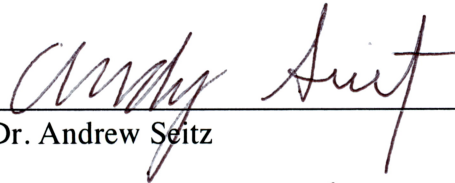


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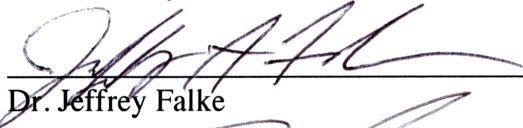
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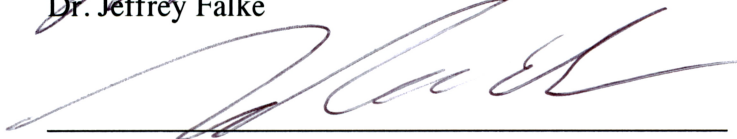
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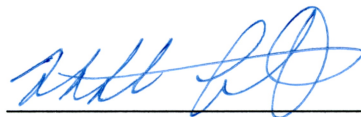
  
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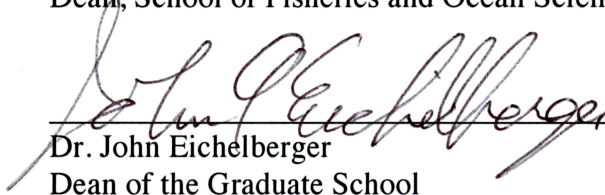
  
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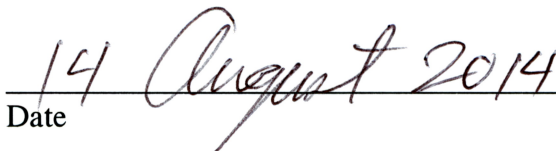
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SEASONAL MOVEMENTS OF ARCTIC GRAYLING IN A SMALL STREAM ON THE  
ARCTIC COASTAL PLAIN, ALASKA

A  
THESIS

Presented to the Faculty  
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

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## Abstract

In watersheds of the Arctic Coastal Plain (ACP) of Alaska, Arctic Grayling adopt a migratory life history strategy to persist in a landscape with long (~ 8 month), cold winters that cause shallow aquatic habitats to freeze solid. We investigated movement patterns of adult and juvenile Arctic Grayling in a shallow beaded stream (Crea Creek), a dominant headwater stream type on the ACP. From 2012–2013 Arctic Grayling ( $N = 1035$ ) were tagged with passive integrated transponder tags and monitored using an array of stream-wide antennae. Migration into Crea Creek peaked immediately after ice break-up in the main channel of the study area. Fish caught within the stream in June were in relatively poor body condition compared to fish captured later in summer. In both years, fish entering the stream during high flow and colder temperatures swam farther upstream than those entering during low flow and warmer temperatures. Migration of adult fish out of the stream was most strongly correlated with decreasing stream discharge, whereas juvenile downstream migration occurred in two peaks and was negatively correlated to minimum stream temperature and discharge. Among juveniles, fish of larger size and higher body condition tended to emigrate earlier. These results indicate that the population level migratory response is strongly tied to seasonal changes in hydrology, though heterogeneity among individuals also influences the response to seasonal change. This work demonstrates the importance of environmental cues, and surface-water flow mediated connectivity during the open-water period, and provides information needed to identify susceptibilities of migratory fishes to climate change and petroleum development on the ACP.



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## Introduction

### *Environmental and individual controls on migration*

Migration is a widespread behavioral adaptation that occurs in many groups within the animal kingdom, and is very common in stream resident salmonids (Gowan et al. 1994; Dingle 1996). It is adaptive at multiple scales. At the evolutionary scale, migration has evolved as a dominant behavior across many taxa because it can increase lifetime reproductive success of individuals in comparison to a sedentary life history (Dingle 1996; Dodson 1997). It is also adaptive to seasonal environmental “priming” and “releasing” factors that cue timing of population level movements (e.g. smolting salmon, McCormick et al. 1998; Sykes et al. 2009). Finally, migration is adaptive at the individual level as physiological differences among individuals can mediate the migratory response (Chapman et al. 2011). For example, freshwater fish are well known to time functional shifts in habitat use (e.g. summer foraging to overwintering) with changing environmental conditions (Gowan et al. 1994; Dingle 1996; Swanberg 1997; Bryant et al. 2009). There is also a growing body of literature indicating that individual differences can influence the migratory response among fish experiencing similar environmental conditions (e.g. fish size, Halttunen et al. 2013; body condition, Brodersen et al. 2008; growth rate, Forseth et al. 1999).

Migration allows individuals to match ontogenic and seasonal life history needs with appropriate habitats in environments with changing abiotic and biotic conditions (Schlosser and Angermeier 1995; Gowan and Fausch 1996). Whereas certain physical habitat features are associated with benefits to occupants (e.g. high flow and increased invertebrate drift available to drift feeding salmonids, Poff and Ward 1991; Dudgeon 1993, or thermal optimum temperature and salmonid growth, Jonsson et al. 2001), these physical features are not static. Hydrology in river networks has strong climate-driven seasonal patterns (Gasith and Resh 1999), and these patterns interact in complex ways within habitats to govern the benefits and costs associated with occupancy of that habitat. Not surprisingly, seasonal changes in hydrology and climate parameters often initiate migratory movements, or “functional shifts” in habitat type by an individual (Homel and Budy 2008). Fish migration has been associated with increases in flow (Albanese et al. 2004), ice formation (Jakober et al. 1998), decreases in water temperature (Huusko et al. 2007), changing photoperiod (Muir et al. 1994), and barometric pressure (Sackett et al. 2007), amongst other seasonal changes.



Fish movements in river networks are also inherently related to connectivity among spatially discrete habitats that may vary seasonally with hydrology and weather patterns (Fullerton et al. 2010). For example, low water conditions, freezing, and anthropogenic disturbance can limit movement between habitats and have pronounced ecological effects at individual, population, and metapopulation levels (Fagan 2002). Alternatively, periodic flooding can connect formerly isolated habitats allowing for dispersal, new habitat exploration, and increased gene flow among metapopulations (Schlosser and Angermeier 1995). Thus, seasonal variation in climatic parameters not only initiates movements amongst habitats, but also can control physical connectivity among those habitats through time.

Both the timing of migration, and whether or not an individual migrates, are also influenced by individual fish characteristics (Chapman et al. 2011). Much of our understanding of these processes comes from research conducted on partially migratory populations, where there exists both resident and migratory components within the same population (Chapman et al. 2011). For example, many populations of salmonids are partially anadromous, where only a portion of the population migrates to sea (Jonsson and Jonsson 1993). While environmental variability plays a role in determining the relative proportion of migrants to residents (Hendry et al. 2003), studies have found the tendency to migrate is often sex-biased toward females (Jonsson and Jonsson 1993) and is correlated with higher individual growth rates (Jonsson 1985) and larger body size (Thériault and Dodson 2003). Similarly, individual characteristics can influence migration timing; for example, experimental feeding led to increased body condition in a group of cyprinids, which subsequently migrated earlier than non-fed conspecifics (Brodersen et al. 2008). Brodersen et al. (2008) concluded that condition dependent decision-making by individuals determined migration timing in this population. Others have found that body size, individual growth rates, and even boldness are important determinants in individual migration timing of fish (Forseth et al. 1999; Chapman et al. 2011; Halttunen et al. 2013). These findings suggest that physiological differences among size classes and heterogeneity in accumulated lipid reserves among individuals mediate the relative costs and benefits of migration for an individual, resulting in differences in migratory behavior (Brodersen et al. 2008). Understanding the factors influencing migration is thereby best understood through multiple levels of analysis (e.g. population and individual).

## *Migration of Arctic Grayling on the Arctic Coastal Plain, Alaska*

Arctic Grayling (*Thymallus arcticus*) is within the family Salmonidae and is widespread throughout Alaska, as well as Arctic and subarctic watersheds of Russia and Canada (Scott and Crossman 1973). The migratory life history of Arctic Grayling is likely one of the major adaptations that has allowed for its successful invasion into Arctic regions of the globe (Tack 1980). Migrations generally involve a complex series of annual movements among three functionally different habitat types, forming a “migratory circuit” (Harden-Jones 1968; Tack 1980; West et al. 1992; Northcote 1995). Fish require deep-water or spring fed areas that retain adequate liquid water and dissolved oxygen for overwintering (West et al. 1992). As winter ice begins to break up and water temperatures rise, adult fish undergo a pre-spawn migration towards spawning habitats (Craig and Poulin 1975; Tack 1980). Spawning is believed to begin as water temperatures reach a threshold level of 3.9°C (Tack 1972), after which males defend spawning territories of 6–7 m<sup>2</sup> (Beauchamp 1990) in predominantly shallow riffled areas. A post-spawn migration ensues shortly after the completion of spawning where spent fish move towards feeding areas to forage and sequester energy reserves. Many juveniles forgo this spawning migration and move directly towards foraging areas after ice break-up, however some larger juveniles (subadults) follow adults through this entire migration (Tack 1980). Tack (1980) suggests this may be a mechanism to imprint this complex migration route across generations. The type of foraging habitats used varies regionally, but is likely related to forage availability (McFarland 2014), temperature (Schallock 1966) and flow preferences (Deegan et al. 1999), and density-dependent competition (Hughes 1992). Size-class specific summer habitat use is also documented, with smaller fish usually found in lower river sections and larger fish further upstream (Tack 1980; Hughes 1999). As environmental cues indicate the approach of winter, fish begin migrating back towards overwintering areas. Whereas general migration patterns of Arctic Grayling are understood, these patterns likely vary amongst watersheds and across geographic areas (Tack 1980) and are dependent on the relative proximity of available habitats. Similarly, climatic differences across the range of Arctic Grayling are dramatic and likely a major factor influencing population level movements and timing of migration.

At the northern extent of their range in Alaska, the overwintering period is elongated and only three to four months of ice-free conditions are available for spawning and foraging in seasonally flowing habitats (Northcote 1995; Buzby and Deegan 2000). Fish at these latitudes

should be particularly well adapted for efficient use of habitats during summer in order to maximize reproductive success and acquire sufficient energy reserves to survive the next winter (Buzby and Deegan 2000). Previous research has shown that during spring and summer, migratory Arctic Grayling move into productive seasonally flowing streams to forage and spawn (Craig and Poulin 1975, Tack 1980); however, fish must time their migrations out of such habitats before freeze-up or low stream flows threaten to leave them isolated in unsuitable winter habitats.

One of the most abundant headwater stream types along the Arctic Coastal Plain (ACP) is the beaded stream (Arp et al. 2012). Beaded streams are formed by melting ice-wedges and surface-flow over polygonized tundra features (Lachenbruch 1966; McNamara et al. 1998). They are characterized by circular or elliptical shaped pools ranging in diameter from one to tens of meters across, connected by narrow, often deeply incised stream channels that resemble a “string-of-beads” (Oswood et al. 1989) (Figure I.1). Pools can reach depths of several meters and may vertically stratify when periods of extended photoperiod warm surface-water and permafrost substrates mediate temperatures at depth (Oswood et al. 1989; Irons and Oswood 1992). In many instances, beaded stream habitats have been lumped together in the “tundra” category coined by Craig and McCart (1975), who classified Arctic streams as either “mountain”, “spring”, or “tundra” based on primary source of water. As such, many fisheries investigations in Arctic regions occurring within beaded stream habitats may not be easily identified, and the role of beaded stream habitat in the migratory circuit of Arctic Grayling remains poorly understood.

Studies specifically mentioning beaded stream habitat in relation to Arctic Grayling use indicate they may be used primarily as summer foraging habitats (Moulton and George 2000; McFarland 2014). Baseline surveys of fish habitats in support of oil and gas development (MJM Research 2004, 2007, 2009) indicate high numbers of Arctic Grayling entering beaded streams during investigations in the Fish Creek watershed. Within these same streams, high densities of ninespine stickleback (*Pungitius pungitius*) were also reported (MJM Research 2004, 2007, 2009). Similarly, Hemming (1996) reported high catch per unit efforts for ninespine stickleback in two beaded streams on the ACP near the Sagavanirktok River drainage in July. Forage abundance, both prey fish and macroinvertebrates, is likely one of the primary factors attracting Arctic Grayling to beaded streams. Whereas Arctic Grayling are known to be opportunistic

foragers, McFarland (2014) recently documented unprecedented rates of piscivory in Arctic Grayling inhabiting beaded streams. In some instances, fish were found with over 80 stickleback within their stomach (Jason McFarland, personal communication). To our knowledge, no study has specifically compared beaded stream macroinvertebrate densities to that of other stream types in ACP drainages, however Huryn et al. (2005) indicates that “tundra” streams host moderate levels of macroinvertebrates in relation to “spring” and “glacial” systems in the Arctic.

Despite a general lack of gravel substrate, Arctic Grayling fry have been found in beaded streams (Moulton and George 2000), indicating beaded streams may also serve as spawning habitat. Tack (1980) hypothesized that the use of “bog” or “tundra” streams for spawning is likely result of their favorable (warm) thermal regimes, and suggests that Arctic Grayling spawn in the most quickly warming location in a watershed. Additionally, one study notes lower densities, yet considerably higher growth rates of young-of-the-year Arctic Grayling in a beaded stream when compared to nearby gravel substrate streams (Moulton and George 2000). The extent to which Arctic Grayling spawn in seasonally flowing beaded streams is not well understood, however there are clear management implications if their use is widespread.

### *Research objectives and significance*

Chapter one reports on population level movements of Arctic Grayling within a seasonally flowing beaded stream (Crea Creek) on the Arctic Coastal Plains of Alaska in relation to surface-water hydrology and fish size. While recent research indicates that beaded streams serve as foraging areas for Arctic Grayling during the summer (McFarland 2014), the extent to which fish use these streams and how movements are matched with changing seasonal conditions remains unknown. Based on the extreme seasonality of Arctic hydrology, where shallow habitats freeze solid for 8-9 months, we predicted a strong seasonal trend in the pattern of Crea Creek use by Arctic Grayling during summer. We expected migration into the stream to correspond with seasonal changes in accessibility (for example ice break-up), and migrations out of the stream to correspond with increasing probability of freezing and restricted access to seasonally connected overwintering areas. Furthermore, we hypothesized that adult and juvenile patterns in migration would differ based on a large body of evidence from populations of Arctic Grayling elsewhere in Alaska (Craig and Poulin 1975; Tack 1980; Northcote 1995).

Chapter two investigates the relationship between individual attributes of fish and migration timing out of the seasonally flowing study stream towards overwintering habitat. Occupancy of seasonally flowing habitats is inherently risky for fish, as low water conditions and freezing can leave them stranded in unsuitable habitats. Thus, as environmental conditions change (e.g. flow, productivity, temperature), the relative risks and rewards (e.g. foraging opportunities, decrease in predator encounter rate) of remaining in the study area also change. We hypothesized that physiological differences among fish would mediate the balance of risks and rewards of migration, resulting in a differential migratory response. We tested the hypotheses that (1) large fish migrate earlier and (2) fish in relatively good body condition migrate earlier, under the presumption that size-specific rates of overwintering mortality (Biro et al. 2004), predation, and the extent of accumulated energy reserves prior to the onset of migration will influence an individual's decision to migrate.

Understanding how local environmental conditions relate to fish migration and use of beaded streams is important in light of significant changes occurring in Arctic ecosystems. Since aquatic connectivity mediates habitat access, and physical habitat features are climate driven (Gasith and Resh 1999), migratory Arctic fish may be sensitive to natural or anthropogenic disturbances in thermal and hydrological regimes. Enhanced evapotranspiration and drying associated with warmer summer temperatures may lead to reduced runoff and disruption of surface-water connectivity and habitat access (Rouse et al. 1997; Reist et al. 2006; Lesack and Marsh 2010). Similarly, road construction associated with oil and gas development could interfere with important migratory pathways of ACP fish (Natural Research Council 2003). Moreover, these effects could be pronounced in small headwater streams (Carpenter et al. 1992) that are even now marginally connected to overwintering habitat.

As Arctic Grayling are a highly prized sport fish throughout their range and are also harvested by subsistence users (Adams et al. 2005), understanding threats and potential human impacts is an important management concern. Additionally, being one of the most abundant and widespread fish across Alaska's ACP, their value is also as an indicator species to better understand the potential effects of climate change on Arctic fish. The extent to which Arctic Grayling use small intermittent beaded streams and how fish time migrations into and out of these streams in relation to changing hydrology is not currently well understood, though is integral to sound management practices and understanding potential effects of climate change.

Thus, the overall goal of this study is to gain insights into migratory behavior of Arctic Grayling in beaded streams at both the population and individual level, providing valuable information to managers and contributing to the general understanding of migratory behavior in stream fishes.

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Figure I.1. Typical beaded stream habitat on the Arctic Coastal Plain, Alaska.



## **Chapter 1: Environmental correlates of Arctic Grayling seasonal movement on the Arctic Coastal plain, Alaska<sup>1</sup>**

### **Abstract**

Seasonal changes in abiotic environmental variables can regulate habitat quality and habitat connectivity, driving locally-adapted fish migrations. In Arctic Coastal Plains (ACP) watersheds, Arctic Grayling migrate to persist in a landscape with long (~ 8 month), cold winters that cause shallow aquatic habitats to freeze solid. How these movements among aquatic habitats (e.g. overwintering, summer foraging) relate to seasonal hydrologic variability is not well understood. We investigated movement patterns of Arctic Grayling in a beaded stream (Crea Creek), which is the dominant low-order stream type on Alaska's ACP. During summers of 2012–2013, 1,035 Arctic Grayling were passive integrated transponder tagged and monitored with stream-width antenna stations to examine migration into the stream, movement within the stream, and migration out of the stream. Migration into Crea Creek peaked immediately after ice break-up occurred in the main channel of the study area in June. In both years, fish that entered the stream during periods of higher flow and colder temperatures swam farther upstream than those entering during low flow and warmer temperatures. Adult migration out of Crea Creek was most strongly correlated with receding stream discharge, while juvenile migration occurred in two peaks and was tied to minimum stream temperature and discharge, though size-specific trends were also evident. This work demonstrates that small stream connectivity during the entire open-water period is integral to the migratory strategy of Arctic Grayling on the ACP, and that structures permitting passage through the full range of flow conditions should be implemented as new roads are constructed across this hydrologic landscape. Results from this study also begin building a basis for predicting how Arctic Grayling and migratory fishes will respond to a changing Arctic climate.

<sup>1</sup>Heim, K. C., M. S. Wipfli, M. S. Whitman, C. D. Arp, J. Adams, and J. A. Falke. Environmental correlates of Arctic Grayling seasonal movement on the Arctic Coastal Plain, Alaska. Submitted to Transactions of the American Fisheries Society.

## Introduction

Directed movements among habitats allow individuals to match ontogenic and seasonal life history needs with appropriate habitats in environments with changing abiotic and biotic conditions (Schlosser and Angermeier 1995; Gowan and Fausch 1996). It follows that many animal movement patterns are closely linked to local shifts in environmental conditions (Dingle 1996). For example, resident stream salmonid movements often correspond with seasonal changes in hydrology (Gowan et al. 1994; Swanberg 1997; Bryant et al. 2009). Similarly, movements are also driven by the availability of food resources and level of predation threat across seasons (Brodersen et al. 2008; Janetski et al. 2011). Not surprisingly, habitat shifts among salmonids are particularly common during the transition from late summer to winter (Young 1998), when rates of environmental change are high.

Fish movements in river networks are also inherently related to connectivity among spatially discrete habitats that may vary seasonally with hydrology and weather patterns (Fullerton et al. 2010; Falke et al. 2012). For example, low water conditions, freezing, and anthropogenic disturbance can limit movement between habitats and have pronounced ecological effects at individual, population, and metapopulation levels (Labbe and Fausch 2000; Fagan 2002). Alternatively, periodic flooding can connect formerly isolated habitats allowing for dispersal, new habitat exploration, and increased gene flow among metapopulations (Schlosser and Angermeier 1995; Lohr and Fausch 1997; Labbe and Fausch 2000; Haynes et al. 2014). Thus, mechanistic explanations of fish movement in rivers and streams should include environmental variation as it may mediate both habitat connectivity and relative differences in habitat quality through time.

Environments with dramatic seasonal differences in habitat connectivity and physical conditions provide an ideal opportunity to examine the relationship of fish movement to seasonal environmental change. A fundamental characteristic of Arctic Coastal Plains (ACP) landscapes is the rapidly shifting extents of surface-water connectivity over short summer seasons (Bowling et al. 2003), which present both benefits and risks to migratory fish. Nearly all bodies of water less than 1.5-m deep freeze solid by the end of winter (Jones et al. 2008), restricting the use of highly productive shallow-water habitats to the short (~ 4 month) summer. In fact, winter ice cover may reduce available freshwater habitats by up to 95% compared to the open-water period (Craig 1989). This open-water period initiates with a sharp peak in runoff generated from

snowmelt, followed by rapidly declining summer flows when evapotranspiration rates often exceed rainfall leading to a negative water balance in these systems (Bowling et al. 2003; Arp et al. 2012). Permafrost-rich soils create extensive surface-water storage in the form of lakes and wetlands and restrict any interaction with much deeper groundwater systems, translating to a vast mosaic of shallow habitats with changing connectivity as snowmelt drains, the surface active-layer (< 1 m) thaws, and water evaporates (Woo and Winter 1993). Timed with snowmelt and river breakup, migratory fish move into productive seasonally flowing stream and lake systems to forage and spawn (Morris 2003). However, fish must time migrations out of such habitats before freeze-up or low stream flows threaten to leave them isolated in unsuitable winter refugia (Craig and Poulin 1975; West et al. 1992).

Arctic Grayling (*Thymallus arcticus*) is a freshwater migratory fish that occupies the northern limit of N. American ACP watersheds. Migration is likely one of the major adaptations that has allowed for their successful colonization of Arctic regions of the globe (Tack 1980). Arctic Grayling overwinter in often-dense aggregations in deep-water lakes and channels of larger river systems that remain unfrozen and provide adequate dissolved oxygen content through winter (Northcote 1995). A spawning migration of adults ensues shortly after ice breakup, while juveniles generally move directly to foraging areas (Craig and Poulin 1975). Adults and juveniles forage on terrestrial and aquatic invertebrates and smaller fish, such as ninespine stickleback (*Pungitius pungitius*), until winter approaches and fish initiate migration back to winter refugia (Morris 2003; McFarland 2014). Foraging success during this short (~ 4 month) period is important for sequestering adequate energy reserves to survive the following winter (Deegan et al. 1999), and recent research indicates that forage-rich beaded stream habitats (Oswood et al. 1989) may be commonly used by Arctic Grayling for this purpose (McFarland 2014). Although this annual migration pattern among functionally different habitats within a watershed is documented through several broad spatial-scale radio-telemetry studies (West et al. 1992; Morris 2003), little is known about the environmental cues and conditions to which migratory fishes are responding.

Understanding how local environmental conditions relate to fish migration and use of aquatic habitat is important in light of significant changes occurring in Arctic ecosystems (Martin et al. 2009). Because surface-water connectivity mediates habitat access, migratory Arctic fish may be sensitive to both changes in land use and climate. For example, road



construction associated with oil and gas development could alter routing of snowmelt runoff or present barriers to channel passage (Natural Research Council 2003). Enhanced evapotranspiration and drying associated with warmer summers could lead to reduced runoff and disruption of surface-water connectivity and habitat access (Rouse et al. 1997; Reist et al. 2006; Lesack and Marsh 2010). Similarly altered water temperature and flow regimes may disrupt migration cues to complete life history requirements during short Arctic summers (Reist et al. 2006). Moreover, these responses could be pronounced in small stream systems (Carpenter et al. 1992), such as beaded streams, that are often marginally connected to overwintering habitat during contemporary climate regimes. More broadly, beaded streams represent major elements of ACP aquatic ecosystems connecting tundra lakes with downstream rivers, and a better understanding of how fish use these connected systems is warranted.

The goal of this study was to gain a better understanding of whether and to what extent Arctic Grayling utilize beaded stream habitats and to determine how movements and migration are related to seasonal stream flow and temperature patterns. We studied fish movement in a beaded stream (Crea Creek) in the National Petroleum Reserve-Alaska where ongoing hydrological and food web research related to future petroleum development provide a strong foundation for this research. Our objectives were to (1) identify peak periods of migration into and out of this system, (2) identify patterns of within-stream summer movements, (3) determine how migration and movement correspond to hydrology and seasonal weather patterns, and (4) gain insights into the life history role (spawning, overwintering, foraging) of beaded streams for Arctic Grayling. The difference between *migration* and *movement* is important and has been examined elsewhere (Dingle 1996), though for the purpose of this study we define movement as the upstream and downstream travel of fish within the beaded stream study area, and migration as the entering or exiting the beaded stream (further discussed in methods).

## **Methods**

### *Study area*

This study was conducted in Crea Creek (70°17'N, 151°20'W), a small lowland tributary to the Ublutuoch River. Crea Creek is a beaded stream characterized by a repeating series of elliptical pools connected by narrow channel runs, appearing as “beads-on-a-string” (Oswood et

al. 1989). The Ublutuoch River flows into the larger Fish Creek, a sand-bedded alluvial river, approximately 5 km upstream of where it enters the Beaufort Sea and just west of the much larger Colville River Delta (Figure 1.1). Crea Creek generally flows from June through September, and is mostly frozen to the streambed during the rest of the year, except for some of its deep pools or “beads” and two lakes that are approximately 2.5 m deep (Jones et al. 2013). It drains a 29.5 km<sup>2</sup> area composed of tussock tundra, thermokarst lakes, and drained thermokarst lake basins. Crea Creek originates from an intermittently connected shallow headwater lake and flows 4.5 km through three other lakes before reaching the Ublutuoch River. The Ublutuoch River is considered to be an important overwintering area and migratory corridor for Arctic Grayling, Broad Whitefish (*Coregonus nasus*), and Burbot (*Lota lota*) (Morris 2003; MJM Research 2007).

#### *Collection of environmental data*

Stream water-level and water temperature were recorded hourly in several pools throughout Crea Creek with remote sensors (Hobo; Model U20) from break-up in early June through freeze-up in late September–October. Stream discharge was measured roughly eight times each summer to describe flow from June through August using a velocity-area method with either an acoustic doppler (SonTek; FlowTracker Handheld-ADV) or electromagnetic velocity meter (Hach; FH950). Using these instruments, velocity and depth were recorded at approximately 20 locations per channel cross-section to calculate stream discharge. These measurements were then used to develop rating curves from water-level data and to generate hourly hydrographs for each year (Whitman et al. 2011). Photoperiod was determined from the US Naval Observatory Astronomical Applications Department online calculator for the latitude and longitude of Crea Creek.

#### *Fish capture and tagging*

The primary fish sampling location was the confluence of Crea Creek and the Ublutuoch River where upstream facing fyke nets were used to capture fish moving into the creek in June, July, and August in 2012 and 2013 (site A, Figure 1). The confluence was chosen as the primary sampling location because all fish entering Crea Creek during the summer pass this point; therefore periodic sampling should provide a representative sample of the population of fish

utilizing Crea Creek. Secondary sampling locations were located in two lakes within Crea Creek, where regular sampling was conducted using fyke nets (site B and C, Figure 1). In addition to fyke net sampling, in 2012, Arctic Grayling were captured via electroshocking and angling at various locations in Crea Creek (McFarland 2014). Electroshocking surveys consisted of a single pass of the entirety of Crea Creek drainage once during June, July and August, using a backpack electrofisher (Model LR-24; Smith Root), and angling was conducted opportunistically with fly-fishing equipment.

All captured Arctic Grayling were anesthetized in a 20–30 ppm clove oil/stream water solution until equilibrium was lost (2–5 minutes) (Morris 2003), measured in millimeters fork length (FL) and weighed to the nearest tenth of a gram. Arctic Grayling in good condition between 120 mm and 179 mm were tagged with 12-mm (0.1 g) passive integrated transponder (PIT) tags, and those  $\geq 180$  mm were tagged with 23-mm (0.6 g) PIT tags to ensure tag/body mass ratio did not exceed 2% (Winter 1996). Once a fish became unresponsive, a small incision was made and a tag was inserted into the body cavity with a syringe. After handling, fish were released into slow water near the sampling location to recover. Tagging and handling appeared to have minimal effects on fish as some were observed foraging less than one hour after being tagged. We used one-way ANOVA and Tukey's *post hoc* HSD test (Zar 1999) and *t*-tests to compare fork lengths of fish captured moving into Crea Creek in different months. Differences were considered significant if  $P < 0.05$  (here, and in all statistical tests throughout analysis).

### *Fish monitoring system*

We used stream-width swim-through PIT tag antennae at seven stations within Crea Creek to monitor fish movements (Figure 1.1). As tagged fish passed through an antenna loop the data logger recorded the date, time, and unique fish ID. Internal data loggers were synchronized to the nearest second, allowing for directionality of movement to be determined based on the chronological sequence of detections. We assigned a numerical value to each station (station 7 is furthest upstream, station 1 is at the Crea Creek confluence) for purposes of calculating detection efficiency and analysis.

In 2012, the seven antenna stations (hereby referred to as the array) were set up between June 16 and June 22 as the spring flood was subsiding. By June 23, the array was fully functional, and by June 24, water levels had dropped to the point where all antennae spanned the

entire width of the stream. Stations 1–7 recorded data through the summer, until August 25, when data loggers were removed from stations 3, 6, and 7 during the last field site visit for the year. Marker tags were placed at remaining stations (except station 2), which periodically emitted a PIT tag signal that showed up in the detection history allowing us to determine if the system was operating properly. These stations were operational well through freeze-up. The last detection at station 2 was on September 20, which corresponds with freeze-up timing of the channel based on hydrology data near that location. We therefore assumed antenna station 2 to be operational through freeze-up.

In 2013, the array was set up between May 30 and June 3, and it was fully operational on June 9 when ice break-up in the main channel of Crea Creek occurred. During June 9 through June 26, stream discharge was exceptionally high, and antennae did not encompass the entire stream width creating potential for missed detections. Additionally, station 4 was inoperable from June 11–June 16 due to technical difficulties. Antenna station 2 was non-operational for several hours on August 20 while repair work was being done. Stations 1, 2, 3, and 4 were operational through freeze-up (based on marker tag detections), and the remaining stations were assumed to be operational through freeze-up based on freeze-up timing and last date of detections at those stations.

### *Monitoring system detection efficiency*

It is important to consider detection efficiency and recognize a potential source of error due to missed detections in analysis (Zydlewski 2006; Connolly et al. 2008). We used the chronological sequence of detections at discrete antenna stations oriented linearly along the stream to quantify individual movements in this study (further description to follow in data analysis); therefore we evaluated the overall error rate of the antenna array in terms of departures from the expected sequences for individual fish. We present a simple method to evaluate array sequence efficiency ( $E_{array\ sequence}$ ) (inclusive of all seven stations):

$$E_{array\ sequence} = \frac{1}{n} \sum_{i=1}^n \frac{S_{c,i}}{S_{c,i} + S_{d,i}}$$

where  $S_{c,i}$  is the sum of all correct detection sequences for fish  $i$ ; for example a sequence 1-2-3-4-3-2-1 indicates a fish swam upstream from station 1 to station 4 then downstream to station 1, in this instance  $S_{c,i} = 6$  since there were 6 correctly ordered sequences.  $S_{d,i}$  is the sum of all known

departures from the expected sequence for fish  $i$ ; for example a sequence 1-2-4-3-2-1, indicates detection was missed at station 3, in this instance  $S_{d,i} = 2$  since the absence of sequence 2-3 as well as 3-4 represent departures from the expected sequence, and  $n$  is the number of individual encounter histories used in estimation. The percent of correctly identified sequences can thus be calculated for each individual's detection records, in order to then calculate an overall mean antenna efficiency ( $E_{array\ sequence}$ ) for all individuals. Where initial fish locations are known (e.g. tagged in a known location) the expected sequence can be adjusted to reflect a priori information on that fish's whereabouts. For example, a fish tagged between station 3 and 4 should be first detected at one of those stations; a detection at any other location would represent an out of order sequence.

#### *Habitat use and site fidelity*

In this analysis we were interested in determining the number of fish that exhibited inter-annual site fidelity to Crea Creek, and whether or not fish overwintered within the stream. Fish known to have migrated out of Crea Creek before freeze-up in 2012, and then later detected at an antenna station in 2013, were deemed to have shown inter-annual site fidelity. To determine if fish successfully used Crea Creek for overwintering habitat, we examined the detection records of each fish not detected migrating out of Crea Creek before freeze-up in 2012. Detections of these fish in 2013 are interpreted as evidence of overwintering survival within Crea Creek.

#### *Within-stream movements*

To examine patterns of within-stream movements in 2012, we counted the total number of upstream and downstream movements between adjacent antennae completed on each day of the study period in 2012 (aggregating movements made by all fish), and depicted results graphically. Here, we only used movements made by the subset of fish tagged at the Crea Creek confluence captured via upstream fyke net in 2012 to generate counts (site A, Figure 1.1). Note that this daily count reflects both the number of individuals moving, and how far those fish are moving since a single fish moving across multiple antenna stations can create multiple movements via these methods. Similar methods are commonly used (Homel and Budy 2008). In instances where fish were known to move past an antenna station undetected (e.g. during periods of spring flooding, or when antenna were non-operational), we adjusted the number of

assigned movements to reflect the number of movements that fish must have made to create the observed sequence of detections (e.g. a fish with detection sequence 1-2-3-4 and 1-2-4 will both be assigned 3 movements). Thus, even though  $E_{antenna\ array}$  was less than 100% at times, movements should be equally represented across time as long as  $E_{antenna\ array}$  was moderately high, since missed detections at one station are likely to be accounted for at others. Since movement counts in 2012 were invariably related to tagging events, we used the subset of fish that showed site fidelity to Crea Creek (after being tagged in 2012) and counted their movements within the stream in 2013, and depicted results graphically. This movement count was not influenced by tagging events, and was used to verify that the pattern of movement observed in 2012 was not generated due to the influence of tagging events. We intentionally use the term *movement* in this analysis rather than *migration*, because within stream movements do not necessarily constitute true migratory movements (though certainly help to identify periods of migration).

We quantified daily upstream and downstream movements for adults and juveniles separately using a FL cut-off of 280 mm to differentiate adults from juveniles. This cutoff length is supported by unpublished length at maturity data collected on site in 2013 and through consulting local expert opinion (L. Moulton, personal communication). However, it is likely that some fish classified as juveniles in 2012 grew into the adult category by 2013. We used a Fabens adaption of the Von Bertalanffy growth model to adjust individual lengths of fish tagged in 2012 by one year, and then reclassified their life stage for use in analysis should they appear in the detection records in 2013 (Fabens 1965). The Fabens growth model is as follows:

$$L_r = L_m + (L_\infty - L_m)(1 - e^{-K\delta t})$$

where  $L_m$  is the FL of the fish at time of marking,  $L_r$  is the FL at recapture,  $\delta t$  is the time at large,  $L_\infty$  is the asymptotic or theoretical maximum length, and  $K$  is the growth coefficient (Fabens 1965). The model parameters were estimated using ordinary least squares methods, using 111 recaptured fish either captured or released in Crea Creek that were at liberty from between six days and six years. These data were collected both during this study and through ongoing sampling efforts by MJM research (Larry Moulton, MJM Research, unpublished data). Once a fitted growth curve was developed, 365 days of growth were applied to lengths at time of tagging for fish tagged in 2012 to produce an estimate for use in 2013. The model produced predictions that averaged 9 mm from observed lengths at recapture.

We used the subset of fish tagged after being captured at the Crea Creek confluence moving upstream (in 2012 and 2013), and determined the furthest upstream antenna station at which each individual was detected in the year it was tagged to determine if there were trends in upstream distance traveled. This distance for each individual was converted to meters based on the linear stream distance from the confluence to that antenna station. We used one-way ANOVA and Tukey's *post hoc* HSD tests to determine if upstream distance traveled differed among fish entering the stream in June, July, and August within years. Spearman's rank correlation was used to determine if upstream distance traveled was related to stream discharge, temperature, and FL at the time fish entered the stream.

#### *Migration into Crea Creek*

We plotted the number of site fidelity fish arriving in the stream per day in 2013, along with stream temperature and discharge, to depict the timing of upstream migration into Crea Creek in relation to seasonal changes in hydrology. For each of the site fidelity fish (tagged in 2012 and returning to Crea Creek in 2013), we defined its arrival date as the first date that it was detected within the stream in 2013. This initial movement of fish into Crea Creek in the spring represents a functional shift in habitat type recurring seasonally (overwintering to shallow summer habitat), and the term *migration* in this instance is appropriate (Dingle 1996).

#### *Migration out of Crea Creek model*

We used an information-theoretic approach to determine which combination of environmental variables best explained the number of Arctic Grayling migrating out of Crea Creek on each day of the study period. We quantified migration with a daily count of movements that met specific criteria intended to help differentiate migratory movements from diel or random movements. Utilizing all fish tagged in 2012 and 2013, we queried the detection records for each individual fish's final movement from antenna station 2 to antenna station 1 (a downstream movement, out of Crea Creek) within each year, and use the detection date at station 1 as that fish's migration date, for that year. We then modeled the number of fish migrating per day as a function of environmental predictor variables for adults and juveniles separately using negative binomial generalized linear models (GLM) in the MASS package of R (Venables and Ripley 2002; R Development Core Team 2011). Note that the response variable is a count that

represents the rate at which a specific event occurs (Zuur et al. 2013), and results of modeling will be discussed as such. Residual autocorrelation was detected, we therefore adjusted coefficient standard errors and  $P$ -values with a Newey-West autocorrelation consistent covariance matrix for lag 2 autocorrelation for each model (Newey and West 1987).

Environmental predictor variables considered included daily mean stream discharge, daily mean stream temperature, daily maximum stream temperature, daily minimum stream temperature ( $T_{min}$ ), photoperiod, year, and season. The seasonal covariate divided the open-water season into two periods (June–July = 0 and August–September = 1), within each year. However, all measures of stream temperature and photoperiod were strongly correlated, and we thus chose to consider only  $T_{min}$  in candidate models, as it represented the strongest biological hypothesis regarding which of these correlated variables might serve as an environmental cue. We also developed an offset term for modeling because fish tagging occurred during several sampling periods each year and the pool of potential migrants was further influenced by how many fish had already migrated. Offsets are used to weight event counts occurring from a non-constant population size or spatial area (Zuur et al. 2013), or in this instance, a changing number of potential migrants that could be observed in the PIT tag records. The offset was quantified for each day ( $d$ ) of the modeling period and included the sum of (1) all fish that migrated on day  $d$  and (2) eventual migrants that were still within the stream on day  $d$ . We also calculated the mean FL of all potential migrants on day  $d$  ( $FL_{pm}$ ). This term represents the average size of tagged fish remaining in the stream across time. As fish returning to Crea Creek after being tagged in 2012 were also included in the migration count for 2013, we used adjusted lengths (as described above, Fabens' methods) to calculate  $FL_{pm}$  when these fish appeared as potential migrants and migrants, and also to distinguish adults from juveniles. All continuous predictor variables were standardized, resulting in coefficient estimates that were interpreted as standardized magnitude of the effects of variables on the response (Schielzeth 2010). Because we included a categorical variable (year), we used two standard deviations to standardize continuous variables, which allowed for comparison between coefficients of categorical and continuous variables (Gelman and Hill 2007; Schielzeth 2010).

We constructed a set of seven a priori candidate models that contained combinations of explanatory variables of potential biological significance, and used Akaike's information criteria (AIC) to select the best approximating model (Burnham and Anderson 2002). The AIC scores



were corrected for small sample size ( $AIC_c$ ), as is strongly recommended as a routine practice (Mazerolle 2006), and Akaike weights ( $w_i$ ) were calculated. To accommodate model uncertainty we used model averaging to calculate parameter estimates and standard errors from top ranking models ( $w_i > 0.05$ ), and made inference based upon those estimates.

## Results

### *Environmental data*

Discharge and stream temperature profiles differed between 2012 and 2013 (Figure 1.2). Ice break-up in the main channel of Crea Creek occurred on June 8 in 2012 and June 9 in 2013. Snowmelt-generated peak flows in June of both years were about two orders of magnitude higher than summer flows, which is typical of ACP rivers and streams. Stream discharge in 2013 was considerably higher through the open-water period than in 2012 and the previous three years (C. Arp, University of Alaska, unpublished data). At no point did stream discharge drop below  $0.01 \text{ m}^3/\text{s}$  in 2013, though discharge was below this level from June 30 through freeze-up in 2012. Despite low flow, the connection to the Ublutuoch River appeared to remain intact throughout the duration of the ice-free period in both years, though time lapse photography and on-site observations revealed the connection became progressively more marginal with decreasing discharge and at times channel depth was  $< \sim 10 \text{ cm}$  (K. Heim, University of Alaska, unpublished data). The area near Crea Creek experiences a photoperiod of 24 hours from around mid-May through late July, at which point an average of 12 minutes is lost each day until late November when the sun stays below the horizon for about 50 days. Mean daily stream temperatures declined after August 18, 2012 and August 11, 2013, concurrent with decreasing photoperiod and local weather conditions (Figure 1.2).

### *Fish capture and tagging*

Over the course of the study 1,035 Arctic Grayling were PIT tagged in Crea Creek (mean FL  $\pm$  standard error =  $224 \pm 2 \text{ mm}$ , range = 120–433 mm) of which 717 (69%) were later detected within the antenna array ( $228 \pm 9 \text{ mm}$ , 120–433 mm). A total of 625 fish were tagged after being captured moving upstream into Crea Creek at the primary sampling location at the confluence with the Ublutuoch River (Table 1.1,1.2), and a total of 313 fish were tagged at lake

sampling sites B, C, and D over the two-year period. The remaining fish were captured in 2012 via electroshocking, angling, and fyke nets at various other locations in Crea Creek.

Mean FL of fish moving into Crea Creek was larger in June than in July in both years (Table 1.1,1.2). Similarly, fish captured in June were larger than those caught in July at sampling site B in 2013 (Site B June:  $254 \pm 18$  mm, Site B July:  $176 \pm 10$  mm;  $t = 4.52$ ,  $df = 188$ ,  $P < 0.001$ ), and C in 2013 (Site C June:  $241 \pm 7$  mm, Site C July:  $190 \pm 5$  mm;  $t = 4.13$ ,  $df = 63$ ,  $P < 0.001$ ). Though standardized methods were not employed to determine reproductive status, we noted in 2012 and 2013 that 12 and 7 Arctic Grayling released milt or eggs during handling, respectively. Young-of-the-year Arctic Grayling were captured in both years during late summer (2012,  $N = 15$ ; 2013,  $N = 5$ ) as far as 3.5 km upstream in Crea Creek.

#### *Detection efficiency*

In 2012 between June 24 and August 24 (the period that all seven antenna stations were in operation)  $E_{array\ sequence}$  was 99.1%. We made no adjustments based on known tagging locations in 2012 because path efficiency ( $E_{path}$ , the probability that moving fish pass *through* the antenna loop) was expected to be 100% during this time period because all antennae spanned the entire stream channel. After August 24, 2012 we removed stations 3, 6, and 7, and did not calculate  $E_{array\ sequence}$  for this time period, however there is no reason to believe rates of detection at remaining stations decreased. In 2013,  $E_{path}$  was undoubtedly less than 100% from June 10 through June 26 during spring flooding.  $E_{array\ sequence}$  during this period was 71.0%; in this calculation, we included adjustments for known a priori initial fish locations. From June 27 through freeze-up in 2013 (when  $E_{path}$  was expected to be 100%),  $E_{array\ sequence}$  (unadjusted) was 98.7%. The array proved to be highly efficient during summer base flow, and moderately efficient during periods of flooding.

#### *Habitat use and site fidelity*

The detection records provided little evidence of PIT-tagged fish surviving the winter of 2012 in Crea Creek, though high rates of inter-annual site fidelity were found for fish that left Crea Creek before freeze-up in 2012. In 2012 there were 299 tagged fish (FL =  $236 \pm 4$  mm) that were last seen moving past antenna station 1, indicating they migrated out of the stream before winter, and 75 tagged fish (FL =  $221 \pm 8$  mm) that were last detected elsewhere within

Crea Creek, suggesting they did not migrate out of the creek before winter. Of the 299 known to have exited Crea Creek in 2012, 155 (FL =  $227 \pm 5$  mm) were later detected within the array in 2013 (53%), indicating they survived winter and exhibited inter-annual site fidelity to Crea Creek. Of the 75 fish not detected leaving, only one (FL = 342 mm) was later detected within the array in 2013 (1%), though further inspection of this detection record in 2012 indicates this fish likely left the stream, but the detection at antenna station 1 was missed.

#### *Within-stream movements*

Observed patterns in upstream and downstream movements were very similar between 2012 and 2013, with peak periods of total movement (upstream and downstream) occurring in June–early July and again in September, with minimal movement occurring during mid summer. Adult and juvenile patterns of movement were similar from June through August; upstream movement peaked shortly after ice break-up while stream discharge was high and temperatures rose dramatically, and downstream movement corresponded with decreasing stream discharge in late June–early July. However, very few movements of adults were recorded after August in either the upstream or downstream direction, while a notable increase in downstream movement of juveniles was observed in late August–September in both years. In 2012 these late season downstream movements occurred in a normally distributed peak corresponding with a gradual decline in stream temperature (Figure 1.2, panel a), while in 2013 late season downstream movements occurred in several peaks, each seeming to correspond with a notable decrease in stream temperature (Figure 1.2, panel c). Interestingly, while stream temperatures began decreasing quickly on August 18, 2012 and August 11, 2013, a noticeable increase in downstream movements was not observed until stream temperatures fell below 5 °C, after which point even slight decreases in temperature appeared to result in increased downstream movements.

Fish tagged in June moved further upstream than fish tagged in July in 2012 (ANOVA:  $F_{1,249} = 276.90$ ,  $P < 0.001$ ; HSD *post hoc* test:  $P < 0.05$ ) and in 2013 (ANOVA:  $F_{2,185} = 12.78$ ,  $P < 0.001$ ; HSD *post hoc* test:  $P < 0.05$ ) (Figure 1.4). Upstream distance traveled by individual fish tagged at the Crea Creek confluence was positively correlated to stream discharge (Spearman rank correlation;  $r_s = 0.65$ ,  $N = 251$ ,  $P < 0.001$ ) and negatively correlated to stream temperature (Spearman rank correlation;  $r_s = -0.56$ ,  $N = 251$ ,  $P < 0.001$ ) at the time of tagging in

2012. In 2013, upstream distance traveled was also positively correlated with discharge (Spearman rank correlation;  $r_s = 0.41$ ,  $N = 190$ ,  $P < 0.001$ ) and negatively correlated with temperature (Spearman rank correlation;  $r_s = -0.26$ ,  $N = 190$ ,  $P < 0.001$ ) at the time of tagging, however the correlations were weaker. In both years there was a weak negative correlation between upstream distances traveled and FL of individual fish (2012 Spearman rank correlation;  $r_s = -0.18$ ,  $N = 251$ ,  $P = 0.004$ , 2013 Spearman rank correlation;  $r_s = -0.16$ ,  $N = 190$ ,  $P = 0.023$ ), indicating that smaller fish tended to travel further upstream.

#### *Migration into Crea Creek*

Upstream migration of fish returning to Crea Creek ( $N = 155$ ) was initiated just one day after ice break-up occurred in the main channel on June 9, and peaked sharply on June 13 when 33 individuals were first detected within the stream (Figure 1.3). Migration into Crea Creek by this subset of fish occurred during peak flow ( $\sim 1 \text{ m}^3/\text{s}$ ) when mean stream temperature increased quickly to  $15 \text{ }^\circ\text{C}$  within a two week period of time. Surprisingly, 10 returning fish ( $\text{FL} = 242 \pm 18$ ) were not seen until September and October, at which point stream discharge estimates were unavailable due to ice formation (on September 14) and stream temperature was  $< 1 \text{ }^\circ\text{C}$ . These late movements are not considered to be migratory, as none of these fish moved upstream past antenna station 2, which is not surprising considering the channel was accumulating ice and stream connectivity to the Ublutuoch River was marginal.

#### *Migration out of Crea Creek*

Juvenile migration out of Crea Creek occurred in two peaks with one in July and another in September in both years (Figure 1.5.). The early peak occurred during high flows and stream temperatures, while the later peak occurred shortly before freeze-up during very low flow. In 2013, there were two days when an unusually high number of juvenile fish migrated, September 15 (20 migrants) and September 21 (26 migrants). Daily minimum temperature on September 14, 2013 was  $3.09 \text{ }^\circ\text{C}$ , but fell to  $1.44 \text{ }^\circ\text{C}$  the next day potentially triggering the increase in migration. After September 15, 2013 mean daily stream temperature remained  $< 1^\circ\text{C}$ . The highest-ranking juvenile migration model ( $w_i = 0.83$ ), given the data, suggested that flow,  $T_{min}$ , season,  $FL_{pm}$ , and year had the strongest influence on daily counts of migrating fish (Table 1.3), though there was also support for the model excluding flow ( $w_i = 0.17$ ). Model-averaged

coefficient values indicate that size of fish within the stream had the strongest effect on migration (Table 1.4), indicating rate of migration increased as mean fish size within the stream decreased. Rate of migration increased as  $T_{min}$  and flow decreased, and note that all 95% CI of model-averaged coefficient values did not overlap zero (except year), indicating confidence in the direction of these effects.

Most adults migrated out of Crea Creek in one peak during late June–early July in both years; however, more adults remained in Crea Creek later in the high water year of 2013 (Figure 1.5.). The highest-ranking adult model ( $w_i = 0.48$ ) suggested that migration was explained best by only flow, although there was also support for models with additional parameters (Table 1.3). However, each model in the confidence set included flow, and of all model-averaged coefficient estimates, flow was the only parameter with a 95% CI that did not overlap zero. These results indicate that rate of adult migration was best explained by decreasing flow.

## **Discussion**

Arctic Grayling began migrating into Crea Creek concurrent with ice break-up, peak flow, and increasing stream temperature. Although fish continued to enter the stream through August, upstream movements were longer and more frequent during high flow and spring flooding, providing evidence that fish selectively travel upstream. Migration out of Crea Creek was also strongly correlated to flow, with adults and larger juveniles migrating at higher rates as flow decreased towards summer base flow level. These results suggest that stream flow has a pervasive influence on how Arctic Grayling utilize small tundra streams during the open-water period. The use of habitats such as Crea Creek constitutes a behavioral risk that is proportional to stream connectivity and associated access to suitable overwintering refuge. These fish appear to be well adapted to mitigate these risks by interpreting environmental cues associated with loss of stream connectivity, while making use of a seasonally available habitat.

### *Migration and movement*

The peak in upstream migration of site fidelity fish in 2013 into Crea Creek immediately after ice break-up may reflect a strategy to maximize time spent in productive foraging habitats. It is believed that fidelity to summer foraging areas is an adaptation to maximize growth during summer, as fish have roughly four months to sequester sufficient energy reserves to sustain them

through winter, and limited time available to explore new habitats (Armstrong 1986; Buzby and Deegan 2000). In this study, 53% of fish known to have exited Crea Creek before freeze-up in 2012 returned to the stream the next year in a strong upstream pulse, suggesting that fish staged at the mouth of Crea Creek until ice break-up permitted access. In addition to site fidelity, accessing productive stream habitats as soon as possible may reflect an adaptation to maximize growth and foraging opportunities during the short summer. This pulse of fish into the stream could also be related to differences in conditions between Crea Creek and the Ublutuoch River during break-up. Break-up in the Ublutuoch River is dominated by mechanical processes, where large pieces of ice are physically broken, dislodged, and transported downstream often resulting in deep scouring of river substrates, whereas break-up within Crea Creek is more thermal in nature, with ice mainly melting in place (Huusko et al. 2007; Brown et al. 2011). Consequently, the observed migration timing could represent a refuge migration away from the unfavorable and potentially dangerous conditions within the Ublutuoch River.

More broadly, the period of spring flooding represents a peak in aquatic connectivity across the ACP, and may be of great importance in facilitating the dispersal of fish from overwintering habitats and the colonization of new habitats (Craig and Poulin 1975; West et al. 1992; Morris 2003). It is well known that floods can increase habitat access to foraging areas (Tempero 2004), and serve an important role in metapopulation dynamics by facilitating dispersal from source habitats to sink habitats (Schlosser and Angermeier 1995). While much of this research has been conducted in the context of dryland watersheds and drought conditions (e.g, Labbe and Fausch 2000; Falke et al. 2012), the relationship of Arctic fishes to ice is strikingly similar to the relationship of dryland fishes to drought (West et al. 1992). We found the strongest peak in within-stream movement was during the spring flooding period in both years, suggesting Arctic Grayling utilize this period to accomplish important life history functions during summer. Furthermore, recent work has shown that discharge-regulated connectivity may be a primary factor influencing community structure of the many seasonally interconnected bodies of water on the ACP, and further work relating aquatic connectivity and movement to population dynamics is warranted (Haynes et al. 2014).

Upstream distance traveled was also greatest during high flow, suggesting that fish may selectively travel upstream based on the relative strength of stream connectivity. Many stream fishes migrate upstream into ephemeral habitats (John 1964; Erman and Hawthorne 1976; Jeffres

et al. 2008), and there are inherent risks to this behavior. In the Arctic, a significant risk is failure to exit shallow streams before ice formation and decreases in flow sever connectivity to suitable winter refugia. As fish require adequate stream flow and depth in order for upstream and downstream passage (Bjornn and Reiser 1991), strong flows at stream outlets may be indicative of strong habitat connectivity. Although fish continued to enter the Crea Creek through August, distances traveled (and upstream movements of any detectable length) markedly decreased after flow reached summer base flow level in mid-July. Given the complexity of ACP watersheds and dramatic seasonal changes in connectivity related to flooding and runoff, selective upstream travel would clearly be an advantageous behavior to avoid getting “stuck” in unsuitable habitats.

Stream flow also appeared to be influential in the timing of migration out of Crea Creek, in particular for adult fish that generally migrated before flows dropped to summer base flow levels. Perhaps adult fish are particularly sensitive to decreasing flow, and the associated loss of stream connectivity, and take a conservative approach to migration and habitat use during summer. In some species risky behavior decreases with ontogeny (e.g. crickets, Niemelä et al. 2012), and differential behavioral responses to ecological processes among size classes of fish (eg. predation risk, Dahlgren and Eggleston 2000) can influence the distribution of mobile species. Indeed, most adults vacated the stream before passage became compromised owing to low water or ice formation. As Arctic Grayling are iteroparous with fecundity increasing with age and body size (Armstrong 1986), lifetime reproductive success is likely maximized through longevity. This appears to be a conservative life history strategy related to the threat of becoming “stuck” in Crea Creek, though the mechanism driving adult migration may also be related to their general preference for higher flow and lower temperatures. Arctic Grayling growth can be positively associated with stream discharge (Deegan et al. 1999) and thermal growth optimum is generally lower for adult salmonids compared to juveniles (Morita et al. 2010). In fact, the combination of low flow and high temperatures can prevent adult Arctic Grayling from gaining weight and even cause them to lose weight (Deegan et al. 1999; Hobbie et al. 1999). As temperatures in Crea Creek can approach 20 °C during summer, adult fish may exit Crea Creek in order to forage in streams with greater discharge and cooler temperatures after mid-summer.

Flow was also an important predictor of juvenile migration rates. Because we modeled the two peaks in juvenile migration simultaneously, the importance of flow was likely driven primarily by larger juveniles that, like adults, migrated concomitant with decreasing stream flow. Interestingly, larger juveniles generally migrated during the same time period in which adults migrated, possibly reflecting an ontogenic progression of behavior as older juveniles begin to behave more like adults. This trend was also noted by Tack (1980) who suggested that the tendency for sub-adults to follow adults along the same migratory route (even to spawning areas) may reflect a method to imprint often-complex migratory behavior across generations. In addition, as larger juveniles become physiologically more similar to adults and show similar foraging tendencies (McFarland 2014), their preferred habitat conditions should become more similar and influence their distribution across available habitats.

The smaller juveniles migrating in the second peak take a more risky approach to migration, depending on correctly interpreting changing seasonal conditions in order to safely access overwintering areas. Unlike adults, many smaller juveniles spent the entirety of the open-water period within Crea Creek, delaying out-migration until freezing was imminent. Many populations of salmonids undergo similar refuge migrations, most often in the downstream direction (Zacharchenko 1973; Peterson 1982; Huusko et al. 2007) that coincide with water temperatures dropping below a certain level, typically between 3 and 6 °C (Huusko et al. 2007). Interestingly, there appeared to be a threshold level of 5 °C below which even slight decreases in stream temperature initiated movements downstream and out of Crea Creek, providing strong evidence that fish are sensitive to the probability of ice formation that may restrict stream passage. As the conditions of Arctic freshwater systems can change rapidly, anchor and frazil ice accumulation could quickly form high velocity conduits of stream flow that may restrict passage (Brown et al. 2011) long before the stream channel freezes solid. Why juveniles take this more risky approach to migration is uncertain, but a principal theorem of behavioral ecology suggests that risky strategies are not undertaken unless costs are outweighed by some potential benefits (Dodson 1997). A simple explanation is that Crea Creek can support rapid growth and allocation of energy more so than alternative habitats within the watershed, perhaps due to its warm temperatures and abundant forage base (McFarland 2014), and extended use into late summer is worth considerable risk. A similar compelling explanation is that since overwintering mortality is often higher for smaller fish (Quinn and Peterson 1996; Biro et al. 2004), they may



accept greater behavioral risks (e.g. later migration) to increase energy reserves prior to the onset of winter, thereby reducing the potential risk of overwintering starvation (Heim et al. 2014). Indeed, among juveniles, smaller fish and those in poor body condition migrated later than larger fish in better condition (Heim et al. 2014).

#### *Habitat use of a model beaded stream*

These results indicate that Crea Creek is used as both a summer foraging habitat (for adults and juveniles) and likely as a spawning habitat for adults, though we found no evidence that fish successfully overwintered within the stream. Partner projects conducted concurrently indicate that Arctic Grayling are foraging heavily in this stream, in particular on ninespine stickleback (*Pungitius pungitius*) (McFarland 2014), and that body condition of Arctic Grayling increases significantly after entering the stream in June (Heim et al. 2014). Clearly, movements into the stream by juveniles reflect a functional habitat switch to access foraging opportunities during summer. Adults also forage within the stream (McFarland 2014), but the presence of young-of-the-year Arctic Grayling far upstream in Crea Creek, and the relatively short bout into Crea Creek are suggestive of a spawning run (Craig 1975). Though lacking gravel substrates, Crea Creek, like many shallow beaded stream habitats, warms rapidly following ice break-up and may provide the earliest spawning opportunities for Arctic Grayling that generally begin spawning as temperatures reach 4 °C (Northcote 1995). Crea Creek is clearly an important habitat in the migratory circuit of a large population of Arctic Grayling that use it during the entire open-water period, and understanding its ecological function helps begin to build an understanding of the role of beaded streams in Arctic ecosystems.

#### *Antenna performance and potential bias*

Because of the large sample size, temporally stratified tagging design, and high efficiency of our monitoring system, we are confident that the results are representative of the general population using Crea Creek; however, there were several limitations to this study. The first is that during the spring of 2013 there was a notable decrease in  $E_{array\ sequence}$  as the antennae did not span the entire floodplain, and only 71% of detections appeared in the expected linear sequence (compared to nearly 99% during the rest of the study). Even so, 71% efficiency is moderately high, especially since this estimate considers seven antenna stations simultaneously. Although

similar studies report detection efficiencies (Zydlewski et al. 2006) of 50–100% at single antenna stations (Connolly et al. 2008; Homel and Budy 2008), many others fail to calculate antenna efficiency altogether (e.g. Skov et al. 2008, Bryant et al. 2009). The temporary decrease in  $E_{array\ sequence}$  is not likely to have influenced our conclusions regarding upstream migration timing and within-stream movement, as data were drawn from seven antenna stations to estimate the arrival date of individual fish, and quantifications of within-stream movements were corrected for missed detections and known initial locations. Additionally, our simple method to estimate  $E_{array\ sequence}$  proved to be an ideal method for evaluating the performance of all seven antenna simultaneously, and may prove useful in future studies utilizing similar technology.

A second limitation is that, as in any observational study, the true influence of individual parameters of interest could not be determined conclusively, in particular when considering a series of simultaneously occurring environmental changes. For example, by nature of the hydrologic regime in ACP watersheds, flows are elevated during early spring and stream temperatures are increasing while fish disperse from overwinter areas (Craig and Poulin 1975; West et al. 1992; Morris 2003; Arp et al. 2012). Consequently, it is not clear how variability in either flow or temperature influences upstream migration into Crea Creek. Similarly, the observed correlations between environmental parameters and fish behavior are also convoluted by life history functions that may also drive movements. For example, while adult migration out of Crea Creek was strongly correlated to decreasing stream flow, it may be that adults depart the stream after spawning is completed, regardless of stream flow conditions. Certainly there are many explanations for the observed trends in this study, however we consider in this discussion the most compelling based on our understanding of Arctic Grayling ecology in the context of ACP hydrology.

### *Implications*

Given the differential patterns in behavior of adult and juvenile Arctic Grayling in Crea Creek, they may be impacted differently by the effects of climate change and development on ACP ecosystems. The effects of climate change are particularly strong in Arctic regions (Nelson et al. 2002), and are likely to result in direct effects (e.g. increased air temperature) as well as indirect effects (e.g. decreased winter snowpack, lower stream levels due to increased rates of evaporation, and a longer open-water period) to Arctic watersheds and biota they support

(Schindler and Smol 2006). Reduced stream flow in late summer could decrease stream connectivity of many shallow low-order streams throughout the ACP and alter the physical attributes of riffle habitats (Bradford and Heinonen 2008) that are critical to the structure of beaded streams. Since adult Arctic Grayling appear to be sensitive to decreasing stream flow, migrating out of Crea Creek as spring flooding recedes, this migration cue would clearly be advantageous if lower discharge disconnects streams earlier following spring breakup. Smaller juveniles migrating later in the summer may be at greater risk; their migration corresponded more strongly to stream temperature. Persistent warm temperatures could delay migration to a point where stream connectivity is marginal or absent resulting in a failure to match migration timing with conditions.

Similarly, Arctic Grayling and other migratory Arctic fish may be impacted by oil and gas development. In fact, recent legislation has approved the construction of an access road into the eastern National Petroleum Reserve-Alaska, which is planned to intersect Crea Creek (USDOI BLM 2014). The results of this study affirm that care should be taken to provide fish passage where roads intersect seemingly inconsequential shallow stream channels, such as the Crea Creek drainage. However, roads do not only create predictable point source issues for fish passage, rather may impact the flow of surface-water (Trombulak and Frissell 2000), and subsequently stream connectivity, across the complex drainage networks in ACP watersheds in ways difficult to predict.

In conclusion, we found that collectively adult and juvenile Arctic Grayling used this small beaded stream habitat during the entirety of the open-water period. Adults used the stream for 2–3 weeks during the period of high flow after ice break-up, while many juveniles remained within the stream until shortly before ice formation in the fall. In this stream where conditions change dramatically in a matter of days, fish appear to be well adapted to interpret environmental cues related to changes in stream connectivity. In particular, stream flow emerged as having a particularly strong influence on how this beaded stream was used during summer. Decreased stream connectivity, regardless of its cause, could have pronounced effects on habitat availability and population dynamics of Arctic Grayling and many other migratory Arctic fish species.

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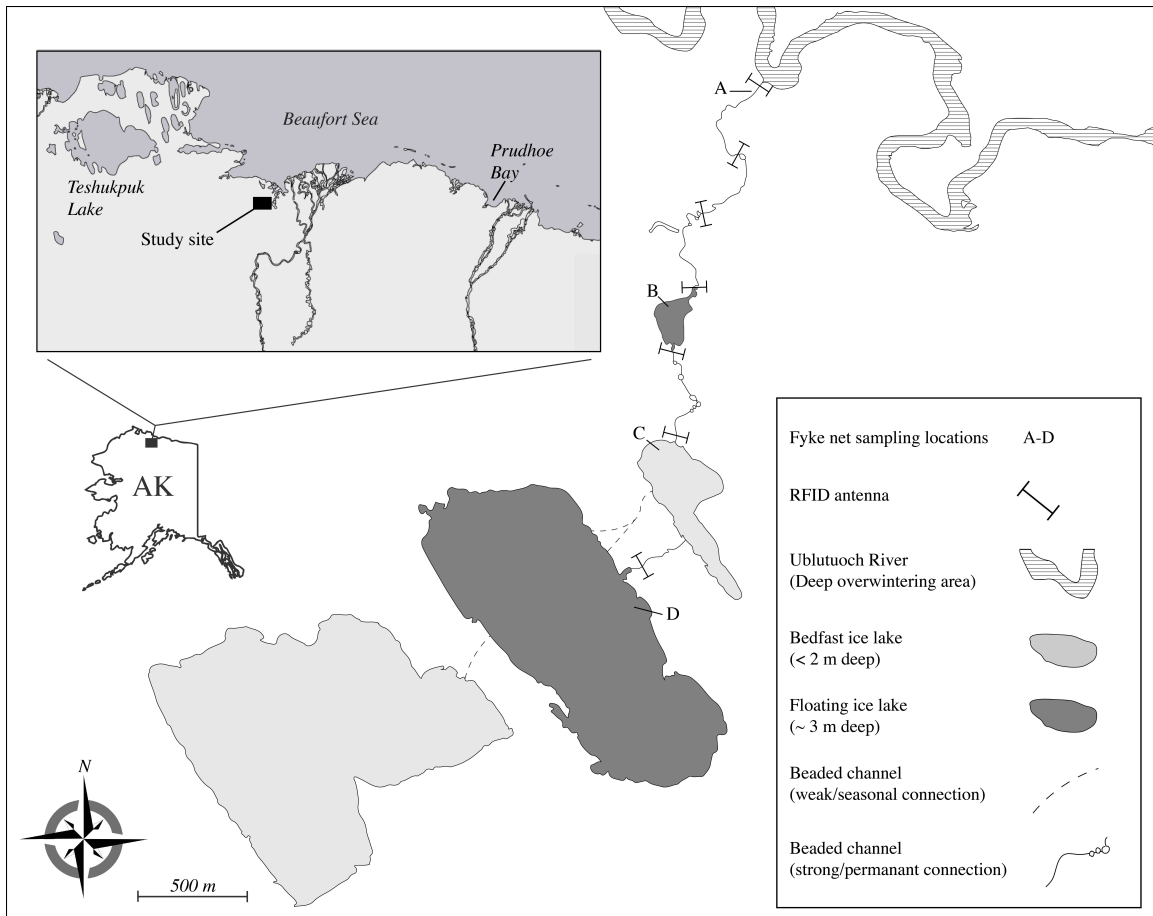


Figure 1.1. Map of Crea Creek drainage showing locations of radio frequency identification (RFID) antennae used to monitor passive integrated transponder (PIT) tagged Arctic Grayling migration and movements. Also shown are fyke net sampling locations and habitat information.

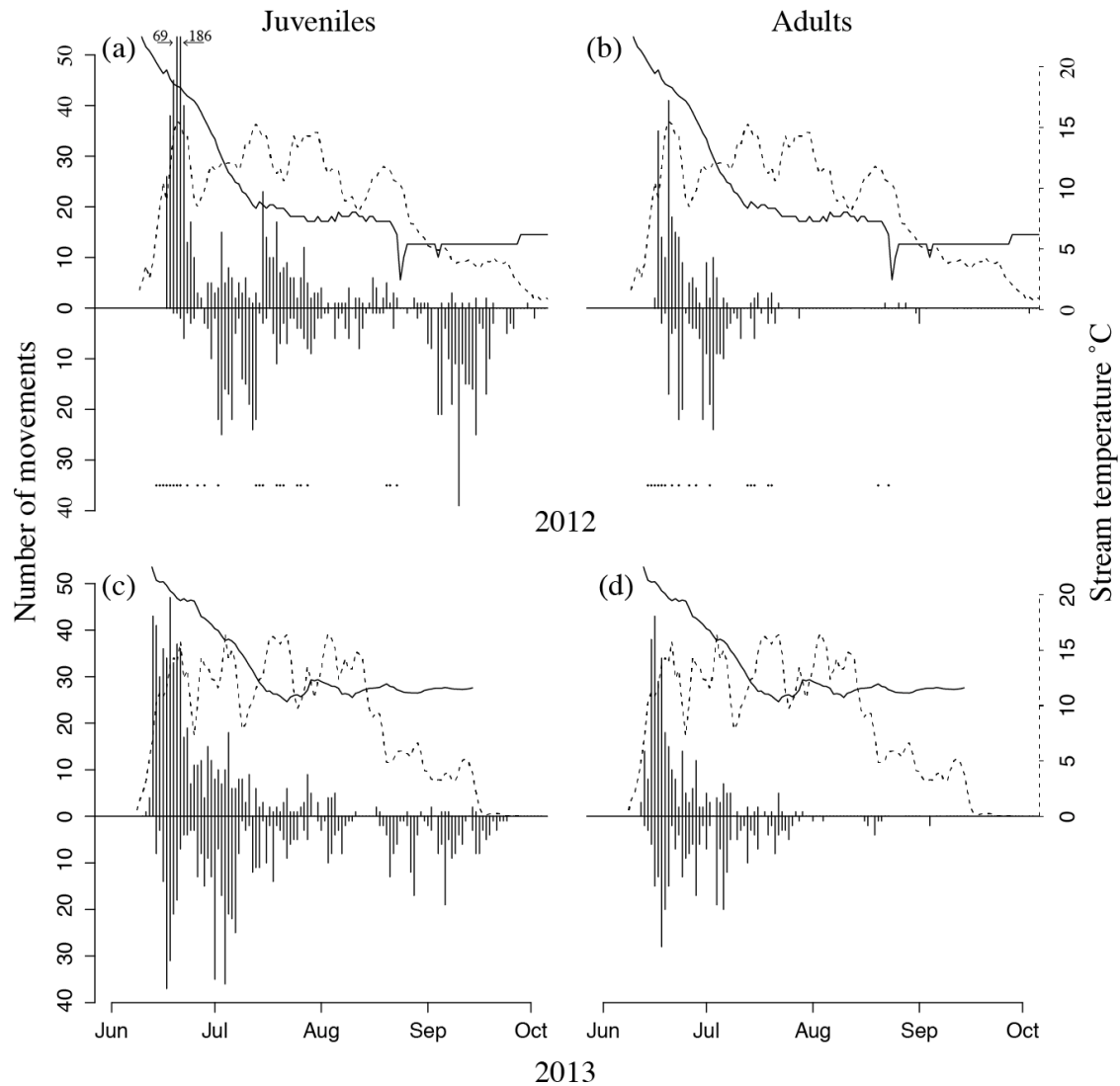


Figure 1.2. Daily number of in-stream movements detected per day for Arctic Grayling PIT tagged in Crea Creek. Vertical bars above zero (left axis) indicate upstream movements, while vertical bars below zero (left axis) indicate downstream movements. Also shown are daily mean stream temperature (broken line, right axis) and log stream discharge (solid line, no axis displayed) measured near the Crea Creek confluence. Panel a and b show movements of fish tagged in 2012 at the Crea Creek confluence, with black dots indicating dates where tagging events occurred. Panel b and c show 2013 movements of fish tagged in 2012 (i.e., fish that showed inter-annual site fidelity).

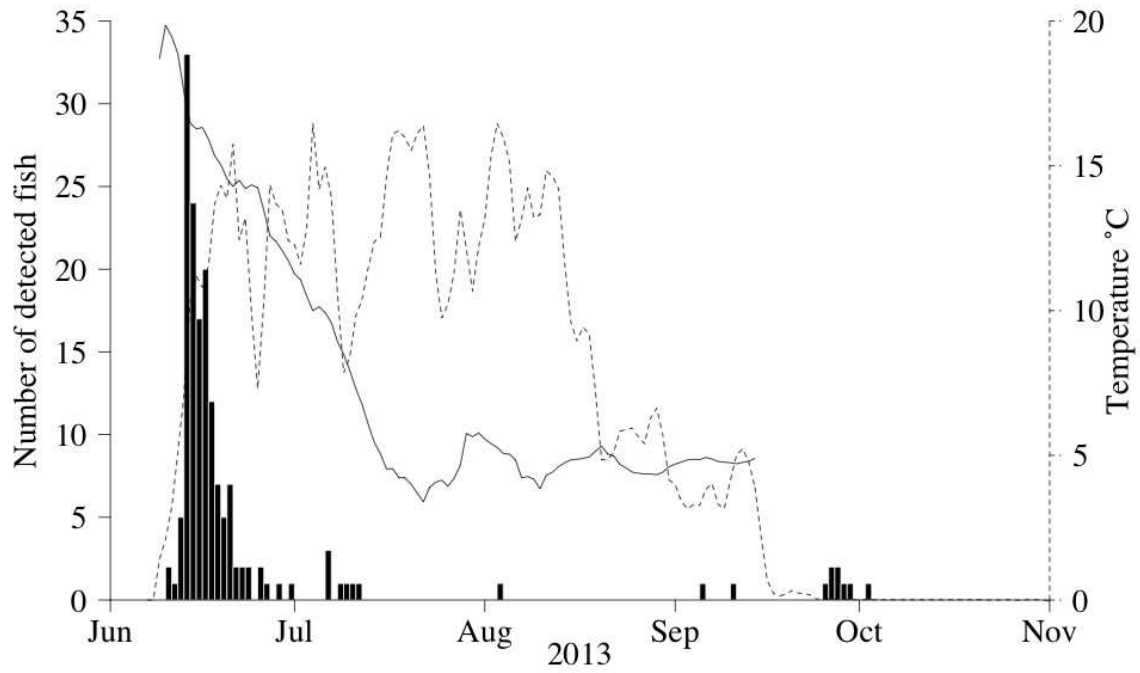


Figure 1.3. Daily count of Arctic Grayling migrating into Crea Creek in 2013 (vertical bars). The distribution was estimated by using the first detection in 2013 of each individual exhibiting inter-annual site fidelity after being tagged the previous year ( $N = 158$ ). Also shown are daily mean temperatures at the Crea Creek outlet (broken line) and the log transformed mean daily discharge (solid line, no axis shown) of Crea Creek.

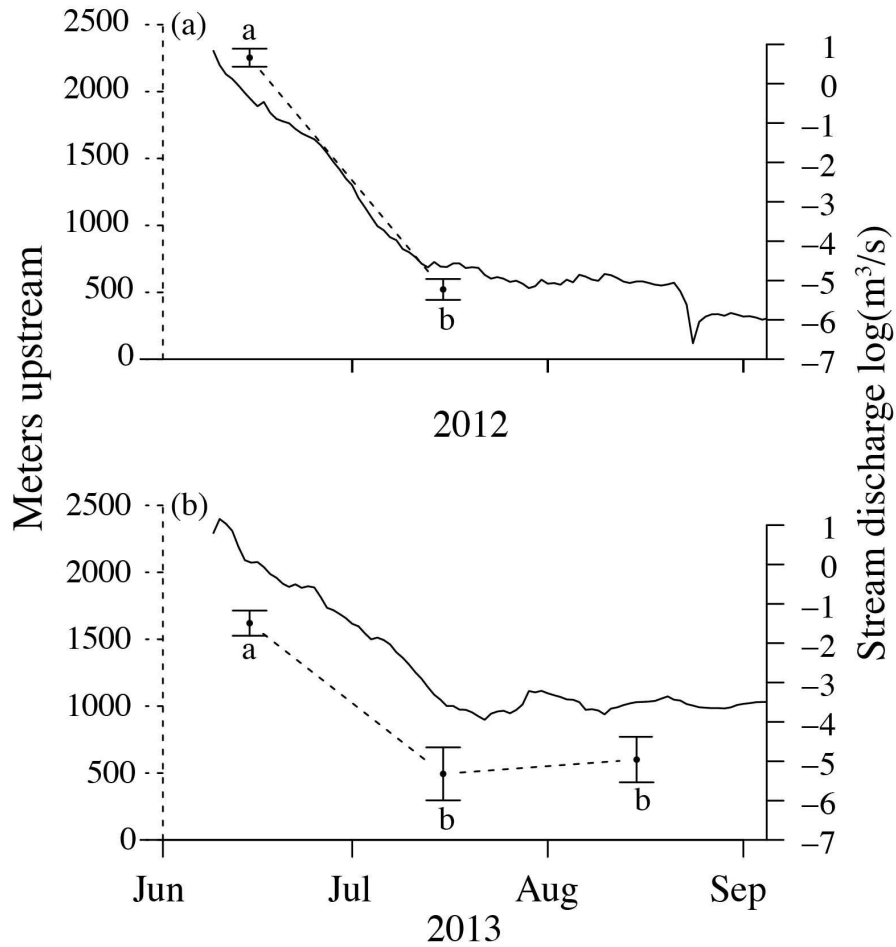


Figure 1.4. Monthly mean (whiskers indicate SE) upstream distance (meters) traveled by (a) fish tagged in June and July 2012 and (b) fish tagged in June, July, and August 2013 in relation to stream discharge (solid line). Data are from all fish captured moving upstream at the Crea Creek confluence. Letters denote significant differences among monthly means within that year (ANOVA, Tukey's HSD *post hoc* test;  $P < 0.05$ ).

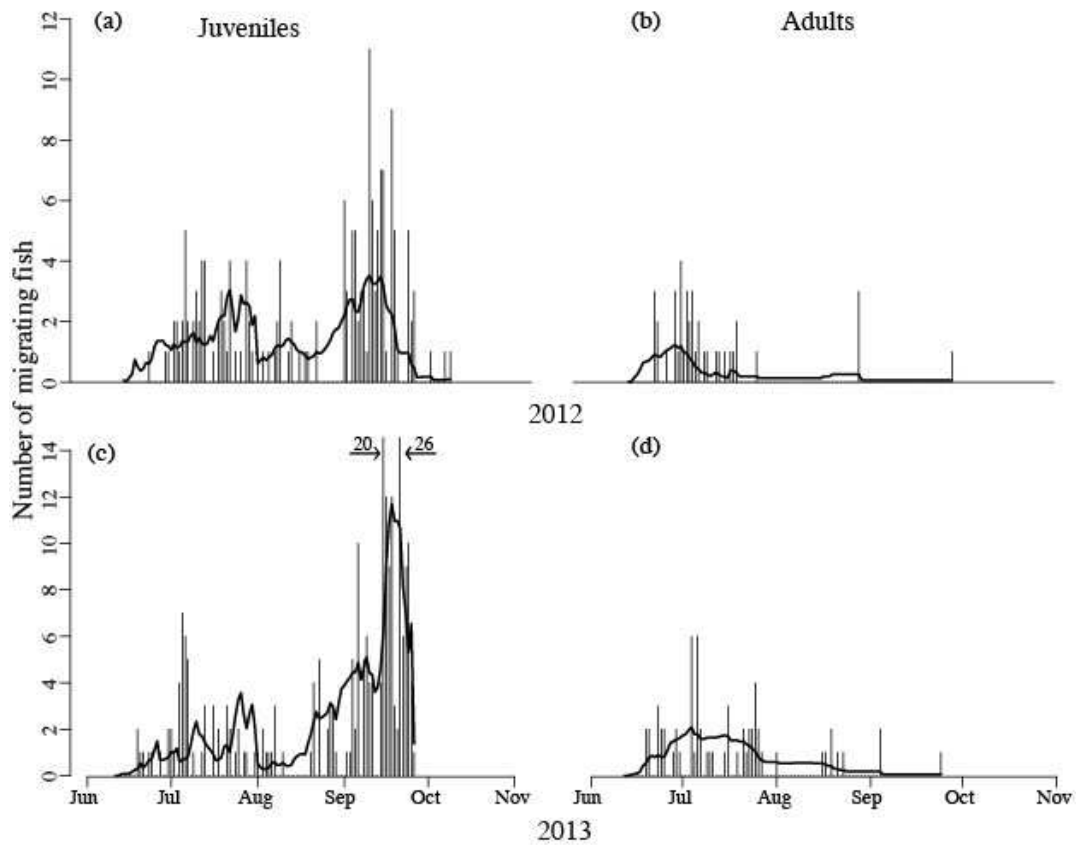


Figure 1.5. Daily counts of juvenile (panels a, c) and adult (panels b, d) Arctic Grayling migrating out of Crea Creek in 2012 and 2013 with highest-ranking negative binomial regression model fitted values (solid line). Model details are presented in Table 2. The juvenile plot and model excludes 2 outliers in 2013 where unusually high numbers of fish migrated (September 15, 20 migrants and September 21, 26 migrants).



Table 1.1. Number and fork lengths (FL) in mm (mean  $\pm$  SE) of Arctic Grayling caught moving upstream into Crea Creek via fyke net during three sampling periods in 2012. Also shown are the number and lengths of fish from these samples that were tagged and those subsequently detected at PIT tag antenna stations.

Sampling Period	2012					
	Caught		Tagged		Detected	
	N	FL*	N	FL	N	FL
June	244	220 $\pm$ 5 a	233	223 $\pm$ 5	155	236 $\pm$ 6
July	266	177 $\pm$ 5 b	129	235 $\pm$ 7	100	241 $\pm$ 8
August	7	303 $\pm$ 22 c	1	392	1	392
Total	517	199 $\pm$ 4	363	228 $\pm$ 4	256	238 $\pm$ 5

\* Values followed by different letters in these columns denote significant differences (ANOVA, Tukey pairwise comparison,  $P < 0.05$ ). Column total is not included in comparisons.

Table 1.2. Number and fork lengths (FL) in mm (mean  $\pm$  SE) of Arctic Grayling caught moving upstream into Crea Creek via fyke net during three sampling periods in 2013. Also shown are the number and lengths of fish from these samples that were tagged and those subsequently detected at PIT tag antenna stations.

Sampling Period	2013					
	Caught		Tagged		Detected	
	N	FL	N	FL	N	FL
June	277	224 $\pm$ 4 a	220	236 $\pm$ 5	153	237 $\pm$ 6
July	32	188 $\pm$ 8 b	27	186 $\pm$ 8	20	188 $\pm$ 9
August	17	164 $\pm$ 9 b	15	171 $\pm$ 8	15	171 $\pm$ 8
Total	326	218 $\pm$ 4	262	227 $\pm$ 4	188	227 $\pm$ 5

\* Values followed by different letters in these columns denote significant differences (ANOVA, Tukey pairwise comparison,  $P < 0.05$ ). Column total is not included in comparisons.

Table 1.3. Summary of model selection statistics for the top five ranking negative binomial regression models relating daily counts of juvenile and adult (separate models) Arctic Grayling migrating out of a small tundra stream in 2012 and 2013 to environmental variables and fish size. Abbreviations are as follows: L-L = log-likelihood;  $AIC_c$  = small sample size corrected Akaike information criterion;  $\Delta AIC_c$  = difference in  $AIC_c$  for a given model compared to top-ranked model;  $w_i$  = Akaike weight;  $K$  = number of parameters;  $FL_{pm}$  = mean fork length of potential migrants within the stream for each day of modeling period;  $T_{min}$  = daily minimum stream temperature.

Model	L-L	$AIC_c$	$\Delta AIC_c$	$w_i$	$K$
<i>Juvenile</i>					
Flow, $T_{min}$ , Season, $FL_{pm}$ , Year (global model)	-365.77	746.05	0.00	0.83	7
$T_{min}$ , Season, $FL_{pm}$ , Year	-368.43	749.25	3.19	0.17	6
Season, $FL_{pm}$ , Year	-375.86	762	15.95	0.00	5
Flow, Season, $FL_{pm}$ , Year	-375.53	763.45	17.4	0.00	6
Flow, $T_{min}$	-390.43	789.04	42.99	0.00	4
<i>Adult</i>					
Flow	-161.55	329.22	0.00	0.48	3
Flow, $T_{min}$	-161.29	330.77	1.56	0.22	2
Flow, $T_{min}$ , Season, $FL_{pm}$ , Year (global model)	-158.31	331.15	1.94	0.18	5
Flow, Season, $FL_{pm}$ , Year	-159.83	332.07	2.85	0.12	4
Season, $FL_{pm}$ , Year	-167.12	344.52	15.31	0.00	3

Table 1.4. Model-averaged parameter estimates, unconditional SE values, and 95% confidence limits (CLs) for covariates predicting daily counts of juvenile and adult (separate models) Arctic Grayling migrating out of a small tundra stream in 2012 and 2013. Juvenile model estimates are based on the top two negative binomial regression models, which accounted for 100% of the collective model weight, while the adult model estimates are based on the top four models again accounting for 100% of the collective model weight (see table 1.3). Abbreviations are as follows:  $T_{\min}$  = the daily minimum stream temperature,  $FL_{\text{pm}}$  = the mean fork length of potential migrants within the stream for each day of modeling period.

Covariate	Parameter estimate	Lower 95% CL	Upper 95% CL
<i>Juvenile</i>			
Intercept	-3.36 ± 0.21	-3.78	-2.94
Flow	-1.08 ± 0.46	-1.99	-0.17
$T_{\min}$	-1.36 ± 0.37	-2.09	-0.63
Season	-1.46 ± 0.28	-2.00	-0.92
$FL_{\text{pm}}$	-1.84 ± 0.25	-2.32	-1.35
Year	0.12 ± 0.26	-0.38	0.62
<i>Adult</i>			
Intercept	-2.88 ± 0.27	-3.41	-2.35
Flow	-1.43 ± 0.40	-2.20	-0.65
$T_{\min}$	-0.47 ± 0.43	-1.31	0.38
Season	-0.89 ± .62	-2.11	0.33
$FL_{\text{pm}}$	-0.15 ± 0.61	-1.35	1.05
Year	-0.46 ± 0.31	-1.07	0.14



## **Chapter 2: Body size and condition influence migration timing of Arctic Grayling<sup>1</sup>**

### **Abstract**

Freshwater fishes utilizing seasonally available habitats within annual migratory circuits time movements out of such habitats with changing hydrology, though individual attributes of fish may also mediate the migratory response to seasonal environmental change. We tagged juvenile Arctic Grayling in a small seasonally flowing stream in Alaska in 2012 and 2013 and recorded migration timing as fish left the study area towards overwintering habitat. We examined the relationship between an individual's migration date and its fork length and body condition index (BCI) for fish tagged in June, July, and August in three separate models. All models indicated that larger fish migrated earlier than smaller fish, however only the model including fish tagged in August indicated a relationship with BCI. In this model, 42% of variability in exit timing was explained by body size and condition alone, and indicated that fish in better condition migrated earlier than those in poor condition. The lack of a strong relationship between BCI and migration date (in June and July models) may be because BCI measured at the time of tagging did not necessarily reflect an individuals' physiological condition at the time of out-migration. These results are interpreted in the context of size and state-specific risk of overwinter starvation, which may influence individuals at greater risk to extend summer foraging in a risky, yet productive, habitat. This research provides further evidence that heterogeneity among individuals within a population can strongly influence migratory behavior, and identifies potential anthropogenic risks to late season migrants in Arctic watersheds.

<sup>1</sup>Heim, K. C., M. S. Wipfli, M. S. Whitman, and A.C. Seitz. Body size and condition influence migration timing of Arctic Grayling. Submitted to Ecology of Freshwater Fish

## Introduction

Many freshwater fish species migrate among habitats to match life history needs with changing environmental conditions (Schlosser and Angermeier 1995). In Arctic watersheds, these migrations generally include movements from overwintering areas to shallow foraging and spawning areas (West et al. 1992; Heim et al. 2014), and can be thought of as a response to the shifting balance of costs and benefits provided by physically and biologically heterogeneous habitats through time (Stearns 1992). At northern latitudes, overwintering habitats must be deep or spring-fed in order to provide adequate unfrozen water, whereas summer habitats must provide ample food in order to replenish energy reserves before the often-extensive (up to nine month) overwintering period (Buzby and Deegan 2000). In some cases, growth may only occur for three months during the short Arctic summer when spring spawning adult fish must also acquire energy necessary for overwinter gonadogenesis (Armstrong 1986; Buzby and Deegan 2000). Fish must therefore coordinate migration timing and habitat use with seasonal conditions in order to maximize growth, while minimizing exposure to predation and likelihood of getting stranded in unsuitable overwintering habitat.

Fish use environmental cues to determine migration timing (Gowan et al. 1994; Swanberg 1997; Bryant et al. 2009; Heim et al. 2014), though studies have also shown timing to be behaviorally plastic and related to heterogeneity in individual characteristics of fish. For example, Brodersen et al. (2008) found that well-fed cyprinids initiated a refuge migration earlier than poorly fed conspecifics. Others have found that body condition, size, and individual growth rates are important determinants in individual migration timing of salmonids (Forseth et al. 1999; Halttunen et al. 2013). These findings suggest that physiological differences among size classes and heterogeneity in accumulated lipid reserves among individuals mediate the relative costs and benefits of migration for an individual, resulting in differences in migratory behavior (Brodersen et al. 2008).

Arctic Grayling (*Thymallus arcticus*) are a widespread and abundant migratory freshwater fish occurring throughout the N. American and Eurasian Arctic and subarctic (Scott and Crossman 1973). Due to their importance as a sport fish, there has been a considerable effort to understand their general ecology and migration patterns (Tack 1980; Northcote 1985). Arctic Grayling move among spawning, foraging, and overwintering habitats as seasonal conditions change (Craig and Poulin 1975; Northcote 1985; West et. al 1992) with many

individuals showing inter-annual fidelity to specific summer foraging locations (Buzby and Deegan 2000). In many watersheds, such as those along the Arctic Coastal Plain of Alaska (ACP), overwintering areas are few in number and can severely limit the distribution of fish during winter (Craig 1989), since nearly all bodies of water less than 1.5 m deep freeze solid by the end of winter (Jones et al. 2009). This restricts the use of productive shallow-water habitats to the short summer, and timing migrations out of such habitats is critical to avoid becoming stranded in unsuitable winter habitat (Tack 1980).

Recent research indicates that low-order beaded stream habitats are used extensively by Arctic Grayling during the short Arctic summer (Heim et al. 2014; McFarland 2014). Beaded streams are characterized by regularly spaced elliptical pools connected by narrow channel runs, appearing as “beads-on-a-string” (Oswood et al. 1989) and are a dominant stream morphology across Alaska’s ACP (Arp et al. 2012). Beaded streams offer good foraging opportunities during the summer (Hemming 1996; McFarland 2014) and generally lack large piscivorous fishes; however, with the exception of deep pools or “beads”, shallow reaches of beaded streams many freeze completely during winter (Jones et al. 2013). Furthermore, despite the persistence of liquid water through winter, these habitats often become anoxic towards late winter (Lilly et al. 2010) and are generally not believed to support overwintering salmonids. Thus prolonged use of these habitats into autumn as water temperatures approach freezing is a substantial risk, though they may provide additional time for growth and accumulation of energy necessary to endure the winter.

In this study, we hypothesized that migration timing of Arctic Grayling from summer habitats into winter refugia was related to both individual size and relative body condition. We examined the relationship between refuge migration timing of individual juvenile Arctic Grayling out of a low-order beaded stream (Crea Creek) on Alaska’s ACP in relation to fork length (FL) and a body condition index (BCI), a proxy for growth and lipid reserves (Pope and Kruse 2007). Given that higher lipid content and larger body size at the onset of winter has been shown to positively influence survival of other salmonids (Quinn and Peterson 1996; Biro et al. 2004), we predicted that (1) large fish will migrate earlier than smaller fish and (2) fish in good condition relative to conspecifics will migrate earlier than those in poor condition. These predictions are based on the premise that smaller fish in poor condition will accept greater risks (i.e., later migration timing) than fish that have already accumulated energy reserves for winter



or are physiologically less susceptible to overwintering mortality.

## **Methods**

### *Study area*

This study was conducted in Crea Creek (70°17'N, 151°20'W), a small tributary in the Fish Creek watershed, which is approximately 20 km west of the Colville River delta in Alaska's ACP (Figure 1). Crea Creek is a beaded stream that generally flows from June through September, and freezes completely during winter except in deep “beads” and two lakes that are approximately 2.5 m deep (Jones et al. 2013). Adults and juvenile Arctic Grayling enter the stream shortly after ice break-up, which usually occurs during early June (Heim et al. 2014). The stream provides excellent foraging opportunities, with both adults and juveniles relying heavily on the small-bodied ninespine stickleback (*Pungitius pungitius*), as well as various aquatic and terrestrial invertebrates (McFarland 2014). Some adults may also spawn within the stream, and most leave before the end of July before stream discharge reaches summer base flow level (Heim et al. 2014). Juvenile fish migrate out of the stream in two peaks, the first coinciding with adult migration in July and the other occurring shortly before freeze-up in September (Heim et al. 2014). Crea Creek is not believed to support overwintering Arctic Grayling (Heim et al. 2014), thus migration out of the stream before freeze-up is critical. Crea Creek initiates from a headwater lake and flows 4.5 km through three other lakes and many large beads before reaching the Ublutuoch River, an important overwintering area and migratory corridor for Arctic Grayling, Broad Whitefish (*Coregonus nasus*), and Burbot (*Lota lota*) (Morris 2003).

### *Fish sampling and tagging*

Fish were captured within Crea Creek from June–August in 2012 and 2013 using fyke nets as the primary sampling method. Additional fish were captured within Crea Creek via opportunistic angling with fly-fishing gear and three single-pass electrofishing surveys in collaboration with an ongoing food web study during 2012. In this analysis, we used only Arctic Grayling 120–280 mm FL, a size at which most Arctic Grayling in the area are still immature, though females generally tend to mature at a smaller size than males (L. Moulton, personal communication). Mature adults were excluded from analysis because length-mass based

measurements of body condition are confounded by sex and allocation of body weight during spawning periods (Morgan 2004). Because Arctic Grayling within and nearby Crea Creek spawn in June, and most migrate out of the study area by mid-July, there is little time to capture unbiased BCI measurements prior to the peak of migration. We therefore focused on juvenile fish to test hypotheses.

Arctic Grayling were anesthetized in a 20–30 ppm clove oil/stream water solution until equilibrium was lost (2–5 minutes) (Morris 2003), measured to the nearest mm in FL and weighed to the nearest tenth of a gram. Arctic Grayling 120-mm through 179-mm were tagged with 12-mm (0.1 g) half-duplex passive integrated transponder (PIT) tags (Oregon RFID, Portland, OR, USA), and those  $\geq 180$  mm were tagged with 23-mm (0.6 g) half-duplex PIT tags to ensure tag/body mass ratio did not exceed 2% (Winter 1996). Once a fish became unresponsive, a small incision was made and a tag was inserted into the body cavity with a syringe. After handling, fish were released into slow water near the sampling location to recover. Tagging and handling appeared to have minimal effects on fish as some were observed foraging less than one hour after being tagged. In total, 1,052 fish were captured within this size range and 781 were PIT tagged.

### *Body condition index*

We used residuals from a length-mass regression as a BCI (Pope and Kruse 2007; Bentley and Schindler 2013). We first used ordinary least squares regression to estimate parameters  $\alpha$  and  $\beta$ , using the linear length-mass equation,

$$\log_e(W_i) = \alpha + \beta \cdot \log_e(L_i),$$

where  $W_i$  is the weight of an individual (g) and  $L_i$  is the FL of an individual (mm). The residual for each individual in this regression was used as its BCI. This process results in a BCI for each fish where positive and negative values indicate a fish is heavier or lighter relative to others at that length. Furthermore, this allows for comparison of relative weight among individuals of different lengths, since residual values are independent of fish length (Bentley and Schindler 2013).

In order to identify seasonal trends in BCI, we first fit a length-mass regression using all 1,052 fish captured during the study to estimate  $\alpha$  and  $\beta$ . We then plotted the calculated BCI values against date of capture. Differences in monthly mean BCI values were determined using

one-way ANOVA and Tukey's *post hoc* HSD test (Zar 1999). Because seasonal and annual trends were clearly evident (Figure 2.2), and we were interested in the condition of fish relative to others during the time period prior to migration, we subset fish into 6 groups (by year and month captured) and re-fit length mass regressions separately to estimate six sets of parameters  $\alpha$  and  $\beta$ , and re-assigned BCI values (Table 2.1). We proceeded to use these time period specific BCI values in modeling.

### *Migration timing*

We used two stream-width swim-through PIT tag antenna stations to determine migration timing out of Crea Creek (Figure 2.1). These consisted of an antenna loop with the bottom anchored to the substrate and the top suspended above water level, connected to a solar powered data logging system (Oregon RFID, Portland, OR, USA) that recorded the date, time, and ID of fish moving through the antenna. Antenna station #2 was located 503 m upstream in Crea Creek from its confluence with the Ublutuoch River, and station #1 was located in Crea Creek at the confluence with the Ublutuoch River. Data logging timekeepers were synchronized to the nearest second, allowing for the direction of fish movement to be determined from the sequence of detections. Antennas were in operation nearly continuously during the summers of 2012 and 2013. Both antennae encompassed the entire stream width during peak periods of downstream migration, and proved to be highly efficient at detecting passing fish (98-99%) according to detection efficiency calculations by methods similar to those presented by Zydlewski et al. (2001) (Heim et al. 2014).

We defined a migratory movement as an individual fish's final movement from antenna station #2 to antenna station #1 in the year it was tagged (a movement out of Crea Creek). As some fish exited and entered the stream several times, or made several movements across antenna station #1, we used this specific sequence to isolate migratory movements from diel or random movements. Thus each fish was only assigned a single migration date and fish that did not travel upstream past antenna #2 were not included. Similarly, any fish not detected moving across antennae in this sequence were not included, which could indicate that fish 1) did not migrate 2) died during the summer or 3) lost its PIT tag. In 2013 many fish tagged in 2012 returned to the stream (i.e. showed inter-annual site fidelity to Crea Creek,  $N = 155$ ), however we excluded these fish from the migration models in 2013 because the length and weight

information for these individuals collected in 2012 may not be representative of their condition in 2013. Furthermore, fish that migrated less than 7 days after being tagged were not used in order to remove fish that may have potentially migrated out of the stream in response to the stress of capture, handling, and tagging. Of the 781 tagged fish over the two year study, we assigned migration dates to 297 based on the above criteria.

### *Data analysis*

We used logistic regression to determine if a binary migratory response (early migrant or late migrant) was related to FL or BCI for fish tagged in June. Early migrants were defined as those that migrated on or before July 15 and late migrants those that migrated after July 15. Year (2012 or 2013) and tagging date (Julian date) were also included as predictors in the model. We used linear regression to predict migration date (Julian date) with BCI, FL, year, and tagging date for fish tagged in July and August in two separate models. In logistic and linear regressions, all continuous predictor variables were standardized, resulting in coefficient estimates that were interpreted as standardized magnitude of the effects of variables on the response (Schielzeth 2010). Because we included a categorical variable (year), we used two standard deviations to standardize continuous variables, which allowed for comparison between coefficients of categorical and continuous variables (Gelman and Hill 2007; Schielzeth 2010). We calculated the variance inflation factor values for covariates in all models and found none greater than 1.3, indicating no violations of model assumptions due to multicollinearity (Zuur et al. 2013) and consider covariates significant in models when  $P < 0.05$ .

## **Results**

### *Body condition index*

Month of capture significantly affected BCI of Arctic Grayling in both years (2012 ANOVA  $F_{2,557} = 256.1, P < 0.001$ , 2013 ANOVA  $F_{2,490} = 223.6, P < 0.001$ ). The mean BCI of fish measured in June (mean  $\pm$  SE, 2012 =  $-0.133 \pm 0.008$ , 2013 =  $-0.066 \pm 0.004$ ) was significantly lower than those measured during July (2012 =  $0.075 \pm .005$ , 2013 =  $0.049 \pm 0.004$ ) and August (2012 =  $0.064 \pm 0.014$ , 2013 =  $0.062 \pm 0.009$ ) within both years, though mean BCI values of fish measured in July did not differ from those measured in August within either year (Tukey *post hoc* HSD,  $P < 0.001$ ) (Figure 2.2 b).

### *Migration timing*

All three models indicated that larger fish migrated earlier than smaller fish, though only the model for fish tagged in August indicated a significant relationship with BCI (Table 2.2; Figure 2.3). The negative coefficient of BCI in the August model indicated that on average, fish in poor body condition migrated later than fish in better body condition. In this model, the effect of FL was twice as great as that of BCI, as determined by comparing coefficient values. The August model re-fit using only FL as a predictor yielded an  $r^2$  value of 0.33. Adding BCI increased  $r^2$  to 0.42, explaining an additional 9% of variability in exit timing by individual fish. Year was only found to be a significant predictor in the July model and predicted that on average fish tagged in July 2012 migrated earlier in 2012 than those tagged in July 2013. All models indicated that migration date was not influenced by tagging date.

### **Discussion**

The three monthly migration models confirmed the prediction that larger juveniles migrate out of Crea Creek earlier than smaller juveniles. This is likely related to a size-mediated functional response to the shifting costs and benefits of remaining in Crea Creek. As minimum stream temperatures approach freezing in September, the risk of becoming stranded in Crea Creek (an unsuitable winter habitat) increases. Thus prolonged residence within this area reflects a behavioral risk that should be balanced by some degree of benefits to later migrants, such as extended foraging opportunities.

Size-dependent overwintering mortality and predation threat provide mechanistic explanations for why smaller fish would take greater risks in their migratory timing. Overwintering mortality is often higher for smaller fish (Oliver et al. 1979; Henderson et al. 1988), and a commonly suggested mechanism is size-dependent starvation endurance. For example, Biro et al. (2004) found that small rainbow trout (*Oncorhynchus mykiss*) had lower lipid reserves, starved earlier, and experienced higher rates of mortality than larger fish in both field and laboratory conditions. If smaller Arctic Grayling in this watershed are more likely to suffer overwinter mortality due to starvation, the risks they take to increase survival during this period should be proportionally greater than larger fish. For smaller fish, extending the length of time in high quality foraging habitats (e.g. later migration) may be a behaviorally adaptive approach to increase body size and pre-winter lipid reserves thereby increasing odds of

overwinter survival (Brodersen et al. 2008). Furthermore the benefits in terms of increased overwintering survival must outweigh the risks of becoming stranded in this unsuitable overwintering habitat. This explanation of this result relies on the assumption that Crea Creek can provide significantly better foraging opportunities than nearby habitats. While no comparative studies exist, the habitat complexity, forage availability, thermal characteristics, and productivity of beaded streams likely provide opportunities for increased juvenile growth relative to larger tundra rivers like the Ublutuoch (Craig and McCart 1975; Oswood et al. 1989).

Alternatively, extended residency in Crea Creek by smaller individuals might be due to differential rates of predation threat once fish reach overwintering areas as compared to within Crea Creek. In Arctic watersheds, overwintering areas are limited to those that do not freeze solid (West et. al 1992) and high densities of fish are likely to occur (Cunjak and Power 1986). In the Fish Creek watershed, overwintering areas used by juvenile Arctic Grayling are likely shared with piscivorous Burbot (*Lota lota*), which poses potential for high rates of predation in winter. Extended residency in Crea Creek may reduce overall predation risk, as very few piscivorous predators are present in Crea Creek during fall (K. Heim, University of Alaska, unpublished data). However, it seems unlikely that delaying migration by 2–3 weeks would provide appreciable benefits in terms of reduced predation threat considering the extensive (9 month) overwintering period. We favor the size-dependent starvation endurance explanation of these results, though realize these explanations are not mutually exclusive and other mechanisms may be at play including size-specific thermal optima and associated habitat choices (Morita et al. 2010) or density dependent processes not considered here.

In support of our second prediction, we found a negative relationship between migration date and body condition in the August model. Fish in poor condition migrated later than fish in good condition, suggesting that a condition dependent mechanism may regulate the migratory response. Recent studies have found that individual condition can influence migration timing. For example, experimental feeding led to increased body condition in a group of cyprinids, which subsequently migrated earlier than non-fed conspecifics (Brodersen et al. 2008). Brodersen et al. (2008) concluded that condition dependent decision-making influenced differences in whether and when fish migrated. Given that the time constraint of a short growing season can result in greater risk taking by individuals preparing for winter (Rowe and Ludwig 1991), and hungry individuals often accept higher risks in order to maximize foraging

(Pettersson and Brönmark 1993; Brown and Kotler 2004), these results are logical. Fish in Crea Creek that have had a successful foraging season and accumulated adequate lipid reserves to survive the winter should be more conservative and migrate earlier, thus avoiding the potential to be stranded in poor overwintering habitat whereas those that lack sufficient lipid reserves continue to forage within Crea Creek at considerable risk. However, support for this body-condition hypothesis was only found for fish tagged in August, while no discernable relationship was found between migration timing and body condition of fish tagged in June and July.

It may be that the metric of body condition used is not representative of accumulated lipid reserves and recent growth for fish that were measured long before they migrated (e.g. fish measured in June, but migrating in September). For example a fish of average weight measured in July may have had excellent foraging success in early August increasing its body condition, then migrated in early September. In this instance, BCI (measured at time of capture) would fail to represent true physiological condition during the time frame when that fish made the decision to migrate. If this were the case, one would expect that fish tagged and measured in August would most accurately reflect physiological condition of fish prior to migration in September. Indeed, the August model is the one in which BCI proved to be significantly related to migration timing.

Furthermore, the use of any length-mass based indices as a proxy for growth and lipid reserves is not without controversy, though we believe adequate precautions were taken to account for potential biases and its use is justified here. Length-mass based condition indices can be influenced by many factors, including maturation status (Morgan 2004), diet (Pothoven et al. 2001), and can vary seasonally due to fluctuating environmental conditions (Gabelhouse 1991). We initially used all 1,052 fish to calculate regression parameters and found that fish mass was much lower per given length for fish measured earlier in the summer within both years. This was expected, as fish in June have only recently moved out of overwintering areas (Craig and Poulin 1975) and are likely in a state of growth compensation (Jobling 1993; Ali et al. 2003) where they forage heavily after a period of starvation. In itself, this was an important result and strengthens the notion that overwintering periods may exert strong selective forces on Arctic fish populations through starvation. We attempted to mitigate these seasonal and annual trends in BCI by re-fitting length mass regressions for different time frames and excluded adult fish in order to remove trends due to maturation status. In addition to these precautions, a recent

study using a southeast Alaskan population of Arctic Grayling found BCI calculated from length-mass regression residuals strongly correlated with instantaneous growth rates (Bentley and Schindler 2013), providing support for its use as a proxy for physiological condition in this species.

The results of this study indicate that small Arctic Grayling in poor body condition are perhaps the most vulnerable to the environmental changes that lead to reduced late season aquatic connectivity. For example, increased rates of evapotranspiration associated with climate change may lead to reduced runoff and disruption of surface-water connectivity and habitat access (Rouse et al. 1997; Reist et al. 2006; Lesack and Marsh 2010), though adequate flows are necessary for upstream or downstream movement (Jonsson 1991; Bradford and Heinonen 2008; Reist et al. 2006) to reach overwintering areas. While Arctic grayling appear to be well adapted to time migrations with seasonal environmental cues (e.g. photoperiod, temperature, flow reduction, Tack 1980; Heim et al. 2014), reduced late season connectivity in tundra watersheds could greatly reduce seasonal access to productive shallow foraging habitats such as beaded streams. If some threshold level of pre-winter lipid reserves determines overwinter survival, attaining this state could become more difficult in future climate scenarios. However, earlier ice break-up timing and a longer open-water period is also predicted in future scenarios that may mitigate reduced late season foraging opportunities by providing earlier access to seasonal habitats in spring (Reist et al. 2006; Prowse et al. 2011). As the effects of development in Arctic freshwater systems will be realized more rapidly than climate change effects, care should be taken to provide late season small-stream connectivity as access roads and drilling areas are constructed across the hydrologic landscape.

In summary we found that size and body condition are important in determining the migratory behavior of an Arctic fish. We also highlighted the dramatic seasonal changes in relative mass per unit length that can occur in a species that spends up to nine months in isolated overwintering areas, and the potential complications this has on length-mass based BCI. The use of more precise, non-lethal measures of the energetic status of individuals (e.g. bioelectric impedance analysis, Cox and Hartman 2005) may prove useful in studies of this nature in the future. This study adds to the growing body of literature examining the relationship between individual attributes and migratory behavior among freshwater fish, and provides empirical evidence to support condition and size dependent migration timing.



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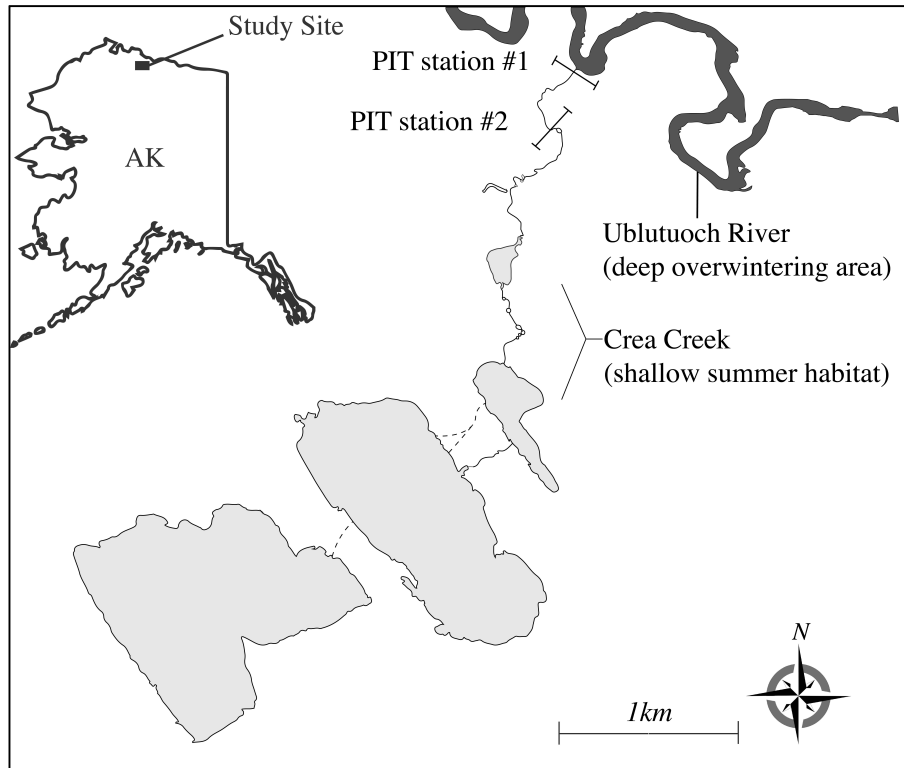


Figure 2.1. Location of the Crea Creek drainage in northern Alaska (inset) to its confluence with the Ublutuoch River, a deep overwintering area for Arctic Grayling. Also shown are the locations of the two passive integrated transponder (PIT) tag antenna stations used to monitor migration timing.

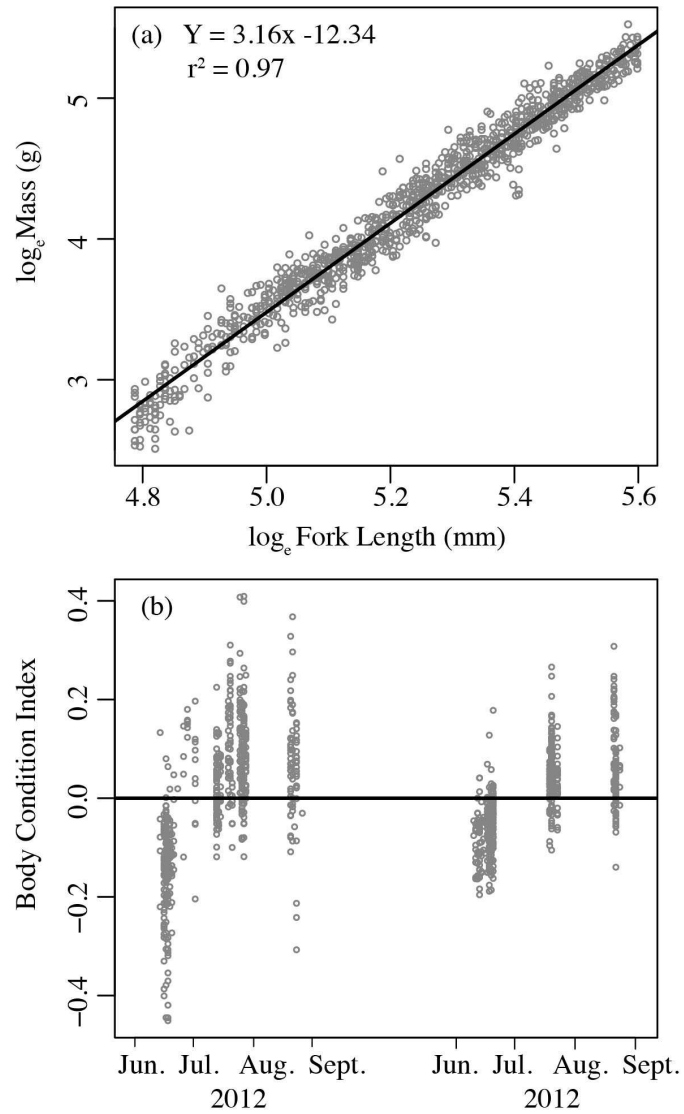


Figure 2.2. Log transformed length mass regression for Arctic Grayling (a) using 1,052 fish between 120-280 mm captured during this study and (b) the resulting body condition index (BCI) for all measured individuals calculated as the residuals of the regression, plotted against date captured (b). Fish in poor condition have negative BCI values; fish in good condition have positive BCI values.

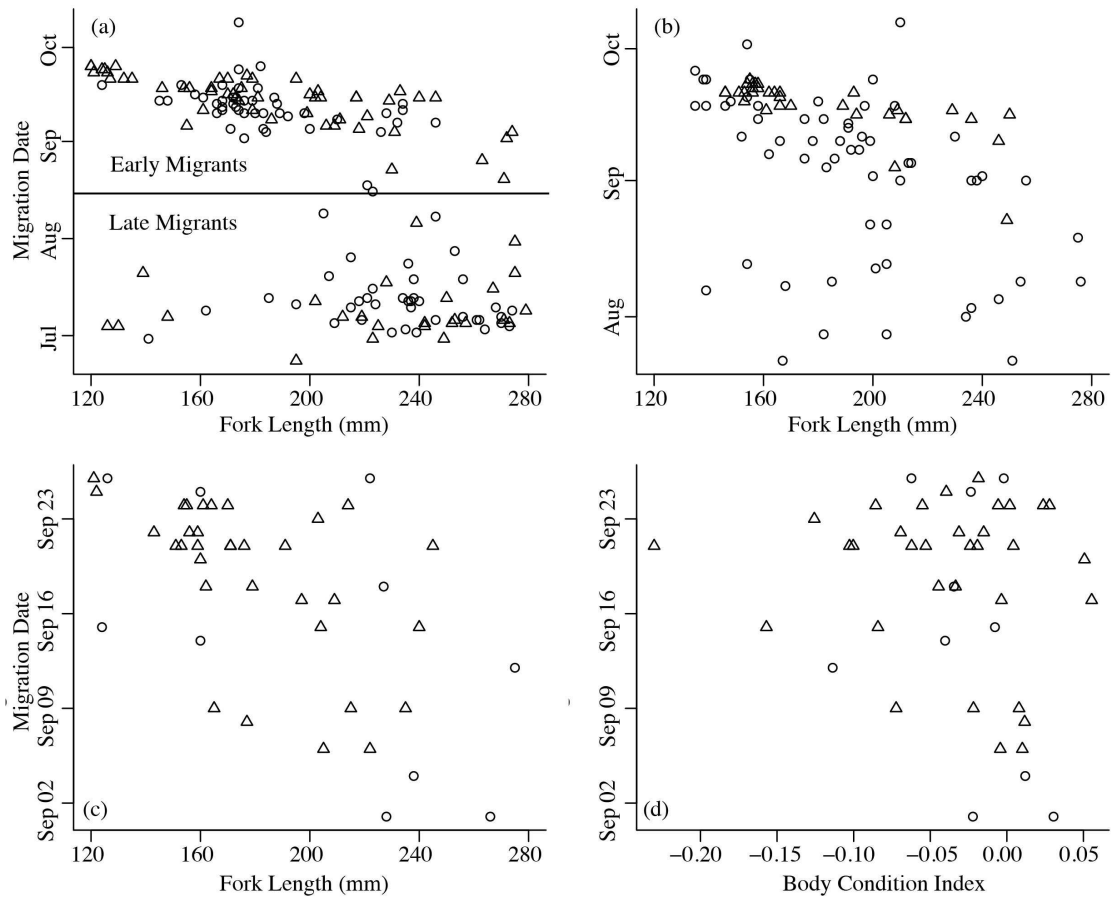


Figure 2.3. Migration date in relation to fork length of individual Arctic Grayling tagged in (a) June, (b) July, and (c) August during 2012 (circles) and 2013 (triangles). Also shown is the relationship between migration date and body condition for fish tagged in August (d). The horizontal line at July 15<sup>th</sup> in panel (a) distinguishes early migrants from late migrants as used in the logistic regression to predict a categorical migratory response (Table 2.2). There was no discernible relationship between migration date and body condition for fish tagged in June and July, and thus no corresponding plots for these groups are displayed.



Table 2.1. Regression coefficients and sample sizes for  $\log_e(\text{weight})$  regressed on  $\log_e(\text{length})$  using subsets of fish caught during different time periods, and all fish captured during this study. A Body Condition Index (BCI) was calculated based on residuals from monthly regressions for each time frame.

Subset	N	$\alpha$ (intercept)	$\beta$ (slope)	$r^2$
Jun. 12	192	-13.13	3.29	0.97
Jul. 12	296	-11.63	3.04	0.98
Aug. 12	71	-13.53	3.41	0.98
Jun. 13	231	-12.89	3.25	1.00
Jul. 13	166	-12.16	3.14	0.99
Aug. 13	96	-12.85	3.27	0.98
All	1,052	-12.34	3.16	0.97

Table 2.2. Monthly models predicting migration timing of Arctic Grayling with predictors fork length (FL), body condition index (BCI), tagging date (Julian date), and year (2012 or 2013). The June model predicts early vs. late migration in a logistic model ( $N = 160$ ), while July ( $N = 94$ ,  $r^2 = 0.33$ ) and August ( $N = 43$ ,  $r^2 = 0.40$ ) models are linear and predict Julian date of migration. All predictor variables were standardized to allow for interpretation of estimates as effect size.

Model	Predictor	Estimate	95% CI	<i>P</i>
June				
	FL	-2.88	-3.91 to -1.98	< 0.001
	BCI	4.27	-1.26 to 10.25	0.14
	Tag date	-0.06	-0.08 to 1.49	0.08
	Year	0.69	-0.87 to 0.73	0.88
July				
	FL	-14.58	-20.62 to -8.53	< 0.001
	BCI	1.11	-4.95 to 7.17	0.72
	Tag date	0.20	-5.94 to 6.34	0.95
	Year	13.739	7.51 to 19.97	< 0.001
August				
	FL	-9.08	-12.85 to -5.30	< 0.001
	BCI	-4.47	-8.05 to -0.86	0.02
	Tag date	0.08	-3.26 to 5.90	0.97
	Year	1.32	-3.67 to 3.84	0.56



## Conclusions

We explored Arctic Grayling migration and movements at both the population and individual level, to understand what factors are influential in determining the timing and extent of this behaviorally adaptive strategy. In the first chapter we found that all population level measures of movement and migration were strongly tied to seasonal changes in hydrology. In the hydrologic landscape of the ACP, seasonal changes in ice-cover, stream flow, and stream temperature occur rapidly and concurrent with weather patterns and photoperiod (Bowling et al. 2003). Not surprisingly, Arctic Grayling appear to be well adapted to these seasonal patterns, initiating movements and migration as seasonal conditions permit in order to maximize time spent in productive foraging habitats and to find timely refuge from adverse winter conditions. For example, upstream migration was strongly correlated with the timing of ice break-up, and our results suggest that fish selectively explore small stream habitats based on flow and temperature experienced at stream outlets. In this “land of extremes” (Huryn and Hobbie 2012), the ability of Arctic Grayling to coordinate life history functions with dramatic seasonality is clearly a behavioral advantage.

We also found that migration timing was related to heterogeneity in individual size and body condition. In chapter 1, we found that adult and juvenile timing of migration out of Crea Creek and their relationship with environmental variables differed. Adults migrated in mid-July and seemed to time migrations with decreasing runoff, with most exiting before the stream reached summer base flow level. Adult migration occurred later in the summer of 2013, a year with much higher flow than 2012, providing further support that adults key in primarily on flow patterns. Among juveniles, larger fish tended to migrate earlier, mimicking the pattern of adult migration corresponding to the same environmental cues. However, smaller juveniles remain in Crea Creek until temperatures approach freezing in late summer. The juvenile migration model was driven by this later peak, and identified minimum stream temperature and flow as important environmental influences on migration. In chapter 2, we further explored juvenile migration timing in relation to size and body condition, and found that among fish experiencing similar environmental conditions, fish that were larger and in better body condition migrated earlier. We explained these results in terms size and condition dependent costs and benefits of remaining in Crea Creek.

The results of this study add considerably to the understanding of the ecological importance of beaded streams, and will be useful to managers as development occurs on the ACP. Fish required passage into and out of Crea Creek during the entire open-water period, with peak periods of migration associated with break-up and freeze-up, indicating a need to provide adequate passage structures where roads intersect small stream channels. The spring upstream migration occurs during peak stream flow, and culverts of adequate size should be used in order to avoid velocity barriers that can occur during high flow (Flemming and Reynolds 1991). Fish also require passage out of small beaded streams in late summer, as fish move towards overwintering areas during a period of very low stream flow. Culverts can create low-water barriers if not installed properly, or are not well maintained, thus care should be taken to provide passage during the entire open-water period across the full range of flow conditions.

Arctic freshwater ecosystems are being influenced by climate change (AMAP 2011), and consequences may be more pronounced in areas where water supply originates primarily from melting snow and ice (Barnett et al. 2005). Predictions for future changes include earlier ice break-up, increased water temperatures, greater evaporative water loss, and delayed freeze-up (Reist et al. 2006; Prowse et al. 2011). How these changes will influence population level processes in beaded streams is difficult to predict, though we speculate that given the adaptive nature of Arctic Grayling migration within seasons and across years in response to variety of conditions, fish have the capacity to adjust timing of migrations in a progressively changing climate. Arctic Grayling are at the northern extent of their range in ACP watersheds, with native populations persisting as far south as Montana (Scott and Crossman 1973). As a species, Arctic Grayling can tolerate much warmer aquatic conditions than those present in North Slope populations, and may be able to adapt to future warmer climate scenarios (Hobbie et al. 1999). Perhaps the biggest threat in ACP watersheds is the loss of habitat access due to reduced stream flow. In tundra watersheds of the ACP, stream flow and associated habitat connectivity is determined by snowmelt and there often exists a negative water balance as rates of evaporation exceed that of summer precipitation (Bowling et al. 2003; Arp et al. 2012). Shallow habitats may become warmer, and may become disconnected from deeper overwintering areas earlier, thus reducing available time available to exploit these productive foraging areas. However, earlier access may mitigate this potential loss of access; perhaps the 3–4 month summer foraging period will simply shift towards an earlier time period.

Though the ecological impacts of climate change are difficult to predict, this study contributes to building a basis for predicting how Arctic Grayling and potentially other fishes will respond to a changing Arctic climate. Currently, beaded streams are used extensively by Arctic Grayling during the entire open-water period, and loss of access appears to be the greatest threat to ACP populations.

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## Appendices

### Appendix A. 2012 IACUC approval



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#### Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

May 15, 2012

To: Mark Wipfli, PhD  
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [309893-5] Seasonal movements of Arctic grayling in the Fish Creek watershed,  
National Petroleum Reserve-Alaska.

The IACUC reviewed and approved the Amendment/Modification referenced above by Designated Member Review.

Received:	May 15, 2012
Approval Date:	May 15, 2012
Initial Approval Date:	May 15, 2012
Expiration Date:	May 15, 2013

This action is included on the May 22, 2012 IACUC Agenda.

*The PI is responsible for acquiring and maintaining all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol, and could result in revocation of IACUC approval.*

*The PI is responsible for ensuring animal research personnel are aware of the reporting procedures on the following page.*



## Appendix B. 2013 IACUC approval



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### Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

April 19, 2013

To: Mark Wipfli, PhD  
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [309893-7] Seasonal movements of Arctic grayling in the Fish Creek watershed,  
National Petroleum Reserve-Alaska.

The IACUC reviewed and approved the Amendment/Modification to the Protocol referenced above by Designated Member Review.

Received:	April 15, 2013
Approval Date:	April 19, 2013
Initial Approval Date:	May 15, 2012
Expiration Date:	May 15, 2014

This action is included on the April 18, 2013 IACUC Agenda.

#### **PI responsibilities:**

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*