How does Eurasian minnow affect the diet of brown trout in streams in northern Sweden?

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How does Eurasian minnow affect the diet of brown trout in streams in northern Sweden?

Hur påverkar elritsa dieten hos öring i vattendrag i norra Sverige?

Flavia Suraci

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Abstract

Brown trout and Eurasian minnow can compete for the same resources, but they may also predate on each other. Minnows are spreading in the Swedish mountain region and their introduction can lead to salmonid extinction. These two species have been studied mainly in lakes and this study aims to achieve a better understanding of their interaction in streams.

Eight streams in the Abisko area were investigated, where brown trout was found in seven out of 13 stretches, and in three of these, the trout were living in sympatry with minnows. We found intermediate/high diet overlap within the sympatric stretches but also between trout that live in allopatry and in sympatry with minnows. No specialization either on prey type or size was observed in sympatric trout compared to allopatric ones. We observed a trend towards lower trout densities when minnow was present. We did not find signs of predation on fish in any of the samples analysed.

Our results give a better insight about the interaction of the two species in steams fundamental for future investigations.

Keywords: diet overlap, competition, predation, streams

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Abbreviations

Abbreviation	Description
DOC	Dissolved Organic Carbon
N	Nitrogen
NMDS	Non-metric Multi-Dimensional Scaling
P	Phosphorous
PERMANOVA	Permutational Multivariate Analysis of Variance
PSI	Proportional Similarity Index
Si	Schoener's Index
SI	Stable Isotope
TOC	Total Organic Carbon

1. Introduction

Globally, biological invasion is a major concern for biodiversity loss and homogenisation, the process by which the similarity of geographically distinct ecosystems increases due to human causes (Pejchar & Mooney 2009; Museth et al. 2010). This is particularly true for the aquatic environments, because our understanding of the processes of homogenisation are not as clear as in the terrestrial environments (Gallardo et al. 2015; Dar & Reshi 2020).

One example of biological invasion that is a concern in the Alpine region of Europe, is the expansion of the Eurasian minnow (*Phoxinus phoxinus*), a small cyprinid (common length 7 cm; Froese & Pauly, 2024) that used to be considered harmless (Museth et al. 2007). This species thrives in a wide variety of cold and well-oxygenated environments, feeds on both plant material and macroinvertebrates, and can reproduce in both gravel areas with flowing water and deep pools with slow currents (Froese & Pauly 2024b). In Scandinavia, *P.phoxinus* is a native species. It probably arrived from central Europe via the Baltic Ice Lake during the last postglacial period, around 10,000 years ago, and the land uplift following the last glaciation had restricted the species natural distribution in non-mountainous regions (Jonsson & Jonsson 2015). However, in recent decades the distribution has expanded in the Swedish mountain area due to human translocation and climate change. Anglers have been using it as live bait, and it has been introduced with stocked trout alevins (Museth et al. 2007). In addition, the rise of water temperature due to climate change is making space for new suitable habitat for the species (Mills 1988). Here, the interaction with salmonids species, particularly brown trout (*Salmo trutta*), is of increasing concern (Museth et al. 2007; Borgstrøm et al. 2010).

Brown trout are anadromous salmonids that thrive in cold, well-oxygenated waters and can typically reach 100 cm in length and 20 kg in weight (Maki-Petäys et al. 2011). Juveniles feed mainly on macroinvertebrates and terrestrial insects while adults can be piscivorous. Lacustrine populations migrate to tributaries to reproduce in well oxygenated gravel areas (Froese & Pauly 2024b). This species exists in many lakes in the Scandinavian mountains, and in the region, it was one of the food sources for early settlers, and it remains important today for its nutritional and recreational value (Jonsson & Jonsson 2015). However, more and more populations are forced to live in sympatry with minnows (Museth et al. 2003; Borgstrøm et al. 2010).

The interaction between the two species is complex: trout can feed heavily on minnows, especially during their reproductive period when minnows are more vulnerable (Museth et al. 2003, 2010). However, they also compete for food and space in the littoral and in tributary habitats (Museth et al. 2007; Borgstrøm et al.

2010), and minnows can prey on trout eggs and fries, leading to the decline or even extinction of salmonid populations (Lien, 1981).

Many have studied the effects of minnow in lentic (lake) ecosystems, focusing on both the predation on native macroinvertebrates (Næstad & Brittain 2010) and on the competition with other fish species (brown trout in Qvenild et al., 2024) and other semi-aquatic vertebrates (small mammals and amphibians in Bello et al., 2024; Osorio et al., 2022).

Less is known about situation in lotic (flowing water) environments: Näslund et al., (2011) state that the density of brown trout, in Swedish streams, is negatively correlated with the number of coexisting fish species. Larsen et al., (2007) found that minnow density did not negatively affect brown trout density over a 10-year period, but it negatively correlated with trout fries' growth, highlighting the possible competitive interaction between the two species, even in riverine environment.

Since the literature focuses more on the lentic environments and examples on lotic environments are sparse, especially when it comes to dietary interactions, the aim of this study is to investigate the interaction between these two species in Swedish mountain streams, focusing on their diet and answering the following three main questions:

i. Does the interaction between the two species change the feeding behaviour of brown trout? More specifically: (i.a.) is there diet overlap between trout and minnows that live in sympatry? (i.b.) Is there a difference in diet between sympatric and allopatric trout? (i.c.) Is there any specialization in diet when minnows are present?

ii. Do trout densities differ between streams with and without minnows?

iii. Is interspecific predation between the two species observed?

We hypothesise that the presence of minnows will negatively affect brown trout by altering their feeding behaviour and reducing their densities as it has been seen in lentic environments (Tiberti et al. 2022). We think the two species will have similar diets, as seen in (Museth et al. 2010), while the diet of sympatric and allopatric trout would differ as seen in Holmen et al. (2003).

We predict that the two species will feed on each other: direct predation by trout on adult minnows (Museth et al. 2003) and by minnows on trout roe (Lien 1981) has been observed in other studies.

Answering these questions would help to understand the processes that take place in these threatened environments and, therefore, actions could be taken to

reduce biodiversity loss and maintain the ecosystem services, such as fisheries, that these environments provide.

2. Material and Methods

2.1 Field work

2.1.1 Selection of sites and stretches

We sampled streams in the area between Riksgränsen and Tornehamn in Norrbotten, Sweden (Abisko area; Figure 1 and 2). The streams were the inlets of lakes, except in two cases, BD02_2 and BAKTA_1, which were outlets. The lakes had been sampled in different studies in the past (Norman 2023; van Dorst, unpublished; Henna Kangosjärvi unpublished). From maps and satellite images of the lakes we assessed the presence of possible inlets and their accessibility before going out in the field.

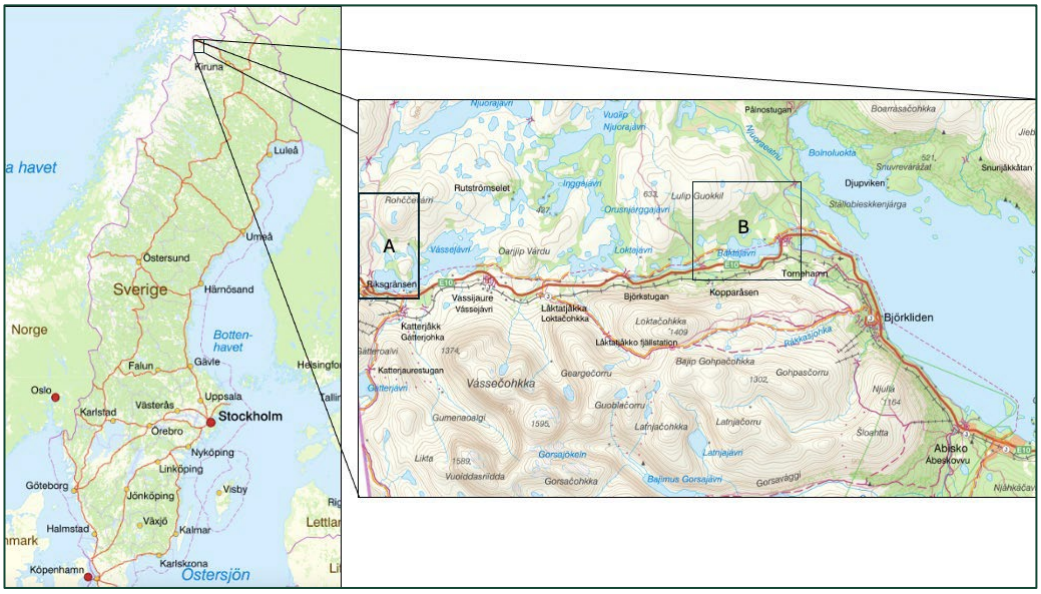

Figure 1. Study area between Riksgränsen and Tornehamn, Norrbotten, Sweden (Abisko area). https://minkarta.lantmateriet.se

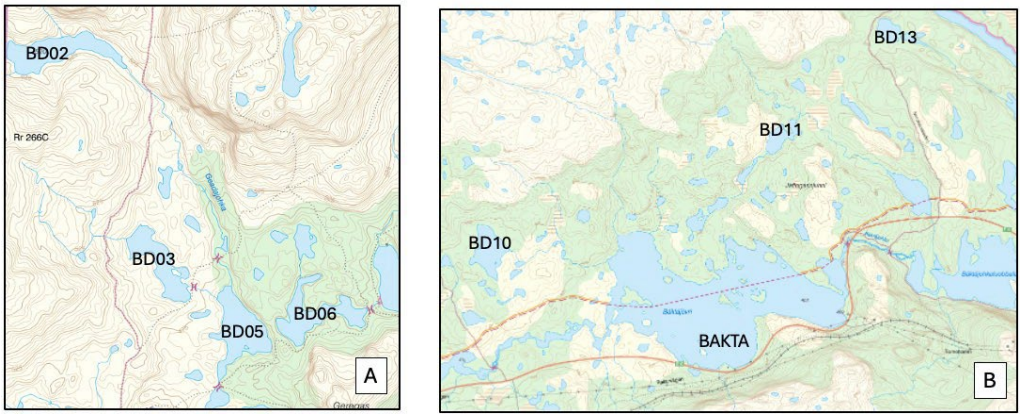

Figure 2. Zoom in on area A close to Riksgränsen and area B close to Tornehamn.

At the site, we verified that the stream was fishable, and we chose a 50 m stretch that included both typical minnows and trout environments (silty and slow flow vs stony and fast flow) if possible. When there were evident migration barriers or other reasons that made a part of the stream unsuitable for sampling (e.g. data logger for another experiment in BAKTA_1) and it was not possible to sample another section of the stream, instead, we sampled a shorter stretch. In one case (BD10_1), different environments were present, but the stream was too short to make two separate stretches, so we sampled a longer one.
Stretches length ranged from 25 to 83 m (Table 1). Stretches were labelled with the name of the lake followed by the number of the stream and the number of the stretch: for example, BD10_1_1 is the first stretch sampled on the first stream of the lake BD10. Each stretch was sampled in two different days. One day, we took water samples, stream parameters, macroinvertebrate samples and stable isotope (SI) samples for both benthic algae and macroinvertebrates. On the other day, we sampled the fish populations, using electrofishing.

Table 1. Streams characteristics. Fish community: minnows (M), brown trout (T) and arctic charr (C). In BD11_1_1 we found one trout that was most likely coming from the lake.

Stretch	Length (m)	Fish community
BD10_1_1	83	M, T, C
BD13_1_1	50	M, T
BD13_1_2	50	T
BD11_1_1	29	M, T (1)
BD11_1_2	45	M
BD03_1_1	40	T
BD05_1_1	32	M, C
BD05_2_1	40	M, T, C
BD06_1_1	25	C
BD06_1_2	40	C
BD02_1_1	50	None
BD02_2_1	50	T
BAKTA_1_1	37.8	T

2.1.2 Water chemistry

Water samples to assess dissolved organic carbon (DOC), total organic carbon (TOC), total nitrogen (N) and total phosphorus (P) were taken first to avoid suspension of material in the water column. For DOC, we filtered 50 ml of water through a Filtropur S 0.45 filter (SARSTEDT AG & Co. KG, Nümbrecht, Germany) attached to a syringe, put it in a Falcon tube and added 0.6 µL of HCl

to stabilize the sample. For TOC and total N and P, we filled two Falcon tubes with 50 ml of water. We preliminarily labelled the tubes in the field. Results are presented in Appendix 1.

2.1.3 Stream characteristics

To describe the stream, we adapted parts of the electrofishing form present in the protocol for sampling fish with electricity provided by the Swedish Standards Institute (2006) to better suits local needs and our study objective. We took the coordinates at the start and end of each stretch (Garmin Alpha 50) and measured water temperature (Tetra TH digital), total length, total width every 10 m and depth at ¼, ½ and ¾ of the width. In one stretch (BD06_1_1), 25 m long, these parameters were measured every 5 m. If the last part of the stretch was shorter than 10 m, we took the measurements at the end of the stretch. We visually assessed all the other parameters. Water level (low, intermediate, high) was assessed by looking for water marks and debris, water visibility was divided in turbid and clear, and water current class in slow, intermediate and rapids. We noted down the habitat types (pool, flat, run, riffles, rapids), dominant and subdominant substrate based on the size (a table was provided in the electrofishing form, see Appendix 2) and if bottom vegetation was present, we noted down if it was sparse, intermediate or rich and the dominant type (algae, mosses, phanerogams). Finally, we noted down weather condition, classification of riparian zone, percentage of shade and presence of large woody debris.

2.1.4 Sampling of macroinvertebrates and algae

To collect macroinvertebrates for quantitative analysis, we used the kick sampling method: we used a net with mesh size 500 µm and kicked for one minute, in the area extending 0.5 meter upstream the net (Feeley et al. 2012). We took one replicate for every 10 m of the stretch, while also making sure we sampled different habitat types, e.g. fast/slow flowing and different substrates. Each sample was poured into a bottle and the characteristics (substrate, vegetation, water flow) of the habitat where the kick sample was taken were noted. The samples of the first three stretches were pooled and put into alcohol (BD10_1_1, BD13_1_1, BD13_1_2). For the subsequent stretches, the kick samples were kept separately for each sample (BD11_1_1, BD11_1_2, BD03_1_1, BD05_1_1, BD05_2_1, BD06_1_1, BD06_1_2, BD02_1_1, BD02_2_1, BAKTA_1_1).

For the macroinvertebrate SI sample, we took different approaches to try to get as many taxonomic groups as possible. We used the kick net in different environments along the stretch, sweeping it in the vegetation in the stream and kicking the substrate on the bottom. We also picked up large stones and directly picked the macroinvertebrates from them with soft tweezers. Everything was

poured into a bottle with water and cooled to be sorted in the lab. For the benthic algae SI sample, we took three fist-size rocks with evident periphyton formations, put them into a clean bucket, brushed them gently with a toothbrush to release the algae, and poured this in a new, clean bottle.
As soon as possible in the lab (at Abisko Scientific Research Station), we sorted the macroinvertebrate kick samples by picking out all macroinvertebrates with soft tweezers from a white tray filled with some water. We then put all the animals in a 70% ethanol solution. At the beginning, we were killing the animals already in the field to avoid predation. We did this by putting them in alcohol. After some attempts, we figured out that it was easier and less time consuming to sort them when they were still alive. Moreover, we did not notice any predation attempt that would affect the results of the analysis. The macroinvertebrates SI sample was sorted in taxonomic groups (*Oligocheta, Plecoptera, Ephemeroptera, Tricoptera, Chironomidea, Diptera, Odonata, Gasteropoda, Bivalvia, Hemiptera, Eurycercus*) and then frozen. Benthic algae SI sample, TOC and total N/P were stored in the freezer, and DOC was stored in the fridge, until further processing and analysis.

2.1.5 Electrofishing

We sampled the fish populations through electrofishing. We followed the Swedish Standard Institute protocol for sampling fish with electricity (Swedish Standards Institute 2006) by which the same person had to fish the same stretch three times. We used a shore-based electrofishing device where the generator and unit were left at the shore - ideally in the middle of the stretch sampled - for practicality. Two people were typically involved in the fishing process: one would fish and the other would coil and uncoil the long cable attached to the pole and carry the bucket with the fish (Lug AB model L1000). Before starting we noted down the voltage at which we were going to fish: it varied between 800 and 1000 V. At the end of each pass, we euthanized the fish with a lethal dose of tricaine mesylate (MS) and sodium hydrogen carbonate (buffer), counted them, and put them in a labelled bag and stored in a cool box until we got back in the lab. In two cases (BD03_1 and BD02_2) and we decided to release some of the trout we caught. After anaesthesia, these fish were measured for total length and, the ones that had a big enough gape size for the syringe to fit (bigger then 3 mm), were stomach flushed. A total of seven trout and one burbot were flushed. The anesthetized fish were put in a bucket with fresh water to give them the opportunity to recover before being released close to the area they were caught.
As soon as in the lab (at Abisko Scientific Research Station), we measured total length, fork length and weight of each fish, noted the species, stretch and pass where it was caught, gave them an individual fish-id, and froze them in separate labelled bags.

2.2 Laboratory work

2.2.1 Processing fish

Later, at the university lab (Sveriges lantbruksuniversitet, SLU Umeå), we defrosted the fish to sample stomachs, otoliths and a piece of muscle tissue for SI analysis. For some minnow we took the caudal fin for possible DNA samples. Working table and tools were cleaned with ethanol between each fish. Stomachs were removed using small scissors and tweezers and stored in a 70% ethanol solution in Eppendorf tubes.
Salmonids have a S-shaped duodenum that highlight the end of the stomach. in contrast this transition is less obvious in minnows, so we made the cut where there was a noticeable difference in the degree of digestion.
We tried to sex the fish once the organs were removed from the abdominal cavity and the stomach sampled, but this was possible only for 38 of the bigger fish out of the total catch of 435 individuals.
Otoliths were sampled using a scalpel and pointy tweezers, stored in a labelled paper bag or in a well plate when very small. Muscle tissue for SI analysis was sampled using a scalpel and some tweezers. The standard way of sampling SI in salmonids is to take a piece of muscle tissue between the dorsal and adipose fins. However, most of the time, in our samples, the standard area was too little, and we had to sample all the muscle tissue behind the dorsal fin. For minnows we sampled the tissue between dorsal and caudal fin. Samples were stored in Eppendorf tubes end frozen. The analyses of stable isotopes, otoliths (growth patterns), DNA and water chemistry will be presented in the master thesis by Valentin Neumann (unpublished) or elsewhere.

2.2.2 Stomachs content analysis

We analysed stomach content under a stereomicroscope, using the relative fullness method (Amundsen & Sánchez-Hernández 2019). We took the stomach out of the alcohol, dried it with a piece of tissue and weighted it (scale accuracy 0.01g). The fullness of the stomach was visually estimated in percentage when it was still intact and then the estimate was adjusted and noted down after opening it. We opened the stomachs with a small scissor and tweezers along the sagittal plane.
At this point, we emptied the stomach and divided the contents in different recognizable categories. For one group we could identify the taxa to genus level (*Eurycercus*), but most of the time it was done to family, order or class (e.g. *Chironomidae, Trichoptera, Gastropoda*). Sometimes, the material was too digested for identification, and it was considered either animal parts or insects' parts. Some fish had organic material, plant and stones in their stomachs (see Appendix 3, list 1 for detailed list). Minnows were deteriorating at a faster rate

than similar sized or smaller trout, and it was more difficult to separate the stomach content into groups for minnows.
Afterwards, we visually estimated the volume (%) of each group, as a part of the total of the fullness estimation (stomach fullness = sum of volume estimation of all prey items). At the end, we measured the length of five biggest prey items to see if there were differences in maximum prey size between stretches with and without minnow. In the stomachs where we could not find enough intact insects due to the digestive process, heads' widths were measured to back-calculate the body length following Smock (1980)

2.2.3 Macroinvertebrate analysis

We analysed macroinvertebrate samples under a Askania stereomicroscope (Mikroskop Technik Rathenow, Germany) equipped with GF/PW 1010×/25 eyepieces, pouring the sample into a Petri dish and sorting the items with tweezers. We divided the animals into taxonomic groups as far as we could identify them, in the same way as we did for the stomach content (see Appendix 4 for detailed list) and estimated the volume percentage of each group. Then, we counted the number of individuals per group and measured the five biggest animals for each group.

2.3 Statistical analyses

2.3.1 Fixing total length measuring error and calculating fitness

On the last day of field work, we figured out that I was measuring the fish total length differently than Renee van Dorst and Valentin Neumann (stretched vs neutral caudal fin position). To solve this problem, we decided to adjust the measures performed with a stretched position to be more similar to the ones in neutral position. We used this formula to back calculate the correct total length of the fish measured with a stretched caudal fin position:

$$TTTT_{FF} = FFTT_{FF} \times \left(\frac{\overline{TTTT}}{\overline{FFTT}_{TT}} \right)$$

Where $TTTT_{FF}$ and $FFTT_{FF}$ are, respectively, the total and fork length of the incorrectly measured fish while $\frac{\overline{TTTT}}{\overline{TTFF}_{TT}}$ is the average ratio between total and fork length of the correctly measured fish.
Fitness of the fish individuals was calculated using Fulton's Condition Factor (K) and we tested, through a Wilcoxon rank-sum test, if there were differences between allopatric and sympatric trout.

2.3.2 Interaction between trout and minnows

We wanted to see if the feeding behaviour of trout was affected by the presence of minnows by testing:

a) if there was diet overlap between the two species,
b) if there were differences between sympatric and allopatric trout in diet overlap (b.1) and stomach fulness (b.2) and
c) if trout would specialize on prey items (c.1) and prey size (c.2) when living in sympatry.

Before performing any test, variance and normality were checked by Levene's and Shapiro-Wilk's tests. The threshold was set to 0.05, and in all cases except when specified, variance was equal and the distribution of data normal.

a. Diet overlap between species

To test if there was diet overlap between trout and minnows that lived in sympatry, we calculated Schoener's index (*Si*) between fish populations occurring in the same stretch.

This index quantifies the niche overlap (diet) between two groups (species), based on their resource use through the following formula:

$$SSSS = 1 - 0.5 \left|\left| p_{iiii} - pp_{iiii} \right|\right|$$

Si is the prey item overlap proportion between trout (*j*) and minnows (*k*). *pij* is the proportion of prey item *i* consumed by trout and *pik* is the proportion of prey item *i* eaten by minnows of the same community.

The similarity is given in a rage from 0 to 1 where 0 is no overlap and 1 is total overlap; values > 0.6 are considered high overlap.

To represent all the variables of our dataset, reducing dimensionality, but preserving the rank order of the dissimilarities, we used the Non-metric Multi-Dimensional Scaling (NMDS) method. A Brey-Curtis dissimilarity matrix was calculated to replicate the differences between the samples. We accepted NMDS ordination with two-dimension representation of the data (k = 2) and stress values below 0.2.

To test the results, we performed a permutational multivariate analysis of variance (PERMANOVA, package vegan, function adonis2) using the same Brey-Curtis dissimilarity matrix. This method test for group differences using permutations. In this case, a reduced model in adonis2 was used because the small dataset allowed a limited number of unique permutations and complete enumeration (testing all possible permutations of the data instead of a random subset).

b.1. Diet overlap between sympatric and allopatric trout

To test if there were diet differences between trout that live in sympatry and allopatry, we calculated the *Si* between the two groups. In this case, *p*j is the proportion of prey item consumed by sympatric trout and *pk* is the proportion eaten by allopatric trout. The results were tested with a PERMANOVA.

b.2. Trout stomach emptiness

To see if trout feeding behaviour was influenced indirectly by the presence of minnow, we performed a two-sample t-test on the mean stomach fulness of trout when minnows were present or absent.

c.1. Trout specialization on prey items

To see if there was any specialization within each population the proportional similarity index was used. It is calculated through the formula:

$$PPSSPP = 1 - 0.5 \text{ ﷺ} pp_{iiii} - qq_{iiii} \text{ﷺ}$$

where pp_{iiii} is the proportion of prey item *j* in individual *i*'s diet, while qq_{ii} is the proportion of prey item *j* in the populations diet. The index gives a rage from 0 to 1, where 1 means high similarity to the community (Bolnick et al. 2002). Stomachs with total fullness < 10% were excluded to avoid disproportionately influencing the results.".

To test if there were differences in PSI between minnow and no-minnow stretches a t-test with the mean PSI of each population was performed.

To further investigate the composition of trout diet compared to what was present in the streams, we ran a PERMANOVA (community matrix ~ minnow presence + sample type, method = Brey-Curtis, permutation = 999) looking at the effect of minnow presence and type of sample. Data were visualized through an NMDS (method = Brey-Curtis; k=2)

c.2. Trout specialization on prey size

Once the total body length of the 5 biggest invertebrates found in each stomach was calculated following Smock (1980), we calculated the mean length per stretch and performed a two-sample t-test between minnows and no-minnows stretches.

2.3.3 Density estimation

We calculated the surface of each stretch by approximating each section to a trapezoidal shape using dplyr package. Widths were used as bases while the distance between each width measurement was the height of the trapezium.
To get an estimated absolute number of fish per stretch we used the "Seber 3" method from the removal function of the FSA package (Ogle et al. 2025). We calculated density estimations per stretch for each species, by dividing the

calculated absolute number of fish by stretch surface. This method could not be used in stretch BD13_1_1 because there was not a linear decline in individuals between each removal. In this case densities were calculated using the number of fish caught. We tested the difference between minnow and no-minnow stretches densities using a two-sample t-test.

3. Results

Allopatric brown trout (n =147) were on average 69.3 mm long (range 28 to 173 mm) and weighed 5.2 g (range 0.2 to 52.3 g), while sympatric trout (n = 65) were 64.0 mm long (range 34 to 184 mm) and weighed 4.8 g (range 0.4 to 57.5 g). Allopatric trout were longer than sympatric ones (W = 5671, p-value = 0.03; median = 60 and 54.4 respectively). Minnows (n = 68) were on average 63.4 mm long (range 43 to 86 mm) and weighed 2.5 g (range 0.7 to 6.2 g).

There was no statistical difference in fitness (Fulton's K) between allopatric and sympatric trout (W = 3646.5, p-value = 0.45; Figure 3).

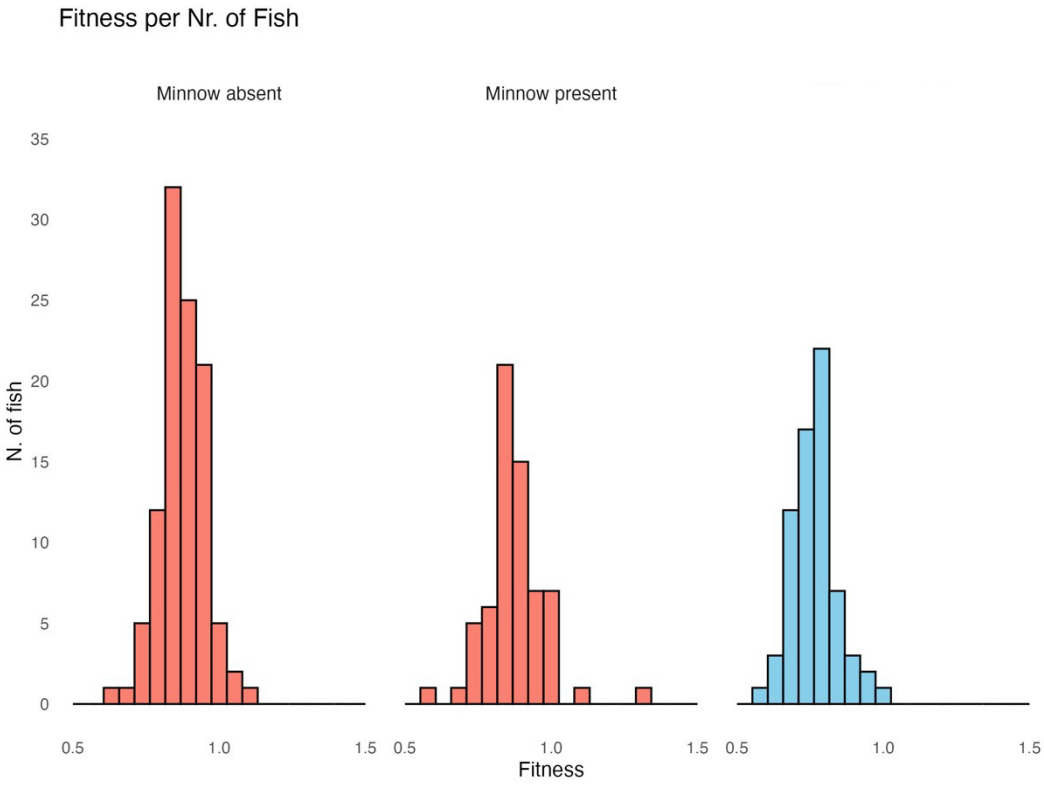

Figure 3. Fitness per number of fish in trout (salmon colour) and minnows (blue colour). Labels on top of the histogram indicate the presence of minnows.

3.1.1 Interaction between trout and minnows

a. Diet overlap between species

Trout and minnow live in sympatry in three out of the seven stretches where trout was found (Table 1). The diet overlap (*Si)* was intermediate or high in all three stretches: *Si* = 0.4, 0.52 and 0.64 respectively. Values between 0.3 and 0.6 are considered intermediate while values above 0.6 are considered high diet overlap.

In stretch BD05_2_1 a large percentage of minnow diet consisted of benthic zooplankton, while this did not seem to be an important prey item for trout in this stretch. Trout on the other hand seemed to rely more on terrestrial insects. In stretch BD10_1_1 minnows fed mainly on terrestrial insects while trout seemed to rely more on insect larvae. In stretch BD13_1_1, the diet overlap between the two species was high. Insect larvae were an important source of food for allopatric trout, but in stretch BD02_2_1 and BD13_1_2 their diet was more varied (Figure 4). In general, trout seemed to rely more on insect larvae then the minnows did, but they seemed to consume similar amounts of terrestrial insects (Figure 5). However, there was no statistical difference between the diet composition of the two species (PERMANOVA: $F= 0.45$, $R^2 = 0.10$, $p = 0.80$, permutation = 719). In contrast, the NMDS (Figure 6, Appendix 5) showed a clear difference in diet between the two species. This incongruence might be due to the small data set (seven stretches in total).

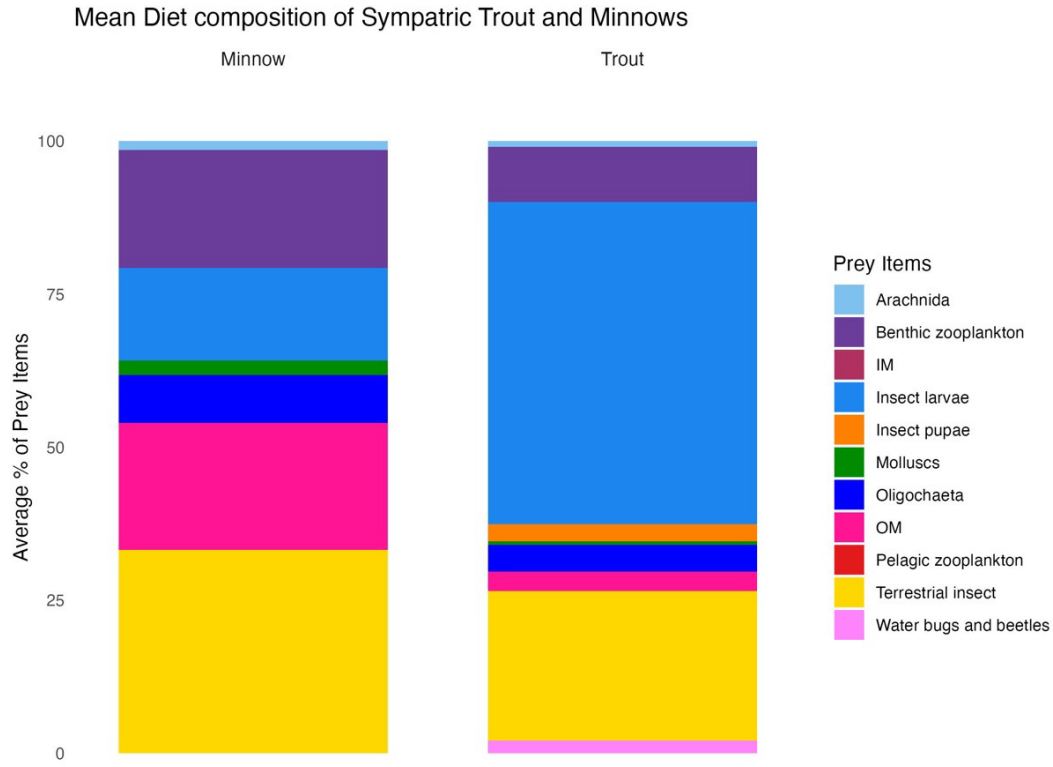

Figure 4. Mean diet composition of trout and minnows that live in sympatry

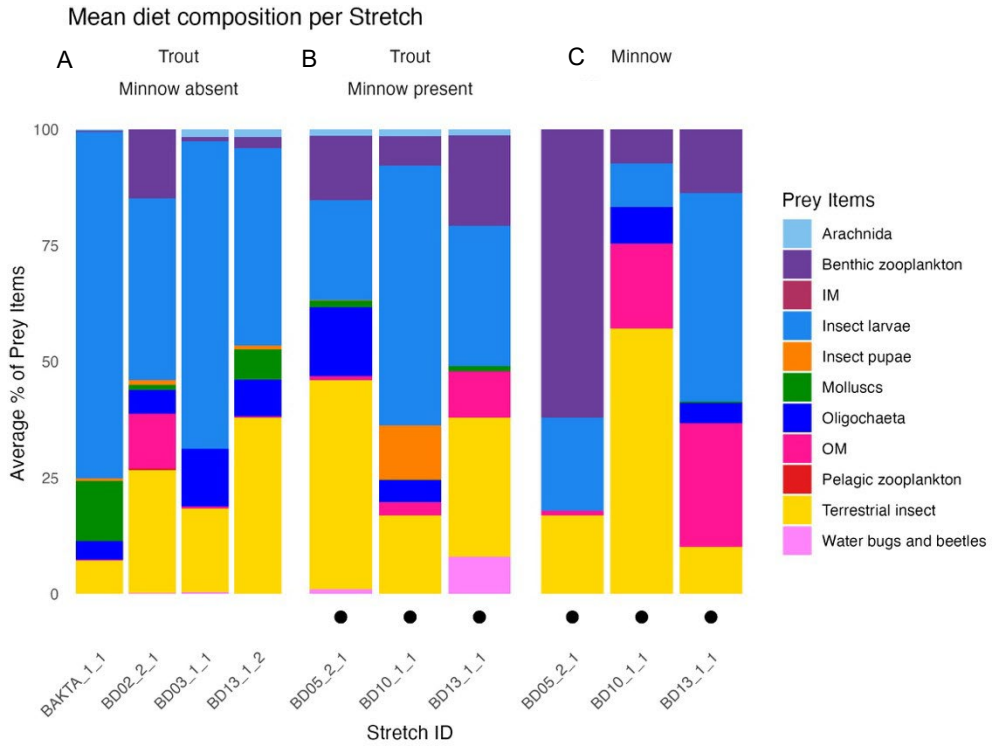

Figure 5. Mean diet composition by stretch of trout and minnows. Black dots highlight the stretches where trout and minnows live in sympatry. A) Allopatric trout; B) Sympatric trout; C) Minnows.

Figure 6. NMDS of trout and minnow diets. Trout is orange and minnow is blue. Plus (+) and solid line is without minnow; triangle (▲) and dotted line is with minnow. Stress = 0.100

b.1. Diet overlap between sympatric and allopatric trout

Diet overlap between sympatric and allopatric trout was high (*Si* = 0.86; Figure 6). Allopatric trout seemed to rely more on insect larvae while the percentage of benthic zooplankton consumed by the sympatric population was higher (Figure 4 panel A and B and Figure 8). Moreover, there was no statistical difference in diet between the two groups (PERMANOVA: F= 1.03, R^2 = 0.22, p = 0.33, n of permutations = 5039).

Figure 7. Mean diet composition of trout in stretches without and with minnow.

b.2. Trout stomach emptiness

There was no difference in mean stomach fullness of trout that live in allopatry (53.9%) or in sympatry (53.2%) with minnow (t(6) = 0.14, p = 0.90; Figure 9). Only three allopatric trout had empty stomachs

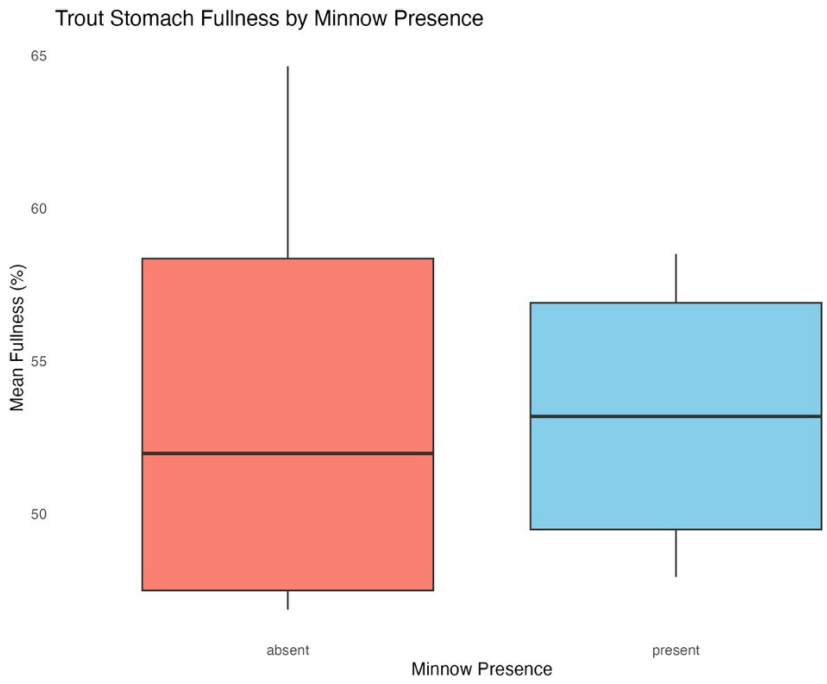

Figure 8. Mean trout stomach fullness (in %) when minnows are absent (salmon colour) and when they are present (blue colour).

c.1. Trout specialization on prey size

The mean length of the five biggest prey items found in allopatric trout stomachs was 5.21 mm, while in sympatric trout stomachs it was 5.19 mm. There was no difference in prey length between the two groups ($t(5) = –0.01$, $p = 0.99$; Figure 12).

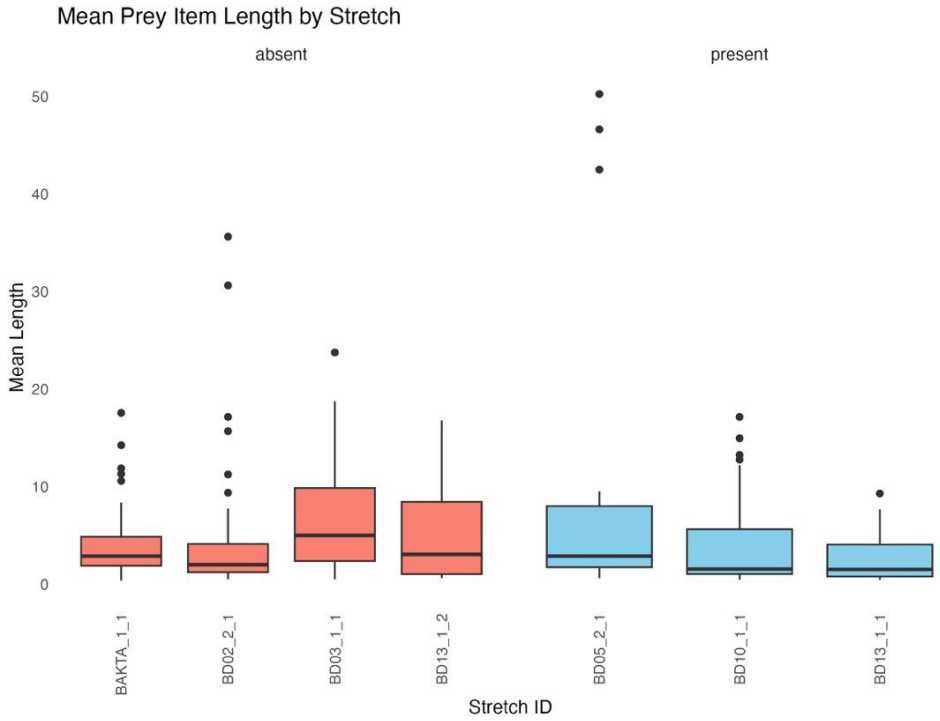

Figure 9. Mean prey item length (mm) by stretch when minnows are absent (salmon colour) and when they are present (blue colour).

c.2. Trout specialization on prey items

There was no difference between the mean Proportional Similarity Index of stretches with and without minnows (0.60 and 0.54 respectively; $t(5) = 1.55$, $p = 0.18$; Figure 10 which means that trout did not specialize more when minnows were present in the streams. However, even though we did not find any adult beetles in the macroinvertebrate samples (Figure 11), in stretches where minnows were present, trout consumption on this prey item was on average 2.5%, reaching 8.0% in stretch BD13_1_1 (Figure 4 panel A and B, and Figure 8).

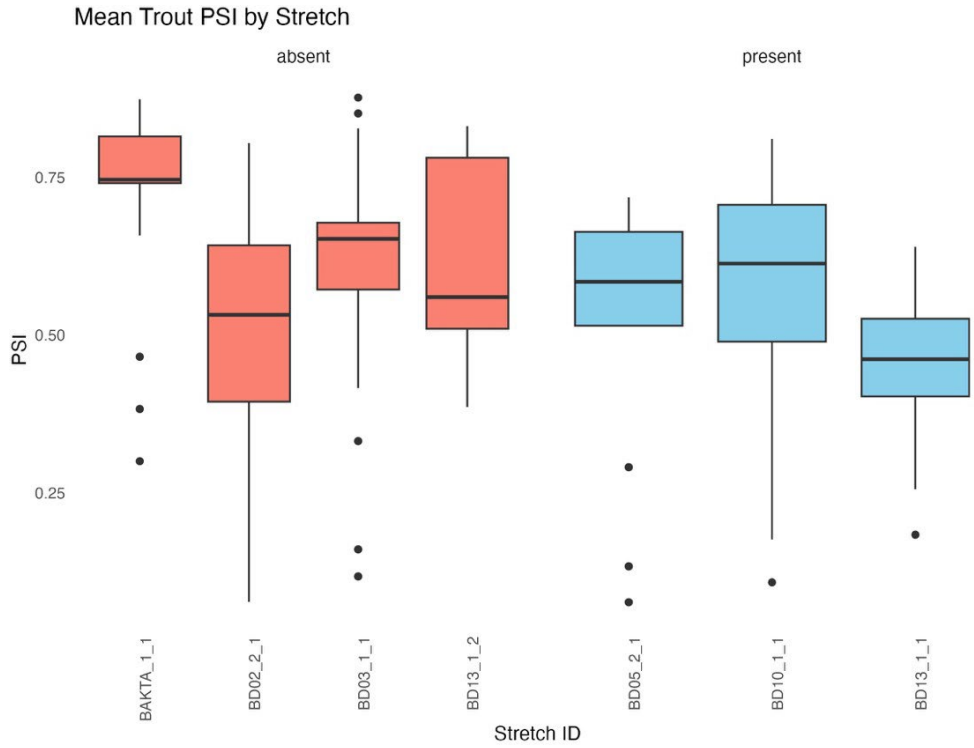

Figure 10. Mean trout Proportional Similarity Index per stretch when minnows are absent (salmon colour) and when they are present (blue colour).

c.3. Comparison of diets and available prey

The PERMANOVA confirm that there was no difference between what was found in the streams and what trout would feed on (Sample type: $F = 2.24$, $R^2 = 0.15$, $p = 0.108$) and that the presence of minnows does not affect the prey community composition (Minnow presence: $F = 1.81$, $R^2 = 0.12$, $p = 0.176$). The interaction between these two terms was not significant (Sample type*Minnow presence: $F = 1.59$, $R^2 = 0.10$, $p = 0.214$) suggesting that the difference between trout stomach content and the stream macroinvertebrate community is not changing whether minnows are present or not (Figure11). However, each factor accounts for 10-15% of the variance that suggests biological trends that might not reach statistical significance due to the small sample size.

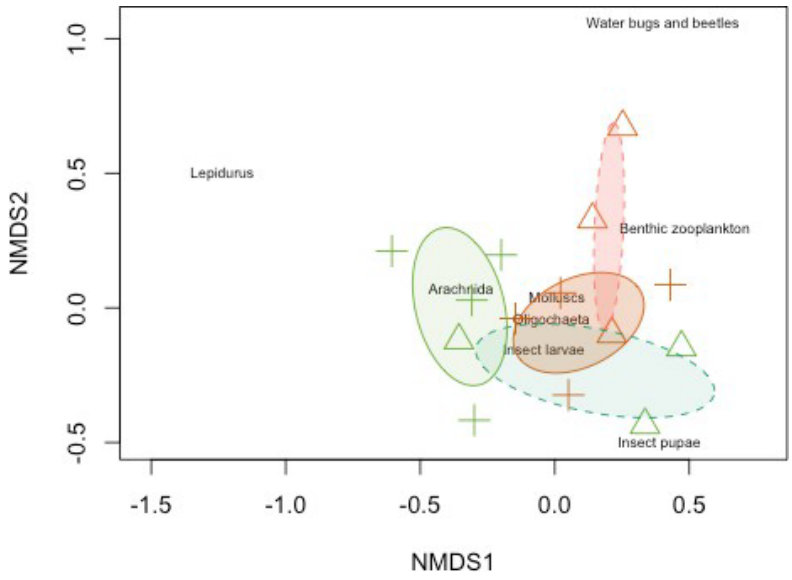

Figure 11. NMDS of trout stomach and macroinvertebrate samples. Trout is in orange and macroinvertebrates are in green. Plus (+) and solid line is without minnow; triangle (▲) and dotted line is with minnow. Stress = 0.138

3.2 Density estimation

In stretches where minnows were present, trout densities were on average lower than when minnows were absent (on average 0.34 individuals/m2 and 0.49 individuals/m2 respectively). However, there was no significant difference between the two groups (two-sample t-test: t(5) = 1.10, p = 0.322).

Table 2. Densities (individuals/m2) and number of fish per stretch.

Stretch ID	Trout		Minnow		Trout + Minnow	
	density	nr. of fish	density	nr. of fish	density	nr. of fish
BD10_1_1	0.53	40	0.29	20	0.82	60
BD13_1_1	0.38	11	0.96	28	1.34	39
BD05_2_1	0.10	14	0.19	20	0.28	34
BD03_1_1	0.26	27	/	/	0.26	27
BD13_1_2	0.53	14	/	/	0.53	14
BD02_1_1	0.63	78	/	/	0.63	78
BAKTA_1	0.56	28	/	/	0.56	28

3.3 Predation

Predation on fish or fish fry and eggs was not observed in any of the minnow or trout stomachs analysed.

4. Discussion

The presence of minnows seems to not have a strong effect on trout feeding behaviour:

i) there was a high or intermediate overlap in diet between sympatric trout and minnows.

ii) No major differences in diet were found between sympatric and allopatric trout.

iii) c) Brown trout did not seem to have a more specialised diet or consume smaller prey items in the presence of minnows.

ii) No differences in densities were found when comparing trout populations that lived with or without minnows.

iii) Piscivory between the species was not observed.

4.1 Interaction between trout and minnows

a. Diet overlap between species

When comparing and visualizing the diet of sympatric trout and minnows there are contrasting results: diet overlap was high in only one of the three stretches which indicate that the competition between the two species is relatively low. However, when the PERMANOVA was applied no difference in diet was detected and we cannot confirm that competition is weak due to the incongruence of the results. At the same time the low number of permutations suggests that our dataset is too small to have statistical power, and further sampling and possibly further statistical analyses should be done.

The PERMANOVA results would be in accordance with Museth et al., (2010) who found high overlap between brown trout parr and minnows in the Øvre Heimdalsvatn system. As they argue, diet overlap studies are not enough to confirm competition between the two species, but they were able to support that there was competition thanks to the long-term dataset of their system which showed shifts in macroinvertebrate community as well as in the densities of the two species. From the diet overlap, densities and macroinvertebrate community data we have it seems that competition is not happening right now. However, since we lack a long-term dataset, we cannot confirm this statement as for the case of the Øvre Heimdalsvatn system.

Minnows crush their food using pharyngal teeth (Scharnweber, 2020) and this may bias observations on minnows' stomach content towards prey items with harder shells or small sizes. This may be relevant for groups like benthic zooplankton that – in our study - were more common in minnow than trout stomachs, although there was no significant difference between the two species.

Moreover, minnows seemed to decompose at a faster rate than trout and this might affect the analysis of the stomachs to a great extent: for example, in one of the minnows sampled we were not able to extract the stomach because it was completely decomposed.

b. Diet in allopatric and sympatric trout

We did not find differences in stomach fullness or fitness between sympatric and allopatric trout. In addition, we found a high overlap between their diet, suggesting trout do not shift their diet when minnow is present. This is in contrast to other studies that have seen dissimilarities in populations that live with similarly competing species like bullhead (*Cottus poecilopus*) in a Norwegian subalpine lake (Holmen et al., 2003). In our systems, trout diet does not seem to be affected by the presence of minnows suggesting that this species may not be a strong competitor as bullheads.

c. Specialization in allopatric and sympatric trout

To further investigates the incongruence regarding the diet of allopatric and sympatric trout, we looked at the individual specialization (PSI) and the composition of trout diet compared to what is available in the stream and the size of the prey they feed on. In contrast to what we expected, we did not find any significant differences between sympatric and allopatric trout.
In comparison, studies conducted in lakes have shown a clear difference in diet between trout that live in allopatry and trout that live in sympatry both with smaller fish prey species like minnows and sticklebacks (*Gasterosteus aculeatus*; Sánchez-Hernández et al., 2017) and bigger competitors like Arctic charr (L'Abée-Lund et al., 1992). The fact that we do not find a difference in the diet of trout populations that exist with or without minnow might be because the minnow expansion has happened recently, and the changes are not yet clearly observable. In fact, in the Øvre Heimdalsvatn system Borgstrøm et al., (2010) have found that trout shifted their diet from big macroinvertebrate like *Gammarus lacustris* and *Lepidurus arcticus* to a more piscivorous diet 10 to 15 years after minnows' introduction, and it is known that trophic adaptations to a new species take time to be observable since both the native and the alien species need to gradually adjust to the new ecological setting (Woodward & Hildrew 2002).

4.2 Density estimation

We did not observe a difference in trout density when minnows were present or absent. This is in contrast to Tiberti et al. (2022) and Qvenild et al. (2024), who found that minnow had a negative effect on salmonid densities in high mountain lakes. The lack of statistical significance may be due to the recency of the invasions: for example, lake BD13 was sampled in 2023 by Henna Kangosjärvi

and minnow where not yet detected, while one year later, in the stream their density was higher than that of the trout (0.96 and 0.38 ind./m^2 respectively). Moreover, there are multiple studies in the Øvre Heimdalsvatn system that look at changes in minnows and trout densities over long periods of time where no visible changes in trout densities were observed at the beginning of the minnow invasion (Lien, 1981; Museth et al., 2010). This is relevant information for the area we sampled, because minnows are most likely still expanding their range. Lake BD03 might be an example of this: it was chosen because it was considered a minnow-free lake but while we did not capture any minnows in the stream sampled, we caught 13 individuals in the lake shore on the opposite side of the lake. It is also worth noting, that while we did not find a difference in trout density depending on if minnows were present or not, the total density of fish seemed to be higher when minnows were present (Table 2, not tested).

4.3 Predation

We wanted to see if either species was predating on the other but no predation on fish was observed. We sampled outside of trout spawning season so no predation on eggs or fry by minnows could be observed. Trout can heavily feed on minnows, especially during their reproductive period when minnows are more vulnerable (Museth et al., 2010). To increase the chances of observing predation, sampling should be performed during the reproductive period of both species (early summer for minnows and autumn for trout; Froese & Pauly, 2024b, 2024a). Moreover, most of the sympatric trout sampled were below the size where they become properly piscivorous (< 130 mm; L'Abée-Lund et al., 1992) and their ability to feed on adult minnow may be limited.

4.4 Conclusion

To further improve the understanding of the trout-minnow interaction in the area, more streams with both allopatric and sympatric trout should be sampled. Moreover, having a long-term dataset will tell if minnows are still expanding and if they are negatively affecting trout. Finally, sampling multiple times during the ice-free season would probably give more chance to observe predation on fish.

In conclusion, we could not statistically confirm any of our hypothesis, but some of the results with the overlap in diet between sympatric trout and minnows, and the trends observed in the difference of the composition of diet, and the different densities in allopatric and sympatric trout, suggest that further research needs to be performed.

With the current knowledge, it seems that trout in the sampled streams are not as negatively affected by the presence of minnows as we thought, but trophic adaptation unfolds over extended periods of time and only a bigger dataset, both

long-term and with more streams sampled, can confirm if this is the case in the Abisko area.

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Popular science summary

We all know the story: big fish eats small fish! But is the opposite possible? Could a tiny fish like the Eurasian minnow affect the survival of the big brown trout by eating their food? Or simply, do trout live better without minnows? And do they eat each other?
We investigated these questions by focusing on the diet of the two species in streams across the northern Swedish mountains.
Our results? Not so clear. So far, it seems that trout are not affected by the presence of minnows. But ecosystems often need time to adjust to the arrival of a new species and we got some hints that changes could still happen.
We tried to get some answers, and we got back with more questions: are trout simply not bothered by the presence of minnows? Or is it just matter of time before we can actually see bigger effects as is often the case in nature?

Appendix 1

ID	No	DOC mg/L	ID	No	TN µg/L	TP µg/L
1	27	2.1	19	11	285	13.0
2	16	3.7	20	15	169	4.7
3	24	5.2	21	13	155	5.0
4	17	8.9	22	14	285	5.2
5	26	4.2	23	16	172	4.8
6	11	4.4	24	5	231	6.0
7	10	7.8	25	4	195	3.8
8	13	5.7	26	7	245	12.0
9	12	3.5	27	17	93	3.1
10	18	8.2	28	9	544	13.8
11	19	2.7	29	8	90	8.2
12	23	4.2	30	12	96	9.3
13	20	2.3	31	18	416	6.6
14	14	2.4	32	6	109	7.3
15	22	2.2	33	10	105	9.0
16	21	7.7	34	1	108	1.8
17	15	2.6	35	2	99	3.0
18	25	6.7	36	3	138	3.2

Appendix 2

Electrofishing protocol

Sampling site, staff and objective	
Sampling site (name, e.g. Abisko)	
Type of water (stream, river, lake, etc)	
River/stream (name)	
Stretch (number)	
Locality co-ordinates Start (GPS)	
Locality co-ordinates End (GPS)	
Team (fishing staff leader and crew members)	
Date (yy-mm-dd)	
Time of the day (beginning and end of electric fishing)	
Other details	

Equipment and prerequisites for electric fishing	
Voltage (V)	
Water level (low, intermediate, high and estimated depth (m))	
Weather conditions (air temperature, precipitation, cloudi- ness, windiness)	
Temperature of water (°C)	
Visibility (colour and/or turbidity of the water, clear/turbid)	

Site characteristics	
Locality length (m; always 50m)	
Average width (of wetted area, m) Look at specific form	

Average depth (m) Look at specific form	
Maximum depth (m) Look at specific form	
Water current class (slow, intermediate, rapids and estimated current speed (m/s))	
Substrate (dominating, subdominant)	
Habitat type (pool, flat, run, riffle, rapid)	
Bottom vegetation (missing, sparse, intermediate, and rich)	
Dominating type of bottom vegetation (algae, mosses, phanerogams)	
The following details are optional	
Classification of surrounding riparian zone	
Shade	
Large woody debris	

Remarks:

Refer to sketch over locality (markings, north point, flow direction, photo-number, etc.):

Substrate classification and explanation

Substrate class	**Particle size**
High Organic	Very fine organic matter
Silt	Mostly inorganic matter, individual particles invisible
Sand	< = 2 mm
Gravel	2 mm to 16 mm
Pebble	16 mm to 64 mm
Cobble	64 mm to 256 mm
Boulder	> 256 mm
Bedrock	Continuous rock surface

Check list

To do list	Date
Electrofishing (2-4 stretches, 3 passage each)	
Macroinvertebrates	
SI benthic algae (1 sample per stream)	
SI macroinvertebrates (1 sample per stream)	
Stream paramiters (width, depth)	
Water sample (1 per stream)	

Appendix 3

List of the division in groups of stomach content items. List 1 represent a finer division at different recognizable taxonomic levels; List 2 regroup stomach content items into functional groups.

List 1:

animal parts, aphidoidea, arachnida, araneae, bivalvia, bosmina, bytotrephes, ceratopogonidae, chironomidae adult, chironomidae larvae, chironomidae pupae, cicadidea, coleoptera adult, coleoptera larvae, diptera adult, diptera larvae, ephemeroptera larvae, ephemeroptera pupae, gastropoda, hemiptera, hymenoptera, insect larvae, insect parts, oligochaeta, organic material, plant, plecoptera adult, plecoptera subadult, plecoptera larvae, simulidea, stones, terrestrial insect, tipulidea adult, trichoptera larvae, trichoptera case.

List 2:

Arachnida, benthic zooplankton, inorganic material (IM), insect larvae, insect pupae, molluscs, oligochaete, organic material (OM), pelagic zooplankton, terrestrial insect, water bugs and beetles.

Appendix 4

List of the division in groups of macroinvertebrate samples. List 1 represent a finer division at different recognizable taxonomic levels; List 2 regroup macroinvertebrate into functional groups.

List 1:
bivalvia, ceratopogonidae, chironomidae larvae, chironomidae pupae, coleoptera larvae, coleoptera imago, diptera larvae, diptera pupae, ephemeroptera, eurycercus, gastropoda, hirudinea, hydrachnidia, lepidurus, odonata, oligochaeta, plecoptera, simulidea, trichoptera.

List 2:
Arachnida, benthic zooplankton, hirudinea, insect larvae, lepidurus, molluscs, oligochaeta.

Appendix 5

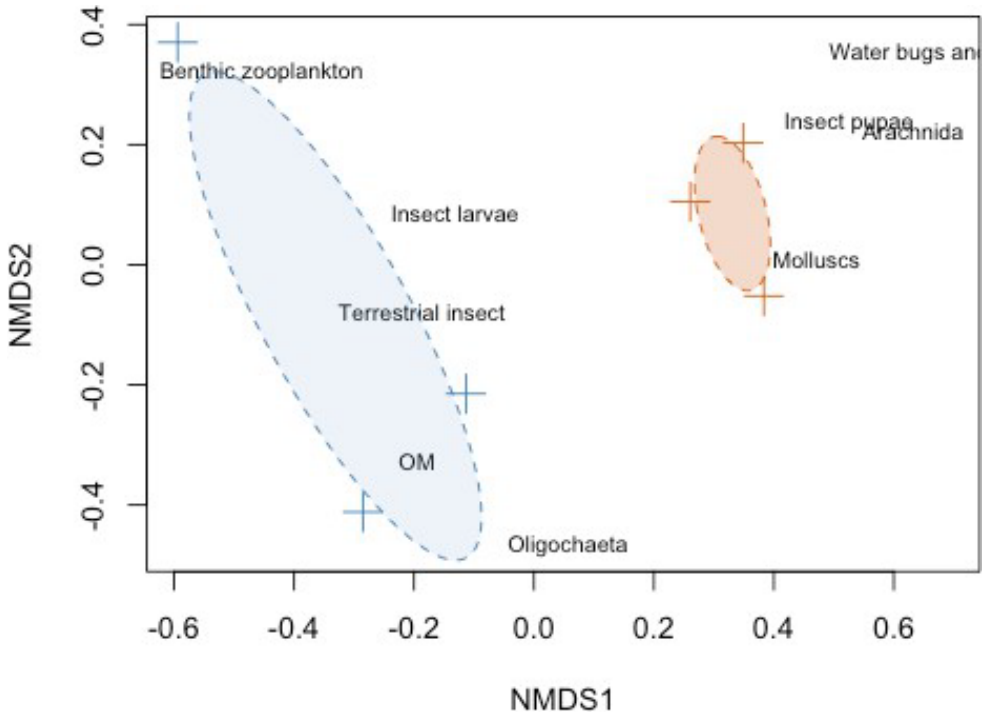

Figure 12. NMDS corresponding to the PERMANOVA between sympatric trout (orange) and minnows (blue). It is evident, as in Figure 6, that trout and minnow have a distinct diet.

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