



**Ecological correlates of diel  
activity in Arctic charr *Salvelinus  
alpinus***

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**Faculty of Life and Environmental Sciences  
University of Iceland  
2016**



# **Ecological correlates of diel activity in stream-dwelling Arctic charr *Salvelinus alpinus***

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Dissertation submitted in partial fulfillment of a  
*Philosophiae Doctor* degree in Biology

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*Salvelinus alpinus*

Diel activity in Arctic charr

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# Abstract

Diel activity, the partitioning of time between periods of activity and rest, gives insights into how organisms compete for resources in time. Some species show plasticity in the rate and timing of their activity, which enables to study associations with ecological factors. Stream-dwelling fishes like salmonids are a textbook example of animals with variable activity patterns. During this Ph.D., I studied the diel activity of individually tagged juvenile Arctic charr in several field experiments and studies, focusing on critical factors for salmonids ecology. I found that Arctic charr increased activity (i) with rising temperature, (ii) when shelters are limited, (iii) in fast current, (iv) under relatively stable waterflow and (v) at high population density. The distribution of activity in time was also affected by ecological conditions in all studies. Flexible activity patterns coincided with modifications of other behaviors (aggregation, foraging mode, habitat selection). Arctic charr sometimes appear to maintain growth under suboptimal conditions by modifying their activity (e.g. limited shelters), whereas in other situations they increase activity under conditions that yield higher growth (high current velocity). In all but one experiment, more active fish grew faster. This relationship depended on the environment. It was stronger in faster currents, and under stable waterflow. These results have important implications for biological fields such as behavioral ecology, by estimating behavioral flexibility, salmonids ecology via food intake and growth under different ecological scenarii, and conservation biology by using behavior to assess the effect of future changes in the physical habitat of stream fishes.



# Útdráttur

Dægursveiflur í virkni lýsa því hvernig dýr deila sólarhringnum á milli virkni og hvíldar, og hvernig þau keppa um auðlindir í tíma. Sumar tegundir sýna sveigjanleika í því hversu virk þau eru og hvenær, og eru hentug til rannsókna á áhrifum vistfræðilegra þátta á virkni. Fiskar í ám, þá sérstaklega laxfiskar, eru skólabókardæmi um dýr sem sýna breytileika í virkni. Í doktorsnáminu rannsakaði ég dægursveiflur í virkni einstaklingsmerktra bleikjuseiða í tilraunum og rannsóknum við náttúrulegar aðstæður, þar sem athuguð voru áhrif þátta sem hafa mikilvæg áhrif á vistfræði laxfiska. Bleikjur voru virkari (i) við herra hitastig, (ii) þar sem felustaðir voru takmarkaðir, (iii) við meiri straumhraða, (iv) þar sem vatnsrennsli var stöðugt, og (v) við hærri þéttleika. Í öllum rannsóknunum höfðu vistfræðilegir þættir líka áhrif á það hvernig virkni dreifðist í tíma. Sveigjanleiki í virkni tengdist líka breytileika í öðru atferli (t.d. árásarhneigð, fæðuháttum og búsvæðavali). Rannsóknirnar sýndu líka að stundum viðheldur bleikja vexti við óhagstæðar aðstæður (fáir felustaðir, hár þéttleiki) með því að breyta virkni sinni en stundum eru þær virkastar við aðstæður hagstæðar fyrir vöxt (meiri straumhraði). Í öllum tilraununum, nema einni, uxu virkari einstaklingar hraðar en þeir sem voru minna virkir. Þetta samband var þó háð aðstæðum, og var t.d. greinilegra við meiri straumhraða og jafnara vatnsrennsli. Niðurstöður þessa verkefnis eru mikilvægar fyrir t.d. (i) atferlisvistfræði (sveigjanleiki í atferli), (ii) vistfræði laxfiska, vegna áhrifa virkni á fæðunám og vöxt við ólíkar aðstæður, og (iii) verndun, vegna þess innsæis sem atferli veitir varðandi áhrif væntanlegra breytinga á búsvæðum fiska.





*This thesis is dedicated to my son Lucas, who I wish sometimes was  
more diurnal.*

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# Abbreviations

HSA: High shelter availability

LSA: Low shelter availability

LWF: Low waterflow

HWF: High waterflow

IWF: Intermediate waterflow



# List of chapters

## **Chapter 1:** Synopsis

**Chapter 2:** Diel activity and aggregation of a stream fish along a temperature gradient among and within populations

Nicolas Larranaga, Stefán Ó. Steingrímsson (In preparation)

Conceived the study: NL SOS. Set up the experiment: NL SOS. Collected the data: NL with help from D. Combot and M. Heath. Analyzed the data: NL SOS. Wrote the paper: NL SOS.

**Chapter 3:** Shelter availability alters diel activity and space use in a stream fish

Nicolas Larranaga, Stefán Ó. Steingrímsson (Published in *Behavioral Ecology*)

Conceived the study: NL SOS. Set up the experiment: NL SOS. Collected the data: NL with help from A. Fingerle, D. Combot and M. Heath. Analyzed the data: NL SOS. Wrote the paper: NL SOS.

**Chapter 4:** Diel activity and growth of Arctic charr (*Salvelinus alpinus*) in contrasting stream habitats

Nicolas Larranaga, Frédéric Hadi, James W.A. Grant, Stefán Ó. Steingrímsson (In preparation)

Conceived the study: NL SOS. Set up the experiment: NL SOS FH. Collected the data: NL FH. Analyzed the data: NL SOS. Wrote the paper: NL SOS JWAG.

**Chapter 5:** Fluctuations in water flow: effects on diel activity, foraging mode and growth in juvenile Arctic charr

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**Chapter 6:** Density-dependent diel activity in stream-dwelling Arctic char *Salvelinus alpinus*

Amy Fingerle, Nicolas Larranaga, Stefán Ó. Steingrímsson (published in *Ecology and Evolution*)

Conceived the study: AF SOS NL. Set up the experiment: AF SOS NL. Collected the data: AF with help from D. Combot and M. Heath. Analyzed the data: AF SOS NL. Wrote the paper: AF SOS NL.

**Chapter 7:** Repeatability and ecological correlates of foraging mode in a stream dwelling fish

Nicolas Larranaga, Amy Fingerle, Stefán Óli Steingrímsson (In preparation)

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# 1 Synopsis

## 1.1 Introduction

Most organisms live in an ever changing environment where their foraging opportunities fluctuate constantly (Shugart 1998). Some of these environmental changes occur periodically, e.g. over the course of a day or across seasons. One particular factor affecting the foraging success of visually oriented predators is light intensity. To cope with the diel periodicity of light intensity, animal species have evolved different patterns of diel activity rhythms (also referred to as circadian rhythms under certain conditions), i.e. strategies of time partitioning over a 24 h period (Schoener 1974, Daan 1981). Diel activity has been the subject of numerous reviews and meta-analyses (Enright 1970, Halle 2000, Reeb 2002, Kronfeld-Schor and Dayan 2003, Halle and Stenseth 2012, Bloch et al. 2013, Bennie et al. 2014). Activity rhythms can have strong implications for biodiversity and ecology, by affecting encounter rates between prey and predators, mediating competition between species with similar ecological niches and affecting the evolution of traits related to the detection and capture of prey (Halle 2000, Kronfeld-Schor and Dayan 2003). Hence, understanding the ecological determinants and the evolutionary implications of activity rhythms is of great significance, especially because recent human-induced changes (e.g. light pollution, rising temperature) may affect the fitness associated with such patterns (Longcore and Rich 2004, Chen et al. 2011).

Activity patterns can be completely rigid, i.e. with very little variation among individuals and over time. For instance, species can be strictly diurnal, nocturnal, or crepuscular. The adaptive value of such patterns lies in individuals being able to anticipate and adapt their response to daily environmental variation (e.g. Horton 2001). Animals also often show morphological and physiological adaptations to activity during a specific period of the day, for instance in terms of eye morphology (Halle 2000, Kirk 2004). Another type of rigid activity pattern is obligately cathemeral, i.e. with obligate activity during both darkness and daylight, Tattersall 2006). Such patterns arise due to e.g.

physiological constraints where organisms have to extend activity over periods when their foraging efficiency is sub-optimal (van Schaik and Griffiths 1996). Competing entities (e.g. species, individuals) may end up exhibiting contrasting activity patterns as a means of temporal niche partitioning, resulting in a cathemeral group composed of units with more rigid activity patterns. This has been evidenced among ecologically similar species (Gutman and Dayan 2005, Bitetti et al. 2009), and among individuals, for instance when different age-classes specialize on different prey resources, potentially available at different hours (Imre and Boisclair 2004).

Opposite to species with strict diel activity patterns, some species can be active facultatively during the day and/or the night (Fox and Bellwood 2011, DeGregorio et al. 2014). Flexibility can exist at different levels. For instance, there can be strong differences among individuals in a population, but low within-individual variability, or the opposite, or variability at both levels. Such flexibility can be adaptive under certain conditions, for instance when resource distribution and dynamics are unpredictable (Bloch et al. 2013). This is particularly true of organisms living at mid to high latitudes that experience a large gradient of photoperiod over the year (from constant darkness to constant daylight, Bennie et al. 2014). Feeding behavior can also impose constraints on activity patterns, e.g. because of long digestive processes (Bloch et al. 2013). Plasticity in activity patterns can be adaptive for species showing large-scale migration, and with distribution ranges expanding over higher latitudes (Steiger et al. 2013). Importantly, not only geographical, but also taxonomic constraints appear to exist on the evolution of plasticity in diel activity patterns. For instance, most birds and mammals exhibit little among- and within-individual variation in diel activity (Daan and Aschoff 1975, Bennie et al. 2014), whereas fish species often switch between activity patterns (Reebs 2002).

Light intensity is not the only ecological factor that fluctuates over the 24 h cycle. A classic example is ambient temperature, which typically increases during daytime. Thermal constraints are important determinants of the rate and timing of activity, through modulations of metabolic demands and the costs of thermoregulation (Angilletta Jr. et al. 2002). Hence, fluctuations in temperature affect diel activity in a variety of taxa, including mammals (Maloney et al. 2005), fish (Breau et al. 2007a), reptiles (Sperry et al. 2013), and insects (Bloem et al. 2006). Other important ecological factors are prey availability and

predator activity (Anholt et al. 2000). The physical habitat of animals can also affect their temporal behavior, e.g. if shelter availability is limited and some individuals have to remain active longer at suboptimal times (Olson and Wallander 2002). Many other ecological factors, including but not limited to humidity (Lane et al. 1995), oxygen (Dalosto and Santos 2011), pH and toxic substances (Williams and Moore 1982) may affect diel activity. Thus, animals may alter their activity in response to a variety of stimuli, some more predictable (e.g. day-night cycles) than others (e.g. extreme events like droughts, floods and eclipses).

Phenotypic traits are known determinants of diel activity. Age and body size are two common examples. For instance, during growth, individuals may progressively use larger prey, potentially active at a different time. Among individuals variation may result from a shift of endogenous rhythms with individual development (Magnan and FitzGerald 1984, Glova and Jellyman 2000, Aragón et al. 2004), or from competitive exclusion where dominant individuals monopolize the optimal windows of activity and force subordinates to be active at other times (Alanärä et al. 2001, David et al. 2007). As individuals get older, they accumulate valuable fitness assets and may be less willing to risk losing them. This has been conceptualized by Clark's (1994) "asset protection principle", sometimes invoked to explain why juvenile individuals are more active than their older counterparts, especially during risky periods. For instance, Atlantic salmon *Salmo salar* are diurnal during their first summer, then become progressively nocturnal to avoid avian and terrestrial predators (Imre and Boisclair 2004), at the cost of reduced prey capture efficiency at night (Elliott 2011). Within a population, males and females can also exhibit contrasting rates and timing of activity. For instance, Aragón et al. (2004) found that male Iberian rock lizards *Lacerta monticola* were more active than females. In the same study, color also predicted activity, as green males were more active than brown males. The net benefits of activity can also be affected by individual state, e.g. injury (Martín and Salvador 1995), or hunger (Nakamuta 1987).

The two previous paragraphs give a brief overview of the variety of extrinsic (abiotic and biotic) and intrinsic (i.e. phenotypic) factors that potentially affect time budgets in wild animals. The equation becomes even more complex considering that extrinsic and intrinsic factors may have interactive effects (Martelo et al. 2013) on diel activity. Identifying the relative importance of each cue that organisms

use to adjust their activity is challenging for several reasons. First, many of these factors are correlated, e.g. days are warmer than nights, and body size is a strong predictor of dominance (Brown and Maurer 1986, Huntingford et al. 1990). Second, recording behavior visually at night under natural conditions is not always possible and using alternative methods such as telemetry may not reflect diel activity patterns if individuals are active but sedentary (Payne et al. 2010). Third, although it is beneficial to record diel activity in laboratory conditions to standardize experimental conditions, animals may display contrasting activity patterns in the wild and in captivity (Levy et al. 2007, Gattermann et al. 2008), e.g. because environmental variation may mask internal rhythms (Mrosovsky 1999, Levy et al. 2007). Still, collecting temporal data *in natura* is important because diel activity may directly affect survival (DeCoursey et al. 2000) and growth (Martin-Smith and Armstrong 2002) in the wild.

An individual approach with repeated measurements of activity is necessary to quantify the link between the diel activity of organisms, their phenotype, their environment and their fitness (Cooke et al. 2004, Bell et al. 2009). However, this type of approach is not always easy to apply in natural conditions, e.g. because individuals are often too small to tag (Leblanc and Noakes 2012), because they use a space too large to be surveyed rapidly (Gervasi et al. 2006), because they cease activity in the presence of an observer (Sugerman and Hacker 1980), because of high densities (Abbott 2005), or because they use habitats where it is hard to detect them (e.g. underground, Goyal 1981; in dense vegetation, Bukombe et al. 2016; in fast water current, Bonneau et al. 1995). Recent technological improvements (e.g. infra-red cameras, smaller and cheaper tags, lower energy limitations) make it possible to monitor a large number of individuals in the wild for relatively long periods of time. I took advantage of these improvements to get repeated individual estimates of diel activity in a stream-dwelling fish.

The overall goal of this thesis is to address specific questions about the variation, the determinants and the consequences of diel activity in natural populations using an individual approach. More specifically, I monitored the behavior of individually tagged juvenile Arctic charr *Salvelinus alpinus* in stream enclosures over the 24 h cycle in several field experiments and a semi-experimental study. In each study, I recreated or modified the local environment using different treatments to study the effect of a particular factor. I also quantified the variation in diel activity among and within individuals.

In addition to activity, I measured several components of the spatial behavior and foraging mode of Arctic charr around the clock to study diel variation in their behavior. Finally, I measured body size at the beginning and at the end of each 10-15 day study period to see if and how activity, coupled with ecological conditions affects growth.

## 1.2 Study system

I performed all the experiments in Icelandic streams. In many ways, Iceland is an ideal place to test predictions about diel activity in freshwater systems. First, it is an island at relatively high latitude, where behavior can be assessed visually around the clock in summertime, without the aid of an artificial light. Second, it is a relatively young island (ca 16M years old and glaciated until 10,000 years ago). Because of its age and distance to the mainland of Europe and North America, few plants and animals inhabit it, leaving relatively simple and species-poor ecosystems. Hence, juvenile freshwater fish have a limited number of predators, including some birds (e.g. Arctic terns *Sterna paradisaea* and red-breasted merganser *Mergus serrator*), minks and potentially older fish. Similarly, inter-specific competition is limited because there are only six freshwater fish species in total, and only three salmonids (Arctic charr, Atlantic salmon and brown trout). The three species use partially distinct ecological niches, Arctic charr inhabiting mostly slow water currents in cold and unproductive streams, whereas Atlantic salmon and brown trout prefer fast and intermediate water currents, respectively, within warmer, more productive streams (Gudjónsson 1990, Heggnes and Saltveit 2007). Finally, the volcanic activity of Iceland, in addition to its northern location offers a wide range of stream conditions, e.g. in terms of water temperature and productivity (Gudjónsson 1990).

### 1.2.1 Salmonid behavior

Teleost fishes are model organisms to study behavioral ecology and have contributed significantly to its development, through an increasing number of studies in the last decades. Salmonids, like many teleost fishes, are visual predators (Rader et al. 2007). In streams, they feed primarily on drifting invertebrates (Kalleberg 1958) and compete with conspecifics for food in both space and time. How salmonids adjust their behavior to ecological conditions, including their habitat (water depth, current velocity, substrate), competition and predation

has generated a vast literature since the seminal work of William S. Hoar (Hoar 1942, Hoar 1954, Hoar 1958). Several aspects of their behavior have been extensively documented. This includes their diel activity (Reebs 2002, Breau et al. 2007a), territoriality (Grant and Kramer 1990, Gunnarsson and Steingrímsson 2011), foraging mode (McLaughlin et al. 1992, Tunney and Steingrímsson 2012), habitat use (Heggenes and Saltveit 1990, Armstrong et al. 2003), and prey selection (Fahy 1980, Schabetsberger et al. 2003). The freshwater habitat of salmonids is especially heterogeneous in space and time, compared to other systems (Allan and Castillo 2007). Some of this variation is predictable (e.g. diel changes in food availability), and some is not (e.g. predation risk, local conditions). Studies have suggested that the flexibility in salmonid behavior reflects the variable conditions they experience, and that their behavioral plasticity is adaptive (Dill 1983, Dolloff et al. 1994, Vehanen 2003).

Arctic charr in particular has been the subject of numerous studies on resource polymorphism, and its ecology, morphology, and life history has been extensively documented in lentic environments (Jonsson et al. 1988, Jonsson and Jonsson 2001, Amundsen et al. 2007). Less is known about the ecology and behavior of Arctic charr in streams. To date, only few studies have focused on the behavior (habitat use, foraging mode, territoriality and movement) of stream-dwelling Arctic charr (e.g. Craig and Poulin 1975, Heggenes and Saltveit 2007, Gunnarsson and Steingrímsson 2011, Tunney and Steingrímsson 2012). These studies suggest that Arctic charr use relatively slow-running waters, and this is reflected in their behavior (Heggenes and Saltveit 2007). Nevertheless, Tunney and Steingrímsson (2012) observed juvenile Arctic charr in water current as fast as 39.9 cm/s, which calls for more information on their behavior in lotic environments.

### **1.2.2 Diel activity of salmonids**

Our knowledge and understanding of the diel activity of juvenile salmonids have changed dramatically over 70 years. Hoar (1942) described “parr” and “smolt” salmon and trout as feeding during the day and sleeping during hours of darkness because of limited access to food. Based on visual observations of brown trout in tanks, Swift (1964) also found that the regularity of feeding had no effect on activity patterns, suggesting that salmonids react primarily to light, and less to food availability. Chaston (1969) found that brown trout of age

2+ or older were mostly active between dusk and dawn (i.e. at night) and explored seasonality of diel activity. Indeed, he reported that daytime activity was higher during the summer than during the winter and the fall. In this study, brown trout increased activity at times of higher food availability (in summertime and at mid-day). Adams et al. (1988) described seasonal effects further by showing that Arctic charr (size range: 5.3-14.1 cm) were almost exclusively nocturnal in late July, but become predominantly diurnal by late August. Walsh et al. (1988) found that young-of-the-year (YOY) brook charr *Salvelinus fontinalis* were mostly diurnal in summertime. These four early studies show that by simply observing fish of different size, at different seasons and under different food availability, one can detect drastic differences in the diel activity of salmonids.

Much has been done since the pioneering work of Hoar (1942). I performed a preliminary study of the literature on the diel activity of salmonids using different combinations of key words such as “diel activity”, “circadian rhythm”, “daily activity”, “salmo”, “salvelinus”, “oncorhynchus”, “thymallus”, “day”, “night”, “crepuscular”, “diurnal”, “nocturnal” and “catheimeral”. This list was progressively updated by including publications I encountered during this work and that did not fit the original criteria. I found that at least 72 publications in peer-reviewed journals contain some information on the activity of juvenile salmonids at different times of the day, or under different treatments of light intensity (not including the publications from this Ph.D.). This variety of publications highlights several points. First, although Salmonidae is a relatively small family, diel activity patterns have been reported for at least 13 different species (Atlantic salmon, brown trout, Arctic charr, chinook salmon, bull charr, cutthroat trout, rainbow trout, coho salmon, brook char, masu salmon, pink salmon, brook trout and grayling), i.e. all *Salmo*, *Oncorhynchus* and *Salvelinus* species. Studying activity at different biological levels offers the possibility to see how much variation exists and how it is distributed. Hence, the rate and timing of activity vary among species (Young et al. 1997a, Jakober et al. 2000), populations (Valdimarsson et al. 2000), age classes (Sempeski and Gaudin 1995, Bradford and Higgins 2001, Imre and Boisclair 2004), individuals (e.g. Breau et al. 2007a), and within individuals (Roy et al. 2013).

Another striking point is the diversity of methods employed to measure activity. In the laboratory, automatic feeders (Alanära et al. 2001), photocell-monitored light beam (Bachman et al. 1979), activity

channels (Godin 1981), radiography (Jørgensen and Jobling 1989), and IR photocells (Mork and Gulbrandsen 1994) are used. In the wild, stomach contents are sometimes used, although precautions need to be taken because the feeding activity may only partially reflect diel activity (Amundsen et al. 1999). Otherwise, field studies consist generally of a mixture of visual observations in viewing rooms (Harwood et al. 2001), underwater observations (Heggenes et al. 1993), pit-tagging (Conallin et al. 2012), radio telemetry (Hiscock et al. 2002) and fluorescent paint tagging (Breau et al. 2007a). The tools and methods used have changed progressively as some topics in biology became more popular. For instance, field measurements are more common now than they were at the onset of diel activity studies. Similarly, tagging methods are increasingly used because currently strong emphasis is placed on behavioral repeatability (Bell et al. 2009).

Methodological details aside, diel activity of salmonids has been studied under variable conditions, with studies focusing on several factors. Such factors can be abiotic, like light intensity (Fraser and Metcalfe 1997), water temperature (Breau et al. 2007a), habitat availability (Bradford and Higgins 2001), cover (Orpwood et al. 2010), rain (Payne et al. 2013), season (Bradford and Higgins 2001) and moon phase (Imre and Boisclair 2005). Biotic factors such as intra- and interspecific competition (Blanchet et al. 2008a), food availability (Orpwood et al. 2006), and predation risk (Railsback et al. 2005) are also reported to affect salmonids diel activity. Phenotypic determinants include age class (Imre and Boisclair 2004), body size (Cromwell and Kennedy 2011), dominance status (Alanära et al. 2001), life history strategy (Valdimarsson and Metcalfe 1999), and hunger (Vehanen 2003). Individual estimates of activity in natural conditions hold great value but remain rare in the salmonid literature and are for the majority quite recent (Breau et al. 2007a, Blanchet et al. 2008a, Roy et al. 2013, Závorka et al. 2016), which means there are opportunities to study further the variation, ecological determinants and consequences of diel activity using semi-experimental approaches where one attempts to control for a large number of factors.

### **1.3 Objectives and predictions**

As described above, the goal of this thesis is fourfold: (i) to better identify some ecological determinants of diel activity, (ii) quantify the extent and the origin of the variation in activity rates and patterns, (iii)



explore how contrasting activity patterns may affect or be linked to other aspects of behavior (e.g. aggregation, foraging mode and habitat use), and (iv) explore potential relationship between activity and growth, using Arctic charr as a model species. I focused on five factors that are critical for the ecology of salmonids and are likely to change in the near future (Jonsson and Jonsson 2009): water temperature, shelter availability, habitat availability (current velocity and water depth), fluctuations in waterflow, and population density. The effect of each factor was explored in a separate study and form the basis of chapters 2 to 6. In addition, I studied the repeatability and ecological correlates of foraging mode of Arctic charr, which relates to their diel activity (e.g. association with light intensity, chapter 7)

*Chapter 2: Diel activity and aggregation of a stream-dwelling fish along a temperature gradient among and within populations.* In this chapter, I monitored Arctic charr in three streams with contrasting temperature profiles (cold 3.6-9.3°C, intermediate 6.8-15.0°C, and warm 11.9-18.7°C). The main value of this work lies in exploring for the first time diel activity both among and within such contrasted streams. Previous work has suggested that differences exist among streams with small differences (1°C in Bremset 2000, 1.5 °C in Sinnatamby et al. 2012, 3 °C in Breau et al. 2007a, 3.5 °C in Reeves, et al. 2010, and 5 °C in Cromwell and Kennedy 2011), suggesting that among-population effects could be even more pronounced. I predicted that activity rates should increase with increasing water temperature, both within and among streams, but that the within-stream effect should be weaker in the warm stream, as Arctic charr gets closer to its thermal tolerance (Breau et al. 2007a). Individuals (age 1+) should be predominantly nocturnal, but from the warm to the cold stream, I also expected fish to be increasingly nocturnal (Fraser et al. 1993, Fraser et al. 1995).

Another aspect of this chapter is the study of the link between water temperature and aggregation. Schooling behavior by salmonids has been observed at high temperature when individuals aggregate in cool stream habitats (Breau et al. 2007b), and at low temperature, possibly because of ice concealment (Cunjak and Power 1986). Water temperature is expected to affect activity rates, and hence the density of potential competitors, which in turn may affect aggression rates and territoriality. Importantly, salmonids have a reduced field of vision at night and interact less with their conspecifics, which causes them to decrease the distance between each other (Valdimarsson and Metcalfe

2001). During the day, they are also more exposed to predators, and may aggregate as a form of anti-predatory behavior (Cresswell 1994). Hence, if there are differences in activity patterns among streams, this could further affect aggregation. Finally, I tested if fish grew faster (i) at high temperature, (ii) when they were more active, and (iii) if they foraged in a group or in isolation.

*Chapter 3: Shelter availability alters diel activity and space use in a stream fish.* Here, I investigated whether Arctic charr modify their diel activity in response to a lack of shelters. In streams, fish can use boulders and woody debris to hide from predators and conspecifics. Boulders and debris also make for more complex habitats, where food availability is usually higher (Negishi and Richardson 2003). Hence, studies have documented the effect of shelter availability on the behavior and growth of salmonids (Imre et al. 2002, Höjesjö et al. 2004, Kemp et al. 2005, Dolinsek et al. 2007, Venter et al. 2008). Surprisingly, however, this has not yet been explored in the context of time partitioning. Orpwood et al. (2010) found that Atlantic salmon were more diurnal in areas with little riparian shading, but the effect of physical hiding structure remains to be investigated. In other taxa, the literature is equivocal, as some studies found significant relationships between shelters and diel activity (Edel 1975, Olson and Wallander 2002), whereas others did not (Walsh and Downie 2005, Fero and Moore 2014). I created two treatments of shelter availability (low and high) using a combination of cobble and moss and recorded diel activity. I predicted that in shelter-poor environments, Arctic charr should be (i) more active because not all individuals can hide simultaneously and (ii) more diurnal (sensu Orpwood et al. 2010).

The presence of shelters alters the space use of salmonids, through effects on their territoriality, as fish detect and interact less often with their conspecifics and have access to more food (Imre et al. 2002, Venter et al. 2008). Therefore I also collected measurements of aggregation, foraging radius, and prey attack rate in the two shelter treatments. I expected fish in shelter-rich enclosures to be less aggregated (Dolan and Butler 2006), and attack prey at shorter distances (Imre et al. 2002) and less frequently (Kemp et al. 2005). Contrasting activity patterns among shelter availability treatments may amplify or hinder such effects, because interactions among individuals and prey detection distance are affected by light intensity (Valdimarsson and Metcalfe 2001, Elliott 2011). Finally, I tested if (i) fish with access to abundant shelters, (ii) more active fish and (iii) fish

foraging in isolation grew faster.

*Chapter 4: Diel activity and growth of Arctic charr in contrasting stream habitats.* In this chapter, I describe the results from an experiment where Arctic charr (age 1+) were placed in enclosures with contrasting current velocity (~5, 15 and 25 cm/s) and water depth (~15 and 30 cm). Habitat variables are central in the study of the energetic costs of swimming and prey intake (Fausch 2014, Piccolo et al. 2014, Rosenfeld et al. 2014). In fast habitats, more potential prey drift in the water column (Nislow et al. 1998), but swimming is more costly (Hill and Grossman 1993). In deep habitats, fish can sample a larger volume of water up to the limit of their detection range (Piccolo et al. 2007). Fast and deep habitat also offer better cover against avian and terrestrial predators (Gregory 1993, Conallin et al. 2014). Studies have repeatedly suggested that salmonids use relatively fast habitats during the day and move to slower water at night, in response to both food availability and predation risk (Metcalf et al. 1997, Polacek and James 2003, Banish et al. 2008, Johnson et al. 2011). Such habitat selection may be limited, e.g. because of the limited ability of juveniles to track habitats (Einum and Nislow 2005, Gowan 2006), because of competitive exclusion (Nakano 1995, Steingrímsson and Grant 2003), or because of man-made structures (Thorstad et al. 2007). In such conditions, salmonids may alter their temporal behavior instead. I tested the prediction that (i) activity rates will increase with current velocity and water depth, and (ii) activity rates will increase more slowly with current velocity and water depth at night than during the day.

In this study, I also measured the individual latency to emerge from a shelter after I started each observation. Indeed, in habitats with high net energy gain, fish may be able to remain longer in a shelter following a perturbation, with little effect on their growth. However, net energy gain and predation risk are often negatively correlated in streams, e.g. fast and deep habitats have more food (Nislow et al. 1998) and are less exposed to predators (Heggenes et al. 1991, Conallin et al. 2014). Thus, fish in habitats with low energy intake may experience higher predation risk and remain hidden longer. When predation risk and food availability vary over the 24h cycle, which is often the case in streams (Metcalf et al. 1999, Giroux et al. 2000), there may also be differences in latency to exit shelters between day and night. Thus, I predicted that fish will resume feeding later after a perturbation in risky conditions, i.e. in slower and shallower habitats

and during the day. Finally, I measured growth to link it to habitat features, and individual activity rates.

*Chapter 5: Fluctuations in water flow: Effects on diel activity, foraging mode and growth in juvenile Arctic charr.* In this chapter I subjected Arctic charr (YOY and age 1+) to either stable (i.e. only natural and moderate fluctuations) or fluctuating waterflow (i.e. low, then high waterflow for two days, repeated once). Freshwater systems display seasonal patterns in discharge (high flow in spring during snowmelt, low flow during summer etc.). These seasonal patterns can be profoundly affected by structures such as dams and reservoirs where water is stored and released, sometimes in an unpredictable manner. Fish can respond to quick habitat modifications by relocating to more suitable areas (Cocherell et al. 2010), but some salmonids show strong site fidelity, even after acute modifications of their local habitat (Pert and Erman 1994, Scruton et al. 2003). Sudden modifications of the waterflow also affect the net benefits of feeding at a given location during the day and the night (e.g. prey detection, swimming costs, predation risk) so fish may adjust their diel activity after such perturbation (see chapter 4). I tested the predictions that the rate and timing of activity will differ among low, intermediate and high waterflow. Thus I set up six enclosures at a specific position where the study stream separates into two channels, with two enclosures at the top serving as control, and two in each channel. The flow was directed to either one or the other side to create the fluctuation.

In this study, I measured foraging mode, i.e. mobility and speed while searching for prey, foraging radius and prey attack rate. Those traits depend directly upon the costs of swimming in different habitats (McLaughlin et al. 1994, Tunney and Steingrímsson 2012), and upon visibility of prey, i.e. light intensity (Metcalf et al. 1997, Mazur and Beauchamp 2003). Thus, I expected to find differences across treatments of waterflow, and between day and night. I also examined if behavioral measurements were similar after consecutive switches of waterflow, and in the two days following a switch, to see if individuals react rapidly or slowly to habitat modifications. Few studies document behavioral adjustments on such short temporal scales in salmonids, but based on previous observations (Keenleyside and Yamamoto 1962), I expected to find differences in activity and foraging mode between the first and the second day after a switch of waterflow. Although the literature is equivocal regarding the effect of waterflow fluctuations on growth, such effects seem to be moderate to non-significant (Flodmark

et al. 2004, Korman and Campana 2009, Puffer et al. 2015). Measurements of activity rates and patterns can bring valuable insights on the effect of waterflow fluctuations on individual fitness.

*Chapter 6: Density-dependent diel activity in stream-dwelling Arctic charr* *Salvelinus alpinus*. The goal of this chapter was to test if and how Arctic charr modify their rate and timing of activity in response to population density (2 ind/m<sup>2</sup> and 6 ind/m<sup>2</sup>). Intra-specific competition increases with density, as more individuals compete for the same amount of prey, which may affect territory size and distribution (López-Sepulcre and Kokko 2005). However, behavioral responses to increased population density are less commonly examined in time and the literature provides equivocal results, as activity rates may (Mobæk et al. 2012) or may not increase (Blanchet et al. 2008a). The timing of activity may also be altered because of intra-specific competition, e.g. through reduced resource availability (Hansen and Closs 2005), or increased energetic requirements (Alanära et al. 2001). Hence we tested the predictions that at high population density (i) fish will be more active, (ii) they will distribute their activity over longer periods, and (iii) growth rate will be similar to low population density.

We also tested how other ecological factors may affect diel activity. We expected activity rates to increase with rising water temperature (e.g. Breau et al. 2007a), and at low light intensity (Imre and Boisclair 2004). We also examined if and how activity changed depending on water level and season.

*Chapter 7: Repeatability and ecological correlates of foraging mode in a stream dwelling fish.* In this chapter, I examined foraging mode across three streams that vary in series of ecological factors (temperature, food availability, habitats), to quantify the variability among and within streams, and individual repeatability. Foraging mode of salmonids is highly variable. Some individuals exhibit a “sit-and-wait” tactic and initiate movement to intercept drifting prey (Kalleberg 1958), but some are more mobile, both while searching for prey and during attack bursts (Grant and Noakes 1987). The shape of the foraging mode distribution can also vary from e.g. a bimodal distribution (e.g. Grant and Noakes 1987), to a distribution skewed towards the sedentary end of the spectrum (e.g. Tunney and Steingrímsson 2012). Variability within individuals, compared with among-individual variability, may be alternatively high (McLaughlin et al. 1992) or low (Biro and Ridgway 2008). This variability may

reflect the different conditions in which foraging mode has been measured (e.g. current velocity, water depth etc.)

I tested the predictions that (i) most of the variability in foraging mode will occur among streams, because I selected streams with contrasting ecological conditions. Within streams, Arctic charr should be more sedentary (ii) at low water temperature (because of increased costs of swimming at low temperature), (iii) at low light levels (because of reduced visibility), and (iv) in fast-running water (because of increased swimming costs and food availability). After accounting for these effects, I expected high individual repeatability of foraging mode (Biro and Ridgway 2008).

## 1.4 Methods

This work consists of both field experiments (chapters 3 to 6) and semi-experimental field work (chapters 2 and 7). All studies were carried out between June and August of 2013, 2014, and 2015. We used five locations in total, all located in Skagafjörður, northern Iceland. These locations included river Deildará (N 65.848333, W 19.215278, chapter 6) and one of its tributaries (N 65.849379, W 19.222297, chapters 2 and 5), river Grímsá (N 65.792379, W 19.844413, chapters 3 and 4) and one of its tributaries (N 65.828795, W 19.869358, chapter 2), and river Myllulækur (N 65.516398, W 19.606433 chapter 2). All three streams have been used previously to study the behavior of salmonids (Gunnarsson and Steingrímsson 2011, Tunney and Steingrímsson 2012). In the field, all studies occurred in a similar way:

1. I erected two to six enclosures (Figure 1.1) at locations that suited Arctic charr requirements, and that fitted the experimental treatments. The enclosures were 4 m long, 1 m wide, and 0.75 m high and were made of nylon with a mesh size of 5 mm. The bottom of the enclosure was covered with local substrate, aiming either for heterogeneous (e.g. in chapters 2 and 6) or relatively homogeneous habitat (e.g. chapters 3 and 4). I tied string at the top of each enclosure to deter avian predators.

2. I collected Arctic charr in the same stream, via electrofishing. All individuals were anaesthetized, measured for body length and body mass, tagged with different color combinations (green, yellow, red and orange of Visible Implant Elastomers (Steingrímsson and Grant 2003),

and were released in the enclosures (Figure 1.2).



*Figure 1.1 Top: 4 m<sup>2</sup> enclosure set up in a tributary of river Grímsá. Bottom: Close up of the inside of an enclosure. Thin metal bars (8 mm) taped at every 10 cm were added to record the position of active individuals. In this experiment, the position and size of shelters was controlled.*

3. I collected measurements of habitat availability (current velocity, water depth and substrate) and repeated these measurements several times in studies where the effect of habitat was examined (e.g. chapters 4 and 5).

4. I also collected drift samples at the beginning of each study. The frequency of these samples varied across studies. In some studies, I collected day and night samples and repeated them several times. In others, I collected eight drift samples (one every three hours) at the beginning and the end of the study.



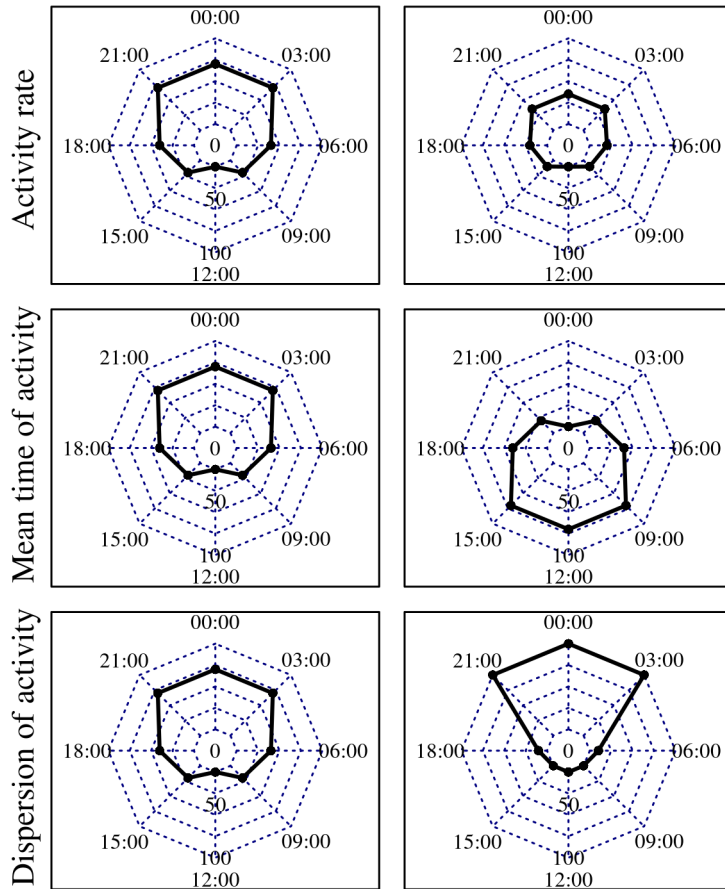
*Figure 1.2 Four Arctic charr *Salvelinus alpinus* of age 1+ tagged with different combinations of colorful Visible Implant Elastomers at two specific positions of the dorsal fin. The tags progressively fade but remained visible throughout each study.*

5. After a period of 24-48 h following the introduction of Arctic charr in the enclosures, I recorded individual behavior for six to ten 24 h periods distributed throughout the experiment. I observed fish eight times a day (every three hours). I obtained the activity status of each individual, and recorded other behaviors, according to the study (e.g. foraging mode, x-y position, habitat features at that position, latency to emerge from a shelter).

6. At the end of each study, I captured all individuals, anaesthetized them, measured their body length and body mass and released them in the stream.

I used several statistical methods to address different questions. I used two types of analyses to test the effect of a given factor (and its treatments) on activity patterns, depending on the power needed to detect an effect and the strength of individual differences. I either used circular ANOVAs based on the circular distribution of activity rates (e.g. chapter 2 and 3), or mixed linear models testing for differences between day (06:00 to 18:00) and night (21:00 to 03:00, chapters 4 and 5). At the individual level, I describe the variation in activity using





*Figure 1.3 Examples of activity patterns showing the level of activity (0 % in the inner ring, 100 % in the outer ring) at different times of the day. In each pair of graphs, one of three factors is modified while the other two are identical. From left to right, the first pair shows high and low activity rate, the right pair shows nocturnal and diurnal activity, and the third pair shows high and low dispersion of activity.*

three metrics, (a) individual activity rates, which is the proportion of observations when a focal individual was active, (ii) the mean time of activity, which indicates at what time of the 24 h cycle an individual was active on average, and (iii) the dispersion of activity, which measures how much an individual spreads its activity around the mean. Figure 1.3 shows examples of individual activity patterns that vary in each of those three aspects. For other analyses, I used mostly mixed linear models, or variants (e.g. zero-inflation models) according to data distribution, normality etc. I used two different metrics of growth, specific growth rate (Ricker 1975) and standardized mass-specific

growth rates (*sensu* Ostrovsky 1995).

## **1.5 Main results and discussion**

### **1.5.1 Diel activity and aggregation of a stream-dwelling fish along a temperature gradient among and within populations**

In chapter 2, I found differences in the rates and timing of activity of Arctic charr, both among, and within streams. First, according to our prediction (*sensu* e.g. Beamish 1964), fish were more active from the cold to the warm stream and with increasing temperature within streams. However, activity rates were particularly high in the warm stream, and no relationship was detected between temperature and activity, perhaps because fish could not increase activity further. Breau et al. (2007a) described a drop in activity rates in unusually warm conditions, but in my study, water temperature remained in the range tolerated by Arctic charr (Jonsson and Jonsson 2009, Elliott and Elliott 2010). Importantly, temperature was correlated to a suite of factors, such as current velocity, body size and food availability. Although it is not an issue within streams, I also discuss how these effects may accentuate or hinder the relationship between activity rate and water temperature. Based on the fact that factors like food availability can be related alternatively positively or negatively to temperature (Anholt and Werner 1995, Nakano 1995), I concluded that such effects should be moderate compared to that of temperature.

Activity rate was similar during the day and the night in the cold stream, but Arctic charr avoided crepuscular times (18:00, 21:00 and 06:00). Fingerle et al. (2016) found similar effects and argued this may be due to diel patterns of food availability. In both the cold and the intermediate streams, activity rates increased with temperature during the day, but not at night, which is in accordance with earlier studies (Fraser et al. 1993, Blanchet et al. 2008a, Fingerle et al. 2016). This could possibly be explained by foraging rates at night being independent of temperature (Fraser et al. 1993), i.e. the benefits of increased activity at high water temperature at low light intensity may be limited (Watz et al. 2014). In the intermediate and the warm stream, fish were predominantly nocturnal, exhibiting moderate activity during the day.

Fish aggregated more in the warm stream than in the cold and intermediate stream. Although aggregation can arise in response to decreasing temperature, e.g. to conserve energy (Shah et al. 2003, Schradin et al. 2006), this is unlikely in streams where water is constantly renewed. Instead, I suggested that among-stream differences rather reflect other factors. For instance, food availability was higher in the warm stream, so fish may not acquire more food via territoriality (Keeley 2000, Gunnarsson and Steingrímsson 2011). In the warm stream, fish were also larger and may display stronger anti-predatory behavior, e.g. via aggregation (Clark 1994). The shape of the relationship between temperature and aggregation varied within streams. Fish were less and more aggregated with increasing temperature in the cold and warm stream, respectively. In the intermediate stream, fish were more aggregated at the extremes of the temperature range. Such contrasting patterns among streams likely reflect a series of factors, e.g. food availability or the costs of territoriality. Valdimarsson and Metcalfe (2001) suggested that salmonids are less aggregated during the day, because they detect prey and conspecifics at a shorter range. However, within streams, contrasting diel patterns of aggregation emerged. Fish were alternatively more, similarly or less aggregated during the night than during the day in the cold, intermediate and warm stream, respectively. Higher aggregation at night in cold conditions, may result from smaller territories. Alternatively, as daytime activity increased from the cold to the warm stream, Arctic charr may aggregate more to limit predation risk (Cresswell 1994).

Studies have suggested that salmonids grow faster at intermediate water temperature (Larsson et al. 2005, Forseth et al. 2009), but I found the opposite pattern. Among stream comparisons of growth should be interpreted carefully, especially because other factors than temperature have to be taken into account (e.g. food availability and habitat). Within streams, I found that more active individuals consistently grew faster than less active individuals, which is in accordance with previous studies (Martin-Smith and Armstrong 2002, Brännäs 2008). In contrast, growth rates were not related to the dispersion of activity or the average distance between a fish and its closest neighbor.

Overall, the novelty of this chapter lies in comparing individual behavior across streams with contrasting temperature profiles. The shape and magnitude of the interaction between water temperature,

diel activity, and aggregation varied for populations living at the lower or higher end of the thermal range of Arctic charr, and may thus affect individual fitness (growth, mortality etc.). An increase in water temperature in warm streams can be a strong limitation to individual fitness, if Arctic charr cannot increase activity beyond a certain maximum. This also has implications for the management of salmonids populations, because Arctic charr respond differently (e.g. diel activity versus aggregation) to an increase in temperature in cold and warm conditions.

### **1.5.2 Shelter availability alters diel activity and space use in a stream fish**

In chapter 3, I tested how Arctic charr modify their diel activity, aggregation and foraging mode in two treatments of shelter availability. Individuals with access to abundant shelters were nocturnal, which is expected of salmonids of age 1+ (Imre and Boisclair 2004, Breau et al. 2007a). However, in shelter-poor environments, fish were more active, mostly diurnal and extended their activity over longer periods. Although it reflects previous work (Orpwood et al. 2010), increasing diurnal activity may seem counter-intuitive because individuals experience higher predation risk (Metcalf et al. 1999). I argued that higher daytime activity may be due to individuals monopolizing shelters and excluding their conspecifics more actively during daytime, because the value of a shelter should be higher.

Arctic charr also modified their spatial behavior when shelters were limited. First, they were more aggregated, which was in accordance with the prediction that open habitats, more exposed to predators, should favour schooling (Dolan and Butler 2006). Second, these fish attacked prey at a shorter distance than fish in shelter-rich environments. This goes against my prediction that fish in complex habitats (i.e. with more shelters) should have a smaller field of vision and foraging area (Imre et al. 2002). I also expected longer foraging radius at low shelter availability because Arctic charr were more diurnal and should thus detect prey more easily (Watz et al. 2014). The results of this experiment may indicate costs associated with foraging in schools at low shelter availability, such as frequent contacts between competitors, and reduced field of vision, leading to shorter foraging radius and reduced prey attack rate.

Smaller fish extended their activity over longer periods, which is consistent with previous results (Alanärä et al. 2001). They were also less likely to be in schools when shelters were abundant. Foraging in isolation can provide several benefits, like increased access to food and reduced aggression. However, limiting shelter availability may increase the costs of such behavior, e.g. through higher predation risk and reduced food availability if isolated individuals use suboptimal habitats. Hence, although small individuals may sometimes take risk to maintain growth, the risk may be too high when shelters are limited.

Arctic charr grew similarly in the two treatments of shelter availability. At low shelter availability, fish were more active, but attacked prey less often. This could result in similar food intake among treatments. Other aspects need to be considered, such as increased stress (Millidine et al. 2006), and decreased food availability (Negishi and Richardson 2003) when shelters are rare. Previous studies suggest that salmonids may adjust their behavior, including their diel activity, to maintain growth in response to e.g. food availability (Orpwood et al. 2006), and intra-specific competition (Blanchet et al. 2008a). However, such behavior comes at the cost of higher exposure to predators (Contor and Griffith 1995, Imre and Boisclair 2005) because individuals are more active and more diurnal. Similarly to chapter 2, more active fish grew faster than those less active (Martin-Smith and Armstrong 2002, Brännäs 2008). Contrary to chapter 2, however, there was also a positive relationship between the distance to the closest neighbor and growth, indicating that individuals in schools grew slower. This could be another indication that Arctic charr foraged in isolation to maintain growth rates. Indeed, although I did not detect an effect of the distance to the closest neighbor on prey attack rate (Eggers 1976), fish staying farther away from other individuals were smaller, and perhaps benefited from such behavior, e.g. through higher foraging success or reduced aggression (DeVries et al. 2004).

The results of this chapter give new insights into the importance of shelters for natural salmonid populations. Responses to shelters have been commonly examined in the context of territoriality, growth and reproductive success (Finstad et al. 2007, Venter et al. 2008, Grimardias et al. 2010). However, temporal effects can be even more pronounced, as I found a twofold increase in activity rates and diametrically opposed times of activity in shelter-poor habitats. Although such adjustments can lead to similar growth rates, it can have long-term effects on individual fitness, especially through

increased mortality risk.

### **1.5.3 Diel activity and growth of Arctic charr in contrasting stream habitats**

In this chapter, I recorded the diel activity of Arctic charr in enclosures with contrasting current velocity and water depth. From slow to fast environments, fish were more active and more diurnal. Some studies suggest that salmonids are more active in fast habitats, but these were mostly correlative, e.g. the results may have reflected an effect of body size or food availability (Nakano 1995, Nislow et al. 1998). Contrasting activity patterns in habitats with different current velocity are in accordance with previous examples of diel habitat selection by salmonids (Polacek and James 2003, Banish et al. 2008, Johnson et al. 2011). However, my results are among the first to show empirically that when salmonids have limited potential for habitat selection, they can alter both the rate and the timing of their activity (Bradford and Higgins 2001, Imre and Boisclair 2004). Water depth did not affect activity rates and activity patterns. This could possibly suggest that my range of depth was relatively small compared to the water depth used by Arctic charr in general (Armstrong et al. 2003, Tunney and Steingrímsson 2012).

A range of hypotheses can be put forward about activity patterns in contrasting habitats. Indeed, one could expect either higher or lower activity rates in fast habitats, depending e.g. on the degree of anti-predatory behavior and need for fast growth. In that regard, it can seem surprising that Arctic charr were more active in fast habitats, because they are typically found in habitats that would correspond to my “slow” or “intermediate” treatments (Heggenes and Saltveit 2007, Tunney and Steingrímsson 2012). In this experiment, Arctic charr were studied in conditions that have rarely been used in previous studies. For instance, Arctic charr is often studied in sympatry with brown trout and Atlantic salmon and is described as less competitive and as using slower running waters (Heggberget 1984, Heggenes and Saltveit 2007). However, in absence of inter-specific competition, they may prefer faster habitats. Similarly, there was no among-cohort competition in my experiment, so charr could not be displaced to slower waters by older individuals. In any case, these results point out the need for more information on the behavior and ecology of Arctic charr in lotic environments. Another important implication of this study is that daytime estimates of population density and habitat

preferences can be biased. For instance, daytime estimates in the present study would have underestimated density more in the slow than in the fast current enclosures.

I also had competing hypotheses about whether fish should emerge earlier or later from a shelter in enclosures with contrasting habitats. Arctic charr took longer to exit shelters in fast and deep habitats, which supports the idea that predation risk rather than energy intake drives this behavior. Fast and deep habitats are less exposed to predators, which may lead Arctic charr to remain feeding, or resume feeding soon after a disturbance (Gotceitas and Godin 1991). I also expected differences in latency to emerge from a shelter between day and night, but found no such effect, neither overall, nor in any habitat type. This prediction reflected the daily activity of Arctic charr's predators, but the presence of an observer (which was distributed equally throughout the 24 h cycle) may be more of a disturbance. This could be another indication that fish react primarily to predation risk, because although there was more food drifting at night, they did not emerge faster from their shelter.

Fish in fast habitats grew faster, which is congruent with their higher activity rate and shorter latency to emerge from a shelter after a disturbance. In fast environments, Arctic charr were also more diurnal, which could lead to higher (through increased prey detection) or lower growth rates (through reduced food availability, see also Young et al. 1997b, Giroux et al. 2000). Growth rates were higher in deep habitats, where the only behavioral difference was that fish emerged from shelters earlier. The literature on growth rates in contrasting habitats is equivocal. So far, higher growth rates have been reported in intermediate (Blanchet et al. 2008b) and fast habitats (Allouche and Gaudin 2001), but Girard et al. (2004) found no relationship between current velocity and growth. Similarly, stream-dwelling fish may grow faster in deep habitats (Harvey et al. 2005), or may have similar growth rates among habitats with contrasting depth (Girard et al. 2004, Blanchet et al. 2008b). As in previous chapters, a positive relationship was detected between activity and growth rates. However, the relationship was strongest in fast habitats, and non-significant in slow habitats. This could be explained by the limited benefits of increasing activity in slow habitats. For instance, food availability can be lower, and higher activity rates may only increase food intake slowly, while costs like aggression may increase faster (Keeley 2000, Gunnarsson and Steingrímsson 2011).

The results of this chapter have several important implications. First, they can be incorporated into foraging models of salmonids by estimating the dynamic profitability of habitats over the 24 h cycle (Railsback et al. 2005, Railsback and Harvey 2011). Second, they challenge the general idea that Arctic charr prefer slow habitats, and suggest that at least when not competing with other salmonids, they may prefer faster-running waters. Third, it gives insight into the potential of salmonids to overcome future habitat modifications (loss, degradation and fragmentation) through behavioral adjustments. Finally, the outcome of this study may be species- and context-dependent and thus needs further investigation.

#### **1.5.4 Fluctuations in water flow: Effects on diel activity, foraging mode and growth in juvenile Arctic charr**

In this chapter, I measured diel activity in relatively stable and in fluctuating waterflow. In the first two days of the study, all enclosures had similar habitats (stable waterflow) and fish displayed similar activity rates (except in one enclosure). In the two control enclosures upstream from the location where the study stream separated into two channels, activity rates also remained similar throughout the study. In the enclosures where the waterflow fluctuated (i.e. water directed from one channel to the other, repeatedly), Arctic charr were primarily active during low flow periods. This is in accordance with Bradford and Higgins' study (2001), but differs from chapter 4. This is surprising because we used fish of similar size ( $57.2 \pm 1.7$  and  $59.4 \pm 5.9$  mm) and under similar temperature ( $6.4 \pm 1.9$  and  $6.7 \pm 1.0$  °C) in chapters 4 and 5, respectively. Habitats were also similar ( $22.2 \pm 4.2$  and  $21.1 \pm 3.3$  cms/s at high flow,  $5.2 \pm 1.9$  and  $4.4 \pm 1.2$  cm/s at low flow in chapters 4 and 5, respectively). Thus, there were three main differences between the two studies, (i) they were carried out in different streams, (ii) there were only individuals of age 1+ in the previous chapter, and both YOY and 1+ individuals in this chapter, and (iii) fish experienced only one habitat type in chapter 4, whereas they experienced high and low waterflow consecutively in chapter 5. Importantly, YOY were never observed active in this experiment, so inter-cohort competition is unlikely to create this difference. Thus, this difference probably reflects population differences in diel activity, or an effect of waterflow stability.



Null activity rates of YOY individuals are also a surprising result, because they were as active as 1+ individuals in previous studies (Imre and Boisclair 2004, Breau et al. 2007a). Hence I suggested that because the study was carried out in a relatively cold tributary, YOY may only need to capture few prey to maintain growth. I found a positive relationship between body mass and activity rates for individuals of age 1+, which further corroborates this explanation. In any case, this study highlights the need for more information on the diel activity of YOY Arctic charr, and the appropriate method to measure it.

Fish were mostly nocturnal, both in the control and at low waterflow, but even more nocturnal at low waterflow, which is consistent both with the literature (Bradford and Higgins 2001, Imre and Boisclair 2004, Riley et al. 2009) and the results from chapter 4. This is probably a response to a combination of higher predation risk during the day in slow habitats, and reduced prey detection at night in fast habitats (Metcalf et al. 1997, Metcalfe et al. 1999). There was also a peak of activity following a switch to low waterflow, which could be due in part to the manipulation of the flow, but this peak lasted up to several hours after the switch. Alternatively, a peak in activity may be due to hunger after two days without feeding at high waterflow, but a peak was also detected after the initial switch from intermediate to low waterflow.

At low waterflow, Arctic charr were more mobile, swam faster during prey search, and attacked prey at longer distance, which reflects the relative costs of swimming in slow and fast habitats (Grant and Noakes 1988, Tunney and Steingrímsson 2012). Fish also swam faster during the day, regardless of the treatment, but did not attack prey at longer distances during daytime (Mazur and Beauchamp 2003). Some of the behaviors measured varied between the first and second switch to low waterflow (activity rate, search mobility, and foraging radius) and between the first and second day after a switch (activity rate and prey attack rate). This suggests that fluctuating waterflow can affect behavior on short temporal scales (i.e. less than 24 h). Hence, frequent hydropeaking events that modify habitat availability may exceed the time needed for Arctic charr to adjust their behavior, which could have important consequences for individual fitness and population ecology (Murchie et al. 2008).

Fish grew at a similar rate in stable and fluctuating waterflow,

which is in accordance with previous studies (Flodmark et al. 2004, Korman and Campana 2009, Puffer et al. 2015). This may suggest that Arctic charr make up for reduced feeding under unfavorable conditions (high waterflow) by increasing activity during favorable conditions to maintain growth. There was a positive relationship between activity rate and growth, but the effect was only detected in the control enclosures. Hence, fluctuating waterflow can greatly affect the benefits of increased activity. For instance, the economic defendability of territories increases with spatial and temporal predictability, so rapidly changing waterflow may mask dominance hierarchies and growth differences (Grant 1993). This should be taken into account e.g. when managing natural salmonid population in fragmented habitats with hydroelectric power plants.

### **1.5.5 Density-dependent diel activity in stream dwelling Arctic charr *Salvelinus alpinus***

The literature suggests that organisms may alternatively increase (Guénard et al. 2012) or decrease activity (Borkowski 2000) in response to increasing population density. In this study, we predicted that juvenile Arctic charr would be more active and distribute their activity over longer periods at high population density, to counter the effect of increased intra-specific competition. Activity rates were low overall, which was expected in this cold stream. In accordance with our predictions, fish at high population density were more active. One previous study (Blanchet et al. 2008a) found no such effect, but its results were based on short observations over narrow intervals (9:00 – 11:00 and 20:30 – 22:30). The importance of monitoring activity at regular short intervals around the clock was especially highlighted in our study, because activity rates increased during crepuscular hours at high population density. As Arctic charr were predominantly nocturnal, this suggests that individuals reduced activity at night, e.g. through competitive exclusion (Alanärä et al. 2001). Higher activity at crepuscular hours also resulted in activity patterns being more dispersed around the clock.

Ecological factors also explained a large part of the variation in activity rates, as fish were more likely to be active at high temperature, during the night, and with increasing water discharge. These results agree with my experiments (e.g. temperature effect in chapter 2, water discharge in chapter 4, but see chapter 5). Arctic charr also progressively increased activity throughout the experiment, which

probably reflected lower food availability. Water temperature and light intensity interacted in their effect on activity rates. Specifically, fish were more likely to be active on warmer than on colder days, whereas activity levels were not affected by water temperature at night (see also Fraser et al. 1993, Breau et al. 2007a, Blanchet et al. 2008a).

Arctic charr grew at similar rate at low and high population density. Density-dependent growth in salmonids has been alternatively documented (Imre et al. 2005, Lindeman et al. 2015) or refuted (Kaspersson et al. 2013). Our results suggest that increased activity at high population density serves to compensate for increased interference and/or exploitative competition. Previous studies suggest similar behavioral responses to changes in competition and food availability (Alanära et al. 2001, Orpwood et al. 2006, Blanchet et al. 2008b). This study is the only one in our series of experiments (including chapters 2 to 5), where more active fish did not grow faster, regardless of population density. This result may be partly explained by the fluctuations in waterflow during the experiment (from 25 to 50 cm). In chapter 5, the relationship between activity rate and growth was non-significant under fluctuating waterflow. Alternatively, this may reflect complex interactions between individual activity patterns and food intake at specific times of the day.

In conclusion, this study demonstrated that intra-specific competition can be mediated by behavioral adjustments in time (higher activity, especially at crepuscular hours). Importantly, the effect of population density on individual behavior is more commonly examined in space, e.g. through territoriality and population distribution. However we found a 1.5 fold increase in activity at high population density, even at cold temperature. This opens interesting research questions, such as the potential interplay between population density, ecological factors such as water temperature and food availability, and behavioral responses of salmonids and its consequences for individual growth, and population dynamics.

### **1.5.6 Repeatability and ecological correlates of foraging mode in a stream dwelling fish**

Monitoring individuals enabled me to collect repeated measurements of foraging mode. I used these data to measure the variation in foraging mode among streams, the individual repeatability within streams, and the relationship with several ecological factors (water

temperature, light intensity, current velocity and water depth). In one stream (Deildará), fish were more mobile during prey search, attacked prey at longer distance and at a slower rate, and fed more often at the surface than in Myllulækur (with intermediate values in Grímsá). This result highlights the coordinated nature of foraging mode among streams (Cooper 2007). Although foraging-related traits are sometimes repeatable (Bell et al. 2009) because behaving in a consistent way can be adaptive (Dall et al. 2004, McElreath and Strimling 2006), among individual variation was relatively low within streams. In other words, Arctic charr could adopt different tactics consecutively and used a wide portion of the local mobile-sedentary continuum. This challenges the common idea that stream-dwelling fish populations consist of a mixture of consistently mobile and consistently sedentary individuals (Morrissey and Ferguson 2011, Young 2011, Booth et al. 2014).

In accordance with previous studies (Grant and Noakes 1988, Steingrímsson and Grant 2011, Tunney and Steingrímsson 2012), Arctic charr were more mobile in slow-running water. They also attacked fewer prey, but at longer distance in slow habitats. They attacked prey at slower rate, over longer distances and more often at the surface in deep habitats (see also Steingrímsson and Grant 2011). Importantly, light intensity and water temperature were strong predictors of foraging mode. This was supported among streams as fish were more mobile in the warmest stream (Tunney and Steingrímsson 2012). Within streams, however, I detected the opposite effect, i.e. fish became more sedentary (based on search mobility and foraging radius) when water temperature increased. This may indicate that more food drifted at high temperature (Winterbottom et al. 1997), thus reducing the need for mobility to capture prey. This is consistent with the fact that Arctic charr also attacked more prey at high temperature. Fish were more mobile during the day, which could also indicate lower drift rates during the day (Elliott 1965, Jenkins Jr. et al. 1970). Arctic charr also attacked prey at longer distances during the day, probably because they could detect remote prey more easily (Watz et al. 2014).

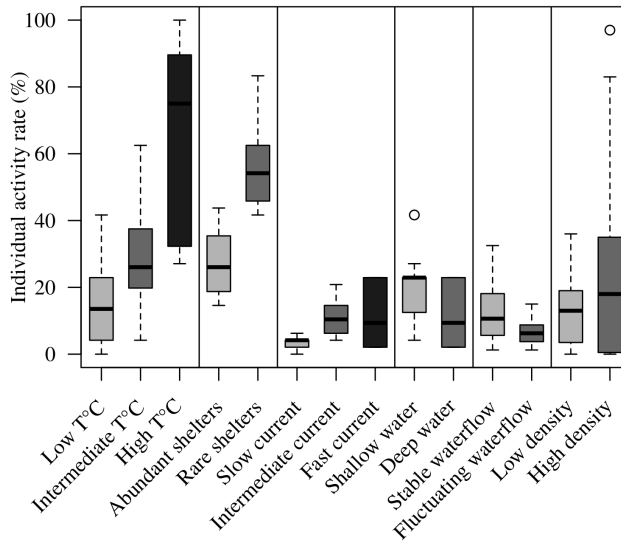
In conclusion, this study shows that the high variability in foraging mode in salmonid populations is due to (i) the variable conditions they experience (day-night, cold-warm, slow-fast habitats, high-low food availability etc.), and (ii) individual flexibility i.e. with individuals being able to use a variety of foraging tactics subsequently. My estimates of repeatability are low and may reflect that Arctic charr is a species with particularly variable ecology and life history. Future

studies could examine this variation further by focusing e.g. on the role of resource specialization (Skúlason and Smith 1995) and on evolutionary history (Stamps et al. 2012).

### **1.5.7 Additional results and conclusions**

In chapters 2 to 6, I place the emphasis on each of five separate experiments, but these datasets can have additional use. One of them is the quantification of the variability in activity among and within individuals across contexts. Among-individual differences in behavior are gaining interest from ecologists and evolutionary biologist, because they seem to be consistent, suggesting an adaptive basis (Dall et al. 2004). Indeed, phenotypic differences in a population are the material upon which natural selection can occur, but this idea has only recently been integrated in the context of behavioral traits (Dall et al. 2004, Reale et al. 2007, Bell et al. 2009, Wolf and Weissing 2012). Estimates of diel activity of salmonids in particular, are rarely collected at the individual level (Alanära and Brännäs 1997, Alanära et al. 2001), especially in natural conditions (Ovidio et al. 2002, Breau et al. 2007a, Roy et al. 2013). The few studies addressing this issue concluded that there exists substantial variation among individuals, even within a cohort. The systematic nature of the data collected during this Ph.D. makes it possible to quantify this variation, examine if it can be affected by ecological conditions and if it relates to individual characteristics (e.g. body size and growth).

In all chapters (but see chapter 6), I measured activity at the population level, e.g. the proportion of fish active during an observation, the mean time of activity based on a whole dataset, independently of individuals, etc. However, one can also calculate these metrics on an individual basis and measure the extent of variation in diel activity among and within individuals. Below, I present several figures where this variation is shown in the five studies. Figure 1.4 shows that ecological conditions can affect not only activity rates, but also the variation among individuals. For instance, there was roughly twice as much variation among individuals in (i) a warm stream than in a cold stream, (ii) under stable than under fluctuating waterflow, (iii) at high than at low density, and (iv) from slow to fast water current.



*Figure 1.4 Distributions of individual activity rates in five studies. All individuals were Arctic charr of age 1+ and their diel activity was monitored at three hour intervals during six-ten 24 h cycles distributed over a period of 10-15 days. The figure only shows values for current velocity in deep habitats, and for water depth in fast water current.*

In Figure 1.5, I show that there is substantial variation in the mean time of activity among individuals. The standard deviation of the distribution was as high as roughly five hours in several studies (e.g. in the cold stream, in slow and deep habitats). Hence, in similar ecological conditions, different individuals could potentially be active at very different moments. Although ecological variables can lead to strong differences in activity patterns (see e.g. the effect of shelter availability and current velocity), the extent of among-individual variation in the mean time of activity is usually less affected. For instance, there was little variation in mean time of activity among individuals in chapter 3 (Figure 1.5B) in each treatment of shelter availability. On the opposite, there was twice as much variation within all treatments of current velocity and water depth in chapter 4, compared to chapter 3 (Figure 1.5C and D). Such differences could reflect population processes like local adaptation, but the studies from chapters 3 and 4 were carried out in the same stream, which suggests that other factors may be at play (e.g. seasonal effects, annual changes in food availability and predation risk, or differential selective pressures on diel activity among cohorts).

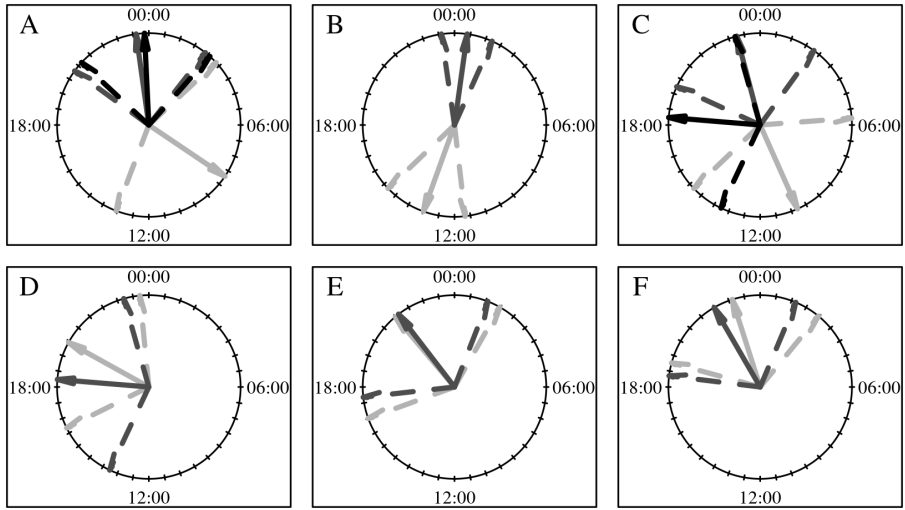
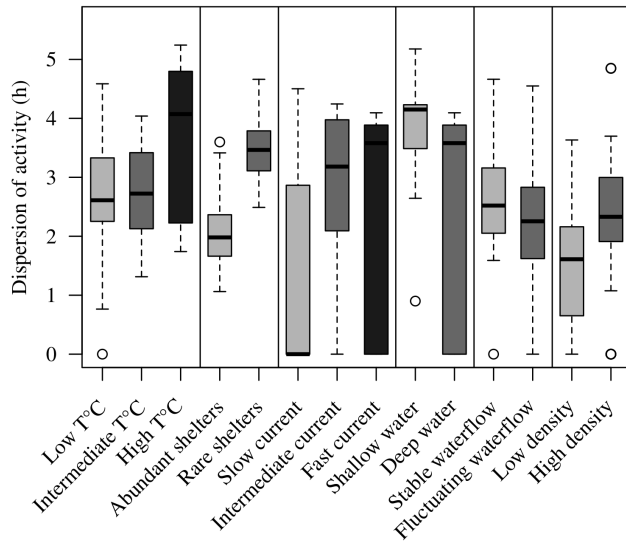


Figure 1.5 Distributions of individual mean time of activity in five studies; A) streams with low (light grey), intermediate (dark grey) and high (black) water temperature, B) at low (light grey) and high (dark grey) shelter availability, C) in slow (light grey), intermediate (dark grey) and fast (black) habitats (deep enclosures only), D) in shallow (light grey) and deep (dark grey) waters (fast enclosures only), E) in stable (light grey) and fluctuating (dark grey) waterflow, F) at low (light grey) and high (dark grey) population density. Solid arrows indicate the mean of the distribution and dotted arrows indicate the standard error.

Figure 1.6 shows how much variation exists in how individuals spread their activity around the clock. Similarly to individual activity rates, individuals in similar ecological conditions can vary greatly in dispersion of activity. Hence, in several studies, some individuals were consistently active at the same time, while other individuals extended their activity over longer periods. Importantly, low dispersion of activity often indicates that an individual was seldom active, which is detected in two ways. First, treatments where individuals were more active also had higher dispersion of activity (Figure 1.7A). Second, in each treatment, I examined possible relationships between individual activity rates and dispersion of activity. This relationship was positive and significant in 9 out of 14 cases (Figure 1.7B). Four of the five non-significant examples were in the study on the effect of habitat availability, where I purposefully limited sample size by selecting only enclosures with a specific treatment of water depth and current velocity (i.e.  $n = 10$  against  $n = 20-40$  in all other studies). This relationship can be a statistical artefact where increasing sample size

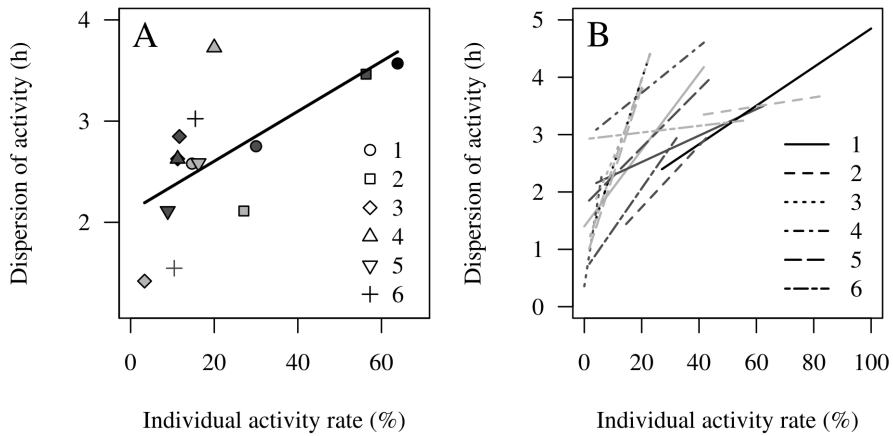


*Figure 1.6 Distributions of individual dispersion of activity in five studies. This metric refers to the standard deviation of the individual circular distribution of activity. All individuals were Arctic charr of age 1+ and their diel activity was monitored at three hour intervals during six-ten 24 h cycles distributed over a period of 10-15 days. The figure only shows values for current velocity in deep habitats, and for water depth in fast water current.*

increases the variation in the distribution. This is especially expected at extremely high activity rates, e.g. a permanently active individual would also have the highest possible dispersion. However, this should not be the case for low to moderate values of activity rates. Hence, by being more active, individuals dispersed their activity more around the clock instead of increasing activity at their preferred activity time. This can indicate that they potentially had to be less active at the specific mean time of their activity window (e.g. because of competitive exclusion) and instead, emerged from their shelters earlier and continued feeding later.

Overall, I detected strong individual variation in activity patterns in the same ecological conditions, which is in accordance with previous studies on salmonids (Ovidio et al. 2002, Breau et al. 2007a, Roy et al. 2013). Some of this variation can be attributed to body size. For instance, Alanärä et al. (2001) found that larger dominant brown trout monopolized the optimal temporal feeding time and forced smaller subordinate individuals to feed at different times. In my datasets, this effect was detected based on body mass (e.g. chapter 3)





*Figure 1.7 Average dispersion of activity against individual activity rates across ecological conditions (A, Pearson correlation test,  $R^2 = 0.642$ ,  $P = 0.013$ ) and regression lines for the effect of activity rate on the dispersion of activity at the individual level (B) in 6 studies (1 water temperature, 2 shelter availability, 3 current velocity, 4 water depth, 5 waterflow fluctuation, 6 population density). Refer to figure 1.5 for information on the color code. The figure only shows values for current velocity in deep habitats, and for water depth in fast water current.*

or not (e.g. chapter 4), so other factors may better predict individual variation in diel activity. Phenotypic differences (age, sex etc.) in circadian rhythms have been extensively documented in humans (Kerkhof 1985, Tankova et al. 1994, Baehr et al. 2000), and have been investigated in other animals (e.g. rodents, Cohen and Kronfeld-Schor 2006). Because freshwater fish exhibit an even higher degree of flexibility in activity patterns (Reebs 2002), these results open interesting research avenues. For instance, one could test how among-individual variation in activity patterns relates to life history strategies (Valdimarsson et al. 1997). Recently, activity rates and patterns have been suggested as a potential component of a pace-of-life syndrome (Réale et al. 2010), i.e. they correlate with faster growth, dispersal tendency and shorter lifespans (Závorka et al. 2015, Závorka et al. 2016).

In chapters 2 to 6, I asked a series of similar questions linking ecological conditions, diel activity patterns and growth. I found that activity rates and diel activity patterns were systematically affected by ecological conditions in all five studies (Table 1.1), which suggests that salmonids are sensitive to various environmental stimuli and

modify their diel activity in consequence. Some effects were detected throughout all studies, e.g. fish were consistently more active at high temperature. Other effects seem to be context-dependent. For instance Arctic charr may alternatively increase (chapter 4) or decrease (chapter 5) activity at high current velocity. Most of the time, the results were in accordance with previous observational studies. Inconsistencies in behavioral responses across chapters also reflect variability in previous results. For instance, contrasting responses to habitat types mirror equivocal conclusions from earlier studies (Nakano 1995, Bradford and Higgins 2001, Imre and Boisclair 2004).

I found that modifications of the physical environment of salmonids can lead to subtle to strong adjustments of diel activity, but what are the consequences of these modifications? First, the foraging behavior (aggregation, foraging mode) of salmonids depends on their activity patterns (Table 1.1). In general, diurnal individuals were more mobile, faster etc. This was expected because of the diel changes in light intensity, water temperature, food availability, density of competitors and predation risk. The results on aggregation are more complex as more diurnal individuals were alternatively more or less aggregated in different streams (chapter 2). This is another example of inconsistency reflecting previous equivocal results. For instance, in chapter 3, I found higher aggregation during the day, whereas Valdimarsson and Metcalfe (2001) found higher aggregation at night. This may reflect different selective pressures in populations with contrasting water temperature or food availability, resulting in different responses to activity during the day. Few studies on salmonid diel activity relate activity patterns to other aspects of individual behavior (Závorka et al. 2016). Relationships between diel activity and other behaviors in stream-dwelling fish deserve further research.

Environmental conditions lead to adjustments in diel activity. In turn, both environmental conditions and their effect on activity can affect foraging behavior. But is there any evidence that such modifications of behavior are adaptive? One way to answer this question is to see if contrasting activity rates among environments lead to different growth rates. This was true in two out of five cases, and a linear effect was detected only in one case (chapter 4). In some cases, activity may serve to maintain growth, as activity rates were sometimes higher in suboptimal conditions (e.g. at low shelter availability and high population density), which enabled Arctic charr to grow as fast as individuals in more suitable conditions.

Alternatively, in two other studies (chapters 2 and 4), fish were more active in environments with higher food availability (warm stream, fast current), which lead them to grow faster than in other environments. This suggests that modifications of the physical and social environment of salmonids may alternatively be coped with (shelter availability, fluctuations in waterflow, population density), or reinforce variability in growth rates (habitat type) via increased activity.

*Table 1.1 Summary of five studies on the effect of ecological conditions on the behavior and growth of juvenile Arctic charr. Green cells indicate significant effects. Red cell indicate that no effect was detected. White cells indicate that no effect was investigated.*

Question	Chapter 2	Chapter 3	Chapter 4	Chapter 5	Chapter 6
Environment → Activity rate?	Increasing activity with increasing temperature	Higher activity at low shelter availability	Increasing activity with increasing current velocity	Lower activity in fluctuating waterflow	Increasing activity at higher population density
Environment → Activity patterns?	Fish more nocturnal in warmer streams	Fish more diurnal at low shelter availability	Fish more nocturnal at low current velocity	Fish more nocturnal in fluctuating waterflow	Activity more dispersed at high population density
Diel activity → Other components of behavior?	Temperature and time of day affected aggregation	Diurnal behavior affected aggregation and foraging mode	No effect detected on the latency to exit shelters	Time of day affected speed while searching for prey	No effect investigated
Environment → Growth?	Different growth rates in three streams	Growth not affected by shelter availability	Faster growth in deep and fast habitats	Growth not affected by fluctuations in waterflow	Growth not affected by population density
Activity rates → Growth?	Yes	Yes	Yes	Yes	No
Environment x Activity → Growth?	No	No	Yes	Yes	No

In four out of five studies, more active fish grew faster (Table 1.4), which is consistent with earlier results (Brännäs 2008, Závorka et al. 2016). More importantly, this relationship may depend on

ecological conditions. For instance, it was stronger at low than at high shelter availability, in fast than in slow habitats, and in stable than in fluctuating waterflow. This could help explain why other studies did not find significant relationships between activity and growth (e.g. Blanchet et al. 2008a). Although I did not measure survival in the wild, I can use several surrogates, e.g. the proportion of daytime feeding, or the distance to other individuals while feeding, both of which affect mortality risk. In general my findings support the idea that higher activity increases predation risk. This is supported by the positive correlation between activity rate and the dispersion of activity across and within ecological conditions (Figure 1.7). Arctic charr of age 1+ are mostly nocturnal, so increasing the dispersion of activity should lead to higher use of daytime to feed, (i.e. more diurnal). Similarly, I found that more active fish were more diurnal in the warmest stream, and hence took more risk (chapter 7). Arctic charr may compensate by being more aggregated while foraging during the day (e.g. chapter 3), but not always (e.g. chapter 2). Whether or not increased predation risk leads to higher mortality is not clear. For instance, Závorka et al. (2016) found that more active individuals not only grew faster, but also had higher survival rates. This could be due to additional benefits of body size, i.e. the competitive ability to acquire territories leading to higher survival (Johnsson et al. 1999). Hence, more studies are needed to understand the consequences of variability in diel activity patterns for the population dynamics and ecology of salmonids.

I analyzed the results from these studies based on previous observations of diel activity of salmonids in streams, and with a strong emphasis on behavioral and ecological theory. Collecting data in a systematic way and repeatedly on tagged individuals and across ecological situations provided alternatively positive or negative evidence of these theories (e.g. flexibility and repeatability of diel activity, asset protection principle, relationship between body size and activity and between activity and growth etc.). These results add new elements to the complex picture of foraging ecology in juvenile salmonids. They also provide qualitative and quantitative estimates that can be implemented in models of growth, abundance and distribution of salmonids. Although some of these models have acknowledged the importance of considering diel activity patterns (Railsback et al. 2005), current foraging models often lack more accurate and complex data on the link between environment, activity, and fitness. One particular application of the data could be to predict how salmonids may overcome future expected changes in their

physical environment (e.g. higher temperature, habitat loss and degradation, increased perturbation of waterflow). These datasets can also be applied to population management and river restoration, e.g. by giving a better understanding of how habitat features (water depth, current velocity, shelter availability, flow regimes) shape the food intake, competition and predation risk of salmonids.

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## 2 Diel activity and aggregation of a stream fish along a temperature gradient among and within populations.

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### Abstract

The way animals exploit habitats and resources in time (e.g. diel activity) and space (e.g. aggregation) affects individual fitness via prey encounter, competition and predation risk. Freshwater fish may respond to daily changes in water temperature by adjusting diel activity and/or aggregation, but these behaviors are rarely examined systematically within and across streams with different water temperature profiles. We monitored individually tagged juvenile Arctic charr *Salvelinus alpinus* in stream enclosures in a cold ( $\sim 5$  °C), intermediate ( $\sim 9$  °C) and warm stream ( $\sim 14$  °C) for two weeks, and measured activity and aggregation at three hour intervals for six 24 h cycles in each stream, as well as individual growth. From the cold to the intermediate, and the warm stream, fish were more active (0.15, 0.23, and 0.64, respectively) and increased activity more at night. Within streams, fish also became more active with rising temperature, but only in the cold and intermediate stream and only during the day. Arctic charr were more aggregated in the warm stream and aggregation declined, declined then increased and increased with temperature in the cold, intermediate and warm stream, respectively. Fish were more, similarly, and less aggregated during the day from the cold to the warm stream. More active fish grew faster in all three streams, but growth was not affected by the distance between individuals. Surprisingly, growth rates were lowest in the stream with intermediate water temperature. Our study demonstrates that stream fishes living at

different temperature may exhibit drastic differences in behavior and respond differently to rising temperature. More generally, limited opportunity for behavioral adjustments (e.g. activity) may have important consequences for ectotherms living near the extreme of their thermal tolerance.

**Keywords:** Activity rates, schooling, Arctic charr, stream enclosures, growth rates

## 2.1 Introduction

Temperature is a critical ecological factor for vertebrates and an important driver of their behavior, physiology, development and distribution (Magnuson et al. 1979). Most behavioral and physiological processes including locomotion and foraging ability are affected by body temperature (Stevenson 1985, Angilletta Jr., Niewiarowski and Navas 2002). Changes in ambient temperature can be coped with in several ways, but adjusting behavior can be a fast and efficient way to do so (Hutchison and Maness 1979), because it enables organisms to track optimal temperatures in time and space (Magnuson et al. 1979). In time, such adjustments may consist in modifying activity, e.g. by foraging for longer periods to meet increased metabolic demands at high temperature, or by being active at specific times (Breau et al. 2007b). In terms of space use, organisms can move across temporarily optimal thermal areas (Young et al. 2010), or become more aggregated to conserve energy (Shah et al. 2003, Schradin et al. 2006). Part of the variation in temperature is predictable in time (e.g. night versus day, winter versus summer). Therefore, organisms should distribute their foraging activity in a predictable manner, leading to diel and seasonal activity patterns and movements (Howze and Smith 2012, Shuai et al. 2014).

Freshwater fish are especially sensitive to fluctuation in temperature, as opportunities for relocation are often limited (Elliott and Elliott 2007). Rising temperatures are expected to have important consequences on several aspects of the behavior and life-history of freshwater fish, including migration, activity, mortality, growth, age and size at maturity (Jonsson and Jonsson 2009, Isaak et al. 2010). It is therefore not surprising that a vast literature is available on the effect of water temperature on the behavior of freshwater fish, especially salmonids (Gibson 1978, Fraser et al. 1993, Fraser et al. 1995, Vehanen et al. 2000, Breau, et al. 2007a, Breau et al. 2007b, Blanchet et al. 2008). One aspect that has received considerable attention is the relationship between temperature and diel activity, i.e. the way individuals distribute their foraging effort over the 24h cycle (Reebs 2002, Zhdanova and Reebs 2005). As a stream gets warmer, fish typically increase their activity in response to increased metabolic demands, although this response reaches a threshold after which fish cease foraging activity and shelter or seek thermal refuges to avoid

excessive energy expenditure and potential mortality (Breau et al. 2007b, Breau, et al. 2011). When temperature decreases, fish not only become less active, but also become gradually nocturnal (Fraser et al. 1993, Fraser et al. 1995).

In streams, spatio-temporal variation in water temperature can result in optimal habitats being sometimes rare and clumped in space (Isaak et al. 2010). Active fish may thus move to and aggregate in small portions of a stream, which in turn can affect local competition. Such observations have been made in summertime in areas 3 – 8 °C colder than ambient stream temperature (Ebersole et al. 2001), as fish avoid potentially lethal zones (Gibson 1966, Breau et al. 2007a). Aggregation also occurs in wintertime, possibly as a result of concealment by ice and low water levels, which, in addition to reducing territoriality and aggression, encourages schooling behavior (Cunjak and Power 1986). These aggregations are expected to be more pronounced as water temperature approaches the extremes of the thermal niche of fish. For instance, fish have been reported to aggregate more at lower temperatures during winter (Cunjak and Power 1986), and at extremely high summer temperatures (Breau et al. 2007a). However, aggregations in response to more moderate changes in temperature have received less attention.

From an ecological perspective, diel activity patterns can also be considered as responses to daily fluctuations in the extent of intra-specific competition (Kronfeld-Schor and Dayan 2003), to which organisms can respond spatially by establishing and defending territories (Wood et al. 2012), moving to new areas, etc. Therefore, space use needs to be considered in a dynamic way and in concert with diel activity. For instance, Larranaga and Steingrímsson (2015) showed that foraging mode and aggregation were affected by shelter availability, through effects on diel activity. Valdimarsson and Metcalfe (2001) also found that individuals active at night were less aggressive, and reduced the distance between them. Water temperature varies over the 24-h cycle and is correlated to the density of active individuals (Breau et al. 2007b). If individuals experiencing contrasting ambient temperature indeed modify their rates and timing of activity, then such response should affect spatial behavior, including aggregation.

Salmonids have an extensive geographic distribution and inhabit rivers with diverse thermal regimes (Metcalfe and Thorpe 1990, Taylor

1991), which offers considerable potential for local adaptation, e.g. in terms of behavior (Taylor 1991, Elliott and Elliott 2010, Quinn 2011). For instance, preferred temperature for different populations of Arctic charr *Savelinus alpinus* have been suggested to vary between 9.2 and 16 °C (Peterson et al. 1979, Larsson 2005). Diel activity of salmonids in summertime has been studied in streams as warm as 27 °C (Breau et al. 2007b), as cold as 5.5 °C (Fingerle et al. 2016) and over ranges as wide as 15 °C (Breau et al. 2007b). However, systematic comparisons of activity in streams with contrasting temperature regimes have seldom been performed, or only over narrow ranges of temperature. For instance, the difference in mean temperature between study streams in summertime was 1°C in Bremset (2000) and in Reeves, Grunbaum and Lang (2010). Similarly, the difference in water temperature between two sites of a river and its tributary was 3 °C in Breau et al. (2007b). Significant differences in behavior were detected among sites in some of these studies, suggesting that among-population effects could be even more pronounced. Comparisons of spatial responses in streams with different temperatures are also rare, but are gaining interest (Gunnarsson and Steingrímsson 2011, Tunney and Steingrímsson 2012). Some studies have also documented the movement and aggregation of fish in relation to temperature in single streams (Cunjak et al. 2005, Breau et al. 2007a).

Because of Iceland's location, geological and volcanic history, water temperature is highly variable among and within Icelandic streams (Gudjonsson 1990). We used this natural variability in patterns of water temperature to study the temporal and spatial behavior of age 1+ Arctic charr in stream enclosures in a cold (3.6 – 9.3 °C) , intermediate (6.8 – 15 °C) and warm (11.9 – 18.7 °C) stream. More specifically, we measured the activity status and position of 20 fish every three hours during six 24-h cycles over a two week period in each stream to test the following predictions. Fish (age 1+) should be predominantly nocturnal in all streams (Bradford and Higgins 2001, Breau et al. 2007b). Activity rates should increase with increasing water temperature both within and among streams, to meet higher metabolic demand. Fish should be more nocturnal in the cold than in the warm stream (sensu Fraser et al. 1995). In every stream, aggregation may increase (sensu Valdimarsson and Metcalfe 2001) or decrease (sensu Larranaga and Steingrímsson 2015) at night. Because other ecological variables may affect activity, and vary across and within the study streams, we also systematically collected measurements of light intensity, current velocity, water depth and food

availability.

## **2.2 Materials and methods**

### **2.2.1 Sampling**

On 28 June and 14 July 2013, and on 6 June 2014, 20 Arctic charr of age 1+ were captured by electrofishing in each of three streams, a tributary of Deildará (cold, N 65.849379, W 19.222297), a tributary of Grímsá (intermediate, N 65.828795, W 19.869358), and Myllulækur (warm, N 65.516398, W 19.606433), in northern Iceland (LR-24 electrofisher, Smith-Root, Inc., Vancouver, Wash., USA). These populations were selected because water temperature differed considerably among the three systems. After capture, individuals were measured for fork length to the closest 0.1 mm with calipers and body mass to the closest 0.01 g (PESOLA® PPS200, CH-6340 Baar, Switzerland). Then, fish were individually tagged with visible implant elastomer (Northwest Marine Technology, Inc., Washington, USA) using different combinations of four colors (yellow, green, orange, and red) and two positions along the dorsal fin (modified from Steingrímsson and Grant 2003), and randomly assigned to two stream enclosures (10 fish/enclosure). On average, fish were 56.0, 66.6 and 80.4 mm (range = 47.5 – 60.9, 57.4 – 76.6 and 64.1 – 92.7 mm) and weighed 1.63, 2.99 and 5.35 g (range = 0.88 – 2.39, 1.89 – 4.65, 2.73 – 8.45 g, Table 2.1) in the cold, intermediate, and warm stream, respectively. Fish were classified as 1+ based on size distributions of Arctic charr populations in each stream. Initial body length and mass differed among streams (p-value < 0.001 for both variables). Prior to the first observation, fish were given 48h to habituate to the enclosures. The experimental bouts were terminated on 13 July, 25 July 2013 and 22 June 2014 in the cold, intermediate, and warm stream, resulting in a study period of 13, 11 and 11 days, respectively. No tag faded too much to impede individual identification of fish during the observations. Finally, after each study bout, all 60 study fish were recaptured, measured for body length and mass and released at their initial sampling location.

*Table 2.1 Characteristics of 60 Arctic charr of age 1+ used in the study and description of the habitats and environmental conditions in experimental enclosures in three study streams: Deildará (cold), Grímsá (intermediate), and Myllulækur (warm). Values are given as Mean  $\pm$  Standard deviation.*

	Deildará		Grímsá		Myllulækur	
Body length (mm)	56.0	4.1	66.6	5.8	80.4	7.3
Body mass (g)	1.63	0.48	2.98	0.84	5.35	1.48
Water depth (cm)	21.5	3.8	24.8	3.7	25.5	4.6
Water depth used (cm)	24.6	2.7	26.8	2.2	26.8	3.1
Current velocity (cm/s)	7.7	3.4	10.0	3.1	15.2	4.2
Current velocity used (cm/s)	8.8	3.1	9.6	1.8	11.0	2.4
Substrate size	6.0	0.6	5.7	0.7	4.9	0.8
Water temperature (°C)	5.6	1.4	9.0	1.5	13.7	1.3
Light intensity (klux)	20.43	26.04	16.68	23.23	33.15	42.23

## 2.2.2 Study design

Streams, and locations within streams were selected to maximise the range of water temperature. However, salmonids in warmer streams often grow faster (over our gradient of temperature, Forseth et al. 2009), so we used fish of the same age, but different size among streams. Because of this size difference, and because larger salmonids typically prefer faster and deeper waters (e.g. Keeley and Grant 1995), we also selected deeper and faster habitats in populations where fish were larger (Table 2.1). Enclosures (4 m long, 1 m wide, and 0.75 m high) were made of 5 mm nylon mesh, which prevents fish from escaping but allows invertebrates to drift through. The behavior of young salmonids has already been described successfully in similar semi-natural environments (Lindeman et al. 2015). String was tied across the top of each enclosure to reduce the risk of predation, presumably without changing the risk perceived by fish. In each stream, enclosures were separated by approximately 40 m (along the stream length) and planted in locations with variable (within enclosures) but similar (among enclosures) habitats (Tunney and Steingrímsson 2012). A grid made of thin 1 m metal bars (width = 8 mm) and taped at every 10 cm was placed at the bottom of each

enclosure. At the beginning of the study, depth and current velocity (Marsh-McBirney Flo-mate™ Model 2000CM, Frederick, MD, USA) were measured at 100 (depth) and 20 (current velocity) x-y coordinates. Water depth measurements were collected every 20 cm on both axes, starting 10 cm from the sides. Current velocity was measured at 40 % of the water depth from the bottom (Davis and Barmuta 1989) every 20 cm along the stream starting at 10 cm from the sides, on 4 transects perpendicular to the flow (every 1 m, starting 50 cm from the up- and downstream sides). Thus, all habitat variables differed among streams according to Kruskal-Wallis tests (p-value < 0.001 in all cases, Table 2.1). Temperature and light intensity were recorded automatically every hour by data loggers positioned at one of the two enclosures (Onset® HOBO® UTBI-001 TidBiTv2 and UA-002-08 HOBO Pendant® Temp/Light,8K, respectively). Water depth was recorded at a fixed point at the top of the upstream enclosure prior to all observations. The mean water depth in each stream varied similarly throughout the study periods (range = 8.5, 8.7 and 6 cm in the cold, intermediate, and warm stream, respectively).

### **2.2.3 Food availability**

Drifting invertebrates were collected every three hours in each stream, at the beginning (1 July 2013, 15 July 2013, and 10 June 2014) and at the end (11 July 2013, 25 July 2013, and 21 June 2014) of the study periods, resulting in a total of 48 food availability samples. Sampling was performed using a 250 µm drift net (net opening = 25 x 40 cm; net length = 100 cm) in front of the upstream enclosure of each stream. Sampling time was 20 min in the cold and intermediate stream and 5 min in the warm stream because the current was faster. Samples were preserved in 70% ethanol and processed at Hólar University College. Food items in each sample were counted under a stereomicroscope and sorted into order and/or family. Some samples from the warm stream contained abundant invertebrates and were subdivided in two or four equal portions before processing (Humboldt Model H-3964, Elgin, USA). All sampled invertebrates were of edible size and type for the fish used in this study (*sensu* Keeley and Grant 1997). Food availability was expressed as the number of prey drifting per minute in a 1 m wide section of the stream (i.e. the width of an enclosure and at their respective current velocity and water depth) in each habitat.



## **2.2.4 Behavioral observations**

Observations were made every three hours (e.g. 00:00, 03:00, 06:00). Each enclosure was visited six times per daytime in total, yielding a total of 48 scans. In northern Iceland, the long daylight in summer allows for unaided visual observation throughout the day/night cycle. The two enclosures in each stream were visited in a random order for each observation. During each observation, we monitored the activity status of all fish. Behavioral observations occurred as follows: To record diel activity, an observer stood motionless in front of an enclosure for 15 min and started recording activity after the first five minutes (Larranaga and Steingrímsson 2015). We calculated overall activity rates as the proportion of active fish during a given scan. An individual was considered active if it was actively feeding for at least one continuous bout of two minutes during the recording time. Hence, active individuals do not include fish that were visible, but simply rested on the bottom without any sign of foraging or mobility. This distinction was facilitated by Arctic charr's foraging behavior, as fish typically behaved consistently throughout a 15 min scan after being detected (i.e., continuously swimming, resting on the bottom, or hiding). We also measured individual activity rates as the proportion of scans in which a focal fish was active. The position of each active fish was determined as the x-y coordinate within the enclosure where it spent the majority of its time during a given scan. After each observation, current velocity and water depth was measured at the position of each active fish in their respective enclosure. We manually removed any accumulated debris and algae from the sides of all enclosure after a round of observations to avoid disturbance prior to the next round.

## **2.2.5 Statistical analyses**

We extracted four variables from the activity data: (i) overall activity rate (ii) individual activity rate, (iii) mean time of activity, which indicates the position of an individual's span of activity around the clock and (iv) the dispersion of activity which describes the tendency of an individual to spread its activity over short or long periods within the 24 h cycle (see also Larranaga and Steingrímsson 2015). We used the circular mean and standard deviation (Batschelet 1981) of individual activity patterns as indexes of the mean time of activity and the dispersion of activity, respectively. Aggregation was measured based on the average distance between individuals and their closest

neighbor, according to Clark and Evans (1954) and modified by Petreere (1985) to account for differences in density of active fish. Values were calculated only if 3 or more individuals from an enclosure were active at the same time (i.e. at least two values of distance between individuals). We calculated standardized mass-specific growth rates (*sensu* Ostrovsky 1995), which allow for adjustment of the scaling of metabolism with body size to account for differences in body size among our study streams. We used an allometric growth rate exponent value of 0.31 (Quinn et al. 2004).

The association between water temperature and behavior was investigated in two ways. First, we built linear mixed models to compare overall activity rates, the dispersion of activity and aggregation across streams. Circular ANOVAs were used to compare mean times of activity across populations. Second, we built two similar models to test for the effect of water temperature on overall activity rates and aggregation within streams. Water temperature, (both linear and quadratic terms) were considered as explanatory variables in the full models. Finally we tested for the effect of individual behavior on growth rates. Individual activity rates, the average distance between a focal individual and its closest neighbor and their interactions were considered as fixed factors. In all analyses, enclosures were included as random factors. Non-significant fixed effects were gradually removed from the full model, and a new model was kept if the difference in AIC was higher than 2. All analyses were run using R 3.0.2 (R Core Team 2013). We used the packages “lme4” (Bates et al. 2008), and “circular” (Agostinelli and Lund 2011) for LMMs and circular analyses, respectively.

## **2.3 Results**

### **2.3.1 Diel activity**

All but two of the 60 study fish were observed active at least once. Those two individuals were in the cold stream (Deildará). Overall activity rates (Mean  $\pm$  SD) were 0.15 ( $\pm$  0.16), 0.30 ( $\pm$  0.23) and 0.64 ( $\pm$  0.31) in the cold, intermediate and warm stream, indicating a significant increase in activity from cold to warm streams (Wilcoxon rank sum test,  $P < 0.001$  in all cases, Table 2.2, Figure 2.1). The average mean time of activity was 8:16 ( $\pm$  5:07), 23:28 ( $\pm$  3:04) and 23:49 ( $\pm$  2:56), from the coldest to warmest stream, respectively

(Figure 2.1, Table 2.2). Only the cold stream was different from the two other ones (circular ANOVA,  $P < 0.001$  in both cases and  $P = 0.750$  between the intermediate and warm streams), i.e. fish were more diurnal in the cold stream (Figure 2.1). The dispersion of activity increased from the cold ( $5:14 \pm 2:17$ ), to intermediate ( $5:30 \pm 1:34$ ) and to warm ( $7:11 \pm 2:37$ ) population. However, the difference was significant only between the warm and the two other streams (circular ANOVA,  $P < 0.001$  in both cases,  $P = 0.678$  between the cold and intermediate stream, Table 2.2).

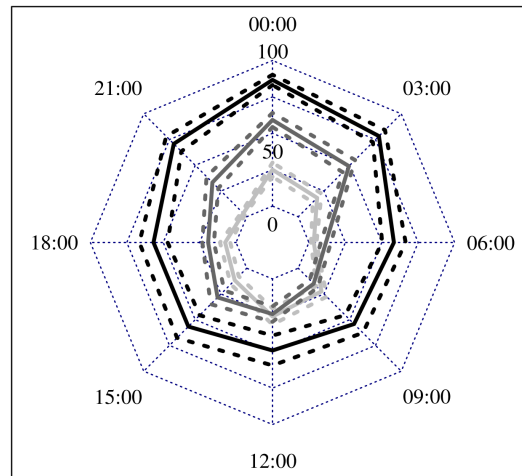


Figure 2.1 Diel distribution of overall activity rates (%) for 60 juvenile (1+) Arctic charr from three Icelandic populations. Deildará, Grímsá, and Myllulækur are represented in light grey, dark grey, and black, respectively. Dotted lines indicate standard error.

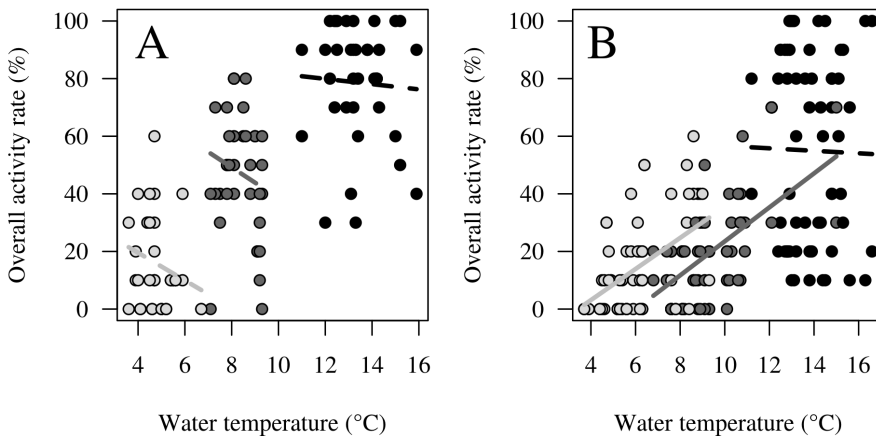
The within-population relationship between water temperature and activity was different among streams (Table 2.3). In the cold stream, overall activity increased with increasing water temperature (LMM, activity =  $0.312 \times \text{water temperature} - 0.265$ ,  $n = 48$ ,  $P < 0.001$ ), but we detected no such effect in the intermediate or warm populations ( $P = 0.436$  and  $0.180$ ). We replicated the analyses separating daytime (06:00 to 18:00) and night (21:00 to 03:00). In the cold and intermediate streams, there was a positive correlation between water temperature and overall activity rates during the day (LMM,  $n=30$ , activity =  $5.401 \times \text{water temperature} - 18.495$ ,  $P < 0.001$  in the cold stream, activity =  $5.900 \times \text{water temperature} - 35.499$ ,  $P < 0.001$  in the intermediate stream, Figure 2.2B), but not at night (LMM,  $n = 18$ ,  $P = 0.171$  and  $0.302$  for the cold and intermediate stream,

respectively, Figure 2.2A). In the warm stream, no effect was detected ( $P = 0.757$  and  $0.897$ ) for night and day values, respectively, (Figure 2.2A and 2.2B).

*Table 2.2 Temporal and spatial behavior of 60 Arctic charr of age 1+ in experimental enclosures in three study streams with contrasting temperature profiles: Deildará (cold), Grímsá (intermediate), and Myllulækur (warm). Values are given as Mean  $\pm$  Standard deviation.*

	Deildará		Grímsá		Myllulækur	
Overall activity rate	0.15	0.16	0.30	0.23	0.64	0.31
Mean time of activity (h:min)	08:16	05:07	23:28	03:04	23:49	02:56
Dispersion of activity (h:min)	05:14	02:17	05:30	01:34	07:11	02:37
Aggregation Index	0.42	1.48	1.38	2.83	-1.32	1.43
Growth rate (%/day)	1.29	0.94	0.03	0.85	0.99	0.92

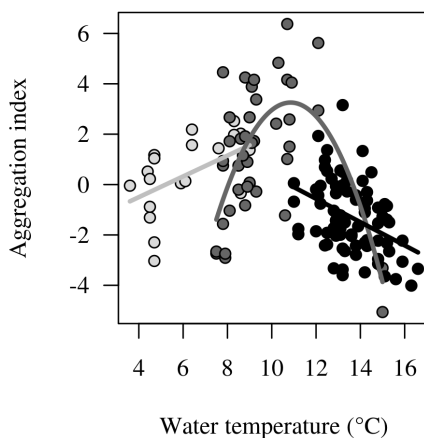
Dispersion of activity is the circular standard deviation of the individual distributions of activity rates. Aggregation is calculated as the Clark–Evans index (Clark and Evans 1954), modified by Petrere (1985). Low values of the aggregation index indicate stronger aggregation.



*Figure 2.2 Association between water temperature and overall activity rates for 60 juvenile Arctic charr from three populations at night (a) and day (b). Deildará, Grímsá, and Myllulækur are represented in light grey, dark grey, and black, respectively. Solid and dashed lines indicate significant and non-significant effects, respectively.*

### 2.3.2 Aggregation

Arctic charr was less aggregated in the cold and intermediate streams, compared with the warm stream (Wilcoxon rank sum test,  $P < 0.001$  in both cases, Figure 2.3). Aggregation was similar between the cold and intermediate stream (Wilcoxon rank sum test,  $P = 0.135$ ). Fish were more, similarly and less aggregated during the night than the day in the cold ( $n = 9$  and  $11$ ), intermediate ( $n = 22$  and  $20$ ), and warm ( $n = 36$  and  $48$ ), respectively (Wilcoxon rank sum test,  $P = 0.046$ ,  $0.080$ , and  $P < 0.001$ , Table 2.3).



*Figure 2.3 Association between water temperature and aggregation for 60 juvenile Arctic charr from three populations. Deildará ( $n = 20$ ), Grímsá ( $n = 42$ ), and Myllulækur ( $n = 84$ ) are represented in light grey, dark grey, and black, respectively. The effects were linear in Deildará and Myllulækur, and polynomial in Grímsá. Low values of the aggregation index indicate more aggregation.*

Similarly to diel activity, aggregation was associated differently with fluctuations in water temperature in different populations. In the cold stream, fish were more aggregated at low water temperature (LMM,  $n = 20$ , aggregation index =  $-2.151 \times \text{Water temperature} + 0.413$ ,  $P = 0.020$ , Table 2.3, Figure 2.3). There was a dome-shaped relationship in the intermediate stream (LMM,  $n = 42$ , aggregation index =  $8.989 \times \text{water temperature} - 0.414 \times \text{water temperature}^2 - 45.510$ ,  $P < 0.001$ , Table 2.3, Figure 2.3), i.e. fish were significantly dispersed at intermediate temperature and became increasingly aggregated when water temperature became either high or low. In the warm stream, fish were more aggregated when water temperature increased (LMM,  $n = 84$ , aggregation index =  $-0.441 \times \text{water}$

temperature + 4.771,  $P < 0.001$ , Table 2.3, Figure 2.3). For each fish, we calculated the average distance to the closest neighbor throughout the study. In the cold and intermediate stream, there was a positive relationship between average distance and individual activity rates ( $R^2 = 0.653$  and  $0.459$  in the cold and intermediate stream, respectively,  $P < 0.001$  in both cases), i.e. isolated fish were more active. In the warm stream, the opposite relationship was found ( $R^2 = -0.805$ ,  $P < 0.001$ ), as isolated fish were less active.

### **2.3.3 Habitat use and food availability**

There were significant differences in habitat use among streams. Arctic charr used shallower habitats in the cold ( $n = 119$ ) than in the intermediate ( $n = 106$ ) and the warm stream ( $n = 614$ , Wilcoxon rank-sum test,  $P < 0.001$  in both cases, Table 2.1), but there was no difference between the intermediate and the warm stream ( $P = 0.824$ ). Similarly, fish used faster habitats in the cold than in the intermediate stream and in the warm than in the intermediate stream (Wilcoxon rank sum test,  $P < 0.001$  in both cases). Hence, in spite of differences in habitat availability among the three study streams, the absolute difference in habitat use among streams was more modest (Table 2.1). Drift rates were  $9.59 \pm 3.51$ ,  $25.33 \pm 14.97$  and  $317.04 \pm 209.33$  organisms / 1 m stream width in the cold, intermediate, and warm stream, respectively, and food availability increased significantly from the cold to the warm stream (Wilcoxon rank sum test,  $n = 16$  in each stream,  $P < 0.001$  for every pair comparison). There was no difference in food availability between day and night, neither overall (Wilcoxon rank sum test,  $P = 0.660$ ), nor in any stream ( $P > 0.05$  in all three cases). Similarly, drift rates did not differ between crepuscular times (06:00, 18:00 and 21:00) and other times (Wilcoxon rank sum test,  $P = 0.688$ ).

### **2.3.4 Growth**

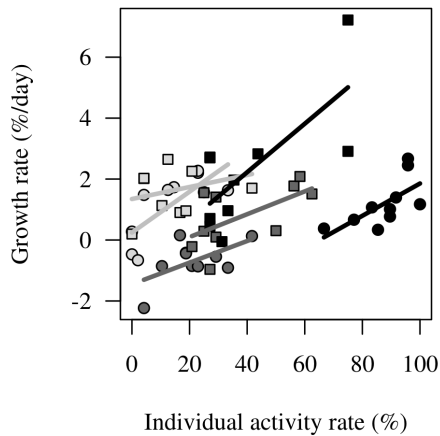
Across all study fish, standardized mass-specific growth rate (Mean  $\pm$  SD) was  $1.09 \pm 1.49$  %/day. Fish grew faster in the cold ( $1.50 \pm 1.02$  %/day) and warm stream ( $1.71 \pm 1.62$  %/day), compared to the intermediate stream ( $0.06 \pm 1.23$  %/day) and these differences were significant ( $n = 20$  in all streams, Wilcoxon rank sum test,  $P < 0.001$  between the intermediate and other streams,  $P = 0.968$  between the cold and warm stream). In general, more active fish grew faster (LMM,  $n = 60$ , growth =  $0.047 \times$  activity + 0.822,  $P < 0.014$ , Figure

2.4). After accounting for among-enclosure differences, significant relationships were found in the three streams (LMM,  $n = 20$  in all streams,  $\text{growth} = 0.047 \times \text{activity} + 0.819$ ,  $P = 0.013$  in the cold stream;  $\text{growth} = 0.043 \times \text{activity} - 1.249$ ,  $P = 0.003$  in the intermediate stream;  $\text{growth} = 0.071 \times \text{activity} - 2.780$ ,  $P < 0.001$  in the warm stream, Figure 2.4). Dispersion of activity was not associated with growth rates in any of the three streams (LMM,  $n = 20$  in all streams,  $P = 0.121$ ,  $0.551$  and  $0.336$  in the cold, intermediate, and warm stream, respectively). There was no effect overall either (LMM,  $n = 60$ ,  $P = 0.228$ ). Similarly, the average distance between a fish and its closest neighbor had no effect on growth rates, neither overall (LMM,  $n = 60$ ,  $P = 0.300$ ), nor in any of the streams (LMM,  $n = 20$  in all streams,  $P = 0.507$ ,  $0.235$  and  $0.252$  in the cold, intermediate, and warm stream, respectively).

*Table 2.3 Qualitative summary of the relationships between water temperature and behavior, and between behavior and growth across three streams and over the complete range of water temperature used in the present study.*

Response variable	Explanatory variable	Deildará	Grímsá	Myllulækur	Overall
Overall activity rate	Water temperature	· · ·	· · ·	· · ·	· · ·
Aggregation index	Water temperature	· · ·	· · · · ·	· · ·	· · · · ·
Individual activity rate	Distance to closest neighbor	· · ·	· · ·	· · ·	· · · · ·
Aggregation index	Daytime (Night → Day)	· · ·	· · ·	· · ·	· · ·
Growth rate	Individual activity rate	· · ·	· · ·	· · ·	· · ·
Growth rate	Dispersion of activity	· · ·	· · ·	· · ·	· · ·
Growth rate	Distance to closest neighbor	· · ·	· · ·	· · ·	· · ·

· · · Positive effect, · · · Negative effect, · · · · · dome-shaped effect, · · · · · U-shaped effect, · · · no effect. In all analyses, enclosures were considered as random factors. Low values of the aggregation index indicate more aggregation.



*Figure 2.4 Association between individual activity rates and specific growth rates for 60 juvenile Arctic charr from three populations. Deildará, Grímsá, and Myllulækur are represented in light grey, dark grey, and black, respectively. For clarity sake, enclosures within streams were separated, using square and round symbols and a regression line for each enclosure.*

## 2.4 Discussion

The primary goal of this study was to examine how water temperature may be linked to diel activity and aggregation. To do this, we recorded the behavior of Arctic charr in relatively natural conditions in three separate streams where we tried to maximize the range in water temperature among streams. This semi-experimental approach imposed several constraints on which environmental variables could be controlled for, and which could not. On one hand, we minimized differences in light intensity and photoperiod by confining observations to similar times of the year (June-July), and we used the same number of fish in all enclosures to limit density-dependent effects. Alternatively, other variables could not be controlled for, and/or were adjusted to the environmental gradient experienced by Arctic charr from cold-unproductive to warm-productive environments. From the cold to the warm stream, fish were bigger and experienced greater food availability. We also provided a gradient of habitats (current velocity and water depth) to take body size differences among streams into account (Armstrong et al. 2003, Mäki-Petäys et al. 2004), but overall, fish selected more similar habitats across all three streams (water depth used was 24.6, 26.8 and 26.8 cm



and current velocity used was 8.8, 9.6 and 11 cm/s in the cold, intermediate, and warm stream, respectively). Hence, although this study focuses on the effect of water temperature, we also address below other factors that may have affected activity and aggregation, particularly among streams.

Examples of adjustments of activity rates along a water temperature continuum are common in salmonids in particular (Fraser et al. 1995, Gries et al. 1997, Breau et al. 2007b) and in freshwater fish in general (Reebs 2002). However, systematic comparisons of activity among streams with contrasting temperature profiles are more rare and usually cover small differences (e.g. 1 °C in Reeves et al. 2010). Some of these studies found significant differences in activity among locations (Reeves et al. 2010), but sometimes differences are not reported, probably because the variability in temperature within sites greatly exceeds among-sites variability (e.g. 3 °C difference among sites, and 14 °C range within sites in a single stream, Breau et al. 2007b). Our results suggest that stream-dwelling fish living at high temperature on average are more active, as we found a 4.26 fold increase in activity rates from a cold to a warm stream, with a difference in average temperature of 10 °C.

In our study, activity increased with temperature in the cold and intermediate streams, but not in the warm stream, which is consistent with the fact that as water temperature increases, activity should initially increase as metabolic demands increase, but then level off at higher temperatures, and even decrease (Breau et al. 2007b). It is also interesting that studies report contrasting relationships between water temperature and activity patterns of young salmonids. For the age class (1+) used in this study, a dome-shaped (Breau et al. 2007b), linear (Roy et al. 2013), and a logistic (Reeves et al. 2010) relationships have been described within streams. In this study, water temperature remained within the range tolerated by Arctic charr (Jonsson and Jonsson 2009, Elliott and Elliott 2010), which can likely explain why fish in the warm stream did not reduce activity at the warm end of the continuum as reported elsewhere (Breau et al. 2007b).

Additional factors may affect activity in this study. First, habitats were deeper and faster from the cold to the warm stream, although differences in habitat use were modest. Studies reporting activity rates in contrasting habitats are equivocal. More food items drift in faster and deeper habitats, which can lead to higher activity (Nakano 1995,

Fingerle et al. 2016, Larranaga et al. submitted, but see Larranaga et al. unpubl. Data). However, studies also suggest that organisms should decrease activity when food availability is high, to limit predation risk (Anholt and Werner 1995, Anholt et al. 2000, Orpwood et al. 2006). Fish were also larger from the cold to the warm stream. Here, one may have expected effects on activity rates opposite to our findings, because larger salmonids are typically less active after having accumulated valuable fitness assets and should be less willing to risk predation (Clark 1994, Imre and Boisclair 2004, but see Nakano 1995). Hence, earlier findings on the determinants of activity are either equivocal (e.g. habitat and food), or unlikely (e.g. body size) to explain the drastic increase in activity rate with increasing temperature.

In the cold stream, there was no difference in activity rates between day and night, but fish avoided crepuscular times (around 18:00, 21:00 and 06:00). Contrary to (Fingerle et al. 2016) who found similar differences, we did not detect lower food availability at those times, so avoidance of crepuscular times may reflect trade-offs between food intake and predation risk (Metcalf et al. 1999). In the intermediate stream, fish increased activity specifically at night and were thus more nocturnal, which challenges our prediction of fish being more nocturnal in cold streams. Water temperature affected activity rates both in the cold and intermediate stream during the day, but there was no such association at night in any of the three streams. Similar daytime-specific effects of water temperature on activity rates have been reported previously. Activity rates increased with increasing temperature only during the day in Fraser et al. (1993), Blanchet et al. (2008) and Fingerle et al. (2016) and only during crepuscular times in Roy et al. (2013). Altogether, our findings and these earlier studies suggest that optimal feeding times may differ among systems, which in turn may affect the benefits of increasing activity at those times. Both night (Breau et al. 2007b, Larranaga and Steingrímsson 2015) and crepuscular times (Conallin et al. 2012, Roy et al. 2013) have been suggested as the safest and preferred feeding time of age 1+ salmonids. However, foraging rates at night have been shown to be independent of water temperature (Fraser et al. 1993), so the benefits of increased activity at higher water temperature under dark conditions may be limited.

Fish aggregated more in the warm stream compared to the cold and intermediate stream. Ectotherms can derive thermal benefits from aggregating (e.g. Shah et al. 2003, Schradin, Schubert and Pillay

2006). However, it is unlikely for stream-dwelling fish which live in constantly renewing water and it would not explain why aggregation also increased at high water temperature. Different levels of aggregation may not reflect water temperature directly, but other factors correlated with temperature. For instance, food availability was more than 13 times higher in the warm stream than in the intermediate stream, which in addition to potentially less food predictability (the warm stream being lake-fed and getting sudden bursts of prey availability, pers.com) may decrease aggression and promote schooling behavior (Grant 1993, Keeley 2000, Gunnarsson and Steingrímsson 2011). Higher activity rates in the warm stream also increased the density of competitors locally (2.1 fold increase from the intermediate to the warm stream), which may also affect the economic defendability of prey and encourage schooling (Grant 1993, Dunbrack et al. 1996). Finally, fish were larger in the warm stream and may be less willing to risk predation (Clark 1994) e.g. via more aggregation (Cresswell 1994).

The association between water temperature and aggregation differed among the three streams. Aggregation declined, declined and then increased, and increased with temperature in Deildará (cold), Grímsá (intermediate) and Myllulækur (warm), respectively. Aggregation often arises as a consequence of patchy distribution of resources. This could explain previous reports of aggregation by salmonids in colder water during warm summer days (Breau et al. 2007a, Dugdale et al. 2015) and in suitable foraging areas during cold winter days (Cunjak and Power 1986, Vehanen et al. 2000). In our study, however, it is likely that similar mechanisms are responsible for the aggregation patterns among and within streams. As temperature increased, more fish were active (i.e. higher density), and food availability may increase. The economic defendability of resources peaks at intermediate values of both population density and prey availability, so fish may be more likely to defend territories in such conditions, leading to decreased aggregation. However, we did not measure aggression in this study, so more information is needed on the aggressive behavior of Arctic charr along a temperature gradient to validate this assumption (Fraser et al. 1993, Nicieza and Metcalfe 1997, Magoulick and Wilzbach 1998).

Previous findings on diel differences in aggregation are equivocal. Valdimarsson and Metcalfe (2001) found that as light intensity decreases, fish become less aggressive and reduce the

distance to their closest conspecific. Alternatively, Larranaga and Steingrímsson (2015) found higher aggregation during daytime, although this effect could also have been triggered by contrasting shelter availability. In the present study, fish were either more, similarly or less aggregated during the night than during the day in the cold, intermediate and warm stream, respectively. This suggests that temperature, daytime and their interaction are important ecological determinants of aggregation. Higher aggregation at night in cold conditions could indicate that fish simply defend smaller territories because they were less likely to detect remote prey and competitors (Metcalf et al. 1997). In the warm stream, we suspect that higher aggregation during daytime was a response to predation risk by avian predators (Larranaga and Steingrímsson 2015), as we observed more predatory birds in Myllulækur (pers.com).

More active individuals were further from their closest neighbor in the cold and intermediate stream, but closer in the warm stream. This results suggests that measuring spatial behavior along with diel activity provides valuable information on the determinants and consequences of behavior in natural populations. For example, more active individuals foraging in isolation could indicate that they were consistently excluded to suboptimal feeding areas and increased their activity to maintain growth (Alanära et al. 2001). Alternatively, fish may grow faster at the cost of higher mortality risk, via more activity and isolation. As active fish were more numerous and aggregated in the warm stream, some costs may be amplified, including lower foraging rates (*sensu* Elliott 2002) and more frequent agonistic acts. Thus, increased activity of fish foraging in large groups may make up for reduced feeding efficiency.

Although most studies on juvenile salmonids report higher growth rates at intermediate water temperature (Larsson et al. 2005, Forseth et al. 2009), we found the opposite pattern (i.e. growth rates highest in the cold and warm stream). Our estimates of growth are based on short periods (between 11 and 13 days) and comparisons across streams should be interpreted carefully, especially because some fish lost weight during the study (e.g. in the intermediate stream). Also, the differences among streams may be caused by other factors than water temperature. For instance, the study in the intermediate stream was carried out later in the summer (July) when growth may slow down (Steingrímsson and Grant 1999). Nevertheless, similar effects of behavior on growth were detected in all three streams. Active

individuals grew faster than inactive ones, which is consistent with previous studies (Brännäs 2008, Larranaga and Steingrímsson 2015, Závorka et al. 2016). Other non-measured components of fitness need to be taken into account, including higher mortality risk for solitary individuals, or via increased daytime activity.

Understanding how water temperature relates to individual behavior is important for predictions on future responses of freshwater fish to increasing global temperature (Jonsson and Jonsson 2009). In our study, the shape and magnitude of the interaction between water temperature, diel activity and aggregation varied for populations existing along the thermal range of Arctic charr, and thus likely affect individual fitness (growth, mortality etc.). Studying populations at different temperature also shows that similar responses can arise in different situations (e.g. aggregation at low temperature in cold streams and at high temperature in warm streams). Our results suggest that the potential for adjusting diel activity may be more limited in warmer streams, as activity rates were already high and did not increase with increasing water temperature. This is an additional limitation in salmonids that show limited potential for local adaptation in heat tolerance among populations (Beacham and Withler 1991, Jonsson and Jonsson 2009). In addition to other ecological consequences of increasing temperature (e.g. phenological shifts, competition with other salmonids), limited opportunity for behavioral adjustments may be critical for the persistence of Arctic charr populations (and other species inhabiting cold waters) living at the upper end of their thermal tolerance.

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### **3 Shelter availability alters diel activity and space use in a stream fish**

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#### Abstract

Shelters are a key component of animal population ecology, as they provide protection from predators and promote visual isolation among competitors. From a behavioral perspective, how shelter availability affects the way individuals allocate their activity in space has been extensively documented. However, how shelters affect the distribution of activity in time (i.e., diel activity) has been less studied in natural conditions. Here, we report results from a field study that used stream enclosures with either high or low shelter availability and stream-dwelling juvenile Arctic charr as a model species. We collected repeated measurements of individual activity 8 times a day (every 3 h) for six 24-h periods during a span of 9 days. In shelter-limited enclosures, fish were more active, became diurnal, and were active over a wider span of time each day, compared with fish with access to abundant shelters. In addition, fish were more aggregated and attacked prey over shorter distances and at lower rate when shelters were limited. Body mass did not affect individual activity rates, but smaller individuals extended their activity over longer periods, possibly as a result of interference competition, and were more isolated. Growth rates were similar across treatments and were positively correlated with individual activity rates and the average distance to the nearest competitor. However, additional nonmeasured effects on fitness may

occur, such as increased predation risk associated with daytime feeding and extended activity in shelter-limited conditions.

**Keywords:** Refuges, activity rates, predation risk, aggregation, Arctic charr, competition



## 3.1 Introduction

Shelters play a major role in regulating population density and species richness (Kohn and Leviten 1976, Jordan et al. 1996). The positive effects of refuges can be explained mainly by reduced predation risk (Lima 1998), intra-specific competition (Bell and McCoy 1991), exposition to unfavorable climatic conditions, and increased habitat complexity (Crowder and Cooper 1982). Because ultimately, the number of shelters influences the frequency of contacts between competitors and between prey and predators, refuges are central in behavioral ecology (Berryman and Hawkins 2006). Increasing shelter availability affects anti-predatory strategies, by decreasing vigilance to predators (Abramsky et al. 1996), but also social behavior, by reducing encounter with competitors (e.g. Venter et al. 2008), and foraging behavior, by increasing prey availability in complex habitats (Crowder and Cooper 1982). Anti-predatory, social and foraging behaviors can be adjusted in response to varying levels of shelter availability both in space and time.

In terms of space use, behavioral adjustments to contrasting numbers of refuges have been repeatedly documented. Indeed, shelters are shown to affect the spatial behavior of organisms through decreased competition (Eason and Stamps 1992, Basquill and Grant 1998). For example, the presence of refuges decreases visual contacts among competitors, which in turn can result in smaller territories, lower resource monopolization, lower intruder pressure, and less aggression (Höjesjö et al. 2004, Dolinsek et al. 2007). In environments with limited shelters, organisms are also often found in larger groups, potentially to evade predation or because individuals follow their conspecifics to locate shelters more efficiently (Dolan and Butler 2006). Such effects of refuges on space use may in turn impair foraging efficiency, through missed feeding opportunities and increased stress (Millidine et al. 2006). Indirect benefits of habitat complexity such as increased food availability (Negishi and Richardson 2003), and reduced maintenance metabolism (Millidine et al. 2006) may also have important consequences for spatial behavior.

In a temporal context, the need and motivation to use shelters may fluctuate as a result of varying ecological conditions such as predation risk or food availability (Metcalf et al. 1999), which lead to non-uniform diel activity patterns (the partitioning of activity within a

24 h cycle). However, a limited number of shelters may also have a strong influence on such patterns, e.g. if individuals cannot find refuges during riskier periods. To date, empirical studies provide mixed evidence for this hypothesis, as some studies suggest that activity rates may be independent of shelters (Walsh and Downie 2005, Fero and Moore 2014), whereas others suggest the opposite (Edel 1975, Olson and Wallander 2002). Importantly, shelter availability may affect how active organisms are, but also how they distribute their activity in time. Indeed, when refuges affect diel activity, individuals may increase their activity either uniformly over the 24 h cycle (Edel 1975) or during specific periods (Orpwood et al. 2010). For example, juvenile Atlantic salmon *Salmo salar* protected by riparian shading increased activity specifically at night (Orpwood et al. 2010). Consequently, if different phenotypes adjust their diel activity patterns differently according to ecological conditions, these patterns may vary in: (i) the overall activity rate, which corresponds to the ratio of time spent foraging versus resting per day and (ii) the allocation of activity over a the 24 h cycle (Daan 1981). The latter is a response to a set of stimuli affecting both the beginning and the end of activity (Pittendrigh and Daan 1976). Hence, a distinction between the overall activity rate, the timing and the compression of activity may yield a more comprehensive understanding of diel activity patterns and their ecological determinants.

Detecting a potential effect of shelter availability on diel activity may be possible only for organisms showing some extent of flexibility in their diel activity patterns. These patterns have long been considered rigid (Kronfeld-Schor and Dayan 2003), as several specific sensory, physiological and morphological adaptations to a particular phase of the day may render activity during other hours sub-optimal (Halle 2000). As a result, both theoretical and empirical studies suggest that intra-specific variability in diel activity patterns is limited and that cathemerality is the exception, rather than the rule (Schoener 1974). Nonetheless, trade-offs between growth and mortality, and growth and competition may favor heterogeneity in diel activity patterns (Kronfeld-Schor and Dayan 2003) and cases of intra-specific partitioning in time are repeatedly documented in many taxa including mammals (Refinetti 2006), birds (Helm and Visser 2010), reptiles (Aragón et al. 2004) and fish (Fox and Bellwood 2011). These studies suggest that under certain conditions, diel plasticity in foraging behavior may be favored for as long as the benefits of this plasticity outweigh the costs of foraging during sub-optimal periods. Such

examples include e.g. animals inhabiting polar environments, or habitats with low environmental variability (Bloch et al. 2013).

Freshwater fish, especially salmonids, have been shown to be a useful model in the activity literature (Reebs 2002, Huusko et al. 2007) because they exhibit a high degree of variation in diel activity, at both the species (Jakober et al. 2000) and population level (Valdimarsson et al. 2000), which highlights the importance of extrinsic factors as determinants of diel behavior. In addition, variation can be found at the cohort (Imre and Boisclair 2004) and the individual level (Breau et al. 2007), which shows that intrinsic factors are also key components in the allocation of foraging effort over time (Nakano 1995). Great attention has been placed on the effect of water temperature on salmonids' diel activity, in part because of its association to climate change (Jonsson and Jonsson 2009), but how additional ecological factors such as shelter availability may affect diel activity is less documented. Monitoring small fish in the wild for extended time is challenging, but improving tagging techniques and appropriate experimental designs help investigate individual activity patterns, space use and foraging (Breau et al. 2007, Roy et al. 2013), and link these to phenotypic characters such as body mass and growth.

To investigate the contribution of shelter availability in shaping individual activity patterns, aggregation and foraging behavior, we monitored juvenile stream-dwelling Arctic charr in a landlocked Icelandic population at low shelter availability (LSA) and high shelter availability (HSA). We tested the prediction that individuals exposed to high shelter availability prefer night time feeding, whereas daytime feeding will be dominant at low shelter availability (*sensu* Orpwood et al. (2010)). We also predicted that at low shelter availability, fish would be more aggregated, as a result of increased predation risk (Dolan and Butler 2006). Visual isolation tends to decrease the size of foraging areas (Imre et al. 2002), so we expected to find reduced foraging radius in shelter-rich environments. In contrast, prey attack rate may (Kemp et al. 2005) or may not increase in open habitats (Imre et al. 2002). Competition for shelters may lead to temporal segregation where dominant individuals should monopolize the most beneficial periods (Alanärä et al. 2001). Therefore, we expected large individuals to exhibit higher compression of activity time than smaller individuals. Finally, we tested for the potential effects of shelter availability and behavior on growth.

## **3.2 Materials and methods**

### **3.2.1 Sampling**

In total, 60 Arctic charr (age 1+) were sampled by electrofishing on 4 and 5 August 2013 in the river Grímsá (Iceland, 65°4'10" N, 19°49'50" W), a tributary to the river Laxá in Skefilsstadarhreppur in northern Iceland (information on the study site can be found in Gunnarsson and Steingrímsson 2011). A landlocked Arctic charr population dominates this small stream and is isolated from downstream populations by a waterfall. Eight fish were caught via electrofishing (Smith-Root LR-24) on 4 August and maintained in a holding tank placed in the river overnight. On 5 August, the other 52 fish were captured and all individuals were measured, tagged, and randomly assigned to six stream enclosures that contained either a high or low number of shelters. We measured fork length to the closest mm and body mass to the closest 0.01 g (PESOLA® PPS200). Fish were on average 7.9 cm in fork length ( $\pm 0.78$ , range = 5.7–9.2 cm) and weighted 4.7 g ( $\pm 1.33$ , range = 1.7–7.8 g) and were determined to be age 1+ based on size distribution. Initial body size did not differ between treatments of shelter availability after accounting for differences between enclosures ( $p$ -value = 0.61 and 0.57 for fork length and body mass, respectively), but there were marginal differences between enclosures (ANOVA,  $p$ -value = 0.06 and 0.08, respectively). We used four colors of visible implant elastomer (red, green, orange and yellow) to individually tag each fish at two specific positions of the dorsal fin (see Steingrímsson and Grant 2003). Tags spread up along the dorsal fin rays, and were thus highly visible during observations. Prior to observation, fish were given 48 h to adjust to the experimental environment. The experiment was terminated on 15 August, when all fish were recaptured, measured and released back in the river. No tag faded too much during the experiment to impede individual identification of fish inside the enclosures.

### **3.2.2 Experimental design**

Observations were conducted from 7 to 15 August 2013 (range of sunrise: 04:04–04:52, range of sunset: 22:10–21:39). We used a nested setup with 3 locations in the river, two enclosures in pair per location, and each pair contained both treatments side by side. The most upstream and downstream pairs were separated by about 200 m. Each enclosure was 4 m long, 1 m wide and 1 m high, with 5 mm nylon

mesh, sufficiently large to allow invertebrates to drift through, but small enough to prevent fish from escaping. The stream was approximately 3 m wide so that enclosures within a pair were separated by around 1 m. Similar enclosures have already proven successful to study the behavior and growth of freshwater fish in natural streams (Yamamoto et al. 2008, Lindeman et al. 2015). Strings were stretched across the top of each enclosure to deter avian predators without altering perceived predation risk. Ten fish were placed in each enclosure, which should be enough for spatial competition to occur among individuals, although Arctic charr also tolerate overlapping areas (Gunnarsson and Steingrímsson 2011). The enclosures were placed in the stream to ensure similar water current velocity and water depth, which correspond to a suitable habitat for Arctic charr (Tunney and Steingrímsson 2012). At the beginning of the experiment, current velocity at 40 % of the water depth from the bottom (Davis and Barmuta 1989) was measured systematically at 5 points along 4 parallel transects perpendicular to the flow with a Marsh-McBirney Flo-mate™ Model 2000CM (Marsh-McBirney Inc., Frederick, MD) current velocity meter. Water depth was measured at 100 coordinates in each enclosure (at 20 cm intervals on each axis, starting at 10 cm from the sides). The average current velocity was 14.4 ( $\pm$  4.17, range = 5–23) cm/s in low shelter availability (LSA) enclosures and 12.8 ( $\pm$  5.6, range = 4–27) cm/s in high shelter availability (HSA) enclosures and the average water depth was 23.2 ( $\pm$  2.76, range = 10.2–30.5) cm in LSA and 21.7 ( $\pm$  4.59, range = 2–28.5) cm in HSA. There were no significant differences in water current velocity and depth when accounting for inter-enclosures differences (mixed linear model with enclosure as a random factor, p-value = 0.07 and 0.401, respectively). The marginal difference in current velocity is due to the number of shelters in the high shelter availability enclosures, because their addition decreased the average current velocity. Water temperature and light intensity were recorded automatically every hour by data loggers positioned at the most downstream (water temperature 10 cm from the bottom + light intensity above the water) and upstream (water temperature only) enclosures (Onset® HOBO® UTBI-001 TidBiTv2 and UA-002-08 HOBO Pendant® Temp/Light,8K, respectively). The average water temperature during the study was 7.1 °C ( $\pm$  1.98, 3.2–12.4 °C) and the average light intensity was 24.0 kilolux ( $\pm$  33.31, 0.0–143.3 kilolux). Light intensity was systematically less than 1.0 lx at 00:00 and 03:00, varied from 0.6 to 6.2 kilolux at 21:00 and 06:00, and from 14.7 to 143.3 kilolux during the rest of the day.

Each parallel pair of enclosures contained the two treatments and the position of each treatment (left or right side) alternated for adjacent pairs. Because fish often use interstitial spaces between rocks as shelters, we sieved the bottom substrate for each enclosure so that the maximum diameter of the gravel was 2 cm. We kept the sides of all enclosures stretched to prevent fish from using these to hide. As shelters, we used a cobble with common water moss, *Fontinalis antipyretic* attached, but this combined structure is a common source of refuges in this river (pers. obs.). The high shelter availability treatment consisted of nine shelters of approximately 0.12 m<sup>2</sup> placed inside each of the three enclosures (covering approximately 27% of the total benthic area of each enclosure). The positions were identical among enclosures. One solitary shelter was placed at the center of each of LSA enclosure (3% of the total area).

### **3.2.3 Behavioral observations**

Observations were made every three hours (00:00, 03:00, etc.). Each enclosure was visited eight times per day during six 24 h cycles, i.e. a total of 48 observations per enclosure. After each observation, algae and debris were removed from the enclosure nets to ensure good water flow and to avoid disturbance immediately prior to a session. Pairs of enclosures were chosen in a random order before every round of observations. To record diel activity, an observer stood motionless in front of an enclosure for 15 min and started recording activity after the first 5 min. For measures of activity, we recorded both individual appearance rates (*sensu* Nakano 1995) and individual activity rates. Individual activity rate is the proportion of scans in which a focal fish actively fed for at least one continuous bout of 2 min during the recording time. Individual appearance rate is the proportion of scans when a fish was visible, which encompasses both activity rates (according to the definition above), and scans during which a fish was visible but simply rested on the bottom and did not feed. This distinction was facilitated by Arctic charr's foraging behavior, as fish typically behaved consistently throughout a 15 min scan (i.e. continuously active, resting on the bottom, or hiding). Thus, individual activity rates only consider scans when a fish was feeding, and exclude situations when it was hiding in a shelter, or resting motionless on the substrate without showing any mobility or foraging effort. We used both indexes (activity and appearance rates) in some analyses because they focus on different aspects of behavior.

Because we needed a total of 90 min in a single session, with an additional 5 min to travel between pairs of enclosures, observations started and finished around 45 min before and after each daytime (e.g. from 14:15 to 15:45 for 15:00). As light intensity decreased at night, the observer used a LED flashlight at 00:00 and 03:00 (VASQ by ELWIS, model S1) during the last four rounds of observation. Depending on the species, such methods may impact salmonid behavior (e.g. Heggenes et al. 1993). To limit the disturbance, we used the flashlight only after the number of active fish had been determined, and only to read the tags. Furthermore, we zoomed in from a large diameter beam, and gradually reduced the diameter to increase visibility to the point where a tag could be read. This procedure was repeated for each unidentified tagged fish and the whole process took less than 20 s per scan. No fish fled as a reaction to the flash light or seemed attracted to the light.

We also collected measurements of space use. First, after each observation, the x-y coordinate of each active fish in each enclosure was recorded to the nearest 5 cm on each axis with the aid of metal bars taped at every 10 cm and placed on the substrate (one bar parallel and 3 bars perpendicular to the flow). The bars were too thin (8 mm) to be used to hide by Arctic charr. At 00:00, 06:00, 12:00, and 18:00, two fish were randomly selected per enclosure to measure their foraging radius and prey attack rate. When an individual was selected, the observer described its foraging activity for approximately 5 min (modified from McLaughlin et al. 1992). Time was kept with a digital timer that emitted a pulse every 5 s. Each individual observation alternated between 5-s intervals of monitoring (between one and three) and a 5-s interval during which the observer recorded notes from the preceding intervals. Each interval was classified as either pursuit or search. Pursuit intervals correspond to a situation where a focal individual made at least one feeding attempt, whereas search intervals correspond to a period where fish searched for prey by maintaining a sit-and-wait position in the water column or via mobile searching (McLaughlin et al. 1992). Prey attack rate was estimated as the proportion of intervals when a focal fish attacked at least one prey. Multiple feeding attempts within a 5-s interval were rare throughout the experiment and were not recorded. During pursuit intervals, we measured the foraging radius (in body lengths) as the distance between a location where attack was initiated and the location where a prey item was intercepted. During the last four 24 h rounds of the experiment, light intensity became too low at 00:00 to measure

foraging radius and prey attack rate without the aid of a flashlight, so we did not collect such data under those circumstances.

### **3.2.4 Data analysis**

In the salmonid literature, activity patterns are often treated as logistic (Breau et al. 2007) or quadratic data (Roy et al. 2013). However, given the cyclical nature of activity patterns, we transformed daytime values into angles and used circular analyses instead (Batschelet 1981). Most individual patterns were unimodal in both treatments. Therefore, we used the circular mean and standard deviation as indexes of the mean time of activity and the compression of activity respectively. The mean time of activity indicates the position of an individual's span of activity around the clock and the compression is a descriptor of its tendency to spread its activity over long or short periods. We used a circular ANOVA to compare the distribution of mean times of activity between the two treatments.

Because all variables were normally distributed (or marginally normally for activity levels, Shapiro-Wilk test) and met the requirements of homoscedasticity of the residual variance, parametric tests were used in all linear analyses. Five types of mixed linear models were performed to analyze the dataset. First, for individual activity rates and compression of activity, we built mixed linear regressions with shelter availability and body mass as fixed factors, and enclosures as a random factor. Second, the full model for distance to the nearest neighbor tested for the effect of shelter availability and body mass. Enclosures and individuals were considered as random factors. The distance between individuals depends on how many are active simultaneously. Therefore, we also calculated aggregation based on the average distance between fish and their nearest neighbor, according to Clark and Evans (1954) and modified by Petrere (1985) to account for differences in local density, and we compared this index between treatments using a mixed linear regression with enclosures as a random factor. Third, the full model for foraging radius encompassed shelter availability, body mass and distance to the nearest neighbor, as well as enclosures and individuals as random factors. Fourth, prey attack rate was considered in a mixed linear regression with shelter availability, body mass, distance to the nearest neighbor and foraging radius as fixed factors, and individuals as random factors nested in their respective enclosure. Finally, we assessed individual growth by calculating Specific Growth Rates (SGR, Ricker 1975) according to



the following equation:  $SGR (\%/day) = (\log_e M_{Final} - \log_e M_{Initial}) * 100 / t$  where  $M$  = Mass and  $t$  is the duration of the experiment in days. Specific growth rates were compared between treatments, and behavioral traits were also included in the full model (values were averaged per individual for distance to the nearest neighbor, foraging radius and prey attack rate) and enclosures were considered as a random factor. In all models, interactions between explanatory variables were also included in the full models. A stepwise selection was applied from the full model, by removing the least significant variable (based on its p-value) and until only significant effects remained (Burnham and Anderson 2002). In addition to those individual based models, we compared activity rates and appearance rates within each treatment. Because these samples are paired, we used a mixed linear model assuming a positive-definite symmetrical correlation between the two rates. All analyses were run using R 3.0.2 (R Core Team 2013). For circular analyses, we used the “Circular” R-package (Agostinelli and Lund 2011). For mixed linear models, we used the lme4 (Bates et al. 2008), or nlme (Pinheiro et al. 2012) package in the case of paired samples.

## 3.3 Results

### 3.3.1 Diel activity

Fish were twice as active at low shelter availability (LSA) than when shelters were abundant (mean activity rate = 0.56 and 0.27, range = 0.42–0.83 and 0.15–0.44 respectively, Table 3.1, Figure 3.1A), and this difference was significant (Table 3.2, model 1). Individual appearance rates were uniformly distributed over the 24 h cycle and high under LSA compared to activity rates after accounting for among-enclosure differences (mixed linear model,  $df = 283.98$ ,  $t$ -value = 7.229,  $p$ -value < 0.001, Figure 3.1B), whereas overall activity and appearance rates did not differ under HSA (mixed linear model,  $df = 283.99$ ,  $t$ -value = 0.281,  $p$ -value = 0.78, Figure 3.1A and B). This discrepancy is due to a large number of inactive fish resting during the night on the bottom outside of the single shelter in the LSA treatment. Indeed, there were never more than four individuals sheltering at the same time. The timing of activity also differed between the two treatments. All fish from the LSA treatment were on average diurnal (range of mean time of activity = 07:54 to 16:54), whereas all those in the HSA treatment were nocturnal (range of mean time of activity = 22:05 to 03:13).

These differences were obviously significant as there was no overlap in the mean time of activity between the two treatments (circular ANOVA,  $df = 1$ ,  $F = 1951$ ,  $p\text{-value} < 0.001$ , Figure 3.1C). Individual activity patterns were also significantly more compressed under HSA ( $p\text{-value} < 0.01$ , Table 3.1 and 3.2, model 2), i.e. individuals from the LSA treatment foraged during a wider spectrum of the 24 h cycle. Because appearance rate is a less accurate estimate of foraging activity, we report only overall activity rate for the subsequent results. Body mass did not have a significant effect on individual activity rates (Table 3.2, model 1), but affected the compression of activity, i.e. small fish extended their activity over longer periods of time (Table 3.2, model 2).

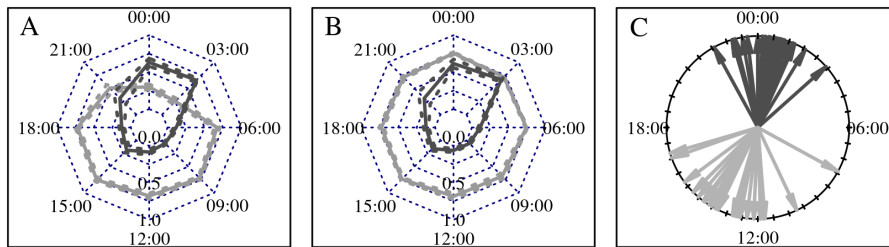


Figure 3.1 Diel distributions of individual activity rates (A), individual appearance rates (B) and individual mean time of activity (C) for 60 juvenile (1+) Arctic charr in river Grímsá, northern Iceland. Light and dark grey represent low and high shelter availability, respectively. Dotted lines indicate the standard error.

### 3.3.2 Spatial and foraging behavior

The availability of shelters also affected spatial and foraging behavior. In the LSA treatment, fish maintained significantly shorter distances between each other (Table 3.2, model 3), and were thus more aggregated (mean modified Clark-Evans index = -1.81 and 1.62, range = -4.84 – 2.67 and -3.32 – 9.54 under LSA and HSA, respectively, Table 3.1). This difference was significant (mixed linear model,  $df = 212.99$ ,  $t\text{-value} = -10.59$ ,  $p\text{-value} < 0.001$ , Table 3.1, Figure 3.2A). Because the aggregation index is based on distances between fish and their nearest neighbor, low values represent strong aggregation and vice versa. At the individual level, body mass affected the distance from fish to their nearest neighbor, i.e. small fish were more isolated and large fish were more likely to be shoaling (Table 3.2, model 3). There was also a significant effect of the interaction between shelter availability and body mass (Table 3.2, model 3). More specifically, the

slope of the relationship between body mass and distance to the nearest neighbor was high under HSA but low under LSA, so that the effect was significant only when shelters were abundant. Under HSA, Arctic charr also attacked prey over longer distances (Foraging radius range = 0 – 1.5 and 0 – 1.75 body lengths in LSA and HSA, Table 3.1 and 3.2, model 4, Figure 3.2B). Finally, prey attack rate was higher under HSA than under LSA (Table 3.1 and 3.2, model 5, Figure 3.2C). Foraging radius and prey attack rate was not related to body mass (Table 3.2). Foraging radius also was positively related to prey attack rate, as fish attacking prey over longer distances also attacked more often (Table 3.2, model 5).

*Table 3.1 Spatial and temporal behavior in the two treatments of shelter availability (LSA = Low Shelter Availability, HSA = High Shelter Availability) and for juvenile Arctic charr.*

	Treatment			
	LSA		HSA	
	Mean	SD	Mean	SD
Individual activity rate	0.56	0.11	0.27	0.09
Individual appearance rate	0.71	0.07	0.26	0.18
Mean time of activity (h:mm)	13:19	01:45	00:31	01:05
Compression of activity (h)	3.46	0.51	2.11	0.65
Aggregation index	-1.81	2.37	1.62	2.06
Foraging radius (body lengths)	0.33	0.34	0.55	0.40
Prey attack rate (proportion)	0.18	0.12	0.30	0.14
Specific Growth Rate (%/day)	0.01	0.65	-0.05	0.57

Compression of activity is the circular standard deviation of the individual distributions of activity rates. Aggregation is calculated as the Clark-Evans-Index (Clark and Evans 1954), modified by Petrere (1985). Prey attack rate is the proportion of 5-s intervals during which a focal fish attacked at least one prey item.

### **3.3.3 Growth**

SGR were on average low (non-significantly different from 0 in both treatments) as some fish grew during the experiment, but others lost weight (Table 3.1). Importantly, the higher overall activity rates observed in the LSA treatment did not translate into a higher growth (range = -0.8 to 2.5 and -1.3 to 0.7 %/day under LSA and HSA respectively, Table 3.2, model 6). However, we did find a positive relationship between activity rates and specific growth rates (Table 3.2,

model 6, Figure 3.3A). Spatial behavior was also related to growth rates through the distance from an individual to its nearest neighbor, i.e. isolated fish grew better (Table 3.2, model 6, Figure 3.3B).

*Table 3.2 Summary of mixed linear models for the effect of shelter availability and body mass on individual behavior, and shelter availability and behavior on SGR in juvenile Arctic charr.*

Model	Response variable	Explanatory variable	Estimate	Std. Error	df	t value	P-value
1	Individual activity rate	Intercept	-0.822	0.120	4.00	-6.830	0.002
		Shelter availability	1.645	0.170	4.00	9.658	< 0.001
2	Compression of activity	Intercept	0.003	0.300	56.99	0.009	0.993
		Shelter availability	1.552	0.162	56.99	9.608	< 0.001
		Body mass	-0.166	0.061	56.99	-2.718	0.01
3	Distance to nearest neighbor	Intercept	0.587	0.062	4.17	9.428	< 0.001
		Shelter availability	-0.852	0.079	2.76	-10.729	< 0.001
		Body mass	-0.136	0.051	82.04	-2.632	0.010
		Shelter availability × body mass	0.140	0.061	150.72	2.290	0.023
4	Foraging radius	Intercept	0.405	0.132	77.16	3.066	< 0.001
		Shelter availability	-0.602	0.161	54.33	-3.731	< 0.001
5	Prey attack rate	Intercept	0.416	0.144	50.99	2.884	0.006
		Shelter availability	-0.714	0.210	50.99	-3.395	0.001
		Foraging radius	0.482	0.106	50.99	4.556	< 0.001
6	Specific growth rate	Intercept	-1.920	0.611	50.21	-3.143	0.003
		Individual activity rate	0.057	0.019	45.69	2.980	0.005
		Distance to nearest neighbor	0.018	0.008	34.05	2.255	0.031

A stepwise selection on p-value was applied from the full model until only significant effects remained. The full models were as follows: Models 1 and 2: Response~Shelter availability+Body mass+Enclosure (random), Model 3: Response~Shelter availability+Body mass+Enclosure (random)+Individual (random), Model 4: Response~Shelter availability+Body mass+Distance to nearest neighbor+Enclosure (random)+Individual (random), Model 5: Response~Shelter availability+Body mass+Distance to nearest neighbor+Foraging radius+Enclosure (random)+Individual (random), Model 6: Response~Shelter availability+Individual activity rate+Compression of activity+Distance to nearest neighbor (averaged)+Foraging radius (averaged)+Prey attack rate (averaged)+Enclosure (random). All first degree interactions between fixed factors were included in the full models.

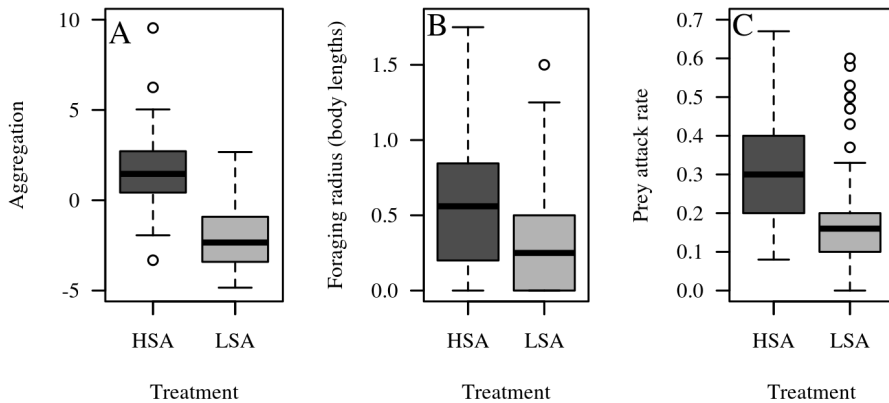


Figure 3.2 Spatial behavior (A, aggregation; B, foraging radius; C, prey attack rate) of juvenile Arctic charr in two treatments of shelter availability. Aggregation is calculated from the average distance between individuals and their nearest neighbor, so that low values represent more aggregation. Prey attack rate is the proportion of 5-s observations intervals for which a focal fish attacked at least one prey item.

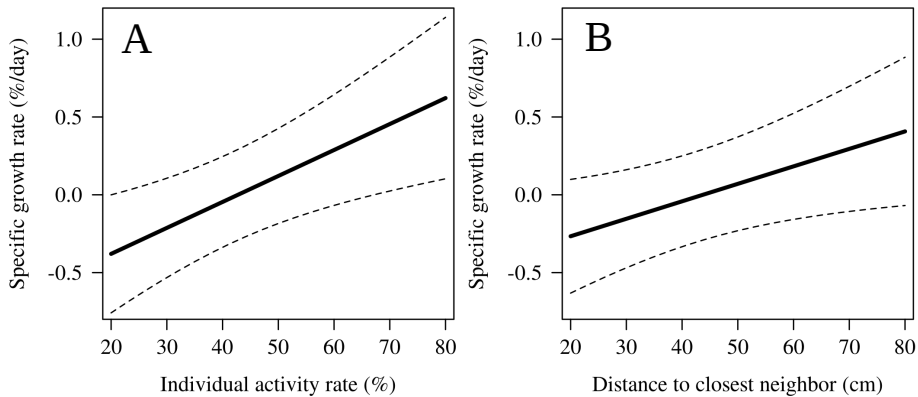


Figure 3.3 Effect size plot for the relationship between specific growth rates of Arctic charr and individual activity rates (A) and distance to the nearest neighbor (B). Values were extracted from mixed linear models where enclosures were included as random factors. Values of distance to the nearest neighbor were averaged per individual. Dotted lines represent 95% confidence intervals.

### 3.4 Discussion

In this experiment, shelter availability affected several aspects of diel

activity. Arctic charr with limited access to shelters had higher individual activity rates, became diurnal and allocated their activity over a wide portion of the 24 h cycle, compared to fish with ample access to shelters. The increase in activity rates under LSA was strongly expected as the experimental conditions in this treatment did not allow many individuals to hide simultaneously. Therefore, our design created important variation in competition and predation risk among treatments and our aim was to investigate how such variation may lead to behavioral adjustments. Specifically, our main prediction derived from Orpwood et al. (2010) was that Arctic charr under low shelter availability would increase their activity during daytime. Indeed we found strong differences in mean time of activity between treatments of shelter availability, i.e. fish were nocturnal when shelters were abundant, and diurnal when shelters were limited.

The literature suggests that individuals should be active primarily during periods that maximize the ratio of food income vs mortality risk (Metcalf et al. 1999). In stream-dwelling fish, the definition of such period is variable because many ecological factors may affect the profitability of a given time of day. For instance, the ability of fish to detect and catch prey decreases with decreasing light intensity (Elliott 2011, Watz et al. 2014), whereas drift rates are also generally higher at night (Elliott 1970). The temporal component of predation risk can also fluctuate significantly, as the type of predators, their diel activity patterns, and the intensity of predation risk may vary among systems (Kadye and Booth 2014). Crepuscular activity has been found to be dominant in some studies on salmonids (05:00 and 20:00, Roy et al. 2013, 03:00-06:00 and 20:30, Conallin et al. 2012). Others suggest that the preferred foraging time depends on a series of additional factors including body size and age (Bradford and Higgins 2001, Imre and Boisclair 2004, Breau et al. 2007). For instance, Breau et al. (2007) recorded activity in Atlantic salmon of size and age similar to our system every two hours and found that activity rates increased linearly from 07:00 to 23:00. Our results are in accordance with their study and suggest that when provided with resting opportunities, nighttime is the optimal feeding period for salmonids of age 1+, because it minimizes encounter rates with predators. Because our observations were initiated at 3 h intervals and each lasted 90 min, we are confident that any potential crepuscular effects would have been detected in this experiment. Moreover, a distinction between day, night and crepuscular time might not be as clear for streams during relatively short nights at high latitude.

Higher activity rates at night in shelter-rich enclosures are in accordance with the results of Orpwood et al. (2010), who found increased nocturnal activity in presence of overhead cover. Such results may not seem intuitive because both riparian shading and boulders used in the present study provide protection against predators. Therefore, when shelters are abundant, daytime activity should be (i) less risky, because salmonids' main predators in this system are diurnal birds, and (ii) preferred due to the increased foraging efficiency (Watz et al. 2014). Predation risk may also elicit additional diurnal foraging behaviors. Common anti-predatory responses in freshwater fish include the use of fast-running water (e.g. Sempeski and Gaudin 1995) and complex habitats during daytime (Stuart-Smith et al. 2008) or reduced activity in presence of predators (Kim et al. 2011). When suitable habitats and opportunities to hide are limited, none of these responses are possible and fish may have to adjust their behavior differently. In this experiment, under low shelter availability, Arctic charr spent most of their time active during the day and rested at the bottom during the night. We interpret this as a behavior consisting in staying alert to flee from potential diurnal predators.

In our study, Arctic charr schooled when sheltering opportunities were rare, but were more dispersed when shelters were abundant, suggesting territorial behavior (Gunnarsson and Steingrímsson 2011). Previous work suggests that aggregation increases with decreasing shelter availability, both to dilute predation risk and locate shelters more efficiently (Dolan and Butler 2006). In terms of foraging behavior, we expected Arctic charr to attack prey over longer distances in open habitats for two reasons. First, in a previous study, fish in complex habitats reduced their foraging areas (Imre et al. 2002). Second, as fish under HSA were primarily nocturnal, they were expected to be less efficient at detecting remote prey (Fraser and Metcalfe 1997, Watz et al. 2014), and should thus attack it over a shorter distance (Metcalfe et al. 1997). However, fish in shelter rich enclosures attacked prey over longer distances in this experiment. This could potentially indicate costs associated with foraging in schools under low shelter availability, such as a reduced field of view, more frequent contacts between competitors, or low motivation to leave schools.

Body mass did not affect individual activity rates, but affected how individuals allocated their activity in time, as large individuals

were active during a narrower interval of the 24 h cycle. Phenotype-dependent effects on diel activity have been previously reported for freshwater fish populations, including salmonids (Alanärä et al. 2001, Brännäs 2008). Such differences may result for instance from different endogenous rhythms (Glova and Jellyman 2000), or from intra-specific competition leading to large dominant individuals monopolizing the most valuable periods (Alanärä et al. 2001). As body mass was correlated only to the compression of activity, without affecting individual activity rates, we suggest that small fish may reduce their activity in the presence of dominant individuals and compensate by extending their activity over longer periods (e.g. Alanärä et al. 2001). In this experiment, smaller fish were also more isolated, albeit only when shelters were abundant. This result suggests that feeding isolated provides certain benefits, like increased access to food, or reduced aggression. However, limiting shelter availability might greatly increase the costs of this behavior, perhaps through increased predation risk, or reduced food availability. Hence, although small individuals may sometimes take risk to gain access to more drifting prey, they may prefer to stay within schools when shelters are rare.

Although we found clear behavioral adjustments in response to a lack of shelters, growth rates were similar between treatments. Limited shelters resulted in a series of costs, some of which were measured, such as lower prey attack rate. Other costs like increased stress and maintenance metabolism, and decreased food availability have also been proposed (Negishi and Richardson 2003, Fortin et al. 2004, Millidine et al. 2006). At high shelter availability, fish were less active, but attacked prey at higher rate, which may result in similar food intake among treatments of shelter availability. In a study by Orpwood et al. (2006), Atlantic salmon were more active under low food availability, which resulted in similar growth rates. Several other studies report that salmonids may adjust their activity to maintain optimal growth trajectories. However, such behavior may lead to higher exposure to predators (Imre and Boisclair 2005) and inter- and intra-specific competition (Blanchet et al. 2008), which suggests that salmonids may forage only to the extent needed to sustain a specific growth threshold. Alternatively, one may argue that the duration of the experiment (nine days) is too short to reveal significant differences, especially because we followed individuals in late summer when prey availability and growth rates typically decrease (Steingrímsson and Grant 1999). Additional non measured costs of limited shelter availability such as increased predation risk may also have important



effects on individual fitness.

Interestingly, in this study, more active fish grew better. Estimates of growth associated with differences in diel activity patterns in natural conditions are rare and not always conclusive. Active Atlantic salmon grew faster than inactive individuals under semi-natural conditions (Martin-Smith and Armstrong 2002), which is in accordance with our results. Similarly, Brännäs (2008) found that more active Arctic charr grew better. However, in another experiment, the level of competition affected diel activity patterns of Atlantic salmon but not foraging and growth rates (Blanchet et al. 2008). We also found that isolated fish grew better than fish in close proximity to their conspecifics. This could be an additional indication that Arctic charr adjust their behavior to maintain growth at the expense of increased predation risk, because small fish were more isolated, and perhaps benefited from such behavior. Although we did not detect an effect of distance to the nearest neighbor on prey attack rate (Eggers 1976), foraging in isolation may provide other non-measured benefits for growth such as higher foraging success, or reduced aggression (DeVries et al. 2004).

In conclusion, this study provides an interesting example of how habitat modifications can drastically alter both temporal (i.e. diel activity patterns, prey attack rate) and spatial (i.e. aggregation, foraging radius) components of behavior in a mobile animal. These results highlight the importance of examining (i) the behavioral consequences of such modifications at the appropriate temporal scale and at sufficient resolution (e.g. throughout the 24 h cycle), and (ii) the possible interactions between time and space (e.g. if spatial behavior is adjusted in response to becoming diurnal). Finally, the individual approach coupled with semi-natural systems should be useful to identify how activity interacts with phenotypic factors such as body size, and components of individual fitness, such as growth and survival.

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# 4 Diel activity and growth of Arctic charr (*Salvelinus alpinus*) in contrasting stream habitats

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Abstract

Diel activity provides insights into how animals exploit and perform in natural habitats. Observational studies have related the activity of stream salmonids to key variables including current velocity and water depth, but experimental studies are lacking. We monitored the diel activity, latency to exit a shelter, and growth of individual juvenile Arctic charr *Salvelinus alpinus* (age 1+) in enclosures established in all combinations of slow (~ 4 cm/s), intermediate (~ 12 cm/s) or fast (~ 22 cm/s) current velocity and shallow (~ 14 cm) or deep (~ 28 cm) habitats. Arctic charr were more active and diurnal in fast, but not deep habitats. Individuals stayed longer in shelters in slow and shallow habitats, but there was no difference between day and night. Fish grew faster in deep and fast habitats, and more active individuals grew faster, but only in fast-running waters. These results suggest that studying diel activity can help explain the habitat use of salmonids. Quantifying activity and growth in different habitats may in turn help predict the abundance and distribution of stream fishes.

**Keywords:** *Salvelinus alpinus*, habitat availability, predation risk, current velocity, water depth

## 4.1 Introduction

Stream-dwelling fishes have long been described as organisms with flexible and diverse diel activity patterns (Reebs 2002), i.e. the way individuals allocate their time towards foraging versus resting over the 24h cycle. Such variability may stem from intrinsic, individual differences such as personality, age or body size (Imre and Boisclair 2004, Závorka et al. 2016) and have effects on individual fitness, such as through predation risk (Fox and Bellwood 2011), and growth (Larranaga and Steingrímsson 2015). Extrinsic, ecological conditions are also important determinants of fish activity. For instance, water temperature and shelter availability can affect both the overall time fish spend active and at what hours they are active, i.e. timing of activity (Breau et al. 2007, Larranaga and Steingrímsson 2015). Two other important habitat characteristics, current velocity and water depth can affect fish behavior, including diel activity. However, studies that link habitat availability to diel activity have focused primarily on shifts in habitat use over the course of the day. For example, stream salmonids use swifter and deeper habitats during the day, because they offer higher food availability (Nislow et al. 1998, Piccolo et al. 2007), and better protection against avian predators (Power 1987, Conallin et al. 2014). During the night, salmonids may move to slower waters, where drifting food is easier to detect (Metcalf et al. 1997, Banish et al. 2008, Johnson et al. 2011).

Freshwater habitats with contrasting current velocity and water depth can vary both in food availability and predation risk. In all habitats, activity rates should indicate the motivation to grow faster at the cost of increasing mortality risk (Kronfeld-Schor and Dayan 2003). In fast waters, food availability increases because more prey items drift per unit of time (Nislow et al. 1998), but prey capture probability and detection distance decrease (Piccolo et al. 2008). Swimming in fast currents also incurs higher energetic costs (Hill and Grossman 1993). Overall, net energetic benefits of drift-feeding stream fish are thought to be highest at intermediate current velocity (Fausch 2014). In terms of mortality, fish may be less conspicuous in fast waters (Heggenes et al. 1991), but they may also use pools with slower currents to limit predation risk (Lonzarich and Quinn 1995). Increasing water depth increases encounter rate with drifting items, as individuals can search a greater volume of water (Rosenfeld and Boss 2001, Piccolo et al. 2007) and provides better protection against avian and terrestrial

predators (Lonzarich and Quinn 1995). There are thus several habitat-related factors that potentially affect activity rates of salmonids.

Relating activity rates to net energy gain is not straight forward as indirect evidence suggests that fish either show higher activity in faster waters with more drifting prey (Nakano 1995), or increase their activity to compensate for reduced feeding rates or increased costs under suboptimal conditions (Orpwood et al. 2006, Blanchet et al. 2008a). Between these two extremes, fish may simply not change their activity in response to fluctuating water current velocity or depth (Blanchet et al. 2008b). Similarly, activity rates typically decrease with increasing predation risk (Lima and Dill 1990), but under some circumstances, salmonids may be more active under higher predation risk (e.g. in shelter-poor environments, Larranaga and Steingrímsson 2015). Furthermore, net energy gain and predation risk may also be negatively correlated, e.g. fast and deep habitats have more food (Nislow et al. 1998) but fish are less exposed to predators (Heggenes et al. 1991, Lonzarich and Quinn 1995), which may have additional consequences for diel activity patterns. These findings illustrate the difficulty of establishing general patterns of activity rates in relation to habitat variables from observational studies.

Salmonids are visual predators and have higher capture rates during the day (Elliott 2011), but experience lower predation risk during nighttime, as the majority of their predators are diurnal (Metcalf et al. 1999). This creates a trade-off where individuals can switch from diurnal to nocturnal behavior in response to diel changes in food availability and/or predation risk, if their activity patterns are plastic (Metcalf et al. 1999). Such a trade-off is likely to be affected by habitat use, because diel changes in food availability and predation by avian and terrestrial predators may differ among habitat types. For instance, low light levels at night are more likely to decrease prey capture efficiency in fast than in slow habitats (Metcalf et al. 1997), i.e. the net benefits of nocturnal activity should be higher in slow habitats. Similarly, shallow habitats are typically more exposed to avian and terrestrial predators (Lonzarich and Quinn 1995), so fish should be more likely to be active at night in those habitats.

Increased activity invariably comes at the cost of reduced time spent sheltering. One way to increase activity is to reduce the time spent refuging after a perturbation such as a predator attack. Resumption of feeding is a response to both food availability and

predation risk (Gotceitas and Godin 1991). Hungry individuals typically resume feeding sooner than satiated individuals (Gotceitas and Godin 1991, Reinhardt and Healey 1999, Roberts et al. 2011). Similarly, smaller individuals that need to grow faster also show shorter residence time in shelters (Mikheev et al. 1994). In habitats with high net energy gain, fish may be able to stay longer in a shelter following a perturbation, with little effect on their growth. However, and as stated above, net energy gain and predation risk are often negatively correlated in streams. Thus, fish in shallow, slow-running habitats with low energy intake may experience higher predation risk and remain hidden for longer periods. When predation risk and food availability vary over the 24h cycle, which is often the case in streams (Metcalf et al. 1999, Giroux et al. 2000), latency to exit shelters may also differ between day and night

Studies focusing on diel activity and growth in habitats of differing water current velocity and depth are rare. Depending on how fish adjust their activity, they may grow differently in contrasting habitats. Some observational studies have suggested that fish in optimal habitats grow faster, via increased activity (Nakano 1995). Alternatively, other studies have found that salmonids may increase activity in sub-optimal conditions like high population density (Fingerle et al. 2016), low shelter availability (Larranaga and Steingrímsson 2015) and low food availability (Orpwood et al. 2006) and reach growth similar to fish in more suitable conditions. Within habitat types, more active fish may also grow faster (Martin-Smith and Armstrong 2002, Larranaga and Steingrímsson 2015).

To examine how habitat features affect optimal diel activity and subsequent growth, we designed a semi-natural experiment where we stocked and monitored individually-tagged Arctic charr *Salvelinus alpinus* of age 1+ in stream enclosures in an Icelandic stream. Locations were selected to create variation in current velocity and water depth among enclosures, but low variation within enclosures. We repeatedly observed fish at different times of the day to quantify activity rates and latency to exit shelters and tested if these attributes were affected by habitat variables (current velocity and depth) and by the time of day (day or night). In addition, we measured initial and final body size to assess how habitat features and activity affect growth. We tested the predictions: (1) Arctic charr will be more active and (2) more diurnal in habitats with low predation risk and high food availability (i.e. deep and fast habitats); and, (3) latency to emerge

from a shelter will increase in risky conditions (i.e. in slow and shallow habitats and during the day). Predictions about growth rates will depend on how Arctic charr adjust their activity in contrasting habitats: (4a) if fish are more active in habitats with high net energy intake, they will grow faster in those habitats; (4b) if fish counter limited access to food or increased energetic costs via increased activity, then growth will be similar across habitats; or (4c) if activity rates are independent of habitat, fish will also grow faster in habitats with higher net energy gain. (5) Finally, within habitats, more active fish will grow faster.

## 4.2 Materials and methods

### 4.2.1 Sampling

On 3 July 2015, we sampled 60 Arctic charr (age 1+) by electrofishing (Smith-Root LR-24) in river Grímsá (Iceland, N 65,79524, W 19,844728), a tributary to the river Laxá in Skefilsstadahreppur in northern Iceland. Arctic charr is the only freshwater fish in this stream and is isolated from downstream populations by a waterfall, which excludes the possibility of inter-specific competition for habitats. Arctic charr do not grow large enough in this stream to present a significant risk of cannibalism, so the main potential predators are diurnal birds, Arctic terns *Sterna paradisaea* and ducks (e.g. *Mergus serrator*, pers.obs). All fish were anesthetized, measured for body length and mass, tagged (see below), and randomly assigned to one of six stream enclosures with different combinations of water depth and current velocity. Age was determined based on the size distribution of Arctic charr in the stream. Fork length was measured to the closest 0.1 millimeter with calipers and body mass to the closest 0.01 g (PESOLA® PPS200). Fish were on average 57.2 ( $\pm$  1.7) mm and 3.2 ( $\pm$  0.3) g; there was no difference among enclosures for body length (ANOVA,  $p = 0.550$ ) or body mass (ANOVA,  $p = 0.457$ ). We used four colors of visible implant elastomer tags (red, green, orange and yellow) at two specific positions of the dorsal fin (Steingrímsson and Grant 2003). Tags spread up along the dorsal fin rays, which enables individual identification during overhead observations. Fish were given 48 h to adjust to the experimental conditions, before the behavioral observations were initiated. The experiment was terminated on 18 July 2015 after 16 days, and all fish were recaptured with dipnets, measured for body length and mass and released back in the

river. Some tags had faded partially, which impeded clear identification during some observations, but all fish could be identified during the final measurement. We used this information to ensure fish were correctly identified in the behavioral dataset.

#### **4.2.2 Experimental design**

Fish were placed in a total of six enclosures which varied in current velocity (slow, intermediate fast; two of each) and water depth (shallow, deep; three of each). The order of the enclosures starting upstream was as follows: intermediate-deep, fast-shallow, slow-shallow, intermediate-shallow, fast-deep and slow-deep. Neighboring enclosures were separated by a stream length of 20-80 m. Enclosures were 4 m long, 1m wide and 0.75 m high and were made of 5 mm nylon mesh (including the bottom). This mesh size is large enough to allow invertebrates to drift through the enclosures, but small enough to prevent fish from escaping. A string was tied across the top of each enclosure to deter avian predators, presumably without affecting the risk perceived by fish. Ten fish per enclosure is a high enough density to expect competition for space or food in a 4 m<sup>2</sup> enclosure (Larranaga and Steingrímsson 2015).

For each active fish, we measured the latency to exit a shelter (see below) after the beginning of an observation. Young salmonids can use interstitial spaces between rocks as shelters (Finstad et al. 2007). Therefore, to control for the availability of refuges, we sieved the bottom substrate and use only gravel  $\leq 2$  cm in diameter to cover the bottom of enclosures (Larranaga and Steingrímsson 2015). We also stretched the sides of each enclosure to prevent fish from using these to hide. Five shelters were then systematically placed in each enclosure, at equal intervals (1 m) along the length of the enclosure and consisted of common water moss *Fontinalis antipyretic* attached to cobbles (approximately 0.12 m<sup>2</sup> and 15% of the total benthic area of each enclosure). This type of structure is commonly used by Arctic charr as a source of shelter in the study stream and has been used in a previous experiment (Larranaga and Steingrímsson 2015). Five shelters per enclosure are sufficient to permit fish to hide at any moment because up to four individuals can hide in one such shelter (Larranaga and Steingrímsson 2015).



### **4.2.3 Habitat availability**

Habitats were selected based on previous observations of Arctic charr in other systems (Heggenes and Saltveit 2007, Tunney and Steingrímsson 2012). At the beginning of the experiment, water depth and current velocity at 40 % of the water depth from the bottom (Davis and Barmuta 1989) were measured systematically at 100 coordinates in each enclosure (at 20 cm intervals on each axis, starting at 10 cm from the sides) with a Flo-Mate™ Model 2000CM (Marsh-McBirney Inc., Frederick, MD) current velocity meter. Similar measurements were collected five other times in all enclosures during the course of the experiment.

Water temperature was recorded automatically every hour to the closest 0.2 °C during the experiment by data loggers positioned at each enclosure (HOBO® TidBiTv2® UTBI-001). Light intensity was also measured every hour by data loggers positioned at the most upstream and downstream enclosures (HOBO® Pendant® Temp/Light, 8K UA-002-08). As there were only minor differences in water temperature and light intensity among enclosures (smaller than the accuracy of the data loggers), we used values from the most upstream data loggers. On average, water temperature was 6.4 ( $\pm$  1.9, range = 2.8 – 11.9) °C and light intensity was 32.8 ( $\pm$  40.2, range = 0.1 – 165.3) kilolux.

### **4.2.4 Food and habitat availability**

Current velocity was 4.4 ( $\pm$  1.2), 12.3 ( $\pm$  3.3) and 22.2 ( $\pm$  4.2) cm/s in the slow, intermediate and fast enclosures, respectively. On average, the shallow and deep enclosures were 14.2 ( $\pm$  1.7) and 28.6 ( $\pm$  3.2) cm at the beginning of the experiment. There were minor but significant differences in current velocity among water depth treatments (ANOVA,  $p$  = 0.016) and marginal differences over time (ANOVA,  $p$  = 0.084). However, there was no difference in depth among current velocity treatments (ANOVA,  $p$  = 0.158), nor was there a difference in water depth over time (ANOVA,  $p$  = 0.318). There were some differences between habitat availability and habitat use. In fast and slow habitats, fish used slower and faster habitats than what was available (Wilcoxon test,  $p$  = 0.005 and  $p$  < 0.001, respectively). There was no such difference in habitats of intermediate current velocity (Wilcoxon test,  $p$  = 0.066). Habitat use and habitat availability did not differ in shallow habitats (Wilcoxon test,  $p$  = 0.061), but fish used shallow habitats relatively more often in deep enclosures (Wilcoxon

test,  $p < 0.001$ ).

*Table 4.1 Invertebrate drift rates (mean number of potential prey drifting per minute in a 1 m wide section of the stream) in different habitats, at day and night. The effect of habitat and time of day were assessed via a three-way ANOVA. Bold p-values indicate significant effects*

Effect	Treatment	Drift rate	SD	P value
Depth	Shallow	5.63	4.72	<b>0.031</b>
	Deep	9.43	8.97	
Current velocity	Slow	2.21	1.34	<b>&lt; 0.001</b>
	Intermediate	6.52	4.22	
	Fast	13.86	8.69	
Time of day	Day	5.71	5.04	<b>0.040</b>
	Night	9.35	8.84	

Drifting invertebrates were collected in each enclosure, at 00:00 and 12:00, at the beginning (7 July), middle (11 July), and end (17 July) of the experiment, resulting in a total of 36 estimates (i.e. samples) of food availability. Sampling was performed using a 250  $\mu\text{m}$  drift net (net opening = 25 x 40 cm; net length = 100 cm) in the middle of each enclosure for 10 min. Samples were preserved in 70% ethanol and processed at Hólar University College. Food items in each sample were counted under a stereomicroscope and sorted into order and/or family. All sampled invertebrates were of edible size and type for the fish used in this study (*sensu* Keeley and Grant 1997). Food availability was expressed as the number of prey drifting per minute in a 1 m wide section of the stream (i.e. the width of an enclosure) in each habitat. Food availability, expressed as drift rates, was 7.53 organisms/min along a 1 m transect on average. Drift rates were higher in deep (ANOVA,  $p = 0.031$ ) and fast habitats (ANOVA,  $p < 0.001$ , Table 4.2). There were also more invertebrates drifting at night (ANOVA,  $p = 0.039$ , Table 4.1).

#### **4.2.5 Behavioral observations**

Observations started on 6 July (12:00) and finished on 17 July 2015 (06:00). Observations were made every 3 h (00:00, 03:00, etc.). Each enclosure was visited 8 times per day during six 24 h cycles, yielding a total of 48 observations per enclosure. Algae and small debris were regularly removed from the enclosures after a round of observations to

ensure good water flow. Enclosures were chosen in a random order before every observation period. To record diel activity, an observer stood motionless in front of an enclosure for 15 min and started recording activity after the first 5 min. Individual activity rate was calculated as the proportion of observations during which a focal fish was active. A fish was considered active when it was feeding, and inactive when it was hiding in a shelter, or resting motionless on the substrate without showing any mobility or foraging effort (this last situation occurred rarely) (Larranaga and Steingrímsson 2015). This distinction was facilitated by Arctic char's foraging behavior, as once fish emerged, their behavior was consistent throughout the rest of the 15 min scan (i.e., continuously active, hiding, or resting on the bottom). We also measured overall activity rate as a proportion of active individuals during each observation. No fish became active more than 9 min after an observation started, so 15 min scans provided a good estimate of activity and latency to exit shelters. Two observers (N. Larranaga and F. Hadi) collected all the data and alternated every three to five observations (i.e. 9 to 15 h), so that each observer collected 50% of the data at each daytime.

Each session of observations lasted 90 min, with an additional time to travel between enclosures. Therefore, observations started and finished around 45 min before and after each daytime (e.g., from 14:15 to 15:45 for 15:00). On four different occasions at 00:00 and 03:00, the observer had to use a LED flash light (VASQ by ELWIS, model S1) to enhance tags that could not be read properly. To avoid affecting behavior of the char, the flash light was used only at the end of the observation, and only very briefly. To limit potential disturbance, we zoomed in from a large diameter beam and slowly reduced the diameter until the tag could be read (Larranaga and Steingrímsson 2015). This procedure was repeated for each unidentified tagged fish, and the whole process took less than 20 s per scan. No fish fled as a reaction to the flash light or seemed attracted to the light.

For each active fish, we measured the latency of fish to exit the shelter if they were not visible from the beginning of an observation. Fish emerging after the beginning of an observation were often seen fleeing to a shelter when the observer approached the enclosure and emerged from the same shelter, so the measurements we collected should accurately represent the latency to emerge from a shelter after a perturbation. It took 20 to 30 sec to scan an enclosure, so those measurements were rounded to the closest 30 s over the 15 min

observations.

#### 4.2.6 Data analysis

Night corresponded to measurements between 21:00 and 03:00, whereas day was determined to occur between 06:00 and 18:00. Light intensity was 26.1 ( $\pm$  21.5) and 3.6 ( $\pm$  4.7) kilolux during the day and the night, respectively (t-test,  $p < 0.001$ ).

During several observations, there were no active fish, so we used a zero-inflation model to assess the effect of water current velocity, depth and time of day on overall activity rates. This model was a mixture between a binomial (zero vs. positive counts, logit link) and a Poisson distribution (positive counts, log link). The model was built using the function *zeroinfl* from the *pscl* package in R (Jackman 2015). The full model included all three variables as well as all first degree interactions. A similar model was used to test for the effect of habitat and time of day on the latency to exit shelter because many fish did not escape when the observer approached the enclosure, which led to a significant proportion of zeros. We doubled the values to round the times in minutes for the analysis and used a Poisson distribution, but we reported only the original values in the results. In this model, individuals were considered as a random factor. We also assessed the effect of current velocity, water depth, individual activity rates and all first degree interactions on specific growth rates.  $SGR (\%/day) = (\ln M_{Final} - \ln M_{Initial}) \times 100/t$ , where  $M$  is the mass and  $t$  is the duration of the experiment in days (Ricker 1975). Individual activity rates were  $\log_{10}$  transformed to fulfill normality. Because this rate equaled zero for some individuals, 0.01 was added to the original value to allow for  $\log_{10}$  transformation. For every model, we tested all the possible combinations of variables and interactions using the function *dredge* from the *MuMin* package in R (Barton 2009), and selected the best model based on its AIC. The difference in AIC values between the best and second best model was always higher than 2 (Burnham and Anderson 2002).

### 4.3 Results

Activity rates of juvenile Arctic charr in this study were low in general (mean = 8.9 %, standard deviation = 14.4 %). The best model explaining overall activity rates included water current velocity, time of day and their interaction (Table 4.2). Hence, activity increased with

increasing current velocity ( $2.7 \pm 9.0$ ,  $8.54 \pm 14.0$ ,  $15.5 \pm 16.3$  % in slow, intermediate and fast habitats, respectively). The probability of observing at least one fish active, as well as the number of active fish increased in habitats with fast-running waters ( $p < 0.001$  and  $p = 0.031$ , respectively, Figure 4.1A). Activity rates were similar in shallow ( $9.0 \pm 15.1$  %) and deep ( $8.8 \pm 13.7$  %) habitats, and water depth had no effect (Table 4.1, Figure 4.1B).

*Table 4.2 Summary of generalized linear models for the effect of habitat on the behavior and growth of Arctic char. Zero-inflated models were used for overall activity rates and the latency to exit shelters because of abundant zero values. Bold p-values indicate significant effects.*

Response variable	Explanatory variable	Df	Deviance	Resid. Deviance	P value
Overall activity rate (Binomial)	Current velocity	2	57.692	323.370	<b>&lt;0.001</b>
	Time of day	1	0.486	322.880	0.486
	Current velocity*Time of day	2	6.381	316.500	<b>0.041</b>
Overall activity rate (Poisson)	Current velocity	2	6.935	847.340	<b>0.031</b>
	Time of day	1	2.150	845.190	0.143
	Current velocity*Time of day	2	12.868	835.320	<b>0.002</b>
Latency to exit shelter (Binomial)	Current velocity	2	7.532	259.590	<b>0.023</b>
	Water depth	1	2.311	302.120	0.128
Latency to exit shelter (Poisson)	Current velocity	2	56.255	1058.400	<b>&lt;0.001</b>
	Water depth	1	8.916	1114.700	<b>0.003</b>
Specific growth rate	Current velocity	2	10.851	23.663	<b>&lt;0.001</b>
	Water depth	1	2.482	34.514	<b>0.009</b>
	Individual activity rate	1	2.140	21.523	<b>0.020</b>
	Individual activity rate*Current velocity	2	2.504	19.019	<b>0.031</b>

Activity rates were similar during the day and the night ( $p = 0.486$  and  $0.143$  for the effect of time of day on the binomial and Poisson components of the model, respectively). However, the interaction between current velocity and time of day was significant, both for the binomial and Poisson components of the model (Table 4.2). Indeed, in agreement with our prediction, there was more activity at night in slow habitats, and more daytime activity in fast habitats ( $p = 0.041$  and  $0.002$  on the Binomial and Poisson components, respectively, Figure 4.1A). The interaction between water depth and time of day did not have a significant effect activity rates (Table 4.2).

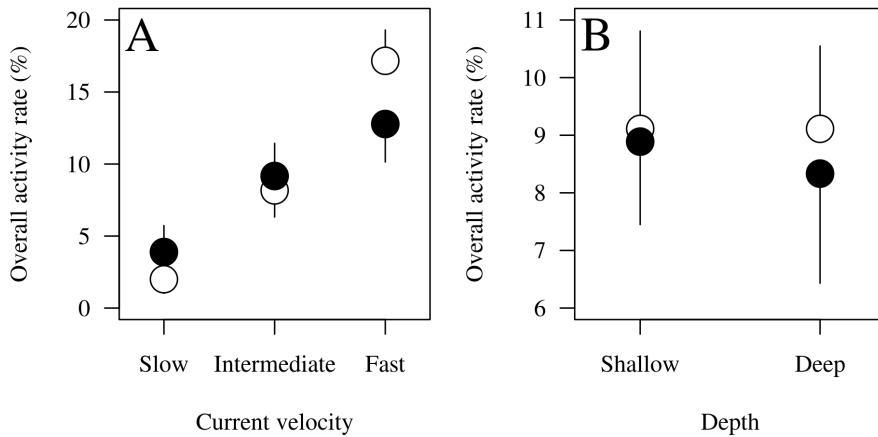


Figure 4.1 Overall activity rate of 60 Arctic charr in stream enclosures with contrasting water current velocity (A) and depth (B) during the day (open circles) and the night (filled circles). Data are given as mean ( $\pm$  standard error).

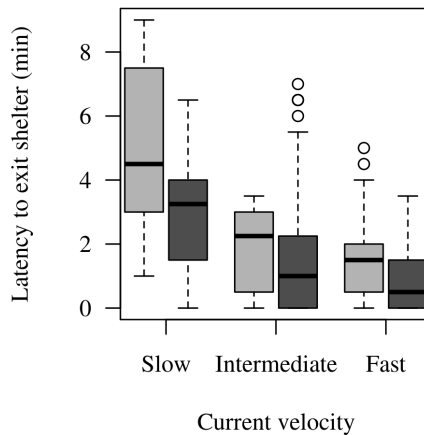
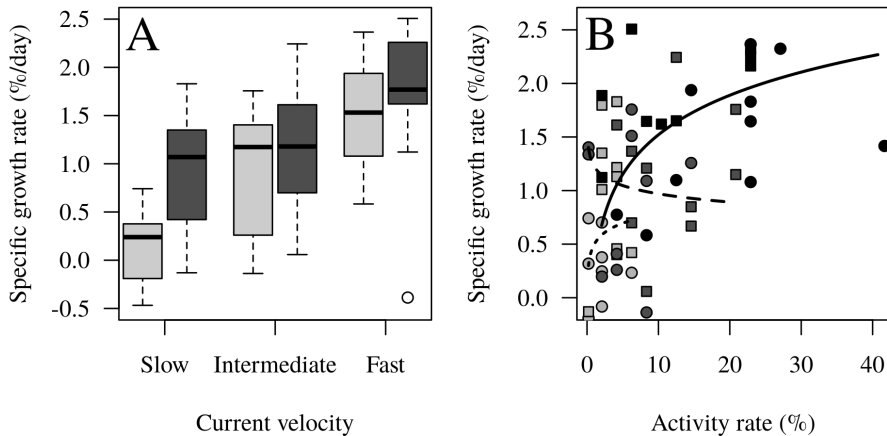


Figure 4.2 Distribution of latency to exit shelters by juvenile Arctic charr in contrasting habitats. Light grey and dark grey represent shallow and deep habitats, respectively. Outliers were not excluded from the analyses.

The latency of fish to exit shelters ranged from 0 to 9 min (mean = 1.8, standard deviation = 2.1, Table 4.2) and was best explained by a model that included water current velocity and depth. In the binomial component, only water current velocity had a significant effect, i.e. fish were less likely to hide when the observer approached an enclosure with fast water current ( $p = 0.023$ , Figure 4.2). In the Poisson component, we found that the latency to exit shelter was

longer in shallow ( $p = 0.003$ ) and slow habitats ( $p < 0.001$ ), ie. fish remained hidden longer in those habitats. Contrary to our prediction, fish took similar time to exit their shelter during the day and the night.



*Figure 4.3 Effect of water current velocity and depth on specific growth rates (A) and predicted interactive effect of current velocity and individual activity rates on growth (B). In Figure A, light and dark grey represent shallow and deep habitats, respectively. In Figure B, light grey (and the dotted line), grey (and the dashed line), and dark grey (and the solid line) represent slow, intermediate and fast habitats, respectively. Circles and squares represent shallow and deep habitats, respectively. Outliers were not excluded from the analyses.*

All but seven fish gained weight during the experiment. Out of these seven fish, four were in the slow-shallow enclosure, one in the fast-deep, one in the intermediate-shallow and one in the intermediate-deep habitat. The average growth rate was  $1.1 (\pm 0.8) \%_{\text{weight}}/\text{day}$ . The best model explaining Arctic charr growth rate included water current velocity, depth, individual activity rates and a positive interaction between current velocity and individual activity rates (Table 4.2). All three variables and the interaction had a significant effect. Fish grew faster in fast ( $p < 0.001$ ) and deep ( $p = 0.009$ ) habitats (Figure 4.3A). More active fish grew better overall ( $p = 0.015$ ), but this effect was primarily due to faster growth of active fish in fast-running waters ( $p = 0.031$  for the interaction between current velocity and individual activity rates, Figure 4.3B). Hence, the effect was detected in fast ( $p = 0.005$ ), but not in intermediate ( $p = 0.997$ ) or slow currents ( $0.298$ ).

## 4.4 Discussion

Our main goal was to test how Arctic charr adjust their diel activity when confined to particular stream habitats, which vary in quality via e.g., net energy intake and predation risk. First, according to our prediction, Arctic charr were more active in fast water currents. Previous studies linking activity rates to water current velocity are only correlative. For instance, Nislow et al. (1998) found that fish increased the time spent foraging and increased their use of high current velocity habitats in a site with greater food abundance. Similarly, Nakano (1995) found that dominant individuals occupied focal positions with higher water current velocity and had higher appearance rates, but this relationship could reflect increased metabolic demands of larger fish. One previous study found the opposite effect, i.e. higher activity rates in a section of a river with slower current (Bradford and Higgins 2001), but they used counts of active fish as a measurement of activity without respect to actual population density. In most of these studies, fish could move in and out of the study site. Therefore, and to our best knowledge, our study is the first to suggest that stream-dwelling salmonids may increase their activity when confined to habitats of high water current velocity.

There was no relationship between water depth and activity rate. Following the same rationale as for water current velocity, fish should be more active in deep habitats, where they have access to more food. Other mechanisms could be responsible for this effect (or lack thereof). Salmonids may be more mobile and swim faster in deep waters (McLaughlin et al. 1994, Steingrímsson and Grant 2011), so this additional energy expenditure may level off with energetic benefits in deep habitats (Piccolo et al. 2007). Another reason could be the small range of water depth used in our study. Our “deep” treatment was around 30 cm, but juvenile Arctic charr can use deeper water (mean depth was 36.5 cm in Tunney and Steingrímsson 2012). Nevertheless, individuals selected relatively shallow waters in the deep enclosures, so it is unlikely to be a strong bias here. Previous studies are equivocal on the link between water level and activity rates in salmonids (Blanchet et al. 2008b, Fingerle et al. 2016). Hence, the behavioral response of stream-dwelling fish to water current velocity and water depth may depend on additional factors, e.g. age, the range of habitat they have access to and how habitat availability fluctuates over time.

Our predictions on the timing of activity in different habitats



were derived from numerous observations of contrasting habitat use by day and night in a variety of salmonid species (Polacek and James 2003, Banish et al. 2008, Johnson et al. 2011). As expected, fish were more diurnal in fast waters, and more nocturnal in slow waters. Several factors can explain this result. For instance, predation risk is higher during the day in slow habitats (Metcalf et al. 1999), which should lead fish to increase activity at night. Also, in fast habitats, prey detection at night should be lower than in slow habitats, so fish should decrease activity at night because it is less profitable (Metcalf et al. 1997). Such explanations have long been suggested as drivers of habitat selection by salmonids (Metcalf et al. 1999), but our study is among the first to show that salmonids adjust their diel activity when confined to particular habitats. (see also Imre and Boisclair 2004). In our study, water depth had no effect on the timing of activity. In contrast, Imre and Boisclair (2004) suggested that fish were more diurnal in shallow habitats. Bradford and Higgins (2001) also found that fish were more diurnal in a section of a river with slower current and lower water level and argued that their effect could be due to differences in diel cycles of food among habitats, contrasting predation risk, or uneven population density. Similarly to the rate of activity, its timing also responds to habitat availability, emphasizing that salmonid behavior varies across species and age classes, both in space (habitat preferences, Armstrong et al. 2003) and in time (diel and seasonal activity, Bremset 2000).

Competing predictions can also be put forward on how fish should adjust their time to resume feeding following a perturbation in different habitats. We found that Arctic charr took less time to exit shelters in fast and deep habitats. This may be a direct indication that this trait is influenced more by predation risk than net energy intake. Indeed, in fast and deep habitats fish are less exposed to avian and terrestrial predators, which may have lead Arctic charr to remain feeding, or resume feeding soon after a disturbance (Gotceitas and Godin 1991). Vaz-Serrano et al. (2011) also argued that resumption of feeding after isolation was more related to boldness than hunger (i.e. access to food). An important implication of our findings is that individuals stranded in slow and shallow habitats may pay a triple price via (i) decreased activity, (ii) limited access to food, and (iii) increased latency to resume feeding than those in fast and deep habitats. There was no difference in latency to exit shelters between day and night in any habitat type. Given our experimental design, avian predators could not attack fish. Coupled with the rare sighting of

such predators, our daily observations were likely the main source of perturbation for Arctic char. The even distribution of these observations over the 24 h cycle may explain the absence of effect of time of day on latency to exit shelters. This result could also be an indication that predation risk is a better predictor of the time to resume feeding, because although there was less food drifting during the day, fish did not resume feeding faster.

This study suggests that Arctic charr grow faster in faster waters. Some habitat-specific costs and benefits may even out and lead to similar growth rates across habitats. For instance, there was more food in fast habitats, but the costs of feeding in fast current should also be higher (Rosenfeld and Boss 2001). Fish were also more active during the day in fast habitats when they detect drifting prey more easily, but there was less food drifting during the day, which is consistent with previous reports (e.g. Young et al. 1997, Giroux et al. 2000). Importantly, two of our findings can contribute to the explanation of this relationship, (i) fish were more active in fast habitats, and (ii) they resumed feeding faster after being perturbed in fast habitats. Our results provide novel insights on the relationship between habitat characteristics and growth, because previous reports of growth rates in contrasting habitats rarely took diel activity into account (e.g. Rosenfeld and Boss 2001, Girard et al. 2004). So far, higher growth rates have been reported in intermediate (Blanchet et al. 2008b) and fast habitats (Allouche and Gaudin 2001), but Girard et al. (2004) found no relationship between current velocity and growth. Similarly, stream-dwelling fish may grow faster in deep habitats (Harvey et al. 2005), or may have similar growth rates among habitats with contrasting depth (Girard et al. 2004, Blanchet et al. 2008b). Some of these differences are certainly due to e.g. age- and species- specific habitat preferences. However, estimates of diel activity in contrasting habitats should increase our understanding of the link between habitat use of salmonids and growth.

More active fish grew faster than those less active, which is consistent with previous findings in semi-natural settings (Martin-Smith and Armstrong 2002, Larranaga and Steingrímsson 2015). Importantly, this relationship was not consistent across habitats with different current velocity. In slow habitats, the absence of correlation may be due to generally low activity rates (maximum individual activity rate = 6.17 %). However, growth was not related to activity in habitats with intermediate current velocity either. Food availability

was low in slow and intermediate habitats, so increasing activity may only increase food intake slowly and come at the expense of greater costs, such as higher aggression (Grant and Noakes 1988, Keeley and Grant 1995, Keeley 2000, Gunnarsson and Steingrímsson 2011), and mobility (Grant and Noakes 1988, Tunney and Steingrímsson 2012). However, in fast habitats, more fish were active simultaneously so density experienced by fish was higher. Hence, several factors potentially affected competition in our study, which in turn may alter the relationship between individual activity and growth.

In previous reports, Arctic charr mostly used habitats that would correspond to our “slow” and “intermediate” treatments (mean = 9.3 cm/s in Tunney and Steingrímsson 2012, and 7.2 cm/s in Heggenes and Saltveit 2007). However, Arctic charr were more active and grew faster in fast habitats in the present experiment. This discrepancy may be due to a lack of inter-specific competition in our study stream. Arctic charr often co-exists with Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* and typically inhabits the slowest water of the three species (Klemetsen et al. 2003). Similarly, fish were not displaced to slower-running habitats by older individuals in our experimental conditions, which can occur under completely natural conditions (Heggenes and Saltveit 2007, Tunney and Steingrímsson 2012). In any case, these findings highlight the need for more information on the behavior of Arctic charr in lotic environments, both in allopatry, and in sympatry with other salmonids. Our results also highlight the importance of incorporating diel activity when visually estimating habitat preferences, as opposed to confining estimates to a particular time of day. For instance, daytime estimates in the present study would have underestimated density more in the slow than in the fast current enclosures.

Foraging models have been successful at predicting the habitat use of salmonids because at any time, net energy intake can be measured in experimental systems and optimal habitats can be identified (Fausch 2014, Piccolo et al. 2014). Estimating the dynamics of profitability of a habitat over the 24 h cycle is a harder task, in part because costs and benefits are measured in different currencies. Yet, activity rates and activity patterns should be important components of these models because they affect food intake and mortality risk. For instance, Railsback and Harvey (2011) found that flexibility in activity patterns affected salmonid biomass more than other ecological factors such as their access to variable habitats, or the effect of dominance

hierarchies. Predictions of diel activity under limited habitat availability are equally as important, but lack experimental data to be integrated in foraging models. Railsback et al. (2005) based their prediction of higher activity under low-flow conditions, especially at night, on previous observations of Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) by Bradford and Higgins (2001). However, our experimental results suggest that at a given density, and for some salmonid species, activity may increase under high flow conditions instead. Hence, behavioral data collected in semi-experimental conditions and on a diel basis could bring valuable input to foraging models to predict the distribution, abundance and growth of salmonids (Rosenfeld et al. 2014).

In conclusion, this study found differences in the rate and timing of activity of salmonids across habitats, which in turn had important consequences in terms of growth. Individual based experiments where juvenile salmonids are monitored over time and their behavior is linked to growth are gaining recognition (Zimmerman and Vondracek 2006, Larranaga and Steingrímsson 2015, Lindeman et al. 2015). This study suggests that studying diel activity can explain how well individuals do in different habitats and the population dynamics of salmonids. Although we tested specifically how salmonids adjust their behavior when confined to particular habitats, our results may have several important implications. First, it challenges the idea that stream-dwelling Arctic charr prefer slow habitats, at least in allopatry (Heggenes and Saltveit 2007, Tunney and Steingrímsson 2012). Second, it should prove useful for the management of salmonid populations, by predicting how salmonids can overcome the loss, degradation, and fragmentation of their habitats through behavioral flexibility (Letcher et al. 2007). Third, it should help to refine existing growth and abundance models of salmonids (Rosenfeld et al. 2014). Finally, Arctic charr exhibits extremely high phenotypic plasticity (Klemetsen 2013) and variable life history compared to other salmonid species (Klemetsen et al. 2003). Future research could focus on how habitat types affect diel activity and growth in species with different habitat preferences and/or with more rigid diel activity patterns and habitat selection.

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# 5 Fluctuations in water flow: effects on diel activity, foraging mode and growth in juvenile Arctic charr

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## Abstract

Waterflow in stream can fluctuate as a result of natural (e.g. rain events) and human-induced events (e.g. hydropeaking). The magnitude, frequency and unpredictability of these events can have drastic consequences for fish populations. We studied how rapid modifications of waterflow affect the diel activity, foraging mode (e.g. search mobility) and growth of juvenile Arctic charr *Salvelinus alpinus* using enclosures positioned where a stream separates into two channels (two control enclosures upstream and two experimental enclosures in each channel). After a two day control period when waterflow was similar across all six enclosures, we repeatedly directed the flow towards one of the two channels (2X2 days of low and high flow in each channel) while the flow remained stable and intermediate in the upstream control enclosures. In fluctuating waterflow, age 1+ Arctic charr increased activity during low flow periods, especially at night, but ceased activity almost completely at high flow. Fish were more mobile and faster during prey search and attacked prey at longer distances at low waterflow. Differences were also noted in activity and foraging mode between the first and second day after reduced waterflow, suggesting that Arctic charr require time to adjust their foraging behavior. Growth rate of 1+ individuals was similar in stable and fluctuating waterflow, however, more active fish grew faster at stable waterflow. This study demonstrates the importance of behavioral flexibility for growth and population ecology in unpredictable environments like regulated rivers.

**Keywords:** *Salvelinus alpinus*, current velocity, stream enclosures, hydro-peaking, behavioral flexibility

## 5.1 Introduction

Freshwater lotic ecosystems are characterized by constant fluctuations in ecological parameters like water temperature, turbidity, depth and current velocity (Poff et al. 1997). Such fluctuations affect the availability and distribution of suitable foraging habitats, to which organisms can respond directly, e.g. by relocating to a different area (Clobert et al. 2001), or modifying their foraging behavior at their current position (Dill 1983). Employing either tactic, or a combination of both should have important effects on individual fitness, e.g. through foraging opportunities, growth, and survival (Dill 1983, O'Brien et al. 1989). Stream salmonids are a particularly well suited model to test the effect of environmental fluctuations on behavior. For instance, they can track new habitats rapidly (Armstrong et al. 1998). Alternatively, some species/and or individuals are more territorial and show strong site fidelity, even after acute modifications of their habitat (Pert and Erman 1994, Scruton et al. 2003) and adjust their foraging behavior accordingly. In spite of this behavioral flexibility, climate changed induced future habitat modifications are expected to have drastic effects on salmonid populations (Jonsson and Jonsson 2009), which highlights the importance of studying the behavior and growth of salmonids in rapidly changing conditions (Young et al. 2011).

Some natural fluctuations in stream waterflow are predictable in time, e.g. spring floods and summer droughts (Poff et al. 1997, Caissie 2006). Salmonids can use these predictable cues to adjust both the extent and the timing of their foraging activity, and/or select specific habitats at different times of the day (Metcalf et al. 1999). Alternatively, fluctuations in waterflow may result from more unpredictable, sometimes extreme events, e.g. glacial floods or lake outbursts (Magoulick and Kobza 2003). Salmonids can also adjust their temporal behavior to sudden changes in their environment, to a certain extent. For instance, rapid modifications of shelter (Larranaga and Steingrímsson 2015), food (Orpwood et al. 2006), or habitat availability (Larranaga et al. unpubl. Data) can affect the diel of activity of salmonids. Natural variation of waterflow can also be altered by human induced changes, including the presence of hydroelectric dams. The rapid and massive modifications of waterflow caused by dams is sometimes predictable in time, e.g. when water is stored during the night, and released during the day to sustain daily power demands. On the other hand, the magnitude, duration, and

frequency of hydropeaking events can change drastically and unpredictably on a day-to-day basis (Morrison and Smokorowski 2002, Taylor et al. 2014). There is a large body of research on the impact of hydroelectric dams on salmonids (Young et al. 2011), including on their mobility (Cocherell et al. 2010), home range (Scruton et al. 2005), habitat use (Riley et al. 2009), and prey selection (Lagarrigue et al. 2002). However, the effect of fluctuations in waterflow on the temporal behavior of salmonids has been less studied (but see Scruton et al. 2005, Riley et al. 2009), and has mostly concentrated on establishing environmentally benign ramping rates to avoid stranding (Saltveit et al. 2001, Halleraker et al. 2003).

Stream salmonids are visual predators (Rader et al. 2007) feeding on drifting invertebrates (Kalleberg 1958). Their ability to detect and capture prey is highest during the day (Fraser and Metcalfe 1997, Elliott 2011, Watz et al. 2014), which can affect their space use and foraging behavior. At night, reduced visibility causes salmonids to decrease aggression (Cromwell and Kennedy 2011) and to reduce the distance between individuals (Valdimarsson and Metcalfe 2001, but see Larranaga and Steingrímsson 2015). Depending on water temperature, prey attack distance is typically shorter at night (Nicieza and Metcalfe 1997). Salmonids can mitigate reduced nighttime foraging efficiency by selecting slower waters where drifting food is easier to detect (Metcalfe et al. 1997, Polacek and James 2003, Banish et al. 2008), which in turn can affect their mobility while searching for and attacking prey (Grant and Noakes 1988, Tunney and Steingrímsson 2012). Fluctuations due to hydropeaking affect the temporal availability and distribution of optimal habitats, as well as food availability (Morrison and Smokorowski 2002, Dodrill et al. 2015). Such changes may have repercussions on the way salmonids distribute their foraging effort in time (diel and seasonal activity) and space (e.g. habitat use).

Habitat use of salmonids is highly size-dependent (Armstrong et al. 2003). Among juveniles, i.e. young-of-the-year (YOY) and parr, larger and older fish often use deeper and faster habitats (Mäki-Petäys et al. 1997 2004). This is in part the result of ontogenic changes in habitat preferences, as larger fish can sample a larger volume of water in deep and fast habitats, with relatively low swimming costs (Morantz et al. 1987, Nislow et al. 1999). Size-based spatial distributions are also due to competitive exclusion by larger dominant fish who occupy preferential positions e.g. near pool inlets and chase their smaller



conspecifics to suboptimal habitats (Hughes 1992, Nakano 1995a). Similarly, YOY fish and older juveniles are typically active at different times of the day. During their first summer, salmonids feed primarily during the day, perhaps at the cost of increased predation (Breau et al. 2007), but then become progressively nocturnal (Imre and Boisclair 2004, Breau et al. 2007) in agreement with the asset protection principle (Clark 1994). Within cohorts, larger fish may also be more nocturnal (Bradford and Higgins 2001, Cromwell and Kennedy 2011, but see Roy et al. 2013, Larranaga and Steingrímsson 2015). Contrasting diel activity patterns among individuals can result from temporal segregation in response to competition, e.g. with larger dominant fish being active at night and forcing smaller subordinates to be active during the day (Alanära et al. 2001, Larranaga and Steingrímsson 2015). Hence, different cohorts, or fish of different size can be affected differently by fluctuations in waterflow, through their potential to select specific habitats when active.

Whether or not hydropeaking affects the growth of stream-dwelling fish is debated (Puffer et al. 2015). Although altered flow regimes have generally negative consequences on fish communities (Anderson et al. 2006), individual species show a range of different responses (Murchie et al. 2008, Young et al. 2011). Studies have alternatively suggested that fish may grow slower (Weyers et al. 2003, Puffer et al. 2014), faster (Finch et al. 2015), or at similar rate (Flodmark et al. 2006, Korman and Campana 2009, Puffer et al. 2015) in altered flow. This discrepancy can be explained in part by the variety of species, their respective habitat preferences, and the magnitude of flow pulses used in these studies. In any case, hydropeaking may have minor influence on the growth of stream-dwelling fish if they relocate to more suitable areas following a change in waterflow, although such movements also affect growth (Puffer et al. 2015). However, the potential for such habitat selection can be limited, either because of competitive exclusion (Nakano 1995a, Nakano 1995b), or highly homogeneous environments in flow regulated streams (Beechie et al. 1994). Under such circumstances, fish may instead alter their temporal behavior to maintain growth, but this has not been investigated in details (but see Larranaga et al. unpubl. Data).

We conducted a 10 day experiment to study the effect of fluctuating waterflow on the diel activity, foraging mode (mobility and speed while searching for prey, foraging radius and prey attack rate),

and habitat selection of individually tagged juvenile Arctic charr *Salvelinus alpinus*. We used stream enclosures where fish were constrained to habitats where the waterflow was stable and intermediate, or fluctuated between high and low water level every other day. We included both YOY and age 1+ fish to address potential age-specific effects of fluctuations in waterflow on behavior. We also measured initial and final body size to study how waterflow fluctuations and behavior affected growth. We tested the predictions that under fluctuating waterflow, (1) fish will alter their activity patterns in response to waterflow, and exhibit greater activity at low waterflow. (2) Arctic charr will be more mobile and swim faster during periods of low waterflow. (3) Growth will be similar in stable and fluctuating environments. Finally, (4), more active individuals will grow faster, regardless of waterflow.

## 5.2 Materials and methods

### 5.2.1 Sampling

On 24 and 25 July 2014, we sampled 24 YOY and 60 1+ Arctic charr, respectively, via electrofishing (Smith-Root LR-24) in a tributary of the river Deildará in northern Iceland (N 65.849379, W 19.222297). Fish were anesthetized with phenoxyethanol, measured for fork length to the closest 0.1 mm (calipers) and body mass to the closest 0.01 g (PESOLA® PPS200) and tagged on an individual basis. On average ( $\pm$  standard deviation), YOY fish were 32.4 ( $\pm$  1.3) mm and 0.23 ( $\pm$  0.03) g. Fish of age 1+ were 59.5 ( $\pm$  5.9) mm and 1.91 ( $\pm$  0.68) g. Age was determined based on the size distribution of Arctic charr in the stream. Fish were tagged using different combinations visible implant elastomers in different colors (red, green, orange and yellow). Tags were injected in two specific positions of the dorsal fin (sensu Steingrímsson and Grant 2003), and spread up along the fin rays, which permitted identification of all individuals during overhead observations. Arctic charr were randomly assigned to one of six stream enclosures, and given 24 h to adjust to the experimental conditions before behavioral observations were initiated. The experiment was terminated on 5 August 2014 after fish were captured, and measured for final body length and body mass. Three of the YOY fish, in three separate enclosures, were not recaptured and either escaped or died during the course of the experiment, but all 1+ fish were successfully retrieved. No untagged fish was found at the end of the study and no

tag had faded to the point of impeding individual identifications during observations.

### **5.2.2 Experimental design**

Six stream enclosures (4 m long, 1 m wide, and 0.75 m high) were erected at a specific position where the study tributary separates into two channels. The bottom of each enclosure was covered with substrate from the study stream. Two enclosures were erected 10 m upstream the divide, side by side, and served as control where the waterflow showed natural and limited fluctuation. Two enclosures were erected in separate locations along the length of each channel. During the first two days of the study (control phase), we ensured that the waterflow was similar in all enclosures (ANOVA,  $p = 0.358$  for current velocity and  $p = 0.383$  for water depth). Enclosures were made of 5 mm nylon mesh, i.e. large enough for invertebrates to drift through, and small enough to ensure most fish remained within their enclosure. A string was tied across the top of each enclosure to deter avian predators, presumably without affecting the risk perceived by fish (Larranaga and Steingrímsson 2015). Each enclosure had four YOY and ten 1+ individuals, which is a high enough density to create competition for food and space in a 4 m<sup>2</sup> enclosure (Larranaga and Steingrímsson 2015, Fingerle et al. 2016).

On the third day of the experiment (waterflow manipulation phase), at 13:30, we used a barrier of cobbles, boulders, and black plastic tarp immediately upstream of the right channel to divert water from the right channel to the left channel (facing downstream) for two subsequent days. Hence, after this switch, two enclosures in one channel had deeper and faster habitats than the control enclosures, while the other two enclosures had shallower and slower habitats (Table 5.1). Then, the flow was switched to the right side at 13:30 for another two days, by moving the barrier upstream of the left channel. This was repeated a second time, so that each channel had had four (2 X 2) days of low flow and four (2 X 2) days of high flow.

### **5.2.3 Habitat availability**

The habitat within stream enclosures was manipulated so that water depth and current velocity in all treatments was expected to be within the range of habitats used by Arctic charr (Heggenes and Saltveit 2007,

Tunney and Steingrímsson 2012). Water depth and current velocity at 40% above the bottom of the water depth (sensu Davis and Barnuta 1989) were measured systematically at the beginning of the experiment. Water depth was measured at 100 x-y coordinates in each enclosure (at 20 cm intervals on each axis, starting 10 cm from the sides). Current velocity was measured at five points along four parallel transects separated by 1 m, starting 50 cm from the top with a Flo-Mate™ Model 2000CM (Marsh-McBirney Inc., Frederick, MD) current velocity meter.

*Table 5.1 Habitat availability in six stream enclosures during the experiment. Measurements were collected every other day at random locations in each enclosure. On the first day, habitats were similar across enclosures (control phase). On Day 3 and 7, the flow was directed to the left side for two days. On Day 5 and 9, it was directed to the right side. Values are given as mean (standard deviation).*

Enclosure	Water depth (cm)					Current velocity (cm/s)				
	Day 1	Day 3	Day 5	Day 7	Day 9	Day 1	Day 3	Day 5	Day 7	Day 9
Control	21.6 (2.6)	28.6 (3.3)	26.5 (3.1)	25.7 (2.8)	26.7 (3.1)	11.0 (2.5)	12.1 (2.7)	11.5 (2.2)	9.8 (1.9)	10.4 (1.7)
	27.3 (4.1)	27.2 (3.5)	23.6 (2.7)	26.8 (2.8)	26.1 (2.9)	11.7 (3.0)	11.5 (2.4)	11.3 (1.9)	11.1 (1.9)	10.6 (1.8)
Right channel	21.4 (2.6)	16.2 (2.8)	34.2 (2.5)	13.5 (1.7)	35.2 (2.8)	21.4 (6.2)	6.2 (1.9)	21.0 (3.5)	5.4 (1.3)	20.1 (2.9)
	24.3 (2.7)	14.5 (2.5)	35.9 (2.8)	13.5 (2.1)	34.7 (3.6)	17.4 (7.1)	6.0 (2.3)	22.2 (2.1)	5.1 (1.3)	22.7 (3.4)
Left channel	23.9 (4.4)	35.8 (3.9)	12.7 (2.8)	30.0 (2.0)	15.9 (2.5)	14.3 (4.1)	21.4 (4.1)	4.4 (1.9)	21.1 (3.6)	5.4 (2.1)
	22.5 (2.9)	33.7 (4.1)	12.7 (1.7)	28.7 (2.3)	14.2 (2.7)	12.3 (4.2)	19.7 (3.2)	4.1 (1.8)	19.9 (2.4)	5.3 (1.4)

During the control phase, the average depth was 23.5 ( $\pm$  3.9) cm and the average current velocity was 14.7 ( $\pm$  6.0) cm/s. After each switch of waterflow from one channel to the other, water depth and current velocity was measured at 24 random locations in each enclosure. In the low waterflow treatment, water depth was 14.2 ( $\pm$  2.7) cm, and current velocity was 5.2 ( $\pm$  1.9) cm/s. At high waterflow, water depth was 33.5 ( $\pm$  3.6) cm and current velocity was 21.1 ( $\pm$  3.3) cm/s. Two enclosures within the same treatment always had similar habitats ( $P > 0.05$  in all cases). Habitat availability within all three treatments of waterflow did not differ between the rounds of measurements (ANOVA,  $P > 0.1$ , for water depth and current velocity in all cases), indicating that the average discharge in the stream

remained stable (Table 5.1).

Water temperature was recorded automatically every hour to the closest 0.2 °C during the experiment by data loggers positioned at each enclosure (Onset® HOBO® UTBI-001 TidBiTv2). Light intensity was also measured every hour by data loggers positioned at the most upstream and downstream enclosures (UA-002-08 HOBO Pendant® Temp/Light, 8K). As there were only minor differences in water temperature and light intensity among enclosures (smaller than the accuracy of the data loggers), we used values from the most upstream data loggers. On average, water temperature was 6.7 ( $\pm$  1.0, range = 5.1 – 9.0) °C and light intensity was 19.7 ( $\pm$  18.3, range = 0.1 – 69.3) kilolux.

#### **5.2.4 Behavioral observations**

Observations started on 26 July 2014 (15:00) and finished on 4 August (12:00). Two persons observed fish in all enclosures every three hours (00:00, 03:00, etc.) during ten days, which yielded a total of 80 measurements of activity rates per enclosure. Bright summer nights in Iceland permitted visual observations and individual identification without the aid of artificial light. Observers alternated every day and hence distributed the observations equally throughout the study. Algae and debris were removed from all enclosures after a round of observations to ensure good waterflow. Enclosures were visited in a random order during each observation period, but the two enclosures in a single treatment were always visited consecutively. During each observation, we remained motionless in front of an enclosure for 5 min and then started recording activity for 10 min. We measured overall activity rates as the proportion of fish active in each enclosure during each scan. An individual was considered active when it was observed feeding actively on prey drifting in or at the surface of the water column, or on the bottom. Hence, inactive fish were either not seen during a scan, or in rare cases, remained motionless on the bottom without showing any sign of foraging effort (Larranaga and Steingrímsson 2015). Once a fish emerged, it was usually active for the rest of the 15 min observation. We also calculated individual activity rates, as the proportion of scans during which a fish was active.

We collected data on habitat use and foraging mode for all active individuals. First, at the end of each scan, we recorded the x-y

coordinates of all active fish to the nearest 5 mm on each axis, with the aid of thin metal bars (8 mm) placed at the bottom of each enclosure (one axis parallel and four axes perpendicular to the flow). The coordinates reflected the location where a focal fish concentrated the majority of its feeding activity (Larranaga and Steingrímsson 2015). At the end of an observation, we measured current velocity and water depth at each of these locations. During each observation, all active fish were consecutively and randomly selected to record their foraging mode during 3 min (*sensu* McLaughlin et al. 1992). When more than three individuals were active simultaneously in an enclosure, observations of foraging mode, but not activity, were extended beyond 15 min. Time was kept with a digital timer that emitted a pulse every 5 s. Each individual observation alternated between one to three consecutive 5 s intervals of monitoring and a 5 s interval where these data were recorded. Each 5 s interval was classified as either pursuit or search. Pursuit intervals correspond to a situation where a focal individual made at least one feeding attempt, whereas search intervals correspond to periods where fish searched for prey from a stationary position or moved without attacking prey (McLaughlin et al. 1992, Tunney and Steingrímsson 2012). Multiple feeding attempts in a single 5 s interval were rare throughout the study and were not distinguished from single attempts. Similarly, the rare 5 s intervals where aggression was detected were excluded from the analyses ( $N = 55$  and 0.58 % of the 5 s intervals). We quantified the mobility during search intervals in number of body lengths. Search mobility corresponds to the proportion of search intervals during which an individual moved one or more body lengths (McLaughlin et al. 1992). Search speed corresponds to the number of body lengths moved during a 5 s search interval (McLaughlin et al. 1992). During pursuit intervals, we measured the foraging radius (in number of body lengths) as the distance between the locations where an attack was initiated and where the prey was intercepted. We also measured prey attack rate as the proportion of intervals when a focal fish attacked at least one prey (Larranaga and Steingrímsson 2015).

### **5.2.5 Data analysis**

The distribution of activity rates was heavily right-skewed because there were many observations with no fish active, so we used a zero-inflation model to assess the effect of waterflow treatment, time of day (day from 06:00 to 18:00, night from 21:00 to 03:00) and their interaction on overall activity rates. This model was a mixture between

a binomial (zero vs. positive counts, logit link) and a Poisson distribution (positive counts, log link). The model was built using the function *zeroinfl* from the *pscl* package in R (Jackman 2015). We used a similar model to test if there was a difference in activity rates between the first and second switch of waterflow, and between the first and second day after the switch in the four enclosures that had fluctuating waterflow. We built mixed linear models using the same explanatory variables, testing the effect on search mobility, search speed, foraging radius, prey attack rate, and habitat use. We used a separate generalized linear model to test the effect of body mass, waterflow and their interaction on individual activity rates, considering a Poisson distribution. The four foraging mode variables were normally distributed. Enclosures, and individuals when necessary, were always considered as random factors. For every model, we tested all the possible combinations of variables and interactions using the function *dredge* from the *MuMin* package in R (Barton 2009), and selected the best model based on its AIC. The difference in AIC values between the best and second best model was always higher than 2, suggesting a single best model in each dataset (Burnham and Anderson 2002). Hence models were of the form:

Model 1: Activity or Foraging mode (zero inflated model, or GLMM) ~ Waterflow treatment \* Time of day + random factors

Model 2: Activity or Foraging mode at low waterflow (zero inflated model, or GLMM) ~ Switch + Number of days since switch + random factors

Model 3: Individual activity rate (GLMM) ~ Body mass \* Treatment + random factors

For each individual, we calculated the circular mean and standard deviation as indexes of the mean time of activity and the dispersion of activity, respectively (Larranaga and Steingrímsson 2015). The mean time of activity indicates the position of an individual's span of activity around the clock, and the dispersion is a descriptor of its tendency to spread its activity over long or short periods. We used a circular ANOVA (Batschelet 1981) to compare the distribution of mean times of activity between treatments. We used a GLMM to assess the effect of body mass, waterflow and their interaction on the dispersion of activity.

We calculated standardized mass-specific growth rates (*sensu* Ostrovsky 1995), which allow for adjustment of the scaling of

metabolism with body size. We used an allometric growth rate exponent value of 0.31 (based on Quinn et al. 2004). First we tested if YOY and age 1+ fish grew differently in the two treatments (control and fluctuating waterflow). Then, we tested the effect of individual activity rates, waterflow treatment, and their interaction on growth rates. Individual activity rates were  $\log_{10}$  transformed to fulfill normality.

## 5.3 Results

During the control phase, the mean overall activity rate (i.e. the average percentage of individuals active at the same time) of 1+ individuals was  $9.4 \pm 12.3$  % (Figure 5.1), and was similar among enclosures except for one of the two upstream control enclosures where fish were significantly more active (Wilcoxon rank sum test,  $P < 0.001$  in all cases,  $P > 0.05$  for all other comparisons between enclosures). During the waterflow manipulation phase, the mean activity rate of 1+ fish was  $10.9 \pm 11.1$  % in the control enclosures with stable intermediate waterflow (IWF) and the difference among enclosures persisted (T test,  $P < 0.001$ , Table 5.1). Activity rates were  $13.8 \pm 14.5$  % at low waterflow (LWF), and were similar among enclosures (T test,  $P = 0.998$ ). However, at high waterflow (HWF), only one fish was seen active, and only once (Figure 5.1). Hence, there were significant differences in overall activity rates of 1+ individuals across treatments of waterflow (GLMM,  $P < 0.001$ , and  $P < 0.001$  for all three pairwise comparisons, Table 5.2, Figure 5.1) during the waterflow manipulation phase. Activity rates remained similar in the upstream control enclosures throughout the study (ANOVA,  $P = 0.127$ , Figure 5.1 and 5.2, Table 5.2). More fish were active during the first day after a switch to LWF (Poisson component) than during the second day, but the probability of finding at least one fish active was similar (Binomial component, Figure 5.1 and 5.2, Table 5.2). This was due mostly to a sudden increase in activity in the first 3-4 h following the switch to LWF (Figure 5.1). Overall, activity increased with body size ( $P = 0.016$ ), and this effect was stronger at IWF than at LWF (body mass\*treatment effect,  $P = 0.042$ ). YOY fish were never observed active during the study, regardless of treatment.

Because of the absence of data at HWF, we only measured the mean time of activity and dispersion of activity at IWF and LWF. During the manipulation phase, and as expected, 1+ fish were



significantly more active at night than during the day, both at IWF and LWF (Table 5.2, Figure 5.3). Overall the mean time of activity was 22:10 ( $\pm$  6:27). The mean time of activity was 21:20 ( $\pm$  5:51) at IWF and 23:27 ( $\pm$  6:51) at LWF and the difference was significant (circular ANOVA,  $P < 0.001$ ). The dispersion of activity was 4:32 ( $\pm$  2:09) overall, 5:10 ( $\pm$  1:57) at IWF, and 4:13 ( $\pm$  2:12) at LWF, and was similar across waterflow conditions (Wilcoxon rank sum test,  $P = 0.136$ ). Hence, over the course of the study, fish were active slightly later when the flow was reduced, but did not extend their activity over longer periods. The dispersion of activity was not affected by body mass, neither overall ( $P = 0.659$ ), nor in specific treatments ( $P = 0.552$  for the interaction between body mass and treatment).

*Table 5.2 Summary of mixed linear models and zero-inflated models fitted to the components of Arctic charr's behavior in stream enclosures. Individual activity rates were used for the model including body mass and body mass \* Waterflow treatment, assuming a Poisson distribution. The default values are given between parentheses. Enclosures, and when necessary individuals were considered as random factors. Coefficients are given for all variables with a significant effect as F-values for overall and individual activity rates, and t-values for all other variables. Significant effects are represented with  $\cdot P < 0.1$ , \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .*

Response variable	Waterflow	Time of day (Day)	Waterflow * Time of day	Switch (First)	Day (First)	Body mass	Waterflow * Body mass
Activity rate (Binomial)	-	-	-	-	-	12.17	4.35
Activity rate (Poisson)	109.7 ***	46.89 ***	8.25 ***	-	17.57 ***	***	*
Search mobility	5.99 ***	-	-2.12 *	-7.15 ***	-	-	-
Foraging Speed	3.78 ***	-3.34 ***	-	-	-	-	-
Foraging radius	2.51 *	-	-	1.66.	-	-	-
Prey attack rate	-	-	-	-	4.79 ***	-	-
Water depth	-20.03 ***	-	-	-	-	-	-
Current velocity	-12.27 ***	-	-	1.66	-2.67 **	-	-

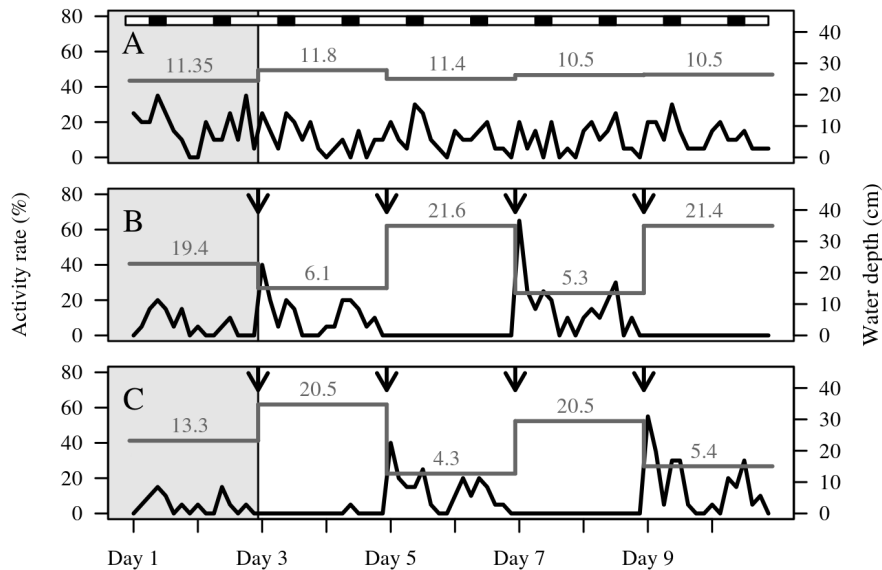


Figure 5.1 Overall activity rates (black lines) of age 1+ Arctic charr measured every three hours under contrasting waterflow regimes (A: upstream control enclosures with stable, intermediate waterflow; B and C: two channels where the flow was diverted alternatively to one channel or the other). During the control phase (two days, grey areas), waterflow was similar in all three sections. On day 3 and 7, the flow was directed towards the left channel (C) for two days each time. On day 5 and 9, the flow was directed towards the right channel (B). Waterflow was switched (arrows) at 13:30 on the respective day. Grey lines indicate the average water depth in a particular section throughout the experiment. Numbers above the grey lines indicate the average current velocity (cm/s). Black and white rectangles in the top graph represent night (from 21:00 to 03:00) and day (from 06:00 to 18:00), respectively.

Because only one fish was detected active at high water flow, we only measured foraging mode at IWF and LWF. As predicted, fish were more mobile during prey search at LWF ( $0.68 \pm 0.21$ ), than IWF ( $0.54 \pm 0.19$ ), but exhibited similar mobility during the day and the night, regardless of treatment (Table 5.2, Figure 5.3). Fish were also less mobile after the second switch to LWF (Table 5.2, Figure 5.2), and swam faster at LWF ( $1.59 \pm 0.29$  body lengths/5s) than at IWF ( $1.42 \pm 0.36$  body lengths/5s). They also swam faster during the day regardless of the waterflow treatment (Table 5.2, Figure 5.3). Fish attacked prey at longer distances at LWF ( $1.30 \pm 0.32$  body lengths) than at IWF

( $1.18 \pm 0.28$  body lengths), regardless of the time of day (Table 5.2, Figure 5.3). Fish attacked prey at similar rate under LWF ( $0.28 \pm 0.06$ ) and IWF ( $0.21 \pm 0.06$ ) and during the day and the night (Table 2). Arctic charr also attacked prey at a faster rate on the second day after a switch to LWF (Table 5.2, Figure 5.2). Body mass was never a significant predictor of foraging mode, regardless of waterflow (Table 5.2).

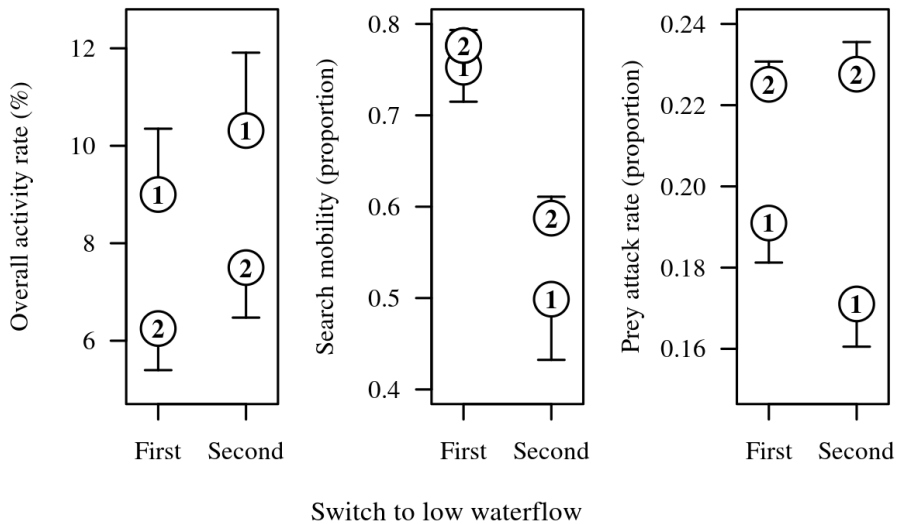


Figure 5.2 Activity and foraging mode (mean  $\pm$  standard error) of age 1+ Arctic charr during the first (symbol 1) and the second day (symbol 2) after the first and second switch to low waterflow.

Habitat availability and habitat use were similar, both at LWF ( $14.1 \pm 2.8$  cm vs  $14.2 \pm 2.7$  cm, T test,  $P = 0.777$ ), and IWF ( $26.3 \pm 4.1$  vs  $24.2 \pm 4.0$ , T test,  $P = 0.080$ ). At LWF and IWF, fish used respectively slightly faster ( $5.9 \pm 2.0$  vs  $5.2 \pm 1.9$  cm/s, T test,  $P = 0.001$ ) and slower ( $10.5 \pm 3.0$  vs  $12.3 \pm 4.5$  cm/s, T test,  $P < 0.001$ ) habitats than the average current velocity in their respective enclosures. Fish were found at similar water depths at LWF after the two switches and the two days following the switch to LWF. Fish used habitats with similar current velocity after the first and second switch to LWF ( $P = 0.09$ ), but used faster habitats the second day after the switch ( $P = 0.004$ , Table 5.2).

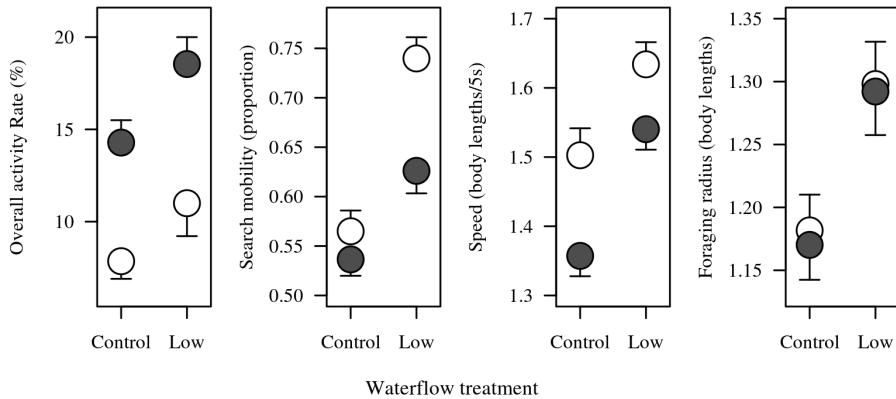


Figure 5.3 Activity and foraging mode (mean ± standard error) of age 1+ Arctic charr during the waterflow manipulation phase at stable and intermediate waterflow (control) and low waterflow, during the day (06:00 to 18:00, white symbols) and the night (21:00 to 03:00, grey symbols).

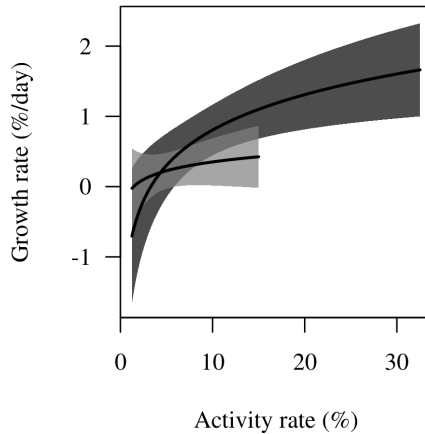


Figure 5.4 Predicted relationship between growth rates of 60 juvenile (1+) Arctic charr and their activity in stable and intermediate (dark grey) and artificially fluctuating waterflow (light grey). Grey areas represent 90% confidence intervals.

The mean growth rate of age 1+ fish was  $0.41 \pm 1.03$  %/day and control fish of age 1+ grew at similar rate ( $0.75 \pm 1.11$  %/day) as fish in fluctuating waterflow ( $0.23 \pm 0.96$ , T test,  $P = 0.085$ ). More active 1+ fish grew faster overall (GLMM,  $P = 0.004$ ), and the interaction between activity rate and waterflow treatment was marginally significant ( $P = 0.060$ ). Hence the relationship between individual activity and growth was significant at IWF but not in fluctuating

waterflow (Figure 5.4). Growth rate of YOY fish was  $2.12 \pm 0.84$  %/day. Hence, in spite of no recorded activity, YOY grew faster than 1+ individuals (T test,  $P < 0.001$ ). They also grew at similar rate in stable ( $1.97 \pm 0.61$  %/day) and fluctuating waterflow ( $2.22 \pm 0.96$  %/day, T test,  $P = 0.483$ ).

## 5.4 Discussion

In this experiment, fluctuations in waterflow affected several components of Arctic charr behavior. In stable waterflow, activity rates of 1+ individuals were comparable to previous studies on Arctic charr in cold streams (Larranaga and Steingrímsson 2015, Fingerle et al. 2016). In fluctuating waterflow, however, 1+ fish increased their activity drastically during low flow periods, but ceased activity almost completely during high flow episodes. In lotic environments, Arctic charr typically use and presumably prefer slow habitats (Heggenes and Saltveit 2007, Tunney and Steingrímsson 2012, but see Larranaga et al. unpubl. Data), so it is not surprising that they restricted their activity to periods of low waterflow. The peaks of activity following switches to low waterflow conditions could also be affected by a combination of factors. Fish were likely hungry after two days without activity at high waterflow (see also Vehanen 2003), although we observed the same phenomenon after a switch from control conditions. Also, the manipulation of the flow between the two channels may also have caused a brief increase in food availability, although that effect should have been similar between the channels. In addition, we observed increased activity up to several hours after the switch, whereas salmonids rapidly decrease their demands in food after it was no longer available (Bolliet et al. 2001).

Curiously, YOY Arctic charr were never detected active throughout this experiment, although their activity rates were similar to parr in previous studies (Imre and Boisclair 2004, Breau et al. 2007). This could alternatively suggest that YOY only need to forage for very short periods to maintain growth (e.g. smaller 1+ individuals were also less active), or that they may require more than 15 min (the length of our observations) to resume activity after being disturbed by an observer. In any case, our results call for further investigation on the activity of YOY in relatively cold streams and the appropriate methodology to quantify it.

Age 1+ fish were mostly nocturnal, which is consistent with previous studies on salmonids of that age class (Imre and Boisclair 2004, Breau et al. 2007), especially in cold conditions (Fraser et al. 1993, Fraser et al. 1995). Studies have suggested that fish in habitats of contrasting current velocity may distribute their activity differently over the 24 h cycle (Bradford and Higgins 2001, Imre and Boisclair 2004, Larranaga et al. in prep). For instance, slow habitats incur higher predation risk by avian and terrestrial predators during the day, which should lead fish to be more nocturnal (Metcalf et al. 1999). Similarly, fish in fast habitats may not detect prey as efficiently at night and should be more diurnal (Metcalf et al. 1997). In our study, fish were active slightly later at night (mean time of activity) under low flow conditions (21:20) than under stable intermediate flow (23:27). This is consistent with Riley et al. (2009) who found higher movement rates (another measure of activity) during the night under low flow conditions, and during daytime in higher flow. Alternatively, Scruton et al. (2005) found no such differences, but their data were collected in wintertime, when foraging activity is typically lower (Valdimarsson et al. 1997).

Fluctuating waterflow also affected the foraging mode of Arctic charr. As expected, fish were more mobile, swam faster during prey search and attacked prey at longer distances under low flow conditions than under stable intermediate waterflow (Grant and Noakes 1988, Tunney and Steingrímsson 2012). Slow-running waters typically result in lower food availability (Nislow et al. 1998), and reduced energetic costs (Hill and Grossman 1993), both of which should favor mobility (Grant and Noakes 1987, Tunney and Steingrímsson 2012), e.g. via a switch from drift-feeding to benthic feeding (Fausch et al. 1997). Arctic charr attacked prey at similar rates in low and intermediate waterflow conditions. In a previous study, Grant and Noakes (1988) reported that brook charr *Salvelinus fontinalis* were more mobile but also fed at slower rate in slow-running habitats. Although reaction distance typically increases with light intensity in salmonids (Metcalf et al. 1997, Mazur and Beauchamp 2003), our study fish did not attack prey at longer range during the day, perhaps because foraging radii were already relatively high (e.g. 2.81 fold increase compared to Larranaga and Steingrímsson 2015).

Fish were less mobile after the second switch to low waterflow conditions, which may reflect the fact that they also used slightly faster habitats, where the costs of swimming are higher. They also attacked

prey at faster rate the second day after a switch to low waterflow. This could result from lower activity rates on the same day, as fewer individuals competed for the same amount of prey (Amundsen et al. 2007). Our results are based on fluctuations in waterflow occurring every other day and suggest that salmonids may require time to adjust their behavior (activity, mobility and prey attack rate). For instance, Keenleyside and Yamamoto (1962) concluded that the establishment of defended territories by Atlantic salmon *Salmo salar* took a minimum of 12 hours after fish were moved to a new environment (in their case, an aquarium). Fluctuating waterflow can thus create temporal variation in behavior, both immediately after a decrease, and on longer scales. Although the duration of low and high flow periods varies considerably across studies (21 days of low flow in Riley et al. 2009, 12 h periods of low and high flow in Scruton et al. 2005), few if any have monitored the changes in behavior over short temporal scales after a fast change of habitat availability. Larranaga et al. (submitted) introduced juvenile Arctic in enclosures with contrasting stream habitats, but only recorded behavior after the first day. Similarly, Kemp et al. (2003) monitored how reversing waterflow affected habitat selection by juvenile Atlantic salmon, but only after 2-3 days. If the frequency of hydropeaking events exceeds the time needed for salmonids to adjust their behavior, notwithstanding the time needed to track new suitable habitats, this could be an additional source of perturbation affecting individual fitness (Murchie et al. 2008).

Although we used enclosures with a limited range of habitats, we found that fish selected slightly slower and faster habitats within their enclosures in intermediate and slow water current conditions, respectively. This suggests that the preferred current velocity of Arctic charr in our study system (with regard to body size, water temperature etc.) is probably between these two values of habitat use (5.9 and 10.5 cm/s, see also Heggenes and Saltveit 2007, Tunney and Steingrímsson 2012, but see Larranaga et al. unpubl. Data). Fish also selected relatively deep habitats in the control, as expected of Arctic charr (Tunney and Steingrímsson 2012), but not under low waterflow where the average water depth was even lower. This could be due to e.g. faster habitats (which were used more) being shallower, or deep habitats being too limited to sustain the higher number of active individuals under low flow conditions.

In this study, fish grew at similar rate in stable and fluctuating waterflow conditions, although fish of age 1+ grew marginally faster

in stable flow conditions. These results are in general accordance with the literature (Flodmark et al. 2004, Korman and Campana 2009, Puffer et al. 2015, Rocaspana et al. 2016). However, we monitored fish only over 10 days, and significant but moderate effects of hydropeaking on growth have been detected on longer periods (Puffer et al. 2014). Altogether, these studies and our results suggest that salmonids may adjust their behavior to maintain growth, in part by altering both their rate and timing of activity (Orpwood et al. 2006, Larranaga and Steingrímsson 2015, Fingerle et al. 2016). Importantly, individuals in fluctuating waterflow were less active overall, which suggests that other factors may explain similar growth rates among treatments of waterflow in our study. Growth of stream-dwelling fish results from complex interactions between a series of factors. For instance, under low flow conditions, Arctic charr were more active, swam more often, faster and over longer distances but the energetic costs of such activity were probably lower (Boisclair and Tang 1993). Similarly, Arctic charr increased activity at night at low waterflow when food is generally more abundant (Young et al. 1997, Giroux et al. 2000), but their ability to detect and capture prey decreases (Elliott 2011). Increased activity at low waterflow may also affect other components of fitness like mortality, through higher exposure to predators. More active fish grew faster, which is consistent with previous studies (Martin-Smith and Armstrong 2002, Larranaga and Steingrímsson 2015). However, this effect was found only at relatively stable (i.e. natural fluctuations) waterflow, indicating that rapidly and massively fluctuating environments can affect the net benefits of increased activity. For instance, the economic defendability of territories increases with spatial and temporal predictability, so rapidly changing waterflow may mask dominance hierarchies and growth differences (Grant 1993).

In conclusion, we showed that rapidly fluctuating waterflow can have a drastic effect on the activity patterns and foraging mode of juvenile salmonids. In this example, Arctic charr in fluctuating waterflow were only active during low flow periods, adjusted their foraging mode (i.e. became more mobile) in response to slow water currents, and ceased activity almost completely at high flow. Importantly, there is strong variation in habitat selection and diel activity patterns among salmonids (Reeb 2002, Armstrong et al. 2003), and among cohorts (Bradford and Higgins 2001, Armstrong et al. 2003). Hence, similar experiments with different fish could produce opposite results, e.g. if they prefer faster currents (e.g. Atlantic



salmon), or are more diurnal (e.g. YOY fish). Our results agree with previous studies showing that fluctuating waterflow has limited effect on fish growth (Puffer et al. 2015), at least on small temporal scales, but can perhaps affect mortality, e.g. through higher exposure to predators during periods of activity (Larranaga and Steingrímsson 2015). Finally, our study demonstrates that behavioral adjustments are key for stream fish populations living in rapidly changing and unpredictable environments like regulated rivers with hydropeaking.

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# **6 Density-dependent diel activity in stream-dwelling Arctic charr *Salvelinus alpinus***

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## Abstract

Intraspecific competition plays a significant role in shaping how animals use and share habitats in space and time. However, the way individuals may modify their diel activity in response to increased competition has received limited attention. We used juvenile (age 1+) Arctic charr *Salvelinus alpinus* to test the prediction that individuals at high population density are more active and distribute their foraging activity over a greater portion of the 24 h cycle than individuals at low population density. Individually-tagged fish were stocked in semi-natural stream enclosures at low (2 fish/m<sup>2</sup>) and high (6 fish/m<sup>2</sup>) density. During each of two 2-week experimental rounds, activity of all fish within each enclosure was recorded every three hours over seven 24 h cycles. At high density, fish were more active and distributed their activity over a greater portion of the 24 h cycle, with increased activity particularly at crepuscular times. Fluctuations in ecological conditions (e.g. water temperature and light intensity) also affected activity. Fish at high density grew as fast as fish at low density. This study demonstrates that individuals exhibit a degree of behavioral flexibility in their response to changes in ecological conditions and suggests that intraspecific competition can cause

animals to modify temporal aspects of their activity to gain access to resources and maintain growth.

**Keywords:** activity rate, resource partitioning, rivers, salmonids, temporal segregation

## 6.1 Introduction

Animals share and compete for resources in both space and time and frequently adopt strategies that reduce conflict among potential competitors (Schoener 1974, Chesson 2000). Coexistence of ecologically similar species is facilitated by e.g. spatial segregation through habitat selection (Rosenzweig 1987, Kneitel and Chase 2004) and temporal segregation through timing of activity (Kronfeld-Schor and Dayan 2003). Animals also compete with conspecifics for access to resources such as food (e.g. Milinski 1982, Lewis et al. 2001), shelters (e.g. Davey et al. 2009), and mates (West-Eberhard 1983, Weir et al. 2011). Spatial responses of animals to intraspecific competition are commonly examined e.g. in the context of territoriality (Hixon 1980, Adams 2001, López-Sepulcre and Kokko 2005) and population distribution (Fretwell and Lucas Jr. 1970, Rodenhouse et al. 1997), but how individuals may modify their diel activity in response to increased competition has received less attention (Guénard et al. 2012).

Diel activity – the allocation of activity and rest within the 24 h cycle (Reebs 2002, Kronfeld-Schor and Dayan 2003) – provides insight into how animals exploit and share habitats and resources in time. Diel activity patterns are influenced by a range of ecological factors such as predation risk (Lima and Bednekoff 1999), prey availability (Brown, Kotler, and Bouskila 2001), temperature (Avenant and Nel 1998) and photoperiod (Kolowski et al. 2007). Importantly, animals may also modify their diel activity in response to competition by adjusting their overall rate of activity, the timing of their activity, or both. To date, studies of how interspecific competition may affect activity patterns primarily focus on temporal partitioning of habitats and resources (e.g. Albrecht and Gotelli 2001, Harrington et al. 2009), whereas at the intraspecific level, more emphasis is placed on whether animals modify their overall activity rates in the presence of conspecifics (e.g. Coulombe et al. 2008, Vera et al. 2011, Guénard et al. 2012).

Intraspecific competition is invariably linked to population density, competition increases as more individuals compete for the same resource (Amundsen et al. 2007), often resulting in increased emigration and mortality, and reduced growth (Grant and Kramer 1990). As intraspecific competition increases, it may be expected that activity rates will increase in response to e.g. reduced food intake due

to reduced availability and quality (Amundsen et al. 2007, Guénard et al. 2012), increased interference (Blanchet et al. 2008), reduced growth efficiency (Guénard et al. 2012), or the use of marginal habitats (Mobæk et al. 2012). Alternatively, it has also been suggested that in certain cases animals may reduce activity to conserve energy if increased competition causes food to be limited or of poor quality (Borkowski 2000, but see Mobæk et al. 2012). To date, several studies on activity patterns of diverse taxa such as ruminants (Mobæk et al. 2012), land snails (Cameron and Carter 1979), fish (Vera et al. 2011, Marchand and Boisclair 1998) and insects (Bailey 1981, Schou et al. 2013), have yielded equivocal results on this topic. Other studies of activity patterns have increased intraspecific competition by varying resource abundance (Howerton and Mench 2014) or energetic requirements (Alanära et al. 2001). However, observations conducted throughout the day/night cycle in relatively natural conditions are rare. Such an approach is necessary for revealing fine-scale shifts in the timing of activity that may occur under conditions of increased competition, and to understand how other ecological variables (e.g. water temperature) affect activity.

Stream salmonids are ideal for studying fine-scale changes in diel activity because of their highly variable activity patterns, and because they typically compete for food and space via territoriality and dominance hierarchies (Grant and Kramer 1990, Nakano 1995, Blanchet et al. 2008). Diel activity differs among species (Reebs 2002), populations (Valdimarsson et al. 2000), cohorts (Bradford and Higgins 2001), and individuals (Breau et al. 2007). By monitoring individual fish over an extended time, which is rarely done in the wild (but see Nakano 1995, Breau et al. 2007, Roy et al. 2013), activity and other behavior can be linked to individual growth rates, which ultimately affect individual survival and fitness (Smith and Griffith 1994). Many studies suggest competition as the primary explanation for the inverse relationship often reported between individual growth rates and density in juvenile salmonids (e.g. Jenkins et al. 1999, Imre et al. 2005), although such relationships are not always detected (e.g. Kaspersson et al. 2013). When competition increases through e.g. increased population density, temporal partitioning of resources may be a viable strategy for maintaining growth (Kronfeld-Schor and Dayan 2003).

Juvenile (age 1+) Arctic charr *Salvelinus alpinus* were used to evaluate if and how individuals modify the rate and timing of activity

in response to increased population density, and if population density affects individual growth rates. Arctic charr exhibits flexibility in activity patterns and social behavior (Valdimarsson et al. 2000, Gunnarsson and Steingrímsson 2011), and has the northernmost distribution of any freshwater fish (Klemetsen et al. 2003). We tested the prediction that at high population density, fish increase their activity rate and spend more time foraging, e.g. to counter increased interference and/or reduced food availability. Activity rates of age 1+ fish should be highest at night when predation risk is lower (sensu Imre and Boisclair 2004, Breau et al. 2007). However, because the cost of increased competition may outweigh the benefits of nocturnal foraging, fish at high density should distribute their activity over a greater portion of the 24 h cycle than at low density. Concurrently, we explored if and how activity is related to ecological conditions (e.g. fluctuations in water temperature, light intensity, and water depth). Finally, we expected that growth rates of fish at high density would be less than or similar to those of fish at low density, depending on the extent to which individuals increase their activity to compensate for increased competition (Guénard et al. 2012, Blanchet et al. 2008).

## **6.2 Materials and methods**

### **6.2.1 Experimental design**

A field experiment was conducted in summer 2013 in a small side channel of Deildará, a run-off river in northern Iceland (65°50'54 N, 19°12'55 W). For more information on this system, see (Gunnarsson and Steingrímsson 2011) and (Tunney and Steingrímsson 2012). The experiment was repeated in time in two consecutive rounds, lasting from 3 to 17 July (15 days) and 20 July to 1 August (13 days). Four nylon mesh enclosures, suitable for behavioral observations (Lindeman et al. 2014), were planted in the stream in pairs, with approximately 70 m between the upstream and downstream pairs and 20 cm between adjacent enclosures. The enclosures (4 m long, 1 m wide, 1 m high) had a stretched mesh size of 5 mm, large enough not to significantly reduce the abundance of invertebrate drift (Keeley and Grant 1997, Zimmerman and Vondracek 2006), but small enough to prevent juvenile fish from escaping. String was stretched across the top of each enclosure to deter potential avian predators, presumably without affecting the risk perceived by fish. Within each enclosure, natural silt, sand, and gravel substrate (diameter < 64 mm) was

overlaid with cobbles (diameter = 64–250 mm) collected from the river bed. The substrate provided ample shelters for the study fish. To facilitate habitat mapping, a coordinate grid made from 1 m metal poles (width = 8 mm) was placed on the streambed within each enclosure (Gunnarsson and Steingrímsson 2011). Bars were marked with tape at every 10 cm and positioned parallel and perpendicular to the enclosure length. Debris was removed from the sides of the enclosures as necessary.

Each pair of enclosures consisted of one enclosure stocked with 8 fish (2 fish/m<sup>2</sup>; low density) and another with 24 fish (6 fish/m<sup>2</sup>; high density). Pairing enclosures and alternating low versus high density treatment enclosures between rounds ensured that other ecological variables were almost identical between treatments (see below). The densities used were close to the average (1.50 fish/m<sup>2</sup>) and slightly above the maximum density (4.14 fish/m<sup>2</sup>) observed at a local scale for juvenile Arctic charr in three Icelandic streams (Gunnarsson and Steingrímsson 2011). At these densities, it is expected that competition should play a role in population regulation (Grant and Kramer 1990).

### **6.2.2 Capture and tagging of study fish**

A total of 128 wild 1+ Arctic charr (mean fork length  $\pm$  SD: 60.0  $\pm$  7.6 mm, range = 42.2–80.0; mean mass  $\pm$  SD: 2.12  $\pm$  0.93 g, range = 0.40–4.96) were electrofished in Deildará and its tributaries before each experimental round (LR-24 electrofisher, Smith-Root, Inc., Vancouver, Wash., USA). Upon capture, fish were anaesthetised with phenoxyethanol and weighed to the nearest 0.01 g (PESOLA PPS200, CH-6340 Baar, Switzerland). Fork length was measured with calipers to the nearest 0.1 mm. All 8 fish in each low density enclosure and 9–10 fish in each high density enclosure were uniquely tagged with small subcutaneous injections of green, orange, red, or yellow visible implant elastomers (Northwest Marine Technology, Inc., Shaw Island, Wash., USA) in two positions along the dorsal fin (sensu Steingrímsson and Grant 2003). Tags spread vertically along the fin rays, were highly conspicuous, and remained visible throughout the experiment. Standardized mass-specific growth rate ( $\Omega$ ; Ostrovsky 1995) was calculated for tagged individuals as  $\Omega = ((M_{\text{Final}b} - M_{\text{Initial}b}) / (b \cdot t)) \cdot 100$ , where M is mass (grams); b is the allometric growth rate exponent, which adjusts for the scaling of metabolism with body size (see Sigourney et al. 2008); and t is the duration of the experimental round in days. The exponent b has not been estimated for



Arctic charr, but has been estimated at 0.308 and 0.31 for brown trout (Elliott 1975) and Atlantic salmon (Elliott and Hurley 1997), respectively, suggesting that  $b = 0.31$  may be appropriate for salmonids generally (Quinn et al. 2004).

Fish were randomly distributed among the enclosures and allowed to habituate for 24 h before observations were made. A new group of fish was captured for the second round, following the procedure described above. After each round, fish in the enclosures were recaptured, measured for mass and length, and released in the area of initial collection. All fish except one untagged fish (high density) were recaptured alive, and all tagged fish were easily identified.

### **6.2.3 Behavioral observations**

Each enclosure was visited eight times per day (at 00:00, 03:00, etc.) during seven 24 h cycles, yielding a total of 56 scans per enclosure during each round. Enclosures were visited in a random order at each time of day by one of three observers, who conducted 71%, 22%, and 7% of the scans, respectively. Any potential observer bias would have negligible effect on the main effect of density, because the effort of each observer was distributed equally between the two density treatments. Before scanning an enclosure, an observer stood motionless on the streambank for 10 minutes to ensure fish resumed normal behavior. The observer then recorded the number of fish and the identity of each tagged fish active within the enclosure. Each scan lasted  $< 15$  s and was a “snapshot” of activity at a particular time. Fish were considered active if they searched for and/or attacked prey, either by holding a position against the current or actively swimming. Fish that were hiding in the substrate were considered inactive. Occasionally, fish rested completely motionless on the substrate (i.e. with no movement of the tail or pectoral fins), typically not facing the water current. These fish were never observed to forage from this position and were considered inactive at that time.

Bright summer nights in Iceland usually permit observations without the aid of artificial light. However, after a fish was located, a flashlight with a blue filter was occasionally used on cloudy nights to briefly enhance tags to ensure accurate identification. Artificial light rarely affected the focal fish, and any such disturbance occurred after a fish was determined to be active or not.

## 6.2.4 Habitat measurements

Fluctuations in environmental conditions were monitored throughout the experiment (Table 6.1). Water temperature was recorded every hour by data loggers positioned at each pair of enclosures (Onset UTBI-001 TidbiT v2, Onset Computer Corp., Mass., USA). Light intensity was recorded hourly by a data logger positioned above the water surface at the upstream enclosure pair (Onset HOBO Pendant Temperature/Light 8K UA-002-08). Water level, an index of fluctuations in water depth, was measured to the nearest mm with a meter stick at a fixed location immediately upstream of each enclosure pair after each set of scans (i.e. at 3 h intervals).

Water depth and current velocity were measured inside each enclosure near the beginning, middle, and end of each sampling round (Table 6.1). Water depth was measured at five points along 21 parallel transects perpendicular to the direction of stream flow (i.e. every 20 cm along both the x- and y-axis of the coordinate grid). Current velocity at 40% water depth (from the substrate, sensu Davis and Barmuta 1989) was measured at four points along seven parallel transects perpendicular to stream flow with an electromagnetic flow meter (Flo-Mate Model 2000, Marsh-McBirney Inc., Frederick, Maryland, USA). Dominant substrate particle size was quantified using a modified Wentworth scale (Degraaf and Bain 1986) for sixty-four 25 cm<sup>2</sup> squares in each enclosure.

Food abundance was estimated by collecting invertebrate drift four times in each enclosure (00:00, 06:00, 12:00, 18:00) throughout four 24 h cycles. Samples were taken 5–6 days into (8 and 24 July) and 3–4 days before the end of (14–15 and 30–31 July) each experimental round for a total of 64 samples. A 250 µm drift net (net opening = 25 x 40 cm; net length = 100 cm) was placed in the downstream half of each enclosure for 10 minutes. Current velocity was measured in the center of the drift net mouth at 50% water depth. Samples were preserved in 70% ethanol and processed at Hólar University College. Food items in each sample were counted under a stereomicroscope and sorted into order and/or family. Because drift samples were composed primarily (mean = 93.8%) of small Chironomid larvae, as well as some Diptera pupae and adults, all sampled invertebrates were of edible size for the fish in this study (sensu Keeley and Grant 1997). Food availability was expressed as drift density, i.e. the number of potential prey items per cubic meter of water (sensu Allan and Russek 1985).

*Table 6.1 Summary (mean and range) of habitat characteristics within each stream enclosure and between population density treatments during the 28-day experiment conducted in Deildará, Iceland in July 2013.*

Enclosure or Treatment	Water temperature (°C)	Light intensity (kilolux)	Water depth (cm)	Current velocity (m/s)	Substrate size <sup>1</sup>	Food availability (items/m <sup>3</sup> )
1	5.2 (2.7-8.8)	35.21 (0.01-209.42)	18.3 (2.3-30.2)	0.09 (0.00-0.26)	5.6 (5-7)	13.9 (3.3-25.2)
2			17.5 (0.9-28.4)	0.10 (0.00-0.30)	5.6 (5-7)	10.6 (3.9-18.7)
3	5.5 (2.7-9.8)	35.21 (0.01-209.42)	15.8 (0.0-35.5)	0.10 (0.00-0.31)	5.7 (5-7)	17.8 (2.0-47.1)
4			17.8 (1.6-38.8)	0.10 (0.00-0.28)	5.7 (5-7)	13.8 (1.4-60.9)
Low	5.4 (2.7-9.8)	35.21 (0.01-209.42)	17.3 (0.0-35.5)	0.09 (0.00-0.31)	5.6 (5-7)	13.8 (1.4-47.1)
High			17.4 (0.0-38.8)	0.09 (0.00-0.28)	5.6 (5-7)	14.3 (2.0-60.9)

<sup>1</sup>Substrate size classified using a modified Wentworth scale (DeGraaf and Bain, 1986): 1 – plant detritus; 2 – clay, < 0.004 mm; 3 – silt, 0.004-0.062 mm; 4 – sand, 0.062-2.0 mm; 5 – gravel, 2.0-64.0 mm; 6 – cobble, 64.0-250.0 mm; 7 – boulder, > 250 mm; 8 – bedrock; 9 – macrophytes.

### 6.2.5 Statistical analysis

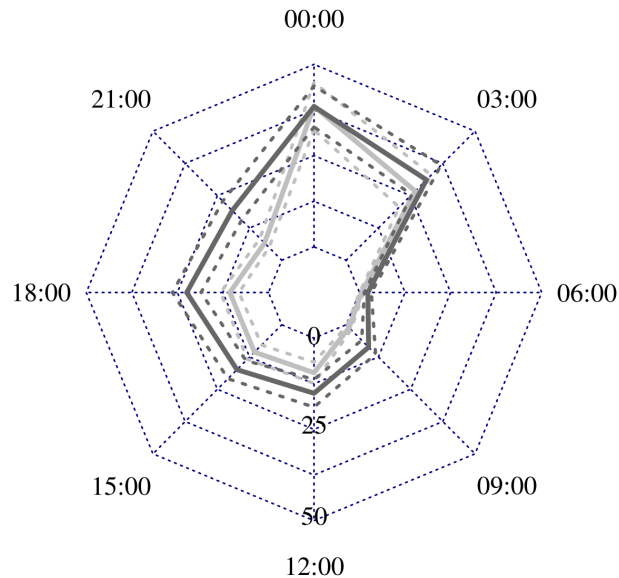
We used two approaches to analyse the data, based on two metrics of activity. First, we analysed how tagged individuals differed in activity and growth between low and high density treatments. Individual activity rates were calculated for tagged fish as the number of scans an individual was observed active divided by the total number of scans in the respective experimental round. Data on diel activity are cyclical by nature, so time values were transformed into angles for circular statistics (Batschelet 1981). Specifically, circular mean was used to determine the mean time of activity of each tagged fish, and circular standard deviation was used to assess how dispersed individual activity rates were over the 24 h cycle. Mean time of activity could not be calculated for two tagged fish that were each observed active only at diametrically opposite times of day (e.g. 00:00 and 12:00), but these fish were included in the analysis of dispersion of activity. The effect of density on individual activity rates and dispersion of individual activity rates was tested using ANOVAs. Because the experimental

design was replicated both in space (two pairs of enclosures) and in time (two rounds), round and pair were included as random effects in the analyses to account for residual variation among rounds, pairs, and enclosures. Hence, ANOVAs were of the form: Response  $\sim$  Density + Error (Round + Pair). The potential effect of density on individual growth rate was evaluated using this model, but with individual activity rate, initial body mass, and an interaction term between density treatment and initial body mass included as covariates (i.e. ANCOVA). Circular ANOVA was used to compare the mean time of activity between treatments.

Second, to evaluate how activity was related to fluctuations in ecological conditions, we used a generalized linear mixed model including density treatment, water temperature, light intensity, water level, Julian date, and first-order interactions (excluding density) as explanatory variables. Enclosure was included as a random factor. Values for each explanatory variable (except density treatment) were converted to standardized z-scores. Overall activity rates, originally calculated as the number of active fish in a particular enclosure during a given scan divided by the total number of fish in the enclosure, were used in this analysis because they could be linked to ecological conditions at a particular time. Importantly, however, no fish were observed active during 49% of scans, which results in a distribution that violates assumptions for traditional modeling approaches. Thus, the model utilized a binomial distribution with a logit link function; i.e. instead of using the original estimates of overall activity, activity was treated as a binomial variable and was rated as “0” when no fish was detected during a scan of a particular enclosure, and as “1” when at least one fish was active. A similar approach is recommended for modeling abundance of rare species and other data with an inflated zero class (see Welsh et al. 1996). If activity is independent of density, the probability of detecting a single active fish should be three times higher at high density. To account for this, different activity thresholds were used for low (1 active fish) and high density (3 active fish) before activity was scored as “1” for a particular scan.

Akaike’s Information Criterion corrected for small sample bias (AICc) was used to evaluate candidate models (see Grueber et al. 2011 and references therein). Model uncertainty was accounted for through model averaging (Bartón 2014), including the top model (that with the lowest AICc score) and models within 2  $\Delta$ AICc values to calculate model-averaged coefficients for each explanatory variable and to

estimate relative variable importance (0.00–1.00) in relation to activity. All analyses were performed in R (version 3.3.1; R Core Team 2014) using packages “circular” (distribution of activity in time, Agostinelli and Lund 2013), “lme4” (generalized linear models, Bates et al. 2014), and “MuMIn” (model averaging, Bartón 2014).



*Figure 6.1 Diel distributions of individual activity rates of juvenile Arctic charr in Deildará, Iceland. Each Y-axis represents the mean individual activity rate (0–50%) for a given time (00:00, 03:00, etc.) of the 24 h cycle. Light grey and dark grey lines represent low and high density, respectively. Dashed lines indicate standard error.*

## 6.3 Results

On average, individual tagged fish were active only 13.2% of the time (range = 0.0–55.4%), and 11 of the 71 tagged fish were never observed active. As predicted, individual activity rates were higher at high density (mean = 15.5%) than at low density (mean = 10.4%) (ANOVA,  $F_{1,67} = 4.475$ ,  $P = 0.038$ , Table 6.2). Fish in the second round (mean = 17.6%) were more active than fish in the first round (mean = 8.7%) (ANOVA,  $F_{1,68} = 12.65$ ,  $P < 0.001$ ). In both density treatments, individual activity rates tended to be higher at night (i.e. from 21:00 to 03:00; high and low density means = 22.3 and 16.5%) than during the day (i.e. from 06:00 to 18:00; high and low density means = 8.7 and 4.4%; Figure 6.1). There was no difference in the mean time of activity

between treatments (circular ANOVA,  $\chi^2 = 0.686$ ,  $P = 0.407$ , Table 6.2), though fish in the second round were more nocturnal (mean time = 23:32) than fish in the first round (mean time = 19:37) ( $\chi^2 = 14.81$ ,  $P < 0.001$ ).

*Table 6.2 Patterns of activity and growth of individually-tagged juvenile Arctic charr under treatments of high and low population density. Bold P values indicate significant differences between the two treatments.*

	Treatment						Df	Mean Sq.	F value	P value
	High density			Low density						
	Mean	SD	n	Mean	SD	n				
Individual activity rate (%) <sup>1</sup>	15.5	13.9	39	10.4	9.3	32	1,67	0.05	4.48	<b>0.038</b>
Mean time of activity (h) <sup>2</sup>	21:59	3:32	32	22:49	3:49	26	1	$X^2 = 0.686$		0.407
Dispersion of diel activity (h) <sup>1</sup>	4:39	2:36	34	3:03	2:23	26	1,56	0	4.64	<b>0.036</b>
Gs (% day-1) <sup>1</sup>	1.6	0.9	39	1.5	0.9	32	1,64	< 0.001	0.2	0.658

<sup>1</sup>Values obtained from ANOVA. These analyses included experimental round and enclosure pair as random effects, and the analysis on growth rate also included individual activity rate, initial body mass, and the interaction between density treatment and initial body mass as covariates. Refer to Appendix S1 for full ANOVA tables.

<sup>2</sup>Values obtained from circular ANOVA.

As predicted, individual activity was more dispersed over the 24 h cycle at high density than at low density (ANOVA,  $F_{1,56} = 4.639$ ,  $P = 0.036$ ; Table 6.2). Although the difference in individual activity rates between treatments was subtle, comparisons between treatments at each time period revealed two to eight times higher crepuscular activity at high density than at low density, specifically at 09:00 (ANOVA,  $F_{1,67} = 6.789$ ,  $P = 0.011$ ), 18:00 ( $F_{1,67} = 6.800$ ,  $P = 0.011$ ), and 21:00 ( $F_{1,67} = 8.788$ ,  $P = 0.004$ ; Figure 6.2).

By pairing low and high density treatment enclosures in the stream, water temperature, light intensity, and water level were essentially identical between treatments. As well, water depth (ANOVA,  $F_{1,3019} = 0.548$ ,  $P = 0.459$ ), current velocity ( $F_{1,668} = 1.336$ ,  $P = 0.248$ ), and substrate size ( $F_{1,508} = 0.002$ ,  $P = 0.963$ ) did not differ

between treatments (Table 6.1). The model-averaged generalized linear mixed model revealed that variability in activity within the study period was not only related to population density ( $P = 0.003$ ), but also to temporal fluctuations in other ecological variables. In fact, all single term variables included in the model had a significant impact on the probability of activity (Table 6.3). Fish were likelier to be active at higher population density, in warmer water, at higher water levels, and later in the season, but less likely to be active as light intensity increased (Figure 6.3). The probability of activity was also affected by an interaction between water temperature and light intensity (Table 6.3). The proportion of active fish was positively correlated with water temperature during the day (Spearman's rank correlation,  $n = 280$ ,  $P < 0.001$ ), but not at night ( $n = 168$ ,  $P = 0.477$ ; Figure 6.4).

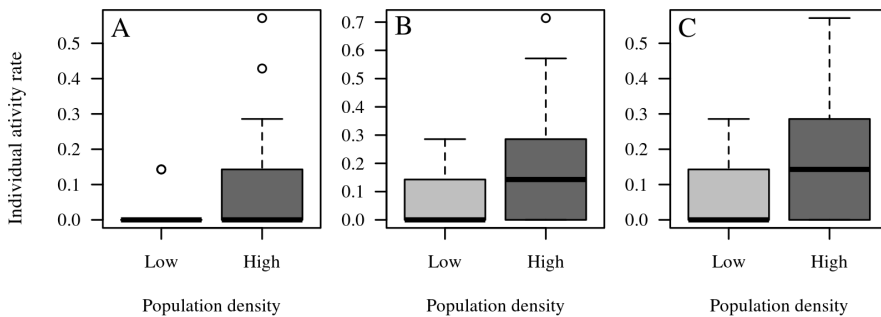


Figure 6.2 Individual activity rates at crepuscular times (A: 09:00, B: 18:00, and C: 21:00) of juvenile Arctic charr in low and high population density treatments in Deildará, Iceland.

There was no difference in food availability (i.e. invertebrate drift density) between treatments overall (ANOVA,  $F_{1,60} = 0.010$ ,  $P = 0.922$ ). Drift density declined from the first round (mean = 17.4 items/m<sup>3</sup>) to the second round (mean = 10.4 items/m<sup>3</sup>) (Wilcoxon rank-sum test,  $n = 64$ ,  $P < 0.019$ ). Drift density was significantly lower at 06:00 than at 12:00 (Wilcoxon rank-sum test,  $n = 16$ ,  $P < 0.001$ ), and marginally lower than at 18:00 ( $n = 16$ ,  $P = 0.068$ ), but there were no differences in food availability between any other times of day (00:00, 12:00, 18:00; Figure 6.5).

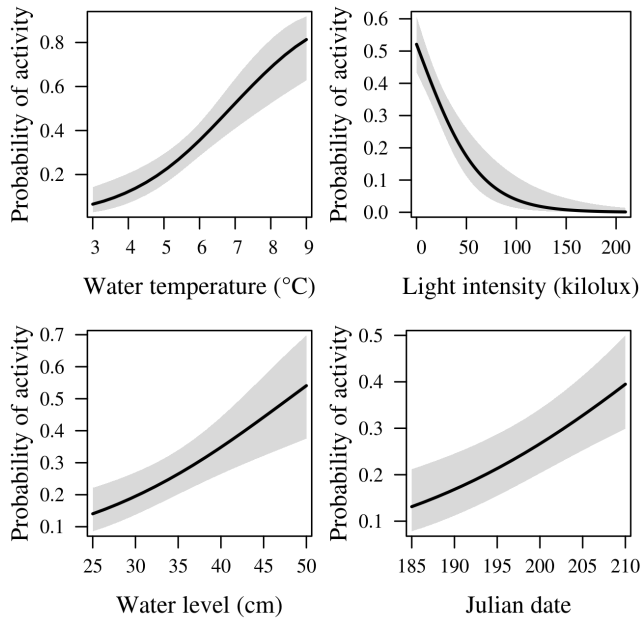


Figure 6.3 Effect size plots from model-averaged generalized linear mixed model showing the probability of observing at least one or three fish (at low and high density, respectively) as a function of water temperature, light intensity, water level, and Julian date. Y-axes have been re-scaled to match the linear distribution of the independent variable. Shaded areas represent 95% confidence intervals.

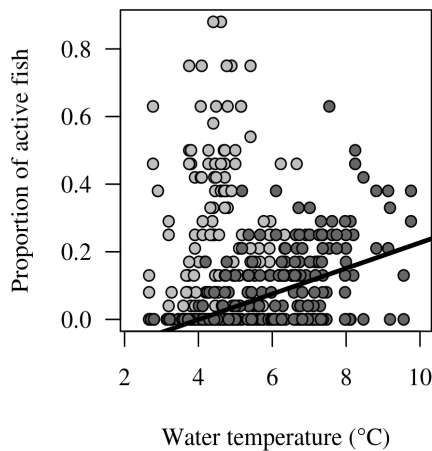


Figure 6.4 The association between activity levels of juvenile Arctic charr and water temperature (°C) in each stream enclosure during the day (i.e. 06:00–18:00; grey circles, solid line) and at night (i.e. 21:00–03:00; black circles).



Fish grew at a similar rate in low and high density treatments (ANCOVA,  $F_{1,64} = 0.197$ ,  $P = 0.658$ ; Table 6.2), with no difference in variance between treatments (Levene's test for homogeneity of variance,  $F_{1,69} = 1.083$ ,  $P = 0.302$ ). Initial mass (ANCOVA,  $F_{1,64} = 3.118$ ,  $P = 0.082$ ) and individual activity rate ( $F_{1,64} = 2.272$ ,  $P = 0.137$ ) had no effect on growth rate (Appendix S1).

*Table 6.3 Results from model-averaged generalized linear mixed model<sup>1</sup> evaluating the effect of the population density treatment and ecological variables on the probability of detecting activity in juvenile Arctic charr, using a threshold of one and three fish at low and high density, respectively. Enclosure was included as a random factor. Bold P values indicate significant impact on activity.*

Source of variation	Relative importance	Estimate	SE	Z value	P value
Intercept	NA	-0.7	0.21	3.340	<b>0</b>
Treatment (low density)	1.00	-0.682	0.229	2.982	<b>0.003</b>
Water temperature	1.00	1.047	0.212	4.929	< <b>0.001</b>
Light intensity	1.00	-1.489	0.297	5.022	< <b>0.001</b>
Water level	1.00	0.457	0.122	3.741	< <b>0.001</b>
Julian date	1.00	0.494	0.130	3.786	< <b>0.001</b>
Water temp.*Light intensity	1.00	0.788	0.186	4.228	< <b>0.001</b>
Light intensity*Julian date	0.41	-0.087	0.143	0.607	0.544
Water temp.*Julian date	0.40	-0.077	0.133	0.584	0.560
Light intensity*Water level	0.25	0.027	0.072	0.373	0.709
Water temp.*Water level	0.23	0.026	0.076	0.343	0.731

<sup>1</sup>Model averaging based on ten candidate models all within 2  $\Delta AIC_c$  values. All ten models included each single term (i.e. treatment, water temperature, light intensity, water level, and Julian date) and the interaction between water temperature and light intensity, but variable combinations of other interactions. Refer to Table S1 for information on each candidate model and Figure S1 for a pairs plot of covariance between environmental variables.

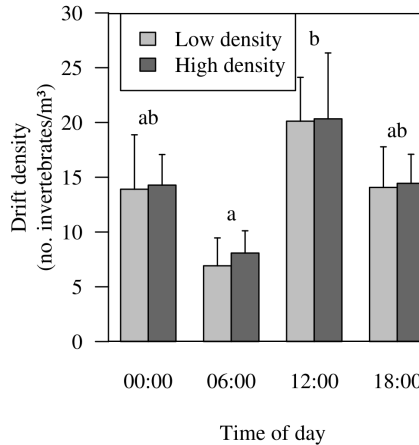


Figure 6.5 Density of invertebrate drift (mean  $\pm$  SE) at different times of day under treatments of low and high population density of juvenile Arctic charr in Deildará, Iceland. Significant differences among times of day (Wilcoxon rank-sum test,  $P < 0.05$ ) are identified with different letters.

## 6.4 Discussion

### 6.4.1 Diel activity and population density

This study demonstrates that individuals can modify both the rate and temporal distribution of their activity in response to increased population density, with fish (i) increasing their activity rate and (ii) extending their activity over a greater range of the 24 h cycle. Recent studies on a variety of taxa show that population density may affect activity rates (e.g. domestic sheep *Ovis aries*, Mobæk et al. 2012, houseflies *Musca domestica*, Schou et al. 2013), but this has not commonly been examined in fish. In two separate studies, the proportion of juvenile Atlantic salmon *Salmo salar* (Armstrong and Griffiths 2001) and adult bullhead *Cottus gobio* (Davey et al. 2009) occupying shelters decreased with increased population density. This trend was explained by increased competition for limited shelters at higher densities, but indirectly suggests that activity may increase with population density. In the present study, activity rates increased with population density even though shelters were abundant.

Alternatively, Blanchet et al. (2008) found no significant intraspecific effect of population density on the activity of juvenile

Atlantic salmon in stream channels, but these findings were based on short observations (5 min each) during narrow time intervals (9:00–11:00 and 20:30–22:30). Activity monitored on a regular basis throughout the 24 h cycle under semi-natural conditions should yield a more comprehensive test of density-dependent activity patterns. In our study, dramatic differences in activity rates between density treatments were observed only at particular times of day. Although some studies on density-dependent activity patterns have been conducted over 24 h cycles (e.g. Cameron and Carter 1979, Bailey 1981, Bahrndorff et al. 2012), this has rarely been done in natural or semi-natural conditions (but see Coulombe et al. 2008) or with fish (but see Vera et al. 2011 for an aquaculture study). Temporal shifts in activity patterns may occur when intraspecific competition increases due to temporal heterogeneity of resources (Craig and Douglas 1984), reduced resource availability (Hansen and Closs 2005, Howerton and Mench 2014), or in response to increased energetic requirements (Alanärä et al. 2001). The idea that intraspecific competition may induce shifts in the timing of activity has, in our opinion, not been addressed at sufficient temporal resolution throughout the day/night cycle.

In this study, Arctic charr were more active at night, with no difference in the mean time of activity between density treatments. However, at high density fish distributed their activity over a greater portion of the 24 h cycle, in part through increased activity at crepuscular times. This suggests that competition for drifting prey and/or interference from other fish may have prevented some individuals from being exclusively nocturnal, although aggression was observed in both low and high density enclosures (A. Fingerle, pers. obs.). In a similar study of juvenile Arctic charr, competition for limited shelters resulted in increased and more dispersed activity (Larranaga and Steingrímsson 2015). Foraging at low light levels may benefit stream salmonids via reduced predation risk (Metcalf et al. 1999) and lower rates of aggression (Fraser et al. 1993, Valdimarsson and Metcalfe, 2001). In contrast, diurnal activity in this system may be risky due to increased vulnerability to predators (Webb 1978). Therefore, crepuscular times may represent a trade-off between increased competition at night and higher predation risk during the day.

#### **6.4.2 Other ecological correlates of activity**

The model-averaged approach confirmed that fish are more active at

high population density, but also showed that other ecological variables play key roles in shaping activity patterns. First, activity increased with water temperature, likely due to increased metabolic demands (Beamish 1964) as well as increased prey capture (Watz and Piccolo, 2011) and position-holding (Graham et al. 1996) abilities. In this study, metabolic demands were likely low because of low water temperatures, resulting in lower activity rates (mean = 13.2%) than have been observed in juvenile salmonids in warmer streams (e.g. mean = 36.8% in Breau et al. 2007, 23% in Roy et al. 2013). In all three studies, activity increased with rising temperatures, though activity may level off at extreme temperatures (e.g. 23°C for Atlantic salmon in Breau et al. 2007). Importantly, in spite of low temperatures and activity rates, the mean densities even of only active fish were still high enough to expect competition under natural conditions (Grant and Kramer 1990, Imre et al. 2005). For example, if we assume each active fish occupied an average territory of 0.558 m<sup>2</sup> (sensu Gunnarsson and Steingrímsson, 2011), the mean habitat saturation at low (PHS = 11.6%) and high (PHS = 51.9%) density yields an 18.1% and 75.5% chance of density dependent mortality, growth, or emigration (sensu Grant and Kramer 1990). This suggests that activity should be taken into account when examining how animals share and compete for habitats, especially in colder regions where activity is generally low.

Second, activity decreased with light intensity. Although salmonids are visual foragers (see Rader et al. 2007) and have higher feeding efficiency (i.e. food intake vs. metabolic expenditure, sensu Metcalfe 1986) at daytime light levels (Fraser and Metcalfe 1997, Watz et al. 2014), fish in this study were more active at night. Salmonids tend to switch from diurnal feeding during their first year of life to more nocturnal feeding later in the juvenile phase. Our findings on 1+ fish, coupled with previous studies (Imre and Boisclair, 2004, Breau et al. 2007), are thus consistent with the asset protection principle (Clark 1994), which states that animals with higher levels of reproductive assets, such as larger body size, should be less willing to risk predation.

Interestingly, water temperature and light intensity interacted in their effect on activity. More specifically, fish were more likely to be active during warmer rather than colder days, as has been found in previous studies (e.g. Gries et al. 1997, Breau et al. 2007, Blanchet et al. 2008), whereas activity levels at night were independent of water temperature (see also Fraser et al. 1993). The ability of fish to avoid

predatory attacks decreases at colder temperatures, but so do gastric evacuation rates (Elliott 1972). Hence, fish may be able to preferentially hide from predators during colder days without sacrificing growth.

Third, activity also increased with rising water levels. Foraging in deeper water may increase prey encounter rate (Piccolo et al. 2007) and provide protection from aerial predators (Bugert and Bjornn 1991, Gregory 1993). However, high water levels may also coincide with fast current velocity and high turbidity, and thus the benefits of foraging may be outweighed by the costs of swimming, causing fish to seek refuge. In a previous study, juvenile Arctic charr were found to be active at a mean water depth of 37.7 cm and at current velocities up to 39.9 cm/s (Tunney and Steingrímsson, 2012). Thus, in the present study water levels may have remained within the range of usable current velocities, resulting in a gradual increase in activity with increased water discharge. Fourth, fish became more active as the season progressed, even after accounting for any effect of water temperature, light intensity, and water level. One potential explanation may be food availability, which significantly decreased from the first (mean = 17.4 items/m<sup>3</sup>) to the second round (mean = 10.4 items/m<sup>3</sup>). Hence, fish may have spent more time foraging later in the season to capture enough prey to meet their energetic requirements.

#### **6.4.3 Population density, activity, and growth**

Population density did not affect growth rates. Although many studies suggest density-dependent growth in juvenile salmonids (e.g. Jenkins et al. 1999, Imre et al. 2005, Lindeman et al. 2014), this result is congruent with other studies that did not detect such an effect (e.g. Kaspersson et al. 2013). Two extremes along a continuum can be proposed for the way activity may shape the relationship between population density and individual growth. At one extreme, individuals at high density could compensate for increased interference (e.g. aggression and territorial defence, sensu Keddy 2001) or reduced food availability as a result of exploitative competition (e.g. shadow competition, Elliott 2002) by spending more time foraging. At the other extreme, individuals could show no flexibility in diel activity patterns and thus grow slower as a result of increased competition. In this study, fish at high density adjusted both the rate and timing of their activity and grew as fast as fish at low density. This suggests that in our study system the former scenario is more likely, which reflects the

findings of previous studies that suggest compensatory behavioral responses to changes in competition (Alanära et al. 2001, Blanchet et al. 2008) and reduced food availability (Nicieza and Metcalfe 1997, Orpwood et al. 2006). Other compensatory mechanisms (i.e. changes in physiology that allow growth to be maintained, see Reznick et al. 2012) are also possible and deserve further exploration. To what degree increased activity levels allow individuals to maintain growth over a greater range of densities and over a longer period of time remains to be examined.

#### **6.4.4 Conclusions**

This study suggests that intraspecific competition is important in shaping diel activity patterns of stream-dwelling salmonids, and animals in general. Using densities high enough to expect high levels of competition (Grant and Kramer 1990, Blanchet et al. 2008), we found that juvenile Arctic charr modified both the rate and timing of their activity and, consequently, maintained growth at higher population density. Ultimately, the difference in activity rates between high and low population density treatments was subtle though significant, and fluctuations in ecological conditions were also important in shaping activity patterns. Future research should attempt to tease apart the interplay between population density and ecological determinants in their effect on activity patterns, as the effect of density may ultimately depend on other ecological variables and could be intensified by e.g. high water temperature and low food availability. This study demonstrates that to obtain a more comprehensive understanding of the role of competition within populations, it is not only necessary to examine spatial patterns (e.g. territory size), but also how individuals modify temporal aspects of their foraging activity to gain access to resources and maintain growth.

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## 6.6 Data Accessibility

We will archive the data associated with this manuscript in the Dryad Digital Repository.

## 6.7 References

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# 7 Repeatability and ecological correlates of foraging mode in a stream dwelling fish

Nicolas Larranaga, Amy Fingerle, Stefán Óli Steingrímsson

## Abstract

Behavior in natural populations is both variable (individuals behave differently on average) and labile (individuals alter their behavior). The nature of this variation can give important insights into individual flexibility and how organisms adjust their behavior in response to varying environmental conditions. In particular, substantial variation exists in the foraging mode of mobile organisms, i.e. sets of coordinated behaviors related to prey search and attack. We repeatedly measured the foraging mode (search mobility, foraging radius, prey attack rate and proportion of attacks directed towards the water surface) of 60 juvenile Arctic charr *Salvelinus alpinus* in three different streams, along with several environmental variables (water temperature, light intensity, water depth and water current velocity). We used these data to quantify the extent and distribution of the variation in foraging mode among populations. We also calculated the individual repeatability of foraging mode in each stream. Most of the variability in foraging mode occurred among populations, but individual repeatability was low within streams. Fish were more sedentary, attacked fewer prey but more often at the surface in fast and shallow habitats. In addition, mobility decreased with both decreasing water temperature and increasing light intensity. Arctic charr also attacked prey at faster rate when temperature increased. The effects of water temperature and light intensity on foraging mode probably reflect higher food availability at high temperature and during the night, which suggests that diel variations in food availability are important components of the foraging behavior of stream-dwelling

fish. Low repeatability of behavior also challenges the general idea of consistent individual differences.

**Keywords:** Search mobility, behavioral flexibility, Arctic charr, habitat use, foraging behavior, temperature, light intensity

## 7.1 Introduction

Behavioral variation, and its structure, is of great relevance for population dynamics and evolutionary ecology (Sutherland 1995, Sih et al. 2004, Réale et al. 2010, Wolf and Weissing 2012). Indeed, this variation can be distributed both among and within individuals in populations, depending on the degree of individual flexibility. For example, the literature on “personality traits” focuses on how consistent behavior is at the individual level (Réale et al. 2010), and shows that behavioral traits, including e.g. foraging, habitat selection and mating behavior, are moderately repeatable (Bell et al. 2009). Alternatively, phenotypic plasticity can be adaptive under certain conditions, so individuals may alter their behavior to cope with fluctuations in their environment either on a short-term basis (e.g. diel or seasonal) or along their development (ontogenic shifts), which suggests some flexibility (Via et al. 1995, Piersma and Drent 2003).

Individual variation in foraging behavior is especially important because it affects prey encounter rates (Huey and Pianka 1981), and has implications for intra- (Nakano 1995) and interspecific interactions (Nakano et al. 1999). Foraging behavior can also affect life-history traits including survival, growth and reproductive rates (Webb et al. 2003). Foraging mode studies are surprisingly under-represented in the research on repeatability of behavior (Bell et al. 2009, Potier et al. 2015), although substantial variation exists both among and within individuals (Bell et al. 2009). Mobile organisms generally adopt one of two discrete foraging modes, or sets of coordinated behaviors (Huey and Pianka 1981, McLaughlin 1989). This dichotomy is typically (albeit not always) based on the mobility of animals while searching for prey. In several taxa, foragers are described as either active searchers (movers) or ambush foragers (stayers, Grant and Noakes 1987, Webb et al. 2003). Although a two-mode paradigm is widely used because of the simple framework it provides for the study of animal behavior and because two adaptive peaks may occur under certain conditions (Gerritsen and Strickler 1977), some theoretical and empirical contributions challenge the bimodality of foraging mode (Perry 1999, Cooper 2005). These studies suggest that foragers may belong to one of more than two modes, or to a behavioral spectrum for which the two modes may be the extremes.

Foraging mode has been extensively described in salmonid

species. Stream-dwelling juveniles typically exhibit a “sit-and-wait” tactic and initiate movement to intercept drifting invertebrates (Kalleberg 1958, Wańkowski and Thorpe 1979, Steingrímsson and Grant 2008), although some individuals actively swim and travel longer distances both while searching for prey and during attack bursts (Grant and Noakes 1987, McLaughlin et al. 1992). Foraging mode variation exists among species (Fausch et al. 1997, Tunney and Steingrímsson 2012), but also at the intra-specific level (Grant and Noakes 1987, Tunney and Steingrímsson 2012). Whether salmonids belong to one of two distinct foraging modes or to a continuum varies. In brook charr *Salvelinus fontinalis*, a well-studied species, considerable literature supports the two-mode view (Grant and Noakes 1987, Grant and Noakes 1988, McLaughlin et al. 1992, McLaughlin et al. 1999, Wilson and McLaughlin 2007, Farwell and McLaughlin 2009, Wilson and McLaughlin 2010). However, for other species and in some studies on *S. fontinalis*, foraging mode is best described by a distribution skewed towards the sedentary end of the continuum (Gunnarsson and Steingrímsson 2011, Tunney and Steingrímsson 2012, Edelsparre et al. 2013).

In salmonids, foraging mode has been studied in a variety of conditions, especially in regard to water current velocity (Grant and Noakes 1988, Tunney and Steingrímsson 2012), water depth (McLaughlin et al. 1994) and prey availability (Fausch et al. 1997). Light intensity and water temperature are two other potential determinants of foraging mode (but see Biro and Ridgway 2009). Koski and Johnson (2002) suggested that kokanee salmon *Oncorhynchus nerka* may switch foraging mode (from particulate to gulp feeding) with increasing light intensity. Likewise, Watz et al. (2014) found that reaction distance of brown trout *Salmo trutta* was affected by water temperature. Although foraging mode has been measured over wide ranges of water temperature (McLaughlin et al. 1994, Watz et al. 2014), data are usually collected only during daytime, which may neglect the activity of some individuals at low light levels. In addition, water temperature and light intensity may have interactive effects on foraging mode (Watz et al. 2012).

The idea that behavior is highly plastic is currently challenged by numerous examples of strong consistency in spatial behavior, including habitat selection, foraging, and exploration (review in Bell et al. 2009). In a study on *S. fontinalis*, repeatability of foraging mode was low but significant (Biro and Ridgway 2008). In addition,

foraging mode may be linked to additional, consistent traits like boldness (Farwell and McLaughlin 2009). Alternatively, McLaughlin et al. (1992) found that only 23.1-33.9 % of the total variation in foraging mode in brook charr was among-individual variation. Residual error, which included within-individual variation, represented up to 74.5 % of the total variation. Consistent inter-individual differences in foraging mode may also be relevant in the context of early diversification in prey selection (Cooper et al. 1985), which may precede morphological differences (Skúlason and Smith 1995) and reinforce behavioral differentiation. For instance, mobile salmonids tend to attack fewer prey (McLaughlin et al. 1994) and to direct more attacks toward the surface or the bottom of the water (Grant and Noakes 1987, McLaughlin et al. 1994, Fausch et al. 1997).

The purpose of the present study is threefold. First we assess the overall variability in foraging mode distribution of Arctic charr using three streams with strong ecological differences (water temperature, food availability, habitat availability). Second, we test if and how this variation relates to ecological conditions (water temperature, light intensity, current velocity, water depth) within streams. Third, we assess the repeatability of foraging mode (prey search and foraging characteristics) in each stream after taking the part of variability explained by ecological determinants into account. To do that, we repeatedly observed the behavior (search mobility, foraging radius, prey attack rate and surface feeding, sensu McLaughlin et al. 1994) of 60 individually tagged juvenile Arctic charr *Salvelinus alpinus* at different times of the day in semi-natural enclosures in three streams. We predict that foraging mode will be repeatable (Biro and Ridgway 2008). In addition, we predict that fish will be more sedentary at low water temperature (because of increased cost of swimming with decreasing temperature), at low light levels (because of reduced visibility) and in fast-running water (because of increased food availability and cost of swimming in fast habitats).

## **7.2 Material and methods**

### **7.2.1 Sampling**

On June 28<sup>th</sup> and July 14<sup>th</sup> 2013, and on June 6<sup>th</sup> 2014, 20 Arctic charr of age 1+ were captured by electrofishing in each of three streams: a tributary of river Deildará (N 65.895971, W 19.277390), a tributary of

river Grímsá (N 65.828795, W 19.869358), and Myllulækur (W 65.516398, W 19.606433), northern Iceland, respectively (LR-24 electrofisher, Smith-Root, Inc., Vancouver, Wash., USA). All three streams are run-off systems with similar width (2-3 m). These populations have been used to describe the behavior of young Arctic charr in two previous studies (Gunnarsson and Steingrímsson 2011, Tunney and Steingrímsson 2012), including foraging mode, and were selected because water temperature differs among these three systems. After capture, individuals were measured for fork length to the closest 0.1 mm and body mass to the closest 0.01 g (PESOLA® PPS200, CH-6340 Baar, Switzerland). Then, fish were individually tagged with visible implant elastomer (Northwest Marine Technology, Inc., Washington, USA) using different combinations of four colours (yellow, green, orange, and red) and two positions along the dorsal fin (modified from Steingrímsson and Grant, 2003), and randomly assigned to two stream enclosures (10 fish/enclosure). On average, fish were 56.0, 66.6 and 80.4 mm (range = 47.5 – 60.9, 57.4 – 76.6 and 64.1 – 92.7 mm) and weighed 1.63, 2.99 and 5.35 g (range = 0.88 – 2.39, 1.89 – 4.65, 2.73 – 8.45 g) in Deildará, Grímsá, and Myllulækur, respectively. Fish were classified as age 1+ based on known size distributions of Arctic charr in these streams, and on the presence of parr marks. Initial body length and mass differed among streams ( $P < 0.001$  for both variables). Prior to the first observation, fish were given 48 h to habituate to the enclosures. The experimental bouts were terminated on July 13<sup>th</sup>, July 25<sup>th</sup> 2013 and June 22<sup>nd</sup> 2014 in the streams Deildará, Grímsá, and Myllulækur, resulting in a study period of 13, 11 and 11 days, respectively. No tag faded too much to impede individual identification of fish during the observations. After each study period, fish were measured for body length and mass and released at their initial sampling location.

## **7.2.2 Study design**

Enclosures (4 m long, 1 m wide, and 0.75 m high) were made of 5 mm nylon mesh, which prevents fish from escaping but allows aquatic invertebrates to drift through. The behavior of young salmonids has already been described successfully in similar semi-natural environments (Lindeman et al. 2015). A string was tied across the top of each enclosure to reduce the risk of predation from birds, presumably without changing the risk perceived by fish. The bottom mesh of each enclosure was covered with substrate from the respective stream. A grid of 1 m metal poles (width = 8 mm) was placed over the

substrate to obtain x-y coordinates of active individuals to the closest 5 cm on both axes. In each stream, enclosures were separated by approximately 40 m (along the stream length) and planted in locations with diverse but similar habitats, suiting Arctic charr requirements (Tunney and Steingrímsson 2012). At the beginning of the study, depth, substrate size, and current velocity (Marsh-McBirney Flo-mate™ Model 2000CM, Frederick, MD, USA) were measured at 100 (depth and substrate size) and 20 x-y points (current velocity) within each enclosure. Water depth and substrate size measurements were collected every 20 cm on both axes, starting 10 cm from the sides. Substrate size was estimated by the modified Wentworth scale (*sensu* Degraaf and Bain 1986). Each value represents the dominant substrate size in a square of 400 cm<sup>2</sup> around each coordinate. Current velocity was measured at 40 % of the water depth from the bottom (Davis and Barmuta 1989) every 20 cm along the stream starting 10 cm from the sides, on 4 transects perpendicular to the flow (every 50 cm, starting 50 cm from the up- and downstream sides). Because of high among-stream variability in fish size, we tried to mirror the variation in habitat availability by selecting sites with deeper and faster water in populations where fish were larger (Mäki-Petäys et al. 1997, Armstrong et al. 2003, Mäki-Petäys et al. 2004, Table 7.1). All habitat variables were thus different among streams according to Kruskal-Wallis tests ( $P < 0.001$  in all cases). Temperature and light intensity were recorded automatically every hour by data loggers positioned at one of the two enclosures (Onset® HOBO® UTBI-001 TidBiTv2 and UA-002-08 HOBO Pendant® Temp/Light,8K, respectively). Water temperature and light intensity varied among populations ( $P < 0.001$  and  $P = 0.03$ , respectively, Table 7.1). Variation in water depth throughout the study was recorded at a fixed point immediately upstream the upstream enclosure prior to all observations in each stream. Water depth varied similarly throughout the study (range = 8.5, 8.7 and 6 cm in Deildará, Grímsá, and Myllulækur, respectively). Thus, we used ranges of habitat availability, temperature and light intensity that would promote variability in foraging mode.

### **7.2.3 Behavioral observations**

Observations were made every three hours (e.g. 00:00, 03:00, 06:00). Each enclosure was visited six times per daytime in total, yielding a total of 48 observations per enclosure. In northern Iceland, the long daylight in summer allows for unaided visual observation throughout the day/night cycle. Enclosures were visited in a random order for each

observation. During each observation, we monitored the foraging activity of all active fish. behavioral observations occurred as follows: An observer stood motionless for 5 min at the side of an enclosure, then visually scanned it and began recording behavior. After an individual was selected randomly, the observer described its foraging mode for approximately 5 min using a procedure *sensu* McLaughlin et al. (1992). Time was kept with a digital timer that emitted a pulse every 5 s. Each individual observation alternated between one to three consecutive 5 s intervals of monitoring and a 5 s interval during which the observer recorded notes from the preceding intervals. 5 s intervals were classified as either pursuit or search. Pursuit intervals correspond to a situation where a focal individual made at least one feeding attempt, whereas search intervals correspond to a period of active searching or a situation where a fish simply maintained position in the water column, without attacking prey. Prey attack rate is estimated as the proportion of intervals when a focal fish attacked at least one prey. Multiple feeding attempts in a single 5 s interval were rare throughout the study and were considered as single feeding attempts, i.e. the foraging radius and feeding position were based on the first feeding attempt of the interval. Similarly, as aggression was not frequent during the study, 5 s intervals where it occurred were excluded from the analyses. During both search and pursuit intervals, we quantified mobility in number of body lengths. Search mobility corresponds to the proportion of search intervals during which an individual moved more than one body length (McLaughlin et al. 1992). During pursuit intervals, we measured the foraging radius (in number of body lengths) as the distance between the location where an attack was initiated and the location where the prey was intercepted. The location of the prey interception in the water column (benthic, mid-water, or surface) was also recorded. After foraging mode was described for a single individual, we estimated an x-y location inside the enclosure where the focal fish spent the majority of the observation. After all foraging mode data had been collected within an enclosure, water depth and current velocity were measured in each of these locations. We manually removed any accumulated debris and algae from the front of an enclosure after an observation to avoid disturbance prior to the next observation periods.

#### **7.2.4 Statistical analyses**

We used general mixed linear models to test for the effect of ecological variables on foraging mode, starting from a full model and gradually



removing the least significant variable until all remaining variables had a significant effect on the response. Stream identity was considered as a random factor to account for the variation in ecological factors among streams. All foraging mode traits were square-root transformed to account for right-skewed distributions. Light intensity values were log-transformed. Then, we extracted the residuals of the models for each foraging mode trait. We had contrasting amounts of observations per individual among streams, so we used only individuals with 5 observations or more and randomly selected 5 values for each individual. We measured the Intra-class coefficient (ICC) in each of the three streams and repeated the analysis 1000 times by selecting 5 random values for each individual. ICC is  $S^2_A / (S^2_A + S^2_W)$ , where  $S^2_A$  is the variance among individuals and  $S^2_W$  is the variance within individuals (Sokal and Rohlf 1995, Wolak et al. 2012). We used the mean ICC, mean lower and upper limits of the 1000 iterations to describe the repeatability of foraging mode. All statistics and simulations were run under R 3.0.2 (R Core Team 2013). More specifically, we used the packages lme4 (Bates et al. 2008), and ICC (Wolak et al. 2012) for GLMMs and ICC repeatability estimates, respectively.

*Table 7.1 Variability of environmental conditions in semi-natural enclosures in three populations of Arctic charr.*

Variable	River	Mean	Range	n
Water temperature (°C)	Deildará	5.62	3.60 – 9.30	47
	Grímsá	8.98	6.80 – 15.00	48
	Myllulækur	13.7	11.00 – 16.60	48
Light intensity (kilolux)	Deildará	20.43	0.10 – 92.10	48
	Grímsá	16.68	0.03 – 88.00	48
	Myllulækur	33.15	0.00 – 220.00	48
Current velocity (cm/s)	Deildará	7.65	0.00 – 20.00	40
	Grímsá	9.95	6.00 – 18.00	40
	Myllulækur	15.23	4.00 – 23.00	40
Water depth (cm)	Deildará	21.47	5.30 – 30.00	200
	Grímsá	24.84	7.30 – 31.50	200
	Myllulækur	25.53	10.00 – 35.00	200

## 7.3 Results

### 7.3.1 Variability and repeatability of foraging mode

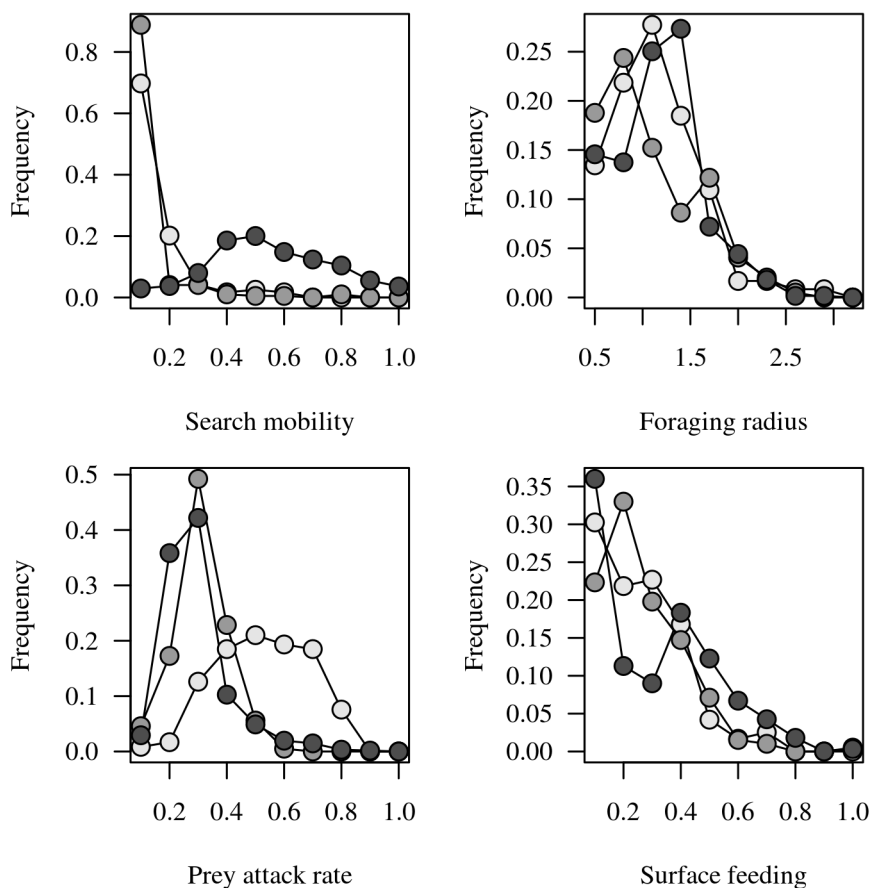


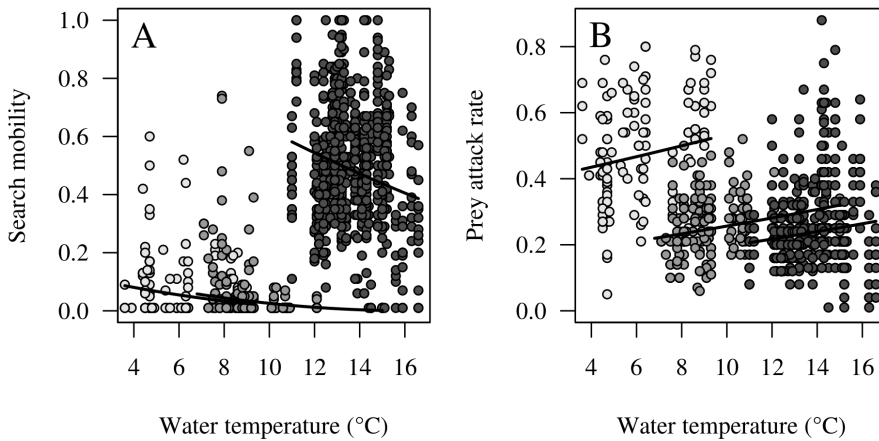
Figure 7.1 Distribution of individual foraging mode in three populations of Arctic charr in northern Iceland. Light, intermediate and dark grey represent populations Deildará, Grímsá, and Myllulækur, respectively. Search mobility, surface feeding and prey attack rate is given as a proportion. Foraging radius is given in body lengths.

In total, we obtained 119, 198 and 614 measurements of foraging mode, yielding an average of 7.0, 9.4 and 30.7 observations per fish in Deildará, Grímsá, and Myllulækur respectively. Foraging mode variables were right-skewed, i.e. the majority of observations were

clustered towards the sedentary side of the foraging mode distribution (Figure 7.1). Hence, fish were mostly sedentary during prey search in two populations (average search mobility = 0.08 and 0.05 in Deildará and Grímsá, respectively, Table 7.2), but more mobile in the third stream (average search mobility = 0.51 in Myllulækur, Table 7.2). Arctic charr also attacked prey over relatively short distances, as 91.6 % of prey interceptions occurred in a radius of less than 2 body lengths, and at very variable rate, as the proportion of 5 s intervals where prey was attacked ranged from 0.05 to 0.80, 0.00 to 0.52 and 0.00 to 0.88 in Deildará, Grímsá, and Myllulækur respectively (Table 7.2). Surface feeding was also common, but benthic feeding was very rarely observed (average = 0.03, 0.01 and 0.02, Table 7.2). Fish used a wide range of habitats, both in terms of water depth and current velocity (Table 7.2).

*Table 7.2 Descriptive statistics for foraging mode and habitat used in semi-experimental enclosures in three populations of Arctic charr. Search mobility, prey attack rate and surface feeding are given as proportions.*

Variable	River	Mean	Range	n
Search mobility	Deildará	0.08	0.00 – 0.60	119
	Grímsá	0.05	0.00 – 0.74	198
	Myllulækur	0.51	0.00 – 1.00	614
Foraging radius (body lengths)	Deildará	0.97	0.08 – 2.85	119
	Grímsá	0.80	0.00 – 2.50	198
	Myllulækur	0.97	0.00 – 5.00	611
Surface feeding	Deildará	0.21	0.00 – 0.69	119
	Grímsá	0.21	0.00 – 1.00	198
	Myllulækur	0.27	0.00 – 1.00	614
Foraging rate	Deildará	0.48	0.05 – 0.80	119
	Grímsá	0.25	0.00 – 0.52	198
	Myllulækur	0.25	0.00 – 0.88	614
Current velocity used (cm/s)	Deildará	8.78	2.00 – 19.00	119
	Grímsá	9.57	1.00 – 14.00	106
	Myllulækur	11.02	2.00 – 24.00	614
Water depth used (cm)	Deildará	24.59	17.00 – 33.00	119
	Grímsá	26.78	16.30 – 30.10	106
	Myllulækur	26.80	9.20 – 34.10	614



*Figure 7.2 The association between water temperature and search mobility (A) and prey attack rate (B) in three populations of Arctic charr (from light to dark grey for populations Deildará, Grímsá, and Myllulækur, respectively). This figure illustrates that foraging mode may be affected differently by water temperature among and within streams. Solid lines are regression lines from general linear mixed models.*

### **7.3.2 Effects of ecological and phenotypic variables**

After accounting for differences in ecological variables among streams and correcting for among-individual differences, foraging mode is affected by a series of ecological factors (current velocity, water depth, water temperature, light intensity, Table 7.3). In contrast to our predictions, within individuals, search mobility, foraging radius and surface feeding decreased with rising water temperature ( $P < 0.001$ ,  $P = 0.006$ , and  $0.001$  respectively, albeit prey attack rate did increase ( $P < 0.001$ , Table 7.3). Thus, individual Arctic charr became more sedentary and attacked more prey with increasing water temperature (Figure 7.2). However, as predicted, they also exhibited greater mobility and attacked prey from farther away with increasing light intensity ( $P < 0.001$  for both variables, Table 7.3). This discrepancy is surprising given the strong positive correlation between water temperature and light intensity (Spearman rank correlation,  $r = 0.82$ ,  $0.65$  and  $0.53$ ,  $N = 48$  and  $P < 0.01$  for all three populations). We found associations between foraging mode and habitat use (Table 7.3). More specifically, when foraging in deeper water, fish attacked fewer prey ( $P < 0.001$ ), over greater distances ( $P = 0.010$ ) and were more likely to

direct attacks at the surface of the water ( $P < 0.001$ ). We also found effects of current velocity on foraging mode, i.e., fish were more sedentary ( $P < 0.001$ ) attacked prey at faster rate ( $P < 0.001$ ) over shorter distances ( $P = 0.036$ ) and less often at the water surface ( $P < 0.001$ ) in faster waters.

*Table 7.3 Results of general linear mixed models for four foraging mode variables. A stepwise backwards selection was applied until only explanatory variables with a significant effect remained. Stream identity was considered a random factor in the models. All response variables were square-root transformed and light intensity vales were log-transformed to fit normal distributions.*

Response variable	Explanatory variable	Estimate	Std. Error	df	t value	P-value	
Search mobility	Intercept	-0.347	1.374	2.0	-0.253	0.088	
	Temperature	-0.213	0.026	834.8	-8.340	<0.001	***
	Light intensity	0.076	0.016	834.8	4.720	<0.001	***
	Current velocity	-3.498	1.218	833.0	-2.870	<0.001	**
Foraging radius	Intercept	0.764	0.145	25.0	-5.264	0.532	***
	Temperature	-0.022	0.008	65.2	-2.810	<0.001	**
	Light intensity	0.029	0.005	490.5	5.566	<0.001	***
	Water depth	0.018	0.003	760.1	5.310	0.010	***
	Current velocity	-1.567	0.403	829.7	-3.887	0.036	***
Surface feeding	Intercept	-0.025	0.082	175.3	-0.307	0.759	
	Water depth	0.024	0.003	336.5	8.803	<0.001	***
	Current velocity	-1.744	0.320	135.4	-5.448	<0.001	***
Prey attack rate	Intercept	0.519	0.094	3.7	5.543	0.006	**
	Temperature	0.007	0.003	810.0	2.487	0.013	*
	Water depth	-0.004	0.001	834.0	-3.202	0.001	**
	Current velocity	0.775	0.150	833.0	5.162	<0.001	***

### 7.3.3 Repeatability of foraging mode

After accounting for population differences and the effect of ecological conditions, we found that repeatability (intra-class coefficient) was consistently low. Confidence intervals (95%) encompassed 0 in 11 out of 12 cases. Hence, only prey attack rate was significantly repeatable, and only in Deildará (Figure 7.3).

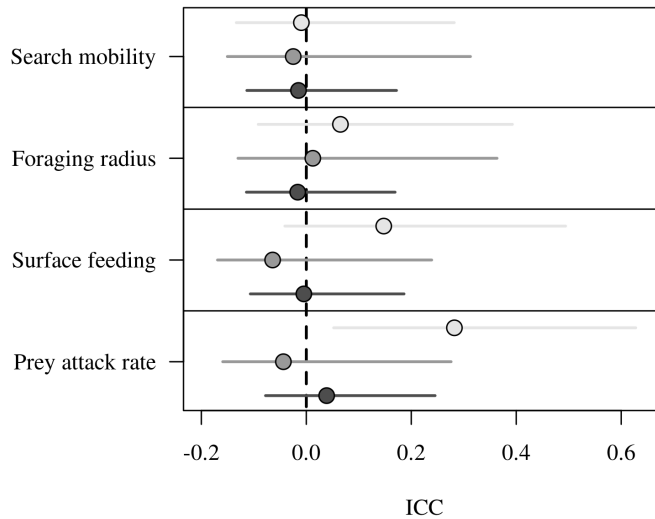


Figure 7.3 Distributions of intra-class coefficients for search mobility, foraging radius, surface feeding and prey attack rate in three populations of Arctic charr (from light to dark grey for populations Deildará, Grímsá, and Myllulækur, respectively). High values of ICC indicate high among-individual variation, i.e. high repeatability. Error bars represent 95% confidence intervals.

## 7.4 Discussion

### 7.4.1 Variability in foraging mode

In this study, Arctic charr remained relatively sedentary during prey search in two streams (Deildará and Grímsá) but were highly mobile in the third one (Myllulækur), which is consistent with the variability detected earlier among Arctic charr populations (Gunnarsson and Steingrímsson 2011, Tunney and Steingrímsson 2012). The range of habitats used was also in accordance with that reported by Gunnarsson and Steingrímsson (2011) and Tunney and Steingrímsson (2012). Although the total (i.e. across populations) distribution of search mobility and surface feeding fits a bimodal distribution, our results suggest that within our study populations, the foraging mode of young Arctic charr belongs to a unimodal behavioral continuum, rather than a two-mode distribution. Nonetheless, the shape and position of this distribution appears system dependent. For instance, a tenfold difference in search mobility was detected between the Grímsá and Myllulækur populations. This difference was consistent across traits,

as search mobility, foraging radius and surface feeding were lowest and highest in Grímsá and Myllulækur, respectively. This suggests a coordinated nature of foraging mode traits, at least among populations (Cooper 2007).

We found substantial variation in Arctic charr's foraging mode. For a large part, this variation was distributed among populations, as among-stream variation represented 72.2 – 99.7 % of the total variance in our dataset (results not shown). A similar pattern has already been described in Tunney and Steingrímsson (2012), where the among-stream variation was 47.9 – 88.6 % of the total variance, but such ranges contrast significantly with other studies on salmonids (e.g. 0.4 – 3.5 % in McLaughlin et al. 1992). This variability may reflect ecological gradients (e.g. water temperature, productivity, habitat availability) as well as phenotypic (e.g. body size) differences across streams. We were also interested in the variation among individuals in each stream (i.e. repeatability). Several studies suggest that behaving consistently may be adaptive (Dall et al. 2004, McElreath and Strimling 2006). Indeed, foraging characteristics have been reported as repeatable in other study models (see Bell et al. 2009 for a review). Interestingly, and contrary to our prediction, among-individual variation in foraging mode was low overall. In fact only prey attack rate was significantly repeatable, and only in one stream. We standardized foraging mode data by accounting for the potential effects of several ecological variables and using the residuals of mixed linear models. However, other variables were not measured (e.g. turbidity, food availability, energetic levels) that may overshadow consistent individual differences. Hence, our results should be examined under the scope of field limitations and show that Arctic charr adopted contrasting foraging mode in different streams, but each individual used a wide portion of the local foraging mode distribution.

Repeatability also varied among streams. For instance, individuals were more consistent in terms of foraging radius, proportion of surface feeding, and prey attack rate, but not search mobility in Deildará than in the two other streams. These differences among populations reflect variability in repeatability of foraging mode reported in previous studies (e.g. high and low among-individual variation in Biro and Ridgway 2008 and McLaughlin et al. 1992, respectively). Mechanisms like early specialization and morphological divergence in a context of resource polymorphism are commonly invoked to explain why juvenile salmonids exhibit consistent foraging

mode (McLaughlin et al. 1999). Repeatable foraging behavior may also reflect dominance hierarchies where individuals with different status or home range characteristics adopt contrasting behavior (Nakano 1995). Additional studies on the movement of stream-dwelling fish describe populations as a mixture of consistently mobile and sedentary individuals (Rodríguez 2002, Morrissey and Ferguson 2011, Young 2011, Booth et al. 2014). Our results, however, suggest relatively low repeatability in the foraging mode of young salmonids.

#### **7.4.2 Ecological correlates of foraging mode**

Low repeatability of foraging mode, in addition to the strong effect of environmental conditions, suggest that ecological determinants play a crucial role in shaping foraging mode. We found that foraging mode was affected by water temperature and light intensity. Importantly, search mobility values were much higher in the warmest stream, which fits previous observations for Arctic charr populations (Tunney and Steingrímsson 2012). Indeed, being mobile should be less costly when temperature increases, because manoeuvre time decreases (Watz and Piccolo 2011) and endurance increases (Ojanguren and Braña 2000) in the range of water temperatures that we used. However, we also predicted that this pattern would be detected within populations. For instance, in a lake population, juvenile brook charr spent more time actively swimming and swam faster as water temperature increased (Biro and Ridgway 1995). Contrary to this prediction, we found that mobility (both search mobility and foraging radius) decreased, although prey attack rate increased with increasing water temperature after accounting for among-population differences. This is also somewhat in contradiction with results by Watz et al. (2012). Indeed, they found that at low temperature, sedentary individuals had higher prey capture success, but this relationship was not significant at temperatures above 10°C. McLaughlin et al. (1994) found no effect of water temperature on foraging mode in still waters, so field studies (especially in lentic environments) may provide equivocal results. Instead, our findings may reflect higher invertebrate activity at higher water temperature for a given daytime, resulting in higher drift rates (Winterbottom et al. 1997) and lower mobility (Vehanen 2003). Hence, fish may be more mobile in warm streams, but may also become more sedentary as more prey drift at higher temperatures, and may capture more prey without spending more energy.

Surprisingly, light intensity and temperature had opposing effects



on mobility and prey attack rate in this study, although these two environmental variables were highly correlated. Hence, fish were more mobile during search and attacked prey at longer distance under bright conditions. Drift rates in streams are generally lower during the day (Elliott 1965, Elliott 1970) and may result in higher mobility to cope with reduced food availability. The positive correlation between light intensity and foraging radius is more intuitive, as the probability of detecting prey increases with light intensity (Elliott 2011), which should result in a longer detection range and hence a greater foraging radius (Metcalf et al. 1997). The same rationale should lead to higher prey attack rate during the day, but we found no relationship between prey attack rate and light intensity, which may also suggest lower food availability during the day (Elliott 1965, Elliott 1970). Although previous studies acknowledged the effect of light intensity on a suite of behavioral characters such as mobility (Young 1999), aggression (Valdimarsson and Metcalfe 2001), and prey attack rate (Elliott 2011), studies on diel patterns of foraging behavior in natural freshwater fish populations are rare (Watz et al. 2014, Larranaga and Steingrímsson 2015). However, monitoring diel behavior is necessary, because individuals may select different periods to feed and might vary in their efficiency at detecting and capturing prey at day or night (Watz et al. 2014). Also, most of the variation in temperature, light intensity, predation risk, and food availability occurs on a diel basis in freshwater systems.

The mobility of stream-dwelling fish is typically assumed to be limited by the increasing costs of swimming with increasing current velocity (Godin and Rangeley 1989), which generally results in increased mobility in habitats with slow-running water (Grant and Noakes 1988, Tunney and Steingrímsson 2012). In turn, prey detection and capture are higher in slow habitats (Piccolo et al. 2008). Our results are in accordance with these studies, as habitat use was an important determinant of foraging mode. Fish were more sedentary, attacked more prey, at shorter distances, and less often at the surface in fast habitats. Prey attack rate decreased with increasing water depth. This is more surprising, because Piccolo et al. (2007) found higher prey capture rates in deep habitats, because of increasing encounter rates. This could suggest that Arctic charr may suffer additional costs in deep habitats (e.g. higher density, Fingerle et al. 2016). This result can also be attributed to a higher proportion of surface feeding in deep habitats, leading to both longer foraging radii, and lower prey attack rate (e.g. through longer return times).

### 7.4.3 Conclusion

This study confirms that monitoring individuals systematically over a wide range of ecological situations is essential to assess the natural range of behavior exhibited in the wild (Bell et al. 2009), especially for species like salmonids, who face very variable conditions (day-night, cold-warm, slow-fast running water etc.). We showed that using a wide range of conditions and repeated estimates can prove useful to understand how behavioral variation is distributed among populations and individuals (Lewis et al. 1990, Husseneder et al. 1998), and how individuals respond to different ecological conditions. Importantly, food availability seems to be the primary driver of foraging mode, as our results show that Arctic charr are more sedentary when food availability is high (fast current, high temperature, low light levels). Further research should examine how behavioral flexibility under natural conditions relates to e.g. the level of specialization (Skúlason and Smith 1995) and evolutionary history (Stamps et al. 2012).

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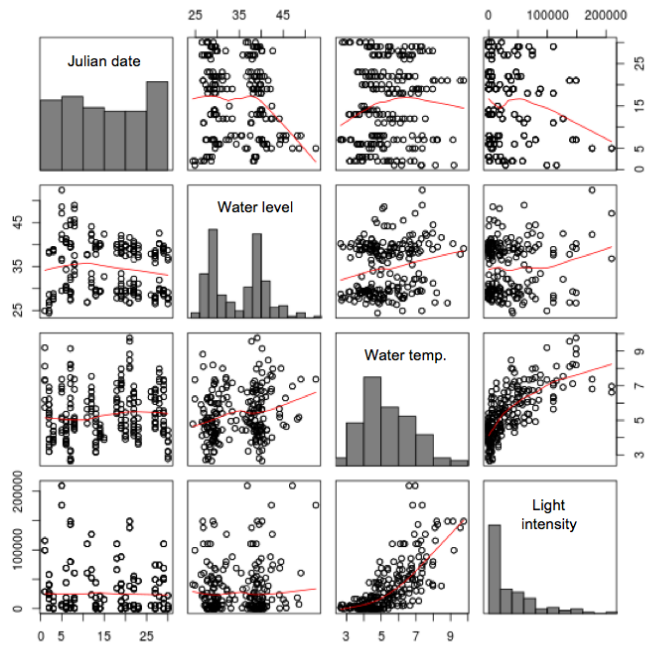
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## 8 Appendices



*Figure S1 (Chapter 6): Pairs plot of covariance between environmental variables included in the model-averaged generalized linear mixed model, evaluating the effect of population density and ecological variables on the probability of detecting activity in juvenile Arctic charr.*

*Table S1 (Chapter 6): Candidate models included in the model-averaged generalized linear mixed model. The effect of population density treatment and ecological variables (see footnote) on the probability of detecting activity in juvenile Arctic charr *Salvelinus alpinus* was tested using a threshold of one and three fish at low and high density, respectively. Enclosure was included as a random factor.*

Candidate models	Df	Log(L)	AICc	Delta AICc	AICc weight
1/2/3/4/5/6/8	9	-230.09	478.62	0.00	0.18
1/2/3/4/5/7/8	9	-230.20	478.84	0.22	0.16
1/2/3/4/5/8	8	-231.69	479.73	1.11	0.10
1/2/3/4/5/7/8/9	10	-229.66	479.86	1.24	0.09
1/2/3/4/5/8/9	9	-230.82	480.08	1.46	0.08
1/2/3/4/5/6/8/10	10	-229.77	480.09	1.47	0.08
1/2/3/4/5/7/8/10	10	-229.86	480.27	1.65	0.08
1/2/3/4/5/6/8/9	10	-229.89	480.33	1.71	0.08
1/2/3/4/5/6/7/8	10	-229.89	480.33	1.71	0.07
1/2/3/4/5/8/10	9	-230.97	480.39	1.78	0.07

Variables included as fixed factors in component models: 1 - Julian date; 2 - Light intensity; 3 - Water temperature; 4 - Water level, 5 - Density treatment; 6 - Light intensity and Julian date; 7 - Water temp. and Julian date; 8 - Water temp. and Light intensity; 9 - Light intensity and Water level; 10 - Water temp. and Water level.

*Appendix S1 (Chapter 6): ANOVA tables testing for the effect of density treatment on (a) individual activity, (b) dispersion of activity, and (c) individual growth rate, including experimental round and enclosure pair as random effects and, in the case of growth, individual activity rate, initial body mass, and the interaction between density treatment and initial body mass as covariates. Bold P values indicate significant impact on dependent variable.*

(a) Individual activity rate: Activity ~ Density + Error (Round + Pair)

Error: Round

	Df	Sum sq.	Mean sq.
Treatment	1	0.139	0.139

Error: Pair

	Df	Sum sq.	Mean sq.
Treatment	1	0.191	0.191

Error: Within

	Df	Sum sq.	Mean sq.	F value	P value
Treatment	1	0.045	0.045	4.475	<b>0.038</b>
Residuals	67	0.675	0.010		

(b) Dispersion of activity: SD of Activity ~ Density + Error (Round + Pair)

Error: Round

	Df	Sum sq.	Mean sq.
Treatment	1	0.002	0.002

Error: Pair

	Df	Sum sq.	Mean sq.
Treatment	1	0.003	0.003

Error: Within

	Df	Sum sq.	Mean sq.	F value	P value
Treatment	1	0.003	0.003	4.639	<b>0.036</b>
Residuals	56	0.035	0.001		

(c) Individual growth rate: Growth ~ Density + Activity + Initial body mass + Density\*Initial body mass + Error (Round + Pair)

Error: Round

	Df	Sum sq.	Mean sq.
Treatment	1	> 0.001	> 0.001

Error: Pair

	Df	Sum sq.	Mean sq.
Treatment	1	> 0.001	> 0.001

Error: Within

	Df	Sum sq.	Mean sq.	<i>F value</i>	<i>P value</i>
Treatment	1	> 0.001	> 0.001	0.197	0.658
Activity rate	1	> 0.001	> 0.001	2.272	0.137
Initial mass	1	> 0.001	> 0.001	3.118	0.082
Density*Initial mass	1	> 0.001	> 0.001	1.355	0.249
Residuals	64	0.005	> 0.001		