

Caves as breeding sites for *Salamandra salamandra*: habitat selection, larval development and conservation issues

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Abstract. Several studies documented the presence of amphibians in caves, yet investigations on the factors determining amphibian distribution and reproduction in underground environments remain scarce. In this study we analyze the environmental features allowing the reproduction of the fire salamander *Salamandra salamandra* in natural caves, and we compare the features of natural and artificial hypogeous springs. We performed surveys to assess salamander distribution and measured environmental variables in 61 natural caves. We recorded larval occurrence in 18% of caves, in waterbodies distant up to 50 m from the entrance. Larvae were associated to the most accessible caves, with gentle slope below the entrance, with waterbodies nearby the entrance and hosting rich macrobenthos communities. Occupied natural and artificial caves had similar environmental features. Larvae metamorphosing in caves attained larger body size than those grown under outdoor conditions. This result shows the key importance of the cave accessibility also for natural caves and confirms the *S. salamandra* ability to breed in underground damp biotopes if placed in a suitable environmental context. However, frequent water catchments for human use prevent the access of animals and threaten these populations.

Keywords: ecology, amphibians, spring, headwater, cave, breeding.

Introduction

The study of underground environments can allow the understanding of how biological processes cope with dominating habitat characteristics, such as the lack of light (Culver & Pipan 2009). Amphibian occurrence in caves and in other hypogeous habitats is well documented. In particular, there are several salamanders known from underground habitats such as caves and phreatic waters in deep aquifers. At least 11 species or subspecies of urodeles, belonging to the families Proteidae and Plethodontidae, are troglobites showing troglomorphy (Romero 2009). Moreover, many species during their life cycles are more or less regularly linked to cave environments and play major roles in cave ecosystems (Peck 1974). For instance, in addition to *Proteus anguinus* and to *Speleomantes* spp., at least 17 species of amphibians that belong to the Italian herpetofauna have been more or less occasionally found in caves or other underground spaces, and several of them occasionally breed in subterranean sites (Bressi & Dolce 1999).

The fire salamander, *Salamandra salamandra*, seems to breed relatively often in subterranean ar-

reas (Uhrin & Lesinsky 1997, Bressi & Dolce, 1999, Razzetti et al. 2001, Gasparo 2002, Manenti 2008, Manenti et al. 2009b). The species has been regularly found both in caves and in other underground habitats. In a few cases caves can act as traps for both adults and larvae (Uhrin & Lesinsky 1997). Nevertheless, there are multiple active mechanisms that can explain the underground occurrence of salamanders. Subterranean habitats can be used as winter shelters, hiding places during the active season, feeding habitats (Krauss 1980, Baumgart 1981, Uhrin & Lesinsky 1997), and also as regular breeding sites (Manenti et al. 2009b). A recent analysis studied artificial hypogeous springs, and evaluated the factors influencing larvae deposition in the fire salamander (Manenti et al. 2009b). However, detailed analyses on salamander reproduction in natural caves remain scarce.

In this paper we analyze the factors affecting the larval deposition of *S. salamandra* in natural caves, and compare natural caves with artificial hypogeous springs. We also present morphological data on larvae found in caves, because they can provide interesting insights on the larval development in these conditions.

Materials and Methods

Study area and surveys

We surveyed the natural caves of the Lecco and Como districts (Lombardy, NW-Italy). We used the data of the CAI Speleo Club of Erba and the annotations of the Regional Speleologic Register to localize the caves and to record preliminary information of them. We used two different approaches to carry out the surveys. First, we examined all the known caves occurring in a relatively restricted karstic area, the catchment basin of the Cosia stream (Como district). Afterwards, we extended our research to all the caves of the two districts in which the speleological registry annotations about hydrography suggest the existence of pools. Overall, we surveyed 61 caves. We performed the surveys from February 2009 to March 2009, from November 2009 to March 2010 and from December 2010 till February 2011. We explored the caves as deeply as possible compatibly with our equipment, or until already existing arming features in the cave, and we performed visual encounter surveys to assess the presence of *S. salamandra* larvae, juveniles and adults (Manenti et al. 2009b). Previous analyses showed that, in small waterbodies, larvae of *S. salamandra* have high detectability using this approach (Manenti et al. 2009a). For each cave we recorded eight environmental variables: altitude, slope of the territory outside the cave below the entrance in a radius of 15 m; slope above the entrance; presence of water inside the cave; distance of water from the entrance; total extension of the cave; richness of the community of benthonic macro-invertebrates, measured as the number of taxonomic units (see Ghetti 1997). In spring, we sampled macrobenthos by moving the substrate for 5-10 minutes, and we used a thin-mesh dip net to collect the invertebrates in the first pool of the cave. Overall, we detected pools or streams in 30 natural caves out of 61. Furthermore we measured forest cover, as the cover of deciduous or mixed forest within 400 m from each sampling point, on the basis of the 1:10000 Vector Map of Lombardy, using the ESRI ArcView 3.2 GIS. Forest is the main habitat of adults, and forest cover at this scale is strongly associated with populations of *S. salamandra* (Ficetola et al. 2009).

We performed surveys and recorded environmental variables also in 21 subterranean artificial springs where salamanders breed (Manenti et al. 2009b). These correspond to 13 springs already identified (Manenti et al. 2009b) and eight additional subterranean springs identified through more recent surveys. Recording the features of these springs allowed us to compare differences between natural and artificial environments.

Measurement of larvae

During 2010, we measured all the larvae that we found in the stages 3A (i.e., initial period of metamorphosis) and 3B (final period of metamorphosis) of Juszczuk & Zakrzewski (1981) in hypogeous environments (10 and 12 respectively). For each larva, we recorded total length, weight and gill length. Each larva was photographed dorsally and laterally for individual recognition following the recommendation of Eitam & Blaustein (2002), in order

to avoid measuring the same larva twice. If possible, each larva was measured once in the 3A stage and once in the 3B stage. However, it was not possible to measure all larvae in both stages.

To compare body size parameters of larvae found in caves with those of larvae growing under outdoor conditions, in March 2010 we collected 11 newborn larvae from four different caves and five larvae from two streams. Larvae were reared under outdoor ambient conditions and fed *ad libitum* with *Chironomus* sp. larvae. On reaching the stage 3B, we recorded weight and total length of reared larvae.

Statistical analyses

First, we used the unequal-variance *t* test to compare the environmental features of occupied and unoccupied caves, and to compare occupied natural and artificial caves. Subsequently, we used an information theoretic approach, based on Akaike's Information Criterion (AIC; Burnham & Anderson 2002), to identify the combination of variables best explaining the presence of larvae in caves. We limited this analysis to natural caves with waterbodies. We built generalized linear models assuming binomial error, including all possible combinations of environmental variables. For each model, we calculated the AIC corrected for small sample size (AICc) and Δ -AICc, which is the difference in AICc between a candidate and the model with lowest AICc (i.e., the best model). The use of AIC/AICc as sole selection criterion may select overly complex models, therefore we considered a complex model only if it had a Δ -AICc lower than the Δ -AICc of all its simpler nested models (Richards et al., 2011). Using AIC instead than AICc would lead to identical results. For each candidate model, we also calculated Nagelkerke's R^2 (R^2_N) as a measure of variance explained, and we assessed significance of environmental variables using likelihood ratio tests. Per each model *i*, we calculated the AIC weight w_i , which is the probability for a model to be the best one among the candidates (Richards et al. 2011). In the results, we present only models with weight > 0.05.

If needed, variables were transformed prior to analyses using logarithms (distance of the water from the entrance; macrobenthos richness) or squareroot-arcsine (forest cover). Finally, we used the analysis of variance (ANOVA) followed by Tukey's post hoc to compare total length and weight among 3B larvae grown in caves with those grown under outdoor conditions. We performed all analyses under the R statistical environment (www.r-project.org).

Results

Natural caves as breeding habitats

In 23 caves the first water bodies were at <30 m from the entrance, while in the other 7 caves they ranged between 30 and 105 m. We found salamander larvae in 10 caves (33% of caves with water). In one site, larvae were found in waterbodies 50 m from the cave entrance. In the other caves we

observed larvae at distances varying from 0 to 20 meters. All the caves in which we recorded larvae but one are emitting caves, constituting a spring that does not receive water from other upstream waters, therefore the presence of larvae cannot be explained by drifting or trapping from epigeous environments. During the surveys we did not record recently metamorphosed individuals, still we observed different developmental stages including some very advanced ones (e.g., metamorphosing larvae at stages 3A and 3B). Furthermore, during winter months, we found adults in 5 caves at distances of 5 to 35 meters from the entrance.

The altitude of the caves used for deposition ranged from 520 to 1020 m a.s.l. In all the occupied caves, the first water-body is within 30 m from the entrance and in 80% of the occupied caves the first water-body is less than 3 m from the entrance; total planimetric development ranged from 6 m to 150 m. Caves used for reproduction are characterized by a relatively gentle slope below the entrance (average slope: 23°) and higher richness of macrobenthos; furthermore, the first waterbody was closer to the entrance, compared to the caves not used for reproduction (Table 1). The best AICc model showed that larvae were associated to caves with the richest macrobenthos communities ($\chi^2_1 = 11.0$, $P = 0.0009$) and gentle slope below the entrance ($\chi^2_1 = 10.2$, $P = 0.001$). This model explained a high proportion of variation ($R^2_N = 0.68$). AIC weights suggests that this model has a good support, given the data (weight = 0.79). A second model with lower support ($\Delta AICc = 5.3$, weight = 0.06) suggested that larvae were associated to caves with gentle slope below the entrance ($\chi^2_1 = 8.1$, $P = 0.005$) and waterbodies nearby the en-

trance ($\chi^2_1 = 5.7$, $P = 0.017$). This model explained a lower proportion of variation ($R^2_N = 0.54$). No other candidate models showed weight > 0.05.

Comparison of natural and artificial caves

We found salamander larvae in 59% of surveyed artificial underground springs (21 springs). For several environmental features, we did not find significant differences between natural and artificial caves occupied by salamander larvae, suggesting that the two environments have similar characteristics from the perspective of larvae (Table 1). However, natural caves were at higher elevation and were surrounded by higher forest percentage. Furthermore, the average slope below the entrance was significantly lower for artificial caves (Table 1).

Body size

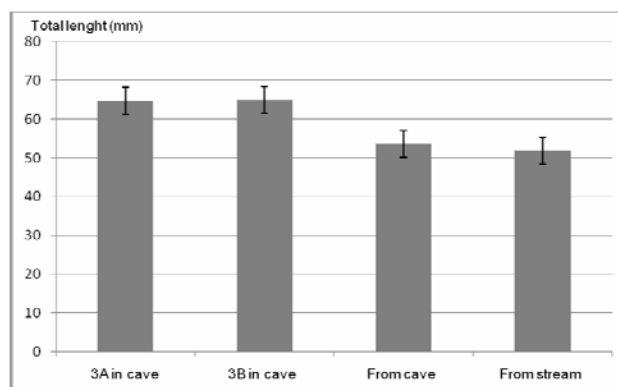
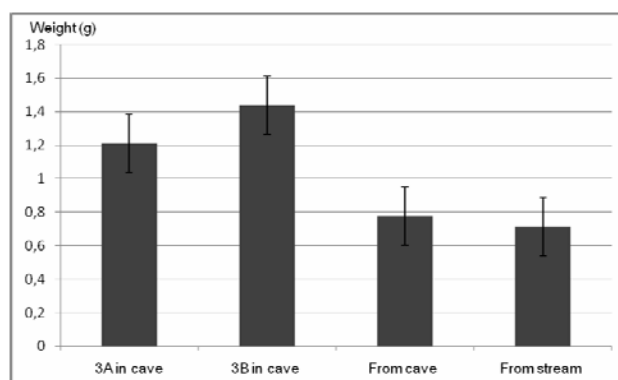
Data on body size of metamorphosing larvae at the development stage 3A and 3B are reported in Table 2. At both stages we recorded multiple larvae exceeding 70 mm of length and with gills still 2-3 mm long. The maximum total length of larvae at the 3B stage was 78 mm. Body size was significantly different among metamorphosing larvae grown in caves, and those grown under laboratory conditions (ANOVA; weight: $F_{2,25} = 14.8$, $P < 0.0001$; total length: $F_{2,25} = 26.5$, $P < 0.0001$) (Table 2). Metamorphosing larvae grown in caves were significantly heavier and longer than those grown in the laboratory (Tukey's post hoc: all $P < 0.001$). Conversely, for larvae reared under laboratory conditions, there were no significant differences among larvae collected in caves or in streams (Tukey's post hoc: all $P > 0.09$). (Fig. 1, 2, Table 2).

Table 1. Mean features of natural caves with water presence: natural, non occupied and occupied by salamander larvae; artificial occupied by larvae, and comparison between cave typologies (unequal variance *t* test).

Feature	Natural, non occupied	Natural, occupied	Artificial	Natural: occupied vs. non occupied			Occupied: natural vs artificial		
				<i>t</i>	df	<i>P</i>	<i>t</i>	df	<i>P</i>
Altitude	744±59	793±55	513±40	-0.6	25.6	0.545	4.1	18.8	0.001
Slope below the entrance (°)	39.1±3.8	23±3.1	10±1.727	3.2	27.2	0.004	3.7	14.7	0.002
Slope above the entrance (°)	60.9±5.3	45±5.8	41±3.549	2.0	22.6	0.061	0.7	16.0	0.497
Planimetric development	264±133	30±14	14±6	1.7	19.4	0.096	1.1	13.2	0.301
Macrobenthos taxa	0.3±0.1	1.9±0.6	2.1±0.3	-3.0	11.7	0.011	-0.8	13.1	0.414
Distance of water from the entrance	31.0±10.7	4.1±2.9	0.2±0.1	3.0	24.7	0.006	2.1	9.7	0.065
Forest cover	0.92±0.03	0.88±0.03	0.66±0.07	-0.4	22.1	0.695	2.7	18.6	0.013

Table 2. Total length and weight of larvae grown in caves and reared under laboratory conditions.

	N	Total length \pm SD (mm)	Weight \pm SD (g)
Stage 3A, grown in caves	10	64.7 \pm 7.2	1.2 \pm 0.3
Stage 3B, grown in caves	12	65.8 \pm 6.7	1.5 \pm 0.5
Stage 3A, born in caves, grown in the laboratory	11	53.6 \pm 3.0	0.8 \pm 0.2
Stage 3A, born in streams, grown in the laboratory	5	47.2 \pm 5.8	0.6 \pm 0.1

**Figure 1.** Total length of larvae grown in caves at stages 3A and 3B compared to that of larvae reared under outdoor laboratory conditions at 3b stage.**Figure 2.** Weight of larvae grown in caves at stages 3A and 3B compared to that of larvae reared under outdoor laboratory conditions at 3b stage.

Discussion

S. salamandra shows a relatively high level of opportunism when choosing breeding sites; it actively uses natural caves for breeding and, in karstic areas with limited superficial streams, the deposition in hypogeous sites seems to be favoured (Bressi & Dolce 1999, Manenti 2008). In a previous study, Manenti et al. (2009b) performed a survey of some artificial hypogeous springs, to evaluate the relationship between the subterranean habitat features and the salamander distribution. They observed that a high percentage of

these underground environments is used for larvae deposition, and showed that salamander larvae are related to the most accessible springs and to relatively rich macrobenthic fauna. In the current study, we extended the research to a larger number of natural caves. A gentle slope below the cave entrance was the most important variable in determining the presence of larvae. This parameter is clearly connected with the level of accessibility of the caves, as the entrance of salamander females is more difficult in caves located in steep areas. The concordance of results obtained in natural and artificial hypogeous springs suggests that ac-

cessibility is the major factor determining salamander reproduction in underground environments.

Furthermore, salamander larvae were associated with waterbodies supporting relatively rich macrobenthos communities. Benthonic invertebrates are preys for larvae, and therefore this relationship is not surprising (see Manenti et al. 2009a, 2009b). The presence of invertebrates can be particularly important in underground habitats, where preys are extremely scarce. In addition, one model with lower support suggests that the frequency of larvae is higher in waterbodies nearby the entrance of caves. This observation further confirms the importance of accessibility of waterbodies for salamander reproduction. Conversely, we did not detect a significant effect of forest cover in the surrounding landscape. Forest cover is an important parameter, because it constitutes the habitat of adults, and may influence water features (Manenti et al. 2009a, Ficetola et al. 2011). On the other hand, all the surveyed sites were in forested areas, and average forest cover was about 90% in both occupied and unoccupied sites (Table 1). This suggests that forest cover is not a limiting factor for these populations, as it happens in human dominated landscapes and mountain or grassland areas.

Despite frequently used as breeding habitat, natural caves are occupied less often than artificial subterranean springs (Manenti et al. 2009b). Only 18% of the natural caves were used for deposition, while larvae were regularly found in more than 59% of the draining galleries. Of course, water presence is the main parameter determining breeding in caves, and only 47% of natural caves had water. Among caves with waterbodies, the frequency of larvae (40%) was closer to the one in the underground artificial springs (59%). The remaining differences could be explained by a lower accessibility. For instance, natural caves were often in more impervious and steep landscapes, compared to the artificial ones, and tended to have waterbodies less close to the cave entrance (Table 1). Furthermore, some pools or streams of natural caves could be temporary, and deserve future monitoring. Conversely, in the study area all the artificial underground springs support permanent waterbodies; moreover, when human activity does not prevent the ease of access, they have a suitable macrobenthic community for the fire salamander, with available preys and no predators (Manenti et al. 2009b). This might be a further factor allowing

the high occupancy of artificial caves.

The presence and abundance of salamanders in caves may also depend on the presence of other salamander populations in areas surrounding the caves, which might allow to maintain occupancy through meta-population dynamics (Ficetola & De Bernardi 2004, Ficetola et al. 2009, Hartel & Öllerer 2009). Unfortunately, fine scale data on salamander distribution through the whole study area are not available, so it was not possible to explicitly test this hypothesis. Nevertheless, analyses performed over a subset of the study area (artificial caves only), for which detailed data on epigeous streams were available, suggested that the presence of nearby streams occupied by salamanders plays a minor role in explaining reproduction in underground springs (Manenti et al. 2009b). This might occur because the fire salamander is well distributed within the study area (Bernini et al. 2004), and all studied caves are surrounded by the major terrestrial habitat of this species (Table 1). Therefore, many caves are probably not far from other salamander breeding sites. Nevertheless, it will be interesting investigating this question in the future.

Larvae developing in underground environments had larger size at metamorphosis, comparing to those reared under outdoor conditions (Table 2, Fig. 1, 2), and showed larger size than several literature records. For instance, in head-water streams near to our study area, the maximum size of metamorphs was about 65 mm (Giovine 1996); Zakrzewski (1987) and Juszczak & Zakrzewski (1981) indicate a maximum length of 60 mm for the metamorphosing larvae, while Joly (1968) reports a maximum length of 70 mm. We recorded several larvae with lengths exceeding 70 mm, with a maximum of 78 mm. These larvae still had developed gills. In several amphibians, a slow larval development determines larger size at metamorphosis (e.g., Alvarez & Nicieza 2002, Ficetola & De Bernardi 2006). Development rate of hypogeous populations of urodeles is slower because of multiple parameters, such as cold temperature, lack of light and scarcity of preys (Clergue-Gazeau 1975). The larger size at metamorphosis is therefore likely to be a consequence of the slow development in the caves. Further studies on the development of salamander larvae in underground environments are necessary.

From a conservationist point of view, these caves are not exploited for tourism, and the principal threat for cave populations are the water

catchments on the springs deriving from the subterranean aquifer. Water uptake is very frequent in emitting caves with high water flow that naturally would originate springs and streams suitable for *S. salamandra* and other animals; these environments can be particularly important in karstic regions with limited superficial water. Out of 110 emitting caves known in the study area, 24 (21.8%) have water catchments and are closed. We surveyed 12 emitting caves with catchments, and only one had larvae inside. Its entrance is closed with a grid and thus accessible to salamanders. The other 11 caves were closed by doors not allowing the entrance of animals, and we did not find larvae inside. These caves also had very poor macrobenthos communities, being in most of the cases limited to stigobiotic taxa. In one of the caves with catchments surveyed, the occurrence of salamander larvae was recorded before the aqueduct construction, while our surveys did not detect larvae. The alteration of cave accessibility is one of the major consequences of human exploitation. We suggest the adoption of simple strategies to minimize the impact of cave water catchments. For example, it is sufficient to close the caves with grids instead of impenetrable doors or, if it is necessary to prevent the access of external organisms, building barriers inside the cave, while leaving suitable pools near the entrance and before the point where water is caught.

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