, would decrease the consumption of freshwater resources and thereby help secure the required e-flows, especially in the dry season, if appropriate mechanisms are in place to ensure that saved water is allocated to the environment (Hayes et al., in prep.).

Hydropeaking rivers are a special case among the regulated rivers. As they exhibit a "dual nature" (Jones, 2014), river restoration approaches must address the consequences of both long- and short-term flow alterations. Hence, there is a need to merge the concepts of "environmental flows" and "hydropeaking mitigation". For example, at the Drava River, an Austrian hydropeaking river, grayling recruitment success was related to spring (base-)flow conditions. In years of good recruitment, spring flow magnitudes were comparably low, while years that produced less juvenile fish were marked by spring floods (Unfer et al., 2011). However, to date, such aspects are hardly considered in hydropeaking mitigation frameworks (CHAPTER 5). Similarly, in many rivers, the base:peak flow ratio may show remarkable seasonal differences due to underlying baseflow conditions (Hauer et al., 2014; Sukhbaatar et al., 2020). Depending on baseflow conditions and bank topography, the same hydropeaking flow volume [$m^3 s^{-1}$] can result in completely different peak amplitudes or dewatered areas (Hauer et al., 2014; Moreira et al., 2020), underlining the urgency of combining hydropeaking thresholds with e-flow considerations.

6.4 Is flow restoration alone sufficient?

Although river flow has been identified as a primary driver of aquatic life, it cannot be considered alone; otherwise it would be sufficient to "just release water in a pipe" (Parasiewicz, personal communication). However, this is not the case as habitat is created by the interaction of river flow with geomorphology and vegetation (e.g., Corenblit et al., 2007). Hence, it is increasingly recognized that (especially in complex river floodplain systems) "habitat availability is not likely to be a simple function of flow" (Whipple, 2018).

Indeed, the papers presented in this thesis underline the need of also incorporating sediment continuity (CHAPTER 3), river morphology and bank sedimentology (CHAPTERS 3–5), as well as river connectivity and critical habitats (CHAPTER 2) into best practice river restoration approaches. This notion is supported by a vast body of literature which advocates that process-based river restoration measures must integrate hydrological and physical approaches (Beechie et al., 2010; De Jalón et al., 2017; Meitzen et al., 2013; Muhar et al., 2007; Whipple and Viers, 2019; Yarnell et al., 2015).

Recently, an integrative assessment of hydropeaking mitigation measures on the national scale of Austria revealed that a combination of hydrological and morphological rehabilitation measures can potentially improve the ecological state of 75–80% of all hydropeaking rivers. Hydrological measures alone, in contrast, would only improve around 30% of the studied river stretches (FIGURE 6.1; Greimel et al., 2017). Similarly, a case study on the Sarine River, Switzerland, showed that a two-year flood peak release combined with sediment replenishment was successful in enhancing hydraulic instream habitat conditions downstream of Rossens hydropower dam (Stähly et al., 2019).

To guarantee flow continuity, river connectivity, as well as sediment and nutrient transport, it is necessary to determine the means of releasing or operationalizing e-flows, as the way that environmental water is allocated (e.g., through a hydropower turbine, weir overflow, sluice gate, fish pass) will determine if and to which degree these ecological functions remain available. Sediment transport and habitat connectivity, for example, are key processes from a basin-wide perspective. However, these processes cannot be guaranteed if the water is (only) released by means that do not support other processes (e.g., through the

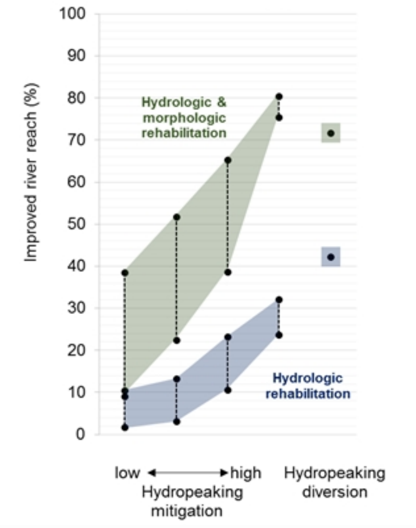

Figure 6.1 Ecological effectiveness of hydropeaking mitigation scenarios (operational restrictions and diversion hydropower plants) with (green) and without (blue) additional morphological measures. Studied river reaches: 294 km of river stretches classified as 'heavily modified' due to hydropeaking (source: Greimel et al., 2017).

powerhouse). Hence, innovative solutions are necessary to adequately address these needs (Hayes et al., in prep.).

Another factor to be considered in river management are the drastic consequences of reservoir flushing operations. Uncontrolled flushing with loads of high suspended sediment concentration can significantly affect aquatic biota. In the short-term, such sediment pulses can cause physiological stress, reduced feeding, or mortality due to hypoxia (Kemp et al., 2011). In the long-term, they can decrease fish and macroinvertebrate populations (Crosa et al., 2010; Grimardias et al., 2017), for example, by clogging spawning gravel layers of lithophilic fish with fine sediments (Kemp et al., 2011) or impacting macroinvertebrate communities through highly mobile particles (Hauer et al., 2018; Leitner et al., 2015). Such adverse effects call for an ecologically-friendly reservoir flushing management.

Fish predation is another factor that is usually not incorporated into river restoration schemes. For example, it has been suggested that piscivorous birds can diminish grayling stocks (e.g., Čech and Vejřík, 2011; Zauner, 1999), and, more recently, predation in general has been identified as a key threat to grayling in the continental biogeographical region of Austria (Aschauer and Bauer, 2019). However, these effects remain to be quantified and set in the context of environmental water allocations and river restoration schemes more generally.

Overall, it has been well established that river flow in combination with different environmental parameters affect aquatic biota – for the better or for the worse. The quantification or prediction of "the interaction between hydrology, sedimentary processes, geomorphology, hydraulics, temperature and ecological variables", however, remains one of major scientific challenges in the field of environmental water management (Arthington et al., 2018b).

6.5 Future research directions

Some recently published guidance documents (e.g., World Bank Group, 2018) specifically include peaking-power releases into their frameworks on integrating e-flows into hydropower projects. Nevertheless, to date, the topics of e-flows and hydropeaking mitigation have hardly been merged (Boavida et al., 2020; Holzapfel et al., 2014; Jones, 2014). This thesis establishes a vital knowledge base for combining e-flows and hydropeaking mitigation, for example, regarding the seasonal aspects of annual and sub-daily flows described in CHAPTERS 3–4. This notion is supported by a study on the Drava River, one of Austria's large hydropeaking rivers, that found a relationship between seasonal baseflows and grayling recruitment: years with higher flows between the end of March to the end of Mai produced only few young-of-year grayling, whereas years with lower flows favored recruitment (Unfer et al., 2011). Although this thesis constitutes a solid foundation for merging the concept of e-flows and hydropeaking mitigation, this topic requires more detailed studies. Future work should, therefore, advance the science and practice of combining e-flows and hydropeaking mitigation.

In order to progress e-flows science, a process-based understanding of riverine ecosystems as presented in CHAPTER 3 is needed. More generally, research has commonly focused on single trophic levels, but analyses of flow-ecology relationships with regards to food-web dynamics are comparably scarce (Davies et al., 2014; Rolls et al., 2017), especially in hydropeaking rivers. For example, studies have assessed the effects of sub-daily flow fluctuations on periphytic algae (Bondar-Kunze et al., 2016), benthic invertebrates (Schülting et al., 2019, 2016) as well as fish (Auer et al., 2017, 2014). To my knowledge, however, no study has yet described the effects of hydropeaking on trophic connections from the basis to consumers to predators. Such research on food-web dynamics is, however, crucial to enhance understanding of the long-term effects of river regulation on aquatic ecosystems and to better guide restoration measures.

But even flow-ecology relationships of single species or organism groups in rarely studied river types require more detailed future investigations. For example, CHAPTER 2 revealed that already low-intensity sub-daily flow fluctuations (hydro-fibrillation) can diminish grayling populations (FIGURE 2.3). As such flow fluctuations can be caused by run-of-river hydropower plants, which are more numerous than storage hydropower plants (Wagner et al., 2015), the resulting ecological effects of these dam operations must be better understood. Hence, there is a need to conduct (comparative) studies in the headwaters (e.g., with brown trout) and in the lowlands (e.g., with cyprinid fish) in order to establish flow thresholds for different river types and species assemblages (Judes et al., 2020). Moreover, it is necessary to expand research into non-temperate areas such as tropical regions, which have received less attention so far (Almeida et al., 2020). Overall, it is also crucial to better understand ecological impacts regarding seasonality (Mihalicz et al., 2019), as well as associated effects of flow regulation, such as seasonal and short-term water temperature changes (Arthington et al., 2018b; Olden and Naiman, 2010; Zolezzi et al., 2011) or sedimentary processes (Arthington et al., 2018b; De Jalón et al., 2017). Moreover, to my knowledge, few studies have yet dealt with the ecological effects of floods and droughts in hydropeaking rivers (but see Sukhbaatar et al. (2020) for a study on the abiotic responses related to ice jams). And only recently, floodplains and vegetation have received more attention (Bejarano et al., 2018).

Another emerging topic in the field of environmental water allocations are flow changes caused by natural shifts and effects related to climate change and other large-scale phenomena. In this regard, it has been argued that the field of hydro-ecology must move beyond the assumptions of climatic and ecological stationary and embrace non-stationary conditions to meet arising e-flow implementation challenges (Capon et al., 2018; Poff, 2018).

Finally, it shall be emphasized that the flow rules presented in this work are targeted at the restoration of modified rivers. These rules present no carte blanche to modify water flows in still free-flowing rivers as the natural flow regime is better capable of sustaining ecosystem integrity than a regime modified by anthropogenic uses.

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Supplementary material 1: SCI journal articles

Other studies published in the course of my Ph.D. studies, but not included in this thesis:

- Englmaier, G.K.*, **Hayes, D.S.***, Meulenbroek, P., Terefe, Y., Lakew, A., Tesfaye, G., Waidbacher, H., Malicky, H., Wubie, A., Leitner, P., & Graf, W. (2020). Longitudinal river zonation in the tropics: Examples of fish and caddisflies from the endorheic Awash River, Ethiopia. *Hydrobiologia*, 847(19), 4063-4090. 10.1007/s10750-020-04400-0 [* equally contributing authors]
- Boavida, I., Díaz-Redondo, M., Fuentes-Pérez, J.F., **Hayes, D.S.**, Jesus, J., Moreira, M., Belmar, O., Vila-Martínez, N., Palau-Nadal, A., & Costa, M.J. (2020). Ecohydraulics of river flow alterations and impacts on freshwater fish. *Limnetica*, 39(1), 213-232. 10.23818/limn.39.14
- Kebede, G., Mushi, D., Linke, R.B., Dereje, O., Lakew, A., **Hayes, D.S.**, Farnleitner, A.H., & Graf, W. (2020). Macroinvertebrate indices versus microbial fecal pollution characteristics for water quality monitoring reveals contrasting results for an Ethiopian river. *Ecological Indicators*, 108, 105733. 10.1016/j.ecolind.2019.105733
- **Hayes, D.S.**, Branco, P., Santos, J. M., & Ferreira, T. (2019). Oxygen Depletion Affects Kinematics and Shoaling Cohesion of Cyprinid Fish. *Water*, 11(4), 642. 10.3390/w11040642
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PRIMARY RESEARCH PAPER

Longitudinal river zonation in the tropics: examples of fish and caddisflies from the endorheic Awash River, Ethiopia

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Abstract Specific concepts of fluvial ecology are well studied in riverine ecosystems of the temperate zone but poorly investigated in the Afrotropical region. Hence, we examined the longitudinal zonation of fish and adult caddisfly (Trichoptera) assemblages in the endorheic Awash River (1,250 km in length), Ethiopia. We expected that species assemblages are structured along environmental gradients, reflecting the pattern of large-scale freshwater ecoregions. We applied multivariate statistical methods to test for differences in spatial species assemblage structure and identified characteristic taxa of the observed biocoenoses by indicator species analyses. Fish and caddisfly assemblages were clustered into highland and lowland communities, following the freshwater ecoregions, but separated by an ecotone with highest biodiversity. Moreover, the caddisfly results suggest separating the heterogeneous highlands into a forested and a deforested zone. Surprisingly, the Awash drainage is rather species-poor: only 11 fish (1 endemic, 2 introduced) and 28 caddisfly species (8 new records for Ethiopia) were recorded from the mainstem and its major tributaries. Nevertheless, specialized species characterize the highland forests,

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whereas the lowlands primarily host geographically widely distributed species. This study showed that a combined approach of fish and caddisflies is a suitable method for assessing regional characteristics of fluvial ecosystems in the tropics.

Keywords Africa · Biodiversity · Biogeography · Species assemblages · Freshwater ecoregions · Indicator species

Introduction

In the early to mid-twentieth century, limnologists intensively described the longitudinal distribution of aquatic communities along rivers (e.g. Thienemann, 1925; Huet, 1949; Harrison & Elsworth, 1958; Illies, 1961a, b; Illies & Botosaneanu, 1963). These studies enhanced the understanding of fluvial ecosystems, and the river continuum concept even became a frequently tested hypothesis in applied fluvial ecology (Vannote et al., 1980). Since then, knowledge on riverine distribution patterns has been used, for example, to establish bioindication systems (e.g. Schmidt-Kloiber & Hering, 2015) and river assessment criteria (e.g. Aarts & Nienhuis, 2003; Welcome et al., 2005).

Nevertheless, taxonomy and taxa differentiation of many biota, as well as their habitat preferences, functional traits, and distribution patterns, are often still poorly understood (Balian et al., 2008). This is especially the case in tropical rivers (e.g. Gibon & Statzner, 1985; Malicky & Chantaramongkol, 1993; Winemiller et al., 2008; Laudee & Prommi, 2011; Skelton & Swartz, 2011; Ochieng et al., 2019). Despite recent advances (Malicky & Chantaramongkol, 1993; Araújo et al., 2009), most conceptual studies on river zonation were conducted in temperate regions of Europe and North America (Hawkes, 1975), which may limit the adoption of established concepts into tropical regions (Araújo et al., 2009). Besides, the lack of knowledge of tropical rivers is a limiting factor in assessing the integrity of these ecosystems. Hence, the scarcity of tropical studies impedes the assessment of diversity and distribution patterns, as well as a comparison to concepts and hypotheses of fluvial ecology of temperate rivers (Ward et al., 2002; Thorp et al., 2006).

At the same time, anthropogenic impacts on aquatic ecosystems are rapidly increasing on a global scale (Darwall et al., 2018; Sabater et al., 2018). The effects of deforestation, intensification of agriculture and other land-use changes, hydropower, river engineering, and water pollution threaten aquatic biodiversity (e.g. Clausen & York, 2008; Fitzgerald et al., 2018; Hayes et al., 2018, 2019; Meulenbroek et al., 2019). These trends can even have visible impacts on large-scale ecosystem processes (Darwall et al., 2018). The serial discontinuity concept was developed to address these pressures (Ward & Stanford, 1983, 1995). It suggests that dams and other anthropogenic stressors can disrupt the underlying natural gradient and cause an upstream or downstream shift of species, as well as divide the river network into discrete zones. However, natural influences such as lakes can also create comparable patterns (Stanford et al., 1988). Hence, it is evident that, in contrast to the assumption of an uninterrupted gradient (Vannote et al., 1980), discontinuities or transition zones constitute a significant component of faunal zonation (Statzner & Higler, 1986). Moreover, certain functional process zones may repeatedly appear along a river and even form comparable patterns within an ecoregion. Beyond the ecoregional level, however, such patterns may be less predictable (Thorp et al., 2006). Therefore, it must be clarified if and to which extent zonation studies conducted in tropical streams and rivers also reveal such discontinuities reported for other systems (Araújo et al., 2009), as well as if the ecoregion regulates community zonation (Thorp et al., 2006).

Fish (Pisces) and caddisflies (Insecta: Trichoptera) are widely used to describe longitudinal changes of community structures (e.g. Harrison & Elsworth, 1958; Lévêque et al., 1983; Stanford et al., 1988). These two organism groups provide the advantage of relatively low sampling effort, the coverage of diverse habitat characteristics in the respective river stretches, and a more profound taxonomic knowledge in comparison to other organism groups. Besides, both groups have a high indicative power regarding environmental conditions. They are therefore implemented within the EU Water Framework Directive (2000/60/EC) as faunistic biological quality elements to assess the ecological status of freshwater systems. Whilst fish mostly respond to mesohabitat characteristics, caddisflies depend more on the availability of microhabitats. Particularly the latter is increasingly used for ecological status assessment of African rivers (e.g. Dickens & Graham, 2002; Masese et al., 2009; Kaaya et al., 2015; Lakew & Moog, 2015; Alemneh et al., 2019). However, ecological studies in riverine ecosystems of the Afrotropical region often rely on a high level of taxonomic resolution, such as family or genus level (e.g. Kaaya et al., 2015; Lakew & Moog, 2015; Alemneh et al., 2019), despite the importance of including species-level information to enhance understanding of distribution patterns (Malicky & Chantaramongkol, 1993). So far, however, species-specific studies throughout the Afrotropical realm mainly focused on taxonomy or a wide biogeographic context (e.g. Roberts, 1975) but rarely covered aquatic communities in entire river systems (Harrison & Elsworth, 1958; Payne et al., 2010).

In this study, we explored the longitudinal zonation of fish and adult caddisfly species in a long (> 1,000 km, sensu Grill et al., 2019) tropical river in East Africa, including its major tributaries. We selected the Awash River in the Main Ethiopian Rift as a case study because of several unique characteristics: the river is an endorheic drainage which flows into the Afar Depression, an arid region; it exhibits a distinctive tectonic setting with a stepwise longitudinal and altitudinal gradient; and the drainage is subdivided into two freshwater ecoregions, the Ethiopian Highlands and the Northern Eastern Rift (Abell et al., 2008). Our overall objective was to describe longitudinal zonation patterns of the fish and caddisfly assemblages in the Awash River drainage by providing species-level information as the most reliable basis for assessment. By using a combined approach of fish, adult caddisflies, and environmental variables, we aimed to answer the following questions: How are fish and caddisfly species distributed longitudinally along a tropic endorheic river and its major tributaries? Can distinct species assemblages be distinguished, and, if yes, which environmental parameters are crucial in steering community composition in the dry season? Besides, we wanted to know if both organism groups show the same distribution and grouping pattern. Moreover, to assist in improved river management, we aimed to detect indicator species characteristic of the observed biocoenoses. Based on theoretical concepts, we expected that species assemblages are structured along environmental gradients and reflect the pattern of large-scale freshwater ecoregions. Accordingly, transition zones between discrete biocoenoses with shared species of both adjacent communities should exist.

Materials and methods

Study area and sampling sites

The Awash River catchment, with an area of 112,696 km^2, is home to approximately 14.9 million people, making it one of the most important and industrialized drainage basins in Ethiopia (Tesfaye & Wolff, 2014; Ministry of Environment, Forest and Climate Change, MEFCC, 2018). The Awash River springs in the Ethiopian Highlands at an altitude of $>$ 3,000 m. It flows for 1,250 km along the northern part of the Main Ethiopian Rift, where it finally drains into saline Lake Abbe at the Ethiopian–Djibouti border at an altitude of around 250 m (Tesfaye & Wolff, 2014; Tadese et al., 2019). Most tributaries originate in the highlands and join the mainstem river from the West (Fig. 1).

In the highlands, the mean annual precipitation amounts to 1,600 mm, and only 160 mm in the northern part of the catchment (Edossa et al., 2010). Similarly, the mean annual air temperature exhibits a spatial variation from 16.7 to 34.5°C (Keraga et al., 2019). The drainage basin consists of two freshwater ecoregions: the Ethiopian Highlands and the Northern Eastern Rift (Abell et al., 2008).

To study the distribution of the fish and caddisfly fauna, we sampled the Awash River from the source region in the Chilimo Forest to the lakes in the Afar Depression, as well as seven of its tributaries, draining the southern slopes of the Ethiopian Highlands into the Main Ethiopian Rift (Fig. 1; Table 1). We selected a total of 24 sampling sites (16 in the Awash River and 8 in the tributaries) based on habitat criteria (natural riparian vegetation, diverse meso- and microhabitat structures), tectonic setting (geomorphological characteristics), minimal direct anthropogenic impact, and accessibility (see Englmaier, 2018). The accessibility of river stretches was restricted by the permission of local authorities, dense riparian vegetation, physiography, water depth, or the presence of abundant crocodiles.

Sites S1–5 (Awash) and T8 (tributary) are located in the Ethiopian Highlands freshwater ecoregion (Abell et al., 2008). These river stretches are usually

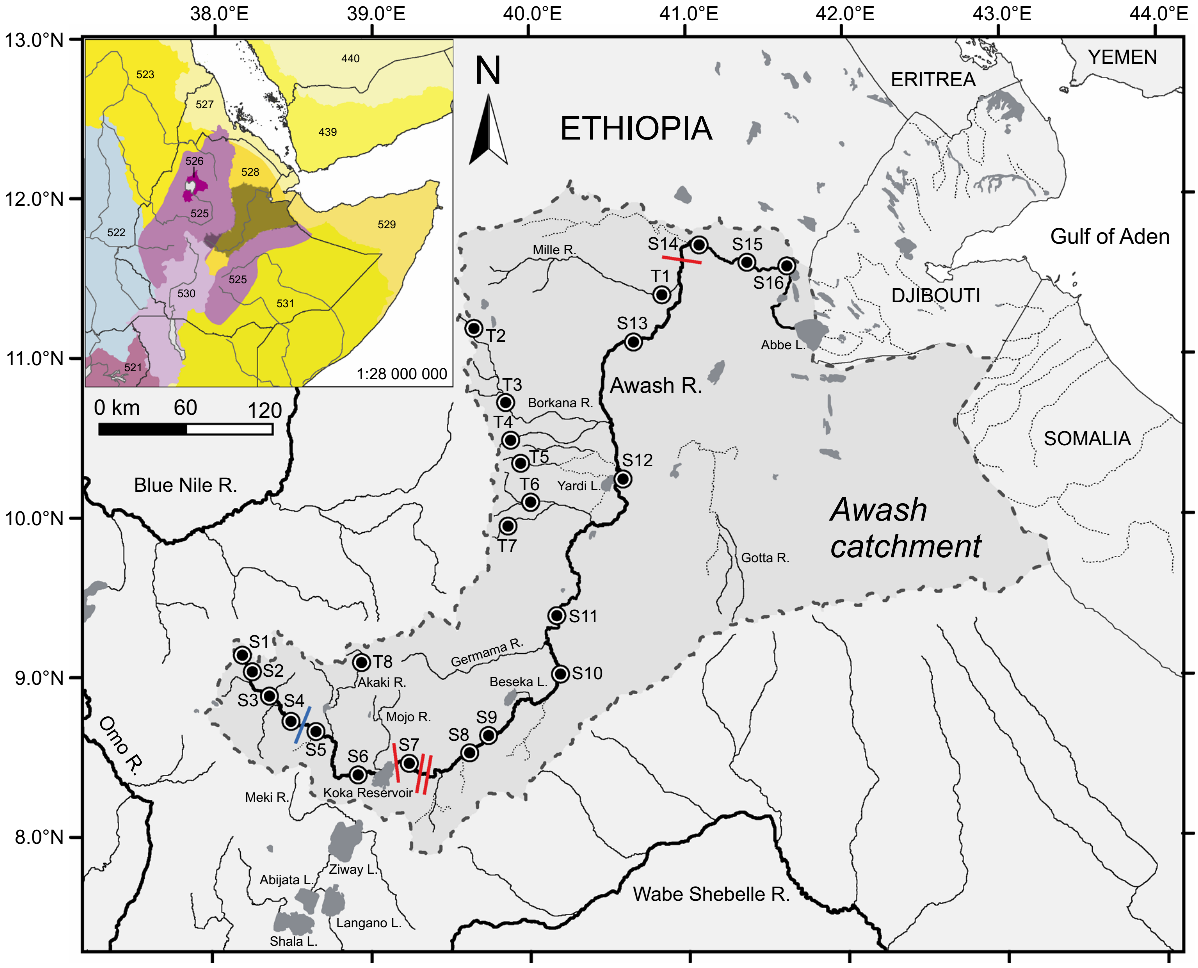

Fig. 1 Map of the study area, location of sampling sites (S1–16, T1–8), dams (red lines), and the cascades at Awash Kunture (blue line). Numbers in the overview map of the Horn of Africa refer to the following freshwater ecoregions (Abell et al., 2008): *439* southwestern Arabian Coast, *440* Arabian Interior, *521* Lake Victoria Basin, *522* Upper Nile, *523* Lower Nile, *525* Ethiopian Highlands, *526* Lake Tana, *527* Western Red Sea Drainages, *528* Northern Eastern Rift, *529* Horn of Africa, *530* Lake Turkana, *531* Shebelle-Juba

characterized by steep gradients, coarse stony substrate (macrolithal to microlithal, see Table 1), and a confined river course (Englmaier, 2018). With the exception of the protected Chilimo Forest (S1, National Forest Priority Area), the region is subject to extensive anthropogenic impacts with intensive agricultural use and overgrazing by livestock, resulting in the loss of natural vegetation (Tafere et al., 2013; Kebede et al., 2020).

The remaining sites are situated in the Northern Eastern Rift freshwater ecoregion (Abell et al., 2008). Here, the Awash River flows through alternating steep and low gradient sections with sequences of confined river stretches and extensive wetlands (Englmaier, 2018). The riverbed consists either of bedrock or sand. In contrast, the tributary sites (T1–7) are characterized by a wide river corridor and coarse substrate (Table 1). In the Northern Eastern Rift, the longitudinal gradient of the Awash River is interrupted by three hydroelectric power plants (Koka Reservoir, Awash II–III) and one irrigation dam (Tendaho Reservoir). At Metahara (downstream of S9), the saline Lake Beseka is artificially connected to the Awash River (Fig. 1).

Field work

We sampled sites during low flow conditions in the dry season over a time frame of 3 years (Table 1). At each

Table 1 Sampling site characteristics

Sampling site characteristics								Water parameters				
Site ID	Name	Survey period[a]	Altitude (m a.s.l.)	Distance from source (km)	Freshwater ecoregion[b]	Geographic coordinates	Slope	pH	DO (%)	DO (mg cm^{-1})	Conductivity (µS cm^{-1})	Water temperature (°C)
Awash River												
S1	Chilimo Forest	A	2,389	5	EH	9° 4′ 1″ N, 38° 8′ 9″ E	4.84	8.4 ± 0.1	95.7 ± 2.2	7.3 ± 0.1	243.9 ± 15.3	15.9 ± 1.8
S2	Gare Arera	A	2,244	14	EH	9° 2′ 23″ N, 38° 6′ 58″ E	1.08	8.8 ± 0.1	126.3 ± 0.8	8.7 ± 0.7	345.3 ± 22.5	20.4 ± 3.6
S3	Awash Belo	A	2,065	73	EH	8° 51′ 39″ N, 38° 23′ 44″ E	0.64	8.7 ± 0.2	107.8 ± 0.2	7.5 ± 0.0	284.7 ± 3.2	20.6 ± 0.6
S4	Awash Kunture	A	2,003	110	EH	8° 42′ 21″ N, 38° 36′ 18″ E	1.24	8.5 ± 0.0	85.7 ± 18.0	6.1 ± 1.1	346.3 ± 31.8	20.3 ± 1.0
S5	Sulula	A	1,916	128	EH	8° 39′ 56″ N, 38° 37′ 58″ E	1.32	8.7 ± 0.1	103.4 ± 6.4	7.3 ± 0.4	360.0 ± 37.0	21.1 ± 0.4
S6	Lafessa	A	1,608	205	NER	8° 23′ 16″ N, 38° 54′ 30″ E	0.20	8.7 ± 0.1	124.1 ± 2.6	8.6 ± 0.1	540.3 ± 75.2	24.2 ± 0.4
S7	Wonji	A	1,552	246	NER	8° 28′ 23″ N, 39° 12′ 43″ E	0.16	8.6 ± 0.2	97.7 ± 1.7	7.3 ± 0.4	286.7 ± 26.8	21.1 ± 2.1
S8	Korkada	A	1,260	311	NER	8° 30′ 2″ N, 39° 33′ 7″ E	0.76	8.7 ± 0.1	103.4 ± 1.2	7.9 ± 0.1	308.7 ± 8.2	21.5 ± 1.1
S9	Nur Sada	B	1,214	328	NER	8° 33′ 9″ N, 39° 38′ 10″ E	0.74	8.8 ± 0.0	109.8 ± 0.2	8.3 ± 0.1	349.7 ± 5.1	21.5 ± 0.1
S10	Yimre	B	797	457	NER	9° 4′ 59″ N, 40° 10′ 3″ E	0.58	8.8 ± 0.0	106.4 ± 0.5	8.1 ± 0.0	941.3 ± 11.2	24.6 ± 0.2
S11	Worer	B	743	507	NER	9° 20′ 6″ N, 40° 10′ 19″ E	0.12	8.5 ± 0.0	65.1 ± 0.6	4.9 ± 0.0	1,206.3 ± 12.4	24.9 ± 0.1
S12	Kada Bada	B	570	738	NER	10° 13′ 53″ N, 40° 34′ 43″ E	0.04	8.7 ± 0.1	75.0 ± 0.1	5.6 ± 0.1	975.3 ± 23.2	26.1 ± 0.5
S13	Adayitu	C	460	926	NER	11° 7′ 48″ N, 40° 46′ 3″ E	0.42	8.2 ± 0.2	100.0 ± 0.5	7.2 ± 0.1	853.5 ± 2.1	30.0 ± 0.3
S14	Dubti	C	378	1,069	NER	11° 41′ 50″ N, 41° 7′ 23″ E	0.18	8.7 ± 0.0	110.8 ± 1.1	7.8 ± 0.3	697.4 ± 5.4	29.2 ± 1.1
S15	Asaita	C	362	1,103	NER	11° 35′ 5″ N, 41° 23′ 47″ E	0.10	8.5 ± 0.1	98.4 ± 0.8	7.0 ± 0.5	692.8 ± 6.2	30.2 ± 0.8
S16	Lake Gamari	C	338	1,159	NER	11° 30′ 50″ N, 41° 38′ 51″ E	0.00	9.5 ± 0.2	101.5 ± 0.7	7.3 ± 0.2	1,710.3 ± 17.4	29.0 ± 1.2
Tributaries												
T1	Lower Mille River	C	482		NER	11° 24′ 50″ N, 40° 45′ 37″ E	0.12	8.7 ± 0.3	104.6 ± 7.3	7.4 ± 0.2	550.4 ± 7.6	31.9 ± 2.2
T2	Upper Borkana River	C	1,902		NER	11° 06′ 10″ N, 39° 41′ 57″ E	2.20	9.8 ± 0.4	114.6 ± 1.4	7.0 ± 0.7	580.2 ± 1.5	28.5 ± 0.1
T3	Middle Borkana River	C	1,417		NER	10° 38′ 09″ N, 39° 55′ 54″ E	0.12	8.7 ± 0.0	94.0 ± 2.4	5.9 ± 0.1	715.1 ± 4.3	31.2 ± 0.8
T4	Jara River	C	1,434		NER	10° 31′ 14″ N, 39° 57′ 13″ E	1.24	9.3 ± 0.5	178.2 ± 1.6	11.9 ± 0.5	410.8 ± 9.4	30.0 ± 0.7
T5	Ataya River	C	1,436		NER	10° 20′ 21″ N, 39° 58′ 16″ E	1.07	9.1 ± 0.1	142.5 ± 0.5	10.1 ± 0.4	510.0 ± 11.8	24.8 ± 0.5
T6	Yewuha River	C	1,138		NER	10° 5′ 50″ N, 39° 58′ 44″ E	1.13	9.4 ± 0.3	183.1 ± 8.6	11.4 ± 1.0	1,509.6 ± 28.4	34.2 ± 0.2
T7	Robit River	C	1,367		NER	9° 57′ 42″ N, 39° 51′ 36″ E	1.20	8.8 ± 0.0	105.1 ± 2.4	7.2 ± 0.2	570.2 ± 5.2	26.2 ± 0.3
T8	Akaki River	C	2,429		EH	9° 5′ 24″ N, 38° 55′ 44″ E	1.43	9.1 ± 0.1	103.4 ± 3.7	7.8 ± 0.4	851.3 ± 34.6	24.2 ± 0.1

Substrate (%)						
Pelal	Psammal	Akal	Microlithal	Mesolithal	Macrolithal	Megalithal
Awash River						
0	5	10	20	25	25	15
5	10	15	20	35	10	5

Table 1 continued

Substrate (%)						
Pelal	Psammal	Akal	Microlithal	Mesolithal	Macrolithal	Megalithal
5	20	25	30	15	5	0
5	15	10	10	5	5	50
0	10	5	5	5	40	35
5	60	15	15	5	0	0
30	40	15	5	5	5	0
0	10	5	0	0	15	70
15	25	15	10	10	10	15
0	15	20	30	20	5	10
50	30	10	5	0	0	5
20	55	20	5	0	0	0
5	35	15	5	10	15	15
15	30	5	5	10	20	15
30	60	5	5	0	0	0
10	70	15	5	0	0	0
Tributaries						
5	20	5	20	20	20	10
0	15	15	15	30	20	5
15	5	5	5	20	30	20
0	10	5	15	20	30	20
0	5	10	20	45	15	5
5	5	10	10	35	20	15
5	15	15	10	30	20	5
30	5	0	0	20	25	20

[a] Surveys conducted during dry season in three periods: A, November and December 2017 (beginning of dry season); B, January 2018 (middle of dry season); C, March 2019 (end of dry season)

[b] Freshwater ecoregions according to Abell et al. (2008), *EH* Ethiopian Highlands, *NER* Northern Eastern Rift

[c] Water parameters given as mean ± SD

ocation, we investigated a representative stretch with a length between 500 and 1,000 m. In order to link fish and caddisfly presence to abiotic variables, we recorded different water parameters. We measured dissolved oxygen concentration (%, mg cm^{-1}), conductivity ($\mu\mathrm{S}\ \mathrm{cm}^{-1}$), pH, and water temperature (°C) with a portable HACH-multimeter (HQ40d) at noon in three consecutive measurement series (three replicates each). The probes were placed in swift current (10 cm sub-surface) at three different points (each 20 m apart) without prior disturbance of the upstream reach. In addition, we classified dominating substrate types: pelal, psammal, akal, microlithal, mesolithal, macrolithal, and megalithal (Moog et al., 1999). We recorded geographic coordinates and altitude of each sampling site with a Garmin VISTA e-trex GPS-system. The distances from the source and slopes of the sampling sites were obtained from Google Earth's digital elevation model (Google Earth Pro v.7.3).

We collected fish from the main river channel, side arms, and the shoreline of lakes. Sampling points included the following mesohabitats: riffles, runs, pools, backwaters, woody debris piles, shoreline vegetation, undercut banks, gravel banks, and inshore areas of lakes. Fishing effort was limited to 100–120 min of active fishing and 2–9 h of passive exposure of gillnets and longlines (where applicable). Wadable stretches were sampled using a back-pack electrofishing unit (Honda GXV 50, direct current 1.5 kW, 300/580 V), seine nets (mesh size 1.5 mm), and frame nets (mesh size 1.5 mm). In deeper waters, fish were collected with gill nets (mesh sizes 80 mm and 60 mm), cast nets (mesh size 15 mm), and longlines. Most fish specimens were identified in the field and released back to the river. A subsample from each locality, including all species and morphotypes, was taken for detailed morphological examination. These specimens were first anesthetized with etheric clove oil diluted in water and later fixed in 6–10% pH neutral formalin or 95% ethanol.

Regarding macroinvertebrates, we chose caddisflies as an indicator group since, aside from their elaborate adult taxonomy, they represent a spectrum of the community that can be attracted and documented by light traps. By targeting adult caddisflies, we aimed at reducing insufficient results due to methodological problems in benthic sampling (e.g. limited accessibility of the entire habitat mosaic of a given site) and due to the low knowledge level on larval taxonomy of African caddisflies in general (e.g. Scott, 1975; Terefe et al., 2018; Ochieng et al., 2019). Only 105 larval stages of 747 Sub-Saharan species of African caddisflies were known by the early 1980s (Scott, 1983). Since then, only twelve additional studies have produced descriptions of larvae for individual species (e.g. Malicky, 1994; Allaya, 2003; Ogbogu, 2008; Ogbogu & Okeze, 2008; Terefe et al., 2018).

We collected adult stages of caddisflies from the riparian zone with sweep nets (at dusk for 30 min, mesh size 1 mm) and light traps. The traps consisted of a fluorescent tube (15 W Blacklight blue tube) attached upon a rectangular pan (40 × 25 × 7 cm), half-filled with water, and containing detergent to reduce the surface tension. The exposure time of light traps was 60 min, starting from sunset. At each site, we used one light trap. We fixed caddisfly samples in 95% ethanol for morphological identification.

No caddisfly samples were obtained from S9, S16 (main channel), T4–6, and T8 (tributaries) due to local restrictions. These sites were therefore excluded from the analyses.

Reference material was stored in the collections of the National Fisheries and Aquatic Life Research Centre, Sebeta, Ethiopia (fish and caddisflies), the Natural History Museum Vienna, Austria (fish), as well as the research collections of H. Malicky (Lunz am See, Austria), W. Graf (University of Natural Resources and Applied Life Sciences, Vienna, Austria) and the Senckenberg Research Institute and Museum of Nature (SMF, Frankfurt am Main, Germany) (caddisflies).

Species identification

All species were identified as morphospecies based on external morphological and meristic traits. The following available literature was used for fish identification: Getahun (2000), Golubtsov et al. (2002), Stiassny & Getahun (2007), Habteselassie et al. (2010), Habteselassie (2012), and Moritz et al. (2019). Caddisfly identification was based on Tobias & Tobias (2008) and the reference collections of the authors, with the assistance of François-Marie Gibon. Direct comparison to museum samples (type specimens, comparative material) included specimens in the collections of the Natural History Museum (BMNH, London, England), the Muséum National D'Histoire Naturelle (MNHN, Paris, France), SMF, and the research collections of H. Malicky and W. Graf.

For polymorphic fish groups (*Garra*, *Labeobarbus*), we followed the group subdivision of Englmaier (2018), which was based on the comparison of 500 bp of the mitochondrial CO1 gene, with the following clarifications: *Garra* sp. was identified as *Garra makiensis* based on the comparison with syntypes at BMNH; *G.* aff. *makiensis* was identified as *Garra aethiopica* based on the comparison with syntypes at MNHN; *Labeobarbus* cf. *intermedius* was identified on species level based on the comparison with the holotype at SMF and the genetic analyses of Beshera & Harris (2014); and *L.* cf. *nedgia* (the sympatric "lipped" form of *L. intermedius*) was provisionally included in *L. intermedius*.

For information on the author and year of description of the identified species, the reader is referred to Tables 2 and 3.

Data analyses

We explored patterns in fish and caddisfly assemblage structure and distribution through a multivariate analysis approach. We analyzed the data based on species presence/absence instead of using relative abundances to avoid a systematic bias due to unequal sampling methods. For each organism group and a combined dataset (fish and caddisflies), we performed two-way cluster analyses [CA, using the Jaccard coefficient and flexible beta linkages ($-$ 0.25)] and non-metric multidimensional scaling (NMDS, using the Jaccard coefficient) to explore and visualize patterns of similarity in the datasets. Both methods were implemented in PC-ORD v.5.33 (McCune & Mefford, 2006). Group circumscription in NMDS was based on individual CA, with subdivisions supported by 37.5% total information used.

Based on the above exploratory tools, we tested the assemblage structure with a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001), with 999 permutations implemented in the R package vegan (Oksanen et al., 2015) in R v.3.4.3 (R Core Team, 2017).

The identification of indicator species is imperative for the classification and assessment of the ecological integrity of a river ecosystem. As species-specific bioindicators are rare or absent in most of the Afrotropical region, we determined characteristic species for the observed biocoenoses of different river sections by conducting an indicator species analysis (Dufrêne & Legendre, 1997) with PC-ORD v.5.33 (McCune & Mefford, 2006). Based on 308 randomizations and 4,999 permutations, only species with an indicator value (IV) of $\geq$ 40 and $P < 0.05$ (Monte Carlo permutation test) were considered significant. The indicator analysis was based on presence/absence data. Group membership of sampling sites was based on the results of the CA. For all tests, we considered $P < 0.05$ as significant.

Results

Faunal characteristics

We recorded a total of 10,111 fish specimens (11 species, 4 families) and 23,757 adult caddisflies (28 species, 7 families). Of the 11 fish species, 9 are native, and 2 introduced (*Cyprinus carpio*, *Coptodon zillii*). Fish species of the family Cyprinidae (three genera, five native species, one introduced species) showed the most dominant occurrence (Table 2). Of these, the genera *Garra* (three species) and *Labeobarbus* (two species) were widely distributed throughout the entire drainage system. At species level, *L. intermedius* was most widespread, with a continuous distribution from S5 to S16 (1,916–338 m) but absent from sampling sites above the cascades at Awash Kunture (upstream of S5). At a few sites (S5, S9–10, and T4), predominantly over coarse substrate, we found the sympatric "lipped" form of *L. intermedius*. *Garra dembeensis* was the only species present in both, the source region in the Chilimo Forest (S1, 2,389 m) and the Lower Awash (S14, 378 m) but showed a highly fragmented distribution restricted to riffles over a stony substrate. *Garra aethiopica* and *Enteromius yardiensis* showed the most restricted distributions. Whilst the former inhabited river stretches > 1,138 m, the latter was found only in lower reaches of the main river channel and aquatic floodplain habitats (S12–16, 570–338 m).

Collections of caddisflies (Table 3) mainly comprised the families Leptoceridae (7 genera, 11 species), Hydropsychidae (3 genera, 8 species), Ecnomidae (1 genus, 3 species), and Hydroptilidae (2 genera, 3 species). A single species was found in each of the remaining families (Dipseudopsidae, Lepidostomatidae, and Polycentropodidae). In total,

Table 2 List of fish species present in the Awash River drainage

Family and species	Authority	Awash River																Tributaries							
		S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	T1	T2	T3	T4	T5	T6	T7	T8
CICHLIDAE																									
(1) *Oreochromis niloticus*	(Linnaeus, 1758)				X		X	X	X		X	X	X	X	X	X	X	X		X		X			
(2) *Coptodon zillii*[a]	(Gervais, 1848)													X		X									
CLARIIDAE																									
(3) *Clarias gariepinus*	(Burchell, 1822)						X	X	X	X	X	X	X	X	X	X	X	X		X			X		
CYPRINDAE																									
(4) *Garra aethiopica*	(Pellegrin, 1927)	X	X	X	X	X	X												X		X	X	X	X	X
(5) *Garra dembeensis*	(Rüppell, 1835)	X	X	X	X	X	X	X	X	X				X	X			X	X	X	X	X	X	X	X
(6) *Garra makiensis*	(Boulenger, 1903)						X	X	X	X	X	X	X	X	X	X	X	X		X	X				
(7) *Labeobarbus beso*	(Rüppell, 1835)		X		X	X			X										X		X	X	X	X	
(8) *Labeobarbus intermedius*	(Rüppell, 1835)					X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	
(9) *Enteromius yardiensis*	Englmaier, Tesfaye & Bogutskaya, 2020												X	X	X		X								
(10) *Cyprinus carpio*[a]	Linnaeus, 1758						X	X	X				X												
POECILIIDAE																									
(11) *Micropanchax antinorii*	(Vinciguerra, 1883)						X	X	X		X	X	X		X	X	X			X					

[a] Introduced species

Table 3 List of caddisfly (Trichoptera) species present in the Awash River drainage

Family and species	Authority	Awash River[a]																Tributaries[a]							
		S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	T1	T2	T3	T4	T5	T6	T7	T8
ECNOMIDAE																									
(1) *Ecnomus nya*[b]	Mosely, 1948				X	X	X	X																	
(2) *Ecnomus similis*	Mosely, 1932				X	X	X	X	X																
(3) *Ecnomus thomasseti*	Mosely, 1932							X				X						X		X					
DIPSEUDOPSIDAE																									
(4) *Dipseudopsis capensis*	Walker, 1852							X					X	X	X	X									
HYDROPSYCHIDAE																									
(5) *Amphipsyche senegalensis*	(Brauer, 1875)							X			X	X	X		X	X				X					
(6) *Cheumatopsyche afra*	(Mosely, 1935)	X	X	X	X	X	X	X	X		X														
(7) *Cheumatopsyche columnata*[b]	Martynov, 1935							X	X		X	X	X	X	X	X			X	X				X	
(8) *Cheumatopsyche falcifera*	(Ulmer, 1930)		X	X		X	X	X	X		X								X	X					
(9) *Cheumatopsyche massa*	Malicky & Graf, 2012	X	X	X		X			X										X	X				X	
(10) *Cheumatopsyche sexfasciata*	(Ulmer, 1904)								X																
(11) *Cheumatopsyche themaz*	Malicky & Graf, 2015	X																							
(12) *Hydropsyche abyssinica*	Kimmins, 1963							X																	
HYDROPTILIDAE																									
(13) *Hydroptila cruciata*[b]	Ulmer, 1912								X						X			X	X	X				X	
(14) *Hydroptila* sp.																								X	
(15) *Orthotrichia thariel*[b]	Malicky & Graf, 2015				X	X	X	X	X		X			X	X			X	X	X				X	
LEPIDOSTOMATIDAE																									
(16) *Lepidostoma scotti*	Ulmer, 1930	X																							

Table 3 continued

Family and species	Authority	Awash River[a]																Tributaries[a]							
		S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	T1	T2	T3	T4	T5	T6	T7	T8
LEPTOCERIDAE																									
(17) *Athripsodes fissus*	(Ulmer, 1912)					X																			
(18) *Oecetis armaros*	Malicky & Graf, 2015	X																							
(19) *Oecetis reticulatella*[b]	Kimmins, 1957						X	X	X		X	X	X		X	X									
(20) *Oecetis tripunctata*	(Fabricius, 1793)						X	X	X																
(21) *Oecetis* sp.																X									
(22) *Setodes squamosus*	Mosely, 1931						X	X																	
(23) *Tagalopsyche aethiopica*	Kimmins, 1963						X	X																	
(24) *Triaenodes serratus*[b]	Ulmer, 1912						X	X	X																
(25) *Trichosetodes tjonnelandi*	Kimmins, 1963						X	X																	
(26) *Trichosetodes truncatus*	Kimmins, 1963										X														
(27) *Parasetodes* sp. (near to *P. respersellus*)											X	X	X	X		X								X	
POLYCENTROPODIDAE																									
(28) *Nyctiophylax armigera*[b]	Jacquemart, 1961						X																		

[a] Sampling sites without collections of adult caddisflies: S9, S16, T4, T5, T6, T8

[b] New species records for Ethiopia

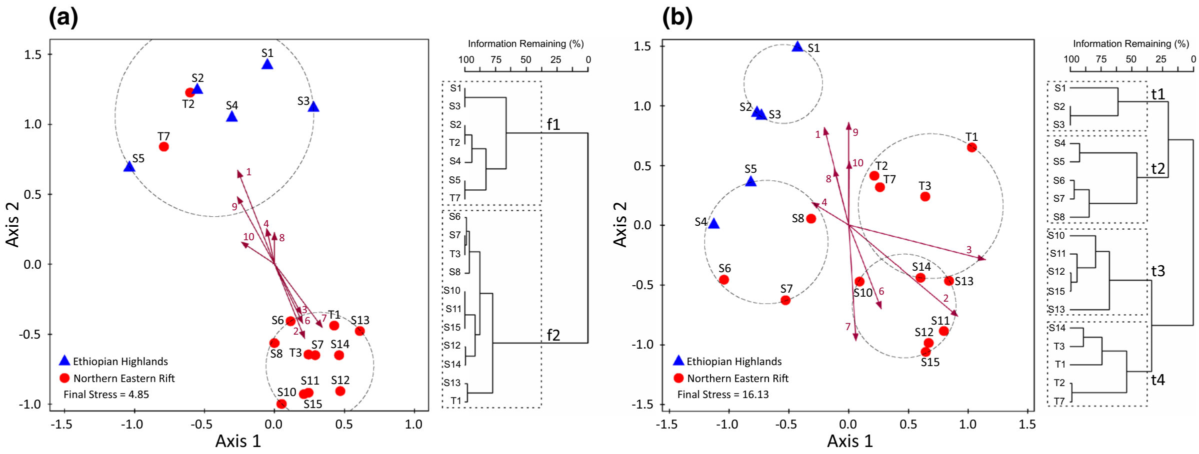

Fig. 2 Non-metric multidimensional scaling (NMDS) dendrogram and two-way cluster analysis (CA) showing zone membership for **a** fish species assemblages and **b** adult caddisfly species assemblages, based on presence/absence data and environmental variables. Group circumscription in NMDS is based on individual CA, with subdivisions supported by 37.5% total information—dashed line. Environmental variables used as following: *1* slope, *2* conductivity, *3* water temperature, *4* dissolved oxygen, *5* pH, *6* %pelal, *7* %psammal, *8* %microlithal, *9* %mesolithal, *10* %macrolithal

27 species were recorded in the main river. We only collected adult caddisflies at four tributary sites; all of the nine species found occurred in the Awash River, except for *Hydroptila* sp., which was detected only in the Robit River (T7). *Lepidostoma scotti*, *Cheumatopsyche themaz*, and *Oecetis armaros* were found exclusively in the Chilimo Forest (S1) and were also absent from the upper tributary reaches (T2–3 and T7, above 1,367 m). *Hydropsyche abyssinica*, *Oecetis tripunctata*, *Setodes squamosus*, *Tagalopsyche aethiopica*, *Triaenodes serratus*, *Trichosetodes tjoennelandi*, and *Nyctiophylax armigera* showed a restricted distribution around the wetland area of the Koka Reservoir (S6–7). *Orthotrichia thariel* was the most widely distributed caddisfly species in the Awash drainage and was found at an altitude range of 2,003–378 m. *Amphipsyche senegalensis* and *Dipseudopsis capensis* were recorded from the main channel of the Awash at altitudes below 1,552 m. They were absent from the tributaries, except for the Borkana River at T3 (1,417 m). The two species of *Hydroptila* (one hitherto undescribed) were most characteristic for some of the tributaries (T1–3, T7, 1,902–482 m) and also found at S8 and S14 in the main channel (Table 3).

Faunal assemblages and zonation

The dataset to assess faunal assemblage and zonation patterns consisted of species presence/absence data for 9 fish species (2 non-native species were excluded) and 28 caddisfly species (Tables 2, 3), 5 environmental parameters (slope, conductivity, water temperature, dissolved oxygen, pH) and dominating substrate types (pelal, psammal, akal, microlithal, mesolithal, macrolithal, megalithal) (Table 1).

Overall, both fish and caddisfly assemblages showed distinct patterns along the longitudinal gradient of the Awash River (Figs. 2, 3; Table 4).

Regarding fish, NMDS and CA revealed a clear separation of the Awash River between sites in the Ethiopian Highlands and the Northern Eastern Rift (Fig. 2a; Table 4). The difference resulted from the absence of *G. aethiopica* downstream of S6 and the upstream limit of *G. makiensis*, *Clarias gariepinus*, and *Micropanchax antinorii* at the same site. The tributaries grouped within similar faunal assemblages of the main river but did not follow the classification of freshwater ecoregions. Whilst *G. aethiopica*, *G. dembeensis*, and *Labeobarbus beso* were dominant in the Upper Borkana River (T2, 1,902 m) and Robit River (T7, 1,367 m), we found typical lowland species in the Lower Mille River (T1, 482 m) and the Middle Borkana River (T3, 1,417 m) (Table 2).

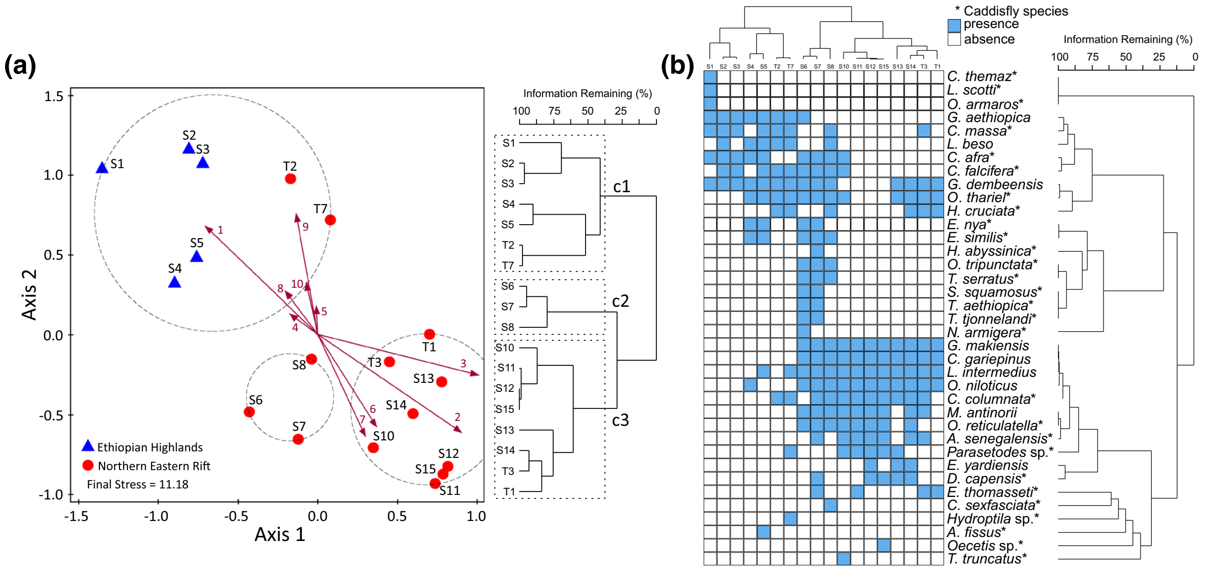

Fig. 3 Non-metric multidimensional scaling (NMDS) dendrogram and two-way cluster analysis showing zone membership for **a** a combined dataset of fish and caddisfly species and **b** two-way cluster analyses showing characteristic assemblages along the river gradient. Group circumscription is based on individual two-way cluster analyses (37.5% information retained—dashed line). Environmental variables used as following: *1* slope, *2* conductivity, *3* water temperature, *4* dissolved oxygen, *5* pH, *6* %pelal, *7* %psammal, *8* %microlithal, *9* %mesolithal, *10* %macrolithal

In contrast to fish, the analyses of adult caddisfly assemblages showed a more detailed assemblage structure with four statistically distinct groups (Fig. 2b; Table 4). In detail, the first three sites (S1–3, > 2,065 m) were distinct, with *Cheumatopsyche afra* and *Cheumatopsyche massa* common to all locations, but *L. scotti*, *C. themaz*, and *O. armaros* restricted to the Chilimo Forest (S1). Sites S4 and S5 of the Ethiopian Highlands freshwater ecoregion grouped with S6–8 of the Northern Eastern Rift region. *Ecnomus nya*, *Ecnomus similis*, *T. serratus*, and *O. tripunctata* were most characteristic for this river stretch. The assemblage structure further downstream was dominated by *D. capensis*, *A. senegalensis*, and *Parasetodes* sp. The fourth group, consisting of the tributaries (T1–3, T7), was separated from the main river (except for S14) by *Hydroptila cruciata* and *Hydroptila* sp.

For the combined dataset of fish and caddisflies, the NMDS and CA revealed three distinct zones (Fig. 3), which were statistically significant (Table 4). Sampling sites S1–5 from the Ethiopian Highlands, including T2 and T7 from the Northern Eastern Rift, form a separate but heterogeneous cluster. The Upper Awash, with a length of approximately 205 km, was clearly distinguished from species assemblages further downstream by *G. aethiopica*, *L. beso*, *C. massa*, *C. afra*, *C. themaz*, *L. scotti*, and *O. armaros*. Altitude ranged from 2,389 to 1,608 m, dissolved oxygen was close to saturation (mean 103.8%), water temperature ranged from 15.9 to 21.1°C, and conductivity was between 234.9 and 360.0 µS cm^{-1}. A sharp increase in water temperature (15.9–20.4°C) and conductivity (243.9–345.3 µS cm^{-1}) was recorded between S1 and S2, which were 9 km apart (Table 1). All sampling sites in the Upper Awash zone were characterized by a coarse substrate (microlithal to megalithal). Only at site S3 (Awash Belo), the riverbed consisted of a high percentage of psammal (20%) and akal (25%).

Sites S6–8, located in the Northern Eastern Rift, form a transition zone (approximately 123 km in length) from the mountains to the lowlands. Here, we recorded the highest species richness (nine fish and 20 caddisfly species) (Fig. 3b; Tables 2, 3). The distribution of some caddisfly species (*Cheumatopsyche sexfasciata*, *H. abyssinica*, *O. tripunctata*, *S. squamosus*, *T. aethiopica*, *T. serratus*, *Trichosetodes tjonnelandi*, and *N. armigera*) was even restricted to this stretch, ranging from an altitude of 1,608 to 1,214 m. Surprisingly, no fish species was particularly

Table 4 PERMANOVA results based on Jaccard dissimilarity using presence/absence data for species assemblage structures using three datasets (fish, caddisflies, and both groups combined)

Factor	df	Sum Sq	R^2	F	P
Fish					
Zones	1	2.738	0.793	61.384	0.001
Residuals	16	0.714	0.207		
Caddisflies					
Zones	3	3.094	0.571	6.209	0.001
Residuals	14	2.325	0.429		
Combined					
Zones	2	2.470	0.550	9.154	0.001
Residuals	15	2.024	0.450		

Degrees of freedom (df), sum of squares (Sum Sq), (R^2), F-ratios, and P-values for the river zones (zones referring to those in Figs. 2, 3a)

characteristic for this zone. The fish fauna included typical lowland elements such as *G. makiensis*, *C. gariepinus*, and *M. antinorii*. *Garra aethiopica* (typical for the Upper Awash) was still present at S6 but disappeared further downstream. In this transition zone, dissolved oxygen was close to saturation (mean 108.4%, max. 124.1% at S6). Water temperature ranged from 21.1°C (S7) to 24.2°C (S6), and conductivity was between 286.7 µS cm^{-1} (S7) and 540.3 µS cm^{-1} (S6). Upstream of Koka Reservoir, both water temperature and conductivity showed a sharp increase (21.1–24.2°C and 360.0–540.3 µS cm^{-1}, respectively) followed by a notable drop below the dam (24.2–21.1°C and 540.3–286.7 µS cm^{-1}, respectively) (Table 1). The dominant substrate ranged from psammal (S6–7) to megalithal (S8).

At altitudes below 1,214 m, the Lower Awash (approximately 922 km in length) was dominated by widely distributed fish species such as *G. makiensis*, *C. gariepinus*, *Oreochromis niloticus*, *M. antinorii*, *L. intermedius*, and *E. yardiensis* (S12–16). Characteristic caddisfly species in this zone were *D. capensis*, *A. senegalensis*, *Cheumatopsyche columnata*, and *Parasetodes* sp. In comparison to the two other zones, dissolved oxygen concentration in the Lower Awash was lower on average (mean 92.6%, range 65.1–110.8%), whereas water temperature was consistently high (> 24°C) with a mean temperature of 27.5°C. Similarly, conductivity exhibited the highest values in the Lower Awash, ranging from 692.8 to 1,206.3 µS cm^{-1} (mean 894.4 µS cm^{-1}). Between sites S9 and S11, we recorded a sharp increase in conductivity (349.7–1,206.3 µS cm^{-1}), followed by a decline to 692.8 µS cm^{-1} (S15). The highest conductivity measurement in the Awash drainage was recorded in Lake Gamari (1,710.3 µS cm^{-1}). In the Lower Awash, pelal, psammal and microlithal were the dominant substrate types.

Faunal assemblages in the main river were not always comparable to those found in tributaries. The latter often showed limited species numbers, especially for caddisflies (Fig. 2b). Besides, the tributaries showed a different substrate composition and a substantially higher water temperature with up to 34.2°C at T6 (Yewuha River, 1,138 m) (Table 1).

Similar to the analyses of the fish dataset, the combined CA grouped the tributary stretches within the faunal zones of the main river (Fig. 3). Tributaries T2 (Upper Borkana River, 1,902 m) and T7 (Robit River, 1,367 m) fall within the Upper Awash, and T1 (Lower Mille River, 482 m) and T3 (Middle Borkana River, 1,417 m) cluster with the Lower Awash.

Indicator species

We found that, in the Awash River, distinct species reflect the biocoenotic separation reported above (Figs. 2, 3; Tables 2, 3).

The individual analysis for fish species allowed us to distinguish two groups along the boundaries of the freshwater ecoregions. *Garra aethiopica* and *L. beso* were most characteristic for mainstem sites in the Ethiopian Highlands (S1–5) and two tributaries (T2, T7). In the Northern Eastern Rift, *G. makiensis*, *L.*

Table 5 Indicator species analysis results for fish (f), caddisflies (t) and the combined (c) dataset (fish and caddisflies): Monte Carlo permutation test of significance of observed maximum indicator value (IV) for each species, based on 308 randomisations and 4,999 permutations (see Dufrêne & Legendre, 1997)

Species	Zone[a]	IV	Mean	SD	*P*	Species	Zone[a]	IV	Mean	SD	*P*
Fish						Combined					
Garra aethiopica	f1	91.7	33.4	10.09	0.0010*	*Garra aethiopica*	c1	75.0	32.0	10.65	0.0012*
Garra dembeensis	f1	61.1	48.2	6.22	0.1126	*Garra dembeensis*	c1	40.0	38.4	4.64	0.5903
Garra makiensis	f2	100	41.6	8.56	0.0002*	*Garra makiensis*	c2	50.0	35.4	9.78	0.0230*
Labeobarbus beso	f1	63.4	28.2	9.3	0.0132*	*Labeobarbus beso*	c1	48.7	28.1	12.38	0.0568
Labeobarbus intermedius	f2	77.8	45.5	8.41	0.0024*	*Labeobarbus intermedius*	c2	43.8	37.7	7.10	0.0910
Enteromius yardiensis	f2	27.3	18.4	8.82	0.2563	*Enteromius yardiensis*	c3	37.5	22.7	11.04	0.1694
Micropanchax antinorii	f2	81.8	36.8	8.91	0.0024*	*Micropanchax antinorii*	c2	57.1	33.0	10.26	0.0150*
Clarias gariepinus	f2	100	41.6	8.56	0.0002*	*Clarias gariepinus*	c2	50.0	35.4	9.78	0.0230*
Oreochromis niloticus	f2	87.5	44.1	8.02	0.0008*	*Oreochromis niloticus*	c2	46.7	36.6	8.63	0.0452*
Caddisflies											
Ecnomus nya	t2	80.0	23.9	11.96	0.0072*	*Ecnomus nya*	c2	46.7	23.8	12.70	0.1424
Ecnomus similis	t2	100.0	24.9	12.55	0.0004*	*Ecnomus similis*	c2	77.8	25.9	12.94	0.0136*
Ecnomus thomasseti	t4	20.0	24.1	12.31	0.5765	*Ecnomus thomasseti*	c3	19.9	23.9	12.55	0.4493
Dipseudopsis capensis	t3	36.0	25.2	12.52	0.2000	*Dipseudopsis capensis*	c3	30.0	26.1	13.17	0.3065
Amphipsyche senegalensis	t3	45.7	27.7	10.68	0.0662	*Amphipsyche senegalensis*	c3	51.9	30.2	11.37	0.0656
Cheumatopsyche afra	t1	45.5	29.1	9.83	0.1476	*Cheumatopsyche afra*	c2	54.4	33.2	10.49	0.1248
Cheumatopsyche columnata	t3	45.5	30.6	7.59	0.0184*	*Cheumatopsyche columnata*	c3	41.9	35.1	9.72	0.3185
Cheumatopsyche falcifera	t2	31.0	29	9.86	0.5181	*Cheumatopsyche falcifera*	c2	54.4	33.1	10.45	0.1218
Cheumatopsyche massa	t1	50.0	28.8	10.02	0.0922	*Cheumatopsyche massa*	c1	55.9	32.1	10.71	0.0778
Cheumatopsyche sexfasciata	t2	20.0	22.3	5.07	1.0000	*Cheumatopsyche sexfasciata*	c2	33.3	16.7	7.52	0.1686
Cheumatopsyche themaz	t1	33.3	22.2	4.96	0.1656	*Cheumatopsyche themaz*	c1	14.3	16.6	7.46	0.5567
Hydropsyche abyssinica	t2	20.0	22.1	4.89	1.0000	*Hydropsyche abyssinica*	c2	33.3	16.7	7.56	0.1702
Hydroptila cruciata	t4	83.3	26.4	12.07	0.0020*	*Hydroptila cruciata*	c3	14.1	28.1	12.48	1.0000
Hydroptila sp.	4	20.0	22.2	4.92	1.0000	*Hydroptila* sp.	c1	14.3	16.7	7.52	0.5529
Orthotrichia thariel	t2	41.7	30.8	6.48	0.0170*	*Orthotrichia thariel*	c2	45.5	36.3	8.62	0.2118
Lepidostoma scotti	t1	33.3	22.2	4.96	0.1656	*Lepidostoma scotti*	c1	14.3	16.6	7.46	0.5567
Athripsodes fissus	t2	20.0	22.2	4.97	1.0000	*Athripsodes fissus*	c1	14.3	16.7	7.51	0.5533
Oecetis armaros	t1	33.3	22.2	4.96	0.1656	*Oecetis armaros*	c1	14.3	16.6	7.46	0.5567
Oecetis reticulatella	t3	40.0	28.4	9.77	0.1522	*Oecetis reticulatella*	c2	61.5	31.9	10.60	0.0088*
Oecetis tripunctata	t2	60.0	22.8	13.02	0.0434*	*Oecetis tripunctata*	c2	100.0	22.7	11.01	0.0016*
Oecetis sp.	t3	20.0	22.3	5.04	1.0000	*Oecetis* sp.	c3	12.5	16.7	7.49	1.0000
Setodes squamosus	t2	40.0	20.2	13.23	0.2216	*Setodes squamosus*	c2	66.7	19.5	10.83	0.0196*

Table 5 continued

Species	Zone[a]	IV	Mean	SD	*P*	Species	Zone[a]	IV	Mean	SD	*P*
Tagalopsyche aethiopica	t2	40.0	20.2	13.23	0.2216	*Tagalopsyche aethiopica*	c2	66.7	19.5	10.83	0.0196*
Triaenodes serratus	t2	60.0	22.8	13.02	0.0434*	*Triaenodes serratus*	c2	100.0	22.7	11.01	0.0016*
Trichosetodes tjonnelandi	t2	40.0	20.2	13.23	0.2216	*Trichosetodes tjonnelandi*	c2	66.7	19.5	10.83	0.0196*
Trichosetodes truncatus	t3	20.0	22.3	5.05	1.0000	*Trichosetodes truncatus*	c3	12.5	16.5	7.37	1.0000
Parasetodes sp.	t3	83.3	26.5	11.97	0.0022*	*Parasetodes* sp.	c3	50.9	28.0	12.60	0.0550
Nyctiophylax armigera	t2	20.0	22.2	4.94	1.0000	*Nyctiophylax armigera*	c2	33.3	16.6	7.42	0.1620

*Significant at $P < 0.05$ level

[a] Zones refer to those in Figs. 2, 3a

intermedius, *M. antinorii*, *C. gariepinus*, and *O. niloticus* were indicative for river stretches downstream of S6 and in tributaries T1 and T3 (Table 5).

Regarding caddisflies, we distinguished four different zones. *Lepidostoma scotti*, *C. themaz*, and *O. armaros* were only recorded from the Chilimo Forest (2,389 m) but were not found indicative for the entire river stretch above 2,063 m (Table 5). Here, *C. massa* was most characteristic. Sites S4–8 were distinguished by *E. similis* and *E. nya*, but also by several species of the family Leptoceridae (Table 5). In the lowlands, *Parasetodes* sp., *C. columnata*, and *A. senegalensis* were most indicative. In contrast to the main channel, tributaries (T1–3, T7) were best characterized by *H. cruciata*.

For the combined matrix of fish and caddisflies, our analyses revealed three zones with the following indicator species (Table 5): *G. aethiopica*, *L. beso*, and *C. massa* were most indicative for the Upper Awash (mainstem) and tributaries T2 and T7, supporting the individual analyses presented above. The transition zone was best characterized by *G. makiensis*, *L. intermedius*, *M. antinorii*, *C. gariepinus*, *O. niloticus*, *E. similis*, *Oecetis reticulatella*, *O. tripunctata*, *S. squamosus*, *T. aethiopica*, *T. serratus*, and *T. tjonnelandi*. Based on the CA, all of the above fish species were found characteristic for the lowland fauna (Fig. 3b). Their presence at an altitude of 1,608 m (S6) represents their upper distribution limit in the Awash River. For the Lower Awash River, the indicator analysis found *Parasetodes* sp. and *A. senegalensis* most characteristic, supporting the individual analysis for caddisflies.

Discussion

The objective of our study was to explore biotic zonation patterns along the endorheic Awash River and its major tributaries in the dry season. By providing species-level information and using a combined approach of fish, adult caddisflies and environmental variables, we were able to assess the species' longitudinal distribution patterns in this tropical river, describe distinct fish and caddisfly assemblages, and detect indicator species relevant for river management.

Biotic zonation patterns and indicator species of the Awash River

Our results show that fish and caddisfly assemblages in the Awash River drainage split into two and four separate groups, respectively. The combined analyses of both organism groups clearly distinguished the species assemblages into highland and rift valley communities, which are separated by an ecotone (transition zone) with highest diversity between 1,200 and 1,600 m. These results would lead us to propose three distinct biocoenotic zones for the Awash River. However, our findings also indicate that the Upper Awash should be further subdivided into two sections, totalling four discrete zones of the mainstem river: the source region (1a), the Upper Awash (1b), a transition zone (2), and the Lower Awash (3) (Fig. 4).

Zone 1a

The Awash River's source region, located in the Chilimo Forest (> 2,389 m), is characterized by caddisflies as fish species (*G. aethiopica*, *G. dembeensis*) were only present up to a small cascade restricting further upstream distribution (Englmaier, 2018). Three of the present caddisfly species (*L. scotti*, *C. themaz*, *O. armaros*), which so far are only known from Ethiopia (Malicky & Graf, 2015; Terefe et al., 2018), exclusively occur at S1 in Chilimo Forest. The headwater community consists of shredders (Lepidostoma) and predators (Leptoceridae: *Oecetis*). As these species inhabit clear water sections over coarse substrate and with lower (< 16°C) water temperatures (Table 1), they disappear in deforested areas downstream with higher proportions of fine sediment (due to erosion), less input of coarse particulate organic matter, and an increase in water temperature.

Zone 1b

The Upper Awash River from S2 to S5 (2,389–1,200 m) is more or less homogeneous regarding fish; *G. aethiopica* and *L. beso* are characteristic species for this reach. Whilst the former is omnivorous, typically scraping off food particles from various substrates (Stiassny & Getahun, 2007), the latter is a specialized scraping feeder associated with stony substrate (Levin, 2012); both are adapted to high flow velocities and cooler water temperatures (Golubtsov et al., 2002). The cascades at Awash Kunture constitute a marked interruption in the river, affecting the upstream distribution of several other fish species. The caddisflies of this section are widely distributed throughout the highlands and already show a transition towards the rift valley communities; *C. massa* and *C. afra* are representatives for the Upper Awash zone. Except for the Chilimo Forest, the rest of the Ethiopian Highlands are under intense anthropogenic pressure due to deforestation and high livestock density (e.g. Kebede et al., 2020). Hence, although we propose that the unique caddisfly fauna in the Chilimo Forest represents a distinct section (zone 1a), the separation of the Upper Awash might also be due to the extensive loss of natural highland forests (Nyssen et al., 2015; Kebede et al., 2020). Overall, slope and mesolithal substrate were the most decisive environmental variables to separate the Upper Awash River from the lower zones.

Zone 2

The section between S6 and S8 (S9) constitutes a transition zone between the upper and lower reaches of the Awash River. Similar to conclusions of other studies (e.g. Statzner & Higler, 1985; Thorp et al., 2006), our data showed that this ecotone offers a high habitat variability (see Table 1), which is influenced by Koka Reservoir and the natural lakes in the central part of the Main Ethiopian Rift, and exhibits the highest species numbers, particularly of caddisflies. Hence, regarding indicator species, the transition zone is predominantly characterized by caddisflies such as *E. similis*, *O. tripunctata*, and *T. serratus*, which were three of the seven indicator caddisfly species for the combined dataset. The fish species present in this zone are all members of the lowland fauna. The significant indicator values for fish in the combined dataset appear overestimated as *G. makiensis*, *C. gariepinus*, and *M. antinorii* have their upstream limit in this zone. Interestingly, the distribution boundary of these fish species is consistent with the upstream limit of crocodiles (Cott & Pooley, 1972; Siege & Koch, 2017), which can be seen as equally indicative for zones 2–3.

Zone 3

In the Lower Awash River (1,214–338 m), species diversity is lower than in the transition zone. Here, in the northern part of the Main Ethiopian Rift, water temperatures are consistently higher than upstream, and conductivity measurements showed a large range. The increase in conductivity between S9 and S10 probably results from the influence of the saline Lake Beseka (conductivity > 6,000 μS cm^{-1}; Goerner et al., 2009), which flows into the Awash River through an artificial channel. The environmental parameters most decisive for the community composition of zone 3 were conductivity, water temperature, and fine-grained sediment (psammal and pelal). The species assemblages typical to the rift valley start to occur downstream of S8 (S9 for fish assemblages) but become marked after the gorge section at S10. In the Lower Awash River, *G. makiensis* and *C. gariepinus*, as well as *A. senegalensis* and *C. columnata*, are most widespread. *Garra makiensis* is predominantly rheophilic but capable of inhabiting limnetic habitats (Golubtsov et al., 2002). All fish species of the Lower Awash seem to tolerate high water temperatures with *G. dembeensis* showing the greatest amplitude (15.9–34.2°C) (Tables 1, 2).

The low number of indicator species for such a comparably long zone is surprising. The geographically wide-spread community in the Lower Awash River presumably results from a combination of different factors, such as geotectonics, water temperature, and alternating dry periods in the history of the Main Ethiopian Rift (Bonnefille et al., 2004; Sagri et al., 2008; Foerster et al., 2014; Benvenuti & Carnicelli, 2015). Regarding the latter, it is likely that parts of the Awash River fell dry in the past, thereby causing species to become locally extinct. After re-wetting, most-probably widely distributed species with high dispersal capacities managed to recolonize the Lower Awash River. Furthermore, it must be noted that the river morphology of zone 3, which is considerably shaped by the geotectonic history of the Main Ethiopian Rift (Bonini et al., 2005; Abbate et al. 2015), is characterized by alternating sections of confined river stretches (including cataracts) and alluvial floodplains as well as low and steep gradients (Fig. 4). As such discontinuities within a similar zone may be of considerable ecological importance (Statzner & Higler, 1986), the densification of sampling sites (e.g. including floodplain water bodies) might expose the presence of smaller patches "within a hierarchy of larger spatiotemporal patches" (Thorp et al., 2006), possibly revealing a fauna distinct from the general pattern of zone 3, which might go hand in hand with a repetition of smaller functional process zones along the river. However, according to the serial

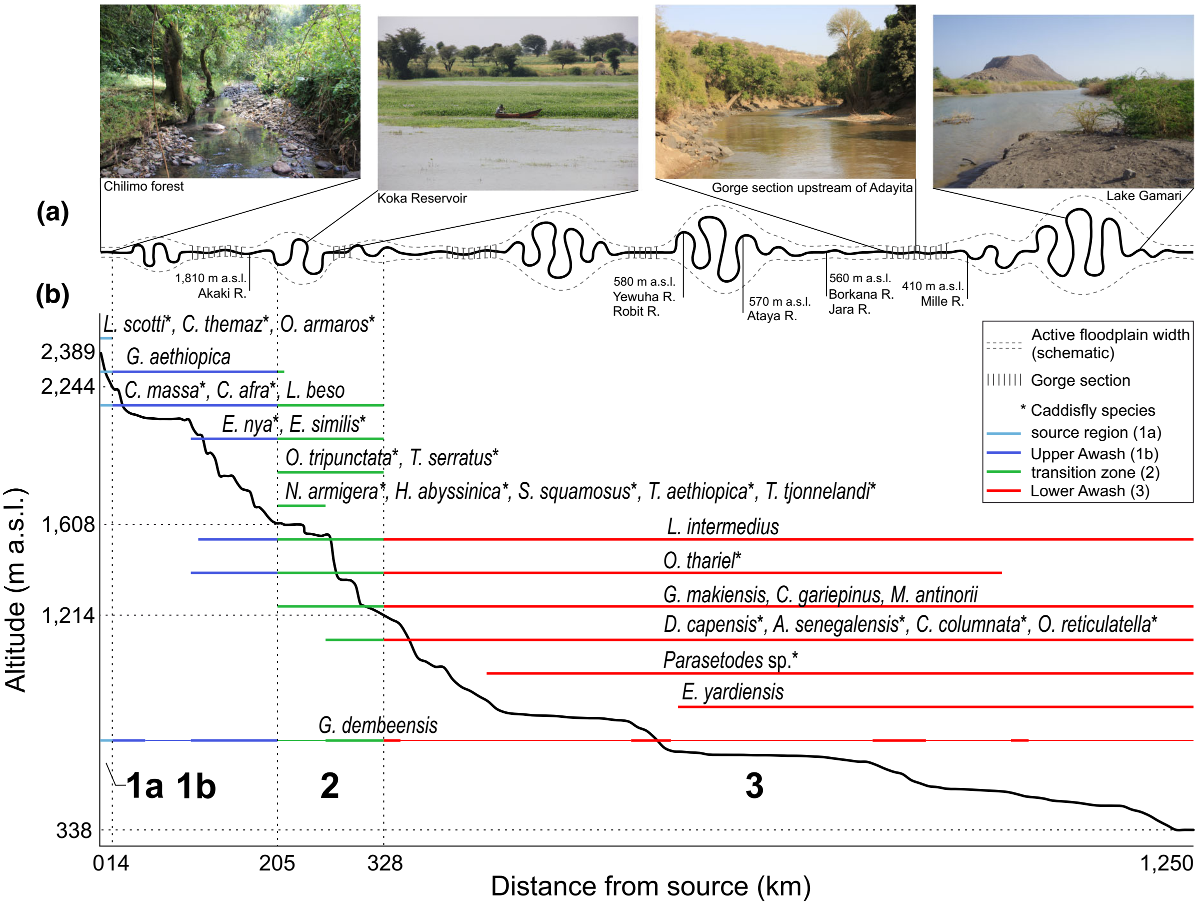

Fig. 4 Schematic representation of the longitudinal zonation of the Awash River, showing typical landscape forms, lateral (**a**) and longitudinal (**b**) river gradient, and characteristic fish and caddisfly species

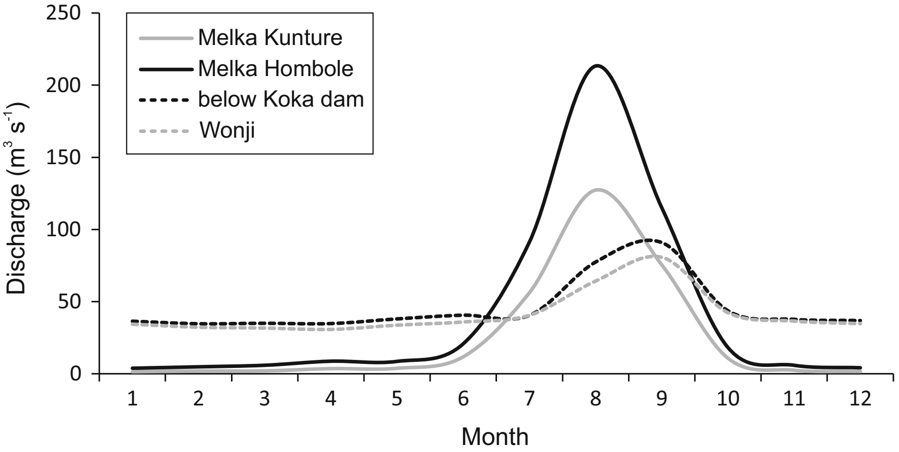

Fig. 5 Mean monthly flow magnitude measured at four gauging stations on the Awash River—in downstream direction: Melka Kunture (8° 42′ 15″ N, 38° 36′ 22″ E), Melka Hombole (8° 22′ 45″ N, 38° 46′ 46″ E; upstream of Koka Reservoir), below Koka Dam (8° 28′ 6″ N, 39° 9′ 33″ E), Wonji (8° 28′ 24″ N, 39° 12′ 48″E). *Data source* Ethiopian Ministry of Water, Irrigation and Electricity (2019)

discontinuity concept (Ward & Stanford, 1983, 1995), the influence of Koka Reservoir and the other impoundments (see Fig. 1) may be another reason for the rather long and homogeneous Lower Awash River section. Not only do these dam structures disrupt the longitudinal river gradient and constitute a recent upstream dispersal barrier, but they also homogenize the flow regime downstream of the reservoir (Fig. 5). These flow regime modifications may have caused changes within the community in the Lower Awash River (e.g. Junk et al., 1989; Winemiller, 2004; Hayes et al., 2018). Besides, the reservoirs may cause, for example, through plankton production (Degefu et al., 2011), considerable alterations in the food resources downstream. In the reservoir itself, the accumulation of fine sediments (Kropáček et al., 2016) may have implications for the aquatic fauna (Jones et al., 2007).

Tributaries

The tributaries of the Northern Eastern Rift (T1–3, T7) exhibit a pattern distinctive of that from the mainstem river zones. Their substrate composition is similar to that of the Upper Awash, dominated by coarse gravel to boulders. However, their riverbeds are much wider and the water temperatures are higher compared to the mainstem Awash River at similar altitudes (Table 1). In the Middle Borkana River (T3) and the Yewuha River (T6) water temperatures exceeded 30°C, which is possibly linked to the presence of hot thermal springs. Caddisfly assemblages tend to be similar to the lowland communities, despite an impressive altitude range of the tributaries (482–1,902 m). Also, fish assemblages show a similar pattern to the Lower Awash River, with the exception of T2 and T7, which are associated to the Ethiopian Highlands. The indicator species of these streams, *H. cruciata*, is apparently associated with coarse substrate and high flow velocities, and is widely distributed throughout Africa (Botosaneanu, 2002).

Several authors have contributed observations from tropical rivers for fish (e.g. Ibanez et al., 2007; Araújo et al., 2009; Payne et al., 2010; Fitzgerald et al., 2018) and caddisflies (e.g. Malicky & Chantaramongkol, 1993; Chaibu, 2000; de Moor et al., 2000; de Moor, 2011), but no common classification of stream sections into general zonation concepts has yet been achieved (Aarts & Nienhuis, 2003). This might be due to the fact that the predictability of zonation patterns becomes more difficult above the ecoregional level (Thorp et al., 2006). In the Awash River, we found that species assemblages in the mainstem were mostly distinct between the two ecoregions but were the same within a single ecoregion (with the exception of the transition zone for the caddisfly dataset). Depending on the dataset used for the analyses, the tributaries—located at the border of both ecoregions—were either grouped with the lowland sites (combined and fish datasets) or showed a separate group (caddisfly dataset). Regarding the first, however, the assemblage of the Upper Borkana River (T2) and Robit River (T7) was clustered with the Upper Awash River in the highlands. Nevertheless, it cannot be completely elucidated if the grouping of sites resulted primarily from their location in the ecoregion or along a steep altitudinal gradient (however, one is not completely independent of the other anyways). This raises the question if precise definitions of zones, such as rhithron and potamon (Illies & Botosaneanu, 1963) are needed and applicable on a global scale (without introducing several specific exceptions). Clearly defined river sections might be applied individually depending on the local characteristics of the respective river. In general, the longitudinal river zonation of biota depends on type, range and interaction of various environmental and/or biotic gradients (e.g. Hawkes, 1975; Malicky & Chantaramongkol, 1993; Araújo et al., 2009). The stronger the gradient, the stronger the demarcation between biocoenoses will be, resulting in distinct zones or patches with more or less sharp transitions. Independent from geographic location and faunal composition, more or less well separated species assemblages will be visible.

Overall, river zonation and measurements of associated indicator species can provide vital information to inform integrated river basin management (Lorenz et al., 2001). In this regard, knowledge on fish and caddisfly diversity, for example, can be used for ecological status assessments (e.g. Lakew & Moog, 2015; Alemneh et al., 2019).

Insights into species diversity

The present findings are one of the first studies to investigate the longitudinal zonation patterns of fish and caddisfly assemblages in the Afrotropical realm on the species level. The following section, therefore, discusses the findings from a biodiversity perspective.

Fish fauna

In comparison to the adjacent Omo-Turkana (79 species), Blue Nile (64 species), White Nile (106 species) and Wabe Shebelle (31 species) drainage systems (Golubtsov & Mina, 2003), the fish diversity in the Awash was exceptionally low (11 species) (see Golubtsov et al., 2002). Furthermore, our results show that the fish fauna is dominated by cyprinids of the genera *Labeobarbus*, *Garra* and *Enteromius*. Except for the widespread *O. niloticus* (Nilo-Sudan), *C. gariepinus* (Pan-African), *G. dembeensis* (Nilo-Sudan), and *L. intermedius* (Nilo-Sudan), the fish species are endemic to Ethiopia (Golubtsov et al., 2002; de Graaf et al., 2007; Stiassny & Getahun, 2007; Englmaier et al., 2020). Indeed, it has been recognized that the northern and central parts of the Main Ethiopian Rift exhibit a fish species composition distinct from the Nilo-Sudan ichthyofaunal province, with affinities to the freshwater ecoregions of the Ethiopian Highlands and the Western Red Sea Drainages (Roberts, 1975; Paugy, 2010). Characteristic families for the Nilo-Sudan ichthyofauna (e.g. Characidae, Mochokidae, Mormyridae, Tetraodontidae) are absent from the Awash; others (e.g. Bagridae, Claroteidae) are extinct (Stewart & Murray, 2017). Two species reported earlier from the Awash, *E. akakianus* and *Aphanius dispar* (see Golubtsov et al., 2002), were not found in the present surveys. Their current status needs clarification.

The highland fauna with *G. aethiopica* (morphologically close to *G. quadrimaculata*), *G. dembeensis*, and *L. beso* is similar to that of the Upper Blue Nile (Golubtsov et al., 2002). The genera *Garra* and *Labeobarbus* are common in the headwaters of all Ethiopian drainages (Habteselassie, 2012). Conversely, however, headwater groups found elsewhere in tropical or southern Africa including *Afronemacheilus*, *Amphilius*, *Chiloglanis*, *Enteromius*, *Kneria* or *Parakneria* (Balon & Stewart, 1983; Skelton, 2001; Bills et al., 2012; Prokofiev & Golubtsov, 2013; Schmidt, 2014) are absent from the Upper Awash.

The Lower Awash is inhabited by widely distributed generalists like *O. niloticus*, *C. gariepinus*, and *L. intermedius*. Others such as *E. yardiensis*, *M. antinorii*, and *G. makiensis* are highly specialized and show affinities to the Nile drainage (Englmaier et al., 2020), the central East African rift (Golubtsov et al., 2002) and the Arabian Peninsula (Englmaier et al., unpublished data) respectively.

Caddisfly fauna

Only 92 species (9 families) of caddisflies are known so far from Ethiopia (Tobias & Tobias, 2008; Terefe et al., 2018; Morse, 2020). Given the higher diversity in South Africa (253 species; de Moor & Day, 2013) and Madagascar (500 species; Benstead et al., 2003), the Ethiopian fauna appears to be either poorly investigated (Terefe et al., 2018) or greatly impoverished. We collected only 28 species (7 families) within the entire Awash drainage, although nearly 1,250 km of the main river and seven tributaries were surveyed. Kimmins (1963), Malicky & Graf (2012, 2015) and Terefe et al. (2018) reported 14 additional species, increasing the number to 42 species in the Awash drainage. However, this number is still low if compared to other tropical rivers such as the Mae Klang Catchment (Northern Thailand) with 171 species (Malicky & Chantaramongkol, 1993; Chaibu, 2000; Chaibu et al., 2002; Malicky, 2014).

In the Awash catchment, species of the families Hydropsychidae and Leptoceridae were most widely encountered. These families make up nearly two thirds of all species. Most species in the Awash are representatives of the Afrotropical region. Some caddisfly species cover huge geographic areas, for example, *H. cruciata* (Cape Verdes, South Africa, Madagascar, Arabian Peninsula), *A. senegalensis* (West Africa, Egypt to South Africa), *D. capensis* and *E. similis* (West Africa, Ethiopia, South Africa), *O. tripunctata* (wide distribution; Portugal to Bali; Malicky, 2005), or elements of Central Africa like *E. nya*, *N. armigera*, *O. reticulatella* (Kjærandsen & Andersen, 1997; Olah & Johanson, 2008; Morse, 2020). Others are, as far as known today, Ethiopian endemics, including *L. scotti*, *O. thariel*, *O. armaros*, *H. abyssinica*, *C. massa*, and *C. themaz* (Malicky & Graf, 2012, 2015; Terefe et al., 2018).

Characteristic species of higher elevations (Upper Awash, > 1,608 m) are *L. scotti*, *O. armaros*, *C. themaz*, *C. afra*, *Cheumatopsyche falcifera*, *C. massa*, *E. nya*, and *E. similis*. Their distribution was, however, not uniform. The first three species solely inhabited the river's source region in Chilimo Forest (Terefe et al., 2018). They apparently disappear in deforested areas as we did not record them further downstream or in the upper sections of tributaries. Nevertheless, species diversity in the forested highland areas might be higher than we recorded. Malicky & Graf (2015), for example, described species such as *Hellyethira marioch*, *Stactobia ruthiel*, *Orthotrichia gudiel*, and *Athripsodes druchas* from a small forest creek north of Addis Ababa. The genus *Lepidostoma* is a characteristic element of the highlands in several African regions (Mosely, 1939; Marlier, 1954). The other species peculiar for the Upper Awash region—*C. afra*, *C. falcifera*, *C. massa*, *E. nya*, and *E. similis*—are more widely distributed throughout Africa and seem to be insensitive to the loss of natural forest cover. Despite being characteristic for the Ethiopian Highlands, those species present a transition to the rift valley community.

Some species, such as *O. tripunctata*, *T. serratus*, *S. squamosus*, *T. aethiopica*, and *T. tjonnelandi*, occurred exclusively in the wetland area of Koka Reservoir. Here, the river morphology changes sharply and the area becomes comparably flat, the river slope and flow velocity are reduced, fine sediment is deposited, and filter feeders with ultra-fine nets (*D. capensis*, *A. senegalensis*) occur here for the first time. Indeed, studies from lakes and reservoirs (Mosely, 1931; Kimmins, 1963) suggest that *T. aethiopica*, *S. squamosus*, *T. tjonnelandi*, and *T. aethiopica* prefer limnetic habitats and fine substrates. Aside from these four species, Kimmins (1963) found six other species in the area around Koka Reservoir: *C. afra*, *C. sexfasciata*, *H. abysinnica*, *D. capensis*, *E. similis* and *A. senegalensis*. As mentioned earlier, the section around Koka Reservoir apparently represents an ecotone where highland and lowland species overlap and coexist. With 29 species currently known from the central part of the Main Ethiopian Rift, this river zone shows a high diversity for the region as it contains elements from the adjacent freshwater ecoregions.

In the Lower Awash River, the number of caddisfly species is reduced (comparable to fish); some species which occur around Koka Reservoir are distributed further downstream, indicating a considerable influence of the reservoir. Members of the rift valley community with a slight overlap to the highlands consist of *O. reticulatella*, *D. capensis*, *A. senegalensis*, and *C. columnata*. In this zone, the river alternately flows through confined reaches and extensive wetlands (Fig. 4). The smooth stream gradient is frequently interrupted by cataracts, resulting in associated changes in substrate composition from fine to large substrates or bedrock. In stony sections, including the tributaries in the Northern Main Ethiopian Rift, we found *H. cruciata*. Though faunal elements of the lowlands are comparable with other river systems in the Afrotropical region (e.g. Gibon & Statzner, 1985; de Moor et al., 2000) the fauna in the Awash River is largely impoverished.

Drivers of diversity

Both, fish and caddisflies exhibited an exceptionally low diversity in the Awash River catchment. Reasons for the apparently low species numbers might be related to the following characteristics.

Anthropogenic impacts

The Awash River is under extreme human pressure. Deforestation, plantations of *Eucalyptus* and *Prosopis*, intensive agricultural use and overgrazing by livestock linked with high nutrient input and erosional processes, as well as industrial and domestic water pollution, are common (Degefu et al., 2013; Keraga et al., 2019). However, this affects mainly the highlands. In the Lower Awash River, livestock is reduced and agriculture is focused at some few irrigated areas. Anthropogenic degradation might therefore be a reason for the low diversity in the Ethiopian Highlands more so than in lowland areas. Studies of reference streams in near-natural environments are not known from Ethiopia, and generally, studies on tropical caddisflies at species level along comparable stretches are rare (e.g. Chaibu et al., 2002).

Geotectonic activities

Geological data give evidence for frequent tectonic and volcanic activities in the history of the Main Ethiopian Rift (Benvenuti et al., 2002; Abbate et al., 2015). These events presumably not only affected the geomorphology and connectivity of the Paleo-Awash (Sagri et al., 2008) but also the distribution of fish species (Beshera & Harris, 2014; Englmaier et al., 2020). Moreover, thermal springs may have considerable influence on the water temperature at higher altitudes (e.g. Middle Borkana River, 31.2°C at 1,417 m), possibly also affecting species composition (Lamberti & Resh, 1985).

River network

The Awash River is an endorheic drainage system, lacking the marine/estuary ecotone. In contrast to large endorheic drainages of Africa such as the Omo (Ethiopia) and the Chad rivers (Central Africa), the Awash does not flow into a large lake basin that supports a rich fauna. Lake Abbe in the Afar Depression is highly saline and an extreme habitat for fish and caddisflies.

Climatic characteristics

The Awash drainage system is located in an area subject to extreme climatic conditions. It is distinguished by high temperatures and exceptionally low precipitation (Fazzini et al., 2015). In the Afar region, the high water temperatures might be a limiting factor for species distribution, potentially exceeding the ecological tolerance of several species. Paleoclimatic and paleohydrological studies have shown frequent lake level changes in the Main Ethiopian Rift (Grove et al., 1975; Le Turdu et al., 1999; Sagri et al., 2008; Benvenuti & Carnicelli, 2015), suggesting a long history of unstable environmental conditions. During dry periods in the past, the Awash River possibly turned ephemeral, thereby limiting faunal persistence. Regarding caddisflies, it seems likely that widely distributed species with high dispersal capacities and broad ecological ranges managed to recolonize old habitats. The specialized fauna of Chilimo Forest, in contrast, indicates that more stable environmental conditions persisted over longer periods.

Possible methodological limitations

We sampled fish and caddisflies over three different years and periods (at the start, middle and end of the dry season) (Table 1). Although this did not seem to influence our results, the effects of temperature or river flow could have influenced species detection. Besides, we investigated species diversity during the dry season only and thereby did not cover the aspect of seasonality. Even though phenological investigations in tropical streams indicate long flight periods for most caddisflies throughout the year (e.g. Malicky, 2019), little is known about flight periods of African species. Kimmins (1963) found *A. senegalensis* during March and April, and Mosely (1948) detected specimens in January and June. However, substantial knowledge gaps regarding seasonality remain. The same is true regarding diurnal activity. This might have increased the change of missing caddisfly species, for example, those which are only active late in the night or early in the morning, in addition to the fact that most sites were only investigated once. Especially the fauna of cataract sections in the Lower Awash needs to be investigated in detail but sampling efforts were limited due to inhibited accessibility.

The best explanation for the species-poor situation of caddisflies in the Awash River is, however, the general poverty of the Afrotropical caddisfly fauna as a whole, which cannot be explained at the present state of knowledge. Exact numbers of species cannot be given because of taxonomic uncertainty of described species, and more new species await discovery. Many widespread caddisfly genera or families are either lacking in tropical Africa (e.g. Rhyacophilidae which are present with hundreds of species in Asia and even non-tropical Europe, or the genus *Psychomyia* with well over 70 species in tropical Asia) or represented only by very few species (e.g. 1 species of *Stenopsyche*, as compared to more than 50 only in western China). Except for some species-poor endemic families or genera in southern Africa (Scott 1986, 1993), only a few widespread species-rich genera are well represented in tropical Africa such as Leptoceridae, *Ecnomus*, *Cheumatopsyche*, *Chimarra*, or *Dipseudopsis*. Rivers in Asia and Europe contain by far more species than the Awash River. For example, 91 species are reported for the Mae Nam Ping in Thailand over a stretch of 120 km (Chaibu & Chantaramongkol, 1999; Chaibu, 2000; Chaibu et al., 2002; Malicky, 2014), 98 species for the Drava River at the border between Hungary and Croatia (Uherkovich & Nógrádi, 2018), 81 species in the Po River in Italy (Bertuetti et al., 2001), or 61 species in the middle part of Danube River in Central Europe (Malicky, 2014).

Conclusion

Our study showed that, in the tropical endorheic Awash River, fish and caddisfly assemblages sampled during the dry season are clearly clustered into highland (Upper Awash) and rift valley (Lower Awash) communities, separated by an ecotone (transition zone) with highest species diversity. The fish and caddisfly assemblages are congruent in their overall distribution patterns, which reflect changes in altitude and jumps between ecoregions. Only caddisflies exhibited a narrower niche in the headwaters, separating the Upper Awash River into a forested and a deforested zone.

Furthermore, we described the most indicative species for the biocoenoses along the mainstem river as well as its tributaries. As species-specific bioindicators are rare or absent in most of the Afrotropical region, these results may constitute a fundamental element for the management of the Awash River and beyond.

Compared to other drainage basins in Eastern Africa, the Awash River is rather species poor, which may result from various natural and anthropogenic factors. Nevertheless, the highland forests seem to be centres of specialized caddisfly species with small-scale distribution, and the Awash lowlands harbour endemic fish species restricted to the Main Ethiopian Rift.

Possible limitations to our study include the aspects of sampling timing and lack of seasonality, which may have oversimplified our results. More studies are needed to understand spatio-temporal effects in distribution patterns in the Afrotropical region.

In summary, we found that a combined approach of fish and caddisflies proved to be a suitable method for identifying longitudinal and regional characteristics of fluvial ecosystems in tropical environments. In the future, East African research must focus on taxonomy, ecology and distribution patterns on species level. Such investigations are urgently needed to foster the development of reliable systems for assessing and monitoring the integrity of tropical river systems and their biodiversity.

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Data availability Data are available from the corresponding authors upon reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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Ecohydraulics of river flow alterations and impacts on freshwater fish

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ABSTRACT

Ecohydraulics of river flow alterations and impacts on freshwater fish

The flow regime is a determinant of the ecological function and natural dynamics of a river system with a prominent effect on freshwater fish. Here, we introduce a number of contributions to the Special Session, "Ecohydraulics of river flow alterations and impacts on freshwater fish," that occurred at the XIX Conference of the Iberian Association of Limnology. The multidisciplinary contributions illustrate the impacts of river flow alteration on aquatic biota, describe mitigation measures and restoration actions to address river flow regulation, and present innovative tools for research in the ecohydraulics field. The research topics debated included environmental flows, river restoration, hydropeaking impacts on aquatic organisms, innovative methods and devices, and hydropeaking mitigation strategies. The importance of ecohydraulics as an emerging science was debated. The bridge between the disciplines of limnology and ecohydraulics was highlighted to understand flow alteration impacts and provide solutions to mitigate those impacts. This Special Session provided an opportunity to embrace ecohydraulic scientists in limnology research.

Key words: Ecohydraulics, limnology, flow alteration, freshwater fish

RESUMO

Ecohidráulica no contexto global das alterações do escoamento do rio e os impactos nos peixes de água doce

O regime de escoamento num rio é determinante para a função ecológica e dinâmica natural do sistema fluvial, com um efeito proeminente nos peixes de água doce. Neste estudo apresentamos as contribuições para a sessão especial - "Ecohidráulica das alterações do escoamento do rio e os impactos nos peixes de água doce", que teve lugar no XIX Congresso da Associação Ibérica de Limnologia, a fim de debater e compreender os efeitos da alteração de escoamento do rio nos peixes. As contribuições multidisciplinares ilustram os impactos da alteração de escoamento do rio no biota aquático, descrevem medidas de mitigação e ações de restauro fluvial para rios regularizados e apresentam ferramentas inovadoras para a investigação na área da ecohidráulica. Os principais tópicos debatidos foram: regime de caudais ecológicos, restauro de rios; impacto dos hidropicos em organismos aquáticos; métodos e ferramentas inovadores; e mitigação dos picos de caudal turbinado. A impor-

tância da ecohidráulica como ciência emergente foi debatida. A ponte entre as disciplinas de limnologia e ecohidráulica foi realçada para analisar os impactos da alteração de escoamento num rio e apresentar soluções de mitigação. Esta sessão especial ofereceu uma oportunidade para incluir a componente ecohidráulica no estudo da limnologia.

Palavras chave: *Ecohidráulica, limnologia, alterações de escoamento, peixes de água doce*

ECOHYDRAULICS

The increasing demand for water resources has resulted in a continuous disruption of natural flow regimes with drastic changes in the physical character of riverine ecosystems. The continued flow alteration has severely changed rivers' hydro-morphological processes (Grant *et al.*, 2013) resulting in uncharacteristic and homogeneous river habitats that adversely affect benthic invertebrates (White *et al.*, 2016); riverine vegetation (Bejarano *et al.*, 2018); and fish activities and critical life-stage events (Murchie *et al.*, 2008; Young *et al.*, 2011) that are likely to amplify to populations, communities, and the entire river ecosystem (Bain *et al.*, 1988). The natural flow regime is therefore a determinant of the ecological function and natural dynamics of riverine systems (Poff *et al.*, 1997). The dynamic role of the biotic (e.g., competition and predation) and abiotic (e.g., chemical and physical factors) partitions at a temporal and spatial scale set the structure of the aquatic ecosystem in which the flow regime plays the primary role (Gasith & Resh, 1999). More difficult to establish, the biotic factors concern biological processes that widely depend on resource availability (Karr, 1981). More predictable and easily measured, the abiotic factors, divided into chemical and physical factors, are vital for the survival and persistence of individuals and affect the distribution of aquatic organisms (Rosenfeld, 2003; Boavida *et al.*, 2011). The interaction of both the abiotic and biotic partitions can only be studied and understood using an integrative set of disciplines ranging from biology and ecology to hydrology and hydraulics, to provide a few examples.

Ecohydraulics emerged from the interface between the disciplines of ecology and hydraulics (Rice *et al.*, 2010; Maddock *et al.*, 2013) to understand the interactions between biotic and abiotic components of a riverine ecosystem that are associated with flow variability. It combines the study of physical properties and processes associated with moving water typical of hydraulic engineering and geomorphology, and their influence on aquatic ecology and biology (Nestler *et al.*, 2016). The multidisciplinarity and interdisciplinarity of ecohydraulics often includes disciplines that are related to aquatic biology (e.g., physiology and evolution), engineering (e.g., hydraulics and hydrology), and other physical sciences (e.g., geomorphology). A survey of the proceeding papers from the International Symposiums on Ecohydraulics (1994–2016) by Casas-Mulet *et al.* (2016) enumerated 10 research macro-topics organized as follows: hydrology; hydraulic modelling; water quality; and flow, physical habitat, vegetation, invertebrate, fish, estuarine and social responses. These broad topics highlight the multidisciplinarity and interdisciplinarity of ecohydraulics research and its relevance for water resources management.

In an effort to determine the ecological responses to flow alteration, multidisciplinary teams have attempted a range of approaches, from numerical modelling (Mouton *et al.*, 2007; Garcia *et al.*, 2011; Boavida *et al.*, 2018a) to empirical laboratory works (Costa *et al.*, 2019a) and field studies (Santos *et al.*, 2006; Ovidio *et al.*, 2008; Alexandre *et al.*, 2016) at various spatio-temporal scales. The spatial range extends from a local-scale (referring to the interaction of aquatic organisms and flow to address microhabitat hydraulics) to a large-scale (e.g., involving geomorphologic processes of erosion and sedimentation). Freshwater fish have always been a primary research target because of their prominence in riverine ecosystems (Pont *et al.*, 2006) as justified primarily by the key role of spatial and temporal variabilities of the natural flow regime to fish population dynamics (Resh *et* *al.*, 1988). Native organisms have evolved life-history strategies and morphological adaptations to respond to these flow variations (Lytle & Poff, 2004). Over time, regulated rivers can better support generalist fish species, typically non-native taxa, compared to indigenous species, providing the former a competitive advantage over the latter (Copp *et al.*, 2005).

Furthermore, in regulated rivers, because of hydroelectricity production, flow is periodically disrupted by extreme and short-duration fluctuations in discharge during daily peaks of energy demand (Cushman, 1985; Young *et al.*, 2011), raising concerns regarding the ability of fish to respond to the quickly changing environment, and the costs and time to react to constant changes (Costa *et al.*, 2019a). In addition, hydroelectric turbines can cause massive fish mortality because of abrupt changes in pressure, cavitation, shear forces, turbulence, and mechanical shock (Havn *et al.*, 2017).

The described impacts associated to flow regulation highlight the need to overcome these problems by forming multidisciplinary teams capable of generating quantitative information regarding these impacts on freshwater fish. Thus, it is imperative to develop innovative methods and tools to describe the aquatic environment and present novel solutions to minimize and mitigate adverse impacts. Promoting successful restoration actions followed by monitoring schemes are also important cues during the process.

The aim of the Special Session, "Ecohydraulics of river flow alterations and impacts for freshwater fish," held at the XIX Conference of the Iberian Association of Limnology was to combine the disciplines of limnology and hydraulics to assess and understand the impacts of river flow alterations on freshwater fish and provide solutions to mitigate these impacts. Limnology is closely related to aquatic ecology and hydrobiology, studying aquatic organisms in particular with regard to their hydrological environment (Wetzel, 1981). Hydraulics focuses on applied engineering using the properties of fluids (Chow, 1973). The interaction between these two disciplines is vital to answer ecohydraulic challenges regarding fish and flow alteration.

ECOHYDRAULIC CONTRIBUTIONS TO LIMNOLOGY

River restoration

The need to maintain the sustainability of aquatic ecosystems by applying local restoration measures has been widely recognized by ecohydraulic research, river management, and environmental policies (Pretty *et al.*, 2003; Nilsson *et al.*, 2007), in particular the EU Water Framework Directive (EU, 2000). Despite the recognition and an increased number of restoration actions, most projects are still undertaken on a trial basis (Downs & Kondolf, 2002), often based on the assumption that implementing a certain restoration action will surely improve the ecological integrity of the aquatic ecosystem. However, scientists and river managers should be aware that undertaking local restoration measures is not a guarantee of success (Maire *et al.*, 2015). Given both the high costs involved and socio-administrative expectations, habitat improvement projects must successfully apply science-based tools. Thus, restoration projects should incorporate a proper assessment of the potential outcome based on the specific ecological attributes of the river (Woolsey *et al.*, 2007) to verify the success of the proposed actions.

Díaz-Redondo *et al.* (2018) used a novel framework to evaluate river restoration in an urban river reach. The authors applied geomorphological metrics and hydraulic variables associated with potential preferential conditions for autochthonous fish fauna, whose populations are greatly reduced (Tánago *et al.*, 1999), to assess the initial natural habitat recovery. Throughout the 20th century, in a similar manner to other urban river segments (Petts, 2007), the Manzanares River in Madrid, Spain, was channelized to allow for intensive urban development, and nine small dams were built to maintain a view of a large deep river. As part of the renaturalization initiative by the Madrid City Council, the opening of urban dam gates during the spring of 2016 potentially allowed for habitat improvement facilitating colonization by vegetation and fauna. First, from the Geographic Information System (GIS) analysis of aerial photographs for the years

2015, 2016, and 2017, geomorphological metrics were applied including areas (m^2) of islands and bars, and shoreline length as the sum of perimeters (m) in contact with water. In addition, the ratios of areas and shoreline lengths per patch (island or bar) were also calculated. Second, hydraulic-habitat models based on species-specific preference curves were applied. Two-dimensional (2D) hydraulic modelling was performed using IBER 2-D (Bladé *et al.*, 2014) and outcomes of water depth, flow velocity, and shear stress were evaluated against the preferences of three target autochthonous fish species - the Iberian barbel (*Luciobarbus bocagei* Steindachner, 1864), Southern Iberian chub (*Squalius pyrenaicus* Günther, 1868), and Southern Iberian spined-loach (*Cobitis paludica* de Buen, 1930). Results from geomorphological metrics indicate that the increase in number, area, and shoreline length of islands and bars was remarkable following the gate opening. Moreover, initially, sedimentation produces many small- and medium-sized patches that later on do not significantly grow in number but, instead, increase in size. All these metrics are an indication of an improvement in habitat quality and availability (Tockner & Stanford, 2002). In this sense, results from 2D hydraulic modelling show that current habitat conditions related to shallower water depths, different velocities within the channel, and new sand sedimentation promote potential preferential habitats for native fish fauna. In conclusion, over a short period of time, the improvement in habitat conditions has been remarkable. Overall, more studies are required regarding the evolution of habitat conditions following urban river rehabilitation, particularly from the perspective that partial recovery of natural habitats in an urban stretch can lead to the improvement of its ecological potential, as required by the Water Framework Directive (Gumiero *et al.*, 2013).

The recognition of river flow alteration worldwide has led to the establishment of environmental flows (hereafter e-flows) (Arthington *et al.*, 2018). An e-flow regime implemented downstream of dams play an essential role in the conservation of freshwater ecosystems (Arthington *et al.*, 2006; Rivaes *et al.*, 2017). Setting an e-flow regime involves identifying the quantity, timing, and quality of water flow required to sustain freshwater and estuarine ecosystems, as well as the human livelihoods and wellbeing that depend upon these ecosystems (Arthington *et al.*, 2018) over time and space. Achieving this level of detail can be resource demanding (Arthington *et al.*, 2006). Boavida *et al.* (2018b) proposed an undemanding method to transfer the inter-annual variability associated with e-flows to another river reach in the same catchment when similar morphodynamic conditions and flow–ecological relations are verified. Several methodologies have been developed to define e-flows with different degrees of effort. According to Tharme (2003), the existing e-flow methodologies can be differentiated into hydrological, hydraulic rating, habitat simulation and holistic methodologies. From an ecohydraulics perspective, habitat simulation methodologies are widely accepted to define e-flows (Acreman *et al.*, 2014). With an emphasis on complex, hydrodynamic habitat modelling, these methodologies require immense amounts of data. The time and resource consumption of these actions (Palmer *et al.*, 2005) highlights the need to implement successful methodologies that require less data or data more easily collected while maintaining the same level of achievement. Transferring flow-ecology relationships can be a successful measure to assist regional-scale e-flow assessments (Chen & Olden, 2018). The habitat availability for a target species in a natural, non-regulated stream acts as the reference condition (guiding image) for comparing the degree to which an environmental flow scenario deviates from the natural flow regime (Boavida *et al.*, 2012). The closer the e-flow scenario is to the reference condition, the "healthier" the e-flow scenario is determined to be (Nilsson *et al.*, 2007). Conversely, the further from the reference condition, the less healthy it will be. Therefore, this study assessed the viability to transfer the pre-defined e-flow regime – set according to the reference habitat availability – proportionally, from an upstream to a downstream river segment. The similarity among the morphodynamic conditions was guaranteed as well as the flow-ecological relationships. The pool of fish species between the two studied reaches was also similar. Finally, inter-annual variability was set the same for both reaches. The results indicated a good adjustment between the e-flow scenario and the reference condition for the river segment that received the e-flow values transferred from the upstream river-segment. This study improves knowledge of the extensive literature on e-flow methodologies. Further, it sets the e-flow based on habitat simulation methodologies by transferring these values among similar river reaches.

Impacts of hydropeaking on aquatic organisms

The impacts of river flow alteration on freshwater fish have been addressed by the ecohydraulic community, with relevance for sub-daily rapid alterations of flow downstream of hydropower stations. Cushman (1985) first referred to hydropeaking as the operational maneuvres that occur in hydropower plants in response to electricity demand to control large and rapid (within minutes) changes in discharge by powering -on or -off hydro-turbines, resulting in rapid flow changes in tailwaters. During non-peak periods, hydropower facilities store water in a reservoir resulting in low flows downstream of the hydropower plant (i.e. environmental flows), while during peak periods, power is generated and water is rapidly released, increasing the velocity and water depth downstream of the facility. The unpredictability and intensity of flow variations are rather permanent and more frequent than those resulting from natural flows, such as rapid snowmelt and precipitation (Shuster *et al.*, 2008). Because of the unpredictability and intensity of flow variations, these rapid flow fluctuations likely influence the natural structure of the riverine ecosystem (Young *et al.*, 2011). Long-term hydropower plant operations result in strong morphological, hydraulic and water quality alterations. These alterations include bank and soil erosion, substrate composition (siltation and armouring of the substrate), and continuous shifts in sediment transport processes (Schmutz *et al.*, 2015) caused by the continuous changes in water level, flow velocity, water turbulence and bed shear stress (Shen *et al.*, 2010). This may lead to severe impairments to fish rearing and growth, fish migration and spawning, and to the benthic invertebrate community (Bruno *et al.*, 2016). Juvenile fish are particularly vulnerable to hydropeaking events, leading to drifting and stranding (Halleraker *et al.*, 2003), which can ultimately reduce recruitment of the entire population (Schmutz *et al.*, 2015). Because of this, during the last decade, research on hydropeaking impacts has rapidly increased (Bejarano *et al.*, 2018). The growing awareness of the impacts of hydropower plants on the downstream ecosystem has increased in parallel with the development of hydropower, given the increasing global demand for hydroelectricity production. Climate change awareness has increased the pressure on hydropower production (Sawin & Martinot, 2010) because of its efficiency, high reliability and predictability, lack of carbon emissions, and low operating costs. These issues point out to an urgent need to overcome this problem by generating quantitative information regarding hydropeaking impacts to find innovative solutions that allow for a sustainable development of hydropower energy. The recognition of this is reflected in the number of contributions describing hydropower impacts and mitigation measures that this Special Session has received. Ranging from field case-studies to laboratory work, research on hydropeaking has never before seen such interest.

To understand fish behaviour when subjected to hydropeaking events, Hayes *et al.* (2018a) used a comprehensive national database to assess the response of juvenile salmonids to natural and artificial flow fluctuations in Austrian Alpine rivers, in which river hydrology ranges from natural flow regimes to extensive hydropeaking, and morphology from natural to channelized. Hydrological metrics were calculated according to Greimel *et al.* (2016), whereby sampling sites were grouped into four categories: (1) reference, (2) hydro-fibrillation (low-intensity flow fluctuations), (3) hydropeaking (high-intensity flow fluctuations), and (4) glacier (natural hydropeaking) (Hayes *et al.*, 2018b). To describe the morphological variability of the assessed river reaches, the coefficient of variation was calculated based on aerial image interpretation of the bankfull river width, which allows comparing the width variability of distinct rivers of different sizes (for details see Greimel *et al.* (2017)). Regarding young-of-the-year brown trout (*Salmo trutta*

Linnaeus, 1758) and European grayling (*Thymallus thymallus* Linnaeus, 1758) abundance in their respective fish zones, initial results showed that sites classified as hydropeaking are distinguished from the three other hydrological categories. Hydro-fibrillation and glacier sites showed lower fish abundances than those of the reference sites, although it was not significant. Downramping rates during mean and high water flow range situations seem to be among the parameters governing juvenile fish abundance, whereby the pattern corresponds with stranding thresholds established through experimental studies (Moreira *et al.*, 2019) particularly for the brown trout in the metarhithral. For the grayling in the hyporhithral it is not as clear, probably because of the number of stressors generally found in this fish region (Schinegger *et al.*, 2018). Results also showed the additional influence of river morphology, whereby more nature-like sites tend to have a higher juvenile abundance than those that are channelized ones (Hayes *et al.*, 2018b) as the former can offer higher habitat suitability than that of the latter (Hauer *et al.*, 2014)

The scientific community as well as fishery and river managers agree with the view, that promoting habitat heterogeneity through more natural sites can effectively mitigate the impacts of hydropeaking and promote self-sustainable fish populations downstream of hydropower dams (Hauer *et al.*, 2014; Alexandre *et al.*, 2016). Experimental flume-based research has proposed morphological measures to mitigate hydropeaking consequences. For example, lateral refuges (Ribi *et al.*, 2014), substrate heterogeneity (Chun *et al.*, 2010), and alternative cover structures (Vehanen *et al.*, 2000) have been studied as refuge for salmonids during hydropeaking events. Still, considerable uncertainty remains regarding the design of effective mitigation measures based on fish responses, particularly when applied to cyprinids, which include a high proportion of endangered species in central Europe and the Iberian Peninsula (Santos *et al.*, 2018). Changes in critical life-cycle events of the Iberian barbel (e.g., growth and reproduction) have been attributed to anthropogenic streamflow variability (Alexandre *et al.*, 2015). For example, smaller home ranges were associated with natural seasonal flow variability of a non-regulated river, whereas wider spatial scale movements were associated with a river affected by hydropeaking (Alexandre *et al.*, 2016). It is certain that flow regulation has extensive impacts on freshwater fish structure and function. However, it remains difficult to understand which changes in the flow components trigger specific movement patterns or habitat preferences. In this sense, the ecologi-

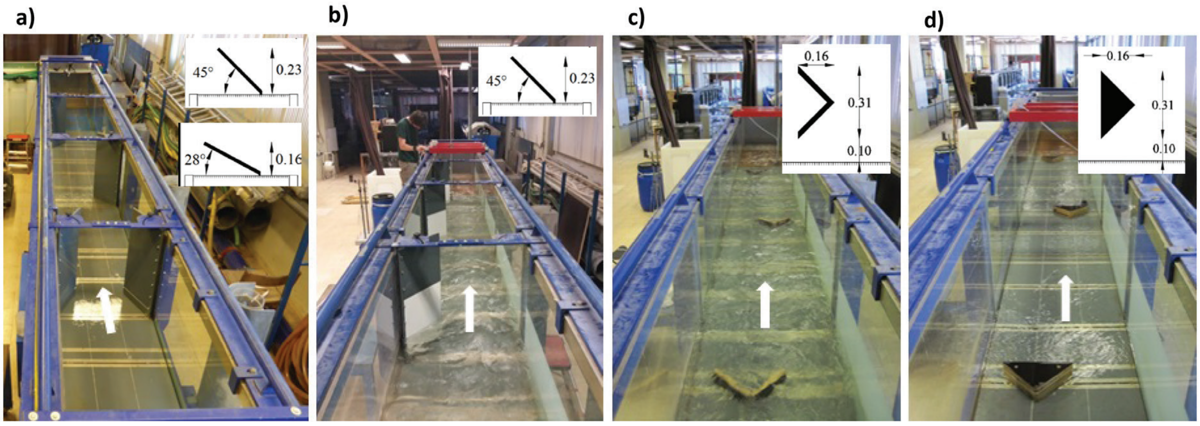

Figure 1. Structure configurations tested according to Costa *et al.* (2018a). (a) and (b) represent the lateral deflectors and (c) and (e) the v-shaped structures and the solid triangular pyramids respectively. A detail of the refuges dimensions (m) is shown. *Configuração das estruturas testadas por Costa* et al. *(2018a). (a) e (b) deflectores laterais e (c) e (d) estruturas em v e pirâmides, respetivamente. A dimensão (m) dos refúgios é apresentada em detalhe.*

cal impacts of hydropeaking and this cause–effect relationship should be further scrutinized to provide the necessary tools for fishery managers to improve population dynamics and conserve endangered fish species.

To fill this gap, Costa *et al.* (2018a) adopted a multidisciplinary approach, in which movement behaviour was combined with a detailed hydraulic characterization to evaluate the use of lateral and instream structures as potential refuges for Iberian barbel (*Luciobarbus bocagei*) affected by rapid flow fluctuations (Costa *et al.*, 2018b; Costa *et al.*, 2019a) (Fig. 1). This consisted of flow field measurements using Acoustic Doppler Velocimetry (ADV) technology and fluid–body interactions with the objective to better interpret fish responses. Using this approach, it was possible to conclude that the movement pattern demonstrated by the Iberian barbel was diverse and not always proportional to the severity of the flow event. For example, during the peak events with structures the individual sprints were more pronounced, whereas group behaviour increased under base flow and hydropeaking conditions without structures. Although the hydraulic characterization showed that lateral deflectors and v-shaped structures provided low velocity areas that could potentially mitigate the severity of peak flows, the flow complexity created by the presence of the structures represented an additional constraint for fish, hindering their ability to find refuge behind the structures. The distinct behavioural patterns were a result of the hydraulic conditions created by the flow event and the structures' configurations. The use of this integrated approach strengthened the interpretation of fish responses and minimized misleading conclusions, thus contributing to the design of more effective mitigation measures in response to hydropeaking consequences.

In addition to affecting fish movements and behaviour as shown by Costa *et al.* (2018a), artificial flow fluctuations decrease the density, composition, and biomass of the macroinvertebrate community (Bruno *et al.*, 2016). Palau-Nadal *et al.* (2018) studied the effects of hydropeaking (ranging from < 2 m^3/s to 12 m^3/s) on the water temperature, macroinvertebrate community, physical habitat, and brown trout population (*Salmo trutta* Linnaeus, 1758) of a Pyrenean river, taking as a reference a near reach of the same river without hydropeaking. The study was conducted during the summers of 2011 and 2012. Hydropeaking affected the macroinvertebrate community through two factors: 1) variations in flow (alteration of the physical habitat) that generate changes in the density, composition, and trophic structure of the community (e.g., an increase in the ratio of grazers/shredders); and 2) changes in water temperature that alter the biological cycle of some aquatic insects in a temporal lag with respect to the reach without hydropeaking (e.g., Heptageniidae and Athericidae). These effects, however, quickly decreased downstream and were barely detected 2 km downstream. The longitudinal variation in the downstream impacts of flow regulation is highly dependent on the existence of a tributary (1 km from the hydropower plant) of sufficient size and flow to alter the upstream discharge and hydraulic lamination. The physical habitat of the brown trout changed in response to the hydroelectric peak flows, particularly the availability of habitat for fish fry decreased as a consequence of the unfavourable hydraulic conditions associated with high flows. However, this change was not reflected in the density and biomass of the trout population in the altered river reach, where both variables presented higher values than those in the reference section, without appreciating the limitations of the adult and juvenile stages. The density and structure of the brown trout population changed between the two years (2011 and 2012) in the reference section, which can be related to a natural flood (of 40 m^3/s) that occurred during April 2012, coinciding with the time of the start of the fry stage in the zone. In contrast, the hydropeaking reach showed few changes between the two years of study, suggesting that its population of brown trout was more resilient and resistant to a natural flood, being in itself confirmed by a low proportion of fry.

Hydropeaking mitigation: regulations and thresholds

Despite the increase in hydropeaking research, with different studies evaluating the effect of flow alteration on aquatic biota and evaluating the success of mitigation measures, knowledge of hydropeaking targets from which an impact occurs remains scarce (Young *et al.*, 2011). Moreira *et al.* (2018) presented an extensive review of the thus far established hydropeaking targets and thresholds regarding outputs from the scientific community (by conducting a Scopus literature search), as well as indicator values from national regulations and guidelines. The study found that only a few European countries (Switzerland and Austria) have legal regulations regarding hydropeaking through flow thresholds (Moreira *et al.*, 2019). Other countries, such as Norway, have environmental legislation that can be used to force hydropeaking mitigation measures. Most mitigation thresholds in the literature address the effect of downramping on stranding of salmonids and were mostly established through trials in experimental channels. Established downramping thresholds range from < 0.1–0.2 cm/min for larvae (of *Salmo trutta* Linnaeus, 1758, *Thymallus thymallus* Linnaeus, 1758) to *ca.* 0.2–0.4 cm for early juveniles (*S. salar* Linnaeus, 1758; *S. trutta* Linnaeus, 1758; *T. thymallus* Linnaeus, 1758; *Oncorhynchus kisutch* Walbaum, 1792; *O. mykiss* Walbaum, 1792). In addition to downramping velocity restrictions, common qualitative goals target the prevention of redd desiccation between peak flows and mitigation approaches aim at increasing base flows and/or decreasing peak flows (Moreira *et al.*, 2019). Regarding other fish group species (e.g., cyprinids) and parameters (e.g., peak duration and time between peaks), a lack of quantitative mitigation thresholds remains. Nevertheless, the literature indicates that multiple aspects have to be considered when assessing such thresholds. To aid in this process, Moreira *et al.* (2018) proposed that mitigation thresholds must be based on key species, including particular features regarding life stage, season, and time of day. These must be combined with site-specific morphological characteristics as the effects of river morphology influences hydropeaking parameters that are essential in defining the thresholds. Thus, the principles laid out in their approach may benefit impacted organism groups in hydropeaking reaches through the establishment of ecologically based relevant mitigation thresholds.

Innovative methods and devices

Better knowledge of fish species movements and behaviour when affected by flow variations is needed to improve the protection of individual fish and achieve self-sustaining fish populations. The planning and design, as well as the probability of success of the proposed mitigation measures, requires innovative monitoring and observational methods, new software tools, and innovative technical devices to enhance the level of assessment and prediction of the measures. Currently, *in situ* analysis of fish habitat preferences is typically based on point measurements of the physical environment (e.g., time averaged velocity, water depth, substrate type, and underwater vegetation presence) (Santos *et al.*, 2018). This discretization may lead to an oversimplification of the hydrodynamic characteristics of the aquatic environment, mainly because these

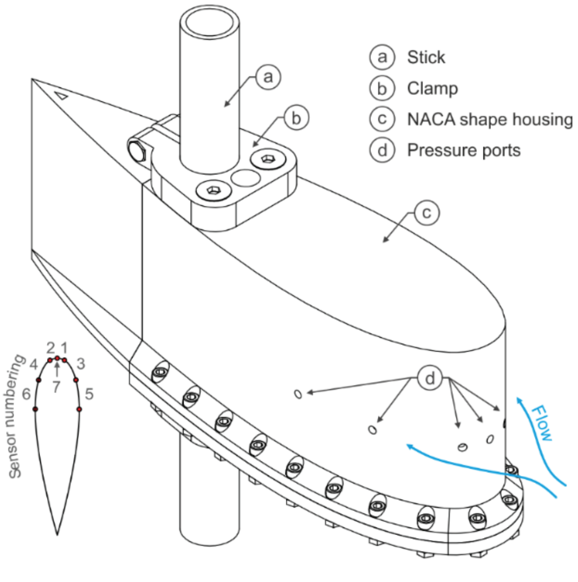

Figure 2. Artificial lateral line probe (modified from Fuentes-Pérez *et al.* (2018)). The NACA025 body shape is outfitted with six differential pressure sensors (1 – 6) and one absolute (7) pressure sensor. *Sonda artificial da linha lateral (modificado de Fuentes-Pérez* et al. *(2018)). A forma NACA025 apresenta seis sensores de pressão diferencial (1-6) e um sensor de pressão absoluta (7).*

metrics ignore the physical interactions between the variables and lack the temporal rate at which fish experience and react to hydrodynamic stimuli. To attempt to address this complex problem, Fuentes-Pérez and Tuhtan (2018) developed a new measuring device based on the sensing principles of fish: the artificial lateral line probe (ALL) (Tuhtan et al., 2016) (Fig. 2).

Fish have evolved in water and unlike terrestrial species they have developed an external sensory system able to sense the water's hydrodynamic characteristics. This physiological adaptation is termed the lateral line (Fig. 3). The lateral line provides sensory input that contributes to many common behaviours in fish, such as prey and predator detection (Coombs *et al.*, 2001; Coomb *et al.*, 2012), obstacle avoidance (Hassan *et al.*, 1992), and rheotaxis (Montgomery *et al.*, 1997) or schooling (Pitcher *et al.*, 1976), among others.

The lateral line probe (LLP) provides a new technology for understanding aquatic ecosystems and is based on the interaction between the sensor, flow, and aquatic environment. Thus, the LLP provides a new type of bio-inspired sensing device for flow measurement (Fuentes-Pérez *et al.*, 2015) and aquatic environment classification The LLP uses a time-synchronized array of rapid pressure sensors installed over a hydrodynamic body (Fig. 2). The benefits of this sensing system to ecohydraulics and water managers are as follows: 1) it performs simultaneous measurements in both space and time in contrast to point measurement devices (e.g., acoustic Doppler velocimeters or propellers); 2) it considers the interaction of the fluid with the body of the probe (spatially distributed sensing) and the surrounding underwater environment (e.g., rocks, plants, and walls); and 3) it measures a sampling rate higher than any other field tool (tested and validated up to 200 Hz) and within the same range of the fish lateral line system. The LLP has the potential to represent the distributed sensing capacity of fish, bringing new sources of flow and underwater environmental information, as well as immediate opportunities to diverse ecohydraulics' fields. For example, in fishway research ALLs have been demonstrated for fish flow preferences and to sample and classify different hydrodynamic scenarios in a vertical slot fishway, contributing to its retrofitting (Tuhtan *et al.*, 2018). In hydropeaking studies, ALLs have shown the availability to characterize the unsteady conditions produced by different hydrodynamic scenarios and relate them to fish behavioural responses (Costa *et al.*, 2019b). Considering these results, ALLs have the potential to become a multipurpose tool to monitor the complex aquatic environment experienced by fish.

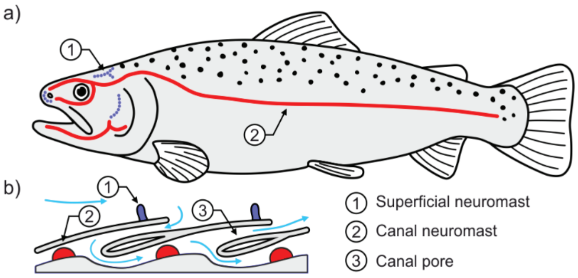

Figure 3. Lateral line system (Tuhtan *et al.*, 2017); (a) Distribution of neuromasts; (b) Superficial and canal neuromasts. *Sistema da linha lateral (Tuhtan* et al.*, 2017); (a) Distribuição dos neuromastos; (b) Neuromastos superficiais e de canal.*

To date, the use of ALLs in the field has been limited to daily monitoring campaigns for fish preference studies or hydrodynamic characterization. Its use for long-term monitoring would require 1) an external datalogging system, 2) a robust design able to handle the target hydrodynamic conditions, and 3) a holding platform. In Ristolainen *et al.* (2018), the described ALL-working principle was successfully implemented in a device (the Hydromast) designed for long-term monitoring of rivers and open oceans.

Alternatively, proactive improvement measures may be needed to guarantee intervention success. Potamodromous fish population survival can be increased using innovative technical solutions based on fish behavioural systems. Non-physical barriers based mostly on different aversive conditions have been tested, namely electric and magnetic fields, water velocity barriers, hypoxia and hypercapnia, pheromones, strobe lights, bubble curtains, and acoustic deterrents (Noatch & Suski, 2012), to reduce fish mortality. The selective study of the repulsive behaviour of a certain species allows one not only to remove fish from traps promoted by the hydraulic structures during their migratory movement, but also allows one to use these same repulsive stimuli to guide the fish, particularly to fishway zones, when functional, but are of reduced attractiveness. Jesus *et al.* (2018b) presented acoustic or luminous stimuli as a repulsive effect for fishes. Both in an isolated and in a combined manner, acoustic (Sweep-up: < 2000 Hz) and luminous (Strobe Light: 600 flashes/minute) stimuli, as well as a bubble curtain, were tested on the salmonid species Brown trout (*Salmo trutta* Linnaeus, 1758) and the cyprinid species northern straightmouth nase (*Pseudochondrostoma duriense* Coelho, 1985) and Iberian barbel (*Luciobarbus bocagei*). In the tests performed with the isolated stimuli, a repulsive sensitivity to the luminous stimulus was verified in the salmonid species (preliminary data under analysis), while the cyprinid species showed a higher sensitivity to the acoustic stimuli (Jesus *et al.*, 2018a). The bubble curtain, in isolation, did not show a behavioral sensitivity in any of the species. In the tests performed in a combined acoustic/light/bubble manner (behavioral barrier), all species showed similar and elevated repulsive sensitivities. These results show the great potential of fish behavioural barriers based on combined systems of acoustics/lights/bubbles, particularly in salmo-cyprinid water courses. The development of behavioural barriers adapted to freshwater species is an important tool to guarantee fish migration, considering the upstream and downstream movement of threatened potamodromous species near dams. These systems will provide conditions for fish to repel from specific structures (channel turbines, pumping systems), avoiding the massive mortality detected in several dams and contributing to the conservation of autochthonous fish populations in regulated rivers.

Fish-based biological indicators

A great number of indexes and metrics have been developed to assess ecological quality in freshwater ecosystems (Benejam *et al.*, 2015); many of these biological indicators have shown to date to be insensitive to flow regime changes or hydrological alterations. Therefore, there is a need to further understand the relationships between such indicators and flow regimes.

Belmar *et al.* (2018b) analysed the relationships between three fish-based biological indicators widely used in Spain and a set of hydrological descriptors, in the low section of a large Mediterranean River using different spatiotemporal scales. The biological indicators were the Indexes of Biotic Integrity in Catalan rivers (IBICAT2010 and IBICAT2b) and the new European Fish Index (EFI+) (EFI+CONSORTIUM, 2009), whereas the hydrological descriptors were water velocity, depth, and a set of sub-daily and daily hydrological indexes (Table 1) modified from Bevelhimer *et al.* (2015) and Olden & Poff (2003), respectively. Fish samples were interannually collected, within a period of 11 years in 6 different transects of the lower Ebro River that were expected to show similar fish communities (except one transect with extreme flow regulation). Hydrological indexes were computed using flow records of different lengths previous to the sampling date. IBICAT2010 was the index most correlated with the flow regimes, but the results were highly dependent on the spatiotemporal scale considered. Daily hydrological indexes showed correlations with biological quality when they were computed using flow records between 9 and 36 months previous to sampling, whereas sub-daily indexes responded better using records between 3 and 9 months. In contrast to that expected, even *a priori* similar sampling transects showed clearer ecohydrological relationships than those of the others, suggesting the influence of hydromorphological variability on the obtained biological quality scores. The transect that provided the clearest relationships showed potential breakpoints for water depth, the mean of the annual minimum flows (ML14), the low flow discharge (ML23), and the standardized maximum hourly ramping rate (dstMHramp). Such breakpoints constitute a separation between "poor" and "bad" status and can be useful to develop management strategies in the Ebro River or other areas. The dependence of the results on the spatial scale highlights the need to improve knowledge regarding the role of channel morphology (including aquatic habitats) on the effects that flow regimes cause in aquatic communities (Belmar *et al.*, 2018a).

Table 1. Hydrological daily indices used to characterise flow regimes, with their units and range (subdaily indices were not computed in the transect with extreme flow regulation) Modified from Belmar *et al.* (2018a). *Indices hidrológicos diários usados para caracterizar o regime de escoamento, com as respectivas unidades e extensão (indices subdiários não foram calculados na secção transversal para as condições extremas de regularização do escoamento. Modificado de Belmar* et al. *(2018a).*

Acronym	Name	Meaning	Range (min – max)	Units
MA3	Variability in daily flows	Coefficient of variation in daily flows	33.63 – 326.20	Dimensionless
MA44	Variability across annual flows	Difference between percentiles 90 and 10 divided by median	0.00 – 141.33	Dimensionless
ML13	Variability across minimum monthly flows	Coefficient of variation in minimum monthly flows	0.00 – 256.37	Dimensionless
ML14	Mean of annual minimum flows	Mean of the lowest annual daily flow divided by median	0.32 – 1.00	Dimensionless
ML23	Low flow discharge	Mean of the percentile 25 divided by median daily flows	0.53 – 1.00	Dimensionless
MH20	Mean annual maximum flows	Mean of the annual maximum flows	343 – 2058	m^3/s
FL1	Low flood pulse count	Number of drops below the percentile 25	0.00 – 25.00	Count
FL3	Frequency of low flow spells	Total number of low spells (5% of mean daily flow)	0.00 – 9.00	Count
FH3	High flood pulse count	Average of daily flows above 3 times the median daily flow	118.86 – 1278.70	m^3/s
FH5	Flood frequency	Number of flow events greater than the median per year	2.00 – 20.00	Count
DL1	Annual minima of daily discharge	Magnitude of minimum annual daily flow	0.00 – 150.16	m^3/s
DL13	Mean of 30-day minima of daily discharge	Mean annual 30-day minimum divided by median flow	0.69 – 13.71	Dimensionless
DH12	Means of 7-day maxima of daily discharge	Mean annual 7-day maximum divided by median flow	0.98 – 29.89	Dimensionless
TL1	Julian date of annual minimum	Julian date of annual minimum	1.00 – 364.00	Day
RA8	Reversals	Number of changes between rising and falling periods	13.00 – 183.00	Count
MA5	Skewness in daily flows	Mean daily flows divided by median daily flows	1.00 – 1.02	Dimensionless
MA12	Mean October flow	Average flow in October	0.00 – 255.03	m^3/s
MA13	Mean November flow	Average flow in November	0.00 – 373.99	m^3/s
MH1	Mean October high flow	Maximum monthly flow in October	0.00 – 1120.15	m^3/s
MH2	Mean November high flow	Maximum monthly flow in November	0.00 - 1539	m^3/s

PERSPECTIVES

Ecohydraulics research has undergone major development during the last decade. A demonstration of this is the recently published papers regarding the "ecohydraulics" topic (Lancaster & Downes, 2010; Nestler *et al.*, 2016; Casas-Mulet *et al.*, 2016) describing contributions from hydraulics, river engineers, ecologists, biologists and geomorphologists. Additionally, the use of the term "ecohydraulics" in Special Issues has appeared in the most relevant journals such as "Ecohydraulics: Recent Research and Applications" in the Journal of Hydro-Environment, "Ecohydraulics: linkages between hydraulics, morphodynamics and ecological processes in rivers" in Ecohydrology, "From microhabitat ecohydraulics to an improved management of river catchments: bridging the gap between scales" and "Bridging the gap between fish behaviour, performance and hydrodynamics: an ecohydraulics approach to fish passage research" in River Research and Applications, and the to be published "Integrating Ecohydraulics in River Restoration: Advances in Science and Applications" in Sustainability.

The ecohydraulics research field appears to address an unanswered question regarding the interaction of aquatic biota with the environment, and consequently, predicts how biota will be affected by changes in river flow. The wide scope of contributions from this Special Session emphasizes the importance of ecohydraulics for freshwater ecosystem management and its contribution to limnology. As limnology integrates physical and biological processes of inland waters, ecohydraulics studies the changes in physical processes caused by flow variability and their influence on the freshwater ecosystem. Based on the global context of river flow alterations and impacts on freshwater fish, the contributions were rather diverse and explored important aspects of the impacts of flow alteration. In particular, the scientific contributions highlighted the need to promote river restoration actions, develop e-flows, and propose mitigation measures that promote self-sustaining fish populations. Hydropeaking impacts on aquatic organisms were also studied by conducting laboratory and field studies as well as covering hydropeaking mitigation thresholds by reviewing existing literature on the subject. In addition, fish-based indicators were assessed. Finally, innovative devices such as procedures to measure the hydrodynamic conditions based on the sensing principles of fish and the use of acoustic or luminous stimuli as a repulsive effect for fishes were proposed.

Regardless, many unanswered questions remain regarding the link between physical processes that occur in this highly unstable environment and the responses of fish biota. To address these and other challenges at the ecology and hydraulics interface there must be equal contribution from both disciplines. In fact, there has been criticism for the lack of ecological relevance to some ecohydraulic approaches (Lancaster & Downes, 2010). While analysing published papers in the ISI Web of Knowledge database between 1997 and 2009, Rice *et al.* (2010) suggested that ecohydraulics is dominated by engineers and physical scientists and that there is less involvement from ecologists and biologists, reinforcing the need to engage these scientists to solve ecohydraulic issues (Casas-Mulet *et al.*, 2016). In contrast, work conducted by ecologists without adequate input from physical engineers will likely result in criticism, particularly considering the misapplication of flow equations. Both contributions are complementary and necessary to understand the effects of flow alterations and impacts on freshwater fish and propose successful mitigation measures. Despite the recognition of this and the efforts to better integrate hydraulic and biological tools to analyse and predict ecological responses to aquatic environmental changes (Lamouroux *et al.*, 2013), there is still a long way ahead. The participation of ecohydraulicians in conferences on inland freshwaters supporting a high level of biodiversity such as the XIX Conference of the Iberian Association of Limnology is more than welcome. Moreover, ecohydraulics lacks fundamental concepts and practices, a problem shared by many new interdisciplines and interdisciplinary academic programs (Nestler *et al.*, 2016). Ecohydraulics focuses on applied research to address practical problems such as the definition of environmental flows, river restoration actions, fish passage design criteria, hydropeaking impacts and mitigation among others (Lamouroux *et al.*, 2010). Ecology is mostly grounded in fundamental science to address the interactions of organisms and the surrounding environment. Ecohydraulics can be integrated into limnology by combining different disciplines to understand the physical processes caused by flow alterations and the consequent ecosystem responses, while incorporating fundamental research to study inland aquatic ecosystems. Therefore, the bridge between the two disciplines is of growing interest.

Ecohydraulics as a field of research is still young; new developments will likely occur in the near future. Fuentes-Pérez & Tuhtan (2018) and Jesus *et al.*, (2018b) foresee more engagement from another field of research with ecohydraulics – electronics and informatics. The development of new tools and devices to assess fish behaviour or the implementation of mitigation and restoration measures needs to be assessed with developers by shortening the bridge between ecohydraulics and emerging technologies. For this we, as ecohydraulicians, need to be more proactive. We need to push boundaries to increase communication and collaboration among different disciplines.

Although new developments are occurring in ecohydraulics a major gap remains between the scientists that conduct science and end users as well as authorities that are responsible for implementation of actions (Casas-Mulet *et al.*, 2016). Moreira *et al.* (2018) presented an overview of the current knowledge and a review of established mitigation thresholds and showed distinct regulations remain largely lacking. This underlines the need to engage both scientists and legislators. Science is driven to address unanswered questions and river managers are the key drivers during the decision-making process. Science is useless without river managers and contrariwise. Most restoration actions and monitoring schemes need to be implemented to assess their success and improve those yet to come, as was shown in Díaz-Redondo *et al.* (2018). Moreover, river managers, hydraulic companies, and environmental agencies are responsible for recognizing knowledge gaps and explaining this need to the scientific community. It should be a win–win process.

Most ecohydraulics research regarding flow alteration is designed to answer practical questions, frequently completed in the field (Alexandre *et al.*, 2016), at a laboratory scale (Ribi *et al.*. 2014), or by applying numerical modelling (Boavida *et al.*, 2017). Often the focus is on the ecological processes that may be influenced by river flow alterations by quantifying the response variables that are directly related to the process and can be isolated. Costa *et al.* (2018a) presented a promising mitigation measure for hydropeaking for an Iberian cyprinid fish. Nevertheless, the results need to be further upscaled or tested in a real environment to improve our understanding of the effectiveness of the implemented measures occurring in nature. How the ecosystem will react to these actions is often the remaining question.

Constant changes in society and environment are followed by a continuous change in the problems that need to be addressed in aquatic ecology. The cost of the application of such measures, methods, or tools in terms of time and resources is a key aspect during the process. There is increasing pressure to solve questions in less time and using fewer resources. Therefore, the need to develop cost-effective measures to improve our knowledge of the aquatic environment is paramount. Examples, such as that presented by Boavida *et al.* (2018b), are needed to optimize the implementation of e-flow regimes in river reaches at a regional scale.

Future research on ecohydraulics should embrace not only a multidisciplinary team of biologists, ecologists, fluvial geomorphologists, hydrologists, hydraulicians, environmental and river engineers, natural resource managers, and conservationists, but ecohydraulics should also move forward and engage using interdisciplinary and transdisciplinary (i.e. engagement with end users) approaches.

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Macroinvertebrate indices versus microbial fecal pollution characteristics for water quality monitoring reveals contrasting results for an Ethiopian river

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Abstract

Awash River is one of the major surface water sources used by millions of people in the central Highlands of Ethiopia. However, numerous pollution sources exert significant pressure on the river. Different approaches for assessing the status of water quality exist, but few studies compared the performance of distinct methods. Therefore, this study aims to evaluate the consistency of fecal indicator bacteria for environmental health assessment of rivers by comparing them to assessments of physicochemical tests as well as newly developed macroinvertebrate indices. Physicochemical, biological (macroinvertebrates) and microbiological (*Escherichia coli* and Enterococci) parameters were assessed at five sites along the upper Awash River. For *E. coli* and Enterococci moderate to strong fecal pollution levels, ranging from 7.9 × 102 to 7.6 × 103 cfu/100 ml and 7.6 × 102 to 1.1 × 104 cfu/100 ml, were observed, respectively. The concentrations of both fecal indicator bacteria exceeded the standards set by the European Union and the World Health Organization for safe recreational water. Hence, all sites were categorized as poor for swimming and recreation. In contrast, three African benthic macroinvertebrate indices (South African Scoring System 5, Tanzanian River Scoring System, Ethiopian Biotic Score) indicated a natural or good water quality with slight ecological degradation at the upstream sites, and a moderate to poor ecological status at the downstream sites. While macroinvertebrate communities were able to reflect anthropogenic disturbances, mainly caused by different land uses, fecal indicator bacteria, most likely driven by the high pressure of extensive livestock fecal emission and overgrazing in the whole catchment, did not. This study underpins the necessity of combining different indicator systems to analyze human pressures in Africa in a holistic way, which can serve as a basis for management and sustainable use of fundamental resources such as water from freshwater ecosystems.

1. Introduction

Rivers and streams are vital ecosystems that sustain the life of humans and animals (Rajiv et al., 2012). In many countries, such as Ethiopia, rivers are essential water sources for domestic, agricultural, industrial and recreational (e.g., open bathing and swimming) purposes (Rochelle-Newall et al., 2015). However, such human uses have inevitably reduced the ecological integrity of lotic ecosystems (Atique and An, 2018, Wang et al., 2013). Although humans depend on intact river systems, numerous anthropogenic activities severely degrade the water quality in many systems (Ebenstein, 2012, Hayzoun et al., 2014, Nhiwatiwa et al., 2017), as the input of pollutants, e.g., through industrial discharges and non-point source like agricultural surface runoff, are common stressors (Bo et al., 2017, Chang et al., 2017, Zhao et al., 2014). Another frequent problem, especially in developing countries, is the microbial fecal pollution of rivers that has wide-ranging impacts on various human activities that require appropriate river water quality (Byamukama et al., 2000, Djuikom et al., 2006, Goshu et al., 2010, Kirschner et al., 2017). For example, in such countries, the local communities often depend on river water for drinking, domestic purposes, crop irrigation and watering of animals (Chigor et al., 2013).

In order to protect people as well as the environment, the water quality must comply with several physicochemical and microbiological standards before water can be used for drinking, farming or recreational purposes (Fewtrell and Bartram, 2001, Jerves-Cobo et al., 2018). Hence, water quality is monitored regularly by assessing different physicochemical, microbiological and biological parameters that are important for ecological and environmental health evaluations (Atique and An, 2018, Popović et al., 2016). Also globally, there is an increasing interest in monitoring freshwater ecosystems, aiming to improve their value for ecological, recreational and economic purposes (WFD, 2000, Lear et al., 2009).

The water quality of rivers depends on their physical, chemical and biological properties, whereby the biological quality is defined by the types of living organisms present in the water, as well as their abundance and diversity. In contrast to traditional physicochemical assessment techniques, biological indicators provide a cumulative measure of ecosystem health resulting from the combined responses of the targeted communities to all stressor types they encounter in the aquatic habitat (Lear et al., 2011, Tanaka et al., 2016). Therefore, by assessing species composition and community structure of a subset of organisms, biological indicators are very useful in providing an overall index of ecosystem health (Lear et al., 2009). Many groups of organisms have been used in the assessment of aquatic ecosystems, including periphyton (McPherson et al., 2005), diatoms (Gonçalves et al., 2008), benthic invertebrates (Armitage et al., 1983, Böhmer et al., 2004, Ofenböck et al., 2004), and fish (Naigaga et al., 2011). In Europe, almost 300 different biological assessment methods, based on various organism groups, are in use (Birk et al., 2012). Successful monitoring requires the ability to accurately describe ecological changes through quantitative indicators (Ryder & Miller, 2005). Therefore, biological indicators, such as fish, macroinvertebrates or diatoms, have been commonly used to provide an integrated measurement of water quality (Bae et al., 2014, Beyene et al., 2009, Lainé et al., 2014, Lear et al., 2009). However, in developing countries, of which many are situated in tropical regions, biomonitoring approaches for assessing river pollution have not yet been studied extensively (Elias et al., 2014), although in some countries, such as Ethiopia, the use of biological indicators to assess water quality is substantially increasing (Ambelu et al., 2013, Lakew, 2015, Lakew and Moog, 2015a, Lakew and Moog, 2015b, Mekonen et al., 2016, Woldeab et al., 2018). Particularly biotic indices using benthic macroinvertebrates have recently been developed and applied for conservation and management of aquatic resources in Ethiopia (Lakew & Moog, 2015b). Nevertheless, though benthic invertebrate indices are widely used in Europe, North America, Australia and South Africa, little information is available on their use and applicability for water quality monitoring in Ethiopia.

Furthermore, indicator bacteria can be used to investigate pollution of aquatic environments (Gotkowska-Plachta et al., 2016, Jin et al., 2004). The most commonly used indicators worldwide are *Escherichia coli* and Enterococci (EU Bathing Water Directive, 2006, Liška et al., 2015, USEPA, 1986). Fecal indicator bacteria are usually counted to evaluate the level of microbial water contamination. The abundance of these fecal indicator bacteria is supposed to correlate with the level of microbial fecal pollution (Byamukama et al., 2000, Byamukama et al., 2005) and health risks associated with river water (Koffi et al., 2011, Teklehaimanot et al., 2014).

The expanding population coupled with the quest for improved livelihoods have resulted in anthropogenic campaigns that have led to the continuous release of pollutants (including sewage) into virtually all environmental matrices (Liyanage & Yamada, 2017). Globally, contaminated water is a serious threat to human health and ecosystem integrity (Sabater et al., 2018). Although different approaches are used worldwide for assessing the status of water quality, their performance has not been empirically compared. To the best of the authors' knowledge, this is the first study to examine the consistency of fecal indicator bacteria as an indicator for the environmental health and human water usage related issues of rivers and compare it with standard physicochemical tests as well as with newly developed macroinvertebrate indices for ecological and biological water quality assessment.

2. Materials and methods

2.1. Description of the study area and sampling sites

This study was conducted along the upper Awash River, located in the central Ethiopian Highlands (Fig. 1). The river's source is on a high plateau of the central highlands west of Addis Ababa, at an altitude of about 3000 m a.s.l. (Kinfe, 1999, WGC and AwBA, 2013). The upper part of the catchment is characterized by headwater streams which are surrounded by indigenous forest (Chilimo forest). Chilimo forest is part of the dry Afro-montane forest dominated by mixed broad-leaved and coniferous trees such as *Juniperus procera*, *Podocarpus falcatus*, *Prunus africanum*, *Olea europaea*, and *Hagenia abyssinica*, and has an overall coverage

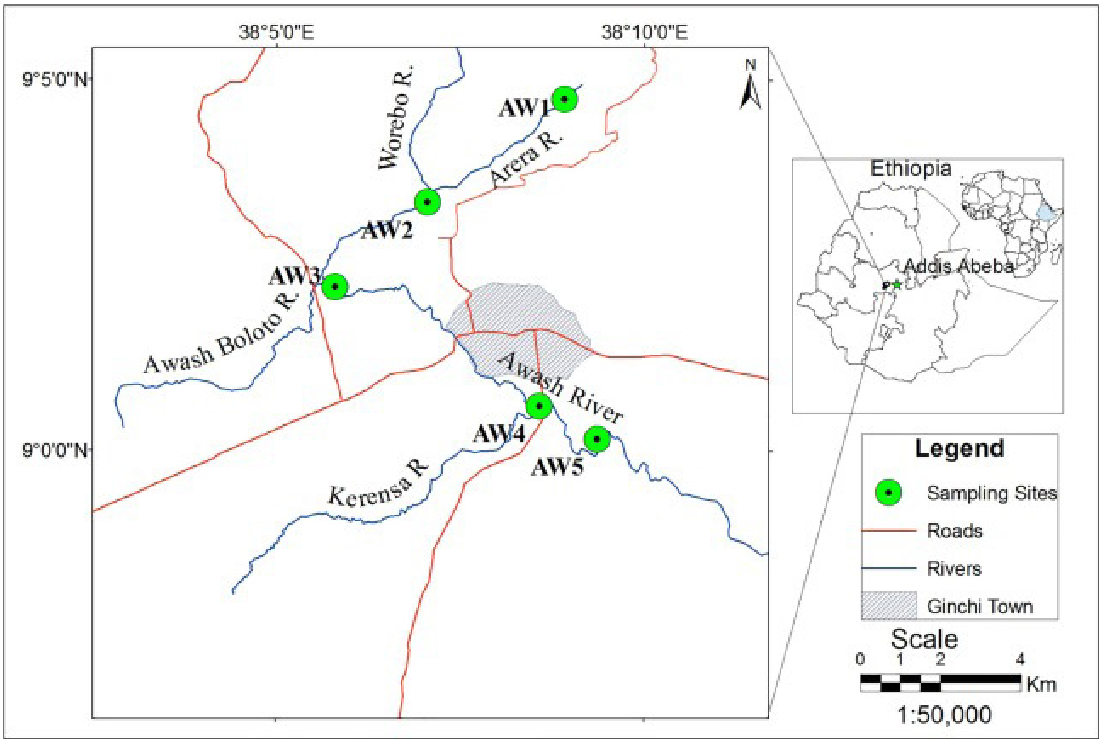

Fig. 1. Location of investigation sites along the upper section of Awash River, Ethiopia.

of about 5000 ha (Ameha et al., 2014, Getacher and Alemtsihay, 2012, Tesfaye, 2015). The lower part of the catchment is subject to a mixture of different anthropogenic activities. Farming, deforestation, urbanization, industrial uses, bathing and grazing are rather common. These anthropogenic activities, however, may lead to an enrichment of fecal bacteria (Paule-Mercado et al., 2016, Rochelle-Newall et al., 2015) and excessive nutrients into Awash River through, among others, open defecation around the riverbanks, in-stream washing of animals (i.e., cattle, donkeys, horses) and automobiles, wastewater releases from households as well as from one factory.

Sampling sites were selected along a pressure-gradient, ranging from river sections with high forest cover and fewer human interventions upstream to more degraded sites affected by multiple stressors downstream. In total, five representative sampling sites along an about 22 km long stretch were identified (Fig. 1; Table 1). The sites were not equidistant from each other because they were carefully chosen based on changes in anthropogenic pressure along the river section stretch. Sampling site AW1 lies within the Chilimo forest which is dominated by indigenous tree species. There are no human settlements in the area, and anthropogenic activities are minimal. Only some grazing livestock and wildlife animals can be occasionally observed. Site AW2 is located downstream of site AW1, at the confluence of two streams, the Arera and Worebo. The second site is mainly characterized by scattered human settlements in the forest and small-scale farming activities (vegetables and cereal crops) in the catchment. The forest around site AW2 is mainly dominated by indigenous (e.g., *J. procera*, *H. abyssinica*, *P. falcatus*) but also exotic (e.g., *Eucalyptus saligna*, *E. camaldulensis*, *Pinus patula*, *Cupressus lusitanica*) tree species. The communities living along AW2 use the river for domestic purposes. Site AW3 is located in the mid-section of the sampling reach, downstream from the inflow of Awash Boloto River, which joins the mainstream after passing through the grazing fields. Site AW4 is located directly downstream of Ginchi town, an urban area with a population of approximately 18,000. Various in-stream activities are present

Table 1. Sampling sites, geographic latitude and longitude, and land use characteristics around the sampling sites.

Sampling sites	Geographic latitude and longitude	Elevation (m a.s.l.)	Land use characteristics
AW1	N 9°05’19.00”, E 38°09’13.01”	2484	No human settlements; near-natural forest mainly dominated by indigenous tree species; wildlife such as monkeys and apes are present, as well as some grazing animals such as cattle and horses.
AW2	N 9°04’07.00”, E 38°08’23.02”	2459	Presence of few human settlements (approximately 75 households) in the mixed forest; small-scale farming; grazing of cattle, donkeys and horses.
AW3	N9°02’21.80”, E 38°05’52.05”	2254	River bank farming and grazing is common.
AW4	N 9°00’47.03”, E 38°08’53.33”	2208	Industrial waste released from a paper mill factory; rain-fed crop farming on the left bank of the river; regular washing of clothes, vehicles, and cattle in the river; animal watering; dumping of domestic wastes on the riverbanks.
AW5	N 9°00’08.94”, E 38°09’23.26”	2181	Rain-fed crop farming on both banks of the river; irrigation (for onions, cabbages, tomato and maize); sand excavation from the riverbed.

at site AW4, including washing of animals and vehicles, animal watering, open defecation, domestic waste dumping, waste disposal from a paper mill factory, and erosion/siltation from rain-fed crop farming. Site AW5 is mainly characterized by agricultural activities, such as rain-fed as well as irrigated crop farming, and sand excavation (Table 1).

2.2. Measuring of physicochemical parameters and fecal indicator bacteria

Measurement of physicochemical and microbiological parameters was conducted from March 2017 to February 2018. For each sampling site (AW1–AW5), twenty-four water samples were collected, respectively. Hence, in total, 120 samples were taken. Regarding physicochemical parameters, water temperature, Wtemp. (°C), dissolved oxygen, DO (mg/l), pH and electrical conductivity, EC (μS/cm) were measured in-situ with a multiparameter probe (Hach HQ 40d, USA). Water samples for the determination of total phosphorous (TP), orthophosphates (PO_4), nitrates (NO_3), and total suspended solids (TSS) were taken below the water surface in free-flowing river sections at a depth sufficient to exclude surface scum but without introducing bottom sediment. All samples were stored in ice-cooled boxes and then transported to the laboratory at Ambo University, Ambo, Ethiopia. Physicochemical parameters were determined following methods as described by EPA (1983).

Sterile glass bottles were used for water sampling to determine the status of fecal indicator bacteria (Goshu et al., 2010). After opening, the bottles were horizontally placed 30 cm below the water surface in a free-flowing river section, while the bottle mouth faced the water current. Bottles were moved against the river flow to capture 500 ml of water for fecal indicator bacteria analysis. All water samples were kept in an ice-cooled box and transported to the laboratory where they were analyzed not later than eight hours after collecting the first sample (Byamukama et al., 2005). Water samples were assessed for *E. coli* and Enterococci using a membrane filtration technique with Chromocult coliform agar for *E. coli*, and Slanetz Bartley medium for Enterococci (Merck, Darmstadt, Germany). To select against possible growth of background bacteria, Cefsulodin (5 mg dm−3 Sigma, Vienna, Austria) was added into Chromocult coliform agar. A range of volumes (0.001 to 100 ml) of water samples was prepared and filtered through 0.45 μm pore size and 47 mm diameter cellulose nitrate membrane filters (Sartorius, Vienna, Austria). For enumeration of *E. coli* and Enterococci, the membrane filters were placed onto the respective agar plates and incubated at 37 °C for 24 h for *E. coli* and 48 h for Enterococci. It should be noted that this study determined *Escherichia coli* and Enterococci concentrations in the investigated river system irrespective of where they come from as there is no guideline(s) currently existing for the techniques that track their source(s) in the environment.

The water quality was classified into one of four classes (Table 2) based on the 90th and 95th percentiles (see Eqs. (1), (2)) of *E. coli* and Enterococci in accordance with the EU Bathing Water Directive (2006). Also, the WHO guideline classification for microbial quality of recreational waters (WHO, 2003) was applied (the WHO guideline focuses only on Enterococcus, for which it requires the 95th percentile). For calculations of the percentiles (P), the arithmetic mean (μ) and standard deviations (σ) of all bacterial counts (log10 values) were obtained.

$$(1) \quad P_{90} = antilog\,(\mu + 1.282 \times \sigma)$$

$$(2) \quad P_{95} = antilog\,(\mu + 1.65 \times \sigma)$$

Table 2. Water quality category limits of the EU Bathing Water Directive (2006) for a colony forming unit (cfu/100 ml) of Enterococci and Escherichia coli in inland waters.

Parameter	Excellent quality	Good quality	Sufficient quality	Poor quality
Intestinal Enterococci (cfu/100 ml)	≤200[a]	201–400[a]	≤330[b]	>330[b]
Escherichia coli (cfu/100 ml)	≤500[a]	501–1000[a]	≤900[b]	>900[b]

a Based on 95th percentile.
b Based on 90th percentile.

2.3. Benthic macroinvertebrate sampling and analysis

Sampling of benthic macroinvertebrates was conducted from 19 to 20 February 2018. Macroinvertebrates were collected with a standard hand net with a frame size of 25 × 25 cm and a mesh size of 500 µs. For each sampling reach of 100 m river length, a multi-habitat sampling (MHS) scheme was implemented to sample all major habitat units according to their proportional representation within the investigation reach. A sample consists of 20 distinct sampling units which are collected from all microhabitat types which have at least a share of 5% of all habitats in the reach (Barbour et al., 1999, Moog, 2007). Sampling was conducted in upstream direction, starting from the most downstream sampling unit. After completion of one multi-habitat sample, the collected specimens of subsamples were combined in one homogenous sample and then preserved in 4% formaldehyde. In the laboratory, each multihabitat sample was passed through a set of sieves to separate different size classes of macroinvertebrates. Specimen of benthic macroinvertebrates were then sorted and counted to the family level, except Baetidae and Hydropsychidae which were identified to genus level. Three well-used African biotic indices were selected to assess the status of water quality and ecosystem health of Awash River, and to compare the results of the respective indices. Therefore, the South African Scoring System version 5 (SASS5) (Dickens & Graham, 2002), the Tanzanian River Scoring System (TARISS) (Kaaya et al., 2015), and the Ethiopian Biotic Score (ETHbios) (Lakew & Moog, 2015b) were used. The scoring systems (TARISS and ETHbios) are based on the SASS, underlining the necessity for index comparison. The score of these three biotic indices was calculated as the sum of sensitivity score of each taxon present in a sample (Eq. (3)).

$$(3)\quad \text{Biotic score} = \sum_{i=1}^{n} Score\ i$$

The Average Score Per Taxon (ASPT) was calculated as a total biotic score divided by the total number of taxa considered in the calculation, where score i is the score of taxon i and n is the number of taxa considered in the calculation (Eq. (4)).

$$(4)\quad \text{ASPT} = \frac{\sum_{i=1}^{n} Score\ i}{n}$$

2.4. Statistical analysis

The physicochemical data collected did not meet the assumptions of parametric tests, as confirmed by Shapiro-Wilk tests. Therefore, non-parametric Kruskal-Wallis H tests were used to determine the overall differences in physicochemical parameters among sites. The Mann-Whitney U test was used to conduct pair-wise post-hoc tests. Pearson correlations were carried out to determine the correlation between the fecal indicator bacteria variables (using the average value from each of the investigated sites) and the biotic scores, as well as between the different diversity indices of benthic macroinvertebrates. The data for the microbiological analysis was log-transformed (log x + 1) prior to analysis. To assess the status of the invertebrate community in relation to land use and environmental variables, a principal component analysis was conducted. All statistical tests were performed with IBM SPSS 20 and PC-ORD Version 5.33.

3. Results

3.1. Physicochemical parameters

Mean values of most physicochemical parameters, such as water temperature, pH, electrical conductivity, total phosphate, nitrate, orthophosphates and total suspended solids slightly increased from upstream to downstream sampling sites (Table 3). Five of eight measured physicochemical variables showed significant differences between the sampling sites ($p < 0.05$, Kruskal-Wallis H test). Only dissolved oxygen, total phosphorus and orthophosphates did not differ between the sites. Comparing AW1 and AW2, electrical conductivity was the only significantly different parameter between the two sites ($p < 0.05$, Mann-Whitney U test).

3.2. Concentrations of fecal indicator bacteria and assessment of bathing water quality

In general, the concentration of fecal indicator bacteria ranged from moderate to strong fecal pollution levels at the five sampling sites, according to the fecal classification scheme for river water (Kirschner et al., 2009), whereas concentration of indicator bacteria increased from upstream to downstream sampling sites (e.g., from 7.9 × 102 cfu/100 ml (AW1) to 7.6 × 103 cfu/100 ml (AW5) for *E. coli*, and from 7.6 × 102 cfu/100 ml (AW1) to 1.1 × 104 cfu/100 ml (AW5) for Enterococci.

The health-related water quality assessment for recreational environments showed that both, *E. coli* and Enterococci concentrations exceeded the threshold set by the EU Bathing Water Directive for the 90th and 95th percentile at all five sampling sites. Similarly, Enterococci concentrations exceeded the maximum WHO threshold at all sampling sites. Hence, based on both documents, all sampling points along the upper Awash River are not qualified for bathing as their water quality was classified as poor (Table 4).

Table 3. Summary statistics of environmental variables for the five sampling sites, showing the mean and the standard deviation (in brackets) for each physicochemical parameter (n = 5 sites × 24 measurements = 120 for all variables, except DO which was only measured 22 times).

Variable	AW1	AW2	AW3	AW4	AW5	Kruskal-Wallis H Test (p value)
Wtemp (°C)	13.05 (±2.49)	14.54 (±2.51)	21.17 (±2.86)	20.30 (±2.76)	19.74 (±2.11)	0.000**
pH	8.35 (±0.54)	8.52 (±0.57)	8.66 (±0.52)	8.48 (±0.61)	8.64 (±0.52)	0.024*
DO (mg l^{-1})	7.54 (±0.71)	7.47 (±0.63)	7.79 (±1.24)	6.91 (±0.86)	7.44 (±1.13)	0.058
EC (μs cm^{-1})	183.67 (±50.65)	247.92 (±94.45)	316.46 (±115.35)	366.13 (±175.28)	365.83 (±172.47)	0.000**
TP (mg·l^{-1})	0.11 (±0.06)	0.19 (±0.35)	0.29 (±0.44)	0.33 (±0.40)	0.37 (±0.47)	0.125
PO_4 (mg l^{-1})	0.037 (±0.026)	0.039 (±0.035)	0.041(±0.048)	0.048 (±0.058)	0.048 (±0.062)	0.942
NO_3 (mg l^{-1})	1.23 (±0.61)	1.37 (±0.81)	2.14 (±1.11)	2.19 (±1.24)	2.28 (±1.08)	0.000**
TSS (mg l^{-1})	62.84 (±104.25)	183.36 (±472.59)	681.99 (±1320.10)	690.20 (±1140.66)	673.96 (±1008.03)	0.000**

Wtemp = water temperature; DO = dissolved oxygen; EC = electrical conductivity; TP = total phosphorus; PO4 = orthophosphate, NO3 = nitrate; TSS = total suspended solids.
* = significant at the 0.05 level. ** = significant at the 0.01 level.

Table 4. Measured concentrations of E. coli and Enterococci in Awash River, and water quality classification based on the 90th and 95th percentiles according to the EU Bathing Water Directive (2006) and WHO guidelines for safe recreational water environments (2003).

Sampling site	Fecal indicator bacteria	Average[a]	±SD[a]	95th Percentile[b]	90th Percentile[b]	EU Bathing Water Directive (based on *E. coli* and Enterococci)	WHO guideline values (based on Enterococci)
AW1	*E. coli*	2.69	0.42	2400	1685	****	*****
	Entrococci	2.66	0.38	1917	1392	****	*****
AW2	*E. coli*	2.90	0.52	5701	3676	****	*****
	Entrococci	2.86	0.62	7549	4478	****	*****
AW3	*E. coli*	3.12	0.72	20,412	11,093	****	*****
	Entrococci	2.97	0.76	16,514	8,706	****	*****
AW4	*E. coli*	3.30	0.59	18,690	11,339	****	*****
	Entrococci	3.29	0.75	33,099	17,577	****	*****
AW5	*E. coli*	3.28	0.77	35,479	18,456	****	*****
	Entrococci	3.02	0.88	29,449	14,017	****	*****

SD = standard deviation.
a Values are log (x + 1 cfu/100 ml) transformed.
b Values are presented as cfu/100 ml.
**** Poor water quality class according to EU Bathing Water Directive.
***** Category D of WHO guideline values for microbial quality of recreational waters.

3.3. Status of benthic macroinvertebrate communities and comparison with microbial water quality classification

A wide range of physicochemical characteristics and land use types determines benthic invertebrate community structure in the Awash River. The principal component analysis showed that the presence of sensitive species (e.g., Leptoceridae, Heptageniidae, Lepidostomatidae, Ecnomidae, Simuliidae and Tipulidae) was associated with forest cover around the sampling site, while the presence of tolerant species (e.g., Oligochaeta, Chironomidae, Corbiculidae and Physidae) correlated with agricultural land (Fig. 2).

Two biotic indices, the South African SAAS5 and the Tanzanian TARISS, classified the five sampling sites exactly the same: AW1 and AW3 were categorized as "natural", AW2 as "good", AW4 as "fair", and AW5 as "poor". According to the Ethiopian ETHbios, the water quality of AW1–AW3 was classified as "good", whereas AW4 and AW5 were classified as "moderate" and "poor", respectively (Table 5). Based on a health-related assessment using the EU Bathing Water Directive and the WHO guideline values, however, all sites were classified as "poor" as the concentrations of fecal indicator bacteria exceeded the established thresholds (Table 5).

Pearson correlations were performed to assess the relation between the fecal indicator bacteria, the biotic indices for macroinvertebrates as well as selected metrics of benthic macroinvertebrates

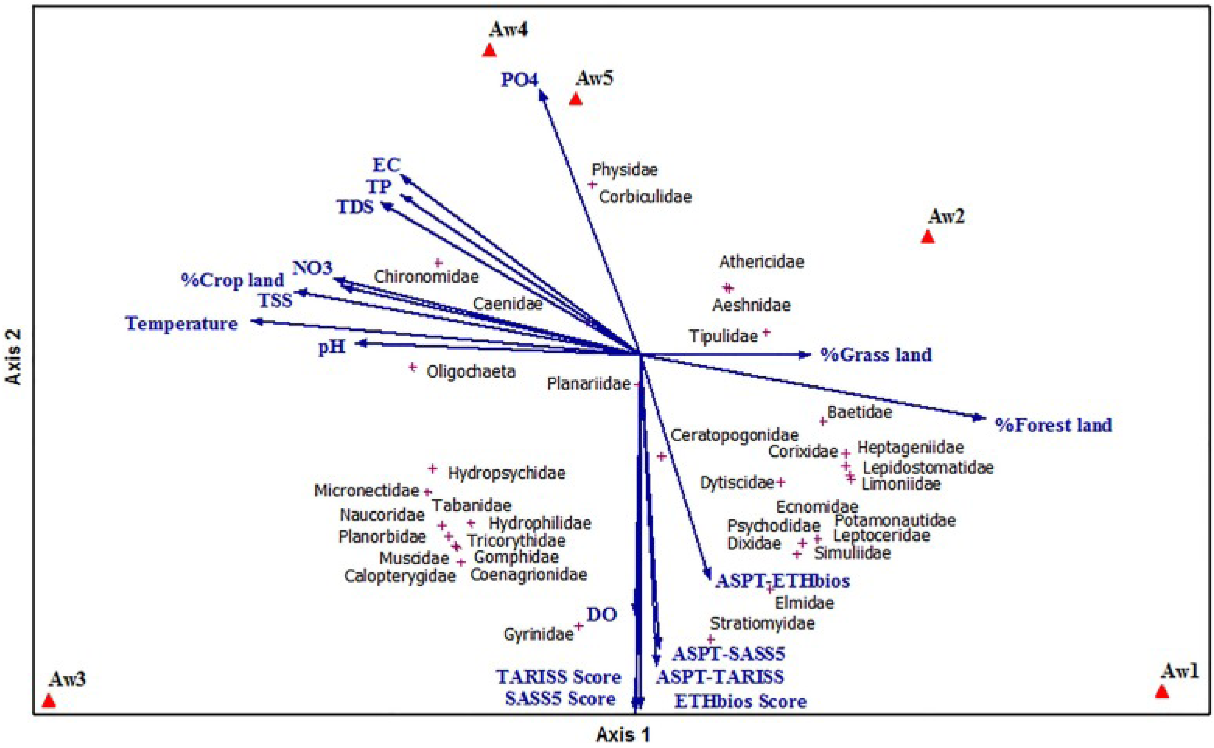

Fig. 2. Principal components analysis (PCA) biplot of macroinvertebrate community in relation to land use and environmental variables along sampling sites in the upper section of Awash River (the first two axes explain 72.15% of the total variance).

Table 5. Water quality classes obtained for each sampling site based on the biotic indices SASS5, TARISS, ETHbios, as well as the EU Bathing Water Directive (2006) and the WHO guideline values for microbial quality of recreational waters (2003).

Sampling Point	SASS5	TARISS	ETHbios	EU Bathing Water Directive (based on *E. coli* and intestinal Enterococci)	WHO recreational water quality guideline (based on intestinal Enterococci)
AW1	*	*	**	****	*****
AW2	**	**	**	****	*****
AW3	*	*	**	****	*****
AW4	***	***	***	****	*****
AW5	****	****	****	****	*****

Classification of ecological status according to the macroinvertebrate indices SASS5, TARISS, ETHbios: * = natural water quality, ** = good water quality with slight ecological degradation, *** = moderate water quality with significant ecological disturbance, **** = poor water quality with major degradation.

Classification of water quality class according to the EU Bathing Water Directive: **** = poor; according to WHO guideline values: ***** = category D.

(no. of taxa, percentage of Ephemeroptera and Trichoptera (ET) taxa). The correlation matrix (Table 6) shows that *E. coli* counts were strongly correlated with Enterococci abundance. However, concentration of both fecal indicator bacteria, *E. coli* and Enterococci, was negatively correlated with metrics of benthic invertebrates, such as number of taxa, percent of ET taxa, as well as the scores and ASPT values of the African biotic indices (SASS5, TARISS, ETHbios). The scores and ASPT values of the three indices were highly correlated with each other (>0.99 and >0.9, respectively), which was significant on the $p < 0.05$ level. The concentrations of fecal indicator bacteria rose as the impact of human pressure increased along the river in downstream direction. In contrast, however, the percentage of ET taxa, biotic scores and ASPT values decreased as the degree of anthropogenic pressures rose from AW1 to AW5.

4. Discussion

4.1. Physicochemical water quality parameters

In this study, we assessed and compared physicochemical water quality parameters, fecal indicator bacteria and benthic invertebrate communities along a pressure-gradient in the Awash River. We found that the levels of various physicochemical parameters increased from upstream to downstream sampling sites. In particular, the two sampling sites below the urban area of Ginchi town had significantly higher values for most physicochemical parameters (e.g., water temperature, electric conductivity, total phosphorus, nitrite and total suspended solids) when compared to upstream sites. Among others, some of these increases can be attributed to the presence of agriculture which often has great effects on water quality. For example, Goshu et al., 2010, Gotkowska-Plachta et al., 2016 reported high values of total suspended solids and electrical conductivity at sites which are mainly impacted by agricultural and urban activities. Furthermore, urbanization and deforestation in the lower sections of Awash River result in increased soil erosion and, subsequently, higher sediment loads and nutrient input into the river systems. The varying concentrations of orthophosphate and total phosphorus between the sampling sites might be caused by different land use types. Similarly, also Gotkowska-Plachta et al. (2016) reported that the lowest concentrations of both forms of phosphorus were measured in forested areas, whereas it was abundant in samples from agricultural and urban areas.

Regarding dissolved oxygen, the levels were the highest in the mid-section of Awash River (AW3), Nevertheless, these slightly higher values could be due to relatively abundant filamentous algae at this site. Similarly, Klose et al., 2012, Morgan et al., 2006 reported high DO concentrations during the day when filamentous algae were present.

4.2. Fecal indicator bacteria

In Awash River, concentrations of fecal indicator bacteria varied depending on the type of land use at immediate catchment area. Concentrations of *E. coli* and Enterococci were higher at sites close to urban and agricultural areas than at sites situated in forested areas. This pattern is similar to other studies which reported that densities of fecal indicator bacteria in the watershed exhibited a clear dependency on the land use type in the surrounding area (Gotkowska-Plachta et al., 2016). For example, Goto & Yan (2011) measured significantly higher concentrations of *E. coli* and Enterococci in the urban section of the stream than in the forested section. Similarly, in the Buffalo and Tyume River, South Africa, higher concentrations of fecal indicator bacteria were observed in lower river reaches as anthropogenic activities, such as

Table 6. Pearson correlation coefficients between pooled data of fecal indicator bacteria, selected macroinvertebrate metrics, and biotic indices for benthic invertebrates.

	E. coli	Enterococci	No. of taxa	% ET taxa	SASS5 score	TARISS score	ETHbios score	ASPT SASS5	ASPT TARISS	ASPT ETHbios
E. coli	1									
Enterococci	0.915*	1								
NO. taxa	−0.578	−0.408	1							
% ET taxa	−0.609	−0.739	−0.240	1						
SASS5 score	−0.628	−0.472	0.993	−0.149	1					
TARISS score	−0.612	−0.456	0.997	−0.176	0.999**	1				
ETHbios score	−0.676	−0.505	0.989	−0.105	0.997**	0.995**	1			
ASPT SASS5	−0.813	−0.699	0.900	0.189	0.941*	0.930*	0.951*	1		
ASPT TARISS	−0.817	−0.714	0.906	0.183	0.944*	0.935*	0.954**	0.998*	1	
ASPT ETHbios	−0.844	−0.697	0.869	0.239	0.914	0.900*	0.932*	0.992**	0.985**	1

* Correlation is significant at the 0.05 level.
** Correlation is significant at the 0.01 level.

urban influence, increased (Chigor et al., 2013, Sibanda et al., 2013). Also, studies conducted on the Belgian Zenne River and the Portuguese Ave River reported high levels of fecal indicator bacteria (*E. coli* and Enterococci) as anthropogenic factors increased along the river in downstream direction (Barbosa-Vasconcelos et al., 2018, Koffi et al., 2011).

According to several studies (e.g., Arnold et al., 2016, Benjamin-Chung et al., 2017), the majority of microorganisms harmful to health present in aquatic systems are of fecal origin. Contamination of bathing waters is, therefore, a serious environmental problem with potential negative effects on water users (Marion et al., 2010). However, in many parts of the world, such as in the Ethiopian Awash catchment, rivers and streams are used as open bathing and recreation areas. The standards of the U.S. Environmental Protection Agency (USEPA, 1986), the EU Bathing Water Directive (2006) and the World Health Organization guidelines for safe recreational water uses (WHO, 2003) are frequently applied for monitoring the bathing water quality criteria regarding bacteria. In Ethiopia, however, there is no guideline to monitor bathing water quality. Hence, in this study, we used the EU Bathing Water Directive and the WHO guidelines for classification of the environmental health status in terms of recreational activities of humans. Our results showed that concentrations of *E. coli* and Enterococci reflected critical to strong fecal pollution levels at the investigated sampling sites. According to EU and WHO water quality standards they had to be classified as poor water quality locations for bathing and recreational activities. According to Mayer et al., 2016, Reischer et al., 2013, this is a common outcome for rivers with a significant input of fecal pollution, such as upstream emissions from communal waste water treatment plants without further disinfection or non-point emissions from intensive livestock farming activities. Even though a study conducted on the Mur River, Austria, obtained concentrations less than those of our study, the numbers of fecal indicator bacteria were still too high at many sampling points, making the river not fit for recreational uses such as bathing (Kittinger et al., 2013). Similarly, high concentrations of fecal bacteria were also reported at some sampling points along the Danube River (Kirschner et al., 2017). Similar to our study, Gotkowska-Plachta et al. (2016) reported that all sampling sites, with the exception of a forested site, of Łyna River, Poland, were characterized by high levels of bacterial contamination and the water quality was, therefore, also classified as poor according to the EU Bathing Water Directive. Studying the Bufalo River, South Africa, Chigor et al. (2013) discovered that 71–79% of all water samples for fecal coliforms and 82–85% of all water samples for Enterococci exceeded the U.S. EPA and South African water quality guideline limits for recreational waters. As a violation of water quality guideline thresholds can pose serious health risk to people, it can be assumed that full contact activities, such as bathing, washing, or domestic uses, can endanger communities living along these rivers. In this regard, recent studies underlined the necessity to monitor the status of fecal indicator bacteria in rivers and streams to prevent unwanted health consequences in recreational areas (Abia et al., 2016, Arnold et al., 2016, Benjamin-Chung et al., 2017, Cordero et al., 2012, Marion et al., 2010). Communities in the upper Awash River basin, and especially the most upstream sampling points, however, not only use river water for outdoor bathing but also for drinking, domestic purposes and washing of clothes.

Recreational water with high fecal-associated bacterial content can lead to outbreaks of serious illnesses, causing hospitalization and even death (Centers for Disease Control and Prevention, 2015). Children, in particular, are among the highest risk group because they tend to play for longer periods in such water bodies and may swallow water during swimming. Moreover, in Eastern Africa, children commonly fetch water for household consumption which increases the frequency they are in contact with the river water. Indeed, Arnold et al. (2016) highlighted that, in the United States, the youngest children showed high gastroenteritis risk and associated burdens related to recreational water exposure. In addition to recreational and household activities, the community in the upper section of Awash River uses water for small-scale irrigation to grow vegetables, such as onions, cabbages and tomatoes, which are consumed fresh. Human pathogens present in irrigation water can, therefore, be transmitted to plants and subsequently passed on to humans through consumption of vegetables irrigated with surface water that may contain pathogens (Pachepsky et al., 2011). According to Herman et al. (2015), such disease outbreaks show a larger association to leafy vegetables than to other food types. Similarly, Chigor et al. (2013) showed that 89% of all water samples of unrestricted irrigation of crops likely to be eaten uncooked exceeded the U.S. EPA and South African water quality guidelines for fecal coliform bacteria. Therefore, the presence of higher fecal indicator bacteria concentrations in the irrigation water of farming communities along the Awash River suggests that fecal pollution levels and thus the potential presence of enteric pathogens are likely a public health threat and thus should be considered in the future.

4.3. Macroinvertebrates

We found that longitudinal diversity of macroinvertebrates was affected by land use and physicochemical parameters. The presence of tolerant species (e.g., Oligochaeta, Chironomidae) was strongly associated with surface area of agricultural land around the sampling site. In contrast, the presence of sensitive species was strongly associated with forested land. Hence, sensitive taxa mostly occurred in the two upstream sampling sites with high forest coverage.

In previously established taxa scores, e.g., ETHbios, sensitive taxa such as Leptoceridae, Heptageniidae, Lepidostomatidae, Ecnomidae and Simuliidae obtained relatively high taxa score values for the same study area in the upper Awash river basin (Lakew & Moog, 2015b). High values of PO_4, NO_3, EC, TP, temperature and TSS were strongly associated with downstream sampling sites where tolerant taxa, such as Oligochaeta and Chironomidae were relatively abundant. Also, Ghani et al. (2018) reported that Oligochaeta, which are very tolerant to pollution were found in high abundance in a polluted urban river. The high presence of sensitive macroinvertebrate taxa at upstream sites, as well as the high abundance of tolerant taxa at the downstream sampling sites, shows that upstream sampling sites are less exposed to human disturbances. A similar pattern was also found in previous studies (Barbosa-Vasconcelos et al., 2018, Herringshaw et al., 2011, Lakew, 2015), which indicates that the land use type within watersheds has considerable effects on biological communities in streams and rivers.

The principal component analysis also showed that the biotic indices were positively correlated with forestland and shrubland on the first axis. In this study, DO content significantly correlated with all biotic indices at the middle section of the river where the concentration of DO is highest, which reflected its desirable association with the macroinvertebrates. Furthermore, the intolerant species such as Ephemeroptera (Baetidae, Caenidae, Heptageniidae and Tricorythidae) and Trichoptera (Hydropsychidae, Lepidostomatidae, Ecnomidae and Leptoceridae) contributed to the high score of the three biotic indices (SAAS 5, TARISS and ETHbios). Hence, calculated biotic indices scores and principal component analysis showed their tendency to classify the upstream section of the rivers as having clean water quality.

The three African benthic macroinvertebrate-based biotic scores indicated a natural or good water quality with slight ecological degradation at the upstream sites, and a moderate to poor ecological status at the downstream sites. Comparing the biological indices, the results revealed that the South African SASS5 and the Tanzanian TARISS classified all sampling sites into the same ecological water quality class. In contrast, the Ethiopian index ETHbios classified two sampling sites different than the other two indices. Therefore, based on water quality classes of each of the sampling sites, ETHbios only had a 60% overlap with SASS5 and TARISS, which indicates that the results of the three biotic indices showed high similarities with each other.

4.4. Comparison of fecal indicator bacteria and benthic macroinvertebrates as indicators of water quality

We hypothesized that, in the Awash River, the population of fecal indicator bacteria and benthic macroinvertebrates would both be a reliable community indicator of ecological health of a freshwater system exposed to different land use types. The results indicate that the benthic invertebrate indices were effective tools for monitoring the biological quality and ecological status of the upper Awash River. All three macroinvertebrate indices were able to reflect the gradient of anthropogenic disturbances, presumably caused by changes in land use type from natural forests in the headwaters to highly modified agricultural landscapes in the lower reaches. In contrast, communities of fecal indicator bacteria were not able to indicate land use changes along the river. Although, in some studies, the fecal indicator bacteria analysis was sensitive to discriminate between the most impacted and the least impacted sites (Barbosa-Vasconcelos et al., 2018, Gotkowska-Plachta et al., 2016), this was not the case in our study, as the occurrence of fecal indicator bacterial, which was mainly driven by the high pressure of extensive livestock overgrazing in the entire catchment, could not distinguish heavily impacted sites by fecal pollution and other anthropogenic pressures from less impacted sites. Hence, this is the first study reporting the contrasting results of water quality status from fecal indicator bacteria and macroinvertebrates during water quality analysis. Consequently, there is a necessity of combining different indicator systems to analyze human pressures from a more holistic perspective, which can serve as a basis for integrated management and sustainable use of fundamental resources such as water from freshwater ecosystems.

5. Conclusion

The study compared physicochemical parameters, fecal indicator bacteria (*E. coli* and Enterococci) as well as benthic macroinvertebrate indices as indicators of water quality in the upper Awash River, Ethiopia. We found that river water quality decreased in downstream direction which reflected the effect of anthropogenic (land use) activities in the catchment which may be attributed to agricultural and urban runoff, waste from a paper mill factory, and various instream activities. Except for dissolved oxygen and water temperature, tested physicochemical parameters and fecal indicator bacteria levels increased from upstream to downstream sampling sites, while biotic indices values decreased. While the assessment of fecal indicator bacteria resulted in a poor classification of all sites if used for bathing and recreational activities, the macroinvertebrate indices generally resulted in better status classes and were able to reflect land use changes along the river. Nevertheless, as the overall bacteriological water quality in Awash River was classified as poor, its use for unrestricted irrigation of fresh produce, full contact recreation, and domestic purposes may cause significant public health hazards. In the interest of public health, future research should focus on the assessment of these surface waters for the presence of bacterial, viral and protozoan pathogens. Also, in order to identify fecal indicator bacteria sources, microbial source tracking should be performed. Provision of adequate sanitary infrastructure and public health education will help to prevent water source contamination from fecal pollution.

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water

Communication

Oxygen Depletion Affects Kinematics and Shoaling Cohesion of Cyprinid Fish

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Abstract: Numerous anthropogenic stressors impact rivers worldwide. Hypoxia, resulting from organic waste releases and eutrophication, occurs very commonly in Mediterranean rivers. Nonetheless, little is known about the effects of deoxygenation on the behavior of Mediterranean freshwater fish. To fill this knowledge gap, we assessed the impact of three different dissolved oxygen levels (normoxia, 48.4%, 16.5% saturation) on kinematics indicators (swimming velocity, acceleration, distance traveled) and shoaling cohesion of adult Iberian barbel, *Luciobarbus bocagei*, a widespread cyprinid species inhabiting a broad range of lotic and lentic habitats. We conducted flume experiments and video-tracked individual swimming movements of shoals of five fish. Our results reveal significant differences between the treatments regarding kinematics. Swimming velocity, acceleration, and total distance traveled decreased stepwise from the control to each of the two oxygen depletion treatments, whereby the difference between the control and both depletion levels was significant, respectively, but not between the depletion levels themselves. Shoaling cohesion showed dissimilarities between the treatments regarding the maximum distance between fish, as the high depletion treatment differed from each of the other two, indicating that under severe oxygen depletion some individuals move away from the shoal. Overall, our results show how oxygen depletion changes fish behavior, which may entail ecological responses, highlighting the need to maintain an unfragmented river network to ensure movement dispersal among habitats, thus providing conditions for species escapement from hypoxia.

Keywords: dissolved oxygen; anoxia; fish behavior; fish school; laboratory flume; video-tracking

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1. Introduction

Mediterranean rivers are characterized by frequent hydrological disturbances, including seasonally predictable drought events, exposing biota to harsh environmental conditions [1]. An extensive period of low summer flows naturally leads to an increase in temperature and primary production, and subsequently to a reduction of oxygen levels [2]. Mediterranean fish populations are adapted to naturally occurring seasonal oxygen fluctuations [1]. However, human activities, such as water abstraction, the discharge of organic wastes, and the diffusion of agricultural fertilizers into aquatic systems, are common problems in Mediterranean rivers, causing further diminishment of oxygen levels of already stressed freshwater systems and possibly leading to hypoxic conditions [3,4] that affect fish and subsequently the entire aquatic community [3–6].

Hypoxic conditions can cause behavioral and physiological stress in fish [7], which can entail many ecological consequences, including impaired reproduction, feeding, and predator avoidance [8,9]. Regarding swimming activity, fish experience a trade-off between activity increase as they try to find more oxygenated water and activity decrease due to lower oxygen availability [10]. When exposed to hypoxia, fish groups may reduce their school density and size as they tend to increase their horizontal spacing to one another in a tentative manner to counteract the limiting effect of oxygen depletion on schools [5]. However, this may cause disadvantages, such as lower coordination or higher energetic costs of locomotion [11]. Both activity changes, individual fish movements and shoaling cohesion, are, however, species-dependent and are influenced by the degree of hypoxia [5,9]. Too low oxygen saturation will at some point be lethal for fish, whereby the lethal concentration also differs between species [12].

The Mediterranean region has been identified as one of the most prominent hot spots of climate change [13]. According to future predictions of climate change for Southern Europe, precipitation will decrease by up to 20% [14], which will also entail significant changes in seasonal runoff asymmetry [15]. Hence, exacerbated and extended summer low flow conditions, in combination with existing human pressures, will likely increase the frequency and duration of hypoxic events in rivers [1,15,16]. To protect and manage rivers, it is vital to understand the impact of deoxygenation on individual fish movements, schooling behavior, and the implications thereof for fish populations, which are a pivotal component of aquatic ecosystems.

To our knowledge, no study has assessed the effects of oxygen depletion on the movements of Mediterranean freshwater fish. Therefore, this work analyzed the impact of three different dissolved oxygen levels on the behavior of a common fish species of the Iberian Peninsula, the Iberian barbel, *Luciobarbus bocagei*. We hypothesized that increasing levels of oxygen depletion would (1) reduce fish movement and (2) decrease the cohesion of fish shoals.

2. Materials and Methods

We conducted flume experiments in a section (2.0 × 1.0 m) of an artificial channel, set at a slope of 3% and a discharge of 28 $L \cdot s^{-1}$, resulting in a water depth of 0.7 m. We caught 75 wild adult Iberian barbel, *Luciobarbus bocagei* (150–250 mm total length), via electrofishing in the Lizandro River, Portugal (33 m a.s.l.), and brought them to the lab facilities (92 m a.s.l.), where they were held in three 800 L tanks (25 fish per tank) in a controlled environment for 48 h before experimentation. After the trials, fish were returned alive to the river. Further details on fish sampling, holding, and the testing facility are given in Branco et al. [17,18] and Santos et al. [19].

In each experiment, we monitored the movement of a shoal of five fish [20] under three levels of dissolved oxygen (DO) conditions: (1) a control level (normoxic condition with DO saturations >80% [21]), (2) a mild depletion level of 48.4% DO saturation (4.4 ± 0.2 $mg \cdot L^{-1}$), and (3) a high depletion level of 16.5% DO saturation (1.4 ± 0.1 $mg \cdot L^{-1}$) (Table 1). These levels allowed for testing along a decreasing gradient, whereby the latter represents a level of extreme oxygen depletion that may induce stress or even death in fish [6,22]. We reduced oxygen values by adding sodium sulfite (Na_2SO_3). This compound is a recognized oxygen scavenger [23] that has been used to create oxygen-deficient conditions in fish research [18,24], as well as in aquatic research more generally [25,26]. Each experiment lasted for eight minutes (six min acclimation [27] plus two min video-tracking) and was replicated five times, whereby a new subset of fish was used for each trial, giving a total of 75 tested fish.

The experiments were conducted in strict accordance with ethical provisions on the welfare of experimental animals enforced by the European Union and were coordinated by J.M. Santos, who holds FELASA level C certification (www.felasa.eu) to direct animal experiments. Fish sampling permits were obtained from the Institute for Nature Conservation and Forests (ICNF). Fish experiments and maintenance in the laboratory and experimental facility were authorized by the Department for Health and Animal Protection (Direcção de Serviços de Saúde e Protecção Animal; permit issued on 6 October 2011) in accordance with the recommendations of the "protection of animal use for experimental and scientific work".

We recorded fish movements with a GoPro Hero 3 Black edition camera mounted above the channel. The camera was set to record at 1280 × 720 pixels. We processed the videos with GoPro Studio to exclude the fisheye effect and then analyzed them at 10 frames per second, resulting in 1200 data points per single fish (Table 1) with the software Tracker (http://physlets.org/tracker/), whereby we calibrated the measurement settings of each video with the size of the channel's bottom tiles (20 × 20 cm).

Table 1. Physiochemical and biological description of the experiments (average values ± SD), and number of analyzed videos and frames per treatment.

	Variable	Treatments		
		Control	**Mild Depletion**	**High Depletion**
Water quality	O_2 (%)	(Normoxia)	48.4 ± 1.9	16.5 ± 1.2
	O_2 ($mg \cdot L^{-1}$)	(Normoxia)	4.4 ± 0.2	1.4 ± 0.1
	Temperature (°C)	19.4 ± 0.4	19.6 ± 0.3	22.7 ± 0.1
	Conductivity ($\mu S \cdot cm^{-1}$)	152 ± 4.5	492 ± 16.4	738 ± 33.4
	pH	8.1 ± 0.1	8.2 ± 0.1	8.4 ± 0.1
Fish	Total length (mm)	202 ± 23.9	213 ± 29.2	191 ± 33.0
	Body mass (g)	81 ± 27.5	94 ± 37.5	70 ± 37.7
Video	Analyzed videos	5	5	4 [1]
	Analyzed frames	30,025	30,025	24,020 [1]

[1] Due to a technical video failure, one replicate of the high depletion treatment level had to be excluded from further analysis.

We calculated kinematics indicators, i.e., mean swimming velocity ($cm \cdot s^{-1}$), acceleration ($cm \cdot s^{-2}$), and distance traveled (cm) for every single fish to investigate spontaneous locomotion activity changes between DO treatments [27]. To test for differences in shoaling cohesion between treatments, we measured the horizontal (XY) inter-individual distance between all fish within a shoal, based on center of mass [27,28], whereby we used the average of the minimum, mean, and maximum values as a proxy for the shoal cohesion. In all analyses, we first tested for overall statistical significance between the treatment levels. If this was detected, it was followed by pair-wise post-hoc tests. For most of the tests, data did not fulfill all assumptions required for parametric tests. Therefore, omnibus tests were conducted with the non-parametric Kruskal-Wallis H test, followed by Dunn's pairwise tests (adjusted using the Bonferroni correction) ($\alpha = 0.05$) using SPSS 24. The dataset to this article can be found online in the Supplementary Material Section (Datasheet S1).

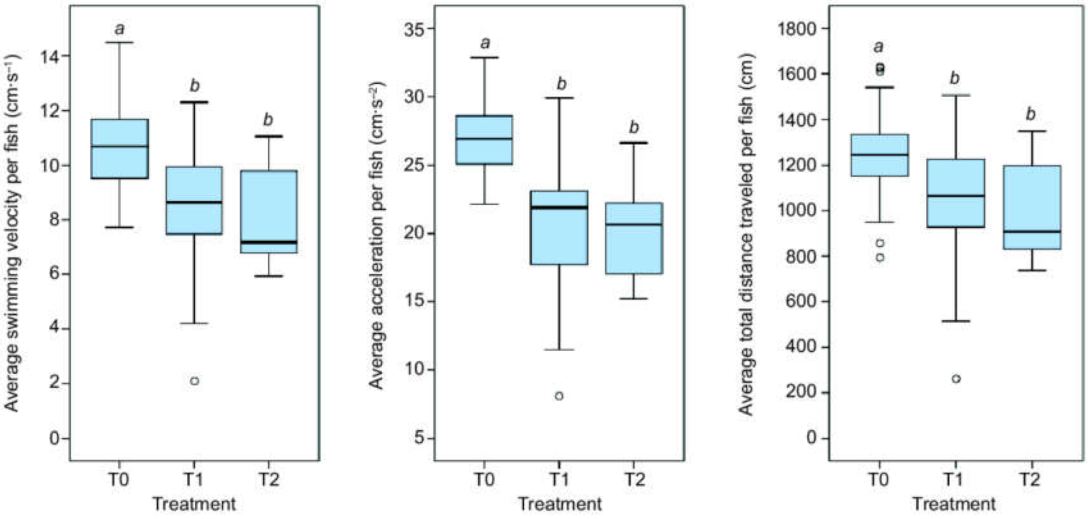
3. Results

3.1. Kinematics

We detected significantly different swimming velocities between the treatments ($\chi^2 = 21.37$, $p < 0.001$, Figure 1a). Pairwise comparison found that fish in the control treatment (T0) swam faster than those in the mild depletion treatment (T1) ($\chi^2 = 18.92$, $p < 0.01$), as well as those in the high depletion treatment (T2) ($\chi^2 = 26.96$, $p < 0.001$), whereas the mild and high depletion treatment (T1 and T2) were not distinct from each other. The average swimming velocity was 10.8 (±0.3 Standard Error (SE)), 8.6 (±0.5 SE), and 7.9 (± 0.4 SE) $cm \cdot s^{-1}$ for T0, T1, and T2, respectively.

For acceleration, we found a similar pattern ($\chi^2 = 34.26$, $p < 0.001$, Figure 1b), whereby the pairwise comparison was highly significant for both T0 and T1 ($\chi^2 = 27.40$, $p < 0.001$), as well as T0 and T2 ($\chi^2 = 32.04$, $p < 0.001$). Average fish acceleration was 27.1 (± 0.6 SE), 20.7 (± 1.0 SE), and 20.3 (± 0.7 SE) $cm \cdot s^{-2}$ for T0, T1, and T2, respectively.

We found significant differences in the total distance traveled by each fish among the treatments ($\chi^2 = 13.10$, $p < 0.001$, Figure 1c), though pairwise comparison revealed that fish only traveled longer distances in T0 (1247 cm ± 44.0 cm SE) when compared to T2 (987 cm ± 45.6 cm SE) (χ^2 = 21.51, $p < 0.001$). T0 and T1 (1055 cm ± 57.2 cm SE) were marginally significant (χ^2 = 13.76, $p = 0.050$).



(**a**) (**b**) (**c**)

Figure 1. Fish kinematics. (**a**) Average swimming velocity, (**b**) acceleration, and (**c**) distance traveled per fish in the three treatment levels: T0 = control, T1 = mild depletion, T2 = high depletion; "a" and "b" above the boxplots indicate a significant difference between two treatments, whereby the same letter indicates no statistically significant difference by Kruskal-Wallis test.

3.2. Shoaling Cohesion

Average minimum distances between fish ranged from 8.5–14.4 cm, mean distances from 46.6–67.8 cm, and maximum distances from 82.2–124.5 cm (Table 2). Regarding the minimum and mean distance between the fish, we did not detect differences between the three treatments. However, for the maximum distance between fish, we found significant dissimilarities between the treatments (Table 2), as the distance between fish was higher in T2 when compared to T0 ($\chi^2 = -15.02$, $p < 0.05$) as well as T1 ($\chi^2 = -16.90$, $p < 0.05$).

Table 2. Average minimum, mean, and maximum distances (cm ± SE) between fish within a shoal during the three treatments.

	Distance (cm ± SE)		
Treatments	**Minimum**	**Mean**	**Maximum**
T0—Control (normoxia)	14.4 ± 2.7 ^{a}	48.3 ± 8.5 ^{a}	82.2 ± 16.0 ^{a}
T1—Mild depletion (48.4% DO)	8.5 ± 0.9 ^{a}	46.6 ± 6.7 ^{a}	88.4 ± 13.0 ^{a}
T2—High depletion (16.5% DO)	10.5 ± 0.4 ^{a}	67.8 ± 15.4 ^{a}	124.5 ± 26.0 ^{b}
Kruskal-Wallis test	$\chi^2 = 1.16$, $p = 0.56$	$\chi^2 = 4.77$, $p = 0.09$	$\chi^2 = 8.89$, $p < 0.01$

"a" and "b" indicate a significant difference between two treatments, whereby the same letter indicates no statistically significant difference by Kruskal-Wallis test.

4. Discussion

Hypoxic events affect Mediterranean rivers worldwide [2,29], and fish, in particular, are highly sensitive to reduced oxygen concentrations [9,30]. The ecological impact of such events ranges from beneficial to mortality [31], but common responses include behavioral alterations [5,9,18].

4.1. Kinematics

Our results showed that swimming velocity, acceleration, and distance traveled significantly differed between the treatment levels. Pair-wise tests revealed that fish in the control treatment exhibited higher spontaneous activity than those in the mild depletion as well as high depletion treatment, which implies that barbel reduce their activity if DO values are lowered. A similar behavioral response is documented for several other species [9,32]. Such lowered activity can be interpreted as an adaptive energy-saving response [33]. *Carassius carassius*, e.g., reduces its locomotor activity to 50% of that during normoxia when exposed to prolonged periods of anoxia, thereby saving 35–40% of total energy consumption [34]. Swimming speed of *Ammodytes tobianus* decreased by 95% after 40 min at the lowest stepwise reduced critical partial pressure of oxygen (3.1 kPa) [32]. Even though the acclimation phase and analysis time in our study were short, fish responded quickly to decreased DO levels by significantly reducing their movement activity.

4.2. Shoaling Cohesion

Under low DO (20%) conditions, school measurements of *Clupea harengus* significantly increased [35]. We found a similar pattern regarding the maximum distance between individuals at the high depletion treatment in comparison to both the control and the mild one, whereas this was not the case for the minimum and average distance. Nevertheless, this might indicate that at approximately 15% DO, some barbel start to depart from the shoal, while others still seem to prefer the close vicinity of the shoal. In such high oxygen depleted situations, individual movement appears to override shoal movements as individuals risk leaving shoal protection to find more oxygenated areas further away, thus reducing shoal integrity by splitting the shoal into two or more groups [11].

4.3. Ecological Implications

In natural situations, fish might try to escape unfavorable conditions. In a hypoxic environment, *Oncorhynchus mykiss* selected lower temperature ranges, enhancing their chance of survival [36]. In the confined flume section of the present study, barbel seemed to reduce their swimming activity, possibly adopting a “sit-and-wait” strategy, which has also been described for other species [5]. In connected pool habitat experiments, however, barbel continued to move despite reduced oxygen levels, possibly searching for higher-oxygenated areas. Nevertheless, the number of movements significantly decreased under low (15%) DO concentrations [18]. Under such oxygen-depleted conditions, isolated habitats may, therefore, cause severe threats to stream fish, highlighting the need to maintain an unfragmented river network to ensure movement dispersal among habitats, and thus providing conditions for species escapement from hypoxia.

In our experiments, the addition of sodium sulfite not only reduced DO levels but also led to an increase in water temperature, conductivity, and pH, making it difficult to completely disentangle the effects of lowered DO from the increase of the other parameters. Nevertheless, similar changes in these variables can often occur with the release of organic stressors, such as sewage, into rivers [18,25]. To increase understanding of fish resistance to oxygen-depleted conditions and its implications for aquatic ecosystems, future studies should investigate the effects of long-term DO depletion on riverine fish species.

Supplementary Materials: The following are available online at http://www.mdpi.com/2073-4441/11/4/642/s1, Datasheet S1: Fish tracking data (kinematics and shoaling).

Author Contributions: Conceptualization, T.F. and P.B.; methodology, T.F., P.B., and J.M.S.; formal analysis, P.B., J.M.S., and D.S.H.; investigation, D.S.H.; data curation, D.S.H.; writing—original draft preparation, D.S.H.; writing—review and editing, D.S.H., P.B., J.M.S., and T.F.; visualization, D.S.H.; supervision, P.B. and T.F.; project administration, T.F., P.B., and J.M.S.; funding acquisition, T.F.

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MANAGEMENT BRIEF

Snorkeling-Based Fish Stock Assessment by Anglers—A Valuable Method for Managing Recreational Fisheries

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Abstract

Periodic assessment of harvested fish populations is essential for their sustainable management. A potential alternative to costly and resource-intensive electrofishing estimates in clearwater streams is the noninvasive snorkeling method. To assess the utility of snorkeling for the angling community, we compared underwater fish counts carried out by novice snorkelers to state-of-the-art electrofishing depletion estimates. Over two consecutive years, we sampled subadult and adult Brown Trout *Salmo trutta* and Rainbow Trout *Oncorhynchus mykiss* with both methods in a fourth-order mountain stream. In each year, a new team of novice snorkelers collected the data. In total, 12 riffle, pool, and run habitats were sampled, and the homogeneity of abundance and size-class distribution between the two methods was analyzed. Over both years, we could detect differences in 6 of 24 habitat × species configurations and in 10 of 72 habitat × species × size-class configurations. Species-specific behavioral traits and differences in the physical character of the habitats were responsible for a divergence in performance between the two methods. Overall, the observed effects were statistically interpreted as weak, as shown by local tests and the indicated low effect sizes. Snorkeling efficiency, however, remained affected by the effort and abilities of the team, as indicated by the year-by-year comparison. We conclude that in clearwater trout streams, snorkeling can be an appropriate substitute method for the widespread, autonomously organized angling community to gather data and build a sound foundation for fisheries-related decision making, if limitations are considered.

The growing threat to freshwater ecosystems (Vörösmarty et al. 2010) and the need to protect and restore them present a major challenge of the 21st century (Dudgeon et al. 2006). A multitude of impacts on freshwater biodiversity has been identified (Dudgeon et al. 2006), including recreational angling, which plays an influential (Cooke and Cowx 2004) and versatile role in the global fish crisis. Although anglers contribute to the conservation of freshwater fish and their habitats (Cooke et al. 2016), anglers' responsibility for biological impacts is increasingly recognized (Lewin et al. 2006). Both aspects frame anglers' area of influence and emphasize their obligation to actively participate in the application of ecosystem-based management practices (Arlinghaus et al. 2002; Pikitch et al. 2004; Hughes et al. 2005). In doing so, the study of quantitative data and life history parameters is crucial for the exploration, monitoring, assessment, and sustainable management of wildlife populations (Lebreton et al. 1992; Ludwig et al. 1993; Post et al. 2002). Especially in Europe, fishing

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rights owners, recreational fishermen, fishing clubs, associations, or reach stewards are responsible for managing the fisheries resources themselves (Arlinghaus et al. 2002). Contrary to their responsibility and due to the elaborate acquisition of data with conventional methods, such as electrofishing (Reynolds 1996), representatives of the angling community often refrain from collecting data on managed (i.e., harvested) fish stocks.

Electrofishing has many advantages, such as the precise measurement of individuals and applicability under a broad spectrum of environmental conditions. However, electrofishing also includes associated disadvantages, such as size selectivity (Mullner et al. 1998; Reynolds and Kolz 2012), the potential for lethal or sublethal harm to the fish (Nielsen 1998; Schreer et al. 2004; Reynolds and Kolz 2012), high cost, and the need for specially trained personnel to achieve safe and effective application (Hankin and Reeves 1988). An alternative method is direct observation by snorkeling. The potential benefits of this survey method include cost and time reductions for acquiring and maintaining equipment (Hankin and Reeves 1988; Thurow et al. 2012), lowering physical disturbance to and impact on the observed populations (Thurow et al. 2012), simultaneous observations of associated microhabitat characteristics (Heggenes et al. 1991), and easier application in remote locations (Dolloff et al. 1996). Considering the lower costs and practicability, counting game fish populations by snorkeling may be a well-suited tool for the angling community to easily acquire data that are relevant for management actions. The knowledge of some stock parameters, such as stock density and population structure, can already be sufficient to provide decision-making aids necessary to implement and adapt fishing regulations, especially if these parameters are regularly monitored (Unfer and Pinter 2018).

In the present study, we compare abundance estimates and the size distribution of Brown Trout *Salmo trutta* and Rainbow Trout *Oncorhynchus mykiss* sampled by electrofishing and snorkeling from three habitat types in a clearwater stream. It is often claimed that the efficiency of an assessment relies on the training and expertise of the snorkelers (Chamberland et al. 2014; Macnaughton et al. 2015). Our snorkeling counts were performed by surveyors with no previous snorkeling experience; this allowed us to test whether inexperienced individuals can generate good-quality data.

METHODS

Study area.— The study river is a fourth-order, prealpine trout stream (Ybbs River) draining off the Northern Limestone Alps in Austria. To determine representative sampling units, we assessed basic habitat characteristics according to Frissell et al. (1986) and Jowett (1993) in September during low-discharge conditions of 2.0 m^3/s between the town of Maierhoefen and the mouth of Seebach, a small tributary (Figure 1). The reach morphology corresponds to the pool–riffle river type described by Montgomery and Buffington (1997). The catchment size at the lower end of the pool–riffle section amounts to 117.9 km^2, with a mean annual discharge of about 4.5 m^3/s. For the method comparison, we chose 12 habitat units (4 pools, 4 riffles, and 4 runs; Figure 1) located within the pool–riffle system; their elevation ranged from 641 to 624 m above sea level. The investigated habitat units had a total length of 1,051 m and were distributed over a range of 5.5 km (Figure 1). The lower six habitats are subject to long-term monitoring (20 years) in which the fish stock is sampled every year using electrofishing (Unfer et al. 2011). The water depth varied between a few centimeters in riffle habitats and up to 4 m in pools. The mean length ± SD of the 12 habitats was 93.1 ± 47.2 m for run units, 81.7 ± 61.4 m for riffles, and 53.1 ± 16.4 m for pools. The habitat widths ranged from 9 to 19 m (Table 1).

Complex cover (e.g., woody debris and root wads) is rare in the stream. The present fish species are the Brown Trout, European Bullhead *Cottus gobio*, European Grayling *Thymallus thymallus*, and nonnative Rainbow Trout. Although the entire fish community is of interest, Brown Trout and Rainbow Trout are of special relevance for recreational fishing.

Electrofishing.— In late September 2012 and 2013 at base flow conditions, we conducted multiple-pass depletion surveys in each of the 12 selected habitat units by following the national guidelines for fish sampling (Haunschmid et al. 2010). We installed a block net at the upper end of each habitat unit to prevent fish from escaping upstream before electrofishing was conducted. Beginning downstream of each habitat, three to four anode handlers waded upstream in a line, with a maximum distance of 4 m between two anodes, to cover the entire cross section. Pool habitats were sampled over the total length, whereas riffle and run habitats were sampled over a representative length (average sampled length of the total habitat lengths for both years was 78% for riffles and 58% for runs), but at least covering a minimum of 50 m, according to the requirements of the European Standard for the sampling of fish with electricity (CEN 2003). Gasoline-powered backpack electrofishing units were used with unpulsed DC (300–600 V; 1.5–2.5 kW). In pools, we additionally used a boat equipped with a 5-kW DC generator to sample deep areas. All units were equipped with a 30-cm hoop anode and a cable cathode. Fish captured from each pass were held separately in live wells at the stream margin. After the last pass of each habitat unit, we identified all fish to the species level and measured them to the nearest millimeter (TL) before returning them to the river. Population estimates were obtained using the maximum-likelihood solution for the two-run removal estimator (Seber and Le Cren 1967). In one

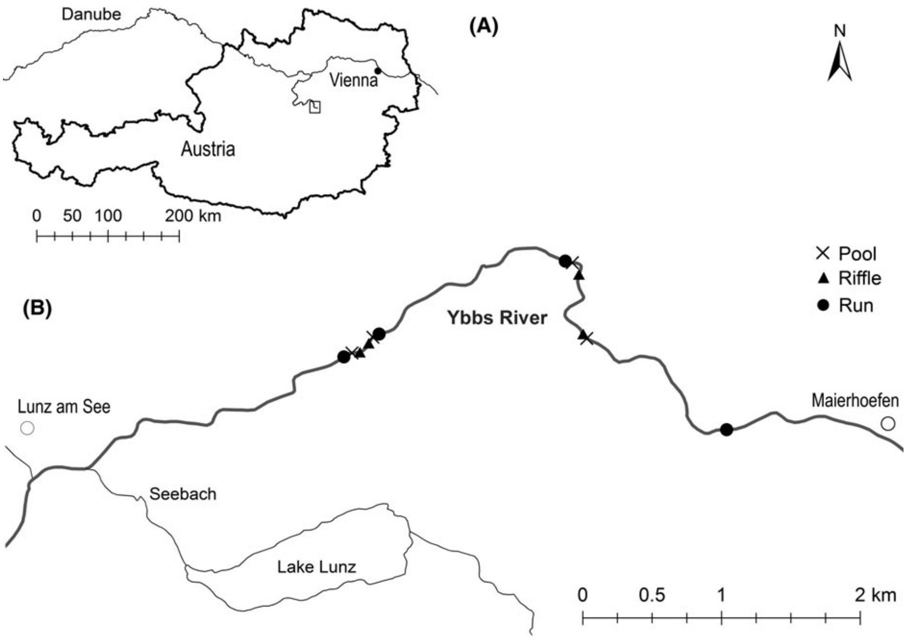

FIGURE 1. Location of **(A)** the Ybbs River in Austria and **(B)** the investigated habitats within the river.

TABLE 1. Habitat characteristics and dimensions of the 12 investigated habitats sampled through electrofishing and snorkeling in the Ybbs River, Austria.

Habitat	Habitat type	Total length (m)	Mean width (m)	Mean maximum depth (cm)	Maximum depth (cm)
1	Pool	51	14	121	>150
2	Pool	27	15	115	>150
3	Pool	56	14	130	>150
4	Pool	55	13	133	>150
5	Riffle	130	18	38	48
6	Riffle	61	19	41	57
7	Riffle	93	15	40	53
8	Riffle	77	16	41	49
9	Run	145	12	71	145
10	Run	94	9	73	91
11	Run	124	13	52	73
12	Run	138	13	55	75

habitat, the catch per pass declined by less than 50%, and a third pass was needed to estimate the population following DeLury (1947).

Snorkeling.— We based the snorkeling procedure, including lateral visibility measurements, on the methodological approach illustrated by Thurow (1994) and conducted the underwater fish counts on the days before the electrofishing surveys. Each year before data collection started, a new team of two novices to snorkeling was briefed on the methodology. During a short training session with an experienced snorkeler, they made themselves familiar with the upstream movement in the water, the identification of fish, and the length size estimation using a known distance (e.g., index finger to thumb; Thurow 1994) until they showed proficiency in these tasks. Their equipment consisted of a diving mask, a snorkel, a dry suit, and an underwater recording board. Block nets were not used. Snorkeling counts were carried out on dry days with good daylight conditions (1000–1600 hours). The underwater visibility allowed for spotting fish at all positions in the river transects and to see the river banks from the position of the snorkelers. To identify fish outside of the range where exact species identification was possible, it was imperative to move toward the individuals and confirm the observation. We followed the protocol of Thurow (1994) to measure the average distance within which a fish could be clearly identified (mean = 3.8 m). Snorkelers carefully entered each sampling site at the lower end and then moved upstream in the middle of the stream, searching for Brown Trout and Rainbow Trout. Each snorkeler counted fish in separate halves of the river cross section. Snorkelers did not proceed shoulder to shoulder but left a gap in between themselves to cover the whole river width. Species and size-class were recorded when a fish passed the observer in the downstream direction. To avoid double counts of fish passing in between the snorkelers, hand signs were used to signal the recording. Due to high fish densities in the pools, the methodology had to be adapted in a way that each snorkeler counted the specimens of one species only. Pool units were counted twice to minimize error related to double-counting fish or missing fish that were present. Riffle and run habitats were snorkeled only once. Pools were snorkeled over the total length. In conformity with the electrofishing standards, a minimum length of 50 m in riffle and run habitat units was sampled in 2012 (average sampled length of the total habitat lengths was 80% for riffles and 64% for runs). In 2013, we sampled their total lengths.

Based on available length-frequency data (Unfer et al. 2011), we distinguished three size-classes: small (<200 mm), medium (200–320 mm), and large (>320 mm). Young of the year were not recorded, as snorkeling had proven to be less effective in accurately counting this age-class (Heggenes et al. 1990; Thurow 1994). In some habitats (e.g., pools), high numbers of fish were present. In such cases, the total number of each species was counted first, and then the percentage distribution of size-classes was estimated and recorded for each species separately. To correctly assign size-classes, snorkelers had to consider an underwater magnification of 25% (Thurow et al. 2012). After a section was completed, data were transferred to a standard data sheet.

Data processing and analysis.— We standardized stock data for each habitat, method, species, and year to 100 m (Figure 2) and created a data set wherein all fish were itemized by habitat, sampling method, species, and assigned size-class and were differentiated by year, resulting in a table of 4,757 lines.

To test the homogeneity of abundance and size-class between the two sampling methods, we established two hypotheses (H_0 = total independence of all variables). Regarding both, it should be noted that the independent variables did not have the same status as the year, which was defined as a control variable (i.e., all tests were separately applied for 2012 and 2013).

The first hypothesis assumed that fish abundance did not differ between the sampling methods, whereby we considered the independent variables of fish species and habitat type. We used cross-table analyses through chi-square and residual tests. Cramér's *V* was used to indicate the effect size. The first dimension of the cross-table was the sampling method, and the second dimension was a

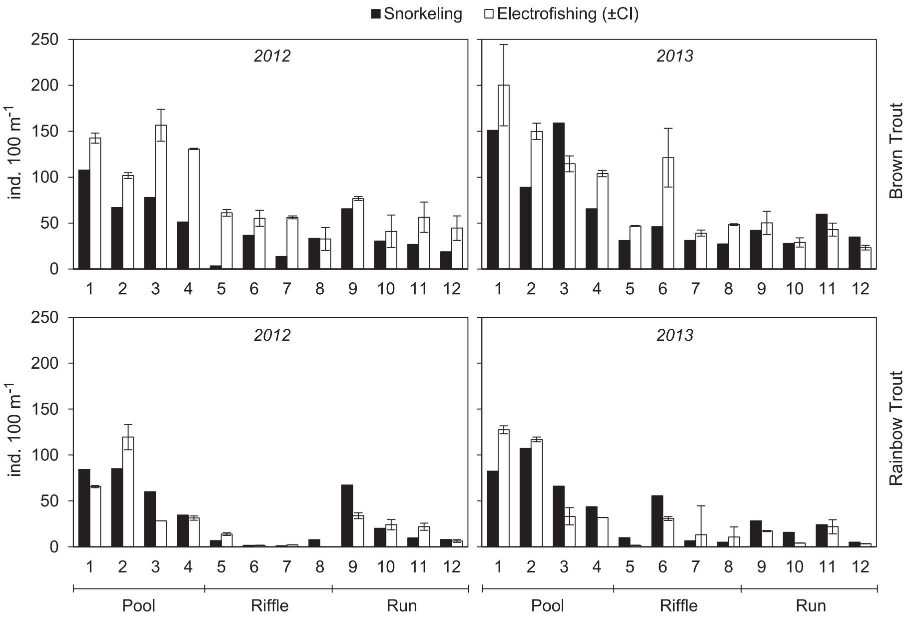

FIGURE 2. Comparison of fish abundance (individuals [ind.]/100 m) by gear type in the 12 investigated habitats separated by year (2012 and 2013) and fish species (Brown Trout and Rainbow Trout). Electrofishing estimates are presented with 95% confidence intervals (CIs). All fish data exclude young-of-the-year individuals.

TABLE 2. Cross-table results for tests of homogeneity of abundance in 2012. The species and habitat variables were grouped in a profile and tested versus the sampling method. Global chi-square test results (χ^2 = 67.88, df = 5, P = 0.000; Cramér's V = 0.137) and post hoc asymptotic binomial residual tests are shown (Obs. = observed cell counts; Exp. = expected cell counts; P' = alpha level for Holm's correction; T = typical/overfrequented; AT = atypical/underfrequented).

Species × habitat	Sampling method	Obs.	Exp.	Asymptotic binomial test	P	P'	T|AT[a]
Brown Trout × Pool	Snorkeling	304	342	−2.21	0.014	0.008	
Brown Trout × Pool	Electrofishing	533	495	1.91	0.028	0.010	
Brown Trout × Riffle	Snorkeling	87	126	−3.58	0.000	0.005	AT
Brown Trout × Riffle	Electrofishing	222	183	3.02	0.001	0.006	T
Brown Trout × Run	Snorkeling	143	150	−0.57	0.284	0.013	
Brown Trout × Run	Electrofishing	224	217	0.48	0.315	0.017	
Rainbow Trout × Pool	Snorkeling	264	206	4.23	0.000	0.004	T
Rainbow Trout × Pool	Electrofishing	241	299	−3.60	0.000	0.005	AT
Rainbow Trout × Riffle	Snorkeling	18	17	0.31	0.378	0.025	
Rainbow Trout × Riffle	Electrofishing	23	24	−0.26	0.398	0.050	
Rainbow Trout × Run	Snorkeling	105	81	2.74	0.003	0.006	T
Rainbow Trout × Run	Electrofishing	93	117	−2.30	0.011	0.007	

[a] Following Krauth (1993): result for the binomial test using Holm's correction (Von Eye et al. 2010).

combination of the following factors: fish species (1 = Brown Trout, 2 = Rainbow Trout) and habitat (1 = pool, 2 = riffle, 3 = run). We generated a two-digit profile variable (so-called "metavariable") from two solitary, single-digit variables. The first hypothesis was tested globally by chi-square tests. Locally, we examined which of the observed cell frequencies in the cross-table were compatible with the hypothesis of total independence. The local tests were post hoc tests and were described under the designation residual test or configuration frequency analysis (Von Eye et al. 2010; Stemmler 2014). We performed all analyses with the "cfa" package (Mair and Funke 2017). All tests were Holm corrected (α = 0.05).

The second hypothesis extended the first hypothesis by the size-class variable. The first dimension of the cross-table was the sampling method, and the second dimension was a combination of the three factors: species (1 = Brown Trout, 2 = Rainbow Trout), habitat (1 = pool, 2 = riffle, 3 = run), and size-class (1 = small, 2 = medium, 3 = large). We conducted global and local testing, as described above.

RESULTS

We recorded a total of 4,757 fish in both years: 2,134 were detected in the snorkeling surveys, and 2,623 were detected through electrofishing (Tables 2, 3). Both sampling methods indicated that Brown Trout were the dominant species in all habitat types. We documented the highest fish abundance for both species in pool habitats, typically followed by run and riffle habitats. The assessment of fish abundance with electrofishing data yielded higher Brown Trout numbers than the snorkeling method. In contrast, snorkeling data yielded higher Rainbow Trout numbers than electrofishing, although on a lower level (Tables 2, 3).

Global tests of the sampling method and species × habitat combination showed a statistically significant influence for both years (2012: P = 0.000; 2013: P = 0.000; Tables 2, 3). The test results further indicated that the model could only explain the observed differences very weakly (2012: Cramér's V = 0.173; 2013: Cramér's V = 0.115). Extending the test procedure to the performance of local tests showed that in 2012, 7 of the 12 cells fulfilled the hypothesis of total homogeneity (Table 2). Deviations from the homogeneity hypothesis were found for Brown Trout in riffles, whereby snorkel counts underrepresented and electrofishing results overrepresented Brown Trout. The opposite deviation was found for Rainbow Trout in pools. Snorkeling overrepresented Rainbow Trout in runs. In 2013, we only observed local differences for the snorkeling method in riffles, with Rainbow Trout being overrepresented (Table 3), indicating that the two sampling methods should be regarded as equivalent in their performance.

Global tests of the sampling method and species × habitat × size-class combination showed a statistically significant influence for both years (2012: P = 0.000, Cramér's V = 0.294; 2013: P = 0.000, Cramér's V = 0.227; Table 4). Local tests highlighted the positioning of the differences; in 2012, 4 of 18 contrasts showed statistically relevant divergences: two contrasts referred to Brown Trout in pools, one referred to Brown Trout in riffles, and one referred to Rainbow Trout in pools. In 2013, one profile showed statistically significant differences regarding large Brown Trout in pool habitats. In total, the local tests from

TABLE 3. Cross-table results for tests of homogeneity of abundance in 2013. The species and habitat variables were grouped in a profile and tested versus the sampling method. Global chi-square test results ($\chi^2 = 32.86$, df = 5, $P = 0.000$; Cramér's $V = 0.115$) and post hoc asymptotic binomial residual tests are shown (Obs. = observed cell counts; Exp. = expected cell counts; P' = alpha level for Holm's correction; T = typical/overfrequented; AT = atypical/underfrequented).

Species × habitat	Sampling method	Obs.	Exp.	Asymptotic binomial test	P	P'	T|AT[a]
Brown Trout × Pool	Snorkeling	464	484	−1.02	0.153	0.013	
Brown Trout × Pool	Electrofishing	534	514	1.00	0.158	0.017	
Brown Trout × Riffle	Snorkeling	135	162	−2.20	0.014	0.005	
Brown Trout × Riffle	Electrofishing	199	172	2.14	0.016	0.006	
Brown Trout × Run	Snorkeling	165	150	1.27	0.102	0.008	
Brown Trout × Run	Electrofishing	144	159	−1.24	0.108	0.010	
Rainbow Trout × Pool	Snorkeling	299	300	−0.08	0.467	0.025	
Rainbow Trout × Pool	Electrofishing	320	319	0.08	0.468	0.050	
Rainbow Trout × Riffle	Snorkeling	77	57	2.64	0.004	0.004	T
Rainbow Trout × Riffle	Electrofishing	41	61	−2.56	0.005	0.005	
Rainbow Trout × Run	Snorkeling	73	59	1.82	0.035	0.006	
Rainbow Trout × Run	Electrofishing	49	63	−1.76	0.039	0.007	

[a] Following Krauth (1993): result for the binomial test using Holm's correction (Von Eye et al. 2010).

TABLE 4. Global chi-square tests and selected post hoc asymptotic binomial residual test results for tests of the homogeneity of size-class abundance in 2012 and 2013 (2012: $\chi^2 = 194.49$, df = 17, $P = 0.000$, Cramér's $V = 0.294$; 2013: $\chi^2 = 128.93$, df = 17, $P = 0.000$, Cramér's $V = 0.227$). Only statistically significant cells (10 of 72) are presented here. For 2013, only the post hoc test assignments are shown. The species, habitat, and size-class variables were grouped in a profile and tested versus the sampling method (Obs. = observed cell counts; Exp. = expected cell counts; P' = alpha level for Holm's correction; T = typical/overfrequented; AT = atypical/underfrequented).

Species × habitat × size-class	Sampling method	Obs.	Exp.	Asymptotic binomial test	P	P'	2012 T|AT[a]	2013 T|AT[a]
Brown Trout × Pool × Large	Snorkeling	42	45	−0.49	0.310	0.006		AT
Brown Trout × Pool × Large	Electrofishing	69	66	0.41	0.340	0.007		T
Brown Trout × Pool × Medium	Snorkeling	81	160	−6.48	0.000	0.001	AT	
Brown Trout × Pool × Medium	Electrofishing	311	232	5.47	0.000	0.001	T	
Brown Trout × Pool × Small	Snorkeling	181	136	3.95	0.000	0.001	T	
Brown Trout × Pool × Small	Electrofishing	153	198	−3.33	0.000	0.002	AT	
Brown Trout × Riffle × Small	Snorkeling	44	74	−3.57	0.000	0.002	AT	
Brown Trout × Riffle × Small	Electrofishing	138	108	2.99	0.001	0.002	T	
Rainbow Trout × Pool × Large	Snorkeling	80	54	3.60	0.000	0.002	T	
Rainbow Trout × Pool × Large	Electrofishing	52	78	−3.01	0.001	0.002	AT	

[a] Following Krauth (1993): result for the binomial test using Holm's correction (Von Eye et al. 2010).

both years ($n = 72$) showed that the homogeneous length-class assignments ($n = 62$) predominated, with a share of around 86% (78% in 2012; 94% in 2013).

DISCUSSION

The objective of the present study was to test whether inexperienced snorkelers were capable of gathering reliable data on fish abundance and the size-class distribution of trout populations in a clear, fourth-order stream in Austria by comparing snorkeling and electrofishing data. We conducted cross-table analysis comparing observed and expected frequencies to test for homogeneity. Considering both years, our results demonstrated that the hypothesis of equivalence between the two methods can be maintained since fish abundance proved to be independent of the sampling method in 18 of 24 configurations (Tables 2, 3). For the size-class distribution, the hypothesis of homogeneity could not be rejected in either year, which was also considered to be statistically supported (Table 4).

However, differences between the years can be seen, with 2013 showing higher consistency in results.

Our observations are broadly consistent with other studies that have assessed the suitability of the snorkeling method for depicting the densities or structure of salmonid populations. Mullner et al. (1998), for example, compared electrofishing and snorkeling by counting Brook Trout *Salvelinus fontinalis*, Rainbow Trout, and Cutthroat Trout *O. clarkii*, and they achieved high correlations ($R^2 \geq 0.90$) for the abundance estimates. Adjusting the frequencies in three length-classes, they also obtained similar results for the length-frequency comparisons (see also Wildman and Neumann 2003 for data on Brook Trout and Brown Trout). Studying Bull Trout *Salvelinus confluentus* stocks, Thurow and Schill (1996) found that size structure estimates were similar between the two methods and that daytime snorkeling produced abundance estimates equivalent to 75% of the electrofishing abundance estimates.

Strengths and weaknesses of the two investigated sampling methods were observed when detailed local tests were applied to identify single effect combinations (Tables 2–4). In our study, conspicuous differences emerged in the case of Brown Trout, whereby the snorkeling method often yielded lower observed frequencies than the electrofishing depletion estimates. This pattern was most evident for riffle habitats during 2012 (Table 2) but also for large- and medium-sized trout in pools. In this context, snorkelers reported a well-known difficulty in locating Brown Trout due to their cryptic coloration and hiding behavior (Pert et al. 1997; Joyce and Hubert 2003). Brown Trout often used interstitial spaces between boulders to hide, which caused sighting difficulties. Low snorkeling detection rates of small Brown Trout in riffles during 2012 may have been due to the difficulty in carefully searching a shallow area of high flow velocity and coarse substrates. Based on similar experiences, Heggenes et al. (1990) emphasized the advantages of the electrofishing method in such habitats. Species-specific behavior may further explain the higher performance of the snorkeling method for Rainbow Trout in pool and run habitats during 2012 and in riffle habitats during 2013. Several authors have reported that variation in observability due to interspecific differences is an essential factor in the success of sampling campaigns (Hankin and Reeves 1988; Pert et al. 1997; Chamberland et al. 2014). Pert et al. (1997) ascribed the higher success in counting Rainbow Trout than Brown Trout to the less-secretive nature of Rainbow Trout. From our observations, we can confirm that Rainbow Trout tended to occupy midwater positions and showed a higher level of activity than Brown Trout.

Aside from biological factors, such as species or fish size, there also exists a broad consensus that the reliability of a sampling method can depend on environmental factors, including water transparency, water conductivity, or habitat complexity (Heggenes et al. 1990; Reynolds 1996), which must be carefully considered when determining the sampling design (Macnaughton et al. 2015). With increasing complexity of environmental parameters (e.g., high species diversity; nature of the physical habitat), reliable data collection becomes more complicated (Orell et al. 2011) and demands the use of more experienced snorkelers.

However, the employment of novice snorkeling crews showed that in the Ybbs River, inexperienced snorkelers were capable of gathering reliable data on trout abundance and size-class distribution, even under conditions of high fish abundance. Our results, therefore, do not concur with those of other authors, who have claimed that the efficiency of snorkeling counts relies heavily on sampling expertise (Chamberland et al. 2014; Macnaughton et al. 2015). The combination of few biotic instream structures (e.g., woody debris, macrophytes, and emergent plants) and high underwater visibility seemed to provide favorable conditions for snorkelers in the Ybbs River.

Ultimately, snorkeling efficiency remains affected by the effort and abilities of the team. The higher accordance of the sampling results in 2013 suggests that working as enthusiastically and carefully as possible is a necessity for high-quality data. We therefore recommend that researchers initially verify the accuracy of snorkel counts with other methods—for example, through electrofishing, repeated counts, or tagging (Orell et al. 2011). To maximize the comparability of data in early and late study years, we further recommend testing snorkeler experience levels to determine the most competent and accurate working team. Yearly repeated snorkel counts can increase experience and thus improve detection rates and enhance sampling efficiency (Orell et al. 2011). Therefore, it is desired to start perennial assessments with the most qualified team but also to conduct periodic validation to estimate reliability.

We conclude that snorkeling has the potential to provide an appropriate method for quantifying trout populations in clearwater streams, such as the Ybbs River, even if the surveyors have no previous snorkeling experience. For fisheries managers, the facilitated access to data acquisition allows for changing harvest regulations based on current production and is thus a promising tool for autonomous inland trout fisheries. Beyond that, snorkeling offers additional advantages over other sampling methods. For example, it provides the possibility to sample large or remote areas, allowing the development of a more holistic picture of underwater habitats. Finally, the direct observation of fish in their natural environment contributes to a better understanding of processes and life underwater, constituting a beneficial insight for conservation-based management of wild fish stocks.

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Supplementary material 2: other research outputs

10.1 Conference proceedings

- **Hayes, D.S.**, Nale, J.P., Schinegger, R. (Eds.) (in prep.). Environmental Flow Assessment and Implementation in India: Sharing Indian, European and International Experiences. *Proceedings of the International E-Flows Workshop organized by GIZ GmbH and IEWP*, 21-22 Oct. 2019, New Delhi, India.
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