



Sit-and-wait foraging is not enough in food-deprived environments: evidence from groundwater and salamanders

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Foraging strategies are fundamental traits that characterize predators, with strong differences between sit-and-wait predators and active-searching predators. Optimal foraging theory predicts that environmental conditions affect the efficiency of these strategies, with active predators being favoured when prey are scarce and difficult to detect. Subterranean habitats are ideal models to study the effectiveness of foraging strategies. Laboratory studies on fish and salamander predators showed that active foraging often characterizes cave-adapted species, but field studies demonstrating the advantages of active foraging for growth and survival are lacking. In this study, we assessed how predators displaying a sit-and-wait strategy can cope with the variable costs of foraging under different ecological contexts, such as cave and surface environments. We performed a cross-environment experiment that was repeated in 3 years by rearing salamander, *Salamandra salamandra*, larvae from caves and surface streams in cages placed in both surface and cave environments. We measured larval growth (weight and total length) repeatedly every 10–20 days, from March to July, and assessed water temperature variation, prey availability and metamorphosis achievement in the rearing sites. Larvae in stream cages grew larger than larvae in subterranean cages, which showed negative growth. Our results suggest that the sit-and-wait strategy does not provide enough prey for development in cave environments, irrespective of larvae origin. In food-deprived environments, active foraging is necessary to obtain the energy required for the basic functions of the organisms exploiting them.

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The study of animals' foraging strategies is a key topic of ecology, zoology and evolution as it aids an understanding of ecosystem functioning, the connections between trophic levels and how animals adapt to different environmental pressures (Bell, 1991). The study of predator–prey interactions has brought forward different theoretical models, which try to explain the behavioural and adaptive patterns regulating these interactions and their effects on the environment (Carroll et al., 2019; Dunn & Hovel, 2020; Ferrari et al., 2009; Guiden et al., 2019; Thaker et al., 2010).

Predators need to optimize their activity budget for foraging by choosing the right strategy and good resource sizes (e.g. many small prey versus few large ones) in order to meet their energetic needs (Bell, 1991; Byrnes et al., 2021; Zoroa et al., 2011). Optimal foraging theory recognizes two basic types of strategies used by predators to find their prey: ambush (also called sit-and-wait) and active (or

'widely foraging') strategy (Bell, 1991). Moreover, a predator may also use a combination of these two strategies (Twardochleb et al., 2020; Zoroa et al., 2011). A typical sit-and-wait predator remains immobile for long periods in order to capture its prey via ambush, while active-searching predators wander throughout the habitat to locate their prey. Common examples of sit-and-wait predators include pike and dragonfly larvae, for which daily activity may be extremely limited except for brief periods when attempting to catch prey (Johansson, 1991; Kennedy et al., 2018; Sahlen et al., 2008; Van Deurs et al., 2017). Examples of active-foraging predators include many species of carnivorous mammal, which may have extensive home ranges in which they wander to locate prey (Switalski, 2003; Vucetich et al., 2012).

Foraging strategy is a fundamental trait characterizing predators and is correlated with different morphological, physiological, behavioural and phenological features. Optimal foraging theory predicts that selective pressures will favour foraging strategies that maximize energy return (Zoroa et al., 2011). How energy return

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affects foraging activity is framed by the marginal value theorem (Charnov, 1976) and by related models of best patch use (Dorfman et al., 2022). When a predator encounters multiple patches showing different prey abundance and quality, it should feed among those patches in a way that equalizes its marginal capture rate between them, i.e. stay in a patch until the advantages, in terms of capture rate and energy intake, diminish below the average capture rate and energetic cost of the environment as a whole (Abramsky et al., 2014; Vijayan et al., 2017). Although well studied in multiple environments (Menezes, 2022; Sanchez & Gillespie, 2022; Vijayan et al., 2018), there are several scenarios in which the marginal value theorem is not validated, only partially corroborated, or not even tested. This is the case of subterranean environments, where the marginal value theorem can improve our understanding of the conditions favouring their colonization by predators living in adjacent surface environments.

When compared with surface habitats, subterranean environments show notable differences in the abundance and distribution of trophic resources, with impacts on food web structure and the foraging strategy of animals (Mammola, 2019; Pipan et al., 2012; Romero, 2020). The availability of prey is generally reduced underground, and thus cave-dwelling predators are predicted to adopt an active foraging strategy (Manenti, et al., 2020). At the same time, in groundwater, the costs of staying in the same foraging patch are lower than in surface streams, because there are fewer predators and the microhabitat is more stable (Manenti & Ficetola, 2013; Pipan et al., 2020; Romero, 2020). Under laboratory conditions, active foraging has been evidenced as the main strategy for several predators strongly adapted to subterranean environments, including the olm, *Proteus anguinus*, which is one of the best known cave-dwelling vertebrates (Uiblein et al., 1992, 1995). However, laboratory results seem to contrast with the limited information collected in the field, which suggests extreme site fidelity of olms, showing yearly displacements not exceeding 5 m (Balazs et al., 2020).

Additional information comes from predators with intermediate degrees of adaptation to the subterranean environments. The spiders of the genus *Meta* inhabit the twilight zone at the entrance of caves, where adults can be considered top predators (Lunghi, 2018; Mammola, 2017; Novak et al., 2010). In addition to the use of orb webs to capture prey, these spiders also perform off-web active hunting (Lipovsek et al., 2019; Smithers, 2005). Such foraging behaviour allows for the exploitation of more patches than their surface relatives, which rely exclusively on the use of webs, providing *Meta* spiders the ability to thrive in food-deprived subterranean environments (Simonsen & Hesselberg, 2021). The behaviour of *Meta* spiders suggests that remaining in the same patch does not provide enough marginal benefits, even if the costs of foraging are low. *Meta* spiders can thus perform different foraging behaviours until their marginal benefits equal their marginal costs, although the frequency and the importance of the combined hunting strategy requires additional studies (Hesselberg & Simonsen, 2019).

Another example is provided by the fire salamander, *Salamandra salamandra*, which breeds both in surface springs and in groundwater environments (Manenti et al., 2011; Manenti & Ficetola, 2013). Larvae from groundwater environments show higher predatory abilities in total darkness and higher behavioural plasticity than surface stream larvae. They are more able to shift from a sit-and-wait foraging strategy (i.e. visually dominated) to a widely active-foraging strategy, preferring the latter under conditions that simulate groundwater environments (such as total darkness) (Manenti et al., 2013). Still, this information derives from laboratory conditions, without evidence from the field. To date, most behavioural and ecological evidence on the importance of wide active foraging in resource-deprived environments like caves comes from studies conducted under artificial conditions.

In the present study, we aimed to verify, under natural conditions, the disadvantages of ambush foraging in food-deprived cave

environments by performing a cross-environment experiment with fire salamanders exploiting both stream and groundwater habitats/environments. We specifically tested whether the energy intake of a surface predator displaying a sit-and-wait foraging strategy is lower when foraging in groundwater relative to surface stream environments, considering that both may provide advantages and disadvantages to an ambush tactic (Fig. 1). The marginal value theorem predicts that, in cave habitats, marginal benefits are low, because prey availability and rates of prey capture are lower than in freshwater surface habitats. Nevertheless, the cost of foraging can also be lower underground due to predator scarcity and habitat stability. Thus, the expected low cost of foraging underground could allow sustaining a strategy where predators devote longer periods to foraging in the same patch, despite limited trophic resources. Conversely, in surface streams, prey availability is high, so marginal benefits are high, and such environments should therefore favour the sit-and-wait strategy. At the same time, the costs of foraging are also high due to environmental variability and higher predation risk (Barzaghi et al., 2020; Knotts & Griffen, 2016; Krause et al., 2017; Manenti et al., 2023), further favouring less risky hunting strategies, such as sit-and-wait predation.

To test these predictions, we measured growth rates in salamander larvae from different environments (cave and stream); in both stream and cave habitats, we limited foraging area so that salamander larvae could only ambush prey entering the area in which they were confined. We predicted (1) that larvae constrained in small patches in caves would suffer a greater disadvantage (limited growth) compared to larvae constrained in small patches in streams and (2) that this effect would influence all larvae, irrespective of their origin. These analyses shed new light on factors allowing cave colonization, improving understanding of the relationships between behavioural and metabolic adaptations of strictly cave-dwelling predators.

METHODS

We performed a cross-environment experiment that was repeated in 3 years: 2010, 2018, 2019. In each year, we collected newborn fire salamander larvae from both cave and stream breeding sites (Fig. 2, Appendix, Table A1). We placed half of the larvae from each breeding site in a distinct surface and cave rearing site, which was different from the one of origin (Appendix, Table A2). In each rearing site, we placed larvae in stainless-steel 3 mm mesh cages to prevent larvae from escaping and prey from entering. At each breeding site, we placed two to six cages (diameter: 40 cm; height: 50 cm). We visually inspected cages and removed predators (dragonfly larvae and crayfish) prior to placement in the water column. The base of each cage was subsequently covered with substrate from the local site. We placed four larvae at the first stages of development in each cage. Each year, larval rearing was performed between March/April and June/July; during this period, we measured the length and weight of each larva on three to six occasions, taking a lateral picture to allow individual identification via unique larval colour pattern. On average (\pm SE), 17.11 ± 0.6 days intercurrent between subsequent surveys. We then assessed larvae daily growth in terms of weight and body size variation between subsequent sampling occasions, calculated as the ratio between the change in total length and weight occurring between two surveys, and the elapsed time (in days). A total of 224 larvae were collected and exposed to the experimental conditions: 32 larvae (16 from three caves, 16 from three surface streams) in 2010; 56 larvae (28 from three caves, 28 from three streams) in 2018; 136 larvae (96 from four caves, 40 from three streams) in 2019.

Overall mortality ranged from 18.7% in streams in 2010 to 39.4% in caves in 2019 (in total 58 larvae died during the experiments). Dead larvae were not replaced and the density of larvae in each cage was noted at each survey. Average mortality per cage was higher in caves

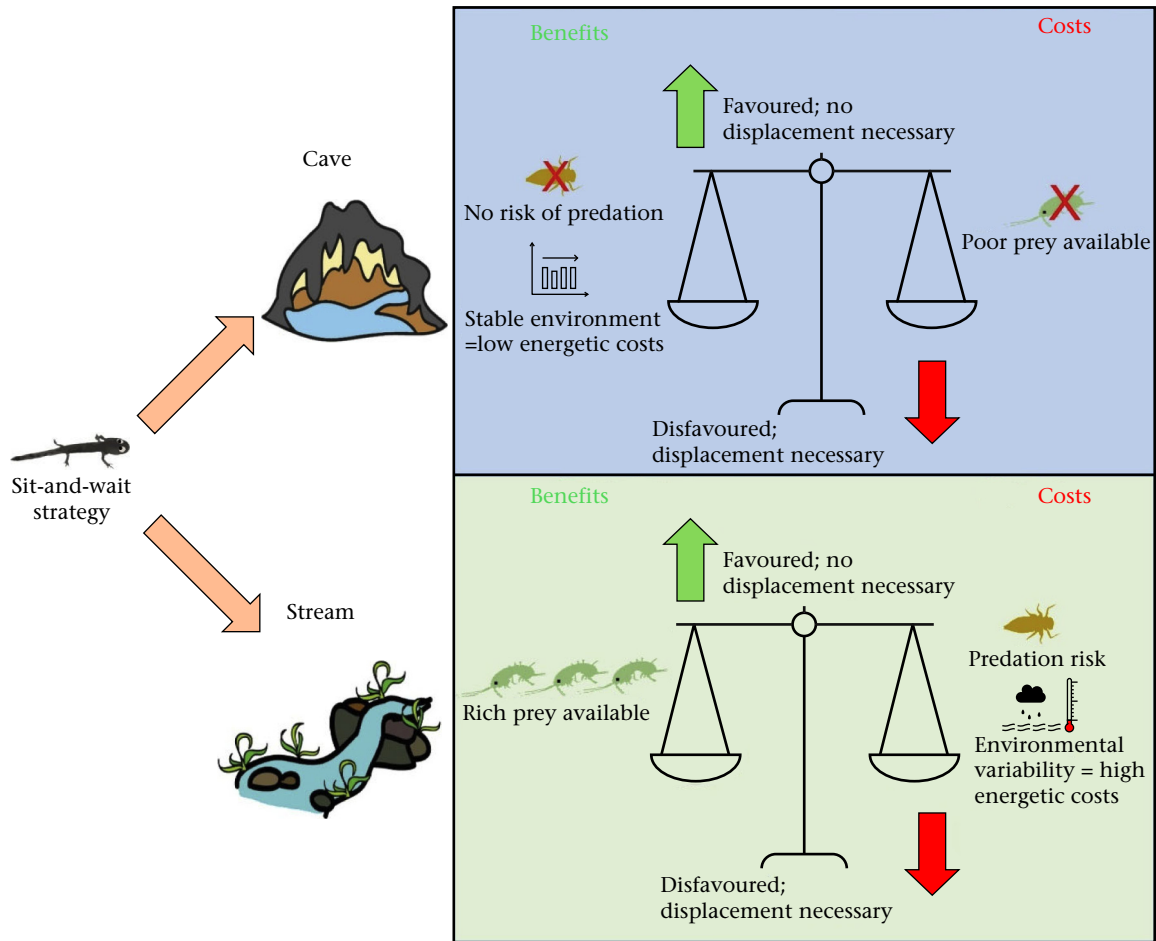


Figure 1. Conceptual workflow of the study. In fire salamander larvae, the sit-and-wait strategy can be favoured or disadvantageous in both cave and stream waters according to the features of the two environments. Potential benefits or costs affecting marginal values of a certain patch exploitation are shown. In caves, benefits potentially favouring a sit-and-wait strategy include low energetic costs afforded by a stable environment; costs include low prey availability that does not guarantee enough energy. In streams, benefits include rich prey availability that could allow a larva to adopt a sit-and-wait strategy while remaining in the same patch; costs include high predation risk and high energetic requirements to cope with environmental instability.

(Appendix, Table A3), but was similar or lower to what is generally observed in these environments (Cogliati et al., 2022; Reinhardt et al., 2018). The highest mortality rate occurred immediately after displacement of larvae to the cages; during at least two consecutive surveys, we assessed growth (in length) of 186 larvae and change in weight of 143 larvae. Variation in larvae density through time was extremely low (average: -0.02 ± 0.003 larvae/day during the entire experiment). At the end of the experiments or when larvae reached the premetamorphosis stage, we released animals at their site of origin. If we recorded null or negative growth of larvae in the same cage during three consecutive surveys, we ended the experiment for that cage and released the larvae at their site of origin after allowing them to feed ad libitum on frozen *Chironomus* sp. larvae. Every rearing site except one, the subterranean site G58 (Appendix, Table A2), was a fire salamander breeding site, where we regularly recorded the occurrence of larvae at premetamorphosis stages during previous studies (Barzaghi et al., 2017; Limongi et al., 2015; Manenti & Ficetola, 2013), suggesting that salamanders successfully achieved metamorphosis there. At each of the rearing sites during 2018 and 2019, we also assessed the presence of larvae at premetamorphosis stages (stages 3A or 3b, described by Jusczyk & Zakrzewski, 1981).

Environmental Features of the Rearing Sites

At each rearing site during 2018 and 2019, we placed a data logger (iButton, DS1923-F5# Hygrochron Temperature and

Humidity Data Logger, iButtonLink, LLC, Whitewater, WI, U.S.A.) in a tube at substrate level, which registered water temperature every 12 h. We recovered data loggers at the end of the experiment; unfortunately, the failure of some data loggers hampered the collection of data from some sites.

After the cross-environment experiment, we kept cages without salamanders inside for 6 months in three of the epigeal rearing sites and three of the cave rearing sites. We then used the pipe sampling technique (Ficetola et al., 2011) to assess prey availability (average density (N/m^2) of macroinvertebrate prey) both inside and outside of the cages. For each rearing site, we performed three to eight random samplings outside the cages using a circular pipe sampler (20 cm of diameter) that we thrust through the water column and into the substrate. We used a fine-mesh net (mesh size 1 mm) to remove all animals from the water column and the first 5 cm of sediment. Net sweeps were collected until at least 10 consecutive empty sweeps occurred. The same sampling strategy was also used inside the cages. We identified the macroinvertebrate systematic units as recommended by the protocol used to assess the extended biotic index (EBI) of Italian watercourses (Ghetti, 1997), and we recorded the density of the potential prey collected at each sampling.

Statistical Analyses

To evaluate whether differences in growth rate could potentially be related to differences in temperature, we used a *t* test to assess

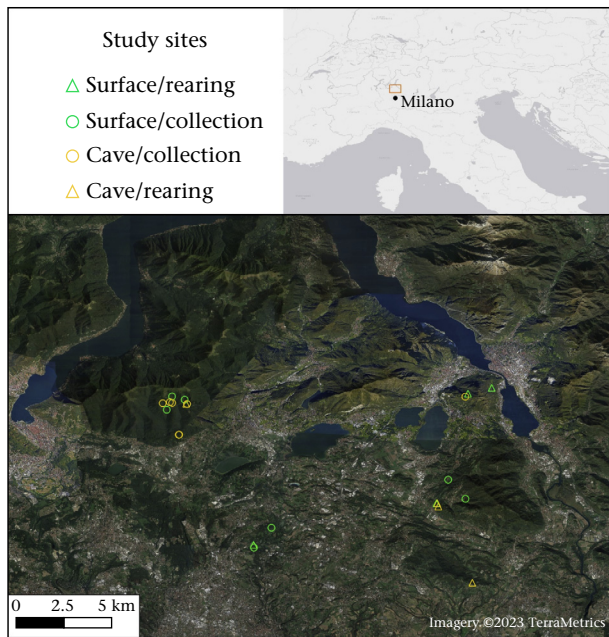


Figure 2. Distribution of the sites of collection and rearing in Lombardy (Italy). Newborn fire salamander larvae were collected at eight surface sites (green circles) and eight cave sites (yellow circles); experimental rearing was conducted in distinct locations, four surface (green triangles) and four cave sites (yellow triangles). Map generated with QGIS (version 3.16.14).

whether water temperatures recorded in cages differed between surface sites and cave sites. To test whether the density of macro-invertebrate prey varied between streams and caves, we built a linear mixed model (LMM). We considered the density of detected prey (N/m^2) as a dependent variable, environment (cave versus stream) as a fixed factor and sampling site as a random factor.

We used linear mixed models (LMMs) to assess the role of rearing environment and environment of origin on fire salamander larvae growth. We built two separate LMMs using daily larval growth in total length or weight as the dependent variable and rearing environment (cave versus stream) and environment of origin (cave versus stream) as fixed factors. We included conspecific abundance (i.e. number of larvae occurring between each survey) as a covariate. Moreover, we included the identity of the larva as a random factor. In preliminary analyses, we also tested more complex models, including additional random factors (cage and site identity). These models yielded nearly identical results, and the additional random factors did not explain a significant amount of variation; thus, we retained the simplest model. For both models, we also tested the occurrence of interactions between larvae origin and cage environment. Dependent variables were transformed using a cubic root transformation to improve normality.

Environmental data are often characterized by strong spatial structure, which can lead to spurious relationships or reflect underlying interpopulation processes not taken into consideration (Ficetola et al., 2012). To confirm that our results were not biased by spatial autocorrelation, we used Moran's I to test the spatial autocorrelation of the models' residuals; we tested the significance of Moran's I residuals using a permutation test (Lichstein et al., 2002), considering four spatial scales (0–50 m, 50–500 m, 500–5000 m, 5000–50 000 m). Lack of significant spatial autocorrelation suggests that our results were not biased by unmeasured spatial processes (Appendix, Table A4).

All analyses were performed in the R environment (R Core Team, 2022) using the packages glmmTMB (Brooks et al., 2017), EcoGenetics (Roser et al., 2017) and lmerTest (Kuznetsova et al., 2017).

Ethical Note

The collection and maintenance of larvae were performed in accordance with the Regional Law 10-31/03/2008 (Lombardy Region) and approved by the regional ethical committee (permit numbers F1.0002091, T1.2015.0001053, T1.2016.0052349 and 18303_2019). At the end of the experiment, we released each larva at the site of collection. The experimental plan was designed following the PREPARE Guidelines; it adheres to ASAB/ABS Guidelines for the Use of Animals in Research. The study design was planned to minimize the number of fire salamander larvae used in the experiment; we performed the experiment across multiple years, minimizing the stress for the individuals and keeping statistical power. Rearing was performed as carefully as possible to maximize the reliability of data collection and minimize fire salamander larvae stress. For this reason, when we recorded null or negative growth of larvae in the same cage during three consecutive surveys we considered the experiment ended for that cage and we released the larvae at their site of origin after allowing them to feed ad libitum on frozen *Chironomus* sp. larvae.

RESULTS

Despite variation in mean water temperature among rearing sites and years (Appendix, Table A5), we did not detect significant differences between surface and subterranean environments (t test: $t_{3,34} = 1.36$, $P = 0.25$). In some sites, data loggers yielded a few unexpectedly high temperatures records. It is possible that this occurred because water level decreased, exposing the data loggers to air conditions.

Available prey taxa were similar outside and inside the cages and, overall, the recorded taxa were generally the same (Appendix, Table A6), but prey density was significantly lower in cave environments than in surface stream habitat ($F_{1, 35} = 20.59$, $P = 0.01$, Fig. 3). During pipe sampling, we recorded the occurrence of some potential predators of salamander larvae, i.e. dragonfly larvae (*Aeshna* and *Cordulegaster* spp.) and the white-clawed freshwater crayfish, *Austropotamobius pallipes*, at surface sites. No predators were detected within caves.

At surface sites, the average (\pm SE) growth of caged larvae between consecutive surveys was 0.12 ± 0.007 mm/day (95% CI: 0.11, 0.14). The maximum size achieved by larvae in surface cages was 56 mm. For larvae reared in surface cages, the average increase in weight was 3.95 ± 0.2 mg/day (95% CI: 3.49, 4.41). Sixteen individuals reached the premetamorphosis stage before being released.

In caves, the average growth between consecutive surveys was -0.02 ± 0.01 mm/day (95% CI: -0.04 , 0.00). The maximum size observed by larvae in caves was 47 mm. The average increase in weight was -3.45 ± 0.5 mg (95% CI: -4.49 , -2.39). Only one individual reached the premetamorphosis stage 3A before being released.

LMMs showed that the cage environment significantly influenced larval growth. Larvae in surface cages grew faster than larvae in cave cages, both in terms of weight and daily growth length (Table 1, Fig. 4). Conversely, we did not detect any effect of larvae origin. Conspecific density had a positive effect on weight variation (Table 1), with a higher density of conspecifics leading to faster larval weight gain, despite increased competition.

Across all rearing sites, we observed wild salamander larvae living outside cages successfully reach the premetamorphosis stages. The only exception was the G58 site, as we did not detect salamander larvae during the rearing period at this site; nevertheless, metamorphosing salamanders were observed in previous years (2013, 2015, 2018).

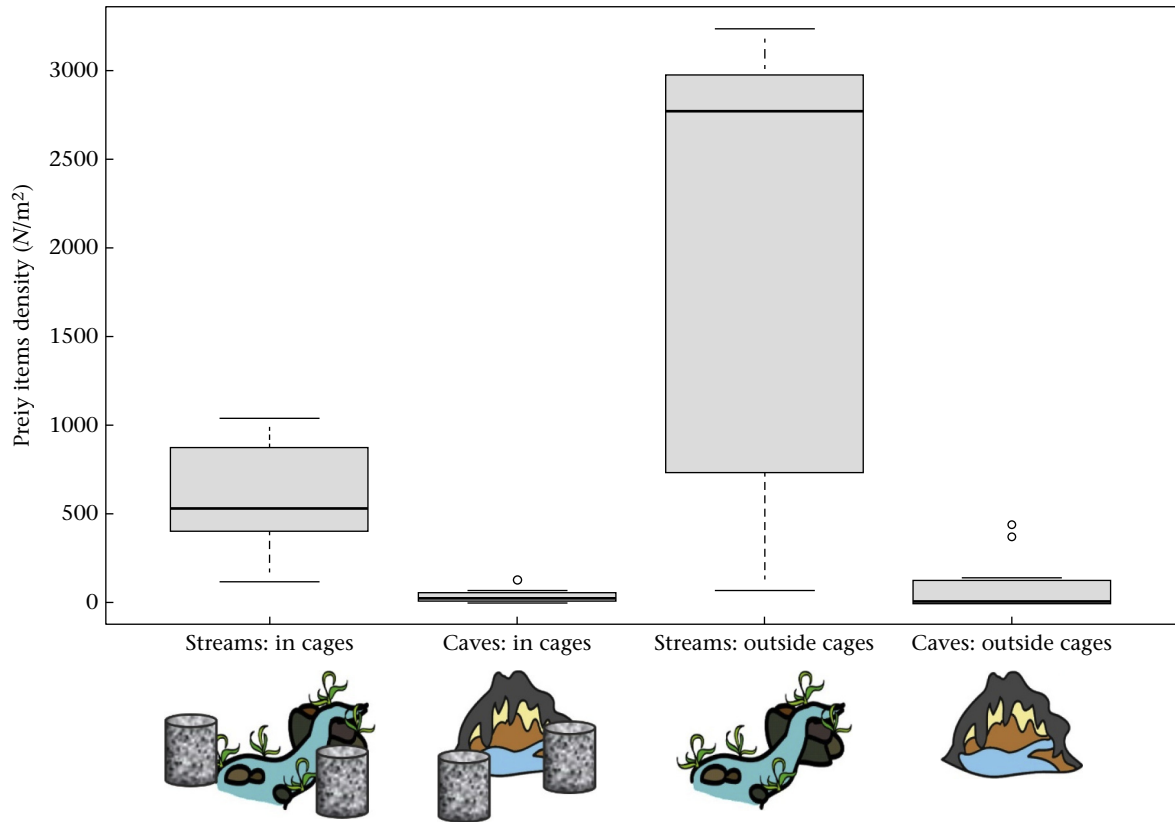


Figure 3. Density of potential prey items for fire salamander larvae occurring inside and outside cages in the subterranean and surficial rearing sites. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

DISCUSSION

Our results provide evidence that limiting the foraging area of salamander larvae to a single patch has a different effect depending on the environment that the larvae are exploiting. The cages used in our experiment forced larvae to rely on prey entering patches; thus, they had to adopt a sit-and-wait foraging strategy, without being able

to actively search for prey in the surrounding environment. Consequently, larvae reared in cave environments grew significantly less than larvae reared in surface environments. Larvae reared in caves even showed a negative growth of both body length and weight, suggesting that resources gained through the sit-and-wait strategy in such a resource-depleted environment were not enough to sustain metabolism and growth, forcing individuals to rely on their reserves. This study, along with previous observations (Barzaghi et al., 2017; Limongi et al., 2015), confirms that salamander larvae can successfully attain metamorphosis in all the study sites used in the present study, indicating that, if salamanders had been able to freely modulate their foraging behaviour, then these environments would harbour enough resources to sustain their development.

In a study of larval development in surface streams and cave pools (including some of the same rearing sites used in this study), Limongi et al. (2015) observed an average growth rate of 4.0 mg/day (range 1.6–8.3 mg/day) in surface pools and 3.3 mg/day in cave pools (range 0.6–12.0 mg/day). In our experiment, larvae reared in streams attained a similar growth, suggesting that cages in surface environments did not impose significant limitations to larval feeding. This was confirmed by the large number of larvae reared in surface cages that successfully reached metamorphosis. The situation differed in caves, where the growth rate was much lower than under natural conditions, and only one larva reached the pre-metamorphosis stage. All the prey taxa recorded in the rearing sites were able to come inside cages, and in caves, prey density was similar inside and outside of cages, suggesting that the low growth of cave-reared larvae was not related to a bias induced by cages. Overall, the observed pattern of larval growth suggests that forcing salamanders to perform sit-and-wait foraging in surface habitats did not prevent their growth; this suggests that fire salamander larvae can rely on a sit-and-wait foraging strategy to develop in

Table 1
Results of LMMs analysis

Factors		Estimate	SE	ndf	ddf	F	P	R ² fixed	R ² random
Total length	Cage environment (cave vs stream)	-0.41	0.03	1	469	117.23	<0.01	0.204	0
	Origin environment (cave vs stream)	0.04	0.03	1	469	1.43	0.23		
	Conspecific abundance	-0.01	0.02	1	469	0.49	0.48		
	Weight	-0.05	0.02	1	339	5.59	0.01	0.037	0
Weight	Cage environment (cave vs stream)	-0.05	0.02	1	339	5.59	0.01	0.037	0
	Origin environment (cave vs stream)	-0.01	0.02	1	339	0.46	0.94		
	Conspecific abundance	0.03	0.01	1	339	5.83	0.01		

Effects of cage environment, larvae origin and larvae density in cages on daily growth (total length) and daily change in weight in fire salamander larvae between each survey. Significant effects are shown in bold.

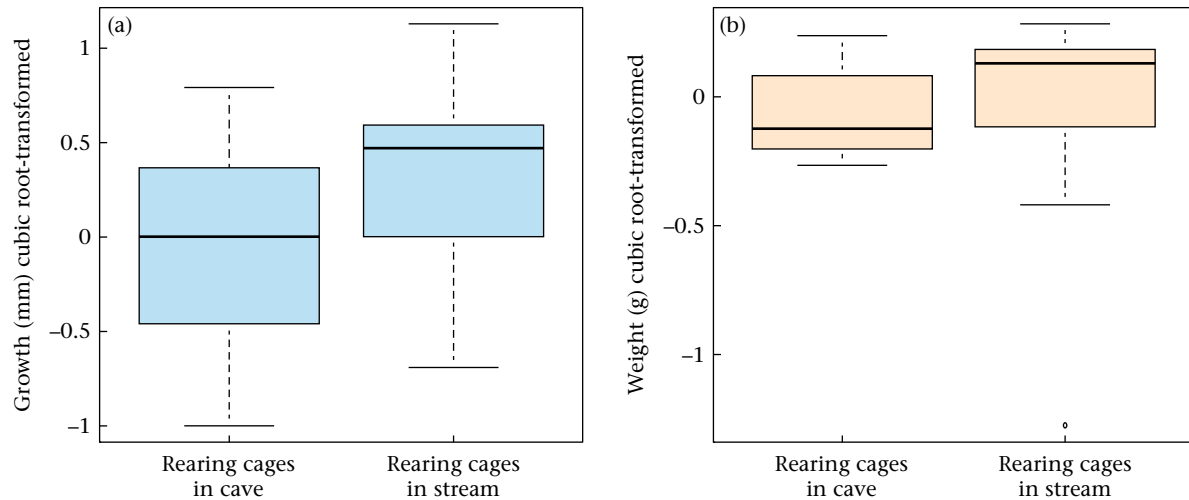


Figure 4. Box plot showing the relationship between cage environment and (a) larvae daily growth and (b) larvae daily change in weight; in the graphs, both variables have been cubic root-transformed as in the analysis. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

environments with rich trophic resources. Conversely, in subterranean habitats, preventing larvae from foraging across multiple patches strongly reduced their food intake, with detrimental effects on growth and development.

The sit-and-wait strategy may be disadvantageous in subterranean pools due to low prey density, making prey encounters less frequent than in surface environments. Lack of light further increases the difficulty of prey detection (Dumas & Chris, 1998). One may argue that subterranean invertebrates/prey are expected to wander more to locate resources (Fiser et al., 2012) because trophic resources are generally limited at all levels of the subterranean food webs (Graening & Brown, 2003; MacAvoy et al., 2016), thus limiting the disadvantages of a sit-and-wait strategy. However, subterranean invertebrates often show patchy distributions (Christman & Culver, 2001; Manenti, Lunghi, et al., 2020), making the effects of the spatial distribution of prey on the foraging dynamics of predators complicated to predict. However, while salamanders encounter multiple predators in streams that could restrict foraging activity (Manenti et al., 2016), fire salamander larvae are top predators in groundwater environments (Manenti et al., 2011; Manenti & Ficetola, 2013), even though cannibalism can also occur (Cogliati et al., 2022). Thus, the advantages of active foraging (exploitation of multiple patches) could outweigh the disadvantages (the risk of encountering predators).

Previous studies have shown that larvae from caves are generally better at detecting prey in total darkness than are larvae from stream environments. Larvae from stream environments tend to exhibit more opportunistic behaviour and are more adaptable in changing their foraging strategy in response to environmental conditions (Manenti et al., 2013; Manenti & Ficetola, 2013; Melotto et al., 2019). This suggests the potential for local adaptation in salamander populations that breed in caves. However, in our analysis, the origin of larvae did not significantly affect their growth (Table 1). Cave-adapted organisms often show reduced metabolic rates and increased resistance to starvation relative to surface-adapted organisms (Issartel et al., 2010; Mali et al., 2013; Wilhelm et al., 2006). Nevertheless, salamander populations from caves may be in the initial stages of adaptation (Manenti & Ficetola, 2013). It is possible that the potential local adaptation of these populations may improve larval performance in food-deprived environments, but such adaptive traits may be insufficient if not paired with key behaviours, such as active search of prey. Furthermore, cave larvae may not differ from surface populations in terms of metabolism and resistance to starving. Adults of stream and cave populations live in nearby

environments, and gene flow likely occurs between them, limiting the development of metabolic adaptations that could allow cave salamanders to have a more efficient balance between the marginal benefits and costs of exploiting the same patch for long periods in subterranean habitats. Detailed behavioural assessments of the foraging activity of species strongly adapted to cave life, like the olm, could allow us to clarify the role of predator–prey interactions in favouring (or preventing) adaptation to subterranean environments.

Active search and sit-and-wait approaches are two extremes of the foraging strategy range, and predators can adjust their behaviour in response to the environment and to prey features (Perry, 1999; Scharf et al., 2006). Salamander larvae are opportunistic predators that can prey upon a broad range of invertebrates (Costa et al., 2015; Reinhardt et al., 2013). In groundwater environments close to the surface, both surface invertebrates, such as crustaceans, planarians and dipterans, and strictly subterranean species may occur and become prey of salamander larvae (Barzaghi et al., 2021; Manenti & Pezzoli, 2019; Mosslacher, 1998; Pipan et al., 2008). However, salamanders can also use strategies offering access to alternative trophic resources, such as intraspecific predation (Melotto et al., 2019) or detritus feeding (Fenolio et al., 2006). At the same time, larvae in surface streams are likely to move more in search of prey, especially at night (Oberrisser & Waringer, 2011). An active search could be advantageous when prey are patchily distributed but disadvantageous when conspecific density is high. Different studies suggest that older and larger larvae can successfully prey upon smaller and younger conspecifics (Barzaghi et al., 2020; Berkowicz & Markman, 2019; Manenti et al., 2015; Reques & Tejedro, 1996). Unexpectedly, weight growth was positively related to the number of conspecifics. This effect might occur because larvae survivorship and growth rate are higher in environments with overall higher prey density.

Temperatures recorded by data loggers, although generally consistent with those expected for both groundwaters and headwaters, registered some anomalous hot peaks, with temperatures higher than those usually occurring in groundwaters of the area (Previati et al., 2022). It is possible that rapid changes in water level, related to flooding and/or dry periods, temporarily exposed some data loggers to ambient air temperature, which, during the study season, was much higher than the water temperature. Some temperature variation also occurred in the subterranean sites, suggesting that the connection with more or less deep groundwater likely varied across seasons. Further investigation, considering sites with varying groundwater levels, could help to reveal the impact of

external conditions on the performance of subterranean animals. Nevertheless, the overall temperature pattern was similar between surface and cave sites, suggesting that microclimatic conditions did not bias the results of our analyses.

Subterranean environments provide excellent conditions to study the mechanisms allowing adaptation to novel habitats or pressures (Mammola et al., 2020; Pipan et al., 2020), even though confirming laboratory experiments with field surveys can be challenging (Blin et al., 2020; Malard et al., 1997; Vandell & Bouillon, 1959). Our study provides evidence that, in environments with low trophic resources availability, the sit-and-wait predatory strategy may be insufficient to ensure capture of enough prey to meet basic energetic requirements, even when marginal costs are strongly reduced. Our study provides a useful resource for further studies comparing the intra- and interspecific foraging strategies of typical cave species and of species currently colonizing caves.

Author Contributions

R.M., G.F.F.: Conceptualization; L.V., C.T., B.L., L.B., B.B.: Methodology, Surveys and Data curation; R.M.: Writing – Original draft; G.F.F., A.M.: Writing – Review & editing.

Data Availability

Data are available at <https://doi.org/10.6084/m9.figshare.22128797.v2>. Code used for the main analysis is available in the Supplementary material.

Declaration of Interest

None.

Acknowledgments

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Supplementary material

Supplementary material associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.anbehav.2023.11.005>.

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Appendix

Table A1

Sites of collection of the fire salamander larvae

Site	Locality	Habitat	Coordinates	Years of collection
G3	Bavaresa cave	Cave	1513605.6 E, 5074707.3 N	2018, 2019
G4	Alpe del Viceré	Cave	1514388.2 E, 5074786.3 N	2010
G5	Burlunga cave	Cave	1513462.5 E, 5074883.3 N	2018
G9	Posca	Cave	1513196.2 E, 5071994.5 N	2010, 2018
G10	Posca	Cave	1513199.5 E, 5072015.9 N	2010
G11	Val Sorda	Cave	1527449.1 E, 5067478.3 N	2019
G18	Tanetta cave	Cave	1512820.1 E, 5075162.7 N	2019
G29	Eremo, Galbiate	Cave	1528958.5 E, 5075318.1 N	2019
R1	Marconaga	Stream	1528031.3 E, 5069133 N	2019
R2	Val del Faè	Stream	1528972.6 E, 5075803.1 N	2018
R24	Pampello	Stream	1518733.7 E, 5065580.2 N	2019
R3	Alpe del Viceré	Stream	1512360.4 E, 5074882.9 N	2010, 2018
R4	Cosia stream, tributary	Stream	1514281.3 E, 5075333.8 N	2019
R5	Cosia stream springs	Stream	1513602.3 E, 5075378.1 N	2019
R6	Bevera stream	Stream	1523475.1 E, 5067231.2 N	2010, 2018
R7	Becogn	Stream	1517852.4 E, 5064130.4 N	2010

Table A2

Rearing sites

Site	Locality	Habitat	Coordinates	Year	Area (m ²)	No. of cages
G11	Val Sorda	Cave	1527449.1 E, 5067478.3 N	2010	3	2
				2018	3	4
				2019	3	6
G27	Lego cave	Cave	1512943.5 E, 5072130.2 N	2010	9	2
				2018	9	2
G58	Ceppo superiore	Cave	1527572.2 E, 5067132.3 N	2019	6	5
G152	Montevecchia	Cave	1527403.8 E, 5063903.3 N	2019	3	5
R2	Val del Faè	Stream	1518733.7 E, 5065580.2 N	2018	8	2
R11	Val Sorda	Stream	1527427.3 E, 5067473.8 N	2010	4	4
				2018	6	4
				2019	6	6
R26	Villa Romanò	Stream	1518474.9 E, 5065700.3 N	2019	10	6
R42	San Michele	Stream	1529088.5 E, 5075275 N	2019	8	6

For each site, habitat features, area and number of cages used during each year of experiment are reported.

Table A3

Average mortality in stream and cave cages according to the year of rearing

	Average mortality		
	2010	2018	2019
Cave	37.5	30.55	39.47
Stream	18.75	25	26.67
Total	28.12	28.57	33.82

Table A4

Spatial autocorrelation

Spatial scale (m)	Standardized mean difference	Observations	<i>P</i>	Size
0–50	17.09	–0.0412	0.87892	104
50–500	235.465	–0.0909	0.61872	52
500–5000	1311.004	0.1752	0.61872	10
5000–50 000	11175.71	–0.0207	0.87892	497

We report correlograms of residuals Moran's *I* derived from the LMM model used to assess the role of cage rearing habitat and of environment of origin on fire salamander larvae growth.

Table A5

Temperature of rearing sites

Site	Year	Water temperature (°C)			
		Recording period	Minimum	Maximum	Average
R11	2018	05 May–10 July	12	36	16.26
R11	2019	28 Mar–10 June	8	14	11.17
G11	2018	05 May–10 July	11	36	14.07
G11	2019	28 Mar–10 June	10	11	10.87
G58	2019	25 Mar–10 June	5	33	11.66
G27	2018	05 May–10 July	9	9	9.00
R26	2018	05 May–10 June	13	15	14.89
G152	2018	05 May–10 June	12	14	12.95

The table shows the maximum, minimum and average water temperature recorded by data loggers in the rearing sites used in 2018 and 2019 and the recording period in which rearing occurred. Note that in sites R26 and G152, the data are reported for 2018, while rearing occurred in 2019, when data loggers did not work.

Table A6
Invertebrate taxa collected inside and outside of cages

Site code	Typology	Cage or pipe outside	Total number of taxa collected	Taxa collected (number of individuals of each taxon)	Number of prey individuals	Number of prey taxa
R26	Epigeal	Cage	5	<i>Austropotamobius pallipes</i> (3), <i>Ephemera</i> (3), <i>Echinogammarus</i> (20), Lumbriculidae (11), <i>Habrophlebia</i> (15)	49	4
R26	Epigeal	Outside	3	Lumbriculidae (1), <i>Habrophlebia</i> (1), <i>Lymnaea</i> (1 clutch of eggs)	2	3
R26	Epigeal	Outside	1	<i>Echinogammarus</i> (10)	10	1
R26	Epigeal	Cage	8	<i>Ephemera</i> (2), Gammaridae (30), Philopotamidae (4), <i>Chironomus</i> (10), <i>A. pallipes</i> (1), <i>Pisidium</i> (10), Sericostomatidae (2), <i>Ephemera</i> (1), Bereidae (1)	50	6
R26	Epigeal	Outside	9	<i>Ephemera</i> (2), Gammaridae (30), <i>Habrophlebia</i> (5), Chironomidae (20), <i>Pisidium</i> (1), <i>Baetis</i> (1), Tubificidae (1), <i>Cordulegaster</i> (1), Elmidae (1)	61	8
R26	Epigeal	Cage	6	Chironomidae (11), <i>Habrophlebia</i> (10), Gammaridae (30), <i>Ephemera</i> (4), Philopotamidae (1), <i>Baetis</i> (5), Lumbriculidae (1)	61	6
R26	Epigeal	Cage	10	Gammaridae (25), <i>Ephemera</i> (30), Chironomidae (10), <i>Niphargus</i> (1), <i>Tubifex</i> (1), Polycentropodidae (1), <i>Habrophlebia</i> (1), Hydropsichidae (1), Lumbriculidae (1)	71	10
R26	Epigeal	Outside	6	<i>Habrophlebia</i> (12), Gammaridae (30), <i>Leuctra</i> (5), <i>Ephemera</i> (200), Elmidae (1), Chironomidae (10)	88	6
R11	Epigeal	Outside	8	Gammaridae (50), <i>Nemoura</i> (10), Sericostomatidae (4), Hydropsichidae (4), Lumbriculidae (2), Chironomidae (10), <i>Baetis</i> (10), Lumbriculidae (1)	91	7
R11	Epigeal	Outside	10	<i>Polycelis</i> (20), Gammaridae (30), Tubificidae (30), Lumbriculidae (1), Hydropsichidae (10), <i>Cordulegaster</i> (2), Philopotamidae (1), Sericostomatidae (1), Limnephilidae (1), Limoniidae (1)	97	8
R11	Epigeal	Outside	6	Bereidae (1), Gammaridae (1), Hydropsichidae (3), Chironomidae (10), <i>Polycelis felina</i> (7), Elmidae (4)	22	5
R11	Epigeal	Cage	5	Gammaridae (2), <i>Cordulegaster</i> (3), Bereidae (1), Chironomidae (10), <i>Ephemera</i> (1)	17	4
R11	Epigeal	Cage	8	Sericostomatidae (1), <i>Cordulegaster</i> (2), Lumbriculidae (15), Chironomidae (5), Gammaridae (50), <i>Ephemera</i> (3), Hydropsichidae (1), Bereidae (1)	75	6
R11	Epigeal	Cage	4	Gammaridae (4), Sericostomatidae (2), <i>Cordulegaster</i> (1), Chironomidae (10)	14	2
R11	Epigeal	Cage	9	Lumbriculidae (20), Gammaridae (20), Sericostomatidae (1), Bereidae (1), Lumbriculidae (1), Chironomidae (5), Tipulidae (1), Hydropsichidae (2), Ceratopogonidae (1)	51	8
R11	Epigeal	Cage	12	<i>Cordulegaster</i> (3), <i>Ephemera</i> (20), Chironomidae (10), Limnephilidae (1), Tabanidae (1), Gammaridae (50), Limoniidae (20), Bereidae (1), Hydropsichidae (1), Lumbriculidae (1), Lumbriculidae (1)	105	9
R11	Epigeal	Cage	10	Polycentropodidae (1), Gammaridae (70), <i>Cordulegaster</i> (3), Chironomidae (30), Limoniidae (10), Tubificidae (10), Sericostomatidae (2), Bereidae (1), Athericidae (1), Lumbriculidae (2)	125	8
G11	Hypogean	Cage	3	<i>Niphargus</i> (1), Elmidae larva (1), Odontoceridae (1)	2	2
G11	Hypogean	Cage	1	<i>Niphargus</i> (1)	1	1
G11	Hypogean	Cage	5	Odontoceridae (1), Chironomidae (1), <i>Pisidium</i> (1), Tubificidae (1), Limoniidae (1)	3	3
G11	Hypogean	Cage	0		0	0
G11	Hypogean	Cage	1	<i>Niphargus</i> (1)	1	1
G11	Hypogean	Outside	0		0	0
G11	Hypogean	Outside	1	Limnephilidae (1)	0	0
G11	Hypogean	Outside	1	<i>Niphargus</i> (4)	4	1
G11	Hypogean	Outside	1	<i>Niphargus</i> (3)	3	1
G27	Hypogean	Cage	0		0	0
G27	Hypogean	Cage	0		0	0
G27	Hypogean	Outside	0		0	0
G27	Hypogean	Outside	0	Philopotamidae (1), <i>Niphargus</i> (4); observed in the whole stream section	0	0
G58	Hypogean	Cage	2	<i>Niphargus</i> (5), Haplotaenidae (10)	15	2
G58	Hypogean	Cage	2	<i>Niphargus</i> (2), Haplotaenidae (3)	5	2
G58	Hypogean	Outside	2	<i>Niphargus</i> (1), Haplotaenidae (10)	11	2
G58	Hypogean	Outside	2	<i>Niphargus</i> (2), anellids (11)	13	2
G58	Hypogean	Cage	1	Anellids (8)	8	1
G58	Hypogean	Outside	2	<i>Niphargus</i> (1), anellids (3)	4	2
G58	Hypogean	Cage	2	<i>Niphargus</i> (2), anellids (5)	7	2
G58	Hypogean	Outside	2	Anellids (2), <i>Tubifex</i> (1)	3	2
G58	Hypogean	Cage	1	Anellids (5)	5	1
G58	Hypogean	Outside	0		0	0
R42	Epigeal	Cage	7	Chironomidae (110), <i>Ephemera</i> (1), <i>Baetis</i> (1), Gammaridae (6), <i>Tubifex</i> (1), <i>Aeshna</i> (1), Limoniidae (10)	129	6
R42	Epigeal	Cage	4	Gammaridae (12), Chironomidae (100), <i>Cordulegaster</i> (1), <i>Physa</i> (2)	113	3
R42	Epigeal	Outside	5	Chironomidae (80), <i>Ephemera</i> (1), Sericostomatidae (1), <i>Physa</i> (2), <i>Pisidium</i> (1)	83	3
R42	Epigeal	Outside	7	Limoniidae (1), <i>Ecdyonurus</i> (1), <i>Physa</i> (5), Chironomidae (80), <i>Cordulegaster</i> (1), Gammaridae (2), <i>Pisidium</i> (4)	89	5