Distribution, discharge and disturbance: new insights into faunal spring ecology

Inauguraldissertation

zur
Erlangung der Würde eines Doktors der Philosophie
vorgelegt der
Philosophisch-Naturwissenschaftlichen Fakultät
der Universität Basel

von

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aus Staufen (Deutschland)

Basel, 2008

Genehmigt von der Philosophisch-Naturwissenschaftlichen Fakultät

auf Antrag von Prof. Dr. Peter Nagel (Fakultätsvertreter) und Prof. Dr. Karl Beierkuhnlein

Basel, den 14.Oktober 2008

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CHAPTER ONE

General Introduction

Spring research in limnology

Springs are unique ecosystems at the interface between groundwater and surface water (Webb, 1998) and between the terrestrial and the aquatic habitat (Cantonati et al., 2006). They are an ecotone providing their own characteristic environment for the organisms living in and around springs (Fischer, 1996; Lindegaard et al., 1998). In contrast to the rhithral and potamal of rivers and streams they provide relatively stable abiotic conditions with small temperature amplitudes, little impact of nutrients and also a relatively stable discharge regime (Gooch & Glazier, 1991; van der Kamp, 1995). Karst springs, which are often intermittent springs, are exceptional, responding quickly to strong rainfalls and drought periods (Zollhöfer et al., 2000; Meyer et al., 2003).

Despite their ubiquitous distribution on earth and their special characteristics, making them “natural laboratories” (Odum, 1971), fewer perennial, natural springs are now found. This in part can be explained by their use in drinking water suppliers. And they still get piped, especially in Switzerland (Zollhöfer, 1997). Moreover, limnological research has shown relatively little interest in spring ecosystems. After comprehensive studies at the beginning of the 20th century (e.g. Steinmann, 1915; Thienemann, 1926; Geijskes, 1935) the interest in springs decreased, aside studies on energy fluxes and trophic relationships in spring ecosystems as excellent models for ecosystems in general (Odum, 1957; Teal, 1957). After this time the main focus of spring research concerned their longitudinal zonation (e.g. Vannote et al., 1980; Resh, 1983; McCabe, 1998), their abiotic stability (e.g. Minshall, 1968; Ward & Dufford, 1979) and their importance as habitats for relict species (e.g. Nielsen, 1950; Fischer, 1996; Hayford & Herrmann, 1998). Although there are some important book publications on springs and springbrooks (Williams & Danks, 1991; Ferrington, 1995; Zollhöfer, 1997; Botosaneanu, 1998), springs are still on the periphery of limnological research. There is a lack of autecological studies and there is no information about the classical limnological questions such as; disturbance, production rates, predator-prey-relationships and food webs. For spring ecology, we therefore are still at an early stage of our understanding.

A brief history of spring research in Europe

Spring research seriously started in Europe with the limnologist August Thienemann, an important researcher for the whole limnology. His trips to the isle of Rügen in the Baltic Sea (1925, 1926) and his research in the German low mountain ranges (1912) and lowlands (1923, 1926) were the first comprehensive studies on springs and their springbrooks. Thienemann was also the first, who invented the theory, that some spring species are glacial relicts that survived in springs because of their stable temperature conditions (1925). Another important study on springs and springbrooks was conducted by Steinmann (1915). He invented the spring typology of rheocrenes as “Sturzquellen”and limnocrenes as “Tümpelquellen”, Thienemann (1924) then added the helocrenes, the typical swamp springs from the north german lowlands. This “trinity” is still the most common ecomorphological spring typology,

Thienemanns student and successor Joachim Illies also conducted comprehensive studies on river systems including springs and springbrooks. He stated that the spring ends where the annual water temperature amplitude exceeds five degrees (1952). This resulted in the famous zonation concept with the krenal as the spring region, the rhithral as the upper river section of the lower mountain range regions and the potamal as the lower river section of the lowlands (1961). He also invented the terms eucrenal as the spring source and hypocrenal as the springbrook (Illies & Botosaneanu, 1963).

After a time of little interest in spring ecosystems a new period of spring research activity started in the late 1980’s. A series of diploma thesis had been initiated and supervised by P. Nagel at the University of Saarbrücken, Germany, in which basic data on spring ecology in the Saarland area of south-western Germany were collected (Röhling, 1990). It culminated in the foundation of the german society “Quellökologie und Quellschutz” with its scientific journal „Crunoecia“ in 1992. Due to a new environmental awareness the pollution of springs, their conservation and restoration and the evaluation of springs came in the focus of wider interest (Verdonschot, 1995; Zollhöfer, 1997; Schindler, 2004). Despite a decrease of interest in our new century some spring research groups in Europe are still active and start investigating springs all over Europe again (e.g. Hoffsten & Malmqvist, 2000; Habdija et al., 2002; Smith et al., 2003; Ilmonen & Paasivirta, 2005; Dumnicka et al., 2006; Mori & Brancelj, 2006). Spring projects currently concentrate in the middle range regions of Bavaria (Beierkuhnlein & Gollan, 1999; Hotzy & Römheld, 2003) and in the alpine region of the German Alps in the Nationalpark Berchtesgaden (Gerecke &

Franz, 2006) and the Italian Alps (Sambugar, 2006; Adamello Brenta Nationalpark, Trentino).

A brief history of spring research in Switzerland

The spring and groundwater research in Switzerland started with the doctoral theses of Bornhauser (1912), Steinmann (1915) and Chappuis (1924). The next comprehensive studies were then conducted by Geijskes (1935) in the Swiss Jura Mountains and Nadig (1942) in the Swiss Nationalpark in the eastern part of Switzerland.

After a long period without any spring research activities Zollhöfer (1997, 1999, 2000) made an important step by designating new spring types for the Swiss Jura Mountains and the Swiss Midlands on the basis of the classical typology of Steinman (1915) and Thienemann (1924). His book "Quellen – die unbekannten Biotope. Erfassen, bewerten, schützen" from 1997 was the first scientific book in Europe exclusively about springs.

At the beginning of the 21th century the spring project "Quellen – Trinkwasserspender und Lebensraum" started in Basel (Baltes et al., 2005). It had a very broad interdisciplinary and even transdisciplinary approach; concerned with all aspects of spring research from hydrogeology through sociology to biology. The goal of the project was to find solutions for springs in areas of conflict between their use as a drinking water resource and between their function as a special ecosystem. Besides the scientific research, (e.g. Contesse & Küry, 2006; von Fumetti et al., 2006; Baltes et al., 2006; Butscher & Huggenberger, 2007) conservation aspects and public relations were an important part of the project. The thesis presented here started during this project with some ideas based on realizations made during the project.

Established hypotheses and new challenges

Since the beginning of spring research some hypotheses determine our perception of springs. We assume that spring species (i.e. krenobionts) are as cold-stenothermic organisms restricted to the eucrenal and are supposed to be relict species, which are adapted to the stable abiotic conditions typical for springs. The cold-stenothermic character of spring species (krenobionts) was first detected and comprehensively discussed by Thienemann (e.g. 1926, 1950). The assumption of species being cold-stenothermic glacial relicts often derives from distribution patterns (e.g. Nielsen, 1950). A publication of Fischer (1996) describes spring species and their origin from pre- or post-glacial times and Di Sabatino et al. (2003) describe endemic water mite species from Italy with a disjunct and relict distribution. The strong interlocking of aquatic and terrestrial habitats, the mosaic structure of springs and the constancy of the milieu also seem to play a role for the krenobiont species (Fischer, 1996; Cantonati et al., 2006). Competition phenomena in springs have also not been widely examined yet, but are known from Crenobia alpina (DANA, 1766) (Lock & Reynoldson, 1976). Furthermore, we still lack autecological studies on spring organisms, which would be helpful and necessary for addressing whether species are stenothermic or not. Phylogenetic studies on the genetic diversity within and between populations is a promising approach, this has started in the last few years (Pauls et al., 2006; Brändle et al., 2007).

Another widely accepted theory is that springs exhibit stable abiotic conditions, especially low temperature amplitudes. The stable temperature regime is thought to be the main reason for the cold-stenothermic character of spring organisms. Since the time of Thienemann many studies described the thermal constancy at the spring source (e.g. Illies, 1952; Minshall, 1968; Ward & Dufford, 1979), and also other physical and chemical factors seem to be quite constant (Odum, 1971; Gooch & Glazier; 1991). However, there is also evidence for a higher variability in the temperature regime of springs (Fischer et al., 1998; Gräsle & Beierkuhnlein, 1999); it was assumed for a long time that abiotic conditions in springs do not change we do not know very much about the reaction of the spring species on possible changes of abiotic conditions. Therefore we can not conclusively say at this point, how stable springs really are. Do they really all stay hydrologically stable under natural undisturbed conditions, as proposed by Thorup & Lindegaard (1977)?

Directly linked to the proposed thermal stability is the concept of the longitudinal zonation dividing springs into the spring source, the eucrenal and the spring brook, the hypocrenal (Illies & Botosaneanu). After Illies' (1952) five degree-border of the krenal, Erman & Erman (1995) defined the border of the eucrenal as the point where the water temperature differs from the water temperature at the source by 2 °C. This has often been cited (e.g. Orendt, 2000; Smith et al., 2003) but not substantiated by data yet. The zonation of the springbrook is one of the most discussed subject in spring research, reviewed by McCabe (1998). We still do not know which species are really restricted to the spring source and where the border to the springbrook is.

We still commonly use the three main ecomorphological spring types rheocrene, helocrene and limnocrene invented by Steinmann (1915) and Thienemann (1924), despite the fact that these ecomorphological types are insufficient for characterizing all springs we find in European landscapes. Furthermore, for spring species other criteria besides the ecomorphological features of a spring seem to be important in their selection of appropriate spring habitats. There are some new promising approaches for better defined spring typologies (Gerecke, 1991; Gauterin, 1999; Zollhöfer, 2000). However, even those are not sufficient for describing all spring habitats in Europe.

After clarifying these unresolved questions we can then start with real ecological problems. For now, we do not have any strong ideas about the food-webs and the ecological relationships between species in springs.

Objectives of the thesis

The goal of the thesis presented here is to verify the generally accepted hypotheses of spring research. I want to give answers to questions concerning the distribution of spring organisms like their longitudinal distribution, their distribution in different kinds of springs and finally the influence of abiotic parameters on the distribution of spring species..

As a first step of the thesis we examine the influence of abiotic parameters on the species assemblages in springs in the Jura Mountains (**chapter 2**). Here, our approach is geographically and scientifically widespread giving us first insights into the situation of the springs in the Swiss Jura Mountains and the parameters influencing the composition of the macroinvertebrate assemblages in springs.

A spring typology based on species composition applicable all over Europe does not yet exist. In **chapter three** we develop a new approach for a faunistic spring typology on the basis of a comprehensive data set over several years from our main research area.

In **chapter four** we question the dogma that springs as stable ecosystems are not influenced by disturbance events. We apply the gypsum dissolution method invented by Muus (1968) and Doty (1971) for oceanic habitats to springs for measuring the discharge in short-term and mid-term periods and monitor the discharge of five natural springs over a one-year period. Additionally we check the influence of discharge and temperature variability on the macroinvertebrate assemblages in the springs.

In **chapter five** we study the longitudinal distribution of species occurring in springs and springbrooks in three different catchments in the Swiss Tabular Jura Mountains. Our goal was to make predictions on the boundary of the eucrenal, the spring source, on the basis of the macroinvertebrate assemblages we find in different distances to the spring source.

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CHAPTER TWO

Factors governing macrozoobenthic assemblages in perennial springs in north-western Switzerland

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Published in *Hydrobiologia*, 568: 467-475, 2006

Abstract

Springs are important freshwater habitats that provide refuge for many rare species. In this study, the fauna and abiotic parameters of 20 perennial springs in north-western Switzerland were investigated. Correlation of abiotic and macrozoobenthos data showed that physicochemical parameters had little impact on macrozoobenthic composition, whereas specific substrate parameters strongly influenced the composition of the macrofauna. Surprisingly, nonmetric multidimensional scaling did not reveal a grouping of springs with similar substrate composition or macrozoobenthic assemblages. However, discharge was identified as the factor significantly determining substrate and the composition of macroinvertebrate assemblages. This justifies the hypothesis that, variation in discharge is the disturbance factor governing the macrofaunal composition temporally and spatially within and between patches.

Key words: macrozoobenthic assemblages, substrate, discharge, typology, springs

Introduction

Springs are an interface between surface and groundwater (Williams 1991, Webb et al. 1998). They provide unique habitats for many rare species (Lindegaard et al., 1998; di Sabatino et al., 2003) and for relict species that have survived in an environment of rather stable ambient conditions (Hynes, 1970; Ito, 1998). The few investigations of spring ecosystems in Switzerland were mostly conducted in the early 20th century (Bornhauser, 1912; Chappuis, 1924; Geijskes, 1935). The only recent comprehensive studies of macroinvertebrate assemblages in springs in Switzerland are those of Zollhöfer (1999), who developed a spring typology based on the work of Steinmann (1915) and Thienemann (1924).

Previous investigations assumed that springs are habitats with nearly stable physical and chemical conditions (Odum, 1957; van der Kamp, 1995). Thermal stability has been thought to be one of the main characteristics of springs and the reason for the presence of cold stenothermic animals (Illies, 1952; Erman & Erman, 1995). However, springs differ in their geomorphological features and their water supply from deep or shallow groundwater. Conditions in springs also change on a temporal scale (Bohle, 1995). Within a spring and between springs, these variabilities lead to a patchy environment with fluctuating conditions for small, isolated populations as described in the patch dynamics concept (Pickett & White, 1985; Townsend, 1989).

Various chemical factors have been identified to influence the specific spring fauna (Glazier, 1991; Williams et al., 1997; Orendt, 2000; Hahn, 2000). And also substrate composition has been regarded as important (Bonettini & Cantonati, 1996; Hahn, 2000; Ilmonen & Paasivirta, 2005). Besides these factors governing the specific spring fauna discharge has been identified to influence macrozoobenthic spring assemblages, especially with regard to its temporal variation (Minshall, 1968; Gümbel, 1976; Danks & Williams, 1991; Smith, 2002; Meyer et al., 2003). Its role relative to other parameters is known neither generally nor specifically for landscape units. This study examines the influence of substrate, discharge, and other physical and chemical variables on the distribution of macroinvertebrates in perennial springs in north-western Switzerland. Our goal was to test whether springs of this region are differentiated into distinct groups and to discover which abiotic parameters are decisive factors for determining the composition of macrozoobenthic assemblages in springs.

Study area

The study area is located around the city of Basel in north-western Switzerland, into the Jura Mountains. The landscape ranges from urban areas near Basel to agricultural areas and forest. The springs are situated between 280 and 630 m above sea level, with an average altitude of 430 m above sea level. The geological underground mainly consists of limestone with groundwater of usually high conductivity. The climate is temperate; winters are moderately cold, and summers are warm and wet (Zollhöfer, 1999). After preliminary investigations, 20 relatively undisturbed, perennial springs (Q1–Q20) were selected. Q1–Q7 are situated near the city of Basel, and Q8–Q20 are located in the Jura Mountains, either in the forest or in rural areas (Table 1). The chosen springs included amongst others limesinter-rheocrenes, karst and alluvial springs, as well as two tubed springs.

Table 1: Selected characteristics of the investigated springs Q1–Q20

Spring	Location (Swiss coordinates)	Altitude above sea level [m]	Geographical region	Mode of outflow	Land use
Q1	617.000/269.650	380	Dinkelberg	Flowing	Forest
Q2	618.775/268.775	450	Dinkelberg	Flowing/seeping	Forest
Q3	618.375/268.750	490	Dinkelberg	Flowing/seeping	Forest
Q4	618.450/269.275	490	Dinkelberg	Seeping	Forest
Q5	616.500/270.050	300	Dinkelberg	Flowing	Floodplain forest
Q6	618.750/271.500	380	Dinkelberg	Artificial pipe	Meadow
Q7	607.275/273.875	280	Rhine valley	Alluvial spring	Floodplain forest
Q8	624.275/263.725	370	Jura Mountains	Seeping	Forest
Q9	624.875/263.525	380	Jura Mountains	Flowing	Forest
Q10	630.55/256.725	430	Jura Mountains	Flowing	Forest
Q11	619.75/260.350	380	Jura Mountains	Flowing	Forest
Q12	618.920/260.290	380	Jura Mountains	Artificial pipe	Edge of forest
Q13	636.775/252.025	630	Jura Mountains	Flowing	Forest
Q14	618.900/251.375	510	Jura Mountains	Artificial pipe	Edge of forest
Q15	619.125/251.475	470	Jura Mountains	Flowing	Edge of forest
Q16	619.500/256.000	470	Jura Mountains	Flowing	Meadow
Q17	604.100/258.275	450	Jura Mountains	Flowing	Forest
Q18	603.975/251.000	370	Jura Mountains	Alluvial spring	Edge of forest
Q19	601.350/251.400	470	Jura Mountains	Seeping	Forest
Q20	633.250/260.000	530	Jura Mountains	Artificial pipe	Edge of forest

Materials and Methods

Macroinvertebrates were quantitatively sampled with a Surber sampler (10x10 cm = 0.01 m^2, 600-µm mesh width), which was constructed specifically for use in springs of very small size. This novel device allowed the recording of a high percentage of the macrofauna of the total habitat without disturbing the entire spring ecosystem. The mesh width was chosen because the study focused on the macrofauna. Meiofauna and minute groundwater species were only collected accidentally as they will be studied in another survey. Four samples from each spring (exceptions noted below) were taken in autumn 2003 and four were taken in spring 2004 within 10 m downstream of the spring source. At each site, a total of 0.08 m² (8 samples × 0.01 m^2) was sampled, exceptions are for technical reasons sites Q1 (5 samples, 0.05 m^2), Q4 (6 samples, 0.06 m^2), Q8 (7 samples, 0.07 m^2) and Q9 (9 samples, 0.09 m^2). All samples were immediately preserved in 70% ethanol, and subsequently sorted and determined in the laboratory. Turbellaria were separated in the field before preservation to allow live identification. Taxonomically demanding groups (e.g., Chironomidae) were not identified to the species level, and early-instar larvae were identified to the most accurate taxonomic level. On each sampling occasion, water temperature (°C), pH value, conductivity (µS cm^{-1}), oxygen concentration (mg l^{-1}), and oxygen saturation (%) were recorded in the field using portable meters (Wissenschaftlich-Technische Werkstätten, Weilheim, Germany). After calibration with our own measurements at some springs using the method of Zollhöfer (2000), discharge was assessed by eye and classified into four classes according to Hoffsten & Malmqvist (2000): 1: <1 l min^{-1}; 2: >1 and <5 l min^{-1}; 3: >5 and <20 l min^{-1}; 4: >20 l min^{-1}. The substrate types (See supplementary material, appendix 1) were categorized into five classes of frequency based on percentage of areal coverage (Hahn 2000): 0: 0%; 1: 1–25%; 2: 26–50%; 3: 51–75%; 4: 76–100. Owing to the three-dimensional nature of a streambed on which the substrates lie, usually more than 100% was obtained.

All statistical analyses were calculated using PRIMER 5.0 (Clarke & Warwick, 2001). Faunistic and abiotic data were correlated using the BioEnv routine. The Bray-Curtis similarity matrix of square-root-transformed abundance data was compared with the Euclidian distance similarity matrix of the abiotic data. The Spearman rank correlation was used for correlating data. The combination of abiotic variables with the highest ρ value best describes the faunistic distribution (ρ between 1 and –1).

Substrate data were analyzed using principal components analysis. Ordination of the springs was conducted using nonmetric multidimensional scaling (nMDS). With nMDS, the similarity index can be chosen freely, and only ranks are compared; it does not assume normal distribution. Distances between springs are relative and illustrate similarities between samples. The Bray-Curtis similarity was used as the similarity index. The similarities between samples were analyzed using the analyses of similarities (ANOSIM) procedure, which is analogous to ANOVA, but relies on a similarity matrix and makes few assumptions on data. The higher the global R value, the larger are the differences between samples.

Results

Physical and chemical variables and substrate composition

The physical and chemical properties of the springs differed slightly. The water temperature ranged from 8.0 to 13.7 °C (mean ± SD: 10.9 ± 1.6 °C). The oxygen concentration ranged from 5.6 to 10.8 mg l^{-1} (mean ± SD: 9.0 ± 1.6 mg l^{-1}), and the oxygen saturation ranged from 47 to 102% (mean ± SD: 84 ± 14.7%). The conductivity was high; only Q8 had a very low conductivity (mean ± SD: 706 ± 334 µS cm^{-1}). Nearly all springs had circum-neutral pH (6.6–8.4), and the discharge ranged from very low (<1 l min^{-1}) in some muddy springs to very high (>20 l min^{-1}) in some springs emerging from an artificial pipe (See supplementary material; appendix 1).

The BioEnv routine (PRIMER 5.0) showed that physicochemical parameters had little influence on the composition of macrozoobenthic assemblages. The substrate parameters anoxic mud, leaf litter, clay, and cobblestones influenced the composition of the macrozoobenthic communities most (ρ= 0.559; p=0.01). Therefore, physicochemical data were not considered in further analyses.

Fauna

A total of 82 species and higher taxa were recorded from 155 samples. We found on average 20 taxa per spring (range: 12–33 taxa; SD= 5.32) with this quantitative sampling, and eight taxa per surber sample (range: 2–20 taxa; SD= 3.47).

Gammarus fossarum was very frequent and occurred in almost every spring and every sample. We determined 22 species of trichoptera. *Crunoecia irrorata* was recorded in 8 springs, but never reached high abundances, whereas *Synagapetus dubitans* was very frequent in 4 springs and occurred in 50% of the springs. The groundwater organisms *Bythiospeum* spp. and *Niphargus* spp. occurred in 13 and 14 springs, respectively. Nemouridae were found in over 75% of the springs.

The population density varied greatly and reached over 17,000 individuals m^{-2} in one spring. Most other springs had population densities of <5,000 individuals m^{-2} (mean ± SD:

8715 ± 5795 individuals m^{-2}). Insects comprised an average of 61% of the taxa recorded per spring (41.7–80%; SD: 10.9%).

An ANOSIM showed that the replicates of one spring are significantly more similar than replicates of different springs (global R = 0.762; p = 0.01). Therefore, we summarized the data of samples of each spring and used the mean value for nMDS and BioENV analyses.

The principal components analysis conducted with the 13 substrate types showed that factors one and two explained 27 and 17% of the variance, respectively. The first three factors together explained 58% of the variance. Component one is dominated by coarse substrate on the positive axis and by biotic and fine substrate on the negative axis. Component two is determined positively by lime sinter and plant structures (roots and dead branches) and negatively by macrophytes (Fig. 1).

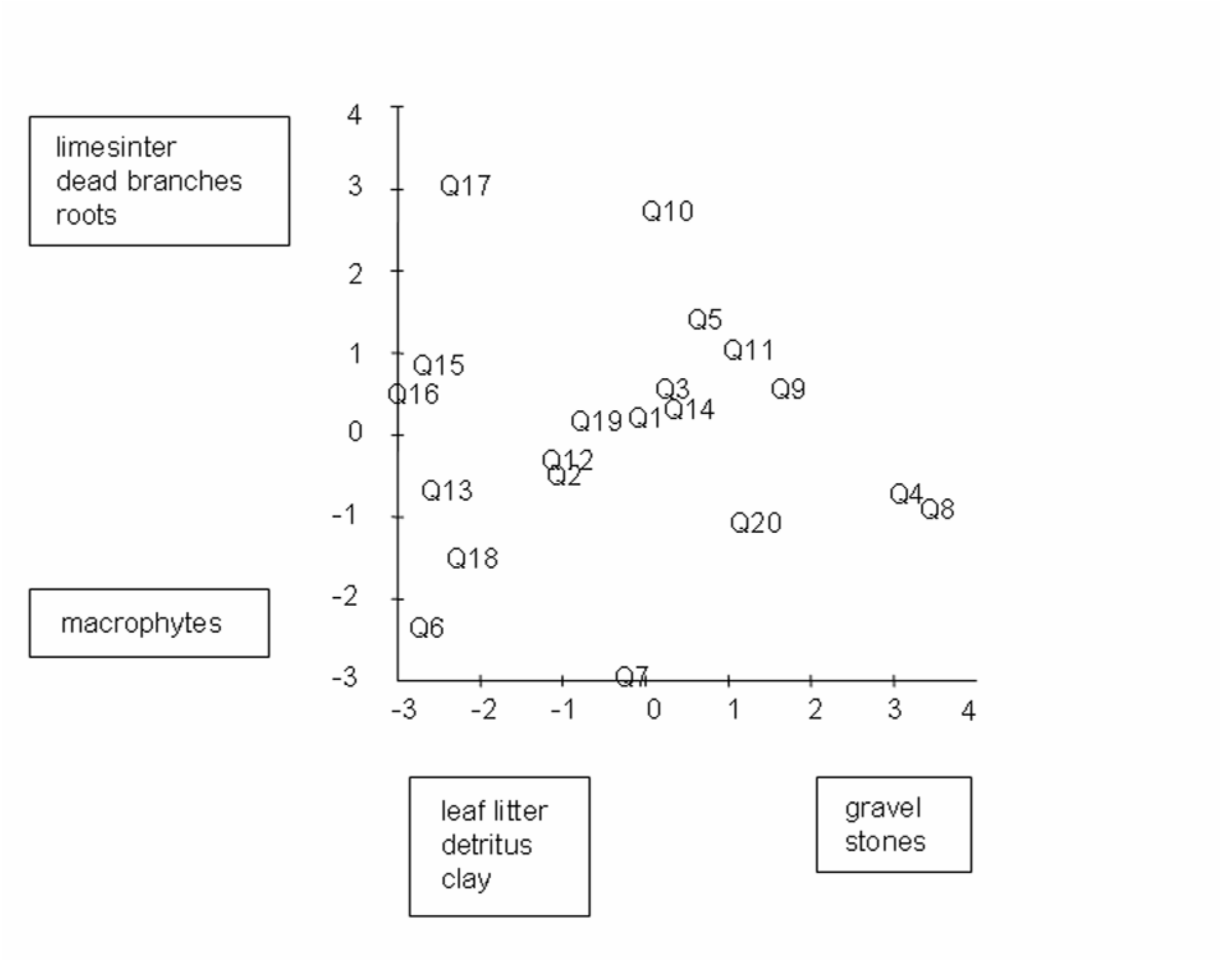

Fig. 1: Principal Components Analysis of the substrates recorded in the 20 investigated springs

The springs could not be classified according to the substrate composition using nMDS. Viewing the graph from the left to the right, a gradient becomes apparent of springs with mainly fine substrate and leaf litter to springs with mostly coarse inorganic substrate. Most of the springs are similar according to their substrate composition. ANOSIM (R = 0.3, p = 0.0013) showed that springs with low discharge (>1 and <5 l min^{-1}) differ significantly from springs with very high discharge (>20 l min^{-1}). Other factors, e.g., physicochemical parameters and the location of the springs, have no influence on the substrate composition and the distribution of the springs on the nMDS graph (Fig. 2).

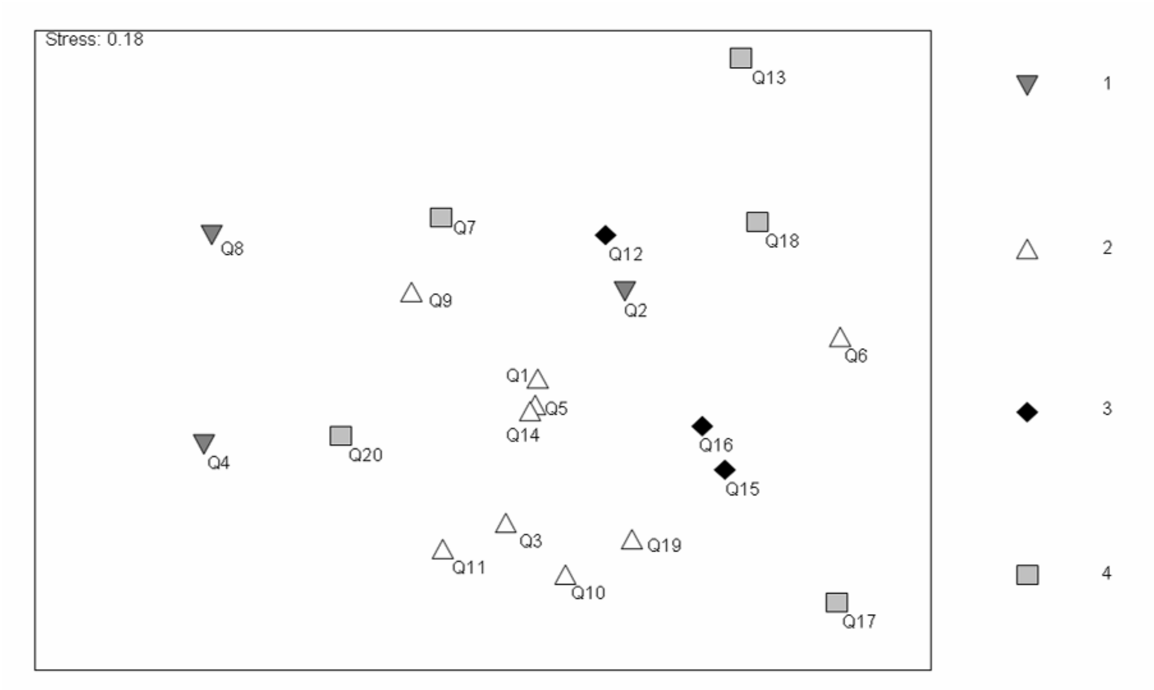

Fig. 2: Nonmetric multidimensional scaling (nMDS) of the investigated springs based on the substrate data. Similarity index: Bray-Curtis; transformation: square root; factor: discharge (1: <1 l min^{-1}; 2: >1 and <5 l min^{-1}; 3: >5 and <20 l min^{-1}; 4: >20 l min^{-1})

Similar results were obtained when faunistic data were used for nMDS (Fig. 3). Classification was not possible, and ANOSIM (R = 0.4, p = 0.0001) showed that springs with low discharge (>1 and <5 l min^{-1}) differ significantly from springs with very high discharge (>20 l min^{-1}). Other factors had no significant influence on the macroinvertebrate composition and the distribution of the springs on the nMDS graph.

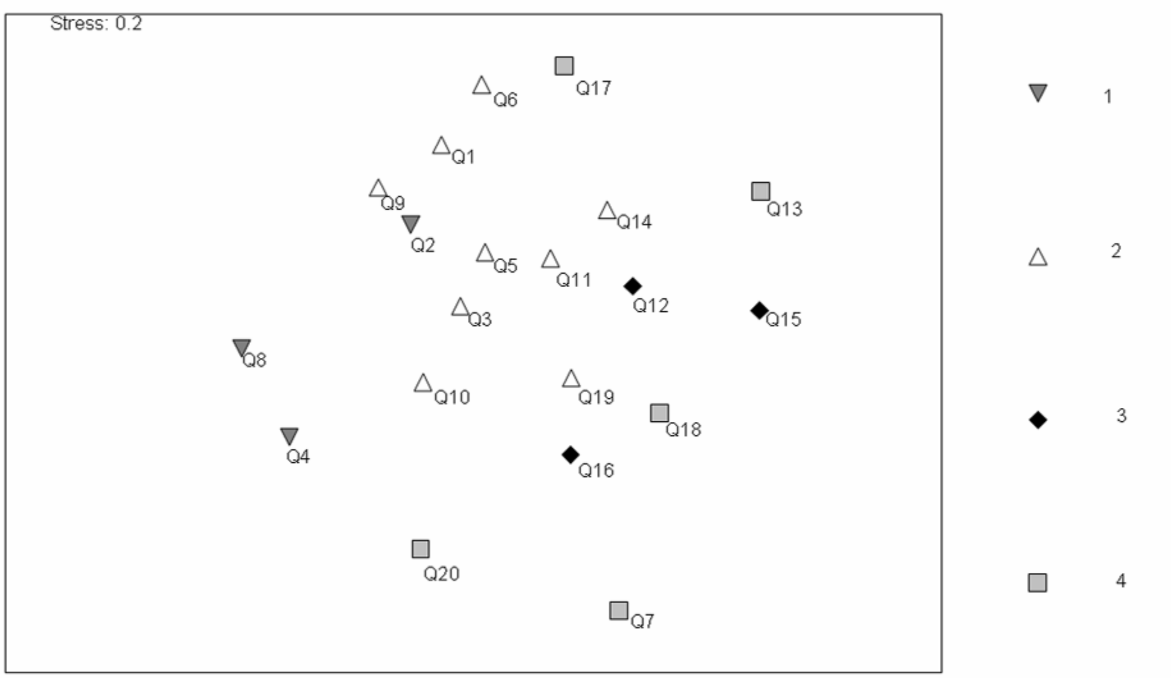

Fig. 3: Nonmetric multidimensional scaling (NMDS) of the investigated springs based on the faunistic data. Similarity index: Bray-Curtis; transformation: square root; factor: discharge (1: <1 l min^{-1}; 2: >1 and <5 l min^{-1}; 3: >5 and <20 l min^{-1}; 4: >20 l min^{-1})

Discussion

In Europe, a few attempts have been made to classify springs limnologically (Thienemann, 1924; Schwoerbel, 1959; Gerecke, 1991; Zollhöfer, 1999; Zollhöfer et al., 2000). In our study the investigated springs could not be differentiated into distinct classes. Due to the geological and geographical homogeneity of the area investigated in this study the chemical conditions of the springs were very similar. Only large-scale investigations in springs with different geological settings or investigations in acidified springs (Baltes, 2000; Hahn, 2000) show distinct differences in spring water chemistry.

And also looking at substrate and macroinvertebrate composition we could not differentiate spring types. The transition from one virtual type to another is gradual, and there is almost a continuum between traditional types, such as helocrene and rheocrene (Steinmann, 1915; Thienemann, 1924). In limestone areas, rheocrenes are often sintered to a certain degree, but this is not a discriminating factor and we can not draw a sharp line between rheocrenes and limesinter-rheocrenes. Non-sintered rheocrenes in other regions might show differences in species composition. For the macroinvertebrate assemblages in the studied springs other substrate factors, e.g., leaf litter and cobblestones, are more important. The appearance of a spring and its macroinvertebrate composition depend on many factors, each of which varies considerably. Therefore, approaches to establish regional spring classifications may best reach their goal by describing a continuum with regionally specific forms of emergence, instead of categorizing rigidly distinct types. The individuality of springs has to be considered.

However, our results confirm that substrate composition plays an important role for macroinvertebrate assemblages as it has been widely documented in literature (Bonettini & Cantonati, 1996; Hahn, 2000; Ilmonen & Paasivirta, 2005; Gerecke et al., 2005) and it is evident that the substrate composition of a spring influences the diversity of macrozoobenthic communities. Detritivores dominate muddy, helocrene-like springs with low discharge, whereas mostly grazers inhabit springs with coarse substrate and high discharge. Leaf litter is particularly important because of its function as a source of energy in an ecosystem with originally little allochthonous material (Rosi-Marshall & Wallace, 2002). Leaf litter is the most common food source, especially for Amphipoda (Cummins et al., 1973). Therefore, it is not surprising that we identified leaf litter as one of the most important substrate components for macrofaunal composition in springs.

As hydrological conditions form spring habitats, discharge is commonly assumed to have an influence on the composition of macrozoobenthic assemblages (Bonettini & Cantonati, 1996; Hoffsten & Malmqvist, 2000; Meyer & Meyer, 2000; Meyer et al., 2003, Ilmonen & Paasivirta, 2005). Constancy of discharge is particularly important for colonization patterns (Danks & Williams, 1991; Smith, 2002; Smith et al., 2003). In shaping the substrate and therefore the habitat structure, discharge also affects macrozoobenthic assemblages indirectly (Smith et al., 2003). In the current study, springs with very high discharge could be significantly separated from springs with low discharge with respect to substrate composition and to the composition of macrozoobenthic assemblages. However, the dynamic character of discharge requires long-term studies for assessing the influence of its constancy on macroinvertebrate assemblages.

The periodical changes of abiotic parameters, such as discharge and substrate composition, lead to temporal and spatial patchiness in springs. The patch dynamics concept (Pickett & White, 1985; Townsend, 1989) has been widely applied to river ecosystems (Downes, 1990; Matthaei & Townsend, 2000; McCabe & Gotelli, 2000; Melo et al., 2003). Investigations on the application of the concept to springs are still lacking.

Patch dynamics are strongly connected with the role of disturbance on macroinvertebrate assemblages. The assumption that springs are relatively stable ecosystems leads to the conclusion that disturbance is not an important factor for the dynamics in spring ecosystems. This is consistent with the intermediate disturbance hypothesis, which predicts a peak in biodiversity at an intermediate disturbance level (Connell, 1978) and low diversity at a lower disturbance level, as in the case of springs. Barquin & Death (2004) support this thesis with the results of their work in northwestern Spain.

However, as we pointed out above, other investigations show the importance of varying discharge for macroinvertebrate communities. As in other running waters, discharge should be the most important disturbance factor in springs, where the span reaches from desiccation in intermittent springs to spates in karst spring systems. Both disturbance events lead to a redistribution of individuals within and between patches of one spring and open up space for new colonists. Because of the periodic disturbance, intermittent springs lack macroinvertebrates with high growth rates in summer or bivoltine, multivoltine or partivoltine animals (Smith & Wood, 2002), and are usually not inhabited by spring specialists (Gooch & Glazier, 1991). However, we did not consider intermittent springs in our study. Perennial springs consist of more patches and therefore associated species (Danks & Williams, 1991) and are refuges for glacial relicts (Fischer et al., 1998; Williams & Williams, 1998). Also hololimnic species are typical for perennial springs because of their lack of flight dispersal (Gooch & Glazier, 1991). The present study confirmed that in springs with very low discharge, merolimnic insects are more frequent than hololimnic species. The Amphipod *Gammarus fossarum* was frequent probably due to the hard water in the investigated springs (Glazier, 1991).

We can also consider a single spring as a patch of a naturally fragmented spring system at landscape scale with temporal, spatial, and functional aspects. Furthermore, the population of one species in one spring forms a part of a metapopulation as described in the metapopulation concept (Hanski & Gilpin, 1997). The genetic differentiation within metapopulations will depend on the dispersal abilities of the animals and on isolation factors, such as the distance between adjacent springs. Initial studies show that among insects, the dispersal ability of a species influences the faunal composition of streams (Hoffsten, 2004) and the genetic diversity within a species (Wilcock et al., 2001; Kelly et al., 2002; Miller et al., 2002).

Studying the distribution and dynamics of the characteristic spring fauna will help to identify the most appropriate measures to mitigate adverse man-made effects on springs.

Conclusion

This study clearly showed the complexity of spring ecosystems. Discharge is one governing factor determining both the substrate composition and the composition of macrozoobenthic assemblages in springs. The springs are also linked because of the influence of the substrate on macroinvertebrate assemblages. Variation in discharge was assumed to be the most important disturbance in springs, where the disturbance may remain predictable over a certain period of time. This would be documented by a characteristic faunal composition. Further investigations will focus on the distribution, disturbance, and dispersal between springs, which are key factors for the dynamics of these unique habitats.

Acknowledgements

We thank the programme “Mensch Gesellschaft Umwelt” from the University of Basel for funding this project. Thanks to Marko and to the other numerous people who helped with the fieldwork. And we also thank Karen Brune, who improved the language and had helpful comments on the manuscript.

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Appendix 1: Physical and chemical characteristics from measurements in autumn 2003 and substrate composition of the 20 investigated springs (Q1–Q20). Discharge (estimated):
1: <1 l min^{-1}; 2: >1 and <5 l min^{-1}; 3: >5 and <20 l min^{-1}; 4: >20 l min^{-1}. Substrate type classes (percentage of areal coverage): 0: 0%; 1: 1–25%; 2: 26–50%; 3: 51–75%; 4: 76–100%.

Site	Physical and chemical characteristics						Substrate composition												
	Discharge (estimated)	Temperature (°C)	pH	Oxygen (mg l^{-1})	Oxygen (%)	Conductivity (µS cm^{-1})	Anoxic mud	Detritus	Leaf litter	Dead branches	Leaf nests	Moss	Roots	Macrophytes	Clay	Sand	Gravel	Stones	Lime sinter
Q1	2	11.6	7.4	9.2	85	1024	0	2	4	3	1	0	0	0	2	2	2	1	0
Q2	1	9.6	8.1	9.4	83	700	0	1	4	2	0	0	0	1	1	1	2	2	0
Q3	2	10.5	8.0	8.8	79	1435	0	3	3	2	1	1	1	1	2	1	1	0	1
Q4	1	10.1	7.4	5.2	47	574	0	3	4	0	3	0	0	0	3	0	0	0	0
Q5	2	13.1	8.0	9.6	91	1315	0	1	3	3	2	0	1	0	1	1	1	1	0
Q6	2	10.6	8.0	8.8	79	710	0	2	1	1	0	1	0	3	3	2	3	3	0
Q7	4	12.8	7.5	7.1	67	804	1	3	2	1	1	0	0	3	1	2	2	0	0
Q8	1	10.4	6.6	8.4	79	76	2	0	4	2	2	0	0	1	3	0	0	0	0
Q9	2	11.2	8.1	10.6	100	791	0	0	4	2	2	0	0	0	3	0	1	1	0
Q10	2	10.2	8.2	10.8	102	412	0	1	3	2	1	0	2	0	2	1	1	1	3
Q11	2	13.7	8.2	10.6	100	356	0	1	3	1	2	0	0	0	2	1	1	0	3
Q12	3	11.1	7.4	9.2	87	651	0	0	2	1	1	0	0	0	0	1	2	1	0
Q13	4	10.2	7.6	9.5	90	500	0	0	1	0	0	1	0	0	0	0	2	2	0
Q14	2	8.5	8.1	10.4	98	581	0	2	4	2	1	0	1	0	3	2	1	1	0
Q15	3	8.0	8.1	10.4	98	463	0	0	1	1	1	1	1	0	1	2	3	1	1
Q16	3	12.0	7.4	5.6	53	564	0	1	1	2	1	1	1	0	2	3	3	2	0
Q17	4	10.5	7.3	9.8	92	786	0	1	3	3	2	2	1	1	0	1	2	3	3
Q18	4	11.4	7.3	7.9	75	566	0	2	3	0	1	0	0	1	0	3	2	3	0
Q19	2	8.8	7.6	9.8	93	570	0	3	3	1	2	1	1	1	3	3	2	1	1
Q20	4	14.0	8.4	9.4	89	1243	0	2	1	1	2	0	1	2	3	1	0	0	0

CHAPTER THREE

A first approach to a faunistic spring typology for a European low mountain range region

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In preparation for submission to *Aquatic Ecology*

Abstract

Springs are unique ecosystems that provide habitats for specialized and rare species. Their classification has ever been in the focus of interest since the beginning of limnological research. In spite of numerous ecomorphological typologies including faunistic parameters, a primary faunistic spring typology is still lacking. During a three-year period we investigated the macroinvertebrate assemblages and the abiotic conditions of springs in a relatively undisturbed valley in north-western Switzerland. Using analysis of similarities and a Cluster-analysis we were able to differentiate four spring groups on the basis of faunistic and abiotic data. In general we can distinguish between springs, which are mostly inhabited by grazers and are characterized by a lotic environment, and springs, which are mostly inhabited by detritivores and filter-feeders and are associated with a lenitic environment. Those spring types are the extremes on a continuum. Special spring forms characterized by key species identified in this study are strongly sintered springs and karstified springs typical for the Swiss Jura Mountains. They lay between those extremes and may offer a more diverse habitat for macroinvertebrates. With this first approach we can now characterize faunistic spring types on the basis of functional feeding groups and give a first foundation for a European spring typology also applicable for conservation aspects.

Key words: faunistic spring typology, macroinvertebrates, classification

Introduction

Springs are unique ecosystems with specific abiotic conditions (Odum, 1971; van der Kamp, 1995) and they are inhabited by organisms adapted to this environment (e.g. Williams & Danks, 1991; Ferrington, 1995). Since the beginning of limnological research in Europe springs were in the focus of interest. Most of the studies were conducted in the northern German low mountain range regions (e.g. Thienemann, 1912; Beyer, 1932) or in the German lowlands (e.g. Thienemann, 1923; Thienemann, 1926). But also studies from the southern German low mountain range regions (Zschokke, 1902), the pre-Alpine low mountain range regions (Bornhauser, 1912; Chappuis, 1924; Geijskes, 1935) and the Alps (Nadig, 1942) exist from these early times. Already then the need for a classification of springs became obvious and the geomorphological types rheocrene – helocrene – limnocrene were invented by Steinmann (1915) and Thienemann (1924). Since then, many other spring typologies for different mid-European regions based on ecomorphological features (Beyer, 1932; Schwoerbel, 1959; Gerecke, 1991), physicochemical (Hahn, 2000) or chemical factors (Roca, 1990; Williams et al., 1997) have been developed. And also some attempts have been made to include faunistic elements (Gerecke & Di Sabatino, 1996; Cantonati, 2003) or whole species assemblages (Gauterin, 1999; Zollhöfer et al., 2000; Martin et al., 2008) in ecomorphological classifications. However, limnological science is still lacking a faunistic spring typology classifying springs on the basis of the spring fauna *a priori*.

As water is the never running out resource of the Alpine region, Switzerland is especially rich of springs. But in north-western Switzerland, for example, only a minimum of the springs are still in a natural or at least near natural condition (Zollhöfer, 1997). In spite of their importance as habitats for specialized species and in spite of their endangered situation there are only a few current studies on natural springs in Switzerland (e.g. Baltes et al., 2006; von Fumetti et al., 2006). Most knowledge derives from a study conducted by Zollhöfer (Zollhöfer, 1999; Zollhöfer et al., 2000). For the Swiss Jura and the Midland he developed an ecomorphological spring typology with seven different spring types based on Steinmanns (1915) and Thienemanns (1924) classification.

The study presented in this publication was part of the Basel Spring Project (Baltes et al., 2005) conducted in north-western Switzerland. Within this project one relatively undisturbed valley near Basel was intensively studied by hydrologists and biologists over several years. The valley gave us the opportunity to investigate many natural, nearly undisturbed springs on a geographically small scale, all within the same drainage area and all emerging from the same geological underground. With these equal prerequisites serving as a common standard for all springs we tested if springs can be classified faunistically independent from the geological underground and the geomorphological features of the springs. This will open us the possibility to develop a spring typology applicable also to other parts of Europe in future research.

Materials and Methods

Study area

The study was conducted in the Röseren valley, a small, relatively undisturbed valley near Basel city in the Jura Mountains, with an average altitude of 400 m above sea level. A comprehensive study on the springs in the Röseren valley was conducted by Geijskes (1935), a short description of the recent situation in the valley and a comparison of the fauna between 1935 and 1990 is given in Küry (1997). Geologically the region belongs to the Swiss Tabular Jura with the Oxfordian aquifer as the main aquifer. The underground is slightly karstified. Because of unkarstified upper geological layers most of the springs do not show the characteristics of typical karst springs. In the whole area 22 springs exist, more than the half is damped as wells for water supply. They were not considered in this study. Recent information on the hydrogeology of these springs is given in Butscher and Huggenberger (2007). All springs investigated in this study are situated in a cultivated forest, partly in non-resident Thuja-forest. During the study period from autumn 2003 until summer 2005 no significant change in the environment happened in the valley. However, due to the economical aspects of the forest, slight changes of the woods around the springs were evident throughout this period.

Macroinvertebrate sampling

Macroinvertebrates were quantitatively sampled with a small surber sampler (0.01 m^2, 500-µm mesh width) according to Von Fumetti et al. (2006) at four times: October 2003, March 2004, October 2004, April 2005. At every sampling occasion four replicates were taken in each spring not more than 5 m away from the source (sampling area per sampling occasion: 0.04 m^2). Some springs were detected not until 2004. Here, only samples from three or even two (Q63, Q64) occasions exist. For technical reasons, some springs could not be sampled at a later sampling occasion (Q4, Q57).

After separation of Turbellaria for live identification, all samples were immediately preserved in 70% ethanol in the field, and subsequently sorted and determined in the laboratory. Taxonomically demanding Dipteran groups (e.g., Chironomidae) were identified to family level, all others were identified to the most accurate taxonomic level. The focus of this survey was on the macrozoobenthos. The meiofaunal taxa Ostracoda, Copepoda and Hydracarina were only caught accidentally. However, as we used the same sampling procedure for every spring, we did not exclude them from our statistical analyses.

Abiotic measurements

At each macrofaunal sampling occasion, water temperature (°C), pH value, conductivity (µS/cm), oxygen concentration (mg/l), and oxygen saturation (%) were recorded in the field using portable meters (Wissenschaftlich-Technische Werkstätten, Weilheim, Germany). Additionally, temperature, conductivity and discharge were recorded bi-weekly during November 2003 and July 2005. Due to the mode of outflow discharge measurements were not possible at Q1. The following Ions were analyzed by the drinking water laboratory of the Cantone Basel-Landscape at least once at every spring: Na^+, K^+, Ca^{++}, Mg^{++}, Cl^-, NO_3^-, NO_2^-, SO_4^-, PO_4^-.

The substrate types moss, detritus, leaf litter, dead branches, leaf nests, roots, macrophytes, anoxic mud, clay, sand, gravel, stones and limesinter were categorized in every spring into five frequency classes: 0: 0%; 1: 1–25%; 2: 26–50%; 3: 51–75%; 4: 76–100% (Von Fumetti et al., 2006). Because of the three-dimensional structure of the streambed, the percentages of the substrate types usually added up to more than 100 %.

Statistical analyses

All statistical analyses described below were calculated using PRIMER 6.0 (Clarke and Gorley, 2006). Ordination of the springs was conducted using non-metric multidimensional scaling (nMDS), on the basis of the analyses of similarities-procedure (ANOSIM), which is analogous to an ANOVA, but relies on a similarity matrix and makes few assumptions on data. For faunistic data the Bray-Curtis similarity and a square root – transformation was used. Abiotic data were normalized but not transformed and the Euclidian distance was used as similarity measure. Detailed information about nMDS and ANOSIM is given in Von Fumetti et al. (2007).

A CLUSTER analysis was performed with the similarity matrix of the summarized faunistic data of the springs using group average. In addition, the SIMPROF-procedure (SIMilarity PROFile) was conducted. This is a series of permutation tests looking for statistically significant evidence of genuine clusters in samples which are *a priori* unstructured. With this procedure every node of the completed dendrogramm is tested to be significant. In the Cluster dendrogramm, samples connected by dashed red lines cannot be significantly differentiated (Clarke & Gorley, 2006).
Test statistic: π - summed absolute distances between the real similarity profile and the simulated mean profile; p = 0.05)

BioENV is a correlation method that shows, which abiotic parameters explain the macroinvertebrate composition best (ρ between 0 and 1). For this procedure the similarity matrix of the summarized faunistic data was correlated with the normalized environmental data using Spearman rank correlation.

With the SIMPER-procedure dissimilarities between and similarities within groups can be explained with individual species and with the composition of the macroinvertebrate assemblages. Species discriminating groups contribute more or less consistently to the distinction of two groups and have a low ratio of the average dissimilarity (diss) and the standard deviation (SD). Species typical for a group highly contribute to the similarity within a group and have a consistent large presence (high ratio diss/SD).

Results

All springs we investigated in this study are cold-temperate springs with an average temperature of 9-10 °C throughout the year (Table 1). In some springs the temperature decreases in winter to almost 6 °C or rises to 12 °C in summer. Here, the amplitude is relatively high, whereas most of the springs have temperature amplitudes of 1–2 °C. All springs had a circumneutral pH (7.2–8.2) and were saturated with oxygen during the sampling occasions. The conductivity was between 270 and 550 µS/cm. The discharge of the springs was between 172 l/min (Q57) and 1 l/min (Q64). The amplitude of the discharge differs from spring to spring and depends on the geographical situation and on the influence of the karstic underground. The amplitude varies between 70 (Q3) and 157 (Q57) (Table 1).
Chemical parameters showed no striking values. In the springs Q59a-c and Q4 high Nitrate- (~40 mg/l) and Chloride-values (~12 mg/l) indicate the use of fertilizers. According to the

BioENV procedure, the chemical parameters did not influence the macrozoobenthic assemblages, so they were not considered for further analyses.

A total of 70 species and higher taxa, among them 11 Trichoptera species and 6 Hydracarina species, were recorded from 149 samples. *Gammarus fossarum* Koch, 1835 was the most abundant, occurring in almost every spring in high densities. On average, 26 taxa were found in each spring (19-32), the Shannon diversity was between 1.5 and 2.2 (Table 1).

Table1: Temperature and discharge range, dominant substrates and diversity parameters of the investigated springs; n. m.: not measured

Spring	Swiss coordinates	Temperature [°C]	Discharge [l/ min]	Dominating substrates	Species richness	Shannon diversity
Q1	619.750/260.350	7.9 - 10.2	n. m.	limesinter, leaves	24	1.602
Q3	619.200/260.250	8.7 - 9.9	13 - 83	limesinter, moss, leaves	30	1.987
Q4	618.920/260.290	9.9 - 10.8	26 - 163	sand, pebbles	26	2.230
Q57	617.775/259.625	8.3 - 10.3	15 - 172	pepples, stones	25	1.508
Q59a	619.150/260.325	9.8 - 12.1	17 - 150	pebbles, dead wood	30	1.867
Q59b	619.150/260.325	9.8 - 12.1	17 - 150	pebbles	32	2.165
Q59c	619.150/260.325	9.8 - 12.1	17 - 150	pebbles, dead wood, srtones	29	2.087
Q61a	618.525/259.950	7.7 - 11.8	2 - 134	coarse clay, FPOM, leaves	29	2.185
Q61b	618.525/259.925	8.0 - 10.5	2 - 91	leaves, dead wood, pebbles	21	2.062
Q62	619.300/260.325	6.9 - 12.0	4 - 91	leaves, limesinter	19	1.898
Q63	617.825/259.650	8.3 - 10.5	2 - 122	leaves, dead wood, stones	25	1.957
Q64	617.550/259.550	6.5 - 11.5	1 - 156	leaves, FPOM, anoxic mud, limesinter	20	2.129

The ANOSIM-procedure showed that the mean value of the macroinvertebrate samples of the different sampling occasions from one spring were significantly more similar than the mean value of the macroinvertebrate samples of the different sampling occasions of different springs (R= 0.448; p= 0.001). Season or sampling occasion were no factors differentiating the samples significantly. During the study period from autumn 2003 until spring 2005 significant differences in the macroinvertebrate assemblages were detected within some springs (Q1, Q3, Q4, q59a, q59b, q59c). However, general patterns like seasonal or temporal shifts from 2003 to 2005 in all springs could not be detected and we assume technical reasons and seasonal fluctuations to be responsible for the differences occurring in some springs. Because of their significant similarity it is therefore adequate to summarize the data of the different sampling occasions of one spring for further statistical analyses.

With the summarized faunistic data from 2003-2005 we can significantly differentiate four different groups of springs using nMDS and ANOSIM (R = 0.849; p = 0.001). Q4 and Q59a, Q59b and Q59c form group 1, Q61a and Q64 form group 2. Group 3 consists of the springs Q57 and Q63 and the springs Q1, Q3, Q61b and Q62 form group 4 (Fig. 1).

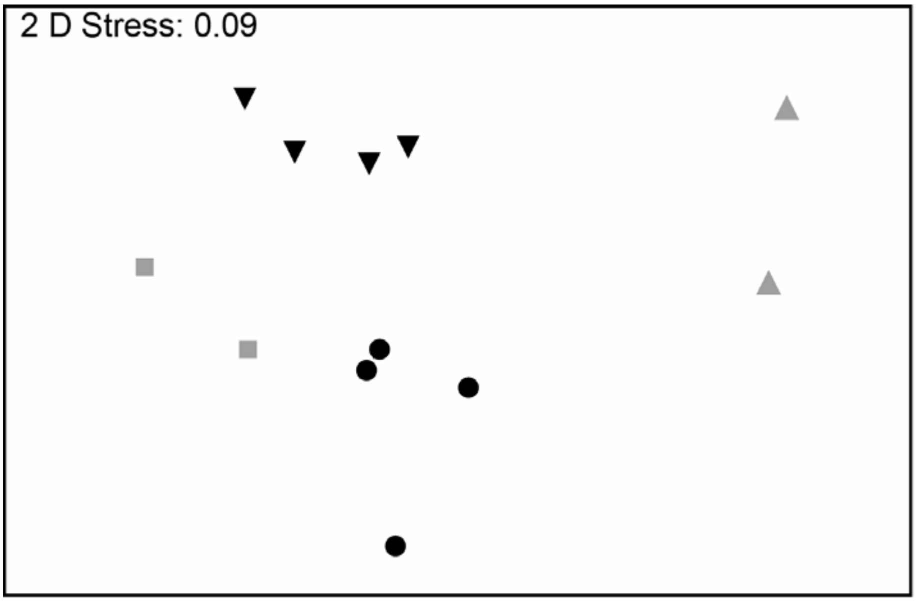

Fig. 1: Non-metric multidimensional scaling (nMDS) of the 12 investigated springs based on the summarized faunistic data; similarity index: Bray-Curtis, transformation: square root; factor: group; ▼ = group 1; ♦ = group 2; ■ = group 3; ▲= group 4; analysis of similarities (ANOSIM): R= 0.849, p= 0.001

A Cluster analysis combined with the SIMPROF procedure on the basis of the faunistic data confirms the groups created by nMDS and ANOSIM *a priori* (p= 0.05). Here, the differentiation of the groups 1 and 3 was not significant (Fig. 2).

With the substrate data and the physicochemical parameters, those groups can also be significantly differentiated from each other (R = 0.849; p = 0.001) (Fig. 3).

The results of the BIOENV procedure underline the importance of minimum temperature, anoxic mud, FPOM, gravel and average discharge for the composition of the macroinvertebrate assemblages (ρ= 0.786; p= 0.01). As mentioned above, chemical parameters have no significant influence.

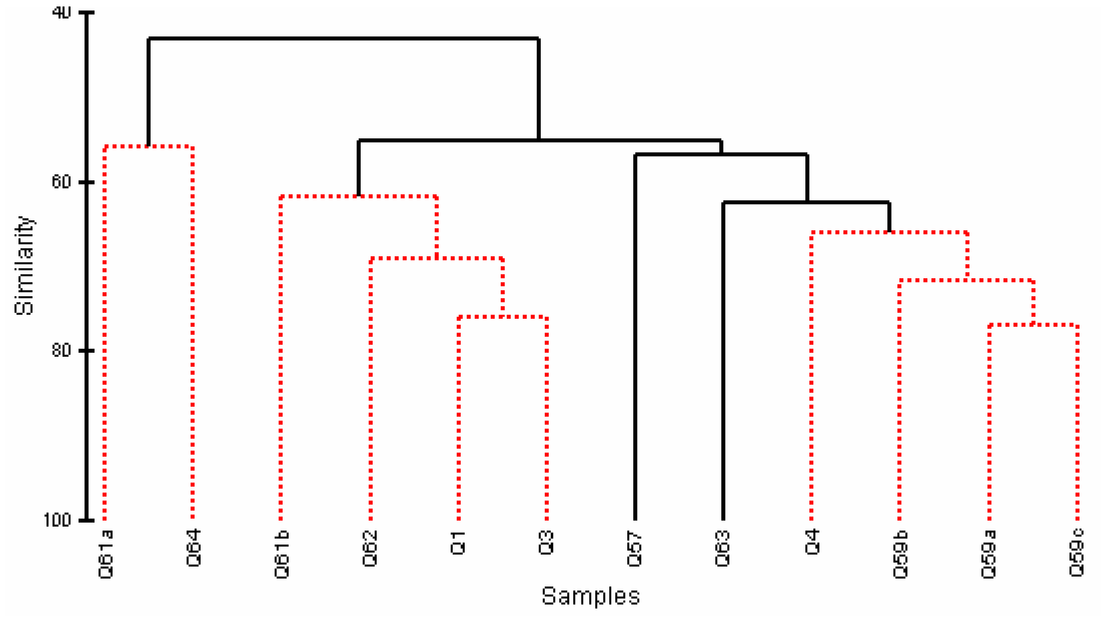

Fig. 2: Cluster-Analysis and SIMPROF-procedure (SIMilarity PROFile) of the summarized faunistic data set of the 12 investigated springs; similarity index: Bray-Curtis, transformation: square root; p = 0.05; samples connected by dotted lines: no significant differences

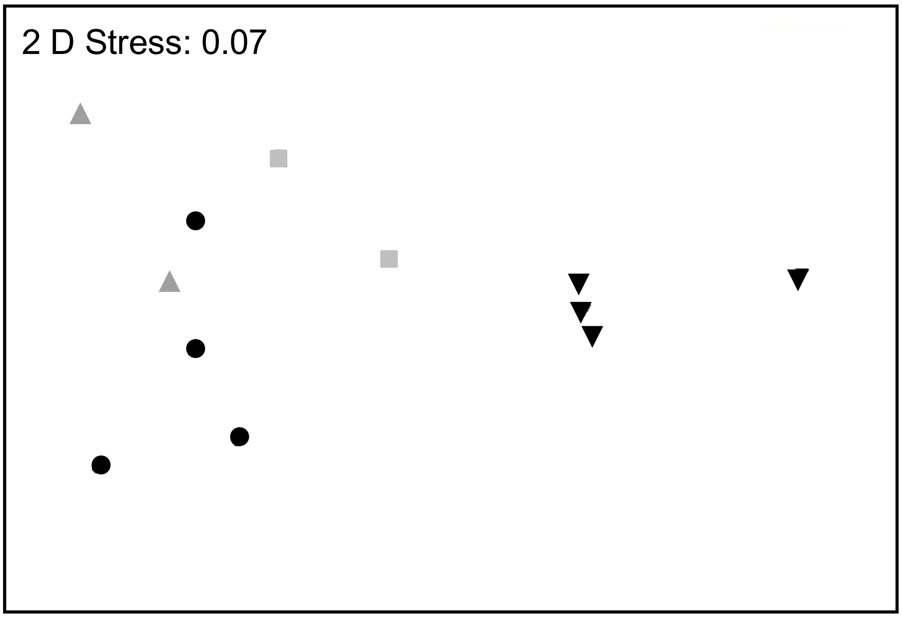

Fig. 3: Non-metric multidimensional scaling (nMDS) of the 12 investigated springs based on the normalised abiotic data (substrate and physicochemical parameters, no chemical parameters); similarity index: Euclidian distance, transformation: none; factor: group; ▼ = group 1; ♦ = group 2; ■ = group 3; ▲= group 4; analysis of similarities (ANOSIM): R= 0.849, p= 0.001

Using SIMPER we calculated the similarity of the faunal assemblages within one spring group and identified key species characteristic for the groups. Most of them also occur in other groups but with lower densities. Group 1 springs (similarity: 70%) are characterized by *Synagapetus dubitans* McLachlan, 1879 and *Elmis rietscheli* Stefan, 1958. Both are typical for lotic environments. *Pisidium cf. personatum* Malm, 1855 and *Sericostoma personatum* Spence, 1826/ *schneideri* Kolenati, 1848 occur in the springs of group 2 (similarity: 56%) in high densities. The snail genera *Bythiospeum spp.* Bourguignat, 1882 and *Bythinella spp.* Moquin-Tandon, 1856 were frequent in the springs of group 3 (similarity: 55%) and in group 4 (similarity: 67%) *Dixa spp*. Meigen, 1818, the mite *Protzia squamosa* Walter, 1908 and Ostracoda reached high densities.

Discussion

Since the beginning of ecological spring research the differentiation of distinct spring types was in the focus of interest. Steinmann (1915) was the first who differentiated springs geomorphologically into rheocrenes and limnocrenes. Thienemann (1924), who mainly worked in the German lowlands, added the helocrenes as spring type. It became soon obvious that this division into three types is oversimplifying the real situation and that the shape of springs depends on many environmental factors, especially the geological and the geographical situation of the springs. In general, the North of Europe is dominated by helocrene-like springs (e.g. Gerecke, 1991; Lindegaard et al., 1998; Ilmonen & Paasivirta, 2005). The siliceous European low mountain range regions are dominated by helocrenes (e.g. Beierkuhnlein & Gollan, 1999) or rheocrenes (Hahn, 2000). In limestone regions, especially in the Alps, and in the Mediterranean regions rheocrene like springs in the widest sense dominate (Gerecke & Di Sabatino, 1996; Zollhöfer, 2000). With this geological background the geomorphological classification of springs was widened in several mid-European regions (Schwoerbel, 1959; Gerecke, 1991; Zollhöfer, 1996; Hahn, 2000), all typologies based on the classical “trinity”. The typology of Schwoerbel (1959) and Gerecke (1991) with the intermediate types rheohelocrene and rheopsammocrene is the most applied one (Di Sabatino et al., 2003; Gerecke et al., 2005; Sambugar et al., 2006).

In the past few attempts have been made to include the fauna and the substrate composition in the classification of springs and to verify a priori defined ecomorphological types with faunistic data a posteriori (Weigand, 1998; Schröder et al., 2006; Dumnicka et al., 2007). Ilmonen and Paasivirta (2005) discriminated lentic, lotic and intermediate spring sites within finnish springs and support the classical typology of Thienemann (1924). The variation between the sites in those springs is related to water flow and substrate characteristics. Most important for Switzerland and adjacent regions is the study of

Zollhöfer (1999, 2000). His regional spring typology for the Swiss Jura and Midland is based on habitat variables and on faunistic parameters. Furthermore he identified key species for each type.

In general we consider, that springs are individuals and that there is a continuous transition between the traditional ecomorphological spring types (Von Fumetti et al., 2006). Intermediate stepping-stone types like the rheohelocrenes and rheopsammocrenes (Schwoerbel, 1959; Gerecke, 1991) can be assumed. But the differentiation of such intermediate spring types does not facilitate the identification of spring types in the field. As the identification of ecomorphological spring types is often difficult, dependent on the geological underground and not useful for the identification of characteristic species assemblages, it is a promising approach to classify springs faunistically. This has the advantage that spring organisms integrate all habitat variables over a longer time period than abiotic parameters, which can usually only be measured punctually. A first attempt for a true *a priori* faunistic spring typology has been made by Gauterin (1996). He proposed a faunistic typology on the basis of faunistic spring evaluation concepts (Fischer, 1996) and plant sociology concepts (e.g. Dierschke, 1994). First approaches for an entomological sociology of aquatic Coleoptera also exist (Hebauer, 1994). In contrast to this approach we propose two steps to be important for a faunistic spring typology: the identification of key species and most important the identification of functional groups dominating different springs.

With our data set of 10 springs investigated over a period of three years we were able to identify four spring groups using all macroinvertebrate data. Our study confirms that springs are inhabited by characteristic macroinvertebrate assemblages visualizing the habitat qualities of the individual springs. Substrate factors, minimum temperature and average discharge were important for the composition of the macroinvertebrate assemblages and also classified the springs significantly in the same pattern. The importance of the substrate composition (Dumnicka, 2007), the discharge (Smith, 2003; Von Fumetti et al., 2006) or both (Minshall, 1968; Bonettini & Cantonati, 1996; Mori, 2006) as factors influencing the composition of macroinvertebrate assemblages in springs has been widely documented.

As we identified other key species or key genera in our investigations than Zollhöfer (1999, 000) did, it is more useful to identify whole species assemblages or functional groups and not single key species to be typical for spring types. This is an important pre-requisite for the application to other parts of Europe. In lotic springs with high and constant discharge and dominating coarse anorganic substrate we found grazers like *Synagapetus dubitans* and *Elmis rietscheli* (Moog, 1995). We therefore generally propose that lotic springs are mainly characterized by grazers like the Glossosomatidae and the Elmidae. Filter-feeders and detritivore species like *Pisidium spp.* or *Beraea pullata* (Curtis, 1834) (Moog, 1995) are typical for lenitic springs with low discharge and dominating organic substrate. With this short overview we have the whole spectrum from lenitic to lotic springs. All other spring types are transitional forms offering a mosaic of habitat types (Fig. 4).

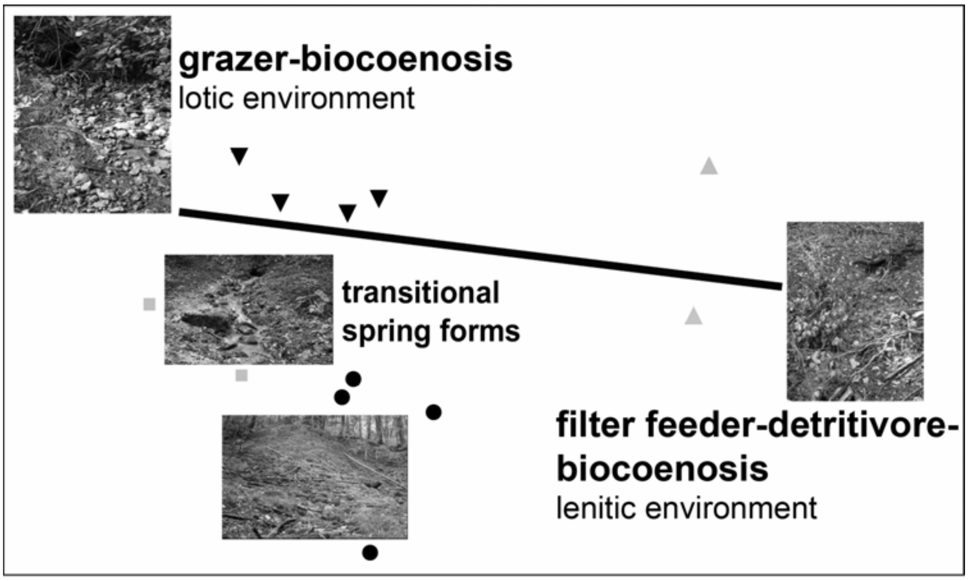

Fig. 4: Spectrum of spring forms occurring in Mid-European regions, inhabited by characteristic biocoenosis

It may be that those intermediate forms are especially rich of crenobionts, because of their diverse biotic and abiotic microhabitats (Di Sabatino et al., 2003). In accordance with Zollhöfer (1999, 2000) we found in our investigations, that the Gastropoda-genera *Bythiospeum spp.* and *Bythinella spp.* are typical for springs exhibiting karst characteristics, even if slight. Those with intermittent dry periods are also inhabited by species, which are adapted to highly fluctuating discharge conditions (Meyer & Meyer, 2000; Wood et al., 2005). Springs with limesinter-terraces, which are typical for the Swiss Jura and other lime-dominated regions, exhibit an upper lotic part and a lower lenitic part and have special conditions because of their high $CaCO_3$-content. According to Zollhöfer (1997) they are characterized by the absence of species. In our study, we did not find less species in sintered springs. We identified the Dixidae as key-family. The water mite *Protzia squamosa* and the Ostracoda we also identified statistically as key species belong to the meiofauna, which was not the main part of our study and only found accidentally. Due to our comprehensive data also from other springs in the Swiss Jura (unpublished data), we would consider Trichoptera without a quiver to be frequent in sintered springs.

Our results show that springs can be classified by characteristic faunistic assemblages or even biocoenosis, which reflect the constitution of different functional feeding groups. They are an integrative measure for the abiotic features in the springs and a measure of functional diversity in springs. Springs with a more or less lotic environment are dominated by grazers like the Glossosomatidae, lenitic springs are dominated by detritivores and filter-feeders. However, some animal groups like the water mites may play a major role in the differentiation of spring types (Gerecke et al., 1998; Di Sabatino et al., 2003).

The main goal for future research will be to develop regional faunistic classification concepts on the basis of functional feeding groups for every landscape unit and transfer it to a higher scale. We will then be able to develop a faunistic spring typology for the whole Swiss Alpine and Pre-Alpine region and for adjacent areas like the geologically very different Black Forest in Germany. This will be transferable to other European regions with similar pre-conditions. Such a faunistic typology can be applied by governmental or non-governmental organisation for the inventory and characterisation of springs and finally for their protection.

Acknowledgements

We thank the program MGU and the Freiwillige Akademische Gesellschaft (FAG) from the University of Basel for funding the project, and the Drinking Water Laboratory for its financial and technical support. We acknowledge numerous people who helped with the fieldwork throughout the years. We thank Peter Martin for identifying Acari and Rüdiger Wagner for identifying Psychodidae.

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CHAPTER FOUR

Disturbance in springs: discharge variability and its impact on macroinvertebrate assemblages

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In preparation for submission to *Freshwater Biology*

Summary

1. Discharge variability has been considered as an important disturbance factor and its impact on macroinvertebrate assemblages has been widely studied in river ecosystems. In comparison, few studies have investigated discharge variability in springs, because they are thought to be relatively stable ecosystems and because the discharge is not easy to measure in this environment.
2. In a one-year-experiment we assessed the discharge regime of five natural, perennial springs using the gypsum dissolution method. After calibration in the laboratory the discharge was calculated from the weight loss of gypsum sphere at a given temperature. Additionally, macroinvertebrate samples were collected during a one year period eight times to assess the impact of discharge variability on the composition of macroinvertebrate assemblages in the investigated springs.
3. The calibration experiments of the gypsum dissolution method revealed significant linear relationships of weight loss and the discharge. In field experiments we could differentiate springs with high discharge variability from springs with low discharge variability. Species diversity was highest in springs with low discharge variability, e.g. little disturbance. The simple number of species was highest in the spring with the highest discharge variability and lowest in the springs with the lowest discharge variability.
4. The gypsum dissolution method is an appropriate method for assessing short-term and medium-term discharge variability in springs, but an accurate calibration is vital. A clear disturbance–diversity relationship as described in the intermediate disturbance hypothesis was not detected.
5. Discharge variability as disturbance events become more important in the context of changes due to global climate change and changes in land use with more drought periods and floods.

Keywords: discharge, disturbance, macroinvertebrate assemblages, gypsum dissolution

Introduction

The influence of disturbance in river ecosystems on macroinvertebrate assemblages has been widely examined in the past, also regarding the intermediate disturbance hypothesis of Connell (1978), which predicts a peak in diversity at an intermediate level of disturbance (e.g. Townsend et al., 1997; McCabe & Gotelli, 2000) and the patch dynamics concept (Pickett & White, 1985; Townsend, 1989; Downes, 1990), describing the temporal and spatial patchiness of habitats. Springs provide relatively stable abiotic conditions for the aquatic fauna (Odum, 1971; van der Kamp, 1995) and are inhabited by species adapted to this environment (Ito, 1998; di Sabatino et al., 2003). However, hydrological disturbances also occur in springs. Drought periods especially in intermittent springs and in karst springs, as well as heavy rainfalls alter the discharge of springs rapidly and may influence the aquatic macroinvertebrates (Meyer et al., 2003). Such affects are also dependent on the geology and the origin of the groundwater. Past investigations found evidence that discharge is the most important factor influencing the composition of macroinvertebrate assemblages (Bonettini & Cantonati, 1996; Smith et al., 2003; Mori & Brancelj, 2006; von Fumetti et al., 2006). Despite the importance of discharge variability of springs on the composition of macroinvertebrate assemblages detailed quantitative discharge measurements have not been investigated. One possible reason might be that accurate, quantitative discharge or flow measurements are difficult in springs with extremely low water levels. However, for assessing the impact of discharge variability on macroinvertebrate assemblages its measurement is vital.

In the past many attempts have been made to assess water motion. This was achieved by measuring the weight loss of plaster or gypsum bodies in the water column. Many of these studies were conducted in the tidal zones of the ocean (Arsenault et al., 1997), in coral reefs (Jokiel & Morrissey, 1993) but also in rivers (Winterbottom et al., 1997) and the hyporheic zone (Angradi & Hood, 1998), but not in springs.

In this study we applied the gypsum dissolution method to springs and tried to establish a new method for getting quantitative discharge measurements or even flow data in natural springs over a long period of time. A constant monitoring of the spring temperature and seasonal sampling of the macroinvertebrate assemblages complemented these surveys. Our main goal was to find a method for measuring the impact of disturbance events on macroinvertebrate assemblages in springs that is reliable, easy to handle and applicable as a tool for environmental impact assessment.

Materials and Methods

Preparation of the gypsum spheres

The gypsum-spheres were made from commercially available calcium sulfate (Quick mix, Bauhaus market Germany) mixed with tap water in 2:1 proportions. After stirring the mixture gently for homogenizing it without producing air bubbles, the slurry was poured into egg-trays obtaining hemispheres of 4 cm - diameter. The trays were tapped several times to release remaining air bubbles before they were left for drying for at least five hours. After removing the hemispheres from the trays they were dried for at least 3 days at room temperature (~20 °C). Drying above 40 °C can lead to a conversion from hydrate to anhydrite in the crystalline structure (Petticrew & Kalff, 1991), we therefore preferred drying at room temperature for a longer period of time. After drying, the bottoms of the hemispheres were sanded and two hemispheres were glued together with commercially available all-purpose glue (UHU Kraft, UHU-Werke Bühl, Germany). In a final step a hole was drilled through each sphere using a drill rig (Dremel, Leinfelden-Echterdingen). The spheres weighed 45.5 g (+/- 3.5 g) on average. After weighing, each gypsum sphere was placed into a ball shaped sieve using a 0.8 mm-ferreous wire and 1cm plastic-tube pieces as spacers (Fig. 1). This construction guaranteed the position of the gypsum spheres in free space within the sieve, and subsequently within the water column during the experiments.

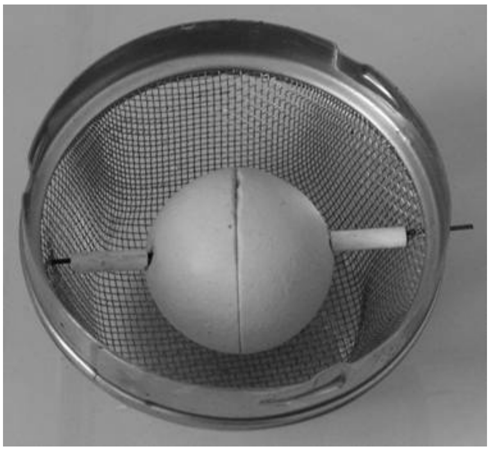

Fig. 1: Gypsum sphere placed in sieve

Calibration experiments

The calibration experiments were carried out in a closed circular flow system in a water laboratory. The system consisted of the flow channel (1.2 m X 0.2 m X 0.2 m), a tube from which the water flowed into a rain barrel of 150 ml content to ensure a water body big enough to prevent saturation of the water with dissolved gypsum (Thompson & Glenn,

1994) a pump for aquaria for pumping the water and for regulating the discharge and a cooling unit for regulating the temperature. The discharge could be adjusted manually at the pump and measured at the tube. The highest possible discharge was 18 l/min and the lowest 10 l/min. For each trial with different discharge and temperature (9-12 °C) values, three sieves containing a gypsum sphere were placed into the last third of the flow channel. Additionally, standing water controls were conducted for every temperature. Here, three sieves hang into the rain barrel ~15 cm above the bottom to ensure the right temperature and to ensure the standing water conditions. For lowering the water movement we let water flow over a sieve dropping then gently onto the top of the water column in the rain barrel. After exposure for 24 hours the gypsum spheres were removed from the sieves and were allowed to dry for at least five days on a laboratory bench at room temperature before weighing again. As the weight loss of gypsum is independent of pH above pH 4 (Crabtree & Trudgill, 1984) we only used tap water for the calibration experiments.

Field experiments

The field experiments were carried out in five natural springs (Q3, Q4, Q59, Q61, Q62) in the the Röseren valley, a single catchment. This is a small, relatively undisturbed valley near Basel city in the Jura Mountains, with an average altitude of 400 m above sea level. All springs that are part of this study are situated in a cultivated forest, partly in non-resident Thuja-forest. Geologically the region belongs to the Swiss Tabular Jura with the main aquifer being of Oxfordian origin. A comprehensive study on the springs in the Röseren valley was conducted by Geijskes (1935), recent information on the hydrogeology of these springs is given in Butscher and Huggenberger (2007).

After weighing the gypsum spheres, they were fixed in a sieve each. Three sieves where then exposed for six days on average (4-8 days) in each spring, always at approximately the same position. Due to the impact of humans and game, especially wild boars, some loss of sieves had to be considered. After the exposure time the gypsum spheres were removed to the laboratory and were allowed to dry for at least five days on a laboratory bench at room temperature before weighing again. In the whole, 22 test series were conducted in each spring from March 2007 until March 2008, at one week intervals between the test series. At the piped spring Q4 the discharge was also recorded as a control by measuring the amount of water entering a plastic bag within three seconds (Zollhöfer, 2000).

The macroinvertebrates in the five investigated springs were quantitatively sampled with a small surber sampler (0.01 m^2, 500-µm mesh width) as in Von Fumetti et al. (2006) every six weeks from March 2007 until October 2007, two additional sampling followed in February and March 2008. At every sampling day four replicates were taken in each spring not more than 5 m away from the source (sampling area per sampling day: 0.04 m^2). After separation of Turbellaria for live identification, all samples were immediately preserved in 70% ethanol in the field, and subsequently sorted and determined in the laboratory. Taxonomically demanding Dipteran groups (e.g., Chironomidae) were identified to family level, all others were identified to the most accurate taxonomic level.

At each macrofaunal sampling day, water temperature (°C), pH value, conductivity (µS/cm), oxygen concentration (mg/l), and oxygen saturation (%) were recorded in the field using portable meters (Wissenschaftlich-Technische Werkstätten, Weilheim, Germany). Additionally, the water temperature was monitored continuously in every spring from March 2007 until March 2008 using data loggers (HOBO Water Temp Pro, MicroDaq).

Data analysis

Using the data from calibration experiments in the laboratory a linear regression discharge – weight loss was plotted for every temperature tested. The linear regression equations were then taken to calculate the discharge in the springs from the given weight loss and temperature.

Species richness (= number of species), abundance, Shannon diversity (H'), Margalef's index (d) and Pielou' s eveness (J') were calculated for each macroinvertebrate sampling day and spring and for the summarized macroinvertebrate data of each spring.

Ordination of the springs was conducted using non-metric multidimensional scaling (nMDS), on the basis of the analyses of similarities-procedure (ANOSIM), which is analogous to an ANOVA, but relies on a similarity matrix and makes few assumptions on data. For the faunistic data the Bray-Curtis similarity and a square root – transformation was used. Detailed information about nMDS and ANOSIM is given in Von Fumetti et al. (2007).

With the SIMPER-procedure dissimilarities between and similarities within groups can be explained with individual species and with the composition of the macroinvertebrate assemblages. Species discriminating groups contribute more or less consistently to the distinction of two groups and have a low ratio of the average dissimilarity (diss) and the standard deviation (SD). Species typical for a group highly contribute to the similarity within a group and have a consistent large presence (high ratio diss/SD).

The regression analysis was done with SPSS 14.0, all other statistical analyses were calculated using PRIMER 6.0 (Clarke & Gorley, 2006).

Results

Calibration experiments

After at least seven trials per temperature we revealed linear equations for each temperature regime using linear regression (Table 1). All linear regressions were highly significant (9°C - 11°C: p= 0.0001; 12°C: p= 0.003).

Table 1: linear regression of the calibration experiments at different temperatures

Temperature [°C]	n trials	linear equation	R^2	significance
9	8	$Y= 0.271x + 0.0741$	0.9742	0.0001
10	9	$Y= 0.260x + 0.0829$	0.9407	0.0001
11	9	$Y= 0.225x + 0.0888$	0.9454	0.0001
12	7	$Y= 0.166x + 0.0974$	0.852	0.003

Field data

The physical and chemical properties of the springs were only slightly different with a circum-neutral pH (6.8-8.5) and a moderately high conductivity (mean ± SD: 418 ± 98 µS cm $^{-1}$). The oxygen concentration was between 51 and 103 % (mean ± SD: 90 ± 8 %), the oxygen concentration ranged from 5.6 to 11 mg l $^{-1}$ (mean ± SD: 9.3 ± 1.5 mg l $^{-1}$). The temperature ranged from 5.9 °C to 14.1 °C. Q61 exhibited the highest, Q59 the lowest temperature amplitude (6.1 and 2.1, respectively) (Table 2).

Table 2: Minimum and maximum discharge (Qmin and Qmax, respectively), discharge amplitude (Qamp) in l/ min and minimum and maximum temperature (Tmin and Tmax, respectively) and temperature amplitude (Tamp) in °C. Extreme (highest and/or lowest) values in bold.

	Qmin	Qmax	Qamp	Tmin	Tmax	Tamp
Q62	0.0	32.9	32.9	**5.9**	12.2	5.3
Q59	0.0	23.6	23.6	**10.1**	12.2	**2.1**
Q3	0.0	**20.9**	**20.9**	6.9	**10.8**	3.9
Q61	0.0	61.5	61.5	8	**14.1**	**6.1**
Q4	**16.8**	**82.3**	**65.5**	10	13.5	3.5

In the field experiments, the highest discharge values were reached in Q4 and Q61 at the beginning of the experiment, just after the snowmelt (Fig. 2). At Aug_1 the discharge could not be measured in Q4 due to a heavy rainfall lasting several days, which flooded the spring. Overall, the discharge amplitude is highest in Q4 (16.8 – 82.3 l/min). Q3 and Q59 are the most constant springs (amplitude: 20.9 and 23.6, respectively), whereas Q61 also exhibits a relatively high discharge amplitude (61.5). The discharge of Q62 varies between 0.00 l/min and 32.9 l/min (Table 2). The zero values are caused by an extremely low weight loss of the gypsum spheres. As negative discharge values calculated from the linear regression are not possible, we set the actually negative discharge values to zero. Here, the discharge of the springs is negligibly small. The linear correlation of gypsum sphere degradation and the discharge of the springs was highly significant (p = 0.0001) (Table 3).

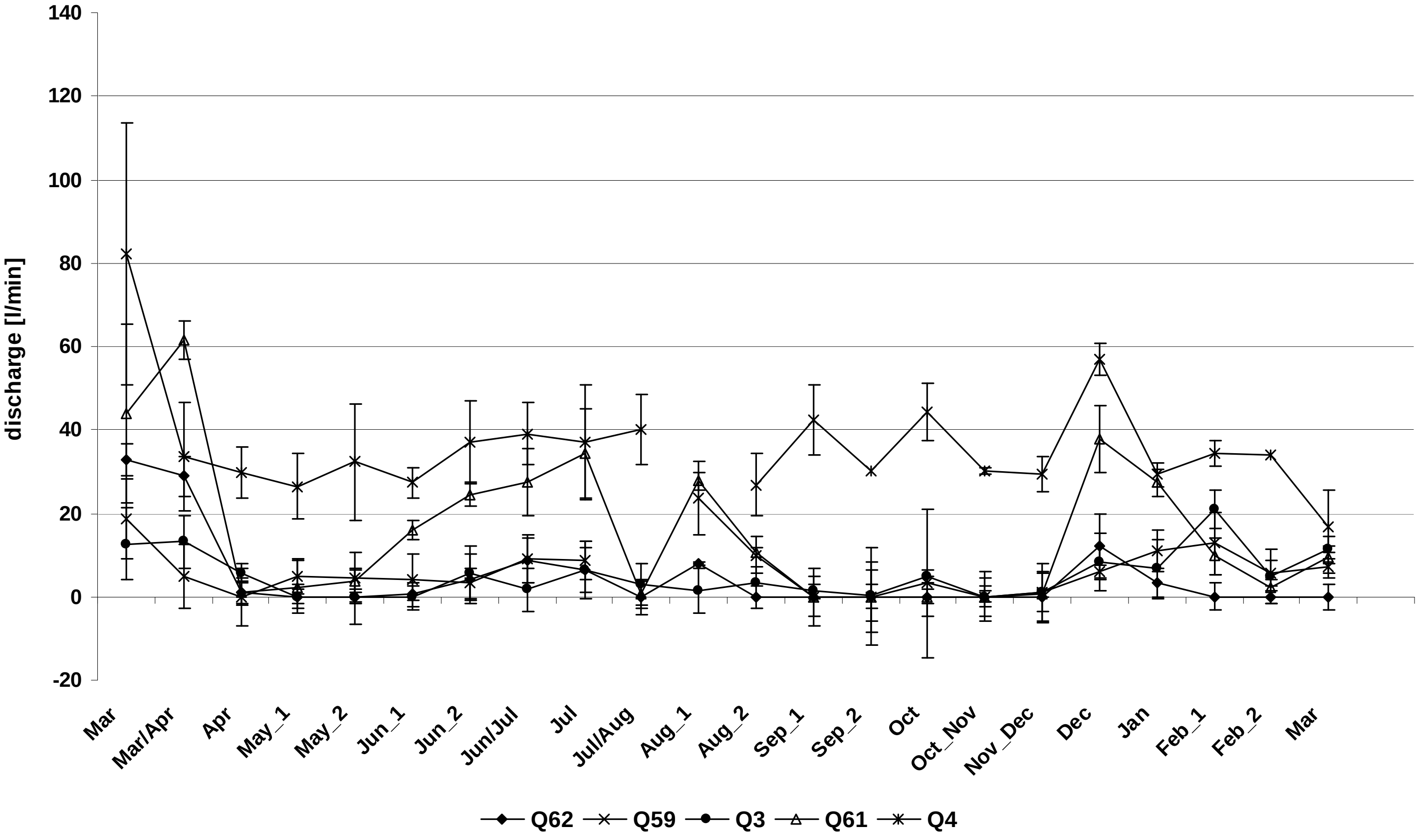

Fig. 2: Discharge of the investigated springs from March 2007 until March 2008 calculated from the regression equations of the calibration experiments

Table 3: Linear regression of the correlation degradation (independent variable) and discharge (dependent variable)

spring	n trials	linear equation	R^2	significance
Q62	22	y = 234.226x - 18.782	0.9581	0.0001
Q59	21	y = 308.63x - 28.568	0.9716	0.0001
Q3	22	y = 262.5x - 22.068	0.8531	0.0001
Q61	22	y = 232.26x - 19.287	0.9889	0.0001
Q4	21	y = 232.61x - 17.447	0.976	0.0001

At Q4, the comparison of the measured and calculated discharge revealed higher values via direct measurement with differences up to 60 l/min. Overall we find approximately the same tendency in the measured and calculated discharge values (Fig. 3)

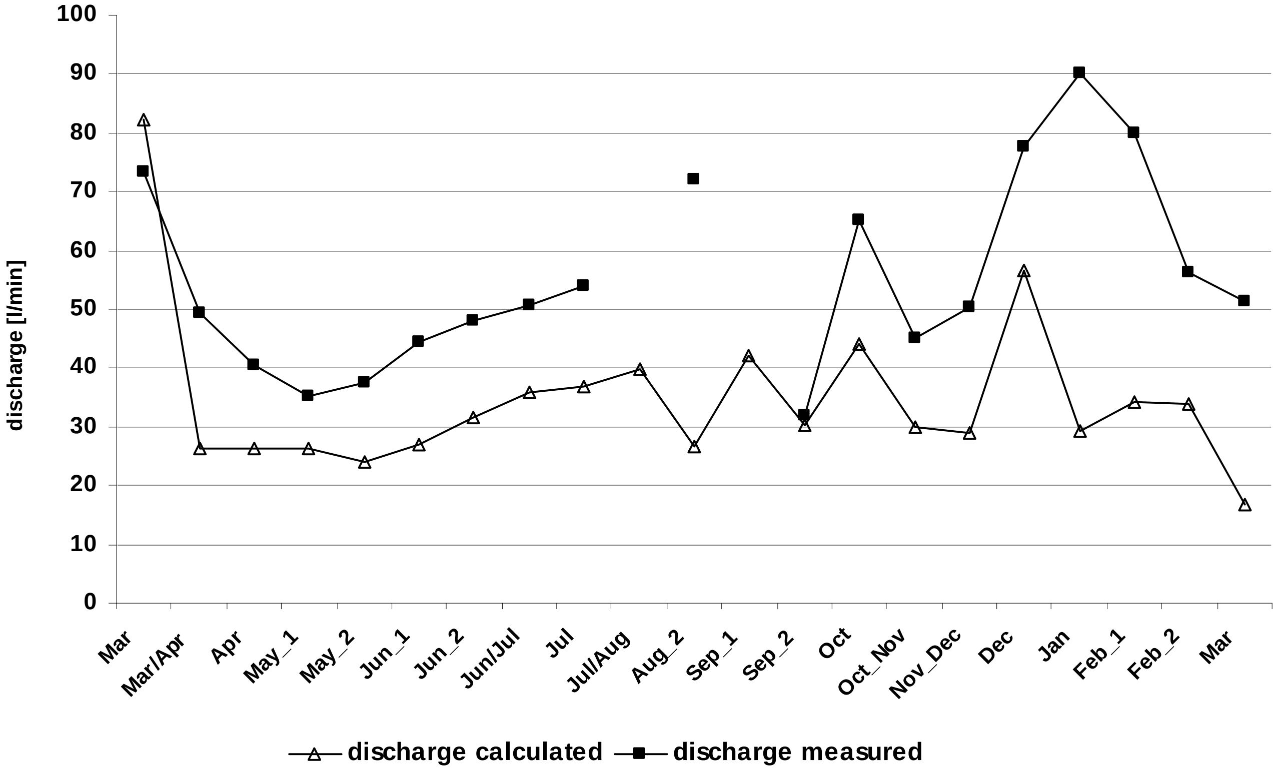

Fig. 3: Comparison of the calculated discharge from the regression equations of the calibration experiments and direct measurements of the discharge at Q4

Faunistic data

A total of 56 species and higher taxa, among them 11 Trichoptera species, were recorded from 120 samples. *Gammarus fossarum* Koch, 1835 was the most abundant, occurring in almost every spring in high densities. On average, 31 taxa were found in each spring (28-35). The average number of species per sampling varied between 12 (Q61) and 16 (Q3), the seasonal range of species numbers was highest in Q4 (8-19 species) and lowest in Q3 (14-19 species). The Shannon diversity was between 1.3 (Q61) and 1.9 (Q59). Margalef's index (d) and Pielou' s eveness (J') were also highest at Q59 and lowest at Q61. The seasonal samples of Q3 had the highest similarity (72.44 %), the seasonal samples of Q4 the lowest similarity (54.44 %) (Table 4).

The nMDS and the Anosim-procedure revealed a significant grouping of the springs using the macroinvertebrate data (Fig. 4). The seasonal samples of one spring were significantly more similar than the seasonal samples of different springs (R= 0.669, p= 0.001). We could also significantly distinguish between the springs with high discharge and temperature variability (Q4, Q61) and the springs with low discharge and temperature variability (Q3, Q59, Q62) (R= 0.328, p=0.001).

Table 4: Diversity parameters of the investigated springs. S_{av} = average number of species per seasonal sample, S_{sum} = overall number of species, N = abundance, d = Margalef' s index, J' = Pielou' s eveness, Sim. = similarity of all seasonal samples of one spring. Highest values in bold.

spring	**S_{av}**	**S_{sum}**	**N**	**d**	**J'**	**H'(loge)**	**Sim. [%]**
59	14	28	33.286	**3.948**	**0.723**	**1.898**	58.20
61	12	31	43.875	3.015	0.527	1.292	61.97
62	13	30	58.250	3.060	0.578	1.485	67.69
4	13	**35**	31.875	3.726	0.636	1.628	54.44
3	**16**	29	**66.625**	3.618	0.652	1.801	**72.48**

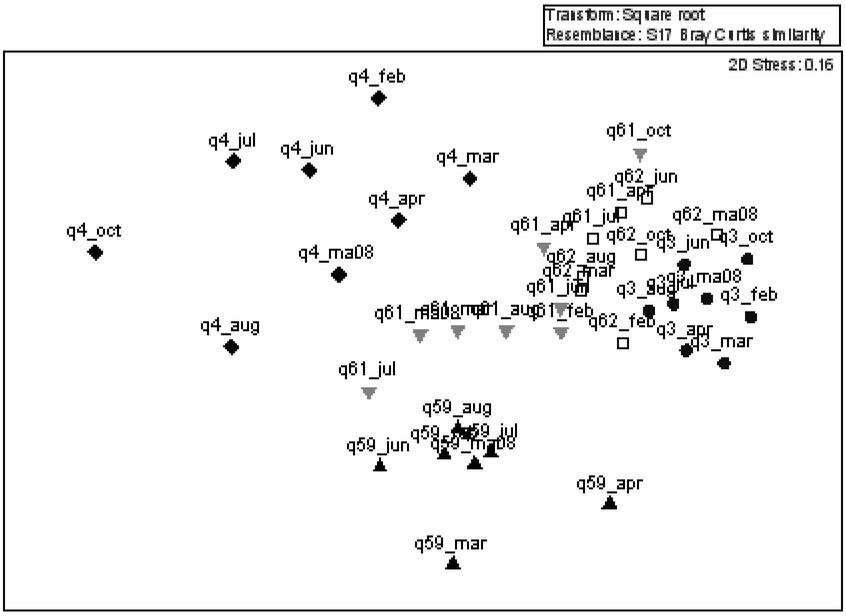

Fig. 5: Non-metric multidimensional scaling (nMDS) of the 5 investigated springs at different sampling occasions; similarity index: Bray-Curtis, transformation: square root; factor: spring; ▼ = Q61; ♦ = Q4; □ = Q62; ▲= Q59; ● = Q3; sampling occasions: mar: march 2007, apr: april 2007, jun: june 2007, jul: july 2007, aug: august 2007, oct: october 2007, feb: febuary 2008, ma 08: march 2008; analysis of similarities (ANOSIM): R= 0.669, p= 0.001

Discussion

In the past many studies found evidence that discharge influences the composition of macroinvertebrate assemblages in springs, either directly or indirectly by determining the substrate composition of springs (e.g. Smith, 2003; von Fumetti, 2006; Mori & Brancelj, 2006). Despite its importance the discharge measurement is often far from accurate as long as the springs are not piped, and many different techniques are used. At free-flowing springs, building a weir is the most exact method, but destroys the natural character of springs and is very time consuming. Zollhöfer (2000) used a plastic bag, which ideally had to cover the whole spring source area, and a stop watch. Other studies assessed the discharge in categories (Hoffsten & Malmqvist, 2000; von Fumetti, 2006) after the calibration at piped springs. Quantitative discharge measurements are hard to obtain. The salt dilution method from Engstrom-Heg (1971) had been used by Erman and Erman (1990) and Smith et al. (2003) used the standard velocity-area technique (Gordon et al., 1992).

The difficulty of quantifying water motion in general concerned researchers also in other fields of limnological research. Muus (1968) and Doty (1971) were the first who used gypsum bodies for assessing water motion in the brackish and tidal zone of coastal waters. In the 1990’s others improved the method and adapted it to other water bodies like the littoral of lakes (Petticrew & Kalff, 1991), coral reefs (Jokiel & Morrissey, 1993) and streams (Winterbottom et al., 1997; Angradi & Hood, 1998). Most of the studies had problems with the calibration and the interpretation of the data, as reviewed by Porter et al. (2000). The most critical part is an accurate calibration of the weight loss – discharge relationship before the use in the field (Porter et al., 2000). As springs flow at a rather steady rate we chose a flow channel for the calibration experiments. Connected to that is the question of which type of regression should be used for a weight loss – water flow correlation. In literature we find different regression types from polynomic (Arsenault et al., 1997), to exponential (Glenn & Doty, 1992) and most often linear (Petticrew & Kalff, 1991; Angradi & Hood, 1998; Porter et al., 2000). In our study, we found strong evidence for a linear relationship in our calibration experiments, and also demonstrated in field experiments. However, in future research it has to be considered that at a weight loss of the gypsum spheres of more than 30 % (Porter et al., 2000) a linear relationship is not given. Another critical point is the question what kind of water motion we are actually measuring with this method. The high standard deviations in some of the trials show that the exposure of each single sphere to the flow in the springs is very important and that the exposure to the flow and the flow itself is quite variable in springs. For future experiments it is therefore important to note the positions of the spheres in the springs and to monitor the water flow in the surrounding area. The lower calculated values in comparison to the direct measurements at the piped spring give an idea of the likely higher discharge values, although also the "plastic bag-method" is susceptible to handling problems. The linear regression of the weight loss – discharge functions of the springs was highly significant. We therefore recommend the gypsum dissolution method as a useful approach, also applicable for short-term measurement of one day or even shorter.

The influence of disturbance frequency and intensity on macrobenthic organisms have been widely discussed in freshwater research (e.g. Wotton, 1998; McCabe & Gotelli, 2000; Matthaei & Townsend, 2000; Thomson, 2002; Melo et al., 2003). In streams, highest diversity at most stable sites (Death & Winterbourn, 1995) have been reported as well as the high diversity at sites with intermediate disturbance intensity and frequency (Townsend et al., 1997). Here, the intermediate disturbance hypothesis (Connell, 1978) could be confirmed, whereas other studies found different, inconsistent results (Death & Winterbourn, 1995; McCabe & Gotelli, 2000). However, the important role of disturbance history for aquatic macroinvertebrates is not disputed, giving also a link to invertebrate patchiness (Townsend, 1989; Matthaei & Townsend, 2000; Melo et al., 2003).

First studies on disturbance events in springs confirm the findings of stream ecosystems with fewer species are found in disturbed sites (Myers & Resh, 2002). Fluctuations in discharge, and also stability of the abiotic features in general lead to lower species richness, especially in intermittent springs (Erman & Erman, 1995; Smith et al., 2003). This is consistent with the findings of Bonettini & Cantonati (1996), who had the highest diversity in springs with low flow variability. The springs in our investigation differed clearly in their discharge and temperature regimes. Some of them exhibited quite stable abiotic conditions while others showed higher amplitudes in discharge and/or temperature. Considering the faunal assemblages of the springs we can also see different degrees of similarity between the seasonal samples of one spring. In general, we can distinguish between springs with high variability in discharge and temperature and those with low variability in discharge and temperature. Considering these two abiotic factors as the important disturbance factors in springs we then have strongly disturbed and less disturbed springs. The highest species diversity was found in the two relatively undisturbed springs Q3 and Q59 and the lowest diversity has been found in a spring with high variability (Q61). Here, the spring species could not persist harsh environmental conditions and were seemingly not yet adapted to intermittent conditions. The stability of the abiotic features increases the constancy of diversity. The intermediate disturbance hypothesis (Connell, 1978) does not seem to fit easily for our spring ecosystems. However, on a broader scale including springs with even higher discharge amplitudes (e.g. intermittent and karst springs) we might have found springs with intermediate levels of disturbance having highest species diversity. Moreover, it is also the question, which species diversity measurement you chose for your investigations. Death & Winterbourn (1995) for example had highest species richness at the stable sides, whereas the eveness peaked at intermediate stability. If we only consider the species number, springs with high disturbance have a high species richness and the less disturbed springs have a low species richness. In the first case the disturbance events may open up space for new species after drought periods or floods and they may also be colonized by stream species, functioning as a refuge for such organisms (Smith & Wood, 2002). Low diversity at low frequency and intensity of disturbance can be due to competitive exclusion (Townsend et al., 1997), like the intermediate disturbance hypothesis

(Connell, 1978) proposes. But we lack any study on this topic in spring ecosystems at this stage.

For future research we have to consider that populations in perennial springs are unaccustomed to intermittent conditions and are therefore vulnerable to desiccation and loss of flowing water habitats in future (Smith & Wood, 2002). This could become problematic if more perennial springs dry out perhaps due to global climate change. The role of disturbance in springs is therefore underestimated and will become more important, if we take into account the anthropogenic influence on disturbance as described by Myers & Resh (2002). With the gypsum dissolution method we developed an easy to handle and reliable method for assessing short-term and medium-term discharge variability and therefore disturbance frequency and intensity in springs. This is a first important step for a monitoring of changes in the discharge regime of perennial springs due to global climate change.

Acknowledgements

We thank the Freiwillige Akademische Gesellschaft (FAG) from the University of Basel for funding the project. We acknowledge numerous people who helped with the fieldwork throughout the year. And we thank Simon Loader, who improved the language and had helpful comments on the manuscript.

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CHAPTER FIVE

Where a springhead becomes a springbrook — a regional zonation of springs

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Published in *Fundamental and Applied Limnology*, 169: 37-48, 2007

Abstract

Springs are important freshwater habitats that provide specific abiotic conditions for many species. These conditions may change very rapidly downstream. Limnologists tend to treat spring sources and their adjacent springbrooks as a unity because of the lack of clear criteria to separate these sections. In this study, we investigated the longitudinal distribution of macroinvertebrate assemblages in ten undisturbed springs in north-western Switzerland at three different distances from the source. Using non-metric multidimensional scaling and analysis of similarities, we detected significant differences between the macroinvertebrate assemblages of the investigated sections in all spring ecosystems, even over short distances. These results stress the importance of distinguishing between the sequential habitats in this upper region of headwaters. Although a complex of abiotic factors is responsible for the distribution of macroinvertebrates, we consider temperature to be of special importance. Based on our faunistic data, we propose that the rheocrene-like springs in the Jura Mountains consist of two sections: the springhead and the springbrook, with the springhead consisting of the source and the upper part of the adjacent downstream section. In accordance with literature and our faunistic and temperature data, we place the beginning of the springbrook at approximately 5 m from the springhead. With this distinction, we justify that springheads and springbrooks are unique, discrete ecosystems, and as such must be considered in conservation legislation.

Keywords: classification, streams stream invertebrates

Introduction

It is widely accepted that springs are freshwater ecosystems with relatively constant physicochemical conditions (Odum, 1971; van der Kamp, 1995; Cantonati et al., 2006). However, rapid changes downstream have been documented (reviewed by McCabe, 2000). The spring source was differentiated from its brook for the first time by Thienemann (1912), but the boundary was not defined exactly. Springs were later considered by Illies (1952, 1961) as one ecosystem, the crenal, with its downstream border at the point where the amplitude of the annual water temperature exceeds 5 °C. Illies & Botosaneanu (1963) defined the crenal as consisting of two sections: the spring as the eucrenal and the springbrook as the hypocrenal. More recently, the boundary of the eucrenal was defined as the point where the water temperature differs from the water temperature at the source by 2 °C (Erman & Erman, 1995).

In many limnological studies, the spring source and the springbrook have not been distinguished or their differentiation has not been consistent. Since the early 20th century, it has been known that springs are inhabited by specially adapted organisms, and there are many systematic and comprehensive studies on macroinvertebrates in springs (e.g. Thienemann, 1912; Nielsen, 1950; Williams & Danks, 1991). However, many publications lack information on where the faunistic or physicochemical samples had exactly been taken (e.g. Steinmann, 1915; Kühn, 1940; Cushing, 1996; Lindegaard et al., 1998). In other studies, samples were taken up to 100 m downstream from the source (Hoffsten & Malmqvist, 2000; Barquin & Death, 2004), a section which would have been defined as the springbrook by others.

Since we assume that the distribution of some species is restricted to the spring source, it should be questioned whether the proposed temperature gradient zonation is also reflected by the organisms. Most studies to date have considered species richness as the relevant parameter for answering this question (Resh, 1983; McCabe & Sykora, 2000; Orendt, 2000; Smith, 2002). Such results are often contradictory and hence a general pattern in the distribution of the species has not emerged.

In this study, we investigated the longitudinal distribution of the faunistic assemblages in ten springs in north-western Switzerland at different distances from the source using diversity measures and multivariate methods. Our goal was to detect zonation patterns for the definition of spring ecosystems in our region.

Materials and methods

Study sites

The study was conducted in three different catchment areas with a more-or-less karstic character, located around the city of Basel in northwestern Switzerland. All of the mostly rheocrene-like springs arise in forested areas, are very small (1–2 m2), and have low discharge (50 l/min).

Springs Q1–Q5 are located in the Röseren Valley, a rather undisturbed area in the Jura Mountains, with an average altitude of approximately 400 m above sea level. The geological underground mainly consists of limestone. All investigated springs have very short springbrooks of 45 m or less. They all flow into the Röserenbach, a small first-order stream of 3185 m length, at the lowest investigated spring, which itself flows into the Ergolz River. In this valley, Geijskes (1935) conducted a comprehensive study, and recent information is given in Baltes et al. (2006).

Springs Q6–Q8 are situated near the city of Basel on the Dinkelberg, which geologically belongs to the Jura Mountains. The springs are situated 450 m above sea level, and they all drain into the same headwater, which flows into the Rhine River. Despite their peri-urban location, the springs can be considered to be near natural. Springs Q9 and Q10 are located on the edge of the Jura Mountains at 400 m above sea level in cultivated forest. The ground consists of loess, and the springbrooks flow into the same headwater after 250 and 120 m (Table 1).

The average annual air temperature in the investigated area reaches approximately 9 °C. The average annual rainfall reaches 700 mm on the Dinkelberg and 1080 mm in the Jura Mountains (REKLIP, 1995).

Abiotic measurements

Simultaneously to macrofaunal sampling in March and October 2005, water temperature (°C), pH, conductivity (µS/cm), oxygen concentration (mg/l), and oxygen saturation (%) were recorded in the field using portable meters (Wissenschaftlich-Technische Werkstätten, Weilheim, Germany). Because of technical problems, conductivity could not be measured at every site. In November/December 2005 and in July 2006, the water temperature in all springs was again recorded, in steps of ≤10 m.

Table 1: Site description. spbr1: springbrook section 1; spbr2: springbrook section 2.

Site	Location (UTM coordinates)	Geographical setting	Spring type	Length of spring stream [m]	Sampling time	Sampling site	Average distance from source [m]
Q1	x: 401612.618636	Jura Mountains	Rheocrene	34	March 2005	Q1_source	3
	y: 5260977.71839					Q1_spbr1	30
						Q1_brook	37
Q2	x: 400980.354391	Jura Mountains	Alluvial spring	21	March 2005	Q2_source	3
	y: 5260615.40167					Q2_spbr1	18
						Q2_brook	22
Q3	x: 400979.853265	Jura Mountains	Rheocrene	40	March 2005	Q3_source	3
	y: 5260590.41198					Q3_spbr1	35
						Q3_brook	45
Q4	x: 401762.557817	Jura Mountains	Calcareous Rheocrene	25	March 2005	Q4_source	2
	y: 5260974.71163					Q4_spbr1	22
						Q4_brook	27
Q5	x: 400274.622289	Jura Mountains	Rheocrene	12	March 2005	Q5_source	2
	y: 5260329.55686					Q5_spbr1	8.5
						Q5_brook	12
Q6	x: 401006.906763	Dinkelberg	Rheocrene	500	March 2005	Q6_source	3
	y: 5269414.71892					Q6_spbr1	20
						Q6_spbr2	50
Q7	x: 401407.24118	Dinkelberg	Rheocrene	550	March 2005	Q7_source	3
	y: 5269431.68173					Q7_spbr1	20
						Q7_spbr2	50
Q8	x: 401349.737564	Dinkelberg	Calcareous Rheocrene	50	March 2005	Q8_source	3
	y: 5269057.84528					Q8_spbr1	15
						Q8_spbr2	30
Q9	x: 406803.649427	Jura Mountains	Helocrene	250	October 2005	Q9_source	5
	y: 5264273.54878					Q9_spbr1	20
						Q9_spbr2	50
Q10	x: 407399.386737	Jura Mountains	Rheocrene	120	October 2005	Q10_source	2
	y: 5264061.60886					Q10_spbr1	20
						Q10_spbr2	50

The temperature minimum, maximum, and amplitude, and the points at which the temperature exceeded the temperature at the source by 1 and 2 °C were calculated using these and additional data from former investigations in 2003–2005.

The substrate types moss, detritus, leaf litter, dead branches, leaf nests, roots, macrophytes, clay, sand, gravel, stones, and sinter of every macroinvertebrate sample were categorized into five frequency classes: 0: 0%; 1: 1–25%; 2: 26–50%; 3: 51–75%; and 4:

76–100% (Von Fumetti et al., 2006). Because of the three-dimensional structure of the streambed, the percentages of the substrate types per macroinvertebrate sample usually added up to >100%.

Faunistic sampling

Macroinvertebrates were quantitatively collected with a small surber sampler (0.01 m2, 500-µm mesh width) according to Von Fumetti et al. (2006). Owing to our focus on macroinvertebrates, meiofauna and minute groundwater species were collected only accidentally. Since we used the same sampling method for all samples, we did not exclude these species from the statistical analysis. In March 2005, four replicates were sampled: 1) from each spring at the source, 2) at approximately 20 m from the source, and 3) at a lower section of the springbrook not exceeding 50 m (Table 1). For technical reasons, only three replicates were taken at the source in spring Q7. Springs Q9 and Q10 were sampled in October 2005. Because of the short length of the springbrooks in the Röseren Valley, the third section was located in the receiving brook (Röserenbach). Since springs Q1 and Q4 as well as Q2 and Q3 are adjacent, their third sections in the Röserenbach were identical. To confirm our results obtained in 2005, an additional, detailed sampling was conducted in July 2006 in springs Q4, Q6, and Q10 in four sections: 0–5 m from the source, 5–10 m from the source, 10–15 m from the source, and 15–20 m from the source.

After separation of Turbellaria for live identification, all samples were immediately preserved in 70% ethanol in the field and subsequently sorted and determined in the laboratory. Taxonomically demanding Dipteran groups (e.g., Chironomidae) were identified to the family level; all others were identified to the most accurate taxonomic level (see supplementary material).

Statistical analyses

All statistical analyses described below were calculated using PRIMER 5.0 (Clarke & Warwick, 2001). Species richness (taxa per section), abundance (ind./m2), the Margalef index (d), and the Shannon diversity index (H’) were calculated for every section.

Ordination of the springs was conducted using non-metric multidimensional scaling (nMDS). With nMDS, the similarity index can be chosen freely, and only ranks are compared; it does not assume normal distribution. Distances between springs are relative and illustrate similarities between samples. The latter were analyzed using the analyses of similarities (ANOSIM) procedure, which is analogous to ANOVA, but relies on a similarity matrix and makes few assumptions on data. This procedure does not require the exclusion of rare species (Clarke & Warwick, 2006). The higher the global R value (between 0 and 1), the larger are the differences between samples. For faunistic data, the Bray-Curtis similarity and a log (x+1) transformation were used. Substrate data were not transformed, and the Euclidian distance was used as distance measure. For testing element-by-element correlations of faunistic and substrate similarity matrices, the RELATE routine was used. This significance test is known as the Mantel test in statistics, and examines how closely related two similarity matrices are (ρ between 1 and –1). It can also examine whether an observed order of samples is a result of seriation, with the locally closest samples being the most similar in their composition.

Results

Abiotic characteristics

When macrofauna were sampled, the water temperature at the sampled sections ranged from 7 to 14.3 °C (mean ± SD: 9.9 ± 1.6 °C). The pH was circumneutral in almost every springbrook (5.5–8.4, median: 7.7); only one spring tended to slight acidity. The conductivity was between 85 and 844 µS/cm (409 ± 162 µS/cm). The oxygen concentration and saturation ranged from 4.1 to 11.3 mg/l (9.6 ± 1.6 mg/l) and from 38 to 101% (88.9 ± 13.5%), respectively.

In some springbrooks, the temperature varied little; in others, the temperature varied greatly throughout 2003–2005 (Table 2). The temperature amplitude was between 1.8 and 17.3 °C, with the highest amplitude calculated for spring Q10, a helocrene. The amplitude exceeded 5 °C at five of the ten spring sources. The 2 °C border between the spring and the spring stream (Erman & Erman, 1995) varied from 3.5 m up to over 50 m. The point at which the water temperature differed from the temperature at the source by 1 °C was between 1.7 m and up to over 50 m. These borders varied in each spring throughout a year (Table 2).

Table 2: Temperature parameters of the investigated springs. Tmin and Tmax are from measurements throughout 2003–2006. The 1- and 2-°C borders were calculated from measurements during faunistic sampling and along the springbrooks in March 2005, November/December 2005, and July 2006.

Site	T_{min} at source (°C)	T_{max} at source (°C)	Amplitude at source	1 °C border (m)	2 °C border (m)
Q1	9.8 (Dec. 03)	12.1 (Sep 04)	2.3	4, 25, >34	11.5, >34
Q2	7.3 (Nov. 05)	12.3 (July 06)	5.0	3.5, >21.5	5, >21.5
Q3	8.0 (March 05)	10.5 (Sep 04)	2.5	2.3, 3.9, >45	5, >45
Q4	6.9 (March 04)	12 (Sep 04)	5.1	9, 11.5, 23.6	13, >25.5
Q5	8.3 (March 05)	10.5 (Aug 04)	2.2	4.5, 7, 7.7	8, >12.5
Q6	6.7 (March 04)	12.4 (Oct. 04)	5.7	8.8, 12.5, 20.5	17, 24, 25
Q7	6.2 (March 04)	10.5 (Oct. 04)	4.3	1.7, 2.7, 50	3.5, 14, >50
Q8	8.0 (April 05)	9.8 (Oct. 04)	1.8	11.5, 16.3, >30	16.5, 23.3, >30
Q9	1.5 (March 04)	18.8 (July 06)	17.3	12.5, >50	20, >50
Q10	4.2 (March 04)	11.2 (Oct. 03)	7	8.8, 11.8, 12.6	18, 21, 35

Faunistic assemblages and diversity patterns

Altogether, we identified 90 species and higher taxa. At the spring sources, we found 56 species and higher taxa in our samples, with *Apatania eatoniana* MCLACHLAN, 1880, *Atractides pennatus* (K. VIETS, 1920), *Satchelliella mutua* (EATON, 1893), *Thaumalea testacea* RUTHÉ, 1831, and a few others restricted to this section. The crenobiont species *Crunoecia irrorata* (CURTIS, 1834) was also abundant up to 50 m downstream from the source in some springbrooks. At approximately 20 and 50 m from the source, we found 60 and 49 species and higher taxa, respectively. Ephemeroptera and also some Coleoptera, e.g., *Riolus cupreus* (P.W.J. MÜLLER, 1806), occurred in higher abundances in the lower sections. Ephemeroptera did not occur at the sources.

There was no indication (see Table 2 and Supplementary Material) for a correlation between the occurrence of the so-called crenobionts and the annual temperature amplitude. The number of taxa and the abundance in every section differed greatly and showed no general patterns (Table 3). No strong trend for the Margalef index and the Shannon diversity index was detected. In one spring, both indices decreased downstream, whereas in another stream, they were both highest in the springbrook at 20 m from the source. Overall, the Shannon diversity index decreased downstream in six of the ten springs.

Table 3: Diversity parameters at the investigated sections. spbr1: springbrook section 1; spbr2: springbrook section 2.

Site	N (taxa/ section)	Abundance (ind/ m^2)	Margalef index (d)	Shannon diversity (H’)
Q1_source	11	4400	1.192	1.605
Q1_spbr1	12	4275	1.316	1.342
Q1_brook	21	11775	2.134	0.873
Q2_source	17	4825	1.886	2.017
Q2_spbr1	11	4825	1.179	1.269
Q2_brook	18	9625	1.853	1.038
Q3_source	16	2550	1.912	1.799
Q3_spbr1	8	1550	0.953	1.472
Q3_brook	18	9625	1.853	1.038
Q4_source	9	5157	0.936	1.861
Q4_spbr1	10	2750	1.136	1.442
Q4_brook	21	11775	2.134	0.873
Q5_source	16	4100	1.803	1.847
Q5_spbr1	15	3350	1.725	2.126
Q5_brook	15	4200	1.678	1.497
Q6_source	16	9700	1.634	1.974
Q6_spbr1	17	14225	1.673	1.789
Q6_spbr2	12	6675	1.249	0.827
Q7_source	18	7825	1.896	1.611
Q7_spbr1	16	5025	1.76	1.504
Q7_spbr2	10	2625	1.143	1.335
Q8_source	14	7433	1.458	1.062
Q8_spbr1	11	5925	1.151	0.862
Q8_spbr2	11	8075	1.112	1.156
Q9_source	20	11050	2.041	2.223
Q9_spbr1	24	5525	2.669	2.55
Q9_spbr2	19	5250	2.101	2.362
Q10_source	12	4425	1.31	1.016
Q10_spbr1	12	3800	1.335	1.313
Q10_spbr2	13	2250	1.555	1.617

Within the faunistic data, we can clearly differentiate the sampled sections in most of the springs in multidimensional space, and the ANOSIM procedure proved overall significant differences between the sections (Fig. 1). In five springs, all sections differed significantly from each other; in two springs, the differences between the spring source and the upper part of the springbrook were not highly significant; and in two springs, the springbrook sections could not be significantly separated from each other. In spring Q5, only the receiving stream, the Röserenbach, could be significantly differentiated from the spring source section. Here, the springbrook only extended 12.5 m before entering the Röserenbach. For springs Q1–Q4, the significant changes in the macroinvertebrate assemblages from the middle to the lowest section are caused by the transition to the receiving stream. At spring Q5 the receiving stream is still very small and is a springbrook itself.

The RELATE procedure showed that, in eight of ten springs, the distribution of the fauna was a result of spatial seriation and that locally adjacent samples were more similar to each other than to more distant samples. Only in two springs was the distribution of the fauna also significantly correlated with the substrate data (Table 4). In our data set, the differences between the macroinvertebrate assemblages in the sections were not a result of changing substrate composition along the springs.

Table 4: Element-by-element correlation of faunistic and substrate similarity matrices and correlation of the faunistic similarity matrices as a result of seriation (RELATE, Clarke & Warwick 2001); ρ between 1 and –1.

	Relate (Substrate)		Relate (Seriation)	
Site	ρ	Sign.level	ρ	Sign.level
Q1	0.372	0.007	0.686	0.001
Q2	0.386	0.008	0.693	0.001
Q3	0.242	0.045	0.358	0.008
Q4	0.709	0.002	0.559	0.001
Q5	0.148	0.114	0.32	0.018
Q6	0.337	0.005	0.616	0.001
Q7	0.342	0.014	0.666	0.001
Q8	0.309	0.04	0.53	0.001
Q9	0.108	0.263	0.33	0.022
Q10	0.042	0.369	0.551	0.002

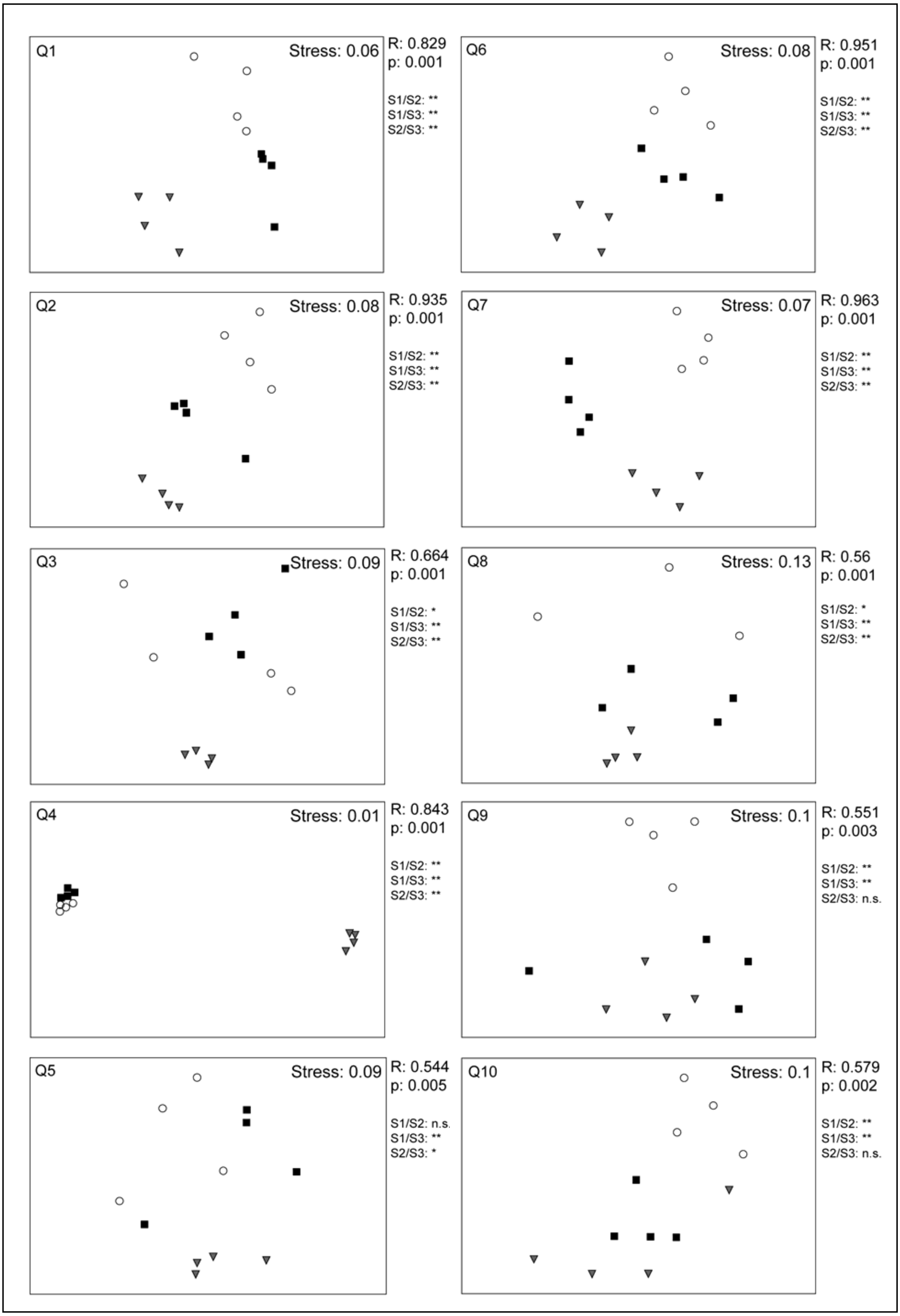


Fig. 1: Non-metric multidimensional scaling and analysis of similarities (ANOSIM) of the sampled sections of the ten investigated spring streams (Q1–Q10) based on the faunistic data. Similarity index: Bray-Curtis; transformation: log (x+1); factor: spring section; ○ = S1: section 1 (at source); ■ = S2: section 2 (first springbrook section); ▼= S3: section 3 (second springbrook section or stream section).

On the additional sampling date in July 2006, the faunistic assemblages in spring Q4 did not differ significantly in the four investigated sections (Fig. 2), and *Thaumalea* spp. occurred up to 20 m downstream from the source. Overall significant differences between the sections were detected for springs Q6 and Q10. In spring Q6, the upper 5 m could be significantly separated from the lower sections. The differences from 5–10 m to 10–15 m and from 5–10 m to 15–20 m were not highly significant. While *Satchelliella mutua* was restricted to the upper 5 m, *Thaumalea* spp. still occurred up to 20 m downstream from the source.

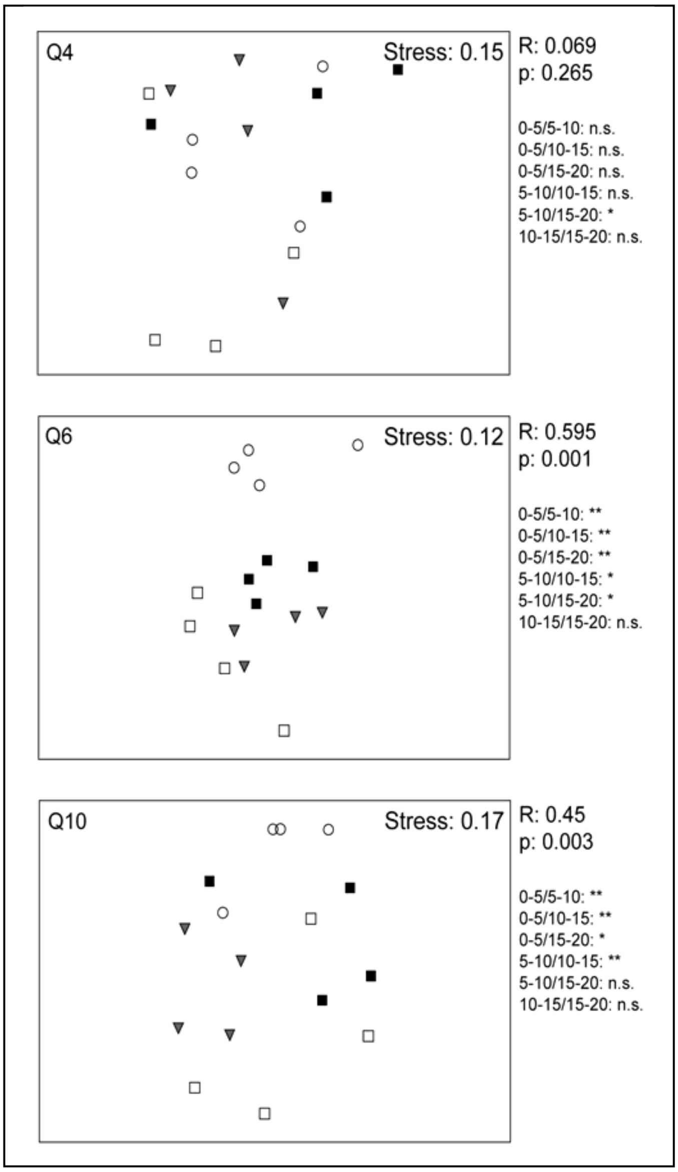


Fig. 2: Non-metric multidimensional scaling and ANOSIM of the additional sampling at springs Q4, Q6, and Q10. ○ : 0–5 m; ■: 5–10 m; ▼: 10–15 m; □ : 15–20 m.

In spring Q10, the differences from 0–5 m to 5–10 m, from 0–5 m to 10–15 m, and from 5–10 m to 10–15 m were highly significant, and the differences between 0–5 m and 15–20 m not highly significant. The differences between the lower sections were not significant. *Crunoecia irrorata* occurred up to 15 m downstream from the source. No general patterns could be detected for the diversity parameters. Again, the Shannon diversity index seemed to be higher directly at the source (Table 4). The RELATE procedure showed only for spring Q6 that the distribution of the fauna was a result of spatial seriation. In spring Q10, there was a slight correlation of the faunistic and the substrate data (Table 5).

Table 5: Diversity parameters and RELATE procedure (Clarke & Warwick 2001) of the additional faunistic sampling in July 2006; ρ between 1 and –1.

	Diversity parameters				RELATE (Substrate)		RELATE (Seriation)	
Site	N (taxa/ section)	Abundance (ind/ m^2)	Margalef index (d)	Shannon diversity (H')	ρ	Sign.level	ρ	Sign.level
Q4_0-5	8	5200	1.772	0.839	0.107	0.164	0.132	0.103
Q4_5-10	9	6450	1.92	0.774				
Q4_10-15	9	9975	1.738	0.525				
Q4_15-20	9	6725	1.901	0.304				
Q6_0-5	8	1425	2.635	1.214	0.208	0.035	0.691	0.001
Q6_5-10	12	3100	3.203	1.352				
Q6_10-15	10	2500	2.796	1.37				
Q6_15-20	11	1250	3.96	1.488				
Q10_0-5	8	1050	2.977	1.534	0.431	0.001	0.19	0.058
Q10_5-10	8	3000	2.058	0.789				
Q10_10-15	12	5900	2.698	0.724				
Q10_15-20	12	5200	2.784	0.679				

Discussion

Zonation patterns have been an important aspect of freshwater research, not only since the publication of the river continuum concept (Vannote et al., 1980). Emphasis has been placed on streams and rivers (e.g. Habdija et al., 2002; Arscott, 2003), but there are also a few investigations on first-order streams (e.g. Meffe & Marsh, 1983; Resh, 1983; McCabe & Sykora, 2000). While the rhithron-potamon concept of Illies (1961) is widely established, the zonation of the uppermost part of streams — the crenal according to Illies (1952) — has only sometimes been the focus of research.

Since the early 20th century, springs have been recognized as locally very restricted habitats with specific abiotic conditions (Thienemann, 1925; Odum, 1957; Van der Kamp, 1995). The first comprehensive studies began in the first decades of the 20th century, many of them conducted by Thienemann (e.g. 1912, 1924, 1926). These studies were mostly descriptive, but he already differentiated between the spring and the springbrook and described the parts in detail. Illies (1952) introduced the concept that the crenal ends where the annual temperature amplitude exceeds 5 °C. Illies & Botosaneanu (1963) split the crenal into the eucrenal and the hypocrenal. Erman & Erman (1995) defined the boundary between the spring and the springbrook as the point at which the temperature exceeds the temperature at the source by 2 °C. The latter has never been further investigated, but has often been cited (Orendt, 2000; Smith et al., 2003; Mori, 2006), and it is the only definition for the lower boundary of a rheocrene spring.

Although the temperature at spring sources is relatively constant in comparison to other freshwater habitats (Nielsen, 1950; Illies, 1952), temperature-based concepts of the crenal are problematic because the defined borders vary from spring to spring or throughout the year or even do not exist in some springs. Even Thienemann (1912), Beyer (1932), and Kühn (1940) detected fluctuations of the water temperature at the source; in some springs, fluctuations exceeded 5 °C within a year. In our study, five morphologically diverse springs located in different catchment areas showed amplitudes higher than 5 °C. The definition of Illies (1952) is only valid for springs with constant discharge, fed by deep groundwater (Fischer et al., 1998). The 2 °C border (Erman & Erman, 1995) varied greatly among the springs we investigated. Even more important than the variance among springs is the annual variance of the 2 °C border along a springbrook; in some springs, we observed a longitudinal shift of the 2 °C border of 20 m or more. No other studies recording the temperature along upper stream sections at distinct points have been published. These serious difficulties minimize the significance of the definition of Illies (1952) and Erman & Erman (1995).

It is widely accepted that many species in springs are cold stenothermic organisms (Nielsen, 1950; Fischer, 1996; Fischer et al., 1998; Zollhöfer, 1999). The temperature regime of a spring will therefore definitely be of relevance to their longitudinal distribution. Some species are without a doubt restricted to the spring source (Gerecke et al., 1998; Ferrington et al., 1995; Di Sabatino et al., 2003), e.g., *Bythinella* spp. in our study. Other organisms seem to be highly variable in their longitudinal distribution through time and space. They might migrate with varying temperature, depending on the specific temperature regime of an individual spring. Even so-called crenobionts, such as *Crunoecia irrorata* and *Thaumalea testacea*, occurred in lower parts of the investigated springbrooks up to 50 m downstream. Only comprehensive autecological studies would show how strongly some species are adapted to the source. *Crenobia alpina* (DANA, 1766), for example, can only reproduce under cold stenothermic conditions, but is also restricted in its distribution through interspecific competition with *Polycelis felina* (DALYELL, 1814) (Lock & Reynoldson, 1976; Williams & Williams, 1998).

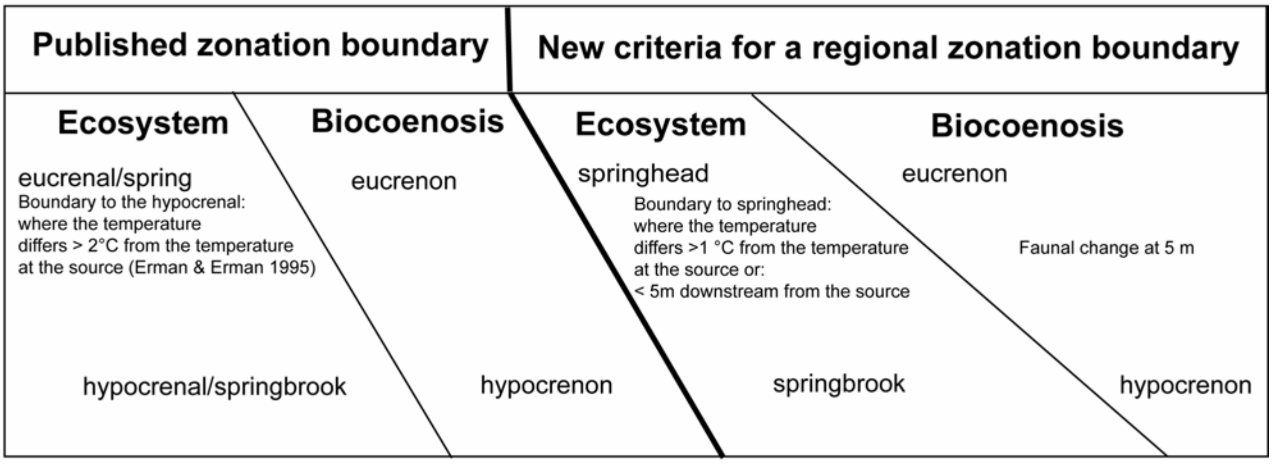
In our study, significant changes in the composition of species assemblages along the springbrooks were detected in all springs. These differences were not caused by changing substrate composition, which would result from changing discharge as a superordinate factor influencing species distribution in springs (Von Fumetti et al., 2006). Changes in discharge and therefore substrate composition were probably responsible, however, for the sharp transition from the springbrook to the Röserenbach in springs Q1–Q4.

Following the intermediate disturbance hypothesis (Connell, 1978), we would expect lower diversity at the source owing to the constant abiotic conditions in springs. While Resh (1983) recorded a decrease of species diversity downstream, others described the opposite (Ward & Dufford, 1979; Meffe & Marsh, 1983; Smith, 2002) or highest species diversity at an intermediate distance along the springbrook (Sloan, 1956; McCabe & Sykora, 2000). In the ten springs investigated, we detected no general patterns of species diversity, but the Shannon diversity index and the Margalef index tended to decrease downstream. This could be caused by the calcareous sinter found in many springs a few meters from the source, but not directly at the source. Zollhöfer (1999) pointed out that these hostile sections do not provide appropriate habitats for many species. Since we could not find any general trend for all springs, we assume that the diversity patterns depend on many factors, including nutrient input, time of sampling, and the location of the spring.

Although the thermal boundary of the spring source area sensu stricto is highly variable throughout time and space and cannot be defined satisfactorily, our faunistic data stress the importance of differentiating this upper part of a spring from the springbrook. It is undisputed that the eucrenal of helocrenes and limnocrenes ends where a channel forms (Gerecke et al., 2005). In the helocrene we investigated, the upper section was significantly separated from the springbrook. For springs that immediately form a channel— rheocrenes in the widest sense — and for all other morphologically different springs, we still must estimate the longitudinal extent of the eucrenal.

Based on our faunistic data, we propose that the typically small, rhoecrene-like springs in the Jura Mountains reach 5 m downstream from the source. We assume that a complex of abiotic factors determine the distribution of macroinvertebrates in springs and springbrooks (Fischer, 1996), but we are certain about the important role of temperature and especially temperature stability because of the results of numerous studies on temperature in springs and because of the lack of data refuting such an important role. Furthermore, in accordance with Glazier (1991), Erman & Erman (1995), and our own results, we propose that a rheocrene-like spring in the Jura Mountains consists of two sections: the springhead (= eucrenal) and the springbrook (= hypocrenal), with the springhead consisting of the source and the upper part of the adjacent downstream section varying <1 °C from the temperature at the source and the springbrook starting at the point where the temperature differs by > 1 °C from the temperature at the source (Fig. 3). In most of the springs studied here, this point was at least 5 m from the source, and we recorded significant changes in the macroinvertebrate assemblages in this range. For practical field work, we recommend that samples should be taken in an area where the temperature does not differ more than 1 °C from the temperature at the source. This can be easily measured in the field.

Fig. 3: New criteria for a regional zonation boundary of rheocrene-like springs.



With this proposal, we justify the observation that springheads are inhabited by distinct species assemblages that differ significantly from those in springbrooks. This is consistent with the finding that main changes in the macroinvertebrate assemblages occur in the first 5–10 m after the source.

Although our survey was only regional, the results can also be applied to other regions in Central Europe. For conservation aspects, we must consider that springheads and springbrooks are discrete ecosystems, and as such they must be protected in the future and addressed in conservation legislation.

Acknowledgements

We thank the Freiwilligen Akademischen Gesellschaft (FAG) from the University of Basel for funding this research. We acknowledge numerous people who helped with the fieldwork. We thank Peter Martin for identifying Acari and Rüdiger Wagner identifying Psychodidae. We also thank Nicole Scheifhacken, Karen Brune and two anonymous reviewers, who improved the English and made helpful comments on the manuscript.

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CHAPTER SIX

General discussion and conclusion

Despite a long history of spring research there are still considerable gaps in our knowledge, particularly concerning the abiotic factors influencing the distribution of spring species.

A one-year survey on the chemical, physical and substrate features and the macroinvertebrate assemblages in springs showed that springs exist along a continuum of a range of ecomorphological forms of appearance. The classic ecomorphological spring typology of Steinmann (1915) and Thienemann (1924) and the classification of Zollhöfer (1999) were not applicable to the springs we investigated. However, we could significantly distinguish species assemblages and the substrate composition of springs with a low discharge from those springs with a very high discharge. These results show that the classic ecomorphological typologies are not sufficient for the classification of small, perennial springs occurring in low range mountain regions in Central Europe and that the discharge regime is of special importance for the species assemblages in springs.

Classifying springs is a topic that still concerns researchers and there are some recent promising approaches (Gerecke, 1991; Williams et al., 1997; Hahn, 2000; Zollhöfer et al., 2000) to refine the ecomorphological spring typology of Steinmann (1915) and Thienemann (1924). Our first study had shown that these ecomorphological typologies are not applicable to the small spring we find in the Swiss Jura Mountains. Classifications of springs based on other measures, such as species composition do not yet exist and have a good potential. We therefore aimed to differentiate distinct spring types a priori on the basis of faunistic data. We developed a spring typology on the basis of functional groups dominating in a lenitic or lotic environment and on the basis of key species. After refining this faunistic spring typology with studies in other parts of Switzerland and adjacent regions (e.g. Black Forest, Vosges) we expect to have a typology applicable to all regions in Central Europe, and not only restricted to specific regions.

Springs are assumed to be stable ecosystems, not influenced by disturbance events. In our first survey we identified in accordance with other studies (e.g. Bonettini & Cantonati, 1996; Smith et al., 2003) that discharge was the decisive factor determining the distribution of the macroinvertebrate assemblages. Discharge variability is a disturbance factor that significantly influences species assemblages in springs, and should be measured accurately in future spring studies. As there is still no standardized method for measuring this important parameter, we applied the gypsum dissolution method (Muus, 1968; Doty, 1971) to springs as a new approach for this measurement. Based on this, we now have the possibility to measure discharge variability on a short-term and mid-term scale. From our results we conclude that the influence of disturbance has been underestimated in springs and it will get more attention if the climatic conditions in Central Europe continue to change and get less stable. Consequently, perennial spring ecosystems responding relatively quickly to heavy rainfalls or drought periods are especially endangered ecosystems. In karst springs in narrower sense the species are mostly adapted to the frequent intermittent situations, in perennial springs they are usually not. The challenge for future research will be in establishing the gypsum dissolution method as a standard approach in spring ecology. And it will be of help in future for refining the faunistic typology concept and for assessing the impact of discharge variability, especially in terms of global change, going along with increasing variations in precipitation.

The boundaries between the eucrenal and the hypocrenal postulated by Illies (1952), Illies & Botosaneanu (1963) and Erman & Erman (1995) have not been questioned, despite weaknesses of the thermal zonation. Our investigation in three different catchments in the Swiss Tabular Jura Mountains shows that the actual spring, the springhead, is limited to only a few meters. The basis of our definition is the change in species assemblages and thermal stability. Unstable abiotic conditions mark the beginning of the springbrook. As a consequence, we can confirm that thermal stability is one of the most prominent features of spring ecosystems. This feature again underlines the unique character of springs. Therefore spring ecosystems should be considered as distinct ecosystems, and afforded protection in conservation legislation.

The thesis presented here gives us a new insight into the fundamental processes that determine the composition and distribution of spring species assemblages. With our investigations we gained evidence that springs are indeed unique and discrete ecosystems, offering thermal stability for characteristic species assemblages or even communities. The discharge variability is the most important disturbance factor influencing species diversity in springs. Discharge will have to be monitored in future research because of expected increases in its variability. Identifying key species for autecological studies that could verify the postulated cold-stenothermic character of krenobionts will also be of special importance for future research. Lastly, genetic investigations will also help to understand the biogeographic and phylogenetic history of spring species.

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SUMMARY

Springs are unique ecosystems at the interface between groundwater and surface water and are said to provide relatively stable abiotic conditions for the species that live there. Despite numerous studies on spring ecology there are still substantial gaps in our knowledge about the functioning of spring ecosystems. Important hypotheses concerning the abiotic stability and the longitudinal extent of springs first described by August Thienemann have never been questioned. Therefore, the goal of this thesis was to revise the dogmas of spring research and to give answers to unresolved questions concerning the composition and distribution of spring species assemblages.

A widespread survey on the chemical, physical and substrate parameters of springs and their influence on the macroinvertebrate assemblages was the first step of the thesis. A nonmetric multidimensional scaling and an analysis of similarities did not reveal a grouping of the springs, neither with the faunistic data nor with the physicochemical and substrate data. However, it was possible to identify that discharge of the springs was the factor that significantly influenced the composition of macroinvertebrate assemblages. The traditional ecomorphological spring typology of August Thienemann is not applicable to the remaining small springs found in the Swiss Jura Mountains that we investigated. We therefore propose to regard springs as existing on a continuous scale of ecomorphological appearance. In consequence the development of a new spring typology based on faunistic parameters and not on the ecomorphological features of springs was the next important goal of the thesis. We took faunistic data collected over three years from springs in our main research area, the Röseren valley. An analysis of similarities and the SIMPER-procedure revealed a grouping of the springs based on the faunistic data, especially on the functional feeding groups and key species characteristic for those springs. Considering that springs occur on a continuous scale we have a continuum of springs from a lenitic to a lotic environment characterized by typical species assemblages.

Our first general survey has shown gaps in our knowledge about the zonation of upstream sections of headwaters. The longitudinal extent and boundary of springs are still discussed in spring research and there are still unresolved questions. We examined the longitudinal zonation of the macroinvertebrate assemblages and the substrate composition in the first 100 meters of three headwater catchments. We could significantly differentiate the springhead section from the springbrook section independent of the substrate composition. A significant change in the composition of the macroinvertebrate assemblages occurred just five meters from the source. In accordance with our temperature measurements and many other studies, we support the hypothesis that temperature stability is one of the most important factors for the distribution of spring species. The springhead as the actual spring can be differentiated from the springbrook and should be considered as a distinct ecosystem in future research.

Springs are said to exhibit stable abiotic conditions in comparison to lower sections of headwaters. Disturbance events have traditionally not seemed to be relevant for explaining the composition of macroinvertebrate assemblages in springs, and it is still a controversial topic in spring research. Because we identified discharge as an important factor for explaining the composition of macroinvertebrate assemblages in springs we consider discharge variability as a disturbance factor highly relevant for understanding spring ecosystems. To verify this hypothesis a scientifically reliable and easy to handle measurement of the discharge is necessary. We applied the gypsum dissolution method developed for oceanic habitats to springs. During a one year period gypsum spheres were exposed in five natural springs in the Swiss Tabular Jura 22 times for six day-periods on average. After a rigorous calibration in the laboratory the calculation of the discharge in the springs was possible. In addition, seasonal faunistic samples had been conducted to investigate the impact of the discharge variability on the spring species diversity. Our results show that there is a relationship between discharge variability and species diversity, a clear correlation as described in the intermediate disturbance hypothesis was not detected. The gypsum dissolution method is an adequate method for measuring the discharge of springs in short-term and mid-term periods. This is of importance for future research, when discharge variability will increase due to climatic change.

With this thesis we are now able to give answers to some of the fundamental questions in spring ecology and provide new insight into the functioning of springs. Springs have to be considered as distinct ecosystems with a longitudinal extent restricted to only a few meters from the source and inhabited by characteristic macroinvertebrate assemblages. They are adapted to the thermally stable environment and their composition is influenced by the discharge regime of the springs. Given predicted global climate change effects, the monitoring of the discharge variability could be an important indicator, and a focus of future research.

ACKNOWLEDGEMENTS

I am very grateful to the former program Mensch - Gesellschaft - Umwelt (MGU) of the Cantone Basel-Landscape that made the spring project “Quellen – Trinkwasserspender und Lebensraum” possible and I thank the Freiwillige Akademische Gesellschaft Basel (FAG) for funding the start of my PhD-thesis.

Many thanks go to Prof. Dr. Peter Nagel for his support in every respect.

I thank Prof. Dr. Carl Beierkuhnlein for taking over the co-report.

I thank all my former colleagues of the MGU-project for a very good team work during and after the project and for helpful comments for my fieldwork.

I very much enjoy being at the Institute of Biogeography. The pleasant working atmosphere facilitates working at such a project in every respect.

I owe many thanks to Björn, Lukas, Tobias, Pascal and other students. Without their help the intensive field and laboratory work would not have been possible.

Special thanks go to Dr. Nicole Scheifhacken who accompanied me all the years since my study period in Freiburg. Without her I would not be where I am.

My parents always supported me and made my study at university possible. Thank you!

Finally, special thanks go to my husband Marko. He accompanied me from the beginning and helped with numerous constructions and comments for the field work. He is my greatest support.

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