Ecosystem effects of invasive domesticated Atlantic salmon (*Salmo salar)* and global warming

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Abstract

Each year large numbers of escaped farmed salmon migrate in Norwegian rivers and some partake in spawning. Offspring with varying degrees of domestication inhabit river systems together with wild conspecifics. As climate warming is another factor that may act synergistically with biological invasions, I studied the impact of domesticated salmon in the context of warmer climate. Although the impact of farmed salmon has been studied extensively, there is little knowledge of the impact of ecosystem functions. In this study, using fully domesticated salmon, I quantified the impact of first feeding salmon in a controlled semi-natural experiment. I estimated the effect of wild and farmed, at todays and the predicted temperature in 100 years, on key stream functions. The effect on leaf-litter decomposition, primary production and macroinvertebrate community was quantified 35 days after salmon emergence. My results indicate overall small effects and sometimes in contradiction to what is expected from other studies.

First, I established that farmed salmon are larger than wild salmon and that increased temperature increases final size differences in stream mesocosms. Final sizes were compared to salmon reared in indoor tanks, fed *ad libitum*. The farmed strain had accelerated growth indoor in comparison to in the more complex habitats, indicating poorer performance in the wild. Second, primary production and microbial decomposition rates were not affected by either treatment, while total decomposition decreased at warmer temperatures. Finally, consumptive or non-consumptive effects on the macroinvertebrate community was not evident in this study. A top-down control of food webs and ecosystem functions could not be established, and the effect of emerging salmon of either origin may be small at this developmental stage.

The wild Atlantic salmon is influenced by multiple human stressors and environmental risk assessments should be concluded at ecosystem level. The findings here indicate small and uncertain effects. Yet, an ecological impact can occur later at later developmental stages as Atlantic salmon holds a complex life-history.

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1 Introduction

Wild Atlantic salmon, *Salmo salar.,* is substantially farmed in Norway and across the globe. Phenotypes showing rapid growth and other traits has been selected for over several generations (Teletchea and Fontaine, 2014). Each year large numbers of farmed salmon escapes fjord-located farms in Norway (Norwegian Directorate of Fisheries; https://www.fiskeridir.no/Akvakultur/Tall-og-analyse/Roemmingsstatistikk). Some migrate to spawning grounds of wild populations in Norway (Carr and Whoriskey, 2006 , Fiske et al. 2006, Karlsson et al., 2016). Escape incidents are likely underreported to official authorities (Skilbrei et al., 2015) and it has been shown that escaped farmed salmon partake in spawning with native spawning stocks of wild salmon (Lura and Saegrov, 1991, Thorstad et al. 1998).

Atlantic salmon is an anadromous specie with a complex life history (Klemetsen et al. 2003, Jonsson and Jonsson 2011, Thorstad et al., 2011). During summer and fall the mature fish migrate to spawn in the same river they were born (natal homing). Fertilized eggs are embedded in surrounding substratum and hatch during spring. Incubation time depends primarily on temperature, but also on other environmental factors, such as oxygen depletion and stress. After hatching, the alevin dwells in the redd until it has consumed most of the yolk sac. Upon consumption, first feeding salmon (fry), migrate through the gravel to the stream bed. The juvenile salmon fry shifts diet and feed opportunistic on small invertebrates (often small *Chironomidae*) (Keeley and Grant 1997, Johnson et al., 2017). After emergence, juveniles seek shelter from fast-flowing water to hold their position and feed successfully. The juveniles inhabit water depths under 15 cm and expands their habitat as they grow (Gibson, 1993). The first period after emergence is a critical period, both habitat availability and presence of available prey species are important for survival (Armstrong and Nislow 2006). After emergence, some individuals drift downstream while some establish and defend territory near the redd (Bujold et al., 2004). Atlantic salmon is a sit and wait predator, feeding on drifting and benthic invertebrates, molluscs and crustaceans (Dineen et al., 2007, Jonsson and Jonsson, 2011). In late summer the fry has developed to parr and spends 2-5 years in their natal river before smoltification and adapts to sea migration.

Selective breeding programs has led to genetic and phenotypic differences in farmed salmon, and domestication of wild Atlantic salmon has significantly impacted life-history traits

(Petersson et al., 1996). Breeding programs have targeted traits aimed to increase production and the Norwegian programs have targeted increased growth rate, food conversion efficiency and avoidance of early maturation (Gjedrem, 2000). Increased growth rate accompanies phenotypic effects as higher activity level, foraging activity and nutrient excretion rates and aggression level (Einum and Fleming, 1997, Lahti et al., 2002). Higher growth rate due to increased growth hormone levels is associated with higher appetite, more risk-willing behavior and increased metabolic rates in transgenic salmonids (Cutts et al., 2002, Fleming et al., 2002, Lahti et al., 2002, Sundt-Hansen et al., 2009). Further, farmed salmon has been documented to impose a negative impact on the wild salmon population, through introgression (Bolstad et al., 2017, Robertsen et al., 2019), and interference competition (Sundt-Hansen et al., 2018, Robertsen et al., 2019, Solberg et al., 2020). However, there is little literature on the ecological impact of escaped farmed salmon on stream ecosystem (Buoro et al., 2016, Cucherousset et al., 2021).

Rivers and streams are influenced by both aquatic and terrestrial processes. Studies have underlined allochthonous input of organic material as a major energy source in streams (Wallace et al., 1997, Leberfinger et al., 2011). Abiotic factors as waterflow, shading, temperature, water chemistry and river substrate forms the ecological framework for the biotic components in aquatic ecosystems. Autochthonous energy is produced by bacteria, macrophytes, algae and water plants. Primary production depends on nutrients and is limited by the overhead canopy. Even though most of the energy originates from allochthonous sources, benthic algae biomass is an important food source for herbivore species and can support herbivore grazers and scrapers due to high turnover rate in algae communities (Gregory, 1980, Pan and Lowe 1994, Guo et al., 2016).

Aquatic invertebrate communities consist of numerous taxa and can be classified to different functional feeding groups and trophic levels in aquatic ecosystems (Meritt and Cummins, 1996, Moog, 2002). Species inhabit different microhabitats and change food sources following changes in ontogeny and size (Hauer, 1996). Grazers/Shredders and decomposers are primary consumers feeding on epiphytic algae and allochthonous leaf-litter. Predatory invertebrates and predatory fish are secondary consumers in freshwater foodwebs. The family Chironomidae is a large taxon with several feeding types; shredders, grazers, filter feeders, gatherer-collector and predators (Kjaerstad et al., 2018). Chironomidae has been reported to feed on leaf-litter and is a common prey of juvenile salmon (62% of diet) (Callisto et al.,

2007, Johnson et al., 2017). Other taxonomic families such as *Trichoptera, Ephemeroptera* and *Plecoptera* belongs to several functional feeding groups and are preyed on by salmonids following ontogeny and season (Dineen et al., 2007, Johnson, 2008).

First feeding Atlantic salmon may impact the ecosystem through consumptive effects on prey community, or non-consumptive effects such as nutrient excretion rates and anti-predator or foraging behavior associated with the presence of salmon. My hypothesis is that juvenile salmon has a top-down control of riverine food webs, and that invasion of intraspecific farmed salmon exhibits a cascade effect through trophic levels, because of phenotypic traits selectively bred for. Increased growth rate gives the farmed salmon a size advantage from swim up, in regards of gap size and size selection of prey. This and a different foraging activity in farmed salmon may lead to a change in macroinvertebrate community structure through top-down control, or through non-consumptive effects on foraging behaviour of prey species. Macroinvertebrate community structure can subsequently change the rate of decomposition of leaf-litter, primary production and other ecological processes associated with primary consumers. In a study from the river Imsa in Norway (Cucherousset et al., 2021) the researchers found that growth-enhanced salmon parr impacted key-ecological processes such as leaf-litter-decomposition and primary production, through consumptive and non-consumptive effects on the macroinvertebrate community.

Global warming is another human induced stressor that act together with biological invasions and affects the abiotic and biotic drivers of ecosystem functioning (Perkins et al., 2010, Antiqueira et al., 2018). Biological invasion and global warming are two major stressors on both terrestrial and aquatic ecosystems (Horreo et al., 2011, Rolls et al., 2017) caused by anthropogenic activity. Global warming may affect ecosystem functions through top-down or bottom-up effects, as phytobenthos biomass has been reported to increase and decrease due to nutrient release and grazing pressure (Kazanjian et al., 2018). Microbial decomposition is also expected to increase with warmer temperature (Irons et al., 1994). Because of this I will also investigate if global warming acts synergistically with the presence of first feeding salmon of farmed origin.

The goal of the study is to test the prediction that global warming and invasion of an alternative phenotype of wild Atlantic salmon influences community structure and ecosystem functioning. Therefore, I will quantify if the ecological impact of escaped farmed salmon

increases with global warming in a semi-natural experiment using stream mesocosms. Phytobenthos biomass, decomposition of leaf-litter and the macroinvertebrate community were studied since it connects elements of stream ecology at different levels.

2 Materials and Methods

2.1 Facility and mesocosm experimental

The experiment was conducted at NINA research station in Ims (referred to as the research station) in southwestern Norway. I designed an experiment to test the impact of two treatments; impact of no fish, wild and farmed salmon fry and the impact of global warming (two levels: current temperature and the predicted future temperature based on IPCC temperature scenarios (IPCC, 2007). The no-fish treatment and current temperature regime functions as a baseline for ecosystem functioning and macroinvertebrate community structure without the presence of first feeding salmon. The current temperature followed the natural temperatures of the nearby lake Liavatn, the warm temperature was approximately 3 degrees warmer (appendix, Figure A-1) (IPCC, 2007, Sundt-Hansen et al. 2018). Water in both treatments was filtered to remove debris and particles, then UV-treated. For the warm water temperature regime, water was heated by the research stations recirculating aquaculture system. From here the current and warmer temperature treatment is referred to as cold and warm temperature regime.

The experiment was conducted in stream mesocosms made of fiberglass, 4.5 meters long and 0.25 meters wide (1.125m^2). Each channel had a vertical meshnet upstream and downstream providing a confined environment, allowing water to flow through and preventing fish and macroinvertebrates from exiting the experimental section. I assigned three stations along the upstream – downstream gradient in each stream mesocosm; A, B and C, where station A was the most upstream location. At each station I placed one ceramic tile and two mesh bags to measure primary production, or phytobentos biomass (green algae, diatoms and cyanobacteria concentrations), and decomposition rates (Figure 1).

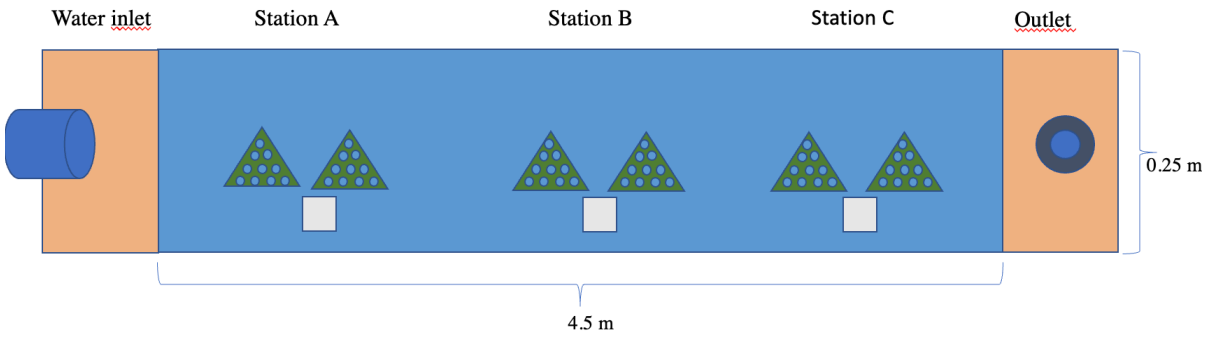

Figure 1: Schematic overview of a stream mesocosm. Inlet, stations A-C with 2 types of meshbags (triangles) and ceramic tiles (square) and outlet. 1,0625m^2.

A total of 24 stream mesocosms were utilized. Each mesocosm is a paired structure divided by a fiberglass wall. Four replicates of each treatment combination (Figure 2) were assigned to different stream mesocosms to account for unmeasured effects of abiotic factors.

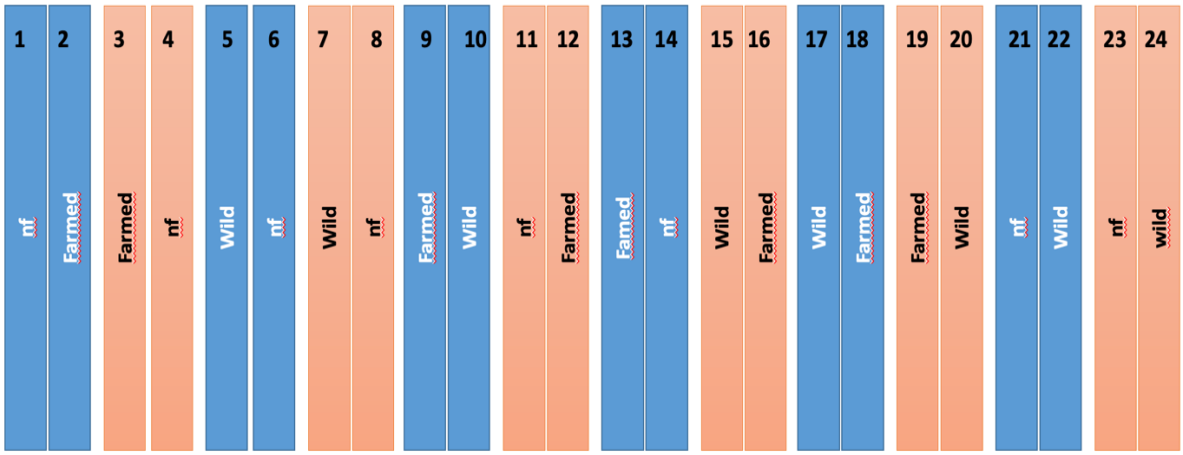

Figure 2. Setup of 24 outdoor stream mesocosm, with stream ID and treatment levels: no-fish, wild and farmed salmon, cold and warm temperature regime. From east (near the shore) to west.

Two and two stream mesocosms shared the same water inlet and because of this every other mesocosm received either the cold or the warm temperature treatment (Figure 3). See appendix table A1-A2 for water flow rate and depth measurements. The mesocosms were covered with standard fish nets to prevent bird predation. Further I added wooden structures over the mesocosms to provide some cover from direct sunshine.

On 29. May 2021 the system that heated water for the warm temperature treatment had a technical issue which led to equal temperatures (cold temperature regime) in all stream mesocosms (appendix, Figure A-1). The issue lasted for approximately 48 hours before it was solved. Other disturbances were not reported during the experiment.

Figure 3: Photo of four stream mesocosms, 5. May 2021. Mesh bag pair and tiles located at each station. Photo: Knut Andreas Bækkelie.

Figure 4: Indoor tanks (n=12) for salmon fed ad libitum. RAS facility with automatic feeders, 5. May 2021. Photo: Knut Andreas Bækkelie.

Inside the research station, twelve 60-litre tanks with salmon were used as a control for the experimental fish (figure 4) with three replicates per treatment level: cold and warm temperature, wild and farmed salmon. A total of 150 individuals was kept in each tank. The tanks were connected to the facility's flow though system and received water from lake Liavant. The indoor fish were fed with automatic feeders, fed as much as they wanted.

The experiment was completed according to the experimental plan without any major disruption (Figure 5). Each day the mesh dividing the inlet and outlet from the mid-section was gently rinsed to keep water level and flow stable. The mesocosms was supervised daily to ensure good animal welfare.

2.2 The experimental fish

The experiment is designed to test the effect of farmed salmon immediately after yolk sac consumption and swim-up. Swim up in river Imsa was estimated to occur 10. May 2021, estimated from when the eggs were acquired (fall 2020) until hatching according to Crisp (1981, 1988). Wild salmon was acquired from the natural population spawning in river Imsa, while the breeding company Aquagen provided eggs from farmed salmon.

Egg and sperm from the natural population spawning in Imsa (wild salmon strain) (10 males and 10 females) of salmon was obtained on 16. November 2020 from the river Ims. The salmon were stripped and after fertilization the eggs were kept under standard hatchery conditions at the research station. Eyed eggs of the farmed strain (offspring of 10 males and 10 females was obtained from Aquagen (farmed salmon strain) (Norwegian breeding company) and delivered to the research station at Ims on February 9. 2021. Both strains were incubated at the same temperature. Family groups within each strain were kept together. Egg development was synchronized as much as possible, so that they would reach the end of the yolk-sac fry stage when the experiment started. Following the models developed by Crisp (Crisp 1981, Crisp 1988), the estimated time of swim up in river Ims was 10. May in 2021 (median), estimated from when the eggs were acquired (fall 2020). On May 5., individuals of both the Aquagen and wild Imsa strain had almost completely consumed their yolk and we decided to start the experiment.

Prior introduction to the stream mesocosms, a subsample of 30 individuals of each strain was euthanized with Benzoak Vet (15-20 ml / 100 L) (ACD Pharmaceuticals AS Leknes, Norway) before being measured (total length). Even though the developmental of both strains were synchronized, the strains differed in length and weight. Family groups within the farmed and wild strain were mixed to control for family effects on length, weight and other traits on 5. May 2021. I carefully released 25 (400 in total) individuals to a predetermined stream mesocosms which had a farmed or wild salmon treatment (Figure 2). 25 individuals correspond to a density of 22 ind. m^2, a density within a range of what can be found in the wild (Teichert, Einum et al. 2013).

In addition to the outdoor experiment in stream mesocosms, juveniles were kept in indoor tanks (n=12, 60L) as a control treatment and fed ad libitum with automatic feeders. The control tanks kept the same temperature regime as the stream mesocosm experiment with six tanks following the natural temperature fluctuations in lake Liavatn and six tanks with a warmer temperature.

2.3 Mesocosm enrichment and inoculation

Natural substrate (cobbles and gravel) was introduced to the empty stream mesocosms. Gravel and cobbles originated from the river Imsa and provided a natural substrate for the juvenile salmon. It had earlier been used in various experiments in several larger mesocosm tanks at the research station, but not that year.

Before the start of the experiments the different stream mesocosms were inoculated with a natural community of invertebrates. This was done by collecting invertebrates the river Imsa using a Surber sampler (a standard quantitative method for sampling macroinvertebrates for estimates of macroinvertebrate taxa pr m^2 (Hauer, 1996). A total area of 0.78 m^2 was sampled and the collected macroinvertebrates were introduced to each stream mesocosm on March 9. 2021 (3 samples) and May 3. 2021 (4 samples). The content of the Surber samples was transferred into 10-liter buckets before being transported to the research station and released upstream to reduce drift of invertebrates. In addition, 4 moss-grown rocks from river Ims were introduced to each stream mesocosm. I sampled the invertebrates in a 30m^2 area with slow flowing water, using a Surber sampler with mesh size of 250 µm.

Further, I saved the content of seven additional Surber samples (subsample) and preserved macroinvertebrates in 96% ethanol. These samples were used to describe the community of macroinvertebrates that was introduced to each stream mesocosm.

2.4 Experimental design and protocol

The experiment lasted from 5. May 2021 until 11. June 2021. During the experiment temperature loggers (HOBO U22-001 Water Temp Pro V2) were placed in the outlet of each stream mesocosm pair at the start of the experiment to record water temperature. Decomposition and phytobentos biomass were measured on 25. May, 2. June and when the

experiment ended on 11. June At each sampling date a random station in each mesocosm was selected for sampling of a ceramic tile and a mesh bag pair (course and fine mesh). I decided to sample phytobenthos biomass and decomposition during the experiment in case that the leaf-litter would be fully consumed prior the experiment ended. See Figure 5 for sampling and preparation dates.

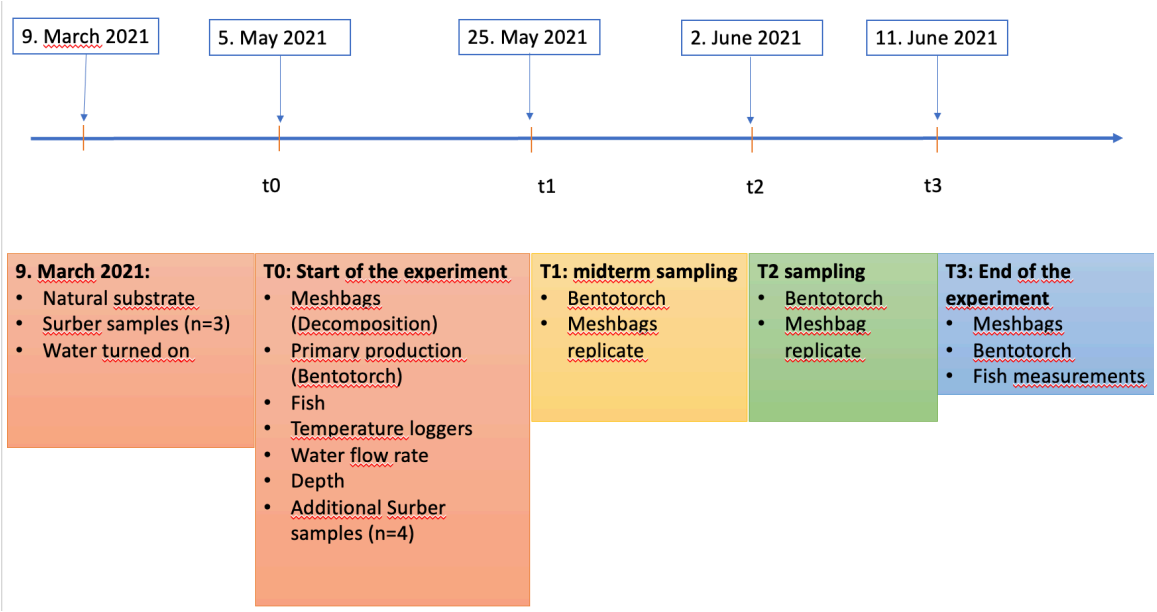

Figure 5: Overview of the experimental protocol from March to June with sampling dates and preparations. T0, start of the experiment 5. May 2021. On 9. March 2021 the stream mesocosms prepared and inoculated. T1, midterm sampling of meshbags and tiles on 25. May 2021. T2 on midterm sampling of ceramic tiles and meshbags on 2. June 2021. T3, the experiment was ended on 11. June 2021 and lasted for 35 days.

2.4.1 Decomposition rates

I placed 1.5 g (sd=0.03 g) of air-dried Gray Alder (*Alnus incana)* leaves in mesh bags of two sizes (Fine mesh; 12mm and coarse mesh; 500 µm) to measure decomposition of leaf-litter in each stream mesocosm (Figure 6). Gray Alder is natural present near the river Imsa. I followed the protocol for the study of decomposition of leaf-litter using mesh bags according to Benfield (1996). A total of six leaf packs were placed in each stream mesocosm and attached to cobbles to prevent drift. At each station a pair of one coarse mesh and one fine mesh leaf pack was placed according to Figure 1. In addition, I measured mesh bags before and after handling and initial leaching to account for loss upon placement in the stream mesocosms. Fine mesh bags allow measurements of mass loss due to microbial activity, since

the mesh size is too small for aquatic invertebrates to enter. While course mesh bags allow quantification of mass loss due to invertebrate and microbial activity (total decomposition).

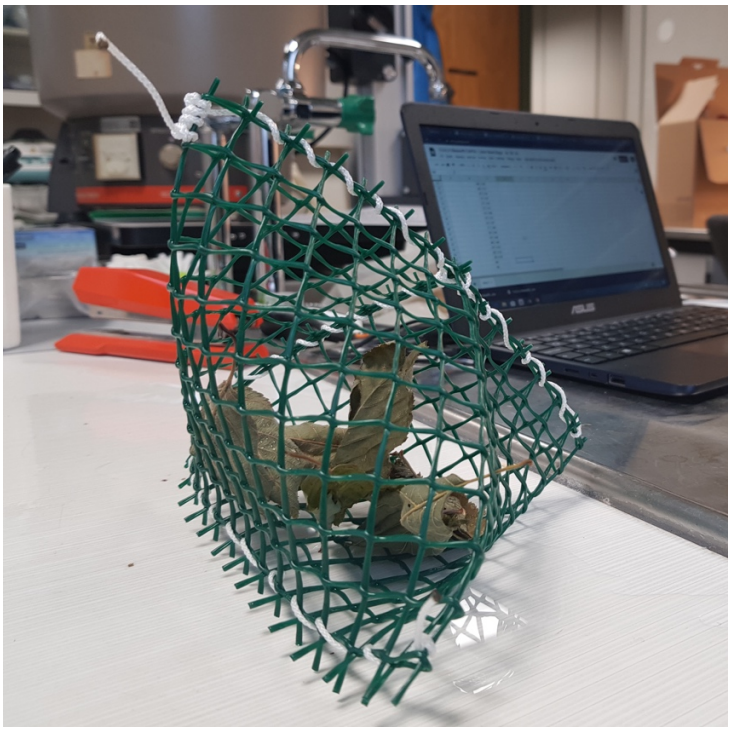

Figure 6: Coarse mesh bag with dried leaf-litter, 9. March 2021, air-dried Gray Alder (Alnus incana).

2.4.2 Primary production

Phytobenthos biomass was measured on unglazed ceramic tiles placed in accordance with Figure 5. The presence and primary production of diatoms, green algae and cyanobacteria was measured using a BenthoTorch®, a portable fluorometer (BenthoTorch, BBE Moldaenke GmbH, Schwentinental, Germany) (Kahlert and McKie, 2014). The device emits light pulses within range of the excitation spectrum of chlorophyll a fluorescence at different wavelengths (470, 525 and 610 nm) and records the pigment response at a wavelength of 690 nm. Density of cyanobacteria, diatoms and green algae is calculated by chlorphyll a measurement of the biofilm. The BenthoTorch® is able to discriminate between cyanobacteria, diatoms and green algae due to distinctive pigments of each target group (phycocyanin for cyanobacteria, chlorophyll c and xanthophylls for diatoms and chlorophyll b for green algae) (Piano et al., 2015).

2.5 Sampling of data

I chose to sample 2/3 of the tiles and mesh bags at T1 and T2 in the case of full consumption of leaf-litter before I ended the experiment. Tiles and mesh bags were carefully sampled during the experiment (T1 and T2) in a non-disturbing manner. Macroinvertebrates was sampled at the end of the experiment due to potential disturbance of salmon. At T3, I first removed the mesh bags and ceramic tiles. Then macroinvertebrates were sampled using Surber sampler. Finally, the juvenile salmon was recaptured using aquarium dip nets.

2.5.1 Sampling of invertebrates at the end of the experiment

On 11. June, I collected three Surber samples (0.1875 m^2) from each stream mesocosm before fish recapture. I sampled each station in the stream mesocosms (total area = 0.1875m^2) and preserved macroinvertebrates in ethanol 96% ethanol. The upstream-downstream gradient was sampled to capture potential microhabitat variation (Benfield, 1996). The invertebrates were identified to the lowest taxonomic group in the lab and classified to a functional feeding group (www.Freshwaterecology.info; Moog, 1995, Moog, 2002, Tachet, 2010, Schmidt-Kloiber and Hering, 2015, Otto Moog, 2017). Since the number of invertebrates from the same taxa (at family and specie level) was low, I assigned each observation of aquatic invertebrates (family level) as either a predator or primary consumer based on their dominant diet.

2.5.2 Sampling of fish

At the end of the experiment, the juvenile fish in the stream mesocosms and the control tanks were recaptured using aquarium dip nets and subsequently euthanized with an overdose of Benzoak Vet (ant. 15-20 ml / 100 L) and measured immediately. A subsample of 30 individuals from each indoor tank (n=12) was recaptured, euthanized and frozen for later body weight and length measurements. The individuals were measured to the nearest mm and 0.01g.

2.5.3 Sampling of mesh bags and ceramic tiles

A pair of coarse- and fine- mesh bags and a ceramic tile was at random sampled on each sampling date, T1-T3. They were removed at random to control for upstream-downstream effects. Each tile was measured 3-4 times with a BenthoTorch® to cover potential variability across the surface and averaged to get concentration per cm^{-2}. The tiles were carefully moved to a plastic container filled with enough water to cover the tiles and measured 3-4 times in areas without overlap.

Mesh bags were kept in zipper bags and frozen after removal before further processing. The samples were gently rinsed with warm water to remove silt, debris and overgrowth by algae. Aquatic insects found in the mesh bags were stored in ethanol and later identified and classified according to its functional group. The leaf-litter samples were kept frozen and dried, weighed and then burned at 550 °C for 6 hours in order to assess ash free dry mass loss (AFDM). All measurements were in grams to four decimals.

2.6 Analyses

The data was analyzed in R (version 4.2.0, R Core Team, 2022) using R studio. Models were compared by Akaike's information criterion (AIC) to find the most parsimonious model (Akaike, 1974). When sample size was low ($N/K < 40$, K is the number of parameters and N is the sample size), I used AICc to choose the most parsimonious model. This was the case for all models except the weight and length models. If the relative difference in AICs or AICc (ΔAIC) was less than 2, the model with fewest parameters was selected for inference. When the difference to the best fit model (ΔAIC) is less than 2, the candidate models is essentially just as good as the best model (Burnham and Anderson, 2004). Decomposition rates and phytobenthos biomass was analyzed using standard linear models, while the macroinvertebrate community was investigated using quasi-Poisson distributed generalized linear models.

Since I am interested in the effect of warmer climate and invasive domesticated salmon, all models include two categorical variables: origin (3 levels: no fish, wild and farmed salmon) and temperature (cold and warm temperature regime). Decomposition and primary production

were measured at different stations when the experiment ended, and station is therefore included as a co-variable in these models.

2.6.1 Salmon size models

A t -test was used to test for difference in the number of recaptured fish of the two salmon strains and temperature regime, and to establish if the farmed strain truly was larger than the Imsa strain at start of the experiment. Differences in length and weight at the end of the experiment was analyzed in a linear mixed effect model (Bates et al., 2015).

I estimated the effect on fish size, at the end of the experiment and included stream mesocosm ID as a random effect to control for heterogeneity among stream mesocosms. Models included two categorical variables: origin and temperature. Random intercept model with additive effects was compared to a random intercept model with an interaction effect between the treatments (appendix, table A-4).

The effect of temperature regime and origin was in addition estimated for the final indoor fish size. Tank ID was used as a random effect to explain among tank heterogeneity. The mixed effect models could, however, not be compared because of singularity (appendix, table A-5). Which means that some parts of the variance-covariance matrix were estimated as zero i.e., no random, or very, small random effect.

2.6.2 Community and ecosystem response

I included upstream to downstream sampling position, temperature regime and origin covariates in the standard linear model for the ecosystem effects (decomposition and total phytobenthos biomass) of escaped farmed salmon. The effect of fish and temperature treatment effect was analyzed using standard linear model. The no-fish and cold temperature treatment were set as the intercept.

Total benthic cholorphyll a concentration (µg chl a. cm^{-2}) was calculated by summing green algae, diatoms and cyanobacteria concentrations into a new variable, as a measure of total phytobenthos biomass. Total cholorphyll a concentration is the dependent variable in this model, additive and interaction models were compared (appendix, table A-6). Since each tile

was measured 3-4 times with the Bentotorch, I averaged the within-tile measurements to avoid pseudo-replication. I could have used a linear mixed model with tile ID as a random effect instead of averaging, but the mixed effect models could not be compared because of singularity.

Daily ash free dry mass loss (k) at T3 is the dependent variable in the decomposition models for both the fine mesh and coarse mesh bags which represents daily microbial and total decomposition. I compared models with an additive and interaction effect between temperature regime and origin with an additive effect of mesocosm position for total decomposition (coarse mesh bags) and microbial decomposition (fine mesh bags) (appendix, table A-7).

The processing coefficient *k* represents leaf-litter decomposition rate and is represented by the formula (Benfield, 1996);

$$K = \frac{\log\left(\frac{AFDM}{iDM}\right)}{T}$$

AFDM is the ash free drymass (g) of the samples, iDM is the initial dry mass (g) corrected for leaching and handling, and T is exposure in days. K represents the exponential decay rate, *K* day^{-1}.

I decided to focus on the most abundant taxonomic families, Elmidae and Chironomidae and functional groups, number of primary consumers and predators, to increase the number of observations. Individual counts of Chironomidae, primary consumers and predator are dependent variables (absolute number of individuals) with temperature regime and origin as covariates in a quasi-Poisson distributed generalized linear model with a log-link function. The no-fish and cold temperature treatment were set as the intercept. I made log-linear models for the community response; number of predators, primary consumers, Chironomidae (family level) collected from Surber samples in the stream mesocosms at the end of the experiment. I decided upon 3 levels of community response (predators, primary consumer and Chironomidae) since the abundance of other taxonomic families were poorly represented.

Initially I compared an additive and interaction generalized linear model using Poisson distribution. Since the models were overdispersed, I decided on using quasi-Poisson distributed models for community response. Quasi-Poisson distributed models cannot be compared using AIC, and I have assumed that the effects are additive (appendix, table A-8).

3 Results

3.1 Salmon size

Before juvenile salmon was introduced to the stream mesocosms, a subsample of 30 individuals of both strains was measured (Figure 7). The two strains differed significantly in size when the experiment started (t-test, p-value$_{weight}$ = 2.2e-16 and p-value$_{length}$ = 5.595e-15) and the farmed salmon was larger. The farmed salmon was on average 2.9 mm longer and 0.06 g heavier more than the wild Imsa strain.

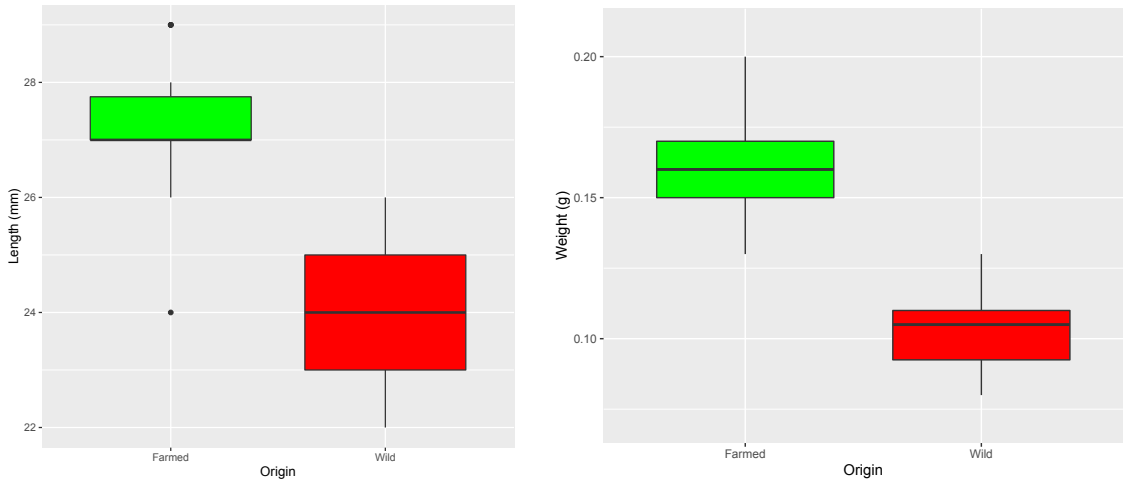

Figure 7: Box and whisker plot of initial wild and farmed salmon) length (mm) and weight (g) distribution at the start of the experiment(T0). N=30. Upper and lower edge of the boxes represents 25th and 75thpercentiles. The vertical lines indicate the min/max value of 1.5 times the interquartile range. Dots represents outliers.

On 11. June 2021 a total of 312 individual salmon juvenile (Figure 8) were recaptured (appendix, A-4), on average 24 farmed and 20 wild individuals, indicating some mortality. At the start of the mesocsm experiment 400 individuals was released. A t-test was used to test recapture success in mesocosms for the treatments. The test showed that mesocosms with farmed salmon had higher recapture success (mean farmed=24, mean wild= 20.1, p-value = 6.7e-05). Recapture success among temperature regimes was also tested and showed that temperature regime did not affect recapture success (mean warm= 22.5, mean cold= 21.88, p-value=0.61).

I estimated the effect of no-fish, farmed and wild salmon and water temperature on final salmon weight and length in the stream mesocosms, at the end of the experiment using linear mixed effects models. The farmed salmon strain was significantly longer (3.49mm, CI =2.39 - 4.59) and heavier (0.07 g, CI=0.04-0.011) than the wild salmon, and warmer temperature had a positive effect on final length (3, CI=1.9 - 4.1) and weight (0.08 g, CI = 0.05 - 0.011). Among stream mesocosm heterogeneity explained approximately 10% of the variance. The models were compared to an interaction model using AIC (appendix, table A-4). The difference between the most parsimonious model (additive model) and the candidate models (interaction model) was less than 2. However, the interaction effect between the farmed salmon and warm temperature treatment was not significant (confidence interval overlap zero) and is therefore not presented.

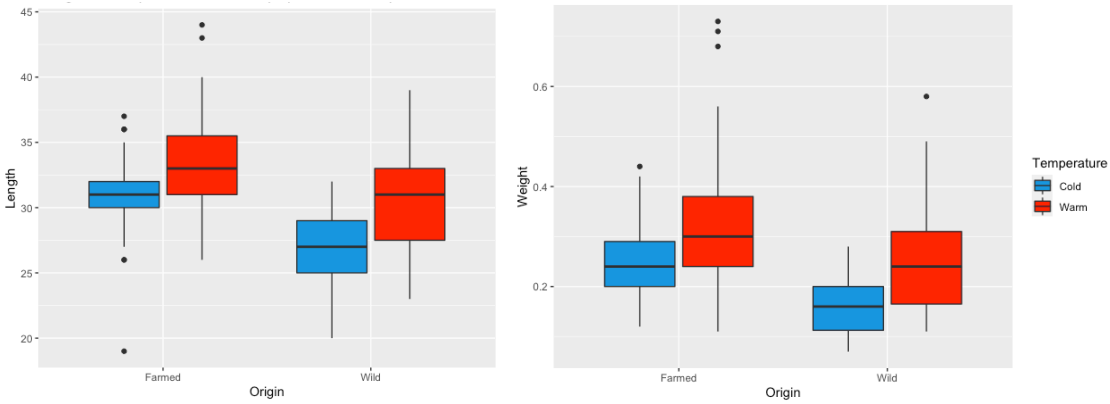

Figure 8: Box and whisker plot of recaptured juvenile salmon length (mm) and weight (g) distribution in the stream mesocosms. Wild and farmed strain, in the cold and warm temperature regime. N = 353. Upper and lower edge of the boxes represents 25th and 75thpercentiles. The vertical lines indicate the min/max value of 1.5 times the interquartile range. Dots represents outliers

Table 1: Estimates from the linear mixed effect models (additive effect of treatments) for individual farmed and wild salmon weight (g) and length (mm). Using the lme4-package function lmer to account for variation in each mesocosm. Intercept in this model represents the wild strain in cold treatment.

	Weight		Length	
Predictors	*Estimates*	*CI*	*Estimates*	*CI*
(Intercept)	**0.17**	**0.14 – 0.19**	**27.24**	**26.28 – 28.20**
Origin [Farmed]	**0.07**	**0.04 – 0.11**	**3.49**	**2.39 – 4.59**
Temperature [Warm]	**0.08**	**0.05 – 0.11**	**3.00**	**1.90 – 4.10**
Random Effects				
σ^2	0.0073		8.32	
τ_{00}	0.0007 $_{\text{Mesocosm}}$		0.87 $_{\text{Mesocosm}}$	
N	16 $_{\text{Mescosm}}$		16 $_{\text{Mesocosm}}$	
Observations	353		353	

In the indoor tanks, I estimated the effect of no-fish, farmed and wild salmon and water temperature on final length and weight (Table 2). The farmed salmon strain was significantly longer and heavier than the wild salmon, and warmer temperature had an additive positive effect on final size (Figure 9). I did not use AIC to compare the additive and interaction model for length and weight of the indoor fish due to singular fits (appendix, A-5). Instead, I assumed that the additive model is the most parsimonious, as the interaction effect was not significant. The mixed effect models for final weight and length shows that farmed salmon was significantly heavier and longer (0.43 g and 9.47 mm bigger) than wild salmon in the cold treatment, and that the warmer temperature treatment had a significant positive effect on length and weight (0.38 g and 7.41 mm). The effects were additive. The among tank heterogeneity contributes to approximately 5% (weight) and 2% (length) of the variance in these models.

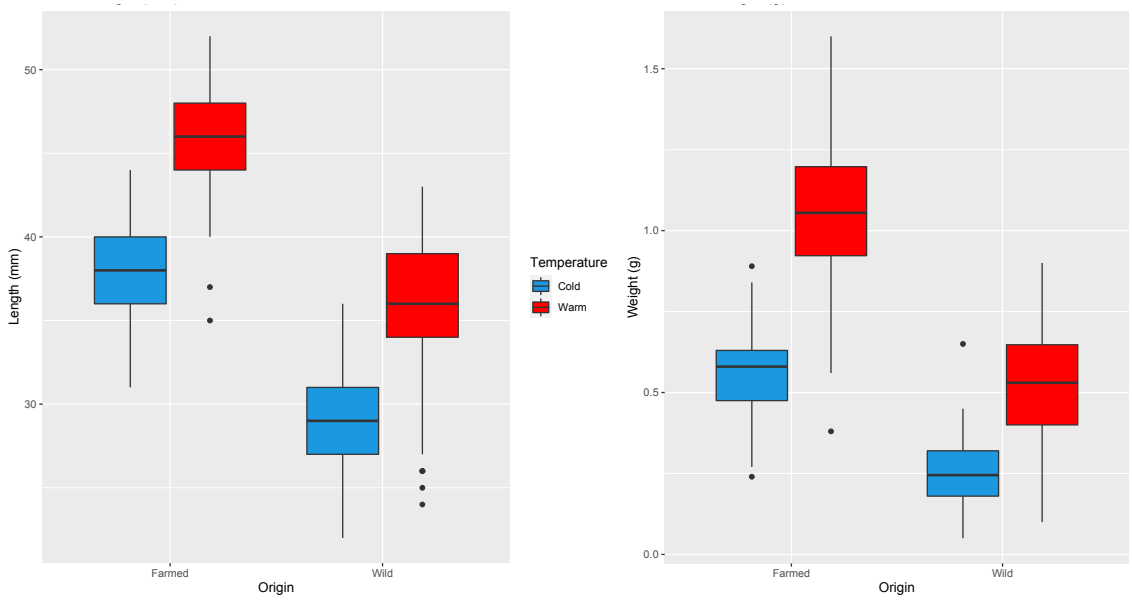

Figure 9: Box and whisker plots showing the indoor control fish length (mm) and weight (g) distribution of the wild and farmed, in cold and warm temperature regime. Upper and lower edge of the boxes represents 25th and 75thpercentiles. The vertical lines indicate the min/max value of 1.5 times the interquartile range. Dots represents outliers.

Table 2: Indoor tank: Estimates from linear mixed effect model of individual farmd and wild salmon weight (g) and length (mm) using the lme4-package function lmer to account for variation in each tank. Intercept represents the wild salmonin the cold treatment. Significant estimates are marker in bold. Predictor variables, estimates and confidence interval.

	Weigth (g)		Length (mm)	
Predictors	*Estimates*	*CI*	*Estimates*	*CI*
(Intercept)	**0.19**	**0.11 – 0.26**	**28.54**	**27.80 – 29.28**
Origin [Farmed]	**0.43**	**0.35 – 0.52**	**9.47**	**8.64 – 10.30**
Temperature [Warm]	**0.38**	**0.30 – 0.46**	**7.41**	**6.57 – 8.24**
Random Effects				
σ^2	0.025		10.14	
τ_{00}	0.005 $_{TankID}$		0.24 $_{TankID}$	
N	12 $_{TankID}$		12 $_{TankID}$	
Observations	425		425	

3.2 Ecosystem effects

3.2.1 Primary production

The total phytobenthos biomass, (µg chl a. m^2) measured on ceramiciles at T3, varied strongly from <1 to <5 µg chl a. m^2 (Figure 10). I estimated the effect of the different treatments, no fish, wild and farmed salmon, and water temperature on total phytbenthos biomass using linear models. The most parsimonious model was the additive model (appendix, table A-6). Total phytobenthos biomass at the end of the experiment (T3) did not differ between treatments (table 3). However, biomass at station B were higher than at other stations.

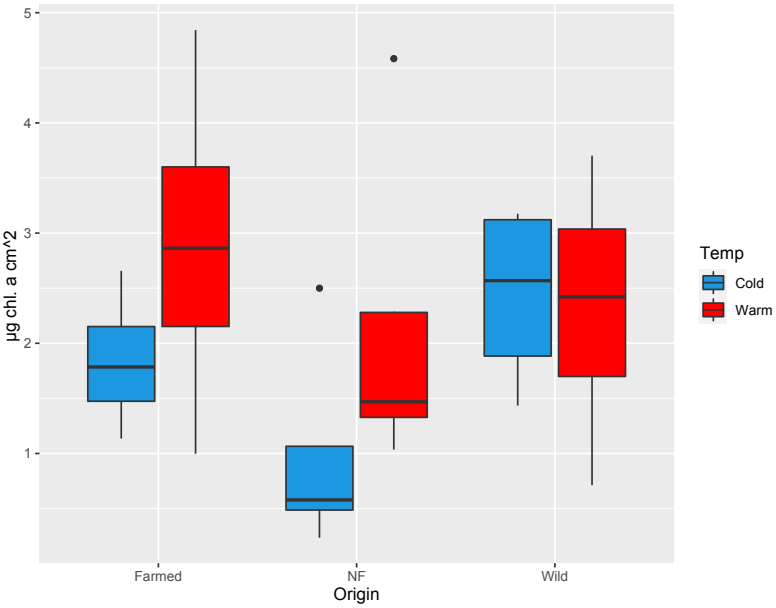

Figure 10: Box and whisker plot total phytobenthos concentrations (µg chl. a cm^{-2}) distribution at each treatment level, at the end of the experiment (T3). Farmed salmon, no-fish and wild salmon treatment at two temperature regimes. Upper and lower edge of the boxes represents 25th and 75thpercentiles. The vertical lines indicate the min/max value of 1.5 times the interquartile range. Dots represents outliers.

Table 3: Standard linear model testing if temperature regime, station B has a significant effect on phytobenthos biomass sampled at T3. Intercept represents the no fish and cold regime sampled at station A. The estimates are expressed in µg chl. a. cm^{-2}. Predictor variables, estimates and confidence interval. Significant estimates are marked in bold.

	Total concentration (µg chl. a cm^{-2})	
Predictors	*Estimates*	*CI*
(Intercept)	0.63	-0.45 – 1.70
Type [Farmed]	0.95	-0.15 – 2.05
Type [Wild]	0.43	-0.70 – 1.56
Temp [Warm]	0.47	-0.43 – 1.38
Stasjon m [B]	**1.56**	**0.42 – 2.71**
Stasjon m [C]	0.43	-0.75 – 1.61
Observations	24	

3.2.2 Decomposition rates

Decomposition rates were determined by the breakdown coefficient *k*, and is expressed per day. There was much variation in total decomposition rates across treatment levels in the coarse mesh bags sampled at the end of the experiment (T3), microbial decomposition varied less in each treatment level (Figure 11).

I estimated the treatment effects on total and microbial decomposition rates using standard linear models. The additive models were the most parsimonious models for both total and microbial decomposition (appendix, table A-7). Farmed salmon and the warmer temperature regime were found to have a significant positive effect on decomposition rate in the coarse mesh bags (Table 4). Stream mesocosms with warmer temperature regime and/or farmed salmon had a decrease in total decomposition (0.001 and 0.0008, K, day^{-1}) compared to the no-fish and cold temperature regime at station A. Decomposition rates measured at station B and C were associated with a significant increase in decomposition rates for samples at these stations. The presence of wild salmon did not have any significant effect on total decomposition in this model. Decomposition rates appears to be lowest in the most upstream section (-0.0018 day^{-1} in no fish cold treatment), while decomposition rates at station B and C were higher (-0.0012 day^{-1} and -0.011 day^{-1}).

Further, the effect of station sampled, the fish treatments (wild or farmed salmon) and warmer temperature regime had no significant effect on microbial decomposition in the most parsimonious model.

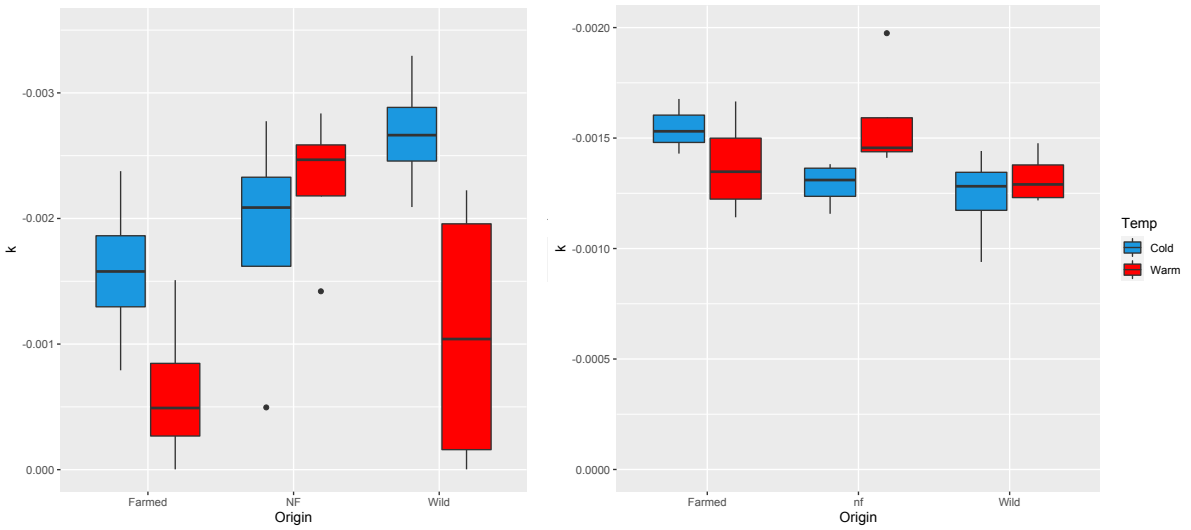

Figure 11: Total decomposition rates (left)) and microbial decomposition rates (right) (K, day^{-1}) after 35 days, at the end of the experiment (T3). Farmed salmon, no-fish and wild salmon treatment, cold and warm temperature. Upper and lower edge of the boxes represents 25th and 75thpercentiles. The vertical lines indicate the min/max value of 1.5 times the interquartile range. Dots represents outliers.

Table 4: Standard linear models estimates of total and microbial decomposition rates (K, day^{-1}). Estimate, confidence interval. Intercepts represents estimate of decomposition rate, in in the no-fish and cold temperature treatment at station A.

	Total decomposition (coarse mesh) (k)		Microbial decomposition (fine mesh) (k)	
Predictors	*Estimates*	*CI*	*Estimates*	*CI*
(Intercept)	**-0.0018**	**-0.0025 – -0.0010**	**-0.0014**	**-0.0016 – -0.0011**
Origin [Farmed]	**0.0010**	**0.0002 – 0.0017**	-0.0001	-0.0004 – 0.0002
Origin [Wild]	0.0005	-0.0003 – 0.0013	0.0002	-0.0001 – 0.0004
Temp [Warm]	**0.0008**	**0.0002 – 0.0014**	-0.0000	-0.0002 – 0.0002
Station [B]	**-0.0012**	**-0.0020 – -0.0004**	-0.0001	-0.0004 – 0.0002
Station [C]	**-0.0011**	**-0.0019 – -0.0003**	-0.0000	-0.0003 – 0.0003
Observations	24		24	

3.2.3 Community structure

A subsample of the Surber samples used for stream inoculation was analyzed to describe the initial macroinvertebrate community. About 5000 ind. m^2 was found in the 7 samples. The most abundant taxas were Chironomidae (74.9%), Elmidae (8.9%), Hydropsychidae (9.7%), Rhyacophilidae (1.9%) and Diptera (3.8%). Figure A-2 in the appendix shows the distribution of functional feeding groups of this subsample.

Macroinvertebrate density sampled in each mesocosm at T3 varied from 175 to 975 ind. m^2. The macroinvertebrate community was dominated by 4 taxa (classes) of predators (Diptera, Trichoptera, Coleoptera and Odonata) and 5 taxa (families) of primary consumers (Chironomidae, Clitellata and Elmidae) (table 5). Next, I estimated if the treatments had a positive or negative impact on the number of primary consumers and predators, and Chironomidae and Elmidae (Figure 12).

First, the effect of each treatment on the number of primary producers and predators was estimated using a generalized linear model (table 6) was estimated. Models fitted using quasi-Poisson cannot be compared using AIC, so I used additive models (appendix, table A-8).

Neither the temperature regime nor the fish regime had a significant effect on the number of primary consumers or predators (table 6).

Then I estimated the effect of each treatment level on the expected number of the most abundant taxas, Chironomidae and Elmidae (table 7). The effect of farmed salmon on the number of Chironomidae was uncertain, while the wild salmon treatment and warmer temperature had a significant negative effect on Chironomidae abundance. For the expected number of Elmidae neither fish presence nor warm temperature had a significant effect.

Table 5: Table of the relative (%) amount of Chironomidae, Elmidae, primary consumers and predators sampled from each stream mesocosm at T3, at each treatment level: no-fish, farmed and wild salmon, and cold and warm temperature regime.

Fish treatment	NF	NF	Farmed	Farmed	Wild	Wild
Temperature	Cold	Warm	Cold	Warm	Cold	Warm
Chironomidae	26.1%	32.9%	17.5%	16.3%	16.8%	16.8%
Elmidae	37.1%	26.6%	34.9%	44.8%	39.1%	40.3%
Clitellata	20.7%	37.1%	15.9%	16.7%	28.4%	34.2%
Primary consumers	95.4%	99.1%	96%	97%	98.5%	94.9%
Predators	4.6%	0.9%	4%	3%	1.5%	5.1%

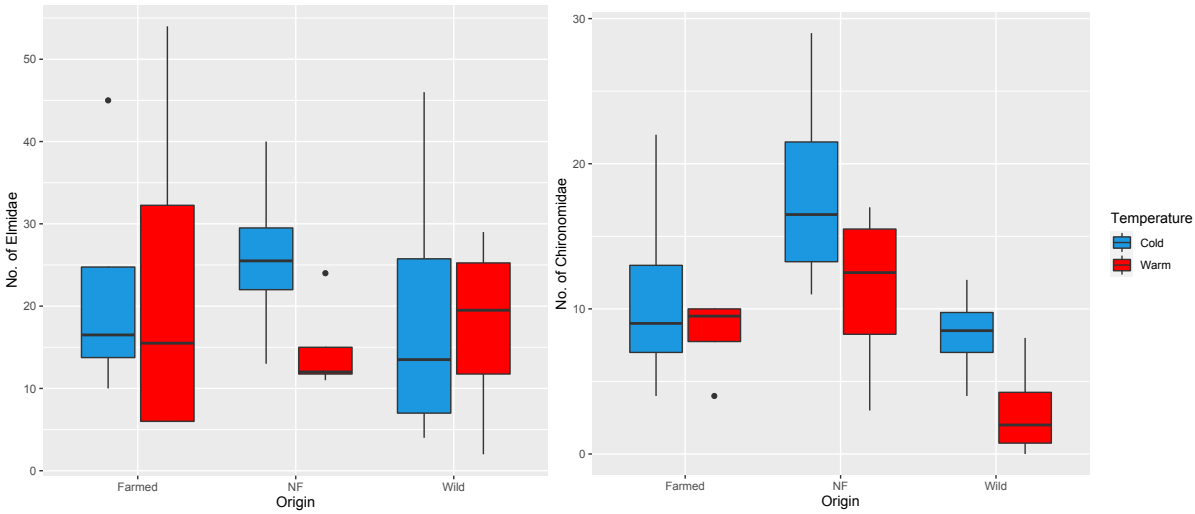

Figure 12: Box and whisker plot of the number of sampled Elmidae (left) and Chironomidae (right) at T3 at each treatment level: no-fish, farmed and wild salmon, cold and warm temperature regime. Upper and lower edge of the boxes represents 25th and 75thpercentiles. The vertical lines indicate the min/max value of 1.5 times the interquartile range. Dots represents outliers.

Table 6: Estimates of the expected number of primary consumers and predators sampled with Surber sampler, T3. Additive quassi-Poisson distributed model using GLM, log-link function. Estimates (rates) and confidence intervals. Significant estimates are in bold.

	Primary consumers		Predator	
Predictors	*Estimates*	*CI*	*Estimates*	*CI*
(Intercept)	**65.45**	**45.84 – 90.70**	**2.22**	**0.78 – 5.03**
Type [Farmed]	0.90	0.59 – 1.39	1.07	0.33 – 3.52
Type [Wild]	0.78	0.50 – 1.22	0.87	0.24 – 2.99
Temp [Warm]	0.86	0.59 – 1.23	0.69	0.25 – 1.84
Observations	24		24	

Table 7: Estimates of the expected number of Chironomidae and Elmidae sampled with Surber sampler, T3. Additive quasi-Poisson distributed model using GLM, log-link function. Estimates (rates) and confidence intervals. Significant estimates are in bold.

	Chironomidae		Elmidae	
Predictors	*Estimates*	*CI*	*Estimates*	*CI*
(Intercept)	**18.44**	**12.86 – 25.59**	**22.42**	**12.14 – 38.06**
Type [Farmed]	0.65	0.40 – 1.05	1.10	0.55 – 2.23
Type [Wild]	**0.38**	**0.21 – 0.66**	0.90	0.43 – 1.88
Temp [Warm]	**0.60**	**0.38 – 0.92**	0.82	0.45 – 1.47
Observations	24		24	

4 Discussion

In this study I estimated the ecosystem effect of first feeding farmed and wild salmon and warmer climate in a controlled semi-natural mesocosm experiment. The findings shows that there was an initial size difference between the farmed and wild strain at the start of the experiment. Both indoor and in the mesocosms, the farmed salmon was larger and temperature increased final size.

The phenotypic effect of farmed salmon and warmer temperature was studied in regards of ecosystem functioning (decomposition and primary production) and structure (macroinvertebrate community). A cascade effect through trophic levels was not evident. I hypothesized that farmed salmon through consumptive or non-consumptive effects would affect prey species and functional feeding groups. Some results are conflicting of what I initially hypothesized and is further discussed in the next sections.

4.1 Juvenile salmon size

Overall, the farmed salmon strain was significantly larger than the wild conspecific and warmer temperature increased size. At the start of the experiment there was a significant size difference between the farmed and wild salmon strain. When the experiment ended, there was a significant positive effect of warmer temperature and farmed salmon on final size. Further, the linear models shows that the size outcome was dependent of both origin and temperature, but also the experimental conditions. Farmed salmon and warmer temperature had a significant positive effect on final weight and length in the indoor tanks and in the mesocosms. However, the effect of farmed salmon and warmer temperature was larger indoor than in the mesocosm experiment. This indicates that the farmed strain performed poorer in more complex environments, which has been reported in other studies with growth hormone treated salmon, and in natural environments using farmed salmon (Fleming and Einum, 1997, Sundstrom et al. 2007, Leggatt et al., 2017, Cucherousset et al., 2021). These findings are likely the result of a trade-of between food acquisition costs and energy return as habitat complexity increases (Finstad et al., 2007, Saikkonen et al., 2011). The recapture success indicate that wild salmon had higher mortality than the farmed strain. It can also be the result of the wild strain being harder to recapture due to smaller size. However, the wild strain in cold water was smaller compared to the warmer treatment and temperature did not affect.

In the stream mesocosms, the farmed salmon was on average longer and heavier than the wild conspecific when the experiment started. The initial weight and length difference is probably due to maternal effects, as both strains were reared in hatchery conditions at similar temperatures. The linear models showed that the effect of farmed salmon and warmer temperature increased final size in the mesocosms experiment. However, the final difference in size is likely described by the initial size advantage of the farmed salmon. At the end of the experiment, the final size difference (3.49 mm and 0.07 g) was almost the same as the initial size difference, indicating that the farmed and wild strain had a relatively equal growth in the mesocosms (in absolute values). Further, the energy demands of the two strains likely differed. As farmed salmon possibly has a higher standard metabolic rate (SMR) and thereby feed more to the grow the same. Although, increased SMR in farmed salmon has not been concluded (Robertsen et al., 2020). At last, higher SMR in prey depleted environments may lead to reduced growth and survival (Vollestad and Quinn, 2003). Reduced survival was not the case for the farmed strain if recapture rates noted here translates to survival. Reduced growth was observed and could therefore indicate a higher SMR, yet this is speculative.

4.2 Ecosystem effects

Decomposition rates, community structure and phytobenthic production are impacted by abiotic and biotic factors. The impact of warmer climate and farmed salmon is first discussed in regards of ecosystem functions and then at community level, as I hypothesized farmed salmon to impact the ecosystem through a change in macroinvertebrate community.

The phenotypic effect of farmed salmon and warmer temperature was studied in regards of ecosystem functioning (decomposition and primary production) and structure (macroinvertebrate community). However, the effect on ecosystem functions was not evident. The presence of both fish treatments and warmer temperature did not have a significant effect on total phytobenthos biomass at the end of the experiment. While fish presence and warm temperature had an uncertain on microbial decomposition rates. Total decomposition rates decreased with farmed salmon present and uncertain for wild salmon. The most surprising was that warmer temperature regime decreased decomposition rates. Regarding community structure, neither treatment affected the number of primary consumers or predatory invertebrates, this finding was also the event for the taxa Elmidae (riffle beetles acquiring

food through scraping). Moreover, the number of Chironomidae decreased in presence of wild salmon and warmer temperature and the effect of farmed salmon was uncertain. These findings are further discussed here.

Phytobenthos biomass measured at T3 did not differ between the treatment levels, the estimate of biomass sampled at station B was the only certain estimate in the most parsimonious model. However, this might have occurred by chance, uneven shading or by unobserved microhabitat variation. As phytobenthos biomass is subject to scraping of macroinvertebrates, it is likely that the number of the most abundant scrapers was not affected by either treatment. The Surber samples gathered on T3 were not marked with station sampled and not included cannot be tested. One of the most abundant group of scrapers weas the taxa Elmidae (*Limnius volckmari* and *Elmis aenea)*, a family of benthic riffle beetles. Juvenile Salmonidae has been reported prey on Elmids, but the taxon is not a major part their diet at this time of year (Dineen et al., 2007, Johnson and Johnson, 2008, Johnson et al., 2017). The effects can be non-consumptive by decreased foraging activity. Although neither treatment had a certain on the number of Elmids. The confidence intervals are wide, and an effect might be concealed by much variation within treaments and little variation among treatment levels. In Kazanjian (2018) the researchers suggest that increase in biomass due to warmer temperature was counteracted by grazing in summer. Temperature increase was expected to increase phytobenthos growth (the experiment was conducted during spring) , other factors not tested here may have limited the effect of either treatments.

In the leaf-litter decomposition experiment neither fish presence or warmer temperature had a significant effect on microbial decomposition, the confidence intervals are narrow and there may be no effect. Microbial (and total) decomposition rates in this study were lower than what has been reported in another study using Gray alder leaves, in Sweden (McKie et al., 2006). As this study was conducted in a controlled semi-natural environment with UV-filtered water it is possible that nutrient conditions or other factors differs in natural streams. This is probably not likely as water was originated from lake Liavatn and was not circulated, Microbial (and total) decomposition rates are expected to increase with temperature (Irons et al., 1994). Friberg et al., (2009) reported increased breakdowns rates in fine mesh bags due to increased microbial activity. In contradiction of what is found in this study.

As Chironomidae are important prey of juvenile salmon fry. I expected that a decrease in abundance was associated with a decrease in total decomposition rates through top-down effects of wild and/or farmed salmon. The effect of farmed salmon on total decomposition rates was uncertain, while wild salmon and warmer temperature decreased total decomposition rates. This is similar to what is reported in other studies with predatory fish where decomposition rates increased (Konishi et al., 2001). A study with growth hormone treated (GH) Atlantic salmon also reported similar results as seen in this study, however; decreased decomposition rates was associated with an increase of Chironomidae (Cucherousset et al., 2021). In their study the salmon fry was larger at release and the phenotypic effect of farmed salmon was imitated by GH-implants. They found that GH treated salmon changed the density of predatory macroinvertebrates and decreased Chironomidae density through consumption. However, no effects of farmed was significant regarding macroinvertebrates in this study. In the other study, the experiment was designed in larger river channels during summer. This and larger size at release might explain the differences. Last, I suggest that warmer temperature reduced decomposition rates through earlier development and emergence of Chironomidae (Nordlie and Arthur 1981), possibly reducing shredding of leaf-litter.

Several individuals of the family Chironomidae were found inside the coarse mesh bags. The family is a diverse taxa and is classified to several functional feeding groups and have been reported to consume leaf-litter (Callisto et al., 2007). As Chironomidae are important prey of juvenile salmon fry, I expected that a decrease in Chironomidae abundance was associated with a decrease in total decomposition rates through top-down effects of wild and/or farmed salmon. However, the diverging effects of fish presence on total decomposition and Chironomidae abundance does not support this. The uncertain of farmed salmon on Chironomidae density can also be explained by preference for other, larger invertebrates. I don’t think this can be concluded as no gut-analysis was performed, and there were overall scarce and insufficient for data analysis.

The most upstream section (A) had the lowest estimate of total decomposition, while the effect at station B and C was similar and increased total decomposition rate. Although higher water flow rate may increase physical abrasion, as reported in other studies (Benfield, 1996, Fonseca et al., 2013), the water flow rate was overall low in each stream mesocosm. It is possible that water temperature increased downstream by heating of sun and thereby

increased breakdown rates. However, the effect of warmer water temperature decreased decomposition rates and contradicts this explanation.

The macroinvertebrate community before and after the experiment was analyzed and described in terms of present species and functional feeding groups. I estimated small treatment effects on the number of primary consumers, predators and Elmids. Overall, there was several zero observations of EPT-species in the mesocosms when the experiment ended. Several taxonomic families of macroinvertebrates, found in the subsample prior the experiment start date, was not recaptured at the end of the experiment. Predatory *Rhyacophiliade* and *Polycentropodidae* was nearly absent when sampled at T3. Densities of the subsample of macroinvertebrates introduced to the stream mesocosms was within the range of what have been reported in Norwegian streams (Kjaerstad et al., 2018, Cucherousset et al., 2021). Which indicates that the initial macroinvertebrate density represents Norwegian streams. At the end of the experiment, I sampled invertebrates at lower densities, indicating a reduction of density. Yet, neither fish treatments nor warm temperature had a significant effect on primary consumer or predator densities in this study. Invertebrates identified as primary consumers was primarily in the family Elmidae and Chironomidae, this likely affected the model for primary consumers. The number of predatory invertebrates presented in this study was lower than what has been reported in another study in Ims (Cucherousset et al., 2021).

The findings presented here indicates that the effect of first feeding juvenile salmon functions is overall small and uncertain in this study. As I could not establish an effect on ecosystem functions through trophic levels. First feeding wild and farmed salmon may be too small to have an effect. I view this as likely since the effects of fish presence are not consistent and does not differ much from the no-fish treatments. This was also the case for the effect of warmer temperatures. Regarding total decomposition and Chironomidae abundance, warmer temperatures reinforced the effect of either salmon treatments. There was no evident effect of either top down or bottom-up effect of warmer temperature on the ecosystem. The effect of global warming was additive in this study. Yet, a synergistic effect of biological invasion and global warming was not supported by the data.

Overall, the experiment was conducted as planned without any major incidences. The 48 hours drop in temperature in warmer treatments likely had small effects on final size of the

juvenile, as the impact on cumulative degree days is small. I designed the experiment with three sampling dates in the case of full leaf-litter consumption. In hindsight, all meshbags and tiles should have been sampled at the end of the experiment. Resulting in simpler models and more precise estimates. The variation was high, within and among replicates of treatment levels, and likely affected some of the results presented. Sampling of meshbags during the experiment, also removed some macroinvertebrates and could therefore and explain some of the results.

Intraspecific invasion of farmed salmon is likely to continue in future and the environmental impact should be studied in the context of human induced stressors. Even though the findings presented here indicates small effects after swim-up, the effect may occur later as they grow. Global warming is expected to increase temperature in Norwegian rivers and act together biological invasions (Perkins et al., 2010, Antiqueira et al., 2018). Therefore, further studies should focus on the impact of farmed salmon in a multiple-stressor approach using controlled manipulation to investigate biological interactions. The impact on ecological functions in streams needs to be further studied at different life-stages to assess the environmental risk of farmed salmon inhabiting Norwegian rivers and streams.

5 Conclusion

First, farmed salmon has a size advantage at start of first feeding, as the wild strain was significantly smaller. Both strains grew faster under warmer temperatures, leading to larger final size. The size difference between farmed and wild salmon was larger in the indoor tanks, indicating, poorer performance in more complex habitats, by comparison of final sizes in indoor tanks and semi-natural stream mesocosms. The growth outcome in the mesocosms indicates that farmed salmon grew as much as the wild strain in a semi-natural environment, and that final size differences in the stream mesocosms is due to the initial size difference.

Further, an impact of the small salmon, both wild and domesticated, on the ecosystem processes was not evident. The ecosystem effect of farmed salmon was overall small and imprecise for total decomposition rates and did not affect microbial decomposition. Estimates of microbial decomposition and phytobenthos biomass was uncertain when salmon (either strain) was present, the effect of temperature was also uncertain. The macroinvertebrate abundance was low when sampled at the end of the experiment, potentially indicating a reduction of macroinvertebrates during the experiment. The presence of salmon, wild or farmed, did not have an effect on the various functional groups and the most abundant taxa. There were also small effects of increased temperature, except for the number of Chironomids, which decreased with warmer temperature. I suggest that this is the result of earlier emergence as developmental rate increases with increasing temperature.

Last, the findings suggest small and uncertain effects of first feeding farmed salmon on key ecosystem functions at emergence and the effect of global warming did not act synergistically.

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A Appendix

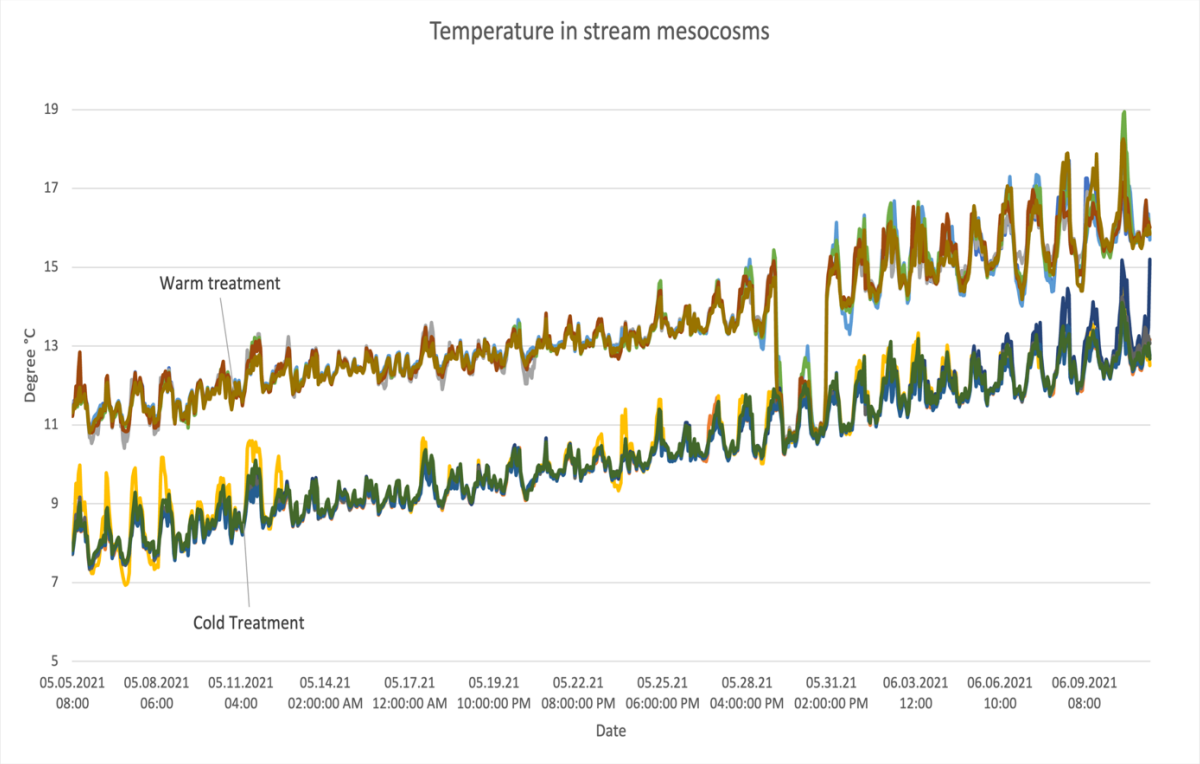

Figure A-1: Temperature (°C) plotted in all stream mesocosms outlet from 5. May 2021, 08:00 to 11. June 2021, 14:00. On 29. May 2021 a technical issue in the heating system led to a drop in water temperature in the warmer treatments and followed the cold temperature regime for approximately 48 hours. Water temperature difference was ca 3 degrees. On 5. May 202,1 the initial temperature was ca. 9 °C and 12 °C. At the end of the experiment (T3), the temperature was ca. 14 °C and 16 °C. Minimum and maximum was ca. 7 and 15 °C in cold treatment and ca 10 and 19 °C in the warm treatment.

Table A-1: Water flow rate measured on May 5. 2021. Water flow rates was measured using a 5-liter bucket. Two and two stream mesocosms share the same inlet. First, all inlets were measured. Then the stream mesocosms with high flow rates were adjusted and then stream mesocosms 17-18, 9-10, 5-6 and 1-2 was re-measured. Stream mesocosm ID (shared inlet for each pair) and liter per second (water flow rate).

Stream mesocosm ID (inlet pair)	Liter pr. second
23-24	3.08
21-22	3.54
19-20	1.48
17-18	1.58
15-16	2.4
13-14	2.9
11-12	2.28
9-10	3.72
7-8	1.88
5-6	3.52
3-4	2.1
1-2	2.92
New measurements after adjustment:	
17-18	2.76
9-10	3.02
5-6	2.98
1-2	2.52

Table A-2: Water depth in cm. The mean of two measurements upstream, downstream and midstream. Stream mesocosm ID, pstream mean (cm), midstream mean (cm) and downstream (cm).

10	Upstream mean (cm)	Midstream mean (cm)	Downstream mean (cm)
1	12.7	8.4	11.1
2	9	7.8	11.1
3	9	9.5	12.6
4	9.25	13.35	10.8
5	11	14.05	12.25
6	10	12	12
7	12.2	10.25	12.75
8	11.85	9.7	12.1
9	10.75	12.25	12.45
10	9.5	9.15	11.95
11	8.2	11	10
12	8	6.6	11.7
13	8.6	10.85	10.3
14	9.5	10	7.6
15	7.8	8.55	9.5
16	9.05	9.45	10.05
17	10.4	11.45	13.25
18	8.7	9.1	11
19	7.5	12.2	11.35
20	7.95	10.45	11.95
21	10.65	8.15	12.1
22	9.35	9.5	10.85
23	7.65	9.95	9.65
24	7.6	10	10.6

Table A-3: Number of recaptured fish from each stream mesocosm. Initially, 25 individuals were introduced in each stream that received the fish treatment, in stream mesocosm number 19, 26 ind. were recaptured. Stream mesocosm ID, number of individuals, origin and temperature.

Stream mesocosm ID	Number of individuals	Origin	Temperature
1	0	nf	Cold
2	24	Farmed	Cold
3	25	Farmed	Warm
4	0	nf	Warm
5	19	Wild	Cold
6	0	nf	Cold
7	21	Wild	Warm
8	0	nf	Warm
9	21	Farmed	Cold
10	22	Wild	Cold
11	0	nf	Warm
12	24	Farmed	Warm
13	24	Farmed	Cold
14	0	nf	Cold
15	21	Wild	Warm
16	24	Farmed	Warm
17	19	Wild	Cold
18	24	Farmed	Cold
19	26	Farmed	Warm
20	18	Wild	Warm
21	0	nf	Cold
22	22	Wild	Cold
23	0	nf	Warm

Table A-4: List of candidate models for fish length and weight recaptured from the stream mesocosms at the end of the experiment. The models are ordered. AIC value, difference to the most parsimonious model and degrees of freedom. Models were compared by maximum likelihood and made using stream mesocosm ID as a random effect. Mesocosm experiment, model structure, AICc, dAICc and degrees of freedom.

Mescosm experiment	*Model structure*	*AICc*	*dAICc*	*df*
Fish weight				
	Weight ~ Origin+Temperature+ (1| Stream mesocosm ID)	-711.2	0.0	5
	Weight ~ Origin*Temperature+ (1| Stream mesocosm ID)	-709.9	1.3	6
Fish length				
	Length ~ Origin+Temperature+ (1| Stream mesocosm ID)	1775.5	0	5
	Length ~ Origin*Temperature+ (1| Stream mesocosm ID)	1775.9	0.4	6

Table A-5: List of candidate models for indoor control fish length (mm) and weight (g) at the end of the experiment. The models are ordered. Since the interaction models were singular fit, I chose the less complex model (additive). Indoor control, odel structure.

Indoor control	*Model structure*
Fish weight	
	Weight ~ Origin+Temperature+ (1| Tank ID)
	Weight ~ Origin*Temperature+ (1| Tank ID)
Fish length	
	Length ~ Origin+Temperature+ (1| Tank ID)
	Length ~ Origin*Temperature+ (1| Tank ID)

Table A-6: List of candidate models for the total phytobenthos concentrations sampled at T3 using standard linear model. AIC value, difference to the most parsimonious model and degrees of freedom. Model structure, AICc, dAIC and degrees of freedom.

	Model structure	*AICc*	*dAIC*	*df*
Total concentration				
	Total conc. ~ (Origin + Temperature + Position)	84.0	0.0	7
	Total conc. ~ (Origin * Temperature + Position)	90.9	6.9	9

Table A-7: List of candidate models for the decomposition parameter, k $^{day1-}$ in a standard linear model. AIC value, AICc, dAIC and degrees of freedom.

	Model structure	*AICc*	*dAIC*	*df*
Coarse mesh				
	K ~ (Origin + Temperature + Position)	-264.6	0.0	7
	K ~ (Origin * Temperature + Position)	-258.2	6.4	9
Fine mesh				
	K ~ (Origin + Temperature + Position)	-284.5	0	7
	K ~ (Origin * Temperature + Position)	-281.1	3.5	9

Figure A-2: Histogram of functional feeding groups in a subsample of the Surber samples used for mesocosm inoculation on March 9. and May 5. 2021. Total area sampled: 0.78m². The samples are a subsample of all Surber samples collected for stream mesocosm inoculation. Groups: cell eater, deposit feeders, active filter feeders, passive filter feeders, grazers, others, parasites, predator, shredder, wood eater. In the subsample ca 15% were classified as predators, 25% as grazers and <3% shredders.

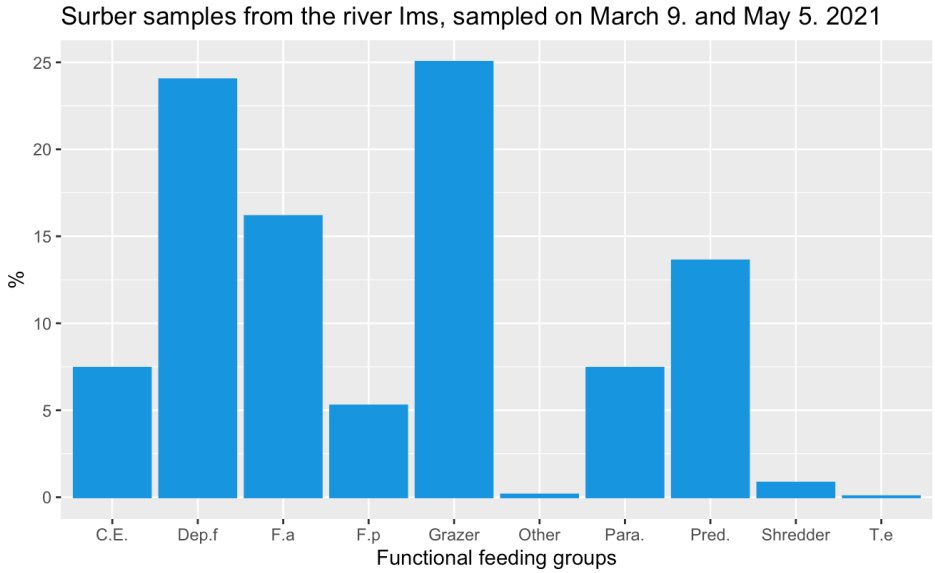

Table A-8: List of candidate models for the macroinvertebrates. All models were made with GLM using quasi-Poisson to avoid overdispersion and cannot be compared using AIC. Instead, I chose the least complex models for all response variables. Model structure.

	Model structure
Predator model	No. predators ~ (Origin + Temperature)
Primary consumer model	No. primary consumers ~ (Origin + Temperature)
Chironomidae	No. Chironomidae ~ (Origin + Temperature)
Elmidae	No. Elmidae ~ (Origin + Temperature)