

TROPHIC PATHWAYS SUPPORTING ARCTIC GRAYLING IN A SMALL  
STREAM ON THE ARCTIC COASTAL PLAIN, ALASKA

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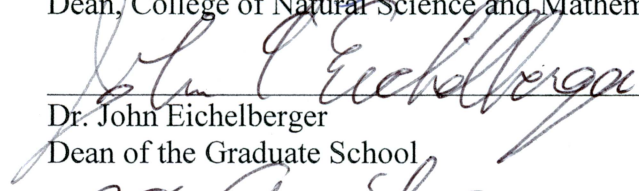
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TROPHIC PATHWAYS SUPPORTING ARCTIC GRAYLING IN A SMALL STREAM ON  
THE ARCTIC COASTAL PLAIN, ALASKA

A  
THESIS

Presented to the Faculty  
of the University of Alaska Fairbanks

For the degree of

MASTER OF SCIENCE

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## Abstract

Arctic Grayling (*Thymallus arcticus*) are widely distributed on the Arctic Coastal Plain (ACP) of Alaska, and are one of the few upper level consumers in streams, but the trophic pathways and food resources supporting these fish are unknown. Grayling migrate each summer into small beaded streams, which are common across the landscape on the ACP, and appear to be crucial foraging grounds for these and other fishes. I investigated prey resources supporting different size classes of grayling in a beaded stream, Crea Creek, where petroleum development is being planned. The specific objectives were to measure terrestrial prey subsidies entering the stream, quantify prey ingested by Arctic Grayling and Ninespine Stickleback (*Pungitius pungitius*), determine if riparian plant species affect the quantity of terrestrial invertebrates ingested by grayling, and determine if prey size and type ingested were a function of predator size. Results indicated that small grayling (< 15 cm fork length (FL)) consumed mostly aquatic invertebrates (caddisflies, midges, and blackflies) early in the summer, and increasing quantities of terrestrial invertebrates (wasps, beetles, and spiders) later in summer, while larger fish (> 15 cm FL) foraged most heavily on stickleback. Riparian plant species influenced the quantity of terrestrial invertebrates entering the stream, however these differences were not reflected in fish diets. This study showed that grayling can be both highly insectivorous and piscivorous, depending upon fish size class, and that both aquatic and terrestrial invertebrates, and especially stickleback, are the main prey of grayling. These results highlight the importance of beaded streams as summer foraging habitats for grayling. Understanding prey flow dynamics in these poorly studied aquatic habitats, prior to further petroleum development and simultaneous climate change, establishes essential baseline information to interpret if and how these freshwater ecosystems may respond to a changing Arctic environment.



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## Chapter 1. General Introduction

Petroleum development and associated infrastructure are rapidly expanding on the Arctic Coastal Plain (ACP) of Alaska (Walker et al. 1987; USDOJ 2013). In addition, the Arctic is experiencing some of the most rapid climate change in the world (Rouse et al. 1997; Nelson et al. 2002, Arctic Climate Impact Assessment 2004; Wrona et al. 2006; Solomon 2007). While the effects of these perturbations are difficult to predict, changes in hydrological regimes (Reist et al. 2006; Schindler and Smol 2006) and vegetation communities are expected (Chapin III et al. 1995; Reynolds and Tenhunen 1996; Jia et al. 2003; Hinzman et al. 2005; Tape et al. 2006; Euskirchen et al. 2009). These changes, in a heretofore relatively pristine environment, are likely to threaten fish habitats (Walker et al. 1987; USDOJ 2013) and ultimately impact freshwater fish populations (Ficke et al. 2007).

Arctic Grayling (*Thymallus arcticus*) are a common and widespread upper-level consumer in streams on the ACP (Moulton 1998, 2007, 2009). Despite the harsh climatic conditions and the abbreviated growing season in this environment, grayling experience rapid summer-time growth and maintain good body condition in these streams (Heim et al. 2014). To accomplish this, grayling forage opportunistically on a wide variety of seasonally and temporally available prey (Dill 1983; Northcote 1995; Stewart et al. 2007), including aquatic and terrestrial invertebrates, fish, and plankton (Bishop 1967; McPhail and Lindsey 1970; De Bruyn and McCart 1974; Stewart et al. 2007). ‘Beaded streams’, which are evenly spaced pools connected by narrow runs that form in ice-wedge networks, are a common type of stream on the ACP (Arp et al. 2012, 2015; Craig and Poulin 1975), and provide foraging and breeding grounds for grayling in summer. Despite their small size (Arp et al. 2015), some beaded streams are known to support as many as several thousand grayling during summer (Moulton 1998, 2007, 2009).

Selecting larger prey (e.g. large insects, fish, mammals) may enhance survival for grayling in regions with a short growing season (Lisi et al. 2014). In northern Canada and Europe, grayling are known to actually predate their own fry (Lindström 2010), as well as non-conspecific forage fish (Miller 1946; Jessop et al. 1993; Olson 2014), particularly Ninespine Stickleback (*Pungitius pungitius*) (De Bruyn and McCart 1974). Stickleback are abundant and widely distributed across the ACP (J. McFarland, personal observation 2010-12; Haynes et al. 2014). Since prey abundance can influence grayling forage patterns (Lisi et al. 2014), stickleback may be an important prey for grayling in these systems.

Terrestrial invertebrates may also be important prey of grayling in the ACP because grayling often forage in small streams (De Bruyn and McCart 1974) where riparian and lotic habitats are in close juxtaposition (Vannote et al. 1980). In fact, grayling have been documented to target terrestrial invertebrates by positioning themselves under overhanging riparian vegetation (Bishop 1967; Hatfield 1972a, b), where infaunal biomass is often greatest (Edwards and Huryn 1996; Nakano and Murakami 2001). In northern Canada, McPhail and Lindsey (1970) found that terrestrial invertebrates were the most important prey supporting grayling, often accounting for over half the biomass they ingested during the summer months. Even in large lakes, where relatively low terrestrial subsidies are logically expected due to the small lake margin to lake surface area ratio, studies have found that terrestrial invertebrates accounted for up to 30% of grayling prey biomass (Rawson 1950), and were by far the most common type of prey ingested (Miller 1946).

Trophic pathways supporting grayling in beaded streams on the ACP are poorly understood. My primary research goal was to quantify prey (terrestrial and aquatic invertebrates, and fish) consumed by grayling in Crea Creek, a beaded stream that is a tributary of the

Ublutouch River on the ACP (Fig. 2.1). My specific objectives were to (i) quantify terrestrial invertebrate in-fall into Crea Creek within prevailing terrestrial vegetation types, (ii) identify and quantify prey (invertebrates, fishes) ingested by Arctic Grayling and Ninespine Stickleback, (iii) determine if riparian plant species locally affected the quantity of terrestrial invertebrates ingested by grayling, and (iv) determine if prey type and size ingested was a function of predator (grayling) size.

This research provides some of the first insight into the foraging ecology of grayling and stickleback in a relatively pristine, beaded stream on the Arctic Coastal Plain. Although the Crea Creek watershed is currently undeveloped, construction of a permanent road over the stream and development of petroleum infrastructure (roads, drilling pads, pipeline, etc.) are anticipated to begin in winter of 2015 (USDOI 2013). Therefore, my research also provides baseline data for comparison of pre and post-development impacts on grayling and their prey in Crea Creek. Further, these data can also be used to predict the environmental effects of development on stream consumers and their prey elsewhere in the ACP.

## **2.1 Literature Cited**

- Arctic Climate Impact Assessment. 2004. Impacts of a warming Arctic-Arctic Climate Impact Assessment. pp. 144. ISBN 0521617782. Cambridge, UK: Cambridge University Press.
- Arp, C. D., Whitman, M. S., Jones, B. M., Kemnitz, R., Grosse, G., and Urban, F. E. 2012. Drainage network structure and hydrologic behavior of three lake-rich watersheds on the Arctic Coastal Plain, Alaska. *Arctic, Antarctic, and Alpine research* 44. 385-398.

- Arp, C., Whitman, M. S., Jones, B. M., Grosse, G., Gaglioti, B. V., and Heim, K. C. 2015. Distribution and biophysical processes of beaded streams in Arctic permafrost landscapes. *Biogeosciences* 12: 29-47.
- Bishop, F.G. 1967. The biology of the Arctic Grayling, (*Thymallus arcticus*), in Great Slave Lake. M.Sc. Thesis, Department of Zoology, University of Alberta, Edmonton, AB.
- Chapin III, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., and Laundre, J. A. 1995. Responses of Arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694-711.
- Craig, P. C., and Poulin, V. A. 1975. Movements and growth of Arctic Grayling (*Thymallus arcticus*) and juvenile Arctic Char (*Salvelinus alpinus*) in a small Arctic stream, Alaska. *Journal of the Fisheries Board of Canada* 32: 689-697.
- De Bruyn, M., and McCart, P. 1974. Life history of the grayling (*Thymallus arcticus*) in Beaufort Sea drainages in the Yukon Territory *Biometrics*. 2: 1-42.
- Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 398-408.
- Edwards, E.D. and Huryn, A.D. 1996. Effect of riparian land use on contributions of terrestrial invertebrates to streams. *Hydrobiologia* 337: 151-159.
- Euskirchen, E., McGuire, A., Chapin III, F., Yi, S. and Thompson, C. 2009. Changes in vegetation in northern Alaska under scenarios of climate change, 2003-2100: implications for climate feedbacks. *Ecological Applications* 19: 1022-1043.
- Ficke, A.D., Myrick, C.A., and Hansen, L.J. 2007. Potential impacts of global climate change on freshwater fisheries. *Reviews in Fish Biology and Fisheries* 17: 581-613.
- Hatfield, C.T., Stein, J.N., Falk, M.R., and Jessop, C.S. 1972a. Fish resources in the Mackenzie

- River Valley, Interim Report 1, Volume 1. Department of the Environment. Fisheries Service. Winnipeg, MB. 249.
- Haynes, T. B., Rosenberger, A. E., Lindberg, M. S., Whitman, M., and Schmutz, J. A. 2014. Patterns of lake occupancy by fish indicate different adaptations to life in a harsh Arctic environment. *Freshwater Biology* 59: 1884-1896.
- Hatfield, C.T., Stein, J.N., Falk, M.R., Jessop, C.S., and Shepherd, D.N. 1972b. Fish resources in the Mackenzie River Valley, Interim Report 1, Volume 2. Department of the Environment. Fisheries Service. Winnipeg, Manitoba. 289.
- Heim, K. C., Wipfli, M. S., Whitman, M. S., and Seitz, A. C. 2014. Body size and condition influence migration timing of juvenile Arctic grayling. *Ecology of Freshwater Fish* doi: 10.1111/eff.12199
- Hinzman, L.D., Bettez, N.D., Bolton, W.R., Chapin, F.S., Dyrurgerov, M.B., Fastie, C.L., Griffith, B., Hollister, R.D., Hope, A. and Huntington, H.P. 2005. Evidence and implications of recent climate change in northern Alaska and other Arctic regions. *Climatic Change* 72: 251-298.
- Jessop, E.F., Chang-Kue, K.T.J., and MacDonald, G. 1993. Fish resource data from Indin Lake, Northwest Territories. *Canadian Data Report of Fisheries and Aquatic Sciences* 907: 52.
- Jia, G.J., Epstein, H.E. and Walker, D.A. 2003. Greening of Arctic Alaska, 1981–2001. *Geophysical Research Letters* 30.
- Lindström, C.J. 2010. Influence of the habitat on the potential for cannibalism and population dynamics in stream-dwelling European Grayling (*Thymallus thymallus L.*). Thesis project, Swedish University of Agricultural Sciences.

- Lisi, P. J., Bentley, K. T., Armstrong, J. B., and Schindler, D. E. 2014. Episodic predation of mammals by stream fishes in a boreal river basin. *Ecology of Freshwater Fish* 23: 622-630.
- McPhail, J.D., and Lindsey, C.C. 1970. Freshwater fishes of northwestern Canada and Alaska. Fisheries Research Board Canadian Bulletin 173: 127.
- Miller, R.B. 1946. Notes on the Arctic Grayling (*Thymallus signifier*) Richardson, from Great Bear Lake. *Copeia* 227-236.
- Moulton, L. 1998. Lakes sampled for fish in and near the Colville River delta, Alaska 1979-1998. Prepared by MJM Research for ARCO Alaska, Inc.
- Moulton, L. 2007. Monitoring fish populations in the Ublutuoch River Drainage in Eastern NPR-A: 2004. Prepared by MJM Research for ConocoPhillips Alaska, Inc.
- Moulton, L. 2009. Fish populations in streams to be crossed by a proposed road to the GMT-1 well pad in Eastern NPR-A: 2009. Prepared by MJM Research for ConocoPhillips Alaska, Inc.
- Nakano, S. and Murakami, M. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America* 98: 166-170.
- Nelson, F., Anisimov, O. and Shiklomanov, N.I. 2002. Climate change and hazard zonation in the circum-Arctic permafrost regions. *Natural Hazards* 26: 203-225.
- Northcote, T. G. 1995. Comparative biology and management of Arctic and European Grayling (Salmonidae, *Thymallus*). *Reviews in fish biology and fisheries* 5: 141-194.
- Olson, K. 2014. Feeding ecology of lenok (*Brachymystax lenok*), Hovsgol Grayling (*Thymallus nigrescens*) and Baikal Grayling (*Thymallus baicalensis*) from the Eg-Uur Watershed, Mongolia (Doctoral dissertation, University of Minnesota).

- Rawson, D.S. 1950. The grayling (*Thymallus signifer*) in northern Saskatchewan. Canadian Fisheries Culturist. 6: 3-10.
- Reist, J.D., Wrona, F.J., Prowse, T.D., Power, M., Dempson, J.B., Beamish, R.J., King, J.R., Carmichael, T.J. and Sawatzky, C.D. 2006. General effects of climate change on Arctic fishes and fish populations. AMBIO: A Journal of the Human Environment 35: 370-380.
- Reynolds, J. and Tenhunen, J. 1996. Ecosystem response, resistance, resilience, and recovery in Arctic landscapes: Introduction. Landscape function and disturbance in Arctic tundra. Springer 3-18.
- Rouse, W.R., Douglas, M.S., Hecky, R.E., Hershey, A.E., Kling, G.W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B.J. and Roulet, N.T. 1997. Effects of climate change on the freshwaters of Arctic and Subarctic North America. Hydrological Processes 11: 873-902.
- Schindler, D.W. and Smol, J.P. 2006. Cumulative effects of climate warming and other human activities on freshwaters of Arctic and Subarctic North America. AMBIO: A Journal of the Human Environment 35: 160-168.
- Solomon, S. 2007. Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC: Cambridge University Press.
- Stewart, D.B., N.J. Mochnacz, J.D. Reist, T.J. Carmichael, and C.D. Sawatzky. 2007. Fish life history and habitat use in the Northwest Territories: Arctic Grayling (*Thymallus arcticus*). Canadian Manuscript Reports of Fish and Aquatic Science 2797.
- Tape, K., Sturm, M. and Racine, C. 2006. The evidence for shrub expansion in northern Alaska and the Pan Arctic. Global Change Biology 12: 686-702.

US Department of the Interior (USDOI), Bureau of Land Management. 2013. Final supplemental environmental impact statement for the Alpine Satellite Development Plan for the proposed Greater Moose's Tooth One development project. DOI-BLM-AK-0000-2013-0001-EIS.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. and Cushing, C.E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.

Walker, D., Webber, P., Binnian, E., Everett, K., Lederer, N., Nordstrand, E. and Walker, M. 1987. Cumulative impacts of oil fields on northern Alaskan landscapes: Moses King.

Wrona, F.J., Prowse, T.D., Reist, J.D., Hobbie, J.E., Lévesque, L.M. and Vincent, W.F. 2006. Climate change effects on aquatic biota, ecosystem structure and function. *AMBIO: A Journal of the Human Environment* 35: 359-369.



## Chapter 2. Trophic pathways supporting Arctic Grayling in a small stream on the Arctic Coastal Plain, Alaska<sup>1</sup>

### 2.1 Abstract

Beaded streams are prominent across the Arctic Coastal Plain (ACP) and are important foraging habitats for stream fishes, yet prey flow and food web dynamics supporting fish are poorly understood. Arctic Grayling (*Thymallus arcticus*) are a widely distributed top stream consumer on the ACP and many migrate into beaded streams to forage during the short 3-month open water season. I investigated energy pathways and primary prey resources supporting grayling in the beaded stream Crea Creek. Considering new petroleum development is being planned in the Crea Creek watershed and climate change is occurring relatively rapidly there, my study provides a basis to better understand how potential impacts may affect beaded stream food webs and the consumers (fishes) they support. I measured terrestrial invertebrate in-fall entering the stream from the most predominant riparian vegetation type-- willow (*Salix spp.*) and sedge (*Carex spp.* and *Eriophorum spp.*) in Crea Creek, a small stream representative of streams across much of the ACP landscape. I investigated the type of prey resources supporting grayling across a range of fish size classes, and measured how riparian plant species and fish size influenced foraging habits in stream reaches bordered by the aforementioned plants. The quantity of terrestrial invertebrates entering the stream was influenced by riparian plant species, however these differences were not reflected in fish diets. Foraging habits varied with fish size and season. Small grayling (< 15 cm fork length (FL)) consumed mostly small aquatic invertebrates (caddisflies, midges, and blackflies) early in the summer, and terrestrial invertebrates (wasps, beetles, and spiders) later in summer, while larger fish (> 15 cm FL) foraged most heavily on Ninespine Stickleback (*Pungitius pungitius*) throughout the summer season, showing that

grayling can be insectivorous and piscivorous, the extent of which depends on fish size and seasonal timing. These findings underscore the potential importance of small, often intermittent streams in Arctic ecosystems as key summer foraging habitats for fish. Understanding trophic pathways supporting stream fishes in these Arctic ecosystems will help interpret if and how petroleum development and climate change may affect energy flow and stream productivity, terrestrial-aquatic linkages, and fish ecology in Arctic ecosystems.

<sup>1</sup> McFarland, J. J., M. S. Wipfli, and M.S. Whitman. Trophic pathways supporting Arctic Grayling in a small stream on the Arctic Coastal Plain, Alaska. Prepared for submission to Ecology of Freshwater Fish.

## 2.2 Introduction

Stream salmonids exhibit broad foraging strategies, and feed on a wide range of prey sizes and prey types, influencing energy flow in stream ecosystems (Dill 1983). As with other predators, salmonids often increase fitness by selecting prey that minimize energy expenditure on capturing and handling, while maximizing energy intake (Charnov 1976; Gill 2003).

Salmonids commonly prey upon a wide range of seasonally and temporally available food resources derived from multiple sources (Wipfli and Baxter 2010). While aquatic and terrestrial invertebrates often account for the majority of their food base (Stewart et al. 2007), salmonids will also opportunistically consume larger prey, such as fish (De Bruyn and McCart 1974; Jessop et al. 1993; Stewart et al. 2007). However, in many stream systems, especially in the Arctic, little is known about prey dynamics within aquatic systems and across the stream-riparian interface.

Terrestrial invertebrates are typically an important prey subsidy for salmonids in many freshwater ecosystems (Wipfli 1997; Kawaguchi and Nakano 2001; Eberle and Stanford 2010), and can be their preferred prey (Hubert and Rhodes 1989; Young et al. 1997). With salmonids in both Alaska and Japan, terrestrial subsidies comprised up to nearly 90% of energy intake during the summer (Wipfli 1997; Allan et al. 2003; Baxter et al. 2005), and as much as 50% of their annual diet and energy budget (Kawaguchi and Nakano 2001; Nakano and Murakami 2001). Much of the terrestrial invertebrate subsidies are found on plants immediately adjacent to the stream, and are influenced by plant community composition (Edwards and Huryn 1996; Wipfli 1997). For example, studies in Southeast Alaska and Oregon showed more terrestrial invertebrates falling into streams with deciduous plant species (e.g. alder, *Alnus* spp.) than coniferous species (Allan et al. 2003; Romero et al. 2005). In Japan, Kawaguchi and Nakano

(2001) showed that the biomass of terrestrial invertebrates falling into a forested stream was up to two times greater than a grassland stream. Because riparian plant communities influence terrestrial invertebrate communities, it follows that changes in riparian vegetation will affect food resources for fishes, especially in small streams that are tightly coupled to their riparian habitats (Vannote et al. 1980).

In the ACP, small streams and riparian plant communities are likely very sensitive to resource development (Maki 1992; Schindler and Smol 2006). Substantial oil and gas exploration has occurred in the 23 million acre National Petroleum Reserve - Alaska (NPR-A) since 2000, with the first development wells and associated infrastructure approved for construction in 2011 (BLM 2015). Petroleum development can affect aquatic ecosystems in several ways. Infrastructure for petroleum development interrupts natural hydrological processes, changing surface and subsurface flow, which in turn affects lotic and lentic ecosystems by affecting surface water storage and runoff, and associated riparian vegetation communities (Walker et al. 1987). Further, road crossings over streams can impede fish passage (Gibson et al. 2005), affecting fish abundance and species richness (Nislow et al. 2011).

In addition to land use changes, climate change is as pronounced in the Arctic as any place on Earth (Nelson et al. 2002; Arctic Climate Impact Assessment 2004). While long-term effects are difficult to predict, substantial changes in thermal regimes, precipitation, runoff patterns, and permafrost are expected by 2100 (Rouse et al. 1997; Wrona et al. 2006; Solomon 2007), and are likely to greatly alter aquatic habitats and riparian plant communities. Climate change will likely influence stream flow regimes and reduce drainage network (surface water) connectivity (Reist et al. 2006; Schindler and Smol 2006), which could severely limit fish access to important summer feeding habitats and restrict critical fish migrations and dispersal (Heim et

al. 2014a, b). Additionally, documented changes in Arctic vegetation, especially widespread increases in shrubs, and greening (Chapin III et al. 1995; Reynolds and Tenhunen 1996; Jia et al. 2003; Hinzman et al. 2005; Tape et al. 2006; Euskirchen et al. 2009) will likely influence terrestrial invertebrate communities and terrestrial prey subsidies to stream fishes. If terrestrial prey subsidies are an important component of stream food webs in the Arctic, as documented in other places throughout the world (Edwards and Huryn 1996; Wipfli 1997; Kawaguchi and Nakano 2001; Eberle and Stanford 2010), trophic pathways are likely to be affected as a consequence of vegetation cover change (Meyer and Pulliam 1992).

Small, lower order streams are particularly susceptible to disturbance (Carpenter et al. 1992). Beaded streams (evenly-spaced pools connected by narrow channels that form in ice-wedge networks) are common across the ACP (Oswood et al. 1989; Arp et al. 2012, 2015) and provide important summer foraging habitat for several ACP fishes (Moulton 1998). These streams may be particularly important foraging areas for Arctic Grayling (*Thymallus arcticus*), a common and widespread aquatic predator within the eastern NPR-A ACP (Moulton 1998, 2007, 2009; Heim et al. 2014a, b). Despite potential petroleum development and climate shift changes to grayling habitat, few studies have focused on understanding their ecology and foraging habitats in beaded streams on the ACP.

I hypothesized that because terrestrial invertebrates are important prey to grayling in other places (McPhail and Lindsey 1970; Stewart et al. 2007), and to other salmonids around the globe (Wipfli 1997; Allan et al. 2003; Kawaguchi and Nakano 2001; Baxter et al. 2005; Eberle and Stanford 2010), they would also be important prey subsidies for grayling in beaded streams on the ACP. However, I also predicted that grayling, as opportunistic feeders, would ingest the entire suite of available prey, both terrestrial and aquatic-sourced. Considering that Ninespine

Stickleback (*Pungitius pungitius*) are highly abundant and widely distributed in these habitats (Haynes et al. 2014), these prey might also be an important food base for Arctic Grayling. The goals of this study were to describe prey flow dynamics, understand the extent to which terrestrial prey subsidies support grayling, assess whether terrestrial vegetation affects terrestrial prey subsidies, and examine trophic pathways (invertebrates and fish) important for supporting grayling in a small stream, Crea Creek, that has been a focal stream of study for other projects on the ACP. Specific objectives were to (i) quantify terrestrial invertebrate in-fall into Crea Creek within prevailing terrestrial vegetation types, (ii) identify and quantify prey (invertebrates, fishes) ingested by Arctic Grayling and Ninespine Stickleback, (iii) determine if riparian plant species locally affected the quantity of terrestrial invertebrates ingested by grayling, and (iv) determine if prey type and size ingested was a function of predator (grayling) size. I chose the relatively pristine and roadless Fish Creek watershed within the NPR-A of the ACP as my model system for this study. This and surrounding watersheds are specifically targeted for petroleum development in the next few years (USDOI 2013). Findings from this study will shed light on prey flow and trophic pathways that support grayling in Arctic ecosystems and will provide baseline information to help predict how petroleum development and climate change may affect these ecosystems in the coming years.

## **2.3 Methods**

### *2.3.1 Study Area*

This study was conducted within the Fish Creek River Drainage (70° 17 N, 151° 20 W), within the NPR-A portion of the ACP, approximately midway between Barrow and Prudhoe Bay, Alaska (Fig. 2.1). Annual precipitation is < 15 cm, mostly snow, and mean annual air

temperature is -12 C (Arp et al. 2012). The ACP is underlain by continuous permafrost (Oswood et al. 2006; Jorgenson and Brown 2005; Jorgenson et al. 2008), and the primary control on most hydrological processes is a function of snowmelt, flat topography, and thermokarst landforms (Arp et al. 2012). A mosaic of drained lake basins, thaw-lakes, wetlands, ponds, rivers, and creeks dominate the treeless, moist-acidic tundra landscape (Walker 2000; Arp et al. 2012).

This study took place in Crea Creek within the Fish Creek watershed during the summer (June–August) of 2011 and 2012. Crea Creek is a first order tributary of the much larger Ublutouch River, originating from headwater lakes, with a low gradient (0.003 m/m) channel composed of evenly spaced pools connected by narrow runs, and several connected lakes along its course. The watershed of Crea Creek is primarily polygenized tussock tundra and drained thermokarst lake basins. Discharge peaks in late spring (June), and is lowest prior to freeze up in early fall (October). In winter, the stream runs generally freeze to the bottom, while liquid water usually persists in pools greater than 1.5 m deep (Arp et al. 2015). Deeper water is considered potential overwintering habitat for most fishes there (Hobbie 1984) however, survival of overwintering fish more likely depends on the quality and depth of liquid water under the ice. Heim et al. (2014a) found no evidence of grayling overwintering in Crea Creek or its lakes. Nine species of fish have been documented to use Crea Creek, with grayling and stickleback being the most common (Moulton 2001, 2009). Moulton (2007) estimated up to several thousand grayling use the stream annually, likely as feeding grounds during the summer. In a grayling movement study, Heim et al. (2014a) found timing of fish migration into and out of Crea Creek was correlated with stream discharge, temperature, and body condition of individual fish.

Two main vegetation types are patchily distributed throughout Crea Creek's riparian habitats; willows (*Salix spp.*; typically < 1.0 m in height), and sedges (*Carex spp.* and *Eriophorum spp.*; typically < 0.5 m in height). Patches of the two vegetation types may be distinct in some areas, or occur in mixed stands of varying size (Table 2.1). From this point forth I will refer to these vegetation communities as willow and sedge, which were defined by the dominant taxa of each.

### 2.3.2 Terrestrial invertebrate inputs

Surface-pan traps (Wipfli 1997; Eberle and Stanford 2010) were used to measure the quantity and composition of terrestrial invertebrates and aerial forms of aquatic invertebrates falling into Crea Creek during June, July, and August of 2011. I selected two vegetation patches dominated by willow and two by sedge. Within each large patch (~ 100 m radius) I deployed four 0.1 m<sup>2</sup> black plastic pan traps (16 total), which were set for a 36-48 hour period each sampling bout. I did not sample the sedge site during June because the vegetation was submerged by unusually high water. To keep invertebrates from climbing or flying out of the pans, 2-3 drops of unscented dish soap were added to the traps, thus breaking the surface tension (Wipfli 1997). Traps were positioned immediately adjacent or below the vegetation type of interest.

In the field, samples were filtered into Whirl-pack® bags filled with 70% ethanol and sorted with a dissection microscope in the University of Alaska Fairbanks (UAF) laboratory. Individuals were identified to the lowest reliable taxonomic level (typically family), measured to the nearest mm, and enumerated. Aquatic insects were not included in the estimate.



### 2.3.3 *Prey ingestion by fishes*

I examined prey composition and mass ingested by grayling in Crea Creek to address diet components of objectives (ii), (iii), and (iv) by establishing ten study reaches, approximately 275 m long (excluding lakes), which encompassed the entire permanently connected length of the stream (Fig. 2.1). I collected up to 10 grayling [5 large (> 15 cm fork length (FL) and 5 small (< 15 cm FL)] per each of the 10 stream reaches, per sampling period in June, (18 total fish captured), July (132 total fish captured), and August (138 total fish captured) of 2011 and 2012.

Prior to sampling, block nets were placed in the stream at the beginning and end of each reach, to ensure fish being caught were indicative of the reach sampled. Fish were collected by backpack electrofishing and were held alive in buckets alongside the creek. Fish were anaesthetized using a clove oil solution (Anderson et al. 1997), weighed (g), and measured for fork length (mm). Nonlethal stomach-content samples were collected via gastric lavage (stomach-flushing) with a modified 10.0 mL syringe (Culp et al. 1988; Wasowicz and Valdez 1994).

In the first year of this study I found that Ninespine Stickleback were important prey for grayling in Crea Creek, and therefore I further examined prey resources supporting stickleback, to help understand the broader food web. To examine prey ingested by stickleback, I collected up to 10 stickleback, in each of the 10 stream reaches, in July (60 total fish) and August (50 total fish) of 2012. No samples were taken in June, due to high water. Stickleback were determined too small to effectively lavage, therefore lethal stomach-content samples were collected by dispatching fish and removing and inspecting stomachs. Prior to stomach removal, stickleback were weighed, and fork length measured.

Stomach contents from grayling and whole stomachs from stickleback were preserved in Whirl-pack® bags filled with 70% ethanol, and later transported to a UAF laboratory, sorted with a dissection microscope, measured to the nearest mm, and enumerated. Prey items were identified to the lowest taxonomic level possible, and invertebrates were categorized as either terrestrial or aquatic.

#### *2.3.4 Influence of riparian vegetation on terrestrial invertebrate consumption*

To examine the influence of riparian vegetation on terrestrial invertebrate consumption by grayling, I first measured the vegetation composition along the length of Crea Creek by estimating the relative cover of the two riparian plants (willow:sedge) through aerial photography. Low elevation aerial photographs were taken during mid-August when willow leaves were turning yellow and easily distinguished from green sedges. Adobe® Photoshop™ was then used to place equal sized grid cells over the photographs to visually estimate percent cover for each grid. Vegetation estimates were totaled and averaged per each of the 10 stream reaches, and presented as relative proportion (willow:sedge) of cover. I used a linear regression to examine the relationship between willow:sedge and the mass of terrestrial invertebrates ingested by fish. For my regressions, I used the willow:sedge proportion from each stream reach as the predictor variable of terrestrial invertebrate mass ingested by grayling within the corresponding reach.

#### *2.3.5 Sample processing and data analysis*

Taxa in fish diet samples were classified as terrestrial or aquatic according to McCafferty (1983), Triplehorn and Johnson (2005), Merritt et al. (2008), and Thorp and Covich (2009).

Aerial stages of aquatic insects were classified as aquatic prey. Dry mass estimates were used in the terrestrial input and diet components of this study. Family groupings were used in my analysis, and invertebrate biomass for each taxon was determined through published length-mass regressions (Rogers et al. 1977, Meyer 1989, Sample et al. 1993, Hodar 1996, Benke et al. 1999, Sabo et al. 2002). Stickleback dry mass was determined by generating a length-mass regression using the allometric formula:

$$W=aL^b$$

where  $W$  is the total dry body weight (g),  $L$  is the total length (cm), and  $a$  and  $b$  are the coefficients of the functional regression between  $W$  and  $L$  (Ricker 1973). I dried stickleback at 60°C until dry (72 hr), then measured mass to the nearest mg, length to the nearest mm, and calculated  $a = 0.00168$ , and  $b = 3.07463$ ,  $r^2 = 0.95$ ,  $p = < 0.01$ ,  $n = 299$ .

Data analyses were conducted using R.3.1.1 (R Development Core Team, 2014), and analyzed with a one-way ANOVA for comparisons between sampling periods and years of prey ingested by different sized grayling and stickleback.  $T$ -tests were used for comparisons over sampling periods and years of terrestrial invertebrate inputs, quantities of terrestrial invertebrates ingested per stream reach, and prey ingested by different sized grayling and stickleback. All statistical tests were two-tailed.  $\text{Log}_{10}(x+1)$  transformations for exact values were performed, if necessary, to standardize variances and improve normality. Non-transformed data are presented unless otherwise stated. For all tests, alpha was set at 0.05.

## 2.4 Results

### 2.4.1 Terrestrial invertebrate inputs

Of the 49 taxa collected in floating surface-pan traps, terrestrial taxa and adult forms of aquatic taxa comprised 52 and 42%, respectively. The remaining 6% taxa could not be reliably attributed to aquatic or terrestrial origin at the level of taxonomic resolution used here.

Invertebrate inputs averaged  $21.7 \pm 3.8 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$  across sites and sampling periods, with maximum inputs in July (Fig. 2.2). Invertebrate inputs from willows were greater than sedge when averaged across July and August sampling periods (willow =  $24.9 \pm 3.6 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ , sedge =  $8.2 \pm 2.5$ ,  $p = 0.02$ ) (Fig. 2.2). The proportion of terrestrial invertebrate mass compared to total invertebrate mass (terrestrial and aquatic) falling into the stream increased over the summer (June =  $27.8 \pm 1.6$ , July =  $38.2 \pm 1.1$ , August =  $41.1 \pm 1.4\%$ ). Estimated dry biomass of terrestrial inputs into Crea Creek averaged across all sites and sampling periods averaged  $8.0 \pm 2.1 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$  (excluding aerial forms of aquatic invertebrates).

### 2.4.2 Prey ingestion by fishes

I analyzed stomach contents from 288 grayling in Crea Creek during the summers of 2011 ( $n = 146$ ) and 2012 ( $n = 142$ ). Fish ranged from 5.3 - 43.3 cm in fork length, with a mean  $\pm$  SE of  $18.4 \pm 7.8$  cm. Grayling consumed prey from 18 orders and 63 families of invertebrates (28 terrestrial, 30 aquatic, and 5 unknown families), and two fish species (Appendix A). 99.8% of all terrestrial taxa found in grayling stomachs were also collected in pan traps.

Stickleback contributed the most mass to grayling diet and accounted for 88% of the total prey biomass consumed in both years, averaged across all fish size classes. Five prey taxa accounted for 99% of the biomass in fish diets [stickleback, 88%; caddisflies (Trichoptera), 4%;

beetles (Coleoptera), 3%; flies (Diptera), 3%; and wasps (Hymenoptera), 1%]. Prey proportions did not differ between years (Fig. 2.3a).

Flies were the most numerically abundant taxon consumed in both years, accounting for 70 and 61% of prey count in 2011 and 2012 (Fig. 2.3b). Flies comprised of 23 different orders, but primarily black flies (Simuliidae) and midges (Chironomidae) (Appendix A). The top five most numerically common taxa were also similar between summers [flies (67%), caddisflies (9%), beetles (8%), stickleback (6%), and wasps (4%)] (Fig. 2.3b).

I analyzed 110 Ninespine Stickleback stomach contents collected from Crea Creek during July and August of 2012. Stickleback fed almost exclusively on aquatic prey. By both mass and total count, the top four prey taxa accounted for 99% of all prey consumed by stickleback, and were zooplankton, flies, mayflies (Ephemeroptera), and caddisflies (Fig. 2.4). Zooplankton (mostly copepods and daphnia) comprised 89% (by count) and 47% (by mass) of all prey consumed (Fig. 2.4). A greater proportion of zooplankton (relative to other prey) were consumed at lake outlets.

#### *2.4.3 Influence of riparian vegetation on terrestrial invertebrate consumption*

The composition of riparian vegetation communities along Crea Creek varied among the 10 stream reaches (Table 2.1). In total, the reaches contained  $39.4 \pm 6.9$  % willows and  $60.6 \pm 6.9$  % sedge.

My linear regression did not show a clear relationship between the mass of terrestrial invertebrates ingested by grayling and willow:sedge proportion ( $r^2 = 0.02$ ,  $p = 0.73$ ). However, when I excluded stream reach 7 from the regression, (which had a relatively high density of large

stream pools; Table 2.1) the relationship became positive, though still not even marginally significant ( $r^2 = 0.06$ ,  $p = 0.52$ ) (Fig. 2.5).

I also compared quantities of terrestrial invertebrates ingested by fish between stream reach 8 (comprised of the greatest amount of willow; 75%), and reach 5 (comprised of the greatest amount of sedge; 93%) (Table 2.1). Fish in the willow-dominated reach consumed greater mass (mean mg/fish  $\pm$  SE: willow =  $5.9 \pm 1.5$  mg vs. sedge =  $3.5 \pm 0.8$  mg) and count (mean count/fish  $\pm$  SE: willow =  $5.7 \pm 1.8$  vs. sedge =  $5.2 \pm 1.2$ ) of terrestrial invertebrates than fish within the sedge reach. However, quantities of terrestrial invertebrates consumed by fish varied considerably between stream reaches of intermediate willow:sedge proportion.

#### 2.4.4 Prey ingestion and fish size

Different sized grayling ingested considerably different size classes and categories of prey. Larger fish ate larger prey (Fig. 2.6), and small grayling ( $n = 121$ ) proportionally consumed more terrestrial invertebrates ( $p < 0.01$ ), and fewer stickleback ( $p = 0.01$ ), than large grayling ( $n = 167$ ) when averaged across sampling periods and years (Fig. 2.7a and b).

Throughout the summer, the proportion of aquatic invertebrates ingested by small fish decreased 67% (June =  $94.2 \pm 19.5$ , July =  $72.0 \pm 21.3$ , August =  $27.1 \pm 7.2\%$ ), and proportion of terrestrial invertebrates increased 22% (June =  $5.7 \pm 2.0$ , July =  $19.3 \pm 5.5$ , August =  $27.4 \pm 3.4\%$ ) (Fig. 2.7a and b). Prey ingested by large fish were dominated by stickleback throughout the summer (Fig. 2.7a and b). Large grayling consumed 15 times more individual invertebrates than numbers of stickleback (mean count/fish: invertebrates =  $36.5 \pm 2.9$ , stickleback =  $2.5 \pm 0.3$ ), yet stickleback accounted for eight times more mass than did invertebrates (mean mg/fish: invertebrates =  $24.1 \pm 5.2$  mg, stickleback =  $189.7 \pm 45.1$  mg) (Fig. 2.8).

## 2.5 Discussion

Beaded streams within the ACP are important summer foraging habitats for Arctic Grayling (Heim et al. 2014a, b) (Fig. 2.9). I found that grayling in these small headwater habitats sequestered the bulk of their energy through piscivory pathways, via stickleback. Terrestrial invertebrates were ingested only to a limited degree by small fish, while aquatic invertebrates were the most important invertebrate prey for both large and small fish. Furthermore, I found that fish size class had considerable influence on prey type and size consumed - small fish ingested mostly small sized prey (e.g. terrestrial/aquatic invertebrates), whereas large fish ingested considerably larger sized prey (e.g. stickleback).

Throughout the summer large grayling consumed primarily stickleback. In other systems, grayling are known to be piscivorous (Miller 1946; Jessop et al. 1993; Lindström 2010), and prey upon stickleback (De Bruyn and McCart 1974) however, these observations are generally considered to be isolated and opportunistic events (De Bruyn and McCart 1974; Olson 2014). In this study system I found that large fish fed consistently, and often exclusively on stickleback. To my knowledge, these results provide some of the first evidence documenting this extent of piscivory. Stickleback were heavily predated all months and summers sampled, accounting for nearly 90% of total biomass consumed by large fish and 17% of the biomass consumed by small fish. These data indicate a size threshold for piscivory, where gap-limited (fish generally < 15 cm FL) or less dominant individuals were generally unable to exploit the resource, commonly seen in fishes (O'Brien 1979; Mittelbach 1981; Abbott et al. 1985)

Given that prey abundance can be indicative of grayling forage patterns (Lisi et al. 2014), and through field observations (J. McFarland, personal observation), I believe that the high degree of piscivory in Crea Creek is a function of stickleback abundance. Haynes et al. (2014)

found that stickleback were the most widespread and ubiquitous fish species in lakes on the ACP. I regularly caught very high numbers of stickleback in sampling nets across sampling periods and years. In the lakes of Crea Creek, I captured up to 3,000 stickleback in fyke nets set overnight, and within the stream over 1,000 stickleback were captured in individual minnow traps set for 4-5 hrs (J. McFarland, personal observations). Further, stickleback abundance in Crea Creek increased over the summer. Stickleback likely overwinter in the deep lakes within the system (Fig. 2.1), and often spawn multiple times early in the summer (Cameron et al. 1973; Heins 2003). I speculate that as stickleback abundance increases and young-of-the-year mature in lakes, so do number of fish entering the stream. Consistent with this, I observed stickleback moving exclusively downstream in groups (up to ~50). These movement patterns illustrate the ecological importance of habitat connectivity amongst lakes and streams on the ACP, for allowing dispersal, colonization, and feeding.

Piscivorous grayling experience larger energetic gains than insectivorous grayling. Mean mass of diet contents in piscivorous fish was 31 times greater (fish lengths were standardized to remove size bias) than non-piscivorous fish, while at the same time having 50% fewer numbers of individual prey than that of insectivorous fish. Moreover, stickleback are higher in energy content than invertebrates (Hanson et al. 1985, Brey et al. 1988, Kidd et al. 1998, Sato et al. 2011). Substantial energetic gains resulting from piscivorous feeding may explain why Heim et al. (2014a, b) found grayling in Crea Creek to experience rapid growth and mass accumulation over the short summer. Heim et al. (2014a) also found that large fish migrated out of the stream earlier in the summer than small fish. I suggest that, while large piscivorous fish are able to sequester sufficient energy early in the season, small fish remain in the stream longer to obtain adequate energy reserves prior to overwintering (Fig. 2.8). Given that piscivorous fish consumed



higher quality prey than insectivorous fish, while at the same time potentially expending less energy to capture fewer prey, stickleback may be a critical prey resource contributing to the annual energy budget - and ultimately grayling abundance and productivity.

Grayling in Crea Creek consumed terrestrial and aquatic sourced prey throughout the summer, with proportions of each inversely changing as the season progressed. From June to August the proportion of terrestrial prey increased by 20%, while the proportion of aquatic prey decreased by nearly 30%. Dependence on terrestrial sourced prey later in the season may be attributed to selective foraging and seasonally changing prey abundance and availability. I found that terrestrial invertebrate individual mean size (collected via pan traps) was greater than that of aquatic invertebrates (collected from drift nets) in Crea Creek, when averaged across sampling periods (terrestrial =  $1.1 \pm 0.2$  mg, aquatic =  $0.7 \pm 0.2$  mg). Salmonids often preferentially select large prey (Edwards and Huryn 1996). For example, Nakano et al. (1999) concluded that differences in prey size among prey categories was the primary factor influencing selective foraging by rainbow trout on terrestrial invertebrates. In addition to prey size selection, aquatic insect phenology (adult emergence over the summer) will temporarily reduce abundance and availability of many aquatic insects, while terrestrial invertebrate phenology will generally increase the abundance and availability over summer (McCafferty 1983; Merritt et al. 2008; Thorp and Covich 2009). My data were consistent with these findings, as the proportion of aquatic and terrestrial invertebrate prey in the diets of small grayling showed a clear, inverse relationship over the summer.

Terrestrial invertebrate prey ingested by grayling were nearly identical to the terrestrial invertebrate fauna captured in pan traps associated with riparian plants along Crea Creek, illustrating a linkage between prey consumption and prey contributed by riparian plants. The

quantity of terrestrial invertebrate prey falling into the stream was greater at willow sites than sedge sites, most likely because willows are generally denser, taller, and overhang the stream surface more, and therefore support a greater abundance of terrestrial invertebrates. However, the mass of terrestrial invertebrates ingested by fish was not reflected in these differences, perhaps due to low sample size. Other studies have shown that streamside vegetation can influence terrestrial prey subsidies entering streams and ingested by fish (Wipfli 1997; Kawaguchi and Nakano 2001; Nakano and Murakami 2001). Studies in both New Zealand and Japan concluded that vegetation composition and the amount of vegetation overhanging the stream explained both greater terrestrial invertebrate inputs in streams and ingested by fish between forested versus grassland stream reaches (Edwards and Huryn 1996; Kawaguchi and Nakano 2001). Evidence from these studies and ours supports the hypothesis that riparian vegetation type influences the amount of terrestrial prey entering the stream, and may likely be a factor driving terrestrial prey subsidies for fishes in small streams on the ACP.

My findings highlight the key prey resources and trophic pathways supporting grayling in a representative stream on the ACP, illustrating that aquatic and terrestrial invertebrates are important for small grayling, and that large prey, primarily stickleback, are a key food base for large grayling. Given the high density of small streams similar to Crea Creek on the ACP and the expansion of petroleum development there, it appears crucial to maintain surface water connectivity among lentic and lotic habitats during development to maintain free movement in drainage networks by aquatic predators and their prey. Road crossings over streams must allow for adequate summer-long fish passage into these important foraging habitats. Maintaining terrestrial-aquatic linkages, and overall surface water connectivity is critical for sustaining food

resources supporting stream fishes and their productivity, and should be a priority for freshwater ecosystem and fish conservation.

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## **2.7 Literature Cited**

- Abbott, J. C., Dunbrack, R. L., and Orr, C. D. 1985. The interaction of size and experience in dominance relationships of juvenile Steelhead Trout (*Salmo gairdneri*). Behaviour 241-253.
- Allan, J. D., Wipfli, M. S., Caouette, J. P., Prussian, A., and Rodgers, J. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences 60: 309-320.
- Anderson, W.G., McKinley, R.S. and Colavecchia, M. 1997. The use of clove oil as an anesthetic for Rainbow Trout and its effects on swimming performance. North American Journal of Fisheries Management 17: 301-307.

- Arctic Climate Impact Assessment. 2004. Impacts of a warming Arctic-Arctic Climate Impact Assessment. pp. 144. ISBN 0521617782. Cambridge, UK: Cambridge University Press.
- Arp, C. D., Whitman, M. S., Jones, B. M., Kemnitz, R., Grosse, G., and Urban, F. E. 2012. Drainage network structure and hydrologic behavior of three lake-rich watersheds on the Arctic Coastal Plain, Alaska. *Arctic, Antarctic, and Alpine research* 44. 385-398.
- Arp, C., Whitman, M. S., Jones, B. M., Grosse, G., Gaglioti, B. V., and Heim, K. C. 2015. Distribution and biophysical processes of beaded streams in Arctic permafrost landscapes. *Biogeosciences* 12: 29-47.
- Baxter, C. V., Fausch, K. D., and Carl Saunders, W. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50: 201-220.
- Benke, A.C., Huryn, A.D., Smock, L.A. and Wallace, J.B. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 308-343.
- Brey, T., Rumohr, H. and Ankar, S. 1988. Energy content of macrobenthic invertebrates: general conversion factors from weight to energy. *Journal of Experimental Marine Biology and Ecology* 117: 271-278.
- Bureau of Land Management (BLM). 2015. Supplemental Environmental Impact Statement for the Alpine Satellite Development Plan for the proposed Greater Mooses Tooth One Development project. Record of Decision. U.S. Department of the Interior, Bureau of Land Management, Anchorage, Alaska.
- Cameron, J. N., Kostoris, J., and Penhale, P. A. 1973. Preliminary energy budget of the Ninespine Stickleback (*Pungitius pungitius*) in an Arctic lake. *Journal of the Fisheries Board of Canada* 30. 1179-1189.

- Carpenter, S. R., Fisher, S. G., Grimm, N. B., and Kitchell, J. F. 1992. Global change and freshwater ecosystems. *Annual Review of Ecology and Systematics* 23: 119-139.
- Chapin III, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., and Laundre, J. A. 1995. Responses of Arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694-711.
- Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. *Theoretical population biology* 9: 129-136.
- Culp, J. M., I. Boyd, and N. E. Glozier. 1988. An improved method for obtaining gut contents from small, live fishes by anal and stomach flushing. *Copeia* 1988: 1079-1082.
- De Bruyn, M., and McCart, P. 1974. Life history of the grayling (*Thymallus arcticus*) in Beaufort Sea drainages in the Yukon Territory. *Biometrics* 2: 1-42.
- Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 398-408.
- Eberle, L.C. and Stanford, J.A. 2010. Importance and seasonal availability of terrestrial invertebrates as prey for juvenile salmonids in floodplain spring brooks of the Kol River (Kamchatka, Russian Federation). *River research and applications* 26: 682-694.
- Edwards, E.D. and Hury, A.D. 1996. Effect of riparian land use on contributions of terrestrial invertebrates to streams. *Hydrobiologia* 337: 151-159.
- Euskirchen, E., McGuire, A., Chapin III, F., Yi, S. and Thompson, C. 2009. Changes in vegetation in northern Alaska under scenarios of climate change, 2003-2100: implications for climate feedbacks. *Ecological Applications* 19: 1022-1043.
- Gibson, R. J., Haedrich, R. L., and Wernerheim, C. M. 2005. Loss of fish habitat as a consequence of inappropriately constructed stream crossings. *Fisheries* 30: 10-17.

- Gill, A. 2003. The dynamics of prey choice in fish: the importance of prey size and satiation. *Journal of Fish Biology* 63: 105-116.
- Hanson, B.J., Cummins, K.W., Cargill, A.S. and Lowry, R.R. 1985. Lipid content, fatty acid composition, and the effect of diet on fats of aquatic insects. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry* 80: 257-276.
- Haynes, T. B., Rosenberger, A. E., Lindberg, M. S., Whitman, M., and Schmutz, J. A. 2014. Patterns of lake occupancy by fish indicate different adaptations to life in a harsh Arctic environment. *Freshwater Biology* 59: 1884-1896.
- Heim, K. C., Wipfli, M. S., Whitman, M. S., and Seitz, A. C. 2014a. Body size and condition influence migration timing of juvenile Arctic grayling. *Ecology of Freshwater Fish* doi: 10.1111/eff.12199
- Heim, K.C., Wipfli, M.S., Whitman, M.S., Arp, C.D., Adams, J. and Falke, J. 2014b. Environmental correlates of Arctic grayling seasonal movement on the Arctic Coastal Plain, Alaska. In review.
- Heins, D. C., Johnson, J. M., and Baker, J. A. 2003. Reproductive ecology of the ninespined stickleback from south central Alaska. *Journal of fish biology* 63: 1131-1143.
- Hinzman, L.D., Bettez, N.D., Bolton, W.R., Chapin, F.S., Dyurgerov, M.B., Fastie, C.L., Griffith, B., Hollister, R.D., Hope, A. and Huntington, H.P. 2005. Evidence and implications of recent climate change in northern Alaska and other Arctic regions. *Climatic Change* 72: 251-298.
- Hobbie, J.E. 1984. Ecology of tundra ponds of the Arctic Coastal Plain: a community profile. Marine Biological Lab., Woods Hole, MA (USA). Ecosystems Center.

- Hodar, J. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta oecologica* 17: 421-433.
- Hubert, W.A. and Rhodes, H.A. 1989. Food selection by brook trout in a subalpine stream. *Hydrobiologia* 178: 225-231.
- Jessop, E.F., Chang-Kue, K.T.J., and MacDonald, G. 1993. Fish resource data from Indin Lake, Northwest Territories. *Canadian Data Report of Fisheries and Aquatic Sciences* 907: 52.
- Jia, G.J., Epstein, H.E. and Walker, D.A. 2003. Greening of Arctic Alaska, 1981–2001. *Geophysical Research Letters* 30.
- Jorgenson, M. and Brown, J. 2005. Classification of the Alaskan Beaufort Sea Coast and estimation of carbon and sediment inputs from coastal erosion. *Geo-Marine Letters* 25: 69-80.
- Jorgenson, M.T., Yoshikawa, K., Kanevskiy, M., Shur, Y., Romanovsky, V., Marchenko, S., Grosse, G., Brown, J. and Jones, B. 2008. Permafrost characteristics of Alaska: Institute of Northern Engineering, University of Alaska Fairbanks.
- Kawaguchi, Y. and Nakano, S. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. *Freshwater Biology* 46: 303-316.
- Kidd, K., Hesslein, R., Ross, B., Koczanski, K., Stephens, G. and Muir, D. 1998. Bioaccumulation of organochlorines through a remote freshwater food web in the Canadian Arctic. *Environmental pollution* 102: 91-103.
- Lindström, C.J. 2010. Influence of the habitat on the potential for cannibalism and population dynamics in stream-dwelling European Grayling (*Thymallus thymallus L.*). Thesis project, Swedish University of Agricultural Sciences.

- Lisi, P. J., Bentley, K. T., Armstrong, J. B., and Schindler, D. E. 2014. Episodic predation of mammals by stream fishes in a boreal river basin. *Ecology of Freshwater Fish* 23: 622-630.
- Maki, A.W. 1992. Of measured risks: the environmental impacts of the Prudhoe Bay, Alaska, oil field. *Environmental Toxicology and Chemistry* 11: 1691-1707.
- McCafferty, W.P. 1983. *Aquatic Entomology: the fishermen's and ecologists' illustrated guide to insects and their relatives*: Jones and Bartlett Learning.
- McPhail, J.D., and Lindsey, C.C. 1970. Freshwater fishes of northwestern Canada and Alaska. *Fisheries Research Board Canadian Bulletin* 173: 127.
- Merritt, R., Cummins, K. and Berg, M. 2008. *An Introduction to the aquatic insects of North America*. 4th (Edition) Kendall Hunt Publishing. Dubuque, Iowa, US.A.
- Meyer, E. 1989. The relationship between body length parameters and dry mass in running water invertebrates. *Archiv für Hydrobiologie* 117: 191-203.
- Meyer, J.L. and Pulliam, W.M. 1992. Modification of terrestrial—aquatic interactions by a changing climate. *Global Climate Change and Freshwater Ecosystems*. Springer 177-191.
- Miller, R.B. 1946. Notes on the Arctic Grayling *Thymallus signifier* Richardson, from Great Bear Lake. *Copeia* 227-236.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62: 1370-1386.
- Moulton, L. 1998. Lakes sampled for fish in and near the Colville River delta, Alaska 1979-1998. Prepared by MJM Research for ARCO Alaska, Inc.
- Moulton, L. 2001. Fish utilization of lakes in Eastern NPR-A: 1999-2001. Prepared by MJM Research for ConocoPhillips Alaska, Inc.

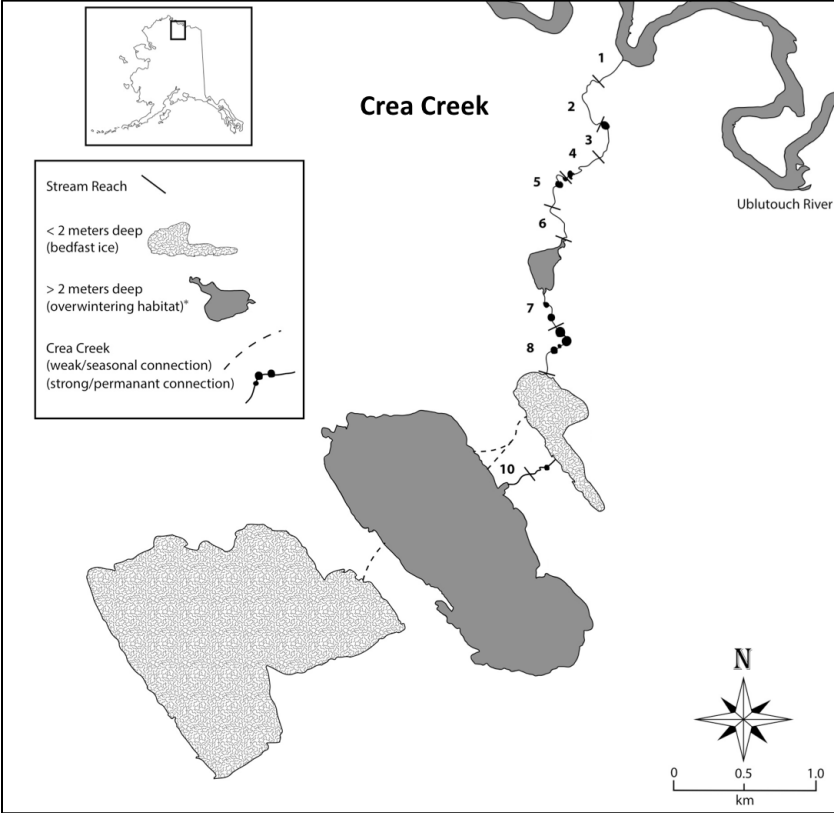


- Moulton, L. 2007. Monitoring fish populations in the Ublutuoeh River Drainage in Eastern NPR-A: 2004. Prepared by MJM Research for ConocoPhillips Alaska, Inc.
- Moulton, L. 2009. Fish populations in streams to be crossed by a proposed road to the GMT-1 well pad in Eastern NPR-A: 2009. Prepared by MJM Research for ConocoPhillips Alaska, Inc.
- Nakano, S. and Murakami, M. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America* 98: 166-170.
- Nakano, S., Kawaguchi, Y., Taniguchi, Y., Miyasaka, H., Shibata, Y., Urabe, H., and Kuhara, N. 1999. Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in northern Japan. *Ecological Research* 14: 351-360.
- Nelson, F., Anisimov, O. and Shiklomanov, N.I. 2002. Climate change and hazard zonation in the circum-Arctic permafrost regions. *Natural Hazards* 26: 203-225.
- Nislow, K.H., Hudy, M., Letcher, B.H. and Smith, E.P. 2011. Variation in local abundance and species richness of stream fishes in relation to dispersal barriers: implications for management and conservation. *Freshwater Biology* 56: 2135-2144.
- O'Brien, W. J. 1979. The predator-prey interaction of planktivorous fish and zooplankton: recent research with planktivorous fish and their zooplankton prey shows the evolutionary thrust and parry of the predator-prey relationship. *American Scientist* 572-581.
- Olson, K. 2014. Feeding ecology of Lenok (*Brachymystax lenok*), Hovsgol Grayling (*Thymallus nigrescens*) and Baikal Grayling (*Thymallus baicalensis*) from the Eg-Uur Watershed, Mongolia (Doctoral dissertation, University of Minnesota).
- Oswood, M.W., Everett, K. and Schell, D.M. 1989. Some physical and chemical characteristics of an arctic beaded stream. *Ecography* 12: 290-295.

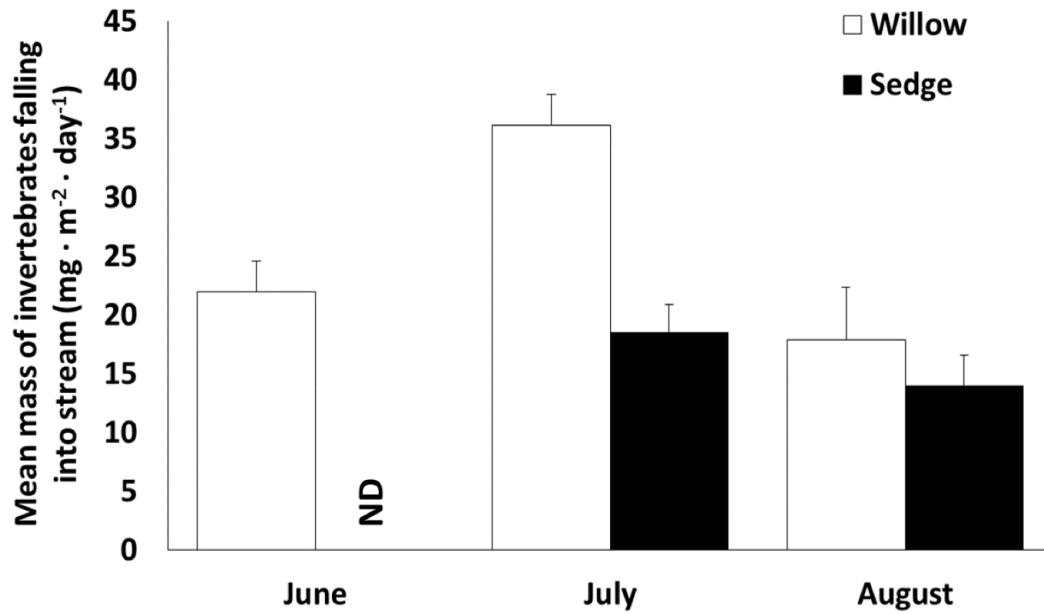
- Oswood, M.W., Irons, J. and Milner, A.M. 2006. River and stream ecosystems of Alaska. River and stream ecosystems of the world. University of California Press, Menlo Park, CA: 9-32.
- R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for statistical Computing, Vienna.
- Reist, J.D., Wrona, F.J., Prowse, T.D., Power, M., Dempson, J.B., Beamish, R.J., King, J.R., Carmichael, T.J. and Sawatzky, C.D. 2006. General effects of climate change on Arctic fishes and fish populations. *AMBIO: A Journal of the Human Environment* 35: 370-380.
- Reynolds, J. and Tenhunen, J. 1996. Ecosystem response, resistance, resilience, and recovery in Arctic landscapes: Introduction. *Landscape function and disturbance in arctic tundra*. Springer 3-18.
- Ricker, W. E. 1973. Linear regressions in fishery research. *Journal of the fisheries board of Canada* 30 409-434.
- Rogers, L., Buschbom, R. and Watson, C. 1977. Length-weight relationships of shrub-steppe invertebrates. *Annals of the Entomological Society of America* 70: 51-53.
- Romero, N., Gresswell, R.E. and Li, J.L. 2005. Changing patterns in coastal Cutthroat Trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1797-1807.
- Rouse, W.R., Douglas, M.S., Hecky, R.E., Hershey, A.E., Kling, G.W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B.J. and Roulet, N.T. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. *Hydrological Processes* 11: 873-902.
- Sabo, J.L., Bastow, J.L. and Power, M.E. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society* 21: 336-343.

- Sample, B.E., Cooper, R.J., Greer, R.D. and Whitmore, R.C. 1993. Estimation of insect biomass by length and width. *American Midland Naturalist*: 234-240.
- Sato, T., Watanabe, K., Kanaiwa, M., Niizuma, Y., Harada, Y. and Lafferty, K.D. 2011. Nematomorph parasites drive energy flow through a riparian ecosystem *Ecology* 92: 201-207.
- Schindler, D.W. and Smol, J.P. 2006. Cumulative effects of climate warming and other human activities on freshwaters of Arctic and Subarctic North America. *AMBIO: A Journal of the Human Environment* 35: 160-168.
- Solomon, S. 2007. *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC*: Cambridge University Press.
- Stewart, D.B., N.J. Mochnacz, J.D. Reist, T.J. Carmichael, and C.D. Sawatzky. 2007. Fish life history and habitat use in the Northwest Territories: Arctic Grayling (*Thymallus arcticus*). *Canadian Manuscript Reports of Fish and Aquatic Science* 2797.
- Tape, K., Sturm, M. and Racine, C. 2006. The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology* 12: 686-702.
- Thorp, J.H. and Covich, A.P. 2009. *Ecology and classification of North American freshwater invertebrates*: Academic Press.
- Triplehorn, C.A. and Johnson, N.F. 2005. *Borror and DeLong's introduction to the study of insects*.
- US Department of the Interior (USDOI), Bureau of Land Management. 2013. Final supplemental environmental impact statement for the Alpine Satellite Development Plan for the Proposed Greater Moose's Tooth One Development Project. DOI-BLM-AK-0000-2013-0001-EIS.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. and Cushing, C.E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.

- Walker, D., Webber, P., Binnian, E., Everett, K., Lederer, N., Nordstrand, E. and Walker, M. 1987. Cumulative impacts of oil fields on northern Alaskan landscapes: Moses King.
- Walker, D. A. 2000. Hierarchical subdivision of Arctic tundra based on vegetation response to climate, parent material and topography. *Global change biology* 6: 19-34.
- Wasowicz, A., and R. A. Valdez. 1994. A nonlethal technique to recover gut contents of roundtail chub. *North American Journal of Fisheries Management* 14: 656-658.
- Wipfli, M.S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 1259-1269.
- Wipfli, M.S. and Baxter, C.V. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. *Fisheries* 35: 373-387.
- Wrona, F.J., Prowse, T.D., Reist, J.D., Hobbie, J.E., Lévesque, L.M. and Vincent, W.F. 2006. Climate change effects on aquatic biota, ecosystem structure and function. *AMBIO: A Journal of the Human Environment* 35: 359-369.
- Young, M.K., Rader, R.B. and Belish, T.A. 1997. Influence of macroinvertebrate drift and light on the activity and movement of Colorado River Cutthroat Trout. *Transactions of the American Fisheries Society* 126: 428-437.

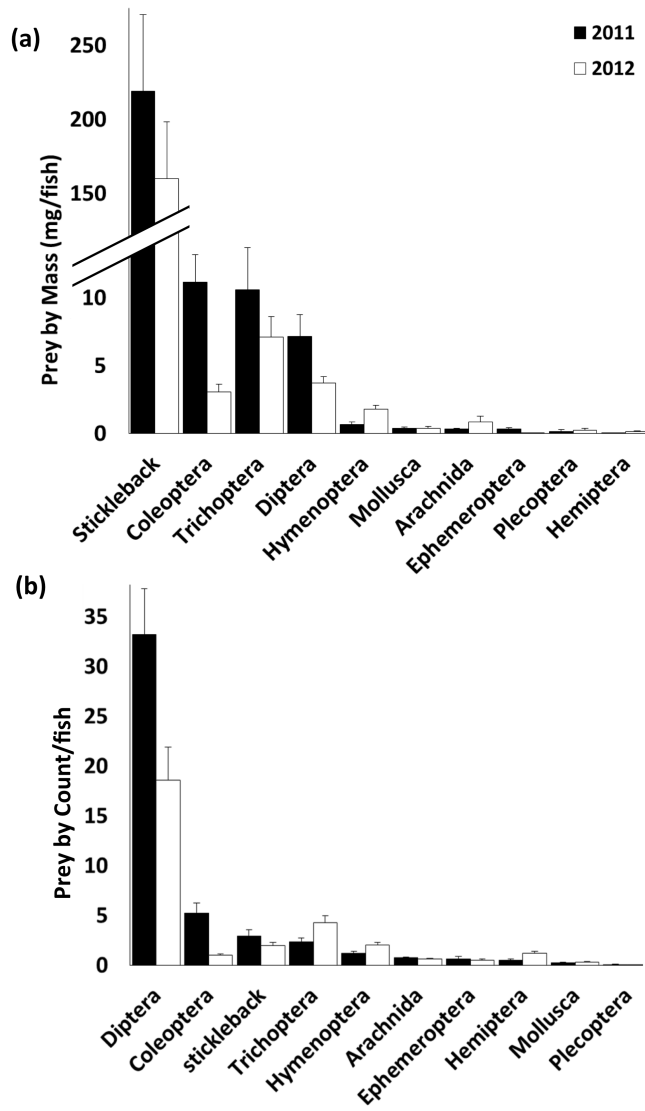


**Figure 2.1.** Study area showing location of ten stream reaches for study along Crea Creek.

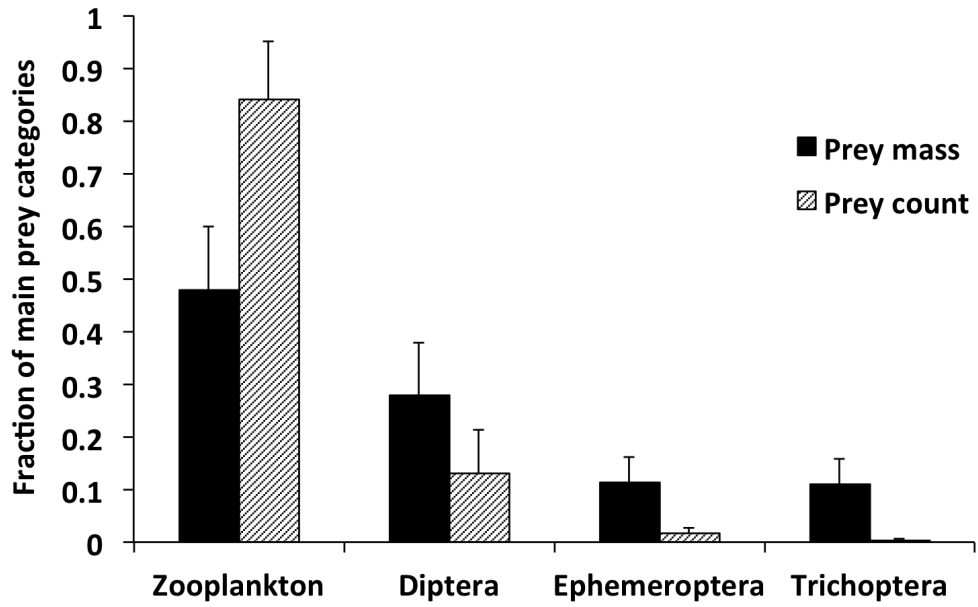


**Figure 2.2.** Mean mass of invertebrates captured in pan traps during the summer of 2011 ( $n = 2$  per site and date). ND = No data because sedge sites were submerged by high water in June.

Bars represent one standard error of the mean.

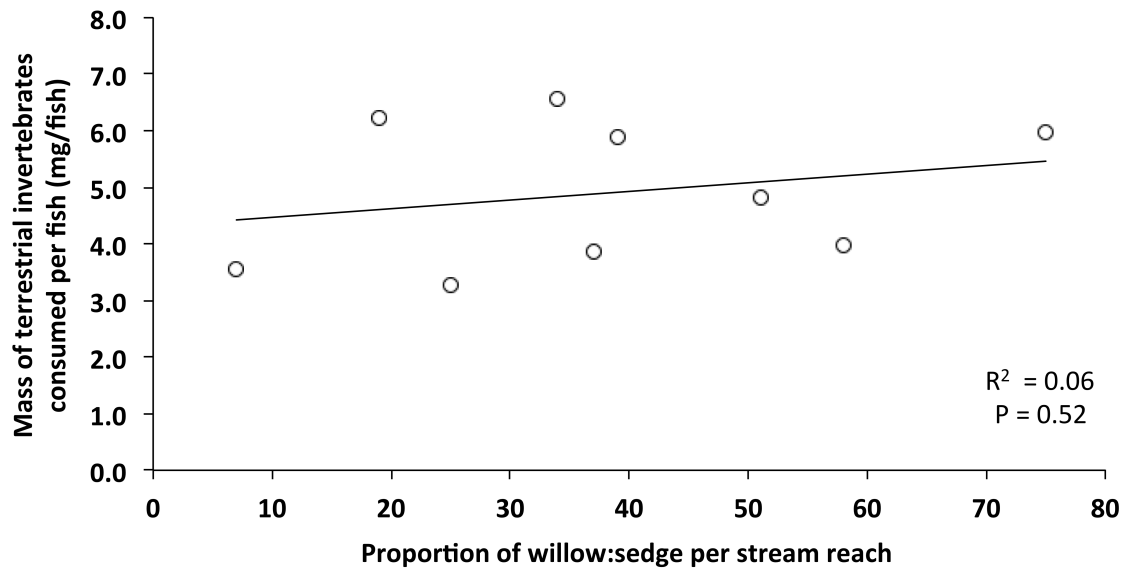


**Figure 2.3.** Mean prey (a) mass and (b) abundance ingested by Arctic Grayling in Crea Creek during 2011 and 2012. Bars represent one standard error of the mean.



**Figure 2.4.** Top four prey taxa accounting for 99% of prey mass and count ingested by Ninespine Stickleback in Crea Creek during 2012. Bars represent one standard error of the mean.





**Figure 2.5.** Relationship between riparian willow:sedge proportion and mass of terrestrial invertebrates ingested by grayling per stream reach.

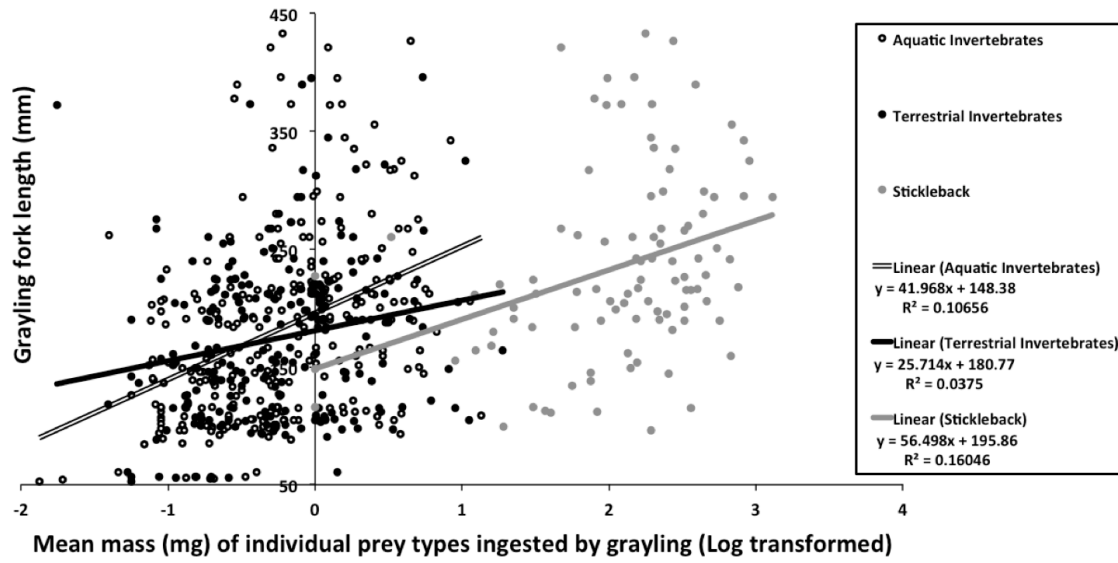
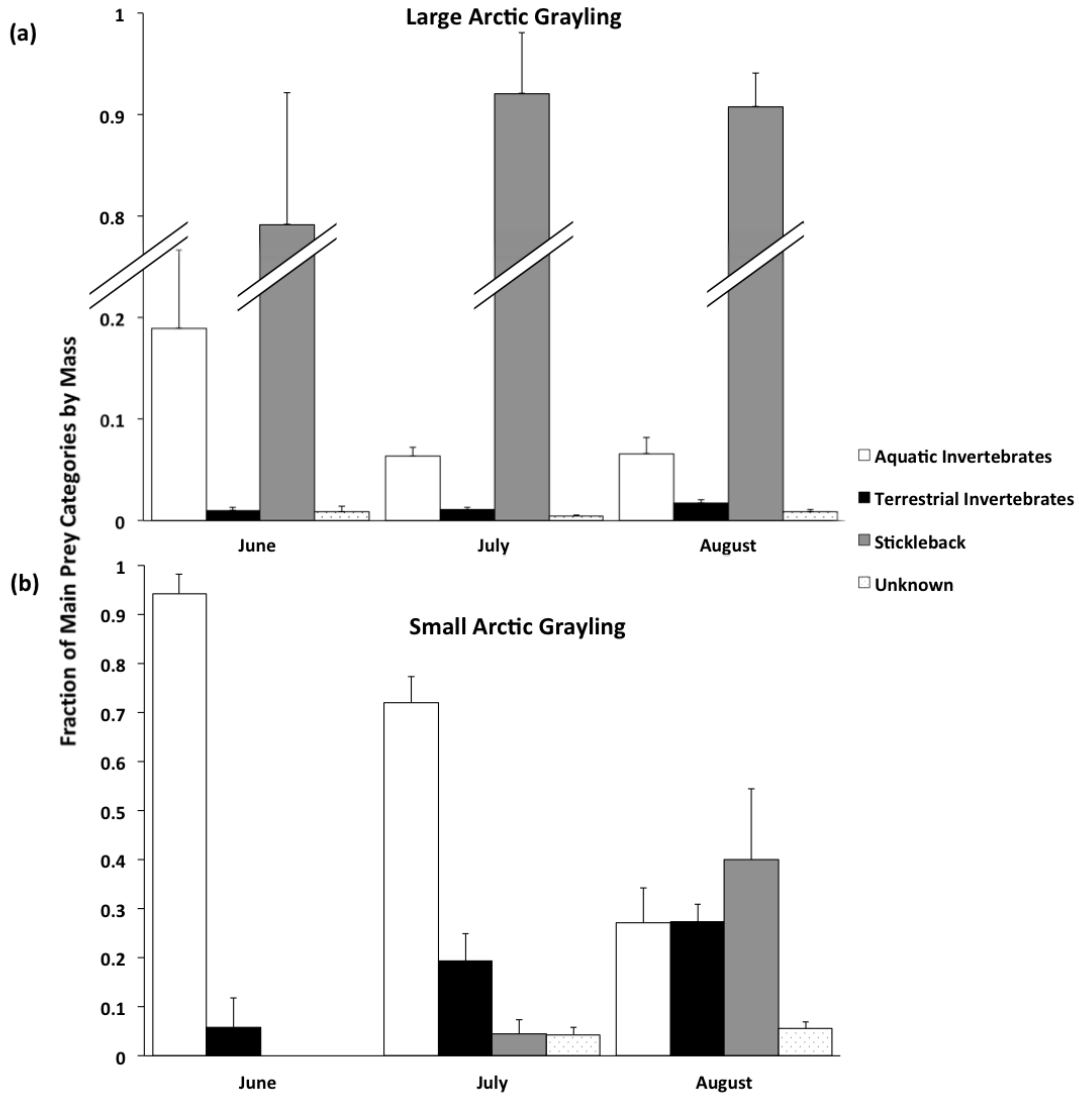


Figure 2.6. Prey size and type ingested by grayling as a function of grayling length.



**Figure 2.7.** Fraction of main prey categories by mass of large (FL > 15 cm) and small (FL < 15 cm) size Arctic Grayling in Crea Creek from 2011 and 2012. Bars represent one standard error of the mean.

(a)

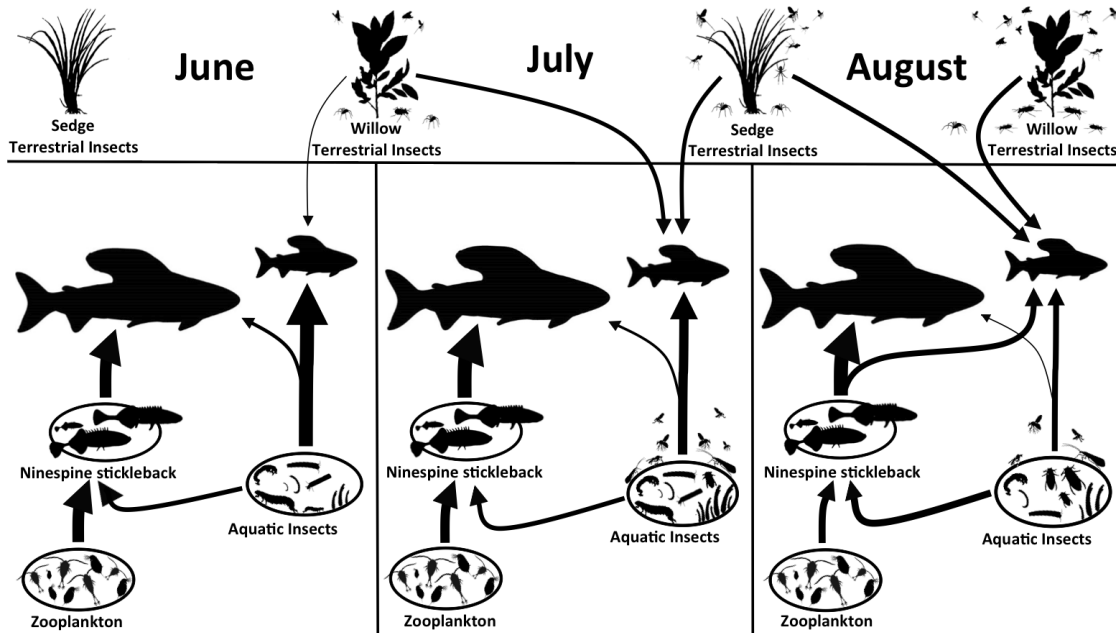


(b)



**Figure 2.8.** Piscivorous Arctic Grayling pictured (a) and its stomach contents (b) containing 73 stickleback and five Limnephilidae larva, illustrating the extent of piscivory that was seen during the study. The 73 stickleback consumed accounted for over 20 percent of the fish's total body mass.

## Prey flow in Arctic Coastal Plain beaded streams



**Figure 2.9.** Simplified summer time beaded stream food web. Different width arrows represent the relative importance of prey for small and large sized Arctic Grayling and Ninespine Stickleback.



**Table 2.1.** Relative percent vegetation cover, mean mass  $\pm$  SE of terrestrial invertebrates consumed by fish ( $n$ ) during the summers of 2011 and 2012, pool density (# of pools  $>$  7 m wide), and gradient (mm/m) per stream reach in Crea Creek. TI = terrestrial invertebrates, ND = no data.

Stream Reach	% Vegetation cover		Mean TI consumption (mg)/fish			Pool Density	Gradient (mm/m)
	Willow	Sedge	June	July	August		
1	25%	75%	1.7 $\pm$ 0.5 $n=11$	2.6 $\pm$ 1.1 $n=17$	4.1 $\pm$ 1.8 $n=14$	0	0.10
2	37%	63%	ND	3.6 $\pm$ 0.9 $n=13$	3.1 $\pm$ 0.8 $n=16$	2	0.05
3	34%	66%	ND	6.7 $\pm$ 2.5 $n=9$	6.2 $\pm$ 1.6 $n=16$	1	0.06
4	39%	61%	ND	8.8 $\pm$ 3.3 $n=19$	4.0 $\pm$ 1.2 $n=21$	2	0.10
5	7%	93%	ND	4.2 $\pm$ 1.5 $n=22$	3.2 $\pm$ 0.7 $n=18$	0	0.11
6	19%	81%	0.2 $\pm$ 0.1 $n=2$	6.1 $\pm$ 2.2 $n=17$	7.3 $\pm$ 2.3 $n=20$	3	0.05
7	73%	27%	1.6 $\pm$ 1.4 $n=4$	2.2 $\pm$ 1.2 $n=12$	1.4 $\pm$ 0.6 $n=9$	12	0.01
8	75%	25%	ND	5.6 $\pm$ 2.0 $n=14$	7.9 $\pm$ 2.9 $n=19$	1	0.07
9	51%	49%	ND	1.5 $\pm$ 0.9 $n=6$	9.7 $\pm$ 6.3 $n=3$	1	0.16
10	58%	42%	ND	0.8 $\pm$ 0.6 $n=3$	10.4 $\pm$ 9.2 $n=2$	0	0.06





### Chapter 3. General Conclusions

This study illustrated trophic pathways supporting Arctic Grayling and Ninespine Stickleback in a beaded stream (Crea Creek), and that these highly abundant systems can serve as important foraging habitats for stream consumers on the ACP. Until now, basic food webs for these stream types had not been characterized. I found that grayling in Crea Creek consumed terrestrial and aquatic sourced prey throughout the summer, with proportions of each changing through the summer, and that the type of prey differed by size of fish. For example, large fish consumed mostly stickleback throughout the summer and relatively few aquatic and terrestrial invertebrates. Conversely, small grayling consumed mostly invertebrates - aquatic invertebrates early in the season, and increasing quantities of terrestrial invertebrates and stickleback as the summer progressed.

My study also provided good evidence that grayling can be highly piscivorous, in contrast to what others have found elsewhere (Miller 1946; De Bruyn and McCart 1974; Jessop et al. 1993; Lindström 2010; Olson 2014). Stickleback accounted for nearly 90% of total prey biomass consumed by large grayling in this study. High degrees of piscivory are likely attributed to prey preference and stickleback availability. Stickleback are significantly greater in size and more energy dense (Hanson et al. 1985, Brey et al. 1988, Kidd et al. 1998, Sato et al. 2011) than invertebrate prey, thus fish sequester much greater energetic value per individual prey. Future studies should focus effort on quantifying stickleback densities and ecology in these freshwater habitats. Given the high abundance and wide distribution of these fish (Haynes et al. 2014), stickleback may be an ecologically important species, driving productivity for not only aquatic consumers (i.e. piscivorous fish), but terrestrial ecosystems (i.e. birds, mammals, etc.) on the ACP.

Grayling consumed nearly the entire suite of terrestrial invertebrate fauna found in the riparian vegetation, thus illustrating the role riparian vegetation plays in grayling food webs in Fish Creek. Terrestrial invertebrates in the diets of fish increased over the summer, likely as a function of aquatic and terrestrial insect phenology and seasonal abundance. I found greater quantities of terrestrial invertebrate entering the stream from willow possibly because their stands are more structurally complex, overhang the stream surface more than sedges, and potentially providing more habitat for invertebrates. Studies around the world have also found that both terrestrial invertebrate infauna and consumption by fish increase over the season (Eberle and Stanford 2010), differ by vegetation type (Edwards and Huryn 1996; Wipfli 1997), and that greater infauna usually occurs in areas with more dense stream-overhanging vegetation (Edwards and Huryn 1996; Kawaguchi and Nakano 2001).

Within these stream systems, maintaining ecological connectivity among aquatic habitats and the stream-riparian interface is important for stream consumers, as illustrated by terrestrial and aquatic pathways, coupled with lake-derived stickleback, supporting different sized grayling. If petroleum development or climate change interrupt or change these connections and prey pathways, freshwater productivity within the ACP will likely be affected, although it is difficult to predict exactly how these changes will influence foraging habitat and prey resources for fish, at this stage. However, given the wide variety of prey resources sequestered by grayling over the course of the summer, these fishes may have the capacity to progressively adapt their foraging ecology, even within a changing environment. One of the most imminent threats to ACP fishes appears to be loss of fish access into productive foraging habitats, such as beaded streams. Stream crossings by roads is known to impede fish passage (Gibson et al. 2005), thus, season-long fish access into these small streams must be maintained. Land managers should consider

connectivity within stream systems when constructing roads and other infrastructure (i.e. culverts and bridges).

Further concerns for Arctic fishes are that climate change may alter hydrological regimes. Warmer temperatures, coupled with longer ice-free seasons may increase evaporation rates on the ACP. Stream discharge is dominated by snowmelt runoff in the early summer with flows declining greatly in the late summer when rainfall is often exceeded by evapotranspiration (Arp et al. 2012). Thus, even now marginally connected small stream sections may become disconnected, reducing or isolating fish foraging habitats.

In conclusion, this study contributes a basis for assessing the response of grayling and other stream consumers to changes within aquatic habitats on the ACP. Considering that this study was conducted immediately prior to major development in the area, it may serve as a springboard for future research investigating how these changes may influence prey flow dynamics in Crea Creek and similar stream systems subject to development in northern Alaska.

### **3.1 Literature Cited**

Arp, C. D., Whitman, M. S., Jones, B. M., Kemnitz, R., Grosse, G., and Urban, F. E. 2012.

Drainage network structure and hydrologic behavior of three lake-rich watersheds on the Arctic Coastal Plain, Alaska. *Arctic, Antarctic, and Alpine research* 44. 385-398.

Brey, T., Rumohr, H. and Ankar, S. 1988. Energy content of macrobenthic invertebrates: general conversion factors from weight to energy. *Journal of Experimental Marine Biology and Ecology* 117: 271-278.

De Bruyn, M., and McCart, P. 1974. Life history of the grayling (*Thymallus arcticus*) in Beaufort Sea drainages in the Yukon Territory. *Biometrics* 2: 1-42.

- Eberle, L.C. and Stanford, J.A. 2010. Importance and seasonal availability of terrestrial invertebrates as prey for juvenile salmonids in floodplain spring brooks of the Kol River (Kamchatka, Russian Federation). *River research and applications* 26: 682-694.
- Edwards, E.D. and Hury, A.D. 1996. Effect of riparian land use on contributions of terrestrial invertebrates to streams. *Hydrobiologia* 337: 151-159.
- Gibson, R. J., Haedrich, R. L., and Wernerheim, C. M. 2005. Loss of fish habitat as a consequence of inappropriately constructed stream crossings. *Fisheries* 30: 10-17.
- Hanson, B.J., Cummins, K.W., Cargill, A.S. and Lowry, R.R. 1985. Lipid content, fatty acid composition, and the effect of diet on fats of aquatic insects. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry* 80: 257-276.
- Haynes, T. B., Rosenberger, A. E., Lindberg, M. S., Whitman, M., and Schmutz, J. A. 2014. Patterns of lake occupancy by fish indicate different adaptations to life in a harsh Arctic environment. *Freshwater Biology* 59: 1884-1896.
- Jessop, E.F., Chang-Kue, K.T.J., and MacDonald, G. 1993. Fish resource data from Indin Lake, Northwest Territories. *Canadian Data Report of Fisheries and Aquatic Sciences* 907: 52.
- Kawaguchi, Y. and Nakano, S. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. *Freshwater Biology* 46: 303-316.
- Kidd, K., Hesslein, R., Ross, B., Koczanski, K., Stephens, G. and Muir, D. 1998. Bioaccumulation of organochlorines through a remote freshwater food web in the Canadian Arctic. *Environmental pollution* 102: 91-103.

- Lindström, C.J. 2010. Influence of the habitat on the potential for cannibalism and population dynamics in stream-dwelling European grayling (*Thymallus thymallus* L.). Thesis project, Swedish University of Agricultural Sciences.
- Miller, R.B. 1946. Notes on the Arctic Grayling *Thymallus signifier* Richardson, from Great Bear Lake. *Copeia* 227-236.
- Olson, K. 2014. Feeding ecology of Lenok (*Brachymystax lenok*), Hovsgol Grayling (*Thymallus nigrescens*) and Baikal Grayling (*Thymallus baicalensis*) from the Eg-Uur Watershed, Mongolia (Doctoral dissertation, University of Minnesota).
- Sato, T., Watanabe, K., Kanaiwa, M., Niizuma, Y., Harada, Y. and Lafferty, K.D. 2011. Nematomorph parasites drive energy flow through a riparian ecosystem *Ecology* 92: 201-207.
- Wipfli, M.S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 1259-1269.



**APPENDIX A.** Prey taxa present in Arctic Grayling diets from Crea Creek; aquatic (A), terrestrial (T), or unknown (U), and by percent composition of abundance and biomass - grouped by habitat type.

	Taxa	Terrestrial/aquatic	% Abundance	% Biomass
Amphipoda	Amphipods	A	0.4	<0.1
Arachnida	Acari	A	1.7	0.1
Arachnida	Pseudoscorpiones	T	<0.1	<0.1
Arachnida	Unidentified spiders	T	0.7	0.1
Cladocera	Daphnia	A	1.3	0.4
Cladocera	Cladocerans	A	<0.1	<0.1
Coleoptera	Amphizoidae	A	<0.1	<0.1
Coleoptera	Carabidae	T	0.1	0.1
Coleoptera	Chrysomelidae	T	<0.1	<0.1
Coleoptera	Dytiscidae	A	1.0	3.3
Coleoptera	Elmidae	A	<0.1	<0.1
Coleoptera	Gyrinidae	A	0.2	<0.1
Coleoptera	Haliplidae	A	<0.1	<0.1
Coleoptera	Hydrophilidae	A	0.1	0.1
Coleoptera	Staphylinidae	T	1.0	0.1
Coleoptera	Unidentified beetles	U	1.7	0.3
Collembola	Collembola	U	0.2	<0.1
Copepoda	Copepods	A	1.4	<0.1
Diptera	Agromyzidae	T	<0.1	<0.1
Diptera	Calliphoridae	T	<0.1	<0.1
Diptera	Ceratopogonidae	A	0.4	<0.1
Diptera	Chironomid	A	31.6	2.2
Diptera	Culicidae	A	0.3	0.1
Diptera	Dixidae	A	0.4	<0.1
Diptera	Dolichopodidae	U	0.8	0.2
Diptera	Empididae	U	0.4	0.1
Diptera	Ephydriidae	U	0.2	0.1
Diptera	Lonchaeidae	T	<0.1	<0.1
Diptera	Muscidae	T	0.2	0.2
Diptera	Mycetophilidae	T	0.3	<0.1
Diptera	Phoridae	T	0.1	<0.1
Diptera	Sarcophagidae	T	<0.1	<0.1
Diptera	Scathophagidae	T	0.2	<0.1
Diptera	Sciaridae	T	0.2	<0.1
Diptera	Sciomyzidae	T	0.1	<0.1

## Appendix A. (Continued)

	Taxa	Terrestrial/aquatic	% Abundance	% Biomass
Diptera	Simuliidae	A	30.7	1.5
Diptera	Sphaeroceridae	T	0.1	<0.1
Diptera	Syrphidae	U	<0.1	<0.1
Diptera	Tipulidae	A	0.2	0.2
Diptera	Xylophagidae	T	0.2	0.1
Diptera	Unidentified flies	U	0.6	0.1
Ephemeroptera	Baetidae	A	0.6	0.1
Ephemeroptera	Unidentified mayflies	A	<0.1	<0.1
Gasterosteiformes	Ninespine Stickleback	A	4.0	88.5
Hemiptera	Aphididae	T	<0.1	<0.1
Hemiptera	Cicadellidae	T	<0.1	<0.1
Hemiptera	Psyllidae	T	1.7	0.1
Hirudinea	Unidentified leeches	A	<0.1	<0.1
Hymenoptera	Apidae	T	<0.1	<0.1
Hymenoptera	Braconidae	T	0.7	0.1
Hymenoptera	Cecidomyiidae	T	<0.1	<0.1
Hymenoptera	Chalcididae	T	<0.1	<0.1
Hymenoptera	Diapriidae	T	0.1	<0.1
Hymenoptera	Ichneumonidae	T	1.9	0.2
Hymenoptera	Megaspilidae	T	0.2	0.1
Hymenoptera	Mymaridae	T	0.2	0.2
Hymenoptera	Unidentified wasps	T	0.1	<0.1
Lepidoptera	Pyralidae	T	<0.1	<0.1
Megaloptera	Sialidae	A	<0.1	<0.1
Mollusca	Gastropods	A	1.2	0.1
Mollusca	Unidentified mollusk	A	0.1	0.1
Nematoda	Nematodes	A	<0.1	<0.1
Ostracoda	Ostracodes	A	0.1	0.3
Plecoptera	Leuctridae	A	0.1	0.7
Plecoptera	Nemouridae	A	<0.1	<0.1
Plecoptera	Perlodidae	A	0.1	0.1
Plecoptera	Taeniopterygidae	A	0.2	<0.1
Salmonidae	Arctic grayling	A	<0.1	0.3
Trichoptera	Brachycentridae	A	4.1	2.4
Trichoptera	Lepidostomatidae	A	<0.1	<0.1
Trichoptera	Limnephilidae	A	4.0	3.1
Trichoptera	Phryganeidae	A	0.3	0.8
Trichoptera	Unidentified caddis	A	0.3	0.1
Unknown	Unidentified insects	U	2.9	0.2