Chapter 13
Caves as Oligotrophic Ecosystems

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13.1 Introduction

> **Box 13.1**
> Hypogean systems are usually relatively energy-limited (Poulson and Lavoie 2000). Most caves are *oligotrophic* with low amounts of available organic matter and low energy density. The trophic structure of these caves is less complex than that of the less common energy- and nutrient-rich *eutrophic* caves, which are characterized by larger amounts of animal faeces (such as bat guano) and plant debris transported into caves by floods and/or gravity. Longer caves, where sections differing in amounts of organic material may be recognized, are called *poecilotrophic* (Humphreys 2000a). Generally, food scarcity along with darkness seems to be the main factors shaping the selective regime in caves (Trontelj 2012).

Oligotrophic systems are environments with low amounts of trophic resources in the form of organic substances. The limited trophic base of such systems leads to low diversity and biomass and less developed biotic communities. Such systems occur in the Arctic, Antarctic and high-mountain tundra where harsh conditions result in very low primary production in both aquatic and terrestrial habitats. Similarly, oligotrophic systems are characteristic of subterranean environments that are relatively isolated from the surface, thus having very limited organic input. Chemolithoautotrophy by bacterial communities in oligotrophic systems is usually negligible. Despite the low organic supply resulting in less developed and less

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diverse biotic communities, oligotrophic cave systems have been in the focus of attention from the beginning of cave explorations. Recently, this attention has even increased as scientists study the composition of the biotic communities of oligotrophic caves, the peculiar adaptations of organisms to this extreme environment and the functional roles of different species in these systems. The focus of this chapter is primarily on cave passages that appear oligotrophic, while examples from food-rich or exceptional caves are included for comparison.

Organization of the trophic structure of oligotrophic caves largely depends on their connectivity and interactions with the epigean environment. Oligotrophic cave systems represent relatively isolated subterranean spaces without extensive above-ground connectivity. In most cases, there is a complicated structure with numerous links between the hypogean environment and its surrounding epigean one (Dunne et al. 2002; Romero 2009). The connectivity between epigean and hypogean environments is relatively high in limestone massifs, where the vadose zone plays an important role as an ecotone. Mostly vertical downwards movement of percolating water is characteristic of this zone.

There are two main routes of organic carbon input to caves: (1) localized flow through sinks and shafts, and (2) diffuse flow through soils, epikarst and the vadose zone. Oligotrophic caves, and their characteristic low-energy biota, are mostly associated with diffuse flow (Simon et al. 2007a). The food base for cave biota in nutrient-poor caves is mostly represented by organic matter transported by percolating water. This includes dissolved organic carbon (DOC), represented by complex molecules of fulvic and humic acids that are metabolized very slowly by actinobacteria. It also includes leached particulate organic matter (POM) that is of low quality and only slowly used (Poulson 2012). Transport of organic matter from the surface is limited, with the quantity progressively reduced with depth below the ground surface. The low amounts of organic matter in the remote and isolated parts of caves create a kind of biotope suitable for troglobionts, which are adapted to cope with low food resources (Deharveng and Bedos 2000, see also further text). In Organ Cave (USA) and Postojnska jama (Slovenia), Simon et al. (2007a) found that most of the organic carbon entering through the epikarst was DOC at concentrations averaging around 1 mg/L. Overall, the amount of DOC in percolation water depends on surface ecosystems and residence times of the water in soil, epikarst and the vadose zone. The amount of DOC in percolation water may be strongly reduced in arid areas such as Cape Range, Australia (Humphreys 2000b; Simon et al. 2007b). DOC and POM are further processed within caves, and probably in all voids of the vadose zone, with an important element for their transformation being microbial films on rocks—"epilithion" (Culver et al. 2012). In addition, percolating water mediates transport of living organisms into subterranean habitats, such as microorganisms, aquatic meiofauna and terrestrial microarthropods (Culver and Pipan 2009; see Chap. 14 for more information on this topic).

13.2   Food Variability and Communities of Biota

Food variability and predictability in caves are different for aquatic and terrestrial habitats. Abiotic input of food by water is represented by plant detritus degraded through the activity of surface decomposers and leaching by water, so bacterial and fungal decomposers are also much reduced. On the other hand, irregular and heavy floods can bring in unleached detritus that may be a food base for the cave communities for 10–100 years. Biotic input of organic material from trogloxenes moving into caves is more predictable, and, although it does not bring as much food, the quality is high (Poulson 2012).

Aquatic species are limited by food that is diluted and dispersed widely, whereas terrestrial species rely on food that remains concentrated in a local area. Intervals at which detritus is renewed at the base of the aquatic food web can be of the order of decades, so there is the selection for long life (Poulson 2012). According to Weber (2000), food scarcity is stronger in the terrestrial than in the aquatic cave habitats. In groundwater, low oxygen supply and food availability are overlapping aspects determining the development of adaptive strategies and distribution patterns of animals (Hervant and Malard 2012).

Generally, in deep subterranean systems food webs depend on diffuse and continual input of very small amounts of dissolved organic matter in percolating water. These cave sections are more oligotrophic and support a small number of species that tend to be long-lived troglobionts which are adapted to cope with low food resources (Deharveng and Bedos 2000; Poulson and Lavoie 2000). Specialized troglobionts can persist in very low-energy environments, being documented even from isolated spaces of the deepest vertical caves such as Lukina jama–Trojama (−1421 m) in Croatia (Bedek et al. 2012; Andersen et al. 2016) and Krubera–Voronja (−2140 m) in Abkhazia, Georgia (Sendra and Reboleira 2012).

Box 13.2

In subterranean environments, food input is not uniformly distributed in space or time. Cave animals share numerous adaptations to the relative food scarcity in their habitat. Hüppop (2012) distinguishes three aspects of food scarcity in caves. *General food scarcity* holds for nearly all caves and occurs especially in caves with limited food input. *Periodic food supply* characterizes caves that are regularly flooded or caves that regularly receive food input from visiting animals. During the wet season, food supply can be very high and even abundant for some weeks or months. After exhaustion of these food reserves, animals in such caves suffer food scarcity like animals in generally food-poor caves. Some cave animals have to cope with *patchy food scarcity*. This means that food is not necessarily limited but is difficult to find and exploit. Under such conditions, cave organisms can be observed aggregated at patchy food resources.

Oligotrophic caves occur in bedrock of all types, i.e. limestones, volcanic (lava tubes) and ferruginous rocks (see Chaps. 17 and 21), and also sandstones. Recent exploration in Venezuelan tepuis, table-top mountains in the Guiana Highlands of South America, provided surprising discoveries of caves and cave systems in quartzite rocks that were formerly assumed to be insoluble substrate. These caves, mainly created by the water currents submerging from the upper plateau and flowing through the tectonic faults, are very scarce in food. Orthoquartzite is characterized by poor buffering capacity, when compared to carbonates, and limited nutrient availability. Barton et al. (2014) observed a significant microbial activity on exposed surfaces within a quartzite cave on Roraima Tepui that appeared to be linked to a stream flowing through the cave. Biospeleothems were described in several Venezuelan tepui caves (Aubrecht et al. 2012), along with a few cave animals such as the troglophilic orthopteran *Hydrolutos breweri*, numerous individuals of which were observed in Cueva de Charles Brewer, one of the greatest quartzite cave systems in Venezuela (Derka and Fedor 2010).

Oligotrophic conditions may be also associated with hypogenic caves (see also Chap. 2). These caves are usually created by the ascending flow of reactive fluids, characterized by deep-seated solutional aggressiveness in soluble lithologies. Hypogenic caves may be also the result of the circulation of meteoric groundwater flow in the uppermost zones of the earth crust. Hypogenic karst thus originates from void-conduit systems occurring at depth and evolves without direct geological linkage with the surface (Palmer 2011; Klimchouk et al. 2017). Hypogenic caves developed by fluids with high concentrations of carbon dioxide, but without sulfidic emanations, are very poor in trophic sources. Such caves are isolated deeper underground and may represent larger networks of fissures and voids or great chambers. Based on the first zoological observations carried out in the eastern Iberian Peninsula by Sendra et al. (2014), it appears that this type of hypogenic cave has a depauperate fauna, consisting of non-cave adapted species. This composition is the result of limited opportunity for faunal colonization during and after genesis of the hypogenic habitats because of their isolation from the surface, i.e. the lack of connection between voids and the surface during the entire history of this type of cave.

13.3   Microorganisms in Oligotrophic Caves

Many caves appear to represent an essentially oxidized and nutrient-limited environment. Consequently, any subaerial microorganisms in these systems likely subsist by scavenging sparse nutrients (Barton et al. 2004, 2007; see also Chap. 5). Cave microorganisms use varying metabolic pathways to obtain nutrients and gain energy. In *autotrophs*, carbon for cellular growth originates by converting inorganic carbon (CO_2, HCO_3^-) to organic carbon. In contrast, some microorganisms, including most fungi, have *heterotrophic metabolism* and use organic compounds for most or all of their carbon requirements. The physiological mechanisms for capturing chemical

energy are diverse, and the distinction between a chemosynthetic and a photosynthetic organism is based on whether the initial source of energy is from inorganic chemicals (litho) or light (photo). Microbes that gain energy through chemosynthesis and fix inorganic carbon are *chemolithoautotrophs*. Some microbes are *mixotrophs*, in which both chemolithoautotrophy and heterotrophy are expressed simultaneously. Microorganisms that gain cellular energy from chemical transformations but use organic carbon compounds for their carbon source are *chemoorganotrophs* (Engel 2012).

Cave microbiota include Bacteria, Actinobacteria, Archaea and Fungi and more rarely some algae and Cyanobacteria. Bacteria often establish their colonies in caves without evident sources of organic material (Northup and Lavoie 2004). Moist surfaces of cave walls and speleothems are colonized by microorganisms in the form of biofilm. In this way, microorganisms contribute significantly to both the creation of speleothems and the erosion of limestone (Cuezva et al. 2009).

Subterranean microbial communities were originally considered to be a subset of soil communities flushed underground by meteoric drip waters, surface streams and air currents or carried by animals into caves. Because of oligotrophic conditions, microbial biomass in caves was considered to be low and insufficient to impact most geological or geochemical processes (Engel 2012). The studies from recent decades, using modern methods for detecting microbial forms and revealing their metabolism pathways, have brought much deeper insight into cave microbial communities in oligotrophic caves and revealed more complex systems than previously thought. Many of the cave microbes are genetically divergent from surface microbes and adapted to the aphotic and oligotrophic cave environment. It was shown that in nutrient-poor caves heterotrophic bacteria dominate the microbial community, accompanied by a number of chemoautotrophs. Bacteria present under the oligotrophic environment of caves survive using complex metabolic pathways (Ortiz et al. 2014; Oliveira et al. 2017; De Mandal et al. 2017). Thus, despite being starved of nutrients, caves contain surprisingly diverse microbial communities. Chapters 5 and 6 provide more details about the diversity of microorganisms in caves.

In addition to having values in their own right, microorganisms play a very important role in subterranean ecosystems as a major food source for other, more complex organisms. Microorganisms stand at the base of the subterranean food web (see further text).

13.4   Faunal Communities in Oligotrophic Caves

In contrast to assemblages of guano and other energy-rich microhabitats (flood debris, root mats) with rich communities of non-troglobiotic/stygobiotic species, oligotrophic microhabitats are characterized by high proportions of the community being troglobiotic or stygobiotic. In Southeast Asia, troglobionts are mainly found foraging around scattered micropatches of food resources, mostly dispersed faeces of swiftlets, bats or rhaphidophorid crickets, and never colonize guano accumulations. Stygobionts are found in subterranean water flows and pools, in phreatic and

percolating waters and more rarely in surface streams which have been filtered through fine boulders. They are usually absent in large tropical sink-resurgence systems, where epigean fauna is often abundant (Deharveng 2004a). This is, however, not the case of some large temperate hydrological systems, such as Postojna-Planina Cave System, which hosts 62 stygobionts (Sket 2012). The pattern of high proportions of troglobionts and stygobionts being associated with oligotrophic habitats is not universal, since a high proportion of troglobionts may sometimes be associated with high amounts of organic debris. For example, root mats often support diverse community of troglobionts, as is the case of Bayliss Cave, a lava tube in North Queensland, Australia (Howarth and Stone 1990; see also Chap. 3).

The food supply in tropical and subtropical caves is richer than in temperate ones because of the higher production of biomass in the tropical biomes (Poulson and Lavoie 2000). As a consequence, selection pressure can be expected to be weaker, the rate of evolution slower and the occurrence of troglobionts limited when compared to caves with low energy input such as temperate ones (Hüppop 2012; see also Chap. 4). However, as emphasized above, patterns are not universal and the rarity of troglobionts in tropical caves may be only the result of sampling error; very few tropical caves have been appropriately sampled.

In spite of the different nature and origin of the various sources of nutrients, the composition of terrestrial troglobiotic communities is rather similar in all oligotrophic habitats for a given underground system, provided that humidity is high (see also Chap. 3). The amount, rather than the nature, of the food supply seems to control the presence of troglobionts and the composition of their assemblages. In most cases, troglobiotic faunas have fewer species than guano communities. In tropical oligotrophic caves, larger predators, such as amblypygids and scorpions, are mostly absent, probably because of the low density of potential prey (Deharveng and Bedos 2000), although some exceptions are found among scorpions (see Chap. 7). Most primary consumers are insects, while predators are arachnids, mainly small spiders. Most of these species exhibit some degree of troglomorphy, particularly the Collembola (Deharveng and Bedos 2000).

13.5 Morphological and Biological Adaptations of the Cave Fauna

In caves, food scarcity acts as a selective force and requires evolutionary adaptations (Deharveng 2004b; Trontelj 2012). Food scarcity in caves is associated with development of morphological adaptations, so-called troglomorphisms (Christiansen 1965, 2012; see also Chap. 4) or more appropriately troglobiomorphisms (Juberthie 1984). The most obvious morphological modifications are longer legs and antennae in arthropods and fins and barbels in fishes. Elongated appendages combined with enlarged or multiplied sensory areas may improve or change food-finding ability and foraging behaviour of animals in hypogean environments through better sensory

perception. Thus, cave animals can detect food faster and at a greater distance from their bodies than their epigean relatives and spend less energy searching for food. As a consequence, when foraging, they have abandoned shoaling and aggregation behaviour and adopted a continuous moving mode to cover a greater area. The benefits of shoaling behaviour in terms of reduced predation risk are lacking in most cave fishes (Timmermann et al. 2004; Hüppop 2012). In contrast to the situation in caves, movement through an interstitial medium is presumably facilitated by shortened appendages and elongated bodies that some troglobionts and stygobionts possess (Hüppop 2012). Reduced scales in stygobiont fish and reduced cuticle in troglobionts are other characteristic traits of cave animals. Weber (2000) argued that the body size of stygobiotic fishes and salamanders, which are usually small in comparison to epigean relatives, is an adaptation to the low food supply. However, the considerable reduction in morphological features is often correlated with the presence of the large amounts of stable food resources. And finally, food scarcity may trigger a switch to individuals with greater dispersal ability (see Chap. 4 for more details).

Special morphological traits have evolved in the inhabitants of moist hygropetric habitats (see also Chap. 3). Conspicuously, troglobiotic leptodirine beetles of the genera *Tartariella*, *Hadesia*, *Nauticiella*, *Radziella* and *Cansiliella* occupy such places in caves of the Eastern Alps and Balkan Peninsula. The hygropetric leptodirines have enlarged and curved claws, and modified mouthparts, characterized by a marked setation and by knee-shaped mandibles. The modified mouthparts are an adaptation for filtering organic particles from the percolating water. A similar set of morphological traits occurs in semiaquatic Diplopoda and in some aquatic crustacean genera of the families Asellidae and Niphargidae (Moldovan et al. 2004; Sket 2004). Another set of morphological modifications for hygropetric habitats is found in the troglobiotic collembolan *Pygmarrhopalites aggtelekiensis*, which is endemic to the Western-Carpathian caves. It has significantly extended antennae and legs with elongated claws that are adapted to move over the slippery surfaces of sediments and speleothems covered with a percolating water film (Kováč et al. 2014). The same habitat is occupied by the strikingly troglomorphic collembolan *Disparrhopalites tergestinus*, found in a single cave in the Eastern Alps (Italy) and *Disparrhopalites* sp., which occurs in several caves in Croatia and Bosnia and Herzegovina and has extremely long antennae.

An extreme case of adaptation to oligotrophic habitats is the chironomid dipteran *Troglocladius hajdi* discovered in Lukina jama–Trojama Cave System in Croatia at 980 m depth. The combination of strongly reduced eyes and large, broad wings is unique and might indicate that the species is able to fly or hover in the total darkness of the cave (Andersen et al. 2016). In vertebrates, there are also extreme cases of adaptations to low food in underground streams. These include the waterfall climbing loach *Cryptotora thamicola*, a troglobiotic fish distributed in a few caves of northern Thailand (Trajano et al. 2002; Fenolio 2016), and the climbing troglophilic catfish *Chaetostoma microps* from Ecuador (Hoese et al. 2015). The loach lives out of water for extended periods, using its well-developed pectoral and pelvic fins to crawl out of the water to feed on bacteria growing on damp rocks; the caves where this species lives often have elevated concentrations of carbon dioxide gas.

Besides a general food scarcity, many cave animals are faced with temporal periodicity of food. The inputs of food in oligotrophic caves may be seasonal, based on periodic flooding, or result from animals, such as bats, visiting the cave sporadically. Hence, cave animals need the ability to survive long periods of starvation, which may be the capacity to accumulate and store large energy reserves as a way of coping with food scarcity (see also Chap. 4). Cave animals can enable their young to survive periods of food shortage by producing eggs with more yolk (Thibaud and Deharveng 1994; Hüppop 2012). This phenomenon has been studied in many invertebrates, such as amphipods, decapods, collembolans and beetles, as well as in salamanders and fishes.

A reduced energy demand is also highly adaptive in caves with limited food sources, and many cave species exhibit striking energy economy (Hüppop 2012). Poulson (1963) demonstrated a decreasing trend in the metabolic rate from the epigean species of the Amblyopsidae family through troglophiles to gradually more cave-adapted troglobionts. The body temperature of troglobionts, which are exclusively ectotherms, is determined primarily by passive heat exchange with its environment. Thus, troglobionts do not spend energy for thermoregulation. Owing to mostly low metabolic rates, the troglobionts are successful in zones with limited resource supplies (food, oxygen, water). Reduction of metabolic rate is associated with prolonged lifetime and iteroparity (multiplied reproduction) (Hüppop 2012).

Another adaptation is that most cave animals exhibit feeding generalism, or dietary shift, compared with surface relatives (Hüppop 2000, 2012; Gibert and Deharveng 2002; Moldovan 2004). To cope with the general food scarcity in caves, the life history of terrestrial and aquatic animals changes towards K-selection and limited energy loss in the relatively predictable and stable habitats. K-selected species have low or no population growth, a reproductive strategy based on fewer but larger eggs, increased hatching time, prolonged larval stage, decreased growth rate, delayed reproduction, iteroparity and increased longevity (Thibaud and Deharveng 1994; Hüppop 2000, 2012). Other features enhancing energy economy include late hatching, protection of eggs and embryos, viviparity and dormancy during dry or cold periods (tardigrades, nematodes). In addition, some aquatic organisms are able to regulate their relatively low oxygen consumption (Albuquerque and Coineau 2004). In amblyopsid fishes, Poulson (1963) observed that population growth rate and density of amblyopsid fishes decrease with phylogenetic age of the cave species, and the population structure shifts towards adults.

Food scarcity and stability of the environment also help explain the tendency for paedomorphosis and neoteny (retention of larval characters) in some subterranean vertebrates (Culver 1982). However, neoteny was also observed in a food-abundant cave microhabitat, namely in tree root mats in Hawaii Island lava caves occupied by cixiid planthopper *Oliarus polyphemus* that have evolved from an ancestor by retaining the beneficial nymphal characters to adulthood (Howarth 1993). Besides the morphological features that characterize this retardation of somatic development, some anatomical changes have been observed in cave fish and amphibians, including reduced muscles and ossification (Moldovan 2004).

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