Stream food webs in a changing climate: the impacts of warming on Icelandic freshwaters

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1 Abstract

Climate change and the accompanying increase in global surface temperatures pose a major threat to freshwater ecosystems, especially at high latitudes where warming is predicted to be particularly rapid. To date many aspects of how rising temperatures can impact fresh waters remain unknown. Information about temperature effects on the level of communities, food webs, ecosystems is especially scarce. The few studies focusing on higher levels of organisation have used either laboratory microcosm experiments, which can lack realism or space-for-time substitution across large ranges of latitude, which can be confounded by bio-geographical effects. This study aimed to overcome these shortcomings by using a “natural experiment” in a set of 16 geothermally heated streams in the Hengill area, South-West Iceland, with water temperatures ranging from 4ºC to 49ºC (mean temperature). Data were analysed for two seasons, August 2008 and April 2009.

The principal goal of this study was to assess the effects of temperature on the structure and functioning of food webs. Additionally the persistence of the community structures along the temperature gradient was examined through time (comparison of previously collected data in August 2004 and August 2008).

Abundances of cold-stenotherm species decreased whereas those of eurythermal species increased with increasing temperatures leading to knock-on effects on abundances of other species. Species community overlap between streams declined as temperature difference between streams increased. The persistence of species composition through time was weakened at the extremes of the temperature gradient. Food webs showed a clear size structuring in analyses of trivariate food webs, abundance and biomass size spectra. Analysis of connectance, complexity, mean link length, mean 2-span, mean community span and slopes and intercepts of linear regressions fitted to the trivariate foods or size spectra revealed the impact of temperature change on freshwater ecosystems.

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3 Table of contents

4 List of figures

5 List of tables

6 General introduction

6.1 Climate Change

The reality of climate change is now widely accepted, and has been confirmed by observations of numerous wide-ranging consequences (IPCC, 2007). The earth has entered a new era named the Anthropocene(Crutzen, 2002; Rockström *et al.*, 2009) in which environmental changes are not solely driven by global geophysical processes, but are heavily influenced by the activity of humankind (Steffen *et al.*, 2011). Since the industrial revolution in the 1850s emissions and anthropogenic influences have increased in manners that lead to a change of the global climate (IPCC, 2007; Steffen *et al.*, 2011). The characteristics of this climate change are multifaceted including sea level rise, increase in extreme weather events, decrease of ice and snow covers and the increase in global surface temperatures (IPCC, 2007). According to the Special Report on Emissions Scenarios by the Intergovernmental Panel of Climate Change (IPCC) a warming of 0.2°C per decade is predicted for the next two decades (IPCC, 2000). The miscellaneous possible effects of climate change on the environment have been the subject of numerous studies (e.g. Prowse *et al.*, 2006; Thomas *et al.*, 2004; Walther *et al.*, 2002). Most research to date has focussed on the lower levels of biological organisation (e.g. individuals to populations) whereas relatively few studies have examined the effect of warming on multispecies systems, such as food webs (but see Dossena *et al.*, 2012; Durance & Ormerod, 2007; Jacobsen, Schultz & Encalada, 1997; Petchey *et al.*, 1999; Yvon-Durocher *et al.*, 2010). At the level of individual changes in phenology, species range shifts, invasion and extinctions of species have been observed (Parmesan, 2006; Parmesan & Yohe, 2003; Walther *et al.*, 2002)

Most of the studies addressing the effects of warming on multispecies systems are based on micro or mesocosm experiments (Dossena *et al.*, 2012; Petchey *et al.*, 1999; Yvon-Durocher *et al.*, 2010). These can lack realism due to the tightly controlled conditions, but one reason restraining these experiments to mesocosms might be theproblems which are inherent in artificial heating on a larger scale. Other studies on effects of changing temperatures have applied time-for-space replacements and therefore tend to be temporally (Durance *et al.*, 2007) or spatially (Jacobsen *et al.*, 1997) confounded. The studies presented here aim to overcome these shortcomings by taking advantage of an existing "natural experiment", consisting of a set of 16 geothermally heated streams in the Hengill area, South-West Iceland, with water temperatures ranging from 4ºC to 49ºC (mean summer and spring temperature).

6.1 Temperature

Temperature has profound effects on all levels of organisation from individuals to communities. Temperature affects the development and growth rates of individual organisms, with most ectotherms growing to smaller size at maturity in a shorter amount of time (Angilletta Jr & Dunham, 2003; Atkinson, 1994, 1995; Ray, 1960). This also leads to a specific distribution of size classes, with larger organisms generally present in colder regions (Ashton, 2002; Ashton, Tracy & de Queiroz, 2000; Bergmann, 1847; Ray, 1960) and warming tending to favour smaller organisms (Daufresne, Lengfellner & Sommer, 2009; Winder, Reuter & Schladow, 2009). This should lead to alterations in species abundance with increasing temperature and potential knock-on effects for predator-prey dynamics (Power, 1992). Global warming can therefore lead to changes in the size spectra of communities, with implications for energy flow through the food web (Dossena *et al.*, 2012; Yvon-Durocher *et al.*, 2011).

Temperature not only affects the size distribution, but also the species distribution, as organisms have species-specific temperature optima and tolerances. Thus, global warming facilitates species range shifts as they are pushed beyond their normal temperature range (Chen *et al.*, 2011; Chevaldonné & Lejeusne, 2003; Root *et al.*, 2003; Walther *et al.*, 2002). Mobile species may move to higher latitudes or altitudes to maintain their thermal optimum (Hickling *et al.*, 2006). Cold-stenotherm species are more likely to be affected by warming as their range of temperature tolerance is narrow, which may even lead to species extinctions (Chevaldonné *et al.*, 2003; Hering *et al.*, 2009). Eurytherms are less affected by warming and warm-stenothermal species can potentially be favoured and invade under the premise of a suitable species pool and no dispersal constraints (Dukes & Mooney, 1999; Francour *et al.*, 1994; Walther *et al.*, 2002).

Effects of warming can be filtered through a community as species are not isolated but interact with each other. Shifts in abundances and the invasion or extinction of a species can result in dramatic changes in community structure via top-down or bottom-up effects (Polis & Holt, 1992; Power, 1992). Consumers have the ability to control abundance of their prey species, which would be defined as a top-down effect (Power, 1992). Examples of top-down effects in the literature range from fish controlling zooplankton and thus phytoplankton populations in lakes (Carpenter, Kitchell & Hodgson, 1985; Carpenter *et al.*, 1987) and sea otters controlling sea urchin populations and thus kelp beds in coastal waters (Estes & Palmisano, 1974). Bottom-up effects can often be observed when nutrient limitation affects primary production, with knock-on effects on the abundance of species at higher trophic levels (Power, 1992). Thus, changes to the abundance or distribution of certain key species, may have the potential to alter community structure through trophic cascades of top-down or bottom-up control (Power, 1992).

The interactions between organisms are also likely to be affected by changes in temperature: handling times of prey and ingestion efficiencies generally decrease with increasing temperatures, whereas attack rates normally increase (Dreisig, 1981; McCoull, Swain & Barnes, 1998; Rall *et al.*, 2010; Thompson, 1978; Vucic-Pestic *et al.*, 2011). The relationships are often hump-shaped over wide temperature ranges as thermal tolerances are reached (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011). Metabolic rate increases with temperature, while smaller organisms have a higher mass-specific metabolic rate (Brown *et al.*, 2004). This leads to increased energetic demands in warmer environments and the need for increased rates of feeding and energy acquisition (Brown *et al.*, 2004; Hairston Jr. & Hairston Sr., 1993). If resources are insufficient to meet these higher energy demands, this may lead to predator starvation in warmer environments (Rall *et al.*, 2010) or greater suppression of resources through increased top-down control (O’Gorman *et al.*, in press)

Thus, warming may lead to alterations in species composition, abundance, body size and energy transfer, which may cause communities exposed to rising temperatures to become less persistent through time. Here, persistence is taken to mean ”a measure of the ability of a system to maintain itself through time” (Loreau *et al.*, 2002). There is a dearth of studies investigating the impact of warming on the temporal stability of natural communities and this is a short-coming that urgently needs to be addressed given the implications for conservation of biological diversity and provisioning of ecosystem services.

6.2 Food web theory

Given the implications of rising temperature for predator-prey interactions discussed above (Hairston Jr. *et al.*, 1993; O'Gorman *et al.*, in press; Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011), it is clear that food web structure may be altered by global warming. The construction of a food web opens up the possibility to explore the energetics and dynamics of the network formed by individual organisms (Belgrano *et al.*, 2005). Aquatic ecosystems are especially suited for exploration of food web properties as they tend to be size-structured, with most consumers feeding on smaller resources (Woodward & Hildrew, 2002). Aquatic environments are also more likely to be influenced by changing temperatures than terrestrial ecosystems due to the greater temperature dependence of respiration rates in aquatic systems (Yvon-Durocher *et al.*, 2012).

Early constructions of food webs were relatively simple, in terms of the number of species (nodes) and links they contained, and most were qualitative, binary "connectance webs" (e.g. catalogues in: Cohen, 1977; Pimm, 1980; Woodward, Speirs & Hildrew, 2005b). The taxonomic resolution of these food webs was relatively low and species were often lumped together in groups of taxonomically or functionally related species (Briand & Cohen, 1984; Schmid-Araya *et al.*, 2002). From the 1980's onwards food web descriptions became better resolved, more complete and correspondingly more complex (Hildrew, Townsend & Hasham, 1985; Polis, 1991; Tavares-Cromar & Williams, 1996). With these developments it became evident that complex food webs were the rule rather than the exception (Berlow *et al.*, 2004; McCann, 2000; Polis & Strong, 1996; Woodward *et al.*, 2005b).This is in contrast to theoretical modelling from the 1970's and early1980's,where simple food webs were regarded as being more stable than complex ones (May, 1972, 1973; Pimm, 1982).These investigations were based on randomly assembled model food webs, however, and it was acknowledged that natural food webs employ non-random structures to facilitate stability with increasing complexity (May, 1972). With the appearance of a growing number of complex food webs due to improved survey techniques a lively discussion on the relationship between complexity and stability arose (Pimm, 1984), and more recent food web models demonstrated how complexity could enhance stability (Pimm, 1984, McCann, 2000; Montoya, Pimm & Sole, 2006), by revisiting some of the conceptual models proposed decades earlier (Elton, 1946; MacArthur, 1955) and parameterising them with empirical patterns of body mass and trophic interactions.

Recently different ways to incorporate body mass and abundance data into food webs have been developed to provide a more complete understanding of the energy flow through a system. So-called trivariate food web plots illustrate the relationship between mean species body mass (Log_{10} M), abundance (Log_{10} N) and trophic interactions. In a trivariate food web, each node represents a species and these are linked in the network via their feeding interactions (Cohen, Jonsson & Carpenter, 2003; Jonsson, Cohen & Carpenter, 2005; Layer *et al.*, 2010; McLaughlin, Jonsson & Emmerson, 2010; O'Gorman & Emmerson, 2010). Trivariate webs generally reflect the size dependence of food web structure in aquatic systems through the ubiquity of small, very abundant basal taxa (e.g. diatoms), and large, rare top taxa (e.g. fish) (Cohen *et al.*, 2009). Trivariate food webs offer the possibility to calculate a wide range of food web statistics ranging from univariate to trivariate measures (Jonsson *et al.*, 2005). Univariate measures include the number of nodes S (i.e. species richness), the number of links L, *connectance* C (i.e. total number of realised links divided by the number of possible links $C = L/S^2$ after Martinez (1991)) and *complexity* ($SC=L/S$)(May, 1972, 1973;

Pimm, 1982; Woodward *et al.*, 2005a). Trivariate measures include the *mean link length*, *mean 2-span*and *community span* capturing the flow of energy from resources to consumers, through an intermediate source (Cohen *et al.*, 2009; Woodward *et al.*, in press). To date, there has been no exploration of temperature impacts on the structure of trivariate food webs in a natural setting. Such a study would greatly enhance our understanding of how future climate change scenarios may erode the stabilising structures of complex communities.

The slope of a linear regression fitted to a trivariate food web plot can give information on the energy transfer within the community, when combined with the intercept of the relationship with the smallest and largest organisms in the community (Yvon-Durocher *et al.*, 2011). In a community, that shares a common resource, abundance (N) typically scales with body mass (M) as $M^{-0.75}$(Brown *et al.*, 2004; Jennings & Mackinson, 2003). Temperature can have profound effects on abundance as well as body size, as described above, and therefore potentially change the body mass - abundance scaling within the community. This also affects the biomass distribution, which is often described as the trophic biomass pyramid. The base of the pyramid is built by a large number of small producers with subsequent trophic levels decreasing in biomass to cumulate at the tip of the pyramid with large rare species as the apex predators (Elton, 1927; Gasol, Giorgio & Duarte, 1997). According to Lindeman (1942) and Slobodkin (1961), approximately 10% of energy is transferred between each trophic level (although this number has been shown to vary between 0% and 25%, with a mean of approximately 10% (Pauly & Christensen, 1995)). This energy transfer efficiency is also affected by temperature as abundance and body mass changes. The different scenarios for alterations to transfer efficiency within the body mass - abundance spectrum are summarised in Figure 1:

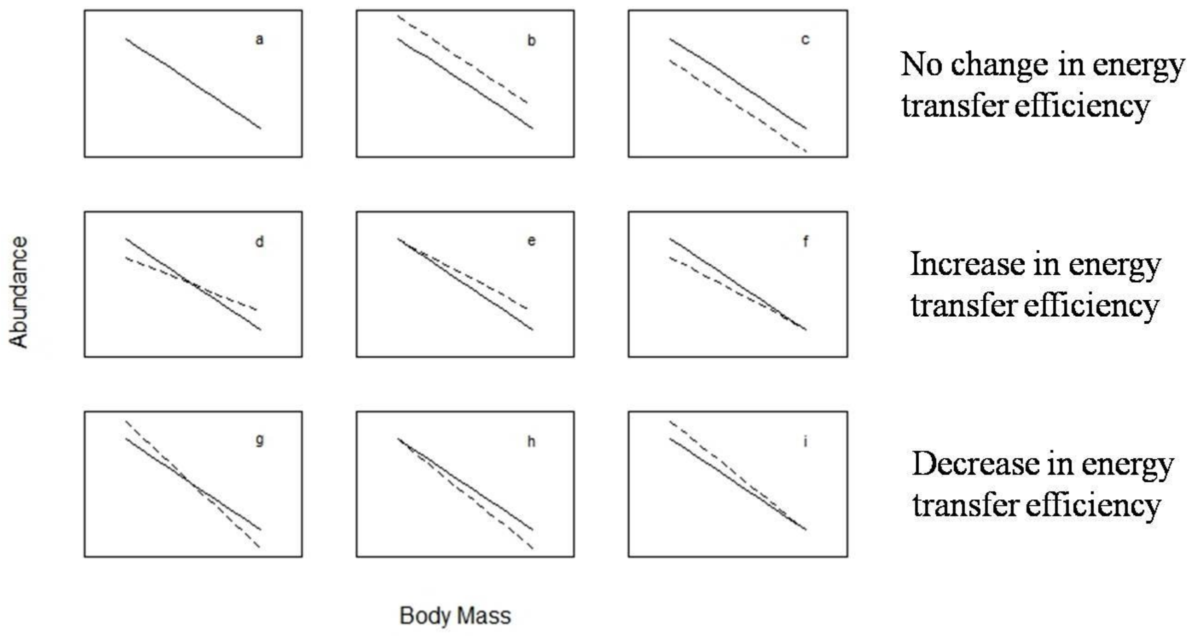

Figure 1 Schematic figure of likely scenarios of change is body mass – abundance scaling. Solid lines represent the reference condition as described in panel (a), dotted lines represent the possible changes of slopes and intercepts combined affecting the energy transfer efficiency.

Panel (a) represents the reference scenario with energy flowing from small abundant organisms to larger rare organisms. Panels (b) and (c) show no change in slope due to parallel alterations in the intercept with the smallest and largest organisms and thus no change in energy transfer efficiency. In scenario (b), resource biomass increases, but this also supports an increased biomass of consumers, maintaining the flow of energy through the system. In scenario (c), resource biomass decreases, but this leads to a parallel decline in consumer biomass, again maintaining the transfer of energy. Panels (d),(e) and (f) represent an increase in energy transfer efficiency. In scenario (d), resource biomass decreases, while consumer biomass increases: fewer resources maintain an increased biomass of consumers representing an increase in energy transfer efficiency. In scenario (e) resource biomass remains on a constant level, but supports and increased consumer biomass. Consumer biomass remains on a constant level in scenario (f), but consumers can maintain their energy levels, being supported by fewer resources. Panels (g), (h) and (i) represent scenarios with a decrease in energy transfer efficiency. In scenario (g) an increased biomass of resources supports a diminished consumer biomass. Resource biomass remains constant in scenario (h) as consumer biomass decreases i.e. fewer consumers are supported by the same amount of energy. In scenario (i) resource biomass increases as consumer biomass remains the same.

The scenarios reflect the variety of possible effects of temperature on mass - abundance scaling and incidental implications for the trophic transfer of energy.

6.3 **Body size**

The determination of body size (i.e. body mass) provides a powerful tool to incorporate several ecological traits, which correlate with body size, into a single measurement. The body size distribution of a community can reveal information on growth rates, productivity, abundances, spatial niche distributions and relationships within an ecological network (Woodward *et al.*, 2005a).The body size distribution within a species (i.e. node) of a food web constrains the ability to ingest certain food types/species and therefore generally the occurrence of feeding links and more specifically the appearances of ontogenetic shifts in the diet (Woodward *et al.*, 2005a). At the individual level, body size influences a variety of biological traits including physiology, behaviour and life history (Brown *et al.*, 2004; Peters, 1983; Woodward *et al.*, 2005a). According to the metabolic theory of ecology (MTE),the metabolic rate of an individual organism is constrained by both its body size and the temperature of the environment (Brown *et al.*, 2004). Thus, body size determines on one hand the structure and dynamics of a food web, whilst on the other it constrains individuals (and by extension the ecosystem) metabolism.

Community ecology research has seen a pre-occupation with taxonomic approaches through the decades, a case of tunnel-vision sometimes referred to as the "curse of the Latin binomial" (Raffaelli, 2007). It is now recognised that condensing the large range of variability associated with individuals of a given species into an average value (e.g. average species body mass) may lead to over-simplification and the possibility to overlook key trends. Thus, a different viewpoint to analysing structure and energy flow in a community is the individual organism or sized-based approach, rather than the taxonomic or community ecology approaches described above (Ings *et al.*, 2009). To date, very few studies have looked at changes in size structure with a combined taxonomic and size-based approach (Ings *et al.*, 2009). This highlights the need for a broader perspective in analyses of community size structure, particularly with regard to potential global warming impacts.

In so-called *size spectra* or *individual size distributions*, nodes represent size classes rather than species (Kerr & Dickie, 2001; Petchey & Belgrano, 2010; Reuman *et al.*, 2008). This method is widely used in fisheries studies to assess the ecosystem status and distance to a reference status (Jennings & Blanchard, 2004; Shin *et al.*, 2005). The spectrum of body masses is evenly divided up into $\log_{10}$ size classes (i.e. size bins), the midpoints of which are plotted on the x-axis against the $\log_{10}$ abundance of individual organisms falling within each size bin. The slope of the linear regression fitted to these size spectra is often examined in fisheries studies of marine ecosystems to identify instances of overexploitation. Here, slopes tend to become steeper (i.e. more negative) following exploitation and over-fishing, as larger bodied fish are selectively removed (Petchey *et al.*, 2010; Shin *et al.*, 2005).

6.4 Goals of this study

The principle aim of this study is to investigate the effects of temperature on the structure and functioning of stream food webs. I sampled the biological community of 16 Icelandic streams covering a temperature gradient between 4ºC to 49ºC at two sampling occasions (end and beginning of reproductive season). The aim is to examine the species composition, food web structure and body mass-abundance using a species as well as a size based approach.

Data chapter 1 of this thesis ("Effects of temperature on community persistence in Sub-Arctic streams") focuses of the effects of temperature on species composition and their abundances whilst tracing the temporal changes of the occurring temperature effects by comparing the 2008-data set with previously obtained data from 2004. Data chapter 2 ("Impacts of warming on the complexity of and energy flow through stream food webs") examines the complexity and energy transfer of 15 stream communities in April 2009 by analysing trivariate food webs representing a species based approach .Data chapter 3 ("Warming alters food web structure and complexity") examines the food web structure of seven trivariate food webs constructed from the combined data of August 2008 and April 2009 representing changes in food web structure of a full growing season along the temperature gradient, whereas Data chapter 4 ("Effects of warming on individual size distributions") examines the individual size distributions representing a size based approach of the same streams.

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7 General methods

7.1 Sampling of biological community

In order to construct the food webs of the streams of the Hengill catchment the different trophic levels of the biological community were sampled for a summer and spring season (August 2008 (27.7.-7.8.2012)and April 2009 (19.4.-12.5.2012)). Samples included diatoms from the biofilm of stones(primary producers), macroinvertebrates (primary and secondary consumers) and fish (top predators).

7.1.1 Biofilm sampling

Two different subsets of biofilm samples were taken: one for the determination of the diatom assemblage and one for calculation standing stock via chlorophyll-*a*.

7.1.1.1 Diatom preparation, identification and measurements

Biofilm was removed from 3 haphazardly chosen stones per stream with a toothbrush, rinsed with stream water and preserved with approx. 1 ml of Lugol’s solution (Kemp, 1993). Stones were photographed (Lumix Panasonic DMC-FZ8) including an absolute scale to calculate the surface area using Image J (Rasband). All preparations for clearing the diatoms frustules of organic matter (e.g. Eminson & Moss, 1980) were conducted under a fume cabinet. For each sample 5 ml of the suspension were place in a 15 ml centrifuge tube, filled up with distilled water and left to settle over night. Supernatant was removed, 1.5 ml nitric acid (65%) added and the pellet resolved. The centrifuge tubes (with non fastened lids) were then placed in a water bath at 70°Cand left to settle over night. Supernatant was carefully removed and replaced with distilled water, the sample was then centrifuged at 1000 rpm for 1 minute. This process of washing the diatom frustules was repeated 3 to 4 times until a neutral pH value was achieved (about 5.5 to 6 for distilled water). Depending of the size of the cleaned diatom pellet the samples were filled up with an appropriate volume of distilled water and the volume noted for later calculations. 500 µl per samples were placed on a round coverslip (15 mm in diameter) and left to dry overnight. The dried coverslip was then mounted with Naphrax (Brunel Microscopes Ltd., Chippenham, U.K.) on a microscope slide under a fume cupboard: the inverted coverslip was placed on a drop of Naphrax on the microscope slide. The slide was heated on a hotplate for a few minutes at a temperature of approx. 70°C to drive off the toluene contained in Naphrax. Slides were left to cool down and dry over night and then inspected for even placing and use of a suitable concentration of the diatom samples. On each slide diatoms were counted and identified in a rectangular transect (100µm wide, 15 mm long) with at least 300 diatom valves using 1000x magnification under a Nikon Eclipse 50i microscope. Identification took place to lowest taxonomic level possible (usually species level) based on Krammer & Lange-Bertalot (1986; 1988, 1991a; 1991b).

To calculate average body masses of the diatoms species 10 measurements of width, length and depth respectively of individual valves (for very rare species sometimes less) per stream were taken with Image J form digital pictures taken with the digital camera set-up on the microscope (Nikon Eclipse 50i). The body volume of each species was calculated after Hillebrand *et al.* (1999) using the mean values of measured length, width and depth. For rare species with no measurements of depth available depth was estimated as equal to width or half the width depending on species (see Appendix..14.5.). Measurements of linear dimensions were taken for all diatom species in April 2009. For August 2008 only the most common species (forming 90 % of total species abundance) were measured in their linear dimensions; measurements for rarer species were inferred from the April 2009 measurements. Body mass (dry mass in mg) for each species was calculated after Reiss & Schmid-Araya (2008).

7.1.1.2 Chlorophyll-*a* content

The algal biomass (mg m^{-2}) in the biofilm was calculated from 10 stones per stream measuring Chlorophyll content as a proxy after Friberg *et al*. (2009). From each stream 10 stones (size of gravel to cobble) were randomly collected, kept in the dark and frozen until chlorophyll extraction at the laboratory. Each stone was then separately covered with 96% Ethanol in a plastic container and stored for extraction of chlorophyll at 5°C in a refrigerator for 12–18 h. The volume of Ethanol used for each stone was determined and a subsample used to measure absorbance at 665nm and 750nm with a DR 5000 Hach-Lange spectrophotometer, whereas measurements at 750nm represent the background absorbance. The surface area of each stone was measured from a digital photograph with absolute scale(Lumix Panasonic DMC-FZ8) using ImageJ (Rasband). The algal biomass as total Chlorophyll was then calculated after:

$$Chlorophyll\ (mg\ m^{-2}) = \left((Abs_{665} - Abs_{750}) \times E \ \times\ 10^{4}\right)/(83.4 \times A)$$

whereAbs_{665}= absorbance at 665 nm, Abs_{750}= absorbance at 750 nm, E= volume of Ethanol (ml), 83.4 = the absorption coefficient for Chlorophyll in Ethanol (l g^{-1} cm^{-1}) and A=surface area of stone (cm^2).

7.1.2 Macroinvertebrate sampling, identification and measurements

To capture the composition of the macroinvertebrate community five random Surber samples (25 x 25 cm, 200µm mesh size) were taken per stream and season. Samples were immediately preserved in 70% Ethanol. In the lab the samples were freed from debris and plant material and the macroinvertebrates sorted out and preserved in 70% Ethanol. Identification took place to the highest possible taxonomic resolution (usually species level) based on a variety of freshwater invertebrate identification keys (Bouchard, 2004; Brooks, Heiri & Langdon, 2007; Cranston, 1982; Gíslason, 1979; Glöer, 2002; Hopkins, 1961; Peterson, 1977; Savage, 1989; Schmid, 1993; Smith, 1989; Usinger, 1956; Wiederholm, 1983). Individuals of the family Chironomidae were separated from the other invertebrate samples in order to clear and mount the head capsules for their identification after Brooks *et al.*(2007). Individual chironomids were placed in a small beaker with 10% Potassium hydroxide (KOH) solution and warmed on a hot plate (set to 70°C) for up to 10 min depending on their size. Subsequently the chironomids were neutralized and further cleared by placing them in Glacial acetic acid. Afterwards they were rinsed in 80% and 100% Ethanol (time in each solution was 5 min) and kept in Euparal essence until mounting. The chironomids were decapitated and head (mentum facing upwards) and body (lateral side facing upwards) of each individual were mounted with Euparal on a microscope slide. Cover slips (6mm diameter) were carefully placed on the individuals and gently pushed down to spread out the mandibles. Each microscope slide could hold up to 8 individuals.

Mean body mass (dry mass in mg) for each species was calculated from linear body dimension measurements using transformation equations (see Appendix 14.6).Adequate linear body dimensions (see Appendix 14.6) e.g. head width were measured for up to 30 individuals (less if only fewer individual were found) per stream.

7.1.3 Fish sampling and measurements

The whole sampling stretch in each stream was depletion fished and total abundances of brown trout, *Salmo trutta* calculated after Seber & Le Cren (1967). Per stream three runs with an electro fisher (230 V using a Honda EX 500 Inverter generator) were conducted moving upstream and sweeping from one side to the other of the river bed and stunned fish caught with a handheld fishing net. The use of stop nets at the end of the sampling stretch was relinquished due to the small depth and width of the river channel. All caught fish were measured in fork length and wet weight (mg) directly at the field site. Wet weight (*ww*) of fish was transformed into dry weight (*dw*) in mg after a equation for wet-dry mass conversions, $dw=1.07ww-0.62$ ($R^2=0.97$) (Edwards, F. K, unpublished).

7.2 Construction of food webs

7.2.1 Trivariate Food webs

The trivariate food webs as in the literature (Cohen, Jonsson & Carpenter, 2003; Jonsson, Cohen & Carpenter, 2005; Layer *et al.*, 2010; McLaughlin, Jonsson & Emmerson, 2010; O'Gorman & Emmerson, 2010)were constructed with the species identified in each of the streams representing the nodes. For each species the $\log_{10}$-transformed mean abundance (log N) per m^{-2} and the $\log_{10}$-transformed mean body mass i.e. dry mass (log M) was calculated. Log N and log M for each species were then plotted against each other with log M on the x-axis and log N on the y-axis. The links representing feeding interactions between species were determined from direct observation where possible, i.e. gut content analysis, with the remaining links inferred from the literature (Bouchard, 2004; Brooks *et al.*, 2007; Di Sabatino, Gerecke

&Martin, 2000; Hopkins, 1962; Ivković, Mičetić Stanković & Mihaljević, 2012; Pretty, Giberson & Dobson, 2005; Proctor & Pritchard, 1989; Smith, 1989; Usinger, 1956; Warren, 1989; Woodward & Hildrew, 2001, 2002).

Feeding links of trout derived from gut content analysis. All trout caught during electro fishing larger than 70mm (fork length) were gut flushed with fine tubing attached to a water-filled syringe using the method after Woodward *et al.*(2010). Gut contents were immediately preserved in 70% Ethanol for the later identification in the laboratory. Gut contents were identified from a total of 63 trout to species level where possible, though identification was often only possible to family level. A detailed table of gut contents found and used for determination of feeding links can be found in Appendix 14.4.1.

Gut contents of macroinvertebrates were identified in a subset of 4 streams (April 2009) for up to 10 individuals per species and stream (less if only fewer individuals of a species were found). No direct determination of feeding links for predatory macroinvertebrates was possible as no identifiable body parts were found in the guts due to prey not being ingested as a whole. The links for these predatory macroinvertebrates therefore had to be inferred from the literature (detailed table can be found in Appendix 14.4.2). The diatoms in the guts of macroinvertebrates whose feeding mode was grazer or collector-gatherer were identified to the lowest taxonomic level possible which was mostly to genus level. In order to support the assumption that feeding on the diatom community was not selective i.e. all diatom species were ingested in the same proportions as they occurred in the biofilm a yield-effort curve (see Appendix 14.4.3) was constructed. The links were added to the trivariate food web plots as lines between the nodes.

Similar yield-effort curves (Cohen *et al.*, 1993; Orians, 1969; Polis, 1991; Woodward, Speirs & Hildrew, 2005b) were constructed for the diatom community and macroinvertebrate community to asses if the sampling effort had been sufficient to capture all species in the food web. Here the number of identified sampling units (x-axis) was plotted against the cumulative number of species identified (y-axis). The order of x values was randomised. 100 randomisations were conducted and the mean of those calculated. A rectangular hyperbola was then fitted to the yield-effort plot to assess the asymptotic value indicating the number of species expected in the community. The constructed yield-effort curves can be found in Appendices14.3.1 and 14.3.2along the comparison of identified and expected number of species in each stream.

7.2.2 Individual size distributions

Body mass – abundance size spectra were constructed as in the literature (Brown *et al.*, 2004; Kerr & Dickie, 2001; Petchey & Belgrano, 2010; Reuman *et al.*, 2008; Shin *et al.*, 2005) with nodes representing size classes rather than species. As described in the biotic characterisation section above not every single individual found was measured for body mass calculations individually. Therefore, a log-normal distribution was plotted for each species using the same mean and standard deviation as calculated from the measured individuals. Body masses for the unmeasured individuals were randomly chosen from within this distribution. These values were then imported into a dataset alongside the measured body mass values which was subsequently used for the statistical analysis. In order to divide the organisms in evenly spaced size classes (i.e. size bins) the lowest and highest $\log_{10}$ M value from all fifteen streams were determined. This body mass spectrum was then divided in evenly-spaced (on a $\log_{10}$ scale) size classes. For each size class the $\log_{10}$ N was calculated from the number of individuals that fell into the respective size class. These values were scaled up to numbers per m^2 using a specific conversion factor for each group (i.e. stone area and sample dilution for diatoms, Surber sample area for macroinvertebrates, and electro fishing reach area for trout).Values for $\log_{10}$ N were regressed against the centre of each $\log_{10}$ M size class (White *et al.*, 2007). In order to make the size spectra of all 15 streams comparable with each other, the same 10 $\log_{10}$ M size classes were used in each stream, resulting in the occurrence of empty size classes.

7.3 Food web analysis

Food web statistics to examine the structure of the webs along the temperature gradient included the univariate measures of *number of nodes S* (i.e. web size (*S*) and species richness), *number of links L*, *connectance C* (i.e. total number of realised links divided by the number of possible links $C = L/S^2$ after Martinez, 1991) and *complexity* ($SC=L/S$) (May, 1972, 1973; Pimm, 1982; Woodward *et al.*, 2005a).

From plots of the trivariate food webs as well as the abundance size spectra values of the slope, small and large intercept values of fitted linear regressions were calculated for each stream. The small intercept value derives from calculating the intercept for the smallest body mass value in the system, whereas the large intercept value derives from calculating the intercept for the largest body mass value. This enables one to make predictions how the intercept values change over the whole gradient of body mass.

Values of these measures were them plotted against the respective mean temperatures of each stream and linear regressions fitted in order to examine how those values change with temperature. From the trivariate food webs in the second and third data chapter additionally, the *mean link length*, *mean 2-span* and *community span* were calculated after Cohen *et al*., 2009. *Link length* was defined as the distance between a resource (*R*) and its consumer (*C*) i.e. the Manhattan distance calculated from |log(M_C) -log(M_R) | + |log(N_C) - log(N_R)|. The Manhattan distance of a tritrophic chain was defined as *2-span* and that of the whole community or food web as *community span* (Cohen *et al.*, 2009; Woodward *et al.*, in press). Values of these measures were again plotted against the respective temperatures of each stream and linear regressions fitted in order to examine changes with temperature.

7.4 Temperature and water chemistry

7.4.1 Water temperature

The water temperature of each stream was monitored in August 2008 for several hours at 1-min intervals using multiparameter sondes TROLL9500 Professional (In-Situ Inc., Ft Collins, CO, USA) and Universal Controller SC100 (Hach Lange GMBF) (Demars *et al.*, 2011). In April 2009 continuous temperature measurements (every hour) using TinyTag loggers over the sampling period were taken for every stream From this data, daily mean temperatures were calculated, which then were used to determine an overall mean temperature for every stream. For changes in calculating mean temperatures in order to make them comparable to pervious data sets or between them find details in the respective chapters.

7.4.2 Water chemistry

Concentrations in mg l^{-1} were determined for Nitrogen (total-*N*), its components Nitrate and Ammonium (N-NO_3, N-NH_4), Phosphorus (total-*P*), its compound Phosphate (P-PO_4), Sulphate (SO_4^{2-}) and other base anions and cations in each stream from water samples collected and filtered with Millipore 0.45 µm pore size on the last day of fieldwork and analysed at the James Hutton Institute, Aberdeen, as in Demars & Edwards (2007). Detailed tables of the water chemistry can be found in Appendix 14.2

7.5 Stable isotope analysis

Stable nitrogen isotope analysis was carried out for the components of the regional food web. Δ_{15}N (‰) represents the naturally occurring ratio of $_{15}$N to $_{14}$N in tissues of organisms which is stepwise enriched by approx. 3‰ as trophic level increases (e.g. DeNiro & Epstein, 1981; Hobson & Clark, 1992).

Macroinvertebrates were sampled from each stream using a pond net (330 μm mesh size) and immediately frozen upon return from the field site. At the laboratory macroinvertebrates were identified, dried for 24 h in a drying-oven at 60°C to constant mass and grinded into a fine powder using a agate pestle and mortar. Large macroinvertebrates e.g. *Potamophylax cingulatus* were treated individually whereas smaller invertebrates e.g. Simulidae and Chironomidae were pooled in groups (3 to 8 individuals) to gain enough powdered material (i.e. at least 0.6 mg) for analysis. Body tissue of brown trout was non-destructively collected from fin-clippings (McCarthy & Waldron, 2000) and additionally from one to two individuals per stream and sampling occasion killed. For the analysis 0.6 mg of powdered material was weighed into sterile tin caps (4 x 3.2 mm). Stable isotope analysis of three samples per species or group were conducted following the method of Ings, Hildrew & Grey (2010) using an elemental analyser (Flash EA,1112 series; Thermo-Finnigan) coupled to a continuous flow mass spectrometer (Finnigan MAT DeltaPlus; Thermo-Finnigan).

7.6 Statistical analysis

All statistical analyses were performed using R 2.15.1 (R Development Core Team, 2011). Multivariate ordination in the first data chapter were performed on $\log_{10}(x+1)$-transformed abundance data, using CANOCO for Windows 4.5 (ter Braak & Šmilauer, 2002). Trivariate food webs were constructed, analysed and plotted by using the R package ‘cheddar’ (Hudson, 2012). Yield effort curves were calculated and plotted using Matlab 7.14 (R2012a) (Mathworks).Further details on the statistical analyses used are given in each individual data Chapter.

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8 Study site description

The study site is a geothermally active area known as Hengill around 45 km southeast of Reykjavík and 8 km northwest of Hveragerði (Nguyen, 2001). This area represents the triple junction and is the meeting point of the Reykjanes Peninsula Volcanic Zone, the Western Volcanic Zone and the South Iceland Seismic Zone (Foulger, 1995).

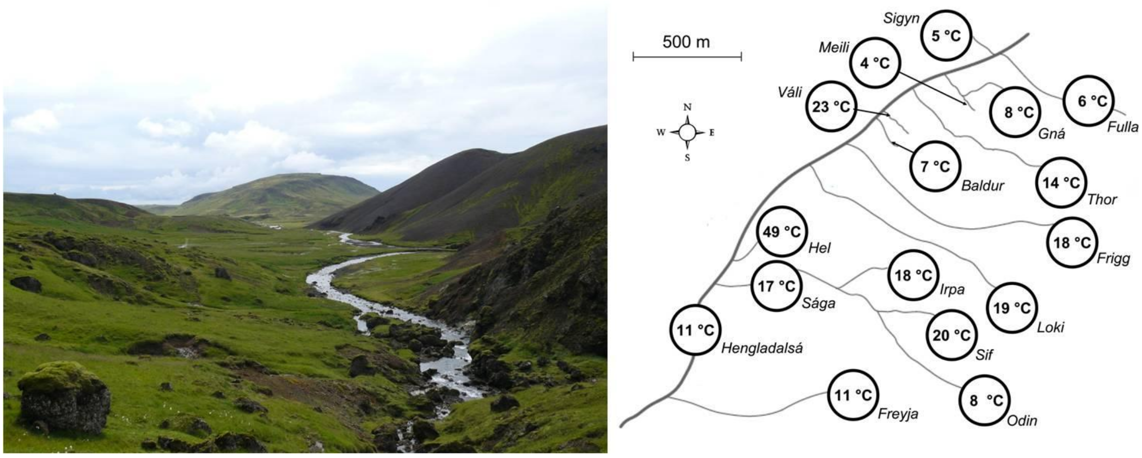

Figure 2*left*: View downstream; main stem (August 2008);*right*: Mean temperatures of the streams in the Hengill area (August 2008 and April 2009 combined) in schematic map

The examined stream system consists of 15 smaller tributaries connected to the mainstem, the Hengladalsá (Figure 2). The 16 streams cover a temperature gradient of aprox. 2°C to 49°C (mean temperature in spring 2009) (Table 1). A temperature of approx. 5 °C reflects the temperature of unheated groundwater in Iceland (Kristmannsdottir & Armannsson, 2004). Each stream is warmed along its whole length by steam from boiling water reservoirs warming the groundwater feeding the streams (Arnason *et al.*, 1969). Due to this form of heating water chemistry over the whole catchment is very similar and not influenced by additional chemical constituents (e.g. sulphur) normally associated with geothermal activity (Demars *et al.*, 2011; Friberg *et al.*, 2009; Woodward *et al.*, 2010).

Stream name	Numbering system of previous studies	mean temperature [°C] 2008/2009	mean temperature [°C] August 2008	mean temperature [°C] April 2009
Meili	IS 10	4.26	5.14	3.38
Sigyn	IS 13	5.48	6.14	4.82
Fulla	IS 14	5.76	9.74	1.79
Baldur	IS 7	6.53	8.24	4.83
Odin	IS 4	8.18	12.69	3.68
Gná	IS 11	8.19	12.81	3.58
Hengladalsá	IS 16	10.87	14.52	7.23
Freyja	IS 12	10.92	15.54	6.31
Thor	IS 9	13.96	18.13	9.80
Sága	IS 1	17.20	22.75	11.65
Frigg	IS 6	17.53	20.95	14.10
Irpa	IS 2	18.14	20.94	15.33
Loki	IS 5	18.91	21.30	16.51
Sif	IS 3	19.70	23.71	15.68
Váli	IS 8	23.08	24.60	21.6
Hel	IS 15	48.73	48.32	49.14

Table 1 Measured mean temperature of streams in August 2008 and April 2009

In each stream a sampling stretch of approx. 25 m was chosen in appropriate distance to the origin and outlet of the streams. Sampling included Surber samples of the benthic macroinvertebrate community, biofilm scrapings of stones, electro fishing and the analysis of water samples (see General methods below).

pH values ranged from 6.8 (Odin, April 2009) to 8.4 (Thor, April 2009) and were relatively similar across the whole stream system (Dr B. Demars, unpublished data).The concentrations of total Nitrogen (total-*N*) ranged from 0.012 µg/ml (Baldur, August 2008) to 0.151µg/ml (Hel, August 2008). Total phosphorus (total-*P*) concentrations varied from 0.006 µg/ml (Fulla, April 2009) to 0.1 µg/ml (Hel, April 2009), and were measured across the 16 streams for both sampling occasions. The chemical characteristics differed somewhat among streams, but were not confounded with the temperature gradient. The generally low nutrient concentrations also reflect the almost "pristine" state of all the streams (Demars *et al.*, 2011; Friberg *et al.*, 2009; Woodward *et al.*, 2010).Detailed tables of the water chemistry in August 2008 and April 2009 can be found in Appendix14.2

The overall macroinvertebrate diversity, with approx. 41 species in the catchment was relatively low compared with those at lower latitudes. The fish population is represented by a single species, the brown trout (*Salmo trutta*). A full species list of the regional species composition can be found in Appendix 14.1

In the following paragraphs I give a brief description based on personal observation, measurements and literature (Demars *et al.*, 2011; Friberg *et al.*, 2009; Woodward *et al.*, 2010) of each stream separately.

Hengladalsá

Figure 3 Hengladalsá in August 2008

Hengladalsá is the mainstem of the catchment and with an approx. width of 8.6 m also the largest of the streams. All other streams are interconnected via Hengladalsá as they are all tributaries of it. This leads to the lack of any dispersal constraints between the streams of the entire catchment. Temperatures measured ranged from approx. 7.2°C in

April to 14.5°C in August. Stream sediment mainly consisted of sand filling the spaces between large gravel and boulders. Values for pH were between 7.4 and 7.9.

Freyja

Figure 4 Freyja in August 20098 looking upstream

Freyja with an approx. width of 2.3 m is the second largest stream of the catchment after Hengladalsá. It is also the furthest away from the other tributaries as it is situated further South downstream Hengladalsá. It has a mean water temperature that lies around 11°C. Sediment mainly consists of gravel.

Sága

Figure 5Sága in April 2009 looking upstream

Sága had temperatures ranging from 11.7°C in April to 22.8°C in August. Its mean width was approx. 2 m.

Irpa

Figure 6 Irpa in August 2008 looking downstream

Irpa is characterised by a very high load of fine silty sediments. This stream does not have any gravel or larger stones which made an examination of stone biofilms i.e.

identification of Diatom species impossible. For this reason the stream was just used for the analysis of its macroinvertebrate community in the first data chapter on persistence and could not be used for the construction of a food web. Irpa has a very dense macrophyte population on which snails and Simulium larvae could be found in abundance. The outflow of Irpa joins Sága. Mean water temperature was 18°C

Sif

Figure 7 Sif in April 2009 looking upstream from outflow in S**á**ga, on the right the out flow of Odin can be seen.

Sif also discharges to Sága. Sif is one of the warm streams with mean temperatures of approx. 20°C. It is habitat to many macrophytes on soft sediment with gravel. Trout are present in Sif in August 2008 and April 2009. Approx. width of Sif is 0.7 m.

Odin

Figure 8 Odin in April 2009 looking upstream

The stream Odin is found in close proximity to the stream Sif. It is a relatively cold stream with mean water temperatures of 8°C. Odin was distinguished by the presence of iron oxide films. Hardly any macrophytes grew in this narrow (approx. 0.6 m) and shallow stream.

Loki

Figure 9 Loki in August 2008 looking upstream

Loki is situated on the grass plain in the east of Hengladalsá. It is a warm and productive stream containing many macrophytes. Mean width is 1 m and mean temperatures ranged from approx. 17°C in April to 21°C in August. Trout were present in this stream.

Frigg

Figure 10 Frigg in August 2008 looking upstream.

A few meters further North from Loki the stream Frigg is situated just before a little hill side. Its streambed was characterised by numerous pepples and boulders. Mean water temperature was 18°C. Trout were caught in this stream in August 2008 but none in April 2009.

Baldur and Váli

Figure 11 Baldur (right) and Váli (left) in April 2009 looking upstream

Baldur and Váli are two adjacent streams about 2m distance from each other. Sediment composition, flow and grade are therefore very similar. Their ecology was very different due to the large difference in temperature. Baldur had a mean water temperature of 7°C and Váli23°C (second warmest stream after Hel). Váli was densely populated by bryophytes whereas Baldur had hardly any macrophytes cover. Trout were only present in Váli.

Thor

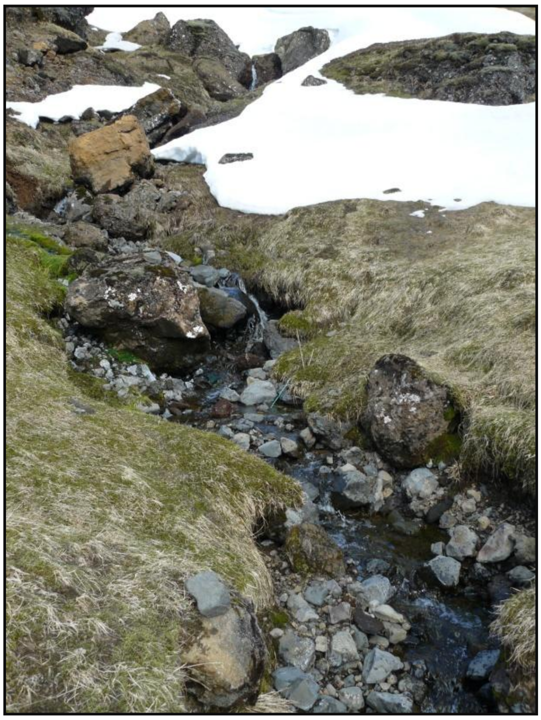

Figure 12 Thor in April 2008 looking upstream

Thor was characterised by its relatively steep grade and presence of abundant large boulders resulting in several cascades in the flow of water. Sandy sediment between the larger stones offers a good habitat for chironomid larvae. A fair amount of bryophyte and macrophyte cover was present. A mean temperature of 14°C was measured.

Meili

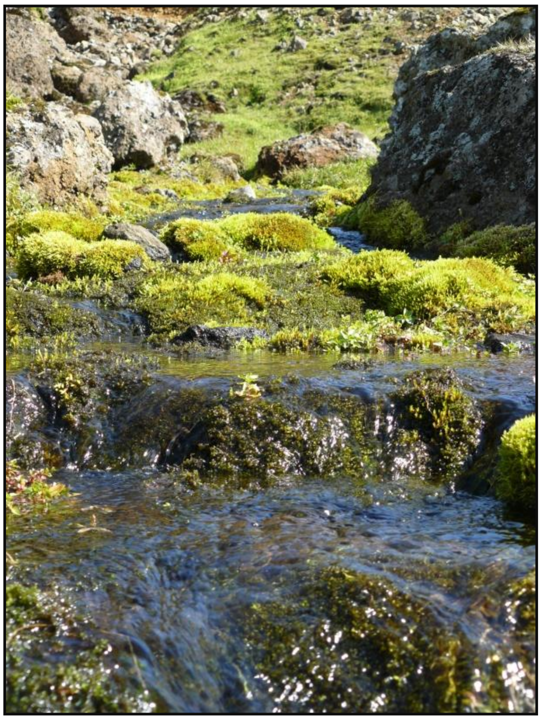

Figure 13 Meili in August 2008 looking upstream

Meili is the coldest of the streams when looking at the mean temperatures combined for April (3.4°C) and August (5.1°C) very close to the general groundwater temperature in Iceland (Kristmannsdóttir & Ármannsson, 2004). The whole stream was characterised by water cascading over large boulders and dense bryophyte cover. This stream discharges into Gná.

Gná

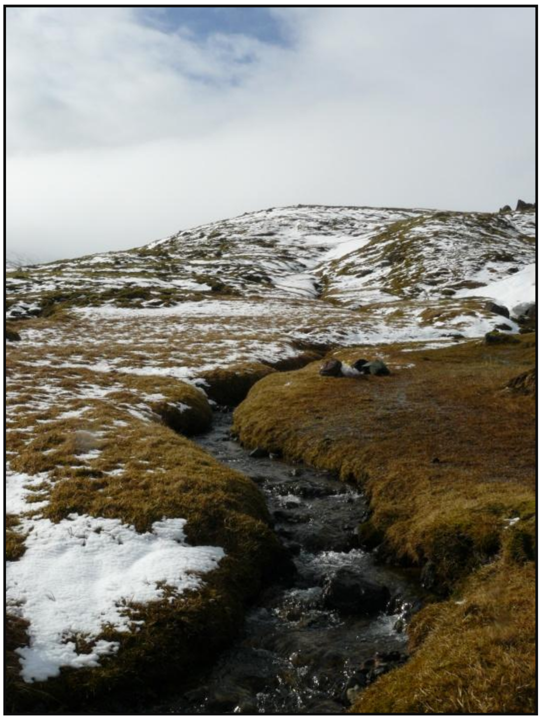

Figure 14 Gná in April 2009 looking upstream

Gná was sampled further upstream from the inflow of Meili. The riverbanks of this stream were relatively high and overhanging providing a good habitat especially for caddis fly pupae. A mean water temperature of 8°C was measured.

Sigyn

Figure 15 Sigyn in April 2009 looking upstream

Sigyn and Fulla are both located on the other side of a smaller mountain from the main valley where all other tributaries are located. Sigyn has an approx. width of 1.2 m and a mixture of sediment types. It contained a wider variety of chironomid species and was a colder stream with mean temperatures of 5°C.

Fulla

Figure 16 Fulla in August 2008 looking upstream

Fulla had a steeper gradient and the sediment was dominated by larger pebbles and boulder. Mean temperatures ranged from 2°C to 10°C. In April 2009 parts of it were still covered in snow which was reflected in the low water temperatures and low abundances of invertebrates found during sampling.

Hel

Figure 17 Hel in August 2008 looking upstream (far left side: Hengladalsá)

Hel was the warmest stream of the Hengill catchment with a mean water temperature of 49°C. Hel represented the generally perceived image of a true geothermal stream. Stones and surface were covered by dense mats of cyanobacteria. Due to the very high water temperature the whole macroinvertebrate community was composed of two species *Scatella thermarum* (synonym *S. tenuicosta*) and chironomid larvae of the *Cricotopus intersectus* - type .

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9 Effects of temperature on community persistence in Sub-Arctic streams

9.1 Introduction

Ecosystems are under increasing stress from a number of anthropogenic (e.g. nutrient enrichment and land use) as well as environmental (e.g. increase in global surface temperatures and sea level rising) sources (Houghton, 2005; Iii *et al.*, 2000; Vitousek, 1994). These stressors are likely to increase the probability that ecosystems and communities are perturbed from their equilibrium states and their stability is reduced. Stability can be defined as the ability of a system to return to or remain in its initial equilibrium after a perturbation (May, 1973; Pimm, 1984). Various measures and subcategories of stability are currently in use, focusing on related but separate aspects of stability (Loreau *et al.*, 2002): *Resistance* is the ability of a system to maintain its equilibrium under the influence of perturbation (Harrison, 1979). *Robustness* is the amount of pressure a system can tolerate before a state switch occurs (Holling, 1973; Loreau *et al.*, 2002).*Resilience* is a measure of how fast a system can return to its equilibrium after perturbation (Webster, Waide & Patten, 1975). The focus of the current study is *persistence*, which is defined as the ability of a system to maintain itself through time, i.e. to remain stable (Loreau *et al.*, 2002).

Persistence is measured by comparing the species composition at two or more time points that are far enough apart to allow analysis at an intergenerational scale (Townsend, Hildrew & Schofield, 1987). Permanent coexistence of species would be the highest level of persistence (Hutson & Law, 1985), whereas complete species turnover would be the lowest level of persistence (Pimm, 1984). Measuring persistence gives an indication of the system's ability to maintain its community structure and function (Loreau *et al.*, 2002; Townsend *et al.*, 1987).

A high turnover rate, i.e. low persistence, may be the result of invasions or extinctions. In the case of invasion, there is a strong likelihood that negative impacts on species diversity and abundance will occur, through processes such as competition, parasitism, hybridisation or habitat alteration (Crooks, 2002; Gribben & Wright, 2006; Grosholz, 2002; Levin, Neira & Grosholz, 2006). Species extinctions may result in an overall reduction in diversity, lowering the complexity of the community. *Sensu* Pimm (1984), complexity of a food web is defined as the combination of species richness and the interactions between species. The influence of complexity on stability has been a long and highly debated topic in the literature (Elton, 1958; May, 1972; McCann, 2000; Pimm, 1984). Recent theoretical studies have shown that, under certain circumstances, diverse and complex systems can be more stable, i.e. more resilient to perturbations (Allesina & Pascual, 2008; McCann, 2000). According to Allesina & Pascual (2008) a complex system is stabilised particularly by the presence of "one ubiquitous type of ecological interaction (i.e. consumer–resource)" and short interaction cycles like predator–prey interaction and self-regulation. Thus, disruptions to the complexity of a community may undermine the long-term stability of the system.

Warming is one of the major environmental stressors affecting the planet and is likely to alter the diversity of a system, as individual species are lost when they are pushed beyond their thermal optimum (Pörtner, 2001). Temperature changes can therefore result in the alteration of community structure, including relative abundance and species composition (Klanderud & Totland, 2005; Parmesan, 2006; Petchey *et al.*, 1999; Pörtner & Farrell, 2008). Cold-stenotherms are more likely to be negatively affected by rising temperatures as they are easily pushed beyond their thermal limits (Chevaldonné

& Lejeusne, 2003; Hering *et al.*, 2009), either decreasing in abundance or becoming extinct. Eurytherms are less likely to be affected by changes in temperature, unless they already exist at the upper bounds of their thermal limit, and may even experience increased abundance due to reduced competition from less thermally-tolerant species. Eurythermal and warm-adapted species are even likely to invade via range expansion under the premise of a suitable species pool and no dispersal constraints (Dukes & Mooney, 1999; Francour *et al.*, 1994; Walther *et al.*, 2002). Thus, it is crucial to investigate the effects of changing temperature on the abundance and composition of species in a community and their persistence through time, especially when considering the imminent threat of warming due to climate change.

Areas of high latitude are especially prone to the consequences of climate change, with global surface temperatures predicted to increase by up to 7ºC in the Arctic, compared to a maximum of 3-5 ºC in temperate regions over the next century (Houghton, 2001; IPCC, 2007). The majority of studies to date have focused on the impact of warming on individuals, populations and species range shifts, while only a few have considered higher levels of organisation, such as communities, food webs and ecosystems (Friberg *et al.*, 2009; Petchey *et al.*, 1999; Woodward *et al.*, 2010; Yvon-Durocher *et al.*, 2010). Numerous studies have demonstrated emergent effects in multispecies systems to date, such as the existence of keystone species and trophic cascades (Polis & Strong, 1996; Power *et al.*, 1996). Interactions in multispecies systems can be described by, for example, intraguild predation (Polis & Holt, 1992), which occurs in food web modules of motifs where species are linked via predation and compete for resources such as niche space (Holt & Polis, 1997; Polis *et al.*, 1992). Top-down as well as bottom-up effects due to changes in species abundances within those motifs have been widely described (Polis *et al.*, 1992; Power, 1992). The presence or change in abundance of a consumer species can regulate the abundance of their prey species. This top-down effect has for example been described for fish regulating zooplankton via predation (Carpenter, Kitchell & Hodgson, 1985; Carpenter *et al.*, 1987). On the other hand the fluctuations in producer abundances limited by nutrient availability can regulate the abundances of consumers via bottom-up effect (Power, 1992). Thus, temperature-induced changes in species composition or abundance, described above, are likely to have knock-on effects at the whole ecosystem scale.

Considering projected global climate change scenarios and the dearth of studies examining the impact of temperature on communities, this study aims to fill gaps in the current understanding of thermal effects on stability and community persistence. Here,the community structure of 14 geothermally heated streams in Iceland were characterised in order to identify potential impacts of warming at multiple levels of biological organisation and at intergenerational scales by comparing data across a temperature gradient and through time, from 2004 and 2008. These streams span a natural thermal gradient from about 5 °C to 24 °C. Each stream has a characteristic temperature throughout its length and the relative temperature differences between streams have remained constant over time. Their physicochemical properties other than temperature have been demonstrated to be similar (Friberg *et al.*, 2009; Woodward *et al.*, 2010). Additionally, there are no dispersal constraints, as all the tributaries are connected to the same main stem. Consequently, the impacts of temperature are not confounded with other environmental variables and thus these streams can be used as a baseline for contemporary reference conditions and also as a space-for-time substitution for predicted future conditions (Woodward *et al.*, 2010).

The following hypotheses were tested to address the effects of temperature at different levels of organisation, from population to community:

1. At the population level, a decrease in abundance of cold-stenothermal species and an increase in abundance of eurythermal species is expected with increasing temperatures.
2. Changes in abundance of predatory species with temperature will alter the abundance of prey species through top-down effects.
3. At the community level, species overlap between streams should decrease with increasing temperature if species composition is determined by temperature.
4. On a temporal scale, species turnover is expected to be higher with warming due to temperature-induced invasions and extinctions, leading to less persistent communities.

9.2 Methods

Study site

The study was conducted in the high-temperature Hengill area, Southwest Iceland in August 2004 and August 2008. This area represents the triple junction of the Reykjanes Peninsula Volcanic Zone, the Western Volcanic Zone and the South Iceland Seismic Zone (Foulger, 1995). 14 streams affected by geothermal activity in this area were chosen; all of them are interconnected by one main river stem, the Hengladalsá. The streams are spring-fed, with the warmed systems being heated through the rock from deep geothermal reservoirs (Arnason *et al.*, 1969), i.e. water is heated in stream channels but not contaminated with additional chemical constituents (e.g. sulphur) normally associated with geothermal activity (see Appendix 14.2). Mean summer temperatures of this set of streams cover a temperature gradient from about 5 to 24 ºC.

Biotic characterisation

For quantification of macroinvertebrate abundance, 5 randomly dispersed Surber samples (sampler area 500 cm^2; mesh size 200 µm) were taken in a 25 m stretch of each stream. Samples were preserved in 70% ethanol and transported to the laboratory for sorting and identification to the highest possible level of taxonomic resolution (usually to species). Chironomids were cleared with KOH and mounted on slides with Euparal for identification using 400-1000x magnification (Brooks, Heiri & Langdon, 2007). All other taxa were identified using 50x magnifications. Identifications were based on a range of freshwater invertebrate keys (Bouchard, 2004; Brooks *et al.*, 2007; Cranston, 1982; Gíslason, 1979; Glöer, 2002; Hopkins, 1961; Peterson, 1977; Savage, 1989; Schmid, 1993; Smith, 1989; Usinger, 1956; Wiederholm, 1983). Further details on the biotic characterisation can be found in the general methods Chapter 7.1.

Details on the methods applied in the previous study in 2004 can be found in the previous publications (Friberg *et al.*, 2009; Woodward *et al.*, 2010). To compare the two data sets adequately, five Surber samples per stream of 2004 were randomly selected for the analysis to make sample size comparable to 2008. Additionally, the resolution of identification was adjusted in 2008 to match the resolution used in 2004.

Temperature and water chemistry

The water temperature of each stream was monitored for several hours at 1-min intervals using multi-parameter sondes TROLL9500Professional (In-Situ Inc., Ft Collins, CO, USA) and Universal Controller SC100 (Hach Lange GMBF) (Demars *et al.*, 2011). Mean temperatures were calculated and compared to temperature data collected in 2004 (Friberg *et al.*, 2009; Woodward *et al.*, 2010). Water temperatures in

2004 and 2008 were highly correlated with each other (Pearson's correlation coefficient $r = 0.99$, $p < 0.0001$)

Concentrations in mg l^{-1} were determined for Nitrogen (total-*N*), its compounds Nitrate and Ammonium ($N\text{-}NO_3$, $N\text{-}NH_4$), Phosphorus (total-*P*), its compound Phosphate($P\text{-}PO_4$), Sulphate (SO_4^{2-})and other base anions and cations in each stream from water samples collected and filtered with Millipore 0.45 µm pore size on the last day of fieldwork and analysed at the James Hutton Institute, Aberdeen, as in Demars & Edwards (2007).

A detailed table of the water analysis can be found in Appendix 14.2.

Statistics

Key species were analysed for changes in their abundances with temperature: the chironomid species *Eukiefferiella minor* Edwards and *Thienemanniella* sp. Kieffer, black fly larvae *Simulium* spp. Latreille and the freshwater snail *Radix balthica* (Linnaeus). These species were chosen because they occurred in relatively high abundances and were present in almost all streams along the temperature gradient. Appropriate regressions for each data series were chosen by comparing different plausible models by their Akaike information criterion (AIC) (Angilletta Jr, 2006; Burnham & Anderson, 2002). AIC was obtained for the linear, polynomial (2nd order) and sigmoidal regression models fitted to the combined dataset from 2004 and 2008. The regression model with lowest AIC was applied separately to data from 2004 and 2008 whenever they were significantly different from each other. Otherwise, a regression was fitted to the combined data (linear regressions for *E. minor* (AIC=45.97 compared to polynomial regression with AIC = 47.90), polynomial (2nd order) regression for *Thienemanniella* sp. (AIC=57.28 compared to linear regression with

AIC=65.80) and *Simulium* spp. (AIC=61.84 compared to linear regression with AIC=63.66) and sigmoidal curve for *R. balthica* (AIC=41.81 compared to linear regression with AIC=67.79 and polynomial regression with AIC=69.25). Fitted regressions were further examined using analysis of variance (ANOVA) in order to identify differences in the trends of fitted regressions, which indicate how abundances are influenced by temperature change between years.

Abundances of two predator-prey motifs, the dance fly *Clinocera stagnalis* Haliday and its respective prey items (Harper, 1980; Smith, 1989), the chironomids *Orthocladius* sp. Wulp (motif 1) and *Chaetocladius* sp. Kieffer (motif 2), were analysed using a three-way ANOVA. For this analysis the temperature gradient was split into three categories: cold (5 ºC -10 ºC), intermediate (12 ºC -17 ºC) and warm (19 ºC -24ºC) temperatures with a buffer of 2ºC between each category. To examine possible cascading effects of species abundances through time driven by the temperature gradient we applied the following model:

$$N_i \sim T_i \times Y_i \times S_i + (1|R_i)$$

where$N$ = *abundance per* m^2 as response and T= *temperature* in *ºC*, Y= *year*, S= *species identity*. The term $(1|R_i)$ describes the nesting of replicates (i.e. Surber samples) in the variable of stream location to avoid pseudoreplication.

The pairwise Sørensen similarity index (SI) (Sørensen, 1948) was used for two types of analyses determining changes in β-diversity (i.e. species overlap) and persistence: firstly, to examine the similarity in communities within a stream between years, and secondly to examine the similarity in communities between streams within a year. The Sørensen similarity index (SI) was calculated as:

$$SI = 2C/(S_1 + S_2)$$

whereS_1 and S_2 represent the total number of species recorded in the first and second community respectively, and C represents the number of species common to both communities. Values of the Sørensen index reach from zero, indicating no common species in the two communities, to one, indicating complete species overlap in the two tested communities. In the first analysis the indices were calculated for the species overlap between the community of each stream with each other within a year. The values were then plotted against the temperature difference between the streams respectively. A linear regression (2004 AIC= -185.16, 2008 AIC=-175.08) was fitted to the index values of each year and tested for significant differences applying an ANOVA to a linear model:

$$SV \sim T \times Y$$

with the values of the Sørensen similarity index (SV) as response and temperature (T) and year (Y) as explanatory variables.

To test the persistence of each community through time the Sørensen index was calculated for each stream comparing its communities of 2004 with 2008. The 14 index values were plotted against the mean temperatures (2004 and 2008 combined) and fitted with a 2nd order polynomial regression (AIC= -34.56 compared to AIC= -29.38 for linear regression)

Multivariate unimodal canonical correspondence analysis (CCA) was performed to investigate correlations among relative abundances of species ($\log_{10}(x+1)$-transformed) and environmental variables. Chemical elements and compounds were incorporated in the ordination as their measured concentrations (mg l^{-1}) (Appendix 14.7.1) whereas for stream location and date (i.e. 2004 or 2008) a binary presence-absence “dummy” code was used. All statistical analyses were performed using R 2.15.1 (R Development Core Team, 2011). Multivariate unimodal (i.e. DCCA) ordinations were performed using CANOCO for Windows 4.5(ter Braak & Šmilauer, 2002).

9.3 **Results**

Absolute abundances of key species, the freshwater snail *Radix balthica*, black fly larvae, *Simulium* spp. and two chironomid species *Eukiefferiella minor* and *Thienemanniella* sp. exhibited a clear response to the temperature gradient in both years (Figure 18). As predicted in the first hypothesis, the more cold-adapted chironomids decreased in abundance and were replaced in terms of dominance by the eurythermal snail *R. balthica* and black fly larvae, *Simulium* spp. Both *R. balthica* ($F_{1,24}$= 0.23, p =0.638) and *Simulium* spp. ($F_{1,24}$= 1.64, p =0.213) showed identical responses to temperature between years. Over the whole temperature gradient, abundances of *E. minor* ($F_{1,24}$ =7.10, P =0.014) and *Thienemanniella* sp. ($F_{1,24}$=7.37, p = 0.012) were significantly higher in 2008 than in 2004, but their form of response to temperature was not significantly different between years ($F_{1,24}$=0.40, P=0.531in *E. minor*, $F_{1,24}$= 0.08, p =0.783 in *Thienemanniella* sp.). Along the temperature gradient, the abundances of these cold adapted chironomids decreased: *E. minor* had highest abundances at 6 °C and *Thienemanniella* sp. at 13 °C.

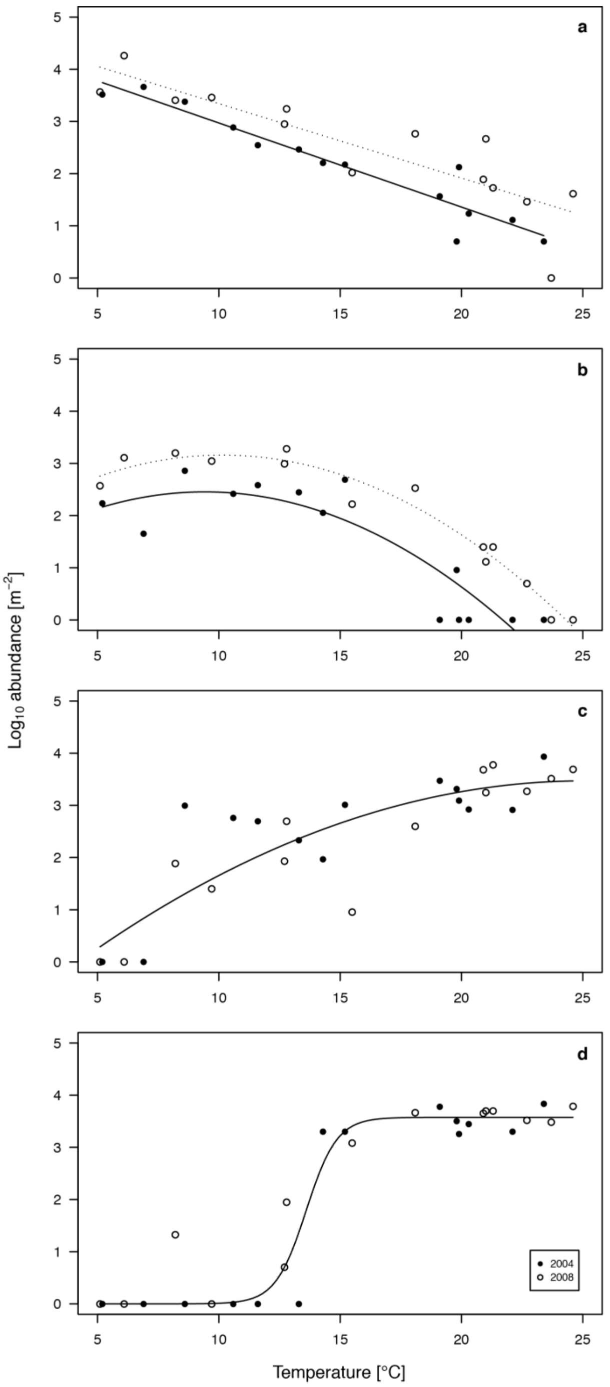

Figure 18 Log$_{10}$-transformed abundances (individuals m^{-2}) against mean water temperature (per stream and year, °C) for **(a)***Eukiefferiella minor*(non-biting midge larvae) with linear regression for 2004 (y = -0.16x+ 4.58, $F_{1,12}$=114.00, *adj.*R^2= 0.90) and 2008 (y = -0.14x + 4.77, $F_{1,12}$=36.78, *adj.*R^2= 0.73)**(b)***Thienemanniella* sp. (non-biting midge larvae) with polynomial (2nd order) regression in 2004 (y = -0.02x^2+ 0.31x + 1.01,$F_{2,11}$=22.97, *adj.* r^2=0.77) and 2008 (y = 1.97 + 1.88x - 3.74x^2, $F_{2,11}$=137.80,*adj.* r^2=0.96**(c)***Simulium* spp. (black fly larvae) with polynomial (2nd order) regression (y = -1.01x^2+ 0.04x - 1.54, $F_{2,25}$= 33.33, *adj.* r^2= 0.71) and **(d)***Radix balthica* (freshwater snail) with sigmoidal regression$\boldsymbol{y = 0.12 + e^{-(x-13.6)/0.63}}$.

A significant difference was found for the three-way interaction of year, temperature and species identity for motif 1 ($F_{1,\ 272}$ = 11.48, P= 0.001) and motif 2 ($F_{1,\ 272}$ = 22.42, P< 0.001). The predatory dance fly larvae shifted from only being present in streams with intermediate and warm temperatures in 2004 to being present at all three temperature categories with highest abundances in the cold streams in 2008. Conversely, abundances of the chironomids were highest in the cold streams in 2004 and lowest in 2008 (Figure 19), suggesting a switch in dominance of predators *versus* prey in 2004 relative to 2008. This confirms the second hypothesis that shifts in the abundance of predators with temperature would alter the abundance of prey species through top-down effects.

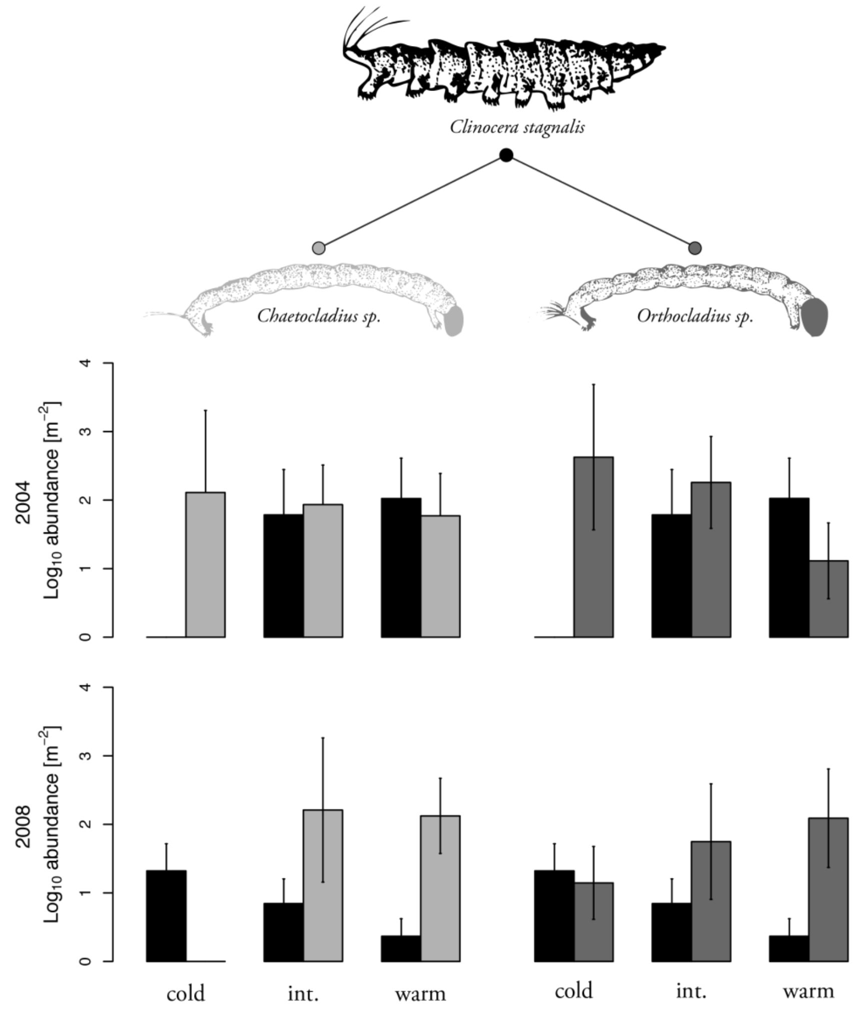

Figure 19 Predator-prey motifs of *Clinocera stagnalis* (black), *Chaetocladius* sp. (light grey) and *Orthocladius* sp. (dark grey) respectively. Bar plots represent $\log_{10}$-transformed abundances in 2004 and 2008 of the particular species. Each panel depicts the abundances of the predatory dance fly larvae and one chironomid species as prey at three temperature categories (cold (5 ºC -10 ºC), intermediate (12 ºC - 17 ºC)abbreviated as int. and warm (20.0 ºC -24.0 ºC). Note: the predatory dance fly larvae went from being most abundant in the warm streams in 2004 to being most abundant in the cold streams in 2008, while the prey species went from being most abundant in the cold streams in 2004 to being most abundant in the warm streams in 2008. The switches in abundances within the motifs between 2004 and 2008 suggest top-down controlled predator-prey cycles.

Species overlap between the stream communities, according to the Sørensen similarity index, decreased with increasing pairwise temperature difference, confirming the third hypothesis. A similar pattern was observed in 2004 and 2008 (Figure 20a). Similarity indices in 2004 were lower overall ($F_{1,178}$= 17.41, P< 0.001) and the slope of the fitted regression line was steeper than in 2008 ($F_{1,\,178}$= 8.07, P= 0.005).

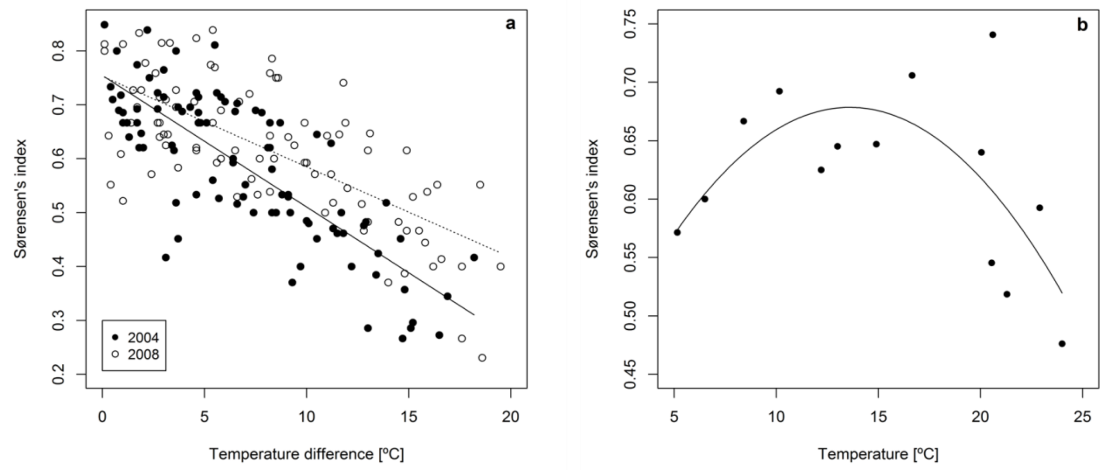

Figure 20(a) Values of Sørensen similarity index between every pairwise combination of streams against their respective temperature differences. Solid circles represent values in 2004 with linear regression fitted (y = -0.02x+ 0.75, $F_{1,89}$ = 153.30, *adj.Rr*^{2}= 0.63), open circles represent values in 2008 with linear regression fitted (y = -0.02x + 0.75, $F_{1,89}$ = 88.40, *adj. R*^{2}= 0.49). **(b)** Values of Sørensen similarity index between communities of same stream in different years (2004 and 2008) against mean temperature of streams with polynomial (2nd order) regression fitted (y = -0.002x^2+ 0.04x + 0.41, $F_{2,11}$ = 4.48, *adj. r*^{2}= 0.35, p = 0.038)

Values for the Sørensen similarity index between the two years (to show species overlap through time) showed a hump shaped response to temperature: i.e. communities in the mid-range of the gradient were most persistent (Figure 20b). This only partially supports the fourth hypothesis, that species turnover should be higher at warmer temperatures and therefore these communities are less stable. While the warmer communities were shown to be less persistent through time, the coldest communities were also found to exhibit reduced persistence. This suggests that extremes of warm or cold are likely to produce greater levels of species turnover and thus less persistent communities.

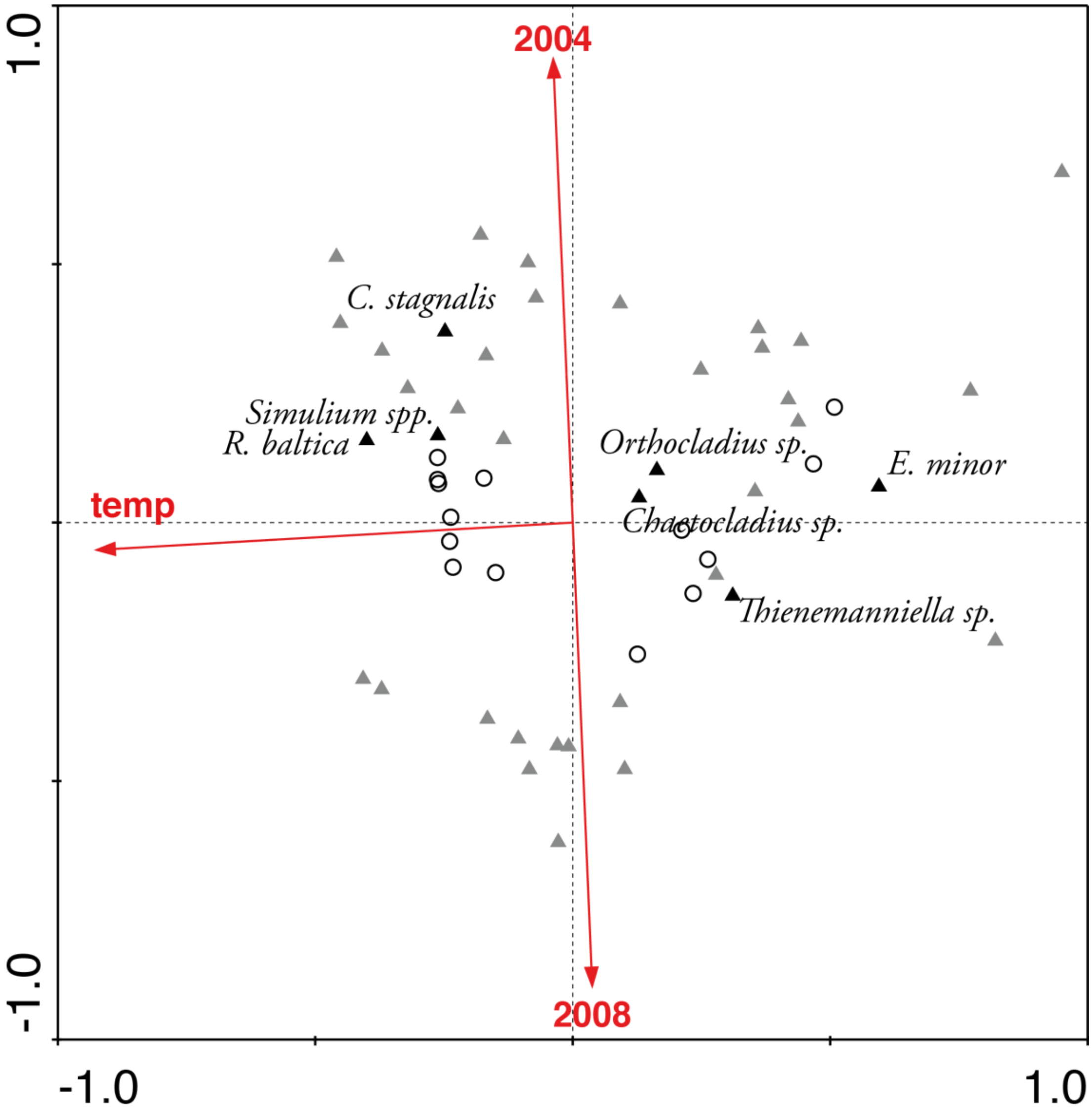

Figure 21 Canonical correspondence analysis (CCA) with species (relative abundances) as solid triangles (highlighted species in black, all others in grey), location (i.e. stream) as open circles and the main determining variables, temperature and date scores (i.e. 2004 and 2008), as arrows.

In the canonical correspondences analysis (CCA), 76.2% of the variability in the data was explained by axis 1 (51.6%) and axis 2 (24.6%) (Figure 21). Axis 1 was highly correlated with temperature (r = -0.91), whereas axis 2 reflected between-year differences (r= ±0.87). Chemical variables added no further significant explanatory power after temperature, year (i.e. 2004 and 2008 respectively) and location (i.e. stream) were incorporated in the model (Appendix 14.7.1).Snails and black fly larvae were strongly associated with the warm streams, whereas the smaller chironomid species (i.e. *E. minor*, *Thienemanniella* sp.) were associated with the cold streams, reflecting their eurythermal and stenothermal life histories, respectively. *Chaetocladius* sp. and *Orthocladius* sp. were associated with more intermediate temperatures.

9.4 **Discussion**

This study provides clear evidence for strong effects of temperature across multiple levels of biological organisation, from populations, to pairwise interactions, to the community as a whole. At the population level, there were negative effects of temperature on two stenothermal chironomid species, with decreasing abundances of *E. minor* and *Thienemanniella sp*. with warming (Figure 18a-b). Rising temperature also had positive effects on some species, with the eurythermal *R. balthica* and *Simulium* spp. increasing in abundance (Figure 18c-d). Shifts in top-down control were observed in some pairwise interactions due to fluctuating abundance of the predatory *C. stagnalis*, which induced reflective changes in its key prey, *Chaetocladius sp*. and *Orthocladius sp.* (see Figure 19). At the community level, species overlap between streams decreased within years as pairwise temperature difference increased (Figure 20a). Community persistence through time declined at the extremes of warm and cold (Figure 20b), suggesting negative impacts of increased temperature variability on system stability. Correspondence analysis also confirmed the importance of temperature and between-year differences in explaining the observed variation in species abundances (Figure 21).

Chironomids are typically shown to be cold stenotherms (Brooks *et al.*, 2007; Ward & Williams, 1986), with their sensitivity to temperature one of the most important variables explaining their distribution and abundance (Brooks & Birks, 2001; Quinlan, Douglas & Smol, 2005; Rossaro, 1991). In accordance with the first hypothesis, the abundance of some key chironomid species decreased with increasing temperature (see Figure 18a-b). This suggests that they became physiologically inhibited at competing for resources in warmer environments, rather than completely excluded due to their thermal limits being exceeded. Similar results have been found by Hogg and Williams (1996) and Tixier *et al*. (2009), where chironomids responded to artificial heating of freshwater streams with a decrease in overall abundance, but not taxonomic richness. Indeed, the changes in abundance shown here may not simply be a direct effect of temperature on the physiology of these chironomid species, rather indirect effects on hatching, growth, emergence, predation or parasitism (Jiang & Kulczycki, 2004; Ward & Stanford, 1982).

The warm streams were dominated by high abundances of the snail *R. balthica* and black fly larvae *Simulium* spp. (see Figure 18c-d). Since these species are considered eurythermal (Becker, 1973; Glöer, 2002), they should in principle be able to occur in high abundance along the whole temperature gradient. However, Fuller and Fry (1991) determined in an experimental setting that *S. vittatum* was restricted in growth at lower temperatures (namely 5 °C), regardless of food quality. This suggests that the Simuliidae in the Icelandic system may be inhibited at low temperatures, while the high productivity and thus availability of resources in the warm streams may sustain the higher abundances found there. *R. balthica* is an efficient grazer (Jonsson & Malmqvist, 2003), whose abundance seems to be dependent on the high levels of algal production provided by the warm streams (O’Gorman *et al.*, in press). Gudmundsdottir *et al*. (2011) showed that bryophyte cover increased dramatically with temperature in the Hengill system, whilst the warmer streams were more dominated by diatoms and green algae. Friberg *et al*. (2009) also showed a linear increase in algal biomass accrual with temperature in the system. These resource-driven dynamics probably contribute to the increased abundance of *R. balthica* with temperature. It is likely that reduced competition for resources, due to the declining abundance of stenotherms such as *E. minor* and *Thienemanniella sp*. (see Figure 18a-b), also contributed to the increasing abundance of both *R. balthica* and *Simulium* spp. with increasing temperature. Alternatively, the high efficiency of grazing by the snails, and indeed increased grazing pressure with temperature (as demonstrated by O'Gorman *et al*., in press), is also likely to contribute to the decrease in chironomid abundance in the warm streams. Here, the rasping feeding behaviour of *R. balthica* is likely to dislodge chironomids from their habitat, while intense competition for algal resources may also limit their success with increasing temperature (Cuker, 1983).

It is also evident from the temporal comparison that the response of species abundance to temperature is consistent on this intergenerational scale. Here, although the stenothermal chironomids showed a quantitative difference in their decreasing abundance between years (see Figure 18a-b), the pattern of decline was qualitatively the same for both years. The increase in abundance of the eurythermal snails and black fly larvae was also remarkably consistent between years (Figure 18c-d), suggesting that these trends are robust. These findings also support climate change research, based on analysis of latitudinal shifts (Root *et al.*, 2003), as species are pushed beyond their thermal optima. These shifts result in altered species composition, which may be due in no small part to changes in predator-prey dynamics, i.e. changes in the abundance of consumers or their resources will have reciprocal effects along the food chain (e.g. Paine 1966, Estes & Palmisano 1974, Power 1992, Walther 2010).

The impact of changes in abundance on predator-prey motifs is clear from this study. Here, a predatory dance fly larva (*C. stagnalis*) exhibited fluctuating top down control and release of its chironomid prey (Harper, 1980) through time at the extremes of warm and cold stream temperature (see Figure 19), supporting the second hypothesis. This predatory larva shifted from being absent in the coldest streams in 2004 to being highly abundant at this temperature category in 2008. Simultaneously, the abundances of two chironomid prey (*Chaetocladius* sp. and *Orthocladius* sp.) were highest in the cold streams in 2004, when the dance fly larva was absent and lowest in 2008 when it was abundant. Conversely, abundances of *C. stagnalis* were highest in the warm streams in 2004 and lowest in 2008, with reciprocal changes in the abundances of the two chironomid prey. Interestingly, the fluctuating abundances seen at the warmest and coldest temperatures in this predator-prey motif suggest a tendency for increased variability and unpredictability of population dynamics at these extremes. This suggests a reduction in temporal stability (as defined by MacArthur (1955)) and may be a major contributing factor in the reduced community persistence through time observed in Figure 20b. Given the rising frequency of extreme weather events and temperature fluctuations (Easterling *et al.*, 2000), this highlights the possibility for reduced stability in consumer-resource dynamics on a more general scale, which may undermine ecosystem functioning and the delivery of ecosystem services (Chapin III *et al.*, 2000; Holmgren *et al.*, 2001).

C. stagnalis is not a very large predator (Bouchard, 2004) and is therefore likely to be limited to relatively small prey items, such as chironomid larvae (Harper 1980). This is the primary reason why a clear effect of top-down control, as described for the two chironomid species above, was not found on larger species like *R. balthica*, *Simulium* spp. or the Tanypodinae. Other small chironomids in the system, such as *Mircropsectra* sp., protect themselves from predation by bearing a tube made of sand (Dillon, 1985), limiting the possibility for strong predator-prey motifs such as those observed in Figure

19. Other possible prey items of *C. stagnalis* were not sufficiently abundant in the coldest streams to investigate a possible top-down effect. It is likely that the community has several other predator-prey motifs, but many of the predators did not occur over the whole temperature gradient to facilitate an analysis of temperature response and persistence through time. A possible explanation for the shift in abundance of *C. stagnalis* in the warmest streams between 2004 and 2008 lies in the fluctuating population dynamics of another predatory species in the system. Larvae of the family Muscidae (house and stable flies) were present in high abundance in the warm streams in 2008, having been absent in 2004. It is possible that these predators out-competed larvae of *C. stagnalis* by occupying the same niche space in the interim of 2004 and 2008. Muscidae larvae are bigger and more efficient predators (Bouchard, 2004; Smith, 1989) and a direct predation effect on *C. stagnalis* is also plausible.

The overlap in species composition between streams decreased with increasing pairwise temperature difference, as predicted by the third hypothesis and supported by previous studies (Friberg *et al.*, 2009; Woodward *et al.*, 2010). This pattern was consistent through time, although the communities became more similar in 2008, with a dampening of the temperature difference effect. Streams with similar temperature regime had high similarity in species composition, with up to 90% of species in common (as also shown by Friberg *et al*. 2009; Woodward *et al*. 2010). Streams with a 15 °C difference in temperature had less than 50% of species in common, however. This also supports the hypothesis that species occurrence and therefore community composition is partly determined by temperature (as shown by Hillebrand *et al*. (2010)). These results suggest that a temperature change of 3-5 °C (as predicted for the next century by the IPCC 2007) could lead to dramatic alterations in freshwater stream communities, with a 10-15% change in species composition likely (as predicted by Figure 19).

Temporal changes in species composition can also be expected at temperature extremes (see Figure 20b). Here, high species turnover through time occurred in the warmest streams as predicted by the fourth hypothesis (and also Townsend *et al.* (1987); Hillebrand *et al.* (2010)), but surprisingly also in the coldest streams. Communities at intermediate temperatures remained quite similar and were therefore more persistent. These findings are supported by the intermediate disturbance hypothesis, which states that biotic diversity is enhanced by moderate levels of disturbance, but inhibited by more severe disturbances (Connell, 1978; Ward & Stanford, 1983). The disturbance in the context of this study is temperature, with the highest and lowest levels of temperature leading to a reduction in beta-diversity (*sensu* Magurran (2004). High levels of disturbance are also known to increase the invasibility of a community (Ewel, 1986; Hobbs & Huenneke, 1992), which could explain the increased species turnover at the extremes of the temperature gradient. For example, eurythermal species like *C. stagnalis* may be able to "invade" streams where they are not normally found (e.g. cold streams in 2004; see Figure 19) if conditions or resources become favourable through the fluctuating population dynamics of other species (leading to high abundances, as found in the same cold streams in 2008; see Figure 19). These “invasions” may then have profound top-down effects on likely prey species, as described above for *C. stagnalis* and its preferred chironomid prey. Further research is required to definitively prove these effects, however.

The ordination shown in Figure 21 summarises many of the key findings of the study visually. Here, temperature and year explain most of the variation in community composition, with no other physical or chemical variable giving further meaningful explanation (in concordance with Friberg *et al*. 2009). Note here that, in contrast to analysing the data with the Sørensen similarity index (which just takes account of the presence and absence of species), the correspondence analysis is sensitive to shifts in species abundance. Thus, the CCA confirms the importance of temperature and between-year differences for explaining the variation in species abundances (as shown in Figure 18 and Figure 19). *E. minor* and *Thienemanniella sp*. are clearly associated with colder temperature in Figure 21, while *R. balthica* and *Simulium* spp. are coupled with warmer water (confirming the patterns shown in Figure 18). *C. stagnalis* abundance (highlighted in Figure 21) is largely driven by warmer temperatures in 2004, highlighting the shift in population dynamics that led to fluctuating top-down control of *Chaetocladius sp*. and *Orthocladius sp*. (see Figure 19). Finally, many species are only associated with the warmest and coldest streams in 2004 and not 2008, leading to the lowest levels of persistence at these extremes of the temperature gradient (see Figure 20b).

All the results shown here accentuate the potential for global warming in the forthcoming decades to severely alter population abundances, predator-prey interactions and top-down control, community composition and persistence of communities through time. Thus, it is critical that we are not just concerned about species extinctions (Petchey *et al.*, 1999) or range shifts (Hickling *et al.*, 2006), but take account of altered abundances and the implications for predator-prey dynamics and the structure and stability of communities. Such an approach is necessary if we are to mitigate the impacts of global change for future generations.

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10 Impacts of warming on the complexity of and energy flow through stream food webs

10.1 Introduction

Increase of global surface temperatures is one of the most severe effects of climate change, with an expected rise of 0.2 °C per decade over the next century (IPCC, 2007). Numerous studies have investigated the effects of climate change, most of which have focussed on phenology and physiology of individuals(Menzel *et al.*, 2006; Visser & Both, 2005) and shifts in species distributions (Hickling *et al.*, 2006; Parmesan & Yohe, 2003), while far fewer have addressed the effects of warming on whole communities (Petchey *et al.*, 1999; Yvon-Durocher *et al.*, 2010). Studies relying on artificial laboratory settings(e.g. Petchey *et al.*, 1999) or small mesocosm communities (e.g. Yvon-Durocher *et al.*, 2010) can lack realism as they cannot reproduce the full complexity of a natural system. Thus, there is a need for studies investigating the ecosystem-level impacts of warming in a natural setting, which are unconfounded by biogeography, latitudinal gradients or physicochemical differences.

Warming is likely to enhance the productivity of aquatic ecosystems due to increased algal growth (Davison, 1991). This should be reflected in measurements of standing stock, with an increased biomass of primary producers, e.g. macrophytes (Gudmundsdottir *et al.*, 2011) or microalgae (Petchey *et al.*, 1999; Yvon-Durocher *et al.*, 2011). Increased resource supply may even result in a greater total biomass of primary consumers, although existing evidence suggests that the high metabolic demands of warmer environments (Brown *et al*. 2004) will inhibit the biomass of consumers (Petchey *et al.*, 1999; Strecker, Cobb & Vinebrooke, 2004; Yvon-Durocher*et* *al.*, 2011), possibly through overexploitation of resources (Beisner, McCauley & Wrona, 1997; Benndorf *et al.*, 2001). Further studies are needed to test these effects in complex natural systems.

Body size is a key parameter known to be affected by warming. The Temperature-Size Rule (Atkinson, 1994) states that the individual body size of ectotherms tends to decrease with increasing temperature. Similarly, Bergmann's Rule states that smaller species are more likely to be found in warmer environments (Bergmann, 1847). This implies that climate change and resulting increases in temperature might alter body mass - abundance scaling in communities if there is a tendency for an increased prevalence of smaller organisms with warming. Previous research has shown a steepening of mass-abundance slopes in response to this effect (Yvon-Durocher *et al.* 2011), with implications for energy transfer through the system.

The flow of energy can be more clearly visualised through the construction of so-called trivariate food webs, which are plots of nodes representing the body mass (Log_{10} M) and abundance (Log_{10} N) of each species, in a community, connected to each other via their feeding interactions (e.g. Cohen *et al.* 2003). There is remarkable consistency in the patterns shown by trivariate webs from marine (O'Gorman & Emmerson 2010), freshwater (Jonsson *et al.* 2005; Layer *et al.* 2010) and terrestrial ecosystems (McLaughlin *et al.* 2010), with energy flowing from small, abundant resources at the base of the web to large, rare predators at the higher trophic levels (see Woodward *et al.* 2005 for an overview). In general, several groups separate out in a trivariate food web plot according to similar abundance and body mass (Cohen, Jonsson & Carpenter, 2003). These clusters represent the different trophic levels in a food web: e.g. primary producers, primary consumers, secondary consumers and apex predators.

Temperature driven changes in body size or abundance can administer knock-on effects on other parts of the community. Top-down effects have often been described for a change in abundance of species with a keystone role in a community (Power, 1992). A keystone species is defined by having a disproportionately large impact on its community or ecosystem relative to its abundance (Power *et al.*, 1996). A famous example is the increase of grazing pressure on benthic macrophytes by sea urchins after the suppression of the sea otter population regulating sea urchin abundances in the near-shore marine communities of Amchitka Island (Estes & Palmisano, 1974). Recent studies suggest that not only the decline of a keystone species can have knock-on effects throughout the whole community, but even just the change in interaction strength between predator and prey facilitated by the reduction of body mass of the predator (Jochum *et al.,* in press).

A number of common statistics have been employed to examine the structure of a food web, including the *number of nodes S* (i.e. species richness), *number of consumer-resource links L*, *connectance C* (i.e. the total number of realised links divided by the number of possible links $C = L/S^2$ after Martinez, 1991) and *complexity* ($SC=L/S$) (May, 1972, 1973; Pimm, 1982; Woodward *et al.*, 2005). Connectance and complexity have both been suggested as surrogate measures of stability in a food web, with lowered connectance shown to reduce the robustness of a food web to secondary extinctions (Dunne, Williams & Martinez, 2002b) and lowered complexity found to increase the fragility of ecological networks (Montoya, Pimm & Sole, 2006). Thus, food web statistics which describe important system-level properties may highlight the health of an ecosystem.

Additional food web properties known as tritrophic statistics have emerged in more recent years to examine the trophic size structure of a community based on the trivariate food web (Cohen *et al*. 2009). Measures here include mean link length, mean 2-span and community span (Cohen *et al.*, 2009; Woodward *et al.*, in press). Mean link lengthis a measure of the average distance in body mass-abundance space between a resource (R) and a consumer (C), calculated by its Manhattan grid distance after $|\log(M_C) - \log(M_R)| + |\log(N_C) - \log(N_R)|$. This equates to the number of orders of magnitude difference in body mass and abundance and thus the flow of energy between the resource and the consumer. Link length represents the relative difference of trophic height between a consumer and a resource, with a shortening of link length indicating that consumers feed on higher trophic levels in the food web. Similarly, mean 2-span measures the distance between a consumer and a resource in a tritrophic interaction, i.e. three nodes on a basal, intermediate and top level connected by two links (Cohen *et al.*, 2009). Changes in 2-span describe an alteration in the flow of energy from resources to consumers through an intermediate source: the greater the 2-span, the farther up the food web energy is travelling in tritrophic chains. Community span measures the Manhattan distance covered by the whole trivariate food web (Cohen *et al.*, 2009) and gives an indication of the trophic span in the community from the smallest, most common resource to the largest, rarest consumer. Tritrophic statistics have thus far been examined for just three ecosystems: Tuesday Lake in Michigan, USA, the Ythan Estuary in Scotland and experimental stream channels in Dorset, UK (Cohen *et al*. 2009; Woodward *et al*. , in press). The latter study showed large impacts of drought, a major component of global change, on the largest species in the system. Here, loss of large, rare species as a result of drought led to fundamental changes in the flow of energy through the web, with a significant decline in mean 2-span compared to control food webs (Woodward *et al*. In press). Given the similar predicted impacts of warming on large organisms high up the food web (Petchey *et al*. 1999), it would be interesting to investigate whether comparable effects are found on mean 2-span and other tritrophic statistics in response to this particular aspect of global change.

The following hypotheses were tested in this study:

1. Warming should lead to an increased biomass of small resources and a reduced biomass of larger consumers.

2. Species diversity should decrease with increasing temperature due to the cold-adaptation of many species in the Icelandic system.

3. Food web complexity and connectance should decrease with increasing temperatures due to higher energy demands.

4. An increased prevalence of small organisms with temperature should lead to a change in body mass-abundance scaling, following scenarios (g) or (i) in Figure 1 in the general introduction, leading to a reduction in energy transfer efficiency through the system.

5. As energetic demands increase with temperatures, values of mean link length, 2-span and community span should shorten as consumers decrease in size and feed on resources that are closer to their own body mass and abundance.

10.2 **Methods**

Studysite

The study site is located in the geothermally active area of Hengill, South-West Iceland. The stream system consists of several tributaries connected via one main stem (the river Hengladalsá). The main stem and 14 of the tributaries selected for this study cover a temperature gradient from 2°C to 49°C (mean temperatures spring 2009). Each stream is warmed along its whole length. The groundwater feeding the streams is warmed through the bedrock by steam from boiling water reservoirs (Arnason *et al.*, 1969). Water chemistry in all streams of the catchment is very similar due to this form of heating, which does not influence the stream water with additional chemical constituents (e.g. sulphur) normally associated with geothermal activity (Demars *et al.*, 2011; Friberg *et al.*, 2009; Woodward *et al.*, 2010b). Sampling of the 15 streams took place in April 2009.

Biotic characterisation

Quantitative measurements for macroinvertebrate species were obtained from 5 haphazardly dispersed Surber samples (sampler area 500 cm^2; mesh size 200 µm) taken in a 25 m stretch of each stream. Samples were preserved in 70% Ethanol and transported to the laboratory for sorting, identification, counting abundances and measuring mean body mass. Individuals were identified to the highest possible level of resolution using a range of freshwater invertebrate keys (Bouchard, 2004; Brooks, Heiri & Langdon, 2007; Cranston, 1982; Gíslason, 1979; Glöer, 2002; Hopkins, 1961; Peterson, 1977; Savage, 1989; Schmid, 1993; Smith, 1989; Usinger, 1956; Wiederholm, 1983). Chironomid head capsules were cleared with Potassium hydroxide (KOH) and mounted on slides with Euparal before identification using a light microscope (400 to 1000x magnification) (Brooks *et al.*, 2007). All other taxa were identified under 50x magnification. Some form of linear dimension of body size (i.e. head width, body length, body width or shell width) was measured for up to 30 individuals (less for species with lower abundance) per species and body mass then calculated from length-mass regressions from the literature (Baumgärtner & Rothhaupt, 2003; Benke *et al.*, 1999; Johnston & Cunjak, 1999; Ramsay *et al.*, 1997; Stoffels, Karbe & Paterson, 2003; Woodward & Hildrew, 2002). Standing stock of biofilm was calculated from 10 stones per stream measuring Chlorophyll *a* concentrations (in mg m^{-2}) as a proxy. The diatom community was examined in their species composition, species abundances and species biomass from 3 randomly selected stones per stream. At least 300 valves per sample were identified to species level based on Krammer & Lange-Bertalot (1986; 1988, 1991a; 1991b) and counted. The cell volume was calculated after Hillebrand *et al.*(1999) using length, width and depth and then transformed into body mass after Reiss & Schmid-Araya (2008) from at least 10 individuals per species and stream.

The fish community was examined in their composition and density by depletion electro fishing (230 V using a Honda EX 500 Inverter generator) in each stream. Fish were measured in terms of fork length, and were then weighed and gut flushed on site before being released. Gut contents were preserved in 70% Ethanol (Woodward *et al.*, 2010a).

A more detailed description of methods used in this study can be found in the General Methods (Chapter 7.1)

Temperature effects on population biomass

To explore the impact of temperature on the prevalence of small organisms, the total biomass of diatoms was calculated for each stream. Here, the average body mass (mg) of each species was multiplied by the total abundance (m^{-2}) of that species. Additionally, the total chlorophyll *a* in each stream was used as a surrogate measure of primary producer biomass (including diatoms, cyanobacteria and green algae). The total biomass of consumers (macroinvertebrates and fish) was also compared across the temperature gradient to explore the impact of warming on larger organisms. Biomass changes with temperature were also investigated for some key species from each trophic level in the system: fish, macroinvertebrates and diatoms. Here, the biomass of the trout *Salmo trutta* was examined as the apex predator in the system. The snail *Radix balthica* is also found in high abundance in many streams and was thus investigated for biomass changes with temperature. Individual diatom species were also explored, with significant trends shown.

Construction of food webs

Nodes were represented by the combination of mean abundance (*y*-axis) and mean body mass (*x*-axis) of each species identified in each of the streams. Feeding links between species, i.e. nodes, were determined from direct observation where possible, i.e. gut content analysis, with the remaining links inferred from the literature (Usinger, 1956; Warren, 1989; Woodward & Hildrew, 2001). The gut content analysis provided a limited amount of directly observed links due to the low number of individuals available in comparison to the large number of individuals needed to capture the entirety of realised links in the food webs (Ings *et al.*, 2009; Woodward *et al.*, 2001).

A more detailed description of the biotic characterisation and the construction of the food webs including the inferring of feeding links can be found in the general methods (Chapters 7.1and 7.2).

Statistical analysis

The trivariate food webs were constructed, plotted and analysed in R 2.15.1 (R Development Core Team, 2011)using the 'cheddar'-package (Hudson, 2012) with $\log_{10}$-transformed values of body mass (Log M) and abundance (Log N). This package provides functions for calculating food web properties such as species and link richness, connectance, complexity, mean link length, mean 2-span and community span. Note that two of the 15 streams, Frigg (14.1°C) and Hel (49.1°C), did not exhibit any tritrophic chains and therefore no calculation of 2-span could be made in these streams. Linear regression analysis was carried out on biomass data, chlorophyll, food web properties (species and link richness, connectance and complexity), mass-abundance scaling exponents (slope and intercepts with the smallest and largest individuals) and tritrophic statistics (mean link length, mean 2-span and community span). In each case, the response variable was plotted against temperature (or other biomasses for correlations between consumer and resource biomass) and significant trends were tested in R 2.15.1 (R Development Core Team, 2011).

10.3 **Results**

There was a significant change in the total biomass of diatoms with increasing temperature ($F_{1,13}$=4.93, P=0.045, *adj.* R^2=0.22; see Figure 22a). The hot stream Hel (~49 °C) was excluded from a second analysis as it is considerably warmer than the other streams and thus likely to drive many of the trends observed in linear regression. There was now no significant change in the total biomass of diatoms with temperature ($F_{1,12}$=0.66, P=0.431, *adj.* R^2=-0.03, see Figure 22b). Concentrations of chlorophyll *a*, as a proxy for standing stock of biofilm, did not show significant changes with temperature ($F_{1,13}$=0.06, P=0.812, *adj.* R^2=-0.07, see Figure 22c). Untransformed concentrations ranged from 2.4 mg/m^2 at the coldest stream (1.8°C, Fulla) to 213.0 mg/m^2 at 4.8°C (Baldur). The hot stream Hel was again excluded from a second analysis, but there was still no significant change in chlorophyll *a* with temperature ($F_{1,12}$=0.01, P=0.931, *adj.* R^2=-0.08, see Figure 23d).

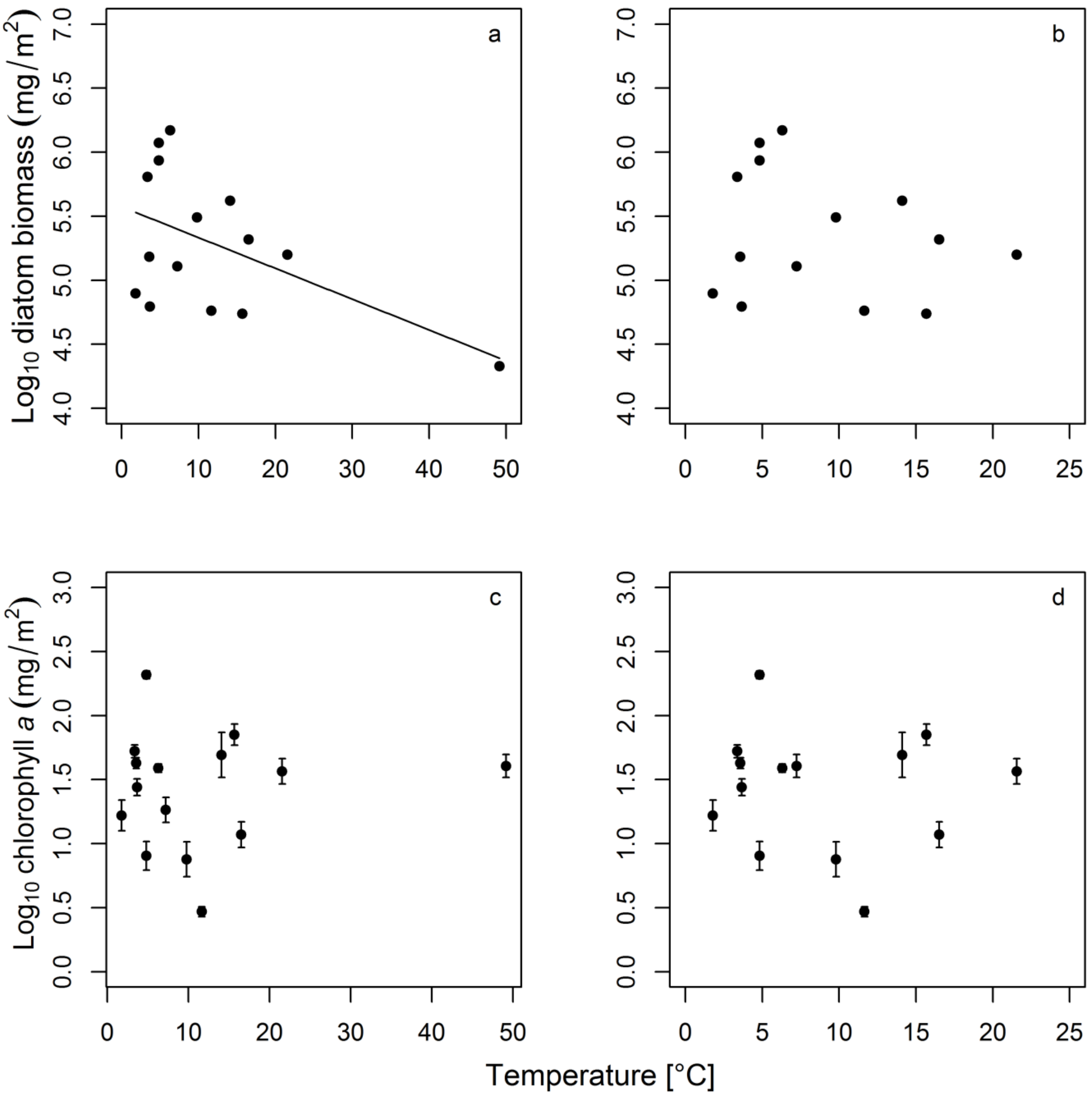

Figure 22 Log$_{10}$-transformed biomass of diatoms in mg/m^2 (panel a and b) of the whole temperature gradient with linear regression y = -0.02x+5.57 (a) and under exclusion of Hel (b) against men temperatures of streams. Log$_{10}$-transformed concentrations of chlorophyll *a* in mg/m^2 with standard error against mean temperatures of streams (panel c and d) .of the whole temperature gradient (c) and under exclusion of Hel (d).

The total biomass of consumers (including macroinvertebrates and fish) did not change significantly with temperature ($F_{1,13}$=0.13, P=0.724, *adj.* R^2=-0.07).Again, the hot stream Hel was excluded from a second analysis, which did show a significant increase of total biomasses with temperature ($F_{1,12}$=10.87, P=0.006, *adj.* R^2=0.43).

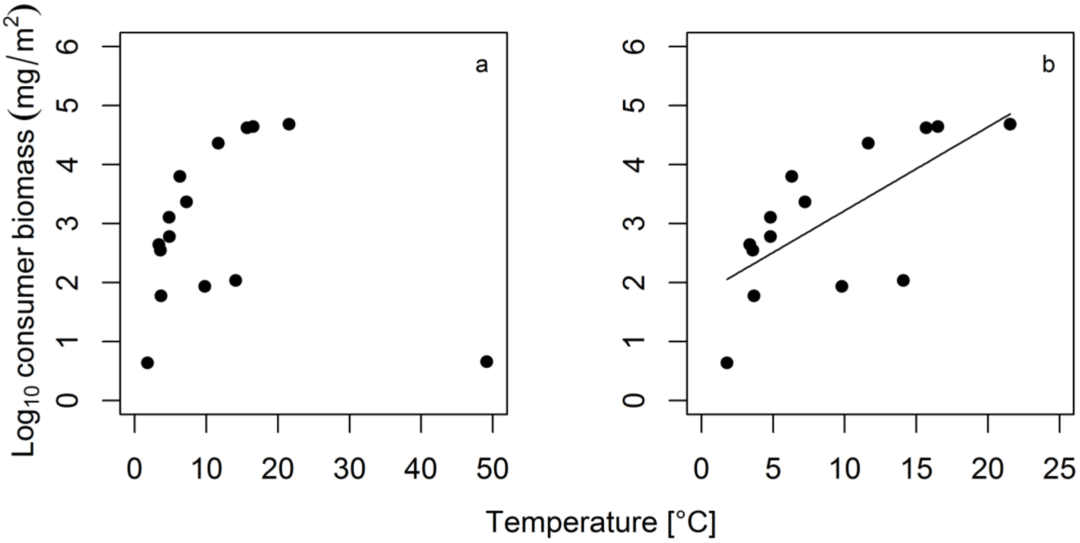

Figure 23 Log_{10}-transformed values of consumer biomass per stream in mg/m^2 against their respective temperatures for the whole temperature gradient in panel (a) and under exclusion of Hel in panel (b) with $y = 0.14x + 1.80$.

No significant correlation could be found between consumer biomass and diatom biomass ($F_{1,13}$=0.47, P=0.504, *adj.* R^2=-0.04, Figure 24a) and consumer biomass and chlorophyll *a* concentrations ($F_{1,13}$=0.17, P=0.686, *adj.* R^2=-0.06, Figure 24b).

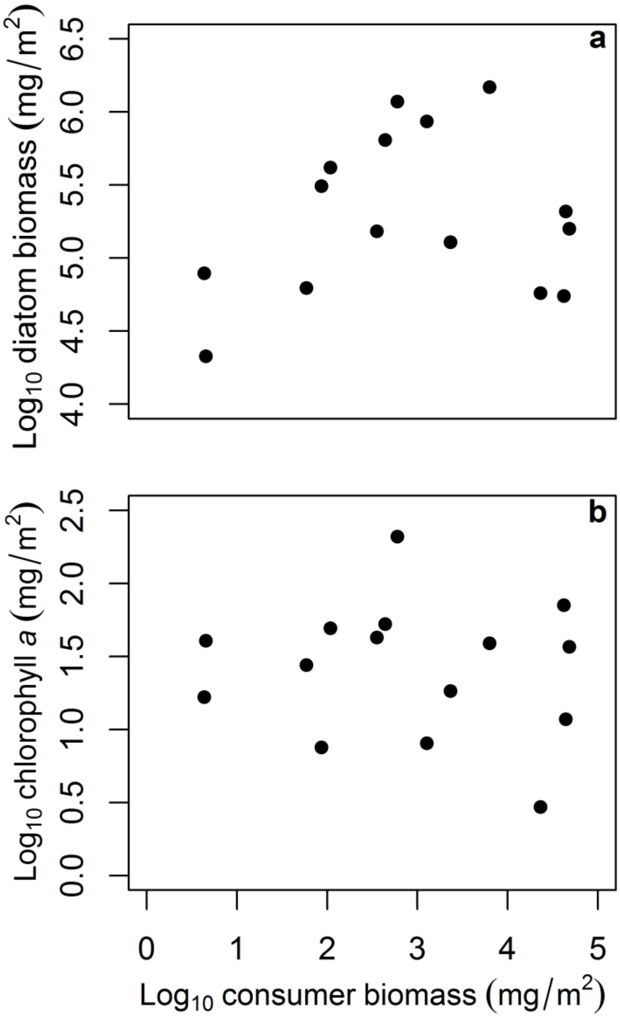

Figure 24 Correlation plots of Log_{10}-transformed consumer biomass against Log_{10}-transformed diatom biomass (panel a) and Log_{10}-transformed consumer biomass against Log_{10}-transformed concentrations of chlorophyll *a*.

Log_{10}-transformed values of brown trout biomass increased significantly with increasing stream temperature ($F_{1,3}$=14.86, *P*=0.031, *adj.* R^2=0.78; Figure 24a). Biomass of *Radix balthica* in streams with brown trout present increased significantly with temperature ($F_{1,3}$=45.64, *P*=0.007, *adj.* R^2=0.97; Figure 24b). Total biomass of diatoms in this set of streams shows a decreasing tendency with increasing temperatures, but this effect was not significant ($F_{1,3}$=1.14, *P*=0.364, *adj.* R^2=0.03).

However, the biomass of three highly abundant diatom species, *Achnanthes lanceolata* (Breb. ex Kütz.) Grun. in Cleve & Grun. 1880 ($F_{1,3}$=29.97, P=0.011, *adj.* R^2=0.88; Figure 24), *Gomphonema type D* ($F_{1,3}$=11.09, P=0.045, *adj.* R^2=0.72; Figure 24) and *Meridion circulare* (Greville) C. Agardh ($F_{1,3}$=32.53, P=0.011, *adj.* R^2=0.89; Figure 24), decreased significantly with increasing temperature.

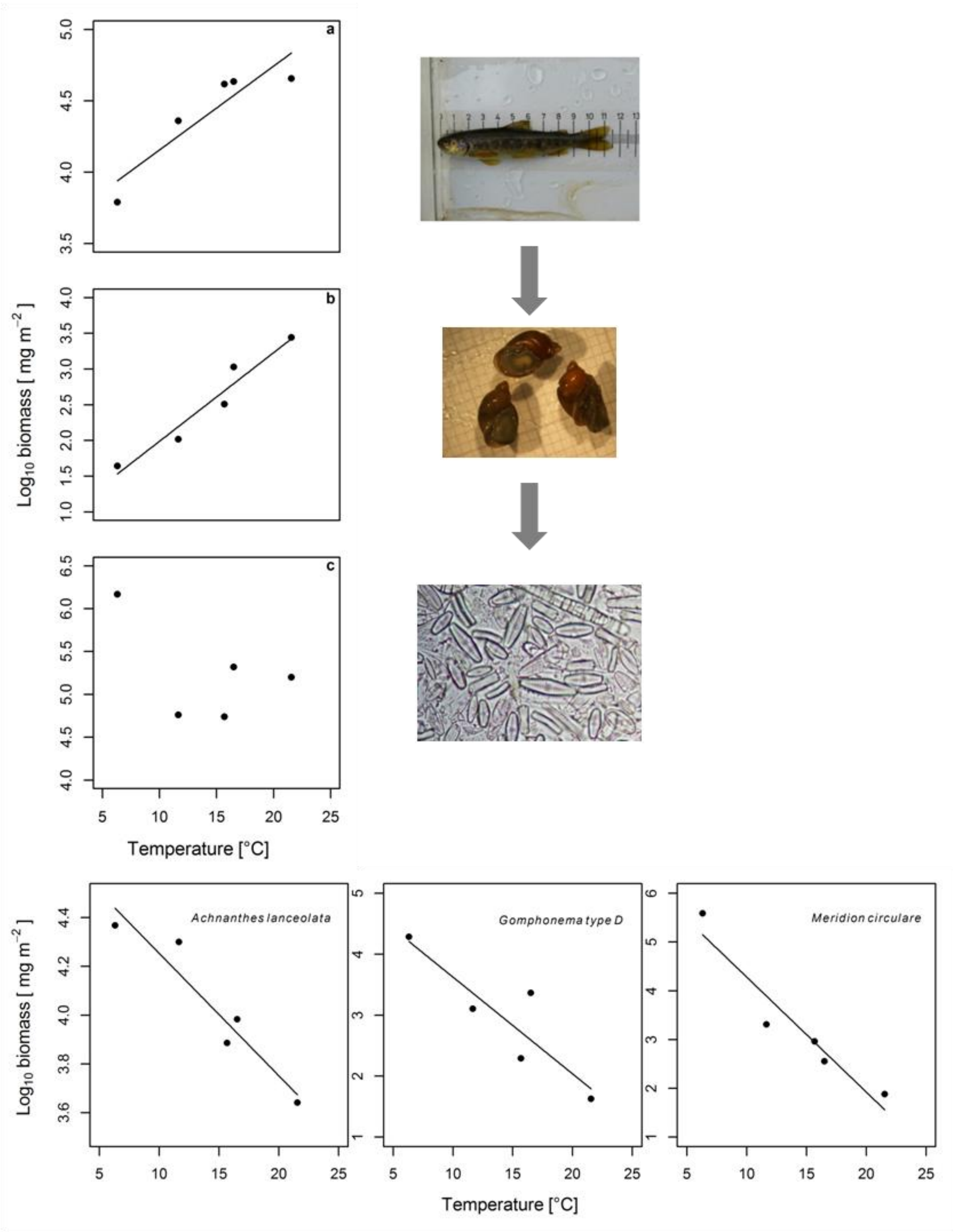

Figure 25 Tritrophic cascade of *Salmo trutta* (brown trout), *Radix balthica* (freshwater snail) and diatoms. Plots represent the $\log_{10}$-transformed biomass [mg m^{-2}] of (a) *Salmo trutta* (y = 0.8x + 3.18), (b) *Radix balthica* (y = 0.18x - 0.27. (c) Total diatoms, (d) *Achnanthes lanceolata* (y = -0.05x+4.76) (e) *Gomphonema type D* (y = -0.16x+5.21) and (f) *Meridion circulare* (y = -0.24x+6.64) against mean stream temperature.

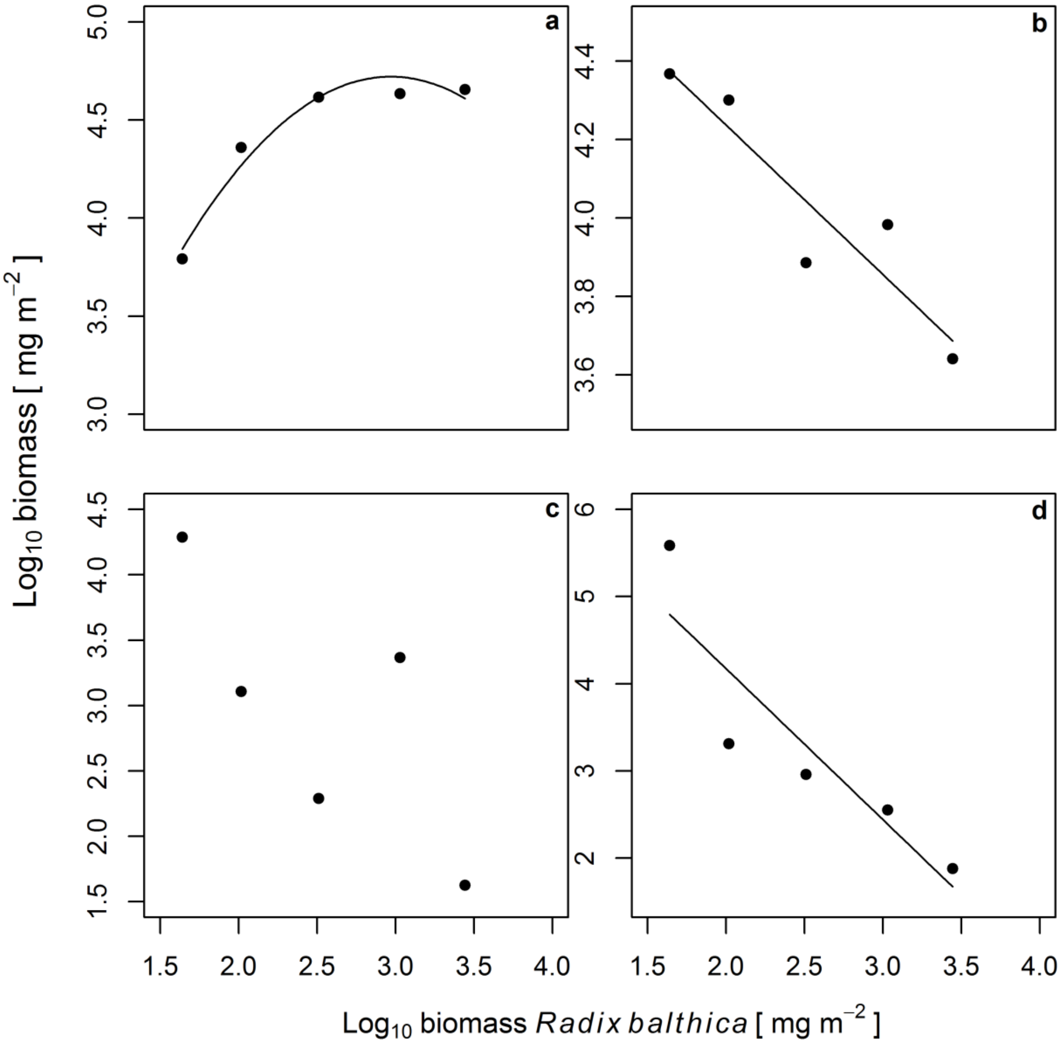

Figure 26 Correlation plots of Log$_{10}$-transformed *Radix balthica* biomass against (a) Log$_{10}$-transformed *Salmo trutta* biomass (polynomial curve (second order): y = 2.95x-0.05x^2+0.33), (b) Log$_{10}$-transformed *Achnanthes lanceolata* biomass (y = -0.38x+5.00), (c)Log$_{10}$-transformed *Gomphonema type D* biomass and (d)Log$_{10}$-transformed *Meridion circulare* biomass (y = -0.24x+6.64)

Evidence supporting the inter-relationship between these changing biomass trends with temperature can be found from correlations of consumer against resource biomass. Here, *S. trutta* and *R. balthica* biomass were significantly correlated ($F_{2,2}$=25.77, *p*=0.037, *adj.* r^2=0.93; Figure 26a), while *R. balthica* biomass was also significantly correlated with *A. lanceolata* ($F_{1,3}$=18.32, *P*=0.023, *adj.* R^2=0.81; Figure 26b)and *M. circulare* biomass ($F_{1,3}$=12.84, *P*=0.037, *adj.* R^2=0.75; Figure 26d), but not

Gomphonema D ($F_{1,3}$=3.99, P=0.140, *adj.* R^2=0.43; Figure 25c). Additionally, the increasing importance of *R. balthica* in the diet of *S. trutta* can be seen from the composition of *S. trutta* prey depicted in Figure 27.

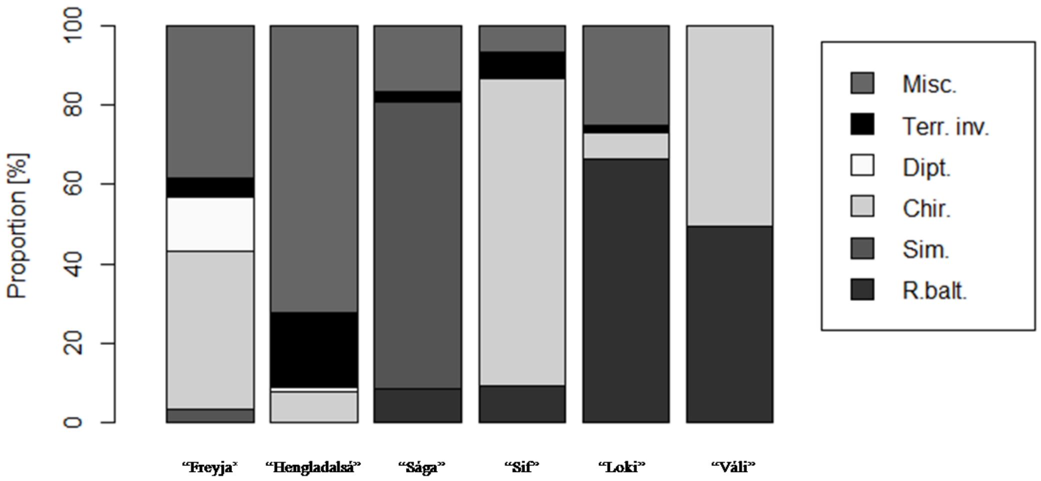

Figure 27 Dietary composition of brown trout depicted as proportions of biomass of prey in gut contents. Groups of prey include *Radix balthica* (R.balt.), Simulidae (Sim.), Chironomidae (Chir.), other Diptera larvae (Dipt.), Terrestrial invertebrates (Terr. inv.) and all other prey items summarised in “Miscellaneous” (Misc.). Streams are ordered from coldest to warmest stream i.e. Freyja (6.3°C) to Váli (21.6°C).

The trivariate plots of all 15 streams revealed a clear size structuring in their food webs (see Figure 28). All webs had groups of abundant small producers, the diatoms, and a group of larger, rarer macroinvertebrate species. In six of the warmer streams, Freyja, Hengladalsá, Loki, Saga, Sif and Váli, brown trout (*Salmo trutta* L.) were present as an apex predator resulting in an additional data point at a large body mass.

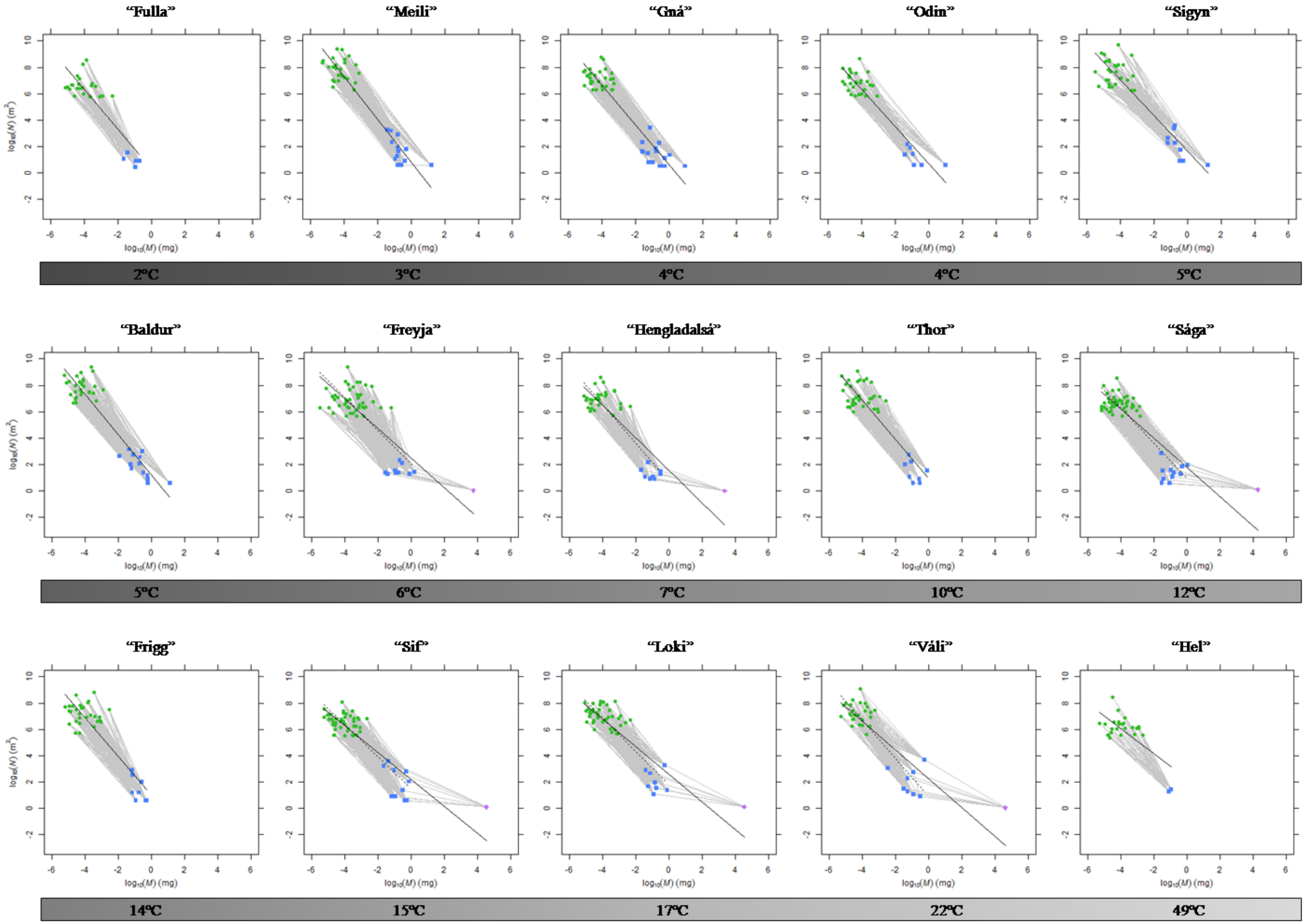

Figure 28 Trivariate food webs of 15 streams (names above each plot) along the temperature gradient. In each plot the $\log_{10}$-transformed abundance per m^2 of each species is plotted against their $\log_{10}$-transformed body mass in mg. Green solid circles represent diatom species, blue solid squares represent macroinvertebrate species and purple solid circles represent the only present fish species, brown trout. Solid lines represent linear regression lines, dotted lines represent linear regressions after exclusion of trout.

The species and link richness of each food web did not change significantly with temperature (species richness:$F_{1,13}$=0.77, P=0.304, *adj.* R^2=-0.02 , link richness:$F_{1,13}$=2.71, P=0.124, *adj.* R^2=0.11, Figure 29). In a second analysis Hel was excluded, but there was still no significant change in species richness ($F_{1,12}$=1.02, P=0.332, *adj.* R^2=0.002) or link richness ($F_{1,12}$=0.06, P=0.808, *adj.* R^2=-0.08).The highest numbers of species and links tended to be found at intermediate temperatures.

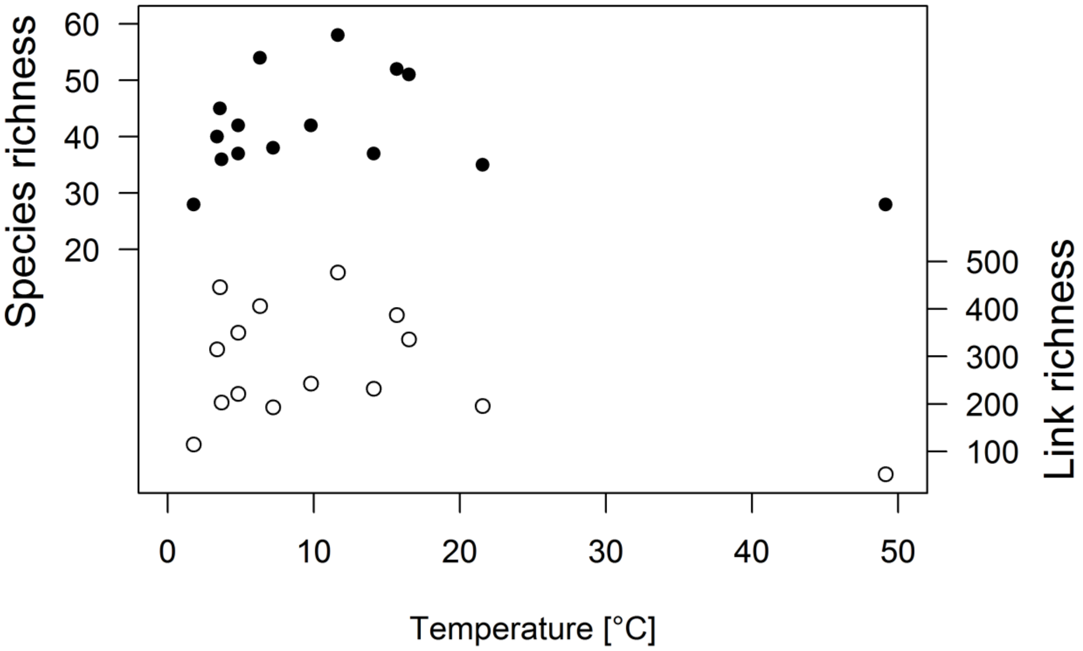

Figure 29 Species and link richness in each food web plotted against the mean temperature of the streams in April 2009.

The number of invertebrate species decreased significantly with temperature ($F_{1,13}$=7.31, P=0.018, *adj.* R^2=0.31; Figure 30), whereas there was no significant change when Hel was excluded in a second analysis ($F_{1,12}$=0.95, P=0.348, *adj.* R^2=-0.004; Figure 30) . The number of diatom species did not respond significantly to temperature (whole temperature gradient:$F_{1,13}$=0.0006, P=0.983, *adj.* R^2=-0.08, exclusion of Hel: $F_{1,12}$=2.09, P=0.174, *adj.* R^2=0.08; Figure 30).

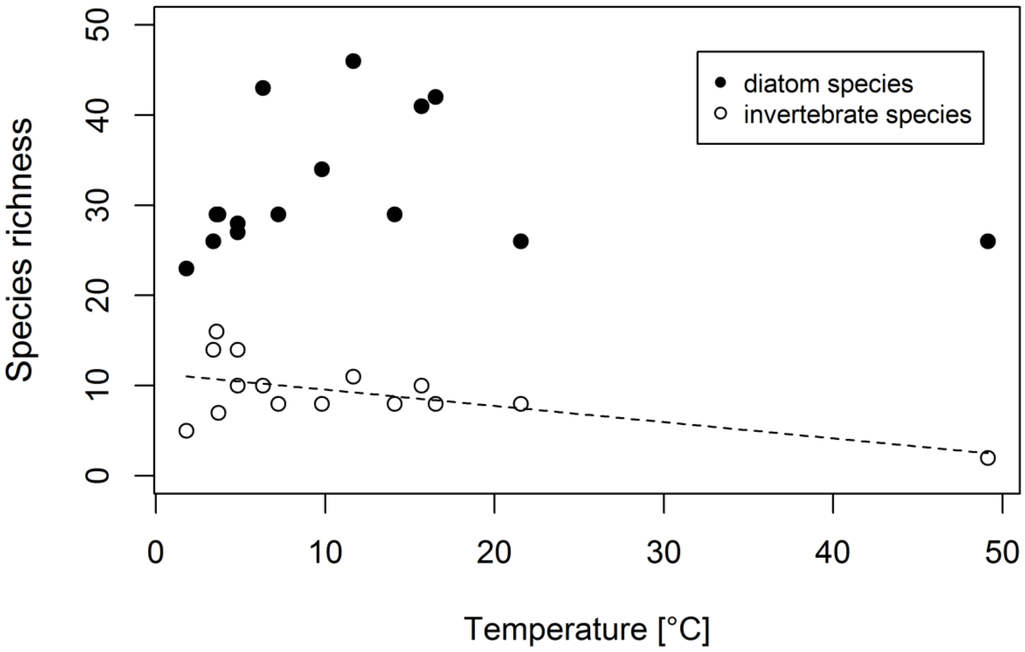

Figure 30 Number of invertebrate (y = -0.18x+11.36) and diatom species along the temperature gradient.

The connectance and complexity (Figure 31) of the food webs decreased significantly when temperature increased (connectance:$F_{1,13}$=14.46, P=0.002, *adj.* R^2=0.49, complexity: $F_{1,13}$=7.21, P=0.019, *adj.* R^2=0.31). Decrease of connectance and complexity with increasing temperatures were only significant for the whole temperature gradient, but not under the exclusion of the warmest stream (Hel, 49.1°C) (connectance:$F_{1,13}$=14.46, P=0.002, *adj.* R^2=0.49, complexity: $F_{1,13}$=7.21, P=0.019, *adj.* R^2=0.31).

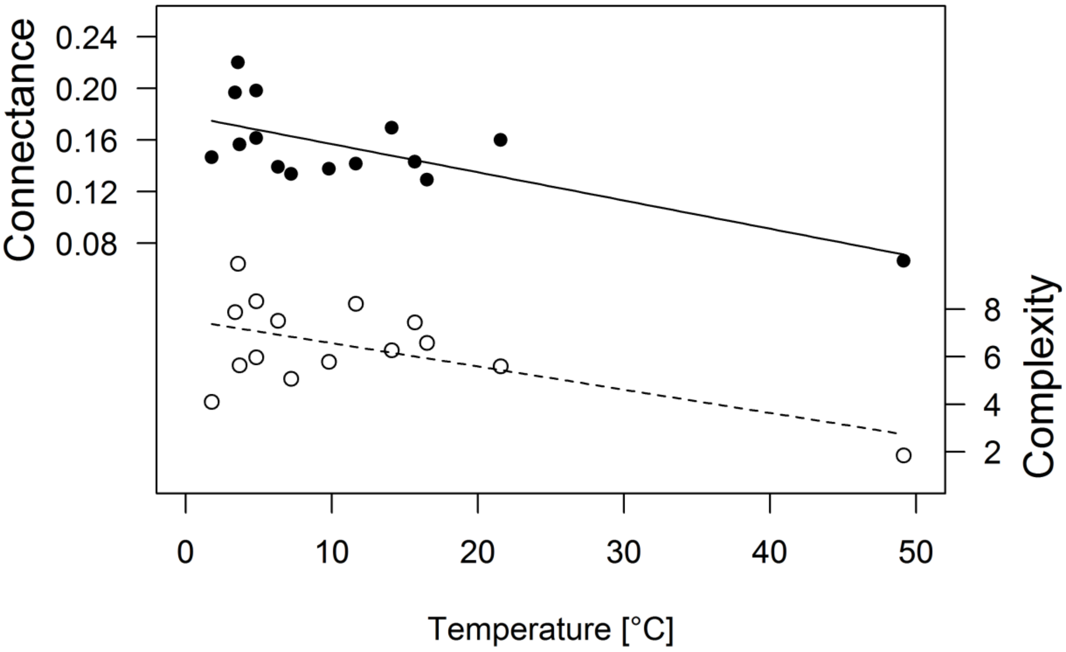

Figure 31 Values of connectance and complexity against respective mean temperatures of streams. Connectance is represented by solid circles (y = -0.002x +0.18, while complexity is represented by open circles (y = -0.10x + 7.55).

The slope of the trivariate webs increased significantly with temperature both with ($F_{1,13}$=11.15, P=0.005, *adj.* R^2=0.42; solid regression line in Figure 32a) and without ($F_{1,13}$=20.59, P=0.001, *adj.* R^2=0.58; dashed regression line in Figure 32a) brown trout included in the analysis. The intercept with the smallest individual in the dataset significantly decreased with increasing temperature both with ($F_{1,13}$=9.22, P=0.010, *adj.* R^2=0.37; solid regression line in Figure 32b) and without($F_{1,13}$=10.67, P=0.006, *adj.* R^2=0.41; dashed regression line in Figure 32b) trout included in the analysis. The intercept with the largest individual in the dataset increased with increasing temperature both with ($F_{1,13}$=9.18, P=0.010, *adj.* R^2=0.37; solid regression line in Figure 32c) and without($F_{1,13}$=10.28, P=0.007, *adj.* R^2=0.40; dashed regression line in Figure 32c) trout included in the analysis.

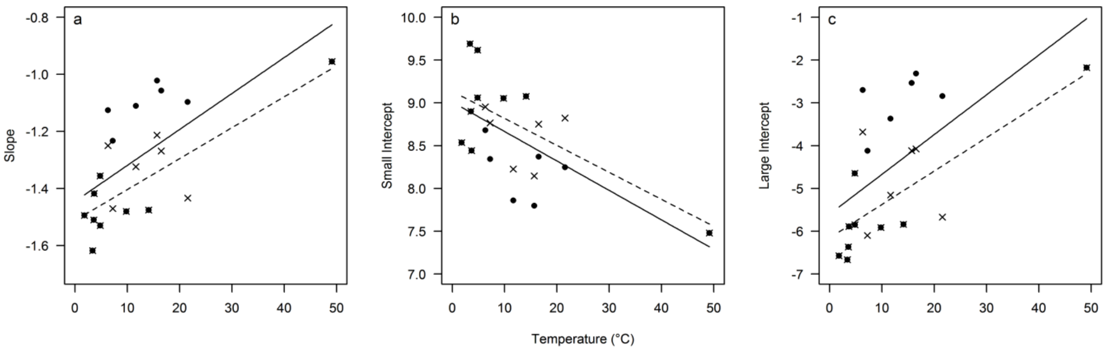

Figure 32 Values of slope and intercepts with smallest and largest individual in the dataset of the linear regressions fitted to the trivariate food webs in Figure 28 against mean temperature of the streams. Solid circles and lines represent the inclusion of trout, whereas crosses and dashed lines represent the exclusion of trout. (a) Trivariate slope values with linear regressions for trout included y= 0.01x-1.45and trout excluded y = 0.01x-1.51 (b) intercept values with smallest individual in the data set with linear regressions for trout included y= -0.03x+9.01and trout excluded y = -0.03x+9.13(c) intercept values with largest individual in the dataset with linear regressions for trout included y= 0.09x-5.60and trout excluded y = 0.01x-1.51.

After exclusion of the hot Hel stream, significant relationships with temperature were only found when the trout data was included. Here, the trivariate slope ($F_{1,12}$=10.77, P=0.007, *adj.* R^2=0.43; Figure 33a) and the intercept with the largest individual in the dataset ($F_{1,12}$=11.13, P=0.006, *adj.* R^2=0.44; Figure 33c) both increased significantly with temperature. There was no significant effect of temperature on either slope ($F_{1,12}$=3.08, P=0.105, *adj.* R^2=0.14; Figure 33a) or the intercept with the largest individual ($F_{1,12}$=2.49, P=0.141, *adj.* R^2=0.11,Figure 33c) when trout were excluded from the analysis. The intercept with the smallest individual in the dataset showed nosignificant change with temperature either with ($F_{1,12}$=4.12, P=0.065, *adj.* R^2=0.19; Figure 33b) or without ($F_{1,12}$=1.26, P=0.284, *adj.* R^2=0.02; Figure 33b) trout included in the analysis.

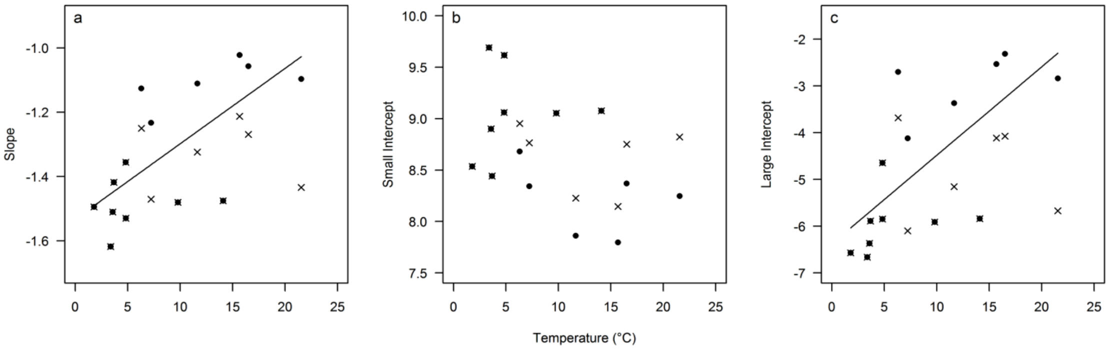

Figure 33 Values of slope and intercepts with smallest and largest individual in the data set of the linear regressions fitted to the trivariate food webs in Figure 28 against mean temperature of the streams, without the hot Hel stream included in the analysis. Solid circles and lines represent the inclusion of trout, whereas crosses and dashed lines represent the exclusion of trout. (a)Trivariate slope values with linear regressions for trout included y = 0.02x-1.53, (b) intercept values with smallest individual in the dataset, (c) intercept values with largest individual in the dataset with linear regressions for trout included y= 0.19x-6.38.

Neither the values of mean link length nor the values of community span showed a significant pattern along the whole temperature gradient when the hot Hel stream was included in the analysis (mean link length: $F_{1,13}$=3.13, P=0.101, *adj.* R^2=0.13, community span: $F_{1,13}$=0.46, P=0.512, *adj.* R^2=-0.04). Note that mean 2-span could not be calculated for the Hel stream because it contained no tritrophic chains. When the hot Hel stream was excluded in the analysis, mean link length did not vary significantly with temperature ($F_{1,11}$=32.16, P=0.121, *adj.* R^2=0.12, Figure 34 a); while mean values of 2-span ($F_{1,12}$=32.16, P<0.001, *adj.* R^2=0.72, Figure 34 b) and community span ($F_{1,12}$=5.28, P=0.041, *adj.* R^2=0.25, Figure 34c) increased significantly with increasing temperatures.

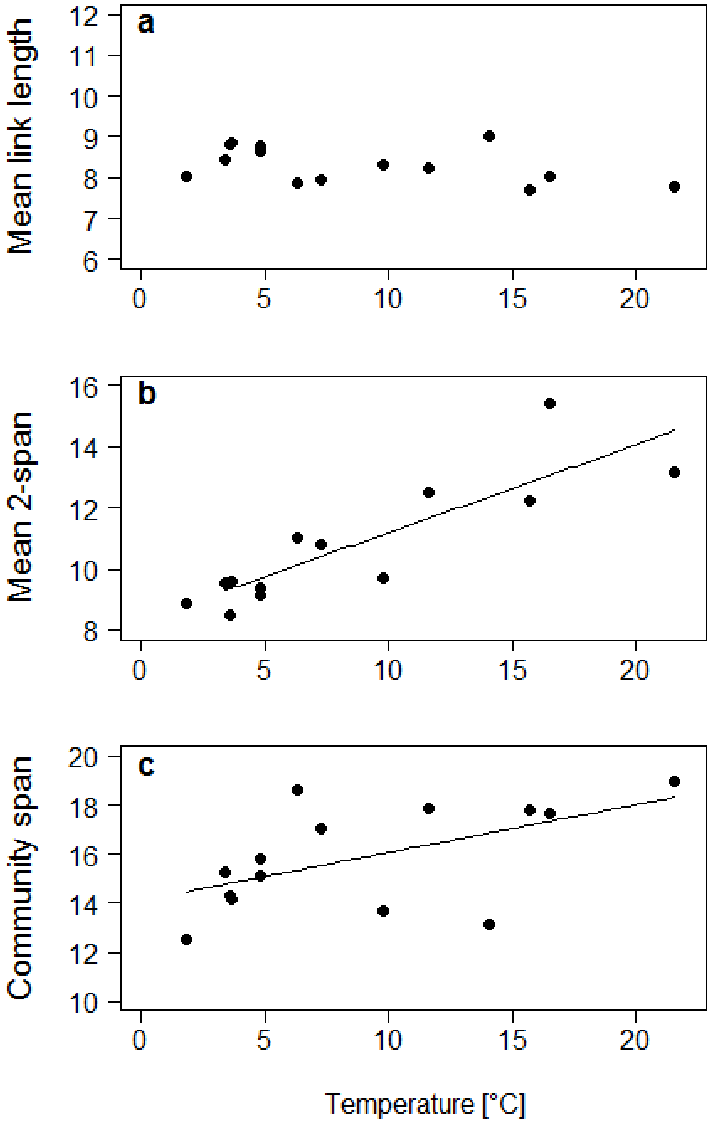

Figure 34 Mean link length (a), mean 2-span (b) and community span (c) against temperature of respective streams with exclusion of warmest stream Hel. Linear regressions: y=0.29x+8.32 for mean 2-span and y=0.20x+14.12 for community span.

10.4 Discussion

This study highlights the importance of temperature-induced changes in population biomass for the flow of energy through the food web. Here, although the total biomass of both consumers and resources remained relatively constant with temperature and did not correlate with each other (see Figure 22, Figure 23, Figure 24), the biomass of a key primary consumer, the snail *R. balthica*, increased with temperature (Figure 25). This had both bottom-up effects on the biomass of trout (FiguresFigure 25a andFigure 26a) and top-down effects on the biomass of some important diatom species (Figure 25d-f and b-d). While there was no change to the species or link richness of the food webs with warming (Figure 29), the dominance of trout and snails with increasing temperature and their associated strong interactions (as shown in O'Gorman *et al.*, in press) appear to reduce the connectance and complexity of the stream webs (Figure 31). There was also a fundamental change in the flow of energy through the system, with steeper mass-abundance slopes and changes to the intercept with the smallest and largest individuals in the dataset leading to increased trophic transfer efficiency (see FiguresFigure 28, Figure 31 and Figure 32). This change in energy flow was further evidenced by the increase in mean 2-span and community-span, which suggest that energy flows further up the food web through intermediate sources as stream temperatures increase.

Species richness showed no response to temperature, in contrast to the second hypothesis. Here, warming was expected to lead to species loss as cold-stenotherm species are pushed beyond their temperature tolerance (Chevaldonné & Lejeusne, 2003; Pörtner, 2001). However, there is also the possibility for invasion by warm stenotherms or eurythermal species (Dukes & Mooney, 1999; Francour *et al.*, 1994; Walther *et al.*, 2002). The previous chapter provided evidence that cold-stenotherm species declined in abundance with increasing temperatures, while eurythermal species increased. This suggests that there is a shift in species dominance, as the niches vacated by cold-adapted species are filled by eurytherms, but the number of species as well as the overall biomass is maintained. Here, it was found that the standing stock of biofilm and the diatom biomass did not change with temperature. The same is true for the consumer biomass including macroinvertebrates and trout. An increase in consumer biomass was found when the hottest stream, Hel, was excluded from the analysis, which is most likely driven by the presence of brown trout in the warmer streams. No correlation was found between the increasing consumer and producer biomass, suggesting no top-down effect of the consumers on producers. These findings contradict the first hypothesis predicting that warming should lead to an increased biomass of small resources and a reduced biomass of larger consumers. Many previous studies suggest that resource biomass should increase and consumer biomass should decrease due to an increased prevalence of smaller bodied organisms with warming (Daufresne, Lengfellner & Sommer, 2009; Strecker *et al.*, 2004; Yvon-Durocher *et al.*, 2010). However, the results shown here from the natural warming experiment at Hengill suggest that these predictions may not be as general as once thought.

In contrast to the overall producer and consumer biomasses, clear changes and correlations of biomass could be determined for some key species. Biomass of *R. balthica* increased significantly with temperature. This species is known for being very adaptable and able to breed continuously (Glöer, 2002; Wullschleger & Jokela, 2002). It provides an important and continuous source of food for the brown trout and is therefore able to support increases in brown trout biomass as more snail biomass becomes available with increasing temperature. A similar bottom-up effect of a key species has previously been demonstrated by Frederiksen *et al.*(2006), where sand eel populations can support an apex predator, here sea birds, by building up high abundances when prey (phytoplankton) availability is sufficient and predation pressure is low.

In addition to this bottom-up effect on the biomass of brown trout, *R. balthica* also had an apparent top-down effect as an effective grazer on the diatom community

(O’Gorman *et al.*, in press; Rosemond, Mulholland & Elwood, 1993). Although the decrease in total biomass of diatoms was not significant, the biomass of key diatom species decreased with temperature, e.g. *A. lanceolata*, *G. type D* and *M. circulare*, all of which are highly abundant in streams with trout present (see Figure 25). The correlation analysis strongly suggests that the biomass of *A. lanceolata* and *M. circulare* were diminished with increasing temperature as biomass of *R. balthica* increased (Figure 26). The gut content analysis of trout in April 2009 also highlighted the importance of *R. balthica* as an important part of the trout diet. Steingrímsson & Gíslason (2002) previously showed that snails become increasingly important in the diet of larger trout. Given that trout are known to get larger with temperature in the Hengill system (O’Gorman *et al.*, in press), it is unsurprising that snails become a more prominent component of their diet in the warmer streams, especially when combined with the increasing biomass of snails observed with increasing temperature (see Figure 25b). The correlation between trout and snail biomass (Figure 26a) also suggests that this is a key food web link, facilitating the existence of apex predators in the warmer streams that otherwise would not have the resources to survive at colder temperatures

Complexity and connectance did not decrease significantly with temperature up to 25 °C as predicted in the third hypothesis (see Figure 31). A significant decrease in these measures was only found with the warmest stream Hel included in the analysis. The lower values of connectance and complexity in the warmest steam Hel (which drive a significant decline in both measures across the temperature gradient; see Figure 31) are likely explained by the low number of macroinvertebrate species in this stream and the complete lack of predator-prey interactions, beyond primary consumption of basal resources. Species and link richness, which are the components that calculations of connectance and complexity are based on, did not change with temperature (Figure 29).

As demonstrated in the previous data chapter, species composition changes, with temperature, which is likely to maintain species richness as well as the connectance and complexity of the system in the face of environmental warming.

Complexity and connectance are both indicators used to assess the stability of a system with higher complexity enhancing stability (Dunne, Williams & Martinez, 2002a; May, 1972; McCann, 2000; Montoya *et al.*, 2006; Pimm, 1984). The fact that neither of these measures decreased with warming in the Icelandic system suggests that the streams may be in a stable state. The lack of a temperature effect on the connectance of the food webs, suggests that the warm streams are as likely to be robust to secondary extinctions as the colder ones (Dunne *et al.*, 2002a). Additionally, given the tight links between complexity and stability (May, 1972, 1973; Montoya *et al.*, 2006), the similar levels of complexity across the temperature gradient suggest a degree of consistency in the stability of these freshwater streams. It should be noted that this food web analysis is for a single snapshot in time (April 2009) and thus may not give an accurate depiction of the true system dynamics. Therefore, it would be valuable to address changes in complexity, connectance and stability on a wider temporal scale, especially given the long-term attributes of stability metrics (Loreau *et al.*, 2002).

In the exploration of body mass - abundance scaling, body mass showed the typical negative scaling with abundance (Dinmore & Jennings, 2004; Hechinger *et al.*, 2011; O'Gorman & Emmerson, 2011; Woodward, Perkins & Brown, 2010c). Significant changes of the body mass – abundance scaling with temperature were found. Slopes of the linear regressions increased significantly with temperature, while intercepts at the small end of the body mass spectrum decreased as intercepts at the large end of the spectrum increased (Figure 32and Figure 33). In comparison with the scenarios for body mass – abundance scaling in Figure 1 in the general introduction, the decrease in small intercepts, the increase in large intercepts and the decrease in slope is equivalent to scenario (d). Thus, as temperature increases fewer small species support more large species resulting in an increase in energy transfer efficiency and/or stronger top-down control. This is in contrast to the prediction of a decrease in energy transfer efficiency with warming as stated in the fourth hypothesis and the findings from previous studies in experimental mesocosms (Yvon-Durocher *et al.*, 2011, although see Dossena *et al.*, 2012) (Dossena *et al.*, 2012). Yvon-Durocher *et al.*(2011) demonstrated a steepening of mass-abundance slopes with warming, implying a decrease in energy transfer efficiency. In contrast to that study no reduction in biomass due to smaller body sizes could be found in this study on a natural system. In fact, the increase in trophic transfer efficiency suggests that, at warmer temperatures, it is possible to sustain a greater consumer biomass. Thus, large predators such as brown trout may be able to prevail at elevated temperatures in spite of their high metabolic demands (Brown *et al.*, 2004; Hairston Jr. & Hairston Sr., 1993).

No significant change was detected for mean link length with temperature (Figure 34a). This indicates that consumers generally do not alter their feeding behaviour in body mass and abundance space, as suggested in the fifth hypothesis. Thus, there was no actual change in the predator – prey body mass ratio, as predators were still feeding on prey of similar mass and abundance when temperature increased. Community span and 2-span in the 14 streams (Hel excluded) increased significantly when temperature increased (Figure 34b-c), a pattern most likely driven by the presence of trout in warmer streams as these measures represent the energy flow in the system through intermediate sources (Cohen *et al.* 2009). In the warm streams the path from diatoms, through *R. balthica* to brown trout becomes the main pathway of energy flow in the system. This suggests that this interaction between *R. balthica* and *S. trutta* is the key interaction driving the energy relationships observed in this system.

The findings of this chapter demonstrate crucial changes in energy flow with temperature, which were often in contrast to theoretical predictions (Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011) and the findings of previous experimental studies (Yvon-Durocher *et al.*, 2011). There were no associated changes in the structure or complexity of stream food webs, suggesting a relatively stable system. However, dramatic changes in population biomass with temperature suggest that energy flow in the system is maintained by just a few key groups. Thus, strong interactions and biological processes have the capacity to overwrite expected temperature-driven impacts in freshwater ecosystems.

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11 Warming alters food web structure and complexity

11.1 Introduction

The Earth is currently undergoing atmospheric warming at an historically unprecedented rate(IPCC, 2007; Parmesan & Yohe, 2003). Average global temperatures are predicted to increase further in the 21st century, with estimates of a 3-5 ºC increase in surface temperature over the next 100 years (IPCC, 2007). Research on the biological impact of climate change has largely focused on the phenology and physiology of individuals and changes in species distribution (Hickling *et al.*, 2006; Menzel *et al.*, 2006; Parmesan *et al.*, 2003; Visser & Both, 2005). However, the impact on higher levels of organisation, such as communities and ecosystems, cannot be predicted from effects on individual organisms alone (Walther, 2010; Woodward, 2009). One way to capture and describe a community is by the construction of its food web, which depicts species and their feeding interactions with each other (Pimm, 1982).

Several measures can be used to describe the structure of a food web. Measures include the *number of nodes* S (i.e. species richness), *number of consumer-resource links* L, *connectance* C (i.e. the total number of realised links divided by the number of possible links $C = L/S^2$ after Martinez, 1991) and *complexity* ($SC=L/S$) (May, 1972, 1973; Pimm, 1982; Woodward *et al.*, 2005). Species richness has been shown to be influenced by warming as individual species are lost when pushed beyond their thermal tolerance (Pörtner, 2001). Especially cold-stenotherm species are likely to be affected by rising temperatures as they are more easily pushed beyond their tolerable temperature limits (Chevaldonné & Lejeusne, 2003; Hering *et al.*, 2009), which would result in decreasing abundances or extinction. Warming has therefore the potential to alter community structure and species composition (Klanderud & Totland, 2005; Parmesan, 2006;

Petchey *et al.*, 1999; Pörtner & Farrell, 2008). These potential alterations in the community structure are likely to be reflected in measures like connectance and complexity. Both these measures have been suggested to be indicative of the stability of a community. A reduction of robustness, i.e. increasing the risks of secondary extinctions, has been described as a consequence of lowered connectance (Dunne, Williams & Martinez, 2002), whereas an increased fragility of ecological networks have been ascribed to the reduction in complexity (Montoya, Pimm & Sole, 2006).

The structure of a community is not random (Elton, 1927) and structure in aquatic food webs in particular is often clearly determined by body size (Cohen, Jonsson & Carpenter, 2003; Woodward *et al.*, 2005), i.e. smaller organisms are typically eaten by larger organisms (Elton, 1927; Jonsson, Cohen & Carpenter, 2005; O'Gorman & Emmerson, 2010). Body size can also be interpreted as a useful proxy for several other key ecological traits, including diet width, productivity and population abundance (Woodward *et al.*, 2005). Many studies to date strongly suggest that a universal response to increasing temperatures is a decrease in body size (Daufresne, Lengfellner & Sommer, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011). According to James's Rule most ectothermic individuals within a species are likely to grow to smaller sizes in warmer environments (Daufresne *et al.*, 2009; James, 1970). The Temperature-Size Rule is an extension of James’s rule, but states not only growth to smaller sizes, but also increased growth rates and has typically been demonstrated in a laboratory setting (Atkinson, 1994, 1995; Atkinson, Ciotti & Montagnes, 2003). On a more global scale it has been shown by Bergmann’s Rule that more species with smaller body size can be found in colder environments (Angilletta Jr & Dunham, 2003; Bergmann, 1847).

Trivariate food web plots illustrate the relationship between mean species body mass (Log_{10} M), species abundance (Log_{10} N) and trophic interactions (Cohen *et al.*, 2003;

Jonsson *et al.*, 2005; Layer *et al.*, 2010; McLaughlin, Jonsson & Emmerson, 2010; O'Gorman *et al.*, 2010). They generally reflect the size dependence of a food web structure by separating out different trophic taxa in clouds of nodes with small, very abundant basal taxa (e.g. diatoms), intermediate taxa (e.g. macroinvertebrates) and large, rare top taxa (e.g. fish) (Cohen *et al.*, 2009). Energy flows predominantly from a larger number of small and abundant species to a smaller number of larger and rarer species (Brown *et al.*, 2004; Cohen *et al.*, 2003). Linear regressions can be fitted to the trivariate plots and the slopes of the regression lines provide information about the efficiency of energy transfer (Cohen *et al.*, 2003). (Allen, Brown & Gillooly, 2002; Brown *et al.*, 2004). In an unwarmed and stable system body mass (M) typically scales with abundance as $M^{-3/4}$ ((Brown *et al.*, 2004; Damuth, 1981; MacMahon & Bonner, 1983), although such scaling is usually only found on a global scale (Blackburn & Gaston, 1997; Cyr, Downing & Peters, 1997). Changes in abundance and body size of species due to warming are expected to be reflected in the body mass – abundance scaling. Different scenarios on the changes of body mass – abundance scaling and their implications on the energy transfer efficiency are summarised in Figure 1 of the General Introduction. Previous studies in an experimental setup did show that, with decreasing body sizes due to warming, the slope of the regression in the body mass – scaling increased, indicating a decrease in energy transfer efficiency (Yvon-Durocher *et al.*, 2011).

Further properties of the structure of food webs can be derived from the trivariate food web plots (Cohen *et al.*, 2009): *Mean link length* is a measure of the average distance between two taxa, i.e. the resource and consumer, calculated by its Manhattan grid distance on the log M – log N plot. Link length therefore represents the relative difference of trophic height between a consumer and a resource, with a shortening of link length indicating that consumers feed on higher trophic levels in the food web. *Mean 2-span* similarly measures the distance covered by a 2-chain (3 nodes: basal, intermediate and top connected by two links) depicting a tritrophic interaction. Changes in 2-span describe an alteration in the flow of energy from resources to consumers through an intermediate source: the greater the 2-span, the farther up the food web energy is travelling in tritrophic chains. *Community span* measures the Manhattan distance covered by the whole trivariate food web (Cohen *et al.*, 2009) and gives an indication of the trophic span in the community from the smallest, most common resource to the largest, rarest consumer.

In this study the following hypotheses were tested:

1. Complexity and connectance should decrease with increasing temperatures. In this cold-adapted system, species richness as well as link richness should decrease with warmer temperatures.
2. Energy transfer efficiency should decrease with warming as an increased prevalence of small organisms with temperature is expected to change the body mass-abundance scaling.
3. Values of mean link length, 2-span and community span should shorten as consumers decrease in size and feed on resources that are closer to their own body mass and abundance due to increased energetic demands with temperature.

11.2 **Methods**

Study site

The study site is located in the geothermally active area of Hengill, South-West Iceland. Seven streams were chosen for this study from the local stream system, connected via one main stem (Hengladalsá). The selected streams cover a temperature gradient from 6°C to 23°C (mean temperatures between summer 2008 and spring 2009). Each stream is warmed along its whole length by steam from boiling water reservoirs that warm the rocks in contact with the ground water that feeds the streams (Arnason *et al.*, 1969). Due to this form of deep heating, the water chemistry is very similar in all streams of the catchment, because it is not perturbed by additional chemical constituents (e.g. sulphur) normally associated with geothermal activity (Demars *et al.*, 2011; Friberg *et al.*, 2009; Woodward *et al.*, 2010). Sampling of the seven streams took place in August 2008 and April 2009.

Biotic characterisation

In order to identify the nodes, i.e. species, of the food webs in each stream the diatom, macroinvertebrate and fish community was examined at the height of summer (August 2008) and immediately after snowmelt (April 2009) in order to capture representative samples for one reproductive season. Diatom species composition was established from three haphazardly collected stones of roughly the same size per stream. The biofilm was scrubbed from the upper stone surface using a tooth brush, rinsed into 15 ml centrifuge tubes with stream water and preserved with approx. 1 ml of Lugol’s solution (Kemp, 1993). Stones were photographed (including an absolute scale) and surface areas calculated using ImageJ (Rasband). Back in the laboratory the diatom frustules were cleared of all organic matter with nitric acid (e.g. Eminson & Moss, 1980), diluted and stored in distilled water. 500 µl of each sample were then dried and mounted on a round slide (15mm in diameter) with Naphrax (Brunel Microscopes Ltd., Chippenham, U.K.). A set transect (100µm wide, 15 mm long) containing at least 300 valves was chosen along the middle of the slide for counting of diatoms and , where possible, identification to species level based on Krammer & Lange-Bertalot(1986; 1988, 1991a; 1991b).

The composition of the macroinvertebrate community was established from five Surber samples (25 x 25 cm quadrat, 200µm mesh size) per stream and sampling occasion. Samples were preserved in 70% Ethanol. Individuals were identified to the highest possible level of resolution using a range of freshwater invertebrate keys (Bouchard, 2004; Brooks, Heiri & Langdon, 2007; Cranston, 1982; Gíslason, 1979; Glöer, 2002; Hopkins, 1961; Peterson, 1977; Savage, 1989; Schmid, 1993; Smith, 1989; Usinger, 1956; Wiederholm, 1983). Chironomids head capsules were cleared with Potassium hydroxide (KOH) and mounted on slides with Euparal before identification using a light microscope (400 to 1000x magnification) (Brooks *et al.*, 2007). All other taxa were identified under 50x magnification.

The examination of the fish community was done by depletion electro fishing (230 V using a Honda EX 500 Inverter generator) of each sampling stretch at both sampling occasions. Fish were measured in terms of fork length, and were then weighed and gut flushed on site before being released. Gut contents were preserved in 70% Ethanol.

A more detailed description of methods used in this study can be found in the General Methods (Chapter 7.1)

Construction of food webs

The food webs were constructed from the species identified in each of the streams, representing the nodes, while the links were determined from direct observation where possible, i.e. gut content analysis, with the remaining links inferred from the literature (Usinger, 1956; Warren, 1989; Woodward & Hildrew, 2001). Just a limited amount of directly observed links was provided per stream and date combination, due to the low number of individuals available in comparison to the large number of individuals needed to capture all the links in the food web directly (Ings *et al.*, 2009; Woodward *et al.*, 2001). The links in the food webs presented here are thus a combination of data obtained from August 2008 and April 2009, to produce a summary food web for the growing season. For each species, node abundance (per m^2) and mean body mass (dry mass in mg) were calculated in each stream using the data collected in 2008 and 2009. For each species and each sampling occasion, up to 30 individuals were measured in some form of linear dimension of body size (i.e. head width, body length, body width or shell width). For macroinvertebrates, body mass was then calculated from length-mass regressions from the literature (Baumgärtner & Rothhaupt, 2003; Benke *et al.*, 1999; Johnston & Cunjak, 1999; Ramsay *et al.*, 1997; Stoffels, Karbe & Paterson, 2003; Woodward & Hildrew, 2002). For diatoms, body volume was calculated after Hillebrand *et al.*(1999) using length, width and depth and then transformed into body mass after Reiss & Schmid-Araya (2008). Wet weight (*ww*) of fish was directly measured at the sampling site and the respective dry weight (*dw*) calculated after the equation for wet-dry mass conversions, dw=1.07ww-0.62 (R^2=0.97) (Edwards, F. K, unpublished).

A more detailed description of the biotic characterisation and the construction of the food webs including the inferring of feeding links can be found in the general methods (Chapter7.1 and 7.2).

Food web statistics

Food web statistics to examine the structure of the webs along the temperature gradient include the univariate measures of *number of nodes S* (i.e. species richness), *number of consumer-resource links L*(i.e. link richness), *connectance C* (i.e. total number of realised links divided by the number of possible links $C = L/S^2$ after Martinez, 1991) and *complexity*($SC=L/S$)(May, 1972; Woodward *et al.*, 2005).

From the trivariate food webs, values of the slope and intercept of fitted linear regressions were calculated for each stream. Additionally, the *mean link length, mean 2-span*and *community span* were calculated after Cohen *et al.*, 2009.

Statistical analysis

Measures were plotted against the respective temperatures of each stream and linear regressions fitted in order to examine how those values change with temperature. The trivariate food webs were constructed, plotted and analysed in R 2.15.1 (R Development Core Team, 2011)using the ‘cheddar’-package (Hudson, 2012) with $\log_{10}$-transformed values of body mass (Log M) and abundance (Log N). All other analyses were also conducted in R 2.15.1.

11.3 **Results**

A range of univariate food web statistics were calculated for the food webs and are summarised in the following table with the respective mean temperature values of the streams:

Stream	**Temperature [ºC]**	**No. of species (*S*)**	**No. of links (*L*)**	**Connectance ($C = L/S^2$)**	**Complexity ($SC==L/S$)**
Sigyn	5.5	55	580	0.19	10.55
Baldur	6.5	61	801	0.22	13.13
Gná	8.2	65	860	0.20	13.23
Thor	14	58	576	0.17	9.93
Sága	17.2	66	560	0.13	8.48
Loki	18.9	70	747	0.15	10.67
Váli	23.1	46	360	0.17	7.83

Table 2 Summary of structural food web properties for the seven stream ordered by their respective temperature.

Complexity of the food webs decreased significantly ($F_{1,5}$ =7.58, P=0.040, *adj.* R^2=0.52) with increasing temperatures (Figure 35), whereas no other measure i.e. species richness, link richness and connectance changed significantly with temperature(species richness:$F_{1,5}$ =0.13, P=0.731, *adj.* R^2=-0.17 , link richness:$F_{1,5}$ =2.90, P=0.149, *adj.* R^2=0.24, connectance:$F_{1,5}$ =6.16, P=0.056, *adj.* R^2=0.46). The lowest total numbers of species and links were found in the warmest stream, Váli.

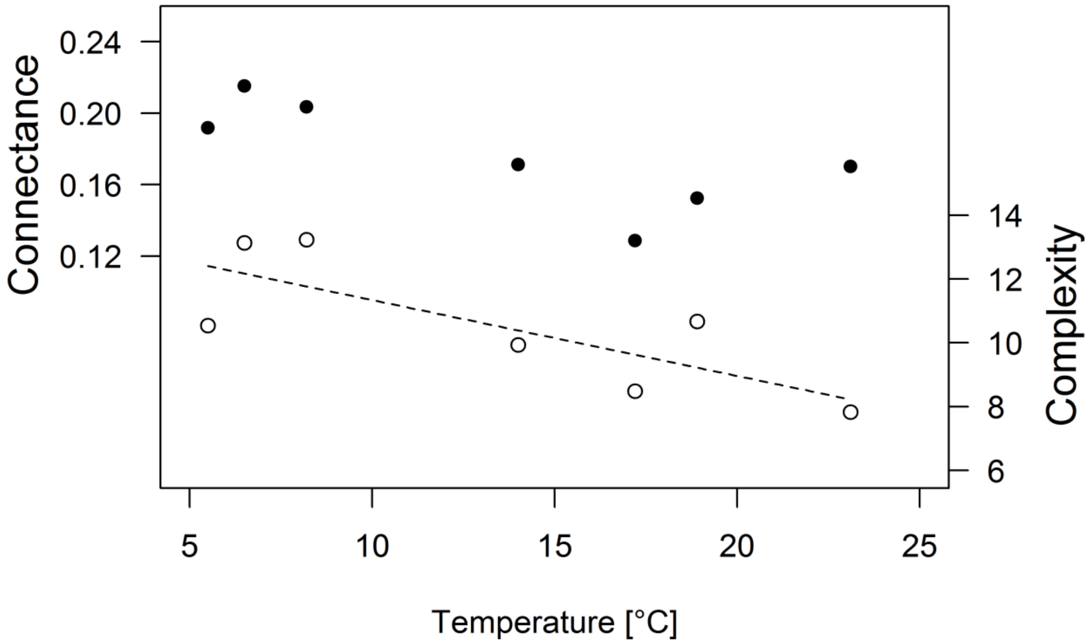

Figure 35 Values of connectance and complexity against respective mean temperatures of streams. Connectance represented by solid circles .Complexity represented by open circles with linear regression y=-0.24x+13.72 ($F_{1,5}$=7.58, P=0.040, *adj.* R^2=0.52).

The exploration of the trivariate food web properties revealed a linear decrease in Log N as Log M increased for all food webs (36). In each web, there was a separation of two or three groups (i.e. clouds of nodes): basal taxa represented by diatoms, intermediate taxa represented by macroinvertebrate taxa and top taxa represented by the only fish species present, the brown trout (*Salmo trutta*L.). The four coldest streams, Sigyn, Baldur, Gná and Thor, were not inhabited by fish and are therefore missing these apex predators. Species numbers of diatoms remained similar over the temperature gradient ($F_{1,5}$= 0.29, P=0.616, *adj.* R^2=-0.14), whereas numbers of macroinvertebrate species decreased significantly ($F_{1,5}$=8.59, P=0.033, *adj.* R^2=0.56):

Stream	**Temperature [ºC]**	**No. of species** **“diatoms”**	**“macroinvertebrates”**	**“fish”**
Sigyn	5.5	36	19	0
Baldur	6.5	38	23	0
Gná	8.2	41	24	0
Thor	14	42	16	0
Sága	17.2	52	13	1
Loki	18.9	51	18	1
Váli	23.1	32	13	1

Table 3 Summary of number of species in the three tropic groups, diatoms, macroinvertebrates and fish ordered by mean temperature of streams

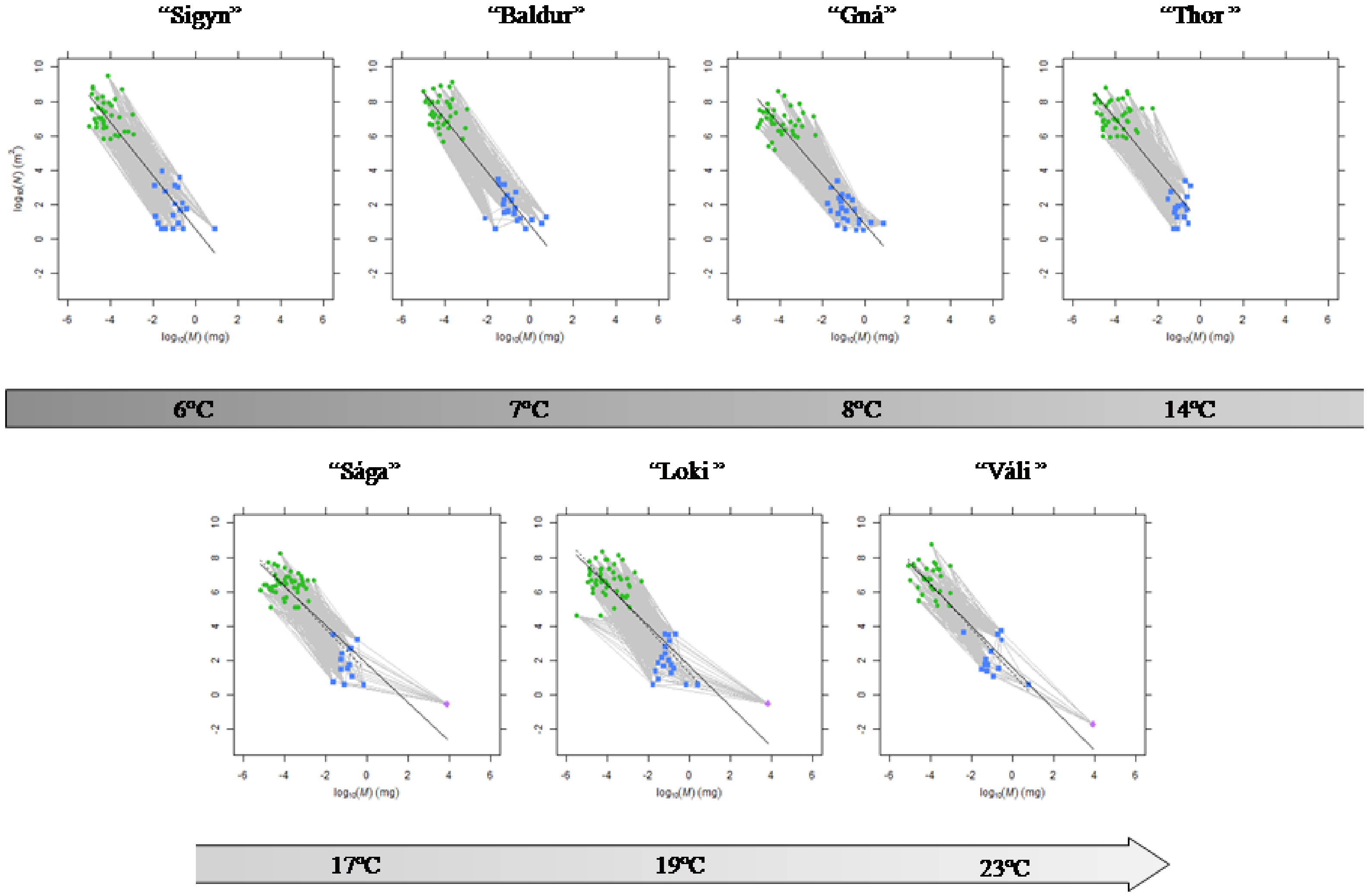

Figure36 Trivariate food webs of seven streams (names above each plot) along temperature gradient. In each plot the log$_{10}$-transformed abundance per m^2 of each species is plotted against their log$_{10}$-transformed body mass in mg. Green solid circles represent diatom species, blue solid squares represent macroinvertebrate species and purple solid circles represent the only present fish species, brown trout. Solid lines represent linear regression lines, dotted lines represent linear regressions with exclusion of trout

Linear regressions were fitted to the trivariate food web of each stream over all present trophic levels of the trivariate food webs and in a second analysis only to diatoms and macroinvertebrates i.e. under the exclusion of brown trout (see Figure36). Slope values increased significantly in both scenarios (trout included: $F_{1,5}$=12.99, P=0.016, *adj.* R^2=0.67, trout excluded: $F_{1,5}$=12.77, P=0.016, *adj.* R^2=0.66) with increasing temperatures (Figure 37a). The intercept values with the smallest individual in the dataset decreased significantly with temperature when trout were included ($F_{1,5}$=7.11, P=0.045, *adj.* R^2=0.51,Figure 37b), whereas the values with the largest individual in the dataset increased significantly ($F_{1,5}$=16.86, P=0.009, *adj.* R^2=0.73). In the analysis with trout excluded the intercepts with the smallest individual in the dataset did not change significantly with temperature ($F_{1,5}$=5.90, P=0.060, *adj.* R^2=0.45), whereas the values with the largest individual in the dataset increased significantly ($F_{1,5}$=19.54, P=0.007, *adj.* R^2=0.76, Figure 37c).

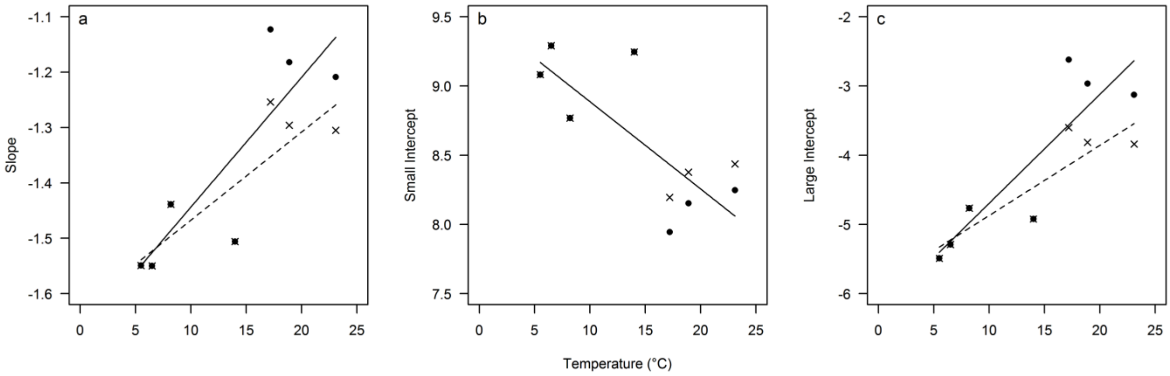

Figure 37 Values of slopeand intercepts with smallest and largest individual in the dataset of the linear regressions fitted to the trivariate food webs in Figure36 against mean temperature values of streams. Solid circles and lines represent the inclusion of trout, whereas crosses and dashed lines represent the exclusion of trout. (a)Trivariate slope values with linear regressions for trout included y = 0.02x-1.67 and trout excluded y = 0.02x-1.63, (b) intercepts with smallest individual with linear regressions for trout included y =-0.06x+9.52, (c) intercepts with largest individual in the data set with linear regression for trout included y= 0.16x-6.27and trout excluded y = 0.10x-5.88.

Further parameters calculated from trivariate food webs of each stream include mean link length, mean 2-span and community span (Figure 38). Mean link length decreased with increasing temperature (*F*$_{1,5}$=11.81, *P*=0.019, *adj. R* ^{2}=0.64), mean 2-span did not show a significant response (*F*$_{1,5}$=5.83, *P*=0.061,*adj. R* ^{2}=0.44), but community span increased (*F*$_{1,5}$=10.07, *P*=0.025, *adj. R* ^{2}=0.55).

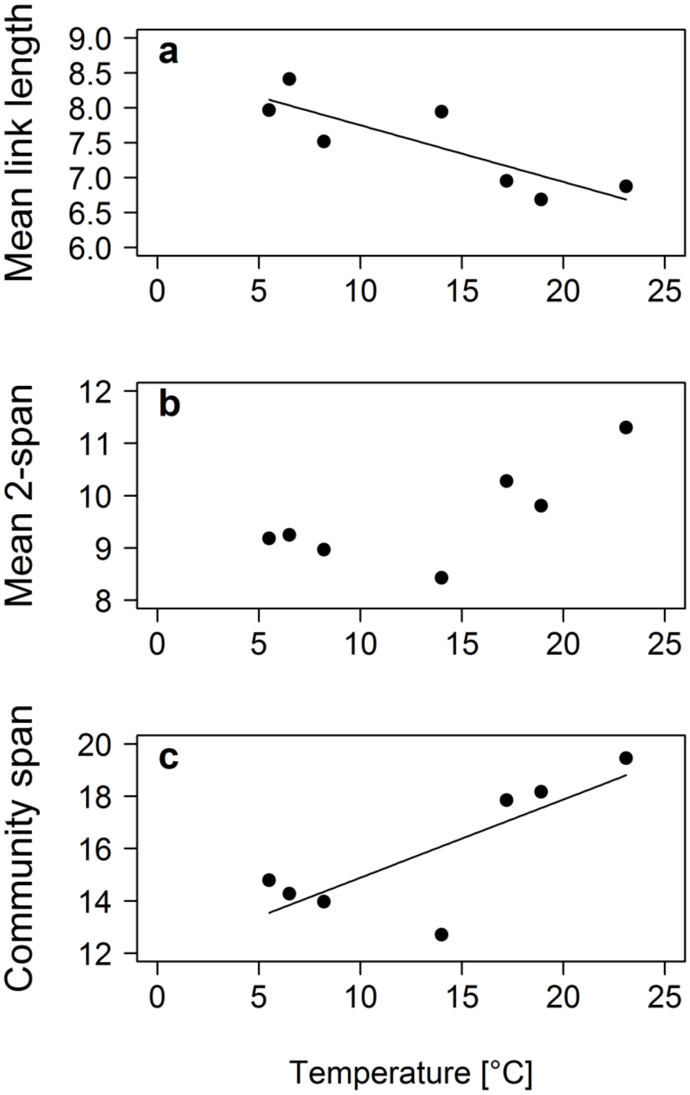

Figure 38 Mean link length (a), mean 2-span (b) and community span (c) against temperature of respective streams. Linear regressions: y=-0.8x+8.56 for mean link length, y=0.10x+8.23 for mean 2-span and y=0.30x+11.91 for community span.

11.4 **Discussion**

Temperature had clear effects on the structure of the food webs in this study. The main changes include the decrease in complexity (see Figure 35), whereas connectance, number of nodes and number of links were not significantly affected by temperature (see Table 2). Energy transfer through the system changed fundamentally as slopes of the body mass-abundance scaling steepened and the intercept with the smallest and largest individuals in the dataset changed significantly. The changes suggested an increase in energy transfer efficiency as temperatures increased (see Figure 37). The change in energy flow was further supported by the increase in community-span with temperature, suggesting that energy can be channelled further up the food web through intermediate sources (see Figure 38c). Mean link length within the food webs decreased significantly suggesting that consumers feed on prey closer to them in mass – abundance space (see Figure 38a). These results generally support the findings of the previous chapter, with results related to energy flow proving much clearer (Figure 37) and additional effects of warming determined on complexity (Figure 35) and mean link length (Figure 38a). Thus, while the number of food webs shown is fewer, the additional temporal resolution of the webs enhances the sensitivity of the analysis of warming impacts and reduces the likelihood of Type II errors. Such an outcome highlights the importance of studying food webs at more than one snapshot in time (Olesen *et al.*, 2010).

Species and link richness were not significantly lower in warmer streams contradicting the first hypothesis (see Table 2). This affirms the findings in the previous chapter, where changes with temperature were examined in 15 streams at one season (April 2009). Here, I investigate the changes for 7 streams but from combined data collected at the height of summer (August 2008) and immediately after snowmelt (April 2009), which should give a more complete picture in terms of temporal resolution (in contrast to greater spatial resolution in the second data chapter) of the streams in their structure and species composition. In the first chapter it was shown that cold-stenotherm species decreased in abundance with warming, whereas abundances of more eurythermal species increased. This suggests that even though species composition changed, species richness remained at a constant level. Connectance, a measure derived from species number and links was consequently not significantly affected by changes in temperature (see Figure 35). Connectance has been described to be indicative of the robustness of a food web to secondary extinctions (Dunne *et al.*, 2002), with more connected food webs found to be more stable and resilient against disturbance. On the other hand the demonstrated decrease in complexity with warming suggests an increase in the fragility of the system as described for ecological networks by Montoya, Pimm & Sole(2006). This finding was not shown for the more spatially resolved food web analysis in April 2009 only, thus highlighting the need for a fine balance between temporal and spatial resolution of food web structure.

Body mass – abundance scaling was affected by temperature. Similar to the findings in the second data chapter, the slopes of the regressions fitted to the trivariate food webs and large intercept values increased significantly, whereas the small intercept values decreased (see Figure 37). This represents scenario (d) as described in Figure 1in the General introduction suggesting an increase in energy transfer efficiency with warming. The changes in slope and large intercept were not just driven by the presence of trout in the three warmest streams as the temperature effect on the slope and large intercept values was still significant when data points of brown trout were excluded in a second analysis. Thus, the higher temporal resolution of this particular study reveals an energy flow pattern that is less driven by the new occurrence of an apex predator in warmer streams, but rather a more general pattern detectable across many other species in the system (Figure36 and Figure 37). These findings contradict the second hypothesis predicting the energy transfer efficiency to decrease with temperature. This hypothesis was based on previous findings form an experimental study where a steepening of mass-abundance slopes with warming was described implying a decrease in energy transfer efficiency (Yvon-Durocher *et al.*, 2011). In this experimental study, the change in slope was driven by a reduction in biomass due to smaller body sizes, which could not be confirmed in the present study on a natural system. Furthermore, the increase in trophic transfer efficiency suggests that it is possible to sustain a greater consumer biomass even at warmer temperatures. This enables large predators such as brown trout to prevail under conditions of the high metabolic demands due to higher temperatures (Brown *et al.*, 2004; Hairston Jr. & Hairston Sr., 1993).

The shortening of link length (see Figure 38a) suggests that predators are forced to alter their feeding behaviour in body mass and abundance space, for example by preying on larger individuals to meet the higher energetic demands of a warmer environment. The increase in community span (Figure 38c) on the other hand supports the increase in energy transfer efficiency as energy can be channelled further up the food web. This pattern is most likely driven by the presence of trout in warmer streams as these measures represent the energy flow in the system through intermediate sources (Cohen *et al*. 2009). This highlights again the key pathway of energy from diatoms through *R. balthica* to brown trout in the warmer streams.

The additional findings in this chapter with a higher temporal resolution in comparison to the findings in previous chapter with a higher spatial resolution are in particular the decrease in complexity (see Figure 35) and the decrease in mean link length (see Figure

38a) as temperature increases, as well as the reduced trout-dependency of the altered energy flow through the system (see Figure 37). This highlights the need to capture food web structure on a more temporally resolved scale, especially when examining complexity and energy flow, if we are to fully understand the dynamic response to temperature change in complex natural systems.

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12 Effects of warming on individual size distributions

12.1 Introduction

Regarding organisms as particles is not a widely used approach in the taxonomic-focused history of ecology (Petchey & Belgrano, 2010). However, there is a growing recognition that we may be constraining our understanding of complex natural systems through the use of an archaic method for classifying organisms, a phenomenon dubbed as the "curse of the Latin binomial" (Raffaelli, 2007). Recent research has made it clear that simply knowing the body size of an organism can already explain many of its functional and ecological traits (Brown *et al.*, 2004; Petchey *et al.*, 2010; Woodward *et al.*, 2005; Yvon-Durocher *et al.*, 2011) and may even allow us to predict interaction strength (O'Gorman *et al.*, 2010), size structure (Gilljam *et al.*, 2011), food web structure (Woodward *et al.*, 2010a) and associated food web properties (Petchey *et al.*, 2008). A popular approach in fisheries science is to ignore species identity and group individuals into size classes (Jennings *et al.*, 2002; Kerr & Dickie, 2001). This approach helps to explain a lot of the variation missed by taxonomic approaches because individuals of a similar size share common characteristics such as abundance, diet breadth, habitat use, home range, nutrient turnover and trophic position (Woodward *et al.*, 2005). There are limitations to the size-based approach, however, as it ignores the fact that some individuals in a size class may have completely different functional roles (predator *vs.* herbivore), physiology (fly larvae *vs.* snail), movement ability (mobile *vs.* sedentary) or indirect effects in the system (e.g. snails passively removing diatoms just from their movement across surfaces). While the taxonomic approach ignores the possibility that individuals of a species completely change their life history, functional roles or gape size, as they grow from larvae or juveniles to adults, individuals of a species often share common characteristics, such as anatomy, physiology, movement, behaviour and feeding mechanisms. Thus, it is important that we consider multiple approaches to the classification of individuals to limit variation and maximise the potential for identifying patterns in complex communities because each has their pros and cons. This thesis has focused on taxonomic approaches to date, but this chapter will be dedicated to the increasingly popular size-based approach.

It is also highly relevant to adopt a size-based approach to investigations of changes in community structure given the likely implications for global warming for the average size of species and individuals. A growing body of research has suggested decreasing body size as a universal response to environmental warming (Daufresne, Lengfellner & Sommer, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011).James's Rule suggests that, within a species, most ectothermic individuals are likely to grow to smaller sizes in warmer environments (Daufresne *et al.*, 2009; James, 1970). In experimental setups, it has been demonstrated that organisms grow to smaller sizes under warmed conditions, but with faster growth rates (Atkinson, 1994, 1995; Atkinson, Ciotti & Montagnes, 2003). It has also been shown by Bergmann’s Rule that more species with smaller body size can be found in colder environments (Angilletta Jr & Dunham, 2003; Bergmann, 1847). Thus, a size-based approach to community ecology may reveal the loss of larger size classes of organisms more readily than a taxonomic approach, which may mask the loss of larger size niches through averaging effects.

Abundance of organisms typically scales with body size in a food web from small, abundant producers to large, rare predators (Brown *et al.*, 2004; Jonsson, Cohen & Carpenter, 2005; Reuman & Cohen, 2004; Reuman & Cohen, 2005). One method to investigate body mass – abundance scaling in a food web based purely on size relies on so-called *individual size distributions* (ISD's)or *size spectra* (Kerr *et al.*, 2001; Petchey *et al.*, 2010; Reuman *et al.*, 2008). In contrast to the trivariate food webs used for abundance (*y*-axis) – body mass (*x*-

axis) scaling in the previous chapters, nodes in ISD's represent size classes rather than a single species. Grouping individuals based on their taxonomic identity might lead to missed patterns, as there is a large amount of size variation within a species that is lost through the calculation of average species body mass. As body size has been shown to be a good measure to capture many physiological and functional traits (Brown *et al.*, 2004; Petchey *et al.*, 2010; Woodward *et al.*, 2005; Yvon-Durocher *et al.*, 2011) it makes sense to investigate changes in size structure using a size based approach.

Energy is predicted to flow from small, abundant organisms to large, rare ones (Brown *et al.*, 2004; Cohen, Jonsson & Carpenter, 2003). As temperature has the potential to increase the prevalence of small organisms, the scaling properties of size spectra are likely to be affected. Changes in the slope or intercept with the smallest and largest organisms are likely to result in an altered flow of energy through the system, similar to the range of possible scenarios described for mass-abundance scaling in Figure 1in the General Introduction and in the previous two chapters. If smaller organisms do become more prevalent with warming (as predicted by Daufresne *et al*. 2009; Gardner *et al*. 2011; Sheridan & Bickford 2011), we may expect to see a reduction in trophic transfer. While evidence from taxonomic-based approaches suggests that this may not be the case in natural ecosystems (see Chapters 2 and 3), a size-based approach may offer a different perspective on the issue.

In a stable system (which is not under warming stress), body mass (M) typically scales with abundance as $M^{-3/4}$(Brown, 1995; Damuth, 1981; MacMahon & Bonner, 1983), although such scaling is usually only found on a global scale (Blackburn & Gaston, 1997; Cyr, Downing & Peters, 1997). Given that body mass also scales with metabolism as $M^{3/4}$(Brown *et al.*, 2004; Enquist, Brown & West, 1998; O'Gorman & Emmerson, 2011) there is a suggestion that mass-abundance scaling may be important for the conservation of energy with respect to body mass (Brown & Gillooly, 2003). Steeper (more negative) mass-abundance slopes should imply a reduction in population energy use with respect to body mass (e.g. $M^{-1} \times M^{3/4} = M^{-1/4}$), leading to a greater biomass of basal resources (as predicted by Daufresne *et al*. 2009; Gardner *et al*. 2011; Sheridan & Bickford 2011). Shallower (less negative slopes) should imply an increase in population energy use with respect to mass (e.g. $M^{-0.5} \times M^{3/4} = M^{1/4}$), leading to a lower biomass of basal resources (as shown in Chapters 2 and 3). These suggested impacts also support the predicted changes in trophic transfer efficiency highlighted in Figure 1 (and in the General Introduction), as more or less energy is funnelled through the food web depending on the scaling of mass-abundance relationships..

In addition to changes in mass-abundance scaling, a reduction in body size with warming may also have consequences for the average trophic height of the food web. For example, predators tend to be larger and have a higher trophic level than prey species which are smaller and lower in trophic height (Dickie, Kerr & Boudreau, 1987; Jennings & Mackinson, 2003; Sheldon, Prakash & Sutcliffe, 1972). Previous research has also found increasing $\delta\ _{15}N$ (‰) values and therefore increasing trophic height with bigger size classes in a marine system (Jennings *et al.*, 2003). Given the likely positive relationship between body mass and trophic height (Jonsson *et al.*, 2005; O'Gorman & Emmerson, 2010), an increased prevalence of smaller organisms with warming (as predicted by Daufresne *et al*. 2009; Gardner *et al*. 2011; Sheridan & Bickford 2011), may lead to an overall reduction in trophic height. Such effects are also likely to have severe consequences for top-down control and the flow of energy through food webs.

The following hypotheses were tested in this study:

1. Individual size distributions should show a negative relationship between size classes and the abundance of individuals making up those size classes.

2. The slope of individual size distributions should become steeper, with a greater intercept with the smallest individual and a lower intercept with the largest individual (as smaller organisms become more abundant with warming) which should result in reduced trophic transfer efficiency.

3. Values of $\delta_{15}N$ (‰) and therefore trophic height should increase as size classes of $\log_{10}$ M increase.

4. Warming should lead to a reduction in $\delta_{15}N$ (‰) if body mass decreases with increasing temperature.

12.2 Methods

Study site

The study site is located in the geothermally active area of Hengill, South-West Iceland. Fifteen streams were chosen for this study from the local stream system, all connected via one main river stem (Hengladalsá). The selected streams cover a temperature gradient from 2°C to 49°C (mean temperatures in spring 2009). Due to the form of heating by steam from boiling water reservoirs (Arnason *et al.*, 1969), each stream is warmed along its whole length and the water chemistry remains very similar between all streams of the catchment (Demars *et al.*, 2011; Friberg *et al.*, 2009; Woodward *et al.*, 2010b). Sampling of the fifteen streams took place in April 2009. For more detailed information on the study site see Chapter 8.

Biotic characterisation

Five haphazardly dispersed Surber samples (sampler area 500 cm^2; mesh size 200 µm) were taken in a 25 m stretch of each stream to capture the macroinvertebrate community. Samples were preserved in 70% Ethanol prior to sorting, identification, counting of abundances and measuring of head width, body length or shell width (depending on species) for the calculation of mean body mass per species. Individuals were identified to the lowest taxonomic level possible using a range of freshwater invertebrate keys (Bouchard, 2004; Brooks, Heiri & Langdon, 2007; Cranston, 1982; Gíslason, 1979; Glöer, 2002; Hopkins, 1961; Peterson, 1977; Savage, 1989; Schmid, 1993; Smith, 1989; Usinger, 1956; Wiederholm, 1983). Body mass was calculated from length-mass regressions from the literature using measured linear dimensions (Baumgärtner & Rothhaupt, 2003; Benke *et al.*, 1999; Johnston & Cunjak, 1999; Ramsay *et al.*, 1997; Stoffels, Karbe & Paterson, 2003; Woodward & Hildrew, 2002). The diatom community examined in their species composition, species abundances and species biomass from three randomly selected stones per stream. At least 300 valves per sample were identified to species level based on Krammer & Lange-Bertalot (1986; 1988, 1991a; 1991b) and counted. The cell volume was calculated after Hillebrand *et al.* (1999) using length, width and depth and then transformed into body mass after Reiss & Schmid-Araya (2008) from up to 10 individuals per species and stream.

Abundances of fish i.e. *Salmo trutta* L. were determined by depletion electro fishing (230 V using a Honda EX 500 Inverter generator) in each stream. Fish were measured in terms of fork length. For a more detailed description of the biotic characterisation see Chapter 7.1.

Individual size distributions

The ISD's were constructed as described in the literature (Brown *et al.*, 2004; Kerr *et al.*, 2001; Petchey *et al.*, 2010; Reuman *et al.*, 2008; Shin *et al.*, 2005). Body mass measurements were not taken for every single individual found, therefore missing body masses had to be estimated or the abundance of individuals within certain size classes would have been underestimated. Here, a log-normal size distribution was plotted for every species using the mean and standard deviation calculated from the measured individuals. Body masses for the unmeasured individuals were randomly chosen from within this distribution. These values were then imported into a dataset alongside the measured body mass values which was subsequently used for the construction of individual size distributions, after scaling up from the area and/or dilution of the sampling unit (i.e. stone area and sample dilution for diatoms, Surber sample area for macroinvertebrates and electro fishing reach area for trout). For example, the Surber sample area was 0.05 m^2, so the body mass of every individual macroinvertebrate was used 20 times in the dataset to scale up to 1 m^2. 24 evenly-spaced size classes (0.5 width on a $\log_{10}$ scale) were allocated, ranging from the lowest and highest $\log_{10}$ M value from all fifteen streams. The midpoints of these size classes were then plotted against the $\log_{10}$number of individuals (N) falling into the respective size class to create the final ISD(White *et al.*, 2007).

<u>*Stable isotope analysis*</u>

Stable nitrogen isotope analysis was carried out for the components of the regional food web. $\delta_{15}N$ (‰) represents the naturally occurring ratio of $_{15}N$ to $_{14}N$ in tissues of organisms which is stepwise enriched by approx. 3‰ as trophic level increases (e.g. DeNiro & Epstein, 1981; Hobson & Clark, 1992; Wada *et al.*, 1987). Macroinvertebrates were sampled from each stream using a pond net (330 μm mesh size) and immediately frozen upon return from the field site. Macroinvertebrates were identified at the laboratory, dried to constant mass and ground into a fine powder. Large macroinvertebrates e.g. *Potamophylax cingulatus* were treated individually, whereas smaller invertebrates e.g. Simulidae and Chironomidae were pooled into groups to gain enough powdered material for analysis. Body tissue of brown trout was non-destructively collected from fin-clippings (McCarthy & Waldron, 2000). Stable isotope analysis of three samples per species or group were conducted following the method of Ings, Hildrew & Grey (2010), using an elemental analyser (Flash EA,1112 series; Thermo-Finnigan) coupled to a continuous flow mass spectrometer (Finnigan MAT DeltaPlus;

Thermo-Finnigan).For further details on stable isotope analysis see general methods (Chapter 7.5).

Species identity was ignored and individuals were pooled into the same 24 size classes used for the ISD's. Note however, that stable isotopes could not be performed on diatoms, so the actual number of size classes containing data was much lower for this analysis. Linear regression analysis was used to explore the relationship between δ_{15}N and (1) the midpoints of the body size classes and (2) temperature.

Statistics

All statistical analyses were conducted in R 2.15.1 (R Development Core Team, 2011). Linear regressions were used to analyse patterns between slope values, small and large intercepts andΔ_{15}N of size classes with temperature

12.3 **Results**

The ISD's of $\log_{10}$-transformed abundances for all 15 streams are presented in Figure 39 ordered by increasing temperature. There was a negative relationship between individual organism body mass and abundance for all streams, with a reduced number of individuals per size class as body mass increased, confirming the first hypothesis.

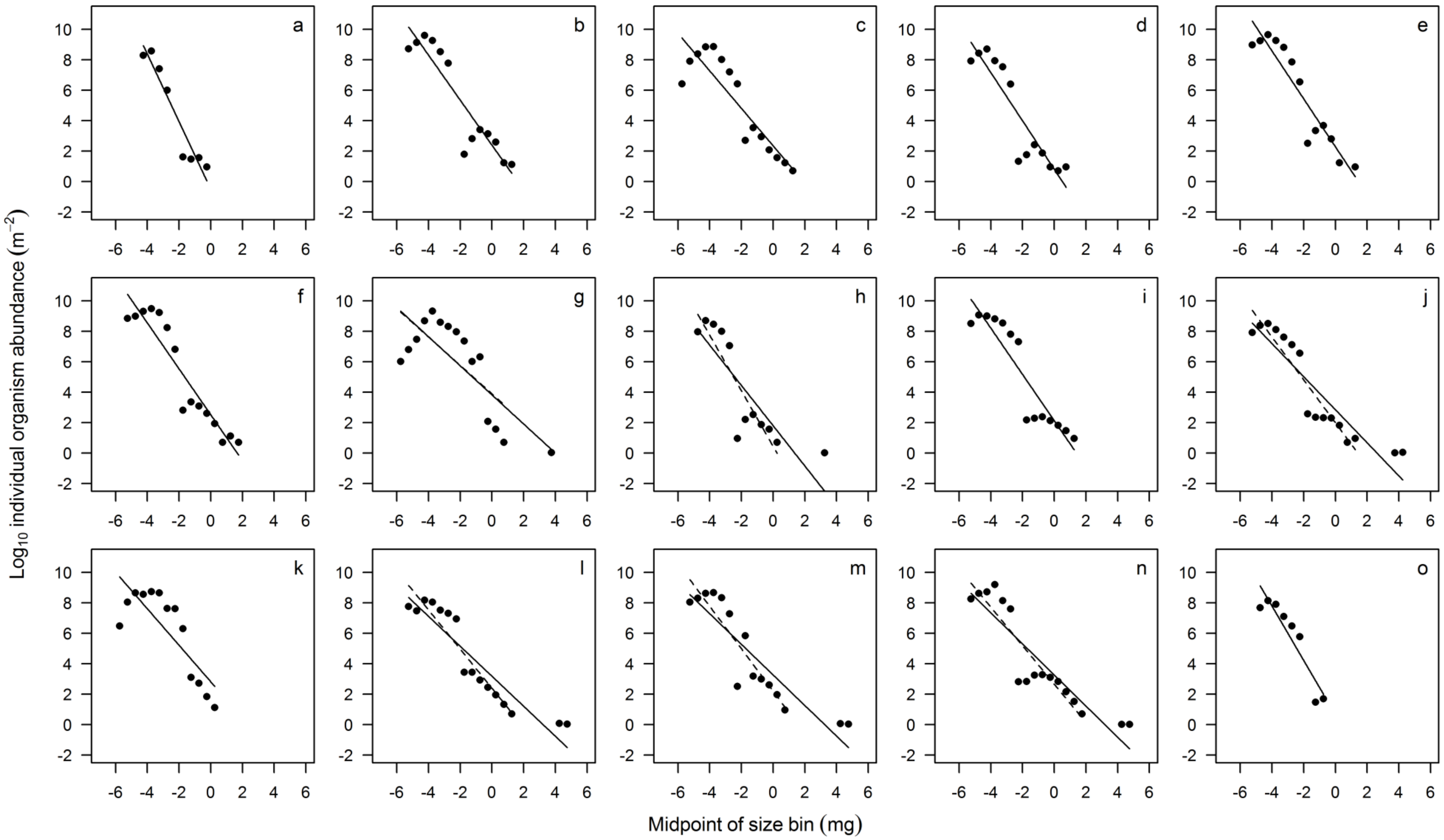

Figure 39 Individual size distributions of fifteen streams along temperature gradient. (a) to (o) from coldest to warmest stream. In each plot the log$_{10}$-transformed abundance per m^2 of each species is plotted against the midpoint of the log$_{10}$-transformed body mass size bin in mg. Solid lines represent linear regression lines fitted to the whole community, dotted lines represent linear regressions with exclusion of trout

Values of slope, intercept with the smallest individual and intercept with the largest individual of the linear regressions did not show any significant changes with temperature when all streams (including the hot stream Hel) were included in the analysis. (Figure 40). The same conclusion was drawn both with and without trout body sizes included in the analysis.

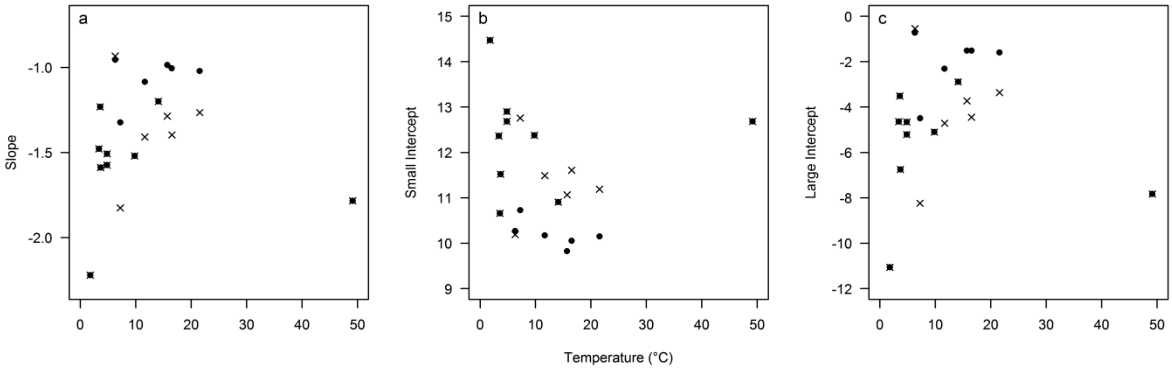

Figure 40 Values of slope (a) and intercepts of the smallest (b) and largest individual (c) in the dataset of the linear regressions fitted to the trivariate food webs in Figure 39 against mean temperature values of streams. Solid circles and lines represent the inclusion of trout body masses, whereas crosses and dashed lines represent the exclusion of trout body masses.

When the hot Hel stream was excluded from the analysis, values of slope ($F_{1,12}$=10.45, P=0.007, *adj.* R^2= 0.42; Figure 41a) and intercept with the largest individual ($F_{1,12}$=9.44, P=0.010, *adj.* R^2=0.39; Figure 41b) increased significantly as temperature increased, whereas the intercept with the smallest individual decreased significantly ($F_{1,12}$=9.53, P=0.009, *adj.* R^2=0.40; Figure 41c). The values of slopes, intercept with the smallest individual and intercept with the largest individual did not show any significant changes with temperature after trout body sizes were excluded from the analysis (slope: $F_{1,12}$=2.75, P=0.123, *adj.* R^2=0.12, intercept with smallest individual: $F_{1,12}$=2.92, P=0.114, *adj.* R^2=0.13, intercept with largest individual: $F_{1,12}$=2.40, P=0.147, *adj.* R^2=0.10, see Figure 41).

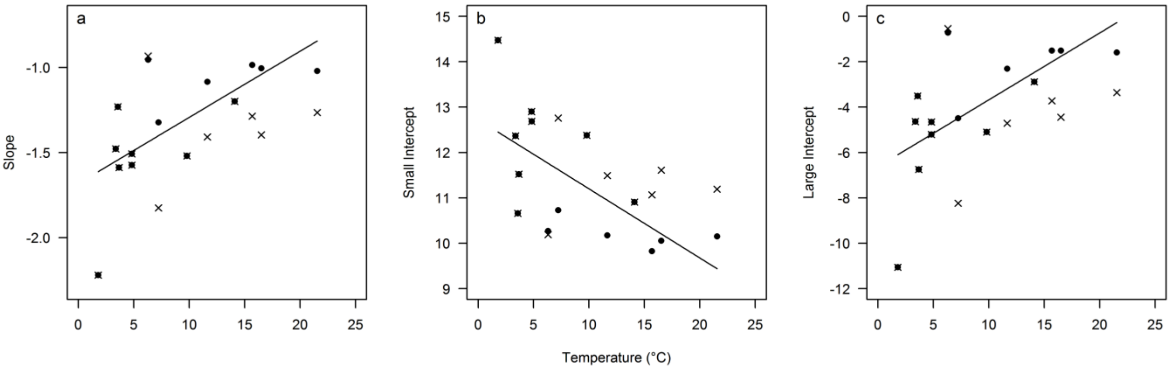

Figure 41 Values of slope (a),intercepts of the smallest (b) and largest individual (c) in the dataset of the linear regressions fitted to the trivariate food webs in Figure 39against mean temperature values of streams. Warmest stream Hel was excluded from analysis. Solid circles and lines represent the inclusion of trout body masses. (a)Trivariate slope values with linear regressions for trout included y = 0.04x-1.68 and trout excluded .(b) intercept values of smallest individual with linear regressions for trout body masses included y = -0.15x+12.72 and trout body masses excluded. (c) intercept values of largest individual with linear regressions for trout body masses included y = 0.29x-6.62and trout body masses excluded.

The δ_{15}N (‰) values were found to increase significantly as the midpoints of the body size classes increased ($F_{1,56}$=29.06, P<0.027, R^2=0.33, see Figure 42a). Similarly, the δ_{15}N(‰) values decreased significantly with increasing temperatures ($F_{1,78}$=7.05, P=0.008, R^2=0.08, see Figure 42b).

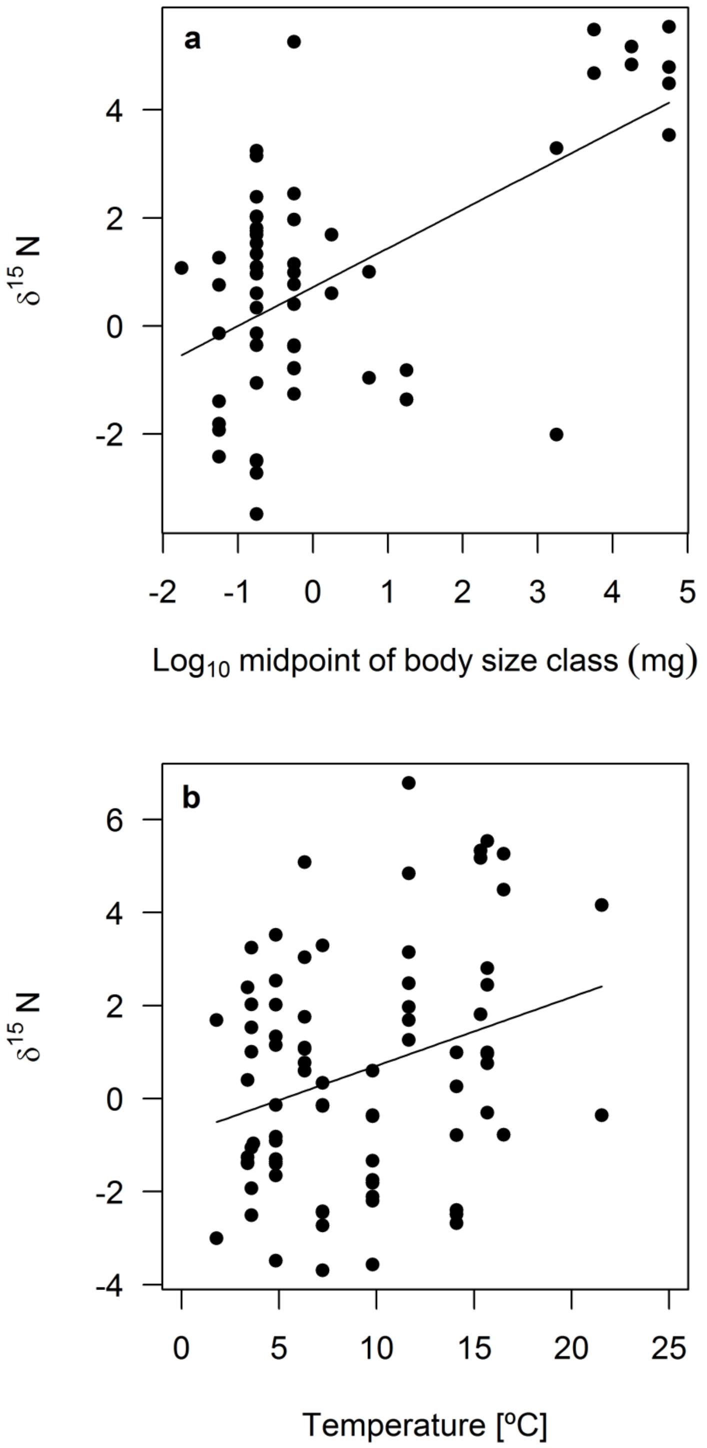

Figure 42(a) δ $_{15}$N (‰) values against the midpoints of the body size classes (y = 0.72x-0.72) and (b) the temperature of streams (y = 0.14x-0.77)

12.4 Discussion

The communities showed a clear size structuring in the ISD's, with a negative relationship between individual organism body mass and abundance of individuals in size classes (see Figure 39),as is typical for aquatic systems (e.g. Blackburn *et al.*, 1997; Cohen *et al.*, 2003; Cyr *et al.*, 1997; Dickie *et al.*, 1987; Sheldon *et al.*, 1972). Characteristics of the ISD's, such as the slope, intercepts with the smallest and largest individual in the dataset of fitted linear regressions were also clearly affected by temperature. Here, the values of slope and intercept with the largest individual increased with temperature, whereas the intercept values with the smallest individual decreased for the temperature gradient up to 25 °C (see Figure 41). These trends represent anincrease in energy transfer efficiency, with fewer resources supporting an increased consumer biomass. This is, in contrast to the second hypothesis, but confirms the conclusions of the taxonomic mass-abundance approach taken in Chapters 2 and 3. None of these patterns in slope and intercepts were significant after the exclusion of trout body masses from the analysis, which highlights the key role of this apex predator in the system. There was evidence for an increase in trophic height with body mass (see Figure 42a), confirming the third hypothesis and patterns previously shown from freshwater (Jonsson *et al.*, 2005) and marine systems (O'Gorman *et al.*, 2010). Additionally, the trophic height of consumers was found to increase with temperature, which contradicts the fourth hypothesis (see Figure 42b).

The ISD’s showed a negative relationship between body mass and abundance of organisms. Similar scaling of body mass and abundance was found for the trivariate food webs based on taxonomy in the previous chapters. This scaling is particularly common in aquatic systems where larger consumers prey on smaller resources (e.g. Blackburn *et al.*, 1997; Cohen *et al.*, 2003; Cyr *et al.*, 1997; Dickie *et al.*, 1987;

Sheldon*et al.*, 1972). In a stable system body mass has been described to typically scale with abundance as $M^{-3/4}$(Brown, 1995; Damuth, 1981; MacMahon *et al.*, 1983). The values of slope found in this study are more negative than the expected value of -0.75. This suggests that population energy use is lower than expected based on the energy equivalence hypothesis, potentially leading to a greater biomass of resources in this system. It also implies that the generality of mass-abundance scaling, mainly found on a global scale (Blackburn *et al.*, 1997; Cyr *et al.*, 1997), might not be transferrable to every system examined on a more regional scale.

The values of slope and intercept with the largest individual increased significantly with temperature, whereas the intercept values with the smallest individual decreased for the temperature gradient up to 25 °C (see Figure 41). This suggests an increase in energy transfer efficiency as described in scenario (d) listed in Figure 1in the General Introduction and shown for the body mass – abundance scaling based on taxonomy in the previous chapters. This contradicts the hypothesis which was based on previous findings in a study from mesocosm experiments (Dossena *et al.*, 2012; Yvon-Durocher *et al.*, 2011). Yvon-Durocher *et al.*(2011) could demonstrate a steepening in slope with warming, which implied a decrease in energy transfer efficiency. The changed slopes of the mass –abundance scaling resulted from a reduced resource biomass due to a prevalence of smaller bodied organisms with warming. In this study in a natural system no prevalence of smaller bodied organisms with increasing temperatures could be found. Less resource biomass was able to support an increased consumer biomass. In particular, brown trout may be able to prevail at elevated temperatures in spite of the high metabolic demands (Brown *et al.*, 2004; Hairston Jr. & Hairston Sr., 1993).

The analysis of the ISD’s highlighted in contrast to the analyses in the previous chapters the key role of brown trout as effects on slopes and intercept values with temperature were removed when the analysis was conducted after exclusion of brown trout. This suggests that brown trout drive many of the described patterns in the energy flow through the system (as observed in Chapter 2) and has to be considered a key species in future work in this system (as also suggested by O'Gorman *et al.* , in press).

The stable isotope analysis of $\delta\ _{15}\mathrm{N}$ (‰) for the size classes showed an increase in values of $\delta\ _{15}\mathrm{N}$ (‰) (see Figure 42a) and therefore also an increase in trophic height(e.g. DeNiro *et al.*, 1981; Hobson *et al.*, 1992) with bigger size classes in this system, as has been previously described for a marine system (Jennings *et al.*, 2003). The increase in trophic height with size can be explained by the ability of consumers to feed on larger prey, i.e. feeding on a higher level of the food chain, due to increased gape size with larger body size. Additionally, the $\delta\ _{15}\mathrm{N}$ (‰) values significantly increased with increasing temperatures (see Figure 42b) contradicting the fourth hypothesis. This surprising result comes about because of the occurrence of the large fish predator, brown trout, in the warmer streams, made possible due to the increased trophic transfer efficiency described in Figure 41. This also confirms previous findings of increased trophic height with temperature in this system calculated from the difference in $\delta\ _{15}\mathrm{N}$ (‰) values between the brown trout, and its common prey species, *Simulium vittatum* (Woodward *et al.*, 2010b). The reduction in $\delta_{15}\mathrm{N}$ (‰) expected in the fourth hypothesis could not be confirmed as body mass did not decrease significantly with increasing temperature (as predicted by Daufresne *et al.* 2009; Gardner *et al.* 2011; Sheridan & Bickford 2011).

The analysis of ISD’s provided similar results on the energy flow of the system observed for the taxonomic approach, highlighting the suitability of body size to capture many structural and functional traits. Additionally the key impact of trout for this system could be detected more clearly with this size-based approach.

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13 General discussion

The main aim of this thesis was to investigate the structural and functional changes on stream communities facilitated by increasing temperatures. Throughout the data chapter a wide range of effects of temperature on different levels of organisation could be demonstrated. The uniqueness of the study site made it possible to examine effects previously reported in experimental setups, but using a "natural experiment". Many of the results obtained contrasted with predictions based on results from experimental studies, and accentuate the need for field based studies in the context of temperature facilitated effects. The results also highlighted the complexity of interactions in a natural system and reinforce the need for further investigation and studies, in particular, to elucidate the role of the main energy pathway between primary producers, snails (*Radix balthica*)and brown trout (*Salmo trutta*).

The first data chapter ("Effects of temperature on community persistence in Sub-Arctic streams.") provided evidence of changes due to increasing temperature across multiple levels of biological organisation, from populations, to pairwise interactions, to the community based on a comparison of data collected in August 2008 and data from a previous study in 2004. Species composition and relative abundances of species changed: cold-stenothermal species were lost or decreased in abundance, whereas the abundances of eurythermal species increased with warming in both years. The loss of cold-stenothermal species was in accordance with previous findings reported in the literature as increased temperatures push these species beyond their thermal tolerance (Chevaldonné & Lejeusne, 2003; Hering *et al.*, 2009; Pörtner, 2001). The increase in eurythermal species in the warmer streams resulted in a balance of species richness across the temperature gradient, i.e. numbers of species did not decrease in warmer streams as it was shown in the following data chapters. In some pairwise interactions due to fluctuating abundance of a predator, shifts in top-down control of the prey items were observed between the years. This highlighted the fact that shifts in abundances were not isolated events but had further implications for the community. Species overlap did not only decrease between streams as the temperature difference increased but also decreased significantly between years at the extremes of the temperature gradient indicating a lower level of persistence at these temperature extremes. A higher species turnover through time was expected in the warmest streams (Hillebrand, Soininen & Snoeijs, 2010; Townsend, Hildrew & Schofield, 1987). The lower persistence in the cold stream could be explained by the intermediate disturbance hypothesis as high levels of disturbance, here cold temperatures, are known to increase the invasibility of a community (Connell, 1978; Ewel, 1986; Hobbs & Huenneke, 1992; Ward & Stanford, 1983).

The subsequent three data chapter investigated the body mass – abundance scaling of the food webs along the temperature gradient in the Icelandic study system based on species based (Chapter 10 and 11) and size based (Chapter 12) approaches.

The second data chapter (Chapter 10: "Impacts of warming on the complexity of and energy flow through stream food webs.") examined the effects of warming on the food web structure, biomass distributions and energy flow through the community by analysing trivariate food webs, i.e. body mass – abundance scaling based on taxonomy, of data derived from 15 streams and one sampling occasion (April 2009). In contrast to this more spatial resolved analysis the trivariate food webs of data derived from 7 streams and two sampling occasions (August 2008 and April 2009) were analysed in a more temporal resolved approach in the third data chapter (Chapter 11: "Warming alters food web structure and complexity.”). The fourth data chapter (Chapter 12: “Effects of warming on individual size distributions”) examined the changes in body mass – abundance scaling with warming in a size-based approach using individual size distributions of the 15 streams used in the second data chapter.

Biomass of producers and consumers remained relatively constant along the temperature gradient, whereas biomass of a key primary consumer, the snail *Radix balthica*, increased with temperature. Profound top-down and bottom-up effects of this species could be demonstrated revealing a key pathway of biomass and energy from diatoms through *R. balthica* to brown trout in this system (see Chapter 10). Alterations with temperature in abundances of predator – prey motifs lead to changes in the structure of the food webs. Connectance and complexity decreased as temperatures increased. In the more spatial resolved dataset (Chapter 10) this was mainly driven by an outlier (the warmest stream Hel), but could be confirmed over a more biologically plausible temperature gradient when averaged over multiple sampling dates (Chapter 11). Decreases in these measures are associated with a reduction in stability (Dunne, Williams & Martinez, 2002; Montoya, Pimm & Sol, 2006) supporting the reduced persistence of warmer stream described in the first data chapter (Chapter 9). Despite the reduction is stability viable communities were still found in the warmer streams even with the ability to support higher trophic levels (fourth data chapter). The main findings on energy transfer from the analysis of body mass – abundance scaling throughout the three data chapters contradicted the hypothesis based on findings in previous experimental studies (Dossena *et al.*, 2012; Yvon-Durocher *et al.*, 2011) and the large body of literature on changes in body size and body size distributions with temperature (Angilletta Jr & Dunham, 2003; Ashton, 2002; Ashton, Tracy & de Queiroz, 2000; Atkinson, 1994, 1995; Bergmann, 1847; Daufresne, Lengfellner & Sommer, 2009;

Gardner *et al.*, 2011; Ray, 1960; Sheridan & Bickford, 2011; Winder, Reuter & Schladow, 2009).The main assumption supporting the prediction of decreasing energy transfer efficiencies with warming was the predicted prevalence of smaller bodied organisms at higher temperatures. This could not be confirmed in this study as the body – mass abundance scaling demonstrated a decrease in intercept values with the smallest individual in the data set and an increase in the intercepts with the largest individuals as temperatures increased suggesting that a decreased producer biomass supported the energy demands of an increased consumer biomass. The changes in these intercept values, supported by decreasing values of slope with temperature, implied an increase in energy transfer efficiency with warming. The increase in energy transfer efficiency is facilitated by the alteration energy flow through the system. As temperatures increased the dominant pathway for energy went though the dominant grazer species, *Radix balthica*, channelling the higher productivity further up through the food web. Increases in 2-span and community span (second and third data chapter) supported the dominance of this pathway with warming. Despite the increased metabolic demands the increase in energy transfer efficiency due to the described pathway of energy enable the communities in warm streams to support large predators like brown trout. These findings bend the metabolic rules of ecology and predictions of warming impacts on the size of individuals and species.

These results highlight the importance and value of studying the effects of warming in a natural context rather than just drawing conclusion from tightly controlled laboratory or mesocosm experiments. In order to begin to make predictions about the future response of ecosystems to climate change further explorations on warming impacts on complex natural communities are needed.

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14 Appendices

14.1 General species list of the Hengill river catchment (2008/2009)

Table 4 Species listof the Hengill river catchment from sampling in August 2008 and April 2009

Order	**Species with authorities**
Bacillariophyta	
	Achnanthes exigua Grunow
	Achnanthes grana Hohn & Hellermann
	Achnanthes lanceolata (Brébissson) Grunow
	Achnanthes lutheri Hustedt
	Achnanthes minutissima Kützing
	Achnanthes minutissima var. *minutissima* Kützing
	Achnanthes nitidiformis Lange-Bertalot
	Achnanthes stolida (Krasske) Krasske
	Amphora inariensis Krammer
	Amphora ovalis (Kützing) Kützing
	Amphora pediculus (Kützing) Grunow
	Aulacoseira italica (Ehrenberg) Simonsen
	Aulacoseira subarctica (O. Müller) Haworth
	Caloneis clevei (Lagerstedt) Cleve
	Caloneis lauta Carter & Bailey-Watts
	Cocconeis pediculus Ehrenberg
	Cocconeis placentula Ehrenberg
	Cocconeis placentula var. *euglypta* Ehrenberg
	Cyclotella sp. (Kützing) Brébissson
	Cymatopleura solea (Brébisson) W.Smith
	Cymbella minuta Hilse
	Cymbella proxima Reimer
	Cymbella sinuata Gregory
	Diatoma mesodon (Ehrenberg) Kützing
	Diploneis ovalis (Hilse) Cleve
	Diploneis pseudovalis Hustedt
	Epithemia sorex Kützing
	Epithemia turgida (Ehrenberg) Kützing
	Eunotia arcus Ehrenberg
	Eunotia bilunaris (Ehrenberg) Mills
	Fragilaria arcus (Ehrenberg) Cleve
	Fragilaria capucina var. *capucina* Desmazières
	Fragilaria capucina var. *rumpens* (Kützing) Lange-Bertalot
	Fragilaria construens (Ehrenberg) Grunow
	Fragilaria pinnata Ehrenberg
	Fragilaria virescens Ralfs
	Frustulia vulgaris (Thwaites) De Toni
	Gomphonema acuminatum Ehrenberg
	Gomphonema angustatum Kützing

Gomphonema clavatum Ehrenberg
Gomphonema clevei Fricke
Gomphonema parvulum Kützing
Gomphonema truncatum Ehrenberg
Gomphonema type D
Melosira undulata (Ehrenberg) Kützing
Melosira varians Agardh
Meridion circulare (Greville) Agardh
Navicula arvensis Hustedt
Navicula atomus (Kützing) Grunow
Navicula atomus var. a*tomus* (Kützing) Grunow
Navicula cryptotenella Lange-Berrtalot
Navicula disjuncta Hustedt
Navicula elginensis (Gregory) Ralfs
Navicula gallica (W. Smith) Lagerstedt
Navicula lucinensis Hustedt
Navicula minima Grunow
Navicula placentula (Ehrenberg) Grunow
Navicula subatomoides Hustedt
Navicula tripunctata (O. F. Müller) Bory
Navicula variostriata Krasske
Navicula viridula (Kützing) Ehrenberg
Navicula viridula var. rostellata (Kützing) Cleve
Nitzschia aequorea Hustedt
Nitzschia amphibia Grunow
Nitzschia dissipata (Kützing) Grunow
Nitzschia fonticola Grunow
Nitzschia frustulum (Kützing) Grunow
Nitzschia inconspicua Grunow
Nitzschia obtusa W. Smith
Nitzschia palea (Kützing) W. Smith
Nitzschia paleacea Grunow
Nitzschia sigmoidea (Nitzsch) W. Smith
Opephora martyi Héribaud
Pinnularia borealis Ehrenberg
Pinnularia ignobilis (Krasske) Cleve-Euler
Pinnularia intermedia (Lagerstedt) Cleve
Pinnularia similis Hustedt
Rhoicosphenia abbreviata (Agardh) Lange-Bertalot
Rhopalodia gibba (Ehrenberg) O. Müller
Stauroneis gracillima Hustedt
Stauroneis pseudosubobtusoides Germain
Surirella angusta Kützing
Surirella ovalis Brébissson
Synedra ulna Ehrenberg
Tabellaria fenestrata (Lyngbye) Kützing
Tetracyclus glans (Ehrenberg) Mills

Diptera

Chaetocladius sp. Kieffer
Clinocera stagnalis Haliday
Cricotopus bicinctus - type (follows Cranston, 1982)
Cricotopus intersectus - type (follows Cranston, 1982)
Diamesa bertrami Edwards
Diamesa zernyi Edwards
Dicranota sp.
Ephydridae indet. (species A)
Ephydridae indet. (species B)
Eukiefferiella claripennis Lundbeck
Eukiefferiella devonica Edwards
Eukiefferiella minor Edwards
Glyptotendipes severini Goetghebuer
Macropelopia sp. Thienemann
Metriocnemus hygropetricus - type (follows Cranston, 1983)
Metriocnemus sp. van der Wulp
Micropsectra sp. Kieffer
Muscidae - Phaoniinae indet.
Orthocladius wetterensis Brundin
Paraphaenocladius sp. Thienemann
Parochlus kiefferi Garrett
Procladius sp. Skuse
Prosimulium ursinum Edwards
Rheocricotopus effesus Walker
Scatella tenuicosta (thermarum) Collin
Simulium aureum Fries
Simulium vernum Macquart
Simulium vittatum Zetterstedt
Thienemanniella sp. Kieffer
Tipulidae - Tipulinae indet.

Heteroptera

Hebridae indet.
Mesoveliidae indet. (species A)
Mesoveliidae indet. (species B)
Naucoridae indet.
Notonectidae indet.

Oligochaeta

Oligochaeta indet.

Plecoptera

Capnia vidua Klapálek

Prostigmata

Sperchon glandulosus Koenike

Pulmonata

Radix balthica Linnaeus

Rhynchobdellida

Helobdella stagnalis Linnaeus

Salmoniformes

Salmo trutta Linnaeus

Trichoptera

Potamophylax cingulatus Stephens

14.2 Physio-chemical properties

Table 5 Physio-chemical properties of streams along mean temperatures in August 2008 and April 2009

	Stream	**mean temp. [°C]**	**pH**	**EC [µS cm^{-1}]**	**DOC [mg l^{-1}]**	**$N\text{-}NH_4$ [mg l^{-1}]**	**$N\text{-}NO_3$ [mg l^{-1}]**	**total-N [mg l^{-1}]**	**$P\text{-}PO_4$ [mg l^{-1}]**	**total–P [mg l^{-1}]**	**Ca^{2+} [mg l^{-1}]**	**K^{+} [mg l^{-1}]**	**Mg^{2+} [mg l^{-1}]**	**Na^{2+} [mg l^{-1}]**	**Si [mg l^{-1}]**	**Cl^{-} [mg l^{-1}]**	**SO_4^{2-} [mg l^{-1}]**
August 2008	Meili	5.14	7.7	129	0.314	0.006	0.002	0.054	0.010	0.018	20.1	0.3	4.7	11.0	6.0	6.6	3.8
	Sigyn	6.14	7.6	201	0.294	0.018	0.001	0.114	0.001	0.006	28.4	0.5	8.9	15.1	9.9	7.2	5.9
	Baldur	8.24	7.6	110	0.208	0.010	0.001	0.012	0.012	0.025	14.1	0.5	4.1	10.6	7.0	7.7	1.5
	Fulla	9.74	8.1	254	0.403	0.010	0.003	0.123	0.001	0.010	35.9	0.5	8.5	17.5	11.4	6.4	5.8
	Odin	12.69	7.7	153	0.465	0.008	0.006	0.041	0.001	0.008	20.3	0.3	5.1	7.4	9.8	7.6	2.9
	Gná	12.81	8.0	624	0.581	0.009	0.001	0.085	0.001	0.015	32.4	2.5	29.5	123.8	25.4	5.7	0.2
	Hengladalsá	14.52	7.9	249	0.318	0.015	0.003	0.068	0.003	0.020	30.5	1.1	8.8	22.0	15.7	6.7	5.8
	Freyja	15.54	7.9	223	0.618	0.012	0.005	0.098	0.001	0.011	25.1	1.4	7.7	19.6	17.6	7.0	2.6
	Thor	18.13	8.1	262	0.263	0.008	0.004	0.036	0.018	0.036	26.9	1.5	6.6	34.6	17.9	6.6	2.7
	Irpa	20.94	8.0	281	0.424	0.010	0.002	0.036	0.006	0.024	32.9	2.0	7.1	37.1	16.8	6.5	4.9
	Frigg	20.95	8.1	283	0.317	0.011	0.002	0.016	0.007	0.028	29.8	2.2	6.4	37.0	19.7	6.5	4.6
	Loki	21.30	8.0	282	0.427	0.006	0.006	0.032	0.002	0.019	31.1	2.2	6.7	36.8	19.8	6.3	4.8
	Sága	22.75	7.8	294	0.767	0.009	0.003	0.062	0.003	0.015	30.8	1.4	7.6	29.0	18.6	6.5	4.9
	Sif	23.71	7.9	275	0.226	0.013	0.004	0.019	0.009	0.028	29.5	1.8	6.5	29.9	19.6	6.4	6.4
	Váli	24.60	8.1	300	0.330	0.009	0.006	0.014	0.012	0.031	28.2	2.6	5.5	37.5	20.2	6.3	3.5
	Hel	48.32	7.6	550	0.956	0.014	0.009	0.151	0.006	0.054	36.4	4.2	10.6	59.9	57.8	6.1	0.8
April 2009	Fulla	1.79	7.8	158	0.551	0.021	0.011	0.048	0.006	0.006	16.2	0.3	3.9	7.1	7.5	5.1	2.7
	Meili	3.38	7.6	78	0.361	0.017	0.011	0.032	0.018	0.025	6.3	0.2	1.6	5.1	5.7	4.7	2.0
	Gná	3.58	8.1	414	0.132	0.018	0.011	0.054	0.009	0.016	34.5	1.2	10.3	33.4	16.9	4.8	0.5
	Odin	3.68	6.8	120	0.265	0.018	0.010	0.037	0.010	0.012	11.9	0.3	2.9	4.8	7.9	6.1	2.3
	Sigyn	4.82	7.2	159	0.444	0.023	0.012	0.048	0.007	0.007	14.1	0.5	4.6	8.1	8.9	6.1	4.0
	Baldur	4.83	7.6	96	0.770	0.019	0.010	0.151	0.022	0.044	8.8	0.4	2.5	7.4	7.2	6.2	1.0
	Freyja	6.31	7.6	84	0.413	0.041	0.088	0.142	0.007	0.016	6.4	0.5	2.1	6.5	7.0	7.1	1.5
	Hengladalsá	7.23	7.4	179	0.479	0.018	0.011	0.033	0.014	0.023	14.9	0.7	4.5	10.2	12.3	5.6	3.8

Thor	9.80	8.4	188	0.498	0.017	0.011	0.043	0.022	0.038	13.1	1.1	3.2	16.9	13.3	5.9	2.1
Sága	11.65	7.2	191	2.271	0.026	0.011	0.108	0.008	0.021	14.2	1.1	3.2	14.7	14.6	5.9	3.5
Frigg	14.10	8.1	199	0.439	0.023	0.010	0.030	0.023	0.042	13.5	1.4	2.9	18.4	15.4	6.1	3.3
Irpa	15.33	7.6	199	1.798	0.023	0.011	0.057	0.015	0.037	13.7	1.4	2.8	17.8	15.9	6.0	3.6
Sif	15.68	7.5	192	0.233	0.019	0.010	0.037	0.021	0.040	13.8	1.3	2.8	16.3	15.0	6.2	3.9
Loki	16.51	7.8	208	2.452	0.019	0.010	0.055	0.018	0.040	12.3	1.3	2.8	17.4	16.2	6.3	3.7
Váli	21.55	8.0	243	0.253	0.032	0.014	0.051	0.024	0.043	15.2	2.1	3.1	22.3	19.5	5.9	2.5
Hel	49.14	7.4	454	0.896	0.031	0.029	0.107	0.026	0.100	21.1	3.9	6.4	39.8	57.2	5.2	0.9

14.3 **Yield effort curves**

14.3.1 Diatoms

Table 6 Values of number of diatom species (n) identified in each stream alongside of values for a, b and R2 of the fitted rectangular hyperbola and the difference between the number of species identified (*n*) and the asymptotic value (*a*) (=expected number of species) in August 2008 and April 2009.

year	**stream**	**no. species *n***	***a***	***b***	R^2	**difference (*n*-*a*)**
2008	Sága	36	38.97	96.42	0.99	-3
	Loki	41	43.13	134.49	0.97	-2
	Baldur	35	35.26	128.73	0.95	0
	Váli	25	27.20	145.11	0.95	-2
	Thor	34	34.00	109.32	0.94	0
	Gná	34	35.69	143.31	0.98	-2
	Sigyn	26	26.68	143.94	0.97	-1
2009	Sága	46	50.63	146.29	1.00	-5
	Sif	41	42.78	78.65	0.99	-2
	Odin	29	30.50	111.74	0.97	-1
	Loki	42	42.52	100.48	0.98	-1
	Frigg	29	29.90	92.40	0.97	-1
	Baldur	28	29.46	89.76	0.98	-1
	Váli	26	27.68	86.22	0.99	-2
	Thor	34	35.96	216.31	0.97	-2
	Meili	26	26.12	98.99	0.96	0
	Gná	29	32.43	95.30	0.99	-3
	Freyja	43	46.69	457.04	0.96	-4
	Sigyn	27	27.17	203.40	0.91	0
	Fulla	23	25.43	160.43	0.99	-2
	Hel	26	36.89	204.10	1.00	-11
	Hengladalsá	29	30.78	87.87	0.98	-2

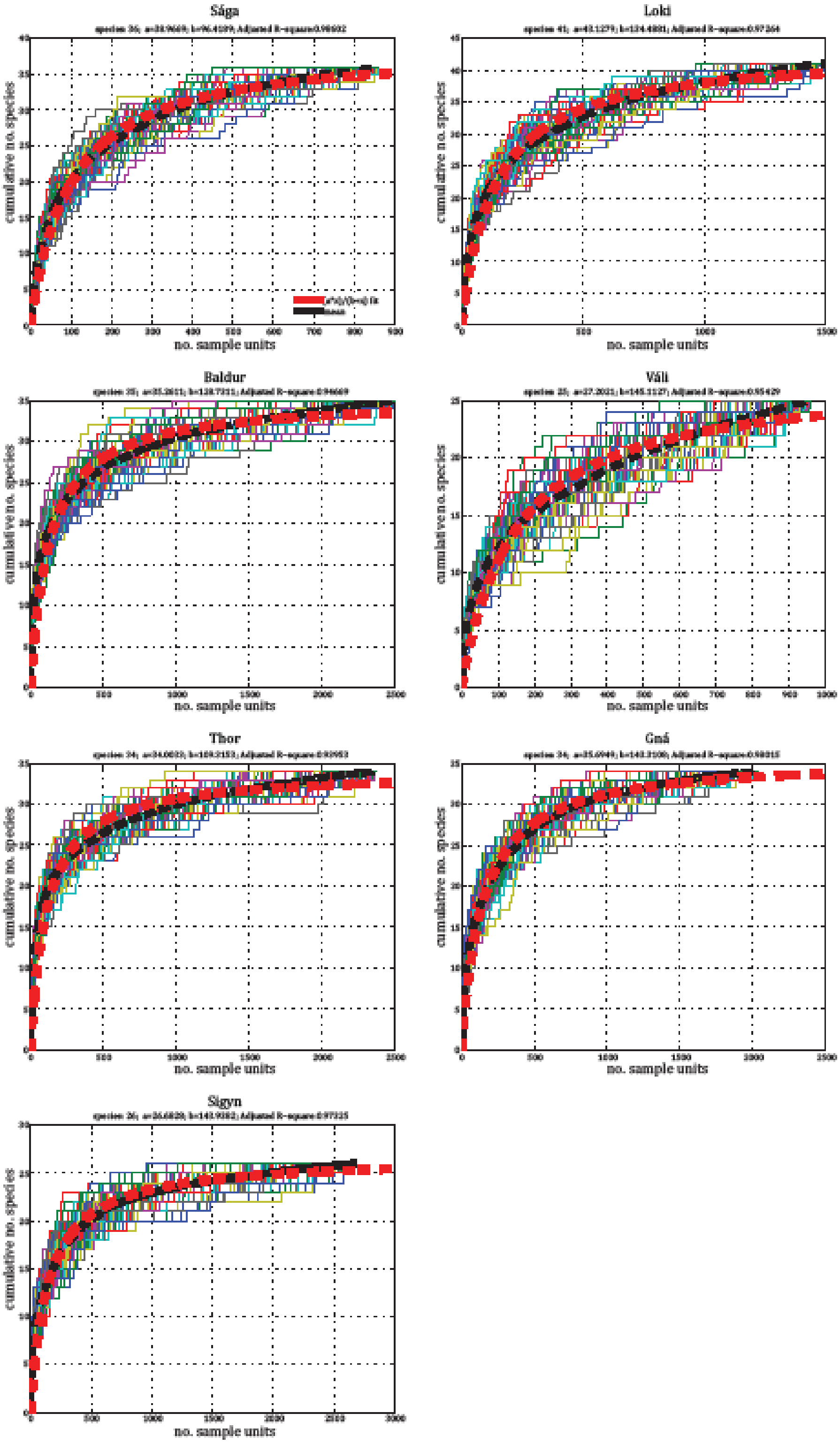

Figure 43 Yield effort curves for diatom communities in 7 streams sampled in August 2008. Number of samples units identified on x-axis against the cumulative number of species found on y-axis. Coloured stepwise lines represent 100 randomisations; black line represents the mean calculated from randomisations; red line represents fitted rectangular hyperbola.

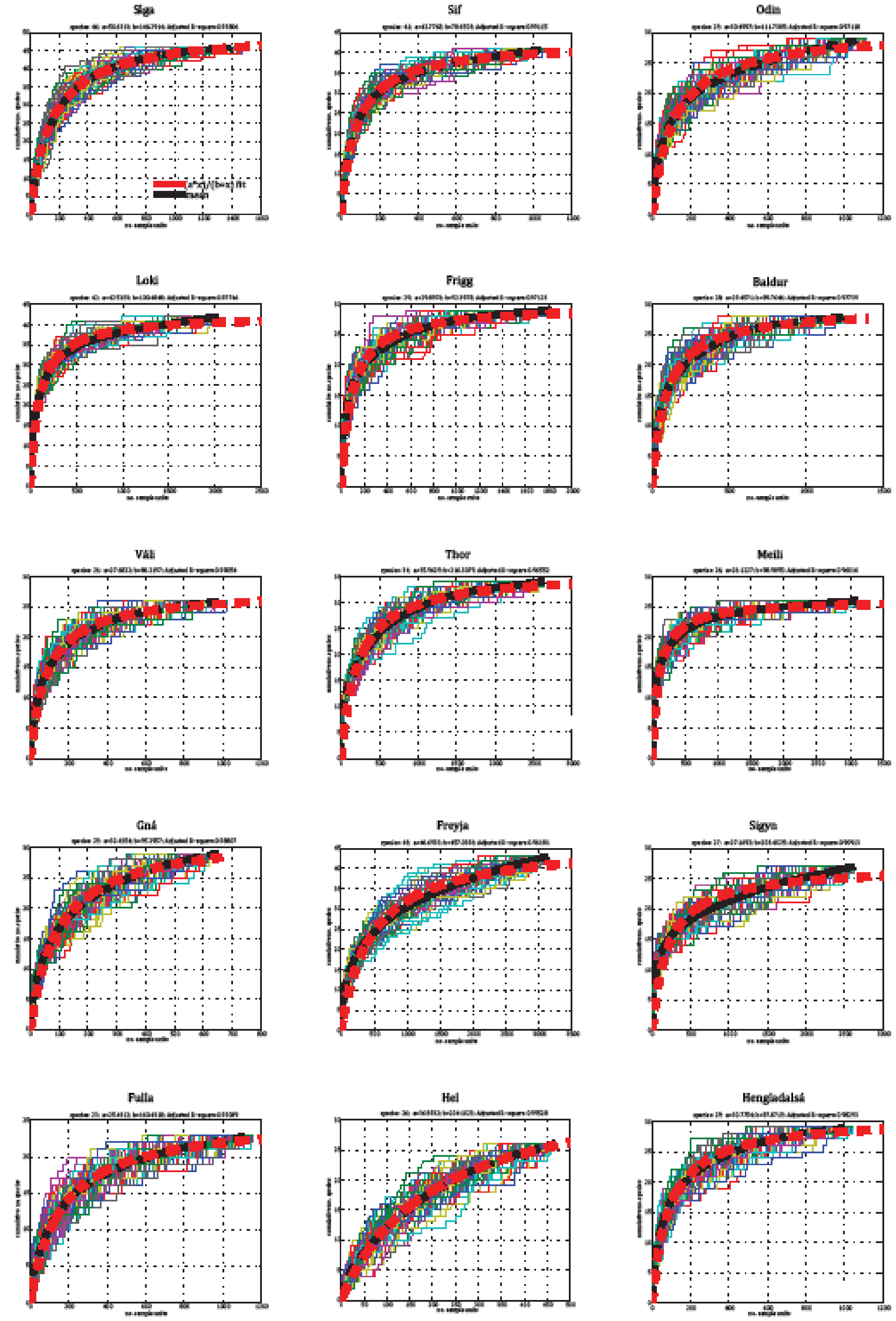

Figure 44 Yield effort curves for diatom communities in 15 streams sampled in April 2009. Number of samples units identified on x-axis against the cumulative number of species found on y-axis. Coloured stepwise lines represent 100 randomisations; black line represents the mean calculated from randomisations; red line represents fitted rectangular hyperbola.

14.3.2 Macroinvertebrates

Table 7 Values of number of macroinvertebrate species (n) identified in each stream alongside of values for a, b and R2 of the fitted rectangular hyperbola and the difference between the number of species identified (*n*) and the asymptotic value (*a*) (=expected number of species) in August 2008 and April 2009.

year	stream	no. species*n*	*a*	*b*	R^2	difference (*n*-*a*)
2008	Sága	11	10.52	61.17	0.85	0
	Irpa	13	13.26	84.46	0.95	0
	Sif	13	12.75	119.71	0.80	0
	Odin	16	16.44	154.96	0.88	0
	Loki	16	15.74	192.64	0.90	0
	Frigg	12	11.23	93.38	0.72	1
	Baldur	20	21.37	194.54	0.98	-1
	Váli	12	11.82	140.47	0.93	0
	Thor	14	14.14	54.91	0.99	0
	Meili	13	12.94	104.89	0.85	0
	Gná	17	17.14	62.58	0.93	0
	Freyja	14	14.57	98.58	0.94	-1
	Sigyn	17	17.64	561.89	0.95	-1
	Fulla	15	14.68	47.86	0.95	0
	Hel	1	-	-	-	-
	Hengladalsá	17	17.71	127.49	0.93	-1
2009	Sága	11	11.96	29.53	0.99	-1
	Irpa	7	6.93	20.69	0.94	0
	Sif	10	9.87	124.54	0.82	0
	Odin	7	7.55	11.78	0.97	-1
	Loki	8	8.29	29.66	0.96	0
	Frigg	7	7.29	53.64	0.88	0
	Baldur	14	13.73	39.19	0.91	0
	Váli	8	8.23	73.30	0.92	0
	Thor	8	8.44	24.98	0.95	0
	Meili	14	14.30	123.34	0.90	0
	Gná	16	16.94	119.73	0.97	-1
	Freyja	10	11.18	10.94	0.99	-1
	Sigyn	10	9.57	49.40	0.85	0
	Fulla	5	6.34	5.78	1.00	-1
	Hel	2	2.25	0.95	0.92	0
	Hengladalsá	8	9.52	12.25	1.00	-2

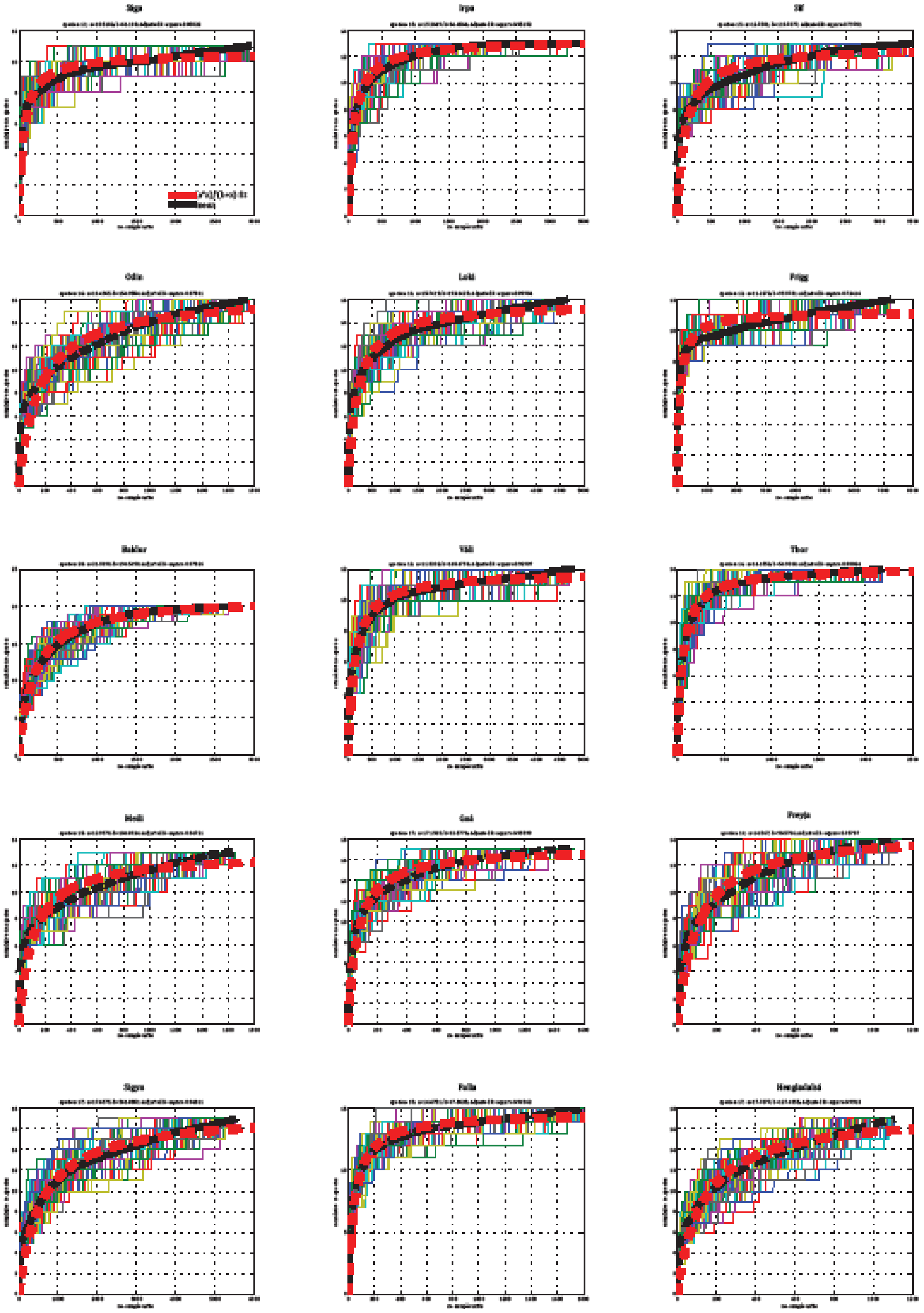

Figure 45 Yield effort curves for macroinvertebrate communities in 15 streams sampled in August 2008 (Hel is excluded as only one species was present). Number of samples units identified on x-axis against the cumulative number of species found on y-axis. Coloured stepwise lines represent 100 randomisations; black line represents the mean calculated from randomisations; red line represents fitted rectangular hyperbola.

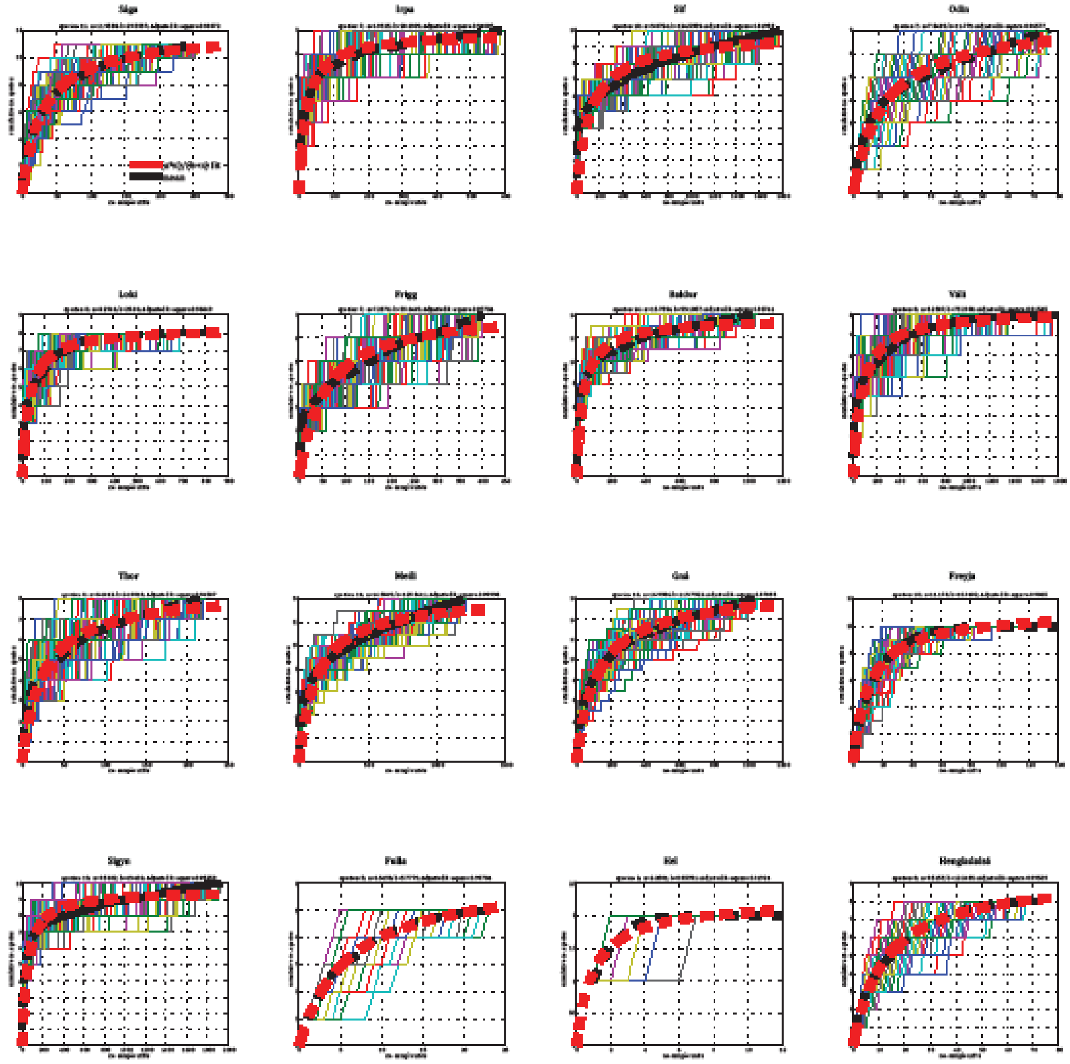

Figure 46 Yield effort curves for macroinvertebrate communities in 16 streams sampled in April 2009). Number of samples units identified on x-axis against the cumulative number of species found on y-axis. Coloured stepwise lines represent 100 randomisations; black line represents the mean calculated from randomisations; red line represents fitted rectangular hyperbola.

14.4 **Links**

14.4.1 Salmo trutta (brown trout)

Table 8 Prey links for *Salmo trutta* in the regional catchment. N = number of *Salmo trutta* stomachs where a given prey item was found. A total of 63 individual *Salmo trutta* stomachs were examined (49 in August 2008, 14 in April 2009).

Prey	**N**	**Prey**	**N**
Capnia vidua	1	Oligochaeta indet.	2
Chironomidae indet.[1]	21	Orthochladinae indet.[1]	47
Chironomidae pupae	17	*Potamophylax cingulatus*	5
Clinocera stagnalis	2	*Radix balthica*	34
Diamesinae indet.[2]	2	Simuliidae[4]	43
Diptera indet.	1	Simuliidae pupae	4
Ephydridae indet.	3	*Sperchon glandulosus*	15
Helobdella stagnalis	3	Tanypodinae indet.[5]	3
Heteroptera indet.[3]	13	Terrestrial invertebrates	34
Micropsectra sp.	27	Tipulidae indet.	2
Muscidae indet.	31	Trichoptera indet.	3

[1] used for inferring to the species of the family Orthochladinae (*Chaetocladius* sp., *Cricotopus bicinctus* – type, *Cricotopus intersectus* – type, *Eukiefferiella claripennis*, *Eukiefferiella minor*, *Metriocnemus hygropetricus* – type, *Orthocladius wetterensis* and *Thienemanniella* sp.

[2] used for inferring to the species of the family (*Diamesa bertrami*, *Diamesa zernyi*.)

[3] used for inferring to the families Mesoveliidae and Naucoridae,

[4] used for inferring to the species of the family (*Simulium aureum*, *Simulium vittatum*, *Prosimulium ursinum*)

[5] used for inferring to the species of the family (*Macropelopia* sp.)

14.4.2 Predatory invertebrates

Table 9 List of references used for inferring links of predatory macroinvertebrates.

Species	**Feeding mode**	**References**
Clinocera stagnalis	Predator	(Bouchard, 2004; Ivković, Mičetić Stanković & Mihaljević, 2012; Smith, 1989; Usinger, 1956)
Dicranota sp.	Predator	(Pretty, Giberson & Dobson, 2005; Smith, 1989; Woodward & Hildrew, 2001, 2002)
Helobdella stagnalis	Predator	(Brose *et al.*, 2005; Young, 1980; Young & Procter, 1986)
Macropelopia sp.	Predator	(Woodward *et al.*, 2001)
Mesoveliidae indet.	Predator	(Bouchard, 2004; Usinger, 1956)
Muscidae – Phaoniinaeindet.	Predator	(Bouchard, 2004; Warren, 1989)
Naucoridae indet.	Predator	(Bouchard, 2004; Usinger, 1956)
Notonectidae indet.	Predator	(Bouchard, 2004; Usinger, 1956)
Procladius sp.	Predator	(Brooks, Heiri & Langdon, 2007; Warren, 1989)
Sperchon glandulosus	Predator	(Di Sabatino, Gerecke & Martin, 2000; Hopkins, 1962; Proctor & Pritchard, 1989)

14.4.3 Collector-gatherers

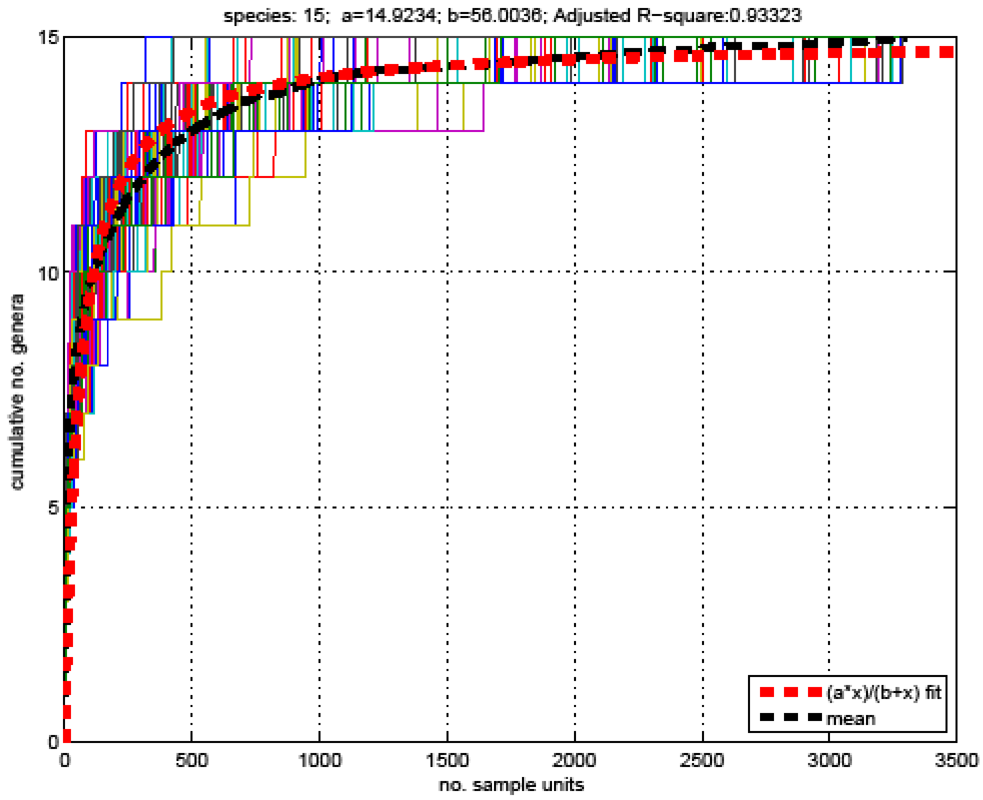

Figure 47 Cumulative number of genera identified against the number of sample units, here diatom valves, identified in four streams in April 2009 from various grazer and collector-gatherer species combined (total of 115 guts, empty guts excluded). Coloured stepwise lines represent 100 randomisations; black line represents the mean calculated from randomisations, red line represents fitted rectangular hyberbola with $y = (14.92*x)/(56.00-x)$, R^2= 0.93. Number of found genera is 15.

14.5 Biovolume and body mass calculations of diatom species

Table 10 Names and authorities of diatom species with the assigned shapes for the calculations of respective biovolumes after Hillebrand *et al.* (1999)Formulas used to calculate biovolume and some additional notes are included at the foot of the table.

Species	assigned shape	biovolume	notes
Achnanthes exigua Grunow	prism on elliptic base	1	3
Achnanthes grana Hohn & Hellermann	prism on elliptic base	1	3
Achnanthes lanceolata (Brébissson) Grunow	prism on elliptic base	1	3
Achnanthes lutheri Hustedt	prism on elliptic base	1	3
Achnanthes minutissima Kützing	prism on elliptic base	1	3
Achnanthes minutissima var. *minutissima* Kützing	prism on elliptic base	1	3
Achnanthes nitidiformis Lange-Bertalot	prism on elliptic base	1	3
Achnanthes stolida (Krasske) Krasske	prism on elliptic base	1	3

Amphora inariensis Krammer	half-elliptic prism	1	3
Amphora ovalis (Kützing) Kützing	half-elliptic prism	1	3
Amphora pediculus (Kützing) Grunow	half-elliptic prism	1	3
Aulacoseira italica (Ehrenberg) Simonsen	cylinder	2	3
Aulacoseira subarctica (O. Müller) Haworth	cylinder	2	3
Caloneis clevei (Lagerstedt) Cleve	prism on elliptic base	1	4
Caloneis lauta Carter & Bailey-Watts	prism on elliptic base	1	4
Cocconeis pediculus Ehrenberg	prism on elliptic base	1	4
Cocconeis placentula Ehrenberg	prism on elliptic base	1	4
Cocconeis placentula var. *euglypta* Ehrenberg	prism on elliptic base	1	4
Cyclotella sp. (Kützing) Brébissson	cylinder	2	3
Cymatopleura solea (Brébisson) W.Smith	prism on elliptic base	1	3
Cymbella minuta Hilse	half-elliptic prism	1	4
Cymbella proxima Reimer	half-elliptic prism	1	4
Cymbella sinuata Gregory	half-elliptic prism	1	4
Diatoma mesodon (Ehrenberg) Kützing	prism on elliptic base	1	3
Diploneis ovalis (Hilse) Cleve	prism on elliptic base	1	4
Diploneis pseudovalis Hustedt	prism on elliptic base	1	4
Epithemia sorex Kützing	half-elliptic prism	1	3
Epithemia turgida (Ehrenberg) Kützing	half-elliptic prism	1	3
Eunotia arcus Ehrenberg	half-elliptic prism	1	3
Eunotia bilunaris (Ehrenberg) Mills	prism on elliptic base	1	3
Fragilaria arcus (Ehrenberg) Cleve	prism on elliptic base	1	3
Fragilaria capucina var. c*apucina* Desmazières	prism on elliptic base	1	3
Fragilaria capucina var. *rumpens* (Kützing) Lange-Bertalot	prism on elliptic base	1	3
Fragilaria construens(Ehrenberg) Grunow	prism on elliptic base	1	3
Fragilaria pinnata Ehrenberg	prism on elliptic base	1	3
Fragilaria virescens Ralfs	prism on elliptic base	1	3
Frustulia vulgaris (Thwaites) De Toni	prism on elliptic base	1	3
Gomphonema acuminatum Ehrenberg	prism on elliptic base	1	3
Gomphonema angustatum Kützing	prism on elliptic base	1	3
Gomphonema clavatum Ehrenberg	prism on elliptic base	1	3
Gomphonema clevei Fricke	prism on elliptic base	1	3
Gomphonema parvulum Kützing	prism on elliptic base	1	3
Gomphonema truncatum Ehrenberg	prism on elliptic base	1	3
Gomphonema type D	prism on elliptic base	1	3
Melosira undulata (Ehrenberg) Kützing	cylinder	2	3
Melosira varians Agardh	cylinder	2	3
Meridion circulare (Greville) Agardh	prism on elliptic base	1	3
Navicula arvensis Hustedt	prism on elliptic base	1	3
Navicula atomus (Kützing) Grunow	prism on elliptic base	1	3
Navicula atomus var. a*tomus* (Kützing) Grunow	prism on elliptic base	1	3
Navicula cryptotenella Lange-Berrtalot	prism on elliptic base	1	3
Navicula disjuncta Hustedt	prism on elliptic base	1	3

Navicula elginensis (Gregory) Ralfs	prism on elliptic base	1	3
Navicula gallica (W. Smith) Lagerstedt	prism on elliptic base	1	3
Navicula lucinensis Hustedt	prism on elliptic base	1	3
Navicula minima Grunow	prism on elliptic base	1	3
Navicula placentula (Ehrenberg) Grunow	prism on elliptic base	1	3
Navicula subatomoides Hustedt	prism on elliptic base	1	3
Navicula tripunctata (O. F. Müller) Bory	prism on elliptic base	1	3
Navicula variostriata Krasske	prism on elliptic base	1	3
Navicula viridula (Kützing) Ehrenberg	prism on elliptic base	1	3
Navicula viridula var. rostellata (Kützing) Cleve	prism on elliptic base	1	3
Nitzschia amphibia Grunow	prism on elliptic base	1	3
Nitzschia aequorea Hustedt	prism on elliptic base	1	3
Nitzschia dissipata (Kützing) Grunow	prism on elliptic base	1	3
Nitzschia fonticola Grunow	prism on elliptic base	1	3
Nitzschia frustulum (Kützing) Grunow	prism on elliptic base	1	3
Nitzschia inconspicua Grunow	prism on elliptic base	1	3
Nitzschia obtusa W. Smith	prism on elliptic base	1	3
Nitzschia palea (Kützing) W. Smith	prism on elliptic base	1	3
Nitzschia paleacea Grunow	prism on elliptic base	1	3
Nitzschia sigmoidea (Nitzsch) W. Smith	prism on elliptic base	1	3
Opephora martyi Héribaud	prism on elliptic base	1	3
Pinnularia borealis Ehrenberg	prism on elliptic base	1	3
Pinnularia ignobilis (Krasske) Cleve-Euler	prism on elliptic base	1	3
Pinnularia intermedia (Lagerstedt) Cleve	prism on elliptic base	1	3
Pinnularia similis Hustedt	prism on elliptic base	1	3
Rhoicosphenia abbreviata (Agardh) Lange-Bertalot	prism on elliptic base	1	3
Rhopalodia gibba (Ehrenberg) O. Müller	prism on elliptic base	1	3
Stauroneis gracillima Hustedt	prism on elliptic base	1	3
Stauroneis pseudosubobtusoides Germain	prism on elliptic base	1	3
Surirella angusta Kützing	prism on elliptic base	1	3
Surirella ovalis Brébissson	prism on elliptic base	1	3
Synedra ulna Ehrenberg	prism on elliptic base	1	3
Tabellaria fenestrata (Lyngbye) Kützing	prism on elliptic base	1	3
Tetracyclus glans (Ehrenberg) Mills	prism on elliptic base	1	3

Biovolume calculation:
[1] biovolume = 4π × length × width × depth
[2] biovolume = 4π × length × $(\text{depth})^2$
Notes:
[3] depth = width
[4] depth = width / 2

14.6 Mass length equations for macroinvertebrates

Table 11 Species names and authorities for macroinvertebrates, along with order, family (and subfamily where applicable). The linear dimensions measured for length are: HW = head capsule width; BL = body length; SW = shell width; and BW = body width. References used to obtain the length-weight (L-W) relationships, log conversions of length (*x*) measurements log conversions and units of weight (*y*) measurements are provided.

Species	Order	Family	Dimension	Reference	*x*	*y*	L-W relationship
Capnia vidua Klapálek	Plecoptera	Capniidae	HW	(Benke *et al.*, 1999)	ln(HW)	ln(mg)	$y = 0.544 + 3.255x$
Chaetocladius sp. Kieffer	Diptera	Chironomidae - Orthocladinae	HW	(Baumgärtner & Rothhaupt, 2003)	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Clinocera stagnalis Haliday	Diptera	Empididae	BL	(Benke *et al.*, 1999)	BL	mg	$y = 0.0066x^{2.437}$
Cricotopus bicinctus - type (follows Cranston, 1982)	Diptera	Chironomidae - Orthocladinae	HW	(Baumgärtner *et al.*, 2003)	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Cricotopus intersectus - type (follows Cranston, 1982)	Diptera	Chironomidae - Orthocladinae	HW	(Baumgärtner *et al.*, 2003)	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Diamesa bertrami Edwards	Diptera	Chironomidae - Diamesinae	HW	(Johnston & Cunjak, 1999)	HW	mg	$y = 4.86x^{3.15}$
Diamesa zernyi Edwards	Diptera	Chironomidae - Diamesinae	HW	(Johnston *et al.*, 1999)	HW	mg	$y = 4.86x^{3.15}$
Dicranota sp.	Diptera	Pediciidae	BL	(Woodward *et al.*, 2002)	ln(HW)	mg	$y = -5.53 + 1.91x$
Ephydridae indet.	Diptera	Ephydridae	BL	(Steingrímsson & Gíslason, 2002)	ln(HW)	mg	$y = -5.17 + 1.8x$
Eukiefferiella claripennis Lundbeck	Diptera	Chironomidae - Orthocladinae	HW	(Baumgärtner *et al.*, 2003)	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Eukiefferiella devonica Edwards	Diptera	Chironomidae - Orthocladinae	HW	(Baumgärtner *et al.*, 2003)	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Eukiefferiella minor Edwards	Diptera	Chironomidae - Orthocladinae	HW	(Baumgärtner *et al.*, 2003)	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Glyptotendipes severini Goetghebuer	Diptera	Chironomidae - Chironomini	HW	(Johnston *et al.*, 1999)	HW	mg	$y = 4.86x^{3.15}$
Helobdella stagnalis Linnaeus	Rhynchobdellida	Glossiphoniidae	BL	(Edwards *et al.*, 2009)	ln(BL)	ln(mg)	$y = -2.74 + 2.12x$
Heteroptera indet.	Heteroptera	Hebridae indet. Mesoveliidae indet. Naucoridae indet. Notonectidae indet.	HW	(Benke *et al.*, 1999)	ln(HW)	ln(mg)	$y = 2.46 + 3.44x$
Macropelopia sp. Thienemann	Diptera	Chironomidae - Tanypodinae	HW	(Johnston *et al.*, 1999)	HW	mg	$y = 4.86x^{3.16}$
Metriocnemus hygropetricus - type	Diptera	Chironomidae - Orthocladinae	HW	(Baumgärtner *et al.*, 2003)	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$

(follows Cranston, 1983)							
Metriocnemus sp. van der Wulp	Diptera	Chironomidae - Orthocladinae	HW	(Baumgärtner *et al.*, 2003)	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Micropsectra sp. Kieffer	Diptera	Chironomidae - Tanytarsini	HW	(Woodward *et al.*, 2002)	$\log_{10}$(HW)	$\log_{10}$(μg)	$y = 3.01 + 1.75x$
Muscidae indet.	Diptera	Muscidae - Phaoniinae	BL	(Steingrímsson *et al.*, 2002)	ln(BL)	mg	$y = -5.17 + 1.8x$
Oligochaeta indet.	Oligochaeta		BL	(Ramsay *et al.*, 1997)	BL	g	$y = (\pi r^2 * 1.05x)/4$
Orthocladius wetterensis Brundin	Diptera	Chironomidae - Orthocladinae	HW	(Baumgärtner *et al.*, 2003)	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Paraphaenocladius sp. Thienemann	Diptera	Chironomidae - Orthocladinae	HW	(Baumgärtner *et al.*, 2003)	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Parochlus kiefferi Garrett	Diptera	Chironomidae - Podonominae	HW	(Johnston *et al.*, 1999)	HW	mg	$y = 4.86x^{3.17}$
*Potamophylax cingulatus*Stephens	Trichoptera	Limnephilidae - Limnephilinae	HW	(Baumgärtner *et al.*, 2003)	ln(HW)	mg	$y = 0.5 + 2.91x$
Procladius sp. Skuse	Diptera	Chironomidae - Tanypodinae	HW	(Johnston *et al.*, 1999)	HW	mg	$y = 4.86x^{3.16}$
Prosimulium ursinum Edwards	Diptera	Simuliidae - Simuliinae	HW	(Woodward *et al.*, 2002)	ln(HW)	ln(mg)	$y = 0.20 + 3.32x$
Radix balthica Linnaeus	Pulmonata	Lymnaeidae - Lymnaeinae	SW	(Baumgärtner *et al.*, 2003)	lnSW	ln(mg)	$y = -3.63 + 3.15x$
Rheocricotopus effesus Walker	Diptera	Chironomidae - Orthocladinae	HW	(Baumgärtner *et al.*, 2003)	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Scatella tenuicosta (thermarum) Collin	Diptera	Ephydridae	BL	(Steingrímsson *et al.*, 2002)	ln(HW)	mg	$y = -5.17 + 1.8x$
Simulium aureum Fries	Diptera	Simuliidae - Simuliinae	HW	(Woodward *et al.*, 2002)	ln(HW)	ln(mg)	$y = 0.20 + 3.32x$
Simulium vernum Macquart	Diptera	Simuliidae - Simuliinae	HW	(Woodward *et al.*, 2002)	ln(HW)	ln(mg)	$y = 0.20 + 3.32x$
Simulium vittatum Zetterstedt	Diptera	Simuliidae - Simuliinae	HW	(Woodward *et al.*, 2002)	ln(HW)	ln(mg)	$y = 0.20 + 3.32x$
Sperchon glandulosus Koenike	Prostigmata	Sperchontidae	BW	(Baumgärtner *et al.*, 2003)	ln(BW)	mg	$y = -1.69 + 1.69x$
Thienemanniella sp. Kieffer	Diptera	Chironomidae - Orthocladinae	HW	(Baumgärtner *et al.*, 2003)	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Tipulidae - Tipulinae indet.	Diptera	Tipulidae	BL	(Woodward *et al.*, 2002)	ln(BL)	mg	$y = -5.50 + 2.36x$

14.7 Ordination

14.7.1 Temperature and chemical variables in CCA

year	stream	stream ID	temperature [°C]	$N\text{-}NH_4$ [mg l^{-1}]	$N\text{-}NO_3$ [mg l^{-1}]	$P\text{-}PO_4$ [mg l^{-1}]	SO_4^{2-} [mg l^{-1}]	total –N [mg l^{-1}]	total-P [mg l^{-1}]	Ca^{2+} [mg l^{-1}]	Cl^- [mg l^{-1}]	total-Fe [mg l^{-1}]	K^+ [mg l^{-1}]	Mg^{2+} [mg l^{-1}]	Na^{2+} [mg l^{-1}]	fish m^{-2}
2004	Sága	1	19.9	0.010	0.010	0.034	15.18	0.140	0.024	13.05	5.38	0.100	1.21	3.87	19.08	0.28
	Irpa	2	20.3	0.010	0.010	0.014	13.79	0.100	0.020	15.23	5.18	0.410	0.43	3.62	6.60	0.04
	Sif	3	22.1	0.012	0.025	0.026	17.10	0.155	0.029	12.14	5.19	0.270	1.58	3.37	21.86	0.00
	Odin	4	13.3	0.015	0.011	0.030	14.45	0.130	0.037	10.74	5.09	0.250	1.69	3.20	23.45	0.00
	Loki	5	19.8	0.010	0.010	0.029	12.56	0.110	0.036	11.06	3.95	0.410	1.33	2.61	18.32	0.31
	Frigg	6	19.1	0.010	0.010	0.032	10.38	0.235	0.044	9.00	4.08	0.260	1.53	2.71	20.47	0.27
	Baldur	7	8.6	0.014	0.016	0.032	4.57	0.135	0.026	7.67	5.64	0.010	0.50	2.10	7.18	0.00
	Váli	8	23.4	0.010	0.013	0.030	7.63	0.125	0.027	10.77	3.68	0.010	1.67	2.75	21.77	0.01
	Thor	9	15.2	0.013	0.013	0.032	7.33	0.115	0.037	9.29	4.68	0.385	0.93	2.60	14.08	0.00
	Meili	10	5.2	0.011	0.019	0.023	11.06	0.135	0.021	7.43	5.35	0.010	0.33	1.95	6.40	0.00
	Gná	11	11.6	0.010	0.010	0.020	2.12	0.105	0.012	13.50	4.61	0.030	1.18	7.90	33.28	0.00
	Freyja	12	14.3	0.014	0.010	0.017	9.25	0.140	0.017	11.91	4.44	0.570	0.95	3.99	11.20	0.19
	Sigyn	13	6.9	0.010	0.015	0.018	15.41	0.200	0.016	13.59	5.01	0.250	0.53	4.54	9.06	0.02
	Fulla	14	10.6	0.010	0.010	0.017	9.96	0.115	0.010	11.54	3.74	0.043	0.31	3.80	7.92	0.05
2008	Sága	1	22.7	0.009	0.003	0.003	4.91	0.062	0.015	30.79	6.54	0.005	1.38	7.64	29.02	0.11
	Irpa	2	20.9	0.010	0.003	0.006	4.86	0.036	0.024	32.85	6.49	0.004	2.04	7.11	37.07	0.09
	Sif	3	23.7	0.013	0.004	0.009	6.39	0.019	0.028	29.52	6.43	0.011	1.84	6.53	29.85	0.06
	Odin	4	12.7	0.009	0.006	0.001	2.94	0.041	0.008	20.25	7.62	0.071	0.33	5.13	7.41	0.00
	Loki	5	21.3	0.007	0.006	0.002	4.82	0.032	0.019	31.13	6.30	0.004	2.17	6.68	36.78	0.22
	Frigg	6	21	0.011	0.002	0.007	4.58	0.016	0.028	29.82	6.53	0.003	2.23	6.43	37.00	0.05

Baldur	7	8.2	0.010	0.001	0.012	1.52	0.012	0.025	14.13	7.67	0.007	0.46	4.13	10.62	0.00
Váli	8	24.6	0.009	0.006	0.012	3.50	0.014	0.031	28.16	6.29	0.000	2.57	5.54	37.51	0.00
Thor	9	18.1	0.008	0.004	0.017	2.69	0.036	0.036	26.94	6.58	0.004	1.523	6.613	34.62	0.00
Meili	10	5.1	0.006	0.002	0.009	3.80	0.054	0.018	20.11	6.56	0.007	0.319	4.700	10.99	0.00
Gná	11	12.8	0.009	0.001	0.001	0.24	0.086	0.015	32.42	5.67	0.001	2.467	29.530	123.80	0.00
Freyja	12	15.5	0.011	0.005	0.001	2.59	0.098	0.011	25.11	7.02	0.081	1.439	7.745	19.62	0.10
Sigyn	13	6.1	0.018	0.001	0.001	5.85	0.114	0.006	28.41	7.20	0.003	0.527	8.949	15.14	0.00
Fulla	14	9.7	0.010	0.003	0.001	5.84	0.123	0.010	35.860	6.414	0.009	0.518	8.460	17.50	0.00

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