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TANJA PIPAN

EPIKARST – A PROMISING HABITAT

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COPEPOD FAUNA, ITS DIVERSITY AND ECOLOGY: A CASE STUDY FROM SLOVENIA (EUROPE)

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EPIKARST –
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COPEPOD FAUNA, ITS DIVERSITY AND ECOLOGY: A CASE STUDY FROM SLOVENIA (EUROPE)

TANJA PIPAN

POSTOJNA – LJUBLJANA
2005

This book is dedicated to my daughter Laura
with all my love.

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FOREWORD

Slovenia is situated in the very northwestern end of the lDinaric area, the site of the richest subterranean fauna in the world. The subterranean fauna increases only slightly to global biodiversity, but is of a high scientific importance in the study of mechanisms of colonisation of extreme environments as well as the nature of adaptations to these environments. I started my scientific career with both the taxonomic and the ecological investigations of copepods in hypogean environments of Slovenia. Copepod crustaceans may be the most abundant metazoans on Earth and can be found in virtually every kind of aquatic habitat from the deepest ocean trenches to damp leaf litter at high altitude in the Himalayas and from hot springs to polar seas. They are frequently found in all kinds of hypogean habitats. My research was aimed at unravelling the spatial structure of copepod fauna in the epikarst. In particular, I was interested in understanding the distribution and the ecology of copepods in the epikarst zone. For understanding of the structure and physico-chemistry of epikarst, I also studied the ecological and microgeographic distribution of epikarst copepods.

Research presented in this monograph was conducted at the Karst Research Institute ZRC SAZU (Postojna) and National Institute of Biology (Ljubljana) within the framework of the Ministry of Education, Science and Sport's programme under the mentorship of Dr. Anton Brancelj and Dr. Andrej Blejec. The hypogean fauna from percolation water and from pools, filled with percolation water from six cave systems in Slovenia, was studied in the period 2000–2003. Besides collecting fauna, parallel measurements of physical properties of the percolation water, performing the chemical analyses of water in the laboratory and the determining of the specimens were conducted. The methodologies used to asses epikarst habitats and fauna living there were also useful for the evaluation of human impacts on the environment, especially karst waters. Research represents the pioneer work on selected ecological aspects of the epikarst fauna.

Field observations and studies are continuing. After concluding my doctoral studies I advanced with my research of the epikarst fauna within the framework of the research programme of the Karst Research Institute ZRC SAZU. I enlarged my studies by participating in the bilateral project USA-Slovenia Cooperation in Science and Technology in years 2003 and 2004 which was supported by the Ministry of Education, Science and Sport (Slovenia) and Karst Waters Institute (USA).

The book has benefited from comments by two referees and discussion with several specialists: Dr. Anton Brancelj, Dr. Andrej Blejec, Prof. Dr. Tone Novak and Dr. Peter

Trontelj who guided me during my PhD work. Dr. Anton Brancelj trained me in taxonomy of copepods.

I would like to express my profound gratitude to Prof. Dr. David C. Culver and Prof. Dr. Horton H. Hobbs III who reviewed the manuscript.

Prof. David C. Culver provided also a revision of the English text. Part of it was reviewed by Dr. Trevor R. Shaw.

I am thankful to Prof. David Culver also for invaluable discussions on the interpretation of the epikarst fauna. I immensely enjoyed all this.

I would like to thank my co-workers at the Karst Research Institute ZRC SAZU for their valuable help and pleasant daily atmosphere. Tadej Slabe, head of the Institute was always interested in my work and helped me with his optimism even when the financial situation was really miserable.

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Last, but not least, I am indebted to Miran and Laura for supporting me in every possible way.

Tanja Pipan

PREFACE

Subterranean environments, especially caves, have long held the attention of biologists because of the many morphological modifications that signal adaptation to subterranean life and because of the harsh nature of the environment in which they must survive. Slovenian cave animals and Slovenian biologists have long played a central role in the study of cave life, beginning with the monumental work of Valvasor in the late 17th century. Dr. Tanja Pipan exemplifies a new generation of Slovenian biologists who continue to make Slovenia the centerpiece of speleobiology internationally.

Epikarst, or the skin of karst as it was called by the French geologist Michel Bakalowicz, has fascinated and perplexed karst scientists for decades. It has enormous importance in the transport of pollutants, in its storage capacity as an aquifer, and as the site of perhaps the most diverse assemblage of obligate inhabitants of subterranean waters (stygobionts) in the subterranean world. Epikarst is especially difficult to study because almost everything we know about it is indirect. The animals that are sampled in drips and pools have left (fallen out of) the epikarst and there is no way to sample them *in situ*. While by no means well know, the epikarst in Slovenian caves has been more intensively sampled than anywhere else, and numerous species have been described by, among others, Kiefer, Petkovski, and more recently Brancelj. In this study, Pipan has sampled more intensively and for longer periods of time than has ever been done before. Not surprisingly, she has documented yet more diversity in an already relatively species rich subterranean habitat.

In my opinion, the importance of Dr. Pipan's work lies not in the documentation of diversity but rather in her rigorous quantitative approach, not only to the question of species diversity, but also to the question of controls on the distribution of the animals.

The study that follows, while modest in tone, makes some real breakthroughs. First, she describes and utilizes techniques for sampling drips and pools that yield many more individual and species than previous work. Second, Dr. Pipan is able to assess how complete sampling is by estimating the number of species remaining to be found, and other measures of sampling completeness. Third, using canonical correspondence analysis, she begins to make sense of the physical and chemical controls on the distribution of individual species. Fourth, she demonstrates the extreme spatial heterogeneity of epikarst copepod distribution, surely a hallmark of this fascinating habitat. The thesis is filled with insightful and provocative observations. For example she points out that coexistence of many competitors is possible in a highly structured habitat like the epikarst even in the absence of habitat variability *per se.*

Like any good pioneering study, she raises as many questions as she answers. She points, and I look forward to decades of continuing groundbreaking work by Dr. Pipan on this fascinating, enigmatic habitat.

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INTRODUCTION

Karst is a landscape on water soluble rocks, e.g. limestone, dolomite, gypsum and salt. Carbonate and sulphate rocks occupy about 15–20 % of the earth's ice-free land surface. Karst areas are among the world's most diverse and fascinating environments. Karst phenomena like caves, gorges and natural bridges are known worldwide.

Karst aquifers are among the world's most important water resources. Karst covers more than a third of Europe and almost half of Slovenia, where more than 8.000 caves have been registered to date. In Slovenia, karst water resources represent more than 50 % of the water supply for the population.

Karst provides unique subsurface habitat to many rare species. Understanding the rarity of the organisms and the fragility of their habitats requires more profound knowledge about karst species, their ecosystems, their sensitivity to environmental contamination and global changes.

Hydrologically we can divide a karst aquifer into several units with different properties and flow regimes. The vadose (unsaturated) zone is the zone above the water table. It is a system of fractures and voids that drain the water from the surface to the water table. The upper layer of this zone, called epikarst, is characterised by a high fracture density and hydraulic conductivity. Water movement and storage in the epikarst zone appears to play an important role in the hydrologic regime of many karst aquifers. This epikarst habitat is exceptionally difficult to sample and exceptionally rich in species. The purpose of this study is to describe an epikarst fauna from karst caves of Slovenia, represented by a numerous specimens of Copepoda (Crustacea), as well as methods for sampling fauna associated with percolating water and to reveal possible environmental factors determining species composition of Copepoda.

The groundwater/surface water ecotones exist in many different types of environments and in all countries. Interfaces, or ecotones, between terrestrial and aquatic ecosystems have an essential role in the movement of water and materials throughout the landscape (Danielopol *et al.*, 1997). For a groundwater ecologist, inputs of water, organic matter and energy into the groundwater system come from the interface to deep water. Ecotones are zones where ecological processes are most intense and resources more diversified. They are also zones which react quickly to human influences and changes of environmental variables. Their starting point is the rainfall which are distributed over the land in two ways: by infiltration when the water percolates through the soil to become groundwater and by surface runoff when the water is collected by the hydrological network (Gibert *et al*., 1997). Three important vertical and horizontal types of groundwater/surface water ecotones are recognized: (1) the soil-karstic aquifer interface, *i.e*., epikarst, (2) springs and the interface between the saturated and unsaturated zones in karstic and porous aquifer and (3) stream underflow, *i.e*., hyporheic zone (Gibert *et al*., 1990). The main characteristics of these interfaces are their great variety of elasticity, permeability, biodiversity and connectivity.

The fact is that in biological researches epikarst is often ignored, even excluded. This lack is partly due to the inaccessibility of epikarst for direct scientific research. The present research is oriented towards biological discovery of the epikarst realm.

INTRODUCTION TO THE EPIKARST

The upper most zone of karst, the skin of karst, is "located within the vadose zone and is defined as the heterogeneous interface between unconsolidated material including soil, regolith, sediment, and vegetative debris, and solutionally altered carbonate rock that is partially saturated with water and capable of delaying or storing and locally rerouting vertical infiltration to the deeper regional phreatic zone of the underlying karst aquifer" (Jones *et al*., 2004).

The epikarst zone represents the stratum that is closest to the surface in the hydrological division of the karst underground (Klimchouk *et al*., 1996) (Figure 1). It is the interface zone between soil and rock characterized by small fractures and solution pockets that may or may not be filled with water. Epikarst is the area of higher porosity and permeability that extends a few meters below the karst surface. Because of the decompression of the rock and direct exposure of the rock to erosion processes, this uppermost part of the karst is densely fractured (Williams, 1983). Its principal characteristic is great heterogeneity, which means that it may rapidly drain the stored water towards the widened fissures or karst channels and in this way form a more or less permanently saturated zone situated close under the surface. It may also reduce the surface runoff by infiltration or the storage of precipitation water and melted snow (Petrič, 2002). Such conditions lead toward the formation of a perched aquifer and to horizontal flow of water towards zones with higher permeability, which drain the water into the saturated zone (Ford & Williams, 1989).

Known for decades by speleobiologists (Sket *et al*., 2004a), water in the epikarst zone was often termed percolating water and included as part of the vadose zone, the zone of karst above the permanently saturated (phreatic) zone. The cavities and cracks in the rock in the epikarst zone may or may not be well integrated in the horizontal direction (Brancelj & Culver, 2004). An extraordinarily complex and heterogeneous structure, it is home to wide array of animals, mostly but not exclusively aquatic, that often rivals in diversity the rest of the karst aquifer (Pipan & Brancelj, 2004a).

DEFINITION OF PROJECT GOALS AND RESEARCH QUESTIONS/HYPOTHESES

In karst caves, organisms can be found that are adapted to the specific macrocavernicolous circumstances. Another group of specially adapted organisms are those present in small cracks and crevices, *i.e.*, microcavernicolous habitats, which exist between the cave passages and the surface. The primary habitat of these species in karst is most probably the subcutaneous zone, *i.e.*, epikarst (Holsinger, 1994) but space there is too small to be investigated *in situ*.

The high level of endemism, as is evident from the literature published to date, and insufficient knowledge about the distribution of species which inhabit the unsaturated karst zone, were two reasons for my decision to focus on the problems and issues related to the distribution and the ecology of the fauna in the epikarst zone. According to rather few explorations, the major part of the fauna in the percolation water is represented by copepods (Crustacea: Copepoda) (Galassi, 2001; Brancelj, 2002). And they amount to more than 80 % of the fauna (Pipan & Brancelj, 2001).

The starting point of my research was the study of the composition of the species and the population dynamics of the copepods in percolating water. By means of systematic and long-term sampling I deepened our knowledge about the ecology of the group of copepods or species from this group and as well as find species new to science. The specific goals were to (1) to detect differences in fauna composition between trickles and pools, (2) to determine whether there are differences of fauna between caves in different geographical areas which are relatively close to each other, and (3) to detect the ecological conditions which are important and influential on the distribution of copepod species in epikarst zone.

The working hypothesis was based upon the ecological, hydrogeological and chemical explorations of the karst unsaturated zone with an emphasis on the ecology of the copepod fauna in the percolating water. At the beginning of my research I made four basic hypotheses:

- the epikarst zone is inhabited by various different species of Copepoda including certain species that have not yet been found,
- the number of species in trickles is different depending on the environmental variables (discharge, precipitation, thickness of the cave ceiling, chemistry of water),
- the copepod community in trickles is a reflection of the epikarst as a habitat; it is only numerical relationships that differ,
- the relationships between the species and the number of specimens in the trickles and pools is different.

I have endeavoured to verify these hypotheses by means of the classical morphological and taxonomic analyses of the animals and by statistical processing of the data. Microgeographic distribution, population dynamics and ecological analysis of the copepods which occur in the epikarst habitats could provide insight into a variety of questions from the above categories.

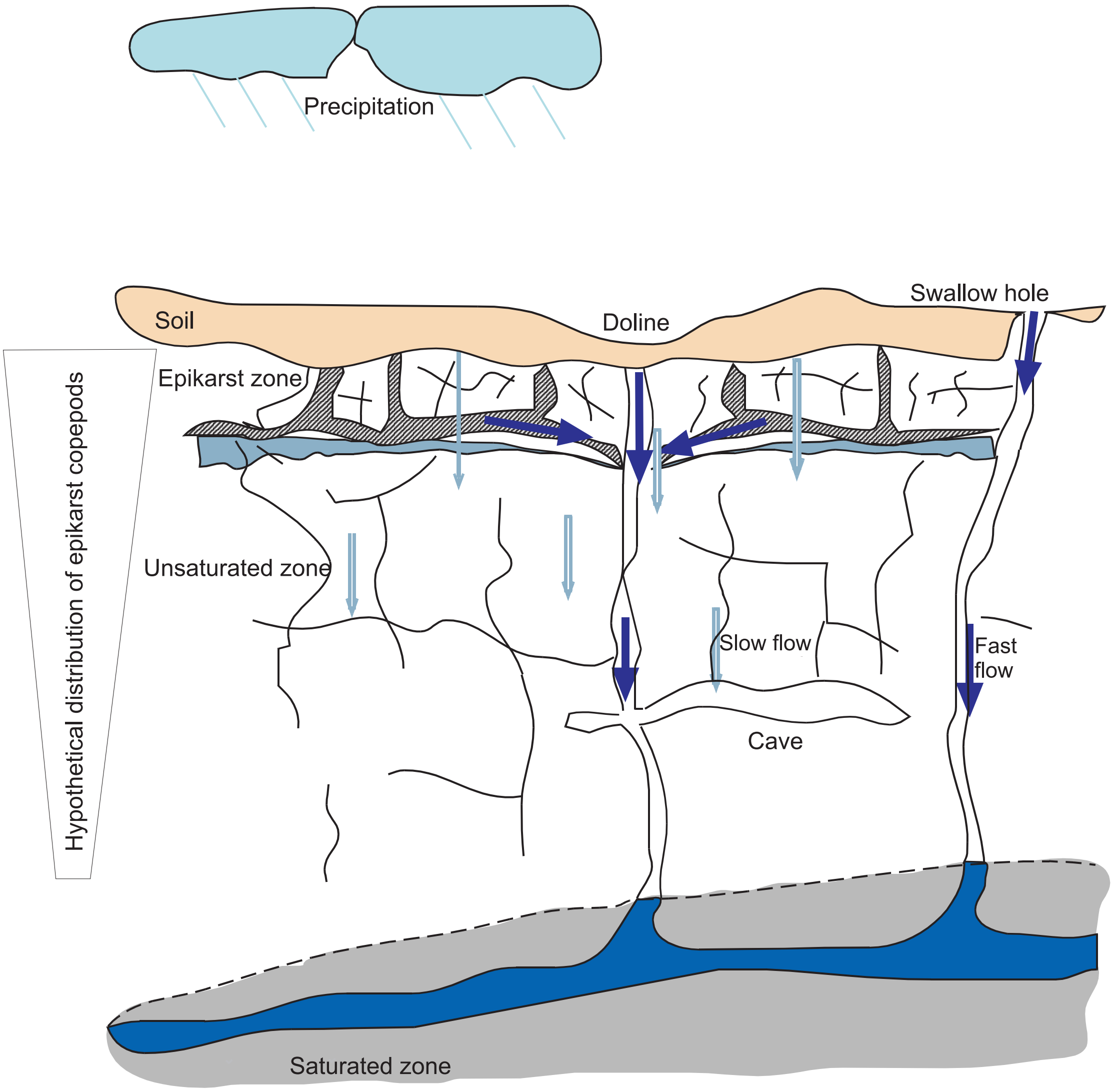

Figure 1: *Conceptual model of the fissured karstic aquifer (after Ford & Williams, 1989) and the epikarst zone as the habitat of copepods*

INTRODUCTION TO THE COPEPODS

The subclass Copepoda belongs to the class Crustacea and comprises ten orders: Calanoida, Cyclopoida, Gelyelloida, Harpacticoida, Misophrioida, Monstrilloida, Mormonilloida, Platycopioida, Poecilostomatoida, and Siphonostomatoida. Over 12.000 species are currently known but this number could easily double by the middle of the twenty – first century (Huys & Boxshall, 1991).

About 2.600 free-living freshwater species belong to four orders: Gelyelloida, Calanoida, Cyclopoida and Harpacticoida. Approximately 650 species of these four orders occupy subterranean fresh water with a high number of stygobiotic and endemic species (Huys & Boxshall, 1991). From percolation water only specimens of Cyclopoida and Harpacticoida are known so far (Brancelj, 2002; Pipan, 2003).

Copepods are aquatic crustaceans which are very diverse and are the most numerous metazoans in the aquatic community. Copepod habitats range from fresh water to hypersaline conditions, from subterranean caves to water collected in bromeliad leaves or leaf litter on the ground and from streams, rivers, and lakes to the sediment layer in the open ocean. Their habitats also range from the highest mountains to the deepest ocean trenches, and from the cold polar ice-water interface to the hot active hydrothermal vents. Copepods may be free-living, symbiotic, or internal or external parasites on almost every phylum of animals in water. Ecologically they are important links in the food chain linking microscopic algal cells to juvenile fish to whales. The usual length of adults is 1–2 mm, but adults of some species may be as short as 0.2 mm and others may be as long as 10 mm (http://www.nmnh.si.edu/iz/copepod).

The name copepod is derived from the Greek words *hope* meaning "oar" and *podos*, meaning "foot" and literraly means "oar-footed". This name refers to their broad, paddle-like swimming legs and forms the basis of their common name in other languages, such as the Slovene "veslonožci".

COPEPODS IN SUBTERRANEAN HABITATS AND THEIR ADAPTATIONS

Subterranean habitats are relatively closed spaces. Within the karstified carbonate area they frequently appear in the form of karst caves with developed systems of rock fissures and cave waters and with the interstitial. Due to the darkness and the limited connections with the surface, primary production is almost non-existent; the quantity of food is fairly limited as well as being poor in quality (Rouch, 1977; Sket, 1996a).

The subterranean space has indeed a distictive fauna (Rouch, 1977). Copepods live in groundwater and can regularly be caught in springs, wells and pools in caves (Huys & Boxshall, 1991) as well as in interstitial, phreatic and hyporheic zones (Pesce, 1985c). Morphological, physiological and ethological adaptations evolve in response to selective pressures from the environment (Dole-Olivier *et al*., 2000). Stygobiotic copepods display various degrees of morphological and biological specialisation.

Depigmentation, thigmotaxis and miniaturisation occur in copepods as preadaptive or exaptive features. Pesce & Galassi (1986a) emphasized the importance of reduction of spinulation on proximal segments of body of Cyclopoida in movement in sandy and muddy sediment. Frequent morphological adaptations of subterranean copepods are lack of pigment and an absence of eyes which indicate stygobiotic environment, whilst elongated and slim body shape indicates interstitial habitats, *i.e*., *Chappuisius inopinus* Kiefer, 1938, *C. singeri* Chappuis 1939, *Parastenocaris phyllura* Kiefer, 1938. Pospisil & Stoch (1999) demostrated detailed morphological analysis of two syntopic species of the *Diacyclops languidoides*-group, of which one species has more stygomorphic characters than other. *D. danielopoli* Pospisil & Stoch 1999 shows several characters in the apomorphic state (e.g. female antennule with shorter segments 7–11, reduction in the number of setae on antennal endopod segment two, absence of exopodal seta on maxillulary palp, longer aesthetascs in male and female antennules, longer dorsal caudal seta, absence of ornamentation on intercoxal sclerites) which could suggest a higher degree of adaptation to the subterranean habitat in comparison to *D. felix* Pospisil & Stoch 1999. Recent observations demonstrated that some epigean species also lack the antennary exopod, while some specialized stygobionts retain this feature (Pospisil & Stoch, 1999). The authors explained this fact probably due to convergence or parallel evolution.

The recently discovered species from Slovenia *Morariopsis dumonti* Brancelj, 2000 and *Parastenocaris andreji* Brancelj, 2000 are described as obligate stygobiotic species (Brancelj, 2000a, 2000b). In specimens of both species a combination of regressive and progressive troglomorphic traits is present: total depigmentation, eye reduction and body and appendage elongation (Turk *et al.*, 1996). Ornamentation is reduced as a result of small interstitial space and possibly also lack of food (Brancelj, 2000b). Inhabiting of small and narrow spaces is supported by relatively short appendages of swimming legs (P2–P4) in *M. dumonti*, while the elongated proximal segments of antennula, antenna and particularly maxillae has *P. andreji*. Elongated appendages help to detect a potential prey earlier which, at the same time, has less chance to escape (Brancelj, 2000b).

The differences in feeding behaviour and swimming behaviour between stygobiotic and epigean copepods are likely adaptations to subterranean life (Stoch, 1995; Ueda & Reid, 2003). Stygobiotic copepods are swimmers, crawlers or burrowers. Interstitial cyclopoids move among sediment particles by pushing their body over the grains to gain propulsion. Harpacticoids are mainly burrowers (Dussart & Defaye, 1995). The worm-like habitus enhances the ability to move in sediments and narrow spaces. An additional pseudosomite and the unfused genital double somite optimise the flexibility of the urosome. Another modification is the shortening of the swimming legs by oligomerisation in some groundwater copepods. Nevertheless, some stygobiotic harpacticoids have relatively long swimming legs (Huys & Boxshall, 1991).

Microcrustaceans display a large variety of feeding habits and food requirements (Einsle, 1996). However, most studies on copepod diets concern marine species or freshwater planktonic specis. Little is known on copepods feeding in lotic benthic and interstitial habitats. Several large cyclopoids are predatory. Predation is rarely found in freshwater harpacticoids but *Phyllognathopus viguieri* (Maupas, 1892) may feed on nematodes. The main food source for harpacticoids is organic matter either as coarse and fine particles and most probably the microbial biofilm associated with it (Dole-Olivier *et al.*, 2000; Gerič *et al.*, 2004).

The annual cycles of a number of species living in subterranean habitats are not yet known and are difficult to study (Sarvala, 1979; Einsle, 1996). Most copepods develop from fertilised eggs (Couch *et al*., 2001; Ueda & Reid, 2003). Fertilisation consists in the attachment of the spermatophore by the male to the copulatory pore of the female. Pre-copulatory mate guarding is common among harpacticoids and cyclopoids. After copulation, sperm is stored in the female seminal receptacle; the eggs are fertilised and usually extruded into egg sacs (Dürbaum, 1995; Berger & Maier, 2001). True groundwater copepods often lack true egg sacs, and egg sacs have never been found among stygobiotic species of the harpacticoid *Pseudectinosoma*, some *Speocyclops* in *Graeteriella* species (Rouch, 1977, 1986; Dole-Olivier *et al*., 2000). In Parastenocarididae two eggs at a time are released onto the substratum, sometimes after previous carrying as in *Parastenocaris phyllura*. Groundwater crustaceans as Copepoda, Amphipoda and Isopoda produce, as a result of K-selection, fewer but larger eggs than epigean species. Large eggs ensure the food supply of nauplii in an oligotrophic environment (Brancelj, 1986c; Culver *et al*., 1995; Turk *et al*., 1996).

Free-living copepods go through six naupliar (N1–N6) and six copepodite stages (C1–C6) (Dahms, 1993) with some exception as in female of *Parastenocaris phyllura* where stage C5 is unknown (Glatzel, 1990). The rate of development is strongly affected by temperature and food supply (Dole-Olivier *et al*., 2000). Among the species studied by Sarvala (1979b), the fastest development time was observed in the cyclopoid *Paracyclops fimbriatus* (Fischer, 1853). Groundwater crustaceans show a general trend toward a prolongation of the life cycle at various stages. Groundwater copepods develop slowly, with one or more generations per year and possible peaks in spring and autumn. Consequently, interstitial and stygobiotic species have long life spans, such as 12 months (*Parapseudoleptomesochra subterranean*), 2,5 years (*Parastenocaris phyllura*), 3 years (*Antrocamptus catherinae* Chappuis & Rouch 1960) and 3,5 years (*Parastenocaris vicesima* Klie 1935) (Glatzel, 1990; Glatzel & Schminke, 1996).

Temperature requirements influence the life cycle and consequently the abundance and distribution of each species in microcrustaceans (Fong & Culver, 1994; Ward & Palmer, 1994). The cold-stenotherm species as *Maraenobiotus vejdovskyi* (Mrazek, 1893), *Epactophanes richardi* (Mrazek, 1893), *Hypocamptus brehmi* (Van Douwe, 1922), *Bryocamptus echinatus* (Mrazek, 1893), *B. typhlops* (Mrazek, 1893) and *B. cuspidatus* (Schmeil, 1893) are common inhabitants of springs and of the rhithron section of streams and rivers. Many stygobiotic harpacticoids seem to have invaded groundwater from surface water as a result of changes in climate during glacial phases (Rouch & Danielopol, 1987; Botosaneanu & Holsinger, 1991).

In interstitial habitats, the role of dissolved oxygen concentration in determining copepod species distribution at different spatial and temporal scales has been stressed by many authors (Ward & Voelz, 1997; Dole-Olivier *et al*., 2000). But, some *Parastenocaris* species tolerate a wide range of oxygen concentration, others as *Diacyclops languidus* s. l. and *D. languidoides* s. l., are very sensitive to low oxygen supply. Rundle (1990) stressed that pH has consistently been shown to influence the species richness of harpacticoid copepods.

DIVERSITY OF HYPOGEAN FAUNA IN THE DINARIC REGION AND DISTRIBUTION PATTERNS OF COPEPODS

In Europe the majority of stygobionts are to be found within the karst regions of the Mediterranean and in the Dinaric region (Sket, 1999c). In Slovenia, karst covers 44 % of all land surface. Karst hypogean habitats constitute quite a significant part of nature there. Despite its small surface area (20.272 km^2), Slovenia represents at the moment one of the most bountiful countries in the world with regard to the number of the specialised inhabitants of subterranean waters (stygobionts) (Sket, 1996a). The particularly rich Slovenian subterranean biodiversity can be important in promoting the conservation of this special biodiversity segment in other areas.

The growing interest in biodiversity has prompted several researchers to consider the question of the number of cave species there are likely to be. Slovenia is on the very northwest end of the Dinaric area, which is by far the richest in the world for subterranean fauna in comparison with other regions of sub-continental size. The richness means approximately 517 recorded species of stygobionts and 783 species of troglobionts in the western Balkans; there are respectively 207 and 166 such species in Slovenia. Among the approximately 207 stygobiotic taxa in Slovenia there are 120 endemic taxa (Sket, 1999c; Culver & Sket, 2000; Sket *et al*., 2004b). Crustacea prevail in the waters, as do Coleoptera in the terrestrial habitats. Beside this, the region abounds in Gastropoda, which are usually scarce elsewhere. Furthermore, stygobiotic representatives of cnidarians, freshwater sponges, freshwater tubeworms and clams can only be found here. Particularly famous and historically important is the only European stygobiotic amphibian *Proteus* with its recently discovered non-troglomorphic race (Sket, 1999b). Causes for a comparatively high diversity could be searched for the lack of competitors, high speciation rates through spatial partitioning, ecological partitioning in the case of co-occurrence, favourable, constant temeperature and a turbulent geological history (Sket, 1999c). Each distribution pattern is the result of one or more geological, paleogeographical, or paleoecological event (Sket, 1994a, 2002).

According to some rough calculations there are among the representatives of Calanoida five stygobiotic species known in Europe (out of total of 79 known species), in Cyclopoida 60 (out of 114 species) and in the group of Harpacticoida 171 stygobiotic species (out of 245 species) (Sket, 1999c). The 233 stygobiotic species of copepods in Europe are not in proportion with the number of the all stygobiotic species of Copepoda in the world, which amounts to 252 others (Botosaneanu, 1986). This is a consequence of the insufficient exploration of the copepods, particularly in the U.S.A. (Culver & Holsinger, 1992; Culver & Sket, 2000).

In the year 2003 the first investigation of epikarst habitat in the Appalachians (U.S.A.) was done (Pipan, 2004; Pipan & Culver, in review). A total of 20 genera of copepods were found from 17 caves in West Virginia.

Some copepod genera found in subterranean water are marine in origin (“thalassoid” species) such as *Parastenocaris*; while others (e.g. *Diacyclops*, *Eucyclops*, *Graeteriella*, *Speocyclops*, *Bryocamptus*, *Elaphoidella*, *Moraria*) colonized the groundwater system directly from superficial fresh waters, during different geologic epochs (Ward & Palmer, 1994; Pesce, 1985c).

Some copepods are cosmopolitan (e.g. *Eucyclops*, *Paracyclops*, *Diacyclops*, *Phyllognathopus*, *Attheyella*, *Epactophanes*, *Canthocamptus*), while others are endemic to a particular biogeographic region. A higher degree of endemism occurs among groundwater taxa, at the ordinal, familial, generic and, more frequently specific, taxonomic levels. Such is the case of many *Diacyclops*, *Speocyclops*, *Graeteriella*, *Nitocrella*, *Elaphoidella* and *Parastenocaris* species. The most interesting family in this regard is the Parastenocarididae. At present it includes five genera, four of which are found exclusively in the South America. On the other hand, *Parastenocaris* is cosmopolitan and includes more than 200 species and subspecies, most of which have very local distributions (Dole-Olivier *et al*., 2000; Williamson & Reid, 2001).

SURVEY OF RESEARCHES OF COPEPODS IN SLOVENIA UP TO THE PRESENT

By the end of 2000 107 species and sub-species of free-living copepods (Copepoda nonparasitica) had been found across the territory of Slovenia, out of which there were 42 subterranean species (Table 1). Due to the numerous newly discovered species, especially in subterranean habitats, the number of copepod species is rapidly increasing. Many of these species are limited exclusively to the Slovene territory (endemics) and frequently even to one single cave or even trickle (habitat). According to the data known up to now there are eight such species.

According to Sket & Brancelj (1992), the presumed number of Calanoida in Slovenia was 25. However, only ten species have been reliably identified. One species, *Troglodiaptomus sketi* Petkovski, 1978, lives exclusively in subterranean waters (Brancelj, 1987, 1996).

In Copepoda Cyclopoida, one of the most omnipresent groups, the number of species and subspecies of Slovenia was 48 (Sket & Brancelj, 1992). Cyclopoids include 18 stygobiotic taxa (Table 1). In the cyclopoid group there are six taxa with a type locality in Slovenia. Ten taxa of cyclopoids, six of them are stygobiotic, are known from a single locality in Slovenia. Cyclopoids have three stygobiotic taxa that are endemic to Slovenia: *Diacyclops hypogeus* (Kiefer, 1930), *D. slovenicus* (Petkovski, 1954) and *Metacyclops postojnae* Brancelj, 1990.

At present 49 species and subspecies of harpacticoid copepods of Slovenia have been found and discoveries of new species are still being made (Brancelj & Pipan, 2001, 2004). From 1996 to 2002 three stygobiotic harpacticoid species of Slovenia have been discovered and described (Stoch, 1998; Brancelj, 2000a, 2000b); and the presence of two other stygophilic species in Slovenia was confirmed. Harpacticoids include 23 stygobiotic taxa (Table 1). In the harpacticoid group there are 15 taxa with a type locality

Table 1: *List of species and subspecies of copepods (Crustacea: Copepoda) found in Slovenia up to the year 2000 (after Brancelj, 1996). Bibliography is added describing the ecology and taxonomy of stygobiotic species/subspecies and some epigean species which are transported into the caves by accident.*

CALANOIDA	stygo-bionts	endemics to SLO	loc. typ. in SLO	single place in SLO
1. *Acanthodiaptomus denticornis* (Wierzejski, 1887)				
2. *Arctodiaptomus alpinus* (Imhof, 1885)				
3. *Arctodiaptomus laticeps* (Sars, 1863)				
4. *Eudiaptomus gracilis* (Sars, 1863)				
5. *Eudiaptomus graciloides* (Lilljeborg, 1888)				
6. *Eudiaptomus hadzici* (Brehm, 1939)				
7. *Eudiaptomus transylvanicus* (Daday, 1890)				+
8. *Heterocope saliens* Lilljeborg, 1863				
9. *Mixodiaptomus tatricus* (Wierzejski, 1883)				
10. *Troglodiaptomus sketi* Petkovski, 1978	+			
CYCLOPOIDA				
11. *Acanthocyclops gordani* Petkovski, 1971	+			+
12. *Acanthocyclops hispanicus* Kiefer, 1937	+			+
13. *Acanthocyclops kieferi* (Chappuis, 1925)	+			
14. *Acanthocyclops robustus* (Sars, 1863)				
15. *Acanthocyclops troglophilus* (Kiefer, 1932)	+			
16. *Acanthocyclops venustus* (Norman in Scott, 1906)	+			
17. *Acanthocyclops venustus stammeri* (Kiefer, 1930)	+		+	
18. *Acanthocyclops vernalis* (Fischer, 1853)				
19. *Cryptocyclops bicolor* (Sars, 1863)				
20. *Cyclops abyssorum praealpinus* (Kiefer, 1939)				+
21. *Cyclops abyssorum tatricus* (Kozminski, 1927)				
22. *Cyclops strenuus* s.lat Fischer, 1851				
23. *Cyclops vicinus* Ulianine, 1875				
24. *Diacyclops bicuspidatus* (Claus, 1857)				
25. *Diacyclops bicuspidatus odessanus* (Schmankevitsch, 1875)				
26. *Diacyclops bisetosus* (Rehberg, 1880)				
27. *Diacyclops charon* (Kiefer, 1931)	+		+	
28. *Diacyclops clandestinus* (Kiefer, 1926)	+			
29. *Diacyclops hiberniae* (Gurney, 1927)	+			
30. *Diacyclops hypogeus* (Kiefer, 1930)	+	+	+	
31. *Diacyclops languidoides* (Lilljeborg, 1901)	+			
32. *Diacyclops languidus* (Sars, 1863)				
33. *Diacyclops slovenicus* (Petkovski, 1954)	+	+	+	

in Slovenia, while 11 taxa are endemic to Slovenia. All but one are stygobiotic. Fourteen taxa of harpacticoids have each a single locality known in Slovenia.

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Pesce in Lattinger (1983), Petkovski (1984a), Stoch (1987b)
Pesce in Galassi (1984), Petkovski (1984a), Brancelj (1986a), Sket (1994a)
Brancelj (1986a, 1987)
Kiefer (1932), Stoch (1985a, 1987a, 1987b, 1988), Brancelj (1992a, 1992b), Sket (1994a)
Stammer (1932), Petkovski (1984a, 1984b), Petkovski & Brancelj (1985)
Kiefer (1930), Brancelj (1987), Stoch (1987a, 1987b)
Dussart (1969)
Dussart (1969)
Dussart (1969)
Dussart (1969)
Dussart (1969)
Kiefer (1938a), Pesce & Fabrizi (1979), Pesce & Maggi (1979), Petkovski (1984b), Stoch (1985a, 1985b), Brancelj (1986a), Pesce & Pagliani (1997)
Stammer (1932), Pesce & Fabrizi (1979), Pesce & Maggi (1979), Pesce & Galassi (1983), Stoch (1983a, 1983b, 1985a, 1985b), Pesce & Galassi (1985), Petkovski & Brancelj (1985)
Stammer (1932), Plesa (1968), Pesce & Fabrizi (1979), Pesce & Maggi (1979), Pesce & Galassi (1983), Petkovski & Brancelj (1985), Stoch (1985a, 1994), Brancelj (1986a), Pesce (1994)
Petkovski (1984b), Stoch (1985a, 1987a, 1987b), Brancelj (1987, 1992a, 1992b), Pesce (1994), Stoch & Dolce (1994)
Stammer (1932), Pesce & Galassi (1983), Petkovski (1984a), Petkovski & Brancelj (1985), Brancelj (1986a, 1987, 1992a, 1997), Stoch (1988), Pesce (1992, 1994), Pesce & Pagliani (1997)
Brancelj (1996)
Kiefer (1930), Petkovski & Brancelj (1985)
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Petkovski (1984a), Petkovski & Brancelj (1985), Brancelj (1986a, 1997), Pesce (1994), Stoch & Pospisil (2000b)
Petkovski (1954, 1984b), Brancelj (1986a, 1992a, 1992b, 1997)

CYCLOPOIDA	stygo-bionts	endemics to SLO	loc. typ. in SLO	single place in SLO
34. *Diacyclops tantalus* Kiefer, 1937	+			+
35. *Diacyclops zschokkei* (Graeter, 1910)	+			
36. *Ectocyclops phaleratus* (Koch, 1838)				
37. *Eucyclops lilljeborgi* (Sars, 1914)				+
38. *Eucyclops macruroides* (Lilljeborg, 1901)				
39. *Eucyclops macrurus* (Sars, 1863)				
40. *Eucyclops serrulatus* (Fischer, 1851)				
41. *Eucyclops speratus* (Lilljeborg 1901)				
42. *Graeteriella unisetigera* (Graeter, 1908)	+			+
43. *Macrocyclops albidus* (Jurine, 1820)				
44. *Macrocyclops fuscus* (Jurine, 1820)				
45. *Megacyclops viridis* (Jurine, 1820)				
46. *Mesocyclops leuckarti* (Claus, 1857)				
47. *Metacyclops gasparoi* Stoch, 1987	+			+
48. *Metacyclops postojnae* Brancelj, 1990	+	+	+	+
49. *Microcyclops varicans* (Sars, 1863)				
50. *Paracyclops affinis* (Sars, 1863)				
51. *Paracyclops poppei* (Rehberg, 1880)				+
52. *Paracyclops fimbriatus* (Fischer, 1853)				
53. *Paracyclops fimbriatus chiltoni* (Thompson, 1882)				
54. *Speocyclops infernus* (Kiefer, 1930)	+		+	
55. *Thermocyclops crassus* (Fischer, 1853)				
56. *Thermocyclops dybowskii* (Lande, 1890)				
57. *Thermocyclops oithonoides* (Sars, 1863)				+
58. *Tropocyclops prasinus* (Fischer, 1860)				
HARPACTICOIDA				
59. *Attheyella crassa* (Sars, 1862)				
60. *Attheyella wierzejskii* (Mrazek, 1893)				
61. *Bryocamptus balcanicus* (Kiefer, 1933)	+			
62. *Bryocamptus cuspidatus* (Schmeil, 1893)				
63. *Bryocamptus dacicus* (Chappuis, 1923)				
64. *Bryocamptus echinatus* (Mrazek, 1893)				
65. *Bryocamptus minutus* (Claus, 1863)				
66. *Bryocamptus pygmaeus* (Sars, 1863)	+			
67. *Bryocamptus pyrenaicus* (Chappuis, 1923)	+			
68. *Bryocamptus rhaeticus* (Schmeil, 1893)				
69. *Bryocamptus tatrensis* Minkiewicz, 1916	+			+
70. *Bryocamptus typhlops* (Mrazek, 1893)	+			
71. *Bryocamptus vejdovskyi* (Mrazek, 1893)				
72. *Bryocamptus zschokkei caucasicus* Borutskii, 1930				

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Brancelj (1986a, 1987)
Stammer (1932), Kiefer (1933b), Petkovski (1984b), Petkovski & Brancelj (1985), Stoch (1985b), Brancelj (1986a, 1992b, 1997), Pesce (1992), Petkovski & Karanovic (1997)
Dussart (1969)
Stoch (1987a), Brancelj (1992b)
Brancelj (1986a)
Brancelj (1986a, 1987)
Kiefer (1933b), Pesce & Fabrizi (1979), Pesce & Maggi (1979), Petkovski (1984b), Petkovski & Brancelj (1985), Stoch (1985a), Brancelj (1986a, 1992b, 1997), Pesce (1992)
Kiefer (1930, 1968), Petkovski (1984a), Brancelj (1986a), Stoch (1987b, 1988, 1997)
Stammer (1932), Chappuis (1936a, 1937), Pesce (1981), Petkovski (1983a, 1984b), Petkovski & Brancelj (1985), Brancelj (1986a, 1986b, 1992a, 1992b), Pesce & Pagliani (1997), Stoch (1998a)
Chappuis (1936a), Petkovski (1983a), Brancelj (1986a, 1986b), Stoch (1997)
Brancelj (1986a, 1986b), Apostolov & Pesce (1989), Galassi (1997), Gerecke et al. (1998)
Chappuis (1933a, 1936a), Petkovski (1984b), Brancelj (1986a, 1992a, 1992b), Stoch (1997)
Dussart (1967)
Chappuis (1929b, 1936b, 1956), Pesce (1981), Petkovski (1983a, 1984b), Brancelj (1986a), Pesce & Galassi (1987), Apostolov & Pesce (1989), Petkovski & Karanovic (1997)
Rouch (1968), Pesce (1983a), Petkovski & Brancelj (1985), Brancelj (1986a, 1986b), Pesce & Galassi (1987), Apostolov & Pesce (1989), Ciccarese & Pesce (1997), Galassi (1997)
Chappuis (1923, 1936a), Kiefer (1933a), Petkovski (1983a), Brancelj (1986a, 1986b)
Dussart (1967)
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Dussart (1967)
Brancelj (1986a)

HARPACTICOIDA	stygo-bionts	endemics to SLO	loc. typ. in SLO	single place in SLO
73. *Bryocamptus zschokkei* (Schmeil, 1893)				
74. *Canthocamptus staphylinus* (Jurine, 1820)				
75. *Ceuthonectes rouchii* Petkovski, 1984	+	+	+	
76. *Ceuthonectes serbicus* Chappuis, 1924	+			
77. *Echinocamptus georgevitchi* (Chappuis, 1924)	+			+
78. *Echinocamptus luenensis* (Schmeil, 1894)				
79. *Echinocamptus pilosus* (Van Douwe, 1910)				
80. *Elaphoidella bidens* (Schmeil, 1894)				+
81. *Elaphoidella cvetkae* Petkovski, 1983	+		+	
82. *Elaphoidella elaphoides* (Chappuis, 1923)				
83. *Elaphoidella franci* Petkovski, 1983	+	+	+	+
84. *Elaphoidella jeanneli* Chappuis 1928	+		+	
85. *Elaphoidella kieferi* Petkovski & Brancelj, 1985	+	+	+	+
86. *Elaphoidella phreatica* (Sars, 1862)				
87. *Elaphoidella stammeri* Chappuis, 1936	+		+	
88. *Epactophanes richardi* (Mrazek, 1893)				+
89. *Maraenobiotus insignipes* (Lilljeborg, 1902)				
90. *Moraria mrazeki* (Scott, 1903)				
91. *Moraria poppei* (Mrazek, 1893)				
92. *Moraria poppei meridionalis* Chappuis, 1929	+		+	+
93. *Moraria radovnae* (Brancelj, 1988)		+	+	+
94. *Moraria stankovitchi* Chappuis, 1924	+			
95. *Moraria varica* (Graeter, 1910)				
96. *Morariopsis dumonti* Brancelj, 2000	+	+	+	
97. *Morariopsis scotenophila* (Kiefer, 1930)	+	+	+	
98. *Nitocra hibernica* (Brady, 1880)				+
99. *Nitocrella hirta* Chappuis, 1924				
100. *Nitocrella slovenica* Petkovski, 1959	+	+	+	
101. *Paracamptus gasparoi* Stoch, 1998	+	+	+	+
102. *Paracamptus schmeili* (Mrazek, 1893)				
103. *Paramorariopsis anae* Brancelj, 1992	+	+	+	+
104. *Parastenocaris andreji* Brancelj, 2000	+			+
105. *Parastenocaris gertrude* Kiefer, 1968				
106. *Phyllognathopus viguieri* (Maupas, 1892)				
107. *Pseudomoraria triglavensis* Brancelj, 1994	+	+	+	+

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Petkovski (1984b), Brancelj (1991b, 1992b)
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Chappuis (1924, 1929b), Petkovski (1983a), Pesce & Galassi (1987)
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Chappuis (1924, 1929a), Petkovski (1956, 1983b), Pesce (1981, 1983c, 1985a), Pesce & Galassi (1983), Pesce & Lattinger (1983), Brancelj (1986a, 1986b, 1988), Pesce et al. (1987), Petkovski & Karanovic (1997)
Petkovski (1983a), Brancelj (1986b), Bole et al. (1993)
Chappuis (1928, 1936a), Kiefer (1930), Stammer (1932), Petkovski (1984b), Brancelj (1986a, 1986b), Stoch (1998a)
Petkovski & Brancelj (1985)
Brancelj (1988)
Chappuis (1936a), Petkovski (1983a), Brancelj (1986a, 1986b), Stoch (1997)
Petkovski (1956), Kiefer (1963), Borutskii (1964), Brancelj (1988)
Dussart (1967)
Petkovski (1956), Brancelj (1988)
Chappuis (1933a), Kiefer (1963), Pesce & Galassi (1983, 1987), Brancelj (1986a, 1986b), Apostolov & Pesce (1989), Galassi (1997), Stoch (1997, 1998a)
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Stoch (1998a)
Chappuis (1933a, 1936a, 1936c, 1937), Petkovski (1983a), Brancelj (1986a, 1986b), Pesce & Galassi (1987), Apostolov & Pesce (1989), Stoch (1998a)
Brancelj (1991b, 1992b)
Brancelj (2000b)
Stoch (2000)
Chappuis (1933a, 1950), Borutskii (1964), Kiefer (1968)
Brancelj (1994)

The first data on subterranean Copepoda in Slovenia were published by Joseph (1882) and Schmeil (1893, according to Wolf, 1934–1938).

Chappuis's (1923, 1924, 1928, 1933a, 1936a, 1936c, 1937) investigations and reports on copepods of seven caves and springs near Novo Mesto (Slovenia) comprised data only on harpacticoids. He found 13 copepod species, mostly of the genus *Bryocamptus* (four species) and *Moraria* (three species). Six of them were stygobiotic, while three species and one subspecies were new for the science. One species and subspecies (e.g. *Elaphoidella stammeri* and *Moraria poppei meridionalis*) were described from specimens from Podpeška jama, two more species (e.g. *Echinocamptus georgevitchi* and *Elaphoidella jeanneli*) were found in Črna jama.

In the 1930's Kiefer (1930, 1931, 1933b) and Stammer (1932) investigated copepod fauna mostly in Škocjanske jame and the Postojna-Planina cave system. Some research was also done in Dimnice cave. Kiefer found and listed 13 copepod species. Škocjanske jame became a type locality for three copepod species and one subspecies (e.g. *Diacyclops hypogeus, Speocyclops infernus, Morariopsis scotenophila* and *Acanthocyclops venustus stammeri*), while Postojnska jama was a type locality for one copepod species and subspecies (e.g. *Diacyclops charon* and *D. languidoides goticus*). Stammer published a list of copepods where he indicated ten species and one subspecies from Škocjanske jame and three species from Črna jama.

Petkovski published his first researches of copepods of Slovenia at the beginning of the 1950s of the twentieth century. In the material from different subterranean habitats, karstic springs and caves such as Škocjanske jame, Planinska jama, Ljubljanica springs and Tominčev izvir (spring) he found and described six new species.

Petkovski (1954) described species *Diacyclops tantalus* f. *slovenica* which was later renamed in *Diacyclops slovenicus*. It was found in Ljubljanica springs near Vrhnika (Slovenia). *Nitocrella slovenica* was described from subterranean waters near Celje (Slovenia), while *Ceuthonectes rouchii* from Tominčev izvir in the catchment area of the Krka river (Petkovski, 1984b). All three mentioned species are stygobionts, known only from Slovenia.

Eight species of Harpacticoida were found in Planinska jama, among them two new species (Petkovski, 1983a). *Elaphoidella cvetkae* and *Elaphoidella franci* were found by filtering of percolation water. Both species are stygobiotic. Further investigations in Planinska jama shown that specimens of *E. cvetkae* are relatively abundant while *E. franci* was never found again (Petkovski, 1983a).

Plesa (1968) was one of the foreign researchers who investigated subterranean fauna of copepods in Slovenia. He found specimens of *Diacyclops bisetosus* in Škocjanske jame.

During the investigation of copepods in Škocjanske jame Petkovski & Brancelj (1985) identified and described one male specimen of harpacticoids as a new species of *Elaphoidella kieferi*. It has been found in only one trickle of percolation water and it seems to be specialized on very distinctive ecological conditions.

Brancelj (1986a, 1986b, 1987) collected copepods from the subterranean river

Pivka and from pools filled with percolation water. The surface runoff has close links with the underflow and the groundwater either along the river sides or in the bottom of rivers. The sinking river in the cave system is inhabited mostly by stygobionts and stygophiles but also accidental species from the surface. From the Postojna-Planina cave system 46 copepods have been found. Two of the listed taxa were found to be new to science (e.g. *Metacyclops postojnae* and *Troglodiaptomus sketi postojnae*). Five species of Harpacticoida and two species of Cyclopoida were discussed from the morphological and taxonomic point of view (Brancelj, 1986b, 1987).

Brancelj (1992a, 1992b) reported some copepods from Osapska jama near Osp and Jama pod Krogom near Mlini at the Croatian-Slovene border and from some springs at the Karst edge. 22 species of copepods were recognized. Among them specimens of *Paramorariopsis anae* were found in small pools rich in organic debris at the entrance of the cave Jama pod Krogom in the SSW part of Slovenia. This was new genus and new species.

In SW Slovenia four springs have been sampled for copepod fauna (Brancelj, 1997). From two springs of the Vipava river, and additional two springs Ajba and Kajža nine specimens of harpacticoids and cyclopoids were found.

Paracamptus gasparoi, the second species of the genus *Paracamptus* found in Europe, was collected in a Slovenian cave, Viršnica, where it inhabited small pools of percolating water as well as a hypogean fast running stream (Stoch, 1998). *Parastenocaris gertrude* was reported from Slovenia for the first time in the Slovenian cave, Pajsarjeva jama, where it inhabited small pools of percolating water and subterranean stream (Stoch, 2000). *P. gertrude* was first discovered in the interstitial groundwaters of some Italian rivers and streams. With the discovery of *P. gertrude* in Italy and Slovenia the known range of the species was extended significantly eastward.

Recently discovered species *Morariopsis dumonti* and *Parastenocaris andreji* are endemic to Slovenia. *M. dumonti* have been found in a small cave, Velika Pasjica, where the copepods inhabits an unsaturated karst zone (Brancelj, 2000a). From the same cave in central Slovenia new species of the genus *Elaphoidella* was found (Brancelj, pers. comm.). *P. andreji* was described upon two adult females from the main cave passage (Brancelj, 2000b).

GEOGRAPHICAL LOCATION OF THE RESEARCH CAVES AND DESCRIPTION OF RESEARCH METHODS

The composition of the epikarst copepod fauna and the environmental factors determining species composition were studied in six caves of the Notranjska, Primorska and Dolenjska karst regions. They were Postojnska jama, Pivka jama, Črna jama, Škocjanske jame, Dimnice and Županova jama (*jama* = *cave*, pl. *jame*) (Figure 2, Table 2). The six caves studied are situated in south and southwest Slovenia. Three caves (Postojnska jama, Pivka jama, and Črna jama) are part of the same cave system and the other three caves were likely to be important sites of epikarst biodiversity because they were important sites for other components of subterranean biodiversity. Two are developed as tourist caves (Postojnska jama and Škocjanske jame) and the others are occasionally shown to tourists. In all the caves, permanent or temporary trickles dripped from the ceiling in several locations. In Postojnska jama there were ten sampling sites, after which five sampling sites were chosen in the other caves (ground plans are in Appendix section). I endeavoured to study Postojnska jama more intensely, and so the ten sites were sampled at weekly intervals.

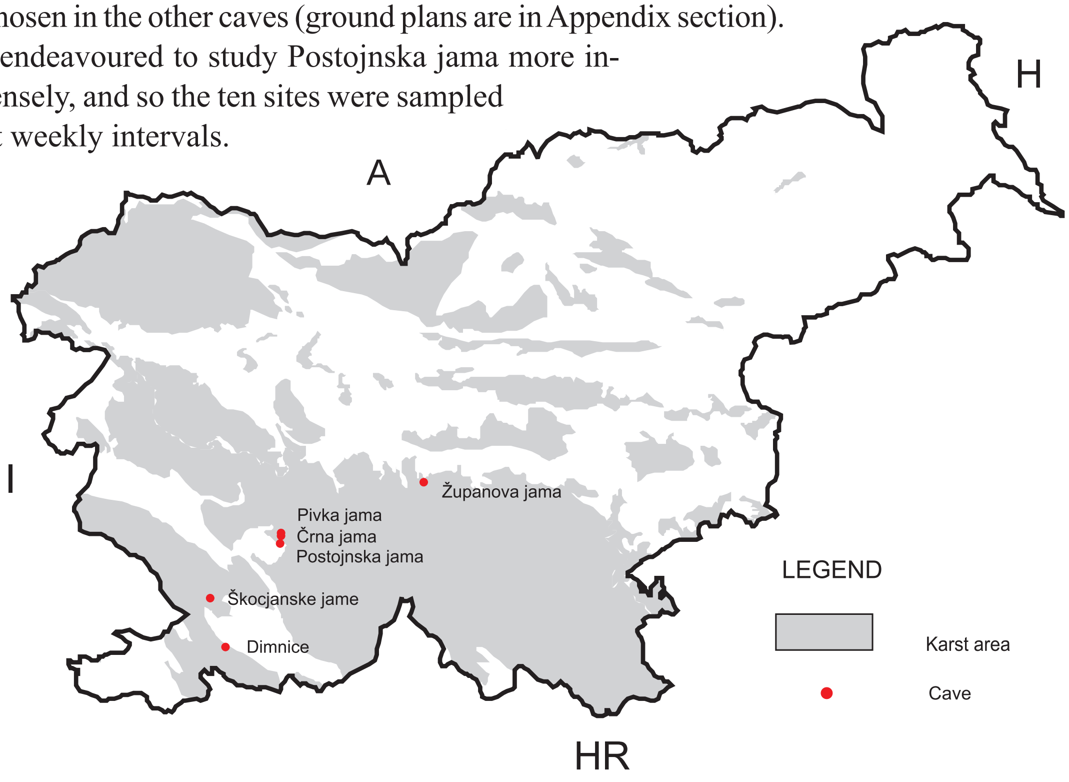


Figure 2: *Geographical location of the research caves in Slovenia*

***Table 2:** Some characteristics of sampling caves*

Cave	Cadastre number	Municipality	Entrance altitude (m a.s.l.)	Length (m)	Depth (m)	Min-max sampling site elevation	Min-max ceiling thickness
Postojnska jama	747	Postojna	530	13500	115	520–530	30–110
Pivka jama	472	Postojna	540	794	77	497–504	50–70
Črna jama	471	Postojna	540	3294	39	512–531	30–65
Škocjanske jame	735	Divača	425	5800	250	300–347	60–110
Dimnice	736	Hrpelje-Kozina	567	6020	134	495–545	60–110
Županova jama	727	Grosuplje	468	682	70	434–465	15–50

In this study I restricted myself to the community of copepods in the fissures and solution pockets in the upper part of the karst. Epikarst represents in the hydrological division of the karst underground the stratum that is closest to the surface and which remains inaccessible using standard research methods. The epikarst fauna was explored indirectly by taking samples of the percolating water and cave pools filled with such water. The samples were taken from the vertical flow of the percolating water and not from the horizontal underground flow of the river. The pools in the fossil part of the cave were filled up by water which seeped down the walls or dripped directly from the ceiling. By sampling these pools I excluded the influence of phreatic groundwater or hypogean rivers on the fauna composition.

Four categories of small water-bodies were distinguished (Figure 3, Figure 4):

- Type A: direct water trickles from the ceiling,
- Type B: permanent small depressions on stalagmites filled with water,
- Type D-i: pools on clay,
- Type D-p: pools on calcite.

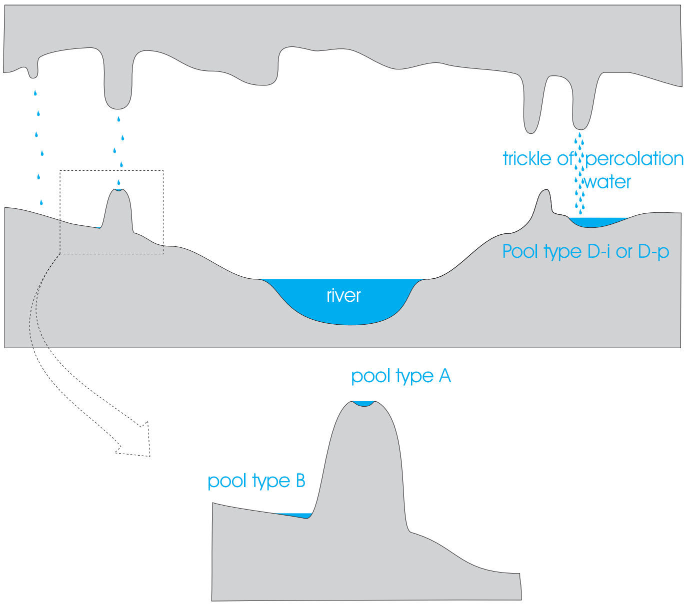


***Figure 3:** Schematic section of the cave with different types of water habitats*

The four types of pools were studied regarding the amount of organic matter, residence time of water in a pool and the pool's size. Pools of type A were the smallest ones, with a low quantity of organic matter and a short residence time. Pools of type B were medium-sized, with a medium quantity of organic matter and a residence time of medium duration. Pools of type D-p had values of all three parameters highest than in pools of type B, and pools of type D-i were higher still.

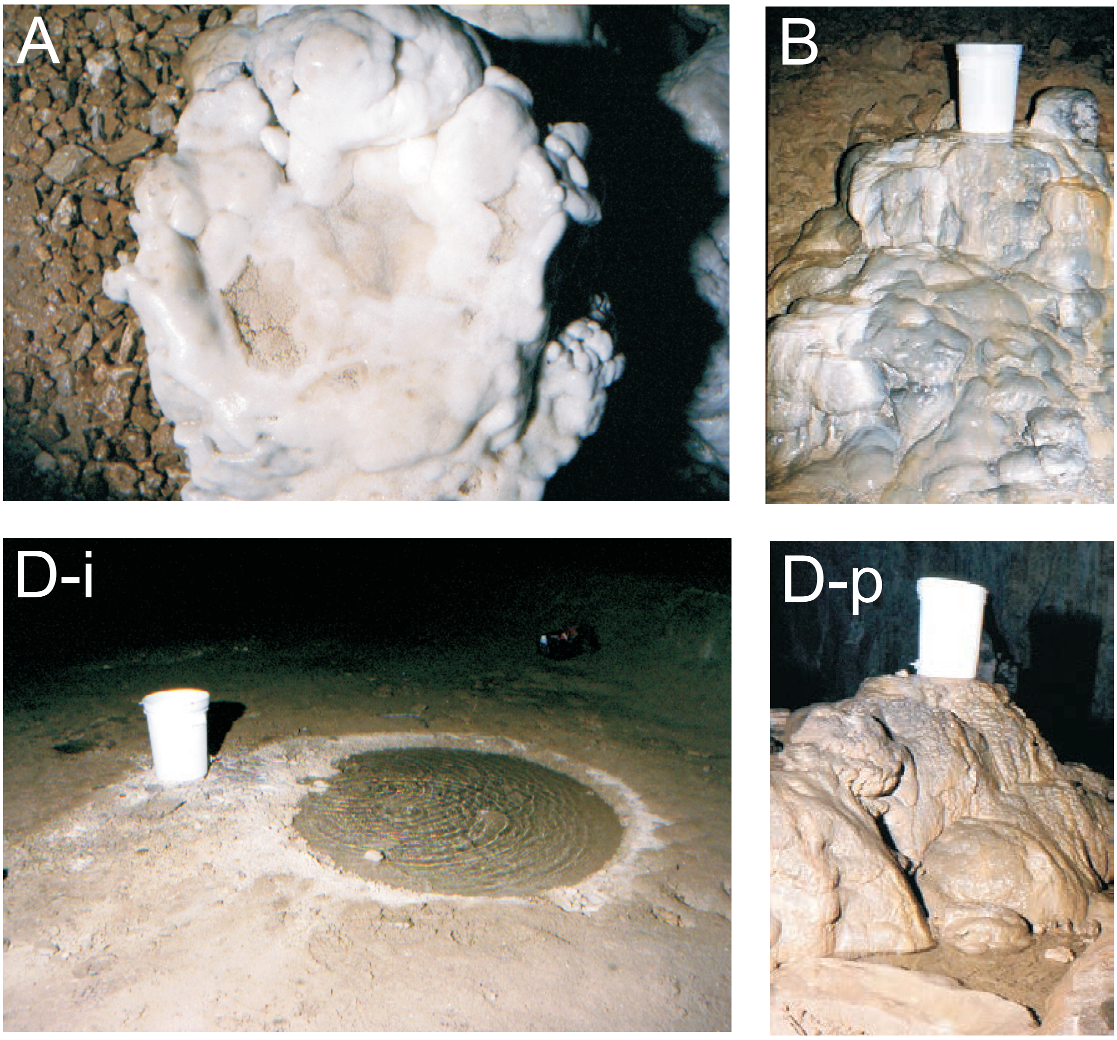


Figure 4: *Four categories of pools*

PRECIPITATION

Precipitation represents the basis for the formation of the karst system's input function (Petrič, 2002). I studied the potential impact of disharge of percolation water caused by precipitation on the composion of epikarst fauna. The Hydrometeorological Survey (Ljubljana, Slovenia) had in operation four precipitation stations within the study area where the precipitation was measured once a day at 7 a.m. The most abundant precipitation in the years 2000/2001 took place in the area of Dimnice (2019 mm), measured at the meteorologic office in Podgrad. The meteorologic office in Postojna, which covers area of the Postojnska jama cave system, measured 1827 mm of annual precipitation; further in Šmarje-Sap 1577 mm was measured and in Kozina 1548 mm of annual precipitation was measured for the area of Županova jama and Škocjanske jame (Figure 5).

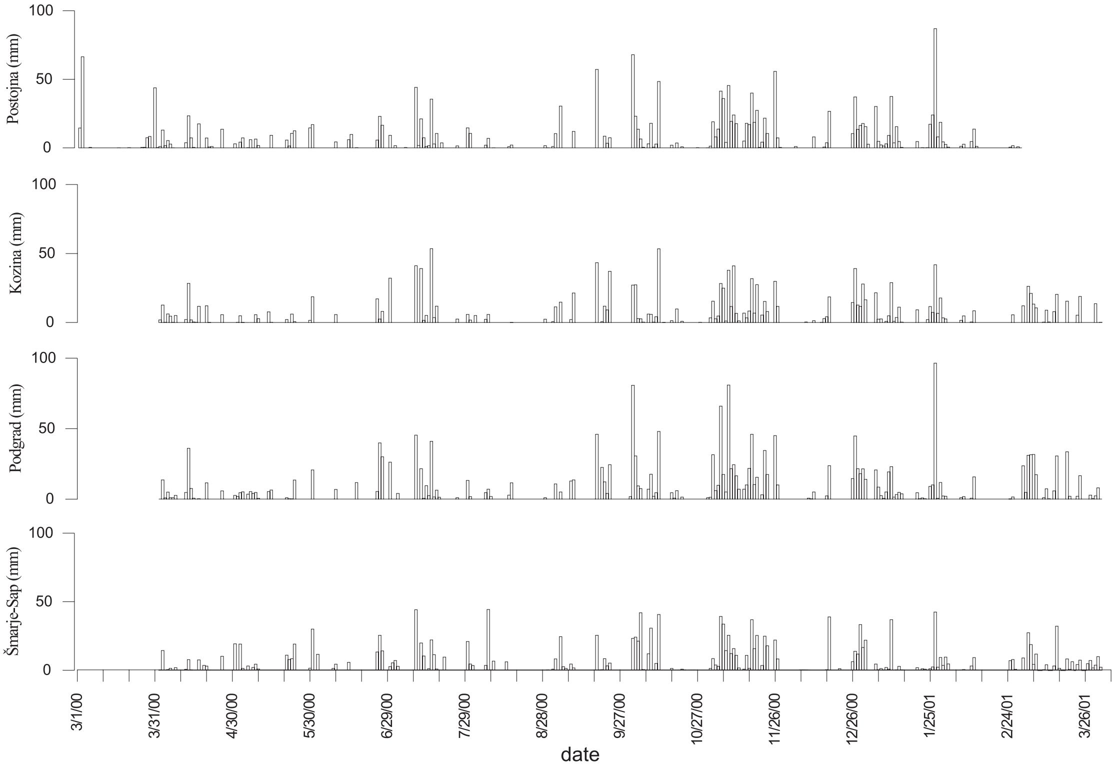


Figure 5: *Diagram of daily precipitation in the period from January 2000 to March 2001 for the four meteorologic offices*

FIELD WORK

In the caves Postojnska jama, Pivka jama, Črna jama, Škocjanske jame, Dimnice and Županova jama I collected samples once a week (Postojnska jama, Pivka jama, Črna jama) or month (Škocjanske jame, Dimnice, Županova jama), during 2000 and 2001. The selection of sampling methods and devices was made primarily to ensure the collection of copepod fauna from the epikarst. Samples of fauna as well as samples for water quality analyses were collected from the container (Figure 6). During the period of one week/month, the water from trickles was directed through a funnel into plastic containers. On two sides, the containers had holes covered with a net (mesh size 60 µm) to retain animals in the container. The contents of the plastic containers was fixed with 4 % final solution of formaldehyde at the sampling site and stored for further processing in the laboratory.

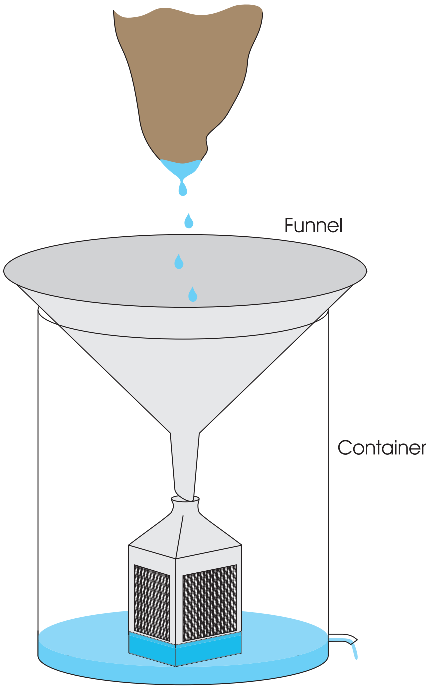


Figure 6: *Sampling container*

Samples from pools were collected separately into plastic containers by means of a modified suction pump (Figure 7). Pools were sampled four times during 2000 and 2001. Various quantities of the pool water at the sampling points were pumped and filtered through a 60 μm net. The samples were then processed in the same way as those from the trickles. Each water trickle or pool was analysed separately.

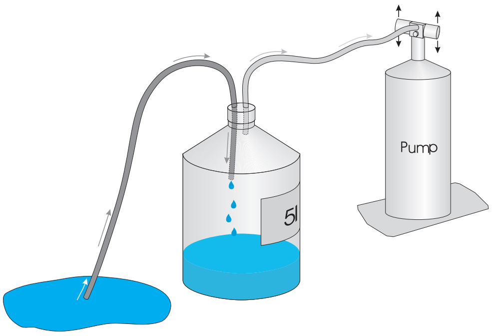


Figure 7: *Suction pump*

LABORATORY WORK

In the laboratory the organisms were separated by means of stereomicroscope at 40× magnification and then stored in 70 % ethanol. Before dissection animals were put into a mixture of glycerol and 70 % alcohol (ratio 1:1) and after some time this was replaced by pure glycerol. Dissection was made at 100× magnification (Olympus SZX12 stereomicroscope). Further processing and identification of the organisms was performed under a compound microscope (Olympus BHS40) at 400× to 1000× magnification. Specimens which were not dissected were deposited in labelled test tubes.

Samples were identified to species using different keys of identification: Borutskii (1964), Dussart & Defaye (1995), Einsle (1993, 1996), Kiefer (1960) and Janetzky *et al*. (1996).

PHYSICAL AND CHEMICAL ANALYSIS

Temperature [˚C], pH, conductivity [μS cm^{-1}] and discharge were measured *in situ* by a conductivity meter (LF 91, WTW) and pH meter (323, WTW). Water samples for analyses, according to "Standard methods" (APHA, 1998), were used for analysing chemical parameters in the samples. The samples were stored in plastic containers and kept at 4 ˚C prior to analysis. An ion chromatograph (761 Compact IC, Metrohm) was used to analyse the concentrations of major ions. Chloride, nitrite, nitrate, phosphate and sulphate were determined on an anion separation column. Sodium, ammonium, potassium, calcium and magnesium were analysed using a cation separation column. Detection limits ranged from 50 to 100 μg l^{-1}. Physical and chemical parameters for each cave are summarized in Appendix 9 and Appendix 10.

BIOLOGICAL ANALYSIS AND STATISTICAL TREATMENT

In the biological analysis the characteristics of each single sampling site and single cave were summarized with a list of the copepod species found together with their abundance, and some ecological and population parameters.

The Shannon-Wiener diversity index (H), which deals with the relative abundance data of single species, shows the copepod communities diversity (Shannon & Weaver, 1949):

$$H = -\sum \frac{n_i}{N} \ln \frac{n_i}{N}$$

where n_i is the number of individuals belonging to species i, N the total number of individuals.

The Shannon-Wiener diversity index increases with the number of species in the community and in theory can reach very large values. The highest hypothetical values of index H is when the abundance of all species in entire collection is equal.

Pearson and Spearman correlation coefficients, and Jaccard similarity coefficient were used (Davis, 1973; Lienert, 1973). Pearson (r) and Spearman (r_S) correlation coefficients were applied to compare two independent random variables. Both these correlation coefficients range from -1 (negative correlation) to +1 (perfect positive correlation), the t test being used to estimate the population ($p \leq 0.05$).

Overall similarity of the epikarst copepods of the different caves was measured using Jaccard's similarity coefficient (S_J). The simplest similarity measures deal only with presence-absence data. Similarity between two caves was expressed as a ratio of the species in common between two locations and the sum of taxa on both locations. The range of the coefficient of Jaccard is supposed to be 0 (no similarity) to 1 (complete similarity):

$$S_J = \frac{a}{a + b + c}$$

where a is the number of common species in both caves (joint occurences), b the number of species in one cave but not in the other, and c the number of species in the second cave but not in the first.

Distribution of copepod population in different types of pools was tested by the Kruskal-Wallis test (KW) (Lienert, 1973; Blejec, 1976):

$$KW = \frac{12}{n(\mathrm{n}+1)} \sum_{i=1}^{k} \frac{R_i^2}{n_i} - 3(n + 1); \quad \chi_p^2(\mathrm{m} = k - 1)$$

where n is the total number of sampling pools, k the number of types of pools, n_i the number of pools of single type, R_i the sum of the ranks of the n_i^{th} type of pool.

When the sample sizes are large and all k populations have the same continuous distribution, then KW has an approximate χ^2 distribution with k-1 degrees of freedom. The Kruskal-Wallis test is a non-parametric method of testing the hypothesis that several populations have the same continuous distribution versus the alternative that measurements tend to be higher in one or more of the populations (Lienert, 1973).

Non-parametric statistical methods (r_S, S_J and KW) were used because of low-diversity communities in samples, and because sample sizes were small and sample distribution was not normal.

Similarity among copepod communities in different caves was calculated using the similarity coefficient of Jaccard, and the grouping method, by the simple average of its similarity values (UPGMA, Unweighted Pair-Group Method, Arithmetic average). Calculation and dendrogram construction were done using adapted program package without data transformation (Davis, 1973; Clarke & Warwick, 1990).

The total expected number of species present in the study caves was calculated using Chao's function S_{Chao2}. This is based on a technique that allows the estimation of total number of species based on the number of species found in two caves and the number of species found in one. Intuitively, the higher the ratio of "doubletons" to "singleton" the fewer "missing" species there are. A widely used formula is due to Chao (1987):

$$S_{Chao2} = S_{obs} + \frac{Q_1^2}{2(Q_2+1)} + \frac{Q_1 Q_2}{2(Q_2+1)^2}$$

or approximately

$$S_{Chao2} = S_{obs} + \frac{Q_1^2}{2Q_2}$$

where S_{obs} is the observed number of species, Q_1 the number of species found in only one cave (singletons) and Q_2 is the number of species found in only two caves (doubletons). See Colwell (2004) for the formulas for variance of the estimates. The approximate equation shows the connection of the estimate with the ratio of singletons to doubletons.

Canonical correspondence analysis (CCA) was used to correlate species data to environmental variables. Significance of environmental variables in CCA was tested by Monte Carlo permutation test. Parametric multivariate analyses were run by the program package CANOCO 4.5 (ter Braak & Verdonschot, 1995; ter Braak & Šmilauer, 2002). The program is based on species data-set and total abundances of copepod communities in relation to data of environmental variables. In analysis of abundance data, counts were transformed by natural logarithms (ln x+1) to down weight highly abundant taxa and to normalize the data.

Results of the CCA were displayed in ordination diagrams of first and second canonical axes, with sites and species represented by points and by triangles, and environmental variables represented by vectors. Species points and the vectors of the environmental variables jointly reflect the species' distribution along each of the environmental variables. Perpendicular projections of species to the chosen environmental vector describe its correlation with the represented ecological factor. Ordination of sampling sites in each of the six caves in diagrams is shown using convex hull (Greenacre, 1983). Convex hull is the smallest convex set containing the points of all the sampling sites of a single cave. Convex hull represents the position of cave in the ordination diagram.

EPIKARST FAUNA FROM SIX CAVES

I collected 17 different major taxa from seeps and drip pools in six caves (Table 3). They belonged to a wide variety of groups and many of them were not identifiable past class or order. In addition to Copepoda in the percolation water samples there were numerous specimens of Nematoda, Oligochaeta, Ostracoda and a few specimens of Turbellaria, Rotatoria, Gastropoda, Araneae, Acarina, Bathynellacea, Isopoda, Amphipoda, Diplopoda, Collembola, Coleoptera, and Diptera larvae. A total of 847 other invertebrates were found in drips and 622 other invertebrates were found in pools. Included among the terrestrial species, presumably ones washed in through the epikarst (Gibert, 1986), were Gastropoda, Acarina, Diplopoda, Collembola and Coleoptera. The small but interesting category of

Table 3: *List of fauna collected at six caves and the number of specimens*

Higher groups /	POSTOJNSKA JAMA		PIVKA JAMA		ČRNA JAMA		ŠKOCJANSKE JAME		DIMNICE		ŽUPANOVA JAMA	
Cave	trickles	pools	trickles	pools	trickles	pools	trickles	pools	trickles	pools	trickles	pools
Turbellaria	3		3	2			12		2			
Nematoda	2	9	158	28	32	30	194	26	29	2	120	17
Rotatoria				2								
Gastropoda		1		12	1	2		1			2	3
Oligochaeta	4	17	21	36	5	25	26	72	34	>150	8	26
Araneae			1		1							
Acarina	2	4	8		10	1	6	4	3	2	3	1
Ostracoda		106	5	3		2	5	15	1	3	8	
Copepoda	11	467	330	1002	194	195	201	297	35	625	188	239
nauplia		37	271	11	97	12	37	121	26	399	127	9
Bathynellacea			1	2								
Isopoda					1			1			6	3
Amphipoda		1	2			1		3			2	
Diplopoda		1	1		3							
Collembola	9	3			2		2		5	1	3	
Coleoptera		2			3							
Diptera-larvae	7	1	3		5		50	1	31		1	
Other Insecta											1	
Total number	**38**	**649**	**804**	**1098**	**354**	**268**	**533**	**541**	**166**	**>1182**	**469**	**298**

stygobionts included the crustaceans Ostracoda, Amphipoda, Isopoda and Bathynellacea. Nematoda and Oligochaeta were among the terrestrial accidentals well represented, since these benthic dwellers presumably find suitable microhabitat in epikarst and in the sediment of drip pools. I paid special attention to copepod crustaceans, most of which were stygobionts, and were the most abundant of all. Only few of the copepods collected were known from epigean or semi-epigean habitats. Taken together, copepods rival all the other invertebrates in abundance. A total 1517 copepods were found in drips and 3414 in pools.

COMPOSITION OF EPIKARST COPEPODS IN SIX KARST CAVES

During my systematic collection of the copepod fauna I identified 37 species (Table 4). Among the copepods six cyclopoids from five genera, and 31 harpacticoids from 11 genera were found. Twenty seven species are stygobionts. Eleven harpacticoids (from the genera *Bryocamptus, Elaphoidella, Maraenobiotus, Moraria, Nitocrella, Parastenocaris* and cf. *Stygepactophanes*) are probable stygobionts and likely to be new species. Their morphological features and distribution indicate they are obligate epikarst species.

Individual caves had between 5 and 14 species found in trickles and 7 and 13 species found in pools (Figure 8). Two stygobiotic epikarst copepods, *S. infernus* and *Parastenocaris* sp. 2*, were found in all six caves and specimens of *B. balcanicus* and *P. nolli alpina* were found from five caves. Of 37 species, 17 are known from a single cave and 9 are known from only two caves. Eight species belonged to genus *Bryocamptus*. Within each of the three genera *Elaphoidella, Moraria* and *Parastenocaris* five species were found.

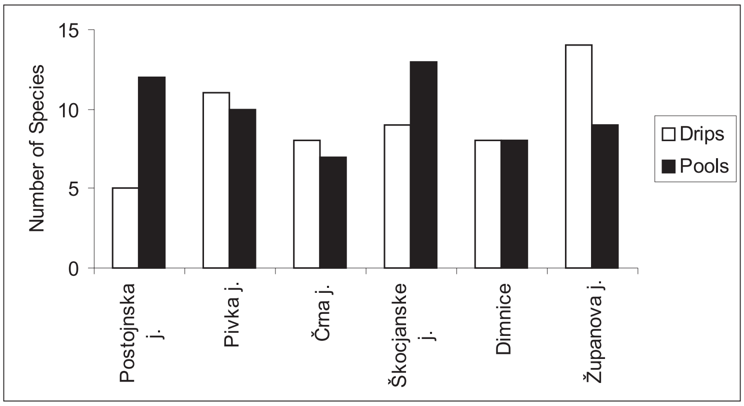


Figure 8: *Distribution of number of copepod species per cave in trickles and in pools*

In all caves together I found 27 species in trickles and 29 species in pools (Table 5, Table 6). 19 species were found both in the trickles and in the pools. The relative abundance of copepod species is evident in Figure 9. In the trickles there were 7 spe-

Table 4: *List of species of copepods and total number of individuals in trickles and pools of percolation water of the six karst caves (species presumed to be new to science are marked with asterisk*). Stygobionts are indicated in bold.*

	POSTOJNSKA JAMA		PIVKA JAMA		ČRNA JAMA	
CYCLOPOIDA	trickles	pools	trickles	pools	trickles	pools
1. ***Acanthocyclops kieferi*** (Chappuis, 1925)		17				
2. ***Diacyclops languidoides*** (Lilljeborg, 1901)		73				
3. *Diacyclops languidus* (Sars, 1863)						
4. *Megacyclops viridis* (Jurine, 1820)						
5. *Paracyclops fimbriatus* (Fischer, 1853)		6				
6. ***Speocyclops infernus*** (Kiefer, 1930)	6	68	78	16	21	43
HARPACTICOIDA						
7. *Attheyella crassa* (Sars, 1862)						
8. ***Bryocamptus balcanicus*** (Kiefer 1933)	1	69	1		77	35
9. ***Bryocamptus borus*** Karanovic & Bobic, 1998						
10. *Bryocamptus dacicus* (Chappuis 1923)		2	68	163		1
11. ***Bryocamptus pygmaeus*** (Sars, 1862)						
12. ***Bryocamptus pyrenaicus*** (Chappuis, 1923)				2		
13. ***Bryocamptus typhlops*** (Mrazek, 1893)		1		5		
14. *Bryocamptus zschokkei* (Schmeil, 1893)			1	4		
15. ***Bryocamptus* sp.***			15	3		
16. ***Elaphoidella cvetkae*** Petkovski, 1983					76	3
17. ***Elaphoidella kieferi*** Petkovski & Brancelj, 1985						
18. ***Elaphoidella stammeri*** Chappuis, 1936						
19. ***Elaphoidella millennii*** Brancelj, in press						
20. ***Elaphoidella* sp.***			3			
21. *Epactophanes richardi* (Mrazek, 1893)				43		
22. ***Maraenobiotus* cf. *brucei****			96	68		
23. *Moraria poppei* (Mrazek, 1893)	1	10	3	687		26
24. ***Moraria stankovitchi* Chap**puis, 1924						
25. *Moraria varica* (Graeter, 1911)		1	10	4		
26. ***Moraria* sp. A***					3	
27. ***Moraria* sp. B***						
28. ***Morariopsis dumonti*** Brancelj, 2000						
29. ***Morariopsis scotenophila*** (Kiefer 1930)		144				84
30. ***Nitocrella* sp.***	2					
31. ***Parastenocaris nolli alpina*** (Kiefer, 1938)			6		3	1
32. ***Parastenocaris* cf. *andreji****						
33. ***Parastenocaris* sp. 1***					2	
34. ***Parastenocaris* sp. 2***	1	2	19		9	
35. ***Parastenocaris* sp. 3***						
36. *Phyllognathopus viguieri* (Maupas, 1892)		3				
37. **cf. *Stygepactophanes* sp.***					3	
juvenile harpacticoids		71	30	17		2
nauplia		37	271	11	97	12
Total number of specimens	11	504	601	1013	291	207
Number of species	5	12	11	10	8	7

	ŠKOCJANSKE JAME		DIMNICE		ŽUPANOVA JAMA	
CYCLOPOIDA	trickles	pools	trickles	pools	trickles	pools
1. ***Acanthocyclops kieferi*** (Chappuis, 1925)						
2. ***Diacyclops languidoides*** (Lilljeborg, 1901)					2	35
3. *Diacyclops languidus* (Sars, 1863)		1				
4. *Megacyclops viridis* (Jurine, 1820)		11				
5. *Paracyclops fimbriatus* (Fischer, 1853)		2				
6. ***Speocyclops infernus*** (Kiefer, 1930)	15	61	6	600		156
HARPACTICOIDA						
7. *Attheyella crassa* (Sars, 1862)		1				
8. ***Bryocamptus balcanicus*** (Kiefer 1933)				1	15	69
9. ***Bryocamptus borus*** Karanovic & Bobic, 1998				6		
10. *Bryocamptus dacicus* (Chappuis 1923)						
11. ***Bryocamptus pygmaeus*** (Sars, 1862)				4		
12. ***Bryocamptus pyrenaicus*** (Chappuis, 1923)				7	8	28
13. ***Bryocamptus typhlops*** (Mrazek, 1893)		51				24
14. *Bryocamptus zschokkei* (Schmeil, 1893)		82				
15. ***Bryocamptus*** **sp.***		10				
16. ***Elaphoidella cvetkae*** Petkovski, 1983	1				6	
17. ***Elaphoidella kieferi*** Petkovski & Brancelj, 1985	5	1				
18. ***Elaphoidella stammeri*** Chappuis, 1936					10	
19. ***Elaphoidella millennii*** Brancelj, in press					2	8
20. ***Elaphoidella*** **sp.***						
21. *Epactophanes richardi* (Mrazek, 1893)						
22. ***Maraenobiotus*** **cf.** ***brucei*** *****						
23. *Moraria poppei* (Mrazek, 1893)	1	31				
24. ***M oraria stankovitchi*** **Chap**puis, 1924					1	
25. *Moraria varica* (Graeter, 1911)						
26. ***M oraria*** **sp. A***	1					
27. ***M oraria*** **sp. B***					1	
28. ***M orariopsis dumonti*** Brancelj, 2000					3	64
29. ***M orariopsis scotenophila*** (Kiefer 1930)		17	2	2		
30. ***Nitocrella*** **sp.***			3			
31. ***Parastenocaris nolli alpina*** (Kiefer, 1938)	30	1	7	2	75	
32. ***Parastenocaris*** **cf.** ***andreji*** *****			1			1
33. ***Parastenocaris*** **sp. 1***			3	1		
34. ***Parastenocaris*** **sp. 2***	113	9	7		11	
35. ***Parastenocaris*** **sp. 3***	4				3	
36. *Phyllognathopus viguieri* (Maupas, 1892)					1	1
37. **cf.** ***Stygepactophanes*** **sp.***	1		6			
juvenile harpacticoids	30	19		2	35	3
nauplia	37	121	26	399	127	9
Total number of specimens	238	418	61	1024	315	248
Number of species	9	13	8	8	14	9

***Table 5:** List of species of copepods, their abundance (#) and ratio [%] based on the total number of taxa recorded from trickles in six karst caves in Slovenia (species presumed to be new to science are marked with asterisk*)*

Species/cave (trickles)	**Pivka jama**		**Črna jama**		**Škocjanske jame**		**Županova jama**		**Dimnice**		**Postojnska jama**		**Total number**
	#	%	#	%	#	%	#	%	#	%	#	%	
1. *Parastenocaris* sp. 2*	19	6.4	9	4.6	113	66.1	11	7.2	7	20.0	1	9.1	160
2. *Speocyclops infernus* (Kiefer, 1930)	78	26.0	21	10.8	15	8.8	15	9.8	6	17.1	6	54.5	141
3. *Parastenocaris nolli alpina* (Kiefer, 1938)	6	2.0	3	1.6	30	17.5	75	49.0	7	20.0			121
4. *Elaphoidella cvetkae* Petkovski, 1983	15	5.0	76	39.2	1	0.6	6	3.9					98
5. *Maraenobiotus* cf. *brucei**	96	32.0											96
6. *Bryocamptus balcanicus* (Kiefer 1933)	1	0.3	77	39.6			15	9.8			1	9.1	94
7. *Bryocamptus dacicus* (Chappuis 1923)	68	22.7											68
8. cf. *Stygepactophanes* sp.*			3	1.6	1	0.6			6	17.1			10
9. *Elaphoidella stammeri* Chappuis, 1936							10	6.5					10
10. *Moraria varica* (Graeter, 1911)	10	3.3											10
11. *Bryocamptus pyrenaicus* (Chappuis, 1923)							8	5.1					8
12. *Parastenocaris* sp. 3*					4	2.3	3	2.0					7
13. *Moraria poppei* (Mrazek, 1893)	3	1.0			1	0.6					1	9.1	5
14. *Parastenocaris* sp. 1*			2	1.0					3	8.6			5
15. *Nitocrella* sp.*									3	8.6	2	18.2	5
16. *Elaphoidella kieferi* Petkovski & Brancelj, 1985					5	2.9							5
17. *Moraria* sp. A*			3	1.6	1	0.6							4
18. *Elaphoidella* sp.*	3	1.0											3
19. *Morariopsis dumonti* Brancelj, 2000							3	2.0					3
20. *Diacyclops languidoides* (Lilljeborg, 1901)							2	1.3					2
21. *Elaphoidella millennii** Brancelj, in press							2	1.3					2
22. *Morariopsis scotenophila* (Kiefer 1930)									2	5.7			2
23. *Bryocamptus* sp.*	1	0.3											1
24. *Moraria stankovitchi* Chappuis, 1924							1	0.7					1
25. *Moraria* sp. B*							1	0.7					1
26. *Parastenocaris* cf. *andreji**									1	2.9			1
27. *Phyllognathopus viguieri* (Maupas, 1892)							1	0.7					1
28. juvenile harpacticoids	▲30				▲30			▲35					95
29. nauplia	▲271		▲97		▲37		▲127		▲26				558
Total number of specimens	**601**		**291**		**238**		**315**		**61**		**11**		**1517**
Species number	**11**		**8**		**9**		**14**		**8**		**5**		

▲ number is out of account of ratio

cies represented with a proportion of more than 5 %: *Parastenocaris* sp. 2* (18.5 %), *S. infernus* (16.3 %), *P. nolli alpina* (14 %), *E. cvetkae* (11.3 %), *M.* cf. *brucei** (11.1 %), *B. balcanicus* (10.9 %) and *B. dacicus* (7.9 %); in the pools there were five such species: *S. infernus* (29.3 %), *M. poppei* (27.8 %), *M. scotenophila* (9.1 %), *B. balcanicus* (6.4 %) and *B. dacicus* (5.8 %). Other species were present with a proportion of less than 5 %.

***Table 6:** List of species of copepods, their abundance (#) and ratio [%] based on the total number of taxa recorded from pools in six karst caves in Slovenia (species presumed to be new to science are marked with asterisk*)*

Species/cave (pools)	**Pivka jama**		**Dimnice**		**Postojnska jama**		**Škocjanske jame**		**Županova jama**		**Črna jama**		**Total number**
	#	%	#	%	#	%	#	%	#	%	#	%	
1. *Speocyclops infernus* (Kiefer, 1930)	16	1.6	600	96.3	68	17.2	61	21.9	6	2.5	43	22.3	794
2. *Moraria poppei* (Mrazek, 1893)	687	69.8			10	2.5	31	11.1			26	13.5	754
3. *Morariopsis scotenophila* (Kiefer 1930)			2	0.3	144	36.4	17	6.1			84	43.5	247
4. *Bryocamptus balcanicus* (Kiefer 1933)			1	0.2	69	17.4			69	29.2	35	18.1	174
5. *Bryocamptus dacicus* (Chappuis 1923)	153	15.5			2	0.5					1	0.5	156
6. *Diacyclops languidoides* (Lilljeborg, 1901)					73	18.4			35	14.8			108
7. *Bryocamptus zschokkei* (Schmeil, 1893)							82	29.5					82
8. *Bryocamptus typhlops* (Mrazek, 1893)	5	0.5			1	0.3	51	18.3	24	10.2			81
9. *Maraenobiotus* cf. *brucei**	68	6.9											68
10. *Morariopsis dumonti* Brancelj, 2000									64	27.1			64
11. *Epactophanes richardi* Mrazek, 1893	43	4.4											43
12. *Bryocamptus pyrenaicus* (Chappuis, 1923)	2	0.2	7	1.1					28	11.9			37
13. *Acanthocyclops kieferi* (Chappuis, 1925)					17	4.3							17
14. *Bryocamptus* sp.*	4	0.4					10	3.6					14
15. *Parastenocaris* sp. 2*					2	0.5	9	3.2					11
16. *Megacyclops viridis* (Jurine, 1820)							11	4.0					11
17. *Paracyclops fimbriatus* (Fischer, 1853)					6	1.5	2	0.7					8
18. *Elaphoidella millennii** Brancelj, in press									8	3.5			8
19. *Elaphoidella cvetkae* Petkovski, 1983	3	0.3									3	1.6	6
20. *Bryocamptus borus* Karanovic & Bobic, 1998			6	1.0									6
21. *Moraria varica* (Graeter, 1911)	4	0.4			1	0.3							5
22. *Parastenocaris nolli alpina* (Kiefer, 1938)			2	0.3			1	0.4			1	0.5	4
23. *Phyllognathopus viguieri* (Maupas, 1892)					3	0.7			1	0.4			4
24. *Bryocamptus pygmaeus* (Sars, 1862)			4	0.6									4
25. *Diacyclops languidus* (Sars, 1863)							1	0.4					1
26. *Attheyella crassa* (Sars, 1862)							1	0.4					1
27. *Elaphoidella kieferi* Petkovski & Brancelj, 1985							1	0.4					1
28. *Parastenocaris* cf. *andreji**									1	0.4			1
29. *Parastenocaris* sp. 1*			1	0.2									1
30. juvenile harpacticoids	▲17		▲2		▲71		▲19		▲3		▲2		114
31. Nauplia	▲11		▲399		▲37		▲121		▲9		▲12		589
Total number of specimens	**1013**		**1024**		**504**		**418**		**248**		**207**		**3414**
Species number	**10**		**8**		**12**		**13**		**9**		**7**		

▲ number is out of account of ratio

In Županova jama the ratio of the number of species in the trickles to that in the pools was 1.5:1, in Pivka and Črna jama 1.1:1, in Dimnice 1:1, in Škocjanske jame 1:1.4 and in Postojnska jama 1:2.4. The difference in proportions reflects both the productivity of trickles in terms of copepods but also the areal extent of the pools as well as copepod density in the pools.

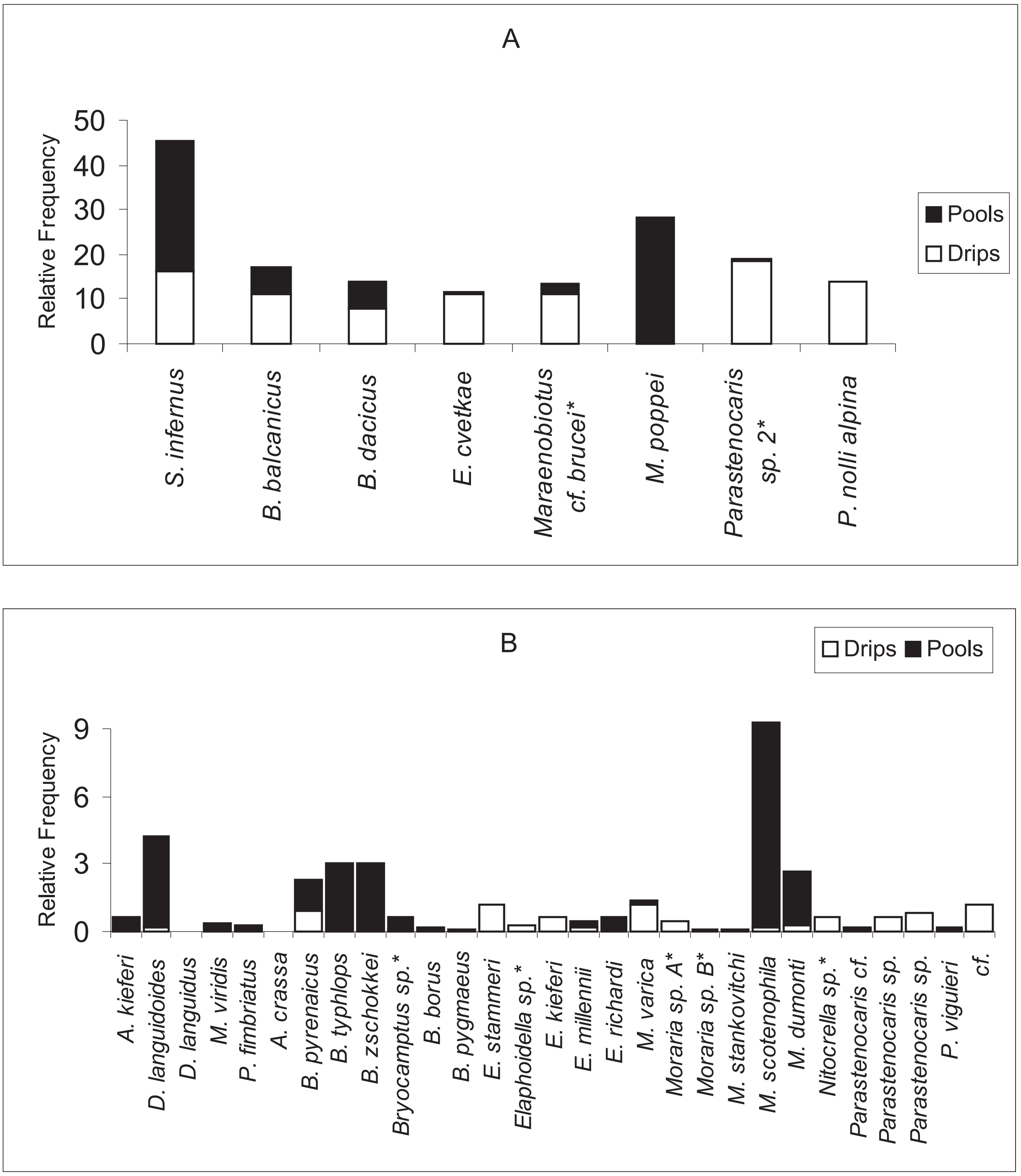


Figure 9: *Bar graph of relative abundance of the 37 copepod species in trickles and in pools*

All species with a relative frequency of more than 10 percent are shown in Figure A, the others are shown in Figure B.

SIMILARITY OF COPEPOD COMMUNITIES

Species overlap among caves was generally low. From a geographical point of view, there is no correlation ($r = -0.38$, $p > 0.05$) between the distance apart of the caves and the similarity of the fauna (using the Pearson correlation coefficient). The mean value for Jaccard index, calculated for trickles and pools combined, was 0.29, and its maximum observed value was only 0.44. Only two pairs of caves (from 15 pairs) had a Jaccard index of 0.40 or higher. The highest similarity was between Dimnice and Črna jama ($S_J = 0.44$) which are 30 km apart (Figure 10). In caves which belong to the same cave system (Postojnska jama, Pivka jama, Črna jama) and in which the sites are within 3 km of each other, the similarity was low and quite similar ($S_J = 0.33 – 0.37$). This low similarity is in spite of the fact that nearby drips are in the same geographical and geological situation, and often similar environmental factors. It strongly suggests that movement of epikarst copepods is quite restricted.

The mean Jaccard index was calculated first for the trickle data, and then for the pool data for the 15 pairs of caves. The mean Jaccard number for trickles was 0.31 and for drips was 0.23. Faunal similarity in trickles was the highest between Črna jama and Škocjanske jame ($S_J = 0.55$) and in pools the highest similarity was between Postojnska jama and Črna jama ($S_J = 0.36$).

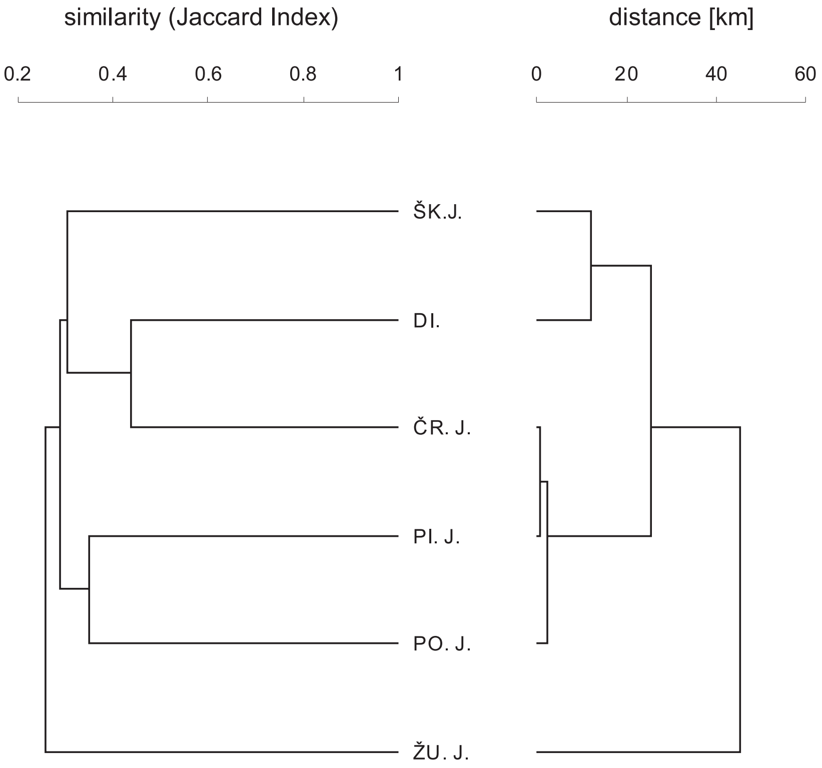
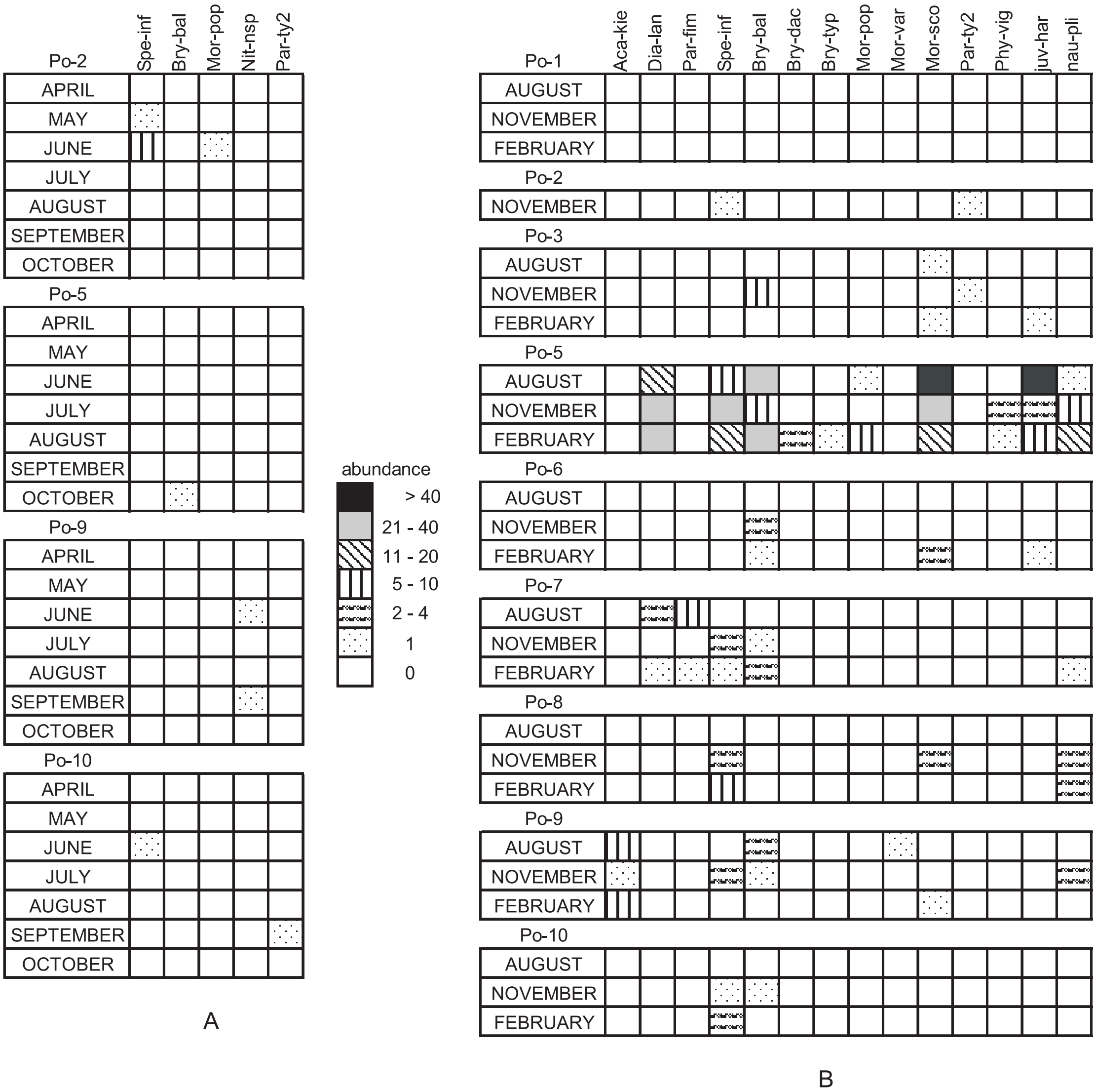


Figure 10: *Dendrogram constructed by data on similarity of copepod community and geographical distance between caves (UPGMA method, standardized on Jaccard similarity coefficient)*

SPATIAL AND TEMPORAL DISTRTIBUTION OF COPEPODS IN TRICKLES AND POOLS FILLED WITH PERCOLATION WATER

POSTOJNSKA JAMA

In Postojnska jama I found copepods only in 4 trickles (Figure 11A) from the 10 sampling sites. A total of 11 specimens of 5 species were found. The most frequent species was *S. infernus*. This was the poorest yield by far of any of the caves studied.



Po-2	Spe-inf	Bry-bal	Mor-pop	Nit-nsp	Par-ty2
APRIL					
MAY	⁘				
JUNE	▥		⁘		
JULY					
AUGUST					
SEPTEMBER					
OCTOBER					
Po-5					
APRIL					
MAY					
JUNE					
JULY					
AUGUST					
SEPTEMBER					
OCTOBER		⁘			
Po-9					
APRIL					
MAY					
JUNE				⁘	
JULY					
AUGUST					
SEPTEMBER				⁘	
OCTOBER					
Po-10					
APRIL					
MAY					
JUNE	⁘				
JULY					
AUGUST					
SEPTEMBER					⁘
OCTOBER					

A

abundance	
■	> 40
▒	21 - 40
▧	11 - 20
▥	5 - 10
▤	2 - 4
⁘	1
□	0

Po-1	Aca-kie	Dia-lan	Par-fim	Spe-inf	Bry-bal	Bry-dac	Bry-typ	Mor-pop	Mor-var	Mor-sco	Par-ty2	Phy-vig	juv-har	nau-pli
AUGUST														
NOVEMBER														
FEBRUARY														
Po-2														
NOVEMBER				⁘							⁘			
Po-3														
AUGUST										⁘				
NOVEMBER					▥						⁘			
FEBRUARY										⁘			⁘	
Po-5														
AUGUST		▧		▥	▒			⁘		■			■	⁘
NOVEMBER		▒		▒	▥					▒		▤	▤	▥
FEBRUARY		▒		▧	▒	▤	⁘	▥		▧		⁘	▥	▧
Po-6														
AUGUST														
NOVEMBER					▤									
FEBRUARY					⁘					▤			⁘	
Po-7														
AUGUST		▤	▥											
NOVEMBER				▤	⁘									
FEBRUARY		⁘	⁘	⁘	▤									⁘
Po-8														
AUGUST														
NOVEMBER				▤						▤				▤
FEBRUARY				▥										▤
Po-9														
AUGUST	▥				▤				⁘					
NOVEMBER	⁘			▤	⁘									▤
FEBRUARY	▥									⁘				
Po-10														
AUGUST														
NOVEMBER				⁘	⁘									
FEBRUARY				▤										

B

Figure 11: *Presence and abundance of copepods in trickles (A) and pools (B) in Postojnska jama*

From 9 pools 500 l of water was filtered. All together in pools 504 copepods of 12 species were found. The most numerous were the specimens and the species in the pool Po-5 (type D-i) (Figure 11B). I took a sample from the pool Po-2 in November, otherwise the pool was empty. In the pools Po-6, Po-8, and Po-10 the August samples were without copepods.

The connection between precipitation, discharge, thickness of the cave ceiling, quantity of pumped water, temperature and number of specimens is summarized in Table 7. Values of the Spearman correlation coefficient (r_s) for trickles were low, a statistically significant correlation ($p<0.05$) between discharge and the number of specimens was found for the sampling points Po-2 and Po-5. This may reflect the fact that some trickles are more directly connected to the surface than others, and this may be the case for Po-2 and Po-5. There was no statistically significant correlation ($p>0.05$) for the other pairs of variables.

Table 7: *Spearman (r_S) correlations for all pairs of the variables in trickles and pools in Postojnska jama*

	sampling points								
	Po-2	Po-3	Po-5	Po-6	Po-7	Po-8	Po-9	Po-10	Cave
precipitation versus drip rate	0.04		–0.05				–0.48	0.18	
drip rate versus abundance	0.56**		0.55**				–0.19	0.24	
precipitation versus abundance	0.22		0.53**				–0.14	0.14	–0.10
ceiling thickness versus drip rate									0.56
ceiling thickness versus abundance									–0.11
volume versus abundance: pools		1.00	–1.00	0.63	0.13	0.50	–0.62	0.62	0.42
temperature versus abundance: pools		–0.50	–0.50	0.88	–0.63	0.50	–0.63	0.13	–0.16

**$p < 0.05$

PIVKA JAMA

In Pivka jama I found 592 specimens of 11 species; most of them were present in the trickles Pi-1 and Pi-2 (Figure 12A). In the trickles Pi-1 and Pi-2 there were specimens of two new species from the genera *Bryocamptus* and *Elaphoidella*. The dominant copepods were *M.* cf. *brucei**, *S. infernus*, *B. dacicus* and *E. cvetkae*.

In Pivka jama 23 l of water was filtered from five pools. Altogether I found 1013 copepods belonging to 10 species. Most of the specimens and species were collected from the pool on calcite (Pi-2), whereas in pools filled up by water which drips from the ceiling (Pi-3, Pi-4) there was a small number of copepods (Figure 12B). From the pools Pi-1, Pi-3 and Pi-5 it was possible to take samples only in November; otherwise the pools were dry. Specimens of the new species *Bryocamptus* were found in the pools Pi-1 and Pi-2, which are away from each other only by some metres. I filtered 936 copepods from only two litres of water from the pool Pi-2. *M. poppei* prevailed with 674 specimens.

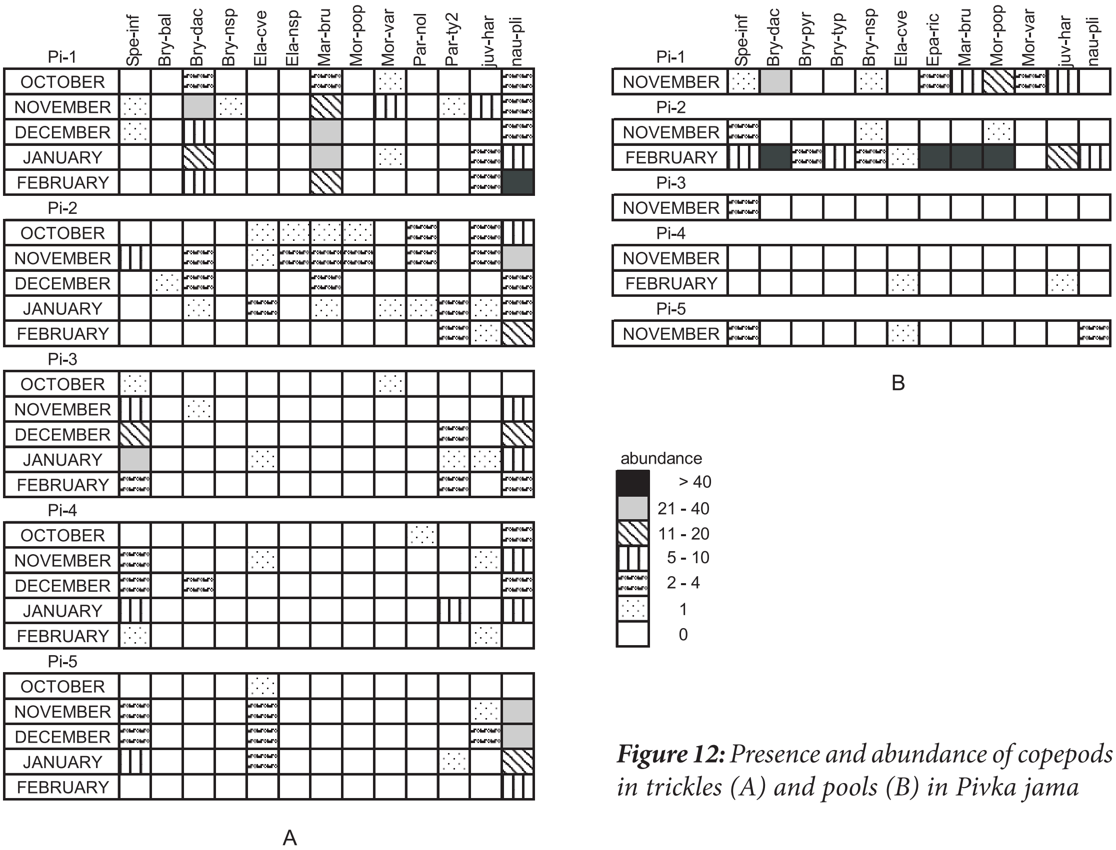


Figure 12: *Presence and abundance of copepods in trickles (A) and pools (B) in Pivka jama*

Results of the correlation analyses, using the Spearman correlation coefficient (r_s) (Table 8), indicate that the precipitation shows highly positive co-variation with the discharge ($p<0.01$) on the one hand and the number of specimens ($r_s = 0.57$, $p<0.05$) on the other hand. Values of the Spearman correlation coefficient for the trickles Pi-2, Pi-3 and Pi-5 were high, and abundance of copepods was positively correlated with the discharge ($p<0.05$). In the present study other physical properties (thickness of the ceiling, temperature and discharge) appeared not have been a crucial factor for the epikarst copepods ($p>0.05$).

Table 8: *Spearman (r_S) correlations for all pairs of the variables in trickles in Pivka jama*

	sampling points					
	Pi-1	Pi-2	Pi-3	Pi-4	Pi-5	Cave
precipitation versus drip rate	0.83**	0.85**	0.87**	0.79**	0.80**	
drip rate versus abundance	0.30	0.56**	0.74**	0.36	0.76**	
precipitation versus abundance	0.36	0.40	0.68**	0.64**	0.73**	0.57**
temperature versus abundance	–0.37	0.18	–0.32	0.12	0.01	–0.70
ceiling thickness versus drip rate						0.43
ceiling thickness versus abundance						0.58

**p<0.05

ČRNA JAMA

In Črna jama I found 292 specimens of 8 species. Most of the specimens and species were from the trickle Čr-5 (Figure 13A). In the trickle Čr-1 I found 4 new species from genera *Moraria, Parastenocaris* and *Stygepactophanes*. *B. balcanicus, S. infernus* and *E. cvetkae* were the most abundant species found in almost all or in more than half of the samples.

207 copepods of 7 species were found in Črna jama where I filtered 68 l of water from five pools. Most of the specimens and species were from the pool Čr-1 (type D-p) (Figure 13B).

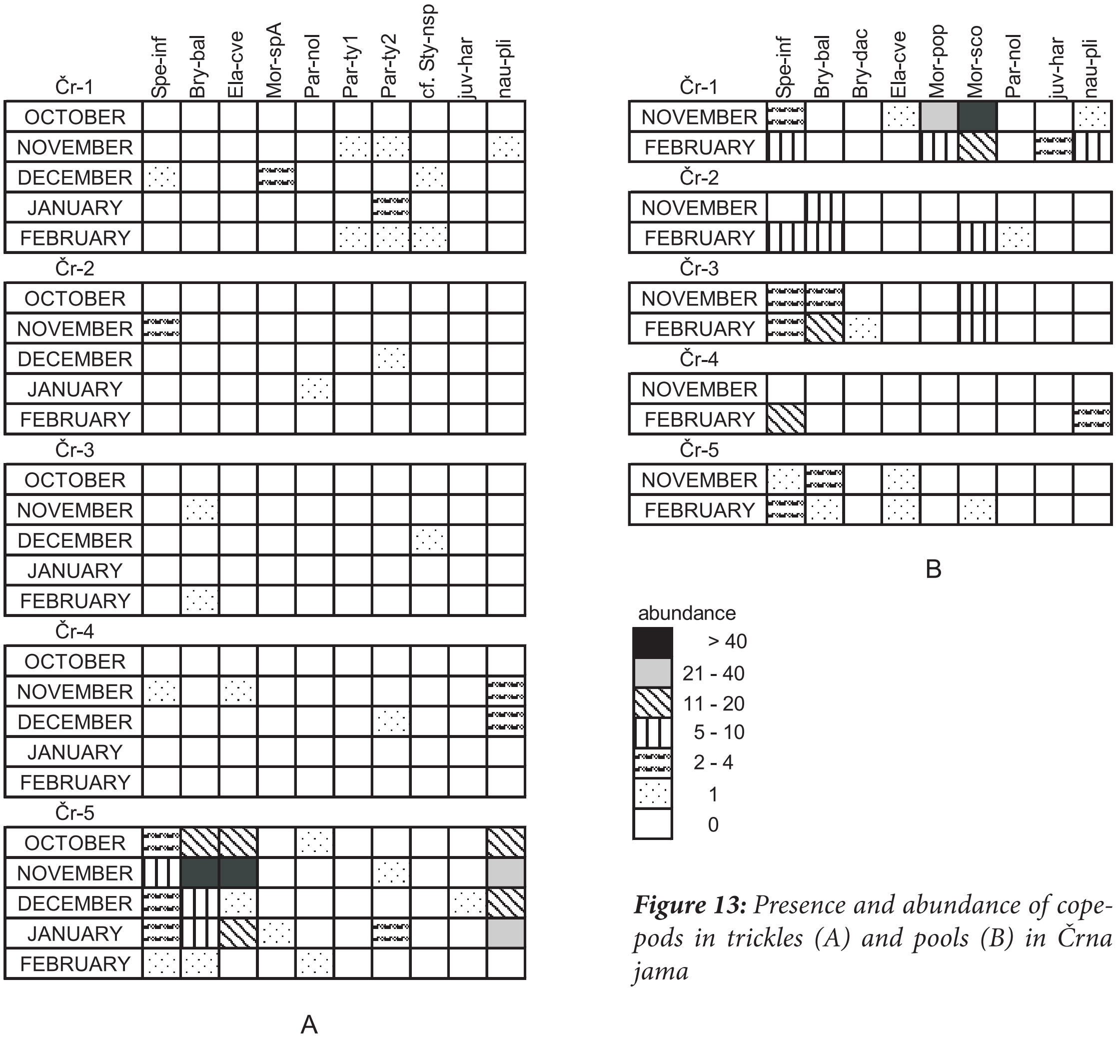


***Figure 13:** Presence and abundance of copepods in trickles (A) and pools (B) in Črna jama*

Results of the correlation analyses are summarized in Table 9. Precipitation shows highly positive co-variation with the discharge ($p<0.05$) on the one hand and the number of specimens ($r_s = 0.79$, $p<0.01$) on the other hand. Abundance of copepods was positively correlated with the discharge ($p<0.05$) at the three sampling points. The correlation between the thickness of the cave ceiling, temperature, discharge and number of specimens was not statistically significant ($p>0.05$).

***Table 9:** Spearman (r_S) correlations for all pairs of the variables in trickles in Črna jama*

	sampling points					
	Čr-1	Čr-2	Čr-3	Čr-4	Čr-5	Cave
precipitation versus drip rate	0.72**	0.56**	0.64**	0.65**	0.81**	
drip rate versus abundance	–0.10	0.58**	0.24	0.59**	0.71**	
precipitation versus abundance	–0.07	0.61**	0.17	0.50	0.78**	0.79**
temperature versus abundance	–0.31	0.23	0.13	0.45	0.20	0.38
ceiling thickness versus drip rate						–0.33
ceiling thickness versus abundance						–0.58

**p<0.05

ŠKOCJANSKE JAME

A total of 238 specimens of 9 species were found in Škocjanske jame. The highest diversity was recognized at the trickle Šk-5 (Figure 14A). Four new species from 3 genera were found: one from the genus *Moraria*, two from the genus *Parastenocaris*, and one from the genus *Stygepactophanes*. The most abundant species were *Parastenocaris* sp. 2*, *S. infernus* and *E. kieferi*.

In Škocjanske jame I filtered 455 l of water from five pools. Altogether I found 419 copepods of 13 species. The highest number of specimens was found at the sampling point Šk-5 (type D-p) and the highest number of species was found in the pool Šk-4 (type B) (Figure 14B).

***Table 10:** Spearman (r_S) correlations for all pairs of the variables in trickles and pools in Škocjanske jame*

	sampling points					
	Šk-1	Šk-2	Šk-3	Šk-4	Šk-5	Cave
precipitation versus drip rate	0.88**	0.82**	0.62	0.96**	0.94**	
drip rate versus abundance	0.71**	0.67	0.76**	0.46	–0.13	
precipitation versus abundance	0.66	0.33	0.40	0.43	–0.14	0.42
temperature versus abundance	0.10	–0.31	–0.68	–0.35	–0.86	–0.50
ceiling thickness versus drip rate						–0.60
ceiling thickness versus abundance						0.70
volume versus abundance: pools	–1.00	0.88	–0.63	–0.63	0.13	0.20
temperature versus abundance: pools	1.00	–0.63	–0.50	1.00	0.50	–0.30

**p<0.05

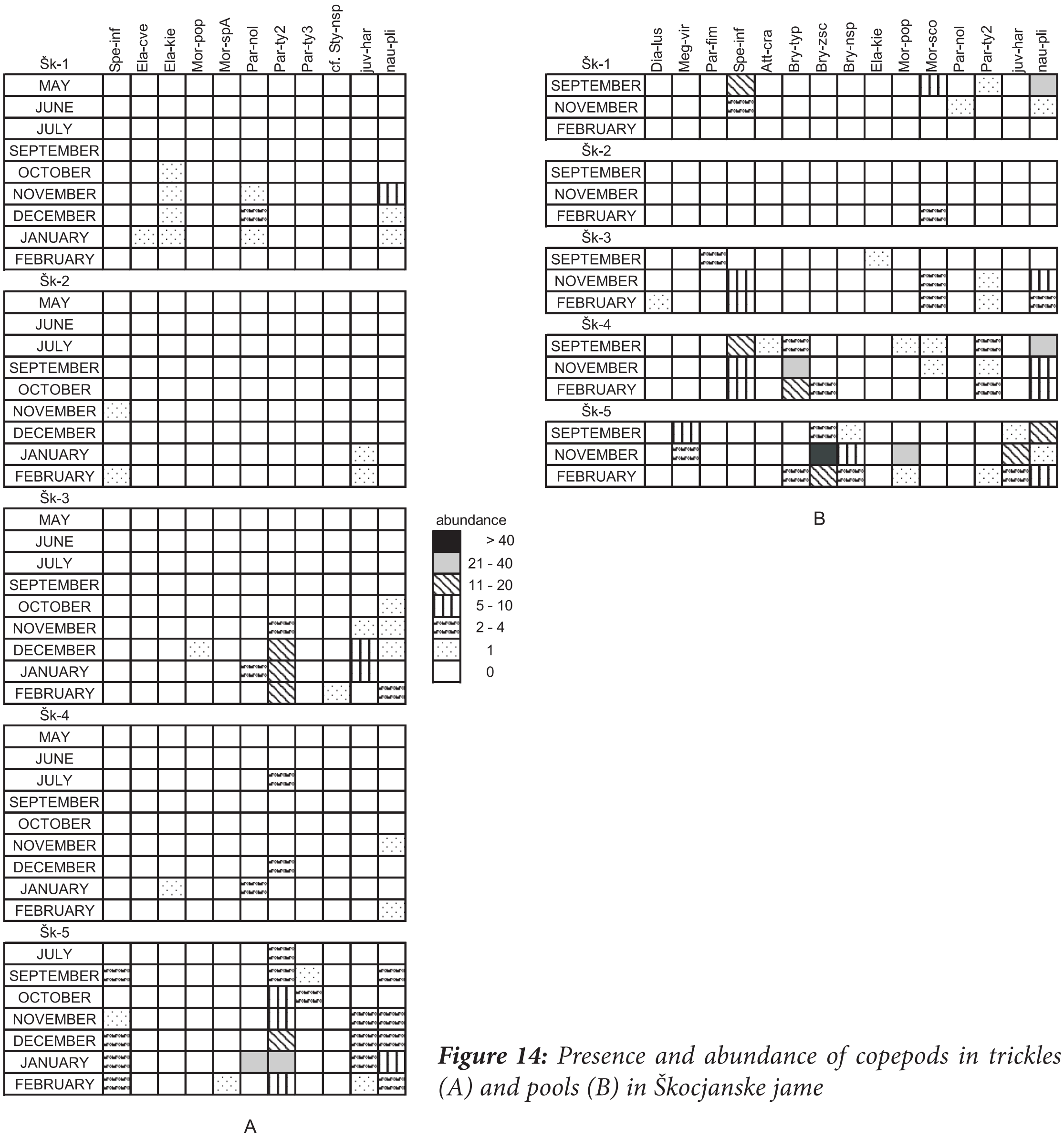


Figure 14: *Presence and abundance of copepods in trickles (A) and pools (B) in Škocjanske jame*

The connection between precipitation, discharge, temperature, thickness of the cave ceiling, quantity of pumped water and number of specimens is summarized in Table 10. Values of the Spearman correlation coefficient (r_s) for trickles indicated that the precipitation shows highly positive co-variation with the discharge ($p<0.05$). There was no statistically significant correlation ($p>0.05$) for the other pairs of variables.

DIMNICE

In Dimnice I found altogether 61 specimens of 8 species. The highest number of copepods were found at the trickle Di-2, whereas the highest number of species was in the trickle Di-1 (Figure 15A). In Dimnice I found the most new species in comparison

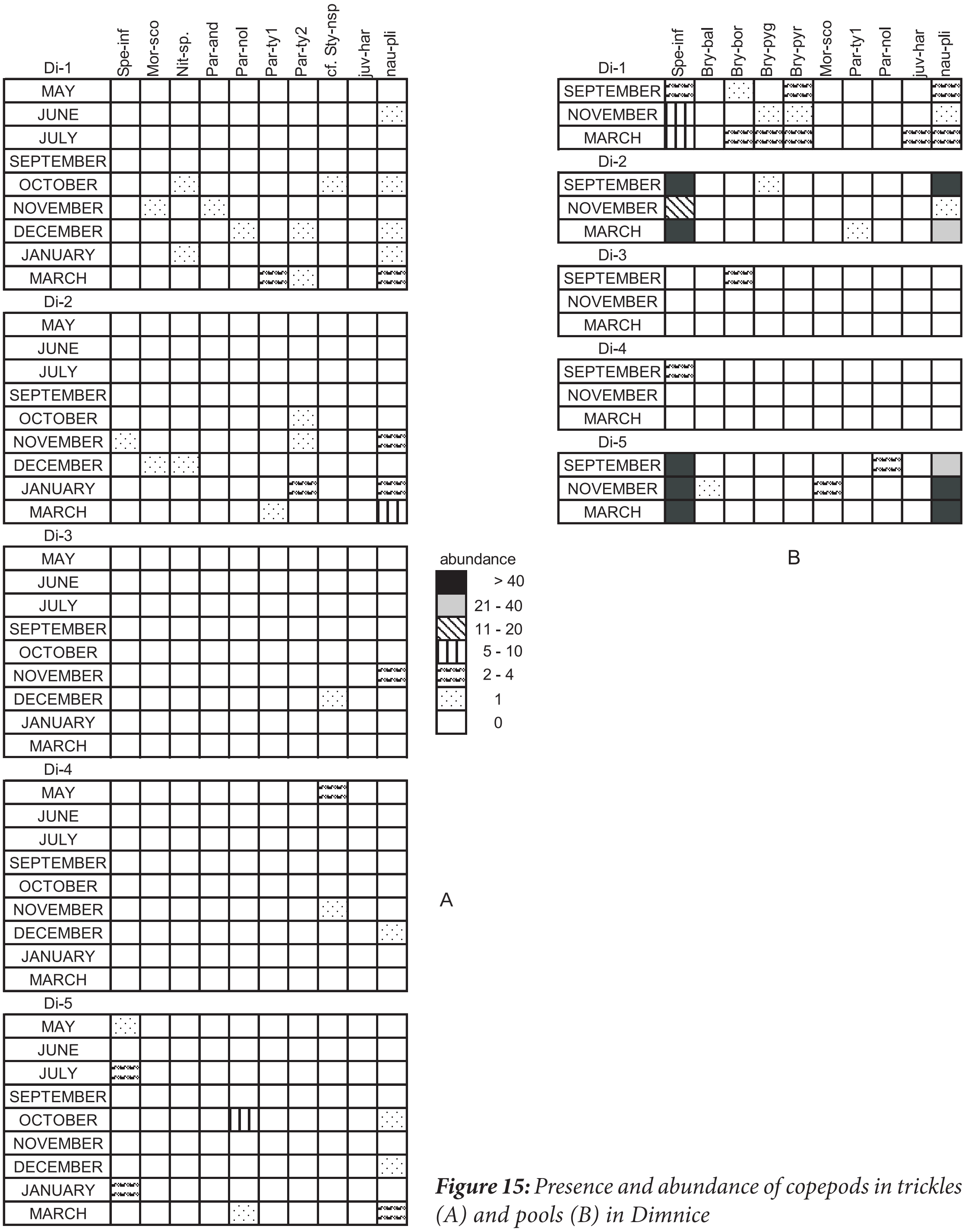


Figure 15: Presence and abundance of copepods in trickles (A) and pools (B) in Dimnice

with the other five caves; there were one species from the genus *Nitrocrella*, one from the genus *Stygepactophanes* and three species from the genus *Parastenocaris*. The most frequent species, which were found in more than half of the samples, were *Parastenocaris* sp. 2* and *S. infernus*.

In Dimnice 156 l of water was filtered from five pools. Altogether I found 1024 copepods of 8 species. The highest diversity was found in the pool Di-5 (type D-p) (Figure 15B).

Results of the correlation analyses, using the Spearman correlation coefficient (r_s), are summarized in Table 11. Precipitation was positively correlated with the discharge at the first three sampling points ($r_s \geq 0.8$, $p < 0.05$). There was no statistically significant correlation ($p > 0.05$) for the other pairs of variables.

Table 11: *Spearman (r_S) correlations for all pairs of the variables in trickles and pools in Dimnice*

	sampling points					
	Di-1	Di-2	Di-3	Di-4	Di-5	Cave
precipitation versus drip rate	0.83**	0.86**	0.87**	0.65	0.50	
drip rate versus abundance	0.21	0.60	0.64	0.62	0.24	
precipitation versus abundance	0.53	0.44	0.62	0.30	0.47	0.60
temperature versus abundance	–0.05	–0.08	0.46	0.39	–0.40	–0.10
ceiling thickness versus drip rate						0.48
ceiling thickness versus abundance						0.13
volume versus abundance: pools	0.50	0.50	–0.63	–0.63	0.50	0.83
temperature versus abundance: pools	–0.50	–1.00			–1.00	–0.43

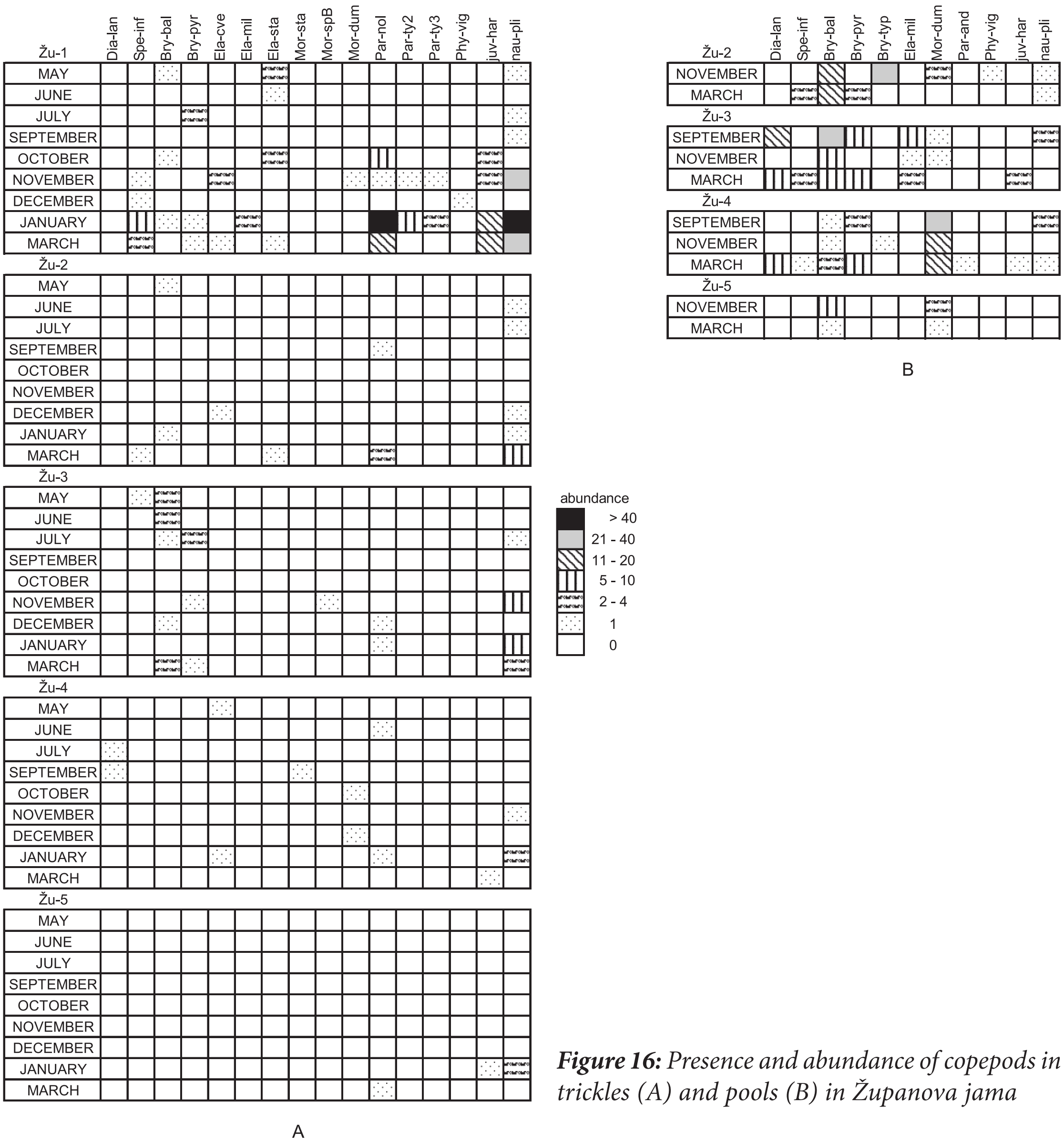
**$p < 0.05$

ŽUPANOVA JAMA

In Županova jama I found 315 specimens of 14 species. Most of them were present in the trickle Žu-1 (Figure 16A). There were 3 new species: one from the genus *Moraria* and two from the genus *Parastenocaris*. The most frequent species were *B. balcanicus*, *P. nolli alpina* and *E. cvetkae*.

In Županova jama 305 l of water was filtered from four pools. 248 copepods of 9 species were found. The highest diversity was found at the sampling points Žu-3 (type D-p) and Žu-4 (type D-i) (Figure 16B). The most frequent species were *B. balcanicus*, *E. millennii* and *M. dumonti*. I was able to take the samples from the pool Žu-5 only twice, otherwise the pool was dry.

Results of the correlation analysis indicate that there was a positive correlation between precipitation and dicharge. Abundance of copepods was positively correlated ($p < 0.05$) with the discharge at the first sampling point. There was no statistically significant correlation ($p > 0.05$) for the other pairs of variables.



Žu-1	Dia-lan	Spe-inf	Bry-bal	Bry-pyr	Ela-cve	Ela-mil	Ela-sta	Mor-sta	Mor-spB	Mor-dum	Par-nol	Par-ty2	Par-ty3	Phy-vig	juv-har	nau-pli
MAY			⁘				≋									⁘
JUNE							⁘									
JULY				≋												⁘
SEPTEMBER																⁘
OCTOBER			⁘				≋				▥				≋	
NOVEMBER		⁘			≋					⁘	⁘	⁘	⁘		≋	▒
DECEMBER		⁘												⁘		
JANUARY		▥	⁘	⁘		≋					■	▥	≋		▨	■
MARCH		≋		⁘	⁘		⁘				▨				▨	▒

Žu-2	Dia-lan	Spe-inf	Bry-bal	Bry-pyr	Ela-cve	Ela-mil	Ela-sta	Mor-sta	Mor-spB	Mor-dum	Par-nol	Par-ty2	Par-ty3	Phy-vig	juv-har	nau-pli
MAY			⁘													
JUNE																⁘
JULY																⁘
SEPTEMBER											⁘					
OCTOBER																
NOVEMBER																
DECEMBER					⁘											⁘
JANUARY			⁘													⁘
MARCH		⁘					⁘				≋					▥

Žu-3	Dia-lan	Spe-inf	Bry-bal	Bry-pyr	Ela-cve	Ela-mil	Ela-sta	Mor-sta	Mor-spB	Mor-dum	Par-nol	Par-ty2	Par-ty3	Phy-vig	juv-har	nau-pli
MAY		⁘	≋													
JUNE			≋													
JULY			⁘	≋												⁘
SEPTEMBER																
OCTOBER																
NOVEMBER				⁘					⁘							▥
DECEMBER			⁘								⁘					
JANUARY											⁘					▥
MARCH			≋	⁘												≋

Žu-4	Dia-lan	Spe-inf	Bry-bal	Bry-pyr	Ela-cve	Ela-mil	Ela-sta	Mor-sta	Mor-spB	Mor-dum	Par-nol	Par-ty2	Par-ty3	Phy-vig	juv-har	nau-pli
MAY					⁘											
JUNE											⁘					
JULY	⁘															
SEPTEMBER	⁘							⁘								
OCTOBER										⁘						
NOVEMBER																⁘
DECEMBER										⁘						
JANUARY					⁘						⁘					≋
MARCH															⁘	

Žu-5	Dia-lan	Spe-inf	Bry-bal	Bry-pyr	Ela-cve	Ela-mil	Ela-sta	Mor-sta	Mor-spB	Mor-dum	Par-nol	Par-ty2	Par-ty3	Phy-vig	juv-har	nau-pli
MAY																
JUNE																
JULY																
SEPTEMBER																
OCTOBER																
NOVEMBER																
DECEMBER																
JANUARY															⁘	≋
MARCH											⁘					

A

abundance	
■	> 40
▒	21 - 40
▨	11 - 20
▥	5 - 10
≋	2 - 4
⁘	1
	0

Žu-2	Dia-lan	Spe-inf	Bry-bal	Bry-pyr	Bry-typ	Ela-mil	Mor-dum	Par-and	Phy-vig	juv-har	nau-pli
NOVEMBER			▨		▒		≋		⁘		⁘
MARCH		≋	▨	≋							⁘

Žu-3	Dia-lan	Spe-inf	Bry-bal	Bry-pyr	Bry-typ	Ela-mil	Mor-dum	Par-and	Phy-vig	juv-har	nau-pli
SEPTEMBER	▨		▒	▥		▥	⁘				≋
NOVEMBER			▥			⁘	⁘				
MARCH	▥	≋	▥	▥		≋				≋	

Žu-4	Dia-lan	Spe-inf	Bry-bal	Bry-pyr	Bry-typ	Ela-mil	Mor-dum	Par-and	Phy-vig	juv-har	nau-pli
SEPTEMBER			⁘	≋			▒				≋
NOVEMBER			⁘		⁘		▨				
MARCH	▥	⁘	≋	▥			▨	⁘		⁘	⁘

Žu-5	Dia-lan	Spe-inf	Bry-bal	Bry-pyr	Bry-typ	Ela-mil	Mor-dum	Par-and	Phy-vig	juv-har	nau-pli
NOVEMBER			▥				≋				
MARCH			⁘				⁘				

B

Figure 16: *Presence and abundance of copepods in trickles (A) and pools (B) in Županova jama*

Table 12: *Spearman (r_S) correlations for all pairs of the variables in trickles and pools in Županova jama*

	sampling points					
	Žu-1	Žu-2	Žu-3	Žu-4	Žu-5	Cave
precipitation versus drip rate	0.66	0.74**	0.80**	0.03	0.84**	
drip rate versus abundance	0.76**	–0.15	0.17	0.24	0.24	
precipitation versus abundance	0.36	–0.27	0.08	0.10	0.17	0.35
temperature versus abundance	–0.63	0.31	–0.17	0.59	0.35	–0.63
ceiling thickness versus drip rate						–0.10
ceiling thickness versus abundance						–0.08
volume versus abundance: pools		–1.00	–0.50	0.50	1.00	1.00
temperature versus abundance: pools				–0.50	–1.00	0.50

**$p<0.05$

CANONICAL CORRESPONDENCE ANALYSES (CCA)

Ordination of species composition from trickles around two main CCA axes was related to the concentrations of ions, *i.e.*, Na^+, NO_3^-, K^+, Ca^{2+}, Mg^{2+}, SO_4^{2-}, Cl^-, and thickness of the cave ceiling, precipitation, discharge, temperature and conductivity (Figure 17, Figure 18). The variables that best explained the variation of 29 taxa from 120 samples in a CCA ordination were the concentrations of Na^+, NO_3^-, K^+ and the thickness of the cave ceiling. Nitrite was generally below the detection limit of 0.01 mg NO_2^--N l^{-1} in all the trickles throughout the year. Ammonium was also seldom detected in percolation water. In general, its concentration was below the detection limit of 0.04 mg NH_4^+-N l^{-1} throughout the year. The ortho-phosphate concentration was also below the detection limit of 0.02 mg PO_4^{3-}-P l^{-1} all year round. Due to the low concentrations of these ions they were not included in research of copepod spatial distribution.

The first canonical axis (CC1) was positively correlated with the sodium concentration and thickness of the cave ceiling, but negatively correlated with the nitrate concentration. The second canonical axis (CC2) was negatively correlated with potassium, sodium, nitrate concentrations and with the thickness of the cave ceiling.

The ordination diagram represents the approximate community composition at the sites. In general, different caves had very different positions in the plane of othe first and second canonical axes. Sampling sites in Pivka jama were distributed along the vector of nitrate (Figure 17). Ordination of sampling sites in convex hulls of Dimnice and Škocjanske jame was strongly influenced by the vector of sodium, which overlapped with the vectors of chloride, magnesium and sulphate. Sampling sites in Županova jama convex hull were dispersed throughout the space.

Ordination of sampling sites in Črna jama, Dimnice and Škocjanske jame were positively correlated with the CC1, and the sites in Pivka jama were negatively correlated with the CC1. CC2 was positively correlated with the sampling sites of Županova jama and Dimnice, and in negative one with the sites of Pivka jama, Črna jama and Škocjanske jame.

Taxa with different affinities or tolerances to four environmental parameters were determined (Figure 18). Four species which were found only in trickles in Pivka jama, (*Bryocamptus* sp.*, *B. dacicus*, *M. varica* and *Maraenobiotus* cf. *brucei**) were positively correlated with the concentration of nitrate. They form a distinctive cluster in the lower left of the graph (Figure 18). Distribution of some species found in Škocjanske jame (*E. kieferi*) and in Dimnice (*M. scotenophila*, *Nitocrella* sp.* and *Parastenocaris* cf. *andreji**) were positively correlated with the sodium concentration. *Moraria* sp. A* from Črna jama had a significantly greater preference for habitats influenced by sodium. In Črna jama and Pivka jama that belong to the same cave system and are 3 km apart there is no geographic trend and have quite different species composition. Species from Županova jama (*B. pyrenaicus, D. languidoides, E. millennii, E. stammeri, M. dumonti, Moraria* sp. B*, *M. stankovitchi* and *P. viguieri*) were frequently present in habitats characterised by lower concentrations of potassium and nitrate and thin thickness of the cave ceiling. The most common species (*i.e.*, *Parastenocaris* sp. 2*, *P. nolli alpina*, *M. poppei*, *E. cvetkae*, *S. infernus*) present in many of the caves were not so dependent on either of the described parameters. Because the species data from Postojnska jama were scarce (5 species) and abundances of the species too low (11 animals) it was not possible to analyse further ordination of species composition related to ecological factors.

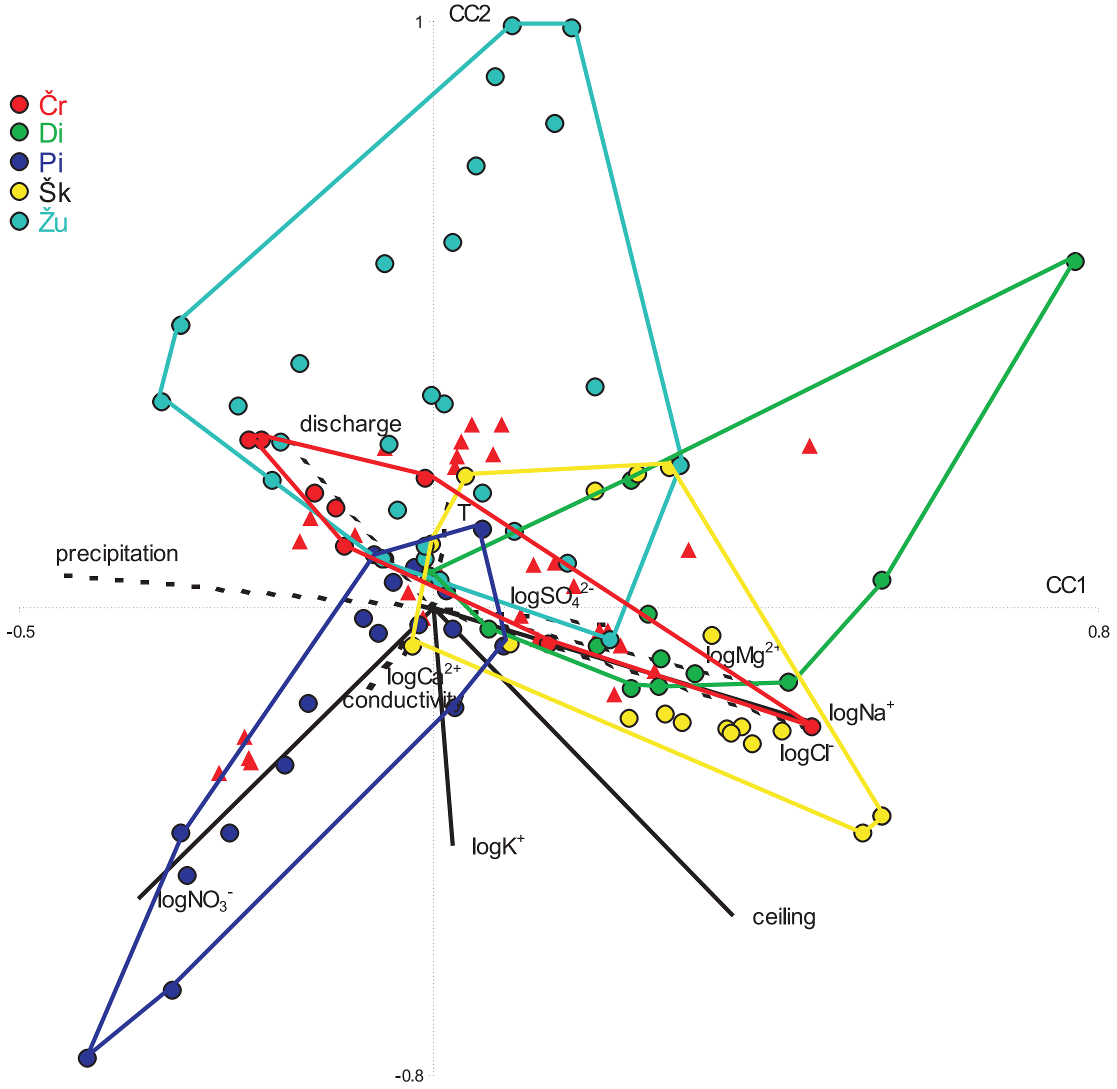


Figure 17: *Ordination diagram based on species composition and abundance data of copepods in trickles showing caves (convex hulls containing sampling sites ○) and species (▲) in relation to the twelve environmental variables (respresented as lines) of the five caves (monthly sampling 2000/2001); cumulative percentage of variance of species - environmental relation with first two axes was 51.9 %*

Legend: CC1 = first canonical axis (canonical eigenvalue = 0.49), CC2 = second canonical axis (canonical eigenvalue = 0.31).

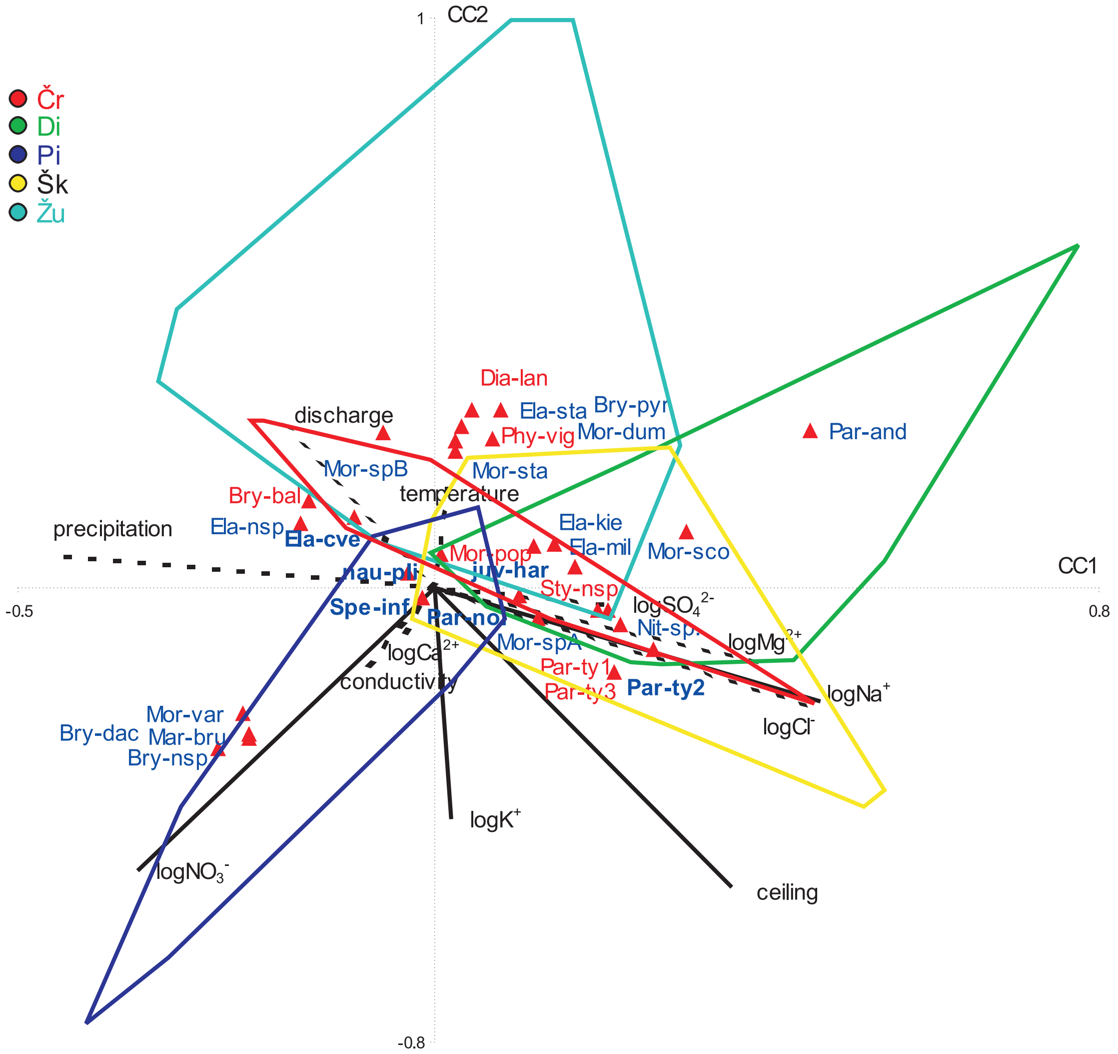


Figure 18: *Ordination diagram based on species composition and abundance data of copepods in trickles in relation to the twelve environmental variables of the five caves (monthly sampling 2000/2001); cumulative percentage of variance of species – environmental relation with first two axes was 51.9 %*

Legend: CC1 = first canonical axis (canonical eigenvalue = 0.49), CC2 = second canonical axis (canonical eigenvalue = 0.31); the species are marked by ▲ and annotated by abbreviated names as they appear in Appendix 1.

The same method was used to relate the copepod communities to environmental parameters in pools. Results of CCA using time integrated data on abundance of 29 taxa from 67 sampled pools and six environmental parameters indicate that, within these parameters, thickness of the cave ceiling, volume of pumped water, conductivity, pH and temperature of water are the most important ecological parameters influencing the distribution of the species.

From Figure 19 we infer that CC1 was positively correlated with the volume, conductivity and temperature. It was also in negative correlation with pH. CC2 was positively correlated with conductivity, temperature, thickness of the cave ceiling and pH. The ordination diagram in Figure 19 allows the following interpretation. Convex hulls of Črna jama, Županova jama, Postojnska jama, Škocjanske jame and Dimnice were positively correlated with CC1, while convex hull of Pivka jama was in negative correlation. CC2 was positively correlated with the sampling sites of Črna jama and Škocjanske jame, but in negative correlation with the sites of Županova jama and Dimnice.

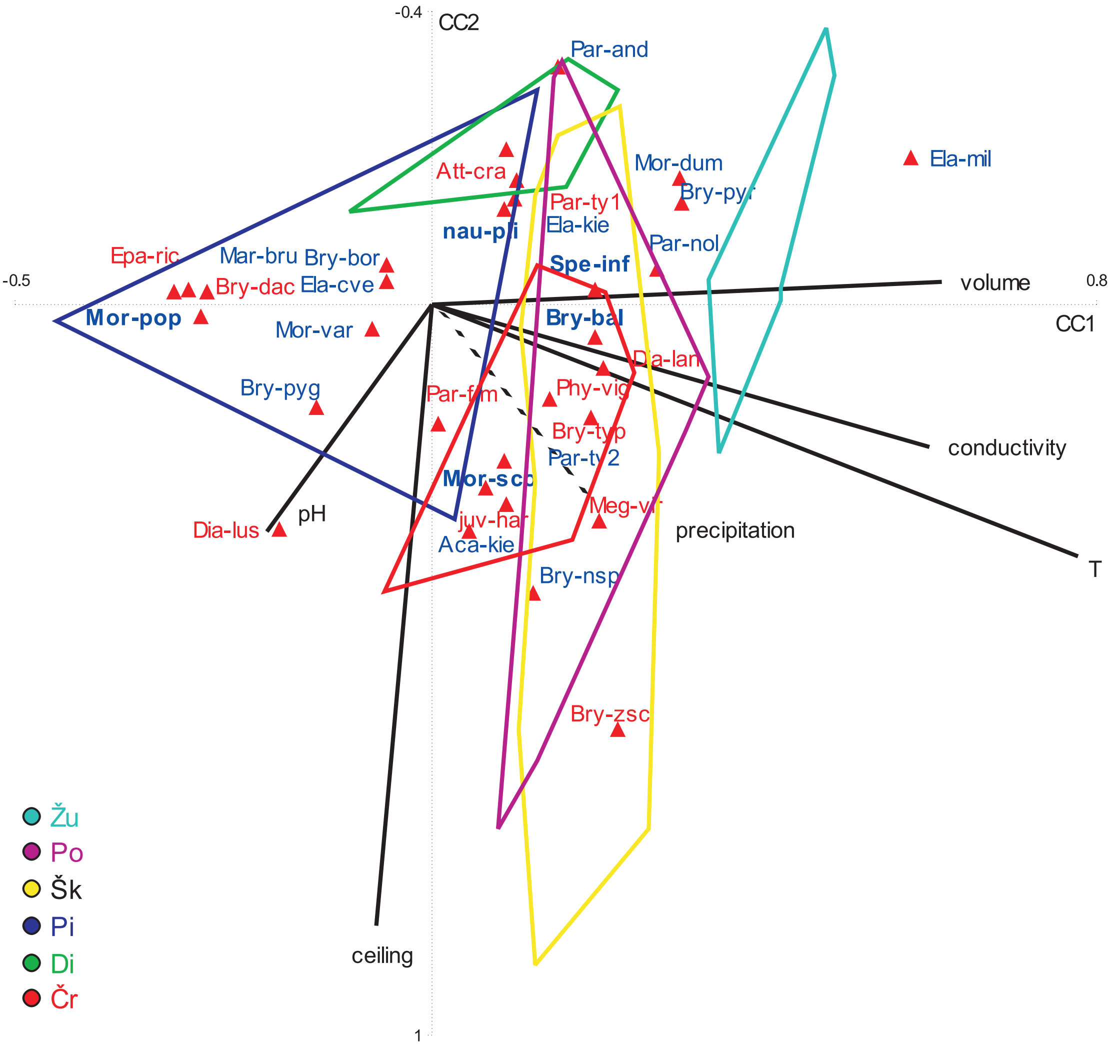


***Figure 19:** Ordination diagram based on species composition and abundance data of copepods in pools showing caves (convex hulls) and species (▲) in relation to the six environmental variables of the six caves (sampled in September, November 2000 and February 2001); cumulative percentage of variance of species – environmental relation with first two axes was 67.3 %*

Legend: CC1 = first canonical axis (canonical eigenvalue = 0.59), CC2 = second canonical axis (canonical eigenvalue = 0.42); the species are marked by abbreviated names as they appear in Appendix 1.

E. millennii, M. dumonti and *P.* cf. *andreji** from Županova jama had the highest weighted average with respect to temperature and conductivity of the water. Abundance of four species *M. viridis, Bryocamptus* sp.*, *B. zschokkei* and *Parastenocaris* sp. 2* from Škocjanske jame and Postojnska jama correlated positively with higher temperature of water. The rest of the copepod species (*i.e., B. borus, B. pygmaeus, E. cvetkae, E. richardi, M.* cf. *brucei*, M. varica, M. poppei, A. crassa, E. kieferi, P. nolli alpina*) were statistically significantly related with the thin thickness of the cave ceiling and were found in small pools with lower temperature and conductivity.

ABUNDANCE IN DIFFERENT TYPES OF POOLS

The Kruskal-Wallis Test was used to test whether sampled pools of different types coded A, B, C and D have an influence on the distribution of copepod fauna. Since the null-hypothesis is not rejected ($KW = 2.49 < \chi^2_{0.005} = 12.84$), I concluded that different types of pools have no statistical significant influence on the abundance of copepods and their distribution.

DIVERSITY OF COPEPOD COMMUNITIES

Shannon-Wiener diversity index was calculated from the numbers of individuals. Results of the Shannon-Wiener diversity index (Table 13) of copepod community in drips show that the highest diversity was recorded in Dimnice, whereas in pools the highest diversity was in Škocjanske jame.

Table 13: *Results of the Shannon-Wiener diversity index (H) of copepod community in drips and pools of the six caves (in the brackets are the hypotethical index valus)*

H	Postojnska jama	Pivka jama	Črna jama	Škocjanske jame	Dimnice	Županova jama
trickles	1.29 (1.61)	1.70 (2.40)	1.36 (2.08)	1.10 (2.20)	1.94 (2.09)	1.23 (2.65)
pools	1.70 (2.48)	1.03 (2.30)	1.40 (1.95)	1.89 (2.57)	0.22 (2.08)	1.74 (2.20)

ESTIMATING EPIKARST COPEPODS' RICHNESS

The thoroughness of sampling can be gained from the species accumulation curve shown in Figure 20. Based on Colwell (2004) sample-based rarefaction, the species accumulation curve together with 95 % confidence intervals is shown. Each sample in this case represented all of the copepods collected in drips and pools at a particular date in a particular cave, resulting in a total of 35 samples. It rapidly begins to reach an asymptote, reaching 75 percent of the maximum after 16 samples, 90 percent of the maximum after 26 samples, and 95 percent of the maximum after 31 of 35 samples.

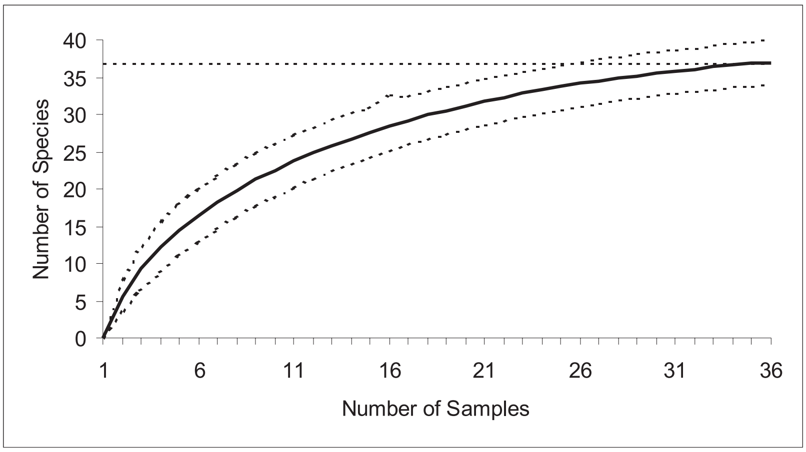


Figure 20: *Copepod species accumulation curve based on Mao-Tau procedure of Colwell (2004). Solid line is the accumulation curve and the two dotted lines are the 95 percent confidence intervals.*

An alternative approach to sampling completeness is to use estimates of total species number, based not on accumulation curves, but rather on the internal structure of species abundance, especially the number of singleton and doubleton species (Chao, 1987). Chao's estimate S_{Chao2} (Table 14) was calculated first for just the trickle data, and then for the combined data (trickles plus pools) for the six study caves. For each of these two data sets, all copepods were considered and then only sygobionts were considered.

A total of 5 of 10 non stygobionts were found in a single cave, based on the combined data. By comparison, 11 of 27 stygobionts were found in a single cave. For trickle data, 3 of 4 non stygobionts were found in a single cave, compared to 13 of 23 stygobionts. The estimates of S_{Chao2} also reflect this difference.

The Chao2 estimate for total numbers of stygobionts suggests that between 34 and 41 stygobionts eventually will be found and that between 60 and 80 percent of them have been found. The range of values reflects the differences in estimates using only trickles and both trickles and pools. The Chao2 estimate of the total number of copepod species was 49 (37 are known).

Table 14: *Estimates of species richness based on Chao's* S_2

	Trickles-All Species	Trickles-Stygobionts	All Habitats-All Species	All Habitats-Stygobionts
Sobs	27	23	37	27
SChao2 + S.E.	52.7+6.5	41.0+6.6	48.7+1.2	34+1.1
Sobs/SChao2	0.52	0.59	0.76	0.79
Singletons	16	13	16	11
Doubletons	4	4	10	8

PATTERNS OF EPIKARST COPEPOD BIODIVERSITY

The discovery of 37 species of copepods belonging to six families and 16 genera supported Sket's findings (1999c) that copepods are represented underground by a large number of families, genera, and species. Prior to this study, knowledge of species richness from epikarst was based on occasional sampling. There are striking omissions from the previous fauna lists, most likely due to inadequate sampling techniques. In most of these collections, the size of the mesh of the collecting nets were not as fine as in the present research.

As a result of the intensive and homogeneous sampling of epikarst copepods, the number of species recorded in percolation water from six caves increased from 24 to 45 (Table 15). When looking only at the five caves that were resampled in the current investigation, 19 species records were confirmed, 16 species records that were not confirmed, and 13 new species records were added (Table 15). The reason for the failure to confirm all previous records could be the transitory nature of the population in pools as Brancelj (1986a, 1986b, 1987) emphasized.

Among the 37 found species, many of them (27) were stygobionts. Most caves have only a handful of stygobionts; caves with ten or more are unusual (cf. Sket, 1999a; Gibert & Deharveng, 2002). Therefore, the discovery of between eight and fifteen species of stygobiotic copepods in each of the study caves indicates that epikarst copepod diversity may overwhelm the diversity of other stygobionts. The findings of this research showed that copepods occurring in the upper most layer or epikarst contribute a major part to the overall species richness from caves.

Clearly, by focusing solely on non-epikarst species or minimal epikarst sampling means that many species would be unreported and the distribution of others incompletely known.

Only two species were found in all six caves: *S. infernus* and *Parastenocaris* sp. 2*. In addition to *A. kieferi, S. infernus* was the only other cyclopoid that was found only in percolation water (Stoch, 1988), although it was also found in one spring (Brancelj, 2001). Species from the genus *Parastenocaris* were in present study often found in trickles of percolation water and in small depressions on stalagmites, but not in larger pools. The same type of habitat, small depressions on the walls, was sampled by Petkovski (1959a). He called it "the realm of *Parastenocaris*". Stoch (2000) reported that despite intensive sampling effort, only few specimens of *Parastenocaris* were collected from hypogean brooks and large pools of percolation water. Because of their small body length they

Table 15: *Review of copepod species found in six caves in percolation water and comparison with literature data*

Legend: ◆ data from presented research
+ /- cited data (+ found in percolation water; – found in undefined type of water habitat)

CYCLOPOIDA Species/cave	PO. J.	PI. J.	ČR. J.	ŠK. J.	DI.	ŽU. J.
1. *Acanthocyclops kieferi* (Chappuis, 1925)	◆ +	+				
2. *Acanthocyclops venustus* (Norman & Scott, 1906)				–		
3. *Diacyclops bicuspidatus odessanus* (Schmankevitsch, 1875)				–		
4. *Diacyclops bisetosus* (Rehberg, 1880)			+	–		
5. *Diacyclops charon* (Kiefer, 1931)	+	+				
6. *Diacyclops clandestinus* (Kiefer, 1926)				–		
7. *Diacyclops hypogeus* (Kiefer, 1930)				–		
8. *Diacyclops languidoides* (Lilljeborg, 1901)	◆ +					◆
9. *Diacyclops languidus* (Sars, 1863)				◆ +		
10. *Diacyclops slovenicus* (Petkovski, 1954)	+					
11. *Megacyclops viridis* (Jurine, 1820)	–			◆ –		
12. *Metacyclops postojnae* Brancelj, 1990	+					
13. *Paracyclops fimbriatus* (Fischer, 1853)	◆ +			◆ +		
14. *Speocyclops infernus* (Kiefer, 1930)	◆ +	◆ +	◆	◆ +	◆ +	◆
HARPACTICOIDA						
15. *Attheyella crassa* (Sars, 1862)			+	◆ +		
16. *Bryocamptus balcanicus* (Kiefer 1933)	◆ +	◆ +	◆ +		◆	◆
17. *Bryocamptus borus* Karanovic & Bobic, 1998					◆	
18. *Bryocamptus dacicus* (Chappuis 1923)	◆	◆	◆ –			
19. *Bryocamptus pygmaeus* (G. O. Sars, 1862)				+	◆	
20. *Bryocamptus pyrenaicus* (Chappuis, 1923)	+	◆			◆	◆
21. *Bryocamptus typhlops* (Mrazek, 1893)	◆	◆		◆ –		◆
22. *Bryocamptus zschokkei caucasicus* Borutskii, 1930	+					
23. *Bryocamptus zschokkei* (Schmeil, 1893)		–	–	◆		

24. *Bryocamptus* sp.*		♦		♦		
25. *Canthocamptus staphylinus* (Jurine, 1820)	+	–		+		
26. *Echinocamptus georgevitchi* (Chappuis, 1924)			–			
27. *Echinocamptus pilosus* (Van Douwe, 1910)	+	–	–	–		
28. *Elaphoidella cvetkae* Petkovski, 1983	+	♦ +	♦	♦ +		♦
29. *Elaphoidella jeannelli* Chappuis, 1928			–	–		
30. *Elaphoidella kieferi* Petkovski & Brancelj, 1985				♦ +		
31. *Elaphoidella stammeri* Chappuis, 1936	+					♦
32. *Elaphoidella millennii* Brancelj, in press						♦
33. *Elaphoidella* sp.*		♦				
34. *Epactophanes richardi* Mrazek, 1893		♦				
35. *Maraenobiotus* cf. *brucei**		♦				
36. *Moraria poppei* (Mrazek, 1893)	♦	♦	♦ +	♦	–	
37. *Moraria stankovitchi* Chappuis, 1924				+		♦
38. *Moraria varica* (Graeter, 1911)	♦ +	♦	+			
39. *Moraria* sp. A*			♦	♦		
40. *Moraria* sp. B*						♦
41. *Morariopsis dumonti* Brancelj, 2000						♦
42. *Morariopsis scotenophila* (Kiefer 1930)	♦		♦ +	♦ +	♦	
43. *Nitocrella* sp.*	♦				♦	
44. *Paracamptus schmeili* (Mrazek, 1893)			+			
45. *Parastenocaris nolli alpina* (Kiefer, 1938)		♦	♦	♦	♦	♦
46. *Parastenocaris* cf. *andreji**					♦	♦
47. *Parastenocaris* sp. 1*			♦		♦	
48. *Parastenocaris* sp. 2*	♦	♦	♦	♦	♦	♦
49. *Parastenocaris* sp. 3*				♦		♦
50. *Phyllognathopus viguieri* (Maupas, 1892)	♦				–	♦
51. cf. *Stygepactophanes* sp.*			♦	♦	♦	

are probably easy prey for the predators, so prefer to live in small pools and crevices of the vadose zone.

B. balcanicus and *M. poppei* were abundant species, found frequently in five and four caves respectively. This pattern of distribution was somewhat surprising given the wider range for *B. balcanicus* as it was known prior to this study. Distribution of *M. poppei*, found in big numbers at the two sampling sites in Pivka jama was probably connected with the food source. Water, gravity, and visitors brought a lot of organic matter to the entrance area of the cave; therefore I can explain the large number of specimens by the specific hydrological and geomorphological characteristics of the cave together with tourist activities. As Gibert & Deharveng (2002) pointed out "biodiversity and its patterns at local and, to some degree, at regional scales are controlled by productivity".

Species which were reproductively active (*Bryocamptus* sp.*, *B. balcanicus*, *B. typhlops*, *B. dacicus*, *B. pyrenacius*, *B. zschokkei*, *M.* cf. *brucei**, *P. fimbriatus*, *M. dumonti*, *D. languidoides*) as precopulatory mating individuals and/or ovigerous females (Figure 21) were often present in the same samples. Such species coexistence in epikarst is easy to explain by habitat patchiness and fragmentation, although scale of coexistence and fragmentation in epikarst is unknown. Physically, the epikarst comprises a series of repeated small solution pockets and vertical and lateral tubes that may fall into several categories based on their temporal stability (Musgrove & Banner, 2004). It is home to a major part of the obligate subterranean fauna that live in microhabitats, filled with water and from where were presumably washed in through the epikarst. The role of differences in trophic position and food specialization is difficult to assess, but typically in food-poor cave systems such as epikarst, the distinction between trophic levels blurs as species diets become more omnivorous and more generalized (Culver, 1985).

Figure 21: *Precopulatory mating individuals of Bryocamptus zschokkei with an ovigerous female*

That the preferred habitat of all found species is in the fissure system of epikarst may not be universal. For example, several precopulatory mating individuals and ovigerous females of *Bryocamptus* sp.* and *B. zschokkei* were found in one pool in Škocjanske jame. Pools may be, at a minimum, alternative habitats to the system of fissures in the epikarst. The coexistence of specimens of various species and their successful reproduction in the same habitat was probably made possible by a large quantity of organic matter due to the presence guano piles nearby.

Among the species, 16 of them are to a certain extent outliers, represented in one single cave. This rarity may be because the species are truly, it may be the result of incomplete sampling, or it may be because epikarst is not the primary habitat for these species. The single cave species can be divided into two ecological groups – generalists (stygophiles, stygoxenes, accidents, and stygobionts from non-epikarst habitats) and stygobiotic epikarstic specialists (Stoch, 1995). Some of the single cave species were generalists, especially *D. languidus, M. viridis, A. crassa, B. pygmaeus, B. zschokkei, E. richardi, E. stammeri* and *M. stankovitchi*. However, some of the species recorded from one cave or even from one trickle are apparently ecological specialists, limited to the epikarst – *A. kieferi, B. borus, E. kieferi, E. millennii, Elaphoidella* sp.*, *M.* cf. *brucei**, *Moraria* sp. B* and *M. dumonti*.

In addition to the variation of the distribution of species, individual drips show a large range of variation with respect to the species richness and ecological specialization of copepods that appear in the drips. While some crevices and drips inhabitants are widely distributed, some others seems to be either narrowly endemic or highly specialized, or both. *E. kieferi*, known only from Škocjanske jame, was found at the same place as in previous research (Petkovski & Brancelj, 1985) and nowhere else in the cave. It is still an open question as to what the important ecological differences are that result in the presence of *E. kieferi* in one small place in a cave. The presence of the species in only one trickle is probably the consequence of one or more geological, paleographical, or paleoecological events and the unique ecological peculiarities of animals. It must also be remembered that not all trickles in Škocjanske jame, or any other cave for that matter, have been sampled. Therefore, the presence in a single trickle can best be interepreted as being present in a small percentage of trickles. A similar example is described by Sket (1999c) and Sket *et al.* (2004a). The amphipod *Niphargobates orophobata* Sket was only known from a single trickle in Planinska jama which is the only known locality for the species. The presence of *N. orophobata* in just a single trickle can only be a consequence of the ecological uniqueness of that trickle among the sampled trickles. Whatever caused this uniqueness, it might be indicated by the highest ratio of terrestrial springtails in this trickle (Sket *et al.*, 2004a). Fact that some species were found only in one trickle suggests the possibility that they are ecologically extremely specialized. According to Sket *et al.* (2004a) this fauna may be more widely distributed, just not yet discovered. Anyway such rare inhabitants as *E. kieferi* and *N. orophobata* particularly increase the conservation value of the epikarst.

Species from the group of specialists were found for the first time in Slovenia (*i.e.*, *B. borus*) and some of them were so scarce as to make conclusions about their range and habits (*Elaphoidella* sp.*, *Maraenobiotus* cf. *brucei**, *Moraria* sp. B*) impossible.

M. dumonti and *E. millenii* were first found in Velika Pasjica jama (Brancelj, 2000a, pers. comm.). For both species, which are endemic to Slovenia, Županova jama is the second cave in which they have been found. It is likely that both species are distributed in the central and eastern part of the Dinaric region. All known species from genus *Morariopsis* live in the unsaturated zone and are frequently found in drips and pools filled with percolation water (Brancelj, 2000a). *M. dumonti* and *M. scotenophila* are allopatric; the first ranges in the narrow zone of central Slovenia, and the other ranges in the western part of it, in Notranjska karst region with the classical Karst area.

In spite of the difficulties of making generalizations about epikarst, it is important to try to arrive at some generalizations about this diverse, threatened habitat. Epikarst fauna is particularly vulnerable due to its almost direct exposure to largely undiluted contaminants from the surface (Sket *et al*., 2004a). Biologists should be fascinated by the peculiarities of epikarst animals. Exceptional richness in copepod species and the high frequency of endemism is probably related to the fragmentation of the epikarst habitat. Such conditions fostered genetic drift in isolated populations, together with the long-term persistence and relative stability of subterranean environment (Gibert & Deharveng, 2002).

DIFFERENCES IN FAUNAL COMPOSITION BETWEEN DRIPS AND POOLS

The drip pools and seeps form a distinct habitat in the cave and they represent window to the epikarst community. Many aquatic species are limited to small pools and trickles and are absent from the main watercourses of a cave probably because they are unable to survive in the stronger current of the larger streams, because of thigmotaxy, or because of a more favourable environmental conditions (Culver & Sket, 2002). The easiest way to sample the epikarst fauna of a cave is to sample pools. Unfortunately, pool sampling is far from an unbiased sample of the epikarst. For example, eight stygobiotic species – *Elaphoidella* sp.*, *E. stammeri*, *Moraria* sp. A*, *Moraria* sp. B*, *M. stankovitchi*, *Nitocrella* sp.*, *Parastenocaris* sp. 3*, cf. *Stygepactophanes* sp.* – were completely missing from the pools. Ten species of copepods were found only in drip pools but only four of them were stygobionts (*A. kieferi*, *B. borus*, *B. pygmaeus*, *B. typhlops*). A total of 37 species of copepods, 19 of these were found in both drips and pools, 15 of them were stygobionts.

Drips provide a more or less unbiased sample. Collections from drips represent animals exiting from the epikarst, in the same sense that harpacticoid copepods collected by drift nets at springs by Rouch (1970) represented both losses from the system and a way to assess the dynamics and diversity of the system. While the animals collected in drips may not be the entire epikarst fauna, it contains no other elements except for the possibility of surface-dwelling species being flushed through the system (Pipan & Culver, in review). By way of contrast, pools not only collect the animals from drips, there is also the possibility of interaction among these animals, as well as reproduction. In addition, there is the possibility that copepods living in other subterranean waters, especially streams, may colonize pools especially during times of flooding. Trickle data has the advantage of having only epikarst species and the disadvantage of smaller numbers. The combined data has the advantage of larger numbers and the disadvantage of containing non-epikarst species.

The reasons for the difference between copepod abundance in drips (1517) and pools (3414) are not clear, but in general abundance in pools is probably mostly a reflection of the amount of volume of pools collected, but the differences between drips may reflect the real differences between the leakage from the epikarst in the two caves. High species richness of epikarst copepods has to be dominated by heterogeneity of microhabitats within epikarst as well as pattern of predator-prey negative correlation. Stoch (1995) pointed out that "spatial heterogeneity and resource richness are correlated with the microcrustacean assemblages".

The non-copepod component of epikarst communities is interesting both because the animals are food input into the cave, especially drip pool and because it is a sample of terrestrial epikarst fauna, only sporadically mentioned. At least in the case of aquatic species, they are still living when they enter the cave, although their existence in any particular set of pools is often quite ephemeral.

Densities of copepods in pools on calcite (D-p) were higher than densities in pools on clay (D-i), although the high amount of water was filtered from pools on clay. This may be due to the effect of heterogeneity of habitat in case of pools on calcite. In contrast, there was more homogeneous habitat in pools on clay. It can be speculated that copepods in epikarst inhabit structured microhabitats similar to interstitial environment. Such microhabitat structure is important for competitive species living together and species in a predator-prey relationship to stably coexist. A classic example of this is Huffaker's (1958) laboratory experiment with a predator-prey pair of mites that could only stably coexist when the available, presumably homogeneous habitat was subdivided by partial dispersal barriers.

It is certainly true that pools are subject to environmental fluctuations (especially drying), that there are some microhabitats that may be quite abundant in pools, and that the relatively simple physical structure of pools may make predation more important (Pipan & Culver, in review).

POPULATION PARAMETERS

In most of the caves females were more frequent than males. Male copepods are commonly smaller than females and are usually outnumbered by females in most habitats (Dussart & Defaye, 2001). Mating has rarely been observed in groundwater copepods (Dole-Olivier *et al*., 2000). Kane & Culver (1992) and Culver *et al*. (1995) wrote that the environmental stimuli that may be the cue for onset of reproduction in amphipod *Gammarus minus* were decreasing temperatures and increasing the influx of organic detritus. In present study precopulatory mating individuals were frequent in the colder period of the year. In contrast, ovigerous females were present in the samples for the whole year. Although these findings are in accordance with Rouch's (1986) observation that females of some stigobiotic copepods lay eggs once a month, and so is the periodicity of copulation, pattern of reproduction is variable and inter and intraspecific variation is present. At this study numbers of reproductively active specimens were too small to make conclusions about the phenology of the species. The majority of the reproductively active specimens were found in pools with a large quantity of organic detritus (roots, fungi, soil, etc.). In general, groundwater copepods develop slowly, with one or more generations per year and possible peaks in spring and autumn. Consequently, stygobiotic species have longer life spans (Glatzel & Schminke, 1996).

A total of ten species of copepods that were reproductively active were found, and of these four were found as ovigerous females and precopulatory mating individuals, all of them from genus *Bryocamptus* (*B. balcanicus*, *B. dacicus*, *B. typhlops*, *B. zschokkei*). In two other species (*B. pyrenaicus*, *Maraenobiotus* cf. *brucei**) precopulatory mating individuals were found, and in four species (*P. fimbriatus*, *M. dumonti*, *D. languidoides*, *Bryocamptus* sp.*) ovigerous females were observed. Egg sacs have never been found among stygobiotic species of the harpacticoid *Pseudoctenisoma* or the cyclopoids *Acanthocyclops venustus westfalicus*, some *Speocyclops* and *Graeteriella* species (Dole-Olivier *et al*., 2000). In the Parastenocarididae two eggs at a time are released on the substratum (Dole-Olivier *et al*., 2000) which may be the reason that ovigerous females were not found also in some species of *Moraria*. The most abundant species present in drips and in pools was *S. infernus*. As the deposition of a spermatophore on female's genital segment is the essence of the mating process, a relatively high number of males of *S. infernus* with mature spermatophores as a reflection of their sexual maturity and copulation readiness were observed.

The relatively high ratio of reproductively active specimens (120) to adult specimens (3575) and nauplii (1147) indicates that the primary habitat of stygobiotic copepods was in the uppermost part of karst. The highly fractured interface between the top-soil and the underlying limestone in karst areas can serve as the primary habitat for a variety of crustaceans, including copepods and amphipods (*Niphargus*, *Stygobromus*) (Fong & Culver, 1994). The troglomorphic characteristics of the taxa indicates that species are adapted on the underground environment and nauplii, copepodids as well as adults were easily washed in caves through the epikarst.

ECOSYSTEM STRUCTURE AND DYNAMICS OF EPIKARST

The effect of geographic distance on community composition was not significant over distances ranges from tens of meters to tens of kilometres. In contrast, Culver *et al.* (in review) in their study found a pattern of similar composition in drips within distances up to 100 m. This relationship broke down at distances greater than 1 km. The difference between the two studies is most likely due to the difference in scales of analysis, and indeed if the geographic connection between communities breaks down at around 1 km, as Culver *et al.* (in review) suggest, then one would not expect a relationship at the broader geographic scale of this study.

Drips are our best and often only window into the epikarst community. The simultaneous monitoring of fauna and environmental parameters for a series of trickles showed that there is extensive heterogenity in the epikarst fauna. Individual drips showed a large range of variation with respect to the abundance of copepods as well as species richness. Looking at the spatial integration of epikarst communities as well as their control by local environmental factors there were precipitation and flow rate of drips that appeared to affect the presence of copepods. In study of Culver *et al.* (in review) of Organ Cave System drips with higher flows and lower temperature were more productive. The considerable differences in drip rates and copepod abundance between drips may be due to an important percolation threshold, caused by a temporary aquifer to form within the epikarst. As Klimchouk (1995) and Klimchouk *et al.* (1996) described, two major features of epikarst are storage and flow concentration at its base. Variability of individual drip diversity can be followed toward hydrologic and transport behaviour of the epikarst. Non-productive drips may be ones that essentially by-pass the aquifer storage system, *i.e.,* holes in the epikarst (Bakalowicz, 2004).

Examination of the results of drip collections showed that heterogeneity of the individual drip or habitat that occurs both within and between caves pronounced the variability of the system.

Aquatic copepod communities in epikarst, encompassing species at different affinities that reflect severe environmental conditions, were studied to extract the pattern of heterogeneity of the system. The significant factor found influencing copepod composition was the chemistry of percolation water and the thickness of the cave ceiling. Epikarst fauna was in permanent contact with the "epikarst water" and could be more influenced by its chemical components. When individual drips were studied, it was clear that thick ceilings probably act as a filter. As very slow moving water has insufficient force to dislodge copepods, thick ceiling reducing the number of animals that get completely dislodged from the epikarst zone (Culver *et al.*, in review).

At the community level, the convex hulls of the six caves indicated that Pivka jama and Županova jama were the most distinct. The abundance of species from Pivka jama was best explained by nitrate concentration. Nitrate, occurring mostly as a result of ammonium oxidation during percolation, indicated more or less permanent and wider areas of pollution. At trickles in the same cave Kogovšek (1987) noticed considerable differences in the water quality. This might be the reason why nitrate could explain a part of the faunal variation within the cave. Unequal degree of purification can be explained by the different paths of percolating water, conditioned by different permeability of the fissures within the epikarst (Kogovšek, 1987). The high concentrations of sodium and chloride at some sites in Dimnice was probable related to agriculture activities in the nearby dolines on the surface. Environmental parameters and fauna assemblage showed significant differences between Županova jama and other caves. Different climatic influences and vegetation on the surface and connected decay of organic matters (Kogovšek, 1990) were maybe the reason for different physical and chemical properties of percolation water in Županova jama.

Some species recorded from pools had preference for high conductivity, high temperature, and a dependence on water volume. It is possible that conductivity is a surrogate for the length of time water has been underground as it picks up ions from the native rock, or it may be an important constraint on the distribution of copepods.

It was clear from a variety of perspectives that the caves were well sampled for epikarst copepods. Thoroughness of sampling is shown by the species accumulation curve. Accumulation curve generated from the data of epikarst copepods from 35 samples reached an asymptote, what happened after 26 samples. This asymptotic relationship is nearly unprecedented and examples of failure of sampling in caves to reach an asymptote abound (Culver *et al.* 2004; Schneider & Culver, 2004).

The ratio of the observed number of species to the total number predicted by Chao's formula also provided a measure of thoroughness of sampling. At all scales there was good agreement between the number of observed species and the total number of predicted species. The Chao2 estimate of the total number of copepod species was 49 (37 are known) while the estimate of the number of stygobionts was 34 (27 are known). This is encouraging because it suggests that sampling in the six caves has captured most of the species. Of course, samples from other caves in the region are likely to yield new species since the ranges of most epikarst copepods are highly restricted. Interestingly many of the rare species were not stygobionts, and their rarity may mean that they are not regular inhabitants of the epikarst. The large ratio of known species to predicted species (80 %) was satisfying, and likely to be a larger percentage than is the case for data for other cave animals. The only other value reported in the literature is that of Schneider & Culver (2004), who reported that the observed number of troglobionts and stygobionts in 65 caves in a 20 km^2 area in West Virginia was less than half of the Chao2 estimate.

CONCLUSIONS

Epikarst displays characteristics of an ecotone since it contains both epigeic and hypogeic meiofaunal species, but in addition they also have characteristic species. This study advances the understanding of structure and dynamics of epikarst communities by providing insights into the richness and distribution of copepod species, environmental determinants of epikarst copepods and assessing the sampling efficiency.

Inputs of water, organic matter and energy into the groundwater system come from the interface to deep water. The surface runoff has close links with the underflow and the groundwater either along the river sides or in the bottom of rivers. An understanding of the physical, chemical, and biological processes under the surface of the earth is an essential element for the protection of caves. The spatial extent of copepod assemblages may also provide some important clues as to the extent of lateral movement of epikarst water during normal flow conditions. Flow paths of contaminants, both vertically and horizontally are highly unpredictable and copepods may provide important clues about the expectations of directions of contaminant flow in different karst areas (Culver *et al.*, in review).

Large number of copepod species found in percolation water, discovery of new epikarst species and their role as indicators of environmental conditions are three interesting ecological entities for a continuation of similar intensive researches of epikarst fauna. The epikarst habitat represents an inexhaustible source of data on the fauna community and a powerful tool for the study of environmental effects.

SUMMARY

The biodiversity, ecology and fauna of copepods in cave systems have rarely been systematically studied even though the subterranean environment all over the world is inhabited by numerous taxa of Copepoda. In Slovenia 107 taxa of Copepoda have been recorded up to now and about one third of these are stygobionts. At present, there are 15 endemics for Slovenia and all but one of them are stygobionts. All but one belong to the Harpacticoida.

I dealt with the ecological and biological explorations that are related to the topic of the copepod communities in percolation waters. Due to the fact that the epikarst habitats are very varied, in certain sense extreme, man may significantly change them and destroy the living place of the epikarst fauna. Waste waters sink from the karst surface and accumulate underground. Therefore the exploration of the impacts on the karst underground and the animal communities that live there is of considerable importance.

The position of epikarst at the top of karst and the typical absence of enterable passages or voids has meant that sampling has had to be indirect. The water exiting from the epikarst often creates pools. Those pools and drips have been collected directly and special sampling devices have been designed to collect copepods and other microscopic invertebrates. Each water trickle or pool filled with water was treated separately. The goals were to find out the total number of taxa in trickles of water in the unsaturated karst zone and to detect differences between trickles and pools. The question was also if there are differences of fauna between caves in different geographical areas which are relatively close to each other. Finally, I tried to detect the ecological conditions which are important and influential on the distribution of copepod species in epikart zone.

The six caves studied are situated in south and southwest Slovenia. In the caves Postojnska jama, Pivka jama and Črna jama I sampled water trickles once per week. In the other three caves (Škocjanske jame, Dimnice, Županova jama) the frequency of collecting samples from the containers was once a month, during 2000 and 2001. In Postojnska jama ten trickles (*i.e.*, ten sampling points) were selected. In the other caves five trickles were selected. The water from a drip was directed through a funnel into a plastic container. A 2 cm by 3 cm area on two sides of the square container were cut out and covered with a net (mesh size of 60 µm) to retain animals in the container. The content of the plastic containers was fixed with a 4 % solution of formaldehyde at the sampling spot and stored for further processing. In the laboratory I separated the organisms by means of a stereomicroscope at 100× magnification and stored them in 70 %

ethanol. Further processing and identification of the organisms was performed under a microscope. Pools within 5 m of the drips were sampled by aspiration of the water filtered through the collecting container described above. The samples were then processed in the same way as those from the trickles.

This research on copepods in six caves in Slovenia indicated a high number of taxa inhabiting percolating water and adjacent pools. From this environment eleven species new to science were recognized. New species living there were particularly restricted in distribution to one or a few trickles of water from the ceiling. In total, 37 taxa were collected in six caves. Ten taxa could be designated as ubiquitous and were found frequently in subterranean environment but transported from their epigean habitats. The rest of the taxa, *i.e.*, 27 of them, are stygobiotic and fifteen are endemic to Slovenia. One species, *Bryocamptus borus*, is new to the Slovenian fauna. Males of *Morariopsis scotenophila* were found for the first time.

Between 11 and 17 different taxa of copepods were found per cave regardless of its length, between 8 and 15 species were stygobiotic. In 680 m long Županova jama 16 taxa was recorded and in the Škocjanske jame, more than 5 km long, 17 taxa were collected.

From 37 taxa, only two, *Speocyclops infernus* and the new species *Parastenocaris* sp. 2* were found in all six caves. In addition two taxa were collected in five caves. The majority of taxa were found in one or two caves only. 16 taxa were found only in one location and eleven of these were stygobiotic ones. The rest were ubiquitous taxa, transported into the caves by accident. Eight taxa, *i.e.*, one fifth of the taxa from the list, were found only in trickles of percolation water. All of them were stygobiotic and all but one are endemic. Some more (ten species) were found only in the pools filled by percolation water. Six of them were cosmopolitan and tolerant to the subterranean environment, the other four taxa are stygobiotic or stygophilic.

It was clear from a variety of perspectives that the caves were well sampled for epikarst copepods. Accumulation curve generated from the data of epikarst copepods from 35 samples reached an asymptote after 26 samples. At all scales there was good agreement between the number of observed species and the total number of predicted species.

The intensive survey of two different types of habitats in six karst caves showed that the ratio of copepod abundance in the trickles of percolation water is different from that in the pools filled with this water. Drips are the best, unbiased and often only window into the epikarst community. The simultaneous monitoring of fauna and environmental parameters for a series of trickles showed that there is extensive heterogenity in the epikarst fauna. High species richness of epikarst copepods is made possible by heterogeneity of microhabitats within epikarst, which allows for coexistence of competitors and stability of predator-prey pairs.

From a geographical point of view, there was no correlation between the distance between the caves and the similarity of the fauna (expressed as a ratio of the species in common between two locations and the sum of taxa on both locations, the Jaccard index).

The highest similarity ($S_J = 0{,}44$) was between caves Dimnice and Črna jama which are approximately 30 km apart. In caves which belong to the same cave system (Postojnska jama, Pivka jama, Črna jama) and are 3 km apart, the index was similar.

The results of the correlation analysis (using the Spearman correlation coefficient) and the nonparametric version of one way ANOVA (using the Kruskal-Wallis Test) indicated that there was no correlation between thickness of the cave ceiling and temperature on the one hand and the number of specimens on the other hand. Precipitation showed a highly positive co-variation with the discharge and with the number of specimens. Copepod abundance in different types of pools was not proportional to the quantity of pumped water. For more precise conclusions about the correlation between the type of pools or quantity of filtered water and the number of specimens, a large number of samples collected in short intervals should be analysed. New data can be obtained from further investigations in trickles of percolation water.

Grouping of copepod species composition around two main axes by canonical community analysis (CCA) was related to physical and chemical parameters in percolation water. Due to the fact that the correlation between single species and ecological parameters, especially ions, was statistically significant, copepods from epikarst zone show high level of ecological specialization. The most common species present in many of the caves were not so dependent on the measured parameters.

In spite of the difficulties of making generalizations about epikarst, this study advances the understanding of structure and dynamics of epikarst communities. The high total number of copepods found in the caves, the high number of species per cave with a dominance of stygobiotic species and very low number of species common to all caves indicate that biodiversity in epikarst is very high. The results and findings of the research represent a fundamental contribution to the understanding of the distribution patterns of stygobiotic copepods in the epikarst zone.

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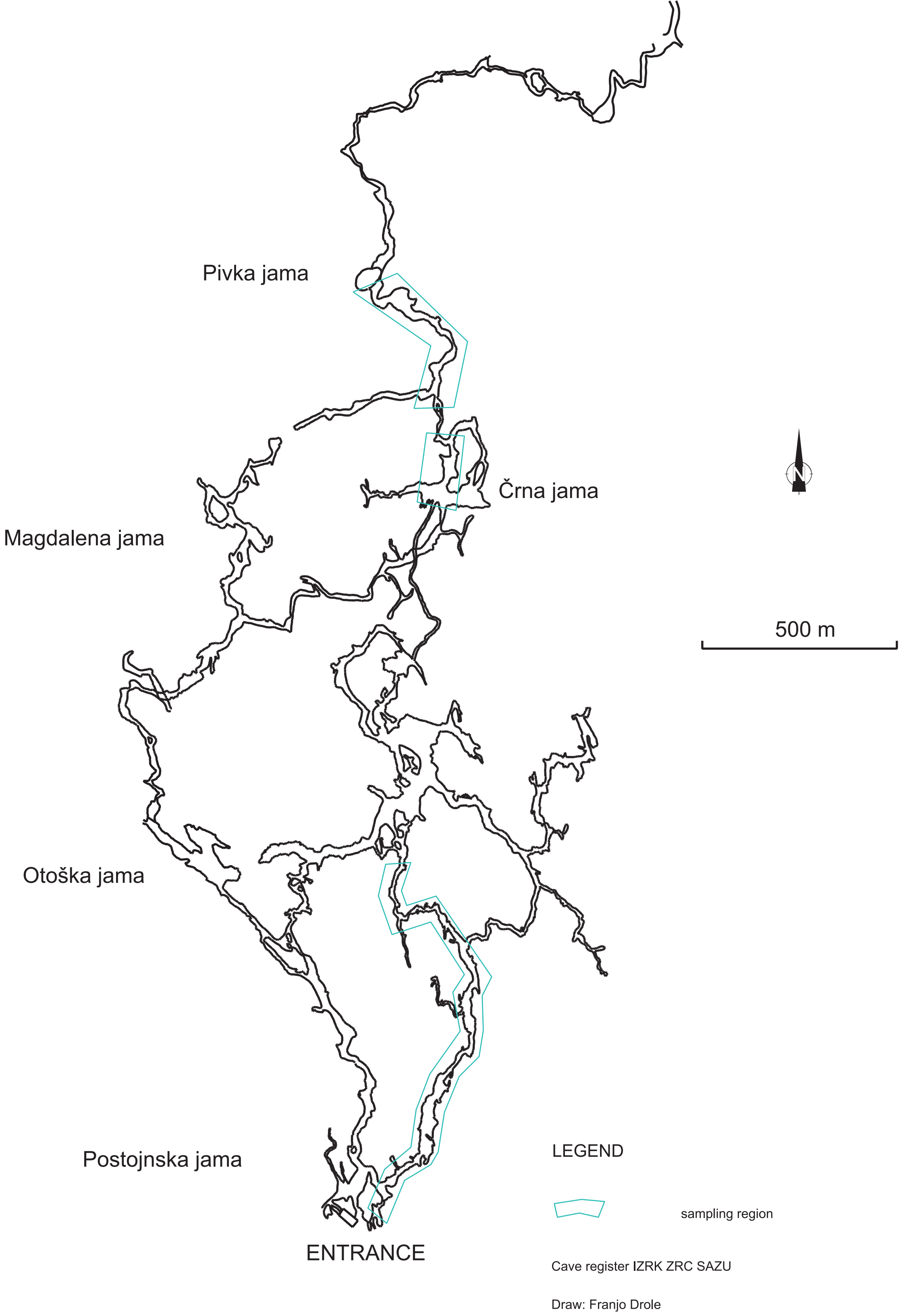
APPENDIX

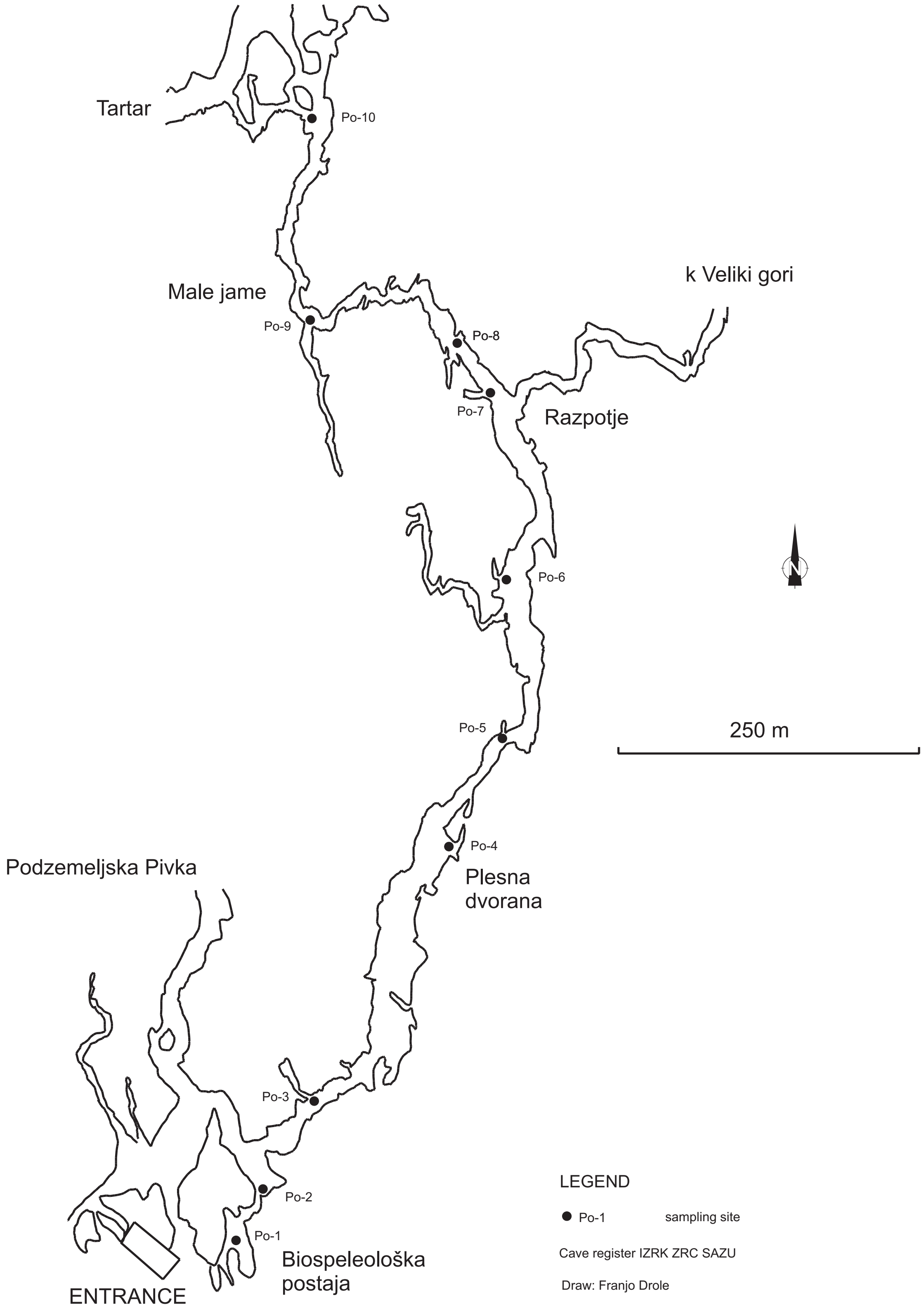
Appendix 1: *Abbreviations used in the figures are:*

Aca-kie	*Acanthocyclops kieferi* (Chappuis, 1925)
Dia-lan	*Diacyclops languidoides* (Lilljeborg, 1901)
Dia-lus	*Diacyclops languidus* (Sars, 1863)
Meg-vir	*Megacyclops viridis* (Jurine, 1820)
Par-fim	*Paracyclops fimbriatus* (Fischer, 1853)
Spe-inf	*Speocyclops infernus* (Kiefer, 1930)
Att-cra	*Attheyella crassa* (Sars, 1862)
Bry-bal	*Bryocamptus balcanicus* (Kiefer 1933)
Bry-bor	*Bryocamptus borus* Karanovic & Bobic, 1998
Bry-dac	*Bryocamptus dacicus* (Chappuis 1923)
Bry-pyg	*Bryocamptus pygmaeus* (G. O. Sars, 1862)
Bry-pyr	*Bryocamptus pyrenaicus* (Chappuis, 1923)
Bry-typ	*Bryocamptus typhlops* (Mrazek, 1893)
Bry-zsc	*Bryocamptus zschokkei* (Schmeil, 1893)
Bry-nsp	*Bryocamptus* sp.*
Ela-cve	*Elaphoidella cvetkae* Petkovski, 1983
Ela-kie	*Elaphoidella kieferi* Petkovski & Brancelj, 1985
Ela-sta	*Elaphoidella stammeri* Chappuis, 1936
Ela-mil	*Elaphoidella millennii* Brancelj, in press
Ela-nsp	*Elaphoidella* sp.*
Epa-ric	*Epactophanes richardi* Mrazek, 1893
Mar-bru	*Maraenobiotus* cf. *brucei**
Mor-pop	*Moraria poppei* (Mrazek, 1893)
Mor-sta	*Moraria stankovitchi* Chappuis, 1924
Mor-var	*Moraria varica* (Graeter, 1911)
Mor-spA	*Moraria* sp. A*
Mor-spB	*Moraria* sp. B*
Mor-dum	*Morariopsis dumonti* Brancelj, 2000
Mor-sco	*Morariopsis scotenophila* (Kiefer 1930)
Nit-sp.	*Nitocrella* sp.*
Par-nol	*Parastenocaris nolli alpina* (Kiefer, 1938)
Par-and	*Parastenocaris* cf. *andreji**
Par-ty1	*Parastenocaris* sp. 1*
Par-ty2	*Parastenocaris* sp. 2*
Par-ty3	*Parastenocaris* sp. 3*
Phy-vig	*Phyllognathopus viguieri* (Maupas, 1892)
Sty-nsp	cf. *Stygepactophanes* sp.*
juv-har	juvenile Harpacticoida
nau-pli	nauplii

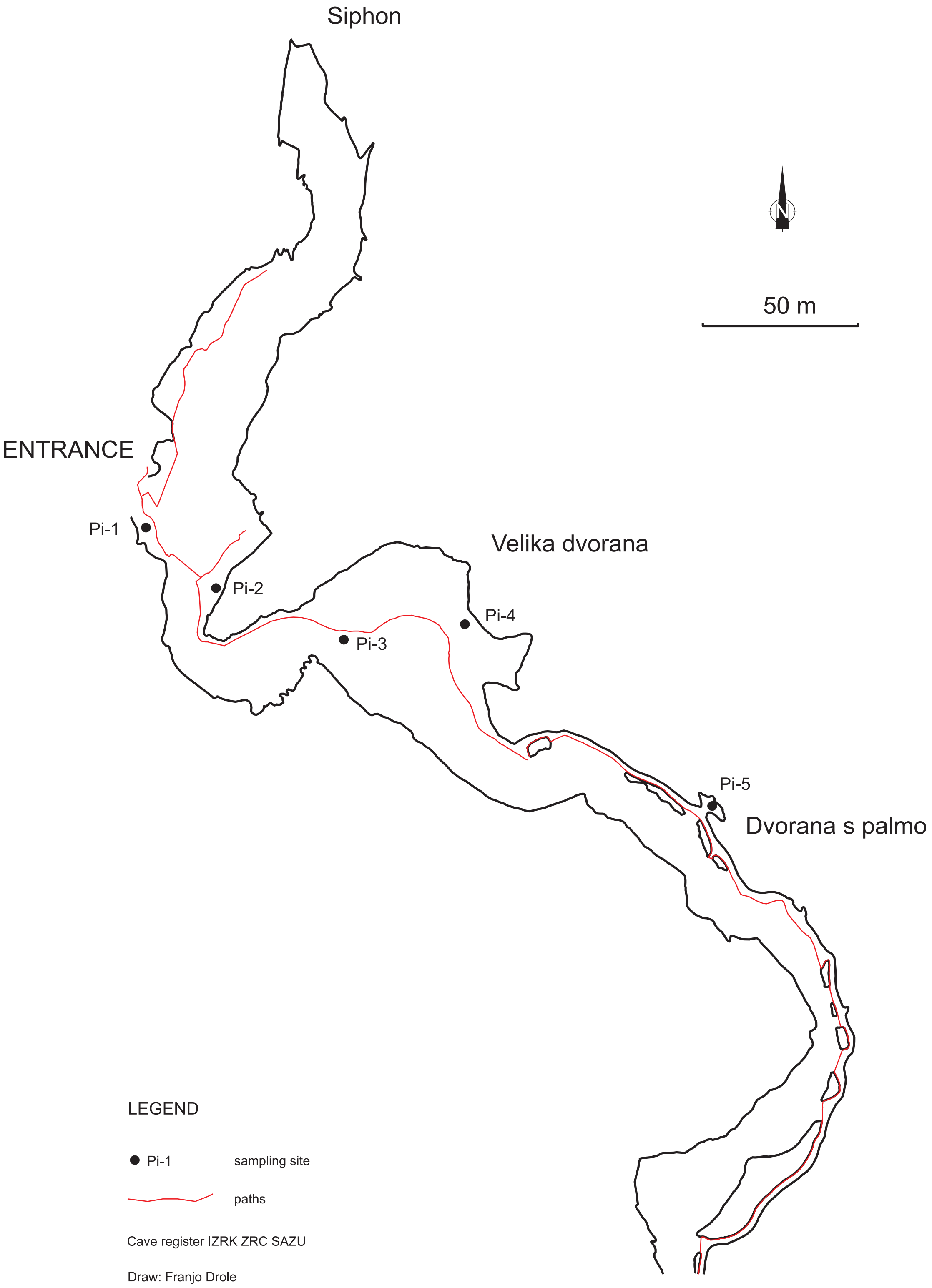
Appendix 2: *Ground plan of Postojnska jama cave system*



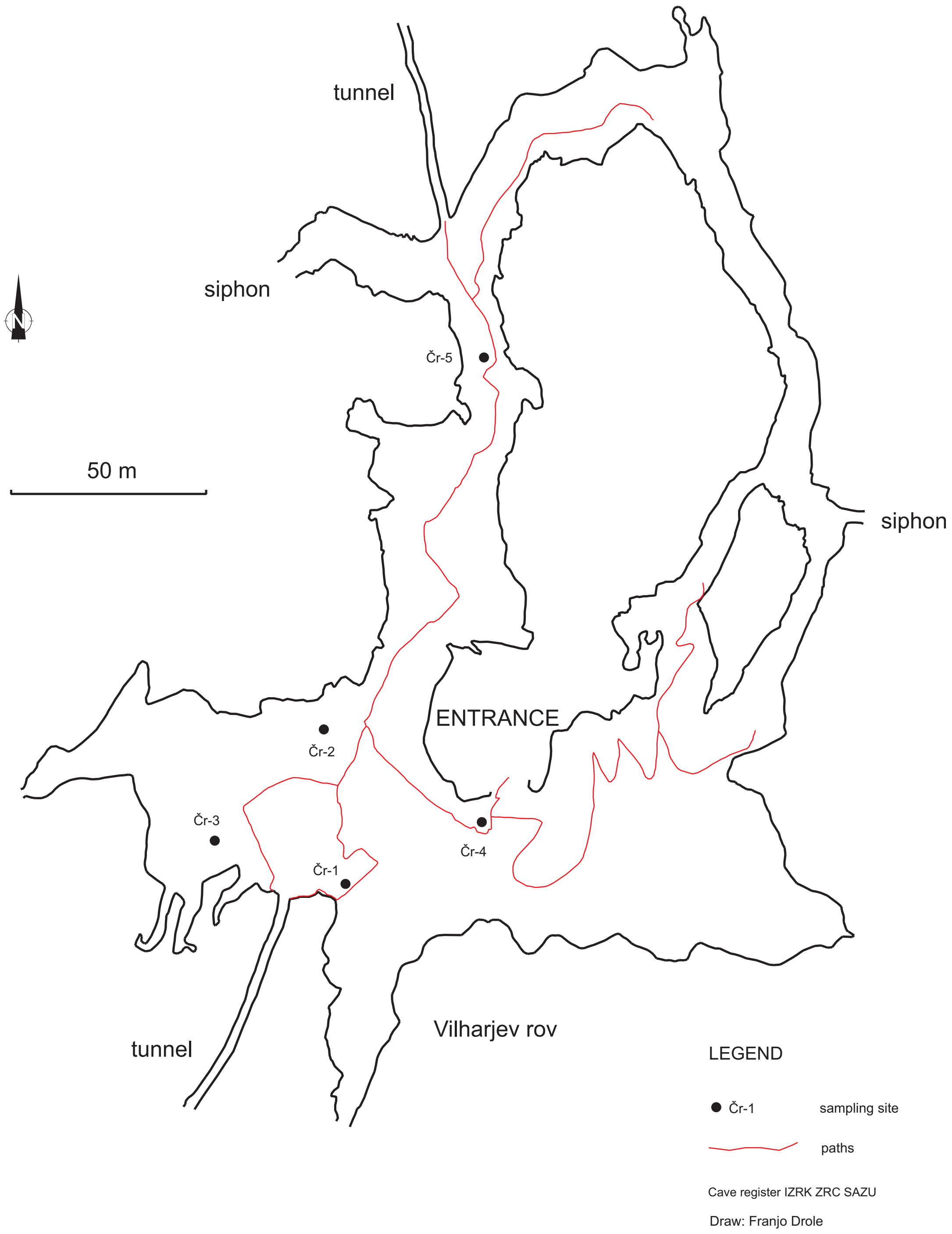
Appendix 3: *Ground plan of Postojnska jama showing sampling sites*



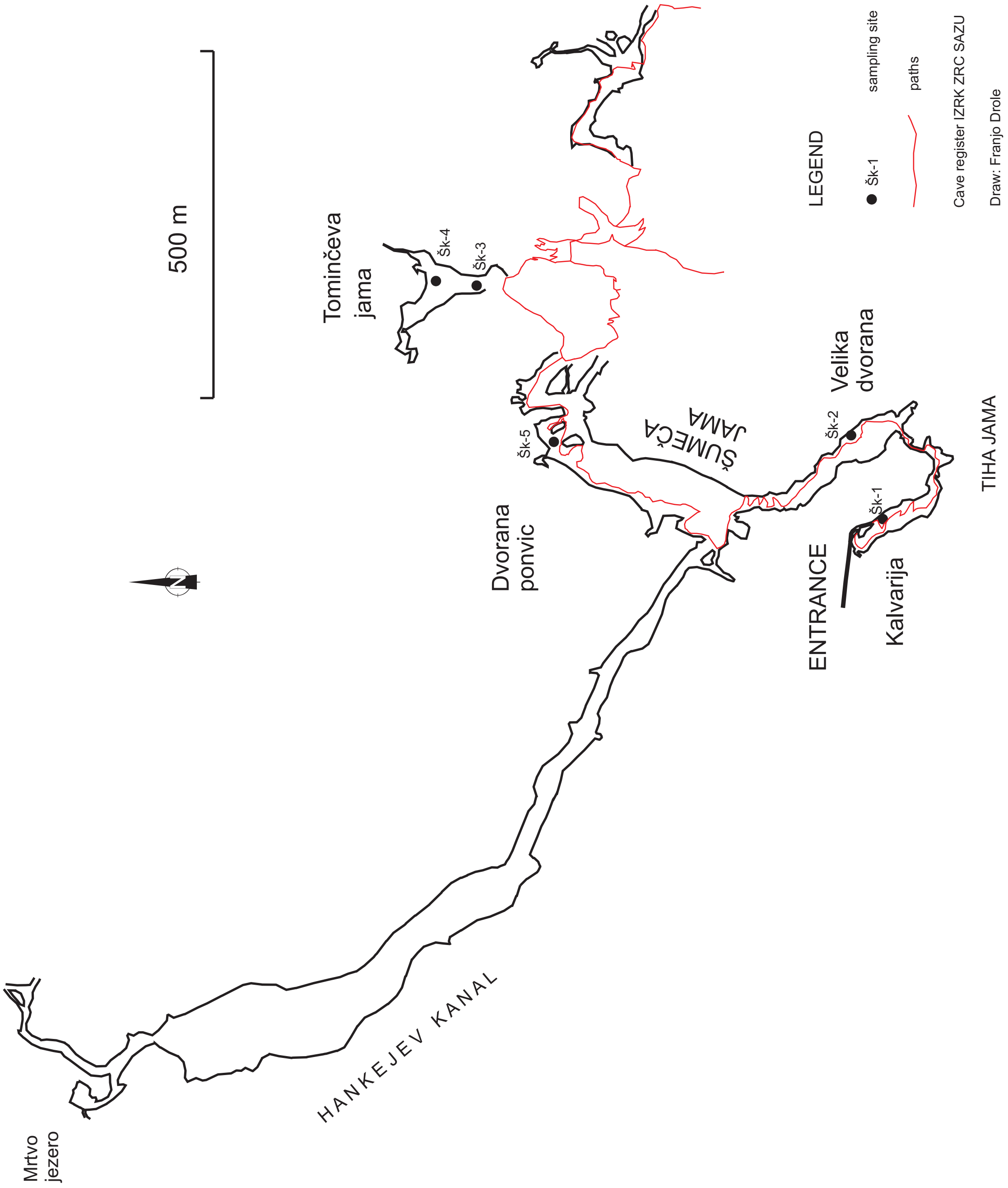
Appendix 4: *Ground plan of Pivka jama showing sampling sites*



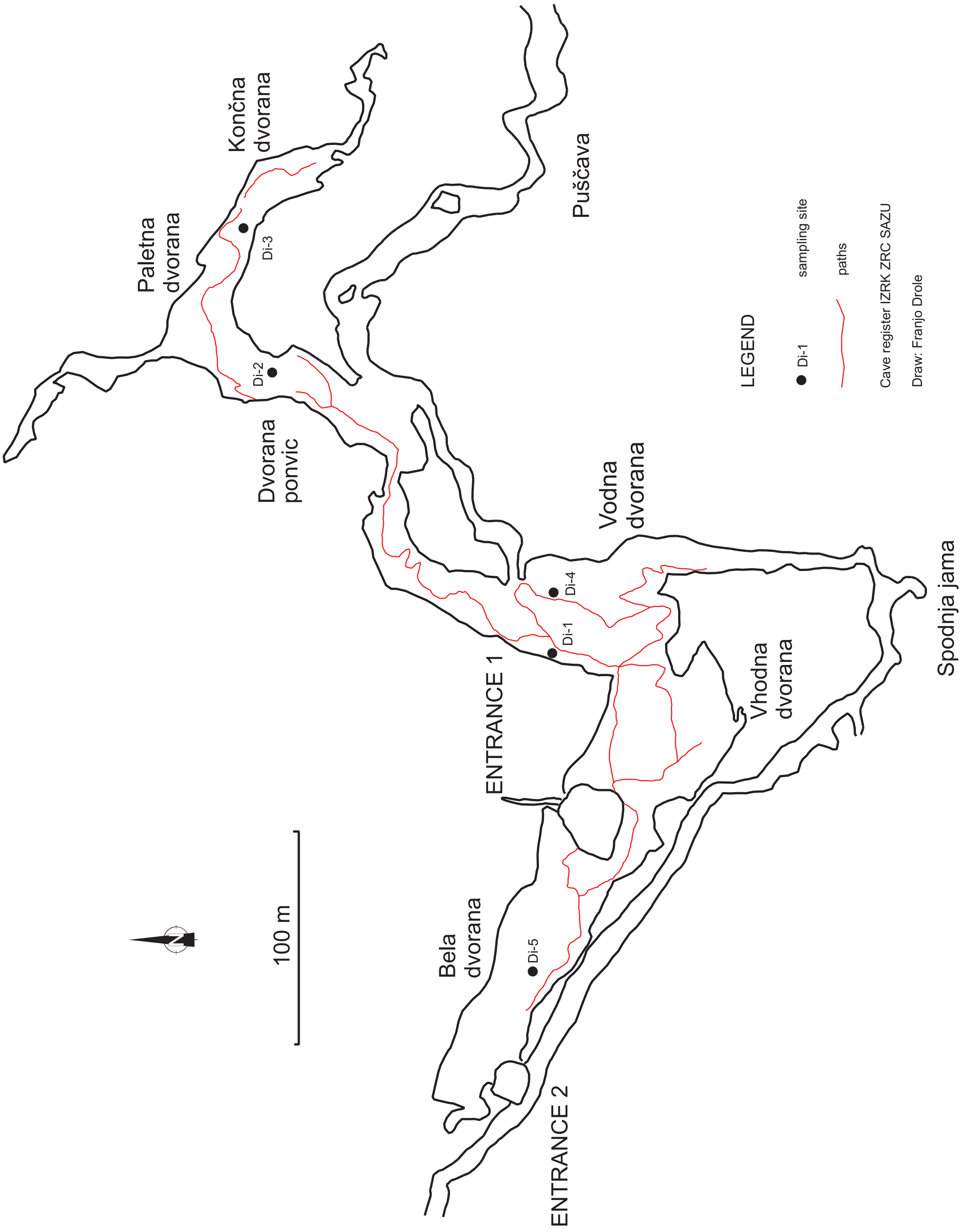
Appendix 5: *Ground plan of Črna jama showing sampling sites*



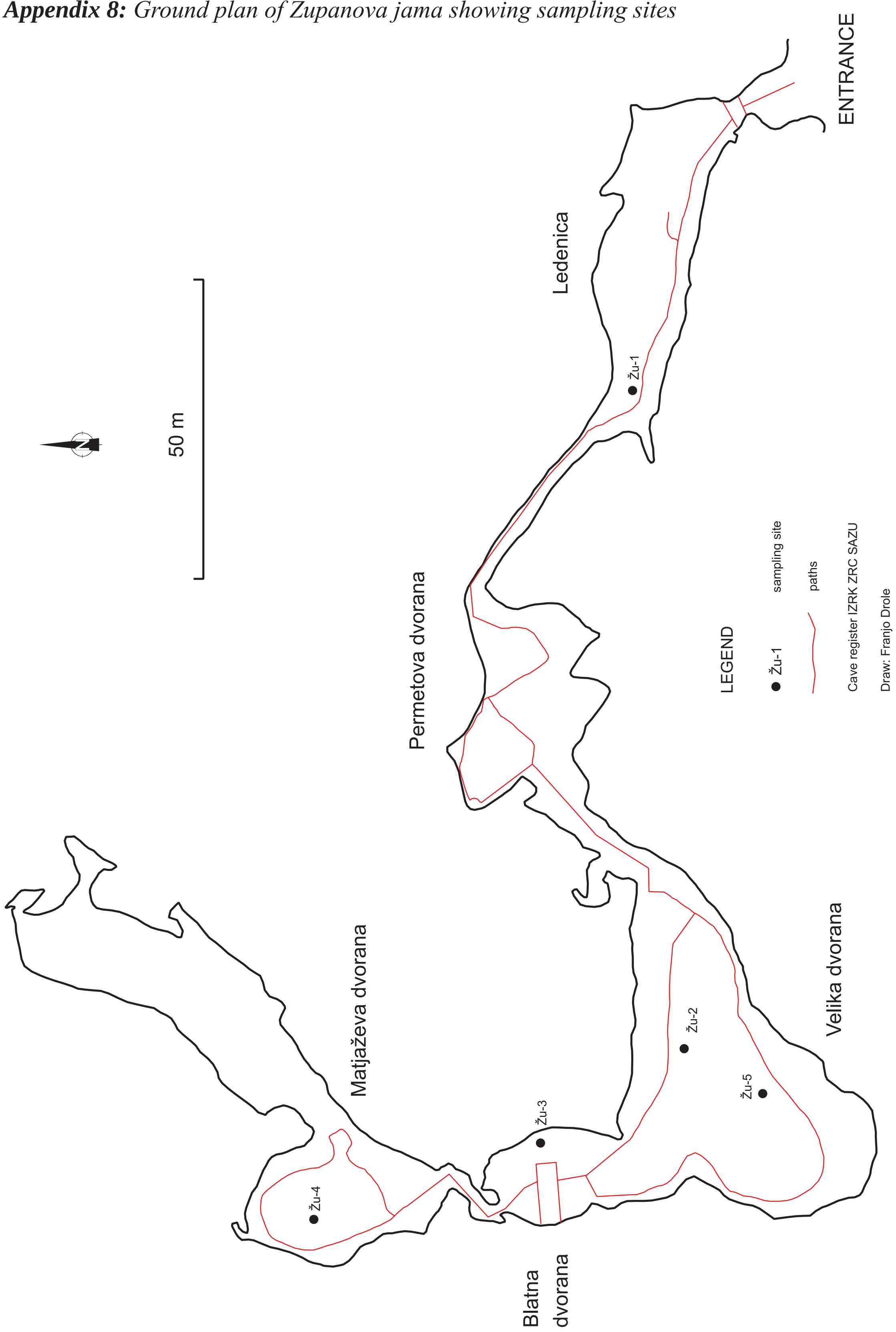
Appendix 6: *Ground plan of Škocjanske jame showing sampling sites*



Appendix 7: *Ground plan of Dimnice showing sampling sites*



Appendix 8: *Ground plan of Županova jama showing sampling sites*



Appendix 9: *Weighted descriptive statistics for a data set of 29 copepod species and six physical parameters from pools (**median**, minimum and maximum, first and third quartile); the species are marked by abbreviated names as they appear in Appendix 1.*

species	n	ceiling [m]		precipitation [mm]		T [°C]		pH		conductivity [µS cm^{-1}]		volume [l]	
Spe-inf	**794**	**59.72**		**1.09**		**7.58**		**7.79**		**374.12**		**24.99**	
		10.11	60.25	0.70	5.11	4.79	7.62	7.69	7.81	271.96	441.89	17.99	25.02
		9.60	110.39	0.68	10.22	0.58	11.92	7.48	8.60	203.81	540.19	0.11	120.01
Mor-pop	**754**	**57.04**		**2.00**		**1.91**		**7.80**		**290.05**		**2.02**	
		56.81	57.26	1.99	2.01	1.86	1.96	7.79	7.81	289.82	290.27	1.91	2.12
		54.65	110.38	0.92	7.62	1.82	11.86	7.59	8.20	220.04	412.32	1.19	50.20
Mor-sco	**247**	**84.38**		**5.21**		**9.29**		**7.71**		**390.18**		**5.02**	
		60.65	85.11	5.09	7.59	6.30	9.31	7.69	7.80	389.92	409.87	4.13	14.95
		10.47	109.25	0.88	10.22	1.69	11.88	7.49	8.41	220.06	525.01	0.04	50.14
Bry-bal	**174**	**60.27**		**2.02**		**8.91**		**7.71**		**392.96**		**11.96**	
		29.54	84.62	1.72	5.70	8.59	9.19	7.69	7.89	375.11	429.99	4.91	24.91
		10.11	99.78	1.36	10.17	2.58	9.52	7.42	8.60	235.84	465.18	0.16	120.08
Bry-dac	**156**	**56.98**		**2.32**		**1.93**		**7.81**		**291.14**		**2.01**	
		56.68	57.21	1.55	2.90	1.85	2.01	7.79	7.82	287.94	294.16	1.81	2.22
		54.73	85.12	0.89	8.70	1.78	8.70	7.71	8.02	285.06	429.38	1.61	15.04
Dia-lan	**108**	**83.23**		**2.00**		**9.08**		**7.70**		**382.41**		**15.38**	
		47.10	86.60	1.60	5.21	8.61	9.31	7.61	7.99	314.85	393.02	14.71	20.32
		27.06	101.56	1.36	7.63	8.58	9.52	7.58	8.02	235.54	442.59	4.61	120.20
Bry-zsc	**82**	**110.93**		**5.09**		**10.91**		**7.90**		**410.54**		**49.71**	
		106.87	114.55	5.08	5.11	10.73	11.15	7.88	7.91	406.93	414.56	47.85	52.04
		69.49	117.00	0.88	5.12	2.11	12.81	7.78	8.31	249.69	417.42	7.55	53.98
Bry-typ	**81**	**73.98**		**5.11**		**8.83**		**7.89**		**420.60**		**4.99**	
		20.99	74.97	2.00	5.68	4.87	11.49	7.81	7.91	355.39	524.60	4.90	5.08
		18.69	110.57	0.88	5.72	1.86	11.89	7.38	8.22	220.67	526.95	0.85	50.03
Mar-bru	**68**	**56.92**		**2.24**		**1.85**		**7.80**		**292.98**		**2.00**	
		56.73	57.14	1.58	2.78	1.24	2.54	7.78	7.83	288.44	298.13	1.98	2.02
		54.60	57.38	0.93	8.53	0.70	9.11	7.76	8.04	280.28	347.83	1.96	2.04
Mor-dum	**64**	**49.72**		**1.58**		**8.99**		**7.52**		**411.79**		**10.11**	
		49.15	50.29	1.43	5.68	8.90	9.09	7.49	7.69	271.15	418.86	5.01	19.91
		14.54	50.99	1.36	5.73	8.78	9.12	7.38	7.90	268.97	440.72	0.28	99.73

species	n	ceiling [m]		precipitation [mm]		T [°C]		pH		conductivity [µS cm^{-1}]		volume [l]	
Epa-ric	**43**	**57.02**		**1.94**		**2.05**		**7.80**		**291.92**		**2.00**	
		56.83	57.19	1.60	2.39	1.56	2.46	7.78	7.81	284.92	295.80	1.99	2.02
		54.61	57.38	0.98	7.74	0.71	8.96	7.76	8.03	280.22	346.92	1.97	2.04
Bry-pyr	**37**	**31.34**		**1.43**		**9.01**		**7.70**		**376.16**		**19.92**	
		29.40	51.32	1.37	1.62	8.88	9.10	7.61	7.78	330.76	441.28	9.89	30.08
		20.73	71.26	0.68	10.22	1.48	9.22	7.48	7.90	269.05	449.76	-0.01	120.14
Aca-kie	**17**	**89.86**		**5.00**		**8.74**		**7.91**		**372.45**		**0.91**	
		88.98	90.79	2.21	5.51	8.69	9.17	7.91	7.98	330.45	374.00	-0.06	29.58
		88.31	91.30	1.60	7.76	8.65	9.51	7.88	8.01	319.72	375.85	-0.45	30.57
Bry-nsp	**14**	**90.12**		**3.12**		**8.12**		**7.85**		**350.23**		**33.23**	
		70.23	110.02	1.99	5.12	5.60	11.17	7.80	7.91	324.85	412.00	11.04	49.96
		55.35	110.27	0.91	7.61	1.73	12.83	7.59	8.30	253.94	412.39	2.40	50.23
Par-ty2	**12**	**74.69**		**0.99**		**9.01**		**7.89**		**354.22**		**19.61**	
		74.06	79.42	0.90	5.10	4.19	11.58	7.79	8.11	322.94	403.03	4.83	49.35
		40.39	110.68	0.88	7.61	1.70	11.90	7.60	8.21	219.60	523.33	1.20	50.39
Meg-vir	**11**	**110.42**		**0.91**		**13.02**		**8.30**		**260.17**		**31.73**	
		109.49	111.02	0.47	1.40	12.61	13.09	8.26	8.32	243.32	271.54	30.97	33.36
		108.37	112.05	0.32	5.72	10.92	13.13	7.84	8.37	233.68	442.56	26.26	50.43
Par-fim	**8**	**97.63**		**5.16**		**9.02**		**7.80**		**270.31**		**19.97**	
		93.35	100.90	1.71	5.27	9.01	9.78	7.78	7.94	268.91	272.49	18.34	20.28
		77.06	103.85	1.03	5.36	8.98	11.80	7.69	8.30	236.81	277.71	17.09	34.52
Ela-mil	**8**	**29.73**		**1.58**		**9.10**		**7.69**		**438.41**		**31.32**	
		29.45	29.94	1.52	1.61	9.01	9.11	7.62	7.71	410.28	444.94	28.66	103.89
		29.41	30.49	1.39	5.73	8.91	9.12	7.60	7.72	373.15	445.92	27.66	122.63
Ela-cve	**6**	**53.43**		**5.32**		**6.42**		**7.80**		**291.01**		**4.08**	
		46.49	58.83	1.55	8.39	5.96	7.24	7.79	7.86	275.03	380.53	4.04	4.63
		44.86	70.10	0.94	8.71	1.89	9.68	7.70	7.98	244.75	539.91	1.91	25.16
Bry-bor	**6**	**64.28**		**1.05**		**7.49**		**7.76**		**285.69**		**0.40**	
		58.90	70.08	0.84	1.06	2.96	9.34	7.72	7.80	249.38	327.48	0.05	2.65
		58.51	71.71	0.71	1.10	0.96	9.44	7.69	7.81	248.50	331.22	-0.42	3.57

Mor-var	**5**	**56.56** 54.15 59.43 50.73 92.46	**7.51** 7.36 7.56 4.82 7.56	**7.95** 7.94 7.96 7.90 8.81	**7.99** 7.99 8.00 7.88 8.00	**342.59** 341.50 343.51 333.78 374.40	**1.85** 1.72 2.17 0.45 2.21
Par-nol	**4**	**32.16** 10.72 53.37 3.79 59.63	**1.69** 1.18 2.87 1.10 4.96	**4.95** 4.44 6.73 3.32 11.64	**7.79** 7.76 7.80 7.71 7.80	**438.99** 427.69 448.99 423.56 449.21	**19.76** 14.90 28.50 5.80 49.26
Phy-vig	**4**	**75.15** 62.18 79.68 24.32 92.19	**6.56** 4.78 7.41 1.65 7.76	**9.13** 8.75 9.48 8.63 9.48	**7.73** 7.62 7.87 7.61 7.99	**394.27** 371.61 402.64 312.78 418.61	**16.51** 13.00 17.71 5.35 18.42
Bry-pyg	**4**	**70.71** 67.98 71.30 61.24 71.64	**0.87** 0.69 3.31 0.63 10.13	**4.07** 1.76 6.93 1.71 8.60	**7.80** 7.71 7.83 7.54 7.84	**338.01** 319.85 369.40 270.37 458.57	**2.94** 2.91 3.21 2.80 4.01
Dia-lus	**1**	**79.56**	**0.88**	**1.70**	**7.89**	**315.81**	**49.92**
Att-cra	**1**	**73.92**	**1.02**	**11.78**	**8.17**	**218.16**	**1.02**
Ela-kie	**1**	**78.47**	**1.00**	**11.84**	**8.15**	**277.61**	**20.05**
Par-and	**1**	**49.41**	**1.38**	**9.00**	**7.78**	**266.80**	**10.09**
Par-ty1	**1**	**59.37**	**0.69**	**7.71**	**7.86**	**276.33**	**24.67**
juv-har	**114**	**85.10** 84.65 85.34 30.25 110.38	**5.19** 2.02 5.20 0.69 7.61	**9.30** 8.61 9.31 1.48 12.79	**7.71** 7.69 7.87 7.58 8.31	**389.80** 348.69 390.45 253.95 412.56	**5.04** 4.87 15.08 1.86 120.20
nau-pli	**589**	**10.57** 9.97 60.29 9.40 110.55	**1.09** 0.71 2.02 0.68 10.22	**4.82** 1.81 8.41 0.58 12.82	**7.71** 7.69 7.81 7.48 8.42	**374.93** 272.16 441.83 203.86 540.13	**24.91** 14.90 29.97 -0.04 50.17

Appendix 10: *Weighted descriptive statistics for a data set of 27 copepod species and 12 physical and chemical parameters from trickles (***median***, minimum and maximum, first and third quartile); the species are marked by abbreviated names as they appear in Appendix 1.*

species	n	ceiling [m]		precipitation [mm]		T [°C]		conductivity [µS cm^{-1}]		discharge [ml min^{-1}]	
Par-ty2	**160**	**80.25**		**5.21**		**7.00**		**312.00**		**32.96**	
		69.92	109.94	5.10	7.01	4.80	10.00	289.01	327.96	19.96	37.01
		14.62	110.40	0.69	17.90	1.50	13.70	212.96	572.24	1.96	500.03
Spe-inf	**141**	**49.94**		**7.80**		**7.43**		**450.50**		**13.03**	
		44.97	50.36	3.15	14.90	5.93	8.96	285.45	494.06	11.01	37.16
		9.65	110.36	0.03	17.90	3.10	12.20	199.96	695.03	0.50	616.68
Par-nol	**121**	**15.39**		**5.21**		**4.41**		**213.18**		**17.01**	
		14.82	59.88	5.18	7.00	4.40	7.00	212.97	312.16	10.97	36.95
		9.49	110.49	0.68	17.89	1.81	11.61	199.84	543.17	0.53	600.05
Ela-cve	**98**	**45.11**		**17.90**		**7.43**		**271.32**		**180.63**	
		44.75	45.50	9.95	17.90	7.43	7.70	270.46	285.33	37.95	180.69
		14.86	70.54	1.40	17.90	3.17	11.30	200.40	520.86	1.98	616.68
Mar-bru	**96**	**55.15**		**3.87**		**5.20**		**318.73**		**2.72**	
		54.94	55.35	3.80	17.87	5.20	6.47	318.56	327.69	1.93	3.03
		54.61	57.26	2.15	17.96	1.34	9.79	315.41	411.39	0.42	293.43
Bry-bal	**94**	**45.10**		**16.39**		**7.43**		**271.03**		**40.09**	
		44.29	45.61	4.13	17.90	7.43	7.69	270.89	285.47	3.59	180.64
		14.35	85.73	1.06	21.39	2.60	9.69	213.09	461.14	0.41	180.77
Bry-dac	**68**	**55.04**		**17.90**		**6.46**		**327.65**		**2.02**	
		54.80	55.27	3.83	17.90	5.20	6.47	318.73	327.76	1.98	2.97
		49.61	57.20	2.20	17.91	1.35	9.66	315.39	546.73	0.46	293.37
Sty-nsp	**10**	**65.62**		**3.28**		**4.51**		**322.28**		**8.05**	
		63.24	66.82	2.97	8.13	4.15	5.88	315.38	402.30	4.04	24.04
		59.53	80.75	0.98	10.53	1.73	9.16	201.84	414.95	3.76	220.14
Ela-sta	**10**	**15.67**		**2.27**		**6.21**		**265.74**		**11.06**	
		15.33	15.91	2.10	6.81	6.11	7.70	260.51	402.78	10.91	34.21
		14.94	20.30	1.48	8.23	3.78	9.18	199.96	416.75	3.02	42.18
Mor-var	**10**	**55.16**		**17.83**		**6.46**		**328.04**		**2.08**	
		55.03	55.25	15.49	18.01	6.10	6.83	326.12	328.96	1.92	2.12
		50.25	56.69	4.68	18.39	3.32	11.57	319.62	694.28	1.17	7.95
Bry-pyr	**8**	**23.77**		**5.81**		**7.70**		**319.12**		**3.11**	
		14.96	30.59	4.26	5.90	5.98	8.98	260.90	399.58	3.01	6.57
		13.54	32.46	1.41	5.93	3.79	9.00	199.84	422.27	2.07	16.96
Par-ty3	**7**	**102.12**		**5.67**		**12.17**		**235.18**		**39.72**	
		6.29	108.25	5.20	8.93	5.30	12.70	218.22	353.37	15.90	40.71
		-0.98	123.48	1.00	8.95	4.38	12.78	211.53	354.80	2.14	201.66
Mor-pop	**5**	**60.11**		**11.38**		**8.85**		**365.44**		**160.62**	
		59.78	64.06	4.82	17.74	8.70	9.18	311.84	410.57	19.92	294.90
		58.89	75.82	4.13	17.82	8.66	9.79	284.97	412.04	-1.05	296.60
Par-ty1	**5**	**60.92**		**1.00**		**3.48**		**322.72**		**6.00**	
		60.12	64.83	0.81	1.56	2.58	5.59	295.69	360.91	3.75	7.45
		59.32	68.75	0.63	2.12	1.69	7.71	268.66	399.10	1.49	8.89

logNO$_3^-$ [mg l^{-1}]		logSO$_4^{2-}$ [mg l^{-1}]		logK$^+$ [mg l^{-1}]		logCa^{2+} [mg l^{-1}]		logNa$^+$ [mg l^{-1}]		logMg^{2+} [mg l^{-1}]		logCl$^-$ [mg l^{-1}]	
-0.55		**1.82**		**-1.17**		**3.18**		**0.10**		**-0.30**		**0.91**	
-1.24	-0.24	1.42	2.05	-1.24	-0.73	2.34	3.90	-0.20	0.42	-0.49	-0.20	0.66	1.07
-2.12	4.01	0.29	2.40	-1.71	0.60	2.11	4.40	-2.40	2.12	-2.12	0.66	-0.89	1.96
1.58		**2.01**		**0.02**		**3.21**		**0.92**		**0.13**		**1.10**	
-0.73	3.72	1.42	2.09	-1.05	0.32	2.70	4.02	0.10	1.75	-0.33	0.26	0.44	1.65
-2.53	4.01	0.10	2.43	-1.77	0.59	1.78	4.65	-4.51	2.12	-2.12	0.98	-1.05	3.12
-0.96		**1.90**		**-0.73**		**3.44**		**0.42**		**0.01**		**0.44**	
-2.04	-0.24	1.90	2.05	-0.89	0.45	2.34	3.95	0.10	0.92	-0.30	0.03	0.43	0.91
-2.30	2.80	0.29	2.47	-1.77	0.45	1.99	4.14	-1.83	1.81	-2.21	0.45	-1.43	2.98
-1.23		**0.91**		**-1.71**		**2.64**		**-2.39**		**-2.12**		**-0.89**	
-1.24	0.84	0.91	1.90	-1.71	-0.78	2.64	3.68	-2.40	0.14	-2.12	-0.46	-0.89	0.72
-2.30	3.72	0.11	2.48	-1.72	0.13	1.78	4.65	-4.51	1.75	-2.21	0.87	-1.43	1.65
1.58		**1.54**		**0.27**		**3.98**		**0.13**		**-0.34**		**-0.05**	
1.57	1.59	1.54	1.56	-0.55	0.32	2.84	3.99	-0.97	0.13	-0.85	-0.34	-0.10	0.26
-1.71	2.18	0.29	2.35	-1.57	0.33	2.41	4.06	-3.82	0.29	-2.20	-0.24	-1.48	1.31
-1.23		**0.91**		**-1.66**		**2.64**		**-1.90**		**-1.27**		**-0.89**	
-1.24	-0.03	0.91	2.21	-1.71	-0.78	2.64	3.78	-2.40	-0.30	-2.12	-0.46	-0.89	0.40
-2.12	1.32	0.72	2.43	-1.72	0.45	2.01	4.13	-2.40	0.95	-2.12	0.62	-1.05	1.33
1.58		**1.54**		**-0.54**		**2.84**		**-0.95**		**-0.84**		**-0.06**	
1.57	1.59	1.54	1.54	-0.55	0.28	2.84	3.98	-0.97	0.13	-0.84	-0.34	-0.09	0.24
-0.07	3.31	0.96	2.34	-1.57	0.38	2.41	4.50	-3.83	1.47	-1.77	0.97	-1.07	1.45
-1.11		**1.77**		**-0.83**		**3.75**		**0.07**		**-0.38**		**0.43**	
-1.53	-0.95	0.69	1.79	-1.35	-0.65	3.31	3.92	-0.55	0.08	-0.80	-0.12	0.10	0.57
-3.52	-0.35	0.01	1.82	-1.71	-0.10	2.87	3.92	-1.28	0.34	-1.45	-0.09	-1.06	0.82
-1.16		**2.11**		**-0.66**		**3.84**		**0.52**		**0.24**		**0.66**	
-1.35	-0.96	1.75	2.11	-0.97	-0.62	3.48	3.85	-0.04	0.95	0.23	0.30	0.04	0.92
-1.61	-0.75	1.64	2.33	-1.00	-0.36	3.44	4.05	-0.34	1.06	0.01	0.32	-0.08	1.15
1.58		**1.54**		**-0.55**		**2.85**		**-0.97**		**-0.85**		**-0.10**	
1.57	1.59	1.09	1.55	-0.60	-0.51	2.84	2.86	-0.98	-0.95	-0.86	-0.85	-0.12	-0.03
-0.07	3.15	0.91	1.55	-1.54	-0.18	2.42	3.23	-3.81	0.96	-1.79	-0.53	-1.12	1.18
-0.96		**2.33**		**-0.87**		**3.95**		**-0.18**		**0.10**		**0.44**	
-1.26	-0.87	2.02	2.34	-0.89	-0.82	3.84	4.13	-0.50	0.65	0.06	0.22	0.15	0.54
-2.04	-0.86	1.90	2.41	-0.89	0.45	2.34	4.15	-0.51	0.92	0.01	0.24	0.01	0.79
-1.36		**1.88**		**-0.77**		**2.31**		**0.22**		**-0.19**		**0.19**	
-1.77	-1.33	0.76	1.97	-1.04	0.36	2.13	2.99	-0.63	0.98	-0.20	0.03	-0.59	0.44
-2.07	1.48	0.75	2.34	-1.05	0.46	2.08	3.76	-0.66	1.66	-0.20	0.39	-0.62	1.37
0.10		**1.20**		**-1.26**		**2.68**		**-0.69**		**-0.87**		**0.27**	
-0.76	0.74	0.96	1.26	-1.27	-1.08	2.54	2.81	-0.74	-0.56	-1.24	-0.71	-0.15	0.37
-1.54	0.87	0.27	1.43	-1.27	-0.60	2.21	3.11	-0.87	-0.21	-2.24	-0.34	-1.35	0.64
-0.34		**1.76**		**-0.74**		**3.83**		**0.03**		**-0.26**		**0.57**	
-0.97	0.09	1.70	1.83	-0.88	-0.72	3.81	3.83	-0.20	0.36	-0.27	-0.24	0.48	1.06
-1.60	0.52	1.65	1.90	-1.02	-0.69	3.80	3.84	-0.43	0.68	-0.27	-0.22	0.38	1.56

species	n	ceiling [m]		precipitation [mm]		T [°C]		conductivity [μS cm^{-1}]		discharge [ml min^{-1}]	
Nit-sp.	**5**	**68.98**		**7.63**		**6.94**		**392.20**		**6.61**	
		65.69	74.61	5.63	8.49	5.33	8.18	332.71	414.17	4.43	15.26
		58.51	88.84	0.04	10.65	3.59	8.81	218.66	415.67	2.98	36.14
Ela-kie	**5**	**59.58**		**6.99**		**11.49**		**311.38**		**48.40**	
		59.43	60.96	5.22	7.02	11.31	11.59	208.81	345.79	24.11	108.53
		58.45	74.57	5.10	8.90	5.32	11.60	206.71	488.24	7.04	600.10
Mor-spA	**4**	**75.83**		**7.05**		**5.66**		**280.61**		**33.25**	
		59.64	92.02	3.49	10.60	5.27	6.05	263.02	298.20	31.45	35.05
		43.44	108.21	-0.07	14.16	4.89	6.43	245.43	315.79	29.64	36.86
Ela-nsp	**3**	**56.39**		**19.49**		**8.84**		**392.56**		**336.39**	
		56.13	56.51	11.91	19.97	8.76	9.25	348.00	405.41	163.86	341.18
		55.87	56.63	4.33	20.46	8.68	9.66	303.45	418.26	-8.66	345.97
Mor-dum	**3**	**44.27**		**5.61**		**8.99**		**462.75**		**5.12**	
		30.29	49.73	5.60	5.66	7.64	9.05	342.71	472.52	4.48	102.55
		16.31	55.19	5.58	5.70	6.29	9.11	222.68	482.30	3.85	199.99
Dia-lan	**2**	**50.08**		**3.81**		**9.16**		**424.13**		**2.02**	
		49.80	50.36	2.39	5.22	9.13	9.19	417.02	431.23	1.43	2.60
		49.52	50.64	0.98	6.63	9.09	9.23	409.92	438.33	0.84	3.19
Ela-mil	**2**	**14.97**		**5.29**		**4.46**		**211.54**		**17.17**	
		14.91	15.03	5.29	5.29	4.46	4.46	210.57	212.50	17.13	17.22
		14.84	15.10	5.29	5.29	4.46	4.46	209.61	213.47	17.09	17.26
Mor-sco	**2**	**66.23**		**8.79**		**7.26**		**377.81**		**23.19**	
		64.10	68.37	8.07	9.50	6.84	7.68	314.43	441.18	9.99	36.40
		61.96	70.50	7.36	10.22	6.42	8.09	251.06	504.56	-3.22	49.60
Bry-nsp	**1**	**55.01**		**17.87**		**6.43**		**327.01**		**2.04**	
Mor-sta	**1**	**49.99**		**1.57**		**9.08**		**406.01**		**0.51**	
Mor-spB	**1**	**30.19**		**5.77**		**8.90**		**396.50**		**5.05**	
Par-and	**1**	**70.41**		**10.24**		**6.23**		**466.33**		**60.82**	
Phy-vig	**1**	**14.94**		**5.64**		**6.40**		**269.86**		**11.13**	
juv-har	**95**	**55.15**		**5.20**		**6.46**		**294.03**		**17.03**	
		15.09	79.76	4.15	7.00	4.40	9.00	213.01	327.59	10.97	33.01
		14.64	110.39	0.90	17.90	1.35	11.60	199.72	520.68	0.50	616.65
nau-pli	**558**	**50.36**		**5.20**		**7.43**		**315.49**		**24.43**	
		41.04	59.69	2.20	13.24	4.40	9.10	261.72	411.36	5.12	200.17
		9.87	110.35	0.70	17.90	1.35	12.60	199.94	572.30	0.31	1299.84

logNO$_3^-$ [mg l^{-1}]		logSO$_4^{2-}$ [mg l^{-1}]		logK$^+$ [mg l^{-1}]		logCa^{2+} [mg l^{-1}]		logNa$^+$ [mg l^{-1}]		logMg^{2+} [mg l^{-1}]		logCl$^-$ [mg l^{-1}]	
-0.98		**1.26**		**-0.81**		**3.45**		**0.08**		**-0.50**		**0.22**	
-1.29	-0.28	0.73	1.74	-1.00	-0.55	3.34	3.61	-0.04	0.19	-0.88	-0.16	0.18	0.43
-1.47	1.07	0.59	1.77	-1.32	-0.06	3.31	3.75	-0.21	0.31	-0.97	-0.15	0.16	0.97
0.44		**1.78**		**-1.06**		**2.51**		**0.15**		**-0.01**		**0.77**	
-0.45	0.50	1.36	2.02	-1.71	-0.81	2.07	3.65	-0.07	0.55	-0.24	0.21	0.77	0.87
-1.00	1.33	1.25	2.47	-1.77	-0.35	1.98	4.07	-1.42	0.65	-1.20	0.74	0.13	1.23
0.48		**2.14**		**-0.96**		**3.84**		**0.17**		**-0.38**		**1.05**	
0.23	0.72	2.04	2.24	-1.11	-0.82	3.80	3.87	0.16	0.17	-0.42	-0.35	1.05	1.06
-0.01	0.96	1.94	2.34	-1.25	-0.68	3.76	3.91	0.15	0.18	-0.45	-0.32	1.04	1.07
0.50		**1.07**		**-1.17**		**2.72**		**-0.68**		**-0.97**		**0.10**	
-0.46	0.78	0.65	1.18	-1.26	-0.84	2.71	3.00	-0.76	-0.68	-1.65	-0.81	-0.74	0.26
-1.41	1.06	0.23	1.29	-1.36	-0.52	2.71	3.27	-0.83	-0.67	-2.32	-0.64	-1.57	0.41
-1.53		**1.95**		**-1.22**		**3.73**		**-0.83**		**0.06**		**0.16**	
-1.58	-1.33	1.80	2.01	-1.26	-1.00	3.48	3.76	-1.04	-0.31	-0.23	0.22	-0.03	0.26
-1.64	-1.14	1.66	2.06	-1.30	-0.77	3.23	3.78	-1.25	0.22	-0.52	0.38	-0.21	0.36
-1.19		**2.25**		**-1.03**		**4.08**		**-0.52**		**0.03**		**-0.24**	
-1.30	-1.08	2.25	2.26	-1.06	-1.00	4.07	4.10	-0.53	-0.51	-0.01	0.08	-0.26	-0.22
-1.41	-0.97	2.25	2.26	-1.09	-0.97	4.05	4.11	-0.54	-0.50	-0.05	0.12	-0.27	-0.20
		1.91		**0.46**		**2.34**		**0.93**		**0.03**		**0.45**	
		1.91	1.92	0.46	0.46	2.33	2.36	0.93	0.93	0.03	0.03	0.45	0.45
		1.90	1.92	0.46	0.46	2.31	2.38	0.93	0.94	0.03	0.03	0.45	0.45
-1.42		**1.25**		**-1.02**		**3.40**		**0.46**		**-0.40**		**0.32**	
-1.73	-1.11	0.93	1.58	-1.10	-0.93	3.32	3.48	0.36	0.57	-0.51	-0.30	0.00	0.64
-2.05	-0.79	0.60	1.90	-1.18	-0.85	3.24	3.56	0.25	0.67	-0.62	-0.19	-0.32	0.96
1.59		**1.56**				**2.85**							
		2.29				**4.05**				**0.11**			
		2.39				**4.20**				**0.24**		**0.20**	
		0.78				**3.23**		**0.71**					
		2.10				**3.48**				**0.03**		**0.41**	
-0.80		**1.90**		**-0.80**		**2.84**		**0.10**		**-0.25**		**0.45**	
-1.31	0.80	1.52	2.02	-1.24	-0.37	2.34	3.57	-0.20	0.44	-0.46	0.03	0.41	0.75
-2.58	3.72	0.29	2.34	-1.38	0.45	2.27	4.65	-0.97	1.75	-2.21	0.87	-1.43	1.65
0.80		**1.90**		**-0.73**		**3.57**		**0.14**		**-0.25**		**0.59**	
-1.24	1.43	1.17	2.23	-1.19	-0.22	2.70	3.99	-0.57	0.42	-0.69	0.24	0.26	0.76
-3.51	4.01	0.02	2.48	-1.77	0.59	1.78	4.65	-4.51	2.12	-2.21	0.98	-1.43	2.98

"The study that follows, while modest in tone, makes some real breakthroughs. First, Dr. Pipan describes and utilizes techniques for sampling drips and pools that yield many more individual and species than previous work. Second, she is able to assess how complete sampling is by estimating the number of species remaining to be found, and other measures of sampling completeness. Third, using canonical correspondence analysis, she begins to make sense of the physical and chemical controls on the distribution of individual species. Fourth, she demonstrates the extreme spatial heterogeneity of epikarst copepod distribution, surely a hallmark of this fascinating habitat. The thesis is filled with insightful and provocative observations."

– from the Preface by David C. Culver,
Professor of Biology, American University
Washington, DC, USA

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