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Think of what lies below, not only of what is visible above, or: a comprehensive zoological study of invertebrate communities of spring habitats

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Abstract
Springs are interface habitats between the surface and subterranean environments, often neglected by zoological studies and generally regarded only from a surface perspective. Springs are also often collected and managed by humans: catching buildings that collect spring water may provide an accessible window over groundwaters. With this paper, we aim to assess the determinants of invertebrates' occurrence in springs using a comprehensive approach and considering the role of catching buildings and of predator occurrence. During 2017 and 2018, we performed six repeated surveys in 44 springs of N-Italy. We distinguished between collected and natural springs, assessed the springs morphological features and recorded the occurrence of predator *Salamandra salamandra* (Linnaeus, 1758) larvae and of four invertebrate taxa corresponding to strictly spring-dwelling, groundwater-dwelling and stream-dwelling groups, such as the gastropod *Graziana alpestris* (Frauenfeld, 1863), the amphipods *Niphargus thuringius* Schellenberg, 1934 and *Gammarus balcanicus* Schäferna, 1922 and dipterans larvae of the family Tipulidae. We used a constrained redundancy analysis to evaluate the relative role of fire salamander occurrence and of springs features on the occurrence of the invertebrate taxa surveyed. Spring typology and fire salamander larvae were the major determinants of spring invertebrates' occurrence. *G. alpestris* was positively related to artificial catching structures. Fire salamander was related to the occurrence of *N. thuringius, G. balcanicus* and Tipulidae larvae. Our results provide evidence that catching spring structures can significantly favour the detection of strictly spring-dwelling species; moreover, we reveal that the breeding of semi-aquatic predators like salamanders may play important roles on the community of invertebrates occurring in the spring habitats.

Keywords: *Gastropod, seepage, headwater, stream, amphibians*

Introduction

Among freshwater habitats, one of the most interesting from both a zoological and management perspective is the spring habitat. Springs have since a while played a fundamental role for humans, being important for the intake of potable water. Currently, spring habitats are defined as groundwater-dependent ecosystems (Eamus & Froend 2006) and are broadly spread worldwide. Generally, springs can be defined as the interface between groundwaters and surface freshwater habitats (Alfaro & Wallace 1994), with both the subterranean and the epigean habitat features that interplay in characterising each spring. However, zoological studies focusing on springs are often approached only under a surface perspective, neglecting the role played by groundwaters (Galassi 2001; Fiasca et al. 2014). From an ecological point of view, springs have been distinguished in three main categories such as (a) flowing springs (also named rheocrenic), in which water flow feeds small streams; (b) pool springs (also named limnocrenic), where the flow is low and creates lentic habitats; and (c) seepage springs (also named helocrenic) that create a shallow damp zone (Thienemann 1922; Martin & Brunke 2012).

Moreover, due to the human action, together with natural springs, there are also different typologies of artificial catchment buildings used, especially in the

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past, to collect and laminate groundwater for agricultural and civil purposes. There are two main typologies of artificial springs: draining galleries and catchment houses (also often called “bottini di presa”). These artificial springs are characterised by a more or less developed accessible part that penetrates the side of a slope, to catch and bring outward water; these buildings collect water directly in the groundwater table. Old artificial springs base their catching activity essentially on gravity and are associated with the urban and agricultural landscape of all the world, with particular importance for Europe, Japan, Asia and Northern Africa (Balland 1992). The importance of old catching buildings other than historical factors may also be significant for zoological studies. Catching buildings often occur in non-karst areas where natural caves or spaces allowing the observation of groundwaters are not available. Catching buildings may thus represent a window over freshwater subterranean environments that could be otherwise accessible only using expensive samplings. As studying distribution and habitats of underground animals is quite complex and is receiving growing interest (Mammola & Leroy 2018; Ficetola et al. 2019), accessible windows to subterranean aquifers may have strong zoological importance. Moreover, from a zoological point of view, old catching buildings may expand the area of the border between the surface and subterranean waters favouring both surface and subterranean populations of organisms related to the spring habitat. When springs are stable and isolated, the environmental conditions may favour the development of a highly specialised fauna; spring-dwelling specialised organisms are often called crenobionts and are organisms that are necessarily associated with spring source habitats to survive and accomplish their life cycles (Di Sabatino et al. 2000; Hoffsten & Malmqvist 2000). Generally, strict crenobiont species are quite rare and are mainly represented by some species of snails of the superfamily Hydrobioidea and by different species of water mites (Roca & Gill 1992; Pezzoli 1996, 2010; Di Sabatino et al. 2000). However, much more organisms are often associated with spring habitats, the springs being often the upper border reached by some stream-dwelling invertebrates and the lower border reached by groundwater-dwelling species. The typical spring-fauna can be composed of different groups such as amphipods, decapods, oligochates, triclads, caddisflies, crane-flies and water beetles (Hirabayashi et al. 2004; Cantonati et al. 2006; Manenti 2014; Nakano et al. 2018; Manenti et al. 2019). Also, some semi-aquatic organisms, like salamanders and some dragonfly species, may often exploit spring habitats for their larval cycles, becoming often the top predator of the source trophic webs (Lowe & Bolger 2002; Gillespie 2013) and contributing substantially to the whole aquatic biomass of springs living organisms (Barzaghi et al. 2017).

In Europe, among the amphibian species that are more strictly connected with spring habitats, there is the fire salamander (*Salamandra salamandra* Linnaeus, 1758) (Manenti et al. 2009a). This species is ovoviviparous and typically breeds in small shallow streams with highly diversified substrate, rich macrobenthos and absence of fish (Manenti et al. 2009b, 2017; Manenti & Ficetola 2013). Several observations have also been reported for different typologies of natural and artificial spring where the larvae of this species may reach strong densities (Limongi et al. 2015). Fire salamander larvae are predators, and their occurrence is likely to affect the composition of the invertebrate fauna.

From a zoological perspective, spring surface organisms are often studied, and communities’ assemblages of the invertebrate fauna of natural springs are available, even if temporarily and spatially fragmented. At the same time, few information is available on the use of springs by typical groundwater fauna, on the use and role of semi-aquatic organisms as amphibians and on the importance that old catching buildings may play for spring-fauna occurrence and observation.

Considering all these aspects, with this paper, we aim to (a) determine if spring catching buildings may affect communities of invertebrates and (b) understand if the occurrence of semi-aquatic predators may affect the distribution of groundwater, crenobiont and surface invertebrates living in springs. We hypothesise that (a) both crenobiont and groundwater organisms may be positively related to catching spring buildings and that (b) all invertebrates’ categories are related to the fire salamander larvae occurrence in springs.

Materials and methods

From November 2017 to March 2018 and from November to December 2018, we performed repeated surveys in 44 springs situated in the Regional Park of Montevecchia (Lombardy, NW Italy; Figure 1). In this area, one of us (EP) performed in the past extensive monitoring of the springs, discovering and describing several important sites, both natural and artificial (Pezzoli 1996,

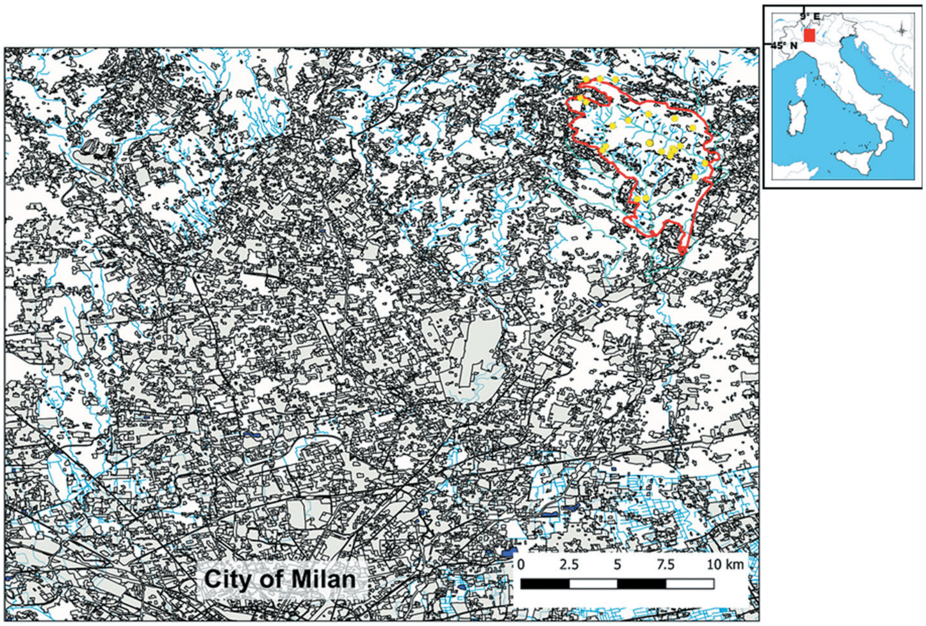

Figure 1. Study area. Soft grey represents urbanised areas; light blue represents hydrographic networks. The borders of the Regional Park of Montevecchia and Curone Valley are represented by the red continuous line. Yellow circles represent the sampling sites; due to geographic proximity, some sites appear superimposed.

2007, 2010). During our research, for each site, we performed six distinct diurnal surveys to assess the occurrence of fire salamander larvae and of four invertebrate taxa such as *Niphargus thuringius* Schellenberg, 1934, *Graziana alpestris* (Frauenfeld, 1863), *Gammarus balcanicus* Schäferna, 1922 and dipterans larvae of the family Tipulidae. *N. thuringius* is a typical groundwater-dwelling species sometimes encountered at springs mouths (Stoch 2000); *G. alpestris* is a typical crenobiont species (Pezzoli 1996, 2007); *G. balcanicus* and Tipulidae larvae are typical of headwaters (Tachet 2010). The occurrence of fire salamander larvae and invertebrates was assessed both visually and by moving substrate with a deep net. Visual surveys lasted 15 min at each sampling, and we performed deep nettings for 10 min. Additionally, in each site, we sifted 2 kg of substrate (or all the substrate if the occurring amount was less than 2 kg) with a sieve of 35 mesh to detect the occurrence of fresh shells of the snail *G. alpestris*. The siftings were repeated two times during the study period.

In natural springs, the surveys were performed in the pool occurring exactly at the mouth of the spring at the interface with groundwaters. In catching buildings, the surveys were performed in all the occurring pools (usually built to laminate the water and filter substrate). During surveys, we recorded two morphological features of the spring such as the maximum area of the pools and the maximum depth of the pools. We assigned the springs to two typologies such as natural springs and collected spring. As natural springs, we considered springs in which no artificial buildings for their collection or structures covering the surface of the mouth occurred, while collected spring was considered those springs occurring in catching buildings. We included in the samplings all the typologies of catching building occurring in the study area such as draining galleries, buildings for water lamination and "bottini di presa".

We used a constrained redundancy analysis (RDA) to evaluate the relative role of fire salamander occurrence, of spring typology and of springs features on the multivariate structure (i.e. species composition) of invertebrate taxa surveyed. RDA is a canonical analysis that is particularly effective as it combines the properties of regression and ordination techniques. RDA allows evaluation of how much of the variation of one dataset structure (e.g. invertebrate community composition in a spring; endogenous dataset) is explained by independent variables (e.g. spring biotic and abiotic features; exogenous datasets) (Borcard et al. 2011). We performed the RDA using the vegan package (Oksanen et al. 2005). In the analysis, we considered one matrix composed of fire salamander occurrence, of the natural or collected spring typology of the pool surface and of pool maximum depth as exogenous matrix, and we used the matrix of invertebrate taxa occurrence as endogenous. We calculated the significance of explained variance by performing ANOVA-like permutation tests (10,000 permutations) (Borcard et al. 2011). We performed the statistical analysis in the R 3.3.2 environment (R Development Core Team 2018).

Results

Twenty-eight out of the 44 springs sampled were catching buildings with different shapes and features. Some buildings hosted multiple pools for the water lamination. *G. alpestris* was detected in 34 sites. The fire salamander was detected in 24 sites, *Gammarus blacanicus* in 7 and *N. thuringius* in 17, and we observed fly larvae of the Tipulidae family in 10 sites. *G. balcanicus* and Tipulidae flies were detected mainly in shallow springs, while we observed *N. thuringius* mainly in smaller pools and the fire salamander in larger pools (Figure 2).

Spring invertebrates were significantly related to the biotic and abiotic spring features considered (permutation test: P = <0.001). The relationship between invertebrate occurrence and spring features explained 25% of the variation. The first RDA axis was represented by spring typology and the second RDA axis by the fire salamander occurrence (Figure 3; Table I). The first RDA axis explained 17% of the variation explained by the RDA, and the second RDA explained 8%. *G. alpestris* occurrence was positively related to collected springs, while *G. balcanicus* and Tipulidae occurrence was related to natural springs. *N. thuringius* showed a weak positive relationship with collected springs (Figure 3; Table II). The occurrence of the fire salamander larvae played a negative role on the occurrence of *N. thuringius* and, at a weaker extent, on the occurrence of *G. balcanicus* and of Tipulidae larvae; on the contrary, no effect was played on *G. alpestris* occurrence (Table II).

Discussion

Our results showed that two major determinants were related to the distribution of spring organisms in the study area. Both the spring typology (natural or with artificial collecting building) and the occurrence of the fire salamander played an

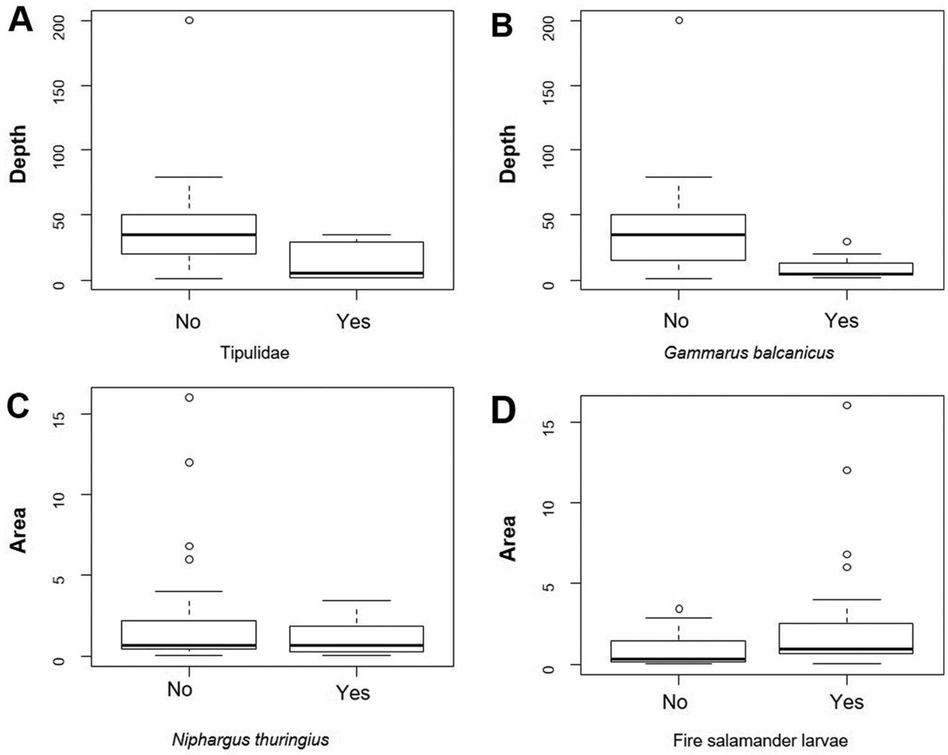

Figure 2. Box whiskers plots of the relationship between taxa occurrence and some spring environmental features recorded. (a) Relationship between Tipulidae larvae occurrence and spring pools depth; (b) relationship between *Gammarus balcanicus* occurrence and spring pools depth; (c) relationship between *Niphargus thuringius* and spring pools area; (d) relationship between fire salamander larvae occurrence and spring pools area.

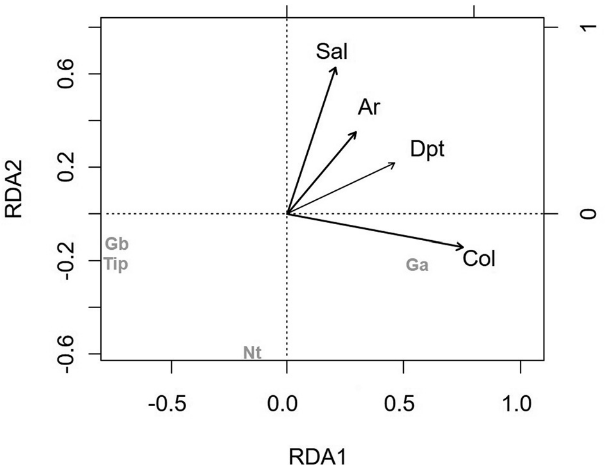

Figure 3. Plot of the RDA showing the relationship between spring features and invertebrate taxa occurrence. Black arrows identify environmental features; dark grey symbols identify invertebrate taxa position with respect to the first two RDA axes. Environmental features: Sal = fire salamander larvae, Ar = pool area, Dpt = pool depth, Col = collected springs with catching buildings. Invertebrates: Gb = *Gammarus balcanicus*, Tip = Tipulidae larvae, Nt = *Niphargus thuringius*, Ga = *Graziana alpestris*.

Table I. Relationships between the variables included in the RDA and the first and second RDA axes.

Variables	RDA1	RDA2
Collected spring	0.94	−0.17
Pool area	0.36	0.44
Maximum depth	0.57	0.27
Fire salamander larvae	0.25	0.79

Table II. Relationships between the invertebrates included in the RDA and the first and second RDA axes.

Invertebrate taxa	RDA1	RDA2
Niphargus thuringius	0.05	−0.58
Graziana alpestris	0.60	−0.23
Gammarus balcanicus	−0.49	−0.11
Tipulidae	−0.63	−0.17

important and differential role on species presence. In the study, we considered multiple categories of organisms including crenobiont species represented by the gastropod *G. alpestris*, stygobiont species often inhabiting groundwaters as the amphipod *N. thuringius* and species generally living in epigean headwaters. The spring typology was related to all the taxa considered, with distinct patterns. We detected a strong positive influence of catching buildings only for *G. alpestris*; a weak positive correlation with *N. thuringius* and a strong negative correlation with *G. balcanicus* and Tipulidae larvae, which are typical epigean taxa.

The emblematic crenobiont species, *G. alpestris* in particular, was positively related to artificial catching buildings. This is a species that may reach high abundances also in springs with the moderate flow (Pezzoli 1996, 2007; Pezzoli & Lemme 2003). Populations of the species are known also for subterranean environments where depigmented and blind individuals may occur, but the species is a typical inhabitant of the interface environment represented by sources (Giusti & Pezzoli 1977, 1980). Water temperature and hardness are important factors for the occurrence of the species that it is rarely observed in sites that exceed 13°C and does not bear water hardness below 5 French degrees (Pezzoli & Spelta 2000; Pezzoli & Lemme 2003; Pezzoli 2007). The species is considered a good bioindicator of the water quality, being able to tolerate only few amounts of organic pollution and being very sensitive to different chemicals (Pezzoli & Spelta 2000). Due to its limited distribution, often linked to local biogeographical factors, the species cannot be used as a biological indicator in biotic indexes for assessing springs quality, but the assessment of its occurrence across time may provide important indications for the springs management at the single-site level. Our results reveal that catching buildings provide important environments for the detection of this species. The high occurrence of *G. alpestris* in artificial catching buildings may be linked both to the fact that artificial springs enlarge the ecotonal habitat available for the species and to the structure of the buildings themselves. They, in fact, usually have one or more pools expressly built for allowing water lamination and sediment collection. These pools are extremely efficient in stockpiling the shells of this gastropod (Pezzoli 1996, 2007; Pezzoli & Spelta 2000). The occurrence of freshly, not concretioned, shells that we collected in the substrate indicates the existence of viable populations. In general, our results show that artificial collecting buildings may be important for allowing the detection of elusive crenobiont species and suggest that their maintenance should be incorporated in management plans dealing with spring source habitats.

Only a weak positive correlation occurred between spring catching buildings and *N. thuringius* occurrence. *Niphargus* is the most various genus of freshwater amphipods, with more than 300 described species (Marković et al. 2018). The genus is widespread and primarily inhabits groundwaters even if some mainly epigean populations and species are known (Marković et al. 2018). *N. thuringius* is a common species in Northern Italy occurring in springs and caves from Po plain lowland areas to Prealps, and it is considered a relatively recent, presumably postglacial, invader of groundwaters (Stoch 2000). Our observations suggest that the exploitation of ecotonal areas between groundwaters and surface waters is possible also for this species as recorded for other species of the genus, especially during night (Fiser et al. 2007). A strong negative correlation occurred between springs catching buildings and the stream-dwelling species. Both *G. balcanicus* and Tipulidae larvae were associated with natural springs. Tipulidae are semi-aquatic insects, using freshwaters for breeding; likely the occurrence of catching building limits reproduction and accessibility for flying adults. *G. balcanicus* is a widespread species occurring in headwaters of Balkans and N-Italy and is often recorded in spring areas (Stoch 2000). Our results suggest that the occurrence of natural not managed springs is important for the species.

Our study reveals also that the occurrence of predators may play an important role for different aquatic organisms more or less linked to the spring habitats. We focused on the occurrence of a semi-aquatic predator, the fire salamander, that generally breeds in headwaters and that can often use also springs and subterranean habitats (Manenti et al. 2009b). Previous studies showed that the fire salamander is often associated with accessible artificial subterranean springs other than emitting caves. The features determining fire salamander larvae occurrence in spring catching buildings are generally the accessibility of the spring itself and the occurrence of prey (Manenti et al. 2011, 2016). Even if both surface and groundwater organisms are negatively related to the fire salamander larvae occurrence, the relationship is strong only with *N. thuringius*. The negative effect played by fire salamander larvae occurrence on *N. thuringius* may indicate that predator presence in springs may limit the exploitation by groundwater-dwelling species of resources closed to the interface between surface and groundwaters. With respect to groundwaters, source mouths can be strongly attractive environments with a relatively high amount of trophic resources available for subterranean organisms (Culver & Pipan 2014). *Niphargus* amphipods occurrence in springs and other surface habitats is generally considered linked to foraging purposes (Marković et al. 2018). Fire salamander larvae may directly prey on *N. thuringius* individuals entering springs from groundwater or create a landscape of fear preventing their exploitation of springs. The weaker negative effect played by fire salamander larvae occurrence on *G. balcanicus* and on Tipulidae larvae may suggest that these surface species have developed antipredator responses; moreover, Tipulidae larvae at older stages are bigger than fire salamander larvae and are not preyed upon. It is also possible that covariation occurs between the habitat where the fire salamander breeds and that of the invertebrates not negatively related to its larvae as perennial accessible shallow springs may represent valuable environments for aquatic and semi-aquatic organisms with different functional roles (Barzaghi et al. 2017). We did not detect relationships between fire salamander larvae occurrence and the crenobiont *G. alpestris*; this small gastropod is able to shelter in interstices (Pezzoli 2007) where it may easily escape predation.

The strong negative relationship that we detected between *N. thuringius* and fire salamander larvae suggests that future studies on this species may be performed in springs with and without the fire salamander larvae, considering the role that the extensions of spring ecotonal areas towards the surface (as happens during night) and the landscape of fear may play in affecting the exploitation of epigean freshwaters by species inhabiting groundwaters.

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Disclosure statement

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