



**Influences of spring type, physicochemical factors, and longitudinal changes in freshwater spring invertebrate ecology**

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# **Influences of spring type, physicochemical factors, and longitudinal changes in freshwater spring invertebrate ecology**

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90 ECTS thesis submitted in partial fulfillment of a  
*Magister Scientiarum* degree in Aquatic Biology

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Influences of spring type, physicochemical factors, and longitudinal changes in freshwater spring invertebrate ecology  
Environmental influences on spring invertebrates

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# Abstract

Springs are unique freshwater ecosystems that present a natural laboratory for testing which environmental variables are important in shaping invertebrate communities. In my study, 22 freshwater springs were sampled throughout Iceland's volcanically active zone. Analysis of environmental variables with invertebrate communities determined that spring type, temperature, and pH were significant in shaping invertebrate communities. The significance of type and temperature were predicted, but pH was surprising as a significant variable.

Although springs are considered constant at their sources, rapid changes in environmental variables have been documented with increasing distance downstream from the rheocrene spring source. Previous studies have attempted to determine where a spring source ends and a springbrook begins, and physical definitions based on temperature and distance have been used to define the boundary between spring source and springbrook. Four rheocrene springs in the Hengill geothermal area were sampled at the source and at various points downstream to determine where invertebrate community shifts occur and the forces driving them. Community changes were observed, but a specific faunistic boundary could not be established for the spring source-springbrook continuum.

# Útdráttur

Lindir eru einstök ferskvatnsvistkerfi, sem í raun má kalla náttúrulega rannsóknarstofu, þar sem hægt er að sjá hvaða þættir eru mikilvægir fyrir mótun smádýrasamfélaga. Í þessari rannsókn voru sýni tekin úr 22 lindum á eldvirka beltí Íslands. Með því að bera saman umhverfisbreytur og smádýrasamfélög kom í ljós að lindargerð, hitastig og pH skiptu mestu máli við mótun samfélaga. Áður hafði verið gert ráð fyrir að lindargerð og hitastig skiptu miklu máli, en það kom á óvart að sjá mikilvægi pH.

Þó svo að lindir séu taldar vera stöðugar, þá hafa rannsóknir sýnt að umhverfisþættir breytast hratt þegar farið er frá lindum niður lindarlæki. Áður hafa rannsóknir reynt að finna hvar vistkerfi lindarinnar endar og vistkerfi lindarlækjarins tekur við. Til að meta þetta hafa vísindamenn notað eðlisfræðilegar breytur eins og hitastig og fjarlægð. Í þessari rannsókn skoðaði ég fjóra lindarlæki í Hengladölum, þar sem að jarðhita gætir. Tekin voru sýni í lindinni og á nokkrum stöðum niður lindalækinn, til að meta hvernig smádýrasamfélög breytast og hvaða þættir skipta þar máli. Niðurstöðurnar sýndu að þó nokkrar breytingar urðu í smádýrasamfélagunum, en þó fundust ekki greinileg skil milli lindar og lindarlækjarins.



*Dedication*

*To Paul and Sheila Govoni.  
They created this.*







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# Abbreviations

## *Chapter 2 study sites*

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<b>Site Abbreviation</b>	<b>Site Name</b>
<b>BOTNAR1</b>	Botnar 1
<b>BOTNAR2</b>	Botnar 2
<b>GRIMSNS2</b>	Grímsnes 2
<b>HLDRVATN</b>	Hlíðarvatn
<b>HRAUN</b>	Hraun
<b>HRAUNA</b>	Hrauná
<b>HUSAFEL1</b>	Húsafell 1
<b>HUSAFEL2</b>	Húsafell 2
<b>HUSAFEL3</b>	Húsafell 3
<b>KLDRBTNR</b>	Kaldárbotnar
<b>KLAPPARA</b>	Klappárós
<b>LKJRBOT1</b>	Lækjarbotnar
<b>LON</b>	Lón
<b>MDHSKGR</b>	Miðhúsaskógur
<b>PRSTHOLR</b>	Presthólar
<b>SANDUR</b>	Sandur
<b>SLTJRN</b>	Sílatjörn
<b>SLNGAPLR</b>	Silungapollur
<b>SKRDSLKR</b>	Skarðslækur
<b>STRMSVK1</b>	Straumsvík 1
<b>STRMSVK2</b>	Straumsvík 2
<b>THVERA</b>	Þverá

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## Chapter 2 taxa

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<b>Taxon Abbreviation</b>	<b>Taxon name</b>
<b>Acari-A</b>	Acari A
<b>Acari-B</b>	Acari B
<b>Arachnid</b>	Arachnida
<b>Cladocer</b>	Cladocera
<b>Coleop</b>	Coleoptera
<b>Collmba</b>	Collembola
<b>Cop-Cant</b>	Copepoda - Harpacticoida
<b>Cop-Cycl</b>	Copepoda – Cyclopoida
<b>Cop-Naup</b>	Copepoda – Nauplii
<b>Empidid</b>	Empididae
<b>Hemipter</b>	Hemiptera
<b>Hymenopt</b>	Hymenoptera
<b>Lepidur</b>	<i>Lepidurus arcticus</i>
<b>Muscidae</b>	Muscidae
<b>Olgchta</b>	Oligochaeta
<b>Ostracod</b>	Ostracoda
<b>Planorb</b>	Planorbidae
<b>Plecop</b>	Plecoptera
<b>Syrphid</b>	Syrphidae
<b>Tanypod</b>	Tanypodinae
<b>Tardigrd</b>	Tardigrada
<b>Thysanop</b>	Thysanoptera
<b>Tipulid</b>	Tipulid
<b>Trichop</b>	Trichoptera
<b>Chaetcl</b>	<i>Chaetocladius</i>
<b>Corynnra</b>	<i>Corynoneura</i>
<b>Cric tib</b>	<i>Cricotopus tibialis</i>
<b>Dia ber</b>	<i>Diamesa bertrami</i>
<b>Dia lat</b>	<i>Diamesa latitarsis</i>
<b>Dia zer</b>	<i>Diamesa bohemani/zernyi</i>
<b>E minor</b>	<i>Eukiefferiella minor</i>
<b>Met eury</b>	<i>Metriocnemus eurynotus</i>
<b>Micrpset</b>	<i>Micropsectra</i>
<b>Orth fri</b>	<i>Orthocladius frigidus</i>
<b>Orth obl</b>	<i>Orthocladius oblidens</i>
<b>Rheocric</b>	<i>Rheocricotopus</i>
<b>Thienema</b>	<i>Thienemanniella</i>
<b>Limnphys</b>	<i>Limnophyes</i>

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*Chapter 3 taxa*

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<b>Taxon Abbreviation</b>	<b>Taxon name</b>
<b>Orthocla</b>	Orthoclaadiinae
<b>Tanytars</b>	Tanytarsini
<b>Acari</b>	Acari
<b>Gastropo</b>	Gastropoda
<b>Tardigra</b>	Tardigrada
<b>Limoniid</b>	Limoniidae
<b>Nematoda</b>	Nematoda
<b>Harpacti</b>	Harpacticoida
<b>Ostracod</b>	Ostracoda
<b>Oligocha</b>	Oligochaeta
<b>Empidida</b>	Empididae
<b>Araneae</b>	Araneae
<b>Collemb</b>	Collembola
<b>Thysanop</b>	Thysanoptera
<b>Plecopte</b>	Plecoptera
<b>Simuliid</b>	Simuliidae
<b>Tanypod</b>	Tanypodinae

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# 1 General introduction – freshwater spring ecology in Iceland

Biodiversity in freshwater is economically (Hunter-Cevera, 1998) and biologically (Dodds, 2002) important. Current species declines may indicate an inability of our planet to support and maintain life (Lawton, 1991). By understanding which factors are important in shaping and maintaining biodiversity in freshwater, we could create ways to mitigate or reverse the loss of biodiversity. Freshwater spring ecosystems present an ideal habitat for testing various theories on the mechanisms responsible for driving biodiversity.

Groundwater becomes surface water in springs by reaching, or at least nearing, the land-atmosphere interface (Springer and Stevens, 2008). Physicochemical properties of springs such as temperature, pH, conductivity, discharge, and dissolved oxygen typically vary by spring location among catchments (Audorff et al., 2011), and it is also possible to find variation from different sources within catchments (Brown et al., 2003). Because groundwater is the source of spring water, springs have physicochemical conditions very similar to the groundwater stores from which they are discharged (Soulsby et al., 2006). Quantifying these physicochemical properties presents a problem for researchers in the study of other lotic systems than springs because stream conditions are very dynamic. Any measurement is essentially a “snapshot” for a specific location in the stream at a certain point in time (Carter et al., 2006). However, this snapshot problem does not seem to exist in springs because their physicochemical constituents remain nearly constant through time (Owen et al., 2008).

Although springs are essentially constant in their composition over time, the same is not true for spring water over physical distances. Physicochemical factors of water in springbrooks have been shown to change markedly with increasing distance from their sources. In spring-springbrook systems in Colorado, USA, total dissolved solids, seston, pH, and temperature all increased with distance from the source (Gray et al., 1983), and Orendt (2000) found that dissolved oxygen increased downstream from the source. Therefore, when studying springs, it is important to sample at or near the source because the conditions at the source are constant there since they are groundwater fed.

Because springs are ecosystems where groundwater and surface water meet, they provide an ecotone to study aquatic macroinvertebrates and the physicochemical factors which potentially affect their community structures (Smith et al., 2003). Ecotones are often areas of great diversity as a result of their transitional habitats (Smith et al., 2001), but springs provide an interesting system for studying biodiversity because the constancy of their conditions sets them apart from other ecotones. One of the most important variables when comparing macroinvertebrate community compositions in spring systems is temperature

(von Fumetti et al., 2007). Vannote and Sweeney (1980) proposed, in their thermal equilibrium hypothesis, that freshwater invertebrates have optimal temperatures at which they have maximum success. The different thermal regimes of springs, which remain constant at their respective sites, could thus provide optimal habitats for certain macroinvertebrates. Teal (1957) found that assimilation of nutrients from organic matter by chironomids was five times greater in a spring than in other freshwater habitats. The author felt that the heightened nutrient usage was the result of chironomids operating at their optimal temperature, which remained almost entirely unchanged because of the constant conditions of the spring. It is plausible, therefore, that along a thermal gradient, community assemblages could be very different simply because of different macroinvertebrate success rates at varying temperatures.

Another important dynamic affecting spring communities is the interaction between substrate composition and flow regime. Discharge and flow velocity shape the substrates of springs, and different substrates have been shown to be quite significant in determining macroinvertebrate assemblages (Malmquist et al., 2000; Smith et al., 2003; Wood et al., 2005; von Fumetti et al., 2006; Barquín and Death, 2008).

As previously mentioned, springs are closely related to the springbrooks to which they are connected. For example, taxa in Colorado, USA springs were found to be more unique at the source than in the springbrooks into which they flowed, and this appeared to be the result of the existence of spring specialists, or “crenobionts” (animals found only in springs) (Gray et al., 1983). Likewise, crenobionts comprised 50% or more of the total species found in four out of five regions in a survey of Italian springs (Di Sabatino et al., 2003). This shows the specific specialization of these animals to the spring habitat, and similar results may thus be found in Icelandic springs.

Iceland is located on a geological “hotspot” on the Mid-Atlantic ridge, and its location is partly responsible for the formation of the island (Sigmundsson and Sæmundsson, 2008). A hotspot is an area on the Earth’s surface that experiences long periods of volcanism due to the upwelling of a mantle plume. In the case of Iceland, this mantle plume occurs in combination with a mid-ocean ridge, where two continental plates are diverging (Ruedas et al., 2004). The formation of Iceland has occurred on a fast geological scale, and Iceland is still a geologically active area (Gudmundsson and Brenner, 2003), which houses newer rock formations younger than 17 million years (Foulger, 2006). The geomorphology of Iceland is shaped by glaciation (Geirsdóttir et al., 2007) and volcanism (Thordarson and Larsen, 2007). High precipitation rates (Koreimann et al., 1996) and porous lava bedrock in the volcanically active zone (Sigurdsson and Stefansson, 2002) have led to the formation of springs throughout Iceland’s volcanically active zone (Einarsson, 1994).

Iceland’s long groundwater residence times (Sveinbjörnsdóttir et al., 2000) lead to homogeneity of the physicochemical properties within a single catchment (Soulsby et al., 2006), but variability among springs in Iceland is still not well understood. Most springs worldwide have temperatures near the mean annual air temperature for their given areas (van der Kamp, 1995), but the geothermal activity of Iceland has, in some locations, caused increases in groundwater temperatures, which have led to the formation of thermal springs (Tuxen, 1944). Although not collectively uniform in temperature, thermal springs have temperatures that are warmer than their mean annual air temperatures (Alfaro and Wallace, 1994; Pentecost, 2005). Hayford and Herrmann (1998) describe springs as “model field

laboratories” because of their unchanging conditions, but this is not entirely accurate because areas with springs typically have more geological activity, leaving the springs susceptible to stochastic events. These dynamics make Iceland an ideal location to carry out spring investigations.

Early classifications (in English) of springs separated this ecosystem into three main types: rheocrene (stream-forming), limnocrene (pool-forming), and helocrene (marsh-forming) (Hynes, 1970). Recently, 12 types of discharge have been described for springs (Springer and Stevens, 2008), in which the three original terms are included. Since this study focused on only rheocrene and limnocrene springs, there should be no ambiguity in the use of these terms.

Rheocrene springs are springs in which groundwater flows directly into a channel to form a stream, while limnocrene springs discharge groundwater directly into a basin forming a pool or pond. It has commonly been suggested that these spring types support different macroinvertebrate assemblages, with limnocrene springs supporting pond- or pool-dwelling species while rheocrene springs support lotic species, especially with increasing distance downstream from the source along the spring-springbrook continuum (Hynes, 1970). Imonen and Paasivirta (2005) found differences in macroinvertebrate assemblages by spring type, but they hedged their conclusion with the caveat that better definitions are needed for spring habitats. Recently, this traditional view has been called into question (von Fumetti et al., 2006), and it has been suggested that spring type is not as important as the various other factors which go into shaping macroinvertebrate assemblages (velocity, substrate composition, water chemistry, etc.).

Lava rocks make up a majority of substrates in springs in Iceland’s volcanically active zone, and their porosity creates a unique habitat for invertebrates. A macroinvertebrate investigation of rocky substrates in Iceland found higher biodiversity and density on rocks with coarser surfaces (Malmquist et al., 2000). Most of the differences in the diversity and density in this study were attributed to differences among chironomids.

Chironomidae is the most dominant freshwater taxon in Iceland (Hrafnisdottir, 2005). Chironomids have been shown to be greatly affected in their growth and survival by temperature (Teal, 1957) and in community dynamics by substrate composition (Malmquist et al., 2000). Chironomids were the most diverse taxon found in two large-scale ecological surveys in Iceland (Lindegaard, 1979a; Lindegaard, 1979b), and a long-term study examined fluctuations in their populations over a 20-year period (Gardarsson et al., 2004) in Mývatn, a spring-fed Icelandic lake. Although several studies have been carried out on chironomids in Iceland, springs have been largely neglected in these investigations. Ferrington (2008) describes springs as potential hot spots for chironomids worldwide, so any spring research conducted in Iceland should consider chironomids carefully.

Iceland is an excellent place to try to gain some clarity on the topic of spring type affecting macroinvertebrate communities. The ubiquity of both types of springs throughout the volcanically active zone presents the opportunity for looking at spring types which are geologically similar but geographically separate. With both rheocrene and limnocrene springs occurring in close proximity to one another, oftentimes in the same catchment in

various regions of the island, spatial confounds cease to be a problem, and physicochemical effects become more salient along with type.

There is ambiguity in the springs literature regarding the definitions of spring sources and springbrooks. In order to study springs as discrete habitats, it seems necessary to get researchers closer to deciding upon commonly accepted definitions of what constitutes spring habitats and springbrook habitats. Erman and Erman (1995) delineated between the two habitats by a change of 2°C from the source, with the source being the point of discharge and the springbrook being anything after the change in temperature. This definition is lacking because of the differences in distances before this change takes place, and the value is seemingly arbitrary because it does not take the biota into account.

An attempt was made to clarify the definitions spring source and springbrook by taking into account physicochemical and faunistic factors (von Fumetti et al., 2007). Unfortunately, the authors only managed to move the boundary from 2°C to 1°C, but they suggested that future investigations look on a smaller scale before this change takes place.

The Hengill geothermal area presents an ideal place to study these changes. Many rheocene springs are present in a small geographical area, and some of the springs are influenced by geothermal activity while others remain unaffected. This allows for the study of both warm and cold spring continua for investigating where community changes take place.

## **1.1 Objectives**

The purpose of my research is to investigate the principles of spring ecosystems and bring clarity to much of the ambiguity that exists in spring studies. More specifically, my objectives are to 1) determine which variables are important in shaping different spring communities at the spring source, and 2) delineate where a spring becomes a springbrook from a faunistic standpoint as opposed to the more common thermal description.



## **2 Assessing the role of ecological factors in shaping invertebrate communities in cold springs**

### **2.1 Introduction**

For many years, Earth's freshwater has experienced an unprecedented decline in biodiversity as the result of alteration, fragmentation, and simplification of habitats. In recent years, changing global climate has exacerbated these declines (Cairns and Lackey, 1992). Habitat and climate constrain diversity and abundance of species, and rapid changes in one or both leads to irreversible changes in species distribution (Vitousek, 1994). In order to understand the overall impact of environmental changes to freshwater ecosystems, it is necessary to understand how specific variables shape the distribution of organisms for different habitat types. One habitat that is lacking in scientific investigation is freshwater spring ecosystems.

Spring ecosystems offer a unique opportunity for the study of community dynamics and the relationship between local geomorphology and biological communities (Smith et al., 2003). However, terminology and definitions regarding spring ecosystems are fraught with ambiguity. Spring systems have been traditionally separated into three categories: limnocene (pool-forming), rheocene (stream-forming), and helocene (marsh-forming) (Hynes, 1970). Recently, spring types have been expanded to 12 varieties (Springer and Stevens, 2008), but the original three types are included in this reclassification. Additionally, there have been attempts to determine where the spring ends and the associated spring system (pool, stream, wetland, etc.) begins (Erman and Erman, 1995; Fumetti et al., 2007). Ilmonen and Paasivirta (2005) differentiated spring types based on invertebrate communities and found that traditional groupings of limnocene, rheocene, and helocene held true. Fumetti et al. (2006), however, found that spring types were difficult to distinguish from one another faunistically and suggested that they form a continuum between the three traditional spring types. Both of these studies sampled springs, but the study areas of the two were different. The former collected samples by dragging nets through the water column, while the later took Surber samples within 10 m of the source. This reflects a common problem with spring ecology studies; the term "spring" is used commonly throughout freshwater literature, but definitions vary on an individual basis.

In studying spring ecology, it is important to understand which habitat can be defined as a discrete spring and how this differs from the whole spring-fed ecosystem. Instead of applying the term spring to any spring-fed ecosystem (e.g., spring-fed stream or spring-fed

lake), I define a spring as the point of discharge of groundwater, or the source of surface water bodies. A further definition of the spring type is based on its associated habitat. Therefore, the term rheocrene spring is used here for sources where a stream forms. The same is true for limnocrene springs, in which a pool forms from the source. This is an important distinction to make since both rheocrene and limnocrene springs were included in the present study and refer to points of discharge of groundwater and not the pools or streams that the springs form.

Rheocrene and limnocrene springs are ubiquitous throughout the Icelandic volcanically active zone because of the island's natural history. Iceland is young on a geological timescale and is still geologically active, with frequent events such as earthquakes and eruptions (Gudmundsson and Brenner, 2003). Rock formations are relatively young and basaltic (Sigurdsson and Stefansson, 2002), with formations younger than 17 million years (Foulger, 2006) dominated by basalts (Sigmundsson and Saemundsson, 2008). The island's topography has been shaped by glaciation, and Iceland has undergone at least 20 periods of glaciation since the Pliocene Epoch (Geirsdóttir et al., 2007).

In addition to glaciation, the primary force shaping the geology of Iceland are volcanic systems, and most geologic processes and events, such as hydrologic cycles, are interconnected with volcanism (Thordarson and Larsen, 2007). Iceland typically receives 200,000 million m<sup>3</sup> of precipitation per year (Koreimann et al., 1996), and large parts of that precipitation fall on the porous lava bedrock within the volcanically active zone (Sigurdsson and Stefansson, 2002). The lava bedrock allows for fast percolation of precipitation into groundwater and increased chemical constituents of the groundwater through weathering (Einarsson, 1994; Gíslason et al., 1994; Flaathen and Gíslason, 2007). This groundwater is commonly discharged in the form of springs throughout Iceland's volcanically active zone (Einarsson, 1994). Iceland's long groundwater residence times (Sveinbjörnsdóttir et al., 2000) have led to homogeneity of the physicochemical properties within a single spring location, but physicochemical variability among springs in Iceland is still not well understood.

The spring habitat, where groundwater becomes surface water, provides a unique environment in which to study aquatic macroinvertebrates and the physicochemical factors that structure invertebrate community dynamics (Smith et al., 2003). Temperature is one of the most important variables when comparing differing macroinvertebrate communities in spring systems (Fumetti et al., 2007). Additionally, discharge and flow velocity shape the substrates of springs, and different substrates have been found to be significant in determining differences between macroinvertebrate assemblages (Smith et al., 2003; Wood et al., 2005; Fumetti et al., 2006; Barquín and Death, 2008). Lava rocks make up a majority of substrates in springs in Iceland's volcanically active zone, and their porosity creates a habitat for invertebrates. A macroinvertebrate investigation of rocky substrates in the littoral zone of Icelandic lakes found higher biodiversity and density on rocks with coarser, less eroded surfaces, commonly found in areas influenced by lava (Malmquist et al., 2000). Most of the differences in the diversity and density in this study were attributed to differences among chironomids.

Chironomidae is the most dominant freshwater taxon in Iceland (Hrafnisdóttir, 2005). Temperature affects chironomid growth and survival rates (Teal, 1957), and substrate composition affects chironomid diversity and abundance (Malmquist et al., 2000).

Although many studies have been carried out on chironomids in Iceland, springs have been largely neglected in these investigations. Ferrington (2008) describes springs as potential hot spots for chironomids worldwide. Therefore, in order to explore the differences in macroinvertebrate community structure of Icelandic springs, I have chosen to add a closer emphasis on chironomids.

## **2.2 Objectives and hypotheses**

The objectives of this study were to develop a consistent method to study the complex spring ecosystem, which is comparable across associated habitat types, and to determine which factors are important in shaping spring invertebrate community composition. I hypothesized that:

1. Spring type (rheocrene or limnocrene) would be an important factor shaping community composition because colonization would first occur in the associated habitat (stream or pool) and then dispersal toward the source would develop slowly over time.
2. Temperature and substrate composition would be the environmental factors with the strongest effect on shaping invertebrate communities, since temperature (Fumetti et al., 2007) and substrate (Dumnicka et al., 2007) have been demonstrated to be instrumental in shaping spring invertebrate communities in previous studies.

## **2.3 Materials and methods**

### **2.3.1 Study sites**

Altogether, 22 springs were sampled in the volcanically active zone of Iceland during the summers of 2004-2006 (Figure 2.1). Local geology is similar throughout the volcanically active zone, with basalts younger than 10,000 years dominating the landscape. The springs for this study were selected from a previous study of Arctic charr (*Salvelinus alpinus*) that looked at more than 30 springs (Kristjansson, 2008). Only permanent rheocrene and limnocrene springs in which a discrete source and spring type could clearly be identified were selected, with a total of 10 rheocrene and 12 limnocrene springs. Although all springs in this study were located in the volcanically active zone, only springs that were not clearly influenced by geothermal activity were used in order to study a narrower temperature range.

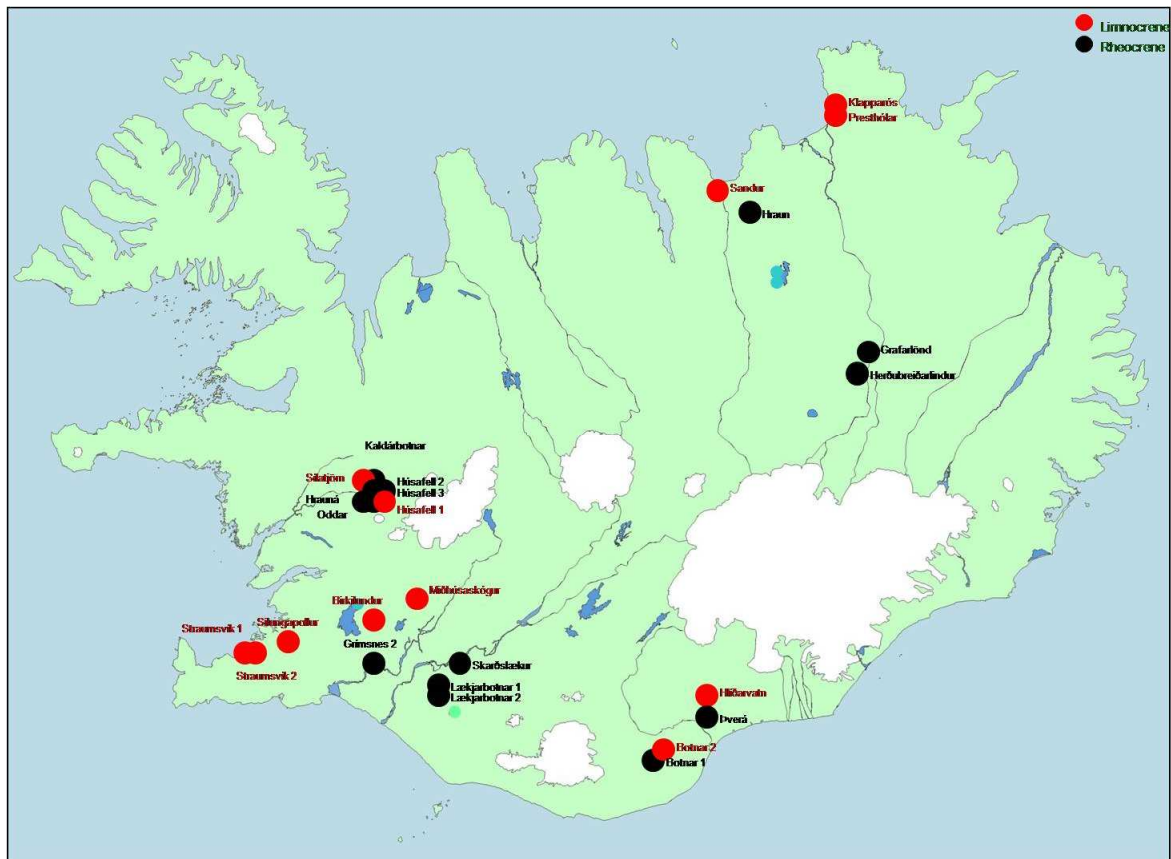


Figure 2.1 Map of Iceland with full names given for sampling locations. Limnocrene springs pictured in red and rheocrene springs pictured in black.

### 2.3.2 Macroinvertebrates and physicochemical parameters

At each study site, spring type was recorded (limnocrene or rheocrene) and temperature, dissolved oxygen saturation, pH, and conductivity were measured using a multi-probe sonde (YSI 600XLM). Substrate complexity and composition were recorded by assessing the percentage of the substrate covered by lava rocks and stone surface roughness. The roughness of stones was assigned a value on a 1-5 scale based on the number and size of pores and the contours of the surface, with 1 being smoothest and 5 being roughest (Malmquist et al., 2000; Kristjánsson, 2008). Stones were also measured for surface area, which was used to calculate density.

Macroinvertebrates were sampled for diversity and abundance estimates at the spring source by scrubbing stones (Kristjánsson, 2008). Six stones were collected at each site. Each stone, upon selection, was placed into a bucket. Stones were scrubbed with a soft brush and rinsed with water. After the initial rinse, a small amount of buffered formalin (<0.5 %) was applied to the stone (Kristjánsson, 2008). This had the effect of coaxing the invertebrates out of the pores of the stones, so they could be scrubbed and rinsed a second time. Collected macroinvertebrates were sieved through 250  $\mu\text{m}$  mesh and fixed in a 5% buffered formalin solution in the field and then rinsed and stored in 70% ethanol in the lab until they were sorted, counted, and identified to the lowest possible taxonomic level. In the laboratory, Chironomidae were mounted on a microscope slide using Hoyer's mounting

medium (Anderson, 1954) and identified to species (Cranston, 1982; Wiederholm, 1983; Schmidt, 1993; Merritt et al., 2008). In samples where chironomid individuals were more numerous than 80, a sub-sample of 50 individuals was taken for mounting and identification.

### 2.3.3 Statistical analyses

Shannon diversity measures were calculated for all stones at each site, and mean Shannon diversities were also calculated for each site (Buckland et al., 2005). Redundancy analysis (RDA) was performed using CANOCO 4.5 (Leps and Smilauer, 2003) to determine which variables affected macroinvertebrate community structure.

## 2.4 Results

### 2.4.1 Physicochemical parameters

The physical and chemical properties of the springs were variable in general (Table 2.1), but there were no clear differences in spring properties by spring type. Temperature ranged from 2.9 to 6.8 °C (mean  $\pm$  SD: 4.4  $\pm$  1.1 °C). Conductivity was low ranging from 61 to 255  $\mu\text{S cm}^{-1}$  (mean  $\pm$  SD: 155  $\pm$  62  $\mu\text{S cm}^{-1}$ ). Each spring in this study was supersaturated with dissolved oxygen, with saturation ranging from 155 to 267% (mean  $\pm$  SD: 161  $\pm$  35%). All springs were slightly alkaline, ranging in pH from 7.9 to 9.7 ((mean  $\pm$  SD: 8.4  $\pm$  0.7).

*Table 2.1 Mean physicochemical values for all sites*

Spring	Temperature (°C)	Conductivity ( $\mu\text{S cm}^{-1}$ )	Dissolved oxygen (%)	pH	% rock	Roughness	Type
BOTNAR1	6.68	241	154.6	7.9	20	1.5	Rheocrene
BOTNAR2	4.54	251	133.8	8.1	10	4.5	Limnocrene
GRIMSNS2	5.81	185	266.7	7.8	25	1.5	Rheocrene
HLDRVATN	5.03	170	154.5	7.8	90	4.5	Limnocrene
HRAUN	4.61	201	146.9	7.7	100	3.5	Rheocrene
HRAUNA	3.75	61	157.9	8.9	99	3.0	Rheocrene
HUSAFEL1	2.88	101	139.2	9.7	60	4.0	Rheocrene
HUSAFEL2	3.05	95	151.0	9.6	100	2.8	Rheocrene
HUSAFEL3	3.17	107	159.2	9.6	100	3.5	Limnocrene
KLDRBTNR	3.53	70	165.8	8.3	90	5.0	Rheocrene
KLAPPARA	3.89	109	143.7	7.7	10	3.3	Limnocrene
LKJRBOT1	4.62	255	164.1	7.6	50	4.0	Rheocrene
LON	4.70	105	149.1	8.2	90	4.0	Limnocrene
MDHSKGR	6.75	121	246.1	9.1	70	2.5	Limnocrene
PRSTHOLR	3.70	124	178.9	8.2	10	3.8	Limnocrene
SANDUR	3.39	203	127.4	7.9	20	3.5	Limnocrene
SLTJRN	4.76	132	146.9	7.9	10	3.2	Limnocrene
SLNGAPLR	3.53	170	133.4	9.1	50	4.7	Limnocrene
SKRDSLKR	5.08	244	185.1	7.7	20	3.1	Rheocrene
STRMSVK1	5.05	199	133.5	8.7	20	2.3	Limnocrene

STRMSVK2	4.43	192	124.1	8.9	99	2.2	Limnocrene
THVERA	4.76	76	188.0	8.0	95	4.0	Rheocrene

## 2.4.2 Macroinvertebrates

I found a total of 57 taxa in this study (Table 2.2). For analysis, rare or semi-aquatic taxa were dropped from data sets, and some taxa with few representatives were combined and recorded at higher taxonomic levels. Once groups were determined for analysis, I found an average of 16 taxa per site, and there was no difference in the number of taxa found between limnocrene and rheocrene springs. Chironomidae was the most abundant taxon in this study, comprising over 45% of individuals in all but two springs. The chironomid *Eukiefferiella minor* was the most abundant taxon, and it was the only taxon found in every spring.

An RDA run on physicochemical factors, spring type, and substrate composition found that three variables significantly explained 36% of the species composition: spring type, pH, and temperature. Spring type explained 14% ( $p = 0.002$ ), pH explained 13% ( $p = 0.002$ ), and temperature explained 9% ( $p = 0.02$ ) of the variability in the data. The RDA with significant variables was plotted with invertebrates to show how they shaped species composition (Figure 2.2).

The RDA showed that all members of the genus *Diamesa* negatively correlated with temperature, which signified that *Diamesa* were found in the coldest sites. Harpacticoid copepods were positively correlated with pH, which suggested that they were found in sites with higher pH. They were found in high abundances in only four springs, and they showed no spring type effect, as two of the springs were rheocrene and two were limnocrene. Cladocerans were negatively correlated with spring type, which meant were found more in limnocrene springs. They were the taxa most strongly associated with type. The two sites in which they were most abundant were where the associated habitats were the deepest calmest pools of all limnocrene spring systems in the study. One type of acari had its highest abundances in three limnocrene systems and was negatively correlated with type, and although one of these systems was separated from the other two by a great geographical distance, these were the three locations which were closest to the sea and may have had a sea water influence in their groundwater.

Shannon diversities were calculated for all stones. Diversity for all sites was relatively low, ranging from 0.35-2.38 (Figure 2.3). Shannon diversity was almost the same for limnocrene springs (1.46) and rhocrene springs (1.42). Since richness was essentially the same for rheocrene and limnocrene springs and  $H^1$  scores were essentially the same for both types of springs, differences in community structures could only be attributed to the presence of different taxa.

Table 2.2 Densities (individuals  $m^{-2}$ ) of invertebrates for all sites

	BOTN ARI	BOTN AR2	GRIM SNS2	HLDR VATN	HRAU N	HRAU NA	HUSA FEL1	HUSA FEL2	HUSA FEL3	KLDR BINR	KLAP PARA	LKJR BOTI	LON	MDHS KGR	PRSTH OLR	SAND UR	SLTJ RN	SLNG APLR	SKR DSL KR	STRM SVK1	STRM SVK2	THVE RA
Acar- A	0.0	0.0	3.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	81.7	15.2	0.0	1.7	0.3	0.5	0.0	21.1	41.0	0.0
Acar- B	6.2	1.0	1.0	1.5	2.4	3.8	1.1	0.0	1.6	0.1	3.7	2.4	0.4	0.0	1.6	2.4	3.7	2.2	4.1	4.4	0.0	7.5
Arach nid	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Cladoc er	0.1	9.6	0.0	5.9	9.4	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.2	1.4	0.0	3.5	2.5	0.0	19.2	45.0	2.8
Coleop	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.2
Collab la	0.0	0.9	0.1	0.0	0.2	0.1	0.0	0.0	0.0	0.2	0.1	0.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	1.0	0.4	0.2
Cop- Cant	0.3	7.1	0.5	8.9	1.3	1.8	37.9	10.0	47.7	44.9	9.1	1.5	0.0	2.9	1.6	0.8	3.7	19.4	5.9	2.1	0.5	3.0
Cop- Cycl	0.1	4.8	0.3	1.1	1.0	0.2	0.5	0.0	0.2	0.0	0.0	0.2	0.0	1.1	3.1	0.0	0.8	1.6	0.4	0.0	2.9	2.6
Cop- Naup	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Empidi d	0.0	0.0	0.4	0.2	0.0	0.1	0.2	0.0	0.1	0.0	0.0	0.4	0.0	0.0	0.0	0.1	0.5	0.3	1.3	0.0	0.0	0.1
Hemip ter	0.0	0.8	0.0	0.0	0.0	0.0	0.3	0.0	0.1	0.4	0.7	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.2	0.0	0.0
Hymen opt	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lepidu r	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Musci dae	0.0	0.2	0.7	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.1	0.0	0.1	0.7	0.0	0.0	2.1
Olgeht a	4.9	13.0	2.2	7.8	6.2	0.1	0.7	0.0	1.0	2.1	13.8	4.5	0.2	1.7	3.8	1.9	1.7	2.9	0.6	4.5	0.3	12.7
Ostrac od	1.3	2.9	0.5	3.3	2.4	0.9	7.6	0.0	0.8	0.4	3.5	1.8	0.6	1.1	12.3	0.4	2.9	3.6	8.6	1.0	0.4	7.3
Planor b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plecop	0.0	0.0	1.8	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.7
Syrphi d	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Tanyph od	0.1	0.1	0.3	0.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.6	0.0	0.2	0.0	0.1	0.1
Tardig rd	0.2	0.3	0.1	0.2	0.9	0.0	0.7	0.0	0.0	0.0	15.6	1.3	0.0	0.0	0.3	0.1	0.1	0.3	2.6	0.0	0.0	1.9
Thysan op	0.0	0.1	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Tipulid	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tricho p	0.3	1.8	0.2	2.3	0.1	1.3	3.0	3.4	0.5	1.2	2.2	0.6	2.6	0.1	1.1	0.2	1.7	1.1	0.9	1.9	0.4	0.3
Chaete lid	0.0	1.4	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.3	0.0	1.1	1.0	0.0	2.3	0.7	0.2
Coryn nra	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cric tib	0.0	3.5	0.0	2.8	15.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	72.2	0.2	0.0	0.5	22.5	0.0	5.1	0.3	3.6
Dia ber	2.5	0.0	0.0	0.0	0.0	1.8	0.0	9.5	2.1	4.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	11.7	0.0	0.0	0.0
Dia lat	0.0	0.0	0.0	0.0	0.4	0.0	0.4	0.0	1.3	4.7	0.0	0.2	0.0	0.0	0.0	0.6	0.5	0.2	0.0	0.0	0.0	4.4

Diazer	2.2	23.9	0.0	0.5	5.8	67.0	27.6	42.9	23.8	5.5	7.3	11.7	0.0	0.0	0.0	3.9	4.1	5.6	7.5	6.9	0.0	0.2	3.7
E minor	80.0	15.2	78.6	12.4	25.8	10.0	8.7	27.2	12.0	31.6	18.2	66.8	8.1	2.0	55.6	73.9	46.9	20.2	2.1	31.2	3.7	24.0	
Met	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.4	0.0
cury	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Micrps	0.4	11.0	7.1	25.2	11.5	0.8	0.0	0.0	0.0	0.0	3.6	2.1	0.1	0.1	3.5	0.0	6.3	0.4	42.4	1.4	1.1	2.0	
et																							
Orth	1.2	2.1	1.4	5.6	7.0	8.0	9.3	5.9	7.4	3.9	6.6	0.1	0.2	2.8	3.3	11.6	10.8	8.3	5.1	3.3	0.8	10.9	
fri																							
Orth	0.1	0.1	0.7	19.8	0.0	0.6	0.7	0.0	0.0	0.3	0.0	2.4	0.0	0.1	0.0	1.1	0.0	0.7	5.7	0.0	0.0	2.1	
obl																							
Rheocr	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
ic																							
Thiene	0.1	0.0	1.1	0.3	9.6	3.4	0.1	0.0	1.6	0.6	15.6	2.6	4.9	0.2	7.2	0.9	8.6	4.3	0.3	0.1	0.7	7.6	
ma																							
Linnp	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	
lys																							



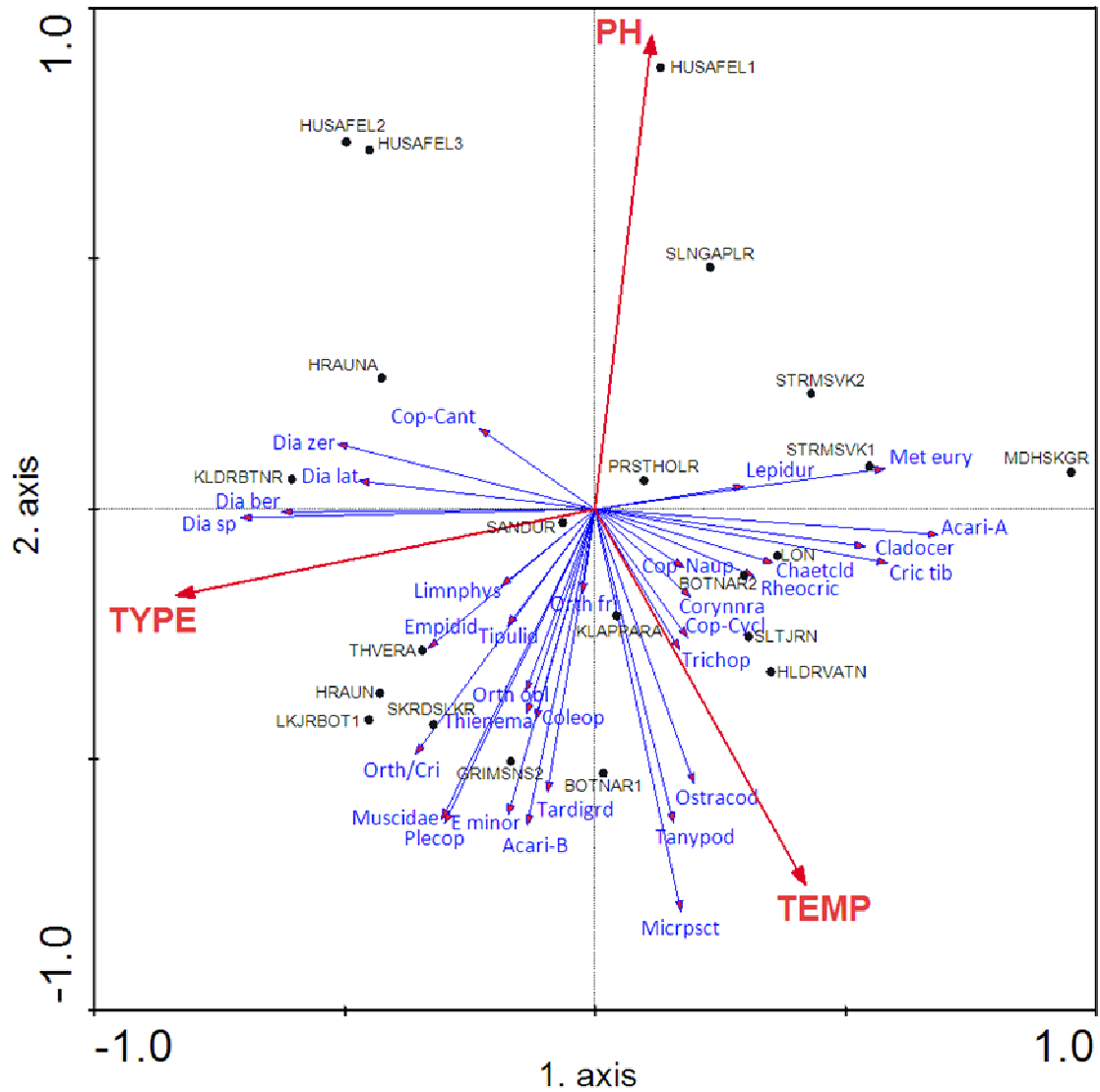


Figure 2.2 RDA ordination diagram of 22 sampling locations (black) and the relationship of the significant environmental variables (red) and invertebrates (blue). Taxa and site names available beginning on page xvi.

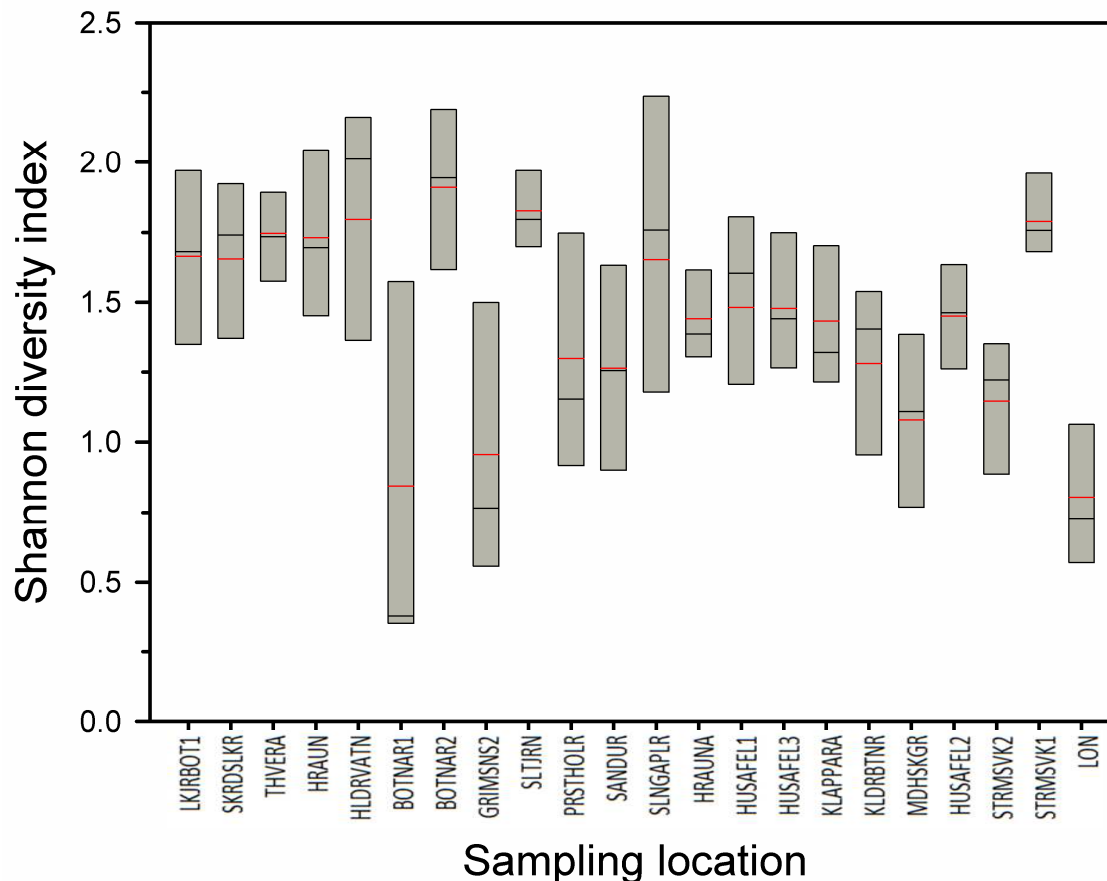


Figure 2.3 Shannon diversity index for all sites, with range of  $H^1$  scores over all stones (gray box), mean  $H^1$  (red), and median  $H^1$  (black). Sampling locations listed in order of principal component axis 1 scores from RDA. Site abbreviations available on page xvi.

## 2.5 Discussion

With this study, I was able to achieve my goal of simplifying the study of a complex ecosystem. By reducing the scope of my study to two easily identifiable spring types and studying only the discretely observable component which both types of systems share, I was able to accomplish this goal. As predicted, I found that spring type significantly affected macroinvertebrate communities at the spring source. Taxa common to lentic systems were found more commonly in limnocene springs, especially cladocerans, and taxa common to lotic systems were found in rheocene springs. This finding is most easily explained by the idea that animals are colonizing the associated habitat of the spring system (pool or stream) and then moving toward the source. Although the source habitat itself, which is constantly discharging water, is lotic, the animals which colonize it come from the ambient habitat.

As predicted, temperature was found to be a significant factor shaping spring invertebrate communities. The finding was most clearly seen in the genus *Diamesa*. Four species of *Diamesa* were found in the coldest sites. Springs often host cold-stenothermic organisms (Orendt, 2000) because of their nearly constant conditions. Although *Diamesa* have been reported to be cold-stenotherms since they are found at the low temperatures (Rosenberg et al., 2004), there is laboratory evidence that suggests that they can grow and survive at higher temperatures than previously believed, and they are simply outcompeted at these higher temperatures in natural settings (Milner, personal correspondence, 2010).

The finding that pH was significant in shaping invertebrate communities was unexpected. Harpacticoid copepods were most strongly correlated with higher pH, and I have been unable so far to explain the mechanism behind this. One study has suggested that some copepods may select for higher pH, but a sufficient explanation for the selection could not be found (Hessen and Nilssen, 1983). Another study (Pipan et al., 2006) claims pH is significant in shaping copepod community structure, but no explanation is ever provided. The freshwater of Iceland has a high pH, so Iceland is a good location for testing theories of high pH on aquatic fauna. Future research should take into account primary producers to determine if the food source available to invertebrates is shaped by pH, and thus is responsible for shaping invertebrate communities.

I have used the term ambient habitat to describe the streams or pools formed by the spring, but the groundwater from which the spring flows should be considered ambient as well. In this study, I found no animals that appeared to be of groundwater origin, so I assumed colonization was only occurring from the surface ambient habitat. Groundwater is typically anoxic or hypoxic (Hynes, 1970) because of respiration taking place in the soil while precipitation percolates to groundwater, but all of my sites were supersaturated with oxygen. It is my hypothesis that since the vadose zone, the region of aeration above the water table, is formed by porous lava rock, as opposed to soil, oxygen trapped in the pores is picked up by precipitation as it percolates to groundwater. Since groundwater is typically oxygen poor, it presents a challenging habitat for animal communities. Oxygen-rich groundwater, however, could support more life than typical groundwater, so Icelandic groundwater communities, which are supersaturated with oxygen, require future study. This need for future study is underscored by the discovery of two new species of groundwater amphipods in Iceland (Kristjánsson and Svavarsson, 2004; Svavarsson and Kristjánsson, 2006).

In the present study, I have determined which factors in spring ecosystems are important for shaping and maintaining biodiversity. The significance of temperature in this study suggests that spring ecosystems will likely be vulnerable to the loss of biodiversity caused by rapid changes in global climate. The pH findings in this project show how changes in chemistry can have significant effects on invertebrate communities. As a result of changing climate, global biogeochemistry of aquatic systems is likely to change (Vitousek, 1994). Since springs are systems of essentially constant physicochemical conditions, the biotic communities housed by them may be vulnerable to abundance and biodiversity losses. If springs, however, are largely unaffected because of deeper groundwaters, they may actually serve as refugia for taxa displaced from other habitats. In either scenario, community structure will experience a shift. Understanding how these shifts are affected may enable us to manage them.

Perhaps the most significant finding of my study comes from the most statistically significant variable in the study, spring type. I was comparing points of groundwater discharge. The fact that spring sources, which were the same habitat in all spring types, had communities shaped by the ambient habitat shows the interconnectedness of all ecological systems. I found that biodiversity is not shaped by one ecosystem process or characteristic, but by several working in concert with one another.

This project succeeded in showing how dynamic spring ecosystems are. Several factors governing invertebrate assemblages have been put forward by others, but there has never really been a consensus regarding what was being studied. In most cases, researchers can look at a forest, river, prairie, or lake and tell you what that system is, with its boundaries and diagnostic features. When, however, five groups of researchers look at a spring, there are likely to be five different definitions given for what a spring is. Some may see a pool and call it a spring, others may see a stream and call it a spring. I saw the source and called it a spring. By doing this, I was able to take a very small portion of a complex and convoluted habitat and study it systematically. What I found is that everything is connected. The source communities are shaped by the ambient habitat, and the ambient habitat is shaped by the physical properties of the source and the local geology. This is true for all freshwater systems; the processes are essentially the same across the board, but the subtle nuances of each system add to the greater understanding diversity in nature.

# **3 Assessing the mechanisms driving faunistic change along a rheocrene continuum**

## **3.1 Introduction**

Running waters have historically received much less scientific attention than lakes (Hynes, 1970), and of the running waters studied, most studies have focused on small headwater streams. Headwater streams are at the mercy of their local conditions and are commonly diverse in flow regimes, light availability, temperature, substrate, and food availability (Meyer et al., 2007). All of these factors affect the conditions of the headwater streams and shape the biodiversity in the streams. Headwater streams offer a wide array of habitats because they are so susceptible to disruption (Connell, 1978) from riparian and local factors (Meyer et al., 2007). By using rheocrene spring systems, which are able to escape disruption to the habitat, it is possible to look at which factors are responsible for shaping invertebrate communities in headwater systems without disturbance.

Some information regarding abiotic factors shaping spring invertebrate communities have already been studied. I have demonstrated previously that spring type, temperature, and pH were significant in shaping spring community composition (Chapter 2) at the spring source. Since spring type, which was defined by the associated habitat, was the most significant variable shaping communities, I believed the next step in my research should be to determine where the spring source ends and the associated habitat begins. In limnocrene springs, water discharged from the source forms a pool. It is therefore difficult to track the exact path of source water once it is discharged. In rheocrene springs however, the discharged water forms a stream (springbrook) from the source, and the source water can easily be traced in its movement down the channel. Because of the ability to clearly follow the path from the source, I decided that the best systems with which to determine where spring sources end and associated habitats begin is rheocrene springs.

Previous studies have attempted to determine where rheocrene spring sources end and springbrooks begin. Erman and Erman (1995) delineated between the two habitats by a change of 2°C. This definition states that the point of discharge and all water downstream until a water temperature change of 2°C as the source. All water after the 2°C change was defined as a springbrook. This definition is seemingly arbitrary because it does not take the biota into account; it's a purely physical definition. The 2°C change may occur in one spring system four meters downstream from the source, while another spring system may not change by 2°C for one kilometer or more. Although the spring continuum has remained thermally constant over this longer distance, the local geology, primary producers, shading,

and stream order may have changed. Invertebrate communities would likely change with changes in these factors, so it would be erroneous to label something as the source when the biological communities have undergone several changes along a continuum. By looking at changes in invertebrate communities and determining which factors are shaping community composition, it would be possible to create definitions of spring and springbrook that are based on both the physical and biological. This was attempted by von Fumetti et al. (2007) but the study only managed to move the boundary from 2°C to 1°C. They also established the boundary at 5 m claiming that this is where the temperature change often occurs. This definition is still using physical parameters (temperature and distance), but the biota do not corroborate the boundaries.

A physical definition of the boundary between spring source and springbrook is only relevant if it is based on the biotic communities in the spring systems. Therefore, a biological definition of the boundaries of spring systems is more logical. While there is no consensus on invertebrate community structure shaping the boundary, there have been studies that have looked at community changes longitudinally along the rheocrene spring continuum. Some studies have found that diversity increased downstream from the source (Ward and Dufford, 1979; Smith, 2000), and they suggested the increase in diversity was in accordance with the principles of the river continuum concept (RCC; Vannote et al., 1980). Using the RCC in this case may be problematic because the studies sampled low order (headwater) streams, and the RCC is based on community changes with changes in stream order. In the RCC, shredders typically dominate the headwaters because of the large amounts of organic matter input. Since spring sources are groundwater fed, there is practically no allochthonous material coming into the spring at the source. The lack of change in stream order and the lack of allochthonous material make the RCC a poor model to base spring system dynamics on. In its most basic form, the RCC could be described as an increase in diversity and evenness with distance downstream (up to a certain point), but this is only analogous if diversity increases downstream.

Not all studies have found an increase in diversity with an increase in distance from the source. von Fumetti et al. (2007) observed a decrease in diversity, but they suggested that it may have been the result of buildup of calcareous sinter downstream from the point of discharge. This problem seems to be limited to karst spring systems, so the results are most likely not applicable to spring systems with bedrock other than limestone. The results seem to be more telling about the local geology than the processes that shape community structure along the spring continuum, so the observed decrease is not expected to be applicable across all spring systems.

Sloan (1956) suggested that intermediate positions along the spring continuum had the greatest invertebrate diversity. This would contradict the finding of a decrease. It would support the idea of an increase up to a certain point in the spring continuum, but without information about distance downstream, it is hard to compare the studies. The finding that diversity was greatest at an intermediate position is problematic because the spring continua were sampled at different locations based on the local environmental conditions. This means that the spring systems were not studied in a systematic way, so the results are essentially anecdotal.

There are two main challenges in trying to draw conclusions from the spring source-springbrook continuum literature. The first challenge is that the literature is very sparse.

There are only a handful of papers that have attempted to determine the boundary between the spring source and the spring brook, and there has never been consensus among authors. The second problem is that the available studies use drastically different methods and sampling distance along the channel.

## **3.2 Objectives and hypotheses**

In this study, I attempted to systematically study the spring-springbrook continuum in rheocrene springs to determine the extent of the spring source and the beginning of the springbrook in relation to the faunal communities. I hypothesized that:

1. The source would have distinct biotic communities because of the constancy of the environmental conditions.
2. The underlying processes shaping community structure would be made by looking at the variables shaping spring communities of different thermal regimes. I believed the most important factors (outside of temperature) would come clearly to the surface.

## **3.3 Materials and methods**

### **3.3.1 Study sites**

I sampled four rheocrene spring systems at the Hengill central volcano (64.083° N, 21.300° W) in southwest Iceland. The geothermal area covers approximately 100 km<sup>2</sup> and is active. Because of this area's groundwater and local geology, there are several rheocrene springs discharging from mountainsides. Some of the springs have geothermally influenced groundwater and others remain cold. It is not uncommon to find adjacent springs differing in temperature by 15 °C or more. Since it is possible to study springs with the same local geology and different thermal regimes, the Hengill system is essentially a natural laboratory in which to test different ideas about what shapes biotic communities along a thermal gradient, so it was a perfect choice to test my ideas about rheocrene spring communities being used to define boundaries within the spring continuum.

Two of the four spring systems sampled in this study had geothermal influence, and two springs were unaffected by the Hengill volcano's geothermal activity. The springs used in this study were used in a previous study (Friberg et al., 2009), and the names were maintained for this study. The springs sampled were IS-6, IS-7, IS-8, and IS-12. IS-6 and IS-8 were geothermal (warm) springs and IS-7 and IS-12 were cold springs.

### **3.3.2 Macroinvertebrates and physicochemical parameters**

A continuous segment of springbrook was established for sampling. Each segment extended from the point of discharge (source) to 20 m downstream. As a continuous segment, there were no other channels joining the springbrook. This ensured that all the water in the springbrook was from the same source. The one exception was the spring system IS-7, which used a 17 m segment instead of 20 m because an adjacent channel joined the springbrook 18 m from the source. In each spring continuum, five macroinvertebrate samples were collected at each sampling station along the springbrook. Sampling stations were located at 0 (source), 5, 10, and 20 m (17 m for IS-7). At each station, macroinvertebrates were sampled for diversity and abundance by scrubbing stones (Kristjansson, 2008). Five stones were collected at each station, and each stone was placed into a bucket, where it was scrubbed with a soft brush and rinsed with water. After the initial rinse, a small amount of buffered formalin (<0.5 %) was applied to the stone (Kristjansson, 2008). This had the effect of coaxing the invertebrates out of the pores of the stones, so they could be scrubbed and rinsed a second time. Collected macroinvertebrates were sieved through 250  $\mu\text{m}$  mesh and fixed in a 5% buffered formalin solution in the field and then rinsed and stored in 70% ethanol in the lab until they were sorted and identified to varying taxonomic levels (commonly order or family).

At each sampling station, temperature, pH, and conductivity were measured using a multi-probe sonde (YSI 600XLM), and flow velocity was measured using a Marsh-McBirney Flo-Mate flow meter. At sampling locations where the channel was too shallow to submerge the sonde, water was collected in a bucket and measured immediately. Substrate complexity and composition were recorded by assessing the percentage of the substrate covered by lava rocks and stone surface roughness. The roughness of stones was assigned a value on a 1-5 scale based on the number and size of pores and the contours of the surface, with 1 being smoothest and 5 being roughest (Malmquist et al., 2000; Kristjansson, 2008). Stones were also measured for surface area, which was used to calculate density.

### **3.3.3 Statistical analyses**

Shannon diversity measures were calculated for all stones at each site, and mean Shannon diversities were also calculated for each site (Buckland et al., 2005). Redundancy analysis (RDA), cluster analysis, and two-way cluster analysis were performed using PC-ORD 6 (Peck, 2010) to determine which variables affected macroinvertebrate community structure.

## **3.4 Results**

### **3.4.1 Physicochemical parameters**

Conductivity ranged between 71 and 330  $\mu\text{S cm}^{-1}$  (maximum conductivity at 25 °C)s. IS-6 and IS-8 (the two geothermal spring systems) had conductivities more than twice those of IS-7 and IS-12 (the two cold spring systems). Conductivity did not change significantly with distance downstream from the source in any of the spring systems studied. The range of pH for all sites was 7.51-8.06, and there were no differences between spring systems or



longitudinally along the spring continuum. Current velocity was low for all sites, with less than 1.0 m/s for all spring systems. The percentage of the substrate covered by lava rocks was variable among and within the spring systems, but there were no discernible patterns related to the substrate composition. Temperature was the variable that had the greatest effect on invertebrate communities (Table 3.1).

IS-6 had a mean temperature of 19.37°C and only changed by a total of 0.07°C from its minimum temperature to its maximum. The mean temperature of IS-8 was 22.98°C, and it changed by 0.10°C. IS-7 had a mean temperature of 5.93°C, with an increase of 1.05°C downstream. IS-12 had a mean temperature of 4.52°C and increased by a total of 1.79°C. The cold spring systems increased in temperature, with distance downstream from the source, much more rapidly than the geothermal springs, which remained essentially unchanged over their 20 m segment.



*Table 3.1 Mean values of environmental variables for all sampling locations in springs IS-6, IS-7, IS-8, and IS-12.*

	IS-6-0	IS-6-5	IS-6-10	IS-6-20	IS-7-0	IS-7-5	IS-7-10	IS-7-17	IS-8-0	IS-8-5	IS-8-10	IS-8-20	IS-12-0	IS-12-5	IS-12-10	IS-12-20
Temperature (°C)	19.34	19.37	19.41	19.35	5.29	6.34	5.77	6.30	23.03	23.00	22.95	22.93	3.72	4.24	4.60	5.51
Conductivity (µS cm <sup>-1</sup> )	282	282	282	281	109	71	108	108	314	313	313	330	120	120	120	119
pH	7.53	7.64	7.66	7.79	8.06	7.94	7.85	7.91	7.51	7.60	7.69	7.73	7.87	7.56	7.61	7.65
Flow velocity (m s <sup>-1</sup> )	0.23	0.33	0.33	0.33	0.1	0.23	0.16	0.15	0.61	0.67	0.84	0.46	0.18	0.08	0.18	0.32
% Rock	90	50	90	60	90	70	60	50	100	60	90	50	20	30	10	50



### 3.4.2 Macroinvertebrates

Abundance did not show any clear patterns with distance from the source (Table 3.2). No spring had its maximum density at the source, but maximum densities did occur at stations 5, 10, and 20 m. Minimum densities occurred at stations 0, 10, and 20m (Figure 3.1). Mean taxa richness, however, increased with distance from the source. In all springs, stations 10 and 20 had greater mean taxa richness than stations 0 and 5. Diversity in spring IS-6 increased by 27.4% (7.3-9.3) and diversity in IS-8 increased by 34.0% (5.0-6.7) from stations 0 and 5 to stations 10 and 20. Diversity in spring IS-7 increased by 100.0% (5.0-10.0) and diversity in IS-12 increased by 139.1% (4.6-11.0) from stations 0 and 5 to stations 10 and 20. Although all springs increased in mean taxa richness, the increases were greater in the cold springs.

The relationships between invertebrates and environmental variables were analyzed by an RDA. The first axis explained 22.3% of the variance in the species data. The second axis explained 11.1% of the species variance. The only significant variable was conductivity, which explained 52.9% of the species data. Conductivity appeared to be closely related to temperature. The warm springs, IS-6 and IS-8, clustered closely together on the left side of the ordination biplot and overlapped in the plot (Figure 3.2). This indicated that these sites have several taxa in common. This indication of faunistic similarity was confirmed by a two-way cluster analysis, which shows the taxonomic overlap by site (Figure 3.3). The presence-absence data in this figure provide the richness value. Tanytarsini chironomids, oligochaets, gastropods, and acari were strongly correlated with the warm springs, IS-6 and IS-8. The cold springs, IS-7 and IS-12, clustered separately and were near each other on the right side of the biplot. Ostracoda were strongly associated with spring IS-12, and chironomids from the subfamily Orthoclaadiinae were strongly correlated with spring IS-7 and to a certain degree with IS-12 (Figure 3.2).



*Table 3.2 Densities for all sampling stations. Abbreviations on page xviii.*

	IS-6-0	IS-6-5	IS-6-10	IS-6-20	IS-7-0	IS-7-5	IS-7-10	IS-7-17	IS-8-0	IS-8-5	IS-8-10	IS-8-20	IS-12-0	IS-12-5	IS-12-10	IS-12-20
<b>Orthocla</b>	1.7	3.9	5.9	1.0	60.9	61.7	79.7	57.8	1.8	7.8	3.3	1.1	11.0	7.9	6.2	17.0
<b>Tanytars</b>	0.4	3.2	0.6	0.5	0.0	0.0	0.0	0.0	0.0	0.8	0.6	0.0	0.0	0.1	0.1	0.2
<b>Acari</b>	5.0	13.9	20.0	8.8	0.2	0.1	0.1	0.1	0.9	19.5	10.9	0.9	0.0	0.1	0.3	0.4
<b>Gastropo</b>	2.5	4.5	3.3	2.3	0.0	0.0	0.0	0.0	0.6	13.3	4.0	0.7	0.1	0.0	0.0	0.0
<b>Tardigra</b>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	2.7
<b>Limoniid</b>	0.0	0.2	0.4	0.2	0.0	0.0	0.0	0.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
<b>Nematoda</b>	0.0	0.0	0.1	0.0	0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.6
<b>Harpacti</b>	1.1	5.4	5.9	2.6	0.4	0.0	0.4	2.3	0.0	0.0	0.0	0.0	0.0	0.4	1.7	4.6
<b>Ostracod</b>	0.0	0.0	0.0	0.0	0.2	0.3	0.1	1.4	0.0	0.0	0.0	0.0	2.8	3.7	1.5	4.9
<b>Oligocha</b>	2.6	32.9	68.4	38.2	0.1	0.0	0.1	0.5	5.5	24.9	5.4	0.2	0.1	0.0	0.3	0.7
<b>Empidida</b>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
<b>Araneae</b>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<b>Collemb</b>	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<b>Thysanop</b>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<b>Plecopte</b>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<b>Simuliid</b>	0.0	0.4	4.5	0.8	0.0	0.0	0.1	0.1	0.0	0.0	2.9	1.6	0.0	0.0	0.0	0.1
<b>Tanypod</b>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0





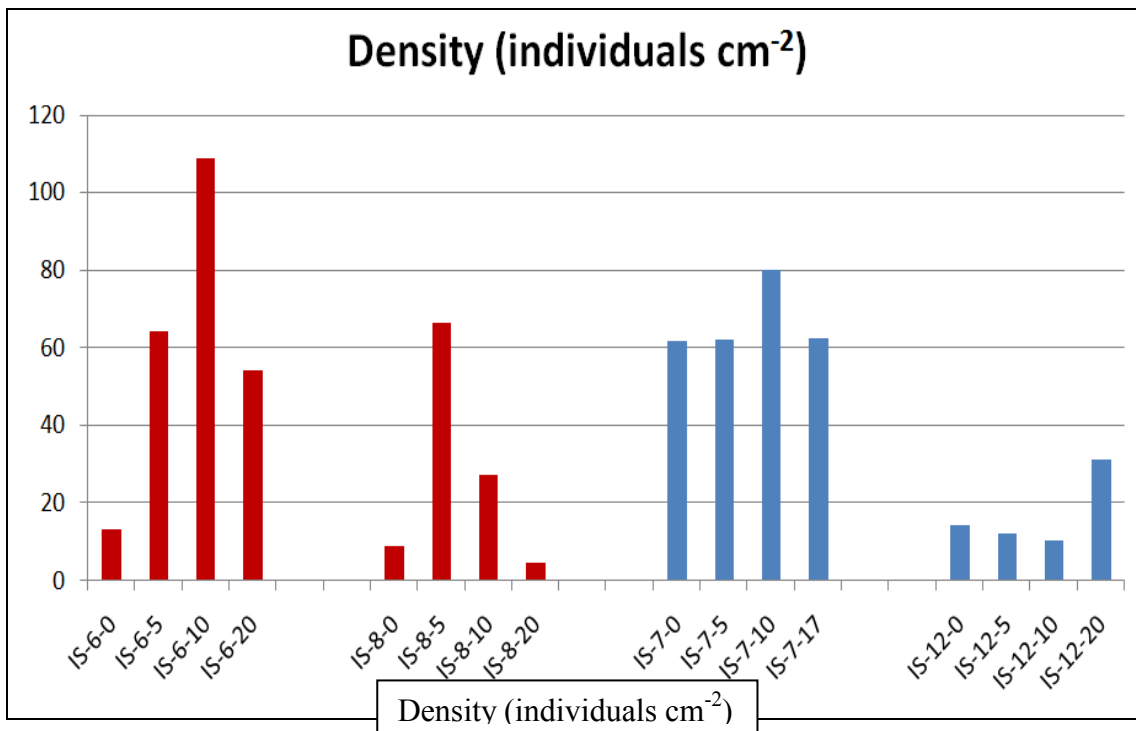


Figure 3.1 Densities for warm springs (red) and cold springs (blue).

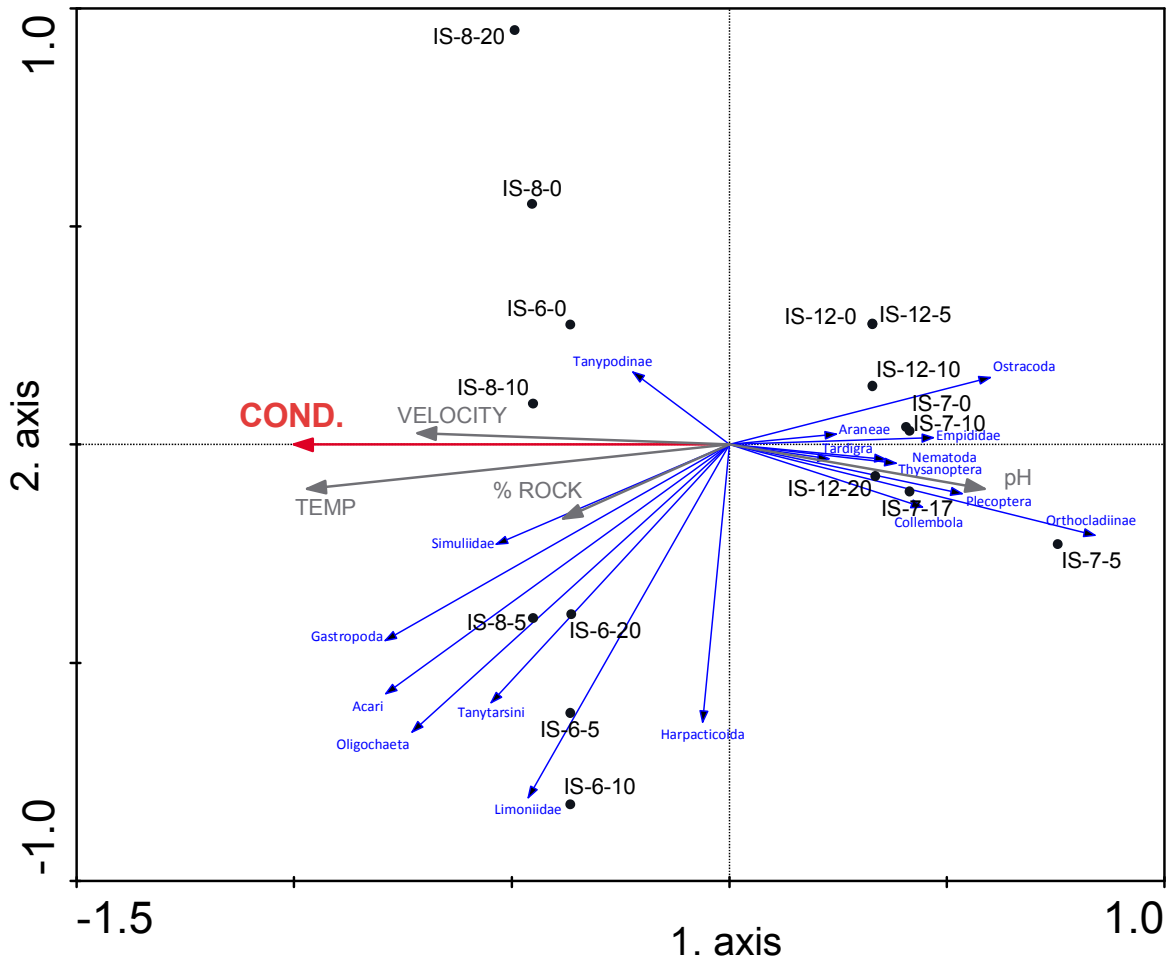


Figure 3.2 RDA ordination diagram for significant (red) and other measured (grey) variables, sites (black), and taxa (blue). Abbreviations available on page xviii.

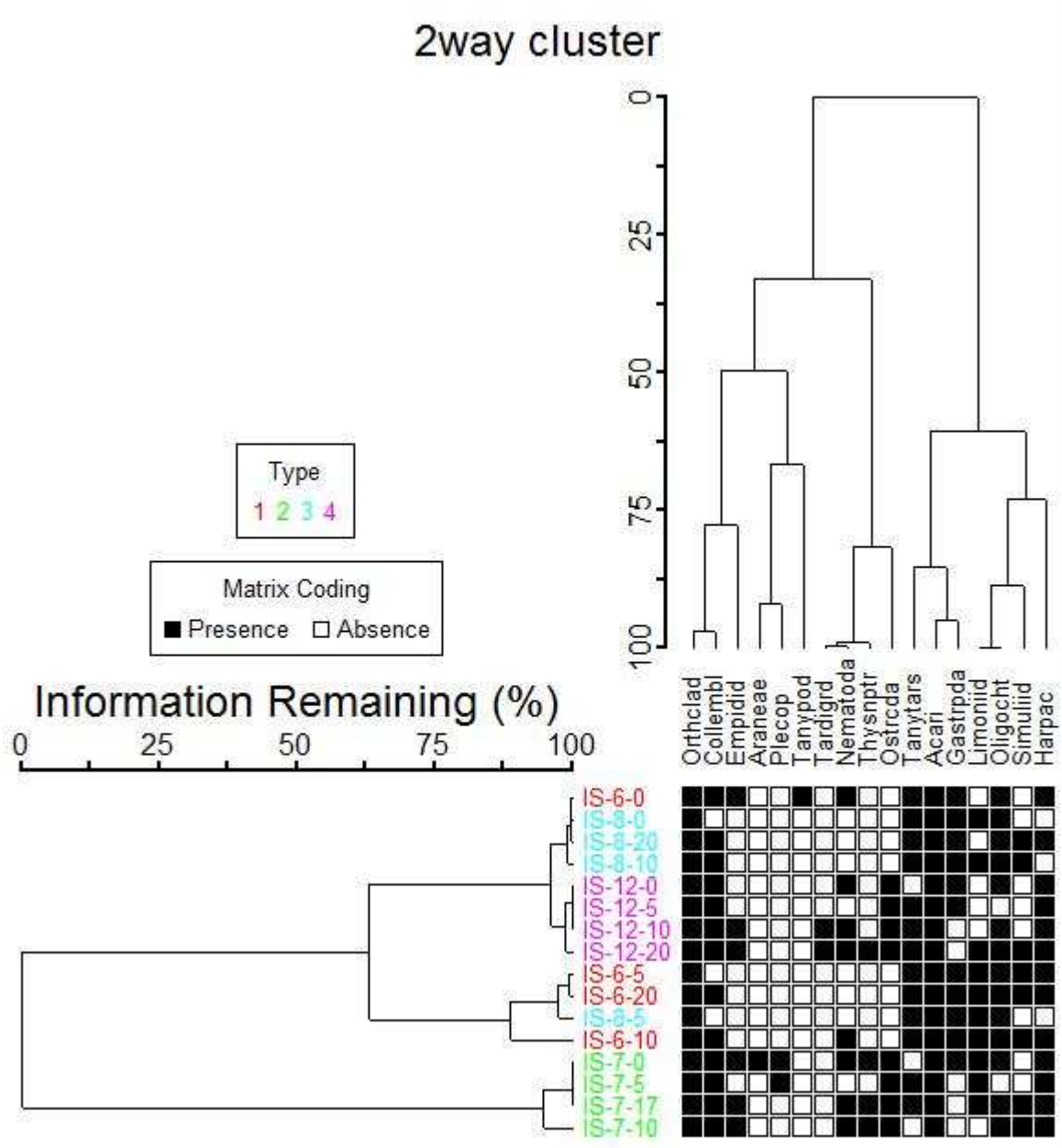


Figure 3.3 Two-way cluster analysis objectively identifying similar groups and showing presence-absence data for richness measures and overlap of IS-6-0 with IS-8 and IS-8-5 with IS-6 (Peck, 2010). Abbreviations available on page xviii.

### 3.5 Discussion

There was nothing present exclusively in the physicochemical data that I felt could provide a definition of the spring source boundary. Conductivity, substrate composition, pH, and flow velocity did not change notably within spring systems downstream from the source, so these variables were not considered to be important shaping community structure within springs. With the exception of pH, this conclusion is consistent with previous results that these variables are not significant in shaping community structure (Chapter 2).

Conductivity appears to be the main variable shaping rheocene spring invertebrate communities, which is not surprising since it is closely linked with temperature, which was a significant variable shaping spring communities in the previous study (Chapter 2) and the previous designations of spring and springbrook have been based on temperature (Erman and Erman, 1995; von Fumetti et al., 2007). The warm springs were closely related in the ordination, and the cold springs were also related but not to the same degree as the warm springs. The warm springs were grouped tightly on both axes and had more similarities among taxa than the cold springs. The shorter horizontal distances, which are a measure of dissimilarity with longer lines representing greater dissimilarity, in the two-way cluster analysis for IS-6 and IS-8 also support this finding. The cold springs were very similar on the first axis in the RDA, but they were less related to one another in relation to the second axis, which suggests there is some factor other than temperature shaping community structure, so substrate composition and pH likely influence cold springs more than warm springs. Cold springs had similar communities, but the dominance of some taxa may have skewed the results. This was probably the case for Orthoclaadiinae in IS-7, where Orthoclaadiinae were in higher proportion than in spring IS-12.

For all sites, maximum taxa richness was at 10 or 20 meters. This finding was much more exaggerated in the cold springs. The cold springs changed in temperature much faster than the warm springs. It is possible that taxa selecting for low temperatures are found at the source (Cantonati et al., 2006) and diversity increases with temperature as less cold-stenothermic taxa colonize the warmer downstream segments of the channel. The constancy of temperature in the warm springs may have led to the smaller changes in taxa richness with distance downstream. Since the changes in temperature are essentially negligible ( $0.07^{\circ}\text{C}$  in IS-6 and  $0.10^{\circ}\text{C}$  in IS-8), there must be some other mechanism responsible for the change in taxa richness. The biggest proportional change in IS-6 comes from the abundance of acari at the source and the gradual decline with distance downstream. For IS-8, the biggest proportional change comes from the abundance of Oligochaeta at the source and their decline downstream. Individuals from these respective groups, acari and Oligochaeta, appear to be selecting for something at the source, but there is not clear indication of what it is.

The most comprehensive investigation of the spring source-springbrook boundary to date had been that of von Fumetti et al. (2007). Their boundary of  $1^{\circ}\text{C}$  and 5 m was not supported by my findings. IS-7 and IS-12, the cold springs, showed the greatest change in community diversity after a change of about  $1^{\circ}\text{C}$ . I also found, however, that the warm springs exhibited community composition changes with a change of only  $0.10^{\circ}\text{C}$ . Therefore, I believe the  $1^{\circ}\text{C}$  boundary is set too high, and my findings suggest that temperature may be an erroneous variable to label the boundary with. The distance boundary may be plausible since changes were found downstream from the source, but the boundary would be different for warm and cold springs, and distance on its own does not explain the shifts in community; it is hard to imagine an insect counting off meters from the source.

Since it was the only variable to have significantly shaped community structure, the difference in conductivity between the warm springs and the cold springs cannot be ignored. Conductivity remained almost completely constant across all sampling stations within each spring, with the exception of one point (IS-7 at the 5 m sampling station), but it

appears to be strongly related to temperature. The two springs with the highest temperatures had higher conductivities as well. I believe the conductivities were higher in these sites because the weathering rates of rock are greater at greater temperatures (White et al., 1999). I believe, based on previous findings (Chapter 2), that temperature would be much more significant in shaping the community structure than conductivity.

With this study, I was able to systematically study the rheocrene spring continuum. I expected to find distinct communities at the source and I expected to see rapid temperature changes with increasing distance downstream from the source. I was not able to determine source-specific communities, and temperature changes did not occur as drastically or rapidly as I expected, especially with respect to the geothermal spring systems. Community changes did occur with distance downstream, but the mechanism for change was not completely clear. I believe the boundaries set by von Fumetti et al. (2007) are incorrect. I think 1°C is too high of a temperature boundary, since I found community changes in a temperature change much lower than 1°C. I also think the 5 m boundary is inaccurate because I saw a change somewhere between 5 and 10 m, and the von Fumetti et al. (2007) boundary was drawn based on a temperature and faunistic estimate and not an actual investigation on the smaller scale. The problem with this research is that it is pattern oriented, and sometimes the pattern is the only thing that can be seen, so the process underlying the pattern is lost.

I believe future research is warranted in this field because there are community changes taking place. I think future projects should take measurements in 1 m increments from the source in order to see changes as they occur on a finer scale. I also think future projects should use a temperature range as wide as the one in this study, but they should find a more continuous spread of temperatures in order to see which factors are shaping changes in community structure. Regardless of the mechanism responsible for shaping these communities, it is clear that the spring ecosystem is a very dynamic system that experiences changes over small areas, which demonstrates the delicate and vulnerable nature of these systems and stresses the importance of their protection and conservation.

## 4 Conclusions

I began this research with the objectives of investigating the principles of spring ecosystems and bringing clarity to much of the ambiguity that exists in spring studies. My specific objectives were to 1) determine which variables are important in shaping different spring communities at the spring source, and 2) delineate where a spring becomes a springbrook from a faunistic standpoint as opposed to the more common thermal description.

In the end, I believe my work has satisfied these objectives. I satisfied objective 1 by systematically studying sources as points of discharge defined by their associated habitats (Chapter 2). I was able to clearly define a “spring” and differentiate it by type, which many previous studies have been ambiguous or erroneous at doing in the past. In this study, I discovered which variables were important in shaping spring source communities.

Although I was unable to clearly describe where a spring sources changes to a springbrook, I believe I still satisfied objective 2. I was able to use faunistic changes to demonstrate changes over an area smaller than the traditional thermal boundary. I also found that the distance definition could not be applied across the board. While I still have not found the mechanism driving the community change in rheocene spring continua, I believe my work has laid the path toward quality research in this field in the future by removing inaccurate definitions.

One of the most interesting concepts of spring ecology is the dichotomy that seemingly exists. Springs are considered constant in their conditions, so there is little disturbance to the flow and the physicochemical parameters, especially when compared to other freshwater systems. The intermediate disturbance hypothesis (Connell, 1978) suggests that an intermediate level of disturbance to a habitat will help maintain maximum biodiversity. In permanent spring systems, like the ones I studied, a lower level of biodiversity should be expected as a result of low disturbance. The constant conditions, however, also lead to endemism in springs (Erman & Erman, 1995). So the very thing that keeps local biodiversity low helps to increase biodiversity overall. The young geologic age of Icelandic surface waters is probably responsible for the lack of endemism in my study sites.

Springs arise from several different types of bedrock, so it may be irresponsible to group them all the same. Karst springs can affect the local biota negatively because of buildup from the physical processes that create the springs (von Fumetii et al., 2007). Perhaps the reason some of my findings were not in accordance with previous findings is because I studied volcanic springs, while other studies have focused on desert springs, forested springs, or karst springs. There may not be one governing set of principles for all “springs.”

Maybe spring type needs to be defined by ambient habitat in a more broad sense than I have done here.

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