

1 **The influence of fire salamander larvae (*Salamandra salamandra*) on**
2 **benthic organisms: evidence of habitat specific differences**

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30
31 **Conflict of Interest**

32 We declare no conflict of interest.

33
34 **Author Contribution**

35 CP, LS & BAC designed the study, CP, LS & JB performed the experiment in the lab,
36 CP analysed the meiofauna community, LS & CP analysed the data, CP created the
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Feeding ecology, meiofauna, habitat adaptation, feeding behavior, niche conformance

Abstract

Salamander larvae can impose a great impact on benthic organisms as they are keystone predators. Previous gut analysis revealed that their diet consists of invertebrates from the water column and benthic taxa. The impact on benthic communities, especially on meiofauna, is, however, not well understood yet, as these organisms cannot be detected reliably in the gut. To avoid this, we investigated the impact of fire salamander larvae on meiofauna by analyzing consumed prey items from a microcosm. Fire salamander larvae can be found in different habitats, such as streams and ponds. To test the impact of fire salamander larvae on the meiofauna and to test whether the effects differ in larvae from different habitats, we collected 20 larvae from both, ponds and streams from the wild and transferred them to the lab. We placed each larva individually into a microcosm with sediment and benthic organisms. We also added control samples without larvae. We kept the larvae either for one week or two weeks and counted the number of nematodes, oligochaetes and rotifers after we removed the larvae. Fire salamander larvae significantly reduced the meiofauna. Furthermore, fire salamander larvae show habitat specific differences, as nematodes were influenced more strongly by pond larvae during the first week. Oligochaetes were mainly influenced by stream larvae, but not by pond larvae, independent of the duration of the experiment. Rotifers were influenced by larvae from both habitats, but only during the first week and not during the second week. Our findings suggest that fire salamander larvae are able to reduce the meiofauna through predation. Furthermore, our finding indicates an adaptation towards the different environmental conditions in the habitat of origin.

Introduction

Salamander larvae are keystone predators in fish-free waters such as temporal ponds or headwater streams (Davic & Welsh, 2004) . The results of numerous studies on the gut contents indicate that their diet includes invertebrates from the water column as well as benthic taxa such as insect larvae (e.g., Chaoboridae, Culicidae and Chironomidae), crustaceans (e.g., Copepoda, Cladocera and Isopoda) and oligochaetes (Cecala et al., 2007; Benoy, 2008; Regester et al., 2008; Reinhardt et al., 2013; Trice et al., 2015) . In addition, cannibalism has been observed (Hoffman & Pfennig, 1999; Wildy et al., 2001) . Fire salamander larvae

can occur in different habitats and food composition of pond and stream larvae can differ greatly (Brophy & Pauley, 1997) . By exerting top-down pressure, salamander larvae can significantly reduce the abundance of certain planktic and macrobenthic taxa in lentic systems (Holomuzki et al., 1994; Benoy, 2008; Regester et al., 2008) , which in turn may have indirect effects on other species of the community (Morin, 1981; Wissinger et al., 1999) . Furthermore, the ingestion of aquatic insect larvae regulates the number of hatching insects and thus also affects surrounding terrestrial habitats (Regester et al., 2008; Reinhardt et al., 2013; Reinhardt et al., 2017) .

With increasing larval development and body size, the prey spectrum also increases, which is often explained by the larger mouth size and thus the ability to handle larger prey (Dodson & Dodson, 1971; Petranksa, 1984; Cecala et al., 2007) .

Bell (1975) studied the feeding habits of newt larvae and attributed this change in food intake to a shift from ambush predation to more active hunting behavior during the course of larval development. Although it is assumed that diet composition largely reflects the composition of prey in the habitat (Deban & Wake, 2000) and corresponding seasonal changes (Brophy & Pauley, 1997) , there are studies that indicate specialized hunting by salamander larvae (Dodson & Dodson, 1971; Takagi & Miyashita, 2019; Struecker et al., 2021) , such as a preference for slower prey. However, the trophic impact of salamander larvae on endobenthic organisms, especially meiofauna like oligochaetes, nematodes or microcrustaceans (benthic organisms that pass through a sieve with 500 μm meshes and are retained by a 20 μm sieve, according to Ptatscheck et al., 2020b), is not yet fully understood and studies from lotic habitats are largely absent (but see Bletz et al., 2016). However, meiofauna is found in high abundances (sometimes > one million ind. m^{-2}) in headwater streams or ponds (Bert et al., 2007; Majdi et al., 2017; Rebecchi et al., 2020) and represents a standing stock of food resources for larger organisms like macroinvertebrates or juvenile fish, but cannot be reliably detected by gut analysis due to their rapid digestion (Ptatscheck et al., 2020a; Ptatscheck, 2021) .

All salamander larvae are suction feeder creating a water inflow by opening their mouths and expanding the buccal cavity to ingest prey organisms at close range (reviewed by Deban & Wake, 2000). The water is then released outwards through the gill slits. Gut analysis of *Desmognathus aeneus* larvae revealed a 16% proportion of detritus in the digestive tract (Donovan & Folkerts, 1972) , showing that the feeding process is not just prey ingestion. At the same time, however, high densities of endobenthic meiofauna, such as nematodes or microcrustaceans were

found in the gut (Brophy, 1980; Brophy & Pauley, 1997; Trice et al., 2015) , whose uptake cannot be explained by selective uptake from the sediment surface or by accidental bycatch alone. Rather, this indicates that sediments could also be ingested directly, and the small prey could be filtered out. In fact, the larvae of several salamander taxa, such as fire salamander (*Salamandra salamandra*) possess gill rakers, spiny protrusions on the gill arches that allow them to retain food particles in the oral cavity (Stadtmüller, 1924; Stebbins & Cohen, 1995; Deban & Wake, 2000) . These structures are already present in embryos and their number on the gill arches and size continue to increase during larval development before being reduced during metamorphosis (Stadtmüller, 1924) . Similar morphological structures also enable bottom-biting fish like carps or gudgeons to effectively filter small organisms from the sediment and affect their abundance, biomass and diversity through strong top-down pressure (Ptatscheck et al., 2020a; Ptatscheck, 2021) .

In our study we investigate the impact of fire salamander larvae on benthic communities, focusing on meiofauna. Fire salamander females deposit fully developed juveniles in both headwater streams as well as in ponds (Weitere et al., 2004; Sabino-Pinto et al., 2019) . In contrast to lotic habitats, ponds are characterized by periodic desiccations, higher temperatures, lower oxygen levels, higher predation risk (e.g., by newts or water beetles) and lower prey availability for salamander larvae (Weitere et al., 2018) . As an adaptation to these unfavorable living conditions, the larvae have a higher birth weight, develop a more pronounced gill system and metamorphose earlier than their relatives in streams (Weitere et al., 2004; Sabino-Pinto et al., 2019; Caspers et al., 2015) . Oswald et al. (2020) showed a more pronounced shelter-seeking behavior for pond larvae and Krause et al. (2011) found larvae reared under poor nutritional conditions to also seek shelter more often than larvae reared under rich nutritional conditions.

In order to investigate the influence of these habitat-related characteristics on the feeding behavior, we perform standardized laboratory experiments in microcosms with both pond and stream larvae. These microcosms were filled with natural sediment, containing a whole benthic community and one salamander larvae was added. After one and two weeks, respectively, the composition, abundance and biomass of the benthic organisms were examined. The identical starting conditions enable us to optimally assess and compare the influence of the respective larvae. Following our preregistration (Ptatscheck et al., 2023) , we assumed that (1) fire salamander larvae reduce the abundance and biomass of benthic invertebrates in

the experimental microcosms through predation. However, (2) this top-down effect will be stronger in treatments with pond larvae because they are adapted to use the few available food resources more efficiently in order to be able to leave their temporary habitat as early as possible. Thus, (2a) they will consume even small organisms like nematodes, while (2b) their stream relatives will consume mainly larger oligochaetes. Additionally, we expected that (3) pond larvae will be less active while foraging, as they are less risk-prone and again, are able to use food resources more efficiently.

Methods

Organisms

The salamander larvae investigated in this experiment originate from populations that colonize headwater streams and temporal ponds (mostly water filled bomb craters) in the Kottenforst, a forest area southwest of Bonn (Germany, N 50°40'50.6748, E 7°7'23.1204). In the spring of 2023, we collected 25 stream and 23 pond larvae of approximately the same size (3.0 - 3.5 cm body length) and took them to the lab for further examination. We collected larvae from two ponds (13 and 10 larvae) and two streams (13 and 12) to avoid any location specific effect (e.g. sibling effect). We were not able to find more larvae of the same size in the two ponds. Larvae that were physically impaired were excluded from this experiment. The larvae were kept individually in microcosms (see below) filled with stream water (from a different location, see below) at a water temperature of 15°C and a light cycle of 12:12 h for one week to acclimate to the laboratory conditions. During this time, the larvae were not fed to achieve a higher trophic effect during the experiments.

Water, sediment and containing benthic organisms were collected from the Johannisbach, a second order headwater in Bielefeld (Germany). Furthermore, we transferred sediment and water to buckets, mixed and filtered the supernatant through a 10 µm sieve, and added the retained material to the sediment already collected (similar to Wulfes et al., 2024). This increases the abundance of benthic organisms. We stored the collected material in a plastic box (60 x 40 cm floor area, 3 cm sediment height), covered with stream water, aerated by air stones and also acclimatized to the laboratory conditions for a week (see above).

Study Design

Before the start of the experiment, the sediment was thoroughly homogenized in a single box. Then we filled the Plexiglas microcosms (10 x 10 x 6 cm) each with 1.5 cm of sediment, which in turn is covered with 3 cm of stream water. We placed one pond larva (LP) in each of the 20 microcosms and one stream larva (LS) in each of the other 20 microcosms (Figure 1). The other larvae (5 from streams and 3 from ponds) served as a reserve to compensate for any losses. We assigned the larvae within the treatment groups (LP, LS) randomly to the microcosms. 20 of the remaining microcosms did not contain larvae and served as control treatments (C). After one week, we sampled 30 microcosms (10 per treatment + 10 controls). Therefore, we placed the larvae, if any, back in their aquarium and transferred the sediment and water to 500 ml PE bottles. The remaining microcosms were treated in the same way after week two (Figure 1). Once a group of larvae left the experiment, we transferred them back to their original habitat in the Kottenforst. Before and after the experiment, we measured the total body length of each larvae and the gill filament length by using a camera and ImageJ.

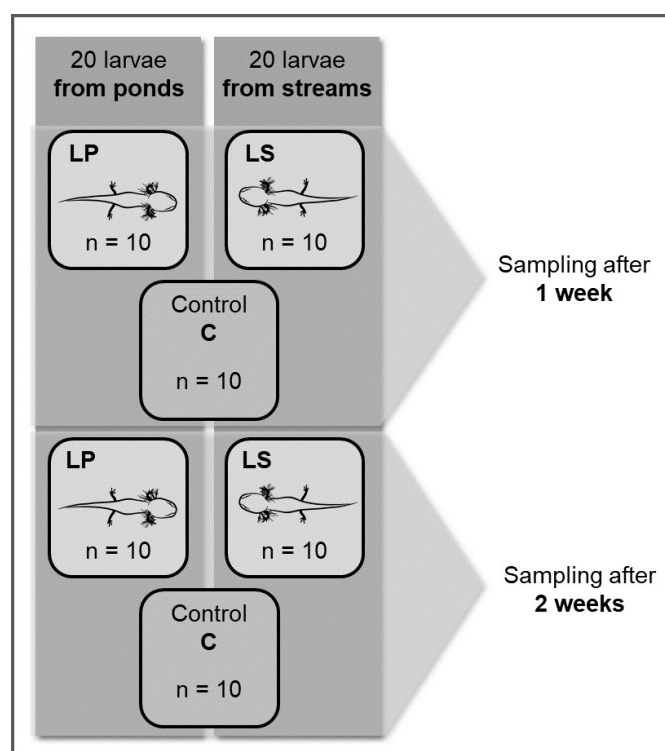


Figure 1: Experimental design. 20 fire salamander larvae (*Salamandra salamandra*) from each habitat type (pond, stream) were placed into individual microcosms filled with sediment and benthic organisms. After one week, 30 microcosms (10 with larvae from ponds, LP, 10 with larvae from streams, LS, and 10 controls, C) were sampled. After another week, the remaining 30 microcosms were sampled.

During the experiment, we also recorded the daytime movement of the larvae with video cameras that were installed above the microcosms. Due to technical difficulties, we could only analyse the records from daytime. We measured the time that the larva was active and inactive and the distance the larva traveled within its microcosm using the software AnimalTA (Chiara & Kim, 2023) Version 2.3.1.

Sample processing and counting of organisms

We stained all samples with Rose Bengal and preserved them in 4% formaldehyde. The benthic organisms were extracted from the sediment by centrifugation (LUDOX TM 50, 1.14 g ml⁻¹, mesh size 10 µm) as described by Pfannkuche & Thiel (1988) and counted in gridded Petri dishes under a Leica S6E stereomicroscope at 45x magnification. Furthermore, we divided all macro- and meiobenthic organisms into taxon-specific size classes to calculate the respective biomass (dry weight) according to (Brüchner-Hüttemann et al., 2020) .

Statistical analysis

We investigated differences in the benthos abundance, biomass and nematodes size classes of the treatments for the first and the second week using a Kruskal-Wallis test and if needed Kruskal MC as post hoc test. Likewise, we calculated differences in the biomass in the first and the second week. To test for differences between the sampling times, we calculated the percentage change in abundance or biomass and used a Mann-Whitney-U test.

For the analysis of the video data, we used a linear mixed effect model (LMM) with the R packages lme4 (Bates et al., 2015) . First, we used the Shapiro Wilk test to test for normality and variance test to test for homogeneity of variance. In case normality of the data is not given, we used the bestNormalize package. We used proportion of time moving or average speed or distance travelled as the dependent variable, habitat type (pond, stream), size and week (week 1, week 2) as well as the interaction between week and habitat type as fixed factor and ID as random factor. All tests were performed using R (version 4.3.2, 2023-10-31). We set the significance level to $\alpha=0.05$.

Results

After week one, we counted on average 1118 metazoans (± 298 , SD) in the control treatments, while the density was slightly lower at the end of week two (833 ± 309 ind.) (Figure 2a & 2c). However, with the exception of rotifers (which were less abundant in week two), we found no significant differences in the abundances of any identified taxon between the controls of week one and week two (Figure 3b). The total organismal biomass in the controls was $1002.6 \mu\text{g}$ ($\pm 447\mu\text{g}$, SD) and $1093 \mu\text{g}$ ($\pm 695 \mu\text{g}$, SD) (Figure 2b & 2d). Nematodes (65.3% and 73.9%) and rotifers (31.6% and 22.1%) predominated the benthic communities in the controls at both sampling times. Oligochaetes (1.9% and 2.7%) as well as chironomid larvae ($< 1\%$ each) represented only a small fraction. In contrast, chironomids (42.2% and 37.2%), oligochaetes (30.8% and 38.3%), but also nematodes (25.5% and 20.3%), made up the major part of the organismal biomass at both sampling times, while the dry weight of the rotifers was low ($< 0.4\%$ at both sampling times). A list of all collected organisms can be found in the supplementary information (Table S1 & S2).

Impact of fire salamander on the benthic community

Already after week one, we observed a significant decrease in total abundance and biomass of benthic taxa in both larval treatments compared to the controls (Figure 2a & 2b). The abundance and biomass of benthic species in the treatments with stream larvae decreased significantly between weeks 1 and 2, while there was only a slight decrease after week 1 in both parameters in the microcosms with pond larvae (Figure 2c & 2d). At the end of the two-week study, the reduction in abundance averaged 81.7% ($\pm 6.8\%$, SD) in microcosms with stream larvae and 76.6% ($\pm 13.4\%$, SD) in the presents of pond larvae. The total biomass decreased by 72.5% ($\pm 14.3\%$, SD) and 49.7% ($\pm 25.3\%$, SD). Overall, we found no significant difference in the total percentage decline of abundance or biomass between both treatments after two weeks (Tables S1 & S2).

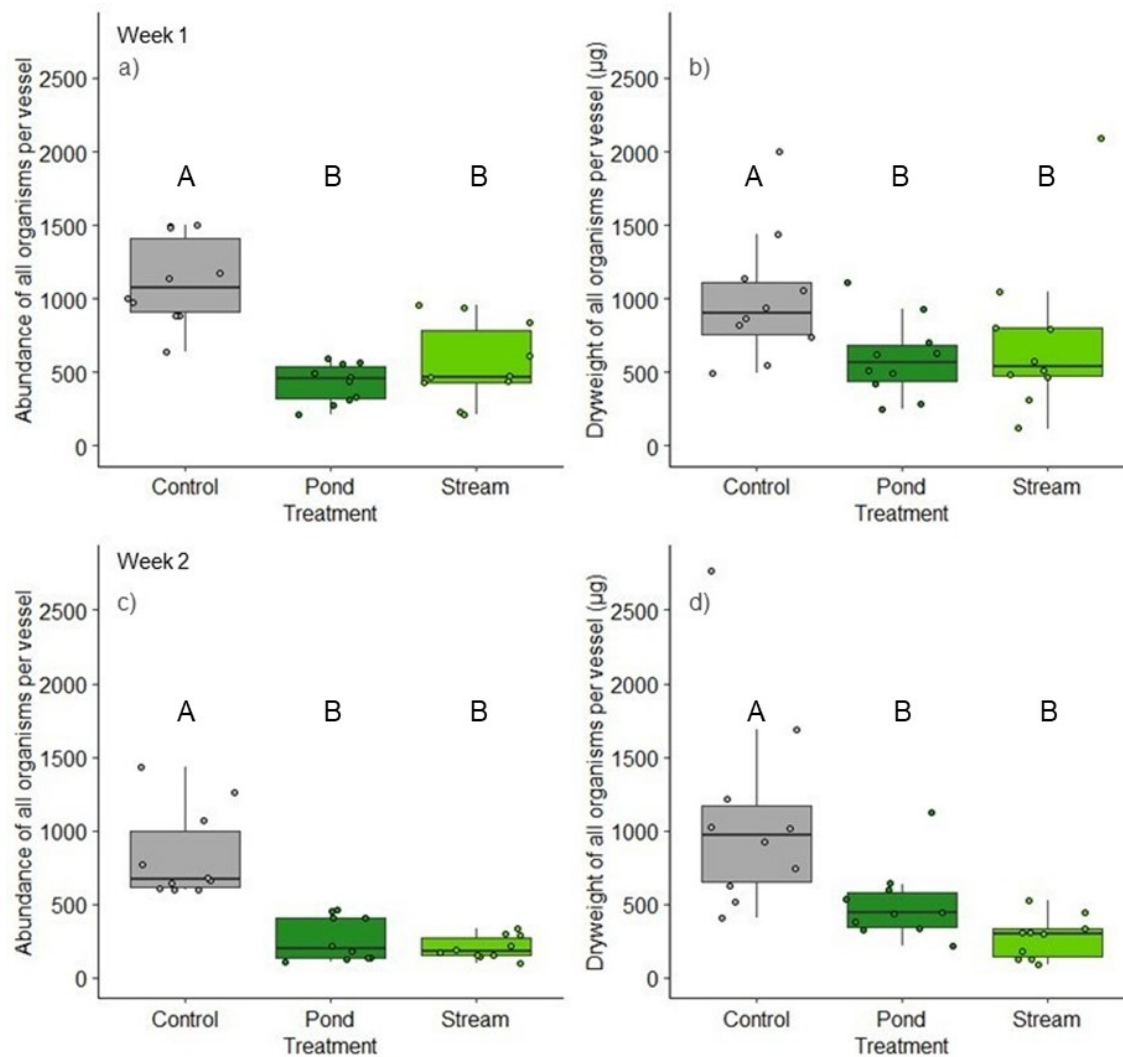


Figure 2: Abundance (left; a & c) and µg dry weight (right; b & d) of all benthic organisms per microcosm for week 1 (top; a & b) and week 2 (bottom; c & d). Boxplots show the upper (75%) and lower (25%) quartiles and the median (horizontal line) for the ten replicates (shown as dots) from the controls and the larval treatments with stream or pond larvae. Different letters above plots indicate significant differences ($p < 0.05$).

The temporal- and treatment-based effect varied between the taxa found, particularly in the nematodes, oligochaetes and rotifers (Figure 3). Nematodes abundance in the treatments with pond larvae showed a significant difference from the control ($p < 0.05$), resulting in a mean reduction of $61.4\% (\pm 13.4\%, \text{SD})$ after the first week and an only slightly higher reduction of $77.3\% (\pm 12.4\%, \text{SD})$ after week two (Figure 3a). In case of Nematodes exposed to stream larvae, there was only a significant ($p < 0.05$) decrease in abundance after two weeks (mean reduction of $80.4\% \pm 13.4\%, \text{SD}$). The abundance of oligochaetes (Figure 3c) was significantly lower than in the controls at both sampling times, but only in the treatments with stream larvae. Here, the mean abundance decreased by $57.2\% (\pm$

28.5%, SD) and 55.2% ($\pm 12.4\%$, SD). In contrast to these results, rotifers (Figure 3b) were similarly affected in both larval treatments. They showed significant lower abundances ($p < 0.05$) after the first week with a mean reduction of 64.9% ($\pm 23.2\%$, SD) in the presence of stream larvae and 65.3% ($\pm 15.1\%$, SD) in microcosms with pond larvae. This effect was no longer detectable at the end of the experiment.

In connection with these abundance reductions, we did not observe any effects on specific size classes, such as the decline of large individuals. All size classes were reduced in proportion to their occurrence. Observed effects on the biomass of the different taxa are largely parallel to the described changes in abundance.

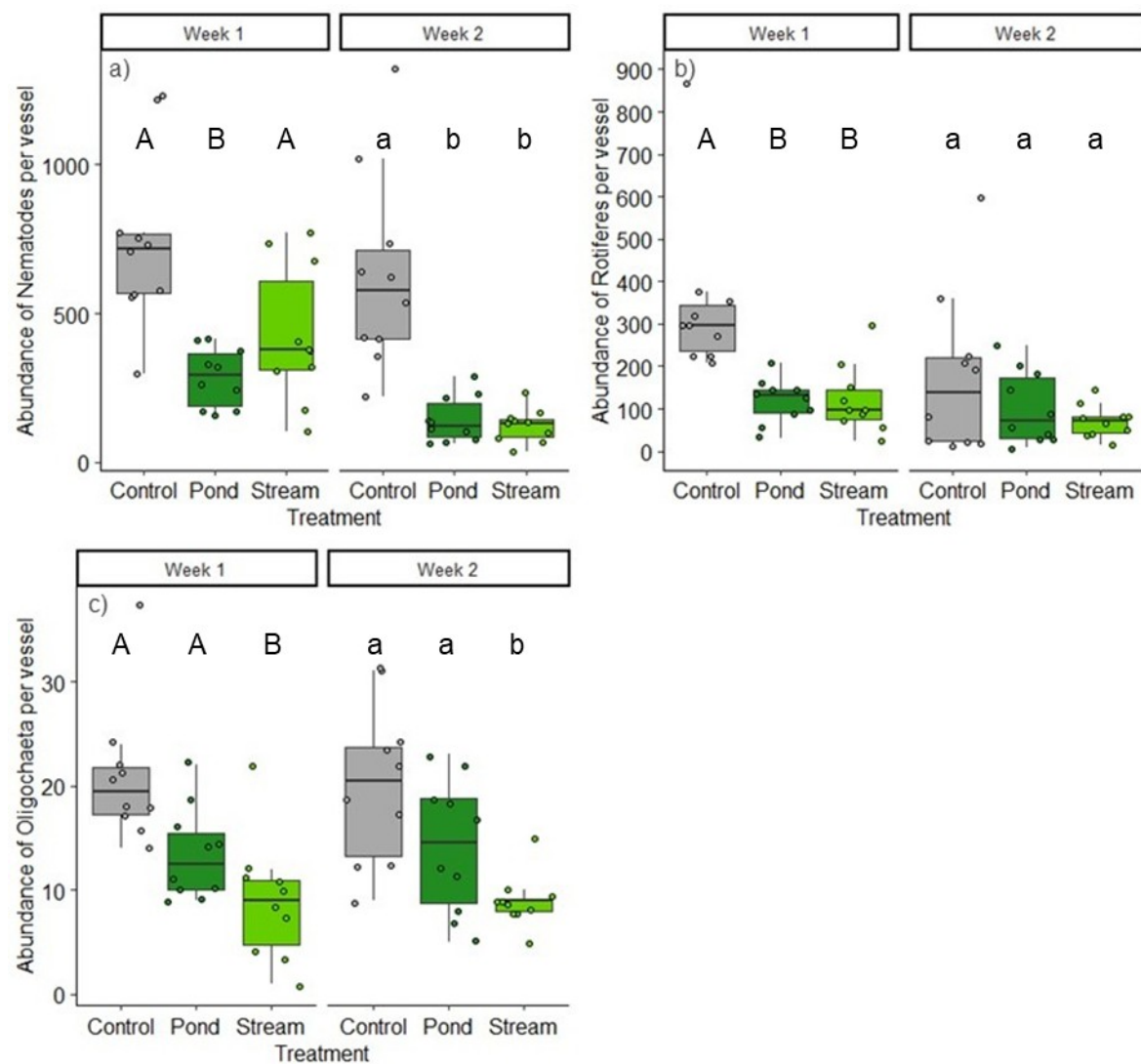


Figure 3: Abundance of nematodes (a), rotifers (b) and oligochaetes (c) per microcosm for week 1 (top) and week 2 (bottom). Boxplots show the upper (75%) and lower (25%) quartiles and the median (horizontal line) for the ten replicates (shown as dots) from the

controls and the treatments with pond or stream larvae. Different letters above plots indicate significant differences ($p < 0.05$; we tested not between the weeks).

Larval body measurements and activity

While the body and gill filament length of the stream larvae didn't change during the course of the study, the size of the pond larvae increased slightly but significantly ($p = 0.01$) after 2 weeks by an average of 1 mm (± 0.08 mm, SD). Additionally, we observed a significant ($p = 0.01$) reduction in the gill filament length of the pond larvae after just one week. The length of the gill filaments decreased by 1.2 mm (± 0.04 mm, SD). When analyzing the larval average speed, their traveled distance and the proportion of time moving, we found a significant interaction between the treatments and the sampling time. All three factors showed consistent values for both larval types after the first week (Figure 4). However, at the second sampling time all values were significant lower ($p < 0.05$) for larvae from streams than from their pond equivalents.

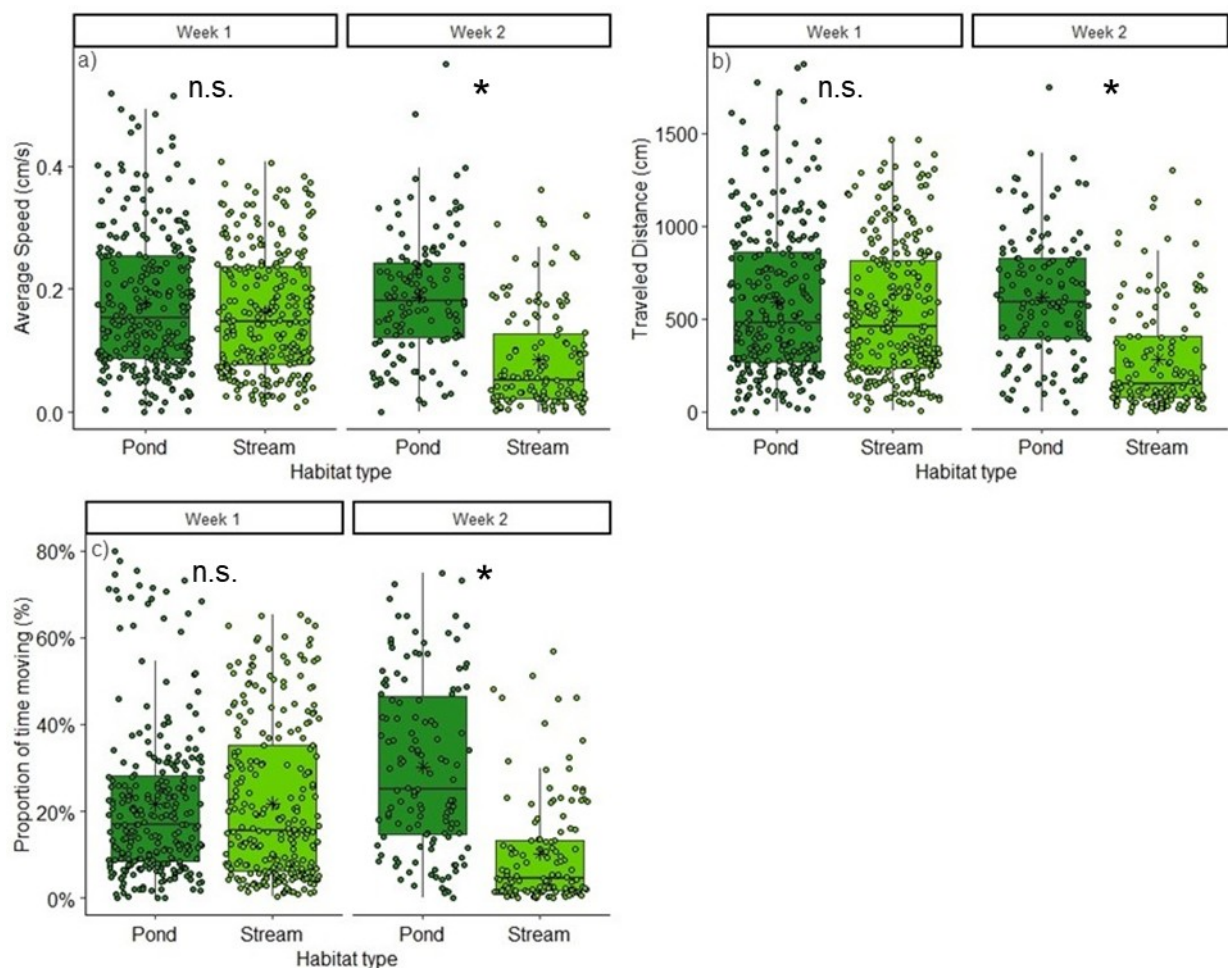


Figure 4: Daytime measurement of average speed (cm/s) (a), traveled distance (cm) (b) and proportion of time moving (%) (c) of the salamander larvae from stream and pond treatments during the first and second week. Boxplots show the upper (75%) and lower (25%) quartiles and the median (horizontal line) while the dots indicate the 260 (week 1) and 130 (week 2) replicates. n.s. = tested pairs not significant, * = $p < 0.05$.

Discussion

Fire salamander larvae can exert a strong impact on meiofaunal and macrofaunal communities. According to our initial assumption (1) in treatments with larvae, the abundance and biomass of the benthic taxa was reduced within one week, especially those of nematodes, rotifers and oligochaetes. Another key finding is the different influence of the two larval types. Contrary to our initial assumption (2), the overall effect on abundance and biomass was similar in both larval treatments. However, in treatments with pond larvae, the abundance of meiofaunal nematodes and rotifers was significantly reduced, whereas stream larvae additionally affected the oligochaetes. Both findings are in line with our hypotheses 2a and 2b. Even though the videos do not show the larval feeding, as we filmed them from above, we assume a trophic interaction, as significantly fewer organisms were found in the sediment in the presence of the larvae compared to the controls. Another potential factor influencing the meiofauna could be chemical or physical effects (e.g., due to substances induced by the larvae, or mechanical disturbance of the sediment). However, in such a scenario, we would expect to find more organismic residues such as body parts of oligochaetes or the cuticle of nematodes. Nevertheless, we will also discuss these factors below.

After just one week, the abundance of benthos in the 100 cm² test microcosms was reduced by over 50% by pond and stream larvae, with body sizes ranging from 3-3.5 cm. At the end of the 14-day study period, the decrease was over 75%. For comparison, Spieth et al. (2011) and Weber & Traunspurger (2014) implemented laboratory experiments with juvenile carps and gudgeons and documented strong effects on the benthic communities. While carps of 9-12 cm body length reduced the abundance by 52% in 2 days, gudgeons (5-7 cm) had a similar effect after 24 h. Both species particularly influenced nematodes and oligochaetes, while unlike in our study, no effect on rotifers was documented. Even though they are consumed as food in aquaculture (Fernández-Reiriz et al., 1993), rotifers do not seem to be influenced by fish and macrobenthic taxa in sediment under natural conditions (reviewed by Ptatscheck et al., 2020a; Ptatscheck,

2021). Therefore, our results, which show an effect at least after the first 7 days, are surprising. Rotifers have a short generation time compared to other benthic organisms, react quickly to environmental influences, and therefore generally exhibit strongly fluctuating population dynamics (Ricci & Balsamo, 2000; Wallace, 2002; Giere, 2009) . This is also evident in their reduced abundances in the control treatments after 2 weeks. Benthic rotifers and nematodes are typical endobenthic organisms rarely entering the water column. Limnic oligochaetes on the other hand, for example from the taxon tubificids, often protrude from the sediment and can serve as prey for visually hunting predators. The individuals we found in the experimental setups mostly had body lengths of over 3 mm, larger than the nematodes (mainly < 1.25 mm) or the rotifers (< 0.25 mm). In lotic waters, oligochaetes represent a significant portion of the food for a salamander larva, alongside various epibenthic organisms like gammarids (Costa et al., 2017) . In temporary ponds, oligochaetes are rare and chironomids, terrestrial insects or residents of the water column like coleopterans and copepods dominates the larval diet (Reinhardt et al., 2013) . Hence, stream larvae are probably already habituated to hunt on oligochaetes which explains the stream, but not pond effect in both weeks. Hoover et al. (2024) already showed that learning behavior of fire salamander larvae affects their foraging strategy. Generally, hunting for prey mostly occurs near the bottom of the aquatic habitat (reviewed by Sánchez-Hernández, 2020).

The intake of endobenthic organisms requires that the sediment is stirred up and the prey is retained by morphologic structures or feeding behavior. The influences of such mechanical sediment reworking and trophic effects are often difficult to separate from each other. Salamander larvae are typically classified as lurking suction feeders (Deban & Wake, 2000; Sanderson & Kupferberg, 1999) , but more active hunting strategies were observed in the absence of light (Hoover et al., 2024) . To the best of our knowledge, there are no studies documenting the process of sediment uptake. Although we were also unable to detect such behavior through the overhead camera footage, clear traces of mechanical deposits such as pits were visible. Palmer (1988) and Schratzberger & Warwick (1999) demonstrated that the mechanical disturbance caused by crabs or fish have a strong impact on meiofauna organisms. In both studies nematodes exhibit a particular sensitivity to the modification of the sediment structure. At the same time, the activity of larger organisms can also lead to the transfer of endobenthic organisms into the water column (Wulfes et al., 2024) , potentially making them targets for predators. It has also been demonstrated in larval salamanders that

certain macrobenthic taxa are more frequently found in the water column in their presence (Oberrisser & Waringer, 2011) . In this context, however, the effect of chemical interactions cannot be ruled out. Studies with newts have shown that the released neurotoxin tetrodotoxin decreases the mobility of benthic macroinvertebrates and affected predator-prey interactions (Gall et al., 2011; Bucciarelli & Kats, 2015) . Regarding fire salamanders, it is generally assumed that toxic alkaloids are mainly restricted to adults. However, these substances have also been detected in prometamorphosis stages and occasionally in young larvae (Reviewed by Lüddecke et al., 2018).

Gut analysis in previous studies clearly revealed that small endobenthic organisms < 1 mm are ingested by salamander larvae (Brophy, 1980; Brophy & Pauley, 1997; Trice et al., 2015) . Since the larvae we examined showed no signs of impending metamorphosis, we assume that their gill rakers were not yet regressed, allowing for the filtration of small prey organisms. The stronger development of gill filaments in the pond larvae may possibly lead to the assumption that the same applies to the remaining gill apparatus. This could be an explanation for the more pronounced decrease in nematodes in the first half of the study, when pond larvae were present. The unselective reduction across all size classes also suggests feeding through filtration. If the larvae were selectively and visually feeding, a stronger effect would have been expected on larger prey organisms. At the same time, the oligochaetes in the treatment with pond larvae were not significantly reduced, while the stream larvae themselves had a reducing impact on the nematodes from the second week of the study. Thus, our results cannot be solely explained by the morphology of the gill apparatus but rather by specific behavioral traits and preferences. As already mentioned above, oligochaetes are a primary food source for stream-dwelling salamander larvae. Therefore, it seems likely that this prey was reduced first before the much smaller and less rewarding nematodes were consumed from the stream larvae. Larvae from temporary ponds, on the other hand, are faced with a significantly lower food supply and rely on consuming all available prey. The consistent high activity of the pond larvae also is in line with such a foraging strategy. Our initial expectation (H3) of higher activity among the stream larvae was not confirmed. The sediment and water used in the study were sourced from a headwater stream and contained no chemical components from predators such as newts, which in ponds, are a reason for reduced activity in fire salamander larvae (Hahn et al., 2023) . Unfortunately, our data cannot be used to determine whether activity was lower at night. At the end of the 14-day study period, the salamander larvae in both treatments reduced the biomass of the

benthos to a similar extent. But we only found length growth in the larvae from the temporary ponds. These larvae may be able to utilize the consumed energy more effectively, which corresponds to their life strategy of starting metamorphosis early before the water dries up. Additionally, the gill lengths decreased, indicating a higher oxygen content in the experimental containers compared to the original habitats. Such restructuring of the gill structures within a few days has already been observed by Bond (1960) and Segev et al. (2019) and perhaps allows the larvae to invest the degraded biomass in length growth.

Based on the assumption that small endobenthic organisms were not selective and visually hunted but that the gill apparatus plays an important role as a filter organ, further clarification (e.g., film records) of the feeding process is needed. Similar to bottom-feeding fish, water drawn into the mouth area of salamander larvae is pushed out through the gill slits, while food particles are retained in the gill apparatus. The number and size of gill rakers, and thus the mesh size of this gill net, can vary greatly among different fish species (Spieth et al., 2011). Additionally, this filtering process is optimized by complex back-flushing of ingested particles, the morphology of the mouth area (e.g., the clamp-like bone structure and the muscular palatal organ) and numerous taste buds to detect suitable food (Sibbing, 1988; Sibbing & Nagelkerke, 2000). Chemical food recognition also plays an important role in fire salamander larvae (Hoover et al., 2024). However, whether the filtering behavior of salamander larvae, with their relatively rigid jaw morphology (Sanderson & Kupferberg, 1999; Deban & Wake, 2000), is as effective as in fish and even capable of retaining rotifers has not yet been investigated.

While the dietary spectrum of salamander larvae has already been described by numerous authors, our study shows the significant effect such predation can have on the benthic community, even on small meiofaunal organisms. Within just a few days, their abundances and biomass were greatly reduced. Due to adaptations to their habitat, this trophic impact differed between larvae from ponds and streams, as did their activity. Overall, larval feeding is still poorly understood, and an important subsequent step is to investigate the results of our microcosm study under field conditions and, for example, over the course of the year. Furthermore, for a more precise interpretation of our results, detailed information about the development of gill rakers in fire salamander larvae from ponds or streams would be crucial, which should be the aim of further studies.

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