Aquatic Shallow Subterranean Habitats: General Features

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Abstract: Shallow (superficial) subterranean habitats, or SSHs are very close to the surface, but are aphotic. Some of these habitats are large cavities, especially lava tubes, while others are small cavity habitats, especially the underflow of streams and rivers (interstitial aquifers), and the soil. But, there is an especially interesting set of SSHs that do not fit into either category, with intermediate sized space with many close connections with the surface. These habitats include talus and scree slopes, milieu souterrain superficiel (MSS), in both carbonate (soluble) and non-carbonate rocks, including volcanic rocks. Epikarst, the uppermost layer of karst formed largely by solutional processes that may be air or water filled, occupies a similar vertical position to that of the MSS, but perhaps with smaller spaces. The most superficial of SSHs are the miniature perched aquifers (isolated wetlands) given the name hypotelminorheic that exit through seepage springs, diffuse discharges when the flow cannot be immediately observed but the land surface is wet compared to the surrounding area. These two SSHs (epikarst and hypotelminorheic), which do not extend beyond a few meters in depth are called strict sense shallow subterranean habitats and will be presented in more detail.

Keywords: Epikarst, Hypotelminorheic, Seepage Springs, Shallow Subterranean Habitats

1. Introduction

Shallow subterranean habitats (SSHs) have close surface connections and are highly variable with respect to temperature and other environmental parameters, and often have high levels of organic carbon [1, 2]. But they harbour highly modified organisms, ones without eyes and pigment and with elongated appendages. Due to this reason, the role of shallow subterranean habitats may be crucial to understand the evolution of subterranean organism (see [3]). The main barrier to colonize subterranean environment is the absence of light, rather than the absence of food or environmental cues. So, the absence of light is the primary selective factor in the evolution of the distinctive morphology of subterranean animals [3].

Among SSHs are aquatic as well as terrestrial habitats (Figure 1), and each of them is relatively quite well studied. These are: epikarst, hypotelminorheic, interstitial habitats and calcrete aquifers as aquatic and terrestrial are MSS, lava tubes and soil. Of course there is a number of cases, that are difficult to categorize in terms of the name of the SSH, or different authors give different names to the same habitat.

Figure 1. Position of the Habitat in Respect to the Size of the Cavity (Space) and Proximity to Soil or Surface.
In this contribution, two well studied aquatic SSHs will be presented, along with general features of SSHs. The shallowest of the SSHs is hypotelminorheic! In 1962, Milan Meštrov who worked on the Medvednica Mountain in Croatia applied the term “hypotelminorheic” to shallow groundwater habitats that are vertically isolated from the water table and are “constituted of humid soils in the mountains, rich in organic matter and traversed by moving water”. Based on his definition and his sketch of the habitat (Figure 2), Culver, Pipan, and Gottstein (2006) proposed that the term hypotelminorheic can be used for habitats with the following major features:

1. A perched aquifer fed by subsurface water that creates a persistent wet spot;
2. Underlain by a clay or other impermeable layer typically 5 to 50 cm below the surface;
3. Rich in organic matter compared with other aquatic subterranean habitats.

The water from the hypotelminorheic exits at a seepage spring (Figure 2). And discharge is typically less than 10 cm$^3$ per second [4].

Hypotelminorheic habitats have been described only from a few sites in Croatia, from the USA (i.e. seepage spring at Scotts Run Park near Washington D. C.) and from Slovenia (Nanos Mountain) where the best studied examples are also known [6]. It is certainly present in other countries and regions, but may be described with different names or just neglected as a habitat.

On a local scale, large numbers of seepage springs can occur but they are highly clustered [7] (Figure 3).

For most of the year, stygobionts can be found in the leaf litter layer. Organisms live in the spaces between fallen leaves and in the dirt and gravel; literally they live in a food. In the particular seepage spring in the Washington area, stygobiotic and trolomorphic snails, isopods, and amphipods are found, along with a few individuals of non-specialist species of amphipods and isopods [2].

Epikarst is the uppermost layer of karst, a more or less permanently saturated zone with a considerable storage capacity (Figure 4). The base of the epikarst is at a depth of 8-12 m, although epikarst on the figure contrasts strongly with many others. The principal characteristic of epikarst as a habitat is its heterogeneity with many semi-isolated solution pockets whose water chemistry is also variable [8]. So, the epikarst habitat itself is highly heterogeneous with respect to water chemistry, residence time of the water, as well as physical structure.

Figure 2. Slightly Modified Sketch of Hypotelminorheic Habitat [5].

Figure 3. Location of 17 Seepage Springs along a 20 Km Stretch of the George Washington Memorial Parkway in the USA, That Are Found in Three Clusters.
Figure 4. Ground Penetrating Radar Profile Through the Hortus Field Test Site (France). A cave, Dipping Rock, a Local Fault, and the Epikarst Are Shown. From [9].

Most what is known about epikarst habitat comes from sampling epikarst drips in caves, and the fauna and chemistry of drips even a few meters apart can be quite different [8, 10]. Results showing the effect of geographic distance on epikarst copepod community composition reveal that similarity increases with distances up to 100 m (Figure 5). At the distances up to 100 m, there is more or less linear increase in similarity. At the distances up to 100-200 m similarity of fauna declines, and after several hundred meters (actually up to 1000 m), the average similarity increased; there is a “resetting” of the community, as “new” communities appeared [11].

Figure 5. Effect of Geographic Distance On Community Composition: Communities of Copepods “Reset” at Scale of 100 to 1000 m (Open Circles). From [11].
Because epikarst is almost impossible to sample directly, epikarst aquatic fauna should be explored indirectly by taking samples of percolation water \[12, 8\]. The easiest way is to collect epikarst fauna from pools, filled up by water which seeps down the walls or drips directly from the cave ceiling. By sampling such kind of pools, the influence of phreatic groundwater fauna or fauna from hypogean river is excluded. Water collected from pools is then filtered through net or filtering bottle to find epikarst fauna.

![Figure 6. Diagram of Filtering Device to Continuously Collect Invertebrates from Drips. From \[12, 8\].](image)

Much more informative can be direct collecting of water exiting epikarst – from ceiling drips. Diagram of the apparatus for such collecting is presented in Figure 6. Water from trickle is directed into a funnel and then in a small plastic bottle with plankton netting (“filtering bottle”). Collected animals and small amount of water remain in the filtering bottle, while most of the water exits into a container. This water can be used for some extra measurements of physical and chemical parameters \[12, 8\].

There is considerable reason to think that epikarst is important source of organic carbon. It was shown that there is a “rain” of coarse particulate organic matter in the form of copepods and other animals from the epikarst \[13\] and that biofilms in cave streams were enriched in nitrogen that came from percolating water \[14\]. The most common and most abundant metazoans in the epikarst are copepod crustaceans \[12, 8\].

2. General Features of Shallow Subterranean Habitats

First, they are aphotic. Light datalogger in a seepage spring at a depth of less than 5 cm in the substrate on Nanos Mountain in Slovenia, where stygobionts were present indicated that no light penetrated the habitat \[2\]. These data suggest that light rarely penetrates more than 5 to 10 cm below the surface.

SSHs have relative close connections to surface environments. These connections have a few impacts. One impact is the influence on chemical and physical factors, like temperature. Figure 7 shows a comparison of surface and seepage water temperature: seepage spring has lower summer temperature as well as higher winter temperature compared to surface water. The coefficient of variation of stream temperature was higher than the coefficient of variation of seepage spring temperature for the same period what suggests the superficial nature of the hypotelminorheic habitat \[15\].

![Figure 7. Hourly Temperature in a Seepage Spring and Adjoining Stream in Prince William Forest Park, Virginia, USA. From \[15\].](image)

The next impact of the close surface-subsurface connection is the availability of organic carbon and nutrients. Information that we have is for dissolved organic carbon (DOC) for some sites on Nanos Mountain in Slovenia. These data can be seen from the table 1, where a hyporheic site is also included for comparison. Concentrations of dissolved
organic carbon in all four types of habitat were quite variable, the result of the very superficial nature of the habitats. The highest average dissolved organic carbon concentration (4.52 mg/L) was at the site with large populations of *Niphargus stygius* and *N. tamaninii* [4]. The lowest dissolved organic carbon concentrations were observed at those sites with few amphipods, either stygobionts or surface dwellers. Intermediate values of dissolved organic carbon were present in small springs dominated by surface-dwelling species and in the hyporheic habitat of a very small stream.

The conceptual model of energy flux in karst (Figure 8) shows the input of DOC and POC (Particulate Organic Carbon) which arrive via two different pathways [16]. Openings such as sinking streams and shafts permit entry of DOC or POC, such as leaves, wood, and fine detritus from streams and soils. Water percolating through soils and the epikarst carries with it DOC, but POC is mostly filtered by soils. POC may arrive from the epikarst in the form of animals that drip into the cave from the epikarst. Deep groundwater may be another source of DOC, but considering the long residence time and distance from organic matter sources, deep groundwater contributes little organic carbon within the karst basin. After input into the karst basin, POC and DOC are used or processed to different forms before they are exported through resurgences.

**Table 1.** Dissolved Organic Carbon (mgL⁻¹) for Seeps, Small Spring, and Hyporheic Site on Nanos Mountain, Slovenia. From [4].

<table>
<thead>
<tr>
<th></th>
<th>Hyporheic</th>
<th><em>Niphargus</em> seep</th>
<th>Other Seep</th>
<th>Small Spring</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>2.77</td>
<td>4.52</td>
<td>1.63</td>
<td>2.72</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>3.79</td>
<td>3.72</td>
<td>0.4</td>
<td>2.48</td>
</tr>
<tr>
<td>Minimum</td>
<td>0.41</td>
<td>0.83</td>
<td>0.4</td>
<td>0.13</td>
</tr>
<tr>
<td>Maximum</td>
<td>10.44</td>
<td>9.89</td>
<td>5.53</td>
<td>7.07</td>
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<tr>
<td>n</td>
<td>6</td>
<td>7</td>
<td>11</td>
<td>12</td>
</tr>
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</table>

We examined Specific UV absorbance (SUVA) at 254 nm and biological index values (BIX) from soil extracts, epikarst drips, sinking streams, cave streams, and resurgence across two karst basins [17]. Soil extracts were characterized by high, but epikarst drips by low SUVA values. SUVA is an indicator of aromatic carbon content. The Biological index values were higher in epikarst drips compared to soils, streams and resurgence. BIX indicates the relative importance of recent microbial contributions relative to terrestrial sources of DOC.

DOC represents the largest input of organic carbon in karst which is used by subterranean communities. The concentration of DOC we found was much higher in sinking streams than in epikarst (Figure 8). But it is important to stress that spatial distribution of percolating water in the epikarst is more widespread than cave streams. Moreover, not all caves have sinking streams and many streams and pools in caves can be fed exclusively by percolating water. In these circumstances the only source of organic carbon in caves would be percolating water. Carbon quality is probably higher in drips than in sinking streams. The importance of organic matter from drips in forming an epilithic biofilm suggests that this may be the case.

**3. Conclusions**

The shallowest of all subterranean habitats are hypotelminorheic habitats and their associated outlets (seepage springs). The chemical signature of hypotelminorheic water is quite distinct as it tends to approximate the mean annual temperature of the region, has moderately high conductivity (350 µScm⁻¹), and near neutral pH. Average concentration of DOC is 4 mgL⁻¹, although it shows spatial and temporal heterogeneity among sites.
Epikarst is a common component of karst areas. Water exiting epikarst typically contains dissolved organic carbon at concentrations of approximately 1.0 mgL\(^{-1}\), and this is the lowest value of DOC in aquatic SSHs. DOC is particularly important in establishment of the biofilm in cave streams and in cave passages without active streams.

All in all, DOC is only one component of the TOC (Total Organic Carbon), but it is typically the dominant component in subterranean waters. As was shown, SSHs are not generally resource-poor habitats. This is especially true for seepage springs and interstitial habitats and in the case of epikarst, resources are not so abundant but there is more DOC than in the epikarst-fed streams.

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