# Icelandic trout:

## adapting to life in warm water

While many readers of *Salmo trutta* have visited Iceland, or have it firmly etched onto the bucket-list, because of the fantastic fish and fishing on offer, here Eoin O'Gorman and Ólafur Patrick Ólafsson recount on very different visits to examine effects of temperature on production of brown trout in geothermally-heated Icelandic streams.

A glistening blanket of white snow undulates over the valleys before us. This is the clichéd vision of Iceland, a country cloaked in flurries and floes. While this may be true in the dark winter months, summertime typically yields lush green valleys that fervently sustain a population of sheep which is more than double that of the 323,000 humans inhabiting the island. The lava fields are drowned in a sea of mosses, sporting the proverbial 40 shades of green. And the rivers are rich in salmon and trout, to the delight of all anglers – though not their pockets, with a day of fishing on several of the Laxá (literally meaning 'salmon river') costing over £1,000. This year (2015) is different though. Iceland has just experienced its worst winter for 93 years and the snow has yet to abandon many of its outposts, even as we reach the middle of June. It's easy to bandy the words 'climate change' about in cases like this, but the increased frequency of extreme events, such as the severe storms and floods we have experienced on our own island this winter, are an ever-increasing reminder that these are now words to be taken very seriously indeed. And it is to study future climate change impacts on brown trout populations that we are setting off across the snow.

Our little team has plodded a lonely furrow through this alabaster landscape for the past six weeks. After an hour of crunching and squelching each day, we stagger into a valley of yellow grasses and flowing waters. The snow has melted away much quicker here because the soil is heated by geothermal energy radiating from beneath the ground. We are now in the Hengill valley, located in southwest Iceland, at the triple junction of the Reykjanes Rift Zone, the Western Rift Zone, and the South Iceland Fracture Zone (see Figure 1). The infamous Eyjafjallajökull ('island mountain glacier'), whose volcanic ash grounded flights across Europe a few years ago, is only an hour's drive away. Luckily for us, hot magma lies a few kilometres beneath the Earth's surface at Hengill, leading to a mixture of cool patches and hot spots in the landscape. There is also no direct upwelling of sulphurous fluids, as seen in more extreme geothermal environments like Yellowstone Park. Fifteen small streams flow into the Hengladalsá ('hanging dales river'), which cuts through the valley between two small mountains. The streams are all within a mile of each other, but with temperatures ranging from 5-25°C (see Figure 2). The chemistry of the streams is typical of Iceland in general and does not vary with temperature. This lets us examine trout populations and the freshwater communities that support them across a range of temperatures, which is representative of the planetary warming we might see in the coming century.

The streams have been studied by researchers for more than a decade and we have amassed great knowledge of temperature-related patterns and the processes that drive them. Brown trout are the only fish in the system and they rarely exceed 30cm fork length in these small streams (about 0.5 lb or two years of growth). Many of the general predictions about warming impacts and broader experimental insight suggests that top predators will decline in abundance, become smaller, or even go extinct with warming. This is because they have to spend more energy to survive in warmer environments. Surprisingly then, we see that trout are rarely found in the coldest streams and actually seem to be bigger and more abundant in the warmest streams. We suspect that this is related to the fact that Iceland is at the northern limit of the geographical distribution of brown trout. The coldest streams in the system are 3-10°C year-round, which is below the optimum temperature for growth in the species of about 11-19°C (as measured in various laboratory experiments). This suggests that trout should actually fare better in warmer streams in Hengill because they provide better conditions for growth. We can even predict how well a trout might do at any given temperature if we can describe its 'thermal performance curve'. This is simply some measure of an organism's 'performance' (for example growth rate) plotted against temperature (see Figure 3). We expect a minimum and a maximum temperature, beyond which the organism cannot function biologically. In between, we expect performance to increase exponentially from the minimum temperature until it reaches an optimum temperature, beyond which performance sharply declines to the critical maximum.

Our Icelandic colleagues (Prof Gísli Már Gíslason and Ólafur Patrick Ólafsson at the University of Iceland) set about measuring the growth rate of trout in as many streams as possible with a mark-recapture study several years ago. This huge undertaking involved electrofishing of all the streams in the system and large stretches of the main river over a period of two weeks. Electrofishing involves passing a small electric current through the water, which makes fish swim towards the equipment, where they can be easily lifted out with a net (see Figure 4). Almost 400 trout were captured, anesthetised, weighed, and implanted with tiny passive integrated transponders (PIT tags), before being released back into the streams at the point where they were caught. The PIT tags enabled the researchers to scan the streams every two weeks and pick up a unique radio signal from the previously tagged fish. After five months of monitoring, the streams were electrofished once more and the remaining tagged trout were weighed again. A total of 59 fish out of 394 tagged were recovered (a typical recapture rate for a study like this carried out over several months). The missing trout may have been eaten by predators such as birds or mink, or they may have migrated down the main river beyond the sampling stretches. Of the fish that were recaptured, only four had moved more than 10 metres in five months. This was a startling discovery, suggesting that once trout find a habitat patch that is suitable for feeding, they are happy to stay there for a very long period of time. This is reflected in the territorial nature of brown trout and salmonids in general.

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The tagging study revealed that the abundance and biomass of trout increased exponentially with stream temperature (from approximately 7-22°C). By measuring the change in weight of the fish over the five months, we were able to calculate their growth rate and found that this also increased exponentially. We would have expected the growth rate to drop off beyond the previously described optimum of 11-19°C, so this suggests that the trout at Hengill have somehow adapted to the environment of the warmer streams to achieve a higher optimum temperature for growth. But what are the mechanisms that contribute to greater biomass and growth rate (and thus production) of trout at these high stream temperatures? We came up with three possibilities: (1) trout change their diet to select for energetically more valuable resources; (2) they rely more on external subsidies in the warmer streams, for example by drift feeding on flies that land on the water surface, more often than they feed on in-stream resources; (3) energy is channelled more efficiently through the food web in the warmer streams so that trout can get more energy for less effort. We have spent several years testing these possible mechanisms.

To assess the in-stream resources available to the trout, we took many Surber samples in different years and seasons. A Surber sampler is a metal square (or quadrat) with a fine mesh bag attached to it. We scrubbed the streambed inside the metal square (which has a known area) and the contents were washed into the bag. We collected these contents in a jar, preserved them with ethanol, and identified them back in the laboratory. We found consistent changes in the composition of the invertebrate communities along the stream temperature gradient. Some species (such as midge fly larvae) become less abundant or disappear completely as stream temperature increases; others (such as the freshwater snail and blackfly larvae) do the opposite. To test our first mechanism about changes in trout diet, we had to take into account these changes in prey composition. We used a selectivity index that relates the biomass of prey in the stomach of a trout to the biomass of that prey item in the stream. To quantify the trout diet, we carried out electrofishing and stomach flushing at similar times to our Surber sample collections. This involved passing

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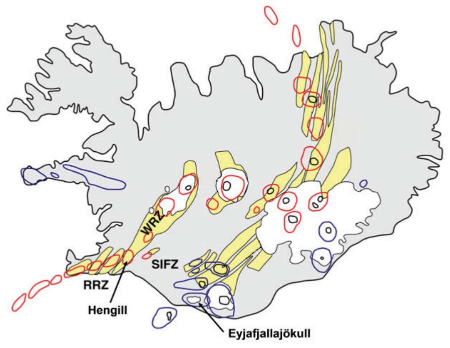
**Figure 1. Map of Iceland showing the position of the Hengill geothermal valley on the triple junction of the Reykjanes Rift Zone (RRZ), the Western Rift Zone (WRZ), and the South Iceland Fracture Zone (SIFZ). The location of the infamous Eyjafjallajökull volcano is also highlighted**



a plastic tube through the mouth of the fish and into the stomach. We then gently forced water through the tube with a syringe until the trout regurgitated its stomach contents into a small sample bag (see Figure 5). We again preserved this in ethanol and identified the contents under a microscope in the laboratory. We found that trout actively selected for blackfly larvae and predatory fly larvae as stream temperature increased, which are the most energetically valuable prey in the streams. Even though snails made up the greatest biomass of prey in the warm streams, trout actively selected against them. This may be because the hard shell is indigestible to trout and so represents a poor quality resource. The trout also actively selected against midge fly larvae and all other prey as stream temperature increased. These results indicate that trout do indeed alter their feeding behaviour to help them grow more rapidly at high stream temperatures.

To test our second mechanism about the importance of external subsidies, we first had to quantify the biomass of flies landing on the surface of the water. We used pan trapping over several sampling periods to achieve this goal. A pan trap is a small rectangular tray, which we propped on rocks just above the surface of the stream. We added some stream water to the pan trap, along with a few drops of surfactant (Fairy Liquid!) to break the surface tension, so that any flies landing on the water surface would sink to the bottom. We collected the traps after 24 hours for identification back in the lab. Even though we have observed more fly larvae in warmer waters and soils at Hengill, we did not expect to see any difference in the biomass of adult flies landing on the surface of streams because air temperatures do not vary in the same way. Surprisingly then, we saw an increase in the biomass of flies landing on the warmer streams. Most of the flies that we identified came from larvae that emerged from the soil, suggesting that this was truly an external subsidy to the streams and not just flies of aquatic origin returning to the same streams they emerged from. We cannot be sure, but perhaps these flies forage close to their natal sites or prefer to feed on the macrophytes associated with the warmer streams. We also identified any adult flies in the stomach contents that we collected from the trout and used the same selectivity index described above to assess its importance in the trout diet. We found that trout actively selected against this external subsidy in the warmer streams, even though it was more readily available, which indicates that our second mechanism does not contribute to increased growth rate of trout at Hengill.

To determine the efficiency of energy flow through the food web, we had to measure production at every trophic level in the ecosystem. First, we quantified the amount of sunlight entering the streams during the summertime with a light meter. We estimated how much of this sunlight was converted into algal resources at the base of the food web by measuring oxygen changes along the length of each stream during day and night time. Algae use sunlight to convert carbon dioxide and water into chemical energy with the release of oxygen (photosynthesis). Thus, by measuring oxygen concentrations in the water under light and dark conditions, we can estimate the gross primary production of a stream. We found that sunlight was converted more efficiently into algae as stream temperature increased. By measuring the change in biomass of stream invertebrates in each stream over the course of a year from our long-term Surber sample data, we were also able to determine secondary production in the system. This is simply a measure of how resources at the base of the food web are converted into animal matter, which we also found to be more efficient as stream temperature increased. It is crudely assumed that only 10% of energy from one trophic level is converted into biomass at the next trophic level.

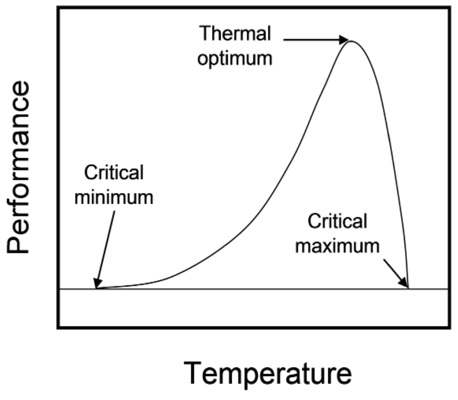


**Figure 3. A hypothetical thermal performance curve, showing the exponential increase in performance of an organism from its critical minimum to the thermal optimum, followed by a sharp decline in performance to the critical maximum temperature at which it can biologically function**

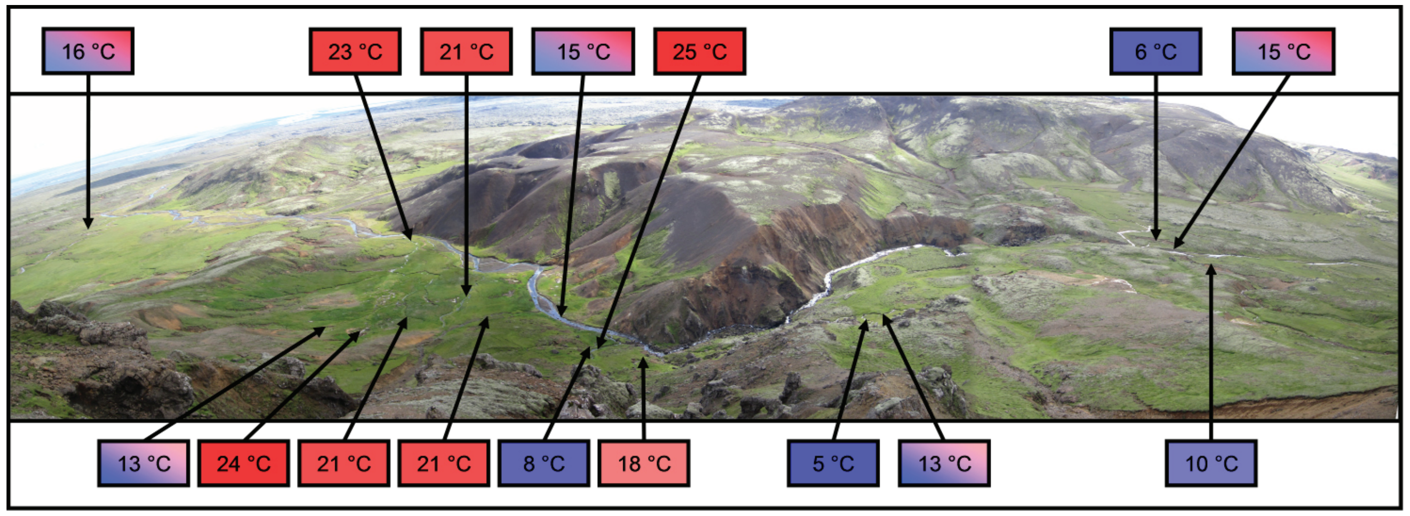


**Figure 2. Aerial view of the Hengill geothermal valley, with the position of the river Hengladalsá and fifteen of its tributaries shown with arrows. The temperature of the streams is provided in the coloured boxes**

Perhaps it is not surprising then that trout populations cannot be sustained in the relatively unproductive environment of the cold streams, while we found approximately 9% of secondary production plus external subsidies was converted to trout production in the warm streams. Interestingly, without the external subsidies, trout would have to convert more than 30% of the in-stream production available to them into biomass to sustain a population, suggesting that adult flies landing on the water surface still have an important part to play in the diet: albeit one that does not become more important as stream temperature increases.

From our studies in Hengill we have shown that brown trout can actively change their diet to target energetically valuable resources and passively benefit from more efficient conversion of energy to biomass throughout the food web. These mechanisms can help them to grow more rapidly in conditions that appear unfavourable for the species and highlight the potential for adaptation in the face of environmental warming. The potential for adaptation must be taken into account in predictive models if we are to accurately anticipate future climate change effects on any given species. It is also clear that we need a broad knowledge of the entire ecosystem occupied by the species because of all the other organisms it interacts with. And a word of warning – the warm streams at Hengill are beyond the lethal limit for development of brown trout embryos (which is about 16°C). Thus, populations at Hengill appear to thrive by taking advantage of rapid growth in the highly productive environment of warm waters before migrating to the cooler main river to continue their life cycle. We need further research to confirm this assumption, but it is an important point when considering our results in the context of future climate change, which may remove the coldwater thermal refugia necessary for trout populations to be sustainable after warming beyond the critical temperature range of any part of their life cycle.

**Figure 5. Stomach flushing of a trout. A plastic tube is passed through the mouth of the fish and into the stomach. Water is gently forced through the tube with a syringe until the trout regurgitates its stomach contents into a small sample bag**

**Figure 4. Electrofishing a Hengill stream. Fish swim towards the metal rod (held in the left hand), which is powered by a generator. They can then be easily removed with the net (held in the right hand) and passed to a bucket on the bank for processing**

This is not the end of our tale. Research always seems to bring more questions than answers and we are already working on some of those. We want to understand all the flows of energy between the streams and the environment around them. During our field visit to Hengill today, we will construct emergence traps, which look like little tents placed in the stream, to quantify the biomass of flies emerging on a weekly basis. In addition to our pan traps, we will also construct gutter traps, which look like half pipes placed under the banks of each stream, to quantify the amount of terrestrial invertebrates falling into the streams. We will also set drift nets, which look like drainage pipes with a mesh bag attached to the end, to quantify the amount of terrestrial material drifting along the surface of each stream. We have carried out fencing experiments to add fish to sections of cold streams and remove them from sections of warm streams. This will help to tell us more about how trout fare in the less productive cold streams and also how much of the change in invertebrate community composition that we observe along the stream temperature gradient is actually due to temperature and how much is due to stronger top down control (i.e. predation) by brown trout.

Our aim over the coming years is to expand the research we have been performing at Hengill to similar geothermal areas, not only in Iceland, but right around the Arctic Circle. A large grant awarded by the Natural Environmental Research Council to Prof Guy Woodward at Imperial College London will explore similarly heated stream systems in Greenland, Svalbard, Alaska, and Russia. By doing the same thing in many places, we can find out if the patterns that we detect at Hengill apply everywhere. We can also see if ecosystems that are more or less diverse and productive respond in the same way. We will continue to use the data we have already collected to build better models to predict how warming will affect trout populations, as well as the structure of plant and animal communities, and the way energy flows through food webs. Most importantly of all, our research provides a new way to understand the unavoidable problem of global warming.

## MORE INFORMATION

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Recent opinion piece in Global Change Biology: *http://onlinelibrary.wiley.com/doi/10.1111/gcb.12602/abstract*

Synthesis paper in Advances in Ecological Research: *http://www.sciencedirect.com/science/article/pii/B9780123983152000028*

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