Impacts of warming on the structure and functioning of aquatic communities: individual- to ecosystem-level responses

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I. ABSTRACT

Environmental warming is predicted to rise dramatically over the next century, yet few studies have investigated its effects in natural, multi-species systems. We present data collated over an eight-year period from a catchment of geothermally-heated streams in Iceland, which acts as a natural experiment into the effects of warming across different organisational levels and spatiotemporal scales. Body sizes and population biomasses of individual species responded strongly to temperature, with some providing evidence to support temperature-size rules. Community composition also changed dramatically across the thermal gradient. Interactions within the warm streams in particular were characterised by food chains linking algae to snails to the apex predator, brown trout. These chains were missing from the colder systems, where snails were replaced by much smaller herbivores and invertebrate omnivores were the top predators. Trout were also subsidised by terrestrial invertebrate prey, which could have an effect analogous to apparent competition within the aquatic prey assemblage. Top-down effects by snails on diatoms were stronger in the warmer streams, which could account for a shallowing of mass-abundance slopes across the community. This may indicate reduced energy transfer efficiency from resources to consumers in the warmer systems and/or a change in predator-prey mass ratios. All the ecosystem process rates investigated increased with temperature, but with differing thermal sensitivities, with important implications for overall ecosystem functioning (e.g. creating potential imbalances in elemental fluxes). Ecosystem respiration rose rapidly with temperature, leading to increased heterotrophy. There were also indications that food web stability may be lower in the warmer streams.

II. INTRODUCTION

A. Climate change: identifying the key drivers and responses

Climate has always shaped the planet's ecosystems, but as we move deeper into the Anthropocene (Steffen *et al.* 2007) the predicted rates of change are unprecedented in recorded human history. One of the most pressing challenges in ecology is to understand and predict the likely consequences of climate, yet we are still surprisingly poorly equipped to do so (Walther 2010). This is partly because climate change operates at large spatiotemporal scales and is also likely to interact with the numerous other anthropogenic stressors that are already imposed across the planet (Woodward *et al.* 2010a). It is also a compound stressor whose component parts (e.g. warming, drought, atmospheric CO_2 change) interact with one another, and often in seemingly unpredictable ways. Given the almost overwhelming task we are faced with, we need to compartmentalise the problem so we can grapple with it in its simplest forms, by exploring one component at a time before attempting to consider its full range of possible effects and potential synergies with other drivers.

Considerable progress has been made recently by tackling climate change in this piecemeal fashion (Ledger *et al*. 2012), but there is still much to do, especially if we are to understand the consequences for multi-species systems, whose behaviour is notoriously difficult to predict. One obvious place to start is to focus on a key component of climate change that we know has profound biological relevance. Environmental warming is the prime candidate here because all biological rates are temperature-dependent, from biochemical reactions at the elemental or molecular level to the carbon cycle in entire ecosystems (Yvon-Durocher *et al.* 2010a, Yvon-Durocher *et al.* 2012). Temperature sets the pace of life by determining the metabolic rate of individual organisms (Brown *et al.* 2004), with ramifications for the higher levels of organisation (Moya-Laraño *et al*. 2012). Metabolism is also determined by individual body mass, which is a critical determinant of other key organismal attributes, such as trophic position in the food web (Jonsson *et al.* 2005, O'Gorman and Emmerson 2010).

Thus, by characterising the size of organisms and the environmental temperature we should be able to capture a large amount of the ecologically meaningful variation of a system within a small number of dimensions. That is not to say these are the only variables that matter, rather they help us to simplify the system into something more tractable, which can also then enable us to identify other potentially important variables (e.g. elemental composition of consumers and resources and effects of increased atmospheric CO_2).

Most climate change research has addressed the lower levels of organisation, which is to be expected in such an embryonic field, but in recent years the focus has shifted towards the higher, multi-species levels (communities, food webs, ecosystems) (Walther 2010). One of the reasons for this change in approach is that although these systems are comprised of individuals, whose size and metabolic requirements we can measure relatively easily, it is now widely accepted that the behaviour of multispecies systems is more than simply the sum of these component parts (Melian *et al.* 2011; Moya-Laraño *et al*. 2012). We therefore need to understand not just the individuals within them but how these individuals combine and interact to produce higher-level phenomena (e.g. community stability, ecosystem respiration). Reductionist approaches are no longer sufficient, and we must now also work at the levels of organisation we wish to understand.

B. The need for multi-scale and multi-level approaches for dealing with multi-species systems

Empirical ecological research is typically carried out over small spatiotemporal scales (Callahan 1984) and rarely across multiple levels of organisation (e.g. individuals to ecosystems), largely due to logistic constraints. This is a major challenge because climate change in natural systems operates at temporal and spatial scales beyond the scope of most research programmes, or indeed the lifetimes of most researchers (Woodward *et al.* 2010a; Moya-Laraño *et al*. 2012). This requires alternative approaches to long-term observation and large-scale experimentation, such as using microbial communities in laboratory microcosms (i.e. scaling by generation time rather than absolute time; Petchey et al. 1999, Reiss *et al* 2010), space-for-time-substitution surveys conducted over large latitudinal gradients (e.g. Yvon-Durocher *et al.* 2012) and *in silico* mathematical simulations of possible future scenarios (e.g. Moya-Laraño *et al*. 2012). In the absence of long-term and large-scale syntheses, our current knowledge is therefore based on a patchwork of different types of evidence and scales of observation. None of these approaches is without its flaws, as they all must make compromises between realism, control and replication, but together they can be used to paint a more coherent picture and hopefully to approach a consensus as to what is likely (and what is not) in the future. By collating smaller-scale studies conducted within a longer-term programme of study we can start bridging the gap between what is desirable and what is feasible.

Building realistic predictions about ecological responses to warming ideally requires a multi-level and multi-scaled approach that combines observations and experiments conducted across different organisational levels (Figure 1) and over a range of spatial and temporal scales (Figure 2), as we aim to do here. Much of the current uncertainty about warming lies in whether short-term responses can accurately predict long-term dynamics: we need to know how physiological and individual responses may be manifested at higher levels of biological organisation and across many generations (e.g. Chapin *et al.* 2000, Hollister *et al.* 2005). Although many studies have focused on either end of this spectrum (i.e. physiological responses to temperature and differences among ecosystems at different temperatures), very few have attempted to span this critical gap. Initial organismal responses to warming (from seconds up to a few generations) may simply represent acclimation of physiological or behavioural traits, whereas long-term warming (many generations) may lead to altered body size distributions, local extinctions and invasions resulting in novel communities and, eventually, evolutionary adaptation (Chapin *et al.* 2000, Parmesan 2006, Durance and Ormerod 2007). To refine our predictions about climate warming we need to identify natural study systems that allow us to investigate warming across temporal scales, without being confounded by large-scale biogeographical differences. One way in which to do this is to use a proxy space-for-time substitution approach (e.g. Meerhoff *et al.* 2012) across a large thermal gradient, but such studies risk being confounded with biogeographical influences unless they can be conducted within a small area without obvious dispersal constraints. Such idealised systems are hard to find in nature, but geothermal ecosystems can provide a solution, if their temperature differences are not confounded by other environmental gradients (e.g. high sulphur concentrations and extreme acidity).

< Figures 1 and 2 near here>

This paper presents a new synthesis of a decade of intensive research conducted in a rare example of just such an ecological model system: the geothermally-heated Hengill area of Iceland (Friberg *et al.* 2009, Olafsson *et al.* 2010, Woodward *et al.* 2010b). Long-term localised heating of streams (Arnason *et al.* 1969) makes this system an ideal 'natural global warming experiment' to study responses from the individual to the ecosystem level. The study streams are part of the same river network, with no dispersal constraints or confounding environmental gradients (other than temperature). Recent studies in this system have revealed strong impacts of temperature on the structure of the macroinvertebrate (Friberg *et al.* 2009, Olafsson *et al.* 2010, Woodward *et al.* 2010b) and primary producer (Gudmundsdottir *et al.* 2011a, 2011b) assemblages, and on ecosystem functioning (Friberg *et al.* 2009, Demars *et al.* 2011a, 2011b, Perkins *et al.* 2012). Further research programmes are currently underway that combine experiments and observations across multiple spatiotemporal scales and organisational levels. Here we build on the initial findings of the earlier studies, by exploring newer and more comprehensive datasets from Hengill. We also discuss the limitations of the work carried out to date in the Hengill system in the context of broad-scale applicability to global warming research.

C. Individuals, populations and environmental warming

At the individual level, body size affects many aspects of an organism's biology, including its physiology, life history, behaviour and ecology (Peters 1983, Brown *et al.* 2004, Woodward *et al.* 2005a, White *et al.* 2007, Sibly *et al.* 2012). Organisms tend to be larger in colder regions (Bergmann 1847, Ray 1960, James 1970, Ashton *et al.* 2000, Ashton 2002), suggesting that global warming may alter the distribution of body sizes via species range shifts (Chen *et al.* 2011) and/or physiological adaptation (Musolin 2007). Several explanations, which are not mutually exclusive, have been proposed for warming favouring the small (Daufresne *et al.* 2009). These include James's Rule, which predicts that the mean body size of a species population will decline with temperature (James 1970). The Temperature-Size Rule is a specific subset of James's Rule and predicts that oxygen demands and different thermal sensitivities in growth and development rate will lead to smaller size at a given age in warmer temperatures (Atkinson 1994).

Individual growth and development rates are dependent on both body size and temperature (Angilletta *et al.* 2004), with most ectotherms growing faster and maturing at a smaller size at warmer temperatures (Ray 1960, Atkinson 1994, 1995, Angilletta and Dunham 2003, Forster *et al.* 2011). Berrigan and Charnov (1994) suggested that relatively rapid growth favours early maturity at small body size if the coefficient of growth and asymptotic size are negatively related, as supported by the differential effects of temperature on anabolism and catabolism (von Bertalanffy 1960, Perrin 1995). Thus, maturing earlier at higher temperatures may be favoured in multi-voltine species (Fischer and Fiedler 2002, Atkinson *et al.* 2003) and thermal constraints on maximal body size can limit growth late in ontogeny, reducing the benefit of delayed maturation (Berrigan and Charnov 1994, Kindlmann *et al.* 2001). Thus, greater fecundity associated with larger body size (Stearns 1992, Roff 2002) may be selected for in cold environments (Angilletta *et al.* 2004).

Van der Have and de Jong (1996) also proposed that differential temperature dependencies in growth and development rates determine size at maturity. Here, if the effect of temperature is greater on development rate than on growth rate, warming should lead to a smaller adult size (Smith 1979, van der Have and de Jong 1996, Davidowitz and Nijhout 2004, Walters and Hassall 2006, Forster *et al.* 2011). This suggests that underlying assumptions of the metabolic theory of ecology, related to many biological rates following a thermal response modelled by the Arrhenius function (Brown *et al.* 2004), may not be complete and this could explain these observed exceptions to the Temperature-Size Rule (van der Have and de Jong 1996, Walters and Hassall 2006). Further, recent models of eco-evolutionary food web dynamics suggest that warm environments might not necessarily always favour smaller organisms (Moya-Laraño et al 2012).

Warming can also lead to community compositional shifts in favour of smaller species that have a competitive advantage at higher temperatures (Daufresne et al 2009). Thus, this general trend for smaller organisms to be favoured by higher temperatures, both across (Bergmann 1847) and within (James 1970, Atkinson 1994) species, may be due to a combination of direct (e.g. activation energies of biochemical reactions) and indirect mechanisms (e.g. metabolic constraints). Given that these responses which act on individuals have ramifications for the higher levels of organisation, we need to consider how warming might mediate connections between populations, communities and ecosystems (Brown *et al.* 2004).

D. Environmental warming impacts on species traits and trophic interactions

Warming may alter species composition via direct and indirect food web effects. Species living near their thermal limits are likely to be excluded as temperatures rise (Chevaldonné and Lejeusne 2003, Hering *et al.* 2009, Somero 2010), whereas more warm-adapted stenotherms and eurytherms could invade via range expansions, given an accessible pool of suitable species (Francour *et al.* 1994, Nehring 1998, Dukes and Mooney 1999, Walther *et al.* 2002, Lejeusne *et al.* 2010). Inhibited aerobic performance is a likely autecological mechanism in freshwaters, which may be overlain with indirect food web effects related to interaction strengths and energetic efficiencies (Rall *et al.* 2010, Vucic-Pestic *et al.* 2011) that could create novel communities in warmed systems. Reductions in the average body mass of a top predator can cause cascading effects on the biomass of lower trophic levels (Jochum *et al.* 2012). Such effects have previously only been associated with the loss of an entire species (reviewed by Heithaus *et al.* 2008) and highlight the potential for temperature-induced changes in body size to dramatically alter community structure. Increased prevalence of small organisms with warming can steepen mass-abundance scaling in community size spectra, potentially altering the flux of energy through the entire food web (Yvon-Durocher *et al.* 2011). Thus, the effects of climate-induced changes in body size can ripple across multiple levels of biological organisation, and its consequences may be manifested at both ecological and evolutionary timescales (Moya-Laraño et al. 2012).

Given that body size influences so many aspects of an organism's autecology (Peters 1983, Woodward and Hildrew 2002, Brown *et al.* 2004, White *et al.* 2007), related aspects of its synecology should also be altered by environmental warming. For example, diets often broaden with body size, particularly in aquatic systems (Scharf *et al.* 2000, Petchey *et al.* 2008), larger predators are capable of faster and more sustained bursts of speed and better visual acuity (Keast and Webb 1966, Webb 1976, Blaxter 1986), while handling times decrease and encounter rates generally increase with consumer size and also with temperature for a given body size (Mittelbach 1981, Beckerman *et al.* 2006). Given that diet breadth is also related to other system-level properties such as connectance (Beckerman *et al.* 2006), if warming leads to more frequent interactions concentrated in fewer links, this could alter both food web structure and dynamics (Dunne *et al.* 2002).

Metabolic rate increases exponentially with temperature (Brown *et al.* 2004) and, when combined with reduced body size (Daufresne *et al.* 2009, Gardner *et al.* 2011, Sheridan and Bickford 2011), this could raise energy requirements across the community, as smaller species have a higher mass-specific metabolic rate (Kleiber 1947, Peters 1983, West *et al.* 1997). Attack rates generally increase, while handling times decrease with warming (Thompson 1978, Dreisig 1981, Gresens *et al.* 1982, McCoull *et al.* 1998, García-Martín *et al.* 2008, Vucic-Pestic *et al.* 2011), although a hump-shaped relationship is expected over very large thermal gradients as thermal tolerances are reached. Consumption rates need to rise to meet the higher energy demands of living in a warmer environment, as observed in laboratory experiments, even though overall energetic efficiencies may decline (Vucic-Pestic *et al.* 2011). Similarly, ingestion efficiencies decrease with temperature, increasing starvation risk (Rall *et al.* 2010). Changes in the distribution and patterning of interaction strengths may lead to a disruption of stabilising mechanisms within the food web (McCann *et al.* 1998, Neutel *et al.* 2002, O'Gorman and Emmerson 2009, Allesina and Tang 2012), creating the potential for long-term shifts in the structure and functioning of communities and ecosystems.

Interaction strength is a commonly used term for ecologists if they want to investigate stability (Layer *et al.* 2010, 2011; Twomey *et al*. 2012), but it can be expressed in multiple ways (Berlow *et al.* 2004). One of the most quantitative measures is the functional response, which returns the per capita feeding rate of consumers based on the resource density (Solomon 1949, Holling 1959). Knowing only the functional responses doesn't give a feedback if systems are dynamically stable or extinctions might occur. Better proxies may be the actual realized mass specific feeding rate (DeRuiter *et al.* 1995, Otto *et al.* 2007) or the relative feeding rate, the ratio of feeding and metabolism (Rall *et al.* 2010, Vucic-Pestic *et al.* 2011), which we will examine in this study (after Rall *et al.* 2012).

E. Linking communities to ecosystems: food web and size structure

In all food webs, a small proportion of species and links dominate most of the biomass flux. In extreme cases such species may act as keystones, if they exert disproportionately strong effects on the system (Paine 1966, Power *et al.* 1996). Experimental manipulations of top predator body size can trigger cascading effects at the lower trophic levels and modification of ecosystem process rates (Jochum *et al.* 2012). Thus, size-mediated changes in trophic interaction may offer one mechanism for potential ripple effects at the community and ecosystem level.

The relationship between body mass and abundance illustrates how biomass is allocated among organisms (White *et al.* 2007) and connects individual- and population-level traits to community structure and ecosystem dynamics (Kerr and Dickie 2001, Woodward *et al.* 2005a). The mass-abundance relationship can be constructed from either individual-based data to describe the size spectrum (Sheldon *et al.* 1972, Kerr and Dickie 2001, Jennings and Mackinson 2003, Yvon-Durocher *et al.* 2011), or via mass-abundance relationships among species populations (Damuth 1981, Blackburn and Gaston 1997, Cyr *et al.* 1997, Schmid *et al.* 2000, Carbone and Gittleman 2002). Only a few studies have considered both simultaneously (Reuman *et al.* 2008, 2009, Layer *et al.* 2010, O'Gorman and Emmerson 2011), as we will do in this paper. Both approaches typically show a negative relationship between body mass and abundance (White *et al.* 2007), the slope of which may be related to the flow of biomass (≈ energy) from small and abundant to large and rare organisms. Steeper slopes can imply an increased prevalence of smaller organisms, resulting in a reordering of the biomass structure of the food web (Yvon-Durocher *et al.* 2011) and/or suppression of the relative abundance of large organisms (Pauly *et al.* 1998). Both outcomes are likely responses to the effects of warming (Petchey *et al.* 1999, Daufresne *et al.* 2009, Yvon-Durocher *et al.* 2011), although disruptions to the efficiency of trophic transfer may alter these effects.

To highlight the possible scenarios leading to a disruption of trophic transfer efficiency, we can consider a simple example involving the typical negative mass-abundance scaling

(White *et al.* 2007) (see Figure 3*a*). If we assume a fixed abundance of the smallest and largest organisms in the system, there are four possible deviations from this reference mass-abundance scaling. The system will exhibit a reduction in trophic transfer efficiency if the same biomass of resources sustains a lower biomass of top predator (Figure 3*b*), or if more resources are consumed (leading to lower resource biomass) to sustain the same biomass of top predator (Figure 3*c*). The system will exhibit an increased trophic transfer efficiency if the same biomass of resources sustains a higher biomass of top predator (Figure 3*d*), or if fewer resources are consumed (increase in resource biomass) to sustain the same biomass of top predator (Figure 3*e*). The same general conclusions should apply whether the scaling is based on average species size and abundance (e.g. Damuth 1981, Blackburn and Gaston 1997, Cyr *et al.* 1997, Schmid *et al.* 2000, Carbone and Gittleman 2002) or individual organism size distributions (e.g. Sheldon *et al.* 1972, Kerr and Dickie 2001, Jennings and Mackinson 2003, Yvon-Durocher *et al.* 2011), although the reference slope and intercept of Figure 3*a* will vary between the two.

< Figure 3 near here>

Despite the potential consequences of warming being varied and complex, recent advancements in the exploration of so-called trivariate food web patterns offer the possibility for a synthesis of these effects at the ecosystem level (Reuman and Cohen 2004, Jonsson *et al.* 2005, Woodward *et al.* 2005b, Layer *et al.* 2010, McLaughlin *et al.* 2010, O'Gorman and Emmerson 2010). Trivariate food webs incorporate relationships between body mass, abundance and all the consumer-resource links in the web and can offer insight into the cumulative effects of alterations to the composition, size, traits and interactions of individuals, populations and communities. They can also reveal important information about the flow of energy and the productivity and stability of the system.

F. Environmental warming and ecosystem processes

Increased metabolic demands at higher temperature are likely to have profound effects on the transfer of energy through the food web, via both autotrophic and detrital-based pathways, leading to ecosystem-level impacts (Mulholland *et al.* 1997, Azevedo-Pereira *et al.* 2006, Perkins *et al.* 2010, Ferreira and Chauvet 2011). Nutrient fluxes and cycles are key measures of ecosystem functioning, especially in aquatic systems (DeAngelis *et al.* 1989, Costanza *et al.* 1997, Chapin *et al.* 2000, Vanni 2002). Attention has focused on the cycling of nitrogen and phosphorous in fresh waters, because they are thought to be most limiting to primary producers and heterotrophic microbes (Smith 1979, Pace and Funke 1991, Suberkropp and Chauvet 1995). Since consumers can have strong effects on nutrient cycling, structural-functional relationships are important in this context (Kitchell *et al.* 1979, McNaughton *et al.* 1997, Vanni *et al.* 1997, Sirotnak and Huntly 2000, Hjerne and Hansson 2002): e.g. nutrient excretion rates should increase with higher metabolic demands in warmed waters (Gardner *et al.* 1981, Wen and Peters 1994, Devine and Vanni 2002). Decreasing body mass could amplify these effects, due to higher mass-specific nutrient excretion rates (Shelby 1955, Lauritsen and Mozley 1989, Wen and Peters 1994, Schaus *et al.* 2002). Increased nutrient uptake and excretion rates could stimulate animal-mediated cycling rates, higher primary production (Grimm 1988, Schindler *et al.* 1993, Vanni 2002), and increased ecosystem resilience (DeAngelis 1980).

Altered rates of energy and nutrient cycling may have serious implications for ecosystem processes and their associated services (e.g. regulation of decomposition, carbon sequestration and fisheries production). Faster decomposition could stimulate the release of stored organic carbon (Kirschbaum 1995, Freeman *et al.* 2001, Davidson and Janssens 2006, Dorrepaal *et al.* 2009), leading to possible positive feedbacks with warming, especially if it emitted as a greenhouse gas (Gudasz *et al.* 2010). Similarly, increased nutrient uptake velocities associated with greater community respiration and net ecosystem metabolism (Hall and Tank 2003) and increased DOC delivery from soil to the stream could also provide positive feedbacks between warming and the carbon cycle.

Net ecosystem metabolism (the balance between photosynthesis and respiration) is influenced by warming. Ecosystem Gross Primary Production (GPP) increases with temperature within normal biological ranges (0-37°C) (Nemani *et al.* 2003, Yvon-Durocher *et al.* 2010b, Demars *et al.* 2011b), although it may also be constrained by nutrient availability (Cox *et al.* 2000) or heat stress (Ciais *et al.* 2005). Similarly, ecosystem respiration (ER) represents the sum of individual respiratory rates of all its autotrophs and heterotrophs (Allen *et al.* 2005, López-Urrutia *et al.* 2006) and also increases with temperature (Yvon-Durocher *et al.* 2010b, Demars *et al.* 2011b, Perkins *et al.* 2012, Yvon-Durocher *et al.* 2012), although it is dependent on community abundance, biomass or other variables (Allen *et al.* 2005, Mahecha *et al.* 2010). Heterotrophic biomass production, and thus respiration, in terrestrial ecosystems is primarily driven by autochthonous primary production, but allochthonous carbon inputs can decouple respiration from photosynthesis in aquatic systems (Yvon-Durocher *et al.* 2012). Thus, terrestrial subsidies may alter the metabolic balance of aquatic ecosystems and their response to temperature. By linking the structure of the autotrophic and heterotrophic communities, the sources and cycling of their energy and nutrients, and measures of ecosystem functioning, we can hope to better understand likely responses to warming in these multi-species systems.

G. Testing hypotheses in the Hengill system

Our overarching aim here is to explore how environmental temperature and warming alters structure (from the individual to the ecosystem level) and functioning across multiple levels of biological organisation (Figure 1) and spatiotemporal scales (Figure 2). A set of specific hypotheses and predictions tested in this paper and how they map onto these different scales and organisational levels are laid out in Table 1. The spatial and temporal scales of measurement vary depending on the study, so the remainder of the paper is organised according to the level of biological organisation, from individuals to the entire ecosystem. This naturally connects temperature effects on structure to those connected with processes. Thus, Figure 1 acts as a road map for the paper, with each numbered box addressed in turn and Hengill employed as a model system.

< Table 1 near here>

III. MATERIALS AND METHODS

A. Study site

This study represents the integration of a large body of work from ongoing research conducted in the geothermally-active Hengill region of southwest Iceland (64°03' N: 21°18' W), which began in August 2002. This research spans different spatial and temporal scales (see Figure 2), which we have collated to provide an in-depth and holistic overview. The Hengill area represents the triple junction of the Reykjanes Peninsula Volcanic Zone, the Western Volcanic Zone and the South Iceland Seismic Zone (Foulger 1995). Our study sites include 15 tributaries of the river *Hengladalsá* (Figure 4), which are mostly spring-fed and heated via deep geothermal reservoirs (Arnason *et al.* 1969); i.e. the water in the stream channels is heated but not contaminated with additional chemical constituents (e.g. sulphur) normally associated with geothermal activity. The streams are similar in their physical and chemical properties (see Appendix A), with temperature being the only variable that is ecologically meaningfully different among them (Friberg *et al.* 2009, Woodward *et al.* 2010b). This study focuses on the main *Hengladalsá* river and 14 of its tributaries: the 15th tributary is far hotter (~50 °C) and is excluded as an extreme outlier, unlikely to be biologically meaningful in the context of natural environmental warming events (after Woodward *et al.* 2010b). Mean summer temperatures of the remaining streams range from about 4 to 25 °C (see Table 2).

< Figure 4 and Table 2 near here>

Two streams in the system are particularly useful for comparing the effects of warming: the warm IS8 (approximate annual range: 21-25 ºC) and cold IS7 (approximate annual range: 4-8 ºC) streams are separated by just 2 m at their closest point (see red dashed ring in Figure 4). These two streams are physically almost identical, apart from their temperature regimes, and thus they represent an important paired case study that we will return to throughout this paper.

B. Biotic characterisation

Data on the species composition of each stream have been collected on several occasions since 2002, but simultaneous sampling of the different assemblages within the food web and ecosystem processes has only been conducted since 2008, as the intensity and integration of research activity has increased. Macroinvertebrates were first sampled in June and August 2002 and 2003 in three of the streams (Olafsson *et al.* 2010). Macroinvertebrates and fish were first sampled in all streams in August 2004, with some of these results published elsewhere (Friberg *et al.* 2009, Woodward *et al.* 2010b). The diatom assemblage was first characterised in the summers of 2006 and 2007 (Gudmundsdottir *et al.* 2011a, 2011b). Ciliates, flagellates and meiofauna were sampled qualitatively in four streams in August 2008 (Perkins *et al.* 2012), but quantified for each tributary for the first time in August 2011, data which are presented here. The most comprehensive sampling of the biotic community to date was undertaken in August 2008 and April 2009 and these two dates account for most of the data presented here. Diatoms, macroinvertebrates and fish were sampled in both 2008 and 2009, although the 2008 dataset contains only seven tributaries, whereas the 2009 dataset contains all

14 and so forms the backbone of this paper. The following paragraphs explain the procedures for sample collection, species identification and measurements of body mass and abundance for these data.

Diatom species composition was established from three stones per stream. The biofilm was scrubbed from the upper surface of each stone using a clean toothbrush and rinsed with stream water into a 15 ml sample tube, topped up with 1 ml of Lugol's solution (after Layer *et al.* 2010). Stones were photographed (including an absolute scale) and projected surface areas calculated using ImageJ (Rasband 2011). The diatom frustules were cleared of all organic matter with nitric acid (e.g. Eminson and Moss 1980), 500 µl of each was diluted with distilled water and the samples were then dried and mounted on a slide with naphrax (Brunel Microscopes Ltd., Chippenham, U.K.). At least 300 valves in a set transect (100 µm × 15 mm) were counted and identified to species level where possible, based on Krammer and Lange-Bertalot (1986, 1988, 1991a, b), using 1000x magnification under a Nikon Eclipse 50i microscope. Photographs were taken of up to 30 individuals per species per slide and linear measurements were taken using ImageJ (Rasband 2011). Individual cells were assigned geometric shapes, and cell volumes were estimated according to Hillebrand *et al.* (1999) using length and width measurements which were then transformed into body mass after Reiss and Schmid-Araya (2008) (see Appendix B). Yield-effort curves to validate the efficiency of diatom sampling in April 2009 are shown in Appendix C.

Characterisation of the ciliate, flagellate and meiofaunal assemblages was carried out on live samples, collected from both hard and soft substrates, which were processed and analysed live. For hard substrates, two stones from each stream were collected, photographed and scraped, as described above, but diluted only with a known volume of distilled water. For soft substrates, sediment samples were collected from each stream using a small-bore corer (internal diameter = 10.3 mm; volume = 5 ml) and transferred to sterile 50 ml tubes. Sample volumes were recorded and shaken for homogenisation prior to sub-sampling. For both substrate types, 1 ml of suspended sediment was transferred to a Sedgwick rafter cell for individuals to be identified and counted by light microscopy using 400x magnification under a Nikon E200 compound microscope. Ciliates, flagellates and meiofauna were identified to genus where possible using Pontin (1978), Foissner and Berger (1996) and Patterson (1996). Linear measurements of live individual ciliates, flagellates and meiofauna were made using an eyepiece graticule. Individuals were assigned geometric shapes and cell volumes were estimated according to Hillebrand *et al*. (1999), and converted to body mass using conversion factors specified in Mullin *et al*. (1966) and Mullin (1969) (see Appendix B).

The composition of the macroinvertebrate assemblage was quantified from five Surber samples (25 × 20 cm quadrat, 200 μm mesh size) per stream on each sampling occasion. Samples were preserved in 70% ethanol. Individuals were identified to the highest possible level of resolution (usually species) using a range of freshwater invertebrate keys (Usinger 1956, Hopkins 1961, Peterson 1977, Gíslason 1979, Cranston 1982, Wiederholm 1983, Savage 1989, Smith 1989, Schmid 1993, Glöer 2002, Bouchard 2004, Brooks *et al.* 2007). Chironomid head capsules were cleared with potassium hydroxide (KOH) and mounted on slides with euparal before identification using a light microscope at 400-1000x magnification (Brooks *et al.* 2007). All other macroinvertebrate taxa were identified at 100x magnification. For each species and each sampling occasion, linear dimensions (i.e. head width, body length, body width or shell width) of up to 30 individuals were measured and these were converted to body mass using published length-mass regressions (Ramsay *et al.* 1997, Benke *et al.* 1999, Johnston and Cunjak 1999, Woodward and Hildrew 2002, Baumgärtner and Rothhaupt 2003, Stoffels *et al.* 2003; see Appendix B). Yield-effort curves to validate the efficiency of macroinvertebrate sampling in April 2009 are shown in Appendix C.

Trout population abundances were characterised using 3-run depletion electrofishing of a 50 m reach within each stream, after Seber and Le Cren (1967). Fork length and body mass measurements were also taken for each fish. Note that many of the streams are less than 50 m in length, so the entire stream was fished in these cases. All electrofishing of the catchment was carried out over a two-day period in both August 2008 and April 2009.

C. Individuals to populations: testing temperature-size rules

James's Rule states that the mean body size of a species should decrease with increasing temperature (James 1970). This rule was tested using the data outlined above by linear regression of the body mass of all individuals of a species against the temperature of each stream. This was carried out for all species of diatoms, macroinvertebrates and fish in April 2009. To account for multiple testing, Bonferroni correction was applied to all significant trends ($p < 0.05$). Here, p was divided by the total number of tests carried out ($n = 66$).

D. Quantifying population-level traits and interactions

The diet of trout was characterised in August 2008 and April 2009, using the same methods applied in the earlier 2004 survey (Woodward *et al.* 2010b). Gut contents from 63 individuals were obtained through live stomach flushing with a plastic syringe and catheter tubing, or dissection of euthanised fish where live sampling was not feasible (for very small individuals), and stored in 70% ethanol. Gut contents were identified to the highest possible taxonomic level and counted under 100x magnification. Biomasses were estimated as described above for macroinvertebrates. Bray-Curtis similarity was calculated between the diet of the trout and the prevalence of potential prey in the same stream as a measure of diet breadth.

A separate study from another geothermal system in Iceland was used to explore differences in the growth rate of *Radix peregra* with temperature (see Box 1). Note here, that we refer to *R. peregra* as conspecific with *Lymnaea peregra* and *R. balthica* after Bargues *et al*. (Bargues *et al.* 2001) and not *R. ovata* as in some descriptions (Remigio 2002).

< Box 1 near here>

The biomass (mg m^{-2}) of species populations were calculated for each stream, by multiplying average species body mass (mg) by population abundance (individuals m^{-2}) in the stream. Linear regression was used to test for responses in these variables to temperature. Patterns in the observed relationships were further explored by correlation of population biomasses to each other to determine if interactions between predator-prey pairs may be driving the changes in biomass.

The snail *R. peregra* is the dominant large grazer in the system, especially in the warmer streams. Thus, the effect of temperature on grazing pressure was examined using results from a previous snail exclusion experiment carried out in August 2004. Here, tiles with a layer of Vaseline around the perimeter to exclude grazing by snails were compared to control tiles with no Vaseline, thus allowing us to estimate net and growth algal accrual rates (after Hladyz *et al.* 2011). The concentration of chlorophyll on the tiles was measured after 28 days of exposure and the log-ratio of chlorophyll in the presence and absence of snails was used as a measure of grazing pressure (see Appendix D and Friberg *et al*. 2009 for further details).

E. Quantifying community-level properties

A matrix of pairwise temperature differences between streams was computed for every combination of the fifteen streams in the study. Sørensen's Index was used to calculate the community similarity for each pair of streams for five different assemblages within the system: diatoms (April 2009 data), ciliates, flagellates, meiofauna (all August 2011 data) and macroinvertebrates (April 2009 data). A Mantel test was used to test for significant differences in community similarity with increasing pairwise temperature difference.

Estimates of interaction strength were calculated for all consumer-resource pairs (see *Quantifying food web structure* below) in the warm IS8 and cold IS7 streams in August 2008 and April 2009. We used general relationships described in a published functional response database (Rall *et al.* 2012) and a well known study on metabolic rates (Brown *et al.* 2004) to calculate the actual mass specific and relative feeding rate (see Appendix D for further details).

Estimates of community biomass were also made for the warm IS8 and cold IS7 streams in August 2008 and April 2009, by summing the biomass of species populations across three different assemblages: diatoms, macroinvertebrates and fish. Trophic biomass pyramids were constructed for each stream in both seasons from these data.

F. Quantifying the food web and size structure: community-ecosystem linkages

Highly resolved food webs were constructed for the warm IS8 and cold IS7 streams, based on the species composition of each stream in August 2008 and April 2009. The trophic links in these webs were determined by a combination of gut content analysis and literature research (see Appendix E). The number of species (S) and links (L), linkage density ($LD = L/S$), connectance ($C = L/S^2$), mean food chain length (calculated as the average short-weighted trophic level; after Williams and Martinez 2004), and the proportions of basal, intermediate and top species were calculated for each food web. Trivariate food webs were also constructed (after Cohen *et al.* 2003, Reuman and Cohen 2004, Woodward *et al.* 2005b, Layer *et al.* 2010, McLaughlin *et al.* 2010, O'Gorman and Emmerson 2010), based on this link information and the average body mass and abundance of each species. Values of the slope and intercept of fitted linear regressions were calculated for each trivariate food web. Intercepts were not determined from the zero point of the x-axis, but rather the smallest species across the entire dataset (*cf.* dashed line in Figure 3) (after Yvon-Durocher *et al.* 2011). Size spectra were computed by dividing the body size data into ten even $\log_{10}$ size bins irrespective of species identity. The mid-points of these size bins were then plotted against the number of individuals per size bin. To ensure any observed patterns were not solely driven by the presence of the largest apex predator, trout, we also removed this species from the analyses and re-calculated both the trivariate food web and size spectra regressions. The triangular and trivariate food webs and approximate size spectra were constructed, plotted and analysed in R 2.14.0 using the ‘cheddar' package (Hudson *et al.* in press).

G. Ecosystem processes: energy and nutrient cycling

Decomposition rates were measured across ten of the streams in August 2004 (see Friberg *et al*. 2009 for details). Here, fine (200 µm aperture) and coarse (10 mm aperture) mesh leaf bags were filled with 2.00 g air-dried green leaves of native Arctic downy birch, *Betula pubescens*. Five each of the fine and coarse mesh leaf bags were placed randomly throughout each stream and secured to the stream bed with a tent peg. After 28 days, the leaf bags were removed, dried to a constant weight at 60 °C and weighed to the nearest 0.01 g. Community and microbial decomposition were estimated from the coarse and fine mesh leaf bags, respectively. Macroinvertebrate decomposition was not calculated in Friberg *et al*. (2009), but it is estimated here according to the following formula: $\ln(1-[(1-p_c)-(1-p_f)])/t$, where p_c and p_f are the proportion of leaf litter remaining in the coarse and fine mesh leaf bags, respectively, and t is the duration of the experiment in days, assuming exponential decay as is typical in most litter breakdown assays (Woodward *et al.* 2012). Decomposition rates were converted to g C day^{-1} using a conversion factor of 0.5 (after Lin *et al.* 2012) to make them more comparable with other ecosystem process rates from the system.

The nutrient uptake rate (mg N or P m^{-2} h^{-1}) of NH_4, NO_3 and PO_4 was measured for the warm IS8 and cold IS7 streams in August 2008 (see Demars *et al.* 2011b for details). To explore the temperature dependencies of cycling for these various nutrients, the percentage change in nutrient uptake rate is estimated here per °C increase in water temperature from the cold to the warm stream.

H. Ecosystem processes: ecosystem metabolism measurements

To investigate the metabolic capacity of assemblages originating from contrasting thermal regimes, benthic biofilms were collected from four Hengill streams in August 2008, spanning a broad temperature range (mean temperatures ~ 6 °C, 13 °C, 21 °C and 25 °C respectively) and incubated in the laboratory at a range of experimental temperatures (see Appendix D and Perkins *et al*. 2012 for details). For each of the 16 experimental subjects (i.e. 4 streams × 4 replicates), biofilm biomass was determined via ash free dry mass determination and converted here to C units by applying an empirical ratio of 0.53 (Wetzel 2001). The stream-specific estimates of average activation energies, E (eV), and average $\ln R(T_c)$, given by the slope and intercept of the Arrhenius model, respectively, were determined using mixed-effects modelling (see Perkins *et al.* 2012 for further methodological details). Expressing respiratory flux as a function of standardised temperature makes the intercept of the relationship, $\ln R(T_c)$, equal to the rate of respiration at standardised temperature, T_c (here T_c = 15 °C = 288.15 K). Here, we also examine the relationship between $\ln R(T_c)$ and biofilm biomass to explore how differences in the latter drive the within-stream variation in respiration rates, which was not examined in the Perkins *et al*. (2012) study.

Daily ecosystem respiration (ER) was calculated from the net metabolism at night (PAR <1μmol photon m^{-2} s^{-1}) scaled to 24 hours. Gross primary productivity (GPP) was derived from subtracting the dark from the light metabolism averaged over 24 h. The daily net ecosystem production (NEP) was calculated as GPP minus ER, with the assumption that autotrophic and heterotrophic respiration were the same under light conditions as those measured at night (see Appendix D and Demars et al 2011 for further details). All ecosystem metabolism measurements from this system have previously been reported in fluxes of O_2 (e.g. Demars *et al.* 2011b), but here we present them as fluxes of C, a more common unit in the climate change literature and for ease of comparison with other ecosystem process measurements in this study. The photosynthetic quotient (P.Q.=$\Delta O_2/-\Delta CO_2$) may vary from 1 (when carbohydrates are the principal product) to as high as 3 (when fats are being synthesised) (Vollenweider 1969p. 78). Similarly, the respiratory quotient (R.Q.= ΔCO_2/- ΔO_2) is 1 when carbohydrates are respired and <1 when fats are respired (Williams and Del Giorgio 2005). Since we do not know the proportion of these metabolic pathways, P.Q. and R.Q. were both fixed at 1 and oxygen units were converted to carbon equivalents using a conversion factor of 0.375 (based on atomic weights; see McCloskey *et al.* 1994).

IV. RESULTS

A. Structure: individuals to populations

There were significant effects of temperature in April 2009 on the body size of individual organisms from three major taxonomic groups: diatoms, macroinvertebrates and fish. Several species complied with James's Rule. Here, the mean body size of the diatoms *Achnanthes lanceolata* ($F_{1,181} = 9.70, p = 0.002$), *A. minutissima* ($F_{1,23} = 10.16, p = 0.004$) and *Amphora pediculus* ($F_{1,67} = 8.82, p = 0.004$), the chironomids *Cricotopus sp. A* ($F_{1,59} = 26.68, p < 0.001$), *Diamesa zernyi* ($F_{1,106} = 5.83, p = 0.018$) and *Eukiefferiella minor* ($F_{1,307} = 4.40, p = 0.037$), oligochaete worms ($F_{1,359} = 11.83, p < 0.001$) and the snail *R. peregra* ($F_{1,301} = 7.10, p = 0.008$) all decreased with increasing temperature (see Figure 5). The remaining species did not comply with James's Rule. Many species showed no response to temperature, while the mean body size of the diatoms *Cocconeis placentula* ($F_{1,62} = 5.99, p = 0.017$), *Diatoma mesodon* ($F_{1,84} = 8.37, p = 0.005$), *Navicula minima* ($F_{1,53} = 4.57, p = 0.037$) and *Nitzschia aquaeore* ($F_{1,5} = 10.01, p = 0.025$), the chironomid *Orthocladius sp.* ($F_{1,56} = 10.04, p = 0.002$), the black fly larvae *Simulium vittatum* ($F_{1,86} = 16.51, p < 0.001$) and the trout *Salmo trutta* ($F_{1,12} = 15.53, p = 0.002$) all showed the opposite trend to theoretical predictions and increased with temperature (see Figure 6). After Bonferroni correction for multiple testing (p / n, where n = the total number of tests carried out), however, only *Cricotopus sp. A* ($p < 0.001$) and oligochaete worms ($p = 0.043$) retained a significant negative trend, while *S. vittatum* ($p =$

0.007) was the only species to retain a significant positive trend. Overall, evidence for James's Rule was thus equivocal at best.

< Figures 5 and 6 near here>

B. Structure: population-level traits

The similarity in the diet of trout to available prey in the benthos increased with temperature in both April ($F_{1,11}$ = 6.78, p = 0.025; Figure 7) and August ($F_{1,44}$ = 4.18, p = 0.047; Figure 7), suggesting they became more generalist in warmer waters, consuming a higher proportion of the available species pool. Note that some of the smallest trout are associated with unusually high similarity at low temperature (grey points in Figure 7), potentially suggesting a different response in juvenile trout. Additionally, the number of data points is low in April, especially at the highest temperatures, suggesting that significant trends should be interpreted with caution.

< Figure 7 near here>

The proportional representation of prey species by biomass in the diet of trout was dominated by just a few groups (see Figure 8). Here, *R. peregra*, Simuliidae, Chironomidae, other Diptera and terrestrial invertebrates form more than 90% of the diet (in terms of the number of individual prey items) in each stream. *R. peregra* and Chironomidae dominated the trout diet in the warmer streams in April, while Simuliidae, other Diptera and terrestrial invertebrates dominated in August. These shifts broadly reflected seasonal variation in the primary food sources for the trout in this system, especially at the warmer temperatures.

< Figure 8 near here>

C. Structure: population-level interactions

Although *R. peregra* body mass decreased with increasing temperature in April 2009 (see Figure 5), there was a significant increase in its population biomass ($F_{1,6} = 53.82$, $p < 0.001$; Figure 9). This might explain the unexpected coincident increase in size (see Figure 6) and population biomass ($F_{1,4} = 7.69$, $p = 0.040$; Figure 9) of *S. trutta* with temperature. The biomass of *S. trutta* and *R. peregra* were also significantly correlated with one another ($F_{1,3} = 12.29$, $p = 0.039$; Figure 10), suggesting a possible bottom-up effect of snails on trout (see Figure 9).

< Figures 9 and 10 near here>

There was also evidence suggesting top-down effects of snails on the basal resources, with a decline in biomass of several diatom species across the temperature gradient. Here, the biomass of *A. lanceolata* ($F_{1,12} = 10.14$, $p = 0.008$), *A. minutissima* ($F_{1,5} = 7.36$, $p = 0.042$), *Gomphonema D* ($F_{1,9} = 7.61$, $p = 0.022$), *Meridion circulare* ($F_{1,38} = 38.38$, $p < 0.001$), *N. atomus* ($F_{1,9} = 13.29$, $p = 0.005$) and *N. atomus var. atomus* ($F_{1,4} = 7.98$, $p = 0.048$) all decreased with increasing temperature (see Figure 9). The biomass of *R. peregra* was also significantly correlated to two of these diatom species, *Gomphonema D* ($F_{1,4} = 9.36$, $p = 0.038$; Figure 10) and *M. circulare* ($F_{1,5} = 10.35$, $p = 0.024$; Figure 10). The possibility of a top-down effect being manifested here is supported from a previous grazing experiment carried out in summer 2004, in which the log ratio of chlorophyll on grazer-excluded tiles relative to grazed tiles significantly increased with temperature ($F_{1,3} = 12.29$, $p = 0.039$; Figure 11), i.e. there was stronger grazing pressure in the warmer streams.

< Figure 11 near here>

Stomach content analysis of the trout (Figure 8), revealed the snail *R. peregra* and Simuliidae black fly larvae were important prey at different times of the year, which was reflected by changes in the relative biomass of each species with temperature. In April, the biomass of Simuliidae showed no significant relationship with temperature ($F_{1,7} = 0.18$, $p = 0.682$; Figure 12), while the biomass of *R. peregra* increased with temperature ($F_{1,6} = 53.82$, $p < 0.001$; Figure 12). In August, the biomass of Simuliidae increased with temperature ($F_{1,4} = 22.65$, $p = 0.009$; Figure 12). While the biomass of *R. peregra* increased with temperature in August ($F_{1,4} = 10.95$, $p = 0.030$; Figure 12), the overall biomass in both colder and warmer streams was at least an order of magnitude lower than in April.

< Figure 12 near here>

D. Structure: community-level properties

Sørensen's index revealed no significant change in species composition as the pairwise temperature difference between diatom assemblages increased in April 2009 (Mantel $r = 0.216$, $p = 0.059$; Figure 13). There was also no significant change in the species composition of the ciliates (Mantel $r = -0.128$, $p = 0.815$), flagellates (Mantel $r = -0.015$, $p = 0.524$) or meiofauna (Mantel $r = 0.184$, $p = 0.089$) as pairwise temperature differences between assemblages increased in August 2011 (see Figure 13). The macroinvertebrates showed a significant decline in similarity as the pairwise temperature difference between assemblages increased in April 2009 (Mantel $r = 0.326$, $p = 0.044$; Figure 13).

< Figure 13 near here>

We compared interaction strengths in two streams at the extremes of the temperature gradient: IS8 (2008-2009 temperature range: 21.6-24.6 °C) and IS7 (2008-2009 temperature range: 4.8-8.2 °C). Mass specific feeding rates increased in the warm relative to the cold stream, with a shift in the distribution towards stronger interactions (see Figure 14*a*, *c*). This pattern disappeared after correcting for metabolism, however, with relative feeding rates (F_{rel}) tending towards weaker interactions in the warm *versus* the cold stream (Figure 14*b*, *d*). Even so, the strongest relative interaction strengths were still found in the warm stream, with *S. trutta* feeding on *R. peregra* ($F_{rel} = 42.75$; all other $F_{rel} < 1$) and predators feeding on Simuliidae ($F_{rel} = 1.98$; all other $F_{rel} < 1$) representing the strongest interactions. Additionally, fewer links were found in the warm streams, as indicated by the lower number of observations in all panels.

< Figure 14 near here>

A qualitative exploration of community biomass highlighted a shift in the structure of trophic biomass pyramids in the warm IS8 and cold IS7 streams. The biomass of diatoms was lower and the biomass of macroinvertebrates was higher in the warm stream in both April 2009 and August 2008 (Figure 15). There was also an additional trophic compartment provided by the presence of trout in the warm stream, making the warm trophic biomass pyramids more top-heavy.

< Figure 15 near here>

E. Structure: communities to ecosystems: food web and size structure

The warm IS8 and cold IS7 food webs highlight some key differences in community structure related to temperature, as representatives of general patterns seen across the full temperature gradient. The warm stream had a much simpler food web structure, with fewer species and links and a lower linkage density and connectance in both April 2009 and August 2008 (see Table 3; Figure 16). The streams had a similar trophic structure in both seasons, with mean food chain lengths virtually identical (see Table 3; Figure 16). Although the warm stream had a much larger apex predator (trout), the proportion of top species was actually lower than the cold stream in both seasons (see Table 3).

< Figure 16 and Table 3 near here>

Trivariate plots of body mass, abundance and trophic links revealed further differences between the two streams. The warm stream had a much shallower (i.e. less negative) slope in both seasons (April = -1.18; August = -1.10; Figure 17, red regression line) relative to the cold stream (April = -1.53; August = -1.82; Figure 17). The *y*-intercept with the smallest species in the dataset was also lower in the warm stream (April = 8.2; August = 8.1) than in the cold stream (April = 9.3; August = 9.2). After excluding fish from the regression, the slope was still shallower in the warm stream (April = -1.43; August = -1.28; Figure 17, black regression lines) and the *y*-intercept with the smallest species was still lower than the cold stream for both seasons (April = 8.5; August = 7.7). These results mirror the reduced energetic efficiency scenario illustrated in Figure 3*c*.

< Figure 17 near here>

To examine how temperature alters some structural properties of the community related to biomass flux, we compared size spectra in the warm IS8 and cold IS7 streams. The warm stream had a much shallower slope (April = -1.08; August = -0.95; Figure 18, red regression line) than the cold stream (April = -1.51; August = -1.55; Figure 18). The *y*-intercept with the smallest individual in the dataset was also lower in the warm stream (April = 8.7; August = 8.1) than in the cold stream (April = 10.0; August = 9.7). Even after excluding fish from the regression, the slope was still shallower in the warm stream (April = -1.21; August = -1.12; Figure 18, black regression lines). The *y*-intercept with the smallest species was also still lower than the cold stream for both seasons (April = 9.0; August = 8.4). These results again mirror the reduced energetic efficiency scenario in Figure 3*c*.

< Figure 18 near here>

F. Ecosystem processes: energy and nutrient cycling

The total ($F_{1,8} = 6.75$, $p = 0.032$; Figure 19*a*) and microbial ($F_{1,8} = 13.52$, $p = 0.006$; Figure 19*b*) decomposition rates increased significantly with increasing temperature in August 2004, but there was no significant change in the macroinvertebrate-mediated decomposition ($F_{1,8} = 2.09$, $p = 0.187$; Figure 19*c*).

< Figure 19 near here>

The cycling rate of NH_4, NO_3 and PO_4 all increased in the warm IS8 stream compared with the cold IS7 stream in August 2008 (Figure 20), with differential temperature dependencies apparent for these three nutrients, with percentage differences per °C for $PO_4 < NH_4 < NO_3$.

< Figure 20 near here>

G. Ecosystem processes: ecosystem metabolism measurements

Biofilm respiratory flux ($\ln R(T_c)$) increased with temperature ($1/kT_c$ - $1/kT$) across substrata taken from different streams (Figure 21*a*). Values of average activation energies, *E*, the fundamental parameter that determines the temperature sensitivity of respiration, were statistically indistinguishable across streams (likelihood ratio test for 'lmer' models, see Perkins *et al*. 2012 for details). Holding slopes constant across streams yielded a common *E* of 0.47 (fitted line; 95% confidence intervals 0.31–0.63 eV), following closely the average activation energy of the respiratory complex (Brown *et al.* 2004). There was a significant correlation between the variation in the intercept of the above relationship, $\ln R(T_c)$, across streams (i.e. residuals around the fitted line in Figure 21*a*) and biofilm biomass (fitted line; $y = 0.69 + 2.05x$, $r = 0.98$, $n = 4$, $p = 0.012$; Figure 21*b*), but not ambient stream temperature ($r = 0.23$, $n = 4$, $p = 0.761$), providing further evidence against physiological thermal adaptation.

< Figure 21 near here>

Daily light availability, measured as PAR, was similar on average for both April 2009 (40 ± 5 mol photon m^{-2} day^{-1}) and August 2008 (38 ± 4 mol photon m^{-2} day^{-1}), suggesting a consistent amount of time available for productivity in the streams (Figure 22*a*). GPP_{max} was strongly and similarly related to observed daily GPP in both April ($F_{1,11} = 250.10$, $p < 0.001$) and August ($F_{1,11} = 87.37$, $p < 0.001$), showing that daily incoming photosynthetic solar radiation was comparable in both seasons at the time of the metabolic studies and food web field sampling (Figure 22*b*).

< Figure 22 near here>

There was no significant effect of temperature on GPP in April 2009 ($F_{1,8} = 0.47$, $p = 0.512$; Figure 23*a*), but temperature caused a significant increase in GPP in August 2008 ($F_{1,11}$

= 5.52, $p = 0.039$; Figure 23*a*) showing seasonal differences in the relationship between temperature and GPP. Mean GPP was also significantly lower in April compared to August ($t_{0.05[18]} = -2.1$, $p = 0.05$; Figure 23*b*), as was true for all but the two coldest streams in the system (Figure 23*c*).

< Figure 23 near here>

Ecosystem respiration fluctuated daily in April 2009 (Figure 24*a*), but was almost constant in August 2008 (Figure 24*c*), reflecting differences in the variability of available light ($r^2 = 0.84$, $p < 0.001$; Figure 24*b, d*) and increased discharge in during spring ice-melt. The NEP was not significantly different from zero (0.26 ± 0.3 g C m^{-2} day^{-1}) in the IS1 stream in April, in sharp contrast to the constant negative NEP in August at the same site (-3.00 ± 0.3 g C m^{-2} day^{-1}), resulting in increased carbon production during summer. This was largely driven by reduced ecosystem respiration in April (-5.63 ± 8.6 g C m^{-2} day^{-1}; mean ± standard error) relative to August (-10.50 ± 4.1 g C m^{-2} day^{-1}).

< Figure 24 near here>

V. DISCUSSION

The data presented here reveal a range of temperature-driven effects that operate across all the levels of organisation investigated, from individuals to the entire ecosystem. We have highlighted impacts of temperature on the mean body size of a number of species (Figures 5 and 6), on the diet breadth of trout (Figures 7 and 8) and on the growth rate of snails (Box 1 Figure). We observed changes in the biomass of some key species with temperature (Figures 9-12), which could lead to increased interaction strengths (Figure 14), greater top down suppression and changes in the structure of trophic biomass pyramids (Figure 15). Increased temperature reduced the similarity of macroinvertebrate assemblages, with particularly little change in the species composition of protozoan and meiofaunal assemblages (Figure 13). Food web structure was simplified at higher temperature (Table 2, Figure 16), with reduced trophic transfer efficiency suggested by shallower mass-abundance scaling (Figures 17 and 18). All ecosystem process rates increased with temperature (Figures 19-24), but at different rates (Figures 20 and 24). These results demonstrate profound effects of temperature on the structure and functioning of ecological communities and we will now discuss their significance in turn in greater detail.

A. Individuals to populations

There was only limited support for James's Rule in Hengill (*cf.* hypothesis 1 in Table 1: decreasing body mass with increasing temperature). While several species of diatoms, chironomids and other macroinvertebrates decreased in size with temperature (Figure 5), most either showed no change or an increase in individual body size in the warmer streams (Figure 6). Additionally, many of the observed negative trends may simply be artefacts of multiple testing, as revealed following Bonferroni corrections. Thus, these data add to the debate about the ubiquity of temperature-size rules, with some authors contesting that the converse relationship is quite common (Mousseau 1997, Bernardo and Reagan-Wallin 2002), i.e. that ectotherms do not benefit from a smaller surface area to volume ratio (associated with a larger mass) reducing heat loss in colder environments (Geist 1987). In particular, Mousseau (1997) argues that a longer growing season in warm environments should lead to a larger individual body size, given the positive relationship between development time and body size frequently observed in ectotherms (Peters 1983), and recent eco-evolutionary modelling results suggest that positive size-temperature relationships could occur due to food web effects (Moya-Laraño *et al*. 2012). Walters and Hassall (2006) show that ectotherms that obey temperature-size rules have a higher temperature threshold for development rate than growth rate, while the exceptions have a lower threshold. This disparity, also seen elsewhere (van der Have and de Jong 1996, Forster *et al.* 2011), may account for some of the responses to temperature in the Hengill system.

Comparisons of growth and development rates in freshwater ectotherms are rare, but experiments by Mackey (1977) showed that larvae of the chironomid *Cricotopus sp.* responded to an increase of temperature from 15 to 20 °C by increasing their development rate, but not growth rate. This corresponds to the significant decrease in body size with temperature for this genus in the Hengill system (Figure 5). Conversely, *S. trutta* embryos do not develop above 16 °C (Ojanguren and Braña 2003), while growth continues up to 19.5 °C (Elliott 1975, 1976), suggesting a lower temperature threshold for development than growth rate, i.e. individual size should increase with temperature, as we see in Hengill (Figure 6). Previous research on Scandinavian trout also demonstrated a positive relationship between temperature and body size (Eklöv *et al.* 1999), suggesting that this may be a common response within this species.

B. Population-level traits

The diet breadth of trout changed with temperature and body size (Scharf *et al.* 2000, Petchey *et al.* 2008). The increase in body size of trout with temperature led to an increase in similarity of the diet with availability of prey in the stream benthos in the warmer systems (Figure 7). Thus, the trout diets broadened with temperature in contrast to our second hypothesis (see Table 1), largely driven by the surprising increase in body mass of trout with increasing temperature (Figure 6). Here, the larger trout should be faster and more adept at spotting a wider range of prey (Keast and Webb 1966, Webb 1976, Blaxter 1986). Consequently, activity and hence encounter rates are also likely to increase with temperature as both the trout and their prey become more active (Vucic-Pestic *et al.* 2011). Given the high metabolic requirements in warmer environments (Brown *et al.* 2004), the trout may be forced to be more generalist, and this could contribute to the reduced diversity and simplicity of the food webs, and especially the loss of intermediate invertebrate consumers, in the warmer streams (Table 3; Figure 16). Overall food web connectance decreased with temperature (Table 3), however, perhaps because other generalists, such as the fly larvae *Dicranota sp*. and water mite *Sperchon glandulosus*, are excluded by trout. These changes in the food webs could have implications for their dynamic stability, potentially making the warmer systems less robust to perturbations and more prone to secondary extinctions (Yachi and Loreau 1999, Dunne *et al.* 2002).

The trout also altered their feeding behaviour over time, with black fly larvae and terrestrial subsidies forming the main component of the diet in summer (Figure 8), reflecting shifts in resource availability. *S. vittatum*, which is the dominant black fly larvae in the system, grows faster at higher temperatures (Fuller and Fry 1991). This may contribute to the increased biomass with temperature in August and thus the predominance of Simuliidae in the diet of trout in the warmer streams (Figures 8 and 12). Terrestrial subsidies can comprise more than 50% of energy intake by stream fishes, particularly during summer (Furukawa-Tanaka 1985, Garman 1991), and are often a preferred prey of salmonids (Hunt 1975). The potential importance of this allochthonous energy source is suggested from the 'dog-leg' in Figure 17, where trout (symbolised by the red points) are far more abundant than would be expected for their body size. This may be due in part to the terrestrial subsidy, which augments the diet of the trout and helps them to maintain a higher population biomass than would be possible based solely on in-stream production, as observed elsewhere and described by the classic “Allen paradox” (Allen 1951, Nakano *et al.* 1999, Baxter *et al.* 2007).

This 'pattern is also found in April, however, when snow cover and freezing conditions limit the input of terrestrial subsidies to the system, suggesting that other mechanisms may also be at play. Fish predation pressure can shift dramatically from terrestrial to aquatic invertebrates when terrestrial subsidies to streams are reduced (Nakano *et al.* 1999), suggesting a more benthic feeding behaviour, as indicated by the prevalence of chironomids and the snail

R. peregra forming the main component of both the diet and the benthos (Figure 8). Thus in-stream prey production may be especially critical outside the summer, and it may be insufficient in the coldest streams to support trout (Figure 23).

Independent evidence from geothermal areas in an Icelandic lake (Lake Mývatn) may help to shed further light on the increasing prominence of *R. peregra* in the warmer Hengill streams (Box 1). Here, warm-origin populations grew faster than cold-origin ones and snails also grew more rapidly in warmer environments (Snail Growth Figure) in support of our third hypothesis (see Table 1), suggesting a combination of both environmental conditions and genetic adaptation (as shown for marine snails by Janson 1982). It would be instructive to explore the population genetics of the snails in Hengill, which has been exposed to warming for up to 50,000 years (Arnason *et al.* 1969). A rapid growth rate may allow the snails to reach sexual maturity at smaller sizes at warmer temperatures (Ray 1960, Atkinson 1994, Angilletta *et al.* 2004, Forster *et al.* 2011), creating a trade-off between high predation pressure and sustaining a viable population over multiple generations (Fischer and Fiedler 2002). Indeed, *R. peregra* are typically uni- or bivoltine (Lam and Calow 1989), but can reproduce continually if conditions are suitable (Lodge and Kelly 1985). If they reproduce continually in the warmer streams, this could lead to a considerable increase in secondary production of prey, which may offset the apparent reduced energy transfer efficiency with warming.

C. Population-level interactions

R. peregra are an increasingly important component in the diet of larger trout (Steingrímsson and Gíslason 2002), as suggested here by the concurrent increase in both species with temperature (Figure 9), the correlation between their respective biomasses (Figure 10) and the increased consumption of snails by trout in the warmer streams (Figure 8). However, the snails really only dominate the diet of the trout in the two warmest streams, (Figure 8), suggesting that other mechanisms may also be driving the increased trout biomass with temperature. Enclosure/exclosure experiments are required to definitively address the factors driving trout dynamics in the system.

The high biomass achieved by the snails in the warmer streams also suppresses the basal resources within the system, as revealed by the negative correlation between snail and diatom biomasses (Figure 10) and changes in grazing pressure demonstrated in a snail exclusion experiment (Figure 11; Friberg *et al.* 2009). In the latter, the biomass of algae increased with temperature in the absence of snail grazing, in contrast to the observed decrease in population biomass of many diatom species in the streams themselves (Figures 10 and 11). Such increases in top down control and grazing pressure with temperature support our fourth and fifth hypotheses (see Table 1). This could lead to energy being channelled rapidly from the base of the web to the apex predators. Further, the high rates of energy and nutrient recycling (Figures 19 and 20; Demars *et al.* 2011b) suggest this energy source, although heavily exploited, is rapidly replenished. Although we have only provided data on epilithic diatoms here, some of the warmer streams also have abundant populations of bryophytes and macrophytes (Gudmundsdottir *et al.* 2011a), which can host large populations of epiphytic diatoms. Indeed, the changes in epilithic diatom biomass with temperature may partly be a product of competition with or shading by other autotrophs (Gregg and Rose 1982, Sand-Jensen *et al.* 1988). A more comprehensive description of the autotrophic communities is now required to address these possibilities.

D. Community-level properties

The similarity in species composition of the macroinvertebrate assemblage decreased with increasing pairwise difference in temperature between streams (partly supporting our sixth hypothesis in Table 1), while all other assemblages remained relatively unchanged (Figure 13). Many cold-adapted stenotherms, such as members of the Orthocladiinae and Diamesinae chironomids (Olafsson *et al.* 2000, 2002, Rossaro *et al.* 2006), are often excluded with increasing temperatures (Chevaldonné and Lejeusne 2003, Hering *et al.* 2009, Somero 2010), while eurytherms such as *Eukiefferiella* spp., *R. peregra* and Simuliidae (Segal 1961, Becker 1973, Olafsson *et al.* 2000, Olafsson *et al.* 2002) become more prevalent (Figure 8; Woodward *et al.* 2010b). These shifts may also be compounded by biotic interactions: e.g. chironomid populations could be suppressed by snail grazing activity, either through direct physical contact and larval displacement or competition for food (Cuker 1983).

This shift in macroinvertebrate community composition from chironomid to *R. peregra* dominance is likely to have repercussions for the diatom assemblage. Chironomids tend to be more selective grazers (Botts 1993), whereas snails are indiscriminate scrapers, capable of altering the species composition and size frequency of the resource base (Hunter 1980, Kesler 1981). Snails can suppress the biomass of all but the smallest diatom species or tougher encrusting forms, with *Cocconeis* spp. being particularly resilient to grazing pressure (Hunter 1980, Kesler 1981). The success of these diatoms in response to grazing pressure by *R. peregra* on their competitors for light and resources may be reflected by the increase in body size of *Cocconeis placentula* with temperature (Figure 6).

The lack of a temperature response in the meiofaunal and protozoan assemblages is surprising, especially as respiration rates increase exponentially with temperature for many meiofaunal (Wieser and Schiemer 1977, Laybourn 1979, Price and Warwick 1980, Moens and Vincx 2000) and protozoan species (Laybourn and Finlay 1976, Caron *et al.* 1986), suggesting increased energetic demands in warmer environments (Brown *et al.* 2004). This raises the likelihood that cold-adapted stenotherms will be excluded in favour of more eurythermal species (Wieser and Schiemer 1977), as energetic demands become too great (Laybourn 1979) and resource biomass is more limited (Figure 15). However, the gross growth efficiency of many protozoa is believed to be independent of temperature within the range for optimal growth (Rogerson 1981, Sherr *et al.* 1983, Caron *et al.* 1986). Given the predominance of bacterivory among protozoa (Sherr *et al.* 1983, Caron *et al.* 1986, Sherr and Sherr 1987, Gonzalez *et al.* 1990, Vickerman 1992) and the generally positive effect of temperature on bacterial growth and abundance (White *et al.* 1991, Shiah and Ducklow 1994), food resources might not be limited with increasing temperature. This suggests they may be responding to other unmeasured gradients and/or there may be far greater diversity present in these systems than we can detect reliably using microscopic techniques. Metagenomic approaches could be instructive in resolving these questions in future studies (Purdy *et al.* 2010).

Most biological rates, including metabolism and feeding, scale with temperature (Brown *et al.* 2004). Current studies, however, show that there is a mismatch in the scaling of feeding and metabolism with temperature leading to a decreased relative feeding rate with warming (Rall *et al.* 2010, Vucic-Pestic *et al.* 2011, Rall *et al.* 2012). These studies are mainly laboratory-based, where predators have only one prey type in one arena and the whole spectrum of prey densities are given. Predators in the field are generally found with much lower prey densities and many different prey species. Generally, it is assumed that prey density decreases with warming (Brown *et al.* 2004, Meehan 2006). Subsequently, the predator has to increase feeding power to balance the decrease in prey density, likely leading to stronger interactions in the system.

Here, an exploration of interaction strengths for the neighbouring cold IS7 and warm IS8 streams revealed a possible shift in the distribution of strong versus weak mass specific interactions (Figure 14*a*, *c*), supporting our seventh hypothesis (see Table 1). Average mass specific interaction strength increased with temperature, which would classically suggest a destabilization of population dynamics and food web stability (May 1972, Vasseur and McCann 2005). This pattern is removed after correcting for metabolism, highlighting the role of increased metabolic demand at higher temperature in driving this effect (Figure 14*b*, *d*). Surprisingly, we found just a small reduction of relative interaction strengths in April and virtually no change in August, contrasting laboratory and model findings that report a 6 to 8 fold reduction over a comparable temperature range for terrestrial arthropods (Rall *et al.* 2010, Vucic-Pestic *et al.* 2011). Strong interactions have the potential to destabilise communities (McCann *et al.* 1998, Neutel *et al.* 2002), possibly leading to increased variability of ecosystem processes, reduced resistance to secondary extinctions and cascading effects (O'Gorman and Emmerson 2009). Weak interactions generate negative covariances and promote community stability by dampening the destabilising potential of strong consumer-resource interactions (McCann 2000, but see Allesina and Tang 2012). Thus, the loss of weak mass specific interactions and the gain of even stronger ones are likely to promote increased instability in the warm streams, via top-down suppression by consumers and fewer alternative resources available (Kondoh 2003). The increased diet breadth of the trout with temperature suggests some adaptive foraging in response to prey availability, which might increase food web stability as temperatures rise (Kondoh 2003).

E. Communities to ecosystems: food web and size structure

The warmer food webs were much less complex than the colder ones, with fewer species and feeding links and a lower linkage density and connectance (Figure 16; Table 3), supporting our eighth hypothesis (see Table 1). Such effects are likely to contribute to reduced stability of the webs in the face of perturbations (Yachi and Loreau 1999, McCann 2000, Dunne *et al.* 2002). Despite having a higher proportion of basal species, the absolute number of diatom species was reduced in the warm streams, perhaps due to heavy grazing by the snails (Figure 11). Similarly, while the proportion of intermediate species stays the same, the absolute number of such species is lower, creating a much narrower triangular structure in the warmed food web (Figure 16). This appears to be a general pattern across the thermal gradient, as revealed by changes in richness within invertebrate (Woodward *et al.* 2010b) and primary producer (Gudmundsdottir *et al.* 2011a, 2011b) assemblages, suggesting that biomass is funnelled through increasingly fewer species as it moves up the food web in the warmer systems. Despite this, the mean length of food chains was relatively consistent between the warm and cold streams (in contrast to hypothesis 8 in Table 1), perhaps because biomass fluxes are not split among so many consumer species in the warmer webs. This may also be indicative of the increased productivity with temperature (Figure 23), as well as the higher rates of energy and nutrient cycling (Figure 19; Figure 20), which may support longer food chains than expected (Kaunzinger and Morin 1998) in spite of apparent reduced trophic transfer efficiency.

Many of the mechanisms discussed above contribute to fundamental changes in the flow of energy through the food web. In contrast to hypotheses 9 and 10 (see Table 1), we did not observe increased slopes and intercepts of either the trivariate food webs (Figure 17) or the individual size spectra (Figure 18). While previous studies have described steeper mass-abundance slopes in response to an increased prevalence of smaller organisms (Yvon-Durocher *et al.* 2011), the inconsistent response of many populations to temperature in the Hengill system (Figures 5 and 6) meant there was no increase in the biomass of the smallest resources. In fact, the population biomass of diatoms decreased with temperature (Figure 15), producing lower intercepts and shallower slopes in both the trivariate webs and size spectra (Figures 17 and 18). This corresponds to the reduced energy transfer efficiency scenario highlighted in Figure 3*c*, suggesting that a greater biomass of resources must be consumed to sustain the same biomass of predators, in line with the increased top down suppression (Figure 9), grazing pressure (Figure 11) and shift towards stronger interactions (Figure 14) identified above.

F. Ecosystem process rates: energy and nutrient cycling

Total decomposition rates of leaf-litter increased with temperature, which was largely driven by the microbes with little effect of macroinvertebrates (Figure 19). This supports hypothesis 11 (see Table 1) and is in line with other research (Mulholland *et al.* 1997, Friberg *et al.* 2009). The macroinvertebrate community showed no response to increasing temperature, in contrast to previous studies (Azevedo-Pereira *et al.* 2006, Perkins *et al.* 2010). This is likely to be because the main invertebrate shredder, the large omnivorous caddis *Potamophylax* *cingulatus*, which often drives breakdown rates (Woodward *et al.* 2012), is found in the colder streams but is excluded when trout are present. This point is emphasised by the high species turnover with increasing temperature in the macroinvertebrate community (Figure 13).

Snails can increase the nutrient uptake length of a system, by reducing algal biomass and thus total nutrient demand (Mulholland *et al.* 1983, Steinman *et al.* 1991, Mulholland *et al.* 1994). The increase in nutrient uptake rates with temperature (Figure 20; Demars *et al.* 2011a, Demars *et al.* 2011b) suggest faster turnover among primary producers as the nutrients they absorb are consumed and excreted at a quicker rate by consumers (supporting hypothesis 12 in Table 1). This is supported by the higher levels of grazing pressure exerted by *R. peregra* with increasing temperature (Figure 11). This faster turnover may maintain a high biomass of snails in spite of a smaller standing stock of epilithic diatoms (Figure 15; similar to Yvon-Durocher *et al.* 2011) and indeed other primary producers such as cyanobacteria and macrophytes (Gudmundsdottir *et al.* 2011a, 2011b). Further work on nutrient cycling and turnover is needed to test these hypotheses more fully.

G. Ecosystem process rates: ecosystem metabolism measurements

Biofilm respiration rates for the Hengill system increased significantly with temperature in laboratory incubations, irrespective of the temperature of the natal stream (Figure 21 *a*), supporting hypothesis 13 (see Table 1). This corresponds to contemporaneous *in situ* measurements of whole stream respiration (Demars *et al.* 2011b). Notably, the laboratory experiment revealed remarkable consistency in the temperature dependence of respiration among biofilm assemblages from the different streams. Here, the biofilm consisted of autotrophic organisms including green algae, cyanobacteria and diatoms, as well as heterotrophic ciliates and meiofauna (Perkins *et al.* 2012), highlighting the ubiquitous nature of the response across multiple taxonomic groups of both unicellular and multicellular organisms with different natal thermal regimes. The differences in absolute respiration rates were uncorrelated with mean stream temperature but were positively correlated with biofilm biomass (Figure 21*b*). Together these results provide compelling evidence against physiological thermal adaptation, but instead highlight that ecosystem-level processes are strongly related to the biomass and metabolic capacity of the microbial assemblage, largely irrespective of its taxonomic composition (Perkins *et al.* 2010, Yvon-Durocher *et al.* 2012).

Only limited exploration of whole ecosystem respiration was possible for April 2009, as many streams were under partial ice cover and subjected to extensive reworking of the substrate during high flows. The effect of this disturbance is clear from two lines of evidence. First, ecosystem GPP is positively related to temperature during summer (Figure 23), in support of hypothesis 14 (see Table 1), but not during spring, as snow cover and freezing conditions lead to low in-stream production. Second, the fluctuating measurements of GPP and ecosystem respiration taken repeatedly at the IS1 stream in April contrast to the more stable ecosystem metabolism measurements from the same stream in August (Figure 24 *c-d*), even though day length was identical (Figure 22).

There is some support for the terrestrial subsidy to the Hengill system leading to reduced carbon sequestration during the summer. Snow cover and freezing conditions limit the input of terrestrial subsidies to the system in April, as supported by the gut content analysis of the trout (Figure 8). Thus, ecosystem respiration should be more dependent on in-stream production during this time of year. The whole-stream metabolism measurements for the IS1 stream in April indicate that this may indeed be the case, with a fine balance between GPP and ecosystem respiration leading to net ecosystem metabolism of close to zero (0.7 ± 0.9 g O_2 m^{-2} day^{-1}; Figure 24). By contrast, the terrestrial subsidy to the system in August may support a higher heterotrophic biomass, partly decoupling respiration from photosynthesis (Yvon-Durocher *et al.* 2012). This is supported by a much higher rate of ecosystem respiration for this stream in August, while GPP is approximately the same level, leading to a negative rate of net ecosystem metabolism (-7.9 ± 0.7 g O_2 m^{-2} day^{-1}; Figure 24). Thus, terrestrial subsidies may have the capacity to override the temperature dependence of the in-stream biota, turning the system into a greater net source of carbon to the atmosphere. This phenomenon of ecosystem respiration increasing faster than photosynthesis with temperature, and leading to greater emission of CO_2, was also demonstrated across a snapshot of several streams at Hengill in August 2008 (Demars *et al.* 2011b) and in a long-term mesocosm experiment (Yvon-Durocher *et al.* 2010a). It should be noted that carbon-concentrating mechanisms may be more important in these systems than the C3 photosynthesis used by Allen *et al.* (2005) to derive the activation energy of photosynthesis (Demars and Trémolières 2009, Raven *et al.* 2011) and the method estimates more total respiration than simply oxygenic respiration (e.g. Canfield *et al.* 2005, p. 199).

H. Caveats and limitations

As the streams at Hengill have been exposed to geothermal heating for up to 50,000 years (Arnason *et al.* 1969), their individual, local communities may have reached equilibrium conditions. The current rapid rates of global warming, however, may be pushing systems beyond their equilibrium conditions into more transient states. Thus, it is important to acknowledge that the impacts of environmental warming described here may represent long-term responses to a range of different "ambient" conditions, rather than more acute warming *per se*.

Logistical constraints and the limitations of funding cycles have traditionally restricted ecological research to small spatial and temporal scales (Callahan 1984). Data on individuals or populations, for instance, are more readily collected than comprehensive explorations of multiple ecosystems. Different pieces of the ecological jigsaw may be assembled over a more extensive sampling campaign, but this requires a commitment from numerous researchers and funding bodies over many years. The advent of long-term ecological research programmes, such as that funded by the National Science Foundation in the USA (Hobbie *et al.* 2003), has helped to alleviate this issue and the value of such projects is increasingly being recognised (Strayer *et al.* 1986, Elliott 1990, Risser 1991, Foster *et al.* 2003, Hobbie *et al.* 2003). Even so, the number of explorations of high quality data encompassing multiple levels of biological organisation (e.g. Hall and Raffaelli 1991, Jonsson *et al.* 2005, Woodward *et al.* 2005b, O'Gorman and Emmerson 2010) or long-term datasets spanning more than five years' duration (reviewed by Hobbie *et al.* 2003, Jackson and Füreder 2006) are still extremely scarce. For a more thorough understanding of the temporal and spatial extent of patterns and processes within ecological networks and how they may be altered by external forces, we need to maximise the resources at our disposal from such long-term projects, and several projects in the Hengill system are now underway to help move us closer to this goal.

I. Looking forward: an international partnership at Hengill

One of the main challenges to producing accurate predictions of ecological responses to global change is disentangling how the short-term responses to warming that we typically measure play out over longer time scales. We need to understand the relative importance of acclimation, adaptation, and species compositional shifts in determining the long-term trajectories of food web and ecosystem properties (Melian *et al.* 2011). Ultimately, it is critical that we characterise how other physical and chemical characteristics (i.e., nutrients, hydrology, disturbance) modulate responses to warming, which is unlikely to occur in isolation. This ambitious research agenda necessitates a diversity of approaches that include further observational synoptic surveys, long-term monitoring, and controlled experimental work at multiple spatiotemporal scales. This task will also require collaborative teams that collectively represent a diversity of backgrounds and perspectives (Resh and Yamamoto 1994, Cullen *et al.* 1999).

The research team at Hengill now comprises a multi-national consortium with expertise on topics ranging from genes to ecosystems, and is currently engaged in conducting observations and experiments across a wider hierarchy of spatial and temporal scales to address many of the remaining gaps highlighted in Figure 2. The Hengill system provides a rare opportunity to study streams that have been exposed to different temperature regimes for potentially thousands of years, in addition to offering opportunities for small-scale and ecosystem-level experiments, reciprocal transplants/common garden experiments, and consumer exclusions, as summarised here.

A crucial validation of many of the responses to warming shown here would be an experimental manipulation of temperature in a natural setting over a much shorter time-scale, i.e. assessing transient responses to temperature change. Whole stream temperature manipulations are extremely rare – we know of only one example to date (Hogg and Williams 1996) – but ongoing research in Hengill is exploring the impact of more rapid temperature change on the community structure and functioning of the ecosystem. The research team is currently in the second year of a three-year whole-stream warming experiment, which will be complemented by a suite of stream-side channel manipulations to provide more control and replication. The whole-system warming experiment takes advantage of the close proximity (~2 meters) of the two focal streams whose food webs are presented here, and uses a heat exchanger placed in the warm IS8 stream to warm the cold IS7 stream by 3-5 °C without altering stream chemistry (Figure 2). The experimental channel experiments will use a similar heat-exchange approach to produce a gradient of temperatures. Both of these systems are gravity-fed, use naturally heated water and require relatively little maintenance once constructed. These experiments will help answer questions related to whether short- to mid-term experiments can predict the patterns seen across the long-term temperature gradient at Hengill. Such comparisons will allow us to make stronger inferences about whether field experiments in general can accurately predict the long-term responses of ecosystems to future climate warming.

Many of the challenges that lie ahead are highlighted by identifying and addressing the gaps that still exist in our structural-functional scheme, as outlined in Figures 1 and 2. One obvious example is that although the Hengill system provides an invaluable field laboratory in the form of a natural experiment, it is still essentially unreplicated at the catchment or regional scale. Expanding the approaches developed here and applying them to other, as yet unidentified, geothermal systems elsewhere in the world would improve the generality and applicability of the study enormously. Such a research programme represents an ambitious objective, but it would provide a uniquely powerful means of assessing the effects of warming in natural ecosystems and could even be used to set up a suite of "sentinel systems" to monitor long-term change.

In addition to the whole-system experiment currently underway, there is also a need to conduct field experiments to explicitly address the mechanisms we have inferred as being behind some of the patterns observed in existing data, and to tighten the connections across scales and levels of organisation. A case in point is the need to conduct fish enclosure/exclosure experiments across the thermal gradient, to quantify their role in the food web under more controlled conditions and to test whether (or not) trophic cascades are as prevalent as we suspect.

There are emerging technologies that could be employed to grapple with some of the other unresolved questions, such as the use of next-generation sequencing (NGS) for characterising the microbial loop using molecular techniques: i.e. are these assemblages relatively insensitive to temperature change, as the current data suggest (Figure 13), or are we simply underestimating their diversity? This could also provide a means with which to link biodiversity more explicitly to ecosystem functioning. For instance, much of the ecosystem respiration we measure will be driven by bacterial activity, yet at present we have no idea how these microbial assemblages respond to warming in terms of community composition. Finally, we need to move from observation and experimentation to more predictive modelling approaches (and validation of those models) to gauge likely future scenarios for multispecies systems as temperatures rise. A key question we still need to address is are the warmer systems less dynamically stable, or are all the stream food webs similarly stable, due to compensatory mechanisms?

J. Conclusion

Many of the findings presented here have revealed powerful effects of warming at different temporal and spatial scales of measurement and across many levels of biological organisation (Figure 2). The interrelationships between so many altered patterns and processes with environmental warming helps to highlight the integrated nature of these studies. Thus, by piecing together the components of long-term ecological research projects, such as those presented here from the Hengill system in Iceland, a more complete understanding of the mechanisms driving the response of complex natural ecosystems to environmental perturbations can be achieved.

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Table 1. Examples of specific predictions based on hypotheses mapped onto different levels of biological organisation and spatiotemporal scales. Citations to the relevant body of theory are: [1] James (1970), [2] Petchey *et al*. (2008), [3] Hairston *et al*. (1969), [4] Parmesan and Yohe (2003), [5] Brown *et al*. (2004), [6] Woodward *et al*. (2010), [7] Cohen *et al*. (2003), [8] Reuman *et al*. (2009), [9] Sterner and Elser (2002).

Hypothesis #	Box in Figure 1	Measurement	Level of organisation	Spatial / temporal scale	Sampling date used here	Predicted response to increased temperature	Body of theory	Ref
1	(1-2)	Body mass	Individual to population	Micro- to macro-habitat / days	April 2009	↓ body mass	Temperature-size rules	[1]
2	(3)	Diet breadth	Population (traits)	Macro-habitat / days	August 2008; April 2009	↓ diet breadth	Foraging theory	[2]
3	(3)	Growth rate	Population (traits)	Meso-habitat / weeks	May-July 2011 (see Box 1)	↑ growth rate	Temperature-size rules	[1]
4	(4)	Population biomass	Interactions (food chain)	Micro- to macro-habitat / days to weeks	August 2008; April 2009	↑ top-down control	Food chain theory	[3]
5	(4)	Grazing pressure	Interactions (food chain)	Meso-habitat / weeks	August 2004	↑ top-down control	Food chain theory	[3]
6	(5)	Community similarity	Community	Micro- to macro-habitat / days	April 2009; August 2011	↓ similarity	Species range shifts	[4]
7	(5)	Interaction strength	Community	Whole system / season	August 2008; April 2009	↑ interaction strength	Metabolic theory	[5]
8	(5)	Food web structure	Community to ecosystem	Whole system / season to years	August 2008; April 2009	↓ diversity, complexity, connectance, mean food chain length	Food web theory	[6]
9	(6)	Mass-abundance scaling coefficient	Community to ecosystem (trivariate food web)	Whole system / season to years	August 2008; April 2009	↑ slope, ↑ intercept	Trivariate food webs	[7]
10	(6)	Mass-abundance scaling coefficient	Community to ecosystem (size spectrum)	Whole system / season to years	August 2008; April 2009	↑ slope, ↑ intercept	Size spectra	[8]
11	(7)	Decomposition	Ecosystem	Meso-habitat / weeks	August 2004	↑ decomposition rate	Metabolic theory	[5]
12	(7)	Nutrient cycling rates	Ecosystem	Patch / days	August 2008	↑ nutrient cycling rates	Ecological stoichiometry	[9]
13	(7)	Respiratory flux	Ecosystem	Whole system / days	August 2008; April 2009	↑ respiration	Metabolic theory	[5]
14	(7)	Gross primary production	Ecosystem	Whole system / days	August 2008; April 2009	↑ productivity	Metabolic theory	[5]

Table 2. Mean stream temperature of the *Hengladalsá* (IS16) and its 15 tributaries (IS1-IS15) during selected sampling periods. Note that stream numbers are the same as the coding used in previous publications related to the area (Friberg *et al.* 2009, Woodward *et al.* 2010, Gudmundsdottir *et al.* 2011a, Gudmundsdottir *et al.* 2011b).

	Temperature (°C)			
Stream	**August 2004**	**August 2008**	**April 2009**	**August 2011**
IS1	19.9	22.7	11.7	21.1
IS2	20.3	20.9	15.3	25.0
IS3	22.1	23.7	15.7	18.2
IS4	13.3	12.7	3.7	18.1
IS5	19.8	21.3	16.5	15.0
IS6	19.1	21.0	14.1	20.6
IS7	8.6	8.2	4.8	7.6
IS8	23.4	24.6	21.6	23.3
IS9	15.2	18.1	9.8	17.8
IS10	5.2	5.1	3.4	4.3
IS11	11.6	12.8	3.6	10.8
IS12	14.3	15.5	6.3	11.7
IS13	6.9	6.1	4.8	11.0
IS14	10.6	9.7	1.8	12.8
IS15	43.0	48.3	49.1	58.0
IS16	NA	14.5	7.2	15.2

Table 3. Properties of the food webs associated with the warm IS8 and cold IS7 streams in April 2009 and August 2008.

	Warm stream		**Cold stream**	
	April	**August**	**April**	**August**
Number of species	35	35	42	50
Number of links	194	194	350	521
Linkage density	5.54	5.54	8.33	10.42
Connectance	0.16	0.16	0.20	0.21
Mean food chain length	1.31	1.38	1.38	1.34
Proportion of basal species	0.74	0.71	0.67	0.68
Proportion of intermediate species	0.20	0.23	0.24	0.20
Proportion of top species	0.06	0.06	0.10	0.12

Figure 1. Conceptual figure highlighting the impact of extrinsic drivers such as temperature on the physiology and behaviour of individual organisms, species, traits and interactions, leading to alterations in community and ecosystem structure. This produces cascading secondary effects on the functioning of the ecosystem and the delivery of ecosystem services, which are themselves often directly altered by the extrinsic drivers, leading to a negative feedback loop.

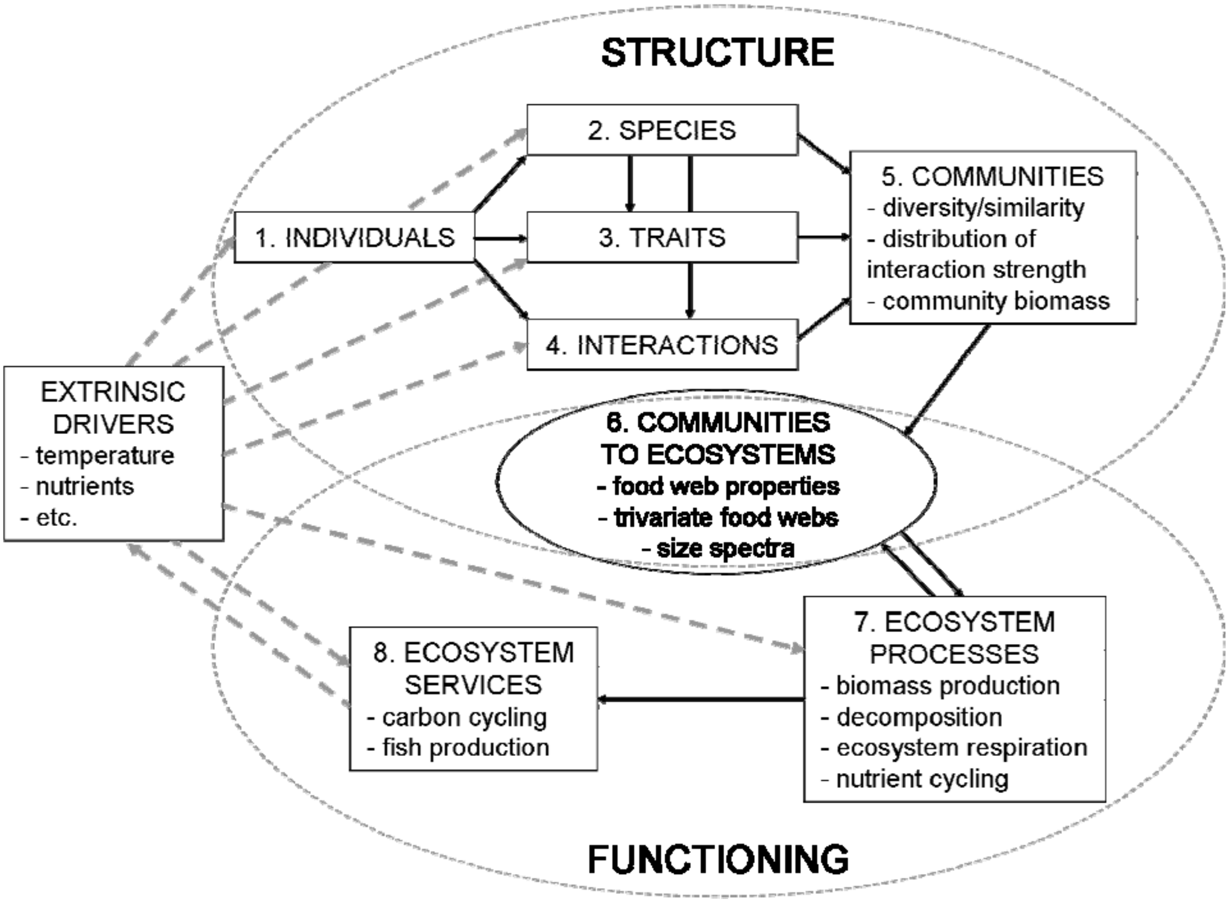


Figure 2. Conceptual figure highlighting the extensive temporal and spatial scales over which sampling of both the structure and functioning of the Hengill system has been carried out since 2002.

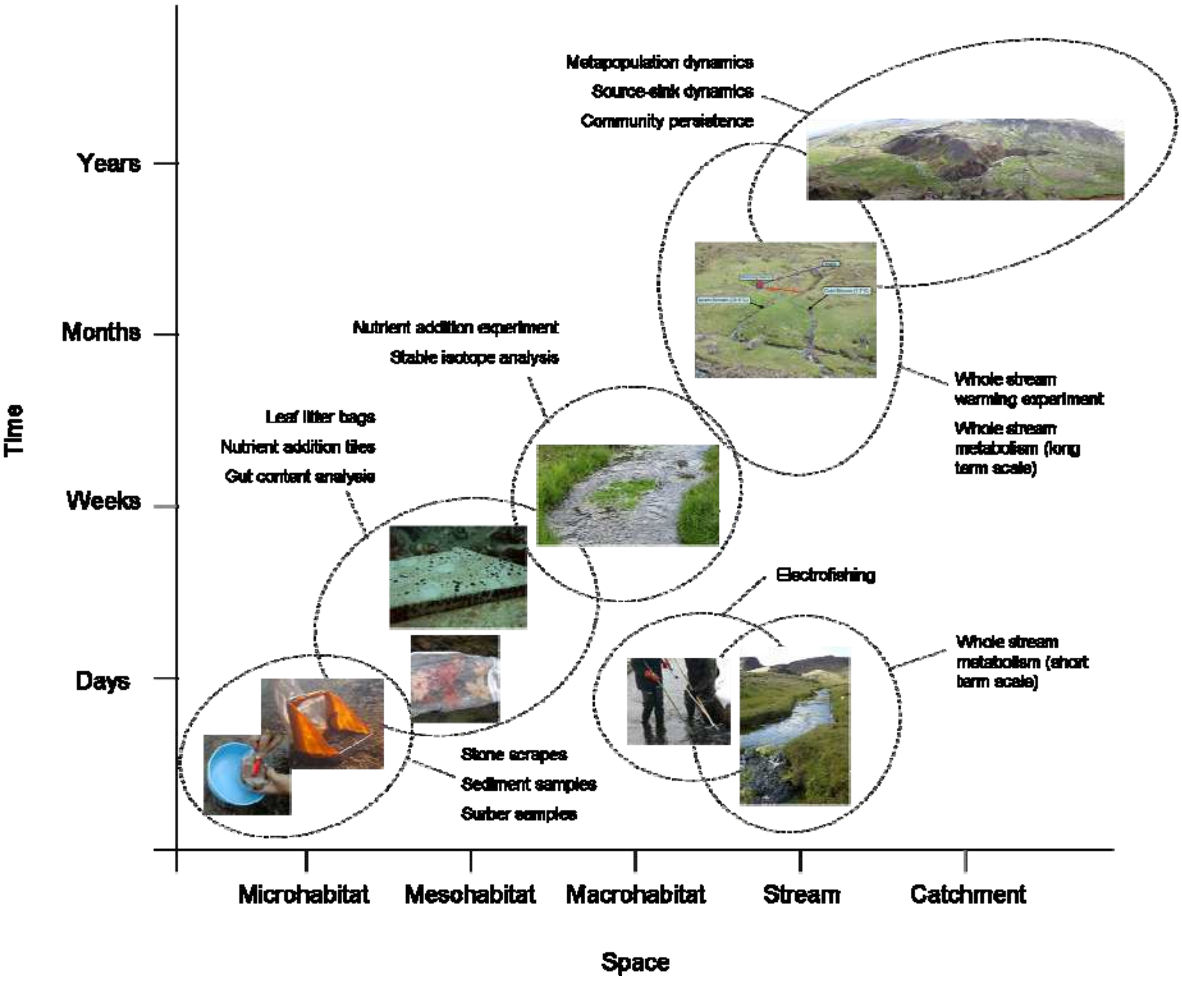


Figure 3. Conceptual figure highlighting (*a*) the typical negative log-log mass-abundance scaling found in nature as a point of reference. The dashed line indicates the *y*-intercept, standardised by the smallest organism. This scaling can apply to individual organism or average species data, although the slope and intercept of the reference panel will vary between the two. Reduced trophic transfer efficiency occurs if: (*b*) the slope becomes steeper while the intercept remains the same (biomass of smallest resources remains constant); or (*c*) the slope becomes shallower while the intercept decreases (biomass of smallest resources declines). Increased trophic transfer efficiency occurs if: (*d*) the slope becomes shallower while the intercept remains the same; or (*e*) the slope becomes steeper while the intercept increases (biomass of smallest resources increases).

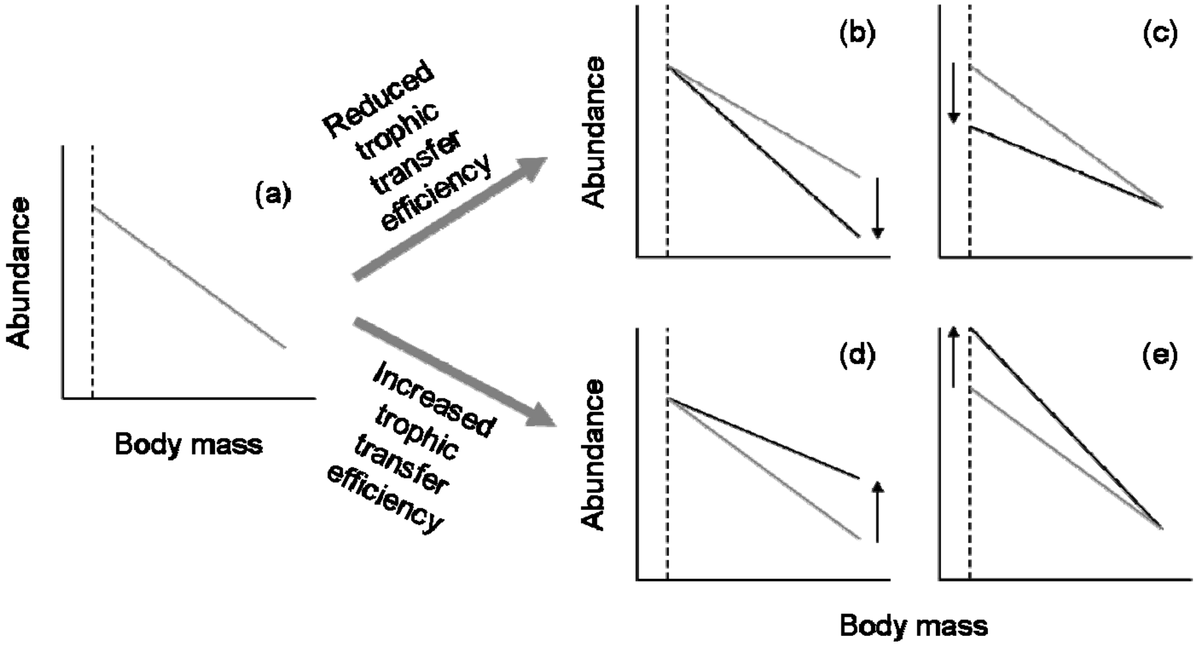


Figure 4. Clockwise from bottom left: (*a*) position of Iceland on the edge of the Arctic circle, with the location of the Hengill field site highlighted by a red dot; (*b*) aerial photograph of the Hengill valley, showing the main *Hengladalsá* river and its tributaries; (*c*) schematic of the geothermal stream system, demonstrating the typical summer time temperature gradient. Two streams at opposite ends of the temperature gradient, yet which are separated by just a few metres are circled with a red dashed line: these are focal systems we return to later for paired comparisons throughout the paper.

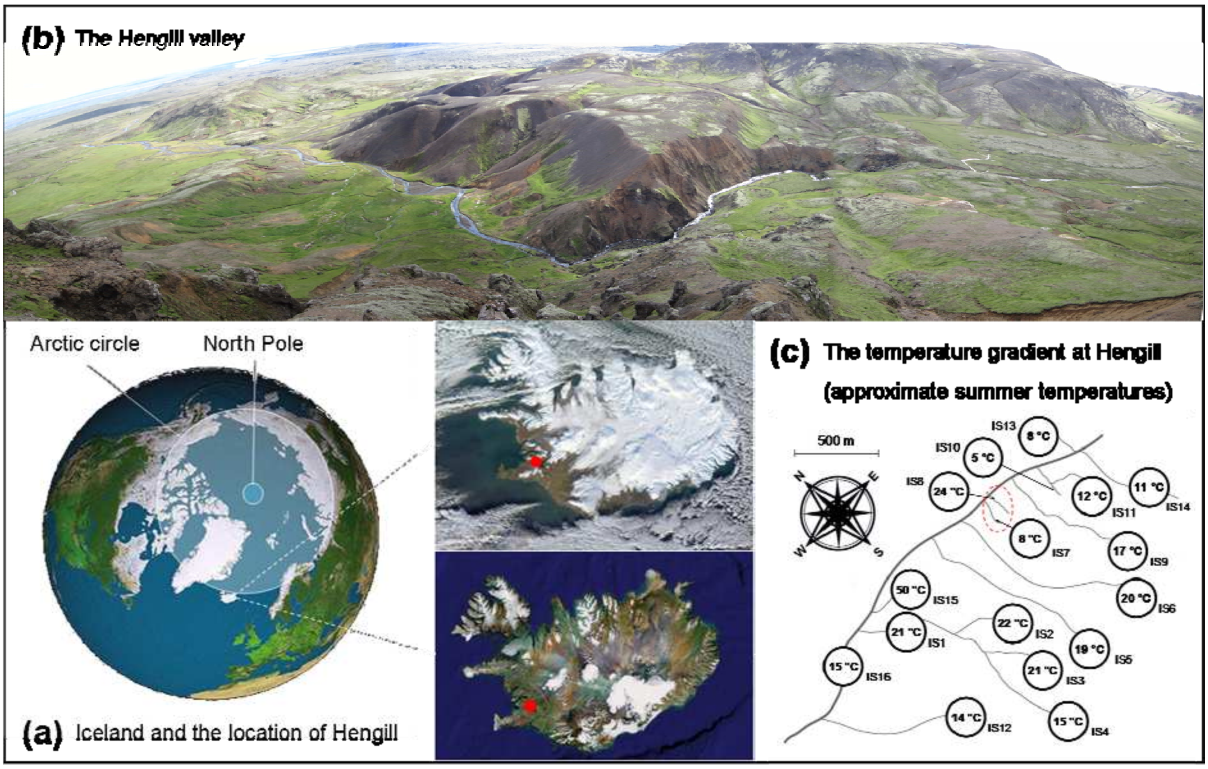


Figure 5. The negative effect of temperature within the Hengill system on the individual organism body mass of the diatoms *A. lanceolata* ($y = 8.5\times10^{-5} - 1.9\times10^{-6}x$, $r^2 = 0.05$, $F_{1,181} = 9.70$, $p = 0.002$), *A. minutissima* ($y = 3.6\times10^{-5} - 1.2\times10^{-5}x$, $r^2 = 0.31$, $F_{1,23} = 10.16$, $p = 0.004$) and *A. pediculus* ($y = 1.3\times10^{-5} - 2.3\times10^{-7}x$, $r^2 = 0.12$, $F_{1,67} = 8.82$, $p = 0.004$), the chironomids *Cricotopus sp. A* ($y = 0.16 - 0.008x$, $r^2 = 0.31$, $F_{1,59} = 26.68$, $p < 0.001$), *D. zernyi* ($y = 0.29 - 0.009x$, $r^2 = 0.05$, $F_{1,106} = 5.83$, $p = 0.018$) and *E. minor* ($y = 0.07 - 0.001x$, $r^2 = 0.01$, $F_{1,307} = 4.40$, $p = 0.037$), oligochaete worms ($y = 0.16 - 0.009x$, $r^2 = 0.03$, $F_{1,359} = 11.83$, $p < 0.001$) and the snail *R. peregra* ($y = 1.17 - 0.045x$, $r^2 = 0.02$, $F_{1,301} = 7.10$, $p = 0.008$). Data used in this analysis are from all streams in April 2009.

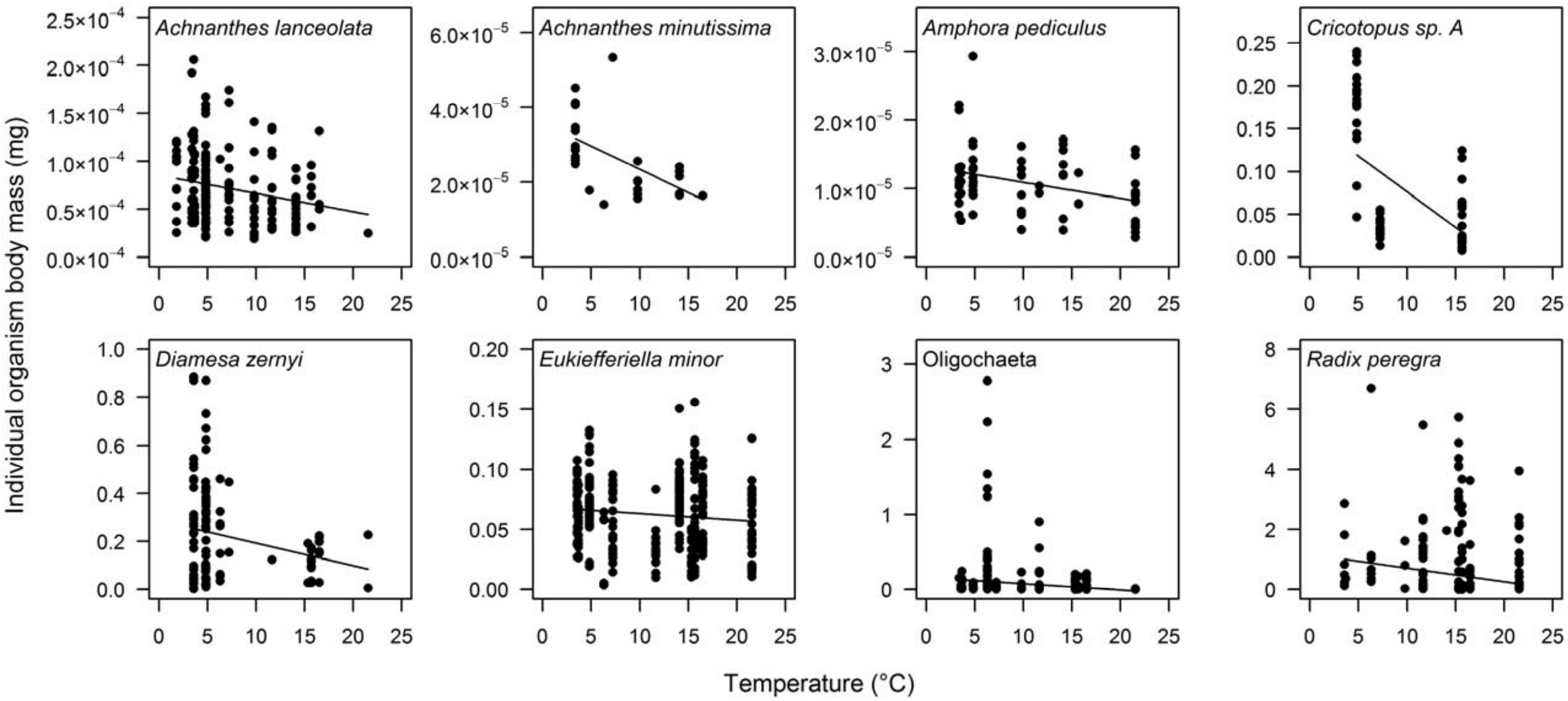


Figure 6. The positive effect of temperature within the Hengill system on the individual organism body mass of the diatoms *C. placentula* ($y = 1.9\times10^{-4} + 1.6\times10^{-5}x$, $r^2 = 0.09$, $F_{1,62} = 5.99$, $p = 0.017$), *D. mesodon* ($y = 3.6\times10^{-4} + 2.3\times10^{-5}x$, $r^2 = 0.09$, $F_{1,84} = 8.37$, $p = 0.005$), *N. minima* ($y = 6.3\times10^{-6} + 9.9\times10^{-8}x$, $r^2 = 0.08$, $F_{1,53} = 4.57$, $p = 0.037$) and *N. aquaeore* ($y = 2.4\times10^{-6} + 1.3\times10^{-6}x$, $r^2 = 0.67$, $F_{1,5} = 10.01$, $p = 0.025$), the chironomid *Orthocladius sp.* ($y = 0.03 + 0.006x$, $r^2 = 0.15$, $F_{1,56} = 10.04$, $p = 0.002$), the black fly larvae *S. vittatum* ($y = 0.32 + 0.021x$, $r^2 = 0.16$, $F_{1,86} = 16.51$, $p < 0.001$) and the trout *S. trutta* ($y = -10148 + 2391x$, $r^2 = 0.56$, $F_{1,12} = 15.53$, $p = 0.002$). Data used in this analysis are from all streams in April 2009.

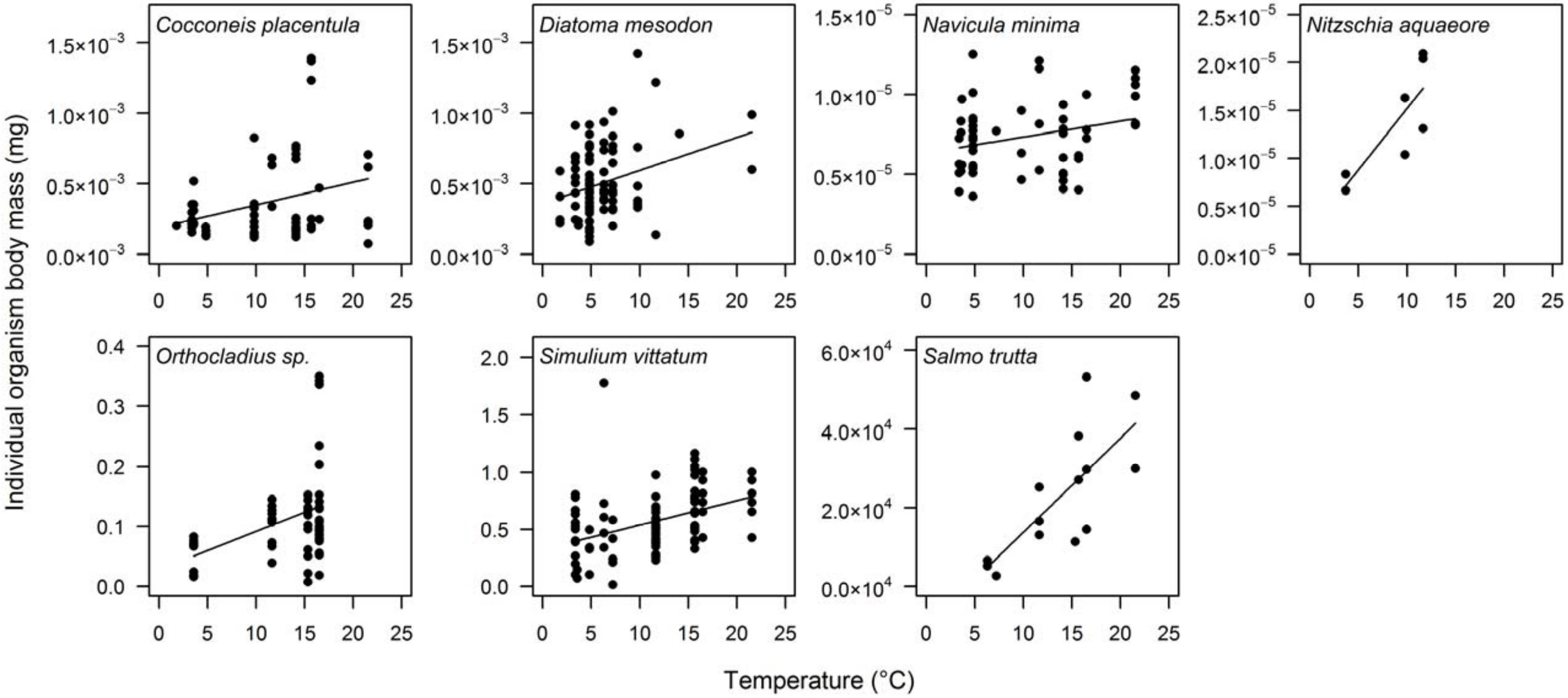


Figure 7. Bray-Curtis similarity in the species composition of trout diet and stream biota with temperature for April 2009 *placentula* ($y = 4.98 + 3.81x$, $r^2 = 0.38$, $F_{1,11} = 6.78$, $p = 0.025$) and August 2008 *placentula* ($y = 0.22 + 1.71x$, $r^2 = 0.09$, $F_{1,44} = 4.18$, $p = 0.047$). The grey points in the August 2008 plot highlight some of the smallest trout in the streams, which appear to exhibit a different trend to the larger fish. The streams used in this analysis are the same as those labelled in Figure 8, which are the only ones in which trout were found.

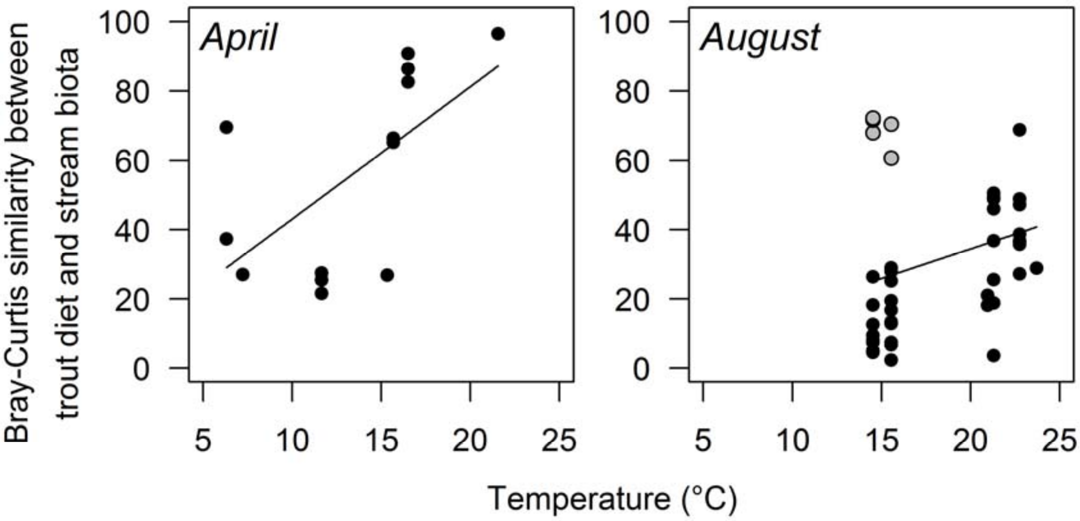
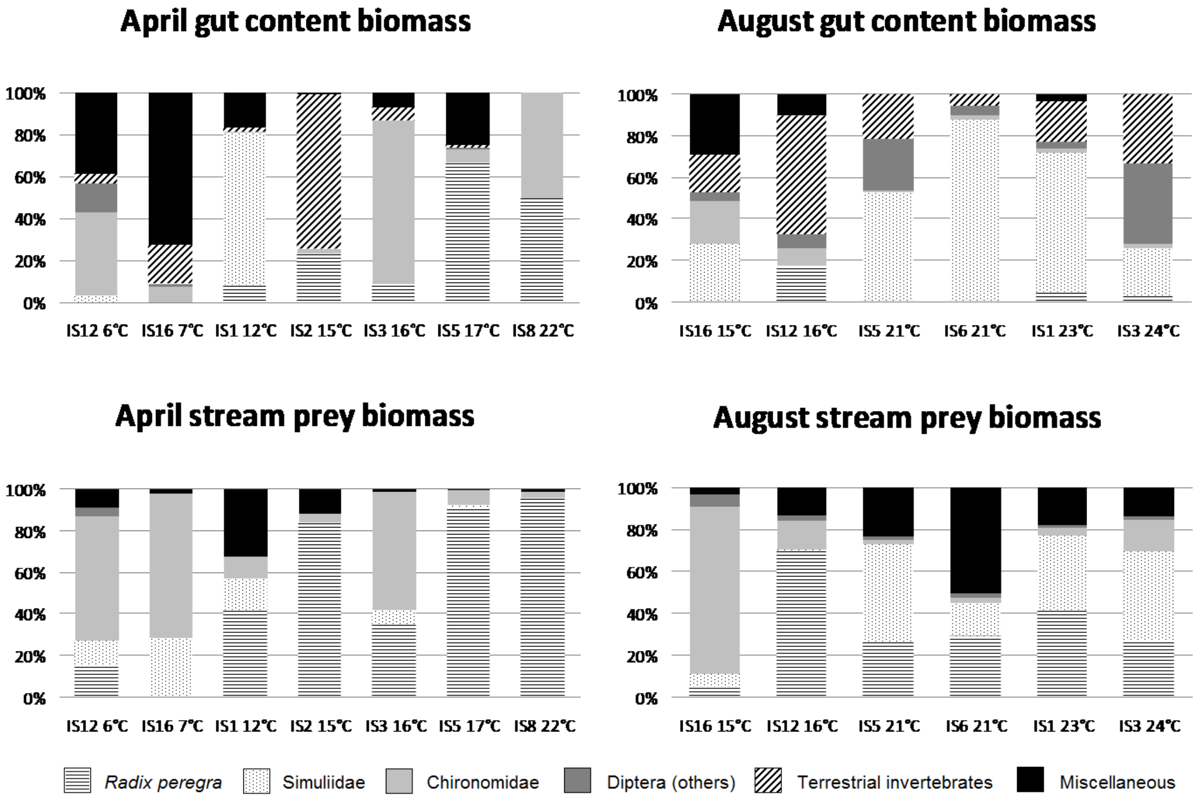


Figure 8. Proportional representation by biomass of six invertebrate groups within the diet of trout during April 2009 and August 2008 (top panels) for all streams that contained fish on those sampling occasions. The proportional representation by biomass of the same six groups within the corresponding streams is also shown for the same time periods (bottom panels). These groups include the snail *R. peregra*, black fly larvae, chironomids, other dipterans, terrestrial invertebrates and all remaining prey taxa found within the guts. The biomass of terrestrial invertebrates in the streams was not quantified due to the benthic surber sampling methods employed.



April gut content biomass

August gut content biomass

April stream prey biomass

August stream prey biomass

Figure 9. Changes in population biomass of the trout *S. trutta* ($y = 1.87 - 0.08x$, $r^2 = 0.60$, $F_{1,4} = 7.69$, $p = 0.040$), the snail *R. peregra* ($y = 0.73 + 0.12x$, $r^2 = 0.90$, $F_{1,6} = 53.82$, $p < 0.001$) and six diatom species, *A. lanceolata* ($y = 4.93 - 0.07x$, $r^2 = 0.46$, $F_{1,12} = 10.14$, $p = 0.008$), *A. minutissima* ($y = 3.62 - 0.11x$, $r^2 = 0.60$, $F_{1,5} = 7.36$, $p = 0.042$), *Gomphonema D* ($y = 4.80 - 0.12x$, $r^2 = 0.46$, $F_{1,9} = 7.61$, $p = 0.022$), *M. circulare* ($y = 5.12 - 0.15x$, $r^2 = 0.76$, $F_{1,38} = 38.38$, $p < 0.001$), *N. atomus* ($y = 3.70 - 0.14x$, $r^2 = 0.60$, $F_{1,9} = 13.29$, $p = 0.005$) and *N. atomus atomus* ($y = 3.06 - 0.17x$, $r^2 = 0.67$, $F_{1,4} = 7.98$, $p = 0.048$), with temperature in the Hengill system. It is hypothesised that the snails support the increased biomass of trout with temperature through a bottom-up effect, while they suppress the biomass of diatoms with increasing temperature through a top-down effect. Data used in this analysis are from all streams where each species was found in April 2009.

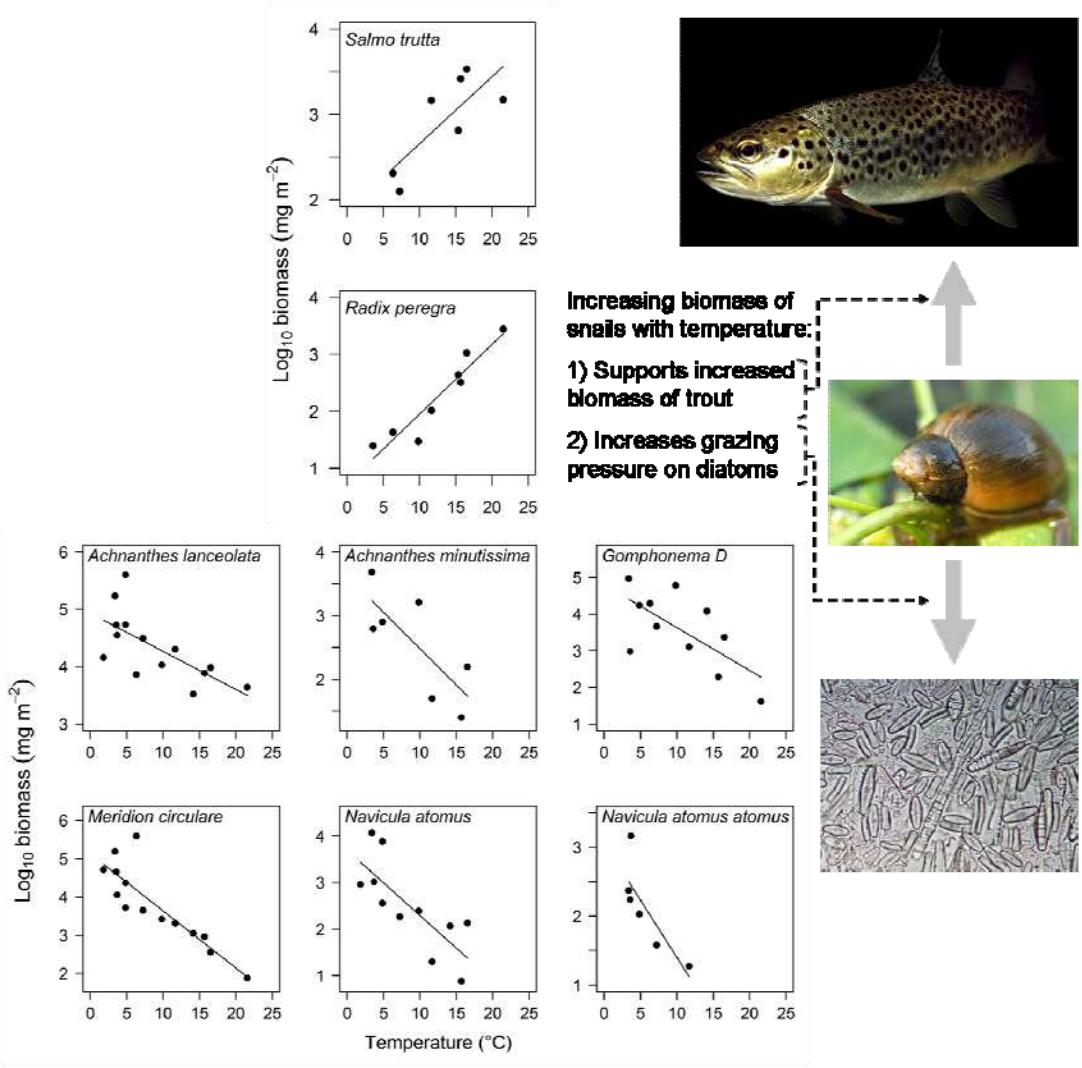


Figure 10. Correlations between the biomass of the snail *R. peregra* and three other species in the Hengill system: the trout *S. trutta* ($y = 3.44 + 2.51x$, $r^2 = 0.80$, $F_{1,6} = 12.29$, $p = 0.039$) and the diatoms *Gomphonema D* ($y = 6.22 - 1.27x$, $r^2 = 0.70$, $F_{1,4} = 9.36$, $p = 0.038$) and *M. circulare* ($y = 6.34 - 1.29x$, $r^2 = 0.67$, $F_{1,5} = 10.35$, $p = 0.024$). Data used in this analysis are from all streams where each species was found in April 2009.

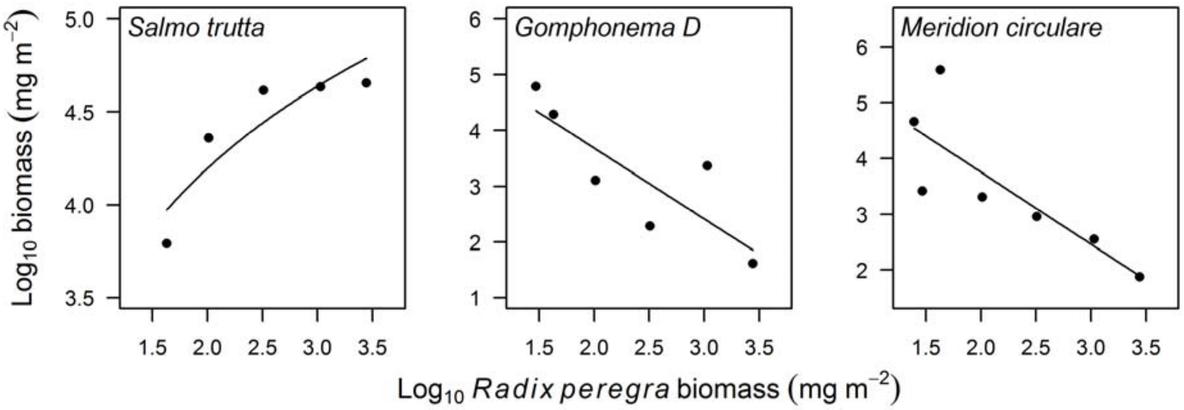


Figure 11. Grazing pressure exerted by the snail *R. peregra* on the biomass of diatoms ($y = -0.12 - 0.021x$, $r^2 = 0.49$, $F_{1,7} = 6.80$, $p = 0.035$), measured as the log ratio of chlorophyll in the presence and absence of snails on tiles used in a snail exclusion experiment at Hengill. Data used in this analysis are from all streams where *R. peregra* was found in April 2009.

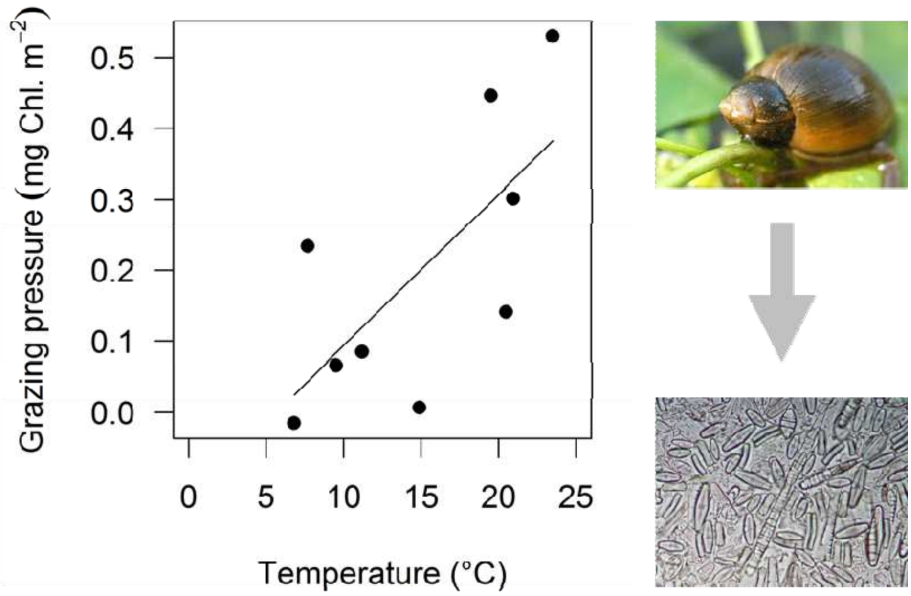


Figure 12. Change in the strength of interactions between the trout *S. trutta* and two key prey (the black fly larvae Simuliidae and the snail *R. peregra*) in April 2009 (Simuliidae: $F_{1,7} = 0.18$, $p = 0.682$; *R. peregra*: $y = 0.73 + 0.12x$, $r^2 = 0.90$, $F_{1,6} = 53.82$, $p < 0.001$) and August 2008 (Simuliidae: $y = -2.50 + 0.23x$, $r^2 = 0.73$, $F_{1,4} = 10.95$, $p = 0.030$; *R. peregra*: $y = -2.78 + 0.21x$, $r^2 = 0.85$, $F_{1,4} = 22.65$, $p = 0.009$) is reflected by changes in their biomass with temperature. This mirrors the shifting importance of these two species in the diet of trout, as suggested by Figure 8. Data are shown for all streams in which these two prey species were found in both years.

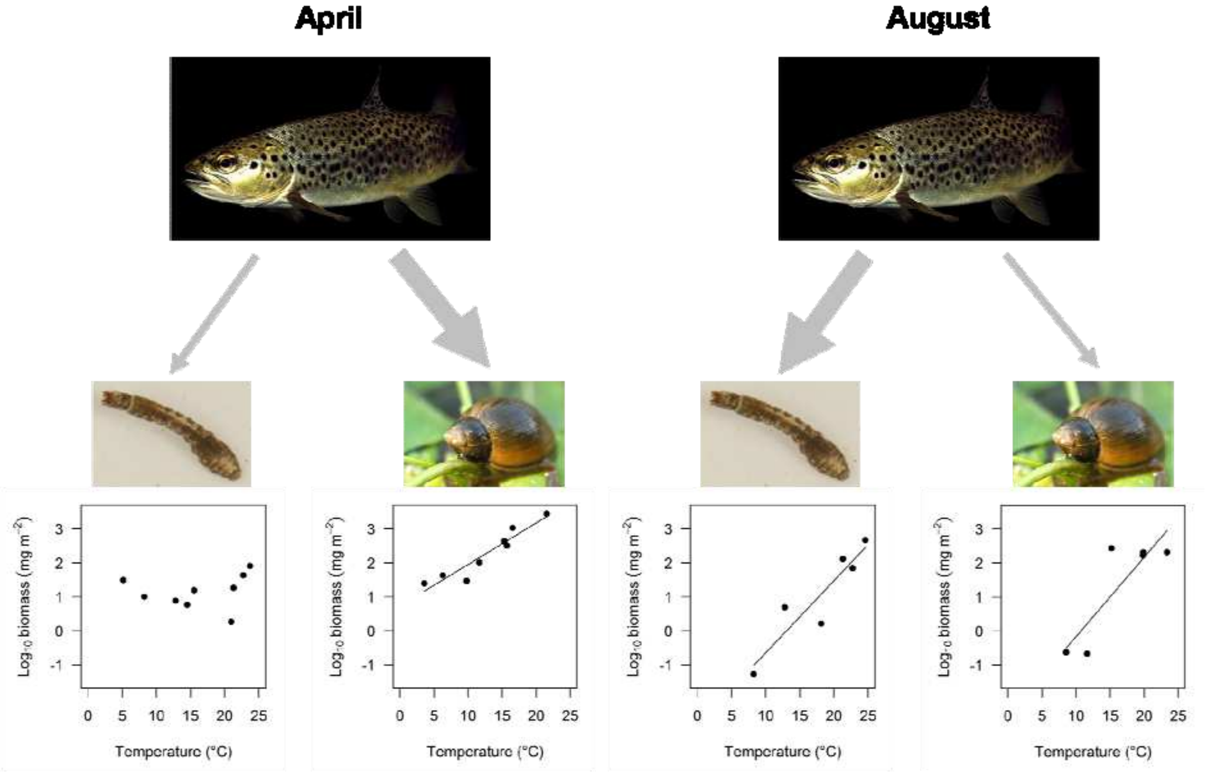


Figure 13. Change in the similarity of the diatom, ciliate, flagellate, meiofaunal and macroinvertebrate communities as the pairwise temperature difference between these streams increases. Only macroinvertebrates showed a significant decline in similarity with increasing pairwise temperature difference. Diatom and macroinvertebrate data used in this analysis are from all streams in April 2009 (except for IS2 in the case of diatoms, which had no stones to perform rock scrapes). Ciliate, flagellate and meiofauna data are from all streams in August 2011.

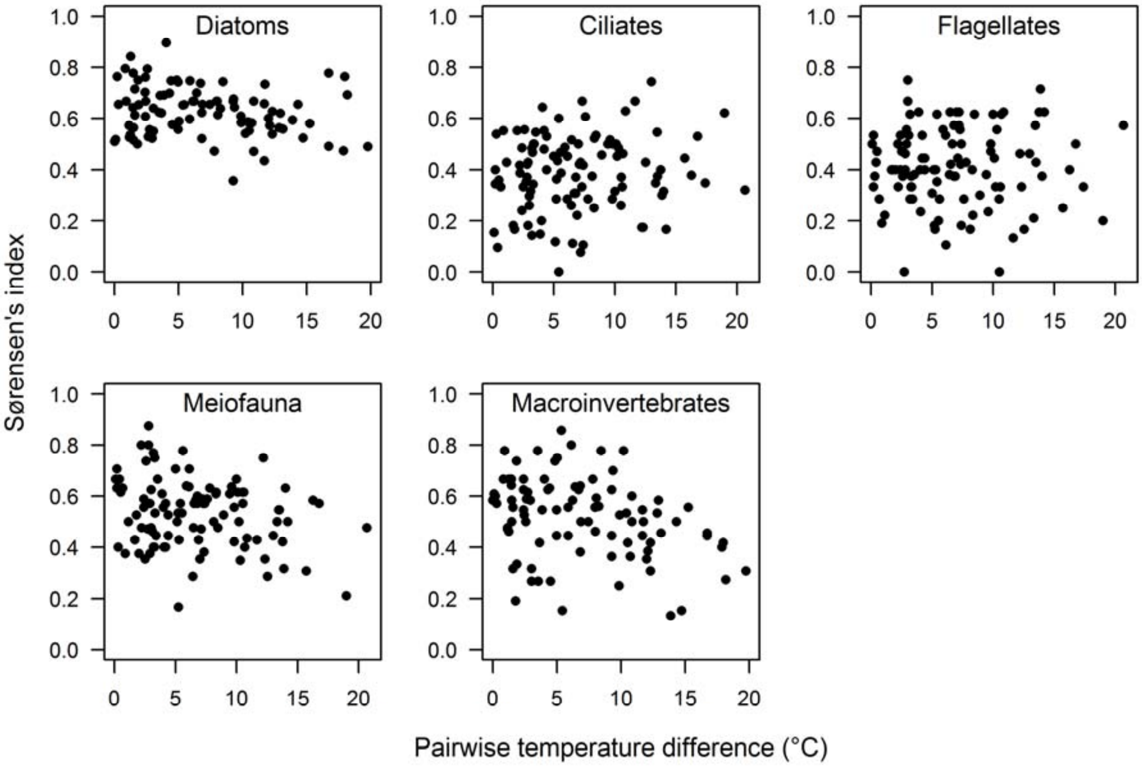


Figure 14. The frequency distribution of the $\log_{10}$ mass specific (*a*, *c*) and the log10 relative interaction strength (*b*, *d*) between the warm IS8 and cold IS7 streams in April 2009 and August 2008. The upper and lower rows show the data from April (*a*-*b*) and August (*c*-*d*), respectively. The blue bars show the distribution of interaction strengths in the cold stream and the dark red bars denote the warm stream. The lines denote unimodal normal distributions for the cold and warm streams.

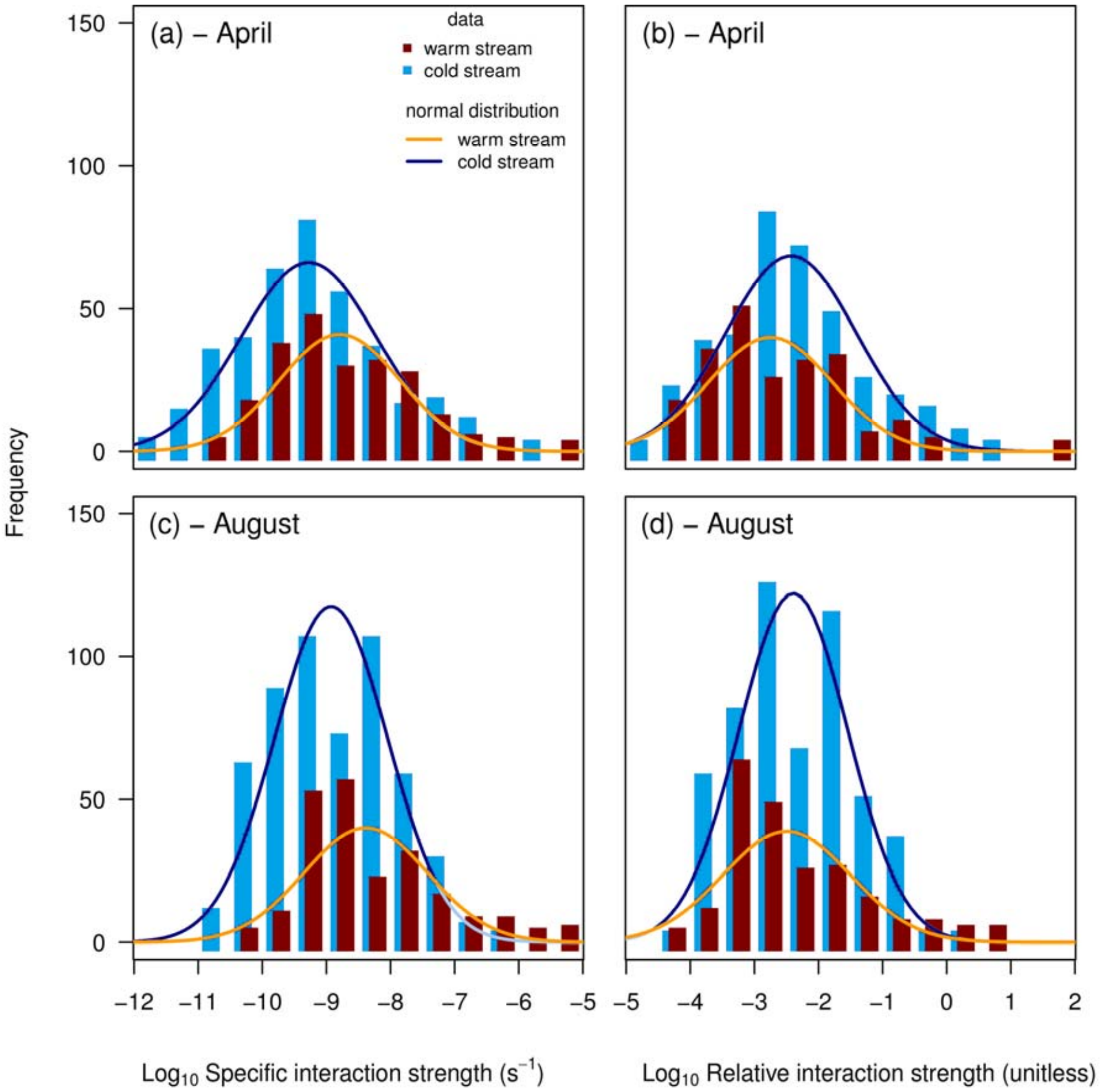


Figure 15. Log$_{10}$ community biomass (mg m^{-2}) of three trophic groups (diatoms, macroinvertebrates and fish) in the warm IS8 (dark red, white writing) and cold IS7 (light blue, black writing) streams in April 2009 and August 2008.

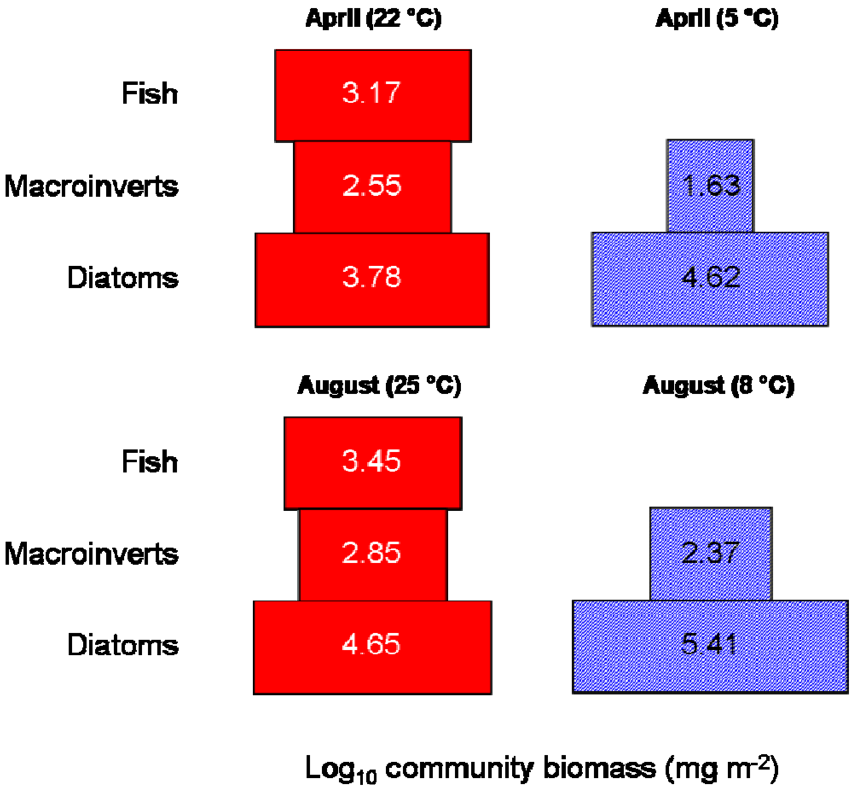


Figure 16. **F**ood web structure of the warm IS8 and cold IS7 streams (shown in the photo) in April 2009 and August 2008. Note the additional top trophic level species in the warm stream and the additional primary consumers and higher complexity of the cold stream food webs. A full list of properties associated with each web can be found in Table 3.

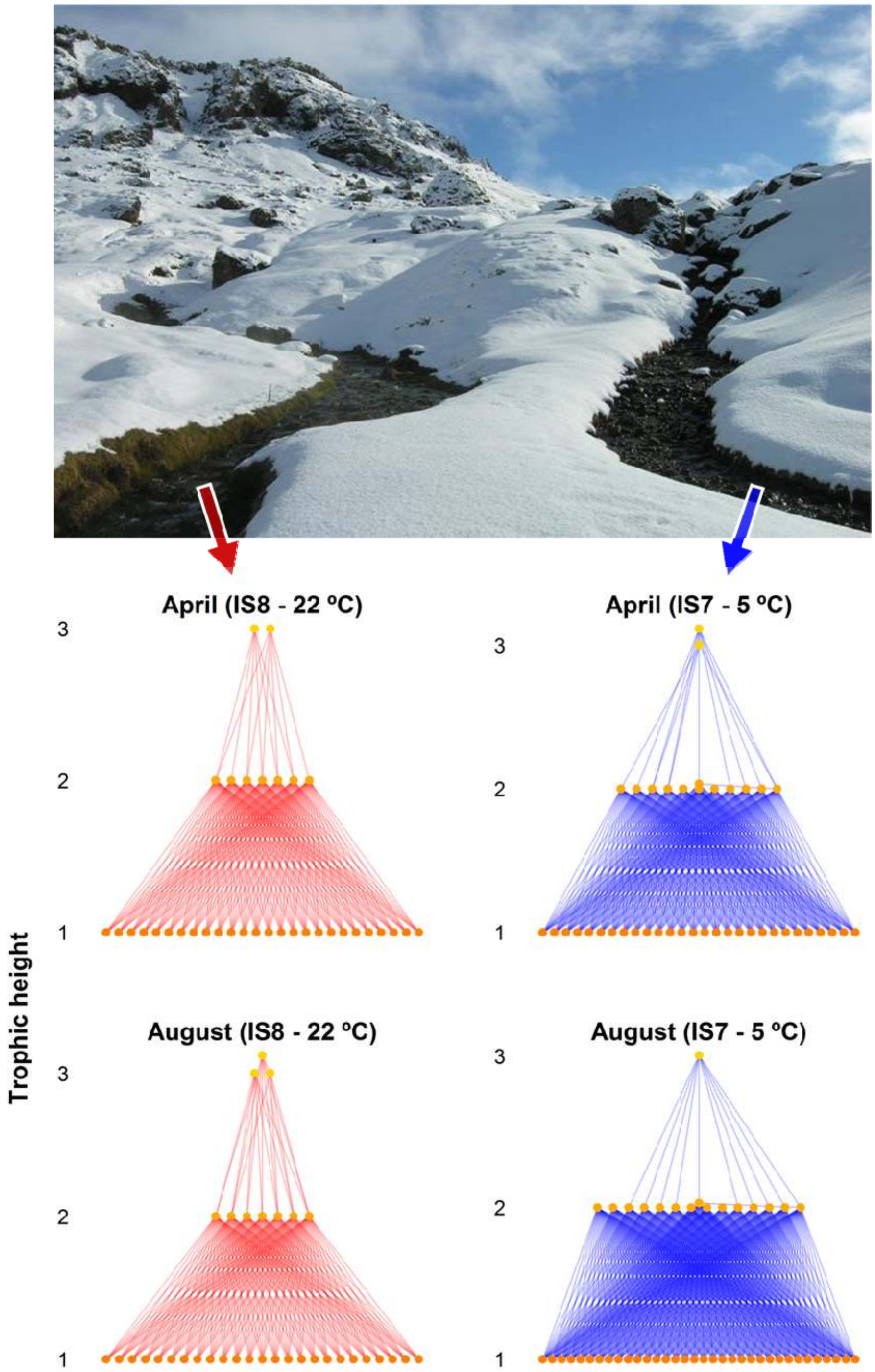


Figure 17. Trivariate food web structure of the warm IS8 and cold IS7 streams in April 2009 and August 2008. The analysis is carried out with trout (red points and regression lines) and without trout included (black regression lines). Note that the regression lines for the warm stream are shallower than the cold stream both with and without trout included. The points on this plot represent the average body mass and abundance of each species in the webs. Regression equations: IS8 (April with trout: $y = 1.89 - 1.18x$, $r^2 = 0.79$, $F_{1,48} = 125.0$, $p < 0.001$; April without trout: $y = 0.95 - 1.43x$, $r^2 = 0.78$, $F_{1,48} = 112.9$, $p < 0.001$; August with trout: $y = 1.76 - 1.05x$, $r^2 = 0.76$, $F_{1,33} = 105.6$, $p < 0.001$; August without trout: $y = 0.91 - 1.28x$, $r^2 = 0.75$, $F_{1,32} = 96.0$, $p < 0.001$); and IS7 (April: $y = 1.22 - 1.53x$, $r^2 = 0.87$, $F_{1,40} = 266.2$, $p < 0.001$; August: $y = -0.44 - 1.82x$, $r^2 = 0.80$, $F_{1,48} = 196.8$, $p < 0.001$).

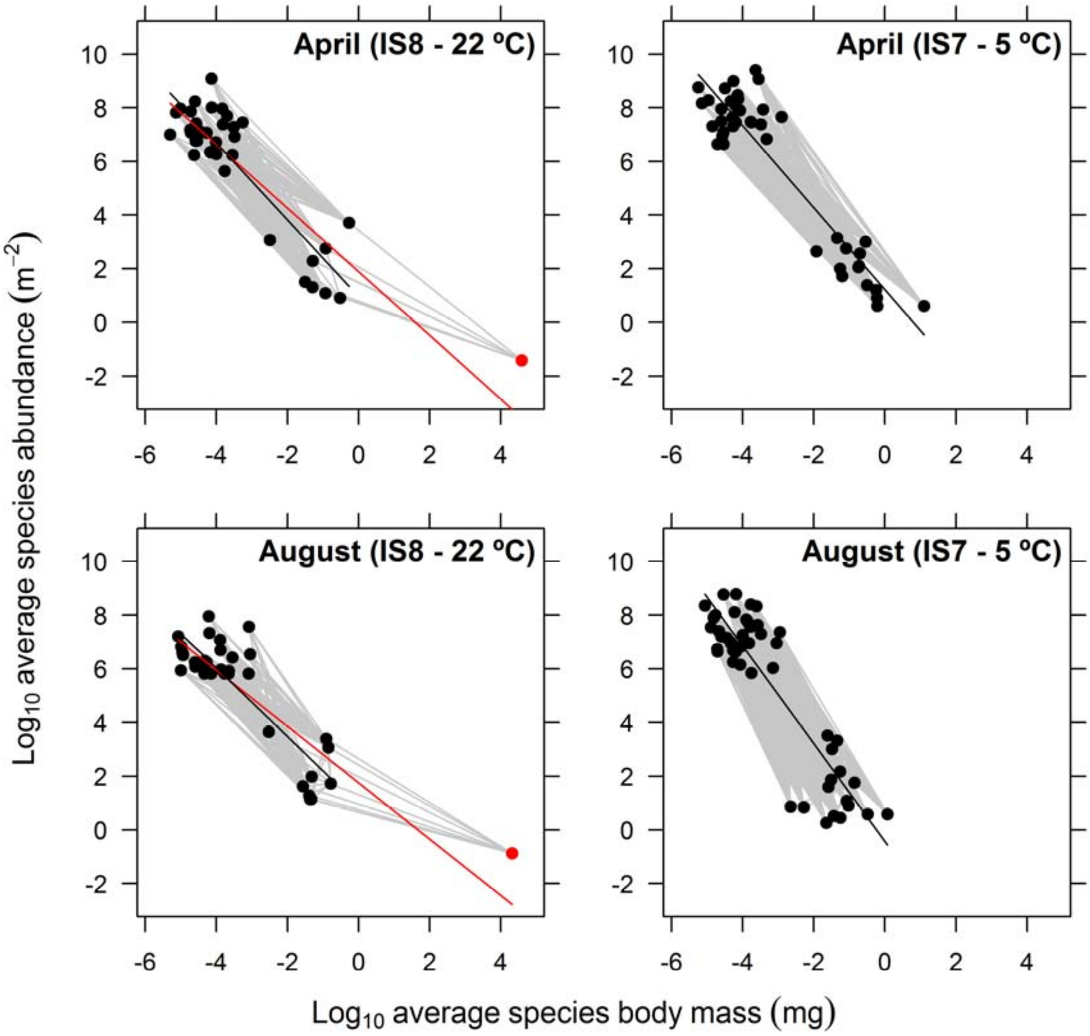


Figure 18. Size spectra of individual organisms in the warm IS8 and cold IS7 streams in April 2009 and August 2008. The analysis is carried out with trout (red points and regression lines) and without trout included (black regression lines). Note that the size spectra slopes for the warm stream are shallower than the cold stream both with and without trout included. The points in this plot represent the midpoint of ten evenly spaced size classes and the number of individuals organisms (irrespective of species identity) within each size bin. Regression equations: IS8 (April with trout: $y = 3.01 - 1.08x$, $r^2 = 0.86$, $F_{1,5} = 30.49$, $p = 0.003$; April without trout: $y = 2.60 - 1.21x$, $r^2 = 0.72$, $F_{1,4} = 10.37$, $p = 0.032$; August with trout: $y = 3.08 - 0.95x$, $r^2 = 0.90$, $F_{1,4} = 35.68$, $p = 0.004$; August without trout: $y = 2.47 - 1.12x$, $r^2 = 0.72$, $F_{1,3} = 7.90$, $p = 0.067$); and IS7 (April: $y = 1.97 - 1.51x$, $r^2 = 0.82$, $F_{1,5} = 23.36$, $p = 0.005$; August: $y = 1.53 - 1.55x$, $r^2 = 0.83$, $F_{1,4} = 18.91$, $p = 0.012$).

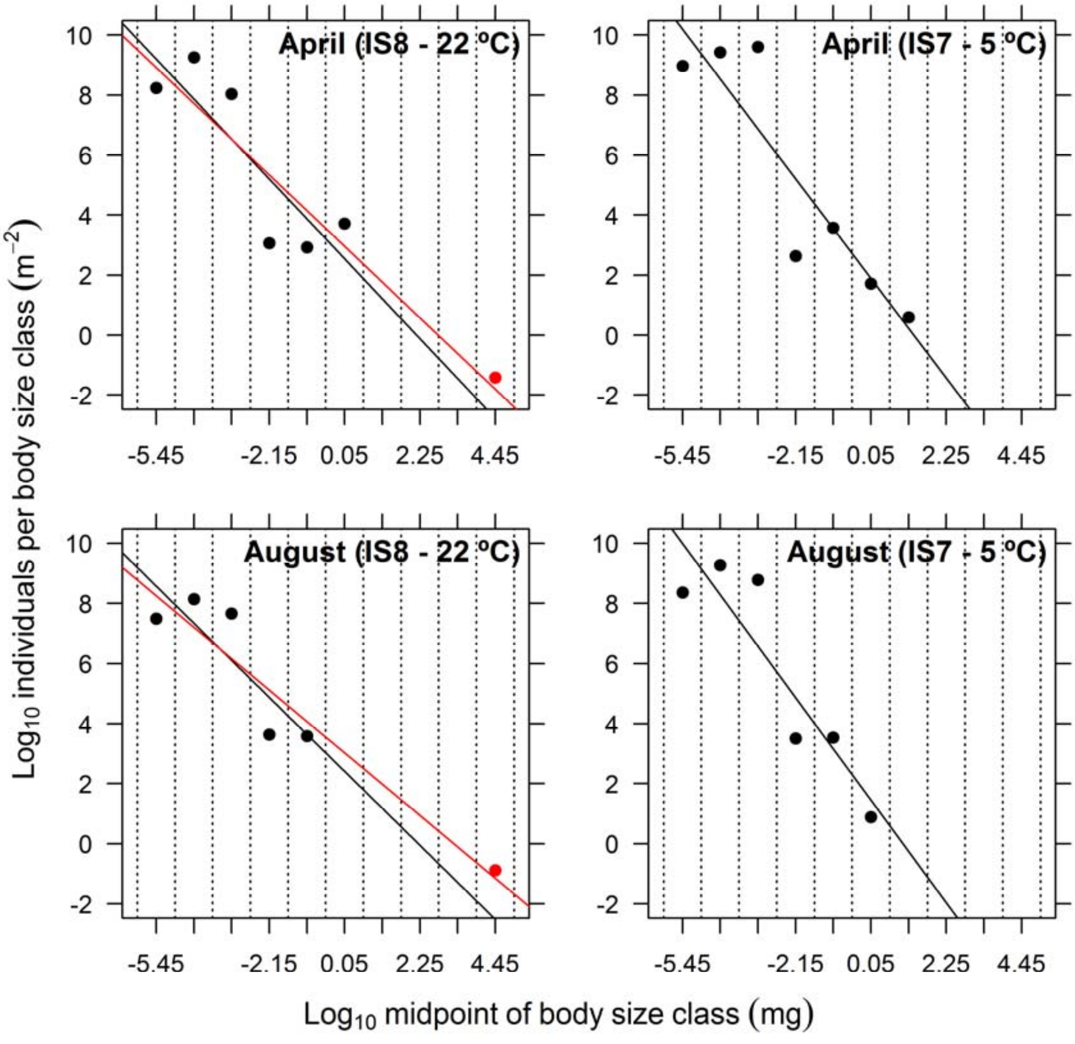


Figure 19. Relationship between decomposition rate and temperature for the (*a*) entire detritivore community ($y = 0.0054 + 0.0008x$, $r^2 = 0.46$, $F_{1,8} = 6.75$, $p = 0.032$); (*b*) microbial assemblage ($y = 0.0056 + 0.0004x$, $r^2 = 0.63$, $F_{1,8} = 13.52$, $p = 0.006$) and (*c*) macroinvertebrate assemblage ($F_{1,8} = 2.09$, $p = 0.187$) in ten streams in August 2004.

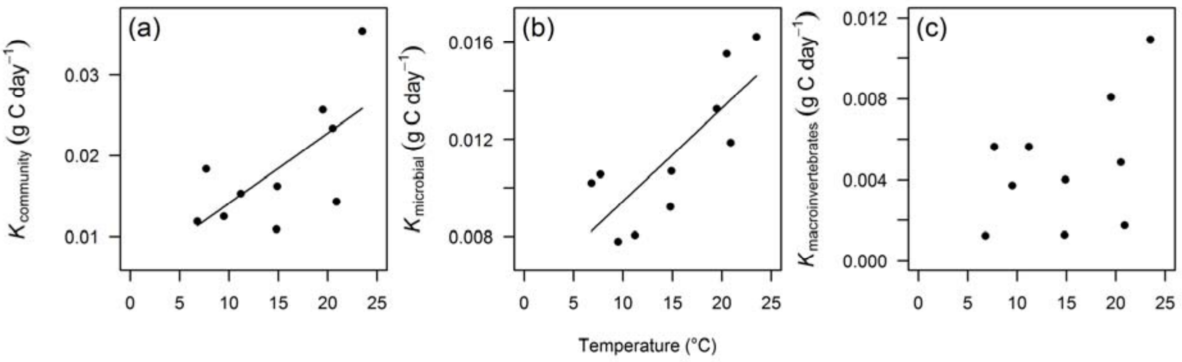


Figure 20. Percentage increase in the cycling rate of NH_4, NO_3 and PO_4 per °C from the cold IS7 stream to the warm IS8 stream in August 2008. The figure highlights the differential temperature dependencies of these three nutrients. Data are based on the average nutrient cycling rate for each stream as measured in Demars *et al*. (2011), thus no error bars are shown.

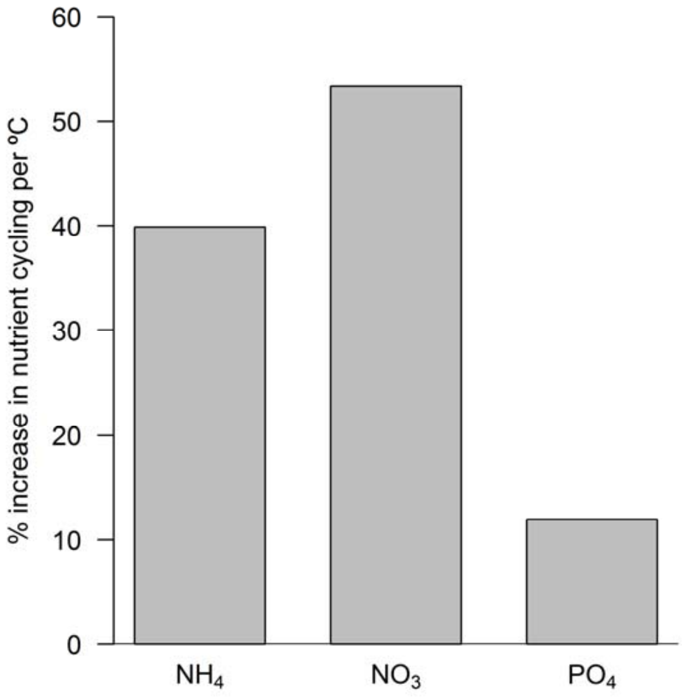


Figure 21. Metabolic capacity of benthic biofilms originating from four geothermal streams contrasting in ambient temperature assessed via laboratory experiments: (*a*) Arrhenius plot representing the relationship between the natural logarithm of biofilm respiratory flux (mg C m^{-2} $hour^{-1}$) and standardised experimental temperature ($1/kT_c$ - $1/kT$) across streams; (*b*) relationship between the rate of respiration at standardised temperature, $\ln R(T_c)$, within each stream and mean biofilm biomass (mg C m^{-2}) with error bars shown as standard error around the mean (redrawn after Perkins *et al*. 2012).

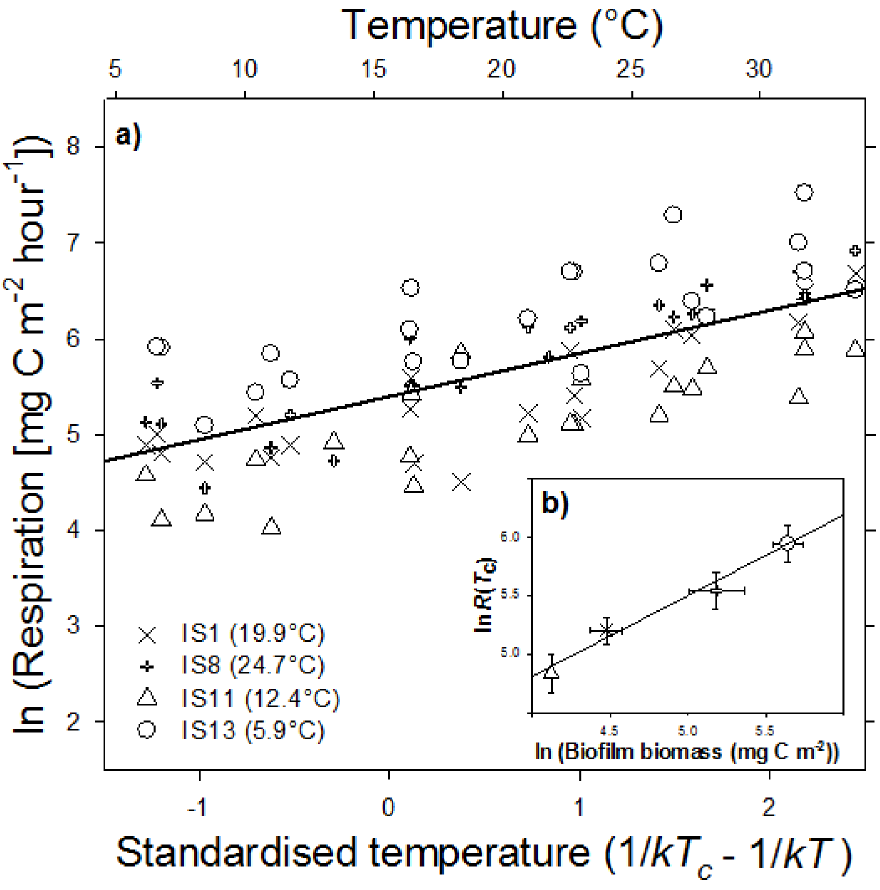


Figure 22. (*a*) Figure highlighting the similarity in daylight hours for both the April and August sampling. (*b*) GPP$_{max}$ was consistently found to be at least three times higher than daily GPP for both August 2008 (grey circles, solid regression line: $y = 0.509 + 1.003x$, $r^2 = 0.96$, $F_{1,11} = 250.1$, $p < 0.001$) and April 2009 (white circles, dashed regression line: $y = 0.570 + 1.036x$, $r^2 = 0.92$, $F_{1,8} = 87.37$, $p < 0.001$). Data are shown for IS1-14 in August 2008 and IS1-10 in April 2009.

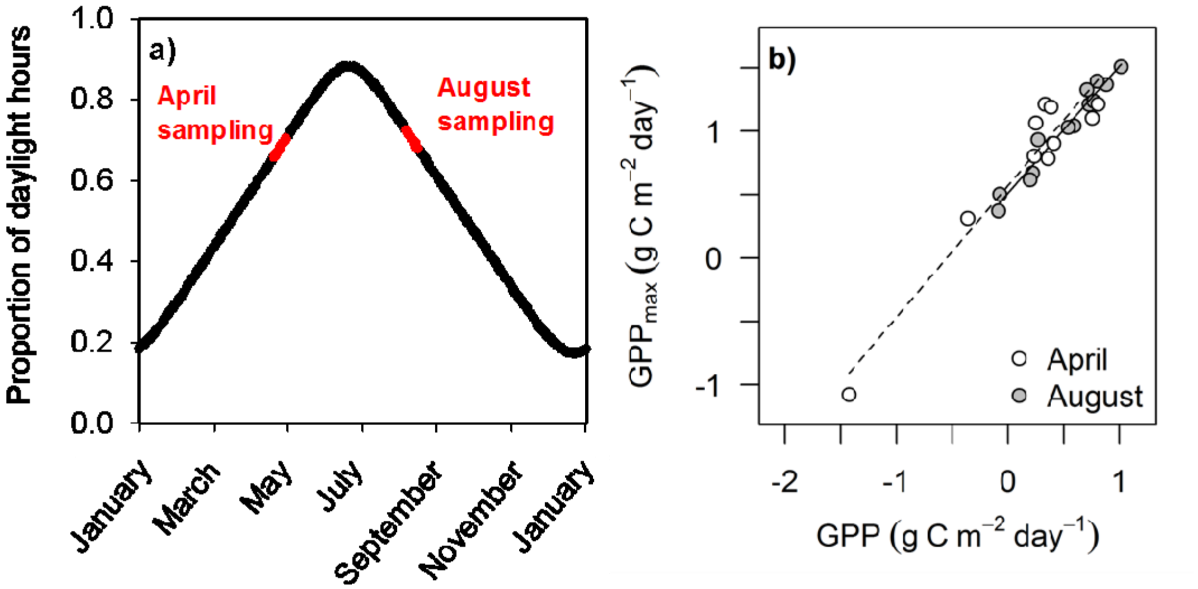


Figure 23. (*a*) GPP was only significantly related to temperature in August 2008 (grey circles, sold regression line: $y = -0.006 + 0.033x$, $r^2 = 0.33$, $F_{1,11} = 5.52$, $p = 0.039$), not April 2009 (white circles: $F_{1,8} = 0.47$, $p = 0.512$). (*b*) GPP was significantly higher per stream and on average across the ten studied streams in August 2008 (grey bars) compared to April 2009 (white bars), except in the two coldest streams: IS7 and IS10. Error bars are given as standard error around the mean. Data in (a) are from IS1-14 in August 2008 and IS1-10 in April 2009.

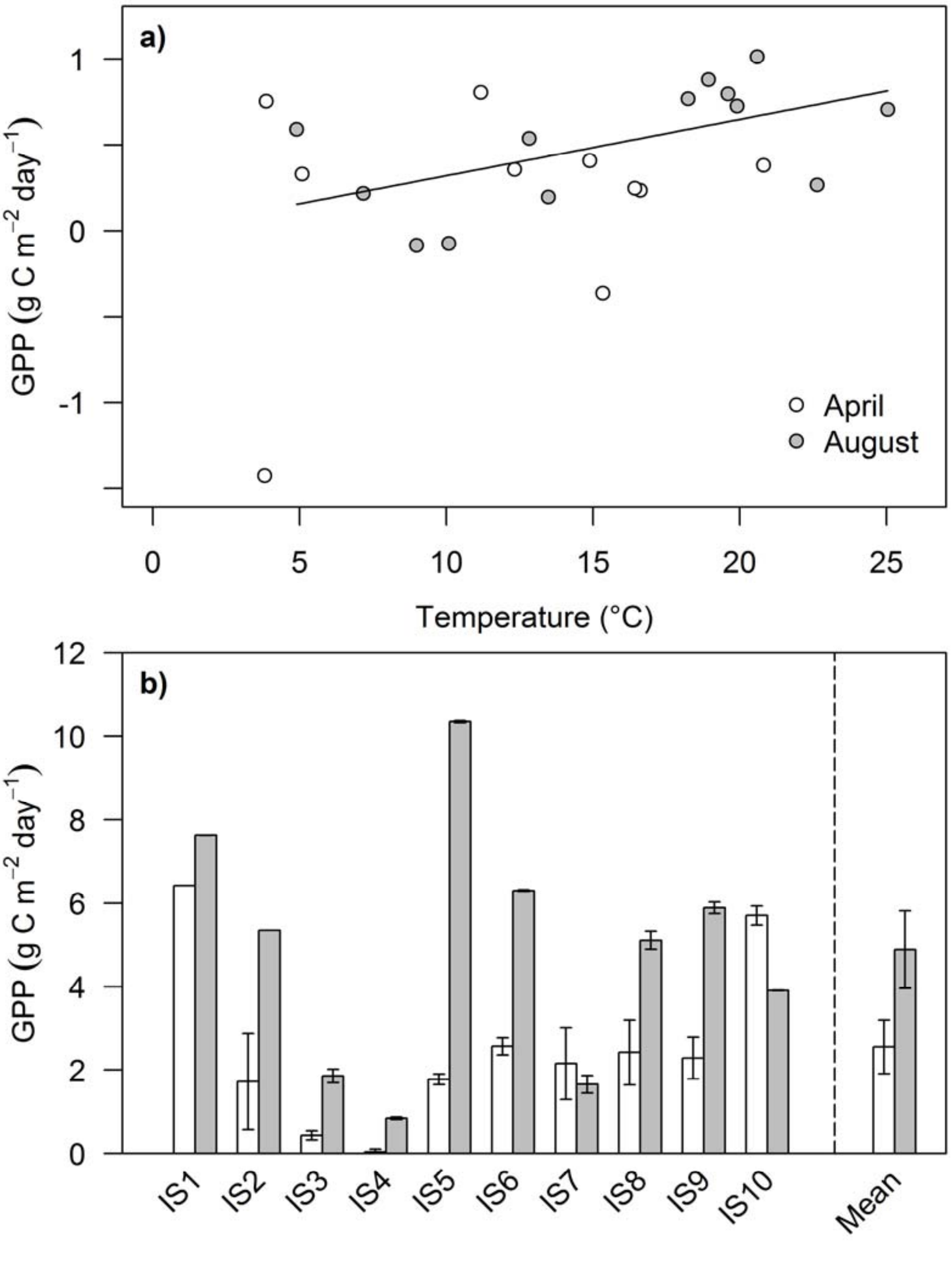
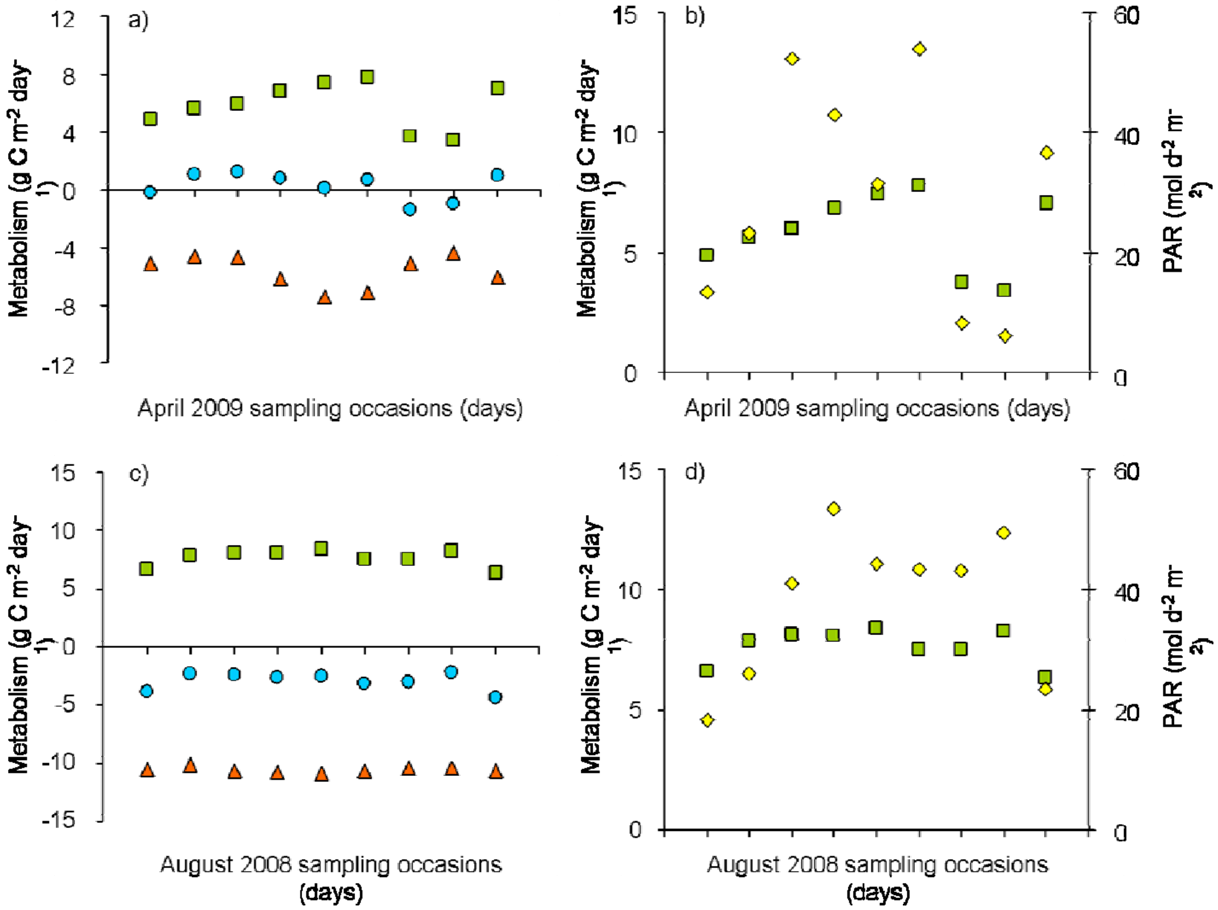


Figure 24. Consistency in GPP (green squares), ecosystem respiration (red triangles) and ecosystem metabolism (blue circles) measurements for the IS1 stream over nine days in (*a*) April 2009 and (*c*) August 2008. The relative consistency of the metabolism measurements may in part be related to the availability of light (yellow diamonds) during the same nine day period (*b*, *d*).



Box 1. *Snail growth rate experiment in geothermally-heated Lake Mývatn*

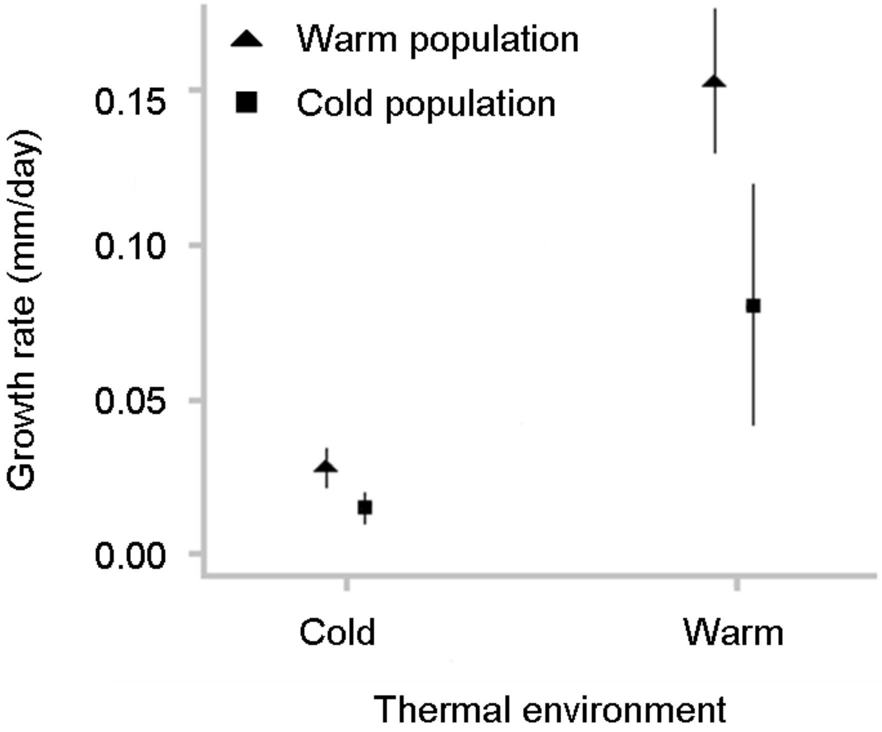
In a bid to understand the prevalence of *R. peregra* at warmer temperatures in both the streams and the diet of the trout (see Figure 8) in Hengill, growth rates of snails were analysed from an experiment at a geothermally-warmed lake in northern Iceland. During May to July 2011, a reciprocal transplant experiment was conducted within Lake Mývatn in northern Iceland. *R. peregra* were sampled along the shoreline from four locations, two cold (6 – 7 °C) and two warm (22 – 23 °C), which fall within the annual range of the cold IS7 and warm IS8 streams in the Hengill system (Table 2). Average shell length at cold locations was 5.38 mm (sd = 0.80) and 6.22 mm (sd = 0.87) at warm locations. The snails were transported to a laboratory where they were kept at 15 °C in two aquaria per sampling location for three weeks to acclimatize them to common temperature. They were fed three times a week with a mixture of spinach and fish food. Water was completely changed two times a week.

The reciprocal transplant experiment had a fully crossed design, i.e. snails from each sampling location were transferred to their own as well as to all other localities. Modified 0.5 l PET bottles were used as experimental units. The bottom of each bottle was cut off and holes were made in the sides to ensure water flow-through. The bottles were surrounded with a fine mesh net to prevent the snails from escaping. Styrofoam rafts held the bottles in place at the treatment sites. All rafts and bottles were placed in the water two weeks prior to the treatment period to allow periphyton to grow in the bottles. During the experiment, periphyton accumulated on the bottle surface provided the sole food source for the snails. A piece of tile was inserted in each bottle to increase the area for periphyton to grow on.

At the start of the experiment two snails from one population were placed in each bottle. They were individually marked with nail polish and photographed at the start (day 0) and at the end (day 25) of the experiment. The length of each individual was measured as the maximal distance starting from the shell apex to the outer shell lip. Each length measurement was taken three times from the photos using ImageJ v1.45s and the average was used in the analyses. Snail growth was analyzed using an ANCOVA with growth (mm/day) as the dependent variable, origin (cold or warm) and treatment location (cold or warm) as independent variables. The length at the start was included in the model as a covariate to correct for initial size. Due to sequential removal of non-significant terms the three-way interaction and the interaction between origin and initial size were removed from the analysis. While the snails from cold and warm origins were sampled at two locations, the random effect of population was weak in the initial analyses, and the data from each thermal habitat type were pooled in the final analysis. The statistical analysis was done in R 2.14.0 using the 'nlme' package (Pinheiro *et al.* 2012).

Snails grew three to four times faster in warm relative to cold environments (two-way ANOVA: treatment factor, $F_{1,63} = 17.04$, $p < 0.001$; Box 1 Figure). Warm-origin snails also had a significantly higher growth rate than cold-origin snails (two-way ANOVA: origin factor, $F_{1,63} = 48.26$, $p < 0.001$; Box 1 Figure), and this effect was more pronounced in the warm environments (two-way ANOVA: origin × treatment, $F_{1,63} = 24.51$, $p < 0.001$; Box 1 Figure). Smaller snails grew faster (two-way ANOVA: initial size factor, $F_{1,63} = 13.93$, $p < 0.001$; Box 1 Figure), particularly in warm environments (two-way ANOVA: treatment × initial size, $F_{1,63} = 6.61$, $p = 0.013$; Box 1 Figure).

Box 1 Figure. Growth rate (mm day^{-1}) of the snail *R. peregra* in an experiment conducted at Lake Mývatn in Iceland in 2011. Mean growth of snails from cold-adapted (squares) and warm-adapted (triangles) populations are shown in two different environments (warm and cold), with error bars shown as standard error around the mean.



Appendix A. Physical and chemical properties of the streams in the Hengill catchment examined in this study.

Table A1. Physical and chemical properties of the streams in August 2008 and April 2009, ordered by mean temperatures.

	Stream	Mean temp. [°C]	pH	EC [µS cm^{-1}]	DOC [mg l^{-1}]	*N-NH₄* [mg l^{-1}]	*N-NO₃* [mg l^{-1}]	total-*N* [mg l^{-1}]	*P-PO₄* [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	IS10	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
	IS13	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
	IS7	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
	IS14	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
	IS4	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
	IS11	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
	IS16	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
	IS12	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
	IS9	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
	IS2	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
	IS6	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
	IS5	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
	IS1	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
	IS3	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
	IS8	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
April 2009	IS14	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
	IS10	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
	IS11	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
	IS4	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
	IS13	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
	IS7	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
	IS12	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

IS16	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
IS9	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
IS1	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
IS6	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
IS2	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
IS3	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
IS5	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
IS8	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

Appendix B. Length-mass relationships and biovolume calculations for the diatom, ciliate, flagellate, meiofaunal and macroinvertebrate assemblages.

Table B1. Diatom species names and authorities, along with the shapes assigned to estimate biovolume. Formulas used to calculate biovolume and some additional notes are included at the foot of the table.

Species	**Shape**	**Biovolume**	**Notes**
Achnanthes exigua Grunow	prism on elliptic base	1	3
Achnanthes grana Hohn and 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 and 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 = $\pi/4 \times \text{length} \times \text{width} \times \text{depth}$

[2] biovolume = $\pi/4 \times \text{length} \times (\text{depth})^2$

Notes:

[3] depth = width

[4] depth = width/2

Table B2. Geometric shapes and formulae for estimating biovolume (V) of microbial loop taxa identified from 16 streams in Hengill in August 2011. For each taxon, length (L) is measured as a straight line along the longest dimension, width (W) is measured as a straight line along the shortest dimension and Z = 0.75 * L is a cross-section of the body of taxa assigned an ellipsoid shape (Hillebrand *et al.* 1999). All dimensions were measured in µm. Fresh/wet mass was calculated by converting to biovolume in μm^3, assuming a mean density of 1.0 for specific gravity (Ruttner-Kolisko 1977; Omori and Ikeda 1984) and a conversion factor of 0.25 (Mullin *et al.* 1966) was applied to convert to dry mass.

Taxa	**Major Group**	**Shape**	**Biovolume formula**
Acineria	Ciliate	Cylinder	$V= \pi W^2 L$
Actinobolina	Ciliate	Ellipsoid	$V= \pi/6(WLZ)$
Actinosphaerium	Ciliate	Sphere	$V=4/3\pi L^3$
Amphileptus	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Aspidisca	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Blepharisma	Ciliate	Cylinder	$V= \pi W^2 L$
Bursellopsis	Ciliate	Sphere	$V=4/3\pi L^3$
Chilodonella	Ciliate	Sphere	$V=4/3\pi L^3$
Chilodontopsis	Ciliate	Cylinder	$V= \pi W^2 L$
Chlamidodon	Ciliate	Cylinder	$V= \pi W^2 L$
Chlamydonellopsis	Ciliate	Cylinder	$V= \pi W^2 L$
Ciliate(A)	Ciliate	Cylinder	$V= \pi W^2 L$
Ciliate(B)	Ciliate	Cylinder	$V= \pi W^2 L$
Ciliate(C)	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Ciliate (D)	Ciliate	Sphere	$V=4/3\pi L^3$
Ciliophrys	Ciliate	Ellipsoid	$V= \pi/6(WLZ)$
Cinetochilum	Ciliate	Ellipsoid	$V= \pi/6(WLZ)$
Coleps	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Colpidium	Ciliate	Sphere	$V=4/3\pi L^3$
Colpoda	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Condylostoma	Ciliate	Cylinder	$V= \pi W^2 L$
Cyclidium	Ciliate	Sphere	$V=4/3\pi L^3$
Dexiostoma	Ciliate	Cylinder	$V= \pi W^2 L$
Dileptus	Ciliate	Cylinder	$V= \pi W^2 L$
Euplotes	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Glaucoma	Ciliate	Sphere	$V=4/3\pi L^3$
Halteria	Ciliate	Ellipsoid	$V= \pi/6(WLZ)$
Holophrya	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$

Holosticha	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Holotrich	Ciliate	Cylinder	$V=\pi W^2 L$
Hypotrich	Ciliate	Cylinder	$V=\pi W^2 L$
Kahliembus	Ciliate	Cylinder	$V=\pi W^2 L$
Litonotus	Ciliate	Cylinder	$V=\pi W^2 L$
Loxodes	Ciliate	Cylinder	$V=\pi W^2 L$
Loxophyllum	Ciliate	Cylinder	$V=\pi W^2 L$
Mesodinium	Ciliate	Ellipsoid	$V=\pi/6(WLZ)$
Metopus	Ciliate	Cylinder	$V=\pi W^2 L$
Nassulopsis	Ciliate	Cylinder	$V=\pi W^2 L$
Ophryoglena	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Oxytricha	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Phascolodon	Ciliate	Cylinder	$V=\pi W^2 L$
Philastrides	Ciliate	Cylinder	$V=\pi W^2 L$
Pleurostomida	Ciliate	Cylinder	$V=\pi W^2 L$
Prorodon	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Pseudomicrothorax	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Sathrophilus	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Spathidium	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Spirostomum	Ciliate	Cylinder	$V=\pi W^2 L$
Stentor	Ciliate	Cylinder+cone	$V=\pi W^2 l+(\pi/12) W^2 L$
Strobilidium	Ciliate	Cone+ ½ sphere	$V=1/3\pi W^2 Z+1/2(4/3\pi)L^3$
Strombidium	Ciliate	Cone+ ½ sphere	$V=1/3\pi W^2 Z+1/2(4/3\pi)L^3$
Suctoria	Ciliate	Sphere	$V=4/3\pi L^3$
Tachysoma	Ciliate	Cylinder	$V=\pi W^2 L$
Uroleptus	Ciliate	Prolate spheroid	$V=\pi/6(W^2 L)$
Urostyla	Ciliate	Cylinder	$V=\pi W^2 L$
Cryptomonadales	Flagellate	Sphere	$V=4/3\pi L^3$
Euglena	Flagellate	Cylinder	$V=\pi W^2 L$
Flagellate(A)	Flagellate	Cone	$V=1/3\pi W^2 L$
Flagellate(B)	Flagellate	Cylinder	$V=\pi W^2 L$
Flagellate (C)	Flagellate	Ellipsoid	$V=\pi/6(WLZ)$
Flagellate (D)	Flagellate	Sphere	$V=4/3\pi L^3$
Gonium	Flagellate	Sphere	$V=4/3\pi L^3$
Oocystis	Flagellate	Prolate spheroid	$V=\pi/6(W^2 L)$
Peridinium	Flagellate	Sphere	$V=4/3\pi L^3$
Acarus	Meiofauna	Prolate spheroid	$V=(\pi/6) W^2 L$
Brachionus	Meiofauna	Cylinder	$V=\pi W^2 L$
Cladocera	Meiofauna	Prolate spheroid	$V=(\pi/6) W^2 L$
Copepoda	Meiofauna	Ellipsoid	$V=\pi/6WLZ$*
Euchlanis	Meiofauna	Ellipsoid	$V=\pi/6WLZ$
Gastrotricha	Meiofauna	Cylinder	$V=\pi W^2 l$
Lepadella	Meiofauna	Prolate spheroid	$V=(\pi/6) W^2 L$
Nematoda	Meiofauna	Cylinder	$V=\pi w^2 l$

Oligochaete	Meiofauna	Cylinder	$V= \pi w^2 l$
Ostracoda	Meiofauna	Prolate spheroid	$V=(\pi/6) W^2 L$
Rotaria	Meiofauna	Cylinder	$V= \pi w^2 l$
Rotifer (A)	Meiofauna	Cylinder	$V= \pi w^2 l$
Tardigrade	Meiofauna	Cylinder	$V= \pi w^2 l$
Testudinella	Meiofauna	Cylinder	$V= \pi w^2 l$
Trichocerca	Meiofauna	Cylinder+cone	$V= \pi w^2 l + (\pi/12) w^2 l$
Turbellaria	Meiofauna	Cylinder	$V= \pi w^2 l$

Table B3. Species names and authorities for the macroinvertebrates identified from all streams, 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. Log conversions of length (x) measurements are provided, as well as log conversions and units of mass (y) measurements. References (Ref) to the studies used to obtain the length-weight (L-W) relationships are: [1] Benke *et al*. (1999); [2] Baumgärtner and Rothhaupt (2003); [3] Johnston and Cunjak (1999); [4] Woodward and Hildrew (2002); [5] Steingrímsson and Gíslason (2002); [6] Edwards *et al*. (2009); [7] Ramsay *et al*. (1997).

Species	**Order**	**Family**	**Dimension**	**Ref**	***x***	***y***	**L-W relationship**
Capnia vidua Klapálek	Plecoptera	Capniidae	HW	[1]	ln(HW)	ln(mg)	$y = 0.544 + 3.255x$
Chaetocladius sp. Kieffer	Diptera	Chironomidae - Orthocladinae	HW	[2]	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Clinocera stagnalis Haliday	Diptera	Empididae	BL	[1]	BL	mg	$y = 0.0066x^{2.437}$
Cricotopus sp. A Cranston	Diptera	Chironomidae - Orthocladinae	HW	[2]	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Cricotopus sp. B Cranston	Diptera	Chironomidae - Orthocladinae	HW	[2]	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Diamesa bertrami Edwards	Diptera	Chironomidae - Diamesinae	HW	[3]	HW	mg	$y = 4.86x^{3.15}$
Diamesa zernyi Edwards	Diptera	Chironomidae - Diamesinae	HW	[3]	HW	mg	$y = 4.86x^{3.15}$
Dicranota sp.	Diptera	Pediciidae	BL	[4]	ln(HW)	mg	$y = -5.53 + 1.91x$
Ephydridae indet.	Diptera	Ephydridae	BL	[5]	ln(HW)	mg	$y = -5.17 + 1.8x$
Eukiefferiella claripennis Lundbeck	Diptera	Chironomidae - Orthocladinae	HW	[2]	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Eukiefferiella devonica Edwards	Diptera	Chironomidae - Orthocladinae	HW	[2]	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Eukiefferiella minor Edwards	Diptera	Chironomidae - Orthocladinae	HW	[2]	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Glyptotendipes severini Goetghebuer	Diptera	Chironomidae - Chironomini	HW	[3]	HW	mg	$y = 4.86x^{3.15}$
Helobdella stagnalis Linnaeus	Rhynchobdellida	Glossiphoniidae	BL	[6]	ln(BL)	ln(mg)	$y = -2.74 + 2.12x$
Heteroptera indet.	Heteroptera	Hebridae indet. Mesoveliidae indet. Naucoridae indet. Notonectidae indet.	HW	[1]	ln(HW)	ln(mg)	$y = 2.46 + 3.44x$
Macropelopia sp. Thienemann	Diptera	Chironomidae - Tanypodinae	HW	[3]	HW	mg	$y = 4.86x^{3.16}$

Metriocnemus hygropetricus type Cranston	Diptera	Chironomidae - Orthocladinae	HW	[2]	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Metriocnemus sp. van der Wulp	Diptera	Chironomidae - Orthocladinae	HW	[2]	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Micropsectra sp. Kieffer	Diptera	Chironomidae - Tanytarsini	HW	[4]	log10(HW)	log10(µg)	$y = 3.01 + 1.75x$
Muscidae indet.	Diptera	Muscidae - Phaoniinae	BL	[5]	ln(BL)	mg	$y = -5.17 + 1.8x$
Oligochaeta indet.	Oligochaeta		BL	[7]	BL	g	$y = (\pi r^2 * 1.05x)/4$
Orthocladius sp. Brundin	Diptera	Chironomidae - Orthocladinae	HW	[2]	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Paraphaenocladius sp. Thienemann	Diptera	Chironomidae - Orthocladinae	HW	[2]	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Parochlus kiefferi Garrett	Diptera	Chironomidae - Podonominae	HW	[3]	HW	mg	$y = 4.86x^{3.17}$
Potamophylax cingulatus Steph.	Trichoptera	Limnephilidae - Limnephilinae	HW	[2]	ln(HW)	mg	$y = 0.5 + 2.91x$
Procladius sp. Skuse	Diptera	Chironomidae - Tanypodinae	HW	[3]	HW	mg	$y = 4.86x^{3.16}$
Prosimulium ursinum Edwards	Diptera	Simuliidae - Simuliinae	HW	[4]	ln(HW)	ln(mg)	$y = 0.20 + 3.32x$
Radix peregra Linnaeus	Pulmonata	Lymnaeidae - Lymnaeinae	SW	[2]	lnSW	ln(mg)	$y = -3.63 + 3.15x$
Scatella tenuicosta (thermarum) Collin	Diptera	Ephydridae	BL	[5]	ln(HW)	mg	$y = -5.17 + 1.8x$
Simulium aureum Fries	Diptera	Simuliidae - Simuliinae	HW	[4]	ln(HW)	ln(mg)	$y = 0.20 + 3.32x$
Simulium vernum Macquart	Diptera	Simuliidae - Simuliinae	HW	[4]	ln(HW)	ln(mg)	$y = 0.20 + 3.32x$
Simulium vittatum Zetterstedt	Diptera	Simuliidae - Simuliinae	HW	[4]	ln(HW)	ln(mg)	$y = 0.20 + 3.32x$
Sperchon glandulosus Koenike	Prostigmata	Sperchontidae	BW	[2]	ln(BW)	mg	$y = -1.69 + 1.69x$
Thienemanniella sp. Kieffer	Diptera	Chironomidae - Orthocladinae	HW	[2]	ln(HW)	ln(mg)	$y = -0.14 + 1.72x$
Tipulinae indet.	Diptera	Tipulidae	BL	[4]	ln(BL)	mg	$y = -5.50 + 2.36x$

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Appendix C. Yield-effort curves to validate the efficiency of diatom and macroinvertebrate sampling in all streams in April 2009, the data which forms the backbone of the current paper.

Table C1. Number of diatom species (*n*) identified in each stream used in the current study from April 2009. The values *a* and *b* are exponents of the rectangular hyperbola fitted to each yield-effort curve, with r^2 values provided for each fitting. The asymptotic value *a* represents the expected number of species in a stream, assuming this form of curve. The difference between the asymptotic value and the number of species identified (*a*-*n*), i.e. the potential under-sampling of the stream, is also provided (with percentage under-sampling in brackets).

Stream	*n*	*a*	*b*	r^2	(*a*-*n*)
IS1	46	50.63	146.29	1.00	5 (10%)
IS3	41	42.78	78.65	0.99	2 (5%)
IS4	29	30.50	111.74	0.97	1 (3%)
IS5	42	42.52	100.48	0.98	1 (2%)
IS6	29	29.90	92.40	0.97	1 (3%)
IS7	28	29.46	89.76	0.98	1 (3%)
IS8	26	27.68	86.22	0.99	2 (7%)
IS9	34	35.96	216.31	0.97	2 (6%)
IS10	26	26.12	98.99	0.96	0 (0%)
IS11	29	32.43	95.30	0.99	3 (9%)
IS12	43	46.69	457.04	0.96	4 (9%)
IS13	27	27.17	203.40	0.91	0 (0%)
IS14	23	25.43	160.43	0.99	2 (8%)
IS16	29	30.78	87.87	0.98	2 (6%)

Figure C1. Yield effort curves for diatom communities in 14 streams sampled in April 2009 (note that there are no stones in the IS2 stream, so epilithic diatoms could not be sampled here). Here, the *x*-axis represents the number of samples units identified and the *y*-axis represents the cumulative number of species found. Coloured stepwise lines represent 100 randomisations; the black line represents the mean calculated from the randomisations; the red line represents the fitted rectangular hyperbola. The name of each stream is given above the panel.

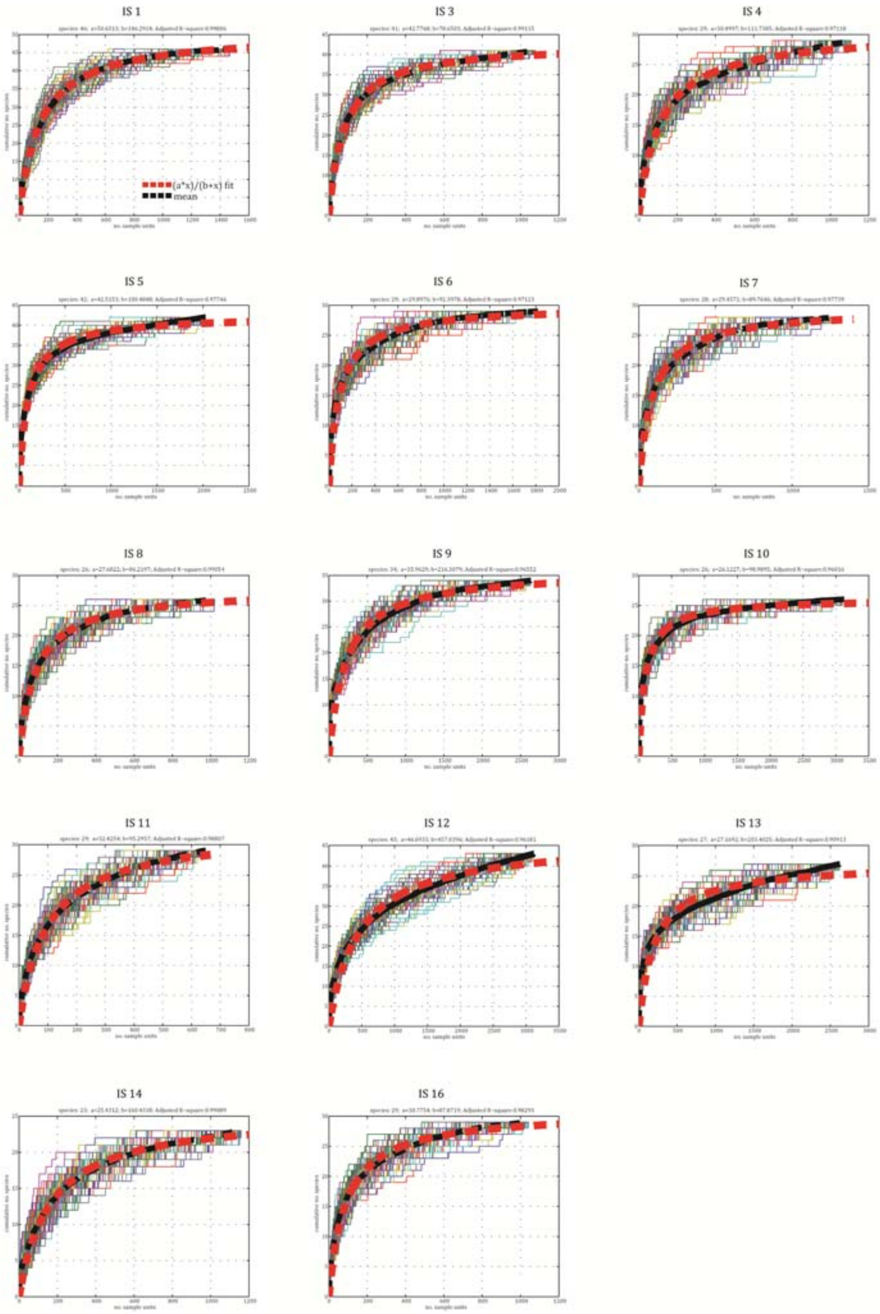
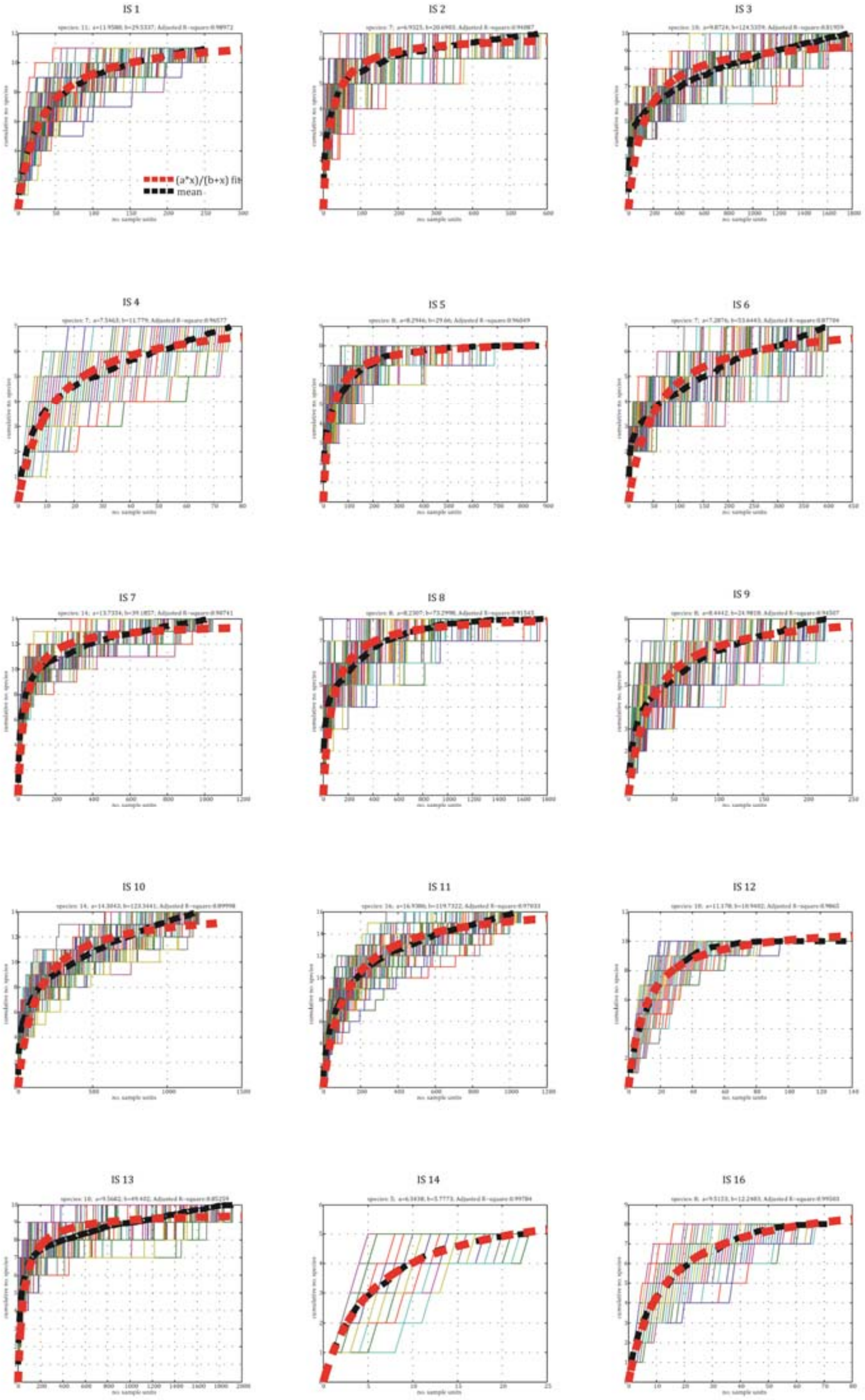


Table C2. Number of macroinvertebrate species (*n*) identified in each stream used in the current study from April 2009. The values *a* and *b* are exponents of the rectangular hyperbola fitted to each yield-effort curve, with r^2 values provided for each fitting. The asymptotic value *a* represents the expected number of species in a stream. The difference between the asymptotic value and the number of species identified (*a*-*n*), i.e. the potential under-sampling of the stream, is also provided (with percentage under-sampling in brackets).

Stream	*n*	*a*	*b*	r^2	(*a*-*n*)
IS1	11	11.96	29.53	0.99	1 (8%)
IS2	7	6.93	20.69	0.94	0 (0%)
IS3	10	9.87	124.54	0.82	0 (0%)
IS4	7	7.55	11.78	0.97	1 (13%)
IS5	8	8.29	29.66	0.96	0 (0%)
IS6	7	7.29	53.64	0.88	0 (0%)
IS7	14	13.73	39.19	0.91	0 (0%)
IS8	8	8.23	73.30	0.92	0 (0%)
IS9	8	8.44	24.98	0.95	0 (0%)
IS10	14	14.30	123.34	0.90	0 (0%)
IS11	16	16.94	119.73	0.97	1 (6%)
IS12	10	11.18	10.94	0.99	1 (9%)
IS13	10	9.57	49.40	0.85	0 (0%)
IS14	5	6.34	5.78	1.00	1 (17%)
IS16	8	9.52	12.25	1.00	2 (20%)

Figure C2. Yield effort curves for macroinvertebrate communities in 15 streams sampled in April 2009. Here, the *x*-axis represents the number of samples units identified and the *y*-axis represents the cumulative number of species found. Coloured stepwise lines represent 100 randomisations; the black line represents the mean calculated from randomisations; the red line represents the fitted rectangular hyperbola. The name of each stream is given above the panel.



Appendix D. Supplementary methods.

Snail exclusion experiment

The impact of grazing in the presence and absence of snails was examined in a nutrient diffusion experiment at Hengill in August 2004. The nine streams used were IS1, 5, 6, 7, 8, 9, 11, 13 and 14. Nutrient diffusion substrates consisted of 90 ml plastic pots containing either 2% agar (controls) or agar to which nitrogen (N) or phosphorous (P) was added. A grazer exclusion treatment was also employed, where the rim of pots containing N was covered with Vaseline. Nitrogen was added as 1 M $NaNO_3$ and phosphorus as 0.06 M KH_2PO_4. The colonisation surface of each pot covered an area of 20 cm^2 and consisted of 200 μm nylon mesh. Twelve pots (three replicates of the N, P, grazer and control treatments) were placed in the downstream reach of each of the nine streams, fitted in random order into a stainless steel frame, which was anchored to the stream bed using large stones. At the end of the experiment, substrates were taken from the streams, colonisation surfaces were removed from the pots and placed into individual plastic containers. The surfaces were kept dark and cool (5 °C) until they were extracted for chlorophyll in 96% ethanol (see Friberg *et al.* 2009 for further details).

Measures of interaction strength

We calculated the actual mass specific and relative feeding rates using a modified multi-prey version (Murdoch and Oaten 1975, Koen-Alonso 2007, Kalinkat *et al.* 2011) of the well known functional response model (Holling 1959):

$$F_{ij} = \frac{\lambda a_{ij} N_j}{(1 + \sum_{k=1}^{k=n} a_{ik} h_{ik} N_k)}$$

F_{ij} is the feeding rate that depends on prey density N_j and the densities of all prey (including predator i and prey j) in the environment N_k. This hyperbolic relationship is parameterized by the attack rate, a_{ij}, a_{ik}, and the handling time, h_{ij}, h_{ik}. We introduced a parameter λ that becomes "0" if the link is not reported in the food web and "1" if the link is reported. As most biological rates, feeding and subsequently the functional response parameters are mass and temperature dependent (see Rall *et al.* 2012 for a review):

$$a_{ij} = a_0 m_i^{b_a} m_j^{c_a} e^{E_a \frac{(T - T_0)}{kTT_0}}$$

$$h_{ij} = h_0 m_i^{b_h} m_j^{c_h} e^{E_h \frac{(T - T_0)}{kTT_0}}$$

where a_0 is a constant, m_i and m_j are the masses of the predator i and a prey j, $b_{a,h}$ and $c_{a,h}$ are the allometric exponents, $E_{a,h}$ is the activation energy, T is the absolute temperature, T_0 is the temperature where the intercept of the model is based and k is the Boltzmann constant.

The mass specific feeding rate is calculated by:

$$F_{spec} = \frac{m_j F_{ij}}{m_i}$$

To calculate the relative feeding rate we need to calculate the metabolic rates of the predators following the Metabolic Theory of Ecology (Brown *et al.* 2004):

$$I_i = I_0 m_i^{b_I} e^{\frac{-E_I}{kT}}$$

where I_i is the metabolic rate, I_0 is a constant and the other parameters are as above. The relative feeding rate is calculated as

$$F_{rel} = \frac{\Omega m_j F_{ij}}{I_i}$$

where Ω is a factor to convert mass (mg) into energy (J) and $\Omega = 7$ (Peters 1983). As a caveat, it should be acknowledged that we use general scaling of functional responses and metabolic rates (Brown *et al.* 2004, Rall *et al.* 2012; see Table D1 below), ignoring quadratic deviations at extreme temperatures for both (Ehnes *et al.* 2011, Englund *et al.* 2011, Rall *et al.* 2012).

Laboratory ecosystem respiration experiment

The Perkins *et al*. (2012) experiment was carried out in August 2008 on streams IS1, 8, 11 and 13, and was designed to assess the direct effects of thermal history (i.e. streams with distinct thermal regimes) on the potential for physiological adaptation of biofilm respiration mediated via changes in the slope (the activation energy, E) and/or intercept (standardised respiration flux, $\ln R(T_c)$) of the Arrhenius model (Brown *et al.* 2004). In the experiment, stones with attached biofilms collected from each of the four selected streams were incubated in opaque chambers at six temperatures (~ 5, 10, 15, 20, 25 and 30 °C) in an increasing sequence starting at the lowest through to the highest temperature. Respiration rates were measured using micro-oxygen electrodes inserted into the lid of each chamber over a 15 minute period at each temperature and converted to carbon (C) equivalents assuming a molar respiratory quotient of 0.85. Measuring respiration rates over the short-term avoided the potential for autotroph and community-level respiratory acclimation to elevated temperature, mediated via possible substrate limitation (Allen *et al.* 2005). Each suite of incubations was repeated four times, each with new biofilms from each of the four donor streams to give a total of 96 experimental units; i.e. 4 streams × 4 replicates × 6 incubation temperatures. Experimental units where r^2 values of the regression between O_2 change over time did not exceed 90% were excluded ($n = 5$ out of 96 experimental units).

Field measurements of ecosystem metabolism and stream hydraulics

Photosynthetically active radiation (PAR) was measured continuously in air and averages logged every 5 minutes (LICOR instruments) for the sampling in both August 2008 and April 2009. These measurements were carried out on streams IS1-14 in August 2008 and IS1-10 in April 2009. To check for bias in daily GPP measurements, the relationship between GPP and PAR (using 5 min time step data) was modelled with a Michaelis-Menten type equation as follows:

$$GPP = \frac{GPP_{MAX} PAR}{k_{PAR} + PAR}$$

where GPP_{MAX} is the maximum GPP and k_{PAR} is the PAR at which half the GPP_{MAX} is realised.

The net metabolism of each stream was quantified in August 2008 and April 2009. Whole stream metabolism estimates (ER and GPP) were based on a modified open-system O_2 change method using two stations corrected for lateral inflows (Odum 1956, Demars *et al.* 2011b). Contrary to previous methods, the in-stream diel oxygen curves were averaged prior to calculations (see below) to circumvent the problem of spatial heterogeneity giving biased results (Demars *et al.* 2011b). Essentially, this is an in-stream mass balance of oxygen requiring measurements of oxygen inflows and outflows along a river reach. Stream metabolism was measured in whole stream reaches (17-51 m long) during 24-48 hours within a short period of time (6-16th August 2008; 22-30th April 2009) as in Demars *et al*. (2011b). The instantaneous net metabolism (NEP_t) at time t (mg O_2 m^{-2} s^{-1}) was calculated as:

$$NEP_t = \left(C_{AV\,t+\tau} - C_{AV\,t} - K_{At}\right)\frac{Q}{wL} - \left(C_g - C_{AV\,t}\right)\frac{Q_g}{wL}$$

with C_{AV} averaged observed oxygen concentration (mg L^{-1}) at time t and $t+\tau$ with τ mean travel time; K_A oxygen re-aeration (mg L^{-1}); Q, discharge (L s^{-1}); w, stream wetted width (m); L, stream reach length (m); C_g groundwater oxygen concentrations (mg L^{-1}); Q_g lateral inflows (L s^{-1}). Typically, oxygen concentrations were measured every minute with optic oxygen sensors (TROLL9500 Professional, In-Situ Inc and Universal Controller SC100, Hach Lange GMBF). Conservative tracer studies (NaCl and propane) were run during the same periods of fieldwork to quantify discharge (Q) at the top and bottom stations, groundwater lateral inflows (Q_g), mean travel time (τ), oxygen exchange coefficient (k_{O_2}), and water transient storage (see below).

Daily ecosystem respiration (ER) was calculated from the net metabolism at night (PAR <1µmol photon m^{-2} s^{-1}) scaled to 24 hours and gross primary productivity (GPP) resulted from subtracting the dark from the light metabolism and averaged over 24 h. The daily net ecosystem production (NEP) was calculated as GPP minus ER, with the assumption that autotrophic and heterotrophic respiration were the same under light conditions as those measured at night. The relative uncertainties (based on 1 standard deviation) in daily ER and GPP were generally around 50% (38-86%) and 20% (1-57%) in August 2008, respectively. Further details about the methods are available in Demars *et al*. (2011a, 2011b).

Water transient storage (amount of temporary storage of water within quiescent zones) is used here as a surrogate for spatial availability for microbes (that is microbial biomass) both in the hyporheic part of the stream as well as on the macrophyte patches. Greater levels of ER and GPP are expected with more water transient storage (Demars *et al.* 2011a). Water transient storage was determined using the upstream–downstream conductivity curves (10 second time step) produced by NaCl slug injections and the equations developed by Bencala and Walters (1983). The equations were solved numerically using the DISCUS method (Manson *et al.* 2001, Demars *et al.* 2011a, Manson *et al.* 2011). The good fit of the model simulations to the experimental data, together with Damkohler numbers within the range 0.5-5 (observed range 0.9-4.3) indicated that the model output was an accurate reflection of the actual stream processes (Hart *et al.* 1999, Argerich *et al.* 2008). To obtain more comparable measurements across streams, the cross-sectional area of the storage zone was normalised by the stream cross-sectional area (A_s:A). Water transient storage was statistically unrelated to temperature both in August 2008 (Demars *et al.* 2011a, 2011b) and in April 2009 ($r^2 = 0.01$, $n = 8$, $p = 0.78$).

Table D1. Parameter values of the allometric models (from Brown *et al.* 2004, Rall *et al.* 2012) used to estimate interaction strengths in this study (see *Measures of interaction strength* above).

Exponent	attack rate*	handling time*	metabolism*
a_0^{**}; h_0^{**}, I_0	$e^{-19.09}$; $e^{-11.71}$	$e^{9.25}$; $e^{5.69}$	$e^{19.75}$; $e^{20.83}$
b	0.58; 0.31	-0.56; -0.46	0.75
c	-0.01; 0.15	0.22; 0.12	
E	0.42	-0.30	0.69

* the first value is for invertebrate predators, the second value is for fish predators.

** a_0 and h_0 are not clearly defined for 2D nor 3D environments (m^2 vs. m^3). We use these values as they normalize the unit in a way that the emerging attack rate unit should be ($m^2 s^{-1}$).

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Appendix E. Trout gut content analysis and source of literature-based and inferred links for the food webs shown in Figures 16 and 17. Yield-effort curves for diatom genera identified in the guts of grazer and collector gatherer species are also shown. Stomach content analysis was performed on individuals captured from the same streams as those shown in Figure 8.

Table E1. Prey links for *Salmo trutta* in the regional catchment. *N* = number of *S. trutta* stomachs where a given prey item was found. A total of 63 individual *S. trutta* stomachs were examined (49 in August 2008, 14 in April 2009), all of which contained prey items. While this number of individuals is low, it represents a large proportion of the trout in the Hengill catchment during this time period. Occurrence of these prey items was also confirmed from stomach content analysis carried out on data from august 2004 (Woodward *et al*. 2010).

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 peregra*	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 prey species from the family Orthochladinae (*Chaetocladius* sp., *Cricotopus sp. A*, *Cricotopus sp. B*, *Eukiefferiella claripennis, Eukiefferiella minor, Metriocnemus hygropetricus type, Orthocladius sp.* and *Thienemanniella* sp.

[2] used for inferring prey species from the family Diamseinae (*Diamesa bertrami*, *Diamesa zernyi*.)

[3] used for inferring prey species from the families Mesoveliidae and Naucoridae,

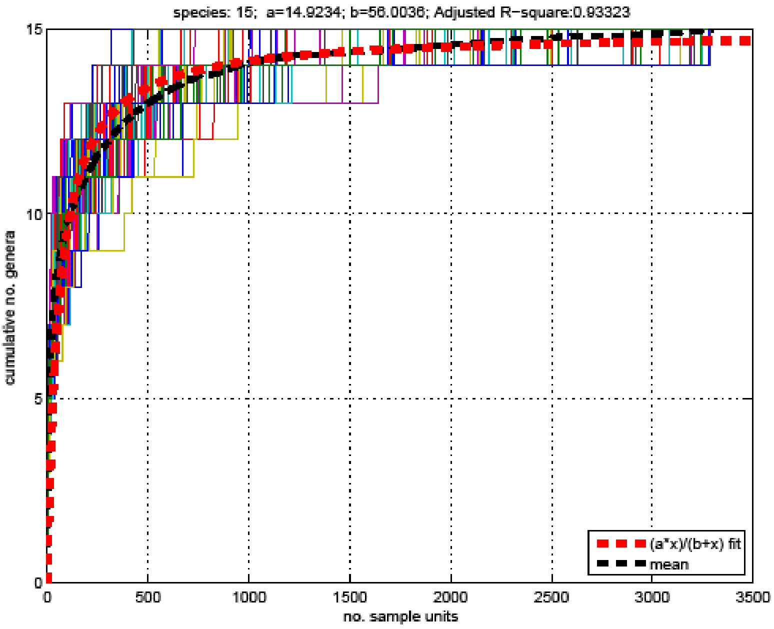
[4] used for inferring prey species from the family Simuliidae (*Simulium aureum*, *Simulium vittatum*, *Prosimulium ursinum*)

[5] used for inferring prey species from the family Tanypodinae (*Macropelopia* sp.)

Table E2. Sources of literature used to infer food web links of predatory macroinvertebrates in the system.

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

Figure E1. 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; the black line represents the mean calculated from the randomisations, the red line represents the fitted rectangular hyperbola with $y = (14.92*x)/(56.00-x)$, $r^2 = 0.93$. The number of genera found was 15, which is equal to the expected asymptotic value, a, from this fitting ($a = 14.92$).



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