Biological diversity in Icelandic groundwater fissures

Jónína Herdís Ólafsdóttir

Department of Aquaculture and Fish biology

Hólar University College
2015

II

Biological diversity in Icelandic
groundwater fissures

Jónína Herdís Ólafsdóttir

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

Advisors
Bjarni Kristófer Kristjánsson
Jón S. Ólafsson

Department of Aquaculture and Fish biology
Holar University College
Hólar, October 2015

Biological diversity in Icelandic groundwater fissures

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

Department of Aquaculture and Fish biology
Hólar University College
Hólar í Hjaltadal
551 Sauðárkrókur
Iceland

Sími (Telephone): 455 6300

Hólar í Hjaltadal, Iceland, November 2015

Abstract

Iceland has an abundance of fissures that are parallel to the Mid-Atlantic ridge where bedrock cracks as a result of continental rifting. In some areas fissures penetrate the aquifer and expose the groundwater within the bedrock. The main objective of the study was to measure the biological diversity in groundwater fissures in Iceland. A large part of the substrate in fissures is rock wall and they often reach great depth. As a result, the sampling sites were at variable depth on both rock wall as well as fissure's bottom. The present study was constrained to macrozoobenthos, while presence or absence of fish was also noted. Invertebrates were found to be living within and around a biofilm that was mostly made of Cyanobacteria and diatoms. Invertebrate assemblages were studied in three fissures: Silfra and Flosagjá in SW Iceland and Stekkjagjá in NE Iceland. All samples and measurements were acquired by scuba diving.

Invertebrate assemblages in fissures varied significantly between geographical regions in regards to taxa richness, density and diversity. All crustacean groups were in significantly greater densities in NE Iceland while chirononmids were found in similar densities in both geographical regions. A closer inspection revealed differences in chironomid assemblages as *Arctopelopia* sp. was only found in NE Iceland while *Diamesa zernyi* gr. was found in significantly greater densities in SW Iceland. Assemblages in fissures in the same region were similar except for differences in densities of cladocerans. *Chydorus* sp. was found in high densities and is the most common cladoceran in Flosagjá while it was almost absent from Silfra and *Alona werestschagini,* the second most common cladoceran in Flosagjá, was entirely absent from Silfra.

Within fissures most taxa were fairly evenly distributed regardless of physical habitat (e.g. depth, rock wall vs. rock bottom). Biofilm mats cover the entire substrate in fissures. These mats are made from Cyanobacteria and benthic diatoms, which are successful under low light conditions and may provide shelter, food and a substrate for animals both at great depth and on rock walls. Rock walls in fissures also have clefts and shelves that may act like bottom while the bottom in fissures is made up of rock rubble which often has vertical or near vertical parts depending on how rocks are positioned. These factors seem to "wipe out" the heterogeneity of the physical habitat and make it more homogenous and this may result in the even distribution of most taxa within fissures. A few species were however found in significant differences in response to depth and rock wall vs. bottom. The chironomid species *Orthocladius frigidus* was found in significantly greater densities at shallow depth (4 m) in Flosagjá and *Cricotopus tibialis* was found in significantly greater densities at shallow depth (2 m) in Stekkjagjá. These species are commonly found in the littoral zone in lakes and possibly cope better with surf conditions in shallow water. In Flosagjá Ostracods were found in significantly greater densities on the bottom than on rock wall. Suitable food resources for ostracods, which feed primarily on detritus, may accumulate more readily at bottom.

One species, *Eucyclops borealis* (Copeoda, Cyclopoida, Eucyclopinae), was documented for the first time in Iceland. This species has previously been documented in Alaska.

Útdráttur

Á Íslandi er gnægð gjáa sem myndast samhliða Mið-Atlantshafshryggnum þar sem berggrunnurinn brotnar við landrek og á sumum svæðum opnast slíkar gjár inn í grunnvatnsgeyminn. Markmið verkefnisins var að lýsa líffræðilegum fjölbreytileika í grunnvatnsfylltum gjám á Íslandi. Stór hluti undirlagsins í gjám er lóðréttur steinveggur og þær ná oft miklu dýpi. Þar af leiðandi voru sýnatökustöðvar ýmist á grjótvegg eða grjótbotn á breytilegu dýpi. Sérstök áhersla var lögð á botnlæga hryggleysingja en tilvist fiska var einnig skráð. Hryggleysingjar héldu til í og á botnlægum lífmottum sem eru að mestu úr blábakteríum og kísilþörungum. Samfélög voru rannsökuð í þremur gjám: Silfru og Flosagjá á SV Íslandi og í Stekkjagjá á NA Íslandi. Öll sýnataka og mælingar voru framkvæmdar með köfun.

Hryggleysingja-samfélög voru marktækt breytileg milli landsvæða þegar kom að fjölda tegunda, þéttleika og fjölbreytileika. Allir hópar krabbadýra fundust í hærri þéttleika á NA Íslandi. Rykmý fannst í svipuðum þéttleika í öllum gjám en samfélög voru engu að síður ólík. *Arctopelopia* sp. fannst eingöngu á NA landi á meðan *D. zernyi* gr. fannst í marktækt hærri þéttleika á SV landi. Enginn marktækur munur var á samfélögum í gjám á sama landsvæði nema með tilliti til þéttleika vatnaflóa. *Chydorus* sp. var algengasta vatnaflóin í Flosagjá en fannst í afar lágum þéttleika í Silfru, og *A. werestschagini* sem var önnur algengasta vatnaflóin í Flosagjá fannst ekki í Silfru.

Innan gjáa voru flestar tegundir og hópar fremur jafndreifðir þrátt fyrir breytileika í búsvæði með tilliti til dýpi og legu undirlags. Líf-mottur úr blábakteríum og botnlægum kísilþörungum þekja undirlagið í gjánum og veita hryggleysingjum mögulega skjól og fæðu. Þessar mottur geta þrifist í litlu ljósmagni og skapað undirlag fyrir lífverur á miklu dýpi sem og á láréttum grjótvegg. Láréttur grjótveggur í gjánum er sprunginn og hefur syllur sem líkjast botni. Á sama tíma er botninn gerður úr stórum grjóthnullungum sem býr til undirlag með mismunandi halla. Þar af leiðandi eru ýmsir þættir sem gera misleitt umhverfi gjánna einsleitara og getur það skýrt fremur jafna útbreiðslu tegunda innan gjánna. Nokkrar tegundir fundust engu að síður í marktækt breytilegum þéttleika á mismunandi dýpi og undirlagi. Rykmýið *Orthocladius frigidus* fannst í marktækt hærri þéttleika í grunnu vatni (4 m) í Flosagjá og *Cricotopus tibialis* fannst í marktækt hærri þéttleika í grunnu vatni (2 m) í Stekkjagjá. Þessar tegundir er algengar á strandsvæðum í íslenskum vötnum og þola ef til vill betur brim og straum í grunnu vatni. Skelkrabbar fundust í marktækt hærri þéttleika á botni í Flosagjá. Möguleg skýring gæti verið að grot sem er helsta fæða skelkrabba safnist fyrir á botni.

Krabbaflóin, *Eucyclops borealis*, fannst í fyrsta skipti á Íslandi. Þessi tegund hefur áður fundist í Alaska.

Dedicated to my parents
and to all lovers of the groundwater fissures in Iceland

Table of contents

List of figures

List of tables

Abbreviations

Abbreviation	Taxa name
Acarina	Acarina
A.harp	*Acroperus harpae*
A.affin	*Alona affinis*
A.quadr	*Alona quadrangularis*
A.werest	*Alona werestschagini*
Arctop	*Arctopelopia* sp.
Chaetocld	*Chaetocladius vitellinus* gr.
Chydor	*Chydorus cf. sphaericus*
Coleopt	Coleoptera
Collemb	Collembola
Copep	Copepoda
Cricot	*Cricotopus tibialis* gr.
C.ovum	*Cyclocypris ovum*
C.opth	*Cypria opthalmica*
Cyprid	*Cypridoidea* sp.
Dia.ber	*Diamesa bertrami*
Dia.zer	*Diamesa zernyi* gr.
Empid	Empididae
E.minor	*Eukiefferiella minor*
Fabaef	*Fabaeformiscandona* sp.
Gastrop	Gastropoda
Hydra	Hydra
I.sord	*Iliocryptus sordidus*
L.sancti	*Limnocytherine sanctipatricii*
Macrop	*Macropelopia* sp.
M.hirsut	*Macrothrix hirsuticornis*
Met.obs	*Metriocnemus obscuripes*
Microp	*Micropsectra* sp.
O.frig	*Orthocladius frigidus*
O.obli	*Orthocladius oblidens*
Plecopt	Plecoptera
P.zschok	*Potamocypris zschokkei*
Rheocr	*Rheocricotopus cf. effusus*
Thienem	*Thienemaniella* sp.
Trichopt	Trichoptera

Abbreviation	Sampling site		
	Fissure	**Transect no.**	**Depth (m)**
F1_1m	Flosagjá	1	1
F1_4m	Flosagjá	1	4
F2_1m	Flosagjá	2	1
F2_5m	Flosagjá	2	5
F3_1m	Flosagjá	3	1
F3_5m	Flosagjá	3	5
F4_1m	Flosagjá	4	1
F4_10m	Flosagjá	4	10
F5_1m	Flosagjá	5	1
F5_5m	Flosagjá	5	5
S1_1m	Silfra	1	1
S1_4m	Silfra	1	4
S2_1m	Silfra	2	1
S2_10m	Silfra	2	10
S3_1m	Silfra	3	1
S3_9m	Silfra	3	9
S4_1m	Silfra	4	1
S4_9m	Silfra	4	9
S5_1m	Silfra	5	1
S5_10m	Silfra	5	10
St1_1m	Stekkjagjá	1	1
St2_1m	Stekkjagjá	2	1
St2_2m	Stekkjagjá	2	2
St3_1m	Stekkjagjá	3	1
St3_10m	Stekkjagjá	3	10
St3_14m	Stekkjagjá	3	14
St4_1m	Stekkjagjá	4	1
St4_7m	Stekkjagjá	4	7
St5_1m	Stekkjagjá	5	1
St5_6m	Stekkjagjá	5	6

Acknowledgements

1. Introduction

1.1 Community ecology

Community ecologists strive to understand which mechanisms are instrumental in shaping distribution, diversity and interactions among species. Estimates of biodiversity include density, evenness and species richness and they can give a wealth of information about community structure (Magurran, 2005). Traditionally local biotic factors such as competition among species were seen as the primary mechanisms shaping communities, while regional factors (*i.e.* history of immigration and emigration, extinction) were mostly ignored. Today however it is understood that both local and regional factors contribute to biodiversity although ecologists still debate which mechanisms are the most important (Shurin, 2000; Bohonak and Jenkins, 2003; Logue *et al*., 2011). The term biodiversity has as well evolved to encompass modern understanding. Instead of being primarily a measure of the number of species as it originally was, it now covers diversity among species, biogeographical dynamics as well as evolutionary processes (Magurran, 2005; Leibold *et al*., 2010).

Ecologists often look to response variables in species assemblages to gain insight into processes within ecosystems (Legendre and Gauthier, 2014). In freshwater studies invertebrates merit special consideration, as they are important for many ecological processes (Richardson and Jackson, 2002). While biodiversity typically decreases towards higher latitudes, the abundance and biomass of aquatic invertebrates there can easily exceed that of invertebrates found at lower latitudes. Noteworthy are the Chironomidae, which are almost as species rich in the Arctic as in temperate regions (Rautio *et al*., 2008). Chironomid distribution reflects their evolutionary history, as they are believed to have originated as cold adapted organisms (Oliver, 1971). Chironomids are considered to be excellent ecological indicators. A good example is the genus *Cricotopus* in North-East America where different species are indicative of a wide range of environmental characteristic such as current, nutrient availability, salinity, oxygen concentration and substrate composition (Boesel, 1983). Chironomids are also suggestive of local pollution and disturbance, and their community assemblages have been useful for the classification of lake types (Lencioni *et al*., 2012; Nyman and Korhola, 2005; Saether, 1979). In this way species assemblages can provide an insight into processes spanning from evolution to the physicochemical environment of taxa.

The understanding of how environmental variables shape biodiversity in communities has increased in recent years (Logue *et al*., 2011; Triantis, 2011). In freshwater springs many environmental factors are considered to be stable and this may result in greater biomass compared to less stable habitats (Aðalsteinsson and Gíslason, 1998; Rautio *et al*., 2008). Substrate composition, detritus, oxygen and nutrients are among environmental variables that have been shown to be important in shaping freshwater crustacean and chironomid communities (Pinder, 1986; Van der Kamp, 1995; Rautio *et al*., 2006; Dumnicka *et al*., 2007; Novichkova *et al*., 2014). Temperature is known especially for having a large role in shaping biodiversity in springs as it influences most ecologically significant factors in some way (Hogg and Williams, 1996;

Bottazzi *et al*., 2011; Govoni, 2011; Stenhouse *et al*., 2012). Species have a temperature optimum at which they perform best in regards to growth, development and metabolism and some taxa are specifically adapted to low temperature (Vannote and Sweeney, 1980; Pinder, 1986; Rautio *et al*., 2008). Species of the chironomid genus *Diamesa* for example are recognized for their strong association with extreme cold habitats (Oliver 1971; Lencioni, 2004; Govoni, 2011). Fully frozen 4th instar larvae of *Dimaesa zernyi* gr. have been collected in alpine streams in Italy only to recover fully after thawing in the laboratory (Lencioni, 2004).

The Equilibrium theory of insular zoogeography, which was published in 1963, was a major hypothesis on biodiversity (MacArthur and Wilson, 1963). It sought to explain species richness on islands and emphasized the importance of dispersal mechanisms, the proximity of islands to a mainland body and the species-area relationship, which states that the larger the area, the greater the number of species found there. This theory has since been expanded to other habitats that are surrounded by dissimilar ecosystems. Studies show that biodiversity is influenced by isolation on spatial scales and this theory is sometimes used to characterize isolated springs (Leibold *et al*., 2004). Lately metacommunity theory has also gained popularity as a way to combine processes occurring on different scales to explain community patterns (Logue *et al*., 2011). Freshwater invertebrates are considered to be suitable metapopulations as they are usually a set of local communities linked by dispersal and often depend on interactions with each other (Bohonak and Jenkins, 2003). Communities in springs and high latitude freshwater systems are simpler than those found in temperate regions. As such they can provide understanding of mechanisms that may be impractical to obtain from more complex systems (Christoffersen *et al*., 2008).

1.2 Spring ecology in Iceland

In Iceland springs are most common in young, volcanically active areas where the bedrock is mostly made up of porous lava. The chemical content of springwater reflects the bedrock it travels through and dissolved chemicals are important for foodweb composition (Marshak, 2008; Hallgrímsson, 2007). Organisms in springs depend on chemoautotrophic processes as well as organic input from surface water and land for survival (Dodds, 2002). The most abundant secondary producers in freshwater are invertebrates (Richardson and Jackson, 2002). In springfed streams in Iceland benthic invertebrate biodiversity is generally greater than in other types of rivers (Gíslason *et al*., 1998). Many insects spend a large part of their life cycle in freshwater and in Icelandic springs the algal-grazing chironomid larvae dominate (Gíslason *et al*., 1998; Brittain *et al*., 2009; Govoni, 2011). Predator species such as water mites can also be found and collectors such as copepods (Petersen *et al*., 1995; Brittain *et al*., 2009). Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) are common fish species (Hallgrímsson, 1973). Spring fed lakes in Iceland are also characterized by high invertebrate biodiversity. The greater animal density and diversity can partly be explained by the occurrence of young lava rock, which has greater surface area than rock in older bedrock areas in Iceland. This lava rock provides a complex microhabitat and a shelter for small animals (Malmquist *et al*., 2003). On the rocky substrate in the littoral zone of the springfed Lake Þingvallavatn, chironomids are the most common taxa followed by oligochaetes and nematodes. Freshwater gastropods, benthic insects, water mites, leeches and cnidarians are also

found but in less abundance (Malmquist *et al.*, 2000). Oligochaeta and other sediment dwelling invertebrates dominate at the profundal bottom, where sediment accumulates (Malmquist *et al.*, 2003).

In 2004 and 2006 two freshwater amphipod species from Icelandic groundwater were described, *Crymostygius thingvallensis* and *Crangonyx islandicus* (Kristjánsson and Svavarsson, 2007a). The first specimen of *C. thingvallensis* was collected in Vatnsvik by Lake Þingvallavatn, where large volumes of groundwater emerge. The species *C. islandicus* has been found in numerous locations within Iceland. These two amphipod species are among the very few endemic species in Iceland. They are thought to have survived in groundwater pockets on a proto-Iceland, which drifted by plate tectonics away from Greenland some 40 million years ago (Kristjánsson and Svavarsson, 2007b; Kornobis *et al.*, 2010a). These findings changed previous ideas about the origin of species in Iceland, as it is a young island marked by recent glaciations, and indicate that species may have arrived here before the Ice age and survived underneath the ice sheet (Guðjónsson and Guðbergsson, 2003; Kristjánsson and Svavarsson, 2007b). Investigations have shown genetic divergence among populations in different geographical regions. *C.islandicus* has been shown to have great mitochondrial DNA diversity and genetic divergence between populations mirrors the geographical distance between them. Populations in NE Iceland show the greatest divergence from others although less variation was observed in a subsequent investigation on RNA genes (Kornobis *et al.*, 2010a; Kornobis *et al.*, 2010b). These findings suggest that connectivity and gene flow is low between populations in Icelandic springs.

1.3 Groundwater fissures

Iceland is a young island with high volcanism due to unique geological and climatological factors (Thordarson and Larsen, 2007). The country straddles the Mid-Atlantic ridge, where the American and Eurasian plates move apart. This causes the bedrock to sink, break and slip, resulting in the formation of numerous faults parallel to the ridge (Marshak, 2008). These commonly suboceanic features are subaerial and clearly visible in many locations in Iceland. This is due to a mantle plume underneath the island contributing great buoyancy and raising the ridge especially high (Sæmundsson, 2011). Fissures are common in the young and porous volcanic rock originating from the plate boundaries (Jóhannesson and Sæmundsson, 2009). Divergent plate boundary fissures that are accessible from land are only known from two places in the world: Iceland and in the Ethiopian Afar Regional State (Dr. Páll Einarsson, personal communication, January 19, 2015; Chorowicz, 2005).

Many of the fissures found in Iceland are dry while a good number penetrate the aquifer and provide an opening into groundwater. Guðmundsson (1986) shares a wealth of information on Icelandic fissures. Fissures vary considerably in length, width and depth: most are relatively short (less than 250m) while a few can reach over 1000m in length. The deepest known accessible point within a groundwater fissure is 60 m. The faults can likely reach a depth of several kilometers in some cases although they are only open to the surface in the uppermost layers of the bedrock (Dr. Páll Einarsson, personal communication, January 19, 2015; Guðmundsson, 1986). Most surface fissures are open to the atmosphere but they often

contain collapsed sections that form caverns with dim light conditions and/or caves where light does not penetrate. Perhaps the most unique feature of the fissures is the substrate, a vertical volcanic rock wall that may create unique habitat for organisms.

Groundwater fissures can be considered as transitional habitats (Ecotones) between groundwater and surface water, and can be defined as springs where groundwater reaches the atmosphere at a natural opening (Spechler and Schiffer, 1995; Springer and Stevens, 2008). Springs have been classified based on various factors such as geology, chemistry and discharge (Batzer and Baldwin, 2012). A suitable classification for ecologists was proposed by Hynes (1970) who defined three kinds of springs based on the systems they feed: streams with current (rheocrene), static pools (limnocrene) and marshes (helocrene). The groundwater fissures can have properties of either rheocrene or limnocrene springs although they don't conform perfectly to this traditional classification of springs. Rather than the water being discharged from a source, the fissures are an opening that exposes the groundwater aquifer within the bedrock. Fissures commonly have a detectable current, while in some the water is more static.

A large part of the substrate within the groundwater fissures is vertical rock wall. This physical feature may potentially affect the distribution of resources and taxa. Detritus in lake bodies readily accumulates at the bottom, while rock walls usually are relatively free of detritus. Detritus is a food source for collectors that filter particle material from the water column (Petersen *et al*., 1995). The distribution of detritus may thus affect the habitat choice of collector species. Also freshwater invertebrates are often adapted to particular environmental factors. In Iceland several species of chironomids are common in habitats with high current or where there is madicolus flow and sometimes have specific physiological adaptations for remaining in such habitat (Giudicelli and Bournard, 1997; Hrafnsdóttir, 2005). Perhaps species that are successful in high flow habitats will also have an adaptive advantage on rock walls, which are characteristics of groundwater fissures.

Most fissures in Iceland have cold (Ólafsson, 1992) and clear water. In these aspects they resemble freshwater systems in the High Arctic (Rautio *et al*., 2008). Numerous freshwater invertebrate species at high latitudes and altitudes are well adapted to life at low temperature, short seasons with variable light availability, and low food supply (Lencioni, 2004). Light drives photosynthesis and is the energy source for most ecosystems (Croce and van Amerongen, 2014). In water light penetration decreases with depth as most of it is scattered by photon-electron interactions and detritus (Jonasz and Fournier, 2007). When light levels decrease, primary production does as well and available resources become scarce. This might affect invertebrate communities within fissures that reach great depth.

Physical habitat has been found to significantly affect invertebrate communities in springs. Govoni (2011) found that spring type was the most important variable in shaping communities in springs in Iceland, whereas animals typically associated with lentic habitats were found in limnocrene springs, while invertebrates associated with lotic habitats were commonly found in rheocrene springs. Different chironomid species in Iceland have also been classified according to the environment they are most often found in (e.g. lentic or lotic waters, thermal springs etc.) (Hrafnsdóttir,

2005). The variability in physical environment both between and within groundwater fissures may create diverse habitats and challenges for organisms.

1.4 Objectives and hypotheses

Rift valley fissures are only accessible from land in very few places in the world. In Iceland they are subaerial and clearly visible in many locations. The fissures focused on in this study contain cold groundwater and most of the substrate is rock wall. Extensive geological and geophysical studies have been made on the fissures (Guðmundsson, 1986), but detailed survey of their ecosystems has been lacking. The objective of this study is to assess biodiversity and compare assemblages between and within groundwater fissures in Iceland: The following hypotheses were made:

1) Physical habitat has been shown to be an important variable in shaping invertebrate communities in springs in Iceland. Therefore assemblages are expected to vary between fissures with different physical characteristics.

2) The fissures often reach great depth and rock walls provide most of the substrate for animals. Decreasing light availability with depth results in less primary production and thus available resources, while rock walls may presen challenges in attaching to substrate and have limited availability of detritus compared to bottom. The physical habitat may thus create a gradient in community structure and therefore assemblages are expected to vary within fissures, both with depth and in response to rock wall vs. bottom.

2. Materials and methods

2.1 Study sites

Geologists have defined a fissure as a fissure body that can be traced from aerial photographs (Guðmundsson, 1986). Such fissure bodies are most commonly part of even larger fissure swarms. Although groundwater fissures may appear continuous from the air, usually there are several collapses and dry sections within them. For this study I collected biological material in continuous open water sections within three large fissures in SW and NE Iceland, all of which are accessible from land (Figure 2.1). A special permit for sampling in protected fissures was obtained from Þingvellir National park.
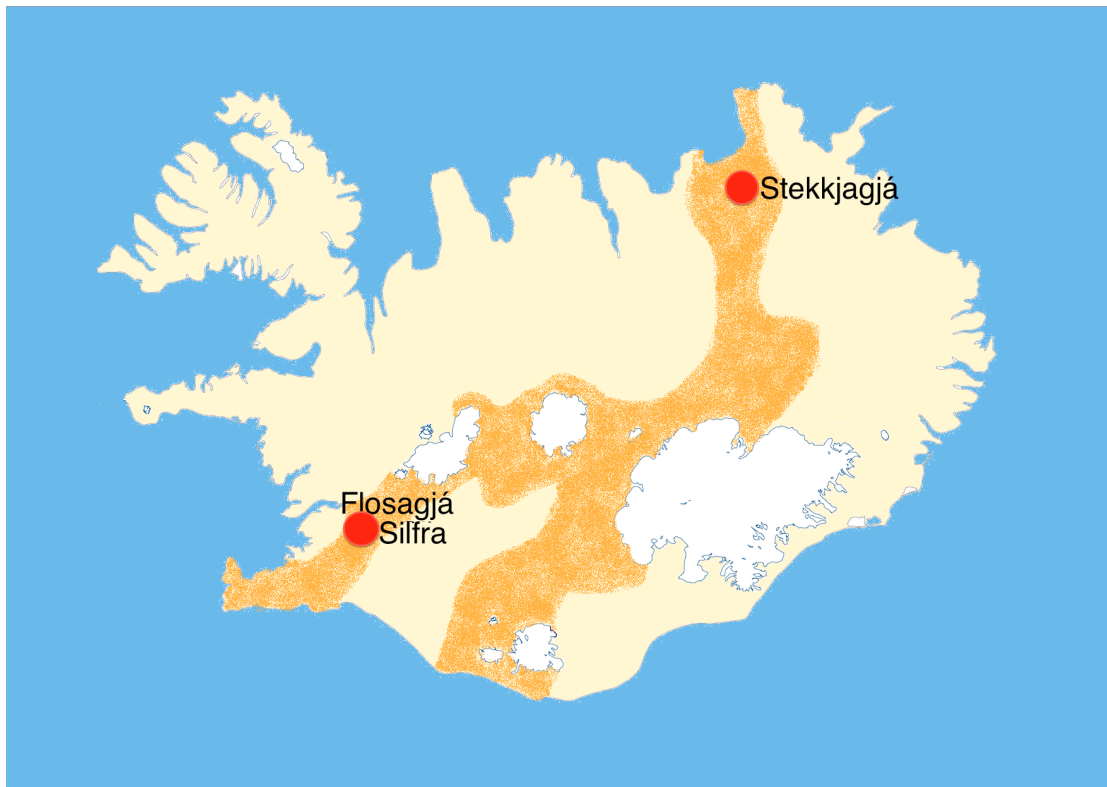
Figure 2.1. *Map of Iceland showing the names (in black) and location (in red) of the three rift valley fissures sampled during this study and the active rift zone (in orange) (adapted from Hjartardóttir, 2013). Cartographic data are from the National Land Survey of Iceland*.

Flosagjá (64°15´46 N, 21°06´46 V) and Silfra (64°15´14 N, 21°07´05 V) are located in 9.000-year-old Eldborg lava flow as part of the Hengill fissure swarm (Thors, 1990; Sigurðsson and Sigbjarnason, 2002; Sinton *et al*., 2005). The two fissures are roughly 300 meters apart. Flosagjá is among the largest fissures in Þingvellir (Figure 2.2a-b). A 330m section between two collapses was sampled, reaching a maximum depth of 18m. Silfra fissure is one of the largest springs opening directly into Lake Þingvallavatn (Malmquist, 2012). Its open water section is about 320 m long with a maximum depth of roughly 20 m. Silfra has several caverns that reach greater depths and the fissure is closed to the surface at its northernmost end forming a cave

reaching 60 m depth, the deepest known accessible point known within a submersed fissure.

Stekkjagjá (66°02´21 N, 16°34´30 V) and Oddagerðisgjá (66°02´34 N, 16°35´42 V) are located in Kelduhverfi in NE Iceland, roughly 300 km away from Flosagjá and Silfra (Figure 2.2c-d). These fissures are in 10.000-year-old Stóravíti lava flow which is part of the Krafla Fissure swarm and are located 35 km away from the central volcano (Hjartardóttir *et al*., 2012; Maclennan *et al*., 2002). Stekkjagjá is just under a kilometer in length, with several collapses and only portions penetrating the groundwater aquifer. A 260 m open water section was sampled with a maximum depth of 14 m. Oddagerðisgjá (is a narrow fissure with a roughly 200 m open water section and a maximum depth of 25 m. The substrate in all the fissures is covered in benthic biofilm mats.

In addition five qualitative samples were taken in a previously undiscovered underground fissure in Þingvellir. The fissure was called Huldugjá (the Hidden fissure).
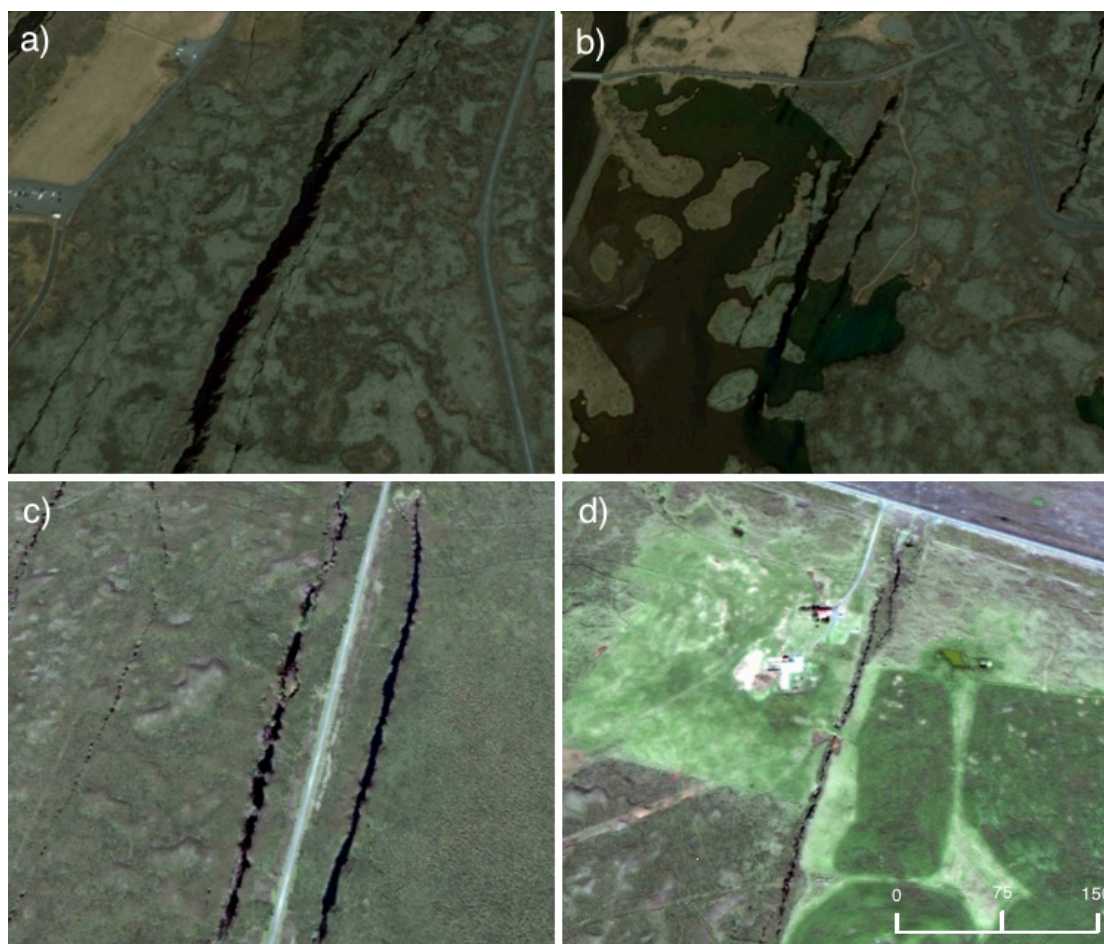
Figure 2.2*. Aerial photographs of study sites: Flosagjá (a) and Silfra (b) at elevation 100-120 m in SW Iceland and Stekkjagjá (c) and Oddagerðisgjá (d) at elevation 20-25m in NE Iceland. North ↑ (Google Earth, 2012).*

2.2 Biological sampling

This study on the biodiversity in submersed groundwater fissures in Iceland was done in collaboration with research on microbial diversity in fissures adjacent to Lake Þingvallavatn (Guðmundsson, 2014), a comparative analysis on methods for sampling invertebrates on rock walls while diving (Þorbjörnsson, 2013) and an investigation into disturbance by SCUBA diver traffic in Silfra fissure (Þorbjörnsson, 2015). Data collection and species sorting was done collaboratively among these studies.

Figure 2.3. *Photograph showing biofilm mats on rock substrate in Flosagjá fissure. Photo by Gísli Arnar Guðmundsson*.

Samples were collected in fissures Flosagjá (22.06-30.06.2013), Silfra (1.07-5.07.2013) and Stekkjagjá (15.07-19.07.2013). All the fissures contain cold groundwater and all samples were acquired by SCUBA diving. Each fissure was divided longitudinally into transects with 10 m between them and from these five transects were chosen randomly. The sampling took place at five replicate transects within each fissure. Within each transect five replicate samples were collected at 1 m, 10 m and bottom. At most transects the depth did not reach 10 m and in these cases samples were taken at the greatest depth at the bottom. Invertebrates and surrounding biofilm (Figure 2.3) was collected into sampling containers using a brush and pump sampler (Þorbjörnsson, 2013) from within a 0,04 m^2 frame taken randomly in the area of each station. The pump sampler was designed to accommodate the challenges of sampling in a submersed area on vertical rock walls while scuba diving (Figure 2.4). The sampling device was made from two plastic hoses, 3 cm in diameter, which were attached to the suction and delivery ends of a small hand-operated bilge suction pump (Munster Simms engineering Ltd. Bangor, N. Ireland). The suction end of the pump had a 190 cm long hose used to vacuum organic material from walls and bottom. The delivery end had a 45 cm long hose attached to a sampling container. The sampling

container was made from plastic PVC pipes, with a volume of 0.5 L with a 125 μm mesh. The container was attached to the plastic hose using a manual threaded valve. This valve could be closed once the sample had been retrieved, thus preventing material from flowing back out of the system and into the surrounding water column. The manual suction pump system was securely attached to a diver with a harness for ease of use in the water. For more detailed information on the pump sampler see Þorbjörnsson (2013). Benthic core samplers were made from 30 cm long PVC pipes with a diameter of 5 cm (0.0019 m^2). One end was carved to make a sharp edge, which cut smoothly through silt. The protruding end was plugged with a plastic plug while the other end was closed with a plug molded from foam plastic. Sampling containers were collected into net bags and brought up to the surface where the material was filtered through a 125 μm sieve and preserved in 70% ethanol for storage.
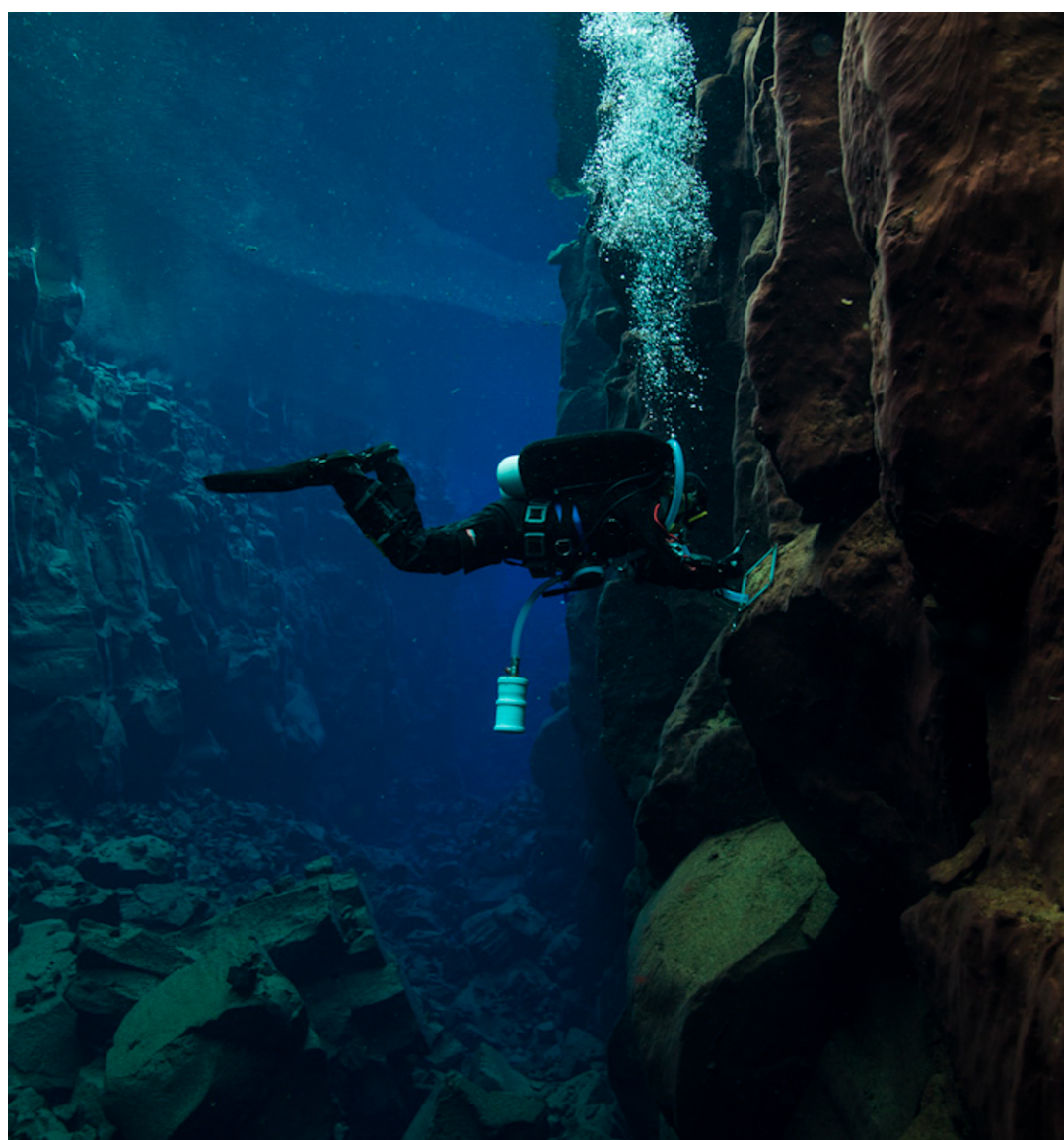
Figure 2.4. Photograph showing setup of sampling device on diver collecting invertebrate samples in *Flosagjá fissure*. Photo by Gísli Arnar Guðmundsson.

Five unbaited minnow traps (Dynamic Aqua Supply Ltd, BC, Canada, mesh size 6.4 and 3.2 mm) were placed into the fissures Flosagjá, Stekkjagjá and Oddagerðisgjá. Fish were released after species identification and counting. Fish sightings were also noted during dives. It was unsuitable to place minnow traps into Silfra fissure due to tourism traffic in the area.
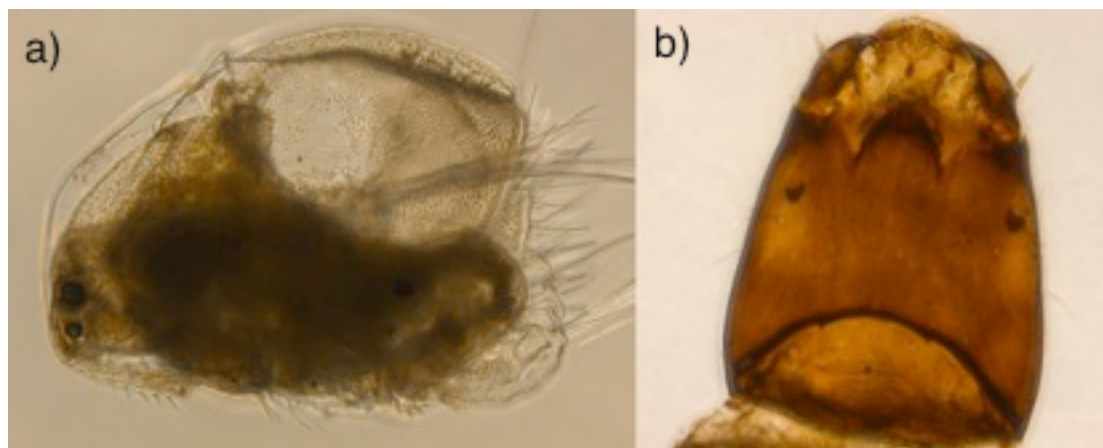
Figure 2.5 *Microscopy photographs of two of the most common species from fissures:* Macrothrix hirsuticornis *from Stekkjagjá (a) and a head capsule of* Diamesa zernyi *gr. from Silfra (b).*

In the laboratory invertebrate samples were transferred on to a Petri dish, the organisms counted and identified to various taxonomic levels (*e.g.* Figure 2.5). The four most common invertebrate groups were identified to the lowest taxonomic level possible. Detailed species identification followed taxonomic keys by Cranston, (1982) and Schmid (1993) for Chironomidae, Alonso (1996) for Cladocera, Alekseev and Defaye (2011) for Copeoda and Meisch (2000) for Ostracoda.

2.3 Physical parameters

Data loggers (HOBO® pendant Temperature/Light 64Kdata logger, Onset computer corporations, USA) were mounted horizontally on to dowel rods using rubber coated electric wire to secure them and placed in the fissures in summer 2014. The sticks had one end carved to a point and were hammered into clefts at 1, 5 and 10 m depth on one transect within each fissure for a gradient. Another two loggers were placed at 1m depth on two other transects for horizontal comparison. Data loggers measured during the period 18.9.2014-4.9.2015 in Flosagjá, 18.9.2014-7.9.2015 in Silfra and 24.11.2014-2.9.2015 in Stekkjagjá. Substrate type was noted at each sampling site. Conductivity, Total dissolved solids and pH was measured with a handheld instrument (YSI Pro 1030 pH/ORP/Conductivity/Temperature Instrument, YSI Incorporated, USA) in Flosagjá (4.9.2015) Silfra (7.9.2015) and Stekkjagjá (2.9.2015).

2.4. Statistical analyses

Proportion of six of the most abundant taxa in assemblages was plotted to highlight differences in community structure. Average densities ($\#/m^2$) were calculated for all species at all stations within fissures. Shannon Wiener diversity index (Equation 1) was calculated, plotted and compared among all fissures and between depth on bottom within all fissures. Shannon diversity index estimates biodiversity from aspects of richness and evenness (Spellerberg and Fedor, 2003; Magurran, 2005).

$$H = -\sum_{i=1}^{S} p_i \log_b p_i$$

Equation 1: *Shannon diversity index.*

p_i- Proportion of species i
S- Number of species
b- Base of the logarithm

Shannon diversity and mean densities of common taxa were compared among fissures using Wilcoxon test with a significance level of $p<0.05$. Communities within fissures were compared between rock wall and bottom using Wilcoxon test with a significance level of $p<0.05$, and between depth on bottom using Spearman rho test with a significance level of $p<0.05$. Ordination analysis was performed to look at trends in macro-invertebrate community structure at the geographical (between fissures in NE vs. SW Iceland) and regional scale (between fissures in SW Iceland), as well as locally within fissures. Mean densities of invertebrate species in all fissures were inspected using principal component analysis (PCA) and communities within fissures were inspected in relationship to potential explanatory physical variables using redundancy analysis (RDA).

All statistical analyses were performed using RStudio Version 0.98.1062, Canoco Version 4.5 and Microsoft Excel Version 14.5.5.

3. Results

3.1 Comparison of assemblages between fissures

A total of 44 invertebrate taxa were found during the study (Table 3.1). In fissures in SW Iceland there were similar numbers of taxa, 25 in Flosagjá and 26 in Silfra. Taxa richness was highest in Stekkjagjá in NE Iceland where 37 taxa was found. 16 taxa were present in all fissures. The proportion of the most common taxa in assemblages varied greatly between geographical regions but was similar in fissures in the same region (Figure 3.1).

Mean densities were calculated for all taxa in fissures and any subsequent discussion about densities of taxa pertains to mean densities (m^2). Chironomidae was the most common taxon in SW Iceland. *D. zernyi* gr. was the most common species there and was closely followed *by Orthocladius frigidus* (Table 3.2). The overall most common taxon in the study was Copepoda, which were dominant in NE Iceland. From samples where groups were fully identified to the species level, the cladoceran *Macrothrix hirsuticornis* was the most common species, especially in Stekkjagjá fissure.

Species data was tested for differences in densities among four of the most common groups: Chironomidae, Cladocera, Copepoda and Ostracoda (Table 3.3). In Stekkjagjá there was significantly greater density of all crustaceans compared to Flosagjá and Silfra while there was no significant difference in density among chironomids. Closer inspection however reveals vast differences in chironomid communities whereas Tanypodinae dominate in the NE while almost absent in SW Iceland. Similarly *D. zernyi* gr. was found in significantly greater density in SW Iceland compared to NE Iceland. There was no significant difference in densities among the most common groups in SW Iceland except for cladocerans, which were found in significantly greater densities in Flosagjá compared to Silfra.

Table 3.1 List of species of Chironomidae, Cladocera, Copepoda, Ostracoda and other taxa groups collected and identified in all fissures (Flosagjá, Silfra and Stekkjagjá) in the current study.

	Flosagjá	Silfra	Stekkjagjá
Family Chironomidae			
Arctopelopia sp.			+
Chaetocladius vitellinus gr. (Kieffer, 1908)		+	+
Cricotopus tibialis gr. (Meigen, 1804)	+		+
Diamesa bertrami Edwards, 1935		+	
Diamesa zernyi gr. Edwards, 1933	+	+	+
Eukiefferiella minor (Edwards, 1929)	+	+	+
Macropelopia sp.	+		+
Metriocnemus obscuripes (Holmgren, 1869)			
Micropsectra sp.	+	+	+
Orthocladius frigidus (Zetterstedt, 1838)	+	+	+
Orthocladius oblidens (Walker, 1856)	+	+	+
Rheocricotopus cf. *effusus* (Walker, 1856)	+	+	+
Thienemaniella sp.	+	+	
Order Cladocera			
Acroperus harpae (Baird, 1834)	+	+	+
Alona affinis (Leydig, 1860)	+	+	+
*Alona quadrangularis (*Müller, 1785)	+	+	+
Alona werestschagini Sinev, 1999	+		+
Chydorus cf. *sphaericus (*Müller, 1776)	+	+	+
Ilyocryptus sordidus (Lieven, 1848)			+
Macrothrix hirsuticornis Norman and Brady, 1867	+	+	+
Subclass Copepoda			
Acanthocyclops robustus (Fischer, 1853)		+	
Bryocamptus pygmaeus (Sars, 1863)			+
Bryocamptus zschokkei (Schmeil, 1823)		+	
Diacyclops bisetosus (Rehberg, 1880)	+		+
Eucyclops borealis (Ishida, 2001)			+
Eucyclops sp.		+	+
Megacyclops viridis (Jurine, 1820)	+	+	+
Paracyclops sp.			+
Class Ostracoda			
Cyclocypris ovum (Jurine, 1820)			+
Cypria opthalmica (Jurine, 1820)			+
Cypridoidea sp.	+	+	+
Fabaeformiscandona sp.	+	+	+
Limnocytherina sanctipatricii (Brady and Robertson, 1869)			+
Potamocypris zschokkei (Kaufmann, 1900)	+		
Other groups			
Acarina	+	+	+
Coleoptera			+
Collembola	+		+
Copepoda	+	+	+
Empididae		+	
Gastropoda			+
Hydra			+
Plecoptera		+	
Salvelinus alpinus (Linnaeus, 1758)	+	+	+
Trichoptera	+	+	+
Total no. taxa	25	26	37
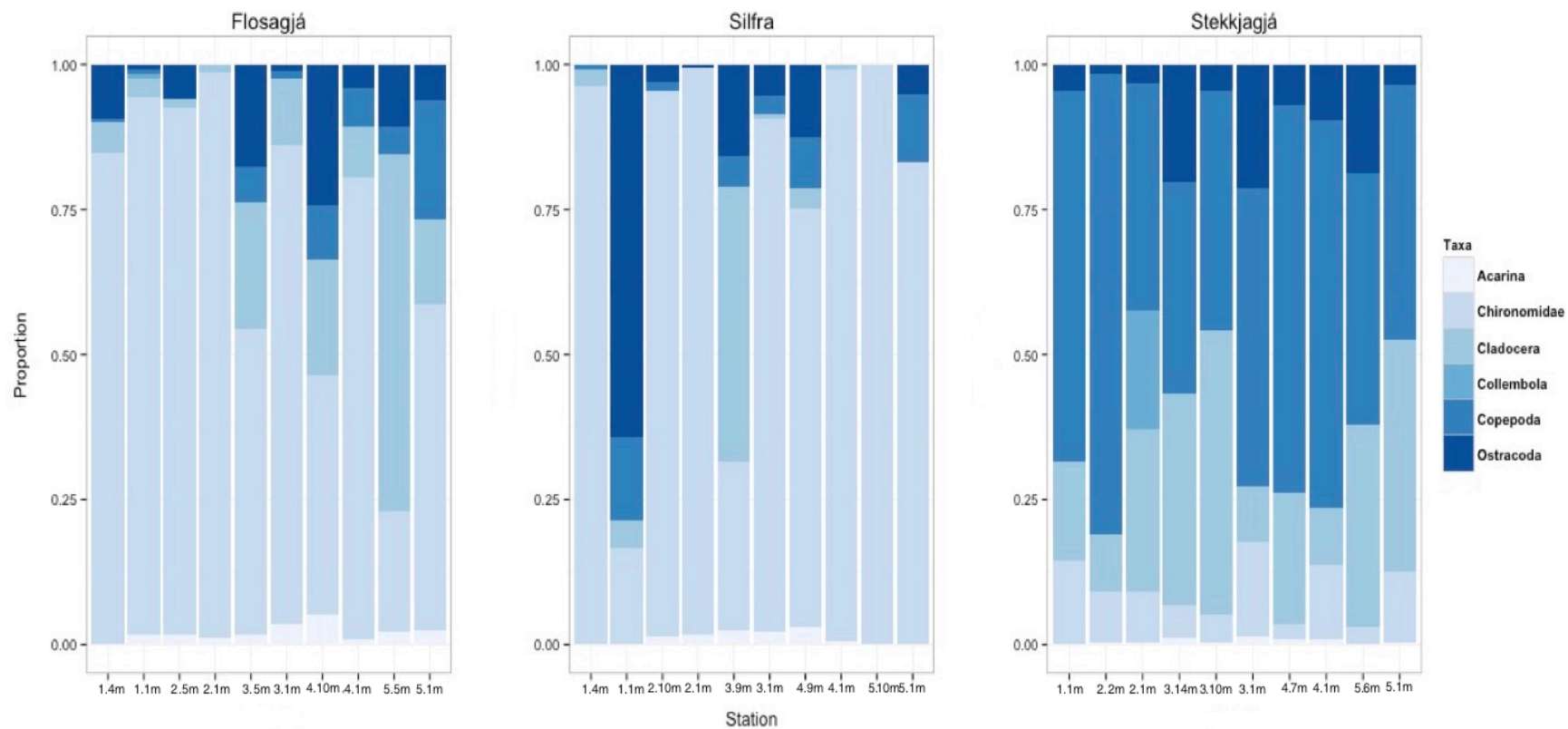
Figure 3.1*. The proportion of the six most common taxa in assemblages within Flosagjá and Silfra (SW Iceland) and Stekkjagjá (NE Iceland) : Acarina, Chironomidae, Cladocera, Collembola, Copepoda and Ostracoda. Sampling station names are shown on page 12*.

Table 3.2 *Mean densities of invertebrate taxa (m^2) in all fissures based on 30 samples for each fissure with standard deviation (SD).*

	Flosagjá		Silfra		Stekkjagjá	
	Mean	SD	Mean	SD	Mean	SD
Chironomidae						
Arctopelopia sp.	0.0	0.0	0.0	0.0	208.3	234.8
Chaetocladius vitellinus gr.	0.0	0.0	8.3	34.8	2.5	10.1
Cricotopus tibialis gr.	59.2	77.0	0.0	0.0	87.5	178.0
Diamesa bertrami	0.0	0.0	0.8	4.8	0.0	0.0
Diamesa zernyi gr.	278.3	253.8	334.2	372.8	5.8	19.3
Eukiefferiella minor	59.2	70.2	167.5	182.0	25.0	38.3
Macropelopia sp.	0.8	4.6	0.0	0.0	15.8	29.7
Metriocnemus obscuripes	0.0	0.0	0.0	0.0	4.2	22.8
Micropsectra sp.	2.5	10.1	10.0	28.9	123.3	134.2
Orthocladius frigidus	340.8	243.0	113.3	119.4	28.3	53.6
Orthocladius oblidens	25.8	51.5	5.0	16.0	31.7	82.2
Rheocricotopus cf. *effusus*	2.5	10.0	1.7	6.7	9.2	22.2
Thienemaniella sp.	1.7	9.2	0.8	4.8	0.0	0.0
Cladocera						
Acroperus harpae	15.0	51.1	5.8	24.6	330.0	629.7
Alona affinis	14.2	36.4	2.5	14.4	213.3	236.1
Alona quadrangularis	4.2	18.7	8.3	18.5	34.2	60.0
Alona werestschagini	69.2	122.6	0.0	0.0	0.8	4.6
Chydorus cf. *sphaericus*	89.2	221.2	1.7	9.6	373.3	378.0
Ilyocryptus sordidus	0.0	0.0	0.0	0.0	0.8	0.0
Macrothrix hirsuticornis	3.3	18.3	6.7	20.6	795.0	1534.7
Ostracoda						
Cyclocypris ovum	0.0	0.0	0.0	0.0	240.0	375.3
Cypria opthalmica	0.0	0.0	0.0	0.0	15.8	29.0
Cypridoidea sp.	52.5	95.9	31.7	71.1	155.8	199.2
Fabaeformiscandona sp.	2.5	7.6	0.8	4.8	0.8	4.6
Limnocytherina sanctipatricii	0.0	0.0	0.0	0.0	40.0	100.6
Potamocypris zschokkei	7.5	23.8	0.0	0.0	48.3	63.6
Other groups						
Acarina	25.0	38.3	12.5	28.0	49.2	55.5
Coleoptera	0.0	0.0	0.0	0.0	1.7	6.3
Collembola	0.8	4.6	0.0	0.0	165.8	894.2
Copepoda	65.0	128.4	40.0	75.7	6377.5	7821.
Empididae	0.0	0.0	0.8	4.8	0.0	0.0
Gastropoda	0.0	0.0	0.0	0.0	5.0	19.0
Hydra	0.0	0.0	0.0	0.0	3.3	14.3
Plecoptera	0.0	0.0	0.8	4.8	0.0	0.0

Shannon diversity index values ranged between 1.6-2.1 and the highest values were found for assemblages in Flosagjá fissure (Figure 3.2). There was a significant difference in Shannon diversity index between assemblages in fissures in different geographical regions, while there was no significant difference between assemblages in fissures in the same region (Table 3.3).

Table 3.3 *Results from Wilcoxon test on mean density of taxa and Shannon diversity index between fissure communities.*

	Difference between fissures in SW Iceland vs. NE Iceland	Difference between fissures in SW Iceland
Mean density		
Chironomidae	0.53	0.63
Copepoda	$2e^{-4}$	0.54
Cladocera	$3e^{-4}$	0.01
Ostracoda	$4e^{-4}$	0.24
D.zernyi gr.	$1e^{-4}$	
Shannon diversity index	0.03	0.22
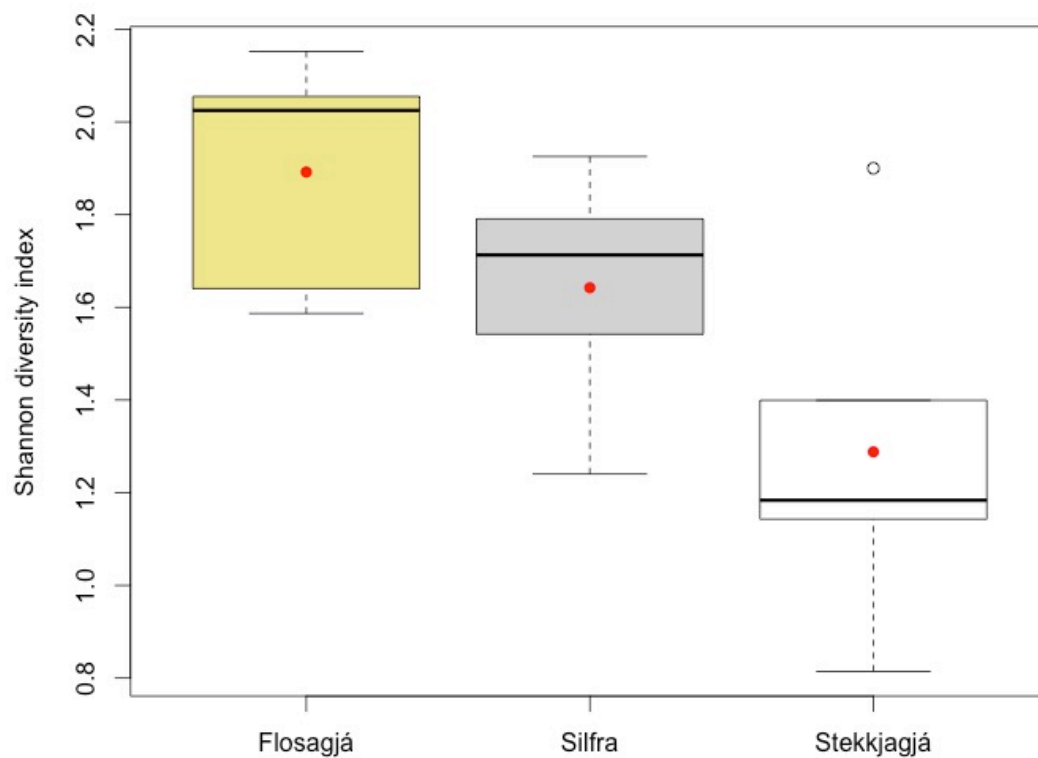
Figure 3.2. *Shannon diversity index for all fissures: Flosagjá (in yellow), Silfra (in gray), Stekkjagjá (in white) with range of values calculated from all sampling stations, mean (red dot) and median (black line). Whiskers reflect variability beyond the upper and lower quartile (the 3rd (Q3) and 1st (Q1) quartiles are demarcated by top and bottom of boxes. The interquartile range (IQR) is the height of boxes from top to bottom. The top whisker is determined by Q3 + 1.5*IQR and the bottom whisker is determined by Q1-1.5*IQR). Empty circles are outliers.*

Communities in fissures were distinct and are spread apart from one another on ordination graph, although assemblages in Flosagjá and Silfra (SE Iceland) overlap to a degree indicating more similarity in assemblages (Figure 3.3). 60.9% of the variance in species composition in all fissures could be explained by principal component 1 (PC1) while 8.7% of the variance could be explained by principal component 2 (PC2). In Flosagjá there were higher densities of the chironomid larval species *D. zernyi* gr., *E. minor* and *O. frigidus* as well as the cladoceran species *A. werestschagini*. No particular species comes out to be in higher density in Silfra while several species are found in high densities within Stekkjagjá fissure.
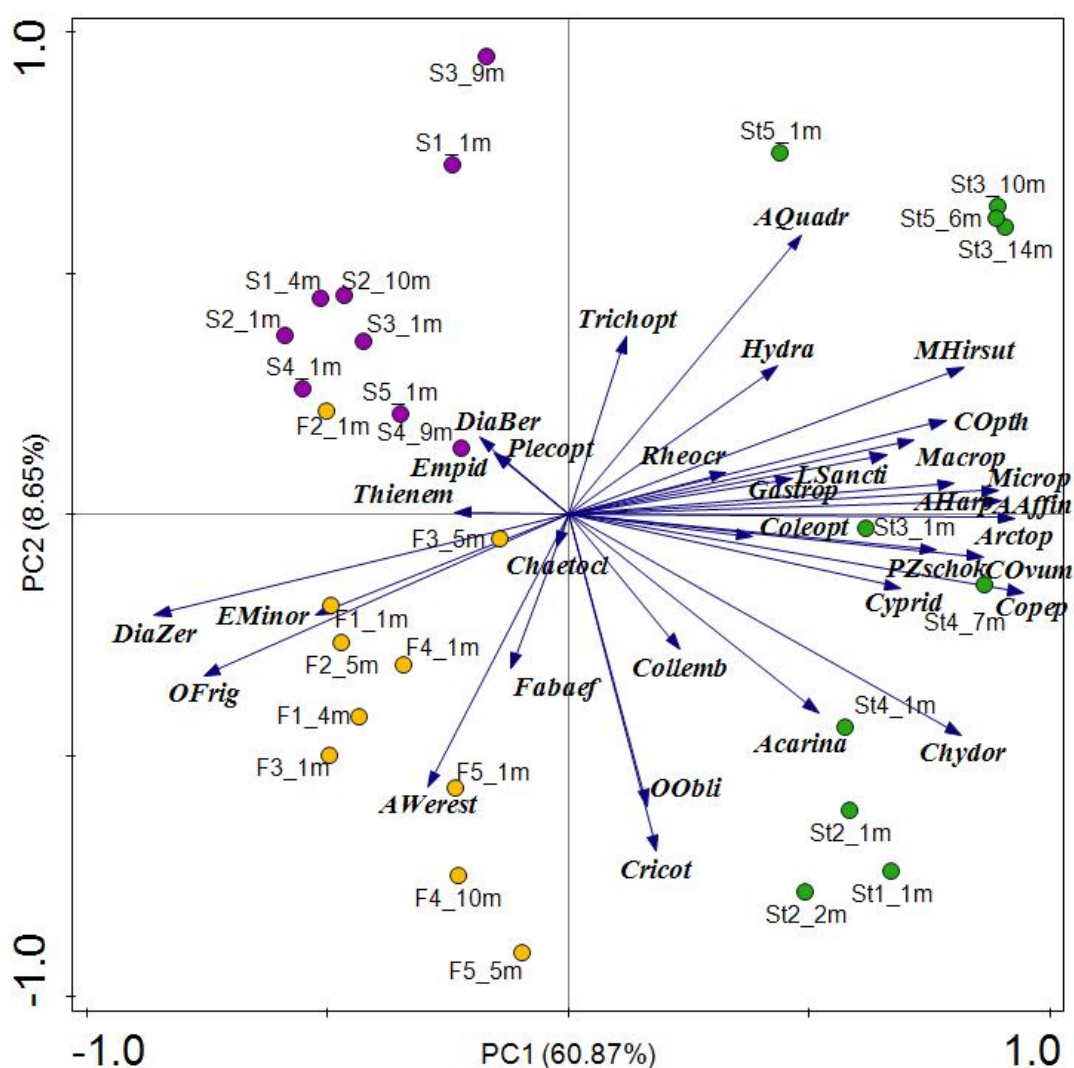
Figure 3.3 *PCA Ordination diagram of all invertebrate species and sampling sites within all fissures: Flosagjá (Yellow), Silfra (Purple) and Stekkjagjá (Green). Taxa and sampling station names are shown on page 11-12.*

In fissures in Þingvellir 31.6% of the variance in assemblages could be explained by principal component 1 (PC1) while 20.8% of the variance could be explained by principal component 2 (PC2) (Figure 3.4). Many of them shallow stations on rock wall, cluster together and are home to dipterous larvae of Empididae, Plecoptera and Trichoptera as well as several species of chironomids. Other stations from Flosagjá, many of them deep with bottom, form a loose cluster where Copepoda and several species of Cladocera and Ostracoda are in higher densities.
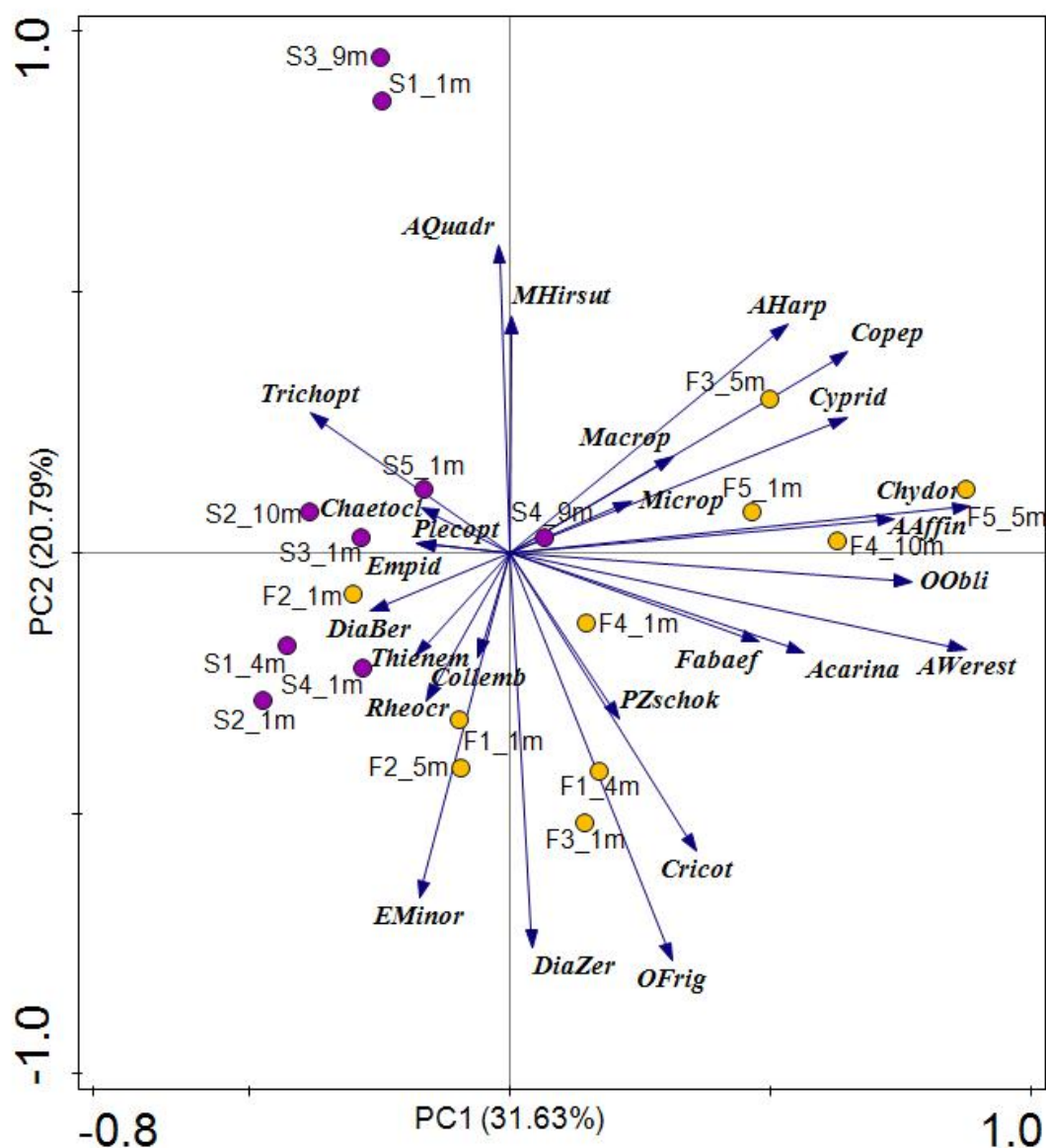
Figure 3.4 *PCA Ordination diagram of all invertebrate species and sampling sites within Flosagjá and Silfra in Þingvellir (SE-Iceland): Flosagjá (Yellow) and Silfra (Purple). Taxa and sampling station names are shown on page 11-12.*

Physicochemical environment was similar inn all fissures but especially so in Silfra and Flosagjá (Table 3.4). The mean annual temperature was 3.6°C in Flosagjá and 3.5°C in Silfra. The highest pH was measured in Flosagjá at 9.8 and was slightly lower in Silfra at 9.5. The water in Stekkjagjá had a higher mean annual temperature, at 4.3 °C, while pH was slightly lower at 8.9. Conductivity and total dissolved solids were lower in fissures in SW Iceland.

Table 3.4 Mean annual temperature, one measurement made per hour in Flosagjá (18.9.2014-4.9.2015), Silfra (18.9.2014-7.9.2015) and Stekkjagjá (24.11.2014-2.9.2015), with standard deviation (SD), minimum values (Min) and Maxium values (Max), as well as pH, conductivity and total dissolved solids measurements from all fissures: Flosagjá (4.9.2015) Silfra (7.9.2015) and Stekkjagjá (2.9.2015).

Fissure	Temperature (°C)				pH	Conductivity (μS cm^{-1})	TDS (mg/L)
	Mean	SD	Min	Max			
Flosagjá	3.61	1.05	4.62	3.26	9.8	83.2	54.0
Silfra	3.53	0.60	3.37	4.10	9.5	70.5	45.2
Stekkjagjá	4.27	3.77	1.44	7.18	8.9	122.6	79.5

3.2 Comparison of assemblages within fissures

Samples were taken at 1m and bottom on each transect. On the deepest transect (14 m within Stekkjagjá) samples were also taken at 10 m depth. Substrate was variable among stations (Table 3.5). All sampling stations were on rock substrate except for one station in Silfra fissure where there was sand substrate. This station was excluded from the final analysis.

Taxa richness was highest on bottom at 10 m depth in Flosagjá, on bottom at 9 m in Silfra and on bottom at 7 m in Stekkjagjá (Figure 3.5).

Table 3.5 Depth and substrate characteristics at each sampling station on all transects within all fissures: Flosagjá, Silfra and Stekkjagjá.

Fissure	Transect no.	Depth (m)	Substrate characteristics
Flosagjá	1	1	Rock wall
Flosagjá	1	4	Bottom
Flosagjá	2	1	Rock wall
Flosagjá	2	5	Bottom
Flosagjá	3	1	Rock wall
Flosagjá	3	5	Bottom
Flosagjá	4	1	Rock wall
Flosagjá	4	10	Bottom
Flosagjá	5	1	Rock wall
Flosagjá	5	5	Bottom
Silfra	1	1	Rock wall
Silfra	1	4	Bottom
Silfra	2	1	Rock wall
Silfra	2	10	Bottom
Silfra	3	1	Rock wall

Silfra	3	9	Bottom
Silfra	4	1	Rock wall
Silfra	4	9	Bottom
Silfra	5	1	Rock wall
Stekkjagjá	1	1	Rock wall
Stekkjagjá	2	1	Rock wall
Stekkjagjá	2	2	Bottom
Stekkjagjá	3	1	Rock wall
Stekkjagjá	3	10	Rock wall
Stekkjagjá	3	14	Bottom
Stekkjagjá	4	1	Rock wall
Stekkjagjá	4	7	Bottom
Stekkjagjá	5	1	Rock wall
Stekkjagjá	5	6	Bottom
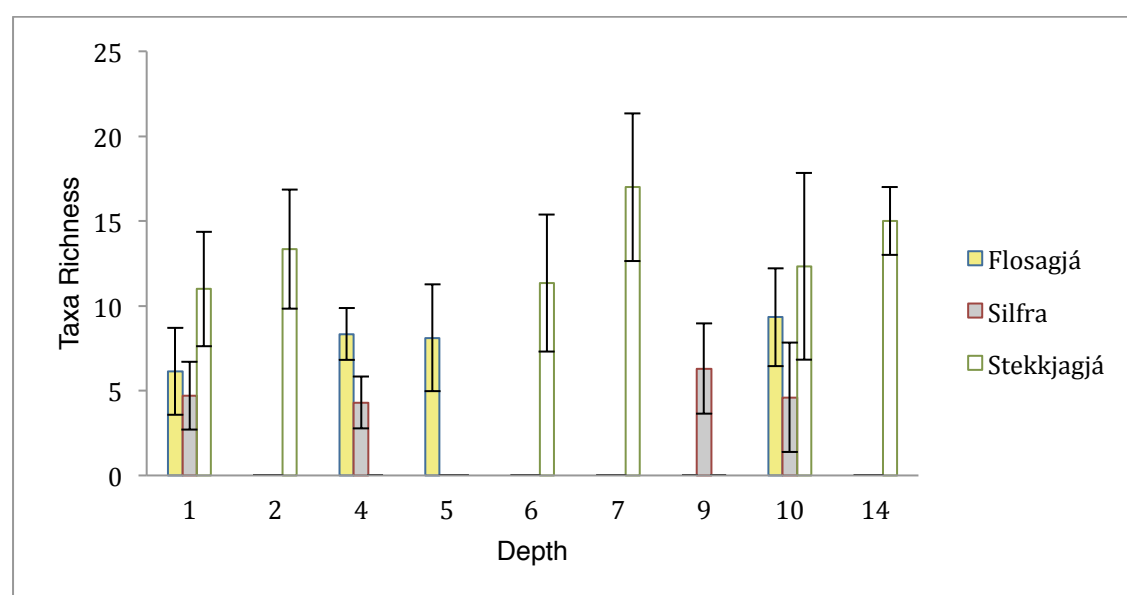
Figure 3.5 *Mean number of taxa (richness) found at each depth within all fissures with standard deviation bars: Flosagjá (yellow), Silfra (gray) and Stekkjagjá (white).*

Mean densities were calculated for all taxa at all sampling stations (Tables 3.7-3.9). Chironomids were most common at shallow or intermediate depth (at 1, 4 and 9 m) while copepods and cladocerans were most common at 9 m. *O. frigidus* was the most common taxon in Flosagjá. This species was found in high densities at 4m (642 animals/m^2) that declined to 75.7 animals/m^2 at 10 m depth. A few species of Cladocera and Ostracoda became more common with depth reaching their greatest densities at 9 and 10 m depth. Densities of the most common taxa in Silfra fissure, *D. zernyi* gr. declined from 483.3 animals/m^2 at 1 m on rock wall, to 47 animals/m^2 at 10 m depth on bottom while *E. minor* and *O. frigidus* were more evenly distributed in response to depth and whether found on rock wall vs. bottom. The densities of the cladoceran *M. hirsuticornis*, the most common taxon within Stekkjagjá fissure, varied greatly with depth but was found in greatest densities at 10 m (3067 animals/m^2).

There was a significant difference in chironomid densities in Flosagjá and Stekkjagjá on bottom at different depth whereas densities of some taxa were higher on shallower

bottom compared to deeper bottom. No other taxa groups varied significantly in densities in response to depth in any of the fissures. The chironomid larvae *O. frigidus* was in significantly higher densities at shallow stations in Flosagjá (Table 3.6). Similarly *Cricotopus tibialis* was found in significantly greater density at shallower stations in Stekkjagjá fissure.

No significant differences were found in densities in response to rock wall vs. bottom in any of the groups in any of the fissures, except among ostracods in Flosagjá, which were found in significantly higher densities on bottom (Table 3.6). This difference cannot be attributed to one distinct ostracod species or group. *Cypridoidea* sp. and *Limnocytherine sanctipatricii* were found in greater densities on bottom although the difference was not statistically significant. *P. zschokkei* was in low densities in Flosagjá but was only found on the bottom.

Table 3.6 *Results from Spearman rho test and Wilcoxon test on mean density of most common taxa and Shannon diversity index within all fissures (Flosagjá, Silfra and Stekkjagjá) in response to substrate characteristics (Rock wall vs. bottom) and depth at bottom.*

	Flosagjá	Silfra	Stekkjagjá
Mean density			
Depth (Spearman rho)			
Chironomidae	0.04	0.15	0.00
Copepoda	0.72	0.93	0.19
Cladocera	0.57	0.09	0.75
Ostracoda	0.72	0.6	0.28
Arctopelopia sp.			0.19
C.tibialis			0.04
D.zernyi gr.	0.22		
Micropsectra sp.			0.87
O.frigidus	0.04		
Substrate (Wilcoxon)			
Chironomidae	0.84	0.55	1.00
Copepoda	0.83	1.00	0.10
Cladocera	0.42	0.52	0.42
Ostracoda	0.02	0.92	0.54
D.zernyi gr.	0.15	0.71	
Cypridoidea sp.	0.14		
Shannon Diversity index			
Depth (Spearman rho p<0.05)	0.22	0.68	0.04
Substrate (Wilcoxon p<0.05)	0.01	0.05	0.37

Table 3.7 *Mean densities of invertebrates (m²) at different depth in Flosagjá with standard deviation (SD).*

	1m		4m		5m		10m	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Chironomidae								
Arctopelopia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetocladius vitellinus gr.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cricotopus tibialis gr.	45.0	67.6	150.0	132.3	61.1	71.9	33.3	28.9
Diamesa bertrami	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diamesa zernyi gr.	335.0	326.9	258.3	101.0	144.4	145.1	233.3	200.5
Eukiefferiella minor	60.0	79.5	125.0	75.0	27.8	47.0	50	66.1
Macropelopia sp.	0.0	0.0	0.0	0.0	2.7	8.3	0.0	0.0
Metriocnemus obscuripes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Micropsectra sp.	1.7	6.5	0.0	0.0	5.6	16.7	0.0	0.0
Orthocladius frigidus	325.0	225.6	641.7	316.0	166.7	227.1	216.7	166.5
Orthocladius oblidens	5.0	14.0	33.3	57.7	19.4	31.7	116.7	118.1
Rheocricotopus cf. *effusus*	1.7	6.5	0.0	0.0	5.6	16.7	0.0	0.0
Thienemaniella sp.	0.0	0.0	0.0	0.0	5.6	16.7	0.0	0.0
Cladocera								
Acroperus harpae	1.7	6.5	16.7	28.9	2.8	91.0	25.0	25.0
Alona affinis	1.7	6.5	16.7	28.9	19.4	60.1	8.3	14.4
Alona quadrangularis	0.0	0.0	8.3	14.4	11.1	33.3	0.0	0.0
Alona werestschagini	50.0	114.2	41.7	14.4	80.6	166.8	75.0	66.1
Chydorus cf. *sphaericus*	33.3	57.2	8.3	14.4	200.0	379.8	66.6	38.2
Ilyocryptus sordidus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macrothrix hirsuticornis	0.0	0.0	0.0	0.0	11.1	33.3	0.0	0.0
Ostracoda								
Cyclocypris ovum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cypria opthalmica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Cypridoidea sp.	16.7	29.4	16.7	14.4	58.3	104.2	208.3	184.3
Fabaeformiscandona sp.	0.0	0.0	8.3	14.4	2.8	8.3	8.3	14.4
Limnocytherina sanctipatricii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Potamocypris zschokkei	3.3	8.8	8.3	14.4	16.7	41.5	0.0	0.0
Other groups								
Acarina	23.3	29.1	0.0	0.0	19.4	38.4	50.0	86.6
Coleoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Collembola	1.7	6.5	0.0	0.0	0.0	0.0	0.0	0.0
Copepoda	75.0	168.5	8.3	14.4	27.8	80.0	91.7	87.8
Empididae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hydra	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plecoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trichoptera	1.6	6.5	0.0	0.0	0.0	0.0	0.0	0.0

Table 3.8 *Mean densities of invertebrate taxa (m^2) at different depth in Silfra with standard deviation (SD).*

	1m		4m		9m		10m	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Chironomidae								
Arctopelopia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetocladius vitellinus gr.	15.0	13.3	0.0	0.0	0.0	0.0	4.1	14.4
Cricotopus tibialis gr.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diamesa bertrami	0.0	0.0	8.3	14.4	0.0	0.0	0.0	0.0
Diamesa zernyi gr.	483.3	440.7	350.0	264.6	245.8	280.4	41.6	72.2
Eukiefferiella minor	190.0	175.3	216.7	203.6	208.3	257.7	45.8	87.8
Macropelopia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metriocnemus obscuripes	10.0	32.0	0.0	0.0	0.0	0.0	0.0	0.0
Micropsectra sp.	6.7	15.3	0.0	0.0	33.3	54.0	0.0	0.0

Orthocladius frigidus	91.7	65.4	225.0	50.0	120.8	160.0	104.2	184.3
Orthocladius oblidens	5.0	10.6	0.0	0.0	12.5	30.6	0.0	0.0
Rheocricotopus cf. *effusus*	1.7	6.7	0.0	0.0	0.0	0.0	4.2	14.4
Thienemaniella sp.	0.0	0.0	0.0	0.0	0.0	0.0	4.2	14.4
Cladocera								
Acroperus harpae	0.0	0.0	0.0	0.0	33.3	28.9	0.0	0.0
Alona affinis	0.0	0.0	0.0	0.0	29.2	48.5	0.0	0.0
Alona quadrangularis	6.7	11.7	0.0	0.0	25.0	31.6	0.0	0.0
Alona werestschagini	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chydorus cf. *sphaericus*	0.0	0.0	0.0	0.0	8.3	20.4	0.0	0.0
Ilyocryptus sordidus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macrothrix hirsuticornis	0.0	0.0	16.7	14.4	25.0	38.7	0.0	0.0
Ostracoda								
Cyclocypris ovum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cypria opthalmica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cypridoidea sp.	45.0	87.4	0.0	0.0	37.5	68.5	8.3	14.4
Fabaeformiscandona sp.	1.7	6.7	0.0	0.0	0.0	0.0	0.0	0.0
Limnocytherina sanctipatricii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Potamocypris zschokkei	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other groups								
Acarina	10.0	23.4	0.0	0.0	33.3	43.8	4.1	14.4
Coleoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Collembola	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Copepoda	38.3	29.2	8.3	14.4	95.8	103.0	4.1	14.4
Empididae	1.7	6.7	0.0	0.0	0.0	0.0	0.0	0.0
Gastropoda	15.0	13.3	0.0	0.0	0.0	0.0	0.0	0.0
Hydra	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plecoptera	1.7	6.7	0.0	0.0	0.0	0.0	0.0	0.0
Trichoptera	5	16.9	0.0	0.0	20.8	33.2	16.6	28.9

Table 3.9 *Mean densities of invertebrate taxa (m^2) at different depth in Stekkjagjá with standard deviation (SD).*

	1m		2m		6m		7m		10m		14m	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Chironomidae												
Arctopelopia sp.	261.7	310.7	83.3	38.2	233.3	14.4	108.3	52.0	125.0	132.3	225.0	175.0
Chaetocladius vitellinus gr.	1.7	6.5	16.7	28.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cricotopus tibialis gr.	130.0	234.0	150.0	152.1	8.3	14.4	58.3	38.2	8.3	14.4	0.0	0.0
Diamesa bertrami	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diamesa zernyi gr.	6.7	20.0	25.0	43.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eukiefferiella minor	21.7	45.2	41.7	14.4	0.0	0.0	41.7	52.0	41.7	38.2	16.7	14.4
Macropelopia sp.	10.0	32.5	0.0	0.0	41.7	14.4	33.3	38.2	16.7	28.9	16.7	28.9
Metriocnemus obscuripes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Micropsectra sp.	118.3	136.8	66.7	52.0	175.0	204.6	100.0	132.3	216.7	200.5	83.3	52.0
Orthocladius frigidus	50.0	68.8	16.7	28.8	8.3	14.4	0.0	0.0	8.3	14.4	0.0	0.0
Orthocladius oblidens	25.0	70.1	141.7	202.1	0.0	0.0	33.3	28.9	8.3	14.4	8.3	14.4
Rheocricotopus cf. *effusus*	8.3	26.2	0.0	0.0	0.0	0.0	25.0	25.0	8.3	14.4	16.7	28.9
Thienemaniella sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cladocera												
Acroperus harpae	40.0	103.4	66.7	94.6	391.7	527.0	916.7	643.4	950.0	1538.5	775.0	690.6
Alona affinis	156.7	183.8	16.7	14.4	433.3	189.3	208.3	137.7	416.7	538.7	275.0	66.1
Alona quadrangularis	35.0	68.7	0.0	0.0	58.3	80.4	8.3	14.4	75.0	75.0	25.0	25.0
Alona werestschagini	0.0	0.0	0.0	0.0	0.0	0.0	8.3	14.4	0.0	0.0	0.0	0.0
Chydorus cf. *sphaericus*	411.7	295.2	316.7	464.6	208.3	177.4	433.3	318.5	550.0	952.6	166.7	180.9
Ilyocryptus sordidus	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macrothrix hirsuticornis	268.3	665.1	50.0	25.0	1850.0	762.8	358.3	448.1	3066.7	4044.2	1283.3	973.5
Ostracoda												
Cyclocypris ovum	331.7	433.7	16.7	14.4	33.3	57.7	150.0	238.5	66.7	76.4	475.0	563.5
Cypria opthalmica	8.3	15.4	0.0	0.0	25.0	43.3	66.7	52.0	16.7	28.9	8.3	14.4
Cypridoidea sp.	78.3	105.6	50.0	43.3	91.7	158.8	325.0	25.0	200.0	229.1	500.0	354.4
Fabaeformiscandona sp.	1.7	6.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Limnocytherina sanctipatricii	23.3	77.0	0.0	0.0	33.3	57.7	8.3	14.4	8.3	14.4	233.3	194.2
Potamocypris zschokkei	33.3	56.4	25.0	25.0	16.7	28.9	108.3	87.8	58.3	80.3	108.3	76.4
Other groups												
Acarina	40.0	47.1	75.0	75.0	50.0	86.6	83.3	57.7	8.3	14.0	75.0	75.0
Coleoptera	1.7	6.5	0.0	0.0	0.0	0.0	8.3	14.4	0.0	0.0	0.0	0.0
Collembola	331.7	1263.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Copepoda	4083.3	3413.9	18883.3	20509.4	11408.3	2496.3	6133.3	3193.4	4316.7	4862.0	2616.7	2264.4
Empididae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropoda	0.0	0.0	8.3	14.4	0.0	0.0	8.3	14.4	33.3	57.7	0.0	0.0
Hydra	0.0	0.0	0.0	0.0	8.3	14.4	0.0	0.0	25.0	43.3	0.0	0.0
Plecoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trichoptera	5.0	14.0	0.0	0.0	0.0	0.0	8.3	14.4	8.3	14.4	16.7	14.4
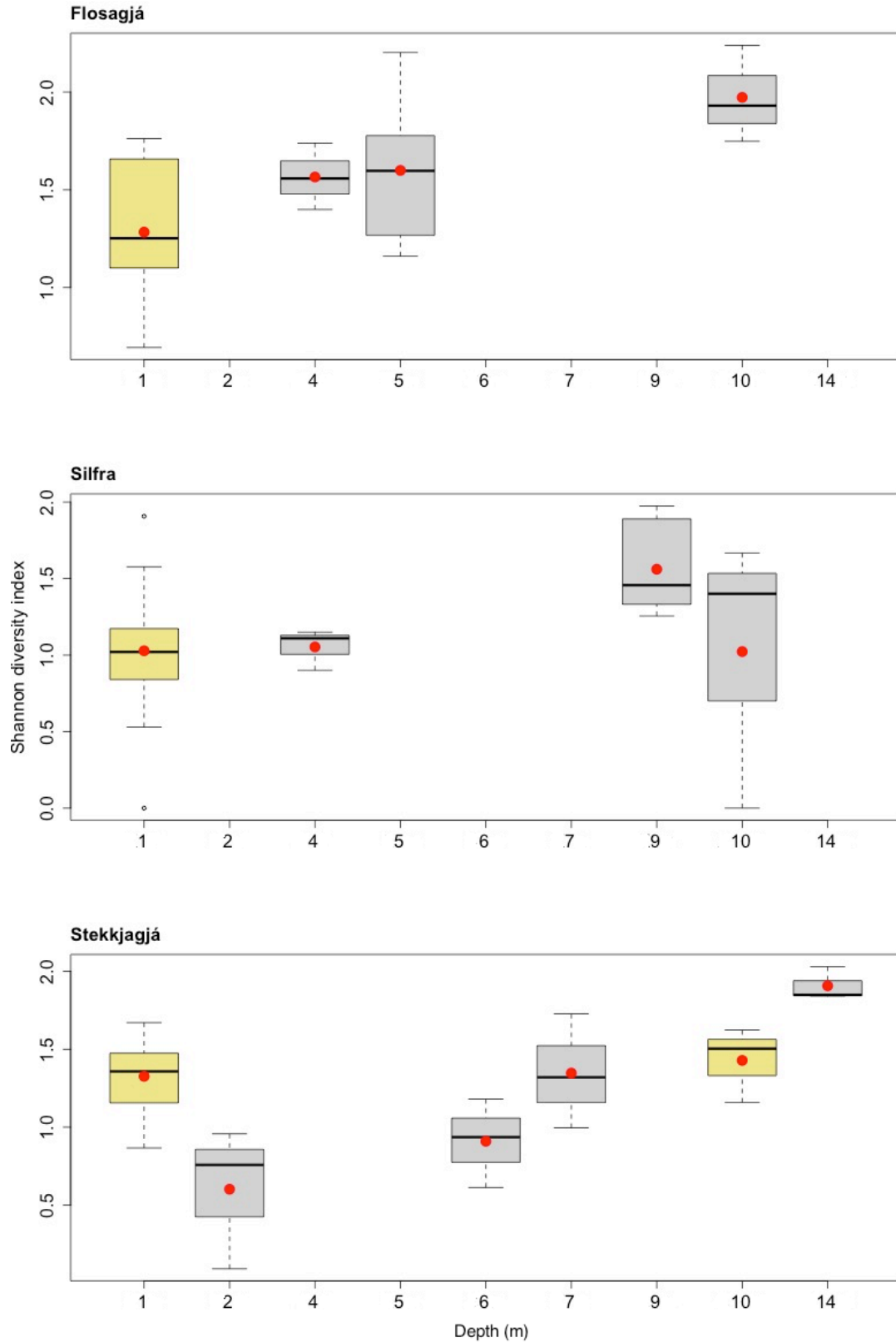
Figure 3.6 *Shannon diversity index for all depths within all fissures. Rock wall stations are shown in yellow and horizontal bottom stations in grey, with mean (red) and median (black line). Whiskers show variability beyond the upper and lower quartile (the 3rd (Q3) and 1st (Q1) quartiles are demarcated by top and bottom of boxes. The interquartile range (IQR) is the height of boxes from top to bottom. The top whisker is determined by Q3 + 1.5*IQR and the bottom whisker is determined by Q1- 1.5*IQR). Empty circles are outliers.*

41

The highest Shannon diversity values of invertebrates was at bottom at the deepest or second deepest stations within all three fissures (10 m within Flosagjá, 9 m in Silfra and 14 m within Stekkjagjá) (Figure 3.6). There was a significant difference in invertebrate diversity (Shannon index) between the rock wall and horizontal bottom in Flosagjá, while no significant difference was between these two habitats in Silfra or Stekkjagjá (Table 3.6). Within Flosagjá and Silfra there was no significant difference in invertebrate diversity (Shannon index) between stations at the bottom habitats at different depths. On the other hand there was a significant difference in invertebrate diversity for the same habitat at different depths in Stekkjagjá.

An RDA analysis was performed on assemblages in response to depth and angle (rock wall vs. bottom) within fissures. Neither variable significantly explained species composition in Silfra and Flosagjá. An RDA analysis on assemblages in Stekkjagjá fissure found depth to significantly explain 26.8% (p=0.01) of the variability in assemblages while angle was insignificant. An RDA diagram was plotted for Stekkjagjá with species data to show how depth shaped assemblages (Figure 3.7). Several ostracod species (*P. zchokkei, L. sanctipatriciii* and *Cypridoidea* sp.) were found in higher densities at greater depth as well as cladoceran *Acroperus harpae* and *M.hirsuticornis*, while the chironomid larvae *C. tibialis* and *D. zernyi* gr. were found in lower densities at greater depth.
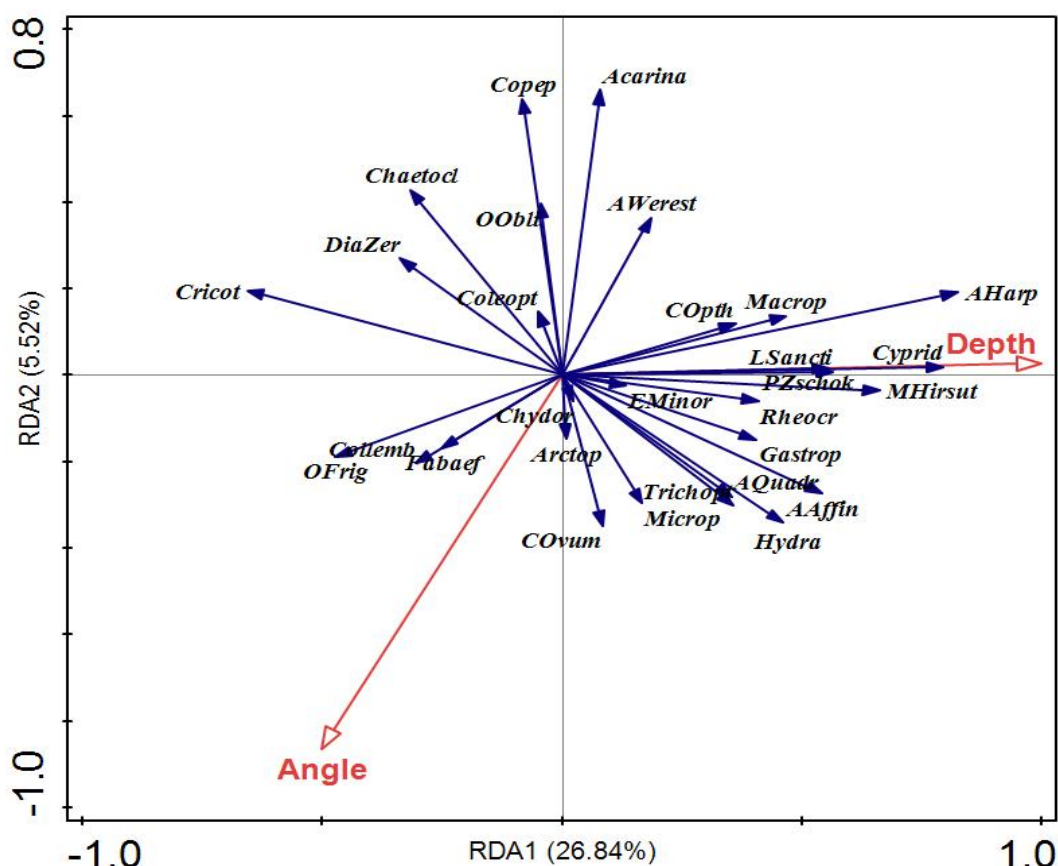

Figure 3.7 *RDA Ordination diagram of invertebrate species (blue arrows) and environmental variables (red arrows) in Stekkjagjá fissure. Taxa names are shown on page 11-12.*

In a PCA analysis on Flosagjá, 51.8% of the variance in species composition could be explained by principal component 1 (PC1) while 13.0% of the variance could be explained by principal component 2 (PC2). Notable is station S3_5m, which is an outlier where high densities of *A. quadrangularis*, *M. hirsuticornis* and *Macropelopia* sp., the only Tanypodinae found in SW Iceland, were found (Figure 3.8). Other stations within Flosagjá form two loose clusters, one has high density of several chironomid species while the other has high density of several crustacean species, Acarina water mites and the chironomids *Micropsectra* sp. and *O. oblidens*. In Silfra 45.4% of the variance in species composition could be explained by principal component 1 (PC1) while 20.8% of the variance could be explained by principal component 2 (PC2) (Figure 3.9). The PCA diagram shows relatively high variability among sampling stations with no distinct clustering (Figure 3.9). The three most common chironomids (*D. zernyi* gr., *E. minor* and *O. frigidus*) were found in higher densities on shallow stations while *Micropsectra* sp. and *O .oblidens* were found in high density on station S4_9m.
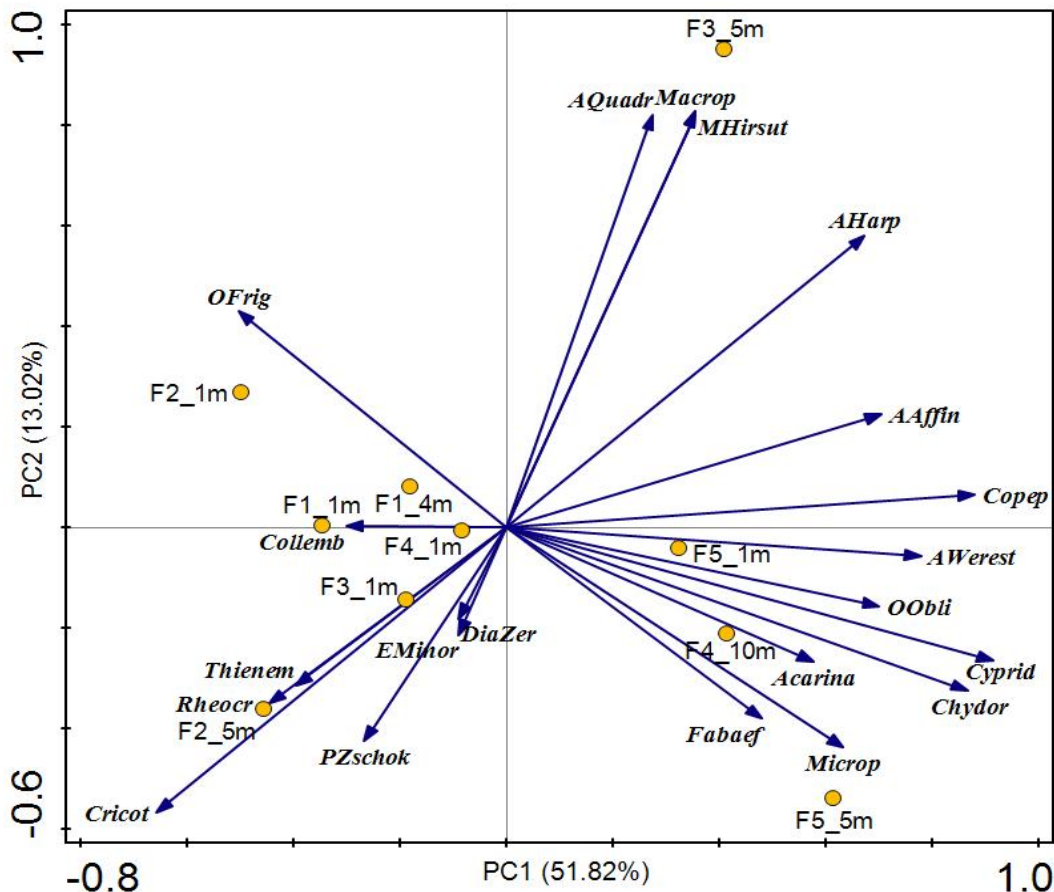

Figure 3.8 *PCA Ordination diagram of all sampling sites (yellow dots) and invertebrate species (blue arrows) in Flosagjá fissure. Taxa and sampling station names are shown on page 11-12.*
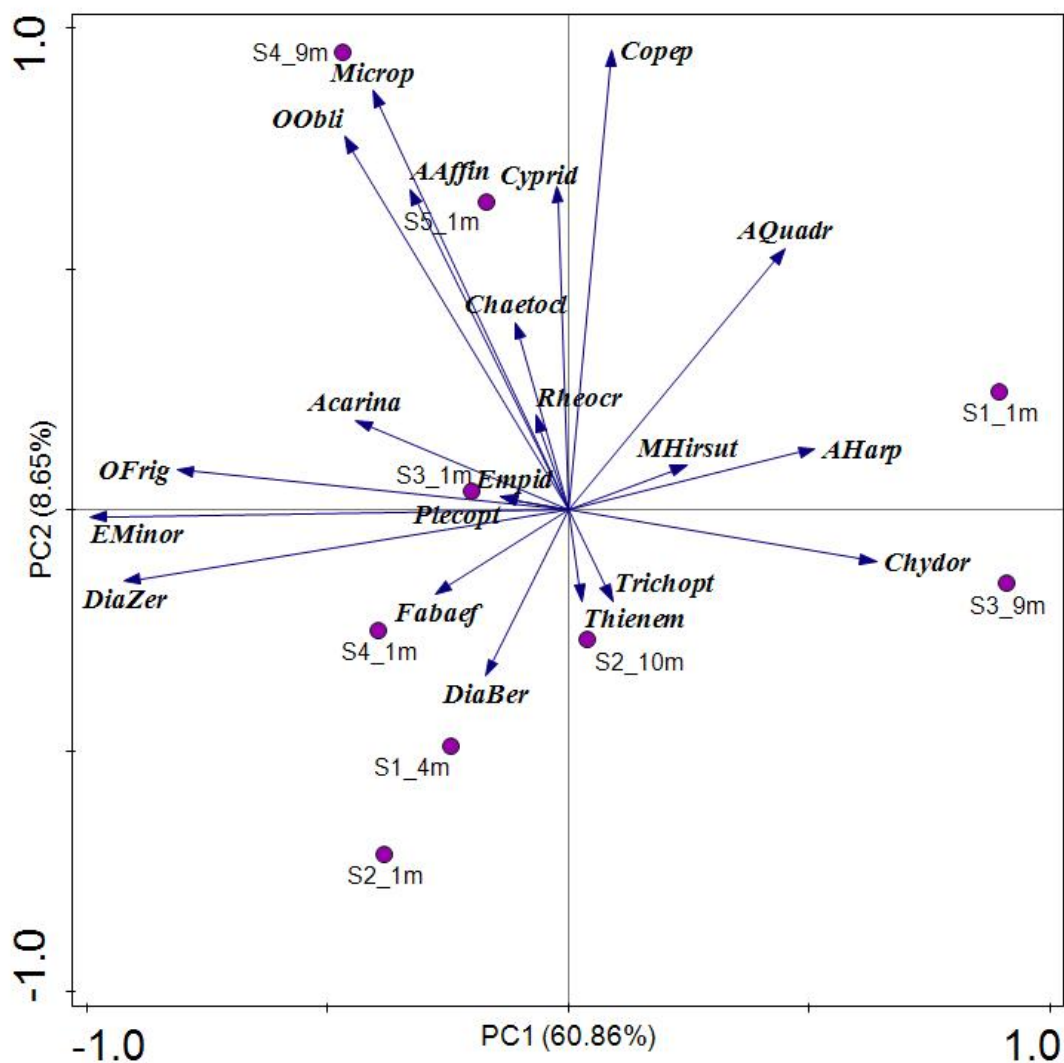
Figure 3.9 *PCA Ordination diagram of all sampling sites (purple dots) and invertebrate species (blue arrows) in Silfra fissure. Taxa and sampling station names are shown on page 11-12.*

4. Discussion

The fissures focused on in this study contain cold groundwater (Ólafsson, 1992) and most of the substrate is rock wall. The two fissures that were sampled in SW Iceland, Flosagjá and Silfra, are roughly 300 meters apart. The section sampled within Flosagjá was 330 m long between two collapses with a maximum water depth of 18 m. Silfra is approximately the same length, 320 m long and has a maximum water depth of 20 m in open water. The section sampled within Flosagjá has no caverns. Silfra however has extensive cavern systems that reach greater depth and the deepest point within the fissure is 60 m within a cave. Silfra connects directly to Lake Þingvallavatn while Flosagjá is landlocked. Therefore these two fissures are quite different in regards to physical habitat. On the other hand the physicochemical environment of Flosagjá and Silfra is similar. The annual mean water temperature is low (3.6°C in Flosagjá and 3.5°C in Silfra) and the temperature was stable throughout the year. The pH of the water in Flosagjá was 9.8 while pH in Silfra was 9.5 and there was slightly lower conductivity and total dissolved solids (TDS) in Silfra compared to Flosagjá.

Additionally a 260 m section within Stekkjagjá fissure was sampled. Stekkjagjá is located in NE Iceland, roughly 300 km away from Flosagjá and Silfra. Stekkjagjá is narrower than the other two fissures, has several collapses, some cavern formations and the maximum water depth is 14 m. Stekkjagjá is located in a different environmental setting. Unlike Flosagjá and Silfra, which are in a National park, Stekkjagjá is located on pastureland. The pH of the water in Stekkjagjá was 8.9 while conductivity and TDS was higher than in SW Iceland. The temperature in Stekkjagjá was slightly higher than in SW Iceland at 4.3°C, and fluctuated more throughout the year.

4.1 Variability in assemblages between groundwater fissures

Assemblages within fissures varied significantly between geographical regions. Shannon diversity was significantly higher in SW Iceland. These high values indicate that densities of taxa are more even in Flosagjá and Silfra despite there being fewer species while Stekkjagjá in NE Iceland, where invertebrate taxa richness was highest, is home to many rare species. The more evenness there is within a community, the more likely it is to recover from changes (e.g. disturbance) and biodiversity is considered to be higher as a result (Magurran, 2005). Cladocerans, copepods and ostracods were found in significantly higher densities in NE Iceland compared to SW Iceland while there was no significant difference in densities of chironomids. On closer inspection however it was clear that chironomid assemblages vary greatly. *Arctopelopia* sp. (Tanypodinae), the most dominant chironomid in Stekkjagjá was not found in SW-Iceland, while *D. zernyi* gr. was found in significantly greater densities in SW Iceland. The larvae of Tanypodinae are predominantly predatory (Baker and McLachlan, 1979). Tanypodine in Stekkjagjá often had ostracods and cladocerans as well as chironomid head capsules in their gut (Figure 4.1). The greater densities of

45

crustaceans in Stekkjagjá may act as a food resource for Tanypodinae and could help explain why they are the dominating chironomid there. Meanwhile Tanypodinae larvae were nearly absent from fissures in SW Iceland, which were crustacean poor compared to Stekkjagjá. Instead there were high densities of grazing chironomids such as *D. zernyi* gr.*, O. frigidus* and *E. minor*. Orthocladiinae and Diamesinae have been found to dominate on rock and gravel surfaces and are especially successful in cold habitats (Pinder, 1986; Govoni, 2011).

Communities in fissures in the same region were similar. There was no significant difference in either Shannon diversity index between fissures or densities of copepods, chironomids and ostracods. Cladocerans however were found in significantly greater densities within Flosagjá fissure. *Chydorus* sp. is the most common cladoceran in SW Iceland mostly because of high densitites in Flosagjá while it was almost absent from Silfra. *A. werestschagini*, which was very recently documented in Iceland for the first time (Novichkova *et al.*, 2014), was entirely absent from Silfra while being the second most common cladoceran in Flosagjá.
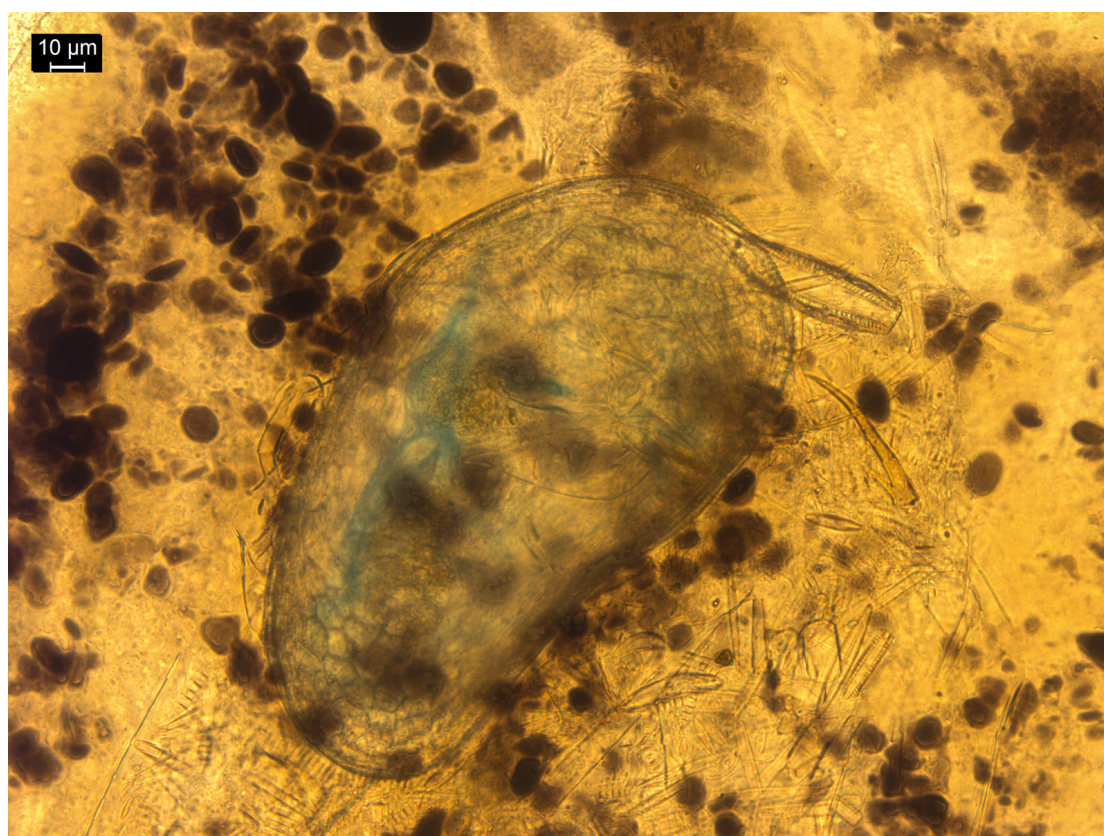
Figure 4.1. *Microscopy photograph of the gut content of* Arctopelopia *larvae from Stekkjagjá showing ostracod Potamocypris zschokkei and diatoms*.

Many factors may help explain the differences between assemblages observed between SW and NE Iceland as the fissures are located in different environmental settings regarding climate, altitude and latitude, all of which are factors that have been shown to shape biodiversity (Van der Kamp, 1995; Jacobsen *et al.*, 1997; Triantis, 2011). One distinct difference between the two geographical regions is that fissures in SW Iceland are within a National park where there is no grazing while Stekkjagjá is located on pastureland. In a study on the effects of environmental factors on species

composition in high altitude springs, pasture led to an increase in invertebrate richness and diversity (Lencioni *et al*., 2012). This was presumably because of additional nutrient input into otherwise oligotrophic systems (Cantonati and Gerecke, 2006). Stekkjagjá has higher taxa richness and densitites of invertebrates than Flosagjá and Silfra although diversity is lower there. Nutrient availability may have been a significant environmental factor in Stekkjagjá and possibly contributed to the higher species richness and densities of invertebrates found there.

Current is also likely to be a significant environmental factor in the fissures and may perhaps explain the observed difference in invertebrate assemblages. There seemed to be fairly strong current in Silfra during the sampling but very mild current in both Flosagjá and Stekkjagjá. Crustaceans are associated with still or slow flowing water. The limited current in Stekkjagjá likely creates a suitable habitat for crustaceans, which are found in much higher densities there compared to fissures in SW Iceland. Slower current in Flosagjá may also help explain the higher density of cladocerans found there compared to the adjacent and faster flowing Silfra. Chironomids are also indicative of environmental characteristics and Hrafnsdóttir (2005) has classified chironomid species in Iceland with respect to habitats they are found in. The present findings fit nicely to Hrafnsdóttir's classification. *Arctopelopia* sp., was the most dominant chironomid in lentic Stekkjagjá and is mentioned as being characteristic of habitats with low current. On the other hand *E. minor* was found in much greater density in Silfra, where the current appeared to be stronger than in the other two fissures. The larvae of *E.minor* are usually found in fast flowing streams and rivers (Garðarsson *et al*., 2004; Lods-Crozet, 2001). Current velocity seems likely to shape assemblages in fissures to a point.

MacArthur and Wilson (1963) hypothesized that communities on islands will reflect the source population and that the rate of dispersal will depend on the islands proximity to a mainland. Springs can be viewed as fairly isolated "islands", which are potentially colonized from a nearby water body "mainland". Variable assemblages in fissures in different geographical regions could reflect a difference in source populations in addition to variability in other ecological characters of the habitat. Stekkjagjá is potentially colonized by nearby Lake Skjálftavatn but very limited information exists about this lake. Fissures in Þingvellir are possibly colonized by nearby and extensively studied Lake Þingvallavatn, although taxa will naturally vary in their dispersal ability depending on their life history (*i.e.* chironomids with winged terrestrial stages compared to macrozoobenthos) (Bohonak and Jenkins, 2003). The most common chironomids in the fissure in SW Iceland have all been documented in L. Þingvallavatn and two of these, *O. frigidus* and *E. minor,* are common in the surf zone of the lake (Lindegaard, 1992). Cladocerans found in the fissures such as *A. harpae* and *C. sphaericus* are also common epibenthic species in the lake (Lindegaard, 1992). One of the most powerful explanatory variables for taxa richness on islands is the size of an area (Triantis, 2011). Although Silfra and Flosagjá are similar in length, Silfra is deeper and thus has a larger volume. Silfra is also directly connected to L. Þingvallavatn while Flosagjá is landlocked, although it presumably connects to other fissure bodies and the lake via underground channels. Silfra's proximity to the lake possibly makes dispersal into the fissure easier, as has been observed with larger morphs of Arctic charr, which frequently swim into Silfra but are unable to access Flosagjá. Therefore there is more than one potential explanation

for the higher taxa richness found in Silfra, although the difference in richness between the fissures was marginal.

Four of the most common groups of invertebrates, in addition to amphipods and fish were identified to species. Copepod was the most common taxa in the study by a margin. This group is challenging, as they often require careful dissection for detailed species identification and currently there is no specialist in copepod identification in Iceland. With external assistance (Identification by Dr. Frank Fiers, February, 2015) a qualitative overview of the Copepoda species present in my samples was obtained from roughly 25% of the samples. For quantitative analysis copepod data was pooled. One species, *E. borealis* (Copeoda, Cyclopoida, Eucyclopinae), was found for the first time in Iceland. This species has previously only been documented in Alaskan ponds and was described in 2001. Another species of this genus, *E. serrulatus*, has been documented in Iceland. Until recently *E. serrulatus* was reported worldwide, but recent revision showed that the species has in fact a much more limited distribution in the Palaearctic (Alekseev and Defaye, 2011), and that recent description from outside this area are likely a result of new invasions. The same authors found no specimens of *Eucyclops* in samples they obtained in Iceland (Alekseev and Defaye, 2011). The copepod *Eucyclops* is recognized among taxonomists as being a difficult and confused genus, which is loaded with flawed descriptions, partly because the original description was deficient (Alekseev *et al.*, 2005). They note that previous records of *E.serrulatus* in Iceland should be re-examined. Due to lack of expertize identification, copepods as a group is underrepresented in Iceland and may include dubious records.

Small benthic charr was found in all three fissures. The behavior and life history of Arctic charr has been studied extensively in Lake Þingvallavatn (Jónsson *et al.*, 1988; Snorrason *et al.,* 2011). The four morphs of charr that inhait the lake are all known to spawn on hard rock in the littoral zone but the small benthic charr is the only morph which spends its entire life there, hiding between rocks and venturing out in search of food in the nighttime (Snorrason *et al.*, 2011). This is a fitting description for their behavior in the fissures where they were frequently observed darting between the rocks in all fissures, in addition to being caught in minnow traps. The small benthic charr is known to feed primarily on the gastropod *Radix balthica* L.1758 (synonym to *Lymnaea peregra*) in Lake Þingvallavatn (Jonsson *et al.*, 1988). Since gastropods were scarce and in most cases entirely absent from the fissures there is reason to believe that other species make up the bulk of the charrs diet in this region. All charr are known to exploit chironomid larvae to a point, especially their nutritious pupae when they start to emerge in springtime (Snorrason *et al.*, 2011). Dwarf charr populations are known to have variable diets depending on their location, sometimes feeding on crustaceans and other insect larvae species in addition to chironomids (Bjarni Kristjánsson and Daniel Govoni, *Lífríki linda*, Náttúrustofur lecture, 2012).

4.2. Variability in assemblages within groundwater fissures in response to a depth gradient and rock wall vs. bottom

In fissures in SW Iceland there was no significant difference found in Shannon diversity with depth, nor was depth significant in RDA constrained analysis. These findings contrast with results from Stekkjagjá where a significant difference was found in Shannon diversity index with depth and depth significantly explained

observed variability in community structure. Densities on bottom of the four most common taxa groups (Chironomidae, Cladocera, Copepoda and Ostracoda) were compared between variable depths in all fissures. Of these Chironomidae in Flosagjá and Stekkjagjá was the only group that was found in different densities at variable depth. Therefore most taxa seem to have relatively even distribution in fissures regardless of depth.

One could expect the fissure setting, which often has great variation in the physical environment (e.g. depth, caverns, rock wall vs. rock bottom) to create a mixture of dissimilar habitat patches that might affect distribution patterns. This however does not appear to be the case and the distribution of various taxa seemed rather homogenous. The biofilm mats that cover the substrate in fissures may help to explain this homogeneity and "wipe out" the effects of the physical terrain. While the clarity of the water in the fissures indicates that not much lives in the water column, these thick benthic mats seem to create favorable habitat for invertebrates and are similar to those commonly found in high latitude freshwater systems. Mat forming diatoms and cyanobacteria have been documented in cold freshwater systems in the Arctic and Antarctica (Ohtsuka *et al*., 2006; Rautio and Vincent, 2007). In systems where the water temperature is below 5°C, the primary production of planktonic cyanobacteria has been shown to be nutrient limited, while benthic mats on the contrary act as a type of microenvironment that is nutrient sufficient and is home to many species (Bonilla, 2005). A study by Rautio and Vincent (2007), which focused on shallow Arctic systems with an oligotrophic water column, found highly productive benthic mats dominated by *Oscillatoria* spp. to be an important carbon source for zooplankton. A similar study on small lakes in sub-Antarctica by Hansson and Travik (2003) found that large copepods feed on benthic algae mats in addition to particulate organic matter. The fissures appear to have much in common with flora in High Arctic freshwater systems. Detailed identification of flora is still lacking but the biofilm mats are mostly made from Cyanobacteria and benthic diatoms. The green algae *Tetraspora cylindrica* and *Klebsormidium* sp. were also observed in Silfra fissure. The Cyanobacteria genus *Oscillatoria* forms algal mats which are known to grow around artesian springs at the bottom of Lake Þingvallavatn where nitrogen rich water is discharged. As long as the nitrogen availability is sufficient cyanobacteria of this genus can photosynthesize under very dim light conditions (Jónsson *et al*., 2011). Cyanobacteria seem to cope well within caverns and in narrow fissures where light penetration is limited. Such biofilm mats appear to act as a shelter and a food source for the array of invertebrate species collected during this study (personal observation). Biofilm mats may continue to provide sufficient habitat and food source for invertebrates even at great depth and this could explain why little difference was observed in densities with depth among most taxa in fissures.

The only taxa that did show significant differences in density in response to depth were chironomids in both Flosagjá and Stekkjagjá. Silfra on the other hand did not follow this trend and no significant difference in chironomid densities was found with depth. One difference that sets these fissures apart is that Silfra endures high levels of dive-use throughout the year while the other two fissures are protected. In Þorbjörnsson's (2015) study on the ecological impacts of dive traffic in Silfra he found chironomids to be the only taxa group that was positively correlated with greater dive-use. This suggests that dive use can in some ways influence chironomid distribution and perhaps it can interfere with the effect that depth gradient would

otherwise have on the distribution of assemblages. The differences observed in chironomid distribution with depth in Flosagjá was mostly due to variable densities of *O. frigidus*, which was found in significantly greater densities at the shallowest bottom station (4 m). The chironomid species *C. tibialis* was also found in significantly greater densities at the shallowest bottom station (2 m) in Stekkjagjá. The higher densities of these species in shallow water in the fissures may be attributed to their ability to cope with current and surf, which is generally greater at shallower sites. This is consistent with Hrafnsdóttir's (2005) classification, which notes that *O. frigidus* and *C. tibialis* are frequently found in the shallow littoral zone in lakes, where surf is high.

The cold adapted *D. zernyi* gr. was the most common chironomid documented in this study. This species is common in lotic habitats and has also been found in madicolous habitats in Iceland (Hrafnsdóttir, 2005). *D. zernyi* sp. may use similar mechanisms to those that make it successful in high flow, to attach to the predominantly vertical rock wall substrate found in the fissures. *D. zernyi* gr. was consistently found in higher densities on rock walls although no significant difference was found in response to rock wall vs. bottom. *Diamesa* sp. are also associated with low temperature in spring habitats and *D. zernyi* gr. is recognized for its tolerance of freezing conditions (Lencioni, 2004; Govoni, 2011) which may help explain their high densities in the cold groundwater fissures.

No significant difference was in densities among the four most common taxa groups in response to rock wall vs. bottom in any of the fissures, except for ostracods within Flosagjá fissure. Flosagjá fissure was also the only fissure where there was significant difference in Shannon diversity in response to rock wall vs. bottom. The difference observed could not be attributed to one particular ostracod taxa, most species were either only found on the bottom or were in greater densities there. Angle (rock wall vs. bottom) was insignificant in constrained RDA analysis supporting that angle has limited influence on species composition in all fissures. The rock wall in fissures is regularly interrupted by uneven surfaces, clefts and shelves which increase surface area and can act as horizontal bottom. The rock wall is also covered in thick algae mats, as was previously mentioned, which appear to act as a shelter for invertebrates. These algae mats create a kind of biofilm substrate. The bottom acts in very much the same way and rather than being level and uniformly horizontal it is made up of large rock rubble where the sides of rocks act as vertical or near vertical substrate depending on how they are positioned. Therefore both rock walls and horizontal rock bottom provide heterogenous habitat patches rendering angle an unfit explanatory variable for patterns in species composition. As previously mentioned ostracods in Flosagjá still preferred bottom substrate. Regardless of substrate heterogeneity, detritus should always accumulate more readily on horizontal bottom while rock walls should stay relatively free of detritus. Ostracods are collectors that filter particle material from the water column and the significantly higher numbers of ostracods found on horizontal bottom in Flosagjá may be explained by greater food availability.

4.3 Huldugjá (The Hidden fissure)

During the project a new underground fissure was discovered in Þingvellir National park and was named Huldugjá (The Hidden fissure). This fissure is approximately 80 m long and 2 m wide and reaches a depth of 40 m making it among the deepest accesible fissures in Iceland (Figure. 4.2). Fissures likely penetrate deep underground to 7-8 km depth and there is reason to believe there are other accessible underground fissures within the uppermost hundreds of meters of the bedrock (Dr. Páll Einarsson, personal communication, January 19, 2015).

Five samples for qualitative analysis were collected in Huldugjá fissure. Two species were found: Copepod *Megacyclops viridis* (Jurine, 1820), which was also common in the open water fissures, and a groundwater amphipod *Crangonyx islandicus* (Svavarsson and Kristjánsson, 2006) that is endemic to Iceland. *C. islandicus* was seen walking around and looked healthy, while the *M.viridis* specimen appeared less healthy and had indications of deterioration of the tissues. This specimen may have been swept into the cave although there is also a slight possibility that sampling equipment was contaminated from earlier sampling procedures. This fissure may prove to be an interesting study site for future research on groundwater ecosystems and cave populations.
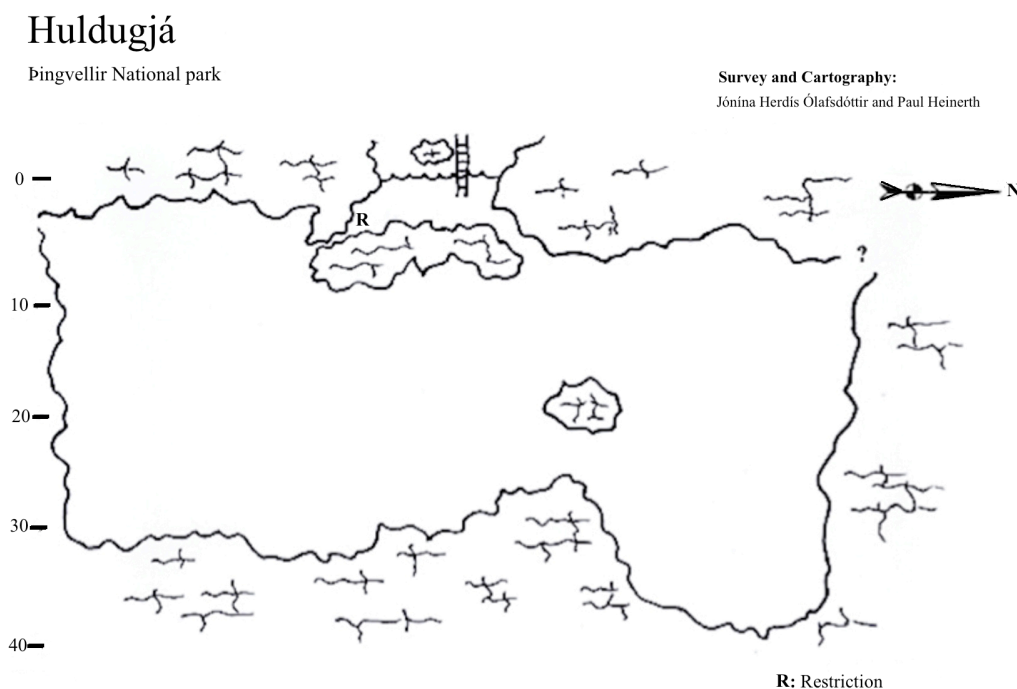

Figure 4.2. *A profile map of Huldugjá fissure (Þingvellir National park) showing depth (m) and restriction (R). North ->. Survey and cartography by Jónína Herdís Ólafsdóttir and Paul Heinerth.*

The systems focused on in this study are unique rift valley fissures. Such fissures are only accessible in two places in the world. Biofilm mats cover the entire substrate in fissures and seem to create favorable shelter for invertebrates. The fissures are also home to endemic species and therefore have a high conservation value. Future studies could focus on quantifying the environmental variables that shape the communities within these systems and could benefit from studying more fissures as well as adding additional sampling stations. Detailed identification of the flora is also still lacking. Fissures may also be suitable natural laboratories to study the effects of local/regional factors in shaping freshwater invertebrate assemblages, as they are stable systems with relatively simple community structure.

5. Conclusions

From a detailed invertebrate community study present in this thesis it was possible to map the diversity within three groundwater fissures in Iceland. There was a significant difference between assemblages in fissures in different geographical regions (Southwest vs. Northeast Iceland) regarding richness, density and diversity. Only chirononmids were found in similar densities in both geographical regions although assemblages varied greatly whereas *Arctopelopia* sp. was only found in NE Iceland and *D. zernyi* gr. was found in significantly greater densities in SW Iceland. Several environmental factors such as surface temperature, precipitation, altitude, latitude and nutrient input (National park vs. pasture land) may help explain the observed differences between fissures in different geographical regions.

Invertebrate communities were similar between the SW Iceland fissures, except for densities of cladocerans, which were significantly greater in Flosagjá. *Chydorus* sp. was found in high densities and is the most common cladoceran in Flosagjá while it was almost absent from Silfra. *A. werestschagini*, the second most common cladoceran in Flosagjá, was entirely absent from Silfra. *A. werestschagini* was documented for the first time in Iceland in 2014. Current may partly explain this difference in assemblages and therefore explain the observed variability between fissures. Crustaceans are associated with slow flowing water and were found in greater abundance in fissures with presumed slow current. Dominant chironomids in fissures with slow current were also species that are associated with lentic water, while the dominating chironomids in the presumed faster flowing Silfra are generally associated with lotic water.

Depth was found to be a significant explanatory variable in Stekkjagjá fissure while it was not a statistically significant environmental variable in fissures in SW Iceland. Rock wall vs. bottom was not found to significantly explain variability in assemblages in any of the three fissures studied. A few species were however found in significant differences in response to depth and rock wall vs. bottom. The chironomid species *O. frigidus* was found in significantly greater densities at shallow depth (4 m) in Flosagjá and *C. tibialis* was found in significantly greater densities at shallow depth (2 m) in

Stekkjagjá. Both of these species are characteristic of the littoral zone in lakes and may cope better with surf conditions in shallow water. Ostracods were found in significantly greater densities on bottom in Flosagjá. Suitable food resources may be more abundant at bottom habitats for ostracods, which primarily feed on detritus. Generally, taxa were fairly evenly distributed regardless of physical habitat. Biofilm mats cover the entire substrate in fissures and seem to provide shelter and a food resource for invertebrates, even at great depth. Meanwhile, clefts and shelves interrupt the rock walls, and the bottom is made from rock rubble, which often has vertical or near vertical parts depending on the position of rocks. These characteristics of the substrate seem to limit heterogeneity of the physical habitat and make it more homogenous. This may explain the even distribution of most taxa within fissures.

One species, *E. borealis* (Copeoda, Cyclopoida, Eucyclopinae), was found for the first time in Iceland. This species has previously been documented in Alaska.

References

Aðalsteinsson, Hákon., Gíslason, Gísli Már. 1998. *Áhrif landrænna þátta á líf í straumvötnum*. Náttúrufræðingurinn 68 (2), 97-112.

Alekseev, Victor R., Defaye, Danielle. 2011. Taxonomic differentiation and world geographical distribution of the *Eucyclops serrulatus* group (Copepoda, Cyclopoida, Eucyclopinae). In: Defaye, Daniella., Suárez-Morales, Eduardo., von Vaupel Klein, J. Carel (eds.). *Studies on Freshwater Copepod: A Volume in Honour of Bernard Dussart*. Brill publishers, Leiden and Boston. 556 pp.

Alekseev, Victor R., Dumont, Henri J., Pensaert, Jeannine., Baribwegure, Deo., Vanfleteren, Jaques R. 2005. *A redescription of Eucyclops serrulatus (Fischer, 1851) (Crustacea: Copepoda: Cyclopoida) and some related taxa, with a phylogeny of the E.serrulatus group*. Zoologica Scripta 35 (2), 123-147.

Alonso, Miguel. 1996. Fauna Iberica Vol.7: *Crustacea, Branchiopoda*. Museo Nacional de ciencias naturales consejo superior de investigaciones científicas, Madrid. 486 pp.

Baker, A.S., McLachlan, A.J. 1979. *Food preferences of Tanypodinae larvae (Diptera: Chironomidae)*. Hydrobiologia 62 (3), 283-288.

Batzer, Darold P., Baldwin, Andrew H. 2012. *Wetland habitats of North America: Ecology and conservation concerns*. University of California Press, Berkeley and Los Angeles. 341 pp.

Boesel, M.W. 1983. *A Review of the genus Cricotopus in Ohio, with a key to adults of species of the Northeastern United States (Diptera, Chironomidae)*. Ohio Journal of Science 83 (3), 74-90.

Bohonak, Andrew J., Jenkins, David G., 2003. *Ecological and evolutionary significance of dispersal by freshwater invertebrates*. Ecology Letters 6, 783-796.

Bonilla, Sylvia. 2005. *Benthic and planktonic algal communities in a high Arctic lake: Pigment structure and contrasting responses to nutrient enrichment*. Journal of Phycology 41, 1120-1130.

Boothroyd, Ian. 2005. *Eumadicole midges- film stars of the freshwater world*. Water and Atmosphere 13 (1), 24-25.

Bottazzi, Elisa., Bruno, Maria Cristina., Pieri, Valentina., Di Sabatino, Antonio., Silveri, Luana., Carolli, Mauro., Rossetti, Giampaolo. 2011. *Spatial and seasonal distribution of invertebrates in Northern Apennine rheocrene springs*. Journal of Limnology 70 (1), 77-92.

Brittain, John E., Bogen, Jim., Khokhlova, Ludmila G., Melvold, Kjetil., Stenina, Angelina S., Gíslason, Gísli M., Brors, Sturla., Kochanov, Sergej K., Ponomarev, Vasily I., Jensen, Arne J., Kokovkin, Alexander V., Petterson, Lars-Evan. 2009. Arctic rivers. In Tockner, Klement., Uehlinger, Urs and Robinson, Christopher T (eds.). *Rivers of Europe 1ˢᵗ. Edition*. Academic Press, Amsterdam.

Cantonati, M., R. Gerecke., E. Bertuzzi. 2006. *Springs of the Alps- sensitive ecosystems to environmental change: from biodiversity assessments to long-term studies*. Hydrobiologia 562, 59–96.

Chorowicz, Jena. 2005. *The East African rift system*. Journal of African Earth Sciences 43, 379-410.

Christoffersen, Kirsten S., Jeppesen, Erik., Moorhead, Daryl L., Tranvik, Lars J. 2008. Food-web relationships and community structures in high latitude lakes. In: Vincent, Warwick F. and Laybourn-Parry, Johanna (eds.). *Polar Lakes and Rivers*. Oxford University Press, Oxford. 346 pp.

Craig, Douglas A. 2003. *Geomorphology, development of running water habitats and evolution of black flies on Polynesian islands*. Bioscience 53 (11), 1079-1093.

Cranston, P.S. 1982. *A key to the larvae of the British Orthocladinae (Chironomidae)*. The Freshwater Biological Association Scientific Publication No. 45, Ambleside, Cumbria. 152 pp.

Croce, Roberta., Van Amerongen, Herbert. 2014. *Natural strategies for photosynthetic light harvesting*. Nature Chemical Biology (10), 492-501.

Dodds, Walter K. 2002. *Freshwater ecology: Concepts and environmental applications*. Academic Press, San Diego. 569 pp.

Dumnicka, Elzbieta., Galas, Joanna., Koperski, Pawel. 2007. *Benthic invertebrates in Karst springs: Does substratum or location define communities?* International Review of Hydrobiology 92 (4-5), 452-464.

Garðarsson, Arnþór., Einarsson, Árni., Gíslason, Gísli Már., Hrafnsdóttir, Thóra., Ingvason, Haraldur R., Jónsson, Erlendur, Ólafsson, Jón S. 2004. *Population fluctuations of chironomids and simuliid Diptera at Myvatn in 1977-1996*. Aquatic Ecology 38, 209-217.

Giller, Paul S., Malmqvist, Björn. 1998. *The biology of streams and rivers*. Oxford University Press, New York. 296 pp.

Gíslason, Gísli Már. 2005. *Origin of freshwater fauna of the North-Atlantic islands: present distribution in relation to climate and possible migration routes*. Verhandlungen des Internationalen verein Limnologie 29, 198-203.

Gíslason, Gísli Már., Ólafsson, Jón., Aðalsteinsson, Hákon. 1998. *Animal communities in Icelandic rivers in relation to catchment characteristics and water chemistry. Preliminary results*. Nordic Hydrology 29, 129-148.

Giudicelli, Jean., Bournard, Michel. 1997. Invertebrate biodiversity in land-inland water ecotonal habitats. In: Lachavan J.B. and Raphaelle, Juge (eds.). *Biodiversity in Land-Inland water ecotones*. UNESCO, Paris and The Parthenon Publishing Group, New York. 326 pp.

Google Earth 7.1.2.2041. 2012. Iceland: 66°02´20.17"N, 16°34´36.73"W, elevation 20m and 64°15´25.80"N, 21°07´08.53"W, elevation 114m. [Viewed 8 May 2015].

Govoni, Dan. 2011. *Influences of spring type, physicochemical factors, and longitudinal changes in freshwater spring invertebrate ecology* (Magister scientiarium thesis). Hólar University College. 61 pp.

Guðjónsson, Sigurður., Guðbergsson, Guðni. 2003. *Verndun búsvæða í fersku vatni á Íslandi: Greinargerð vegna náttúruverndaráætlunar*. Veiðimálastofnun, Reykjavík. 21 pp.

Guðmundsson, Ágúst. 1986. *Sprungurnar á Þingvöllum og myndun þeirra*. Náttúrufræðingurinn 56 (1), 1-18.

Guðmundsson, Kjartan. 2014. *Environmental microbial diversity and anthropogenic impact on Lake Thingvallavatn basin* (Magister Scientiarium thesis). University of Iceland, Reykjavik. 97 pp.

Hallgrímsson, Helgi. 2007. *Þörungtal: Skrá yfir vatna og landþörunga á Íslandi samkvæmt heimildum*. Fjölrit Náttúrufræðistofnunar 48. 94 pp.

Hallgrímsson, Helgi. 1973. *Heimur hins ferska vatns*. Týli 3, 19-28.

Hansson, Lars-Anders., Travik, Lars J. 2003. *Food webs in sub-Antarctic lakes: a stable isotope approach*. Polar Biology 26, 783-788.

Hjartardóttir, Á.R., Einarsson, P., Bramham, E., Wright, T.J. 2012. *The Krafla fissure swarm, Iceland and its formation by rifting events*. Bulletin of Volcanology 74 (9), 2139-2153.

Hjartardóttir, Ásta Rut. 2013. *Fissure swarms of the Northern Volcanic Rift zone, Iceland* (Philosophiae Doctor thesis). University of Iceland. 138 pp.

Hogg, Ian D., Williams, D. Dudley. 1996. *Response of stream invertebrates to a global warming thermal regime: An ecosystem-level manipulation*. Ecology 77 (2), 395-407.

Hrafnsdóttir, Þóra. 2005. Diptera 2 (Chironomidae). *The Zoology of Iceland III, 48b*. 1-169.

Hynes, H.B.N. 1970. *The ecology of running waters*. Liverpool University Press. Inc. New York, London. 555 pp.

Jacobsen, Dean., Schultz, Rikke., Encalada, Andrea. 1997. *Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude*. Freshwater Biology 38, 247-261.

Jóhannesson, Haukur., Sæmundsson, Kristján. 2009. *Geological map of Iceland 1:500.000 Bedrock geology*. Náttúrufræðistofnun Íslands, Garðarbær.

Jonasz, Miroslaw and Fournier, Georges. 2007. *Light scattering by particles in water: Theoretical and Experimental foundations*. Elsevier Inc., London. 714 pp.

Jonsson, Bror., Skúlason. Skúli., Snorrason, Snorri., Sandlund, Odd Terje., Malmquist, Hilmar J., Jónasson, Pétur M. 1988. *Life history variation of polymorphic Arctic charr (Salvelinus alpinus) in Thingvallavatn, Iceland*. Canadian Journal of Fisheries and Aquatic Science. 45, 1537-1547.

Jónsson, Gunnar Steinn., Gunnarsson, Karl., Jónasson, Pétur M. 2011. Life on the lake bottom. In: Jónasson P.M. and Hersteinsson. P (eds.). *A unique world evolving Thingvallavatn: A world heritage site*. Opna Publishing, Reykjavík. 326 pp.

Kornobis, Etienne., Pálsson, Snæbjörn., Kristjánsson, Bjarni K., Svavarsson, Jörundur. 2010a. *Molecular evidence of the survival of subterranean amphipods (Arthropoda) during ice age underneath glaciers in Iceland*. Molecular Ecology 19, 2516-2530.

Kornobis, Etienne., Pálsson, Snæbjörn., Sidorov, Dmitry A., Holsinger, John A., Kristjánsson, Bjarni K. 2010b. *Molecular taxonomy and phylogenetic affinities of the groundwater amphipods Crangonyx islandicus and Crymostygius thingvallensis*. Molecular Phylogenetics and Evolution 58, 527-539.

Kristjánsson, Bjarni Kristófer., Svavarsson, Jörundur. 2007a. *Grunnvatnsmarflær á Íslandi*. Náttúrufræðingurinn 76 (1-2), 22-28.

Kristjánsson, Bjarni Kristófer., Svavarsson, Jörundur. 2007b. *Subglacial refugia in Iceland enabled groundwater amphipods to survive glaciations*. The American Naturalist, 170 (2), 292-296.

Legendre.,P., Gauthier, Olivier. 2014. *Statistical methods for temporal and space-time analysis of community composition data*. Proceedings of the Royal Society 281 (1778), 1-9.

Leibold, Mathew A., Economo, Evan P., Peres-Neto, Pedro. 2010. *Metacommunity phylogenetics: separating the roles of environmental filters and historical biogeography*. Ecology Letters 13, 1290–1299.

Leibold, Mathew A, Holyoak, M., Mouquet, N., Amarasekare. P., Chase. J.M., Hoopes. M.F., Holt. R.D., Shurin. J.B., Law.R., Tilman. D., Loreau. M., Gonzales. A. 2004. *The metacommunity concept: a framework for multi-scale community ecology*. Ecology Letters 7, 601-613.

Lencioni, Valeria. 2004. *Survival strategies of freshwater insects in cold environments*. Journal of Limnology 63 (Suppl.1), 45-55.

Lencioni, Valeria., Marziali, Laura., Rossaro, Bruno. 2012. *Chironomids as bioindicators of environmental quality in mountain spring*s. Freshwater Science 31 (2), 525-541.

Lindegaard, Claus. 1992. Zoobenthos ecology of Thingvallavatn: vertical distribution, abudance, population dynamics and production. Oikos 64, 257-304.

Lods-Crozet, B., Lencioni, V., Ólafsson, J.S., Snook, D.L., Velle, G., Brittain, J.E., Castella, E., Rossaro, B. 2001. *Chironomid (Diptera: Chironomidae) communities in six European glacier-fed streams*. Freshwater Biology 46, 1791-1809.

Logue, Jurg B., Mouquet, Nicolas., Peter, Hannes., Hillebrand, Helmut. 2011. *Empirical approaches to metacommunities: a review and comparison with theories*. Trends in Ecology and Evolution, 26 (9), 1-10.

MacArthur, Robert H., Wilson, Edward O. 1963. *An equilibrium theory of insular zoogeography*. Evolution 17 (4), 373-387.

Maclennan, J., Jull, M., McKenzie, D., Slater, L., Grönvold, K. 2002. *The link between volcanism and deglaciation in Iceland*. Geochemistry, Geophysics, Geosystems, an Electric Journal of the Earth Sciences 3 (11), 1525-2027.

Magurran, Anne M. 2005. *Biological diversity*. Current Biology 15 (4), 116-118.

Malmquist, Hilmar J. 2012. *Vöktun á lífríki og vatnsgæðum Þingvallavatns: Yfirlit yfir fimm fyrstu vöktunarárin 2007-2011 og samanburður við eldri gögn*. Fjölrit nr. 3. Náttúrufræðistofa Kópavogs. 67 pp.

Malmquist, Hilmar J., Ólafsson, Jón S., Guðbergsson, Guðni., Antonsson, Þórólfur., Skúlason, Skúli., Snorrason, Sigurður S. 2003. *Vistfræði- og verndarflokkun íslenskra stöðuvatna, verkefni unnið fyrir rammaáætlun um nýtingu vatnsafls*. Náttúrufræðistofa Kópavogs. 33 pp.

Malmquist, Hilmar J., Antonsson, Thórólfur., Gudbergsson, Gudni., Skúlason, Skúli.,Snorrason. Sigurður S. 2000. *Biodiversity of macroinvertebrates on rocky substrate in the surf zone of Icelandic lakes*. Verhandlungen des Internationalen Verein Limnologie 27, 121-127.

Marshak, Stephen. 2008. *Earth: Portrait of a planet, 3rd edition*. W.W. Norton and Company. 880 pp.

Meisch, Claude. 2000. *Freshwater Ostracoda of Western and Central Europe*. Spektrum Akademischer Verlag, Heidelberg, Berlin. 522 pp.

Novichkova, Anna., Chertoprud, Elena., Gíslason, Gísli Már. 2014. *Freshwater Crustacea (Cladocera, Copepoda) of Iceland: taxonomy, ecology and biogeography*. Polar Biology 37, 1755-1767.

Nyman, Marjut T., Korhola, Atte A. 2005. *Chironomid-based classification of lakes in western Lapland*. Boreal Environment Research 10, 239-254.

Ohtsuka, Taisuke., Kudoh, Sakae., Imura, Satoshi., Ohtani, Shuji. 2006. *Diatoms composing benthic microbial mats in freshwater lakes of Skarvsnes ice-free area, East Antarctica*. Polar Bioscience 20, 113-130.

Oliver, D.R. 1971. *Life history of the Chironomidae*. Annual Review of Entomology 16, 211-230.

Ólafsson, Jón. 1992. *Chemical characteristics and trace elements of Thingvallavatn*. Oikos 64, 151–161.

Petersen, Robert C., Gíslason, Gísli Már., Vought, Lena B.M. 1995. Rivers of the Nordic countries. In: C.E. Cushing., K.W. Cummins and G.W. Minshall (eds.). *Ecosystems of the world* (22). Elsevier, Amsterdam, 296-341.

Pinder, L.C.V. 1986. *Biology of freshwater chironomidae*. Annual Review of Entomology 31, 1-23.

Power, Michael., Reist, James D., Dempson, J. Brian. 2008. Fish in high latitude Arctic lakes. In: Vincent, Warwick F. and Laybourn-Parry, Johanna (eds.). *Polar Lakes and Rivers*. Oxford University Press, Oxford. 346 pp.

Rautio, Milla., Bayly, Ian A..E., Gibson, John A.E., Nyman, Marjut. 2008. Zooplankton and zoobenthos in high latitude water bodies. In: Vincent, Warwick F. and Laybourn-Parry, Johanna (eds.). *Polar Lakes and Rivers*. Oxford University Press, Oxford. 346 pp.

Rautio, Milla., Dufresne, France., Laurion, Isabelle., Bonilla, Sylvia., Vincent, Warwick F., Christoffersen, Kirsten S. 2006. *Shallow freshwater ecosystems of the circumpolar Arctic*. Ecoscience 18 (3), 204-222.

Rautio, Milla., Vincent, Warwick F. 2007. *Isotopic analysis of the sources of organic carbon for zooplankton in shallow subarctic and arctic waters*. Ecography 30, 77-87.

Richardson, John S., Jackson, Michael J. 2002. Aquatic invertebrates. In: Perrow, Martin R., Davy, Anthony J. (eds.) *Handbook of ecological restoration*. Cambridge University Press, New York. 464 pp.

Sæmundsson, Kristján. 2011. Thingvallavatn catchment- geology. In: Jónasson P.M. and Hersteinsson. P. (eds.) *A unique world evolving Thingvallavatn: A world heritage site*. Opna publishing, Reykjavík. 326 pp.

Saether, Ole A. 1979. *Chironomid communities as water quality indicat*ors. Holarctic Ecology 2, 65-74.

Scher, O., Defaue, D., Korovchinsky. N.M., Thiéry. A. 2000. *The Crustacean fauna (Branchiopoda, Copepoda) of shallow freshwater bodies in Iceland*. Vestnik Zoologii 34 (6), 11-25.

Schmid, P.E. 1993. A key to the larval chironomidae and their instars from Austrian Danube region streams and rivers, Part 1. In: *Waasser und abwasser, supplementband 3/93*. Federal Institute for Water Quality, Wien. 513 pp.

Shurin, Jonathan B. 2000. *Dispersal limitation, invasion resistance and the structure of pond zooplankton communities*. Ecology 81 (11), 3074-3086.

Sigurðsson, Freysteinn., Sigbjarnason, Guttormur. 2011. Groundwater inflow. In: Jónasson P.M. and Hersteinsson. P (eds.) *A unique world evolving Thingvallavatn: A world heritage site*. Opna Publishing, Reykjavík. 326 pp.

Sinton, John., Grönvald, Karl., Sæmundsson. Karl. 2005. *Postglacial eruptive history of the Western Volcanic Zone, Iceland*. Geochemistry, Geophysics, Geosystems 6 (12), 1525-2027.

Snorrason, Sigurður S., Malmquist, Hilmar J., Skúlason, Skúli. 2011. Arctic charr. In: Jónasson P.M. and Hersteinsson. P (eds.) *A unique world evolving Thingvallavatn: A world heritage site*. Opna publishing, Reykjavík. 326 pp.

Spechler, Rick.M., Schiffer, Donna M. 1995. *Springs of Florida*. U.S. Geological Survey Fact Sheet, Tallahassee, Florida. 2 pp.

Spellerberg, Ian F and Fedor, Peter J. 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' Index. *Global Ecology & Biogeography* 12, 177–179.

Springer, Abraham E., Stevens. Lawrence E. 2008. *Spheres of discharge of springs*. Hydrogeology Journal 17 (1), 83-93.

Stenhouse, Steven A., Bean, Caitlin E., Chesney, Willima R., Pisano, Mark S. 2012. *Water temperature thresholds for coho salmon in a spring-fed river, Siskiyou County, Califronia*. California Fish and Game 98 (1), 19-37.

Svavarsson, Jörundur., Kristjánsson, Bjarni K. 2006. <u>*Crangonyx islandicus sp. nov.*</u>*, a subterranean freshwater amphipod (Crustacea, Amphipoda, Crangonyctidae) from springs in lava fields in Iceland*. Zootaxa 1365, 1-17.

Thordarson, T., Larsen. G. 2007. *Volcanism in Iceland in historical time: Volcano types, eruption styles and eruptive history*. Journal of Geodynamics 43(1), 118-152.

Thors, Kjartan. 1990. Bedrock, sediments and faults in Thingvallavatn. In: Jónasson, Pétur M. (ed.), *Thingvallavatn*. The Icelandic Literature Society, Copenhagen. 437 pp.

Triantis, Kostas A. 2011. *Symposium summary: Island biogeography*. Frontiers of Biogeography, 3 (1), 21-22.

Van der Kamp, Garth. 1995. *The Hydrogeology of springs in relation to the biodiversity of spring fauna: A review*. Journal of the Kansas Entomological Society 68 (2), 4-17.

Vannote. Robin L., Sweeney. Bernard W. 1980. *Geographic analysis of thermal equilibria: A conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities*. The American Naturalist 115(5), 667-695.

Þorbjörnsson, Jóhann Garðar. 2013. *Comparison of two methods for sampling invertebrates on submerged vertical walls with diving* (Baccalaureus Scientiarium project). University of Iceland. 26 pp.

Þorbjörnsson, Jóhann Garðar. 2015. *Impacts of scuba divers in the Silfra groundwater fissure: Ecological disturbance and management* (Magister scientiarium thesis). Hólar University College. 83 pp.