



Eurasian minnow (*Phoxinus phoxinus*) in brown trout (*Salmo trutta*) nursery streams

Impacts on juvenile trout life history, trophic position, density and prey availability in the Abisko area

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Elritsa (Phoxinus phoxinus) i öringens (Salmo trutta) uppväxtområden. Inverkan på livshistoria, trofisk position, täthet och bytestillgänglighet för juvenil öring i Abiskoområdet.

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Abstract

Eurasian minnow (*Phoxinus phoxinus*) are spreading into brown trout (*Salmo trutta*) lakes in the Swedish Arctic due to bait releases from anglers or possibly due to habitat improvement induced by climate change. Previous studies have shown that introduced minnow can negatively affect trout through resource and habitat competition and predation. We investigated lake-adjacent trout nursery streams in the Abisko area where minnow are colonizing lake systems. My aim was to uncover possible impacts of the newly established minnow on trout growth, age structure, condition, density, trophic position and niche width, as well as impacts on the prey community. We electrofished several lake inlets and measured weight and length of the caught trout and minnow. We also collected macroinvertebrates. I analyzed trout otoliths for age estimation and conducted a stable isotope analysis to assess trout and minnow diets. I found that trout in stretches where minnow were present had a shorter length-at-age at 3+ and possibly 4+ than trout in allopatry, suggesting slower growth. I found multiple tendencies that hint at further influences of minnow on trout, e.g. differing age structures between stretches with and without minnow, which indicate that trout in sympatry leave their nursery streams earlier. There also seems to be a tendency for fewer rare macrobenthos taxa in the presence of minnow, which suggests an influence of minnow on trout prey. I could not confirm an influence of minnow presence on trout condition, density or prey size, possibly due to the small sample size ($n = 7$). This thesis can serve as the foundation for a long-term study with more investigated streams that could reveal if minnow have a more severe impact on trout in this area.

Keywords: Abisko, brown trout, competition, Eurasian minnow, invasion, otoliths, *Phoxinus phoxinus*, *Salmo trutta*, stable isotope analysis, stream

Table of contents

List of tables	i
List of figures	ii
Abbreviations	iv
1. Introduction	1
2. Materials and Methods	4
2.1 Study area.....	4
2.2 Data collection.....	4
2.2.1 Stretch selection	5
2.2.2 Electrofishing	5
2.2.3 Macroinvertebrate and benthic algae for SIA	6
2.2.4 Macroinvertebrates for resource levels	6
2.2.5 Stream parameters	6
2.2.6 Water samples	7
2.3 Laboratory analysis	8
2.3.1 Fish	8
2.3.2 Otoliths.....	8
2.3.3 Stable Isotope Analysis	8
2.3.4 Macroinvertebrates	9
2.4 Statistical analysis.....	9
2.4.1 Measuring error	9
2.4.2 Environmental variables	10
2.4.3 Length, age and condition analysis	10
2.4.4 Stable Isotope Analysis	11
2.4.5 Density estimation	11
2.4.6 Macroinvertebrates	12
3. Results	13
3.1 Environmental variables.....	13
3.2 Does length, body condition or age of trout differ between presence and absence of minnow?.....	14
3.2.1 Influence on length	14
3.2.2 Influence on body condition	16
3.2.3 Age and length distribution	18
3.3 Are trophic position and niche width of trout shifted between presence and absence of minnow?	19
3.3.1 Trophic positions.....	20
3.3.2 Niche width	22
3.4 Does trout density differ between presence and absence of minnow?	23

3.5	Does the presence of minnow influence stream prey community?	24
3.5.1	Macroinvertebrate diversity and abundance.....	24
3.5.2	Macroinvertebrate size	30
4.	Discussion	31
4.1	Age, length and condition	31
4.1.1	Influence on length	31
4.1.2	Influence on condition.....	32
4.1.3	Age and length distribution	32
4.2	Trophic position and niche width.....	33
4.2.1	Trophic position	33
4.2.2	Niche width	35
4.3	Trout density	36
4.4	Prey community	36
4.4.1	Prey diversity and abundance	36
4.4.2	Prey size	38
4.5	Limitations	38
4.6	Conclusion	39
5.	Outlook.....	40
	References	41
	Popular science summary.....	47
	Appendix 1	48
	Appendix 2	49
	Appendix 3	50
	Appendix 4	51
	Appendix 5	52
	Appendix 6	55
	Appendix 7	56
	Appendix 8	57
	Appendix 9	58
	Appendix 10	59
	Appendix 11	60
	Appendix 12	61
	Appendix 13	63
	Appendix 14	66

List of tables

Table 1. Levels of different stretch parameters.....	7
Table 2. Dissolved Organic Carbon (DOC) in mg/L and Total Nitrogen (TN) as well as Total Phosphorus (TP) in μm across stretches.	7
Table 3. Output from Model 1 with trout fork length as response variable and stream as random effect. Estimated age and every interaction are significantly correlated with trout fork length.	15
Table 4. Post-hoc test results for the interaction between age and minnow presence from Model 1 with length as response variable. The contrast is not significant from age classes 0+ to 2+ and significant in 3+ and 4+.	15
Table 5. Output from Model 1 with Fulton's K as response variable and stream as random effect. Fulton's K is only significantly correlated to the dominant type of bottom vegetation: trout are in a better condition when mosses dominate.	17

List of figures

Figure 1. Stream positions in the study area between Abisko and Riksgränsen in Norrbotten, Sweden. Two enlarged windows show each stretch depicted in blue. The town of Abisko is shown for reference. (willcwelch 2019; QGIS Geographic Information System 2025).....	4
Figure 2. MP and MA-stretches in the first two dimensions of a PCoA that has been conducted with the Gower's distances of their environmental parameters. Red dots depict MA-stretches and blue dots depict MP-stretches. The stretches are spread across the first dimension and split between 0.0-0.1 of the second dimension.....	13
Figure 3. Hierarchical clustering applied to the stretches' Gower's distances. Three clusters are visible: BD02_2_1 to BD03_1_1, BAKTA_1_1 to BD10_1_1 and the individual stretch BD13_1_1.....	14
Figure 4. Left: Model-predicted trout fork length (mm) for each age with 95 %-CI in MP and MA-stretches. The length differences increase with age. Right: Trout fork length (mm) over age with a linear regression line across stretches. BAKTA_1_1 and BD05_2_1 show stronger positive relationships in contrast to BD10_1_1. BD13_1_2 contained only one age class.....	16
Figure 5. Left: Trout condition factor of individuals in MP and MA-stretches with confidence intervals of a fitted linear model depicted in grey. The condition factor varies strongly at age 0+ and the confidence intervals overlap almost everywhere. Right: Trout condition factor over age with a linear regression line across stretches. BD13_1_1 shows a stronger positive relationship then the other stretches. BD13_1_2 only contained 0+ individuals with a wide condition factor range.....	17
Figure 6. Age distributions of trout in all MP and MA-stretches. In one group of stretches the number of trout is declining from 0+ while in the other group the distribution peaks later. There is no clear difference between MP and MA-stretches.....	18
Figure 7. Length distributions of trout in all MP and MA-stretches. The distributions largely match the age distributions and show the same pattern of some stretches peaking at 0+ and some later, independently of minnow presence.....	19
Figure 8. Isotope biplot showing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in trout, minnow, macroinvertebrates and benthic algae. The hulls show 95%-CI for the position of individuals for each species. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in trout differ substantially between stretches while they are more consistent in minnow. Invertebrates and algae differ massively in $\delta^{13}\text{C}$	20

Figure 9. $\delta^{15}\text{N}$ per stretch. Most trout and minnow in MP-stretches seem to have a slightly higher $\delta^{15}\text{N}$ than trout in MA-stretches. Only trout in BD13_1_2 have exceptionally high $\delta^{15}\text{N}$	21
Figure 10. Relationship between $\delta^{15}\text{N}$ and fork length (mm) per stretch and separated in MA and MP. A few very short individuals from both MP and MA-stretches have a very high $\delta^{15}\text{N}$ in comparison to larger individuals.	22
Figure 11. SEAc of trout in MP and MA-stretches. Trout in BD10_1_1 had a SEAc many times larger than in any other stretch. Except for this, no pattern between MP and MA-stretches is visible.	23
Figure 12. Trout and minnow density (n/m^2) per stretch. Densities were varying in MP and MA-stretches. The two stretches in BD11_1 contained only minnow and differed greatly with BD11_1_2 having had by far the highest fish density of all stretches.	24
Figure 13. Normalized prey abundance and prey volume per taxon in MP and MA-stretches. The stretches seem to vary independently from minnow presence. Large taxa appear proportionally larger in prey volume in comparison to small taxa.	25
Figure 14. Shannon index for macroinvertebrate communities in MP (blue) and MA-stretches (red). The index seems on average to have a higher value in MA-stretches. BD10_1_1 has an exceptionally low index.	26
Figure 15. Simpson index for macroinvertebrate communities in MP (blue) and MA-stretches (red). Similarly to the Shannon index, the Simpson index seems on average to have a higher value in MA-stretches. Again, BD10_1_1 has the lowest index.	27
Figure 16. NMDS showing the differentness of macroinvertebrate communities between stretches. The MA-stretches (red polygon) are distinct from MP-stretches (blue polygon). Most stretches containing only minnow and only charr appear more similar to MA-stretches.	28
Figure 17. NMDS showing the contribution of single taxa to the differentness of macroinvertebrate communities between stretches. One group of taxa is closer to the center of the plot while the other spreads around it.	28
Figure 18. Cumulative contribution of taxa to the differentness between stretches. Chironomidae contribute by far most to variation between stretches, followed by Ephemeroptera and Oligochaeta. Starting at Coleoptera the contribution is close to none.....	29

Abbreviations

Abbreviation	Description
DOC	Dissolved Organic Carbon
FAMD	Factor Analysis of Mixed Data
HCL	Hydrochloric Acid
MP	Minnow Present
MA	Minnow Absent
SIA	Stable Isotope Analysis
TN	Total Nitrogen
TOC	Total Organic Carbon
TP	Total Phosphorus

1. Introduction

Invasive species heavily contribute to global biodiversity loss (McGeoch et al. 2010; Bellard et al. 2016; Mollot et al. 2017; Sesay et al. 2024) and constitute one of the biggest ecological issues of our time. Consequences for invaded ecosystems are diverse: invasions can induce trophic cascades (Gallardo et al. 2016), affect ecosystem stability and resilience and have a direct impact on humans by disrupting ecosystem services (Levin & Crooks 2011). Common interactions between invasive and native species are competition for food and habitat as well as predation (Simon & Townsend 2003; Carmona-Catot et al. 2013; Lewis et al. 2024). Speed and frequency of invasion vary: remote aquatic ecosystems like small mountain streams have a comparably low invasion pressure (Keller et al. 2011). Beneficial traits of the invader are among others high phenotypic plasticity (Arismendi et al. 2014) as well as generalism (Hayes et al. 2024).

Eurasian minnow (*Phoxinus phoxinus ssp.*, from here on “minnow”) from the *Cyprinidae* family is a species complex with high phenotypic plasticity (Garcia-Raventós et al. 2020) and multiple different genetic lineages, which is why it is under active taxonomic revision (Palandačić et al. 2017; Cheng et al. 2022). It is widespread across Eurasia (Paško et al. 2014) and native to parts of the Swedish north (Sveriges lantbruksuniversitet [SLU], Institutionen för akvatiska resurser 2025). However, minnow are spreading further into mountain lake systems that they have not occupied before. It is not clear whether voluntary introductions have taken place, as described for Norwegian lakes and parts of the Iberian Peninsula (Museth et al. 2007; Garcia-Raventós et al. 2020), but it is documented that they have been accidentally released by anglers in parts of Sweden (in Jämtland, Filipsson 1994). According to Comte et al. (2013), *Cyprinidae* benefit most from climate change in comparison to all other studied fish taxa, indicating that their natural range may be expanding with climate change. Range expansions of invasive species that are both human-mediated and climate change-driven are happening especially fast in comparison to native species (Bradley et al. 2024). This synergy between human introduction and benefiting from climate change could benefit introduced minnow populations in northern Sweden.

The fish community in mountain lake systems of the Swedish Arctic often only consists of brown trout (*Salmo trutta*, from here on “trout”) and Arctic charr (*Salvelinus alpinus*, from here on “charr”) in sympatry or allopatry. Like minnow, trout have very high phenotypic plasticity (Gabrielsen et al. 2021). They can use different freshwater as well as saltwater habitats and switch between them within their life cycle (Jonsson 1989). Trout diet ranges from invertebrates to fish, depending on life stage and availability (Jensen et al. 2012). Trout in mountain lake systems in Arctic Sweden are adfluvial; they use small streams for spawning

and as nurseries where they are available (Halvorsen & Jørgensen 1996). As minnow spread into these systems, they may overlap with trout and charr in diet and habitat and thereby impact the native fish populations.

In lakes in the Alps and the Pyrenees as well as the geographically closer Norwegian lakes *Øvre Heimdalsvatn* and *Lake Skjerja*, a negative impact of introduced minnow on the existing trout populations in mountain lakes could be observed (Lien 1981; Borgstrøm et al. 1996, 2010; Tiberti et al. 2022; Qvenild et al. 2024). Invasions by minnow led to reduced recruitment, reduced annual growth and lowered biomass in trout due to resource competition (Borgstrøm et al. 1996; Qvenild et al. 2024) and possibly minnow predation on trout eggs or alevins (Museth et al. 2007; Borgstrøm et al. 2010; Tiberti et al. 2022). These effects on trout seemed to be correlated with minnow abundance (Qvenild et al. 2024), and the reduced annual growth can result in piscivory setting in later in the life cycle of trout (Jonsson et al. 1999). The combination of resource competition and predation could lead to the gradual replacement of trout in lakes that have been invaded by minnow (Tiberti et al. 2022). Minnow have also been found to influence the composition and structure of littoral benthos in lakes (Næstad & Brittain 2010), where *Chironomidae* and *Oligochaeta* have increased in relative abundance. Apparently, introduced minnow can affect trout life history, density and resource availability through competition and predation.

Like juvenile trout, minnow use habitat in lake tributaries, leading to competition for resources in the trout's early life stages (Museth et al. 2010), especially if the two species overlap in size (Larsen et al. 2007). Energetically constrained by competition, juvenile trout may leave their nursing streams earlier and migrate to the adjacent lake (Jonsson & Jonsson 2011). In contrast to most other studies about the species' interaction, Näslund et al. (1998) found that in streams in central Sweden trout growth during the ages 0+ to 3+ was increased in sympatry. However, they add that growth is correlated with temperature, resource availability and density which is why their finding is not universally applicable.

The interaction between trout and minnow has been studied in multiple instances but rarely in northern Swedish ecosystems. Also, most research so far has been conducted in lakes while nursery stream interactions have not been focused on. Varying environmental conditions in streams like width, depth and stream slope possibly influence both species and how their impact on each other manifests (Jonsson & Jonsson 2011). Minnow will likely continue to expand their range and enter new lake systems. To understand how juvenile trout might be affected by non-native minnow in lake-adjacent streams in northern Sweden, the species' interaction needs to be studied in situ. Trout in lakes seem to be negatively affected in several ways, among other things in terms of growth, recruitment, life history and prey availability. To potentially detect similar interactions in trout nursery streams, I investigated several lake tributaries in the

Abisko area that are reported to either contain or lack minnow to answer the following questions:

1. Does length, body condition or age structure of trout in streams differ depending on the presence or absence of minnow?
2. Do Trophic Position and niche width of trout in streams differ depending on the presence or absence of minnow?
3. Does trout density differ depending on the presence or absence of minnow?
4. Does the presence of minnow influence the stream prey community in terms of diversity, abundance or size?

2. Materials and Methods

2.1 Study area

In August 2024, we sampled streams in the area between Abisko and Riksgränsen in Norrbotten in northern Sweden (Figure 1). Before we went into the field, we used satellite images to identify one or multiple possible tributaries to lakes we know to contain trout or both trout and minnow from previous field work by Renee van Dorst, Sven Normann and Henna Kangosjärvi. We also assessed accessibility and the weather forecast.

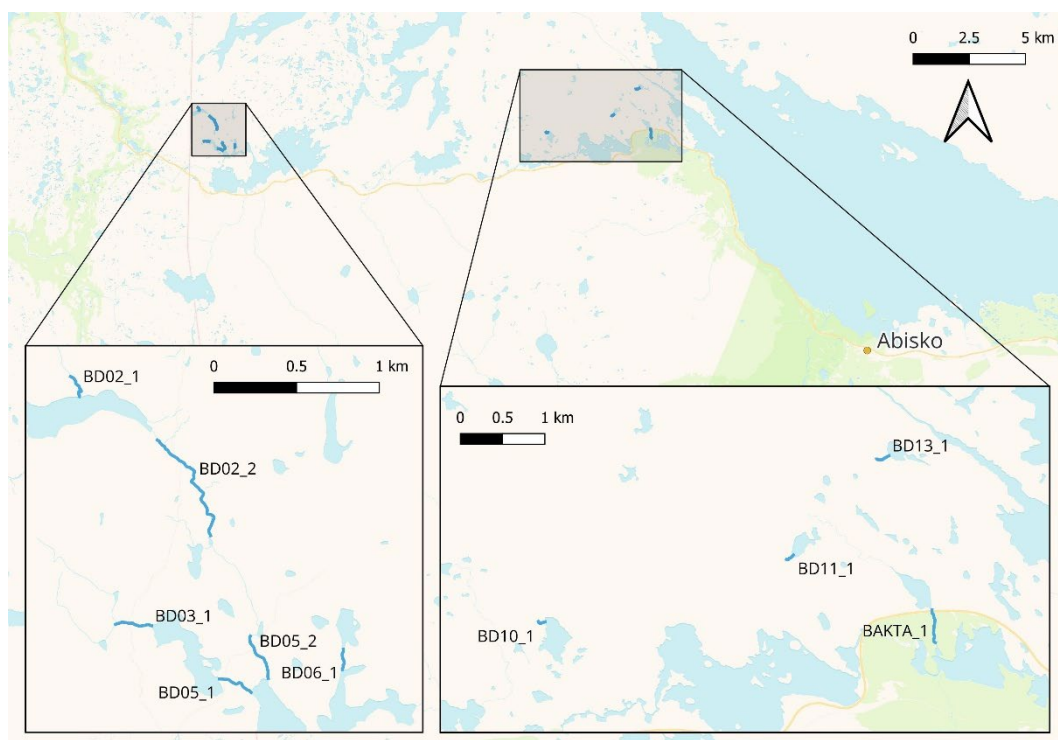


Figure 1. Stream positions in the study area between Abisko and Riksgränsen in Norrbotten, Sweden. Two enlarged windows show each stretch depicted in blue. The town of Abisko is shown for reference. (willc Welch 2019; QGIS Geographic Information System 2025)

We sampled 10 streams with 13 subunits in total (Appendix 1, Supplementary figure 1).

2.2 Data collection

We performed two days of sampling for each stream: The first day we sampled macroinvertebrates and benthic algae for prey density estimation and stable isotope analysis (SIA), stream parameters and water chemistry. On the second day

we conducted electrofishing. With this setup, we did not disturb the water with kicknet sampling on the day we electrofished.

2.2.1 Stretch selection

We selected delimited stretches as smaller units within a stream. For the purpose of electrofishing, we decided that a stretch should ideally contain a variety of habitats, e.g. silty and slow flowing spots as well as fast flowing with gravel. With this, we tried to minimize a sampling bias since species and abundance can be habitat-specific (Valtonen et al. 2002). Initially, we decided a stretch should measure 50 m but realized that almost no stream allowed that, they were mostly too short. BD10_1 measured more than 50 m but not enough for two stretches, so we treated it as one stretch. The stretches ranged from 30 m to 80 m. The names give information about stretch and stream numbers: e.g. BD02_2_1 is the first stretch in the second stream adjacent to lake BD02 in our sampling order. To be fishable, they could not have too much debris in them or be too overgrown. When we found an obvious migration barrier like a large cascade or a long smooth rock surface with a sufficient slope and very little water, we used it as the natural end or beginning of a stretch.

2.2.2 Electrofishing

We acquired density estimates of trout and minnow, and individual measurements (size, weight, stomach contents, tissue samples for SIA, and otoliths for ageing) by electrofishing the stretches. We conducted electrofishing in accordance with *SVENSK STANDARD SS-EN 14011:2006* (Standard - Vattenundersökningar - Provtagning av fisk med elektricitet SS-EN 14011, 2003). We used the electrofishing unit *Lug AB model L 1000*.

We performed three removals for later density estimation. The same person fished all three passes to ensure consistency. We started downstream to avoid affecting fish upstream. In each pass the fisher evenly pulled the activated anode through the water a few steps in front of them towards the net. This was done over the whole width of the stream in a standardized manner to make comparison possible. The fisher also pulled the anode through every reachable location where fish could hide like crevices and cavities under the stream bank. Behind the fisher, one person carried the cable and uncoiled or coiled it as well as carried the bucket in which the caught fish were put. In between passages the caught fish would be killed with the anesthetic tricaine mesylate (MS 222) mixed with hydrogen carbonate as buffer in a separate bucket, put in one bag per passage and cooled. If we already caught many trout, we only anaesthetized the fish, measured total length and occasionally regurgitated them to not influence the population too heavily. Only fish with a minimum gape size of 3 mm could be regurgitated because of the diameter of the syringe. The regurgitated stomach contents were

put into Falcon tubes with 75 % ethanol. After measuring (and regurgitating) the anaesthetized fish were put into a bucket with fresh water to recover and subsequently released sufficiently far downstream of the fished stretch.

2.2.3 Macroinvertebrate and benthic algae for SIA

To calculate the trophic positions and niche widths of trout and minnow, we tried to sample benthic algae, *Oligochaeta*, *Chironomidae* and *Trichoptera* in each stretch as a baseline for SIA. We took one benthic algae sample for SIA in each sampled stream except BD05_2. For this, we brushed algae off three fist-sized stones from the stream into a bucket, added 500 ml of water and filled it into a bottle. We cooled the algae sample until we arrived in the lab and froze it. We tried to avoid any moss or sediment in the sample.

We collected macroinvertebrates for SIA in each stream in multiple ways and covered all habitats within a stream. We collected benthic material with a kicknet and later picked macroinvertebrates from the moss and debris. Also, we collected macroinvertebrates from larger stones. If we caught macroinvertebrates in the net during electrofishing, we collected those as well. After sorting them, they were frozen.

2.2.4 Macroinvertebrates for resource levels

We also collected macroinvertebrates to measure prey abundance, diversity and size in each stretch. We took one sample for every 10 m in a stretch. The samples were taken in differing habitats within the stretch so that the samples were representative of the whole macroinvertebrate community. We placed a kicknet downstream from the designated spot and kicked within 1 m upstream from the net for 1 min. We rinsed the net and filled the contents of each sample into bottles. We documented the substrate, vegetation and flow at each sample spot. The samples were cooled until we arrived at the lab.

We started taking individual samples per 10 m after three stretches, so the individual samples in the first three stretches BD10_1_1, BD13_1_1 and BD13_1_2 were pooled.

2.2.5 Stream parameters

In each stretch we measured or estimated multiple parameters as described in *SVENSK STANDARD SS-EN 14011:2006 (Standard - Vattenundersökningar - Provtagning av fisk med elektricitet SS-EN 14011 2003)* to include as covariates in the statistical analysis (Table 1). We estimated the following parameters with multiple levels for each stretch:

Table 1. Levels of different stretch parameters.

Water current	Substrate	Habitat type	Bottom vegetation	Dominating type of bottom vegetation
slow	high organic	pool	missing	algae
intermediate	silt	flat	sparse	mosses
rapids	sand	run	intermediate	phanerogams
	gravel	riffle	rich	
	pebble	rapid		
	cobble			
	boulder			
	bedrock			

Further we estimated water level, weather conditions, visibility, shade, composition of the riparian zone and amount of large woody debris in the water. We measured water temperature and start and end coordinates. For later fish population density estimation, we measured width and depth at $\frac{1}{4}$, $\frac{1}{2}$ and $\frac{3}{4}$ of the width every 10 m of the stretch.

2.2.6 Water samples

We took water samples to analyze Total Organic Carbon (TOC), Dissolved Organic Carbon (DOC) and total Phosphorus (TP) and Nitrogen (TN) (Table 2). We did this at the beginning of each sampled stream but far enough from the inlet into the lake so that an influence from the lake water was unlikely. For TOC, TN and TP, we filled two 50 ml Falcon tubes. For the DOC, we filtered 50 ml of water with a 0.45 μg syringe filter and added 0.6 ml of hydrochloric acid (HCL) to stabilize the water. All three water samples were cooled until we arrived at the lab. There, we froze the TOC and TP and TN samples and refrigerated the DOC.

Table 2. Dissolved Organic Carbon (DOC) in mg/L and Total Nitrogen (TN) as well as Total Phosphorus (TP) in μm across stretches.

Stretch	DOC (mg/L)	TN ($\mu\text{g/L}$)	TP ($\mu\text{g/L}$)
BAKTA_1	4.2	138	3.2
BD02_2	2.2	93	3.1
BD03_1	2.7	99	3.0
BD05_2	2.6	105	9.0
BD10_1	2.3	109	7.3
BD13_1	6.7	544	13.8

2.3 Laboratory analysis

2.3.1 Fish

We identified the fish to species, measured total and fork length, weighed them and gave them an individual ID (Appendix 2). After taking these measures, the fish were either frozen, or further samples were taken immediately.

If possible, we took the stomach, a tissue sample for SIA and the otoliths of each fish. Stomachs were stored in 75 % ethanol and stomach contents were analyzed by Flavia Suraci (2025). The tissue sample was ideally taken from dorsal muscle tissue between the dorsal and adipose fin in trout and behind the dorsal fin in minnow (Hanisch et al. 2010). In most of the fish we sampled this body area did not contain enough tissue so that we had to take dorsal and ventral tissue between dorsal and caudal fin. Occasionally we had to take tissue from both sides of the fish. To not contaminate the SI sample all instruments and surfaces were cleaned after every fish. The otoliths of each fish were either stored in paper bags for further drying or put into assay plates if they were too small.

The condition factor of trout was calculated as Fulton's K in accordance with Fulton (1904):

$$K = \left(\frac{W}{L^3} \right) \times 100$$

K is the condition factor, W the weight (g) and L the total length (mm) of the fish.

2.3.2 Otoliths

The otoliths were aged to acquire information about the age structure among and within stretches and to be able to estimate growth. We aged all otoliths under a stereo microscope (Olympus Corporation, model SZX2-ILLTQ, Tokyo, Japan). The otoliths were placed in contrast liquid to make the differentiation between summer and winter increments easier. Every winter growth increment that was visible was counted as one finished year and for the current, unfinished year a "+" was added to the individual's age. The two otoliths from one individual were analyzed independently. Magnus Kokkin from SLU Aqua provided expertise in the age estimation.

2.3.3 Stable Isotope Analysis

I filtered and picked out all debris or zoobenthos from the algae samples for SIA after thawing them. All samples were dried in a laboratory freeze-drier (Appendix 3) Fish samples were homogenized through a 212 μm sieve and macroinvertebrate and algae samples with a grinder. After homogenization, I weighed the samples with a microscale. The samples were then processed using an Elemental Analyzer with an Isotope ratio Mass Spectrometer (EA-IRMS; Flash EA 2000 and DeltaV,

Thermo Fisher Scientific, Bremen, Germany) (Werner et al. 1999) in the SLU Stable Isotope Laboratory (SSIL).

2.3.4 Macroinvertebrates

The macroinvertebrate samples were kept in 75 % ethanol. We used an Askania stereomicroscope (Mikroskop Technik Rathenow, Germany) with GF/PW 1010×/25 eyepieces for processing the samples. We separated each sample into taxonomic groups (Appendix 4). I counted the number of individuals in each group and measured each group's five largest individuals per sample. I also visually estimated the contributed volume of each group to the whole sample.

2.4 Statistical analysis

All statistical analyses were performed with *R Statistical Software* (R Core Team 2023). Plots were created with the *tidyverse* package (Wickham & RStudio 2023). I used *nlme* (José Pinheiro (S version) et al. 2025) for modelling.

I analyzed most variables on stretch-level. I included BD13_1_2 in the MA-stretches since we only caught trout in it, even though the stretch lies in the same stream as BD13_1_1 which contained minnow.

2.4.1 Measuring error

We used different approaches to measure the total length of fish, resulting in a measuring error which we corrected in the following way: we agreed that the correct way to measure it was to spread the caudal fin in a way that approximates how the fish would look swimming in the water. We calculated the relative length difference between total length and fork length for every fish and calculated the average of this per species and measurer. Since the average difference between total and fork length in the correctly measured fish was slightly smaller than in the incorrectly measured fish, we estimated a new total length (TL_n) of the wrongly measured fish with the relation between total length (TL) and fork length (FL_b) of the correctly measured fish. FL_a is the fork length of the incorrectly measured fish and N is the total number correctly measured fish.

$$TL_n = FL_a * \frac{1}{(\sum_{i=1}^N FL_b / TL) / N}$$

We tested this on the correctly measured fork lengths and calculated the proportion between calculated and measured total length. The range of proportion is 0.972 to 1.028 with a mean of 1. We continued with these new estimated total lengths.

2.4.2 Environmental variables

Since stream morphology may affect trout and minnow interaction, I assessed to what degree the measured stretches differ from each other and if there was a difference between stretches with only trout (Minnow Absent, MA) and trout and minnow (Minnow Present, MP). I calculated the Gower's distance between all environmental variables of all stretches from which I created a dissimilarity matrix (Gower 1971). With this, I performed a PCoA to assess differences in environmental variables between the stretches. I also performed hierarchical clustering and a silhouette analysis with the *cluster* package (Maechler et al. 2025).

When investigating the influence of minnow presence on different response variables, I could not include all environmental variables that we measured or estimated as covariates in the models because the small sample size in different parts of the analysis would otherwise result in perfect fits (overfitting). To filter the variables and decide on a smaller number to use in the analysis I performed a Factor Analysis of Mixed Data (FAMD) with the *FactoMineR* (Husson et al. 2024) and *factoextra* (Kassambara & Mundt 2020) packages. Based on contribution to stretch differences and correlation between variables, I decided to only include *water current class* and *dominant type of bottom vegetation* as covariates in further analyses (Appendix 5, Supplementary figure 1). I decided against model selections in the statistical analysis since the covariates are already preselected. Instead, I provided one model with all covariates (Model 1) and one with only minnow presence (Model 2) as predictors where I used linear models or linear mixed models:

1. $response\ variable \sim minnow\ presence + water\ current\ class + dominant\ type\ of\ bottom\ vegetation$
2. $response\ variable \sim minnow\ presence$

Where I could not use stream as random effect, Model 2 was similar to a one-way ANOVA.

2.4.3 Length, age and condition analysis

To detect the effects of minnow presence on length and condition, I tested the effect of minnow presence on age, length and condition in linear mixed models as in Model 1 and Model 2. I used an interaction between *age* and every other predictor. I included a random intercept for the streams to account for stream-dependent effects on individuals:

1. $Fork\ length/Body\ condition \sim minnow\ presence * age + water\ current\ class * age + dominant\ type\ of\ bottom\ vegetation * age + (I|Stream)$
2. $Fork\ length/Body\ condition \sim minnow\ presence * age + (I|Stream)$

When model diagnostics suggested heteroscedacity in the data, I used the *varIdent* function class to allow for varying variances among streams and avoid violation of model assumptions. Post-hoc tests were conducted with the *emmeans* package (Lenth et al. 2025).

Since the estimated trout age was an ordinal variable, I used two cumulative link mixed models from the *ordinal* package (Christensen 2024) structured as Model 1 and 2 to test for an influence of minnow presence on the difference in trout age distributions.

We caught one 6+ trout in BD05_2_1 and no individual older than 4+ in any other stretch. I decided to exclude this individual since it had a large impact on averages and likely entered the stream from the lake. Like this, the age range of MP and MA stretches was the same.

2.4.4 Stable Isotope Analysis

I used the original $\delta^{15}N$ value as proxy for trophic position. I decided against the formula proposed by Post (2002) to calculate the trophic position of organisms because I had no suitable baseline. I did not use macroinvertebrates as baseline since no taxon was available in every stretch. *Trichoptera* was available for almost every stretch but their $\delta^{15}N$ level in BD03_1_1 was higher than that of all trout so they could not serve as baseline. I also could not use benthic algae since the $\delta^{13}C$ range between stretches was strikingly wide.

I used linear mixed models for testing the relationship between trout trophic position and minnow presence. I included fork length as a fixed effect in Model 1 and Model 2 and stream as a random effect. I used another linear mixed model with $\delta^{15}N$ as response variable, fork length as fixed effect and stream as random effect to test for the relationship between $\delta^{15}N$ and length: $\delta^{15}N \sim Fork\ length + (I|Stream)$.

I plotted a stable isotope biplot to visualize the niche width of species in each stretch and additionally used the *SIBER* package (Jackson & Parnell 2023) to calculate the corrected Standard Ellipse Areas (SEAc) from the $\delta^{15}N$ and $\delta^{13}C$ as a proxy for niche width. The SEAc served as a proxy for trophic niche width.

2.4.5 Density estimation

To estimate trout and minnow population sizes per stretch, I used the *Seber3* method in the *removal* function from the *FSA* package (Ogle et al. 2015). This method is designed for three removals and a declining catch size. In BD13_1_1 the catch size did not decline after each removal (5, 15, 8 for trout and 4, 2, 5 for

minnow) which is why the *Seber3* method could not be used for this stretch. I used the absolute catch size instead (Appendix 6). From the measured length and width every 10 m we estimated each stretch's surface. We calculated density by dividing the estimated number of fish by the calculated stretch surface (m²).

I tested the effect of minnow presence on trout density with Model 1 and Model 2 without random effects since the low sample size (n = 7) resulted in NAs. I also tested if there was a relationship between the total fish density with both species in stretches and minnow presence and density with an ANOVA.

2.4.6 Macroinvertebrates

The macroinvertebrate data from BD11_1, BD02_1_1 and BD05_1_1 were not considered in this data set since we either found no fish there, or only minnow and/or charr were present. Unidentifiable invertebrates were also not considered. Since we pooled the macroinvertebrate samples of BD10_1_1, BD13_1_1 and BD13_1_2, I analyzed the data set on stretch level.

To analyze if minnow presence is influencing macroinvertebrate community diversity, I used the *diversity* function from the *vegan* package to calculate the Shannon and Simpson index for each macroinvertebrate community. The Shannon index is more sensitive to rare species while the Simpson index gives more insight into species evenness, thus they complement each other. I used linear models as in Model 1 and 2 to identify relationships between the indices and minnow presence. I did not include random effects since the low sample size would result in NAs (n = 7).

To visually and statistically detect any effect of minnow presence on macroinvertebrate community composition, I performed a NMDS, SIMPER analysis and PERMANOVA using the *vegan* package. I conducted two PERMANOVA with the Bray-Curtis dissimilarity matrix with the Model 1 and Model 2 predictor combinations.

I calculated the mean size of the five biggest individuals per species within each stretch to determine if minnow presence influences the size of taxa. Only in the taxa *Trichoptera*, *Ephemeroptera* and *Chironomidae* were there enough observations for creating models based on this. I built Model 1 with average maximum size as response variable and without a random effect for stream since the low sample size would result in NAs again (n = 7). Additionally, I performed a one-way ANOVA with minnow presence as predictor.

3. Results

3.1 Environmental variables

MP and MA-stretches are not noticeably different in their environmental conditions. A PCoA with the Gower's distance matrix of environmental variables shows a relatively even distribution of the MP and MA stretches across the first two PCoA dimensions (Figure 2).

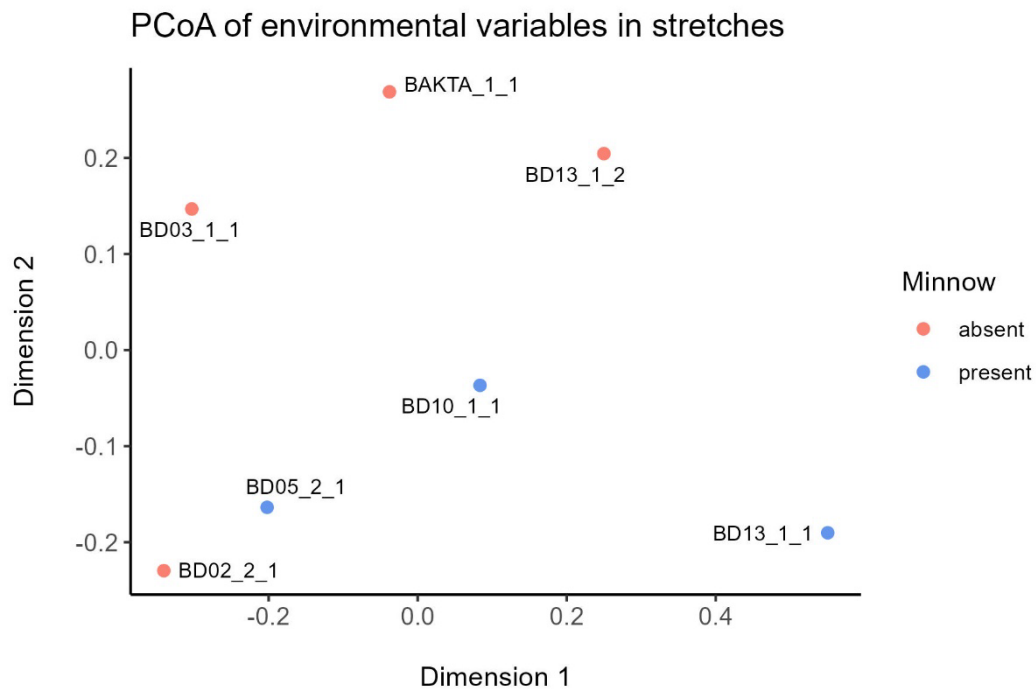


Figure 2. MP and MA-stretches in the first two dimensions of a PCoA that has been conducted with the Gower's distances of their environmental parameters. Red dots depict MA-stretches and blue dots depict MP-stretches. The stretches are spread across the first dimension and split between 0.0-0.1 of the second dimension.

In the first dimension there are no apparent clusters. BD13_1_1 is comparably separate from the rest. In the second dimension there are seemingly two groups: one with BD03_1_1, BAKTA_1_1 and BD13_1_2 and another one with the rest.

Hierarchical clustering shows three different clusters: BD02_2_1, BD05_2_1 and BD03_1_1 in the first, BAKTA_1_1, BD13_1_2 and BD10_1_1 in the second and BD13_1_1 as the only stretch in the third cluster (Figure 3). The first two clusters are more similar to each other than either of them to the third cluster.

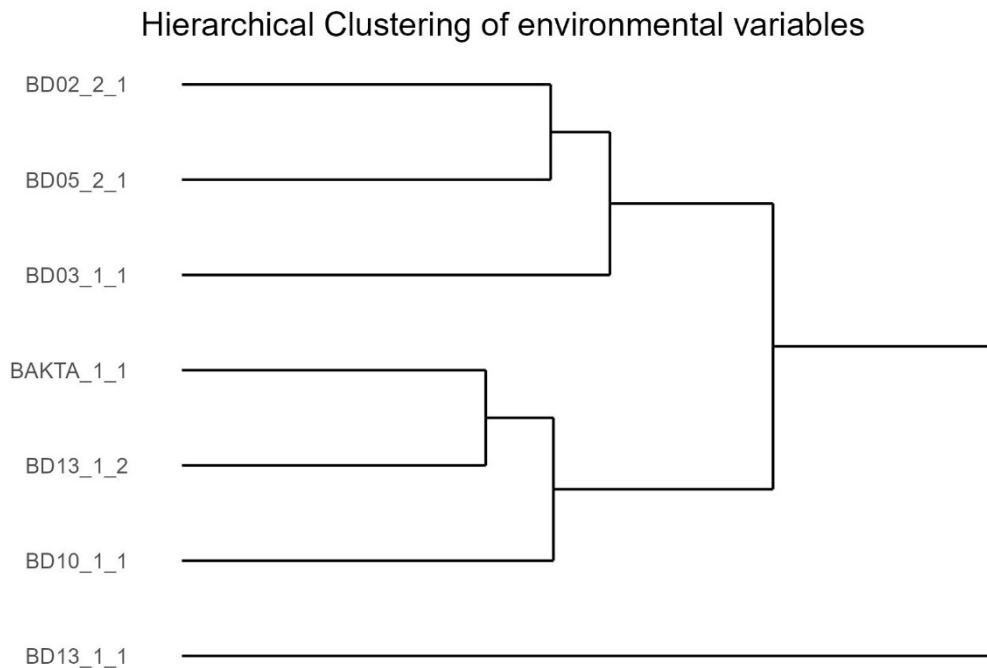


Figure 3. Hierarchical clustering applied to the stretches' Gower's distances. Three clusters are visible: *BD02_2_1* to *BD03_1_1*, *BAKTA_1_1* to *BD10_1_1* and the individual stretch *BD13_1_1*.

These clusters are in accordance with stretch positions along the first dimension in the PCoA. They seem to be independent from minnow presence.

A silhouette analysis however suggests that two clusters capture the dissimilarities best: one consisting only of *BD13_1_1* and the other one of the other stretches.

3.2 Does length, body condition or age of trout differ between presence and absence of minnow?

3.2.1 Influence on length

Model 1 ($n = 157$) showed that where minnow were present trout length-at-age is significantly lower than where they are absent (Table 3). Trout length increased significantly with age. In stretches where mosses dominate, length-at-age is significantly higher in comparison to where algae dominate stretches. Length-at-age is significantly lower where phanerogams dominate. There was a significant negative relationship between length-at-age and the water current class. Stream as random effect explained a considerable amount of variability (intercept variance = 177.26, residual variance = 70.17).

Table 3. Output from Model 1 with trout fork length as response variable and stream as random effect. Estimated age and every interaction are significantly correlated with trout fork length.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	43.476	28.195	1.542	0.125	-12.261, 99.213
estimated age	55.575	6.469	8.591	<0.001	42.788, 68.362
minnow present	3.844	18.91	0.203	0.839	-33.537, 41.226
water current class	0.362	6.194	0.058	0.954	-11.883, 12.606
mosses	-11.232	16.292	-0.689	0.492	5.035, 12.820
phanerogams	-12.982	3.939	-3.295	0.239	-20.769, -5.194
mosses:age	8.928	1.969	4.534	<0.001	5.035, 12.820
phanerogams:age	-12.982	3.939	-3.295	0.001	-20.769, -5.194
minnow present:age	-17.888	2.983	-5.997	<0.001	-23.784, -11.992
water current class:age	-8.878	1.601	-5.544	<0.001	-12.043, -5.712

A post-hoc test showed that the contrast in length between trout in MP and MA-stretches increased with age class (Table 4, Figure 4). The difference was insignificant in age classes 0+ to 2+ while 2+ showed a tendency towards significance. The contrast was statistically significant in the age classes 3+ and 4+.

Table 4. Post-hoc test results for the interaction between age and minnow presence from Model 1 with length as response variable. The contrast is not significant from age classes 0+ to 2+ and significant in 3+ and 4+.

Age	Estimate	SE	p-value
0+	-3.84	18.9	0.8392
1+	14.04	18.8	0.4554
2+	31.93	19.1	0.0965
3+	49.82	19.9	0.0132
4+	67.71	21.0	0.0016

There are differences in the relationship between age and length across the stretches (Figure 4). In BAKTA_1_1 and BD05_2_1 there is a visibly stronger positive relationship than in BD10_1_1 or BD13_1.

Relationship between trout length and minnow presence across age classes

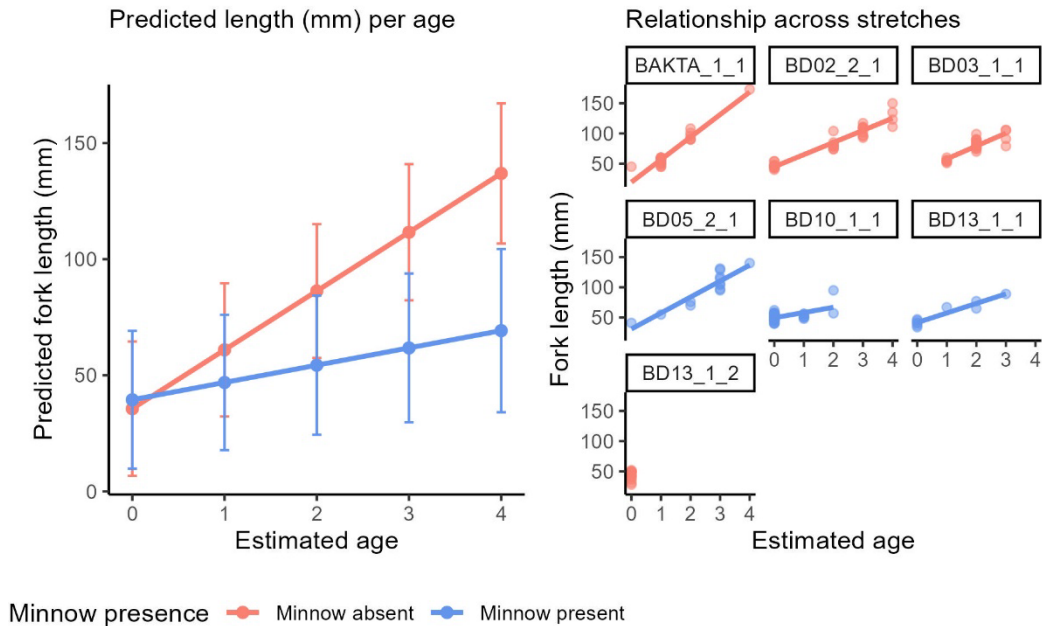


Figure 4. Left: Model-predicted trout fork length (mm) for each age with 95 %-CI in MP and MA-stretches. The length differences increase with age. Right: Trout fork length (mm) over age with a linear regression line across stretches. BAKTA_1_1 and BD05_2_1 show stronger positive relationships in contrast to BD10_1_1. BD13_1_2 contained only one age class.

Model 2 showed a negative effect of minnow presence on trout length-at-age as well ($n = 157$, $\beta = -5.124$ mm, $SE = 1.610$, $p = 0.002$) (Appendix 7, Supplementary table 12). Here, stream affiliation only explains a fracture of the variance (intercept variance = 16.892, residual variance = 233.843).

3.2.2 Influence on body condition

Model 1 with Fulton's K as response variable ($n = 157$) shows no significant correlation with any predictor except for mosses (Figure 5, Table 5): the condition of trout is higher in stretches where mosses dominate in comparison to stretches where algae dominate regardless of age.

Relationship between trout condition and minnow presence across age classes

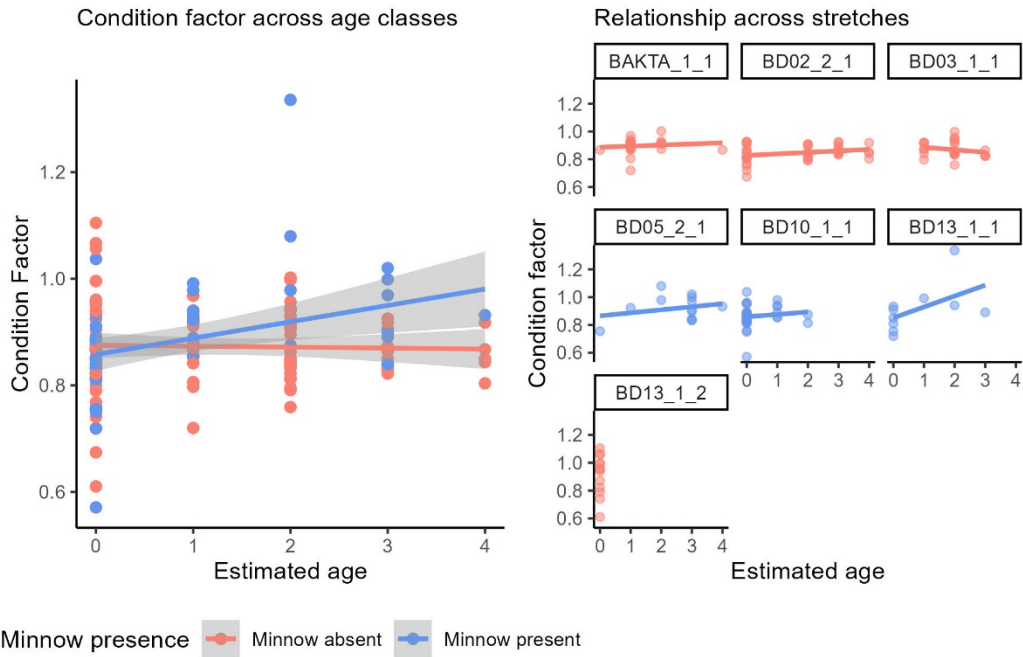


Figure 5. Left: Trout condition factor of individuals in MP and MA-stretches with confidence intervals of a fitted linear model depicted in grey. The condition factor varies strongly at age 0+ and the confidence intervals overlap almost everywhere. Right: Trout condition factor over age with a linear regression line across stretches. BD13_1_1 shows a stronger positive relationship than the other stretches. BD13_1_2 only contained 0+ individuals with a wide condition factor range.

Table 5. Output from Model 1 with Fulton's K as response variable and stream as random effect. Fulton's K is only significantly correlated to the dominant type of bottom vegetation: trout are in a better condition when mosses dominate.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	0.828	0.065	12.710	<0.001	0.7, 0.958
estimated age	0.043	0.037	1.177	0.241	-0.029, 0.116
minnow present	0.031	0.026	1.205	0.23	-0.02, 0.082
water current class	0.000	0.016	-0.02	0.984	-0.032, 0.031
mosses	0.068	0.025	2.790	0.006	0.02, 0.117
phanerogams	-0.008	0.067	-0.126	0.9	-0.141, 0.124
mosses:age	-0.017	0.013	-1.299	0.196	-0.042, 0.009
phanerogams:age	0.046	0.046	0.994	0.322	-0.046, 0.138

minnow	-0.003	0.018	-0.164	0.87	-0.038, 0.032
present:age					
water current	-0.008	0.009	-0.896	0.372	-0.026, 0.01
class:age					

The random effect explains almost no variance in condition (intercept variance < 0.001, residual variance = 0.003).

Model 2 showed no significant correlation (n = 157). The random effect explained slightly more variation, but the residual variance remains higher (intercept variance = 0.001, residual variance = 0.003) (Appendix 8, Supplementary table 13).

3.2.3 Age and length distribution

The mean of stretch age means in minnow absence is 1.207 and in minnow presence 1.205. A two-sample t-test shows no significant difference (n = 7, p = 0.999). The cumulative link mixed models structured as Model 1 and 2 did not show a significant influence of minnow presence on trout age distribution either (Appendix 9). However, looking at the stretches individually it becomes clear that there seem to be two types of age distributions, independent of minnow presence: One where most individuals are in the 0+ age class and the distribution flattens out towards older age classes and one where an older age class dominates in number (Figure 6).

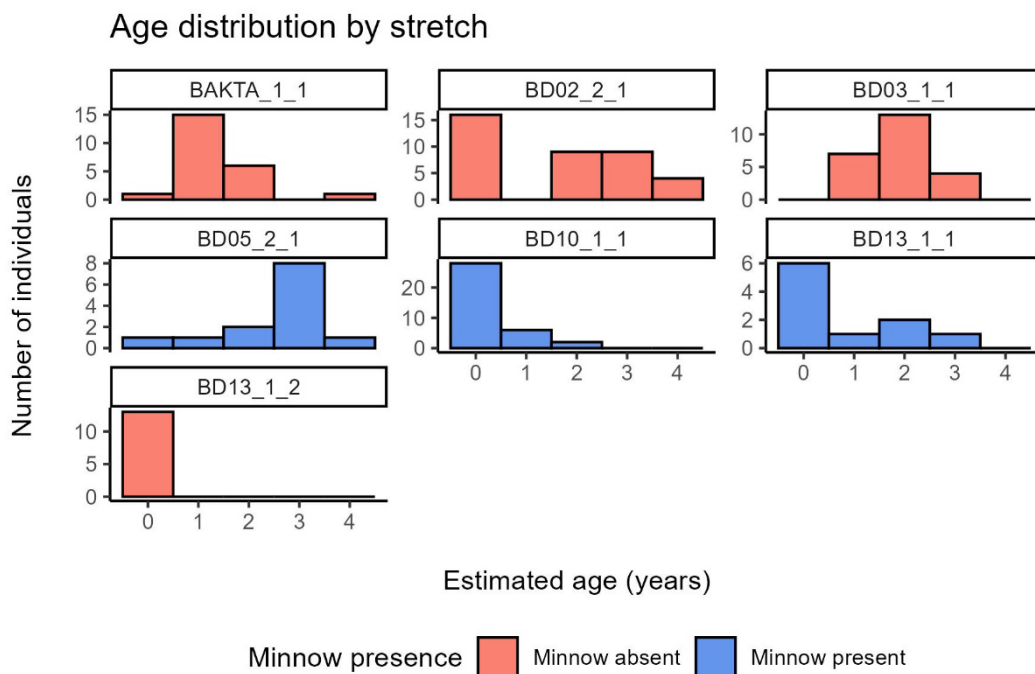


Figure 6. Age distributions of trout in all MP and MA-stretches. In one group of stretches the number of trout is declining from 0+ while in the other group the distribution peaks later. There is no clear difference between MP and MA-stretches.

In BD02_2, BD10_1, BD13_1_1 and BD13_1_2 most individuals are 0+ and the next age classes had gradually fewer individuals in them. BD13_1_2 contained only 0+. In contrast, in BAKTA_1, BD03_1 and BD05_2_1 the majority of individuals was in the age classes 1+, 2+ or 3+.

The length distributions were very similar to the age distributions (Figure 7). The gap of BD02_2_1 in 1+ is not visible in the length distribution and instead of a sharp decline after an initial peak in BD13_1_1 the length curve declines more evenly in contrast to the stretch's age curve.

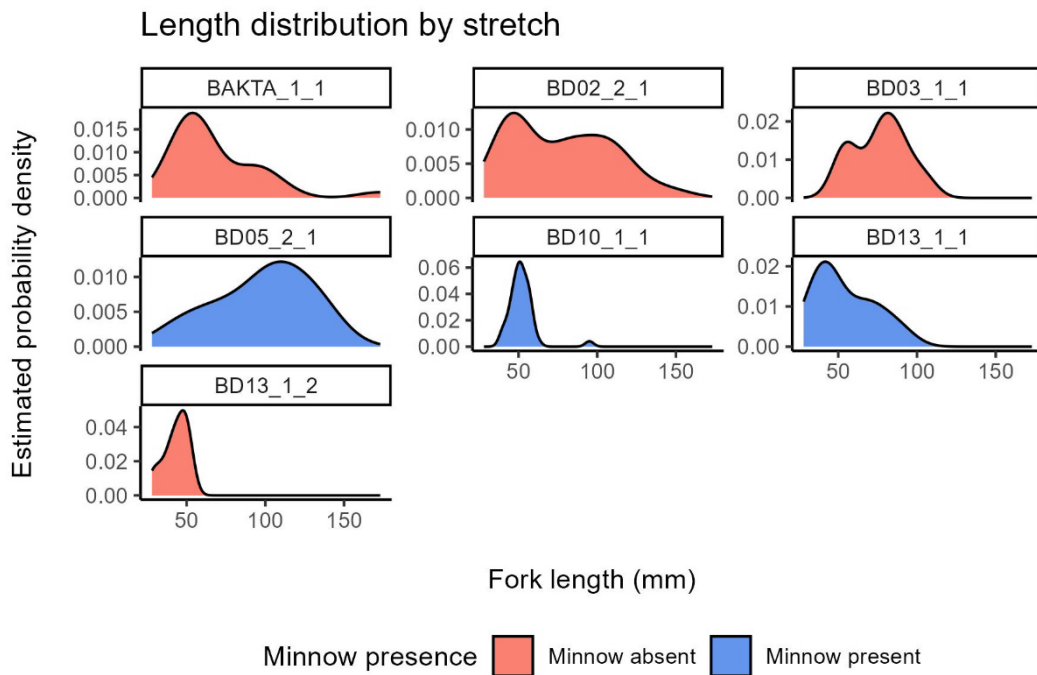


Figure 7. Length distributions of trout in all MP and MA-stretches. The distributions largely match the age distributions and show the same pattern of some stretches peaking at 0+ and some later, independently of minnow presence.

3.3 Are trophic position and niche width of trout shifted between presence and absence of minnow?

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ content in trout and minnow tissue varies a lot between stretches (Figure 8). The ranges within trout differ considerably between stretches while they seem to be more constant within minnow. BD10_1_1 had a particularly wide $\delta^{13}\text{C}$ range. In BD05_2_1 minnow and trout seemed most separated while in BD10_1_1 they fully overlapped. $\delta^{15}\text{N}$ in BD13_1_2 was highest from all stretches.

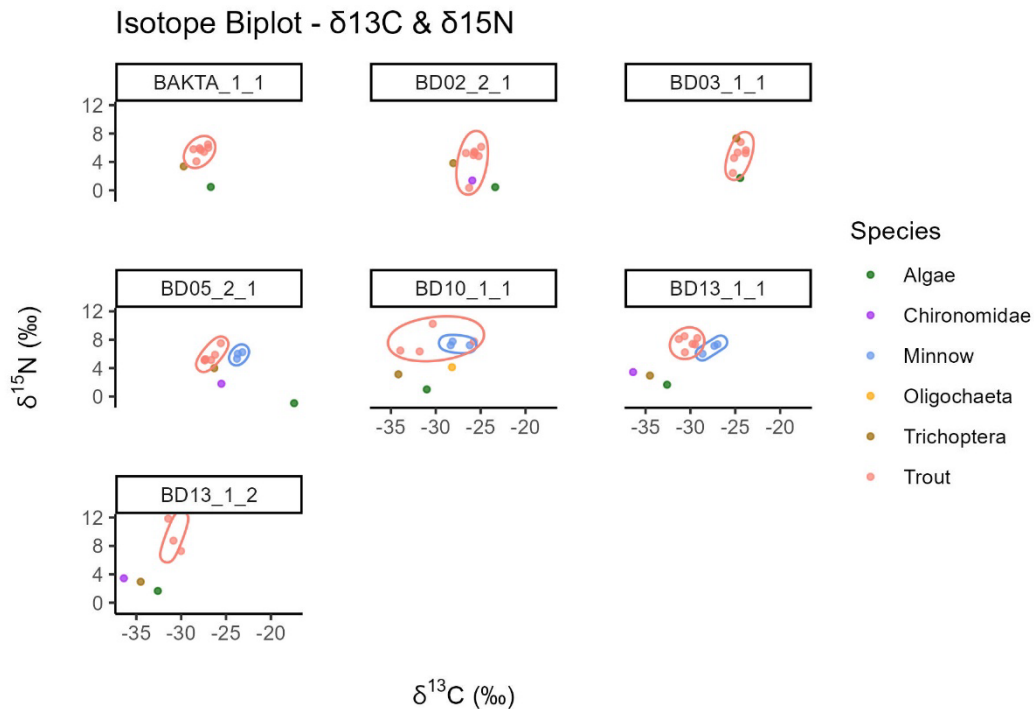


Figure 8. Isotope biplot showing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in trout, minnow, macroinvertebrates and benthic algae. The hulls show 95%-CI for the position of individuals for each species. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in trout differ substantially between stretches while they are more consistent in minnow. Invertebrates and algae differ massively in $\delta^{13}\text{C}$.

Trichoptera seem to vary between stretches in both dimensions as well (while it is important to remember that BD13_1 has only one baseline). *Trichoptera* in BD03_1_1 have a higher $\delta^{15}\text{N}$ ratio than trout. The *Chironomidae* samples from BD13_1 and from BD05_1 differ strongly in $\delta^{13}\text{C}$. Benthic algae was relatively constant with low $\delta^{15}\text{N}$ while varying substantially in $\delta^{13}\text{C}$.

3.3.1 Trophic positions

Trophic position (from here on $\delta^{15}\text{N}$) differed between stretches (Figure 9). In both Model 1 (intercept variance = 4.066, residual variance = 1.658) and the Model 2 (intercept variance = 3.064, residual variance = 1.689) the stream identity as random effect explained a high amount of variation in $\delta^{15}\text{N}$ ($n = 48$). Neither Model 1 nor Model 2 with stream as random effect showed a significant relationship between either fixed effect and $\delta^{15}\text{N}$ (Appendix 10).

Trout in BD13_1_2 have substantially higher $\delta^{15}\text{N}$ than the other ones in absence of minnow and most individuals lie higher than fish in stretches with minnow. BD03_1_1 and BD02_2_1 contained some individuals with comparably low $\delta^{15}\text{N}$ values.

Trophic Position ($\delta^{15}\text{N}$) of Trout and Minnow per Stretch

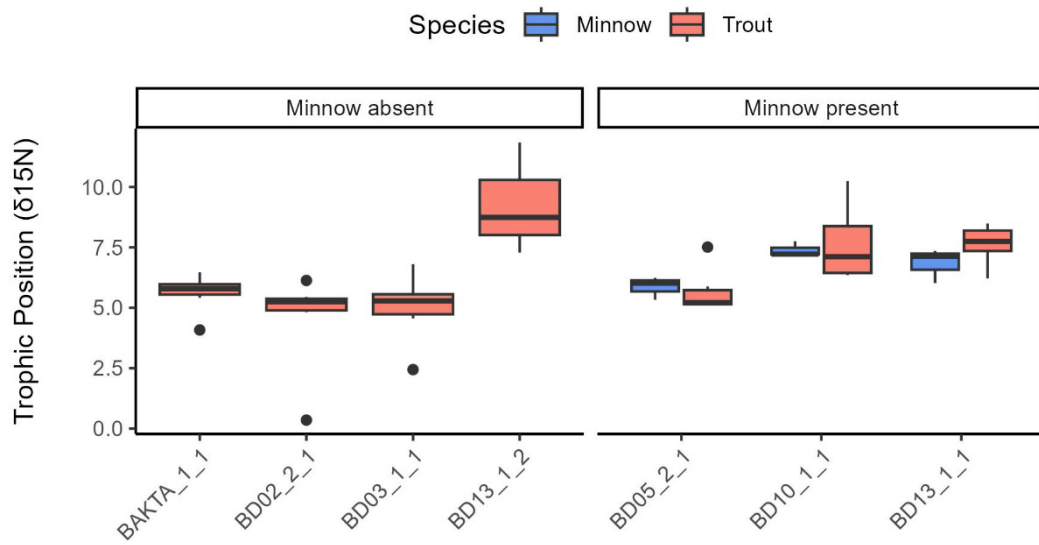


Figure 9. $\delta^{15}\text{N}$ per stretch. Most trout and minnow in MP-stretches seem to have a slightly higher $\delta^{15}\text{N}$ than trout in MA-stretches. Only trout in BD13_1_2 have exceptionally high $\delta^{15}\text{N}$.

I also tested if there was a difference in $\delta^{15}\text{N}$ between minnow and trout: Model 2 with $\delta^{15}\text{N}$ as response variable, species as fixed effect and stream as random effect showed no significant difference between $\delta^{15}\text{N}$ stretch means between trout and minnow, while the mean $\delta^{15}\text{N}$ of minnow is higher than that of trout (6.698, 6.504).

I looked at how fork length is correlated to $\delta^{15}\text{N}$ to see if the visible patterns stem from a correlation between $\delta^{15}\text{N}$ and length (Figure 10).

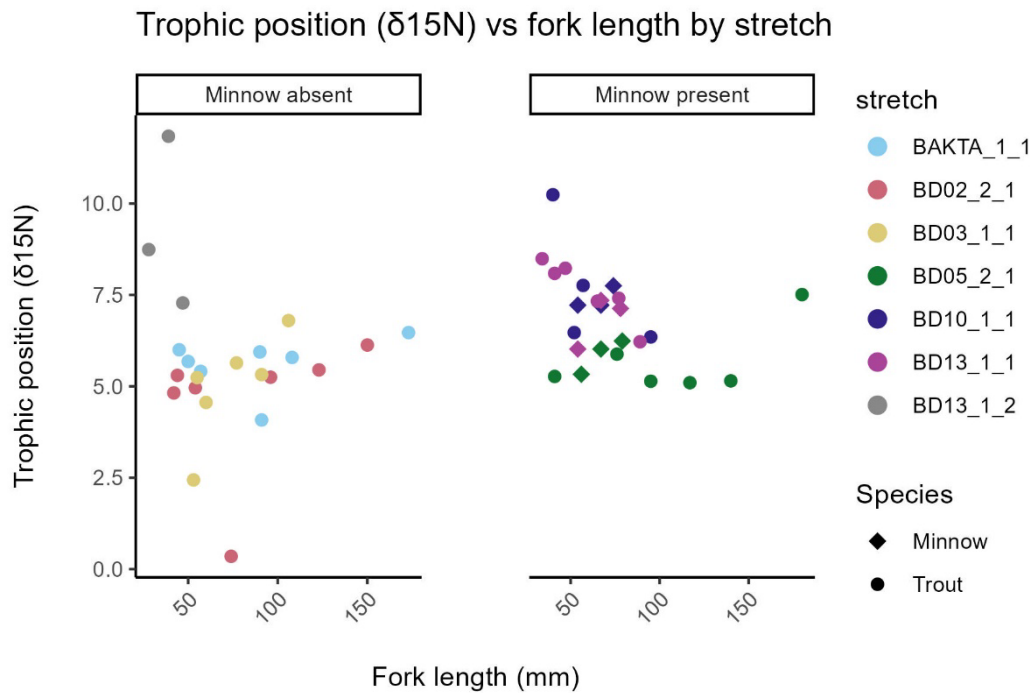


Figure 10. Relationship between $\delta^{15}\text{N}$ and fork length (mm) per stretch and separated in MA and MP. A few very short individuals from both MP and MA-stretches have a very high $\delta^{15}\text{N}$ in comparison to larger individuals.

BAKTA_1_1, BD02_2_1, BD05_2_1 and BD03_1_1 all increased in $\delta^{15}\text{N}$ with increasing length to varying degrees. BD13_1_2, BD10_1_1 and BD13_1_1 on the other hand tended to decrease. $\delta^{15}\text{N}$ was not significantly influenced by fork length according to a linear mixed model with $\delta^{15}\text{N}$ as response variable, fork length as fixed effect and stream as random effect (Appendix 10).

3.3.2 Niche width

Niche width of trout seems to be relatively similar across stretches with BD10_1_1 being the only strong exception (Figure 11).

SEAc for trout by minnow presence

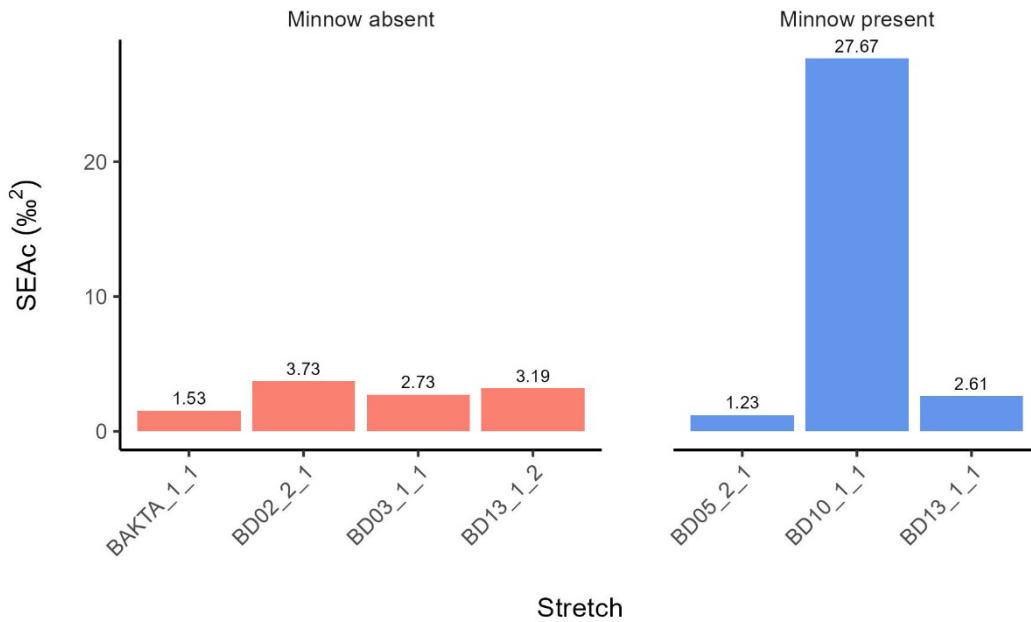


Figure 11. SEAc of trout in MP and MA-stretches. Trout in BD10_1_1 had a SEAc many times larger than in any other stretch. Except for this, no pattern between MP and MA-stretches is visible.

Niche width was not significantly influenced by minnow presence, water current class or the dominant type of bottom vegetation in Model 1 or 2 ($n = 7$) (Appendix 11).

There was a niche overlap between trout and minnow in one out of three stretches where they live in sympatry: In BD10_1_1 trout and minnow had a niche overlap of 61.68 % while in BD05_2_1 and BD13_1_1 there was no overlap at all. Pearson correlation shows that there is a 32.02 % correlation between niche overlap and trout $\delta^{15}\text{N}$.

3.4 Does trout density differ between presence and absence of minnow?

Trout density in MP-stretches was on average slightly lower than in MA-stretches (MP: 0.335 n/m^2 , MA: 0.493 n/m^2). However, Model 1 and Model 2 (a one-way ANOVA in this case) showed no significant relationship between trout density and minnow presence and either water current class or the dominant type of bottom vegetation ($n = 7$). The same was true for both models with minnow density instead of minnow presence as predictor. (Appendix 12)

Minnow density differs considerably between stretches (Figure 12). In the two stretches in BD11_1 where minnow live in allopatry their density ranges from 0.12 n/m^2 to 2.56 n/m^2 .

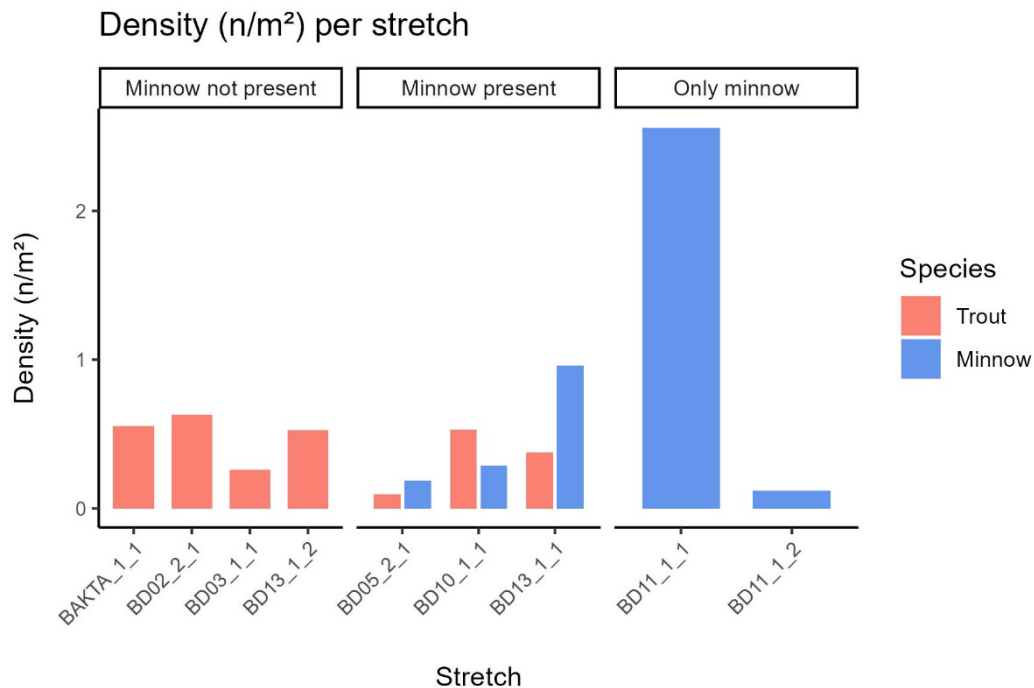


Figure 12. Trout and minnow density (n/m^2) per stretch. Densities were varying in MP and MA-stretches. The two stretches in BD11_1 contained only minnow and differed greatly with BD11_1_2 having had by far the highest fish density of all stretches.

The total fish density in stretches was not correlated with minnow presence either (Appendix 12).

3.5 Does the presence of minnow influence stream prey community?

3.5.1 Macroinvertebrate diversity and abundance

BAKTA_1_1 and BD10_1_1 are distinct from the other stretches in their composition of taxa (Figure 13). In BAKTA_1_1, the proportion of *Gastropoda* and *Bivalvia* is considerably higher than in any other stretch, while the relative number of *Chironomidae* is lowest of all stretches. Conversely, almost all individuals in BD10_1_1 are *Chironomidae*. *Eurycercus* in BD05_2_1 made up almost 50 % of all individuals while there were almost none in other stretches. Proportions of other taxa like *Ephemeroptera* or *Oligochaeta* varied as well among stretches. The stretches varied in taxa proportions but there is no distinctive pattern visible between MA and MP stretches.

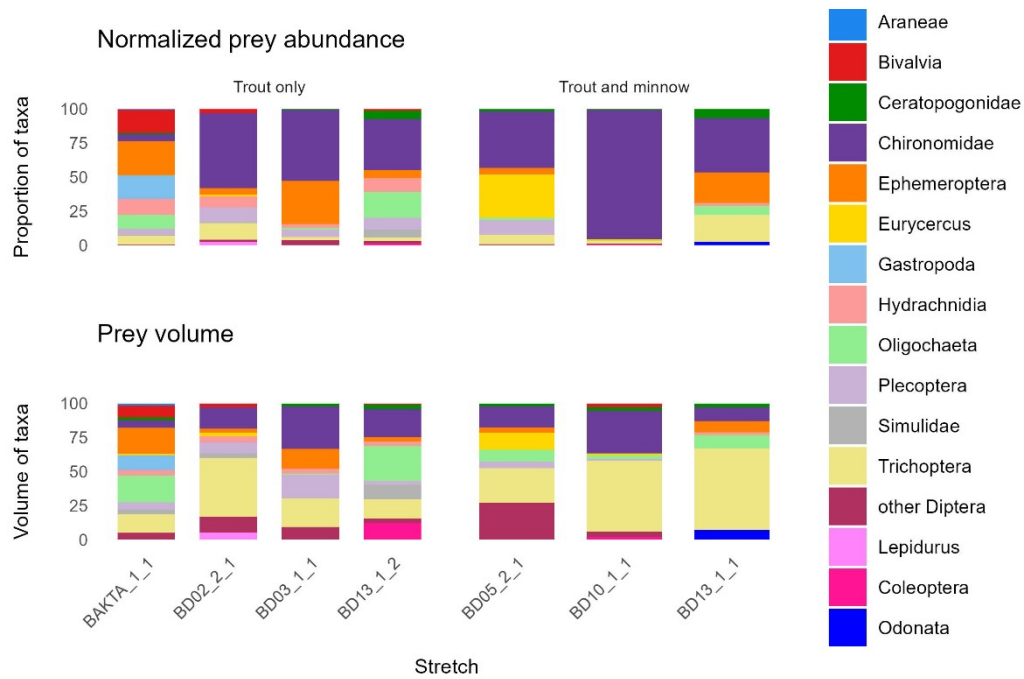


Figure 13. Normalized prey abundance and prey volume per taxon in MP and MA-stretches. The stretches seem to vary independently from minnow presence. Large taxa appear proportionally larger in prey volume in comparison to small taxa.

There is a visible difference in the Shannon index of MP and MA-stretches (Figure 14). However, Models 1 and 2 did not show a significant relationship between Shannon index and minnow presence, water current class or dominant type of bottom vegetation (Appendix 13). The MA-stretches BD02_2_1 and BD03_1_1 have similar values to the MP-stretches BD05_2_1 and BD13_1_1 around 1.4. The difference between groups stems from the other four stretches: BAKTA_1_1 and BD13_1_2 increase the mean value of the group without minnow. BD10_1_1 decreases it for the group with minnow, having the lowest index of all stretches.

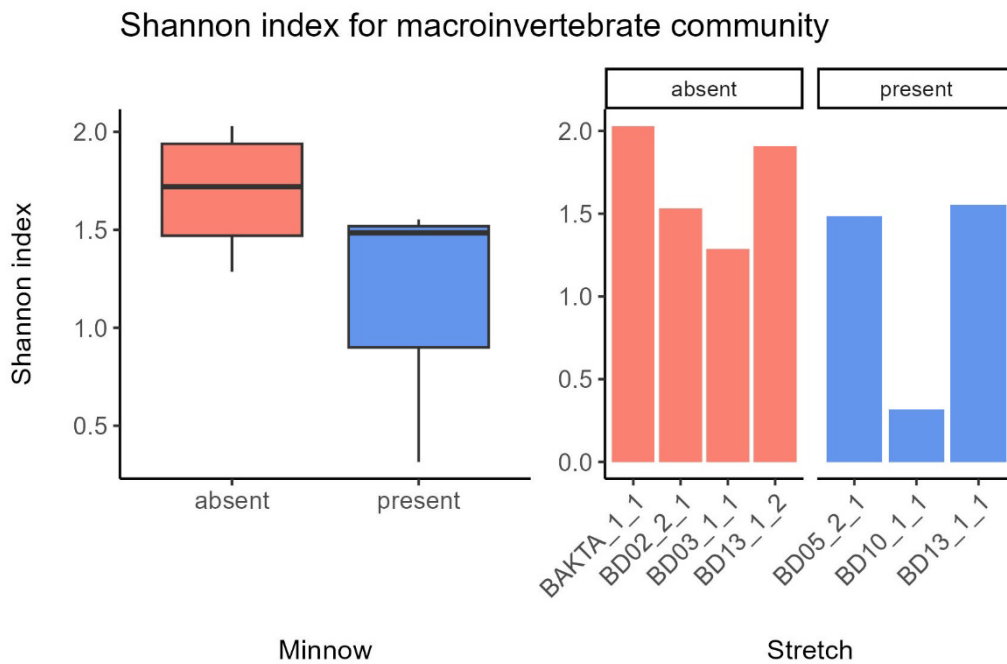


Figure 14. Shannon index for macroinvertebrate communities in MP (blue) and MA-stretches (red). The index seems on average to have a higher value in MA-stretches. BD10_1_1 has an exceptionally low index.

The Simpson index of the two groups have a similar relationship to each other as the Shannon index (Figure 15). Again, Models 1 and 2 did not show a significant relationship between Shannon index and minnow presence (Appendix 13).

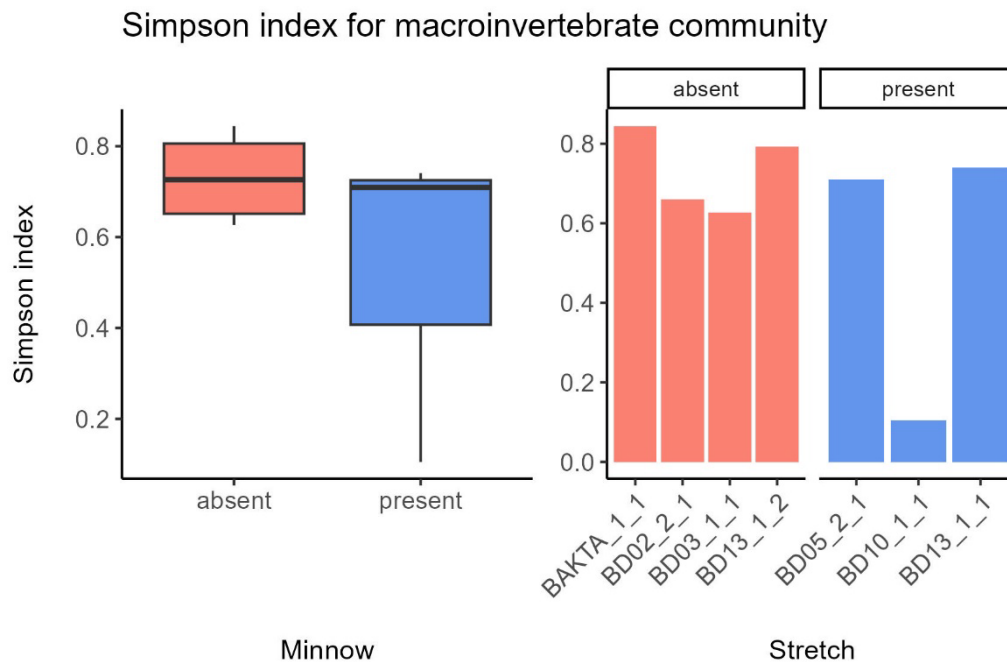


Figure 15. Simpson index for macroinvertebrate communities in MP (blue) and MA-stretches (red). Similarly to the Shannon index, the Simpson index seems on average to have a higher value in MA-stretches. Again, BD10_1_1 has the lowest index.

An NMDS using a matrix with taxa abundance per stretch shows a visible separation between MA and MP-stretches (Figure 16). NMDS1, which explains most variation between stretches, shows that there was essentially one stretched cluster containing both MP and MA stretches. Only BD13_1_1 was apart, and BD02_2_1 was also standing out slightly in the opposite direction. There was a separation between MP and MA stretches along NMDS2, only BD03_1_1 seemed to be more similar to MP stretches on NMDS2. This separation was also true for stretches that contained only charr or only minnow, all of them were closer to MA stretches on NMDS2. BD06_1_1 was closer to the MP stretches, making up the only exception.

The same NMDS with taxa positions in the multivariate space shows taxa in different distances to the center of both axis and to the two polygons (Figure 17).

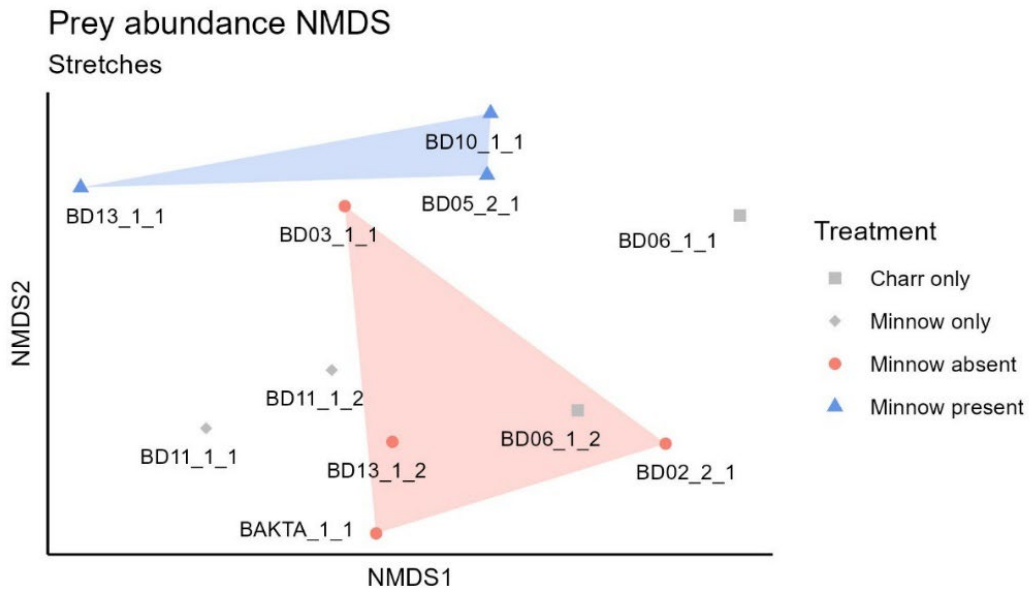


Figure 16. NMDS showing the differentness of macroinvertebrate communities between stretches. The MA-stretches (red polygon) are distinct from MP-stretches (blue polygon). Most stretches containing only minnow and only charr appear more similar to MA-stretches.

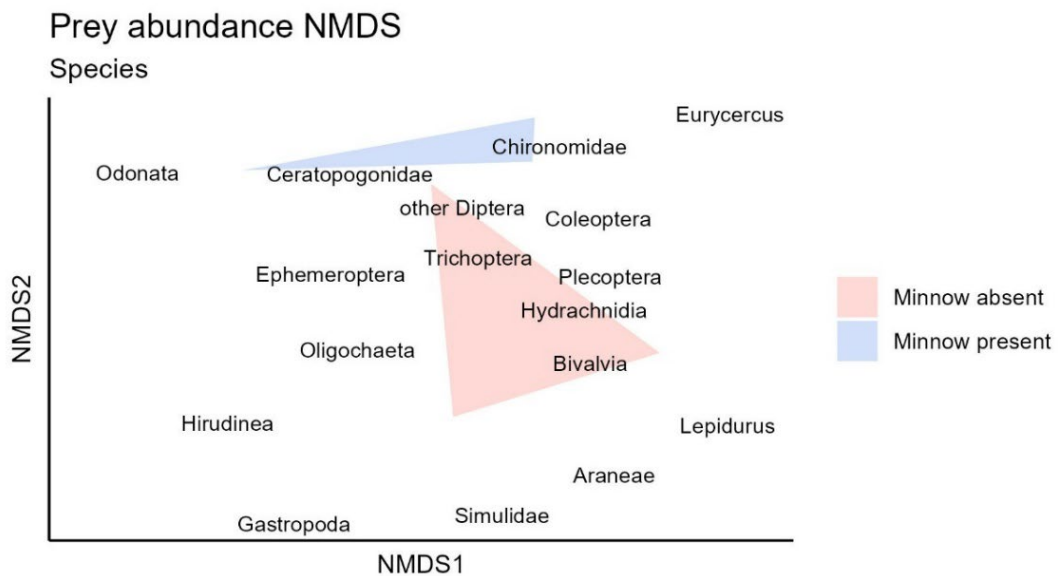


Figure 17. NMDS showing the contribution of single taxa to the differentness of macroinvertebrate communities between stretches. One group of taxa is closer to the center of the plot while the other spreads around it.

The taxa that are furthest away from the center of the multivariate space are largely overlapping with taxa whose variation among stretches explains least according to the SIMPER analysis (Figure 18). The SIMPER analysis further shows that *Chironomidae* alone explain more than 40 % of the total variation. *Ephemeroptera* explain more than 10 % and every other taxon explains less than 10 % of variation in macroinvertebrate abundance between the stretches.

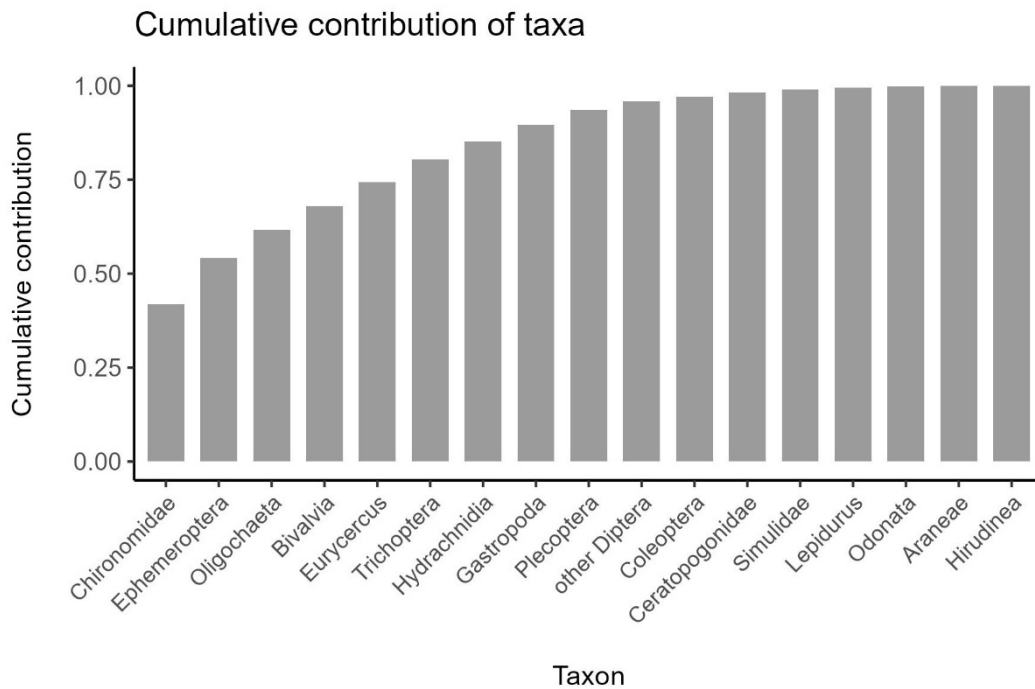


Figure 18. Cumulative contribution of taxa to the differentness between stretches. *Chironomidae* contribute by far most to variation between stretches, followed by *Ephemeroptera* and *Oligochaeta*. Starting at *Coleoptera* the contribution is close to none.

The full PERMANOVA with minnow presence, water current class and dominant type of bottom vegetation as predictors did not show that any of the predictors can significantly explain variation in macroinvertebrate abundance between stretches ($n_{MA} = 4$, $n_{MP} = 3$, $F(4,2) = 0.642$, $R^2 = 0.562$, $p = 0.882$, permutations = 5039). The PERMANOVA with only minnow presence as predictor also did not show any significant explanation of minnow presence ($n_{MA} = 4$, $n_{MP} = 3$, $F(1,5) = 1.007$, $R^2 = 0.168$, $p = 0.457$, permutations = 5039). According to the *betadisper()* function, the group variances of MP and MA stretches do not differ significantly, so I assume that the PERMANOVA results are produced by differences between the group centroids and not differences in dispersion.

3.5.2 Macroinvertebrate size

Model 1 with minnow presence, water current class and dominant type of bottom vegetation as predictors and model 2 with minnow presence as the only predictor returned no significant relationships between the mean size of *Ephemeroptera*, *Trichoptera* or *Chironomidae* and the presence of minnow ($n = 7$) (Appendix 13). There was also no relationship between any covariate and macroinvertebrate mean size. *Chironomidae* in stretches with phanerogams as the dominant type of bottom vegetation were almost significantly larger than in stretches with algae as the dominant vegetation ($\beta = 3.489$ mm, SE = 1.115, $p = 0.089$).

4. Discussion

This study has shown that minnow seem to affect juvenile trout in the investigated streams in some regards. Most interactions between trout and minnow that have been observed in lakes or hypothesized for streams could not be confirmed in these streams. However, I discovered that the length-at-age of trout from age class 3+ in stretches without minnow was significantly higher than where the two species live in sympatry, suggesting that minnow slow trout growth in their nursery streams. Condition-at-age on the other hand was not significantly related to minnow presence. Neither trout trophic position, trophic niche width or density seemed to be significantly affected by the presence of minnow. Lastly, I could not confirm that minnow significantly influenced the macroinvertebrate community of the investigated streams.

4.1 Age, length and condition

4.1.1 Influence on length

In the age classes 3+ and 4+ trout seemed to have a shorter length-at-age in the presence of minnow (Table 3, Table 4, Figure 4). This suggests slower annual growth of trout and is in accordance with the findings of Borgström et al. (1996) and Qvenild et al. (2024) who suggest resource competition as an influencing factor. However, there was only one individual in BD05_2_1 from an MP-stretch in the age class 4+. Therefore, the significant relationship between minnow presence and trout length-at-age can only be confidently established in the age class 3+. I did not observe any indication for increased trout growth between the age classes 0+ to 3+ in the presence of minnow as reported by Näslund et al. (1998). Trout in MP and MA-stretches started off with similar lengths at 0+ but the difference in length-at-age between both groups increased with each age class. A possible explanation for the delayed impact of minnow on trout length-at-age from age class 3+ is that resource competition with minnow did not set in immediately after the trout hatch. The habitat use of juvenile trout changes within their first years of life, as it moves from shallow to deeper parts of the stream (Maki-Petäys et al. 1997). Perhaps trout moved to a habitat that is occupied by minnow after trout reached the age class 2+, and only then started competing for resources, resulting in slower growth after they changed habitats. Alternatively, smaller trout were less sensitive to competition for food because they had lower energetic demands and were able to cope with lower resource levels (Persson & De Roos 2006).

4.1.2 Influence on condition

While trout condition was not significantly related to minnow presence (Table 5), a tendency was visible where condition-at-age from age class 1+ on was higher in stretches with minnow (Figure 5). This may however have been the result of a steep positive slope between age and condition in the MP-stretch BD13_1_1: one individual from the age class 2+ had an exceptionally high body condition (1.3) and possibly influenced the linear regression applied across MP-stretches considerably towards a positive slope. As mentioned in 4.1.1, there was only one individual in the age class 4+ among MP-stretches. At the same time there were multiple 4+ individuals in MA-stretches. While the relatively low condition in trout in the age class 4+ from MA-stretches influenced the MA-regression towards a more negative slope, there was only one individual in the age class 4+ to model body condition in MP-stretches. Therefore, the visible trend towards a better condition-at age in the presence of minnow was possibly influenced by missing data points for the age class 4+ in MA-stretches.

Trout in the age class 0+ had a considerable range in Fulton's K (0.571 - 1.104) while the condition-at-age seemed to become more similar in higher age classes, independently of minnow presence (Figure 5). This could have been the result of differing environmental advantages or disadvantages after hatching which evened out while the trout grew. It could have also stemmed from measuring inaccuracy of individuals at 0+. In small individuals measuring differences of few millimeters get translated into large differences when calculating Fulton's K. The influence of these measuring inaccuracies on Fulton's K gets smaller the longer the trout are, so the effect of measuring inaccuracies is strongest when the fish are the smallest.

According to the model (Table 5), trout in stretches where mosses dominated the bottom vegetation had a significantly better body condition than where algae or phanerogams dominated. This indicates that vegetation and possibly other environmental parameters in these streams had a clearer effect on trout condition than the presence of minnow, e.g. food availability and quality (Pender & Kwak 2002), parasite load (Stauffer et al. 2017) or other stream parameters (Kristensen & Closs 2008).

4.1.3 Age and length distribution

The age and size structure of trout differed strongly across stretches but not significantly between MP and MA-stretches (Figure 6, Figure 7). Jonsson and Jonsson (2011) suggest that juvenile trout possibly leave their nursery stream prematurely to avoid resource competition. There was only one individual in BD05_2_1 in the age class 4+ across all MP-stretches while there were multiple in the MA-stretches BAKTA_1_1 and BD02_2_1. Also, most individuals in the MP-stretches BD10_1_1 and BD13_1_1 were in the age class 0+, which is in line

with the findings of Jonsson and Jonsson (2011). However, the MP-stretch BD05_2_1 contained mostly individuals in the age class 3+, showing a later peak in the age distribution than any other stretch. In addition, the MA-stretch BD13_1_2 contained only individuals in the age class 0+ and has the lowest age average. Therefore, the age structure in BD05_2_1 and BD13_1_2 contradicted the notion that juvenile trout leave nursery streams earlier in the presence of minnow. Having said that, it is important to note that BD13_1_1 and BD13_1_2 lie in the same stream which overall contains minnow. Arguably, environmental parameters influenced the occurrence of certain age classes in different habitats (Maki-Petäys et al. 1997). Effects of environmental parameters potentially covered the effects the presence of minnow had on trout age and size structure leading to a mixed result. I propose that juvenile trout left their nursery stretches early when in competition with minnow, but abundant suitable habitat and resources in some streams like BD05_2_1 allowed higher age classes that need more resources to use the stretch. Conversely, there might not have been enough suitable habitat in stretches like BD13_1_2 to support older age classes than 0+.

According to Kaspersson & Höjesjö (2009) fewer individuals that are older than 0+ result in 0+-individuals having access to better microhabitats. This could on one hand mean that there were fewer younger individuals because more older individuals claimed good habitat and restrained 0+ trout in BD05_2_1 as well as BD03_1_1. On the other hand, it could indicate that there were more young individuals in stretches like BD10_1_1 and BD13_1_1 because older individuals were largely missing.

The silhouettes of trout age and length distributions (Figure 6, Figure 7) overlapped relatively well for each stretch, suggesting that the age estimation by otoliths was accurate. However, there was a gap in the age distribution for the age cohort 1+ in BD02_2_1 which was not visible in the length distribution hinting at an estimation error or an anomaly in the stretch.

4.2 Trophic position and niche width

4.2.1 Trophic position

Museth et al. (2010) reported trout and minnow diet to overlap in trout nursery streams. If this resulted in strong resource competition it could shift trout diet towards including new food items and thereby change its trophic position. This would be visible in a changed trout $\delta^{15}\text{N}$. However, I did not find a significant effect of minnow presence on the trophic position ($\delta^{15}\text{N}$) of trout estimated through SI analyses in the investigated streams (Figure 9, Appendix 10). This is in line with Suraci (2025) who found a high diet overlap between trout from MP and MA-stretches. Museth et al. (2010) also summarized from existing literature that high dietary overlap can on the one hand be viewed as an indicator for

interspecific competition because both species compete for access to their food source. A possible sign for this could have been the observed lower length-at-age of trout in MP-stretches. On the other hand, it could show missing competition since the species can both fill this niche. As observed by Museth et al. (2010), Suraci (2025) found the diet overlap between minnow and trout in the investigated streams to be intermediate to high and in this study I found that the trophic positions of minnow and trout in the investigated stretches did not significantly differ. Considering that trout and minnow diet and trout diet between MP and MA-stretches did not significantly differ, it is possible that even though the two species overlapped in diet, potential food competition did not lead to a diet change in trout. Perhaps this is why trout $\delta^{15}\text{N}$ did not differ depending on if minnow were present. However, the MA-stretch BD13_1_2 contained individuals with the highest $\delta^{15}\text{N}$, while the other MA-stretches seemed slightly lower in $\delta^{15}\text{N}$ than MP-stretches. Also, BD13_1_2 lies in a stream that contains minnow making it impossible to exclude an effect of minnow on stream-level. When BD13_1_2 was excluded from the linear mixed model described in 3.3.1, trout in MP-stretches had a higher $\delta^{15}\text{N}$ than trout in MA-stretches ($p = 0.059$), bordering on statistical significance at the $p = 0.05$ threshold (Appendix 14).

Trophic position generally increases with increasing age and a changing diet (Woodward & Hildrew 2002; Romanuk et al. 2011; Sánchez-Hernández et al. 2016), so I expected a positive slope between trout length and $\delta^{15}\text{N}$ (Figure 10). However, BD13_1_2, BD13_1_1 and BD10_1_1 did not follow this pattern and had individuals in the age class 0+ that were highest in $\delta^{15}\text{N}$ in their respective stretch. The comparably high trophic position of 0+ individuals from BD13_1_2 could not be explained by the individuals' diet: Suraci (2025) found the stomach content of trout in this stretch to consist mainly of *Chironomidae* with medium to full stomachs. It needs to be considered though that stomach contents only reflect an individual's recent diet. BD13_1_1 and BD10_1_1 contained a few individuals with noticeably high $\delta^{15}\text{N}$ as well and did not show any particularities in their diet either. One possible explanation for unexpectedly high $\delta^{15}\text{N}$ values, which I used as proxy for trophic position, is starvation or physiological stress (Colborne & Robinson 2013; Karlson et al. 2018). This is specifically true for species like trout that undergo large changes in life history (Bowes et al. 2014). Possibly, the high $\delta^{15}\text{N}$ in trout from BD13_1_2, BD13_1_1 and BD10_1_1 were artifacts from a starvation period earlier in 2024 since all noticeable individuals were in the age cohort 0+. In a post-hoc analysis I found an insignificant negative relationship between $\delta^{15}\text{N}$ and Fulton's K, where I used K as a measure for starvation (Appendix 14). BD13_1_1 and BD13_1_2 had the strongest negative relationship between body condition and $\delta^{15}\text{N}$, possibly indicating that starvation was the reason for their high $\delta^{15}\text{N}$ contents. This is supported by the fact that the two stretches are located in the same stream and factors leading to starvation

likely influenced the whole stream. BD10_1_1 on the other hand showed a positive relationship between body condition and $\delta^{15}\text{N}$, contradicting the hypothesis that starvation is the reason for the unusually high $\delta^{15}\text{N}$ values. I cannot eliminate the possibility that starvation, i.e. resource limitation in the past led to the unusually high $\delta^{15}\text{N}$ levels in BD13_1_2 and BD13_1_1 but it does not appear to have been responsible for the high level in BD10_1_1.

Another possible explanation for the unusually high $\delta^{15}\text{N}$ values in the individuals from BD13_1_1, BD13_1_2 and BD10_1_1 is that we introduced a positive bias in $\delta^{15}\text{N}$ when taking tissue samples from fish with a total length smaller than ~ 90 mm (Schielke & Post 2010) since all individuals that had unusually high $\delta^{15}\text{N}$ values were below 90 mm in length.

4.2.2 Niche width

The isotopic niche width of trout was not influenced by minnow presence, water current class or dominant type of bottom vegetation (Appendix 11). Except for BD10_1_1 the niche widths across stretches were fairly similar (Figure 11). I used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to calculate the isotopic niche width. I discussed $\delta^{15}\text{N}$ in 4.2.1 since I used it as proxy for trophic position. The wide $\delta^{13}\text{C}$ range in BD10_1_1 could indicate that trout in this stretch fed on isotopically distinct carbon sources with different origins (Post 2002). Hill et al. (2008) found in stream experiments that algal $\delta^{13}\text{C}$ is strongly influenced by light and nutrients. This is likely also visible in the varying levels of algal $\delta^{13}\text{C}$ in my analysis (Figure 8), which range from $-17.4 \delta^{13}\text{C}/\text{‰}$ in BD05_2 to $-32.6 \delta^{13}\text{C}/\text{‰}$ in BD13_1. BD10_1_1 was the longest stretch sampled (80 m) and thus contained a variety of habitats, that likely vary in light exposure and nutrient availability. This could have created areas within the stretch where algae differed in $\delta^{13}\text{C}$ and as part of the trophic base these differences in $\delta^{13}\text{C}$ were transferred to higher trophic levels. Possibly, the trout from BD10_1_1 that I used for SIA were feeding in different $\delta^{13}\text{C}$ -areas which resulted in a large $\delta^{13}\text{C}$ range and in turn a wide trophic niche. BD10_1_1 was also the only stretch out of the three MP-stretches where there was any niche overlap between trout and minnow. Since the $\delta^{13}\text{C}$ in minnow was consistently between $-23 \delta^{13}\text{C}/\text{‰}$ and $-30 \delta^{13}\text{C}/\text{‰}$ the niche overlap between minnow and trout in BD10_1_1 was possibly a result of differing $\delta^{13}\text{C}$ sources for trout along the stretch and the resulting wide niche. In BD05_2_1 and BD13_1_1 it seems like trout generally had lower $\delta^{13}\text{C}$ than minnow. Since the trophic position and diet of trout and minnow was relatively similar (Suraci 2025) this could indicate that trout and minnow fed on the same prey items but foraged in different areas of the stream, resulting in different $\delta^{13}\text{C}$ signatures. However, Suraci (2025) note that trout generally seemed to rely more on terrestrial insects in their diet than minnow, even if not significantly. $\delta^{13}\text{C}$ from terrestrial input is distinguishable from algal $\delta^{13}\text{C}$ (Finlay 2001) and visible in a more negative signature (Besser et

al. 2022). Thus, the more positive $\delta^{13}\text{C}$ -value of minnow in BD05_2_1 and BD13_1_1 could be explained by less intake of terrestrial input than trout. Terrestrial insects were a larger part of trout diet in BD10_1_1 than any other stretch and BD10_1_1 also contained the individual with the lowest $\delta^{13}\text{C}$ -value, supporting this notion.

4.3 Trout density

I could not detect a significant influence of minnow presence or density on trout density in the studied streams, even though differences in trout density between stretches were visible (Figure 12). Neither water current class nor the dominant type of bottom vegetation were significant factors. These findings did not change when taking into account that I could not use the *Seber3* method to estimate the number of individuals in BD13_1_1 and only considered the absolute catch size. Previous studies have shown reduced trout recruitment and biomass after the introduction of minnow through either resource competition (Borgstrøm et al. 1996; Qvenild et al. 2024) or predation of eggs and alevins (Museth et al. 2007; Borgstrøm et al. 2010; Tiberti et al. 2022). If minnow had a strong impact on recruitment through predation of trout eggs or alevins, this should have been visible in these stretches and would have resulted in lower trout density. As I could not detect a difference in density between MP and MA-stretches predation of trout in early life stages was not supported. This aligns with Suraci (2025) who did not find any indication of interspecific predation in the investigated streams.

A variety of trout density predictors apart from minnow presence has been described in previous studies (Beard & Carline 1991; Hesthagen et al. 1999; Jutila et al. 2001; Kristensen & Closs 2008; Louison & Stelzer 2016). They suggest that trout density is dependent on a variety of biotic and abiotic factors and thereby highly stream dependent. I assume that in the streams we investigated, minnow presence and density were at least not strong factors influencing trout density at the time of sampling.

4.4 Prey community

4.4.1 Prey diversity and abundance

When comparing the individual Shannon and Simpson index values of each stretch, there seemed to be higher diversity in MA-stretches (Figure 14, Figure 15). However, this difference was not statistically significant (Appendix 13) and largely driven by BD10_1_1, which had by far the lowest diversity according to both indices: most invertebrates we collected there were *Chironomidae* larvae or pupae (Figure 13). This is surprising since it was the longest stretch we measured (80 m), and we expected it to cover comparably many habitats in the stream and display high macroinvertebrate diversity. It was also the stretch with by far the

highest isotopic niche width in the trout's diet. Næstad & Brittain (2010) documented an increased dominance of *Chironomidae* and *Oligochaeta* in a formerly allopatric trout lake four years after the introduction of minnow. We have no information about the first appearance of minnow in the streams we investigated but possibly, the colonization of BD10_1 by minnow happened sufficiently long ago so that minnow could have had a similar effect on the macroinvertebrate community and shift the composition towards being dominated by *Chironomidae*. However, this was not a general pattern, as the relative abundance of *Chironomidae* varied between stretches (Figure 13). This SIMPER analysis confirmed that *Chironomidae* abundance explained most differences between stretches among taxa (Figure 18) but there was not a clear differentiation between MP and MA-stretches. *Oligochaeta* even seemed to have been slightly more abundant in MA-stretches (Figure 13).

The NMDS showed no overlap between the polygons of MP and MA-stretches, indicating a separation between the two groups (Figure 16). But it is visible that differences within the two groups were in part larger than between them: BD03_1_1 is closer to the MP-polygon than to the other MA-stretches. In the NMDS showing the position of individual taxa in the multivariate space (Figure 17) a group of taxa is visible that is situated further away from the center of the multivariate space, with the MA-polygon between them and the MP-polygon: *Lepidurus*, *Araneae*, *Simulidae*, *Gastropoda* and *Hirudinea*. This means that these taxa were mainly present in at least some MA-stretches and less or not at all in MP-stretches. Since these are mostly taxa that contributed very little variation according to the SIMPER analysis and were very few in number (Appendix 4), it seems like a lot of differentness in the NMDS between stretches comes from few rare taxa that were only found in MA-stretches. This aligns with previous results: the Shannon index differed more between MP and MA-stretches than the Simpson index, emphasizing the presence of rare taxa in MA-stretches. Additionally, the relative abundances were visibly more diverse (Figure 13). This could be the result of higher pressure on the macroinvertebrate community when minnow were present. When the generalist minnow (Oscoz et al. 2006) colonized these streams where they overlapped in diet with generalist trout (Suraci 2025), the predation pressure on all available prey species probably increased. In consequence of this, macroinvertebrate species that naturally occur in low numbers were potentially preyed upon until they were locally extinct or until their numbers were so low that it was unlikely to detect them. Thus, one possible effect of minnow presence on the macroinvertebrate community is a negative influence on the abundance of rare taxa. This is in accordance with Osorio et al. (2022) who found non-native minnow to be responsible for negatively influencing the occurrence of multiple taxa. However, this apparent relationship between the absence of rare taxa and the presence of minnow was not clear enough in the

overall differentness between MP and MA-stretches to be significant in the conducted PERMANOVA.

The differences in macroinvertebrate community might have also been influenced by environmental variables like canopy cover and resource supply (Tonkin 2014) or conductivity and stream size measures (Melo 2009) which I did not consider in my analysis. A comparison of the PCoA of environmental variables (Figure 1) and the prey abundance NMDS (Figure 16, Figure 17) hints at this: there was a considerable overlap between the relative positions of stretches to each other in both multivariate spaces. BD13_1_1 was relatively isolated, BD02_2_1 was on the other side from BD13_1_1 of the first dimension while BAKTA_1_1 was in the center of it in the vicinity of BD13_1_2. While this was not true for all stretches, it hints at a potential influence of environmental variables on the macroinvertebrate community in the investigated stretches.

4.4.2 Prey size

I did not detect any significant influence of minnow presence on the average size of the five largest individuals of *Ephemeroptera*, *Trichoptera* or *Chironomidae* (Appendix 13). Water current class and the dominant type of bottom vegetation were not significantly influential either. Suraci (2025) also found that trout prey item lengths did not significantly differ between MP and MA-stretches. Næstad & Brittain (2010) explain how visual predators hunt large macroinvertebrates that are easy to see. Many *Ephemeroptera*, *Trichoptera* and *Chironomidae* species are comparably large so an impact on the size structure of these taxa could be expected after the colonization of the investigated stretches by visually foraging minnow (Huhta et al. 1999). Possibly, the effect of minnow presence on taxon size was hidden by the low taxonomic resolution I used for the macroinvertebrates. Since I calculated the average taxon size from the five biggest individuals in each taxon, smaller species in the taxon might have been systematically discriminated and a change in species size was possibly hidden.

4.5 Limitations

The low sample size of stretches with ($n = 3$) and without minnow ($n = 4$) possibly obscured interactions on stretch-level in my models. Also were the stretches we investigated very diverse in environmental conditions so that effects of minnow presence could have been hidden by effects from environmental differences. We took the samples in a time frame of 20 days in late August. This means seasonal changes like insect hatches could have happened during our sampling and thus resulted in false differences between stretches. Another limiting factor is that there is almost no information on when minnow first appeared in many streams in this area. Possibly, the investigated streams are in

different stages of minnow colonization and thus show differing effects of their presence.

4.6 Conclusion

Comparing my results with the literature revealed multiple relevant tendencies next to the sole statistically significant finding that trout in the presence of minnow were smaller in the age class 3+: I discovered that trout possibly left their nursery streams earlier when in sympatry with minnow, which could have influenced trout age structure. Also, the trophic position of trout in allopatry was not significantly different from trout in sympatry, but this could have been due to the high trophic positions in one specific stretch which was adjacent to a stretch with minnow present. If this anomalous stretch was excluded, the trophic positions of trout in sympatry might have been higher than of trout in allopatry. The $\delta^{13}\text{C}$ signature of minnow and trout in sympatry differed, suggesting that the two species fed in different parts of the stream. Lastly, there seemed to have been fewer rare macroinvertebrate taxa present in stretches with minnow. This could indicate that minnow presence influences the trout prey community in terms of rare species occurrence. I could, however, not find any influence of minnow on trout condition, density or prey size.

5. Outlook

Despite its limitations, I could show a significant influence of minnow presence on the trout populations in the study area as well as multiple insignificant tendencies. Trout in the Swedish Arctic face several threats in the Anthropocene. As a cold-water species, brown trout are increasingly impaired by rising average temperatures. Being additionally affected by non-native species like minnow could negatively impact their ability to cope with climate change and other anthropogenic challenges. Possibly it is a question of time until the impact of minnow which has been described in previous studies starts to fully act in the investigated area.

It becomes clear that to protect native trout and to fully capture the effects non-native minnow have on trout in their nursery streams continued research is needed. Repeatedly investigating a larger number of streams that ideally are similar in their environmental parameters could uncover interactions that this thesis missed. At the same time, streams that are not yet colonized by minnow need to be monitored to capture the moment when colonization happens. This way, progressive change can be documented. This thesis serves as a foundation for such a long-term study. If viable, the knowledge generated can be used for minnow-removal projects in the future.

References

- Arismendi, I., Penaluna, B.E., Dunham, J.B., García de Leaniz, C., Soto, D., Fleming, I.A., Gomez-Uchida, D., Gajardo, G., Vargas, P.V. & León-Muñoz, J. (2014). Differential invasion success of salmonids in southern Chile: patterns and hypotheses. *Reviews in Fish Biology and Fisheries*, 24 (3), 919–941. <https://doi.org/10.1007/s11160-014-9351-0>
- Beard, T.D., Jr. & Carline, R.F. (1991). Influence of Spawning and Other Stream Habitat Features on Spatial Variability of Wild Brown Trout. *Transactions of the American Fisheries Society*, 120 (6), 711–722. [https://doi.org/10.1577/1548-8659\(1991\)120<0711:IOSAOS>2.3.CO;2](https://doi.org/10.1577/1548-8659(1991)120<0711:IOSAOS>2.3.CO;2)
- Bellard, C., Cassey, P. & Blackburn, T.M. (2016). Alien species as a driver of recent extinctions. *Biology Letters*, 12 (2), 20150623. <https://doi.org/10.1098/rsbl.2015.0623>
- Besser, A.C., Elliott Smith, E.A. & Newsome, S.D. (2022). Assessing the potential of amino acid $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis in terrestrial and freshwater ecosystems. *Journal of Ecology*, 110 (4), 935–950. <https://doi.org/10.1111/1365-2745.13853>
- Borgström, R., Brittain, J., Hasle, K., Skjølås, S. & Dokk, J. (1996). qve. *Nordic Journal of Freshwater Research*, 72, 30–38
- Borgström, R., Museth, J. & Brittain, J.E. (2010). The brown trout (*Salmo trutta*) in the lake, Øvre Heimdalsvatn: long-term changes in population dynamics due to exploitation and the invasive species, European minnow (*Phoxinus phoxinus*). *Hydrobiologia*, 642 (1), 81–91. <https://doi.org/10.1007/s10750-010-0161-7>
- Bowes, R.E., Lafferty, M.H. & Thorp, J.H. (2014). Less means more: nutrient stress leads to higher $\delta^{15}\text{N}$ ratios in fish. *Freshwater Biology*, 59 (9), 1926–1931. <https://doi.org/10.1111/fwb.12396>
- Bradley, B.A., Beaury, E.M., Gallardo, B., Ibáñez, I., Jarnevich, C., Morelli, T.L., Sofaer, H.R., Sorte, C.J.B. & Vilà, M. (2024). Observed and Potential Range Shifts of Native and Nonnative Species with Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 55 (Volume 55, 2024), 23–40. <https://doi.org/10.1146/annurev-ecolsys-102722-013135>
- Carmona-Catot, G., Magellan, K. & García-Berthou, E. (2013). Temperature-Specific Competition between Invasive Mosquitofish and an Endangered Cyprinodontid Fish. *PLOS ONE*, 8 (1), e54734. <https://doi.org/10.1371/journal.pone.0054734>
- Cheng, L., Wang, E., Li, W., Yu, X. & Liao, X. (2022). The Complete Mitochondrial Genome of Eurasian Minnow (*Phoxinus* cf. *Phoxinus*) from the Heilongjiang River, and Its Phylogenetic Implications. *Animals*, 12 (21), 2960. <https://doi.org/10.3390/ani12212960>
- Christensen, R.H.B. (2024). *ordinal: Regression Models for Ordinal Data* (2023.12-4.1). <https://cran.r-project.org/web/packages/ordinal/index.html> [2025-09-01]
- Colborne, S.F. & Robinson, B.W. (2013). Effect of nutritional condition on variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values in Pumpkinseed sunfish (*Lepomis gibbosus*) fed different diets. *Environmental Biology of Fishes*, 96 (4), 543–554. <https://doi.org/10.1007/s10641-012-0040-3>
- Comte, L., Buisson, L., Daufresne, M. & Grenouillet, G. (2013). Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. *Freshwater Biology*, 58 (4), 625–639. <https://doi.org/10.1111/fwb.12081>
- Filipsson, O. (1994). NYA FISKBESTÅND GENOM INPLANTERING ELLER SPRIDNING AV FISK. *Information från Sötvattenslaboratoriet*, 2, 1–65

- Finlay, J.C. (2001). Stable-Carbon-Isotope Ratios of River Biota: implications for Energy Flow in Lotic Food Webs. *Ecology*, 82 (4), 1052–1064. [https://doi.org/10.1890/0012-9658\(2001\)082\[1052:SCIROR\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1052:SCIROR]2.0.CO;2)
- Fulton, T.W. (1904). *The Rate of Growth of Fishes*.
- Gabrielsen, S.-E., Lennox, R.J., Wiers, T. & Barlaup, B.T. (2021). Saltwater spawning grounds of sea-run brown trout (*Salmo trutta*) in tidal waters of a major Norwegian river. *Environmental Biology of Fishes*, 104 (10), 1207–1213. <https://doi.org/10.1007/s10641-021-01147-y>
- Gallardo, B., Clavero, M., Sánchez, M.I. & Vilà, M. (2016). Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology*, 22 (1), 151–163. <https://doi.org/10.1111/gcb.13004>
- Garcia-Raventós, A., Martins, F.M.S., Teixeira, A., Sousa, R., Froufe, E., Varandas, S., Lopes-Lima, M., Beja, P. & Filipe, A.F. (2020). Origin and history of Phoxinus (Cyprinidae) introductions in the Douro Basin (Iberian Peninsula): an update inferred from genetic data. *Biological Invasions*, 22 (8), 2409–2419. <https://doi.org/10.1007/s10530-020-02279-5>
- Gower, J.C. (1971). A General Coefficient of Similarity and Some of Its Properties. *Biometrics*, 27 (4), 857–871. <https://doi.org/10.2307/2528823>
- Halvorsen, M. & Jørgensen, L. (1996). Lake-use by juvenile Atlantic salmon (*Salmo salar* L.) and other salmonids in northern Norway. *Ecology of Freshwater Fish*, 5 (1), 28–36. <https://doi.org/10.1111/j.1600-0633.1996.tb00034.x>
- Hanisch, J.R., Tonn, W.M., Paszkowski, C.A. & Scrimgeour, G.J. (2010). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Signatures in Muscle and Fin Tissues: Nonlethal Sampling Methods for Stable Isotope Analysis of Salmonids. *North American Journal of Fisheries Management*, 30 (1), 1–11. <https://doi.org/10.1577/M09-048.1>
- Hayes, C., Mitchell, A., Mellin, C., Booth, D.J., Ravasi, T. & Nagelkerken, I. (2024). Ecological generalism and physiology mediate fish biogeographic ranges under ocean warming. *Proceedings of the Royal Society B: Biological Sciences*, 291 (2015), 20232206. <https://doi.org/10.1098/rspb.2023.2206>
- Hesthagen, T., Heggenes, J., Larsen, B.M., Berger, H.M. & Forseth, T. (1999). Effects of Water Chemistry and Habitat on the Density of Young Brown Trout *Salmo trutta* in Acidic Streams. *Water, Air, and Soil Pollution*, 112 (1), 85–106. <https://doi.org/10.1023/A:1005068404832>
- Hill, W.R., Fanta, S.E. & Roberts, B.J. (2008). ^{13}C dynamics in benthic algae: Effects of light, phosphorus, and biomass development. *Limnology and Oceanography*, 53 (4), 1217–1226. <https://doi.org/10.4319/lo.2008.53.4.1217>
- Huhta, A., Muotka, T., Juntunen, A. & Yrjönen, M. (1999). Behavioural interactions in stream food webs: the case of drift-feeding fish, predatory invertebrates and grazing mayflies. *Journal of Animal Ecology*, 68 (5), 917–927. <https://doi.org/10.1046/j.1365-2656.1999.00339.x>
- Husson, F., Josse, J., Le, S. & Mazet, J. (2024). *FactoMineR: Multivariate Exploratory Data Analysis and Data Mining* (2.11). <https://cran.r-project.org/web/packages/FactoMineR/index.html> [2025-06-18]
- Jackson, A. & Parnell, A. (2023). *SIBER: Stable Isotope Bayesian Ellipses in R* (2.1.9). <https://cran.r-project.org/web/packages/SIBER/index.html> [2025-04-28]
- Jensen, H., Kiljunen, M. & Amundsen, P.-A. (2012). Dietary ontogeny and niche shift to piscivory in lacustrine brown trout *Salmo trutta* revealed by stomach content and stable isotope analyses. *Journal of Fish Biology*, 80 (7), 2448–2462. <https://doi.org/10.1111/j.1095-8649.2012.03294.x>

- Jonsson, B. (1989). Life history and habitat use of Norwegian brown trout (*Salmo trutta*). *Freshwater Biology*, 21 (1), 71–86. <https://doi.org/10.1111/j.1365-2427.1989.tb01349.x>
- Jonsson, B. & Jonsson, N. (2011). *Ecology of atlantic salmon and brown Trout: habitat as a template for life histories*. Springer. (Fish and fisheries series; 33)
- Jonsson, N., Næsje, T.F., Jonsson, B., Saksgård, R. & Sandlund, O.T. (1999). The influence of piscivory on life history traits of brown trout. *Journal of Fish Biology*, 55 (6), 1129–1141. <https://doi.org/10.1111/j.1095-8649.1999.tb02064.x>
- José Pinheiro (S version), Douglas Bates (up to 2007), Saikat DebRoy (up to 2002), Deepayan Sarkar (up to 2005), EISPACK authors (src/rs.f), Siem Heisterkamp (Author fixed sigma), Bert Van Willigen (Programmer fixed sigma), Johannes Ranke (varConstProp()), & R Core Team (2025). *nlme: Linear and Nonlinear Mixed Effects Models* (3.1-168). <https://cran.r-project.org/web/packages/nlme/index.html> [2025-06-12]
- Jutila, E., Ahvonen, A. & Julkunen, M. (2001). Instream and catchment characteristics affecting the occurrence and population density of brown trout, *Salmo trutta* L., in forest brooks of a boreal river basin. *Fisheries Management and Ecology*, 8 (6), 501–511. <https://doi.org/10.1046/j.1365-2400.2001.00253.x>
- Karlson, A.M.L., Reutgard, M., Garbaras, A. & Gorokhova, E. (2018). Isotopic niche reflects stress-induced variability in physiological status. *Royal Society Open Science*, 5 (2), 171398. <https://doi.org/10.1098/rsos.171398>
- Kaspersson, R. & Höjesjö, J. (2009). Density-dependent growth rate in an age-structured population: a field study on stream-dwelling brown trout *Salmo trutta*. *Journal of Fish Biology*, 74 (10), 2196–2215. <https://doi.org/10.1111/j.1095-8649.2009.02227.x>
- Kassambara, A. & Mundt, F. (2020). *factoextra: Extract and Visualize the Results of Multivariate Data Analyses* (1.0.7). <https://cran.r-project.org/web/packages/factoextra/index.html> [2025-06-18]
- Keller, R.P., Geist, J., Jeschke, J.M. & Kühn, I. (2011). Invasive species in Europe: ecology, status, and policy. *Environmental Sciences Europe*, 23 (1), 23. <https://doi.org/10.1186/2190-4715-23-23>
- Kristensen, E.A. & Closs, G.P. (2008). Environmental variability and population dynamics of juvenile brown trout (*Salmo trutta*) in an upstream and downstream reach of a small New Zealand river. *New Zealand Journal of Marine and Freshwater Research*, 42 (1), 57–71. <https://doi.org/10.1080/00288330809509936>
- Larsen, B.M., Sandlund, O.T., Berger, H.M. & Hesthagen, T. (2007). Invasives, Introductions and Acidification: The Dynamics of a Stressed River Fish Community. In: Brimblecombe, P., Hara, H., Houle, D., & Novak, M. (eds) *Acid Rain - Deposition to Recovery*. Springer Netherlands. 285–291. https://doi.org/10.1007/978-1-4020-5885-1_31
- Lenth, R.V., Banfai, B., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Piaskowski, J., Riebl, H. & Singmann, H. (2025). *emmeans: Estimated Marginal Means, aka Least-Squares Means* (1.11.1). <https://cran.r-project.org/web/packages/emmeans/index.html> [2025-06-19]
- Levin, L.A. & Crooks, J.A. (2011). 7.03 - Functional Consequences of Invasive Species in Coastal and Estuarine Systems. In: Wolanski, E. & McLusky, D. (eds) *Treatise on Estuarine and Coastal Science*. Academic Press. 17–51. <https://doi.org/10.1016/B978-0-12-374711-2.00704-X>
- Lewis, S.T., Salerno, J.D., Sanderson, J.S. & Kanno, Y. (2024). An experimental test of intra- and inter-specific competition between invasive western

- mosquitofish (*Gambusia affinis*) and native plains topminnow (*Fundulus sciadicus*). *Freshwater Biology*, 69 (8), 1131–1143.
<https://doi.org/10.1111/fwb.14295>
- Lien, L. (1981). Biology of the minnow *Phoxinus phoxinus* and its interactions with brown trout *Salmo trutta* in Øvre Heimdalsvatn, Norway. *Ecography*, 4 (3), 191–200. <https://doi.org/10.1111/j.1600-0587.1981.tb00997.x>
- Louison, M.J. & Stelzer, R.S. (2016). Use of first-order tributaries by brown trout (*Salmo trutta*) as nursery habitat in a cold water stream network. *Ecology of Freshwater Fish*, 25 (1), 133–140. <https://doi.org/10.1111/eff.12197>
- Maechler, M., original), P.R. (Fortran, original), A.S. (S, original), M.H. (S, Hornik [trl, K., maintenance(1999-2000)), ctb] (port to R., Studer, M., Roudier, P., Gonzalez, J., Kozłowski, K., pam()), E.S. (fastpam options for & Murphy (volume.ellipsoid({d >= 3})), K. (2025). *cluster: “Finding Groups in Data”: Cluster Analysis Extended Rousseeuw et al. (2.1.8.1)*. <https://cran.r-project.org/web/packages/cluster/index.html> [2025-04-07]
- Maki-Petäys, A., Muotka, T., Huusko, A., Tikkanen, P. & Kreivi, P. (1997). Seasonal changes in habitat use and preference by juvenile brown trout, *Salmo trutta*, in a northern boreal river. *Canadian Journal of Fisheries and Aquatic Sciences*, 54 (3), 520–530. <https://doi.org/10.1139/f96-311>
- McGeoch, M.A., Butchart, S.H.M., Spear, D., Marais, E., Kleynhans, E.J., Symes, A., Chanson, J. & Hoffmann, M. (2010). Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. *Diversity and Distributions*, 16 (1), 95–108.
<https://doi.org/10.1111/j.1472-4642.2009.00633.x>
- Melo, A.S. (2009). Explaining dissimilarities in macroinvertebrate assemblages among stream sites using environmental variables. *Zoologia (Curitiba)*, 26, 79–84. <https://doi.org/10.1590/S1984-46702009000100013>
- Mollot, G., Pantel, J.H. & Romanuk, T.N. (2017). Chapter Two - The Effects of Invasive Species on the Decline in Species Richness: A Global Meta-Analysis. In: Bohan, D.A., Dumbrell, A.J., & Massol, F. (eds) *Advances in Ecological Research*. Academic Press. 61–83.
<https://doi.org/10.1016/bs.aecr.2016.10.002>
- Museth, J., Borgstrøm, R. & Brittain, J.E. (2010). Diet overlap between introduced European minnow (*Phoxinus phoxinus*) and young brown trout (*Salmo trutta*) in the lake, Øvre Heimdalsvatn: a result of abundant resources or forced niche overlap? *Hydrobiologia*, 642 (1), 93–100.
<https://doi.org/10.1007/s10750-010-0162-6>
- Museth, J., Hesthagen, T., Sandlund, O.T., Thorstad, E.B. & Ugedal, O. (2007). The history of the minnow *Phoxinus phoxinus* (L.) in Norway: from harmless species to pest. *Journal of Fish Biology*, 71 (sd), 184–195.
<https://doi.org/10.1111/j.1095-8649.2007.01673.x>
- Næstad, F. & Brittain, J.E. (2010). Long-term changes in the littoral benthos of a Norwegian subalpine lake following the introduction of the European minnow (*Phoxinus phoxinus*). *Hydrobiologia*, 642 (1), 71–79.
<https://doi.org/10.1007/s10750-010-0160-8>
- Näslund, I., Degerman, E. & Nordwall, F. (1998). Brown trout (*Salmo trutta*) habitat use and life history in Swedish streams: possible effects of biotic interactions. *Canadian Journal of Fisheries and Aquatic Sciences*, 55 (4), 1034–1042. <https://doi.org/10.1139/f97-313>
- Ogle, D.H., Doll, J.C., Wheeler, A.P. & Dinno, A. (2015). FSA: Simple Fisheries Stock Assessment Methods. <https://doi.org/10.32614/CRAN.package.FSA>
- Oscoz, J., Leunda, P., Miranda, R. & Escala, M. (2006). Summer feeding relationships of the co-occurring *Phoxinus phoxinus* and *Gobio lozanoi* (Cyprinidae) in an Iberian River. *Folia Zoologica*,
<https://www.semanticscholar.org/paper/Summer-feeding-relationships-of->

- the-co-occurring-in-Oscoz-Leunda/bde6b3a90a0c9ab1b561c3326d4bc018f740e651 [2025-08-11]
- Osorio, V., Puig, A., Buchaca, T., Sabás, I., Miró, A., Lucati, F., Suh, J., Pou-Rovira, Q. & Ventura, M. (2022). Non-native minnows cause much larger negative effects than trout on littoral macroinvertebrates of high mountain lakes. *Biological Conservation*, 272, 109637–109637. <https://doi.org/10.1016/j.biocon.2022.109637>
- Palandačić, A., Naseka, A., Ramler, D. & Ahnelt, H. (2017). Contrasting morphology with molecular data: an approach to revision of species complexes based on the example of European Phoxinus (Cyprinidae). *BMC Evolutionary Biology*, 17 (1), 184. <https://doi.org/10.1186/s12862-017-1032-x>
- Paško, Ł., Kuszniery, J., Maślak, R., Tagayev, D., Sergiel, A., Pietras-Lebioda, A. & Borczyk, B. (2014). Morphometric Exploration of Diversity of the Eurasian Minnow *Phoxinus phoxinus*: A Case Study of a Widely Distributed Palaearctic Fish. *Annales Zoologici Fennici*, 51 (4), 399–412. <https://doi.org/10.5735/086.051.0401>
- Pender, D.R. & Kwak, T.J. (2002). Factors Influencing Brown Trout Reproductive Success in Ozark Tailwater Rivers. *Transactions of the American Fisheries Society*, 131 (4), 698–717. [https://doi.org/10.1577/1548-8659\(2002\)131<0698:FIBTRS>2.0.CO;2](https://doi.org/10.1577/1548-8659(2002)131<0698:FIBTRS>2.0.CO;2)
- Persson, L. & De Roos, A.M. (2006). Food-dependent individual growth and population dynamics in fishes. *Journal of Fish Biology*, 69 (sc), 1–20. <https://doi.org/10.1111/j.1095-8649.2006.01269.x>
- Post, D.M. (2002). Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology*, 83 (3), 703–718. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)
- QGIS Geographic Information System (3.30) (2025). QGIS Association. <http://www.qgis.org>
- Qvenild, T., Hesthagen, T. & Museth, J. (2024). A long-term study of the impact of the invasive species Eurasian minnow *Phoxinus phoxinus* on brown trout *Salmo trutta* production in a high mountain lake, Southern Norway. *Fauna norvegica*, 43, 1–11. <https://doi.org/10.5324/fn.v43i0.5826>
- R Core Team (2023). *R: A Language and Environment for Statistical Computing* (R version 4.3.0 (2023-04-21 ucrt)). R Foundation for Statistical Computing. <https://www.R-project.org/>
- Romanuk, T.N., Hayward, A. & Hutchings, J.A. (2011). Trophic level scales positively with body size in fishes. *Global Ecology and Biogeography*, 20 (2), 231–240. <https://doi.org/10.1111/j.1466-8238.2010.00579.x>
- Sánchez-Hernández, J., Eloranta, A.P., Finstad, A.G. & Amundsen, P. (2016). Community structure affects trophic ontogeny in a predatory fish. *Ecology and Evolution*, 7 (1), 358–367. <https://doi.org/10.1002/ece3.2600>
- Schielke, E.G. & Post, D.M. (2010). Size matters: comparing stable isotope ratios of tissue plugs and whole organisms. *Limnology and Oceanography: Methods*, 8 (7), 348–351. <https://doi.org/10.4319/lom.2010.8.348>
- Sesay, R.E.V., Sesay, F., Azizi, M.I. & Rahmani, B. (2024). Invasive Species and Biodiversity: Mechanisms, Impacts, and Strategic Management for Ecological Preservation. *Asian Journal of Environment & Ecology*, 23 (9), 82–95. <https://doi.org/10.9734/ajee/2024/v23i9600>
- Simon, K.S. & Townsend, C.R. (2003). Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. *Freshwater Biology*, 48 (6), 982–994. <https://doi.org/10.1046/j.1365-2427.2003.01069.x>
- Standard - Vattenundersökningar - Provtagning av fisk med elektricitet SS-EN 14011 (2003). Svenska institutet för standarder, SIS.

- <https://www.sis.se/produkter/miljo-och-halsoskyddsakerhet/vattenkvalitet/undersokning-av-vattens-biologiska-egenskaper/ssen14011/> [2025-02-12]
- Stauffer, J., Bruneaux, M., Panda, B., Visse, M., Vasemägi, A. & Ilmonen, P. (2017). Telomere length and antioxidant defense associate with parasite-induced retarded growth in wild brown trout. *Oecologia*, 185 (3), 365–374. <https://doi.org/10.1007/s00442-017-3953-x>
- Suraci, F. (2025). *How does Eurasian minnow affect the diet of brown trout in streams in northern Sweden?* (Master's thesis in Biology). SLU, Department of Wildlife, Fish, and Environmental Studies.
- Sveriges lantbruksuniversitet (SLU), Institutionen för akvatiska resurser (2025). Svenskt elfiskeregister – SERS. <http://www.slu.se/elfiskeregistret> [2025-05-20]
- Tiberti, R., Buchaca, T., Cruset Tonietti, E., Iacobelli, L., Maini, M., Ribelli, F., Pou Rovira, Q. & Ventura, M. (2022). Minnow introductions in mountain lakes result in lower salmonid densities. *Biological Invasions*, 24 (8), 2285–2289. <https://doi.org/10.1007/s10530-022-02783-w>
- Tonkin, J.D. (2014). Drivers of macroinvertebrate community structure in unmodified streams. *PeerJ*, 2, e465. <https://doi.org/10.7717/peerj.465>
- Valtonen, K., Mononen, T., Tirri, H., Erkinaro, J., Jokikokko, E., Kuikka, S. & Romakkaniemi, A. (2002). A Study of Electroshocking Bias in Terms of Habitat and Abundance Using Information-Theoretic Tools. https://www.semanticscholar.org/paper/A-Study-of-Electroshocking-Bias-in-Terms-of-Habitat-Valtonen-Mononen/c60e59f9bf001793a2b671403bed6d87544cce2c?utm_source=consensus [2025-06-30]
- Werner, R.A., Bruch, B.A. & Brand, W.A. (1999). ConFlo III – an interface for high precision $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis with an extended dynamic range. *Rapid Communications in Mass Spectrometry*, 13 (13), 1237–1241. [https://doi.org/10.1002/\(SICI\)1097-0231\(19990715\)13:13<1237::AID-RCM633>3.0.CO;2-C](https://doi.org/10.1002/(SICI)1097-0231(19990715)13:13<1237::AID-RCM633>3.0.CO;2-C)
- Wickham, H. & RStudio (2023). *tidyverse: Easily Install and Load the “Tidyverse”* (2.0.0). <https://cran.r-project.org/web/packages/tidyverse/index.html> [2025-03-25]
- willwelch (2019). Voyager [no labels] (retina) TMS, OpenStreetMap. <https://cartodb.com/basemaps/>
- Woodward, G. & Hildrew, A.G. (2002). Body-size determinants of niche overlap and intraguild predation within a complex food web. *Journal of Animal Ecology*, 71 (6), 1063–1074. <https://doi.org/10.1046/j.1365-2656.2002.00669.x>

Popular science summary

Young Brown trout in Abisko streams probably grow slower when non-native Eurasian minnow are around and are affected in several other ways. It is unclear when minnow arrived there and whether they were left as bait by anglers or hitched a ride on birds as eggs, but they are there to stay. The negative impact of introduced minnow on trout has been documented in several lakes and streams from Norway to Spain, slowed growth being only one symptom of many. That is why the finding of this thesis is crucial: it is a warning that trout in Abisko might be in for the same development as in places where non-native minnow already threaten trout. Hopefully, the gained knowledge from our study engages researchers to continue monitoring minnow colonization in this area. Knowledge on this issue can ultimately be used to inform policy makers who decide on actions like minnow removal programs.

Appendix 1

Supplementary table 1. Coordinates of stretch beginning and ending locations in the EPSG:3006 coordinate system.

Stretch	Start coordinates (X, Y)	End coordinates (X, Y)
BAKTA_1_1	647929	647933
	7596357	7596394
BD02_1_1	627830	627800
	7597504	7597542
BD02_2_1	628363	628331
	7597120	628331
BD03_1_1	628253	628215
	7596083	7596085
BD05_1_1	628842	628837
	7595685	7595690
BD05_2_1	628954	628957
	7595773	7595831
BD06_1_1	629407	629411
	7595816	7595842
BD06_1_2	629419	629414
	7595860	7595888
BD10_1_1	643343	643274
	7596483	7596472
BD11_1_1	646272	646260
	7597272	7597256
BD11_1_2	646246	646215
	7597244	7597214
BD13_1_1	647381	647363
	7598440	7598422
BD13_1_2	647349	647312
	7598417	7598398

Appendix 2

Supplementary table 2. Catch sizes per species and stretch.

Stretch	Brown Trout	Minnow	Arctic Charr	Burbot
BAKTA_1_1	28			
BD02_2_1	78			
BD03_1_1	27			
BD05_1_1		7	6	
BD05_2_1	14	20	1	
BD06_1_1			7	
BD06_1_2			3	
BD10_1_1	40	20	1	1
BD11_1_1	1	102		
BD11_1_2		5		
BD13_1_1	11	28		
BD13_1_2	14			

Appendix 3

Supplementary table 3. Samples collected for SIA. Not all samples could be collected in each stretch.

BD10_1	BD03_1	BAKTA_1	BD02_2	BD13_1	BD05_2	BD05_1
Benthic algae	Benthic algae	Benthic algae	Benthic algae	Benthic algae	Benthic algae	
Oligochaeta						
			Chironomidae	Chironomidae		Chironomidae
Trichoptera	Trichoptera	Trichoptera	Trichoptera	Trichoptera		Trichoptera

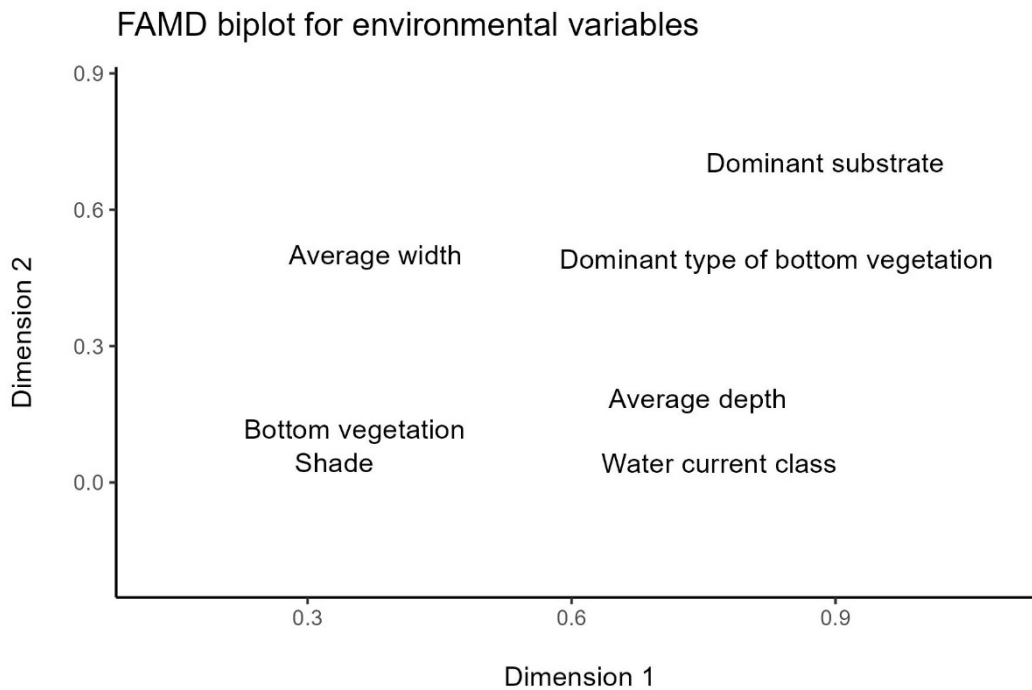
Appendix 4

Supplementary table 4. Number of individuals of each taxon per stretch.

Taxon	BAKTA_1_1	BD02_2_1	BD03_1_1	BD05_2_1	BD06_1_1	BD06_1_2	BD10_1_1	BD11_1_1	BD11_1_2	BD13_1_1	BD13_1_2
Ephemeroptera	113	6	43	6		1	1	13	20	10	4
Chironomidae	23	71	71	49	14	146	574	66	27	18	26
Trichoptera	30	16	3	8	6	30	11	26	7	9	2
Oligochaeta	46		1	2		18	1	20	23	3	13
Plecoptera	19	14	8	13	2	3	1	10	7		6
Bivalvia	79	4			1	4	1		19		1
Gastropoda	79							4	3		
Eurycercus	1	2		37	7	16	6				
Araneae	1					1					
Hydrachnidia	54	10	4		3	9		1	1	1	7
Ceratopogonidae	4		1	2		1	4	1	1	3	4
Other Diptera	2	2	5	1		2	5		14		1
Simuliidae	3	1									4
Lepidurus		3				3					
Coleoptera					2	1	2	7	3		1
Odonata								1		1	
Hirudinea								1			

Appendix 5

Supplementary figure 1. Variable coordinates of environmental variables in the first two FAMD dimensions.



Supplementary table 5. Contribution of continuous environmental variables to FAMD dimensions

Variable	Dim 1	Dim 2	Dim 3	Dim 4	Dim 5
average width	8.785	25.647	3.615	2.981	0.002
average depth	17.321	8.000	1.518	0.024	8.683
water current class	17.885	0.008	0.040	1.175	6.436
shade	7.694	0.093	32.608	0.179	31.720

Supplementary table 6. Representation of continuous environmental variables per FAMD dimension.

Variable	Dim 1	Dim 2	Dim 3	Dim 4	Dim 5
average width	0.377	0.459	0.051	0.037	0.000
average depth	0.744	0.143	0.021	0.000	0.051
water current class	0.768	0.000	0.001	0.015	0.037
shade	0.330	0.002	0.461	0.002	0.185

Supplementary table 7. Correlation between continuous environmental variables.

Variable	average width	average depth	water current class	shade
average width	1.000	-0.256	0.489	-0.209
average depth	-0.256	1.000	-0.675	0.487
water current class	0.489	-0.675	1.000	-0.601
shade	-0.209	0.487	-0.601	1.000

Supplementary table 8. Contribution of qualitative environmental variables to FAMD dimensions.

Variable	Dim 1	Dim 2	Dim 3	Dim 4	Dim 5
boulders	4.198	11.131	1.333	3.334	8.524
cobble	0.100	22.716	0.372	9.477	3.589
high	16.394	3.088	1.072	2.907	4.249
organic					
intermediate	2.980	0.368	16.571	3.035	15.401
rich	5.227	3.210	1.346	25.954	1.066
sparse	0.018	0.654	35.885	5.191	15.306
algae	1.063	12.653	2.412	35.125	0.251
mosses	1.941	9.345	2.157	7.711	0.524
phanerogams	16.394	3.088	1.072	2.907	4.249

Supplementary table 9. Representation of qualitative environmental variables per FAMD dimension.

Variable	Dim 1	Dim 2	Dim 3	Dim 4	Dim 5
boulders	0.617	0.284	0.021	0.042	0.023
cobble	0.020	0.776	0.008	0.160	0.013
high	0.943	0.031	0.007	0.014	0.004
organic					
intermediate	0.544	0.012	0.329	0.047	0.052
rich	0.616	0.066	0.017	0.262	0.002
sparse	0.004	0.024	0.816	0.093	0.059

algae	0.162	0.335	0.040	0.458	0.001
mosses	0.434	0.363	0.052	0.148	0.002
phanerog	0.943	0.031	0.007	0.014	0.004
ams					

Appendix 6

Supplementary table 10. Number of caught trout and Seber3-estimations from the FSA-package per stretch. Catch sizes in BD13_1_1 did not strictly decline with each removal so an estimate could not be calculated.

Stretch	Estimate	catch size	upper CI (95%)
BAKTA_1_1	33.03	28	43.11
BD02_2_1	102.31	78	131.96
BD03_1_1	27.92	27	30.53
BD05_2_1	15.24	14	19.08
BD10_1_1	43	40	48.65
BD13_1_1		11	
BD13_1_2	17.16	14	26.1

Supplementary table 11. Number of caught minnow and Seber3-estimations from the FSA-package per stretch. Catch sizes in BD13_1_1 did not strictly decline with each removal so an estimate could not be calculated.

Stretch	Estimate	catch size	upper CI (95%)
BD05_2_1	29.23	20	52.89
BD10_1_1	23.43	20	31.59
BD11_1_1	107.61	102	114.71
BD11_1_2	5.217	5	6.54
BD13_1_1		28	

Appendix 7

Supplementary table 12. Output from Model 1 with trout fork length as response variable, age and minnow including their interaction as fixed effects and stream as random effect. Estimated age and the interaction between age and minnow presence are significantly correlated with trout fork length.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	43.608	2.291	19.035	<0.001	39.081, 48.135
estimated age	20.493	0.798	25.695	<0.001	18.917, 22.069
minnow present	2.262	2.794	0.81	0.419	-3.259, 7.783
age:minnow present	-5.124	1.610	-3.182	0.002	-8.307, -1.942

Appendix 8

Supplementary table 13. Output from Model 2 with Fulton's K as response variable, age and minnow including their interaction as fixed effects and stream as random effect. Neither age nor minnow presence significantly influenced Fulton's K.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	0.865	0.016	53.999	<0.001	0.833, 0.896
estimated age	0.006	0.005	1.131	0.26	-0.005, 0.017
minnow present	-0.005	0.028	-0.201	0.841	-0.06, 0.049
age:minnow present	0.02	0.013	1.513	0.133	-0.006, 0.046

Appendix 9

Supplementary table 14. Output from a cumulative link mixed model with trout age as response variable, minnow presence, water current class and dominant type of bottom vegetation as fixed effects and stream as random effect. No fixed effect significantly influenced trout age.

Fixed effects	Estimate	SE	z-value	p-value	CI (95%)
minnow present	0.87	2.548	0.341	0.733	-4.124, 5.864
water current class	0.943	0.863	1.094	0.274	-0.747, 2.634
mosses	-0.902	2.149	-0.42	0.675	-5.115, 3.31
phanerogams	2.178	2.026	1.075	0.282	-1.793, 6.149

Supplementary table 15. Output from a cumulative link mixed model with trout age as response variable, minnow presence as fixed effects and stream as random effect. Minnow presence did not significantly influence trout age.

Fixed effects	Estimate	SE	z-value	p-value	CI (95%)
minnow present	2.054	1.198	1.714	0.086	-0.294, 4.401

Appendix 10

Supplementary table 16. Model output from Model 1 with TP as response variable and stream as random effect. TP was not significantly correlated with either fixed effect or interaction.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	8.057	4.262	1.891	0.067	-0.578, 16.692
minnow present	0.612	2.894	0.211	0.834	-5.252, 6.476
water current class	-0.966	0.926	-1.043	0.304	-2.843, 0.911
mosses	1.433	2.476	0.579	0.566	-3.584, 6.451
phanerogams	-2	2.008	-0.996	0.325	-6.068, 2.068

Supplementary table 17. Model output from Model 2 with TP as response variable and stream as random effect. TP was not significantly influenced by minnow presence.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	6.556	0.819	8.002	< 0.001	4.902, 8.211
minnow present	-1.041	0.760	-1.369	0.179	-2.578, 0.495

Supplementary table 168. Model output from Model 2 with TP as response variable, species as fixed effect and stream as random effect. Species was not significantly influencing TP.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	5.887	0.786	7.49	0.001	3.866, 7.907
species	0.401	0.669	0.6	0.591	-1.727, 2.529

Supplementary table 19. Linear mixed model output with $\delta^{15}N$ as response variable, fork length as fixed effect and stream as random effect. Length did not significantly influence $\delta^{15}N$.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	5.934	0.736	8.06	<0.001	4.447, 7.421
fork length	0.002	0.006	0.318	0.752	-0.011, 0.015

Appendix 11

Supplementary table 20. Output from Model 1 with SEAc as response variable and stream as random effect. SEAc was not significantly influenced by either fixed effect.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	-6.351	25.537	-0.249	0.827	-116.229, 103.526
minnow present	14.5	17.55	0.826	0.496	-61.024, 90.023
water current class	2.52	5.551	0.454	0.694	-21.363, 26.403
mosses	0.435	15.031	0.029	0.98	-64.24, 65.109
phanerogams	-8.057	17.553	-0.459	0.691	-83.581, 67.466

Supplementary table 21. Output from Model 2 with SEAc as response variable and stream as random effect. SEAc was not significantly influenced by minnow presence.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	2.795	4.721	0.592	0.580	-9.341, 14.930
minnow present	7.708	7.211	1.069	0.334	-10.83, 26.246

Appendix 12

Supplementary table 22. Output from Model 1 with trout density per stretch as response variable without a random effect. Trout density was not significantly influenced by either fixed effect.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	0.815	0.529	1.541	0.263	-1.461, 3.091
minnow present	-0.385	0.364	-1.059	0.401	-1.949, 1.18
water current class	-0.046	0.115	-0.403	0.726	-0.541, 0.448
mosses	-0.213	0.311	-0.685	0.564	-1.553, 1.126
phanerogams	-0.006	0.364	-0.016	0.989	-1.57, 1.559

Supplementary table 23. Output from one-way ANOVA with trout density per stretch as response variable, minnow presence as predictor and with no random effect. Trout density was not significantly influenced by minnow presence.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	0.493	0.094	5.262	0.003	0.252, 0.734
minnow present	-0.157	0.143	-1.1	0.322	-0.525, 0.210

Supplementary table 24. Output from Model 1 with trout density per stretch as response variable, minnow density as main predictor and without a random effect. Trout density was not significantly influenced by either fixed effect.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	0.548	0.563	0.974	0.433	-1.875, 2.971
minnow density	-0.674	1.609	-0.419	0.716	-7.597, 6.25
water current class	-0.007	0.129	-0.057	0.96	-0.564, 0.549
mosses	-0.077	0.353	-0.217	0.849	-1.596, 1.443
phanerogams	0.485	1.28	0.379	0.741	-5.02, 5.991

Supplementary table 25. Output from Model 2 with trout density per stretch as response variable, minnow density as main predictor and without a random effect. Trout density was not significantly influenced by minnow density.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	0.446	0.091	4.878	0.005	0.211, 0.681

minnow density	-0.102	0.237	-0.429	0.686	-0.71, 0.507
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Supplementary table 26. Output from Model 1 with overall fish density per stretch as response variable without a random effect. Fish density was not significantly influenced by either fixed effect.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	0.512	0.598	0.857	0.482	-2.06, 3.084
minnow presence	0.002	0.411	0.006	0.996	-1.766, 1.771
water current class	-0.008	0.13	-0.062	0.956	-0.567 0.551
mosses	-0.102	0.352	-0.289	0.8	-1.616, 1.413
phanerogams	0.834	0.411	2.029	0.18	-0.934, 2.602

Supplementary table 27. Output from Model 2 with overall fish density per stretch as response variable without a random effect. Fish density was not significantly influenced by minnow presence.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	0.408	0.182	2.247	0.075	-0.059, 0.874
minnow presence	0.369	0.277	1.330	0.241	-0.344, 1.081

Appendix 13

Supplementary table 28. Linear model output with Shannon index as response variable and minnow presence, water current class and dominant type of bottom vegetation as predictors. No predictor significantly influenced the Shannon index of a stretch.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	2.819	0.977	2.885	0.102	-1.386, 7.024
minnow presence	-1.115	0.672	-1.659	0.239	-4.005, 1.776
water current class	-0.322	0.212	-1.515	0.269	-1.236, 0.592
mosses	-0.005	0.575	-0.009	0.994	-2.48, 2.47
phanerogams	0.17	0.672	0.254	0.824	-2.72, 3.06

Supplementary table 29. One-way ANOVA output with Shannon index as response variable and minnow presence as predictor. Minnow presence did not significantly influence the Shannon index of a stretch.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	1.689	0.257	6.577	0.001	1.029, 2.349
minnow presence	-0.571	0.392	-1.456	0.205	-1.58, 0.437

Supplementary table 30. Linear model output with Simpson index as response variable and minnow presence, water current class and dominant type of bottom vegetation as predictors. No predictor significantly influenced the Simpson index of a stretch.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	1.121	0.535	2.098	0.171	-1.178, 3.421
minnow presence	-0.426	0.367	-1.159	0.366	-2.006, 1.155
water current class	-0.115	0.116	-0.994	0.425	-0.615, 0.384
mosses	0.018	0.315	0.057	0.960	-1.336, 1.372
phanerogams	0.16	0.367	0.436	0.705	-1.42, 1.741

Supplementary table 31. One-way ANOVA output with Simpson index as response variable and minnow presence as predictor. Minnow presence did not significantly influence the Simpson index of a stretch.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
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intercept	0.731	0.12	6.078	0.002	0.422, 1.04
minnow presence	-0.213	0.184	-1.157	0.3	-0.685, 0.26

Supplementary table 32. Output from linear model with mean Ephemeroptera length per stretch as response variable without a random effect. Ephemeroptera length was not significantly correlated with either fixed effect.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	3.903	3.833	1.018	0.416	-12.589, 20.396
minnow presence	-0.792	2.635	-0.301	0.792	-12.128, 10.544
water current class	0.412	0.833	-0.494	0.670	-3.997, 3.173
mosses	0.915	2.256	0.406	0.724	-8.793, 10.623
phanerogams	-0.424	2.635	-0.161	0.887	-11.76, 10.912

Supplementary table 33. Output from linear model with mean Ephemeroptera length per stretch as response variable without a random effect. Ephemeroptera length was not significantly correlated with minnow presence.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	3.147	0.676	4.657	0.006	1.41, 4.885
minnow presence	-1.002	1.032	-0.97	0.377	-3.656, 1.652

Supplementary table 34. Output from linear model with mean Trichoptera length per stretch as response variable without a random effect. Trichoptera length was not significantly correlated with either fixed effect.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	9.589	10.182	0.942	0.446	-34.222, 53.399
minnow presence	-0.343	6.999	-0.049	0.965	-30.456, 29.77
water current class	0.033	2.213	0.015	0.99	-9.49, 9.555
mosses	-4.061	5.993	-0.678	0.568	-29.848, 21.726
phanerogams	1.447	6.999	0.207	0.855	-28.666, 31.56

Supplementary table 35. Output from linear model with mean Trichoptera length per stretch as response variable without a random effect. Trichoptera length was not significantly correlated with minnow presence.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	6.657	1.795	3.709	0.014	2.044, 11.271
minnow presence	3.136	2.742	1.144	0.305	-3.911, 10.183

Supplementary table 36. Output from linear model with mean Chironomidae length per stretch as response variable without a random effect. Chironomidae length was not significantly correlated with either fixed effect.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	6.437	1.622	3.969	0.058	-0.54, 13.414
minnow presence	-0.542	1.115	-0.486	0.675	-5.338, 4.254
water current class	-0.304	0.353	-0.861	0.48	-1.82, 1.213
mosses	-0.329	0.955	-0.345	0.763	-4.436, 3.777
phanerogams	3.489	1.115	3.13	0.089	-1.307, 8.284

Supplementary table 37. Output from linear model with mean Chironomidae length per stretch as response variable without a random effect. Chironomidae length was not significantly correlated with minnow presence.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	5.127	0.779	6.58	0.001	3.124, 7.13
minnow presence	1.323	1.19	1.112	0.317	-1.736, 4.383

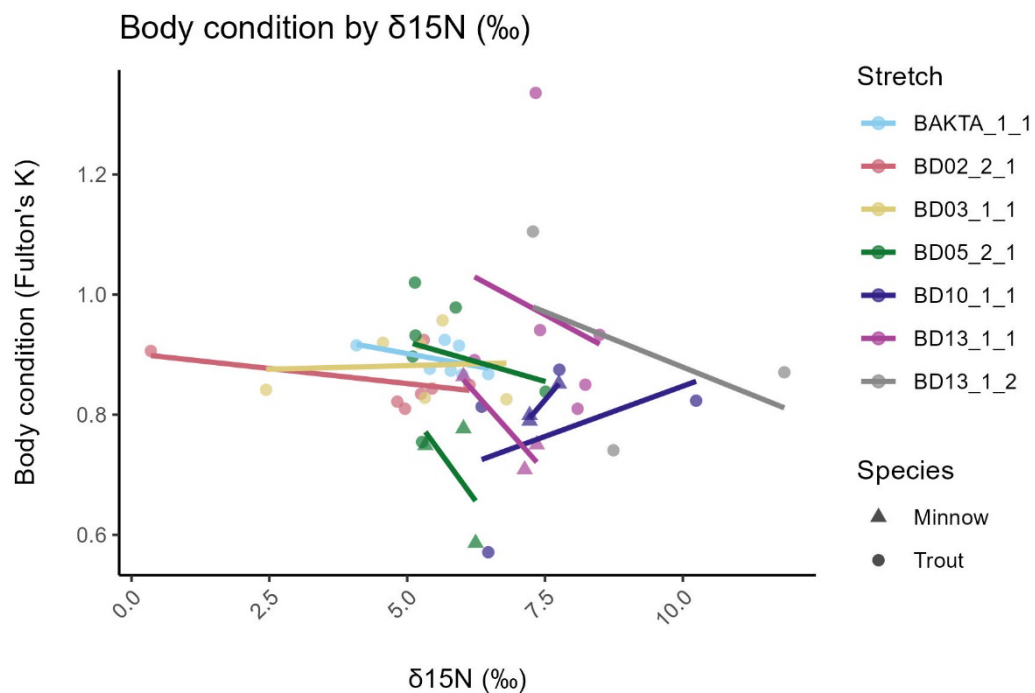
Appendix 14

Supplementary table 38. Output from linear model with trout $\delta^{15}N$ as response variable and stream as a random effect excluding the stretch BD13_1_2. Minnow presence only influenced trout $\delta^{15}N$ above the $p=0.05$ -significance threshold.

Fixed effects	Estimate	SE	t-value	p-value	CI (95%)
intercept	5.079	0.499	10.179	< 0.001	4.06, 6.098
minnow presence	1.884	0.723	2.606	0.06	-0.123, 3.89

Supplementary table 39. Spearman test showing an insignificant negative correlation between K and $\delta^{15}N$ (‰).

Variable 1	Variable 2	Spearman's ρ	p-value	n
Fulton's K	$\delta^{15}N$ (‰)	-0.129	0.434	39

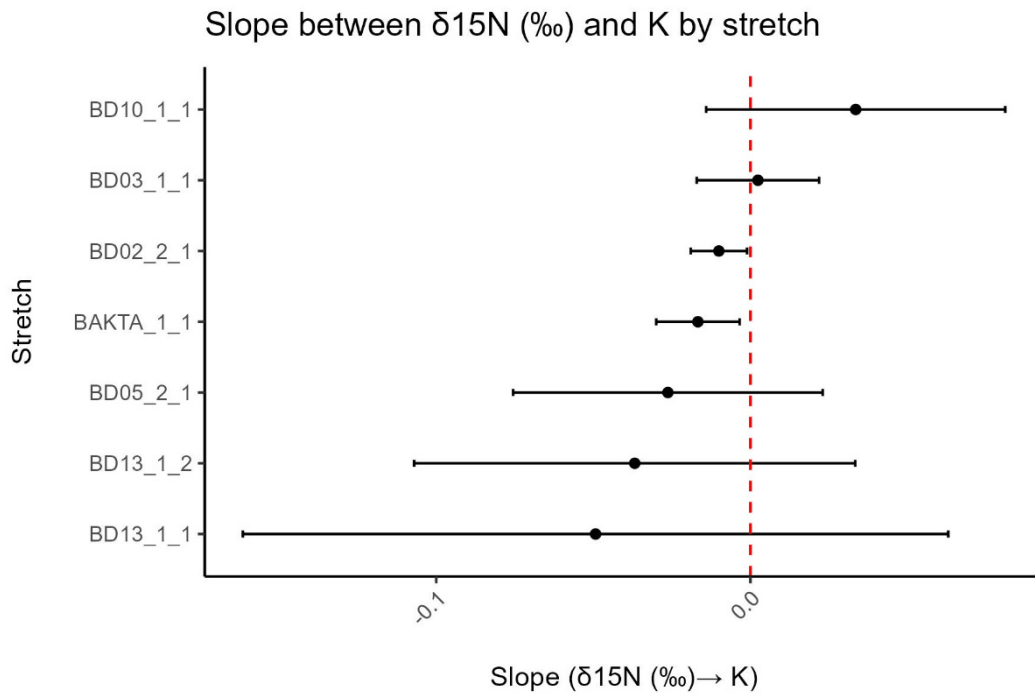


Supplementary figure 2. Relationship of Fulton's K and $\delta^{15}N$ (‰) per stretch and species. All stretches except BD10_1_1 and BD03_1_1 show a negative slope for both trout and minnow.

Supplementary table 40. Results from a one-sided t -test testing if the mean of slopes between Fulton's K and $\delta^{15}N$ (‰) is significantly less than zero. It shows that the mean is not significantly less than zero.

t-value	degrees of freedom	p-value	n
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-1.432 6 0.101 7



Supplementary figure 3. Slopes between $\delta^{15}\text{N}$ (‰) and K with standard errors per stretch. All relationships between $\delta^{15}\text{N}$ and K are negative except for BD03_1_1 and BD10_1_1. The standard error from almost all stretches crosses a slope of 0.

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