



Original Research Article

Fish biodiversity in different types of tributary mouths located within impounded sections of Swedish boreal rivers

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ABSTRACT

Large boreal rivers in Sweden are generally impounded by hydropower dams and a large proportion of main stem shallow flowing habitats have been lost. Tributaries often contain the last undisturbed habitats and could be important for the conservation of species diversity. In particular, tributary mouth areas could be biodiversity hot-spots, due to their vicinity to the main stem and favorable environmental conditions. In this study, we investigate whether tributary mouth areas in two impounded boreal rivers (Ume River and Lule River) could be regarded as biodiversity hot-spots for fish. Based on standardized electrofishing in 20 tributary mouths, we find that overall fish diversity is generally low. The highest species richness and diversity was found in mouth areas dominated by intermediate substrate sizes (gravel – cobble). Few, if any, species were found in areas where fine sediments (smaller than sand) dominated. The tributary mouth areas had similar species richness and diversity as areas in the tributaries located 1-km upstream of the mouth, but the fish community composition often differed between these two types of sites. Management action favoring fish diversity in the tributary mouth areas could include protection or rehabilitation of areas dominated by medium sized substrate and reduction of erosion and transport of fine sediments in the tributaries. Overall, we find no support for tributary mouths being hot-spots for fish biodiversity and while some patterns in diversity gives hints on suitable management action, it is important to further understand impacts in tributaries and their mouths and the temporal dynamics of the fish community.

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1. Introduction

Large rivers are important ecosystems for aquatic biodiversity, typically housing a higher fish biodiversity than smaller rivers, with some species being adapted

specifically for habitats characteristic of these larger systems (Jackson et al. 2001; Oberdorff et al. 2011; Miranda et al. 2019). The biodiversity of many of these large ecosystems has been negatively impacted during the last century as they have been heavily exploited for many purposes, including energy production (Grill et al. 2019). While damming of main stem rivers can secure large amounts of affordable energy for society (Rex et al. 2014; Schäfer 2021), damming also disrupts longitudinal connectivity and al-

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ters hydrological, hydrogeomorphological, and thermal conditions (Baxter 1977; Ligon et al. 1995; Vörösmarty et al. 2010; Anderson et al. 2015). The result is spatially and seasonally homogenized, slow-flowing river sections between dams, with severely disrupted connection among them, which reduces their overall biodiversity (Poff et al. 2007; Malm Renöfält et al. 2010).

The northern European large rivers discharging into the Baltic Sea are today generally exploited for large-scale hydropower production, with only a few remaining in a completely or near free-flowing state (Dynesius & Nilsson 1994; Grill et al. 2019). In Sweden, hydropower development in these Baltic rivers was initiated in the early- to mid-1900s, without much regard to the ecology of the river ecosystems, and today constitute the most important source of hydropower in the country (Ödmann et al. 1982; Schäfer 2021). With national and international legal requirements for sustainable hydropower (GOS 2020) and riverine ecosystem functioning (EC 2000), the pressure to restore riverine biodiversity and processes is high. Sweden is a net-exporter of energy, with hydropower making up an important proportion of the energy production, and sources of renewable energy are increasingly important in light of climate change (SEA 2021). Hence, while complete restoration to reference conditions is unfeasible in these heavily modified rivers, rehabilitation measures and mitigation of continued biodiversity loss are still required to secure a good ecological potential (EC 2000, 2020; GOS 2020). Such management action, however, requires much information about the current ecological state of different areas in relation to their hydro- and geomorphology, so that restoration and rehabilitation measures can be optimally directed to those with the strongest positive effects on biodiversity (e.g. Borg et al. 2007; Jansson et al. 2007; Renschler et al. 2007; Widén et al. 2016).

Tributaries to large impounded rivers often have a lower degree of habitat alteration and more natural sediment transport, flow dynamics, and temperature regimes, as compared to the main stem, given that they themselves are not impounded (Rice et al. 2008; Ziv et al. 2012; Pracheil et al. 2013; Marques et al. 2018; Vasconcelos et al. 2021). Protection of unaltered tributaries and restoration of ecologically degraded tributaries could thereby retain or improve the remaining ecological values of impounded large rivers. Focus on this potential source of biodiversity has mainly been proposed for large tributaries in very large river systems (Ziv et al. 2012; Pracheil et al. 2013; Dunn & Paukert 2021), where network dispersal (extensive upstream dispersal in tributaries) is more likely than in small tributaries (Grenouillet et al. 2004). Nevertheless, similar effects may also be achievable in smaller systems where the main stem-tributary movements of species mainly relates to confluence exchange (localized movements near confluences), if conditions are favorable (Rice et al. 2008; Thornbrugh & Gido 2010; Laub et al. 2018). The confluence areas of tributaries (mouth) and the main stem have previously been described as important for habitat heterogeneity and biodiversity in the main stem, due to e.g. aggradation, concentrated nutrient flow, favorable thermal and chemical conditions, and environmental features allowing prey species to shelter from large-sized

predators (Power & Dietrich 2002; Wipfli & Gregovich 2002; Kiffney et al. 2006; Rice et al. 2006). Tributary confluences can indeed constitute significant biological 'hot-spots' in riverine ecosystems (Power & Dietrich 2002; Benda et al. 2004; Kiffney et al. 2006). The value of tributaries for biodiversity is particularly pronounced in e.g. species-rich neotropical river systems (e.g. Marques et al. 2018; Azevedo-Santos et al. 2020; Vasconcelos et al. 2021; da Luz Soares et al. 2022), but the pattern could potentially be the same in relatively species-poor boreal river systems. Previous studies have shown that species richness of benthic invertebrate fauna is high at tributary confluences in reaches below impoundments in the main stem (e.g. Greenwood et al. 1999; Vinson 2001; but see Milner et al. 2019). Studies of fish also suggest that species richness can be higher in tributary segments near main stem confluences (Thornbrugh & Gido 2009; Miranda et al. 2019), and that these areas can be important spawning areas for fish (da Luz Soares et al. 2022). These patterns make tributary mouths possible focal areas for 1) conservative management plans when intact, 2) restorative actions when degraded, or 3) ecological compensation measures when the main stem is degraded and there is still potential to increase biodiversity (Allan & Castillo 2007; Rice et al. 2008; Erkinaro et al. 2017; Sandin et al. 2017; Miranda et al. 2019).

The tributaries themselves (i.e. sections upstream from the mouth) often have lower species richness than the main stem (Czeplédi et al. 2016; Miranda et al. 2019), but can nevertheless be important for biodiversity in the river network. For instance, tributaries can be highly heterogeneous in terms of flow and environmental features, offering a variety of habitats (Jackson et al. 2001; Wohl 2017). They also offer refuge from extreme temperature- and flow events in the main stem, contain spawning grounds or juvenile habitat, and create migration corridors between the main stem and upstream lakes and smaller streams (Jackson et al. 2001; Fausch et al. 2002; Meyer et al. 2007; Rice et al. 2008; Wohl 2017).

Management action to improve habitats in the main stems of these rivers are often costly and incongruous with hydropower production, at least with high production, but measures in their tributaries may be more feasible from a socio-economic perspective. Hence, tributaries, and the tributary mouth areas in particular, are possibly key target areas for restoration and rehabilitation activities. The aim of this study was to provide baseline information about fish biodiversity in tributary mouths in two heavily impounded boreal rivers in northern Sweden, Ume- and Lule River, both of which are classified as strongly affected by fragmentation (Dynesius & Nilsson 1994). We investigate the effects of some key environmental characteristics (hydrogeomorphology and bottom substrate) of tributary mouth areas on the fish fauna composition. More specifically, we aimed to:

- 1) Assess the number of species and diversity of fish in tributary mouth areas to collect initial data on whether these areas could be viewed as fish biodiversity hot-spots (i.e. in relation to the known species in the main stem).

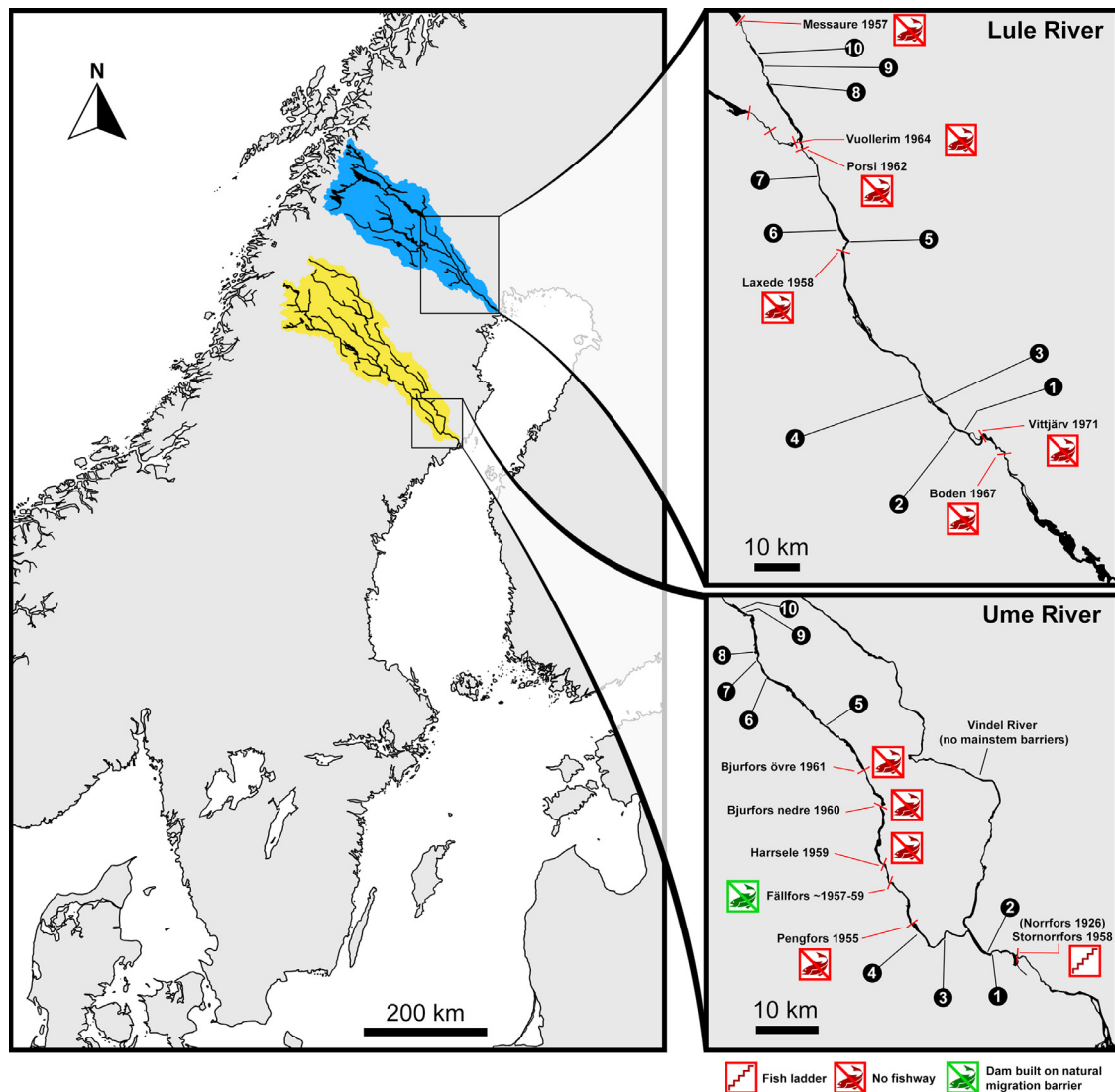


Figure 1. Map over Sweden with the locations of the study areas within the catchments of Ume- (yellow) and Lule (blue) Rivers. Artificial barriers are marked with red bars across the rivers in the maps. The tributaries investigated in the study are marked with numbers (for details see Table 2).

- 2) Investigate which tributary mouth habitats are the richest in fish diversity and abundance, with particular focus on sites dominated by erosional (non-aggraded) vs. depositional (aggraded) processes.
- 3) Investigate the association of different fish guilds to habitat characteristics in tributary mouth areas.
- 4) Compare diversity in tributary mouth areas with sites located further upstream in the tributaries (ca. 1 km upstream of the confluence).

2. Materials and methods

2.1. Survey areas

The surveyed tributaries belong to two large Swedish boreal rivers, Ume River and Lule River (Fig. 1), located in the Svecofennian Orogen province of the Baltic Shield. Both

rivers transverse the country in a northwest-southeast direction, starting in the alpine region near Norway and draining into the Baltic Sea (Bothnian Sea and Gulf of Bothnia, respectively). The rivers are of similar size (Table 1), have similar hydro-climatic variation within their catchments (SMHI 2022), and have multiple hydropower impoundments along a large portion of each river (Fig. 1). In the downstream parts of both rivers, power production follows a run-of-the-river scheme, with the flow being regulated by storage reservoirs in the upper parts of the catchments.

The tributaries included in this study were limited to the region between the first hydroelectric dam from the sea and the highest coastal line after the Weichselian glaciation, so as to be able to work with comparable fish communities. In this geographical area, the river margins of both rivers are dominated by erosion sensitive ma-

Table 1

Details about Ume- and Lule River (SMHI 2010; SERS 2020). MMQ: mean monthly discharge; MHQ: mean annual high discharge.

	Ume River	Lule River
Position (mouth), WGS84 dec (N, E)	63.75502, 20.322304	65.700975, 21.805115
Catchment area, km ²	26782	25262
Length (source to sea), km	449	457
MMQ (1900's), m ³ ·s ⁻¹	443	506
MHQ (1900's), m ³ ·s ⁻¹	1365	1040
Number of electrofishing records*	2378	224

* from the Swedish Electrofishing Register (SERS 2020–10–14)

terials; sandy substrates in the more upstream sections, with an increased occurrence and dominance of silt and flood sediments as the rivers flow further downstream (SGI 2022). Much of the surrounding land consists of moraine, glacial river sediments and peat (SGU 2022). Tributaries in Ume River were distributed over a main stem distance of 84 km (most downstream tributary located 30 km from the sea) and tributaries in Lule River were distributed over a main stem distance of 104 km (most downstream tributary located 50 km from the sea) (Fig. 1).

2.2. Site selection

Tributaries entering Ume- and Lule Rivers have mouth areas that can be broadly classified as either aggrading or non-aggrading, based on the presence or absence of sediment plumes at the confluence, using digital aerial map surveys from public web-services (<https://maps.google.se/>; <https://eniro.se/>). We identified candidate tributary mouths based on the aerial photographs, extracted information on mean discharge (MQ) for each candidate from the S-HYPE model of national hydrological statistics (Bergstrand et al. 2014) and thereafter selected a set of tributaries along a wide range of MQ for both confluence types. Impoundments with only one type of tributary (aggrading/non-aggrading) were excluded and tributaries assessed as too deep for wading, or culverted or dammed directly at the mouth, were not considered. From the candidate set, we selected tributaries so that each confluence type was represented by equal numbers of streams (5 of each type in each of the two rivers), covering similar ranges of MQ. Assessment of tributary mouth type was also made in the field (see 2.5. *Environmental survey methodology*), and final designation was based on the combined information. The selected tributaries were located in two impoundments in Ume River and three impoundments in Lule River (Table 2).

2.3. Fish communities

Fish communities in the two river systems are similar (Table 3). The main differences are the absence of alpine bullhead *Cottus poecilopus* in Ume River records, and the absence of river lamprey *Lampetra fluviatilis* in Lule River records (GBIF 2020). River lamprey, however, does not occur upstream of the first dam in Ume River. Anadromous salmonids (Atlantic salmon *Salmo salar* and brown trout *S. trutta*) can use a fishway to pass the same dam, reaching the most downstream surveyed impoundment

of Ume River, but are either not expected in the survey area (*S. salar*, which mainly migrates up the large tributary Vindel River) or have local non-migratory populations (*S. trutta*), making species presence effectively equivalent in both rivers. Arctic charr *Salvelinus alpinus* mainly occurs in the alpine region of the catchments and populations in the lower parts are likely stocked into lakes, and hence not expected in the river tributaries. Two non-native salmonid species are present in the area, rainbow trout *Oncorhynchus mykiss* and brook charr *Salvelinus fontinalis*; the former does not reproduce and stems from unintentional escape-events from aquaculture net-pens; the latter was intentionally introduced during the 19–20th centuries and established in some tributaries. With respect to historical electrofishing data, Lule River is less surveyed than Ume River (Table 1; SERS 2020). However, the sources of presence/absence data for the catchments include more than electrofishing surveys (Lundberg 1899, Ekman 1922; Widén et al. 2016; GBIF 2020), and the species list is in accordance with recent national distribution maps (Kullander et al. 2012).

For each species, we collected additional information about tolerance, Red List status (classification of the extinction risk of a given species within a specified geographic area), and habitat preference. Tolerance, reflecting species sensitivity to impacts related to altered flow regime, nutrient regime, habitat structure and water chemistry, was based on assignments within the European Fish Index (FAME Consortium 2004; Pont et al. 2006). Red List status was obtained from the most recent lists of Sweden (ArtDatabanken 2020) and Europe (IUCN 2020). Feeding habitat and rheophily were obtained from the freshwater ecology.info database (Schmidt-Kloiber & Hering 2015). We modified the classification of brook charr to rheophilic (eurytopic in the database); this species is eurytopic in its native distribution range in North America (Scott & Crossman 1973), but naturalized Swedish populations are primarily found in headwater streams (Kullander et al. 2012).

2.4. Fish survey methods

Multipass wading electrofishing surveys were conducted once at each site, in autumn (August–September) by professional electrofishing consultants (equipment: straight-DC bank-side aggregates; Lug AB L-1000, Luleå; 700–800 V, 0.3–0.4 A), following Swedish standard practices (the so-called three-pass protocol; Bergquist et al. 2014). In each tributary, one site at the tributary mouth (i.e. near the confluence with the main stem)

Table 2

Surveyed tributaries used in the study. For location, refer to Fig. 1 following the column '# Fig. 1'. Note that three tributaries share the same name; these are arbitrarily numbered for identification. Note that three different tributaries are all named "Kvarnbäcken" and distinguished based on which impoundment they are located in ("S", ".B", and ".V").

Tributary	# Fig. 1	Impoundment	Mouth type	MQ	Width, mouth (m)	Width, 1-km upstream (m)
<i>Ume River</i>						
Kvarnbäcken.S	1	Stornorrfors	Non-aggrading	0.08	1.8	1.5
Gubbölebacken	2	Stornorrfors	Aggrading	0.08	2.0	2.8
Trinnan	3	Stornorrfors	Aggrading	0.67	6.5	9.0
Pengån	4	Stornorrfors	Non-aggrading	1.56	7.5	NA
Stomdalsbacken	5	Bjurfors övre	Aggrading	0.10	2.7	2.1
Vidbäcken	6	Bjurfors övre	Non-aggrading	0.20	8.0	6.0
Kvarnbäcken.B	7	Bjurfors övre	Non-aggrading	0.12	2.5	2.0
Byssjan	8	Bjurfors övre	Aggrading	2.00	20.4	16.8
Nyrningsbacken	9	Bjurfors övre	Aggrading	0.24	1.2	1.0
Illbäcken	10	Bjurfors övre	Non-aggrading	0.29	6.0	3.5
<i>Lule River</i>						
Norbäcken	1	Vittjärv	Non-aggrading	0.22	15.0	2.0
Degerbäcken	2	Vittjärv	Aggrading	0.39	18.0	6.0
Kvarnbäcken.V	3	Vittjärv	Aggrading	0.06	4.0	2.0
Bjurbäcken	4	Vittjärv	Aggrading	0.20	7.0	2.0
Forsträskbäcken	5	Laxede	Non-aggrading	0.45	3.0	3.0
Görjeån	6	Laxede	Aggrading	3.89	25.0	20.0
Lagnäsån	7	Laxede	Non-aggrading	1.52	22.0	5.0
Kistabäcken	8	Porsi	Non-aggrading	0.22	2.0	2.0
Andrensbäcken	9	Porsi	Aggrading	0.49	4.0	4.0
Kanibäcken	10	Porsi	Non-aggrading	0.31	5.0	4.0

Table 3

Summary of historical information on the fish species in the surveyed catchments, and the species general tolerance, Red list status and habitat preference (feeding habitat and rheophily).

Species	Tolerance	Red List status	Habitat	Other	Ume River	Lule River
<i>Abramis brama</i>	Tolerant	S-LC, Eu-LC	B, L		Yes	Yes
<i>Alburnus alburnus</i>	Tolerant	S-LC, Eu-LC	W, L		Yes	Yes
<i>Anguilla anguilla</i>	Tolerant	S-CR, Eu-CR	B, E	D	Yes ^a	Yes ^{a†}
<i>Coregonus albula</i>	Intolerant	S-LC, Eu-LC	W, L		Yes	Yes
<i>Coregonus maraena</i>	Intolerant	S-LC, Eu-VU	W, E		Yes	Yes
<i>Cottus gobio</i>	Intolerant	S-LC, Eu-LC	B, R		Yes	Yes
<i>Cottus poecilopus</i>	Intolerant	S-NT, Eu-LC	B, R		No	Yes
<i>Esox lucius</i>		S-LC, Eu-LC	W, E		Yes	Yes
<i>Gymnocephalus cernua</i>		S-LC, Eu-LC	B, E		Yes	Yes
<i>Lampetra fluviatilis</i>	Intolerant	S-LC, Eu-LC	B, R	D	Yes ^{a†}	No†
<i>Lampetra planeri</i>	Intolerant	S-LC, Eu-LC	B, R		Yes	Yes
<i>Leuciscus idus</i>		S-LC, Eu-LC	W, R		Yes	Yes
<i>Leuciscus leuciscus</i>		S-LC, Eu-LC	W, R		Yes	Yes
<i>Lota lota</i>		S-VU, Eu-LC	B, E		Yes	Yes
<i>Oncorhynchus mykiss</i>		-	W, R	N	Yes ^{a,b}	Yes^b
<i>Perca fluviatilis</i>	Tolerant	S-LC, Eu-LC	W, E		Yes	Yes
<i>Phoxinus phoxinus</i>		S-LC, Eu-LC	W, R		Yes	Yes
<i>Pungitius pungitius</i>	Tolerant	S-LC, Eu-LC	W, L		Yes ^a	Yes
<i>Rutilus rutilus</i>	Tolerant	S-LC, Eu-LC	W, E		Yes	Yes
<i>Salmo salar</i>	Intolerant	S-LC, Eu-VU	W, R	D	Yes ^a	Yes [†]
<i>Salmo trutta</i>	Intolerant	S-LC, Eu-LC	W, R		Yes	Yes
<i>Salvelinus alpinus</i>	Intolerant	S-LC, Eu-LC	W, E		Yes ^c	Yes ^c
<i>Salvelinus fontinalis</i>	Intolerant	-	W, R	N	Yes	Yes
<i>Stizostedion lucioperca</i>		S-LC, Eu-LC	W, E		Yes ^a	Yes
<i>Thymallus thymallus</i>	Intolerant	S-LC, Eu-LC	W, R		Yes	Yes

Red list status: S = Sweden, Eu = Europe, LC = least concern, DD = data deficient, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered; non-native species not considered. Feeding habitat: B = benthic, W = water column; rheophily: R = rheophilic, L = limnophilic, E = eurytopic; other: D = obligate diadromous life cycle, N = non-native.

^a Only recorded outside of the surveyed area.

[†] Migration into the survey area hindered by dam.

^a Historically rare.

^b Non-reproducing.

^c Native to the catchment, but likely stocked within the surveyed area, native populations exists in the alpine region of the river. Record sources: GBIF (2020), Lundberg (1899), Ekman (1922), Widén et al. (2016). Species captured in this study are marked in boldface in their respective river column.

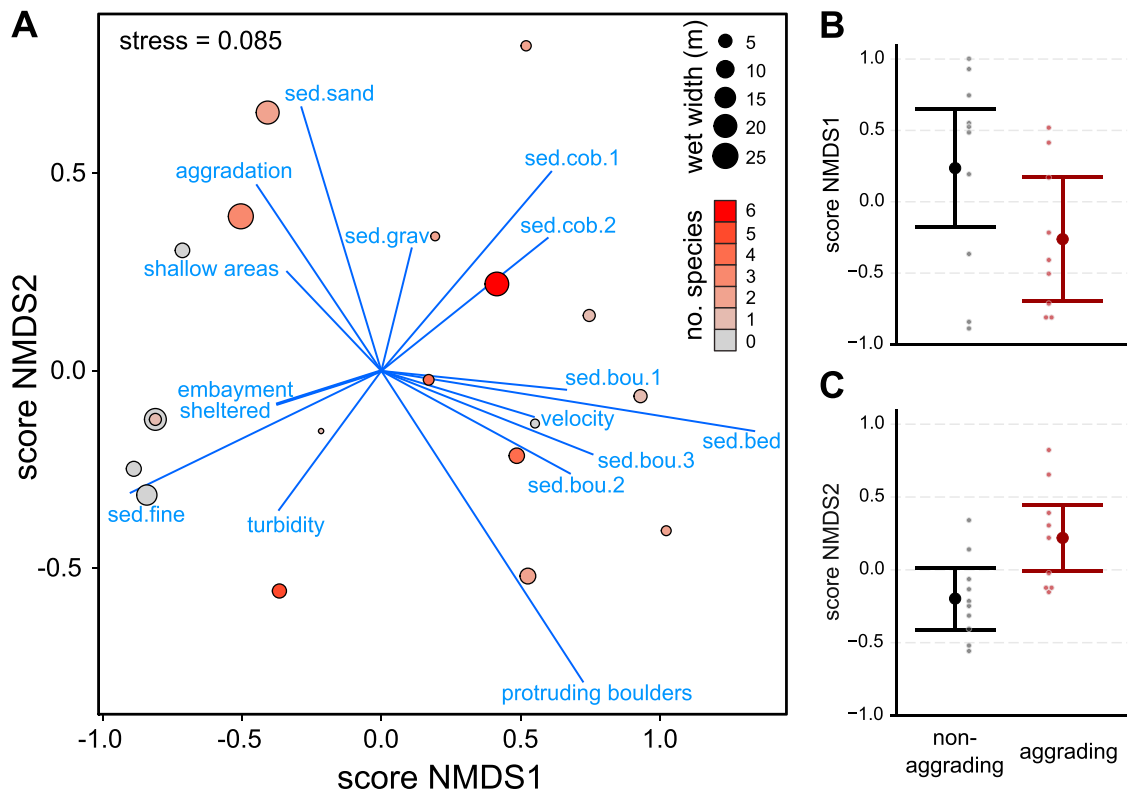


Figure 2. Non-metric multidimensional scaling (NMDS) and its relationship to classified aggradation status in tributary mouth areas. A) NMDS ordination in relation to number of species at each site. B) Relationship between mean score of NMDS1 and aggradation classification. C) Relationship between mean score of NMDS2 and aggradation classification. Error bars show 95% confidence interval. Key to the NMDS: 'sed.[class]' = sediment class on ordinal rank scale (ranks: 0 - absent, 0% coverage; 1 - scant, <5% coverage; 2 - moderate, 5–50% coverage; 3 - ample, >50% coverage; classes: fine = fine sediment <0.2mm; sand = sand 0.2–2 mm; grav = gravel 0.2–2 cm; cob.1 = cobble 2–10 cm; com.2 = cobble 10–20 cm; bou.1 = boulders 20–30 cm; bou.2 = boulders 30–40 cm; bou.3 = boulders 40–200 cm; bed = boulders >200 cm and bedrock); 'aggradation' = binary aggradation classification (0 = non-aggrading; 1 = aggrading); 'protruding boulders' = presence of boulders protruding the surface (0 = no; 1 = yes); 'shallow areas' = presence of shallow areas (0 = no; 1 = yes); 'embayment' = tributary mouth located in a mainstem embayment (0 = no; 1 = yes); 'sheltered' = tributary mouth sheltered from the mainstem flow; 'turbidity' = ordinal rank of turbidity (0 = clear, <1 FNU; 1 = turbid, 1–2.5 FNU; 2 = very turbid, >2.5 FNU); 'velocity' = ordinal rank of flow velocity (0 = slow, <0.2 m s⁻¹; 1 = moderate, 0.2–0.7 m s⁻¹; 2 = rapid, >0.7 m s⁻¹).

and one site located 1 km upstream of the mouth were electrofished. Fished areas ranged between 55 and 760 m², depending on the size of the tributary (smaller areas in smaller tributaries and vice versa; see Fig. S3) and environmental characteristics limiting electrofishing. At sites with deep sections, the survey was limited to the wadable section along one of the banks, in line with Swedish standard methodology. One upstream site remained unfished, as it was too deep for wading when visited. For each electrofishing pass at a given site, all fish caught were counted, identified to species, and measured for length and mass.

2.5. Environmental survey methodology

Coordinated with the electrofishing survey, a standardized environmental survey was conducted at each site, following the Swedish electrofishing protocol (Bergquist et al. 2014). Within this protocol, the dominant sediment types in the top-layer of the bottom substrate are classified by ocular inspection across-channel transects, which are located every 10 meters along the survey site.

From the overall survey site data, the three most dominant sediment classes are summarized into an ordinal scale relating to overall coverage (D1–D3) with associated classification of areal coverage (see figure text to Fig. 2), which provides a coarse but generally accurate picture of the general sediment dynamics (fine scale sediment cover data is, however, not available). In addition, a more detailed investigation of the tributary mouths was made in association to a parallel study on vascular plants in and around the same tributaries (R. Jansson, B. Malm-Renöfält, *in prep.*). Based on field observations, each mouth area was classified as 1) aggrading or non-aggrading, 2) sheltered or non-sheltered, 3) situated in an embayment or not, 4) having boulders protruding above the water surface at low flow or not, and 5) having shallow fine sediment areas (< 1 m deep, from high water level; sand or finer substrate; > 5 m² area) or not. Altitude for each site was obtained from 2-m resolution altitude raster images over each catchment (GSD-Höjddata, grid 2+; The Swedish Mapping, Cadastral and Land Registration Authority, Gävle) in GIS (QGIS 3.16, QGIS Development Team 2021).

Table 4
Factors used in the statistical modelling.

Factor	Abbreviation	Factor type	Levels	Units
River identity	RIVER	Categorical	2 (Ume R., Lule R.)	
Impoundment identity	IMP	Categorical	5 (Table 2)	
Site in tributary	SITE	Categorical	2 (0K, 1K)	-
Tributary identity	TRIB	Categorical	20 levels (Table 2)	-
Fished area	FLAR	Continuous	-	m ²
Channel width	CH.WI	Continuous	-	m
Mean annual discharge	MQ	Continuous	-	m ³ .s ⁻¹
Altitude above main stem	ΔALT	Continuous	-	m
Aggradation at tributary mouth	AGGR	Categorical	2 (yes, no)	-
Habitat; NMDS score, axis 1*	NMDS1	Continuous	-	-
Habitat; NMDS score, axis 2*	NMDS2	Continuous	-	-

* See section: *Statistical analyses: Dimension reduction of habitat variables, and Fig. 2.*

2.6. Data handling and calculations

Density of fish individuals per 100 m² was estimated for each species at each site using the sequential removal model for three passes of removal in the FAS R-package ('Seber3' model) (Seber 1982; Ogle et al. 2020). Fish species density estimates from each site were used to calculate the Shannon Diversity index (H') (Shannon 1948), using the vegan R-package (Oksanen et al. 2019). Shannon's H' is an estimate of the uncertainty of species identity when drawing a random individual (fish) from the data set (fish community at the site) and increases with species abundance and evenness (higher values = higher diversity). Based on H' , Pielou's evenness (J') (Pielou 1966) was also calculated (dividing H' with $H'_{\max}$), as a measure of how close the number of individuals of each species are to each other at a site.

2.7. Statistical analyses

2.7.1. General procedures

All statistical analyses were conducted in R Studio 1.2.5033 (RStudio, Inc., Boston). Types of models are abbreviated as follows: linear models – LM; linear mixed models – LMM; generalized linear models – GLM; and generalized linear mixed models – GLMM. For statistical models with more than a single factor (Table 4), the initial global models specified below were reduced based on the relative Akaike Information Criterion (modified for small sample size; AIC_c) of all subordinate models (including the global model and the intercept-only model), using the MuMIn R-package (Bartoń 2020) to avoid uninfluential factors and thereby increase the residual degrees of freedom. To reduce the risk of excluding influential factors, the most complex model within two AIC_c-units from the most parsimonious model was used for interpretation. When models were run as Poisson-regressions (i.e. for count data), overdispersion was tested using a one-sided DHARMA nonparametric dispersion test (Hartig 2021). If significant overdispersion was indicated, GLMs were re-constructed as quasi-Poisson regressions (Ver Hoef & Boveng 2007) and GLMMs were fitted with an additional observation-level random effect (Harrison 2014). Mixed models were constructed using the lme4 R-package (Bates et al. 2020), marginal means and contrasts were obtained using the

emmeans R-package (Lenth 2021), and data processing and visualization were done within the tidyverse-suite for R (Wickham et al. 2019).

2.7.2. Dimension reduction of habitat variables in tributary mouths

To characterize and summarize habitat features in the tributary mouths, we conducted a non-metric multidimensional scaling (NMDS) analysis, using the vegan R-package (Oksanen et al. 2019). Habitat variables included: i) ordinal ranks of nine different sediment classes, ii) aggradation status (aggrading/non-aggrading); iii) presence/absence of protruding boulders, iv) presence/absence of shallow areas, v) binary classification of embayment, vi) binary classification of whether or not the mouth was sheltered, vii) ordinal rank of water turbidity, and viii) ordinal rank of flow velocity (see Fig. 2 for a key to the variables). We extracted two dimensions ($k = 2$) based on Bray-Curtis dissimilarity. Results were centred and half-scaled, variation was maximized in the first dimension by principal component rotation. Stress-value was derived based on the type I-approach (weak ties).

2.7.3. Nuisance factors for species abundance

Initially, we ran a suite of simple one-factor Poisson-GLMs to investigate factors suspected, based on previous studies, to generally influence species abundance in the catches at the 0K and 1K sites, to make informed decisions on whether or not to include any of the factors in the construction of models specified below. Factors investigated were fished area FLAR (Reynolds et al. 2003), channel width CH.WI (Trigal & Degerman 2015), mean annual discharge MQ (only at 0K) (Dunn & Paukert 2021), and altitude above the main stem ΔALT (only at 1K) (Lipsey et al. 2005); all but ΔALT were log₁₀-transformed. No significant overdispersion was indicated in any model (all $p > 0.064$).

2.7.4. Environmental effects on fish diversity in tributary mouths

Differences in number of species and diversity (Shannon H') between aggrading and non-aggrading tributary mouth areas were tested using Poisson-GLMM/GLM and LMM/LM, respectively. Global models included RIVER, AGGR,

and $\log_{10}(\text{FI.AR})$ as fixed factors and IMP as a random factor (Table 4). Shannon H' values were positively skewed and $\log_{10}$ transformed (Shannon $H' + 1$) prior to analysis, which reduced, but did not eliminate the skew, due to a relatively high number of 0-values; hence interpretation of parameter estimates should be made with caution. The model reduction procedures led to exclusion of RIVER for the species-model (GLMM) and exclusion of RIVER, $\log_{10}(\text{FI.AR})$, and the random factor IMP for the diversity model (turning it from a LMM to a LM) (see supplementary material: Table S1-S2). The final species-model was not significantly overdispersed (dispersion = 0.77, $p = 0.42$).

Broader environmental effects, as described by the two extracted NMDS axes, on number of species caught and diversity (Shannon H') were modelled using Poisson-GLMM/GLM and LMM/LM, respectively. Global models included RIVER, NMDS1, NMDS2, and $\log_{10}(\text{FI.AR})$ as fixed factors and IMP as a random factor (Table 4). The factors NMDS1 and NMDS2 were fitted as second order polynomials and the interaction between NMDS-terms was included [in lme4-syntax: $\text{poly}(\text{NMDS1}, 2) * \text{poly}(\text{NMDS2}, 2)$]. As in previous analyses, Shannon H' values were $\log_{10}$ transformed (Shannon $H' + 1$). The purpose of the modelling was descriptive rather than a test of a specific hypothesis; hence, all terms were allowed to be removed in the model reduction. The final reduced models for both number of species caught and Shannon diversity included $\text{poly}(\text{NMDS1}, 2)$ and $\log_{10}(\text{FI.AR})$. No overdispersion of the reduced Poisson-model was indicated (dispersion = 0.65, $p = 0.80$). For model reduction details, see supplementary material: Table S3-S4.

Absence of a species or presence of only single species led to Pielou's evenness (J') not being applicable to a substantial proportion of the sites ($N = 9$). Therefore, no models were constructed for this index. Instead, Pielou data are graphed in relation to NMDS-scores, with tendencies evaluated based on loess regression and Spearman rank correlations.

2.7.5. Broader environmental effects on fish densities in tributary mouths

Environmental effects, as described by the two extracted NMDS axes, on densities of fish were modelled using LMM/LM. Fish densities were transformed as $\log_{10}(\text{density} + 1)$ and analysed for six different groupings of species: i) all fish species combined, ii) tolerant species, iii) intolerant species, iv) benthic species, v) rheophilic species, and vi) species included in the Swedish Red List (see Table 3 for group classifications). Global models included RIVER, NMDS1, and NMDS2 as fixed factors and IMP as a random factor. NMDS1 and NMDS2 were fitted as second order polynomials, and their interaction was included, as described for previous analyses. All factors were allowed to be removed in the model reduction, see reduction procedure in supplementary material: Table S5-S10. The final reduced models were constructed as follows:

- All species: $\log_{10}(\text{density} + 1) \sim \text{NMDS1} + \text{NMDS2}$
- Tolerant species: $\log_{10}(\text{density} + 1) \sim 1$ (intercept-only)
- Intolerant species: $\log_{10}(\text{density} + 1) \sim \text{poly}(\text{NMDS1}, 2) + \text{RIVER}$

- Benthic species: $\log_{10}(\text{density} + 1) \sim \text{poly}(\text{NMDS1}, 2)$
- Rheophilic species: $\log_{10}(\text{density} + 1) \sim \text{poly}(\text{NMDS1}, 2) + \text{RIVER}$
- Red-listed species: $\log_{10}(\text{density} + 1) \sim \text{poly}(\text{NMDS1}, 2)$

Final models were tested against intercept-only models using likelihood ratio tests to assess their fit to the data. Densities were also investigated specifically in relation to NMDS1 using loess regression.

2.7.6. Differences between tributary mouth and upstream tributary sites

To compare average species richness between 0K and 1K sites within tributaries, a GLMM (Poisson, log-link) was used to model species count as dependent on SITE (fixed factor) and TRIB (random intercept); no overdispersion was indicated (dispersion = 1.08, $p = 0.66$). The same model structure was used in a LMM to model Shannon diversity (H'), using $\log_{10}$ transformed data (Shannon $H' + 1$). Sign tests (two-sided) were used to compare changes (positive or negative) in species richness and Shannon H' for 0K and 1K sites.

3. Results

3.1. Captured fish fauna

In total, 12 species of fish (11 bony fishes and 1 lamprey) were recorded in the surveys (Table 5). In Ume River, 8 species were caught in total, 6 at the 0K-sites and 5 at the 1K-sites; the species caught at most sites were common bullhead *C. gobio* and burbot *L. lota*, each caught at 7 sites (Table 5). In Lule River, 11 species were caught, 9 at the 0K-sites and 8 at the 1K-sites; the species caught at most sites was brown trout *S. trutta*, found at 8 sites (Table 5). Non-native species (rainbow trout *O. mykiss* and brook charr *S. fontinalis*) were only caught in the Lule River system, and only at one 1K-site each; *O. mykiss* ($N = 1$; 204 mm TL) likely originated from an aquaculture net-pen in an upstream lake and *S. fontinalis* ($N = 37$) were naturalized, as indicated by the presence of age 0+ individuals (51–68 mm TL).

3.2. Dimension reduction of habitat variables in tributary mouths

A two-dimensional ordination of environmental variables in the tributary mouth areas resulted in a final stress value of 0.085, indicating a good ordination in combination with the Shepard plot derived from the analysis (Fig. S1; Clarke 1993). The first NMDS axis (NMDS1) largely ordered sites along a substrate size and water velocity gradient, with high values being associated with large substrate sizes and high velocity, and low values with small-sized substrate (Fig. 2A). Other features like turbidity, shallow areas, and embayment, to some extent loaded in the same direction as small substrates, as did the binary classification of aggradation status. Modelling NMDS1-scores as dependent on binary classified aggradation status revealed that NMDS1 did not differ significantly between sites classified as aggrading and non-aggrading, although

Table 5

Species caught in Ume- and Lule River, based on the number of OK (tributary mouth) and 1K (1-km upstream) sites containing each species and the total number of individuals caught.

Species	Ume River				Lule River			
	OK sites (N)	1K sites (N)	OK ind. (N)	1K ind. (N)	OK sites (N)	1K sites (N)	OK ind. (N)	1K ind. (N)
<i>Cottus gobio</i>	3	4	26	26	1	1	12	1
<i>Cottus poecilopus</i>	0	0	0	0	3	1	27	2
<i>Esox lucius</i>	1	0	1	0	1	1	1	1
<i>Lampetra planeri</i>	2	1	2	1	0	0	0	0
<i>Lota lota</i>	6	1	8	1	2	0	2	0
<i>Oncorhynchus mykiss</i>	0	0	0	0	0	1	0	1
<i>Perca fluviatilis</i>	3	0	7	0	1	0	1	0
<i>Phoxinus phoxinus</i>	3	0	12	0	3	2	24	21
<i>Rutilus rutilus</i>	0	0	0	0	1	0	5	0
<i>Salmo trutta</i>	0	2	0	18	4	4	90	129
<i>Salvelinus fontinalis</i>	0	0	0	0	0	1	0	37
<i>Thymallus thymallus</i>	0	1	0	1	2	2	44	56

a tendency for aggrading sites having lower values was seen (ANOVA: $F_{1,17} = 3.06$, $p = 0.098$; Fig. 2B). The second NMDS axis (NMDS2) was mainly described by the presence of protruding boulders loading in the negative direction of the axis, and sandy to small cobble substrates and aggradation status loading in the positive direction of the axis (Fig. 2A). Modelling NMDS2-scores as dependent on their binary classified aggradation status revealed that NMDS2 significantly differed between sites classified as aggrading and non-aggrading (ANOVA: $F_{1,17} = 8.04$, $p = 0.011$; Fig. 2C).

3.3. Nuisance factors for species abundance

For OK-sites, channel width did not have a significant effect on the number of species caught [$\log_{10}(\text{CH.WI})$: $z = 1.494$, $p = 0.135$], but mean annual discharge and fished area had positive effects [$\log_{10}(\text{MQ})$: $z = 2.802$, $p = 0.005$; $\log_{10}(\text{FLAR})$: $z = 1.987$, $p = 0.047$] (Fig. S2A–D). For 1K-sites, channel width and fished area had significant effects on number of species caught [$\log_{10}(\text{CH.WI})$: $z = 2.319$, $p = 0.020$; $\log_{10}(\text{FLAR})$: $z = 3.162$, $p = 0.002$], but altitude (in relation to the mainstem) did not (ΔALT : $z = -0.924$, $p = 0.356$) (Fig. S2E–H). Looking at all sites combined, channel width, mean annual discharge, and fished area were all strongly correlated with each other (all $r > 0.7$, all $p < 0.05$; Fig. S3). Hence, these three variables appear to largely represent the same thing (i.e. size of the tributary), and since fished area consistently had a positive effect on number of species caught, this variable was used in the more detailed modelling.

3.4. Environmental effects on fish diversity in tributary mouths

Models investigating effects of binary aggradation status of the tributary mouth area indicated no statistically significant effects on number of species (ANODEV; AGGR: $\chi^2 = 0.26$, $p = 0.61$; $\log_{10}(\text{FLAR})$: $\chi^2 = 1.67$, $p = 0.20$; Fig. S4a). Similarly, no significant effect on diversity, as indicated by Shannon H' , was found (ANOVA; AGGR: $F_{1,18} = 0.45$, $p = 0.51$; Fig. S4b).

The model for number of species indicated significant effects of the second-order polynomial term $\text{poly}(\text{NMDS1}, 2)$ ($\chi^2 = 15.8$, $p < 0.001$) and $\log_{10}(\text{FLAR})$ ($\chi^2 = 5.26$, $p = 0.022$). Parameter estimates indicated a concave down relationship between number of species caught and NMDS1 (Fig. 3A; parameter estimates: $\beta_{\text{intercept}} = -3.43$, $\beta_{\text{NMDS1:1}} = 2.26$, $\beta_{\text{NMDS1:2}} = -2.94$, $\beta_{\log_{10}(\text{FLAR})} = 1.56$). As the first axis of the NMDS generally relates to substrate classes and their associated habitat characteristics, the pattern suggests that the intermediate substrate size is associated with the highest number of species. The number of species caught also increases with fished area, as also indicated in the previous analyses. The factor NMDS2 was not retained after model reduction, indicating that it is not influential on the number of species present (see relationship in Fig. S5A).

The model for Shannon diversity (H') also indicated significant effects of the second-order polynomial term $\text{poly}(\text{NMDS1}, 2)$ ($F_{2,15} = 5.49$, $p = 0.016$) and $\log_{10}(\text{FLAR})$ ($F_{1,15} = 5.71$, $p = 0.030$). Parameter estimates indicated a concave down relationship with NMDS1 (Fig. 3B; parameter estimates: $\beta_{\text{intercept}} = -0.47$, $\beta_{\text{NMDS1:1}} = 0.25$, $\beta_{\text{NMDS1:2}} = -0.28$, $\beta_{\log_{10}(\text{FLAR})} = 0.25$). In accordance with number of species, the pattern suggests that intermediate substrate size is associated with higher diversity, and increased diversity with fished area. The factor NMDS2 was not retained after model reduction (see relationship in Fig. S5B). Pielou's evenness (J') was not significantly rank-correlated with any of the investigated environmental variables [NMDS1, NMDS 2, FLAR, and CH.WI], with all Spearman rank correlations having $p > 0.46$ (see Fig. S6 for details and visualization of loess-regressions).

3.5. Broader environmental effects on fish densities in tributary mouths

For the model of total fish density (all species combined), the factor NMDS1 was significant, indicating increasing density with increasing values of NMDS1 (Fig. 4A), while NMDS2 was non-significant (Table 6). Based on the loess regression fit, the significant positive relationship appears largely driven by low fish densities in sites dominated by fine sediment, with associated environmental fea-

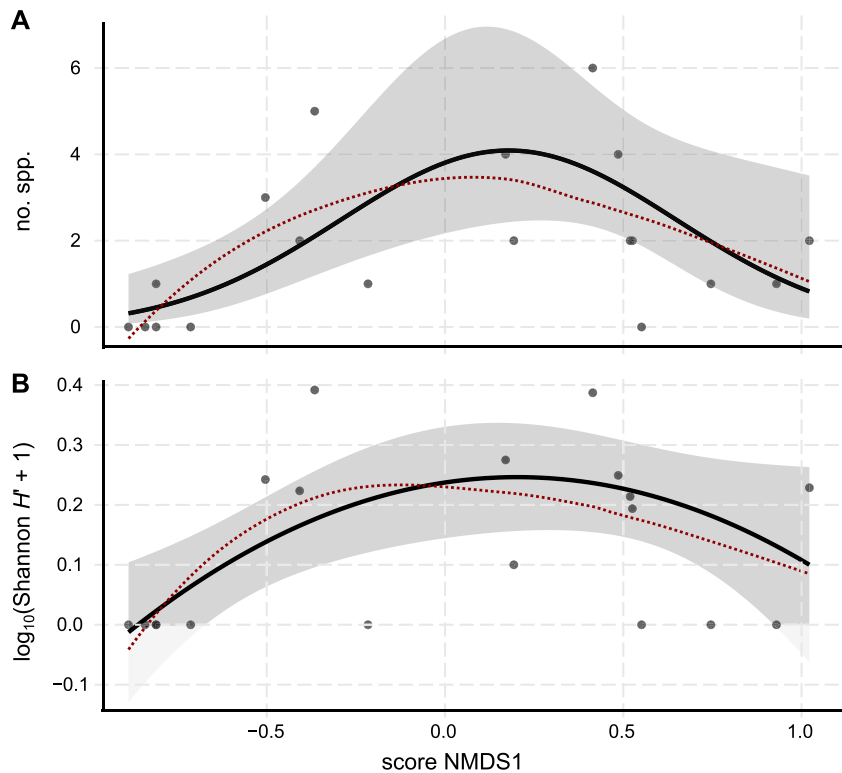


Figure 3. A) Effect of the first NMDS axis (NMDS1) scores on the number of species caught. Black line shows the modelled effect from a Poisson GLM, with 95% confidence bands in grey. Red dotted lines show a loess regression on raw data.

Table 6
Summary of analyses of fish densities, with model fit (comparison with intercept-only model), significance of model terms, and parameter estimates from the linear models.

Group	Model fit	Model terms			Parameter estimates		
		Term	F	p	Parameter	β (SE)	p
All	$p = 0.020$	INTERCEPT	31.63	<0.001	INTERCEPT	0.783 (0.139)	<0.001
		NMDS1	6.38	0.022	NMDS1	0.552 (0.219)	0.022
		NMDS2	1.47	0.242	NMDS2	0.461 (0.379)	0.242
Tolerant	-	INTERCEPT	23.87	<0.001	INTERCEPT	0.783 (0.160)	<0.001
Intolerant	$p < 0.001$	INTERCEPT	31.68	<0.001	INTERCEPT	0.978 (0.174)	<0.001
		poly(NMDS1,2)	6.60	0.009	poly(NMDS1,2)1	1.832 (0.550)	0.005
					poly(NMDS1,2)2	-0.900 (0.550)	0.123
		RIVER	10.01	0.006	RIVER (Ume)	-0.822 (0.260)	0.006
Benthic	$p = 0.004$	INTERCEPT	19.47	<0.001	INTERCEPT	0.416 (0.094)	<0.001
		poly(NMDS1,2)	5.65	0.014	poly(NMDS1,2)1	0.635 (0.411)	0.142
					poly(NMDS1,2)2	-1.227 (0.411)	0.009
Rheophilic	$p < 0.001$	INTERCEPT	39.05	<0.001	INTERCEPT	1.072 (0.172)	<0.001
		poly(NMDS1,2)	7.74	0.005	poly(NMDS1,2)1	1.797 (0.543)	0.005
					poly(NMDS1,2)2	-1.257 (0.543)	0.035
Red-listed	$p = 0.037$	RIVER	10.61	0.005	RIVER (Ume)	-0.835 (0.257)	0.005
		INTERCEPT	12.46	0.003	INTERCEPT	0.265 (0.075)	0.003
		poly(NMDS1,2)	3.29	0.063	poly(NMDS1,2)1	0.242 (0.327)	0.470
					poly(NMDS1,2)2	-0.804 (0.327)	0.026

Note that estimates for polynomial terms [poly()] relate to orthogonal polynomials.

tures (i.e. sites with the lowest values on the NMDS1-scale). For all other sites, no apparent trend was indicated in the loess fit (Fig. 4A).

For tolerant species, only four sites had tolerant species present (Fig. 4B), which is inadequate for modelling the influence of environmental factors. The model selection procedure ended with selection of the intercept-only

model, and hence, no factors were specifically investigated (Table 6).

In the model of intolerant species density, the polynomials of NMDS1 and RIVER were retained in the model selection procedure (which was designed to allow for some model complexity; not always selecting the most parsimonious model) and both terms were significant. Parameter

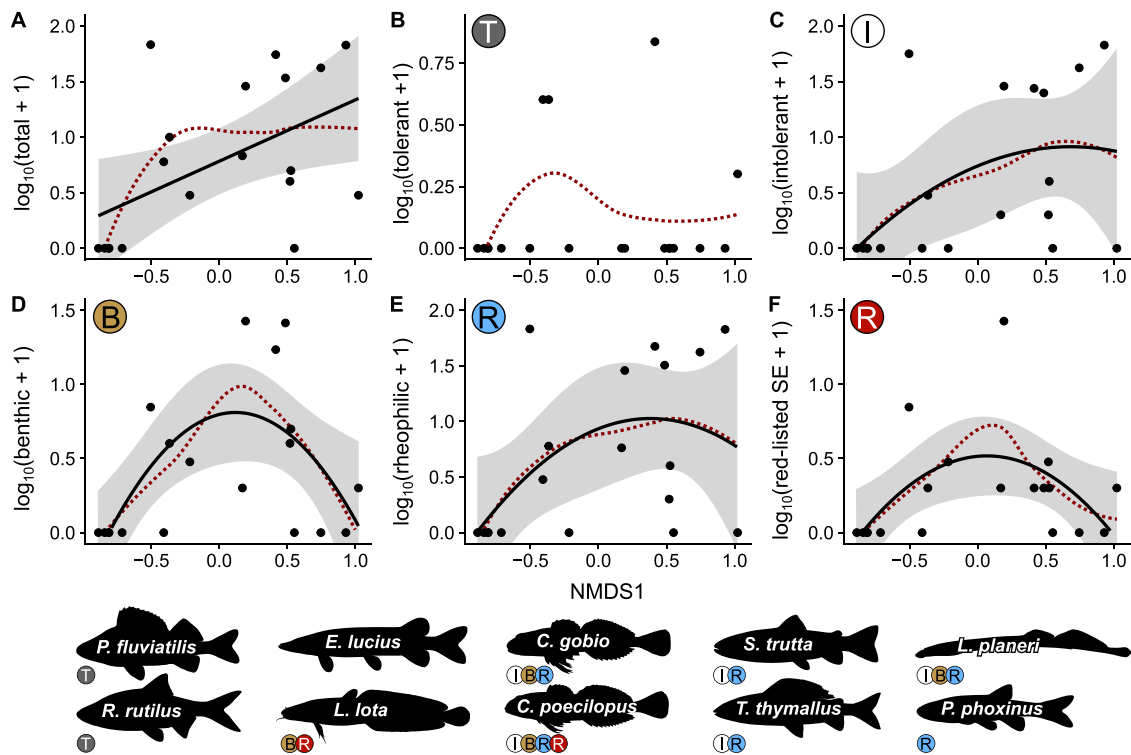


Figure 4. Densities of different fish guilds (including lampreys) along the first NMDS axis (finer to coarser substrate, from left to right): A) total density of fish, B) density of tolerant species, C) density of intolerant species, D) density of benthic species, E) density of rheophilic species, F) density of species listed in the Swedish Red List (Artdatabanken 2020). Black lines: regression lines from linear models, with grey-shaded areas representing the 95% confidence band (not provided in B; tolerant species were only present at four sites). Red dotted lines: loess regression lines based on raw data. Species present in the data illustrated with silhouettes, scientific name and the categories to which they belong (labels under the silhouettes matching labels in the graphs).

estimates, however, indicate that the polynomial relationship with NMDS1 is not significantly different from a linear fit (Table 6; Fig. 4C). This is supported by the fact that neither a likelihood ratio test (LRT) nor AIC_c -comparisons indicate that the fit of the polynomial model is significantly better than a linear fit (LRT: $p = 0.102$; $\Delta AIC_c = 0.64$). Loess regression suggests that the fit may be driven largely by a lack of intolerant species in the sites with the lowest NMDS1-scores. For sites with higher NMDS1-scores (> -0.5), there is no trend, and intolerant species' densities vary substantially throughout this range (Fig. 4C). Ume River had a lower fish density in general (Table 5).

Density of benthic species showed a concave down relationship with NMDS1 (Table 6; Fig. 4D). This pattern was also supported by the loess regression.

Density of rheophilic species was modelled using a polynomial function of NMDS1, and this model indicated a potential concave down relationship (Table 6; Fig. 4E). While the polynomial fit is not obviously different from a positive linear fit, both LRT and AIC_c comparisons of the models indicate that the fit of the polynomial model is significantly better (LRT: $p = 0.021$; $\Delta AIC_c = 2.04$). Similar to density of intolerant species (which constitute a subset of the rheophilic species), assessment of the loess regression suggests that the fit can be driven largely by the lack of rheophilic species in the sites with the lowest NMDS1-scores. An effect of RIVER was also detected, with

Ume River having a lower density of rheophilic species (Table 6).

Density of red-listed species followed the same concave down relationship with NMDS1 as the density of benthic species (Table 6; Fig. 4F). This result is consistent with the fact that red-listed species constitute a subset of the benthic species.

From a local conservation perspective, presence of specific species in relation to habitat characteristics can be of importance. Hence, we present a graphical representation of each species caught within this study in the Appendix (Fig. A1).

3.6. Differences between tributary mouth- and upstream sites

Neither species richness nor Shannon diversity differed significantly between 0K- and 1K sites (species richness: $z = -1.542$, $p = 0.123$; Shannon H' : $t = -1.546$; $p = 0.139$; Fig. 5). Based on preliminary analyses of possible nuisance factors (see above), altitude was not considered in the models and further support for this decision is found in the lack of a correlation between the change in species richness or Shannon H' and the change in altitude ΔALT between 0K- and 1K sites (species richness: $r = -0.267$, $p = 0.269$; Shannon H' : $r = -0.173$, $p = 0.479$). Sign tests comparing general patterns of increase or decrease be-

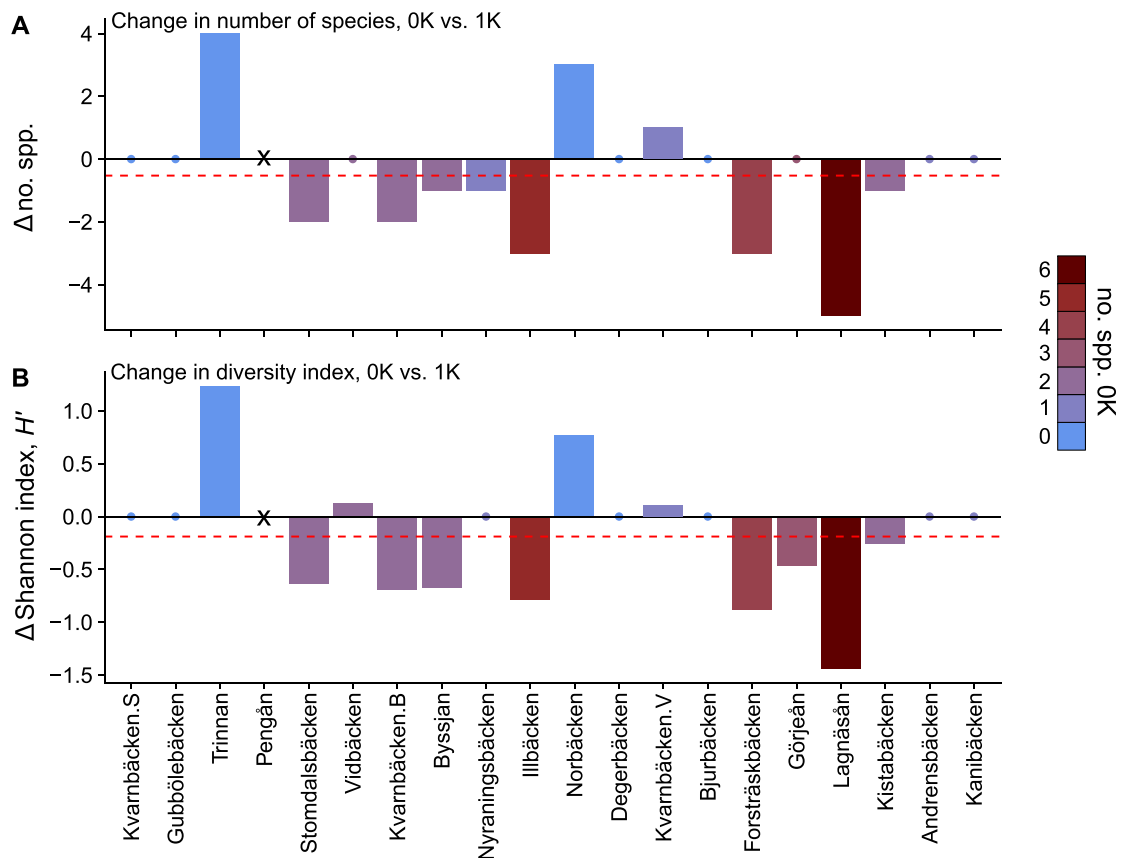


Figure 5. Comparison between sites located at the mouth of tributaries (0K) and sites located ca. 1 km upstream these tributaries (1K). A) Difference in species richness. B) Difference in Shannon index (diversity). Positive values indicate an increase from 0K- to 1K-sites and negative values indicate a decrease. Color scale represents number of species at the 0K sites. Red dashed lines show the arithmetic mean difference. In Pengån, no 1K site could be sampled (marked 'X').

tween 0K- and 1K sites did not indicate any significant differences (species richness: $z = 1.508$, $p = 0.132$; Shannon H' : $z = 1.155$; $p = 0.248$; Fig. S7), in line with the GLMM/LMM analyses above. Generally, the species present at the mouth of the tributary were not the same species as encountered upstream (Fig. A2). Regressing change in species richness as dependent on the species richness at the 0K site gives a slope of -0.87 (95% CI: $-0.50 - -1.23$), which suggests a strong regression-to-the-mean effect, which could be due to a more or less random distribution of data for 0K and 1K sites (e.g. Barnett et al. 2005).

4. Discussion

The overall number of fish species present in the catchment areas of the rivers is substantially higher than the numbers observed in the tributary surveys (typically, only 2 or fewer species were detected at each tributary site). Hence, the species diversity observed in the tributaries areas, as indicated by the electrofishing catches, does not support the notion that tributaries are hot-spots for fish species diversity. Nevertheless, when environmental conditions are favorable, these areas may still be important for

the biodiversity and ecology of the river systems for other reasons, which we discuss below.

4.1. Fish biodiversity in relation to habitat characteristics

Tributary mouths characterized by intermediate sediment-sizes (gravel-cobble) had the highest α -diversity (species richness) of fish. The Shannon diversity index, which incorporates the relative abundance of the species present, showed a similar pattern, although not statistically significant. Areas dominated by the intermediate substrate sizes also tended to harbor higher densities of benthic species, which generally may be favored by high environmental complexity (possibly with the exception of brook lamprey *L. planeri*, which bury in finer sediments). In line with this observation, the two red-listed species (Artdatabanken 2020), burbot *L. lota* (VU) and alpine bullhead *C. poecilopus* (NT), both benthic species, showed higher densities at intermediate substrate sizes. While abiotic effects often dictate the ecological community in freshwater ecosystems (Jackson et al. 2001), a similar study from a more species-rich river system in central Europe found no clear detectable effects of habitat

structure on species richness (Czeglédi et al. 2016). The difference in effects suggests that the importance of local habitat may differ depending on biogeographical factors (Grenouillet et al. 2004) and extrapolation of results outside of the investigated geographic region may be difficult.

Our initial classification based on aggradation status, i.e. presence/absence of sediment plumes at the tributary mouth, did not relate to any clear statistical differences in fish diversity. This classification mainly predicted the pattern on the second NMDS axis (NMDS2), and analyses including NMDS2 instead of the binary aggradation class did not suggest any relationship between this axis and species richness or Shannon H' .

4.2. Fish abundance

Densities of fish in general increased with coarser substrate, but it is not clear whether densities increase continuously with increasing sediment size (NMDS1 value), or if there is a non-linear saturating or step-wise effect where densities increase from fine sediments to gravel substrate, and then remain at a stable level with increasing substrate size (as indicated by the non-linear loess regression in Fig. 4A). In many cases, non-linear effects in response to habitat complexity are expected (Soukup et al. 2022), but more detailed investigations are needed to resolve this question. Species contributing to high densities in coarser-substrate tributary mouth areas were rheophilic and intolerant to anthropogenic impacts (these two guilds have largely overlapping species composition; Pont et al. 2006; Schmidt-Kloiber & Hering 2015). When large-sized substrates dominate, stream power (streamflow $\times$ slope) is typically higher as compared to when smaller substrates dominate (Lane 1955), which can explain why occurrence of rheophilic species is higher at sites with higher values of NMDS1 (i.e. characterized by larger substrate).

With regards to two rheophilic taxa of national management concern, the bullheads (*C. poecilopus* and *C. gobio*) and brown trout (*S. trutta*), we noted that the former are found at their highest densities at intermediate NMDS1 values (cobble to gravel, or even sandy habitats), while the latter have their highest densities at high NMDS1 values (i.e. boulder habitats). These patterns fit with previous observations in Norwegian subalpine rivers (Hesthagen et al. 2004). The differences in habitat preference for these two taxa, which both are important for environmental management, illustrate the importance of maintaining environmental variation across sites.

Predominantly limnophilic species were not common in this study, not even in slow-flowing tributary mouths dominated by finer substrates. Slow-flowing sites were generally shallow over substantial areas so, for limnophilic species, the main stems or lakes may be more suitable as habitats within the river systems. Moreover, it was not possible to electrofish deep areas when they occurred, and this may be biasing our results as indicated in other studies (Cooke et al. 2012). Limnophilic species may also be more mobile, only inhabiting tributary mouth areas temporarily, which decreases the probability of being caught during single electrofishing surveys. Seasonal and diel

changes in habitat-specific species composition have been described in several river systems (Copp & Jurajda 1999; Nunn et al. 2010; Salas & Snyder 2010). Hence, a sampling over a broader period of time might have produced a different picture of fish biodiversity in tributary mouths.

4.3. Fish α - and γ -diversity in broader context

The number of fish species found in each tributary mouth ranged between 0 and 6 (typically 2 or fewer), indicating a generally low α -diversity compared to the overall number of species known to be present in the river systems (Table 3). At sites located 1 km upstream of the tributary mouths, species richness ranged between 0 and 4, but without any clear decline within a given tributary. Furthermore, the species present generally differed between the mouth and the upstream site in the tributaries. Hence, the species found in the upstream areas are not typically a subset of the species present in the mouth-area, but may constitute a different type of community. To some extent, these findings contrast with results from central Europe, where a decline in tributary fish α -diversity could be detected from the mouth to sites located 1 km upstream (Czeglédi et al. 2016), but studies over a larger geographic area are probably needed to draw such a conclusion.

Low species richness likely reflects the overall γ -diversity in these boreal rivers. Only 24 species in total are known from the two investigated river systems (Table 3), out of which four are not expected in the survey areas due to downstream migration barriers (*A. anguilla*, *S. salar*, *L. fluviatilis*) or alpine distributional limits (*S. alpinus*). Considering that the α -diversity at a given tributary mouth area constitutes only 0–30% of the expected γ -diversity and that no systematic differences were found between mouth and upstream sites, it is nevertheless questionable, at best, whether the tributary mouth areas can be considered biodiversity hot-spots for fish in these river systems. These results contrast with studies from e.g. Neotropical rivers, where tributaries are often found to be hot-spots for fish diversity (Marques et al. 2018; Azevedo-Santos et al. 2020; Vasconcelos et al. 2021; da Luz Soares et al. 2022). However, the Neotropical rivers have a much higher taxonomic richness and functional specialization of fishes overall, due to comparatively long historical stability (on an evolutionary time scale) (Rodrigues-Filho et al. 2018), which may explain the differences.

4.4. Caveats and future research requirements

The present study focuses on tributary mouth fish diversity in impounded boreal rivers in Sweden, as assessed from electrofishing surveys. As such, the study constitutes an initial insight into the fish diversity in these areas, but some key information is still missing – especially for designing appropriate management action. For instance, the study does not provide information about the biodiversity in unimpacted reference systems. To gain this knowledge future studies could survey the tributaries in the few remaining unimpacted boreal rivers (or river sections) in Europe. Surveys in the present study did not include biodiver-

sity in the main stems, due to lack of comparable methods between shallow tributaries and deep habitats in the main stem. Boat electrofishing could be considered in future studies, but differences in species-specific capture bias between wading- and boat electrofishing present a large problem for comparisons. Furthermore, efficient boat electrofishing is only possible to a depth of a couple of meters, making it difficult to survey the main stem fish fauna representatively. Hence, our conclusion that the tributary mouth areas are not hot-spots for fish biodiversity in these two regulated rivers is based on a general qualitative comparison with the overall number of species known to be present in the main stems.

Surveys conducted at different times is another focus area that could be approached in future studies to improve our knowledge about the importance of tributary mouth areas as habitat. Many juvenile species use the shallower habitats mainly at night (Copp & Jurajda 1999), and given that we only have survey data from daytime here, information about this is currently lacking. These studies would likely require a different survey method since wading electrofishing at night can be hazardous. Environmental DNA metabarcoding surveys could detect more species, but detailed studies of tributary mouth biodiversity may be obscured by DNA contamination from upstream sections (David et al. 2021). Nevertheless, eDNA metabarcoding may give insights into short-term changes in species presence. Other survey methods like e.g. snorkeling transects, trapping, or possibly seining may be better suited; all of which, however, may be primarily applicable in deep, slow-flowing, areas. Similarly, we do not have information about usage of these habitats during spring, summer, or winter, and seasonal differences have at least been detected in a similar study from a more species-rich system in central Europe (Czeglédi et al. 2016). Future studies, extending on the present results, should incorporate a wider temporal coverage.

4.5. Management considerations

While tributary mouth areas in general were found to be relatively species-poor, several rheophilic species found in these areas are disfavored in impounded rivers since their typical habitats, riffles and rapids, are often either inundated, or completely or partially dried out when eliminated, modified, or bypassed by hydropower infrastructure (Malm Renöfält et al. 2010; Göthe et al. 2019; Widén et al. 2021). To maintain as high ecological potential as possible in these river systems, natural tributary mouths characterized by flowing habitats and medium to large sediment substrate could be protected from further anthropogenic impacts, as they may constitute near-main stem refuges for rheophilic species. Where degraded (e.g. by dams or culverts near the confluence), these types of habitats could also be rehabilitated or restored. These actions would be in line with the European Water Framework Directive (Directive 2000/60/EC) and national river restoration goals associated with the European Biodiversity Strategy for 2030.

To promote the currently red-listed species present in the area, *L. lota* and *C. poecilopus*, habitat measures

may consist of ensuring a medium-sized sediment habitat. Habitat restoration efforts in Swedish boreal rivers typically promote brown trout habitats (i.e. coarser-sediment habitats) (Degerman & Näslund 2021), which might disfavor bullhead given the apparent competition between trout and bullheads (Hesthagen et al. 2004). Tributary mouth areas could possibly be appropriate target areas for (re-)creating intermediate sediment-size habitats, and trout may instead be targeted in the upstream areas of the tributaries. Also the burbot might find a refuge from negative temperatures, flows- and pollution in the main stem (Stapanian et al. 2010; Dugdale et al. 2013; Koizumi et al. 2013; Artdatabanken 2020; Wang et al. 2020).

To promote γ -diversity in river systems at large, we need to collect and compile knowledge about the diversity patterns in these rivers, e.g. how different species are distributed through river networks. It could, in fact, be important to maintain a range of different types of tributary mouths to benefit a wide variety of species with different habitat requirements. Management activities must also consider other taxa than fish, including invertebrates, plants, semi-aquatic vertebrates, etc., in both the aquatic environment and the riparian zone. Restorative measures gain cumulative value if considered on a catchment scale rather than local efforts (Gann et al. 2019; Cid et al. 2022). Therefore, when a pristine reference state is unachievable, a combination of measures could be suggested. For example, reconstruction of road culverts at the tributary mouth will likely lead to a more natural flow regime with associated sediment dynamics (Widén et al. 2016), and recreating natural stream morphology with riparian zones in currently straightened and channelized sections of tributaries will likely reduce erosion and unnatural transport of fine sediment to the tributary mouths (Beschta & Platts 1986). Both measures may also help retain the water in the tributary to avoid negative effects of drought on the ecosystem.

5. Conclusions

With this study, we have gained information about the diversity of fish in tributary mouth areas within large impounded boreal river systems. We found that fish species richness and diversity were relatively low but variable, with variation being primarily explained by habitat features related to sediment grain size. Highest diversity was found in mouths with intermediate grain size (gravel-cobble). Fine sediment habitats often contained few, if any, fish species during the time of our surveys. The species composition at the mouth was generally not the same as upstream the tributary, nor were the species present upstream a subset of the species at the mouth. Overall, we find no clear evidence supporting that the tributary mouth areas are biodiversity hot-spot for fishes in relatively species-poor regulated boreal rivers.

Data Availability Statement

Data from the electrofishing surveys are deposited in the Swedish Electrofishing Register (<http://www.slu.se/elfiskeregistret>). Collated data sets used for analyses and R code are deposited in the figshare database: <https://>

doi.org/10.6084/m9.figshare.20103155 <https://figshare.com/s/1c373beb5b0ba497f9bc>.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that

could have appeared to influence the work reported in this paper.

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Appendix

Figures A1 and A2

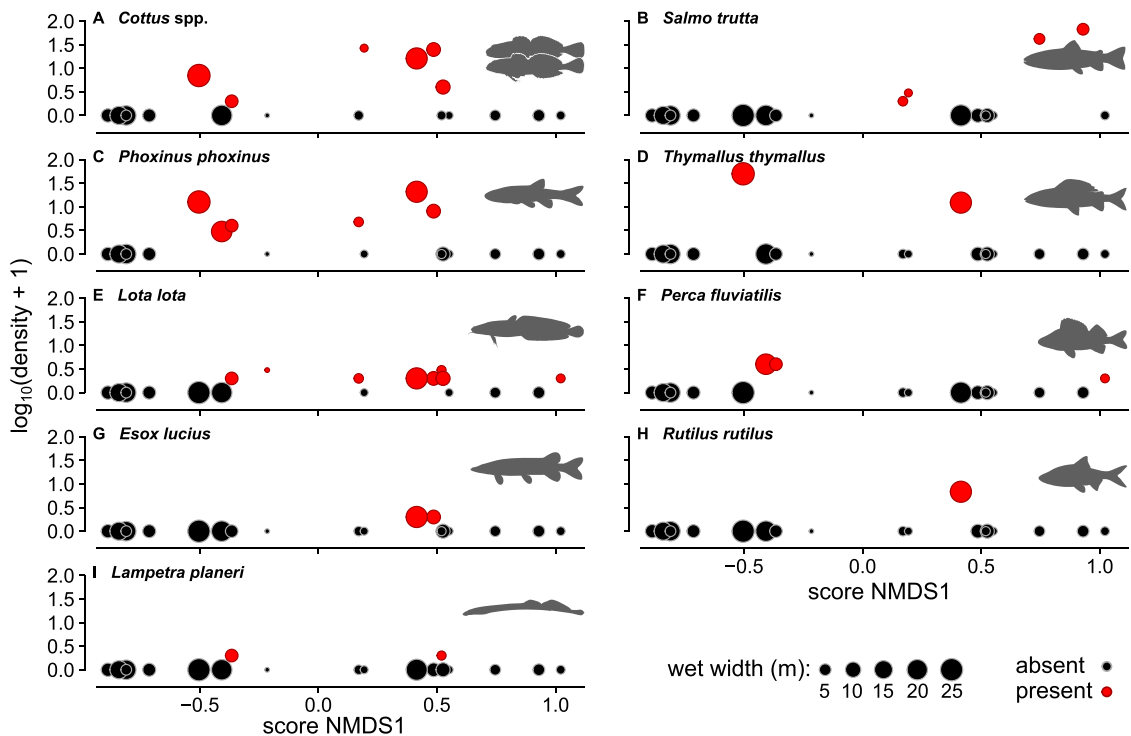


Figure A1. Density estimates of the different fish species caught in the tributary mouth areas, in relation to the first NMDS axis (x-axis) and wet width of the tributary at the mouth (size of the dots). Densities for *Cottus gobio* and *C. poecilopus* were pooled due to similar autecology, but only partially overlapping distribution.

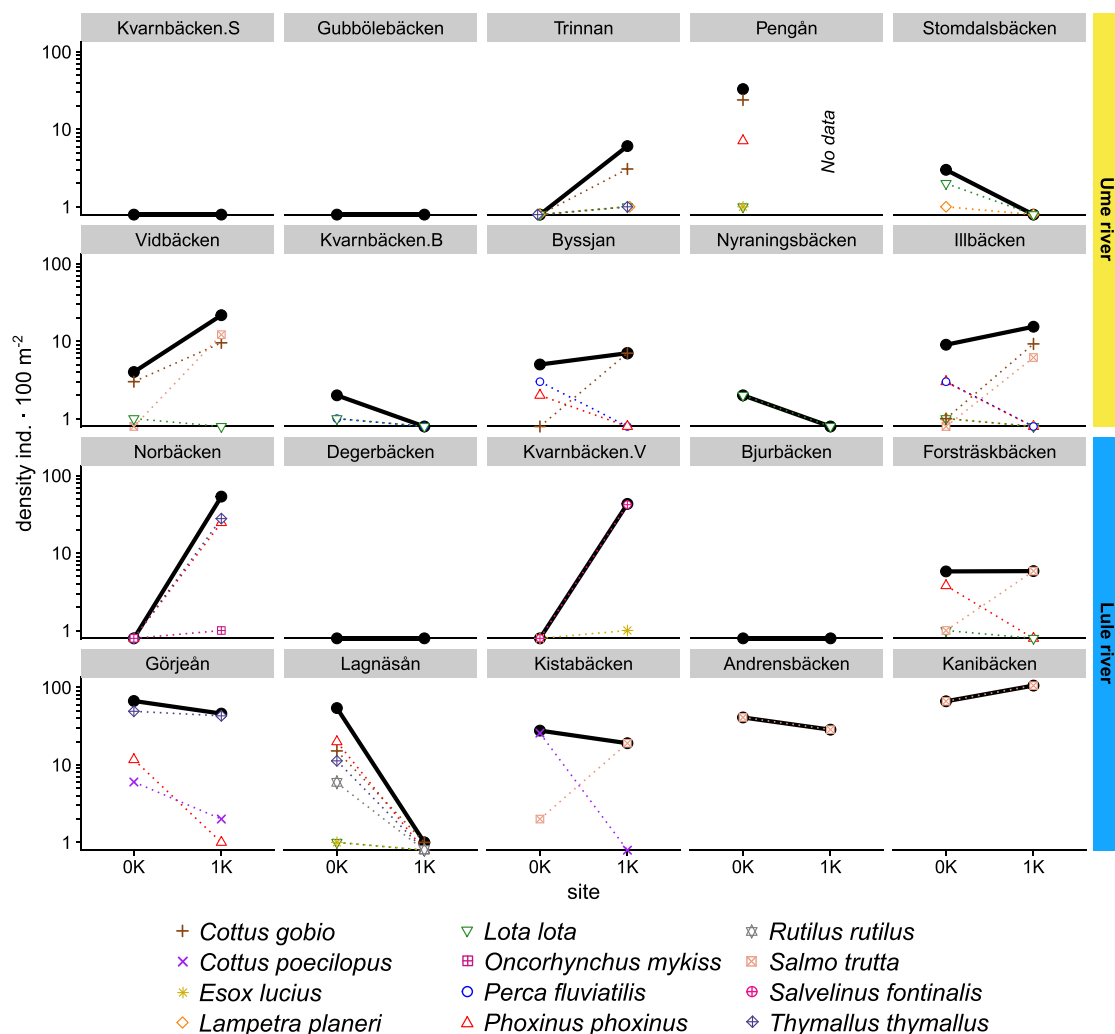


Figure A2. Densities of fish in the surveyed tributaries, at the tributary mouth (0K) and 1 km upstream the mouth (1K). Black symbols show total fish density and colored symbols show each individual species caught. Species with no catches at either site in a given tributary are not shown. Note that the y-axes are logarithmic.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.ecohyd.2022.11.004](https://doi.org/10.1016/j.ecohyd.2022.11.004).

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