Water Resources Research

RESEARCH ARTICLE

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Key Points:

- Bypassed reaches (BRs) at hydropower stations cause major habitat loss for rheophilic species by dewatering high-gradient reaches
- Ca. 75% of Swedish BRs lack minimum discharge, and 88% of the remainder have discharge <2 m^3/s, often insufficient for rheophilic fish
- Restoring flow in BRs is key to support high value riverine habitats that are biodiversity hotspots

Supporting Information:

Supporting Information may be found in the online version of this article.

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Silenced Rapids and Waterfalls: Habitat Loss and Management of Bypassed Reaches in the Regulated Rivers of Sweden

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Abstract Habitat destruction is a global driver of biodiversity loss. In rivers, damming and river regulation for hydropower have caused extensive loss of high gradient, riffle, rapid and waterfall habitats. Restoring these habitats, which support unique biodiversity, should be an urgent priority, but inadequate documentation hampers evaluation of different management strategies. Focusing on Sweden, where river regulation affects most catchments, we mapped and quantified characteristics (e.g., slope, length, discharge) of 968 bypassed reaches (BRs), that is, river sections that are dewatered due to diversion of discharge for hydropower production. The extent of habitat loss associated with BRs is substantial, summing to a total length of 1,256 km, 94% of which is predominantly comprised of former riffles, rapids and waterfalls. BRs are typically located in larger rivers at central river network positions, highlighting their potential importance for hydrological and ecological connectivity. These habitat losses are poorly addressed by current management: three quarters of Swedish BRs have no mandated minimum discharge. Of the remainder, 88% have a discharge <2 m^3/s, a flow threshold below which, on average, the proportion of rheophilic fish decline rapidly in Swedish BRs. Based on these findings for Sweden, and given the ubiquity of hydropower elsewhere, we suggest that the thousands of kilometers of mostly dry high-gradient habitat linked to diversion hydropower worldwide likely represent high value restoration targets. Increased, ecologically meaningful, flow releases in these reaches has great potential to rehabilitate essential habitat for threatened rheophilic organisms and ecosystem functioning of regulated rivers.

Plain Language Summary Human activities are degrading rivers around the world, and one major cause is hydropower dams that divert water away from natural channels. In this study, we investigated losses of river habitat associated with water diversion in Sweden, a country where most rivers are regulated for hydropower. We focused on nearly 1,000 “bypassed reaches,” which are stretches of river left largely dry because water is rerouted through hydropower plants. Together, these reaches add up to more than 1,250 km of lost river ecosystem, most of which were once fast-flowing habitats like rapids and waterfalls that support specialized plants and animals. We found that these lost habitats often sit in important positions within river networks, meaning their loss can disrupt how water, species, and nutrients move through entire catchments. Current management struggles to address this problem effectively: most bypassed reaches receive no guaranteed water flow, and where water is released, it is usually much too little to support fish that depend on strong currents. Restoring water to these dry river reaches could be a straight-forward method to improve ecological health and biodiversity in thousands of kilometers of river habitat, not only in Sweden but wherever hydropower diverts water from valuable river habitats.

1. Introduction

Hydropower is regarded as both a key element in the transition to a non-fossil fuel energy system (IEA, 2021) and as a driver of environmental degradation and biodiversity loss (e.g., Dudgeon & Strayer, 2024; Palmer & Ruhi, 2019; Reid et al., 2019). In Sweden, hydropower provides ca. 43% (ca. 16,400 MW installed capacity) of electricity generation (Puharinen et al., 2024). At the same time, hydropower is also recognized as a threat to at least 35 species (e.g., European eel, *Anguilla anguilla*) protected by international conventions and/or Swedish law (Swedish Government and Ministry of the Environment, 2020). Impacts of hydropower on biodiversity are most often attributed to altered flow regimes and river network fragmentation associated with dams (e.g., Grill et al., 2019; Reid et al., 2019; Tickner et al., 2020). However, the direct loss of higher gradient reaches (riffles, rapids and water falls), key habitats for rheophilic species (i.e., species requiring fast flows), associated with hydropower development is often overlooked (Birnie-Gauvin et al., 2017; but see e.g. Bunn & Arthington, 2002; Gibeau et al., 2017; Kibler & Tullos, 2013; Xie et al., 2018). Many rivers in Sweden (Renöfält et al., 2010; Widén, Malm-Renöfält, et al., 2022) and elsewhere (e.g., Kibler & Tullos, 2013; McManamay et al., 2016; Xie et al., 2018) are characterized by series of hydropower dams along the main river channel. The dams are most often built on higher gradient reaches, and result in losses of riffles, rapids and waterfalls and the diversity they support, due to both dewatering of reaches downstream of the dam and inundation upstream by the reservoir (e.g., Englund & Malmqvist, 1996; Swedish EPA, 2014). Rehabilitating of such lost habitats should be an urgent priority, but is hindered by the inadequate documentation of the extent and type of habitat loss, which limits evaluation of possible management strategies (e.g., dam removal, hydrological and geomorphological restoration). In this study we aim to address this knowledge gap and discuss the role that extensive loss of high-gradient lotic habitats could have in the loss of biodiversity in hydropower regulated rivers.

In free-flowing rivers, riffle, rapid and waterfall reaches are characterized by turbulent flows that oxygenate the water (Baxter, 1977). These habitats have a predominance of rocky substrates and often support higher biodiversity compared to soft-bottomed, slower flowing, deeper reaches (Brown & Brussock, 1991; Vinson & Hawkins, 1998). Furthermore, these reaches are hotspots of ecosystem function, supporting river carbon cycling and nutrient processing. Their shallow, turbulent waters promote atmospheric gas exchange and primary production (e.g., Finlay et al., 1999), while strong currents favor filter-feeding invertebrates that remove fine particulate organic matter from the water (Wotton et al., 2003). Riffles and rapids serve as principal spawning habitats for many temperate and boreal fish species (Birnie-Gauvin et al., 2017; Kondolf et al., 2008; Tamario et al., 2021), and all three "torrential habitat types", including the spray zone of waterfalls, constitute unique habitats that host a specially adapted, but understudied, biota (Clayton & Pearson, 2016; Rackeman et al., 2013). The biodiversity value of riffles, rapids and waterfalls is likely to be influenced by their position within the river network. Centrally positioned reaches (e.g., main river stem, and central stems of sub-catchments) may support higher local α-diversity than headwaters (Kuglerová et al., 2015), due to greater size (more discharge and thus more habitat area) and their role as "dispersal nodes" between headwaters, downstream habitats and the ocean (Altermatt, 2013; Gotelli & Taylor, 1999; McGarvey & Ward, 2008; Schmera et al., 2018). Unfortunately, these steep, centrally positioned, reaches have been disproportionately targeted for hydropower development, as they allow creation of large hydraulic head in reaches with high discharge at relatively low investment cost (Englund & Malmqvist, 1996; McManamay et al., 2016; Swedish EPA, 2014).

At many hydropower stations, water is diverted through artificial channels, tunnels or pipelines (penstock) to the turbines, which results in a partially or wholly dewatered "bypassed reach" (BR) downstream of the diversion dam (McManamay et al., 2016). BRs are also referred to as diversion reaches, dewatered reaches, or depleted reaches (Gibeau et al., 2017) and may comprise several kilometers of formerly productive, high gradient habitat. However, even if some water remains, the structure and functioning of biological communities persisting in BRs is typically highly degraded (e.g., Anderson et al., 2015; Gibeau et al., 2017; Göthe et al., 2019). One approach for maintaining some level of biodiversity and ecosystem functioning in BRs is to apply a minimum discharge; whereby a defined amount of water is released into the BR (Poff et al., 1997; Renöfält et al., 2010). A minimum discharge based on a binding court decision is referred to as a mandated minimum discharge (MMD). Historically, MMDs have typically been static, meaning that discharge was kept constant throughout the year (Poff et al., 1997). However, dynamic minimum discharges, which mimic the variability of the natural flow regime (e-flows), are generally better at supporting natural biodiversity and ecosystem functioning (Poff et al., 1997, 2010) and are increasingly favored around the world (Acreman et al., 2014; Tickner et al., 2020). So called functional flows, that is, MMDs designed to support key hydrogeomorphic and ecological functions of the natural flow regime rather than perfectly mimicking the natural hydrograph, may be particularly applicable in rivers under large anthropogenic pressure, for example, from extensive hydropower development (Yarnell et al., 2015).

In Sweden, many BRs still completely lack any MMD (Göthe et al., 2019; Renöfält et al., 2010). At the same time, MMDs equal to the natural base flow (approximated as the mean annual low flow—MLQ, see Table 2 for details) are increasingly advocated as a reasonable minimum requirement for good ecological status classification under the EU Water Framework Directive (WFD) (Kling, 2015; Swedish Government and Ministry of the Environment, 2020). Hydropower permits do not expire in Sweden, and therefore many hydropower stations operate under legislation from 1918 (Vattenlag 1918:523), or on no other legal basis than "by tradition", with little or no

10.1029/2025WR040752

consideration of ecosystem impacts (Puharinen et al., 2024; Renöfält et al., 2010; Widén, Malm-Renöfält, et al., 2022). Hence, to reach compliance to WFD requirements, a largely cooperative process has been initiated where all hydropower permits are set to be relicensed in Swedish environmental courts over the coming 20 years. The goal is to achieve maximum improvement in ecosystem health at minimum cost in terms of reduced hydropower generation. However, given the predefined very restrictive criteria set for the maximum acceptable reduction of national hydropower generation (no more than 2.3% reduced production) (Puharinen et al., 2024; Swedish Government and Ministry of the Environment, 2020), there is a need for a systematic approach to allocate MMDs among BRs by prioritizing those with the greatest ecological rehabilitation potential.

The objectives of this study are to (a) document the quantity and location of riffle, rapid and waterfall habitats dewatered downstream of hydropower dams as BRs, (b) assess variation among BRs in habitat characteristics, management (e.g., MMDs, additional restoration measures), other water sources (e.g., tributaries), and the presence of anthropogenic catchment stressors. This information is then used to (c) evaluate to what degree current MMDs can motivate good ecological status classification of the BRs under the WFD and meet the flow-requirements of model rheophilic species. First we identify and map the BRs in Sweden, and compile data on their intrinsic (prior to hydropower development) hydrogeographic characteristics (e.g., slope, river network position, discharge, elevation) to identify former likely rocky, high gradient habitat. We also calculate BR size metrics and compile data on current flow conditions (e.g., MMD), whether any additional restoration measures have been completed in the BR, and presence of additional anthropogenic stressors. The latter two factors have potential to alter the success of flow restoration. To our knowledge, such a detailed large-scale quantification of habitat loss from BRs has not been undertaken previously. Finally, we use an existing, highly resolved, flow-ecology relationship to assess the efficacy of current MMDs in favoring rheophilic fish, i.e. an organism group encompassing top predators, endangered species (e.g., sea lamprey, *Petromyzon marinus*), and species with high cultural value, such as brown trout (*Salmo trutta)* and Atlantic salmon (*Salmo salar*).

We hypothesize that (a) most BRs represent former high quality, steep and rocky habitats, and (b) are located mainly in larger, centrally positioned, river reaches. We further expect to find (c) spatial variation in these potential habitat qualities and in BR size, anthropogenic stressors and BR management (e.g., allocation of water for MMDs, presence of additional restoration measures)—driven by, for example, regional differences in the history of hydropower development (larger hydropower stations and longer BRs in the north). Finally, we hypothesize that (d) existing MMDs often are too small and inconsistent to create habitat favorable to rheophilic fish or to motivate good ecological status classification under the WFD.

2. Methods

2.1. Identification and Digitization of BRs

We compiled a geospatial database of BRs in Sweden. This was based on (a) a data file with 425 BRs identified in an earlier project (Göthe et al., 2019), (b) a data set on reaches subject to water abstraction (909 reaches) and (c) a data set with locations of power stations in Sweden (1803 hydropower stations). Data set b was provided by the by the Swedish Meteorological and Hydrological Institute (SMHI) and data set c by the Swedish Agency for Marine and Water Management. An external stakeholder panel (with representatives from county administrative boards, water authorities, water regulation companies and relevant energy companies) suggested 41 additional potential BRs. After accounting for overlap among these data sources, the final total of potential BRs was 1038, which were digitized in ArcGIS© v10.7.1. (ESRI Inc. Redlands, CA).

Validation of the BR presence at each site was carried out in two-steps. First, we crosschecked delineations against aerial photographs ("GSD-Ortofoto, 1m färg", 2016) and the national 2 × 2 m digital elevation model ("GSD-Höjddata grid 2+", 2019) supplied by the Swedish Land Survey. We excluded river reaches where the natural channel was not substantially bypassed (<10% of discharge diverted). For the remainder, we defined a BR as beginning immediately downstream of the diversion dam, while the end-point was defined where the tailrace/outlet channel of the power station reconnected with the dewatered river channel. However, if the potential BR and tailrace both emptied into a downstream lake or reservoir, the endpoint of the BR was set where it entered the lake/reservoir at full water level. In a few cases where a very long BR was interrupted by lakes or large pools (with the tailrace/outlet channel reconnecting with the BR downstream of these lentic water bodies), the BR was split up into subsections, and larger lentic water bodies (minimum distance inlet to outlet: 4.3 km) were not considered part of the BR. Also, potential BRs with a length shorter than 20 m were removed from the database. In a second validation step, we consulted with the external stakeholder panel, for corroboration of BR presence. The panel also provided data on the application (presence/absence) and magnitude (quantity in m^3/s) of MMDs when available. After final validation, 968 individual BRs remained, and we received information on MMDs for 607 of these.

2.2. BR Characteristics

We compiled two sets of variables describing our BRs. Set 1 incorporated descriptors of intrinsic (pre-hydropower development) hydrogeographic characteristics, comprising ecologically relevant variables including for example, slope, elevation, river network position, hydrology, and catchment geology (Table 1). Set 2 compiled descriptors of present day BR characteristics, including BR size (i.e., length, area) and additional anthropogenic pressures (Table 2). For reaches with a MMD, we cataloged information on discharge magnitude and variability (maximum and minimum discharges for MMDs varying throughout the year). Finally, we compiled information on completed restoration measures in the BR from the Swedish restoration database (Table 2).

2.3. Statistical Analyses

2.3.1. Classification of BRs Based on Intrinsic Hydrogeographic Properties

To investigate spatial variation in MMDs, other restoration measures, and stressors (Objective b), we grouped BRs into "*Reach types*" based on intrinsic hydrogeographic characteristics utilizing K-means cluster analysis, visualized in a principal components analysis (PCA) Biplot (Figures S3.1.1–S3.1.4 in Supporting Information S1). Seven reach types were identified and subsequently labeled according to their dominant characteristics (see Section 3.1 for details): 1. *Southern platformal*, 2. *Southern coastal*, 3. *Southern steeply sloped*, 4. *Southern inland*, 5. *Northern inland*, 6. *Northern large rivers* and 7. *Northern alpine*.

Some variables were characterized by outliers (boxplots in Figure S3.3 of Supporting Information S1), but all data points were considered true variation and were retained in our analyses. We excluded three BRs missing data on one or more intrinsic hydrogeographic parameters.

Cluster analysis and PCAs were conducted in R v4.2.2 (R Core Team, 2021) using the built-in *kmeans* function and PCA function in the *FactoMineR* package v2.9 (Lê et al., 2008), respectively. The optimal number of clusters (2–20) was evaluated using 30 indices in the *NBClust* function, *NBClust* package v3.0.1 (Charrad et al., 2014).

2.3.2. Classification of BRs Based on Water Availability

To investigate how intrinsic hydrogeographic characteristics varied among BRs with and without MMD (Objective b) we grouped BRs in three "*Water Availability categories*", reflecting differences in the reliability and sources of water. This includes a category encompassing BRs without MMD but with significant inputs of water from other sources:

1. "*MMD*"–BRs with a verified MMD.
2. "*Other water*"–BRs without a MMD but with inputs from tributaries, and/or from structural aspects of the hydropower facility, for example, weir-like diversion dams or spillover from intake channels (Table 2). Such inputs can show high seasonal variability.
3. "*No water*"–BRs lacking MMD and "other water" inputs. These may sporadically receive water inputs from for example groundwater upwelling, dam leakage or operational flow releases (i.e., "spill"), but these sources of water are less reliable than MMDs.

2.3.3. Hypothesis Testing

Differences in frequencies of MMD allocation and the occurrence of other water among reach types (Hypothesis c) were analyzed using non-parametric Pearson χ^2 tests, as were differences in application of additional restoration measures (Table 2). Expected frequencies <5 was used as a cut-off for designating a χ^2 approximation as unreliable (Franke et al., 2012). Significant χ^2 tests ($P < 0.05$) were followed by analysis of means for proportions (ANOMP, Nelson et al., 2005) to identify which categories differed significantly from the total mean. ANOMP and χ^2 tests were run in JMP© Pro 15 (SAS Institute Inc., Cary, NC).

Two-way analysis of variance (ANOVA) tested for effects of reach type and water availability category on continuous variables quantifying key intrinsic hydrogeographic characteristics (Hypothesis c), for example,

Table 1
Intrinsic Hydrogeographic Characteristics of the Bypassed Reaches (BRs), That is, Variables Characterizing Habitat Type and Quality Prior to Hydropower Development

Variable	Unit	Description	Details	Data sources
Meters above sea level (masl)	m	Proxy for climate.		National 2×2 m digital elevation model.
BR slope	%	Intrinsic water velocity conditions.		
Riffle, rapid or waterfall dominance	Present/absent		Slope needed for ≥50% prob. of riffles, rapids or waterfalls = $3.791 * CA^{-0.408}$ (Equation 1) CA = catchment area (km2). An area specific discharge of 8–12 l/s * km^2 is assumed (Widén, Ahonen, et al., 2022).	
Classical stream order	Dimensionless	Measure of river network centrality.	Bottom up (or Horton) stream order, that is, 1 at river mouth, increasing as river branches moving upstream.	SVAR (Svenskt VattenARkiv), version 2016: http://vattenwebb.smhi.se/.
Relative BR catchment area	%		The ratio (%) of the catchment area of the BR (Catchment $area_{BR}$) and catchment area at the river mouth (Catchment $area_{River\ Mouth}$).	
Longitude	WGS84 decimal degrees	Proxy for climate.	Calculated for midpoint of BR.	
Latitude				
Caledonian bedrock in catchment	Fraction	Proxy for intrinsic water chemistry (e.g. Sandström et al., 2024; Weldon & Meriggi, 2023).	Caledonian bedrock is from the most recent orogeny in Scandinavia, forming the Scandinavian mountain range.	Swedish lithotectonic units (“Berggrund 1:1000000”, 2020) supplied by Geological survey of Sweden.
Platformal sedimentary cover rocks in catchment				
Peat soil in catchment				Swedish soil map (“Jordarter 1:1000000”, 2020) supplied by Geological survey of Sweden.
Mud-moraine/silt soil in catchment			Two soil types with high content of mud and/or silt. Deposits of mud-moraine of glacial origin, deposits of mud-silt of postglacial origin.	
Natural[a] mean annual discharge (MQ)	m^3/s	Descriptors of natural flow regime (Poff et al., 1997). MQ is also a proxy for river size.	Mean over a period of years (1981–2010).	Modeled (S-HYPE 2019) data. Data source: SVAR (Svenskt VattenARkiv), version 2016: http://vattenwebb.smhi.se/.
Natural[a] mean annual low flow (MLQ)			Annual minimum discharge (mean of a day). Mean over a period of years (1981–2010). MLQ sometimes used as an estimate of the base flow of Swedish river reaches (Kling, 2015).	
Natural[a] mean annual high flow (MHQ)			Annual maximum discharge (mean of a day). Mean over a period of years (1981–2010).	
MLQ/MQ	Fraction		Relative mean annual low flow.	
MHQ/MQ			Relative mean annual high flow.	

[a]“Natural” indicates that the national S-HYPE (2019) hydrological model has utilized a scenario of no anthropogenic diversion or storage of water (e.g., from hydropower) upstream in the catchment. Thus, the model gives the hypothetical unregulated discharge for the whole modeled time period.

average slope and natural mean annual discharge (MQ), along with BR length and additional stressors (proportion anthropogenic land use in catchment). The same model was used for quantitative MMD metrics. Response variables were transformed (log, Box-Cox or square-root) when required to meet normality and homoscedasticity assumptions. ANOVAs were conducted in R v4.2.2 (R Core Team, 2021), and significant results ($P < 0.05$) were

Table 2
Present Day BR Descriptors, Including Characteristics of Mandated Minimum Discharge (MMD), Size Metrics, Additional Pressures and Restoration Measures

Variable	Unit	Description	Details	Data sources
MMD_{Min}	m^3/s	Minimum MMD.	In some BRs the MMD was higher some times of the year (MMD_{Max}) and lower at other times (MMD_{Min}).	See Sections 2 and 2.1.
MMD_{Max}		Maximum MMD.		
MMD_w		The weighed mean annual MMD.	MMD_w was calculated as: $MMD_w = (MMD_{Max} * d_{Max} + MMD_{Min} * d_{Min})/365$ (Equation 2) where d_{Max} and d_{Min} are number of discharge days with MMD_{Max} or MMD_{Min} respectively. If number of discharge days with MMD_{Max} had not been supplied to us we assumed a 50/50 MMD_{Max}/MMD_{Min} proportion.	
MMD_w/MQ	%	Relative measure of MMD allocation.	Relates MMD_w to the natural mean annual discharge (MQ).	See Sections 2 and 2.1 and Table 1.
$MMD_{Min} < 2\ m^3/s$	Present/absent	Indicators of MMDs adequacy for rheophilic fish.	On average,the proportion of rheophilic fish declines rapidly in Swedish BRs as MMD_{Min} falls below $2\ m^3/s$, while lentic fish increase (Donadi et al., 2025).	See Sections 2 and 2.1.
$MMD_{Min} < 0.1\ m^3/s$			MMDs $< 0.1\ m^3/s$ are highly unlikely to favor rheophilic fish (Donadi et al., 2025).	See Sections 2 and 2.1
$MMD_{Min} < MLQ$		Relates MMD_{Min} to the natural base flow (MLQ).	$MMD_{Min} = MLQ$ proposed as a minimum requirement for BR good ecological status classification under the EU Water Framework Directive (WFD) (e.g. Kling, 2015).	See Sections 2 and 2.1 and Table 1.
Other water		BRs with an identified input of water from tributaries, and/or from structural aspects of the hydropower facility.	BRs that had no MMD were evaluated. Only cases where it was evident that water always flowed into the BR (e.g. weir-like diversion dam, obvious spillover from intake channel, etc.) was classified as having other water due to structural characteristics of diversion dam.	Aerial photographs from the Swedish Land Survey and Swedish stream network: SVAR (Svenskt VattenARkiv), version 2016: http://vattenwebb.smhi.se/
BR Length	km			
Length BRs with MMD		Total length of BRs with a MMD.		See Sections 2 and 2.1.
Length BRs with other water		Total length of BRs with other water divided by 2.	Based on the conservative assumption that if a tributary empties into the BR, on average, this happens at the midpoint of the BR.	
Length BRs in large rivers		Total length of BRs in large rivers.	Large rivers are those with a $MQ \geq 20\ m^3/s$, as defined by Swedish EPA (2020).	

Table 2
Continued

Variable	Unit	Description	Details	Data sources
BR Area	km^2	BR Length * width.	BR Width calculated with following equation: Log $W = 0.487 * \text{Log CA} + 0.016 * R - 0.203$ (Equation S2.1 in Supporting Information S1). W = Width (m), CA = Catchment area (km^2), R = Runoff (l/s * km^2). Further details in Text S2 of Supporting Information S1.	SERS (Swedish Electrofishing RegiSter), retrieved 2020: http://www.slu.se/elfiskeregistret
Area BRs in large rivers		Total area of BRs in large rivers.	See above.	See above.
Anthropogenic land use	%	Proportion of anthropogenic land use in catchment.	Anthropogenic land uses = Agricultural land + urban area + other hard surfaces (e.g. roads, roofs).	SVAR (Svenskt VattenARkiv), version 2016: http://vattenwebb.smhi.se/.
Completed restoration measures	Present/absent	Restoration measures in the BR.	Included measures reported as finished, or initiated in 2010 or earlier, in the categories “hydrological restoration”, “biotope enhancement” (i.e. addition of gravel, large boulders or woody habitat elements) or “fishway” (i.e. the construction, improvement or repair of a fishway or the partial or complete removal of a dam or other migration barrier).	Swedish restoration database, retrieved 11.12.2020: https://www.atgardervatten.se/.

followed by Tukey HSD (*TukeyHSD* function) post hoc tests to identify significant differences among categories, with *p*-values adjusted for multiple pairwise comparisons.

We also evaluated the potential of current MMDs to (1) motivate good ecological status classification under the WFD and (2) sustain rheophilic biota, focusing on fish (Hypothesis d). The first question was assessed by identifying BRs with MMD_{Min} values below the approximate base flow (MLQ; see Tables 1 and 2). The second was assessed by identifying BRs with MMD_{Min} below 2 m^3/s, a threshold below which the proportion of rheophilic fish, on average, declines sharply in Swedish BRs, while lentic fish increase (Donadi et al., 2025).

One of the identified reach types, the Southern platformal group (see Section 3), contained very few BRs and was excluded from ANOVAs and χ^2 tests, but is included in graphs, for reference.

3. Results

3.1. Defining the Reach Types

The optimal solution of the cluster analysis identified seven groups (or reach types) of BRs labeled in Figure 1, based on their main distinguishing intrinsic hydrogeographic characteristics (Table 3). Means and boxplots for all included variables are found in Table S3.2 and Figure S3.3 of Supporting Information S1.

Four of the BR groups were predominantly southern (Figure 1). The *Southern platformal* group comprised low elevation sites characterized by catchments with a high proportion of sedimentary rocks and mud-moraine/silt soils (Table 3). The *Southern coastal* group was characterized especially by high river network centrality and a predominantly coastal distribution extending into the north (Figure 1, Table 3). The *Southern steeply sloped* group comprised high gradient, low elevation BRs with low but highly variable discharge, and catchment soils relatively high in mud elements and low in peat (Table 3). Finally, BRs in the *Southern inland* group mostly occupy a peripheral river network position, with a low proportion of peat in catchment soils (Table 3).

The remaining three clusters were predominantly northern (Figure 1). The *Northern inland* group mainly encompass BRs situated in boreal forests, with a high proportion of peat in catchment soils and the largest relative high flows (Table 3), while the *Northern large rivers* group had high river network centrality and very high MQ (Table 3). Finally, the *Alpine group* comprised higher elevation BRs located toward the Scandinavian mountain range. Both the Northern large and the alpine reach types had a high proportion of Caledonian bedrock in the catchment (Table 3).

3.2. Water Availability — Variation Among Reach Types

More than three quarters (77%) of the 607 BRs for which we acquired information on MMD lacked minimum discharge. Similarly, among BRs without a MMD, three quarters (74%) also lacked inflow from other water sources (see methods Section 1 and 2 and Figure S4.1 in Supporting Information S1). However, where other inflows were present, they could be substantial, for example, a maximum of 7.1 m^3/s inflow (MQ from tributaries) into a BR with no MMD and a MQ of 43.3 m^3/s was observed (further details in Text S4 of Supporting Information S1). Expressed by reach length, 33% (416.1 km) of the total length of all BRs had a verified MMD and an additional ca. 24% (300.6 km) could be expected to have some continous input of water from other sources. Additional descriptive statistics of MMDs and other water are supplied in Table S6.3.2 of Supporting Information S1.

BRs in the Southern coastal group had the highest incidence of MMDs (36%) compared to the other reach types (Figure 2a and Table 4 also, Figure S5.1 in Supporting Information S1). The presence of other water was more frequent among BRs in the Northern alpine and inland rivers groups (50% and 37% incidence respectively), but lower in the Southern steeply sloped and inland groups (11% and 21% incidence respectively), compared to the overall frequency (Figure 2b and Table 4, also Figure S5.2 in Supporting Information S1).

Among BRs for which verified quantitative information on MMD was available (N = 135, see Figure S4.1 in Supporting Information S1), mean MMD_w (weighed mean MMD, see Table 2) was 1.49 m^3/s (SE ± 0.30 m^3/s) and mean MMD_w/MQ at the reach was 6.2% (±0.6%). MMD_w was higher for the Northern large rivers and alpine reach types compared to the Southern inland group while MMD_w/MQ was markedly the lowest for the Northern large rivers reach type (Table 4, Figures 3a and 3b).

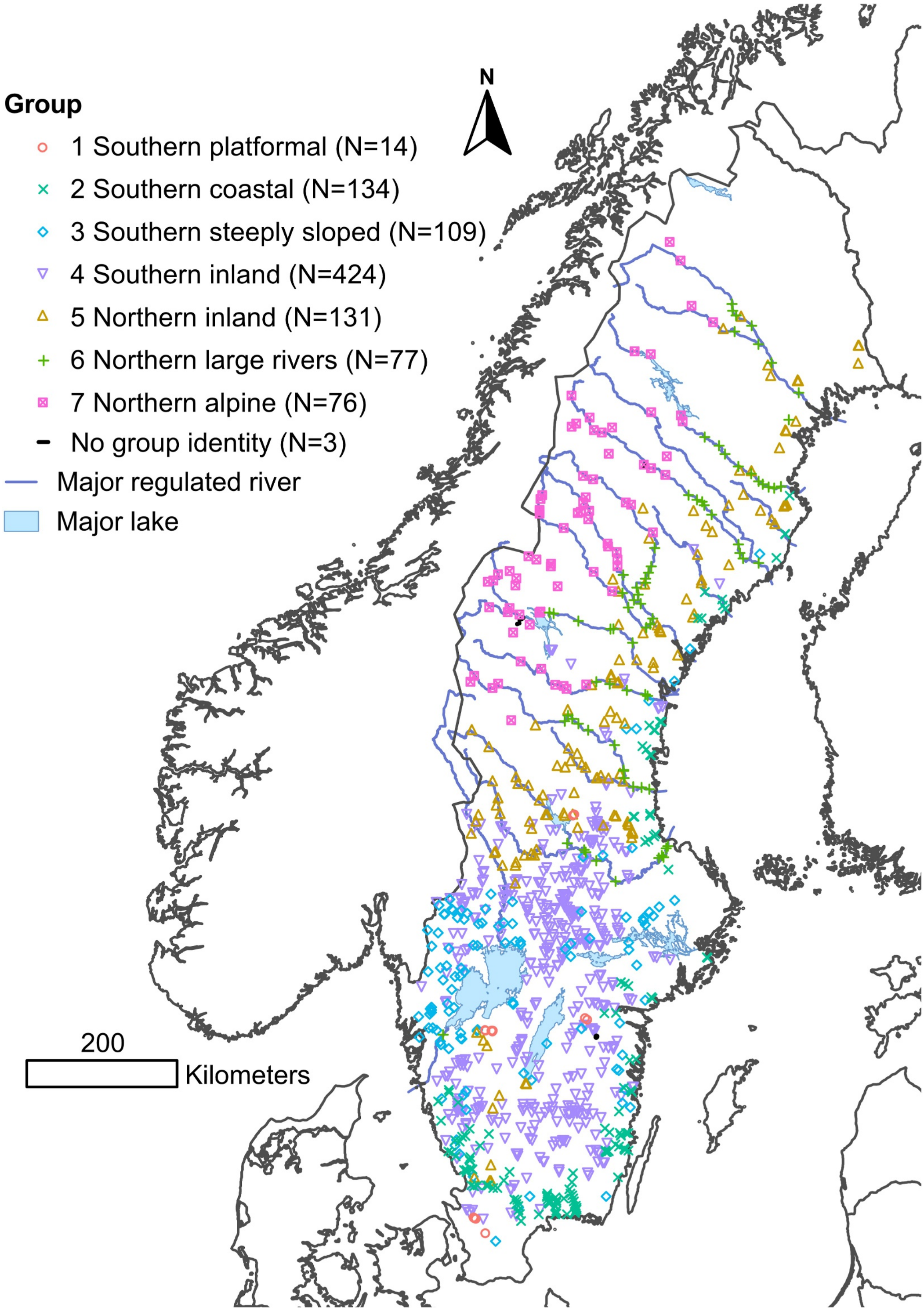

Figure 1. Location of bypassed reaches (BRs) within Sweden, classified into seven groups (reach types). Information on the defining intrinsic hydrogeographic habitat characteristics of each reach type is available in Table 3 (means and boxplots for all included variables in Table S3.2 and Figure S3.3 of Supporting Information S1, respectively). N = number of BRs that belong to that group.

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Table 3
Summary of Main Intrinsic Hydrogeographic Characteristics Distinguishing the Seven Groups (Reach Types) Identified From Cluster Analyses

Group	Catchment geology	Catchment soils	River network centrality	Elevation & slope	Natural flow regime
1. Southern platformal ($N = 14$)	High proportion Platformal sedimentary cover rocks (65%)	High proportion mud-moraine/silt (8%)		Low elevation (75 m asl)	High relative base flows (MLQ/MQ = 0.27)
2. Southern coastal ($N = 134$)			Central position (Relative BR catchment area = 82%)	Low elevation (46 m asl)	
3. Southern steeply sloped ($N = 109$)		High proportion mud-moraine/silt (16%), low proportion peat (3%)		Low elevation (63 m asl) but steep (gradient 5%)	Low MQ (6.0 m^3/s), high relative flow variability (MLQ/MQ = 0.12, MHQ/MQ = 5.2)
4. Southern inland ($N = 424$)		Low proportion peat (4%)	Peripheral position (Relative BR catchment area = 7.5%)		
5. Northern inland ($N = 131$)		High proportion peat (12%)			High relative discharge maximum (MHQ/MQ = 5.8)
6. Northern large rivers ($N = 77$)	High proportion Caledonian bedrock (45%)		Central position (Relative BR catchment area = 65%)		Very high MQ (236 m^3/s), high relative base flows (MLQ/MQ = 0.28)
7. Northern alpine ($N = 76$)	High proportion Caledonian bedrock (92%)			High elevation (387 m asl)	High MQ (49.9 m^3/s)

Note. All numbers represent mean values for the reach type. Attributes are listed when they are relatively more associated with one or more reach types compared to the others, designations such as “high” or “low” are thus relative to the other reach types. Means for all variables and reach types and boxplots supporting these categorizations are available in Table S3.2 and Figure S3.3 of Supporting Information S1. N = number of BRs that belong to that group.

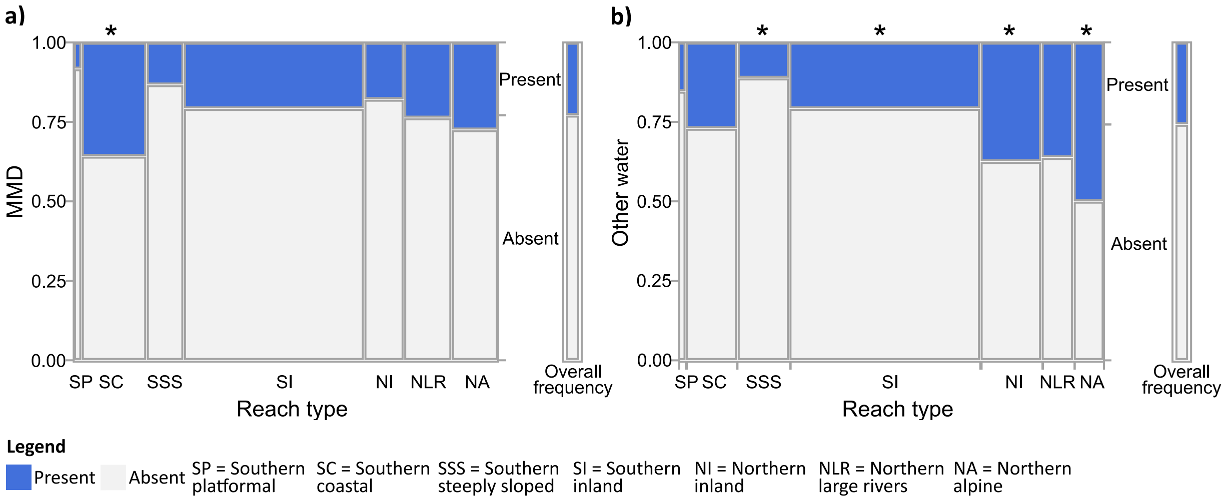

Figure 2. Mosaic plots of the frequency of a mandated minimum discharge (MMD) (panel a) and other water sources (panel b) across reach types. Overall frequencies (i.e., pooling all reach types) are indicated by the bars to the right. Asterisks (*) denote frequencies significantly different from the overall frequency. Column widths indicate the number of observations per reach type, and bar heights represent the frequency of the attribute within each group. BRs in the SP (Southern platformal) reach type were included in figures but excluded from χ^2 tests. Test statistics are found in Table 4.

MMDs varied over the year in 41% of BRs with a MMD (58 of 135, see Figure S4.1 in Supporting Information S1), with more water typically being discharged in summer or autumn than in winter. Across all BRs with a MMD, MMD_{Min} was lower than the base flow at the reach (MLQ) in 94%, less than 2 m^3/s in 88%, less than 0.1 m^3/s in 24% and 0 m^3/s for some periods over the year in 11%. Incidences of MMD_{Min} and MMD_w below more values within the range of 0–2 m^3/s are provided in Table S6.3.2 of Supporting Information S1. Higher summer or autumn discharge (MMD_{Max}) was maintained for on average 4.5 months (range 2–7 months). No inter-annual variation in MMDs was reported.

3.3. Intrinsic Hydrogeographical Characteristics

Mean BR slope was 2.17% (±0.08%). A slope and MQ indicative of former dominance of riffle, rapid or waterfall habitat characterized 91% of BRs (878 out of 968), representing approximately 94% of the combined BR length (1,184.6 km). Riffle-rapid-waterfall dominance was high across all reach types (86%–95% incidence), although BRs with no water were generally steeper than those in the "other water" category (Figure 4a, Table 4).

Relative BR catchment area, as a measure of river network centrality (Table 1) averaged 23.9% (±1.0%). Also, classical (bottom up) stream order was 1 or 2 in 76% of all BRs (1 in 37% and 2 in 39%), representing 77% of the total BR Length. Mean relative BR catchment area ratio was 21.6% for BR without water, 22.3% for BRs with other water sources, and 36.2% for BR with a MMD, with these differences near significance ($p = 0.0659$) (Table 4, Figure 4b). Among BRs in reach types with high river network centrality (i.e., Southern coastal and Northern large rivers groups), 100% in the former group and 89.6% in the latter had classical stream order 1, with the remainder being stream order 2.

Mean MQ was 32.6 m^3/s (±2.3 m^3/s). Twenty-six percent of the BRs were located in large rivers (MQ > 20 m^3/s, see Table 2), these represented 45% of total BR length (562.8 km) and 83% of total BR area (53.2 km^2). Large rivers occurred in every reach type. BRs with no water had significantly lower MQ than BRs with a MMD (Table 4, Figure 4c). Additional descriptive statistics of slope, river network centrality and MQ for all BRs are found in Table S6.3.1 of Supporting Information S1.

3.4. BR Size

Mean BR length was 1.3 km (±0.1 km) and mean BR area was 0.066 km^2 (±0.008 km^2). Additional descriptive statistics can be found in Table S6.3.2 of Supporting Information S1. The longest BRs were found in the Northern large rivers and alpine groups (Figure 5a, Table 4). Furthermore, BRs with no water were almost one order of magnitude shorter than BRs in the other water availability categories. An interaction between reach type and

Table 4
Statistical Tests of Effects of Reach Type and Water Availability Categories as Factors, With Interaction Effect, on MMD Descriptors, Hydrogeographic Variables, BR Length, Stressors, and Restoration Measures

Type of variable	Variable	Test		Reach type	Water availability category	Reach type * water availability category
MMD and other water	MMD	Pearson χ^2	Pearson χ^2	13.39	–	–
			p	**0.0200**	–	–
			N	594	–	–
	Other water		Pearson χ^2	45.81	–	–
			p	**<0.0001**	–	–
			N	812	–	–
	MMDw	Two way ANOVA	F	4.233	–	–
			p	**0.0014**	–	–
			Residual	127	–	–
	MMDw/MQ		F	8.254	–	–
			p	**<0.0001**	–	–
			Residual	127	–	–
Intrinsic ecological values	Slope	Two way ANOVA	F	43.82	8.234	1.236
			p	**<0.0001**	**0.0003**	ns
	Relative BR catchment area		F	156.0	2.727	1.610
			p	**<0.0001**	0.0659	0.0988
	MQ		F	165.9	7.552	1.600
			p	**<0.0001**	**0.0006**	ns
BR size metrics	Length	Two way ANOVA	F	74.03	159.2	3.41
			p	**<0.0001**	**<0.0001**	**0.0002**
Other stressors	Anthropogenic land use	Two way ANOVA	F	131.4	6.961	2.539
			p	**<0.0001**	**0.0010**	**0.0051**
Restoration measures in the BR	Restoration measures in the BR	Pearson χ^2	Pearson χ^2	30.27	53.11	–
			p	**<0.0001**	**<0.0001**	–
			N	951	951	–

Note. Categorical variables tested with Pearson χ^2; continuous variables with two-way ANOVA. Pearson χ^2 = test statistic, F = ANOVA statistic, p = probability (bold letters indicate significance), N = sample size, ns = not significant. Degrees of freedom: reach type = 5, water availability = 2, interaction = 10; ANOVA residual = 933 unless noted. Southern platformal BRs are excluded from the statistical analysis.

water availability was also apparent: In northern reach types, BRs with a MMD were longer than those with other water, whereas the reverse was true in southern reach types (Figure 5a). BR area showed a very similar pattern to BR length (Figure S6.2; Table S6.2 in Supporting Information S1).

3.5. Catchment Anthropogenic Land Use

The proportion of catchment anthropogenic land use averaged 7.1% (±0.3%) across all BRs. BRs in the southern reach types had higher proportion of anthropogenic land use in the catchment than those in the northern reach types (Table 4, Figure 5b). Also, BRs with no water had a higher proportion of catchment anthropogenic land use (mean 7.8 ± 0.4%) than those in the remaining water availability categories (combined mean 6.0 ± 0.5%).

3.6. Other Restoration Measures

One or multiple restoration measures had been carried out in ca. 10% of the BRs in our data set (multiple restoration measures in ca. 2%) “Fishways” (see Table 2) was the most frequent type of restoration measure (73%, 69 out of 95 restored BRs), habitat enhancement the second most frequent (38%, 36 out of 95 BRs) and hydrological restoration the least frequent (11%, 10 out of 95 BRs, with increased MMD part of the restoration in

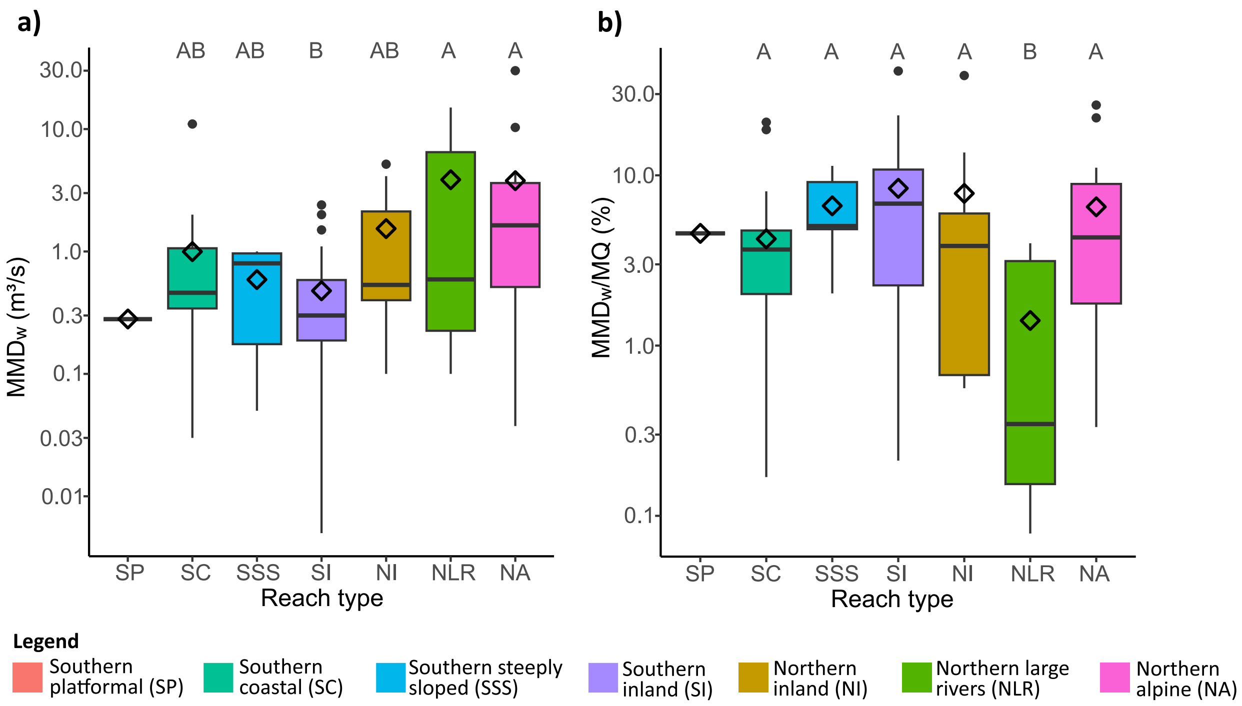

Figure 3. Differences in MMD_w (panel a) and MMD_w/MQ (panel b) between reach types. MMD_w = weighed annual mean mandated minimum discharge, MQ = annual mean natural discharge (see Tables 1 and 2). *Y*-axes are log transformed. Mean values are indicated by rhomboids and medians by horizontal lines. Boxplot hinges indicate the 25th and 75th percentiles; whiskers extend to 1.5 × IQR (inter-quartile range), with outliers plotted individually. Letters above the bars (A, B, AB) denote homogeneous subsets identified by Tukey's post hoc test for differences among reach types: groups sharing a letter do not differ significantly from one another. BRs in the Southern platformal reach type were excluded from the statistical analysis but included in the figures for reference. Test statistics are found in Table 4.

six). The frequency of completed restoration measures was significantly higher for Southern coastal BRs (20.1%), and in BRs with a MMD (25.9%), compared with the overall frequency (Figures 6a and 6b, Table 4; Figures S5.3 and S5.4 in Supporting Information S1).

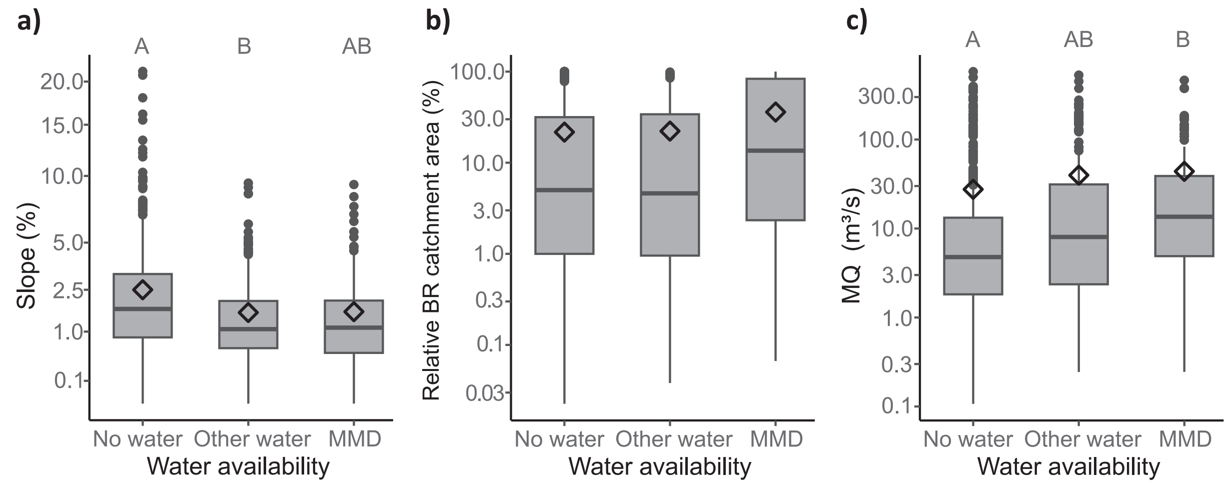

Figure 4. Differences in slope (panel a), relative BR catchment area, a measure of river network centrality (panel b), and natural mean annual discharge (MQ) (panel c) among water availability categories. *Y*-axes are either square root (a) or log (b, c) transformed. MMD = BRs with a mandated minimum discharge, Other water = BRs without MMD but with inflow of water from tributaries or due to structural characteristics of the hydropower facility, No water = BRs with no identified inflow of water. Mean values are indicated by rhomboids and medians by horizontal lines. Boxplot hinges indicate the 25th and 75th percentiles; whiskers extend to 1.5 × IQR, with outliers plotted individually. Letters above the bars (A, B, AB) denote homogeneous subsets identified by Tukey's post hoc test for differences among water availability categories: groups sharing a letter do not differ significantly from one another. Test statistics are found in Table 4.

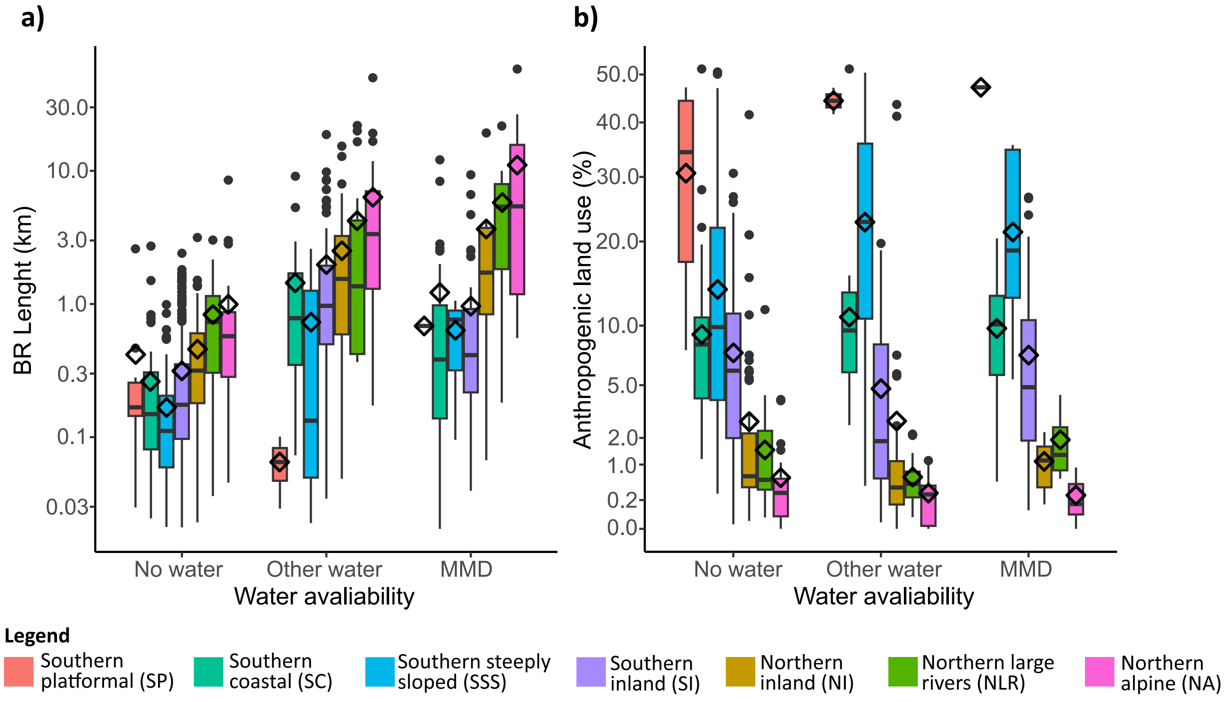

Figure 5. Differences in BR length (panel a) and proportion of anthropogenic land use in the catchment (panel b) among reach types and water availability categories. *Y*-axes are either log (a) or square-root (b) transformed. Mean values are indicated by rhomboids and medians by horizontal lines. Boxplot hinges indicate the 25th and 75th percentiles; whiskers extend to 1.5 × IQR, with outliers plotted individually. BRs in the Southern platformal reach type were excluded from the statistical analysis but included in the figures for reference. Test statistics are found in Table 4.

4. Discussion

Our analyses highlight how the construction of hydropower dams on steeply sloped river reaches has resulted in the systematic removal of high gradient habitats from river networks. The results support hypotheses a and b regarding the high potential habitat quality for rheophilic organisms and the central river network position of Swedish BRs, with 94% of total BR length consisting of former riffle-rapid-waterfall dominated reaches, 77% of

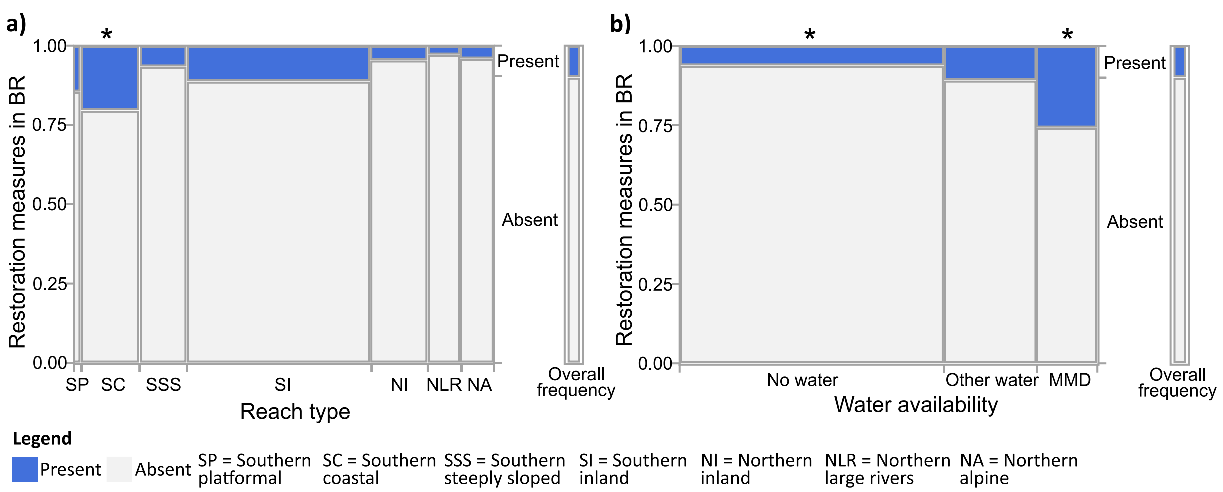

Figure 6. Mosaic plots of differences in frequency of implementation of restoration measures in BRs among reach types (panel a) and water availability categories (panel b). Overall frequencies (i.e., pooling all reach types) are indicated by the bars to the right. Asterisks (*) denote frequencies significantly different from the overall frequency. Column widths indicate the number of observations per category (reach type or water availability category), and bar heights represent the frequency of the attribute within each category. BRs in the SP (Southern platformal) reach type were included in figures but excluded from χ^2 tests. Test statistics are found in Table 4.

BRs occupying central river network positions (classical stream orders 1–2) and 83% of total BR area (53 of 64 km^2) located in large rivers. Our analyses further demonstrate how substantial these losses are in Sweden, whether quantified as loss of habitat area, length or as amount of water diverted. For example, the total length of BRs in our database was 1,256 km, equivalent to the total length of the two longest rivers in Sweden added together (Göta älv/Klarälven 731 km and Dalälven 557 km). Also, the sum of MQ diverted from the BRs totaled ca. 31,500 m^3/s, or five times more water than the average discharge of the Danube at the river mouth ($MQ = 6{,}488\ m^3/s$). Furthermore, given an estimate of average densities of rheophilic fish in Swedish unregulated rivers of ca. 50 individuals/100 m^2 (e.g., Donadi et al., 2025), 64 km^2 of BRs translates into the potential loss of tens of millions of rheophilic fish, such as brown trout (*S. trutta*) and Atlantic salmon (*S. salar*), from regulated rivers. We further emphasize that our estimates of losses of high gradient habitat due to BRs represent only a subset of the total loss of high gradient habitat from Swedish regulated rivers. This is because former riffles, rapids and waterfalls inundated by hydropower reservoirs, or by the more than 10,000 non-hydropower dams in the country (Beletti et al., 2020; Swedish Government and Ministry of the Environment, 2020) still remain to be quantified.

Our analyses further highlight that current flow management practices in Swedish BRs are inadequate (Hypothesis d). MMDs are either absent or imperfectly applied (i.e., with discharge interruptions) in most Swedish BRs: 77% lack a MMD altogether and 11% of those with an MMD have a MMD_{Min} of 0 m^3/s during parts of the year. Consequently, most BRs are either completely dewatered or frequently dry out (example images in Figure S8 of Supporting Information S1). Such reaches are likely to exhibit altered food web structure and function (McHugh et al., 2010; Palmer & Ruhi, 2019; Sabo et al., 2010; Truchy et al., 2020) and cannot support a diverse fish community including environmentally sensitive native rheophilic species (Göthe et al., 2019). Furthermore, in 88% of BRs with a MMD the discharge was periodically or continually below 2 m^3/s, identified as a threshold MMD in Swedish BRs below which the proportion of rheophilic fish species on average declines sharply, with lentic species instead favored (Donadi et al., 2025). Even at MMDs exceeding 2 m^3/s, the proportion of rheophilic fish in BRs generally remains lower compared to unregulated reference conditions (Donadi et al., 2025), likely reflecting an impact from sudden high flows (hydropeaking) or other hydro-morphological impairments (e.g., Bätz et al., 2023; Benejam et al., 2016; Donadi et al., 2025). Minimum discharges were also periodically or continually lower than reach base flow (MLQ) in 94% of BRs with a MMD, and thus insufficient to motivate good ecological status classification under the WFD (Kling, 2015; Swedish Government and Ministry of the Environment, 2020). While 41% of BRs with a MMD had a variable MMD, this was typically binary, with lower discharge in the winter and higher in summer-autumn. There were no examples of dynamic MMDs mimicking the natural flow regime (e-flows) in our database. However, environmental flows (e-flows) were implemented in 2021 (for the first time in Sweden) in the BR of River Juktån, Alpine group, after our data compilation was completed (Widén et al., 2023).

Though completely dry BRs may be particularly common in Sweden, inadequate flow management in BRs is an issue in many countries. This includes Finland, where the historical development (with little initial environmental consideration) and legal regulation (i.e., old permits that do not expire) of hydropower are similar to Sweden (Puharinen et al., 2024). Elsewhere, McManamay et al. (2016) documented a 43% incidence of diversion hydropower stations in the USA (compared to ca. 50% in Sweden, additional details in Text S6.1 of Supporting Information S1), that were associated with 975 km of dewatered BR habitat. Similarly, water availability remains restricted in most BRs globally. Although e-flows are increasingly implemented in regulated rivers (Acreman et al., 2014; Tickner et al., 2020), BRs with no or a small static MMD remain common. Apart from Sweden, BRs without a MMD are reported in for example, Finland (Vehanen et al., 2019), China (Kibler & Tullos, 2013), Czech Republic (Kubecka et al., 1997), Canada (Hall et al., 2011) and USA (Hill & Platts, 1998; McManamay et al., 2016). Unfortunately, the possibilities to pursue the “hydropower by design” approach suggested by Opperman et al. (2015), aimed at minimizing environmental impacts of new hydropower development, are limited in existing facilities. Nevertheless, the restoration potential of BRs is often very high. For example, although Swedish BRs regularly are associated with additional or preexisting geomorphological modification (e.g., channelization, closing of side channels, losses of finer grained substrates (Nilsson et al., 2005)), other key geomorphic features, including high channel slope and hard stone substrates, typically remain intact. This underscores the potential for rehabilitating the thousands of kilometers of BRs occurring in Sweden and elsewhere as hard-bottomed torrential habitat, contributing to efforts to “bend the curve” of freshwater biodiversity loss, by accelerating the implementation of environmental and functional flows.

Although other sources of water entering BRs were not uncommon (ca. 26% incidence), tributaries typically do not enter at the start of the BR and are likely to exhibit high seasonal variability in discharge. Thus, other sources of water are likely rarely sufficient in magnitude and/or reliability to provide habitat conditions optimal for rheophilic organisms, and cannot be considered as a substitute for active flow management (e.g., as sufficiently large dynamic MMDs). Rather, since natural geomorphic processes may remain intact in tributaries which can replenish the BR with different size classes of bottom substrates, and since tributaries may act as refugia for naturally occurring biota allowing for swift recolonization of the BR if flow conditions are improved, BRs with intact tributaries could be especially attractive for expanded hydrological restoration (Yarnell et al., 2015).

Complete dam removal is ultimately the best approach for restoration of former riffles-rapids-waterfalls inundated upstream, or dewatered downstream, of hydropower dams, but at the cost of ceased hydropower generation. In contrast, applying MMDs, ideally as e-flows or functional flows, is a relatively simple restoration measure that increases and improves habitat for sensitive rheophilic species in BRs while allowing energy production to continue (Widén, Malm-Renöfält, et al., 2022). BRs occur across all three Swedish biogeographical regions (Alpine, Boreal and Continental) and in all river habitat types (alpine, large and small rivers) defined under the EU Habitats directive (Swedish EPA, 2020). Rivers covering this biogeographic range, encompassing variation in for example, natural flow regimes, and key soil and bedrock catchment characteristics (Table 3, Table S3.2 and Figure S3.3 in Supporting Information S1) known to govern water chemistry (e.g., Sandström et al., 2024; Weldon & Meriggi, 2023), are likely to differ substantially in community composition. Accordingly, a national-scale BR restoration effort could enhance both local scale α-diversity and larger scale β-diversity. Ultimately, more ambitious e-flows are likely needed to fully protect a broader range of rheophilic diversity (Poff et al., 2010; Tickner et al., 2020). This is exemplified by the recent restoration of the BR in R. Juktån (Alpine rivers group), where preliminary results indicate that the establishment of a dynamic e-flow, with a pronounced spring flood, have promoted rapid recovery of riparian vegetation and resident brown trout (*S. trutta*) populations (Widén et al., 2023).

Supporting our Hypothesis c, BRs in the centrally positioned Southern coastal, but not the Northern large rivers, groups are already characterized by a relatively high incidence of both MMDs and completed restoration measures including fishways (Figures 2a and 6a). Still, substantial opportunities for combining MMDs with complementary additional restoration exists for BRs in all reach types. Ecological outcomes from MMDs, including e-flows and functional flows, are likely enhanced by simultaneous application of complementary morphological (e.g., regenerating gravel beds) and connectivity (e.g., fishway installation) restoration measures. Migration barriers elsewhere in the river network are particularly likely to limit fish responses to local discharge improvements by restricting migration and isolating populations (e.g., Tamario et al., 2021; Törnblom et al., 2017). Thus, expanded flow management in BRs is best planned concurrently with measures to restore longitudinal connectivity. Kling (2015) reported that ca. 90% of Swedish hydropower stations lack fishways, and measures to restore longitudinal connectivity have been implemented at fewer than 7% of BRs in our database, with most exhibiting poor hydrological connectivity (Figure S7.2g in Supporting Information S1). Integrating MMDs with restoration of connectivity is especially important for centrally positioned BRs, such as those in the Southern coastal and Northern large river reach types, to support endangered anadromous fish like the European eel (*A. Anguilla*) and sea lamprey (*P. marinus*). However, an attempt to increase critical spawning habitat for wild "Gullspång salmon"; the world's largest sized variety of landlocked Atlantic salmon (*S. salar*), at Gullspång hydropower station (Southern inland group), through combined implementation of increased MMD in the BR and measures to improve connectivity have only been partially successful (Hutchings et al., 2019; Magnusson, 2022).

Additional pressures on the BR ecosystem can hamper restoration success (e.g., Bätz et al., 2023; Benejam et al., 2016; Göthe et al., 2019; Palmer & Ruhi, 2019). However, aside from impaired longitudinal connectivity and flow regime, most BR reach types in our database had quite low levels of additional anthropogenic pressures from land use and riparian degradation (Figure 5b and Figure S7.2 in Supporting Information S1) that otherwise might undermine the success of morphological and hydrological restoration (Göthe et al., 2019). This was especially pronounced for the northern reach types, due to the very low intensity of additional human impacts (Figure 5b and Figure S7.2 in Supporting Information S1), confirming our Hypothesis c. In particular, Northern alpine BRs are located within or in close proximity to the Scandinavian mountain range (Figure 1), an area sometimes described as "the last wilderness of Europe" (Kuuluvainen et al., 2017). Despite this, the conservation status of large rivers within the Swedish alpine biogeographical region is unsatisfactory or in decline (Swedish EPA, 2020). BRs in the Northern alpine group were also notably long and had the highest incidence of inflow from tributaries (Figures 2b and 5a), potentially adding to their suitability for expanded hydrological restoration (Yarnell et al., 2015). Overall, the very low application of MMDs not only in the Northern alpine, but also in Southern steeply sloped BRs, illustrates a concerning lack of environmental consideration in management of the highest gradient river reaches, including former waterfall habitats, while also highlighting their untapped potential for restoration. Although waterfalls are typically unsuitable habitat for rheophilic fish and may have acted as natural migration barriers, they support unique flora and fauna (Clayton & Pearson, 2016; Rackeman et al., 2013) and their restoration can disproportionately increase β-diversity at larger scales. Intact waterfalls also oxygenate water, benefiting downstream ecosystems. Additionally, in our database, BRs—including those in the Southern steeply sloped group—rarely consist of a single bypassed waterfall, but typically include adjacent bypassed riffle-rapid stretches. Consequently, habitat for rheophilic fish is often lost alongside the waterfall's unique biota.

Regulatory frameworks such as the WFD, and hydropower relicensing processes (such as the process initiated in Sweden), have proved to be effective incentives to improve environmental conditions in regulated rivers. However, there may be a risk that these incentives inspire an unfortunate “all or nothing” thinking. For example, if achieving good ecological potential in a BR that has been classified as a “heavily modified” waterbody (details in Text S7.1 of Supporting Information S1) is deemed unfeasible due to excessive costs, the WFD permits exceptions and the establishment of less stringent environmental standards (e.g., Puharinen et al., 2024). Therefore, long BRs at large hydropower stations in Sweden have typically been excluded from consideration for future MMD allocation motivated by the negative consequences implementation of MMDs equal to MLQ, or alternatively 5% of MQ, would have for national hydroelectricity generation and regulation capacity (e.g., Swedish Energy Agency, 2016; Swedish Government and Ministry of the Environment, 2020). We suggest that the length and area of these BRs should make them more, not less, attractive as targets for restoration, given their potential to provide additional critical habitat for rheophilic species. Also, more modest MMD allocations than MLQ or 5% of MQ may still be sufficient to support a rheophilic fish community (Donadi et al., 2025), facilitate upstream fish migration (*sensu* Wolter & Schomaker, 2018), and buffer impacts of additional stressors (e.g., riparian degradation) on river biota (Göthe et al., 2019). Nearly all of the BRs in the Northern large and alpine groups are long enough to potentially harbor self-sustaining populations of brown trout (*S. trutta*) with the allocation of water for a MMD < MLQ (Törnblom et al., 2017). With trout populations established, this would make these BRs potential habitats for freshwater pearl mussel (*Margaritifera margaritifera*), a protected species with populations in decline all over Europe, that require young salmonid fish to complete their life cycle (e.g., Degerman et al., 2013). Attaining good ecological status/potential according to the WFD may be beyond reach for some BRs. Nevertheless, substantial improvements in the health of BRs through expanded flow releases in combination with other restoration measures is realistic, with cumulative benefits for the river ecosystem as a whole, and for a plethora of unique northern-European rheophilic species.

5. Conclusion

The global decline of riffle-rapid-waterfall habitats is recognized as a major threat to freshwater biodiversity, particularly rheophilic species (e.g., Birnie-Gauvin et al., 2017; Bunn & Arthington, 2002). Our mapping of BRs in Sweden reveals extensive losses of such habitats. Most BRs in our database are characterized by steep slopes, and many also occupy central river network positions—features that once made them likely hotspots of biodiversity and ecosystem function. These habitats must not be entirely lost; rehabilitation through environmental or functional flows could help restore networks of riffle, rapid, and waterfall habitats, supporting and protecting threatened rheophilic species and valued biodiversity for future generations.

Current management of Swedish BRs remains inadequate: few have MMDs, existing MMDs are low both in absolute terms and relative to MQ, and almost no MMDs mimic natural flow regimes. This presents considerable potential for improved discharge management to drive large gains in productive, well oxygenated habitat for rheophilic biota, and enhance longitudinal connectivity. Achieving this requires (a) increased allocation of resources for BR rehabilitation, including MMDs and complementary geomorphological and other restoration measures, and (b) a framework for prioritizing MMDs among BRs based on their potential to deliver positive ecological outcomes. Our systematic mapping and characterization of habitats lost to BRs provides a foundation for such a framework, but further research is needed on both the effectiveness of different MMD regimes and how mapped factors—anthropogenic stressors, complementary restoration, and catchment position—influence MMD outcomes to enable science-based prioritization.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

In accordance with AGU's data policy, the data are made accessible in SND (Swedish National Data service), a repository of research data (https://doi.org/10.5878/fgz3-v727).

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