Alpine springs under pressure?

Assessing the environmental drivers of species assemblages

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Prof. Dr. Jörg Schibler

Dekan

To my family

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CHAPTER ONE

General introduction

Spring research in limnology

Springs are spatially restricted ecotones located at the interface between surface and groundwater (Williams 1991, Webb et al. 1998). Compared to most other freshwater habitats, springs are ecologically unique because they are characterised by a relatively low variability of abiotic conditions especially in terms of relatively low water temperature amplitudes (Odum 1971, van der Kamp 1995). Discharge stability and discharge variability are important abiotic factors influencing the spring fauna directly and indirectly (e.g. Smith et al. 2003, von Fumetti et al. 2006, Mori and Brancelj 2006). Springs exhibit a high-level of individuality regarding their uniquely distinct macroinvertebrate assemblages (Cantonati et al. 2006, Robinson et al. 2008). Springs are characterised by a mosaic-like substrate composition and therefore macroinvertebrate composition is even more heterogeneous (Cantonati et al. 2006, Robinson et al. 2008).

The organisms inhabiting springs are closely adapted to the prevailing environmental conditions (e.g. Williams and Danks 1991, Ferrington 1995). One of the main characteristics of springs fed by deep groundwater (Fischer et al. 1998) and at high altitudes are their thermal stability (Thienemann 1950). This was thought to be the reason for the presence of cold-stenothermal species (Illies 1952, Erman and Erman 1995). However, more recent studies suggest that there is more variability in the temperature regime of springs than originally postulated (Fischer et al. 1998, Gräsle and Beierkuhnlein 1999, von Fumetti et al. 2007, von Fumetti and Blattner 2016, Küry et al. 2016). The thermal variability of spring water depends on different influential parameters such as the mode of flow, the length of time water is underground (Pitty 1976) and the different sources of the spring water (Frisbee et al. 2013). Most notably, springs at higher altitude show substantial seasonal changes of water source contributions, which therefore also influence the amount of discharge (Frisbee et al. 2013). Although discharge amounts can be studied relatively easily, the processes in the aquifer, after precipitation and infiltration in the groundwater till the discharge of the water, remain relatively unknown.

Alpine spring research

Alpine springs are young biotopes of postglacial origin (Cantonati et al. 2006) and therefore tend to be mostly populated by various kinds of flying insect larvae with a high dispersal ability (Glazier et al. 2014). Springs usually have a small spatial extent, but are inhabited by a species-rich community (Cantonati and Ortler 1998, Cantonati et al. 2006, Gerecke and Franz 2006). In contrast to springs at lower elevation mountain ranges, springs at high altitudes are usually fed by an individual mix of groundwater, snowmelt and glacial meltwater in different proportions (Brown et al. 2003, Hannah et al. 2007, Frisbee et al. 2013). This also affects the degree of individuality of these systems (Bonettini and Cantonati 1996). Snow cover in winter isolates springs for several months from the surface. Due to their spatial isolation and fragmentation, alpine springs are vulnerable to changing environmental conditions (Woodward et al. 2010). Furthermore, crenobiont species with a restricted distribution are potentially endangered (Hering et al. 2009). There is a lack of knowledge about the processes going on under snow cover during winter. Additionally, detailed information about macroinvertebrate distribution over several altitudinal belts would be necessary to extrapolate possible future changes caused by global warming. Alpine springs are still poorly investigated habitats due to their remoteness, the aggravated accessibility and the short investigation period.

The first detailed investigation of alpine springs was conducted in Switzerland’s National Park by Nadig (1942). Further investigations were also conducted in the Swiss canton of Graubuenden by Weber (2004), von Fumetti and Felder (2014) and von Fumetti and Blattner (2016). Gerecke and Franz (2006) investigated springs in Germany’s Berchtesgaden National Park. Austria’s

Gesäuse National Park was recently examined by Gerecke et al. (2012). Mori and Brancelj (2006) surveyed macroinvertebrate communities in karst springs in the Slovenian Alps. Springs in the Italian Alps have also been investigated well, both flora (Tomaselli et al. 2011) and fauna (Spitale et al. 2012). The French Alps are clearly under-investigated and there has yet to be any study conducted regarding the macroinvertebrate distribution in springs. Freshwater springs were examined in the Cantabria Mountains in Northern Spain (Barquín and Death 2006a). Cantonati et al. (2006) gave a transnational review of European spring research in alpine regions. Other studies in high alpine areas were implemented in the Andes Mountains in Ecuador (Madsen et al. 2015) and in Mount Taranaki of Egmont National Park in New Zealand (Barquín and Death 2006b).

Compared to the rest of the world, central Europe is the most comprehensively investigated area concerning alpine springs. Therefore, it is astonishing that no detailed faunistic investigation of high elevation springs has been conducted in the Swiss Alps apart from the studies conducted in the Swiss National Park. In order to close this research gap, the thesis presented here provides a first insight into the macroinvertebrate assemblages of natural springs in the Central Swiss Alps.

Consequences of global warming on alpine freshwaters

Climate change, especially climate warming, affects alpine regions twice as intensely as other regions (IPCC 2014). Alpine freshwater ecosystems are significantly affected due to their sensitivity towards climate variability and their strong dependence of snow packs, glacier mass-balance and atmospheric forcing (Hannah et al. 2007). Many studies concentrated on the influence of the physico-chemistry and the influence of glacial melt water input on river ecosystems induced by climate warming (e.g. Füreder et al. 2001, Robinson et al. 2004). Very few studies focused on the influences of climate change on alpine springs or springbrooks (e.g. Gerecke and Franz 2006).

Water temperature and channel stability are thought to be the most important stream characteristics influencing benthic communities (Milner et al. 2001). Additionally, there is some evidence that freshwater species have exhibited temperature induced range shifts in response to climate change (Heino et al. 2009). In boreal regions, a horizontally northwards shift of warm-water species is very likely and conversely cold-water species may go extinct in the southern aspects of boreal regions (Heino et al. 2009). Alpine aquatic ecosystems are very suitable for monitoring because of their temperature sensitivity (Khamis 2014). They enable us to detect early signals of climate-induced ecosystem shifts (Khamis 2014). In addition to the strong influence air temperature has on water temperature, springs are also strongly influenced by precipitation changes (BAFU 2012). As the climate changes further, the Central Alps are predicted to experience less summer precipitation, leading to summer droughts but with higher winter precipitation (IPCC 2014, BAFU 2012). Therefore accordingly, a shift in the water sources of alpine rivers can be expected and is already observed (Brown et al. 2007, Viviroli et al. 2011). Higher runoff induced by a rapid melt of glacial ice, permafrost and snow can have dramatic effects on discharge (Zappa and Kan 2007). These changes are likely to significantly affect the fauna, since faunistic patterns are strongly dependent on the water temperature and suspended sediment concentration (Brown et al. 2006). Additionally, the increasing intensity and number of predicted extreme events will affect channel stability, which could negatively affect freshwater communities.

This study shall investigate how in alpine regions, climate induced species shifts might occur in an altitudinal direction, as observed for terrestrial alpine plant communities (Jentsch and Beierkuhnlein 2003, Körner 2003), and shall be investigated in this study. Especially in cold-adapted, small-scale and isolated ecosystems, species shifts may lead to species extinctions (IPCC 2014). Due to the large uncertainties about the magnitude of climate change induced impacts on mountain ecosystems, further environmental monitoring at high altitudes is pointed out to be of the utmost importance during the changing times ahead (Viviroli et al. 2011).

Objectives of the thesis

The aim of this thesis is to investigate the macroinvertebrates composition of alpine springs in order to understand the driving mechanisms influencing the species assemblages in alpine springs.

Due to the minimal amount of marginal studies of alpine springs in Switzerland, a pilot study **(chapter two)** was conducted to document a preliminary baseline of high alpine Swiss springs. During this pilot study, a small-scale area with a high spring density was surveyed intensely. The goal was to detect patterns in the macroinvertebrate composition and the abiotic environmental conditions. The pilot study also served to test and adjust the methodology for investigating alpine springs.

Afterwards, the investigation area was expanded to an entire alpine valley (**chapter three**). In this larger scale study, distribution patterns of macroinvertebrates of springs along an altitudinal gradient were investigated. The objective was to detect if the spring fauna is dependent on the altitude, or other factors which are strongly linked to altitude such as temperature, precipitation, or vegetation. Such a dependence on altitude would hint at probable species shifts with changing climatic conditions.

In **chapter four**, possible influences of the variability of water temperature and other physico-chemical parameters on macroinvertebrates at different altitudes were investigated. For this purpose, a comparison of long-term logger data and three macroinvertebrate samplings were performed. Knowing the dependence of the spring fauna on the variability and stability of the environmental parameters, enables predictions of possible future shifts due to climate change.

Using previously existing investigation techniques, it is difficult to measure many important processes influencing the macroinvertebrate assemblages in springs, such as groundwater recharge, flow time and flow path of groundwater. In **chapter five** a non-invasive method was tested using high resolution signals from water loggers and meteorological data as a novel solution to measure spring processes previously difficult to measure. This novel approach aimed at correlating the data with a time series analysis and thereby extrapolating the time lag of the water temperature compared to the air temperature. The time lag can thus be interpreted as the groundwater flow time. This new knowledge will help to understand the spring's source water composition, consisting of melt water and groundwater, which is evidentially important for the macroinvertebrate communities in alpine freshwater ecosystems.

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CHAPTER TWO

Fabian Wigger[1] und Stefanie von Fumetti[1]

Quellen und ihren Lebensgemeinschaften in den Berner Alpen

1. Einleitung

Alpine Quellen sind Ökotone postglazialen Ursprunges, d.h. Übergangshabitate an der Schnittstelle zwischen Oberflächenwasser und Grundwasser (Cantonati et al. 2006, Gerecke & Franz 2006). In der Schweiz wurden erstmals durch Nadig (1942) alpine Quellen im Schweizerischen Nationalpark untersucht. Weitere Untersuchungen alpiner Quellen wurden im Nationalpark Berchtesgaden (Gerecke & Franz 2006), in den Julischen Alpen in Slowenien (Mori & Brancelj 2006) und im Nationalpark Gesäuse in Österreich (Gerecke et al. 2012) durchgeführt. Eine allgemeine Publikation zu alpinen Quellen liegt von Cantonati et al. (2006) vor. Verglichen mit Untersuchungen von Gletschervorfeldern oder Bergbächen (z.B. Füreder 2001) sind Quellen in den Alpen, insbesondere in der Schweiz, relativ schlecht untersuchte Biotope.

Alpine Quellen stehen seit jeher unter einem starken Nutzungsdruck. Viele Quellen wurden gefasst, um Alphütten oder Viehtränken mit Wasser zu versorgen oder schlicht, um vernässte Wiesen trockenzulegen. Natürliche, unbeeinflusste Quellen sind auch im Alpenraum kaum mehr vorhanden (Zollhöfer 1997).

Aufgrund ihrer Temperaturstabilität sind Quellen besonders geeignete Indikatoren, um die Auswirkungen des Klimawandels zu untersuchen (Gerecke & Franz 2006). Durch ihre kleinräumige Struktur und isolierte Lage sowie durch die hohe Anfälligkeit auf Störungen jeglicher Art sind Quellen wertvolle Biotope und bedürfen deshalb eines besonderen Schutzes. Jedoch sind naturnahe Quellen in der Schweiz nach geltendem Recht in keiner Weise geschützt (Zollhöfer 1997).

In der vorliegenden Arbeit wurde eine allgemeine Feldaufnahme alpiner Quellen im Berner Oberland hinsichtlich der Quellfauna und Quellmorphologie durchgeführt. Dabei wurde versucht, die Quellen hinsichtlich der Störungsintensität und der Störungsfrequenz durch den Menschen und das Vieh zu analysieren. Zudem wurde die Rolle der Schüttung und deren Stabilität bezüglich deren Beeinflussung der Quellfauna untersucht. Als Untersuchungsobjekt wurde eine extensiv genutzte Hochebene westlich des Giessbachtals ausgewählt.

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2. Untersuchungsgebiet

Das Untersuchungsgebiet liegt südlich des Brienzersees und nördlich der Faulhorngruppe im Berner Oberland auf dem Gemeindegebiet von Iseltwald. Abgegrenzt wird das Untersuchungsgebiet durch die Fangisalp, Schönegg, Blättenalpburg, Litschgiburg und Harzisboden *(Abb. 1)*. Die untersuchte Fläche hat eine relativ hohe Quelldichte und liegt auf einer Hochebene auf 1850–2100 m ü.M. Insgesamt wurden 13 unterschiedliche Quellen für die Untersuchung ausgeschieden.

Das Untersuchungsgebiet liegt in der tektonischen Einheit der Helvetischen Decken, welche den nördlichen Rand der Alpen bilden. Das Untersuchungsgebiet liegt in der Axendecke, einer Untereinheit der Helvetischen Decken. Die aufgeschlossenen Schichtfolgen im Gebiet stammen einerseits aus der Kreide, und werden durch den Valangienkalk (heute Betlis-Kalk) und den Valangienmergel (heute Vitznau-Mergel) repräsentiert (Seeber 1911), und andererseits aus dem Jura. Die deutlich härteren und verwitterungsbeständigeren Schichten des Valangienkalkes bilden die markante Wandflue *(Abb. 2)*. Die weicheren Valangienmergel sind deutlich zurückgewittert und umschliessen die Wandflue. Bedingt durch den hohen Tonanteil sind diese Schichten grundwasserstauend. Aus diesem Grund

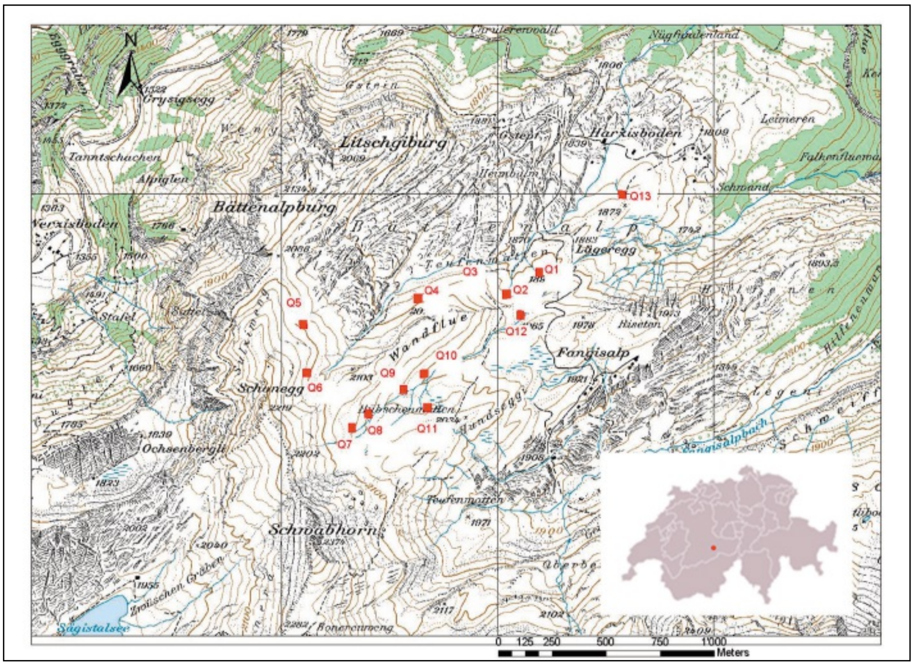


Abbildung 1: Topographische Karte des Untersuchungsgebietes mit den untersuchten Quellen im Massstab 1:25000 (Reproduziert mit Bewilligung von swisstopo (BA13023).

Abbildung 2: Die Valangienkalke der Wandflue, die Schichtgrenze befindet sich in der Bildmitte unter der Felswand.

sind die meisten Quellen auch an der Schichtgrenze zwischen den Kalken und dem Mergel zu finden und können als Schichtquellen bezeichnet werden.

Das harsche Klima des Untersuchungsgebietes bestimmt im Wesentlichen die kurze Vegetationsperiode. Die Schneebedeckung hält im Mittel sechs Monate lang an. Die Jahresmitteltemperatur beträgt –2,2 °C bei einer jährlichen mittleren Niederschlagssumme von 2100 mm, wobei der Grossteil des Niederschlages im Winterhalbjahr als Schnee anfällt. Eine Begehung des Untersuchungsgebietes im Winter hat gezeigt, dass die untersuchten Quellen vollständig durch Schnee bedeckt waren *(Abb. 6)*. Die komplett schneefreie Zeit dauert daher nur rund drei Monate. Das jährliche Niederschlagsminimum im Spätsommer führt zu einem Schüttungsminimum oder gar Trockenfallen von Quellen (intermittierende Quellen). Dies konnte in der Voruntersuchung sowie auch in der Untersuchungsperiode beobachtet werden.

3. Material und Methoden

Die Quell- und Umfeldkartierung wurde mit dem Bayerischen Quellerfassungsbogen (BAYQEB 2004) durchgeführt. Der Kartierbogen erfasst die verschiedenen Substrattypen, die Quellschüttung sowie die chemischen und physikalischen Faktoren. Die abiotischen (Steine, Kies, Sand, Ton) und biotischen Substrate (v.a. Moose und feines partikuläres organisches Material) wurden visuell durch prozentuales Abschätzen des Vorkommens aufgenommen. Die Feldparameter, wie zum Beispiel die elektrische Leitfähigkeit und der Sauerstoffgehalt, wurden mit mobilen Messgeräten (WTW, Weilheim, Deutschland) gemessen. Diese Felddaten wurden jeweils unmittelbar nach der faunistischen Probenahme im Frühjahr und im Herbst 2009 erhoben. Zusätzlich wurde im Frühjahr 2009 von jeder Quelle eine Wasserprobe entnommen, um die Nährstoffverhältnisse der Quellen zu untersuchen. Diese wurden durch das Analytische Zentrallabor für Umwelt- und Geochemie (AZUG) des Departements Umweltwissenschaften der Universität Basel analysiert.

Die Schüttung wurde mit Hilfe eines Plastiksackes und eines Messzylinders ermittelt. Dabei wurde das Wasser mit dem Plastiksack über fünf Sekunden abgeschöpft und die Menge anschliessend mit dem Messzylinder abgemessen (ZOLLHÖFER 1997, FUMETTI VON & NAGEL 2012).

Die faunistischen Probennahmen fanden im Frühjahr und im Herbst 2009 statt. Im Herbst 2008 wurde eine Voruntersuchung durchgeführt, um geeignete Quellen zu eruieren. Für die quantitative Beprobung wurde ein Surber-Sampler mit einer Grundfläche von 10x10 cm und einer Maschenweite von 500 µm eingesetzt. Es wurden in jeder Quelle jeweils vier Proben im Frühjahr und Herbst genommen, um die verschiedenen Substrattypen der Quellen berücksichtigen zu können. Zusätzlich wurde eine qualitative Probennahme im Herbst 2009 durchgeführt. Sowohl die qualitative als auch die quantitativen Beprobungen wurden vom unteren Quellbereich zum Quellmund hin durchgeführt, um Trübungen durch aufgewirbeltes Substrat zu vermeiden. Als Definition des Quellbereiches wurde die Klassifikation nach FUMETTI VON ET AL. (2007) verwendet. Als Quelle werden dabei nur die ersten fünf Meter nach dem Quellaustritt bezeichnet.

Die Abschätzung der Störungsintensität einer Quelle wurde indirekt über die Aufnahme der Störungsintensität des Quellumfeldes erhoben. Dabei wird vorausgesetzt, dass das Quellumfeld und die Quelle derselben Störung durch das Vieh oder den Menschen ausgesetzt sind. Quellen mit geringer Störung werden bei dieser Untersuchung meist von mesophilen subalpinen Zwergstrauchheiden begleitet. Steigt die Störungsintensität, wird das Quellumfeld von mit Viehgangeln dominierten alpinen Magerrasen durchzogen. Eine hohe Störungsintensität zeigt sich durch das Auftreten von Fettwiesen oder vegetationslosen Böden (DELARZE & GONSETH 2008).

Die statistische Auswertung wurde mit Primer V 6.1.6 (CLARKE & GORLEY 2006) und Statistica (STATSOFT 2008) gerechnet. Als Datengrundlage wurden die Artenlisten der beiden quantitativen Feldaufnahmen und der qualitativen Beprobung summiert und mit presence/absence kodiert. Dies hat den Vorteil, dass die kombinierte Taxaliste aus den beiden quantitativen und der qualitativen Taxalisten auf drei Beprobungen fundiert und die Wahrscheinlichkeit zunimmt, die tatsächliche Artenzusammensetzung der einzelnen Quellen zu repräsentieren.

Die abiotischen, beziehungsweise nicht faunistischen Daten wurden in drei Intensitätsstufen klassifiziert. Dabei gilt 1 als schwache und 3 als starke Ausprägung des jeweiligen Merkmales.

4. Ergebnisse

Die Analyse der morphologischen Ausprägung ermöglicht eine Quelltypologie nach Steimann (1915) und Thienemann (1924). Quellen mit einem hohen Anteil an organischer Substanz im Substrat, geringer Neigung und flächiger Ausprägung können als Helokrene bezeichnet werden. Gute Beispiele dieses Quelltyps sind die Quellen 1 und 10 *(Abb.5)*. Eine eher von Steinen dominierte Quelle mit länglicher Ausprägung und starker Neigung wird als Rheokrene beschrieben. Quelle 4 und 10 sind typische Rheokrenen. Es lassen sich aber längst nicht alle Quellen mit dieser Quelltypisierung ausreichend charakterisieren. Bei den untersuchten Quellen handelt es sich vielmehr um Übergangsformen einzelner Quelltypen.

Die mittlere Wassertemperatur betrug im Frühling 4,4 °C und im Herbst 5,8 °C. Der Temperaturunterschied der zwei Beprobungen betrug also 1,6 °C. Die grösste saisonale Temperaturamplitude wurde in der Quelle 11 mit 5,6 °C gemessen.

Die Schüttung der untersuchten Quellen reichte von 0,25 l/sec bis 4 l/sec. Im Frühjahr war die Schüttung bei allen Quellen höher als im Herbst. Drei Quellen (Q7, Q8, Q9) sind im Herbst 2009 gänzlich ausgetrocknet.

Der pH erreichte im Frühjahr Werte von 7,5 bis 8,4 und im Herbst von 5,7 bis 7,6, er war im Herbst wesentlich tiefer als im Frühjahr. Die Leitfähigkeit wies im Frühjahr und im Herbst erhebliche Schwankungen auf (Frühjahr: 199–1992 µS/cm; Herbst: 298–1960 µS/cm).

Der Sauerstoffgehalt betrug im Frühjahr im Mittel 9 mg/l (89,62%). Der höchste Wert wurde in der Quelle 4 mit 13,4 mg/l (127%), der niedrigste Wert in der Quelle 12 mit 5,8 mg/l (55%) gemessen *(Tab. 1)*.

Insgesamt konnten 43 Taxa nachgewiesen werden *(Tab. 2)*. Bei der quantitativen Beprobung wurden 22 Taxa im Frühjahr und 18 Taxa im Herbst gezählt. Die qualitative Untersuchung ergab 26 verschiedene Taxa. Im Folgenden werden die wichtigsten Taxa näher beschrieben.

Turbellaria (Strudelwürmer): *Crenobia alpina* wurde in allen untersuchten Quellen in hohen Abundanzen nachgewiesen. Diese Art ist quelltypisch und zeigt eine alpine Verbreitung.

Im Gegensatz dazu war *Dendrocoelum hercynicum* nur in der Quellfassung der Quelle 10 zu finden. Diese Art ist an dunkle, kalte Lebensräume wie Brunnenschächte angepasst. Beide Arten ernähren sich wie alle Strudelwürmer räuberisch.

Acari (Wassermilben): Mit acht Arten sind die Süsswassermilben recht zahlreich vertreten. *Lebertia maculosa*, *Sperchon mutilus* und *Sperchon squamosus* sind krenobionte Arten, haben also ihren Verbreitungsschwerpunkt in Quellen (Sambugar et al. 2006). Das Vorkommen von Süsswassermilben ist ein Indikator für stetig schüttende Quellen (gerecke & Franz 2006).

		Laborwerte					**Frühling**						**Herbst**					
Quelle	Höhe ü.A.	DOC mg/l	NH_4 mg/l	NO_3 mg/l	Cl mg/l	SO_4 mg/l	Wassertemperatur (°C)	pH-Wert	Leitfähigkeit (µS/cm)	Sauerstoffgehalt (mg/l)	Sauerstoffsättigungsindex (%)	Schüttung (l/sec)	Wassertemperatur (°C)	pH-Wert	Leitfähigkeit (µS/cm)	Sauerstoffgehalt (mg/l)	Sauerstoffsättigungsindex (%)	Schüttung (l/sec)
Q1	1906	0.467	0	0.229	0.673	3.444	3.4	7.94	285	6.5	62	1	5.3	5.74	298	1.75	18	0.25
Q2	1921	0.464	0	0.315	0.196	4.5	3	7.92	199	8.8	85	1	4.7	7.57	1960	3.11	31	0.25
Q3	1972	0.815	0.07	0.559	0.453	6.163	7	7.93	816	10.6	115	1	6.2	5.82	325	2.51	26.4	0.25
Q4	1970	–	–	–	–	–	2.7	8.3	1314	13.4	127	0.5	5.7	6.76	301	3.1	32.1	0.5
Q5	2044	0.403	0.059	0.371	0.142	5.353	3	8.04	1451	13	123	2	7.5	6.01	314	2.53	27	0.5
Q6	2100	0.456	0	0.16	0.115	4.941	4.9	7.55	285	7.2	72	0.5	6.2	6.72	340	3.5	37	0.25
Q7	2055	0.375	0.058	0.237	0.623	4.875	3.5	7.77	273	8	79	4	–	–	–	–	–	–
Q8	2051	0.441	0.032	0.418	0.16	3.146	3.5	7.6	335	7.2	70	1	–	–	–	–	–	–
Q9	2019	0.471	0.015	0.407	0.695	3.733	4	7.52	285	6.8	67	1	–	–	–	–	–	–
Q10	2007	0.679	0.03	5.678	0.511	9.323	3.8	7.54	1992	10.5	104	2	4.4	7.27	397	3	29.7	1
Q11	2011	0.465	0.032	0.206	0.58	8.538	11.7	8.37	204	10.2	119	3	6.1	7.48	397	3.46	36.9	0.5
Q12	1912	0.662	0.015	0.18	0.469	6.931	3.1	7.45	381	5.8	55	1	4.5	7.57	455	4	41	0.5
Q13	1820	1.27	0.059	<0.1	0.534	3.473	4	8.15	267	9.5	87	0.5	7.4	7.31	354	1.94	20.7	0.5
Mittelw.	**1983.69**	**0.58**	**0.03**	**0.73**	**0.43**	**5.37**	**4.43**	**7.85**	**622.08**	**9.04**	**89.62**	**1.42**	**5.80**	**6.83**	**514.10**	**2.89**	**29.98**	**0.45**

Tabelle 1: Physikochemische Analyse im Frühjahr und Herbst mit den gemessenen Laborwerten.

Abbildung 3: Eine Ansammlung von Köcherfliegen in Strömungsrichtung ausgerichtet.

Coleoptera (Wasserkäfer): Es wurden fünf verschiedene Wasserkäferarten nachgewiesen. *Agabus biguttatus* und *Helophorus* spp. waren dabei relativ häufig und wurden in gut der Hälfte der Quellen aufgefunden. Ein einziges Exemplar eines *Agabus bipustulatus* und eines *Hydroporus nigrita* wurde in der Quelle 1 nachgewiesen. Bei allen Arten handelt es sich um typische Räuber in Quellen.

Plecoptera (Steinfliegen): Insgesamt konnten vier Taxa bestimmt werden: Perlodidae, *Nemurella pictetii, Nemoura mortoni* und *Leuctra* spp. Bis auf die Quelle 7 konnte in jeder Quelle mindestens eine Art nachgewiesen werden. Mit Ausnahme der *Perlodidae* sind alle nachgewiesenen Steinfliegen krenophil. *Neumoura mortoni* ist besonders in höheren Lagen zu finden und weist eine alpine Verbreitung auf (GERECKE & FRANZ 2006).

Trichoptera (Köcherfliegen): Es konnten vier verschiedene Arten nachgewiesen werden. Es handelt sich um *Pseudopsilopteryx zimmeri, Limnephilus coenosus, Brachycentrus montanus* und *Limnephilus hirsutus. Pseudopsilopteryx zimmeri* und *Limnephilus hirsutus* sind quelltypische Taxa, wobei *P. zimmeri* zudem eine alpine Verbreitung aufweist *(Abb. 3).*

Taxa		**Q1**	**Q2**	**Q3**	**Q4**	**Q5**	**Q6**	**Q7**	**Q8**	**Q9**	**Q10**	**Q11**	**Q12**	**Q13**
Turbellaria (Strudelwürmer)	*Crenobia alpina* (Dana, 1766)	1	1	1	1	1	1	1	1	1	1	1	1	1
	Dendrocoelum hercynicum (Flossner, 1959)										1			
Moluska (Mollusken)	*Radix* spp. Montfort, 1810	1	1	1	1	1	1	1			1	1	1	1
	Valvata piscinalis alpestris (Kuester, 1853)			1		1					1			
	Pisidium spp. C. Pfeiffer, 1821	1	1	1							1	1	1	1
Oligochaeta (Wenigborster)	Oligochaeta	1	1	1			1		1		1			
Acari (Wassermilben)	*Hydrovolzia placophora* (Monti, 1905)										1			
	Hygrobates norvegicus (Thor, 1897)		1								1			
	Lebertia elsteri Schwoerbel, 1957													1
	Lebertia maculosa Koenike, 1902												1	
	Lebertia schechteli Thor, 1913										1		1	
	Sperchon mutilus Koenike, 1895			1	1						1			
	Sperchon squamosus Kramer, 1879		1				1							1
	Sperchon (s.str.) sp. Kramer, 1877											1		
Crustacea (Krebstiere)	Ostracoda	1	1	1	1	1					1	1	1	1
	Copepoda										1			
	Gammarus fossarum Koch, 1835	1												
	Niphargus spp. Schioedte, 1849								1	1	1			
	Asellus aquaticus Racovitza, 1919		1	1	1						1			
Ephemeroptera (Eintagsfliegen)	*Ecdyonurus* spp. Eaton, 1868				1		1				1	1		
	Baetis alpinus (Pictet, 1843)		1		1	1	1				1	1		1

Plecoptera (Steinfliegen)	Perlodidae	1	1											
	Nemurella pictetii Klapalek, 1900	1	1	1	1	1	1		1	1	1	1	1	1
	Nemoura mortoni Ris, 1902		1	1	1							1		1
	Leuctra spp. Stephens, 1836			1	1		1							
Coleoptera (Käfer)	*Agabus biguttatus* (Olivier, 1795)	1	1	1			1				1	1	1	1
	Agabus bipustulatus (Linnaeus, 1767)	1												
	Dytiscidae	1												
	Helophorus spp. Fabricius, 1775	1		1			1			1	1	1		1
	Hydroporus nigrita (Fabricius, 1792)	1												
Trichoptera (Köcherfliege)	*Brachycentidae*		1									1		
	Limnephilus coenosus Curtis, 1834					1	1	1	1	1	1	1	1	1
	Limnephilus hirsutus (Pictet, 1834)	1	1											
	Pseudopsilopteryx zimmeri (McLachlan, 1876)				1		1		1			1		
	Limnephilidae	1		1	1	1					1	1	1	
Diptera (Zweiflügler)	Ceratopogonidae		1											
	Chironomidae	1	1	1	1	1	1	1	1	1	1	1	1	1
	Empididae					1	1						1	1
	Limoniidae			1	1				1	1	1	1		
	Pedicia spp. Latreille, 1809	1	1	1		1					1	1		1
	Psychodidae gen sp.		1	1	1	1	1				1	1	1	
	Simulium spp. Latreille, 1802	1	1	1	1		1		1	1	1		1	1
	Oxycera spp. Meigen, 1803					1	1		1					
	Tipulidae					1					1			

Tabelle 2: Artenliste aus den zwei quantitativen und der qualitativen Beprobung. 1 = vorhanden

Diptera (Zweiflügler): Die Bestimmung der Larven konnte jeweils nur auf Familienniveau vorgenommen werden. Die Dipteren sind mit elf Taxa die Grossgruppe mit den meisten nachgewiesenen Familien der Untersuchung. Eine hohe Individuendichte und eine hohe Artenzahl sind typisch für Quellen (Zollhöfer 1997).

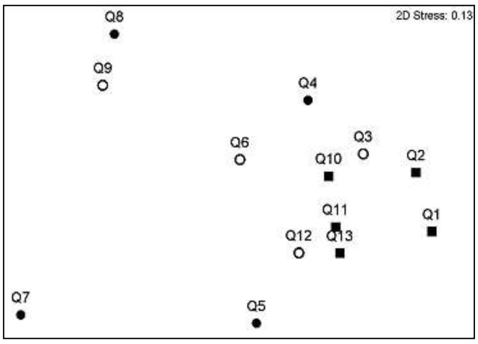
Zu Beginn der Analyse wurde eine Hauptkomponentenanalyse (PCA) durchgeführt. Dabei sollen die abiotischen Faktoren, welche einen grossen Einfluss auf die Fauna haben könnten, herausgefiltert werden. Die beiden Faktoren Substratdiversität und organisches Substrat werden dabei in erster Linie als dominierend ausgeschieden. Ausserdem sind der Isolationsgrad und der Viehtritt sowie die anthropogene Störung zu erwähnen.

Ein anschliessende Rangkorrelationsanalyse (BioENV) zeigte, dass die Schüttungsstabilität, der Viehtritt und die anthropogene Störung, die Schüttung sowie der Sauerstoffgehalt einen starken Einfluss auf die Zusammensetzung der Fauna haben (σ=0,621 und p=0,01). Anschliessend wurde eine nMDS (nichtmetrische Multidimensionale Skalierung) mit der Taxaliste als Datengrundlage durchgeführt und getestet, welche der als wichtig eruierten abiotischen Faktoren aus der PCA und der BioENV eine Gruppierung der Quellen erklären.

Der Faktor Schüttungsstabilität zeigt, dass die stark schüttenden, perennierenden Quellen 1, 2, 10, 11 und 13 untereinander eine hohe Ähnlichkeit aufweisen *(Abb. 4)*. Die intermittierenden und im Herbst trockengefallenen Quellen zeigen unter sich den stärksten Unterschied. Die dazugehörige Ähnlichkeitsanalyse (ANOSIM) zeigt einen signifikanten Unterschied zwischen den Quellgruppen mit unterschiedlicher Schüttungsstabilität (R:0,53; p:0.002) *(Abb. 4)*.

Zudem haben die Viehtrittintensität (R=0,59), die Störung durch Mensch und Vieh (R=0,30), der Anteil an organischem Substrat (R=0,62) und die Substratdiversität (R=0,50) einen signifikanten Einfluss auf die Zusammensetzung der Quellfauna (p=0,001).

Eine Varianzanalyse (ANOVA) mit Fischers LSD-Test mit der Taxaliste und dem Faktor Viehtrittintensität ergab einen signifikanten Unterschied von p=0,0112 (F=7,2705; df=2).



Schüttungstabilität
● = 1
○ = 2
■ = 3

Abbildung 4: nMDS mit Schüttungsstabilität als Faktor und der Taxaliste als Datengrundlage (1 = schwache, intermittierende Schüttung, 2 = schwache perennierende Schüttung, 3 = starke perennierende Schüttung).

5. Diskussion

Die Quellen im Berner Oberland sind starken saisonalen Abflussschwankungen unterworfen und unterliegen einem nivalen Abflussregime. Dabei spielt die Schneeschmelze im Frühsommer eine zentrale Rolle. Die Schüttung erreicht dann ihr jährliches Maximum. Das jährliche Niederschlagsminimum hingegen ist im Spätsommer oder im Herbst. Im Herbst kann es daher zu einer Austrocknung von einzelnen Quellen kommen. Im Jahresgang sind Schwankungen der Schüttung um den Faktor 5 bis 30 möglich (ZOLLHÖFER 1999).

In unserer Untersuchung wurde die stärkste Schüttung im Juli, während der Schneeschmelze beobachtet. Der Oberboden war dabei noch teilweise gefroren und es war ein direktes Einfliessen des Schmelzwassers in die Quelle zu beobachten *(Abb. 5)*. Aufgrund der meist muldenförmigen Ausprägung der Quellen war ausserdem zu beobachten, dass gerade im Bereich des Quellaustrittes der Schnee am längsten überdauert hat.

Die Schneeschmelze ist starken täglichen Schwankungen unterworfen, was mit den Temperaturschwankungen im Tagesverlauf und der Sonnenscheindauer zusammenhängt. Die Schüttung der Quellen ist im Frühjahr somit sehr variabel und besteht zu einem grossen Teil aus meteorischem Wasser. Eine Quelle weist während der Schneeschmelze somit einen ähnlichen Tagesgang wie ein Gletscherfluss im Gletschervorfeld auf. Dieser Einfluss des kalten Schmelzwassers ist auch ein

Abbildung 5: Helokrene mit Schmelzwasserbeeinflussung.

Hauptgrund für die starken Temperaturschwankungen des Quellwassers. Im Winter sind die Quellen mehr als sechs Monate durch eine geschlossene Schneedecke bedeckt *(Abb. 6)*. Während dieser Zeit bewegen sich die Temperaturen des Quellwassers um den Gefrierpunkt.

Loggermessungen und direktes Beproben haben zudem eine minimale Schüttung zu dieser Zeit gemessen. Die Temperaturschwankungen der Quellen variierten im Mittel um 1,5 °C. Einzelne Quellen zeigen aber eine wesentlich höhere Temperaturamplitude. Quellen werden als sehr konstant bezüglich ihrer Wassertemperatur und Schüttung beschrieben (Steinmann 1915), für alpine Quellen trifft dies aber offensichtlich nur bedingt zu. Gräsle & Beierkuhnlein (1999) und Fumetti von & Nagel (2012) dokumentieren grosse Temperaturschwankungen aber auch in Quellen im Frankenwald bzw. im Schweizer Jura. Möglicherweise steigt die Temperaturamplitude der Quellen mit zunehmender Höhe, da die saisonalen und täglichen Lufttemperaturunterschiede und die unterschiedliche Besonnung im Winter und Sommer extremer werden und der Einfluss der Schneeschmelze zunimmt.

Das Minimum der Schüttung, die damit verbundene geringe Fliessgeschwindigkeit und das Lufttemperaturmaximum fallen im Spätsommer zusammen. Dies äussert sich in einer erhöhten Wassertemperatur im Herbst. Das Risiko für das Austrocknen der Quellen ist somit sehr hoch. Unsere Untersuchung konnte nachweisen, dass ein starker Zusammenhang zwischen einer stabilen Schüttung und der Biodiversität besteht. Wasserentnahmen im Quellbereich für Viehtränken im

Abbildung 6: Schneehöhenmessung im Winter.

Sommer haben daher einen stark negativen Einfluss auf die Fauna. Quellen mit perennierender Schüttung weisen eine höhere Abundanz und Diversität auf als intermittierende.

Im Frühjahr konnte eine höhere Nährstoffzulieferung im Zusammenhang mit der Schneeschmelze festgestellt werden, was auch bei Quellen in Berchtesgaden beobachtet wurde (Gerecke & Franz 2006). Eine Untersuchung im Alptal hat gezeigt, dass im Schnee viele Nährstoffe gebunden werden (Waldner et al. 2000). Diese können im Frühjahr in die Quelle eingewaschen werden. Alpines Quellwasser ist normalerweise sehr nährstoffarm, somit ist auch eine Saisonalität der Nährstoffverfügung zu verzeichnen.

Die Quellfauna wird neben der Konstanz der Wassertemperatur auch durch den Eintrag von Falllaub beeinflusst (Smith et al. 2003). Die Diversität der Habitatstrukturen und die Substratzusammensetzung beeinflussen die Quellfauna direkt. Je grösser die Diversität von Kleinstlebensräumen, desto grösser ist die Biodiversität. Auch in dieser Untersuchung konnte ein starker Einfluss der Substratdiversität nachgewiesen werden. Ilmonen & Paasivirta (2009) zeigen zudem, dass in Moos dominierten Helokrenen die höchste Taxazahl und Abundanz auftritt. Als Ursache werden die mosaikartige Struktur der Moospolster und deren Schutzwirkung, die vertikale Zonierung und das vielseitige Nahrungsspektrum genannt. Jedoch werden nur gering gestörte Quellen von Moosen dominiert.

Grundsätzlich weisen ungestörte Quellen mit einer stetigen Schüttung und einer vielfältigen Habitatstruktur die grösste Biodiversität auf. Gerade diese Standorte jedoch sind sehr selten geworden. Quellfassungen oder Drainagen zerstören die natürlichen Habitatstrukturen oder setzen die Schüttungsstabilität herab. Die verbliebenen Quellen werden gleichzeitig stärker durch Wildtiere und das Vieh frequentiert. In der Regel werden gefasste, aber nicht mehr verwendete Quellfassungen nicht rückgebaut.

Wissenschaftliche Prognosen für die Schweiz zeigen für die nächsten Jahrzehnte einen Anstieg der Sommertemperaturen und einen gleichzeitigen Rückgang des Niederschlags im Sommer. Dies bedeutet für die Quellen ein erhöhtes Risiko, auszutrocknen (Qinquai et al. 2005). Quellen, welche nicht austrocknen, laufen Gefahr, einer erhöhten Störung durch das Vieh zu unterliegen, da diese möglicherweise häufiger aufgesucht werden. Zudem werden die Winterniederschläge zunehmen, was für alpine Regionen über 1500 m ü.M. zu einer erhöhten Schneemenge führen kann (OcCC-Report 2007). Die Schneeschmelzeereignisse im Frühling werden somit intensiver und über einen längeren Zeitraum ablaufen. Die Quellen werden auch dadurch einer erhöhten Störung unterliegen. Die Bedeutung des Quellschutzes wird deshalb umso wichtiger, um negative anthropogene Eingriffe möglichst zu minimieren und die Quellen als wertvolle Biotope nicht zusätzlich zu beeinträchtigen. Renaturierungen von Quellen sowie das Auszäunen von Quellen oder das Freilegen gefasster und ungenutzter Quellen könnten helfen, die Biodiversität dieser kaum bekannten Biotope zu erhalten. Weitere Langzeitstudien im Giessbachtal sollen helfen, Ansätze für den zukünftigen Umgang mit

Quellen zu finden. Die Untersuchung von Quellen auf unterschiedlicher Höhe und des Winteraspekts sind dabei von zentraler Bedeutung.

6. Zusammenfassung

Alpine Quellen sind in der Schweiz noch sehr schlecht untersuchte Biotope. Der Nutzungsdruck durch den Menschen und die Beweidung sowie die Klimaänderung wirken sich negativ auf diese kleinräumigen, isolierten Lebensräume aus. Viele Quellen sind durch den Menschen bereits stark zerstört oder verschwunden. Naturnahe Quellen unterliegen in der Schweiz keinerlei gesetzlichem Schutz.
Im Rahmen dieser Untersuchung wurden im Frühjahr und Herbst 2009 13 Quellen mit unterschiedlichem Nutzungsdruck und somit unterschiedlichem Störungsregime faunistisch und strukturell untersucht. Parallel dazu wurden alle relevanten abiotischen Parameter der Quellen und die Vegetationsstrukturen sowie die geologischen Verhältnisse des Quellumlandes aufgenommen. In den Jahren 2011 und 2012 wurden die Untersuchungen an weiteren Quellen fortgeführt.

Insgesamt konnten bisher 43 Taxa nachgewiesen werden. Die einzelnen Quellen weisen eine sehr heterogene Taxazahl auf. Quellen mit hohem organischem Anteil und stetiger mässiger Schüttung sowie einer hohen Substratdiversität weisen die höchste Biodiversität auf. Die Schüttung und Wassertemperatur alpiner Quellen ist variabler als in Quellen in Mittelgebirgen und wird durch die Schneebedeckung und Schneeschmelze beeinflusst.

Die halbjährliche Schneebedeckung und die damit verbundene fehlende Solarstrahlung, das Wegfallen von organischen Einträgen im Winter, die starke Schüttung durch die Schneeschmelze im Frühling und die sehr geringe Schüttung während der herbstlichen Trockenheit stellen extreme Bedingungen dar, welche auf die Quellfauna einwirken. Aus diesen Gründen unterscheiden sich alpine Quellen bezüglich Temperaturverlauf und Schüttung stark von Quellen im Flachland und in Mittelgebirgen.

Klimaprognosen gehen von einer verstärkten Sommertrockenheit und einem erhöhten Niederschlag im Winter aus. Für die Quellen bedeutet dies ein erhöhtes Austrocknungsrisiko im Herbst und eine verstärkte Beeinflussung durch Schmelzwasser. Beides kann die Biodiversität negativ beeinflussen. Auch eine rückläufige Bewirtschaftung der Alpweiden und eine Verschiebung der Waldgrenze stellen künftige Herausforderungen für die äusserst sensiblen Quellorganismen dar.

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Macroinvertebrate assemblages of natural springs along an altitudinal gradient in the Bernese Alps, Switzerland

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Abstract – Alpine springs are sensitive ecotones which are inhabited by highly adapted organisms. Studies on how the species assemblages change vertically have not been conducted previously. We investigated 35 natural springs along an altitudinal gradient of about 2000 m in a valley in the Bernese Alps over 2 years. The aim of this study was to investigate the changes of the macroinvertebrate assemblages of natural springs along this gradient and to find out which environmental factors determine the distribution of the species along the altitudinal gradient. The spring fauna was quantitatively sampled three times and a wide range of environmental parameters were measured. The species richness significantly decreased with increasing altitude and the composition of the species assemblages changed distinctively along the altitudinal gradient. The low-elevation springs were dominated by crenobiont species, whereas high-altitude springs were mostly inhabited by taxa typical for Alpine headwaters in general. The mid-altitudinal range was a transition zone where crenobiont and alpine species co-existed. The water temperature was an important factor determining the species richness and the composition of macroinvertebrate assemblages of the springs at different altitudes. Moss, stones and the degree of forestation also had a significant influence on the composition of the macroinvertebrate assemblages. This study helps to understand the distribution of the spring fauna along altitudinal gradients. Knowing the current distribution ranges is an important prerequisite to predict potential changes of the species distribution, caused by global change, in the future.

Key words: Macroinvertebrate assemblages / alpine springs / water temperature / climate change

Introduction

Alpine springs are usually small but complex and species-rich ecotones (Cantonati *et al.*, 2006; Gerecke and Franz, 2006). They often exhibit a mosaic-like substrate composition and a high degree of individuality regarding their macroinvertebrate assemblages (Cantonati *et al.*, 2006). Crenobiont macroinvertebrate species exclusively occur in springs, while crenophiles favour springs, but can also be found in springbrooks (Cantonati *et al.*, 2006). Surveys in the German and Italian Alps (Cantonati and Ortler, 1998; Gerecke and Franz, 2006; Sambugar *et al.*, 2006; Bottazzi *et al.*, 2011) and the French Pyrénées (Brown *et al.*, 2007) demonstrated a high α- and β-diversity for Alpine springs. This is caused by spatial and temporal hydro-ecological heterogeneity (Lassen and Savoia, 2005). Glacially fed rivers on the same altitude are dominated by snowmelt and glacial meltwater. The macroinvertebrate assemblages of those rivers differ strongly from those of groundwater-fed springs (Brown *et al.*, 2003; Hannah *et al.*, 2007). Due to their isolation and spatial fragmentation, springs are particularly vulnerable to changing environmental conditions (Woodward *et al.*, 2010). Crenobiont species are potentially endangered by impacts of climatic changes, especially if they have a restricted distribution area (Hering *et al.*, 2009). Until now, studies referring to climatic changes in the context of freshwaters either concentrate on single species (Taubmann *et al.*, 2011), a species group (Altermatt *et al.*, 2014) or focus on general aquatic ecosystems (Daufresne *et al.*, 2007; Khamis *et al.*, 2013).

Some studies investigating at the macroinvertebrate species composition along altitudinal gradients in aquatic systems exist (Burgherr and Ward, 2001; Henriques-Oliveira and Nessimian, 2010; Obertegger *et al.*, 2010), but until now no studies have been conducted in springs and springbrooks. As crenobionts are usually thought to

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be cold-water adapted species, a high occurrence of crenobionts in high Alpine, cold-water springs can be assumed. It is, however, still unclear whether or how the composition of the macroinvertebrate assemblages of springs changes along altitudinal gradients. One of the reasons may be owing to the lack of fine-grained faunistic data and information on the thermal preferences of the species (Hering *et al.*, 2009). In our study, we investigated natural springs along an altitudinal gradient of about 2000 m in a valley in the Bernese Alps. The aim of the study was to investigate the macroinvertebrate assemblages and corresponding environmental parameters of natural springs at different altitudes. We had two leading questions, namely: (1) Does the faunistic composition significantly change along the altitudinal gradient? (2) Is the water temperature the driving environmental factor for this potential change? Possible consequences of climatic changes for springs and their inhabitants in Alpine regions are then discussed.

Methods

Field investigations

Thirty-five springs were located with the help of topographic maps and a direct search in the field in summer and autumn 2010 (Fig. 1) (Table 1). Subsequently we mapped suitable springs, *i.e.*, natural springs and their surroundings. The mapping of the springs was conducted with an evaluation sheet developed for springs in Bavaria, Germany (Hotzy and Römheld, 2008). This comprises, for example, the substrate composition of the springs, anthropogenic impacts such as cattle trampling or water withdrawal and mapping of the surrounding vegetation. The substrate composition was determined by visually estimating the percentage of coverage of each substrate present within the first 5 m of the outflow. The percentage of coverage was categorized into three intensity classes given in the evaluation sheet: 0 = 0% coverage; 1 = 1–10% coverage; 2 = 10–50% coverage; 3 ≥ 50% coverage. As the focus of the study was on natural springs, the anthropogenic impacts were low and we only classified if they were present (= 1) or not (= 0). The vegetation in the surrounding perimeter of approximately 5 m around the outflow of the spring was mapped. The percentage of coverage of conifers, deciduous forest and grassland was determined (0 = 0% coverage; 1 = 1–10% coverage; 2 = 10–50% coverage; 3 ≥ 50% coverage) and from that the total forest coverage around the spring was assessed. Moreover, the vascular plants were determined to species level within 1 m around the springs (Lauber and Wagner, 2001). Mosses and not flowering grasses were disregarded. Summer and winter shading were assessed photographically by taking a photograph of the sky above the spring. The percentage of shading was assessed and categorized as follows: 0 = 0% shading; 1 = 1–10% shading; 2 = 10–50% shading; 3 ≥ 50% shading (Table 2).

Water temperature (°C), oxygen concentration and saturation (mg.L^{-1} and%, respectively), pH and conductivity (μS.cm^{-1}) were measured in the field using a Multi-Parameter Water Quality Meter (Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, WTW 3500i). Discharge was determined by measuring the amount of water entering a plastic bag in 5 s (Zollhöfer, 1997). The discharge of the investigated springs was classified in three levels: 1 < 0.5, 2 = 0.5–2 and 3 > 2 L.s^{-1}.

The nutrient parameters phosphate (PO_4^{3-}), ammonia (NH_4^+) and nitrate (NO_3^-) were analyzed in the field with a portable photometer (MERCK Spectroquant NOVA 60).

The macroinvertebrates of all springs were quantitatively sampled in spring 2011, autumn 2011 and summer 2012 with a small Surber sampler (0.01 m^2, 500 μm mesh width). At each sampling occasion four samples were taken proportionally to the main substrate types in the first 5 m after the outflow (von Fumetti *et al.*, 2007). Samples were taken by gently shoveling the substrate within the 10 × 10 cm-frame of the surber sampler into the net of the sampler. After flushing the samples into a white dish the samples were washed with spring water and immediately preserved in 70% ethanol (von Fumetti *et al.*, 2006). In the laboratory, they were sorted and the organisms were identified to the most precise taxonomic level possible (*e.g.*, Aubert, 1959; Schmedtje and Kohmann, 1988; Studemann *et al.*, 1992; Tachet, 2000; Glöer, 2002; Waringer and Graf, 2011; Lubini *et al.*, 2012).

Data processing and analysis

All of the investigated springs were categorized into three altitudinal classes: lowland springs from 500 to 1600 m a.s.l., intermediate springs from 1600 to 1950 m a.s.l. and high Alpine springs above 1950 m a.s.l. The intermediate level is the transition zone where the treeline is located. It separates the lower zone, dominated by dense mixed forest, from the higher zone, dominated by open meadows with few single conifers and shrubs.

The faunistic data of the four samples we took from each spring, on each sampling occasion, were pooled. The three seasonal samples were subsequently also pooled. The final data set thus consisted of one data point per spring, originally derived from 12 single samples.

We performed a linear correlation analysis with the abiotic parameters, the number of macroinvertebrate taxa and the number of macroinvertebrate individuals as a function of altitude in PAST 2.09 (PAleontological STatistcs Version 2.09, Hammer, 2011).

Combined environmental and macroinvertebrate assemblages data were analyzed using Canonical Correspondence Analysis (CCA) with CANOCO 5.0 (ter Braak and Šmilauer, 1998). The distance of the species dissimilarity is measured by their chi-square. All species data were (log*e* + 1)-transformed prior to analyses, which were performed with a forward selection of explanatory variables.

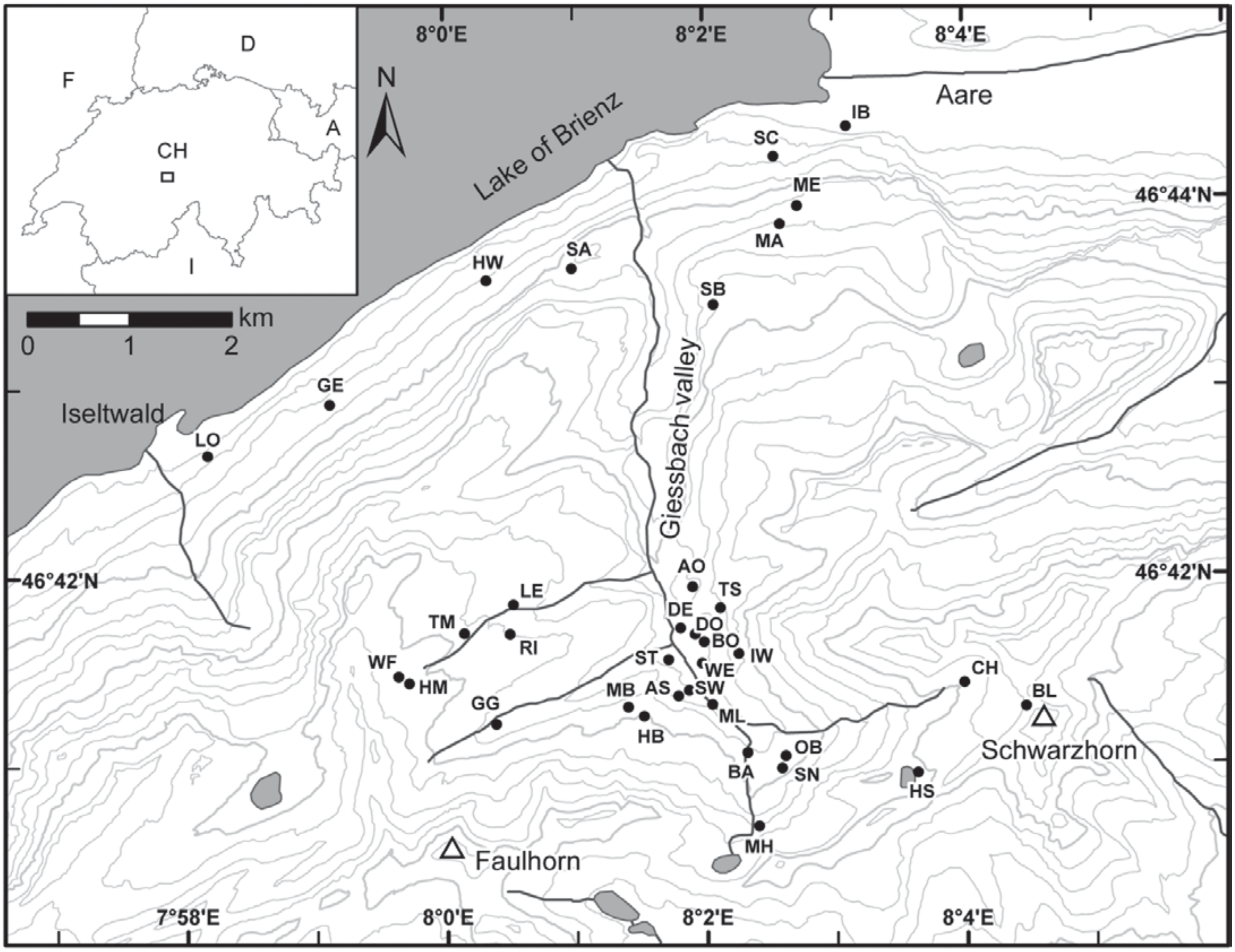

Fig. 1. Map of the investigation area in the Bernese Alps (Switzerland). ● = spring sites; 100 m isolines, based on DHM25 (Swisstopo).

All further statistical analyses described below were calculated using PRIMER 6.0 (Clarke and Gorley, 2006). Ordination of the springs, based on the faunistic data, was conducted using non-metric multi-dimensional scaling (nMDS). An analysis of similarities-procedure (ANOSIM), which is analogous to an ANOVA, but relies on a similarity matrix and makes few assumptions on data, was used for testing the grouping of the springs. The similarity matrix was calculated from Loge $(x+1)$ – transformed abundance data, using the Bray–Curtis similarity index. We tested for differences of the macroinvertebrate assemblages among the three altitudinal zones. The Global Test gives the overall observed R statistic, whereas the pairwise test directly compares rank dissimilarities between and within two groups (Clarke and Gorley, 2006).

We subsequently ran a Similarity Percentages (SIMPER) analysis to assess dissimilarities between and similarities within altitudinal zones, and to identify the taxa that discriminate between the zones. The lower the similarity within groups and the higher the dissimilarity between groups is, the higher the β-diversity is.

Results

Environmental parameters

The pH of the springs ranged from 7.3 (spring BA) and 8.9 (spring ML) and the oxygen saturation ranged from 49% (springs MH and TM) to 95% (spring ME). The conductivity ranged from 18 $\mu S.cm^{-1}$ (spring MH) to 519 $\mu S.cm^{-1}$ (spring MA). The number of vascular plants was highest around the spring SA at 1050 m a.s.l. At some springs above 1950 m a.s.l. no vascular plants were present around the springs (Table 1).

The linear correlation analysis revealed an inverse correlation of water temperature with altitude (*r*, -0.760; *P*, 0.0001). The springs at the intermediate altitudinal range situated around the treeline showed a higher heterogeneity of water temperature.

The linear correlation analysis of vascular plant diversity and altitude showed a significant inverse correlation (*r*, -0.533; *P*, 0.001). Likewise, conductivity also significantly decreased with altitude (*r*, -0.517; *P*, 0.002).

Table 1. Location and measured environmental parameters of the investigated springs.

	Code	Altitude (m)	Coordinates (WGS_84)	pH	Oxygen saturation (%)	Oxygen content (mg.L^{-1})	Temperature (°C)	Conductivity (µS.cm^{-1})	Phosphate (mg.L^{-1})	Ammonia (mg.L^{-1})	Nitrate (mg.L^{-1})	No. of vascular plants
Blaugletscherli	BL	2700	46°41.22′N, 8°4.4′E	8.0	68	7.3	1.2	80	< 0.1	< 0.01	< 0.1	0
Chessel	CH	2510	46°41.35′N, 8°3.93′E	8.0	78	7.5	1.8	20	n.m.	0.01	3.5	3
Häxeseeli	HS	2464	46°40.87′N, 8°3.56′E	8.0	57	4.9	1.4	169	0.18	0.01	2.5	3
Mittagshorn	MH	2200	46°40.59′N, 8°2.34′E	7.9	49	4.2	2.6	18.3	n.m.	0.01	1.4	3
Wandflue	WF	2011	46°41.39′N, 7°59.57′E	7.7	65	6.7	4.3	330	< 0.1	< 0.01	< 0.1	0
Schwarzenboden	SN	2010	46°40.9′N, 8°2.52′E	8.3	82	8.7	3.5	294	0.18	0.01	1.2	6
Hübschenmatten	HM	2077	46°41.18′N, 8°1.46′E	7.5	65	6.8	4.3	339	< 0.1	< 0.01	< 0.1	0
Hüttliboden	HB	1990	46°41.23′N, 8°1.34′E	8.1	70	7.3	2.6	39.8	n.m.	0.01	1.7	10
Marchboden	MB	1974	46°41.62′N, 8°0.43′E	7.7	94	9.9	3.6	186.7	0.05	0.06	0.4	4
Riseten	RI	1950	46°41.62′N, 8°0.08′E	7.4	54	5.2	7.4	456	0.12	0.08	1.0	5
Teufenmatte	TM	1906	46°40.96′N, 8°2.55′E	7.9	12	0.8	7.1	321	< 0.1	< 0.01	< 0.1	0
Oberberg	OB	1880	46°41.24′N, 8°1.98′E	7.05	65	6.2	9.2	112	0.2	0.01	1.0	8
Mittlisten	ML	1860	46°41.14′N, 8°0.32′E	8.9	93	8.8	8.9	44.8	0.1	0.04	1.0	12
Geissgang	GG	1857	46°41.77′N, 8°0.46′E	7.9	90	8.7	7.2	240	0.06	n.m.	< 0.1	8
Lägeregg	LE	1854	46°40.98′N, 8°2.25′E	7.8	75	7.3	6.6	462	0.24	0.02	0.9	9
Blatti	BA	1820	46°41.51′N, 8°2.19′E	7.3	60	5.9	7.2	155.8	0.12	0.02	0.5	7
Im Wengen	IW	1772	46°41.28′N, 8°1.72′E	7.8	90	9.7	6.2	211	0.15	0.05	1.2	7
Am Schweiffi	AS	1750	46°41.31′N, 8°1.8′E	8.2	81	8.1	7.2	263	0.07	0.01	1.0	9
Schweiffi	SW	1710	46°41.75′N, 8°2.05′E	8.2	94	10.1	4.6	188.2	0.13	0.04	0.6	7
Torwangspitz	TS	1748	46°41.46′N, 8°1.91′E	8.2	92	9.9	3.9	35.2	0.43	0.02	2.7	10
Wehri	WE	1680	46°41.61′N, 8°1.85′E	8.1	83	8.5	6.5	223	0.06	0.01	1.0	8
Dürrenegg Ost	DO	1645	46°41.48′N, 8°1.65′E	8.0	83	8.4	6.7	270	0.07	0.01	0.6	9
Schärmtanni	ST	1630	46°41.64′N, 8°1.74′E	8.0	92	9.1	7.6	229	n.m.	n.m.	1.0	6
Dürrenegg	DE	1625	46°41.57′N, 8°1.92′E	7.9	69	7.4	5.5	220	0.22	0.04	1.5	18
Bödeli Ost	BO	1625	46°41.86′N, 8°1.84′E	8.2	91	9.5	5.5	184.7	0.05	n.m.	1.0	10
Alpogli	AO	1550	46°43.36′N, 8°2.01′E	8.0	94	10	5.3	224	0.1	< 0.01	1.8	12
Schwarzenberg	SB	1380	46°43.78′N, 8°2.53′E	8.1	85	8.8	6.6	506	0.2	0.01	1.2	7
Margel	MA	1200	46°43.88′N, 8°2.66′E	7.8	82	8.6	6.7	519	0.08	0.08	1.1	10
Meyerhofstatt	ME	1100	46°43.55′N, 8°0.92′E	7.8	96	10.1	8	472	0.39	0.36.	1.2	11
Schweibealp	SA	1050	46°42.84′N, 7°59.05′E	7.5	55	5.7	7.8	431	0.08	0.08	1.6	20
Geeri	GE	900	46°43.49′N, 8°0.26′E	8.3	93	9.6	9.2	326	0.15	0.15	0.6	8
Hagweid	HW	850	46°44.14′N, 8°2.48′E	8.0	93	10.2	7.5	258	0.15	0.15	2.3	11
Schwendli	SC	750	46°42.57′N, 7°58.11′E	7.8	52	4.9	12	386	0.08	0.08	0.9	8
Louberli	LO	650	46°44.3′N, 8°3.04′E	8.4	92	9.2	12.2	374	0.11	0.05	1.3	8
Im Brunnen	IB	550	46°41.36′N, 7°59.65′E	7.9	58	6.7	7.5	308	0.19	0.01	0.7	12

n.m., not measured; < 0.1 and < 0.01, below detection limit.

Species richness

A total of 114 species and higher taxa were found in the 35 investigated springs (Supplementary material). The number of taxa ranged between 4 in the highest elevated spring BL (2700 m a.s.l.) and 32 in the spring SW (1710 m a.s.l.) (mean ± SD: 20.2 ± 7). The number of individuals found in each spring was highest in the spring MH at 2200 m a.s.l. with 1963 individuals and lowest in BL at 2700 m.a.s.l. with 24 individuals (mean ± SD: 527 ± 419). Generally, Chironomidae was the most abundant taxon in all springs and especially in spring MH.

Overall, the number of taxa was highest at the lowest altitudinal level up to 1400 m a.s.l. and lowest in the high Alpine springs above 1950 m a.s.l. The number of taxa showed a significant correlation with altitude (*r*, − 0.402; *P*, 0.018). The number of individuals did not show a significant correlation with altitude (*r*, 0.170; *P*, 0.341), although we observed a slight increase with altitude.

The lowest springs situated between 500 and 1600 m a.s.l. were characterized by crenobiont taxa such as the trichopterans *Crunoecia irrorata* (Curtis, 1834), *Beraea maurus* (Curtis, 1834) and the gastropod *Bythinella* sp. Moreover, some crenobiont water mites were only present in these lowest springs. For example, *Sperchon squamosus* Kramer, 1879 only occurred in the springs ME (1100 m a.s.l.) and SC (750 m a.s.l.) and *Protzia squamosa* Walter, 1908 only occurred in the spring GE at 900 m a.s.l.

The springs located above 1900 m a.s.l. were inhabited by many Alpine species not restricted to springs. For example, *Consorophylax consors* (McLachlan, 1880), *Drusus biguttatus* (Pictet, 1834) and *Rhyacophila intermedia* McLachlan, 1868 were most abundant in high Alpine springs. The highest abundance of Chironomidae was found in the highest elevation springs.

The intermediate altitudinal zone can be considered as a transition zone, where typical crenobiont species, *e.g.*, *Beraea pullata* (Curtis, 1834), and high Alpine species, *e.g.*, *Drusus discolor* (Rambur, 1842), co-exist. At the intermediate altitude species richness of the water mites was highest. Some species such as *Lebertia schechteli* Thor, 1914 occurred from 1600 m a.s.l. upwards, whereas others such as *Sperchon longirostris* Koenike, 1895 occurred exclusively at the intermediate altitude.

The nMDS-plot, based on the faunistic data, revealed a clear separation of the altitudinal classes in assemblages' composition (Fig. 2). The corresponding ANOSIM significantly separated the three altitudinal ranges (Global *R*, 0.47; *P*, 0.001). The pairwise test showed that the species assemblages of springs at high and low altitudes, as well as of springs at intermediate and high altitudes differed, significantly (*R*, 0.557; *P*, 0.001; R: 0.544, *P*: 0.001, respectively). Low and intermediate springs were less clearly, but still significantly, separated (*R*, 0.324; *P*, 0.002).

In the SIMPER analysis group 1 (high springs) had an average similarity of 26%, group 2 (intermediate springs) of 42% and group 3 (low springs) of 26%. The β-diversity was therefore lowest in the intermediate springs. The average dissimilarity scored 69% between groups 1 and 2, 79% between groups 1 and 3, and 84% between groups 2 and 3, indicating a high β-diversity along the altitudinal gradient. Generally all groups were dominated by Chironomidae.

Relationship between species and environmental variables

All environmental variables together explained 71.9% of the variance (the adjusted explained variation is 20.3%) in the CCA. The significant explanatory variables accounted for 32.9% of the variance. The first four canonical axes explained 28.4% of the species variation (the explained fitted variation is 39.6%; Table 3). On all axes the permutation test was significant (pseudo-*F*, 1.4; *P*, 0.002). The CCA clearly separated three groups of springs primarily based on the variation in temperature, moss availability and altitude. Furthermore, the amount of stones, the degree of forestation and the ammonia content had a significant explanatory power (Fig. 3(a)). These three groups more or less represent the three altitudinal levels, with the lowest springs being influenced mainly by forestation, high ammonia contents and the water temperature. The springs at high altitudes were dominated by moss.

The taxon biplot identified the taxa associated with the three springs' groups (Fig. 3(b)). For example, the caddisfly *C. irrorata*, the amphipod *Gammarus fossarum* Koch, 1836 and certain water mite species only occurred in the forested springs. The limnephilid caddisflies *D. biguttatus* and *C. consors* were only present in the high Alpine springs dominated by moss. The Stratiomyidae *Oxycera morrisii* Curtis, 1833 and *Beris vallata* (Forster, 1771), and the stonefly *Nemoura mortoni* Ris, 1902 were present in the third group of springs around the forest located at the intermediate altitude between 1600 and 1950 m a.s.l.

Discussion

The composition of species assemblages clearly changed along the altitudinal gradient with characteristic species assemblages in each altitudinal zone. We recorded a significant decrease of species richness with increasing altitude.

Springs in the Alps at lower elevations were characterized by a typical crenal biocoenosis: the lowest springs situated between 500 and 1600 m a.s.l. were characterized by crenobiont taxa. Especially many water mite species are restricted to springs and are even adapted to certain spring types (Gerecke and Di Sabatino, 1996). For example, *Partnunia steinmanni* Walter, 1906 and *S. squamosus* are restricted to springs below 1400 m a.s.l. (Gerecke and Martin, 2006). *P. squamosa* is a typical crenobiont species of forested helocrenes and rheocrenes (Gerecke and Martin, 2006).

Table 2. Classified environmental parameters.

	Discharge	Dead wood	Moss	Leaf litter	Needles	Detritus	Calcareous tufa	Stones	Gravel	Conifers	Deciduous forest	Grassland	Shading winter	Shading summer	Utilization	Cattle damage
Blaugletscherli	3	0	0	0	0	0	0	3	3	0	0	0	3	1	0	0
Chessel	3	0	2	0	0	0	0	3	3	0	0	3	2	2	0	0
Häxeseeli	3	0	1	0	0	0	0	3	2	0	0	3	3	1	0	0
Mittagshorn	3	0	3	0	0	0	0	3	3	0	0	0	3	2	0	0
Wandflue	3	0	3	0	0	0	2	0	1	0	0	2	1	1	0	1
Schwarzenboden	3	0	3	0	0	0	0	2	2	0	0	3	2	1	0	0
Hübschenmatten	3	0	3	0	0	3	0	1	0	0	0	3	1	1	1	0
Hüttliboden	3	0	3	0	0	0	0	3	3	0	0	3	3	1	0	0
Marchboden	2	3	0	0	0	2	0	1	1	0	3	1	0	0	0	0
Riseten	1	2	0	0	0	1	3	3	2	0	3	0	0	0	1	0
Teufenmatte	2	0	1	0	0	1	0	1	0	0	0	2	0	0	0	0
Oberberg	2	2	0	0	0	1	0	0	1	0	2	1	1	1	1	0
Mittlisten	2	2	3	0	1	2	0	0	3	0	0	3	2	1	0	0
Geissgang	3	2	0	0	0	2	0	1	2	1	3	1	1	1	0	0
Lägeregg	3	2	0	0	0	1	1	1	2	1	3	1	0	0	2	1
Blatti	2	2	0	0	0	2	0	3	2	1	3	2	1	1	1	1
Im Wengen	2	2	1	1	1	2	0	3	2	2	2	2	1	1	0	0
Am Schweiffi	2	2	0	0	0	2	0	2	1	2	3	2	1	1	0	0
Schweiffi	2	0	3	0	0	2	0	2	1	3	0	3	2	2	0	0
Torwangspitz	3	3	3	1	1	0	0	0	0	3	0	2	3	2	0	0
Wehri	3	3	0	0	0	1	0	1	2	2	2	2	1	1	1	1
Dürrenegg Ost	2	2	2	2	1	1	0	1	1	2	3	2	3	3	0	0
Schärmtanni	2	2	1	1	1	3	0	2	2	2	3	3	2	2	0	1
Dürrenegg	3	2	3	0	1	1	0	0	2	2	0	2	2	2	0	0
Bödeli Ost	1	2	1	1	1	1	0	2	2	1	3	3	2	2	0	0
Alpogli	3	3	3	0	2	0	0	2	2	3	0	3	3	3	0	0
Schwarzenberg	3	3	3	3	2	2	3	0	0	2	1	0	3	3	0	0
Margel	2	2	3	1	1	1	3	1	0	2	1	2	2	2	1	1
Meyerhofstatt	3	2	3	1	1	0	3	3	2	2	0	2	3	2	0	0
Schweibealp	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geeri	3	3	3	3	1	0	3	0	0	1	1	2	3	2	0	1
Hagweid	1	3	2	3	1	0	0	2	2	1	1	2	3	3	0	0
Schwendli	1	2	2	1	1	1	0	1	0	1	0	2	3	3	0	1
Louberli	2	2	3	1	1	3	3	1	1	1	1	0	3	2	1	0
Im Brunnen	1	3	1	3	1	2	2	2	2	1	1	2	2	3	0	0

Discharge: 1 (low) < 0.5 $L.s^{-1}$, 2 (intermediate) = 0.5–2 $L.s^{-1}$, 3 (high) > 2 $L.s^{-1}$; Substrate composition and surrounding vegetation: 0 = 0% coverage, 1 = 1–10% coverage, 2 = 10–50% coverage, 3 ≥ 50% coverage; Shading summer and winter: 0 = 0% shading, 1 = 1–10% shading, 2 = 10–50% shading, 3 ≥ 50% shading; Utilization and cattle damage: 1 = present, 0 = not present.

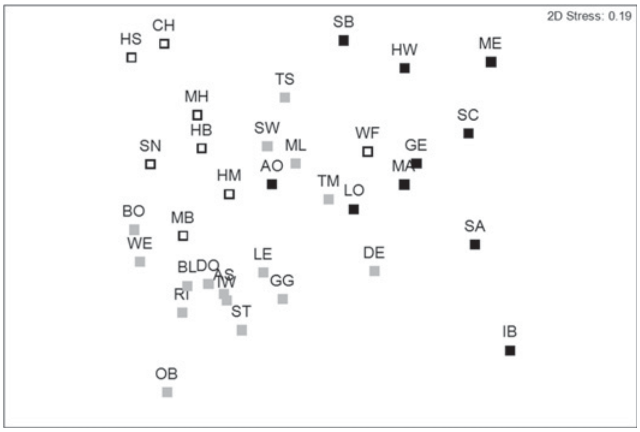

Fig. 2. nMDS of the investigated springs based on the faunistic data. Similarity index: Bray–Curtis; transformation: square root; factor: altitudinal level (■ = low altitudinal level: 500–1600 m a.s.l.; ▨ = intermediate altitudinal level: 1600–1950 m a.s.l.; □ = high altitudinal level: > 1950 m a.s.l.).

Springs in the Alps at high elevations were characterized by a typical Alpine rhithral biocoenosis: the springs located above 1900 m a.s.l. are inhabited by many Alpine species which are adapted to constant low water temperatures. *Consorophylax consors*, *D. biguttatus*, *Drusus monticola* McLachlan, 1876 and *R. intermedia* are adapted to the crenal and rhithral zones of high Alpine headwaters (Graf *et al.*, 2006). It is known that especially the subfamily Diamesinae of the Chironomidae is adapted to constantly low water temperatures and is the first to colonize glacier-fed brooks (Ward, 1994; Füreder *et al.*, 2001).

The transitional intermediate altitudinal zone was inhabited by typical crenobiont species as well as high Alpine species. *Drusus discolor* and *N. mortoni* are typical Alpine species (Bottazzi *et al.*, 2011; Waringer and Graf, 2011). *Oxycera morrisii*, *B. vallata* and *B. pullata* are not limited to the Alps, but can be considered as crenophile or even crenobiont species (Rozkosny, 2000; Waringer and Graf, 2011).

The water temperatures of the investigated springs decreased with increasing altitude as it has been shown previously, for instance, for springs in the Swiss National Park (Robinson *et al.*, 2008) and the Adamello-Brenta Natural Park (Cantonati, 1998). At the intermediate altitude (1600–1950 m a.s.l.) the springs exhibited a greater heterogeneity of water temperature than those at lower and higher altitudes. This is probably due to the patchy structure of the landscape: the springs at the intermediate level are located around the treeline and therefore some springs are situated in dense forest, whereas others emerge on open countryside and are influenced by solar radiation to a higher degree.

Water temperature is one of the factors which strongly influences the species composition in freshwater ecosystems in general (*e.g.*, Jacobsen *et al.*, 1997; Jacobsen, 2003). For springs, the water temperature has been identified as an important environmental variable explaining the composition of species assemblages both on the small (Bottazzi *et al.*, 2011) and large spatial scale (Gathmann *et al.*, 2009; Ilmonen *et al.*, 2009). The results of our study revealed a strong temperature dependence of species assemblages. Water temperature mainly determined the faunal transition along the altitudinal gradient, from crenobiont species at low altitudes to Alpine, cold-water-adapted species at higher altitudes. These also occurred in the rhithral reaches of high Alpine streams. Crenobionts are confined to springs for a number of reasons, such as habitat stability (van der Kamp, 1995), competition (Fischer, 1996; Wagner *et al.*, 1998) and substrate availability (Hahn, 2000; Ilmonen and Paasivirta, 2005). We therefore conclude that the adaptation to low water temperatures is not the main reason for crenobiosis, *i.e.*, the restriction of occurrence in springs.

We recorded a strong influence of the presence of moss and stones on the species assemblages. Moss is

Table 3. Summary of CCA eigenvalues, cumulative percentage of variance explained on the first four canonical axes, significance of all canonical axes and significant environmental variables identified by a forward selection of the explanatory variables.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.37	0.27	0.21	0.19
Species environment correlation	0.98	0.98	0.99	0.95
Cumulative percentage of variance				
Explained variation (cumulative)	10.04	17.36	23.14	28.44
Explained fitted variation (cumulative)	13.96	24.15	32.2	39.57
	F ratio			
Significance of all canonical axes	1.4**			
Significant environmental variables				
Altitude	2.6**			
Moss	2.3**			
Temperature	1.7*			
Stones	1.5*			
Forestation	1.6*			
Number of plants	1.4*			
Calcareous tufa	1.4*			
Ammonia	1.5*			

*$P < 0.05$; **$P < 0.005$.

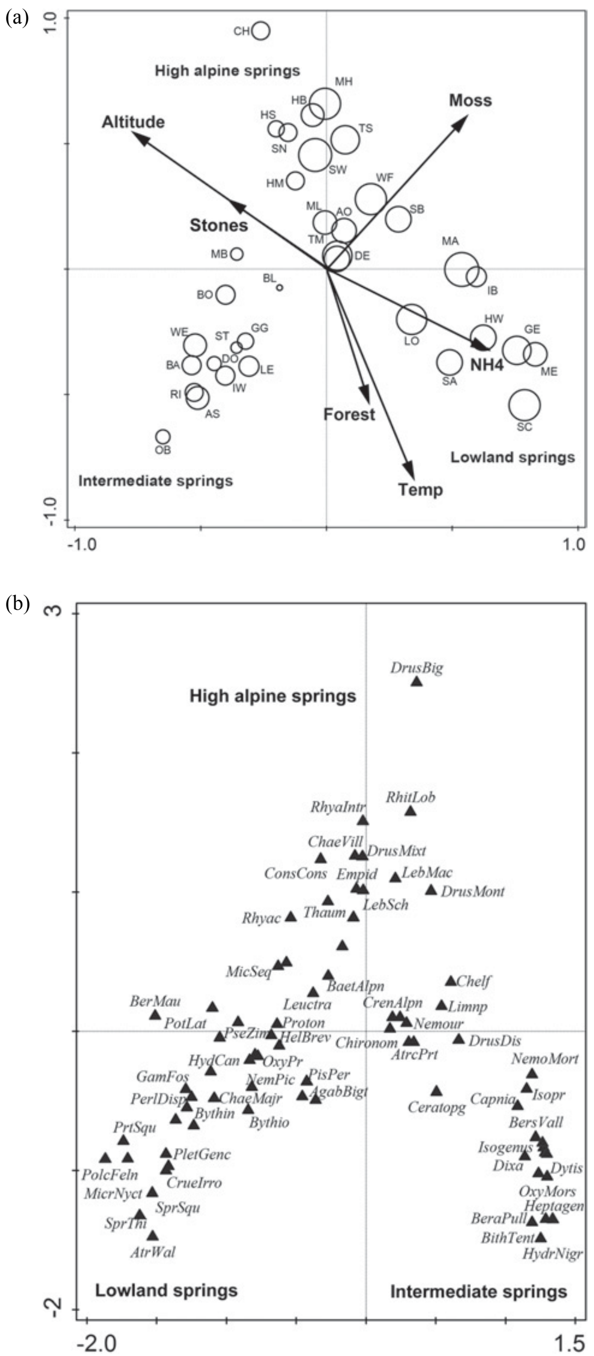

Fig. 3. a, b: Ordination of (a) 35 sites and (b) 108 taxa by a CCA. The environmental variables with the highest explanatory power in the model are indicated by arrows. The size of the circles (a) displays the number of taxa present. A few taxa near the center with low explanatory power, and taxa with single occurrences, have been omitted.

an important factor, which positively influences species richness, functioning as a food source and habitat for example for the caddisfly *C. irrorata* (Ilmonen and Paasivirta, 2005) and for many water mites (Gerecke and Di Sabatino, 1996) in springs. The surface of stones is colonized by diatoms, which are subsequently consumed by scrapers, which dominate at high altitudes (Füreder *et al.*, 2001). Moreover, the CCA revealed a significant influence of the degree of forestation on the composition of the species assemblages. A significantly higher number of vascular plants were found around the springs at the lower altitudes. This leads to a higher input of allochthonous coarse particulate organic matter (CPOM) into the springs, which is especially important for shredders such as *G. fossarum* (*e.g.*, Simcic and Brancelj, 2006). Indeed, this very important species for the food web of headwaters (Dangles *et al.*, 2004), providing fine particulate organic matter (FPOM) for gathering collectors and filtering collectors, was only present in this study in lower springs situated in a beech forest. Another reason for the absence of *G. fossarum* may be found in the last glaciation: the central Alps still have to be recolonized by amphipods (Cantonati *et al.*, 2006).

Studies predict that montane regions will be affected more strongly by climatic changes than the lowlands (*e.g.*, Bush *et al.*, 2012; Perroud and Bader, 2013; CH2014-Impacts, 2014). Range shifts have already been shown for freshwater species (*e.g.*, Vittoz *et al.*, 2013). However, adaptation via range shifts is constrained by catchment boundaries and the dispersal capabilities of the single species (Bush *et al.*, 2012). We conclude that an upwards migration of spring species in the Alps will potentially be possible for species in low altitudinal springs. An upwards migration is, however, not possible for species already living in the highest springs (*i.e.*, summit trap phenomenon (Thuiller *et al.*, 2005; Bässler *et al.*, 2010)). They are at risk of going extinct in the future (Vittoz *et al.*, 2013).

Conductivity decreased with increasing altitude. Changes in conductivity may indicate a changing ratio of ground water, snow melt and glacial meltwater contribution to stream flow (Brown *et al.*, 2003; Hannah *et al.*, 2007), with increasing contributions of meltwater with increasing altitude. High meltwater contributions lead to a decrease of the α-diversity (Brown *et al.*, 2007). For high altitudes we can conclude that a decreased contribution of snow and glacial meltwater will increase the α-diversity (Brown *et al.*, 2007). The β-diversity will decrease due to the lower habitat heterogeneity caused by the recession of extreme habitats (Brown *et al.*, 2007; Jacobsen and Dangles, 2012). Springs at intermediate altitudes around the treeline exhibited the lowest β-diversity. This may be caused by the vertical dispersal of taxa from higher and lower springs, *i.e.*, crenobiont and alpine rhithral species. Those springs may be additionally affected by land use changes. Forest expansion is mainly driven by the abandonment of grasslands in the Alps (Guidi *et al.*, 2014). In our study area the patchy open land structures are becoming visibly overgrown mostly by *Alnus viridis* (Fabian Wigger, personal observation). This could further diminish the β-diversity, as the reduced landscape patchiness could reduce the spring habitat diversity and lead to a standardization of the faunistic assemblages. It is unclear how Alpine freshwaters will exactly respond to the proceeding global change. Based on the current state of research it can be assumed that climatic changes will have severe impacts on the spring fauna at all altitudinal levels.

Conclusions

This is one of the first studies investigating the distribution pattern of macroinvertebrate assemblages in springs along an altitudinal gradient. The composition of the marcoinvertebrate assemblages clearly changed along the altitudinal gradient; we found characteristic species assemblages at each altitudinal level, with the crenobiont species occurring in the lowest springs, Alpine species occurring in the highest springs and both crenobiont and Alpine species occurring in the springs at the intermediate altitudes. Furthermore, we were able to show that the water temperature has a large influence on the fauna composition of the springs along an altitudinal gradient. Although we have been able to shed some light into the current composition of macroinvertebrate assemblages of springs along an altitudinal gradient, it is not clear what effect global change will have. The current situation is complex and detailed field research is still necessary to understand the functioning of Alpine spring ecosystems.

Supplementary material 1a, 1b, 1c

List of presence (+) and absence (−) of the 108 taxa at each investigated site.

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	BL	CH	HS	MH	WF	SN	HM	HB	MB	RI	TM	OB	ML	GG	LE	BA	IW	AS	SW	TS	WE	DO	ST	DE	BO	AO	ScB	MA	ME	SA	GE	HW	SC	LO	IB
Turbellaria																																			
Crenobia alpina (Dana) 1766	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Polycelis felina (Dalyell) 1814	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–
Mollusca																																			
Bithynia tentaculata (Linnaeus) 1758	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Bythiospeum	–	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	+	+	+	+	+	+	–
Galba truncatula (O.F. Müller) 1774	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Gyraulus Charpentier, 1837	–	–	–	–	+	–	–	–	–	–	–	–	–	–	+	–	+	+	–	+	–	+	–	–	+	–	+	–	–	+	+	+	+	+	+
Gyraulus crista (Linnaeus) 1758	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	+	+	–	–	+	–	+
Radix sp.	–	–	–	–	+	–	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	+	+	–
Valvata piscinalis alpestris (Küster) 1852	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–
Bythinella sp. Moquin–Tandon, 1856	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	–	–	+	–	+	–	+
Pisidium cf. *personatum* Malm, 1855	–	–	–	–	+	–	+	–	–	–	+	+	–	–	–	–	–	+	+	–	–	–	+	+	–	–	–	+	–	+	–	–	–	–	+
Oligochaeta																																			
Eiseniella tetraedra (Savigny) 1826	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	+	+	–
Acari																																			
Atractides sp. Koch, 1837	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Atractides protendens K. O. Viets, 1955	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+
Atractides walteri (K.Viets, 1925)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
Hydrovolzia cancellata Walter, 1906	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–
Hydrovolzia placophora (Monti) 1905)	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hygrobates norvegicus (Thor) 1897	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Lebertia cuneifera Walter, 1922	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Lebertia cf. *elsteri* Schwoerbel, 1957	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Lebertia lativentris K. Viets, 1922	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–
Lebertia maculosa Koenike, 1902	–	+	–	+	–	+	–	–	–	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lebertia schechteli Thor, 1913	–	–	–	+	–	+	+	+	–	–	–	–	+	–	–	–	–	–	+	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Panisus michaeli Koenike, 1896	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Partnunia steinmanni Walter, 1906	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	–	–	–	–	+	–	–	–
Protzia squamosa Walter, 1908	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Sperchon (s.str.) sp.	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sperchon longirostris Koenike, 1895	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	+	+	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Sperchon mutilus Koenike, 1895	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Sperchon squamosus Kramer, 1879	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–
Sperchon thienemanni Koenike, 1907	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
Crustacea																																			
Gammarus fossarum Koch, 1836	–	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	+	+	+	+	+	+	+
Asellus aquaticus Linnaeus, 1758	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	–	–	–	+	–

	BL	CH	HS	MH	WF	SN	HM	HB	MB	RI	TM	OB	ML	GG	LE	BA	IW	AS	SW	TS	WE	DO	ST	DE	BO	AO	ScB	MA	ME	SA	GE	HW	SC	LO	IB
Ephemeroptera																																			
Heptageniidae	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhithrogena lobata – group	–	+	–	–	+	–	–	–	–	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ecdyonurus sp. Eaton, 1868	–	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Baetis alpinus (Pictet) 1843	–	–	+	+	–	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	+	–	+	+	–	–	–	–	–	–
Paraleptophlebia sp.	–	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Plecoptera																																			
Capnia sp.	–	–	–	–	–	–	–	–	+	–	–	–	–	+	+	+	+	+	–	–	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Leuctra sp.	–	+	–	+	+	–	–	+	+	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	–	+	–	+	–	+	+	+	+	+	+
Nemoura sp.	–	+	+	+	+	+	+	+	+	+	+	–	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	+	+	–	+	–
Nemoura mortoni Ris, 1902	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Nemurella pictetii Klapalek 1900	–	–	–	–	+	–	–	–	–	–	+	–	–	+	+	–	–	–	+	–	–	–	–	+	–	–	–	+	+	–	+	–	+	–	–
Protonemura sp.	–	–	–	+	+	–	–	+	–	–	+	–	+	+	–	–	–	–	+	+	–	–	–	–	–	+	+	+	+	–	+	–	+	+	–
Perlodidae	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	+	–	–	+	–	–	–	–
Perlodes sp.	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–
Dictyogenus sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Isoperla sp.	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Coleoptera																																			
Dytiscidae	–	–	–	–	–	–	–	–	–	+	–	–	–	+	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Agabus biguttatus (Olivier) 1795	–	–	–	–	+	–	–	–	–	–	+	+	+	–	+	–	–	–	–	+	–	–	–	+	–	–	–	+	–	+	–	–	–	+	–
Agabus bipustalatus (Linnaeus) 1767	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Helophorus brevipalpis Bedel, 1881	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–	–	–
Hydraena nigrita Germar, 1824	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hydraena minutissima Stephens, 1829	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Trichoptera																																			
Beraea maura Curtis, 1834	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+
Beraea pullata (Curtis) 1834	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Glossosomatidae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Lithax niger (Hagen) 1859	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Crunocia irrorata (Curtis) 1834	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	+	–	–
Leptoceridae	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	–	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Limnephilidae	–	+	+	+	–	+	–	+	+	–	+	+	–	–	+	+	+	+	–	–	+	+	+	+	+	+	–	+	–	+	+	–	–	–	–
Limnephilini	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acrophylax zerberus Brauer, 1867	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Allogamus uncatus (Brauer) 1859	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetopteryx major McLachlan, 1876	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–
Chaetopteryx villosa (Fabricius) 1798	–	–	+	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Consorophylax consors (McLachlan) 1880	–	–	+	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Drusus sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–

	BL	CH	HS	MH	WF	SN	HM	HB	MB	RI	TM	OB	ML	GG	LE	BA	IW	AS	SW	TS	WE	DO	ST	DE	BO	AO	ScB	MA	ME	SA	GE	HW	SC	LO	IB
Trichoptera																																			
Drusus biguttatus (Pictet) 1834	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Drusus discolor (Rambur) 1842	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	+	–	–	–	–	+	–	–	–	–	–
Drusus mixtus Pictet, 1834	–	+	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Drusus monticola McLachlan, 1876	–	+	–	+	–	–	–	+	+	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	+	+	–	–	–	–	–	–	–	–	–
Leptotaulius gracilis Schmid, 1955	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–	–
Limnephilus coenosus Curtis, 1834	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Micropterna lateralis (Stephens) 1837	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	+	+	–	–
Micropterna nycterobia McLachlan, 1875	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
Micropterna sequax/lateralis Schmid, 1957	–	–	+	+	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	+	–	+	–	–	–	+	–	–	–	–	+
Pletrocnemia geniculata McLachlan, 1871	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–
Potamophylax latipennis (Curtis) 1834	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+
Potamophylax rotundipennis (Brauer) 1857	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–
Parachiona picicornis Pictet, 1834	–	–	–	–	+	–	–	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–	–
Pseudopsilopteryx zimmeri (McLachlan) 1876	–	–	–	+	+	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	+	–	+	+	+	+	–	–	–	–	–	+
Rhyacophila sp. Pictet 1834	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Rhyacophila intermedia McLachlan, 1868	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sericostoma cf. *personatum* Spence, 1826	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Diptera																																			
Ceratopogonidae	+	–	–	+	+	+	+	–	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	–	+	–	–	+	+	+	+	–
Atrichopogon sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Chironomidae	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Chironominae	–	+	–	+	+	–	+	+	+	+	+	–	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Dixidae	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	+	+	–	–	–	–	–	+	–	+	+	–	+	+	+	–	–
Dixa sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Empididae	–	+	–	–	+	+	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	–	–	–	–	–	–	+	–
Clinocerinae	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–
Chelifera sp.	–	+	–	+	–	+	–	–	–	+	–	–	–	+	–	+	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–
Limoniidae	+	+	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	+	–	–	–	–	–	+	+	+	+	–	–	+	+	–	–
Antocha sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	+	–
Dicranota sp.	–	–	–	+	+	–	+	+	+	–	+	+	–	+	+	+	–	–	+	–	+	–	–	–	+	+	–	–	–	–	+	–	+	+	–
Pedicia sp.	–	–	–	–	+	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	+	–
Rhypholophus sp.	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scleroprocta sp.	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Oxycera morrisi Curtis, 1833	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oxycera cf. *pardalina* Meigen, 1809	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	+	–	+	–	+	–	+	+	–	+	+	–
Beris vallata (Forster) 1771	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Psychodidae	–	–	–	–	+	+	–	+	–	+	–	–	–	–	+	–	+	+	+	+	+	–	–	–	–	+	+	+	+	+	+	+	+	+	–
Simulium sp.	–	–	+	+	+	–	+	+	–	+	+	–	+	+	–	+	+	+	+	+	–	–	–	+	–	+	+	+	–	+	–	+	–	+	–
Tabanidae	–	–	–	+	+	+	–	+	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	+	–	+
Tipulidae	–	–	+	–	–	–	–	–	–	–	+	–	+	–	+	–	–	–	+	–	–	–	–	–	–	–	–	+	–	+	–	–	+	+	+
Thaumaleidae	–	+	+	+	–	–	–	–	–	–	+	–	+	–	–	–	+	–	+	–	–	–	–	–	–	–	+	–	–	–	–	+	+	+	–

CHAPTER FOUR

Temperature variability and its influence on macroinvertebrate assemblages of alpine springs

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Abstract

Constant water temperature is meant to be a key factor for macroinvertebrates inhabiting springs. Springs in low mountain ranges are usually fed by deep groundwater. At high altitudes they are often fed by surface-near aquifers and are influenced by snow and permafrost meltwater. In this study we examined thirteen springs in the Bernese Alps in Switzerland during one year. The aim of the study was to investigate the variability of water temperature and other physico-chemical parameters and their influence on macroinvertebrate assemblages of alpine springs at different altitudes. Water temperature and solar radiation were continuously monitored, electrical conductivity, pH and oxygen were measured, and a quantitative sampling of the macroinvertebrates was conducted three times from June 2010 to July 2011. A generalized linear model revealed a significant decrease of the variability of water temperature along the altitudinal gradient. Electrical conductivity was significantly lower in springs at high altitude indicating an influence of snow and permafrost meltwater. The percentage of alpine species significantly increased with altitude. Taxon richness and the percentage of crenobiont taxa were not significantly correlated with any physico-chemical parameter. Monthly temperature amplitude and snow cover had a

significant influence on the composition of macroinvertebrate assemblages distinguishing high alpine springs from those at lower altitude. Harsh environmental conditions with low but constant water temperatures foster alpine rhithrobiont species, also in springs.

Introduction

Natural springs are unique ecotones at the interface between surface water and groundwater (Webb et al. 1998; Gerecke and Franz 2006), which are characterised by low variability of abiotic conditions (Odum 1971; van der Kamp 1995). Thermal stability has been identified as the outstanding feature characterizing springs fed by deep groundwater (e.g. Illies 1952; van der Kamp 1995; Fischer et al. 1998) and separating them from the adjacent springbrook (e.g. Erman and Erman 1995; Von Fumetti et al. 2007). This is thought to be the reason for the presence of cold-stenothermal species (Illies 1952; Erman and Erman 1995). However, there is also evidence for some variability in the temperature regime of springs, independently of the spring type (Fischer et al. 1998; Gräsle and Beierkuhnlein 1999; von Fumetti et al. 2007). Due to their ecotonal character springs are mainly inhabited by spring specialists, so-called crenobionts, and by species also occurring in springbrooks (i.e. crenophiles). Also groundwater associated stygobiont species, species occurring in adjacent streams (i.e. rhithrobionts) and species adapted to the transition zone between land and water are found as well.

Alpine springs, i.e. springs, which are situated at the subalpine and alpine slope of mountains, can host species rich communities (Cantonati and Ortler 1998; Cantonati et al. 2006). Despite the importance of groundwater-fed springs for alpine aquatic biodiversity studies were mainly conducted on the peculiarities of glacier-fed streams (e.g., Burgherr and Ward 2001; Uehlinger et al. 2010; Jacobsen and Dangles 2012; Brown et al. 2015). Minimum temperature and channel stability were identified as main drivers for macroinvertebrate colonisation in high-alpine, glacially influenced streams (Milner et al. 2001; Brown et al, 2007). Based upon the conceptual model of Ward (1994) a classification has been proposed differentiating stream types according to contributions of glacial melt water (kryal), snow melt water (nival) and groundwater (krenal) (Brown et al. 2003; Hannah et al. 2007). Frisbee et al. (2013) found evidence that spring water is also composed of several water sources to different proportions such as unsaturated flow and snowmelt and never solely of groundwater. Recently Wigger et al. (2015) demonstrated a significant decrease of the mean water temperature and the species richness of springs along an altitudinal gradient. It is, however, still not clear, if the variability of the water temperature, i.e. the amplitude, also changes and how the macroinvertebrate assemblages are affected. In high alpine springs kryal and nival contributions to water flow may lead to a higher abiotic variability throughout the year.

In this study we investigated natural springs in the Bernese Alps at an altitudinal range from 500 up to 2500 m a.s.l. We aimed at examining, if the variance of the water temperature influences the composition of the macroinvertebrate assemblages. We hypothesize (a) that the variability of the water temperature is higher in springs at high elevation than in springs at lower altitudinal ranges and (b) that this variability leads to varying macroinvertebrate assemblages at higher elevation. Implications for possible consequences of climate induced changes of the flow regime are then discussed.

Materials and Methods

Study area: The study was conducted in the Bernese Alps in Switzerland in an area situated at the southern slope of Lake Brienz reaching up to the Schwarzhorn (Fig. 1). Geologically the area belongs to the Helvetic Shields, which form the edge of the northern Alps. These layers from the Cretaceous period mostly consist of limestone and marl (Labhart 1992). The vegetation is dominated by common spruce (*Picea abies)*. Above tree line dwarf shrub heath and marsh area associated with fens dominate. Especially the marsh areas are extensively used for grazing, whereas the steep rough pastures are almost never frequented by cattle. The vegetation period is short and the snow cover lasts six months on average. The mean precipitation amounts to 2094 mm a^{-1}, mostly falling as snow (www.meteosuisse.ch, version July 2012). The study area is rich in natural springs. However, even at high altitudes springs are partly subject to anthropogenic impacts such as trampling by cattle.

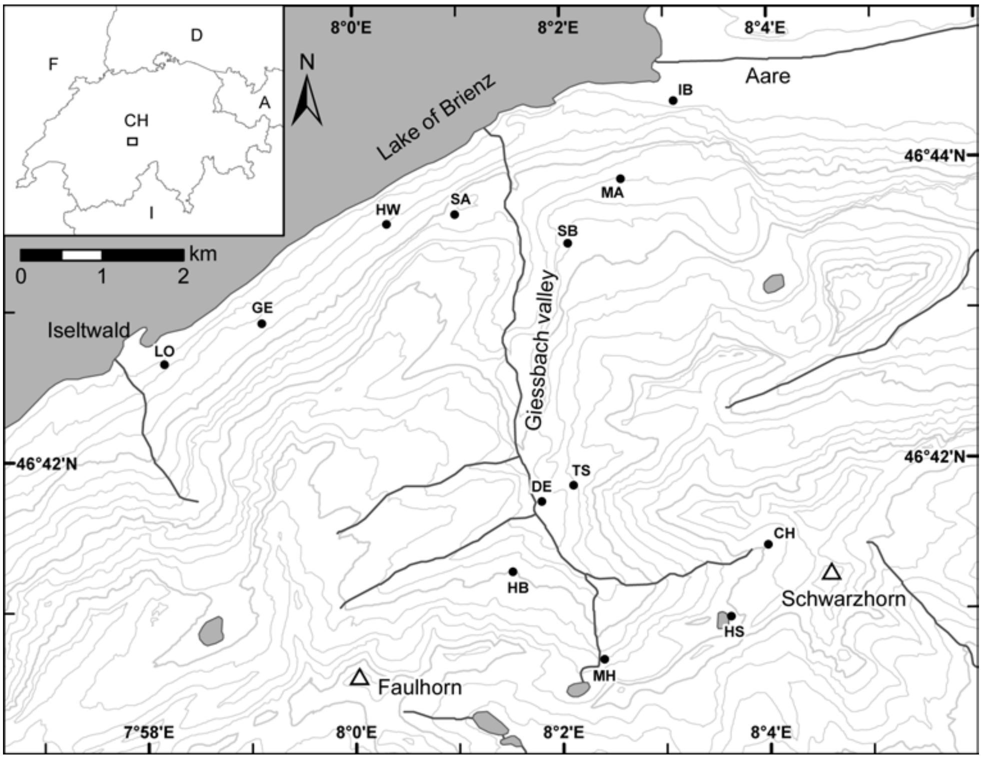

Fig. 1: Map of the investigation area in the Bernese Alps. ● = spring sites, codes are given in table 1; 100 m isolines, based on DHM25 (Swisstopo).

Environmental monitoring: Thirteen springs were selected for this study. They were mapped using an evaluation sheet originally developed for springs in Bavaria, Germany, which also considers alpine springs (Hotzy et al. 2008). Small loggers for monitoring water temperature and solar radiation (HOBO® Pendant temperature/light-logger, UA-002-64) were placed into the springs on the 1st of August 2010 and retrieved on the 12th of June 2011 (316 days). The loggers were placed in the springs at locations where we not expected a drying-out during the study period. They were fixed in the substrate with a large nail and a short thick string. A metal net was installed below the water surface above the loggers in order to prevent leaf litter from shadowing the loggers. Solar radiation measurements were used to assess the duration of the period, when the springs were covered with snow. No measured solar radiation means complete snow cover. Water temperature and solar radiation were measured four times each day: 12:00 a.m., 6:00 a.m., 12:00 p.m. and 6:00 p.m. Oxygen concentration and saturation (mg L^{-1}), pH and electrical conductivity (µS cm^{-1}) were measured in the field at each sampling occasion using a Multi-Parameter Water Quality Meter (Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, WTW 3500i). Owing to technical reasons the electrical conductivity of the uppermost springs was only measured once. The influence of the substrate composition on the macroinvertebrate assemblages of the springs considered in this study was thoroughly investigated in Wigger et al. (2015) and will not be subject of the current study.

Macroinvertebrate sampling: Macroinvertebrates were quantitatively sampled three times in June 2010, September 2010 and June 2011 with a small surber sampler (0.01 m^2, 500-µm mesh width). The possible sampling period is very restricted in high alpine areas, an earlier start of the macroinvertebrate sampling was not possible. In June we started with the springs at lowest elevation and in September we started with the springs at highest elevation to avoid a sudden onset of winter. This sampling time is in concordance with recommendations of Lubini et al. (2014). At each sampling occasion four samples were taken in each spring in the first five meters after the outflow (von Fumetti et al. 2007; Wigger et al. 2015). Samples were taken proportionally to the main substrate types mapped with the evaluation sheet of Hotzy et al. (2008). All samples were separately preserved in 70 % ethanol. In the laboratory samples were washed, specimens were separated from the substrate using a stereomicroscope and identified to species or at least genus level whenever possible (e.g. Waringer and Graf 2011; Glöer 2002; Studemann et al. 1992; Aubert 1959).Taxonomically demanding taxa such as Chironomidae and small instars were only identified to family level.

Data processing and analysis: Mean water temperatures and total as well as monthly temperature amplitudes were calculated from the logger data, whereupon negative values were not considered. Temperatures below zero were interpreted as a periodically drying-out of a spring; the inverse value was indicated as the number of wet days for each spring. The monthly and total temperature amplitude are a measure of temperature variability in each spring. The boxplot (Fig. 2) illustrating the variability of the monthly temperature amplitude in each spring was generated using PAST Version 2.09 (Hammer, 2011).

The abundance data of each spring was pooled (a) for each sampling occasion, i.e. from four samples, and (b) in total, i.e. from three sampling occasions (= 12 samples). The number of taxa and the Shannon diversity (H') per spring were calculated for each sampling occasion as well as in total.

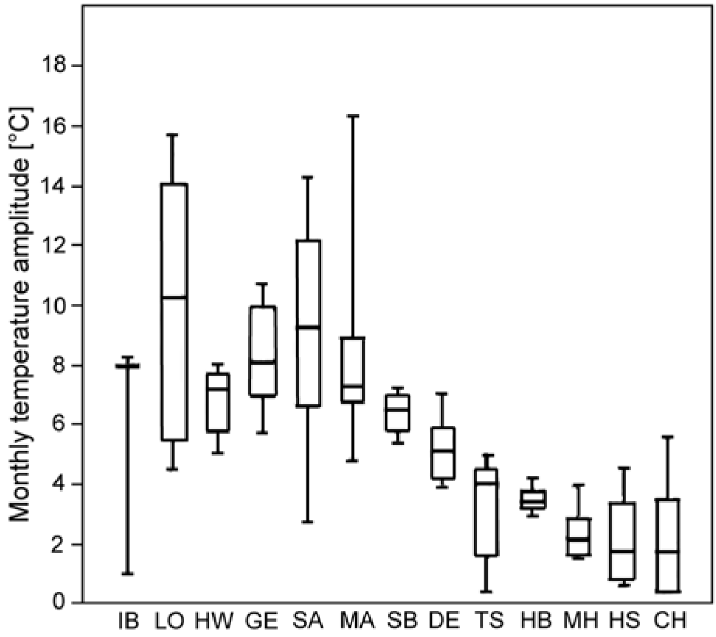

Fig. 2: Boxplot of the monthly temperature amplitude in each spring. Monthly temperature amplitudes were calculated for each month from August 2010 until May 2011.

Using the SIMPER-procedure (SIMilarityPERcentages) included in PRIMER 6.0 (Clarke and Gorley 2006) the percentage similarity of the macroinvertebrate assemblages of the three sampling occasions within each spring was calculated. We also calculated the percentage of taxa occurring only in one sampling occasion in a spring. The percentage of similarity and the percentage of single occurrences were interpreted as a measure of macroinvertebrate assemblage variability in a spring. We finally calculated the percentage of alpine and spring species within a spring in order to get insight into the composition of the macroinvertebrate assemblages. Autecological information for each taxon was derived from Moog (1995) and Schmedtje and Colling (1996).

We used generalized linear models (GLM) to identify correlations between physico-chemical parameters and to identify those parameters, which significantly influence the calculated diversity measures. The GLMs were performed with CANOCO 5.0 (ter Braak and Šmilauer 1998) using Gaussian distribution with identity link function.

Combined environmental and macroinvertebrate assemblages data were analysed using Redundancy Analysis (RDA) with CANOCO 5.0. The distance of species dissimilarity is measured by their chi-square. All species data were (log e+1)-transformed prior to analyses which was performed with a forward selection of explanatory variables.

Results

Physico-chemical parameters: Mean temperatures in the springs ranged from 1.4 ± 1.3 °C (spring CH) to 7.3 ± 1.7 °C (spring GE). Minimum and maximum temperature amplitudes were measured in springs HB and MA (Table 1). The variability of the temperature differed greatly between the springs: springs HW, SB, DE, HB and MH were extremely stable and the temperature amplitude did not exceed 4 °C. LO, SA and MA were the least stable springs with overall temperature amplitudes of up to 16.3 °C. Water temperature did not exceed 5.5 °C in springs above 1700 m a.s.l. (Fig. 2).

Median pH of the springs was between 7.5 ± 0.06 (spring SA) and 8.3 ± 0.8 (spring GE). Mean electrical conductivity was between 262 ± 6 µS cm^{-1} (spring HW) and 1142 ± 954 µS cm^{-1} (spring HB). Oxygen content ranged from 5.8 ± 4.8 mg l^{-1} (spring HB) to 11.2 ± 2.7 mg l^{-1} (spring LO). The most snow days were counted in the highest springs HS and CH and the number of wet days was lowest in spring IB, which was dry for almost seven weeks (Table 1). The GLMs with altitude as explanatory variable (DF: 1, 11) revealed a significant negative effect on the mean and median water temperature (T = -7.24, p (T) = 0.00002; T = -12.37, p

(T) = <0.00001, respectively) and a significant negative effect on the monthly amplitude of the water temperature (T = -7.61, p (T) = 0.00001). The GLM also showed a significant negative effect of the altitude on the electrical conductivity (T = -3.45, p (T) = 0.005) (Table 2).

Table 1: Location and measured abiotic characteristics of the investigated springs. Snowdays: number of days without solar radiation reaching the logger indicating a snow cover, Wetdays: number of days with temperatures above 0 °C indicating the logger to lie in the water; For technical reasons the conductivity of the springs DE-CH was measured once.

Spring	Code	Altitude [m]	Coordinates (WGS_84)	Temperature mean ± SD [°C]	Temperature amplitude [°C]	pH median	Conductivity mean ± SD [μS cm^{-1}]	Oxygen mean ± SD [mg l^{-1}]	No. of Snowdays	No. of Wetdays
Im Brunnen	IB	550	46° 41.36' N 7° 59.65' E	5.4 ± 3.7	8.2	7.7	319 ± 21	6.5 ± 1.2	44	268
Louberli	LO	650	46° 44.30' N 8° 3.04' E	7.2 ± 4.4	15.5	8.0	395 ± 66	11.2 ± 2.7	66	316
Hagweid	HW	850	46° 44.14' N 8° 2.48' E	6.3 ± 1.1	3.4	8.0	262 ± 6	10.3 ± 0.1	146	316
Geeri	GE	900	46° 43.49' N 8° 0.26' E	7.3 ± 1.7	6.1	8.3	358 ± 61	10.1 ± 2.5	111	316
Schweibealp	SA	1050	46° 42.84' N 7° 59.05' E	7.0 ± 3.6	14.2	7.5	439 ± 7	5.9 ± 0.4	22	297
Margel	MA	1200	46° 43.88' N 8° 2.66' E	6.2 ± 2.4	16.3	7.5	525 ± 12	9.1 ± 2.2	0	303
Schwarzenberg	SB	1380	46° 43.78' N 8° 2.53' E	6.0 ± 0.7	3.2	7.7	506 ± 4	9.9 ± 1.6	8	316
Dürrenegg	DE	1625	46° 41.57' N 8° 1.92' E	4.7 ± 0.9	3.9	7.9	232	8.9 ± 1.9	0	316
Torwangspitz	TS	1748	46° 41.46' N 8° 1.91' E	2.2 ± 1.5	4.9	8.2	35	10.2 ± 0.4	178	309
Hüttliboden	HB	1990	46° 41.23' N 8° 1.34' E	3.1 ± 0.3	1.7	8.1	40	5.8 ± 4.8	179	316
Mittagshorn	MH	2200	46° 40.59' N 8° 2.34' E	2.0 ± 0.8	3.1	8.2	18	7.4 ± 4.5	185	316
Häxeseeli	HS	2464	46° 40.87' N 8° 3.56' E	1.6 ± 0.9	3.9	8.0	169	7.2 ± 3.3	250	316
Chessel	CH	2510	46° 41.35' N 8° 3.93' E	1.4 ± 1.3	5.5	8.0	20	8.7 ± 1.7	234	314

Table 2: Generalized linear models with altitude as explanatory variable. Expected distribution: Gaussian with identity link function; DF of F statistic: 1, 11; b: regression coefficient estimates, SE: estimates of their standard error, T: T-statistics, p (T) estimated with Wald test. Tmean: mean water temperature throughout the logging period, Tmedian: median water temperature throughout the logging period, Tamp: amplitude of the water temperature throughout the logging period, MonthTamp: monthly amplitude of the water temperature, T_SD: standard deviance of the mean water temperature throughout the logging period, El cond: electrical conductivity.

Response variable	F statistic	p(F)	Fitted model deviance	Null model deviance	Parsimony (AIC-like)	b	SE	T	p(T)
Tmean	52.403	0.00002	11.043	63.652	43.438	-0.0031042	0.0004288	-7.24	0.00002
Tmedian	2.2678	0.16025	5.4261	80.867	34.201	-0.0037172	0.0003006	-12.37	<0.00001
Tamp	9.2836	0.01111	261.38	315.27	84.573	-0.0031416	0.0020862	-1.51	0.16025
MonthTam	57.931	0.00001	15.597	97.738	47.927	-0.0038788	0.0005096	-7.61	0.00001
T_SD	11.937	0.00538	9.9313	18.313	42.059	-0.001239	0.0004066	-3.05	0.01111
El cond	152.94	<0.00001	200630	418340	170.93	-0.19969	0.0577983	-3.45	0.00538

Macroinvertebrate parameters: In total 71 species and higher taxa were identified (Appendix 1). The total number of taxa in a spring varied between 13 in spring HS and 31in spring DE. The lowest mean number of taxa was derived in spring IB (7.3 ± 3.2) and the highest in spring MH (16.3 ± 4.5). The percentage of alpine species was lowest in spring LO (4 %) and highest in spring HS (39 %). The percentage of spring species varied between 7 % (IB) and 38 % (HW). The lowest similarity of all sampling occasions in a spring was found in spring HW (28 %) and the percentage of taxa occurring only at one sampling occasion was also highest in spring HW (71 %). The Shannon diversity was lowest in spring GE (0.658 ± 0.26) and highest in spring MA (2.147 ± 0.3) (Table 3).

Table 3: Biotic characteristics of the investigated springs. Alpine taxa: taxa restricted to alpine streams, spring taxa: taxa restricted to springs; % Similarity: similarity of the taxon assemblages of the three sampling occasions analysed by the SIMPER-procedure, % single occurrence: percentage of taxa recorded at one sampling occasion; H'(loge): Shannon diversity. Codes are given in table 1.

		IB	LO	HW	GE	SA	MA	SB	DE	TS	HB	MH	HS	CH
No. of taxa	Spring 2010	11	15	14	10	12	13	13	21	12	15	21	6	14
	Autumn 2010	5	15	11	11	13	17	10	15	15	12	12	9	9
	Spring 2011	6	14	4	12	10	12	13	13	17	19	16	9	7
	Total	14	24	21	20	21	28	24	31	26	22	30	13	17
	Mean ± SD	7.3 ± 3.2	14.7 ± 0.6	9.7 ± 5.1	11 ± 1.0	11.7 ± 1.5	14 ± 2.6	12 ± 1.4	16.3 ± 4.1	14.7 ± 2.5	15.3 ± 2.1	16.3 ± 4.5	8 ± 1.7	10 ± 3.6
% Alpine taxa		14	4	5	5	5	14	17	19	15	27	27	39	24
% Spring taxa		7	25	38	30	24	32	25	32	31	19	23	23	24
% Similarity		40	58	28	57	36	35	38	42	40	55	54	62	50
% Single occurence		64	50	71	55	52	68	63	60	46	36	60	38	47
H'(loge)	Total	2.14	1.59	1.92	0.59	2.26	2.62	2.34	2.19	2.14	2.14	1.16	1.58	1.32
	Mean ± SD	1.5 ± 0.6	1.6 ± 0.4	1.6 ± 0.2	0.7 ± 0.3	1.6 ± 0.3	2.2 ± 0.3	1.9 ± 0.2	1.9 ± 0.2	1.9 ± 0.4	1.8 ± 0.03	1.1 ± 0.3	1.4 ±0.1	1.3 ± 0.2

Macroinvertebrate – environmental relationships: The GLMs of the percentage of alpine species and the physico-chemical parameters (F statistic = 24.24, DF = 8, 4, p (F) = 0.004) revealed a significant relationship with altitude (T = 5.81, p (T) = 0.004), mean and median water temperature (T = -4.85, p (T) = 0.008; T = 5.19, p (T) = 0.007, respectively). The GLMs of other faunistic parameters did not reveal any significant relationship.

All environmental variables of the constrained RDA explained 69.2 % of the total variance (adjusted explained variation: 26 %). All RDA axes were significant (Monte-Carlo test: F = 1.6; p = 0.02). The first four axes explained 57.18 % of the variance, the explained fitted variation was 87.86 %. A forward selection revealed two significant explanatory variables accounting for 36.4 % of the total variance: monthly temperature amplitude ($p < 0.005$) and number of snow days ($p < 0.05$) (Table 4). The first axis separates the springs and their macroinvertebrate assemblages according to the altitude - also indicated by the number of snowdays and wetdays - and the monthly amplitude of the water temperature. Springs with a high amplitude of the water temperature are situated at lower elevation, they are also characterized by a higher electrical conductivity and higher water temperatures in general (Fig. 3).

As shown in the RDA plot (Fig. 3), the crenobiont caddisflies *Crunoecia irrorata* and *Beraea maura* and the amphipod *Gammarus fossarum* only occurred in springs LO, HW and GE at lower elevation. Other spring specialists such as some Stratiomyidae, e.g. *Oxycera morrisii* and *Beris vallata*, and the Trichoptera *Wormaldia occipitalis* were only present in springs MA, SB and SA at the middle altitudinal range. The Trichoptera *Consorophylax consors*, *Drusus monticola* and *Drusus muelleri* were mainly present in springs above 1700 m a.s.l.

Table 4: Summary of RDA eigenvalues, cumulative percentage of variance explained on the first four canonical axes, significance of all canonical axes and significant environmental variables identified by a forward selection of the explanatory variables.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.27	0.11	0.10	0.09
Species environment correlation	0.93	0.94	0.95	0.96
Cumulative percentage of variance				
Explained variation (cumulative)	27.33	38.44	48.60	57.18
Explained fitted variation (cumulative)	42.00	59.07	74.68	87.86
	F ratio			
Significance of all canonical axes	1.6*			
Significant environmental variables				
MonthAmp	3.8**			
Snowdays	1.7*			

* $P < 0.05$; ** $P < 0.005$

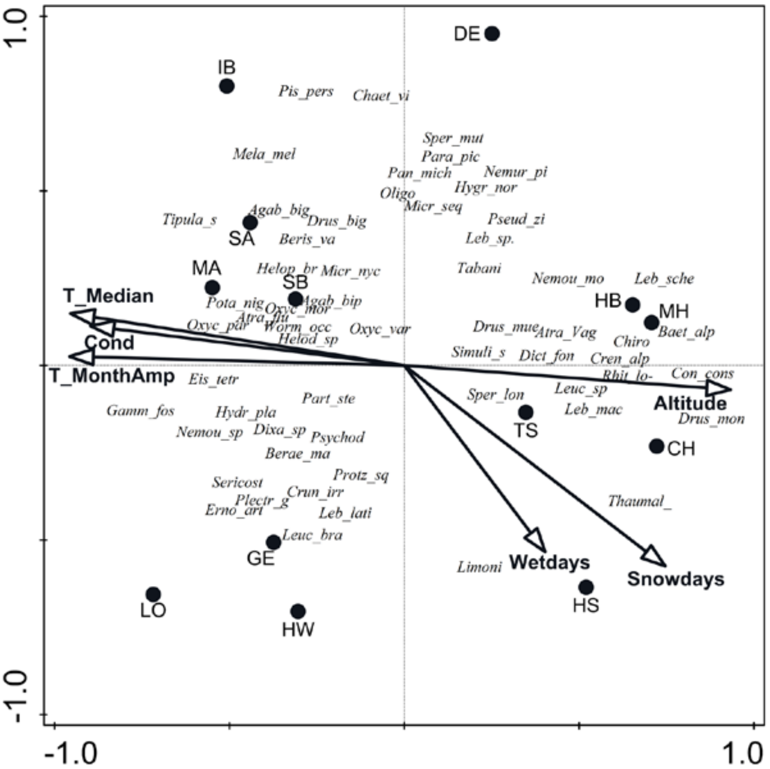

Fig. 3: Ordination of 12 sites and 71 taxa by a redundancy analysis (RDA). The environmental variables are indicated by arrows

Discussion

Thermal variability: The water temperature of the investigated springs decreased significantly with altitude, both looking at the mean and the median over the ten-month period. This was not surprising and found before for alpine springs (Cantonati 1998; Wigger et al. 2015).The water temperature of springs is meant to reflect the mean annual air temperature of the region, being cool in summer and warm in winter, no matter if at low or high elevation (Ward 1994). This is, however, especially true for springs fed by deep groundwater, which are usually located in low mountain ranges or in the lowlands (Cantonati et al. 2006). Frisbee et al. (2013) concluded from their research that all springs are not solely composed of groundwater but also to different degrees of other water sources such as superficial unsaturated flow or snowmelt. Springs at higher altitudes are to a larger extent than springs at lower altitudes, fed by a mix of groundwater, interflow and surface-runoff

(Beierkuhnlein and Gollan 1999). In early summer, when the top soil is still frozen, a direct flow of snow meltwater into the spring can indeed be observed. This is cooling the water additionally.

Besides a decrease of the mean water temperature we hypothesized a decrease of temperature stability with altitude due to the above mentioned increased influence of meltwater and surface-runoff. Our results revealed the opposite, the amplitude of the water temperature was significantly lower in the springs at higher elevation. A half-year pattern can be observed in those springs: In *winter* the period of snow cover lasts almost six months and isolates the springs at high altitude. The buffering effect of snow was also monitored by Füreder (2007). In early *summer* the input of snowmelt and in late summer the meltwater input from permafrost is highest (Brown et al. 2003). A higher variability could have therefore been expected for the summer half of the year. However, our data shows that meltwater input has a regulating effect on high alpine springs by stabilizing the run-off and leading to a constantly cold water temperature. Springs at lower altitudes heat up in summer and, due to the lack of a permanent isolating snow cover, they also cool down in winter. Some of those springs, which had instable temperature conditions, even fell dry at least once during the monitoring period. This underlines the higher abiotic variability of these springs. Overall it can be concluded that the lower water temperatures throughout the year as well as the lower temperature variability indicate an increased influence of snow melt and permafrost meltwater on high alpine springs. This can also be seen by looking at the electrical conductivity, which is significantly lower in the springs at higher elevation. Low electrical conductivity indicates a kryal influence, i.e. a glacial meltwater input into a spring (Brown et al. 2003). The seasonal shifts from harsh environmental conditions in summer to a constant environment in winter described by Füreder et al. (2001) for glacier-fed streams may also be crucial for high alpine groundwater-fed springs.

Influence of thermal variability on the macroinvertebrate assemblages: The macroinvertebrate composition of springs at high altitude differed considerably from those in springs at lower altitude. The percentage of alpine species significantly increased along the altitudinal gradient, whereas the percentage of spring specialists did not significantly change. They occurred in all springs in relatively small percentages, which is not unusual (von Fumetti 2014). The equal occurrence of crenobiont taxa in springs with high and low temperature variability as well as in springs with a certain contribution of meltwater underlines the special character of springs. It confirms the observation that crenocoenosis, the obligatory occurrence of taxa in springs, cannot solely be explained by the adaptation to constant water temperatures (Fischer et al. 1996; Wigger et al. 2015). Other abiotic factors such as substrate availability are just as important (Cantonati et al. 2006; von Fumetti and Blattner 2016).

Based on our hypothesis that springs at high altitudes exhibit higher temperature variability we also hypothesized higher variability, e.g. lower similarity of the three sampling occasions, of the macroinvertebrate assemblages in those springs. The springs at higher altitudes tended to be more stable showing higher similarity of their macroinvertebrates during the sampling period and a lower proportion of taxa only occurring once. They had relatively high proportions of alpine as well as spring specialists. Against our expectation they were the least variable springs considering the macroinvertebrate assemblages. The constantly cool water temperatures favor a pool of adapted rhitrobiont species such as *Drusus monticola* or *Drusus muelleri*. The constant but harsh environmental conditions also favor fast developing organisms such as Chironomids. Looking at their diversity in springs would be very promising. It is known, that Diamesinae dominate in glacier-fed streams with water temperatures below 4 °C (Milner et al. 2001; Clitherow et al. 2013), whereas other sub-families such as the Orthocladiinae dominate in groundwater-fed streams (Milner et. al 2001; Füreder et al. 2001). We expect that Diamesinae also dominate in constantly cold springs at high altitude. Semivoltine taxa and those with an interposed Diapause in winter will survive in the high alpine springs underneath the sheltering snow cover most probably within the hyporheic zone. In a winter survey of few springs investigated in this study, which was conducted by digging out the springs, a similar composition of the macroinvertebrate assemblages was found (unpubl. data).

Implications for possible future developments: The relatively high abiotic stability make alpine springs susceptible to changes of mean values and temporal variability of climatic parameters such as precipitation and temperature. Predictions of future climatic changes include more rain in winter instead of snow and a shorter duration of the snow cover (Barnett et al. 2005). The lack of a sheltering snow cover and a decreased meltwater input (Hannah et al. 2007) will increase the temperature variability in high alpine springs. This may also lead to a shift of the discharge peaks and a severely reduced discharge can be expected. In the Swiss Alps the summer heatwave in 2003 caused a demonstrably reduced runoff in alpine groundwater-fed basins, whereas the discharge of glacier-fed basins was above average (Zappa and Kan 2007). A decrease of stability with less flow during summer was also observable in the extremely dry summer 2015. Many springs, which still were flowing in summer 2003, fell dry for some weeks in 2015.

What could be the consequences for the inhabitants of alpine springs? From our results we conclude that crenobiont species will be less affected by increased temperature variability or increased water temperatures in general. It is more likely that more frequent intermittency may be problematic for spring specialists and will further promote univoltine, fast developing taxa. We further conclude that those taxa, which are adapted to constantly cold water temperatures, are endangered. Brown et al. (2007) predicted a loss of endemic alpine species in Pyrenean glacier-fed rivers. Within the Trichoptera especially endemic, stenoecious taxa will be affected by climate change impacts (Hering et al. 2009). Climate change could lead to an extinction of endemic alpine species such as *Drusus muelleri*. Other taxa may have the possibility to disperse to more stable, still constantly cold habitats. For future research it is therefore important to study in more detail the dispersal abilities of such taxa potentially affected by climatic changes.

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Appendix 1. List of taxa recorded in the investigated springs in spring 2010 (S10), autumn 2010 (A10) and spring 2011 (S11). Codes of the springs according to Table 1; + = present.

	Alpine	Crenobiont	BR_S10	BR_A10	BR_S11	LB_S10	LB_A10	LB_S11	HW_S10	HW_A10	HW_S11	G_S10	G_A10	G_S11	SA_S10	SA_A10	SA_S11	M_S10	M_A10	M_S11	SB_S10	SB_A10	SB_S11	DE_S10	DE_A10	DE_S11	TWS_S10	TWS_A10	TWS_S11	HB_S10	HB_A10	HB_S11	MH_S10	MH_A10	MH_S11	HS_S10	HS_A10	HS_S11	CH_S10	CH_A10	CH_S11
Crenobia alpina (Dana, 1766)	x	x	-	-	-	+	-	-	+	-	-	+	+	-	+	+	-	+	+	-	+	+	-	+	+	-	+	+	+	+	+	+	+	+	-	+	+	-	+	+	-
Oligochaeta			+	-	+	+	+	+	+	+	-	-	-	+	-	+	-	+	+	+	+	+	+	+	+	+	-	+	+	-	-	+	-	-	+	+	+	-	+	-	+
Eiseniella tetraedra (Savigny, 1826)			-	-	-	-	-	+	-	-	-	-	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nematomorpha			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Pisidum cf. personatum (Malm, 1855)			+	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	+	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acari			-	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-	+	-	-	+	+	-	+	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-
Atractides fluviatilis (Szalay, 1929)			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Atractides vaginalis (Koenike, 1905)	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Hydrovolzia placophora (Monti, 1905)		x	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hygrobates norvegicus (Thor, 1897)		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lebertia lativentris K.Viets, 1922		x	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lebertia schechteli Thor, 1913		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	+	-	+	-	+	+	+	-	-	-	-	-	-	-
Lebertia cuneifera Walter, 1922		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lebertia maculosa Koenike, 1902	x		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-
Lebertia sp. Neumann, 1880			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Panisus michaeli Koenike, 1896		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Partnunia steinmann i Walter, 1906		x	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+	+	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	+	-	-
Protzia squamosa Walter, 1908		x	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sperchon mutilus Koenike, 1895	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sperchon longirostris Koenike, 1895		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Gammarus fossarum Koch, 1835			+	+	+	+	+	+	-	+	-	+	+	+	+	+	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Copepoda			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ostracoda			-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	+	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Baetis alpinus (Pictet, 1843)	x		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	+	+	+	+	+	-	+	+	-	-	-
Rhithrogena lobata -group			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	+	-
Perlodidae juv.			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Dictyogenus fontium (Ris, 1896)		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Leuctra spp. Stephens, 1836			-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	-	+	-	-	-	+	+	+
Leuctra gr. braueri-muranyii		x	-	-	-	-	-	-	+	+	+	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nemoura spp. Latreille, 1796			-	-	-	+	+	+	-	+	+	+	-	-	-	-	+	+	-	+	+	+	-	-	+	+	-	+	+	+	-	-	-	+	-	-	-	-	+	+	-
Nemoura mortoni (Ris, 1902)	x		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	+	-	-	-	-	+	+	+	+	+	+	-	+	-	-	-	-
Nemurella pictetii (Klapalek, 1900)			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-
Protonemura spp. Kempny 1898			-	-	-	+	-	+	-	-	-	+	+	+	-	-	-	+	+	+	+	-	+	-	-	-	-	-	+	+	+	+	+	+	+	-	-	-	-	-	-
Agabus biguttatus (Olivier, 1795)			-	-	-	-	-	+	-	-	-	-	-	-	+	-	+	-	+	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Agabus bipustulatus (Linnaeus, 1767)			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elodes spp. Latreille, 1796			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Helophorus brevipalpis Bedel, 1881			-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	Alpine	Crenobiont	BR_S10	BR_A10	BR_S11	LB_S10	LB_A10	LB_S11	HW_S10	HW_A10	HW_S11	G_S10	G_A10	G_S11	SA_S10	SA_A10	SA_S11	M_S10	M_A10	M_S11	SB_S10	SB_A10	SB_S11	DE_S10	DE_A10	DE_S11	TWS_S10	TWS_A10	TWS_S11	HB_S10	HB_A10	HB_S11	MH_S10	MH_A10	MH_S11	HS_S10	HS_A10	HS_S11	CH_S10	CH_A10	CH_S11
Beraea maura (Curtis, 1834)		x	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chaetopteryx villosa/fusca (Fabricius, 1798)/ Brauer, 1857			-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Consorophylax consors (McLachlan 1880)	x	x	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	+	+	-	+	+	-	+	+	+	+	+	+	-
Crunocia irrorata (Curtis, 1834)		x	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Drusus biguttatus (Stephens, 1837)			+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Drusus muelleri McLachlan 1868	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-
Drusus monticola (McLachlan, 1876)	x		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+
Ernodes articularis (Pictet, 1834)		x	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Limnephilidae juv.			+	+	-	-	-	-	+	-	-	-	-	-	-	+	+	+	-	-	+	+	-	+	-	+	+	-	-	+	+	-	+	+	+	+	-	+	-	-	+
Limnephilus coenosus (Curtis, 1834)			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melampopylax melampus (McLachlan 1876)			+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	-	-	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Micropterna nycterobia McLachlan, 1875			-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Micropterna sequax/lateralis McLachlan, 1875/ (Stephens, 1837)			+	-	-	-	-	-	+	-	-	-	-	-	-	+	+	-	-	-	-	-	+	-	-	+	-	-	+	-	+	+	-	-	+	-	-	+	-	-	-
Plectrocnemia geniculata McLachlan, 1871		x	-	-	-	-	-	-	+	+	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Potamophylax nigricornis (Pictet, 1834)		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Parachiona picicornis (Pictet, 1834)		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pseudopsilopteryx zimmeri (McLachlan 1876)	x		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Rhyacophilidae juv.			-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-
Rhyacophila intermedia McLachlan, 1868			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Rhyacophila pubescens Pictet, 1834		x	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Sericostoma personatum/schneideri Spence, 1826/ Kolenati, 1848			-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Wormaldia occipitalis (Pictet, 1834)		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Atrichopogon spp. Kieffer, 1906			+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ceratopogoninae			-	-	-	+	+	+	+	-	-	+	-	-	-	-	-	+	+	-	-	-	-	-	+	-	+	-	+	-	-	-	-	-	+	-	-	-	-	-	-
Chironomidae			-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Dixa spp. Meigen, 1818			-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	+	-	+	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Empididae			-	-	-	+	-	+	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	+	-	-	-	-	-	+	+	+
Limoniidae			-	-	-	+	-	-	-	+	-	-	-	-	-	-	+	+	-	-	-	+	-	-	-	-	+	+	-	-	-	-	+	-	-	+	+	+	-	+	-
Dicranota spp. Zetterstedt, 1838			-	-	-	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	-	+	+	-	+	-	-	-	+	-	-
Pedicia spp. Latreille, 1809			-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Oxycera morrisi Curtis, 1833		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxycera cf. pardalina (Meigen, 1822)		x	-	-	-	-	+	-	-	-	-	-	+	-	-	+	-	+	+	+	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxycera varipes Loew, 1870		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Beris vallata (Forster, 1771)		x	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychodinae			-	-	-	+	+	+	-	+	-	+	+	-	+	-	-	-	+	-	+	-	-	-	-	-	+	-	+	-	+	+	-	-	+	-	-	-	-	-	-
Simulium spp. Latreille, 1802			-	-	-	+	+	-	-	+	-	-	-	-	-	+	-	-	+	-	+	-	-	-	+	-	-	+	+	+	+	+	-	-	+	-	-	+	-	-	-
Tabanidae			+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Tipulidae			+	-	-	-	+	+	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Thaumalea spp. Ruthe, 1831		x	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	+	-	+	-	-	+	+	-	-

CHAPTER FIVE

The benefit of data loggers for hydro-ecological monitoring of alpine springs

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Abstract

In remote alpine areas it is elaborate and difficult to get fine-grained environmental data for hydro-ecological analyses of natural springs. This is, however, of special importance for the analysis of flow-pathways and the relationship of climatic parameters such as precipitation and hydro-morphological parameters in springs. A new non-invasive approach to determine groundwater flowtime of alpine springs was tested in this study. Therefore alpine springs at different altitudinal levels in the Bernese Alps in Switzerland were equipped with different aquatic loggers for two winter half years. Data from air temperature loggers and meteorological stations were incorporated in the data analysis. The aim of the study was to analyze the reaction time, i.e. the time lag of the springs on meteorologically induced signals. To statistically evaluate such trends in our data we used cross-correlation analyses. Thereby two parameters or signals were compared with each other. The results show, that best results can be archived with centrally measured air temperature and the water temperature of springs. Springs with stable and constant discharge can be separated from intermittent springs with considerable temperature fluctuations. Analyzing logger measurements have the advantage to be non-invasive and to give

continuous information during seasons, when field investigations are not possible. Improving the tested logging method is worthwhile and can contribute to gain information about the sparsely investigated processes in the aquifer of alpine springs.

Introduction

Alpine springs are small scaled and isolated aquatic habitats (Cantonati et al., 2006; Gerecke and Franz, 2006). Water temperature is the most mentioned abiotic factor influencing springs (Jacobsen et al., 1997; Jacobsen, 2003; Wigger et al., 2015; Küry et al., 2016). In field research temperature is mostly punctually measured during field investigation with portable meters. Often springs are therefore characterized based on several single temperature measurements. Since Gräsle and Beierkuhnlein (1998), Smith et al. (2003) and von Fumetti et al. (2007, 2012) we know that the dogma of temperature stability not pertains for all springs. Especially alpine springs may show high temperature variability (Constantz, 1998). Thermal variability of the spring water is dependent on the mode of flow and the duration that water is under ground (Pitty, 1976; Luhmann et al., 2011).

Measurements of the duration of groundwater flow are financially and personally sophisticated. Established methods for examining the flow path of precipitation before recharging springs are dye tracing with chemicals or age determination using isotopes (Hiscock and Bense, 2014). Both methods have the disadvantage that they are point measurements and do not figure out the continuous characterization of groundwater flow. Moreover an implementation in winter with a complete snow cover is not possible.

Preud'homme and Stefan (1992) and Martin and Dean (1999) investigated a non-invasive method to detect the flow rate of water with temperature as a natural tracer in rivers. A karstic river was equipped with temperature loggers upstream and downstream in a river section, where the water seeps away for certain distance and flows underground. Both temperature signals were compared to detect time lag. This time lag enables to calculate the flow time within the aquifer. The tracing was successfully repeated with logging the electrical conductivity (Martin and Dean, 1999). A similar investigation was implemented for rivers in the Jura Mountains (Chalier, 2012) and for glacial runoffs (Brown et al., 2004). A strong correlation between long-term air and stream temperature was shown in a stream in USA (Maheu et al., 2015). Spring water temperature was found to react with a certain delay on air temperature changes (Küry et al., 2016), but until now no study concentrating on computing this delay was implemented yet. In contrast to the river investigation of Martin and Dean (1999) the catchment area of springs cannot be logged directly as there is no open water for the initial measurement. Many studies showed a strong correlation between air temperature and groundwater temperature in a karstic region at positive air temperatures (Johnson, 1971; Crisp and Howson, 1982; Webb, 1987; Tulipano, 1988; Erickson and Stefan, 1996; Mohseni and Stefan, 1999; O'Driscoll and DeWalle, 2006).

In order to understand the processes in the aquifer, especially the residence time of groundwater, this study aims at testing a new method which shall answer the following questions: Are logger data suitable for examining spring water temperature regimes? Which aquatic and which meteorological parameters correlate best?

Methods

Logging: Nine selected springs were equipped with aquatic loggers from 07.10.2013 (logging period one: P1) to 27.04.2014 and from 1.11.2015 to 15.05.2016 (logging period two: P2). The selected springs differ in their location and altitude (Table 1). Five springs are situated below 1200 m.a.s.l. in the forested mountainside above Lake of Brienz. The other five springs are located above 1625 m.a.s.l. on an elevated weak afforested plain (Fig.1). Due to very little discharge we replaced the investigation site OB with SW in the second period. The investigation area is dominated by karstic limestone layers filled with moraine material, particularly up to the tree line. Above tree line dark slate layers dominate. In one hour resolution we logged oxygen content (mg L^{-1}), electrical conductivity (µS cm^{-1}), solar radiation (Lux) and water temperature (°C). HOBO Pendant Temperature Data Loggers (UA-001-xx) were used for water temperature and solar radiation, HOBO U24 Conductivity Logger (U24-001) for electrical conductivity and HOBO Dissolved Oxygen Logger (U26-001) for measuring the oxygen content.

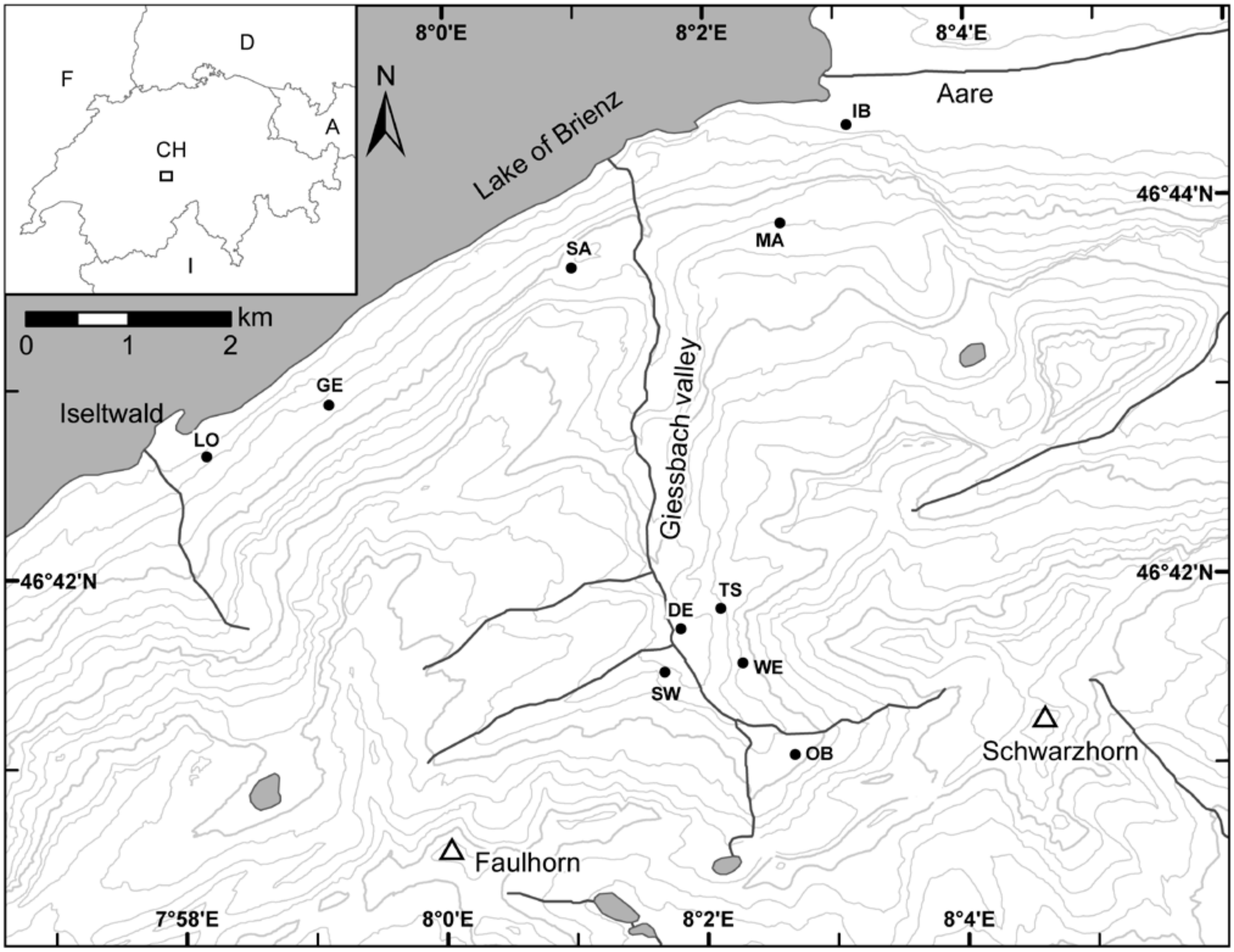

Fig. 1: Map of the investigation area in the Bernese Alps (Switzerland). ● = spring sites; 100 m isolines, based on DHM25 (Swisstopo).

Table 1: Investigated springs with the corresponding code, altitude and coordinates.

Name	Code	Altitude [m]	Coordinates (WGS_84)
Oberberg	OB	1880	46° 41.24' N 8° 1.98' E
Schweiffi	SW	1710	46° 41.75' N 8° 2.05' E
Torwangspitz	TS	1748	46° 41.46' N 8° 1.91' E
Wehri	WE	1680	46° 41.61' N 8° 1.85' E
Dürrenegg	DE	1625	46° 41.57' N 8° 1.92' E
Margel	MA	1200	46° 43.88' N 8° 2.66' E
Schweibealp	SA	1050	46° 42.84' N 7° 59.05' E
Geeri	GE	900	46° 43.49' N 8° 0.26' E
Louberli	LO	650	46° 44.3' N 8° 3.04' E
Im Brunnen	IB	550	46° 41.36' N 7° 59.65' E

In the second logging period we also measured air temperature at each spring site with HOBO Pendant Temperature Data Loggers (UA-001-xx). We placed and fixed these loggers two meters above ground on a shaded spot like a crevice or on the northern side of a near tree.

Due to limited storage space of the loggers and restricted battery capacity based on low ambient temperature longer continuous logging periods were not possible. Alpine springs are known to vary in discharge. Therefore it was important to fix the loggers with a u-shaped wire-bow at the bottom of the springs. An overflow of the loggers was thus also given during minor discharge. The solar radiation and temperature loggers were additionally fixed with a wire bow so that the solar radiation sensor constantly stayed upturned. We also formed a semispherical protection with wire mesh to prevent the loggers to get overlaid by leaf litter.

Station analyses: To find out which meteorological station reflects the catchment area of the springs best a correlation analysis was conducted with Past 2.09 (PAleontological STatistcs Version 2.09, Hammer, 2011). Thereby discharge measurements of Giessbach (L s^{-1}) and precipitation measurements (mm) of the stations Interlaken, Brienz and Meiringen in the time period 01.05.2002 to 01.11.2002 were analyzed. Data basis for the correlation analysis were the daily mean values calculated by the hourly data. The analysis with older data was necessary because the hydrological station was abolished in 2003. The Giessbach is the on-site preflooder of the investigation area (Fig. 1). Further data analyses were conducted with the data of the best fit meteorological station. Meteorological stations usually measure air temperature two meters above soil. Station Interlaken also takes hourly data from near-ground air temperature. We used both temperature progressions to analyze our logger data. For the second logging period we additionally used the logged air temperature of each spring. Moreover a comparison of different meteorological stations shows the meteorological distinctness of alpine valleys.

Statistical analyses: To determine the reaction time of the springs on environmental influences we conducted cross-correlation (xcorr (x,y)) using MATLAB R2014b (Natick, Massachusetts). Cross-correlation measures the degree of correlation of two data series. . Thereby the shift of one series to the other is calculated as temporal delay also denoted as time lag. The investigated data series have the same starting and terminal point and an equal temporal resolution of one hour.

The maximum cross-correlation (max xcorr) indicates the point in time, when the signals are best aligned with each other. To compare the different signals, data first has to be standardized (xorr coeff) (1).

$$\text{xcorr (a,b, coeff)=xorr(a,b)/[norm(a)*norm(b)]} \tag{1}$$

The absolute values of the data series were therefore normalized (2)

$$\text{norm (a)*norm(b)=sqrt(sum(abs(a)}^{2}\text{*sum(abs(b)}^{2}\text{))} \tag{2}$$

,where *abs* means all absolute values of the data series, which were calculated for both series (a,b). *Sqrt* is the shortcut for square root.

All resulting values lie between 0 and 1, whereas 1 means hundred percent accordance of the two data series and would thus conform to an autocorrelation of one data series with itself.

The corresponding time lag can be interpreted as flow time or residence time of the groundwater in the aquifer. We conducted cross-correlations with the logger data and both meteorological air temperatures, two meters and five centimeters above soil, of the meteorological station Interlaken (577 m a.s.l.). For the second logging period we additionally used air temperature directly measured at the spring sites.

Results

Station analyses: The correlation analyses of the meteorological stations and the discharge of the Giessbach resulted in that station Interlaken (p: 0.36) fitted best. Meiringen (p: 0.21) and Brienz (p: 0.27) show distinctly weaker coherences (Table 2). Internal analyses of the stations showed a correlation of Brienz and Meiringen of p: 0.86 and Brienz and Interlaken of 0.76. The weakest correlation was between Interlaken and Meiringen (p: 0.73).

Table 2: Results of the correlation analysis of Giessbach discharge and the meteorological stations Meiringen, Interlaken and Brienz.

	Giessbach discharge	Meiringen precipitation	Interlaken precipitation	Brienz precipitation
Giessbach discharge	1.00	0.22	0.36	0.27
Meiringen precipitation	0.22	1.00	0.73	0.86
Interlaken precipitation	0.36	0.73	1.00	0.76
Brienz precipitation	0.27	0.86	0.76	1.00

Therefore we further analyzed our data of the first logging period with the temperature data from the station Interlaken. Comparing the hourly air temperature of station Interlaken two meters above soil (T_{2m}) and five centimeters above soil (T_{5cm}) shows a larger variation and lower mean temperature (T_{5cm}: 3.25°C, SD : 7.59, T_{2m}: 4.24°C, SD: 5.76) Fig.2. In the second period mean T_{2m} was 4.84 °C (SD: 4.93).

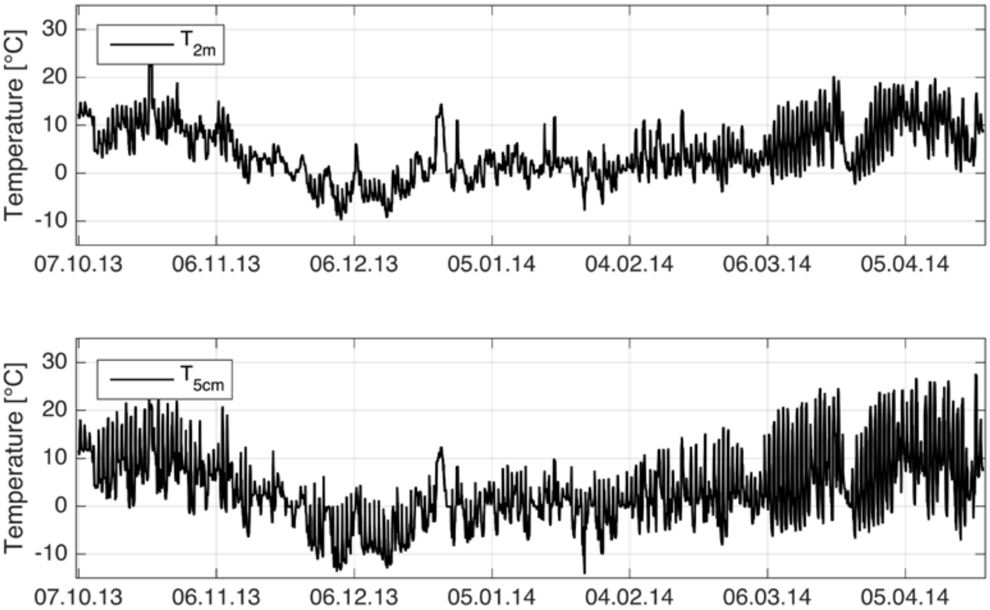

Fig. 2: Comparison of air temperature two meters (T_{2m}) and five centimeters above soil (T_{5cm}) of the meteorological station Interlaken during the first investigation period (Data provided by MeteoSwiss)

We visualized the temperature progressions of the nine investigated springs for both logging periods (Appendix 1 and 2). For the second logging period we also visualized the air temperature of the springs (Appendix 3). The corresponding statistical values are presented in Table 3. To compare the first and the second logging period (P1, P2) average water temperature and standard deviation was calculated on the same timeframe from 01.11 to 21.04. P1 revealed an average temperature of 4.86 °C (SD: 2.69), and P2 of 5.48 °C (SD: 0.85). Analogous, the air temperature values were calculated for P1: 3.37 °C (SD 5.48), and P2: 4.10 °C (SD 4.40).

Time series analysis: Cross-correlation with air temperature showed positive values in analyzing spring temperature and electrical conductivity in P1 (Table 4). The xcorr coeff value is uniformly larger with the T_{2m} than T_{5cm} data. For T_{2m} and the water temperature of the springs the cross-correlation is visualized in Fig. 3. Thereby springs TS and GE showed highest and springs DE and LO lowest xcorr coeff values in T_{2m} and T_{5cm}. Electrical conductivity is only positively correlated with T_{2m} values (Table 4). The xcorr coeff values are uniformly lower compared to the analysis with the water temperature of the springs.

Table 3: Mean and standard deviation (SD) of water temperature (W) and air temperature (A) from investigation period one (P1) and period two (P2). The data is shortened to the same timeframe from 01.11 to 21.04. Missing values are marked with *.

	DE	TS	GE	IB	LO	MA	WE	SA	OB	SW
Mean P1 W	5.38	3.10	6.68	6.56	9.16	5.54	5.67	6.37	2.65	*
SD P1 W	4.37	5.03	3.59	4.16	2.69	4.22	4.44	4.61	5.04	*
Mean P2 W	4.52	1.56	6.41	7.60	7.07	6.79	3.83	8.75	*	3.37
SD P2 W	0.51	1.22	0.99	1.57	1.28	0.76	0.91	0.13	*	0.33
Mean P2 A	-0.49	1.64	4.26	3.25	5.44	3.27	1.95	2.84	*	0.34
SD P2 A	5.41	5.54	4.46	4.96	4.29	5.12	6.15	5.54	*	3.55
Mean W P1+P2/2	4.95	2.33	6.55	7.08	8.11	6.17	4.75	7.56	*	*
SD W P1+P2/2	2.44	3.13	2.29	2.86	1.99	2.49	2.68	2.37	*	*

In the second logging period we repeated cross-correlation with T_{2m}, the local air temperature around the springs and the electrical conductivity (Table 5). The higher value of max xcorr in P2 for T_{2m} and electrical conductivity in comparison to P1 indicates a generally higher influence of air temperature on the springs. Analyzing T_{2m} and spring water temperature, the springs TS and GE showed again the highest xcorr values, whereas the lowest were found in DE and WE. Analysing oxygen saturation and solar radiation did not provide suitable results due to fragmentary or weak data.

Table 4: Results of the normalized xcorr analysis of the first logging period. T = Air temperature (°C), WT = water temperature (°C), Int. = meteorological station Interlaken, Cond. = conductivity, Lag (h) = temporal delay of the signal in hours, xcorr coeff = maximal normalized correlation coefficient.

	T_{2m} Int., WT Spring		T_{5cm} Int., WT Spring		T_{2m} Int., Cond Spring	
	xcorr coeff	Lag (h)	xcorr coeff	Lag (h)	xcorr coeff	Lag (h)
DE	0.59	0	0.40	1	0.56	0
IB	0.65	3	0.47	4	0.63	116
LO	0.60	1	0.40	4	0.58	0
MA	0.66	0	0.49	2	0.65	149
WE	0.61	0	0.41	1	0.55	0
OB	0.64	83	0.51	86	0.62	136
SA	0.67	1	0.51	194	0.63	201
TS	0.77	5	0.61	7	0.63	84
GE	0.73	3	0.54	4	0.51	2

Table 5: Results of the normalized xcorr analysis of the second logging period. T = Air temperature (°C), WT = water temperature (°C), Int. = meteorological station Interlaken, Cond. = conductivity, Lag (h) = temporal delay of the signal in hours, xcorr coeff = maximal normalized correlation coefficient.

	T_{2m} Int., WT Spring		T_{2m} Spring, WT Spring		T_{2m} Int., Cond Spring	
	xcorr coeff	Lag (h)	xcorr coeff	Lag (h)	xcorr coeff	Lag (h)
DE	0.68	0	0.16	-3552	0.68	0
IB	0.71	2	0.58	0	0.69	7
LO	0.78	6	0.86	3	0.74	0
MA	0.71	1	0.54	0	0.65	-274
WE	0.68	2	0.35	2	0.66	-22
SW	0.69	0	0.34	-3575	0.69	-23
SA	0.70	0	0.46	0	0.70	0
TS	0.81	27	0.50	25	0.69	36
GE	0.78	2	0.78	0	0.72	2

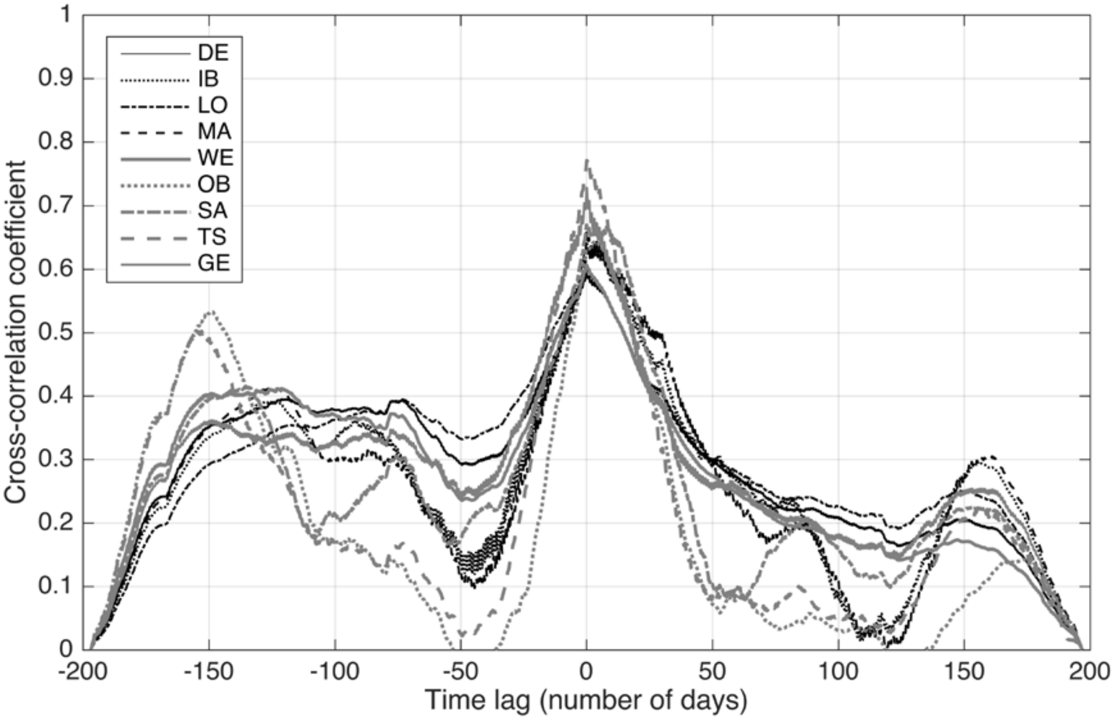

Fig.3: Visualization of normalized cross-correlation analysis with air temperature T_{2m} from meteorological station Interlaken and the water temperature of the springs of the first investigation period (P1).

Discussion

Air and water temperature interferences: Comparing the air temperature of both logging periods within the same time frame, the second period was warmer and more stable. This also pertains for water temperature. The distinctly more stable water temperatures resulted from the improved positioning of the loggers in the second logging period. In the first logging period some loggers were not stationed ideally, it is thus possible that the loggers sporadically were not under water in phases of minor discharge. So we assess the data quality of the second period to be better. Generally water temperature showed less variation than air temperature in both periods. To compute the residence time of groundwater we conducted cross-correlations with the logger data exposed to the spring water and temperature of a central meteorological station in period one and additionally air temperature measured at each spring site in the second logging period. In the first logging period the logger data were analysed with air and precipitation data from a central meteorological station. To find out which meteorological station reflects the climatic conditions of the investigation area best we conducted a station analysis with three near meteorological stations and used discharge measurements of the on-site preflooder Giessbach. Interlaken was found to fit best and was therefore used in cross-correlation analysis with the first logging period. The three meteorological stations are all situated in the same valley and are within 20 kilometer distance from each other. Brienz is the nearest station to the investigation area, but is influenced by periodically winter föhn winds. This is also true for station Meiringen (Richner and Hächler, 2013). The investigation area and the station Interlaken are not affected by föhn and therefore show the highest coincidence. Alpine valleys often show heterogenic, small-scaled climatic distinctions of air temperature and precipitation (Richner and Hächler, 2013). As these events have an influence on spring water temperature and discharge future investigation could be promising. Time series analyses of the first logging period were conducted with air temperature two meters and five centimeters above soil. Our analysis always revealed better results with the two meters air temperature. Soil temperature underlies larger daily variation due to enhanced heating up during daytime and enhanced cooling down during the night. Therefore the signal underlies a large daily variation and shows less coherence with spring water temperatures.

Time series analyses: The two springs TS and GE showed the highest xcorr coefficients in the first logging period. Both springs are completely shadowed by spruces. The spring DE shows the lowest coefficient. It is fully sunlit, but shows a very stable temperature regime during the investigation period. This spring seems to be relatively independent concerning air temperature, solar radiation and snow cover. A main reason could be the high discharge, which may buffers external influences (Mohseni and Stefan, 1999). TS and GE are characterized by low and turbulent discharge and thus are more influenced by air temperature. The observed time lag of several hours of these springs supports the assumption that spring water reacts delayed on air temperature changes.

Analogous to Martin and Dean (1999) we conducted cross-correlation analyses with air temperature and the electrical conductivity. The xcorr coefficients are generally lower and less variable compared to air temperature. It is apparent that high xcorr coefficients values express long time lags and small xcorr coefficient express ambiguous time lags. As solubility is temperature dependent this could be an evidence on groundwater residence time. Based on our data and with regard to the heterogeneity of the geological conditions of the investigation area and the effect of snowmelt on conductivity (Hiltbrunner, 2005) further examinations are necessary for ensured assertions.

In the second logging period we additionally measured air temperature directly at each spring site. Against our expectation the comparison with spring water temperature values showed a higher coherence with the air temperature data of the meteorological station Interlaken than with the locally measured air temperature. A reason for that might be that the temperature values from the meteorological station are hourly mean values from measured one-minute values and the measurements at the spring sites are hourly point measurements. Mean values tend to smoothen outliers. Moreover the infield measurement of air temperature, especially on open land with no forestation, was challenging. Possibly the loggers were exposed to punctual solar radiation despite of carefully placing. As the water temperature is higher and less fluctuating than air temperature during winter in general, the more stable data from meteorological station fits better in cross-correlation analyses than the direct measured air temperature at each spring site.

In the second logging period again springs TS and GE and also LO showed highest xcorr coefficient analyzing air temperature two meters above soil of meteorological station Interlaken and spring water temperature. Coincidently TS and LO belong to the springs with the highest water temperature fluctuations.

DE, WE, SW and SA show low xcorr coefficients and are the most stable springs regarding water temperature.

It is conspicuous that springs with low xcorr coefficients generally slow a short time lag and are preferably stable concerning water temperature. They are independent regarding environmental influences. Springs with higher xcorr coefficients exhibit positive time lags and are more likely variable regarding the water temperature. Especially in the second period, regarding xcorr of air temperature measured at spring sites and water temperatures, it is obvious that springs at high elevation have low coefficients and springs situated lower have higher coefficients. A reason for that might be that in the generally warmer second period the lower springs were not covered with snow and thus were stronger affected by temperature than the springs at higher altitude witch are completely covered. Snow cover was found to have a buffering effect on alpine running waters (Füreder, 2007) and springs (von Fumetti et al., *in prep.*).

We conclude that low xcorr coefficients combined with low time lags mean only slight or no influence of air temperature on water temperature and therefore indicate stable, perennial springs. Time series analysis by cross-correlation of water temperature and air temperature can thus help to gain more information about groundwater processes and help to characterize temperature regimes, especially during winter when no surface measurements are possible. Superficial drying out, which can occur in alpine springs during winter (Wigger and von Fumetti, 2013), can only be detected by a continuously logging during this time.

Summary and Outlook: We showed that logger data are suitable for gaining information about the temperature regime of springs. With a higher logging interval and a longer phase of logging the results might be improved. The storage and battery capacity of the loggers are limiting but exchanging the loggers during summer time could solve this problem.

In this study we found the best correlation between air temperature two meters above soil of a near meteorological station and spring water temperature. Measuring precipitation temperature instead of air temperature could help to align the temperature signals of spring water, but this is very elaborate to measure and could only gather data during raining events. For determining flow duration of groundwater, logging during the summer half could give clearer results as precipitation in winter is a mixture of rain and snow. A delay due to snowmelt sophisticates time lag analysis additionally (Frisbee et al. 2013).

For initial values, it is also conceivable to bury the loggers into the soil in the catchment area instead of measuring air temperature.

Disturbance by solar radiation could be inhibited and moreover soil temperature might be more relevant for water temperature than air temperature (Cartwright, 1974).

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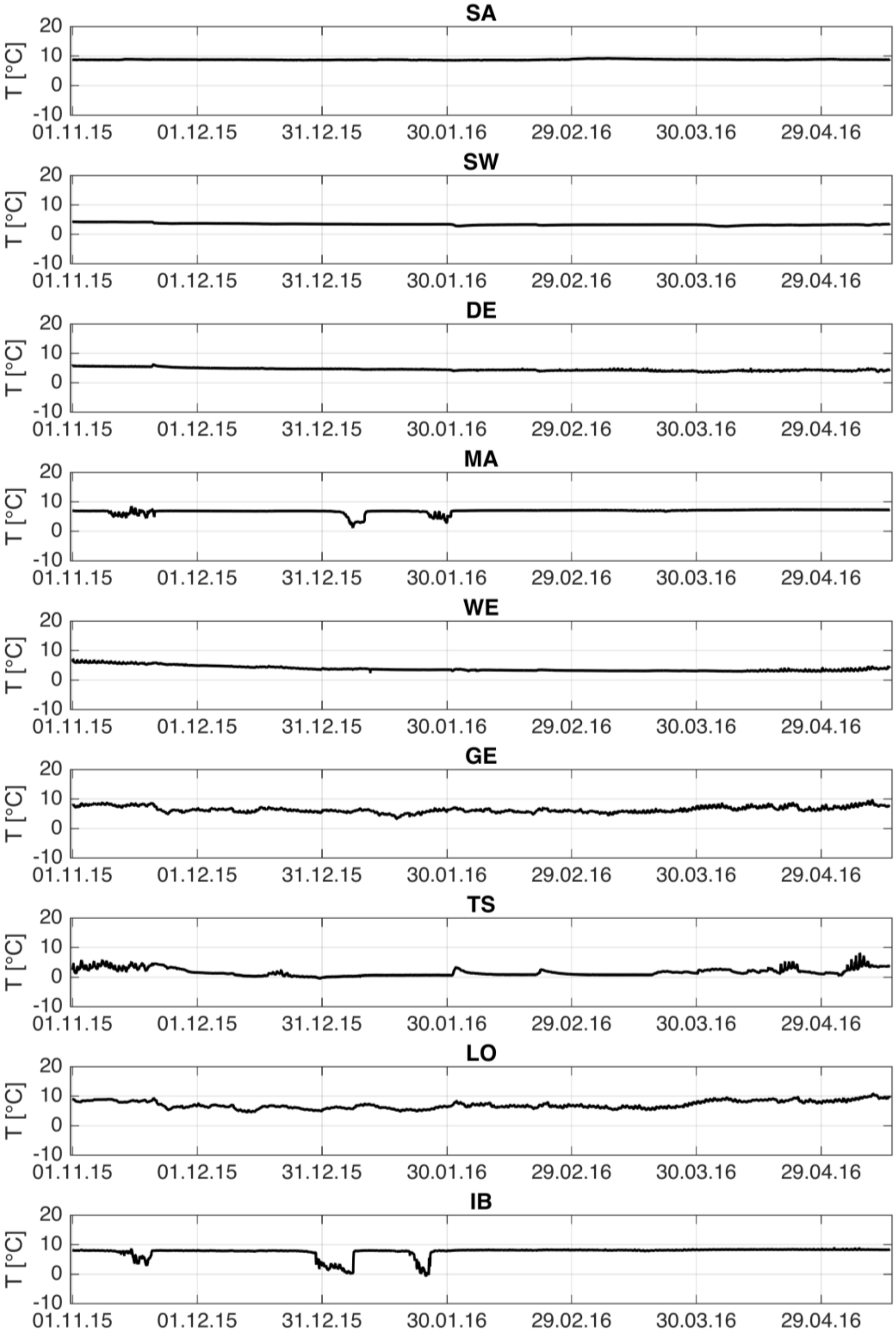
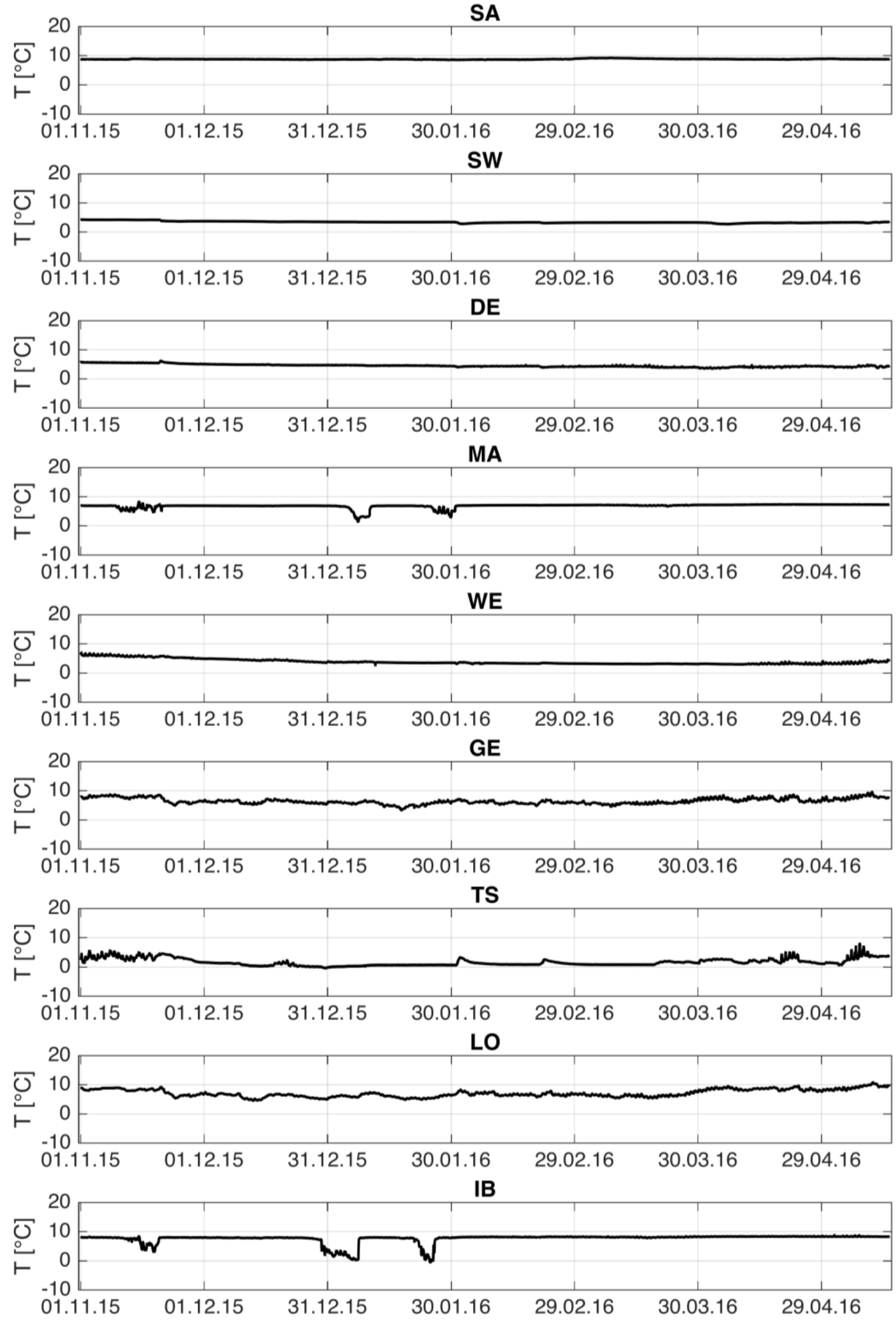
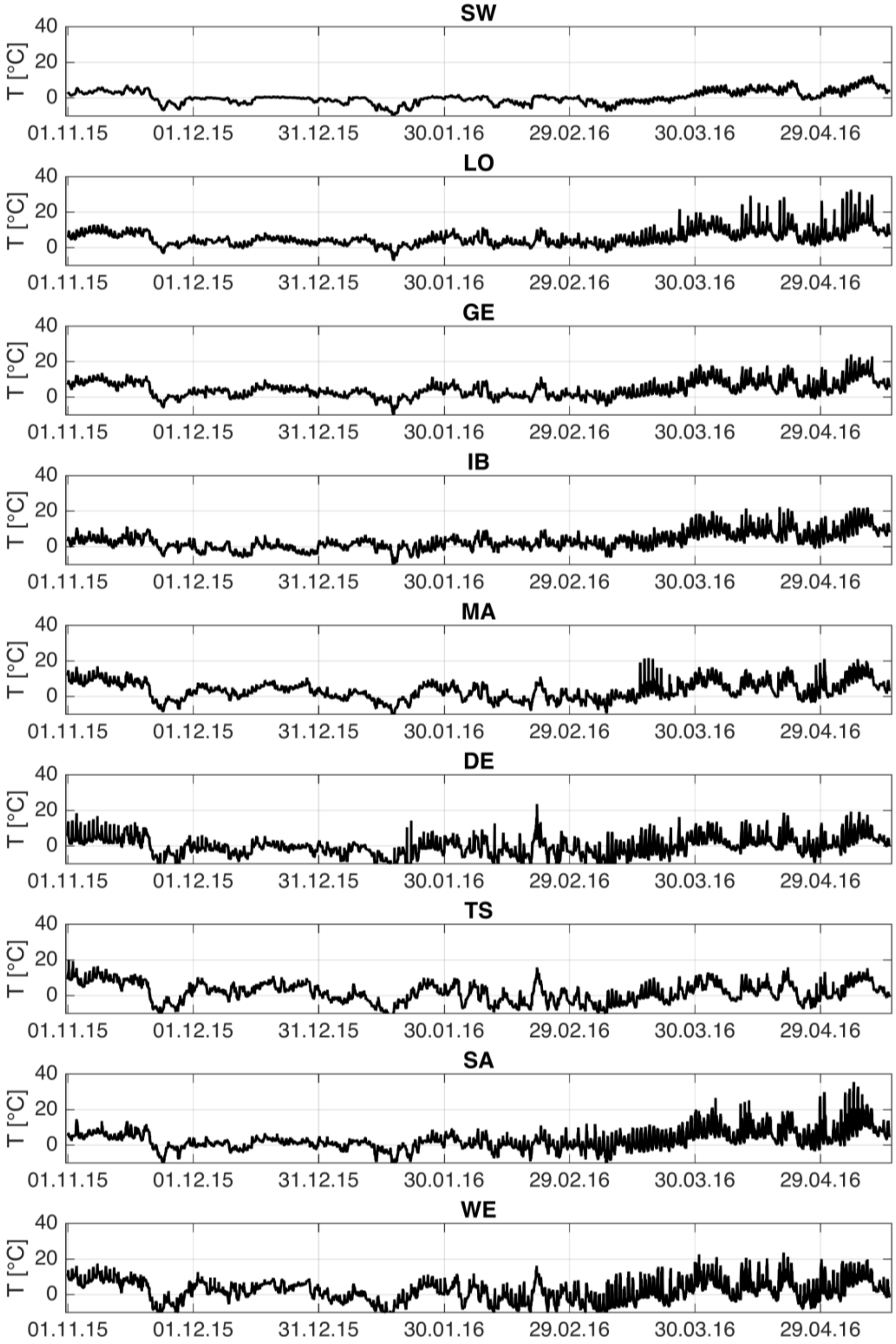
Appendix 1. Water temperature regime of the investigated springs in P1 sorted by increasing standard deviation.



Appendix 2. Water temperature regime of the investigated springs in P1 sorted by increasing standard deviation.



Appendix 3. Air temperature regime of the investigated springs in P2 sorted by increasing standard deviation.



CHAPTER SIX

General discussion and conclusions

Compared to other European alpine spring ecosystems, alpine springs in the central Swiss Alps are relatively poorly understood. On one hand, there is only little information regarding the macroinvertebrate assemblages on different altitudinal ranges, and on the other hand, the driving ecological factors influencing such assemblages are not known in detail. For understanding the ongoing rapid changes in alpine regions induced by global change, this knowledge is imperative to a better understanding of the changes ahead.

A pilot-study clearly showed heterogenic macroinvertebrate assemblages in a small-scale investigation area. Macroinvertebrate assemblages were found to be positively influenced by a high substrate diversity, the presence of organic material, the amount of dissolved oxygen and perennial discharge conditions. Disturbance by cattle and anthropogenic changes were found to have negative effects on taxa number. Substrate composition and substrate availability were also found to play an important role in other studies concentrating on alpine springs (Cantonati et al. 2006, von Fumetti and Blattner 2016). The pilot study documented relatively unstable environmental conditions regarding the amount of discharge, source of the spring water and water temperature. This contradicts the current theory describing springs as stable, perennial ecosystems with low amplitudes of water temperature (Odum 1971, van der Kamp 1995). The increased influence of the harsh winter season at high altitudes, compared to lowland springs, was identified as a main reason for the high environmental variability and disturbance regime in springs: High elevated springs also were found to be completely covered by snow over several months during winter. This was also confirmed by a winter survey, in which springs were investigated after digging them out for monitoring.

Along an altitudinal gradient, the macroinvertebrate assemblages changed considerably. Generally, the number of taxa showed a significant decrease with increasing altitude, whereas the number of individuals showed a slight increase. This was confirmed by a recent experimental study in the Andes (Madsen et al. 2015). Low alpine springs are characterised by the highest number of crenobiont species, whereas high alpine springs are dominated by alpine freshwater species, which are not exclusively bound to springs. Intermediate springs around the tree line are characterised by high species richness with a mixture of macroinvertebrates occurring in low and high altitudinal springs. Besides structural parameters such as the presence of stones and moss, the water temperature was found to be a main driver for changing macroinvertebrate assemblages along the altitudinal gradient. Water temperature as a main driver of macroinvertebrate assemblages was also described for springs in montane areas (Gathmann et al. 2009, Ilmonen et al. 2009, Bottazzi et al. 2011). Ongoing climatic changes, which lead to more intense and frequent increased air temperature in alpine areas, will have significant effects on species assemblages. A potential temperature induced upwards migration of species in low alpine springs can be expected. Species only occurring in high alpine springs are at risk of going extinct in the future (Vittoz et al. 2013). Moreover, the expected increased meltwater contribution in the future will lead to a decrease of alpha and beta diversity and will additionally negatively affect high alpine springs due to changed precipitation regimes (Brown et al. 2007).

Water temperature amplitude was found to be lowest in the highest springs. This can be explained by the buffering effect of insulating snow cover in winter (Füreder 2007), and the regulating effect of the input of cold water by melted snow and permafrost in early summer. Significant lower electrical conductivity values in high alpine springs compared to lower springs also indicates a higher meltwater influence. Lower springs cool down in winter due to the lack of snow cover and heat up in summer due to less meltwater contribution and higher air temperatures. Comparing macroinvertebrate assemblages of three different sampling occasions, the highest springs showed the lowest variability. Due to the equal occurrence of crenobiont species in all springs, crenobiosis cannot solely be explained by the adaption to constant water temperatures (Fischer et al. 1996). The constantly low water temperatures in the higher situated springs favor rhithtrobiont species such as *Drusus monticola* or *Drusus muelleri*. The harsh environmental conditions also promote fast developing organisms such as Chironomids.

Duration of the winter period and the temperature of the water are the key factors understanding high alpine springs. Logging the water and air temperature and the electrical conductivity can generate additional information about the processes in the aquifer and the spring water composition. The discharge of springs is composed of different sources of water, whereas groundwater is a significant but not the only component (Frisbee et al. 2013). By computing the residence time of the groundwater, perennial and intermitted springs can be distinguished even when a direct observation or access is not possible. Snow covered springs could be separated from springs not covered with snow as the latter exhibit a stronger correlation when analysing by logging air and water temperature data using time series analysis. Additionally, valuable information about the exact duration of the snow cover can be gained by measuring solar radiation. Hence the approach of temperature as a natural tracer (Martin and Dean 1999) was refined and adapted for springs. High alpine springs showed no response to air temperature regarding water temperature as they were covered by snow during winter. Lower springs without snow cover exhibit a stronger correlation of air and water temperature. Generally, time series analysis with data loggers is a useful method to gain information about the hydrological processes in the aquifer. Further measurements during summer would complement the insight we gained from the winter data. Moreover, the successfully tested method could possibly be improved by measuring soil instead of air temperature.

In summary, the current thesis gives information about macroinvertebrate assemblages in the central Swiss Alps. With this investigation, we showed that springs are heterogenic concerning their macroinvertebrate assemblages along an altitudinal gradient and that the water temperature of the springs and the processes ongoing in winter are the main influencing factors. Snow cover and snow cover duration, the influence of meltwater on the habitat structures, and the processes in the aquifer have been shown to be important for the macroinvertebrate assemblages in springs, but there is still a significant lack of understand these factors interact with one another to determine the observed macroinvertebrate community. The ongoing global changes, with enhanced effects in alpine regions (IPCC 2014), concern just these ecologically relevant factors: Higher temperatures in winter leads to less snow cover and shorter snow cover duration and therefore to a reduced buffering effect for the most elevated springs. Additionally, it is also predicted that higher temperatures and less summer precipitation and the missing melt water contribution lead to more frequent droughts in summer. Moreover, the changing climatic conditions influence the quality and availability of ground water (Hannah et al 2007), which reinforces the negative effects on macroinvertebrate assemblages and additionally reduces discharge. Alpine springs are found to be vulnerable to changing groundwater recharge-discharge processes due to the altered precipitation regimes associated with the changing climate (Clements et al. 2016). A better understanding of alpine springs is not only a tool to investigate the mechanisms of Global Climate Change itself, but also helps to develop actions to attenuate negative effects on biodiversity.

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Summary

The objective of this thesis is to shed light on the previously under-investigated natural alpine spring ecotones of Central Switzerland. The study focuses on investigating macroinvertebrate assemblages at different altitudinal levels in order to determine if macroinvertebrate assemblages in alpine springs differ along an altitudinal gradient. If there was a certain pattern in the macroinvertebrate assemblages, the study also aims to determine the relevant driving environmental factors and gain a better understanding of how the interaction of these factors influence macroinvertebrate assemblages. As environmental conditions, especially in alpine regions, change rapidly due to global warming, this study's goal is to contribute new knowledge to detecting possible climate-induced changes of macroinvertebrate assemblages in alpine springs.

The results show that macroinvertebrate assemblages differ clearly along the altitudinal gradient. The number of taxa decreases with increasing altitude. Crenobiont species occur predominantly in the lower situated springs, whereas high situated springs are increasingly dominated by alpine freshwater species. Besides structural parameters such as the presence of moss and stone, stability of the water temperature was found to be an important factor influencing macroinvertebrate assemblages. Generally, higher situated springs exhibit lower water temperatures than lower springs. As for the variation of water temperature across the altitudinal gradient, this study also determined the highest springs to be the most stable compared to lower elevated. The buffering effect of insulating snow cover in winter and the contribution of cooling snowmelt and permafrost in summer, were found to be the driving factors for water temperature stability in high alpine springs. Additionally, a continuous measuring of air and water temperature enables the characterization of perennial and intermittent springs, especially during seasonal periods where the springs are not easily accessible.

This thesis contributes to the current state of knowledge concerning macroinvertebrate assemblages through providing possible explanations for faunistic patterns found in alpine springs. Ongoing climatic changes, which affect alpine areas twice as intense as lower altitude ecosystems, will lead to changing environmental conditions within these springs, and thus, significantly affect the driving factors influencing alpine spring habitats. This is especially the case for alpine springs due to multiple driving factors changing simultaneously. Most notably an increase in temperature and changing precipitation characteristics is to be expected. Future research should focus on the influencing factors of species distribution and adaptability. A better understanding of natural springs can be used as an opportunity to study climate-change induced changes to biodiversity, as well as offer insights into how to minimize the negative consequences of Global Change on biodiversity and hydrological processes.

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