

Háskóli Íslands  
Verkfræði- og náttúruvísindasvið  
Líf- og umhverfisvísindadeild



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**Territorial and foraging behaviour of juvenile salmonids in Icelandic streams**

**By**

**Guðmundur Smári Gunnarsson**

M.Sc. thesis  
Advisors: Dr. Stefán Ó. Steingrímsson  
and Dr. Sigurður S. Snorrason

Reykjavík  
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## **Yfirlýsing**

Hér með lýsi ég því yfir að ritgerð þessi er samín af mér og að hún hefur hvorki að hluta né í heild verið lögð fram áður til hærri prófgráðu.

Undirskrift: \_\_\_\_\_

## **Abstract**

Territoriality and foraging behaviour can play a major role in determining the abundance and distribution of mobile animals. To date, territorial behaviour of young-of-the-year (YOY) salmonids is typically described for sit-and-wait individuals that defend territories from a single foraging station, but ignored for individuals that are more mobile or use several foraging stations. In this study, I describe the territorial and foraging behaviour of 61 YOY Arctic charr (31) and brown trout (30), in relation to key ecological factors in six rivers (three rivers per species) in NW-Iceland. Individual territory size was estimated, irrespective of mobility, based on locations of all observed foraging and aggressive acts over 40 minutes. Territories were generally larger for Arctic charr than for brown trout, which corresponded with high and low mobility, respectively. Also within each species, more mobile individuals used larger territories. Territories were also influenced by ecological correlates: i.e. territory size generally increased with body size, declined with increased food abundance, but surprisingly, increased as intruder pressure increased. Interestingly, Arctic charr territories overlapped more and appeared to be defended less efficiently than brown trout territories. In general, this study suggests that mapping territories for all individuals, irrespective of whether they remain sedentary at a single foraging station or exhibit more mobility, provides a novel view on territoriality in stream-dwelling salmonids. Multiple central-place territories and territories of widely foraging individuals may not always pertain to the same laws as single central-place territories and highlight the need for further studies on local space use of stream-dwelling salmonids and its population consequences.

## Samantekt

Óðals- og fæðuatferli er almennt talið hafa mikil áhrif á þéttleika og dreifingu dýra. Hingað til hefur óðalsatferli ungra laxfiska helst verið lýst fyrir þá einstaklinga sem sitja-og-bíða á tiltekinni fæðustöð og ráðast á fæðu og keppinauta sem hætta sér of nærri. Rannsóknir ná því sjaldan til hreyfanlegri einstaklinga sem synda um í leit að fæðu eða nota margar fæðustöðvar. Í þessari rannsókn lýsi ég óðals- og fæðuatferli hjá vorgömlum (0+) laxfiskum, 31 bleikju og 30 urriðum, og athuga tengsl atferlis þeirra við vistfræðilegar breytur í sex ám (þrjár ár fyrir hvora tegund) á NV-landi. Óðalsstærð var metin fyrir hvern einstakling, óháð hreyfanleika og fjölda fæðustöðva, með því að kortleggja fæðunám og árásir á aðra einstaklinga yfir 40 mínútna tímabil. Bleikja notaði stærri óðul en urriði og var einnig hreyfanlegri við fæðunám. Ennfremur voru hreyfanlegri einstaklingar innan hvorrar tegundar með stærri óðul en þeir sem sátu-og-bíðu eftir fæðu. Stærð óðala var einnig háð vistfræðilegum þáttum: óðul stækkuðu eftir því sem einstaklingar voru stærri, minnkuðu við aukið fæðuframboð og voru, ólíkt því sem spáð var, stærri við háan þéttleika fiska. Þá virtust óðul bleikju skarast meira en hjá urriða og ekki vera eins vel varin. Almennt má segja að óðul sem eru kortlögð fyrir alla einstaklinga, þ.e. óháð því hvort þeir séu hreyfanlegir við fæðunám eða sitji-og-bíði á einni fæðustöð veiti nýstárlegar upplýsingar um óðalsatferli laxfiska í straumvatni. Óðul einstaklinga sem eru hreyfanlegir eða nota margar fæðustöðvar lúta þannig ekki alltaf að sömu lögmálum og óðul sem kortlögð eru frá einni stöð, t.d. hvað varðar fylgni við vistfræðilega þætti. Greinileg þörf er á frekari rannsóknum á slíkum óðulunum til að kanna áhrif þeirra á þéttleika, vöxt, afföll og far einstaklinga, og aðra þætti er móta stofnvistfræði laxfiska.

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## **Table of contents**

Yfirlýsing .....	ii
Abstract .....	iii
Samantekt.....	iv
Acknowledgment .....	v
Table of contents .....	vi
List of Tables .....	viii
List of Figures .....	ix
<b>Chapter 1 – General Introduction.....</b>	<b>1</b>
<b>Chapter 2 – Territorial and foraging behaviour of young-of-the-year Arctic charr (<i>Salvelinus alpinus</i>) and brown trout (<i>Salmo trutta</i>) in Icelandic rivers .....</b>	<b>6</b>
Introduction.....	6
Material and methods.....	10
General information .....	10
Behavioural observations .....	11
Habitat measurements .....	13
Spatial analysis.....	14
Statistical analysis .....	15
Results.....	16
Territorial and foraging behaviour.....	16
Foraging mode and territory size .....	17



Territory size and ecological factors .....	18
Patterns of territorial defence .....	20
Discussion .....	21
Variation in territory size and foraging behaviour .....	21
Territory size and ecological factors .....	23
Territorial defence .....	25
Population ecology of stream-dwelling salmonids .....	27
<b>Chapter three – General Discussion and Conclusions.....</b>	<b>40</b>
<b>References .....</b>	<b>43</b>

## List of Tables

Table 2.1. Behavioural characteristics of Arctic charr and brown trout in six Icelandic rivers in NW-Iceland .....	29
Table 2.2. Ecological characteristics for the territories used by Arctic charr and brown trout in six rivers in NW-Iceland .....	30
Table 2.3. A multivariate analysis testing for the influence of species and ecological predictors on territory size for Arctic charr and brown trout in six Icelandic rivers .....	31
Table 2.4. Spatial distribution of aggressive acts within territories of 21 Arctic charr and 20 brown trout in 6 Icelandic rivers .....	32

## List of Figures

Figure 1.1. A hypothetical depiction of the benefits (B) and costs (C) of defending a territory .....	5
Figure 2.1. Location of the six study rivers in NW-Iceland. Rivers for Arctic charr and brown trout populations .....	33
Figure 2.2. Variability in territory size for Arctic charr and brown trout in six Icelandic rivers.....	34
Figure 2.3. Territory size for the study populations of Arctic charr and brown trout in NW-Iceland.....	35
Figure 2.4. The relationship between territory size and mobility prior attacking prey for Arctic charr and brown trout in six rivers in NW-Iceland.....	36
Figure 2.5. Territory size for 31 Arctic charr and 30 brown trout as a function of foraging radius, based on six rivers in NW-Iceland.....	37
Figure 2.6. Territory size for Arctic charr and brown trout in six Icelandic rivers as a function of ecological factors.....	38
Figure 2.7. Estimated percent habitat saturation for Arctic charr and brown trout in six Icelandic rivers .....	39

## **Chapter 1 – General Introduction**

To describe the population ecology of animals it can be useful to study individual behavioural traits in relation to environmental variables. Specific behaviours of animals are favoured by natural selection through individual fitness maximization, whereas population ecology has been criticized for lacking such an over-all theory to explain and predict how and why populations fluctuate or vary in abundance and distribution (Sutherland 1996). Species distribution can for instance be determined by foraging behaviour (Huey and Pianka 1981, Nakano 1999) and territorial behaviour can determine the density of species or populations (Patterson 1980).

Animals often defend resources by excluding, inter- and/or intraspecifically, other individuals from specific areas. These resources can e.g. be food, shelter, mates and breeding sites or an area that otherwise increases the fitness of the defending individual (Noakes 1978). Territorial behaviour is not only beneficial for individuals but has costs as well, e.g. predation risk, energy expenditure and risk of injury. Brown (1964) reported that individuals should only defend territories when the benefits are greater than the costs and that the optimal territory size should yield the maximum net gain (Schoener 1983) (Figure 1.1). The maximum net gain and thus territorial defence (e.g. territory size and aggression) can depend on and vary with ecological characteristics, i.e. the costs and benefits differ between habitats and competitive scenarios (Davies and Houston 1984; Krebs and Davies 1993). Economic defendability is generally believed to decrease with increased competitor density, but increases as resources become more abundant, predictable and clumped in space (Grant 1997). Interestingly, long- and

short-term territories can be defended differently, e.g. holders of short-term territories often respond faster to temporal variation in resources (Patterson 1980).

Species typically classified as territorial may also include individuals that do not defend territories. Such variation within species exist for example in brown trout (*Salmo trutta*) (Elliott, 1990) and oystercatchers, (*Haematopus ostralegus*) (Ens et al. 1992) where individuals “float” between the territories of other individuals (floaters). Floaters have been reported for feeding (Elliott 1990), mating (Smith and Arcese 1989) and breeding (Ens et al. 1992) territories. Puckett and Dill (1985) also report individuals that are aggressive but do not defend territories (non-territorial). Often, floaters and non-territorial individuals are found in the same environment as territory holders but for some reason not all individuals hold territories. Possible reasons for this behavioural variability include dominance hierarchies and reduced economic defendability where competitors are in high number (Krebs and Davies 1993).

Animals also show great variance in how they search for and attack prey, both within and among species (Helfman 1990). Pianka (1966) introduced two foraging modes common among mobile animals, one is the “sit-and-wait” mode where an individual is sedentary and ambushes prey and attacks when it is close enough. Alternatively, “widely foraging” individuals cruise around searching actively for food (Huey and Pianka 1981). In general, consumers are likely to sit-and-wait when prey is mobile and predictable in space. Alternatively, when prey is less mobile and less predictable spatially, the widely foraging mode should be more beneficial (Huey and Pianka 1981). Importantly, at least for some species, individuals can switch between these foraging modes when ecological conditions change (Fausch et al. 1997; Nakano et al. 1999). Mobile foragers are often assumed

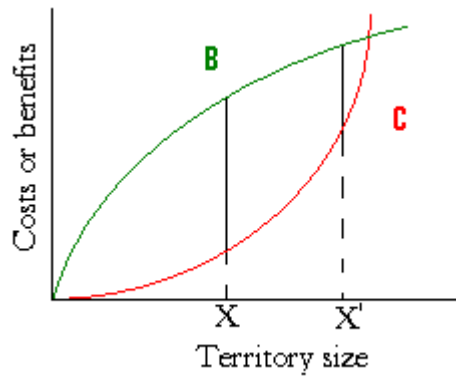
to use bigger home ranges than sit-and-wait foraging individuals although this has rarely been confirmed (but see Katano 1996; Verwajen and Van Darnme 2008) In addition to foraging mode variability, the foraging effort of mobile animals may either be initiated from a single central-place (e.g. nest, burrow; Andersson 1981) or multiple central-places (e.g. sleeping sites and chicks; Chapman et al. 1989; McLaughlin and Montgomerie 1989).

A great variation in territorial and foraging behaviour of juvenile salmonids (Puckett and Dill 1985; Grant and Noakes 1987; Nakano et al. 1999; Tunney 2008), and their relatively small home ranges (Minns 1995), provide a good opportunity to study how these behavioural traits covary, and depend on ecological conditions. Juvenile salmonids may e.g. sit-and-wait for drifting prey (Elliott 1990; Grant et al. 1989; Keeley 2000) or actively seek out prey (i.e. forage widely) (Grant and Noakes 1987; Tunney 2008). Furthermore, sit-and-wait salmonids may either attack prey from one foraging station (*sensu* the central-place territorial model, CPTM) (Elliott 1990; Grant et al. 1989; Keeley 2000) or from multiple stations (*sensu* the multiple CPTM) (Steingrímsson and Grant 2008). To date, however, most studies attempt only to map space use around a single foraging station, whereas very few studies attempt to map territories of widely foraging salmonids, or sit-and-wait individuals that use multiple foraging stations (but see e.g. Armstrong et al. 1999; Økland et al. 2004 for studies that map space use via PIT or radio tag-technology without direct observations of foraging behaviour). The territorial behaviour of young-of-the-year (YOY) salmonids in the wild has rarely been studied outside of the CPTM, perhaps because they have not been tagged individually in behavioural studies until recently. This sampling bias is unfortunate, because information on space use behaviour can provide important insights on the

population regulation of stream-dwelling salmonids, especially during early life history, where mortality and/or migration may occur frequently due to limited energy reserves and intense competition for space (Elliott 1994; Steingrímsson and Grant 1999). A recent tagging technique, however, has made it possible to individually tag YOY salmonids (see e.g. Steingrímsson and Grant 2003), and makes it possible to observe more mobile individuals in the wild.

Icelandic freshwater systems are only inhabited by five (or seven, see Jónsson and Pálsson 2006) fish species, three of which are salmonids: Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*), and Atlantic salmon (*Salmo salar*) (Guðbergsson and Antonsson 1996). In contrast, however, Icelandic freshwater systems are very variable in ecological and physical characteristics, e.g. due to variable age and permeability of the bedrock. Hot and cold springs also influence many rivers, whereas others are made of glacial and/or run-off waters (Gardarsson 1979). Situations where few species live in a highly variable environment, provide an interesting opportunity to observe behaviour over a wide range of ecological conditions, and in the presence or absence of interspecific competition. These features make Icelandic freshwater very suitable for behavioural studies on salmonids.

In this study, territoriality and foraging behaviour of YOY Arctic charr and brown trout were observed in six rivers in northern Iceland, three for each species. Territory size and territorial behaviour in Arctic charr has not been studied in natural systems before, whereas for YOY brown trout, territory size has only been reported with focus on the single CPTM method. In addition, no studies are currently available on territorial behaviour of stream-dwelling fish in Icelandic rivers.



**Figure 1.1.** A hypothetical depiction of the benefits (B) and costs (C) of defending a territory. The optimal territory size can be found where the net gain of defence (benefits – costs) is maximized (X). Defending other territory sizes (for instance X') is not as economically beneficial. The graph is modified from Schoener (1983).



## **Chapter 2 – Territorial and foraging behaviour of young-of-the-year Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in Icelandic rivers**

### **Introduction**

Animals may increase their fitness by defending resources such as food, shelter and mates (Davies and Houston 1984). Such aggressive behaviour can result in competition for space (i.e. territories) which provides access to these resources, and may play a role in determining local density and even population size (Patterson 1980). Importantly, the size and defence of territories, and thus their effect on population regulation, often depend on a range of ecological and environmental factors, e.g. body size (Harestad and Bunnell 1979), food abundance (Hixon 1981; Kodric-Brown and Brown 1978) and competitor density (Sutherland 1996). More specifically, territory size typically increases with body size (Schoener 1983), but decreases when food availability and consumer density increase in a variety of taxa (Stimson 1973; Dill et al. 1981; Tricas 1989; Mayers et al. 1979). However, although territory size is reported in many studies, these less often include detailed information on how these areas are exploited and defended (but see Meadows 2001; Stamps and Krishnan 1998)

Insights into how individuals exploit territories and other local areas can e.g. be gained from the foraging mode literature. Pianka (1966) introduced two common foraging modes among mobile animals, the “widely forage” and the “sit-and-wait” modes (see also: Huey and Pianka 1981). Pianka (1983) also assumed

that sit-and-wait individuals have smaller home ranges than those that forage widely. Empirical data connecting home range size and foraging mode are scarce but do however support this assumption for lizards (Verwajen and Van Darnme 2008) and fish (Katano 1996). In general, studying territory size and foraging mode concurrently should yield a more comprehensive understanding of how individuals respond to variation in ecological conditions.

Territorial behaviour of juvenile salmonids in streams (Kalleberg 1958) has mainly been described via the central-place territory model (CPTM) which assumes that sit-and-wait individuals forage and attack intruders from, and return to, a single foraging station (Grant et al. 1989; Keeley 2000; Elliott 1990; but see Keeley and Grant 1995; Nakano 1995). Young-of-the-year (YOY) salmonids, however, have been reported to use other behavioural tactics, such as mobile foraging (Grant and Noakes 1987; Nakano et al. 1999), where individuals search actively for prey, and multiple central-place foraging, where individuals sit-and-wait for prey but switch among several foraging stations (i.e. multiple CPTM; see Steingrímsson and Grant 2008). Individuals that exhibit such variation have rarely been included in studies that map space use behaviour of YOY salmonids (but see e.g. Nakano 1995 for older individuals). This lack of information on individuals that do not conform to the CPTM may exist because these fish have, until recently, been difficult to monitor in the wild (but see Steingrímsson and Grant 2008). Consequently, the current knowledge on how the territory size of YOY salmonids varies across ecological situations is also largely based on single central-place territories.

The effect of ecological factors on territory size of YOY salmonids with focus on the single CPTM has been documented several times. In general,

individuals are believed to increase their fitness by adjusting territory size and foraging behaviour in accordance to ecological conditions. For instance, larger fish defend larger territories presumably to gain access to enough food to meet their metabolic demands, whereas territory size decreases with increased food abundance for similar reasons, i.e. individuals can maintain their food intake on a smaller territory in higher food abundance (Keeley and Grant 1995; Keeley and McPhail 1998; see Grant and Kramer 1990 for a review). Territories have also been reported to decrease with increased intruder pressure, especially at relatively high densities (Keeley 2000). Low visibility, e.g. due to large substrate on the river bottom, may also decrease territory size (Kalleberg 1958; Valdimarsson and Metcalfe 2001; Imre et al. 2002). In terms of foraging mode, individuals are typically more mobile where prey is sedentary (i.e. in slow-running water) but sit-and-wait where prey is more mobile (i.e. in fast-running water) (Grant and Noakes 1987). Based on the few available studies, territories of individuals that forage from several stations may be larger, influenced by dominance status (Nakano 1995), but less clearly so with e.g. body size (Steingrímsson and Grant 2008).

Only three native salmonid species exist and overlap in Icelandic freshwater systems, i.e. Arctic charr, brown trout and Atlantic salmon (Guðbergsson and Antonsson 1996). Arctic charr are generally found in less productive rivers and in slower-running water than the brown trout and Atlantic salmon, which are found in more productive streams in the intermediate and the fastest water flow, respectively (Guðjónsson 1990). In contrast with the low number of freshwater fish species (5-7; Guðbergsson and Antonsson 1996; Jónsson and Pálsson 2006), the freshwater systems they inhabit are highly diverse due to bedrock of varying age and permeability, resulting in variation in water

conductivity and food abundance. Hot or/and cold springs influence many streams as well as melting glacial water and run-off water (Garðarson 1979). The limited number of species and the variable habitats of salmonids in Iceland give good opportunities to study the effect of key ecological factors (e.g. food availability, intruder pressure) on their behaviour. To date, however, we are only aware of a single study where direct behavioural observations have been made of salmonids in Icelandic rivers (Tunney 2008).

My general goal in this thesis is to describe and compare territorial and foraging behaviour of two salmonid species in Icelandic streams, Arctic charr and brown trout, and to examine how these behaviours relate to key ecological variables, such as body size, food availability, water current velocity and intruder pressure. First, I predict that because Arctic charr are generally found in less productive and slower running water than brown trout, the former species should use larger territories and be more mobile while foraging. Second, I predict that more “widely foraging” individuals of both species should use larger territories; in this study, widely foraging behaviour is measured as increased mobility prior to attacking prey and increased distance at which prey is attacked (i.e. foraging radius). Third, I predict that territory size should increase with body size but decrease with increased food abundance, intruder pressure and current velocity. Finally, patterns of defence will be examined for both species. If for instance, Arctic charr territories are, as predicted, larger than brown trout territories, we should expect them to be defended less efficiently.

## **Material and methods**

### ***General information***

Wild populations of Arctic charr and brown trout were studied in six rivers in northern Iceland, three for each species, from June to August in 2007 and 2008. In total, 31 YOY Arctic charr and 30 YOY brown trout were observed (10-11 fish in each river). All six rivers are in the vicinity of Skagafjörður in NW-Iceland (Figure 2.1). The rivers were selected to ensure that individuals of both species were observed under highly variable conditions in terms of physical characteristics and stream productivity. Within each river, potential study sites/individuals were initially searched for via snorkelling or by walking along the riverbanks. Again, study sites within streams were selected to represent as variable environments as possible in terms of water flow and depth, therefore side channels and tributaries were searched and used as well. Overall YOY salmonids appeared to be clumped in space and in some rivers only few areas were available for observation.

In each river, several potential study fish were captured with dip nets, either by snorkelling or from the riverbank and then anesthetized for a short period of time in a phenoxyethanol solution. Fork length was measured and is reported to the nearest 0.1 cm. Fish were individually tagged by injecting fluorescent elastomer paint (Northwest Marine Technology, Inc.; colours: red, green or orange) into two of six potential tagging location on each fish (see Steingrímsson and Grant 2003). When fish had recovered from anaesthesia, it was returned in a dip net to the exact location of capture. No fish was observed for behaviour until at least one day after tagging.

In situations where fish density was low and the risk of confusing untagged individuals was deemed minimal, untagged fish were also observed (26 out of the total 61 focal fish). For untagged Arctic charr (14 fish) a picture of the individual was drawn for identification to avoid a risk of confusion with other individuals; this was possible because of often distinct and easily recognizable individual parr marks in YOY Arctic charr. However, untagged brown trout (12 fish) are harder to recognize, and if the focal fish disappeared and there were any doubts about its identification upon reappearance, the observation was cancelled and not used. Occasionally, untagged fish were not caught after observation (nine Arctic charr and six brown trout). In these cases, body size was visually estimated with regards to measured benthic landmarks (e.g. substrate).

### ***Behavioural observations***

Observations were recorded on waterproof mylar sheets (28 individuals) or by videotaping the focal fish (33 individuals). Each fish was observed for approximately 40 min (range = 37-43 min), either from the stream bank or by snorkelling. Observation started no earlier than 10 min after fish identification to ensure that the observer would not affect the behaviour. During the 40-min period aggressive and foraging behaviour was observed by documenting the direction (1 – 12 o'clock, 12 being upstream) and the radius (body lengths) of each noticed foraging and aggressive act. The vertical location of foraging attempts in the water column was also recorded, i.e. whether the fish fed from the river substrate, water column or water surface. I also observed whether the focal fish started the prey attack from a sit-and-wait position or while moving. If a fish had moved

continuously more than one body length before attacking the prey, that foraging attempt was classified as mobile. Alternatively, if fish moved one body length or less before attacking prey, the foraging attempt was categorized as a sit-and-wait attempt (see Tunney 2008). After the 40-min observation, the focal fish was watched for additional 1-5 min where foraging attempts were counted to estimate foraging rate.

Mapping of territories was facilitated by placing a coordinate grid in each study site, typically at least a day before observation. The grid was composed of several 1-m long black metal poles (width = 1 cm), marked with grey duct taped at every 10 cm, which were placed along, and perpendicular, to the stream flow on the river substrate. If the focal fish did not use distinct foraging stations, location of each foraging attempt and aggressive act was recorded based on its position (i.e., x-y coordinate) within the grid. If the focal fish used fixed foraging stations, the location of each station was marked on a map drawn of the river substrate. Each station was then measured (to the nearest 1 cm) using the coordinate grid, or by stringing a measuring tape through the territory, and measuring the distance from the tape to each foraging station (see similar methods in Steingrímsson and Grant 2008). For fish using foraging stations, the actual x-y coordinate of each foraging attempt and aggressive act was thus estimated based on the location of each station, and the vector of the attempt (radius and direction, see above). Twenty-two Arctic charr were observed by using the coordinate grid and nine were mapped based on their foraging stations. One brown trout was mapped using the grid, 26 based on the location of their foraging stations and three by using both systems.

### ***Habitat measurements***

The habitat of each territory was measured for several important ecological variables (Table 2.2). Water current velocity was measured over three 5-sec intervals for each fish at 40% depth from the bottom with a current velocity meter (Marsh-McBirney FLO-MATE Model 2000). Water depth was measured to the nearest centimetre using a meter stick. Dominant substrate size was estimated in four equal areas, in 50 cm radius from the middle of the territory. The classification was as follows: 1: clay and silt = <0.0625 mm, 2: sand = 0.0625 - 2 mm, 3: gravel = 2 - 16mm, 4: pebble = 16 - 64 mm, 5: cobble = 64 - 256 mm, 6: bolder = >256 mm, 7: bedrock (see DeGraaf and Bain 1986). Water temperature was measured with a portable thermometer to the nearest 0.1°C. Intruder pressure was measured by counting the number of fish in approximately 1m radius from the focal fish on a regular basis (mean = 5.9 times) over the 40-min observation.

Food abundance was estimated by placing a 250 µm drift net (net opening = 25 x 40 cm) in the middle of each territory for 20 min after observing the focal fish. During sampling, current velocity was measured at three different locations (middle, right and left) in the mouth of the drift net at 50% of the drift net depth. Drift samples were stored in 70% ethanol solution and processed in the laboratory. All food items collected in the drift net were counted and analyzed under a stereo microscope, categorizing them into families. Food items that were considered to be too big (based on Keeley and Grant 2001) for YOY fish to eat were removed and not included in the count. Finally, food abundance (i.e. invertebrate drift rate) was calculated as the number of food items per minute entering the drift net area. If the net opening was not fully submerged in the water during sampling, drift rate was prorated to the net height.



### *Spatial analysis*

A digital map for each territory was created in ArcView GIS 3.2 (with the Animal Movement extension added; Hooge and Eichenlaub 2000) for every observed fish. Territory size was estimated via the minimum convex polygon method (MCP) (Schoener 1981) using the location of every aggressive and foraging act (MCP<sub>100%</sub>). For a comparison, territory size was also estimated after removing 5% of spatial outliers for each territory (MCP<sub>95%</sub>). Because the two estimates were highly correlated for both species (Arctic charr:  $\log_{10}\text{MCP}_{100\%} = -0.483 + 0.983\log_{10}\text{MCP}_{95\%}$ ,  $n = 31$ ,  $r^2 = 0.864$ ,  $p < 0.001$ ; Brown trout:  $\log_{10}\text{MCP}_{100\%} = -1.432 + 1.105\log_{10}\text{MCP}_{95\%}$ ,  $n = 30$ ,  $r^2 = 0.889$ ,  $p < 0.001$ ), and both estimates were related to relevant ecological correlates in a similar manner, only MCP<sub>100%</sub> will be reported for territory size analyses. For individuals that showed aggression during the study period, I also calculated the territory size based on the mean distance travelled towards an intruder from a foraging station (i.e. mean aggressive radius<sup>2</sup> \*  $\pi$ ), a method typical for previous central-place studies (Keeley 2000; Keeley and Grant 1995). In this study, this single central-place territory-size estimate area will be referred to as “aggressive area”.

Two main methods were used to examine if territories were defended differently by the two species. First, I examined the distribution of aggressive acts directed toward conspecifics within the territory. To do this, the MCP boundary for all foraging attempts was drawn for 100%, 75% and 50% foraging area (MCP<sub>FOOD</sub>) by removing 0%, 25% and 50% of spatial outliers, respectively, and counting aggressive acts inside and outside of each MCP<sub>FOOD</sub>. The proportion of aggressive acts outside each MCP<sub>FOOD</sub> was then calculated for each individual and the mean for each MCP<sub>FOOD</sub> for both species calculated (see Steingrímsson and Grant 2008).

Second, I estimated percent habitat saturation (PHS) to examine how and if territories were overlapping or shared among individuals. For each individual, PHS was calculated as:

$$\text{PHS} = (D_c / D_{\text{max}}) * 100$$

where  $D_c$  is counted fish density per  $\text{m}^2$  and  $D_{\text{max}}$  is calculated maximum density per  $\text{m}^2$  assuming all neighbouring fish defended a territory of the same size as the focal fish, i.e. maximum density ( $\text{fish. m}^{-2}$ ) =  $1 / \text{territory size (m}^2)$  (see Grant and Kramer 1990 for similar methods for cohorts). A PHS that exceeds 100%, suggests that territories are likely to overlap or be shared, or even that fish may simply not defend specific areas.

### ***Statistical analysis***

Behavioural and ecological traits are summarized and reported as mean and range for each trait. If data were not normally distributed, these were either  $\log_{10}$  or square root transformed (Sokal and Rohlf 1994).  $\text{MCP}_{100\%}$ , fork length, foraging radius, proportion of mobile forages and food abundance were thus  $\log_{10}$  transformed whereas current velocity and intruder pressure were square root transformed. Because the proportion of mobile forages was equal to zero for some individuals, 0.01 was added to the original value to allow for  $\log_{10}$  transformation. For normally distributed data, means were tested with t-tests but otherwise Mann-Whitney (Wilcoxon) tests were used. To examine the effect of ecological factors on territory size, I first tested if the slopes between each ecological factor and territory size differed between the species by examining if there was an interaction between the two variables (ANCOVA<sub>species x ecological factor</sub>). Second, to examine the

influence of all measured predictors of territory size simultaneously, a general linear model was constructed with  $\log\text{MCP}_{100\%}$  as a dependent variable and species (as a categorical factor), fork length, drift rate, current velocity, intruder pressure, substrate size and water depth as independent variables. To simplify these results, this model was driven stepwise backwards, excluding variables with a p-value over 0.15; importantly, the same independent variables contributed significantly to the overall model irrespective whether these non-significant variables were included or not. Finally, a simple linear regression was used to describe the relationship between the territory size and significant ecological factors (from the multivariate analysis) for each species.

## **Results**

### ***Territorial and foraging behaviour***

For YOY Arctic charr, the location of 4077 foraging attempts and 169 aggressive acts were recorded for 31 fish (fork length: mean = 4.4 cm) during a total of 1244 minutes of observation. For YOY brown trout, the location of 6870 foraging attempts and 83 aggressive acts were recorded in total for 30 YOY brown trout (fork length: mean = 4.0 cm) over 1200 minutes of observation.

Territory size ( $\text{MCP}_{100\%}$ ) was on average 4.4 times larger for Arctic charr (mean =  $0.558 \text{ m}^2$ ) than for brown trout (mean =  $0.127 \text{ m}^2$ ) (Table 2.1; Figure 2.2;  $\log_{10}\text{MCP}_{100\%}$ : t-test:  $t = 5.346$ ,  $df = 59$ ,  $p < 0.001$ ). These territory size patterns also emerge when the mean territory size is examined across the study populations; the Arctic charr populations had consistently larger territories (range in mean territory size =  $0.287\text{-}0.780 \text{ m}^2$ ) than the brown trout populations (range in mean

territory size = 0.089-0.177 m<sup>2</sup>) (Figure 2.3). Importantly, MCP<sub>100%</sub> territories for Arctic charr and brown trout are on average 8.3 and 2.3 times larger, respectively, than the respective aggressive areas, based on the mean aggressive radius, assuming circular territories and that all aggressive acts originate from one central-place (i.e. the circular method; see methods) (Table 2.1). No statistical difference was detected between the two species in the size of these aggressive areas (t-test,  $t = 0.534$ ,  $df = 38$ ,  $p = 0.59$ ).

Arctic charr and brown trout fed predominantly on drifting invertebrates and only occasionally on benthic prey. More specifically, Arctic charr attacked prey 6.1 times per minute on average (Table 2.1), of which 92.5% (range: 38.1-100%) attempts were directed toward the water column, 4.1% (range: 0.0-63.4%) toward the water surface and only 3.7% (range: 0.0-35.2%) towards benthic prey. Similarly, brown trout attacked prey 8.4 times per minute (Table 2.1), of which 92.1% (range: 55.6-100%), 1.7% (range: 0.0-8.7%) and 6.3% (range: 0.0-39.4%) were directed towards the water column, water surface and the river substrate, respectively.

### ***Foraging mode and territory size***

This study supports the assumption that widely foraging individuals use larger territories than sit-and-wait individuals. First, at the species level, Arctic charr use larger territories than brown trout (Figure 2.4) and are also more mobile ( $\log_{10}$  proportion mobile forages + 0.01; t-test:  $t = 5.541$ ,  $df = 55$ ,  $p < 0.001$ ). Second, a similar trend is observed at the individual level for both species where territory size increases with higher proportion of mobile forages (Linear regression: Arctic charr:

$\log_{10}$  territory size ( $\text{m}^2$ ) = 0.805  $\log_{10}$  (proportion mobile forages + 0.01) – 0.105, n = 27, p = 0.004; brown trout:  $\log_{10}$  territory size ( $\text{m}^2$ ) = 2.035  $\log_{10}$  (proportion mobile forages + 0.01) + 0.934, n = 30, p < 0.001) (Figure 2.4).

If greater foraging radius is used as indicator of foraging “widely”, the results are less clear. The two species do not differ in the distance at which they attacked food, i.e. foraging radius (in body lengths) (Table 2.1;  $\log_{10}$  foraging radius: t-test, t = -0.194, df = 59, p = 0.847). Also, although a relationship was detected between territory size and foraging radius for brown trout (Linear regression:  $\log_{10}$  territory size ( $\text{m}^2$ ) = 2.375  $\log_{10}$  foraging radius (body lengths) – 2.841, n = 30, p = 0.013) no such relationship was detected for Arctic charr (Linear regression:  $\log_{10}$  territory size ( $\text{m}^2$ ) = -0.330  $\log_{10}$  foraging radius (body lengths) – 1.006, n = 31, p = 0.727) (Figure 2.5).

### ***Territory size and ecological factors***

A multivariate analysis reveals that the variation in territory size is explained by species differences and three ecological variables; fork length, food abundance and intruder pressure (Table 2.2; Table 2.3). First, as expected, territories of YOY Arctic charr were larger than territories of YOY brown trout, even after removing the effects of fork length, food abundance and intruder pressure (see Table 2.3; p = 0.002). Second, and as predicted, territory size increased with body size (i.e. fork length) after removing the effects of species, food abundance and intruder pressure (Table 2.3; p = 0.003; Figure 2.6a). The slope of this relationship did not differ between species (ANCOVA<sub>species x fork length</sub> :  $F_{1,57} = 0.361$ , p = 0.551). However, when the two species were analysed separately, territories increased with body size

for brown trout (Linear regression:  $\log_{10}$  territory size ( $\text{m}^2$ ) = 4.745  $\log_{10}$  fork length (cm) – 8.965,  $n = 30$ ,  $p = 0.035$ ), but not significantly so for Arctic charr (Linear regression:  $\log_{10}$  territory size ( $\text{m}^2$ ) = 3.019  $\log_{10}$  fork length (cm) – 5.526,  $n = 31$ ,  $p = 0.067$ ) (Figure 2.6a). Third, as predicted, territory size decreased with increased food abundance, even after removing the effects of other independent variables (Table 2.3;  $p = 0.002$ ). Between the two species, the slope of this relationship did not differ significantly (ANCOVA<sub>species x food abundance</sub>:  $F_{1,57} = 0.58$ ,  $p = 0.449$ ). For the species separated, the relationship was significant for Arctic charr (Linear regression:  $\log_{10}$  territory size ( $\text{m}^2$ ) = -0.376  $\log_{10}$  drift rate ( $\text{no. min}^{-1} \cdot \text{net}^{-1}$ ) – 0.812,  $n = 31$ ,  $p = 0.048$ ) but not for brown trout (Linear regression:  $\log_{10}$  territory size ( $\text{m}^2$ ) = -0.057  $\log_{10}$  drift rate ( $\text{no. min}^{-1} \cdot \text{net}^{-1}$ ) – 2.333,  $n = 30$ ,  $p = 0.857$ ) (Figure 2.6b). Fourth, unexpectedly, territory size showed a general increase with intruder pressure after the effects of species, fork length and food abundance were removed (Table 2.3;  $p = 0.010$ ). Again, the slope of this relationship did not differ between the species (ANCOVA<sub>species x intruder pressure</sub>:  $F_{1,57} = 1.23$ ,  $p = 0.271$ ). When analysed separately, however, there was a significant relationship between territory size and intruder pressure for brown trout (Linear regression:  $\log_{10}$  territory size ( $\text{m}^2$ ) = 0.658 intruder pressure<sup>1/2</sup> – 3.61,  $n = 30$ ,  $p = 0.019$ ) but not for Arctic charr (Linear regression:  $\log_{10}$  territory size ( $\text{m}^2$ ) = 0.196 intruder pressure<sup>1/2</sup> – 1.417,  $n = 31$ ,  $p = 0.517$ ). Finally, current velocity, water depth and substrate size did not have significant effects on territory size (Table 2.3).

### *Patterns of territorial defence*

Of 31 Arctic charr, 21 showed aggressive behaviour whereas 20 out of 30 brown trout were aggressive. The rate of aggression (Table 2.1) did not differ between Arctic charr and brown trout (Mann-Whitney:  $Z = 0.63$ ,  $n = 41$ ,  $p = 0.514$ ). In general, aggression rate tended to increase with increasing intruder pressure (Arctic charr: Spearman's  $r = 0.417$ ,  $n = 26$ ,  $p = 0.034$ ; brown trout: Spearman's  $r = 0.342$ ,  $n = 27$ ,  $p = 0.081$ ).

The location of aggressive acts compared to 100% and 75% MCP<sub>FOOD</sub> (minimum convex polygon for location of recorded foraging attempts with 0% and 25% spatial outliers removed) did not vary between the species (100% MCP<sub>FOOD</sub>: Mann-Whitney:  $Z = 0.21$ ,  $n = 41$ ,  $p = 0.829$  and 75% MCP<sub>FOOD</sub>: Mann-Whitney:  $Z = 0.08$ ,  $n = 41$ ,  $p = 0.935$ ). However, the location of aggressive acts compared to 50% MCP<sub>FOOD</sub> differed between the two species (Mann-Whitney:  $Z = 4.8$ ,  $n = 41$ ,  $p < 0.001$ ) (Table 2.4) indicating Arctic charr attack a higher proportion of intruders (20%) than brown trout (7%) deep within their territory.

Mean percent habitat saturation (PHS), which indicates how much of local habitat around each focal fish is occupied by territories was significantly greater for Arctic charr (85.6% habitat saturation) than brown trout (20.8% habitat saturation) ( $\log_{10}$  PHS; t-test:  $t = 4.178$ ,  $df = 59$ ,  $p < 0.001$ ) (Figure 2.7). These species differences in habitat saturation were also reflected in the number of fish which appear to be experiencing overlapping territories; i.e. PHS exceeded 100% for 10 Arctic charr (maximum: 312%) but only for one brown trout (maximum: 104%). Hence, Arctic charr appear to share their local habitat to a much higher degree than brown trout.

## Discussion

### *Variation in territory size and foraging behaviour*

This study is among the first to examine territory size of YOY salmonids outside of the typical single central-place framework, and supports the idea that the CPTM may in some cases underestimate their space use (Steingrímsson and Grant 2008; but see e.g. Keeley and Grant 1995). First, for brown trout, this study yielded larger territories (mean = 0.127 m<sup>2</sup>) than the single central-place estimates from Elliott (1990) (0.049 m<sup>2</sup>; assuming a mean fork length of 4 cm as in this study), or when my data were mapped via the circular method (mean aggressive area = 0.055 m<sup>2</sup>). Second, for Arctic charr, this study shows a clear difference between territory size obtained by mapping the true location of all foraging and aggressive acts via the minimum convex polygon method (mean = 0.558 m<sup>2</sup>) or by mapping the respective data via the circular method (mean = 0.067 m<sup>2</sup>). Third, similar trends arise when YOY Atlantic salmon territories are mapped for individuals using multiple foraging stations (Steingrímsson and Grant 2008); these territories are considerably larger than previous territory size estimates for Atlantic salmon (Kalleberg 1958; Keeley and Grant 1995). Hence, mapping territories of salmonids via the circular method can be useful to study minimum space use requirements of stream salmonids (Grant et al. 1989; Keeley and McPhail 1998) but may not always provide accurate estimates on the local space use of YOY salmonids.

By mapping salmonid territories via the circular method, previous studies often assume territorial individuals are sit-and-wait foragers that ambush prey from a single foraging station (e.g. Keeley and McPhail 1998). Consequently, this method may not be useful to link territory size to foraging mode and mobility



because it constrains the results to sedentary individuals at one end of the foraging mode spectrum. Alternatively, this study samples tagged individuals irrespective of their mobility and suggests that differences in territory size, both at the individual and species level, are directly related to foraging mode. Hence, as predicted, Arctic charr use considerably larger areas than brown trout, and are also more mobile during foraging (see also Tunney 2008); a similar trend has been detected among species of lizards (Verwaijen and Van Darnme 2008). Furthermore, within each species, this study demonstrates that more mobile (i.e. widely foraging) individuals use larger areas (see also Pianka 1983 and Katano 1996 for a fish example).

Territory size is less clearly associated with foraging radius than with mobility; i.e. brown trout territories are positively related to foraging radius but no relationship was detected for Arctic charr. These findings may be explained by a greater tendency toward central-place foraging and smaller territories among brown trout than Arctic charr. Hence in situations where individuals use one or few foraging stations, increased foraging radius may have direct influence on territory area by extending the boundaries of the MCP area. Similarly, in single central-place territories foraging radius is typically positively related to aggressive radius which determines the territory size (Grant et al. 1989). Alternatively, the foraging radius may have less effect on the size of large territories, which may rather be affected by mobility or the number of and distance between foraging stations (Steingrímsson 2004).

In this study, brown trout generally used fixed foraging stations whereas Arctic charr more frequently moved around when foraging or did not return to station from which the foraging attack was initiated (personal observation). These behavioural differences are highlighted by the fact that most brown trout could be

mapped from one or several foraging stations, whereas Arctic charr were in most cases mapped by a grid on the stream bottom (see e.g. Figure 2.2). This behavioural variability in Arctic charr resembles the behaviour of a closely related species, brook charr (*Salvelinus fontinalis*) (Grant and Noakes 1987), whereas the use of fixed foraging stations by brown trout is more similar to Atlantic salmon (Keeley and Grant 1995; Steingrímsson and Grant 2008). These findings may suggest systematic differences in territorial behaviour among salmonid species, an issue that needs to be studied further in general.

### ***Territory size and ecological factors***

In this study, territories of YOY Arctic charr and brown trout appear to be affected by several ecological variables, and either contradict or agree with former studies, which mapped territories via the CPTM (e.g. Keeley 2000) or focused on multiple central-place foragers (Steingrímsson and Grant 2008). First, as predicted, larger individuals of both species used larger territories. These findings are in agreement with previous single central-place studies on YOY salmonids (e.g. Grant et al. 1989; Keeley and McPhail 1998; Keeley 2000). Interestingly, when analysed separately brown trout showed an allometric increase in territory size whereas Arctic charr did not. Because Arctic charr use larger territories than brown trout, these findings suggest that large territories of widely foraging YOY salmonids (and of multiple central-place foragers; see Steingrímsson and Grant 2008) may not be strongly related to body size.

Second, as predicted, territory size showed an overall decline with increasing food abundance. These findings are consistent with several studies on

YOY salmonids, (Keeley and Grant 1998; Keeley 2000; but see Dill et al. 1984), other species of fish (Hixon 1981) and other taxa (Simon 1975), and show that this relationship may also emerge when territories are mapped outside the CPTM (see also Steingrímsson 2004). This study, however, also highlights that species may vary in their response to prey density as the decline in territory size was primarily driven by Arctic charr and not detected for brown trout. Why some species respond to changes in food availability and others do not remains unclear. However, increased territory size at low food abundance can be mediated through several factors, such as (i) increased foraging and aggressive radii (Keeley and Grant 1995; Keeley 2000), (ii) increased mobility, (e.g. Arctic charr in this study), and (iii) longer distance travelled between foraging stations of multiple central-place territories (Steingrímsson 2004). Although territories of brown trout are positively associated with both foraging radius and mobility, it remains unclear why territory size does not respond to food density.

Third, this study yielded an unexpected positive relationship between intruder pressure and territory size. In this case a negative relationship was expected because increased intruder pressure should increase defence cost and make smaller territories more economical (Hixon 1980). Results of earlier studies either show no relationships at relatively low population density (Keeley and Grant 1995: Mean: 3.2 fish/m<sup>2</sup>; Keeley and McPhail 1998: Mean: 2.9 fish/m<sup>2</sup>; for comparison, mean density in this study is 3.7 and 3.6 fish/m<sup>2</sup> for Arctic charr and brown trout, respectively), or a negative relationship at high densities under experimental conditions (Keeley 2000: 5.3, 10.2 and 21.1 fish/m<sup>2</sup>). Hence, a negative relationship between territory size and population density should be more likely to emerge during situations of intense competition, e.g. when individuals

compete for space during high habitat saturation. When Arctic charr and brown trout were examined separately, territory size increased intruder pressure for both species, but not significantly so for Arctic charr (see Figure 2.5c). Considering the high habitat saturation for Arctic charr, a negative relationship would be expected, whereas for brown trout, in low habitat saturation, a positive or no relationship is perhaps less surprising. One potential explanation for Arctic charr, is that large areas at high densities may be a result of more individuals being attacked and forced to use alternative areas/stations (personal observation). Hence, this may resemble situations where subordinate individuals use more foraging stations and larger areas than dominant individuals (Nakano 1995). Unfortunately, although aggression was indeed more frequent at higher densities in this study, no data were collected on dominance hierarchies.

### ***Territorial defence***

One way to estimate how territories are defended is to examine how aggression toward intruders is distributed within the territory (see Steingrímsson and Grant 2008). This study showed a subtle difference in where the two species attacked intruders; i.e. Arctic charr attacked intruders slightly deeper inside their territories (80% of attacks outside the 50% core foraging area) than brown trout (93%). Thus, brown trout may defend their territories better than Arctic charr, which used larger areas that are generally more costly to defend (Schoener 1983). Interestingly, however, the slightly less efficient defence of Arctic charr territories compared to brown trout can not entirely be explained by territory size differences. Hence territories of YOY Atlantic salmon which are considerably larger (mean =

0.932m<sup>2</sup>) than territories of both Arctic charr and brown trout appear to be defended just as well as brown trout in this study (92.8% outside the 50% foraging area; Steingrímsson and Grant 2008). Hence, these results suggest different patterns of defence for Arctic charr than for brown trout and Atlantic salmon which used smaller and larger territories, respectively.

Another way to investigate how territories are defended is to calculate percent habitat saturation (PHS) which indicates the percent of the river bottom occupied by territories. Hence, a PHS over 100% suggests that territories occupy more than the available area, which in turn suggest that territories overlap and are poorly defended. In this study, PHS was much higher for Arctic charr (mean = 85.6%) than brown trout (mean = 20.8%). More importantly, PHS exceeded 100% for 10 Arctic charr (max = 312.3%) but only for one brown trout (max = 103.6%). Hence, again, Arctic charr appear to defend their territories differently, i.e. less efficiently, than brown trout. Because PHS is high for Arctic charr, a negative relationship would be expected between territory size and intruder pressure if territories were exclusive; which was not the case in this study. Alternatively, a high PHS for Arctic charr may also result from individuals defending three-dimensional territories throughout the water column and not being restricted to the river substrate (see also Nakano 1995), especially in pools (Grant and Kramer 1990). In this study, Arctic charr were indeed found in deeper waters than brown trout (see Table 2.2) which might partly explain this high PHS for Arctic charr. In summary, my findings raise the question whether Arctic charr are actually defending their whole territory or if only a fraction of the area is defended at any given time.

### ***Population ecology of stream-dwelling salmonids***

Because territorial behaviour plays a major role in the population regulation of stream-dwelling salmonids, several studies are available on this topic (e.g. Grant and Kramer 1990; Elliott 1990). Majority of these studies have used the CPTM to estimate territory size which is a key predictor of important aspects of population ecology of stream-dwelling salmonids, such as local population densities, growth, emigration and/or mortality (Grant and Kramer 1990; Elliott 1990; but see Steingrímsson and Grant 2008). However, although these single central-place estimates may be good predictors of the minimum space-use requirements of YOY salmonids (Grant and Kramer 1990) they do not accurately reflect the considerable variability that exists in salmonid behaviour and often ignore individuals that forage widely, or from several foraging stations (Elliott 1990; Keeley 2000). This study (see also Steingrímsson and Grant 2008), however, observed individuals irrespective of their foraging tactic. These two different approaches have their strengths and weaknesses. Because the single CPTM reflects the minimum spatial requirements, it may be a better indicator of maximum density, and thus density-dependent emigration and mortality. Alternatively, mapping territories outside of the CPTM may give a better picture of how (and if) territories overlap in space, and thus the degree to which habitats are shared among individuals. This approach has also the potential to provide better insights into how territorial behaviour is linked to foraging mode, social status, growth and fitness of stream-dwelling fish (see also Nakano 1995). Finally, territories mapped outside of the CPTM do not always associate with ecological factors in the same way as studies that focus on central-place territories (see also Steingrímsson and Grant 2008). In summary, the effect of territorial behaviour of multiple central-place and mobile individuals on the

population ecology of stream-dwelling salmonids remains largely unexplored and warrants further study.

**Table 2.1.** Summary of behavioural variation for 31 Arctic charr and 30 brown trout from six rivers in NW-Iceland.

Variable	Arctic charr		Brown trout	
	Mean	Range	Mean	Range
Territory size (MCP <sub>100%</sub> , m <sup>2</sup> )	0.558	0.015-1.725	0.127	0.012-0.542
95% territory size (MCP <sub>95%</sub> , m <sup>2</sup> )	0.365	0.008-1.660	0.069	0.005-0.477
Foraging rate (attacks.min <sup>-1</sup> )	6.1	1.8-14.0	8.4	2.8-13.8
Aggression rate (attacks.min <sup>-1</sup> )	0.13	0.00-0.55	0.06	0.00-0.28
Proportion of mobile forages	0.25	0.00-0.91	0.02	0-0.07
Foraging radius (body lengths)	1.22	0.76-1.93	1.22	0.75-1.51
Aggressive radius (body lengths)	3.17	1.00-5.60	3.10	1.67-5.00
Aggressive area (m <sup>2</sup> ) <sup>a)</sup>	0.068	0.005-0.195	0.055	0.012-0.146

a) Aggressive area is based on mean aggressive radius<sup>2</sup> \*  $\pi$  for 21 Arctic charr and 20 brown trout that showed aggressive behaviour.



**Table 2.2.** Summary of ecological characteristics for the territories used by Arctic charr and brown trout in NW-Iceland.

Variable	Arctic charr		Brown trout	
	Mean	Range	Mean	Range
Fork length (cm)	4.4	3.4-5.4	4.0	3.3-4.6
Drift rate (food items.min <sup>-1</sup> .net <sup>-1</sup> ) <sup>a)</sup>	41.5	0.1-443.6	44.0	1.5-179.6
Intruder pressure <sup>b)</sup>	3.7	0.3-12.0	3.6	0.0-6.7
Substrate size <sup>c)</sup>	3.8	1.0-6.0	3.3	1.0-5.0
Current velocity (cm.s <sup>-1</sup> )	5.2	0.0-15.0	15.3	0.7-35.0
Temperature (C°)	14.2	9.8-18.2	15.5	11.6-19.0
Water depth (cm)	35.9	18.0-60.0	23.0	5.0-36.0

a) Size of the drift net was 25x40 cm with 250 µm mesh size.

b) Number of fish in 1 m radius from fish under study.

c) The classification of the substrate was: 1: clay and silt = <0.0625 mm, 2: sand = 0.0625 - 2 mm, 3: gravel = 2 - 16mm, 4: pebble = 16 - 64 mm, 5: cobble = 64 - 256 mm, 6: bolder = >256 mm, 7: bedrock (see DeGraaf and Bain 1986).

**Table 2.3.** A multivariate analysis (ANCOVA) testing for the influence of species and several potential ecological predictors on territory size for 31 Arctic charr and 30 brown trout. The model was driven stepwise backwards with species as categorical factor

Variable	Coefficient	Std Error	F	P
Species	0.468	0.145	10.403	0.002
Fork length	3.464	1.128	9.424	0.003
Drift rate (food items.min <sup>-1</sup> .net <sup>-1</sup> ) <sup>a)</sup>	-0.627	0.191	10.754	0.002
Intruder pressure <sup>b)</sup>	0.518	0.193	7.199	0.010
Current velocity (cm.s <sup>-1</sup> )	2.209	1.293	2.917	0.093
Substrate size <sup>c)d)</sup>	-0.066		1.322	0.255
Water depth (cm) <sup>d)</sup>	-0.155		0.234	0.631

a) Size of the drift net was 25x40 cm with 250 µm mesh size.

b) Number of fish in 1 m radius from the focal fish.

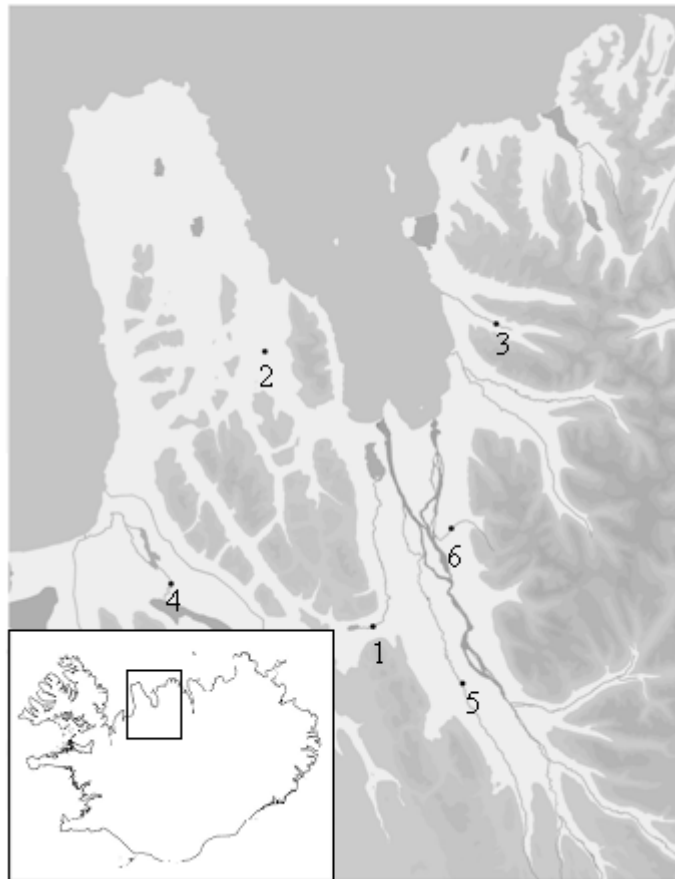
c) The classification of the substrate was: 1: clay and silt = <0.0625 mm, 2: sand = 0.0625 - 2 mm, 3: gravel = 2 - 16mm, 4: pebble = 16 - 64 mm, 5: cobble = 64 - 256 mm, 6: bolder = >256 mm, 7: bedrock (see DeGraaf and Bain 1986).

d) Variables were removed from the model if P value was higher than 0.15.

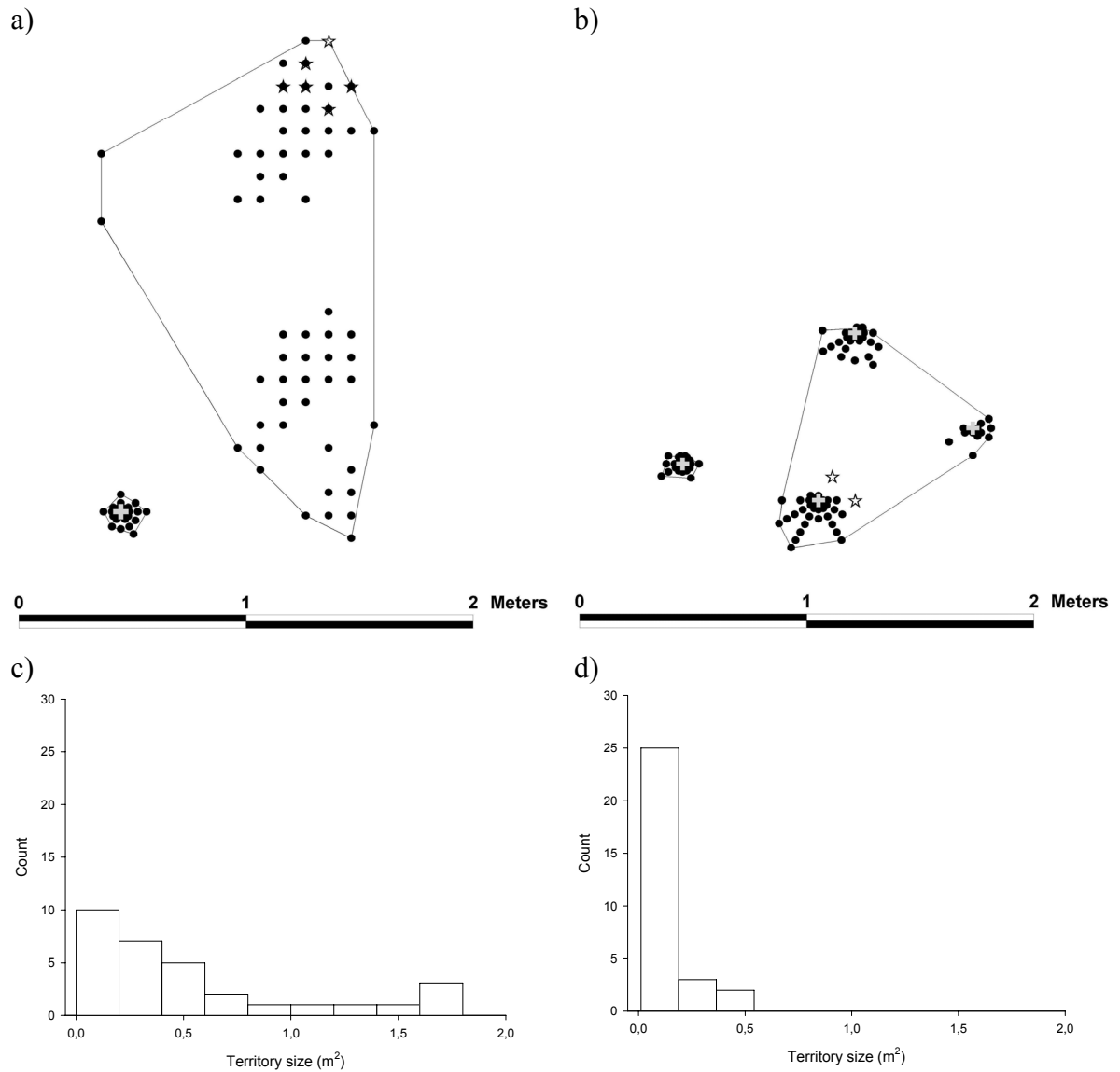
**Table 2.4.** Summary of the spatial distribution of aggressive acts with regards to 100, 75 and 50% of the foraging area calculated as the average frequency of aggressive acts outside foraging area<sup>a)</sup>.

	Arctic charr (n = 21)	Brown trout (n = 20)
% Aggression outside 100% foraging area	34	31
% Aggression outside 75% foraging area	71	72
% Aggression outside 50% foraging area	80	93

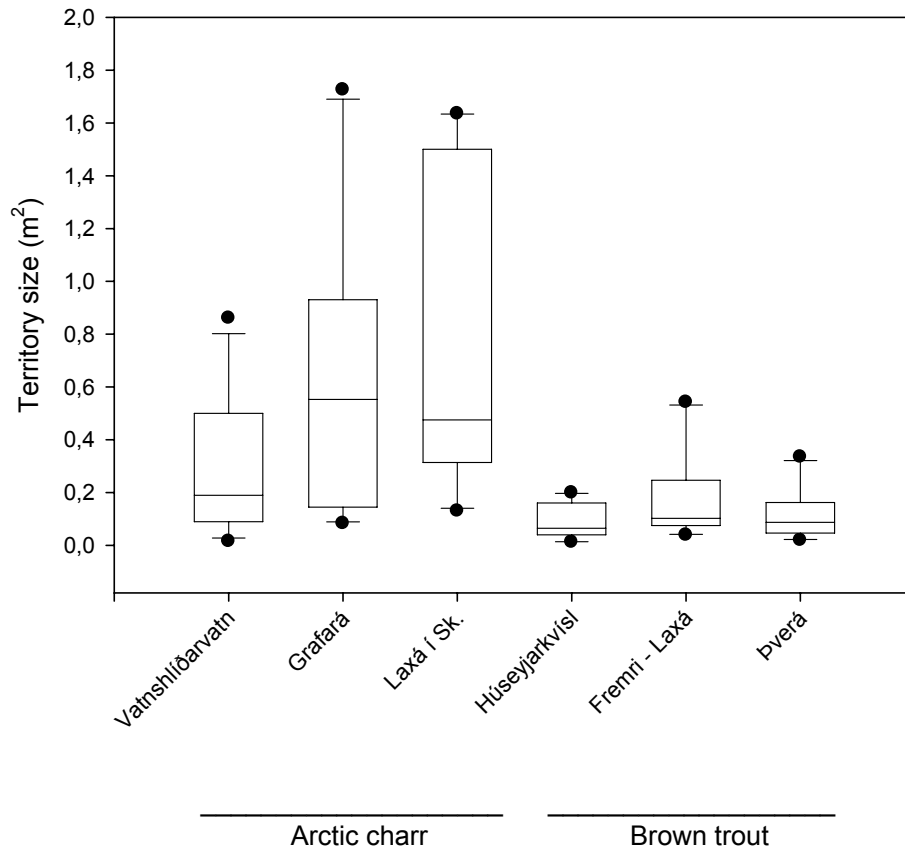
a) The foraging area is the minimum convex polygon area based on location of documented foraging attempts. The three areas (100, 75 and 50%) were established by removing 0, 25 and 50% of foraging attempts outliers, respectively.



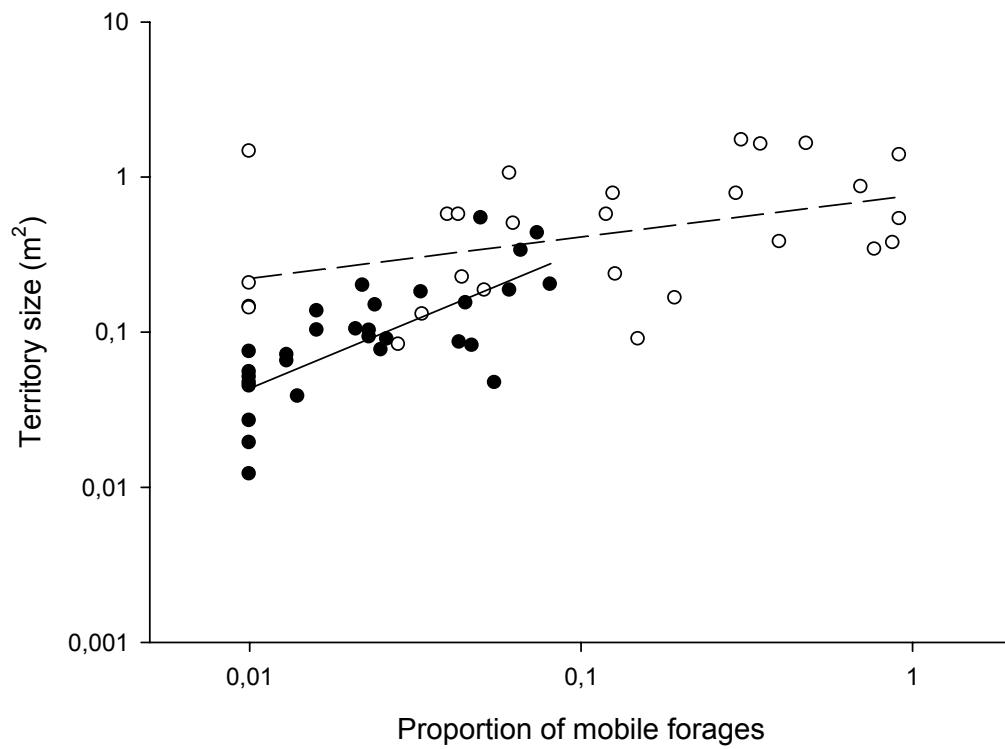
**Figure 2.1.** Location of the six study rivers in NW-Iceland. Rivers for Arctic charr populations are: 1. Myllulækur, 2. Laxá í Skefilsstaðahreppi, 3. Grafará. Rivers for brown trout populations are: 4. Fremri - Laxá, 5. Húseyjarkvísl, 6. Þverá. The picture in the bottom left corner shows a map of Iceland with the study area outlined.



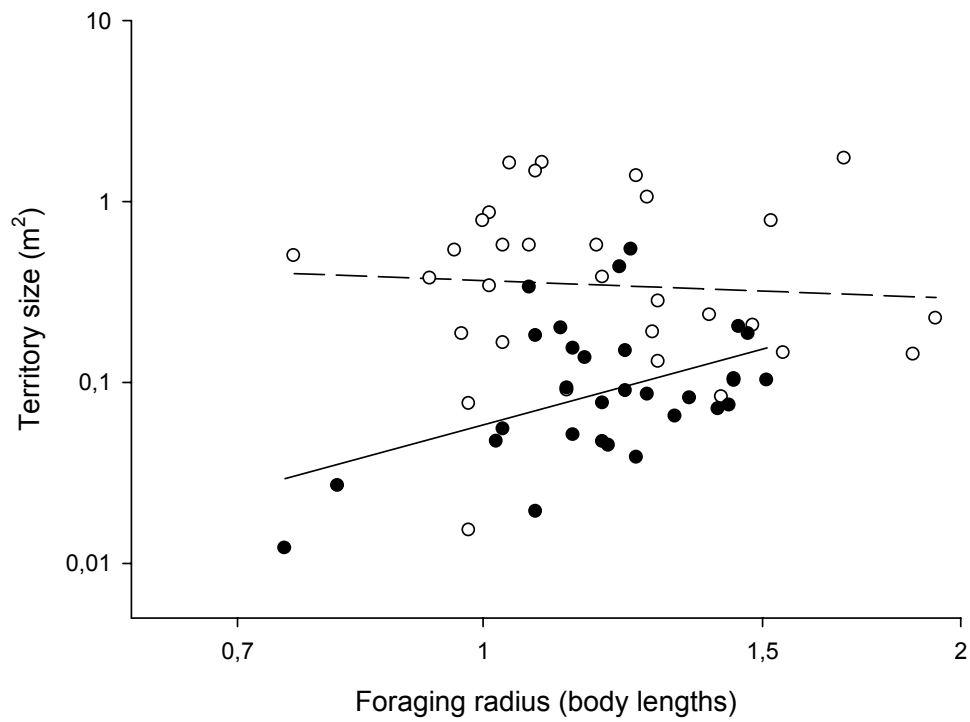
**Figure 2.2.** Variability in territory size for Arctic charr and brown trout in six Icelandic rivers. The maps show the smallest and biggest territories for Arctic charr (a) and brown trout (b), where the location of foraging attempts, aggressive acts and foraging stations are represented by a solid circle, a star and a grey cross, respectively. The two histograms show the frequency distribution of territory sizes for Arctic charr (c) and brown trout (d).



**Figure 2.3.** Territory size for the study populations of Arctic charr (Creek Myllulækur, River Laxá í Skefilsstaðahreppi and River Grafará) and brown trout (River Húseyjarkvísl, River Fremri – Laxá and River Þverá) in NW-Iceland. The boxes show the 25<sup>th</sup> and 75<sup>th</sup> percentile, whereas the line inside each box represents the median. Error bars above and below indicate the 90<sup>th</sup> and 10<sup>th</sup> percentile, respectively, whereas the dots show extreme values.

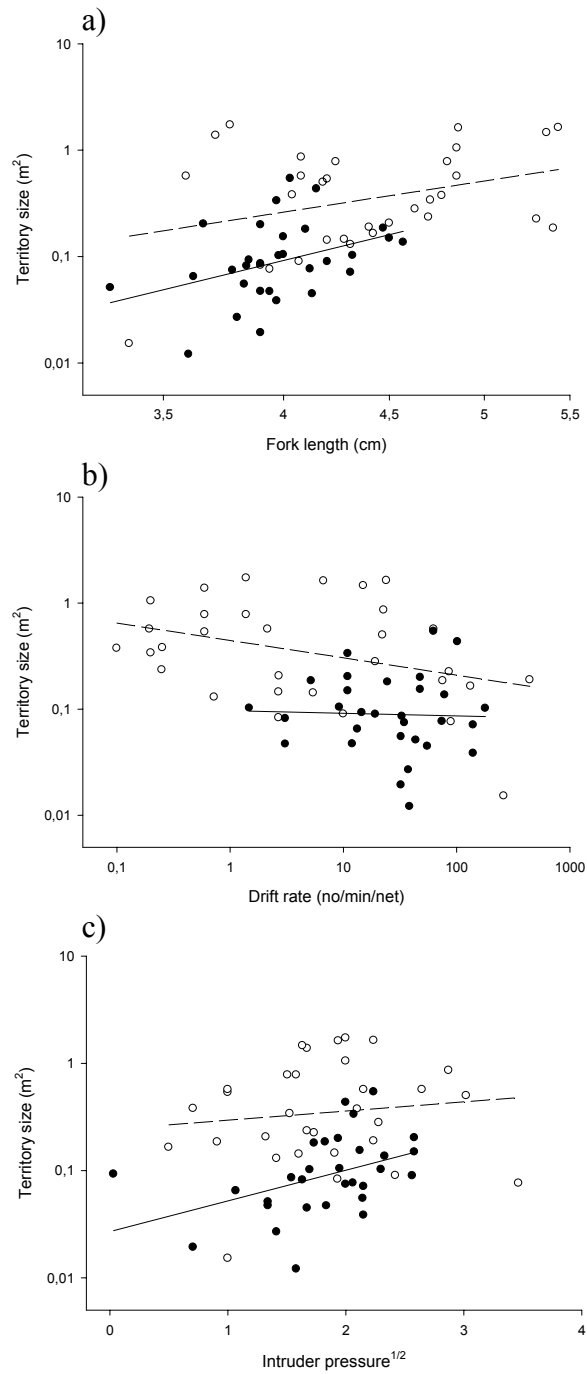


**Figure 2.4.** The relationship between territory size and mobility prior attacking prey for Arctic charr (open circles and long-dashed line) and brown trout (solid circles and line) based on six rivers in NW-Iceland.

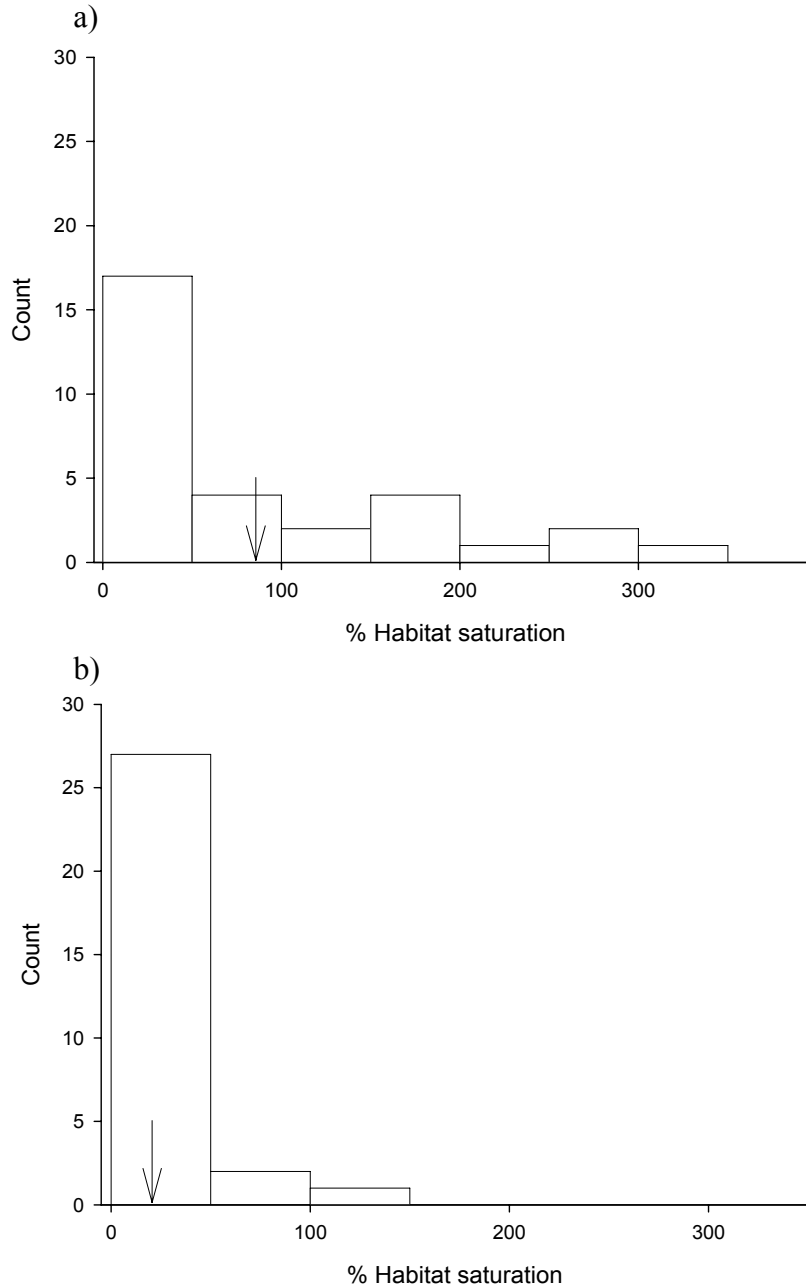


**Figure 2.5.** Territory size for 31 Arctic charr (open circles and long-dashed line) and 30 brown trout (solid circles and line) as a function of foraging radius, based on six rivers in NW-Iceland.





**Figure 2.6.** Territory size for 31 Arctic charr (open circles and long-dashed line) and 30 brown trout (solid circles and line) in six Icelandic rivers as a function of fork length (a), drift rate (b) and intruder pressure (c).



**Figure 2.7.** Estimated percent habitat saturation (PHS) for YOY Arctic charr (a) and YOY brown trout (b) in six Icelandic rivers. PHS indicates the proportion of the habitat covered by territories based on fish density and territory size for each individual. The arrows show average PHS.

### **Chapter three – General Discussion and Conclusions**

This study provides a novel description of territoriality and local space use of stream-dwelling salmonids by focusing on several unexplored aspects of their behaviour. First, territories were mapped irrespective of foraging mode, i.e. most studies have focused on individuals feeding by a sit-and-wait position from a single foraging station causing the literature to be biased towards these individuals (e.g. Elliott 1990). Second, this is the first time where foraging mode is related to territory size of salmonids (see Katano 1996 for study on other fish). Third, and surprisingly, space use behaviour has never been mapped for YOY Arctic charr before, and in fact very limited literature is available on this species in stream environments (but see Heggenes and Saltveit 2007 for a study on habitat use of older fish). Finally, this is the first study to map territories of YOY brown trout outside of the single central-place approach.

This study provides several novel and interesting findings on behaviour of stream salmonids. First, the two salmonid species examined vary in the size and use of their territories. Arctic charr used larger territories than brown trout and were more mobile. Furthermore, a similar trend was detected within both species, where more mobile individuals used larger territories. Hence, there obviously exists a considerable inter- and intraspecific variability in the territory size of salmonids (see also Elliott 1990; Keeley and Grant 1995; Keeley 2000; Steingrímsson and Grant 2008), which this study clearly links with variability in how individuals exploit their local environment via different foraging modes. Second, this study suggests that territories mapped outside of the single CPTM may also vary depending on ecological conditions, and not necessarily in the same manner as previously believed. More specifically, territory size increased with body size,

decreased with food abundance and, surprisingly, increased with intruder pressure. Large areas at high population densities are not easily explained, but may partly be due to more aggressive acts, which can cause (or force) individuals to explore other areas/stations after such events (personal observation). Finally, territorial defence appears to differ between the two study species, where territories of Arctic charr overlap more and seem to be less efficiently defended than for brown trout. Hence, the unusually high percent habitat saturation for Arctic charr suggest that territorial behaviour in this species may not be as efficient in regulating local population density, as it is for most other salmonid species (Grant and Kramer 1990).

This is the first study to map territorial and space use behaviour of salmonids in Icelandic rivers using direct behavioural observations (but see Tunney 2008 for a study on foraging mode). Although Icelandic salmonids overlap in distribution, they utilize different habitats on a small spatial scale and the behaviour varies between species (Guðjónsson 1990; Tunney 2008). In this study, Arctic charr had a greater range in most behavioural components than brown trout, a pattern that was also reported by Tunney (2008), who found that Arctic charr were more variable in foraging mode than brown trout and Atlantic salmon. Moreover, several studies have shown that Arctic charr are also highly variable in morphology and life history (Skúlason et al. 1993; Skúlason et al. 1996; Snorrason et al. 1994). Together, these studies suggest that Arctic charr may be well suited, and perhaps better suited than many other salmonids, to handle the wide range of ecological conditions offered by Icelandic freshwater systems.

Several studies are available on the importance of territorial behaviour in population ecology of stream-dwelling salmonids, but most focus on single central-place territories (Elliott 1990; Keeley and Grant 1995; but see Steingrímsson and

Grant 2008). Behavioural studies, such as this one, which focus on territoriality and foraging behaviour, help us gain better understanding of the population ecology of species (Sutherland 1996). On one hand, knowledge on territorial behaviour helps us to understand how individual behaviour can affect density-dependent responses of populations, and hence the regulation of population density. On the other hand, foraging behaviour improves our knowledge on how individuals use their local habitats, which in turn may affect their larger scale distribution. Based on my findings, it is clearly helpful to map territories across a species' true range in foraging mode, to gain a more comprehensive view of how these behaviours influence salmonid population ecology.

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