

Master's thesis



*The effect of water temperature on the
feeding behaviour of Arctic char
(Salvelinus alpinus) in a natural stream:
Potential effects of climate change*

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Ísafjörður, May 2013

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45 ECTS thesis submitted in partial fulfilment of a Master of Resource

Management degree in Coastal and Marine Management at the University Centre of the Westfjords, Suðurgata 12, 400 Ísafjörður, Iceland

Degree accredited by the University of Akureyri, Faculty of Business and Science, Borgir, 600 Akureyri, Iceland

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Printing: Háskólaprent, June 2013

Declaration

I hereby confirm that I am the sole author of this thesis and it is a product of my own academic research.

Sarah Jane Kennedy

Abstract

Climate change is a generally accepted phenomenon that will likely influence a wide range of organisms and ecosystems worldwide through shifts in current temperature regimes. Such temperature shifts are believed to have a particular impact on the freshwater ecosystems in the Arctic. The biggest threat to salmonids, and other freshwater fish species, is that many are geographically isolated and their biology is highly dependent on the surrounding water temperature. I observed how water temperature, and other ecological variables, affected the activity, food intake, and foraging mode of young-of-year (YOY) Arctic char (*Salvelinus alpinus*) in a relatively warm stream in Northern Iceland. Arctic char did not increase their mid-day feeding activity with increasing temperatures, perhaps because they may maintain high activity over the narrow range of high temperatures experienced within the study stream over the period of observation (late July- late August). Individual foraging rate was higher at high water temperatures and light levels earlier in the summer suggesting that these variables may play an important role for the underlying metabolic need for, and the ability of Arctic char to forage on drifting invertebrates; respectively. In addition, mobility during foraging decreased significantly as water temperature and light levels decreased towards the end of the summer. This study shows that although Arctic char survive and grow at high water temperatures (*i.e.*, above 10 °C), their repertoire of potential behavioural responses to deal with a further increase in water temperatures may be reduced. Increasing our knowledge on the role water temperature plays in altering salmonid behaviour will eventually allow us to gain a better understanding of best management practices for fish and fish habitats likely to be effected by rising temperatures due to global climate change.

Útdráttur

Loftslagsbreytingar eru almennt viðurkennt fyrirbæri sem er líklegt til að hafa áhrif á fjölmargar tegundir lífvera og vistkerfa um jörð alla. Breytingar á hitastigi eru taldar hafa sérstök áhrif á ferskvatnsvistkerfi á norðurlægum breiddargráðum. Stærsta ógnin gagnvart laxfiski og öðrum ferskvatnstegundum er sú að margar þessara tegunda eru landfræðilega einangraðar og líf þeirra er mjög háð vatnshita. Ég rannsakaði hvernig hitastig vatns og aðrar vistfræðilegar breytur hafa áhrif á virkni, fæðuinntöku og hreyfanleika við fæðunám hjá bleikjuseiðum (*Salvelinus alpinus*) í hlýrri á á Norðurlandi. Bleikjan jók ekki virkni sína með hækkandi hitastigi, hugsanlega af því að virknin hefur haldist mjög há yfir það þrönga bil af háum vatnshita sem einkenndi rannsóknartímabilið frá seinnihluta júlí fram í seinnihluta ágúst. Tíðni fæðuinntöku var hærri í hlýrra vatni og á bjartari dögum snemma sumars, sem bendir til þess að þessar umhverfisbreytur gegni mikilvægu hlutverki með áhrifum sínum á undirliggjandi efnaskipahraða annarsvegar, og getu bleikju til að ráðast á og nýta sér hryggleysingja á reki sem fæðuuppsprettu. Að auki reyndist hreyfanleiki við fæðunám minni þegar hitastig árinna og birtustig lækkaði þegar nær dró hausti. Þessi rannsókn sýnir að þótt bleikja lifi og dafni í hlýju vatni (þ.e.a.s. yfir 10°C), þá er getur verið að atferlisfræðilegum valkostum hennar fækki þegar bregðast þarf við enn frekari hækkun í vatnshita. Aukin þekking á hlutverki vatnshiti í að móta atferli laxfiska veitir okkur betri skilning á þeim kostum sem í boði eru þegar kemur að verndun náttúrulegra fiskistofna og búsvæða þeirra í kjölfar loftslagsbreytinga og hækkandi hitastigs.

This thesis is dedicated to my family, my biggest supporters throughout this process.

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Acknowledgements

First and foremost, I would like to thank my supervisor, Dr. Stefán Óli Steingrímsson, for all his guidance and support throughout this entire thesis. I would also like to thank his Ph.D student, Nicolas Larranaga, for his assistance during my field work and his guidance. I would also like to acknowledge the support of Hjalti Karlsson and the Marine Research Institute of Iceland (Ísafjörður) for providing the laboratory facilities for my use. A special thanks to my mom and dad for not only their financial support but also their encouragement throughout this process. I would also like to thank my sisters Amy and Megan for their constant support, as well as my friends who have helped me with this study; this thesis would not have been completed without you: Chelsea Dawn Boaler, Astrid Fehling, and Maik Brötzmann. Special thanks to the staff of the University Centre of the Westfjords: Dagný Arnarsdóttir, Albertína Elíasdóttir, Guðrún Matthíasdóttir, Kristín Ósk Jónasdóttir, and Peter Weiss. This study was partially supported by a project grant issued to Stefán Óli Steingrímsson from the Icelandic Research Fund (120235022) and Holar University College.

1 Introduction

1.1 Climate change

Climate change is a generally accepted phenomenon that will likely influence a wide range of organisms and ecosystems worldwide. Recent climate warming has altered abundance, population dynamics and the distribution of many aquatic and terrestrial organisms (Thackeray, *et al.*, 2012). Over the next century northern Europe's mean temperature is predicted to increase approximately 3 °C, altering almost all biological processes (Moss, *et al.*, 2003).

Climate change is projected, on average, to warm up much of the Earth's surface and will continue to alter aquatic habitats by increasing salinization, modifying thermal regimes, changing stream flow, and causing changes in the current vegetation. (Eaton & Scheller, 1996; Rahel, Biernagen, & Tanguchi, 2008). When combined with other ecological stressors such as pollution and habitat loss, climate change is expected to weaken the resilience of many organisms (Scheffer & Carpenter 2003). This can lead to a sudden re-organization of communities and drastically alter ecosystem function and structure. This shift can allow detrimental environmental conditions to occur, which *i.e.*, may have the ability to modify the distribution and virulence of diseases-causing organisms and parasites in aquatic environments (Rahel, Biernagen, & Tanguchi, 2008). Warming has also exacerbated the effects of existing diseases in many species of fish. Examples include brown trout in Switzerland, where an increase in the occurrence of temperature-dependent proliferative kidney disease (PKD) can be attributed to warming temperatures (Rahel, Biernagen, & Tanguchi, 2008). In Iceland, the first report of PKD was reported in 2008, with wild populations of Brown trout and Arctic char affected. An increase in temperature related to global warming was cited as a potential factor strengthening the effect of PKD on these salmonid populations (Kristmundsson, Antonsson, & Árnason, 2010).

Climate change is of particular concern for freshwater systems. This is due to the habitat vulnerability and the limited relocation abilities of many freshwater organisms, requiring them to deal with environmental stress at a local scale (Reist, 2007). One critical question to ask is; do freshwater systems have the capacity to adjust to future

changes in key climatic variables (Prowse, *et al.*, 2012). Changes due to climate change have already become apparent. A freshwater example would be the lakes within northeastern Ontario which has already undergone an annual air temperature rise of 2 °C and a decrease in ice cover during the winter months (Chu, Mandrak, & Minns, 2005). Climate change will likely affect individuals, populations, and ecosystems within these freshwater systems and impact freshwater fishes in particular. Such changes include shifts in geographical species distribution, and changes in growth and bioenergetics (Chu, Mandrak, & Minns, 2005). Other general effects of climate change on these systems include decreased dissolved oxygen levels, and more importantly, an increase in water temperatures (Ficke, Myrick, & Hansen, 2007). Such changes in water temperature will likely have an effect on the physiology and behaviour of individual organisms within these freshwater ecosystems (Ulvan *et al.*, 2012). Water temperature plays a central role in defining the distributions of aquatic organisms since most are ectothermic, meaning that their body temperature will vary with the temperature in their surrounding habitats (Rahel, Biernagen, & Tanguchi, 2008). Rahel, Biernagen, & Tanguchi (2008), say that aquatic ectotherms differ in the maximum temperature they can endure and in ideal temperatures for growth. Therefore some species will likely be favored during shifts in temperature regimes, albeit at the expense of others. Globally, climate change has already had significant effects on freshwater and anadromous fish species. In 2001, there was a major anadromous fish die-off of brook char in the Hudson's Bay river in northern, Ontario, Canada. This die-off was due to an increase of temperatures during the summer months, resulting in changes to the surrounding freshwater and marine ecosystems (Gunn & Snucins, 2010).

In terms of conservation and management of aquatic salmonids, climate change will be particularly tricky to navigate. One issue of interest are species that are restricted to a particular area such as freshwater lakes, rivers, wetlands, and species in protected areas and reserves. Unlike most terrestrial and marine species such species are much more vulnerable to changes in the earth's climate (Saunders, Meeuwig, & Vincent, 2001). Although little is known of what is actually going to happen, it is thought that the warm water salmonids will migrate to cooler temperatures, where the cold water salmonids will be limited to increasingly higher elevations, and will eventually run out of habitat (Rahel, Keleher, & Anderson, 1996; Krajick, 2004). These observations

suggest from a management perspective, that a more proactive management paradigm should be adapted in areas of such concern. Preventing an influx of invasive species in these areas by creating migration barriers, executing habitat improvements that diminish the effects of climate change, translocating species to newly suitable habitats, and developing action plans to help detect and eliminate new invasive species are examples of efforts that can be implemented, alleviating some stress brought on by the ever changing climate (Rahel, Bierwagen, & Taniguchi, 2008).

1.2 Climate change and the Arctic and Sub-Arctic ecosystems

The Arctic covers a significant area of the Northern Hemisphere, including high-, low-, and sub-Arctic areas, which have a number of distinct features in terms of climate and geology (Reist *et al.*, 2006a). Arctic climate is extreme; for example, daylight extremes are characterized by continuous sunlight in summer months, and prolonged darkness in winter months (Wrona, *et al.*, 2006).

Freshwater sources vary in the Arctic, but originate mostly from rainfall in southerly lands during the summer, and winter snowfall at northern latitudes. Precipitation is the most important input of fresh water into Arctic aquatic ecosystems, where the annual spring melt can contain a majority of the total annual flow in a fairly short period of time. Maritime locations generally receive greater quantities of snow and rain than continental regions and during the summer months, *i.e.* via groundwater discharge, thawing permafrost, glaciers, and late or perennial snow patches. As temperatures increase due to climate change, these seasonal freshwater inputs may become more significant contributors to the overall annual water budget of Arctic ecosystems (Prowse *et al.*, 2006).

Faunal and floral species have adapted to survive in the extreme conditions present in Arctic and sub-Arctic habitats. These habitats are characterised by a relatively short growing season and limited species diversity in comparison to other regions of the world (Hassol, 2004). Due to the harsh conditions, many Arctic and sub-Arctic species have become resilient to current fluctuations in temperature but if such fluctuations

become magnified, resulting in a decrease in available habitat, these Arctic and sub-Arctic species may become more vulnerable to climate change (Prowse *et al.*, 2006).

In the past two decades, the average air temperature has increased almost twice as fast in the Arctic, compared to the rest of the world (Hassol, 2004). Although climate varies due to natural causes, the strength of these changes has been influenced by anthropogenic activities in the last decade. Climate change is taking place within the context of other ecosystem changes resulting from pollution, overfishing and habitat alteration, which increases overall concurrent pressure on these ecosystems. Combined threats overwhelm the adaptive capacity of these Arctic and sub-Arctic ecosystems (Prowse *et al.*, 2006). Apparent changes, such as rising permafrost temperatures, the melting of glaciers, and limited sea ice in the winter are some of the strongest and most significant indicators of global warming due to climate change (Hassol, 2004).

Climate change has a particular impact on the freshwater ecosystems in the Arctic. The two different freshwater ecosystems present in the Arctic; lentic (*i.e.* lakes, ponds, wetlands) and lotic (*i.e.* streams, rivers and estuaries), demonstrate diverse physical and chemical characteristics (Prowse *et al.*, 2006). The Arctic has numerous permanent and semi-permanent streams and rivers that drain from mountains, glaciated areas, highlands and some of the largest rivers in the world (Wrona *et al.*, 2006). Within these Arctic systems, productivity tends to be lower than in freshwater systems of temperate latitudes. Low temperatures and low levels of nutrient inputs of Arctic systems result in slower growth and longer-lived organisms (Prowse *et al.*, 2006). Some species, specifically in fish, will display migratory behaviour that can be triggered by environmental cues, such as a drastic decrease in temperature. Such behavioural changes are interpreted as adaptation strategies to cope with severe conditions.

Freshwater fishes within the Arctic are considered a key part of the ecosystem and are of great social and economic significance to local human populations (Reist *et al.*, 2006a). There are approximately 99 species in 48 genera of freshwater and diadromous Arctic fishes (Reist *et al.*, 2006a; Wrona *et al.*, 2006). This number of species may be conservative, where some species contain complexes of incompletely resolved species or are represented by local polymorphic forms that may act as a

species biologically (Reist *et al.*, 2006a). For example, there are four distinct morphs of Arctic char in Thingvallavatn, Iceland (Sandlund *et al.*, 1992). Each morph displays significant morphological and behavioural specialization, which may be a result of the discreteness habitats and available resources in the lake and possibly enhanced by paucity of interspecific competing fish species in Iceland (Skulason & Smith, 1995). Salmonidae is the most species rich family within the Arctic with over 33 species, where the majority is important to the food fisheries for northern people and economically to the national commercial fisheries. Cyprinidae is the second species-rich family with 23 species, but are not as important economically. This family is only being fished on a local scale, with the remaining families having significantly less species diversity and a much lower economic value (Reist *et al.*, 2006a). Some studies suggest that climate change will affect these freshwater fish species the greatest, especially the anadromous fish that inhabit the freshwater ecosystems but rely on marine and estuarine habitats as well. Climatic changes can influence their migration routes and timing and success of other key life functions (Reist *et al.*, 2006a). Their ability to migrate may cause them to be greatly affected by climate change as they traverse different habitats, and because they are not in one stationary location predicting and monitoring these fish becomes much more difficult (Reist *et al.*, 2006a; Prowse *et al.*, 2006). The Intergovernmental Panel on Climate Change (IPCC) has determined that freshwater fish found primarily in river and stream systems are on the limits of their geographical distributions (such as Arctic and sub-Arctic species), and will be the first groups of fishes to react to the effects of climate change (Arnell *et al.*, 2010; Reist *et al.*, 2006a).

Freshwater fish and other Arctic biota will experience direct and indirect effects of climate change. The combination of these changes with increased pressure from other anthropogenic impacts will blend together, effecting how fish will react (Reist *et al.*, 2006a). Biological changes in organisms may include faster temperature-driven growth and a lower maturation age, an expansion of available of habitat for invasive species, and reductions in winter mortality (Reist *et al.*, 2006a). These changes will benefit some of the sub-Arctic species, by creating a higher over-wintering survival rate, a bigger range of habitat, and an increase in productivity in some areas. However, these changes will most likely harm the true northern, or Holarctic, species, including

Arctic char (*Salvelinus alpinus*), by increased competition from more southerly species that extend in to the northward habitats (Reist *et al.*, 2006b).

In general, although scientists are able to make predictions on how Arctic freshwater fish and ecosystems will respond to climate change, it is almost impossible to project exactly what is going to happen since our understanding of such systems is so elementary (Reist *et al.*, 2006a).

1.3 Climate change and salmonids

Freshwater fishes, particularly salmonids, are hypothesized to be the main group of fish affected by climate change (Jonsson & Jonsson, 2009). Salmonids are present over a large range of habitats; some migrate between habitats while others are residential to a particular area. Due to this, many salmonids have developed life strategies that are somewhat unique to the habitat in which they have settled, making them more vulnerable to any changes to these habitats (Bryant, 2009). In particular, freshwater fish may be vulnerable to direct impacts of changing climate, including changes in temperature, and precipitation levels. Potential indirect impacts of climate change affecting salmonids include shifts in geographical species distribution (Rahel & Olden, 2008), decreased dissolved oxygen concentrations (Ficke, Myrick, & Hensen, 2007), modification of surface currents and zooplankton distribution due to changing wind patterns (Mangel, 1993), reduced stream flow, vegetation changes, and reduced shading (Eaton & Scheller, 1996). Jonsson and Jonsson (2009) suggest the change in temperature could be more noticeable over land than the ocean, which in turn would create greater changes in freshwater than in marine habitats. Inland freshwater habitats may experience droughts, where coastal regions may receive higher amounts of precipitation (Bryant, 2009). Additionally, the intensity of rainfall could bring changes in winter snow packs and the spring-time melt. Such climatic factors, namely temperature and hydrology, play a vital role in the development of salmonid stocks and control multiple important life-cycle stages (Bryant, 2009). Changes in temperature are the biggest threat to salmonids as many are geographically isolated, while thermal limits are species specific (Jonsson & Jonsson, 2009). As a result, two

types of thermal shifts, to which populations of freshwater fish have to respond, can occur; geographical shifts and temporal shifts in seasonal temperature profiles (Jeppensen *et al.*, 2012). A study based on streams located in the United States predicted a 50 percent loss of cool- and cold-water-fish thermal habitat and up to a 14.2 percent loss of warm-water-fish thermal habitat. The decrease in warm-water-fish thermal habitat was less expected and could be explained because warm water fish located in the lower end of their thermal tolerance are very similar to many cool water species, making them similarly sensitive to climate warming (Eaton & Schellor, 1996; Bryant, 2009). The success rate of these fish depended on the percentage of habitat loss, their exposure to climatic anthropogenic stressors, including the introduction of an invasive species (Bryant, 2009).

Additionally, due to the ectothermic nature of freshwater fish, their physiology is linked to their surrounding temperature. Previous papers (Hasnain, Minns, & Shuter, 2010; Pörtner & Peck, 2010) suggest that many fish (particularly salmonids) have adapted to a specific temperature range that maximizes performance. Many freshwater fish have not only upper and lower temperature boundaries in which they can survive, they also have optimal growth and preferred temperatures, which are both normally located closer to the upper limit of the boundary (Larsson *et al.*, 2005; Hasnain, Minns, & Shuter, 2010; Pörtner & Peck, 2010). Many salmonids have evolved to grow, interact, and thrive in specific habitat niches and hydrology regimes, where temperature changes can serve as an ecological timer that will initiate behavioural reactions, such as migrations to different habitats (Ficke *et al.*, 2007; Jonsson & Jonsson, 2009). This means an initial increase in temperature may initially optimize salmonid growth and activity, but as temperature continues to rise, the threshold of optimal temperature will be surpassed, and the fish will eventually be constrained by the limited amount of oxygen in the water (Jonsson & Jonsson, 2009).

Although disadvantages still exist, warm-water salmonids will benefit the most from climate change. These fish may have a much wider distribution due to range expansion, where many have the ability to tolerate higher temperatures, unlike cold-water species (Eaton & Scheller, 1996). Many cool- and cold-water species have developed behavioural and physiological strategies that have been shaped by the extreme conditions of some freshwater habitats, especially during the winter months.

Warming brought on by climate change will have a significant impact on these specialized species during warmer and longer summers paired with potentially shorter winters (Shuter *et al.*, 2012; Pörtner and Peck, 2010). The impact on community structures could isolate or eliminate cold-water salmonids altogether (Bryant, 2009). Changes in fish communities and range shifts will occur, where effects are anticipated to be intensified for species with the smallest initial distribution, as they will lose the greatest percentage of habitat (Eaton & Scheller, 1996). Genetic change could also occur, being the only biological option for fishes unable to migrate or acclimate (Ficke, Myrick, & Hensen, 2007).

It is important to understand how climate change could alter these important freshwater ecosystems. In this study we are looking more closely at one of the main factors affecting climate change, which is temperature. I did this by looking at how water temperature affected behaviour of young-of-the-year Arctic char in a stream located in the north of Iceland. More specifically, I examined how temperature may affect foraging activity, foraging rate and foraging mode. Studying temperature and foraging mode should help produce a more complete understanding of how animals, particularly freshwater salmonids respond to the different ecological conditions, particularly an exposure to higher than average temperatures. This is important because although freshwater salmonids are ectotherms, they may have the ability to adapt to environmental changes, such as altered temperatures, through a variety of responses (Larsson *et al.*, 2005).

2 Theoretical overview

2.1 Iceland

Iceland is located in the middle of the North Atlantic Ocean between 63° 23' and 66° 32' N (Jóhannesson, *et al.*, 2007). The country covers an area of 103,100 km² of which glaciers are almost 11% (Jóhannesson, *et al.*, 2007), and is characterized as a mountainous island of volcanic origin located between warm and cold ocean currents (Ólafsson, Furger, & Brümmer, 2007). The Irminger current is the warm current that encircles much of the island once it branches off from the Gulf Stream. The East Greenland and East Icelandic currents are cooler currents coming from the Arctic. These oceanographic conditions directly influence climate on the country's coasts and inland, through the air masses that arrive in Iceland, after passing over the sea (Einarsson, 1984). Although Iceland is considered to be a sub-arctic ecosystem, factors such as ocean currents, sea surface temperature, sea ice, precipitation, and air temperature create a relatively mild climate throughout the country (Jóhannesson *et al.*, 2007). Iceland's climate is characterized as maritime, where winds speeds often vary from less than 5 m/s to over than 25 m/s. The mean daily air temperature in Iceland ranges from approximately 0 °C in the winter to 10 °C in the summer (Ólafsson, Furger, & Brümmer, 2007). The air temperature is considerably lower in the northern part of the country, as it is more affected by Atlantic, Polar, and Arctic waters, whereas the southern part of Iceland is exposed mostly to relatively warm Atlantic waters (Jóhannesson, *et al.*, 2007).

2.1.1 Rivers in Iceland: classification and characteristics

Icelandic lakes and rivers cover approximately 2,300 km², making up roughly 2.2% of the total area of the island (Gíslason, Ólafsson, & Aðalsteinsson, 1998), and share many similarities in physical characteristics and biota with the Arctic and alpine regions of northern Norway (Gíslason, Ólafsson, & Aðalsteinsson, 2002). There are three different types of rivers present in Iceland, categorized by origin: glacier rivers, run-off rivers, and spring-fed rivers (Jóhannesson *et al.*, 2007). Glacier rivers are derived from glacier melt-water, and thus show great annual and diurnal fluctuations. Run-off rivers are derived from water that accumulates on the lands surface (*i.e.*

rainwater and meltwater) (Ólafsson, Gíslason, Aðalsteinsson, 2002). Spring-fed rivers can be classified into those that flow directly from the spring to the sea and those flowing through a lake (Gíslason, 1994). The chemical composition of the water within Iceland's rivers is influenced by the catchment areas, but also by the percolation time and the temperature of the water. The isolation of the island, its relatively young bedrock and recent de-glaciation has shaped the freshwater flora and fauna. The presence of lakes, vegetation cover, and catchment basins also influence the animal communities and overall productivity of these rivers (Gíslason, Ólafsson, & Aðalsteinsson, 1998).

Glacial rivers have the greatest amount of discharge of all river types and are dominated by glacial ice-melt (Gíslason, Ólafsson, & Aðalsteinsson, 1998). This is most prominent during the summer with extensive sediment transport, where large quantities of sand and silt are deposited on the river bed (Gíslason, 1994). Glacial rivers have unstable bottom substrate with coarse silt eroding the bottom, limiting algal growth and production (Gíslason, Ólafsson, & Aðalsteinsson, 1998). Other characteristics of glacial rivers include great annual and diurnal fluctuations in temperature and low pH, conductivity, and biodiversity (Ólafsson, Gíslason, & Aðalsteinsson, 2002).

The non-glacier-fed rivers consist of run-off rivers and spring-fed rivers. Both river types are generally clear all year round, but may turn brown with silt during floods (Gíslason, 1994). Run-off rivers in Iceland constitute networks of small tributaries, and dominate the older rock formations outside the volcanic active zone (Gíslason, 1994). Discharge can fluctuate considerably with daily precipitation, but averaged over longer periods it is generally greatest during the spring and lowest during frost-periods in winters and or during dry summers (Gíslason, Ólafsson, & Aðalsteinsson, 1998). The substrate is usually unstable and productivity is associated with the steepness, topography and length of the area through which the water flows. Normally, the fluctuating nutrient discharge results in relatively unproductive rivers (Gíslason, 1994). However, productivity can vary, from short rivers with little influence from lakes or wetlands, to rivers that originate from well vegetated wetland plateaus and are buffered by ponds and lakes, causing them to have medium fluctuations in discharge and

temperature but relatively high conductivity and biodiversity (Ólafsson, Gíslason, & Aðalsteinsson, 2002).

Spring-fed rivers are most common in relatively young geographical areas with permeable bedrock formations along the volcanic belt extending from the Southwest to the Northeast of Iceland (Guðbergsson & Antonsson, 1996). Compared to glacial and direct-run-off rivers, the water discharge is relatively even, with little seasonal fluctuation, where floods rarely occur. These rivers remain open all year, except when there is severe frost. Once the temperature approaches 0 °C, the ice will once again disappear. Productivity in rivers that flow through lakes can be much higher than in rivers that flow directly to the sea. This is related to the biological production of the lake which in turn depends a lot on the retention time in the lake. Springfed rivers that flow directly to the sea often demonstrate similar productivity levels to that of run-off rivers (Gíslason, 1994). Although similar to many Nordic streams, they differ in that the spring-fed rivers from spring-fed lakes in the volcanic zone of Iceland are much higher in productivity (Gíslason, 1994) and when comparing freshwater biota to other Nordic countries, Iceland showed a much lower species diversity (Gíslason, Ólafsson, & Aðalsteinsson, 1998). Generally speaking, spring-fed rivers in Iceland demonstrate high biodiversity, pH, and conductivity (Ólafsson, Gíslason, & Aðalsteinsson, 2002).

2.1.2 Climate change and Iceland

Within the last several decades there has been significant warming in Iceland, which can potentially be attributed to climate change. From 1975-2008, air temperatures in Iceland increased by about 1.2 °C, which is approximately 0.35 °C per decade. This increase is about 0.2 degrees above the average global trend, illustrating how vulnerable this sub-Arctic country is to global warming (Björnsson & Gíslason, 2010). Sea ice used to be common in the vicinity of Iceland but has been rare in the last few decades (Jónsdóttir, 2012).

Recent models in climatology suggest that within Iceland, air temperatures may rise between 1.4 and 2.5 °C in the 21st century (Björnsson & Gíslason, 2010). Precipitation is also anticipated to increase by 0.4 to 0.8 percent per decade. The winter is predicted to be warmer with less snow and warmer summers will become more common (Jónsdóttir, 2012). It is also predicted that there will be an early onset of melting in

spring which can cause changes in glacier and run-off rivers, in particular (Björnsson & Gíslason, 2010). Recently, the Marine Institute of Iceland conducted a study demonstrating a considerable rise in summer 2012 sea surface temperatures, compared to the last 20-year average for the northern part of the Icelandic and Greenland waters, whereas some areas demonstrated an increase of up to 3 °C (Nottestand *et al.*, 2012).

Short-term negative impacts of climate change have not been sufficiently predicted for Iceland. In fact, rising air temperatures will most likely be immediately favourable for industries such as agriculture and fishing. In the agriculture industry, productivity of plants and grains will likely increase, and changes in sea temperatures will allow for some marine species to expand or shift in range (Jónsdóttir, 2012). Twenty-six new fish species have been found in Icelandic seawaters in recent years (Björnsson & Gíslason, 2010). For example, the Atlantic mackerel has expanded to Icelandic waters, where warming of the ocean has likely played a substantial role, resulting in new opportunity within the fishing industry and at least a temporary financial benefit for the nation (Björnsson & Gíslason, 2010; Nottenstand *et al.*, 2012).

The future of fisheries is uncertain and the effects of climate change may not be all positive. Although warming may lead to greater productivity in some fishing sectors, the ability of stocks to thrive may be ceased by increased ocean acidification (Jónsdóttir, 2012). Seabird stocks, for example, are speculated to be in decline due to ecosystem changes which have caused a decrease in their abundance of prey, the recent appearance of the Atlantic Mackerel is believed to have contributed to the collapse of the sand eel; an important food source for many seabird species (Jónsdóttir, 2012). Due to the milder winters and warmer summers, there also seems to be a northerly range shift of birds (Parmeson, 2006; Björnsson & Gíslason, 2010; Jónsdóttir, 2012). Most of the glaciers in Iceland are gradually melting and some are even expected to almost, if not completely, disappear during the next 100-200 years (Björnsson & Gíslason, 2010; Jónsdóttir, 2012). These range shifts will also be confounded by additional global issues such as sea level rise and the vertical stratification in the upper layer of the Arctic Ocean (Björnsson & Gíslason, 2010).

Icelandic rivers are likely already being altered considerably due to the above discussed effects of climate change. Such alterations are putting extra stress on these

ecosystems and are further exacerbated by anthropologic activities that likely began shortly after the first settlement in the 9th century. Such activities include: the development of roads, bridges and mining; changes in vegetation cover of catchments, and soil erosion due to overgrazing; draining of lakes, ponds, and wetlands for farmland; development of hydroelectricity through diverting rivers between catchment, and changing water-flow regimes; and perhaps by the the introduction of invasive, wild or farmed, populations of fish (Ólafsson, Gíslason, & Aðalsteinsson, 2002).

2.2 Arctic char

Arctic char is the most northern of all freshwater fishes, and has a wide distribution range throughout the northern hemisphere. Arctic char is the only species with a circumpolar distribution in both anadromous and freshwater forms, and are establish throughout the Arctic, sub-Arctic, boreal, and temperate areas of the Holarctic (Parker & Johnson, 1991; Klemetsen *et al.*, 2003; Heggenes & Saltveit, 2007; Ulvan *et al.*, 2012). Arctic char are found in inshore marine waters, lakes, and rivers. There are an estimated 50,000 populations throughout the world, most of which are found in Scandinavia, with approximately 30,000 populations in Norway, 13,000 in Sweden, 3,500 in Canada, and about 1,000 in Russia, Greenland, and Iceland combined (Klemetsen *et al.*, 2003). The high number of populations reflects how efficient this species has been in adapting to new areas and local environments. This diversity is an important aspect to keep in mind when managing specific Arctic char populations (Ulvan *et al.*, 2012). Arctic char is an important species for many indigenous peoples of the north and has become an important commercial fishery in Canada. Furthermore, Arctic char has aquaculture potential in many countries including Norway, Canada, and Iceland (Klemetsen *et al.*, 2003).

2.2.1 Arctic char ecology

Arctic char are described as trout-like with a somewhat rounded body, a large mouth, small cycloid scales, and a slightly forked caudal fin (Frost, 2001). Arctic char is possibly the most colourful of all the northern fishes. Colouration can vary between populations and can depend on environmental conditions, fat content, and fish growth. Both sexes can have strong colours that range from white/silvery to orange, yellow,

and red throughout the year. Males and females may become brightly coloured when spawning, though males are often more ornamented, whereas non-breeding individuals are usually pale and non-descript (Frost, 2001; Klemetsen *et al.*, 2003). Arctic char are opportunistic feeders that eat a variety of organisms, including both vertebrates and invertebrates (McCart, 1980). They are visual feeders and undergo seasonal and diel fluctuation in feeding activity. During the spring, summer, and autumn, Arctic char will feed primarily during the day, with peaks in activity presumably around dusk and dawn (Alanara & Brannas, 1997; Bjornsson 2001); this pattern, however, changes during the winter months when Arctic char may become nocturnal. Alanara and Brannas (1997) state that this could be a result of a seasonal shift in the density of prey, as well as a form of protection from predators. In many northern temperate areas, the drift activity of insects is mostly nocturnal, and the colder temperatures during the winter make the fish less responsive (Alanara & Brannas, 1997). The optimum temperature for growth of parr and adult char ranges around 11-14 °C. Although they can feed and grow at temperatures as low as 3 degrees Celsius, growth is gradually restricted outside the preferred temperature range (Langeland *et al.*, 1991; Finstad & Hein, 2012). Arctic char can also exhibit great variability in life history and show a high degree of morphological variability. Such differences are greatly influenced by niche shifts and large variation in habitat use, feeding behaviour and other ecological traits and, as a result, can induce differences in growth rates as well as age and size at sexual maturation between populations (Reimer, 1986; Klemetsen *et al.*, 2003). Arctic char also have the largest size variation among adult fish of any other species of fish, where mature fish can range from 3 grams to more than 12 kilograms (Klemetsen *et al.*, 2003).

There are both anadromous and non-anadromous forms of Arctic char. About 13,000 populations of Arctic char are considered anadromous (Klemetsen *et al.*, 2003). During the spring, once the anadromous form reaches smolt stage, these fish migrate to the sea to feed. Arctic char can spend up to two months in coastal areas, and then return to the same freshwater lake (or stream) to avoid the sub-zero temperatures of the ocean in the winter (Reimer, 1986; Parker & Johnson, 1991; Finstad & Hein, 2012). Non-anadromous Arctic char are called “resident” and will stay in freshwater throughout their entire life. Some northern populations live in rivers and streams, but the typical environment of landlocked char are lakes (Klemetsen *et al.*, 2003).

Freshwater forms tend to be smaller than the anadromous Arctic char due to higher levels of competition and limited resources (McCart, 1980). The proportion of migratory individuals in lake populations can be quite variable and depend heavily on the physical characteristics of the migratory route and environmental conditions (Finstad & Hein, 2012). Char tend to spawn in September or October and often choose shallow, rocky or gravel substrates in lakes or in pools within rivers and streams (Frost, 2001).

In Iceland, Arctic char tend to inhabit slow-running sections of relatively cold and unproductive rivers; brown trout are usually found in intermediate conditions, whereas Atlantic salmon inhabit relatively fast-running waters of warmer, more productive streams (Tunney & Steingrímsson, 2012). Non-anadromous Arctic char are the only freshwater fish species found in the high Arctic, because it is the only species capable of surviving such rigorous environmental conditions (Parker & Johnson, 1991). Studies suggest that the capacity of Arctic charr to adapt to such extreme conditions of northern waters is partly due to their generalist and opportunistic characteristics; their ability to exploit many diverse habitats and diets (Parker & Johnson, 1991; Heggenes & Saltveit, 2007).

2.2.2 Arctic char in Iceland

Arctic char are often an important component of fish communities in lakes through their Holarctic range. Within Iceland, in particular, they are one of only three native salmonids that exist in freshwater systems (Tunney & Steingrímsson, 2012). Moreover, Arctic charr are found as several different morphs, taking advantage of different ecological niches (Winfield, Fletcher, & James, 2008). For example, in Iceland, there are four different morphs of Arctic char present in Lake Thingvallavatn (Sandlund *et al.*, 1992). Arctic char often coexist with brown trout and Atlantic salmon in many streams, rivers, and lakes, by utilizing the colder uppermost parts of these habitats (Heggenes & Saltveit, 2007).

2.2.3 Effect of climate change on Arctic char

Although Arctic char have the ability to adapt to various environmental conditions, they are still likely candidates to be affected by climate change. Due to the temperature

requirements of this species, there is concern that warming due to climate change will cause negative impacts on local populations (Winfield *et al.*, 2010). For example, migration patterns of anadromous Arctic char may be affected by climate change. Finstad and Hein (2012) state that migratory behaviour in char is likely influenced by freshwater productivity, i.e. the lower the productivity, the more likely char will benefit from migration. Climate change is predicted to initially increase productivity of boreal and subarctic lakes, therefore decreasing the net benefit of migration. There have already been examples of climate change affecting char populations. In particular, a review of the status of this species within the United Kingdom showed that at least 12 out of 258 populations of Arctic char in Scotland, four of 12 native populations in England, and one of three native populations in Wales is now extinct (Maitland *et al.*, 2007). Many anthropogenic factors, including pollution, acidification, aquaculture, and exploitation, were named along with climate change as probable factors that have led to these extinctions (Winfield, Fletcher, & James, 2008).

It is difficult to accurately predict how climate change will impact this species in the future due to the lack of long-term data (Finstad & Hein 2012), however, gaining a better understanding of how changes in climate and temperature will affect Arctic char will help to gradually fill these gaps and answer important questions regarding the future of this species.

2.3 Temperature

In order to better understand the effects climate change will have on species, particularly salmonids, it is useful to study individual behavioural traits in relation to environmental variables. Temperature is an important ecological factor that plays a key role in determining the distribution of aquatic organisms. Temperature increase due to climate change will result in both biological and abiotic changes, influencing numerous species of freshwater fish. Understanding this influence is of particular importance for many key Arctic fish species due to the lack of basic knowledge available regarding the role temperature plays on these species (Rahel, Biernagen, & Tanguchi, 2008).

Organisms often live within a narrow range of temperatures, limiting the geographical distribution of many species (Farrel, 2009; Jonsson & Jonsson, 2009; Finstad *et al.*, 2011). Temperature is a key characteristic of the habitat of an organism, but can also be viewed as a factor that will affect individual physiological and behavioral processes (Reist *et al.*, 2006b). Altered thermal regimes may influence the outcome of competitive interactions among species (Rahel & Olden, 2008). Overall fitness and survival of non-native species may also be influenced, either negatively or positively, by altered thermal regimes. Invasions of non-native species could present unfamiliar resource competition with native species, increase the introduction of invasive parasites, and influence predator-prey relationships, *i.e.* through an increase in consumption of native prey by non-native predators (Rahel, Biernagen, & Tanguchi, 2008; Rahel & Olden, 2008).

Relatively consistent water temperatures are important for ectothermic animals, as they rely on external sources of heat, rather than metabolic process, to maintain an optimal body temperature, effecting rates of biochemical reactions. Temperature can influence characteristics such as rates of growth, development and associated traits, and trigger behavioural reactions such as marine migrations of anadromous fishes (Jonsson & Jonsson, 2009; Finstand & Hein, 2012; Spares *et al.*, 2012). Ectothermal animals are only able to survive in a range of temperatures and will spend the majority of their lives in a temperature at which physiological processes function optimally. This temperature is referred to as the preferred temperature, where the relatively narrow range of temperatures in which the species inhabits is called its thermal niche (Larsson, 2001; Reist *et al.*, 2006b).

Fish can be classified into a thermal guild based on the level of temperature they can tolerate; warmwater species' ideal temperature is > 28 degrees Celcius, coolwater species' is between 20 and 28 degrees Celcius, and coldwater species' is < 20 °C (Rahel & Olden, 2008). Thermal limits for salmonids are species-specific, where fish may adjust to altered temperature conditions through a variety of reactions before reaching their lethal thermal limit. If individuals are outside of their lower and upper limit of temperature, the fish will eventually die (Larsson, 2001; Larsson *et al.*, 2005; Jonsson & Jonsson, 2009). Fish are highly dependent on water temperature for maintaining physiological and life history processes, through its effects on growth rate,

digestion, muscle efficiency, reproduction, and food intake (Larsson, 2001; Larsson *et al.*, 2005; Reist *et al.*, 2006b; Handeland, Imsland, & Stefansson, 2008; Hasnain, Minns, & Shuter, 2010). Indirectly, through its effects on growth, temperature can eventually influence age and size at smolting and sexual maturation in salmonids (Jonsson & Jonsson, 2009).

2.3.1 Temperature and Salmonid Behaviour

Temperature is one of the most influential abiotic factors affecting stream living fishes and can have a substantial effect on their behaviour and choice of habitat (Heggenes *et al.*, 1993). Within this study, we looked at how temperature can influence a number of behavioural traits, including fish activity, foraging rate, and foraging mode.

2.3.2 Feeding activity

Levels of feeding activity relate to when and how often an individual is active within its habitat, a pattern which can be affected by numerous ecological variables. The overall level of activity in fish has obvious consequences at an individual and population level, because it may affect an individual's food intake and growth, as well as its survival when faced with risk of predation (Jonsson & Jonsson, 2009; Hedger *et al.*, 2012).

Most fish are active throughout a range of temperatures, although their overall level of activity is influenced by water temperature. For example, many fish are more active during high temperatures (Valdimarsson *et al.*, 1997; Larsson *et al.*, 2005), but if water temperature becomes too high and reaches levels that are close to lethal, activity may be reduced and stop all together (Sloat & Osterback, 2012). Additionally, seasonal changes in temperature can influence the diel activity of many salmonids. It has *i.e.*, been suggested that during late autumn and early winter, lower water temperatures trigger a change in activity from primarily diurnal to nocturnal (Heggenes *et al.*, 1993; Fraser *et al.*, 1995). It is thought that activity should increase with temperature since higher metabolic rates are linked to higher temperatures; this requires the fish to feed more, therefore increasing their overall level of activity (Larsson *et al.*, 2005).

2.3.3 Foraging rate

Foraging is the process by which organisms obtain nutrients and energy by feeding (Kramer, 2001). In stream salmonids, and freshwater fish in general, water temperature is likely to be a key determinant of foraging rate. The rate at which ectothermal animals forage is an important component of the foraging behaviour and has obvious consequences in terms of growth and it is thought that higher water temperatures should increase the amount salmonids have to forage due to an increase in metabolic demands (Larsson *et al.*, 2005). Hence, at higher water temperatures, young-of-the-year salmonids should increase their foraging rates in order to meet their metabolic demands. Foraging rate is also expected to be affected by other ecological variables, including drift density, current velocity, and light intensity.

2.3.4 Foraging mode

Animals, including stream salmonids, may exhibit a wide range in foraging modes, *i.e.* the way organisms search for, attack and ingest their prey. In short, predators are often characterized as mobile or sedentary foragers (Huey & Pianka, 1981; Grant & Noakes, 1987). Sedentary predators remain relatively immobile and will only move short distances to attack prey that move into their field-of-view, whereas mobile foragers will move longer distances, searching for their prey over a larger area (Huey & Pianka, 1981; Grant & Noakes, 1987; Killen, Brown, & Gamperl, 2007).

An animal's growth and fitness, as well as the ability for similar species to coexistence through habitat segregation and resource division, are all influenced by foraging mode (Nakano, Fausch, & Kitano, 1999; Tunney & Steingrímsson, 2012). Due to their variable foraging behaviours, young salmonids in streams present a good opportunity to study how foraging behaviour may change in reaction to shifting ecological conditions, *e.g.*, via changes in water temperature. To date, foraging mode (mobility) of salmonids has mostly been related to ecological variables, such as water current velocity and prey availability but rarely to water temperature. Salmonids are known to become sedentary predators in faster, more productive waters to conserve energy. The reason is due to the fact that food is brought to them with the current, making it unnecessary to spend energy via increased mobility or to search for prey over a wider area. (Grant & Noakes, 1897; McLaughlin, Grant, & Kramer, 1992; Nakano, Fausch, & Kitano, 1999; Killen, Brown, & Gamperl, 2007). Water

temperature, however, may be associated with foraging mobility both directly and indirectly. More specifically, salmonids may, at lower temperatures, switch from mobile foraging to sedentary foraging to conserve energy, because mobile foraging is energetically more costly at cold temperatures (Frasier *et al.*, 1995). I also expect that foraging mode will be affected by other ecological variables, including Julian date, light intensity, water current velocity, and drift density.

2.4 Goals of this Study

The aim of this study is to identify, via direct behavioural observations, how fish deal with water temperature changes at a local scale. To achieve this, young-of-the-year (YOY) Arctic char were observed in a single stream in Northern Iceland. The reason why I focused on juvenile salmonids and water temperature in particular was because I felt that understanding temperature tolerance in freshwater fish, particularly in a cold water salmonid like Arctic char, may increase our knowledge of how animals may react and potentially adapt to environmental change.

The questions addressed in this study include:

- Will rising water temperatures affect the density of actively feeding Arctic char?
- Will the amount of foraging attempts per time unit increase with temperature?
- Does foraging mode (*i.e.* mobility) change with changing water temperature?

Predictions:

First, I hypothesis that there will be a positive correlation between feeding activity of Arctic char and water temperature, *i.e.*, as water temperatures increase so will overall activity. Secondly, I predict that Arctic char will forage at a faster rate at higher water temperatures than fish found at lower temperatures. Finally I predict that water temperature will influence foraging mobility and that foraging mobility of the Arctic char will decrease as temperature and light levels decrease. I tested the above temperature related predictions, while, when possible, measuring and estimating other habitat variables that may affect these behaviours, such as light levels, water current velocity, water depth, the coarsness of the bottom substrate (*i.e.*, substrate size) and the density of invertebrate prey.

3 Materials and Methods

3.1 Study area and study population

A wild population of Arctic char was studied in stream Myllulækur, in the northwest of Iceland (Figure 1). The stream is lake-fed by a small, shallow lake named Vatnshlíðarvatn, and is highly productive, both in terms of invertebrates and fish, resulting in a very high density of young-of-the-year (YOY) Arctic char. This stream is also ideal for studying the effect of water temperature on fish behaviour because it shows a great range in water temperature and can get very warm following extended periods of favourable weather conditions. The abundance of YOY Arctic char in the lake and stream may be due to high productivity and the noticeable absence of the threespine stickleback (*Gasterosteus aculeatus*), a common fish competitor in similar lakes in Iceland (Jónsson & Skúlason, 2000). Vatnshlíðarvatn has a number of streams feeding into it, whereas Myllulækur is the only outlet. Like many Arctic lakes, Vatnshlíðarvatn only contains one fish species, Arctic char; however there are two specific forms of char, the brown form and the silver form (Jónsson & Skúlason, 2000). Jónsson and Skúlason (2000) observed that unlike the brown form; which is residential to the lake, the silver form display remnants of smolt transformation and migration, explaining why during the fall, many adults from the lake migrate to stream Myllulækur and spawn there. Thus, this relatively simple stream system provides an interesting natural setting for behavioural observations of Arctic char. All observations were done in a study area extending about 760m downstream from the lake outlet (Figure 1.0).

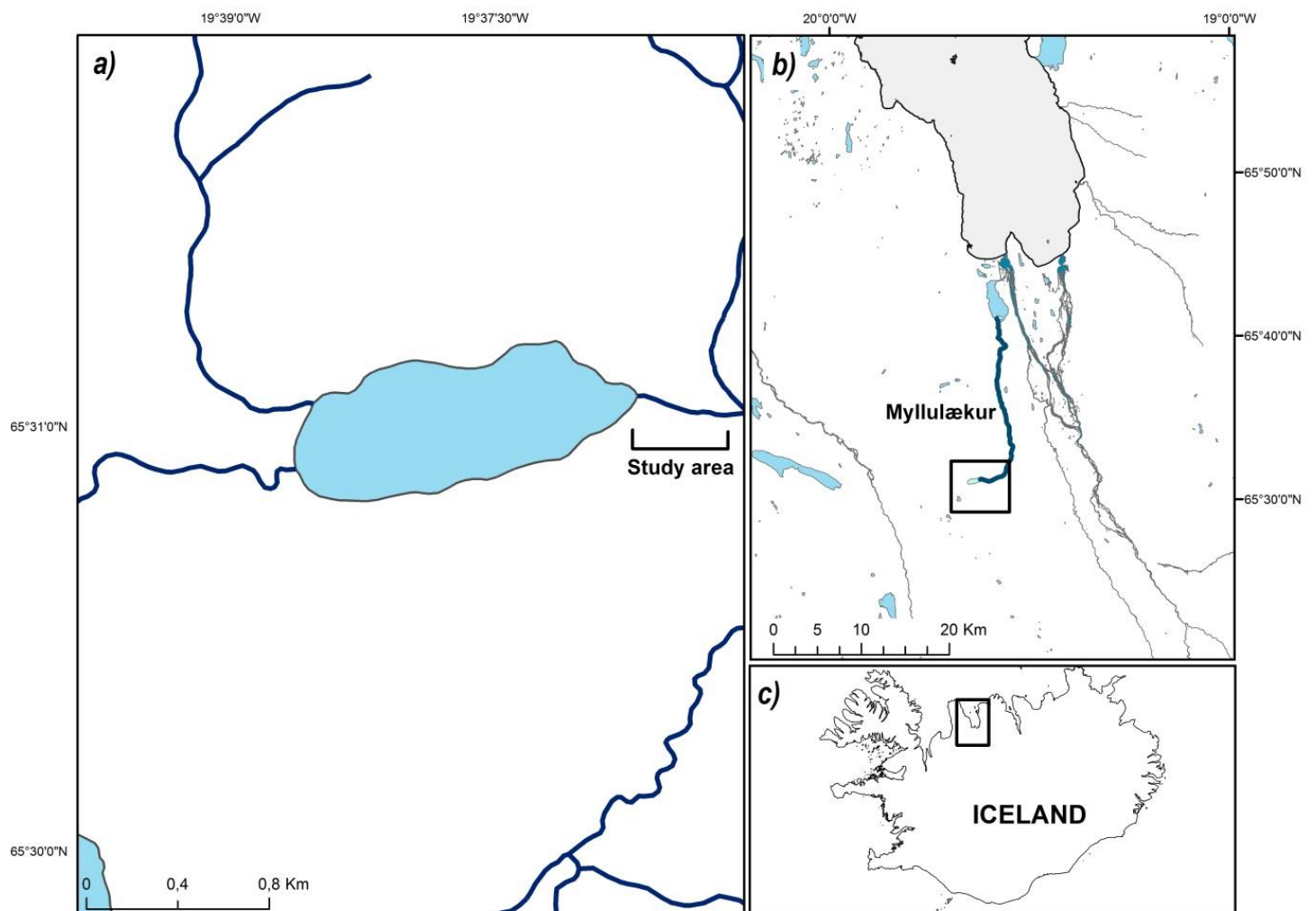


Figure 1.0 The study area within the stream Myllulækur a), the location of the study stream in Skagafjörður, Northern Iceland b) and the location of Skagafjörður within Iceland

3.2 Observations of activity

The activity of young-of-the-year (YOY) Arctic char was observed in stream Myllulækur via snorkeling observations from 23 July to 27 August, 2012. The number of Arctic char was recorded in four different study sites, located serially along the length of the study area, in order to cover a good range of habitats (Figure 1.0). For three of the study sites fish were counted on an area of approximately 250 cm², whereas the fourth site was 1000 cm². Following each observation water temperature and light intensity were also recorded. Data collection was done as a team effort with Nicolas Larranga as the observer and Sarah J. Kennedy assisting him. The observer in dry suit would enter the water 1-2 m downstream and cautiously move towards the designated study site. The observer would then wait for five minutes to allow the fish to adjust to his presence. After the initial five minute period, activity was then observed for an additional five minutes by recording the number of active fish within the study site. A fish was considered active if it was seen within the study site swimming actively against the current and/or feeding during the five minute observational period. Observations were conducted at different times of the day (11:00, 13:00, 15:00, and 17:00) with seven observations in total per site. Prior to statistical analysis, the counts for the four sites were combined for each time interval in each of the seven surveys to give an overall value of activity (*i.e.* number of active young-of-the-year Arctic charr) across the four study sites at each time interval, resulting in a total of 28 observations.

3.3 Observation of foraging behaviour

Foraging behaviour of 40 YOY Arctic char was recorded in the study area either by observations from the stream bank or snorkeling. Observations were conducted in a time period spanning 12 days, from 14 – 26 August at different water depths and in fast and slow waters so that fish could be observed over a wide range in ecological conditions. The distribution of the focal fish along the length of the stream was not evenly spread across the whole study area, and more fish were observed in habitats where density was higher, but the probability of observing the same individual during

different observation periods was minimal due to the extremely high density of YOY char in the study area. The same fundamental protocol was used prior to all foraging observations irrespective of whether these were conducted from the stream bank or via snorkeling. A stream bank observer would approach the river cautiously and would situate themselves in a position that gave them a clear view of the stream. To find a focal fish, the stream bank observer would then scan the water for a foraging YOY Arctic char. Similar, during snorkeling, the observer would enter the water and gradually and slowly move upstream until a focal fish was detected. Once an actively foraging YOY char was found the observer lay motionless 1-2 m downstream, so as to not disturb the surrounding environment (Steingrímsson & Grant 2008; Tunney & Steingrímsson, 2012). For both methods, once a focal fish was detected, the observer would wait for five minutes before starting the observations, so that the fish would be accustomed to and not disturbed by his/her presence (Steingrímsson & Grant 2008). After the adjustment period, the fish was observed for five minutes and every foraging attempt made by the focal fish would be recorded on waterproof paper (See similar methods in Tunney & Steingrímsson 2012). If sight of the focal fish was lost during the observations and the fish did not return after a time period of 30 seconds, or if there was any doubt of its identity upon its reappearance the observation would be cancelled. Once the observation was finished the site was marked with a flag to avoid returning to the exact same site for observing another focal fish and then the habitat features were measured. Observations were all conducted during the day between 1,100 and 1,600 h by Sarah J. Kennedy (stream bank observations; 32 fish) and Nicolas Larranaga (snorkeling; eight fish).

The two main behavioural variables measured during the 5 minute observation intervals were (1) foraging rate and (2) mobility prior to prey attack. Foraging rate was estimated by observing the number of foraging attempts the focal fish would undertake in 5 minutes. A foraging attempt by the focal fish was defined as any rapid movement to catch a potential food item (Grant & Noakes, 1987; Tunney & Steingrímsson, 2012). McLaughlin, Grant, & Kramer (1992) defines foraging attempts as a foraging observation that includes prey inspection and missed attacks, meaning the attempt was not always successful. The decision to observe foraging rate using foraging attempts is based on the fact that in natural environments, capture and ingestion can be difficult to observe and the number of foraging attempts, is typically related to ingestion rate

(McLaughlin, Grant, & Noakes, 2000). Hence in this study foraging rate is measured as the number of foraging attempts initiated over a five minute period.

Mobility of the fish prior to initiating a foraging attempt was also measured during this observational period. This behaviour was measured by distinguishing foraging attempts into two separate categories, those initiated while fish were mobile and those initiated while fish were stationary. In short, attempts were classified as mobile if the fish moved continuously more than one body length before attacking its prey, but were considered stationary (*i.e.* sit-and-wait) if the fish had moved a body length or less immediately before the attack (Grant & Noakes, 1987; Gunnarsson & Steingrímsson 2011). Mobility prior to prey attack was calculated as the proportion of mobile forages by dividing the total amount of mobile forages by the total number of foraging attempts.

3.4 Habitat measurements

Immediately following each observation a variety of measurements were taken at the location of the focal fish; including water temperature, light intensity, water depth, water current velocity, substrate size, and food availability. Additional information about the weather conditions was also recorded. Water temperature was recorded to the nearest 0.1°C using a digital thermometer. Light intensity was measured using a digital lux tester that had a range of about 20 000 Lux (Beha 93-1065L Model). The light meter was held just above the water line, facing downwards to test for luminance, and then turned so it would be facing upwards, to test the illuminance; in this study we report luminance. Water depth was measured with a meter stick to the nearest centimeter. Water current velocity was measured at 40% depth from the bottom over three five second intervals using a current velocity meter (FLO-MATE model 2000, Marsh-McBirney Inc., Frederick, MD., USA). The substrate type where the focal fish was observed was scored using the modified Wentworth scale of grain size categories. The classification was as follows: 1: plant detritus and clay = <0.004 mm, 2: Silt and sand = <2.0 mm, 3: Gravel = 2 – 16 mm, 4: Pebble = 17 – 64 mm, 5: cobble = 65 – 256 mm, 6: bolder > 256 mm (see DeGraaf & Bain, 1986).

The abundance of potential food items drifting by the location of each focal fish was estimated using a 250 μm drift net with a net opening of 25 cm (depth) X 40 cm (width). The net was placed immediately upstream to the fish location and invertebrate drift was sampled for five minutes. The water depth at the drift net location was measured using a meter stick and the current velocity was measured at three locations across the drift net opening (left, middle and right) for five seconds. If the net was fully submerged, then the velocity was calculated at 50% of the drift net depth (*i.e.* at 12.5 cm of the total 25 cm depth of the drift net). When the net was only partly submerged the current velocity was then measured at 50% of the total height of the water column with the drift net (Gunnarsson & Steingrímsson 2011). Once the samples were collected they were stored in a 70% ethanol solution and kept at room temperature until processed in the laboratory. During processing, samples were rinsed with water in a 250 μm sieve and placed in petri dishes mixed with water. Samples were then scanned under a microscope for potential prey items. All prey items were classified into categories (Copeopoda, Ostracoda, Blackfly larvae, Blackfly pupae, Blackfly imago, Cladocera, Acarina, Chironomidae larvae, Chironomidae pupae, and other). Debris items were excluded right away as they only got in the way of the processing and food items too small to be eaten were not counted (Keeley & Grant, 1995). Drift density was calculated based on the number of prey and volume of water entering the drift net during the five minute sampling time and reported as the total number of potential prey items per volume (m^3) of water.

3.5 Statistical analysis

All analyzes were performed with R 2.15.3 and ecological variables are summarized and reported as mean and ranges for each variable. Behavioural data are summarized as total counts (*i.e.*, number of active fish or number of foraging attempts in 5 min) or the proportion of mobile forages. Variables that were not normally distributed were either \log_{10} - (light intensity and invertebrate drift density), or square root transformed (current velocity, and depth) (Sokal & Rohlf, 1994). Due to the fact that very still water sometimes yielded negative values in the current velocity, 0.01 was added to the original values to allow for the square root transformation to be performed. To

examine the influence of water temperature on activity, the activity counts from the four study sites were combined in four categories of temperature, 10-12 °C, 12-14°C, 14-16 °C and $t > 16$ °C. An ANOVA was performed with water temperature as an independent categorical variable and the number of active fish as a dependent variable. Post hoc Tukey's tests were then performed to describe any differences between temperature intervals. A simple linear regression was used to test for relationships between activity, Julian date and light intensity. A Principle Component Analysis (PCA) analysis was done to explore the relationship between the ecological variables and the behaviours we were observing, which included foraging rate and percent mobility. Julian date, water temperature, light intensity, water depth, water current velocity, invertebrate drift density, and substrate size were all of the variables included in the PCA. This was done because correlations were expected between factors such as temperature and light level, and unlike a simple linear regression, PCA is a method that accounted for these variables. A variable factors map was then produced to describe the type and degree of correlation between the predicting variables, which consisted of Julian date, water temperature, light intensity, water depth, water current velocity, invertebrate drift density, and substrate score.

4 Results

4.1 Activity Patterns

Young-of-the-year Arctic char in the four study sites were counted seven times from 23 July to 27 August, each at four time intervals (11:00, 13:00, 15:00 and 17:00) resulting in a total of 28 activity estimates. The number of active young-of-the-year Arctic char did not change significantly with increasing water temperature (ANOVA, $P = 0.177$) (Fig 2.0). As expected from the ANOVA, *Post hoc* Tukey tests yielded no significant differences in activity among any of the four temperature intervals ($P > 0.05$ in all cases); the only comparison that was close to statistical significance was between intervals 12-14°C and 14-16°C where the latter tended to be slightly higher ($P = 0.059$). No significant relationship was detected between the number of active fish and Julian date (Linear regression: Number of active fish = $0.277 \text{ Julian date} - 10.606$, $n = 28$, $R^2 = 0.125$, $P = 0.064$) or light intensity (Linear regression: Number of active fish = $50.763 - 0.00119 \text{ light intensity}$, $n = 28$, $R^2 = 0.019$, $P = 0.490$), respectively.

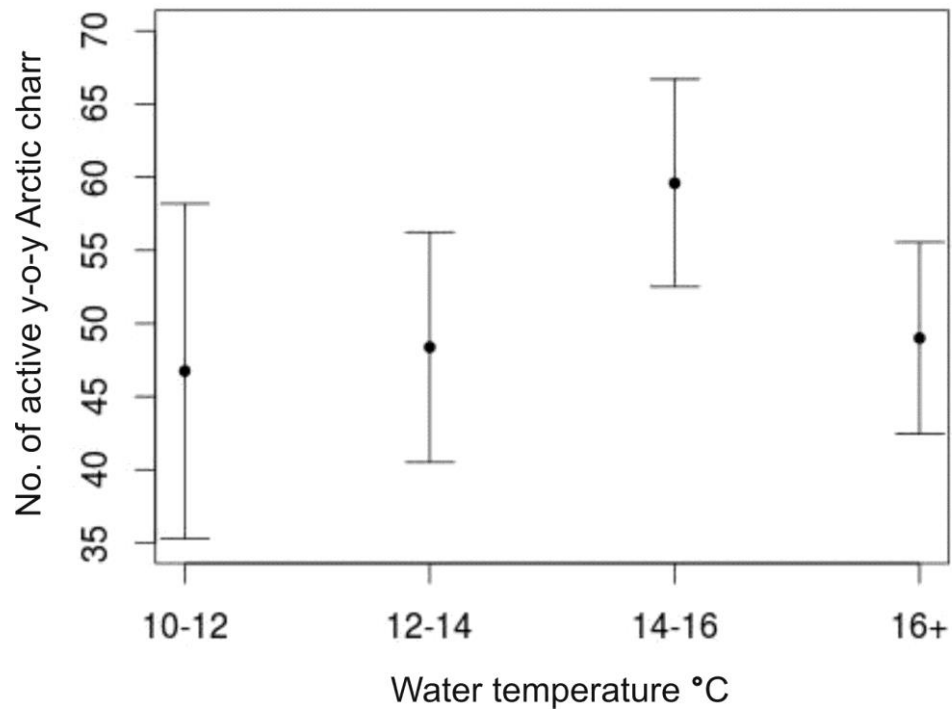


Figure 2.0. Average number of active young-of-the-year (y-o-y) Arctic char in the observation areas (dots) at four temperature intervals in Myllulækur, Northern Iceland. The lines are the standard error bars within the particular temperature interval. The number of observation for active y-o-y char at each temperature interval was 10-12 = 3, 12-14 = 16, 14-16 = 5, and 16+ = 3.

4.2 PCA Analysis and Foraging Behaviour

For young-of-the-year (YOY) Arctic char, the frequency of foraging attempts (Total = 1469; Mean = 36.7) and type of foraging mode (Mobile = 520, Stationary = 949) attempts were recorded for 40 fish during a total of 200 minutes of observation. The study fish were observed under variable environmental conditions and habitats (Table 1.0). More specifically, foraging behaviour of Arctic charr was observed over a wide range of water temperatures (5.0 to 18.3 °C) and at variable water depths (13.0 to 52.0 cm) (Table 1.0). Analysis of the drift density showed that the drifting invertebrates which were available to Arctic char in stream Myllulækur consisted primarily of blackfly larvae (30.0 % of the number of organisms), cladocera (28.9%), and copepoda (26.8 %).

Table 1.0 Summary of ecological variables of the habitat used by 40 Arctic char during behavioural observations in Myllulækur, Northern Iceland. Observations were made in the time period of 14 - 26 August.

Habitat variable	Mean	Median	Standard Deviation	Range
Density of invertebrate drift (no./m ³)	95.0	65.9	183.3	15.0 - 1200.0
Substrate size ^{a)}	3.9	4.0	1.2	1.0 - 6.0
Current Velocity (m s ⁻¹)	0.063	0.060	0.039	0.000 - 0.100
Water temperature (°C)	12.4	12.5	3.4	5.0 - 18.3
Water Depth (cm)	31.5	27.3	11.8	13.0 - 52.0
Light Intensity (lux)	2159	1366	2354	360 - 14100

a) The classification of the substrate was 1: plant detritus and clay = <0.004 mm, 2: Silt and sand = <2.0 mm, 3: Gravel = 2 – 16 mm, 4: Pebble = 17 – 64 mm, 5: cobble = 65-256 mm, 6: bolder > 256 mm (see DeGraaf and Bain, 1986).

A PCA analysis was used to examine the association between the ecological variables measured in this study. As illustrated by a factors map the first axis contrasts water temperature and light intensity, and to some extent drift density against Julian date (see Figure 3.0). In other words, water temperature was negatively correlated with Julian date (*i.e.* decreased with season), but positively related with light intensity and drift. The second axis mostly describes contrasts of habitat features, *i.e.* such as water depth against substrate score, water current velocity, and the density of invertebrate drift (see Figure 3.0). This is very logical. Assuming a certain discharge rate faster currents are expected in shallower waters and faster currents lead to coarser bottom substrates. Furthermore, assuming a certain amount of drift for each cubic metre discharged a faster current yields higher density of invertebrate prey.

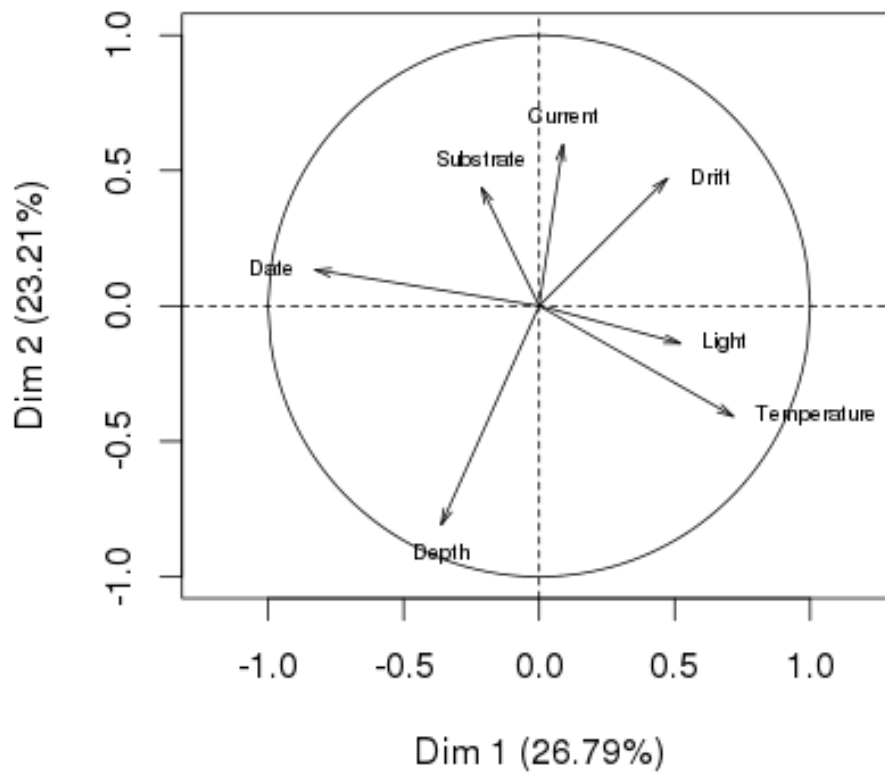


Figure 3.0: Variables factor map (PCA) explaining the relationship among the habitat variables measured for each of the 40 focal fish in Myllulækur, Northern Iceland. The correlation circle shows habitat variables according to the correlations within the PCA axes, and the length and the direction of the arrows indicates the strength of each variable and its association with other variables, respectively. The first PCA axis (Dim 1) consists mainly of Julian date (Date), Water temperature (Temperature) and light intensity (Light), whereas the second PCA axis (Dim 2) is associated with water depth (Depth), water current velocity (Current), invertebrate drift density (Drift) and substrate size (Substrate).

4.3 Foraging rate of Arctic char

The foraging rate of young-of-the-year Arctic char in Myllulækur increased with higher scores on coordinate axis 1 ($t = 2.116$; $P = 0.041$) from the PCA (Figure 4.0a). This shows that the YOY Arctic char foraged more frequently earlier on in the season, when water temperatures and light levels were higher. There was no significance association between the rate of foraging and the habitat variables dominating axis 2 ($t = 0.102$; $P = 0.909$) (Figure 4.0b). In short, habitat variables including water depth, water current velocity, invertebrate drift densities, and substrate size did not affect the foraging rate of YOY Arctic charr.

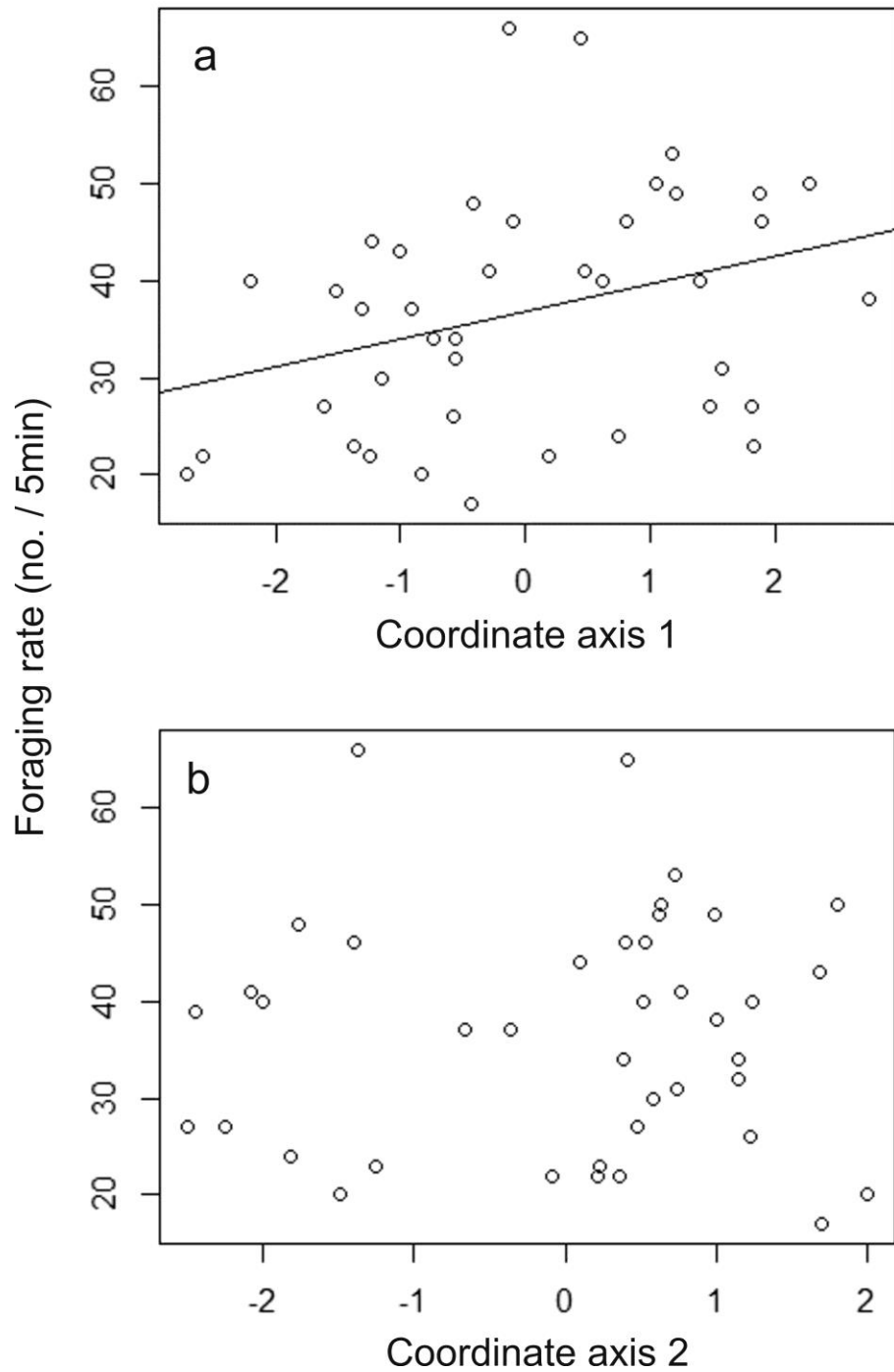


Figure 4.0 Scatterplots of the foraging rate of individual active young-of-the-year Arctic char versus their scores on axis 1 (a) and 2 (b) from the PCA analysis. The foraging rate is shown as the number of foraging attempts initiated by an active Arctic char over a five minute period. The line in (a) shows the least squares linear fit to the data.

4.4. Foraging mobility of active feeding Arctic char

The foraging mobility of the actively feeding young-of-the-year Arctic char in Myllulækur was positively related to individual scores on axis one (PCA 1) ($R^2 = 0.028$, $P = 0.028$) (Figure 5.0a), indicating that the mobility decreased significantly as the summer progressed, temperature decreased, and as light levels dropped. Foraging mobility was also significantly correlated with axis two (PCA 2) ($R^2 = 0.034$, $P = 0.034$) (Figure 5.0b), indicating that the habitat variables within this axis (*i.e.* water depth, water current velocity, invertebrate drift densities, and substrate type) significantly affect the feeding mode of the YOY char, *i.e.* whether or not the actively feeding char were mobile while foraging.

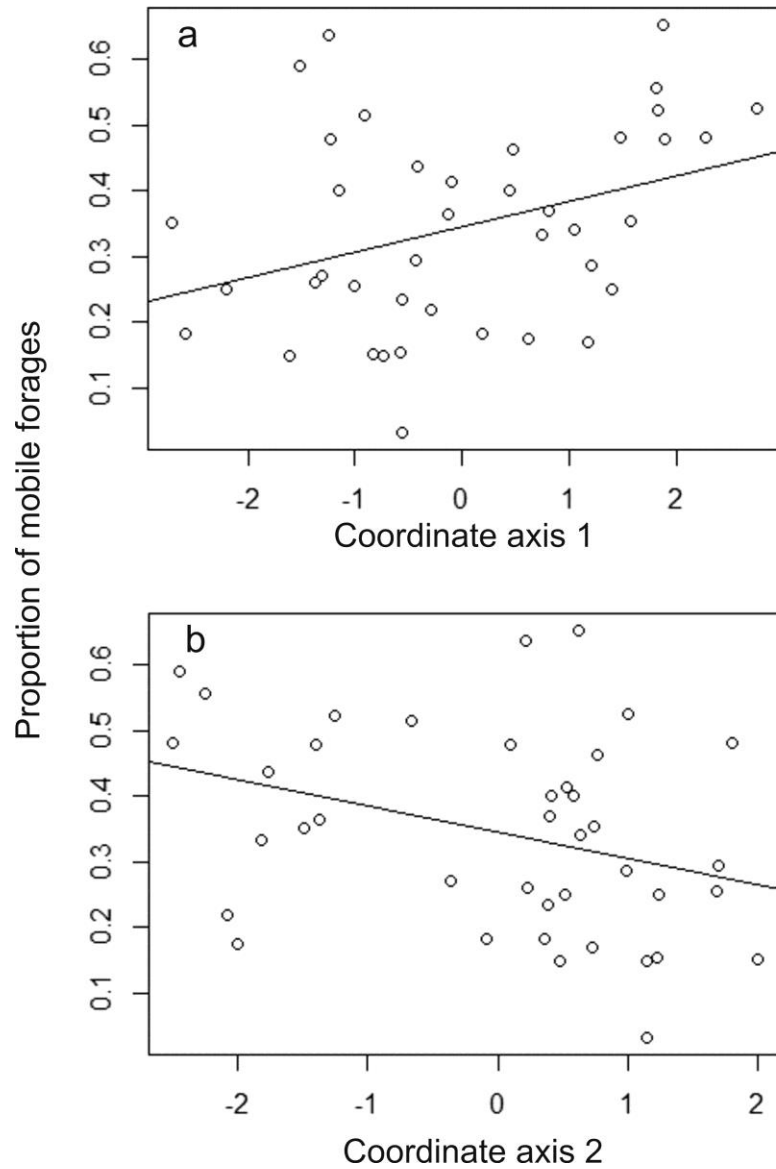


Figure 5.0 The significant relationships between Scatterplots of the mobility of individual young-of-the-year Arctic char versus their scores on axis 1 (a) and 2 (b) of the PCA Analysis. Mobility is shown as the ratio of mobile forage attempts over the total number of foraging attempts measured over a five minute observation period. A foraging attempt was considered mobile if a fish moved continuously more than 1 body length prior to prey attack. The lines show the least squares linear fit to the data.

5 Discussion

Water temperature affects important biological and ecological characteristics of ectothermal freshwater organisms, both at the individual and population level. This study attempts to understand the influence of water temperature and other ecological variables on a population of Arctic char in a small stream in Northern Iceland. More specifically, I examined how these ecological variables affected (i) feeding activity, (ii) foraging rate and (iii) the foraging mobility of YOY Arctic charr. Water temperature is probably the most important abiotic ecological factor to consider when observing the foraging activity and behaviour of stream salmonids because, together, these behavioural variables are likely to affect characteristics such as growth rates, and life history (Jonsson & Jonsson, 2009; Finstand & Hein, 2012; Spares *et al.*, 2012).

5.1 Feeding activity

In this study, my initial hypothesis claimed that there would be a positive correlation between feeding activity and water temperature; *i.e.*, as temperature increased, so would activity (Fraser, Metcalfe, & Thorpe, 1993; Heggenes *et al.*, 1993; Fraser *et al.*, 1995). In short, my study did not support this hypothesis, as no relationship between activity and water temperature for YOY Arctic char was detected. One reason why activity did not increase with temperature may be the fact that during the study period, the water temperature in the study stream remained quite high compared to most Arctic char streams. More specifically, during the observation period between 23 July and 27 August, the water temperature never dropped below 10 °C during the day (Min = 10.3 °C) and reached temperatures as high as 18.0 °C. Although, Arctic char can survive over a range of water temperatures, their preferred temperature (*i.e.* the range at which they are most active and spend most of their time) has been reported as, 9.2 °C by Peterson, Sutterlin, & Metcalfe, (1979) and as 11.3 °C by Larsson (2001), while their optimum temperature (which optimizes their growth efficiency, *sensu* Larsson, 2005) may range between 11 °C – 16 °C (Langeland *et al.*, 1991; Larsson & Berglund 1998; Larsson, 2005; Finstad & Hein, 2012). In summary, due to the consistently high temperatures within the study stream, which fell approximately within the preferred or

optimum temperatures of the Arctic char, the study fish may have already been highly active at the lowest temperatures recorded.

Interestingly, this study also suggests that Arctic char may exhibit limited flexibility in their overall activity as temperature increases above 10°C. This idea, that fish may not adjust their overall activity levels further once certain water temperatures are reached, may be of concern in the light of any potential future rise in temperature levels. More specifically, if there is an increase in stream temperatures due to changes in global climate, Arctic char may eventually lack the behavioural flexibility to deal with higher temperatures, which could result in reduced growth and increased mortality. Sloat and Osterback (2013) examined how salmonids, particularly steelhead trout, responded to a range of stream temperatures. They concluded that these fish alter their behaviour to reduce energetic costs associated with activity. A slight increase in water temperature would promote an increase in time and energy that juvenile steelhead spent foraging. However, feeding activity declined sharply around 24 – 25 °C, indicating that they had reached their maximum temperature limit. Importantly, at the maximum temperatures recorded in this study (18.0 °C), activity levels of Arctic charr had levelled off, but not yet started to decrease. The highest number of active fish (albeit not significantly) were recorded at 14 – 16 °C which corresponds with water temperature where food intake and growth in Arctic char is predicted to be at its greatest (Larsson, 2001).

Finally, activity did not relate to either Julian date or light intensity. As the season progressed and the light levels dropped, Arctic char continued to be active. This may also be a result of the water temperature, meaning fish continued to be active while the stream temperature remained high, regardless of the light intensity or time of the year.

5.2 Foraging rate

In this study, foraging rate of YOY Arctic char was primarily associated with ecological variables such as Julian date, water temperature, and light intensity, whereas no association was detected for habitat characteristic such as water depth, water current velocity, substrate size, and invertebrate drift density. The former results are consistent with the published literature which states that water temperature and

light intensity play an important role for the ability of fish to forage on drifting invertebrates (See: Fraser *et al.*, 1995; Gries *et al.*, 1997; Valdimarsson *et al.*, 1997; Metcalfe, Fraser, & Burns, 1999; Bremset, 2000). Alternatively, it is quite surprising that foraging rate did not increase significantly in habitats where water current velocity is greater and drifting prey is more abundant. These latter findings contradict several papers on drift-feeding salmonids, which show that foraging rate often increases in faster, more productive waters (Grant & Noakes 1988; Steingrímsson & Grant 2011). One potential reason for this discrepancy may be caused by the relatively low number of fish observed in this study compared to at least some of the earlier studies (*i.e.*, Grant & Noakes, 1988). Importantly, however, in our PCA analysis, invertebrate drift also contributed to axis 1, along with Julian date, water temperature and light levels. We therefore cannot exclude the possibility that drift density contributed to higher foraging rates, along with higher temperature and light earlier in the season.

As predicted, Arctic char foraged faster at higher water temperatures and greater light levels earlier in the season. As the season progressed, however, temperature and light intensity decreased, resulting in a drop in foraging rate. Various studies suggest that temperature is the most influential abiotic environmental factor for stream salmonids in terms of behaviour, especially foraging rate (Heggens *et al.*, 1993; Fraser *et al.*, 1995; Bremset, 2000). We predicted that foraging rate would decrease as temperature decreased because fish have higher metabolic needs in warmer waters (Larsson, 2001), which are typical of late spring and summer. Under these warmer conditions, young-of-the-year salmonids should become more active in order to meet their metabolic needs and obtain most of their food during the day (Fraser, Metcalfe, & Thorpe, 1993; Breau, Weir, & Grant, 2007). Declining water temperatures may cause a drop in daytime foraging rates, as metabolic needs decrease (Breau, Cunjak, & Bremset, 2007) and young salmonids may switch from a diurnal towards a nocturnal activity pattern, suggesting another reason for any potential drop in daytime foraging activity in later summer (Fraser, Metcalfe, & Thorpe, 1993; Heggens *et al.*, 1993; Valdimarsson *et al.*, 1997; Bremset, 2000). Importantly, in this study YOY Arctic char lowered their foraging rate as summer progressed and temperatures dropped, whereas no decrease was detected in the overall activity levels. Finally, light intensity has been known to have an impact on the feeding behaviour of stream salmonids as salmonids are visual foragers, resulting in higher foraging rates when light levels are higher (Gries *et al.*,

1997; Metcalfe, Fraser, & Burns, 1999; Bremset, 2000; Valdimarsson & Metcalfe, 2000).

Changes in water temperature, whether seasonal or diurnal, may also cause shift in the diel patterns of foraging behaviour. As mentioned above, low water temperatures may have direct physiological effects on stream-dwelling fish causing slower digestion rates, reduced swimming capacity, and reduced daily energy requirements, which in turn may influence food intake and growth (Fraser, Metcalfe, & Thorpe, 1993; Bremset, 2000). In fact, in some cases, reduced metabolic demands due to cold waters may result in salmonids being able to feed only at night, thereby lessening predation risk (Valdimarsson *et al.*, 1997). Alternatively, as water temperature increases, higher metabolic requirements can no longer be met by feeding at night and daytime foraging will resume (Valdimarsson *et al.*, 1997). In this study stream, however, YOY Arctic char remained primarily active and had consistently higher foraging rates during the day than during the night (Nicolas Larranaga, personal observation, 07/2013), a pattern more common among YOY salmonids than older salmonids (*i.e.*, Breau, Weir, & Grant, 2007).

5.3 Foraging mode

Several studies suggest that foraging mode variation is at least partly determined by a species' local environmental conditions, and not necessarily related to differences in body shape and size (McLaughlin, Ferguson & Noakes, 1999). More specifically, individual organisms can display flexibility in foraging, shifting their prey type and size, foraging mode, and habitat in response to changes to these environmental conditions (Nakano, Fausch, & Kitano, 1999). Juvenile salmonids are a good example of such flexibility and show great variation in foraging mobility as they can adjust to environmental changes by switching between foraging modes there by altering the amount of energy spent on foraging (Grant & Noakes, 1987; McLaughlin, Grant, & Kramer, 1992; Nakano, Fausch, & Kitano, 1999); Killen, Brown & Gamperl, 2007). Salmonids within streams provide a good opportunity to study this behaviour, being that they are visual hunters that can select from a wide range of habitats in relatively small and confined areas (Grant & Noakes, 1987). Sit-and-wait foragers tend to

encounter and eat more active, fast-moving organisms, whereas mobile foragers spend more energy and demonstrate significantly higher mobility as they move about their environment in search for more sedentary or slow moving prey (Huey & Pianka, 1981; Grant & Noakes, 1987; Killen, Brown & Gamperl, 2007).

In this study, we examined if water temperature affected the foraging mode (*i.e.* mobility) of YOY Arctic char. Our results indicate that foraging mobility of the Arctic char decreased significantly as temperature and light levels decreased towards the end of the summer, supporting the idea that water temperature may in fact affect mobility. One potential reason for my finding may be associated with the energetics of mobility at different temperatures. More specifically, the physiological costs of fish movement are believed to be higher at lower temperatures, which could explain why mobility may decrease at lower water temperatures later in the season (Fraser *et al.*, 1995; Killen, Brown & Gamperl, 2007). In addition, light intensity may affect foraging mode because salmonids are visual feeders and are less efficient at feeding at lower light levels (Fraser & Metcalfe, 1997). As light decreases, their ability to search and locate food is limited (Valdimarsson & MetCalfe, 2000).

Our results also show a significant relationship between foraging mobility and habitat characteristics, which is in agreement with the literature. Multiple studies suggest that habitat characteristics such as water current velocity, availability of invertebrate drift, and water depth, may all play a substantial role in determining the foraging mobility of stream salmonids (Grant & Noakes, 1988; Killen, Brown & Gamperl, 2007; Steingrímsson & Grant 2011). In particular, water current velocity and invertebrate drift may be of great importance. More specifically, observations made over a range of current velocities and drift abundance suggest that salmonids become less mobile as current velocity increases across the habitat (Grant & Noakes, 1988; Fausch, Nakano, & Kitano, 1997). It has also been hypothesized that mobility will decrease with an increase in drift density (Huey & Pianka, 1981; Grant & Noakes, 1987; Killen, Brown, & Gamperl, 2007). Drift density can affect the mobility of salmonids because at high prey densities, an individual has a very high chance of encountering and capturing drifting prey items in a relatively small area. These conditions may motivate individuals to become sedentary and ambush prey from one foraging station, and thus save energetic costs associated with high mobility. Alternatively, fish may switch to

mobile foraging in order to increase their prey encounter rate under conditions where the amount of drifting prey is limited (Huey & Pianka, 1981; Grant & Noakes, 1988; Fausch, Nakano & Kitano, 1997; Killen, Brown, & Gamperl, 2007). In short, my results support the idea that foraging mobility will decrease with increased water current velocity and prey density (Grant & Noakes, 1987).

5.4 Final Remarks

Salmonids may deal with thermal stress in a variety of ways, and not only by modifying their foraging activity and behaviour at a local scale. Fish may respond to higher temperatures by altering their thermal habitats through geographical shifts (Jeppensen *et al.*, 2012). As water temperature increases, anadromous salmonids in warm-water habitats may potentially migrate to cooler waters, whereas cold-water salmonids have a more limited range and run the risk of eventually running out of suitable habitats (Rahel, Keleher, & Anderson, 1996; Krajick, 2004). Salmonids, which do not have the ability to migrate out of their respective river system, may seek thermal refuges by temporarily or permanently relocating to cooler headwater or tributaries within the river or stream system they reside (Breau, Cunjak, & Bremset, 2007; Sloat & Osterback, 2012). Salmonids may also deal with an increase in water temperature by altering their diel activity and potentially change from primarily diurnal to nocturnal, becoming more active during the night when temperatures are cooler (Fraser, Metcalfe & Thorpe, 1993).

Increasing water temperatures have the potential to affect rates of growth, life history processes, as well as entire population dynamics (Jonsson & Jonsson, 2009; Finstand & Hein, 2012; Spares *et al.*, 2012). For many salmonids, as water temperature nears their lethal level, feeding along with food absorption and conversion declines rapidly, limiting growth rate (Sloat & Osterback, 2012). High water temperatures can also cause weight loss, limit muscle efficiency, and increase the risk of disease and occurrence of parasites, such that warmer waters allow parasites and other disease-causing organisms to more rapidly complete their life cycles (Larsson *et al.*, 2005; Reist *et al.*, 2006b; Rahel & Olden, 2008). If salmonids are already stressed, in this case by higher water temperatures, they may be unable to cope with a second stressor *i.e.* disease and parasites, and anthropogenic factors, such as pollution leading to

toxicity or reduced water oxygen levels, increasing their chance of mortality (Richer & Kolmes, 2005). Rising water temperatures also have the ability to facilitate the invasion of non-native species into salmonid habitat. Such introductions can limit food resources for native species and create competitive displacement of species that are unable to adapt to the prevailing temperatures (Rahel & Olden, 2008). Life history processes can also be altered, whereas any ecological change in one life stage can have significant effects on later life stages as most life-stage transitions are intertwined (Jonsson & Jonsson, 2009). Understanding how salmonids deal with rising temperatures and how these behavioural and physiological shifts extrapolate from an individual to population level will add to the overall understanding of how fish species are able to adapt to potentially warming environments.

6 Conclusion

The aim of this study was to identify how fish deal with water temperature changes at a local scale. This was achieved through behavioural observations of young-of-the-year (YOY) Arctic char in a single stream in Northern Iceland. With this study, I hoped to gain new information regarding how freshwater fish, particularly juvenile salmonids, are able to cope with changing temperatures by modifying key aspects of their foraging behaviour. Importantly, shifts in fish behaviour due to temperature changes on local levels may not be suitable for extrapolation to global climate change scenarios. However, by increasing our knowledge of how fish react in general to environmental changes and ecological variation may help contribute to future management considerations of marine and coastal systems.

Understanding temperature tolerance in fish, especially cold water salmonids like Arctic char, is of particular importance as animals will respond differently to environmental change based on their particular physiology. Water temperature is an important environmental factor for aquatic organisms because shifts in temperature patterns have the potential to affect individual behaviour and physiology, which on a longer time scale can also affect population parameters and biogeography (Rahel & Olden, 2008). Climate change may act upon fish directly through climate-induced changes in the environment or even indirectly through altering interactions on the community level with other taxa (Hedger *et al.*, 2012). Climate change is expected to warm much of the earth and as air temperatures increase, water temperatures will also rise, altering aquatic habitats by changing both thermal and water flow regimes. In the northern latitudes, this warming may create stressful conditions for the cold-water fish, promoting invasive warm-water fish to shift into new habitats, creating resource competition between native and non-native species (Rahel & Olden, 2008). Fish that are isolated and unable to migrate will have to alter their behaviour by relocating to cooler areas of their river or stream, when possible, to deal with the increasing temperatures (Breau, Gunjak, & Bremset, 2007). Eventually, the existence of isolated freshwater populations and species may depend on how fast these environmental changes occur, and how rapidly these organisms may adapt and evolve to tolerate higher temperatures and other ecological changes (Winfield *et al.*, 2010).

This study provides several findings on the behaviour of stream salmonids and how they may react to increasing water temperatures and other environmental variation. Interestingly, no relationship was found between YOY Arctic char feeding activity and water temperature. This finding could be due to relatively high stream temperatures during the observations, but may also suggest that Arctic char are limited in the flexibility of their overall activity as temperature increases above 10°C. Hence, Arctic char may already be highly active at these temperatures and may eventually lack the flexibility in this behavioural component to deal with the higher temperatures that may occur due to climate change. Importantly though, our study did suggest that YOY Arctic char adjust their foraging rate and foraging mode to changes in ecological variables such as water temperature, Julian date, and light intensity. This means that once fish are active at 10 C, they may deal with even higher temperatures by foraging more frequently on drifting invertebrates to meet their metabolic demands, or by shifting their behavioural tactic towards more mobile foraging. At this point, however, any explanations on the biological mechanism underlying increased mobility at higher temperatures remain speculative.

My findings are relevant for conservation. Although Arctic char have the ability to survive in a variety of environments and over a large range of water temperatures, this does not mean that high water temperatures are not already having negative effects, especially in colder-water environments (Larsson & Berglund, 2005; Winfield *et al.*, 2008; Jeppensen *et al.*, 2010; Winfield *et al.*, 2010). Some Arctic charr populations and salmonid species are already living at maximum temperatures, where their behavioural armoury of dealing with thermal stress (*i.e.*, activity and foraging rate) may already be at its limits. Increasing our knowledge on the role water temperature plays on salmonid behaviour, survival and ecology in general will allow us to gain a better understanding on how such shifts alter fish behaviour and activity, thus leading to more robust management strategies and practices as it relates to climate.

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