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Can a piscicide treatment alter stream ecosystem functioning through trophic cascading effects on benthic invertebrates?

A field experiment exploring leaf litter decomposition and invertebrate diversity in enclosed leaf packs in a sub-arctic watercourse.

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Cover page photos. Front: Kavelelva, Skibotn. Front panels top to bottom: 1, Juvenile Atlantic salmon (*Salmo salar*); 2, The stonefly *Diura nansenii*; 3. The stonefly *Taeniopteryx nebulosa*; 4, Coarse- and fine mesh litter bags used in the experiment. Back: Kjusakelva, Nordkjösbotn.

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2 Abstract

Processing of detritus is an important ecosystem function in freshwaters. In rivers and streams, the activity of shredding invertebrates play an important role in processing of coarse-particulate organic matter such as leaf litter. In stream food webs, fish may act as top predators and control activity of consumers such as shredders top down. This top-down effect may be of a directly consumptive nature, or indirect and mediated by species traits.

Most studies on trophically cascading effects in stream ecosystems are done in small scale, either in small laboratory setups, or in in-stream experimental units such as cages or flow through channels. These setups are very useful in exploring specific effects and relationships, but might not be adequate to document effects on whole stream or catchment scale.

I utilized a management-imposed rotenone treatment of the sub-arctic watercourse Skibotn catchment in Troms, northern Norway, as a setup for a large scale field experiment. Using pairs of coarse- and fine-meshed plastic litter bags filled with dry birch (*Betula pubescens*) leaf litter, I measured decomposition rates (kd^{-1}), and collected and identified leaf litter colonizing invertebrates in riffle habitats in the autumn one year before (2014), and one year after (2017) the treatment. Nordkjøs catchment, an untreated catchment in the adjacent area, was studied simultaneously.

Shredding invertebrates contributed to litter decomposition in both years in all but one stream, but I found no significant change in invertebrate-mediated decomposition between the two years on catchment scale. There was no marked change in density or diversity of invertebrates in the litter bags between the two years, while fish had a diverse diet dominated by Baetid mayflies. However, young of the year salmonids were present already in a few sites after the treatment.

Results of this field experiment indicate that fish did not have a strong top-down effect on shredding invertebrates in Skibotn catchment. The most likely explanation is that fish densities were low and their diets were not dominated by the most important shredder species. The studied streams are heterogenic environments and subject to natural stochasticity that might outweigh any small ecological effects, emphasizing the importance of good background data when performing before-after- impact control studies.

3 Introduction

Rivers and streams represent only a fraction of the total freshwater in the world, and only 0.06% of Earth's non-glaciated land surface (Allen and Pavelsky 2018). Yet, these systems contribute to the transport and cycling of energy and matter across vast geographical scales and through several biological levels of organization (Vannote et al. 1980, Shiklomanov 2000, Wohl 2017, Allen and Pavelsky 2018). Like other freshwater systems, they contain disproportionately high biologic diversity relative to their geographic extent (Reid et al. 2019), and contribute to important ecosystem services such as food and clean freshwater in addition to recreational and and spiritual services (Thorp et al. 2010).

Processes or combinations of processes such as primary production, processing and recycling of detritus, and production of animal biomass in ecosystems, can be termed ecosystem functions. Ecosystems include interactions between and within species assemblages and their non-living environment (Lawrence 2005), and species within an ecosystem can be connected by their trophic interactions in a food web, through which energy and matter is processed (Pimm et al. 1991). Such functions involving the processing of energy and matter contribute to the overall 'functioning' of ecosystems, by retaining the nature and properties of the system, while also contributing to global bio- and geochemical cycles (Lecerf and Richardson 2010). Ecosystem services are in practice those functions of ecosystems that are of high relevance for human societies (Jax 2005). For example, the way detritus, dead organic material, is processed in streams relates both to the quality of the water for human consumption, the diversity and biomass production of animals that live there and its role as a sink or source of carbon to the atmosphere (Allen and Pavelsky 2018) or adjacent aquatic and terrestrial ecosystems (Vannote et al. 1980, Marks 2019).

Human activities pose a multitude of interactive stressors on freshwater systems worldwide (Carpenter et al. 2011). Stressors such as pollution (Fernández et al. 2015), habitat alteration (Frainer et al. 2018), climate change (Follstad Shah et al. 2017) and spread of invasive alien species (McIntosh and Townsend 1996) can on their own or simultaneously affect the biological diversity and functioning of freshwater ecosystems. Scientific attention has therefore been led to the relationship between biologic diversity, food-web structure and ecosystem functioning (Gessner et al. 2010, Lecerf and Richardson 2010, Duffy et al. 2017 and references within), including potential top-down

effects of predators on consumer guilds.

The processing of detritus of both autochthonous (in-stream) and allochthonous (terrestrial input) origin is a key ecosystem function in freshwater food webs (Marcarelli et al. 2011). A substantial part of annual photosynthetic product in both terrestrial and aquatic ecosystems is not consumed directly, and therefore enters the food web as detritus (O'Neill and Reichle 1979, Wetzel 1995, Cebrian 1999). Watersheds consist of a continuum of streams of increasing order (Strahler 1957, Vannote et al. 1980), and in lower order streams, the surface area available for photosynthetic production on the stream bottom is low relative to the terrestrial-aquatic interface in the riparian zone. This means that allochthonous carbon from the watershed and riparian zone are important supplies to the food web, especially when autochthonous production is restricted due to seasonality effects like shading by tree foliage in summer, and a reduced light and temperature regime in combination with ice formation in winter. Indeed, a long-term study by Wallace et al. (2015) shows that biomass production of stream invertebrates is positively affected by inputs of terrestrial leaf litter.

In temperate, boreal and sub-Arctic catchments with deciduous forest, leaf litter abscised in autumn may be transported to streams and rivers by wind and rainwater, or by falling directly into them. In these aquatic ecosystems leaf litter undergoes decomposition through an array of physical and biotic processes, transforming it from coarse- to fine- particulate organic matter. First, water soluble compounds leach out of leaves rapidly after submersion, leading to substantial mass loss (Gessner et al. 1999). Then, as time passes, leaf litter is colonized by microbial decomposers, most importantly aquatic hyphomycetes, and later by detritivorous invertebrates.

Aquatic hyphomycetes have a large influence on decomposition of leaf litter. Fungal accrueling of biomass leads to the up-taking and enriching of leaf litter with several nutrients, such as nitrogen and phosphorous, the respiration of carbon, and the cleaving of structural molecules such as cellulose and lignin (Danger et al. 2016). Since this activity of aquatic hyphomycetes normally increases the food quality of leaf litter for invertebrates by making it more palatable and nutritious, it is often called “conditioning” (Bärlocher and Kendrick 1975). This however undermines the fact that microbes are responsible for a large part of leaf litter mass loss regardless of other detritivores. In fact, aquatic fungi can compete by interference with invertebrates for the same nutrients by producing toxic secondary metabolites (Trienens and Rohlfs 2012).

Macroinvertebrates, most of them insects and crustaceans, are important primary consumers in freshwater ecosystems. Stream invertebrate species can be assigned to guilds according their feeding strategies (Cummins 1974): 1) Shredders feed on coarse particulate organic carbon (CPOM), including fallen leaf litter and other dead plant tissues, 2) Predators feed on live prey, mainly other invertebrates or small fish, 3) gatherers/collectors feed on sedimented fine particulate organic matter (FPOM), and 4) grazers feed mainly on endolithic and epilithic algae, as well as biofilms, and partially on FPOM and aquatic plant tissues. A division of invertebrates into distinct feeding guilds is sometimes sufficient, but omnivory is prevalent, with some single species acting as both shredders, gatherers and predators depending on seasonal food availability. Leaf litter in streams is utilized by different invertebrates as a food source and habitat in a succession-like manner throughout the course of its decomposition (Haapala et al. 2001, Marks 2019).

Although predacious invertebrates can be the top predator in some systems and some settings (e.g. Cobbaert et al. 2010), the main top predators in streams are fish. Both top predator fish and intermediate predator invertebrates are present in most streams (Power 1990). Amphibians, birds, and rodents can also feed on aquatic invertebrates, but their direct effect on food webs in non-perennial headwater streams on the northern hemisphere is restricted compared to that of fish due to ice cover in winter (Parker and Huryn 2006).

Predators can have trophically cascading effects on stream ecosystem functioning, for example on leaf litter decomposition rates (Konishi et al. 2001) or standing crop of periphyton (Power 1990). These cascading effects on the activity of consumers can be directly mediated by density alteration when the predator decreases the density of the consumer (Konishi et al. 2001), or may be trait mediated, for example when predator-avoidance behaviour decreases feeding efficiency of prey (Wellnitz 2014). Trait-mediated effects may be triggered by predator chemical cues (Paterson et al. 2013), or by direct interference. For example, *Diura nanseni*, a common predatory invertebrate in northern rivers and streams, prefers to prey on small invertebrates like chironomid midges and blackfly-larvae (simuliidae), but can still have antagonistic non lethal predation effects on larger taxa, including shredding stoneflies (Malmqvist 1993).

Effects of fish on ecosystem functioning can also cascade through intermediary trophic levels, by releasing a consumer from a predatory invertebrate (Power 1990) or from interspecific competition

(Ruetz et al. 2002). The direction and strength of trophic cascades is variable between systems, and depends on interactive effects of species assemblages (Ruetz et al. 2002), food-web structure (Jabiol et al. 2013) and productivity (Peckarsky et al. 2013). Other biotic and abiotic conditions may further affect the strength and direction of trophic cascades. For example, food availability may impact the predatory activity of omnivores (Hellmann et al. 2013), and water current velocity can reduce activity of predators, thus reducing their antagonistic effect on consumers (Wellnitz 2014).

Most results describing top-down effects on leaf litter decomposition in streams come from small lab experiments, or controlled small-scale field experiments. Manipulative field experiments on trophic relationships in streams are often restricted to designs with small experimental units where predator presence or absence, predator density, or the access of naturally occurring predators is manipulated using flow-through channels, mesh-bags or cages. In such experiments predator evasion behaviour in consumers might be confused as a consumptive top-down effect (Meissner and Muotka 2006), and actual consumptive effects can be overestimated by using artificially high fish densities in an enclosed homogenous habitat. While laboratory experiments are valuable in untangling relationships and documenting effects, field experiments can be necessary to find out if trophic cascades actually occur outside a controlled lab environment, and if their effect on functioning in real natural ecosystems can be separated from natural variation in time and space.

Large-scale management-imposed piscicide treatments can be used as ‘natural’ field experiments to explore effects of fish removal on the whole stream and even on watershed levels. In Norway, different solutions containing rotenone, a plant based piscicide, have been used for management purposes in freshwaters intended to extirpate invasive or unwanted fish species or their parasites (Bardal 2019). Rotenone inhibits the activity of cells used in gill respiration and is lethal to almost all fish (Hamilton 1941). Rotenone is also toxic to many invertebrates (Kjærstad and Arnekleiv 2011), but studies show that lotic invertebrate communities can recover quite rapidly (within 1 year) after rotenone treatments when treatments are restricted to the lower stretches of a larger watershed or smaller parts of a system of aquatic habitat patches (Kjærstad et al. 2016, Woods et al. 2016, e.g. Pham et al. 2018). Thus, a rotenone treatment might be used to assess a situation where fish are extirpated from a catchment or stream, while invertebrates rapidly reestablish.

In this study, I take advantage of a large scale rotenone treatment that aimed to eradicate the

monogenean parasite *Gyrodactylus salaris* from rivers in Storfjord region, northern Norway. The treatment lead to the extirpation of all fish in anadromous reaches of the sub-Arctic watercourse River Skibotn (Adolfson et al. 2021). Leaf litter decomposition and community composition of invertebrates inhabiting leaf packs were studied in the rotenone treated catchment and a control catchment simultaneously before and after the treatment, to explore and document decomposition of leaf litter in a situation of top-predator release for shredding invertebrates. I hypothesized that extirpation of fish communities would lead to changes in decomposition rates of leaf litter via density- or trait-mediated effects of fish on invertebrates, provided that invertebrate communities in the treated catchment recover within the first year after the treatment.

4 Methods

4.1 Study area

The study was conducted in the lower reaches (<70m asl.) of two catchments in Troms and Finnmark county, northern Norway (~69°N, 20°E): the Skibotn catchment and the Nordkjøs catchment, with the main experimental sites in Skibotn and the control sites in Nordkjøs (Table 1). Main rivers in the two catchments are named river Skibotn and river Nordkjøs, respectively, while original Norwegian names are used for tributary streams, the suffix “-elva” translating to “river” or “stream”.

The lower reaches of both catchments run in northeast-to-southwest oriented valleys (Figure 1) with boreal mixed forest dominated by birch (*Betula pubescens*), with alder (*Alnus incana*), rowan (*Sorbus acuparia*) and several willow species (*Salix* spp.) also present. There is some pine (*Pinus sylvestris*) and patches of Norway spruce (*Picea abies*) locally, especially in Skibotn. The lower reaches of both main rivers and tributaries in these catchments are also spawning habitats for anadromous Atlantic salmon (*Salmo salar*, hereafter referred as salmon), brown trout (*Salmo trutta*, hereafter referred as trout), and Arctic charr (*Salvelinus alpinus*, hereafter referred as charr). Juveniles of trout, salmon and charr are the common fish encountered at the studied sites.

River Skibotn runs for 35km through the Skibotn valley from the outlet at Gálggojávri (500 m asl.) to the river mouth in Skibotnbukta, Storfjorden. The lower reaches are characterized by slow flow and fine-particle substrate, while the upper reaches have coarser substrate and higher current velocities (Kristoffersen et al. 2005). The Skibotn hydropower plant collects water from larger lakes in the catchment, and the outlet is at Kavelnes, 11 km from the river mouth. Two sites were sampled in the main river stem, ~500m apart, in one of several branches in a braided section of the river above the hydropower outlet. Four tributaries were included in the study. Tributaries Kavelelva and Lullelva mouth to the main river upstream of the hydropower outlet and were sampled with two sites each, approximately 500m apart. Tributaries Haskielva and Olderelva, each with a single sampling site, mouth to the river below the hydropower outlet but are not themselves subject to any runoff regulation.

River Nordkjøs runs for 21km from the outlet in lake Dápmotjávri (263 m asl.) in the Tamok valley to the river mouth in Nordkjøsbotten, Balsfjorden. Three sites were studied in Nordkjøs catchment, one in a small side-branch of the main river stem, and two in the tributaries Kjusakelva and Øverelva.

Øverelva is a distributary from Kjusakelva, and both streams were sampled below the point of bifurcation, where they alternate between riffles and small pools. The mouths of these two tributaries, as well as the studied site in the main river are all located in the lower 7km of River Nordkjøs.

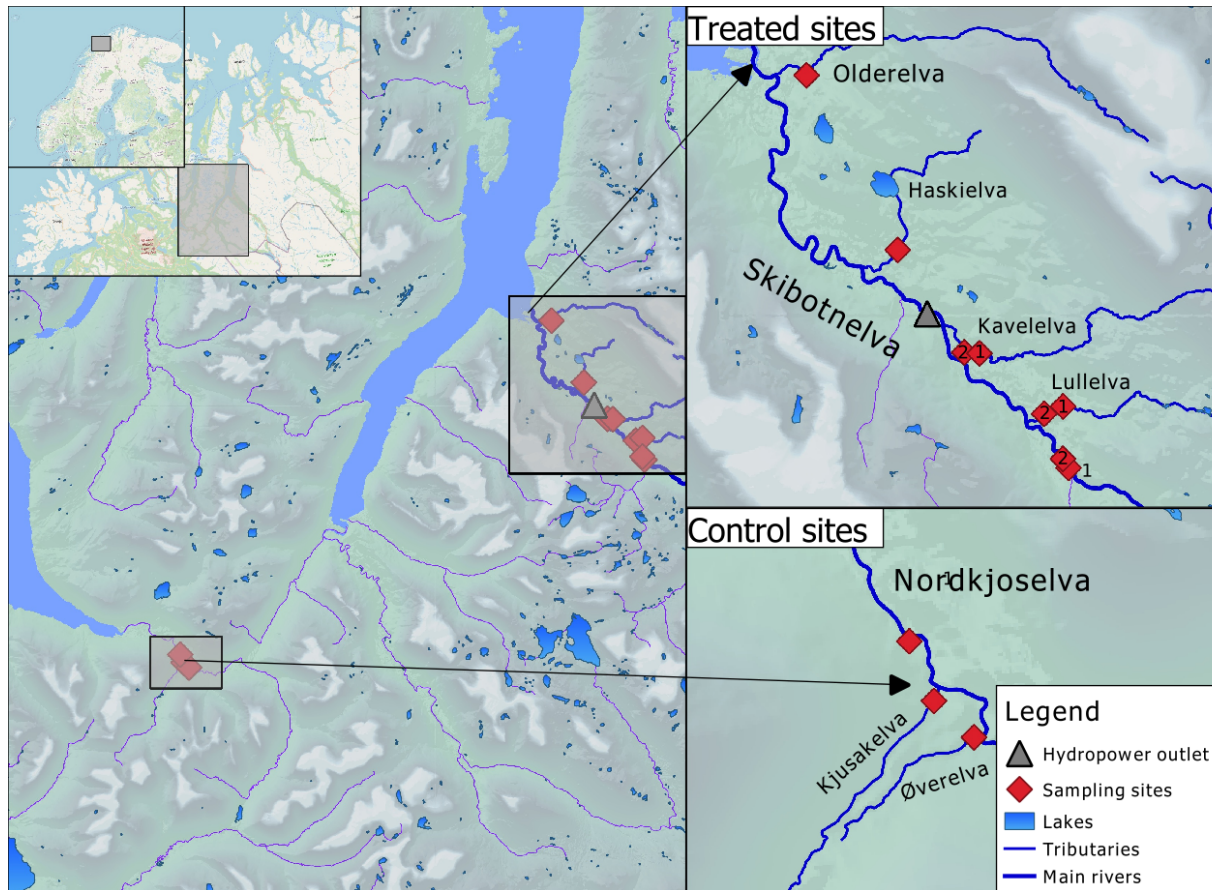


Figure 1: Map showing sampling sites in the rotenone treated Skibotn catchment and the control, Nordkjøs catchment. Sites in River Skibotn and its tributary streams Lullelva and Kaveelva are marked: 1, upstream; 2, downstream, when two sites are sampled in the same stream. Streams have original norwegian names in the map, the suffix ”-elva” translates to river or stream.

4.2 Field experiment

A field experiment was conducted before (2014) and after (2017) rotenone treatments in Skibotn catchment in 2015-2016 (for details about rotenone treatment see Adolfsen et al. 2021). Leaf litter decomposition and community composition of litter colonizing invertebrates was studied by deploying leaf packs enclosed in plastic litter bags in the rivers and tributary streams. Experiments were initiated around the time of abscission, which is often mid september to early october in this

Table 1: Overview of sites included in the field experiment in Skibotn catchment and Nordkjøs catchment. Where specified, the "upper" site is 500m upstream of the "lower" site.

Catchment		Site	Site description
Skibotn	(Treated)	River Skibotn	Main river branch (upper)
		River kibotn 2	Main river branch (lower)
		Lullelva 1	Tributary (upper)
		Lullelva 2	Tributary (lower)
		Kavelelva 1	Tributary (upper)
		Kavelelva 2	Tributary (lower)
		Haskielva	Tributary
		Olderelva	Tributary
Nordkjøs	(Control)	Øverelva	Tributary
		Kjusakelva	Tributary
		River Nordkjøs	Main river branch

region, and ended in november before rivers and streams were completely covered with ice. The duration of the experiment was 41 days in 2014 (from 1.10 to 11.11) and 35 days in 2017 (from 03.10 to 06.11). In the same time period (23-24.09 in 2014 and 24.10 in 2017), fish community composition was assessed at all sites by qualitative electrofishing surveys. Air temperatures at the closest weather station in Skibotn (20m asl.) decreased steadily throughout the study periods from a mean of 9°C at the beginning in September to -2°C at the end in November (see Appendix Figure 10, Based on data from MET Norway).

4.2.1 Litter bags: measuring decomposition and collecting invertebrates

Freshly abscised birch (*Betula pubescens*) leaf litter was collected in Telegrafbukta, Tromsø, in autumn 2014, and air dried until constant mass. It has been stored dry, cool and dark since then. Small tetrahedral mesocosms, about 5 * 15cm, constructed with plastic net of two different mesh sizes: coarse (~9mm) and fine (~0.5mm), were filled with dried, homogenized and weighed leaf litter from this same collection in both years of the study. Only undamaged leaves were selected, and litter was moistened before being put in the litter bags to prevent fragmentation.

The purpose of the coarse-mesh bags is to assess overall decomposition rate of leaf litter in the streams by allowing shredding invertebrates access to the litter, combining the effect of physical abrasion,

microbial-mediated decomposition and invertebrate-mediated decomposition. Fine-mesh bags are meant to assess microbial decomposition rates by excluding shredding invertebrates from the leaf litter. One coarse- and one fine-mesh bag was paired for each replicate in the study to approximate invertebrate-mediated decomposition using the difference between mass loss in the two different bags.

Litter bags were deployed on the stream bottom in shallow riffles and kept in place (~0.5m between replicates) by a rope tied between two metal poles. This way, they simulated the way leaf litter in streams forms packs in and on the stream bottom substrate. Riffles were chosen as a standardized habitat to find comparable sites in all streams, instead of finding the local effects of individual pools (Frainer et al. 2014). In the main river stems, sites were selected where the river divided into several branches, in an attempt to find sampling sites comparable to the tributaries.

Sampling effort differed slightly between the two years: In 2014 the bags were each filled with $4 \text{ g} \pm 0.05 \text{ g}$ of litter. Five replicates of paired litter bags were deployed per site. To ensure that all samples had leaf litter of even quality, also for potential extra years of sampling, total amount of leaf litter in each litter bag was reduced to $3 \text{ g} \pm 0.05 \text{ g}$ in 2017, and number of replicates per site was reduced to four.

When retrieved, each pair of litter bags was placed in a plastic zip-lock bag, transported from Skibotn to Tromsø by car, and frozen. Later, each replicate was defrosted and contents of litter bags were emptied into white trays with tap water. Birch leaf litter remains were rinsed carefully by hand under running water and stored in paper envelopes. Envelopes with leaf litter were later dried at $60 \text{ }^\circ\text{C}$ for 48 hours and leaf litter, having reached constant mass, was removed and weighed on a digital scale at 0.001 g precision. One fine mesh bag had a mass loss of approximately 47%. This was regarded as measurement error and the bag was omitted from the data.

Leaf litter decomposition can be approximated to a negative exponential decay model (Petersen and Cummins 1974) where the rate coefficient kd^{-1} can be calculated with the following equation:

$$Kd^{-1} = -\frac{\ln\left(\frac{M_t}{M_0}\right)}{t} \quad (1)$$

where t is the time in which decomposition has happened, in this case the duration of the field experiment in days, and M_0 and M_t are the dry weight of the leaf litter at times 0 and t , respectively.

When coarse and fine mesh bags are paired, the fine mesh bag can be used as a negative control and the rate coefficient for invertebrate-mediated decomposition ($K_i d^{-1}$) can be estimated using Frainer's (2016) modified equation, calculated with the following equation:

$$K_i d^{-1} = -\frac{\ln\left(\frac{C_t + F_0 - F_t}{C_0}\right)}{t} \quad (2)$$

where C_0 and C_t are the dry mass of leaf litter from the coarse mesh bag at times 0 and t , while F_0 and F_t are dry mass of leaf litter from the fine mesh bags at times 0 and t . In this case as well t is the duration of the experiment in number of days. The calculation incorporates mass loss from both bags in each replicate, and a zero or negative value indicates no significant contribution of invertebrate activity to total decomposition rate in the coarse mesh bag, while positive values may be used as an estimate of how much invertebrates contribute to litter decomposition at the site.

Mass loss by leaching in the dried birch leaves was estimated in a lab experiment. Four replicates, each consisting of $3\text{g} \pm 0.05\text{g}$ of homogenized dry leaf litter from the same collection used in the field experiments, were submerged in distilled water and kept at $4\text{ }^\circ\text{C}$ for 24 hours to simulate leaf submersion streams in autumn. Another four replicates were subject to the same treatment for 144 hours. After incubation, the leaf litter was dried at $60\text{ }^\circ\text{C}$ for 48 and weighed at 0.001g precision.

Invertebrate collection from the litter bags differed slightly between the two years of the study due to practical issues. In 2014, after leaf litter from the coarse mesh bag was rinsed and removed for drying, all remaining debris in plastic trays was obtained by filtering and stored on ethanol. Invertebrates could then be picked out later under a stereomicroscope. In 2017, Invertebrates visible to the eye were picked out directly from the tray using tweezers or a plastic pipette. The smallest invertebrates were therefore found in higher densities in 2014 than in 2017. Early instars of most invertebrates are hard to identify further than family level so invertebrates shorter than 4mm in length were omitted from the analysis to avoid methodic bias in the data (Appendix table 4). All Acari, Psychodidae, Dicranota, and other small Diptera were therefore left out from the analysis in this study. Chironomids were also removed from the analysis, since they could not be identified to a meaningful taxonomic level. A single terrestrial oligochaete was found in 2014, and a single Dixidae in 2017. These were regarded as random occurrences and omitted, together with Simuliidae pupae which were attached to the litter bags in some cases.

Remaining invertebrates (>4mm) from the coarse litter bags were identified visually under stereomicroscope to genus and species level using relevant taxonomic identification keys (Plecoptera: Lillehammer 1988, Ephemeroptera, Coleoptera and Diptera: Nilsson 1996 & Nilsson (1997), Trichoptera: Rinne and Wiberg-Larsen 2016). Some species could with certainty be identified to species level, but many invertebrates could only be identified to genera. This taxonomic level is kept for *Baetis*, *Nemoura*, *Capnia*, *Leuctra*, *Potamophylax*, and *Isoperla* in all analyses and result presentations. Analysis of the feeding traits (using the freshwater ecology.info database: Schmidt-Kloiber and Hering 2019) within these genera indicate little or no variation. Thus, their identification at genus level does not remove much, if any, information on functional diversity at the resolution used in this study.

Due to 1g dry-weight difference in leaf-pack mass in litter bags used between the two years, invertebrate abundances were recalculated to density per gram dry weight of the initial leaf pack. This approach was selected since Ruetz III et al. (2006) found 5g leaf packs to contain more shredders than 3g leaf packs, while the biomass of invertebrates per dry mass of leaf litter remained somewhat constant.

Mean shredder density and diversity, as well as predator density, was calculated per sampling site. All species categorized as partly shredding in the freshwater ecology database (Schmidt-Kloiber and Hering 2019) were counted as shredders in this study while only *Diura nanseni*, *Rhyacophila nubila* and *Isoperla* sp., categorized as predominantly predators, were counted as predators (see Table 2). This means that *Isoperla* was counted as both a predator and a shredder, but only a few individuals were found throughout the whole study. Shredder species diversity was calculated as the richness (species number per litter bag) and using Simpsons (1949) diversity index, based on the following equation:

$$1/D = 1/ \sum (p_i)^2 \quad (3)$$

where p_i is the proportion of species i in the community. In this interpretation of Simpsons diversity index the maximum possible value equals the species richness in the study. It works as a good compromise between richness and evenness, and was therefore chosen for this study. Shredder taxonomic diversity indices were calculated using the diversity() function in the R package vegan

(Oksanen et al. 2019).

Fuzzy coded feeding trait scores (score from 1-10 for each trait category, making the total 10 for each species) were retrieved from the freshwater ecology database (Schmidt-Kloiber and Hering 2019, Table 2). These traits were assigned to each taxa and community weighted mean (CWM) values were calculated for each trait and each replicate using the R package FD (Laliberté and Legendre 2010, Laliberté et al. 2014). These values weight the trait values with by species abundances in each sample, summarizing its functional composition.

Functional dispersion (*FD_{is}*) of shredders was also calculated using the R package FD (Laliberté and Legendre 2010, Laliberté et al. 2014). In this index, a multidimensional trait space is assessed, where each species is characterized based on the distribution of its trait values. A centroid is calculated among all species found in a sample based on species abundances dissimilarity of their traits. The centroid is placed where the distance to each species is as small as possible, but since abundance is weighted, the centroid is placed closer to the more abundant species. The *FD_{is}* value for the sample is then calculated as the mean distance from the centroid to each individual animal in the sample (Laliberté and Legendre 2010). It works as an estimate of trait diversity or evenness, since *FD_{is}* decreases when species have the same traits or if a few similar species dominate the sample.

4.2.2 Electrofishing and fish diets

A qualitative electrofishing survey was conducted on all sites during the study periods in 2014 and 2017. The aim was to assess fish community composition in 2014, and to check if fish were present in the studied sites in Skibotn catchment in 2017. On each site, a 100m² river section was fished over with backpack-electrofishing gear a single time. Sections for electrofishing were selected >50m downstream of the litter bags to prevent any effects on fish and invertebrates in and close to the litter bags. In some sites, an upstream section was selected when downstream was not possible. Fish were kept for stomach content analysis, in 2014 stored frozen, and in 2017 on ethanol.

Fish were identified to species in the lab, weighed (± 0.1 g) and had their total body length measured (± 0.1 cm). After cutting open the body cavity, fish stomachs, cut at pyloric sphincter and esophagus behind the gills, were removed and preserved in 70% ethanol. Upon opening with small scissors, the fullness of the stomach was visually determined as percentage (0-100%) of total stomach volume.

Table 2: Fuzzy coded feeding trait values extracted from the freshwater ecology.info database (Schmidt-Kloiber and Hering 2019) for species identified in litter bags in the field experiment. Trait scores for feeding add up to a total of ten for each species.

Order	Species	Grazer	Shredder	Gatherer	Predator
Plecoptera	<i>Diura nanseni</i>	0	0	0	10
	<i>Isoperla</i> sp.	1	1	1	7
	<i>Nemoura</i> spp.	0	7	3	0
	<i>Capnia</i> spp.	2	6	2	0
	<i>Protonemura meyeri</i>	3	5	2	0
	<i>Leuctra</i> spp.	3	3	4	0
	<i>Taeniopteryx nebulosa</i>	3	2	5	0
Trichoptera	<i>Rhyacophila nubila</i>	0	0	0	10
	<i>Potamophylax</i> sp.	2	6	0	2
Ephemeroptera	<i>Ephemerella aroni</i>	4	1	5	0
	<i>Baetis</i> spp.	5	0	5	0
Diptera	<i>Prionocera</i> sp.	0	5	5	0

Prey items were identified visually under stereomicroscope and their contribution to the total fullness of the stomach was determined by visual approximation on a percentage scale (Amundsen and Sánchez-Hernández 2019). Prey items were categorized to closest taxonomic level possible, but some were grouped: the groups “Other Ephemeroptera” and “Other Plecoptera” contain unidentified individuals or remains of these orders, while unidentified Trichoptera are divided between the two groups “Case-building Trichoptera” and “Other free-living Trichoptera”. The group “Terrestrial arthropods” contains ants (Formicidae), spiders (Arachnida) and unidentified winged insects. Fish were divided into two length groups: >70mm and <70mm, based on a maximum total length of 64mm for young of the year from Skibotn found in 2017. However, due to a low sample size, fish of all sizes and all the three salmonid species were pooled by year and catchment for diet analysis.

4.3 Statistical analysis

All statistical analysis and all result presentations were produced in the R software (R Core Team 2021). Effects of the pesticide treatment on decomposition rates mediated by invertebrates was tested using mixed-effect models. Decomposition rate coefficient kd^{-1} was tested as a response to the year (2014 or 2017), litter bag mesh size (coarse or fine), and their interaction term, estimating changes in the difference in decomposition rate between the two mesh sizes between years and thus, changes in

invertebrate-mediated decomposition. Due to unbalanced sampling effort between the treated catchment and the control, one model was made for each catchment separately. To correct for differences owing to background variation among the streams, stream identity was added as a random factor. The mixed effect models were made using the `lmer()` function in the R package `lme4` (Bates et al. 2015). The tributary stream Haskielva in Skibotn catchment had no fish in 2014 or 2017 and much lower decomposition rates than all the other sites, and was therefore not included in the model since there was no logical reason to test the hypothesis there. Assumptions of normality were tested by visual inspection of plots created with the `check_model()` function from the R package `performance` (Lüdtke et al. 2021). P-values are not presented for mixed-effect model estimates in this study. Instead, 95% confidence intervals were calculated for model effect estimates using the `lme4` function `confint.merMod()` and interpreted.

I used non-metric multidimensional scaling (NMDS) to visualize and assess overall changes in invertebrate species composition between the two years in each stream, using the `metaMDS()` function in the R package `vegan` (Oksanen et al. 2019). A Bray-Curtis dissimilarity index was used by default since it is recommended for community data. NMDS is a distance-based ordination method, that calculates dissimilarity between all samples and places them in two dimensional space. It is a useful method for comparative analysis when many sites are sampled for species abundances. Samples with no invertebrates were omitted prior to this analysis. When plotting the two axes, samples with similar species composition cluster together. To simplify visualisation, data points were grouped by stream and year, and ellipses were calculated using the `stat_ellipse()` function in the `ggplot2` package (Wickham 2016) in R. No ellipse could be made for stream-year combinations where less than 4 samples had one or more invertebrate taxa.

I used principal components analysis (PCA) with the calculated community weighted mean trait values in the R package `vegan` (Oksanen et al. 2019) to assess changes in functional composition of invertebrate communities between the two years in each catchment. A principal components analysis is an ordination method based on regressions in multivariate data. Regressions are summarized to as few axes as possible, and if the two first axes (PC1 and PC2) explain a significant amount of the variance in the data, they can be used to plot multivariate data in a two-dimensional space. I performed two separate PCA's. One for each catchment, but with data from both years. Then, for

visual purposes, results from each PCA was subsetted by year and presented in separate biplots.

5 Results

5.1 Leaf litter decomposition rates

Average decomposition rates were similar in the two catchments, however more variation was observed in Skibotn catchments, where more sites were sampled. Decomposition rates in the litter bags overall ranged from 0.0032 to $0.013kd^{-1}$ (Figure 2). For comparison, mean mass loss by leaching in the lab was 12% (range: 11–13%) after 24 hours and 14% (range: 13–14%) after 144 hours. A mass loss of 12% over 35 days would equal a decomposition rate $-0.0037Kd^{-1}$. Only a single litter bag had a decomposition rate lower than this.

Decomposition rates were overall higher in coarse- than fine mesh bags, and increased overall from 2014 to 2017 in both catchments, as indicated by positive effects of mesh and year in the mixed effect models (Figure 3; Appendix tables 5 and 6). The increase between years was especially evident in Nordkjøs catchment. Further inspection of results from Skibotn catchment indicate that this overall increase between years was present in the main river, but diluted by inter-site variation in the tributaries (Figure 4).

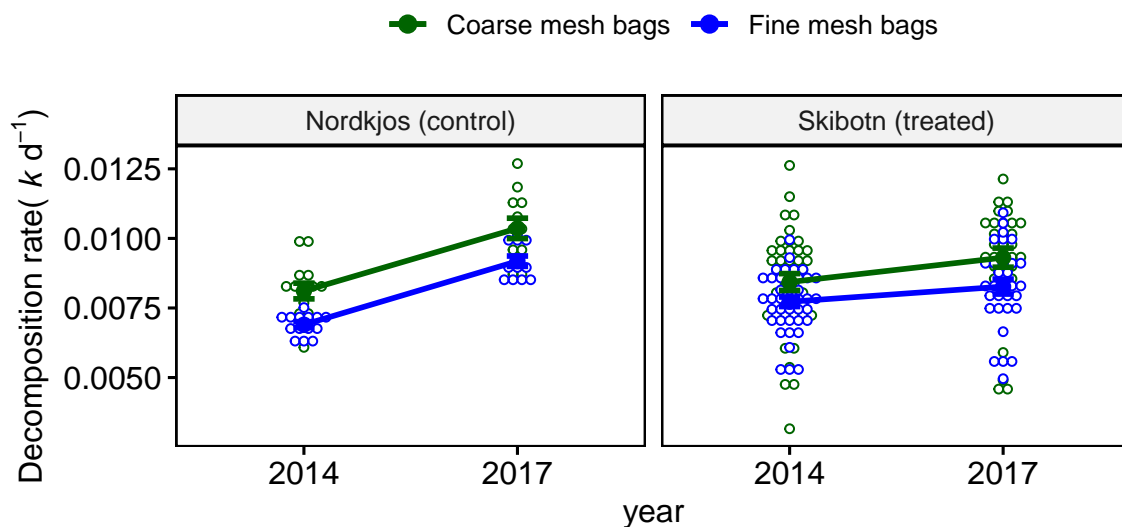


Figure 2: Decomposition rates (kd^{-1}) in fine- (blue) and coarse-mesh (red) bags in 2014 (left) and 2017 (right) in Skibotn catchment and Nordkjøs catchment, Full circles with error bars representing the mean and standard error for each catchment, while open circles represent individual litter bags.

The mixed effects models suggest no significant change in invertebrate-mediated decomposition, as

indicated by the interaction term “mesh*year” (Figure 3; Appendix tables 5 and 6). The 95% confidence interval for the interaction term crossed zero in both models. However, the estimate was indicative of a weak positive effect in Skibotn catchment as opposed to Nordkjøs catchment where the estimate was equal to zero. Although this effect was not statistically significant, indications of potential interaction effects were observed in tributaries Olderelva and especially Lullelva, when plotting their data separately (Figure 4). In these two tributaries decomposition rates in coarse-mesh bags increased more than those in fine mesh bags. However, invertebrate-mediated decomposition rates in these two streams were close to zero in 2014.

Invertebrate-mediated decomposition as calculated with equation 2, ranged from $-0.0013 K_i d^{-1}$ to $0.0036 K_i d^{-1}$, deviating around the estimated effect of mesh size in the models, and constituting only a minor part of total mass loss in the coarse mesh bags (Figure 5). Both inter- and intra-site variation was large.

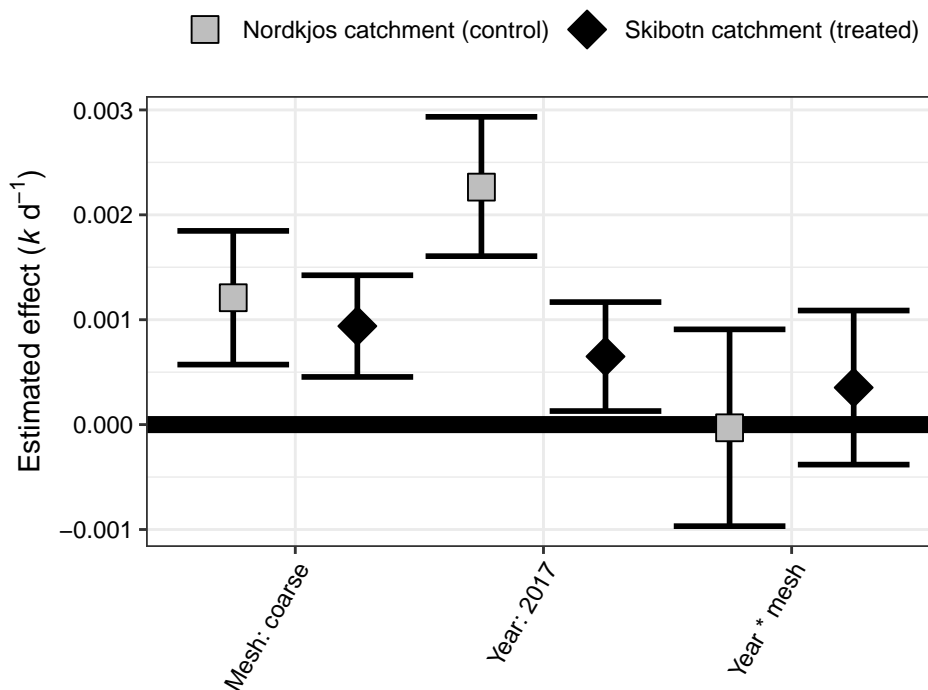


Figure 3: Estimated effects (with 95% confidence intervals represented by error bars) of year, mesh size and their interaction term “year*mesh” on decomposition rates ($k d^{-1}$), from the two mixed effect models for Skibotn and Nordkjøs catchments, separated by colour and shape.

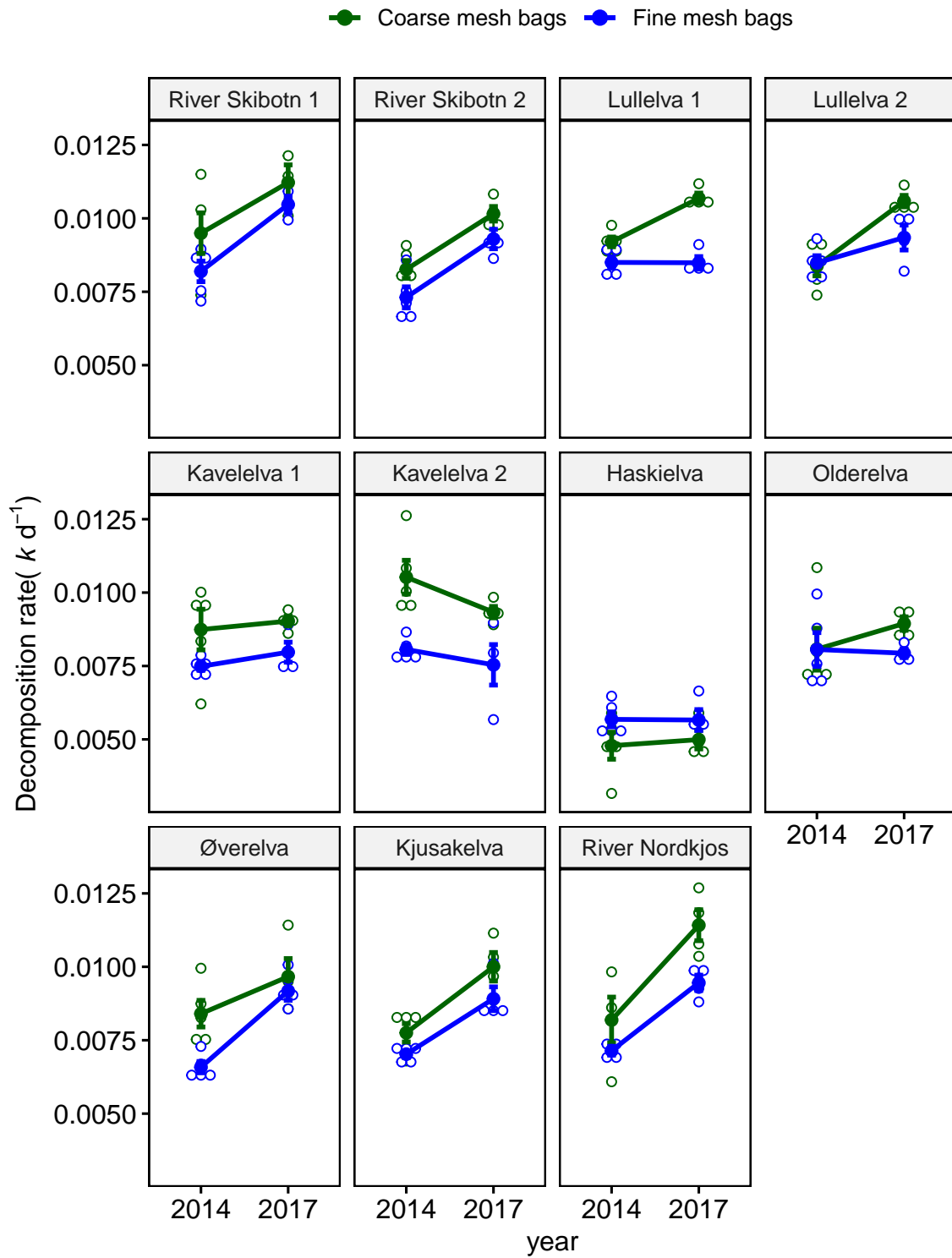


Figure 4: Decomposition rate (kd^{-1}) in fine (blue) and coarse (red) mesh bags in 2014 (left) and 2017 (right), plotted separately for each sampling site. The upper eight panels are sites in Skibotn catchment, while the three lower panels are sites from Nordkjøs catchment. Full circles represent the mean, error bars representing the standard error. Smaller open circles represent the values from individual litter bags.

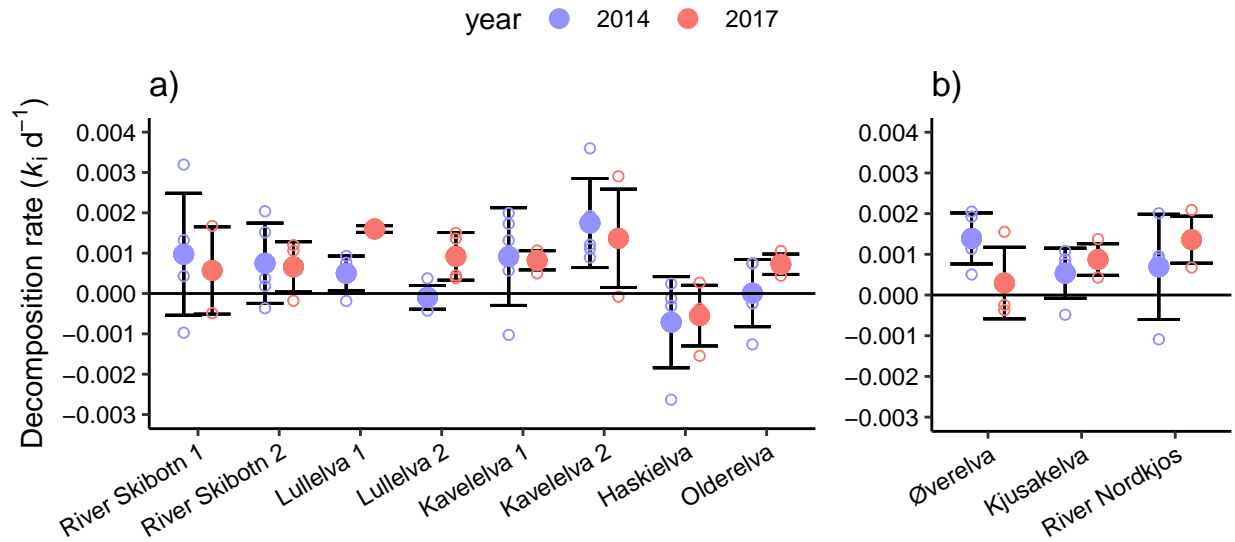


Figure 5: Invertebrate-mediated decomposition ($K_i d^{-1}$) in main rivers and tributaries of a) Skibotn catchment and b) Nordkjøs catchment, in 2014 and 2017. Results from the two years are placed side by side for each sampling site. Full circles represent mean per site and year, error bars show standard deviation, while open circles represent single replicates.

5.2 Invertebrate community composition and functional diversity

Shredder densities in the litter bags ranged from 0 to 5 individuals per gram dry weight of leaf litter, however the average density across all samples was 1.1 ± 1 per gram dry weight. Shredders were patchily distributed across sampling units, as indicated by the large standard deviations compared to mean values (Table 3). Species richness ranged from 1 to 6 species per litter bag while most litter bags had between 1 and 3 shredder species (mean, 1.7; SD, 1.1). In total 12 invertebrate species were recorded. According to the fuzzy coding, 8 of these can be considered as shredders, 4 as predators, 8 as grazers and 9 as gatherers (Table 2), indicating a high degree of generalism in diet.

Most of the 12 invertebrate species were found in both catchments, but *Prionocera* sp. was found only in Nordkjøs catchment, while *Potamophylax* sp., *Isoperla* sp. and *Nemoura* sp. were found only in Skibotn catchment. Nemourids smaller than 4mm (and therefore not analyzed in this study) were found also in Nordkjøs catchment (Appendix table 4), indicating that *Nemoura* are not absent from that watercourse. The most common predators were *Diura nanseni* and *Rhyacophila nubila*, found in low densities across all sites in both catchments.

In the main river site in River Nordkjøs, *Capnia* sp. was the most abundant shredder in 2014, followed by *Taeniopteryx nebulosa* which was only found in high density in one litter bag. *Protonemura meyeri* was most abundant in 2014, when the large bodied *Prionocera* sp. was also found. In the tributaries Kjusakelva and Øverela, *Taeniopteryx nebulosa* and *Protonemura meyeri* were the most abundant shredders in both years (Appendix figures 11 and 12).

In the main river site River Skibotn 1, *Ephemerella aroni* and *Protonemura meyeri* were the most abundant shredder species. *Protonemura meyeri* was also most abundant in Skibotn 2. In 2017 *Protonemura meyeri* was missing from these sites, and *Ephemerella aroni* was the dominant shredder. In the tributary site Lullelva 1, *Capnia* sp., *Protonemura meyeri* and *Ephemerella aroni* were most abundant in 2014, While *Potamophylax* sp. was most abundant in 2017. In Lullelva 2, density and diversity was lower, while many of the same species were present in both years. *Taeniopteryx nebulosa* was the most abundant shredder in the two sites in Kavelelva in 2014, while *Nemoura* sp. was more abundant in Kavelelva site 2 in 2017. In Haskielva, only low densities of *Nemoura* sp. and *Potamophylax* sp. were found in 2014, and no invertebrates larger than 4mm were found in 2017. In Olderelva, *Nemoura* sp. was most abundant, while *Capnia* sp. was also present (Appendix figures 11 and 12).

Despite some variation in mean density, Simpson's diversity index and functional dispersion within each sites (Table 3), there was no large change in community composition from year to year visible in the NMDS ordinations, where samples clustered together in the middle, and ellipses representing sites and years overlapped (Figure 6). Similarly, functional composition of feeding traits in leaf colonizing invertebrates, as estimated by community weighted trait values, did not change noticeably in Skibotn catchment or Nordkjøs catchment according to visual interpretation of results from the principal components analysis (Figure 7). Most samples clustered in the middle of the biplots, while just a few individual samples deviated from this pattern, in some cases due to higher density of obligate predatory invertebrates *Diura nanseni* or *Rhyacophila nubila* (See figures 11 and 12. The clustering is likely due to the low resolution of the functional traits used, and the fact that many of the species observed in the litter bags were omnivores (Table 2), but it also indicates that the composition of functional feeding groups of invertebrates in the litter bags was overall quite similar.

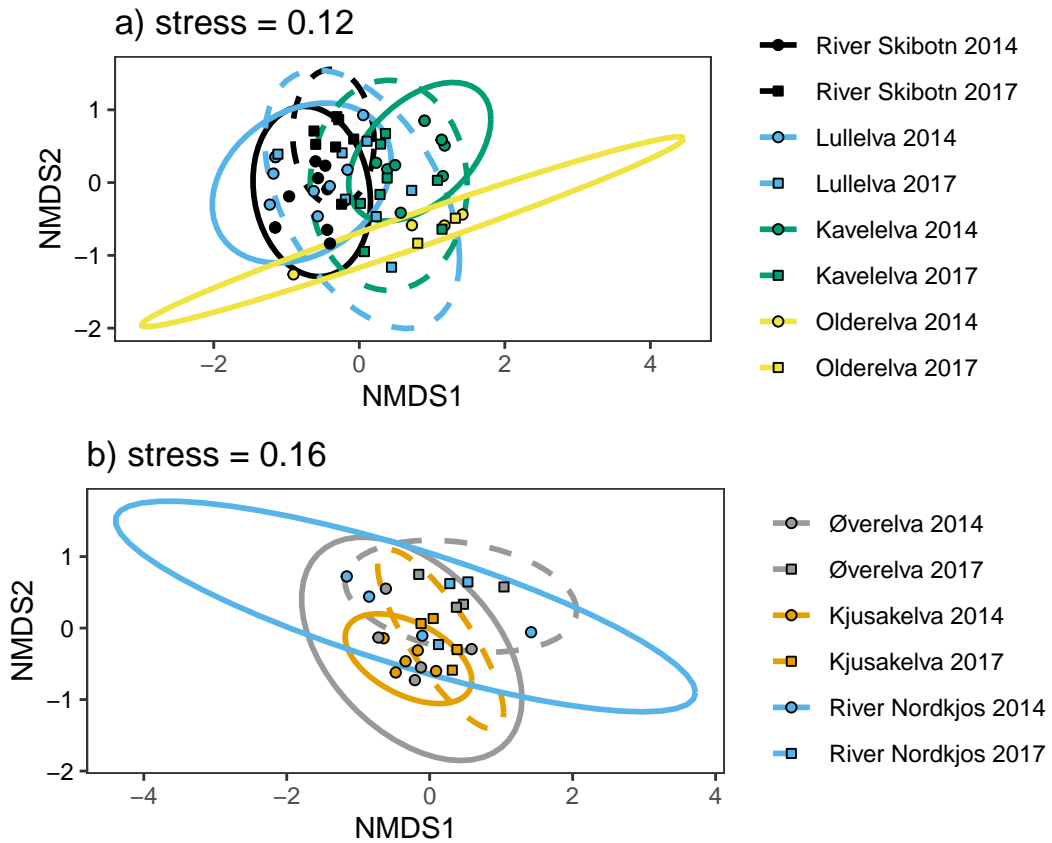


Figure 6: Non-metric multidimensional scaling plots with benthic invertebrates in coarse mesh litter bags from a) Skibotn and b) Nordkjøs catchments.

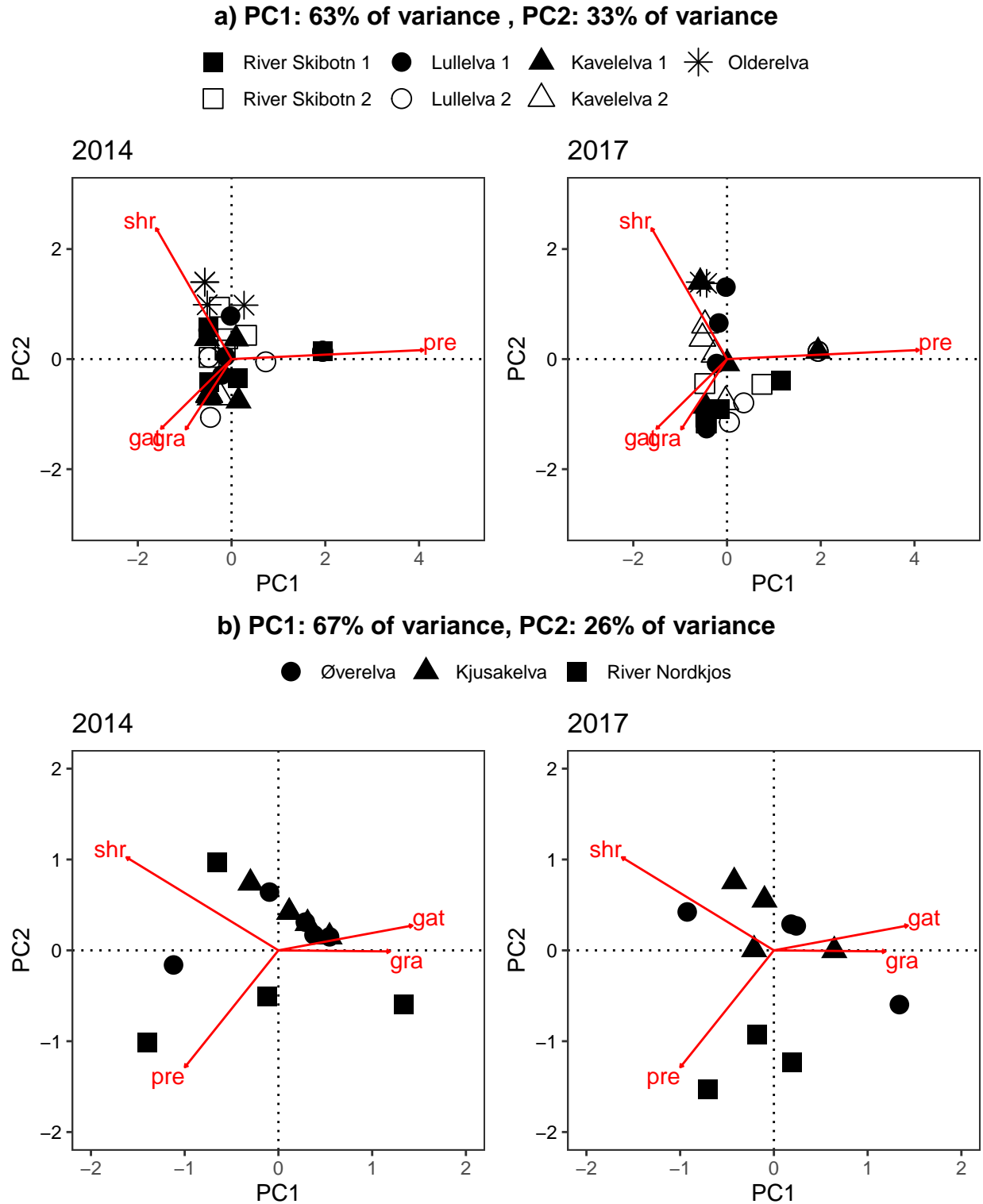


Figure 7: Biplots subsetting by year featuring results from the same principal components analysis (PCA) on community weighted mean feeding trait values in a) Skibotn and b) Nordkjøs catchments. Trait scores are abbreviated: shr = “shredding”; pre = “predator”; gra = “grazing”; gat = “gathering”.

Table 3: Invertebrate community parameters (mean \pm 1SD per replicate) calculated for each site and each year. ”-” is inserted where no invertebrates were included in the analysis.

	Shredder Density (ind/g litter)		Shredder Species richness		Shredder diversity (1/Simpson)		Shredder FDis		Predator density (ind/g litter)	
	2014	2017	2014	2017	2014	2017	2014	2017	2014	2017
River Skibotn 1	0.8 \pm 1	1 \pm 0.9	2 \pm 1	1 \pm 1	1 \pm 1	0.8 \pm 0.8	0.9 \pm 1	1 \pm 1	0.1 \pm 0.1	0.3 \pm 0.3
River Skibotn 2	0.9 \pm 0.5	1 \pm 0.6	2 \pm 0.7	1 \pm 0.5	2 \pm 0.4	1 \pm 0.3	2 \pm 0.5	1 \pm 1	0.1 \pm 0.1	0.08 \pm 0.2
Lullelva 1	1 \pm 0.7	0.5 \pm 0.3	3 \pm 2	1 \pm 0.5	2 \pm 1	1 \pm 0.4	1 \pm 0.8	1 \pm 1	0.1 \pm 0.1	0 \pm 0
Lullelva 2	0.2 \pm 0.3	0.08 \pm 0.2	0.8 \pm 0.8	0.2 \pm 0.5	0.8 \pm 0.8	0.2 \pm 0.5	0.7 \pm 1	1 \pm 1	0.1 \pm 0.1	0.3 \pm 0
Kavelelva 1	1 \pm 1	0.5 \pm 0.3	2 \pm 0.8	1 \pm 1	2 \pm 0.5	1 \pm 1	2 \pm 1	0.9 \pm 1	0.1 \pm 0.1	0.2 \pm 0.2
Kavelelva 2	1 \pm 2	2 \pm 2	1 \pm 0.4	3 \pm 0.5	1 \pm 0.1	2 \pm 0.6	0.2 \pm 0.5	2 \pm 0.3	0.1 \pm 0.2	0.08 \pm 0.2
Haskielva	0.8 \pm 0.7	-	2 \pm 0.7	-	1 \pm 0.3	-	0.4 \pm 0.6	-	0 \pm 0	-
Olderelva	0.4 \pm 0.1	0.8 \pm 0.7	1 \pm 0	2 \pm 0.7	1 \pm 0	1 \pm 0.4	0.6 \pm 1	0.5 \pm 0.7	0.06 \pm 0.1	0 \pm 0
Øverelva	1 \pm 0.9	2 \pm 2	2 \pm 1	2 \pm 1	2 \pm 0.9	1 \pm 0.8	1 \pm 0.8	1 \pm 0.9	0.05 \pm 0.1	0.08 \pm 0.2
Kjusakelva	2 \pm 0.9	2 \pm 1	2 \pm 0.4	2 \pm 1	2 \pm 0.4	2 \pm 0.8	0.9 \pm 0.6	1 \pm 0.5	0 \pm 0	0.08 \pm 0.2
River Nordkjøs	0.8 \pm 0.7	1 \pm 0.5	2 \pm 2	2 \pm 0.6	1 \pm 1	2 \pm 0.2	1 \pm 1	3 \pm 0.1	0.1 \pm 0.1	0.6 \pm 0.2

5.3 Fish and fish diets

Fish were found in 9 sampling sites (2 in Nordkjøs, 7 in Skibotn) In 2014. All fish were juvenile salmonids, ranging from 41mm to 141mm total length. Both trout, salmon and charr were found, but trout and salmon dominated the catches (Figure 8). No fish were caught in the Nordkjøs tributary Kjusakelva, where the sampling site was above a bridge with a culvert. In Skibotn catchment, no fish were caught in Haskielva (see discussion and methods). Only trout were caught in Olderelva, while trout and salmon were caught in the main river, and charr was found in addition, in tributaries Kavelelva and Lullelva.

Surprisingly, less fish were caught in the control sites in 2017 than 2014 (Figure 8). Only two trout >70mm were caught in the tributary Øverelva, and no fish were caught in the main river. In addition, several fish were caught in the rotenone treated sites in Skibotn catchment. In River Skibotn and Lullelva, small trout and salmon <70mm, and a single charr <70mm were caught.

Fish diet was not dominated by important shredders in this study (Figure 9). Baetid mayflies were the most abundant prey in both years while fish also fed on stoneflies (mainly Perlodidae and small *Nemoura*), different Trichoptera (both case-building and free-living) as well as chironomids. Most

stoneflies and case-building caddis in the stomachs were rather small. Predatory invertebrates like stoneflies belonging to the Perlodidae, and the caddisfly *Plectrocnemia conspersa* were found also in stomachs of the small fish caught in 2017.

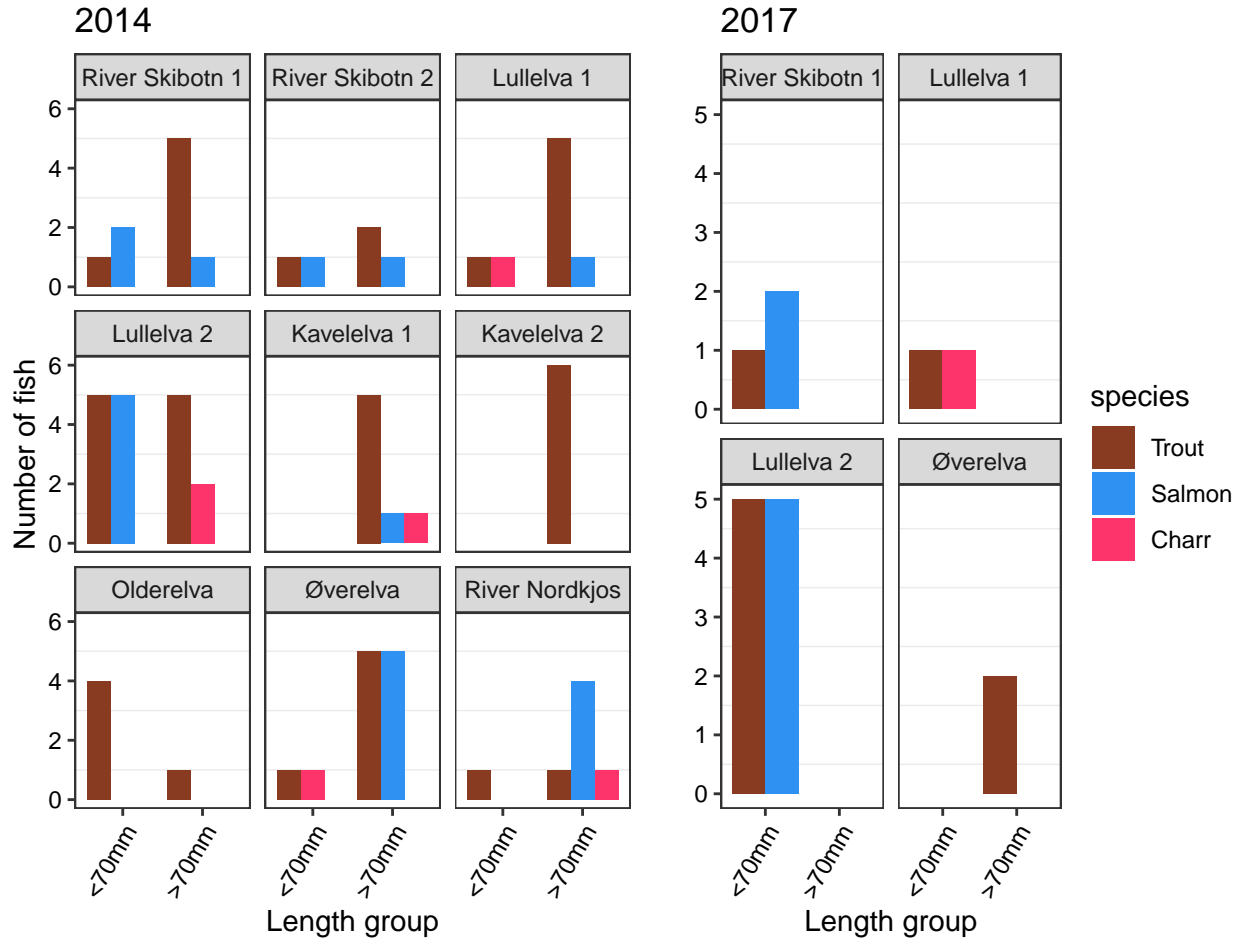


Figure 8: Numbers of fish by species (trout, charr and salmon) and by fish length (smaller or larger than 70mm total length) captured in each stream by electrofishing during the study period in 2014 (left) and 2017 (right). Fish are divided in length groups “<70mm”, representing young of the year, and “>70mm” representing older fish up to 141mm.

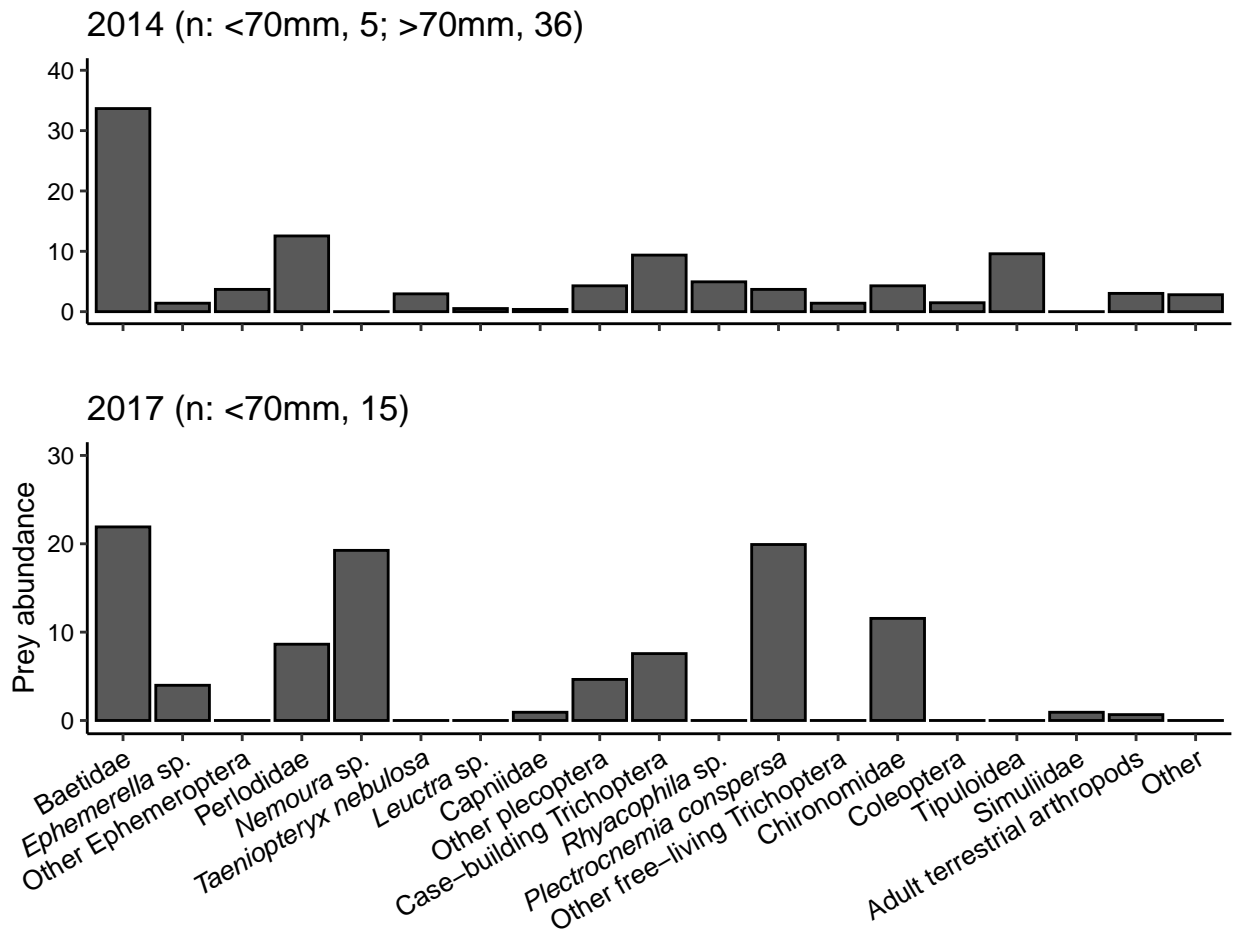


Figure 9: Prey abundances by proportion of total stomach content in fish captured at studied sites in Skibotn catchment in 2014 and 2017. All prey items except “Adult terrestrial arthropods” are aquatic insect larvae.

6 Discussion

The results of the field experiments suggested no significant effect of the rotenone treatment on leaf litter decomposition mediated by shredding invertebrates, despite theoretical expectations linking trophic cascades with changes on ecosystem functioning. However, the lack of evidence does not necessarily mean that no top-down effects of fish on leaf litter decomposition were present in this system. Results from large scale field studies are challenging to interpret, since they are subject to site- and stream-specific interannual variation. Although all fish were extirpated from the studied sites in Skibotn catchment in early autumn 2016, fish were found there in autumn 2017. In addition, fewer fish were registered in the two fish holding control sites in Nordkjøs catchment in 2017 than 2014.

The fish in Skibotn catchment in 2017, all <70mm, likely originated from post-treatment stocking or from natural spawning by sea run fish the autumn before. Downstream dispersal of fish from upstream untreated reaches was registered in Skibotn catchment in 2015, after the first year of the rotenone treatment, but these fish were extirpated in the next year of the treatment (Adolfson et al. 2021). Still, I expected an effect of the treatment, since fish were extirpated both in 2015 and 2016, leaving the streams in Skibotn catchment fish-less throughout autumn 2016, and with only young of the year present through spring and summer 2017 in a few sites. While the introduction of fish post-treatment made the hypothesis hard to assess in this system, the study still corroborates that a rotenone treatment can be useful for further studies on predator effects on functioning, if study design is planned well ahead.

Fish densities are generally low in northern rivers and streams (Power 1973), likely making consumptive top down effects less evident in catchment scale experiments than in experimental setups in cages or flow through channels. For example, the fish-less site in tributary Kjusakelva in the control catchment Nordkjøs did not differ significantly from its fish bearing neighbour stream Øverelva in shredder density, predator density or species composition in the litter bags. Meissner and Muotka (2006) found fish to have negative impacts on the density of predatory invertebrates in streams in northern Finland. However, in my study I observed no large change in shredder or predator density in litter bags in the Skibotn tributaries Olderelva and Kavelelva, where fish were found before, but not after the treatment, despite the fact that both small and larger salmonid juveniles fed on predatory invertebrates like *Diura* and *Rhyacophila*. However, the density of predatory invertebrates

was very low in the litter bags.

The systems studied in this experiment may have had lower fish densities than normal in the study period. In River Nordkjøs, the salmon and sea-run trout populations had declined during the study period (Rune Muladal, pers.comm.), which might explain the fact that so few fish were caught in the electrofishing surveys. In River Skibotn, fish densities, and thus fish effect on invertebrates, might already have been lower than usual due to the *Gyrodactylus salaris* parasite and its lethality to juvenile salmon in Norway (Johnsen and Jenser 1991). In addition, the narrow tributaries and branches of braided main rivers studied in this field experiment have a relatively steep gradient, which may restrict the access of fish to riffles. When electrofishing, more fish were found in pools and runs than in riffles. Large parts of the stream area may be available for invertebrates, but not directly for fish feeding, further reducing the potential effect of a low-density fish population on invertebrate populations on catchment scale.

A direct density mediated top-down effect of fish on leaf litter decomposition was found by Konishi et al. (2001), when comparing 1 * 1m cages with and without fish in slow flowing pools in a Japanese stream. An amphipod was both the dominant shredder and the most abundant fish prey. Experimental fish densities of 5 fish per cage, well above what can be expected in sub-Arctic streams, led to a decrease in density of the amphipod, which again led to significantly lower decomposition rates of leaves in litter bags (Konishi et al. 2001). In my study, the shredder assemblages in the streams contained a variety of species, while fish also had a varied diet. Baetid mayflies, known to be grazers and collectors, were the most abundant fish prey. However, I had a limited sample for diet analysis. Small salmonids in sub-Arctic Norwegian streams are also known to feed extensively on *Ephemerella aroni*, previously named *Ephemerella aurivilli* (Gabler and Amundsen 2010), which was categorized as a shredder, and found in litter bags in this study. *E. aroni* was however, where it occurred, present in litter bags in both years of the study. The specific combination of stream morphometry, shredder community, fish community, and fish diet that likely made a trophic cascade possible in the study by Konishi et al. (2001) was nothing similar to the conditions in my studied sites in Skibotn and Nordkjøs catchments.

No clear indications of trait mediated effects of fish via invertebrates on decomposition rates were detected in this study. However, traits like body size, predator evasion behaviour or predator

resistance were not measured for the studied species assemblages, while the prevalence of omnivory made multivariate analysis of feeding traits hard to interpret. Late instars of some case-building caddisfly larvae are known to be quite resistant to predation from small fish. In a laboratory experiment by (Jabiol et al. 2013), two stonefly shredders decreased their feeding activity when exposed to fish scent, while a large cased caddisfly did not. The predator resistance of large bodied case-building caddisfly larvae was also demonstrated by Ruetz et al. (2002) in a field experiment where a large case-building caddisfly was found in higher densities, and led to higher decomposition rates, in litter bags that were exposed to predatory fish. This increased density and shredding activity of the caddisfly in fish-exposed cages was explained as a response to release from interspecific competition with other invertebrates with stronger responses to predator cues (Ruetz et al. 2002).

A marked increase in invertebrate-mediated decomposition was observed in the Skibotn tributary Lullelva from 2014 to 2017. In the site Lullelva 1, the case-building caddis *Potamophylax* sp. was only slightly more abundant, but had fewer potential competitors in the litter bags in 2014 than 2017, as indicated by decreases in shredder species richness and shredder density. Here, decomposition rates in coarse-mesh bags increased more than those in fine-mesh bags. While differing in size composition, fish were present in the stream both before and after the rotenone treatment. Hence, it is unlikely that this was an effect of fish removal, since invertebrates in this stream were probably exposed to fish scent in both years of the study. Fish scent as a predator cue is shown to affect invertebrate activity in a wide range of contexts and concentrations (Paterson et al. 2013). Only two small fish were caught in the upstream site Lullelva 1, downstream of the sample site, so an effect of fish removal cannot be completely depreciated. However, a more likely explanation is that the observed changes in invertebrate-mediated decomposition and shredder species assemblage reflect interannual variation.

The communities of shredding invertebrates seemed in 2017 to have reestablished after the rotenone treatment. In the treated Skibotn catchment, shredding invertebrates were found in all but one site in 2017, and decomposition rates were higher in coarse- than fine- mesh bags in both years. The lethality of rotenone to specific invertebrate species is dependent on the rotenone concentration and water temperature in the microhabitat, as well as different tolerance levels of invertebrates on species and instar level (Kjærstad and Arnekleiv 2011). On a watershed metapopulation level, the resilience of a community, in other words its ability to recover to its original state following a disturbance, can be

maintained by downstream dispersal of eggs and larval instars from undisturbed reaches upstream (Woods et al. 2016, Pham et al. 2018). Only one species found in Skibotn in 2014, was not found in 2017 (*Protonemura meyeri*), but the species was not extinct from the watercourse (Gaute Kjærstad, unpublished data). However, as no density estimates from other samples than the litter bags were included in this study, I cannot determine whether the low abundances of *P. meyeri* in Skibotn catchment in 2017 are a result of the rotenone treatment or interannual variation.

The invertebrates present in a litter bags at the time of retrieval do not necessarily reflect all invertebrates that have or could have contributed to its decomposition. Invertebrates feed selectively on combinations of litter and fungal species, and shredder species composition in leaf packs may change successively throughout the decomposition period, depending on the food quality of the litter compared to availability of other sources (Marks 2019). Therefore invertebrates found in enclosed leaf packs do not represent a random subsample of shredders, collectors and predators in a stream. They should therefore if possible and desired, be complemented with e.g benthic surber samplings (Di Sabatino et al. 2014). It should be noted that invertebrates were patchily distributed, and shredders were missing from many litter bags, while invertebrate-mediated decomposition values still indicated shredder presence. Unpublished data from kick sampling in River Skibotn in the period 2015-2017 indicate but that many possible shredder species that I did not find in litter bags were indeed abundant in the river system, while the relative density of shredders in litter packs did not reflect their relative density in kick samples (Gaute Kjærstad, pers. comm.).

Comparing rates of litter decomposition between studies and stream is not straight forward. Decomposition rates can vary within the same stream context, depending on the species of leaf used (Frainer et al. 2015), or the choice of habitat (see Frainer et al. 2014 for riffle-pool comparison). Decomposition rates in this study were overall lower than values from sites in temperate Europe, but comparable with e.g studies from small forested streams in boreal parts of Sweden (Frainer et al. 2014) and Finland (Haapala et al. 2001). Invertebrate-mediated decomposition rates estimated for birch litter in this study, are in the lower range of the values estimated for black alder (*Alnus glutinosa*) and oak (*Quercus robur*) in a large scale pan-European field-experiment (Woodward et al. 2012).

The tributary stream Haskielva in Skibotn catchment deviated from the patterns in all the other

streams. In 2017, only a few chironomids and a small early instar caddisfly larvae were found in litter bags there. This is a tributary where no fish were found, likely due to its susceptibility to heavy silting, as observed especially in the upper parts, creating a hostile environment for invertebrates and fish alike. Even after washing in sink water, the leaf litter from Haskielva was whitish in colour, presumably from chalk deposits. Nonetheless, litter mass loss in Haskielva was, although low, slightly higher than estimated mass loss by leaching in both fine- and coarse-mesh bags, except for a single coarse mesh bag in 2014. Decomposition rates here were the lowest estimated in the whole study and comparable to those estimated by Robinson and Jolidon (2005) in glacial streams in the Swiss Alps. Microbial decomposition caused most of the mass loss this field study. In some sites it seemed to be the main driver of interannual change in decomposition rates. In Nordkjøs catchment and the main river site River Skibotn, the increase in decomposition rates between years was similar in coarse- and fine- mesh bags, indicating that the increase is not mediated by change in community composition or activity of invertebrates, but rather a change in microbial decomposition. The same pattern was not evident in tributaries to the rotenone treated River Skibotn, where decomposition in fine mesh bags did not increase as much. Species identity and diversity of aquatic hyphomycetes can directly affect decomposition rates in streams (Duarte et al. 2006), while also perhaps having indirect effects on invertebrate-mediated decomposition due to detritivores feeding selectively on leaf litter colonized by specific species (Lecerf et al. 2005).

The streams studied in this experiment have a tendency to form ice slurry on the stream bottom in late autumn. This can lead to the litter bags being covered with ice during longer or shorter periods. Ice formation in and on the litter bags may kill off invertebrates or restrict their movement and activity, thus leading to reduced decomposition rates in coarse-mesh as opposed to fine mesh bags. In fact, an additional sampling site in Olderelva was excluded from the study since ice formation made it impossible to retrieve the litter bags in 2014. Ice may form during the study period in some sites and melt later, leaving the event unobserved when litter bags are not monitored throughout the study period. This especially complicates the interpretation of invertebrate-mediated decomposition rates that are already on a very small scale in these systems.

Continuous background data spanning several years might be necessary to distinguish actual effects from random variation. Stream systems are subject to prominent stochasticity, with variation in

temperature and precipitation in the catchment highly affecting the stream on short and long time scale. Changes in abiotic conditions affect ecosystems both directly, and indirectly via effects on species and species interactions (Rosillon 1989). Invertebrate species with different phenology might not only react differently to change, but also have naturally fluctuating abundances (Briers et al. 2004). A study with only a single year of sampling before and after the disturbance or alteration of interest might not be enough to gain viable results in rivers and streams, even when a control site is selected with care to be similar to the treated site (Smokorowski and Randall 2017).

The magnitude of interannual variation complicates the assessment of effects on ecosystem functioning in streams. Gessner and Chauvet (2002) suggested that changes in leaf litter decomposition rates in a stream should surpass a threshold of 70-133% of the average value for the system to be explained as an effect on ecosystem functioning, and not just normal deviation. This means that an effect of a perturbation has to be strong to be picked up in field experiments and observational studies. Yeung et al. (2018) later expanded on this and stated that interannual variation in leaf litter decomposition rates in undisturbed streams sometimes exceeded documented effects of disturbances like, for example, nutrient pollution. The highest decomposition values estimated in River Nordkjøs in 2017 exceeded 133% of the mean in 2014, while none of the increases or decreases in decomposition rates in coarse-mesh bags in Skibotn catchment surpassed such values. One exception was invertebrate-mediated decomposition rates in Lullelva, which were much higher in 2014 than 2017, but this increase was within the range of inter-site variation in Skibotn catchment, supporting the conclusion that the rotenone treatment and fish extirpation had no significant effect on invertebrate-induced decomposition rates that could with certainty be untangled from the observed inter-site and inter-annual variation.

In conclusion, large scale field studies utilizing management-imposed piscicide treatments have potential to reveal top-down effects on ecosystem functioning beyond the limitations of small experimental units. It is unlikely that fish have a top down effect of significant strength on leaf litter decomposition in the studied sites in Skibotn catchment. If such effects are present, they were likely masked by natural variation in time and space. Hence, extended sampling to map the extent of natural variation and stochasticity is necessary to pick up such effects with certainty.

7 Contributions

The experiment was designed and initiated by André Frainer. Field work and preparations was done by André Frainer, Karin Strand Johannesen, Laina Dalsbø, Rune Knudsen, Javier Sánchez-Hernández and Roar Kristoffersen. In 2014 litter bags were processed by Laina Dalsbø, André Frainer and Karin Strand Johannesen. I processed litter bags from 2017, identified all invertebrates, processed fish and dish diets, and performed all data analysis, under the supervision of André Frainer and Per-Arne Amundsen.

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9 Appendix

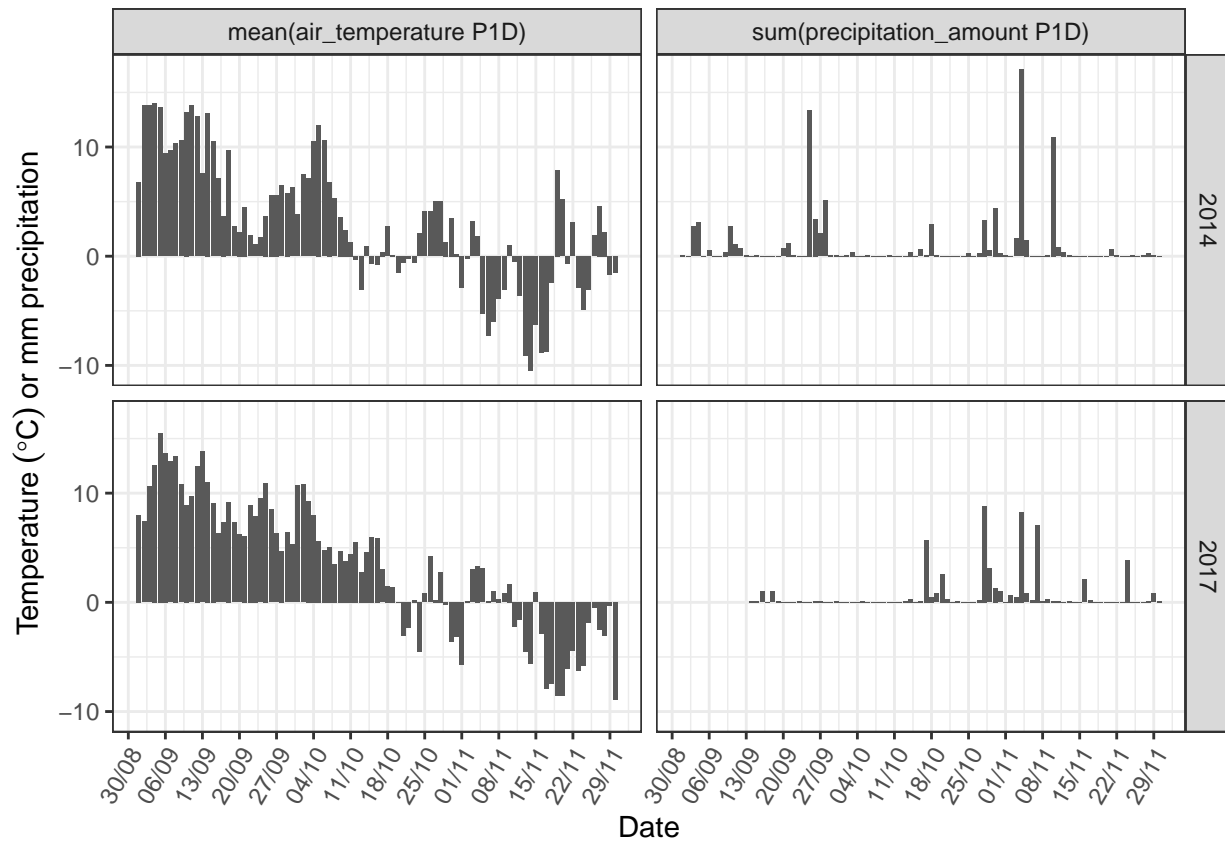


Figure 10: Weather data (mean daily air temperature, left; daily precipitation sum, right) from a weather station in Skibotn in the study periods in autumn 2014 (top) and 2017 (bottom). Based on data from MET, Norway.

Table 4: Mean (± 1 SD) number of invertebrates that were removed from further analysis due to their size($<4\text{mm}$) or taxonomy. See further explanation in methods. The group "Other" includes Dicranota, Psychodidae, Simuliidae, other small Diptera, Acari, and Oligochaeta.

	Ephemeroptera		Plecoptera		Trichoptera		Chironomidae		Other	
	2014	2017	2014	2017	2014	2017	2014	2017	2014	2017
River Skibotn 1	4 \pm 2	1 \pm 2	16 \pm 10	2 \pm 2	3 \pm 5	0 \pm 0	42 \pm 39	0 \pm 0	0.6 \pm 1	2 \pm 1
River Skibotn 2	2 \pm 0.8	0 \pm 0	3 \pm 2	1 \pm 0.8	0.2 \pm 0.4	0.5 \pm 0.6	77 \pm 82	0 \pm 0	0.6 \pm 0.9	2 \pm 2
Lullelva 1	11 \pm 8	0.5 \pm 0.6	48 \pm 20	8 \pm 10	3 \pm 3	0.2 \pm 0.5	101 \pm 7	0.5 \pm 1	16 \pm 12	1 \pm 1
Lullelva 2	2 \pm 0.8	1 \pm 2	30 \pm 22	14 \pm 9	0 \pm 0	0 \pm 0	45 \pm 37	2 \pm 2	3 \pm 4	2 \pm 3
Kavelvelva 1	12 \pm 14	4 \pm 3	69 \pm 47	15 \pm 3	1 \pm 1	0.5 \pm 1	12 \pm 8	4 \pm 1	3 \pm 2	4 \pm 2
Kavelvelva 2	26 \pm 24	13 \pm 8	57 \pm 51	14 \pm 5	0.2 \pm 0.4	0 \pm 0	9 \pm 9	5 \pm 3	2 \pm 2	0.2 \pm 0.5
Haskielva	0 \pm 0	0 \pm 0	4 \pm 2	0 \pm 0	0.4 \pm 0.9	0.8 \pm 1	15 \pm 8	3 \pm 5	0.4 \pm 0.5	0 \pm 0
Olderelva	0 \pm 0	0 \pm 0	11 \pm 7	2 \pm 0	0.2 \pm 0.4	0.2 \pm 0.5	12 \pm 10	4 \pm 3	0 \pm 0	0.8 \pm 2
Øverelva	0.6 \pm 0.9	0 \pm 0	1 \pm 2	11 \pm 2	0 \pm 0	0 \pm 0	2 \pm 3	10 \pm 4	1 \pm 1	2 \pm 2
Kjusakelva	0 \pm 0	0 \pm 0	1 \pm 1	8 \pm 6	0 \pm 0	0 \pm 0	33 \pm 27	11 \pm 7	0 \pm 0	3 \pm 2
River Nordkjøs	0 \pm 0	2 \pm 3	2 \pm 1	14 \pm 7	0 \pm 0	0 \pm 0	2 \pm 2	10 \pm 10	0.2 \pm 0.5	10 \pm 8

Table 5: Effect estimates of year, mesh size and the interaction term "year*mesh" on decomposition rate (kd^{-1}) with upper and lower limits of 95% confidence intervals (CE) and estimated degrees of freedom (DF) from the mixed effects model with decomposition data from the control sites in Nordkjøs catchment in 2014 and 2017. The intercept value represents a coarse mesh bag in 2014.

	Lower CE	Estimate	Upper CE	DF
(Intercept)	0.0064	0.0069	0.0075	7.6
Year: 2017	0.0016	0.0023	0.0029	46.0
Mesh: coarse	0.0006	0.0012	0.0018	45.9
Year * mesh	-0.0010	0.0000	0.0009	45.9

Table 6: Effect estimates of year, mesh size and the interaction term "year*mesh" on decomposition rate (kd^{-1}) with upper and lower limits of 95% confidence intervals (CE) and estimated degrees of freedom (DF) from the mixed effects model with decomposition data from rotenone treated sites in Skibotn catchment in 2014 and 2017. The intercept value represents a coarse mesh bag in 2014.

	Lower CE	Estimate	Upper CE	DF
(Intercept)	0.0074	0.0080	0.0085	6.1
Year: 2017	0.0001	0.0006	0.0012	116.8
Mesh: coarse	0.0005	0.0009	0.0014	116.8
Year * mesh	-0.0004	0.0004	0.0011	116.8

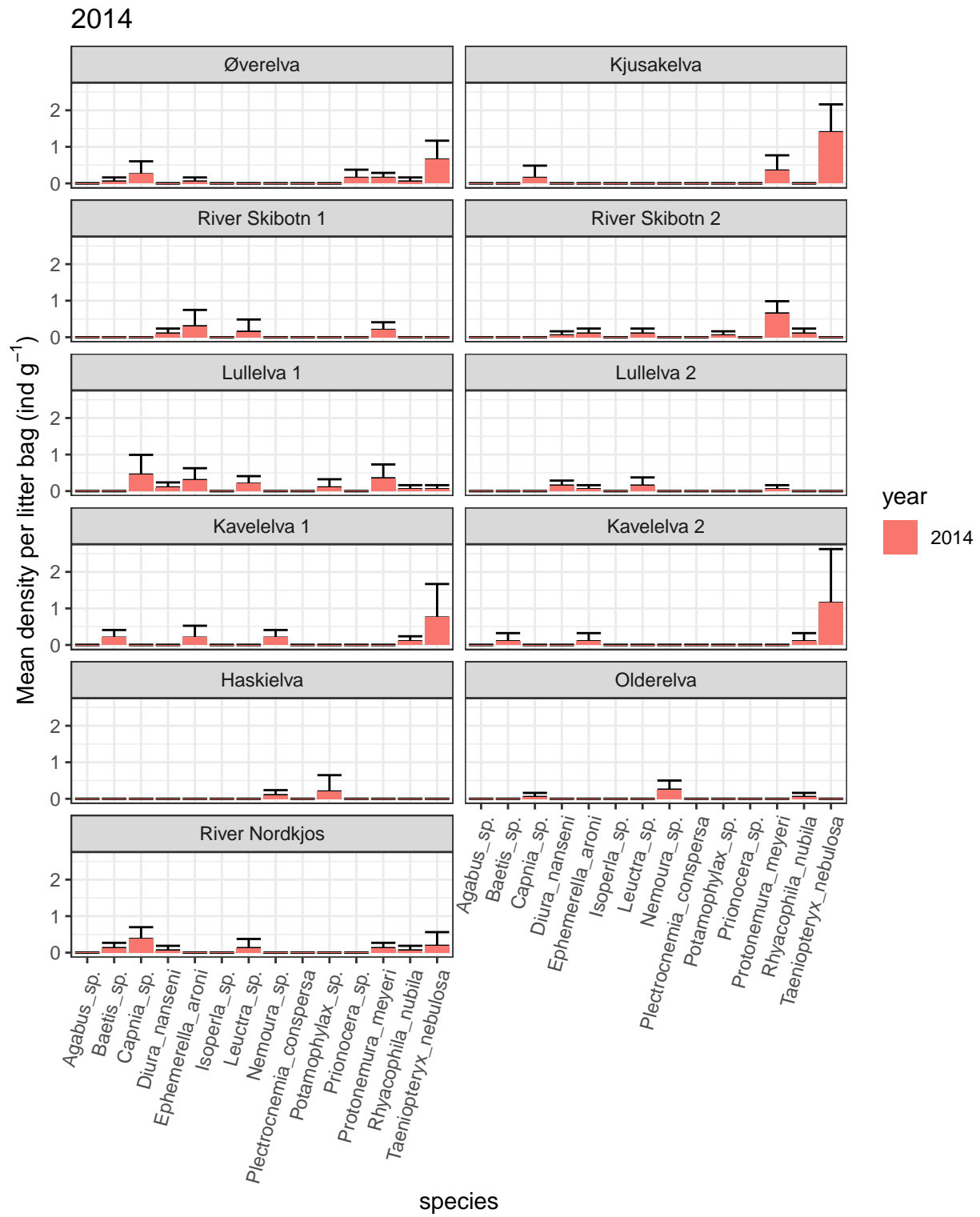


Figure 11: Mean density (ind g^{-1} initial leaf litter) of the studied invertebrates per litter bags per in sites in 2014

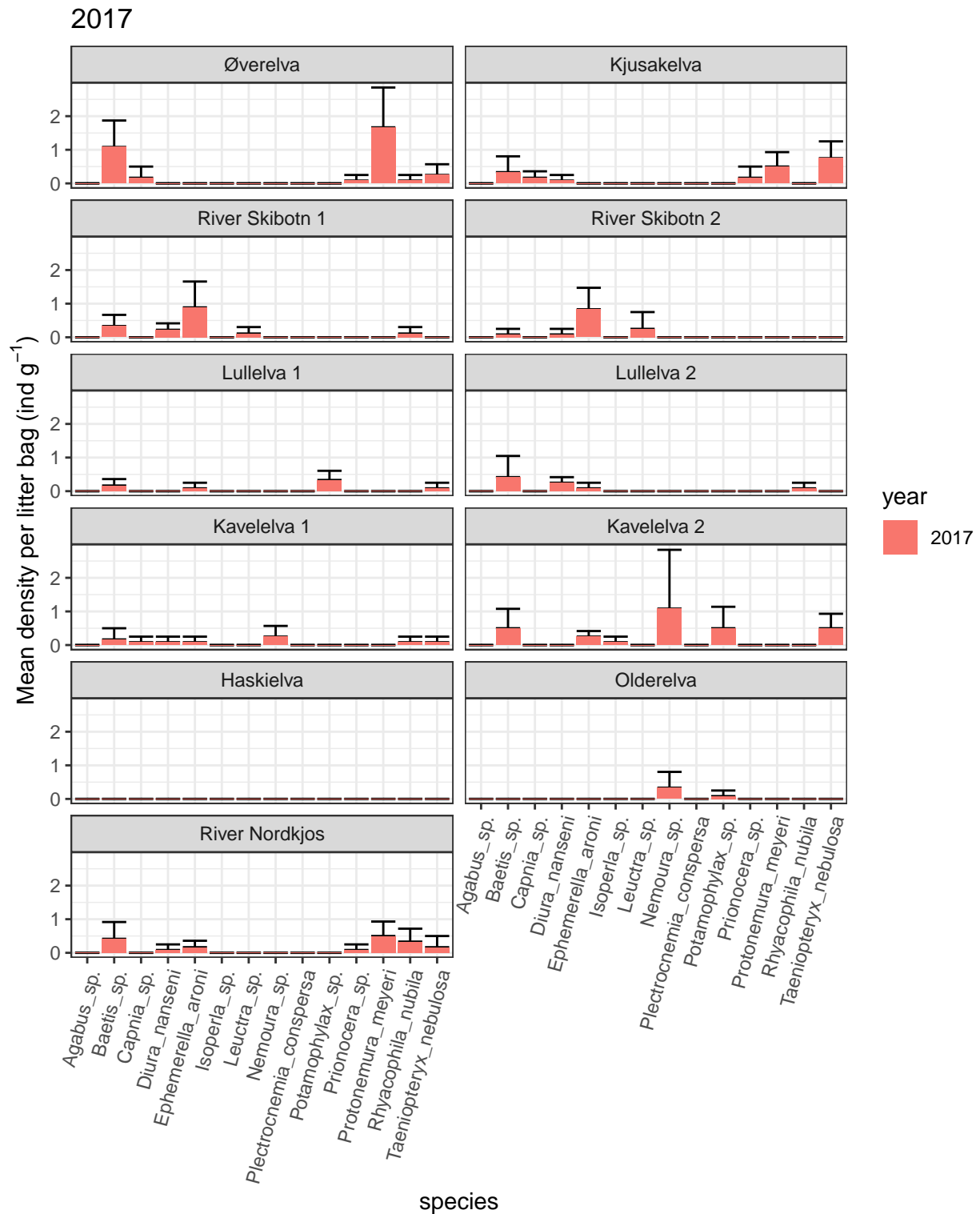


Figure 12: Mean density (ind g^{-1} initial leaf litter) of the studied invertebrates in per litter bag in the sites in 2017

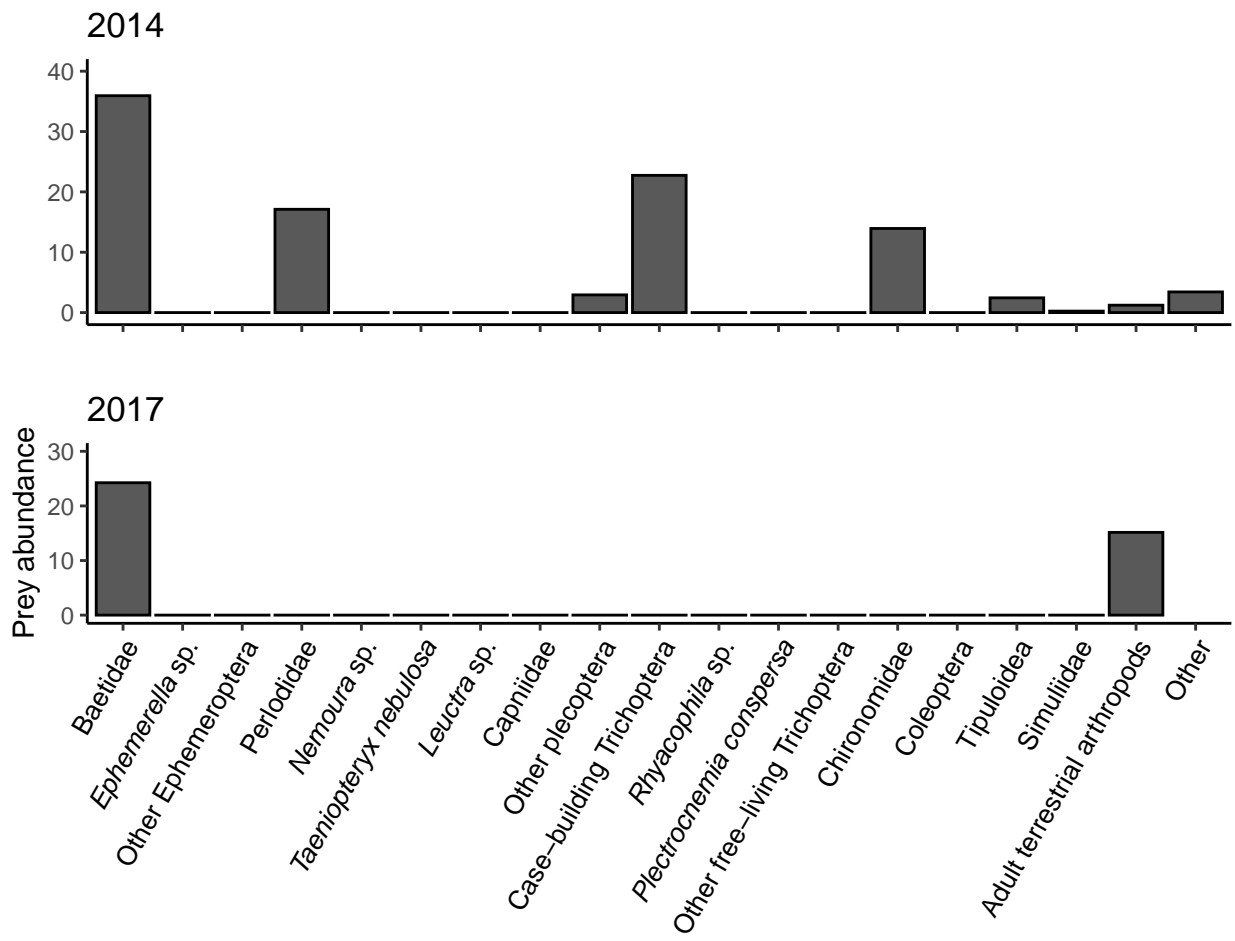


Figure 13: Prey abundances by proportion of total stomach content in fish captured at studied sites in Nordkjos catchment in 2014 (n: <70mm, 3; >70mm, 13) and 2017 (n: <70mm, 0; >70mm, 5). All prey items except “Adult terrestrial arthropods” are aquatic insect larvae.