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Balancing hydropower production and ecology – ecological impacts, mitigation measures, and programmatic monitoring

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Abstract – Hydropower is a vital renewable energy source but has substantial ecological impacts on rivers, lakes, and surrounding ecosystems. It alters hydrogeomorphology, disrupts connectivity, and changes water physicochemical properties such as temperature and dissolved gas concentrations. Historically, the environmental impact has been of less concern compared to energy production, and there is an urgent need to adapt hydropower production to reduce impacts on aquatic ecosystems. While various mitigation measures exist, a systematic understanding of their efficiency is lacking. Here, we extensively review both the environmental effects of hydropower and the scientific base for mitigation measures. We then list key abiotic and biological candidates for systematic monitoring before outlining a programmatic monitoring approach to evaluate the efficiency of mitigation measures. This programmatic monitoring approach involves monitoring packages based on specific mitigation measures. A set of abiotic parameters and biological indicators are monitored with standardized methods and monitoring designs over the long-term and at several sites, covering different river types and hydropower configurations. The proposed program serves to inform ongoing and future remedial measures, expand our mechanistic understanding of the ecological effects, facilitate knowledge transfer, and allow for more reductionist monitoring approaches outside of the program.

Keywords: Environmental flow / fish passage / temperature effects / gas supersaturation / remedial measures / restoration

1 Introduction

Hydropower has been important for human civilization for hundreds of years, and today constitutes a cornerstone for low-carbon, renewable energy production (Lenders *et al.*, 2016; Moran *et al.*, 2018), producing about 15% of the world's electricity (IEA, 2024). Over 90 000 hydropower plants are estimated to be in operation or under construction worldwide (Couto and Olden, 2018) with many more planned for the future (Zarfl *et al.*, 2015). Consequently, hydropower dams, together with other impoundments, affect the majority of the world's large river systems (Nilsson *et al.*, 2005), encompassing an estimated 16 million reservoirs (>0.01 ha) worldwide (Lehner *et al.*, 2011) and an instream barrier every 1.35 river kilometer in Europe (Belletti *et al.*, 2020). While constituting an indispensable source of electricity, hydropower production has wide-ranging impacts on the ecology in rivers and regulated lakes (He *et al.*, 2024).

In many countries, the environment has historically been of secondary concern compared to the production of hydroelectricity, and there is an urgent need to adapt hydropower production to reduce impacts on the aquatic ecosystems (Lindström and Ruud, 2017; Schäfer, 2021). This process can take the form of policies and general environmental legislation (*e.g.*, EU Water Framework Directive; 'WFD'). Specifically, it can be directly coupled with environmental licensing of hydropower production (Tonka, 2015; Carvalho *et al.*, 2019; Vogel and Jansujwicz, 2022). In Sweden, for example, the implementation of the WFD has prompted a modernization of

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environmental legal requirements through a national relicensing process for existing hydropower facilities (commonly referred to as 'NAP'), a process which is expected to necessitate extensive remedial measures (Sundin *et al.*, 2025).

The upcoming process to mitigate ecological effects of hydropower requires a systematic understanding of the efficiency of mitigation measures (Richter *et al.*, 2006; Rogosch *et al.*, 2024). Despite this requirement, and the well-documented impacts from hydropower on biota in rivers and lakes (He *et al.*, 2024), systematic monitoring of the ecological communities is relatively scarce, particularly in relation to the efficiency of mitigation measures (Clifford, 2007; Weber *et al.*, 2018). At the same time, systematic monitoring and assessment is needed to confirm and improve the general functionality of existing remedial measures and to inform future mitigation efforts within a framework of both case-specific- and central (agency directed) adaptive management. Monitoring is required for demonstration of successful mitigation and, in the end, improved ecological status of impounded rivers and regulated lakes (Keefer *et al.*, 2021; Tirkaso and Gren, 2022; Rogosch *et al.*, 2024).

In this paper, we first present a narrative review of ecological effects of hydropower on a wide range of organism groups, covering both habitat and connectivity effects. We then summarize mitigation measures related to these effects. Finally, we discuss potential abiotic and biological indicator candidates for systematic monitoring before outlining a programmatic monitoring approach to evaluate the efficiency of mitigation measures. The paper has a general focus on the European, in particular the Nordic, situation. Examples, however, are drawn from the global literature and discussions have global implications. Recurringly, we build on knowledge synthesized in a set of high quality literature reviews, for example on hydropower impacts on biodiversity (He *et al.*, 2024), general impacts from hydropeaking (Bipa *et al.*, 2023), ecological impacts from water level fluctuations (Carmignani and Roy, 2017; Cott *et al.*, 2008a), effects of hydropeaking on riverine plants (Bejarano *et al.*, 2018), gas supersaturation (Li *et al.*, 2022; Pulg *et al.*, 2018) and fish passage (Coutant and Whitney, 2000; Silva *et al.*, 2018).

2 Flow, hydropower and the river system ecology

Hydropower plants vary widely in design and operation, which shapes their ecological footprint on riverine ecosystems. Some hydropower plants are associated with large water storage reservoirs, allowing large-scale regulation of discharge, while others are run-of-the-river plants, which directly utilize water arriving from upstream (He *et al.*, 2024). Commonly, run-of-the-river type plants still have the ability to temporarily store a limited amount of water within their impoundment areas, which can lead to substantially altered flow patterns over shorter time frames (*e.g.*, through hydropeaking) (Widén *et al.*, 2021). The hydropower plant itself can be located either adjacent to the dam or at a substantial distance downstream, fed with water through channels or tunnels. The latter situation often creates extended bypassed river reaches with lowered, highly variable, or even no discharge in the original riverbed. (He *et al.*, 2024).

2.1 Flow regulation

River reaches upstream of hydropower dams are transformed from lotic to lentic habitats, while flow regulation alters the magnitude and rate of discharge, as well as the frequency and duration of high- and low-flow events in downstream reaches. For example, spring floods are often cut short or eradicated, while water levels in summers can be unnaturally high affecting also the river-floodplain exchange of water, sediment, and nutrients (He *et al.*, 2024). Hydropeaking affects both the upstream and downstream reaches of a dam and results in both small or large discharge and water level fluctuations at hourly, or even sub-hourly, timescales to optimize production according to short-term changes in demand (Ashraf *et al.*, 2018). Sometimes this even involves the decoupling of flow and water level (Widén *et al.*, 2021). Hydropeaking, in addition to the flow and water level fluctuations, can also result in hydrogeomorphological changes downstream the dam, *e.g.*, loss of substrate diversity, erosion of banks soil, and bed armoring (Harby and Noack, 2013; Fig. 1d). As river water is temporary abstracted for hydroelectric power production, long or short river reaches downstream are bypassed and left dry or with substantially reduced water levels (Malm Renöfält *et al.*, 2015; Widén *et al.*, 2022; He *et al.*, 2024: Fig. 1b). Tailrace reaches can, instead, be subject to sudden changes in flow coupled with the operation of the turbines, and often have their morphology simplified to increase the flow of water (Widén *et al.*, 2021).

As hydropower production disrupts the natural hydrological regime and alters erosion and sedimentation processes to which riparian and aquatic organism are adapted (Poff and Zimmerman, 2010; Kiernan *et al.*, 2012), it can fundamentally restructure riverine ecosystems and result in declines or local extinctions across the organism spectrum (Tab. 1). Indeed, flow regulation has documented effects on the composition of macrophytes (Biggs, 1996; French and Chambers, 1996), diatoms (Truchy *et al.*, 2022), macroinvertebrates (Kennedy *et al.*, 2014, Englund *et al.*, 1997), and fish (Liew *et al.*, 2016; Mims and Olden, 2013; Benejam *et al.*, 2016). Reduced flow velocities or increased winter flows with reduced ice cover can cause increases in macrophyte growth (Rørslett *et al.*, 1989) while high flow velocities or drying can cause declines in macrophyte abundance (Chambers *et al.*, 1991; Biggs, 1996). The macroinvertebrate community is shaped by flow as well as the effect of flow on substrate compositions (Mihalicz *et al.*, 2019; Wang *et al.*, 2020). They are affected by habitat loss under reduced flow conditions and from flushing and drying during hydropeaking (Robinson *et al.*, 2004; Gibbins *et al.*, 2007; Bruno *et al.*, 2013). As a consequence, flow regulations often cause macroinvertebrate diversity to decrease as species adapted to fast flow decline, while taxa tolerant anthropogenically-altered environmental conditions taxa may increase in abundance (Poff and Zimmerman, 2010; Mihalicz *et al.*, 2019; Wang *et al.*, 2020). Sensitive groups such as Ephemeroptera, Plecoptera, Trichoptera, and Hemiptera are particularly impacted by flow regulation (Krajenbrink *et al.*, 2019; Mihalicz *et al.*, 2019; Wang *et al.*, 2020). Similarly, mussels are impacted by the change in sediment characteristics imposed by flow regulation, such as the accumulation of fine sediment at reduced flows or the sediment armouring caused by temporary high flows and can suffer from reduced oxygen levels in impounded low flow reaches

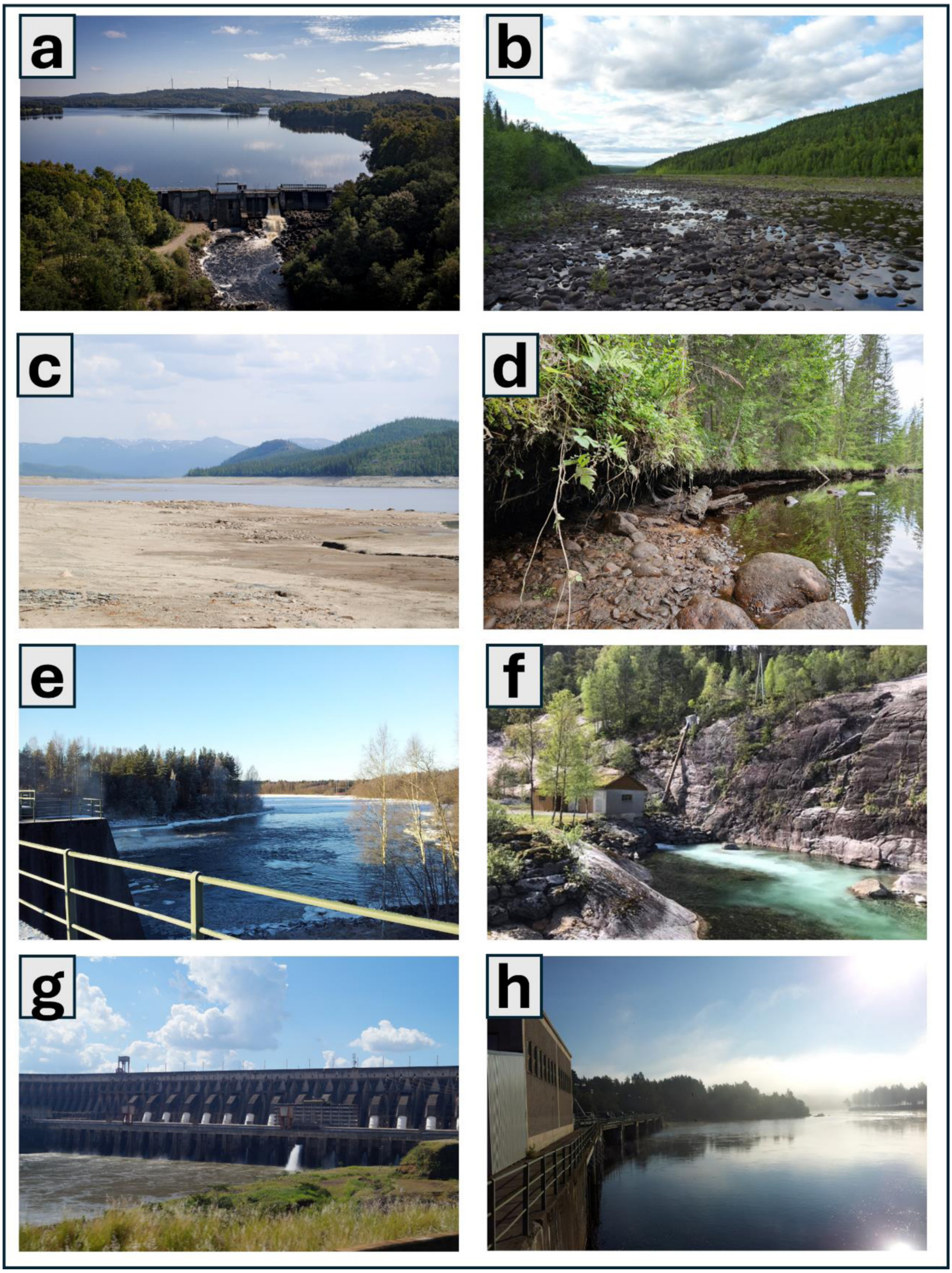

Fig. 1. Hydropower production has a range of effects in regulated river systems. Including transforming water reaches from lentic environments to lotic (a; Ätraforsdammen, Sweden), bypassed river reaches with reduced or no flow (b; Lilla Piteälven, Sweden), water level fluctuations in reservoirs (c; Umeälven, Sweden), hydropeaking with resulting erosion of the river banks (d; Oreälven, Sweden), increased winter temperatures and changed ice dynamics downstream bottom spills (e; Klarälven, Sweden), supersaturated water in tailraces or downstream spillgates (f; Stølselva, Norway),barriers to upstream fish movements (g; Parana river, Brazil), barriers to downstream fish movement (h; Klarälven, Sweden). Photos: Duncan Philpott (a), Olle Calles (b,g), Johan Östergren (c), Emil Nordström (d), NORCE LFI (f), Daniel Nyqvist (e,h).

Table 1. Key findings on impacts from flow regulation.

Group	Impact	References
Riperian vegetation	Flow regulation cause shifts in riparian vegetation composition.	Bejarano *et al.*, 2018; Bipa *et al.*, 2023
	Flow regulation reduces the extent and cover of riparian vegetation.	Jansson *et al.*, 2000; Widén *et al.*, 2022
	Prolonged low flows can result in more drought-tolerant species replacing the typical riparian species.	Poff and Zimmerman, 2010
	Encroachment of the inundation sensitive Norway spruce (*Picea abies*) due to lack of flooding.	SEPA, 2011; Vlahakis, 2023
	Unnatural flooding displace or injure plants, and can drown roots causing oxygen deficit, resulting in lower growth and mortality among plant species.	Johansson and Nilsson, 2002; Nilsson and Svedmark, 2002
	Flow fluctuations related to hydropeaking reduce growth and survival in many, but not all, plant species.	Baladrón *et al.*, 2022
	River sites adjacent to regulated rivers have lower riparian plant diversity and cover than similar sites in unregulated rivers.	Nilsson and Jansson, 1995; Jansson *et al.*, 2000; Nilsson and Svedmark, 2002
	Hydropeaking intensity negatively correlated with summer decomposition rates	Nordström *et al.*, 2025
	Flow regulation can replace the natural riparian zonation with a narrow band of tolerant species, leaving barren soil in the most flow/level variation exposed section.	Nilsson *et al.*, 1991; Bejarano *et al.*, 2018
	Species rich riparian forests and the willow shrub zones are disproportionately negatively affected by flow regulation as these are the zones created by seasonal high flow events that often are lacking in regulated rivers.	Malm Renöfält and Jansson, 2023
Macro-phytes	Flow is an important determinant for the presence and composition of macrophyte species in the river, both directly and mediated through effects on erosion and sedimentation	Bunn and Arthington, 2002
	Excessive flow velocities, as well as drying, cause the reduction or disappearance of macrophytes.	Chambers *et al.*, 1991; Biggs, 1996
	Reduced flow velocities can result in substantial increase in macrophyte occupancy in the river.	Rørslett *et al.*, 1989
	Different species have different flow velocity preferences, for example aquatic mosses preferring higher water velocities, and modified flow velocities can change the composition of macrophytes.	Biggs, 1996; French and Chambers, 1996
	Discharge fluctuation influences the macrophyte community, with some species being more, and other less, tolerant to water level variation.	Walker *et al.*, 1994; Mjelde *et al.*, 2013
Benthic algae	In reaches subject to hydropeaking, diatom abundance is substantially reduced in the desiccation zone, although re-wetting can quickly increase this abundance.	Bondar-Kunze *et al.*, 2015
	Different diatom species react differently to the flow regulation related to hydropower with both seasonal flow regulation and short term hydropeaking influencing diatom composition.	Truchy *et al.*, 2022
	Diatom species richness is lower after compared to before dam construction and in regulated compared to more natural river reaches.	Wu *et al.*, 2009; 2010
Macro-inverte-brates	Flow regulation has an important impact on the macroinvertebrate community with hydropower production often resulting in altered species richness and diversity downstream of dams.	Mihalicz *et al.*, 2019; Wang *et al.*, 2020
	Reduction or other alteration of naturally fast flowing water results in the disappearance or decline of species adapted to this environment as flow interacts with, and forms, substrate conditions that shape the macroinvertebrates community composition.	Englund *et al.*, 1997
	Large variation in discharge associated with hydropeaking can cause flushing and drying of the individual macroinvertebrates present.	Robinson *et al.*, 2004; Gibbins *et al.*, 2007; Bruno *et al.*, 2013
	Hydropeaking causes changes the composition of the macroinvertebrate community. For example, species sensitive to disturbance and emerging insects (as compared to non-insect macroinvertebrates) reduced with hydropeaking intensity and closeness to the dam.	Kennedy *et al.*, 2014; Abernethy *et al.*, 2021

Table 1. (continued).

Group	Impact	References
	Flow regulation often causes diversity to decrease while abundance can even increase, when sensitive groups disappear and individuals of tolerant taxa increase in numbers.	Poff and Zimmerman, 2010; Mihalicz *et al.*, 2019; Wang *et al.*, 2020; Jones 2013; Holt *et al.*, 2015
	Reduced flow increases the proportion of fine substrate (sand and silt) and reduces the availability of coarse substrate and with this important habitat and food resources for macroinvertebrates.	Wang *et al.*, 2020
	Mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera), and true bugs (Hemiptera) are particularly negatively affected by hydropower.	Krajenbrink *et al.*, 2019; Mihalicz *et al.*, 2019; Wang *et al.*, 2020
Mussels	Dams can modify the composition of the mussel community in impacted catchment areas and also generally reduce their abundance, sometimes resulting in local extirpations of certain species.	Layzer *et al.*, 1993; Randklev *et al.*, 2016; Sousa *et al.*, 2020
	Mussels are impacted by the change in sediment characteristics imposed by flow regulation, such as the accumulation of fine sediment at reduced flows or the sediment armouring caused by temporary high flows, and can suffer from reduced oxygen levels in impounded low flow reaches.	Layzer *et al.*, 1993; Wegscheider *et al.*, 2019; Sousa *et al.*, 2020).
	Lowered water levels can cause general mussel mortality from drying or increased predation pressure.	Sousa *et al.*, 2018
	Individual mussels may be flushed away at high discharge.	Sousa *et al.*, 2020
Fish	When fast-flowing lotic environments are lost or reduced, so are the associated rheophilic fish species.	Liew *et al.*, 2016
	Lower diversity and density of shallow water fish in regulated than unregulated river reaches. No such effects among fish inhabiting deep waters.	Travnichek and Maceina, 1994
	Reaches downstream of dams with reduced discharge can have lower fish abundance, as well as altered species composition, favoring generalists, limnophilic species, or species adapted to more stable environments compared to free flowing reaches.	Mims and Olden, 2013; Benejam *et al.*, 2016
	Hydropeaking and related flow variation frequently causes stranding related mortality and downstream displacement of fish.	Schmutz *et al.*, 2015
	In relation to hydropeaking, even if all life stages can be flushed away at high discharges, eggs and larvae run a particularly high risk of being stranded or freeze at low winter water levels	Young *et al.*, 2011; Barton *et al.*, 2023; Pander *et al.*, 2023
	In relation to hydropeaking, stranding rates are typically higher at more extreme down-ramping rates but are also affected by environmental conditions.	Young *et al.*, 2011; Führer *et al.*, 2022
	In relation to hydropeaking, the likelihood of stranding is higher over lower sloping shores, at colder temperatures, in otherwise stable discharge conditions, and in environments with shelters and potholes.	Saltveit *et al.*, 2001; Nagrodski *et al.*, 2012; Auer *et al.*, 2017
	Stranding rates in relation to hydropeaking can vary between day and night; this effect seems to vary both among and within species, and is likely dependent on specific local habitat characteristics.	Young *et al.*, 2011
	In relation to hydropeaking, variable channel morphology (*e.g.*, side-channels) and in-stream structures (larger-sized sediments or large woody debris) can function as flow-shelter, protecting fish from downstream displacement during high flows, but may also constitute ecological traps if fish choose to remain sheltered instead of following the receding water.	Heggenes, 1988; Young *et al.*, 2011; Harby and Noack, 2013; Cousin *et al.*, 2025
	Abrupt flow variation may contribute to reproduction failures through dewatering of spawning habitat, disruption of migratory cues, and disturbance of spawning behavior.	Schmutz *et al.*, 2015; Barton *et al.*, 2022; Pander *et al.*, 2023
	Through repeated hydropeaking events accumulation of relatively modest effects can lead to transformation of the affected fish community.	Young *et al.*, 2011
	River reaches subject to hydropeaking was associated with higher habitat overlap and more use of deep pools compared to more natural controls in Cypriniformes fish.	Leite *et al.*, 2025
	Flow regulation can impact the overall fitness of fishes, through direct or indirect effects on growth and survival. As habitat availability is under frequent change	Bätz *et al.*, 2024; Daufresne *et al.*, 2015;

Table 1. (continued).

Group	Impact	References
	under hydropeaking, more mobile species and life-stages are forced into repeated movements in search of suitable habitats, which may result in wasted energy and lost foraging opportunities. For territorial species, like juvenile salmonids, it may also lead to repeated loss of territory access and costs related to competition to regain good territories. In addition, increased mobility can increase exposure rate to predators.	Puffer *et al.*, 2015; Schmutz *et al.*, 2015
Birds	Breeding success, female condition, and breeding timing of pied flycatchers (*Ficedula hypoleuca*) were lower in regulated rivers compared to natural rivers.	Strasevicius *et al.*, 2013
	Construction of small hydropower stations reduced the number of white-throated dippers (*Cinclus cinclus*) at the sites, but this could be compensated for by the placement of nest-boxes.	Walseng and Jerstad, 2011, 2014
	Water regulation effects on downstream wetlands can impact bird reproduction in riparian habitats.	Kingsford and Auld, 2005; Graf, 2006
Terrestrial and amphibious animals	Changed flooding regime changed the composition but not the taxonomic richness of terrestrial arthropods.	Ellis *et al.*, 2001
	Total abundance of terrestrial invertebrates was lower along regulated rivers compared to unregulated controls.	Jonsson *et al.*, 2013
	Southern dune tiger beetle (*Cicindela maritima*) and giant riverbank wolf spider (*Arctosa cinerea*) are threatened due to river flow regulation and artificial armouring of riverbanks, preventing floods that causes habitat loss.	Åström *et al.*, 2017
	River breeding frogs can be negatively affected by flow regulations through both desiccation and flushing. They were more likely to be found in free flowing than in regulated rivers, and early life mortality correlated with flow variability.	Kupferberg *et al.*, 2012
	In semi-aquatic mammals, hydropower production has been reported to affect distribution, fitness, movement, nutrition and reproduction, mainly through its effects on available habitat.	Altanov *et al.*, 2025
	Marsh deer (*Blastocerus dichotomus*) and hippos (*Hippopotamus amphibius*) have been reported to decline following damming and associated flooding of habitats.	Andriolo *et al.*, 2013; Bempah *et al.*, 2022
	Catches of caddisflies (after emergence) in light traps correlate with river regulation regime.	Kennedy *et al.*, 2016

(Layzer *et al.*, 1993; Wegscheider *et al.*, 2019; Sousa *et al.*, 2020). Lowered water levels can cause general mussel mortality from drying or increased predation pressure (Sousa *et al.*, 2018), and individual mussels may be flushed away at high discharges (Sousa *et al.*, 2020). Among fish, reduced flows result in the replacement of rheophilic with limnophilic or generalist species (Mims and Olden, 2013; Benejam *et al.*, 2016). At the same time, hydropeaking can cause widespread stranding and displacement, particularly affecting eggs and juveniles (Young *et al.*, 2011; Pander *et al.*, 2023), an effect which can be amplified by channelization of downstream river sections (Cousin *et al.*, 2025). Hydropeaking can also disrupt spawning, dewater habitats, increase predation risk, and force repeated energy-expensive movements (Schmutz *et al.*, 2015; Bätz *et al.*, 2024).

Along the river, riparian vegetation that relies on floods for water supply, seed and sediment deposition, and seedling recruitment, is affected when the timing of floods no longer aligns with plant phenology (Mahoney and Rood, 1998; Bejarano *et al.*, 2020). Such alterations can shift vegetation composition (Bejarano *et al.*, 2018; Bipa *et al.*, 2023), and reduce vegetation cover (Jansson *et al.*, 2000; Widén *et al.*, 2022) and diversity (Nilsson and Jansson, 1995; Jansson *et al.*, 2000; Nilsson and Svedmark, 2002). Reduced flows can promote encroachment by flood-sensitive species, such as Norway spruce (SEPA, 2011; Vlahakis, 2023), while unnatural floods and hydropeaking can result in plant displacements, damages, or growth reductions (Johansson and Nilsson, 2002; Baladrón *et al.*, 2022). Flow regulation often leads to a narrow riparian zone dominated by tolerant species, leaving barren the flow variation exposed zone (Nilsson *et al.*, 1991; Malm Renöfält and Jansson, 2023). Within the riparian environment, terrestrial arthropods relying on riparian areas, may decline due to habitat loss from reduced flooding and the coupled change in sedimentation, erosion, and plant community (Åström *et al.*, 2017; Feld *et al.*, 2011; He *et al.*, 2024), while birds are affected mainly through changes to nesting habitats and prey availability (Strasevicius *et al.*, 2013; Walseng and Jerstad, 2014). In semi-aquatic mammals, hydropower production has been reported to impact distribution, fitness, movement, nutrition and reproduction, mainly through its effects on available habitat (Altanov *et al.*, 2025).

2.2 Reservoirs and regulated lakes

The reservoir changes the biological community from one adapted to flowing water to one that is more lake-like (He *et al.*, 2024). Typically, this means decreased abundance and diversity of specialist rheophilic species in concert with increase in generalists and lentic species (Franssen and Tobler, 2013;

Turgeon *et al.*, 2019; Knott *et al.*, 2024) while macrophytes and benthic primary producers decline and phytoplankton increases (He *et al.*, 2024). Even if a reservoir in itself causes important ecological impacts, it constitutes a lake-like ecosystem that can be more or less heavily compromised. Indeed, in the WFD, this is formalized through the possibility of declaring reaches with indispensable hydropower production as heavily modified waters. This means that a reservoir created in a former river section should be managed and assessed as a lake, rather than a river reach, and the legal demands relate to 'ecological potential' instead of 'ecological status' (Borja and Elliott, 2007). Consequently, while being a heavily altered river reach, the reservoir is also a lake-like system subject to its own stressors from hydropower production, often shared by regulated natural lakes.

In reservoirs and regulated lakes, large artificial water level fluctuations typically constitute the main anthropogenic pressure (Keto *et al.*, 2008; Fig. 1c). Storage reservoir water is typically retained in the reservoir to be discharged when it can be most profitably used for the energy system or the hydropower producer. In alpine, arctic, and temperate regions, this traditionally meant filling up the reservoir during snowmelt in spring, maintaining high water levels over summer, followed by a continuous lowering over winter (winter drawdown). In parallel, short-term water level fluctuations related to hydropeaking are increasingly important in hydropower production (Cott *et al.*, 2008a). The littoral zone is particularly exposed to water level fluctuations (Keto *et al.*, 2008). Here, anthropogenic water level fluctuations cause erosion and loss of sediment in the littoral zone, expose part of the littoral for repeated drying (sometimes coupled with freezing), and make complex habitats (tree roots, boulders, dead woody debris, etc.) temporarily unavailable to aquatic organisms (Cott *et al.*, 2008a; Carmignani and Roy, 2017). Artificially high water levels may push the limits of the photic zone closer to the surface, decrease the light conditions in the littoral zone, and inundate naturally dry habitats in the riparian zone (Leira and Cantonati, 2008). In pelagic and profundal waters, regulated water levels may affect water circulation, stratification, oxygen availability, and temperature regimes (Cott *et al.*, 2008b; Leira and Cantonati, 2008; Poikane *et al.*, 2020). As in natural lakes, stratification can also result in oxygen free areas under the thermocline in reservoirs and regulated lakes (Malm Renöfält and Ahonen, 2013), and recent measurements indicate that oxygen deficit can arise also in relatively shallow areas (Widén and Malm Renöfält, in prep). While, impoundments initially cause increases in nutrient loads as submerged organic material is broken down (Zohary and Ostrovsky, 2011), water level regulation often results in oligotrophication of the regulated water body as nutrient exports from land to the aquatic environment are disrupted (Carmignani and Roy, 2017; Rydin *et al.*, 2008).

In the reservoir or regulated lake, unnatural water level fluctuations can impact the ecosystems in multiple ways, changing the composition of the ecological community, particularly in the littoral zone (Tab. 2). Changes in flooding magnitude, frequency, and duration, together with associated erosion, often reduce riparian vegetation diversity, hinder recruitment, and cause physical damage through processes such as ice scour that damage, break or uproot plants (Hill *et al.*, 1998; Nilsson and Keddy, 1988; Bejarano *et al.*, 2018, 2020). Drying, freezing, and scouring often, but not always, reduce macrophyte abundance particularly of sensitive species, such as large quillworts, in the littoral zone (Poikane *et al.*, 2020; Turner *et al.*, 2005; Keto *et al.*, 2006; Mjelde *et al.*, 2013). Macroinvertebrates in the littoral are also strongly affected by desiccation, erosion, and loss of macrophytes, roots, woody debris, and loss of wetted area, often reducing diversity, while tolerant or mobile taxa may increase (Furey *et al.*, 2006; Zohary and Ostrovsky, 2011; Poikane *et al.*, 2020; Roy *et al.*, 2021). Similarly, littoral feeding or spawning fish are heavily impacted by desiccation and loss of structural complexity and food resources in the littoral zone, associated with large artificial water level amplitude (Hirsch *et al.*, 2017; Sutela and Vehanen, 2008; Sutela *et al.*, 2011; Logez *et al.*, 2016; Yamamoto *et al.*, 2006). Fish eggs and juveniles suffer desiccation, with impacts varying by season and drawdown amplitude (Modde *et al.*, 1997; Sutela and Vehanen, 2008; Sutela *et al.*, 2002, 2011; Logez *et al.*, 2016; Linløkken and Sandlund, 2016; Westrelin *et al.*, 2018). Birds foraging for macrophytes, macroinvertebrates, or fish in the littoral zone may be affected by the impacts on these groups and associated change in feeding opportunities (Cott *et al.*, 2008a), and birds nesting near the water surface can be sensitive to unnatural water level fluctuations that drown nests or expose chicks and eggs to terrestrial predators (Keto *et al.*, 2008; Leira and Cantonati, 2008; Walseng and Jerstad, 2014). Pelagic fish, the planktonic community, and deeper-living macroinvertebrate assemblages often remain relatively unaffected (Cott *et al.*, 2008a; Tavsanoğlu *et al.*, 2017; Sutela *et al.*, 2013), although trophic effects of water level regulation can transmit also to pelagic communities (Milbrink *et al.*, 2011; Rydin *et al.*, 2008). Reservoirs can also act as hotspots and stepping stones for invasive species, and in some cases, non-native fish are intentionally stocked to benefit fisheries impacted by hydropower, potentially triggering cascading ecological effects in the reservoir and beyond (Gozlan *et al.*, 2010; Vander Zanden *et al.*, 2024).

2.3 Temperature effects

Depending on the dam operation, temperatures downstream of the dam can be affected in different ways. In particular, temperature effects downstream of reservoirs may depend on the vertical placement of spill gates and turbine intakes (depth-origin of the spilled/turbined water), reservoir stratification regime, volume, surface area, and water surface albedo. Relatively wide impounded water surfaces above low head dams and reaches with reduced discharge levels can be heavily influenced by heat exchange with the air. This can, for example, result in substantial increases of river temperature downstream during summers (Zaidel *et al.*, 2021). An opposite effect is achieved at larger dams where water is released via turbines or spill gates from below the hypolimnion in stratified reservoirs, resulting in higher-than-normal temperature in winter and colder-than-normal temperatures in summer in the downstream river stretches (Heggenes *et al.*, 2021; He *et al.*, 2024). During winter, increased temperature can alter ice dynamics, replacing stable surface ice conditions with open water and dynamic in-stream ice-formation (Heggenes *et al.*, 2021; Fig. 1e). The water temperature changes can be detected tens of kilometers downstream of the dam (Heggenes *et al.*, 2021). Upstream the dam, reservoirs, in turn, can be warmed or

Table 2. Key findings on impacts from unnatural water level fluctuation in hydropower reservoirs and regulated lakes.

Group	Impact	References
Riperian vegetation	Lowered diversity, more non-native species, and fewer rare shoreline herbs compared to a natural shore.	Hill *et al.*, 1998
	Flood duration affects vegetation cover and composition.	Nilsson and Keddy, 1988
	Flood magnitude and frequency impact recruitment and survival of plants, excluding flood-sensitive species. Initial promotion of flood-tolerant species can later be counteracted by continuous erosion.	Bejarano *et al.*, 2020
	Extended lowered water levels can cause water stress and reduced growth and survival of plants.	Bejarano *et al.*, 2018
	Erosion of fine sediment, associated with water level regulation, can hinder plant recruitment.	Bejarano *et al.*, 2018
	Increased ice chafing against the reservoir or river margins, associated with water level regulation, cause physical injury to plants through breakage and uprooting.	Bejarano *et al.*, 2018
Macro-phytes	Overall macrophyte richness and abundance can be reduced by water level fluctuations.	Poikane *et al.*, 2020; Keto *et al.*, 2006
	Increase of more water level fluctuation tolerant species and decrease or disappearance of more sensitive species.	Cott *et al.*, 2008a; Zohary and Ostrovsky, 2011; Mjelde *et al.*, 2013
	Large quillworts (*Isoetes* spp.) are particularly sensitive to water level fluctuations.	Turner *et al.*, 2005; Keto *et al.*, 2006; Mjelde *et al.*, 2013
	Artificially reduced water level fluctuations can cause changes in macrophyte composition, inducing the dominance of erect aquatic macrophytes.	Wilcox and Meeker, 1992
	Water level fluctuations of 1-3 m promote macrophyte diversity, while winter drawdowns of >3 m has been suggested to be detrimental for the macrophytes community	Rørslett, 1991; Hellsten and Mjelde, 2009; Mjelde *et al.*, 2013; Sutela *et al.*, 2013
Benthic algae	Water level fluctuations reduce colonizable surface areas for benthic algae, leading to reduced contribution to the reservoir food web.	Turner *et al.*, 2005
Macro-Inverte-brates	Desiccation effects restrict many speciesto deeper, permanent wetted areas.	Cott *et al.*, 2008a; Leira and Cantonati, 2008
	Community composition alterations and diversity reduction due to erosion, disconnection from arse substrates (roots, woody debris, etc.), and reduction of macrophytes; mediated direct impacts and decreased habitat and food availability and diversity.	Brauns *et al.*, 2008; Zohary and Ostrovsky, 2011; Poikane *et al.*, 2020; Roy *et al.*, 2021
	Increase in drought-resistant and mobile taxa, as well as organisms with short life cycles. Seasonal drawdowns lead to higher density and biomass of tolerant taxa such as chironomids, oligochaetes and nematodes.	Furey *et al.*, 2006
	Accumulation of organic material. Reduced outflow of reservoir- or lake derived plankton and coarse and particulate organic matter may starve downstream sections of nutrients.	He *et al.*, 2024; Gerwing and Plate, 2019
Fish	Loss of access to structural complexity (roots, boulders, macrophytes) and food resources in the littoral zone associated with large artificial water level amplitude.	Hirsch *et al.*, 2017
	Littoral benthic feeding and nest building fishes (*e.g.*, common minnow, ruffe, bullheads, and juvenile burbot), are sensitive to artificial water level fluctuation.	Sutela and Vehanen, 2008; Sutela *et al.*, 2011; Logez *et al.*, 2016
	Phytophilic juvenile fish (*e.g.*, cyprinid larvae), can be sensitive to loss of macrophytes in the littoral zone.	Yamamoto et al., 2006
	Loss of spawning habitat or desiccation of eggs (observed *e.g.*, in kokanee salmon *Oncorhynchus nerka* and whitefish *Coregonus* sp.).	Modde *et al.*, 1997; Sutela *et al.*, 2002; Linløkken and Sandlund, 2016
	For pelagic fish, water level fluctuations per se do not seem to be an important stressor and several studies fail to indicate notable regulation-dependent behavioral effects in habitat generalist predatory fish.	Vehanen and Lahti, 2003; Westrelin *et al.*, 2018; Roy *et al.*, 2021; Sutela *et al.*, 2013

Table 2. (continued).

Group	Impact	References
	Water level fluctuations affect pelagic fish with littoral life-stages, and can cause habitat shifts and influence predator-prey interactions in the littoral.	Fischer and Öhl, 2005; Klobucar and Budy, 2016
	Water level regulation, by disruption of nutrient exports from land to the aquatic environment, results in oligotrophication of reservoirs and regulated lakes, with effects on the planktonic food web and fish growth, size, and biomass.	Milbrink *et al.*, 2011; Rydin *et al.*, 2008
	For riverine species that persist in reservoirs, changed selection pressures may cause evolutionary change in the affected populations.	Haas *et al.*, 2010
Birds	Birds foraging for macrophytes, macroinvertebrates, or fish in the littoral zone may be affected by the impacts on these groups and associated change in feeding opportunities.	Cott *et al.*, 2008a
	Birds that nest on or very close to the water are typically adapted to the natural water level variations and can be sensitive to unnatural water level fluctuations that drown nests or expose chicks and eggs to terrestrial predators.	Keto *et al.*, 2008; Leira and Cantonati, 2008; Walseng and Jerstad, 2014
	Unpredictable change of water level from the time of nest establishment to the time chicks leave the nest can result in failed breeding and make the regulated river site into an ecological trap. Loons (Gaviidae) and some gulls (Laridae), for example, nest close to the water surface and are considered sensitive to water level increases of just a few dm.	Keto *et al.*, 2008; Walseng and Jerstad, 2014

cooled as a particular depth strata is being used for hydropower production or spilled past the dam (Hirsch *et al.*, 2017).

Since most biological processes of ectotherms are dependent on the environmental temperature (Ward and Stanford, 1982; Huey and Kingsolver, 1989; Brown *et al.*, 2004), altered water temperatures will inevitably affect physiology and behavior of ectothermic aquatic animals (Gillooly *et al.*, 2002; Watz and Piccolo, 2011). In macroinvertebrates, colder summer temperatures can disrupt egg development, hatching, and maturation, and risks affecting their presence in the watercourse (Brittain and Saltveit, 1989). In winter, the absence of temperatures close to freezing can disrupt development triggers, and hence the ontogeny of affected species (Olden and Naiman, 2010). Warmer winter temperatures can also result in abnormally increased growth (given that food is available) followed by too early emergence (*e.g.*, in winter rather than in spring) with potential lethal consequences for the emerging insects, and temporal trophic mismatch in the ecosystem (Ward and Stanford, 1982; Olden and Naiman, 2010). Temperature effects have been reported to cause changes in the aquatic macroinvertebrates community (Lessard and Hayes, 2003), including losses of many taxa (Olden and Naiman, 2010). In fish, reduced temperatures due to flow regulation has been reported to disrupt spawning and suppress fry recruitment (King *et al.*, 1998). and increased winter temperatures can increase development rates of egg and fry with potentially detrimental impacts on timing of hatching and subsequent survival (Heggenes *et al.*, 2021). Also, reduced ice-cover has the potential to modify fish behavior, making fish more susceptible to predation and therefore reduce their activity (predator exposure) in winter (Watz *et al.*, 2016). In addition, changed temperatures can transform host-pathogen dynamics, for example increasing fish mortalities in warmer waters (Löhmus and Björklund *et al.*, 2015; Bruneaux *et al.*, 2017). At a fish community level, dam related temperature modifications have resulted in declines in cold water fish species, such as brown trout (*Salmo trutta*), at high latitudes, while cold water release has extirpated warm water species at lower latitudes (Lessard and Hayes, 2003; Olden and Naiman, 2010).

2.4 Gas supersaturation

Under some conditions, the passage of water through turbines or spill gates can cause gas supersaturation in the water, with negative effects on fish and other biota (Pulg *et al.*, 2018; Li *et al.*, 2022; Fig. 1f). The occurrence and level of gas supersaturation depend on facility geometry, turbine intakes, clogging debris, and the downstream environment, and hence vary both over time and between sites (Pulg *et al.*, 2016; Li *et al.*, 2022). Supersaturated water can disperse several kilometers downstream of dams (Feng *et al.*, 2018).

Gas supersaturation causes gas bubble disease in fish and other organisms. This can cause direct mortality or increased susceptibility to predation and pathogens (Weitkamp and Katz, 1980; Pulg *et al.*, 2018). Different organisms display different tolerance levels, but important effects on survival are reported for levels above 110 – 120%. Salmonid fish seem to be generally more sensitive than cyprinid species, and invertebrates appear relatively tolerant (Weitkamp and Katz, 1980; Pulg *et al.*, 2018). Fish can recuperate from exposure to supersaturation, and, even if the mechanism is unknown, also display avoidance behavior by going to deeper waters where supersaturation is less of a problem (Weitkamp and Katz, 1980; Heggberget, 1984; Beeman and Maule, 2006).

2.5 Dissolved oxygen

Hydropower regulation can affect decomposition, river flow, and temperature in ways that lower dissolved oxygen levels in rivers. At construction, dams inundate terrestrial areas, causing an increasing decomposition and oxygen demand (Baxter, 1977). At places where summer temperatures increase, *e.g.*, in impoundments, downstream surface spills, or in river reaches with reduced discharge, the oxygen levels follow suit. Reduced discharge and flow, for example in bypassed river reaches, also reduces the in-mixing of oxygen from the air while respiration rates can remain high (Widén *et al.*, 2021). Together or in isolation, these factors may contribute to low levels of dissolved oxygen in regulated rivers. Although little investigated, this phenomenon has recently been documented in several regulated rivers in northern Sweden (Å. Widén and B. Malm-Renöfält, in prep), with potentially important effects on river biota (Croijmans *et al.*, 2021; Franklin 2014).

2.6 Connectivity

Connectivity in riverine systems occurs over three spatial dimensions – longitudinal, lateral, and vertical – and constitutes the movement of water, sediment, nutrients and organisms (Ward, 1989). On top of this, variation and continuity over time is superimposed (temporal connectivity).

Longitudinal connectivity refers to the movement of organisms and materials along the upstream–downstream axis of a river. Dams disrupt this connectivity by blocking upstream and downstream movement of fish and other organisms while also trapping sediments, nutrients, and woody debris, thereby causing ecological effects that extend far beyond the dam itself (He *et al.*, 2024; Figs. 1g–1h). A range of organisms are affected by the disrupted longitudinal connectivity, including insects (Brooks *et al.*, 2018), riparian plants (Nilsson *et al.*, 2010), mussels (Dobbs *et al.*, 2024), crustaceans (Fièvet, 2000), and mammals (Mijangos *et al.*, 2022). The situation is, however, both better investigated and particularly precarious for fish that depend on in-stream longitudinal movements for migration and dispersal.

Fish migrate for feeding, reproduction and refuge, often in response to environmental or developmental changes (Lucas *et al.*, 2001). The scale of fish migration varies from meters to thousands of kilometers and can occur in the marine environment, in freshwater or between freshwaters and the sea (Lucas *et al.*, 2001; Morais and Daverat, 2016; Herrera-R *et al.*, 2024). During the last centuries, the construction of dams has hindered fish from migrating between habitats and caused declines and sometimes even local extinctions of migratory species (Jonsson *et al.*, 1999; Lenders *et al.*, 2016). Ideally, non-migrating fish should also be allowed to pass dams to maintain genetic diversity and natural dispersal in the river system (Jones *et al.*, 2021), and also allows fish to adapt to changing environmental conditions by movement (Schiavon *et al.*, 2024). Blocked fish movements can have cascading effects in the form of disrupted nutrient transport and changed trophic interactions (Tonra *et al.*, 2015). Riverine mussel larvae are typically transported upstream attached to fish (Rock *et al.*, 2025; Salonen *et al.*, 2017; Schneider, 2017), and blocking the movement of host fish also effectively prevents the upstream dispersal of these mussel species (Watters, 1996; Dobbs *et al.*, 2024). Hence, restoring longitudinal connectivity is an important aspect of conserving fish and fish-associated species, and consequently ecological integrity, in regulated rivers (McIntyre *et al.*, 2015; Bastino *et al.*, 2021).

Lateral connectivity concerns the interaction between the river channel and the riparian or floodplain system (Ward, 1989). Overbank flows connect surrounding floodplains and the river, causing erosion and sedimentation, transfer of nutrients, and open up important habitat for fish and other organisms (Junk *et al.*, 1989; McCabe *et al.*, 2025). The regulation of river discharge and lake levels can disrupt natural flood patterns, and hence interrupt the lateral connectivity with widespread effects on the ecological communities (Thieme *et al.*, 2024). For example, many fish enter highly productive floodplains for reproduction, with the environment offering a food rich and protected environment for growing fry (Opperman *et al.*, 2010; McCabe *et al.*, 2025). Also, as already been discussed above, the riparian plant community depends on floods for recruitment, irrigation, species filtering, and nutrients (Junk *et al.*, 1989; Mahoney and Rood, 1998; Bejarano *et al.*, 2020). Lateral connectivity and natural flood pulses also creates habitat diversity necessary for a range of invertebrate species (Ellis *et al.*, 2001; Åström *et al.*, 2017).

Vertical connectivity concerns the movement of nutrients and organisms between stream water in the river channel, and groundwater in the aquifer (Ward, 1989; Hancock, 2002). Groundwater and stream water mix in the hyporheic zone, which is an important habitat for microorganisms, macroinvertebrates and bivalves, and fish (Boulton *et al.*, 1998; Ward *et al.*, 2002) making vertical connectivity a defining habitat characteristic. Many salmonids, for example, burrow their eggs in gravel while many insect species spend their larval stage partly or entirely in the interstitial habitat (Ward *et al.*, 2002; Hancock, 2002). Hyporheic flows are affected by river discharge and may therefore be directly impacted by flow regulations (Calles *et al.,* 2007; Hancock, 2002; Boulton *et al.*, 1998). In particular, reduced flows from hydropower can cause sedimentation and clogging of the river bed, with negative consequences for natural occurring species in the habitat (Wang *et al.*, 2020; Mathers *et al.*, 2021).

2.7 Interconnectedness

Importantly, effects on one species, or type of organism, are not isolated events. Other organisms are likely influenced by the same abiotic factors, or effects on one organism type result in cascading effects on others. For example, a reduction in macrophytes and macroinvertebrates in the littoral zone of reservoirs or regulated lakes, can reduce the food and shelter availability of fish, resulting in changed composition of the fish community (Cott *et al.*, 2008a). Alternatively, regulated flow can result in decreased densities or changed composition of macroinvertebrates with negative effects on fish (Wang *et al.*, 2020). Even on land, flow regulation effects on the riparian plant composition can, for instance, affect the availability of species-specific host plants for butterfly larvae, and hence the butterfly population (Appelqvist and Bengtsson, 2007).

Of relevance to all types of hydropower effects on aquatic biota, rivers and their fringing riparian zones are also not independent ecosystems; they are intimately reliant on linked exchange pathways of matter, energy, and organisms (Ward and Stanford, 1995; Lafage *et al.*, 2019; Baxter *et al.*, 2005). Aquatic insects often emerge with very high abundance and biomass, and are composed of relatively labile, high-quality organic matter (Nakano and Murakami, 2001). Accordingly, these aquatic insects represent an important food resource for terrestrial arthropods (Henschel *et al.*, 2001; Paetzold *et al.*, 2006), lizards (Sabo and Power, 2002), birds (Iwata *et al.*, 2003; Alberts *et al.*, 2013), and bats (Fukui *et al.*, 2006), and hence an important element in the cycling of carbon and nutrients from water to land. This means that any effects on aquatic biota will also potentially impact the surrounding terrestrial ecosystem. Indeed, studies has shown that flow regulation can lower emergent insect biomass relative to unregulated reaches resulting in a decrease in the abundance or breeding success of riparian arthropod predators and insectivorous birds (Jonsson *et al.*, 2013; Strasevicius *et al.*, 2013).

In the opposite direction, the riparian plant community is instrumental for life in the river and lake (Sass, 2009; Zaidel *et al.*, 2021; Rodríguez-González *et al.*, 2022). The riparian zone retains pollutants and sediments, provides shade that can lower water temperature, subsidy the river with organic material (*e.g.*, large woody debris and leaves) that serves as food, shelter and substrate in the aquatic ecosystem (Feld *et al.*, 2011; Rodríguez-González *et al.*, 2022). Terrestrial arthropods entering rivers and streams (via gravity, wind, or other vectors) also provide high-quality food resources for aquatic consumers, including benthic invertebrates (Kraus, 2010) and fish (Mason and Macdonald, 1982; Baxter *et al.*, 2005; Kawaguchi and Nakano, 2001).

The characteristics of the land as well as the anthropogenic land use also shapes the ecology of the river (Extence *et al.*, 1999; Sandin, 2009). Land use constitutes additional human stressors relating to nutrient and sediment loads, pollution, hydrological alterations, and riparian degradation (Feld *et al.*, 2011). Land use, river characteristics, and additional stressors shape the biological communities present, and often interact with ecological effects of hydropower (Carmignani and Roy, 2017). Effects of hydropower production can therefore differ from site to site, depending on other stressors and river characteristics (Feld *et al.*, 2011; Göthe *et al.*, 2019). Hence, ecological effects of hydropower can be both site-specific and general, underlining the need for research and monitoring to define suitable mitigation measures.

3 Remedial measures

The master tool for rehabilitating rivers affected by hydropower production is the removal of dams and ceasing of production (Silva *et al.*, 2018). Dam removal, a common measure of restoration, has resulted in thousands of dams, mostly small and old, being removed in North America and Europe (Ryan Bellmore *et al.*, 2017; Ding *et al.*, 2019). Dam removal has immediate effects on flow, temperature and the longitudinal connectivity, and shift impounded river reaches back to their lotic state (Feld *et al.*, 2011), but often also comes with short term detrimental effects, mainly in form of excessive sediment loads (Carlson *et al.*, 2018; Rubin *et al.*, 2017). Over decadal time scales, however, dam removal and the associated restoration of natural flow patterns, should restore conditions to which native organisms are adapted and enable sustained ecological recovery (Poff *et al.*, 1997; Wohl *et al.*, 2015). Despite decades of research, significant knowledge gaps remain about the rate and extent of riverine ecosystem responses to dam removal and, crucially, about when negative effects are likely to occur. These uncertainties hinder the development and application of regulations and standards (Gillette *et al.*, 2016) and complicate decision-making around dam removal. Understanding biological responses to dams and their removal is important for quantifying ecosystem impacts and guiding mitigation efforts, as these responses reflect the spatial scale of the impact and provide benchmarks for measures to mitigate the effects of dams on biodiversity and ecosystem function.

Dam removal is, however, often not feasible from a societal perspective, and therefore a range of remedial measures are instead applied. Remedial measures then focus on the coexistence of hydropower production, and associated dams with the natural river ecology. A diverse, but under-studied, toolbox is available (Trussart *et al.*, 2002), with both different environmental flow and physical adaptation among the remedial measures discussed in the following sections.

3.1 Environmental flows

The natural riverine ecosystem depends on a natural variation of magnitude, rate of change, frequency, duration, and timing of flows (Poff *et al.*, 1997; Richter *et al.*, 1997). Environmental flow mitigation based on this multifaceted natural variability, for example by allowing only minor deviations from the natural flow regime, is widely promoted (Richter *et al.*, 1996; Acreman *et al.*, 2014). In practice, minimum flows, or flow variation adapted to one or a few target species is more commonly applied as flow mitigation measures (Richter *et al.*, 1997; Arthington *et al.*, 2006). While remediating some effects of flow regulation, this simplified approach also risks disregarding ecologically important flow characteristics (Acreman *et al.*, 2014).

Adjustment of downstream flows can be achieved by directly regulating hydropower production or reservoir storage, or by the use of retention basins that capture water and balance the flow downstream (Harby and Noack, 2013; Bruder *et al.*, 2016; Reindl *et al.*, 2023). Discharge regulation and flow mitigation occurs both in whole river reaches downstream of reservoirs and, more radically, in river reaches where all or a large proportion of water is channeled away from the natural river (Widén *et al.*, 2022; He *et al.*, 2024). Even if the latter bypassed river reaches are typically heavily impacted, they also constitute potentially important habitat for organisms living in fast flowing water, especially as this habitat has been severely restricted by the damming of rivers (Birnie-Gauvin *et al.*, 2017a). Some of this potential can be fulfilled even by allocating only a fraction of the natural discharge (Malm Renöfält *et al.*, 2015). In general, flow and water level mitigation measures are in need of robust evaluation in the field (Richter *et al.*, 1997; Bruder *et al.*, 2016; Souchon *et al.*, 2008).

3.2 Minimum flow

Completely dry river reaches or very low flow is a fundamental problem for riverine life (Widén *et al.*, 2022). Consequently, minimum flow regulation is commonly applied to save downstream river reaches from complete desiccation by retaining at least some water at all times (Richter *et al.*, 1997; Renöfält *et al.*, 2010). Minimum flows of 10%, 30%, and >60% of mean annual flow have been used as, relatively arbitrary, thresholds to achieve basic survival, good habitat, or excellent habitat respectively (Richter *et al.*, 1997). In Sweden, however, most hydropower projects lack minimum flow requirements or, where present, 5% of discharge is the most common requirement (Renöfält *et al.*, 2010). Although reductionist in relation to recommendations, even a low minimum flow offers more riverine habitat than a dry riverbed. Application of minimum flow can substantially increase macroinvertebrate density and diversity (Weisberg *et al.*, 1990; Bednarek and Hart, 2005) and rewetting of previously dry river reaches can result in rapid recolonization of periphyton, macroinvertebrates, and fish (Decker *et al.*, 2008). Indeed, minimum flow requirements have been associated with higher fish growth and condition factor, presumably as a consequence of higher macroinvertebrate prey abundance (Weisberg and Burton, 1993). On a fish community level, implementation of minimum flow, and the associated reduction in flow fluctuations, increased species richness and the proportion of fluvial specialists in the southern USA (Travnichek *et al.*, 1995), and the presence and magnitude of minimum flow in bypassed river reaches was positively correlated to fish diversity and density in northern Sweden (Göthe *et al.*, 2019). Importantly, the effect of minimum discharge can be influenced by additional stressors, such as land use and riparian vegetation (Göthe *et al.*, 2019). Sometimes, habitat restoration measures within the bypassed river reach can be needed to improve conditions for fish and other biota in a system receiving substantially less water than what was naturally the case (Renöfält *et al.*, 2017; Decker *et al.*, 2008). Also, release of minimum flow can be used to mitigate low water quality in water stressed river reaches (Lind *et al.*, 2007).

3.3 Dynamic flow variation

Flow variation adapted to one or a few target species, or to a flow component deemed particularly important, is sometimes applied to mitigate the effect of flow regulation (Richter *et al.*, 1997; Arthington *et al.*, 2006). Release of spring floods have been used to promote fish migration or reproduction as well as the recruitment of riparian vegetation (Rood *et al.*, 2005; Arthington *et al.*, 2024). High flows can also reconnect the river to flood plains, provide moisture to plants, purge non-wanted species, as well as deposit and flush material (Loire *et al.*, 2021; Richter *et al.*, 2006), including sediment to maintain vertical connectivity (Hancock, 2002). In general, an environmental flow based on natural flow dynamics is deemed preferable to a narrow focus on a target species, as the latter approach may come to the detriment of other organism groups (Tonkin *et al.*, 2021).

3.4 Hydropeaking mitigation

In relation to hydropeaking, flow mitigation measures are often focused on reducing the rate of change to avoid stranding and flushing, reduce the magnitude or frequency of change, or limiting maximum and minimum discharge during critical periods (Nagrodski *et al.*, 2012; Moreira *et al.*, 2019; Bartoň *et al.*, 2023). Along these lines, reducing the frequency of down-ramping events has been used to mitigate hydropeaking effects on juvenile salmonids (Connor and Pflug, 2004), with thresholds for rate of change of $0.1 - 0.3$ cm/s being used (Moreira *et al.*, 2019). Also, maintaining discharge levels during spawning similar to the predicted discharge during incubation is implemented to avoid spawners depositing eggs in areas which will later become air-exposed (Moreira *et al.*, 2019). Minimum-flow is also used to mitigate effects of hydropeaking, in particular zero-flow events (Widén *et al.*, 2021).

Not directly flow related, the habitat downstream can be restored or manipulated to mitigate against extreme flows. At a relatively large scale, floodplain channels have been shown to mitigate effects of hydropeaking on juvenile chub (*Squalus cepahlus)* abundance (Cousin *et al.*, 2025). At the site scale, physical flow deflectors, small weirs, submerged trees, and coarse gravel can reduce the rate of change, offer protection to high flows, and retain water during low discharge periods (Heggenes, 1988; Harby and Noack, 2013). Boulders and other large structures can also reduce bank erosion and ice-scouring effects on macrophytes and riparian vegetation (Bejarano *et al.*, 2020), and flow deflectors protecting spawning grounds from high flow velocities increased egg survival in asp (*Leuciscus aspius;* Bartoň *et al.*, 2023). Shelters in the drying zone can, however, increase the risk of stranding (Harby and Noack, 2013), and refuge habitats ("potholes") on the river bank can increase both the risk of stranding and drift (Auer *et al.*, 2017).

3.5 Temperature

The cold-water or warm-water pollution associated with river regulation can be mitigated by a range of measures. For hypolimnetic released water, aeration or pumping in the reservoir can prevent stratification and therefore the sharp shift in temperature from above and downstream the reservoir (Olden and Naiman, 2010), and have been used to restore natural fish populations downstream dams (Miles and West, 2011). The same effect can, theoretically, be achieved by multi-level or floating intakes and spill gates, or by using submerged weirs to force surface water down and prevent the exit of bottom water (Olden and Naiman, 2010; Heggenes *et al.*, 2021). For smaller reservoirs, and river reaches with reduced flow, tall riparian vegetation that provides shade can buffer against warming effects (Poole and Berman, 2001).

3.6 Dissolved gases

Gas supersaturation can be caused both in turbined and spilled water (Beeman and Maule, 2006; Pulg *et al.*, 2018; Li *et al.*, 2022). For turbined water, excluding air from the intake and maintaining clean intake racks can reduce gas supersaturation (Pulg *et al.*, 2018). Gas supersaturation can be mitigated by exposing the supersaturated water to air, for example spilling in cascades as well as aerating or directing the supersaturated water to regions near the surface (Pulg *et al.*, 2018; Li *et al.*, 2022). Low dissolved oxygen levels, on the other hand, has been mitigated by aeration weirs downstream the dam or by venting turbine water, resulting in increases in the proportion of Ephemeroptera, Plecoptera, and Trichoptera species (Bednarek and Hart, 2005).

3.7 Reservoirs

For reservoirs, potential mitigation follows the same principle as river flow mitigation. To reduce the amplitude and adapt the timing of water level fluctuations, following more natural rhythms, can limit the ecological effects of the regulation (Hill *et al.*, 1998; Garron *et al.*, 2024). With an explicit fish focus, avoiding lowering water levels from mid-April has been recommended for protecting spawning Eurasian perch (*Perca fluviatilis*) (Westrelin *et al.*, 2018), but this type of recommendation could likely be applied to several species spawning in littoral habitats (*e.g.*, northern pike *Esox lucius* and whitefish *Coregonus* sp.; Hellsten *et al.*, 2002; Glover *et al.*, 2012). Limiting water level fluctuations to 3-5 m has been suggested to reduce detrimental effects on littoral biotic communities (Smith *et al.*, 1987; Mjelde *et al.*, 2013; Sutela *et al.*, 2013), but this is likely site dependent.

Floating islands have been used to compensate for complex littoral habitat lost from water level fluctuations. Such islands have been associated with high abundance of juvenile Eurasian perch and roach (*Rutilus rutilus*), typically habiting the littoral (de Moraes *et al.*, 2023). Floating platforms are also used to offer nesting sites to aquatic birds (Baxter 1977). A layered floating island, constituting both a terrestrial part and several underwater levels containing soil and plants, resulted in higher macroinvertebrate richness, diversity and abundance as well as higher juvenile northern pike occurrence compared to littoral control reaches (Salmon *et al.*, 2022; 2024). The same structure did not show higher densities of juvenile fish, typical of the littoral zone, compared to the reservoir littoral, potentially due to its relatively small size (70 m^2) and large distance from the shore (Salmon *et al.*, 2025). This underlines the need to evaluate different design characteristics of this remedial measure. Another open question, that goes beyond the communities inhabiting the individual structure, is how much of such a habitat mitigation measure that constitutes meaningful mitigation at the reservoir or lake scale.

The so-called lake-in-a-reservoir concept has been applied in reservoirs. Here, a weir is constructed within the reservoir to make a portion of the reservoir littoral unaffected by water level fluctuations (Baxter, 1977). This mitigation has been applied to benefit both macroinvertebrates, fish and birds but lacks scientific evaluation (Grimås, 1965; Helland *et al.*, 2019). Other reservoir restoration measures include compensatory habitat- or substrate rehabilitation (*e.g.*, addition of spawning gravel for salmonid fish), increasing connectivity with reservoir tributaries, and mechanical protection against erosion (Helland *et al.*, 2019). Sometimes fertilization of oligotrophic reservoirs is also considered a mitigation measure, at least when a reduction in nutrients is caused by water regulation (Gerwing and Plate, 2019; Rydin *et al.*, 2008).

3.8 Fish passage

Dam removal typically opens up the river for migratory or dispersing fish, as well as drifting invertebrates and plant propagules. Related to fish, dam removals have, for example, allowed the return of diadromous lamprey (Hess *et al.*, 2021), salmon (Liermann *et al.*, 2017), eel (Hitt *et al.*, 2012), and herring species (Hogg *et al.*, 2015) to upstream river reaches, but can also increase life-history variation, abundance, and growth of migrating fish already present (Brenkman *et al.*, 2019 Birnie-Gauvin *et al.*, 2017b). Importantly, also river resident or short distance migrating fish can benefit from the increased movement possibilities from dam removal (Hogg *et al.*, 2015). Dam removal is, however, often not a feasible option (Silva *et al.*, 2018). In face of this, fishways and other fish passage solutions are instead used to pass fish over hydropower dams (Katopodis and Williams, 2012; Noonan *et al.*, 2012).

The need for fishways and other passage solutions to facilitate two-way fish passage at migration barriers has been acknowledged for hundreds of years (Montgomery, 2004). Although remedial measures are still missing at many dams, this need has resulted in development of both technical and more nature-like fishways, as well as downstream bypass solutions (Katopodis and Williams, 2012; Calles *et al.*, 2013a; Nieminen *et al.*, 2016). A functional fish passage solution must ensure safe passage routes that a substantial portion of the migrating fish will use (Castro-Santos *et al.*, 2009; Silva *et al.*, 2018). Common for both upstream and downstream fish passage is that it is a process that depends on local conditions (*e.g.*, operation, discharge, temperature, physical structures), as well fish characteristics (species, size, life stage, motivation) (Silva *et al.*, 2018).

Even at dams with fishways, migrating fish might experience barrier-related migratory failure (Bunt *et al.*, 2012; Noonan *et al.*, 2012). Upstream migrating fish typically follow the dominant flow of the river, which can, if the fishway is erroneously placed, result in the fish getting stuck in the tailrace of the powerhouse or downstream spillways instead of finding the fishway entrance (Lundqvist *et al.*, 2008; Hagelin *et al.*, 2019). Once having found the fishway, the fish needs to be a sufficiently strong swimmer (and not behaviorally deterred) or it will not be able to enter and ascend the fishway (Volpato *et al.*, 2009; Katopodis *et al.*, 2019). Even after having exited the fishway, the fish may face the risk of falling back downstream again (Naughton *et al.*, 2006; Frank *et al.*, 2009). Fallbacks can be particularly problematic in human aided passage over multiple dams, as in trap-and-transport solutions (Hagelin *et al.*, 2016).

Downstream passage solutions were neglected for a long time, but have received increased attention during the last decades (Calles *et al.*, 2013a). While upstream passage typically is limited to one fishway, the downstream migrants often face the choice between multiple routes, often associated with different site- or operation specific mortality risks (Algera *et al.*, 2020; Knott and Pander, 2023). Turbine passage may cause injury and mortality from abrupt pressure changes, cavitation, shear forces, turbulence, and blade-strike (Coutant and Whitney, 2000; Mueller *et al.*, 2017). Although spill passage is often considered a safe route, it can also result in injuries or mortality (Algera *et al.*, 2020). As downstream migrating fish typically follow bulk flow, and this is often used for electricity production, most of them are bound to follow the water through turbines, unless successfully guided to a safe route downstream, often a dedicated bypass (Coutant and Whitney, 2000). Different physical screens are the standard solution to guide fish to bypass openings that guide them downstream (Harbicht *et al.*, 2022).

Both upstream- and downstream passage are associated with delays (Venditti *et al.*, 2000; Marschall *et al.*, 2011; Nyqvist *et al.*, 2016a) that may cause increased susceptibility to disease, predation and fishing mortality (Gowans *et al.*, 1999, 2003). Also, the lentic environments upstream impoundments can be important sources of mortality of migrating fish (Norrgård *et al.*, 2024; Schwinn *et al.*, 2018). Additional energy expenditure and injuries related to passage may also result in post-passage mortality (Caudill *et al.*, 2007; Roscoe *et al.*, 2011; Stich *et al.*, 2015).

Although engineering guidelines for constructing fishways are available (Dvwk, 2002; Larinier *et al.*, 2002; DWA, 2005; Ebel *et al.*, 2013; Schmutz and Mielach, 2013), the final product is based on local design compromises (Algera *et al.*, 2020). In fact, the in-situ functionality of fishways is often not known or is highly variable (Bunt *et al.*, 2012; Noonan *et al.*, 2012).

Important to note in relation to dams and fish passage is that dams may also prevent, or at least delay, the spread of non-native invasive species. Therefore, caution is warranted when building fishways connecting isolated native species with downstream non-native or invasive populations. In Italy, for example, strong native barbel populations mainly remain upstream of barriers where the non-native barbel species has not yet arrived (Antognazza *et al.*, 2023). In North European waters, this could be of concern, for example, in relation to the spread of the invasive signal crayfish (*Pacifastacus leniusculus*) (Kerr *et al.*, 2021), round goby (*Neogobius melanostomus*) (Hirsch *et al.*, 2017), and pink salmon (*Oncorhynchus gorbuscha*) (Staveley and Ahlbeck Bergendahl, 2022). Relatedly, it is also important not to build fishways that bring fish species to river reaches that they historically did not have access to, with a natural ecosystem shaped in their absence.

4 Monitoring

Hydropower production impacts a wide range of organisms within and around river systems, but remedial measures can mitigate these effects, helping to restore ecological integrity and safeguard key ecological values even in heavily altered rivers (Acreman *et al.*, 2014). Many mitigation measures, however, lack robust scientific basis, and there is a general need for both short- and long-term monitoring and evaluation of their effects (Clifford, 2007). Monitoring and evaluation serve to refine remedial measures at site, and to identify what works and what does not work to inform future mitigation measures elsewhere (Richter *et al.*, 2006; Bruder *et al.*, 2016). In fact, increased knowledge about the functionality of mitigation measures is the basis for cost-efficiently improved ecological status of regulated rivers and lakes, and for sustainable hydropower production (Tirkaso and Gren, 2022; Rogosch *et al.*, 2024). To understand the ecological effects there is a need to study both impacted organisms as well as the abiotic factors that ultimately drive these impacts (England *et al.*, 2008).

4.1 Abiotic monitoring

Hydrological factors directly manipulated by hydropower production include route specific discharge (spill, turbine, bypass, *etc*) and water level. Flow velocities at focal sites should be related to discharge data, either through manual measurements or hydrodynamic modeling validated with field data (Tarena *et al.*, 2024). River temperature is affected by hydropower production both through reservoir discharge and in low-flow reaches (Heggenes *et al.*, 2021). The extent of this impact is poorly understood making systematic monitoring of temperature upstream and downstream of dams urgently needed to obtain temperature data related to dam size, depth, intake/spill depth, and route-specific discharge (Olden and Naiman, 2010). Gas supersaturation can occur in both spilled and turbined water, persisting several kilometers downstream and causing injuries or mortality in fish and other biota (Pulg *et al.*, 2018; Li *et al.*, 2022). Despite its ecological significance, its occurrence is poorly mapped, and continuous logging in running water is recommended (Pulg *et al.*, 2018). Low oxygen levels may occur in reservoirs or downstream of dams affecting habitat availability and survival for aquatic animals. Although under-studied, recent work data (In prep. Å.Widén and B. Malm-Renöfält) suggests this problem is more widespread than previously thought, underlining the need for systematic monitoring.

In addition, hydropower production, through fluctuations in flow and water level, also influence erosion, sediment transport, and deposition, benthic habitats in streams (Vörösmarty *et al.*, 2003), at the same time as river morphology influence impacts from hydropower (Cousin *et al.*, 2025). Ecological effects of hydropower are also shaped by local conditions, and biological communities are often subject to more than one anthropogenic stressor (Feld *et al.*, 2011; He *et al.*, 2024). Local habitat, climate, river size, slope, land-use, and chemical pollutants can have important impacts on river ecology while not being directly related to hydropower production (Hynes, 1975; Woolsey *et al.*, 2007; Feld *et al.*, 2011; Wang *et al.*, 2011). Nutrient status and pH also strongly affect biological communities (*e.g.*, Masouras *et al.*, 2021; Ritterbusch *et al.*, 2022). Collecting chemical and geomorphological data is hence a fundamental part of the monitoring process, and can help explain observed biological responses to mitigation measures, as well as to predict expected biological communities in the system (Hawkins *et al.*, 2010).

4.2 Biological indicators

To describe ecological effects, indicators should be sensitive to impacted conditions and relatively stable over time (Poff and Zimmerman, 2010; Blabolil *et al.*, 2017). Incorporating indicators that are socially valued can also help justify and support mitigation efforts (Olden *et al.*, 2014). To ensure consistency and reliability, sampling procedures for indicator taxa should be standardized, user-friendly, and repeatable across time and locations (Birk *et al.*, 2012; Gann *et al.*, 2019). In addition, sample sizes should be sufficiently large to detect important ecological impacts and change (Gann *et al.*, 2019).

Given the important effects of hydropower production on many different organisms groups, a large set of biological indicator candidates are available. Riparian vegetation is especially important, as it regulates temperature, stabilizes banks, filters runoff, and supplies organic matter to aquatic food webs. Functioning riparian zones also support high biodiversity and influence the outcome of restoration measures such as minimum flow provisions or dam removals (Rodríguez-González *et al.*, 2022; Göthe *et al.*, 2019; Widén *et al.*, 2022). Macrophytes both respond strongly to water level fluctuations and flow changes (Bunn and Arthington, 2002; Poikane *et al.*, 2020) and constitute habitat and food resources for other organism (Wilcox and Meeker, 1992; Dibble *et al.*, 1997). Benthic diatoms are ubiquitous, taxonomically diverse, primary producers. They have taxa specific environmental requirements and are easily sampled and therefore commonly used as bioindicators (Rimet and Bouchez, 2012; Masouras *et al.*, 2021; Bondar-Kunze *et al.*, 2021) though their value for describing hydrogeomorphological change is less established (Johnson *et al.*, 2025).

Macroinvertebrates constitute important links between primary producers, detrital deposits, and higher trophic levels (Miler *et al.*, 2013) and constitute a taxonomically and functionally diverse group of animals adapted to a wide variety of different hydrogeomorphological conditions (Extence *et al.*, 1999; Armanini *et al.*, 2014). Simple categories of sensitive and tolerant taxa, proportion of key taxa (Ephemeroptera, Plecoptera, and Trichoptera; Carlson *et al.*, 2018), ratios of animals belonging to different hydrodynamic preference groups (Extence *et al.*, 1999; Armanini *et al.*, 2011, 2014) or functional traits (Carlson, 2025) are used as indices describing hydrogeomorphological impacts. Freshwater mussels play key roles in river ecosystems by filtering water, cycling nutrients, stabilizing sediments, and providing food and habitat for other organisms (Vaughn *et al.*, 2008; Atkinson and Vaughn, 2015) and their long lifespan integrates environmental conditions over decades, while the presence of juveniles show that the present conditions are suitable for reproduction and recruitment (Svensson, 2016).

Higher trophic levels indicate both direct and cascading effects, and charismatic animals attract wide sympathy and interest outside of research and management, helping to motivate mitigation measures (Greenwood, 2007). Fish are well-known mobile animals with a diversity of trophic positions and environmental preferences and requirements that are extensively used as indicators (Ritterbusch *et al.*, 2022). Birds are impacted by river regulation through its effect on their prey and nest sites (Keto *et al.*, 2008; Strasevicius *et al.*, 2013), and potentially respond swiftly to environmental change resulting from hydropower production or mitigation measures (Egwumah *et al.*, 2017). Similarly, bats also respond to changed river conditions mediated by emergent prey availability and can serve as a terrestrial indicator organism (Jones *et al.*, 2009; Hooker *et al.*, 2024). Also land invertebrates can be impacted by water regulation, for example by habitat loss (Åström *et al.*, 2017), and show a different aspect of the ecological impact of hydropower.

The availability, robustness, and level of method standardization varies between organism groups. Riparian vegetation is typically surveyed in field campaigns and to some extent using remote sensing (Cupertino *et al.*, 2024; Rowan *et al.*, 2006). Macroinvertebrates are collected using, for example, kick-nets, surber samplers, colonization baskets, litterbags, or terrestrial traps for emerging life-stages (Carlson *et al.*, 2018). Mussels are monitored through visual surveys, diving, or drone-based detection (CEN, 2017; Hedger *et al.*, 2023, and fish sampling includes electrofishing, gill nets, and trawling, hydroacoustics, and video recording (*e.g.*, Bohlin *et al.*, 1989, Golpour *et al.*, 2022; Näslund *et al.*, 2024; Prchalova *et al.*, 2009). Birds and bats are typically monitored using visual or acoustic censuses but passive acoustic recorders with automated species identification are quickly developing (Sethi *et al.*, 2024; Gallacher *et al.*, 2021). DNA-based methods can substantially accelerate present-absence surveys and are becoming more common for groups such as macroinvertebrates (Duarte *et al.*, 2021), fish (Moody *et al.*, 2025), diatoms (Masouras *et al.*, 2021), and even terrestrial arthropods (Leandro *et al.*, 2024).

Macrophytes, diatoms, macroinvertebrates, and fish are mandated bioindicators within the WFD, and typically evaluated through various multimetric indices (Birk *et al.*, 2012), while other organismal groups are less commonly monitored but may still have indicative value. Indeed, for multimetric indices used in ecological status assessment, it is crucial to assess whether they accurately reflect the relevant impacts for the monitoring program. Some indices are developed for impact specific effects (*e.g.*, Armanini *et al.*, 2011, 2014; Carlson 2025), while others are developed to measure general anthropogenic impacts (Birk *et al.*, 2012) without possibility to assess *e.g.*, antagonistic interactions between impact factors. Some indices have also been shown to have inbuilt flaws for certain type-specific impact assessments (*e.g.*, having presence of generally tolerant, but hydropower-sensitive species, as indicators of poor ecological status; Näslund *et al.*, 2022).

4.3 Evaluation of fish passage solutions

The performance of fish passage solutions needs to be monitored and evaluated to ensure that longitudinal connectivity is functionally restored, particularly when dealing with less known species or untested designs (Roscoe and Hinch, 2010). Indeed, fish passage science and design is still evolving, and high passage performance is typically achieved in the interplay between design, management, and monitoring (Nyqvist *et al.*, 2017a; Keefer *et al.*, 2021).

A simple and general form of fishway evaluation is conducted by trapping or by other means detecting fish upstream and downstream the fishway and comparing these fish communities or the presence/absence of target species over time. This can be done by capturing fish (Tamario *et al.*, 2019), or using eDNA (Yamanaka and Minamoto, 2016). Trapping fish ascending the fishway is another common but work-intensive method to quantify fish using the fishway (Benitez *et al.*, 2015; Baumgartner *et al.*, 2020). During the last decade, electronic fish counters have become a widely used tool for this kind of evaluation, producing numbers, species, and length distribution of passing fish, as well as the seasonal timing of passage without handling the fish (Eggers *et al.*, 2024; Haas *et al.*, 2024). This data can demonstrate that the fishway is ascendable by at least some individuals of the recorded species and sizes (Haas *et al.*, 2024). Passage events can then be correlated with environmental or operational conditions to improve understanding both of the fishway performance and the fish movements as such (Peterson *et al.*, 2017; Stuart and Marsden, 2019).

The drawback of these presence-, capture-, and detection methods is that they do not account for the fish that fail to use the fishway. Trapping data on size-and-species composition of fish caught downstream and upstream (or in the downstream end or upstream end of the fishway) can be used to get rough and comparable performance estimates of this kind (Jansen *et al.*, 1999; Baumgartner *et al.*, 2020) but is practically difficult to achieve. Several electronic tagging techniques (telemetry) are available that can give even more detailed understanding of the functionality of the fishway (see Thorstad *et al.*, 2013; Eggers *et al.*, 2024). Common telemetry-based evaluation metrics that account for previously caught and tagged fish that succeed/fail to use fishways are attraction (*i.e.*, the proportion of fish that are successfully guided to a particular passageway), entrance (*i.e.*, the proportion that enter the fishway after finding it) and passage efficiency (*i.e.*, the proportion that successfully pass from having entered) (Bunt *et al.*, 2012; Noonan *et al.*, 2012; SIS, 2021). Delay is another important fish passage performance metric that typically requires tagging of fish (Calles *et al.*, 2012; Nyqvist *et al.*, 2016b). Tracking fish also allows to estimate the migratory success post-passage as direct and delayed mortality, as well as fallback rates (Hagelin *et al.*, 2016; Algera *et al.*, 2020). Telemetry allows a more precise evaluation of fishway performance, including the quantification of passage probabilities over time and under shifting conditions (Hagelin *et al.*, 2019; Eggers *et al.*, 2024), which can form both the impetus and knowledge to allow for improved fish passage facilities (Nyqvist *et al.*, 2017a).

For downstream movements of fish, route specific mortality is an important part of the fish passage puzzle. This can be modelled based on previous data (Amaral *et al.*, 2018), evaluated by capturing fish that exit specific passage routes (Janáč *et al.*, 2013), or by using telemetry techniques tracking tagged fish to determine passage routes and the resulting post-passage survival (Nyqvist *et al.*, 2016a; b).

While the persistence and health of migrating and resident fish populations is the most robust confirmation of a functional fish passage solution (Pelicice and Agostinho, 2008), this might fall outside the responsibility of the fishway owner, and does not directly inform on how to improve the passage facilities. The evaluation effort might also need to be adapted to the fish populations concerned. In river reaches without important migratory populations, using data from traps or fish counters might be enough to qualitatively demonstrate that a wide range of the local fish fauna successfully enter, ascend, and exit the fishway. For migratory populations that need to reach spawning or feeding areas on the other side of the dam, the quantitative passage success and passage times are fundamental elements of the evaluation, and telemetry techniques should therefore preferably be applied (CEN, 2021). Similarly, where high mortality passage routes exist, their use and its associated mortality need to be evaluated, to safeguard against excessive mortality.

Even if reduced longitudinal connectivity is a problem also for plants, and to some extent invertebrates and mammals, mitigation measures (excluding dam removal) have been almost exclusively focused on fish. Fish are also the main riverine group actively moving upstream only in water (as compared to both mammals and insects that typically can travel on land or in air). As a consequence, while other animal groups are also important, longitudinal connectivity monitoring has a natural focus on fish. This does not exclude, also monitoring seed transport and insect drift, according to approaches discussed above.

5 Programmatic monitoring

Lessons and experience from the evaluation of nature restoration efforts have been collected in an approach termed programmatic monitoring (Weber *et al.*, 2018; Roni *et al.*, 2018). This approach is focused on coordination across projects to allow for a systematic comparison and the generalization of results. Surveys are standardized within the program regarding both methodology and indicators. Indicators are then chosen based on their robustness, acceptance and ease of measurement as well as on the anticipated spatial-temporal effects of restoration. Data storage is coordinated and centralized. A programmatic monitoring approach should also facilitate transfer of results between projects, collaborative learning, and coordinated adaptive management (Weber *et al.*, 2018). Below features of a programmatic monitoring approach to hydropower mitigation (Fig. 2) is discussed.

5.1 Monitoring packages

For monitoring the effects of remedial measures in relation to hydropower, we suggest monitoring packages focused on particular mitigation measures (O'Neal *et al.*, 2016). Such monitoring packages could, for example, target dam removal, fish passage, environmental flow, and reservoir water level regulations. A number of sites within each package should be chosen and systematically monitored with a focus on detecting effects of specific remedial measures.

5.2 Similarity and variability

Although similar, no hydropower facility or remedial measure is identical (Noonan *et al.*, 2012). Also, land-use, climate, river dimensions and many other non-directly hydropower related conditions influence the effects of hydropower as well as the restoration measures (Extence *et al.*, 1999; Sandin, 2009; Göthe *et al.*, 2019). This means that conclusions from individual case studies are not always transferable to other systems. In contrast, to draw general conclusions on effects of mitigation measures, several sites, both similar and different, need to be monitored. The latter approach results in data replicated among sites for a similar mitigation measure and would allow the incorporation of variation between sites in the analysis of the result (England *et al.*, 2008). This opens up for increased understanding of the mechanisms behind result variability and has the potential to show when and where a particular measure is effective. At the programmatic monitoring level, mapping hydropower configurations, river types, and applied remedial measures can guide the selection of representative sites to be included in the monitoring program.

5.3 Long term monitoring

Restoration monitoring is a long term endeavor as it can take everything from weeks to several decades before the effects of the restoration effort are seen (Daufresne *et al.*, 2015; Marttila *et al.*, 2016), and short-term monitoring data can be misleading (Weber *et al.*, 2018). Long-term monitoring also allows monitoring under a range of natural (and regulation induced) conditions. This is important as the functionality of a mitigation

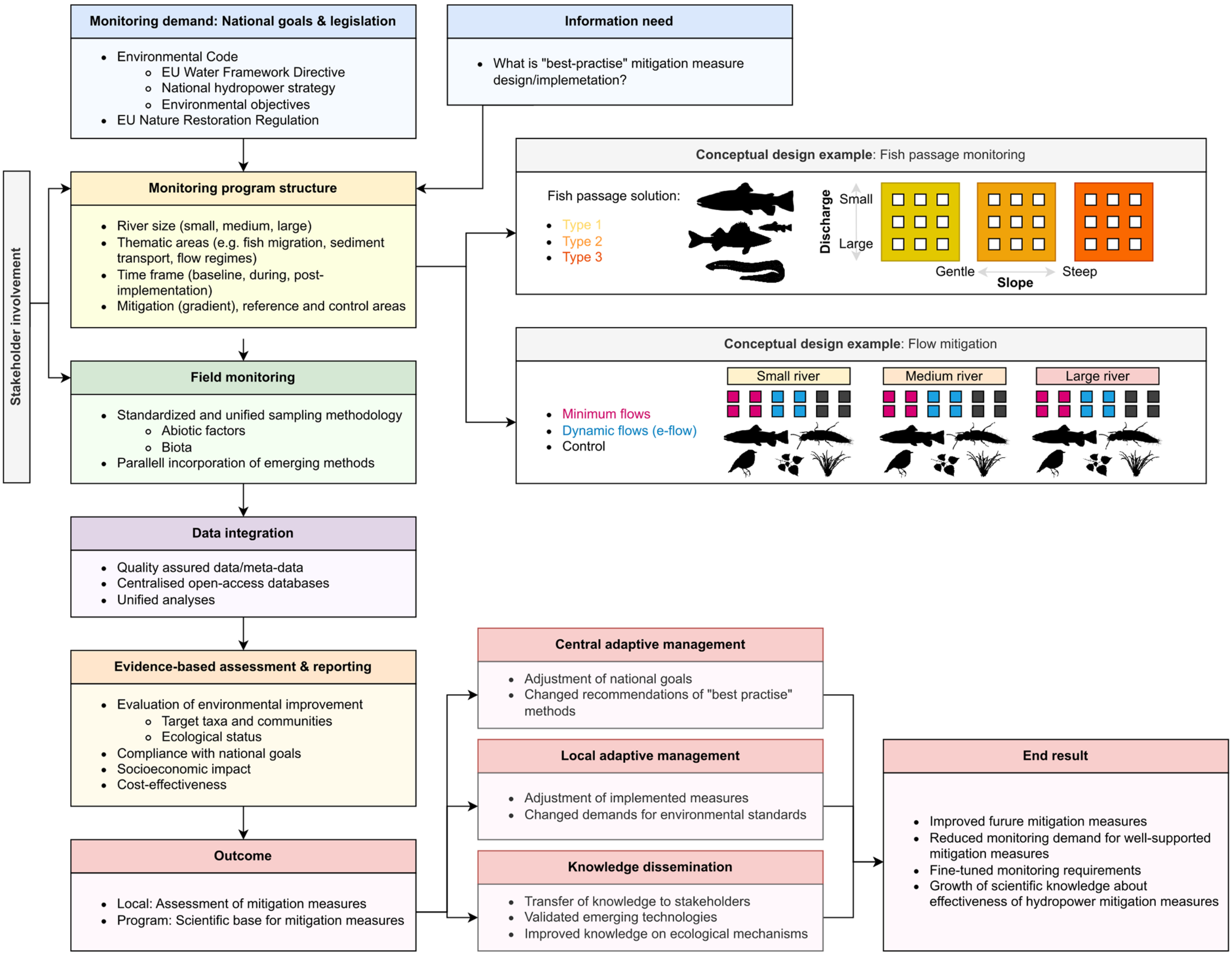

Fig. 2. A conceptual figure over the outline and benefits of programmatic monitoring of ecological effects of mitigation measures related to hydropower. Silhouette from phylopic.org.

can vary with environmental conditions, such as flow and water level, and single year studies risk to hide the real efficiency of a remedial measure (Souchon *et al.,* 2008; Vehanen *et al.*, 2010; Hagelin *et al.*, 2019). Ideally, data should be collected before the mitigation, followed by a long-term monitoring commitment (Roni *et al.,* 2018). The monitoring package could, however, be flexible, and there is no need for every project to start in the same year. On the contrary, different starting dates reduce the temporal correlation and should make the analysis of the actual mitigation measure easier to analyze. Data from other facilities, using similar methodology, could also complement the data collected in the monitoring program.

5.4 Controls and references

Hydropower facilities without the implementation of restoration measures can serve as negative controls (Weber *et al.*, 2018; Roni *et al.,* 2018). These controls should encompass the general conditions of the facilities subject to mitigation measures and can be spread over similar catchments or even upstream within the same catchment (Jähnig *et al.,* 2011; Karlsson and Leonardsson, 2014). Given the uncertainty of how long such unmitigated controls will persist, some redundancy might be needed (that is, extra sites). Timely replacement of control sites could also be an alternative.

In addition, comparing the outcome of the remedial measures with natural references, natural or least-disturbed conditions, can be used as a target measuring stick for restoration success (Feld *et al.*, 2011). However, due to natural variation and different levels of disturbance even on less disturbed sites, such direct comparisons may be problematic (Hawkins *et. al.,* 2010; O'Neal *et al.,* 2016). Instead, predicted reference conditions, based on regional and river/reservoir characteristics may be more useful (Hawkins *et. al.,* 2010). Such an approach is typically used in monitoring for the WFD (Acreman and Ferguson, 2010).

5.5 Transfer of knowledge

Another advantage of this cross-site monitoring program is that it involves a larger number of stakeholders. Centralized data repositories and analysis together with the inclusion of facilities from different companies and county boards should facilitate the spread of experiences throughout the industry (Souchon *et al.,* 2008). In this way, monitoring results as well as monitoring methodology can be organically disseminated among stakeholders. As follows, knowledge from the monitoring can directly inform future mitigation measures as well as independent evaluation measures.

5.6 Emerging methods and redundant sampling

As already briefly mentioned above, several relatively novel techniques (*e.g.*, eDNA, remote sensing, drone surveys, and fish counters) promises to facilitate future monitoring but require calibration against traditional methods. eDNA is a rapidly developing methodology for detecting aquatic biota (Duarte *et al.*, 2021; Pont *et al.*, 2021), often cheaper and more effective than traditional surveys (Li *et al.*, 2019; Golpour *et al.*, 2022). It can indicate species presence and provide coarse abundance estimates across lakes, rivers, and reservoirs (Li *et al.*, 2019; Golpour *et al.*, 2022, Pont *et al.*, 2021). Hydropower related applications already include assessing fishway use (Tolonen *et al.*, 2024) and fish present upstream and downstream of fishways (Yamanaka and Minamoto, 2016). For the evaluation of mitigation measures, a range of methodological limitations and uncertainties are, however, associated with the use of eDNA. These include the potential for eDNA to travel long distances, become diluted by high flows, and to be sensitive to contamination (Wilcox *et al.*, 2016; Pont *et al.*, 2018), along with uncertainties related to species identity, life stage, and species-specific shedding rates (Wilcox *et al.*, 2016; Hering *et al.*, 2018), all of which must be considered when designing monitoring programs. Remote sensing satellite data is applied to monitor riparian vegetation (Cupertino *et al.*, 2024), primary production (Sayers *et al.*, 2021), water temperatures (Sharma *et al.*, 2015), and to estimate water flow in rivers (Cavallo *et al.*, 2025). From a hydropower monitoring perspective, this tool is an underutilized resource at the same time as the spatial resolution the data pose a challenge to be overcome. In parallel, drone footage is used to rapidly map riparian vegetation (Cupertino *et al.*, 2024), macrophytes (Kislik *et al.*, 2020), mussels (Hedger *et al.*, 2023), and even fish movements (Zhang *et al.*, 2022). Underwater drones (remotely operated underwater vehicles; "ROV") or cameras are also beginning to be used to monitor ecological communities in riverine environments (Guedes and Araújo, 2022). In relation to fish passage, fish counters, with their limitations and possibilities, are already starting to be a go-to method for fishway evaluation (Haas *et al.*, 2024; Eggers *et al.*, 2024; Fuentes-Pérez. 2025).

Integrating emerging methods with traditional approaches within the programmatic monitoring offers an excellent possibility to validate and refine these in relation to already established methods. This holds the potential to both improve precision and reduce costs of future monitoring and evaluation projects. Along the similar lines, with an inclusive sampling design within the program, correlation between indicators may emerge, as well as a better understanding of the time-scales required for the environment to respond to the mitigation measures (Feld *et al.*, 2011; Ryan Bellmore *et al.*, 2017; Garron *et al.*, 2024). This in turn, may allow a taxonomically and temporally much more limited monitoring outside of the program.

5.7 Towards an evidence based standard for adaptive management

As a large number of mitigation measures are anticipated during the upcoming years, and these mitigation measures need to be evaluated to confirm their functionality, there is a lot to be gained from a programmatic monitoring approach. Today evaluation of mitigation measures are generally scarce, and the need to evaluate individual solutions is high. With data from the proposed monitoring, standard solutions may emerge as well as knowledge about under which conditions they are not suitable. This will inform future mitigation measures but can also lower the evaluation requirements for mitigation measures outside the program that follows a now evidence based approach. Along similar lines, the programmatic monitoring results can also serve as a reference for the evaluation of independent remedial measures.

5.8 Cheap and expensive

Adaptive management is a widely lauded approach to conservation for improving resource management by learning from management outcomes (Bernie-Gauvin *et al.*, 2017c; Westgate *et al.*, 2013). The anticipated widespread implementation of mitigation measures in relation to hydropower (*e.g.*, in Sweden; Sundin *et al.*, 2025) offers a unique opportunity for monitoring the efficiency of these mitigation measures and programmatic monitoring a way to implement a society and industry wide adaptive management (Westgate *et al.*, 2013). The programmatic monitoring approach is ambitious and costly, but the alternatives may be even more costly. Already substantial resources are invested in site-specific monitoring and environmental impact assessments with data only exceptionally used to widen our systematic understanding (Botelho *et al.*, 2017). For the industry as whole, if re-licensing of hydropower production comes with ambitious monitoring requirements, a plethora of site specific monitoring projects with a diversity of methodologies will amount to enormous costs. An "everyone for themselves" approach will likely also result in huge diversity in monitoring methods, making inter-project comparisons and generalizations difficult (O'Neal *et al.*, 2016). Scaled-back experiments and subsequent knowledge gaps or erroneous conclusions risk resulting in insufficient mitigation measures, or over-investment in suboptimal mitigation approaches (Konrad *et al.*, 2011). This of course, would carry a cost for the river ecology but also for the individual companies and the industry as a whole – inviting active industry involvement. Given that mitigation measures are typically shaped by compromises or trade-offs between environmental benefits and economic costs (Venus *et al.*, 2020), understanding what works and under what conditions is very valuable, at both a local and a national level. Afterall, improved understanding of ecological responses to mitigation measures underpins more efficient resource allocation and reduces costs for both industry and society (Souchon *et al.*, 2008).

5.9 From principle to monitoring

While programmatic monitoring has the potential to contribute substantially to our understanding of remedial measures in relation to hydropower it will unavoidably constitute a compromise between available resources and need for knowledge (Fig. 2). A diverse range of hydropower configurations are in operation in different sized rivers placed in different geographical contexts (He *et al.*, 2024; Hynes 1975). Upon these hydropower facilities, different mitigation measures are implemented. Hence, a programmatic monitoring program needs to prioritize monitoring packages. Environmental flow is a widely implemented mitigation measure, often in the form of minimum flows, although more dynamic flows being widely promoted. Including sites with more and less generous environmental flow regimes can help reveal the ecological benefits of the additional water. Hydropeaking mitigation is another monitoring package candidate with hydropeaking having important ecological effects while being promoted as a balancing force in an electricity grid dependent on solar and wind power. Sites where hydropeaking is prohibited, mitigated by in-river structures, and subjected to reduced ramping rates could all be included in a monitoring program. In the reservoir, water level regulation is the main issue. Limiting regulation and structural compensation (floating islands, lake-in-reservoirs) may be the immediate mitigation measures to include in a reservoir focus monitoring package. For longitudinal connectivity, upstream passage solutions and downstream passage solutions may constitute two separate fish passage focused monitoring packages. For upstream passage, variation in fishway types, slope, discharge (especially in proportion to total discharge) could be covered in the monitoring package. Similarly, for downstream passage, variation in guidance racks (including angle, bar spacing, and type), spill-based solutions, and low-mortality turbines could be candidates for inclusion among the sites in the monitoring package. For all work packages, a spread in river size and geography will be necessary. Obviously, not all sites are subject to all mitigation measures associated with the different monitoring packages. Some sites may, therefore, be included in all monitoring packages, while others only in one or two. When possible, however, including the same site in several monitoring packages has logistical and economic advantages.

A detailed, monitoring methodology for abiotic conditions and biological indicators then need to be designed for the program as a whole, and applied for the relevant monitoring packages and sites. Among all the candidate indicators listed above, merits and weaknesses need to be thoroughly studied, to select those most relevant (Czúcz *et al.*, 2021). This includes their ecological and instrumental relevance, sensitivity and directionality in relation to the disturbance, and detectability against natural noise. Robust, repeatable, precise, and if available, standard, sampling methodologies must be used. While data allowing for very complex analysis will be collected, the program should strive for simplicity to allow results to directly communicate with practitioners (Czúcz *et al.*, 2021).

Even if the term programmatic monitoring is relatively recent, systematic and standardized monitoring programs to evaluate restoration efforts have been called for also previously (Weber *et al.*, 2018; Souchon *et al.*, 2008). Many of its principles have long been implemented in, for instance, the Swedish program *Integrated Studies of the Effects of Liming Acidified Waters* (ISELAW). This program has been running for over 30 yr and involves the standardized monitoring of abiotic factors, macroinvertebrates, fish, and plankton in both limed and reference lakes and streams while incorporating geographic variability in the water body selection (Appelberg and Svensson, 2001; Drakare *et al.*, 2022). Another example is the long term monitoring of salmon rehabilitation projects in the Pacific USA, allowing direct comparisons of the efficiency of different rehabilitation measures (O'Neal *et al.,* 2016). These, and other large standardized monitoring programs (Roni *et al.,* 2018), may serve both as inspiration and proof of concept for the implementation of programmatic monitoring of remedial measures in relation to hydropower.

6 Conclusions

Hydropower is currently indispensable for electricity production but has wide-ranging impacts on the ecology in rivers and regulated lakes (He *et al.*, 2024). Implementation of remedial measures to improve the ecological status of hydropower hosting river systems is both urgently needed and anticipated. A large portfolio of remedial measures with variable evidence-based support are available while a systematic understanding of their efficiencies are scarce. A programmatic monitoring approach where a range of indicator organisms and abiotic factors are systematically monitored in a standardized way in relation to a set of remedial measures has the potential to provide invaluable information for river management. Evidence based mitigation measures could emerge that can make future mitigation more efficient and facilitate the improvement of existing remedial measures. Increased knowledge about ecological responses can allow for more reductionist monitoring outside the program. Overall, a programmatic monitoring approach to hydropower mitigation holds the potential to greatly enhance our ability to mitigate the environmental impacts of hydropower production in a world where it is deemed indispensable.

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