

LARVAL DEVELOPMENT AND HABITAT USAGE OF STREAM-BREEDING FIRE SALAMANDERS IN AN URBAN ENVIRONMENT

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Urbanisation adversely affects the abiotic and biotic characteristics of watercourses, including freshwater streams that support the development of stream-breeding salamanders. We conducted a study over four years on an isolated fire salamander population inhabiting a stream valley northwest of Budapest, Hungary. Our aim was to understand aspects of larval development and habitat usage within this population. The maximum number of larvae was observed in April and the first weeks of May. Due to drifting caused by heavy rainfall, there was a mean decrease of 63.3% in the number of larvae. The abundance of larval salamanders within 16 stream segments showed strong temporal and spatial variation, and there was a strong relationship between larval abundance and the % cover of fine gravel substrate. Some of the larvae could escape drift by entering pools with slower water flow and shelter. Larvae were predominantly solitary in smaller pools but occasionally aggregated in high numbers in some segments. The first larvae with yellow spots (indicative of metamorphosis) appeared in June, and by early September, all larvae were metamorphosing. Our results show that in this urbanised environment, larval development through to metamorphosis is occurring, but increasing urbanisation and alterations to stream flow threaten the persistence of the local population.

Key words: aggregation, drifting, larval density, metamorphosis, stream habitat, *Salamandra salamandra*, urbanisation.

INTRODUCTION

Many amphibian species, including urodeles breed in streams where the impact of agriculture, forestry and expanding urbanisation has been well documented (WILSON & DORCAS 2003a, PRICE *et al.* 2006, MILLER *et al.* 2007). Stream-breeding amphibians are under increasing pressure from habitat loss, fragmentation, isolation, and degradation of habitat quality caused by urbanisation (HAMER & McDONNELL 2008), and salamander communities in urban catchments have been observed to decrease in diversity and density

(BARRETT *et al.* 2010a). Urbanisation has a strong effect on the physical and biological conditions of streams (PAUL & MEYER 2001, WALSH *et al.* 2005, BARRETT & GUYER 2008). BARRETT *et al.* (2010a) showed that increased spate (i.e. high water flow) frequency and poor water quality as a result of urbanisation can substantially decrease salamander densities in urban streams. Climate change and inappropriate water management interventions, especially in hilly and montane streams, may also lead to the periodic drying out of streams, which can eliminate breeding habitats and reduce the chances of successful larval development through to metamorphosis. In several salamander species, survivorship appears to be low during the larval phase (BARRETT *et al.* 2010a). The food sources of salamander larvae, such as macroinvertebrate communities, can be severely depleted in urban streams due to water pollution and high water flows (WALSH *et al.* 2001). Conversely, however, urbanisation can have apparently positive effects on some species, such as the two-lined salamander (*Eurycea cirrigera*) (BARRETT *et al.* 2010b), largely due to increased growth rates arising from increased water temperature and decreased intraspecific competition in the urban streams examined.

The dispersal of organisms in lentic water can occur almost freely in three-dimensional space, whereas in lotic water movement, it is mainly restricted to the longitudinal direction via drifting with the stream current (REINHARDT *et al.* 2018). Three types of drift can be distinguished: random, behavioural and catastrophic (NAMAN *et al.* 2016, VEITH *et al.* 2019). To avoid predators, salamander larvae hide under stones and other covered objects and are mostly inactive during the day (PETRANKA 1983). In catastrophic drift, an organism is carried away by an unusually strong current (e.g. as a result of heavy rainfall) and drifts downstream (ARNOLD 1983, THIESMEIER 1992, REINHARDT *et al.* 2018). Urban streams often have flows with greater magnitude and frequency during rain events (BARRETT *et al.* 2010a). These stormflows can cause long-term changes in water quality, exert stress on stream communities, and often lead to shifts in community assemblages and decreased abundance of salamanders (WILLSON & DORCAS 2003, BARRETT *et al.* 2010a).

Drift is a risky dispersal strategy because individuals may become more conspicuous to predators, or may be unable to re-enter previously occupied habitat, potentially resulting in mortality (REINHARDT *et al.* 2018). Drift may have a major impact on larval population dynamics, leading to the restructuring of populations, and favouring species that have evolved specific strategies for drift compensation or avoidance (VEITH *et al.* 2019). The effect of drift on larval populations of fire salamanders has been previously demonstrated (e.g. ARNOLD 1983, THIESMEIER & SCHUHMACHER 1990, BAUMGARTNER *et al.* 1999). Drift compensation is an active behavioural process. Upstream movements of organisms are usually the result of positive rheotaxis, which allows them to hold their position in streams rather than drifting downstream (VEITH *et al.*

2019). Salamander larvae have not developed specific morphological features (e.g. enlarged oral discs or belly suckers that are present in some lotic anuran larvae) as an adaptation to the water current (ALTIG & McDIARMID 1999, VEITH *et al.* 2019). Modification of body shape (moderately flattened and elongated body shape, lower body and dorsal tail fins) is the primary evolutionary option salamanders possess to withstand drift (e.g. GRIFFITHS 1996, THIESMEIER 2004). Small urodela larvae are more prone to drift (BRUCE 1985), while up- and downstream movements of various distances and with different water velocities have been documented for several species (JOHNSON & WALLACE 2005, LOWE 2008, CECALA *et al.* 2009). In a near-natural experiment, SCHAFFT *et al.* (2022) found that upstream movements of fire salamander larvae did not exceed more than 30 cm.

The fire salamander (*Salamandra salamandra*) is a widespread amphibian in Central, Eastern and Southern Europe and is larviparous in Central Europe. Females deposit fully developed larvae mainly into permanent streams between March and May (VEITH 1996). Fire salamanders have been shown to use alternative breeding and larval feeding sites, such as small ponds, ephemeral ponds in addition to streams (THIESMEIER 2004, WEITERE *et al.* 2004, EITAM *et al.* 2005, REINHARDT *et al.* 2013, CASPERS *et al.* 2015, KRAUSE & CASPERS 2015). THIESMEIER & SCHUHMACHER (1990) stated that the rate of larval drift fluctuated between 19% and 41% in a stream. Larvae of the fire salamander are typically stream-dwelling sit-and-wait predators (THIESMEIER & SCHUHMACHER 1990, MANENTI *et al.* 2013), often aggregating in pools along streams with better conditions for ambushing prey (THIESMEIER & SOMMERHÄUSER 1995, BAUMGARTNER *et al.* 1999). Larvae complete metamorphosis within 3–5 months, depending on temperature and nutrition (THIESMEIER 2004, THIESMEIER & GROSSENBACHER 2004, KRAUSE *et al.* 2011). REBELO & LECLAIR (2003) found that dissimilar-sized larvae at deposition attained metamorphosis at different times, but there was no difference in body size. After metamorphosis, the fire salamander is entirely terrestrial, with only females visiting the stream to deposit larvae in early spring (VEITH *et al.* 2019).

In Hungary, the distribution of the fire salamander is restricted to the Northern Middle Range and to western Transdanubia (VÖRÖS *et al.* 2010). Population declines have occurred in many areas, but in the absence of detailed studies, it is difficult to estimate the extent of the decrease (VÖRÖS *et al.* 2015). The unusually small number of Hungarian studies deal mostly with empirical reviews of distribution, morphological characteristics, life cycle (e.g. SZABÓ 1959, DELY 1967), population structure and dynamics of adult fire salamanders (e.g. KISS *et al.* 2021, 2022). Only one study has examined the effect of density on fire salamander larval development (CSILLÉRY & LENGYEL 2003).

A geographically as well as genetically isolated population (Vörös *et al.* 2016) occurs in an urbanised catchment within the Buda Hills northwest of

Budapest, where a short, forested stream provides suitable habitats for fire salamander larvae and adults (Kiss *et al.* 2021, 2022). We conducted a six-year study on this local population (see Kiss *et al.* 2021, 2022), during which we conducted larval surveys over four years.

Our main aim here was to understand aspects of larval development of the fire salamander population in this urbanised stream. We sought to determine: (1) the temporal and spatial patterns of change in larval number, density and spatial distribution from larval deposition to metamorphosis in successive years; (2) environmental characteristics of stream segments and their effect on larval abundance; (3) the effect of drift on the spatial and temporal variation in salamander larval abundance and aggregation.

MATERIAL AND METHODS

Survey area

An isolated fire salamander population inhabits a 7.3-ha area at the northwest border of Budapest (Hungary) in the Buda-Hill region close to the east side of “Hűvös-ér” stream. This stream catchment collects the groundwater of the surrounding, mainly urbanised area. The stream valley flowing through a patch of oak-hornbeam forest is partly surrounded by buildings and roads (see map in Kiss *et al.* 2021, 2022).

Stream characteristics

The “Hűvös-ér” stream emerges from a stormwater pipe near the edge of houses of the stream valley in a short stretch of paved bed and then meanders through the forest in a natural channel about 500 metres long (Fig. 1). The course of the channel bed changes slightly from year to year due to the erosive effect of water, especially after sudden heavy rainfall. A silt trap was built in the middle section, above which the stream spreads out widely. The final ~130 m section of the 630 m long “Hűvös-ér” stream flows outside of the forest cover, as a concrete-bottomed watercourse alongside a busy two-lane road, before joining the longer “Paprikás” stream. The occurrence of metamorphosed fire salamanders in the vicinity of the “Paprikás” stream was only recently determined, but whether they drifted as larvae from the “Hűvös-ér” stream or were migrating terrestrial individuals is unknown. The average inclination of the “Hűvös-ér” stream is approx. 1.87° (235–215 m a.s.l.). No predatory fish have been recorded in the stream. With the exception of rainfall events, the stream is slow-flowing and generally unpolluted, free from human influence. The average water depth of the stream ranged between 10–15 cm, but reached 20–30 cm within smaller pools. The maximum water depth was 50–60 cm. The numerous small pools provide low-velocity aquatic microhabitats for larvae. There are several water steps along the length of the stream, after which the water velocity accelerates slightly, but decelerates closer to pool segments. During the spring period, when larvae were deposited, water temperature ranged between 8–10°C. The estimated availability of macrozoobenthos food sources (especially gammarids, water louses, different insect larvae and worms) is likely to be sufficiently high to sustain larval development (FORRÓ, L. and MURÁNYI, D. unpublished data). Invertebrates that have the potential to eat or injure salamander larvae occur in the stream in low densities, e.g. water scorpions (*Nepa cinerea*).

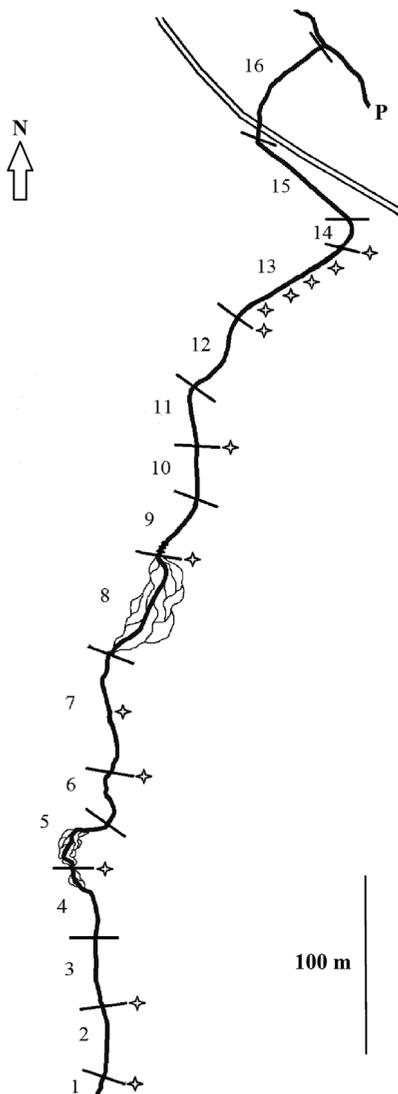


Fig. 1. Segments of “Húvös-ér” stream, where *Salamandra salamandra* larvae were surveyed. (Numbers indicate individual stream segments, bold meandering line = main branch of the stream, thin branching line = tributaries of the stream, straight lines = segment boundaries, four-pointed stars at segment boundaries and in the stream bed = water steps, double line = main road between Budapest and Solymár, P = “Paprikás”-stream)

The stream was divided into 16 segments (Fig. 1), each with varying environmental features: segment length and area, stream width, number of pools, presence of riffles, streambed substrate, slope (based on metres above sea level at the start and at the end of the stream transect), and presence of steep water-steps. Stream substrate composition was estimated visually in each stream segment and recorded as the percentage cover of stream bottom covered by stones, fine gravel, sand, mud, tree roots/woody debris, garbage (i.e. artificial debris) or concrete.

Larval sampling

Surveys for salamander larvae were conducted every 10 days (17 surveys in 2011, 18 in 2012, 17 in 2013, 20 in 2014) in the evening from March–April to September 2011–2014. The 72 sample occasions were classified into three decades of months (1–10, 11–20, 21–31). Visual encounter surveys (HEYER *et al.* 1994) started after dusk at 20 or 21 hours, depending on the season and time of sunset. After dusk, the larvae emerged from hiding places and were detected with torch light and were not captured or marked. We recorded the EOV coordinates of larvae with Meridian Golds (2011–2012) and later (2013–2014) with Garmin eTrex 30 devices. Geographical coordinates were assigned either to separate individuals or to a group of larvae aggregating to within 1 m. However, care was taken to avoid double counting individuals. For instance, the surveys commenced at the downstream end and observers moved slowly upstream, where possible, along the banks of the stream so as to prevent the stirring of sediment that might otherwise reduce the visibility through the water column. Furthermore, larvae moved only several centimetres at most when exposed to light, and salamander larvae generally do not move towards disturbance and typically move to retreats near the point of observation (HUTTON *et al.* 2020). We recorded the developmental stage of each sighted individ-

ual: larvae with yellow spots on the dorsum with or without external gills were considered to be metamorphosing individuals, whereas individuals coloured grey-black with external gills were designated as non-metamorphosing larvae.

Data processing and statistical analyses

The data was organised and processed in MS Excel (MICROSOFT CORPORATION 2018). A total of 14 780 larvae were recorded over the four years. Altogether 3848 EOVS geographical coordinates of larval occurrences were used for analysis. The location of the larvae in the 16 segments of the stream was sorted and plotted using the QGIS 3.16.3 program (QGIS DEVELOPMENT TEAM 2020).

We used a N-mixture model to estimate the mean number of larvae each year, and to assess potential relationships between abundance in the 16 stream segments and the physical characteristics of the stream. Models were constructed according to the formulation of ROYLE (2004), ROYLE *et al.* (2005) and WENGER and FREEMAN (2008), as implemented by MACKLEEM *et al.* (2020) to estimate salamander abundance in urban streams. True but imperfectly observed abundance ($N_{i,t}$) was modelled as a Poisson distribution of $\lambda_{i,t}$, which was calculated as a log-linear function of the following covariates: (1) stream segment area; (2) distance downstream of a stream segment; (3) mean slope of a stream segment (a proxy for stream velocity); and (4) the principal component scores from a principal component analysis (PCA) of stream substrate composition. Component scores from the first PC axis were subsequently used as site values for this covariate in the modelling. A random effects term for overdispersion and unexplained variation in abundance among sites (ϵ_i) was included in the models, which also accounted for the spatial non-independence of stream segments. Four models were constructed, each consisting of a single covariate due to the small sample size.

The probability of detection was modelled as a logit-link function in each model of the number of days that had elapsed between a survey occasion and the start of the breeding season (1 February each year; days). A quadratic term for days was also included to account for a potential peak in the detectability of larvae in the middle of the season (days²). All covariates were standardised as z scores (mean = 0; SD = 1). Observed abundance $y_{i,t}$ was modelled as a Poisson random variable. Because the 16 stream segments were repeatedly surveyed over four years, we accounted for potential temporal dependence in abundance by including an auto-logistic term (ϕ ; ROYLE & DORAZIO 2008), which specified the correlation between $z_{i,j,t}$ and $z_{i,j,t+1}$ (see MACKLEEM *et al.* 2020).

The mean and standard deviation of the model coefficients derived from the four models are presented, and the 2.5th and 97.5th percentiles of the posterior distribution, which represents a 95% Bayesian credible interval (BCI). Parameter estimates of covariates with a BCI that did not overlap zero were clearly important, whereas estimates with a BCI overlapping zero had greater uncertainty and considered to be less important. The most influential covariate on mean larval abundance was the one with the highest beta coefficient and clearest BCI. Modelling was performed using the software program JAGS (version 4.3.0, PLUMMER 2017) called via the R2jags package (SU & YAJIMA 2015) from program R (version 4.1.2, R Core Team 2019). Each model was run using three replicate Markov chain Monte Carlo (MCMC) iterations to generate 300 000 samples from the posterior distribution of each model after discarding a 'burn-in' of 50 000 samples, with a thinning rate of 5. Convergence of the Markov chains was checked by visual inspection of trace plots and the Brooks-Gelman-Rubin statistic (\hat{R}); acceptable convergence was achieved when $\hat{R} < 1.05$

(BROOKS & GELMAN 1998, GELMAN & RUBIN 1992). To improve model convergence, original survey data ($n = 72$) were truncated to exclude seven surveys in which no larvae were detected (typically surveys at the start or end of a season).

RESULTS

Patterns of larval abundance, aggregation and metamorphosis

The deposition of larvae was triggered by early spring rains in the middle of March (2014), the beginning of April (2012) and the middle of April (2011 and 2013) (Fig. 2). Larval deposition ceased within a few weeks, however in 2012 deposition extended to the beginning of May. The pattern of changes in the number of larvae were very similar in successive years. The maximum number of larvae in 2011 ($n = 502$) and 2012 ($n = 499$) was observed in the first decade of May, while in 2013 ($n = 505$) in the third decade of April and 2014 ($n = 775$) in the first decade of April (Fig. 2).

The rainy spring period typical in Hungary from May to the beginning of June caused a drastic drifting of larvae (Fig. 2). From the end of April to the beginning of May, the annual average 10-day cumulative rainfall rose almost continuously, with each year and each decade often receiving 50–100% more rainfall per day than the four-year average. Considering the size of the watershed, this resulted in the occasional release of considerable amounts of water into streams, significantly increasing streamflow. The number of larvae decreased but stabilised in June and the first decade of July. Taking into account

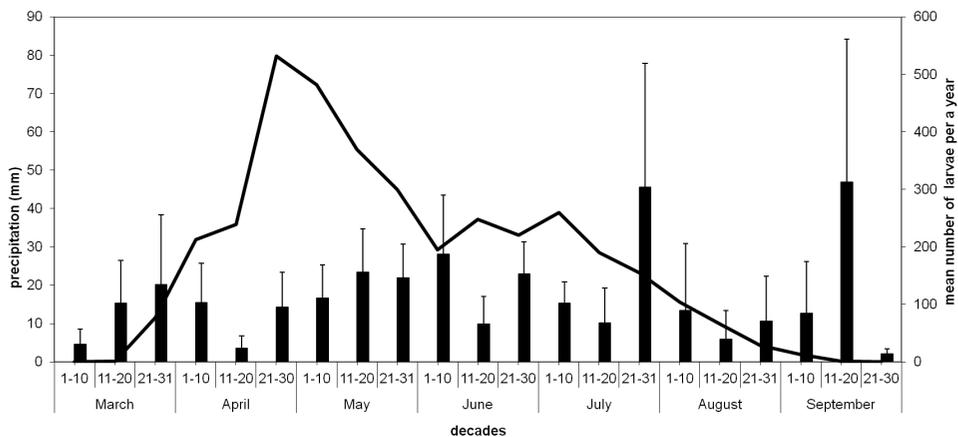


Fig. 2. Changes in the number of salamander larvae and rainfall. The bold black continuous line shows the mean number of salamander larvae detected during the surveys in the three 10 day intervals of months in Húvös-ér stream, 2011–2014. The bar graph shows the mean amount (and SD) of precipitation (mm) during the three 10-day intervals of months

the highest and lowest values of the total number of larvae observed in the last decade of April and the first decade of June over the four years, there was a 63.3% decrease in the number of larvae. Taking the same decades and analysing each year separately, the rate of decline varied – it was highest in 2011 (80.6%) and 2014 (80.2%), while much lower in 2012 (37.1%) and 2013 (46.1%). The number of larvae due to the onset of metamorphosis and the heavy rains gradually decreased from the beginning of July, and the last metamorphosing specimens were found in the beginning of September (2011, 2012, 2014) or the middle of September (2013).

Depending on the date of larval deposition, the first indicators of metamorphosis (yellow spots on the larval dorsum) appeared in June. During this early phase of metamorphosis larvae have well-developed external gills. Approximately four weeks later, in July, the yellow colouration is brighter and the gills have gradually reduced. A few days after the disappearance of gills, the larvae can leave the water and start terrestrial life. Larval development through to metamorphosis takes four weeks and ceases by the middle of September. By late August/early September, 63–67% of all larvae observed were metamorphosing.

A total of 3856 sampling points were available to assess the aggregation behaviour of larvae. On 1122 occasions, larvae were observed as solitary individuals. The number of co-occurrences of multiple larvae decreased exponentially, e.g. 5 individuals occurred together only 244 times, 10 individuals 42 times, and 20 individuals only 8 times. Aggregations of larger numbers were rarely observed, mostly only after heavy rainfall in deeper pools (especially in segment 9). There were no substantial differences in aggregation size between 2012, 2013 and 2014.

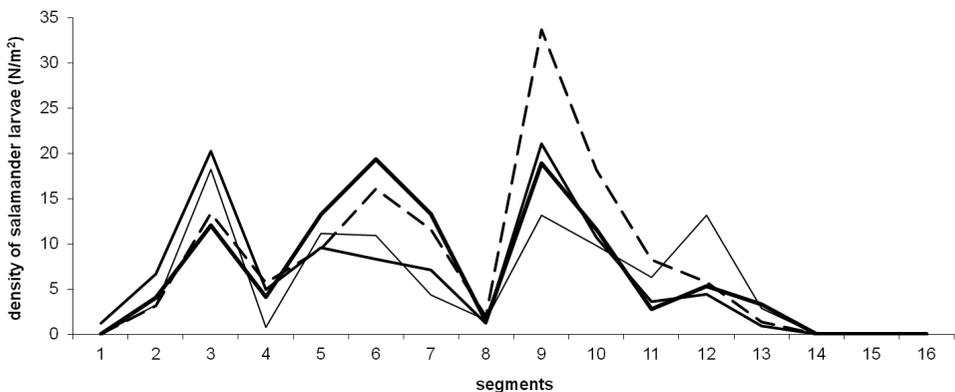


Fig. 3. Mean density of salamander larvae (number of larvae/m²) detected in the 16 segments during surveys every 10 days in "Húvös-ér" stream, 2011–2014 (2011: thin line, 2012: medium line, 2013: bold line, 2014: dashed line)

The dispersion pattern of larvae and the drift effect

In segment 1, salamander larvae were present only during one sampling occasion in 2012. In segments 2–13, larvae were found during at least half of the sampling occasions. There was a fairly continuous increase in larval density from segment 2 to 8–9 each year, followed by a decrease in segments 10–13 (except in 2011; Fig. 3). The highest larval densities were recorded in segments 2, 3, 5, 7, 8 and 9 while lower densities were recorded in segments 4, 6, 10 and 13. We detected no larvae in segments 14, 15, 16 situated downstream close to the road and in the concrete section of the stream.

The relative abundance of salamander larvae was influenced by the different environmental conditions of each stream segment. The first axis (PC 1) from the stream substrate PCA explained 32.2% of the variation among the seven variables, with % fine gravel (positive factor loading) and % concrete (negative factor loading) most strongly correlated with this axis (Fig. 4).

There was a strong positive relationship between estimated mean abundance and PC1 ($\lambda = 1.376$, 95% BCI: 0.562–2.290; Table 1). There was also support for the effect of segment area on abundance but with a slight overlap

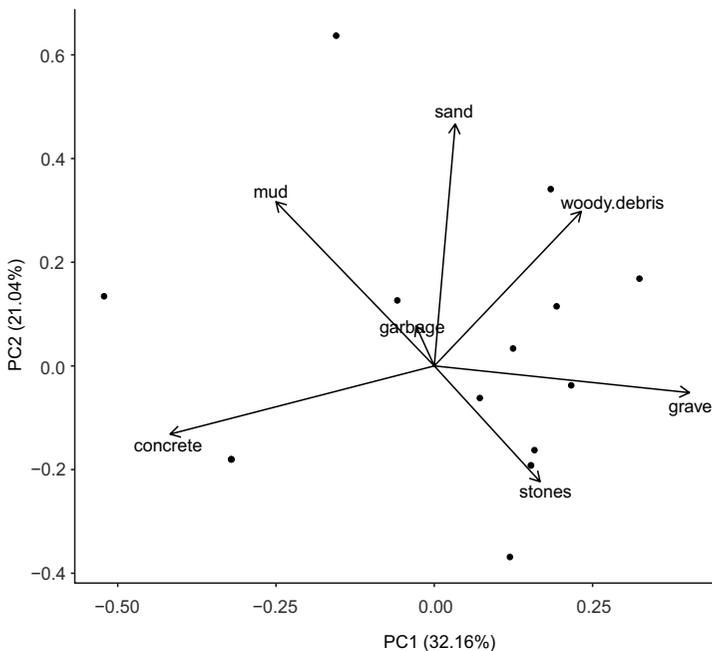


Fig. 4. Principal components analysis of stream substrate composition at 16 stream segments, “Hűvös-ér” stream. PC1 described a gradient from stream segments with a high % cover of fine gravel to segments with a high % cover of concrete. PC2 described a gradient from segments with a high % cover of sand to segments with a high cover of stones

Table 1. Summary of parameters for abundance (λ) and detection (p) of the larvae of *Salamandra salamandra*. Estimates include 95% Bayesian credible intervals (BCI: 2.5th and 97.5th percentiles). Clear relationships for parameters are where the 95% BCI does not overlap zero. SD = standard deviation. PC1 = principal components scores from stream substrate PCA; Area = stream segment area; Distance = stream segment distance down-stream from top of stream; Slope = mean slope of stream; Days = days since 1 February; Days² = quadratic effect of Days.

Model	Parameter	Covariates	Mean	SD	2.5th	97.5th
1	λ	PC1	1.376	0.443	0.562	2.29
2	λ	Area	0.718	0.459	-0.106	1.679
3	λ	Distance	0.224	0.336	-0.417	0.908
4	λ	Slope	-0.019	0.364	-0.730	0.709
1	p	Days	0.294	9.902	-19.121	19.777
1	p	Days ²	8.129	6.002	0.444	22.560

of the 95% BCI with zero ($\lambda = 0.718$, 95% BCI: -0.106–1.679; Table 1). Stream substrate composition, therefore, had the strongest effect on larval abundance over the four years of surveys, with the highest larval abundance in segments containing a high % substrate cover of fine gravel and the lowest abundance in segments with a concrete streambed.

There was a strong positive relationship between the probability of individual detection and a quadratic effect of the number of days ($p = 8.129$, 95% BCI: 0.444–22.560; Table 1), indicating a sharp peak in detectability mid-season. Estimates of the auto-logistic parameter suggested that abundance in

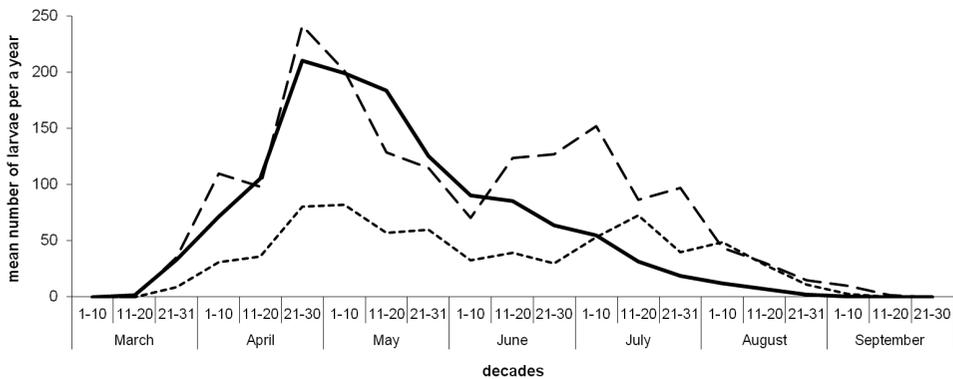


Fig. 5. Mean number of salamander larvae detected per a year in the “releasing” 2–6 upper segments (continuous bold line), in the “strong collector” middle segments: 7–9 (dashed line) and the “weak collector” lower segments: 10–13 (dotted line) during surveys every 10 days in “Hűvös-ér” stream between 2011–2014. Data from segment 1 have not been plotted because larvae were present at only one time point

a particular year was positively related to abundance in the previous year ($\varphi = 1.840$, 95% BCI: 0.310–3.516).

Mean abundance across all years was estimated at 55.3 salamander larvae per stream segment (95% BCI: 4.2–437.8).

Larval drift from the upper to the lower segments of the stream was sudden and continuous from the end of April until May (Fig. 2). Water steps were at a height that larvae could not traverse to move to the upper reaches, so a decline in larval numbers in the upper reaches of the stream was a continuous pattern. Two main types of segments could be distinguished according to their larval holding capacity. In the “releasing segments” larvae were discharged due to heavy rains, and their numbers decreased rapidly at first, but then stabilised. In the “collecting segments”, the accumulation of larvae for shorter or longer periods was observed after the heavy rains. The upper, releasing segments (2–6) retained larvae that were present before the spring storms, but later on the observed number of larvae gradually decreased over the study period (Fig. 5). The middle segments and some lower segments of the stream were able to retain some of the downstream drifting larvae, in varying numbers in June and July. These “collectors” include segments 7–9 (“strong collectors”) where the number of larvae increased, and segments 10–13 where numbers increased only slightly (“weak collectors”) (Fig. 5). Due to individuals metamorphosing, the number of larvae steadily decreased during the metamorphic period.

DISCUSSION

The timing of larval deposition by fire salamander females is influenced by the developmental stage of larvae, the physiological status of the female and environmental factors such as favourable temperatures and early spring rainfall (THIESMEIER 2004). In our study area, larval deposition was observed from mid-March until early May. Increased rainfall in late March, early April, late April and early May may have been important triggers for females to disperse towards the stream and deposit larvae. The maximum number of larvae observed was very similar in 2011–2013 ($n = 502$, 499 and 505, respectively) and higher in 2014 ($n = 775$). Occasionally larvae were found after early May, indicating that some females may have deposited larvae beyond the peak period, as also observed in Germany (REINHARDT *et al.* 2018). The abundance of larvae increased until the mid-larviposition phase in May. BAUMGARTNER *et al.* (1999) found that young larvae appeared at the end of April, with full-sized individuals observed into the second decade of May.

BAUMGARTNER *et al.* (1999) found that larvae commenced metamorphosis from the end of June, while REINHARDT *et al.* (2018) observed the first larvae at the beginning of the metamorphosing process in early June, with completely

metamorphosed individuals leaving the stream in late August/early September. In our study, the number of larvae gradually decreased from early July, partly due to the metamorphic period commencing. However, it cannot be discounted that the decline in the number of larvae may also be partly due to stream drift. At the beginning of August, 39.4% of the observed larvae were metamorphosing, while by the end of August 62.8% were metamorphosing, with a steady decrease in the number of larvae observed owing to individuals leaving the water. Previous data on metamorphic success, largely based on estimates (e.g. THIESMEIER & SCHUHMACHER 1990), were confirmed by REINHARDT *et al.* (2018), who stated that only 6.9% of a year's larval cohort metamorphosed successfully. REBELLO and LECLAIR (2003) stated that recently deposited larvae that varied markedly in size differed in time needed to reach metamorphosis, but not in size at metamorphosis.

We showed that the distribution of larvae along the length of the stream became heterogeneous within a short time following initial larval deposition, both spatially and temporally. We found that larval numbers and densities were higher in the upper and middle segments of the stream until early to mid-May, but then declined steadily in June and July. The higher number of larvae in the middle segments and fewer numbers in the lower segments in the second period of larval development could be due to drift. REINHARDT *et al.* (2018) found that segments closest to the headwaters were depleted of salamander larvae, while lower stream segments contained up to 57% of the larval population. Our study showed that 65.2% of the 14780 larvae observed along the entire length of the stream were recorded in the first half of the larval development period and 34.8% in the second half. The decrease in the observed numbers between developmental periods could be partly due to drift and metamorphosis occurring since July. Based on the changes in the number of larvae observed in each segment after the heavy rains in May, two main types of segments were described (releasing and collector). We were also able to distinguish between two groups of collector-type segments based on the number of larvae present in each stage, thus finding strong and weak collector segments. Analysed over the whole larval development period, the upper stream releasing type segments accounted for 35% of the total observed larvae, while 64.9% were present in the collector type middle and lower stream segments. In the releasing upper stream segments, 78.8% of the larvae were found in the first half of the larval development period, while only 21.2% were found in the second half. In the lower stream collector type segments 57.9% of the larvae were detected in the first period, with 42.1% detected in the second period, indicating that a significant proportion of larvae were still in the second developmental period, likely as a result of drift and accumulation.

The strong temporal and spatial variation of larval density was possibly partly due to the drift effect. According to REINHARDT *et al.* (2018) random

drift of salamander larvae is usually rare but can have the greatest impact on newborn larvae (THIESMEIER & SCHUHMACHER 1990). Behavioural drift may also be present (VEITH *et al.* 2019), but did not result in a strong restructuring of larval distribution. The main cause of the drift was due to heavy rainfall, which probably washed some of the larvae downstream with the sudden increase in water flow. Local weather conditions can vary yearly, so the risk of drift may also vary in some years. Heavy rains at the end of May significantly reduced larval density, especially at sites near the source (BAUMGARTNER *et al.* 1999). Over the four-year period of our study, we observed similar trends in larval declines from early to mid-May. Larvae flushed downstream become more susceptible to mortality from predation and unsuitable foraging areas (VEITH *et al.* 2019, BARRETT *et al.* 2010a). THIESMEIER and SCHUHMACHER (1990) showed that 19–41% of all larvae drifted downstream into sections occupied by trout, where predation pressure may drastically increase. Fish are not present in the stream we studied, and the number of invertebrate predators was low, so larval mortality may be attributed to unfavourable aquatic conditions in the lowest stream segments (e.g. low food availability). We do not exclude the possibility that larvae, drifting in shallow water in the paved, concrete section of the lowest segments of the stream, are also subject to predation by terrestrial predators.

BARRETT *et al.* (2010a) found that larvae on sand-based substrates common in urban streams were flushed to a larger extent at lower velocities than larvae on rock-based substrates from an artificial stream. We found a strong relationship between mean larval abundance and a high cover of fine gravel substrate in segments, whereas abundance was estimated to be substantially lower in concrete-lined segments. Fine-gravel substrates likely provide sufficient habitat complexity for larvae to avoid being flushed during high-flow events while also providing suitable foraging areas. In our study area, the stream flow increased dramatically during heavy rainfall events, which was because a large part of the catchment area is urbanised, with roofs and concrete surfaces preventing rainwater run-off from seeping into the ground, and large amounts of rainwater suddenly entering the stream in a short period of time. The accelerated flow washes some segments of the stream down to the harder bedrock, eliminating the natural detritus that serves as a shelter for salamander larvae.

Catastrophic events of high spring and summer precipitation could have a strong influence on larval fitness, which appears to be the most relevant cause of mortality for salamander larvae (THIESMEIER & SCHUHMACHER 1990, STEINFARTZ *et al.* 2007, REINHARDT *et al.* 2018). Heavy rains may flush more than 90% of all larvae downstream (THIESMEIER 1992). THIESMEIER and SCHUHMACHER (1990) stated that most (83%) drifting larvae were hatchlings or in very young stages. On the contrary, REINHARDT *et al.* (2018) claimed that the movement of newborn larvae was minimal in these stages, as instead they

sought refuge. The rate of decline from the maximum observed number of larvae in April and early May was on average 63% over the four years of our study due to the heavy rains, but exceeded 80% in 2011 and 2014. This represents a significant loss of the reproductive potential of the salamander population, especially as drift continues until metamorphosis. The extent of this loss is more difficult to detect because of the parallel reduction in total numbers as metamorphosed larvae leave the stream.

It is widely believed that female salamanders can reduce the risk of drift by depositing their larvae in the upper segments of streams. REINHARDT *et al.* (2018) stated that selective areas with low densities of conspecifics may override the benefits of larvipositing upstream with a drift buffer. Our study also did not confirm this previous assumption, as we have observed females depositing their larvae in all but the last few segments (13–16). However, the number of deposited larvae was higher in both the upper and middle segments of the stream and lower in the downstream segment. This indicates that the upper two thirds of the stream were preferred by females for larval deposition. Our parallel studies showed that the most favourable habitat conditions for adults were found in the same areas (KISS *et al.* 2021, 2022). However, the distribution of larvae in stream sections may also be facilitated by the fact that females may visit several habitats when laying larvae as part of a risk-spreading strategy (CASPER *et al.* 2015).

Salamander larvae in headwater streams are specifically adapted to avoid involuntary drift (REINHARDT *et al.* 2018). In the absence of specific adhesive or anchoring organs, they have adapted primarily through behavioural mechanisms. Larvae favour microhabitats exposed to only minor hydraulic stress (BAUMGARTNER *et al.* 1999), which can be found in pools. In other studies, the number of pools within a stream positively affected the abundance of larvae (BAUMGARTNER *et al.* 1999, WERNER *et al.* 2014, SCHMIDT *et al.* 2015, WAGNER *et al.* 2020). In our study, the number of pools in a stream segment was strongly correlated with the cover of stony substrate ($r = 0.67$) and woody debris ($r = 0.47$), which all increase aquatic habitat complexity and provide larvae with shelter and foraging microhabitats, and we found that larvae predominantly inhabited segments with multiple pools. A total of 106 natural and constructed pools along the entire length of the stream likely contributed to improved conditions for larval survival. The largest number (30) of pools were in segment 2, 25 in segment 5 and 15 in segment 8. Not only the presence of pools but also the water steps may change the longitudinal distribution of larvae in the stream. Pools often form immediately upstream of water steps which increases the area of larval habitat; however, water steps are a barrier to upstream movement. VEITH *et al.* (2019) found that larvae can actively move upstream, but they found significantly more larvae drifted downstream with the increasing water flow volume.

During our surveys, we found that larvae were most often solitary in smaller pools. The co-occurrence of several larvae decreased exponentially. Such aggregative behaviour occurred more frequently in deeper water and larger pools where there was sufficient shelter for the larvae. Consecutive drift events during the season narrow the range of suitable habitats for larvae to survive (THIESMEIER & SCHUHMACHER 1990). At sites with higher discharge, larvae are restricted to sheltered microhabitats (BAUMGARTNER *et al.* 1999). High flows of water caused by heavy rains can carry larvae relatively substantial distances; in one study, the mean drift distance in recaptured larvae was 150 m, while the maximum was attained at 318 m (REINHARDT *et al.* 2018). In our study area, this could mean that larvae are almost completely washed out from a relatively short 485-m long stream segment; however, the presence of numerous pools likely prevented larval flushing from the stream. These larval dispersal distances also correspond fairly well with the observed distances moved by adult males, females and juvenile salamanders in the study area (KISS *et al.* 2022), and suggest that the population is largely restricted to the stream environment and adjoining terrestrial habitats. A similar finding was made for stream-adapted salamanders in another population within central Europe (HENDRIX *et al.* 2017).

Salamander larval densities can show large differences between habitats, years, and segments of a stream in space and time. REINHARDT *et al.* (2018) found that initial larval densities in different localities were 0.12–0.27 individuals/m² in April, which increased to a maximum of 0.45–0.95 ind./m² in May. From June, larval densities successively decreased. They did not find a significant effect of the number of pools, stream width or average depth on the density of larvae. In our survey, we found that the highest density value (0.69 ind./m²) was recorded in late April and early May (0.62 ind./m²), then dropped significantly due to drifting down to early June (0.25 ind./m²), and was almost the same until early July, after which it started to decrease again. Very high density values were observed in segment 9 in all four years, with an annual average value of 33.7 ind./m² peaking in 2014. THIESMEIER and SOMMERHÄUSER (1995), in an extreme case, found up to 383 larvae/m², but the average densities were 18.1 and 19.0 larvae/m² in flowing sections and pools, respectively. In our survey, the average density was 8.3 ind./m² for segments 1–13 over the four years.

Ensuring the successful recruitment of fire salamander larvae to the terrestrial stage requires conservation management within the study catchment. The priority is to preserve the stream in its current state, which is in an unprecedented environmental condition in the region. This includes protecting, maintaining and restoring the vegetation structure of the valley. The extent of the residential areas surrounding the stream valley should not be further increased, as this would increase the amount of impervious surface cover, which would reduce the usable drainage area, decreasing the stream's recharge but

also potentially increasing the volume of runoff. Extending the sewerage network must be prevented so that polluted water is not discharged into the stream. Implementation of a stormwater management plan would outline the conservation actions necessary to ensure that urban stormwater is directed to the soils and not into the drainage system, where it may negatively impact fire salamander larvae and their habitats. Finally, increasing the number of pools in the stream with gravelly substrate may increase larval survival and hence population size and, ultimately, recruitment into the terrestrial population.

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