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Temporal and spatial differences in the food web of Atlantic salmon rivers

Trophic relationships of Atlantic salmon

Fæðuvefur Atlantshafslaxins

breytileiki í tíma og rúmi

Sum Yi Lai

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Temporal and spatial differences in the food web of Atlantic salmon rivers

Sum Yi Lai

Dissertation submitted in partial fulfilment of a
Philosophiae Doctor degree in Biology

Supervisors
Hlynur Bárðarson
Jón S. Ólafsson

Ph.D. Committee
Arnar Pálsson
Ingi Rúnar Jónsson
Jóhannes Guðbrandsson

Opponents
Stefán Óli Steingrímsson
Lee Brown

Faculty of Life and Environmental Sciences
School of Engineering and Natural Sciences
University of Iceland
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Faculty of Life and Environmental Sciences
School of Engineering and Natural Sciences
University of Iceland
Sturlugata 7
102, Reykjavik
Iceland

Telephone: 525 4000

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Author ORCID: 0000-0002-0203-2634
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Abstract

Atlantic salmon is an anadromous species that spend most of their life in freshwater and migrates out to sea for 1-2 years before returning to the river as a spawning adult. In recent decades, Atlantic salmon populations are declining. This ecologically and economically important species has a broad distribution and complex life cycle. The aim of this thesis is to increase our understanding of the impact of prey availability on juvenile populations and the Atlantic salmon's role in the riverine food web, with a focus on salmon in northern, low-productivity rivers. Predator-prey relationships of Atlantic salmon were investigated in NE Iceland and food webs of Atlantic salmon rivers in the North Atlantic were compared over space and time.

Chironomidae (Insect: Diptera) were the most abundant benthic invertebrates and constituted the majority of the diet of juvenile salmon in NE Iceland. Juvenile salmonids had high dietary overlap and were consuming chironomids due to their high availability. The predator-prey relationships in a nutrient-poor river in NE Iceland were found to be mostly similar over a 23-year period. However, prey availability in the river started to decrease after 1997, possibly due to climate change. A peak in productivity during the late summer period was also observed in the Vesturdalsá river, which matches the growth and development of freshwater species in the system. Food webs were found to be spatially similar within and between rivers in Iceland, owing to its biogeographical isolation and homogenous catchment characteristics. Food webs in the North Atlantic were also shown to have increasingly complex trophic interactions with decreasing latitudes, which corresponds to increases in temperature and vegetation.

Juvenile Atlantic salmon populations located in cold, northern latitudes have low food availability and simple food webs; thus, making them highly vulnerable and lack adaptability to the climate change impacts. Researchers could use northern salmon populations as suitable 'sentinel' systems for monitoring and predicting global trends of salmon population dynamics and their prey availability.

Útdráttur

Atlantshafs laxinn dvelur fyrstu ár lífsferils síns í straumvatni, en hverfur síðan til sjávar þar sem hann dvelur í 1 – 2 ár uns hann kemur aftur í uppeldisána sína. Líkt og fyrir allar lífverur er framboð á fæðu einn af mikilvægustu þáttum fyrir afkomu og vöxt laxins. Atlantshafslax er í niðursveiflu, og telst sumstaðar í útrýmingarhættu. Laxinn er bæði vistfræðilega og efnahagslega mikilvæg tegund með víðtæka útbreiðslu og flókinn lífsferil. Markmið þessa doktorsverkefnis er að auka skilning fæðuvef laxins og á áhrifum fæðuframboðs á ungviði hans með áherslu á laxastofna á norðlægum slóðum og í ám með litla framleiðni. Til að ná settu markmiði beindist rannsóknin að gerð fæðuvefjar fyrir Alantshafslax í ám á Norðausturlandi. Auk þess að bera saman fæðuvefi Atlantshafslaxins í ám í löndum við norðanvert Atlantshaf.

Skordýralirfur af ætt rykmýs (Diptera: Chironomidae) voru algengasta fæða laxaseiða og stóðu þær undir meirihluta fæðu laxaseiða í ám á Norðausturlandi. Einnig var mikil skörun í fæðu mismunandi tegunda laxfiska og samanstóð fæðan aðallega af rykmýstegundum vegna mikils þéttleika þeirra. Samband afræningja og bráðar í næringarsnauðri á Norðausturlandi, reyndist stöðugt milli ára. Hins vegar virðist fæðuframboð hafa farið minnkandi frá því 1997, mögulega vegna loftslagsbreytinga. Hámark var í framleiðni í fæðuvef árinnar síðsumars (seint í júlí og byrjun ágúst) sem passar við vöxt og þroskun laxa á rannsóknarsvæðinu. Fæðuvefir laxaseiða reyndust vera svipaðir bæði innan áa sem og á milli þeirra á Norðausturlandi. Einnig var sýnt fram á sífellt flóknari samspili lífvera milli fæðuþrepa innan fæðuvefja frá norðlægri til suðlægrar breiddargráðu, sem fer saman við hækkandi hitastig og aukna gróðuþekju á landi.

Seiðastofnar Atlanshafslax á köldum norðlægum breiddargráðum þar sem fæðuframboð er lítið og tilheyra einföldum fæðuvefum eru viðkvæmir fyrir áhrifum loftslagsbreytinga. Niðurstöðurnar benda til þess að mikilvægt sá að nota þessi norðlægu vistkerfi til að spá fyrir um áhrif loftslagsbreytinga á laxastofna.

This thesis is dedicated to

My loved ones

And the Atlantic salmon who love their food

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Paper II: Lai, S.Y., O´Gorman, E.J., Guðbergsson, G., Woodward, G., Jónsson, I.R., Guðbrandsson, J., Ólafsson, J.S., & Bárðarson, H. Signs of warming and temporal stability of predator-prey relationships of sub-Arctic Atlantic salmon river. Manuscript.

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Author Contributions:

Paper I: Conceptualisation & Developing methods: SYL, AP, GG, IRJ, JSO, HB. Conducting the research: SYL, JSO, HB. Data analysis: SYL, HB. Data interpretation: SYL, AP, IRJ, JSO, HB. Preparation figures & tables & Writing: SYL. All authors reviewed, edited, and approved the manuscript.

Paper II: Conceptualisation & Developing methods: SYL, EJG, GG, GW, IRJ, JG, JSO, HB. Conducting the research: SYL, JG, JSO, HB. Data analysis: SYL. Data interpretation: SYL, EJG, GW, IRJ, JG, JSO, HB. Preparation figures & tables & Writing: SYL.

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我知道你们一定好困难也很担心让你们的女儿飞到那么远的地方。从小到大，芯宜都让你们担心不能照顾自己，但芯宜长大了，有办法去照顾自己也认识了很多照顾我的人,所以现在可以让芯宜来照顾你们了。女儿很抱歉这四年为了追梦而没能通常回家孝顺你们。多谢你们多年来的支持和爱。无论我在哪里，你们永远都是我的家，我的避难所。我希望我让你感到骄傲，也可以帮Boogie赚零食钱了。

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1. Introduction

Food supply is one of the most important factors determining the survival of many species and the health of populations. Studies have shown that food limitations can influence the dynamics of fish populations, and in some cases, be the limiting factor for the carrying capacity for certain areas (Amundsen & Gabler, 2008; Le Pape & Bonhommeau, 2015; Okamoto et al., 2012). Food availability studies can therefore help identify areas in which populations become vulnerable due to limited prey items. Atlantic salmon populations are well monitored and of high economic importance, but due to their complex life cycles covering large spatial distributional ranges and different habitat types, most studies in food availability of juvenile salmon have only been covered in a small part of their distributional range, one snap-shot in time, and only focused on salmon and their prey rather than the whole food web (Amundsen et al., 2000; Johnson & Ringler, 2016; Marsh et al., 2022). Knowledge of spatial and temporal variability in interspecies interactions in the ecosystem is lacking for most systems but is important especially when it comes to applying ecosystem-based management. This thesis explores freshwater habitat food availability as one of the main drivers of juvenile population change and a focus for river management.

1.Study Species: Atlantic Salmon in Iceland

The Atlantic salmon (*Salmo salar*; *Figure 1*) is an anadromous species, belonging to the family Salmonidae (Jonsson & Jonsson, 2011). Their global distribution spans across North America, northern Europe, and the Baltic region (ICES, 2023). The anadromous Atlantic salmon has a complex life history which varies between populations (Birnie-Gauvin et al., 2019; Jonsson & Jonsson, 2011; *Figure 2*). In fact, a recent study exploring different life-histories of salmon populations in Norway identified 141 unique life-history types across the 179 rivers analysed (Persson et al., 2023). In general, Atlantic salmon populations in southern regions, such as Spain, France, UK, and Ireland, tend to stay in freshwater for a shorter period (~1-2 years) than in northern regions, such as Iceland and Norway (ICES, 2023; Metcalfe & Thorpe, 1990). Therefore, the juveniles in these southern regions tend to smoltify much earlier (at a younger age) and at a larger size (Hutchings & Jones, 1998). Around June to early August, the juveniles will then migrate out to the sea as smolts during optimal conditions and after developing tolerance to saline waters (Antonsson & Gudjonsson, 2002; Davies et al., 2004; IUCN Red List, 2009; Kallio-nyberg & Koljonen, 2020; Olafsson et al., 2014). Most salmon experience most of their growth within 1-2 years at sea, with some examples of populations that stay longer before returning. Thus, oceanic environmental variables are also important drivers of changes in anadromous fish stocks and survival (Antonsson et al., 1996) that need to be considered by managers as well. Adults will then migrate back to their natal river for spawning. Atlantic salmon normally spawn in the autumn and eggs develop in gravel on the river bottoms through the winter (Saltveit & Brabrand, 2013).

Figure 1: Juvenile Atlantic salmon (Salmo salar) across age classes from the top 0+ to 4+ in River Vesturdalsá.

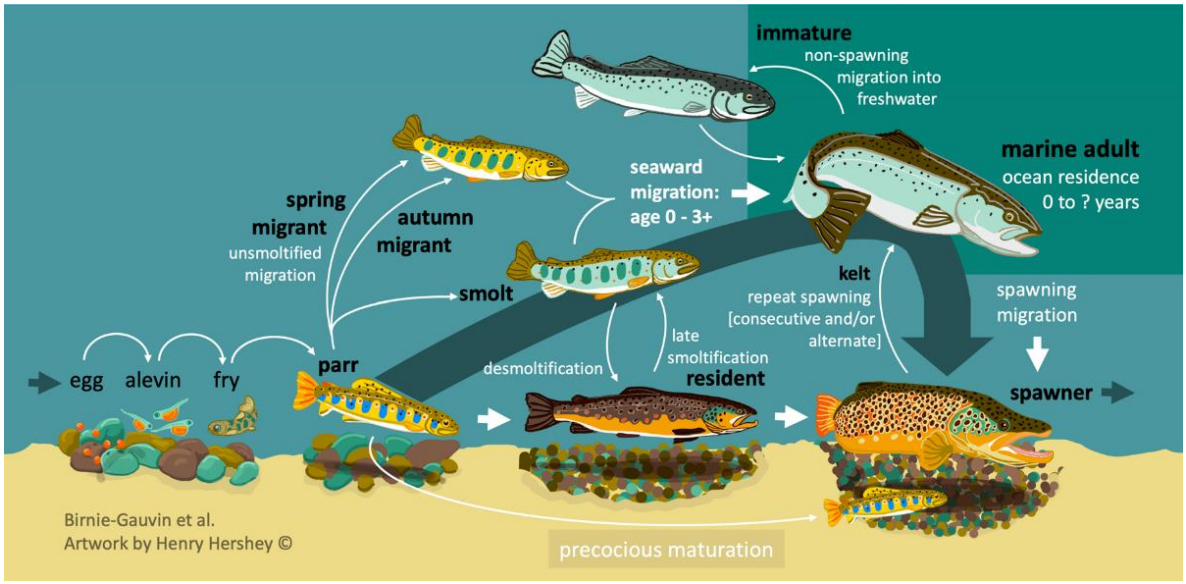

Figure 2: Possible life cycles paths of Atlantic salmon from an egg to a spawning adult (Birnie-Gauvin et al., 2019). As a parr, salmon can experience several different life cycle strategies, including going through smoltification, becoming an unsmoltified migrant, staying in the river as a resident, or going through precocious maturation. As a resident, they may also choose to smoltify later on and migrate to sea or sexually mature as a spawning adult. As a smolt, they

may stay at sea for several years before migrating back to the river to spawn or return to the river as an immature individual.

Atlantic salmon stocks are an important source of food and income for countries along the North Atlantic Ocean. They are an important resource for angling, tourism, and commercial exploitation (Butler et al., 2009; Kochalski et al., 2023; McGinnity et al., 2003). Fishing season is usually 90 days from around 1 July to 20 September every year in the Northeast rivers in Iceland but the allowable number of days for salmon rod fishing in Icelandic rivers is 105 each season (Alþingi, 2006; Heidarsson et al., 2006). Exploitation rates of Atlantic salmon have decreased in the last decades and have remained low since 2001, whereas the production of farmed salmon has increased (ICES, 2023). For example, a recent study on the economic importance of freshwater angling in Iceland found that the total value of angling to be approximately 170.5 billion krona (1.2 billion USD) a majority of which (83%) are from salmon-dominated rivers (Jóhannesson, 2018). Importantly, recreational fishing has increased in popularity in the world and its economic value can be higher than that from commercial fisheries (Andersson et al., 2020).

Many salmon populations in southern outskirts of the species distribution have recently gone extinct or are currently close to extinction (Jonsson & Jonsson, 2011). Additionally, in north European rivers, it has been observed that the growth of juvenile salmon in freshwater has decreased over the past 50 years and that juvenile salmon are spending on average 1-2 more years in the river before migrating out to sea (Alioravainen et al., 2023). Atlantic salmon has also been predicted to shift their distribution northward into the Arctic with changing climates and vagrant Atlantic salmon has been found in Arctic rivers in Canada (Bilous & Dunmall, 2020; Jonsson & Jonsson, 2009). Climate change, habitat alteration, invasive alien species, stocking, disease, and spread of sea lice are some of the threats to wild Atlantic salmon populations (Forseth et al., 2017; Thorstad et al., 2021). Whilst salmon fisheries can be called an important ecosystem service, they can also have negative impacts to wild salmon populations. Catch-and-release angling could cause Atlantic salmon to become fatally stressed and die within 24 hours (Booth et al., 1995), but some studies have also shown that catch-and-release angling does not affect salmon migratory behaviour or growth rates of parr (Jensen et al., 2010; Whoriskey et al., 2000). Additionally, aquaculture could be another risk to wild salmon populations with increased risk of sea lice epidemics, genetic mixing of spawning stock with farmed escapees and pollution of freshwater habitats (Jackson et al., 2013; Karbowski et al., 2019; Parrish et al., 1998; Skaala et al., 2014). Understanding factors that influence changes in sizes of Atlantic salmon populations could help managers to know what type of management process may be best in sustaining stocks of gradually decreasing wild populations (Chaput et al., 2019; ICES, 2022; Parrish et al., 1998). Migration barriers such as the construction of dams and weirs could affect the survival and time spent by adults to reach spawning sites (Thorstad et al., 2008). Of course, there are many more factors that affect the population dynamics of wild Atlantic salmon, which should be considered when investigating the species or when implementing proper management methods.

Salmon populations in Iceland are considered to be at the northern boundaries for the species' natural distribution. The populations of Atlantic salmon in Iceland significantly contributes to the global stock production and the revenue for fishing associations in Iceland, whilst the health of the population has also been relatively stable compared to a generally

declining global salmon populations (ICES, 2023). Atlantic salmon in Icelandic rivers will lay their eggs in the autumn. The fry will emerge from the egg in the spring, and they stay in the river as a parr on average for 2-5 years (Antonsson et al., 2010; Olafsson et al., 2016). Salmon in north Icelandic rivers migrate to the sea from mid-June to early August (Antonsson & Gudjonsson, 2002). Most salmon only spawn once, with only a small number of individuals that become repeat spawners (iteroparity), which return out to sea and repeat the migration again. In the study by Persson et al. (2023) mentioned above, the frequency of iteroparity in Atlantic salmon across the 179 rivers in Norway ranged between 0 to 26% with an average of 3.8% adult survival in each river. A smaller study from Icelandic populations also found the frequency of repeated spawning to be very similar in frequency or from 0 – 25% when analysed from scale samples of Atlantic salmon from eight rivers, between the years 1989 – 2006 (Kjartansdóttir & Einarsson, 2009).

Most Atlantic salmon populations are partly migratory as some individuals may reside around the spawning area all year round and not migrate out to sea (Jonsson & Jonsson, 2011; Nevoux et al., 2019). These residents could include young males that mature sexually as parr (precocious males) providing an alternative male reproductive strategy (Fleming, 1996; Jonsson & Jonsson, 2011; Mobley et al., 2021). These individuals are often called sneakers, as they do not exhibit courtship behaviour and would spawn near large fish when females release their eggs (Birnie-Gauvin et al., 2019). They may become precocious males again during the next spawning season or smoltify and migrate out to sea and then return as adults and even become repeat spawners (Fleming, 1996). The occurrence of precocious male parr may be quite high in some populations, as a study showed that precocious males make up 80% of the population in Little Murray, Newfoundland (Myers, 1984). Whereas in the Armorican river, France, the occurrence of precocious maturity was <5% (Bagliniere & Maisse, 1985). Some Atlantic salmon populations may also be landlocked or non-anadromous. These populations go through smoltification and leave their natal spawning rivers but stay in freshwater lakes until precocious sexual maturation (Lumme et al., 2015; Nilsen et al., 2003). There are very few examples of truly non-migrating forms of Atlantic salmon and landlocked populations are usually managed to support sustainable fishing and conservation targets (Hutchings et al., 2019). Notably, there are no landlocked populations of Atlantic salmon in Iceland, but other salmonid species have established such populations on the island (Lumme et al., 2015).

Atlantic salmon, in Iceland or otherwise, spend a considerable amount of time of their lifecycle in the freshwater environment. Therefore, the quality of the riverine habitat are important determinants to the sustainability of these populations.

a. Diet of Juvenile Salmon in Freshwater

Atlantic salmon parr are sit-and-wait predators in rivers where they stay within a feeding territory picking invertebrates in the bottom substrate, capture prey that drifts downstream, or alternate between these two strategies depending on the availability of prey (Akbaripasand et al., 2014; Gerwing & Plate, 2019; Johnson & Waldt, 2014; Jonsson & Jonsson, 2011). Observational study in a river in northern Iceland showed that in comparison to the Arctic charr and brown trout, juvenile Atlantic salmon were less mobile and less likely to travel long distances to hunt prey (Tunney & Steingrímsson, 2012). Whereas adults are opportunistic pelagic feeders that often forage close to the surface and utilise many different prey items at sea (Guðjónsson et al., 2015; Haugland et al., 2006; Rikardsen & Dempson, 2011). Juvenile salmon usually feed on aquatic and terrestrial insects and invertebrates with some also feeding on other

smaller salmonids. Salmonid species feed on similar resources and may show competition between species for specific prey or habitats (Johnson et al., 2017; Mookerji et al., 2004). The observed diet of salmonids is naturally reflected in the invertebrate community of the local freshwater ecosystem (Syrjänen et al., 2011). In terms of available prey, Atlantic salmon rivers in Iceland are dominated by Chironomidae (Insecta: Diptera), Simuliidae (Diptera), Trichoptera and predatory Acarina (Govoni et al., 2018; Jonsson & Jonsson, 2011; Kreiling et al., 2022; Lárusdóttir et al., 2000). Studies on the stomach contents of Arctic charr and brown trout in Iceland have also found that they mainly consume chironomids, cladocerans, bivalves, and water snails (Björnsson, 2001; Gíslason & Steingrímsson, 2004; Kreiling et al., 2021). Furthermore, salmonids within the same water body have also been shown to overlap in prey diet items (Björnsson, 2001; Malmquist et al., 1992). Atlantic salmon in these Icelandic rivers are mostly preying on small larval midges and black flies (Antonsson et al., 2010). Icelandic freshwater macroinvertebrate communities are also lower in biodiversity than other Atlantic salmon rivers in the North Atlantic (Ministry for the Environment & The Icelandic Institute of Natural History, 2001). Therefore, the diversity of prey available to salmonids in Icelandic rivers may be lower in comparison to other countries, due to its biogeographical isolation (Laske et al., 2022). The high abundance of chironomids found in these systems shows the importance of the chironomid community in driving changes in the Icelandic freshwater food webs (Govoni et al., 2018).

Prior studies suggest that juvenile Atlantic salmon select prey based on size (Wańkowski, 1979, 1981). This can manifest in several ways. It has been observed that drifting prey was mostly being consumed by larger juveniles in River Teno, Finland (Erkinaro & Erkinaro, 1998). In addition, in some cases, juvenile salmonids start to consume other smaller salmonids once they reach a certain size that may lead to them predating on others of their own kind (Falkegård et al., 2023; Näslund et al., 2015; Wańkowski, 1979; Wańkowski & Thorpe, 1979). Similar ontogenetic shift behaviour was also observed for Arctic charr, where they would consume larger-sized snails with increasing fish size, which shows the ontogenetic gape limitations of salmonids (Malmquist et al., 1992). Terrestrial prey are most commonly found in streams with deciduous forests (Syrjänen et al., 2011). Studies have also shown that salmonids are quite opportunistic, which may change prey selection depending on what kind of prey items are available, habitat type, size of the fish, and also inter- and intra-specific competition (Jonsson & Jonsson, 2011). Therefore, prey choice of salmonids is usually expected to reflect the species composition of prey items in their habitat. This is for instance demonstrated very clearly in the habitat use of different morphs of Arctic charr in Iceland, which is reflected in their diet (Kristjánsson & Leblanc, 2018; Sandlund et al., 1987).

2. Status of Atlantic Salmon Populations in NE Iceland

Atlantic salmon populations are in decline globally. Estimates of Atlantic salmon population abundance and fisheries landings have shown declines since the 1990s (Chaput et al., 2019; ICES, 2023). In addition, there has been declines in numbers of multi-sea-winter fish and survival of post-smolts over time. Whereas, the current population trends of Atlantic salmon in Iceland are shown to be stable over time, high fluctuations are observed in the most recent years (of the available time-series) (Bárðarson et al., 2023; Þórðardóttir & Guðbergsson,

2023). Notably, the proportion of Atlantic salmon caught in tributaries and proportion of multi-sea-winter salmon in rod catch for river systems in northeast Iceland has declined (Kristinsson et al., 2015; Þórðardóttir & Guðbergsson, 2023).

The smolt-age of Atlantic salmon have been decreasing in the Burrishoole catchment in Ireland (Rinaldo et al., 2023) and this was also seen in some rivers in Iceland (Björnsson et al., 2023), which could be linked to increased juvenile growth rates. It has also been observed that smolts are usually older in northern and colder habitats (Antonsson & Gudjonsson, 2002). Based on data spanning from 10 to 22 years prior to 2001, juvenile Atlantic salmon in SW and NW Iceland were on average longer than juvenile salmon from the W and NE regions, whereas relative density and biomass were higher in SW and W regions than NW and NE (Antonsson et al., 2005). Most of the major salmon rivers in Iceland are located in western regions, but several major sports fishing rivers are located in lowland areas at NW, NE, and S of Iceland (DELWP, 2017). Many Atlantic salmon rivers are lake-fed, direct run-off, or spring run-off rivers and few from glacial streams, but they still contribute to the annual catch of salmon.

3.Freshwater Food Webs

Food webs describe the predator-prey relationships in a community and help picture the way in which the community is put together (Pimm et al., 1991). Food webs in freshwater ecosystems are usually made up of three trophic levels- primary producing algae, invertebrates, and fish. Reconstruction of food webs helps researchers understand the structure and dynamics of trophic interactions among organisms, and the transfer of energy within ecosystems (Gibert, 2019; Woodward et al., 2010a). River conservation management methods usually target one species but many other ecosystem factors can also be affected by those management methods (Wootton, 2012). Thus, research on climate change impacts on food webs should be expanded to consider more than two trophic levels, and include responses in addition to population abundance and biomass, and a wider collection of environmental variables (Cameron et al., 2019). There are several ways to study food webs such as through using stomach/gut content analysis, stable isotope ratios, and biochemical markers (Fry, 1991; Jake Vander Zanden & Fetzer, 2007; Pasquaud et al., 2007; Rosi-Marshall & Wallace, 2002; Woodward et al., 2010a). Food web studies to date have mostly been situated in USA and Europe (Cameron et al., 2019), where there is a high abundance of case studies for cross comparisons in these areas.

Ecological stoichiometry offers an alternative approach to understand trophic interactions (Perkins et al., 2010). Most food web studies use species- or size-averaged data for both species nodes and trophic links rather than individual-based data, but species averaging can obscure structural regularities due to intraspecific size variation whereas individual-based approaches could provide clearer insights to seasonal and ontogenetic shifts (Woodward et al., 2010a). In this study, biomass: abundance trivariate food webs are reconstructed which provides measures of both community structure and how a community responds to environmental stressors (Perkins et al., 2018). Trophic interactions and structure of food webs are largely determined by the respective sizes of consumers and resources, with the majority of trophic interactions being the consumption of smaller, more abundant prey by larger and rarer predators (Woodward et al., 2005). Additionally, the strength of trophic links increases with predator body size (Woodward et al., 2005).

Food webs could also differ by either ´bottom-up´ or ´top-to-bottom´ control of the river ecosystem, which can dictate the size-structuring, prey availability, and productivity level of the ecosystem (Brose et al., 2012; Shurin et al., 2012). Knowledge about what type of trophic cascade exists in a river can help managers identify the best way to manipulate productivity of certain species of interest. Changes in primary productivity level, such as due to warming, can affect fish communities depending on the strength of the 'top-to-bottom' control of the ecosystem (Kratina et al., 2012; Polis, 1994). The seasonal changes in resource availability could influence food web complexity and ingestion rates, both of which peaks in the summer when generations of freshwater populations overlapped, and started declining when prey became scarer or outgrew their predators (Woodward et al., 2005). The low resource availability (Hannesdóttir et al., 2013; Johnson et al., 2017) and low condition factor and somatic energy of juvenile salmonids during the winter (Morash et al., 2021) could also impact the energy flow within freshwater food webs. Kratina et al. (2012) has shown that trophic cascades seem to vary seasonally with warming leading to stronger trophic cascades during the winter and weaker algae blooms in the summer. Whilst understanding that food webs vary seasonally within rivers and most likely impact the growth of juvenile salmon, there are currently limited studies on juvenile Atlantic salmon in the winter (Cunjak, 1996). A study has also shown that an introduction of a top predator into a chalk stream in the UK created a cascading effect that slowed the detrital processing rate (Woodward et al., 2008). Trophic interactions of food web may also be disrupted by phenological mismatches between consumer and resources (Perkins et al., 2010).

Climate change and changes in hydrology can restructure food webs, which alters species diversity and the strength and patterning of trophic interactions (Perkins et al., 2010). Food webs can also differ between simple and high-diversity community structures, in which the addition of terrestrial subsidies plays a primary role in increasing the species diversity within a food web (Hladyz et al., 2011; Johansen et al., 2005). Changes in abundance, composition, and diversity of species have consequences for food web stability and the transfer of resources through the food web (Perkins et al., 2010). For food webs in Icelandic rivers though, terrestrial subsidies play less of a role due to the lack of riparian vegetation surrounding riverine habitats. Additionally, some food webs may be able to compensate for species loss by gaining new species through range shifts, but large species such as fishes have limited dispersal ability, therefore large predators (such as the Atlantic salmon) in freshwater food webs may not be easily substituted or shifted (Perkins et al., 2010).

4. Drivers of Population Dynamics of Juvenile Atlantic Salmon

There are many different drivers of changes in population dynamics of juvenile Atlantic salmon, which includes food availability, temperature, water discharge, habitat change, and river management. Population dynamics refer to the continuous change in abundance of animals and plants over space and time (Fogarty, 2001). This thesis will be focusing on the factors that influence food availability and variation in food availability over space and time. Therefore, in the following, I will explain how food availability has been known to affect juvenile salmonid populations. I will also discuss management strategies that may influence the food availability within rivers and how future climate change impacts may affect food availability for juvenile salmonids.

a. Food Availability and its Management in Rivers

Vegetation, catchment characteristics and autochthonous material, and thereby primary productivity, can determine the density and diversity of invertebrates (Gíslason et al., 1999; Lárusdóttir et al., 2000). The availability of nutrients within streams constraints the productivity of the food web. Resource requirements of juvenile Atlantic salmon changes throughout their life history as they grow, as increasing body size can increase their resource requirements and higher amounts of prey allows for greater size and higher growth rates (Arnekleiv et al., 2006; Einum & Nislow, 2011). Diet also varies seasonally over time in many systems, as food availability can differ due to changes in productivity. Predictably, the stomach content of salmonids does vary seasonally depending on food availability (Björnsson, 2001; Kreiling et al., 2021). Seasonal variations in food availability can affect the condition factor and growth of salmonids (Gíslason & Steingrímsson, 2004). Terrestrial invertebrates are usually found in the drift column during the summer (Johnson et al., 2017). A study in River Teno/Tana, Finland/Norway, has shown that food consumption increases from May to a peak in July and August and declines during autumn (Amundsen & Gabler, 2008). Food quantity and quality are important drivers as salmonids are most abundant in the most productive areas of a river with a high invertebrate biomass. Prey availability also changes seasonally and with temperature (Kallio-nyberg & Koljonen, 2020). Additionally, high competition for food and territory space in rivers with high fish densities can limit the number of resident Atlantic salmon in an area (Grant et al., 2017; Nevoux et al., 2019). Salmonids inhabiting the same area may have to share and exploit more resources and have different diets to adapt and compete in those areas (Amundsen & Gabler, 2008; Fausch, 1998; Fausch & White, 1981; Miyasaka et al., 2003; Mookerji et al., 2004).

In terms of management, some actions have been proven to affect prey availability. River management methods such as increasing riparian vegetation, in-stream vegetation, and nutrient enhancements acting as a subsidy have been used to influence the food supply of juvenile salmon and the productivity of food webs (Allan et al., 2003; Marsh et al., 2022). Additionally, high macrophyte cover can provide more resources for juvenile salmon and reduce the negative effect of interspecific competition (Marsh et al., 2022). River management approaches built on these principles, such as shading of watersheds to lower temperatures, may allow species to survive and sustain diversity in ecosystems at risk from increasing temperature due to climate change (Parmesan et al., 2023). In the context of Iceland, where cold climates and nutrient poor lands do not promote fast growth of riparian vegetation, increased production and growth of invertebrates could in theory be achieved through production of benthic algae within rivers (B-Béres et al., 2023; Fuller et al., 1986). Observational studies have shown that large-bodied invertebrates such as Simuliidae, which provides the one of the largest energy contents for juvenile salmon, mainly feed on the drifting algae (diatoms) and detritus from lakes (Gíslason & Jóhannsson, 1991). Other studies have shown the addition of inorganic nutrients could produce large diatom populations that could be grazed by aquatic invertebrates, leading to increased biomass in treated areas (Armitage, 1995). The promotion of natural production of macroinvertebrate stocks is the most suitable and sustainable strategy for boosting the food availability and should be highly encouraged (Deegan et al., 1997; Marsh et al., 2022). Therefore, depending on primary productivity and temperature, river management can enhance the production of macroinvertebrates prey within rivers. Although it is important to mention that only increasing food abundance may not be an efficient method in increasing salmonid populations as salmonids are territorial predators (Grant et al., 2017), therefore the increase in

suitable habitats for salmonids are also necessary for sustainable population growth of salmonids.

b. Climate Change and the Food Web

The local climate in Iceland is classified as cool temperate maritime and the warmest average monthly temperature is just above 10°C, and coldest mean temperature being close to 0°C (Brittain et al., 2009). Due to climate change, models predict greater warming in the north of Iceland than the south. Indeed, air temperatures have increased between 1.0 to 1.7°C from years 1986 to 2015, with a projected average of 1.0°C per century and greater warming in the winter than summer (Björnsson et al., 2023).

Temperature is a strong driver in population dynamics of Atlantic salmon, either through direct effect on the fish, or through aspects of the ecosystem, primarily the food web. Temperature can influence the food productivity within a river (O'Gorman et al., 2016). Changes in temperature can also affect fish directly and those impacts can vary between stages of development. Climate change might be one of the main environmental impacts to salmon populations, which could affect their metabolism, growth, life history, survival, behaviour, food availability, abundance, and shifts in range (Einum & Nislow, 2011; Heino et al., 2016; Jonsson & Jonsson, 2011; Nevoux et al., 2019; Sundt-Hansen et al., 2018). Atlantic salmon are thermally sensitive, oxygen demanding, need cold, clean waters and are sensitive to extremes in flows (Nicola et al., 2018). It has been hypothesized that climate change, especially at higher latitudes, could have a larger seasonal impact on Atlantic salmon populations (McGinnity et al., 2009). Curiously, a study has shown that there were no effects of increased temperature on Atlantic salmon populations in northern Europe, whereas populations of brown trout have been found to increase and replace Arctic charr populations in rivers (Svenning et al., 2022). A local study of landlocked brown trout populations in Iceland found an increase in biomass, abundance, growth rate, and production, that correlated with increasing stream temperature, which the data indicated was largely driven by increases in resource availability (O'Gorman et al., 2016). Global warming can also cause changes in freshwater ecosystem properties and responses, such as earlier development of phytoplankton and earlier spawning of fish in spring and extension in the growing season (Parmesan et al., 2023). Additionally, climate change can increase the chances of floods and droughts in rivers, which can affect the habitats of fish. Warming can also affect the ocean distribution of Atlantic salmon and shift individual migration routes (Strøm et al., 2019b). Many studies show that increasing river temperatures increases metabolism cost, prevalence of proliferative kidney disease, food requirements, decreases age at smoltification, and affect reproductive behaviour (Kallio-nyberg & Koljonen, 2020; Kristmundsson et al., 2023; Nevoux et al., 2019; Nicola et al., 2018; Olmos et al., 2019; Sundt-Hansen et al., 2018).

Like all animals, Atlantic salmon has thermal limits, that affect survival, feeding and growth. Temperatures reaching near lethal or close to sub-lethal thresholds (>25.0 °C) can increase mortality (Beechie et al., 2012; Elliott & Elliott, 2010; Nicola et al., 2018). Temperatures above or below optimum egg development temperature (0 – 16°C) could change sizes of fry with insufficient energy reserves and higher mortalities. But Atlantic salmon can adapt to some extent, by matching energy demands by laying eggs of appropriate size, slowing development rates, shifting egg development to earlier emergence time, or by adjusting

spawning time (Bøe et al., 2019; McGinnity et al., 2009; Saltveit & Brabrand, 2013). Throughout the distribution range of Atlantic salmon, thermal limits are different for each population, geographical origin, and life stage (Elliott & Elliott, 2010; Jonsson & Jonsson, 2011; Strøm et al., 2019a; Verspoor et al., 2007). Natural selection on standing genetic variation will likely lead to shifts in relevant traits (possibly even the optimum temperature of growth) for Atlantic salmon to adapt to rising temperatures. Temperature change can shift the timing of migration, reproduction, age-at-maturity, age-at-juvenile migration, growth, and survival (Parmesan et al., 2023; Rinaldo et al., 2023).

The current climate change projections indicate warmer winters and earlier springs with increases in water temperature in rivers and lakes (Parmesan et al., 2023), which may lead to improved feeding opportunities of juvenile salmonids in the northern edge of the species range (Jonsson & Jonsson, 2011). Seasonal fluctuations could affect trophic dynamics and temperature increases due to climate change may alter the community and primary production in rivers, thus affecting Atlantic salmon production and growth (Jonsson & Jonsson, 2011; Nelson et al., 2017a; Nevoux et al., 2019; Verspoor et al., 2007). Furthermore, temperature influences the availability of macroinvertebrates within streams, and studies have shown that warming will increase the production of larger-bodied, slower-growing taxa such as snails and Simuliidae larvae, whereas small-bodied taxa with higher growth rates such as Chironomidae larvae may decrease (Nelson et al., 2017b). Warming could also change the emergence pattern of chironomids (Hannesdóttir et al., 2010), therefore affecting the availability of larvae within streams during growing seasons. However, in the southernmost salmon populations, where the fish experience severe consequences of climate change, the growth of juveniles may be constrained due to very high water temperatures during the summer that may even cause population extinction due to extreme heat waves (Bednar-Friedl et al., 2022; Jonsson & Jonsson, 2011; Parmesan et al., 2023). Warming has also been shown to change community compositions and length of food chains in Icelandic freshwater ecosystems (Woodward et al., 2010b).

5.Study Area: Rivers in Iceland

The study rivers for the project include River Vesturdalsá, Hofsá, Selá, Miðfjarðará, Krossá and Elliðaár. 14 additional rivers in the North Atlantic were also included for comparative analysis for chapter 1.3.b in this thesis. The main focal area of the project was in Northeast Iceland, which included Vesturdalsá, Hofsá, Selá, and Miðfjarðará (*Figure 3*). These four rivers were chosen because they contain some of the most northernly distributed Atlantic salmon populations in the world. In these rivers, Brown trout (54,005 individuals) had the highest rod catch, followed by Atlantic salmon (43,183 individuals) and Arctic charr (26,348 individuals) in 2022 (Bárðarson et al., 2023). There are usually more variable climatic conditions in NW and NE regions of Iceland than W and SW regions (Antonsson et al., 2005). Growth rates of salmonids also vary between different regions in Iceland (Antonsson & Gudjonsson, 2002). In addition, there is little riparian vegetation in Iceland (Brittain et al., 2009; Petersen et al., 1995). As referred above, beside Atlantic salmon, two other salmonids are found in these rivers, brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*).

Rivers of Northeast Iceland represent the main riverine habitat of salmon populations in one of the northernmost outskirts of their distribution. This makes them interesting to study as

these populations are relatively stable in number whilst living at the edge of their optimal environmental conditions. Due to extensive monitoring, ~40 years of data on the salmon population on some of these rivers have been collected by the Marine and Freshwater Research Institute (MFRI) in Iceland (Bárðarson et al., 2023; Thordardottir & Guðbergsson, 2017). The long-term monitoring ecological protocol and low species diversity of Vesturdalsá in NE Iceland also makes it good for studying, and thus, it is the main study river in this PhD project. Furthermore, Vesturdalsá is an index river used by MFRI and ICES to monitor the state of Atlantic salmon stocks in Iceland (Bárðarson et al., 2023; ICES, 2023). Similarly, the salmon stocks in Vesturdalsá have been used by the Working Group on North Atlantic Salmon (WGNAS) within ICES as one of the stocks being monitored for the return rate of smolts to adults (ICES, 2023). The salmon rivers in this area (Northeast Iceland) are wetland heath streams shared with other freshwater fish such as Arctic charr and brown trout (Brittain et al., 2009; Petersen et al., 1995). Each river usually is dominated by one freshwater fish species and is dominated by relatively few species at each trophic level (Gíslason & Steingrímsson, 2004). The rivers are fertile, have relatively stable water discharges (an average flow of 5.0 m^3/s (Rist, 1990)) and catchment areas are well vegetated, by Icelandic standards (not forested) (Antonsson et al., 2010; Antonsson & Gudjonsson, 2002). These river systems have a high density and low diversity of macroinvertebrates (Gíslason et al., 1999). In addition, the chemical composition and nutrient availability in Icelandic rivers are determined by the geology, topography, and vegetation cover (Gíslason et al., 1999).

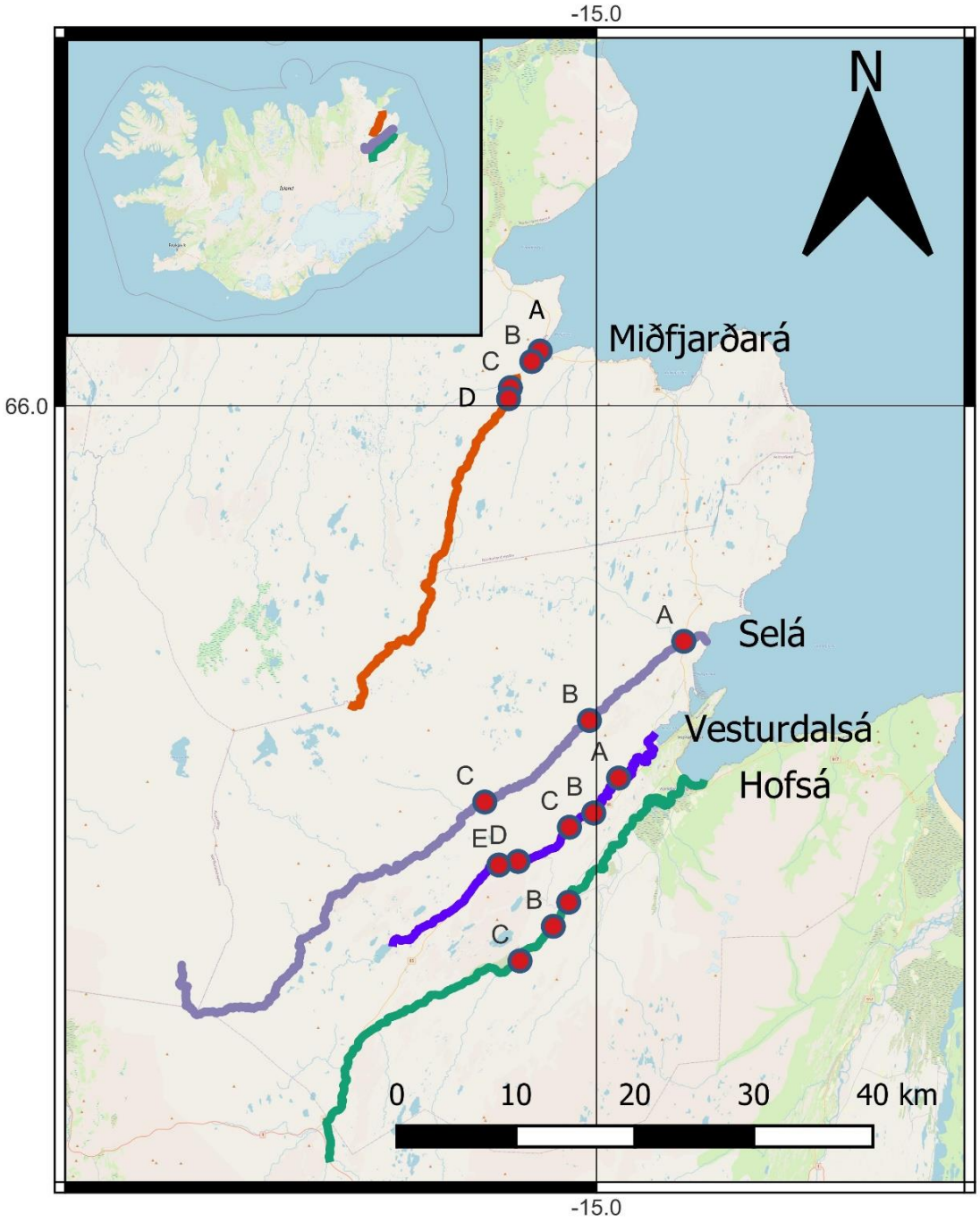

Figure 3: Map of the four study rivers- Vesturdalsá, Hofsá, Selá, and Miðfjarðará, in Northeast Iceland. Top-left inset shows a map of Iceland with the four rivers.

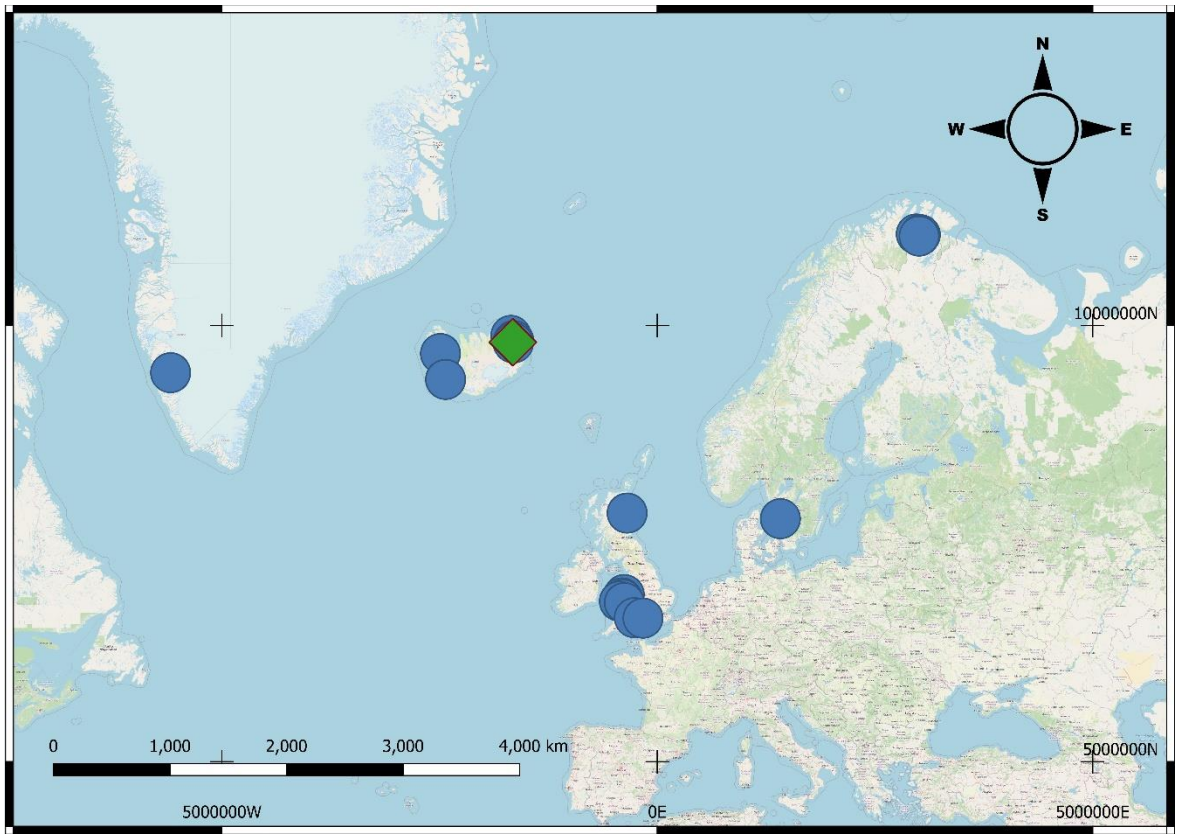

Figure 4: Map of the 20 Atlantic salmon study rivers in the North Atlantic that were analysed in this thesis, with the main study river, Vesturdalsá, highlighted as a green diamond. The 20 rivers are listed in Table 1.

Table 1: List of the 20 study rivers in the North Atlantic, ordered from the highest to lowest latitudinal degree.

River	Country	Latitude (°N)
Badda	Finland/Norway	69.95
Vidgaveädji	Finland/Norway	69.92
Teno	Finland/Norway	69.92
Utsjoki	Finland/Norway	69.87
Midfjardará	Iceland	66.04
Selá	Iceland	65.83
Vesturdalsá	Iceland	65.75
Hofsá	Iceland	65.73
Krossá	Iceland	65.27
Kapisillit	Greenland	64.43
Elliðaár	Iceland	64.13
Fiddich	United Kingdom	57.44
Högvadsån	Sweden	57.13
Nant Pen y Cwm	United Kingdom	52.64
Afon Bidno	United Kingdom	52.43
Afon Marteg	United Kingdom	52.33
Afon Berwyn	United Kingdom	52.22
Upper Duhonw	United Kingdom	52.13
Mill Stream	United Kingdom	51.17
Test	United Kingdom	51.14

2. Aims of the Thesis

The main objective of this thesis is to study the impacts of food availability on juvenile Atlantic salmon populations and their role in freshwater food webs in the North Atlantic over space and time. Specifically, to compare differences over time in the food web structure over the summer period and from 1997-2020, and to explore differences in food webs within and between rivers in Iceland, and between rivers in the North Atlantic.

6. **Paper I** explored the invertebrate composition and prey choice of juvenile Atlantic salmon in nutrient-poor streams. The hypotheses include:
    a. The abundance and biomass of prey available to juvenile salmon differ between and within rivers but have similar invertebrate assemblages.
    b. Prey items consumed by juvenile salmon differ in size.
    c. Juvenile salmon in these systems show no selectivity for the most abundant prey items, but high selectivity for large-bodied prey items.
    d. The most abundant prey item consumed is Chironomidae, which is the main prey choice for juvenile salmon in NE Iceland.
7. I investigated the trophic relationships of juvenile Atlantic salmon over time in a cold, low-productivity, salmon-dominated river in **Paper II**. The hypotheses are:
    a. The salmonid-invertebrate predator-prey relationships will vary between years and along temperature gradients in Vesturdalsá with higher productivity and prey availability in later years due to warming.
    b. Food webs in Vesturdalsá changes over the summer period due to the increase in growth of macroinvertebrates and primary productivity, therefore affecting the prey choice and population of juvenile Atlantic salmon.
8. In **Paper III**, I examined the spatial similarity of predator-prey relationships in Atlantic salmon sink food webs by comparing trophic relationships within and between rivers in Northeast Atlantic. I hypothesise that Atlantic salmon food webs are:
    a. Similar within rivers in cold and northern latitudes and have a simple structure (Woodward et al., 2010b) due to similar catchment characteristics in comparison to temperate rivers (Ólafsson et al., 2002).
    b. Alike within Iceland as rivers share similar physicochemical characteristics and ecology within the country.
    c. Different across latitudinal, temperature, and vegetation density gradients in the North Atlantic because of differing productivity levels and freshwater macroinvertebrate communities. The food webs will increase in complexity of food web structure with decreasing latitude and increasing temperature and vegetation productivity, such as decreasing food chain length and increasing connectivity in rivers at lower latitudes (Jake Vander Zanden & Fetzer, 2007; Shah et al., 2015).

3. Summary of Methods

First, I describe, in brief, the field sampling methods and statistics used in this thesis. I used both field-collected data in Iceland and algae, invertebrate, and fish population abundance and biomass data from published literature and population monitoring reports. Further descriptions of data collection, source, lab processing, and statistical analysis in the following chapters.

1.Field Sampling in Rivers in NE Iceland

Table 2: Summary of field sampling conducted in the four rivers in the summer of 2020, including across sampling sites and over 4 periods in Vesturdalsá[1].

River	Site	Period 1	Period 2	Period 3	Period 4
		9-14 June	1-4 July	27-31 July	20-29 August
Vesturdalsá	A	*a,b,d,e,f*	*a,b,d,e,f*	*a,b,d,e,f*	*a,b,c,d,e,f,g*
	B	*a,b,d,e,f*	*a,b,d,e,f*	*a,b,d,e,f*	*a,b,c,d,e,f,g*
	C	*d,f*	*d,f*	*d,f*	*a,b,c,d,e,f,g*
	D	*d,f*	*d,f*	*d,f*	*a,b,c,d,e,f,g*
	E	*a,b,d,e,f*	*a,b,d,e,f*	*a,b,d,e,f*	*a,b,c,d,e,f,g*
Hofsá	3 sites				*a,b,d,f,g*
Miðfjarðará	4 sites				*a,b,d,f,g*
Selá	3 sites				*a,b,d,f,g*

Table 3: Number of samples taken at each sampling site, the total number of samples collected, and total number of samples processed for each sampling method in the summer of 2020.

Sampling method	Samples per site	Total samples	Samples processed
Algae identification	2	48	46
Benthotorch measurements	30	709	709
Chlorophyll	10	50	50
Invertebrate drift	2	60	56
Invertebrate stone scrapes	10	140	95
Invertebrate surber	10	150	77
Invertebrate kick	2	28	25
Fish Stomach-pumping	25	691	691

[1] *a*: Algae identification samples, *b*: Benthotorch algae measurements, *c*: Chlorophyll-α samples, *d*: invertebrate drift samples, *e*: Invertebrate stone and kick sampling, *f*: electrofishing and stomach pumping, *g*: Invertebrate surber sampling

Field sampling was conducted in the summer of 2020 in the four study rivers, and the materials used for **Papers I, II, and III** (Table 2). Three sites were sampled in Hofsá and Selá, whereas four sites were sampled in Miðfjarðará, and five sites were sampled across four time points from June until August in Vesturdalsá. In addition, samples of invertebrate and fish populations from sites B and E in Vesturdalsá that were taken yearly since 1997 were also used for comparison analysis. Algae concentrations and populations were measured using a BenthoTorch (bbe Moldaenke, GmbH, Germany) and with stone scrapes (Adams et al., 2013; Lento et al., 2022a; O'Gorman et al., 2017). BenthoTorch *in vivo* fluorometer was used for measuring periphyton biomass and algal community composition. Measurements were made on three different sides of ten randomly picked stone in a 15 m long transect at each sampling site. Chlorophyll-α measurements (µg cm^{-2}) were made to compare with the algae concentration results from the BenthoTorch. Therefore, measurements from BenthoTorch may be different from algae samples. Chlorophyll-α samples were taken from a quadrat (8.64 cm^2) from another ten randomly picked stones inside the transect. Samples were collected and drained using a filter paper and was frozen until processing. Chlorophyll-*α* concentration was measured using a UV-Vis spectrophotometer (HACH DR 5000^{TM}) and the absorbance of each sample was measured at 665 and 750 nm wave lengths, and then was repeated after adding 1N HCl acid to correct for pheophytins. Chlorophyll-*α* concentration (µg cm^{-2}) was calculated using: $C = \frac{A*K*((665_b-750_b)-(665_a-750_a))*V}{S*l}$, where *A* is the absorption coefficient of chlorophyll-α, *K* is the factor of correction for acidification, 665_x and 750_x is absorbance at 665nm and 750nm respectively, *V* is volume of ethanol, *S* is area of quadrat, and *l* is length of path light through cuvette (EPA, 1991; Ritchie, 2006; Weber, 1973). This showed that BenthoTorch chlorophyll measurements were on average higher than the measurements from algae samples (**Paper III**). Other studies have also shown that algae mat thickness can affect the BenthoTorch measurements and the community composition and thus, may not reflect the true concentration (Kahlert & McKie, 2014; Kaylor et al., 2018). Algae samples for species identification and abundance count were also collected by scraping algal content off of three quadrats from two randomly picked stones. The samples were preserved in Lugol solution.

Invertebrate populations were sampled using drift net, Surbers sampler, kick net, and stone scrape at each sampling station. Drift nets were used to gather data on the availability of prey items for juvenile salmonids in the drift column (Johnson & Ringler, 2016; Weber et al., 2017). Samples were collected for 5 minutes using nets (48 × 33 cm with 363 µm mesh size) situated at two locations along the sampling transect. Velocity (m/s) at each sampling site of the river were also measured using a YSI© Sontek Flowtracker Handheld Acoustic Doppler Velocimeter (Ohio, USA). Two invertebrate samples were taken using kick nets (25 × 25 cm with 250 µm mesh size) by kicking for 30 seconds. Ten stones were randomly chosen, and all the content of the surface of the stone were scrubbed off and collected. Ten additional areas were sampled using Surber sampler (25 × 25 cm with 250 µm mesh size) during sampling in August at all sites. Invertebrates from stone scrape and Surber samples were compared for the August 2020 dataset and showed that sampling with stone scrapes had a lower species diversity than using Surber sampler (Shannon diversity of stone scrapes: 0.610; Shannon diversity of Surber samples: 0.866). Stone scrapes also had lower individual biomass of species in comparison to collection of invertebrates through Surbers (detailed results comparing methodology found in **Paper II**). I kept the analysis of data collected using these two methodologies separate, therefore there was no cross analysis using both stone scrape and Surber datasets and does not further affect in the interpretation of results. All samples collected

were preserved in 70% ethanol solution and processed in the lab to get density and individual biomass data.

Single-pass electrofishing was conducted in each site at each period to sample the salmonid population and to collect gut content samples. First, the fish were identified to species level and their fork length and weight measured. Scale and otolith samples were also dissected from one fish at each size class to get an estimate of age. Only fish with fork length above 5 cm were stomach pumped, whereas a maximum of five fish below that size were killed, dissected and gut content collected. Stomach-flushing was done with a water pump linked to a rubber tube with a plastic pipette tip. This method of collecting gut content should harm the fish as little as possible, and is highly effective in removing stomach content of salmon (Kamler & Pope, 2001). The area (m^2) electrofished was measured to enable calculation of the salmonid density index (Bárðarson et al., 2023). All the fish caught were able to recover and was released back at site-of-capture (except around five individuals per station that were sacrificed because they were below 5 cm).

I used the density index estimate from the August sampling period in 2020 as an estimate of true abundance of juvenile Atlantic salmon in the river during the summer. It was assumed that the catchability of fish at all sizes were highest due to their growth and favourable water flow. Additional tagging studies of Atlantic salmon in the river showed that juvenile salmon migrated little in between sites (Bárðarson, n.d.), therefore the density of fish at each sampling site is assumed to be relatively stable during the summer sampling period. The age classes of fish from the electrofishing surveys were used the estimate age proportions of fish at each sampling site. In order to correct for the density of age 0+ salmon in Vesturdalsá due to the difficulty in capturing them during electrofishing (Niemelä et al., 2000), I had to estimate the date of emergence and first feeding to find out when they started becoming a part of the food web in the river. The emergence of 0+ Atlantic salmon and their first feeding were also estimated in Vesturdalsá using growth equations based on water temperature of the river (CRISP, 1981; Gorodilov, 1996). Spawning was assumed to be on the 1st of November and the alevin were estimated to have absorbed the yolk sac on 15th July in 2020. Arctic charr densities were calculated using electrofishing in the same area as such data strongly reflects studied charr migration patterns (Johnson, 1980; Jonsson & Antonsson, 2005) and there is a high catchability of charr using electrofishing due to their habitat preferences (Heggberget, 1984; Heggenes & Saltveit, 2007).

2.Processing of samples and identification

Drift and benthic invertebrate and gut content samples were counted and identified to family or order using identification keys (Bouchard, 2004; Kriska, 2013; Macan, 1960), except for terrestrial input which was separated into a one general broader category. Invertebrates' body length and head width (mm) were also measured using an eyepiece graticule. Biomass of invertebrates was estimated using published length-mass regression relationships (Baumgärtner & Rothhaupt, 2003; Benke et al., 1999; Burgherr & Meyer, 1997; Kang & Kang, 1997; O'Gorman & Emmerson, 2010). Chironomidae (Diptera) larvae from benthic samples in NE Icelandic rivers were also mounted using Hoyer´s Solution (Anderson, 1954) and identified to the lowest possible taxonomic level using identification keys (Cranston, 1983; Heiri, 2013; Oliver & Roussel, 1983; Schmid, 1993) for **Paper I**. Equal volumes of algal samples were put under a microscope where abundances of diatoms were counted (individuals m^{-2}). Samples of

chironomids, simuliids, and Trichopterans (Diptera) larvae were dissected, and the digestive system removed and mounted onto slides to identify their diatom gut content under a microscope. Diatoms were identified to genus level. Sizes of diatoms were measured using Image J (Schneider et al., 2012), which was then used to calculate the individual biomass using established biovolume equations from Hillebrand et al. (1999). Chlorophyll samples were measured using a spectrophotometer (further detailed methodology of preparing the samples for measurement is mentioned in **Paper III**).

3.Reconstructing Food Webs

Using the abundance and individual biomass of species, I am able to reconstruct food webs to compare them over space and time. Building mass-abundance food webs require using population densities and biomass data (Hudson et al., 2013; O'Gorman et al., 2019; Perkins et al., 2018). Furthermore, I also expanded the temporal and spatial range beyond data that was collected in the field in order to make broader comparisons and used population biomonitoring data that had been collected before using published literature to get estimates of population density and biomass data to reconstruct those food webs.

Population densities were calculated using the following equation for relative invertebrate number per volume (D; individuals m^{-3}): $D = \frac{N}{t \times w \times d \times v}$, where N was the abundance of each invertebrate group, t was drifting time (secs), w and d was frame width (m) and depth (m) of drift net in the water respectively, and v was the velocity of the water. The relative densities of benthic invertebrates and juvenile salmonids (D; individuals m^{-2}) were calculated using: $D = N/A$, where N was abundance of organisms at each site and A was the area sampled. Population biomass (B) of invertebrates and juvenile salmonids (mg m^{-2}) using: $B = M \times D$, where M is mean individual biomass.

Furthermore, previously available data gathered at the MFRI was used for **Papers II and III**. For **Paper III**, data on algae, invertebrate, and salmonid population data taken from previous annual surveys in two other rivers (Krossá (datasets from 2012-2020) and Elliðaár (datasets from 2011-2022)) and the same sampling methodology was used (Einarsson et al., 2020; Hansen & Eiríksdóttir, 2021; Ingimarsson, 2022; Sturlaugsson, 2023). **Paper II** also uses salmonid stomach content data and diatom, invertebrate, and salmonid data from Vesturdalsá from the 1997-2018 taken from previous reports by the MFRI (Antonsson, 2015; Bárðarson et al., 2023; Hansen & Eiríksdóttir, 2021). In **Paper III**, I compared predator-prey relationships of Atlantic salmon rivers from the North Atlantic, that relied on algae, invertebrate and salmonid population data from the published literature and reports (Anon, 2023; Arnekleiv et al., 2019; Bergh, 2022; Ekologigruppen Ekoplan AB, 2021; Environmental data MVM, 2023; Erkinaro & Erkinaro, 1998; Perkins et al., 2018; Woodward et al., 2021). These datasets were measured using similar sampling methodologies such as surbers and electrofishing to gather population abundance and biomass data, therefore allowing these datasets to be comparable across rivers. Known individual biomass of invertebrates and diatoms from literature (Benke et al., 1999; Méthot et al., 2012; Perkins et al., 2018) was used to fill-in missing data. See more details in **Paper II and III** below.

Food webs were reconstructed using *cheddar* R package (Hudson et al., 2013), which was also used to calculate different food web components and characteristics for **Papers II and III**. The 'nodes' of the food web were calculated as $\log_{10}$-transformed averages of population

abundance and individual biomasses of each taxonomic group. Gut content data of invertebrates and fish were used to build trophic links between 'nodes', and others were gathered from literature (Benke et al., 1999; Méthot et al., 2012; Perkins et al., 2018). Linear regression analysis of log-log mass-abundance (M-N) relationships of 'nodes' were used to get the food web properties, where the M-N slope, connectance, mean trophic level, mean chain length, and mean link angle were extracted. For **Paper II**, the M-N slope, mean chain length, and mean link angle of juvenile salmon trophic relationships were also calculated.

4. Statistical Analyses

All statistical analysis were carried out using R version 4.3.3 (2024-02-29) (R Core Team, 2023), run in the R-studio environment (2023.12.1+402) on a PC. In **Paper I**, prey selectivity (α) was calculated for prey items of Atlantic salmon in NE Iceland using the Manly-Chesson Index (Chesson, 1983): $\alpha = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j}$. r_i and n_i were proportions of food item *i* in the gut content of fish and the environment (benthic and drift prey items) and *m* was the number of prey categories. Prey selectivity values ranged from 0 to 1, from never eaten to complete preference. If α=1/m, then juvenile salmon exhibited no prey preferences, if α>1/m, there was prey selection, but if α<1/m, then there was avoidance of the prey item (Minder & Pyron, 2018; Syrjänen et al., 2011). Dietary niche overlap was also calculated between salmon and other coinhabiting salmonids in the NE rivers in Iceland for **Paper I**. The Freeman-Tukey (*FT*, (Smith & Zaret, 1982)) index: $FT = \sum \sqrt{p_{1j} \times p_{2j}}$ was used to calculate this. p_{1j} and p_{2j} were the mean proportion of prey resource (*j*) found in stomachs of species 1 and 2, respectively. FT values ranged from 0 of no overlap to 1 which was complete overlap (Marsh et al., 2022; Smith & Zaret, 1982). For **Paper III**, Diversity of prey items found in stomachs of juvenile salmon and other salmonids in Vesturdalsá were calculated using the Shannon-Weiner Index with the *vegan* package (Oksanen et al., 2022).

The distribution of various data was checked using the Shapiro-Wilk´s method, and non-parametric tests was used if normality assumptions were not met. Outliers were also removed from analysis, using Principal Components Analysis (PCA) plots, boxplots and further confirmation using Grubbs´s test. Non-parametric Kruskal-Wallis tests and/or Analysis of Covariances (ANOVA), and further Tukey and/or Dunn tests, were used in comparisons of abundances and biomass of diatoms, invertebrates, and salmonids between rivers, sites, and sampling periods during the summer for **Paper I, II, and III**. Gut content samples of juvenile salmonids were also compared between rivers, site, and sampling periods during the summer. In general, p-values from post-hoc analyses were adjusted with Bonferroni corrections, to account for multiple tests. Unpaired Wilcoxon signed-rank test was used to compare prey choice of salmon using invertebrate and gut content data. It was also used to compare FT indices between salmonid species in **Paper I**. In **Paper II and III**, The M-N scaling of food webs was compared using Linear Mixed Effects (LME) models and ANOVA routines in the *lmerTest* package (Bates et al., 2015; Kuznetsova et al., 2017). 'Nodes' and 'river' were included as a random effect in the model. Post-hoc Tukey tests were also used for further comparisons. **Paper I** also investigates the relationships between salmon stomach content and their weight using linear regression models. Additionally in **Paper II and III**, linear and polynomial models were used to compare feeding behaviour of salmon in different sites in Vesturdalsá and comparing food web properties between latitudes, temperature, vegetation levels, and years using the *lm*

function from the *stats* package. Average air temperature (°C) data of each river were extracted from the WorldClim database using the *raster* package (Hijmans, 2023). Estimates of mean water temperature (°C) of Vesturdalsá during the summer from 1997-2020 were available (Bárðarson et al., 2023). Productivity levels were also compared using Normalised Difference Vegetation Index (NDVI; hereafter referred to as vegetation productivity), and data were extracted from MODIS datasets (Didan, 2021) and extracted using QGIS (QGIS.org, 2023). Models were selected based on likelihood ratio tests.

4. Main Results and Discussions

Here I will go through the main results of the thesis chapter by chapter. First, I will cover the findings on the invertebrate composition and prey choice of juvenile Atlantic salmon in NE Iceland, which presented in **Paper I**. Secondly, I will present the temporal changes in trophic relationships of juvenile Atlantic salmon in a cold, low-productivity river, which includes the results of **Paper II**. Thirdly, the spatial comparisons of food webs of Atlantic salmon rivers in the North Atlantic are presented in **Paper III**, which also provides additional detailed spatial analysis of the food web community within Vesturdalsá.

1. Prey availability and stomach content of juvenile Atlantic salmon in NE Iceland

The first main aim of the thesis and of **Paper I** is to identify the invertebrate composition and prey choice of juvenile Atlantic salmon in nutrient-poor streams, which will give the base understanding of the structure of the trophic relationships between Atlantic salmon and their prey.

The data showed remarkably similar food availability for juvenile Atlantic salmon between the four rivers in NE Iceland studied here. In the same vein, the macroinvertebrate community was very similar in these rivers. The abundance of invertebrates differed however, with Miðfjarðará having the lowest invertebrate abundance in comparison to the other rivers ($p<0.05$; *Figure 5b* and *d*). Miðfjarðará also had a lower population biomass of benthic invertebrates than other rivers ($p<0.001$; *Figure 6d*), but there was no significant difference in the biomass of drifting invertebrates between rivers ($p=0.119$; *Figure 6b*). Benthic and drift invertebrates were found to mainly be composed of Chironomidae (Diptera) as shown in *Figure 5* and *Figure 6*, which concur with other studies on freshwater invertebrates in Iceland (Gíslason et al., 1998; Gíslason & Gardarsson, 2010; Kreiling et al., 2022). After chironomids, the second most abundant invertebrates were Oligochaeta, Gastropoda, terrestrial subsidies, and large-bodied Dipterans. The results supported that there is a low invertebrate species diversity in Iceland (Gíslason et al., 1999; Ministry for the Environment & The Icelandic Institute of Natural History, 2001), which could be largely driven by their island biogeographical isolation (Lento et al., 2022a). There was also no difference in abundance of benthic macroinvertebrates between sites in these four rivers, on the other hand, only the population biomass of macroinvertebrates in Midfjardará ($p<0.01$) and Selá ($p<0.05$) vary between sites. Post-hoc Dunn testing showed that there were lower biomasses of invertebrates in site B than site A ($p<0.05$) and C ($p<0.01$) in Midfjardará, and that the population biomass in site A was higher than in C ($p<0.05$) in Selá (Supporting Information of **Paper I**). Furthermore, Chironomidae *Eukiefferiella minor* and *Orthocladius spp.* had the highest abundance and population biomass (additional figures found in the Supporting Information of **Paper I**), which were similarly found in streams in the Hengill valley system in Iceland (Hannesdóttir et al., 2010). The population of larval Chironomidae did not differ between rivers in the drift column (abundance: $p=0.091$, biomass: $p=0.802$) but differed in the benthic population (abundance: $p<0.001$, biomass<0.001). Again, I observed that

the abundances of benthic chironomid larvae did not differ between sites within rivers, and only the population biomass of chironomids in Midfjardará differed ($p<0.01$). Thus, chironomids have been shown to play a significant role in the ecosystem in these low-productivity rivers (Gíslason et al., 1998; Gíslason & Gardarsson, 2010; Kreiling et al., 2022; Lai et al., 2024). Whereas the freshwater macroinvertebrate communities in southern temperate regions had a much higher diversity.

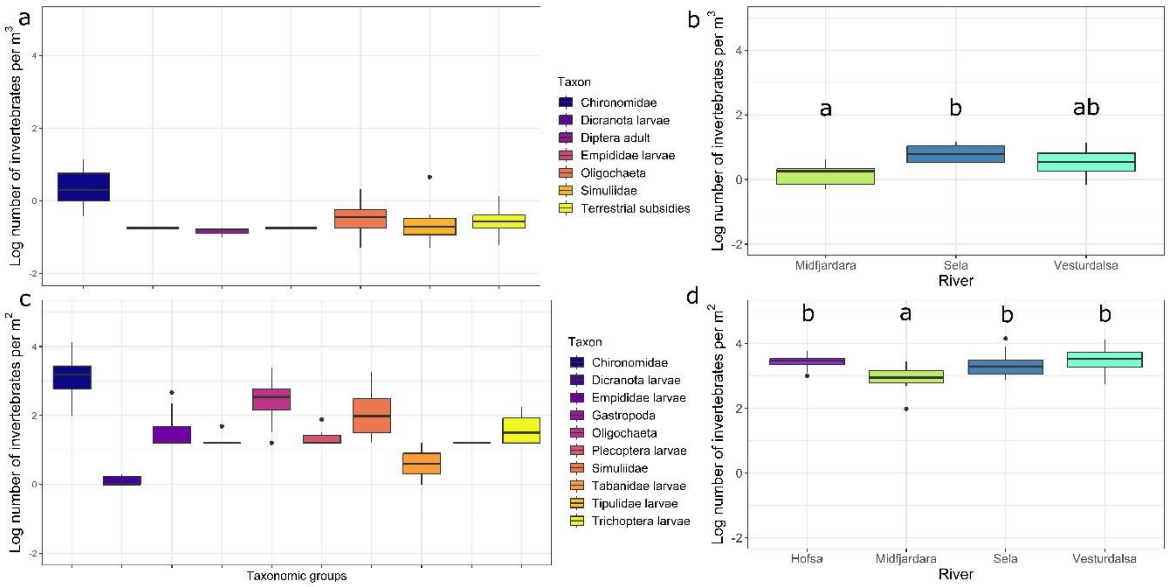

Figure 5: Variation in abundance of invertebrates in four rivers, caught in the drift (top; log_{10} of number of individuals/m^3) and benthic (bottom; log_{10} of number of individuals/m^2), by taxonomic groups (left) and rivers (right). Log_{10} abundances of different taxonomic groups of invertebrates differed significantly a) in the drifting column ($p<0.001$) and c) in the bottom substrate ($p<0.001$) in all four rivers. Log_{10} abundances found b) in the drift and d) in the bottom substrate were also significantly different between rivers ($p<0.05$ and $p<0.001$ respectively). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

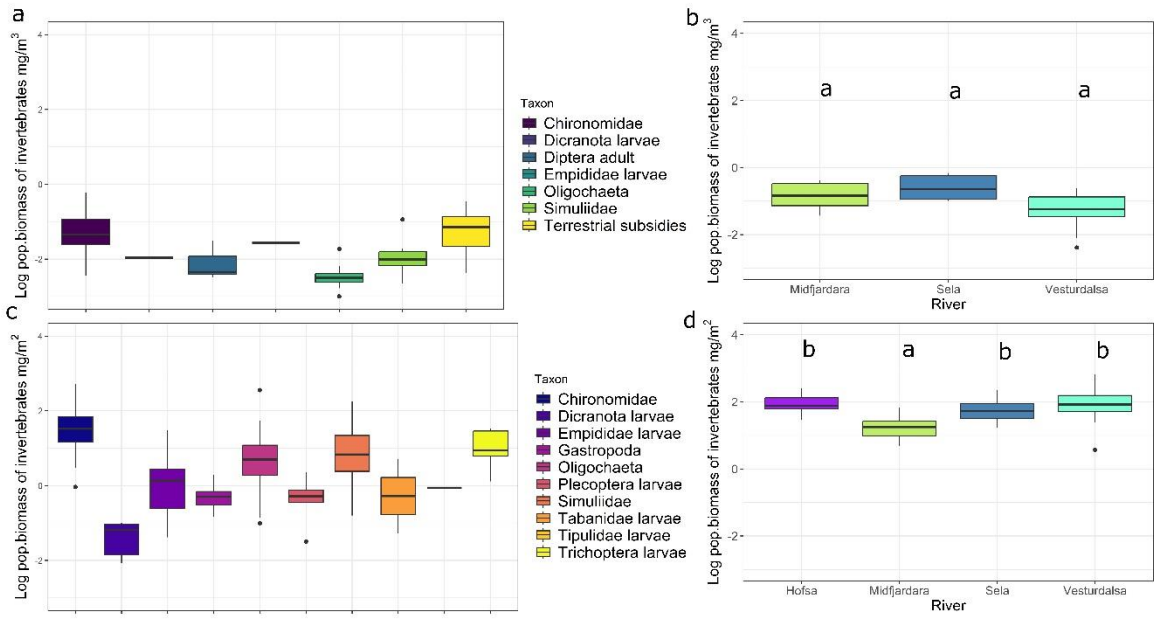

Figure 6: Variation in population biomass of invertebrates in four rivers caught with drift (top; $log_{10}(mg/m^3)$) and benthic (bottom; $log_{10}(mg/m^2)$) sampling, by taxonomic groups (left) and rivers (right). Log_{10} biomass of different taxonomic groups of invertebrates differed significantly a) in the drifting column ($p<0.001$) and c) in the bottom substrate ($p<0.001$) in all four rivers. Log_{10} biomass found b) in the drift was not significantly different between rivers ($p=0.119$) but was significantly different d) in the bottom substrate ($p<0.001$). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

With regards to the prey diet of juvenile Atlantic salmon, the prey availability clearly reflects the gut content of juvenile salmonids in these rivers, as they mostly consumed the Diptera larvae of the family Chironomidae in this study. Of them, the sub-family Orthocladiinae was found to be the most abundant and had the highest biomass in prey content of juvenile Atlantic salmon. This was also shown to be similar to juvenile salmon populations in the south and another NE river in Iceland, where they had consumed similarly, chironomids, simuliids, and freshwater snails (Kreiling et al., 2021). The largest biomass prey item was salmonid fry. Salmon in these rivers also vary in the abundance ($p<0.001$) and total biomass ($p<0.001$) of prey they consume, as shown in *Figure 7* and *Figure 8*. Juvenile salmon in Hofsá seem to consume larger Diptera, Trichoptera, and Simuliidae. Juveniles in Selá had consumed the most prey items, both when estimated as abundance and biomass. Salmon in Hofsá had consumed a higher proportion of large macroinvertebrates. The abundance ($p<0.001$) and biomass ($p<0.01$) of prey consumed by juveniles also varied between sites within Vesturdalsá, where a higher abundance was found upstream than downstream. Consistently, juveniles in Midfjardará showed a similar trend, a higher biomass of prey was consumed in upstream sites ($p<0.001$). Furthermore, the amount of chironomids consumed by juvenile Atlantic salmon also differed between sites across all rivers (abundance: $p<0.05$, biomass: $p<0.05$), with less abundance found downstream than upstream, except for Selá. Additionally, the results did not show that

resources were limiting in these study rivers, but Bárðarson et al. (2023) showed that the variations in juvenile Atlantic salmon populations in these rivers could be due to the fluctuations in temperature, which has an additional impact on food availability. O'Gorman et al. (2016) showed that increased temperature caused an increase in the growth and abundance of brown trout in a natural warming experiment in Iceland, which is likely due to higher trophic transfer efficiency and resource availability in warmer streams. Furthermore, the results stress the importance on chironomid productivity and its impact on food availability for juvenile salmon. I had also found that smaller-sized salmon consumed a higher diversity of prey items than larger fish, as larger fish consumed mainly chironomids. The juvenile Atlantic salmon also differed in average size between rivers ($p<0.001$). Juvenile Atlantic salmon in Hofsá was the largest across all age classes, whereas Atlantic salmon in Midfjardará was smallest in average size. There was a weak positive relationship between abundance of prey items and $\log_{10}$-transformed weight of juvenile Atlantic salmon (Adjusted $r^2=0.016$, $p<0.05$) and there was no relationship with biomass of prey items (Adjusted $r^2=0.00146$, $p=0.232$). Whereas juvenile brown trout in Laxá, another NE river in Iceland, was shown to consume larger prey as they grew larger (Steingrímsson & Gíslason, 2002), which was different to what was observed in the salmon in the NE study rivers.

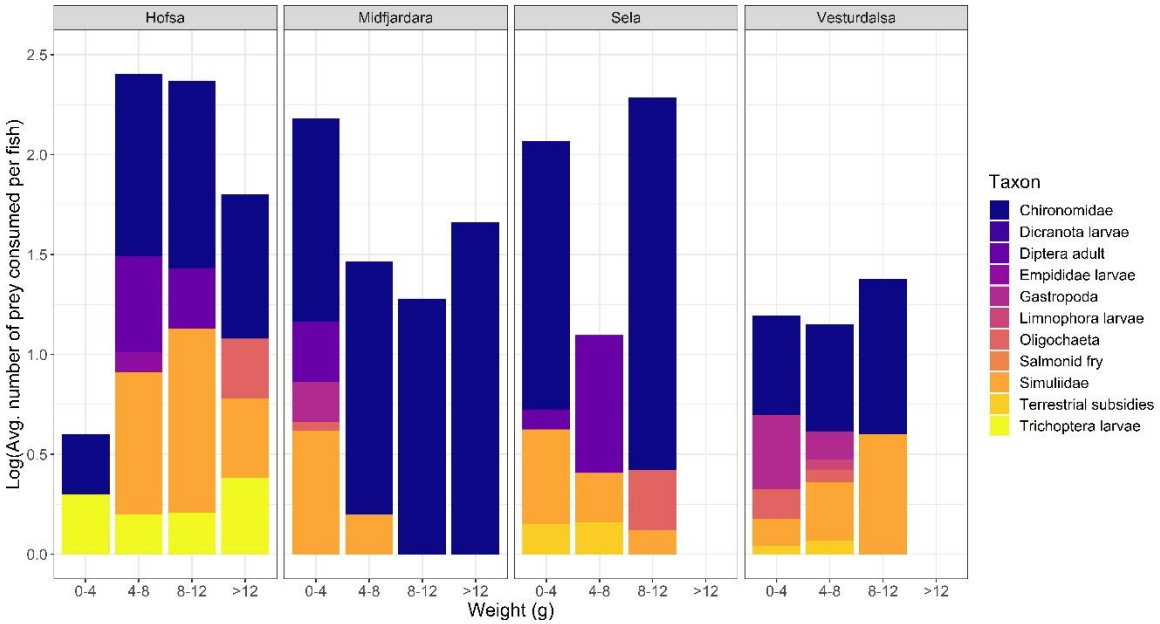

Figure 7: Log_{10} average number of prey items found in stomachs of juvenile Atlantic salmon (Salmo salar) differed significantly across rivers ($p<0.001$) and by fish weight (three size groups, $p<0.001$). The number of prey items consumed increased with weight ($p<0.05$). Log_{10} abundance also varied between taxonomic groups for all rivers ($p<0.001$) with Chironomidae being the most abundant in comparison.

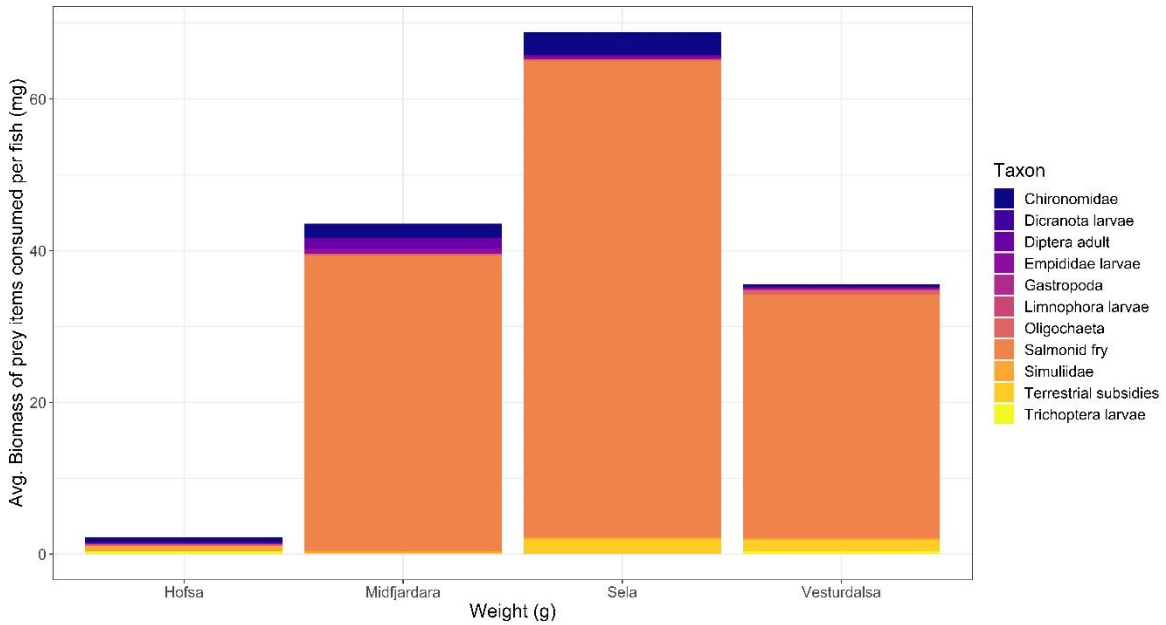

Figure 8: The average biomass of prey consumed per juvenile Atlantic salmon (Salmo salar) was significantly different between rivers ($p<0.001$). Biomass did not vary between different weight groups of juvenile fish ($p=0.232$).

Additionally, the data revealed high dietary niche overlap between salmonid species in this system. In terms of absolute numbers there was higher overlap between juvenile Atlantic salmon and brown trout (FT=0.908) than Atlantic salmon and Arctic charr (FT=0.964), but this was not formally significant (p=0.071). Juvenile Arctic charr seems to rely more heavily on drifting prey. Juvenile trout was significantly larger than other salmonids ($p<0.001$). The juvenile salmonid species in NE Iceland were all highly dependent on the consumption of chironomids and this indicates strongly how limited prey choices are in these low-productivity rivers. In comparison, there was a lower dietary niche overlap in the Frome (Armitage et al., 2017; Bowes et al., 2005; Marsh et al., 2022), a highly productive salmonid river in the United Kingdom, than in these four NE Iceland rivers. Salmon in these Icelandic rivers had to share more resources between individuals than their more southern counterparts, most likely due to a lower productivity and less prey diversity. Additionally, salmonids in more productive rivers are usually more dependent on terrestrial prey rather than larval aquatic prey because the banks are usually surrounded by riparian vegetation (Amundsen & Gabler, 2008; Dineen et al., 2007; Grunblatt et al., 2019; Johnson et al., 2017), but the riparian zone of rivers in Iceland have limited vegetation (nearly no forests (Gíslason et al., 1998; Gudjonsson, 1990)) and terrestrial prey items are rare. There is also a higher growth rate of juvenile Atlantic salmon in a more productive stream like the Frome (Mann, 1989). The species diversity of Iceland and its rivers is also low due to its isolated island biogeography and high latitude (Lento et al., 2022b; Ministry for the Environment & The Icelandic Institute of Natural History, 2001). Which results in Chironomidae being their main prey item consumed and suggests that the production of Chironomidae could largely influence the salmon population in these low-productivity rivers. Hannesdóttir et al., (2010) showed that temperature change can influence the production and development of chironomids, thus the main prey item of juvenile salmon in Iceland could be vulnerable to anthropogenic impacts.

a. Prey Choice of Juvenile Atlantic Salmon

Juvenile Atlantic salmon are known to feed on drifting animals, but occasionally they consume benthic organisms (Akbaripasand et al., 2014; Rader, 1997; Syrjänen et al., 2011). Prey selectivity of juvenile Atlantic salmon on benthic invertebrates varied significantly between the four different rivers ($p<0.05$) but did not for drifting invertebrates ($p=0.156$), as shown in *Figure 9*. Juvenile salmon did not exhibit any selection preference for chironomids. Additionally, for Oligochaeta there were also no preference and some slight prey avoidance as they were usually buried within the sediments and are less likely to be hunted (Bouchard, 2004). Smaller-sized juvenile Atlantic salmon were also less likely to be able to consume large-bodied invertebrates like Oligochaeta due to their inability to swallow them (Wańkowski & Thorpe, 1979). Juvenile Atlantic salmon had a higher prey preference for larger dipterans (such as Simuliidae), Trichoptera, and Gastropoda but these were not highly abundant prey items within the river systems in NE Iceland. Juveniles in Hofsá seemed to also avoid consuming chironomids or would rather consume bigger food items like dipterans. Therefore, juvenile salmonids in these rivers were shown to be more diet generalists (Andreassen et al., 2001), as they were consuming what was most abundant rather than spending more energy and effort to hunt for larger prey items.

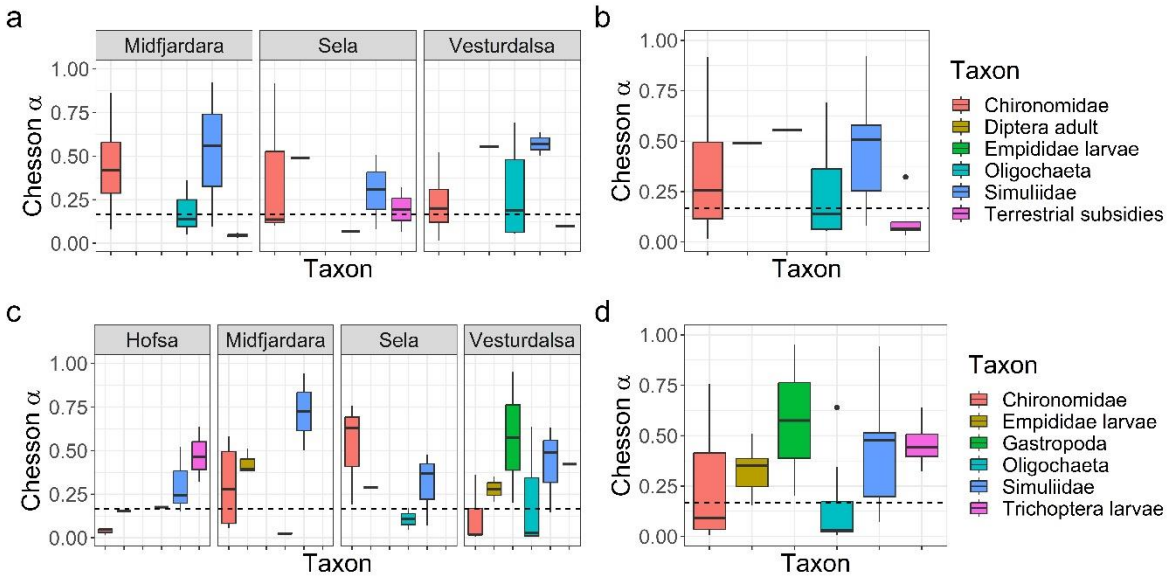

Figure 9: Variation in prey selectivity (Manly-Chesson α) of juvenile Atlantic salmon (Salmo salar) estimated for drift samples a) across rivers and b) combined between rivers, and benthic samples c) across rivers and d) combined between rivers. Values α=0.167 show no selectivity, α>0.167 shows prey preference, and α<0.167 indicates prey avoidance. Kruskal-Wallis test showed that the selectivity for different taxonomic groups differed significantly for benthic samples (p<0.05), but not drift.

2. Temporal Variations in Salmon Trophic Interactions in a Low-Productivity River in the Sub-Arctic

Having explored the invertebrate composition and prey choice of juvenile Atlantic salmon in a low-productivity river, the second main research question was to ask how much temporal variation was in the trophic relationship in a specific low-productivity salmon river at the northern range of the species distribution. To analyse this, data from 1997 to 2020 in Vesturdalsá was used for **Paper II**. In short, there was little temporal variation in trophic relationships and food web structure in Vesturdalsá for the study period. This further underlines the relatively simple food web structure of this river and impending adverse impacts of warming on the ecosystem of these rivers and the Atlantic salmon populations.

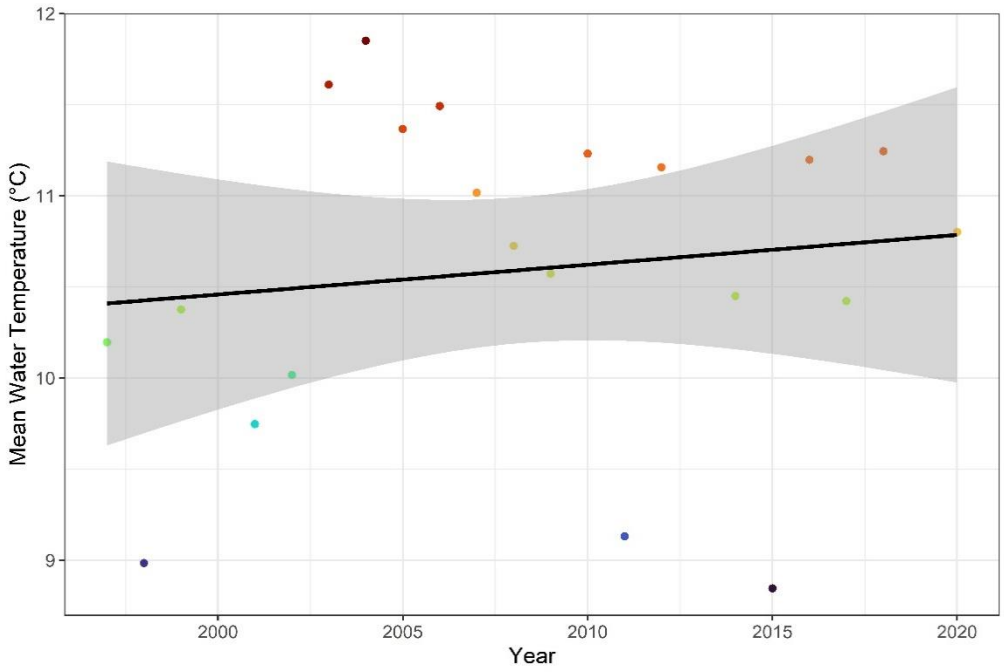

Figure 10: Average water temperature (°C) during the summer (June to August) in Vesturdalsá from 1997 to 2020.

a. Change in Predator-Prey Relationships Over Years in Vesturdalsá

The first main question for **Paper II** is whether predator-prey relationships in Vesturdalsá vary over time and temperature change from 1997 to 2020. The data indicated minor changes in predator-prey relationships over the summer (1997 to 2020) in Vesturdalsá. There were no significant differences in the M-N predator-prey relationship between years in Vesturdalsá ($F_{(22,214)}$=1.17, p=0.279), but there were significant differences in $\log_{10}$ abundance of aquatic species within the river between 1997-2020 ($F_{(22,214)}$=2.91, p<0.001). Post-hoc Tukey tests showed that the species abundance in 1997 and 2017 were significantly higher than most of the other years, which includes 1998, 2010, and 2013, as shown in *Figure 11* (further information

on post-hoc tests found in Supporting Information of **Paper II**). Species abundance in 2017 were also significantly higher than in 2008. Whereas abundances of species in other years were found to be similar. A previous study (Antonsson, 2015) on part of the same data from Vesturdalsá, reported that in 1997, juvenile Atlantic salmon consumed comparatively more of Simuliidae and other Diptera than in other years, and therefore the high productivity during that year seems to have also influenced their diet. Furthermore, there were no significant differences in M-N relationships and temperature (SE=0.00564, t=-0.681, p=0.497), thus it is unlikely that changes in M-N relationships were driven strongly by temperature fluctuations.

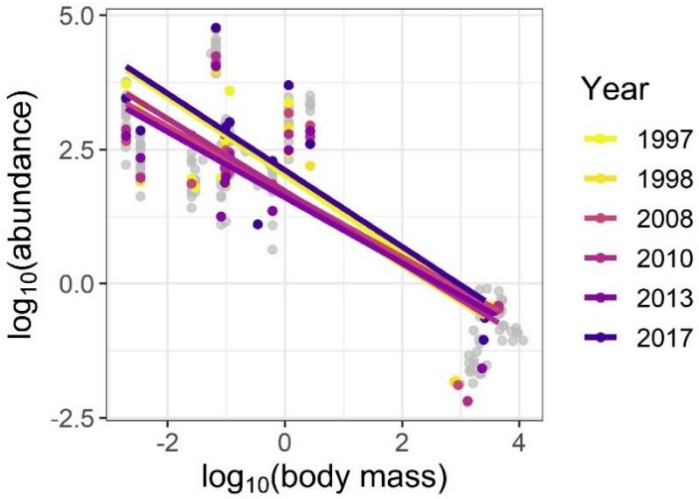

*Figure 11: Relationship between biomass and abundance in the Vesturdalsá salmon river over years. Shown here are the significantly different abundances within linear regressions of log-log M-N trophic relationships in 1997, 1998, 2008, 2010, 2013, and 2017 in Vesturdalsá. The greyed-out points are non-significant relationships (further information found in Supporting Information in **Paper II**).*

Additionally, some of trophic relationships properties were found to differ over time or with temperature. Except the mean trophic level and connectance of trophic relationships, which neither differed significantly over time (from 1997 to 2020) nor changed with temperature in Vesturdalsá. *Figure 12* and *Figure 13* shows the linear regressions of the slope, mean chain length, and mean link angle of trophic relationships and of juvenile Atlantic salmon trophic relationships over years and average water temperature, respectively. The slope (R^2=0.295, p<0.01) and mean link angle (R^2=0.273, p<0.01) of Atlantic salmon trophic interactions in Vesturdalsá significantly increased over time. On the other hand, in the same dataset, the mean chain length of trophic relationships significantly decreased over time (R^2=0.145, p<0.05). The slope of M-N relationship (R^2=0.153, p=0.09) and link angle (R^2=0.312, p<0.05) of salmon trophic relationships related to temperature, as 2nd-order polynomial relationships, but only link angle had a significant relationship with temperature. The change in chain lengths reflects the resource availability for juvenile salmon that increases with increasing temperatures (Doi, 2012; Doi et al., 2009; Pimm et al., 1991; Ward & McCann, 2017), but when the river temperature surpasses an optimum, resources could start to decrease

again. The shortening of chain length with increasing temperature has also been found in other studies on the impact of warming on food webs in other rivers (Arim et al., 2007; Petchey et al., 1999). The increase in the mean link angle of salmon trophic relationships over time and with increasing temperature also indicates that in this system, increased temperature leads to a decrease in prey resource for juvenile salmon. The rate of biomass depletion (estimated as slope) was also found to decrease over time but did not relate significantly with temperature. Thus, there may be other drivers affecting resource availability (Albertson et al., 2018; Dineen et al., 2007; Shurin et al., 2012). The changes in food web properties over time also seems to reflect the changes in diet of juveniles, for example, in 2005, the chain length and link angle of the food web was higher and juveniles also consumed a lot more large-bodied invertebrates (Antonsson, 2015).

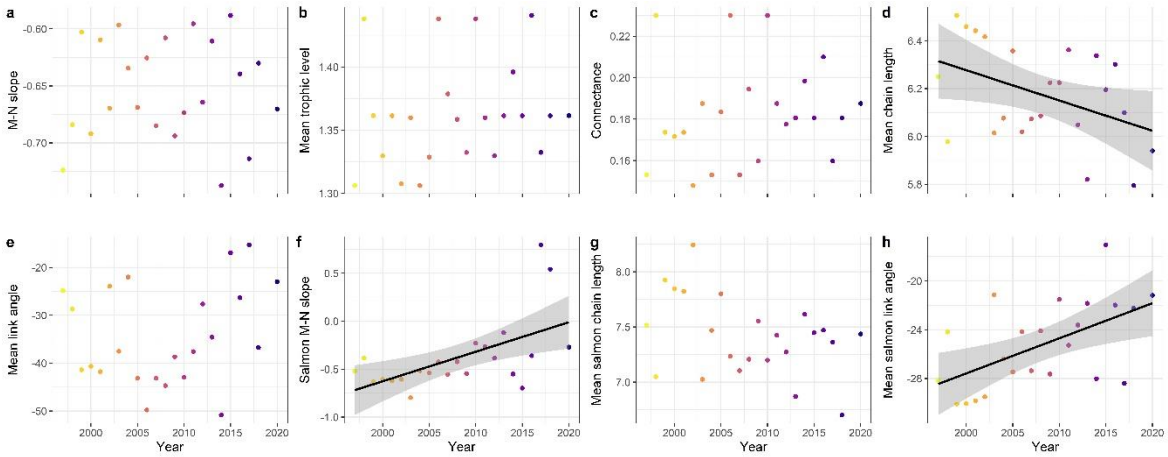

Figure 12: Change in reconstructed food web properties in Vesturdalsá over 23 years. Shown are the estimates of a) slope (p=0.893), b) mean trophic level (p=0.411), c) connectance (p=0.533), d) mean chain length (p<0.05), e) mean link angle (p=0.314) of overall trophic relationships, and the f) slope (p<0.01), g) mean chain length (p=0.0674), h) mean link angle (p<0.01) of salmon trophic relationships over years (1997-2020) in Vesturdalsá. Only significant linear regressions are shown.

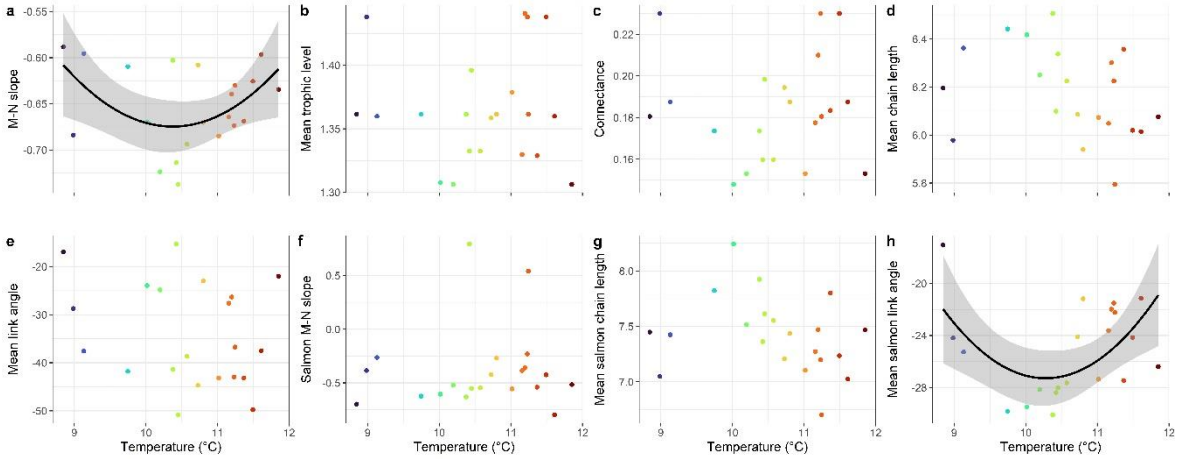

Figure 13: Change in reconstructed food web properties in Vesturdalsá over 23 years. Shown are the estimates of a) slope (p=0.0866), b) mean trophic level (p=0.959), c) connectance (p=0.430), d) mean chain length (p=0.141), e) mean link angle (p=0.263) of overall trophic relationships, and linear regressions of the f) slope (p=0.714), g) mean chain length (p=0.110), h) mean link angle (p<0.05) of salmon trophic relationships in across average summer water temperatures (°C) in Vesturdalsá. Only significant or close-to-significant relationships are shown.

In summary, although I did not see large changes in trophic relationships over these 23 years for Vesturdalsá, there is evidence that the prey availability for juvenile Atlantic salmon have decreased over time and one of the main reasons for that may be variation in temperature. Warming could cause lower prey availability and choice for juvenile salmon and further adverse impacts to the whole ecosystem (O'Gorman et al., 2023; Woodward et al., 2010a). The results of this study also further illustrate the relatively simple structure of the food web in Vesturdalsá. The river may have limited scope for adaptability and may become more fragile due to warming (Closs & Lake, 1994; Perkins et al., 2010; Warren, 1989; Woodward et al., 2010a).

b. Change in Food Webs Over the Summer of 2020 in Vesturdalsá

The second main research aim of **Paper II** was to investigate if and how the food web in Vesturdalsá varies from June till August in 2020. To address this, I focused on the food web in Vesturdalsá over the summer of 2020. The data shows significant changes, with peak productivity during the late summer (late July and August). Weber et al. (2017) has also shown similarly a peak in drift density and biomass of macroinvertebrates in the John Day River Basin in central Oregon, USA. Importantly, (*Figure 14*) the M-N relationship during the summer showed no significant differences between sampling periods ($F_{(3,69)}$=1.78, p=0.159), but the species abundance was found to be different ($F_{(3,69)}$=6.68, p<0.001). Abundances in early July were significantly lower compared to other months. The properties of food webs in Vesturdalsá did not differ significantly over time in the summer, however, the mean link angle (p=0.073) of the food web decreased whereas mean chain length (p=0.084) of juvenile salmon trophic relationships increased over the summer, but neither of these were found to change significantly over the summer. The changes in chain length and link angle reflects the change in river

productivity over time during the summer, which was also observed in other Icelandic rivers and streams (Kreiling et al., 2021; Robinson et al., 2021), where prey availability is the highest in late summer.

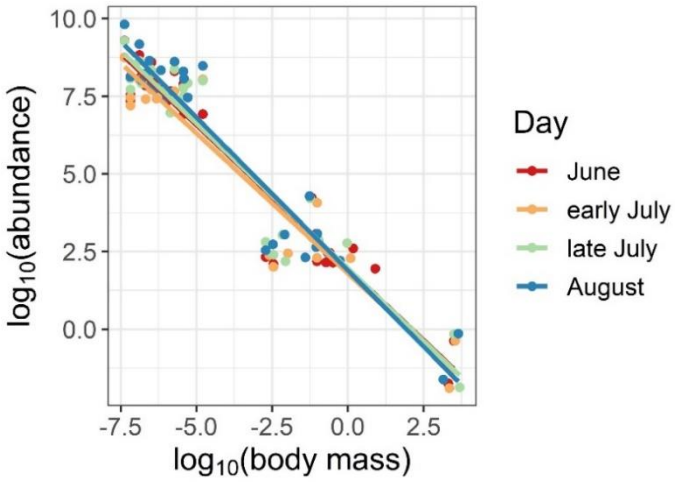

Figure 14: Linear regressions of log-log M-N food webs in different sampling periods during the summer in Vesturdalsá.

Additionally, no major changes were observed in the productivity of freshwater species during the summer in Vesturdalsá. The biggest changes over the summer were seen in the primary productivity of the river. In *Figure 15b*, the concentrations of Cyanobacteria were significantly higher in August (χ^2=30.9, df=3, p<0.001). Diatom concentrations were also found to be higher in the late summer period (χ^2=72.8, df=3, p<0.001), where concentrations were the highest overall in August (p<0.001) and concentrations in late July were higher than early July (p<0.05).

Furthermore, densities and biomasses of benthic invertebrate changed little over the summer period (*Figure 15c*). **Paper I** showed that the most abundant invertebrate in Vesturdalsá was the chironomid in August, which was also found to be the case throughout the summer and was consistent with other studies of rivers in the Hengill river systems (Friberg et al., 2009) and the Skarðslækur stream (Kreiling et al., 2021) in Iceland. The density of Simuliidae was significantly higher in August than in early July (χ^2=8.66, df=3, p<0.05), but the population biomass did not vary over time (χ^2=3.13, df=3, p=0.373). Whereas the population biomass of Chironomidae was significantly lower in August than early July (χ^2=12.4, df=3, p<0.01), but their abundance did not differ over the summer (χ^2=2.32, df=3, p=0.509). Similarly, drifting invertebrates were found to change little during the summer (*Figure 15d*). Only the abundance (χ^2=9.86, df=3, p<0.05) and population biomass (χ^2=11.3, df=3, p<0.05) of chironomids differed significantly between sampling periods in the summer, with more drifting chironomids in early July than in August. Overall, the benthic and drifting

invertebrate community composition exhibited little variability during the summer, except for populations of simuliids and chironomids.

The invertebrate availability within the river was also reflected in the stomach content of juvenile Atlantic salmon in Vesturdalsá from June till August in 2020 (*Figure 15e*). Chironomids appear to be the most consumed prey by both Atlantic salmon and Arctic charr in prey consumption studies of salmonid rivers in Iceland (Antonsson, 2015; Kreiling et al., 2021), This is congruent with the findings of **Paper I**, see above. Therefore, this reemphasises the importance of the production of chironomids throughout the summer as the main food source for juvenile salmonids in these low-productivity rivers in the sub-Arctic (Erkinaro & Erkinaro, 1998). Notably, prey consumed by juvenile Arctic charr did not vary over the summer, but the prey consumed by juvenile Atlantic salmon varied. The abundance (χ^2=48.7, df=3, $p<0.001$) and biomass (χ^2=56.4, df=3, $p<0.001$) of chironomids consumed by salmon varied over the summer, with the lowest consumption of chironomids being in August ($p<0.001$). The abundance of chironomids that were consumed were also lower in June than early July ($p<0.01$) and total biomass was lower in late July than early July ($p<0.05$). In addition, the total biomass of Simuliidae eaten by juvenile salmon also differed between sampling times over the same summer (χ^2=16.3, df=3, $p<0.001$), as biomass was significantly lower in late July than June ($p<0.05$) and early July ($p<0.01$). Juvenile Arctic charr in the river also showed high stability in their population growth due to their consistent consumption of macroinvertebrates and density numbers over the summer season. On the other hand, juvenile Atlantic salmon showed high variability, most likely due to their high population numbers which changes the food web and community structure of the river during the summer.

Abundance of juvenile salmonids was similar over the summer, as shown in *Figure 15f*, with higher abundances of juvenile Atlantic salmon than Arctic charr during the sampling period. Abundance of Atlantic salmon was the lowest in early July, which coincides with the main smolt migration period (Bárðarson et al., 2019). In addition, the mass of juvenile Atlantic salmon was also lower in late July than early July (χ^2=49.8, df=3, $p<0.001$). In contrast, the mass of juvenile Arctic charr was the lowest in August (χ^2=15.0, df=3, $p<0.01$).

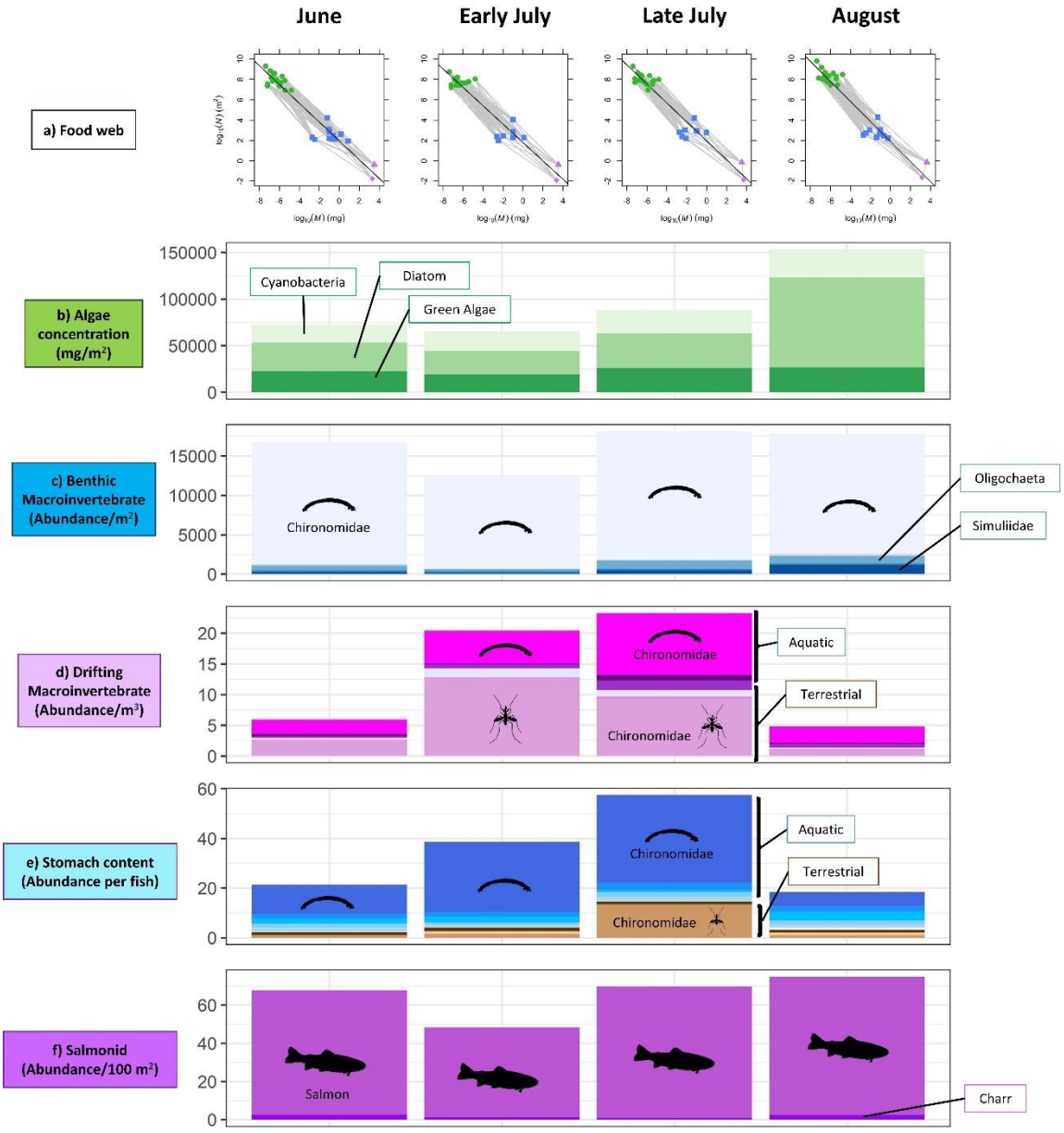

Figure 15: a) Linear regressions of log-log M-N trivariate food webs across sampling periods in Vesturdalsá (green circles ●: primary producers, blue squares ■: invertebrates, purple triangle ▲: juvenile Atlantic salmon, purple diamonds ◆: other salmonid species). Bar plots of average b) algae concentrations (µg) per m^2, c) abundance of benthic invertebrates per m^2, d) abundance of drifting invertebrates per m^3, e) abundance of prey items found in the stomachs of juvenile salmon, f) abundance of juvenile salmonids per 100 m^2.

Overall, the abundance of freshwater organisms was low in early July but increased during the late summer period, which was when the young-of-the-year fish started feeding and increasing in biomass before winter. The difference in abundance over the summer also matches the differing growth and development of freshwater species. Predation of prey species by

juvenile salmonids may also contribute to the lower abundance of prey species that was observed in the summer, but the data provide no indication that predation is limiting the density of invertebrate species in the river. Changes in benthic algae production is also reflected in the changes in invertebrate populations during the summer (Gíslason & Gardarsson, 2010). Additionally, the variations in resource availability during the summer is crucial to the development and growth of juvenile Atlantic salmon in cold low-productivity rivers (Elliott et al., 1998). Thus, intervention to increase the salmon population by altering resource productivity could be focused on increasing productivity during the early summer period, so that juvenile Atlantic salmon will have more stable supply of prey over time. Juvenile Atlantic salmon also have the highest growth rates in the summer, when temperature is the highest in the year (Bacon et al., 2005; Ebersole et al., 2006; Jones et al., 2002). Further studies are still needed to estimate the mortality rate of juvenile salmon during the summer, and to test whether it is impacted by food availability in the river. Juvenile mortality is usually the highest in locations with extreme climates and when temperatures reaches below or above their optimum (Antonsson et al., 2005). Multiple studies have shown that food availability could impact juvenile salmonids' behaviour (Orpwood et al., 2006), distribution, growth (Arnekleiv et al., 2006; Riley et al., 2009), density (Johansen et al., 2005; Piccolo et al., 2014), and smoltification (Jones et al., 2015). Reiriz et al. (1998) has even shown that juvenile Atlantic salmon that were previously feeding on reduced ratios, grew faster by increasing their food intake rates when having access to full rations. Additionally, Jonsson et al. (2012) have shown that richer food availability in marine environments could decrease the age maturation for female adult salmon. Stability of food supply throughout the whole summer could in theory promote the highest growth possible and lower mortality rates during this critical period of the juvenile salmon's life cycle. A caveat of this, is that stable food availability requires high and stable control of the nutrient supply and primary productivity of a river such as using nutrient enhancement in nutrient-poor streams to promote salmonid fish stocks, and could be difficult to achieve successfully and sustainably (Gerwing & Plate, 2019).

3. Spatial Comparisons of Food Webs in Atlantic Salmon Rivers

The first two chapters focused on prey choice and composition for juvenile salmon and changes in trophic relationships over time for low-productivity rivers. The following chapter will discuss the spatial similarity of trophic relationships in salmon sink food webs in the North Atlantic, by reconstructing food webs for multiple rivers, and further comparing the trophic relationships of those food webs within and between rivers. The results demonstrated that the trophic relationships between juvenile salmonids and their prey in northern Europe varied due to the difference in environmental characteristics and macroinvertebrate communities.

a. Spatial Similarity in Food Webs in Iceland

First, I aimed to reconstruct and compare the food webs of different sites within Vesturdalsá, in which I found that there were spatial similarities in food webs between sites in

the river. The results differed from what was described by the River Continuum Concept (RCC), which predicts that there is a latitudinal gradient in the topology of animal communities within streams due to their physical and biophysical characteristics, in which there is a high reliance on terrestrial resources in headwaters, to autochthonous sources in mid-orders, and to suspended materials in larger rivers (Rosi-Marshall et al., 2016; Sánchez-Hernández, 2023; Vannote et al., 1980). RCC was found to be more accurately describing temperate and forested rivers (Doretto et al., 2020; Rosi-Marshall et al., 2016), rather than the cold, nutrient-poor rivers such as those found in Iceland (Brittain et al., 2022; Peterson & Martin-Robichaud, 1995). The ANCOVA model of log-log M-N scaling showed that there were no significant differences between sites within Vesturdalsá ($F_{(4,87)}$=1.81, p=0.135; *Figure 17a*). Juvenile Atlantic salmon abundance (p=0.786) and biomass (p=0.104) also did not differ between sites and the characteristics of the food web also remained similar throughout (*Figure 18*). A similar trend was also observed for other rivers in NE Iceland (which was not included in the results of **Paper III**), where there were no differences in the M-N relationship between sites within rivers. The abundances of species varied between sites for two of the rivers, Selá ($F_{(2,44)}$=23.1, p<0.001) and Midfjardará ($F_{(3,55)}$=4.44, p<0.01), but did not differ for Vesturdalsá ($F_{(4,87)}$=1.01, p=0.406) and Hofsá ($F_{(1,15)}$=0.465, p=0.506) (further information and figures of reconstructed food webs found in Appendix 3).

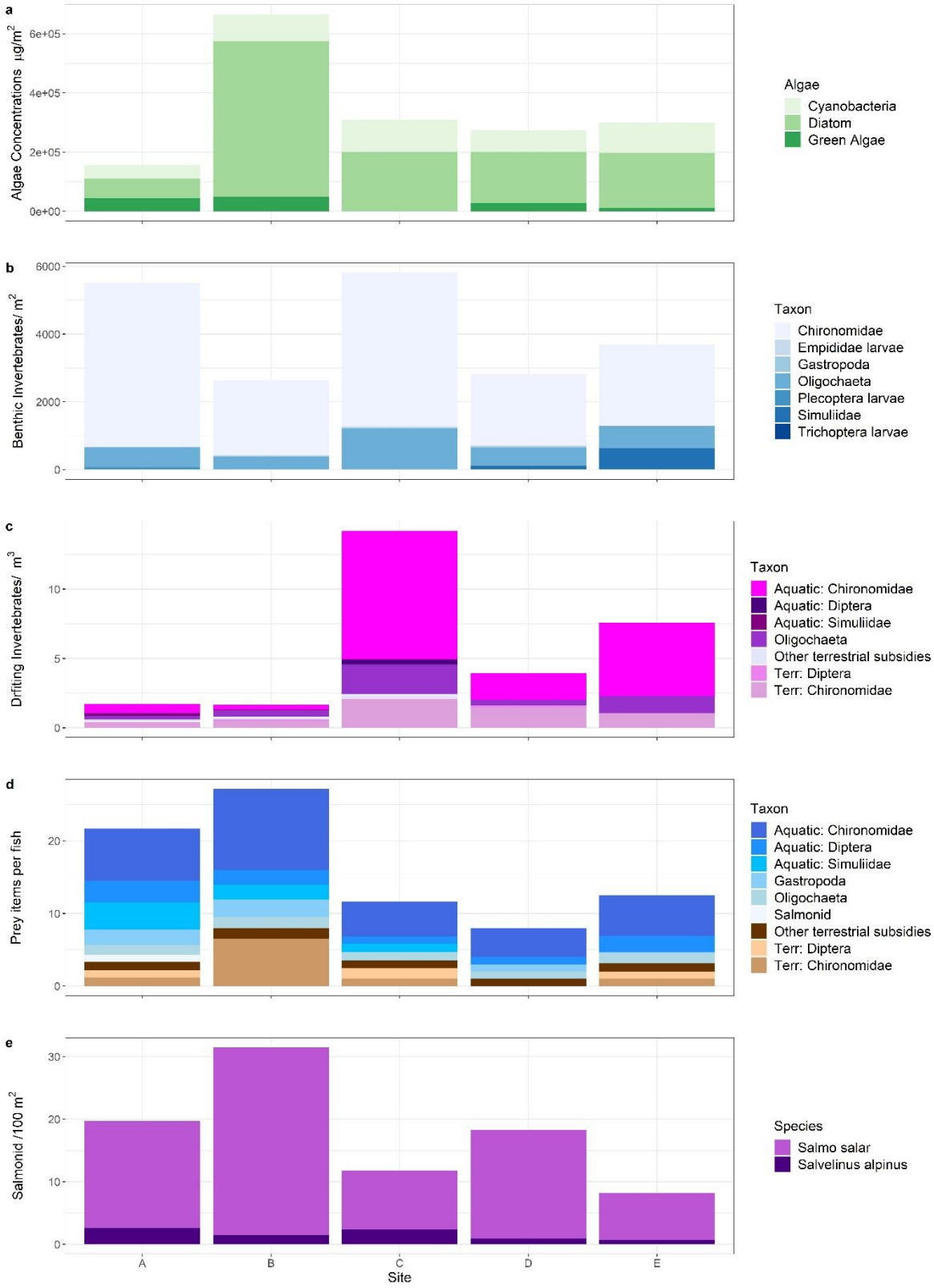

Figure 16: Bar plots of average a) algae concentrations (µg) per m^2, b) abundance of benthic invertebrates per m^2, c) abundance of drifting invertebrates per m^3, d) abundance of prey items found in the stomachs of juvenile salmon, e) abundance of juvenile salmonids per 100 m^2 in sites along Vesturdalsá. Sites are from downstream (closest to sea) to upstream, refer to Figure 3 for location of sites.

Further detailed analysis of the freshwater community (which was not included in **Paper III**) also suggests minor difference between sites in Vesturdalsá. Concentrations of periphyton pigments, used as a proxy for periphyton biomass, of Cyanobacteria (χ^2=26.9, df=4, p<0.001) and diatom (χ^2=64.0, df=4, p<0.001) varied between sites (*Figure 16a*). There were significantly more Cyanobacteria in the middle site (C) than downstream (site A; p<0.001) and upstream (site D; p<0.01). There were also overall less Cyanobacteria downstream (site A) than upstream (site E) (p<0.01). Diatoms were also much lower in concentration in downstream (site A) than other sites, whereas site B had the highest concentration and was significantly higher than upstream (site E; p<0.001). Additionally, invertebrate community composition was also mostly similar between sites (*Figure 16b*). Except for the abundance of Oligochaeta, which was significantly higher in site C than B (p<0.05), whereas the population biomass of Oligochaeta which was significantly higher in site A than B (p<0.05). Chironomidae population biomass was also higher in site A than it was upstream (site D (p<0.05) and E (p<0.05)). Population biomass of Empididae was higher in site B than D as well (p<0.05). On the other hand, the drifting invertebrate population did not significantly differ between sites in Vesturdalsá (*Figure 16c*), but there was a decrease in drift abundance from upstream to downstream. The prey items consumed by juvenile Atlantic salmon differed a bit between sites. Only the abundance of chironomids consumed in site D was significantly higher than B (p<0.01) and C (p<0.05), whereas all other amount of prey consumed was not significantly different. There is also a higher density of juvenile Atlantic salmon in downstream sites than upstream, whereas Arctic charr populations were similar throughout the river (*Figure 16e*). The mass of juvenile Atlantic salmon was also significantly lower in downstream (χ^2=30.0, df=4, p<0.001), whereas the biomass of Arctic charr was lower in midstream (site C; χ^2=19.6, df=4, p<0.001). The results further support the conclusion that rivers in Iceland and other with similarly low-productivity do not follow the RCC model as rivers in more temperate and forested areas do.

Additionally, there were also spatial similarity among rivers in Iceland. The LME models indicated that the M-N relationship in food webs bordered on being significantly different from each other ($F_{(5,122)}$=2.24, p=0.0545; *Figure 17b*), and abundances of species were found to differ significantly between rivers ($F_{(5,122)}$=10.7, p<0.001). There was also only nominal indication in the data of a relationship between salmon abundance (p=0.0967) and biomass (p=0.0890) with latitude (*Figure 18b*). Although the results were insignificant, I saw a trend in decreasing juvenile Atlantic salmon biomass with increasing latitude which was also found to be the case for other sub-Arctic rivers in Norway (Hedger et al., 2013). Whereas mean link angle had a significant negative linear relationship with latitude (R^2=0.742, p<0.05; refer to Supporting Information of **Paper III**). Both Elliðaár and Krossá are rivers situated in lower latitude relative to the four rivers in NE Iceland and had higher (i.e. shallower) mean link angle in comparison. Elliðaár and Krossá also had a higher abundance of invertebrates and salmonids than the more northern rivers. It is likely due to a warmer climate and high abundance of invertebrates, that Atlantic salmon in southern and western Iceland are on average a larger size (Antonsson et al., 2005; Gíslason et al., 1999; Stefánsson & Ólafsson, 1991). Other food web properties did not appear to differ along the latitudinal gradient within Iceland. Additionally, the primary productivity was found differ significantly among the four salmon rivers in NE Iceland (*Figure S20*; *Table S4*), with the periphyton biomass of Cyanobacteria, diatom, and green algae in Hofsá being higher in comparison to other rivers. Macroinvertebrates in Hofsá were also larger in size

in comparison to invertebrates in other rivers, which could be due to the high primary productivity of Hofsá providing the necessary resources for larger-bodied invertebrates such as trichopterans, as was shown in **Paper I**.

The results suggest that the bedrock and vegetation of Icelandic rivers are quite similar, both within and between them. This is likely driven by the low productivity environment and species diversity due to being biogeographically isolated, resulting in a lack of diverse invertebrate functional feeding groups (Gíslason et al., 1999; Lento et al., 2022b; Ministry for the Environment & The Icelandic Institute of Natural History, 2001). The relatively weak spatial differences that were observed in the structure of food webs between Icelandic rivers shows that these rivers could be used as monitoring stations for changes in trophic interaction for other similar sub-Arctic, low-productivity salmon rivers.

b. Spatial Similarity and Differences in Food Webs in the North Atlantic

Next, I expanded the spatial range by including rivers outside of Iceland in the North Atlantic, covering a larger proportion of the latitudinal range of the species distribution of juvenile Atlantic salmon. The main research question was whether trophic relationships of salmon sink food webs in the North Atlantic varied with temperature and by productivity levels? Food webs of six Atlantic salmon rivers in Iceland and eight in United Kingdom (UK) did not differ significantly between countries ($F_{(1,330)}$=1.36, p=0.244), latitudes (p=0.147; *Figure 17c*), air temperatures (p=0.310) and vegetation productivity (p=0.0544). The biomass of Icelandic freshwater species were also lower, but abundances were higher than species in the UK. Predictably, more species diversity was found in UK rivers (Perkins et al., 2022; Shah et al., 2015). In addition, terrestrial inputs are highly important to the productivity of Atlantic salmon rivers in the UK (Woodward et al., 2008). One of the UK Atlantic salmon rivers included is the Mill Stream, a chalk stream with high species diversity and productivity, that has a higher level of primary production (Bowes et al., 2005; Marsh et al., 2022; Wright et al., 1992). Connectance (R^2=0.621, p<0.001) and mean trophic level (R^2=0.467, p<0.01) decreased negatively with increasing latitude (figures shown in Supporting Information of **Paper III**). Mean link angle had a second-order polynomial regression along the latitudinal gradient (R^2=0.772, p<0.001). Following the trend in latitudinal gradient, there was a significant decrease in connectance (R^2=0.535, p<0.01; *Figure 18*c), mean trophic level (R^2=0.363, p<0.05; *Figure 18*c), and mean link angle (R^2=0.616, p<0.001) with colder temperatures. There was a positive relationship between vegetation productivity and connectance (R^2=0.348, p<0.05; *Figure 18*d). Mean trophic level also slowly increases when vegetation productivity reaches above 0.6 (R^2=0.563, p<0.01; *Figure 18*d). Whereas mean link angle decreases until vegetation productivity level is above 0.63 and then increases (R^2=0.351, p=0.0579). Long, southern Atlantic salmon rivers in the UK have a higher primary production than the Icelandic rivers (Bowes et al., 2005; Elliott et al., 1998; Lamberti & Steinman, 1997), but no significant relationship was found between Atlantic salmon productivity and latitude, temperature, or vegetation levels. Even though there is variability in food web structure, productivity of juvenile Atlantic salmon remains similar between these regions.

Furthermore, looking at predator-prey relationships across the North Atlantic, there were significant differences between countries and rivers. The log-log M-N relationship of fish

and invertebrates were significantly different across latitudes ($p<0.05$), temperature ($p<0.01$; *Figure 17e*), and between countries ($F_{(4,220)}=3.39$, $p<0.05$; *Figure 17d*). Tukey post-hoc tests showed that there were significant differences between Iceland and the UK ($p<0.001$) and Sweden ($p<0.01$). This also manifested as differences between rivers ($F_{(19,190)}=2.67$, $p<0.001$). The Högvadsån river in Sweden has a low abundance of invertebrates and fish, but higher species diversity due to high riparian vegetation and warmer climates (Bergh, 2022; Ekologigruppen Ekoplan AB, 2021; Elliott et al., 1998; Eriksson et al., 1983). Salmon rivers in northern and cold regions, such as those in Greenland and northern Nordic region, were not found to differ significantly in trophic interactions due to their similar productivity levels and lack of dense vegetation (Elliott et al., 1998). They also consist of similar macroinvertebrate communities with mainly small Dipterans, which also becomes the main prey item of salmonids in these rivers (Arnekleiv et al., 2019; Erkinaro & Erkinaro, 1998; Friberg et al., 2001). There was also no significant relationship between M-N relationships and vegetation density ($p=0.844$; *Figure 17*f). Furthermore, comparison of food webs of rivers within the Teno/Tana system in Finland/Norway showed that there were no significant differences between the food webs ($F_{(3,14)}=0.642$, $p=0.601$). The Teno/Tana system has different habitats and amount of terrestrial inputs into the streams (Einarsson et al., 1990; Erkinaro et al., 1995; Halvorsen & Svenning, 2000; Jørgensen et al., 2000), resulting in a difference in prey availability and growth rates of juvenile Atlantic salmon (Erkinaro & Niemelä, 1995), which contradicts the results of the study likely due to terrestrial resources being excluded in food web models.

Population abundance of Atlantic salmon did not vary between latitudes ($p=0.254$), but average biomass of individual salmon did ($R^2=0.247$, $p<0.05$). The biomass of Atlantic salmon were lower with increasing temperatures ($R^2=0.262$, $p<0.05$; *Figure 19a*), which aligns with findings on juvenile Atlantic salmon populations in cold rivers in high latitudes, that have to spend more time in rivers and grow to a larger size before migrating as smolts (Elliott et al., 1998). At higher latitudes and colder temperatures, there were steeper M-N slopes ($R^2=0.280$, $p<0.05$) and longer mean chain lengths ($R^2=0.271$, $p<0.05$), and lower connectance ($R^2=0.386$, $p<0.01$) and mean trophic level ($R^2=0.647$, $p<0.001$, *Figure 19a*). Salmon in cold and northern salmon rivers have little prey choice, and thus have less adaptability to warming (Erkinaro & Erkinaro, 1998; Gilbert, 2009; Steingrímsson & Gíslason, 2002). Lower mean trophic level in high latitudes and cold environments also show that they have fewer species with multiple trophic interactions, whereas southern rivers with higher productivity have a higher diversity of fish species and prey items that help break up the food chain and create higher flexibility in the food web (Kortsch et al., 2019). Furthermore, there was a positive relationship between connectance and NDVI vegetation productivity ($R^2=0.248$, $p<0.05$; *Figure 19*b). The M-N slope also has a close-to-significant second order relationship with vegetation levels with the slope increasing with vegetation level until vegetation levels is higher than 0.69 and then started decreasing ($R^2=0.233$, $p=0.0533$; *Figure 19*b). Whereas mean chain length had a negative relationship ($R^2=0.452$, $p<0.01$). Mean trophic level also decreases with vegetation levels and then increases when vegetation levels are above 0.61 ($R^2=0.400$, $p<0.01$; *Figure 19*b).

The differences in trophic relationships observed in different Atlantic salmon rivers appear to be related to variations in temperature and vegetation density. The results from **Paper III** shows that due to the impacts of warming, food webs in Atlantic salmon rivers may become simplified and decrease biodiversity (O'Gorman et al., 2023). Simple food webs are also found in rivers with lower vegetation, colder climates, and at higher latitudes. Therefore, these northern food webs with a simple structure are less adaptable from climate change impacts than complex food webs, as they cannot rely on a high diversity of species and ecosystem functions

to use as a buffer from changes (Petchey et al., 1999). Juvenile Atlantic salmon population management should focus on sustaining current benthic macroinvertebrate diversity and population by increasing primary productivity within the river so that juveniles could rely on a sustainable food source (Albertson et al., 2018; Thompson et al., 2018). River managers could also use northern Atlantic salmon rivers as ´sentinel´ systems for climate change, where an increased reliance on small dipteran larvae in northern systems may mean a decrease in prey options also in southern systems (Perkins et al., 2010; Rolls et al., 2017). Thus, frequent monitoring of northern salmon populations and their respective trophic interactions could help better predict anthropogenic impacts. The study did not examine the changes in inter-specific interactions between fish species, which will also impact the trophic structure of the river and the productivity of Atlantic salmon populations (Armstrong et al., 2003; Fausch, 1998; Forseth et al., 2017). Therefore, further investigations are needed to understand how inter-specific competition differ across spatial scales.

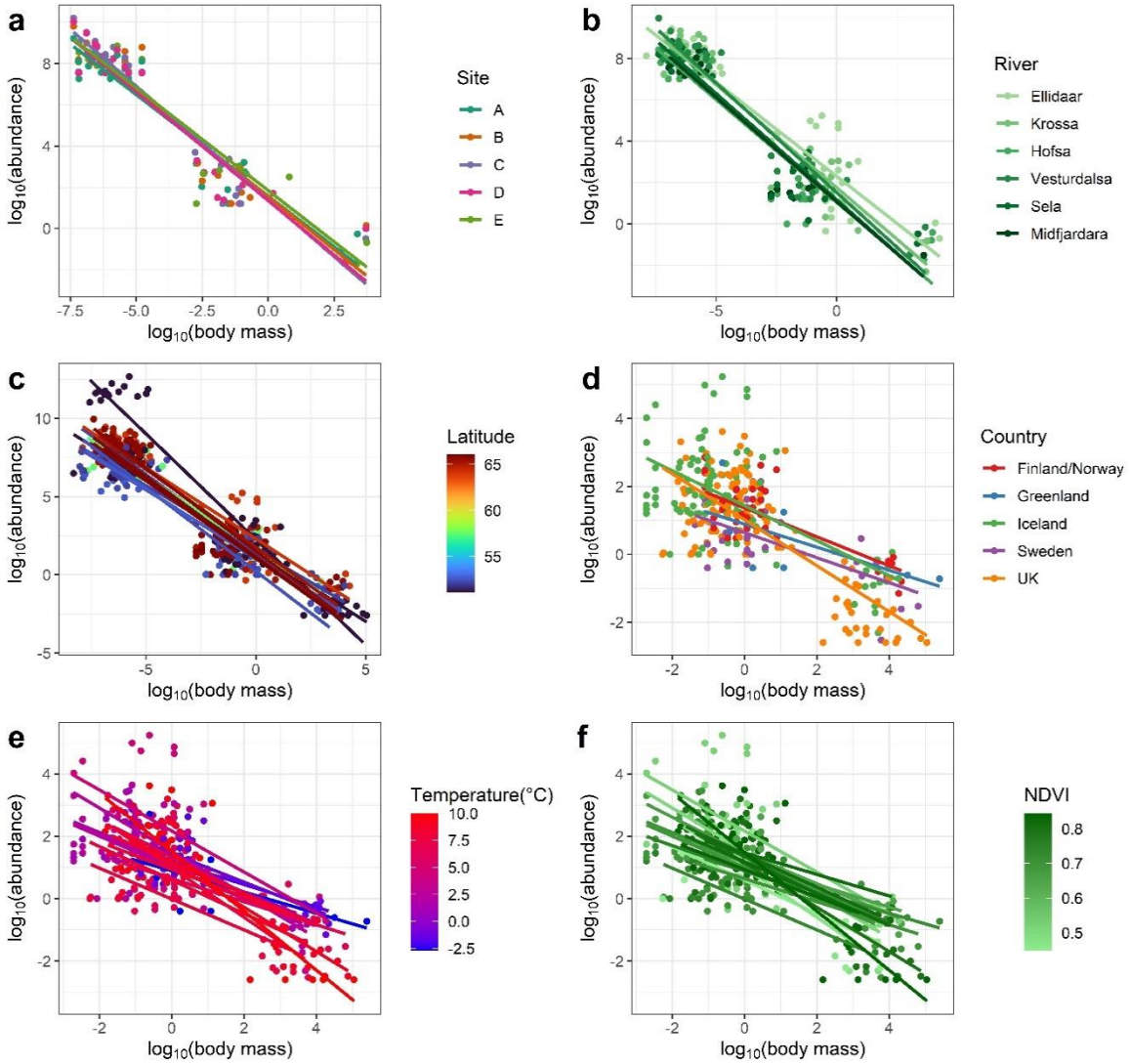

Figure 17: Linear regressions of log-log M-N food web relationship of a) food webs across sites in Vesturdalsá (p=0.135), b) across Atlantic salmon rivers in Iceland along the latitudinal gradient (high to low; p=0.0545), c) food webs across the latitudinal gradient in Iceland and UK (p=0.147). Linear regressions of log-log M-N predator-prey relationships of salmon rivers in d) different countries (p<0.05), e) the temperature gradient (p<0.01), and f) the productivity gradient (p=0.844) in the North Atlantic.

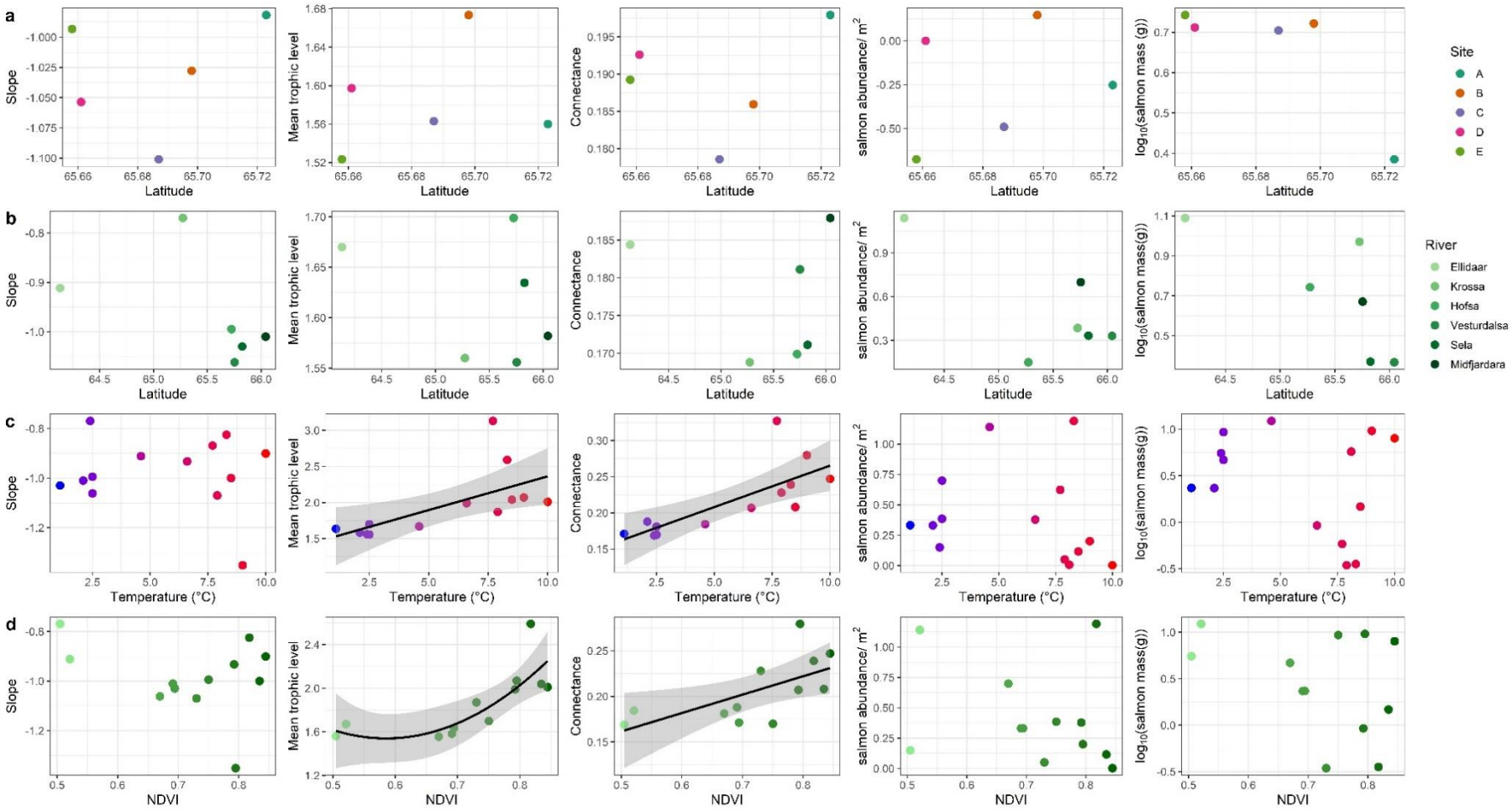

Figure 18: Linear and polynomial regressions of trivariate community food web properties (slope, mean trophic level, connectance) and characteristics (salmon abundance and mass) along the latitudinal gradient in increasing spatial scales from a) sites within Vesturdalsá to b) rivers in Iceland. Linear regressions of trivariate food web properties and characteristics of rivers in Iceland and UK were also compared along c) temperature and d) NDVI gradient.

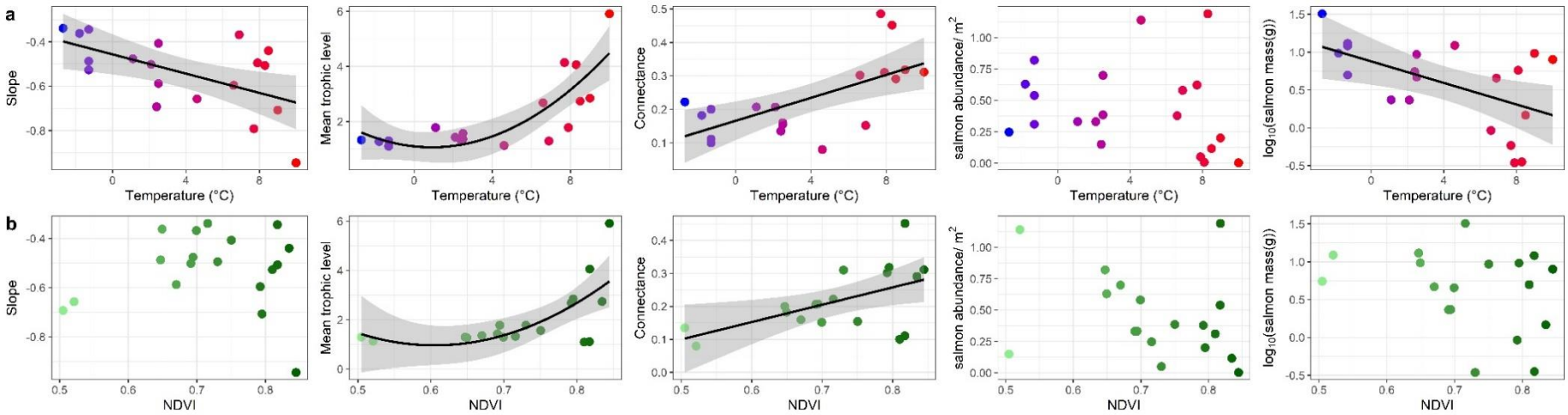

Figure 19: Linear and polynomial regressions of animal-animal food web properties (slope, mean trophic level, connectance) and characteristics (salmon abundance and mass) along the a) temperature, and b) NDVI gradient for all rivers in the North Atlantic.

5. Conclusions and Future Perspectives

The main aim of this thesis is to investigate how food availability affects the Atlantic salmon population in cold, nutrient-poor rivers and how the food web differs spatially and temporally in these rivers. Juvenile Atlantic salmon in cold, nutrient-poor rivers, such as those found in NE Iceland, are highly vulnerable to climate change and heavily rely on the production of small benthic invertebrate (Constable et al., 2022; Lai et al., 2024; Perkins et al., 2010). The results from this thesis suggest that the food webs within these streams have simple structures and relationships with low species diversity, which rhymes with literature reviewed here (Lento et al., 2022a; Perkins et al., 2010; Rypel & David, 2017; Woodward et al., 2010b). The main conclusions of the thesis are listed below. I will also discuss future perspectives and related topics.

In **Paper I**, it was reported that juvenile Atlantic salmon in NE Icelandic rivers were consuming Chironomidae larvae during the summer, which was also the most abundant benthic and drifting macroinvertebrate. This supports what was also found in other studies in other Icelandic rivers and sub-Arctic rivers as well (Friberg et al., 2001; Gíslason & Gardarsson, 2010; Kreiling et al., 2022; Lento et al., 2022a). Thus, the production of chironomids could be one of the important indicators to the future trends of fish stocks in the sub-Arctic low-productivity rivers (Armitage, 1995), and also for the growth and production of juvenile Atlantic salmon. Studies have shown that macroinvertebrate communities have an effect on Atlantic salmon productivity (Descroix et al., 2010; Riley et al., 2009), and it is reasonable to assume that the dominant species in low diversity ecosystems, such as the Chironomidae in Icelandic rivers, may become the main limiting factor. It was found that macroinvertebrate abundance and density were lower in Midfjardará, but otherwise invertebrate composition was found to be similar between the four rivers. It was also shown that juvenile Atlantic salmon did not have a high feeding preference for chironomids, but rather just consumed what was readily available. There was also a high dietary overlap between the species of juvenile salmonids within the rivers. These results reveal the lower importance of riparian vegetation compared to benthic macroinvertebrate communities as a food subsidy for juvenile Atlantic salmon in these rivers.

As shown in **Paper I**, Vesturdalsá, like other sub-Arctic rivers, has a relatively simple food web. The food web structure in Vesturdalsá had a predictable peak in productivity in the late summer but otherwise did not seem to change much over the summer. This peak period coincides with the beginning of feeding for young-of-the-year Atlantic salmon (Gorodilov, 1996), in which the salmon´s development matches the high prey availability during the summer season. The changes in food web chain length and link angle that were found in **Paper II** reflect the life cycle fluctuations of invertebrates during the summer in low-productivity Icelandic rivers (Kreiling et al., 2021).

Paper II showed that within Vesturdalsá there were generally only slight changes in interspecies interactions over time and with warming. However, there is an apparent decrease

in prey availability for juvenile Atlantic salmon since 1997 and with increasing temperature, as reflected by the inverse relationship between food web chain length and link angle. Therefore, with increasing warming over time, Vesturdalsá and other similarly oligotrophic rivers, may become more vulnerable as food webs are unable to adapt to the same extent as those in more productive and higher species diversity rivers (Closs & Lake, 1994; Warren, 1989), decreasing the food supply available for juvenile Atlantic salmon.

Furthermore, I found that the food webs of juvenile Atlantic salmon rivers in Iceland are spatially similar in **Paper III**. Food webs were similar within rivers and within the surrounding region within the country. In **Paper II** and **III**, it was shown that the food webs in Vesturdalsá are largely similar over some decades and along the river. This has overall been a very stable and homogenous river, which is also reflected in stable Atlantic salmon stock and catches with little fluctuations over the years (Bárðarson et al., 2023). The food webs of rivers in Iceland were also found to be rather similar to one another, most likely due to the homogenous catchment characteristics across the island (at least among the rivers studied here). In contrast, the trophic structure of predator-prey relationships of rivers in multiple countries that drain into the North Atlantic were different and varied with latitude. These results showed that trophic structure becomes increasingly simpler from south to north and with decreasing temperature and vegetation density. This is highlighted by high-latitude salmon rivers having lower connectance, trophic level, and link angle. On the other hand, temperate Atlantic salmon rivers, such as those in the UK, have higher prey diversity and additional terrestrial subsidies, and thus, higher productivity and rate of biomass depletion, and more consumers within the food web.

The results here provide important knowledge on sustainable management of Atlantic salmon populations situated in their northern distributions serving as 'sentinel' systems for other salmon rivers (Perkins et al., 2010; Woodward et al., 2010b). Impacts of climate change on Atlantic salmon rivers in Iceland should be assessed on a whole-ecosystem level to effectively manage rivers (Laske et al., 2022). Measuring food supply through estimating benthic and drift macroinvertebrate abundance should be encouraged when monitoring salmon populations (Weber et al., 2017). Management methods focusing on the productivity of benthic algae or high biomass macroinvertebrates would be better suited for Icelandic salmon rivers, due to its oligotrophic trait and the lack of dense riparian vegetation (Gerwing & Plate, 2019). Additionally, this thesis demonstrates the importance of having intensive monitoring of sub-Arctic freshwater communities over time, as these rivers experience northern expansion and encroachment of warm-water adapted species due to climate change (Laske et al., 2022). Temporal and spatial trends from this thesis could also be used to identify periods and areas of food limitation that could reduce the risk of overharvesting in vulnerable salmon populations (Okamoto et al., 2012). Finally, this thesis also provides a platform for predicting future trends in changes in food availability and trophic interactions of juvenile salmon in the North Atlantic.

Several questions still remain to be answered. Does competition between and within salmonid species impact the Icelandic salmon populations? And how does competition consequentially impact the food web? Will invasive species such as pink salmon threaten the balance of food web dynamics in low-productivity rivers? How will changes in distribution ranges of freshwater species due to climate change impact the food web? What are the impacts of aquaculture on freshwater food webs and the prey availability of wild juvenile salmon? What will these observed changes and differences of food webs over space and time look like under different warming scenarios? Will we see similar trends in marine food webs and how do they impact the growth and density of adult Atlantic salmon?

Future research on the effects of food competition between juvenile salmonids could potentially reveal inter-specific interactions within rivers with low food productivity. Sub-Arctic rivers usually have few fish species other than Atlantic salmon competing for food resources within the river (Bárðarson et al., 2023; Björnsson, 2001; Guðbergsson, 2015), unlike some other southern temperate rivers (Mann, 1989). Therefore, interspecies competition may have trivial effects on juvenile salmon populations, but this may change with the invasion of pink salmon into rivers in Iceland and elsewhere around North Atlantic, potentially leading to altered nutrient balance and food availability (Amoroso et al., 2017; Björnsson et al., 2023; Dadswell et al., 2022; Diaz Pauli et al., 2023). Another cause for changes in nutrient composition of juvenile salmonid habitats and increases in the proliferation of diseases are aquacultural practices near rivers (Ackefors & Enell, 1994; Kristmundsson et al., 2023), which was not discussed in this thesis as the rivers included were not located near aquaculture practices. There is evidence that increased production of farmed salmon leads to a decrease in the survival and abundance of Atlantic salmon of many global populations (Ford & Myers, 2008), further supporting the need to examine how the presence of aquaculture will impact trophic interactions of wild juvenile Atlantic salmon. Furthermore, species distributions of Arctic freshwater fish populations are likely to shift northwards due to increases in temperature from impacts of climate change (Reist et al., 2006). A shift in distributional range may alter fish diets and resources available in the newly inhabited regions, which could have consequential effects on local trophic dynamics in the rivers. Although Atlantic salmon population are stable over time in northern latitudes (Svenning et al., 2022), Arctic charr populations are vulnerable and decreasing over time, which could impact freshwater food webs and prey availability, due to the role of Arctic charr as an additional food source for juvenile Atlantic salmon.

The temporal variation project in the thesis (**Paper II**) only utilised one study river. Therefore, using other rivers in the sub-Arctic with long-term time series food web data could be highly beneficial in further testing the conclusions presented in this thesis. Future work should include old and new data of freshwater ecosystems to investigate changes in observed patterns and consequences of inter-species trophic relationships (Laske et al., 2022). Better spatio-temporal coverage of monitoring protocols and models could help further improve and inform management decisions (Ouellet et al., 2020). Additionally, further research into how management methods affect the overall freshwater food webs could also provide further clarity what methods are suitable for providing sustainable food availability for juveniles.

This thesis focused on the freshwater phase of the salmonid life cycle, but this is only one piece of the puzzle. The marine phase of the salmon life cycle is where the most growth occurs and dictates the ability of salmon to return to spawning rivers (Jonsson & Jonsson, 2011). Therefore, just as food availability in rivers is key for juvenile Atlantic salmon to successfully smoltify and migrate out to sea, food availability in the sea drives the return of adult salmon back to rivers to continue the production of salmon (Thorstad et al., 2021). Research on changes in food webs at sea over time and due to climate change could also further accurately predict trends in salmon population change. The thesis also does not cover the marine environment that Atlantic salmon spend their adult phase in, therefore further research could usefully explore how changes in food availability in the marine environment affect Atlantic salmon populations (Dadswell et al., 2022; Strøm et al., 2023).

The findings of this thesis have a number of important implications for future practices and research:

1) Spatio-temporal trends of food webs in Atlantic salmon rivers could be established and used as a baseline for further cross comparisons between rivers in the North Atlantic and to predict future changes in trophic interactions.
2) Intensive and ecosystem-based monitoring of populations in freshwater ecosystems is recommended to inform on changes in food availability and trophic relationships of juvenile Atlantic salmon.
3) Management of low-productivity rivers should be focused on increasing or maintaining benthic productivity to create a sustainable food supply for juvenile Atlantic salmon populations due to the lack of surrounding dense riparian vegetation and terrestrial subsidies.
4) Further research should examine the spatio-temporal food web dynamics across all life stages of Atlantic salmon populations and should consider future climate change impacts on the environment.

References

Ackefors, H., & Enell, M. (1994). The release of nutrients and organic matter from aquaculture systems in Nordic countries. *Journal of Applied Ichthyology*, *10*(4), 225–241. https://doi.org/10.1111/j.1439-0426.1994.tb00163.x

Adams, G. L., Pichler, D. E., Cox, E. J., O'Gorman, E. J., Seeney, A., Woodward, G., & Reuman, D. C. (2013). Diatoms can be an important exception to temperature-size rules at species and community levels of organization. *Global Change Biology*, *19*(11), 3540–3552. https://doi.org/10.1111/gcb.12285

Akbaripasand, A., Ramezani, J., Lokman, P. M., & Closs, G. P. (2014). Can drifting invertebrates meet the energy requirements of drift-feeding fish? A Case Study on Galaxias fasciatus. *Freshwater Science*, *33*(3), 904–914. https://doi.org/10.1086/676957

Albertson, L. K., Ouellet, V., & Daniels, M. D. (2018). Impacts of stream riparian buffer land use on water temperature and food availability for fish. *Journal of Freshwater Ecology*, *33*(1), 195–210. https://doi.org/10.1080/02705060.2017.1422558

Alioravainen, N., Orell, P., & Erkinaro, J. (2023). Long-Term Trends in Freshwater and Marine Growth Patterns in Three Sub-Arctic Atlantic Salmon Populations. *Fishes*, *8*(9), 441. https://doi.org/10.3390/fishes8090441

Allan, J. D., Wipfli, M. S., Caouette, J. P., Prussian, A., & Rodgers, J. (2003). Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(3), 309–320. https://doi.org/10.1139/f03-019

Alþingi. (2006). *61/2006: Lög um lax- og silungsveiði*. https://www.althingi.is/lagas/nuna/2006061.html

Amoroso, R. O., Tillotson, M. D., & Hilborn, R. (2017). Measuring the net biological impact of fisheries enhancement: Pink salmon hatcheries can increase yield, but with apparent costs to wild populations. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(8), 1233–1242. https://doi.org/10.1139/cjfas-2016-0334

Amundsen, P. A., & Gabler, H. M. (2008). Food consumption and growth of Atlantic salmon *Salmo salar* parr in sub-Arctic rivers: Empirical support for food limitation and competition. *Journal of Fish Biology*, *73*(1), 250–261. https://doi.org/10.1111/j.1095-8649.2008.01932.x

Amundsen, P. A., Gabler, H. M., Herfindal, T., & Riise, L. S. (2000). Feeding chronology of Atlantic salmon parr in subarctic rivers: Consistency of nocturnal feeding. *Journal of Fish Biology*, *56*(3), 676–686. https://doi.org/10.1006/jfbi.1999.1187

Anderson, L. E. (1954). Hoyer's Solution as a Rapid Permanent Mounting Medium for

Bryophytes. *The Bryologist*, *57*(3), 242. https://doi.org/10.2307/3240091

Andersson, A., Greenberg, L. A., Bergman, E., Su, Z., Andersson, M., & Piccolo, J. J. (2020). Recreational trolling effort and catch of Atlantic salmon and brown trout in Vänern, the EU's largest lake. *Fisheries Research*, *227*(105548), 109. https://doi.org/10.1016/j.fishres.2020.105548

Andreassen, P. M. R., Martinussen, M. B., Hvidsten, N. A., & Stefansson, S. O. (2001). Feeding and prey-selection of wild Atlantic salmon post-smolts. *Journal of Fish Biology*, *58*(6), 1667–1679. https://doi.org/10.1006/jfbi.2001.1576

Anon. (2023). *Status of the Tana/Teno River salmon populations in 2022*. https://brage.nina.no/nina-xmlui/bitstream/handle/11250/3041641/Tana report 2023-1.pdf?sequence=1&isAllowed=y

Antonsson, T. (2015). Fæða laxa- urriða- og bleikjuseiða: Gögn úr Vesturdalsá, Hofsá og Selá í Vopnafirði og úr Elliðaám og Leirvogsá við Faxaflóa. In *Veiðimálastofnun*. https://www.hafogvatn.is/static/research/files/faeda_laxa.pdf

Antonsson, T., Arnason, F., & Einarsson, S. M. (2005). Comparison of density, mean length, biomass and mortality of Atlantic salmon (*Salmo salar L.*) juveniles between regions in Iceland. *Icelandic Agricultural Sciences*, *18*, 59–66.

Antonsson, T., Guðbergsson, G., & Gudjonsson, S. (1996). Environmental Continuity in Fluctuation of Fish Stocks in the North Atlantic Ocean, with Particular Reference to Atlantic Salmon. *North American Journal of Fisheries Management*, *16*(3), 540–547.

Antonsson, T., & Gudjonsson, S. (2002). Variability in Timing and Characteristics of Atlantic Salmon Smolt in Icelandic Rivers. *Transactions of the American Fisheries Society*, *131*(4), 643–655. https://doi.org/10.1577/1548-8659(2002)131

Antonsson, T., Heidarsson, T., & Snorrason, S. S. (2010). Smolt Emigration and Survival to Adulthood in Two Icelandic Stocks of Atlantic Salmon. *Transactions of the American Fisheries Society*, *139*(6), 1688–1698. https://doi.org/10.1577/t08-200.1

Arim, M., Bozinovic, F., & A. Marquet, P. (2007). On the relationship between trophic position, body mass and temperature: Reformulating the energy limitation hypothesis. *Oikos*, *116*(9), 1524–1530. https://doi.org/10.1111/j.0030-1299.2007.15768.x

Armitage, P. D. (1995). Chironomidae as food. *The Chironomidae*, 423–435. https://doi.org/10.1007/978-94-011-0715-0_17

Armitage, P. D., Bass, J. A. B., Coleman, J. W., Jones, John, I., & Kaplan, T. L. (2017). Faunal and floral response to the dredging of a River Frome floodplain ditch (Dorset, UK). *Proceedings of the Dorset Natural History & Archaeological Society*, *138*(October), 67–76.

Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M., & Milner, N. J. (2003). Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research*, *62*(2), 143–170. https://doi.org/10.1016/S0165-7836(02)00160-1

Arnekleiv, J. V., Davidsen, J. G., Sheehan, T. F., Lehnert, S. J., Bradbury, I. R., Rønning, L., Sjursen, A. D., Kjærstad, G., Lubinski, B. A., & Nilssen, K. J. (2019). Demographic and genetic description of Greenland's only indigenous Atlantic salmon *Salmo salar* population. *Journal of Fish Biology*, *94*(1), 154–164. https://doi.org/10.1111/jfb.13887

Arnekleiv, J. V., Finstad, A. G., & Rønning, L. (2006). Temporal and spatial variation in growth of juvenile Atlantic salmon. *Journal of Fish Biology*, *68*, 1062–1076. https://doi.org/10.1111/j.0022-1112.2006.00986.x

B-Béres, V., Stenger-Kovács, C., Buczkó, K., Padisák, J., Selmeczy, G. B., Lengyel, E., & Tapolczai, K. (2023). Ecosystem services provided by freshwater and marine diatoms. *Hydrobiologia*, *850*(12–13), 2707–2733. https://doi.org/10.1007/s10750-022-04984-9

Bacon, P. J., Gurney, W. S. C., Jones, W., Mclaren, I. S., & Youngson, A. F. (2005). Seasonal growth patterns of wild juvenile fish: Partitioning variation among explanatory variables, based on individual growth trajectories of Atlantic salmon (Salmo salar) parr. *Journal of Animal Ecology*, *74*(1), 1–11. https://doi.org/10.1111/j.1365-2656.2004.00875.x

Bagliniere, J. L., & Maisse, G. (1985). Precocious maturation and smoltification in wild Atlantic salmon in the Armorican massif, France. *Aquaculture*, *45*(1–4), 249–263. https://doi.org/10.1016/0044-8486(85)90274-1

Bárðarson, H. (n.d.). *Tagging data from River Vesturdalsá, Iceland*.

Bárðarson, H., Guðbergsson, G., Njarðardóttir, E., & Helgason, S. Ó. (2019). *Research on fish stocks in several rivers at North-East Iceland 2018*.

Bárðarson, H., Helgason, S. Ó., & Njarðardóttir, E. (2023). *Research on fish stocks in several rivers at North-East Iceland 2022*.

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Baumgärtner, D., & Rothhaupt, K. O. (2003). Predictive Length-Dry Mass Regressions for Freshwater Invertebrates in a Pre-Alpine Lake Littoral. *International Review of Hydrobiology*, *88*(5), 453–463. https://doi.org/10.1002/iroh.200310632

Bednar-Friedl, B., Biesbroek, R., Schmidt, D. N., Alexander, P., Børsheim, K. Y., Carnicer, J., Georgopoulou, E., Haasnoot, M., Cozannet, G. Le, Lionello, P., Lipka, O., Möllmann, C., Muccione, V., Mustonen, T., Piepenburg, D., & Whitmarsh, L. (2022). Europe. In: Climate Change 2022: Impacts, Adaptation and Vulnerability. In *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. https://doi.org/10.1017/9781009325844.015

Beechie, T., Imaki, H., Greene, J., Wade, A., Wu, H., Pess, G., Roni, P., Kimball, J., Stanford, J., Kiffney, P., & Mantua, N. (2012). Restoring Salmon Habitat for a Changing Climate. *River Research and Applications*, *30*(January), 132–133. https://doi.org/10.1002/rra

Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-mass relationships

for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, *18*(3), 308–343. https://doi.org/10.2307/1468447

Bergh, R. (2022). *Biologisk undersökning av fiskfaunan inom Högvadsåns kalkningsprojekt 2022*. https://catalog.lansstyrelsen.se/store/24/resource/179

Bilous, M., & Dunmall, K. (2020). Atlantic salmon in the Canadian Arctic: potential dispersal, establishment, and interaction with Arctic char. *Reviews in Fish Biology and Fisheries*, *30*(3), 463–483. https://doi.org/10.1007/s11160-020-09610-2

Birnie-Gauvin, K., Thorstad, E. B., & Aarestrup, K. (2019). Overlooked aspects of the Salmo salar and Salmo trutta lifecycles. *Reviews in Fish Biology and Fisheries*, *29*(4), 749–766. https://doi.org/10.1007/s11160-019-09575-x

Björnsson, B. (2001). The trophic ecology of arctic char (Salvelinus alpinus) and brown trout (Salmo trutta) in Ellidavatn, a small lake in Southwest Iceland. *Limnologica*, *31*(4), 281–288. https://doi.org/10.1016/S0075-9511(01)80030-X

Björnsson, H., Ólafsdóttir, A. H., Sugurðsson, B. D., Katrínardóttir, B., Davíðsdóttir, B., Gunnarsdóttir, G., Aðalgeirsdóttir, G. T., Sigurðsson, G. M., Ögmundardóttir, H., Pétursdóttir, H., Bárðarson, H., Heiðmarsson, S., & Matthíasdóttir, T. (2023). *Umfang og afleiðingar hnattrænna loftslagsbreytinga á Íslandi. Fjórða samantektarskýrsla vísindanefndar um loftslagsbreytingar*.

Bøe, K., Power, M., Robertson, M. J., Morris, J., Brian, J., Pennell, C. J., & Fleming, I. A. (2019). The Influence of temperature and life stage in shaping migratory patterns during the early marine phase of two Newfoundland (Canada) Atlantic salmon (Salmo salar) populations. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(12), 2364–2376.

Booth, R. K., Kieffer, J. D., Tufts, B. L., Davidson, K., & Bielak, A. T. (1995). Effects of late-season catch and release angling on anaerobic metabolism, acid–base status, survival, and gamete viability in wild Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *52*(2), 283–290. https://doi.org/10.1139/f95-029

Bouchard, R. W. (2004). *Guide to Aquatic Invertebrate Families of Mongolia. Identification Manual for Students, Citizen Monitors, and Aquatic Resource Professionals*.

Bowes, M. J., Leach, D. V., & House, W. A. (2005). Seasonal nutrient dynamics in a chalk stream: The River Frome, Dorset, UK. *Science of the Total Environment*, *336*(1–3), 225–241. https://doi.org/10.1016/j.scitotenv.2004.05.026

Brittain, J. E., Bogen, J., Khokhlova, L. G., Melvold, K., Stenina, A. S., Gíslason, G. M., Brørs, S., Kochanov, S. K., Ólafsson, J. S., Ponomarev, V. I., Jensen, A. J., Kokovkin, A. V., & Pettersson, L. E. (2009). Arctic Rivers. In *Rivers of Europe* (pp. 337–379). https://doi.org/10.1016/B978-0-12-369449-2.00009-6

Brittain, J. E., Heino, J., Friberg, N., Aroviita, J., Kahlert, M., Karjalainen, S. M., Keck, F., Lento, J., Liljaniemi, P., Mykrä, H., Schneider, S. C., & Ylikörkkö, J. (2022). Ecological correlates of riverine diatom and macroinvertebrate alpha and beta diversity across Arctic Fennoscandia. *Freshwater Biology*, *67*(1), 49–63. https://doi.org/10.1111/fwb.13616

Brose, U., Dunne, J. A., Montoya, J. M., Petchey, O. L., Schneider, F. D., & Jacob, U. (2012). Climate change in size-structured ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1605), 2903–2912. https://doi.org/10.1098/rstb.2012.0232

Burgherr, P., & Meyer, E. I. (1997). Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Archiv Fur Hydrobiologie*, *139*(1), 101–112. https://doi.org/10.1127/archiv-hydrobiol/139/1997/101

Butler, J. R. A., Radford, A., Riddington, G., & Laughton, R. (2009). Evaluating an ecosystem service provided by Atlantic salmon, sea trout and other fish species in the River Spey, Scotland: The economic impact of recreational rod fisheries. *Fisheries Research*, *96*(2–3), 259–266. https://doi.org/10.1016/j.fishres.2008.12.006

Cameron, E. K., Sundqvist, M. K., Keith, S. A., CaraDonna, P. J., Mousing, E. A., Nilsson, K. A., Metcalfe, D. B., & Classen, A. T. (2019). Uneven global distribution of food web studies under climate change. *Ecosphere*, *10*(3). https://doi.org/10.1002/ecs2.2645

Chaput, G., Carr, J., Daniels, J., Tinker, S., Jonsen, I., & Whoriskey, F. (2019). Atlantic salmon (Salmo salar) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence , northwest Atlantic. *ICES Journal of Marine Science*, *76*(4), 1107–1121. https://doi.org/10.1093/icesjms/fsy156

Chesson, J. (1983). The estimation and analysis of preference and its relationship to foraging models. *Ecology*, *64*(5), 1297–1304. https://doi.org/10.2307/1937838

Closs, G. P., & Lake, P. S. (1994). Spatial and Temporal Variation in the Structure of an Intermittent-Stream Food Web. *Ecological Monographs*, *64*(1), 1–21. https://doi.org/10.2307/2937053

Constable, A. J., Harper, S., Dawson, J., Holsman, K., Mustonen, T., Piepenburg, D., & Rost, B. (2022). Cross-Chapter Paper 6: Polar Regions. In *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. https://doi.org/10.1017/9781009325844.023.2319

Cranston, P. S. (1983). A Key to the Larvae of the British Orthocladiinae (Chironomidae). In *Freshwater Biological Association Scientific Publication No. 45. 152*. Ambleside: The Freshwater Biological Association.

CRISP, D. T. (1981). A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. *Freshwater Biology*, *11*(4), 361–368. https://doi.org/10.1111/j.1365-2427.1981.tb01267.x

Cunjak, R. A. (1996). Winter habitat of selected stream fishes and potential impacts from land-use activity. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(SUPPL. 1), 267–282. https://doi.org/10.1139/cjfas-53-s1-267

Dadswell, M., Spares, A., Reader, J., McLean, M., McDermott, T., Samways, K., & Lilly, J. (2022). The Decline and Impending Collapse of the Atlantic Salmon (Salmo salar)

Population in the North Atlantic Ocean: A Review of Possible Causes. *Reviews in Fisheries Science and Aquaculture*, *30*(2), 215–258. https://doi.org/10.1080/23308249.2021.1937044

Davies, C., Shelley, J., Harding, P., McLean, I., Gardiner, R., & Peirson, G. (2004). *Freshwater Fishes in Britain: The Species and their Distribution* (C. Davies (ed.)). Harley Books.

Deegan, L. A., Peterson, B. J., Golden, H., McIvor, C. C., & Miller, M. C. (1997). Effects of fish density and river fertilization on algal standing stocks, invertebrate communities, and fish production in an arctic river. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(2), 269–283. https://doi.org/10.1139/f96-268

DELWP. (2017). *Draft Implementation Plan for Consultation*. *September*.

Descroix, A., Desvilettes, C., Bec, A., Martin, P., & Bourdier, G. (2010). Impact of macroinvertebrate diet on growth and fatty acid profiles of restocked 0+ Atlantic salmon (*Salmo salar*) parr from a large European river (the Allier). *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(4), 659–672. https://doi.org/10.1139/F10-012

Diaz Pauli, B., Berntsen, H. H., Thorstad, E. B., Homrum, E. ì, Lusseau, S. M., Wennevik, V., & Utne, K. R. (2023). Geographic distribution, abundance, diet, and body size of invasive pink salmon (Oncorhynchus gorbuscha) in the Norwegian and Barents Seas, and in Norwegian rivers . *ICES Journal of Marine Science*, *80*(1), 76–90. https://doi.org/10.1093/icesjms/fsac224

Didan, K. (2021). *MODIS/Aqua Vegetation Indices 16-Day L3 Global 250m SIN Grid V061 [Data set]*. NASA EOSDIS Land Processes Distributed Active Archive Center. https://doi.org/10.5067/MODIS/MYD13Q1.061

Dineen, G., Harrison, S. S. C., & Giller, P. S. (2007). Diet partitioning in sympatric Atlantic salmon and brown trout in streams with contrasting riparian vegetation. *Journal of Fish Biology*, *71*, 17–38. https://doi.org/10.1111/j.1095-8649.2007.01441.x

Doi, H. (2012). Resource productivity and availability impacts for food-chain length. *Ecological Research*, *27*(3), 521–527. https://doi.org/10.1007/s11284-012-0941-9

Doi, H., Chang, K. H., Ando, T., Ninomiya, I., Imai, H., & Nakano, S. I. (2009). Resource availability and ecosystem size predict food-chain length in pond ecosystems. *Oikos*, *118*(1), 138–144. https://doi.org/10.1111/j.1600-0706.2008.17171.x

Doretto, A., Piano, E., & Larson, C. E. (2020). The river continuum concept: Lessons from the past and perspectives for the future. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(11), 1856–1864. https://doi.org/10.1139/cjfas-2020-0039

Ebersole, J. L., Wigington, P. J., Baker, J. P., Cairns, M. A., Church, M. R., Hansen, B. P., Miller, B. A., LaVigne, H. R., Compton, J. E., & Leibowitz, S. G. (2006). Juvenile Coho Salmon Growth and Survival across Stream Network Seasonal Habitats. *Transactions of the American Fisheries Society*, *135*(6), 1681–1697. https://doi.org/10.1577/t05-144.1

Einarsson, S. M., Guðbrandsson, J., & Guðmundsdottir, Á. K. (2020). *Viðmiðunarmörk hrygningar í Krossá á Skarðsströnd*.

https://www.hafogvatn.is/static/research/files/1579074817-hv2020-03.pdf

Einarsson, S. M., Mills, D. H., & Johannsson, V. (1990). Utilisation of fluvial and lacustrine habitat by anadromous Atlantic salmon, Salmo salar L., in an Icelandic watershed. *Fisheries Research*, *10*(1–2), 53–71. https://doi.org/10.1016/0165-7836(90)90015-N

Einum, S., & Nislow, K. H. (2011). Variation in Population Size Through Time and Space: Theory and Recent Empirical Advances from Atlantic Salmon. In Ø. Aas, S. Einum, A. Klemetsen, & J. Skurdal (Eds.), *Atlantic Salmon Ecology* (pp. 277–298). Blackwell Publishing Ltd.

Ekologigruppen Ekoplan AB. (2021). *Bottenfaunaundersökning i Hallands län 2021*. https://catalog.lansstyrelsen.se/store/24/resource/165

Elliott, J. M., & Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: Predicting the effects of climate change. *Journal of Fish Biology*, *77*(8), 1793–1817. https://doi.org/10.1111/j.1095-8649.2010.02762.x

Elliott, S. R., Coe, T. A., Helfield, J. M., & Naiman, R. J. (1998). Spatial variation in environmental characteristics of Atlantic salmon (*Salmo salar*) rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(SUPPL.1), 267–280. https://doi.org/10.1139/d98-001

Environmental data MVM. (2023). *National data host lakes and watercourses, and national data host agricultural land*. Swedish University of Agricultural Sciences (SLU). https://miljodata.slu.se/mvm/2023-10-11

EPA. (1991). *ESS Method 150.1: Chlorophyll - Spectrophotometric*.

Eriksson, F., Hörnström, E., Mossberg, P., & Nyberg, P. (1983). Ecological effects of lime treatment of acidified lakes and rivers in Sweden. *Hydrobiologia*, *101*(1–2), 145–163. https://doi.org/10.1007/BF00008667

Erkinaro, H., & Erkinaro, J. (1998). Feeding of Atlantic salmon, *Salmo salar L.*, parr in the subarctic River Teno and three tributaries in northernmost Finland. *Ecology of Freshwater Fish*, *7*(1), 13–24. https://doi.org/10.1111/j.1600-0633.1998.tb00168.x

Erkinaro, J., & Niemelä, E. (1995). Growth differences between the Atlantic salmon parr, Salmo salar, of nursery brooks and natal rivers in the River Teno watercourse in northern Finland. *Environmental Biology of Fishes*, *42*(3), 277–287. https://doi.org/10.1007/BF00004921

Erkinaro, J., Shustov, Y., & Niemelä, E. (1995). Enhanced growth and feeding rate in Atlantic salmon parr occupying a lacustrine habitat in the River Utsjoki, northern Scandinavia. *Journal of Fish Biology*, *47*(6), 1096–1098. https://doi.org/10.1111/j.1095-8649.1995.tb06032.x

Falkegård, M., Lennox, R. J., Thorstad, E. B., Einum, S., Fiske, P., Garmo, Ø. A., Garseth, Å. H., Skoglund, H., Solberg, M. F., Utne, K. R., Vollset, K. W., Vøllestad, L. A., Wennevik, V., & Forseth, T. (2023). Predation of Atlantic salmon across ontogenetic stages and

impacts on populations. *Canadian Journal of Fisheries and Aquatic Sciences*, *80*(10), 1696–1713. https://doi.org/10.1139/cjfas-2023-0029

Fausch, K. D. (1998). Interspecific competition and juvenile Atlantic salmon (Salmo salar): On testing effects and evaluating the evidence across scales. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(SUPPL.1), 218–231. https://doi.org/10.1139/d98-006

Fausch, K. D., & White, R. J. (1981). Competition Between Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*) for Positions in a Michigan Stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*(10), 1220–1227. https://doi.org/10.1139/f81-164

Fleming, I. (1996). Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fish Biology and Fisheries*, *6*, 379–416. https://doi.org/10.1007/BF00164323

Fogarty, M. J. (2001). Dynamics Of Exploited Marine Fish Populations. *Encyclopedia of Ocean Sciences*, 774–781. https://doi.org/10.1006/RWOS.2001.0455

Ford, J. S., & Myers, R. A. (2008). A global assessment of salmon aquaculture impacts on wild salmonids. *PLoS Biology*, *6*(2), 0411–0417. https://doi.org/10.1371/journal.pbio.0060033

Forseth, T., Barlaup, B. T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., Hindar, A., Mo, T. A., Rikardsen, A. H., Thorstad, E. B., Vøllestad, L. A., & Wennevik, V. (2017). The major threats to Atlantic salmon in Norway. In *ICES Journal of Marine Science* (Vol. 74, Issue 6). https://doi.org/10.1093/icesjms/fsx020

Friberg, N., DybkjÆr, J. B., Olafsson, J. S., Gislason, G. M., Larsen, Sø. E., & Lauridsen, T. L. (2009). Relationships between structure and function in streams contrasting in temperature. *Freshwater Biology*, *54*(10), 2051–2068. https://doi.org/10.1111/j.1365-2427.2009.02234.x

Friberg, N., Milner, A. M., Svendsen, L. M., Lindegaard, C., & Larsen, S. E. (2001). Macroinvertebrate stream communities along regional and physico-chemical gradients in Western Greenland. *Freshwater Biology*, *46*(12), 1753–1764. https://doi.org/10.1046/j.1365-2427.2001.00857.x

Fry, B. (1991). Stable Isotope Diagrams of Freshwater Food Webs. *Ecology*, *72*(6), 2293–2297. https://doi.org/10.2307/1941580

Fuller, R. L., Roelofs, J. L., & Fry, T. J. (1986). The Importance of Algae to Stream Invertebrates. *Journal of the North American Benthological Society*, *5*(4), 290–296. https://doi.org/10.2307/1467481

Gerwing, T. G., & Plate, E. (2019). Effectiveness of nutrient enhancement as a remediation or compensation strategy of salmonid fisheries in culturally oligotrophic lakes and streams in temperate climates. *Restoration Ecology*, *27*(2), 279–288. https://doi.org/10.1111/rec.12909

Gibert, J. P. (2019). Temperature directly and indirectly influences food web structure. *Scientific Reports*, *9*(1), 1–8. https://doi.org/10.1038/s41598-019-41783-0

Gilbert, A. J. (2009). Connectance indicates the robustness of food webs when subjected to

species loss. *Ecological Indicators*, *9*(1), 72–80. https://doi.org/10.1016/j.ecolind.2008.01.010

Gíslason, G. M., & Gardarsson, A. (2010). The production of chironomids and blackflies in a subarctic river. *Proc 15th International Symposium on Chironomidae*, 45–54. http://www.hi.is/~gmg/Serprent/Gislason-Gardarsson_2010_Produ_Chir_Blackflies_Proceedings_Chir.pdf

Gíslason, G. M., & Jóhannsson, V. (1991). Effects of food and temperature on the life cycle of Simulium vittatum Zett. (Diptera: Simuliidae) in the River Laxá, N-Iceland . *SIL Proceedings, 1922-2010*, *24*(5), 2912–2916. https://doi.org/10.1080/03680770.1989.11899196

Gíslason, G. M., Ólafsson, J. S., & Adalsteinsson, H. (1998). Animal communities in Icelandic rivers in relation to catchment characteristics and water chemistry: preliminary results. *Nordic Hydrology*, *29*(2), 129–148. https://doi.org/10.2166/nh.1998.0008

Gíslason, G. M., Olafsson, J. S., & Hokon, A. (1999). Macroinvertebrate communities in Rivers in Iceland in Biodiversity in Benthic Ecology. *Proceedings from Nordic Benthological Meeting in Silkeborg, Denmark, 13-14 November 1997. NERI Technical Report No. 266, November*, 53–61.

Gíslason, G. M., & Steingrímsson, S. Ó. (2004). Seasonal and spatial variation in the diet of brown trout (*Salmo trutta L.*) in the subarctic River Laxá, north-east Iceland. *Aquatic Ecology*, *38*(2), 263–270. https://doi.org/10.1023/B:AECO.0000032052.04874.fb

Gorodilov, Y. N. (1996). Description of the early ontogeny of the Atlantic salmon, Salmo salar, with a novel system of interval (state) identification. *Environmental Biology of Fishes*, *47*(2), 109–127. https://doi.org/10.1007/BF00005034

Govoni, D. P., Kristjánsson, B. K., & Ólafsson, J. S. (2018). Spring type influences invertebrate communities at cold spring sources. *Hydrobiologia*, *808*(1), 315–325. https://doi.org/10.1007/s10750-017-3434-6

Grant, J. W. A. A., Weir, L. K., & Steingrímsson, S. Ó. (2017). Territory size decreases minimally with increasing food abundance in stream salmonids: Implications for population regulation. *Journal of Animal Ecology*, *86*(July), 1308–1316. https://doi.org/10.1111/1365-2656.12737

Grunblatt, J., Meyer, B. E., & Wipfli, M. S. (2019). Invertebrate prey contributions to juvenile Coho Salmon diet from riparian habitats along three Alaska streams: Implications for environmental change. *Journal of Freshwater Ecology*, *34*(1), 617–631. https://doi.org/10.1080/02705060.2019.1642243

Guðbergsson, G. (2015). *Catch statistics for Atlantic salmon Arctic charr and brown trout in Icelandic rivers and lakes 2015*.

Gudjonsson, S. (1990). Classification of Icelandic watersheds and rivers to explain life history strategies of Atlantic salmon [Oregon State University]. In *Ph.D. Thesis. Oregon State University, Corvallis, Oregon.* http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/37370/GudjonssonSigurdur

1991.pdf?sequence=1

Guðjónsson, S., Einarsson, S. M., Jónsson, I. R., & Guðbrandsson, J. (2015). Marine feeding areas and vertical movements of Atlantic salmon (*Salmo salar*) as inferred from recoveries of data storage tags. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(7), 1087–1098. https://doi.org/10.1139/cjfas-2014-0562

Halvorsen, M., & Svenning, M. A. (2000). Growth of Atlantic salmon parr in fluvial and lacustrine habitats. *Journal of Fish Biology*, *57*(1), 145–160. https://doi.org/10.1006/jfbi.2000.1296

Hannesdóttir, E. R., Gíslason, G. M., & Ólafsson, J. S. (2010). Life cycles of Eukiefferiella claripennis (Lundbeck 1898) and Eukiefferiella minor (Edwards 1929) (Diptera: Chironomidae) in spring-fed streams of different temperatures with reference to climate change. *Fauna Norvegica*, *31*, 35–46. https://doi.org/10.5324/fn.v31i0.1367

Hannesdóttir, E. R., Gíslason, G. M., Ólafsson, J. S., Ólafsson, Ó. P., & O'Gorman, E. J. (2013). Increased Stream Productivity with Warming Supports Higher Trophic Levels. In *Advances in Ecological Research* (Vol. 48). https://doi.org/10.1016/B978-0-12-417199-2.00005-7

Hansen, I., & Eiríksdóttir, E. S. (2021). *Ástandsflokkun straumvatna út frá tegundasamsetningu kísilþörunga*. https://www.hafogvatn.is/static/research/files/hv2021-11.pdf

Haugland, M., Holst, J. C., Holm, M., & Hansen, L. P. (2006). Feeding of Atlantic salmon (*Salmo salar L.*) post-smolts in the Northeast Atlantic. *ICES Journal of Marine Science*, *63*(8), 1488–1500. https://doi.org/10.1016/j.icesjms.2006.06.004

Hedger, R. D., Sundt-Hansen, L. E., Forseth, T., Ugedal, O., Diserud, O. H., Kvambekk, Å. S., & Finstad, A. G. (2013). Predicting climate change effects on subarctic-arctic populations of atlantic salmon (salmo salar). *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(2), 159–168. https://doi.org/10.1139/cjfas-2012-0205

Heggberget, T. G. (1984). Habitat selection and segregation of parr of Arctic charr (Salvelinus alpinus), brown trout, (Salmo trutta) and Atlantic salmon (Salmo salar L.) in two streams in north Norway. In L. Johnson & B. L. Burns (Eds.), *Biology of the Arctic Charr: Proceedings of the International Symposium on Arctic Charr* (pp. 217–231). Univ. Manitoba Press.

Heggenes, J., & Saltveit, S. J. (2007). Summer stream habitat partitioning by sympatric Arctic charr, Atlantic salmon and brown trout in two sub-arctic rivers. *Journal of Fish Biology*, *71*(4), 1069–1081. https://doi.org/10.1111/j.1095-8649.2007.01573.x

Heidarsson, T., Antonsson, T., & Snorrason, S. S. (2006). The Relationship between Body and Scale Growth Proportions and Validation of Two Back-Calculation Methods Using Individually Tagged and Recaptured Wild Atlantic Salmon. *Transactions of the American Fisheries Society*, *135*, 1156–1164.

Heino, J., Erkinaro, J., Huusko, A., & Luoto, M. (2016). Climate change effects on freshwater fishes, conservation and management. In G. P. Closs, M. Krkosek, & J. D. Olden (Eds.), *Conservation of Freshwater Fishes* (pp. 76–106). Cambridge University Press.

Heiri, O. (2013). The Larvae of Chironomidae of the Holarctic Region – Keys and diagnoses. In T. Wiederholm (Ed.), *CHIRONOMUS Journal of Chironomidae Research* (Issue 26). Publishing House of the Swedish Research Councils. https://doi.org/10.5324/cjcr.v0i26.1656

Hijmans, R. J. (2023). *raster: Geographic Data Analysis and Modeling*. https://rspatial.org/raster

Hillebrand, H., Dürselen, C. D., Kirschtel, D., Pollingher, U., & Zohary, T. (1999). Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology*, *35*(2), 403–424. https://doi.org/10.1046/j.1529-8817.1999.3520403.x

Hladyz, S., Åbjörnsson, K., Chauvet, E., Dobson, M., Elosegi, A., Ferreira, V., Fleituch, T., Gessner, M. O., Giller, P. S., Gulis, V., Hutton, S. A., Lacoursière, J. O., Lamothe, S., Lecerf, A., Malmqvist, B., McKie, B. G., Nistorescu, M., Preda, E., Riipinen, M. P., … Woodward, G. (2011). Stream Ecosystem Functioning in an Agricultural Landscape. The Importance of Terrestrial-Aquatic Linkages. In *Advances in Ecological Research* (Vol. 44). https://doi.org/10.1016/B978-0-12-374794-5.00004-3

Hudson, L. N., Emerson, R., Jenkins, G. B., Layer, K., Ledger, M. E., Pichler, D. E., Thompson, M. S. A., O'Gorman, E. J., Woodward, G., & Reuman, D. C. (2013). Cheddar: Analysis and visualisation of ecological communities in R. *Methods in Ecology and Evolution*, *4*(1), 99–104. https://doi.org/10.1111/2041-210X.12005

Hutchings, J. A., Ardren, W. R., Barlaup, B. T., Bergman, E., Clarke, K. D., Greenberg, L. A., Lake, C., Piironen, J., Sirois, P., Sundt-Hansen, L. E., & Fraser, D. J. (2019). Life-history variability and conservation status of landlocked atlantic salmon: An overview. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(10), 1697–1708. https://doi.org/10.1139/cjfas-2018-0413

Hutchings, J. A., & Jones, M. E. (1998). Life history variation and growth rate thresholds for maturity in Atlantic salmon, Salmo salar . *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(S1), 22–47. https://doi.org/10.1139/d98-004

ICES. (2022). Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*, *4*(39), 39. https://doi.org/http://doi.org/10.17895/ices.pub.19697368

ICES. (2023). Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*, *5*(41), 477. https://doi.org/https://doi.org/10.17895/ices.pub.22743713

Ingimarsson, F. (2022). *Vöktun á lífríki Elliðaánna Náttúrufræðistofa Kópavogs*. *4*. https://www.hafogvatn.is/static/research/files/hv2023_42.pdf

IUCN Red List. (2009). *Salmon and Climate Change: Fish in hot water*.

Jackson, D., McDermott, T., Kane, F., O'Donohoe, P., & Kelly, S. (2013). Evaluation of the impacts of aquaculture and freshwater habitat on the status of Atlantic salmon stocks in Ireland. *Agricultural Sciences*, *04*(06), 62–67. https://doi.org/10.4236/as.2013.46a010

Jake Vander Zanden, M., & Fetzer, W. W. (2007). Global patterns of aquatic food chain length. *Oikos*, *116*(8), 1378–1388. https://doi.org/10.1111/j.0030-1299.2007.16036.x

Jensen, J. L. A., Halttunen, E., Thorstad, E. B., Næsje, T. F., & Rikardsen, A. H. (2010). Does catch-and-release angling alter the migratory behaviour of Atlantic salmon? *Fisheries Research*, *106*(3), 550–554. https://doi.org/10.1016/j.fishres.2010.08.013

Jóhannesson, S. (2018). *Skýrsla nr. C18:07 Virði lax- og silungsveiða*.

Johansen, M., Elliott, J. M., & Klemetsen, A. (2005). Relationships between juvenile salmon, *Salmo salar L.*, and invertebrate densities in the River Tana, Norway. *Ecology of Freshwater Fish*, *14*(4), 331–343. https://doi.org/10.1111/j.1600-0633.2005.00107.x

Johnson, J. H., DiRado, J. A., Mackey, G., & Abbett, R. (2017). Comparative diets and foraging strategies of subyearling Atlantic salmon, brown trout, and rainbow trout during winter. *Journal of Applied Ichthyology*, *33*(6), 1158–1165. https://doi.org/10.1111/jai.13488

Johnson, J. H., & Ringler, N. H. (2016). Comparative diets of subyearling Atlantic salmon and subyearling coho salmon in Lake Ontario tributaries. *Journal of Great Lakes Research*, *42*(4), 854–860. https://doi.org/10.1016/j.jglr.2016.05.007

Johnson, J. H., & Waldt, E. M. (2014). Examination of the influence of juvenile Atlantic salmon on the feeding mode of juvenile steelhead in Lake Ontario tributaries. *Journal of Great Lakes Research*, *40*(2), 370–376. https://doi.org/10.1016/j.jglr.2014.03.005

Johnson, L. (1980). The arctic charr, Salvelinus alpinus. In E. K. Balon (Ed.), *Perspectives in Vertebrate Science* (Vol. 1, pp. 15–98). Dr. W. Junk, The Hague.

Jones, D. A., Bergman, E., & Greenberg, L. (2015). Food availability in spring affects smolting in brown trout (Salmo trutta). *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(11), 1694–1699. https://doi.org/10.1139/cjfas-2015-0106

Jones, W., Gurney, W. S. C., Speirs, D. C., Bacon, P. J., & Youngson, A. F. (2002). Seasonal patterns of growth, expenditure and assimilation in juvenile Atlantic salmon. *Journal of Animal Ecology*, *71*(6), 916–924. https://doi.org/10.1046/j.1365-2656.2002.00679.x

Jonsson, B., Finstad, A. G., & Jonsson, N. (2012). Winter temperature and food quality affect age at maturity: An experimental test with Atlantic salmon (salmo salar). *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(11), 1817–1826. https://doi.org/10.1139/f2012-108

Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. *Journal of Fish Biology*, *75*(10), 2381–2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x

Jonsson, B., & Jonsson, N. (2011). *Ecology of Atlantic Salmon and Brown Trout* (D. L. G. Noakes (ed.); Fish and F). Springer Netherlands. https://doi.org/10.1007/978-94-007-1189-1

Jonsson, I. R., & Antonsson, T. (2005). Emigration of age-1 Arctic charr, Salvelinus alpinus, into a brackish lagoon. *Environmental Biology of Fishes*, *74*(2), 195–200. https://doi.org/10.1007/s10641-005-7693-0

Jørgensen, L., Halvorsen, M., & Amundsen, P. A. (2000). Resource partitioning between lake-dwelling Atlantic salmon (Salmo salar L.) parr, brown trout (Salmo trutta L.) and Arctic charr (Salvelinus alpinus (L.)). *Ecology of Freshwater Fish*, *9*(4), 202–209. https://doi.org/10.1111/j.1600-0633.2000.eff090402.x

Kahlert, M., & McKie, B. G. (2014). Comparing new and conventional methods to estimate benthic algal biomass and composition in freshwaters. *Environmental Science: Processes and Impacts*, *16*(11), 2627–2634. https://doi.org/10.1039/c4em00326h

Kallio-nyberg, I., & Koljonen, I. S. M. (2020). Increasing temperature associated with increasing grilse proportion and smaller grilse size of Atlantic salmon. *Journal of Applied Ichthyology*, *00*, 1–10. https://doi.org/10.1111/jai.14033

Kamler, J. F., & Pope, K. L. (2001). Nonlethal Methods of Examining Fish Stomach Contents. *Reviews in Fisheries Science*, *9*(1), 1–11. https://doi.org/10.1080/20016491101663

Kang, H.-K., & Kang, Y. J. (1997). Length and Weight Relationship of Acartia steueri(Copepoda: Calanoida) in ilkwang Bay, Korea. *Korean Journal of Fisheries and Aquatic Sciences*, *30*(5), 30(5), 906–908. https://www.koreascience.or.kr/article/JAKO199723607645201.page

Karbowski, C. M., Finstad, B., Karbowski, N., & Hedger, R. D. (2019). Sea Lice in Iceland: Assessing the Status and Current Implications for Aquaculture and Wild Salmonids. *Aquaculture Environment Interactions*, *11*, 149–160. https://doi.org/10.3354/aei00302

Kaylor, M. J., Argerich, A., White, S. M., VerWey, B. J., & Arismendi, I. (2018). A cautionary tale for in situ fluorometric measurement of stream chlorophyll a: Influences of light and periphyton biomass. *Freshwater Science*, *37*(2), 287–295. https://doi.org/10.1086/697239

Kjartansdóttir, H., & Einarsson, S. M. (2009). Endurtekin hrygning hjá íslenskum laxastofnum. *Fræðaþing Landbúnaðarins*, *6*, 175–183.

Kochalski, S., Riepe, C., & Arlinghaus, R. (2023). Perceived socio-cultural ecosystem services provided by wild Atlantic Salmon populations in four European countries. *Aquatic Ecosystem Health and Management*, *25*(3), 12–21. https://doi.org/10.14321/aehm.025.03.12

Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A. V., & Planque, B. (2019). Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. *Ecography*, *42*(2), 295–308. https://doi.org/10.1111/ecog.03443

Kratina, P., Greig, H. S., Thompson, P. L., Carvalho-Pereira, T. S. A., & Shurin, J. B. (2012). Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology*, *93*(6), 1421–1430. https://doi.org/10.1890/11-1595.1

Kreiling, A. K., Govoni, D. P., Pálsson, S., Ólafsson, J. S., & Kristjánsson, B. K. (2022). Invertebrate communities in springs across a gradient in thermal regimes. *PLoS ONE*, *17*(5 May), 1–20. https://doi.org/10.1371/journal.pone.0264501

Kreiling, A. K., O'Gorman, E. J., Pálsson, S., Benhaïm, D., Leblanc, C. A., Ólafsson, J. S., & Kristjánsson, B. K. (2021). Seasonal variation in the invertebrate community and diet of a

top fish predator in a thermally stable spring. *Hydrobiologia*, *848*(3), 531–545. https://doi.org/10.1007/s10750-020-04409-5

Kriska, G. (2013). Freshwater Invertebrates in Central Europe. In *Freshwater Invertebrates in Central Europe*. https://doi.org/10.1007/978-3-7091-1547-3

Kristinsson, K., Gudbergsson, G., & Gislason, G. M. (2015). Variable migration and delay in two stock components of an Atlantic salmon population. *Environmental Biology of Fishes*, *98*(6), 1513–1523. https://doi.org/10.1007/s10641-015-0378-4

Kristjánsson, B. K., & Leblanc, C. A. (2018). Variation in the magnitude of morphological and dietary differences between individuals among populations of small benthic Arctic charr in relation to ecological factors. *Ecology and Evolution*, *8*(3), 1573–1581. https://doi.org/10.1002/ece3.3761

Kristmundsson, Á., Rut Svavarsdóttir, F., Árnason, F., Antonsson, Þ., Guðbergsson, G., Magnúsdóttir, H., & Andrew Freeman, M. (2023). Tetracapsuloides bryosalmonae and proliferative kidney disease in Icelandic salmonids – Comparative data from two different time periods. *International Journal for Parasitology*, *53*(4), 207–220. https://doi.org/10.1016/j.ijpara.2022.11.011

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/JSS.V082.I13

Lai, S. Y., Pálsson, A., Guðbergsson, G., Jónsson, I. R., Ólafsson, J. S., & Bárðarson, H. (2024). The prey availability and diet of juvenile Atlantic salmon (Salmo salar L .) in low-productivity rivers in northern Europe. *Journal of Fish Biology*, 1–13. https://doi.org/10.1111/jfb.15757

Lamberti, G. A., & Steinman, A. D. (1997). A comparison of primary production in stream ecosystems. *Journal of the North American Benthological Society*, *16*(1), 95–104. https://doi.org/10.2307/1468241

Lárusdóttir, G., Adalsteinsson, H., Ólafsson, J. S., & Gíslason, G. M. (2000). River ecosystems in Iceland — catchment characteristics and river communities. *SIL Proceedings, 1922-2010*, *27*(3), 1607–1610. https://doi.org/10.1080/03680770.1998.11901510

Laske, S. M., Amundsen, P. A., Christoffersen, K. S., Erkinaro, J., Guðbergsson, G., Hayden, B., Heino, J., Holmgren, K., Kahilainen, K. K., Lento, J., Orell, P., Östergren, J., Power, M., Rafikov, R., Romakkaniemi, A., Svenning, M. A., Swanson, H., Whitman, M., & Zimmerman, C. E. (2022). Circumpolar patterns of Arctic freshwater fish biodiversity: A baseline for monitoring. *Freshwater Biology*, *67*(1), 176–193. https://doi.org/10.1111/fwb.13405

Le Pape, O., & Bonhommeau, S. (2015). The food limitation hypothesis for juvenile marine fish. *Fish and Fisheries*, *16*(3), 373–398. https://doi.org/10.1111/faf.12063

Lento, J., Culp, J. M., Levenstein, B., Aroviita, J., Baturina, M. A., Bogan, D., Brittain, J. E., Chin, K., Christoffersen, K. S., Docherty, C., Friberg, N., Ingimarsson, F., Jacobsen, D., Lau, D. C. P., Loskutova, O. A., Milner, A., Mykrä, H., Novichkova, A. A., Ólafsson, J.

S., … Goedkoop, W. (2022a). Temperature and spatial connectivity drive patterns in freshwater macroinvertebrate diversity across the Arctic. *Freshwater Biology*, *67*(1), 159–175. https://doi.org/10.1111/fwb.13805

Lento, J., Laske, S. M., Lavoie, I., Bogan, D., Brua, R. B., Campeau, S., Chin, K., Culp, J. M., Levenstein, B., Power, M., Saulnier-Talbot, É., Shaftel, R., Swanson, H., Whitman, M., & Zimmerman, C. E. (2022b). Diversity of diatoms, benthic macroinvertebrates, and fish varies in response to different environmental correlates in Arctic rivers across North America. *Freshwater Biology*, *67*(1), 95–115. https://doi.org/10.1111/fwb.13600

Lumme, J., Ozerov, M. Y., Veselov, A. E., & Primmer, C. R. (2015). The Formation of Landlocked Populations of Atlantic Salmon. In T. Vladic & E. Petersson (Eds.), *Evolutionary Biology of the Atlantic salmon* (pp. 26–39). CRC Press. https://doi.org/10.1201/b18721

Macan, T. T. (1960). *A Guide to Freshwater Invertebrate Animals*. Longmans.

Malmquist, H. J., Snorrason, S. S., Skulason, S., Jonsson, B., Sandlund, O. T., & Jonasson, P. M. (1992). Diet Differentiation in Polymorphic Arctic Charr in Thingvallavatn, Iceland. *The Journal of Animal Ecology*, *61*(1), 21. https://doi.org/10.2307/5505

Mann, R. H. K. (1989). Mann 1989 Fish population dynamics in the river Frome. *Regulated Rivers: Research and Management*, *4*, 165–177.

Marsh, J. E., Lauridsen, R. B., Gregory, S. D., Kratina, P., Scott, L. J., Cooling, D., & Jones, J. I. (2022). High summer macrophyte cover increases abundance, growth, and feeding of juvenile Atlantic salmon. *Ecological Applications*, *32*(2). https://doi.org/10.1002/eap.2492

McGinnity, P., Jennings, E., DeEyto, E., Allott, N., Samuelsson, P., Rogan, G., Whelan, K., & Cross, T. (2009). Impact of naturally spawning captive-bred Atlantic salmon on wild populations: Depressed recruitment and increased risk of climate-mediated extinction. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1673), 3601–3610. https://doi.org/10.1098/rspb.2009.0799

McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., Maoiléidigh, N. Ó., Baker, N., Cotter, D., O'Hea, B., Cooke, D., Rogan, G., Taggart, J., & Cross, T. (2003). Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1532), 2443–2450. https://doi.org/10.1098/rspb.2003.2520

Metcalfe, N. B., & Thorpe, J. E. (1990). Determinants of Geographical Variation in the Age of Seaward-Migrating Salmon, Salmo salar. *The Journal of Animal Ecology*, *59*(1), 135. https://doi.org/10.2307/5163

Méthot, G., Hudon, C., Gagnon, P., Pinel-Alloul, B., Armellin, A., & Poirier, A. M. T. (2012). Macroinvertebrate size-mass relationships: How specific should they be? *Freshwater Science*, *31*(3), 750–764. https://doi.org/10.1899/11-120.1

Minder, M., & Pyron, M. (2018). Dietary overlap and selectivity among silver carp and two native filter feeders in the Wabash River. *Ecology of Freshwater Fish*, *27*(1), 506–512.

https://doi.org/10.1111/eff.12365

Ministry for the Environment, & The Icelandic Institute of Natural History. (2001). Biological diversity in Iceland - National Report to the Convention on Biological Diversity. In *Natural History*. https://www.cbd.int/doc/world/is/is-nr-01-en.pdf

Miyasaka, H., Nakano, S., & Furukawa-Tanaka, T. (2003). Food habit divergence between white-spotted charr and masu salmon in Japanese mountain streams: Circumstantial evidence for competition. *Limnology*, *4*(1), 1–10. https://doi.org/10.1007/s10201-002-0088-4

Mobley, K. B., Aykanat, T., Czorlich, Y., House, A., Kurko, J., Miettinen, A., Moustakas-Verho, J., Salgado, A., Sinclair-Waters, M., Verta, J. P., & Primmer, C. R. (2021). Maturation in Atlantic salmon (*Salmo salar*, Salmonidae): a synthesis of ecological, genetic, and molecular processes. In *Reviews in Fish Biology and Fisheries* (Vol. 31, Issue 3). https://doi.org/10.1007/s11160-021-09656-w

Mookerji, N., Weng, Z., & Mazumder, A. (2004). Food partitioning between coexisting Atlantic salmon and brook trout in the Sainte-Marguerite River ecosystem, Quebec. *Journal of Fish Biology*, *64*(3), 680–694. https://doi.org/10.1111/j.1095-8649.2004.00333.x

Morash, A. J., Speers-Roesch, B., Andrew, S., & Currie, S. (2021). The physiological ups and downs of thermal variability in temperate freshwater ecosystems. *Journal of Fish Biology*, *98*(6), 1524–1535. https://doi.org/10.1111/jfb.14655

Myers, R. A. (1984). Demographic consequences of precocious maturation of atlantic salmon (Salmo salar). *Canadian Journal of Fisheries and Aquatic Sciences*, *41*(9), 1349–1353. https://doi.org/10.1139/f84-165

Näslund, J., Aldvén, D., & Závorka, L. (2015). Eggs from anadromous adults provide marine-derived nutrients to Atlantic salmon and brown trout parr in late autumn – observations from a Swedish coastal stream. *Environmental Biology of Fishes*, *98*(12), 2305–2313. https://doi.org/10.1007/s10641-015-0436-y

Nelson, D., Benstead, J. P., Huryn, A. D., Cross, W. F., Hood, J. M., Johnson, P. W., Junker, J. R., Gíslason, G. M., & Ólafsson, J. S. (2017a). Experimental whole-stream warming alters community size structure. *Global Change Biology*, *23*(7), 2618–2628. https://doi.org/10.1111/gcb.13574

Nelson, D., Benstead, J. P., Huryn, A. D., Cross, W. F., Hood, J. M., Johnson, P. W., Junker, J. R., Gíslason, G. M., & Ólafsson, J. S. (2017b). Shifts in community size structure drive temperature invariance of secondary production in a stream-warming experiment. *Ecology*, *98*(7), 1797–1806. https://doi.org/10.1002/ecy.1857

Nevoux, M., Finstad, B., Davidsen, J. G., Finlay, R., Josset, Q., Poole, R., Höjesjö, J., Aarestrup, K., Persson, L., Tolvanen, O., & Jonsson, B. (2019). Environmental influences on life history strategies in partially anadromous brown trout (*Salmo trutta*, Salmonidae). *Fish and Fisheries*, *20*(6), 1051–1082. https://doi.org/10.1111/faf.12396

Nicola, G. G., Elvira, B., Jonsson, B., Ayllón, D., & Almodóvar, A. (2018). Local and global

climatic drivers of Atlantic salmon decline in southern Europe. *Fisheries Research*, *198*, 78–85. https://doi.org/10.1016/j.fishres.2017.10.012

Niemelä, E., Julkunen, M., & Erkinaro, J. (2000). Quantitative electrofishing for juvenile salmon densities: Assessment of the catchability during a long-term monitoring programme. *Fisheries Research*, *48*(1), 15–22. https://doi.org/10.1016/S0165-7836(00)00113-2

Nilsen, T. O., Ebbesson, L. O. E., & Stefansson, S. O. (2003). Smolting in anadromous and landlocked strains of Atlantic salmon (Salmo salar). *Aquaculture*, *222*(1–4), 71–82. https://doi.org/10.1016/S0044-8486(03)00103-0

O'Gorman, E. J., & Emmerson, M. C. (2010). Manipulating Interaction Strengths and the Consequences for Trivariate Patterns in a Marine Food Web. *Advances in Ecological Research*, *42*(C), 301–419. https://doi.org/10.1016/B978-0-12-381363-3.00006-X

O'Gorman, E. J., Ólafsson, Ó. P., Demars, B. O. L., Friberg, N., Guðbergsson, G., Hannesdóttir, E. R., Jackson, M. C., Johansson, L. S., McLaughlin, Ó. B., Ólafsson, J. S., Woodward, G., & Gíslason, G. M. (2016). Temperature effects on fish production across a natural thermal gradient. *Global Change Biology*, *22*(9), 3206–3220. https://doi.org/10.1111/gcb.13233

O'Gorman, E. J., Petchey, O. L., Faulkner, K. J., Gallo, B., Gordon, T. A. C., Neto-Cerejeira, J., Ólafsson, J. S., Pichler, D. E., Thompson, M. S. A., & Woodward, G. (2019). A simple model predicts how warming simplifies wild food webs. *Nature Climate Change*, *9*(8), 611–616. https://doi.org/10.1038/s41558-019-0513-x

O'Gorman, E. J., Zhao, L., Kordas, R. L., Dudgeon, S., & Woodward, G. (2023). Warming indirectly simplifies food webs through effects on apex predators. *Nature Ecology & Evolution*, *7*(12), 1983–1992. https://doi.org/10.1038/s41559-023-02216-4

O'Gorman, E. J., Zhao, L., Pichler, D. E., Adams, G., Friberg, N., Rall, B. C., Seeney, A., Zhang, H., Reuman, D. C., & Woodward, G. (2017). Unexpected changes in community size structure in a natural warming experiment. *Nature Climate Change*, *7*(9), 659–663. https://doi.org/10.1038/nclimate3368

Okamoto, D. K., Schmitt, R. J., Holbrook, S. J., & Reed, D. C. (2012). Fluctuations in food supply drive recruitment variation in a marine fish. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1747), 4542–4550. https://doi.org/10.1098/rspb.2012.1862

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, D. M., Durand, S., … Weedon, J. (2022). *vegan: Community Ecology Package* (R package version 2.6-4). https://cran.r-project.org/package=vegan

Ólafsson, J. S., Adalsteinsson, H., Gíslason, G. M., Hansen, I., & Hrafnsdóttir, T. (2002). Spatial heterogeneity in lotic chironomids and simuliids in relation to catchment characteristics in Iceland. *SIL Proceedings, 1922-2010*, *28*(1), 157–163. https://doi.org/10.1080/03680770.2001.11902566

Olafsson, K., Einarsson, S. M., Gilbey, J., Pampoulie, C., Hreggvidsson, G. O., Hjorleifsdottir, S., & Gudjonsson, S. (2016). Origin of Atlantic salmon (Salmo salar) at sea in Icelandic waters. *ICES Journal of Marine Science*, *73*(6), 1525–1532.

Olafsson, K., Pampoulie, C., Hjorleifsdottir, S., Gudjonsson, S., & Hreggvidsson, G. O. (2014). Present-Day Genetic Structure of Atlantic Salmon (Salmo salar) in Icelandic Rivers and Ice-Cap Retreat Models. *PLoS ONE*, *9*(2), 1–12.

Oliver, D. R., & Roussel, M. E. (1983). *THE INSECTS AND ARACHNIDS OF CANADA The Genera of Larval Midqes*. Agriculture Canada.

Olmos, M., Payne, M. R., Nevoux, M., Prévost, E., Chaput, G., Du, H., Guitton, J., Sheehan, T., Mills, K., & Rivot, E. (2019). Spatial synchrony in the response of a long range migratory species (*Salmo salar*) to climate change in the North Atlantic Ocean. *Global Change Biology*, *26*, 1319–1337. https://doi.org/10.1111/gcb.14913

Orpwood, J. E., Griffiths, S. W., & Armstrong, J. D. (2006). Effects of food availability on temporal activity patterns and growth of Atlantic salmon. *Journal of Animal Ecology*, *75*(3), 677–685. https://doi.org/10.1111/j.1365-2656.2006.01088.x

Ouellet, V., St-Hilaire, A., Dugdale, S. J., Hannah, D. M., Krause, S., & Proulx-Ouellet, S. (2020). River temperature research and practice: Recent challenges and emerging opportunities for managing thermal habitat conditions in stream ecosystems. *Science of the Total Environment*, *736*. https://doi.org/10.1016/j.scitotenv.2020.139679

Parmesan, C., Morecroft, M. D., Trisurat, Y., Adrian, R., Anshari, G. Z., Arneth, A., Gao, Q., Gonzalez, P., Harris, R., Price, J., Stevens, N., & Talukdar, G. H. (2023). Terrestrial and Freshwater Ecosystems and Their Services. In H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama (Eds.), *Climate Change 2022 – Impacts, Adaptation and Vulnerability* (pp. 197–378). Cambridge University Press. https://doi.org/10.1017/9781009325844.004

Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D., & Reeves, G. H. (1998). Why aren't there more Atlantic salmon (Salmo salar)? *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(SUPPL.1), 281–287. https://doi.org/10.1139/d98-012

Pasquaud, S., Lobry, J., & Elie, P. (2007). Facing the necessity of describing estuarine ecosystems: A review of food web ecology study techniques. *Hydrobiologia*, *588*(1), 159–172. https://doi.org/10.1007/s10750-007-0660-3

Perkins, D. M., Durance, I., Edwards, F. K., Grey, J., Hildrew, A. G., Jackson, M., Jones, J. I., Lauridsen, R. B., Layer-Dobra, K., Thompson, M. S. A., & Woodward, G. (2018). Bending the rules: exploitation of allochthonous resources by a top-predator modifies size-abundance scaling in stream food webs. *Ecology Letters*, *21*(12), 1771–1780. https://doi.org/10.1111/ele.13147

Perkins, D. M., Hatton, I. A., Gauzens, B., Barnes, A. D., Ott, D., Rosenbaum, B., Vinagre, C., & Brose, U. (2022). Consistent predator-prey biomass scaling in complex food webs. *Nature Communications*, *13*(1). https://doi.org/10.1038/s41467-022-32578-5

Perkins, D. M., Reiss, J., Yvon-Durocher, G., & Woodward, G. (2010). Global change and food webs in running waters. *Hydrobiologia*, *657*(1), 181–198. https://doi.org/10.1007/s10750-009-0080-7

Persson, L., Raunsgard, A., Thorstad, E. B., Østborg, G., Urdal, K., Sægrov, H., Ugedal, O., Hindar, K., Karlsson, S., Fiske, P., & Bolstad, G. H. (2023). Iteroparity and its contribution to life-history variation in Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *80*(3), 577–592. https://doi.org/10.1139/cjfas-2022-0126

Petchey, O. L., McPhearson, P. T., Casey, T. M., & Morin, P. J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, *402*(6757), 69–72. https://doi.org/10.1038/47023

Petersen, R. C. J., Gíslason, G. M., & Vought, L. B.-M. (1995). Rivers of the nordic countries. *Ecosystems of the World: 22. River and Stream Ecosystems*, *February*, 295–341.

Peterson, R. H., & Martin-Robichaud, D. J. (1995). Yolk utilization by Atlantic salmon (Salmo salar L.) alevins in response to temperature and substrate. *Aquacultural Engineering*, *14*(1), 85–99. https://doi.org/10.1016/0144-8609(94)P4428-E

Piccolo, J. J., Frank, B. M., & Hayes, J. W. (2014). Food and space revisited: The role of drift-feeding theory in predicting the distribution, growth, and abundance of stream salmonids. *Environmental Biology of Fishes*, *97*(5), 475–488. https://doi.org/10.1007/s10641-014-0222-2

Pimm, S. L., Lawton, J. H., & Cohen, J. E. (1991). Food web patterns and their consequences. In *Nature* (Vol. 350, pp. 669–674).

Polis, G. A. (1994). Food webs, trophic cascades and community structure. *Australian Journal of Ecology*, *19*(2), 121–136. https://doi.org/10.1111/j.1442-9993.1994.tb00475.x

QGIS.org. (2023). *QGIS Geographic Information System*. http://qgis.org

R Core Team. (2023). R: A Language and Environment for Statistical Computing. In *R Foundation for Statistical Computing* (p. https://www.R-project.org). R Foundation for Statistical Computing,Vienna, Austria. http://www.r-project.org

Rader, R. B. (1997). A functional classification of the drift: Traits that influence invertebrate availability to salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(6), 1211–1234. https://doi.org/10.1139/f97-025

Reiriz, L., Nicieza, A. G., & Braña, F. (1998). Prey selection by experienced and naive juvenile Atlantic salmon. *Journal of Fish Biology*, *53*(1), 100–114. https://doi.org/10.1006/jfbi.1998.0688

Reist, J. D., Wrona, F. J., Prowse, T. D., Power, M., Dempson, J. B., King, J. R., & Beamish, R. J. (2006). An overview of effects of climate change on selected Arctic freshwater and anadromous fishes. *Ambio*, *35*(7), 381–387. https://doi.org/10.1579/0044-7447(2006)35[381:AOOEOC]2.0.CO;2

Rikardsen, A. H., & Dempson, B. (2011). Dietary Life-Support: The Food and Feeding of

Atlantic Salmon at Sea. In Ø. Aas, A. Klemetsen, S. Einum, & J. Skurdal (Eds.), *Atlantic Salmon Ecology* (pp. 115–143). John Wiley & Sons.

Riley, W. D., Pawson, M. G., Quayle, V., & Ives, M. J. (2009). The effects of stream canopy management on macroinvertebrate communities and juvenile salmonid production in a chalk stream. *Fisheries Management and Ecology*, *16*(2), 100–111. https://doi.org/10.1111/j.1365-2400.2008.00649.x

Rinaldo, A., de Eyto, E., Reed, T., Gjelland, K. Ø., & McGinnity, P. (2023). Global warming is projected to lead to increased freshwater growth potential and changes in pace of life in Atlantic salmon <scp> *Salmo salar* </scp>. *Journal of Fish Biology*. https://doi.org/10.1111/jfb.15603

Rist, S. (1990). Viðauki I. Vatnasvið Íslands. In *Vatns er pörf* (pp. 203–234). Bókaútgáfa Menningarsjóðs.

Ritchie, R. J. (2006). Consistent sets of spectrophotometric chlorophyll equations for acetone, methanol and ethanol solvents. *Photosynthesis Research*, *89*(1), 27–41. https://doi.org/10.1007/s11120-006-9065-9

Robinson, S. I., Mikola, J., Ovaskainen, O., & O'Gorman, E. J. (2021). Temperature effects on the temporal dynamics of a subarctic invertebrate community. *Journal of Animal Ecology*, *90*(5), 1217–1227. https://doi.org/10.1111/1365-2656.13448

Rolls, R. J., Hayden, B., & Kahilainen, K. K. (2017). Conceptualising the interactive effects of climate change and biological invasions on subarctic freshwater fish. *Ecology and Evolution*, *7*(12), 4109–4128. https://doi.org/10.1002/ece3.2982

Rosi-Marshall, E. J., Vallis, K. L., Baxter, C. V., & Davis, J. M. (2016). Retesting a prediction of the River Continuum Concept: Autochthonous versus allochthonous resources in the diets of invertebrates. *Freshwater Science*, *35*(2), 534–543. https://doi.org/10.1086/686302

Rosi-Marshall, E. J., & Wallace, J. B. (2002). Invertebrate food webs along a stream resource gradient. *Freshwater Biology*, *47*(1), 129–141. https://doi.org/10.1046/j.1365-2427.2002.00786.x

Rypel, A. L., & David, S. R. (2017). Pattern and scale in latitude-production relationships for freshwater fishes. *Ecosphere*, *8*(1). https://doi.org/10.1002/ecs2.1660

Saltveit, S. J., & Brabrand, Å. (2013). Incubation, hatching and survival of eggs of Atlantic salmon (Salmo salar) in spawning redds influenced by groundwater. *Limnologica*, *43*(5), 325–331. https://doi.org/10.1016/j.limno.2013.05.009

Sánchez-Hernández, J. (2023). Fresh perspectives on the River Continuum Concept require trophic ecology approaches focussed on food web structure and energy mobilisation routes. *Journal of Animal Ecology*, *92*(5), 957–964. https://doi.org/10.1111/1365-2656.13928

Sandlund, O. Ter, Jonsson, B., Malmquist, H. J., Gydemo, R., Lindem, T., Skúlason, S., Snorrason, S. S., & Jónasson, P. M. (1987). Habitat use of arctic charr Salvelinus alpinus

in Thingvallavatn, Iceland. *Environmental Biology of Fishes*, *20*(4), 263–274. https://doi.org/10.1007/BF00005297

Schmid, P. E. (1993). *A Key to the Larval Chironomidae and Their Instars from Austrian Danube Region Streams and Rivers: Part 1, Diamesinae, Prodiamesinae and Orthocladiinae* (K. Werner (ed.); Wasser und). Federal Institute of Water Quality.

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Shah, D. N., Tonkin, J. D., Haase, P., & Jähnig, S. C. (2015). Latitudinal patterns and large-scale environmental determinants of stream insect richness across Europe. *Limnologica*, *55*, 33–43. https://doi.org/10.1016/j.limno.2015.11.001

Shurin, J. B., Clasen, J. L., Greig, H. S., Kratina, P., & Thompson, P. L. (2012). Warming shifts top-down and bottom-up control of pond food web structure and function. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1605), 3008–3017. https://doi.org/10.1098/rstb.2012.0243

Skaala, Ø., Johnsen, G. H., Lo, H., Borgstrøm, R., Wennevik, V., Hansen, M. M., Merz, J. E., Glover, K. A., & Barlaup, B. T. (2014). A conservation plan for Atlantic salmon (Salmo salar) and anadromous brown trout (Salmo trutta) in a region with intensive industrial use of aquatic habitats, the Hardangerfjord, western Norway. *Marine Biology Research*, *10*(3), 308–322. https://doi.org/10.1080/17451000.2013.810758

Smith, E. P., & Zaret, T. M. (1982). Bias in Estimating Niche Overlap. *Ecology*, *63*(5), 1248–1253. https://doi.org/10.2307/1938851

Stefánsson, U., & Ólafsson, J. (1991). Nutrients and fertility of Icelandic waters. *Rit Fiskideildar*, *January 1991*, 1–56. http://books.google.is/books/about/Nutrients_and_fertility_of_Icelandic_wat.html?id=uMs4GwAACAAJ&pgis=1

Steingrímsson, S. Ã., & Gíslason, G. M. (2002). Body size, diet and growth of landlocked brown trout, Salmo trutta, in the subarctic River Laxá, North-East Iceland. *Environmental Biology of Fishes*, *63*(4), 417–426. https://doi.org/10.1023/A:1014976612970

Strøm, J. F., Rikardsen, A. H., Campana, S. E., Righton, D., Carr, J., Aarestrup, K., Stokesbury, M. J. W., Gargan, P., Javierre, P. C., & Thorstad, E. B. (2019a). Ocean predation and mortality of adult Atlantic salmon. *Scientific Reports*, *9*(1), 1–11. https://doi.org/10.1038/s41598-019-44041-5

Strøm, J. F., Thorstad, E. B., & Rikardsen, A. H. (2019b). Thermal habitat of adult Atlantic salmon Salmo salar in a warming ocean. *Journal of Fish Biology*. https://doi.org/10.1111/jfb.14187

Strøm, J. F., Ugedal, O., Rikardsen, A. H., & Thorstad, E. B. (2023). Marine food consumption by adult Atlantic salmon and energetic impacts of increased ocean temperatures caused by climate change. *Hydrobiologia*, *850*(14), 3077–3089. https://doi.org/10.1007/s10750-023-05234-2

Sturlaugsson, J. (2023). *Ellíðaár 2022- Rannsóknir á fiskistofnum vatnakerfisins*. https://www.laxfiskar.is/images/stories/skyrslur/Ellidaar_2022-Fiskirannsoknir-Johannes_Sturlaugsson-Laxfiskar_april2023.pdf

Sundt-Hansen, L. E., Hedger, R. D., Ugedal, O., Diserud, O. H., Finstad, A. G., Sauterleute, J. F., Tøfte, L., Alfredsen, K., & Forseth, T. (2018). Modelling climate change effects on Atlantic salmon: Implications for mitigation in regulated rivers. *Science of the Total Environment*, *631–632*, 1005–1017. https://doi.org/10.1016/j.scitotenv.2018.03.058

Svenning, M. A., Falkegård, M., Dempson, J. B., Power, M., Bårdsen, B. J., Guðbergsson, G., & Fauchald, P. (2022). Temporal changes in the relative abundance of anadromous Arctic charr, brown trout, and Atlantic salmon in northern Europe: Do they reflect changing climates? *Freshwater Biology*, *67*(1), 64–77. https://doi.org/10.1111/fwb.13693

Syrjänen, J., Korsu, K., Louhi, P., Paavola, R., & Muotka, T. (2011). Stream salmonids as opportunistic foragers: The importance of terrestrial invertebrates along a stream-size gradient. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*(12), 2146–2156. https://doi.org/10.1139/F2011-118

Thompson, M. S. A., Brooks, S. J., Sayer, C. D., Woodward, G., Axmacher, J. C., Perkins, D. M., & Gray, C. (2018). Large woody debris "rewilding" rapidly restores biodiversity in riverine food webs. *Journal of Applied Ecology*, *55*(2), 895–904. https://doi.org/10.1111/1365-2664.13013

Thordardottir, G., & Guðbergsson, G. (2017). Catch statistics for Atlantic salmon Arctic charr and brown trout in Icelandic rivers and lakes 2016. In *Marine & Freshwater Research Institute in Iceland*. https://www.hafogvatn.is/static/research/files/hv2019-42.pdf

Thorstad, E. B., Bliss, D., Breau, C., Damon-Randall, K., Sundt-Hansen, L. E., Hatfield, E. M. C., Horsburgh, G., Hansen, H., Maoiléidigh, N., Sheehan, T., & Sutton, S. G. (2021). Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(9), 2654–2665. https://doi.org/10.1002/aqc.3624

Thorstad, E. B., Økland, F., Aarestrup, K., & Heggberget, T. G. (2008). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries*, *18*(4), 345–371. https://doi.org/10.1007/s11160-007-9076-4

Tunney, T. D., & Steingrímsson, S. Ó. (2012). Foraging mode variation in three stream-dwelling salmonid fishes. *Ecology of Freshwater Fish*, *21*(4), 570–580. https://doi.org/10.1111/j.1600-0633.2012.00577.x

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1), 130–137.

Verspoor, E., García de Leániz, C., & McGinnity, P. (2007). Genetics and habitat management. In E. Verspoor, L. Strandmeyer, & J. L. Nielsen (Eds.), *The Atlantic Salmon: Genetics, Conservation and Management* (pp. 399–424). Blackwell Publishing Ltd.

Wańkowski, J. W. J. (1979). Morphological limitations, prey size selectivity, and growth response of juvenile atlantic salmon, Salmo salar. *Journal of Fish Biology*, *14*(1), 89–100. https://doi.org/10.1111/j.1095-8649.1979.tb03498.x

Wańkowski, J. W. J. (1981). Behavioural aspects of predation by juvenile Atlantic salmon (*Salmo salar L.*) on particulate, drifting prey. *Animal Behaviour*, *29*(2), 557–571. https://doi.org/10.1016/S0003-3472(81)80119-4

Wańkowski, J. W. J., & Thorpe, J. E. (1979). The role of food particle size in the growth of juvenile Atlantic salmon (*Salmo salar L.*). *Journal of Fish Biology*, *14*(4), 351–370. https://doi.org/10.1111/j.1095-8649.1979.tb03530.x

Ward, C. L., & McCann, K. S. (2017). A mechanistic theory for aquatic food chain length. *Nature Communications*, *8*(1). https://doi.org/10.1038/s41467-017-02157-0

Warren, P. H. (1989). Spatial and Temporal Variation in the Structure of a Freshwater Food Web. *Oikos*, *55*(3), 299. https://doi.org/10.2307/3565588

Weber, C. I. (1973). *Biological field and laboratory methods for measuring the quality of surface waters and effluents* (Issue Environmental Monitoring Series).

Weber, N., Bouwes, N., & Jordan, C. (2017). Accounting for spatial and temporal variation in macroinvertebrate community abundances when measuring the food supply of stream salmonids. *Freshwater Science*, *36*(2), 364–376. https://doi.org/10.1086/692012

Whoriskey, F. G., Prusov, S., & Crabbe, S. (2000). Evaluation of the effects of catch-and-release angling on the Atlantic salmon (*Salmo salar*) of the Ponoi River, Kola Peninsula, Russian Federation. *Ecology of Freshwater Fish*, *9*(1–2), 118–125. https://doi.org/10.1034/j.1600-0633.2000.90114.x

Woodward, G., Blanchard, J., Lauridsen, R. B., Edwards, F. K., Jones, J. I., Figueroa, D., Warren, P. H., & Petchey, O. L. (2010a). Individual-based food webs. Species identity, body size and sampling effects. In *Advances in Ecological Research* (Vol. 43, Issue C). Elsevier Ltd. https://doi.org/10.1016/B978-0-12-385005-8.00006-X

Woodward, G., Dybkjær, J. B., Ólafsson, J. S., Gíslason, G. M., Hannesdóttir, E. R., & Friberg, N. (2010b). Sentinel systems on the razor's edge: Effects of warming on Arctic geothermal stream ecosystems. *Global Change Biology*, *16*(7), 1979–1991. https://doi.org/10.1111/j.1365-2486.2009.02052.x

Woodward, G., Morris, O., Barquín, J., Belgrano, A., Bull, C., de Eyto, E., Friberg, N., Guðbergsson, G., Layer-Dobra, K., Lauridsen, R. B., Lewis, H. M., McGinnity, P., Pawar, S., Rosindell, J., & O'Gorman, E. J. (2021). Using Food Webs and Metabolic Theory to Monitor, Model, and Manage Atlantic Salmon—A Keystone Species Under Threat. *Frontiers in Ecology and Evolution*, *9*(December), 1–10. https://doi.org/10.3389/fevo.2021.675261

Woodward, G., Papantoniou, G., Edwards, F., & Lauridsen, R. B. (2008). Trophic trickles and cascades in a complex food web: Impacts of a keystone predator on stream community structure and ecosystem processes. *Oikos*, *117*(5), 683–692. https://doi.org/10.1111/j.0030-1299.2008.16500.x

Woodward, G., Speirs, D. C., & Hildrew, A. G. (2005). Quantification and Resolution of a Complex, Size-Structured Food Web. *Advances in Ecological Research*, *36*, 85–135. https://doi.org/10.1016/S0065-2504(05)36002-8

Wootton, J. T. (2012). River Food Web Response to Large-Scale Riparian Zone Manipulations. *PLoS ONE*, *7*(12). https://doi.org/10.1371/journal.pone.0051839

Wright, J. F., Gunn, R. J. M., Symes, K. L., Matthews, A. M., Furse, M. T., Blackburn, J. H., & Winder, J. M. (1992). *Invertebrate survey and classification of rivers for nature conservation*. https://nora.nerc.ac.uk/id/eprint/12886

Þórðardóttir, G., & Guðbergsson, G. (2023). *Lax- og silungsveiðin 2022*.

Appendix 1: Statistical comparison of algae concentrations across rivers in NE Iceland

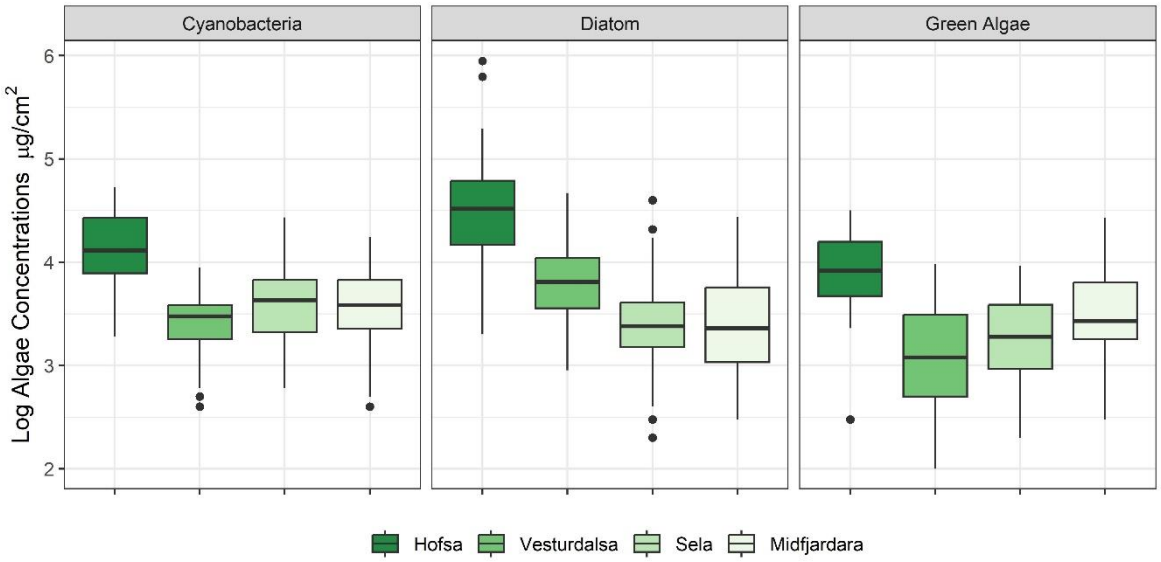

Figure S20: Log$_{10}$ algae concentrations of cyanobacteria, diatom, and green algae of Atlantic salmon rivers in NE Iceland.

Table S4: Statistical output of comparison of log$_{10}$ algae concentrations in different rivers using Kruskal-Wallis tests. Summary tables are shown with X^2 values (chi-squared), DF values (degree of freedom), and P values.

	X^2	df	p-value
Cyanobacteria	157	3	***
Diatom	203	3	***
Green Algae	49.7	3	***

Table S5: Statistical output of post-hoc Dunn test on comparisons of log$_{10}$ cyanobacteria concentrations between rivers. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	adjusted p-value
Hofsá – Miðfjarðará	8.82	***
Hofsá – Selá	8.09	***
Miðfjarðará – Selá	-0.186	1.00
Hofsá – Vesturdalsá	12.3	***
Miðfjarðará – Vesturdalsá	3.55	**

Selá – Vesturdalsá	3.46	**

Table S6: Statistical output of post-hoc Dunn test on comparisons of log_{10} diatom concentrations between rivers. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	**adjusted p-value**
Hofsá – Miðfjarðará	12.5	***
Hofsá – Selá	12.0	***
Miðfjarðará – Selá	0.268	1.00
Hofsá – Vesturdalsá	7.11	***
Miðfjarðará – Vesturdalsá	-6.27	***
Selá – Vesturdalsá	-6.05	***

Table S7: Statistical output of post-hoc Dunn test on comparisons of log_{10} green algae concentrations between rivers. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	**adjusted p-value**
Hofsá – Miðfjarðará	2.96	*
Hofsá – Selá	5.07	***
Miðfjarðará – Selá	3.53	**
Hofsá – Vesturdalsá	5.94	***
Miðfjarðará – Vesturdalsá	4.88	***
Selá – Vesturdalsá	1.33	1.00

Appendix 2: Figures of food webs and predator-prey relationships

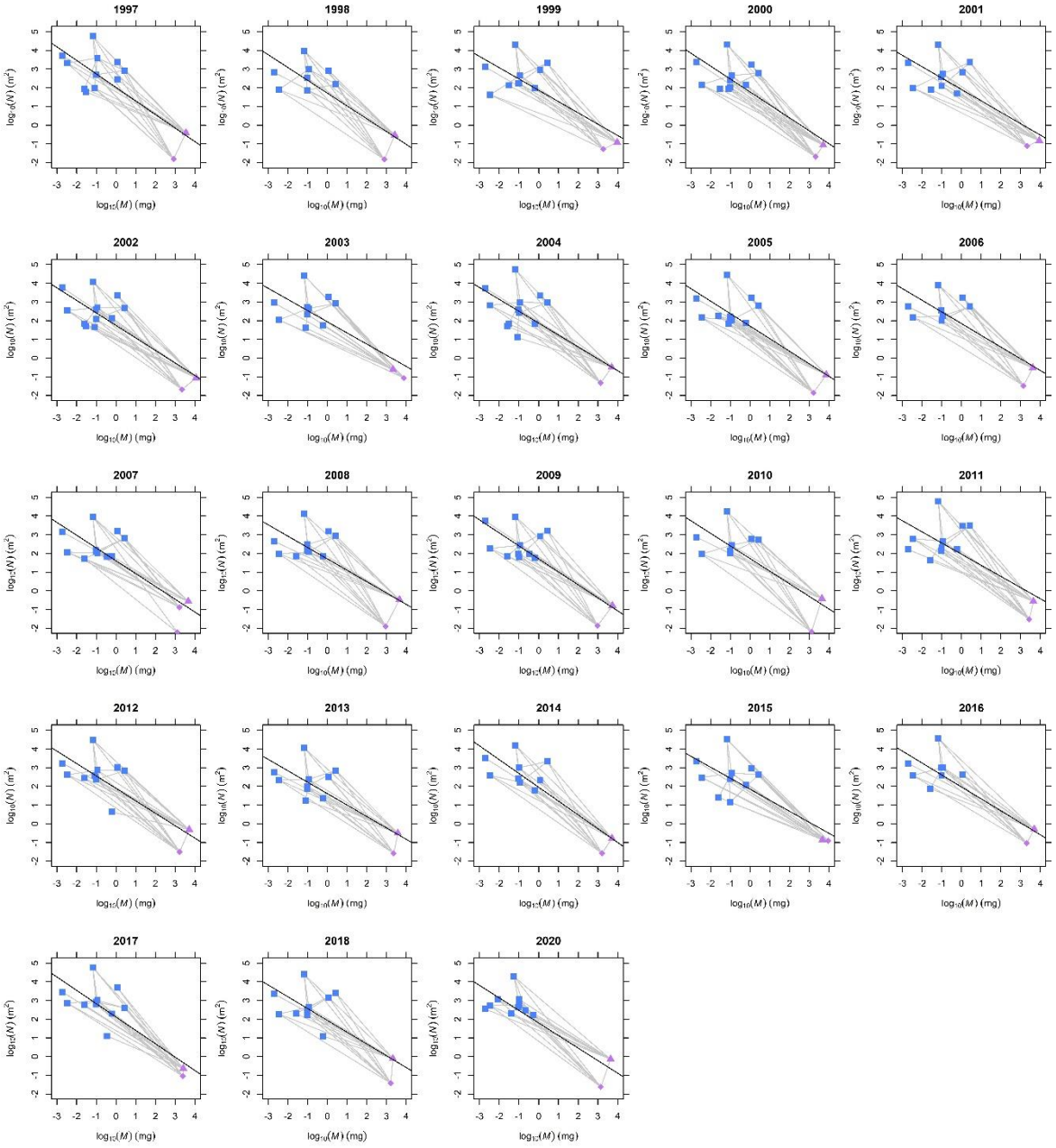

Figure S21: Log_{10} M-N predator-prey relationships from 1997 to 2018 and 2020 in Vesturdalsá (Blue squares ■: invertebrates, purple triangle ▲: juvenile Atlantic salmon, purple diamonds ◆: other salmonid species).

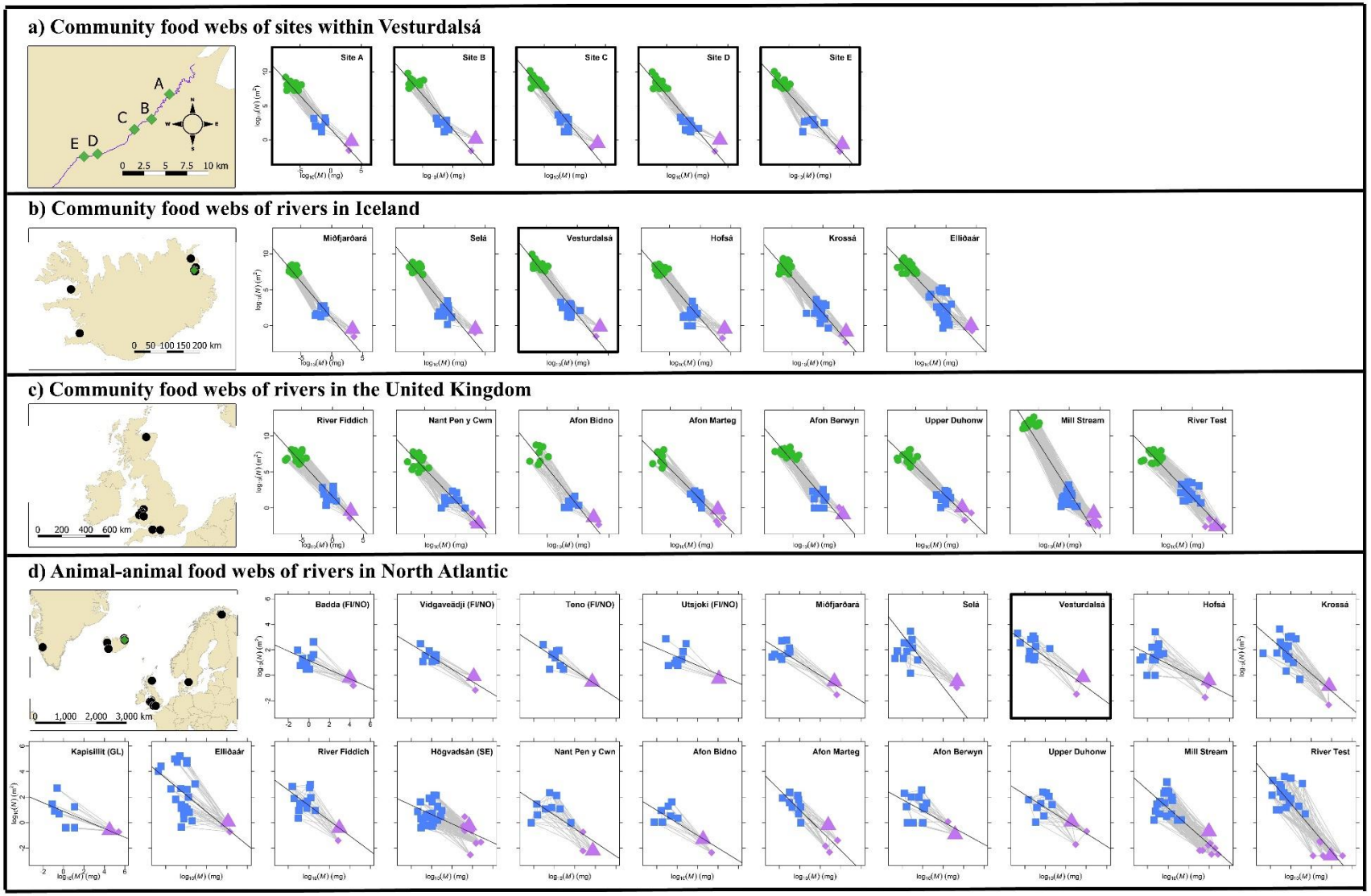
a) Community food webs of sites within Vesturdalsá
A
B
C
D
E
0 2.5 5 7.5 10 km
Site A
Site B
Site C
Site D
Site E
b) Community food webs of rivers in Iceland
0 50 100 150 200 km
Miðfjarðará
Selá
Vesturdalsá
Hofsá
Krossá
Elliðaár
c) Community food webs of rivers in the United Kingdom
0 200 400 600 km
River Fiddich
Nant Pen y Cwm
Afon Bidno
Afon Marteg
Afon Berwyn
Upper Duhonw
Mill Stream
River Test
d) Animal-animal food webs of rivers in North Atlantic
0 1,000 2,000 3,000 km
Badda (FI/NO)
Vidgaveädji (FI/NO)
Teno (FI/NO)
Utsjoki (FI/NO)
Miðfjarðará
Selá
Vesturdalsá
Hofsá
Krossá
Kapisillit (GL)
Elliðaár
River Fiddich
Högvadsån (SE)
Nant Pen y Cwn
Afon Bidno
Afon Marteg
Afon Berwyn
Upper Duhonw
Mill Stream
River Test

Figure S22: Log_{10} M-N trivariate community food webs with increasing spatial scale a) from within sites of Vesturdalsá, to b) salmon rivers in Iceland, and c) salmon rivers in the United Kingdom. d) Log_{10} M-N animal-animal food webs of salmon rivers in the North Atlantic. Black points on the map to the left shows the sites/rivers of the food webs, and the green diamond is Vesturdalsá. Food webs of Vesturdalsá are also highlighted. Left to right figures in decreasing latitude. Green circle points represent producer species, blue square points represent macroinvertebrate species, purple triangle point represent Salmo salar, and purple diamond points represent other fish species, grey lines show feeding interactions, and the black line represents the slope of the food web.

Appendix 3: Summary properties, figures, and statistical outputs of food webs within rivers in NE Iceland

Table S8: Food web properties of sites within Hofsá.

Site	Overall M-N slope	M-N Slope of producer	M-N Slope of invertebrate	M-N Slope of salmonids	Mean trophic level	Connectance	Mean chain length	Mean link angle
B	-0.978	-0.172	0.173	2.70	1.74	0.200	9.76	-43.8
C	-0.982	-0.0946	0.459	3.83	1.73	0.163	9.46	-46.1

Table S9: Statistical output from ANOVA analysis of linear mixed effects model across different sites in Hofsá. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and site were fixed effects. 'Nodes' were a random effect. The summary table is shown with DF values (degree of freedom), F values, and P values.

	DF	F value	P value[†]
(Intercept)	1	324	***
log_{10}(Mass)	1	191	***
Site	1	0.465	0.506
log_{10}(Mass) × Site	1	0.202	0.660

[†] if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

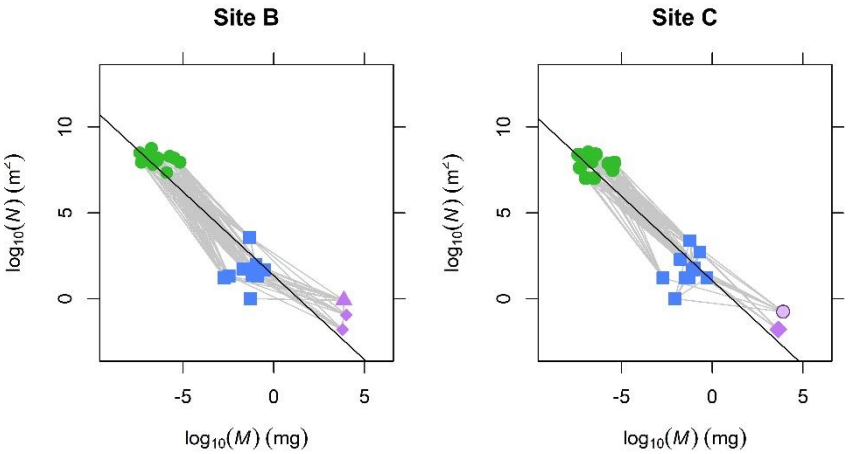

Figure S23: Log_{10} mass-abundance trivariate food webs of sites in Hofsá, with green points representing producer species, blue diamond points representing macroinvertebrate species (circles: Simuliidae, Chironomidae, and Oligochaeta), purple points representing salmonid species (circle: Salmo salar), grey lines show feeding interactions, and the black line represents the slope of the food web.

Table S10: Food web properties of sites within Selá.

Site	Overall M-N slope	M-N Slope of producer	M-N Slope of invertebrate	M-N Slope of salmonids	Mean trophic level	Connectance	Mean chain length	Mean link angle
A	-1.08	-0.109	0.556	NA	1.67	0.198	9.23	-50.3
B	-1.01	-0.105	0.626	1.43	1.60	0.191	9.54	-49.8
C	-0.985	-0.0322	0.235	-2.29	1.59	0.182	9.30	-49.3

Table S11: Statistical output from ANOVA analysis of linear mixed effects model across different sites in Selá. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and site were fixed effects. 'Nodes' were a random effect. Summary table is shown with DF values (degree of freedom), F values, and P values.

	DF	F value	P value[†]
(Intercept)	1	583	***
log_{10}(Mass)	1	202	***
Site	2	23.1	***
log_{10}(Mass) × Site	2	0.709	0.498

[†] if p<0.05 it is shown with *, if a p<0.01 it is shown with **, and if a p<0.001 it is shown with ***, non-significant p-values are written out.

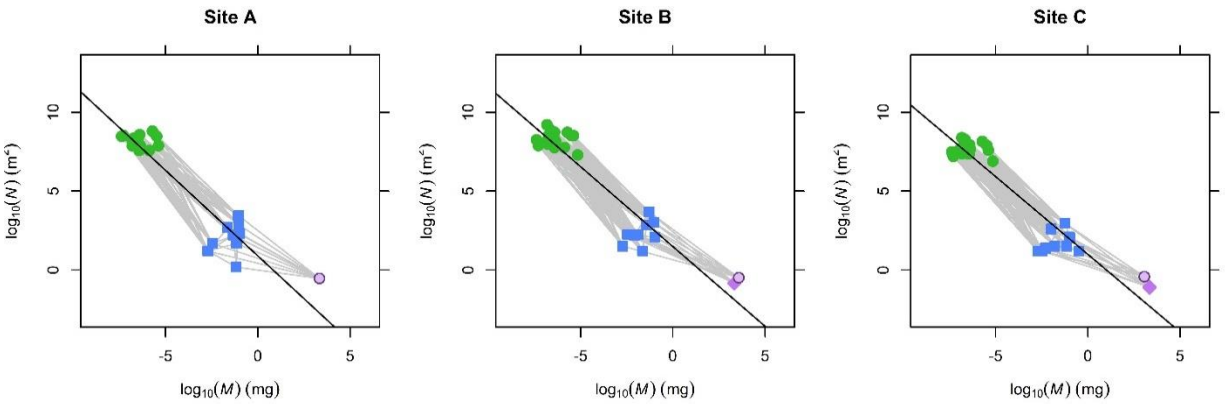

Figure S24: Log_{10} mass-abundance trivariate food webs of sites in Selá, with green points representing producer species, blue diamond points representing macroinvertebrate species (circles: Simuliidae, Chironomidae, and Oligochaeta), purple points representing salmonid species (circle: Salmo salar), grey lines show feeding interactions, and the black line represents the slope of the food web.

Table S12: Food web properties of sites within Miðfjarðará.

Site	Overall M-N slope	M-N Slope of producer	M-N Slope of invertebrate	M-N Slope of salmonids	Mean trophic level	Connectance	Mean chain length	Mean link angle
A	-1.03	-0.0212	0.486	NA	1.61	0.209	9.36	-47.0
B	-1.06	0.00202	0.298	NA	1.54	0.187	9.46	-50.9
C	-0.984	-0.263	0.339	-1.71	1.60	0.168	9.40	-47.5
D	-1.03	-0.0265	0.232	3.72	1.66	0.179	9.19	-47.4

Table S13: Statistical output from ANOVA analysis of linear mixed effects model across different sites in Miðfjarðará. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and site were fixed effects. 'Nodes' were a random effect. The summary table is shown with DF values (degree of freedom), F values, and P values.

	DF	F value	P value[†]
(Intercept)	1	642	***
log_{10}(Mass)	1	217	***
Site	3	4.44	**
log_{10}(Mass) × Site	3	0.870	0.462

[†] if p<0.05 it is shown with *, if a p<0.01 it is shown with **, and if a p<0.001 it is shown with ***, non-significant p-values are written out.

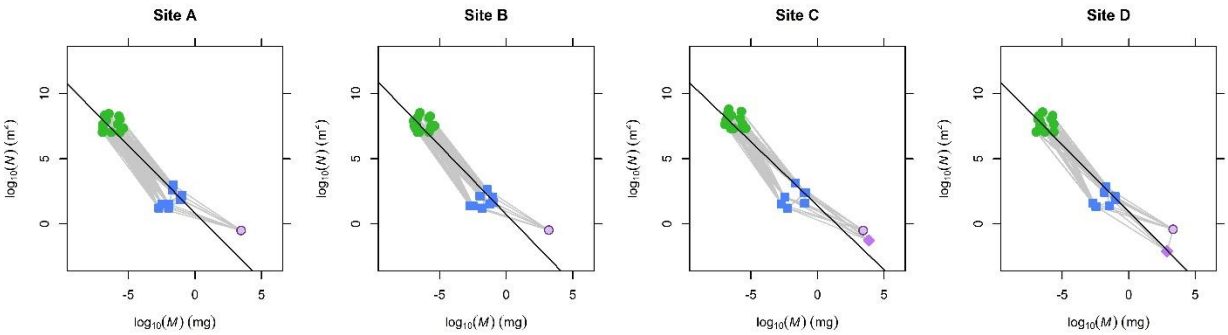

Figure S25: Log_{10} mass-abundance trivariate food webs of sites in Miðfjarðará, with green points representing producer species, blue diamond points representing macroinvertebrate species (circles: Simuliidae, Chironomidae, and Oligochaeta), purple points representing salmonid species (circle: Salmo salar), grey lines show feeding interactions, and the black line represents the slope of the food web.

Paper I

The prey availability and diet of juvenile Atlantic salmon (*Salmo salar L.*) in low-productivity rivers in northern Europe

Sum Yi Lai, Arnar Pálsson, Guðni Guðbergsson, Ingi Rúnar Jónsson, Jón S. Ólafsson, and Hlynur Bárðarson

Author Contribution Statement:

Conceptualisation & Developing methods: SYL, AP, GG, IRJ, JSO, HB. Conducting the research: SYL, JSO, HB. Data analysis: SYL, HB. Data interpretation: SYL, AP, IRJ, JSO, HB. Preparation figures & tables & Writing: SYL. All authors reviewed, edited, and approved the manuscript.

Article Title: The prey availability and diet of juvenile Atlantic salmon (*Salmo salar L.*) in low-productivity rivers in northern Europe

Authors:

Sum Yi Lai[1,2] (sammi.lai@hafogvatn.is)

Arnar Pálsson[2] (apalsson@hi.is)

Guðni Guðbergsson[1] (gudni.gudbergsson@hafogvatn.is)

Ingi Rúnar Jónsson[1] (ingi.runar.jonsson@hafogvatn.is)

Jón S. Ólafsson[1] (jon.s.olafsson@hafogvatn.is)

Hlynur Bárðarson[1] (hlynur.bardarson@hafogvatn.is)

1. Marine and Freshwater Research Institute, Hafnarfjördur, Iceland
2. University of Iceland, Reykjavík, Iceland

Corresponding author:

Name: Sum Yi Lai

Address: Marine and Freshwater Research Institute, Fornubúdir 5, 220 Hafnarfjördur, Iceland

Email: sammi.lai@hafogvatn.is

Funding information: This study was funded by Six Rivers Iceland.

Abstract:

The availability of resources varies across a species distributional range, and a low-productivity area can make a species more vulnerable. We investigated the invertebrate composition and prey choice of juvenile Atlantic salmon (*Salmo salar L.)* in low-productivity rivers at Northeast Iceland, which is one of the species´ most northerly distributions. By sampling benthic and drift invertebrate populations, we found that prey availability was similar within and between rivers. Gut content samples showed that the main prey choice for juvenile *S. salar* was the Chironomidae. The type of food items consumed varied across different weight groups of *S. salar*, with smaller juveniles having more diverse diet. *S. salar* did not have a selection preference for chironomids, which indicate that they were eating the highly available prey in their environment, rather than hunting high biomass items such as terrestrial invertebrates and large Dipterans. Estimates of dietary niche showed that *S. salar* in these low-productivity rivers relied on consuming what was most readily available, the chironomids, and that they must share resources with other salmonid species. This may be due to the low diversity of freshwater invertebrates (fewer prey options), whereas *S. salar* in nutrient-rich rivers could rely more on terrestrial invertebrates as an additional subsidy in their diet. In conclusion, with limited prey choices, juvenile *S. salar* in nutrient-poor rivers, especially in a biogeographically isolated region with low species diversity, may increase in vulnerability and decrease in adaptability to environmental change. Management methods that increase benthic prey abundance and diversity are recommended for conserving *S. salar* population in a nutrient-poor river.

Keywords: Atlantic salmon, food availability, invertebrates, Northeast Iceland, prey selectivity, productivity

Introduction:

Populations of Atlantic salmon (*Salmo salar L.)* in rivers worldwide vary temporally and spatially in abundance, growth, and structure. Understanding the factors that influence these variations is vital for sustainable management of *S. salar* populations. Globally, there are many threats to freshwater ecosystems. Climate change, changes in water flow, pollution, eutrophication, and habitat alteration primarily affect juvenile *S. salar* populations, all of which could affect the growth, age-at-maturity, migration timing, and survival of populations (Bednar-Friedl et al., 2022; Birnie-Gauvin et al., 2019; Parmesan et al., 2023; Vollset et al., 2022). The culmination of these threats during the freshwater phase has contributed to a decrease in the abundance of wild *S. salar* in the North Atlantic (ICES, 2023). Despite many studies on the different drivers of these changes in *S. salar* (Arnekleiv et al., 2006; Johnson & Ringler, 2016; Suttle et al., 2004), including temperature, water discharge, habitat use, and competition, many questions remain unanswered (Armstrong et al., 2003; Baum et al., 2005; Dolinsek et al., 2007; Elliott & Elliott, 2010; Jonsson & Jonsson, 2009; Mookerji et al., 2004; Stich et al., 2015), including what are the impacts and relative importance of these drivers on different populations? An important driver that determines the growth and sustainability of *S. salar* populations is the availability of food resources.

Detailed studies on the effect of food availability on *S. salar* populations in nutrient-poor streams are lacking. Icelandic freshwaters are species-poor due to their isolated island biogeography; therefore, food webs are simpler in comparison to other northern European freshwater habitats (Lento et al., 2022; Ministry for the Environment & The Icelandic Institute of Natural History, 2001). Freshwater ecosystems in Iceland are also less studied compared to the

more productive southern *S. salar* riverine ecosystems with free immigration and emigration of freshwater species.

Additionally, stress factors such as warming could reduce prey options for *S. salar* populations in high-productivity rivers owing to decreases in invertebrate biodiversity and abundance. Thus, looking at a low prey diversity system such as the rivers in Iceland offers an interesting perspective on a vulnerable population at risk (ICES, 2023). It has also been projected that there will be a loss of key species in the Arctic because of warmer water temperatures, which could increase productivity and oxygen loss in oligotrophic systems (Bednar-Friedl et al., 2022). Recent IPCC reports (Bednar-Friedl et al., 2022; Parmesan et al., 2023) showed that freshwater species shifted their range to higher latitudes and the change in freshwater habitats could cause a loss of cold-dependent fish due to climate change. Therefore, *S. salar* populations in northern Iceland offer an opportunity to examine the food availability and prey choice of juveniles in a cold and nutrient-poor environment.

Many *S. salar* populations across the North Atlantic have shown a steady decline over time (Dadswell et al., 2022; ICES, 2023). However, populations in NE Iceland have remained relatively stable compared to other North Atlantic populations (Bárðarson et al., 2023). *S. salar* has an anadromous life cycle, and in Iceland, they spend approximately three to five years in a freshwater environment before migrating to the ocean as smolts and return either after one or two years at sea to the same natal river as spawning adults (Antonsson et al., 2010; ICES, 2023; Olafsson et al., 2016). Their juvenile life stage in the freshwater ecosystem is important, as growth during the juvenile stage can be associated with the survival rates of smolts and, therefore, the number of adults returning to the rivers (Antonsson et al., 2010; Gregory et al., 2019).

Juvenile salmonids feed mainly on invertebrates in the drift column of rivers (Rader, 1997; Reiriz et al., 1998). Invertebrate input into the drift comes from benthic and terrestrial resources and even pelagic resources if there is a lake upstream of the river. If these resources are reduced or depleted, the growth and abundance of the salmonid population may be affected. Invertebrate communities differ between rivers due to differences in physical and environmental characteristics and chance; thus, prey availability and type of salmonids vary even by neighbouring rivers (Kreiling et al., 2021). Additionally, food availability differs seasonally and abundance tends to peak in the spring and early summer, which is the main growth period of juvenile *S. salar* (Bacon et al., 2005; Dineen et al., 2007). Body size can also affect the structure of the food web, as *S. salar* of different sizes (reflecting their age and conditions) will have different food preferences, and small predators usually have narrower diet preferences than larger predators (Wańkowski, 1979; Wańkowski & Thorpe, 1979). Knowing the food availability within an *S. salar* river with low-productivity can inform river managers which resources are highly important to the *S. salar* populations and thereby implement the appropriate management plan to increase productivity.

In addition to the *S. salar*, two other native salmonid species inhabit rivers in NE Iceland, Arctic charr (*Salvelinus alpinus L.*) and brown trout (*Salmo trutta L.*). Only two other fish species belong to the native fish-fauna in freshwater ecosystems i.e. three-spined sticklebacks (*Gasterosteus aculeatus*) and eel (*Anguilla anguilla*) and more recently flounder (*Platichthys flesus*) and pink salmon (*Oncorhynchus gorbuscha*) have arrived within these rivers (Bárðarson et al., 2023). Sharing resources creates an overlap in resource consumption and decreases prey availability between species and individuals, which could affect their growth and survival (Johnson & Ringler, 2016; Mookerji et al., 2004). Thus, fish inhabiting the same space with the

same resources may need to consume a large variety of prey items to meet their energy demand. The three salmonid species found in Iceland use many of the same food items (Antonsson, 2015). This study showed that *S. alpinus* consumed more terrestrial input from drifts. In contrast, *S. trutta* had prey choices similar to *S. salar*, and *S. trutta* may have competed directly for resources with *S. salar* (Fausch, 1998; Hesthagen et al., 2017). Studies on other salmonid populations have indicated that they are size-selective opportunistic predators feeding on either large individuals with high mass or smaller individuals that are easier to catch (Andreassen et al., 2001; Syrjänen et al., 2011). A study in Iceland indicated that *S. alpinus* was the top predator in an *S. alpinus*-dominated system and selected the most abundant prey irrelevant to size, which was the Chironomidae (Diptera) (Kreiling et al., 2021). Juvenile salmonids in rivers may also rely mainly on terrestrial prey as a supplement, particularly if the river is situated in riparian habitats (Grunblatt et al., 2019). It is crucial to understand resource partitioning between species and its impacts on the ecosystem, as resource depletion in a low-productivity environment could increase inter-specific competition and put those species further at risk of population decline.

[Figure 1 here]

Therefore, the aim of this study was to investigate the invertebrate composition in nutrient-poor streams and prey choice of juvenile *S. salar*; to increase our knowledge of food availability in the species' most northerly distributed rivers. To this end, we sampled the stomach contents of juvenile *S. salar* and invertebrates from four rivers in NE Iceland to measure the prey availability (Figure 1). This study also provides a highly detailed analysis of food availability and prey choice of juvenile *S. salar* in a low-productivity freshwater ecosystem, in comparison to previous studies of more productive salmonid rivers (Marsh et al., 2022; Mookerji et al., 2004; Riley et al., 2009). Our hypotheses were: 1) the abundance and biomass of prey available for *S.*

salar differ between and within rivers, but will have similar invertebrate assemblages (Gisli M. Gíslason et al., 1999; Gísli Már Gíslason et al., 1998; Ólafsson et al., 2002; Petersen et al., 1995); 2) prey items consumed by juvenile *S. salar* differ in body size; 3) juvenile *S. salar* in these systems show non-selectivity for the most abundant prey items, but high selectivity for large-bodied prey items; and 4) the most abundant prey item consumed is Chironomidae, which represents the main choice of prey item for juvenile *S. salar* in NE Iceland.

Materials and Methods:

Ethical Statement:

The research was carried out under consent of research licence (2018-12-12-2777) and (2022-11-17-2389/2.3.2) to the Marine and Freshwater Research Institute, given by the Directorate of Fisheries according to the Icelandic law No 61/2008 article 26.

Study area:

The study was conducted in four direct runoff rivers located in NE Iceland (Antonsson et al., 2005; Rist, 1990) (Figure 1). These rivers are River Vesturdalsá, Hofsá, Midfjardará, and Selá. The prey composition in the drift in Vesturdalsá and Hofsá is influenced by lakes located 11 and 57 km from the closest sampling site, respectively. Five sites were sampled in Vesturdalsá, four in Midfjardará, and three in Selá and Hofsá in August 2020. Sites were chosen based on previously established *S. salar* populations at each site and are long-term population monitoring sites. The descriptions of each site are presented in Table S1. Vesturdalsá is also an ICES index river for marine-return rates *S. salar* (ICES, 2023). The juvenile *S. salar* density indices across each age group are similar across rivers, whereas the biomass of juvenile *S. salar* differs across rivers, with Hofsá having a higher individual body mass than the other rivers

(Bárðarson et al., 2018). *S. salar* was found to be the most abundant salmonid species in the studied rivers. *S. alpinus* is also found in all four rivers, but only brown trout is found in Hofsá. These rivers were chosen as they represent one of the northerly distributed populations *S. salar* worldwide.

Field sampling:

In August 2020, we collected invertebrate samples and surveyed fish density, size, and food consumption. Sampling was conducted at similar time periods during the day at each sampling site. Invertebrate samples were collected using both a surber sampler and drift net at each site. The Surber sampler (25 × 25 cm with 250 µm mesh size) provides a density of macroinvertebrates living at the bottom of these rivers. At each sampling site a total of ten surber replicate samples were collected, and each sample was from randomized coordinates along a 15 m transect within the sampling site. Drift nets were chosen because studies have shown that salmonids are predominantly drift-feeders (Akbaripasand et al., 2014; Rader, 1997; Reiriz et al., 1998). Samples were collected using drift nets (48 × 33 cm with 363 µm mesh size) at two locations at each sampling site, one in the middle of the river and the other next to the riverbank. The drift nets were positioned with the top of the frame slightly above the water surface to collect organisms drifting on the surface of the river. The nets were placed for five minutes, and velocity (m/s) was measured using a Sontek Flowtracker Handheld Acoustic Doppler Velocimeter (YSI©, Ohio, USA) where the net was placed. The water depth (m) at each drift net sampling location was measured. The samples were preserved in 70% ethanol until further processing.

Electrofishing (Arnason et al., 2005; Bohlin et al., 1989) was conducted at all sampling sites. Stomach samples from at least 25 fish across different weight groups and salmonid species

were collected from each site. The fish were anesthetized with 2-phenoxyethanol (300ppm). The fork length and wet weight of each fish were measured, and each fish was speciated. Fish fork lengths above 5.0 cm were stomach-pumped, whereas fish that were below 5.0 cm (usually 0+ parr) were dissected, and all stomach samples were collected, which could provide more detailed diet information (Traugott et al., 2020). The stomach contents of the fish were collected by inserting a plastic pipette tip attached to a pump into the mouth of the fish as close to the stomach as possible and flushing the stomach contents with water until the stomach was empty. Scale and otolith samples were taken from a maximum of eight fish from each site to determine length-age relationships, and all other fish were able to recover after being processed and was released back into the river where they were originally caught.

Sample processing and data analysis:

The invertebrate samples were counted, sorted, and identified closest to family or order levels using identification keys (Bouchard, 2004; Kriska, 2013; Macan, 1960). All terrestrial invertebrates were grouped into a separate category. Drift samples collected from Hofsá were excluded from analysis because of sample degradation. The Chironomidae (Diptera) larvae within samples were identified to the lowest possible taxonomic level using identification keys (Eggermont, 2008; Green & Cranston, 1983; Heiri, 2013; Oliver & Roussel, 1983; Schmid, 1993) to provide a more detailed description of the food web, as they represented the majority of the species composition. The invertebrates body length, width, height, and head width (mm) were measured using an eyepiece graticule. The densities of invertebrates (D; abundance/m^3) sampled using drift nets were calculated according to the following formula: $D = \frac{N}{t \times w \times h \times v}$, where N is the abundance of each invertebrate group, t is sampling time (s), w and h are the frame width (m) and height (m) of the drift net situated underwater respectively, and v is the

velocity of the water (Baxter et al., 2017). Invertebrate density (*D*; abundance/m^2) of surber samples was calculated using: $D = N/A$, where *N* is the abundance of invertebrates and *A* is the area of the surber frame (Merritt et al., 2017). The invertebrate biomass was estimated using length-mass regression relationships from the literature (Baumgärtner & Rothhaupt, 2003; Benke et al., 1999; Burgherr & Meyer, 1997; Kang & Kang, 1997; O'Gorman & Emmerson, 2010). Additionally, the population biomass (*B*; mg/m^2) of species was calculated using: $B = M \times D$, where *M* is the mean body mass. Copepoda, *Daphnia*, Ostracoda, and Acarina individuals were excluded from the analysis because their true abundances were likely underestimated because of the chosen mesh size of our sampling gear. The exclusion of these species could underestimate the true amount of prey available and consumed by salmonids, as previous studies have found that these species were found in <10% of the stomach samples of *S. alpinus* and contributed to ~21% of the benthic macroinvertebrate population in Icelandic rivers (Kreiling et al., 2021, 2022).

Prey selectivity (α) was calculated for all prey items using the Manly-Chesson Index (Chesson, 1983): $\alpha = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j}$; where r_i and n_i are proportions of food item *i* in stomach content and the environment, and *m* is the number of prey categories. Prey selectivity of juvenile *S. salar* was calculated using both benthic and drift samples. Values of α can range from 0 to 1, from never eating the prey item to complete preference. If α=1/m, then it indicates no preference and *S. salar* is feeding on what is available, α>1/m indicates selection, and α<1/m indicates avoidance of the prey item (Minder & Pyron, 2018; Syrjänen et al., 2011). Dietary niche overlap was calculated both between *S. salar* and *S. trutta* and *S. salar* and *S. alpinus* using the Freeman-Tukey (FT) index: $FT = \sum \sqrt{p_{1j} \times p_{2j}}$; where the p_{1j} and p_{2j} are the mean proportion of prey resource (*j*) found in stomachs of species 1 and 2 respectively. The FT values range from 0 (no

overlap) to 1 (complete overlap) (Marsh et al., 2022; Smith & Zaret, 1982). Because of the low number of stomach content samples of *S. trutta* in Hofsá, an additional 348 stomach content samples from both juvenile *S. salar* and *S. trutta* that were sampled during previous annual surveys taken in the same sampling month from 2000 to 2014 conducted by the Marine and Freshwater Research Institute were used to compare differences in dietary niche overlap (Antonsson, 2015). The samples were extracted from juvenile salmonids of the same age classes as in our study. However, the prey items from stomach contents taken from previous years were only identified to the genus or family level. The gut content was also estimated as a percentage of total gut content.

The population density and biomass of invertebrates found in the river and in the stomachs of fish were compared between rivers. The abundance and biomass of invertebrates found in the bottom substrate and stomach samples were also compared between sites in each river to assess spatial variation within rivers. In addition, analysis of stomach contents included variations in abundance and biomass of stomach items of different weight ranges of *S. salar* representing age classes. Prey selectivity indices were also compared between taxonomic groups for the benthic and drift samples. The normality of the data was checked using the Shapiro-Wilk´s method, to see if it met assumptions for the parametric tests used. Since all data did not meet the normality assumption, analyses were made using non-parametric Kruskal-Wallis tests, when comparing invertebrate densities and population biomasses across different rivers, taxonomic groups, and sites (only for benthic invertebrate and stomach contents data). A post-hoc analysis with non-parametric Dunn test was used to test hypothesis and make comparisons between rivers and sites. All p-values from post-hoc analyses were adjusted with Bonferroni corrections. Linear regressions were used for analysing stomach content abundance and biomass data across weights

of juvenile *S. salar*. The distribution of residuals was analysed to check assumptions. An unpaired Wilcoxon signed-rank test was used to compare environmental invertebrate data to stomach content abundance and biomass data to evaluate prey choice for juvenile *S. salar*. An unpaired Wilcoxon signed-rank test was also used to compare dietary niche overlap (FT) index between *S. salar* and *S. trutta* and between *S. salar* and *S. alpinus*. Statistical analysis was conducted using various packages within R (R Core Team, 2023).

Results:

Prey availability: Invertebrate composition

We assessed the prey availability in all rivers using surber (Vesturdalsá: n=25; Midfjardará: n=20; Selá: n=16; Hofsá: n=16) and drift (Vesturdalsá: n=10; Midfjardará: n=8; Selá: n=6; Hofsá: n=6) sampling where possible. We found that the most abundant and highest population biomass prey in the four rivers was Chironomidae (Diptera; Figure 2 and 3). Oligochaeta, Gastropoda, terrestrial subsidies, and large Dipterans made up most of the rest of the macroinvertebrate community. The abundance of prey items was found to differ significantly between rivers, both for the drift column (Kruskal-Wallis test, $\chi^2=6.63$, df=2, $p<0.05$) and the bottom substrate ($\chi^2=25.4$, df=3, $p<0.001$) (Figure 2). Post-hoc tests showed significantly lower benthic invertebrate abundances in Midfjardará than other rivers (Dunn test, $p_{adj}<0.05$). Furthermore, Midfjardará had the lowest abundance of drifting invertebrates but only differed significantly from Selá (Dunn test, $p_{adj}<0.05$). However, the population biomass of invertebrates in the drift did not vary between rivers (Kruskal-Wallis test, $\chi^2=4.25$, df=2, $p=0.119$), but varied in the benthos ($\chi^2=32.1$, df=3, $p<0.001$). Post-hoc tests showed similar results as above, where Midfjardará had a significantly lower population biomass of benthic invertebrates (Dunn test, $p_{adj}<0.05$). Within river variation was also tested and we found that the abundances of benthic

invertebrates did not vary between sites for all rivers (Figure S1). Conversely, the population biomasses of benthic invertebrate in Midfjardará (Kruskal-Wallis test, χ^2=15.0, df=3, p<0.01) and Selá (χ^2=6.15, df=2, p<0.05) were found to differ significantly between sites (Figure S2). Further post-hoc testing showed that the population biomass of benthic macroinvertebrates was lower in site B than site A (Dunn test, p_{adj}<0.05) and C (p_{adj}<0.01) in Midfjardará. The population biomass of benthic invertebrates in site A of Selá was significantly higher than site C (Dunn test, p_{adj}<0.05), which is situated further upstream.

[Figure 2 here]

[Figure 3 here]

P*rey availability: Chironomidae larvae composition*

When looking at the Chironomidae larvae, their population abundance (Kruskal-Wallis test, χ^2=4.8, df=2, p=0.091) and biomass (χ^2=0.442, df=2, p=0.802) in the drift column did not differ between rivers (Figure S3 and S4). The individual abundance (Kruskal-Wallis test; Drift: χ^2=48.881, df=16, p<0.001; Benthic: χ^2=125, df=21, p<0.001) and biomass (Drift: χ^2=32.5, df=16, p<0.01; Benthic: χ^2=120, df=21, p<0.001) of drifting and benthic chironomid larvae differed between taxonomic groups. Chironomidae Tanypodinae and of the genus *Diamesa* had the highest population biomass, whereas the chironomid species *Eukiefferiella minor* and of the genus *Orthocladius* were the highest in abundance. Additionally, the abundance (Kruskal-Wallis test, χ^2=11.7, df=3, p<0.001) and population biomass (χ^2=17.8, df=3, p<0.001) of Chironomidae larvae in the bottom substrate was significantly different between rivers, with abundances in Midfjardará being significantly lower than other rivers (Dunn post-hoc test, p_{adj}<0.05). Additionally, there were no significant differences in abundance of benthic

Chironomidae larvae between sites within rivers (Table S11). Only the population biomass of chironomids in Midfjardará was significantly different between sites (Kruskal-Wallis test, χ^2=11.4, df=3, p<0.01; Figure S5).

In summary, the most abundant benthic and drifting macroinvertebrate were the chironomids. They also make up most of the biomass that are found in these rivers. *Eukiefferiella minor* and *Orthocladius spp.* make up most of the chironomid community in these rivers. The abundance of macroinvertebrate was found to differ little spatially, but the overall macroinvertebrate community was similar. Furthermore, the abundance and biomass of Chironomidae larvae found in the bottom substrate was also different between rivers.

Stomach content of juvenile S. salar:

The second main objective was to analyse the prey consumed by juvenile *S. salar*. Juvenile salmon in these rivers were significantly different in size (Kruskal-Wallis test, χ^2=228, df=3, p<0.001), with the salmon in Hofsá and Midfjardará being (on average) largest and smallest respectively. Juvenile sizes also differed between sites for all rivers (Kruskal-Wallis test; Vesturdalsá: χ^2=27.7, df=4, p<0.001; Selá: χ^2=13.9, df=2, p<0.001; Midfjardará: χ^2=24.7, df=3, p<0.001; Hofsá: χ^2=20.1, df=2, p<0.001). Analyses of gut content collected from stomach pumps and dissections of 328 (Vesturdalsá: n=124; Midfjardará: n=87; Selá: n=60; Hofsá: n=57) juvenile salmon showed Chironomidae larvae were the main prey in all four rivers (Figure 4). Additionally, *S. salar* in Hofsá consumed a higher proportion of large-bodied macroinvertebrates such as Trichoptera and Simuliidae. Abundance of prey items consumed varied by rivers (Kruskal-Wallis test, χ^2=90.3, df=3, p<0.001). There were fewer prey items in stomachs of juveniles in Vesturdalsá and more in Selá, whereas the number of prey items consumed in Hofsá and Miðfjarðará were similar (Figure 4). Also, the total biomass of prey items in each stomach

varied by rivers (Kruskal-Wallis test, χ^2=80.1, df=3, p<0.001; Figure 5) and post-hoc tests showed that *S. salar* in Hofsá and Vesturdalsá consumed similar biomass of prey and salmon in Selá consumed the highest biomass of prey. To test for variation within river, we took stomach samples from *S. salar* at all sampling sites in the four study rivers. We found that there were significant differences in both abundance (Kruskal-Wallis test, χ^2=37.1, df=4, p<0.001) and biomass (χ^2=15.3, df=4, p<0.01) in stomach contents between sites in Vesturdalsá, with higher abundance in sites upstream of the river but very similar in biomass between sites (Figure S6 and S7). Additionally, juvenile salmon in Miðfjarðará consumed a higher total biomass of stomach contents in upstream than downstream sites (Kruskal-Wallis test, χ^2=33.4, df=3, p<0.001; Figure S7). The prey type with the highest biomass was salmonid fry, followed by chironomids and terrestrial subsidies. A linear regression revealed a weak positive relationship between abundance of prey items and $\log_{10}$(weight) of juveniles, (Adjusted r^2=0.016, p<0.05), but biomass did not associate with weight (Adjusted r^2=0.00146, p=0.232). Smaller-sized *S. salar* consumed a higher variety of prey items than larger fish.

[Figure 4 here]

[Figure 5 here]

The abundance (Kruskal-Wallis test, χ^2=133, df=3, p<0.001) and total biomass (χ^2=120, df=3, p<0.001) of Chironomidae larvae, consumed by juvenile *S. salar*, differed significantly between rivers (Figure S8). The abundance (Kruskal-Wallis test, χ^2=1.29, df=2, p=0.525) and biomass (χ^2=4.45, df=2, p=0.108) differed between sites within rivers, but not for Selá (Table S27 and S29). There were no significant differences in the abundance (Adjusted r^2=0.004, p=0.158) and mass (Adjusted r^2=-0.002, p=0.447) of larvae consumed across the weight groups of *S. salar* for all rivers.

Prey preference:

Using the Manly-Chesson prey selectivity index, we found that the prey selectivity was significantly different between rivers for benthos (Kruskal-Wallis test, χ^2=13.9, df=5, p<0.05), but not for drifts (χ^2=8.01, df=5, p=0.156) (Figure 6). There was no preference of Chironomidae for juveniles overall, although with varying results across rivers as *S. salar* in Selá and Midfjardará showed some preference for the prey item. We also found that there was no preference for Oligochaeta and even showing slight prey avoidance. There was also evidence of prey avoidance for terrestrial subsidy prey items for juvenile salmon. Additionally, juvenile *S. salar* had a high preference for the larger *Diptera spp.*, Trichoptera, and Gastropoda. In Hofsá, the *S. salar* avoided Chironomidae and favoured Simuliidae and Trichoptera.

[Figure 6 here]

Dietary Niche Overlap:

To study the overlap in prey items between salmonid species, we calculated the dietary niche overlap (FT) index of each sampling site for each river. Gut content taken from 20 *S. alpinus* and 17 *S. trutta* in all four study rivers in addition to the 348 stomach samples from Hofsá taken from previous years were used in this analysis. The mean dietary niche overlap across rivers between *S. salar* and *S. trutta* was 0.908 (SE=0.022), and the niche overlap between *S. salar* and *S. alpinus* was 0.864 (SE=0.036). The mean dietary niche overlap between *S. salar* and *S. trutta* in Hofsá calculated using data from previous surveys was 0.628 (SE=0.114), which did not differ significantly from the FT index of our study samples (unpaired Wilcoxon signed-rank test, W=14, p=0.071). There were no significant differences in the FT index of *S. salar* and *S. alpinus* and *S. salar* and *S. trutta* (unpaired Wilcoxon signed-rank test, W=9, p=0.786). There were also no significant differences in FT index between *S. salar* and *S. alpinus* by rivers

(Kruskal-Wallis test, χ^2=5.597, df=3, p=0.133). Juvenile trout was also significantly larger than other salmonid species (Kruskal-Wallis test, χ^2=24.611, df=2, p<0.001). The data suggests that in these rivers, the *S. salar* chooses the same food items as *S. alpinus* and *S. trutta*, which also rely highly on the consumption of Chironomidae.

Discussion:

Temperature, habitat use, river discharge, and food availability are the main limiting factors of population dynamics for juvenile *S. salar* (Amundsen & Gabler, 2008; Dunham & Vinyard, 1997; Egglishaw & Shackley, 1985; Grant et al., 1998; Johansen et al., 2005; Kocik & Ferreri, 1998; Mann, 1989). We studied the food availability of four rivers in NE Iceland, Hofsá, Vesturdalsá, Selá, and Midfjardará using extensive sampling and methodologies. The data indicates very similar food availability for juvenile salmon in the rivers. Even though abundances of prey types varied by rivers, the total available biomass was similar across rivers. Chironomidae having the highest density overall is consistent with earlier findings from studies on freshwater invertebrates in rivers and springs across Iceland (Gísli Már Gíslason et al., 1998; Gísli Már Gíslason & Gardarsson, 2010; Kreiling et al., 2022). The chironomid species *E. minor* and *E. claripennis* are the most abundant in run-off and spring-fed streams in Iceland (Hannesdóttir et al., 2010), as was found in the present study. The invertebrate community and the riverine food webs in Iceland differ vastly from communities in its southern counterparts due to a lower diversity of invertebrate fauna (Brown et al., 2018; Ministry for the Environment & The Icelandic Institute of Natural History, 2001), and the data showed that chironomids in low-productivity rivers play a major role in the ecosystem. Macroinvertebrates in Iceland mainly consume algae, detritus and other invertebrates, therefore productivity of primary producers

could be a main determinant in the production of the main prey item of juvenile *S. salar* (Bouchard, 2004; Hannesdóttir et al., 2010).

Although the prey consumed by *S. salar* varied between and within rivers, our study does not suggest food is limiting, but further research on food limitations on population density in species poor rivers is encouraged. Juvenile population density and growth in the study rivers have shown responses linked to fluctuation in temperature based on results of annual surveys (Bárðarson et al., 2023). The temperature fluctuations and its interaction with food availability and the effect that it has on salmonid juvenile populations need to be incorporated into annual surveys of salmon populations. Consistent with food availability, the juvenile *S. salar* in these rivers mainly consumed chironomids. Similarly, salmonids in a stream in the south of Iceland were also highly dependent on the most abundant prey (Chironomidae) during the summer. Specifically, Chironomidae Orthocladiinae were found most abundantly and had highest biomass in the stomachs of juvenile salmon, again matching the high abundancy in the environment (Kreiling et al., 2021). Decreases in chironomid production may have consequences for the production of *S. salar* within Icelandic rivers and other similarly low-productivity rivers. The amount and type of prey consumed varies spatially, between rivers and within Vesturdalsá and Midfjardará. Choice of prey also varies across weight groups, as larger salmon mainly consumed chironomids, whereas smaller fish had a higher variety of food items in their stomachs. A study on *S. trutta* in Iceland showed a tendency for a shift towards consuming larger prey items as they grew larger (Steingrímsson & Gíslason, 2002), which was contrary to our findings as larger juvenile *S. salar* in NE Iceland consumed the most abundant prey item (Chironomidae) while smaller salmon had variously sized prey in their stomach. Further work is needed to test whether there are seasonal changes in prey choice and food availability in these rivers and if that affects

the survival and population dynamics of juvenile salmon, as our study focuses only on one sampling period.

Juvenile *S. salar* in highly diverse riverine environments have access to many different types of prey items such as those in the River Frome in Dorset, United Kingdom, which is a chalk stream that is highly productive and has a high diversity in invertebrates (Table S2; (Armitage et al., 2017; Bowes et al., 2005; Woodward et al., 2010)). The Frome has a high productivity of algae, macrophytes, and aquatic invertebrates, thus, food availability is not considered a strong limiting factor, which translates into higher growth rates of juvenile *S. salar* (Mann, 1989). This was different from the juvenile salmon populations in our study rivers as they were comparatively lower in productivity and food diversity. Additionally, juvenile salmonids in in high productivity streams in Alaska and Ireland depend more highly on terrestrial prey rather than larval aquatic prey, due to the high amount of riparian vegetation surrounding the streams (Dineen et al., 2007; Grunblatt et al., 2019). Salmonids in sub-Arctic streams can use terrestrial prey as a substitute food source during the summer to compensate for the low nutrient levels and colder climates, whereas in the winter, salmonids would have to rely more on aquatic insects (Amundsen & Gabler, 2008; Johnson et al., 2017; Johnson & Ringler, 2016).

However, riparian vegetation around Icelandic rivers, especially in the NE, are sparse in comparison and terrestrial prey items are rare, therefore, salmonids will have to rely on aquatic insects throughout the year. There was a low availability of terrestrial subsidies in these low-productivity rivers, making it more difficult for *S. salar* to have access to those resources, even though they are high in biomass. Additionally, the species diversity of endemic fauna and flora in Iceland is low owing to its island biogeography, high latitude, and low species diversity of invertebrates (Lento et al., 2022; Ministry for the Environment & The Icelandic Institute of

Natural History, 2001). As shown here, the most abundant invertebrate, Chironomidae larvae, was the main prey item for juveniles. Whereas larger prey items such as the Oligochaeta was shown to be less often consumed and may even be avoided to some degree, which may reflect them often being buried within sediments (Bouchard, 2004). Note, smaller-sized juvenile salmon may avoid consuming large Oligochaeta due to their inability to swallow them (Wańkowski, 1979; Wańkowski & Thorpe, 1979).

Prey selectivity for juveniles showed no preference for chironomids, indicating that they consumed the most abundant prey within the rivers rather than targeting larger-sized prey items. Studies on salmonids in Finland indicated that they were opportunistic foragers where their diet reflects the prey composition of benthic and drift samples (Syrjänen et al., 2011). Diet specialization of juvenile fish can be due to experience and learning, whereas diet generalisation may be caused by hunger (Andreassen et al., 2001). Therefore, the juvenile *S. salar* in Vesturdalsá, Selá, Hofsá, and Midfjardará in NE Iceland seem to be diet generalists, consuming what is readily available, as they have few prey choices. Even though the juveniles in the NE Iceland rivers showed a high preference for consuming large Diptera macroinvertebrates, which were low in abundance in the river systems, their diet mainly consisted of chironomids. In concordance with our results, *S. trutta*, in another NE Iceland river (Laxá) with similar productivity levels, was found to mostly eat benthic invertebrates, which included mainly blackfly larvae, chironomids, and freshwater snails (Gísli Már Gíslason & Steingrímsson, 2004). River management focusing on river primary productivity, such as those increasing algal production, altering habitat to promote the growth of algae, and using large woody debris, are possible options in creating a sustainable food source for the main macroinvertebrate prey items of juvenile *S. salar* (Thompson et al., 2018; Wootton, 2012). Thereby, the conservation and

production of large-bodied benthic macroinvertebrates could promote the growth of *S. salar* populations.

We observed a high dietary niche overlap between juvenile *S. salar* and other salmonids, which all mainly consumed Chironomidae and are proportioning the consumption of this main prey item. Our results further emphasize the importance of chironomids to the growth of juvenile salmon in these nutrient-poor systems. Although, the degree and nature of competition for food and habitat between the salmonid species found within these rivers is poorly understood, and further research will be needed to describe and quantify competition for resources between the salmonids, the high number of shared resources between salmonid species in NE Iceland shows how limited prey choices are. Therefore, it may be more likely that the production of one prey item can largely influence the population of juvenile salmon in this type of environment, in which the low-productivity environment becomes a barrier to *S. salar* population recovery. For example, changes in temperature could affect the production and development of chironomids (Hannesdóttir et al., 2010), and therefore the main food supply for juvenile salmon in Iceland may be vulnerable to the impacts of climate change. Interspecific competition for resources was shown to affect growth and survival of juvenile *S. salar* due to changes in diet (Fausch, 1998; Johnson & Ringler, 2016). The FT index of *S. salar* with *S. trutta* in the Frome (Marsh et al., 2022) is comparatively lower than that was found in rivers in NE Iceland, as resources are more shared in the latter, which is due to the difference in productivity and prey diversity between these rivers. Competition for food could also lead to competition for space and shelter as habitat can affect foraging and sharing resources with other salmonid species (Marsh et al., 2022).

Conclusion

Through exploring the food availability and prey choice of juvenile *S. salar* populations in a nutrient-poor ecosystem and one of the species' northern distributional ranges using detailed analysis of invertebrate population and salmonid gut content sampling, we found that food availability was similar between and within rivers and the main food item for juvenile *S. salar* was the Chironomidae. The type of food items consumed also varied between weight groups. Juvenile salmon did not select for chironomids, and their high consumption most likely owing to the high chironomid abundance in the environment. Our results could provide important knowledge to the conservation of sub-Arctic *S. salar* populations especially in low-productivity rivers such as those in Iceland. Currently, terrestrial inputs have less of a role as a food supply to juvenile salmon in Icelandic rivers in comparison to others especially as there are low number of invertebrate species that can process leaf litter (Ministry for the Environment & The Icelandic Institute of Natural History, 2001). The production of chironomids is of high importance to the growth and production of *S. salar* in their most northerly distributed rivers. Salmonids in nutrient-poor ecosystems in a low species diversity and biogeographically isolated environment may have no choice but to rely on their one main food source, which may alter the growth and development during their juvenile phase and might make them highly vulnerable and difficult to adapt to other emerging threats (Bednar-Friedl et al., 2022; Lento et al., 2022; Parmesan et al., 2023).

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Supporting Information:

Additional supporting information can be found in the online version of this article.

Figure S26: Log_{10} abundances of benthic invertebrates (number of individuals/m^2) did not significantly differ between sites at each study river (Hofsá: p=0.352; Midfjardará: p=0.051; Selá: p=0.075; Vesturdalsá: p=0.238).

Figure S2: Log_{10} population biomass (mg/m^2) of benthic invertebrates at different sites at each river in NE Iceland. There were no significant differences between sites for Hofsá (p=0.650) and Vesturdalsá (p=0.105). On the other hand, there were significant differences between sites for Midfjardará (p<0.01) and Selá (p<0.05). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

Figure S27: Variations in abundance of drifts (number of individuals/m^3) and benthic (number of individuals/m^2) Chironomidae larvae, by taxonomic groups (left) and rivers (right). Log_{10} abundances of drift (top panels) and benthic chironomids (bottom panels). Log_{10} abundances of different taxons of chironomids differed significantly a) in the drifting column (p<0.001) and c) in the bottom substrate for all rivers (p<0.001). Log_{10} abundances found b) in the drift did not

differ between rivers (p=0.091), but d) abundance in the bottom substrate differed (p<0.001). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

Figure S28: Variations in population biomass of drifts (mg/m^3) and benthic (mg/m^2) Chironomidae larvae, by taxonomic groups and rivers. Log_{10} biomass of drift (top panels) and benthic invertebrates (bottom panels). Log_{10} biomass of different taxons of chironomids differed significantly a) in the drifting column (p<0.01) and c) in the bottom substrate (p<0.001). Log_{10} biomass found b) in the drift were not significantly different between rivers (p=0.802) but was different d) in the bottom substrate (p<0.001). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

Figure S29: Log_{10} population biomass (mg/m^2) of benthic Chironomidae larvae at different sites at each study river. There were no significant differences between sites for Hofsá (p=0.599), Selá (p=0.204), and Vesturdalsá (p=0.491), but there were significant differences for Midfjardará (p<0.01). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

Figure S30: Log_{10} number of prey items consumed by juvenile salmon at different sites at each study river. There were no significant differences between sites for Hofsá (p=0.088), Selá (p=0.729), and Midfjardará (p=0.066), but there were significant differences for Vesturdalsá (p<0.001). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are

significantly different.

Figure S31: Log_{10} biomass (mg) of prey items consumed by juvenile salmon at different sites at each study river. There were no significant differences between sites for Hofsá ($p=0.0838$) and Selá ($p=0.283$). In contrast, there were significant differences between sites for Midfjardará ($p<0.001$) and Vesturdalsá ($p<0.01$). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

Figure S32: a) Log_{10} average number ($p<0.001$) and b) biomass (mg; $p<0.001$) of Chironomidae larvae consumed per juvenile salmon (Salmo salar) was significantly different across rivers. Abundances also differed between sites ($p<0.05$) for all rivers except for Selá ($p=0.368$). There was no difference in abundance ($p=0.158$) and biomass ($p=0.447$) of larvae consumed across different weight groups of juvenile fish.

Table S1: Descriptions of sites at each study river. Substrate classification broken down into: gravel (2-16 mm), pebble (17-64 mm), cobble (65-256 mm), and boulder (>256 mm) (Bain et al., 1985).

Table S2: Invertebrate family groups found in Vesturdalsá and Frome.

Table S3: Kruskal-Wallis of invertebrate taxonomic groups between rivers and taxonomic groups.

Table S14: Kruskal-Wallis of benthic invertebrate taxonomic groups between sites within study rivers.

Table S5: Bottom substrate: pairwise comparison of log_{10} (abundance) between rivers.

Table S6: Bottom substrate: pairwise comparison of $\log_{10}$ (population biomass) between rivers.

Table S15: Bottom substrate: pairwise comparison of $\log_{10}$ (population biomass) between sites in Midfjardará.

Table S16: Bottom substrate: pairwise comparison of $\log_{10}$ (population biomass) between sites in Selá.

Table S17: Drift: pairwise comparison of $\log_{10}$ (abundance) between rivers.

Table S10: Kruskal-Wallis of Chironomidae larvae between rivers and taxonomic groups.

Table S18: Kruskal-Wallis of benthic taxonomic groups of Chironomidae larvae between sites within study rivers.

Table S19: Bottom substrate: pairwise comparison of $\log_{10}$ (population biomass) of Chironomidae larvae between sites in Midfjardará.

Table S13: Bottom Substrate: pairwise comparison of $\log_{10}$ (abundance) of Chironomidae larvae between rivers.

Table S14: Bottom Substrate: pairwise comparison of $\log_{10}$ (biomass) of Chironomidae larvae between rivers.

Table S20: Comparison of weight (g) of juvenile salmon sampled across rivers (Kruskal-Wallis test and Dunn test).

Table S21: Comparison of weight (g) of juvenile salmon sampled across sites in Vesturdalsá (Kruskal-Wallis test and Dunn test).

Table S22: Comparison of weight (g) of juvenile salmon sampled across sites in Selá (Kruskal-Wallis test and Dunn test).

Table S23: Comparison of weight (g) of juvenile salmon sampled across sites in Midfjardará (Kruskal-Wallis test and Dunn test).

Table S19: Comparison of weight (g) of juvenile salmon sampled across sites in Hofsá (Kruskal-Wallis test and Dunn test).

Table S24: Log_{10} number and biomass of prey items found in stomachs of juveniles across rivers (Kruskal-Wallis test and Dunn test).

Table S25: Number of prey items in stomachs of juveniles across sites in different rivers (Kruskal-Wallis test and Dunn test).

Table S26: Log_{10} number of prey items in stomachs of juveniles across taxonomic groups across rivers (Kruskal-Wallis test).

Table S27: Log_{10} biomass of prey items in stomachs of juveniles across sites in different rivers (Kruskal-Wallis test and Dunn test).

Table S28: Log_{10} biomass of prey items in stomachs of juveniles across taxonomic groups in River Vesturdalsá (Kruskal-Wallis test).

Table S29: Linear model of prey items found stomachs of juveniles ~ log_{10}(weight of fish).

Table S26: Number and biomass of Chironomidae larvae found in stomachs of juveniles across rivers (Kruskal-Wallis test and Dunn test).

Table S30: Number of Chironomidae larvae in stomachs of juveniles across sites in different rivers (Kruskal-Wallis test and Dunn test).

Table S31: Number of Chironomidae larvae in stomachs of juveniles across taxonomic groups across different rivers (Kruskal-Wallis test).

Table S32: Biomass of Chironomidae larvae in stomachs of juveniles across sites in different rivers (Kruskal-Wallis test and Dunn test).

Table S33: Biomass of Chironomidae larvae in stomachs of juveniles across taxonomic groups across different rivers (Kruskal-Wallis test).

Table S34: Linear model of Chironomidae larvae found stomachs of juveniles ~ $\log_{10}$ (weight of fish).

Table S35: Chesson α compared across different taxonomic groups for benthic and drift samples (Kruskal-Wallis test).

Table S36: Comparison of weight (g) of different species of juvenile salmonids (Kruskal-Wallis test and Dunn test).

Table S37: Comparison of FT indices using unpaired Wilcoxon signed-rank test.

Table S38: Comparison of FT indices across rivers (Kruskal-Wallis test).

Author Contribution Statement:

Conceptualisation & Developing methods: SYL, AP, GG, IRJ, JSO, HB. Conducting the research: SYL, JSO, HB. Data analysis: SYL, HB. Data interpretation: SYL, AP, IRJ, JSO, HB. Preparation figures & tables & Writing: SYL. All authors reviewed, edited, and approved the manuscript.

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References:

Akbaripasand, A., Ramezani, J., Lokman, P. M., & Closs, G. P. (2014). Can drifting invertebrates meet the energy requirements of drift-feeding fish? A Case Study on Galaxias fasciatus. *Freshwater Science*, *33*(3), 904–914. https://doi.org/10.1086/676957

Amundsen, P. A., & Gabler, H. M. (2008). Food consumption and growth of Atlantic salmon *Salmo salar* parr in sub-Arctic rivers: Empirical support for food limitation and competition. *Journal of Fish Biology*, *73*(1), 250–261. https://doi.org/10.1111/j.1095-8649.2008.01932.x

Andreassen, P. M. R., Martinussen, M. B., Hvidsten, N. A., & Stefansson, S. O. (2001). Feeding and prey-selection of wild Atlantic salmon post-smolts. *Journal of Fish Biology*, *58*(6), 1667–1679. https://doi.org/10.1006/jfbi.2001.1576

Antonsson, T. (2015). Fæða laxa- urriða- og bleikjuseiða: Gögn úr Vesturdalsá, Hofsá og Selá í Vopnafirði og úr Elliðaám og Leirvogsá við Faxaflóa. In *Veiðimálastofnun*. https://www.hafogvatn.is/static/research/files/faeda_laxa.pdf

Antonsson, T., Arnason, F., & Einarsson, S. M. (2005). Comparison of density, mean length, biomass and mortality of Atlantic salmon (*Salmo salar L.*) juveniles between regions in Iceland. *Icelandic Agricultural Sciences*, *18*, 59–66.

Antonsson, T., Heidarsson, T., & Snorrason, S. S. (2010). Smolt Emigration and Survival to Adulthood in Two Icelandic Stocks of Atlantic Salmon. *Transactions of the American Fisheries Society*, *139*(6), 1688–1698. https://doi.org/10.1577/t08-200.1

Armitage, P. D., Bass, J. A. B., Coleman, J. W., Jones, John, I., & Kaplan, T. L. (2017). Faunal

and floral response to the dredging of a River Frome floodplain ditch (Dorset, UK). *Proceedings of the Dorset Natural History & Archaeological Society*, *138*(October), 67–76.

Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M., & Milner, N. J. (2003). Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research*, *62*(2), 143–170. https://doi.org/10.1016/S0165-7836(02)00160-1

Arnason, F., Antonsson, T., & Einarsson, S. M. (2005). Evaluation of single-pass electric fishing to detect changes in population size of Atlantic salmon (Salmo salar L.) juveniles. *Icelandic Agricultural Sciences*, *18*, 67–73.

Arnekleiv, J. V., Finstad, A. G., & Rønning, L. (2006). Temporal and spatial variation in growth of juvenile Atlantic salmon. *Journal of Fish Biology*, *68*, 1062–1076. https://doi.org/10.1111/j.0022-1112.2006.00986.x

Bacon, P. J., Gurney, W. S. C., Jones, W., Mclaren, I. S., & Youngson, A. F. (2005). Seasonal growth patterns of wild juvenile fish: Partitioning variation among explanatory variables, based on individual growth trajectories of Atlantic salmon (Salmo salar) parr. *Journal of Animal Ecology*, *74*(1), 1–11. https://doi.org/10.1111/j.1365-2656.2004.00875.x

Bain, M. B., Finn, J. T., & Booke, H. E. (1985). Quantifying Stream Substrate for Habitat Analysis Studies. *North American Journal of Fisheries Management*, *5*(3B), 499–500. https://doi.org/10.1577/1548-8659(1985)5<499:qssfha>2.0.co;2

Bárðarson, H., Helgason, S. Ó., & Njarðardóttir, E. (2023). *Research on fish stocks in several rivers at North-East Iceland 2022*.

Bárðarson, H., Helgason, S. Ó., Njarðardóttir, E., & Jónsson, I. R. (2018). *Research on fish*

stocks in several rivers at North-East Iceland 2017.

Baum, D., Laughton, R., Armstrong, J. D., & Metcalfe, N. B. (2005). The effect of temperature on growth and early maturation in a wild population of Atlantic salmon parr. *Journal of Fish Biology*, *67*(5), 1370–1380. https://doi.org/10.1111/j.0022-1112.2005.00832.x

Baumgärtner, D., & Rothhaupt, K. O. (2003). Predictive Length-Dry Mass Regressions for Freshwater Invertebrates in a Pre-Alpine Lake Littoral. *International Review of Hydrobiology*, *88*(5), 453–463. https://doi.org/10.1002/iroh.200310632

Baxter, C. V., Kennedy, T. A., Miller, S. W., Muehlbauer, J. D., & Smock, L. A. (2017). Macroinvertebrate Drift, Adult Insect Emergence and Oviposition. In F. R. Hauer & G. A. Lamberti (Eds.), *Methods in Stream Ecology: Third Edition* (3rd ed., Vol. 1, pp. 435–456). Elsevier. https://doi.org/10.1016/B978-0-12-416558-8.00021-4

Bednar-Friedl, B., Biesbroek, R., Schmidt, D. N., Alexander, P., Børsheim, K. Y., Carnicer, J., Georgopoulou, E., Haasnoot, M., Cozannet, G. Le, Lionello, P., Lipka, O., Möllmann, C., Muccione, V., Mustonen, T., Piepenburg, D., & Whitmarsh, L. (2022). Europe. In: Climate Change 2022: Impacts, Adaptation and Vulnerability. In *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. https://doi.org/10.1017/9781009325844.015

Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, *18*(3), 308–343. https://doi.org/10.2307/1468447

Birnie-Gauvin, K., Thorstad, E. B., & Aarestrup, K. (2019). Overlooked aspects of the Salmo salar and Salmo trutta lifecycles. *Reviews in Fish Biology and Fisheries*, *29*(4), 749–766. https://doi.org/10.1007/s11160-019-09575-x

Bohlin, T., Hamrin, S., Heggberget, T. G., Rasmussen, G., & Saltveit, S. J. (1989). Electrofishing - Theory and practice with special emphasis on salmonids. *Hydrobiologia*, *173*(1), 9–43. https://doi.org/10.1007/BF00008596

Bouchard, R. W. (2004). *Guide to Aquatic Invertebrate Families of Mongolia. Identification Manual for Students, Citizen Monitors, and Aquatic Resource Professionals*.

Bowes, M. J., Leach, D. V., & House, W. A. (2005). Seasonal nutrient dynamics in a chalk stream: The River Frome, Dorset, UK. *Science of the Total Environment*, *336*(1–3), 225–241. https://doi.org/10.1016/j.scitotenv.2004.05.026

Brown, L. E., Khamis, K., Wilkes, M., Blaen, P., Brittain, J. E., Carrivick, J. L., Fell, S., Friberg, N., Füreder, L., Gislason, G. M., Hainie, S., Hannah, D. M., James, W. H. M., Lencioni, V., Olafsson, J. S., Robinson, C. T., Saltveit, S. J., Thompson, C., & Milner, A. M. (2018). Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover. *Nature Ecology and Evolution*, *2*(2), 325–333. https://doi.org/10.1038/s41559-017-0426-x

Burgherr, P., & Meyer, E. I. (1997). Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Archiv Fur Hydrobiologie*, *139*(1), 101–112. https://doi.org/10.1127/archiv-hydrobiol/139/1997/101

Chesson, J. (1983). The estimation and analysis of preference and its relationship to foraging models. *Ecology*, *64*(5), 1297–1304. https://doi.org/10.2307/1937838

Dadswell, M., Spares, A., Reader, J., McLean, M., McDermott, T., Samways, K., & Lilly, J. (2022). The Decline and Impending Collapse of the Atlantic Salmon (Salmo salar) Population in the North Atlantic Ocean: A Review of Possible Causes. *Reviews in Fisheries Science and Aquaculture*, *30*(2), 215–258. https://doi.org/10.1080/23308249.2021.1937044

Dineen, G., Harrison, S. S. C., & Giller, P. S. (2007). Diet partitioning in sympatric Atlantic salmon and brown trout in streams with contrasting riparian vegetation. *Journal of Fish Biology*, *71*, 17–38. https://doi.org/10.1111/j.1095-8649.2007.01441.x

Dolinsek, I. J., Grant, J. W. A., & Biron, P. M. (2007). The effect of habitat heterogeneity on the population density of juvenile Atlantic salmon *Salmo salar L. Journal of Fish Biology*, *70*(1), 206–214. https://doi.org/10.1111/j.1095-8649.2006.01296.x

Dunham, J. B., & Vinyard, G. L. (1997). Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(5), 1025–1030. https://doi.org/10.1139/cjfas-54-5-1025

Eggermont, H. (2008). The Identification and Use of Palaearctic Chironomidae Larvae in Palaeoecology. In *Freshwater Biology* (Vol. 53, Issue 10). Quaternary Research Association. https://doi.org/10.1111/j.1365-2427.2007.01926.x

Egglishaw, H. J., & Shackley, P. E. (1985). Factors governing the production of juvenile Atlantic salmon in Scottish streams. *Journal of Fish Biology*, *27*(sA), 27–33. https://doi.org/10.1111/j.1095-8649.1985.tb03229.x

Elliott, J. M., & Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: Predicting the effects of climate change. *Journal of Fish Biology*, *77*(8), 1793–1817. https://doi.org/10.1111/j.1095-

8649.2010.02762.x

Fausch, K. D. (1998). Interspecific competition and juvenile Atlantic salmon (Salmo salar): On testing effects and evaluating the evidence across scales. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(SUPPL.1), 218–231. https://doi.org/10.1139/d98-006

Gíslason, Gisli M., Olafsson, J. S., & Hokon, A. (1999). Macroinvertebrate communities in Rivers in Iceland in Biodiversity in Benthic Ecology. *Proceedings from Nordic Benthological Meeting in Silkeborg, Denmark, 13-14 November 1997. NERI Technical Report No. 266, November*, 53–61.

Gíslason, Gísli Már, & Gardarsson, A. (2010). The production of chironomids and blackflies in a subarctic river. *Proc 15th International Symposium on Chironomidae*, 45–54. http://www.hi.is/~gmg/Serprent/Gislason-Gardarsson_2010_Produ_Chir_Blackflies_Proceedings_Chir.pdf

Gíslason, Gísli Már, Ólafsson, J. S., & Adalsteinsson, H. (1998). Animal communities in Icelandic rivers in relation to catchment characteristics and water chemistry: preliminary results. *Nordic Hydrology*, *29*(2), 129–148. https://doi.org/10.2166/nh.1998.0008

Gíslason, Gísli Már, & Steingrímsson, S. Ó. (2004). Seasonal and spatial variation in the diet of brown trout (*Salmo trutta L.*) in the subarctic River Laxá, north-east Iceland. *Aquatic Ecology*, *38*(2), 263–270. https://doi.org/10.1023/B:AECO.0000032052.04874.fb

Grant, J. W. A., Steingrímsson, S. Ó., Keeley, E. R., & Cunjak, R. A. (1998). Implications of territory size for the measurement and prediction of salmonid abundance in streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(SUPPL.1), 181–190. https://doi.org/10.1139/cjfas-55-s1-181

Green, J., & Cranston, P. S. (1983). A Key to the Larvae of the British Orthocladiinae (Chironomidae). In *The Journal of Applied Ecology* (Vol. 20, Issue 2). Freshwater Biological Association. https://doi.org/10.2307/2403541

Gregory, S. D., Ibbotson, A. T., Riley, W. D., Nevoux, M., Lauridsen, R. B., Russell, I. C., Britton, J. R., Gillingham, P. K., Simmons, O. M., Rivot, E., & Durif, C. (2019). Atlantic salmon return rate increases with smolt length. *ICES Journal of Marine Science*, *76*(6), 1702–1712. https://doi.org/10.1093/icesjms/fsz066

Grunblatt, J., Meyer, B. E., & Wipfli, M. S. (2019). Invertebrate prey contributions to juvenile Coho Salmon diet from riparian habitats along three Alaska streams: Implications for environmental change. *Journal of Freshwater Ecology*, *34*(1), 617–631. https://doi.org/10.1080/02705060.2019.1642243

Hannesdóttir, E. R., Gíslason, G. M., & Ólafsson, J. S. (2010). Life cycles of Eukiefferiella claripennis (Lundbeck 1898) and Eukiefferiella minor (Edwards 1929) (Diptera: Chironomidae) in spring-fed streams of different temperatures with reference to climate change. *Fauna Norvegica*, *31*, 35–46. https://doi.org/10.5324/fn.v31i0.1367

Heiri, O. (2013). The Larvae of Chironomidae of the Holarctic Region – Keys and diagnoses. In T. Wiederholm (Ed.), *CHIRONOMUS Journal of Chironomidae Research* (Issue 26). Publishing House of the Swedish Research Councils. https://doi.org/10.5324/cjcr.v0i26.1656

Hesthagen, T., Larsen, B. M., Bolstad, G., Fiske, P., & Jonsson, B. (2017). Mitigation of acidified salmon rivers – effects of liming on young brown trout *Salmo trutta*. *Journal of Fish Biology*, *91*(5), 1350–1364. https://doi.org/10.1111/jfb.13454

ICES. (2022). Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*, *4*(39), 39. https://doi.org/http://doi.org/10.17895/ices.pub.19697368

ICES. (2023). Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*, *5*(41), 477. https://doi.org/https://doi.org/10.17895/ices.pub.22743713

Johansen, M., Elliott, J. M., & Klemetsen, A. (2005). Relationships between juvenile salmon, Salmo solar L., and invertebrate densities in the River Tana, Norway. *Ecology of Freshwater Fish*, *14*(4), 331–343. https://doi.org/10.1111/j.1600-0633.2005.00107.x

Johnson, J. H., DiRado, J. A., Mackey, G., & Abbett, R. (2017). Comparative diets and foraging strategies of subyearling Atlantic salmon, brown trout, and rainbow trout during winter. *Journal of Applied Ichthyology*, *33*(6), 1158–1165. https://doi.org/10.1111/jai.13488

Johnson, J. H., & Ringler, N. H. (2016). Comparative diets of subyearling Atlantic salmon and subyearling coho salmon in Lake Ontario tributaries. *Journal of Great Lakes Research*, *42*(4), 854–860. https://doi.org/10.1016/j.jglr.2016.05.007

Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. *Journal of Fish Biology*, *75*(10), 2381–2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x

Kang, H.-K., & Kang, Y. J. (1997). Length and Weight Relationship of Acartia steueri(Copepoda: Calanoida) in ilkwang Bay, Korea. *Korean Journal of Fisheries and Aquatic Sciences*, *30*(5), 30(5), 906–908. https://www.koreascience.or.kr/article/JAKO199723607645201.page

Kocik, J. F., & Ferreri, C. P. (1998). Juvenile production variation in salmonids: Population dynamics, habitat, and the role of spatial relationships. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(SUPPL.1), 191–200. https://doi.org/10.1139/cjfas-55-s1-191

Kreiling, A. K., Govoni, D. P., Pálsson, S., Ólafsson, J. S., & Kristjánsson, B. K. (2022). Invertebrate communities in springs across a gradient in thermal regimes. *PLoS ONE*, *17*(5 May), 1–20. https://doi.org/10.1371/journal.pone.0264501

Kreiling, A. K., O'Gorman, E. J., Pálsson, S., Benhaïm, D., Leblanc, C. A., Ólafsson, J. S., & Kristjánsson, B. K. (2021). Seasonal variation in the invertebrate community and diet of a top fish predator in a thermally stable spring. *Hydrobiologia*, *848*(3), 531–545. https://doi.org/10.1007/s10750-020-04409-5

Kriska, G. (2013). Freshwater Invertebrates in Central Europe. In *Freshwater Invertebrates in Central Europe*. https://doi.org/10.1007/978-3-7091-1547-3

Lento, J., Culp, J. M., Levenstein, B., Aroviita, J., Baturina, M. A., Bogan, D., Brittain, J. E., Chin, K., Christoffersen, K. S., Docherty, C., Friberg, N., Ingimarsson, F., Jacobsen, D., Lau, D. C. P., Loskutova, O. A., Milner, A., Mykrä, H., Novichkova, A. A., Ólafsson, J. S., … Goedkoop, W. (2022). Temperature and spatial connectivity drive patterns in freshwater macroinvertebrate diversity across the Arctic. *Freshwater Biology*, *67*(1), 159–175. https://doi.org/10.1111/fwb.13805

Macan, T. T. (1960). *A Guide to Freshwater Invertebrate Animals*. Longmans.

Mann, R. H. K. (1989). Mann 1989 Fish population dynamics in the river Frome. *Regulated Rivers: Research and Management*, *4*, 165–177.

Marsh, J. E., Lauridsen, R. B., Gregory, S. D., Kratina, P., Scott, L. J., Cooling, D., & Jones, J. I. (2022). High summer macrophyte cover increases abundance, growth, and feeding of juvenile Atlantic salmon. *Ecological Applications*, *32*(2). https://doi.org/10.1002/eap.2492

Merritt, R. W., Cummins, K. W., & Berg, M. B. (2017). Trophic Relationships of Macroinvertebrates. In F. R. Hauer & G. A. Lamberti (Eds.), *Methods in Stream Ecology: Third Edition* (3rd ed., Vol. 1, pp. 413–433). Elsevier. https://doi.org/10.1016/B978-0-12-416558-8.00020-2

Minder, M., & Pyron, M. (2018). Dietary overlap and selectivity among silver carp and two native filter feeders in the Wabash River. *Ecology of Freshwater Fish*, *27*(1), 506–512. https://doi.org/10.1111/eff.12365

Ministry for the Environment, & The Icelandic Institute of Natural History. (2001). Biological diversity in Iceland - National Report to the Convention on Biological Diversity. In *Natural History*. https://www.cbd.int/doc/world/is/is-nr-01-en.pdf

Mookerji, N., Weng, Z., & Mazumder, A. (2004). Food partitioning between coexisting Atlantic salmon and brook trout in the Sainte-Marguerite River ecosystem, Quebec. *Journal of Fish Biology*, *64*(3), 680–694. https://doi.org/10.1111/j.1095-8649.2004.00333.x

O'Gorman, E. J., & Emmerson, M. C. (2010). Manipulating Interaction Strengths and the Consequences for Trivariate Patterns in a Marine Food Web. *Advances in Ecological Research*, *42*(C), 301–419. https://doi.org/10.1016/B978-0-12-381363-3.00006-X

Ólafsson, J. S., Adalsteinsson, H., Gíslason, G. M., Hansen, I., & Hrafnsdóttir, T. (2002). Spatial heterogeneity in lotic chironomids and simuliids in relation to catchment characteristics in Iceland. *SIL Proceedings, 1922-2010*, *28*(1), 157–163.

https://doi.org/10.1080/03680770.2001.11902566

Olafsson, K., Einarsson, S. M., Gilbey, J., Pampoulie, C., Hreggvidsson, G. O., Hjorleifsdottir, S., & Gudjonsson, S. (2016). Origin of Atlantic salmon (Salmo salar) at sea in Icelandic waters. *ICES Journal of Marine Science*, *73*(6), 1525–1532.

Oliver, D. R., & Roussel, M. E. (1983). *THE INSECTS AND ARACHNIDS OF CANADA The Genera of Larval Midqes*. Agriculture Canada.

Parmesan, C., Morecroft, M. D., Trisurat, Y., Adrian, R., Anshari, G. Z., Arneth, A., Gao, Q., Gonzalez, P., Harris, R., Price, J., Stevens, N., & Talukdar, G. H. (2023). Terrestrial and Freshwater Ecosystems and Their Services. In H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama (Eds.), *Climate Change 2022 – Impacts, Adaptation and Vulnerability* (pp. 197–378). Cambridge University Press. https://doi.org/10.1017/9781009325844.004

Petersen, R. C., Gíslason, G. M., & Vought, L. B. M. (1995). River and Stream Ecosystems. In C. E. Cushing, K. W. Cummins, & G. W. Minshall (Eds.), *Ecosystems of the World* (pp. 295–341). Elsevier.

R Core Team. (2023). R: A Language and Environment for Statistical Computing. In *R Foundation for Statistical Computing* (p. https://www.R-project.org). R Foundation for Statistical Computing,Vienna, Austria. http://www.r-project.org

Rader, R. B. (1997). A functional classification of the drift: Traits that influence invertebrate availability to salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(6), 1211–1234. https://doi.org/10.1139/f97-025

Reiriz, L., Nicieza, A. G., & Braña, F. (1998). Prey selection by experienced and naive juvenile Atlantic salmon. *Journal of Fish Biology*, *53*(1), 100–114. https://doi.org/10.1006/jfbi.1998.0688

Riley, W. D., Pawson, M. G., Quayle, V., & Ives, M. J. (2009). The effects of stream canopy management on macroinvertebrate communities and juvenile salmonid production in a chalk stream. *Fisheries Management and Ecology*, *16*(2), 100–111. https://doi.org/10.1111/j.1365-2400.2008.00649.x

Rist, S. (1990). Viðauki I. Vatnasvið Íslands. In *Vatns er pörf* (pp. 203–234). Bókaútgáfa Menningarsjóðs.

Schmid, P. E. (1993). *A Key to the Larval Chironomidae and Their Instars from Austrian Danube Region Streams and Rivers: Part 1, Diamesinae, Prodiamesinae and Orthocladiinae* (K. Werner (ed.); Wasser und). Federal Institute of Water Quality.

Smith, E. P., & Zaret, T. M. (1982). Bias in Estimating Niche Overlap. *Ecology*, *63*(5), 1248–1253. https://doi.org/10.2307/1938851

Steingrímsson, S. Ã., & Gíslason, G. M. (2002). Body size, diet and growth of landlocked brown trout, Salmo trutta, in the subarctic River Laxá, North-East Iceland. *Environmental Biology of Fishes*, *63*(4), 417–426. https://doi.org/10.1023/A:1014976612970

Stich, D. S., Kinnison, M. T., Kocik, J. F., & Zydlewski, J. D. (2015). Initiation of migration and movement rates of Atlantic salmon smolts in fresh water. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(9). https://doi.org/10.1139/cjfas-2014-0570

Suttle, K. B., Power, M. E., Levine, J. M., & McNeely, C. (2004). How fine sediment in

riverbeds impairs growth and survival of juvenile salmonids. *Ecological Applications*, *14*(4), 969–974. https://doi.org/10.1890/03-5190

Syrjänen, J., Korsu, K., Louhi, P., Paavola, R., & Muotka, T. (2011). Stream salmonids as opportunistic foragers: The importance of terrestrial invertebrates along a stream-size gradient. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*(12), 2146–2156. https://doi.org/10.1139/F2011-118

Thompson, M. S. A., Brooks, S. J., Sayer, C. D., Woodward, G., Axmacher, J. C., Perkins, D. M., & Gray, C. (2018). Large woody debris "rewilding" rapidly restores biodiversity in riverine food webs. *Journal of Applied Ecology*, *55*(2), 895–904. https://doi.org/10.1111/1365-2664.13013

Traugott, M., Thalinger, B., Wallinger, C., & Sint, D. (2020). Fish as predators and prey: DNA-based assessment of their role in food webs. *Journal of Fish Biology*, *43*(0), 1–43. https://doi.org/10.1111/jfb.14400

Vollset, K. W., Urdal, K., Utne, K., Thorstad, E. B., Sægrov, H., Raunsgard, A., Skagseth, Ø., Lennox, R. J., Østborg, G. M., Ugedal, O., Jensen, A. J., Bolstad, G. H., & Fiske, P. (2022). Ecological regime shift in the Northeast Atlantic Ocean revealed from the unprecedented reduction in marine growth of Atlantic salmon. *Science Advances*, *8*(9), 1–10. https://doi.org/10.1126/sciadv.abk2542

Wańkowski, J. W. J. (1979). Morphological limitations, prey size selectivity, and growth response of juvenile atlantic salmon, Salmo salar. *Journal of Fish Biology*, *14*(1), 89–100. https://doi.org/10.1111/j.1095-8649.1979.tb03498.x

Wańkowski, J. W. J., & Thorpe, J. E. (1979). The role of food particle size in the growth of

juvenile Atlantic salmon (*Salmo salar L.*). *Journal of Fish Biology*, *14*(4), 351–370. https://doi.org/10.1111/j.1095-8649.1979.tb03530.x

Woodward, G., Blanchard, J., Lauridsen, R. B., Edwards, F. K., Jones, J. I., Figueroa, D., Warren, P. H., & Petchey, O. L. (2010). Individual-based food webs. Species identity, body size and sampling effects. In *Advances in Ecological Research* (Vol. 43, Issue C). Elsevier Ltd. https://doi.org/10.1016/B978-0-12-385005-8.00006-X

Wootton, J. T. (2012). River Food Web Response to Large-Scale Riparian Zone Manipulations. *PLoS ONE*, *7*(12). https://doi.org/10.1371/journal.pone.0051839

Figures:

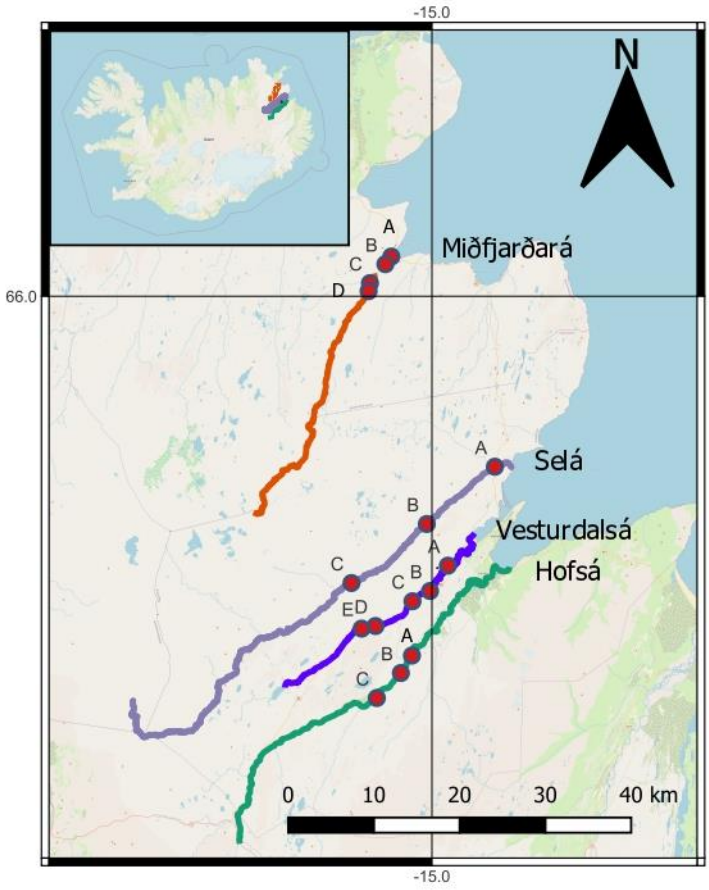

Figure 1: Map of the four study rivers in NE Iceland. Each point is labelled and represents a sampling site.

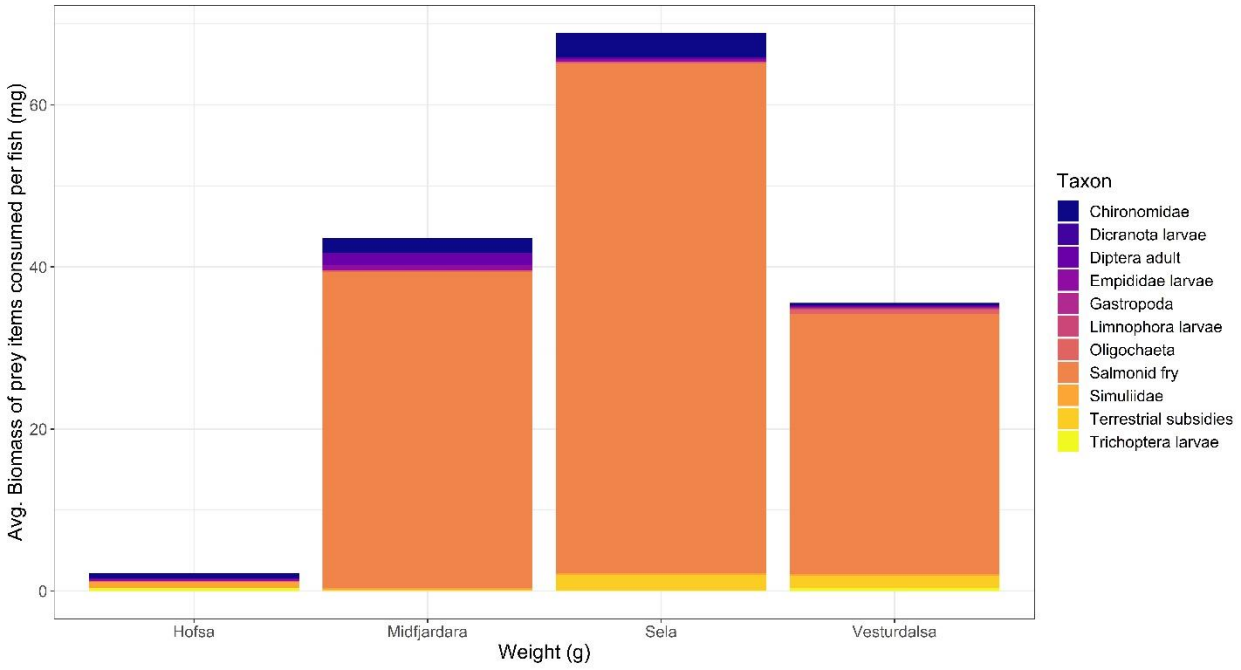

Figure 2: Variations in abundance of invertebrates caught in the drift (top; log_{10} of number of individuals/m^3) and benthic (bottom; log_{10} of number of individuals/m^2), by taxonomic groups (left) and rivers (right). Log_{10} abundances of different taxonomic groups of invertebrates differed significantly a) in the drifting column (n=30; $p<0.001$) and c) in the bottom substrate (n=77; $p<0.001$). Log_{10} abundances found b) in the drift and d) in the bottom substrate were also significantly different between rivers ($p<0.05$ and $p<0.001$ respectively). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

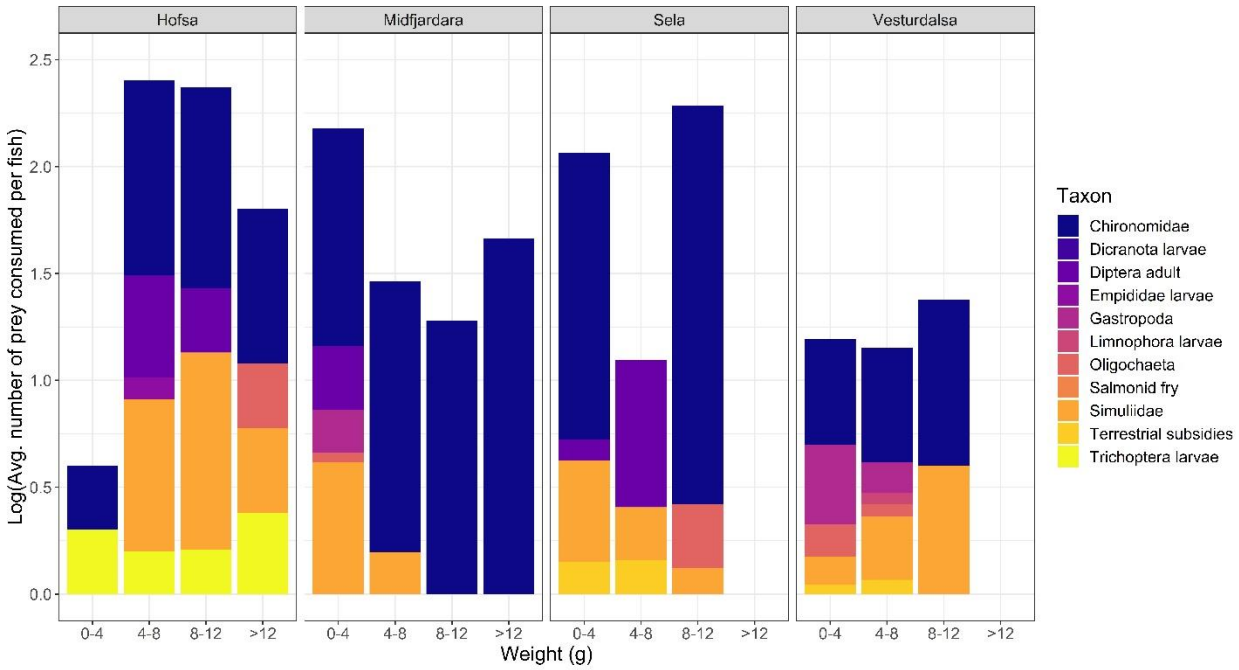

Figure 3: Variations in population biomass of invertebrates caught with drift (top; $log_{10}(mg/m^3)$) and benthic (bottom; $log_{10}(mg/m^2)$) sampling, by taxonomic groups (left) and rivers (right). Log_{10} biomass of different taxonomic groups of invertebrates differed significantly a) in the drifting column (n=30; $p<0.001$) and c) in the bottom substrate (n=77; $p<0.001$). Log_{10} biomass found b) in the drift was not significantly different between rivers ($p=0.119$) but was significantly different d) in the bottom substrate ($p<0.001$). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

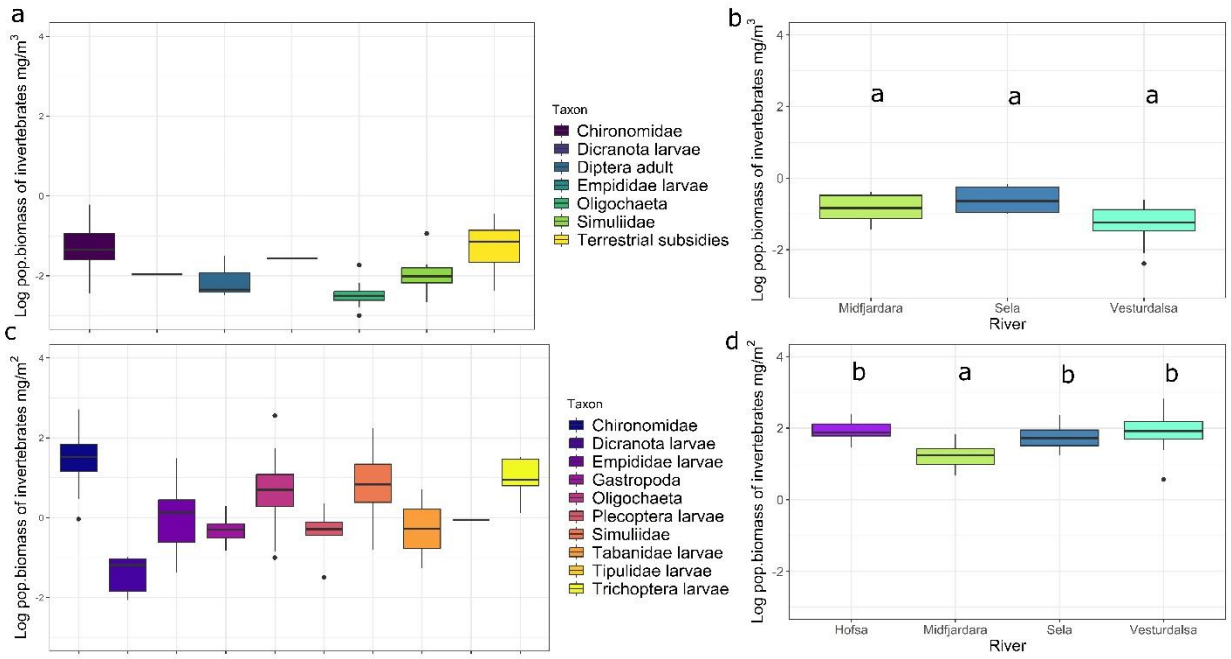

Figure 4: Log_{10} average number of prey items found in stomachs of juvenile Atlantic salmon (*Salmo salar*) was differed significantly across rivers (n=328, $p<0.001$) and by weight ranges ($p<0.001$). The number of prey items consumed increased with weight ($p<0.05$). Log_{10} abundance also varied between taxonomic groups for all rivers ($p<0.001$) with abundances of Chironomidae higher in comparison.

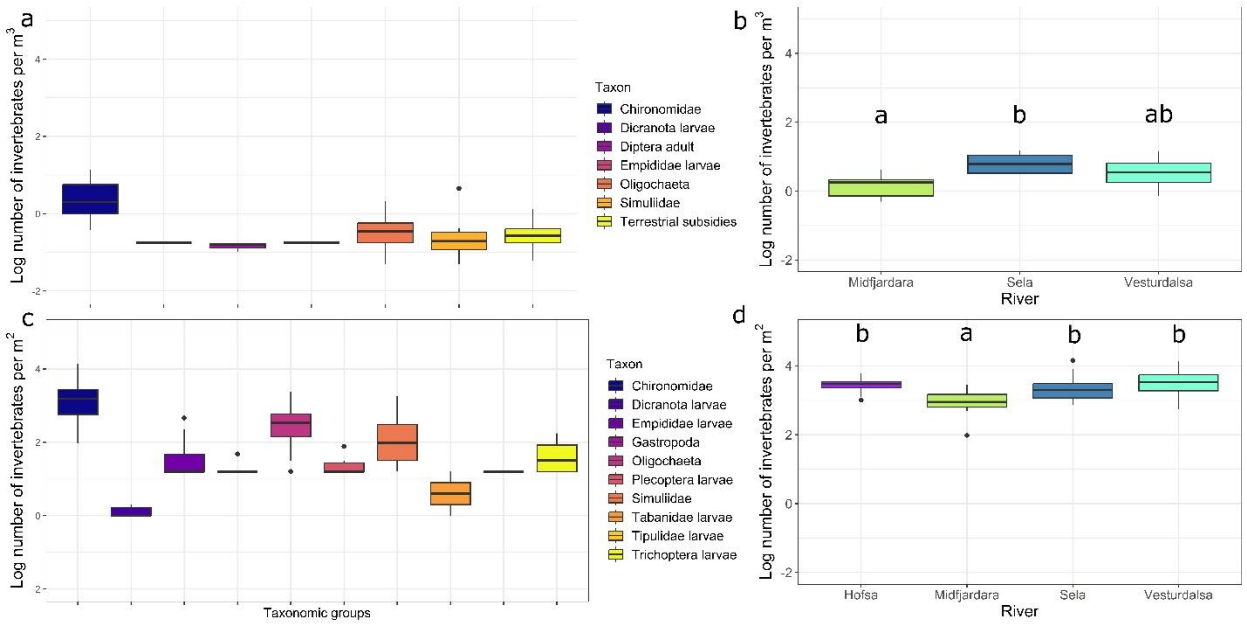

Figure 5: The average biomass of prey consumed per juvenile Atlantic salmon *(Salmo* salar) was significantly different between rivers (n=328; p<0.001). Biomass did not vary between different weight groups of juvenile fish (p=0.232).

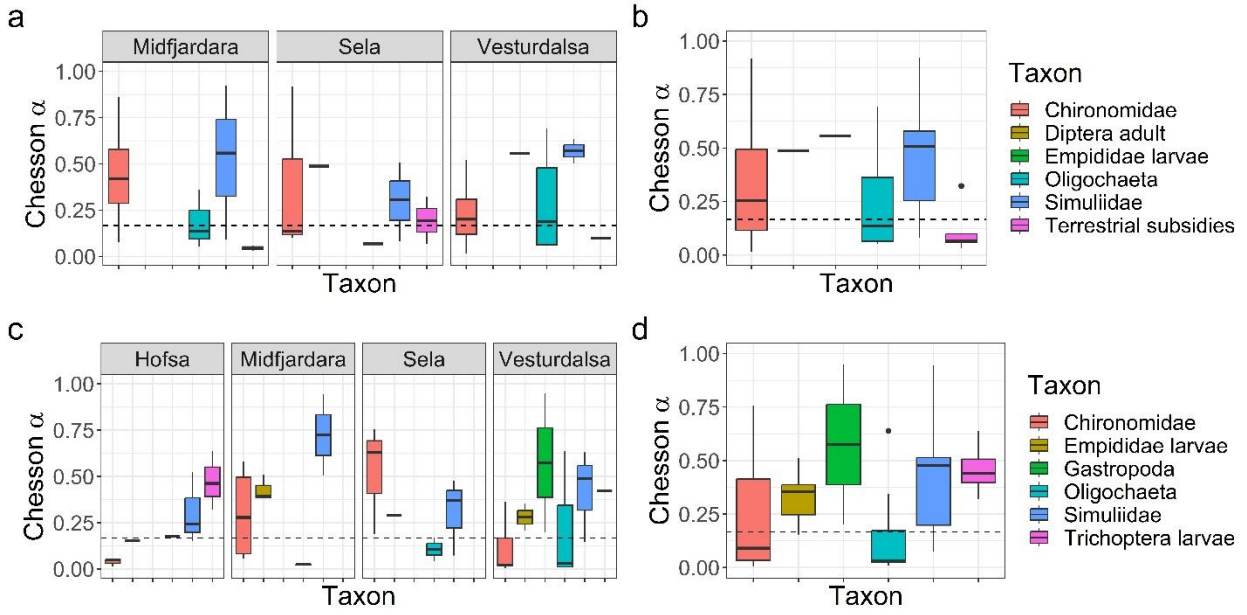

Figure 6: Variation in prey selectivity (Manly-Chesson α) of juvenile Atlantic salmon (*Salmo*

salar) estimated for drift samples a) across rivers and b) combined between rivers, and benthic samples c) across rivers and d) combined between rivers. Values $\alpha=0.167$ show no selectivity, $\alpha>0.167$ shows prey preference, and $\alpha<0.167$ indicates prey avoidance. Kruskal-Wallis test showed that the selectivity for different taxonomic groups differed significantly for benthic samples ($p<0.05$), but not drift.

Supporting Information:

Supporting Figures:

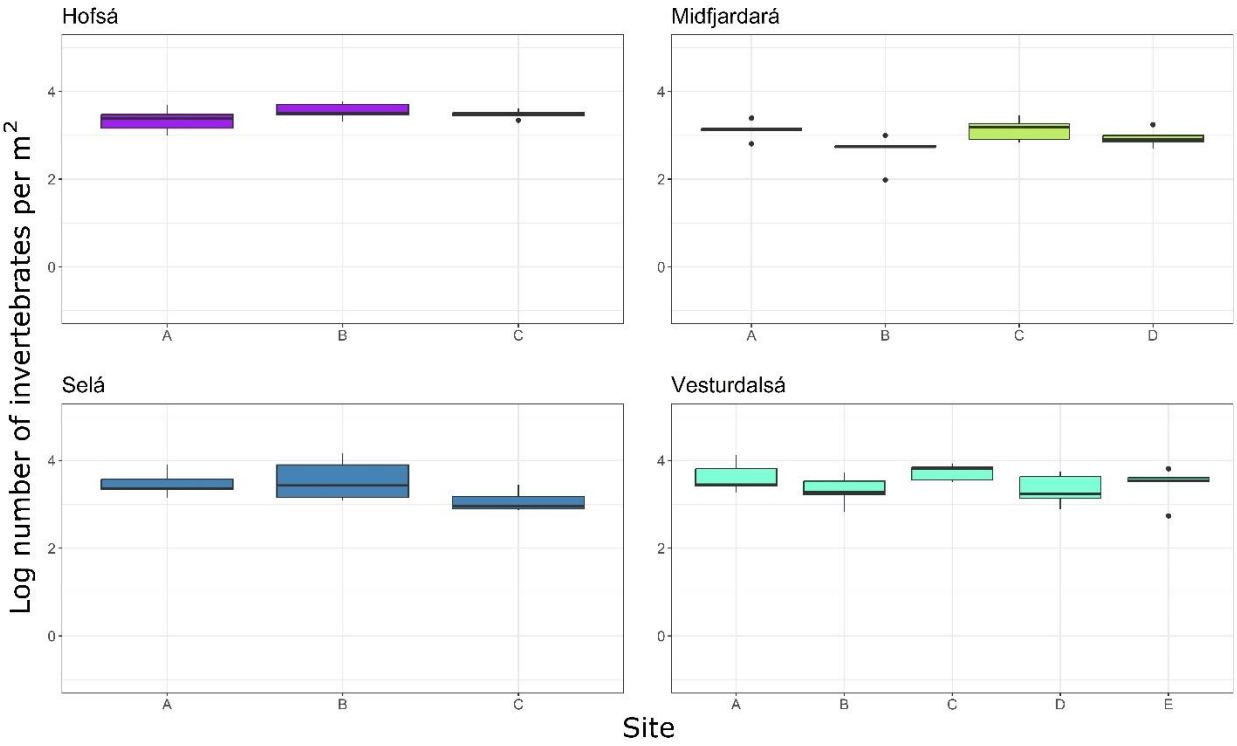

Figure S1: Log_{10} abundances of benthic invertebrates (number of individuals/m^2) did not significantly differ between sites at each study river (Hofsá: p=0.352; Midfjardará: p=0.051; Selá: p=0.075; Vesturdalsá: p=0.238).

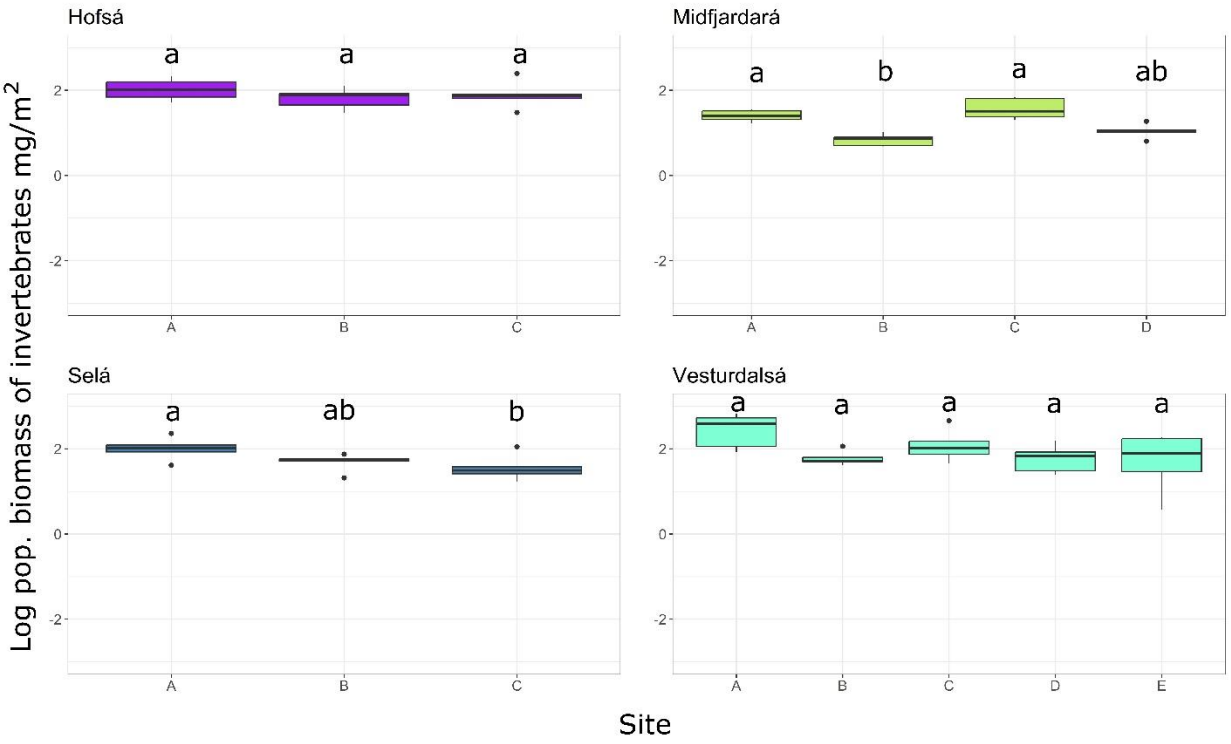

Figure S2: Log_{10} population biomass (mg/m^2) of benthic invertebrates at different sites at each river in NE Iceland. There were no significant differences between sites for Hofsá ($p=0.650$) and Vesturdalsá ($p=0.105$). On the other hand, there were significant differences between sites for Midfjardará ($p<0.01$) and Selá ($p<0.05$). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

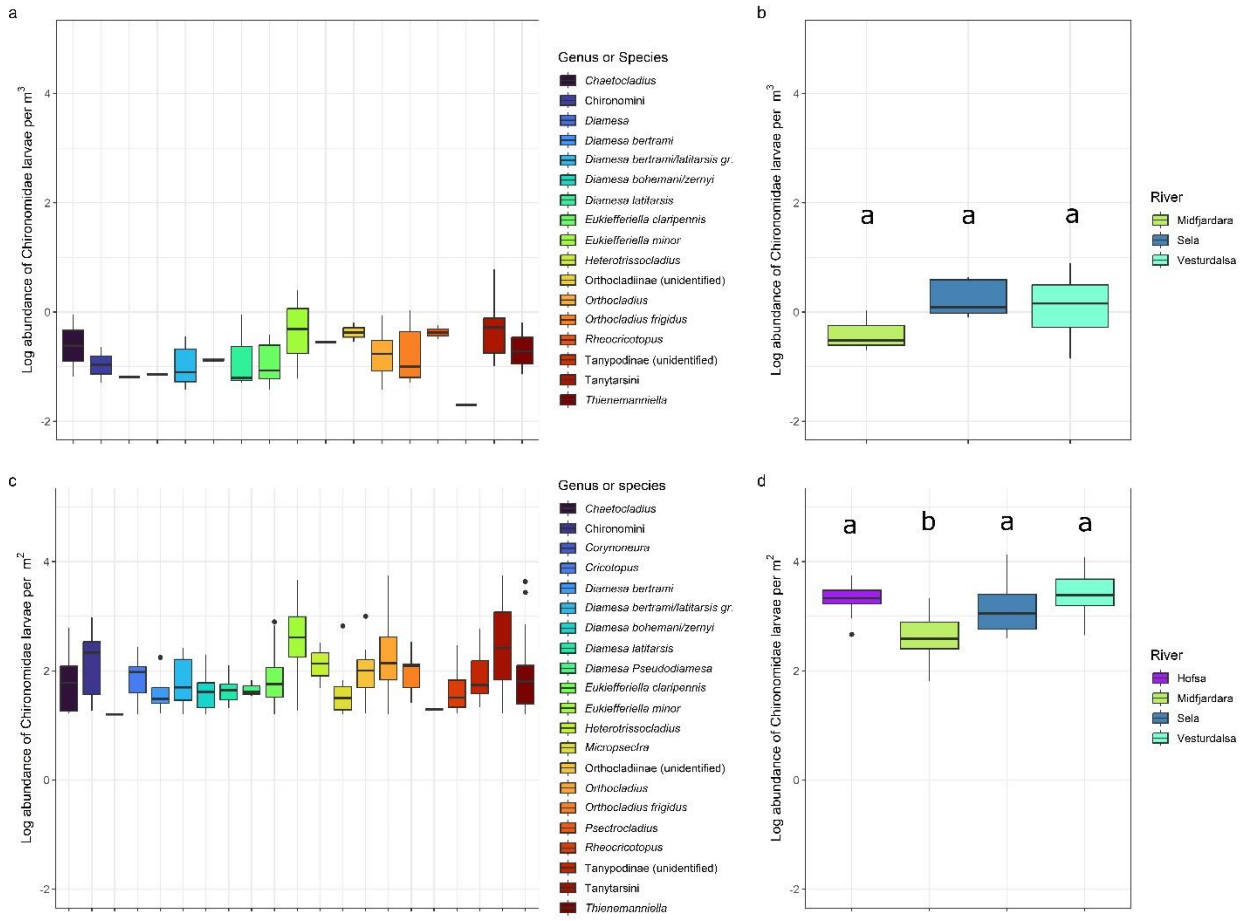

Figure S3: Variations in abundance of drifts (number of individuals/m^3) and benthic (number of individuals/m^2) Chironomidae larvae, by taxonomic groups (left) and rivers (right). Log_{10} abundances of drift (top panels) and benthic chironomids (bottom panels). Log_{10} abundances of different taxons of chironomids differed significantly a) in the drifting column ($p<0.001$) and c) in the bottom substrate for all rivers ($p<0.001$). Log_{10} abundances found b) in the drift did not differ between rivers ($p=0.091$), but d) abundance in the bottom substrate differed ($p<0.001$). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

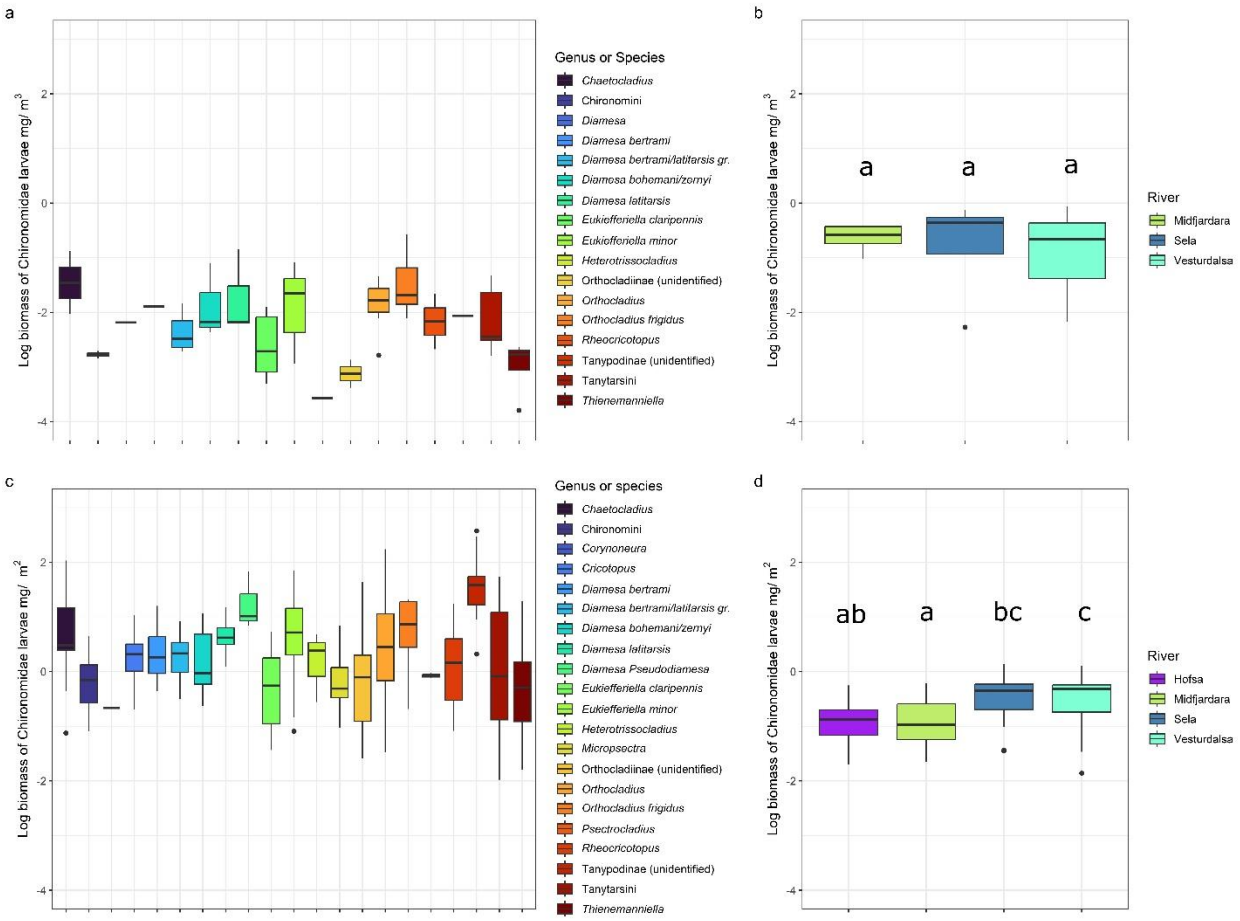

Figure S4: Variations in population biomass of drifts (mg/m^3) and benthic (mg/m^2) Chironomidae larvae, by taxonomic groups and rivers. Log_{10} biomass of drift (top panels) and benthic invertebrates (bottom panels). Log_{10} biomass of different taxons of chironomids differed significantly a) in the drifting column ($p<0.01$) and c) in the bottom substrate ($p<0.001$). Log_{10} biomass found b) in the drift were not significantly different between rivers ($p=0.802$) but was different d) in the bottom substrate ($p<0.001$). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

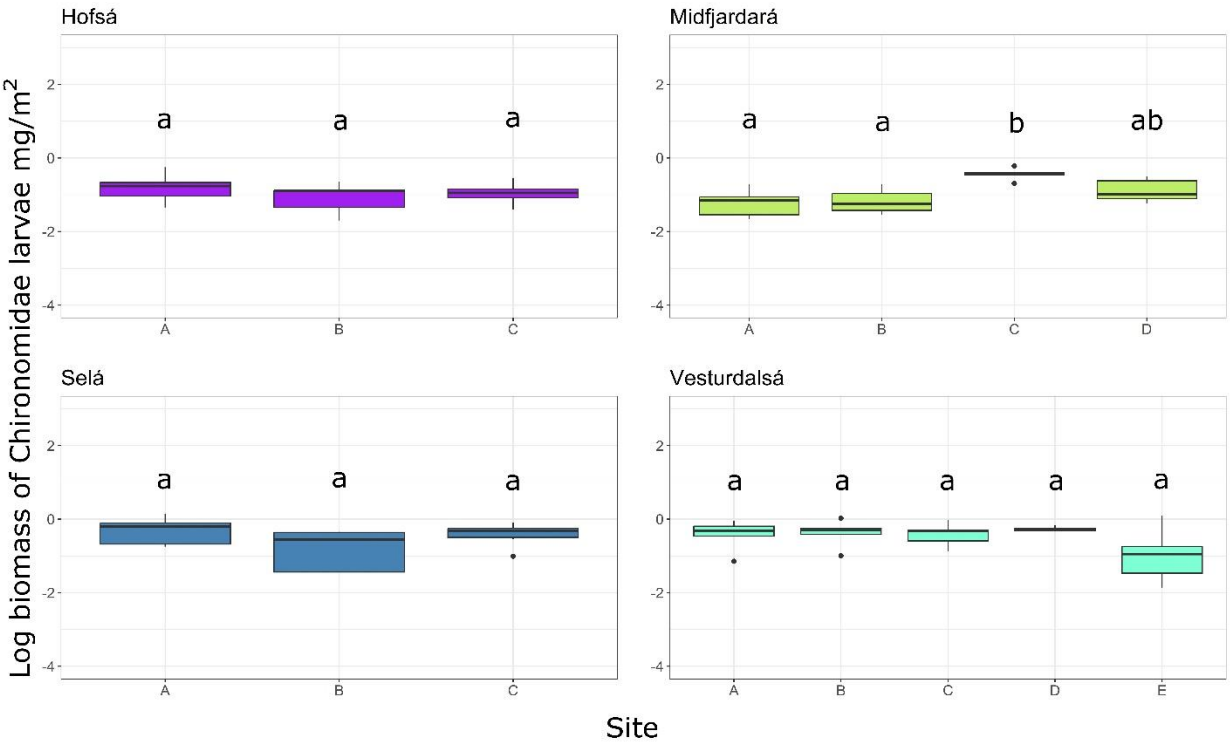

Figure S5: Log_{10} population biomass (mg/m^2) of benthic Chironomidae larvae at different sites at each study river. There were no significant differences between sites for Hofsá ($p=0.599$), Selá ($p=0.204$), and Vesturdalsá ($p=0.491$), but there were significant differences for Midfjardará ($p<0.01$). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

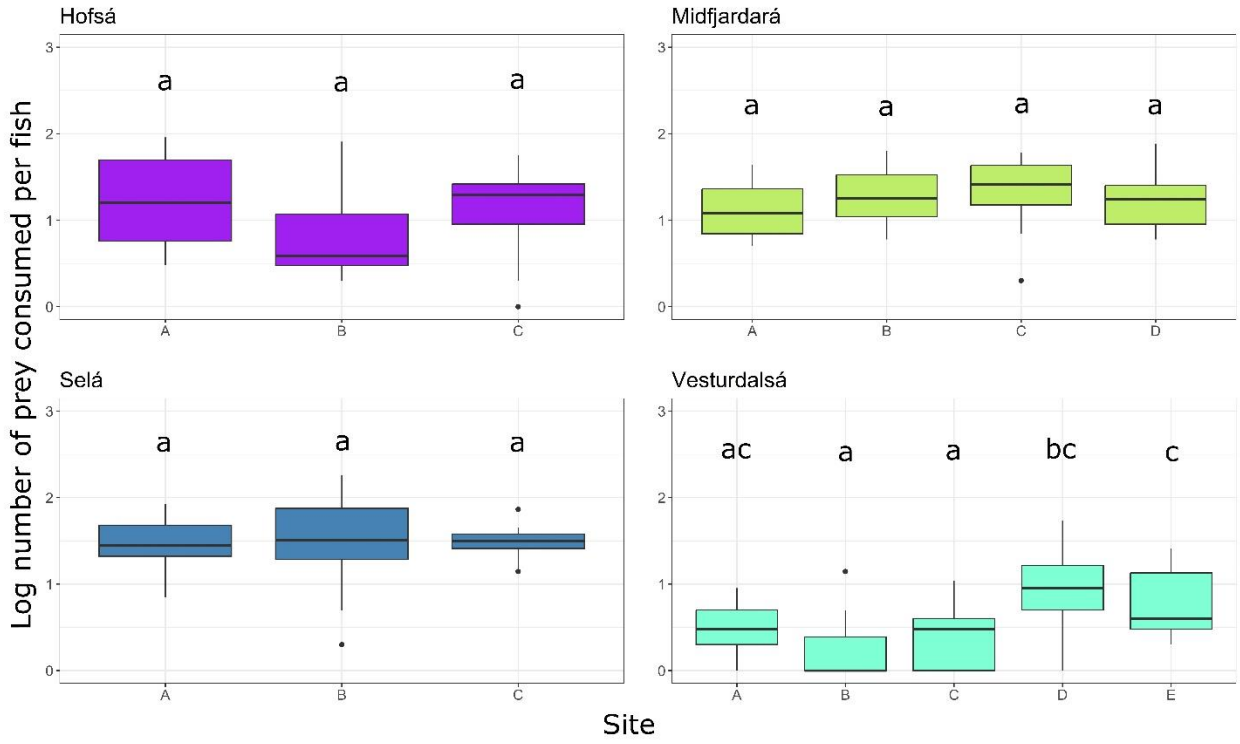

Figure S6: Log_{10} number of prey items consumed by juvenile salmon at different sites at each study river. There were no significant differences between sites for Hofsá ($p=0.088$), Selá ($p=0.729$), and Midfjardará ($p=0.066$), but there were significant differences for Vesturdalsá ($p<0.001$). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

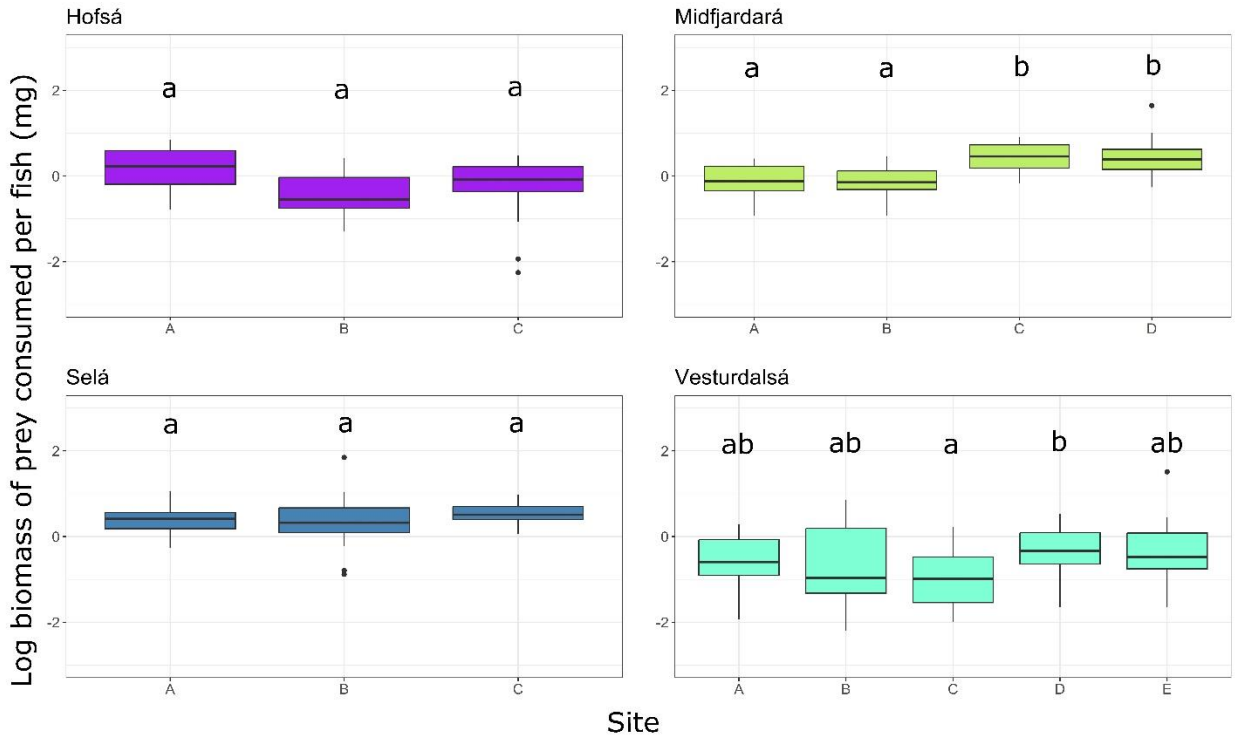

Figure S7: Log_{10} biomass (mg) of prey items consumed by juvenile salmon at different sites at each study river. There were no significant differences between sites for Hofsá ($p=0.0838$) and Selá ($p=0.283$). In contrast, there were significant differences between sites for Midfjardará ($p<0.001$) and Vesturdalsá ($p<0.01$). Letters above boxplots show significant differences from post-hoc tests, with same letters indicating no significant differences between means, variables with different letters are significantly different.

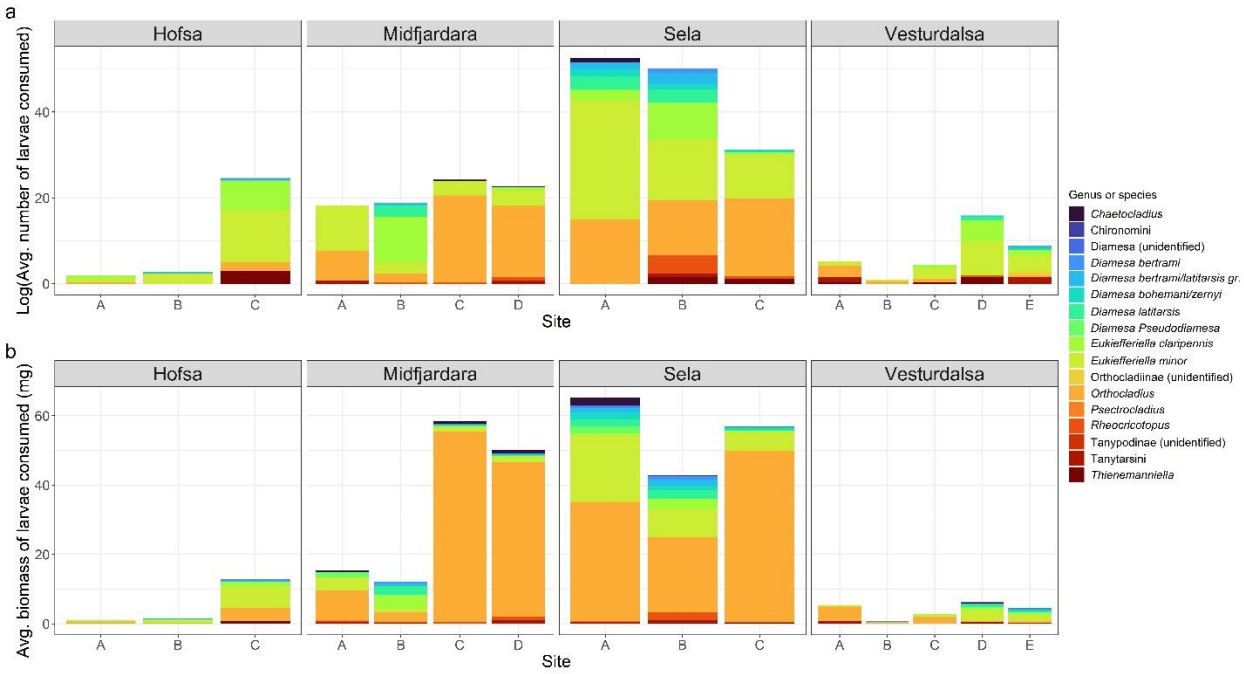

Figure S8: a) Log_{10} average number ($p<0.001$) and b) biomass (mg; $p<0.001$) of Chironomidae larvae consumed per juvenile salmon (Salmo salar) was significantly different across rivers. Abundances also differed between sites ($p<0.05$) for all rivers except for Selá ($p=0.368$). There was no difference in abundance ($p=0.158$) and biomass ($p=0.447$) of larvae consumed across different weight groups of juvenile fish.

Supporting Tables:

1. Site Descriptions in each study river in NE Iceland

Table S1: Descriptions of sites at each study river. Substrate classification broken down into: gravel (2-16 mm), pebble (17-64 mm), cobble (65-256 mm), and boulder (>256 mm) (Bain et al., 1985).

River	Site	Degrees (N)	Degrees (W)	Elevation (m)	Width (m)	Water Depth (m)	Area Sampled (m)	Temperature (°C)	pH	Conductivity	Velocity (m/s)	Benthic substrate description	Benthic vegetation description	Vegetation on banks
Vesturdalsá	A	65.7234	-14.9597	0	20.4	0.165	257	10.2	7.89	100	0.0805	100% gravel	100% benthic algae	wetland, grassland
	B	65.6973	-15.0046	0	12.6	0.475	118	9.57	8.00	114	0.338	50% gravel, 50% pebble	100% benthic algae	heathland
	C	65.6867	-15.0487	50	9.60	0.255	198	9.73	8.07	112	0.150	100% cobble	60% benthic algae	grassland, heathland
	D	65.6610	-15.1417	170	8.13	0.345	97.1	10.2	8.05	108	0.683	70% cobble, 30% boulder	50% benthic algae	grassland
	E	65.6584	-15.1764	200	14.7	0.235	307	10.8	8.17	106	0.438	60% cobble, 40% boulder	20% benthic algae	wetland, heathland
Midfjardará	A	66.04054	-15.1019	0	10.7	0.155	193	11.1	7.84	71.5	0.169	80% gravel, 20% pebble	100% benthic algae	heathland, wetland, grassland
	B	66.0328	-15.1169	0	6.70	0.370	103	11.2	7.79	68.8	0.320	50% pebble, 50% cobble	100% benthic algae	heathland, grassland
	C	66.0134	-15.1556	60	11.5	0.370	150	10.8	7.69	67.5	0.186	100% cobble	40% benthic algae	grassland
	D	66.0052	-15.1590	60	10.4	0.380	130	10.7	7.66	67.3	0.639	70% cobble 30% boulder	20% benthic algae	heathland, wetland
Selá	A	65.8254	-14.8416	0	8.40	0.240	198	12.95	8.22	67.4	0.169	gravel and little pebble	100% benthic algae	wetland, heathland
	B	65.7664	-15.0127	100	7.10	0.310	158	12.0	8.22	67.9	0.0445	50% pebble, 50% cobble	70% benthic algae	heathland
	C	65.7055	-15.2020	320	13.0	0.240	173	10.1	7.73	69.8	0.232	80% cobble, 20% boulder	30% filamentous algae, 30% benthic algae	heathland, grassland
Hofsá	A	65.6305	-15.0501	40	6.90	0.435	89.7	10.3	8.67	94.8	0.249	90% pebble, 10% boulder	40% filamentous algae, 20% benthic algae	wetlands, heathland
	B	65.6124	-15.0778	60	4.90	0.450	63.7	8.95	8.55	94.6	0.0700	100% cobble	80% benthic algae	heathland
	C	65.5864	-15.1382	100	12.0	0.335	188	8.20	8.49	91.5	0.0650	80% cobble, 20% boulder	80% benthic algae	heathland

2. Species list between River Vesturdalsá, Iceland and River Frome, UK

Table S2: Invertebrate family groups found in Vesturdalsá and Frome.

Vesturdalsá	**Frome (Woodward et al., 2010)**
Chironomidae	Trichoptera
Empididae	Gastropoda
Gastropoda	Annelida
Oligochaeta	Aphelocheirus aestivalis
Plecoptera	Asellus aquaticus
Simuliidae	Baetidae
Trichoptera	Odonata
Hydracarina sp.	Dicranota
Tipulidae	Elmis aenea Lv.
	Empididae
	Ephemeroptera
	Erpobdella
	Gammarus
	Glossiphonia
	Gyrinidae
	Hydracarina sp.
	Plecoptera
	Limnius
	Oligochaeta
	Oulimnius tuberculatus Lv.
	Piscicola
	Pisidium
	Simuliidae
	Tipulidae

3. Statistical outputs of Kruskal-Wallis tests of invertebrate abundance and biomass comparisons

Table S3: Kruskal-Wallis test of invertebrate taxonomic groups between rivers and taxonomic groups.

Bottom substrate (Surber):	χ^2	**df**	**p-value** †
Log_{10} (Abundance)~River	25.374	3	***
Log_{10} (Biomass) ~River	32.115	3	***
Log_{10} (Abundance)~Taxonomic group	179.710	9	***
Log_{10} (Biomass) ~Taxonomic group	131.670	9	***
Drift:			
Log_{10} (Abundance)~River	6.629	2	*
Log_{10} (Biomass) ~River	4.253	2	0.119
Log_{10} (Abundance)~Taxonomic group	29.114	6	***
Log_{10} (Biomass) ~Taxonomic group	33.889	6	***

Table S4*:* Kruskal-Wallis test of benthic invertebrate taxonomic groups between sites within study rivers.

Hofsá:	χ^2	**df**	**p-value**†
Log_{10} (Abundance)~Site	2.090	2	0.352
Log_{10} (Biomass) ~Site	0.863	2	0.650
Midfjardará:			
Log_{10} (Abundance)~Site	7.786	3	0.051
Log_{10} (Biomass) ~Site	15.046	3	**
Selá:			
Log_{10} (Abundance)~Site	5.188	2	0.075
Log_{10} (Biomass) ~Site	6.146	2	*
Vesturdalsá:			
Log_{10} (Abundance)~Site	5.524	4	0.238
Log_{10} (Biomass) ~Site	7.658	4	0.105

† if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

3.1. Dunn test pairwise comparison outputs of invertebrates between rivers and taxonomic groups

Table S5: Bottom substrate: pairwise comparison of log_{10} (abundance) between rivers.

Comparison	Z	adjusted p-value†
Hofsá – Midfjardará	3.951	***
Hofsá – Selá	1.189	1.000
Midfjardará – Selá	-2.697	*
Hofsá – Vesturdalsá	-0.241	1.000
Midfjardará – Vesturdalsá	-4.674	***
Selá – Vesturdalsá	-1.554	0.721

Table S6: Bottom substrate: pairwise comparison of log_{10} (population biomass) between rivers.

Comparison	Z	adjusted p-value†
Hofsá – Midfjardará	4.601	***
Hofsá – Selá	1.327	1.000
Midfjardará – Selá	-3.202	**
Hofsá – Vesturdalsá	-0.010	1.000
Midfjardará – Vesturdalsá	-5.155	***
Selá – Vesturdalsá	-1.476	0.839

Table S7: Bottom substrate: pairwise comparison of log_{10} (population biomass) between sites in Midfjardará.

Comparison	Z	adjusted p-value†
Site A – Site B	2.940	*
Site A – Site C	-0.428	1.000
Site B – Site C	-3.367	**
Site A – Site D	1.871	0.368
Site B – Site D	-1.069	1.000
Site C – Site D	2.298	0.129

† if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

Table S8: Bottom substrate: pairwise comparison of log_{10} (population biomass) between sites in Selá.

Comparison	Z	adjusted p-value†
A – B	1.528	0.380
A – C	2.463	*
B – C	0.867	1.000

Table S9: Drift: pairwise comparison of log_{10} (abundance) between rivers.

Comparison	Z	adjusted p-value†
Midfjardará-Selá	-2.859	*
Midfjardará-Vesturdalsá	-1.983	0.142
Selá-Vesturdalsá	1.169	0.728

4. Statistical outputs of Kruskal-Wallis test of comparisons of abundances and biomass of Chironomidae larvae

Table S10: Kruskal-Wallis test of Chironomidae larvae between rivers and taxonomic groups.

Bottom substrate (Surber):	χ^2	df	p-value†
Log_{10} (Abundance)~River	11.698	3	***
Log_{10} (Biomass) ~River	17.844	3	***
Log_{10} (Abundance)~Taxonomic group	125.420	21	***
Log_{10} (Biomass) ~Taxonomic group	119.760	21	***
Drift:			
Log_{10} (Abundance)~River	4.800	2	0.091
Log_{10} (Biomass) ~River	0.442	2	0.802
Log_{10} (Abundance)~Taxonomic group	48.881	16	***
Log_{10} (Biomass) ~Taxonomic group	32.541	16	**

Table S11: Kruskal-Wallis test of benthic taxonomic groups of Chironomidae larvae between sites within study rivers.

Hofsá:	χ^2	df	p-value †
Log_{10} (Abundance)~Site	5.677	2	0.059
Log_{10} (Biomass) ~Site	1.024	2	0.599
Midfjardará:			
Log_{10} (Abundance)~Site	7.454	3	0.059
Log_{10} (Biomass) ~Site	11.366	3	**
Selá:			

† if p<0.05 it is shown with *, if a p<0.01 it is shown with **, and if a p<0.001 it is shown with ***, non-significant p-values are written out.

Log_{10} (Abundance)~Site	5.259	2	0.072
Log_{10} (Biomass) ~Site	3.181	2	0.204
Vesturdalsá:			
Log_{10} (Abundance)~Site	5.947	4	0.203
Log_{10} (Biomass) ~Site	3.412	4	0.491

Table S12: Bottom substrate: pairwise comparison of log_{10} (population biomass) of Chironomidae larvae between sites in Midfjardará.

Comparison	**Z**	**adjusted p-value†**
Site A – Site B	-0.053	1.000
Site A – Site C	-2.940	*
Site B – Site C	-2.886	*
Site A – Site D	-1.176	1.000
Site B – Site D	-1.122	1.000
Site C – Site D	1.764	0.466

4.1. Dunn test pairwise comparison outputs of Chironomidae larvae between rivers and taxonomic groups

Table S13: Bottom Substrate: pairwise comparison of log_{10} (abundance) of Chironomidae larvae between rivers.

Comparison	**Z**	**adjusted p-value†**
Hofsá – Midfjardará	4.401	***
Hofsá – Selá	1.280	1.000
Hofsá – Vesturdalsá	-0.293	1.000
Midfjardará – Selá	-3.052	*
Midfjardará – Vesturdalsá	-5.234	***
Selá – Vesturdalsá	-1.707	0.527

Table S14: Bottom Substrate: pairwise comparison of log_{10} (biomass) of Chironomidae larvae between rivers.

Comparison	**Z**	**adjusted p-value†**
Hofsá – Midfjardará	-0.067	1.000
Hofsá – Selá	-2.623	0.052
Hofsá – Vesturdalsá	-3.143	*
Midfjardará – Selá	-2.699	*
Midfjardará – Vesturdalsá	-3.279	**
Selá – Vesturdalsá	-0.246	1.000

5. Statistical output of size comparisons of juvenile salmon in NE Iceland

Table S15: Comparison of weight (g) of juvenile salmon sampled across rivers (Kruskal-Wallis test and Dunn test).

Kruskal-Wallis test			χ^2	**df**	**p-value**[†]
Weight (g) ~ River			228.25	3	***
Dunn test					
Comparison	**Z**	**adjusted p-value†**			
Hofsá – Midfjardará	14.705	***			
Hofsá – Selá	10.753	***			
Midfjardará – Selá	-2.914	*			
Hofsá – Vesturdalsá	10.487	***			
Midfjardará – Vesturdalsá	-5.713	***			
Selá – Vesturdalsá	-1.974	0.290			

Table S16: Comparison of weight (g) of juvenile salmon sampled across sites in Vesturdalsá (Kruskal-Wallis test and Dunn test).

Kruskal-Wallis test			χ^2	**df**	**p-value†**
Weight (g) ~ Site			27.731	4	***
Dunn test					
Comparison	**Z**	**adjusted p-value†**			
Site A- Site B	-2.115	0.344			
Site A- Site C	-0.546	1.000			
Site B- Site C	1.633	1.000			
Site A- Site D	-0.863	1.000			
Site B- Site D	1.602	1.000			
Site C- Site D	-0.239	1.000			
Site A- Site E	-4.161	***			
Site B- Site E	-1.124	1.000			
Site C- Site E	-3.516	**			
Site D- Site E	-3.982	***			

[†] if p<0.05 it is shown with *, if a p<0.01 it is shown with **, and if a p<0.001 it is shown with ***, non-significant p-values are written out.

Table S17: Comparison of weight (g) of juvenile salmon sampled across sites in Selá (Kruskal-Wallis test and Dunn test).

Kruskal-Wallis test			χ^2	**df**	**p-value**†
Weight (g) ~ Site			13.897	2	***
Dunn test					
Comparison	**Z**	**adjusted p-value**†			
Site A- Site B	-3.310	**			
Site A- Site C	0.402	1.000			
Site B- Site C	3.073	**			

Table S18: Comparison of weight (g) of juvenile salmon sampled across sites in Midfjardará (Kruskal-Wallis test and Dunn test).

Kruskal-Wallis test			χ^2	**df**	**p-value**†
Weight (g) ~ Site			24.740	3	***
Dunn test					
Comparison	**Z**	**adjusted p-value**†			
Site A- Site B	4.721	***			
Site A- Site C	0.812	1.000			
Site B- Site C	-3.499	**			
Site A- Site D	0.862	1.000			
Site B- Site D	-3.581	**			
Site C- Site D	0.020	1.000			

Table S19: Comparison of weight (g) of juvenile salmon sampled across sites in Hofsá (Kruskal-Wallis test and Dunn test).

Kruskal-Wallis test			χ^2	**df**	**p-value**†
Weight (g) ~ Site			20.061	2	***
Dunn test					
Comparison	**Z**	**adjusted p-value**†			
Site A- Site B	3.847	***			
Site A- Site C	3.947	***			
Site B- Site C	-0.772	1.000			

† if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

6. Statistical outputs for juvenile Atlantic salmon stomach contents analysis

Table S20: Log_{10} number and biomass of prey items found in stomachs of juveniles across rivers (Kruskal-Wallis test and Dunn test).

Kruskal-Wallis test			χ^2	**df**	**p-value**[†]
Log_{10} (abundance of stomach prey items) ~ River			90.282	3	***
Dunn test					
Comparison	**Z**	**adjusted p-value**[†]			
Hofsá – Midfjardará	-1.297	1.000			
Hofsá – Selá	-4.041	***			
Midfjardará – Selá	-3.264	**			
Hofsá – Vesturdalsá	4.263	***			
Midfjardará – Vesturdalsá	6.534	***			
Selá – Vesturdalsá	9.139	***			
Kruskal-Wallis test			**X^2**	**df**	**p-value†**
Log_{10} (biomass of stomach prey items) ~ River			80.142	3	***
Dunn test					
Comparison	**Z**	**adjusted p-value†**			
Hofsá – Midfjardará	-2.713	*			
Hofsá – Selá	-5.282	***			
Midfjardará – Selá	-3.181	**			
Hofsá – Vesturdalsá	2.303	0.128			
Midfjardará – Vesturdalsá	5.879	***			
Selá – Vesturdalsá	8.465	***			

[†] if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

6.1. Abundance of prey items in stomachs for juvenile salmon across sites and invertebrate taxonomic groups

Table S21: Number of prey items in stomachs of juveniles across sites in different rivers (Kruskal-Wallis test and Dunn test).

River Vesturdalsá		χ^2	**df**	**p-value†**
Log_{10} (abundance) ~Site		37.134	4	***
Dunn test				
Comparison	**Z**	**adjusted p-value†**		
Site A- Site B	1.954	0.508		
Site A- Site C	0.856	1.000		
Site B- Site C	-1.183	1.000		
Site A- Site D	-3.355	**		
Site B- Site D	-5.113	***		
Site C- Site D	-4.294	***		
Site A- Site E	-2.107	0.352		
Site B- Site E	-3.965	***		
Site C- Site E	-3.029	*		
Site D- Site E	1.309	1.000		
River Selá		χ^2	**df**	**p-value†**
Log_{10} (abundance) ~Site		0.634	2	0.729
River Midfjardará				
Log_{10} (abundance) ~Site		7.187	3	0.066
River Hofsá				
Log_{10} (abundance) ~Site		4.850	2	0.088

Table S22: Log_{10} number of prey items in stomachs of juveniles across taxonomic groups across rivers (Kruskal-Wallis test).

River		χ^2	**df**	**p-value†**
Vesturdalsá	Log_{10} (abundance) ~Taxon	68.559	10	***
Selá		78.487	7	***
Midfjardará		73.703	7	***
Hofsá		34.217	6	***

† if p<0.05 it is shown with *, if a p<0.01 it is shown with **, and if a p<0.001 it is shown with ***, non-significant p-values are written out.

6.2. Biomasses of prey items in stomachs for juvenile salmon across different rivers, sites, and invertebrate taxonomic groups

Table S23: Log_{10} biomass of prey items in stomachs of juveniles across sites in different rivers (Kruskal-Wallis test and Dunn test).

River Vesturdalsá		χ^2	**df**	**p-value†**
Log_{10} (biomass) ~Site		15.299	4	**
Dunn test				
Comparison	**Z**			**adjusted p-value†**
Site A- Site B	1.685			0.921
Site A- Site C	2.451			0.143
Site B- Site C	0.563			1.000
Site A- Site D	-0.760			1.000
Site B- Site D	-2.448			0.144
Site C- Site D	-3.333			**
Site A- Site E	-0.101			1.000
Site B- Site E	-1.841			0.656
Site C- Site E	-2.665			0.077
Site D- Site E	0.692			1.000
River Selá		χ^2	**df**	**p-value†**
Log_{10} (biomass) ~Site		2.529	2	0.283
River Midfjardará				
Log_{10} (biomass) ~Site		33.403	3	***
Dunn test				
Comparison	**Z**			**adjusted p-value†**
Site A- Site B	-0.080			1.000
Site A- Site C	-4.398			***
Site B- Site C	-4.089			***
Site A- Site D	-4.032			***
Site B- Site D	-3.749			**
Site C- Site D	0.295			1.000
River Hofsá		χ^2	**df**	**p-value†**
Log_{10} (biomass) ~Site		4.960	2	0.0838

† if p<0.05 it is shown with *, if a p<0.01 it is shown with **, and if a p<0.001 it is shown with ***, non-significant p-values are written out.

Table S24: Log_{10} biomass of prey items in stomachs of juveniles across taxonomic groups in River Vesturdalsá (Kruskal-Wallis test).

River		χ^2	df	p-value†
Vesturdalsá	Log_{10} (biomass) ~Taxon	28.942	10	**
Selá		72.153	7	***
Midfjardará		73.298	7	***
Hofsá		2.891	6	0.822

6.3. Abundances and biomasses of prey items in stomachs across weights of juvenile salmon

Table S25: Linear model of prey items found stomachs of juveniles ~ log_{10}(weight of fish).

Abundance	Estimate	SE	t-value	p-value†
(Intercept)	16.031	2.136	7.506	***
Log_{10} Weight (g)	0.905	0.372	2.433	*
			Adjusted r^2: 0.016, p-value: *	
Biomass	**Estimate**	**SE**	**t-value**	**p-value†**
(Intercept)	1.650	0.520	3.173	**
Log_{10} Weight (g)	0.109	0.091	1.199	0.232
			Adjusted r^2: 0.00146, p-value: 0.232	

† if p<0.05 it is shown with *, if a p<0.01 it is shown with **, and if a p<0.001 it is shown with ***, non-significant p-values are written out.

7. Statistical outputs for the analysis of Chironomidae larvae in stomachs of juvenile Atlantic salmon

Table S26: Number and biomass of Chironomidae larvae found in stomachs of juveniles across rivers (Kruskal-Wallis test and Dunn test).

Kruskal-Wallis test		χ^2	**df**	**p-value**†
Log_{10}(abundance of stomach prey items) ~ River		133.57	3	***
Dunn test				
Comparison	**Z**		**adjusted p-value**†	
Hofsá – Midfjardará	-1.592		0.669	
Hofsá – Selá	-5.827		***	
Midfjardará – Selá	-5.466		***	
Hofsá – Vesturdalsá	3.615		**	
Midfjardará – Vesturdalsá	6.717		***	
Selá – Vesturdalsá	11.420		***	
Kruskal-Wallis test		χ^2	**df**	**p-value**†
Log_{10} (biomass of stomach prey items) ~ River		119.64	3	***
Dunn test				
Comparison	**Z**		**adjusted p-value**†	
Hofsá – Midfjardará	-4.153		***	
Hofsá – Selá	-6.841		***	
Midfjardará – Selá	-3.709		**	
Hofsá – Vesturdalsá	1.413		0.945	
Midfjardará – Vesturdalsá	7.123		***	
Selá – Vesturdalsá	10.076		***	

† if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

7.1. Abundance of Chironomidae larvae in stomachs for juvenile salmon across different rivers, sites, and invertebrate taxonomic groups

Table S27: Number of Chironomidae larvae in stomachs of juveniles across sites in different rivers (Kruskal-Wallis test and Dunn test).

River Vesturdalsá		χ^2	**df**	**p-value†**
Log_{10} (abundance) ~Site		10.893	4	*
Dunn test				
Comparison	**Z**			**adjusted p-value†**
Site A- Site B	1.281			1.000
Site A- Site C	0.369			1.000
Site B- Site C	-0.979			1.000
Site A- Site D	-2.022			0.432
Site B- Site D	-2.774			0.055
Site C- Site D	-2.339			0.193
Site A- Site E	-0.679			1.000
Site B- Site E	-1.795			0.727
Site C- Site E	-1.034			1.000
Site D- Site E	1.357			1.000
River Selá		**X^2**	**df**	**p-value†**
Log_{10} (abundance) ~Site		1.288	2	0.525
River Midfjardará		**X^2**	**df**	**p-value†**
Log_{10} (abundance) ~Site		12.163	3	**
Dunn test				
Comparison	**Z**			**adjusted p-value†**
Site A- Site B	-1.364			1.000
Site A- Site C	-3.069			*
Site B- Site C	-1.598			0.661
Site A- Site D	-2.788			*
Site B- Site D	-1.350			1.000
Site C- Site D	0.232			1.000
River Hofsá		χ^2	**df**	**p-value†**
Log_{10} (abundance) ~Site		17.800	2	***
Dunn test				
Comparison	**Z**			**adjusted p-value†**
Site A- Site B	1.013			0.934
Site A- Site C	-1.705			0.265
Site B- Site C	-4.180			***

† if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

Table S28: Number of Chironomidae larvae in stomachs of juveniles across taxonomic groups across different rivers (Kruskal-Wallis test).

River Vesturdalsá	χ^2	**df**	**p-value**[†]
Log_{10} (abundance) ~Taxon	24.641	14	*
River Selá			
Log_{10} (abundance) ~Taxon	134.680	15	***
River Midfjardará			
Log_{10} (abundance) ~Taxon	94.570	13	***
River Hofsá			
Log_{10} (abundance) ~Taxon	17.055	6	**

[†] if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

7.2. Biomasses of Chironomidae larvae in stomachs for juvenile salmon across different rivers, sites, and invertebrate taxonomic groups

Table S29: Biomass of Chironomidae larvae in stomachs of juveniles across sites in different rivers (Kruskal-Wallis test and Dunn test).

River Vesturdalsá		χ^2	**df**	**p-value†**
Log_{10} (biomass) ~Site		10.065	4	*
Dunn test				
Comparison	**Z**			**adjusted p-value†**
Site A- Site B	2.341			0.192
Site A- Site C	2.166			0.303
Site B- Site C	-0.673			1.000
Site A- Site D	0.210			1.000
Site B- Site D	-2.284			0.224
Site C- Site D	-2.117			0.343
Site A- Site E	1.186			1.000
Site B- Site E	-1.513			1.000
Site C- Site E	-1.080			1.000
Site D- Site E	1.066			1.000
River Selá		χ^2	**df**	**p-value†**
Log(biomass) ~Site		4.448	2	0.108
River Midfjardará				
Log_{10} (biomass) ~Site		40.828	3	***
Dunn test				
Comparison	**Z**			**adjusted p-value†**
Site A- Site B	0.220			1.000
Site A- Site C	-4.599			***
Site B- Site C	-4.568			***
Site A- Site D	-4.456			***
Site B- Site D	-4.436			***
Site C- Site D	0.078			1.000
River Hofsá		χ^2	**df**	**p-value†**
Log_{10} (biomass) ~Site		14.975	2	***
Dunn test				
Comparison	**Z**			**adjusted p-value†**
Site A- Site B	1.382			0.501
Site A- Site C	-1.118			0.790
Site B- Site C	-3.869			***

† if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

Table S30: Biomass of Chironomidae larvae in stomachs of juveniles across taxonomic groups across different rivers (Kruskal-Wallis test).

River Vesturdalsá	χ^2	**df**	**p-value†**
Log_{10} (biomass) ~Taxon	48.634	14	***
River Selá			
Log_{10} (biomass) ~Taxon	163.890	15	***
River Midfjardará			
Log_{10} (biomass) ~Taxon	134.830	13	***
River Hofsá			
Log_{10} (biomass) ~Taxon	17.055	6	***

7.3. Abundances and biomasses of Chironomidae larvae in stomachs across weights of juvenile salmon

Table S31: Linear model of Chironomidae larvae found stomachs of juveniles ~ log_{10} (weight of fish).

Abundance	**Estimate**	**SE**	**t-value**	**p-value†**
(Intercept)	44.255	11.559	3.829	***
Log_{10} Weight (g)	3.105	2.190	1.418	0.158
	Adjusted r^2: 0.004, p-value: 0.158			
Biomass	**Estimate**	**SE**	**t-value**	**p-value†**
(Intercept)	1.428	0.186	7.672	***
Log_{10} Weight (g)	-0.029	0.036	-0.762	0.447
	Adjusted r^2: -0.002, p-value: 0.447			

8. Comparison of Manly-Chesson α prey selectivity index across taxonomic groups

Table S32: Chesson α compared across different taxonomic groups for benthic and drift samples (Kruskal-Wallis test).

	χ^2	**df**	**p-value†**
Benthic: Chesson α~Taxon	13.934	5	*
Drift: Chesson α~Taxon	8.013	5	0.156

† if p<0.05 it is shown with *, if a p<0.01 it is shown with **, and if a p<0.001 it is shown with ***, non-significant p-values are written out.

9. Statistical output of size comparisons of different salmonid species in NE Iceland

Table S33: Comparison of weight (g) of different species of juvenile salmonids (Kruskal-Wallis test and Dunn test).

Kruskal-Wallis test			χ^2	**df**	**p-value†**
Weight (g) ~ River			24.611	2	***
Dunn test					
Comparison	**Z**	**adjusted p-value†**			
Salmon - Charr	-0.355	1.000			
Salmon – Trout	-4.960	***			
Charr – Trout	-3.492	**			

10. Dietary niche overlap (FT) index comparison between juvenile salmon and other salmonid species and between rivers

Table S34: Comparison of FT indices using unpaired Wilcoxon signed-rank test.

Comparison	**W**	**p-value†**
FT of salmon and trout – salmon and charr	9	0.786
FT of salmon and trout in Hofsá from current – previous years	14	0.071

Table S35: Comparison of FT indices across rivers (Kruskal-Wallis test).

	χ^2	**df**	**p-value†**
FT index ~ River	5.597	3	0.133

† if p<0.05 it is shown with *, if a p<0.01 it is shown with **, and if a p<0.001 it is shown with ***, non-significant p-values are written out.

References:

Bain, M. B., Finn, J. T., & Booke, H. E. (1985). Quantifying Stream Substrate for Habitat Analysis Studies. *North American Journal of Fisheries Management*, *5*(3B), 499–500. https://doi.org/10.1577/1548-8659(1985)5<499:qssfha>2.0.co;2

Woodward, G., Blanchard, J., Lauridsen, R. B., Edwards, F. K., Jones, J. I., Figueroa, D., Warren, P. H., & Petchey, O. L. (2010). Individual-based food webs. Species identity, body size and sampling effects. In *Advances in Ecological Research* (Vol. 43, Issue C). Elsevier Ltd. https://doi.org/10.1016/B978-0-12-385005-8.00006-X

Paper II

Signs of warming and temporal stability of predator-prey relationships of sub-Arctic Atlantic salmon river

Sum Yi Lai, Eoin J. O´Gorman, Guðni Guðbergsson, Guy Woodward, Ingi Rúnar Jónsson, Johannes Guðbrandsson, Jón S. Ólafsson, and Hlynur Bárðarson

Author Contribution Statement:

Conceptualisation & Developing methods: SYL, EJG, GG, GW, IRJ, JG, JSO, HB. Conducting the research: SYL, JG, JSO, HB. Data analysis: SYL. Data interpretation: SYL, EJG, GW, IRJ, JG, JSO, HB. Preparation figures & tables & Writing: SYL.

Abstract:

There is a global population decline of worldwide Atlantic salmon (*Salmo salar)* populations in the past four decades and changes in food availability and climate change could alter the trophic interactions between Atlantic salmon and its prey. Thus, we wanted to know whether trophic relationships of Atlantic salmon differed over years (from 1997 to 2020) and during the summer. We compared trophic relationships between years and four periods during the summer in a relatively cold, oligotrophic, low-productivity, and Atlantic salmon-dominated river, which was the Vesturdalsá river in Northeast Iceland. Our results showed that trophic relationships varied little over time, both over the 23-year window studied and during the summer of 2020, demonstrating the temporal stability in sub-Arctic low-productivity rivers. Changes in slope, mean chain length, and mean link angle revealed decreasing prey availability for juvenile salmonids over time. Our results showed a peak in river productivity during late summer (late July to August), in which juvenile Atlantic salmon were able to feed on a higher availability of prey. Thus, the productivity during the late summer period is crucial to the productivity of the Atlantic salmon population. Even though, Vesturdalsá experienced little change in predator-prey relationships over time, it is evident that there were decreases in prey availability and adaptability in the ecosystem, suggesting that other sub-Arctic rivers with oligotrophic and species-poor systems may be vulnerable to lack of prey and resources due to climate change.

Keywords: food webs, trophic relationships, salmonids, Atlantic salmon, temporal, Northeast Iceland

Introduction:

Evidence shows that, Atlantic salmon (*Salmo salar*) populations across the globe are declining over the past four decades (Guðbergsson, 2015; ICES, 2023), and researchers are both monitoring this carefully and investigating the potential reasons for this decline (Gregory et al., 2017; Thorstad et al., 2021). Habitat loss, aquaculture, migration barriers, pollution, diseases, overexploitation, and warming are just some of the potential reasons for this decline (Ford & Myers, 2008; Forseth et al., 2017; ICES, 2023; Thorstad et al., 2019, 2021). Changes in food availability in rivers has been identified as one of the main drivers to changes in populations of juvenile Atlantic salmon, but its relative importance could vary between rivers or years (Erkinaro & Erkinaro, 1998; Orpwood et al., 2006; Riley et al., 2009). Additionally, resource availability studies are becoming increasingly more challenging to examine processes and effects on juvenile salmon populations due to the complex interactions of different threats (Ficke et al., 2007; Reist et al., 2006), especially across temporal and spatial scales (Mellard et al., 2021).

Atlantic salmon rivers in high latitudes are important study and monitoring systems as they can serve as ´sentinel´ systems for climate change impacts on inter-species interactions in the ecosystem (Perkins et al., 2010; Rolls et al., 2017; Woodward et al., 2010). These systems rivers are relatively simple with lower species diversity, compared to the highly productive temperate rivers (Perkins et al., 2010). This is particularly evident in Iceland, where biogeographical isolation leads to an exceptionally low species level diversity (Lento et al., 2022; Ministry for the Environment & The Icelandic Institute of Natural History, 2001; Woodward et al., 2010). These high latitude, low-productivity rivers could also be used as a population change indicator. If warming compounds seasonal variations and affects limited resources due to climate change, organisms in these low-productivity and oligotrophic rivers

will have to acclimate or adapt. Improper management of such populations could further lead to collapses in local salmonid stocks (Gerwing & Plate, 2019; Reist et al., 2006). Freshwater productivity and communities in Iceland, and others in similar latitudes are changing as rivers are becoming increasingly warmer and temperature is only projected to further increase in the near future (Bednar-Friedl et al., 2022; Constable et al., 2022; Hrafnkelsson et al., 2012; Parmesan et al., 2023). Consequentially, trophic relationships and invertebrate communities are also changing and further affecting the food availability and growth of juvenile Atlantic salmon (Durance & Ormerod, 2007; O'Gorman et al., 2016, 2019). Thus, temporal variability of trophic relationships of Atlantic salmon in a nutrient-poor environment still needs to be better understood for proper population management.

Therefore, we chose a low-productivity, sub-Arctic, salmon-dominated stream in Northeast Iceland with long-term biomonitoring of their freshwater community as our study system (Figure 1). Vesturdalsá is a 42 km long direct run-off river with a catchment area of 190 km^2 and runs into the Iceland Sea (Rist, 1990). Two salmonid species (Atlantic salmon and the Arctic charr, *Salvelinus alpinus*) spawn in the river but Atlantic salmon are more abundant of the two (Bárðarson et al., 2023). The Arctic charr is a cold-adapted species and more vulnerable to high temperatures than Atlantic salmon and recent studies are showing the global population decreasing and species range shrinking, most likely due to warming, and may likely be replaced by juvenile Atlantic salmon or brown trout in northern Europe (Reist et al., 2006; Svenning et al., 2022). In comparison, the Atlantic salmon population in Iceland has been relatively stable for the past three decades (Bárðarson et al., 2023; Svenning et al., 2022), but it may still nonetheless be vulnerable to environmental change.

Vesturdalsá is also a long-term ICES index river for Atlantic salmon populations (ICES, 2023), and thus, have more than 40 years of data on the salmonid community and 20 years of

data on the macroinvertebrate community available (Bárðarson et al., 2023). Most research studies have only been a snapshot of the freshwater ecosystem at a certain point in time as it is challenging monitoring trophic interactions over space and time (Olivier et al., 2019), and rather few long-term biomonitoring datasets are available for northern Atlantic salmon rivers. There are limited studies describing environmental change over numerous years in freshwater Atlantic salmon habitats (Naman et al., 2022). Additionally, the summer in Iceland (with a mean temperature of 6.5°C in Vopnafjörður in May-July 2020) with extended photoperiods as it rests just south of the Arctic circle (North 65°) (Bjornsson et al., 2007; Einarsson, 1899) is a crucial for to the growth of juvenile Atlantic salmon due to the peak in productivity and food availability (Elliott et al., 1998; Kreiling et al., 2021).

The aim of this study is to examine the trophic relationships of juvenile Atlantic salmon over time in Vesturdalsá by comparing properties of trophic interactions over years (1997 to 2020) and during the summer growth period (June to August). Reconstructed mass-abundance food webs are a useful way to representatives in the efficiency of the flow of energy through the an ecosystem (O'Gorman et al., 2019; Thompson et al., 2012; Woodward et al., 2021). They can also reveal inter-species trophic interactions of predators (like juvenile Atlantic salmon) and how these interactions impact the Atlantic salmon's growth and population over time (Naman et al., 2022; Olivier et al., 2019). We utilised multiple datasets of algae, macroinvertebrate, and juvenile salmonid populations during the summer. Our hypotheses are: 1) the salmonid-invertebrate predator-prey relationships will vary between years and along temperature gradients in Vesturdalsá, with higher productivity and prey availability in later years due to climate change (Constable et al., 2022; Lento et al., 2022; O'Gorman et al., 2016; Parmesan et al., 2023), and 2) food webs in Vesturdalsá changes over the summer period due to the increase in growth of macroinvertebrates and primary productivity with high

temperatures, affecting the prey choice and population of juvenile Atlantic salmon (Hannesdóttir et al., 2010; Kreiling et al., 2021; Kreivi et al., 1999; Saunders et al., 2018).

Materials and Methods:

Field data collection:

Two main datasets are analysed in this study, a time series over one summer, and a yearly series over several decades (described below). For the former, four repetitive sampling sessions (every three weeks) was conducted in three sites (A, B, and E, Figure 1), situated in Vesturdalsá from June to August of 2020 to monitor temporal changes over the summer in the freshwater food web. For the latter, data on the benthic macroinvertebrate and fish populations of two sites, situated upstream (E) and midstream (B), has been monitored consistently in late summer (3 week of August) every year. We had therefore used fish and macroinvertebrate population datasets from 1997 to 2020.

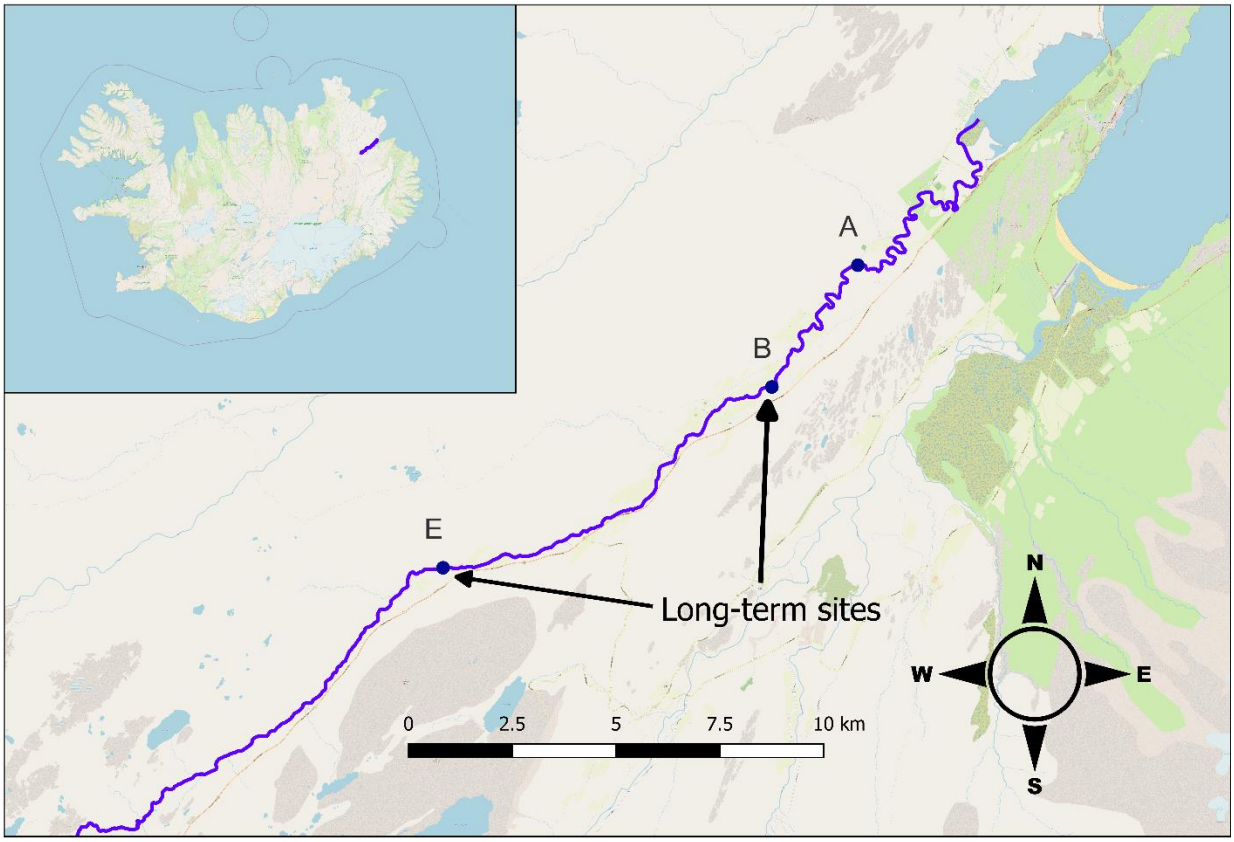

Figure 1: Map of sampling sites in Vesturdalsá, NE Iceland, the river drains to the lagoon and then into the Norwegian Sea (Map of Iceland with Vesturdalsá is shown in the top left). Site E is around 9 km from site B, and site B is around 3 km from site A. Site A was around 5km from the lagoon (Lai et al., 2024).

During the summer of 2020, the salmonid populations were sampled across these sites using single-pass electrofishing, where each fish was anesthetised, speciated, and measured in length (cm) and weight (g). The area electrofished was also measured to calculate a density index (individuals m^{-2}). Aging of fish populations were done using otoliths were extracted from at least five fish of each species for each site and sampling date. Gut contents of at least 25 juvenile salmonids were also collected at each site and sampling period through stomach flushing to estimate stomach content. Additionally, gut content samples of fish were also collected in previous years to get a rough percentage of each type of prey item consumed. All fish that were caught and not used for otolith sampling recovered and were released back to the catch site after processing.

We used the electrofishing density index estimate from late August (20-29th) 2020 as an estimate of true abundance of juvenile Atlantic salmon in the river over the summer period, because we conjecture that the catchability of fish from all size classes was highest due to the growth and size of young-of-the-year fish. The water flow was also more favourable during that sampling period. Furthermore, according to on-going tagging studies of juveniles in the river, the movement during the summer is very limited, and therefore, the in and out migration of juveniles at each sampling site is assumed to be limited and the density relatively stable through the study period (Bárðarson, n.d.). We used the age proportions of juveniles from the electrofishing surveys during field sampling to calculate the numbers of fish per each age classes at each site. We also had to estimate when age 0+ fish became a part of the river food web during our sampling period. We assumed spawning was on the 1st of November (Bárðarson et al., 2021, 2023) and estimated that the alevin will absorb the yolk sac and start actively feeding on 15th of July. This is based on using temperature measurements of the river and applying egg-development and growth equations published by CRISP (1981) and Gorodilov (1996). Thus, we added age 0+ Atlantic salmon to the density estimates for the late July sampling period and assumed that they did not migrate to another part of the river soon after emergence. We kept the observed juvenile Arctic charr densities from electrofishing surveys because it closely reflects the true abundance in the river. There is a higher catchability of Arctic charr in comparison to Atlantic salmon due to the difference in habitat preferences that allow Arctic charr to be more easily caught with electrofishing (Heggberget, 1984; Heggenes & Saltveit, 2007), and the data also supports the known behavioural patterns and habitat preferences of Arctic charr (Johnson, 1980; Jonsson & Antonsson, 2005). The juvenile Arctic charr in the river represented a small proportion (~9%) of the total salmonids in the river (Bárðarson et al., 2023).

The benthic macroinvertebrate community was sampled over the same four timepoints in the summer of 2020 with stone scrapes. At each site, 10 stones were randomly picked along a 15 m transect in the river. Each stone was scrubbed and the surface organisms on the stones were collected. The outline of each stone was traced to calculate the surface area for density index calculations (individuals m^{-2}). We collected drift net samples (48 × 33 cm with 363 µm mesh size) of drifting macroinvertebrates for five minutes at two locations along the transect at each site. Velocity (m/s) was measured at each net placement using a YSI© Sontek Flowtracker Handheld Acoustic Doppler Velocimeter (Ohio, USA). All macroinvertebrate samples were preserved in 70% ethanol solution. Additional samples of invertebrates collected using stone scrapes at each site were preserved using formaldehyde to build trophic links between invertebrates and diatoms for constructing the food web.

Benthic algae were sampled using stone scrapes as well for each site and sampling time. Three stones were again randomly selected in the transect for processing and algae were scraped off from within three quadrats (805 mm^2) from each stone. Two of the algae samples were preserved using Lugol and other with formaldehyde for diatom identification. Algae concentrations (µg cm^{-2}) of cyanobacteria, diatoms, and green algae were additionally measured from 10 stones at each site and sampling period using a BenthoTorch (bbe Moldaenke, GmbH, Germany).

Lab processing:

Diatoms from algae scrape samples were identified to the genus level (Spaulding et al., 2021) and was counted under a microscope to get a density index (individuals m^{-2}) of the diatom community. Sizes of diatoms were measured in Image J (Schneider et al., 2012) and biomass was estimated using biovolume equations taken from Hillebrand et al. (1999).

Macroinvertebrate samples taken using stone scrapes and drift nets were counted and sorted to family level or higher, and terrestrial invertebrates were separately categorised. Gut content collected from salmonids were also similarly identified and processed. Head width and body length of macroinvertebrates and prey items were also measured to the nearest millimetre to estimate biomass using length-mass regression relationships from published literature (Baumgärtner & Rothhaupt, 2003; Benke et al., 1999; Burgherr & Meyer, 1997; Kang & Kang, 1997; O'Gorman & Emmerson, 2010; Ramsay et al., 1997).

Statistical analysis:

Due to contaminated samples of benthic invertebrates taken using stone scrapes in site B in August, we used the average individual biomass data from the corresponding surber sampling taken at the same site and time (Lai et al., 2024) and further, used the average densities of benthic invertebrate samples taken from stone scrapes described in previous years (1997-2019) for food web reconstruction (summary of data used can be seen in Table S1). Note importantly that sampling by stone scrapes and surbers yield some differences in biomasses of Chironomidae (Diptera) and Oligochaeta, which tend to be lower using the former sampling method, thus the biomass estimate of macroinvertebrates in site B in August may be higher than depicted (Table S2). Densities (D; individuals m^{-2}) of juvenile salmonids and benthic invertebrates were also estimated, and population biomass (B) of invertebrates (mg m^{-2}) and juvenile salmonids (g m^{-2}) were also calculated using: $B = M \times D$, where M is mean individual body mass. Densities (individuals m^{-3}) and population biomasses (mg m^{-3}) of drifting invertebrates were also calculated using the same methodology.

All statistical analysis and food webs were analysed and created using R (R Core Team, 2023). Food webs of each year and sampling period during the summer of 2020 were created with their respective averages of population abundances and individual biomasses of each

taxonomic group using the *cheddar* package (Hudson et al., 2013). Biomasses of individuals for invertebrates were not measured for all years, therefore the biomasses taken from the August 2020 invertebrate dataset was used instead for previous years. Trophic links were inferred from gut content data and from published literature (Bouchard, 2004; Di Sabatino et al., 2000; Proctor & Pritchard, 1989). Food web properties were also calculated using the linear-regressions of $\log_{10}$-transformed individual biomass against $\log_{10}$-transformed average abundance (or the M-N relationship) of taxonomic group as 'nodes' for each sampling time and year using *cheddar*. The slope of the M-N relationship, mean trophic level, connectance, mean link angle, and mean chain length were extracted to describe the overall food web and the interspecific relationships. The slope of the M-N relationship, mean chain length, and mean link angle of juvenile Atlantic salmon were also measured as they can reveal changes in the trophic relationship that juvenile Atlantic salmon have with their prey over time or between sites.

M-N relationships of food webs were compared over time (including years and over the summer of 2020) and average summer water temperature using Linear Mixed Effects (LME) models from the *lmerTest* package (Bates et al., 2015; Kuznetsova et al., 2017) and Analysis of Covariance (ANCOVA). 'Nodes' were included as a random effect in the LME model (O'Gorman et al., 2017). Post-hoc Tukey tests were used to further compare between years and sampling times. Average summer water temperatures (°C) of the Vesturdalsá were taken from water temperature measurements from the Marine and Freshwater Research Institute and their published reports (Bárðarson et al., 2023). Trophic properties from predator-prey relationship in 2000 and 2013 were excluded from the temperature comparisons as summer water temperature data were missing for those years. Food web properties were additionally compared over time using linear or polynomial models. Best-fit models were selected using likelihood

ratio tests. Furthermore, we compared the density and population biomasses of benthic and drifting invertebrates, individual salmonid biomass, and algae concentrations between sampling periods during the summer of 2020 using Kruskal-Wallis tests. Post-hoc Dunn tests were used for pair-wise comparisons between sampling times. Abundance and biomass of gut content of juvenile Atlantic salmon and Arctic charr were also compared between sampling times. The statistical significance was set at 5% level. P-values from post-hoc analyses were adjusted with Bonferroni corrections.

Results:

Temporal Resemblance and Variations in Trophic Relationships in River Vesturdalsá from 1997-2020

Although the M-N relationships were not significantly different between years ($F_{(22,214)}$=1.17, p=0.279), the $\log_{10}$ abundances of invertebrate and fish species varied significantly different ($F_{(22,214)}$=2.91, p<0.001, Figure 2). Post-hoc Dunn testing showed that species abundance in 2017 was significantly higher than that of earlier years including 1998 (p<0.01), 2008 (p<0.05), 2010 (p<0.01), and 2013 (p<0.001). Species abundance in 1997 was also higher than that in 1998 (p<0.05), 2010 (p<0.05), and 2013 (p<0.01). Additionally, there was also no significant relationship between the M-N relationship and mean water temperature each summer (SE=0.00564, t=-0.681, p=0.497).

Interestingly, some of the properties of trophic relationships (Table S6 and S7) varied over years as shown in Figure 3. The slope, mean trophic level, connectance, and mean link angle of the M-N relationship showed no significant relationship with years. The mean chain length decreased significantly over time (R^2=0.145, p<0.05). On the other hand, the slope

(R^2=0.295, p<0.01) and mean link angle (R^2=0.273, p<0.01) for Atlantic salmon trophic relationships increased significantly since 1997. Comparisons of food web properties with average water temperature showed that mean link angle (R^2=0.312, p<0.05; Figure 4h) of Atlantic salmon trophic relationships associated significantly with temperature, as a second-order polynomial curve. Figure 4a may indicate a second-order polynomial regression between the slope of the M-N relationship and temperature but was on the cusp of significance (R^2=0.153, p=0.0866). In sum, most food web properties in Vesturdalsá do not change significantly with water temperature or over this 23-year study period.

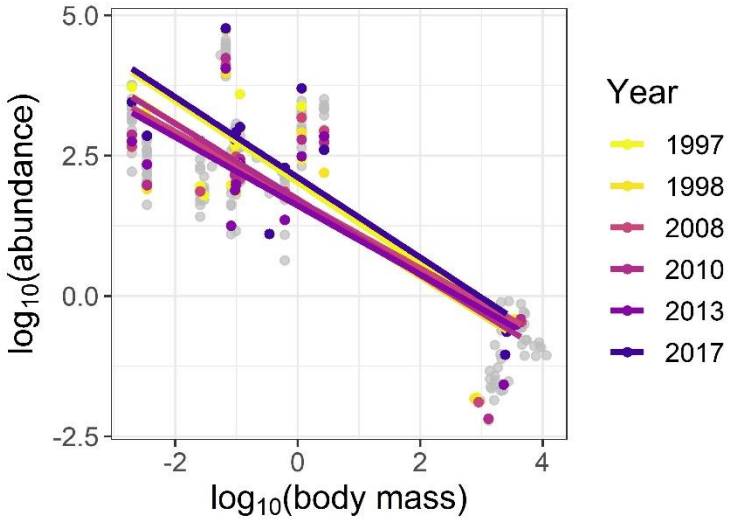

Figure 2: Linear regressions of significantly different species abundance of log-log M-N trophic relationship in 1997, 1998, 2008, 2010, 2013, and 2017 in Vesturdalsá. The greyed-out points are of non-significantly different M-N relationships (Table S3).

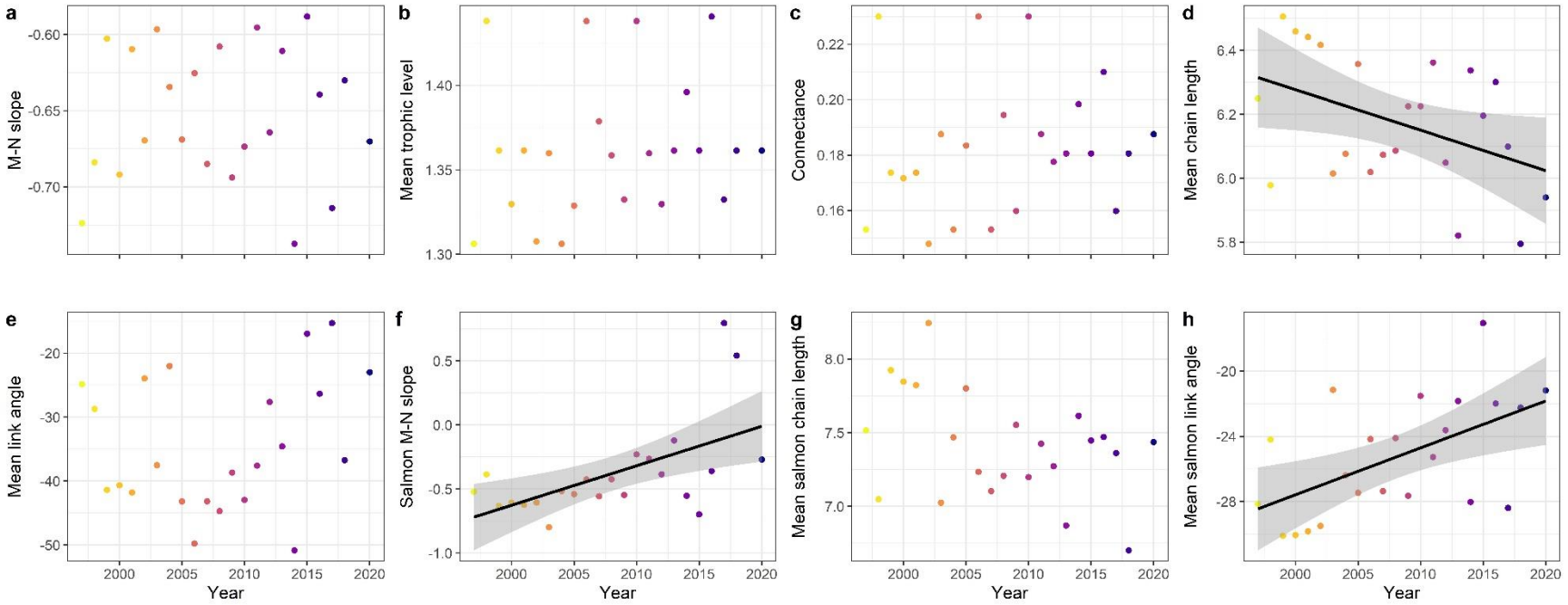

Figure 3: Changes in several aspects of the reconstructed food web properties in Vesturdalsá from 1997 to 2020. Shown are the estimates per year, with significant linear regressions of the d) mean chain length, and linear regressions of the f) slope and h) mean link angle of Atlantic salmon trophic relationships over the 23 years (Table S6).

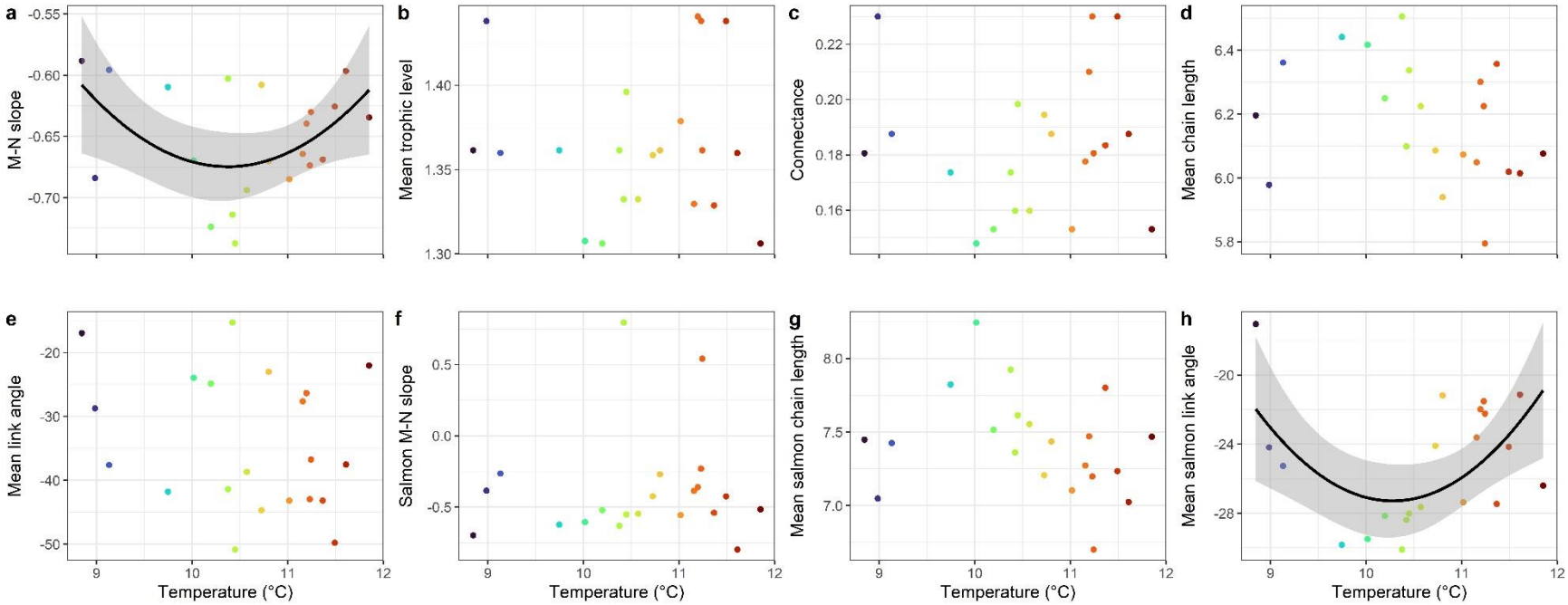

Figure 4: Temperature associated changes in several aspects of the reconstructed food web in Vesturdalsá. Depicted are the estimates for each year (1997 to 2020) and a) close-to-significant polynomial regressions of the slope and of overall trophic relationships and h) significant polynomial regressions of the mean link angle of Atlantic salmon trophic relationships across average summer water temperatures (°C) (Table S7).

Changes in Food Webs of Vesturdalsá During the Summer 2020

Next, we estimated food webs for the high productivity season, June to August, with data from the summer of 2020. The LME model showed that the M-N relationships in Vesturdalsá were not significantly different between sampling times ($F_{(3,69)}$=1.78, p=0.159), but abundances of species were found to be significantly different over time ($F_{(3,69)}$=6.68, p<0.001; Figure 5). Post hoc tests showed that the abundance of species in early July were the lowest during the summer (Table S10). Additionally, linear models of food web properties over time showed no significant relationships, indicating very similar food web structures during this summer period (Table S11). The possible exceptions being that the mean link angle of the whole food web (p=0.073) decreased over time, and the mean chain length of Atlantic salmon trophic relationships (p=0.084) increased over time, but neither of these relationships were significant with alpha = 0.05.

Detailed in-depth analysis agreed. There were significant differences in the abundance and biomass of each trophic level over time during the summer. Kruskal-Wallis tests showed that the concentrations of cyanobacteria (χ^2=30.9, df=3, p<0.001) and diatom (χ^2=72.8, df=3, p<0.001) were significantly higher in August (Figure 6b). The diatom concentration was also significantly higher in late July than in early July (p<0.05). On the other hand, most densities and population biomasses of benthic invertebrates did not differ significantly over the summer (Figure 6c), except for simuliids (χ^2=8.66, df=3, p<0.05) and chironomids (χ^2=12.4, df=3, p<0.01). Simuliidae (Diptera) densities were significantly higher in August than in early July (p<0.05), whereas population biomass of Chironomidae were significantly lower in August relative to early July (p<0.05). The population biomass of Chironomidae in early and late July was also found close to be significantly different (p=0.0510). Correspondingly to the results of benthic invertebrate populations, the abundance and biomass of drifting invertebrate mostly did not differ over time,

shown in Figure 6d. Additionally, only the abundance (χ^2=9.86, df=3, $p<0.05$) and total biomass (χ^2=11.3, df=3, $p<0.05$) of drifting chironomids differed over time, with a higher abundance and biomass of chironomids in late July than in August. Terrestrial inputs did not differ over the summer. Thus, the benthic and drifting invertebrate community composition in the river was very similar over the summer.

Therefore, the gut contents of juvenile salmonids varied little over time. Both salmonid species consumed mostly chironomids during the summer period. Only the total abundance (χ^2=48.7, df=3, $p<0.001$) and biomass (χ^2=56.4, df=3, $p<0.001$) of Chironomidae eaten by juvenile Atlantic salmon varied over time (Figure 6e). Juveniles consumed the lowest abundance and biomass of chironomids during August. Additionally, the abundance of chironomids consumed was lower in June than in early July ($p<0.01$) and the biomass consumed was lower in late July than early July ($p<0.05$). The amount of terrestrial resources consumed by juvenile Atlantic salmon did not differ over time. On the other hand, the total biomass of Simuliidae consumed by juvenile Atlantic salmon varied over time (χ^2=16.3, df=3, $p<0.001$), with significantly lower total biomass of simuliids consumed in late July than June ($p<0.05$) and early July ($p<0.01$). On the other hand, the amount of prey consumed by juvenile Arctic charr did not vary during the summer. The abundance of salmonids was found to be similar over time, with juvenile Atlantic salmon making up most of the salmonid population at 55.9 ± 38.9 individuals/100m^2, whereas juvenile charr had 2.08 ± 1.71 individuals/100m^2 (Figure 6f). Abundance of salmonids were the lowest in early July. The average mass of Atlantic salmon was also significantly higher in early July and late July (χ^2=49.8, df=3, $p<0.001$), whereas the average mass of Arctic charr was the lowest in August (χ^2=15.0, df=3, $p<0.01$).

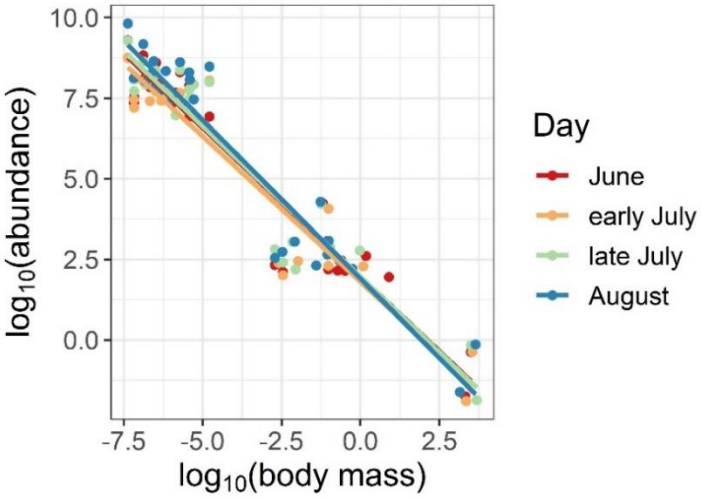

Figure 5: Linear regressions of log-log M-N food webs did not vary significantly in different sampling days in Vesturdalsá (Table S9 and S10).

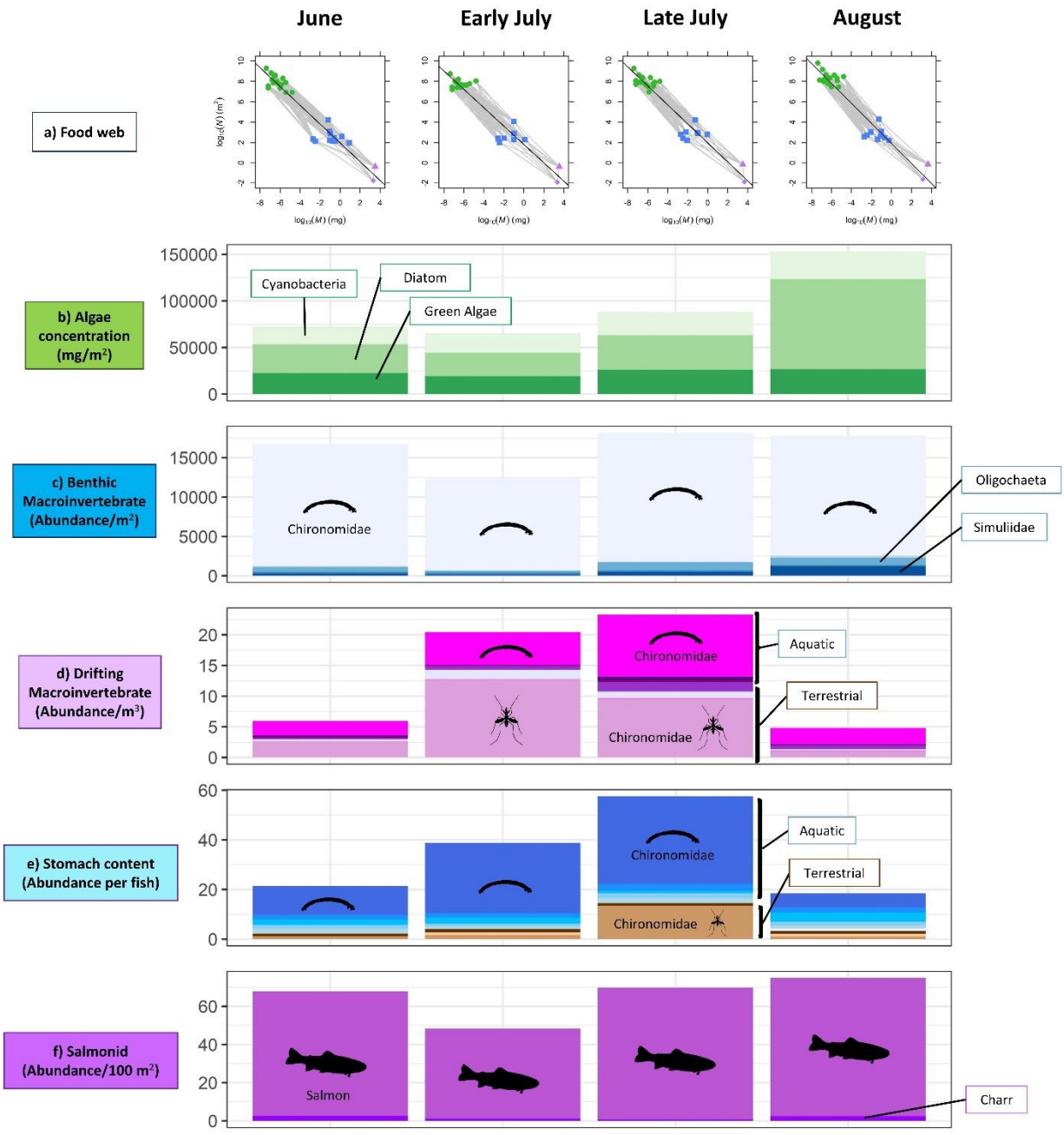

Figure 6: Comparison of food webs, populations, and stomach content of juvenile Atlantic salmon over the summer period in Vesturdalsá. a) Linear regressions of log-log M-N trivariate food webs across sampling periods in Vesturdalsá (green circles ●: primary producers, blue squares ■: invertebrates, purple triangle ▲: juvenile Atlantic salmon, purple diamonds ◆: juvenile Arctic charr). Bar plots of average b) algae concentrations (µg) per m^2, c) abundance of benthic invertebrates per m^2, d) abundance of drifting invertebrates per m^3, e) abundance of prey items found in the stomachs of juvenile Atlantic salmon, f) abundance of juvenile salmonids per 100 m^2.

Discussion:

Relatively few studies have investigated changes in freshwater food webs and trophic relationships over time (Mellard et al., 2021; Olivier et al., 2019), and even fewer have specifically looked at Atlantic salmon (Weber et al., 2017). This study on the changes in trophic interactions over time in Vesturdalsá shows how a sub-Arctic low-productivity river with a simple food web varies little in structure over the study period, both the summer months and a 23-year window. More importantly, it shows how monitoring of trophic interactions over time could give insight to how environmental variables may affect the food availability of salmonids across a community-scale.

IPCC reports have shown that mean temperatures in in northern Europe, including Iceland, have increased ~0.4°C per decade since 1980 and is projected to continue doing so and at a faster rate under current warming scenarios (Bednar-Friedl et al., 2022; Constable et al., 2022). Although the water temperatures in Vesturdalsá have not been increasing over time, water temperatures have been shown to highly fluctuate especially during the summer months (Bárðarson et al., 2023), which will likely fluctuate more over time due to climate change (Bednar-Friedl et al., 2022). The results showed that the predator-prey trophic relationships in Vesturdalsá are similar over the 23-year period, which did not support our first hypothesis. The changes observed over the years do not seem be completely driven by changes in temperature, as the changes in the mean chain length over years did not vary with water temperature. However, the mean chain length, which is the average of orders of magnitude of difference in body mass and population density between consumers and resources (Cohen et al., 2009), decreased towards the present, which may be due increasing temperature variability and changing resource availability (Doi et al., 2009; Hette-Tronquart et al., 2013). Changes in temperature can affect the population of benthic invertebrates with increases in abundance of

large, slow-growing invertebrates and decreases in productivity of small, fast-growing invertebrates (Nelson et al., 2017), thereby affecting prey available to salmonids in rivers. Years with cold summers have shorter mean chain lengths and years with an average water temperature of around 10°C have longer chain lengths, which follows patterns was found in the Hengill river system in Iceland, where food chains lengthened with warmer temperatures (Woodward et al., 2010). However, in this study of Vesturdalsá, the mean chain length decreases between 10 and 11°C. Therefore, consumers have more resources available with increasing temperatures but when temperatures reach a certain tipping point, resources start depleting, which was more similarly reflected in temperate regions (Arim et al., 2007; Petchey et al., 1999). Furthermore, the mean link angle of Atlantic salmon trophic relationships increased over time and as mean water temperatures increased above 10°C in Vesturdalsá. This was most likely reflecting the decrease in amount of prey resources for each salmonid consumer when temperature increases the period, and therefore leading to the observed decrease in mean chain length. The slope of M-N relationships of Atlantic salmon trophic relationships also became shallower (less negative) over time, which showed that the rate of biomass depletion was decreasing over time. But this does not seem to vary significantly with temperature, so there may be other drivers causing the rate of biomass depletion to decrease over time. Factors other than temperature could also drive the changes we saw in trophic relationships, such as changes in habitat (Albertson et al., 2018; Dineen et al., 2007) and primary productivity (Shurin et al., 2012). The predator-prey relationships were mostly structurally stable over time, as the freshwater species community did not vary much over these years. But there was a decrease in mean chain length and increase in mean link angle over time in the Vesturdalsá system, which showed that there were likely already decreases, albeit little, in prey availability for salmonids over time even with just a small increase in mean water temperature of Vesturdalsá due to climate change. The observed changes in food web metrics from 1997 to 2020 suggests that

resource availability for Atlantic salmon could further decrease in Vesturdalsá due to climate change especially with increasing fluctuations in temperatures.

Furthermore, food web changes over the summer period were more prominent revealing the importance of the summer season in the growth of juvenile Atlantic salmon in Vesturdalsá, which supports our second hypothesis. A peak in productivity was observed during late summer (late July and August), with the macroinvertebrate and salmonid community having access to a high amount of resources before temperature drops for the winter. Although the overall M-N relationships of the food web does not vary over the summer, we can observe a grazing cycle in the growth of primary producers from late July and a subsequent increase in the abundance of freshwater organisms later in the summer. But we did not observe any grazer impact on the primary producers in our study, as both invertebrates and algae populations were high in August. Populations of most invertebrates varied little during the summer, except for the Chironomidae populations, where benthic and drifting chironomids were the most abundant invertebrates (Friberg et al., 2009; Kreiling et al., 2021; Lai et al., 2024) and was the highest in population during late July and decreased in August. Densities of simuliids had also increased in August. This change in population of chironomids and simuliids is most likely due to the seasonal change in benthic algae production that was observed during the summer in these cold Icelandic rivers (Gíslason & Gardarsson, 2010). Stomach contents of juvenile salmonids also did not vary over time the summer, with only the amount of chironomids and simuliids consumed varying over time, where more chironomids and less simuliids were eaten during late summer. Juvenile salmonids were also mostly eating chironomids during the summer, especially in late summer (Antonsson, 2015; Kreiling et al., 2021; Lai et al., 2024), which further emphasises the importance of the production of chironomids as juvenile Atlantic salmon main food source in low-productivity rivers in the sub-Arctic (Erkinaro & Erkinaro, 1998).

Fluctuations in food availability during the summer period, is crucial to the growth and development of juvenile Atlantic salmon populations (Elliott et al., 1998). Feeding during the late spring and summer season have been shown to contribute to most of the growth during the juvenile phase of an Atlantic salmon´s life cycle (Bacon et al., 2005; Jones et al., 2002). The abundance of salmonids did not vary much over the summer, but the structure of the age class varied, with higher average individual weight across all year classes of Atlantic salmon in July and decreases in August. Similarly for Arctic charr, there was a decrease in average mass in August, which was mainly due to the emergence of 0+ salmonids into the river and the emigration of smolting juveniles.

The food web properties were very similar over time and only the mean link angle of the M-N relationship of the food web decreased over the summer and vice versa for the mean chain length of Atlantic salmon trophic relationships, which reflected the changes in river productivity seasonally (Kreiling et al., 2021; Robinson et al., 2021). The mean chain length was the highest in the late summer, whereas the mean link angle of the food web was the lowest. This is consistent with our findings that the prey availability and abundance was the highest in late summer starting in late July, which is a crucial period of growth for juvenile Atlantic salmon. Thompson & Townsend (1999) also observed similar seasonal changes in food web attributes, with the increase in mean chain length during late summer/autumn period of rivers in New Zealand.

Thus, to summarise, Vesturdalsá is a simple system that have not undergone large structural changes in predator-prey relationships over time but is showing worrying signs of decreases in resource availability, and experiences large productivity cycles during the summer. The river productivity during the late summer period vastly contributes to the growth of juvenile salmonid population in Vesturdalsá. Climate change with further warming and increasing

fluctuations in temperature can cause juvenile Atlantic salmon to rely on little available prey items and choices, which can create further negative impacts on the whole ecosystem level (O'Gorman et al., 2023; Woodward et al., 2010). Vesturdalsá has experienced little changes in food web structure for the last 20 years due to its simplistic food web structure in comparison to other more productive and species-rich systems (Closs & Lake, 1994; Warren, 1989), but have shown its lack of flexibility and will become increasingly vulnerable without proper sustainable management that helps increase the Atlantic salmon population´s ability to adapt to climate change (Perkins et al., 2010; Woodward et al., 2010). This also highlights the potential vulnerability of other similar sub-Arctic, low-productivity salmonid streams due to future warming.

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References:

Albertson, L. K., Ouellet, V., & Daniels, M. D. (2018). Impacts of stream riparian buffer land use on water temperature and food availability for fish. *Journal of Freshwater Ecology*, *33*(1), 195–210. https://doi.org/10.1080/02705060.2017.1422558

Antonsson, T. (2015). Fæða laxa- urriða- og bleikjuseiða: Gögn úr Vesturdalsá, Hofsá og Selá í Vopnafirði og úr Elliðaám og Leirvogsá við Faxaflóa. In *Veiðimálastofnun*. https://www.hafogvatn.is/static/research/files/faeda_laxa.pdf

Arim, M., Bozinovic, F., & A. Marquet, P. (2007). On the relationship between trophic position, body mass and temperature: Reformulating the energy limitation hypothesis. *Oikos*, *116*(9), 1524–1530. https://doi.org/10.1111/j.0030-1299.2007.15768.x

Bacon, P. J., Gurney, W. S. C., Jones, W., Mclaren, I. S., & Youngson, A. F. (2005). Seasonal growth patterns of wild juvenile fish: Partitioning variation among explanatory variables, based on individual growth trajectories of Atlantic salmon (Salmo salar) parr. *Journal of Animal Ecology*, *74*(1), 1–11. https://doi.org/10.1111/j.1365-2656.2004.00875.x

Bárðarson, H. (n.d.). *Tagging data from River Vesturdalsá, Iceland*.

Bárðarson, H., Helgason, S. Ó., & Njarðardóttir, E. (2023). *Research on fish stocks in several rivers at North-East Iceland 2022*.

Bárðarson, H., Helgason, S. Ó., Njarðardóttir, E., & Árnason, F. (2021). *Research on fish stocks in several rivers at North-East Iceland 2020*. https://www.hafogvatn.is/static/research/files/hv2021-18.pdf

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects

models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Baumgärtner, D., & Rothhaupt, K. O. (2003). Predictive Length-Dry Mass Regressions for Freshwater Invertebrates in a Pre-Alpine Lake Littoral. *International Review of Hydrobiology*, *88*(5), 453–463. https://doi.org/10.1002/iroh.200310632

Bednar-Friedl, B., Biesbroek, R., Schmidt, D. N., Alexander, P., Børsheim, K. Y., Carnicer, J., Georgopoulou, E., Haasnoot, M., Cozannet, G. Le, Lionello, P., Lipka, O., Möllmann, C., Muccione, V., Mustonen, T., Piepenburg, D., & Whitmarsh, L. (2022). Europe. In: Climate Change 2022: Impacts, Adaptation and Vulnerability. In *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. https://doi.org/10.1017/9781009325844.015

Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, *18*(3), 308–343. https://doi.org/10.2307/1468447

Bjornsson, H., Jonsson, T., Gylfadottir, S. S., & Olason, E. O. (2007). Mapping the annual cycle of temperature in Iceland. *Meteorologische Zeitschrift*, *16*(1), 45–56. https://doi.org/10.1127/0941-2948/2007/0175

Bouchard, R. W. (2004). *Guide to Aquatic Invertebrate Families of Mongolia. Identification Manual for Students, Citizen Monitors, and Aquatic Resource Professionals*.

Burgherr, P., & Meyer, E. I. (1997). Regression analysis of linear body dimensions vs. dry mass

in stream macroinvertebrates. *Archiv Fur Hydrobiologie*, *139*(1), 101–112. https://doi.org/10.1127/archiv-hydrobiol/139/1997/101

Closs, G. P., & Lake, P. S. (1994). Spatial and Temporal Variation in the Structure of an Intermittent-Stream Food Web. *Ecological Monographs*, *64*(1), 1–21. https://doi.org/10.2307/2937053

Cohen, J. E., Schittler, D. N., Raffaelli, D. G., & Reuman, D. C. (2009). Food webs are more than the sum of their tritrophic parts. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(52), 22335–22340. https://doi.org/10.1073/pnas.0910582106

Constable, A. J., Harper, S., Dawson, J., Holsman, K., Mustonen, T., Piepenburg, D., & Rost, B. (2022). Cross-Chapter Paper 6: Polar Regions. In *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. https://doi.org/10.1017/9781009325844.023.2319

CRISP, D. T. (1981). A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. *Freshwater Biology*, *11*(4), 361–368. https://doi.org/10.1111/j.1365-2427.1981.tb01267.x

Di Sabatino, A., Gerecke, R., & Martin, P. (2000). The biology and ecology of lotic water mites (Hydrachnidia). *Freshwater Biology*, *44*(1), 47–62. https://doi.org/10.1046/j.1365-2427.2000.00591.x

Dineen, G., Harrison, S. S. C., & Giller, P. S. (2007). Diet partitioning in sympatric Atlantic salmon and brown trout in streams with contrasting riparian vegetation. *Journal of Fish*

Biology, *71*, 17–38. https://doi.org/10.1111/j.1095-8649.2007.01441.x

Doi, H., Chang, K. H., Ando, T., Ninomiya, I., Imai, H., & Nakano, S. I. (2009). Resource availability and ecosystem size predict food-chain length in pond ecosystems. *Oikos*, *118*(1), 138–144. https://doi.org/10.1111/j.1600-0706.2008.17171.x

Durance, I., & Ormerod, S. J. (2007). Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology*, *13*(5), 942–957. https://doi.org/10.1111/j.1365-2486.2007.01340.x

Einarsson, M. Á. (1899). Climate of Iceland. *Quarterly Journal of the Royal Meteorological Society*, *25*(110), 175–177. https://doi.org/10.1002/qj.49702511010

Elliott, S. R., Coe, T. A., Helfield, J. M., & Naiman, R. J. (1998). Spatial variation in environmental characteristics of Atlantic salmon (*Salmo salar*) rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(SUPPL.1), 267–280. https://doi.org/10.1139/d98-001

Erkinaro, H., & Erkinaro, J. (1998). Feeding of Atlantic salmon, *Salmo salar L.*, parr in the subarctic River Teno and three tributaries in northernmost Finland. *Ecology of Freshwater Fish*, *7*(1), 13–24. https://doi.org/10.1111/j.1600-0633.1998.tb00168.x

Ficke, A. D., Myrick, C. A., & Hansen, L. J. (2007). Potential impacts of global climate change on freshwater fisheries. In *Reviews in Fish Biology and Fisheries* (Vol. 17, Issue 4). https://doi.org/10.1007/s11160-007-9059-5

Ford, J. S., & Myers, R. A. (2008). A global assessment of salmon aquaculture impacts on wild salmonids. *PLoS Biology*, *6*(2), 0411–0417. https://doi.org/10.1371/journal.pbio.0060033

Forseth, T., Barlaup, B. T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., Hindar, A., Mo, T. A., Rikardsen, A. H., Thorstad, E. B., Vøllestad, L. A., & Wennevik, V. (2017). The major threats to Atlantic salmon in Norway. In *ICES Journal of Marine Science* (Vol. 74, Issue 6). https://doi.org/10.1093/icesjms/fsx020

Friberg, N., DybkjÆr, J. B., Olafsson, J. S., Gislason, G. M., Larsen, Sø. E., & Lauridsen, T. L. (2009). Relationships between structure and function in streams contrasting in temperature. *Freshwater Biology*, *54*(10), 2051–2068. https://doi.org/10.1111/j.1365-2427.2009.02234.x

Gerwing, T. G., & Plate, E. (2019). Effectiveness of nutrient enhancement as a remediation or compensation strategy of salmonid fisheries in culturally oligotrophic lakes and streams in temperate climates. *Restoration Ecology*, *27*(2), 279–288. https://doi.org/10.1111/rec.12909

Gíslason, G. M., & Gardarsson, A. (2010). The production of chironomids and blackflies in a subarctic river. *Proc 15th International Symposium on Chironomidae*, 45–54. http://www.hi.is/~gmg/Serprent/Gislason-Gardarsson_2010_Produ_Chir_Blackflies_Proceedings_Chir.pdf

Gorodilov, Y. N. (1996). Description of the early ontogeny of the Atlantic salmon, Salmo salar, with a novel system of interval (state) identification. *Environmental Biology of Fishes*, *47*(2), 109–127. https://doi.org/10.1007/BF00005034

Gregory, S. D., Nevoux, M., Riley, W. D., Beaumont, W. R. C., Jeannot, N., Lauridsen, R. B., Marchand, F., Scott, L. J., & Roussel, J. M. (2017). Patterns on a parr: Drivers of long-term salmon parr length in U.K. and French rivers depend on geographical scale. *Freshwater Biology*, *62*(7), 1117–1129. https://doi.org/10.1111/fwb.12929

Guðbergsson, G. (2015). *Catch statistics for Atlantic salmon Arctic charr and brown trout in Icelandic rivers and lakes 2015*.

Hannesdóttir, E. R., Gíslason, G. M., & Ólafsson, J. S. (2010). Life cycles of Eukiefferiella claripennis (Lundbeck 1898) and Eukiefferiella minor (Edwards 1929) (Diptera: Chironomidae) in spring-fed streams of different temperatures with reference to climate change. *Fauna Norvegica*, *31*, 35–46. https://doi.org/10.5324/fn.v31i0.1367

Heggberget, T. G. (1984). Habitat selection and segregation of parr of Arctic charr (Salvelinus alpinus), brown trout, (Salmo trutta) and Atlantic salmon (Salmo salar L.) in two streams in north Norway. In L. Johnson & B. L. Burns (Eds.), *Biology of the Arctic Charr: Proceedings of the International Symposium on Arctic Charr* (pp. 217–231). Univ. Manitoba Press.

Heggenes, J., & Saltveit, S. J. (2007). Summer stream habitat partitioning by sympatric Arctic charr, Atlantic salmon and brown trout in two sub-arctic rivers. *Journal of Fish Biology*, *71*(4), 1069–1081. https://doi.org/10.1111/j.1095-8649.2007.01573.x

Hette-Tronquart, N., Roussel, J. M., Dumont, B., Archaimbault, V., Pont, D., Oberdorff, T., & Belliard, J. (2013). Variability of water temperature may influence food-chain length in temperate streams. *Hydrobiologia*, *718*(1), 159–172. https://doi.org/10.1007/s10750-013-1613-7

Hillebrand, H., Dürselen, C. D., Kirschtel, D., Pollingher, U., & Zohary, T. (1999). Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology*, *35*(2), 403–424. https://doi.org/10.1046/j.1529-8817.1999.3520403.x

Hrafnkelsson, B., Morris, J. S., & Baladandayuthapani, V. (2012). Spatial modeling of annual

minimum and maximum temperatures in Iceland. *Meteorology and Atmospheric Physics*, *116*(1–2), 43–61. https://doi.org/10.1007/s00703-010-0101-0

Hudson, L. N., Emerson, R., Jenkins, G. B., Layer, K., Ledger, M. E., Pichler, D. E., Thompson, M. S. A., O'Gorman, E. J., Woodward, G., & Reuman, D. C. (2013). Cheddar: Analysis and visualisation of ecological communities in R. *Methods in Ecology and Evolution*, *4*(1), 99–104. https://doi.org/10.1111/2041-210X.12005

ICES. (2023). Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*, *5*(41), 477. https://doi.org/https://doi.org/10.17895/ices.pub.22743713

Johnson, L. (1980). The arctic charr, Salvelinus alpinus. In E. K. Balon (Ed.), *Perspectives in Vertebrate Science* (Vol. 1, pp. 15–98). Dr. W. Junk, The Hague.

Jones, W., Gurney, W. S. C., Speirs, D. C., Bacon, P. J., & Youngson, A. F. (2002). Seasonal patterns of growth, expenditure and assimilation in juvenile Atlantic salmon. *Journal of Animal Ecology*, *71*(6), 916–924. https://doi.org/10.1046/j.1365-2656.2002.00679.x

Jonsson, I. R., & Antonsson, T. (2005). Emigration of age-1 Arctic charr, Salvelinus alpinus, into a brackish lagoon. *Environmental Biology of Fishes*, *74*(2), 195–200. https://doi.org/10.1007/s10641-005-7693-0

Kang, H.-K., & Kang, Y. J. (1997). Length and Weight Relationship of Acartia steueri(Copepoda: Calanoida) in ilkwang Bay, Korea. *Korean Journal of Fisheries and Aquatic Sciences*, *30*(5), 30(5), 906–908. https://www.koreascience.or.kr/article/JAKO199723607645201.page

Kreiling, A. K., O'Gorman, E. J., Pálsson, S., Benhaïm, D., Leblanc, C. A., Ólafsson, J. S., & Kristjánsson, B. K. (2021). Seasonal variation in the invertebrate community and diet of a

top fish predator in a thermally stable spring. *Hydrobiologia*, *848*(3), 531–545. https://doi.org/10.1007/s10750-020-04409-5

Kreivi, P., Muotka, T., Huusko, A., Mäki-Petäys, A., Huhta, A., & Meissner, K. (1999). Diel feeding periodicity, daily ration and prey selectivity in juvenile brown trout in a subarctic river. *Journal of Fish Biology*, *55*(3), 553–571. https://doi.org/10.1006/jfbi.1999.1018

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/JSS.V082.I13

Lai, S. Y., Pálsson, A., Guðbergsson, G., Jónsson, I. R., Ólafsson, J. S., & Bárðarson, H. (2024). The prey availability and diet of juvenile Atlantic salmon (Salmo salar L .) in low-productivity rivers in northern Europe. *Journal of Fish Biology*, 1–13. https://doi.org/10.1111/jfb.15757

Lento, J., Culp, J. M., Levenstein, B., Aroviita, J., Baturina, M. A., Bogan, D., Brittain, J. E., Chin, K., Christoffersen, K. S., Docherty, C., Friberg, N., Ingimarsson, F., Jacobsen, D., Lau, D. C. P., Loskutova, O. A., Milner, A., Mykrä, H., Novichkova, A. A., Ólafsson, J. S., … Goedkoop, W. (2022). Temperature and spatial connectivity drive patterns in freshwater macroinvertebrate diversity across the Arctic. *Freshwater Biology*, *67*(1), 159–175. https://doi.org/10.1111/fwb.13805

Mellard, J. P., Henden, J. A., Pedersen, Å. Ø., Marolla, F., Hamel, S., Yoccoz, N. G., & Ims, R. A. (2021). Food web approach for managing Arctic wildlife populations in an era of rapid environmental change. *Climate Research*, *86*, 163–178. https://doi.org/10.3354/cr01638

Ministry for the Environment, & The Icelandic Institute of Natural History. (2001). Biological diversity in Iceland - National Report to the Convention on Biological Diversity. In *Natural History*. https://www.cbd.int/doc/world/is/is-nr-01-en.pdf

Naman, S. M., White, S. M., Bellmore, J. R., McHugh, P. A., Kaylor, M. J., Baxter, C. V., Danehy, R. J., Naiman, R. J., & Puls, A. L. (2022). Food web perspectives and methods for riverine fish conservation. *Wiley Interdisciplinary Reviews: Water*, *9*(4), 1–21. https://doi.org/10.1002/wat2.1590

Nelson, D., Benstead, J. P., Huryn, A. D., Cross, W. F., Hood, J. M., Johnson, P. W., Junker, J. R., Gíslason, G. M., & Ólafsson, J. S. (2017). Shifts in community size structure drive temperature invariance of secondary production in a stream-warming experiment. *Ecology*, *98*(7), 1797–1806. https://doi.org/10.1002/ecy.1857

O'Gorman, E. J., & Emmerson, M. C. (2010). Manipulating Interaction Strengths and the Consequences for Trivariate Patterns in a Marine Food Web. *Advances in Ecological Research*, *42*(C), 301–419. https://doi.org/10.1016/B978-0-12-381363-3.00006-X

O'Gorman, E. J., Ólafsson, Ó. P., Demars, B. O. L., Friberg, N., Guðbergsson, G., Hannesdóttir, E. R., Jackson, M. C., Johansson, L. S., McLaughlin, Ó. B., Ólafsson, J. S., Woodward, G., & Gíslason, G. M. (2016). Temperature effects on fish production across a natural thermal gradient. *Global Change Biology*, *22*(9), 3206–3220. https://doi.org/10.1111/gcb.13233

O'Gorman, E. J., Petchey, O. L., Faulkner, K. J., Gallo, B., Gordon, T. A. C., Neto-Cerejeira, J., Ólafsson, J. S., Pichler, D. E., Thompson, M. S. A., & Woodward, G. (2019). A simple model predicts how warming simplifies wild food webs. *Nature Climate Change*, *9*(8), 611–616. https://doi.org/10.1038/s41558-019-0513-x

O'Gorman, E. J., Zhao, L., Kordas, R. L., Dudgeon, S., & Woodward, G. (2023). Warming indirectly simplifies food webs through effects on apex predators. *Nature Ecology & Evolution*, *7*(12), 1983–1992. https://doi.org/10.1038/s41559-023-02216-4

O'Gorman, E. J., Zhao, L., Pichler, D. E., Adams, G., Friberg, N., Rall, B. C., Seeney, A., Zhang, H., Reuman, D. C., & Woodward, G. (2017). Unexpected changes in community size structure in a natural warming experiment. *Nature Climate Change*, *7*(9), 659–663. https://doi.org/10.1038/nclimate3368

Olivier, P., Frelat, R., Bonsdorff, E., Kortsch, S., Kröncke, I., Möllmann, C., Neumann, H., Sell, A. F., & Nordström, M. C. (2019). Exploring the temporal variability of a food web using long-term biomonitoring data. *Ecography*, *42*(12), 2107–2121. https://doi.org/10.1111/ecog.04461

Orpwood, J. E., Griffiths, S. W., & Armstrong, J. D. (2006). Effects of food availability on temporal activity patterns and growth of Atlantic salmon. *Journal of Animal Ecology*, *75*(3), 677–685. https://doi.org/10.1111/j.1365-2656.2006.01088.x

Parmesan, C., Morecroft, M. D., Trisurat, Y., Adrian, R., Anshari, G. Z., Arneth, A., Gao, Q., Gonzalez, P., Harris, R., Price, J., Stevens, N., & Talukdar, G. H. (2023). Terrestrial and Freshwater Ecosystems and Their Services. In H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama (Eds.), *Climate Change 2022 – Impacts, Adaptation and Vulnerability* (pp. 197–378). Cambridge University Press. https://doi.org/10.1017/9781009325844.004

Perkins, D. M., Reiss, J., Yvon-Durocher, G., & Woodward, G. (2010). Global change and food webs in running waters. *Hydrobiologia*, *657*(1), 181–198. https://doi.org/10.1007/s10750-

009-0080-7

Petchey, O. L., McPhearson, P. T., Casey, T. M., & Morin, P. J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, *402*(6757), 69–72. https://doi.org/10.1038/47023

Proctor, H., & Pritchard, G. (1989). Neglected Predators: Water Mites (Acari:Parasitengona:Hydrachnellae) in Freshwater Communities. *Journal of the North American Benthological Society*, *8*(1), 100–111. https://doi.org/10.2307/1467406

R Core Team. (2023). R: A Language and Environment for Statistical Computing. In *R Foundation for Statistical Computing* (p. https://www.R-project.org). R Foundation for Statistical Computing,Vienna, Austria. http://www.r-project.org

Ramsay, P. M., Rundle, S. D., Attrill, M. J., Uttley, M. G., Williams, P. R., Elsmere, P. S., & Abada, A. (1997). A rapid method for estimating biomass size spectra of benthic metazoan communities. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(8), 1716–1724. https://doi.org/10.1139/cjfas-54-8-1716

Reist, J. D., Wrona, F. J., Prowse, T. D., Power, M., Dempson, J. B., King, J. R., & Beamish, R. J. (2006). An overview of effects of climate change on selected Arctic freshwater and anadromous fishes. *Ambio*, *35*(7), 381–387. https://doi.org/10.1579/0044-7447(2006)35[381:AOOEOC]2.0.CO;2

Riley, W. D., Pawson, M. G., Quayle, V., & Ives, M. J. (2009). The effects of stream canopy management on macroinvertebrate communities and juvenile salmonid production in a chalk stream. *Fisheries Management and Ecology*, *16*(2), 100–111. https://doi.org/10.1111/j.1365-2400.2008.00649.x

Rist, S. (1990). Viðauki I. Vatnasvið Íslands. In *Vatns er pörf* (pp. 203–234). Bókaútgáfa Menningarsjóðs.

Robinson, S. I., Mikola, J., Ovaskainen, O., & O'Gorman, E. J. (2021). Temperature effects on the temporal dynamics of a subarctic invertebrate community. *Journal of Animal Ecology*, *90*(5), 1217–1227. https://doi.org/10.1111/1365-2656.13448

Rolls, R. J., Hayden, B., & Kahilainen, K. K. (2017). Conceptualising the interactive effects of climate change and biological invasions on subarctic freshwater fish. *Ecology and Evolution*, *7*(12), 4109–4128. https://doi.org/10.1002/ece3.2982

Saunders, W. C., Bouwes, N., McHugh, P., & Jordan, C. E. (2018). A network model for primary production highlights linkages between salmonid populations and autochthonous resources. *Ecosphere*, *9*(3). https://doi.org/10.1002/ecs2.2131

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Shurin, J. B., Clasen, J. L., Greig, H. S., Kratina, P., & Thompson, P. L. (2012). Warming shifts top-down and bottom-up control of pond food web structure and function. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1605), 3008–3017. https://doi.org/10.1098/rstb.2012.0243

Spaulding, S. A., Potapova, M. G., Bishop, I. W., Lee, S. S., Gasperak, T. S., Jovanoska, E., Furey, P. C., & Edlund, M. B. (2021). Diatoms.org: supporting taxonomists, connecting communities. *Diatom Research*, *36*(4), 291–304. https://doi.org/10.1080/0269249X.2021.2006790

Svenning, M. A., Falkegård, M., Dempson, J. B., Power, M., Bårdsen, B. J., Guðbergsson, G.,

& Fauchald, P. (2022). Temporal changes in the relative abundance of anadromous Arctic charr, brown trout, and Atlantic salmon in northern Europe: Do they reflect changing climates? *Freshwater Biology*, *67*(1), 64–77. https://doi.org/10.1111/fwb.13693

Thompson, R. M., Dunne, J. A., & Woodward, G. (2012). Freshwater food webs: Towards a more fundamental understanding of biodiversity and community dynamics. *Freshwater Biology*, *57*(7), 1329–1341. https://doi.org/10.1111/j.1365-2427.2012.02808.x

Thompson, R. M., & Townsend, C. R. (1999). The Effect of Seasonal Variation on the Community Structure and Food-Web Attributes of Two Streams: Implications for Food-Web Science. *Oikos*, *87*(1), 75. https://doi.org/10.2307/3546998

Thorstad, E. B., Bliss, D., Breau, C., Damon-Randall, K., Sundt-Hansen, L. E., Hatfield, E. M. C., Horsburgh, G., Hansen, H., Maoiléidigh, N., Sheehan, T., & Sutton, S. G. (2021). Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(9), 2654–2665. https://doi.org/10.1002/aqc.3624

Thorstad, E. B., Bliss, D., Damon-Randall, K., Hatfield, E. M. C., Horsburgh, G., Hansen, H., Maoiléidigh, N. Ó., & Sutton, S. (2019). *Managing the Atlantic salmon in a rapidly changing environment - management challenges and possible responses* (Issue 19).

Warren, P. H. (1989). Spatial and Temporal Variation in the Structure of a Freshwater Food Web. *Oikos*, *55*(3), 299. https://doi.org/10.2307/3565588

Weber, N., Bouwes, N., & Jordan, C. (2017). Accounting for spatial and temporal variation in macroinvertebrate community abundances when measuring the food supply of stream salmonids. *Freshwater Science*, *36*(2), 364–376. https://doi.org/10.1086/692012

Woodward, G., Dybkjær, J. B., Ólafsson, J. S., Gíslason, G. M., Hannesdóttir, E. R., & Friberg, N. (2010). Sentinel systems on the razor's edge: Effects of warming on Arctic geothermal stream ecosystems. *Global Change Biology*, *16*(7), 1979–1991. https://doi.org/10.1111/j.1365-2486.2009.02052.x

Woodward, G., Morris, O., Barquín, J., Belgrano, A., Bull, C., de Eyto, E., Friberg, N., Guðbergsson, G., Layer-Dobra, K., Lauridsen, R. B., Lewis, H. M., McGinnity, P., Pawar, S., Rosindell, J., & O'Gorman, E. J. (2021). Using Food Webs and Metabolic Theory to Monitor, Model, and Manage Atlantic Salmon—A Keystone Species Under Threat. *Frontiers in Ecology and Evolution*, *9*(December), 1–10. https://doi.org/10.3389/fevo.2021.675261

Supporting Information

6. Data used within study

Table S1: Summary of data used for each food web reconstruction and analysis for each time point, with shaded areas representing data that was collected using the specified sampling method.

Data/sampling type	summer 1997-2019	June 2020	early July 2020	late July 2020	August 2020
algae scrape					
invertebrate stone scrape					using an average density from 1997-2019 as a substitute
invertebrate surber					only biomass estimates
invertebrate drift					
fish stomach pump					
fish electrofishing					

7. Comparison of benthic sampling methods

Table S2: Statistical output of comparison of log_{10} average individual biomasses of macroinvertebrates between different benthic sampling methods (stone scrapes and surbers) using Kruskal-Wallis tests from the August 2020 dataset. Summary tables are shown with X^2 values (chi-squared), DF values (degrees of freedom), and P values.

	X^2	DF	P value
Chironomidae	8.43	1	<0.01
Simuliidae	1.64	1	0.200
Oligochaeta	11.4	1	<0.001
Gastropoda	0.194	1	0.660

8. Change in average water temperature over years (1997-2020) in Vesturdalsá

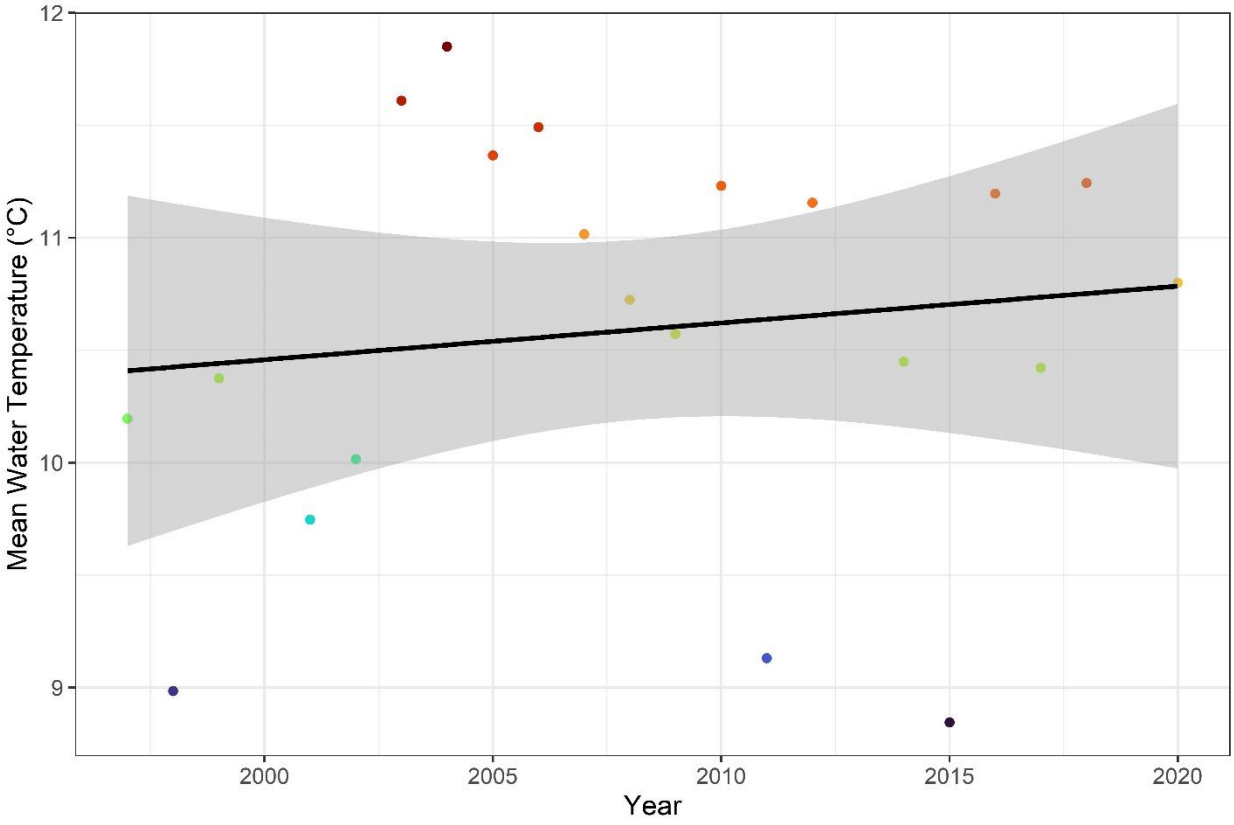

Figure S1: Average water temperature (°C) in Vesturdalsá from 1997 to 2020.

Table S3: Statistical output of linear models of average water temperature over years. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	Estimate	SE	t value	p value
Intercept	-22.3	57.3	-0.398	0.702
Year	0.0164	0.0285	0.574	0.573

9. Figure of predator prey relationships over years (1997-2020)

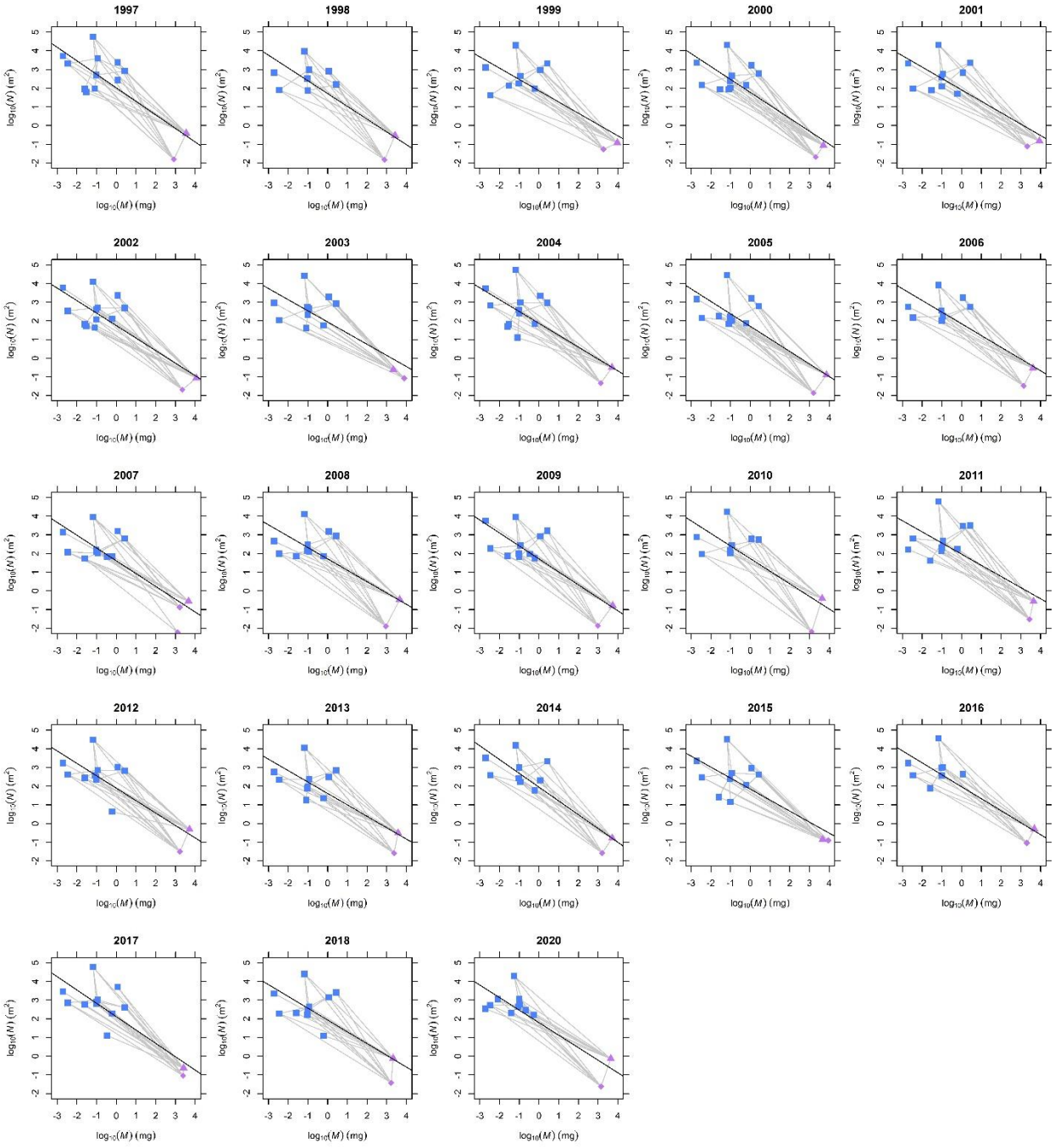

Figure S2: Log_{10} M-N predator-prey relationships from 1997 to 2018 and 2020 in Vesturdalsá (Blue squares ■: invertebrates, purple triangle ▲: juvenile Atlantic salmon, purple diamonds ◆: other salmonid species)

10. Comparison of predator-prey relationships over years

Table S4: Statistical output from ANOVA analysis of linear mixed effects model of predator-prey mass-abundance relationships between years. Log_{10}(species abundance) was the dependent variable and log_{10}(mass (g)) and year were considered fixed effects. Species identity was a random effect in the model. The summary table is shown with DF values (degree of freedom), F values, and P values. Post-hoc output of food web comparison between years in Vesturdalsá using pairwise comparisons and Tukey adjustments is attached as a separate excel file.

	DF	F value	p value
Intercept	1	51.9	<0.001
log_{10}(Mass)	1	4.39	<0.05
Year	22	2.91	<0.001
log_{10}(Mass) × Year	22	1.17	0.279

Table S5: Statistical output from linear mixed effects model of mass-abundance relationships in Vesturdalsá across the temperature gradient. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and average summer water temperature (°C) were fixed effects. 'Nodes' were a random effect in the model. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	Value	SE	t-value	p value
Intercept	1.70	0.386	4.40	0.000
log_{10}(Mass)	-0.252	0.175	-1.44	0.151
Temperature	0.0110	0.0280	0.394	0.694
log_{10}(Mass) × Temperature	0.000514	0.0142	0.036	0.971

Table S6: Properties of estimated predator -prey relationships in the food web, over years the study period (1997-2020) in Vesturdalsá.

Year	M-N slope	mean trophic level	Connectance	Mean chain length	Mean link angle	Salmon M-N slope	Mean salmon chain length	Mean salmon link angle
1997	-0.724	1.306	0.153	6.250	-24.838	-0.520	7.515	-28.151
1998	-0.684	1.438	0.230	5.978	-28.715	-0.385	7.049	-24.189
1999	-0.603	1.361	0.174	6.506	-41.391	-0.632	7.924	-30.095
2000	-0.692	1.330	0.172	6.459	-40.654	-0.606	7.845	-30.057
2001	-0.610	1.361	0.174	6.442	-41.773	-0.623	7.823	-29.824
2002	-0.670	1.308	0.148	6.417	-23.945	-0.605	8.243	-29.491
2003	-0.597	1.360	0.188	6.014	-37.518	-0.797	7.025	-21.140
2004	-0.634	1.306	0.153	6.076	-22.008	-0.516	7.468	-26.397
2005	-0.669	1.329	0.183	6.357	-43.167	-0.539	7.801	-27.463
2006	-0.625	1.438	0.230	6.020	-49.765	-0.424	7.234	-24.162
2007	-0.685	1.379	0.153	6.073	-43.163	-0.556	7.103	-27.360
2008	-0.608	1.359	0.194	6.086	-44.692	-0.424	7.207	-24.099
2009	-0.694	1.332	0.160	6.225	-38.670	-0.546	7.553	-27.637
2010	-0.674	1.438	0.230	6.225	-42.970	-0.230	7.198	-21.515
2011	-0.595	1.360	0.188	6.362	-37.581	-0.264	7.424	-25.268
2012	-0.664	1.330	0.178	6.049	-27.640	-0.385	7.272	-23.621
2013	-0.611	1.361	0.181	5.821	-34.581	-0.120	6.870	-21.836
2014	-0.737	1.396	0.198	6.337	-50.827	-0.552	7.614	-28.018
2015	-0.588	1.361	0.181	6.196	-16.948	-0.698	7.447	-17.053
2016	-0.639	1.441	0.210	6.301	-26.326	-0.360	7.470	-21.978
2017	-0.714	1.332	0.160	6.099	-15.304	0.794	7.361	-28.386
2018	-0.630	1.361	0.181	5.795	-36.745	0.541	6.702	-22.236
2020	-0.670	1.361	0.188	5.940	-22.985	-0.270	7.436	-21.179

Table S7: Statistical output of linear models of properties of a) M-N slope, b) mean trophic level, c) connectance, d) mean chain length, e) mean link angle, f) salmon M-N slope, g) mean salmon chain length, and h) mean salmon link angle over years. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

Dependent variable		Estimate	SE	t value	P value
a) M-N slope	Intercept	-1.04	2.82	-0.367	0.717
	Year	0.000191	0.00141	0.136	0.893
b) Mean trophic level	Intercept	-0.857	2.65	-0.324	0.750
	Year	0.00111	0.00132	0.838	0.411
c) Connectance	Intercept	-0.796	1.55	-0.515	0.612
	Year	0.000488	0.000770	0.633	0.533
d) Mean chain length	Intercept	31.6	11.7	2.70	<0.05
	Year	-0.0127	0.00583	-2.17	<0.05
e) Mean link angle	Intercept	-695	640	-1.09	0.290
	Year	0.329	0.319	1.03	0.314
f) Salmon M-N slope	Intercept	-62.2	19.3	-3.22	<0.01
	Year	0.0308	0.00964	3.20	<0.01
g) Mean salmon chain length	Intercept	48.3	21.2	2.28	<0.05
	Year	-0.0204	0.0106	-1.93	0.0674
h) Mean salmon link angle	Intercept	-603	190	-3.18	<0.01
	Year	0.288	0.0946	3.04	<0.01

Table S8: Statistical output of linear and polynomial models of properties of a) M-N slope, b) mean trophic level, c) connectance, d) mean chain length, e) mean link angle, f) salmon M-N slope, g) mean salmon chain length, and h) mean salmon link angle across average summer water temperatures (°C) in Vesturdalsá. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

Dependent variable		Estimate	SE	t value	P value
a) M-N slope	Intercept	-0.653	0.00895	-73.0	<0.001
	poly (Temperature, 2)1	-0.0125	0.0410	-0.306	0.763
	poly (Temperature, 2)2	0.0964	0.0410	2.35	<0.05
b) Mean trophic level	Intercept	1.37	0.123	11.1	<0.001
	Temperature	-0.000597	0.0116	-0.051	0.959
c) Connectance	Intercept	0.178	0.0721	2.47	<0.05
	Temperature	0.000491	0.00679	0.072	0.943
d) Mean chain length	Intercept	6.94	0.499	13.9	<0.001
	Temperature	-0.0722	0.0569	-1.54	0.141
e) Mean link angle	Intercept	-0.572	29.2	-0.020	0.985
	Temperature	-3.17	2.75	-1.15	0.263
f) Salmon M-N slope	Intercept	-0.776	1.069	-0.726	0.477
	Temperature	0.0374	0.101	0.371	0.714
g) Mean salmon chain length	Intercept	-7.42	0.0713	104	<0.001
	poly (Temperature, 2)1	-0.382	0.327	-1.17	0.257
	poly (Temperature, 2)2	-0.550	0.327	-1.68	0.110
h) Mean salmon link angle	Intercept	-25.2	0.668	-37.7	<0.001
	poly (Temperature, 2)1	0.737	3.06	0.241	0.812
	poly (Temperature, 2)2	8.72	3.06	2.85	<0.05

11. Comparison of food webs over time during summer of 2020

Table S9: Properties of trivariate food webs in Vesturdalsá over the summer period from June till August.

Time	M-N slope	Mean trophic level	Connectance	Mean chain length	mean link angle	Salmon M-N slope	Mean salmon chain length	Mean salmon link angle
June	-0.923	1.63	0.180	9.64	-39.4	0.000227	6.86	-24.3
early July	-0.902	1.54	0.193	9.36	-39.7	0.564	6.93	-16.2
late July	-0.933	1.53	0.163	9.12	-44.5	-1.60	7.47	-17.4
August	-0.983	1.58	0.198	9.45	-44.7	-0.270	7.44	-21.2

Table S10: Statistical output from ANOVA analysis of linear mixed effects models of trivariate food webs between sampling times during the summer. Log_{10}(species abundance) was the dependent variable and log_{10}(mass (g)) and time were fixed effects. 'Nodes' were a random effect in the model. Summary tables are shown with DF values (degree of freedom), F values, and P values.

	DF	F value	P value
(Intercept)	1	1050	<0.001
log_{10}(Mass)	1	302	<0.001
Time	3	6.68	<0.001
log_{10}(Mass) × Time	3	1.78	0.159

Table S11: Post-hoc output of food web comparison between sampling times and Log_{10}(species abundance) in Vesturdalsá using pairwise comparisons and Tukey adjustments.

	SE	t ratio	P value
early July-June	0.0991	2.82	<0.05
late July-June	0.0933	-0.086	1.000
August-June	0.0920	-1.67	0.349
late July-early July	0.0996	-2.89	<0.05
August-early July	0.0991	-4.37	<0.001
August-late July	0.0931	-1.56	0.407

Table S12: Statistical output of linear models of properties of a) M-N slope, b) mean trophic level, c) connectance, d) mean chain length, e) mean link angle, f) salmon M-N slope, g) mean salmon chain length, and h) mean salmon link angle over time during the summer. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

Dependent variable		Estimate	SE	t value	P value
a) M-N slope	Intercept	-0.904	0.0205	-44.0	<0.001
	Time	-0.000904	0.000460	-1.96	0.188
b) Mean trophic level	Intercept	1.59	0.0438	36.3	<0.001
	Time	-0.000605	0.000982	-0.616	0.601
c) Connectance	Intercept	0.180	0.0155	11.6	<0.01
	Time	0.0000964	0.000347	0.278	0.807
d) Mean chain length	Intercept	9.508	0.196	48.5	<0.001
	Time	-0.00328	0.00439	-0.746	0.533
e) Mean link angle	Intercept	-39.0	1.12	-34.8	<0.001
	Time	-0.0877	0.0251	-3.50	0.0730
f) Salmon M-N slope	Intercept	0.138	0.843	0.164	0.885
	Time	-0.0130	0.0189	-0.687	0.563
g) Mean salmon chain length	Intercept	6.83	0.131	52.0	<0.001
	Time	0.00951	0.00294	3.23	0.0840
h) Mean salmon link angle	Intercept	-20.9	3.63	-5.76	<0.05
	Time	0.0310	0.0814	0.381	0.740

12. Comparisons of algae concentrations between sampling times

Table S13: Statistical output of Kruskal-Wallis tests on comparisons of log_{10} algae concentrations (mg m^{-2}) between sampling times. Summary tables are shown with X^2 values (chi-squared), DF values (degree of freedom), and P values.

	X^2	DF	p-value
Cyanobacteria	30.871	3	<0.001
Diatom	72.762	3	<0.001
Green Algae	1.992	3	0.574

Table S14: Statistical output of post-hoc Dunn test on comparisons of log_{10} cyanobacteria concentrations between sampling times. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	adjusted p-value
June-early July	-0.0154	1.000
June-late July	-2.15	0.188
early July- late July	-2.13	0.198
June-August	-4.82	<0.001
early July-August	-4.80	<0.001
late July-August	-2.74	<0.05

Table S15: Statistical output of post-hoc Dunn test on comparisons of log_{10} diatom concentrations between sampling times. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	adjusted p-value
June-early July	1.687	0.550
June-late July	-1.01	1.000
early July- late July	-2.70	<0.05
June-August	-6.49	<0.001
early July-August	-8.105	<0.001
late July-August	-5.504	<0.001

13. Comparison of benthic invertebrate between sampling times

Table S16: Statistical output of Kruskal-Wallis tests on comparisons of log_{10} benthic invertebrate density (individuals m^{-2}) between sampling times. Summary tables are shown with X^2 values (chi-squared), DF values (degree of freedom), and P values.

	X^2	df	p-value
Chironomidae	2.32	3	0.509
Simuliidae	8.66	3	<0.05
Oligochaeta	6.922	3	0.0744
Trichoptera	1	1	0.317
Gastropoda	1.5	1	0.221

Table S17: Statistical output of post-hoc Dunn test on comparisons of log_{10} Simuliidae density between sampling times. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	adjusted p-value
June-early July	0.928	1.000
June-late July	-0.442	1.000
early July- late July	-1.148	1.000
June-August	-2.24	0.152
early July-August	-2.83	<0.05
late July-August	-1.38	0.998

Table S18: Statistical output of Kruskal-Wallis tests on comparisons of log_{10} benthic invertebrate population biomass (g m^{-2}) between sampling times. Summary tables are shown with X^2 values (chi-squared), DF values (degree of freedom), and P values.

	X^2	df	p-value
Chironomidae	12.4	3	<0.01
Simuliidae	3.13	3	0.373
Oligochaeta	2.73	3	0.435
Trichoptera	1	1	0.317
Gastropoda	1.5	1	0.221

Table S19: Statistical output of post-hoc Dunn test on comparisons of log_{10} Chironomidae population biomass between sampling times. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	adjusted p-value
June-early July	-2.26	0.145
June-late July	0.708	1.000
early July- late July	2.63	0.0510
June-August	1.31	1.000
early July-August	2.95	<0.05
late July-August	0.651	1.000

14. Comparison of drift invertebrate between sampling times

Table S20: Statistical output of Kruskal-Wallis tests on comparisons of log_{10} drifting invertebrate density (individuals m^{-3}) between sampling times. Summary tables are shown with X^2 values (chi-squared), DF values (degree of freedom), and P values.

	X^2	df	p-value
Chironomidae	9.86	3	<0.05
Simuliidae	3.682	3	0.298
Oligochaeta	5.681	3	0.128
Empididae	1	1	0.317
Diptera adult	2.96	2	0.227
Terrestrial	5.78	3	0.123

Table S21: Statistical output of post-hoc Dunn test on comparisons of log_{10} Chironomidae density between sampling times. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	adjusted p-value
June-early July	-1.45	0.878
June-late July	-1.90	0.345
early July- late July	-0.468	1.000
June-August	0.739	1.000
early July-August	2.30	0.129
late July-August	2.77	<0.05

Table S22: Statistical output of Kruskal-Wallis tests on comparisons of log_{10} drifting invertebrate population biomass (g m^{-2}) between sampling times in downstream (A) site. Summary tables are shown with X^2 values (chi-squared), DF values (degree of freedom), and P values.

	X^2	df	p-value
Chironomidae	11.3	3	<0.05
Simuliidae	4.47	3	0.215
Oligochaeta	3.39	3	0.335
Empididae	1	1	0.317
Diptera adult	1.49	2	0.475
Terrestrial	6.85	3	0.0770

Table S23: Statistical output of post-hoc Dunn test on comparisons of log_{10} Chironomidae population biomass between sampling times. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	adjusted p-value
June-early July	-1.31	1.000
June-late July	-1.92	0.326
early July- late July	-0.638	1.000
June-August	0.998	1.000
early July-August	2.43	0.0916
late July-August	3.06	<0.05

15. Statistical outputs for stomach content of juvenile Atlantic salmon between sampling times

Table S24: Statistical output of Kruskal-Wallis tests on comparisons of log_{10} abundance of prey items consumed by juvenile salmon between sampling times. Summary tables are shown with X^2 values (chi-squared), DF values (degree of freedom), and P values.

	X^2	df	p-value
Chironomidae	48.7	3	<0.001
Simuliidae	2.34	3	0.505
Oligochaeta	2	3	0.572
Empididae	1.79	2	0.409
Dicranota	0.75	2	0.687
Gastropoda	0.781	3	0.854
Terrestrial	5.30	3	0.151

Table S25: Statistical output of post-hoc Dunn test on comparisons of log_{10} abundance of Chironomidae in salmon gut content between sampling times. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	adjusted p-value
June-early July	-3.58	<0.01
June-late July	-2.55	0.0655
early July- late July	0.764	1.000
June-August	2.91	<0.05
early July-August	6.42	<0.001
late July-August	5.20	<0.001

Table S26: Statistical output of Kruskal-Wallis tests on comparisons of log_{10} biomass (g) of prey items consumed by juvenile salmon between sampling times. Summary tables are shown with X^2 values (chi-squared), DF values (degree of freedom), and P values.

	X^2	df	p-value
Chironomidae	56.4	3	<0.001
Simuliidae	16.3	3	<0.001
Oligochaeta	4.76	3	0.190
Empididae	2.61	2	0.271
Dicranota	3.314	2	0.191
Gastropoda	6.183	3	0.103
Terrestrial	7.03	3	0.0708

Table S27: Statistical output of post-hoc Dunn test on comparisons of log_{10} biomass of Chironomidae in salmon gut content between sampling times. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	adjusted p-value
June-early July	-2.35	0.113
June-late July	0.578	1.000
early July- late July	2.75	<0.05
June-August	5.15	<0.001
early July-August	7.39	<0.001
late July-August	4.23	<0.001

Table S28: Statistical output of post-hoc Dunn test on comparisons of log_{10} biomass of Simuliidae in salmon gut content between sampling times. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	adjusted p-value
June-early July	-1.35	1.000
June-late July	3.02	<0.05
early July- late July	3.40	<0.01
June-August	2.16	0.183
early July-August	2.63	0.0505
late July-August	-1.73	0.499

16. Statistical outputs for stomach content of juvenile Arctic charr between sampling times

Table S29: Statistical output of Kruskal-Wallis tests on comparisons of log_{10} abundance of prey items consumed by juvenile charr between sampling times. Summary tables are shown with X^2 values (chi-squared), DF values (degree of freedom), and P values.

	X^2	df	p-value
Chironomidae	3.65	3	0.302
Oligochaeta	2	2	0.368

Table 30: Statistical output of Kruskal-Wallis tests on comparisons of log_{10} biomass (g) of prey items consumed by juvenile charr between sampling times. Summary tables are shown with X^2 values (chi-squared), DF values (degree of freedom), and P values.

	X^2	df	p-value
Chironomidae	2.24	3	0.524
Oligochaeta	2	2	0.368

1. Comparison of salmonid mass between sampling times

Table S31: Statistical output of Kruskal-Wallis tests on comparisons of log_{10} mass (g) of salmonids between sampling times. Summary tables are shown with X^2 values (chi-squared), DF values (degree of freedom), and P values.

	X^2	df	p-value
Salmon	49.8	3	<0.001
Charr	15.0	3	<0.01

Table S32: Statistical output of post-hoc Dunn test on comparisons of log_{10} mass of juvenile salmon between sampling times. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	adjusted p-value
June-early July	-4.37	<0.001
June-late July	-3.01	<0.05
early July- late July	0.688	1.000
June-August	1.50	0.804
early July-August	6.10	<0.001
late July-August	4.24	<0.001

Table S33: Statistical output of post-hoc Dunn test on comparisons of log_{10} mass of juvenile charr between sampling times. Summary tables are shown with Z test statistic value and Bonferroni adjusted p-values.

	Z	adjusted p-value
June-early July	-0.868	1.000
June-late July	-1.52	0.764
early July- late July	-0.784	1.000
June-August	2.12	0.203
early July-August	2.69	<0.05
late July-August	2.91	<0.05

Paper III

Spatial trends in the trophic relationships of Atlantic salmon rivers across the North Atlantic

Sum Yi Lai, Daniel Perkins, Eoin J. O'Gorman, Gaute Kjærstad, Guðni Guðbergsson, Guy Woodward, Hans Schibli Lundahl, Ingi Rúnar Jónsson, Jaako Erkinaro, Jan Grimsrud Davidsen, Jo Arnekleiv, Jón S. Ólafsson, Rasmus B. Lauridsen, and Hlynur Bárðarson

Author Contribution Statement:

Conceptualisation & Developing methods: SYL, EJG, GG, GW, IRJ, JSO, HB. Contribution of data: DP, GK, HSL, JE, JGD, JA. Conducting the research: SYL, JSO, HB. Data analysis: SYL, EJG. Data interpretation: SYL, EJG, GW, IRJ, JSO, HB. Preparation figures & tables & Writing: SYL. All authors reviewed, edited, and approved the manuscript.

Abstract:

The impacts of climate change vary across latitudinal gradients; therefore, research on the ecology and management methods for Atlantic salmon populations will differ depending on the local geographical regions. Current studies on Atlantic salmon (*Salmo salar*) food webs lack comparisons over large geographical scales that cover their species distribution. We compared food web structures over a large spatial scale around the North Atlantic. Our findings showed that Icelandic rivers with relatively simple food web structures had little spatial variation within and between rivers, most likely due to geographical isolation and few species of fish competitors and available prey species. Food web structures in colder riverine systems were simpler with lower connectance and mean trophic levels, whereas temperate Atlantic salmon rivers had both greater prey diversity and terrestrial inputs, and thus higher productivity and more complex food web structures. Differences in trophic structure between rivers could also be due to the density of riparian vegetation, interspecific competition, and climate. Nevertheless, temperature explained the greatest variation across the North Atlantic. These findings suggest that productivity of salmon populations in cold high-latitude rivers could be strained and vulnerable to the impacts of warming and should be continually monitored for changes in trophic interactions as early warning indicators of broader impacts on freshwater ecosystems and global Atlantic salmon populations.

Keywords: Atlantic salmon, trivariate food webs, predator-prey relationships, spatial similarity, productivity, temperature, salmonids, latitudinal gradient

Introduction:

It is clearly evident from many studies and reports that climate change has been impacting freshwater ecosystems, and those impacts differ across latitudes (Heino et al., 2016; Parmesan et al., 2023; Todd et al., 2011; Woodward et al., 2010; Wrona et al., 2006). Studies have also shown that species are shifting further northward due to climate change (Kubelka et al., 2022), but that can be challenging for anadromous salmonids, such as the Atlantic salmon (*Salmo salar*), due to their complex life cycles and inter-specific competition. For example, the length of time that juvenile Atlantic salmon populations spend in the freshwater phase varies spatially between populations depending on the climate they inhabit across the North Atlantic (Elliott et al., 1998).

Populations of Atlantic salmon are declining globally (ICES, 2022), making it all the more imperative to understand possible population bottlenecks and for the management of stocks. The productivity of a river can determine the availability of food for Atlantic salmon populations, which can become a limiting factor under warming (Constable et al., 2022; O'Connor et al., 2009; O'Gorman et al., 2016; Parmesan et al., 2023). Northern latitude populations may become more threatened over time due to a low food supply (Kubelka et al., 2022). Atlantic salmon are often highly abundant in sub-Arctic rivers, but riverine productivity can also be limited by the harsh environmental conditions (Amundsen & Gabler, 2008) and typically nutrient-poor status with less prey available than in southern regions (Elliott et al., 1998). These northern open rivers in tundra ecosystems have a highly different productivity than forested streams, such as those found further in temperate regions. Thus, due to the difference in productivity and catchment characteristics, we can also expect to see differing food web structures along the latitudinal gradient. For example, a higher species diversity in the riverine system is likely to have higher food web connectivity (Lento et al., 2022b; Shah et

al., 2015). Therefore, certain patterns are expected to be observed along the latitudinal gradient of Atlantic salmon rivers.

The northernmost Atlantic salmon populations in the North Atlantic could experience the largest impacts from climate change as the northern latitudes are experiencing the largest winter warming, decrease in river ice, and reduction in habitat availability of cold-adapted species (Bednar-Friedl et al., 2022; Constable et al., 2022). Warming has shifted species distributions and altered food web structure and food and space competition in high-latitude regions (Constable et al., 2022), for example, there has been a decrease in the proportions of Arctic charr (*Salvelinus alpinus*) and increased proportions of brown trout (*Salmo trutta*) in the catch composition of anadromous salmonids for the past 25 years in northernmost European rivers (Svenning et al., 2022). Additionally, climate change is generally predicted to increase diversity and growth rates of macroinvertebrates in the Arctic, which could ultimately increase salmonid biomass (Hannesdóttir et al., 2013), but Iceland may exhibit a different trend due to its biogeographical constraints (Lento et al., 2022a). Furthermore, Haase et al. (2023) found that although there had been overall increases in species richness and abundance in Europe before 2010s, these increases has since plateaued suggesting that future projections of macroinvertebrate prey availability within rivers are becoming limited, which can lower the growth rate of juvenile salmonids (Amundsen & Gabler, 2008).

Here, we use mass-abundance (M-N) relationship within food webs to understand how trophic interactions and energy flow varies spatially 1) within a northern latitude Atlantic salmon river in Iceland and 2) compare how similar fluvial food webs are across various spatial, temperature, and productivity gradients across the North Atlantic area. We investigated the spatial similarity of predator-prey relationships in Atlantic salmon sink food webs by comparing trophic relationships within and between rivers in the North Atlantic. We

hypothesize that: 1) Atlantic salmon food webs in the North Atlantic increases in complexity of food web structure with decreasing latitude and increasing temperature and vegetation productivity, such as decreasing food chain length and increasing connectivity in rivers at lower latitudes (Jake Vander Zanden & Fetzer, 2007; Shah et al., 2015) ; 2) food web structures of Atlantic salmon rivers are comparable within and between rivers for cold and northern regions due their relatively simple food web structure, homogenous physiochemical and catchment characteristics (Elliott et al., 1998; Lento et al., 2022; Ministry for the Environment & The Icelandic Institute of Natural History, 2001), which suggests that the food web parameters of Atlantic salmon rivers in Iceland do not differ from one another.

Materials and Methods:

Study area and data collection:

The focal river for this study was River Vesturdalsá in Northeast (NE) Iceland. Other rivers used in this study include both main stem rivers and their tributaries across the North Atlantic area (Table S1). Utsjoki, Vidgaveädji and Badda are all tributaries of the main stem of the large River Teno/Tana in Finland/Norway. Additionally, Högvadsån is one of the main tributaries of the River Ätran in Sweden. We have selected Atlantic salmon rivers across a latitudinal gradient with varying catchment areas and productivity. Several of them are used as ICES index rivers for Atlantic salmon population assessments (ICES, 2022).

Fieldwork to collect samples of algae, invertebrates, and salmonid fishes was conducted in August 2020 in the main study river, Vesturdalsá, which is a direct run-off river. The river has a length of 42 km, a catchment area of 190 km^2, and drains into the North Atlantic (Rist, 1990). Five locations were sampled across the river, which stretched a total of 15.1 km (Figure

1). At each site, the sampling was conducted for each site along a 15 m reach. For measuring the algal assemblages, we randomly collected rocks from within the sampling reach. The biofilm was scrubbed off each stone within a quadrat of 805 mm^2. Three such samples were collected from each stone. Two replicate stones were also collected for the algal samples. The samples were preserved in Lugol for algal identification. Macroinvertebrates were sampled using Surber sampler, with 25 × 25 cm frame and 250 µm mesh size net. Surber samples were collected at 10 replicated random coordinates within each sampling reach. The macroinvertebrate samples were preserved in 70% ethanol solution until processing. Additionally, we collected separate invertebrate samples for identifying gut content items of Chironomidae, Simuliidae and Trichoptera (Diptera), which were preserved in a weak formalin solution. These invertebrates were selected as they were the most abundant within Icelandic macroinvertebrate communities (Gíslason et al., 1999).

For fish gut content, density, assemblages, and to obtain length-weight relationships, we sampled salmonids by using single-pass electrofishing in all the sampling sites in Vesturdalsá (Antonsson et al., 2005). Fish were anesthetized with 2-phenoxyethanol (300ppm). The area of electrofishing was measured to calculate an index of fish density. The fork length and wet weight of each fish was measured, and the species recorded. Fish gut content of 25 salmonids randomly selected across their size range were obtained by gut flushing of fish caught above 5 cm in length and smaller fish were overdosed with 2-phenoxyethanol and dissected to identify feeding links (Dineen et al., 2007; Traugott et al., 2020). Fish caught and not dissected recovered and then released back at their original fished area after measurements.

Lab processing and density and biomass calculations:

Abundances of diatoms were estimated using the algae samples collected. Algae samples, taken using the same methodology mentioned above, from previous studies and annual

surveys in Selá, Hofsá, Midfjardará, and Ellidaár taken by the Marine and Freshwater Research Institute were additionally processed to collect diatom population data. Equal volumes of algae were extracted from the samples for subsampling and abundances were counted across a transect under a microscope (individuals m^{-2}). Diatoms were identified to genus level (Spaulding et al., 2021). Sizes of diatom were also measured using ImageJ (Schneider et al., 2012) with pictures taken by Leica Application Suite and individual biomass (mg m^{-2}) were estimated using established biovolume equations from published literature (Hillebrand et al., 1999).

We counted and identified the invertebrates in the Surber samples to family or order level. We calculated the relative density of invertebrates (D, individuals m^{-2}) and juvenile salmonids using: $D = N/A$, where N was abundance of organisms at each site and A was the area sampled. The biomass of invertebrates was estimated using measured body length and head width and length-mass regression relationships from published literature (Baumgärtner & Rothhaupt, 2003; Benke et al., 1999; Burgherr & Meyer, 1997; Kang & Kang, 1997; O'Gorman & Emmerson, 2010; Ramsay et al., 1997). The digestion system of Chironomidae, Simuliidae and Trichoptera larvae larger than 3 mm was removed, and mounted for gut content identification to identify trophic links between these invertebrates and algae using a high-resolution microscope (Rosi-Marshall et al., 2016).

Building food webs:

The abundance and individual biomass data of diatom, macroinvertebrates and fish in rivers with Atlantic salmon populations across the North Atlantic area were gathered to compare food webs across various spatial scales (References to published data sources in Table S1; (Anon, 2023; Arnekleiv et al., 2019; Bárðarson et al., 2021; Bergh, 2022; Einarsson et al., 2020; Ekologigruppen Ekoplan AB, 2021; Environmental data MVM, 2023; Erkinaro &

Erkinaro, 1998; Hansen & Eiríksdóttir, 2021; Ingimarsson, 2022; Perkins et al., 2018; Sturlaugsson, 2023; Woodward et al., 2021)). Average biomasses of macroinvertebrates and diatoms from published literature (Benke et al., 1999; Méthot et al., 2012; Perkins et al., 2018) was used for filling in missing data in the food web. Population abundance and individual biomasses were averaged across 'nodes' (individual taxa) for each site and river.

Trophic links between 'nodes' were assigned based upon gut content data where available and missing trophic links of other invertebrates were identified using information gathered from the literature (Bouchard, 2004; Di Sabatino et al., 2000; Proctor & Pritchard, 1989). We created and compared food webs between sites and different rivers using the *cheddar* package (Hudson et al., 2013; O'Gorman et al., 2019). We used the $\log_{10}$-transformed average abundance and body mass of each 'node' within each food web. Linear regression analysis of $\log_{10}$ individual body mass against $\log_{10}$ abundance of each 'node' (hereafter referred as M-N relationship) was used to get the food web properties of each site and river. The M-N slope of the food web was extracted to compare the rate of biomass depletion between rivers. Connectance were also calculated to show the possible interactions that the predator has with their prey within the river (Cohen et al., 2009). The mean link angle were used to show the ratio of consumer to resource and a shallow or less negative angle shows that consumers have a relatively higher abundance compared to their resources (O'Gorman et al., 2023; Perkins et al., 2018). Mean link length were also used to show the magnitude of difference in body mass and abundance between resources and consumers in the system (Cohen et al., 2009).

Statistical analysis:

We used Linear Mixed Effects (LME) models and Analysis of Covariance (ANCOVA) to analyse the M-N relationship in the food web to test for differences between sites, rivers, and countries using the *lmerTest* package (Bates et al., 2015; Kuznetsova et al., 2017). We used

'nodes' and 'river' as a random effect in the M-N relationship model to account for differences in abundances between species (O'Gorman et al., 2017). Pairwise comparisons with Tukey adjustments were used as post-hoc tests for the model. Food web properties and Atlantic salmon abundance (individuals m^{-2}) and average individual biomass (g) were compared between latitudes, temperature (°C), and productivity levels using the *lm* function from the *stats* package. Mean monthly air temperature values from 1970 to 2000 were extracted using the *raster* package (Hijmans, 2023). Normalised Difference Vegetation Index (NDVI) values were used as a measurement of productivity were taken from MODIS datasets (Didan, 2021) and extracted using QGIS (QGIS.org, 2023). NDVI was used as direct effects of climatic conditions on spatio-temporal biomass and phenological patterns of vegetation are frequently assessed using NDVI (Huang et al., 2021; Pettorelli et al., 2005). We had selected models using the likelihood ratio tests. Collinearity was also tested between latitude and temperature in the linear regression models by calculating the variance inflation factor (VIF). High collinearity was found between latitude and temperature and therefore the linear regression plots with latitude in the model were excluded from the results section. Temperature was kept as it is a good indicator of differences in environmental and biophysical processes between regional populations (Elliott et al., 1998). Temperature and productivity data was assessed for outliers using boxplots and Grubbs´s test, in which the productivity value for Afon Marteg, an Atlantic salmon river in the UK, was found to be an outlier and was subsequently removed from the productivity linear regression analyses (Figure S1). Statistical significance was set at 5% level. All statistical analysis was conducted using R (R Core Team, 2023).

Results:

[Figure 1 here]

[Figure 2 here]

Spatial similarity in the food web of Vesturdalsá:

The food web properties of each site were very similar to each other in Vesturdalsá, and the ANCOVA model of the M-N relationship showed that there were no significant differences in the slope of the M-N relationship between sites ($F_{(4,87)}$=1.81, p=0.135; Figure 1a and 2a). There was no significant relationship in juvenile Atlantic salmon abundance (p=0.786) and body mass (p=0.104) over the latitudinal gradient of the river (Table S4). As shown in Figure 3a, there were no significant relationships between food web properties (Table S4) and the latitude of each site in Vesturdalsá, indicating that they remained similar within the river. However, Vesturdalsá had a high ratio of resources to consumers, with a higher abundance of resources found further upstream than downstream, but overall was not significantly different between locations (Figure S2a). The difference in ratios of resources to consumers could be due to higher abundances of primary producers in upstream sites.

Spatial similarity across rivers in Iceland:

Looking at a larger scale, food webs in rivers in Iceland were similar to one another (Figure 1b, Table S5). The linear regressions of different rivers overlap with one another (Figure 2b), and there was weak evidence for a difference between Atlantic salmon abundance (p=0.0967) and biomass (p=0.0890) in Icelandic rivers along the latitudinal gradient (Table S7). Additionally, there were little evidence that food web properties differed across latitudes in Iceland, except for mean link angle which had a significant negative linear regression along the latitudinal gradient (R^2=0.742, p<0.05; Table S7). Ellidaár and Krossá both had a higher mean link angle than rivers in the NE, with Ellidaár having the highest link angle. Mean link angle and abundances of species in the food web were significantly different along latitudinal

gradients in Iceland. The M-N relationships between rivers were also close to being significantly different ($F_{(5,122)}$=2.24, p=0.0545). Therefore, the trophic interactions in Atlantic salmon rivers in Iceland were shown to be comparable to one another.

[Figure 3 here]

Spatial similarity across rivers in the North Atlantic:

First, we compared the food web data of Atlantic salmon rivers only in Iceland and United Kingdom (Figure 1b and 1c) using the model selection procedure, based upon likelihood ratio tests, highlighted that the M-N relationship of these rivers in the two countries had no significant relationship along the latitudinal gradient (Figure 2c, p=0.147), air temperature (p=0.310), and productivity (p=0.0544). There were also no differences found between rivers in Iceland and the UK ($F_{(1,330)}$=1.36, p=0.244). Food web connectance, mean trophic level and mean link angles in rivers in the UK were higher in comparison to Icelandic rivers. Connectance (R^2=0.535, p<0.01), mean trophic level (R^2=0.363, p<0.05), and mean link angle (R^2=0.616, p<0.001) had a positive linear relationship with air temperature (Figure 3c). There was also a positive relationship between connectance (R^2=0.348, p<0.05) with productivity (Figure 3d). Mean trophic level also remains similar until productivity reaches a value of 0.60 but starts increasing as productivity increases (R^2=0.563, p<0.01). Likewise, mean link angle decreases with productivity and starts increasing when productivity is above 0.63 (R^2=0.351, p=0.0579).

[Figure 4 here]

Second, we compared predator-prey relationships of all study rivers within the North Atlantic, which includes rivers in Iceland, UK, Greenland, Norway/Finland, and Sweden. The predator-prey trophic relationships found in Atlantic salmon rivers were different across countries and food webs (Figure 1d). The results from the LME model showed that the log-log

M-N relationship of fish and macroinvertebrates were significantly different across latitudes ($p<0.05$), temperature (Figure 2e; $p<0.01$), and between countries (Figure 2d; $F_{(4,220)}=3.39$, $p<0.05$), and thus, was also significantly different between rivers ($F_{(19,190)}=2.67$, $p<0.001$). Further post-hoc testing showed that there were significant differences in the M-N relationship between Iceland and the UK ($p<0.001$) and Sweden ($p<0.01$). Furthermore, there were no significant differences in the M-N relationship between rivers on the Teno/Tana system ($F_{(3,14)}=0.642$, $p=0.601$). Although we saw significant differences between countries and along temperature and latitudinal gradients, there were no significant relationships with productivity (Figure 2f; $p=0.844$). Mean juvenile Atlantic salmon mass ($R^2=0.262$, $p<0.05$), slope ($R^2=0.280$, $p<0.05$), and mean chain length ($R^2=0.271$, $p<0.05$) also significantly decreased with increasing temperatures (Figure 4a). On the other hand, connectance increased with increasing temperatures ($R^2=0.386$, $p<0.01$). Mean trophic level also decreases with increasing temperature and starts increasing when temperature reaches above 1°C ($R^2=0.647$, $p<0.001$). Additionally, as shown in Figure 4b, connectance increases with increasing productivity levels ($R^2=0.248$, $p<0.05$), whereas mean chain length decreases ($R^2=0.452$, $p<0.01$). Mean trophic level along the productivity gradient shows similar trends as temperature, where mean trophic level decreases with productivity until productivity is higher than 0.61 and starts increasing ($R^2=0.400$, $p<0.01$). Although the relationship was non-significant, the slope of the food web also increases with productivity and starts decreasing when productivity level reaches above 0.69 ($R^2=0.233$, $p=0.0533$).

Discussion

Atlantic salmon rivers in the North Atlantic have a range of diverse habitats and environmental variables (Elliott et al., 1998). A broader geographical scale of food web

comparisons is needed to further our understanding of the trophic relationships of Atlantic salmon, as the majority of food web studies are focused on temperate streams of Europe and North America (Thompson et al., 2012a). Our study rivers encompass a wide latitudinal gradient from 50° to 70° north, and thus, there is a large contrast in temperature and productivity, and covers the North Atlantic distributional range of Atlantic salmon (MacCrimmon & Gots, 1979). We found spatial similarity in food webs within Atlantic salmon rivers, particularly within our model system, Vesturdalsá, and across other high-latitude rivers across Iceland. There may be node-level differences between food webs, such as changes in abundance and biomass of individual species along the river, but the community-level M-N relationships of the food webs were not significantly different at the river or country scale. At the continental scale, however, there were differences in mass-abundance scaling and food web properties, such as mean trophic level and connectance, which were largely underpinned by temperature and productivity. The global spatial trends in Atlantic salmon sink food webs can help predict global trends in trophic relationships and fish stocks. Inadequate monitoring of biodiversity and community changes in freshwater over broad geographical ranges makes it difficult to predict changes in ecosystem services and trophic relationships (Heino et al., 2020). Establishing spatial trends in food webs will fill these gaps and provide a comparative baseline for spatial differences in trophic relationships (Laske et al., 2022).

Similarity in the food web structure for the Vesturdalsá and additionally rivers within the Teno/Tana system mirrors patterns for other high-latitude rivers (Elliott et al., 1998; Kahlert et al., 2022; Laske et al., 2022). The low habitat complexity and productivity of high-latitude Atlantic salmon rivers create a highly homogenous food web structure, whereas low-latitude rivers have a greater diversity of habitats and more complex food webs (Elliott et al., 1998; Rypel & David, 2017). Indeed, the similarity in M-N relationship throughout Icelandic freshwater ecosystems may be largely driven by biogeographical isolation (Lento et al., 2022a).

Productivity was consistent between these Icelandic rivers because of the similar cold environments and the lack of diverse invertebrate functional feeding groups (Gíslason et al., 1999; Ministry for the Environment & The Icelandic Institute of Natural History, 2001). Thus, a low regional species pool would have similar communities occupying similar available niche spaces in these high-latitude rivers (Vincent et al., 2008). The spatial differences in trophic structures were small enough that it can be assumed that monitoring trophic relationships in these Icelandic rivers could be a good indicator of change for other rivers in Iceland, as these rivers follow similar patterns in food web structures. On the other hand, the similarities in M-N relationships of food webs of rivers within the Teno/Tana system seen in our results contradicts what was shown by Erkinaro & Niemelä (1995) that high differences in prey availability and growth rates of juvenile Atlantic salmon were found between different river orders in the Teno/Tana system. The difference in results is likely due to the lack of allochthonous prey being represented in our models, as the rivers in northern latitudes have similar benthic compositions but differing terrestrial inputs due to the differences in fluvial and lacustrine habitats (Einarsson et al., 1990; Erkinaro et al., 1995; Halvorsen & Svenning, 2000; Jørgensen et al., 2000).

Terrestrial inputs also play a larger role in contributing to the productivity of Atlantic salmon rivers with high riparian vegetation in the UK (Woodward et al., 2008). There are greater allochthonous subsidies to supplement fish diets in temperate climates (Closs & Lake, 1994; Syrjänen et al., 2011), which could help maintain higher metabolic demands rather than simply relying on in-stream production, such as in low-latitude systems with low vegetation cover. In unproductive streams of Alaska, terrestrial invertebrates represent roughly half of the diet of juvenile coho salmon (*Oncorhynchus kisutch*) during the growing season, which also helps support higher fish production (Allan et al., 2003). Mill Stream is a chalk stream in the UK, which has high species diversity and productivity (Bowes et al., 2005; Marsh et al., 2022;

Wright et al., 1992); therefore, it had a higher abundance of primary producers than other rivers. Atlantic salmon rivers in the UK, especially towards the south and longer rivers, have higher primary productivity levels than in Iceland (Bowes et al., 2005; Elliott et al., 1998; Lamberti & Steinman, 1997), but there were no significant relationships between the abundance and mass of Atlantic salmon abundance with latitude, temperature, and vegetation level. However, studies (Jonsson & Jonsson, 2009; Klemetsen et al., 2003) have shown that there are higher individual growth rates of Atlantic salmon in warmer, southern river, which suggests a higher mortality rate and less time spent in the freshwater environment for those populations, and also explains the lack of relationship with fish density and mass that we saw in our findings. Although there are differences in the structure of the food web and freshwater fish species assemblage (including juvenile Atlantic salmon), productivity remain similar in these countries, which could be driven by decreased interspecific competition and increased food availability at higher latitudes (ICES, 2023; Rypel & David, 2017).

We also found that predator-prey trophic relationships varied across temperature and productivity gradients. The M-N scaling of predator-prey relationships was not only significantly different between Iceland and the UK, but also with Sweden. Högvadsån in Sweden had a lower abundance of macroinvertebrates and fish species than Iceland, but a higher species diversity due to the high riparian vegetation and warmer climate (Bergh, 2022; Ekologigruppen Ekoplan AB, 2021; Elliott et al., 1998; Eriksson et al., 1983). Other northern and cold rivers have similar productivity levels, low vegetation, and the same latitudinal gradient as Iceland, thereby having similar Atlantic salmon trophic relationships (Elliott et al., 1998). Macroinvertebrate communities in these cold and nutrient-poor streams mainly consists of small Diptera larvae which is the main prey item of juvenile salmonids (Arnekleiv et al., 2019; Erkinaro & Erkinaro, 1998; Friberg et al., 2001).

The M-N relationship also differed with temperatures, but not vegetation productivity. Food webs of Atlantic salmon rivers in warmer climates have higher production and diversity of macroinvertebrates (Elliott & Elliott, 2010; Rypel & David, 2017). In contrast to other studies (Johansen et al., 2005), our results showed that Atlantic salmon production did not vary with changes in the amount of riparian vegetation, in which higher productivity levels with additional terrestrial subsidies can support higher species richness whilst having similar fish production (Sabo et al., 2005). The mass of juvenile Atlantic salmon also increased with decreasing temperatures, because juveniles in colder rivers and northern latitudes have to spend a longer time in the river and grow to a larger size before migrating out to the sea as smolts (Antonsson et al., 2010; Metcalfe & Thorpe, 1990; Thorstad et al., 2012). In colder climates, the connectance within a food web is lower, which shows that there is little diversity of prey options for salmonids to feed on within the system, and that there may be less robustness to changes in the food web, especially with the added threat of warming (Erkinaro & Erkinaro, 1998; Gilbert, 2009; Steingrímsson & Gíslason, 2002). The mean trophic level increased with temperature, which showed that there were fewer species with many trophic interactions and were less able to sustain Atlantic salmon populations in high-latitude rivers, whereas at lower latitudes, there was a higher diversity of fish species that helped break up the food chain and created more flexibility in selecting prey items (Kortsch et al., 2019). This trend was also similar to that of productivity, with trophic levels decreasing with increasing productivity and vice versa, suggesting that Atlantic salmon rivers in warmer climates could support higher trophic levels, including top predators such as juvenile salmonids (Fretwell, 1987; Jake Vander Zanden & Fetzer, 2007). Warmer climates also have sufficiently high productivity levels to meet the demands of fish species and allow numerous predatory invertebrates to thrive in the face of stronger top-down control. Our results was different to what was found in the study of O'Gorman et al. (2019), where the opposite was found that in warmer streams had simplified

food web structures with lower connectance and mean trophic level than colder streams in the Hengill river systems in Iceland, which was a smaller latitudinal gradient in comparison to our study. Across a large latitudinal gradient, productivity increases at lower latitudes, supporting more complex food webs. This is evident in the case of a longer food chain length (which relates to the overall trophic level of the food web, such that shorter chains have a lower mean trophic level) of rivers found at higher latitudes (Jake Vander Zanden & Fetzer, 2007). This emphasises the importance of studies comparing temperature effects on food web structures across different baseline climates. Freshwater food web studies have mostly been conducted at small spatial scales, and thus there is a need to take an expanded range approach to study food web energetics (Thompson et al., 2012b).

Warming of freshwater ecosystems can simplify food webs and create biodiversity loss (Gibert, 2019; O'Gorman et al., 2023), which we have evidently observed in this study as northern rivers with low vegetation productivity and cold climates reflects the characteristics of a simple food web. Shifting to simpler food webs could suggest that streams are becoming oligotrophic (Gerwing & Plate, 2019; Kosten et al., 2012). Food webs in low biodiversity systems have little temporal variability owing to their simple structure (Nordström et al., 2009). Thus, these northern river systems are predicted to be more adversely affected by climate change because they already have simple food webs and cannot rely on the diversity of species and ecosystem functions to act as a buffer for ecosystem changes, unlike nutrient-rich rivers with larger food webs further south (Petchey et al., 1999). Additionally, McCann et al. (2005) have shown that trophic interactions in simple food webs usually lead to instabilities and vulnerability. Furthermore, the productivity of large predators such as juvenile Atlantic salmon plays a large role in promoting stability and balance within a food web (McCann & Rooney, 2009), which further highlights the importance of conserving the Atlantic salmon populations in North Atlantic rivers, especially in northern regions. Management of high-latitude and cold

Atlantic salmon rivers should focus on increasing or maintaining the species diversity that juveniles can feed on as a sustainable food source, such as by increasing primary productivity (Albertson et al., 2018; Thompson et al., 2018). The management of temperate Atlantic salmon populations could also use fish behaviour and ecology in the north as a warning against climate change impacts; for example, an increase in reliance in Atlantic salmon diet on small larval dipterans in a northern river may suggest decreasing prey options for temperate systems (Perkins et al., 2010; Rolls et al., 2017). Additionally, differences in trophic structures between Atlantic salmon populations could be due to climate, vegetation differences, and competition with other fish species. Habitat and interspecific interactions should also be considered when understanding the population dynamics of Atlantic salmon (Armstrong et al., 2003; Fausch, 1998; Forseth et al., 2017).

Conclusion

This study provides new knowledge into the spatial trends in food web structure of Atlantic salmon rivers along temperature and productivity gradients. Furthermore, showing that temperature and vegetation could predict future trends and changes in trophic relationships of these food webs. Cold Atlantic salmon rivers have simpler food web structures than temperate rivers, thus making them less flexible to the effects of warming. Regular monitoring of northern Atlantic salmon populations in riverine ecosystems should be encouraged to better predict changes in Atlantic salmon rivers that are less monitored (Heino et al., 2020; Laske et al., 2022). Management strategies should consider the local climate, interspecies interactions, and habitat, as they affect the trophic interactions of juvenile Atlantic salmon and their prey. Whilst the scopes of this study were highly spatial comparing food webs from within rivers to over the North Atlantic, it was also limited to the spatial perspective of changes in food web structure, which further describes the impacts of warming on Atlantic salmon sink food webs. Future

research should explore the long-term changes in food web structure under different climate change scenarios while considering different levels of productivity and environmental characteristics.

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References:

Albertson, L. K., Ouellet, V., & Daniels, M. D. (2018). Impacts of stream riparian buffer land use on water temperature and food availability for fish. *Journal of Freshwater Ecology*, *33*(1), 195–210. https://doi.org/10.1080/02705060.2017.1422558

Allan, J. D., Wipfli, M. S., Caouette, J. P., Prussian, A., & Rodgers, J. (2003). Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(3), 309–320. https://doi.org/10.1139/f03-019

Amundsen, P. A., & Gabler, H. M. (2008). Food consumption and growth of Atlantic salmon *Salmo salar* parr in sub-Arctic rivers: Empirical support for food limitation and competition. *Journal of Fish Biology*, *73*(1), 250–261. https://doi.org/10.1111/j.1095-8649.2008.01932.x

Anon. (2023). *Status of the Tana/Teno River salmon populations in 2022*. https://brage.nina.no/nina-xmlui/bitstream/handle/11250/3041641/Tana report 2023-1.pdf?sequence=1&isAllowed=y

Antonsson, T., Arnason, F., & Einarsson, S. M. (2005). Comparison of density, mean length, biomass and mortality of Atlantic salmon (*Salmo salar L.*) juveniles between regions in Iceland. *Icelandic Agricultural Sciences*, *18*, 59–66.

Antonsson, T., Heidarsson, T., & Snorrason, S. S. (2010). Smolt Emigration and Survival to Adulthood in Two Icelandic Stocks of Atlantic Salmon. *Transactions of the American Fisheries Society*, *139*(6), 1688–1698. https://doi.org/10.1577/t08-200.1

Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M., & Milner, N. J. (2003). Habitat

requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research*, *62*(2), 143–170. https://doi.org/10.1016/S0165-7836(02)00160-1

Arnekleiv, J. V., Davidsen, J. G., Sheehan, T. F., Lehnert, S. J., Bradbury, I. R., Rønning, L., Sjursen, A. D., Kjærstad, G., Lubinski, B. A., & Nilssen, K. J. (2019). Demographic and genetic description of Greenland's only indigenous Atlantic salmon *Salmo salar* population. *Journal of Fish Biology*, *94*(1), 154–164. https://doi.org/10.1111/jfb.13887

Bárðarson, H., Helgason, S. Ó., Njarðardóttir, E., & Árnason, F. (2021). *Research on fish stocks in several rivers at North-East Iceland 2020*. https://www.hafogvatn.is/static/research/files/hv2021-18.pdf

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Baumgärtner, D., & Rothhaupt, K. O. (2003). Predictive Length-Dry Mass Regressions for Freshwater Invertebrates in a Pre-Alpine Lake Littoral. *International Review of Hydrobiology*, *88*(5), 453–463. https://doi.org/10.1002/iroh.200310632

Bednar-Friedl, B., Biesbroek, R., Schmidt, D. N., Alexander, P., Børsheim, K. Y., Carnicer, J., Georgopoulou, E., Haasnoot, M., Cozannet, G. Le, Lionello, P., Lipka, O., Möllmann, C., Muccione, V., Mustonen, T., Piepenburg, D., & Whitmarsh, L. (2022). Europe. In: Climate Change 2022: Impacts, Adaptation and Vulnerability. In *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. https://doi.org/10.1017/9781009325844.015

Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, *18*(3), 308–343. https://doi.org/10.2307/1468447

Bergh, R. (2022). *Biologisk undersökning av fiskfaunan inom Högvadsåns kalkningsprojekt 2022*. https://catalog.lansstyrelsen.se/store/24/resource/179

Bouchard, R. W. (2004). *Guide to Aquatic Invertebrate Families of Mongolia. Identification Manual for Students, Citizen Monitors, and Aquatic Resource Professionals*.

Bowes, M. J., Leach, D. V., & House, W. A. (2005). Seasonal nutrient dynamics in a chalk stream: The River Frome, Dorset, UK. *Science of the Total Environment*, *336*(1–3), 225–241. https://doi.org/10.1016/j.scitotenv.2004.05.026

Burgherr, P., & Meyer, E. I. (1997). Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Archiv Fur Hydrobiologie*, *139*(1), 101–112. https://doi.org/10.1127/archiv-hydrobiol/139/1997/101

Closs, G. P., & Lake, P. S. (1994). Spatial and Temporal Variation in the Structure of an Intermittent-Stream Food Web. *Ecological Monographs*, *64*(1), 1–21. https://doi.org/10.2307/2937053

Cohen, J. E., Schittler, D. N., Raffaelli, D. G., & Reuman, D. C. (2009). Food webs are more than the sum of their tritrophic parts. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(52), 22335–22340. https://doi.org/10.1073/pnas.0910582106

Constable, A. J., Harper, S., Dawson, J., Holsman, K., Mustonen, T., Piepenburg, D., & Rost,

B. (2022). Cross-Chapter Paper 6: Polar Regions. In *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. https://doi.org/10.1017/9781009325844.023.2319

Di Sabatino, A., Gerecke, R., & Martin, P. (2000). The biology and ecology of lotic water mites (Hydrachnidia). *Freshwater Biology*, *44*(1), 47–62. https://doi.org/10.1046/j.1365-2427.2000.00591.x

Didan, K. (2021). *MODIS/Aqua Vegetation Indices 16-Day L3 Global 250m SIN Grid V061 [Data set]*. NASA EOSDIS Land Processes Distributed Active Archive Center. https://doi.org/10.5067/MODIS/MYD13Q1.061

Dineen, G., Harrison, S. S. C., & Giller, P. S. (2007). Diet partitioning in sympatric Atlantic salmon and brown trout in streams with contrasting riparian vegetation. *Journal of Fish Biology*, *71*, 17–38. https://doi.org/10.1111/j.1095-8649.2007.01441.x

Einarsson, S. M., Guðbrandsson, J., & Guðmundsdottir, Á. K. (2020). *Viðmiðunarmörk hrygningar í Krossá á Skarðsströnd*. https://www.hafogvatn.is/static/research/files/1579074817-hv2020-03.pdf

Einarsson, S. M., Mills, D. H., & Johannsson, V. (1990). Utilisation of fluvial and lacustrine habitat by anadromous Atlantic salmon, Salmo salar L., in an Icelandic watershed. *Fisheries Research*, *10*(1–2), 53–71. https://doi.org/10.1016/0165-7836(90)90015-N

Ekologigruppen Ekoplan AB. (2021). *Bottenfaunaundersökning i Hallands län 2021*. https://catalog.lansstyrelsen.se/store/24/resource/165

Elliott, J. M., & Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*,

brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: Predicting the effects of climate change. *Journal of Fish Biology*, *77*(8), 1793–1817. https://doi.org/10.1111/j.1095-8649.2010.02762.x

Elliott, S. R., Coe, T. A., Helfield, J. M., & Naiman, R. J. (1998). Spatial variation in environmental characteristics of Atlantic salmon (*Salmo salar*) rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(SUPPL.1), 267–280. https://doi.org/10.1139/d98-001

Environmental data MVM. (2023). *National data host lakes and watercourses, and national data host agricultural land*. Swedish University of Agricultural Sciences (SLU). https://miljodata.slu.se/mvm/2023-10-11

Eriksson, F., Hörnström, E., Mossberg, P., & Nyberg, P. (1983). Ecological effects of lime treatment of acidified lakes and rivers in Sweden. *Hydrobiologia*, *101*(1–2), 145–163. https://doi.org/10.1007/BF00008667

Erkinaro, H., & Erkinaro, J. (1998). Feeding of Atlantic salmon, *Salmo salar L.*, parr in the subarctic River Teno and three tributaries in northernmost Finland. *Ecology of Freshwater Fish*, *7*(1), 13–24. https://doi.org/10.1111/j.1600-0633.1998.tb00168.x

Erkinaro, J., & Niemelä, E. (1995). Growth differences between the Atlantic salmon parr, Salmo salar, of nursery brooks and natal rivers in the River Teno watercourse in northern Finland. *Environmental Biology of Fishes*, *42*(3), 277–287. https://doi.org/10.1007/BF00004921

Erkinaro, J., Shustov, Y., & Niemelä, E. (1995). Enhanced growth and feeding rate in Atlantic salmon parr occupying a lacustrine habitat in the River Utsjoki, northern Scandinavia.

Journal of Fish Biology, *47*(6), 1096–1098. https://doi.org/10.1111/j.1095-8649.1995.tb06032.x

Fausch, K. D. (1998). Interspecific competition and juvenile Atlantic salmon (Salmo salar): On testing effects and evaluating the evidence across scales. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(SUPPL.1), 218–231. https://doi.org/10.1139/d98-006

Forseth, T., Barlaup, B. T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., Hindar, A., Mo, T. A., Rikardsen, A. H., Thorstad, E. B., Vøllestad, L. A., & Wennevik, V. (2017). The major threats to Atlantic salmon in Norway. In *ICES Journal of Marine Science* (Vol. 74, Issue 6). https://doi.org/10.1093/icesjms/fsx020

Fretwell, S. D. (1987). Food Chain Dynamics: The Central Theory of Ecology? *Oikos*, *50*(3), 291. https://doi.org/10.2307/3565489

Friberg, N., Milner, A. M., Svendsen, L. M., Lindegaard, C., & Larsen, S. E. (2001). Macroinvertebrate stream communities along regional and physico-chemical gradients in Western Greenland. *Freshwater Biology*, *46*(12), 1753–1764. https://doi.org/10.1046/j.1365-2427.2001.00857.x

Gerwing, T. G., & Plate, E. (2019). Effectiveness of nutrient enhancement as a remediation or compensation strategy of salmonid fisheries in culturally oligotrophic lakes and streams in temperate climates. *Restoration Ecology*, *27*(2), 279–288. https://doi.org/10.1111/rec.12909

Gibert, J. P. (2019). Temperature directly and indirectly influences food web structure. *Scientific Reports*, *9*(1), 1–8. https://doi.org/10.1038/s41598-019-41783-0

Gilbert, A. J. (2009). Connectance indicates the robustness of food webs when subjected to

species loss. *Ecological Indicators*, *9*(1), 72–80. https://doi.org/10.1016/j.ecolind.2008.01.010

Gíslason, G. M., Olafsson, J. S., & Hokon, A. (1999). Macroinvertebrate communities in Rivers in Iceland in Biodiversity in Benthic Ecology. *Proceedings from Nordic Benthological Meeting in Silkeborg, Denmark, 13-14 November 1997. NERI Technical Report No. 266, November*, 53–61.

Haase, P., Bowler, D. E., Baker, N. J., Bonada, N., Domisch, S., Garcia Marquez, J. R., Heino, J., Hering, D., Jähnig, S. C., Schmidt-Kloiber, A., Stubbington, R., Altermatt, F., Álvarez-Cabria, M., Amatulli, G., Angeler, D. G., Archambaud-Suard, G., Jorrín, I. A., Aspin, T., Azpiroz, I., … Welti, E. A. R. (2023). The recovery of European freshwater biodiversity has come to a halt. *Nature*, *620*(7974), 582–588. https://doi.org/10.1038/s41586-023-06400-1

Halvorsen, M., & Svenning, M. A. (2000). Growth of Atlantic salmon parr in fluvial and lacustrine habitats. *Journal of Fish Biology*, *57*(1), 145–160. https://doi.org/10.1006/jfbi.2000.1296

Hannesdóttir, E. R., Gíslason, G. M., Ólafsson, J. S., Ólafsson, Ó. P., & O'Gorman, E. J. (2013). Increased Stream Productivity with Warming Supports Higher Trophic Levels. In *Advances in Ecological Research* (Vol. 48). https://doi.org/10.1016/B978-0-12-417199-2.00005-7

Hansen, I., & Eiríksdóttir, E. S. (2021). *Ástandsflokkun straumvatna út frá tegundasamsetningu kísilþörunga*. https://www.hafogvatn.is/static/research/files/hv2021-11.pdf

Heino, J., Culp, J. M., Erkinaro, J., Goedkoop, W., Lento, J., Rühland, K. M., & Smol, J. P.

(2020). Abruptly and irreversibly changing Arctic freshwaters urgently require standardized monitoring. *Journal of Applied Ecology*, *57*(7), 1192–1198. https://doi.org/10.1111/1365-2664.13645

Heino, J., Erkinaro, J., Huusko, A., & Luoto, M. (2016). Climate change effects on freshwater fishes, conservation and management. In G. P. Closs, M. Krkosek, & J. D. Olden (Eds.), *Conservation of Freshwater Fishes* (pp. 76–106). Cambridge University Press.

Hijmans, R. J. (2023). *raster: Geographic Data Analysis and Modeling*. https://rspatial.org/raster

Hillebrand, H., Dürselen, C. D., Kirschtel, D., Pollingher, U., & Zohary, T. (1999). Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology*, *35*(2), 403–424. https://doi.org/10.1046/j.1529-8817.1999.3520403.x

Huang, S., Tang, L., Hupy, J. P., Wang, Y., & Shao, G. (2021). A commentary review on the use of normalized difference vegetation index (NDVI) in the era of popular remote sensing. *Journal of Forestry Research*, *32*(1), 1–6. https://doi.org/10.1007/s11676-020-01155-1

Hudson, L. N., Emerson, R., Jenkins, G. B., Layer, K., Ledger, M. E., Pichler, D. E., Thompson, M. S. A., O'Gorman, E. J., Woodward, G., & Reuman, D. C. (2013). Cheddar: Analysis and visualisation of ecological communities in R. *Methods in Ecology and Evolution*, *4*(1), 99–104. https://doi.org/10.1111/2041-210X.12005

ICES. (2022). Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*, *4*(39), 39. https://doi.org/http://doi.org/10.17895/ices.pub.19697368

ICES. (2023). Working Group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*,

5(41), 477. https://doi.org/https://doi.org/10.17895/ices.pub.22743713

Ingimarsson, F. (2022). *Vöktun á lífríki Elliðaánna Náttúrufræðistofa Kópavogs*. *4*. https://www.hafogvatn.is/static/research/files/hv2023_42.pdf

Jake Vander Zanden, M., & Fetzer, W. W. (2007). Global patterns of aquatic food chain length. *Oikos*, *116*(8), 1378–1388. https://doi.org/10.1111/j.0030-1299.2007.16036.x

Johansen, M., Elliott, J. M., & Klemetsen, A. (2005). Relationships between juvenile salmon, *Salmo salar L.*, and invertebrate densities in the River Tana, Norway. *Ecology of Freshwater Fish*, *14*(4), 331–343. https://doi.org/10.1111/j.1600-0633.2005.00107.x

Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. *Journal of Fish Biology*, *75*(10), 2381–2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x

Jørgensen, L., Halvorsen, M., & Amundsen, P. A. (2000). Resource partitioning between lake-dwelling Atlantic salmon (Salmo salar L.) parr, brown trout (Salmo trutta L.) and Arctic charr (Salvelinus alpinus (L.)). *Ecology of Freshwater Fish*, *9*(4), 202–209. https://doi.org/10.1111/j.1600-0633.2000.eff090402.x

Kahlert, M., Rühland, K. M., Lavoie, I., Keck, F., Saulnier-Talbot, E., Bogan, D., Brua, R. B., Campeau, S., Christoffersen, K. S., Culp, J. M., Karjalainen, S. M., Lento, J., Schneider, S. C., Shaftel, R., & Smol, J. P. (2022). Biodiversity patterns of Arctic diatom assemblages in lakes and streams: Current reference conditions and historical context for biomonitoring. *Freshwater Biology*, *67*(1), 116–140. https://doi.org/10.1111/fwb.13490

Kang, H.-K., & Kang, Y. J. (1997). Length and Weight Relationship of Acartia

steueri(Copepoda: Calanoida) in ilkwang Bay, Korea. *Korean Journal of Fisheries and Aquatic Sciences*, *30*(5), 30(5), 906–908. https://www.koreascience.or.kr/article/JAKO199723607645201.page

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar L.*, brown trout *Salmo trutta L.* and Arctic charr *Salvelinus alpinus* (L.): A review of aspects of their life histories. *Ecology of Freshwater Fish*, *12*(1), 1–59. https://doi.org/10.1034/j.1600-0633.2003.00010.x

Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A. V., & Planque, B. (2019). Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. *Ecography*, *42*(2), 295–308. https://doi.org/10.1111/ecog.03443

Kosten, S., Huszar, V. L. M., Bécares, E., Costa, L. S., van Donk, E., Hansson, L. A., Jeppesen, E., Kruk, C., Lacerot, G., Mazzeo, N., De Meester, L., Moss, B., Lürling, M., Nõges, T., Romo, S., & Scheffer, M. (2012). Warmer climates boost cyanobacterial dominance in shallow lakes. *Global Change Biology*, *18*(1), 118–126. https://doi.org/10.1111/j.1365-2486.2011.02488.x

Kubelka, V., Sandercock, B. K., Székely, T., & Freckleton, R. P. (2022). Animal migration to northern latitudes: environmental changes and increasing threats. *Trends in Ecology and Evolution*, *37*(1), 30–41. https://doi.org/10.1016/j.tree.2021.08.010

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/JSS.V082.I13

Lamberti, G. A., & Steinman, A. D. (1997). A comparison of primary production in stream

ecosystems. *Journal of the North American Benthological Society*, *16*(1), 95–104. https://doi.org/10.2307/1468241

Laske, S. M., Amundsen, P. A., Christoffersen, K. S., Erkinaro, J., Guðbergsson, G., Hayden, B., Heino, J., Holmgren, K., Kahilainen, K. K., Lento, J., Orell, P., Östergren, J., Power, M., Rafikov, R., Romakkaniemi, A., Svenning, M. A., Swanson, H., Whitman, M., & Zimmerman, C. E. (2022). Circumpolar patterns of Arctic freshwater fish biodiversity: A baseline for monitoring. *Freshwater Biology*, *67*(1), 176–193. https://doi.org/10.1111/fwb.13405

Lento, J., Culp, J. M., Levenstein, B., Aroviita, J., Baturina, M. A., Bogan, D., Brittain, J. E., Chin, K., Christoffersen, K. S., Docherty, C., Friberg, N., Ingimarsson, F., Jacobsen, D., Lau, D. C. P., Loskutova, O. A., Milner, A., Mykrä, H., Novichkova, A. A., Ólafsson, J. S., … Goedkoop, W. (2022a). Temperature and spatial connectivity drive patterns in freshwater macroinvertebrate diversity across the Arctic. *Freshwater Biology*, *67*(1), 159–175. https://doi.org/10.1111/fwb.13805

Lento, J., Laske, S. M., Lavoie, I., Bogan, D., Brua, R. B., Campeau, S., Chin, K., Culp, J. M., Levenstein, B., Power, M., Saulnier-Talbot, É., Shaftel, R., Swanson, H., Whitman, M., & Zimmerman, C. E. (2022b). Diversity of diatoms, benthic macroinvertebrates, and fish varies in response to different environmental correlates in Arctic rivers across North America. *Freshwater Biology*, *67*(1), 95–115. https://doi.org/10.1111/fwb.13600

MacCrimmon, H. R., & Gots, B. L. (1979). World Distribution of Atlantic Salmon, *Salmo salar*. *Journal of the Fisheries Research Board of Canada*, *36*(4), 422–457. https://doi.org/10.1139/f79-062

Marsh, J. E., Lauridsen, R. B., Gregory, S. D., Kratina, P., Scott, L. J., Cooling, D., & Jones, J.

I. (2022). High summer macrophyte cover increases abundance, growth, and feeding of juvenile Atlantic salmon. *Ecological Applications*, *32*(2). https://doi.org/10.1002/eap.2492

McCann, K. S., Rasmussen, J. B., & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. *Ecology Letters*, *8*(5), 513–523. https://doi.org/10.1111/j.1461-0248.2005.00742.x

McCann, K. S., & Rooney, N. (2009). The more food webs change, the more they stay the same. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1524), 1789–1801. https://doi.org/10.1098/rstb.2008.0273

Metcalfe, N. B., & Thorpe, J. E. (1990). Determinants of Geographical Variation in the Age of Seaward-Migrating Salmon, Salmo salar. *The Journal of Animal Ecology*, *59*(1), 135. https://doi.org/10.2307/5163

Méthot, G., Hudon, C., Gagnon, P., Pinel-Alloul, B., Armellin, A., & Poirier, A. M. T. (2012). Macroinvertebrate size-mass relationships: How specific should they be? *Freshwater Science*, *31*(3), 750–764. https://doi.org/10.1899/11-120.1

Ministry for the Environment, & The Icelandic Institute of Natural History. (2001). Biological diversity in Iceland - National Report to the Convention on Biological Diversity. In *Natural History*. https://www.cbd.int/doc/world/is/is-nr-01-en.pdf

Nordström, M., Aarnio, K., & Bonsdorff, E. (2009). Temporal variability of a benthic food web: Patterns and processes in a low-diversity system. *Marine Ecology Progress Series*, *378*, 13–26. https://doi.org/10.3354/meps07872

O'Connor, M. I., Piehler, M. F., Leech, D. M., Anton, A., & Bruno, J. F. (2009). Warming and

resource availability shift food web structure and metabolism. *PLoS Biology, 7*(8), 3–8. https://doi.org/10.1371/journal.pbio.1000178

O'Gorman, E. J., & Emmerson, M. C. (2010). Manipulating Interaction Strengths and the Consequences for Trivariate Patterns in a Marine Food Web. *Advances in Ecological Research, 42*(C), 301–419. https://doi.org/10.1016/B978-0-12-381363-3.00006-X

O'Gorman, E. J., Ólafsson, Ó. P., Demars, B. O. L., Friberg, N., Guðbergsson, G., Hannesdóttir, E. R., Jackson, M. C., Johansson, L. S., McLaughlin, Ó. B., Ólafsson, J. S., Woodward, G., & Gíslason, G. M. (2016). Temperature effects on fish production across a natural thermal gradient. *Global Change Biology*, *22*(9), 3206–3220. https://doi.org/10.1111/gcb.13233

O'Gorman, E. J., Petchey, O. L., Faulkner, K. J., Gallo, B., Gordon, T. A. C., Neto-Cerejeira, J., Ólafsson, J. S., Pichler, D. E., Thompson, M. S. A., & Woodward, G. (2019). A simple model predicts how warming simplifies wild food webs. *Nature Climate Change*, *9*(8), 611–616. https://doi.org/10.1038/s41558-019-0513-x

O'Gorman, E. J., Zhao, L., Kordas, R. L., Dudgeon, S., & Woodward, G. (2023). Warming indirectly simplifies food webs through effects on apex predators. *Nature Ecology & Evolution*, *7*(12), 1983–1992. https://doi.org/10.1038/s41559-023-02216-4

O'Gorman, E. J., Zhao, L., Pichler, D. E., Adams, G., Friberg, N., Rall, B. C., Seeney, A., Zhang, H., Reuman, D. C., & Woodward, G. (2017). Unexpected changes in community size structure in a natural warming experiment. *Nature Climate Change, 7*(9), 659–663. https://doi.org/10.1038/nclimate3368

Parmesan, C., Morecroft, M. D., Trisurat, Y., Adrian, R., Anshari, G. Z., Arneth, A., Gao, Q.,

Gonzalez, P., Harris, R., Price, J., Stevens, N., & Talukdar, G. H. (2023). Terrestrial and Freshwater Ecosystems and Their Services. In H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama (Eds.), *Climate Change 2022 – Impacts, Adaptation and Vulnerability* (pp. 197–378). Cambridge University Press. https://doi.org/10.1017/9781009325844.004

Perkins, D. M., Durance, I., Edwards, F. K., Grey, J., Hildrew, A. G., Jackson, M., Jones, J. I., Lauridsen, R. B., Layer-Dobra, K., Thompson, M. S. A., & Woodward, G. (2018). Bending the rules: exploitation of allochthonous resources by a top-predator modifies size-abundance scaling in stream food webs. *Ecology Letters*, *21*(12), 1771–1780. https://doi.org/10.1111/ele.13147

Perkins, D. M., Reiss, J., Yvon-Durocher, G., & Woodward, G. (2010). Global change and food webs in running waters. *Hydrobiologia*, *657*(1), 181–198. https://doi.org/10.1007/s10750-009-0080-7

Petchey, O. L., McPhearson, P. T., Casey, T. M., & Morin, P. J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, *402*(6757), 69–72. https://doi.org/10.1038/47023

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution*, *20*(9), 503–510. https://doi.org/10.1016/j.tree.2005.05.011

Proctor, H., & Pritchard, G. (1989). Neglected Predators: Water Mites (Acari:Parasitengona:Hydrachnellae) in Freshwater Communities. *Journal of the North*

American Benthological Society, *8*(1), 100–111. https://doi.org/10.2307/1467406

QGIS.org. (2023). *QGIS Geographic Information System*. http://qgis.org

R Core Team. (2023). R: A Language and Environment for Statistical Computing. In *R Foundation for Statistical Computing* (p. https://www.R-project.org). R Foundation for Statistical Computing,Vienna, Austria. http://www.r-project.org

Ramsay, P. M., Rundle, S. D., Attrill, M. J., Uttley, M. G., Williams, P. R., Elsmere, P. S., & Abada, A. (1997). A rapid method for estimating biomass size spectra of benthic metazoan communities. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(8), 1716–1724. https://doi.org/10.1139/cjfas-54-8-1716

Rist, S. (1990). Viðauki I. Vatnasvið Íslands. In *Vatns er pörf* (pp. 203–234). Bókaútgáfa Menningarsjóðs.

Rolls, R. J., Hayden, B., & Kahilainen, K. K. (2017). Conceptualising the interactive effects of climate change and biological invasions on subarctic freshwater fish. *Ecology and Evolution*, *7*(12), 4109–4128. https://doi.org/10.1002/ece3.2982

Rosi-Marshall, E. J., Wellard Kelly, H. A., Hall, R. O., & Vallis, K. A. (2016). Methods for quantifying aquatic macroinvertebrate diets. *Freshwater Science*, *35*(1), 229–236. https://doi.org/10.1086/684648

Rypel, A. L., & David, S. R. (2017). Pattern and scale in latitude-production relationships for freshwater fishes. *Ecosphere*, *8*(1). https://doi.org/10.1002/ecs2.1660

Sabo, J. L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Heffernan, J., Jani, A., Katz, G., Soykan, C., Watts, J., & Welter, J. (2005). Riparian zones increase regional species

richness by harboring different, not more, species. *Ecology*, *86*(1), 56–62. https://doi.org/10.1890/04-0668

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Shah, D. N., Tonkin, J. D., Haase, P., & Jähnig, S. C. (2015). Latitudinal patterns and large-scale environmental determinants of stream insect richness across Europe. *Limnologica*, *55*, 33–43. https://doi.org/10.1016/j.limno.2015.11.001

Spaulding, S. A., Potapova, M. G., Bishop, I. W., Lee, S. S., Gasperak, T. S., Jovanoska, E., Furey, P. C., & Edlund, M. B. (2021). Diatoms.org: supporting taxonomists, connecting communities. *Diatom Research*, *36*(4), 291–304. https://doi.org/10.1080/0269249X.2021.2006790

Steingrímsson, S. Ã., & Gíslason, G. M. (2002). Body size, diet and growth of landlocked brown trout, Salmo trutta, in the subarctic River Laxá, North-East Iceland. *Environmental Biology of Fishes*, *63*(4), 417–426. https://doi.org/10.1023/A:1014976612970

Sturlaugsson, J. (2023). *Elliðaár 2022- Rannsóknir á fiskistofnum vatnakerfisins*. https://www.laxfiskar.is/images/stories/skyrslur/Ellidaar_2022-Fiskirannsoknir-Johannes_Sturlaugsson-Laxfiskar_april2023.pdf

Svenning, M. A., Falkegård, M., Dempson, J. B., Power, M., Bårdsen, B. J., Guðbergsson, G., & Fauchald, P. (2022). Temporal changes in the relative abundance of anadromous Arctic charr, brown trout, and Atlantic salmon in northern Europe: Do they reflect changing climates? *Freshwater Biology*, *67*(1), 64–77. https://doi.org/10.1111/fwb.13693

Syrjänen, J., Korsu, K., Louhi, P., Paavola, R., & Muotka, T. (2011). Stream salmonids as

opportunistic foragers: The importance of terrestrial invertebrates along a stream-size gradient. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*(12), 2146–2156. https://doi.org/10.1139/F2011-118

Thompson, M. S. A., Brooks, S. J., Sayer, C. D., Woodward, G., Axmacher, J. C., Perkins, D. M., & Gray, C. (2018). Large woody debris "rewilding" rapidly restores biodiversity in riverine food webs. *Journal of Applied Ecology*, *55*(2), 895–904. https://doi.org/10.1111/1365-2664.13013

Thompson, R. M., Brose, U., Dunne, J. A., Hall, R. O., Hladyz, S., Kitching, R. L., Martinez, N. D., Rantala, H., Romanuk, T. N., Stouffer, D. B., & Tylianakis, J. M. (2012a). Food webs: Reconciling the structure and function of biodiversity. *Trends in Ecology and Evolution*, *27*(12), 689–697. https://doi.org/10.1016/j.tree.2012.08.005

Thompson, R. M., Dunne, J. A., & Woodward, G. (2012b). Freshwater food webs: Towards a more fundamental understanding of biodiversity and community dynamics. *Freshwater Biology*, *57*(7), 1329–1341. https://doi.org/10.1111/j.1365-2427.2012.02808.x

Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., & Finstad, B. (2012). A critical life stage of the Atlantic salmon Salmo salar: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, *81*(2), 500–542. https://doi.org/10.1111/j.1095-8649.2012.03370.x

Todd, C. D., Friedland, K. D., MacLean, J. C., Hazon, N., & Jensen, A. J. (2011). Getting into Hot Water? Atlantic Salmon Responses to Climate Change in Freshwater and Marine Environments. In *Atlantic Salmon Ecology*. https://doi.org/10.1002/9781444327755.ch16

Traugott, M., Thalinger, B., Wallinger, C., & Sint, D. (2020). Fish as predators and prey: DNA-

based assessment of their role in food webs. *Journal of Fish Biology*, *43*(0), 1–43. https://doi.org/10.1111/jfb.14400

Vincent, W. F., Hobbie, J. E., & Laybourn-Parry, J. (2008). Introduction to the limnology of high-latitude lake and river ecosystems. In *Polar Lakes and Rivers* (pp. 1–17). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199213887.003.0001

Woodward, G., Morris, O., Barquín, J., Belgrano, A., Bull, C., de Eyto, E., Friberg, N., Guðbergsson, G., Layer-Dobra, K., Lauridsen, R. B., Lewis, H. M., McGinnity, P., Pawar, S., Rosindell, J., & O'Gorman, E. J. (2021). Using Food Webs and Metabolic Theory to Monitor, Model, and Manage Atlantic Salmon—A Keystone Species Under Threat. *Frontiers in Ecology and Evolution*, *9*(December), 1–10. https://doi.org/10.3389/fevo.2021.675261

Woodward, G., Papantoniou, G., Edwards, F., & Lauridsen, R. B. (2008). Trophic trickles and cascades in a complex food web: Impacts of a keystone predator on stream community structure and ecosystem processes. *Oikos*, *117*(5), 683–692. https://doi.org/10.1111/j.0030-1299.2008.16500.x

Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: Impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2093–2106. https://doi.org/10.1098/rstb.2010.0055

Wright, J. F., Gunn, R. J. M., Symes, K. L., Matthews, A. M., Furse, M. T., Blackburn, J. H., & Winder, J. M. (1992). *Invertebrate survey and classification of rivers for nature conservation*. https://nora.nerc.ac.uk/id/eprint/12886

Wrona, F. J., Prowse, T. D., Reist, J. D., Hobbie, J. E., Lévesque, L. M. J., & Vincent, W. F. (2006). Climate change effects on aquatic biota, ecosystem structure and function. *Ambio*, *35*(7), 359–369. https://doi.org/10.1579/0044-7447(2006)35[359:CCEOAB]2.0.CO;2

Figures:

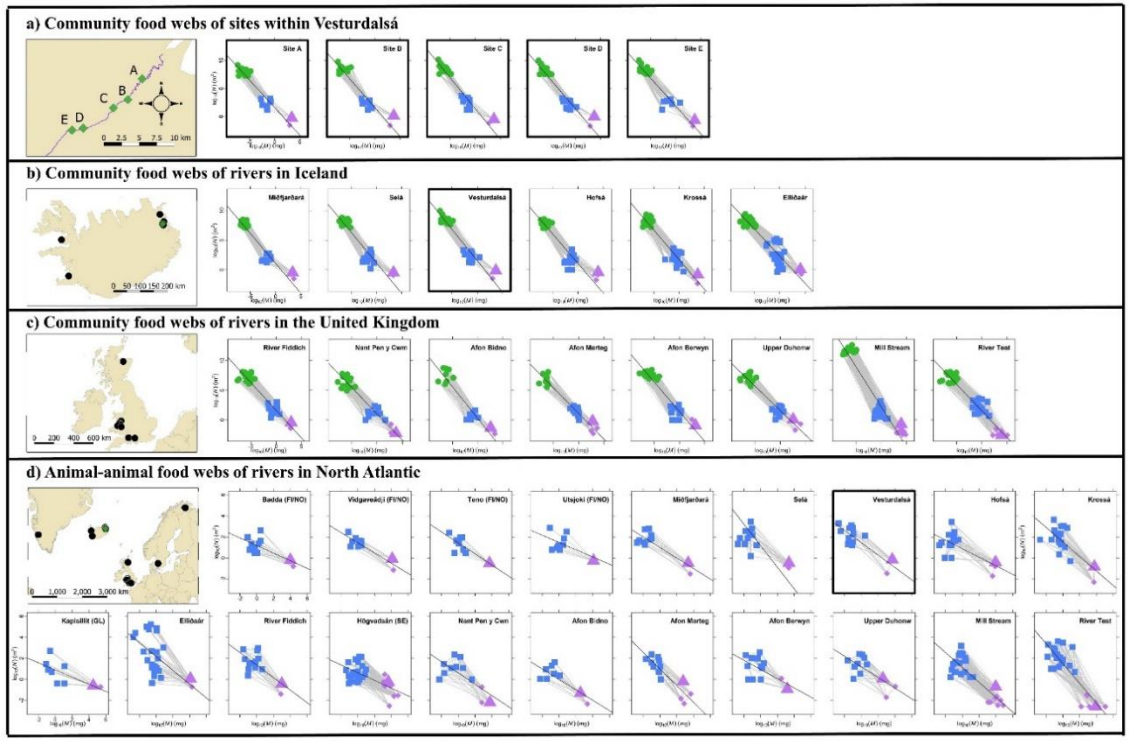

Figure 1: Log_{10} M-N trivariate community food webs with increasing spatial scale a) from within sites of Vesturdalsá, to b) Atlantic salmon rivers in Iceland, and c) Atlantic salmon rivers in the United Kingdom. d) Log_{10} M-N animal-animal food webs of Atlantic salmon rivers in the North Atlantic. Animal-animal food webs represent the invertebrate and fish predator-prey relationships within the river. Black points on the map to the left shows the sites/rivers of the food webs, and the green diamond is Vesturdalsá. Food webs of Vesturdalsá are also highlighted. Left to right figures in decreasing latitude. Green circle points represent producer species, blue square points represent macroinvertebrate species, purple triangle point represent Salmo salar, and purple diamond points represent other fish species, grey lines show feeding interactions, and the black line represents the slope of the food web.

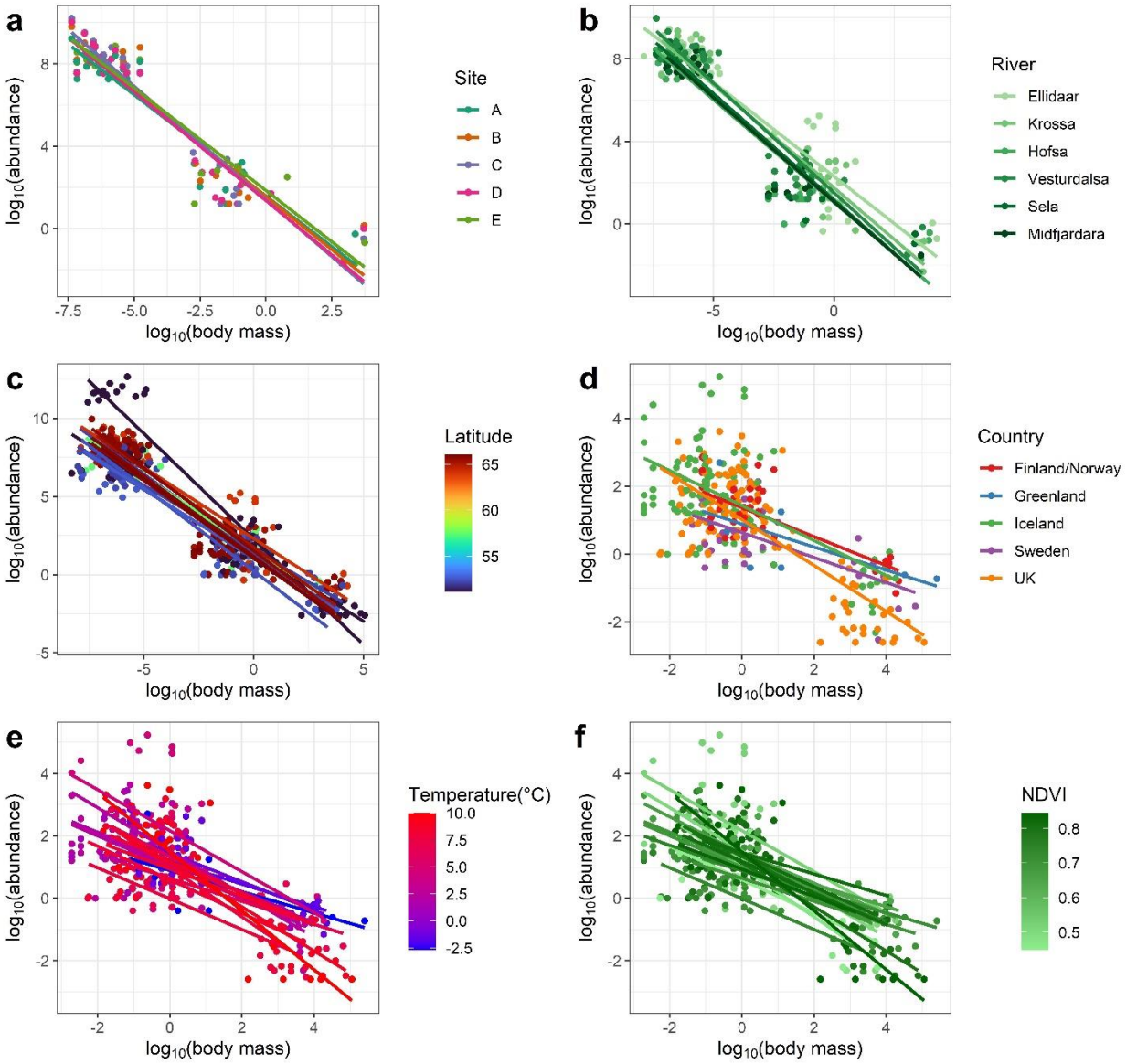

Figure 2: Linear regressions of log-log M-N food web relationship of a) food webs across sites in Vesturdalsá, b) food webs across the latitudinal gradient in Iceland, c) food webs across the latitudinal gradient in Iceland and UK. Linear regressions of log-log M-N predator-prey relationships of Atlantic salmon rivers in d) different countries, e) the temperature gradient, and f) the productivity gradient in the North Atlantic.

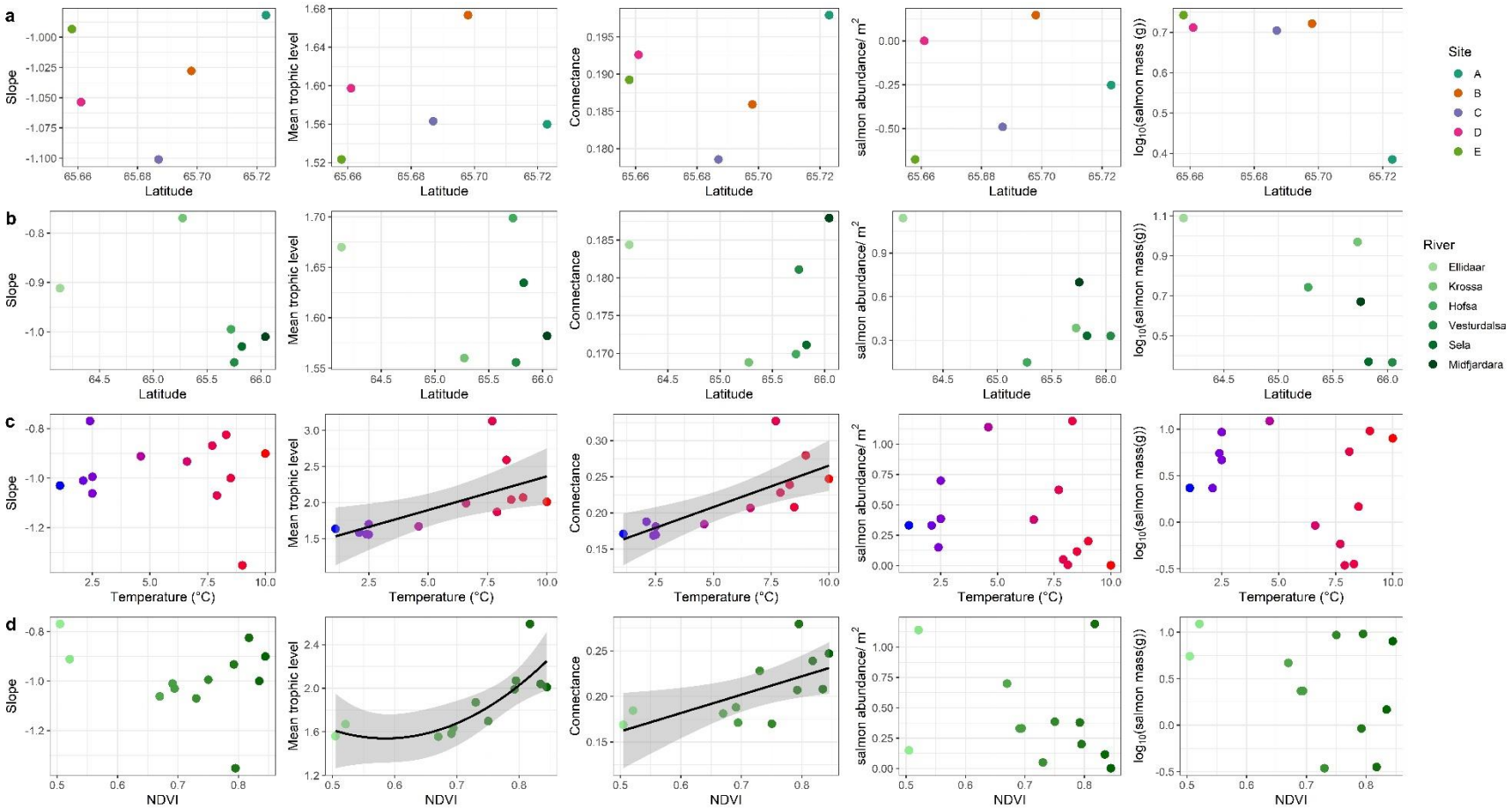

Figure 3: Linear and polynomial regressions of trivariate community food web properties (slope, mean trophic level, connectance) and characteristics (Atlantic salmon abundance and mass) along the latitudinal gradient in increasing spatial scales from a) sites within Vesturdalsá to b) rivers in Iceland. Linear regressions of trivariate food web properties and characteristics of rivers in Iceland and UK were also compared along c) temperature and d) NDVI gradient.

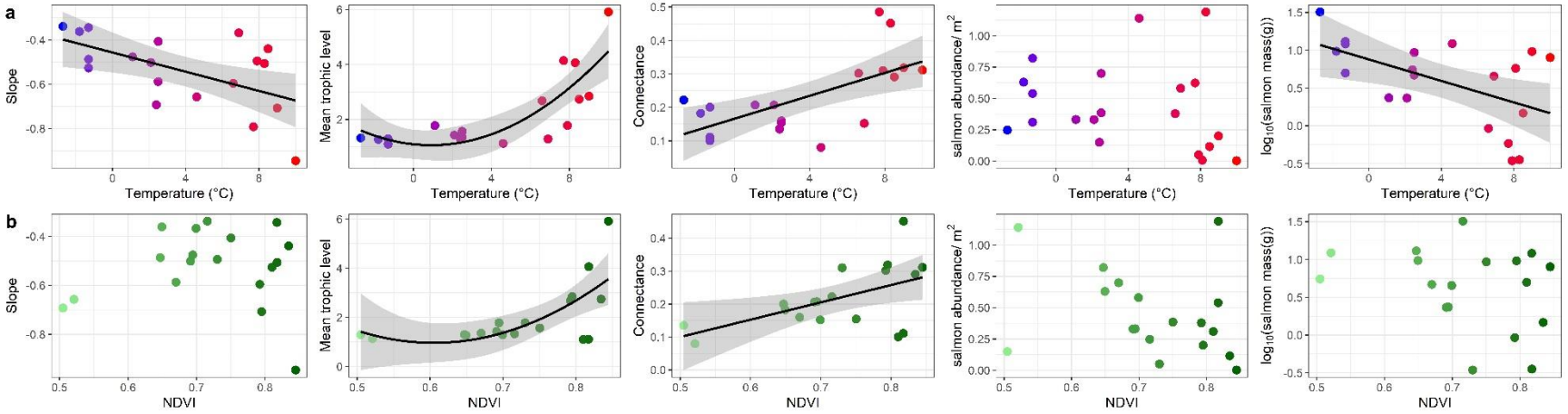

Figure 4: Linear and polynomial regressions of animal-animal food web properties (slope, mean trophic level, connectance) and characteristics (Atlantic salmon abundance and mass) along the a) temperature, and b) NDVI gradient for all rivers in the North Atlantic.

Supporting Information:

17. Dataset sources of food webs

Table S1: List of datasets used to build food webs for different rivers. 1: (Arnekleiv et al., 2019); 2: (Anon, 2023); 3: (Erkinaro & Erkinaro, 1998); 4: (Hansen & Eiríksdóttir, 2021); 5: data provided by Jón S. Ólafsson; 6: (Einarsson et al., 2020); 7: (Ingimarsson, 2022); 8: (Sturlaugsson, 2023); 9: (Perkins et al., 2018); 10: (Swedish University of Agricultural Sciences (SLU), 2023); 11: (Bergh, 2022; Ekologigruppen Ekoplan AB, 2021); 12: (Bárðarson et al., 2023)

River	Diatom data		Invertebrate data		Fish data		
	Density	size	Density	size	Density	size	Gut content/trophic links
Kapisillit			✓[1]		✓[1]	✓[1]	✓[1]
Badda			✓[2]		✓[2]	✓[2]	✓[3]
Vidgaveädji			✓[2]		✓[2]	✓[2]	✓[3]
Teno			✓[2]		✓[2]	✓[2]	✓[3]
Utsjoki			✓[2]		✓[2]	✓[2]	✓[3]
Krossá	✓[4]		✓[5]		✓[6]	✓[6]	✓[6]
Elliðaár	✓	✓	✓[7]		✓[8]	✓[8]	✓[8]
Afon Berwyn	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]
Afon Bidno	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]
Fiddich	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]
Afon Marteg	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]
Nant Pen y Cwn	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]
Test	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]
Upper Duhonw	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]
Mill Stream	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]	✓[9]
Högvadsån			✓[10,11]		✓[11]	✓[11]	
Vesturdalsá	✓	✓	✓	✓	✓[12]	✓[12]	✓
Selá	✓	✓	✓	✓	✓[12]	✓[12]	✓
Hofsá	✓	✓	✓	✓	✓[12]	✓[12]	✓
Midfjardará	✓	✓	✓	✓	✓[12]	✓[12]	✓

18. Food web properties and statistical output of comparison between sites within Vesturdalsá

Table S2: Food web properties of sites in Vesturdalsá.

Site	Overall M-N slope	M-N Slope of producer	M-N Slope of invertebrate	M-N Slope of fish	Mean trophic level	Connectance	Mean chain length	Mean link angle
A	-0.982	-0.245	0.123	3.05	1.56	0.198	9.68	-45.0
B	-1.03	-0.0208	-0.470	2.39	1.67	0.186	9.58	-47.8
C	-1.10	-0.54	-0.817	0.645	1.56	0.179	9.69	-47.9
D	-1.05	-0.470	-0.415	2.01	1.60	0.193	9.87	-46.5
E	-0.993	-0.414	0.171	2.77	1.52	0.189	10.1	-49.1

Table S3: Statistical output from ANOVA analysis of a linear mixed effects model across different sites in Vesturdalsá. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and site were fixed effects. 'Nodes' were a random effect in the model. The summary table is shown with DF values (degree of freedom), F values, and P values.

	DF	F value	P value[†]
(Intercept)	1	886	***
log_{10}(Mass)	1	287	***
Site	4	1.01	0.406
log_{10}(Mass) × Site	4	1.81	0.135

[†] if p<0.05 it is shown with *, if a p<0.01 it is shown with **, and if a p<0.001 it is shown with ***, non-significant p-values are written out.

Table S4: Statistical output of linear models of a) salmon abundance per m^2, b) log_{10} mean salmon mass (g), c) slope, d) connectance, e) mean chain length, f) mean link angle, and g) mean trophic level of food webs along the latitudinal gradient in Vesturdalsá. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	Estimate	SE	t value	P value†
a) LM with salmon abundance per m^2				
Intercept	-202	685	-0.295	0.787
Latitude	3.09	10.4	0.296	0.786
b) LM with log_{10} mean salmon mass (g)				
Intercept	293	127	2.32	0.104
Latitude	-4.46	1.93	-2.31	0.104
c) LM with slope				
Intercept	-30.2	65.4	-0.463	0.675
Latitude	0.445	0.995	0.447	0.685
d) LM with connectance				
Intercept	-3.99	9.89	-0.403	0.714
Latitude	0.0636	0.151	0.422	0.701
e) LM with mean chain length				
Intercept	372	162	2.30	0.105
Latitude	-5.51	2.46	-2.24	0.111
f) LM with mean link angle				
Intercept	-2470	1640	-1.50	0.230
Latitude	36.8	25.0	1.47	0.237
g) LM with mean trophic level				
Intercept	-32.7	77.0	-0.425	0.700
Latitude	0.522	1.17	0.445	0.686

19. Food web properties of salmon rivers

Table S5: Food web properties of salmon rivers in Iceland (IS) and United Kingdom (UK).

River	Country	Overall M-N slope	M-N slope of producer	M-N slope of invertebrate	M-N slope of fish	Connectance	Mean trophic level	Mean chain length	Mean link angle
Vesturdalsá	IS	-1.06	-0.380	-0.284	2.09	0.181	1.56	10.0	-47.0
Hofsá	IS	-0.995	-0.0514	0.454	3.39	0.170	1.70	9.46	-48.3
Selá	IS	-1.03	-0.128	0.137	15.3	0.171	1.63	9.17	-48.0
Midfjardará	IS	-1.01	-0.169	0.357	-4.25	0.188	1.58	9.49	-47.9
Krossá	IS	-0.770	0.091	-0.304	-2.10	0.169	1.56	12.0	-42.7
Elliðaár	IS	-0.912	-0.282	-0.795	-4.42	0.184	1.67	10.2	-41.1
Mill Stream	UK	-1.35	0.186	-0.145	-0.111	0.280	2.07	11.6	-39.0
Afon Berwyn	UK	-1.00	-0.210	0.0208	-1.54	0.208	2.04	9.96	-38.3
Afon Bidno	UK	-1.07	0.201	0.338	-1.26	0.228	1.87	9.15	-34.0
Fiddich	UK	-0.933	-0.0152	0.0408	9.18	0.207	1.99	9.13	-33.8
Afon Marteg	UK	-0.869	0.141	-0.648	0.0505	0.327	3.13	8.51	-26.2
Nant Pen y Cwm	UK	-0.889	-0.162	0.0474	-0.769	0.226	2.11	9.34	-34.2
Test	UK	-0.901	0.0933	-0.208	-0.243	0.247	2.01	8.77	-36.1
Upper Duhonw	UK	-0.825	0.0216	0.301	-0.212	0.239	2.59	8.76	-30.4

20. Statistical output of food webs in Iceland.

Table S6: Statistical output from ANOVA analysis of a linear mixed effects model across different rivers in Iceland. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and rivers were fixed effects. 'Nodes' were a random effect in the model. The summary table is shown with DF values (degree of freedom), F values, and P values.

	DF	F value	P value†
(Intercept)	1	1900	***
log_{10}(Mass)	1	703	***
River	5	10.7	***
log_{10}(Mass) × River	5	2.24	0.0545

Table S7: Statistical output of linear models of properties of a) log_{10} mean salmon abundance per m^2, b) log_{10} mean salmon biomass (g), c) slope, d) connectance, e) mean trophic level, f) mean chain length, and g) mean link angle of food webs in Iceland. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	Estimate	SE	t value	P value†
a) LM with mean salmon abundance per m^2				
Intercept	25.2	11.4	2.21	0.0920
Latitude	-0.378	0.175	-2.16	0.0967
b) LM with log_{10}(mean salmon mass (g))				
Intercept	21.6	9.36	2.31	0.0819
Latitude	-0.320	0.143	-2.24	0.0890
c) LM with slope				
Intercept	4.26	4.30	0.989	0.379
Latitude	-0.0798	0.0658	-1.21	0.292
d) LM with connectance				
Intercept	0.305	0.384	0.795	0.471
Latitude	-0.00196	0.00587	-0.333	0.756
e) LM with mean trophic level				
Intercept	3.50	2.66	1.32	0.258
Latitude	-0.0288	0.0406	-0.710	0.517
f) LM with mean chain length				
Intercept	45.8	44.3	1.03	0.360
Latitude	-0.547	0.677	-0.807	0.465
g) LM with mean link angle				
Intercept	218	62.2	3.50	*
Latitude	-4.03	0.950	-4.24	*

† if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

21. **Comparison of food webs of salmon rivers across the North Atlantic.**

Table S8: Statistical output from linear mixed effects model of food webs in rivers in UK and Iceland across latitudes. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and latitudinal degree were fixed effects. 'Nodes' and 'river' were a random effect in the model. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	value	SE	t value	P value†
(Intercept)	0.121	0.785	0.155	0.877
log_{10}(Mass)	-1.22	0.174	-6.98	0.00
Latitude	0.0246	0.0136	1.81	0.0713
log_{10}(Mass) × Latitude	0.00438	0.00301	1.45	0.147

Table S9: Statistical output from linear mixed effects model of food webs in rivers in UK and Iceland across the temperature gradient. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and temperature (°C) were fixed effects. 'Nodes' and 'river' were a random effect in the model. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	value	SE	t value	P value†
(Intercept)	1.68	0.235	7.12	0.00
log_{10}(Mass)	-0.928	0.0492	-18.8	0.00
Temperature	-0.0231	0.0297	-0.779	0.437
log_{10}(Mass) × Temperature	-0.00655	0.00644	-1.02	0.310

Table S10: Statistical output from linear mixed effects model of food webs in rivers in UK and Iceland across the NDVI gradient. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and NDVI were fixed effects. 'Nodes' and 'river' were a random effect in the model. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	value	SE	t value	P value†
(Intercept)	1.63	0.409	3.99	0.0001
log_{10}(Mass)	-0.812	0.0874	-9.29	0.00
NDVI	-0.151	0.554	-0.273	0.785
log_{10}(Mass) × NDVI	-0.232	0.120	-1.93	0.0544

† if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

Table S11: Statistical output from ANOVA analysis of linear mixed effects models of food webs in rivers between UK and Iceland. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and country were fixed effects. 'Nodes' and 'river' were a random effect in the model. Summary tables are shown with DF values (degree of freedom), F values, and P values.

	DF	F value	P value†
(Intercept)	1	2480	***
log_{10}(Mass)	1	1320	***
Country	1	3.85	*
log_{10}(Mass) × Country	1	1.38	0.240

Table S12: Statistical output of linear and polynomial models of properties of a) mean salmon abundance, b) log_{10} mean salmon mass, c) slope, d) connectance, e) mean trophic level, f) mean chain length, and g) mean link angle of food webs in Iceland and UK along the latitudinal gradient (Figure S3). Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	Estimate	SE	t value	P value†
a) LM with mean salmon abundance per m^2				
Intercept	-0.362	0.943	-0.383	0.708
Latitude	0.0131	0.0161	0.813	0.432
b) LM with log_{10}(mean salmon mass (g))				
Intercept	-1.39	1.26	-1.10	0.291
Latitude	0.0310	0.0215	1.45	0.174
c) LM with slope				
Intercept	-1.15	0.373	-3.08	*
Latitude	0.00289	0.00633	0.456	0.657
d) LM with connectance				
Intercept	0.548	0.0736	7.45	***
Latitude	-0.00568	0.00125	-4.55	***
e) LM with mean trophic level				
Intercept	4.77	0.836	5.71	***
Latitude	-0.0481	0.0142	-3.39	**
f) LM with mean chain length				
Intercept	7.43	2.67	2.77	*
Latitude	0.0389	0.0454	0.857	0.410
g) LM with mean link angle				
Intercept	-39.4	0.955	-41.3	***
poly(Latitude,2)1	-20.7	3.44	-6.02	***
poly(Latitude,2)2	-8.67	3.44	-2.52	*

† if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

Table S13: Statistical output of linear and polynomial models of properties of a) mean salmon abundance, b) log_{10} mean salmon mass, c) slope, d) connectance, e) mean trophic level, f) mean chain length, and g) mean link angle of food webs in Iceland and UK along the temperature gradient. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	Estimate	SE	t value	P value†
a) LM with mean salmon abundance per m^2				
Intercept	0.526	0.231	2.28	*
Temperature	-0.0217	0.0353	-0.614	0.551
b) LM with log_{10}(mean salmon mass (g))				
Intercept	0.685	0.317	2.16	0.0515
Temperature	-0.0461	0.0485	-0.951	0.360
c) LM with slope				
Intercept	-0.951	0.0875	-10.9	***
Temperature	-0.00495	0.0137	-0.362	0.724
d) LM with connectance				
Intercept	0.151	0.0191	7.92	***
Temperature	0.0115	0.00298	3.85	**
e) LM with mean trophic level				
Intercept	1.43	0.213	6.69	***
Temperature	0.0934	0.0334	2.80	*
f) LM with mean chain length				
Intercept	10.1	0.630	16.0	***
Temperature	-0.0715	0.0985	-0.726	0.483
g) LM with mean link angle				
Intercept	-49.8	2.61	-19.1	***
Temperature	1.83	0.407	4.50	***

Table S14: Statistical output of linear and polynomial models of properties of a) mean salmon abundance, b) log_{10} mean salmon mass, c) slope, d) connectance, e) mean trophic level, f) mean chain length, and g) mean link angle of food webs in Iceland and UK along the NDVI gradient. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	Estimate	SE	t value	P value[†]
a) LM with mean salmon abundance per m^2				
Intercept	1.08	0.782	1.39	0.196
NDVI	´-0.930	107	-0.867	0.406
b) LM with log_{10}(mean salmon mass (g))				
Intercept	1.73	1.04	1.67	0.127
NDVI	-1.78	1.42	-1.25	0.239
c) LM with slope				
Intercept	-0.701	0.286	-2.46	*
NDVI	-0.398	0.392	-1.02	0.334
d) LM with connectance				
Intercept	0.0606	0.0560	1.08	0.305
NDVI	0.202	0.0769	2.62	*
e) LM with mean trophic level				
Intercept	1.86	0.0581	31.9	***
poly(NDVI, 2)1	0.701	0.201	3.48	**
poly(NDVI, 2)2	0.406	0.201	2.01	0.0749
f) LM with mean chain length				
Intercept	13.2	1.82	7.30	***
NDVI	-4.78	2.49	-1.92	0.0839
g) LM with mean link angle				
Intercept	-40.5	1.46	-27.8	***
poly(NDVI, 2)1	9.44	5.05	1.87	0.0946
poly(NDVI, 2)2	10.7	5.05	2.11	0.0637

[†] if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

Table S15: Properties of predator-prey trophic relationship and mean salmon abundance and biomass of rivers in decreasing latitudes in the North Atlantic. IS- Iceland, UK- United Kingdom, GL- Greenland, FI/NO- Finland/Norway, SE- Sweden.

River	Country	Latitude	Overall M-N slope	M-N slope of invertebrate	M-N slope of fish	Connectance	Mean trophic level	Mean chain length	Mean link angle	Mean salmon abundance per 100 m^2	Mean salmon biomass (g)
Badda	FI/NO	69.95	-0.362	0.263	-1.66	0.182	1.27	5.64	-16.7	63.0	9.68
Vidgaveädji	FI/NO	69.92	-0.487	-0.338	-7.11	0.200	1.3	5.98	-22.3	82.0	13.0
Teno	FI/NO	69.92	-0.526	-0.549	NA	0.100	1.1	5.59	-27.0	31.0	5.0
Utsjoki	FI/NO	69.87	-0.344	0.0656	NA	0.111	1.11	5.90	-23.4	54.0	12.1
Midfjardará	IS	66.04	-0.502	0.357	-4.25	0.207	1.43	5.69	-29.5	33.0	2.33
Selá	IS	65.83	-0.476	0.137	15.3	0.207	1.78	4.66	-35.9	33.2	2.34
Vesturdalsá	IS	65.75	-0.588	-0.284	2.09	0.160	1.36	5.52	-23.4	69.9	4.69
Hofsá	IS	65.73	-0.407	0.454	3.39	0.154	1.57	5.31	-42.4	38.5	9.34
Krossá	IS	65.27	-0.693	-0.304	-2.1	0.135	1.3	6.72	-34.2	14.9	5.53
Kapisillit	GL	64.43	-0.339	-0.615	-0.129	0.222	1.33	5.89	-3.86	24.7	32.1
Elliðaár	IS	64.13	-0.657	-0.795	-4.42	0.0799	1.13	6.98	-26.1	114	12.3
Fiddich	UK	57.44	-0.596	0.0408	9.19	0.302	2.68	3.82	-0.34	37.8	0.923
Högvadsån	SE	57.13	-0.368	0.209	-0.997	0.152	1.29	5.54	-22.0	58.1	4.53
Nant Pen y Cwm	UK	52.64	-0.536	0.0474	-0.769	0.403	2.98	4.34	-6.15	0.615	5.76
Afon Bidno	UK	52.43	-0.495	0.338	-1.26	0.310	1.78	4.50	-6.36	4.97	0.345
Afon Marteg	UK	52.33	-0.792	-0.648	0.0505	0.485	4.14	3.99	-7.30	62.3	0.585
Afon Berwyn	UK	52.22	-0.440	0.0208	-1.54	0.291	2.74	3.99	-1.19	11.6	1.47
Upper Duhonw	UK	52.13	-0.507	0.301	-0.202	0.451	4.06	3.65	-10.5	1.19	0.355
Mill Stream	UK	51.17	-0.707	-0.145	-0.111	0.318	2.85	4.83	-16.9	20.0	9.63
Test	UK	51.14	-0.945	-0.208	-0.243	0.311	5.91	5.48	-27.9	0.255	8.00

Table S16: Statistical output from linear mixed effects model of food webs in rivers in the North Atlantic across latitudinal gradient. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and latitudinal degree were fixed effects. 'Nodes' and 'river' were a random effect in the model. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	value	SE	t-value	P value[†]
(Intercept)	-0.553	0.529	-1.05	0.296
log_{10}(Mass)	-1.12	0.276	-4.05	***
Latitude	0.0259	0.00865	2.99	**
log_{10}(Mass) × Latitude	0.0106	0.00463	2.29	*

Table S17: Statistical output from linear mixed effects model of food webs in rivers in the North Atlantic across temperature gradient. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and temperature (°C) were fixed effects. 'Nodes' and 'river' were a random effect in the model. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	value	SE	t-value	P value†
(Intercept)	1.09	0.117	9.37	0.00
log_{10}(Mass)	-0.373	0.0623	-5.99	0.00
Temperature	-0.0193	0.0157	-1.23	0.221
log_{10}(Mass) × Temperature	-0.0249	0.00813	-3.07	**

Table S18: Statistical output from linear mixed effects model of food webs in rivers in the North Atlantic across NDVI gradient. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and NDVI were fixed effects. 'Nodes' and 'river' were a random effect in the model. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	value	SE	t-value	P value†
(Intercept)	1.40	0.338	4.15	0.00
log_{10}(Mass)	-0.544	0.191	-2.84	**
NDVI	-0.637	0.467	-1.36	0.174
log_{10}(Mass) × NDVI	0.0516	0.261	0.197	0.844

[†] if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

Table S19: Statistical output from ANOVA analysis of linear mixed effects models of predator-prey trophic relationships across countries in the North Atlantic. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and country were fixed effects. 'Nodes' and 'river' were a random effect in the model. Summary tables are shown with DF values (degree of freedom), F values, and P values.

	DF	F value	P value†
(Intercept)	1	72.7	***
log_{10}(Mass)	1	118	***
Country	4	6.31	***
log_{10}(Mass) × Country	4	3.39	*

Table S20: Post-hoc output of food webs comparison across countries in the North Atlantic using pairwise comparisons and Tukey adjustments.

	SE	DF	t ratio	P value†
Finland/Norway – Greenland	0.367	220	0.966	0.870
Finland/Norway – Iceland	0.195	220	-2.10	0.222
Finland/Norway – Sweden	0.237	220	1.68	0.451
Finland/Norway – UK	0.179	220	1.40	0.626
Greenland – Iceland	0.352	220	-2.17	0.194
Greenland – Sweden	0.379	220	0.115	1.00
Greenland – UK	0.347	220	-0.297	0.998
Iceland – Sweden	0.208	220	3.89	**
Iceland – UK	0.143	220	4.62	***
Sweden – UK	0.195	220	-0.751	0.944

Table S21: Statistical output from ANOVA analysis of a linear mixed effects model across different rivers in the Teno/Tana system. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and latitudinal degree were fixed effects. 'Nodes' were a random effect in the model. The summary table is shown with DF values (degree of freedom), F values, and P values.

	DF	F value	P value†
(Intercept)	1	71.3	***
log_{10}(Mass)	1	116	***
Latitude	19	4.96	***
log_{10}(Mass) × River	19	2.67	***

† if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

Table S22: Post-hoc output of predator-prey relationships comparison between rivers in the North Atlantic using pairwise comparisons and Tukey adjustments.

	SE	DF	t ratio	P value†
Afon Berwyn - Afon Bidno	0.343	190	2.96	0.266
Afon Berwyn - Afon Marteg	0.312	190	0.749	1.000
Afon Berwyn - Badda	0.341	190	-0.286	1.000
Afon Berwyn - Ellidaár	0.282	190	-4.65	**
Afon Berwyn - Fiddich	0.312	190	-1.05	1.000
Afon Berwyn - Hofsá	0.311	190	-0.688	1.000
Afon Berwyn - Högvadsån	0.271	190	0.221	1.000
Afon Berwyn - Kapisillit	0.373	190	0.401	1.000
Afon Berwyn - Krossa	0.287	190	-2.43	0.635
Afon Berwyn - Midfjardará	0.359	190	-0.450	1.000
Afon Berwyn - Mill Stream	0.279	190	-0.926	1.000
Afon Berwyn - Nant Pen y Cwn	0.320	190	1.56	0.991
Afon Berwyn - Sela	0.351	190	-1.37	0.998
Afon Berwyn - Teno	0.345	190	-0.544	1.000
Afon Berwyn - Test	0.274	190	-2.26	0.757
Afon Berwyn - Upper Duhonw	0.318	190	-0.254	1.000
Afon Berwyn - Utsjoki	0.363	190	-1.22	1.000
Afon Berwyn - Vesturdalsá	0.342	190	-1.72	0.975
Afon Berwyn - Vidgaveädji	0.345	190	-0.504	1.000
Afon Bidno - Afon Marteg	0.351	190	-2.22	0.783
Afon Bidno - Badda	0.377	190	-2.95	0.272
Afon Bidno - Ellidaár	0.323	190	-7.19	***
Afon Bidno - Fiddich	0.350	190	-3.84	*
Afon Bidno - Hofsá	0.347	190	-3.54	0.0592
Afon Bidno - Högvadsån	0.317	190	-3.01	0.238
Afon Bidno - Kapisillit	0.407	190	-2.12	0.840
Afon Bidno - Krossa	0.329	190	-5.20	***
Afon Bidno - Midfjardará	0.391	190	-3.00	0.241
Afon Bidno - Mill Stream	0.323	190	-3.94	*
Afon Bidno - Nant Pen y Cwn	0.355	190	-1.45	0.996
Afon Bidno - Sela	0.384	190	-3.90	*
Afon Bidno - Teno	0.380	190	-3.16	0.166
Afon Bidno - Test	0.319	190	-5.12	***
Afon Bidno - Upper Duhonw	0.357	190	-3.06	0.211
Afon Bidno - Utsjoki	0.398	190	-3.66	*
Afon Bidno - Vesturdalsá	0.375	190	-4.26	**
Afon Bidno - Vidgaveädji	0.380	190	-3.13	0.181
Afon Marteg - Badda	0.348	190	-0.954	1.000
Afon Marteg - Ellidaár	0.291	190	-5.30	***
Afon Marteg - Fiddich	0.321	190	-1.75	0.970
Afon Marteg - Hofsá	0.320	190	-1.40	0.998
Afon Marteg - Högvadsån	0.281	190	-0.618	1.000

Afon Marteg - Kapisillit	0.379	190	-0.223	1.000
Afon Marteg - Krossa	0.298	190	-3.13	0.180
Afon Marteg - Midfjardará	0.367	190	-1.08	1.000
Afon Marteg - Mill Stream	0.290	190	-1.70	0.977
Afon Marteg - Nant Pen y Cwn	0.326	190	0.807	1.000
Afon Marteg - Sela	0.359	190	-1.99	0.901
Afon Marteg - Teno	0.351	190	-1.20	1.000
Afon Marteg - Test	0.282	190	-3.02	0.230
Afon Marteg - Upper Duhonw	0.324	190	-0.972	1.000
Afon Marteg - Utsjoki	0.371	190	-1.83	0.954
Afon Marteg - Vesturdalsá	0.350	190	-2.35	0.700
Afon Marteg - Vidgaveädji	0.351	190	-1.16	1.000
Badda - Ellidaár	0.318	190	-3.81	*
Badda - Fiddich	0.348	190	-0.661	1.000
Badda - Hofsá	0.343	190	-0.338	1.000
Badda - Högvadsån	0.308	190	0.511	1.000
Badda - Kapisillit	0.397	190	0.623	1.000
Badda - Krossa	0.324	190	-1.86	0.947
Badda - Midfjardará	0.388	190	-0.165	1.000
Badda - Mill Stream	0.316	190	-0.507	1.000
Badda - Nant Pen y Cwn	0.353	190	1.69	0.979
Badda - Sela	0.380	190	-1.01	1.000
Badda - Teno	0.373	190	-0.241	1.000
Badda - Test	0.313	190	-1.66	0.982
Badda - Upper Duhonw	0.355	190	0.0478	1.000
Badda - Utsjoki	0.385	190	-0.897	1.000
Badda - Vesturdalsá	0.371	190	-1.32	0.999
Badda - Vidgaveädji	0.361	190	-0.210	1.000
Ellidaár - Fiddich	0.290	190	3.39	0.0907
Ellidaár - Hofsá	0.280	190	3.92	*
Ellidaár - Högvadsån	0.235	190	5.84	***
Ellidaár - Kapisillit	0.351	190	4.16	**
Ellidaár - Krossa	0.252	190	2.43	0.639
Ellidaár - Midfjardará	0.333	190	3.45	0.0769
Ellidaár - Mill Stream	0.247	190	4.26	**
Ellidaár - Nant Pen y Cwn	0.297	190	6.09	***
Ellidaár - Sela	0.324	190	2.56	0.540
Ellidaár - Teno	0.323	190	3.48	0.0697
Ellidaár - Test	0.244	190	2.83	0.341
Ellidaár - Upper Duhonw	0.299	190	4.12	**
Ellidaár - Utsjoki	0.342	190	2.54	0.554
Ellidaár - Vesturdalsá	0.314	190	2.31	0.726
Ellidaár - Vidgaveädji	0.323	190	3.52	0.0626
Fiddich - Hofsá	0.318	190	0.359	1.000
Fiddich - Högvadsån	0.281	190	1.38	0.998
Fiddich - Kapisillit	0.379	190	1.26	0.999

Fiddich - Krossa	0.296	190	-1.25	0.999
Fiddich - Midfjardará	0.365	190	0.455	1.000
Fiddich - Mill Stream	0.288	190	0.242	1.000
Fiddich - Nant Pen y Cwn	0.326	190	2.53	0.564
Fiddich - Sela	0.358	190	-0.429	1.000
Fiddich - Teno	0.351	190	0.400	1.000
Fiddich - Test	0.282	190	-1.03	1.000
Fiddich - Upper Duhonw	0.327	190	0.756	1.000
Fiddich - Utsjoki	0.370	190	-0.311	1.000
Fiddich - Vesturdalsá	0.348	190	-0.743	1.000
Fiddich - Vidgaveädji	0.351	190	0.439	1.000
Hofsá - Högvadsån	0.275	190	0.996	1.000
Hofsá - Kapisillit	0.373	190	0.975	1.000
Hofsá - Krossa	0.285	190	-1.70	0.977
Hofsá - Midfjardará	0.342	190	0.152	1.000
Hofsá - Mill Stream	0.285	190	-0.156	1.000
Hofsá - Nant Pen y Cwn	0.325	190	2.19	0.802
Hofsá - Sela	0.329	190	-0.814	1.000
Hofsá - Teno	0.349	190	0.0752	1.000
Hofsá - Test	0.280	190	-1.45	0.996
Hofsá - Upper Duhonw	0.328	190	0.406	1.000
Hofsá - Utsjoki	0.366	190	-0.626	1.000
Hofsá - Vesturdalsá	0.322	190	-1.16	1.000
Hofsá - Vidgaveädji	0.349	190	0.115	1.000
Högvadsån - Kapisillit	0.342	190	0.262	1.000
Högvadsån - Krossa	0.245	190	-3.10	0.193
Högvadsån - Midfjardará	0.330	190	-0.673	1.000
Högvadsån - Mill Stream	0.229	190	-1.39	0.998
Högvadsån - Nant Pen y Cwn	0.288	190	1.52	0.994
Högvadsån - Sela	0.320	190	-1.69	0.978
Högvadsån - Teno	0.312	190	-0.793	1.000
Högvadsån - Test	0.229	190	-2.96	0.263
Högvadsån - Upper Duhonw	0.289	190	-0.487	1.000
Högvadsån - Utsjoki	0.332	190	-1.52	0.994
Högvadsån - Vesturdalsá	0.309	190	-2.09	0.858
Högvadsån - Vidgaveädji	0.313	190	-0.745	1.000
Kapisillit - Krossa	0.355	190	-2.39	0.668
Kapisillit - Midfjardará	0.412	190	-0.755	1.000
Kapisillit - Mill Stream	0.349	190	-1.17	1.000
Kapisillit - Nant Pen y Cwn	0.383	190	0.907	1.000
Kapisillit - Sela	0.405	190	-1.56	0.991
Kapisillit - Teno	0.396	190	-0.850	1.000
Kapisillit - Test	0.347	190	-2.21	0.789
Kapisillit - Upper Duhonw	0.385	190	-0.597	1.000
Kapisillit - Utsjoki	0.419	190	-1.41	0.997
Kapisillit - Vesturdalsá	0.397	190	-1.86	0.947

Kapisillit - Vidgaveädji	0.401	190	-0.806	1.000
Krossa - Midfjardará	0.335	190	1.60	0.988
Krossa - Mill Stream	0.254	190	1.73	0.972
Krossa - Nant Pen y Cwn	0.304	190	3.94	*
Krossa - Sela	0.327	190	0.665	1.000
Krossa - Teno	0.328	190	1.56	0.991
Krossa - Test	0.250	190	0.319	1.000
Krossa - Upper Duhonw	0.304	190	2.03	0.885
Krossa - Utsjoki	0.347	190	0.738	1.000
Krossa - Vesturdalsá	0.317	190	0.355	1.000
Krossa - Vidgaveädji	0.328	190	1.60	0.988
Midfjardará - Mill Stream	0.338	190	-0.285	1.000
Midfjardará - Nant Pen y Cwn	0.371	190	1.77	0.965
Midfjardará - Sela	0.372	190	-0.860	1.000
Midfjardará - Teno	0.392	190	-0.0657	1.000
Midfjardará - Test	0.334	190	-1.37	0.998
Midfjardará - Upper Duhonw	0.374	190	0.217	1.000
Midfjardará - Utsjoki	0.407	190	-0.690	1.000
Midfjardará - Vesturdalsá	0.364	190	-1.17	1.000
Midfjardará - Vidgaveädji	0.392	190	-0.0302	1.000
Mill Stream - Nant Pen y Cwn	0.296	190	2.56	0.543
Mill Stream - Sela	0.329	190	-0.679	1.000
Mill Stream - Teno	0.320	190	0.221	1.000
Mill Stream - Test	0.239	190	-1.51	0.994
Mill Stream - Upper Duhonw	0.296	190	0.600	1.000
Mill Stream - Utsjoki	0.340	190	-0.544	1.000
Mill Stream - Vesturdalsá	0.318	190	-1.03	1.000
Mill Stream - Vidgaveädji	0.321	190	0.264	1.000
Nant Pen y Cwn - Sela	0.363	190	-2.69	0.438
Nant Pen y Cwn - Teno	0.356	190	-1.93	0.926
Nant Pen y Cwn - Test	0.288	190	-3.87	*
Nant Pen y Cwn - Upper Duhonw	0.333	190	-1.73	0.972
Nant Pen y Cwn - Utsjoki	0.376	190	-2.50	0.583
Nant Pen y Cwn - Vesturdalsá	0.354	190	-3.06	0.212
Nant Pen y Cwn - Vidgaveädji	0.356	190	-1.89	0.938
Sela - Teno	0.384	190	0.765	1.000
Sela - Test	0.324	190	-0.424	1.000
Sela - Upper Duhonw	0.366	190	1.10	1.000
Sela - Utsjoki	0.400	190	0.0965	1.000
Sela - Vesturdalsá	0.356	190	-0.295	1.000
Sela - Vidgaveädji	0.385	190	0.801	1.000
Teno - Test	0.316	190	-1.36	0.998
Teno - Upper Duhonw	0.356	190	0.300	1.000
Teno - Utsjoki	0.387	190	-0.659	1.000
Teno - Vesturdalsá	0.376	190	-1.06	1.000
Teno - Vidgaveädji	0.376	190	0.0371	1.000

Test - Upper Duhonw	0.289	190	1.86	0.945
Test - Utsjoki	0.336	190	0.524	1.000
Test - Vesturdalsá	0.314	190	0.104	1.000
Test - Vidgaveädji	0.318	190	1.40	0.998
Upper Duhonw - Utsjoki	0.376	190	-0.962	1.000
Upper Duhonw - Vesturdalsá	0.357	190	-1.42	0.997
Upper Duhonw - Vidgaveädji	0.358	190	-0.260	1.000
Utsjoki - Vesturdalsá	0.391	190	-0.367	1.000
Utsjoki - Vidgaveädji	0.387	190	0.695	1.000
Vesturdalsá - Vidgaveädji	0.376	190	1.10	1.000

Table S23: Statistical output from ANOVA analysis of a linear mixed effects model across different rivers in the North Atlantic. Log_{10}(abundance) was the dependent variable and log_{10}(mass (g)) and 'River' were fixed effects. 'Nodes' were a random effect in the model. The summary table is shown with DF values (degree of freedom), F values, and P values.

	DF	F value	P value[†]
(Intercept)	1	57.7	***
log_{10}(Mass)	1	15.2	**
River	3	0.281	0.838
log_{10}(Mass) × River	3	0.642	0.601

[†] if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

Table S24: Statistical output of linear models of properties of a) log_{10} mean salmon abundance per m^2, b) log_{10} mean salmon biomass (g), c) slope, d) connectance, e) mean trophic level, f) mean chain length, and g) mean link angle of predator-prey trophic relationships in the North Atlantic along the latitudinal gradient (Figure S5). Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	Estimate	SE	t value	P value[†]
a) LM with mean salmon abundance per m^2				
Intercept	-0.313	0.641	-0.488	0.631
Latitude	0.0123	0.0105	1.18	0.254
b) LM with log_{10}(mean salmon mass (g))				
Intercept	-1.82	0.905	-2.02	0.0591
Latitude	0.0398	0.0148	2.69	*
c) LM with slope				
Intercept	-1.18	0.290	-4.07	***
Latitude	0.0105	0.00471	2.23	*
d) LM with connectance				
Intercept	0.967	0.140	6.90	***
Latitude	-0.0120	0.00228	-5.29	***
e) LM with mean trophic level				
Intercept	10.5	1.73	6.10	***
Latitude	-0.137	0.0280	-4.91	***
f) LM with mean chain length				
Intercept	0.0998	1.45	0.069	0.946
Latitude	0.0841	0.0235	3.58	**
g) LM with mean link angle				
Intercept	32.7	20.7	1.58	0.133
Latitude	-0.857	0.336	-2.55	*

[†] if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

Table S25: Statistical output of linear models of properties of a) log_{10} mean salmon abundance per m^2, b) log_{10} mean salmon biomass (g), c) slope, d) connectance, e) mean trophic level, f) mean chain length, and g) mean link angle of predator-prey trophic relationships in the North Atlantic along the temperature gradient. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	Estimate	SE	t value	P value[†]
a) LM with mean salmon abundance per m^2				
Intercept	0.495	0.107	4.60	***
Temperature	-0.0146	0.0187	-0.780	0.446
b) LM with log_{10}(mean salmon mass (g))				
Intercept	0.878	0.147	5.98	***
Temperature	-0.0711	0.0256	-2.78	*
c) LM with slope				
Intercept	-0.457	0.0429	-10.6	***
Temperature	-0.0217	0.00766	-2.83	*
d) LM with connectance				
Intercept	0.166	0.0274	6.06	***
Temperature	0.0172	0.00489	3.51	**
e) LM with mean trophic level				
Intercept	2.11	0.180	11.7	***
poly(Temperature, 2)1	4.05	0.785	5.16	***
poly(Temperature, 2)2	2.28	0.785	2.90	*
f) LM with mean chain length				
Intercept	5.72	0.251	22.8	***
Temperature	-0.124	0.0448	-2.77	*
g) LM with mean link angle				
Intercept	-23.2	3.63	-6.40	***
Temperature	0.920	0.648	1.42	0.174

[†] if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

Table S26: Statistical output of linear models of properties of a) log_{10} mean salmon abundance per m^2, b) log_{10} mean salmon biomass (g), c) slope, d) connectance, e) mean trophic level, f) mean chain length, and g) mean link angle of predator-prey trophic relationships in the North Atlantic along the NDVI gradient. Summary tables are shown with model-predicted values, SE (standard errors), t value, and P values.

	Estimate	SE	t value	P value[†]
a) LM with mean salmon abundance per m^2				
Intercept	1.20	0.598	2.01	0.0614
NDVI	-1.04	0.822	-1.27	0.222
b) LM with log_{10}(mean salmon mass (g))				
Intercept	1.77	0.953	1.85	0.0822
NDVI	-1.57	1.31	-1.20	0.247
c) LM with slope				
Intercept	-0.524	0.0320	-16.4	***
poly(NDVI, 2)1	0.0170	0.136	0.125	0.902
poly(NDVI, 2)2	-0.364	0.136	-2.68	*
d) LM with connectance				
Intercept	-0.163	0.149	-1.10	0.290
NDVI	0.526	0.205	2.57	*
e) LM with mean trophic level				
Intercept	2.00	0.231	8.67	***
poly(NDVI, 2)1	2.93	0.979	2.99	**
poly(NDVI, 2)2	2.04	0.979	2.09	0.0544
f) LM with mean chain length				
Intercept	9.96	1.21	8.23	***
NDVI	-6.44	1.66	-3.87	**
g) LM with mean link angle				
Intercept	-52.0	20.4	-2.55	*
NDVI	43.7	28.0	1.56	0.138

[†] if $p<0.05$ it is shown with *, if a $p<0.01$ it is shown with **, and if a $p<0.001$ it is shown with ***, non-significant p-values are written out.

22. Supporting Figures

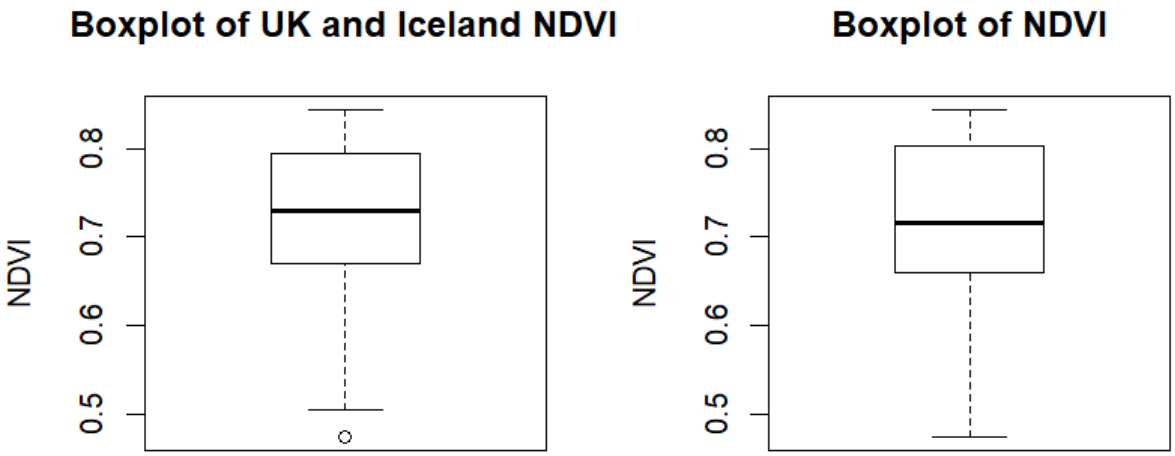

Figure S1: Boxplots of NDVI values to identify outliers (Outlier: 0.473 in Afon Marteg).

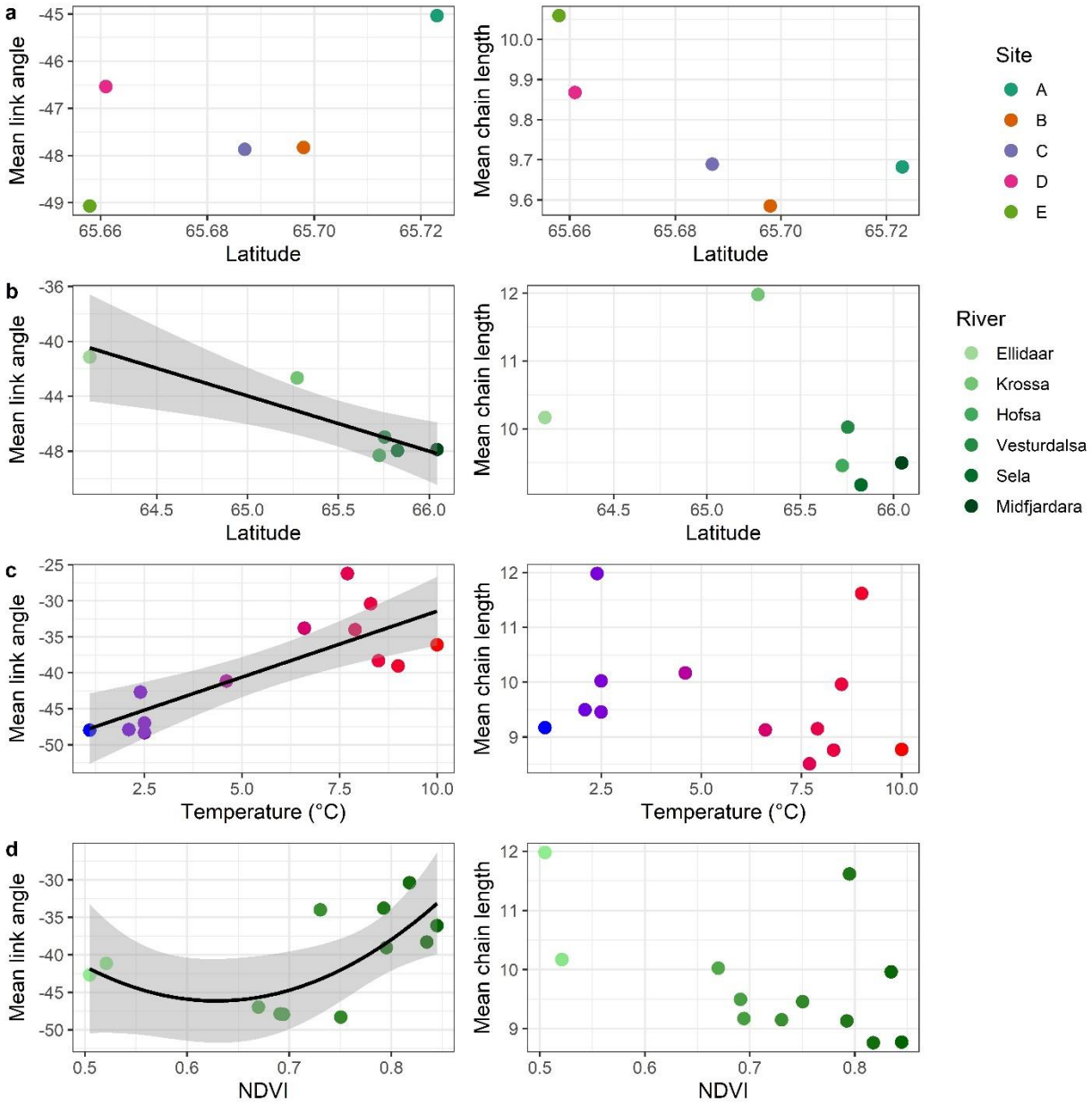

Figure S2: Linear and polynomial regressions of mean link angle and chain length of trivariate community food webs along the latitudinal gradient in increasing spatial scales from a) sites within Vesturdalsá to b) rivers in Iceland. Linear regressions of trivariate food web properties and characteristics of rivers in Iceland and UK were also compared along c) temperature and d) NDVI gradient.

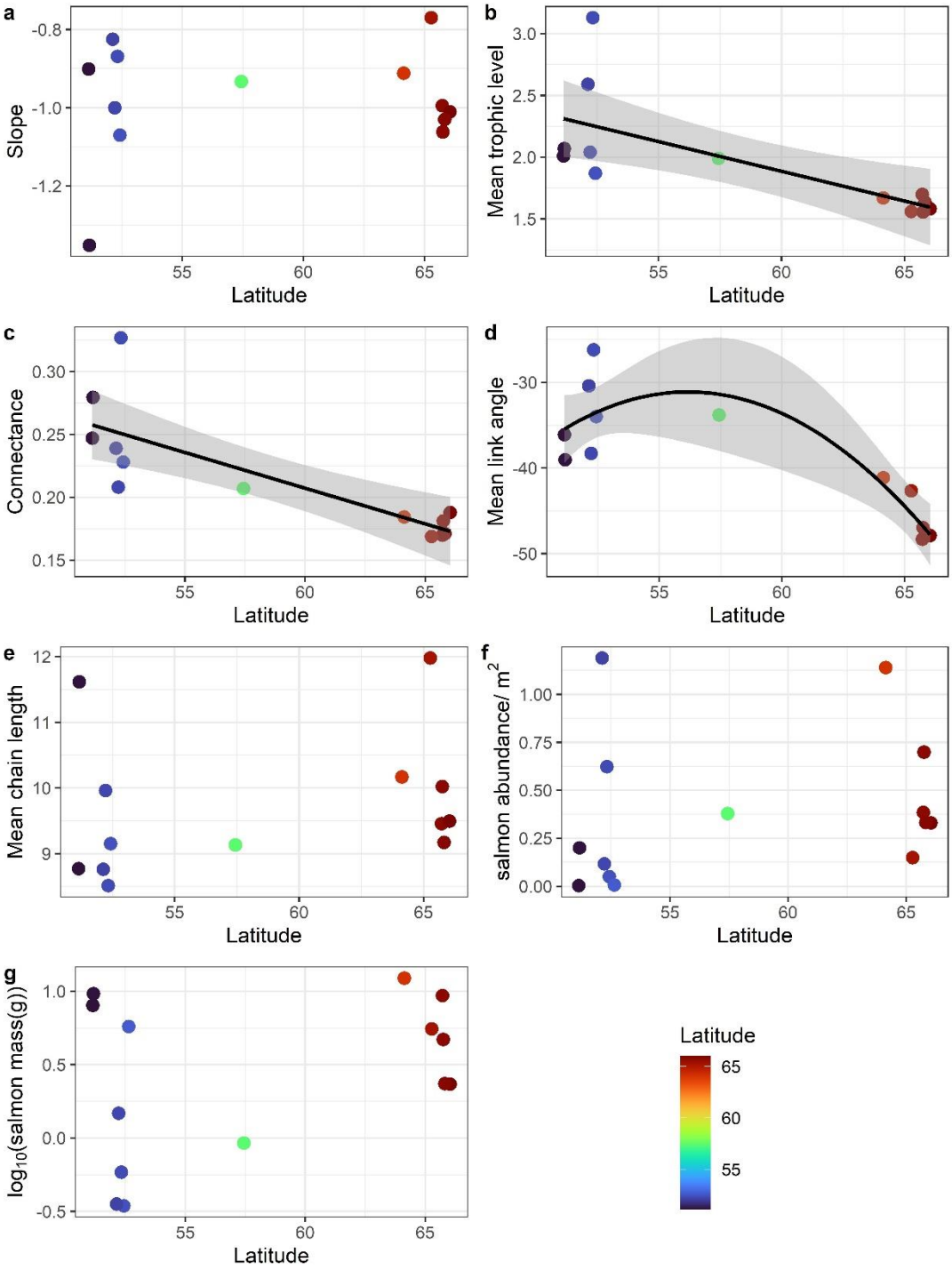

Figure S3: Linear and polynomial regressions of trivariate community food web properties (a) slope, b) mean trophic level, c) connectance, d) mean link angle, and e) mean chain length) and f) salmon abundance and g) mass along the latitudinal gradient in Iceland and UK.

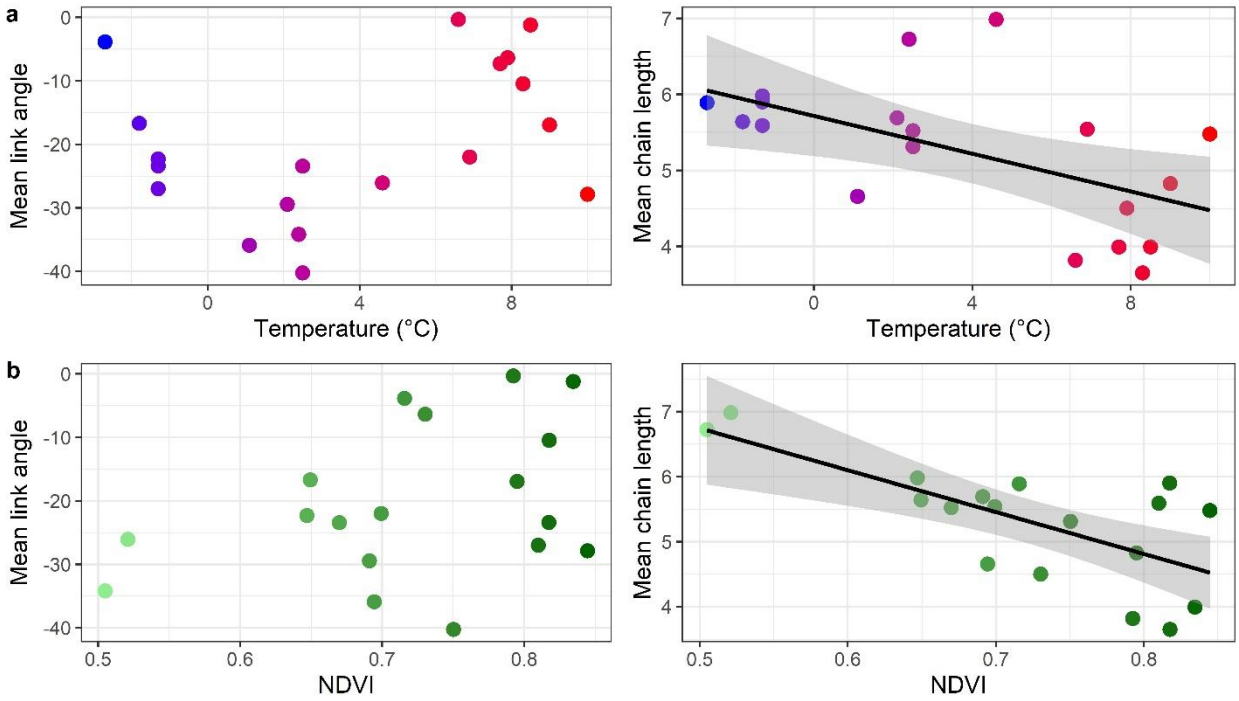

Figure S4: Linear regressions of mean link angle and chain length of animal-animal food webs along the a) temperature, and b) NDVI gradient.

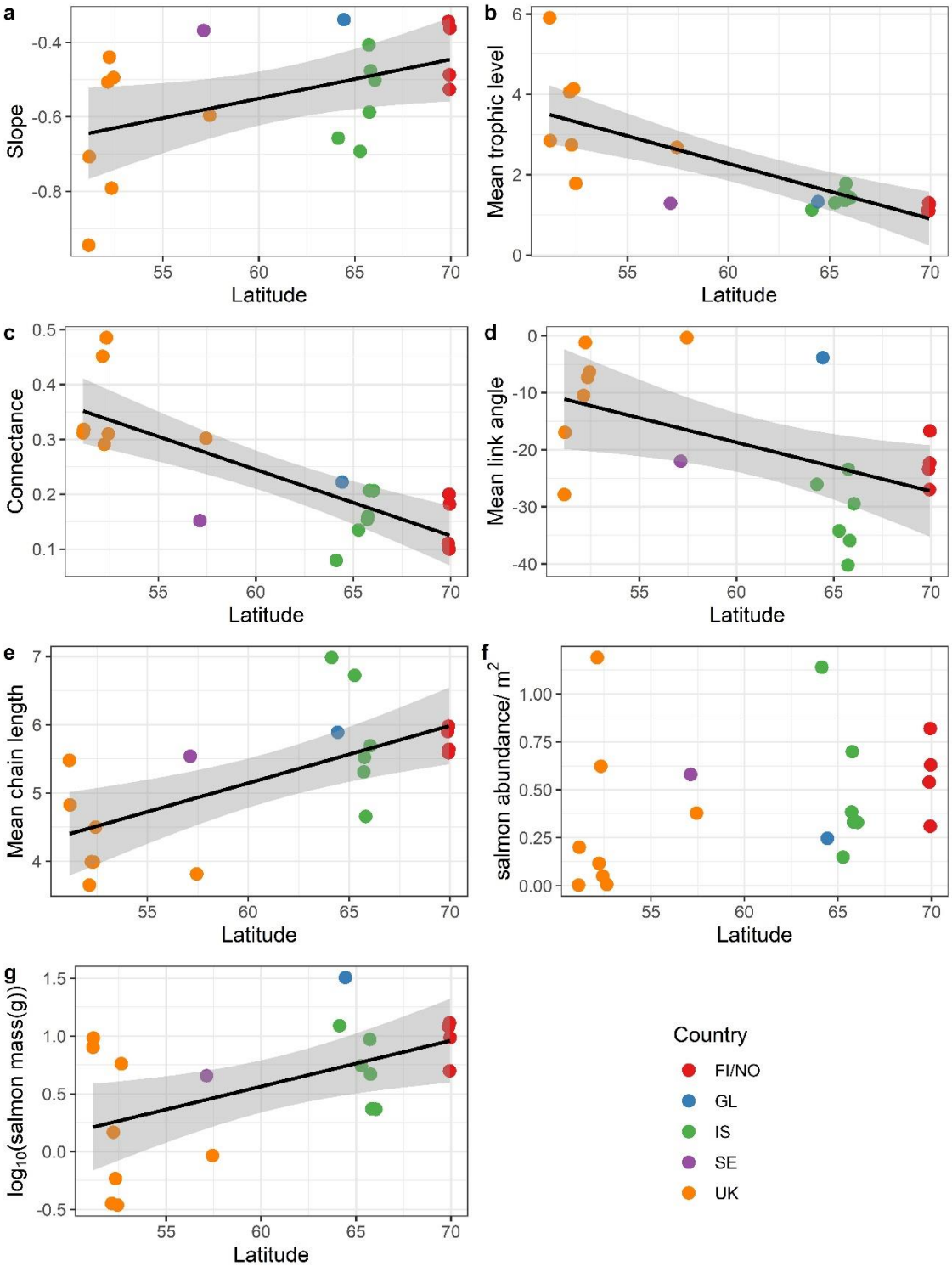

Figure S5: Linear regressions of animal-animal food web properties (a) slope, b) mean trophic level, c) connectance, d) mean link angle, and e) mean chain length) and f) salmon abundance and g) mass along the latitudinal gradient.

References:

Anon. (2023). *Status of the Tana/Teno River salmon populations in 2022*.

Arnekleiv, J. V., Davidsen, J. G., Sheehan, T. F., Lehnert, S. J., Bradbury, I. R., Rønning, L., Sjursen, A. D., Kjærstad, G., Lubinski, B. A., & Nilssen, K. J. (2019). Demographic and genetic description of Greenland's only indigenous Atlantic salmon Salmo salar population. *Journal of Fish Biology*, *94*(1), 154–164. https://doi.org/10.1111/jfb.13887

Bárðarson, H., Helgason, S. Ó., & Njarðardóttir, E. (2023). *Research on fish stocks in several rivers at North-East Iceland 2022*.

Bergh, R. (2022). *Biologisk undersökning av fiskfaunan inom Högvadsåns kalkningsprojekt 2022*.

Einarsson, S. M., Guðbrandsson, J., & Guðmundsdottir, Á. K. (2020). *Viðmiðunarmörk hrygningar í Krossá á Skarðsströnd*.

Ekologigruppen Ekoplan AB. (2021). *Bottenfaunaundersökning i Hallands län 2021*.

Erkinaro, H., & Erkinaro, J. (1998). Feeding of Atlantic salmon, Salmo salar L., parr in the subarctic River Teno and three tributaries in northernmost Finland. *Ecology of Freshwater Fish*, *7*(1), 13–24. https://doi.org/10.1111/j.1600-0633.1998.tb00168.x

Hansen, I., & Eiríksdóttir, E. S. (2021). *Ástandsflokkun straumvatna út frá tegundasamsetningu kísilþörunga*.

Ingimarsson, F. (2022). *Vöktun á lífríki Elliðaánna Náttúrufræðistofa Kópavogs*. *4*.

Perkins, D. M., Durance, I., Edwards, F. K., Grey, J., Hildrew, A. G., Jackson, M., Jones, J. I., Lauridsen, R. B., Layer-Dobra, K., Thompson, M. S. A., & Woodward, G. (2018).

Bending the rules: exploitation of allochthonous resources by a top-predator modifies size-abundance scaling in stream food webs. *Ecology Letters*, *21*(12), 1771–1780. https://doi.org/10.1111/ele.13147

Sturlaugsson, J. (2023). *Elliðaár 2022- Rannsóknir á fiskistofnum vatnakerfisins*.

Swedish University of Agricultural Sciences (SLU). (2023). *Miljödata-MVM*.