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Foraging mode of wild salmonids in Icelandic streams

By

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MSc. thesis
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Declaration

I hereby declare that this thesis is based on my own observations, is written by me and has not been previously submitted, either in part or as a whole, at a postgraduate level.

Signature:_____

Abstract

Foraging mode provides important insights into the space use of animals, their functional role within ecosystems, and may be crucial for understanding the processes that mediate diversity in nature. I directly observed the foraging mode of wild Arctic charr, brown trout and Atlantic salmon in their first year of life, over a range of habitats, and among ten natural Icelandic streams. Several novel findings emerged from this study. First, although Icelandic stream salmonids typically sit-and-wait to ambush drifting prey from short distances, Arctic charr were more mobile during prey search and prior to attacking prey than Atlantic salmon, whereas, brown trout showed an intermediate pattern. Second, in all three species, individuals that were mobile while searching for prey were also likelier to be mobile when initiating forages. However, the three species clearly differ in the way their search movements relate to foraging, as Arctic charr was the only species where more mobile individuals traveled longer distances when pursuing prey. Third, foraging mode varied among species as generally expected by their habitat use, the least mobile species, Atlantic salmon, were found in the fastest water flows, whereas Arctic charr and brown trout use slower-running waters and were most mobile and intermediate in behaviour, respectively. These findings offer a promising behavioural basis for future work to explicitly identify the mechanisms that influence habitat use, diversity and distribution of Icelandic salmonids in the wild.

Samantekt

Fæðuhættir veita mikilvæga innsýn í það hvernig dýr nýta umhverfi sitt, hlutverk þeirra í viðkomandi vistkerfi, og auka skilning á þeim þáttum er ýta undir fjölbreytileika lífvera. Gerðar voru beinar athuganir á fæðuháttum villtrar bleikju, urriða og lax á þeirra fyrsta sumri í fjölbreytilegum búsvæðum í tíu ám á Íslandi. Helstu niðurstöður þessarar rannsóknar voru eftirfarandi: Í fyrst lagi, þó laxfiskategundirnar þrjár sýni allar það atferli að sitja-og-bíða eftir bráð og ráðast á hana af stuttu færi, þá er bleikja hreyfanlegri við fæðuleit og fæðunám heldur en lax, og urriðinn liggur þar á milli. Í öðru lagi, hjá öllum þremur tegundunum voru þeir einstaklingar sem sýndu mikinn hreyfanleika við fæðuleit, einnig hreyfanlegri við upphaf atlögu að bráð. Tengsl fæðuleitar og fæðunáms virðist þó vera ólíkt á milli tegunda, þar sem bleikja var eina tegundin þar sem samband fannst á milli hreyfanleika við fæðuleit og vegalengdar sem fiskar ferðuðust við fæðunám. Í þriðja lagi virðast fæðuhættir tegundanna þriggja vera í samræmi við það sem búast mátti við út frá búsvæðanotkun þeirra. Bleikja hélt sig í lygnasta vatninu og hreyfði sig mest, á meðal lax var í mesta straumnum og hreyfði sig minnst. Þessar niðurstöður mynda atferlislegan grunn að frekari rannsóknum á þeim þáttum er móta búsvæðaval, fjölbreytileika og útbreiðslu íslenskra laxfiska við náttúrulegar aðstæður.

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Chapter One - General Introduction

Animals adopt varying behavioural tactics, called foraging modes, when searching for and attacking prey (McLaughlin 1989, Helfman 1990, O'Brien et al. 1990, Helfman 1994, Hart 1997, Perry and Pianka 1997, Perry 1999). Some individuals remain still as they "sit-and-wait" and then ambush prey that enter within striking distance. Alternatively, "widely foraging" animals may travel more expansively, searching out and attacking prey while on the move (Pianka 1966, Huey and Pianka 1981). Potentially, foraging mode can provide an important link between individual behaviour and processes that organize life across the landscape (Koehl 1989 , Lima and Zollner 1996, Sutherland 1996, Scharf and Ovadia 2006). For instance, movement tactics may provide insights into adaptations related to use of novel ecological conditions considered important when animal lineages diversify (Vitt and Pianka 2005). Equally, foraging mode constraints may limit where and what animals eat, and may thus influence patterns of habitat use and animal distribution (Huey and Pianka 1981, Robinson and Holmes 1982, Wellborn et al. 1996, Nakano et al. 1999). Furthermore, the relationships between foraging mode and other behavioural, morphological (McBrayer 2004), physiological (Nagy et al. 1984, Secor and Nagy 1994, Belliure et al. 1996) and life history characteristics (Eckhardt 1979, Huey and Pianka 1981, McLaughlin 1989, Webb et al. 2003) has led some researchers to claim that it is among the most important characteristics of an animal's natural history (Eckhardt 1979). Surprisingly though, few researchers take the initial step to establish variation in animal foraging mode in the wild. Therefore, the links between foraging mode and the diversity of ecosystems remain largely open to discovery.

Several studies demonstrate that the way salmonid fishes search for and capture prey can vary among species (Nakano et al. 1999), populations (Biro and

Ridgway 1995) and individuals (Grant and Noakes 1987, McLaughlin et al. 1992). Stream salmonids typically sit-and-wait and then dart out to intercept invertebrate prey carried by water currents (Kalleberg 1958, Wankowski and Thorpe 1979), while salmonids in still waters, such as lakes, typically forage more widely as some individuals cruise almost continually (Biro and Ridgway 1995). Furthermore, some salmonids appear to adopt one mode of movement, whereas others appear flexible as individuals switch modes to track resource availability and habitat variation through space and time (Fausch et al. 1997, Nakano et al. 1999). Interestingly, even individuals occupying relatively homogenous habitat may adopt strikingly different levels of mobility if they feed on different resource types (McLaughlin et al. 1992, McLaughlin 1994). Today, new insights into foraging mode should be useful, as researchers increasingly attempt to link behaviour to performance and distribution of salmonids in the wild (Nislow et al. 1998).

Despite a considerable knowledge base, there are still many good reasons to study salmonid foraging mode. First, and perhaps the most simple of these is that very little is known about how many otherwise well studied salmonid species actually forage in the wild. Here, basic descriptive studies that establish foraging mode patterns may provide information that can be adopted to ground broader ecological and evolutionary studies in nature. Second, most studies of salmonid foraging mode focus on single species, and as a result, a lack of direct interspecific comparisons begs that more studies address the question of how species compare in their foraging tactics. This knowledge is of broad interest in understanding both the interactions among competing species, as well as among predators and their prey. Third, although different components of foraging mode, such as mobility during prey search and attack, can exhibit similar patterns (McLaughlin et al. 1992, Biro and Ridgway 1995),

studies rarely examine if or how these variables are correlated. This is unfortunate, because further investigation of the coordinated nature of behavioural components of foraging mode may lead to a more complete understanding of their consequences for animals (Cooper 2007). Fourth, it is necessary to identify factors that influence foraging mode and other reasons for movement. Predictions made from behaviour and habitat variability details may help explain why broader habitat use and diversity patterns occur. Together, it seems inevitable that further *in situ* studies will continue to uncover novel elements of salmonid foraging mode.

Here I examine the foraging mode of three salmonid species in several Icelandic streams. In general, Icelandic streams are simple in taxanomic diversity and contain only 6 freshwater fish species (Gudbergsson and Antonsson 1996, Albert et al. 2006). Because half of the species are salmonids (Arctic charr *Salvelinus alpinus,* brown trout *Salmo trutta,* and Atlantic salmon *Salmo salar*), it is likely that this group of fish play a major role in the ecology of these stream environments. Yet, although species are few, diverse habitats provide fish with a wide range of conditions that can potentially be exploited in different ways. As an example, both the biotic and abiotic characteristics of these rivers differ drastically among and within watersheds depending on the age and permeability of the bedrock, influence of hot and cold water springs, glacial melt-water, and run-off from the mountainous landscape (Gardarsson 1979, Gudjonsson 1990). Few species and diverse habitats are believed to play an important role in the evolution and ecology of Icelandic freshwater fish (Gudjonsson 1990, Skulason et al. 1992, Skulason and Smith 1995). For example, limited interspecific competition and open niches are believed to promote the extreme intraspecific variation observed in salmonids in Iceland's freshwater lakes by the process of resources polymorphism (Skulason et al. 1992, Skulason and Smith 1995).

Similarly, in terms of ecology, there is clear evidence of habitat segregation and geographical distribution differences among Icelandic stream salmonids (Gudjonsson 1990). Hence, Arctic charr are observed in slow side-water pools or near the stream bank of low productive streams, whereas brown trout and Atlantic salmon are found in the more productive streams, in intermediate and faster water flows, respectively (Gudjonsson 1990, see also: Heggenes and Saltveit 2007). To date, however, very little is known of the behavioural ecology of Icelandic stream fish. In summary, foraging mode observations may provide new insights into how this guild of fishes differs in their means of exploiting resources and their use of Icelandic stream habitats.

In this thesis, I take the first steps in unravelling the behavioural ecology of Iceland's wild stream salmonids by examining their foraging mode. My general question is simple: How do young-of-the-year Arctic charr, brown trout and Atlantic salmon seek out and capture prey in Icelandic streams? To address this question, I observed individual fish over two summers in a total of 10 streams and monitored their movement patterns. In doing so, I make the first direct comparison of the foraging mode of Arctic charr, brown trout, and Atlantic salmon. That these species may adopt some similar foraging tactics is expected based on their stream existence, but a comparison of foraging mode may provide some new insights into how these species use stream habitats differently.

Chapter Two - Foraging mode variation within a guild of three stream-dwelling salmonid fishes

Introduction

Foraging mode can be defined as a set of coordinated behavioural traits that reflect the variability in how animals seek out and capture prey (Eckhardt 1979, Helfman 1990). Most often, foraging mode is examined along a sedentary-mobile continuum (Janetos 1982, Pianka 2000) and animals are classified according to the two extremes as "sit-and-wait" or "widely foraging" predators (Pianka 1966, Huey and Pianka 1981). In general, whether an animal adopts a sedentary or mobile foraging mode is believed to be tied to the costs and benefits of moving when using specific habitats and resources (Helfman 1990). Consequently, because foraging mode should influence an animal's growth and fitness in a particular habitat, it may serve as a mechanistic link between individual behaviour and broad-scale patterns of diversity in nature (Tilman 1987, Sutherland 1996, Wellborn et al. 1996, Schmitz 2007). For instance, foraging mode may form a behavioural basis for understanding how similar species coexist via habitat segregation and resource partitioning (Pianka 1966, Nakano et al. 1999).

Juvenile stream-dwelling salmonid fishes exhibit great intra- and interspecific variability in foraging mode. Many studies indicate that stream salmonids search for prey from a stationary (i.e., sit-and-wait) position near the streambed (Kalleberg 1958), from which they pursue and capture drifting invertebrates via short bouts of burst swimming (Grant and Noakes 1987; Fausch 1984; Wankowski and Thorpe 1979). Alternatively, some salmonids may forage more widely as they actively travel to locate prey, which they pursue while on the move, from relatively longer distances

(Grant and Noakes 1987, McLaughlin et al. 1992, Biro and Ridgway 1995). In addition, mobility may be linked to resource use if mobile individuals consume more prey from the stream bottom or the waters surface than sedentary individuals (Grant and Noakes 1987, McLaughlin 1994, Katano 1996, Nakano et al. 1999). Hence, salmonids obtain prey using different sets of behaviour that vary between sedentary and more mobile foraging modes.

Based on the typical two mode paradigm (i.e., sit-and-wait vs. widely foraging), salmonids may adopt mobility that can be visualized on a coordinate plane bound by two axes ranging from no movement to constant movement, where the axes reflect search mobility and mobility while initiating foraging attempts, respectively (Figure 2.1ab). In this scenario, a sit-and-wait tactic reflects limited movement in both the search and attack components of behaviour whereas widely foraging fish exhibit the opposite extremes. Such a two-dimensional framework of foraging mode has been proposed for mobile animals (Cooper 2005, 2007), but not yet formally so for salmonid fishes. According to this framework, salmonid tactics could, at least hypothetically, vary beyond a two mode description to include individuals that may either be mobile between pursuits, but only attack prey from a sedentary position (e.g., traveling among multiple ambush sites), or search from a stationary position for long periods only to move for short periods prior to initiating a foraging attempt (Figure 2.1cd). Therefore, examining the coordination of two or more behaviours may provide new insights into salmonid foraging mode.

Explicit species comparisons of foraging mode are useful for understanding how salmonid species share habitats and resources in streams (Nakano et al. 1999). To date, however, salmonid foraging mode studies typically focus on a single species. As a result, although several studies reveal striking intraspecific variation in foraging

mode (Grant and Noakes 1987, McLaughlin et al. 1992, Biro and Ridgway 1995), they may not be ideal for comparing species because of methodological discrepancies. Moreover, even if methods are consistent, single-species sometimes categorize foraging mode qualitatively and lack the necessary detail to compare similar species (McLaughlin 1989, see: Biro and Ridgway 1995, for intraspecific comparison study). Hence, comparative studies are more reliable for evaluating how similar species differ in their exploitation of stream habitats (Biro and Ridgway 1995, Fausch et al. 1997, Nakano et al. 1999).

Only three native salmonids, Arctic charr (*Salvelinus alpinus* L), brown trout (*Salmo trutta* L) and Atlantic salmon (*Salmo salar* L) exist and overlap in the relatively species-poor streams that carve Iceland's volcanic landscape (Gudbergsson and Antonsson 1996). Icelandic streams, however, offer a wide range of fish habitats as they vary drastically among and within watersheds depending on the age and permeability of the bedrock, influence of hot and cold water springs, glacial melt-water, and run-off from the mountainous landscape (Gardarsson 1979, Gudjonsson 1990). General observations suggest that Arctic charr is often found in slow-running sections of relatively cold and unproductive waters, brown trout at intermediate conditions, and Atlantic salmon is most abundant in fast waters in warmer and more productive rivers (see also: Gudbergsson and Antonsson 1996, see also: Heggenes and Saltveit 2007). Because stream-salmonids tend to adopt a sedentary foraging mode in swift water flows and be more mobile in slow waters, it is reasonable to expect Icelandic stream-salmonids to vary in foraging mode. So far, the behaviour of stream fishes in Iceland remains largely unexplored in natural situations (but see: Sigurjonsdottir and Gunnarsson 1989, for a lake study).

In this thesis, I examine how the foraging mode of young-of-the-year (YOY) Arctic charr, brown trout, and Atlantic salmon compares in stream environments. First, I describe and compare the foraging mode of the three species by summarizing the following four aspects of their foraging behaviour: (1) mobile searching, (2) mobile foraging attempts, (3) pursuit distance, and (4) the tendency to make foraging attempts toward benthic, mid-water or surface prey. Second, I evaluate whether salmonids coordinate their behaviour along a sedentary-mobile continuum bound by the two extremes sitting-and-waiting and widely foraging for prey. To test this hypothesis I use bivariate data to determine whether search and pursuit behaviours covary for individuals in each species. Specifically, I predict that salmonids that tend to be sedentary while they search (i) make fewer foraging attempts while moving, (ii) have relatively shorter pursuit distances, and (iii) eat less prey from the benthos than more mobile searching individuals. Finally, I briefly examine how the foraging mode of the three salmonid species and the different study populations relate to water flow, a key aspect of their habitat. Based on water flow preferences, I expect Arctic charr to exhibit the greatest mobility while searching for and pursuing prey, brown trout to be intermediate, and Atlantic salmon to be least mobile. Similarly, for each species, I expect populations that are found in slower running waters to exhibit greater mobility during search and prior to attacking prey.

Methods

General information

Wild populations of young-of-the-year (YOY) Arctic charr, brown trout and Atlantic salmon were studied in ten streams in Iceland between June and September of 2005

and 2006 (Figure 2.2). I surveyed fast and slow waters at different depths in variable habitats within each stream in attempt to observe fish over a range of conditions (Table 2.1, see methods for habitat measurements below). I directly observed 153 individuals (61 Arctic charr, 42 brown trout, and 50 Atlantic salmon) via snorkelling and stream bank observations. I visually estimated fork length (i.e. body size) with the aid of a ruler placed in stream or a nearby object that was later measured, as a reference for scale. Following each observation, I attempted to capture the focal fish and if successful, I anaesthetized it with phenoxyethanol and measured the fork length with callipers to the nearest 0.01mm. My visual estimates of fork length were accurate to an absolute mean difference of < 2 mm for all three species. Finally, I marked the foraging site with a flag, measured its habitat features (see below) and released the fish back to its exact location of capture.

Observation of foraging mode

I made a single 10-20 minute observation of individual fish between 9:00 and 20:00. To observe fish, I (1) snorkelled, where I lay motionless underwater downstream from the focal fish and recorded observations on plastic mylar sheets, or (2) sat behind a blind on the stream bank, and recorded behaviour on a digital voice recorder or a video camera. Prior to an underwater observation, I gradually moved upstream until a foraging YOY salmonid was spotted. I then held a position 1-2 m downstream from the focal fish, so that behaviours could be recorded without disturbing the fish or its environment. For stream bank observations, I visually scanned the water from the bank. Once a foraging YOY salmonid was spotted I set up a blind to prevent the fish from being disturbed by any sudden movement. Before each observation, I waited for

at least 5 minutes to allow focal fish to resume their natural foraging behaviour. The same set of behaviours was recorded independent of whether I observed fish from the stream bank or while snorkelling. Also, for fish recorded on video, I made observations in the lab from a single play of each video recording using the same observation methods as in the field. My choice of observation technique depended on stream conditions, such as stream depth and visibility, and the location of foraging fish.

I used a procedure similar to McLaughlin et al. (1992, 1994) and Biro and Ridgway (1995) to measure the time spent on different foraging behaviours. Time was monitored with a digital watch timer which emitted a single pulse alarm at five second intervals. In general, I alternated the total observation time between five second intervals where I monitored behaviour and subsequent intervals where I recorded my observations. The behaviour of each fish for each five second interval was classified into three categories: pursuit, aggression and search. Salmonids swim rapidly toward a point location often accompanied by opening and closing their mouth to make foraging attempts. If a focal fish made a foraging attempt during a five second interval it was classified as a pursuit. Periods where focal fish chased or fled from another fish were considered periods of aggression and intervals without foraging attempts or aggression were classified as search.

In this study I measure four behaviours associated with the foraging mode: (1) the proportion of time spent moving while searching for prey, (2) the proportion of foraging attempts initiated from a moving start, (3), the distance traveled during pursuit of prey, and (4) the location where foraging attempts were directed (benthos, mid-water or surface). I identified specific behaviours during observation by the following criteria. (i) Fish that moved greater than one body length during a search

period were considered mobile for that interval, while fish that moved one body length or less were considered immobile. I chose one body length as my definition of mobility to account for slight movements that may simply be related to fish holding a position in flowing water. (ii) An interval of pursuit where a fish moved greater than one body length prior to a foraging attempt was considered a mobile forage, while intervals where attempts were fish moved one body length or less before attacking prey were considered sedentary prey pursuits. (iii) Pursuit distance was recorded as the total number of body lengths travelled during a 5 second interval classified as pursuit. (iv) If during a foraging attempt the mouth of a fish made contact with the streambed or surface of the water, the foraging attempt was classified as benthic or surface, respectively. All other foraging attempts were classified as mid-water.

For analyses, I calculated the proportion of mobile searching for each focal fish as the number of 5 second search intervals where a fish moved greater than one body length divide by the total number of 5 second search intervals. The proportion of mobile foraging attempts and benthic, mid-water and surface foraging were similarly calculated for individuals as the number of times I observed each type of foraging attempt divided by the total number of foraging attempts. Finally, I calculated mean pursuit distance for individual fish based on the body lengths traveled in each 5 second pursuit interval averaged over all pursuit intervals recorded for that individual.

Habitat measurement

Immediately following observation, I measured water flow, water depth, substrate size, and water temperature at the exact location of each fish. The average water flow rate was measured at 60% of the water depth (measured from the water surface)

(Davis and Barmuta 1989) using a Marsh-McBirney Flo-mate™ Model 2000CM current velocity meter. I determined water flow by averaging three consecutive flow measurements recorded to the nearest 0.001 $m.s^{-1}$; where each measurement represents the average flow over a 15 second time interval. I measured water temperature with a digital thermometer to 0.1 °C and water depth with a meter stick to the nearest millimetre. I then estimated substrate size by placing of a square piece 30 x 30 cm of clear plastic divided into four sections on the streambed centred on the foraging location. The dominant substrate size in each of the four sections was estimated based on the modified Wentworth scale into grain size categories (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).

Data Analysis

To examine foraging mode, I first summarized behavioural traits and reported mean, median, and range for each trait. Second, I examined the distribution these traits with simple histograms of untransformed data. Third, I tested for differences among species for single behavioural traits with ANOVA or Kruskal-Wallis on ranks. If necessary, I used arcsine square-root transformation on proportion data in attempt to obtain a normal distribution for parametric statistical analysis. Fourth, I used Kruskal-Wallis test to examine differences among benthic, mid-water and surface forages both within and among species.

Associations between behavioural traits were determined with simple Pearson product moment correlations. When required, I transformed variables or used

Spearman rank correlations (Sokal and Rohlf 1994). I first tested for correlations at the species level and if a predicted pattern occurred, I then examine these patterns within each species at the stream-level. Analysis of covariance ANCOVA was used to compare the slope of the relationships between corresponding traits among species. For figures, bivariate plots of behavioural data display transformed behavioural variables but axes were back-transformed for interpretation purposes.

I report univariate summaries of four untransformed habitat variables. I used ANOVA to determine whether differences exist among species in water flow, water temperature, and water depth. When necessary, I used $\log_{10}$-transformation to achieve a normal distribution for continuous habitat variables. Kruskal-Wallis analysis of variance on ranks was used to test for differences in substrate size categories among species which did not meet ANOVA assumptions after transformation. I used Systat 11, Sigma Stat 9.0 and Sigma Plot 9.0 for statistical analysis.

Results

Univariate approach

YOY Arctic charr (fork length, mean = 44.1mm, range = 33.4 - 58.0mm), brown trout (fork length = 38.0mm, range = 30.3 - 45.8mm) and Atlantic salmon (fork length = 37.1mm, range = 29.8 - 46.0mm) in ten Icelandic streams exhibit important intra- and interspecific variability in key components of their foraging mode. First, the three species differed significantly in the mobility they exhibit during search for prey (ANOVA, $F_{2,153} = 14.269$, df = 2, $p < 0.001$; Table 2.2; Figure 2.3). Arctic charr was the most mobile species during prey search (mean = 27%), and significantly more so than brown trout (Tukey HSD, $p < 0.001$) and Atlantic salmon (Tukey HSD, $p <$

0.001) which had the lowest search mobility value of the three species (mean = 12%). A post hoc test did not reveal significant differences in the search mobility of brown trout and Atlantic salmon (Tukey HSD, $p = 0.999$). Even though very mobile individuals were found within each species (Arctic charr, max = 84%; brown trout, max = 56%; Atlantic salmon, max = 77%), many fish were sedentary as 28% of Arctic charr, 59% of brown trout and 64% of Atlantic salmon spent less than 10% of their time moving while searching for food. As a result, the search time mobile was positively skewed with more values distributed toward the sedentary end of the movement scale in all three species, but more so for brown trout and Atlantic salmon than for Arctic charr (Figure 2.3).

Second, salmonid species also differed in their propensity to attack prey while moving (Kruskal Wallis, $H_{2,153} = 18.855$, $p < 0.001$; Table 2.2; Figure 2.4). Mobile foraging attempts were higher in Arctic charr compared to Atlantic salmon (Dunn's Q = 4.143, $p < 0.05$). Brown trout, however, had intermediate values for the proportion of mobile forages, which were not significantly different from those found for Arctic charr or Atlantic salmon (Dunn's Q =, $p > 0.05$). For all three species, the frequency distribution for the proportion of mobile foraging was positively skewed toward low values as most fish ambushed prey from a stationary position (Figure 1.4). Although there are clear differences among species, all species exhibit a wide range in time spent moving prior to making foraging attempts (Table 2.2; Figures 2.4). For example, although Arctic charr were the most mobile on average, one particular brown trout had the highest individual proportion of mobile forages.

Third, pursuit distance differed among the three study species (Kruskal Wallis, $H_{2,153} = 13.840$, $p < 0.001$; Figure 2.5). Brown trout had significantly longer pursuit distances than Atlantic salmon (Dunn's Q = 3.711, $p < 0.05$) whereas Arctic charr

were intermediate to Atlantic salmon (Dunn's Q = 1.630, $p > 0.05$) and brown trout (Dunn's Q =2.323, $p > 0.05$). Pursuit distance appeared normally distributed within all three species based on histograms, but was not statisctically so in brown trout (Arctic charr, K-S p = 0.192; brown trout K-S p = 0.009; Atlantic salmon, K-S p = 0.214).

Fourth, typical of what might be expected of stream salmonids, all three species foraged predominantly from the midwater, but only occasionally attacked benthic prey and rarely fed on prey on the waters surface (Figure 2.6; Table 2.3). Yet the proportion of benthic (Kruskal Wallis $H_{2,153} = 15.183$, df = 2, $p < 0.001$), midwater (Kruskal Wallis $H_{2,153} = 15.712$, df = 2, $p = <0.001$) and surface (Kruskal Wallis $H_{2,153} = 11.769$, df = 2, p = 0.003) feeding differed slightly, but significantly, among species. More specifically, Atlantic salmon had a higher proportion of benthic feeding than Arctic charr (Dunn's, Q = 3.263, $p < 0.05$), whereas brown trout did not differ from Atlantic salmon (Dunn's, Q = 0.704, $p > 0.05$), or Arctic charr (Dunn's, Q = 2.370 , $p > 0.05$). Similarly, Arctic charr had a higher proportion of midwater foraging attempts compared to brown trout (Dunn's, Q = 3.571, $p < 0.05$) and Atlantic salmon (Dunn's, Q = 3.075, $p < 0.05$) which did not differ (Dunn's, Q = 0.618 , $p > 0.05$). Post hoc analysis did not identify specific species differences in the proportion of surface foraging.

Bivariate approach

As predicted, YOY salmonids that were mobile during search for prey tended to be more mobile prior to prey attacks (Figure 2.7). Despite a very low number of individuals from each stream, the above trend was also moderately supported at the

stream level (Table 2.3). More specifically, the correlation between mobility during search and attack was always positive, and significantly so in three of four Arctic charr streams, one of three brown trout streams and two of three Atlantic salmon streams (Table 2.3).

Although mobility during search and prior to prey pursuit were positively correlated within each species, the strength (Figure 2.7) and slope of this relationship differed among the three species (ANCOVA, $F_{2, 153} = 3.963$, $p = 0.021$). Of the three species, Arctic charr clearly exhibited the strongest association among the two above aspects of foraging mode, ranging from being extreme sit-and-wait predators that rarely move while searching and always ambush prey, to being highly mobile while searching and attacking most prey from a moving start (Figure 2.7a). In contrast, brown trout showed a relatively weak relationship between search and pursuit mobility, which was highly influenced by one individual that exhibited an unusually high proportion of mobile foraging attempts. Brown trout also differed from the other species, as four individuals that showed no movement while searching for prey exhibited considerable mobility just prior to attacking prey (Figure 2.7b). In Atlantic salmon, the association between search and foraging mobility appears to have a shallower slope than for Arctic charr. Hence, although several individuals exhibited considerable mobility during search, they rarely attacked prey from a moving start (Figure 2.7).

The prediction that pursuit distance should increase with search mobility was only statistically supported in Arctic charr (Figure 2.8). Similarly, stream level associations were not significant for any species although all correlation coefficients were positive (Spearman rank correlation; $p > 0.05$ in all cases). Finally, there was no indication that the proportion of benthic foraging was higher in individuals that were

more mobile during search, neither within species nor populations (Spearman rank correlation; $p > 0.05$ in all cases).

Habitat and foraging mode

The YOY salmonids in this study, were monitored at a range of stream conditions (see Table 2.1). As expected, the three species were found at different average water flow rates (ANOVA, $F_{2, 153} = 32.3$, $p < 0.001$); Arctic charr used the slowest moving waters, and brown trout and Atlantic salmon were found in intermediate and the fastest flows, respectively. More specifically, post hoc analyses revealed that both Arctic charr and brown trout were observed at significantly lower flow rates than Atlantic salmon (Tukey test, $p < 0.001$ in both cases), whereas Arctic charr and brown trout did not differ statistically (Tukey test, $p = 0.962$) in this respect. Similarly, as expected, I observed among-species differences in water temperatures (ANOVA, $F_{2,153} = 38.829$, $p < 0.001$; Table 2.1), as Arctic charr were observed in colder waters than brown trout and Atlantic salmon (Tukey test, $p < 0.001$ in both cases). Finally, no significant evidence of species differences was detected in the use of water depth (ANOVA, $F_{2,153} = 0.888$, $p = 0.413$) or grain size of the substrate (Kruskal Wallis, $H_{2,153} = 5.695$, $p = 0.058$).

I predicted that species and populations inhabiting slower waters should be more mobile than those in faster waters. In agreement with my prediction, Arctic charr use slower waters and are more mobile during search and prior to foraging than Atlantic salmon, whereas brown trout tend to be intermediate (see results above). A similar trend is observed across populations, where a significant overall decrease in mobile foraging attempts was detected with increased water flow (Spearman $r = -0.733$, $n = 10$, $p = 0.010$) (Figure 2.9b). The same trend, but not significant, was

detected between mobile search and water flow (Spearman r = -0.523, n = 10, p = 0.129) (Figure 2.9a). Also, for all three species the populations found at the slowest water flow typically had the lowest proportion of mobile search and mobile foraging attempts. Finally, Arctic charr appear to exhibit a greater among-population variability in mobility and water flow use than brown trout, and particularly, Atlantic salmon (Figure 2.9).

Discussion

Behavioural components of foraging mode

This first comparison of the foraging mode of wild YOY Arctic charr, brown trout and Atlantic salmon in streams reveals that although all three species tend to be sedentary and attack prey drifting in the water column, there are important differences in several aspects of their foraging mode. For instance, Arctic charr are clearly more mobile as they search for food (27% of search time) than both brown trout (13%) and Atlantic salmon (12%). These findings were expected, because search mobility is thought to decrease with water flow (Grant and Noakes 1988), and Arctic charr and Atlantic salmon typically inhabit the slowest and fastest waters, respectively (Gudbergsson and Antonsson 1996, Heggenes and Saltveit 2007). Because methodology varies considerably among studies a broader comparison of search mobility needs to be taken with some reservation. However, the low search mobility observed in brown trout and Atlantic salmon in this study is consistent with sedentary trends in young brown trout (14%) (Bachman 1984) and brook charr (*Salvelinus fontinalis*) (<20%) monitored over a range of water flow in streams (Grant and Noakes 1988). Arctic charr, however, appear to be slightly more mobile than most

stream-dwelling salmonids but less mobile than brook charr observed in still water pools in streams (44%) (McLaughlin et al. 1992), and in lake habitats (50%) (Biro and Ridgway 1995). Together these findings build a strong case for the idea that salmonids become less mobile as water flow increases across habitats, from lakes to streams, and from slow to fast-running stream habitats.

Classifying foraging mode by search mobility can be somewhat arbitrary, but one study classifies brook charr as stayers (sit-and-wait) if they are mobile <10% of the time, as movers (widely foraging) if they spend greater than 50% of their time mobile and the remainder were considered intermediate and adopted both behaviours (Grant and Noakes 1988). Based on these individual criteria, many Arctic charr, brown trout and Atlantic salmon would be considered sedentary (28%, 60%, 64%) and only few (16%, 4%, 2%) would be considered mobile. For a broader comparison among cold-blooded animals, lizard species considered sit-and-wait foragers often spend on average 10-15 % or less of their time moving while they search for prey (Butler 2005, Cooper 2005). Hence, if I use the larger lizard literature as a guideline then Arctic charr can be classified as "widely foraging" species, whereas brown trout and Atlantic salmon likely fall within the sit-and-wait category.

Monitoring mobility just prior to attempts at capturing prey is useful to compare variability among sit-and-wait and widely foraging predators, but is rare in the general foraging mode literature (Cooper 2007). My finding that Arctic charr (85%), brown trout (91%) and Atlantic salmon (97%) initiate most foraging attempts while still, supports the general view that salmonids typically ambush prey in flowing waters (Kalleberg 1958, Wankowski and Thorpe 1979). Additionally, these values are higher than respective values for search mobility and thus provide a clearer idea of how these species actually attack prey in streams. Similar to search mobility, species

patterns in mobility prior to attack are consistent with expectations based on water flow as Arctic charr are more mobile than Atlantic salmon while brown trout are intermediate. Alternatively to my findings for stream-dwelling salmonids, golden shiner (*Notemigonus crysoleucas*) larvae in still waters characteristically pause while they actively search for food but rarely attack prey from this sedentary position (1-10%) (Browman and O'Brien 1992). From this contrast, it is clear that recording mobility prior to attack in addition to search mobility is useful to differentiate between animals that pause while they actively search but only attack prey as they move, from those that are mobile while searching but stop prior to ambushing prey. Although variability in mobility prior to prey attack is a recognized as an important aspect of the different foraging modes salmonids adopt (Grant and Noakes 1988), I am unaware of any other salmonid study that explicitly monitors this behaviour.

In this study, Atlantic salmon had the shortest pursuit distances (1.62 body lengths) while the two species found in slower water, Arctic charr and brown trout, pursued prey from slightly longer distances (1.86 and 2.20 body lengths, respectively). Furthermore, brook charr in still water pools in streams (McLaughlin et al. 1992) and in lakes (Biro and Ridgway 1995) have even greater pursuit distances (mean body lengths = 2.94 and 3.28, respectively) than the salmonids observed in this study. These differences are in harmony with the idea that pursuit distance should be less in fast-flowing water where salmonids wait for drifting prey. Alternatively, variation in pursuit distance in juvenile salmonids has been attributed to water column use, visibility against background habitat and prey characteristics (McLaughlin 1994). Because a predator’s success is also related to the prey’s ability to escape, detection mechanisms and mobility of common prey types could also be a factor (Dangles et al. 2006).

My finding that the three salmonid species in Icelandic rivers tend to attack prey located in the mid-water is in harmony with previous studies on brown trout and Atlantic salmon in flowing waters (Bachman 1984, Nislow et al. 1998). This study, however, is the first to show that stream-dwelling Arctic charr feed primarily on prey drifting in the water column. Interestingly, the three study species vary slightly in their propensity for attacking benthic or drifting prey. Most notably, Atlantic salmon (21%) and brown trout (20%) attacked more prey on the streambed than Arctic charr (11%). These findings are surprising because Arctic charr use slow waters where access to drifting invertebrates may be limited (Elliott 1970) and because they regularly forage on benthic prey in lakes (Malmquist et al. 1992, Klemetsen et al. 2003) and in captivity (Jorgensen and Jobling 1990). Initially, the high proportion of benthic foraging among Atlantic salmon may be surprising considering their use of fast waters where drifting prey should be abundant. My findings, however, fall within a wide range of benthic foraging in previous studies of Atlantic salmon (Keeley and Grant 1995), < 1% to 39% (Nislow et al. 1998). One potential contributor to benthic foraging is that Atlantic salmon have large pectoral fins that allow them to hold an ambush position closer to the streambed, and thus in more proximity to benthic prey, than is typical for other salmonids (Arnold et al. 1991, Hojesjo et al. 2005).

The correlated behaviours of foraging mode

This study indicates that the three salmonid species in Icelandic rivers are similar, but show notable discrepancy, in the way search mobility is associated with actual feeding behaviour, i.e. the mobility they exhibit just prior to attacking prey and the distance of prey pursuits. Importantly, that mobile search and mobile foraging attempts increase accordingly among individuals in all three species, agrees with the

idea that salmonid foraging modes reflect a set of coordinated behaviours (Eckhardt 1979, McLaughlin 1989, McLaughlin et al. 1992). However, some subtle species differences do emerge when I examine the results in the context of the conceptual foraging mode framework presented earlier (Figure 2.1). Similar to what might be expected from previous studies on mobile animals (Eckhardt 1979, McLaughlin 1989, McLaughlin et al. 1992, Cooper 2007), individual Arctic charr continuously varied between being extreme sit-and-wait predators that rarely move while searching and always ambush prey (see scenario in Figure 2.1a) to being highly mobile both while searching and attacking prey (Figure 2.1b). In comparison, however, although search and pursuit mobility are also correlated for brown trout and Atlantic salmon, the slope and consistency of this relationship clearly differs among species. Most brown trout, for example, behave as sit-and-wait foragers and show limited mobility both during search and prior to prey attack (Figure 2.1a) and the bivariate relationship is highly influenced by one very mobile individual (Figure 2.1b). In addition, a few brown trout differed from both Atlantic salmon and Arctic charr as they did not move during search, but made several mobile foraging attempts (Figure 2.1d). Similar to the behaviour of brown trout, most Atlantic salmon sit-and-wait for prey both during search and prior to foraging. In contrast to Arctic charr and brown trout, however, the few salmon that exhibit high mobility during search show a limited increase in mobility prior to pursuit (see Figure 2.1c; although no extreme individuals were observed). These findings agree with Steingrimsson and Grant (in press) which suggested that YOY Atlantic salmon are multiple central-place foragers that attack prey primarily from a sit-and-wait position, but can be very mobile as they frequently switch among ambush sites. This foraging mode alternative may be more common

among mobile animals than previously thought, as a similar tactic was recently proposed for wolf spiders foraging in agricultural fields (Samu et al. 2003).

Although, the relationship among search and pursuit is not implicit in the foraging mode argument, so far, two studies of brook charr report pursuit distances were longer for more mobile searching individuals (McLaughlin et al. 1992, Biro and Ridgway 1995). In this study, Arctic charr that are more mobile during search, traveled further during pursuit, whereas such association was not detected for Atlantic salmon or brown trout. Thus, it is clear that species may vary in the way pursuit distance relates to mobility and further work is necessary to determine why only some species increase their pursuit distance as they switch to a more mobile foraging mode. Alternative to Arctic charr and brook charr, in a comparison of bird species, passive searchers that initiated pursuits from a perch site to capture immobile prey from surfaces (sit-and-wait) were found to have larger attack radii than more mobile searchers that captured airborne prey (Eckhardt 1979). To conclude, I would argue that the role of pursuit distance as part of a coordinated set of behaviours needs further examination in animals, especially in the context of how foraging mode is influenced by food and habitat features.

Search mobility and benthic foraging were not correlated in any species in this study. In theory, salmonids should move when feeding on sedentary benthos to increase their prey encounters (Grant and Noakes 1987) if nearby prey organisms are depleted by consumption (Wooster and Sih 1995, Dahl and Greenberg 1996). To date, empirical studies have shown an indirect link between search mobility and benthic feeding as both behaviours are negatively associated with water flow (Grant and Noakes 1987, Katano 1996). However, these studies did not attempt to correlate individual search mobility with benthic foraging. Hence, a detailed study where

individual foraging mode is linked to habitat features and the characteristics of benthic prey may be necessary. Interestingly, mobility may not covary with the proportion of benthic foraging if increased mobility also allows fish to encounter more mid-water or surface prey in slow or still waters (Grant and Noakes 1987, McLaughlin 1994).

My findings suggest that in some cases foraging mode components covary in a similar way at the species and the population level. In this study, the tendency for mobile searcher to be more mobile prior to attacking prey is not solely due to an additive effect of many different populations, but may also exist within the populations themselves. This finding is important for understanding foraging mode in a general sense, as the question of how a continuum of variation at the species level comes about is still widely debated (Perry 1999).

Foraging mode, habitat and population differences

This study is the first to systematically compare the foraging mode of several salmonid species across an environmental gradient in streams. As predicted, Arctic charr, brown trout and Atlantic salmon adopted the most mobile, intermediate, and the least mobile foraging mode as they were found in the slowest to fastest water flow, respectively (Heggberget 1984, Gudbergsson and Antonsson 1996, Heggenes and Saltveit 2007). This trend, where mobility increases as water flow decreases was also detected across the ten study populations, at least when mobility is measured just prior to prey attack. However, due to the observational nature of this study, a further examination of my data needs to examine the potential effects of other ecological factors than water flow, such as body size, water temperature and prey availability. For example, it is reasonable to expect that prey may be important, given that the

number of drifting prey increases with water flow (Elliott 1970, Wankowski and Thorpe 1979, Grant and Noakes 1987) and prey characteristics can influence the foraging mode (Katano 1996, Fausch et al. 1997) and distribution and abundance of salmonids in streams (Cada et al. 1987, Poff and Huryn 1998). In addition, water temperature may also affect mobility as metabolic demands related to swimming may increase with water temperature (Webb 1978). Furthermore, water temperature can limit the distribution of salmonids among watersheds (Fausch et al. 1994), and seems to be important on a stream level in Iceland where Artic charr tend to reside in the coldest waters (Gudjonsson 1990).

Although not conclusive, the population differences observed for the three species are of considerable interest. Most notably, greater differences were found in the mobility and water flow use among the four Arctic charr populations, than for Atlantic salmon that consistently exhibited low mobility in relatively fast waters. Greater variability in the foraging mode of Arctic charr, both at the individual and population level, agrees with evolutionary studies that consider Arctic charr highly variable in behaviour (Skulason et al. 1993), morphology (Skulason et al. 1989, Snorrason et al. 1994), and life history (Skulason et al. 1996), showing significant divergence within populations. These studies emphasize the importance of the interaction of foraging and habitat, and provide substantial evidence that Arctic charr variation is driven by a diverse feeding ecology (Skulason et al. 1992, Skulason and Smith 1995). In the least, I suspect that variability in Arctic charr behaviour may allow them to exploit a wider range of habitats compared to a less variable species such as Atlantic salmon. In this context, an animal's ability to adopt sedentary and mobile foraging tactics may improve its performance (ie. fitness) when using a broad range of habitats and resources than those more restricted (Helfman 1990, Helfman

and Winkelman 1991). Because foraging mode is related to habitat it is reasonable to assume that behavioural differences among these salmonids and their populations should influence their growth and fitness in slow and faster flowing waters. Together, I believe that my findings form a useful basis for building a mechanistic understanding of the links between individual behaviour and broad-scale patterns of diversity and the distribution of Arctic charr, brown trout and Atlantic salmon in Icelandic freshwaters, as well as in other freshwater systems .

Chapter Three - General Discussion and Conclusions

My findings make new contributions to stream salmonid research by providing the first comparison of Arctic charr, brown trout and Atlantic salmon foraging behaviour. In particular, knowledge about Arctic charr in streams is scarce (Klemetsen et al. 2003). In agreement with earlier ideas of stream salmonid behaviour (Kalleberg 1958, Wankowski and Thorpe 1979, Bachman 1984), these species were relatively sedentary searchers and ambushed prey via short bursts of swimming. However, like studies of birds (Eckhardt 1979, Robinson and Holmes 1982), lizards (Huey and Pianka 1981, Butler 2005), and fish (Fausch et al. 1997) my study reveals that species vary in foraging mode. In comparison, Arctic charr were more mobile during prey search and prior to attacking prey than Atlantic salmon, whereas brown trout were intermediate. Thus, emphasizing that detailed species comparisons are necessary to understand salmonid foraging in streams. Cooper (2007) suggested that quantifying movements as animals attack prey should be useful in foraging mode studies. My data support his claim and clearly add to literature by showing that mobility of stream-salmonids may be more restricted immediately before foraging bouts than during search. I also put forward a new visual framework (Figure 2.1) for how individual behavioural components related to search and foraging may covary, and thus contribute to a more complete view of foraging mode. In this context, empirical data suggest that even though more mobile searching individuals were also likelier to make mobile foraging attempts in all species, the slope and consistency of this relationship varies among species. Furthermore, as individuals increased their search mobility, only Arctic charr showed an increase in the distances traveled during prey pursuits.

Individual behavioural studies provide a new framework for studying animals in Icelandic freshwaters streams. Previously, habitat use and distribution of salmonids

in Icelandic streams is reported to vary where Arctic charr inhabit slower waters of cold low productive streams, whereas brown trout and Atlantic salmon reside in more productive waters at intermediate and high water flows respectively (Gudjonsson 1990, Gudbergsson and Antonsson 1996). Using a behavioural approach, I examined if the foraging mode differences reported above were in harmony with the prediction that mobility should decrease with increased water flow (Grant and Noakes 1988). I found that Arctic charr, brown trout and Atlantic salmon overlap in some habits but clearly exhibit different foraging behaviour, which varies according to water flow use. As predicted, Arctic charr and brown trout use slower waters and were the most mobile and intermediate in behaviour respectively, whereas Atlantic salmon were found in the fastest waters, and were least mobile. My approach compliments earlier studies as a means to form predictions about how individuals should perform under different habitat conditions (Fausch et al. 1997, Nislow et al. 1998, Nakano et al. 1999). Consequently, under the theory of natural selection the performance of individuals should influence why some species may occupy one habitat and not another (Sutherland 1996) and thus ultimately a more mechanistic understanding of salmonid distributions can be developed. Hence, an individual-based framework may improve understanding of why demographic patterns exist, why exceptions may arise, and how salmonids might respond to novel conditions, such as human induced changes. On the whole, a behavioural approach is of value to understanding the habitat use and the distribution of salmonids in Iceland, as it shifts focus from describing patterns of where salmonids are found to a more biological understanding that links salmonid characteristics to stream habitat conditions.

Overall my research argues for the use of individual-based comparisons of foraging mode in attempts to establish diversity among similar predator species.

Beyond a comprehensive examination of foraging mode, identifying key environmental factors that influence individual mobility should also provide helpful insights into space use. In addition to water flow, food and social interactions can be important determinants of foraging behaviour in stream habitats (McLaughlin 1994, Nakano 1995, Fausch et al. 1997, Nislow et al. 1998). Subsequently, the consequences of foraging mode for growth and fitness in relation to habitat characteristics should also be investigated. My findings advocate that distinguishing foraging mode among similar species may require detailed descriptions beyond the two extremes of a sedentary-mobile continuum (Janetos 1982, Pianka 2000). Once armed with these details researchers may make better predictions about the role of movement tactics in the ability of salmonids to utilize variable conditions in freshwater environments. For example, the knowledge that brown trout seem to remain sedentary even in slow waters may mean that these habitats are only exploited where food is abundant (Helfman 1990). In conclusion, by definition species are expected to differ, but establishing how animal characteristics vary is an important first step to understanding their ecology. In this context, my investigation fills some important knowledge gaps in the behaviour of these three species. Future work may build on the descriptive basis of my observations to form a more mechanistic understanding about the processes that influence the habitat use, diversity and distribution of these salmonids in the wild.

Tables 2.1 – 2.4

Table 2.1 Habitat characteristics of three species of young-of-the-year salmonids observed in 10 Icelandic streams.

Species	Water Flow ($cm.s^{-1}$)	Water Depth (cm)	Water Temperature (°C)	Substrate Size
Arctic charr	9.3 (0.1 - 39.9)	37.7 (8.5 - 86.5)	11.8 (6.6 -18.7)	3.7 (1 - 6)
Brown trout	9.9 (0.0 - 51.3)	21.5 (8 - 60.5)	16.2 (11.6 - 19.7)	4.3 (3 - 5)
Atlantic salmon	26.6 (2.3 - 65.7)	36.5 (10 - 88)	15.1 (12.3 - 20.4)	4.4 (1 - 7)

Note: Data were pooled for 4 Arctic charr streams (n = 61), 3 brown trout streams (n = 42), and 3 Atlantic salmon streams (n = 50). Mean and range (in parenthesis) are reported. Substrate size values reflect categories assigned using a modified Wentworth scale 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 2.2 Univariate summaries of foraging behaviour of young-of-the-year salmonids in Icelandic streams

Foraging Behaviour	Species	Mean	Median	Range
Proportion of Mobile Searching				
	Arctic charr	0.27	0.24	0 - 0.84
	brown trout	0.13	0.08	0 - 0.56
	Atlantic salmon	0.12	0.08	0 - 0.77
Proportion of Mobile Forages				
	Arctic charr	0.15	0.07	0 - 0.69
	brown trout	0.09	0.04	0 - 0.93
	Atlantic salmon	0.03	0.00	0 - 0.27
Pursuit Distance (body lengths)				
	Arctic charr	1.86	1.82	0.09 - 5.00
	brown trout	2.20	2.15	0.78 - 4.57
	Atlantic salmon	1.62	1.53	0.40 - 3.09
Proportion of Benthic Forages				
	Arctic charr	0.11	0.05	0 - 0.63
	brown trout	0.20	0.13	0 - 0.80
	Atlantic salmon	0.21	0.13	0 -0.79

Note: Species summaries include 61 Arctic charr, 42 brown trout and 50 Atlantic salmon

Table 2.3 Statistical comparison of the proportion of benthic, mid-water and surface foraging made by three salmonids in ten Icelandic streams based on Kruskal Wallis Analysis of Variance on ranks.

Species	Kruskal Wallis Statistic (H)	Pairwise Comparison	Dunn's Q	P-value
Arctic charr	129.96			<0.001
		Benthic-surface	4.706	<0.05
		mid-water-benthic	5.105	<0.05
		midwater-surface	9.811	<0.05
brown trout	99.024			<0.001
		Benthic-surface	4.706	<0.05
		mid-water-benthic	5.105	<0.05
		midwater-surface	9.811	<0.05
Atlantic salmon	91.123			<0.001
		Benthic-surface	2.522	<0.05
		mid-water-benthic	6.658	<0.05
		midwater-surface	9.179	<0.05

Note: Based of df = 2 for Arctic charr = 61, brown trout = 42, Atlantic salmon = 50

Table 2.4 Spearman Rank correlations between mobile searching and mobile foraging attempts for young-of-the-year salmonids in 10 Icelandic streams

Species	Stream	N	Coefficient	P-value
Arctic charr	Myllulækur	18	0.484	0.041
	Norðurá	13	0.916	< 0.001
	Grafará	15	0.367	0.171
	Brúnastaðará	15	0.840	< 0.001
Brown trout	Húseyjarkvísl	16	0.722	< 0.001
	Þverá	11	0.083	0.797
	Fremri-Laxá	15	0.058	0.832
Atlantic salmon	Laxá á Ásum	19	0.478	0.0374
	Tungá	15	0.338	0.209
	Mýrarkvísl	16	0.713	< 0.001

Figures 2.1 – 2.9

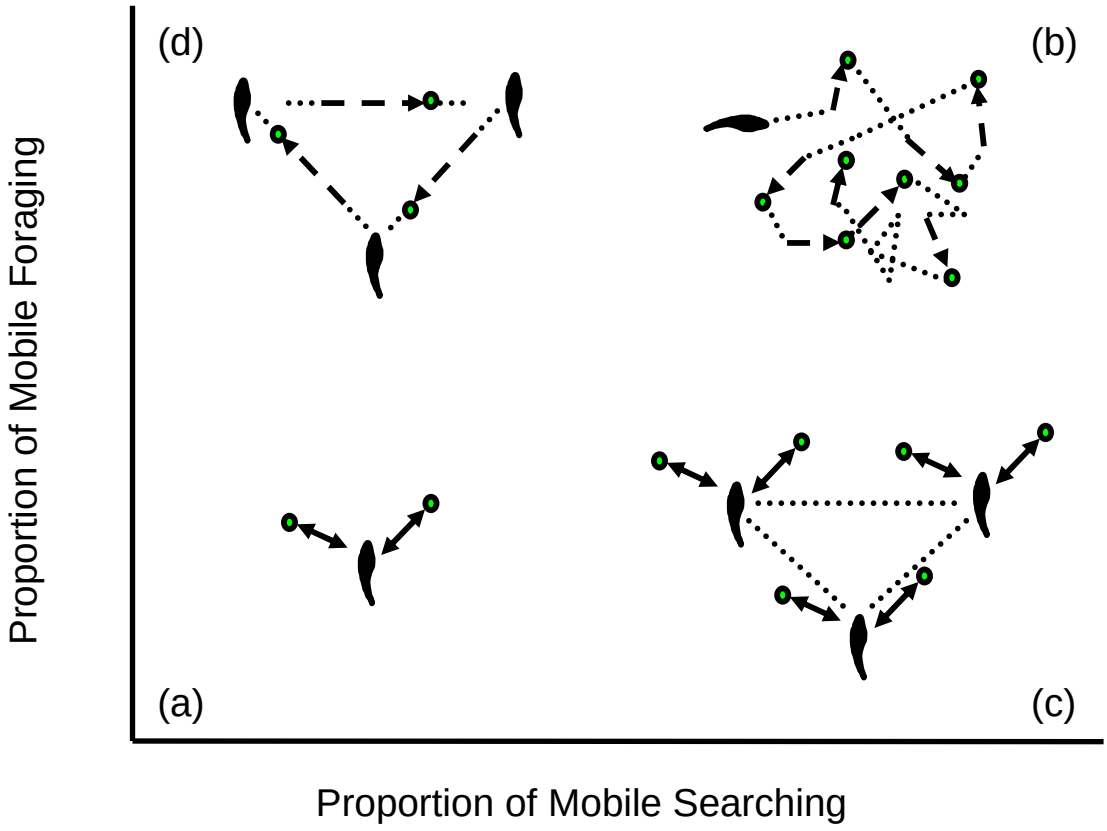

Figure 2.1. Conceptualized view of the potential variability in the mobility of stream-dwelling salmonids as they search for and pursue prey. The extreme foraging modes, sit-and-wait and widely foraging are depicted in a) and b), respectively. Hypothetical situations where individuals c) move between pursuits but only attack prey from ambush sites and d) never move except prior to attacking prey are proposed. Small circles, dotted lines, solid and dashed arrows represent intercepted prey items, movement during search, and attacks on prey from a stationary position and a moving start, respectively. Both axes represent a hypothetical range from no movement to constant movement.

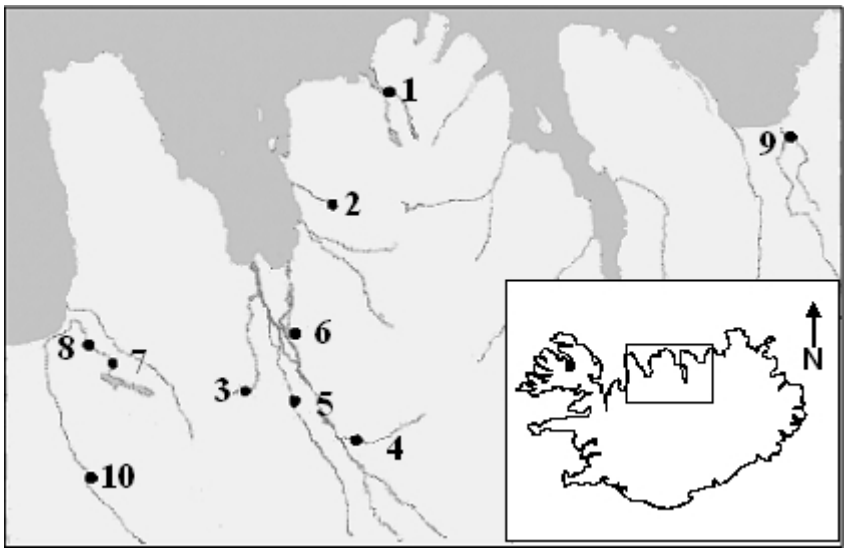

Figure 2.2. Map of the ten study streams in northern Iceland. The rivers (●) are labeled with numbers for Arctic charr: 1. Brúnastaðará, 2. Grafará, 3. Myllulækur, 4. Norðurá; brown trout: 5. Húseyjarkvísl, 6. Þverá, 7. Fremri-Laxá; and Atlantic salmon: 8. Laxá á Ásum, 9. Mýrarkvísl, 10. Tungá. Bottom right corner contains a map of Iceland with the study area outlined.

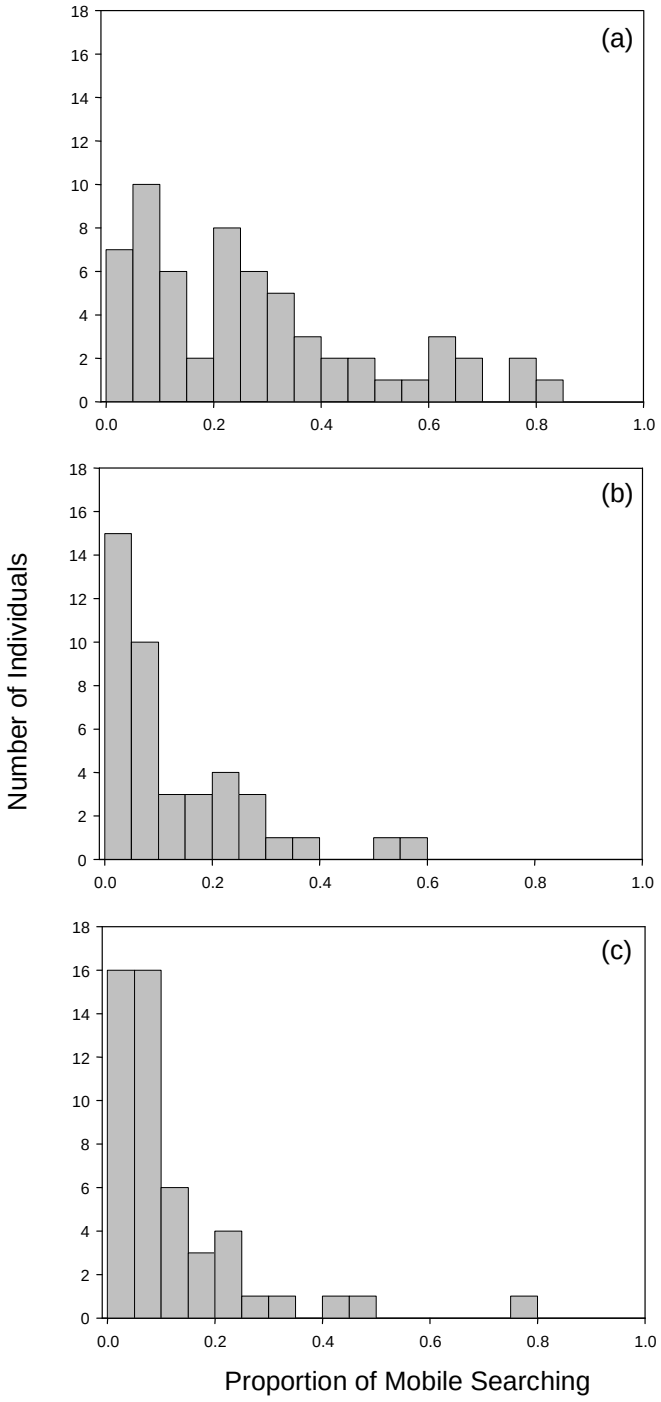

Figure 2.3. The search mobility of three species of young-of-the-year salmonids in Icelandic streams. The frequency distributions show untransformed data for (a) 61 Arctic charr (*Salvelinus alpinus*) from 4 streams, (b) 43 brown trout (*Salmo trutta*) from 3 streams and (c) 50 Atlantic salmon (*Salmo salar*) from 3 streams. Search mobility was estimated based on the proportion of 5-second search intervals where a focal fish moved more than 1 body length)

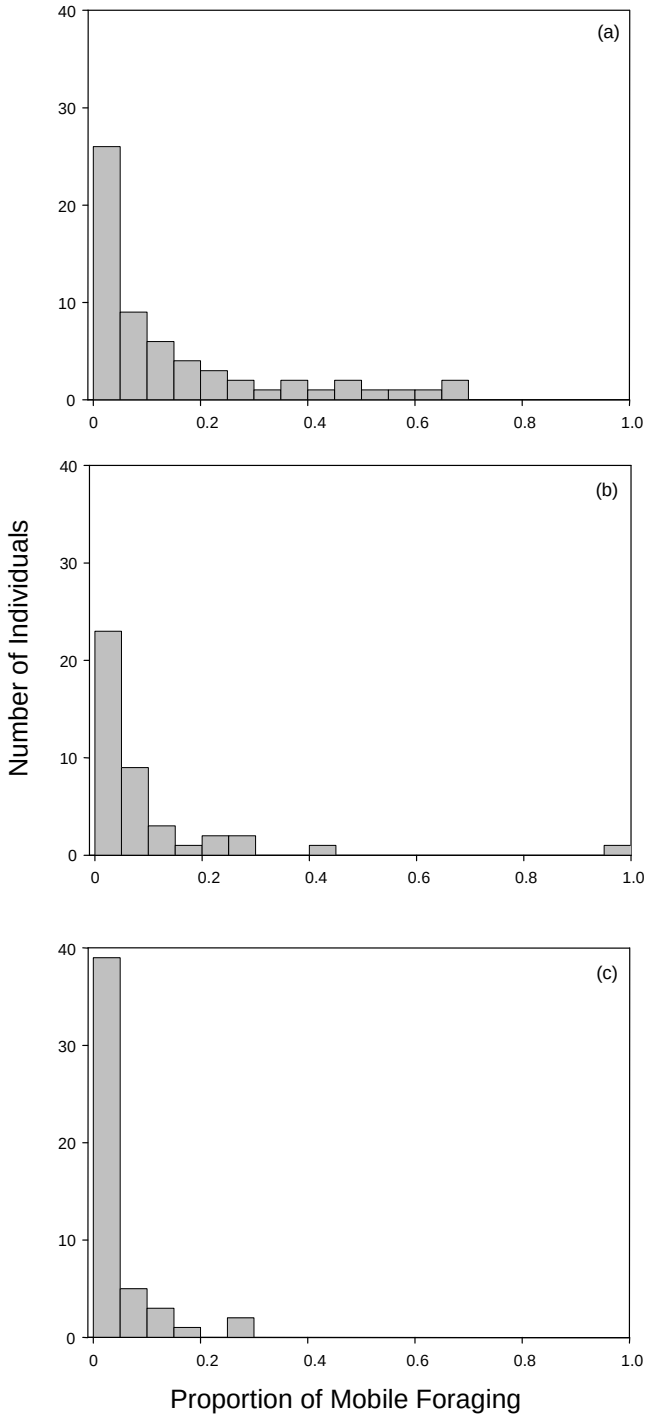

Figure 2.4. The mobile foraging attempts of three species of young-of-the-year salmonids in Icelandic streams. Frequency distributions show untransformed data for (a) 61 Arctic charr (*Salvelinus alpinus*) from 4 streams, (b) 43 brown trout (*Salmo trutta*) from 3 streams and (c) 50 Atlantic salmon (*Salmo salar*) from 3 streams.

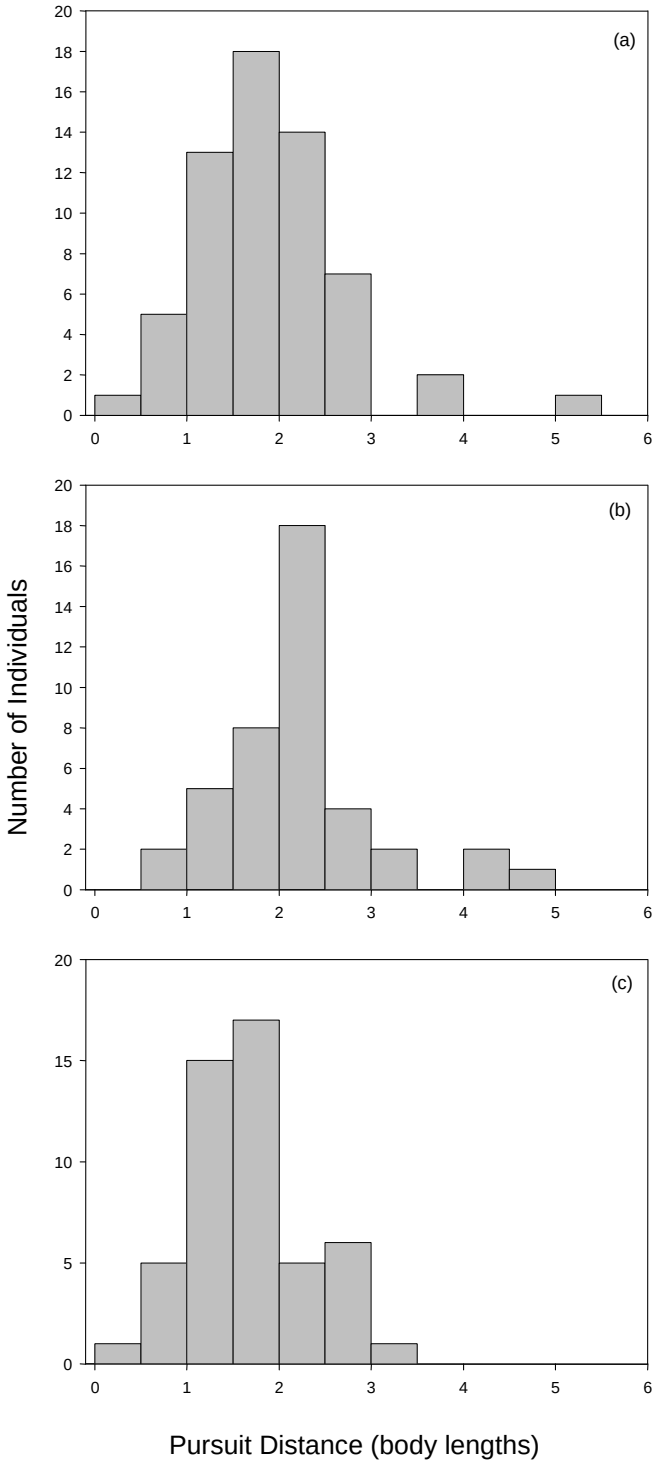

Figure 2.5. The mean pursuit distance of three species of young-of-the-year salmonids in Icelandic streams. Frequency distributions show untransformed data for (a) 61 Arctic charr (*Salvelinus alpinus*) from 4 streams, (b) 43 brown trout (*Salmo trutta*) from 3 streams and (c) 50 Atlantic salmon (*Salmo salar*) from 3 streams.

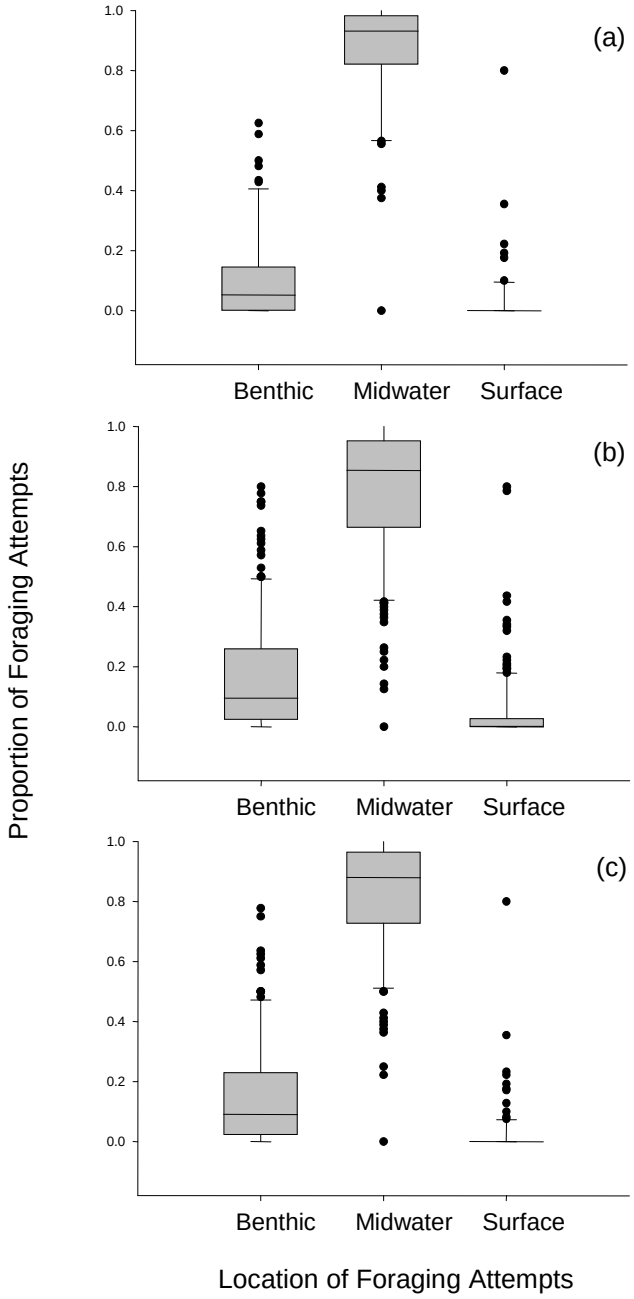

Figure 2.6. The benthic, mid-water, and surface forages for three species of young-of-the-year salmonids in Icelandic streams. Box plots show the median value (line), the 25% and 75% quartile (box), 95 % quartile (line) and individual extreme values (stars) for (a) 61 Arctic charr (*Salvelinus alpinus*) from 4 streams, (b) 43 brown trout (*Salmo trutta*) from 3 streams and (c) 50 Atlantic salmon (*Salmo salar*) from 3 streams.

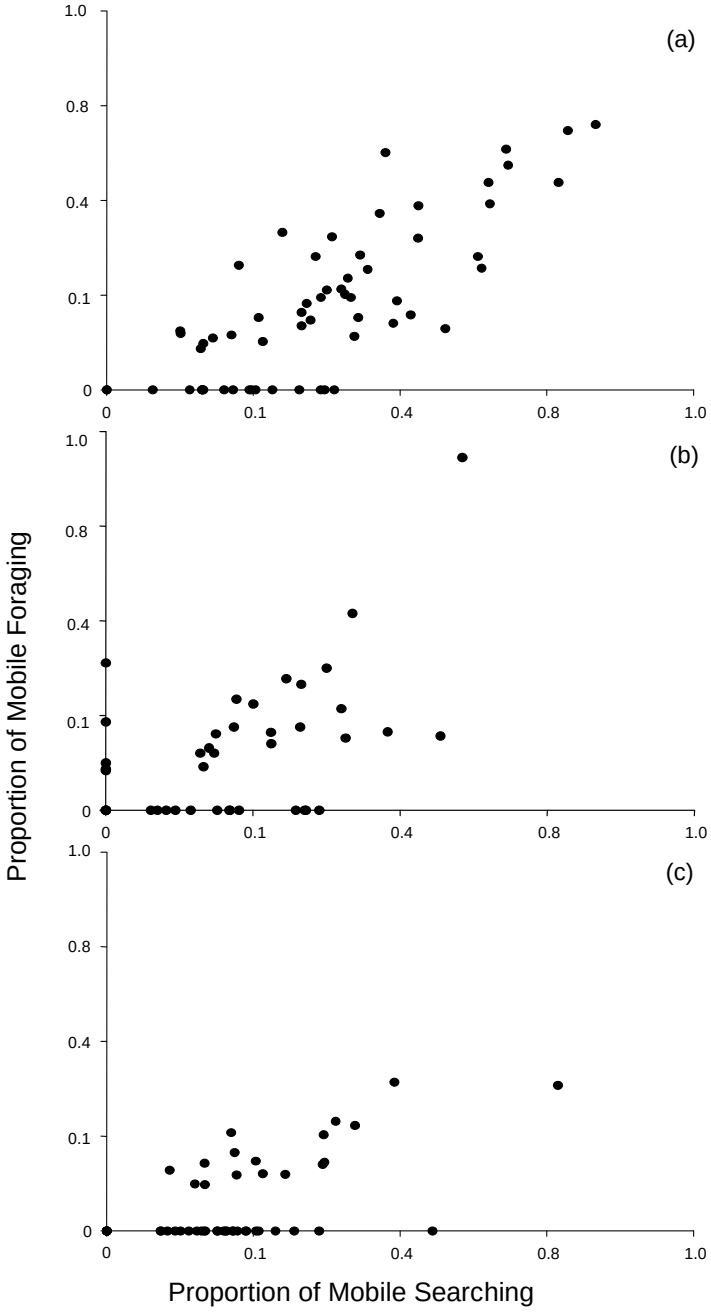

Figure 2.7. The association between search mobility and mobile foraging attempts for young-of-the-year salmonids in Icelandic streams. Scatterplots show (a) 61 Arctic charr from 4 streams (Pearson´s r = 0.80, P < 0.001), (b) 43 brown trout from 3 streams (Pearson´s r = 0.51, P < 0.001 and (c) 50 Atlantic salmon from 3 streams (Pearson´s r = 0.62, P < 0.001). Axes values were back-transformed from arcsine square root transformations of proportion data.

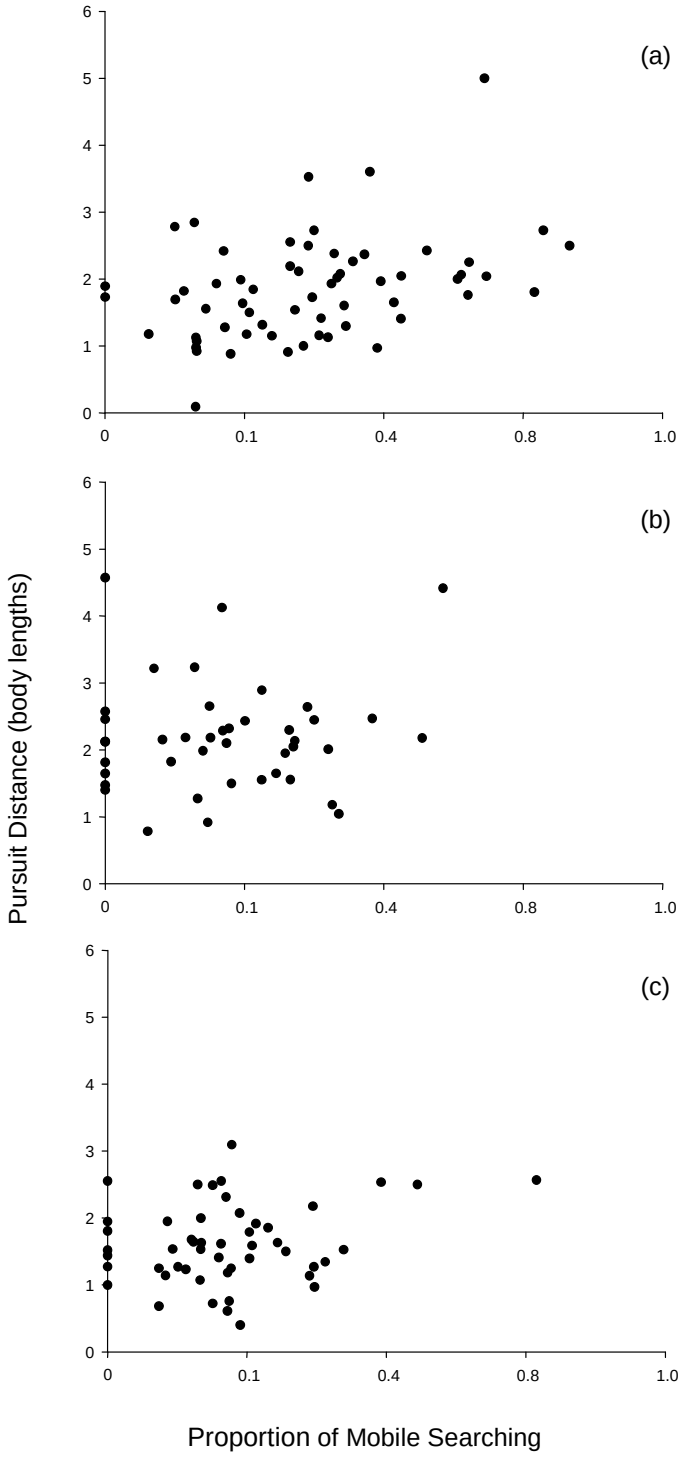

Figure 2.8. The association between search mobility and pursuit distance for young-of-the-year salmonids in Icelandic streams. Scatterplots show (a) 61 Arctic charr (Pearson´s r = 0.37, P < 0.01), (b) 43 brown trout (Pearson´s r = 0.08, P = 0.61, (c) 50 Atlantic salmon (Pearson´s r = 0.23, P = 0.1). X axis was back-transformed from arcsine square root transformations of proportion data.

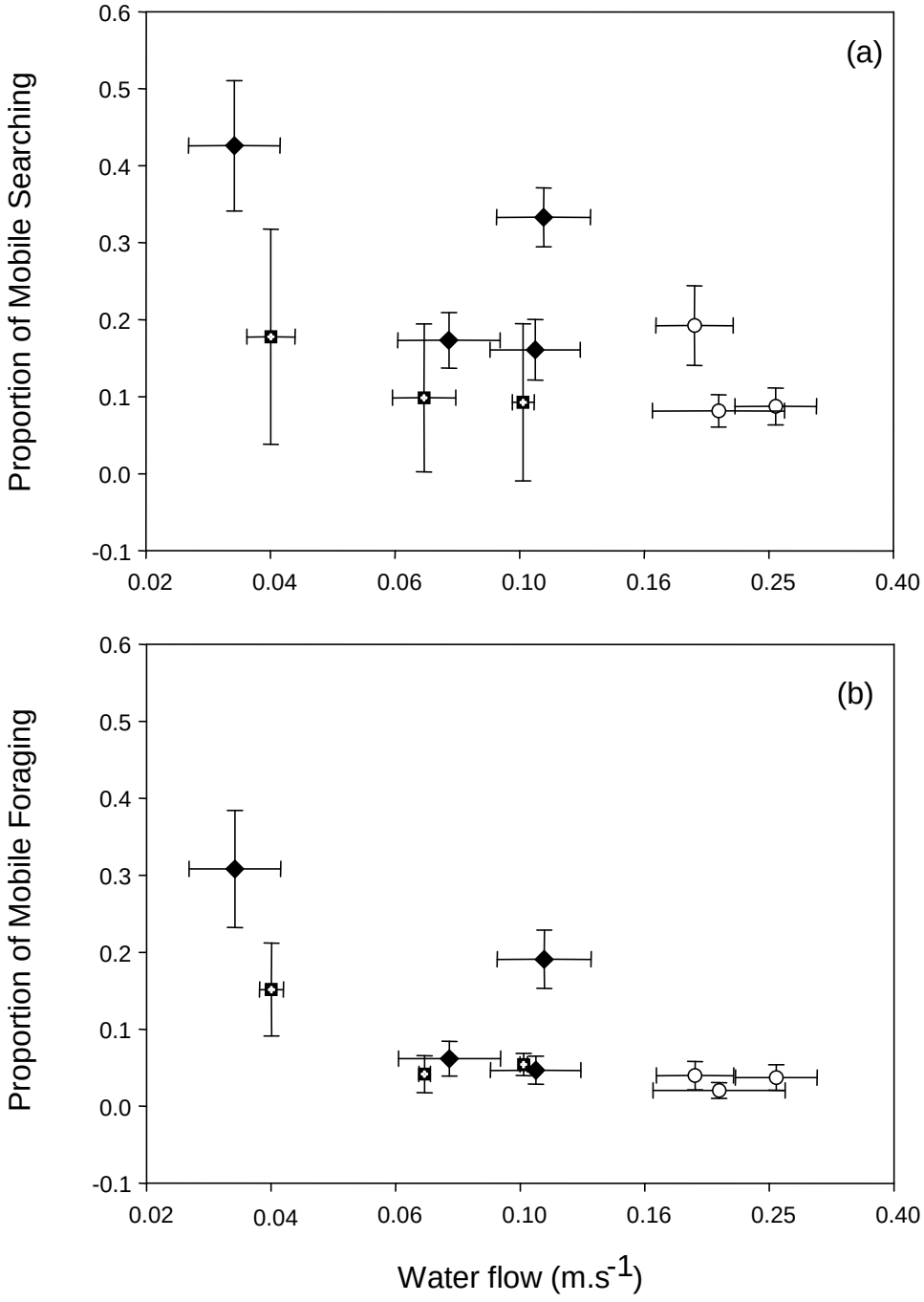

Figure 2.9. Mobility exhibited by young-of-the-year salmonids in Icelandic during (a) prey search and (b) prior to attacking prey plotted against mean water flow used by fish in each stream. Symbols show mean of Arctic charr in 4 streams (◆), brown trout in 3 streams (◘), and Atlantic salmon in 3 streams (○). Error bars represent the standard error of the mean. X axis was back-transformed from log-transformations of water flow.

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