TERRESTRIAL INVERTEBRATE PREY FOR JUVENILE CHINOOK SALMON: ABUNDANCE AND ENVIRONMENTAL CONTROLS IN AN INTERIOR ALASKA RIVER

By

Laura Gutierrez

RECOMMENDED: ______________________________
Dr. Arny L. Blanchard

____
Dr. Amanda E. Rosenberger

____
Dr. Mark S. Wipfli, Advisory Committee Chair

____
Dr. Christa P. H. Mulder, Chair, Department of Biology and Wildlife

APPROVED: ______________________________
Dr. Paul W. Layer, Dean of the College of Natural Science and Mathematics

____
Dr. Lawrence K. Duffy, Dean of the Graduate School

Dec 6, 2011
____
Date

TERRESTRIAL INVERTEBRATE PREY FOR JUVENILE CHINOOK SALMON: ABUNDANCE AND ENVIRONMENTAL CONTROLS IN AN INTERIOR ALASKA RIVER

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

Laura Gutierrez, B.S.

Fairbanks, Alaska

December 2011

Abstract

Terrestrial prey subsidies can be a key food source for stream fish, but their importance and environmental controls on their abundance have not been widely documented in high latitude ecosystems. This study investigated terrestrial invertebrate prey availability and predation by age-0+ juvenile Chinook salmon (*Oncorhynchus tshawytscha*), overlap between terrestrial infall and drift to diet, and the relationship between diet to stream temperature and discharge in the Chena River, interior Alaska. Terrestrial infall, drift, and juvenile Chinook diet varied widely through the summers (May-Sept) of 2008 and 2009. Drift was comprised of 33% terrestrial and 67% aquatic invertebrate mass, while juvenile Chinook diet contained 19% terrestrial, 80% aquatic, and 1% unidentifiable invertebrate mass. The proportion of terrestrial invertebrate mass consumed increased through summer and, at times, made up to 39% of total diet. Low similarity of invertebrates in diet and infall, and diet and drift suggested that fish were, in part, prey-selective, selecting hymenopterans and chironomid midges (Diptera). In both years, prey mass consumed and discharge varied inversely, but no correlation was found between proportion of terrestrial invertebrates consumed and discharge. However, the two sampling dates with the highest proportion of terrestrial invertebrates consumed occurred shortly after a 60-year flood, indicating that terrestrial invertebrates may be important during rain and associated high water. This study found that, although terrestrial infall and drift are highly variable, terrestrial invertebrates are an important prey resource for rearing Chinook salmon in this high latitude riverine system, especially later in the summer.

Table of Contents

List of Figures

List of Tables

Acknowledgements

Throughout this document, “we” refers to primary author Laura Gutierrez and co-authors Dr. Mark S. Wipfli, Dr. Arny L. Blanchard, Dr. Nicholas F. Hughes, and Elizabeth C. Green. Drs. Wipfli, Blanchard, Rosenberger and Hughes served on Ms. Gutierrez’s advisory committee. Ms. Gutierrez conducted the research and analysis described here, and wrote the majority of this document. Drs. Wipfli and Hughes, with co-investigator Matt Evenson, conceived the original idea for this project and secured funding for it. Dr. Blanchard provided much support, primarily in the area of statistical analysis. Dr. Wipfli and Ms. Green also contributed editorial comments. Dr. Rosenberger was very helpful in discussions about the scope, organization, and analysis of this research project. We thank the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative and the Alaska Department of Fish and Game for funding and technical support, as well as Matt Evenson, James Savereide, Audra Brase, Virgil Davis, James Riedman, Melody Durrett, TJ Fayton, Katie Skogen, Stephanie Fischer, Emily Benson, Jason Neuswanger, Megan Perry, and Dave Roon for help in the field and lab. Thanks to Dr. Abby Powell and the members of the spring 2010 Biology 694: Scientific Writing class at University of Alaska Fairbanks for commenting on and improving an earlier draft of this manuscript. The sampling method was approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC # 07-21) and by the Alaska Department of Fish and Game (Fish Resource Permits: SF2008-133 and SF2009-141).

Any use of trade firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

General Introduction

Riparian areas have long been recognized as contributing basal resources to flowing-water ecosystems such as leaf litter and woody debris that are used by aquatic organisms including plants, aquatic invertebrates, and fish (Cummins *et al.*, 1989; Naiman & Decamps, 1997; Wallace *et al.*, 1997). One of the most researched areas of terrestrial inputs into streams is the contribution of detritus as a food and habitat source for aquatic invertebrate communities (Vannote *et al.*, 1980; Cummins *et al.*, 1989; Wallace *et al.*, 1997). More recently, terrestrial invertebrates directly falling into streams and rivers have also been recognized as an important food source for fish (Garman, 1991; Nielsen, 1992; Edwards & Huryn, 1995; Wipfli, 1997; Baxter *et al.*, 2005). These invertebrates fall into the stream by accidentally dropping from riparian vegetation directly into the water or are swept in via overland flow (Layzer *et al.*, 1989; Edwards & Huryn, 1995).

A study conducted in a New Zealand stream determined that the annual aquatic invertebrate production appeared insufficient to support the stream's brown trout population; this discrepancy became known as "Allen's Paradox" (Allen, 1951). Part of the solution to "Allen's Paradox" is thought to be the supplemental food that terrestrial invertebrates provide to fish (Edwards & Huryn, 1995; Bridcut, 2000; Allan *et al.*, 2003). The quantity and rate of terrestrial invertebrate consumption by stream consumers has been the subject of many recent salmonid foraging studies (Nielsen, 1992; Wipfli, 1997; Nakano *et al.*, 1999; Kawaguchi *et al.*, 2003; Allan *et* *al.*, 2003; Baxter *et al.*, 2005; Rundio & Lindley, 2008). Wipfli (1997) reported terrestrial invertebrates made up over 30% of prey ingested and 50% of the biomass consumed by Dolly Varden (*Salvelinus malma malma*), juvenile coho salmon (*Oncorhynchus kisutch*), and cutthroat trout (*O. clarkii*) in Southeast Alaska. In Japan, Kawaguchi and Nakano (2001) found terrestrial invertebrates composed 49% (in the forest) and 53 % (in grasslands) by mass in the annual diet of masu salmon (*O. masou)*, rainbow trout (*O. mykiss*), white-spotted char (*S. leucomaenis leucomaenis*), and Dolly Varden. Allan et al. (2003) found in southeast Alaska that terrestrial invertebrates provided roughly half of juvenile coho's energy supply in summer. Nakano et al. (1999) found when terrestrial invertebrate input was blocked, fish consumption of aquatic invertebrates increased, thereby concluding that, during summer, the rate of terrestrial invertebrate input into the stream controlled the effects of fish on top down food web processes.

Terrestrial invertebrate input is also thought to have consequences for fish production (Edwards & Huryn, 1996; Wipfli, 1997; Allan *et al.*, 2003). Often larger and with a higher caloric content then aquatic invertebrates (Cummins & Wuycheck, 1971), terrestrial invertebrate contribution to juvenile salmon diets may be energetically important. Most growth of fish takes place in summer, and body size in juvenile fish is positively related to overwinter survival and may lead to increased marine survival (Reimers, 1963; Mason, 1976; Quinn & Peterson, 1996; Ruggerone *et al.*, 2009). A study examining the bioenergetics of brook trout in West Virginia found that models simulating reduced terrestrial invertebrate consumption gave rise to predictions of negative fish growth over summer, leading to decreased energy stores and overwinter survival (Sweka & Hartman, 2008).

Due to the energetic importance of terrestrial invertebrates for fish, it is important to note that terrestrial invertebrate input and consumption is highly variable by season (Nelson, 1965; Cloe & Garman, 1996; Nakano *et al.*, 1999; Bridcut, 2000; Nakano & Murakami, 2001; Rundio & Lindley, 2008; Eberle & Stanford, 2010; Rosenberger *et al.*, 2011). Peaks of terrestrial infall and consumption by fish occur in late spring, summer, and fall in temperate zones (Nelson, 1965; Cloe & Garman, 1996; Bridcut, 2000). In addition, peaks in terrestrial infall and consumption were documented in the fall in northern Japan and Russia (Nakano & Murakami, 2001; Eberle & Stanford, 2010). Terrestrial invertebrate input and consumption may also fluctuate with environmental variables such as stream discharge. High discharge and floods may result in an increase of terrestrial invertebrate infall by increasing the wetted perimeter of a river bank and sweeping terrestrial invertebrates into the river via overland flow (Layzer *et al.*, 1989; Edwards & Huryn, 1995).

Changes in land use can also affect terrestrial and aquatic invertebrate abundance, and potentially fish populations. Different vegetation types support different types and numbers of terrestrial invertebrate taxa (Edwards & Huryn, 1996; Wipfli, 1997; Allan *et al.*, 2003; Romero *et al.*, 2005). Deciduous vegetation supports a greater number of terrestrial invertebrates than conifers (Mason & Macdonald, 1982; Allan *et al.*, 2003; Romero *et al.*, 2005), and natural grasslands and forests are known to provide greater terrestrial infall than pasture (Edwards & Huryn, 1995;

Edwards & Huryn, 1996). A study in western US contrasting two types of cattle grazing found that one type of grazing regime had greater terrestrial infall and consumption along with greater fish biomass than the other type of grazing regime (Saunders & Fausch, 2007). The Saunders and Fausch (2007) study highlights that riparian land management can have an impact on terrestrial infall and consumption as well as fish biomass.

The work in this master's project examined the dietary ecology of juvenile Chinook salmon *(Oncorhynchus tshawytscha)* by studying the invertebrates available to juveniles in stream drift and terrestrial invertebrates falling into the river from the surrounding riparian area. We then investigated what food juvenile Chinook consumed by directly examining their stomach contacts. We focused primarily on terrestrial invertebrate availability and consumption by juvenile Chinook because, as previously mentioned, terrestrial invertebrates are recognized as an important and sometimes primary food source for juvenile salmonids (Kawaguchi & Nakano, 2001; Kawaguchi *et al.*, 2003; Webster & Hartman, 2005; Rundio & Lindley, 2008). This master's study was part of a larger project on the ecology and demographics of juvenile Chinook salmon in the Chena River, a tributary to the Tanana and Yukon Rivers in interior Alaska. The larger project's goal was to improve our understanding of how ecological processes may regulate population size and generate annual variability in the abundance of Chinook salmon. Research on other fish species suggest the mortality that regulates abundance of Chinook salmon is due to competition for space or food during the summer months that juveniles spend rearing in freshwater (Grant, 1993; Elliott, 1994; Milner *et al.*, 2003). Understanding the availability and consumption of terrestrial invertebrates in the diet of juvenile Chinook should provide insight into which ecological processes influence juvenile Chinook population size; terrestrial invertebrates may be a necessary component of juvenile Chinook salmon's growth and survival. Furthermore, insight on the availability and consumption of terrestrial invertebrates should aid riparian management.

References

Allan, J.D., Wipfli, M.S., Caouette, J.P., Prussian, A. & 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.

Allen, K.R. (1951) The Horokiwi stream: a study of a trout population. *New Zealand Marine Department Fisheries Bulletin,* **10,** 1-231.

Baxter, C.V., Fausch, K.D. & Saunders, C.W. (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology,* **50,** 201-220.

Bridcut, E.E. (2000) A study of terrestrial and aerial macroinvertebrates on river banks and their contribution to drifting fauna and salmonid diets in a Scottish catchment. *Hydrobiologia,* **427,** 83-100.

Cloe, W.W. & Garman, G.C. (1996) The energetic importance of terrestrial arthropod inputs to three warm-water streams. *Freshwater Biology,* **36,** 104-114.

Cummins, K.W., Wilzbach, M.A., Gates, D.M. & Perry, W.B. (1989) Shredders and riparian vegetation: leaf litter that falls into streams influences communities of stream invertebrates. *Biosciences,* **39,** 24-30.

Cummins, K.W. & Wuycheck, J.C. (1971) *Caloric equivalents for investigations in ecological energetics,* Mitt. Int. Ver. Limnol.

Eberle, L.C. & 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. & Huryn, A.D. (1995) Annual contribution of terrestrial invertebrates to a New Zealand trout stream. *New Zealand Journal of Marine and Freshwater Research,* **29,** 467-477.

Edwards, E.D. & Huryn, A.D. (1996) Effect of riparian land use on contributions of terrestrial invertebrates to streams. *Hydrobiologia,* **337,** 151-159.

Elliott, J.M. (1994) *Quantitative ecology of the brown trout,* Oxford University Press.

Garman, G.C. (1991) Use of terrestrial arthropod prey by a stream-dwelling cyprinid fish. *Environmental biology of fishes,* **30,** 325-331.

Grant, J.W.A. (1993) Self-thinning in stream-dwelling salmonids. *Canadian Special Publication of Journal of Fisheries and Aquatic Sciences,* **118,** 99-102.

Kawaguchi, Y. & 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.

Kawaguchi, Y., Taniguchi, Y. & Nakano, S. (2003) Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. *Ecology,* **83,** 701-708.

Layzer, J.B., Nehus, T.J., Pennington, W., Gore, J.A. & Nestler, J.M. (1989) Seasonal variation in the composition of the drift below a peaking hydroelectric project. *Regulated Rivers: Research & Management,* **3,** 29-34.

Mason, C.F. & Macdonald, S.M. (1982) The input of terrestrial invertebrates from tree canopies to a stream. *Freshwater Biology,* **12,** 305-311.

Mason, J.C. (1976) Response of underyearling coho salmon to supplemental feeding in a natural stream. *Journal of Wildlife Management,* **40,** 775-788.

Milner, N.J., J.M. Elliott, J.D. Armstrong, R. Gardiner, J.S. Welton & Ladle, M. (2003) The natural control of salmon and trout populations in streams. *Fisheries Research,* **62,** 111-125.

Naiman, R.J. & Decamps, H. (1997) The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics,* **28,** 621-658.

Nakano, S., Miyasaka, H. & Kuhara, N. (1999) Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology,* **80,** 2435-2441.

Nakano, S. & 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, J.M. (1965) A seasonal study of aerial insects close to a moorland stream. *Journal of Animal Ecology,* **34,** 573-579.

Nielsen, J.L. (1992) Microhabitat-specific foraging behavior, diet, and growth of juvenile salmon. *Transactions of the American Fish Society,* **121,** 617-634.

Quinn, T.P. & Peterson, N.P. (1996) The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. *Canadian Journal of Fisheries and Aquatic Sciences,* **53,** 1555-1564.

Reimers, N. (1963) Body condition, water temperature, and over-winter survival of hatchery-reared trout in Convict Creek, California. *Transactions of the American Fisheries Society,* **92,** 39 - 46.

Romero, N., Gresswell, R.E. & 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.

Rosenberger, A.E., Dunham, J.B., Buffington, J.M. & Wipfli, M.S. (2011) Persistent effects of wildfire and debris flows on the invertebrate prey base of rainbow trout in Idaho streams. *Northwest Science,* **85,** 55-63.

Ruggerone, G.T., Nielsen, J.L. & Agler, B.A. (2009) Linking marine and freshwater growth in western Alaska Chinook salmon (*Oncorhynchus tshawytscha*). *Journal of Fish Biology,* **75,** 1287-1301.

Rundio, D.E. & Lindley, S.T. (2008) Seasonal patterns of terrestrial and aquatic prey abundance and use by *Oncorhynchus mykiss* in a California coastal basin with a mediterranean climate. *Transactions of the American Fisheries Society,* **137,** 467-480.

Saunders, W.C. & Fausch, K.D. (2007) Improved grazing management increases terrestrial invertebrate inputs that feed trout in Wyoming rangeland streams. *Transactions of the American Fisheries Society,* **136,** 1216 - 1230.

Sweka, J.A. & Hartman, K.J. (2008) Contribution of terrestrial invertebrates to yearly brook trout prey consumption and growth. *Transactions of the American Fisheries Society,* **137,** 224-235.

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

Wallace, J.B., Eggert, S.L., Meyer, J.L. & Webster, J.R. (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science,* **277,** 102-104.

Webster, J.J. & Hartman, K.J. (2005) The role of terrestrial invertebrates in allopatric brook trout headwater streams in central Appalachian mountains. *Journal of Freshwater Ecology,* **20,** 101-107.

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.

Chapter 1: Terrestrial invertebrate prey for juvenile Chinook salmon: Abundance and environmental controls in an interior Alaska River[1]

Summary

1. During summer (May-September), we investigated the dynamics of terrestrial invertebrate prey availability and predation by age-0+ juvenile Chinook salmon (*Oncorhynchus tshawytscha*), overlap between terrestrial infall and drift to diet, and the relationship between stream temperature and discharge with diet in the Chena River, interior Alaska.

2. Four sites were chosen for study within a 55-km mid-section of the river. We deployed surface pan traps to collect terrestrial invertebrate infall into the river, collected drifting invertebrates via 250-µm drift nets, and sampled juvenile Chinook salmon diet via gastric lavage during the summer seasons of 2008 and 2009.

3. Terrestrial infall, drift, and consumption by juvenile Chinook varied widely through the season. Mean terrestrial infall was 25 ± 5 mg dry mass m^{-2} d^{-1}. By mass, drift was composed of 33% terrestrial and 67% aquatic invertebrates, while juvenile Chinook diet contained 19% terrestrial, 80% aquatic, and 1% invertebrates of unidentifiable origin. The proportion of terrestrial invertebrates consumed generally increased throughout the summer and, on some sampling dates, made up to 39% of total juvenile Chinook diet.

[1] Gutierrez, L., M. S. Wipfli, A. L. Blanchard, N. F. Hughes, and E. C. Green. Terrestrial invertebrate prey for juvenile Chinook salmon: Abundance and environmental controls in an interior Alaska River. Prepared for submission to Freshwater Biology.

4. Low similarity between invertebrate taxa in diet and infall, and diet and drift suggested that fish were disproportionately selecting some prey types over others, such adult hymenopterans and all life stages of chironomid midges.

5. Stream temperature and discharge had varied influences on juvenile Chinook diet. Total invertebrate prey consumed was negatively related to discharge in both years, and negligible correlation was found between discharge and proportion of terrestrial invertebrates consumed. Yet, the two sampling dates with the highest proportion of terrestrial invertebrates consumed occurred after a late summer 60-year flood indicating that terrestrial invertebrates may be more available as prey after periods of unusually high discharge.

6. This study found that although terrestrial infall and drift are highly variable throughout the summer, terrestrial invertebrates can be an important prey resource for these fish, particularly as the summer season progresses.

Introduction

From small headwater streams to large braided rivers, moving waters are connected to surrounding riparian areas by the exchange of materials and organisms. Stream food webs derive the base of their energy not only from autochthonous (in stream) sources, but also allochthonous (external) sources (Vannote *et al.*, 1980). The basic components of food webs (nutrients, detritus, and organisms) all cross spatial boundaries (Polis *et al.*, 1997). In mixed-coniferous and deciduous forests, terrestrial subsidies to rivers include invertebrates, coniferous needles, deciduous leaves, and woody materials. These terrestrial subsidies act as basal resources for many aquatic organisms (Cummins *et al.*, 1989; Naiman & Decamps, 1997; Wallace *et al.*, 1997). Fish directly consume these subsidies in the form of terrestrial invertebrates (Garman, 1991; Cloe & Garman, 1996; Wipfli, 1997; Kawaguchi *et al.*, 2003) that fall into streams and rivers from the surrounding riparian zone by accidentally dropping from riparian vegetation or via overland flow (Layzer *et al.*, 1989; Edwards & Huryn, 1995).

Terrestrial invertebrates are an important food source for fish in headwater and small streams, where there is generally a large amount of overhanging riparian vegetation (Nielsen, 1992; Cloe & Garman, 1996; Wipfli, 1997; Kawaguchi & Nakano, 2001; Allan *et al.*, 2003; Romero *et al.*, 2005). For example, in small coastal streams in southeast Alaska, terrestrial invertebrates made up over 30% of the number of prey ingested, and 50% of the total prey mass consumed by Dolly Varden charr (*Salvelinus malma*), juvenile coho salmon (*Oncorhynchus kisutch*), and cutthroat trout (*O. clarki*) (Wipfli, 1997). Also in coastal southeast Alaska, Allen *et al.* (2003) found that terrestrial invertebrates made up 50% of the abundance of prey ingested by juvenile coho salmon in summer. A study in a headwater stream in Japan found that terrestrial invertebrates comprised 51% by mass of the annual diet of fish in these streams (Kawaguchi & Nakano, 2001). However, few studies have evaluated terrestrial invertebrate infall and the importance of terrestrial invertebrates as prey for fish in larger river systems (Baxter *et al.*, 2005; Paetzold *et al.*, 2008).

In small streams, terrestrial invertebrate infall and its availability to fish varies seasonally (Edwards & Huryn, 1995; Wipfli, 1997; Bridcut, 2000). In early spring and late fall, terrestrial invertebrate infall is an important source of prey for salmonids in temperate regions (Cloe & Garman, 1996; Nakano *et al.*, 1999a; Bridcut, 2000; Romero *et al.*, 2005). In an arid climate, terrestrial infall and consumption by steelhead trout *(O. mykiss)* also peaked in early summer and late fall (Rundio & Lindley, 2008). In northern Japan, terrestrial infall and consumption only peaked in late fall when aquatic invertebrate production was low (Nakano & Murakami, 2001). Several studies have been conducted in northern latitudes: in Russia, the terrestrial invertebrate proportion of juvenile coho and Dolly Varden diet was highest in the fall (Eberle & Stanford, 2010), and in southeastern Alaska, the proportion of terrestrial invertebrates in salmonid diet increased from May to October (Wipfli, 1997). One other juvenile salmonid study in southeast Alaska found no particular seasonal trend in invertebrate infall or consumption (Allan *et al.*, 2003). Again, all these studies were conducted in small streams and only a few were conducted in northern latitudes. The seasonal variation and contribution of terrestrial invertebrate infall in larger river systems and in northern climates could be greatly different, but has not been adequately investigated.

In spite of previous research documenting the importance of terrestrial infall as a prey resource for fish in temperate areas, little is known about the availability and use of terrestrial invertebrates by juvenile Chinook salmon (*O. tshawytscha*) in interior Alaska. Because of the extreme climatic conditions in interior Alaska, most river systems freeze over in winter (Oswood, 1997); thus, the availability of terrestrial invertebrates is limited to the summer season. The objectives of this study were to understand the dynamics that govern terrestrial prey for fish in the Chena River, interior Alaska to determine: 1) terrestrial invertebrate infall into pool habitats where foraging salmonids reside, 2) the contribution of terrestrial invertebrates to stream invertebrate drift, 3) the contribution of terrestrial invertebrates to the diet of age-0 juvenile Chinook salmon, 4) the relationship between invertebrate prey composition in the infall and drift to that ingested by juvenile Chinook, and 5) the effects of discharge and stream temperature on juvenile Chinook prey consumption during the summer season (May-September). Understanding the role of terrestrial invertebrates in the prey base of juvenile Chinook is significant in terms of understanding salmonid food webs and the sources of prey important for riverine salmonids.

Methods

Study Area

This study was conducted on the Chena River, a subdrainage of the Yukon River in interior Alaska. It flows roughly 252 km from the uppermost reach of the East Fork to the confluence with the Tanana River at the edge of the city of Fairbanks, Alaska. The Chena River watershed covers approximately 5,130 km^2 and is composed of five major tributaries (Fig. 1; Cai *et al.*, 2008). Annual discharge at the USGS Two-Rivers gauging station on the East Fork of the Chena River averages approximately 20 $m^3 s^{-1}$ with daily mean flows ranging from 0.6 to over 496 $m^3 s^{-1}$. The banks of the lower 40 km of the river have been developed extensively, and there is limited road access along the lower two-thirds of the river.

The Chena River supports three species of fish in the family Salmonidae: Arctic grayling (*Thymallus arcticus*), Chinook salmon, and chum salmon (*O. keta*). The Chena River is an important spawning and rearing river for Yukon River Chinook salmon in interior Alaska (The United States and Canada Yukon River Joint Technical Committee, 2009), with adults spawning in the lower 150 km of the river (Brase & Doxey, 2006). Age-0 juvenile Chinook salmon emerge from the gravel in mid-May from redds where eggs were deposited by adult spawning salmon (M. Evenson, Alaska Department of Fish and Game, personal communication).

Site Selection

In 2007, two study reaches were selected that contained the largest concentrations of juvenile Chinook in summer. Sampling occurred at two sites in the upstream reach (Site 1: N 64°53'35.16", W 146°38'43.44"; Site 2: N 64°52'45.70", W 146°44'55.54"; all in WGS84) and two in the lower reach (Site 3: N 64°49'18.80, W 147° 4'32.45"; Site 4: N 64°48'16.67", W 147° 7'57.97). The study sites were located at river bends with a large proportion of root wads, fallen trees, and mats of woody debris which provided ample quality habitat for juvenile Chinook. Sites ranged from 214 to 530 m long. We measured the width of the river in each site at five evenly distributed points, and the average river wetted width ranged from 30 to 43 m.

Sampling Scheme

We sampled invertebrate infall, drift, and juvenile Chinook salmon diet approximately every other week from 6 June to 25 September 2008 and from 12 May to 15 September 2009, for a total of eight sampling events each summer (Table 1).

We continuously measured water temperature with data loggers at each site during both summers (Hobo Water Temp Pro v2, Onset Corp, MA and Hach Environmental Hydrolab DS5 Water Quality Sonde, CO). We obtained stream discharge data from USGS gauging stations at Hunts Creek (near sites 1 and 2) and Moose Creek Dam (near sites 3 and 4).

Field Methods

Terrestrial invertebrate infall

We sampled invertebrate infall with floating pan traps at our four study sites for a 24-h period preceding each diet sampling event. Pan traps were designed to catch invertebrates falling into the stream; they consisted of a black plastic pan (34.3 x 29.2 x 13.3 cm) filled with ~5 cm water and 2-3 drops of dish soap to break the surface tension to prevent invertebrates from escaping. Each pan trap was floated within a blue insulation foam frame. We placed four traps at each site for a total of 16 possible samples per sampling date. Traps were placed on the cut bank side of the river in locations where juvenile Chinook salmon were observed. Traps were tethered with nylon cord to overhanging tree limbs, vegetation, or woody debris approximately 0.5-1.0 m from the cut bank. After the

24-h deployment, the contents of each pan were sieved through a 250 µm mesh and stored in at least 80% ethanol. For our analysis, we calculated terrestrial invertebrate infall, aquatic invertebrate infall (adult winged forms), and total invertebrate infall (both terrestrial invertebrates and adult winged forms of aquatic invertebrates) by calculating the biomass and number of each category of invertebrates that fell into the traps per sampling date and site.

Terrestrial invertebrates in drift

Invertebrate drift was collected for a 24-h period concurrent with pan trap sampling. We placed one drift net at each site in 2008 and two in 2009. Each drift net (250-µm mesh) was attached to a circular pipe (13-cm diameter) anchored 30 cm below a floating rectangle of blue insulation foam. The entire drift float was tethered to overhanging branches or large woody debris approximately 0.5-3.0 m from the bank. At the end of the 24-h sampling period, we collected the nets, brought them to the lab, and stored each drift sample in 80% ethanol. We measured stream flow at the mouth of the pipe before and after nets were placed in the river with a flow meter (Marsh-McBirney Flo-Mate 2000, Hach, CO) to estimate the amount of water flowing through the net over the 24-h period. We estimated drift per cubic meter of water per date by dividing the biomass and number of invertebrates caught in the drift net by the mean stream discharge for the 24-hour sampling period. In our analysis, we used the mean invertebrate biomass (per cubic meter of water per date), the source type (terrestrial vs. aquatic), and the percent source type in each sample.

Terrestrial invertebrates ingested by juvenile Chinook salmon

We trapped fish and collected their stomach contents 24 hours after the end of drift and terrestrial infall sampling to reduce the effects of disturbance on fish due to sampling for prey availability. Fish were captured on two consecutive days between 10:00 and 16:00. We used dip nets and seines to catch fish because minnow traps were not effective in the beginning of the summer (May to mid-July); from mid-July through September, we used baited minnow traps to capture fish. In 2008, we measured fish fork length to the nearest 1 mm; in 2009, we measured fish fork length, again to the nearest 1 mm, as well as fish weight, to the nearest 0.1 g. To collect stomach contents, fish less than 40 mm long were sacrificed and preserved in 80% ethanol, with an incision in their stomachs to prevent further digestion or degradation of the stomach contents. Fish greater than 40 mm were anaesthetized with MS-222 (tricane methanesulfonate), and stomach contents were collected by gastric lavage with a 10-ml pipette and preserved in 80% ethanol (Meehan & Miller, 1978). Once diet sampling was complete, we transferred the fish to a holding tub until they recovered and swam normally, and then returned them to the location of capture.

We calculated the biomass, number, and frequency of invertebrates consumed per fish by sampling date and site, and the proportion of the diet that was terrestrial or aquatic (mg invertebrates dry mass / mg total dry mass). Over both summers, we only had five empty stomach samples. These five were included in our analysis and results. The juvenile Chinook salmon in this study were consistently growing throughout the summer, on average about 5 mm every two weeks (Table 1). We standardized biomass consumed by fish length and found the same patterns and statistical results as when using the non-length standardized values. Thus for conciseness and clarity, we are only presenting the values of biomass and proportions consumed. The index of relative importance (*IRI*) was calculated to determine which invertebrate taxa were most important to the juvenile Chinook diet in each sampling year. *IRI* is a compound index that combines the percent number, mass, and frequency of each taxon to calculate an importance ranking (Pinkas *et al.*, 1971; Liao *et al.*, 2001). *IRI* was calculated with the equation:

$$IRI = (\%\,N + \%\,M) \times (\%\,F)$$

where N is the percent by number, M is the percent by mass, and F is the percent of frequency of occurrence.

Laboratory Procedures

For invertebrate infall samples, specimens were identified to order except for those that have both aquatic and terrestrial members such as Coleoptera, Diptera, Hemiptera, and Lepidoptera, which were identified to family level. For the diet and drift samples, invertebrates were identified to the nearest convenient taxonomic group (primarily family). Drift samples were sieved through a 1mm sieve and then subsampled down to 1/16 of the original sample, while still maintaining a minimum of 500 invertebrates per sample. All invertebrates were counted, measured by length, and categorized as either aquatic or terrestrial based on larval origin (Wipfli, 1997). Dipterans in the following families were assumed to be aquatic: Ceratopogonidae, Chironomidae, Empididae, Psychodidae, and Tipulidae. All adult and larval stages of aquatic insects were excluded from the terrestrial source category (Wipfli, 1997). We estimated invertebrate dry mass (mg) using length-weight regressions (Rogers *et al.*, 1976; Uye, 1982; Meyer, 1989; Sample *et al.*, 1993; Hodar, 1996; Burgherr & Meyer, 1997; Hodar, 1997; Kawabata & Urabe, 1998; Benke *et al.*, 1999; Johnson & Strong, 2000; Sabo *et al.*, 2002; Baumgärtner & Rothhaupt, 2003; Gruner, 2003; Miyasaka *et al.*, 2008; Wipfli, unpublished data)

Statistical Analysis

We used a repeated measures analysis of variance (rm ANOVA) with date as the repeated measures factor to test for significant differences by site, date, and year of invertebrate mass by source. An rm ANOVA was conducted for infall, drift, and juvenile Chinook diet. Invertebrate infall and diet data were ln(x+1) transformed, while drift data were fourth root transformed to meet the assumptions of normality and variance of the ANOVA. We used a Bonferroni correction of $\alpha = 0.05 / 3$ (= 0.017) to account for testing multiple hypotheses (mass of terrestrial, aquatic, and total invertebrates) from the same data set. Since using a Bonferroni correction increases the risk of committing a type II error, we reported p-values of $\alpha = 0.10 / 3 = 0.033$ as marginally significant. Pearson's correlation coefficient was used to test if the total mass consumed and the proportion of terrestrial prey consumed was positively or negatively associated with sampling date. Pearson's correlation coefficient was also used to test the association between total and the proportion of terrestrial prey mass consumed and the environmental variables of stream discharge and temperature, as well as the relationship between discharge and water temperature. For the Pearson's correlations using discharge and water temperature, we used the mean daily discharge and mean water temperature for each sampling date. We used a Bonferroni correction of $\alpha = 0.05 / 3$ (= 0.017) to take into account the multiple comparison between 2008, 2009, and the combination of both years. P-values of $\alpha = 0.10 / 3 = 0.033$ were reported as marginally significant.

To determine if juvenile Chinook salmon consumed invertebrate prey according to their availability, we conducted a multidimensional scaling (MDS) ordination (McCune & Grace, 2002; Brodeur *et al.*, 2010). We used the MDS ordination to visualize the similarities in invertebrate composition data between infall, drift, and juvenile Chinook salmon diet. We created two different ordinations based on a Bray-Curtis dissimilarity matrix of the mean proportion by mass of the top 95% invertebrate taxa and life stage per sample type (i.e. infall, drift, or diet), date, and year. We did not use site as a variable because we were concerned with prey consumption and availability as a whole, and not site-to-site variability. Each point on the ordination represents the combination of sample type-date-year. Sample points plotted closer together have greater similarity in invertebrate community composition. The first ordination included all invertebrate taxa, while the second ordination included only terrestrial taxa. In the second ordination, we only used sampling dates were terrestrial invertebrates were present. An ordination with stress less than 0.20 was considered to be suitable for interpretation; a stress value is comparable to standard deviation (McCune & Grace, 2002; Brodeur *et al.*, 2010). We then used a similarity percentage (SIMPER) analysis on both ordinations to determine the percent dissimilarity between invertebrate community composition of diet compared to drift, and diet compared to infall. Two sample points which share no species have a very high dissimilarity, and two sample points which share the same species in similar abundances have a low dissimilarity (Clarke, 1993). We also used SIMPER on both ordinations to determine which prey taxa accounted for the largest difference in the invertebrate community composition between comparisons of infall to diet and drift to diet.

The repeated measures ANOVAs were done using SAS® software, version 9.1 of SAS System for Windows (SAS Institute Inc., Cary, NC, USA). Pearson's correlation coefficient tests were done using R, an open-source statistical program (R Core Development Team). The MDS ordination and SIMPER analysis were done using the PRIMER v6 software (Clarke, 1993). Hereafter all means are reported as mean ± standard error (SE).

Results

Terrestrial invertebrate infall

In 2008, terrestrial invertebrate infall mass peaked during late August (8/12), whereas, in 2009, terrestrial infall peaked earlier in late June (6/22) and then again mid-August (8/18, Fig. 2). The mass of adult-winged aquatic and terrestrial invertebrate infall generally followed similar patterns within summer in both 2008 and 2009. In 2008, terrestrial invertebrate infall ranged from 6-51 mg dry mass $m^{-2}d^{-1}$ with a mean of 17 ± 5 mg dry mass m^{-2} d^{-1} (Fig. 2). In 2009, terrestrial invertebrate infall ranged from 0-72 mg dry mass m^{-2} d^{-1} with a mean of 33 ± 8 mg dry mass m^{-2} d^{-1}. Terrestrial infall mass was significantly higher in 2009 than 2008, varied significantly by sampling date, and marginally by date*year (rm ANOVA, year: $P = 0.003$, sampling date: $P < 0.001$; date*year: $P = 0.018$; Table 2), but not by site. The top five taxa by mass of terrestrial invertebrate infall in 2008 were adult Hymenoptera, followed by adult Collembola, Araneae, Hemiptera, and Coleoptera Staphylinidae. The top five taxa by mass for terrestrial invertebrate infall in 2009 included the same taxa as in 2008, but in a different order with adult Coleoptera Staphylinidae having the highest mass, followed by adult Hymenoptera, Araneae, Collembola, and Hemiptera.

Contribution of terrestrial invertebrates in the drift

In 2008, terrestrial invertebrates in the drift peaked in early June (6/11) and then again in mid-August (8/12), whereas in 2009 the mass of terrestrial invertebrates was variable and had peaks in each month (Fig. 3). The greatest peak of terrestrial invertebrate drift (8/12) was concordant with the greatest peak of terrestrial invertebrate infall, but in 2009 the peaks of terrestrial infall and drift did not consistently match (Fig. 2 and 3). However in the beginning of both summers, there was an initial peak of aquatic invertebrate drift primarily made up larval chironomids (Diptera), although this first peak was almost two weeks later in 2009 than in 2008 (Fig. 3).

In 2008, terrestrial invertebrate drift ranged from 0.01-0.4 mg dry mass m^{-3}, had a mean of 0.12 ± 0.04 mg dry mass m^{-3}, and was 20 ± 6% of the invertebrate drift (Fig. 3).

During 2009, terrestrial invertebrates drift ranged from 0.01-0.24 mg dry mass m^{-3}, had a mean of 0.07 ± 0.02 mg dry mass m^{-3}, and was 27 ± 6% percent of the drift. Unlike terrestrial infall, terrestrial drift did not vary significantly by date nor was significantly higher in 2009 than in 2008. Furthermore, terrestrial drift did not vary seasonally in a similar manner both years (rm ANOVA, date*year: $P = 0.004$; Table 2). In the 2008 drift, the top five terrestrial taxa by mass were adult Hymenoptera, followed by adult Hemiptera, Diptera in the families Xylophagidae and Sciaridae, and Araneae. In the 2009 drift, the top five terrestrial taxa by mass were adult Hymenoptera, followed by adult Hemiptera, Coleoptera Staphylinidae, Araneae, and Lepidoptera.

Contribution of terrestrial invertebrate prey to juvenile Chinook diet

We sampled juvenile Chinook salmon for stomach contents, obtaining a total of 360 samples ($n = 118$ in 2008, $n = 233$ in 2009) from fish 28-87 mm in length (Table 1). Both summers, juvenile Chinook consumed a low mass of aquatic and terrestrial prey in the beginning of the summer and then consumed an increasing but variable mass throughout the rest of the season (Fig. 4). In 2008, juvenile Chinook consumed terrestrial invertebrates in a range of 0.05 - 3.67 mg dry mass $fish^{-1}$, with a mean 1.4 ± 0.4 mg dry mass $fish^{-1}$. In 2009, juvenile Chinook once again consumed a similar terrestrial invertebrate mass ranging from 0 - 3.30 mg dry mass $fish^{-1}$; however, with a lower annual mean of 0.75 ± 0.26 mg dry mass $fish^{-1}$. Although marginally significant, juvenile Chinook consumed more terrestrial invertebrate mass in 2008 than in 2009 (rm ANOVA, $P = 0.028$; Table 2). This was also reflected in the proportion of their total diet made up by terrestrial invertebrates, with terrestrial invertebrates making up 24 ± 4% of total juvenile Chinook diet in 2008 versus 16 ± 4% in 2009. Consumption of terrestrial invertebrates varied significantly by site and date (rm ANOVA, site: $P < 0.001$; date: $P < 0.001$; Table 2), and varied marginally by year and by the site between years (rm ANOVA, year: $P = 0.028$; year * site: $P = 0.028$; Table 2).

Juvenile Chinook consumed a wide range of invertebrate prey, consisting of 16 orders and at least 47 families. Using the calculated IRI to determine the importance of differing taxa to juvenile Chinook diet, we found that chironomids (Diptera) in all their life stages (larva, pupa, and adult) as well a chloroperlids (Plecoptera) ranked in the top five most important taxa for both 2008 and 2009 (Table 3). Two terrestrial taxa ranked in the top ten most important taxa consumed per year: adult Hymenoptera and Araneae in 2008, as well adult aphids (Hemiptera) and Hymenopterans in 2009.

During both summers, the proportion of terrestrial invertebrates in the diet was initially low, generally increased throughout the season (Fig. 5), and was positively correlated to sampling date (Pearson's correlation; 2008: $r = 0.35$, $P < 0.001$; 2009: $r = 0.36$, $P < 0.001$). In 2008 on two different sampling dates (8/13 and 8/27), terrestrial invertebrates made up 39% of the total diet (Fig. 5). These two dates with the highest proportion of terrestrial invertebrates consumed in the total diet followed a 60-year flood that peaked on July 31 with a discharge of 250.1 $m^3 s^{-1}$, a twelve-fold increase from the mean annual flow. In 2009, the largest proportion of terrestrial invertebrates consumed that year occurred in late August with terrestrial invertebrates making up 38% of the total diet.

Relationship between infall, drifting invertebrates, and predation by fishes

The first ordination comparing aquatic and terrestrial invertebrate availability (via infall and drift) to consumption by juvenile Chinook resulted in clustering by sample type (Figure 6-a). Clustering by sample type, i.e. infall, drift, and diet, signified that invertebrate community composition was more similar in abundance and composition by sample type rather than across samples types, dates, or years. This also signified that there was low overlap between the invertebrate community represented in the comparisons of infall to diet and diet to drift. Juvenile Chinook diet and drift had approximately 23-28% similar taxa and abundance levels (SIMPER, mean percent dissimilarity of invertebrate composition: 77% in 2008 and 72% in 2009). SIMPER determined that hymenopterans in 2008 and adult chironomids in 2009 contributed the most dissimilarity between invertebrate composition of juvenile Chinook diet to drift. In both summers, juvenile Chinook consumed a higher proportion of both hymenopterans and adult chironomids than the proportion of either available in the drift. Additionally in both summers, black fly larva (Diptera: Simuliidae) and water mites (Acari: Hydracarina) were highly abundant by proportion in the drift. Yet, juvenile Chinook consumed black fly larva at levels lower than their availability, and rarely consumed water mites.

Juvenile Chinook diet and invertebrate infall also had low total overlap with 22-27% similar taxa and abundance levels (SIMPER, mean percent dissimilarity of invertebrate composition: 78% in 2008 and 73% in 2009). Both in 2008 and 2009, adult chironomids contributed the most dissimilarity between diet to infall, with a higher proportion of adult chironomids in infall samples than in juvenile Chinook diet. Adult aquatic stoneflies (Plecoptera) also contributed to the dissimilarity between diet and infall, with a higher proportion of adult stoneflies in infall than in juvenile Chinook diet. As a whole, juvenile Chinook diet had a low, but comparable overlap with both drift and infall (SIMPER, mean percent dissimilarity of 2008 and 2009 combined, diet to drift: 74% and diet to infall: 75%).

When examining only terrestrial taxa in the second ordination, diet and drift samples loosely clustered with some overlap. This signified greater overlap of terrestrial invertebrate composition and quantity between diet and drift (Figure 6-b). Terrestrial infall had some overlap with the terrestrial invertebrate composition and abundance of diet and drift, but did not cluster with them (Figure 6-b). SIMPER analysis determined that in both years Hymenoptera was the taxon that contributed the most dissimilarity between diet to drift and diet to infall. In 2008, the proportion of hymenopterans was higher in both drift and infall than in the juvenile Chinook diet. However in 2009, the proportion of hymenopterans in the diet was slightly higher than the proportion in drift and almost twice as much as the proportion in the infall. The percent dissimilarity of terrestrial taxa between diet to drift was lower than the percent dissimilarity between diet to infall in both years (respectively, 2008: 65% vs. 70%; 2009: 51% vs. 77%), indicating that terrestrial invertebrates consumed by juvenile Chinook were more closely represented by terrestrial invertebrates in the drift than in infall samples. This lack of overlap between infall and diet was primarily due to differences in levels of abundance between sample types, not differences in terrestrial invertebrate taxa.

Effects of discharge and stream temperature on predation by juvenile Chinook

Total prey mass consumed was negatively correlated with river discharge in 2009 and both years combined, but was negligibly correlated in 2008 (Pearson's correlation; 2008: $r = -0.10$, $P = 0.29$, 2009: $r = -0.35$, $P < 0.001$; combined: $r = -0.23$, $P < 0.001$). The proportion of terrestrial prey mass consumed was negligibly correlated with discharge in 2008 and in both years combined, but had a marginal negative correlation with discharge in 2009 (Pearson's correlation; 2008: $r = 0.05$, $P = 0.65$; 2009: $r = -0.14$, $P = 0.02$, combined: $r = 0.07$, $P = 0.17$).

Total invertebrate prey mass consumed was positively correlated with water temperature for 2009 and both years combined, and had a non-significant positive correlation in 2008 (Pearson's correlation; 2008: $r = 0.09$, $P = 0.38$; 2009: $r = 0.26$, $P < 0.001$; combined: $r = 0.22$, $P < 0.001$). The proportion of terrestrial prey mass consumed was not significantly correlated with water temperature in either 2008 or 2009, but had a marginal negative correlation with the water temperature of both years combined (Pearson's correlation; 2008: $r = -0.13$, $P = 0.18$; 2009: $r = 0.03$, $P = 0.65$; combined: $r = -0.11$, $P < 0.04$). In addition, water temperature and discharge were negatively correlated for each individual year and both years combined (Pearson's correlation; 2008: $r = -0.25$, $P = 0.01$; 2009: $r = -0.51$, $P < 0.001$; combined: $r = -0.47$, $P < 0.001$).

Discussion

Availability of terrestrial invertebrates via infall and drift

Terrestrial invertebrate infall in the Chena River was highly variable throughout the summer and between years, showing no consistent pattern between the two years of our study. However within each summer, we observed a similar pattern by date between the mass of aquatic and terrestrial invertebrates, even though the life history (e.g. hatches, number of generations per summer, and emergence dates) are presumably different between these two distinct categories. That we observed both aquatic and terrestrial invertebrates following the same pattern of infall into the Chena suggests that climate (i.e. wind patterns, air temperature, humidity, and precipitation) may have greater control on invertebrate infall than an individual taxon's life history. Also related to climate, we observed higher terrestrial invertebrate infall in 2009 relative to 2008. This could be due to lower air temperatures in 2008. On average near the Chena River, the air temperature in May-September was 2.5° C cooler in 2008 than in 2009. Previous research documented increasing air temperatures coinciding with an increase in quantity of invertebrates entering streams (Nelson, 1965; Edwards & Huryn, 1995; Romero *et al.*, 2005).

The mean terrestrial infall for both summers (25 ± 5 mg dry mass m^{-2} d^{-1}) was on the low end compared to published values of summer terrestrial infall, ranging from 1.3 mg dry mass m^{-2} d^{-1} in a small New Zealand pasture stream to a high of 112 mg dry mass m^{-2} d^{-1} in the Horonai Stream in Japan (Baxter *et al.*, 2005). A study of small coniferous streams in southeast Alaska found a mean terrestrial infall of 37 mg dry mass $m^{-2}d^{-1}$

(Wipfli 1997). Another study, also in Alaska, found a mean terrestrial infall of 83.3 mg dry mass m^{-2} d^{-1} in small to mid-size coniferous streams (Allan *et al.*, 2003). Several plausible ecological mechanisms could explain the low mean terrestrial infall mass into the Chena River compared to other lotic systems. One of the reasons we found decreased terrestrial inputs per unit area may be due to the Chena River being a larger river system than the streams in the previously mentioned Alaskan studies. The river continuum concept predicts that allochthonous inputs decrease per unit area as one heads downstream because of the increased volume of water relative to the stream edge, which most likely would result in decreased allochthonous inputs per unit area (Vannote *et al.*, 1980; Polis *et al.*, 1997; Baxter *et al.*, 2005). A study in Virginia that examined the difference in terrestrial infall rate in different order (e.g. size) streams found that a 2^{nd} order stream site had over 5 times the mean mass of infall than a 6^{th} order river site (Cloe & Garman, 1996). Another possible reason could be due to our sample design of leaving our pan traps out for only one day, which resulted in the potential for missing pulses of terrestrial infall. In other terrestrial infall studies conducted in Alaska, pan traps were left out for one to two weeks (Wipfli, 1997; Allan *et al.*, 2003). We chose to collect infall samples over a relatively short 24 h period to avoid disturbance from regular motor boat traffic since we were concerned about our pan traps getting swamped.

Drift of terrestrial invertebrates was highly variable by date and year, and we found few consistent or discernible patterns within two years of sampling. Both summers we saw an early season peak in terrestrial and aquatic invertebrate drift which may have been related to invertebrate life cycles or thermal mechanisms such a number of degree days, water, and air temperature (Mason & Macdonald, 1982; Brittain & Eikeland, 1988). Terrestrial invertebrates composed approximately 24% of the total drift for both years. Yet, on occasion, the mean mass of terrestrial invertebrate drift nearly equaled the mean mass of aquatic invertebrate drift. The relative proportion of terrestrial invertebrate drift was comparable to other studies conducted in temperate streams which showed similar trends that at times terrestrial invertebrates contributed as high or greater mass to the drift than aquatic invertebrates (Cloe & Garman, 1996; Romaniszyn *et al.*, 2007). In temperate zones, terrestrial invertebrate drift is known to peak in availability during the summer (Cloe & Garman, 1996; Bridcut, 2000).

Terrestrial invertebrates as prey for juvenile Chinook

The quantity of terrestrial invertebrates in the diet of juvenile Chinook varied throughout the summer, with a mean of 19 ± 3% terrestrial invertebrate mass consumed in both summers combined. Late in the summer, terrestrial invertebrates comprised up to 38% of the total diet on several dates. In small streams, juvenile salmonid diet has been found to consist of up to 50%-72% terrestrial invertebrates of the prey mass consumed (Wipfli, 1997; Nakano *et al.*, 1999b; Eberle, 2007). Although the highest proportion of terrestrial invertebrates consumed was lower in the Chena than in many smaller streams, the reality that terrestrial invertebrates contributed up to 39% of the total juvenile Chinook diet is notable because of the magnitude and since few studies have examined the importance of terrestrial invertebrates for juvenile fish in mid-size or large rivers (Baxter *et al.*, 2005; Paetzold *et al.*, 2008).

Juvenile Chinook consumed more terrestrial invertebrates towards the end of the summer season. Higher consumption of terrestrial invertebrates has been observed in late summer and fall in Oregon, West Virginia, Kamchatka, and Idaho (Romero *et al.*, 2005; Webster & Hartman, 2005; Eberle & Stanford, 2010; Rosenberger *et al.*, 2011). The increase in terrestrial invertebrate consumption in the Chena may have been due to decreased aquatic invertebrate availability in 2008 since the increase in terrestrial invertebrate consumption coincided with an overall decrease in drifting aquatic invertebrate mass. However, we did not see this pattern in 2009 where a late summer increase in terrestrial invertebrate consumption occurred, even though a decrease in drifting aquatic invertebrate mass was not observed. The increase in terrestrial invertebrate consumption could also be due to increased gape size of the fish with summer growth and, therefore, a greater ability to capture large forms of prey such as terrestrial invertebrates (Elliott, 1994). Terrestrial invertebrates are recognized to be a larger and higher energy food source than aquatic invertebrates, and drift feeding fish are known to preferentially select large prey (Edwards & Huryn, 1996; Nakano *et al.*, 1999b). An increase in terrestrial invertebrate consumption could be important bioenergetically as summer is when fish store fat and increase body size which is important for overwinter survival (Reimers, 1963; Mason, 1976). Larger body length and rapid growth in juvenile salmonids have been found to increase overwinter survival and most likely lead to increased marine survival (Quinn & Peterson, 1996; Ruggerone *et al.*, 2009). Thus, terrestrial prey may provide an important energy subsidy at a critical stage for survival.

The terrestrial invertebrates that were important prey items for juvenile Chinook in the Chena River were adult Hymenoptera, Araneae, and aphids (Hemiptera). An outbreak of aphids in 2009 (Gutierrez, personal observation) was reflected in the infall traps, the drift, and in the diet, suggesting that juvenile Chinook can capitalize and respond to incidents of high abundances of terrestrial invertebrates. Still, the main staple of the juvenile Chinook diet were chironomids in all their life stages. A study investigating the diet of juvenile Chinook smolts in a nearby Alaskan river (the Salcha River) reported finding that chironomids were the main prey item consumed early in the season as well (Loftus & Lenon, 1977).

Relationship between invertebrate infall, drift, and predation by fishes

The composition of invertebrate taxa in the infall and drift did not match well with the composition of prey consumed by juvenile Chinook salmon. The mean percent dissimilarity between drift and diet, and infall and diet was 74% and 75%, respectively, suggesting that neither sampling method collected invertebrates that overlapped completely with the juvenile Chinook diet. This makes sense as infall samples primarily catch terrestrial and winged adult aquatic invertebrates, while drift samples theoretically mimic what invertebrates are drifting in the river, but may be excluding terrestrial invertebrates floating on the water surface and may be composed of invertebrates post fish-selection (i.e. the fish already consumed invertebrates out of the drift). However, the ordination comparing only terrestrial invertebrates showed a higher overlap between invertebrates in the drift and diet rather than invertebrates in the infall. This suggests that terrestrial invertebrates in the juvenile Chinook diet were more closely related in quantity and composition to terrestrial invertebrates in the drift than those captured by the pan traps.

SIMPER analysis of all invertebrates consumed determined that adult chironomids and hymenopterans were the taxa that had the most dissimilar proportions between diet to drift and diet to infall. In the diet to drift comparison for both 2008 and 2009, juvenile Chinook consumed a greater proportion of chironomids and hymenopterans than were in the drift implying selectivity for these taxa and that these taxa might have been consumed before entering the drift. These results support our findings from the IRI analysis which showed that chironomids and hymenopterans were in the top six most important taxa consumed by juvenile Chinook in both years. Our SIMPER results comparing diet to infall showed a larger proportion of chironomids in the infall samples than the proportion consumed which suggests that juvenile Chinook consumed adult chironomids at a lower proportion than was falling in, although this difference could be an artifact of the sampling method. Pan traps may collect higher proportions of certain taxa such as winged Diptera and thus might suggest a higher availability in the environment than is actually there (Edwards & Huryn, 1995; Wipfli, 1997). Another possible bias in a comparison between a predator and its potential prey is that the comparison assumes that the collection methods are spatially and temporally compatible. By site and date, the drift nets were set out at different distances from the riverbank depending on woody debris presence and river discharge, e.g. when discharge was high we anchored the drift nets closer into the bank due to water velocity being too fast where we had previously placed the drift nets at lower discharge. Yet, the infall traps were consistently set out at the same distance from the bank over the course of the study. Indirectly, the constantly changing distance of the drift nets may have better mimicked the opportunistic foraging habits of juvenile fish.

Our SIMPER analysis of only terrestrial invertebrates consumed placed Hymenoptera as the taxa that had the most dissimilar abundance between diet to drift and diet to infall. By IRI, the importance of Hymenoptera was rated 6th out of the top 10 most important taxa for both 2008 and 2009. Several diet studies have recently documented one or two species of terrestrial invertebrates as being particularly important for the diet of fish in their region. Studies in West Virginia streams noted the importance by mass of adult terrestrial Lepidoptera in the diet of brook trout (Webster & Hartman, 2005; Utz & Hartman, 2007), as well as the Coleopteran family Scarabaeidae by bioenergetic estimates (Utz *et al.*, 2007). In California during March through July, terrestrial Isopoda was identified as the taxa with the highest proportion mass in the diet of juvenile steelhead trout (Rundio & Lindley, 2008). In our study, we documented through the measure of mass, as well as IRI and SIMPER analysis, that adult hymenopterans are one of the most important terrestrial invertebrate prey items for juvenile Chinook salmon in the Chena River.

Effects of discharge and stream temperature on predation by juvenile Chinook

Stream temperature and discharge had variable influences on juvenile Chinook predation. Total mass consumed by juvenile Chinook was not correlated with river discharge in

2008, but was negatively correlated in 2009 and both years combined. A negative correlation between total mass consumed and discharge indicates that, at high discharge, fish are consuming a lower mass of invertebrates, and vice versa. Yet, high discharge also increases the availability of benthic and aquatic invertebrates, which may result in more prey available to fish (O' Brian & Showalter, 1993; Romaniszyn *et al.*, 2007). High discharge, however, may pass threshold levels at which physical factors begin to scour the stream bed causing a delayed decrease in aquatic invertebrate availability and taxonomic richness, as well as a decrease in prey consumption (Scrimgeour & Winterbourn, 1989; Quinn & Hickey, 1990; Perry *et al.*, 2003). In addition, high discharge can cause increased turbidity, and high turbidity has been shown to reduce fish's consumption of available prey (Berg *et al.*, 1985). In the Chena River, spates of high discharge may have caused a temporary decrease in aquatic invertebrate availability and reduced juvenile Chinook's ability to detect and capture prey leading to our result of a negative correlation between total mass consumed and discharge.

Particularly high discharge and flood events may increase terrestrial invertebrate infall by increasing the wetted perimeter of a river bank and sweeping terrestrial invertebrates into the river by overland flow (Layzer *et al.*, 1989; Edwards & Huryn, 1995). Although we found no significant correlation between the proportion of terrestrial invertebrates consumed and discharge, our study found that the two sampling dates with the highest proportion of terrestrial invertebrates consumed by juvenile Chinook occurred after a late summer 60-year flood in 2008. A possible explanation for this is that a high discharge threshold was reached, and the flood may have scoured the stream bed, decreasing the amount of aquatic invertebrates, which may have caused the juvenile Chinook to switch to terrestrial prey. Several studies suggested that fish may switch to terrestrial invertebrates when aquatic invertebrate abundance or mass are low (Cloe & Garman, 1996; Nakano & Murakami, 2001; Romero *et al.*, 2005). A comparison between terrestrial invertebrate availability in both summers reveals that the mass of terrestrial infall and the proportion of terrestrial invertebrates in the drift were higher in 2009 than in 2008. Thus, availability was higher in 2009 than in 2008, but a greater mass of terrestrial invertebrates were consumed in 2008. One potential explanation is that the 60-year flood in 2008 may have caused an increase in the yearly mean of terrestrial invertebrates consumed. This is circumstantial evidence as we were not able to sample diet, infall, or drift during the flood since the discharge was too high for sampling. However, this indicates that terrestrial invertebrates may not only be more important later in the summer, but also after high discharge events.

We also evaluated stream temperature as a possible factor of how important terrestrial invertebrates are to juvenile Chinook, as fish are known to have higher metabolic needs and consume greater amounts as temperature increases (Elliott, 1994). Our results support this: we found a positive correlation between water temperature and mean mass consumed for 2008 and 2009, and for both years combined. However, when we examined the relationship between proportion of terrestrial invertebrates consumed and water temperature, we found no significant correlation in each individual year and a negative correlation for both years combined. Our results also showed a strong negative correlation between river discharge and water temperature. The negative correlation between terrestrial invertebrates consumed and water temperature may have been driven by the inverse relationship between water temperature and discharge. When water temperature dropped due to periods of high discharge, the scouring of the stream bed may have led to a decrease in aquatic invertebrate abundance and therefore an increase in the proportion of terrestrial invertebrates consumed.

Conclusions

Terrestrial infall, drift, and predation by juvenile Chinook in the Chena River were highly variable by date and by season. The diet of age-0+ juvenile Chinook salmon was primarily made up by aquatic invertebrates, largely all life stages of chironomids. Adult hymenopterans were the most important terrestrial prey for juvenile Chinook, which also capitalized in 2009 on an increased availability of aphids. This illustrates the link between riparian forests, the invertebrates they support, and the flow of terrestrial prey into rivers that subsidizes the prey base for aquatic consumers, in this case, fish. Terrestrial invertebrate consumption by juvenile Chinook in the Chena River should not be discounted as the percent of prey mass consumed reached up to 38% on three different sampling dates. Our study indicates that both aquatic and terrestrial invertebrates are important prey resources for juvenile Chinook salmon in the Chena River, with terrestrial prey ingestion increasing through the summer and potentially after periods of high discharge. As terrestrial prey subsidies can be a key food source for stream fish, it is important to understand what may drive the variability of terrestrial infall, drift, and consumption by fish.

Table 1. Sample size of terrestrial infall, drifting invertebrates, and juvenile Chinook salmon diet samples collected in the Chena River, Alaska during the summers of 2008 and 2009. Mean (± SE) length and weight are also reported for the juvenile Chinook salmon.

Date	Terrestrial infall	Invertebrate drift	Juvenile Chinook diet		
	n	*n*	*n*	Length	Weight*
2008					
11-Jun	15	3	10	38.1 ± 0.6	na
16-Jun	12	3	15	42.5 ± 1.0	na
30-Jun	14	4	16	52.0 ± 1.3	na
14-Jul	14	4	16	62.6 ± 1.2	na
12-Aug	13	2	14	69.7 ± 1.0	na
25-Aug	16	3	12	72.4 ± 0.7	na
9-Sep	15	4	15	73.4 ± 1.8	na
25-Sep	na	4	7	69.0 ± 2.2	na
2009					
26-May	9	6	25	37.6 ± 0.4	0.3 ± 0
8-Jun	14	8	39	37.3 ± 0.4	0.3 ± 0
22-Jun	11	5	15	39.8 ± 0.9	0.4 ± 0
6-Jul	11	6	34	42.6 ± 1.3	0.8 ± 0.1
20-Jul	21	6	31	52.5 ± 2.5	2.0 ± 0.2
3-Aug	16	7	37	66.4 ± 0.7	3.2 ± 0.1
18-Aug	16	7	36	71.9 ± 0.7	4.2 ± 0.1
14-Sep	15	6	16	77.8 ± 1.4	5.5 ± 0.3

*Weight data from 2008 were not available (na).

Table 2. Repeated measures ANOVA of the effects of site, year, year*site, date, and date*year on the mass of aquatic (AI), terrestrial (TI), and total (both AI and TI) invertebrates by infall (mg / m^2), drift (mg / m^3), and juvenile Chinook salmon diet (mg / fish).

		Infall			Drift			Diet		
		AI	**TI**	**Total**	**AI**	**TI**	**Total**	**AI**	**TI**	**Total**
Site	df	3, 205	3, 205	3, 205	3, 77	3, 77	3, 77	3, 330	3, 330	3, 330
	F	3.14	0.67	2.49	2.18	1.07	1.65	2.56	6.63	4.18
	P	0.044	0.580	0.085	0.233	0.457	0.313	0.065	**< 0.001**	**0.010**
									***	*
Year	df	1, 205	1, 205	1, 205	1, 77	1, 77	1, 77	1, 330	1, 330	1, 330
	F	67.58	11.18	82.01	0.59	2.12	0.99	0.13	5.14	0.94
	P	**< 0.001**	**0.003**	**< 0.001**	0.485	0.219	0.377	0.721	**0.028**	0.338
		***	**	***					*	
Year * Site	df	3, 205	3, 205	3, 205	3, 77	3, 77	3, 77	3, 330	3, 330	3, 330
	F	1.10	2.48	2.98	4.36	6.41	4.12	0.13	3.22	0.59
	P	0.369	0.086	0.052	0.094	0.052	0.103	0.940	**0.030**	0.625
									*	
Date	df	28, 205	28, 205	28, 205	28, 77	28, 77	28, 77	27, 330	27, 330	27, 330
	F	1.51	2.53	1.64	3.47	2.33	3.02	3.09	3.86	4.03
	P	0.067	**< 0.001**	0.035	**0.005**	0.036	**0.010**	**< 0.001**	**< 0.001**	**< 0.001**
			***		**		**	***	***	***
Date * Year	df	25, 205	25, 205	25, 205	21, 77	21, 77	21, 77	21, 330	21, 330	21, 330
	F	2.34	1.81	2.52	4.49	3.78	4.58	2.66	1.49	2.23
	P	**0.001**	**0.018**	**< 0.001**	**0.001**	**0.004**	**0.001**	**< 0.001**	0.081	**0.002**
		**	*	***	**	**	**	***		**

* *P* values in bold are significant. The stars (*, **, ***) indicate the level of significance. *P* * < 0.03, *P* ** < 0.017, *P* *** < 0.001

Table 3. Top 10 invertebrate prey consumed by juvenile Chinook salmon in the Chena River in the summers of 2008 and 2009. Prey importance for invertebrate taxa in the diet was determined using the Index of Relative Importance which combines proportion by weight, proportion by number, and frequency of prey occurrence to form one compound index (Pinkas, Oliphant, & Iverson, 1971). Terrestrial taxa are highlighted in bold.

IRI rank	Order	Family	Life stage	Source	Prop. mass	Prop. number	Freq.
2008							
1	Diptera	Chironomidae	larva	aquatic	0.04	0.50	0.66
2	Plecoptera	Chloroperlidae	larva	aquatic	0.05	0.03	0.24
3	Diptera	Chironomidae	adult	aquatic	0.03	0.09	0.36
4	Ephemeroptera	Baetidae	larva	aquatic	0.04	0.04	0.24
5	Diptera	Chironomidae	pupa	aquatic	0.03	0.13	0.30
6	**Hymenoptera**	**unknown**	**adult**	**terrestrial**	**0.08**	**0.01**	**0.09**
7	Diptera	Simuliidae	larva	aquatic	0.02	0.06	0.34
8	Plecoptera	Perlodidae	larva	aquatic	0.05	0.01	0.09
9	**Araneae**	**unknown**	**adult**	**terrestrial**	**0.03**	**0.01**	**0.09**
10	Diptera	Empididae	adult	aquatic	0.07	0.01	0.07
2009							
1	Diptera	Chironomidae	adult	aquatic	0.30	0.39	0.63
2	Diptera	Chironomidae	larva	aquatic	0.06	0.30	0.82
3	Diptera	Chironomidae	pupa	aquatic	0.03	0.10	0.67
4	**Hemiptera**	**Aphididae**	**adult**	**terrestrial**	**0.02**	**0.07**	**0.41**
5	Plecoptera	Chloroperlidae	larva	aquatic	0.05	0.03	0.30
6	**Hymenoptera**	**unknown**	**adult**	**terrestrial**	**0.11**	**0.01**	**0.14**
7	Diptera	Empididae	adult	aquatic	0.05	0.01	0.13
8	Plecoptera	unknown	larva	aquatic	0.03	0.01	0.16
9	Ephemeroptera	Baetidae	larva	aquatic	0.02	0.01	0.17

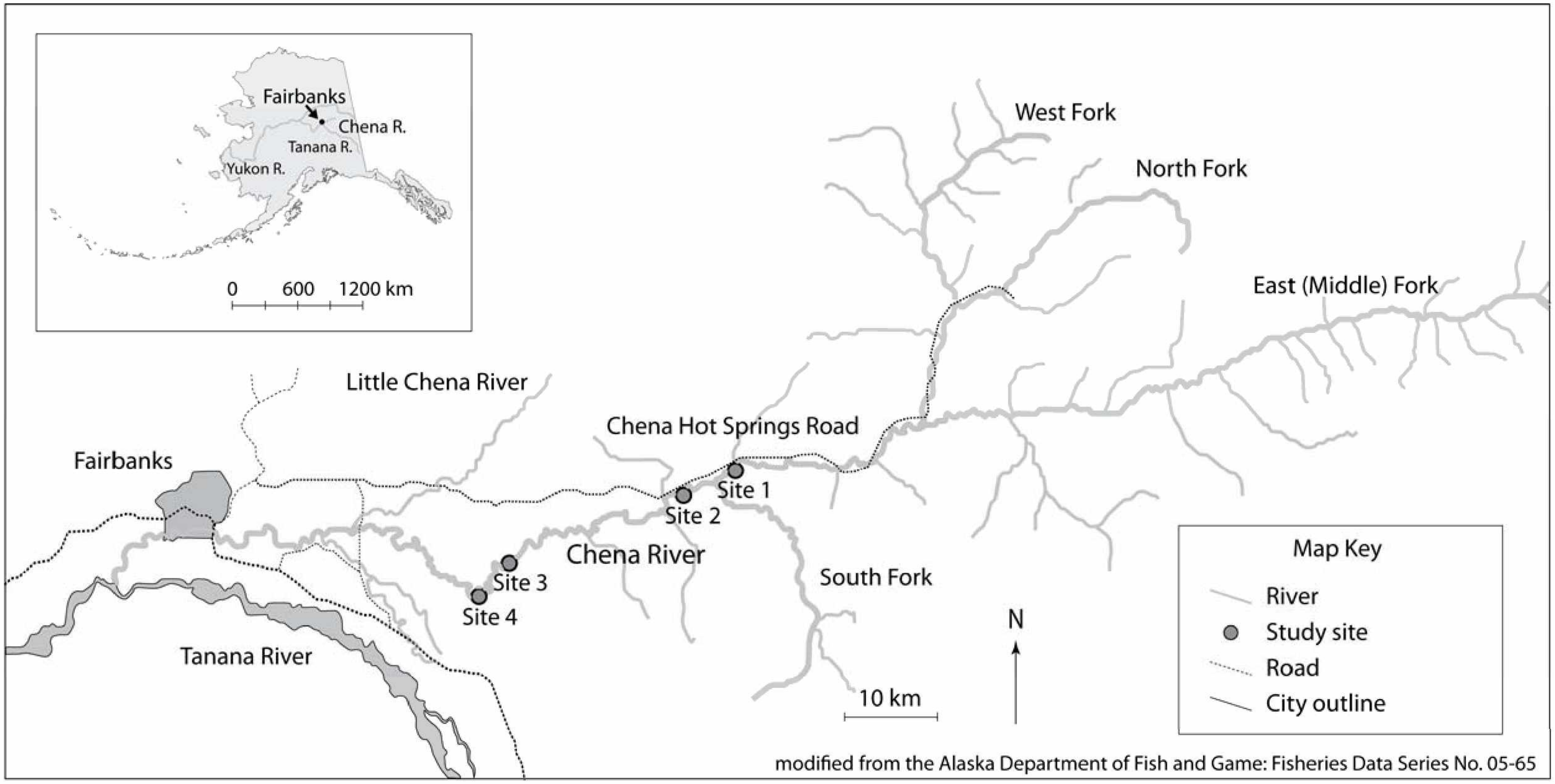

Fig. 1 Sample sites for a study on terrestrial infall, invertebrate drift, and juvenile Chinook diet on the Chena River, Alaska 2008-2009.

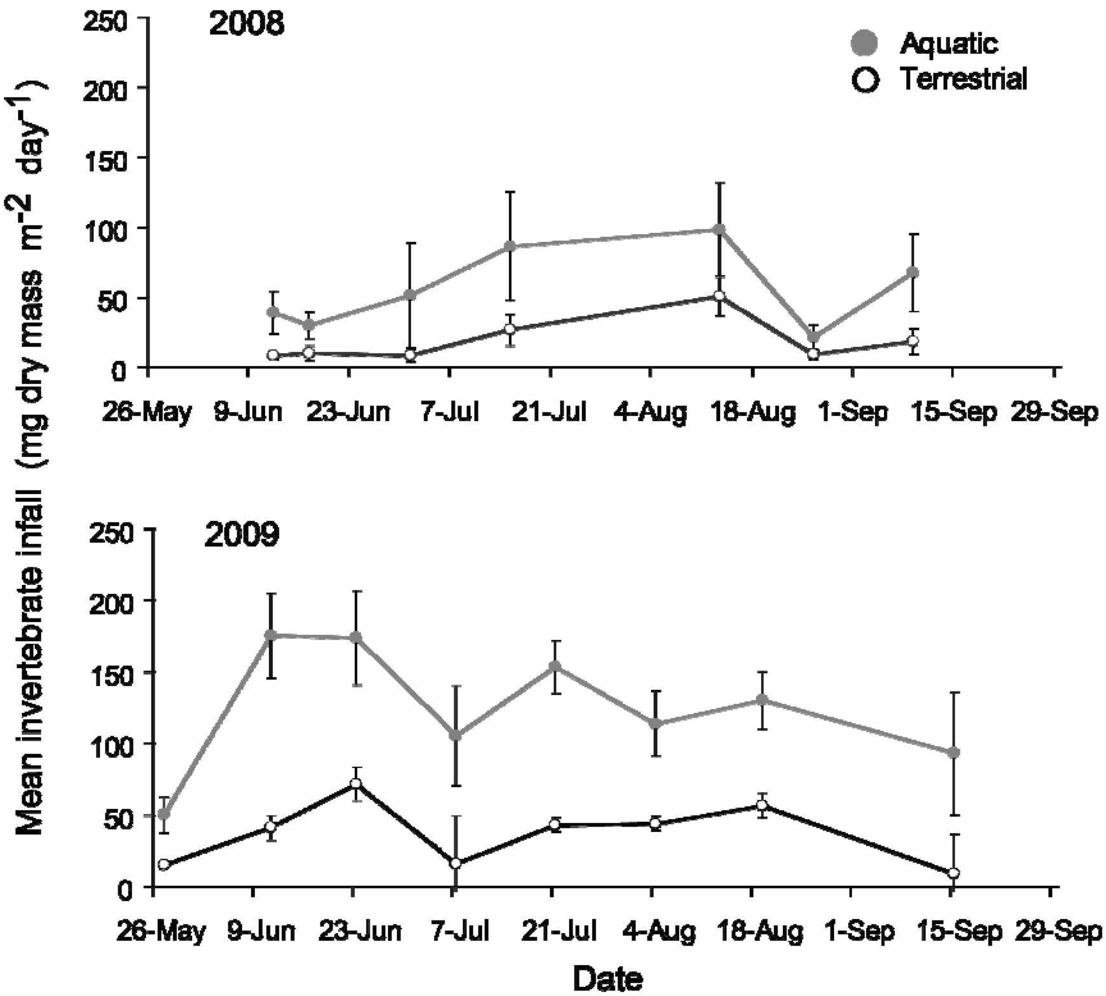

Fig. 2 Invertebrate infall (mean ± SE) by origin source (aquatic and terrestrial) into the Chena River, Alaska during the summers of 2008 and 2009.

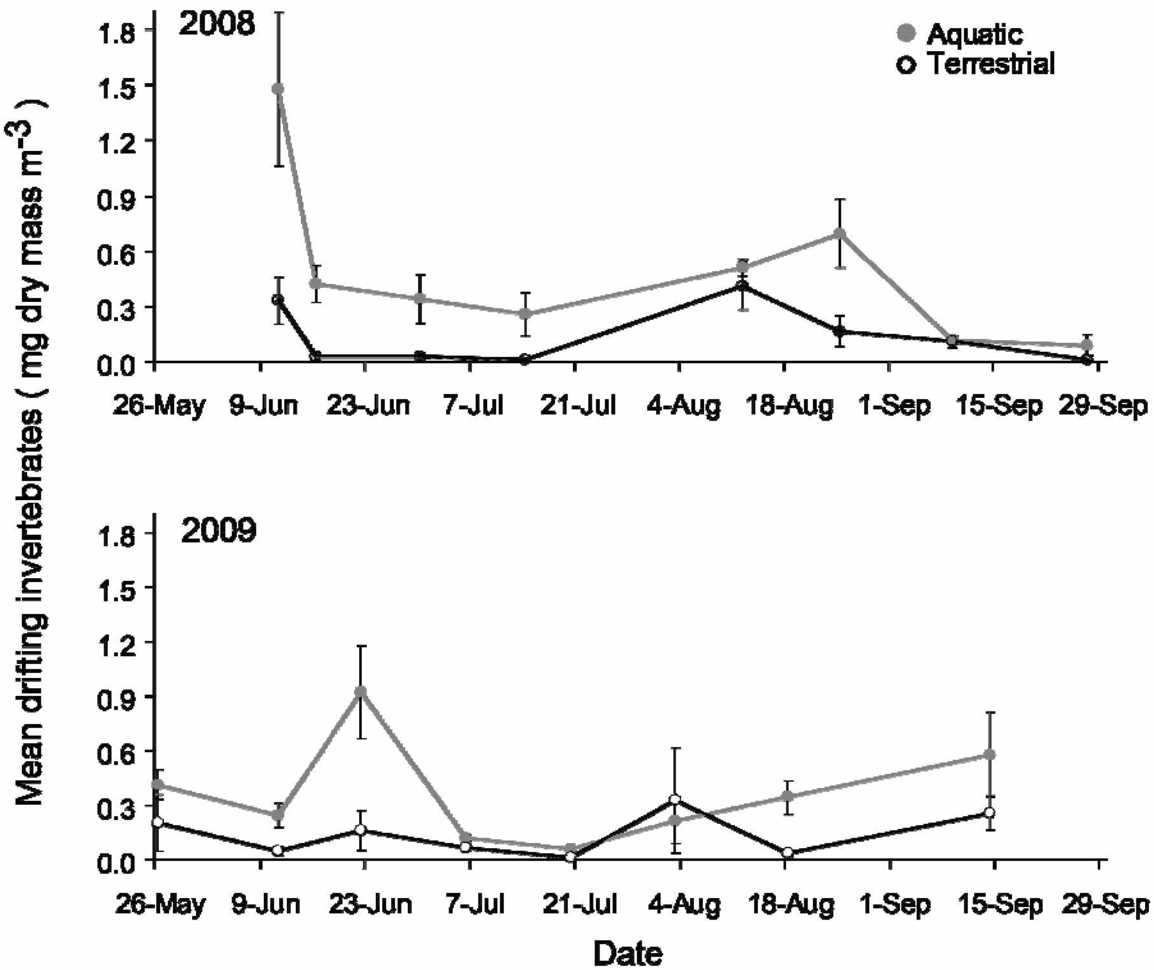

Fig. 3 Drifting invertebrates (mean ± SE) by origin source (aquatic and terrestrial) in the Chena River, Alaska during the summers of 2008 and 2009.

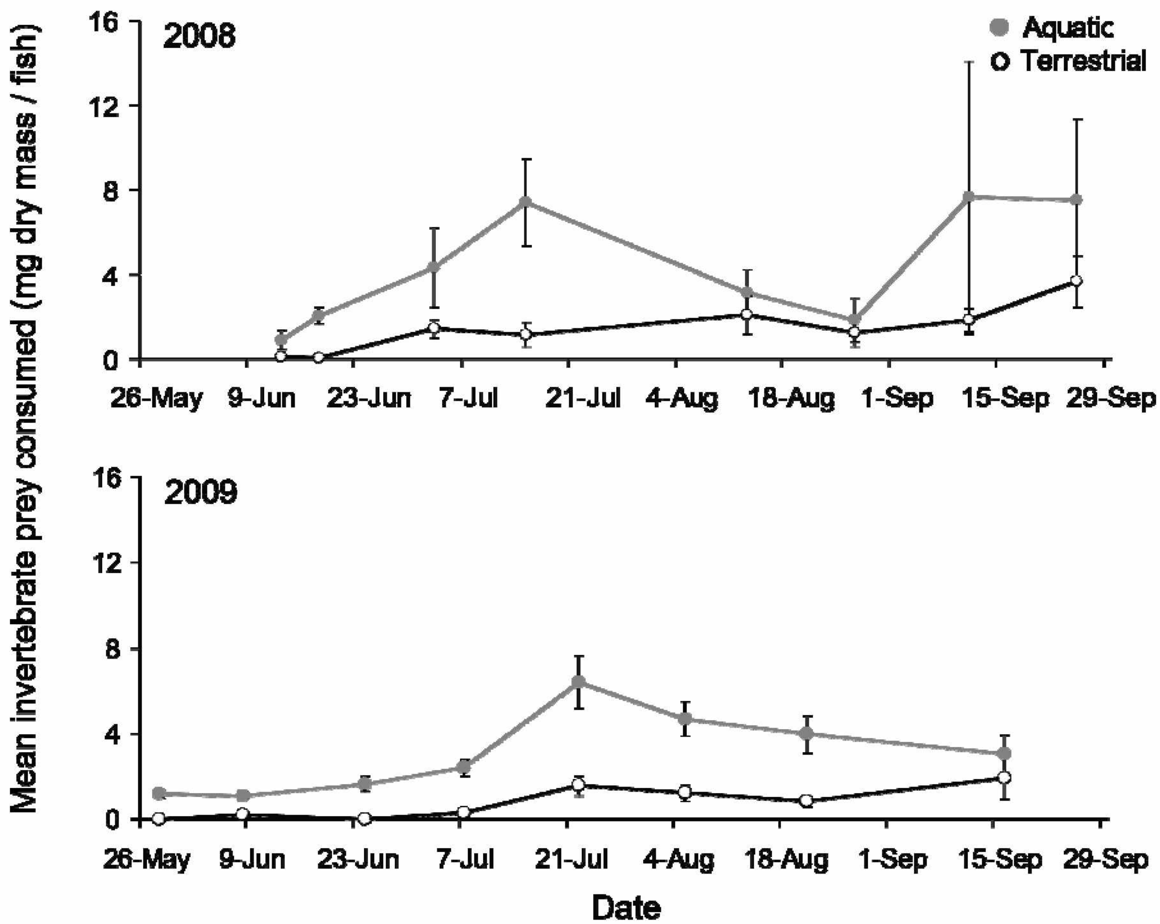

Fig. 4 Prey mass consumed (mean ± SE) by juvenile Chinook salmon broken down into origin source (aquatic and terrestrial) in the Chena River, Alaska during the summers of 2008 and 2009.

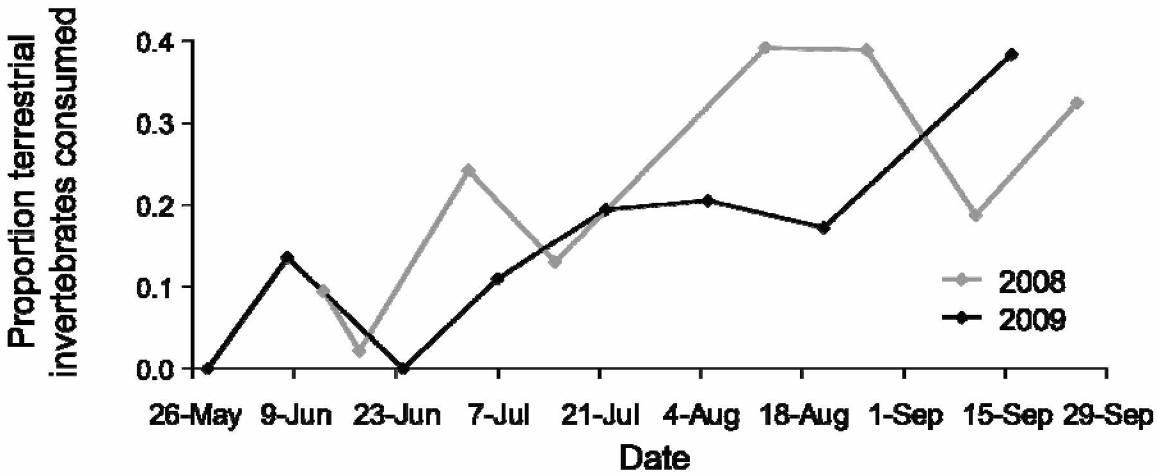

Fig. 5 Proportion terrestrial invertebrates consumed by juvenile Chinook salmon in the Chena River during the summers of 2008 and 2009.

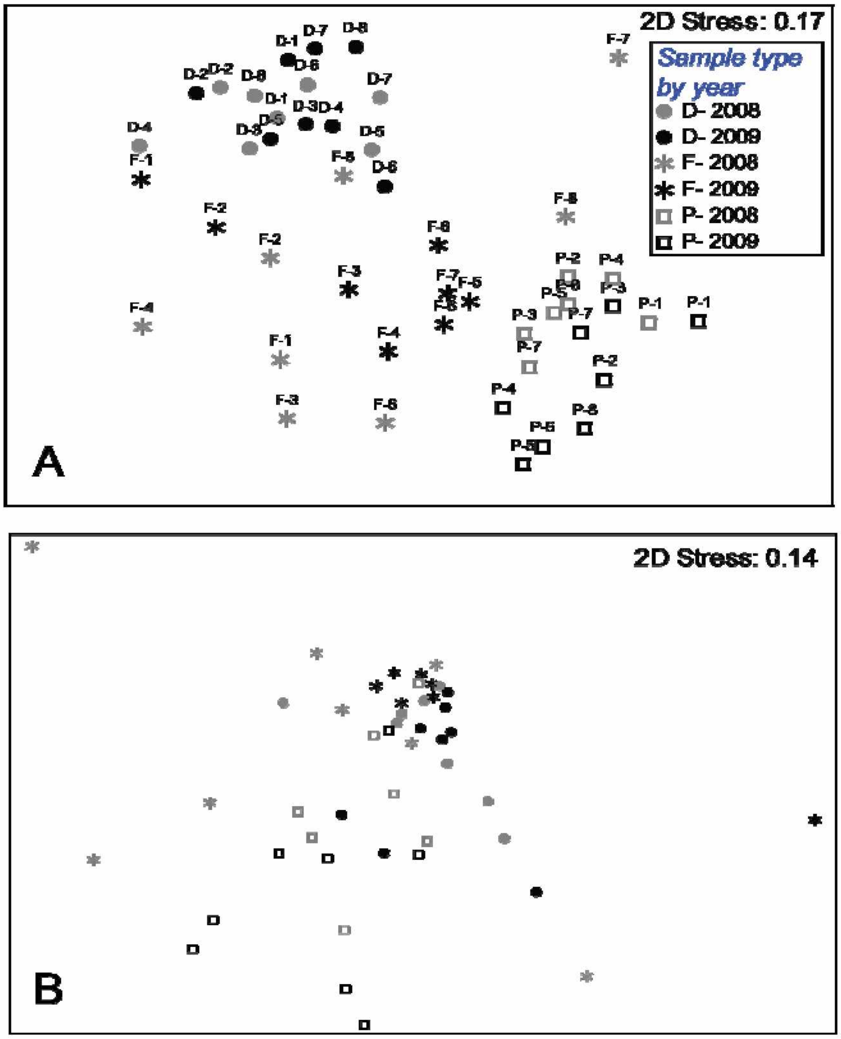

Fig. 6. Multidimensional scaling ordination of the mean proportion by mass of the top 95% invertebrate families and life stages for each sample date in the Chena River, Alaska during the summers of 2008 and 2009. Sample type refers to F = fish diet, D = invertebrate drift, P = invertebrate infall; sample date 1-8 represents each of 8 sampling events between May-September. Graph (a) includes all invertebrate taxa, and graph (b) includes only taxa of terrestrial origin. Samples points that are plotted closer together have greater similarity in invertebrate community composition.

References

Allan, J.D., Wipfli, M.S., Caouette, J.P., Prussian, A. & 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.

Baumgärtner, D. & Rothhaupt, K.O. (2003) Predictive length-dry mass regressions for freshwater invertebrates in a pre-alpine lake littoral. *International Review of Hydrology,* **88,** 453-463.

Baxter, C.V., Fausch, K.D. & Saunders, C.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. & 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,* **18,** 308-343.

Berg, L. & Northcote, T.G. (1985) Changes in territorial, gill-flaring, and feeding behavior in juvenile Coho-salmon *(Oncorhynchus kisutch)* following short-term pulses of suspensed sediment. *Canadian Journal of Fisheries and Aquatic Sciences,* **42,** 1410-1417.

Brase, A.L.J. & Doxey, M. (2006) Salmon studies in the Chena, Chatanika, Delta, Clearwater, and Salcha Rivers, 2004 and 2005. Alaska Department of Fish and Game). Fishery Data Report No. 06-61.

Bridcut, E.E. (2000) A study of terrestrial and aerial macroinvertebrates on river banks and their contribution to drifting fauna and salmonid diets in a Scottish catchment. *Hydrobiologia,* **427,** 83-100.

Brittain, J.E. & Eikeland, T.J. (1988) Invertebrate drift - A review. *Hydrobiologia,* **166,** 77-93.

Brodeur, R.D., Daly, E.A., Benkwitt, C.E., Morgan, C.A. & Emmett, R.L. (2010) Catching the prey: Sampling juvenile fish and invertebrate prey fields of juvenile coho and Chinook salmon during their early marine residence. *Fisheries Research,* **108,** 65-73.

Burgherr, P. & Meyer, E.I. (1997) Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Archiv für Hydrobiologie,* **139,** 101-112.

Cai, Y., Guo, L., Douglas, T.A. & Whitledge, T.E. (2008) Seasonal variations in nutrient concentrations and speciation in the Chena River, Alaska. *Journal of Geophysical Research,* **113,** 1-11.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology,* **18,** 117-143.

Cloe, W.W. & Garman, G.C. (1996) The energetic importance of terrestrial arthropod inputs to three warm-water streams. *Freshwater Biology,* **36,** 104-114.

Cummins, K.W., Wilzbach, M.A., Gates, D.M. & Perry, W.B. (1989) Shredders and riparian vegetation: leaf litter that falls into streams influences communities of stream invertebrates. *Biosciences,* **39,** 24-30.

Eberle, L.C. (2007) *The importance and seasonal variation of terrestrial invertebrates as prey for juvenile salmonids on the Kol RIver floodplain, Kamchatka, Russian Federation.* M.S., The University of Montana, Missoula, MT.

Eberle, L.C. & 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. & Huryn, A.D. (1995) Annual contribution of terrestrial invertebrates to a New Zealand trout stream. *New Zealand Journal of Marine and Freshwater Research,* **29,** 467-477.

Edwards, E.D. & Huryn, A.D. (1996) Effect of riparian land use on contributions of terrestrial invertebrates to streams. *Hydrobiologia,* **337,** 151-159.

Elliott, J.M. (1994) *Quantitative ecology of the brown trout,* Oxford University Press.

Garman, G.C. (1991) Use of terrestrial arthropod prey by a stream-dwelling cyprinid fish. *Environmental Biology of Fishes,* **30,** 325-331.

Gruner, D.S. (2003) Regression of length and width to predict arthropod biomass in the Hawaiian islands. *Pacific Science,* **57,** 325-336.

Hodar, J.A. (1996) The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica,* **17,** 421-433.

Hodar, J.A. (1997) The use of regression equations for the estimation of arthropod biomass in diet studies of insectivore vertebrates. *Miscellania Zoologica,* **20,** 1-10.

Johnson, M.D. & Strong, A.M. (2000) Length-weight relationships of Jamaican arthropods. *Entomological News,* **111,** 270-281.

Kawabata, K. & Urabe, J. (1998) Length-weight relationships of eight freshwater planktonic crustacean species in Japan. *Freshwater Biology,* **39,** 199-205.

Kawaguchi, Y. & 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.

Kawaguchi, Y., Taniguchi, Y. & Nakano, S. (2003) Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. *Ecology,* **83,** 701-708.

Layzer, J.B., Nehus, T.J., Pennington, W., Gore, J.A. & Nestler, J.M. (1989) Seasonal variation in the composition of the drift below a peaking hydroelectric project. *Regulated Rivers: Research & Management,* **3,** 29-34.

Liao, H., Pierce, C.L. & Larscheid, J.G. (2001) Empirical assessment of indices of prey importance in the diets of predacious fish. *Transactions of the American Fisheries Society,* **130,** 583-591.

Loftus, W.F. & Lenon, H.L. (1977) Food habits of the salmon smolts, *Oncorhynchus tshawytscha* and *O. keta*, from the Salcha River, Alaska. *Transactions of the American Fisheries Society,* **106,** 235 - 240.

Mason, C.F. & Macdonald, S.M. (1982) The input of terrestrial invertebrates from tree canopies to a stream. *Freshwater Biology,* **12,** 305-311.

Mason, J.C. (1976) Response of underyearling coho salmon to supplemental feeding in a natural stream. *Journal of Wildlife Management,* **40,** 775-788.

McCune, B. & Grace, J.B. (2002) *Analysis of Ecological Communities,* MjM Software Design, Gleneden Beach, OR.

Meehan, W.R. & Miller, R.A. (1978) Stomach flushing: effectiveness and influence on survival and condition of juvenile salmonids. *Journal of Fisheries Research Board of Canada,* **35,** 1359-1363.

Meyer, E. (1989) Relationship between body length parameters and dry mass in running water invertebrates *Archiv für Hydrobiologie,* **117,** 191-203.

Miyasaka, H., Genkai-Kato, M., Miyake, Y., Kishi, D., Katano, I., Doi, H., Ohba, S. & Kuhara, N. (2008) Relationships between length and weight of freshwater macroinvertebrates in Japan. *Limnology,* **9,** 75-80.

Naiman, R.J. & Decamps, H. (1997) The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics,* **28,** 621-658.

Nakano, S., Miyasaka, H. & Kuhara, N. (1999a) Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology,* **80,** 2435-2441.

Nakano, S. & 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. & Kuhara, N. (1999b) Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in northern Japan. **14,** 351-360.

Nelson, J.M. (1965) A seasonal study of aerial insects close to a moorland stream. *Journal of Animal Ecology,* **34,** 573-579.

Nielsen, J.L. (1992) Microhabitat-specific foraging behavior, diet, and growth of juvenile salmon. *Transactions of the American Fish Society,* **121,** 617-634.

O' Brian, W.J. & Showalter, J.J. (1993) Effects of current velocity and suspended debris on the drift feeding of Arctic Grayling. *Transactions of the American Fish Society,* **122,** 609-615.

Oswood, M.W. (1997) Streams and rivers of Alaska: a high latitude perspective on running waters. In: *Freshwaters of Alaska: Ecological Syntheses.* (Eds. A.M. Milner & M.W. Oswood), pp. 331-356. Ecological Studies Series. Springer, New York.

Paetzold, A., Sabo, J.L., Sadler, J.P., Findlay, S.E.G. & Tockner, K. (2008) Aquatic-terrestrial subsidies along river corridors. In: *Hydroecology and Ecohydrology: Past, Present, and Future.* (Eds. P.J. Wood, D.M. Hannah & J.P. Sadler), pp. 57-73. John Wiley & Sons, Ltd., New York, U.S.A.

Perry, R.W., Bradford, M.J. & Grout, J.A. (2003) Effects of disturbance on contribution of energy sources to growth of juvenile chinook salmon (*Oncorhynchus tsawytscha*) in boreal streams. *Canadian Journal of Fisheries and Aquatic Sciences,* **60,** 390-400.

Pinkas, L., Oliphant, M.S. & Iverson, I.L.K. (1971) Food habits of albacore, bluefin tuna, and bonita in California waters. *California Department of Fish and Game Fish Bulletin,* **152,** 1-105.

Polis, G.A., Anderson, W.B. & Holt, R.D. (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematic,s* **28,** 289-316.

Quinn, J.M. & Hickey, C.W. (1990) Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research,* **24,** 411-427.

Quinn, T.P. & Peterson, N.P. (1996) The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. *Canadian Journal of Fisheries and Aquatic Sciences,* **53,** 1555-1564.

Reimers, N. (1963) Body condition, water temperature, and over-winter survival of hatchery-reared trout in Convict Creek, California. *Transactions of the American Fisheries Society,* **92,** 39 - 46.

Rogers, L.E., Hinds, W.T. & Buschborn, R.L. (1976) A general weight vs. length relationship for insects. *Annals of the Entomological Society of America,* **69,** 387-389.

Romaniszyn, E.D., Hutchens, J.J. & Bruce Wallace, J. (2007) Aquatic and terrestrial invertebrate drift in southern Appalachian Mountain streams: implications for trout food resources. *Freshwater Biology,* **52,** 1-11.

Romero, N., Gresswell, R.E. & 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.

Rosenberger, A.E., Dunham, J.B., Buffington, J.M. & Wipfli, M.S. (2011) Persistent effects of wildfire and debris flows on the invertebrate prey base of rainbow trout in Idaho streams. *Northwest Science,* **85,** 55-63.

Ruggerone, G.T., Nielsen, J.L. & Agler, B.A. (2009) Linking marine and freshwater growth in western Alaska Chinook salmon (*Oncorhynchus tshawytscha*). *Journal of Fish Biology,* **75,** 1287-1301.

Rundio, D.E. & Lindley, S.T. (2008) Seasonal patterns of terrestrial and aquatic prey abundance and use by *Oncorhynchus mykiss* in a California coastal basin with a Mediterranean climate. *Transactions of the American Fisheries Society,* **137,** 467-480.

Sabo, J.L., Bastow, J.L. & Power, M.E. (2002) Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of North American Benthological Society,* **69,** 387-389.

Sample, B.E., Cooper, R.J., Greer, R.D. & Whitmore, R.C. (1993) Estimation of insect biomass by length and width. *American Midland Naturalist,* **129,** 234-240.

Scrimgeour, G.J. & Winterbourn, M.J. (1989) Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia,* **171,** 33-44.

The United States and Canada Yukon River Joint Technical Committee (2009) Yukon River salmon 2008 season summary and 2009 season outlook. Regional Information Report No. 3A09-01. Alaska Department of Fish and Game, Anchorage, AK.

Utz, R. & Hartman, K. (2007) Identification of critical prey items to Appalachian brook trout (*Salvelinus fontinalis*) with emphasis on terrestrial organisms. *Hydrobiologia,* **575,** 259-270.

Utz, R.M., Ratcliffe, B.C., Moore, B.T. & Hartman, K.J. (2007) Disproportionate relative importance of a terrestrial beetle family (*Coleoptera: Scarabaeidae*) as a prey source for central Appalachian brook trout. *Transactions of the American Fisheries Society,* **136,** 177 - 184.

Uye, S. (1982) Length-weight relationships of important zooplankton from the inland Sea of Japan. *Journal of the Oceanographical Society of Japan,* **38,** 149-158.

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

Wallace, J.B., Eggert, S.L., Meyer, J.L. & Webster, J.R. (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science,* **277,** 102-104.

Webster, J.J. & Hartman, K.J. (2005) The role of terrestrial invertebrates in allopatric brook trout headwater streams in central Appalachian mountains. *Journal of Freshwater Ecology,* **20,** 101-107.

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.

General conclusions

This study found that terrestrial invertebrates were important for the diet of juvenile Chinook salmon in the Chena River, Alaska. Multiple studies have documented the importance of terrestrial invertebrates for fish (see review by Baxter *et al.*, 2005), and this study extended these findings to a mid-size, high latitude river. Terrestrial invertebrate consumption made up to 38% by mass of juvenile Chinook diet on several sampling dates, and generally increased from the beginning of the summer to late summer. The quantity of terrestrial invertebrate infall and drift was highly variable with no particular pattern throughout the season or by year. The variability of terrestrial infall and drift most likely was due to insect phenology and climatic patterns of precipitation, temperature, and wind (Bale *et al.*, 1997).

Adult Hymenoptera was the terrestrial taxon most consumed by juvenile Chinook in both years. Of total prey consumed, juvenile Chinook consumed a higher proportion of hymenopterans and adult chironomids in both 2008 and 2009 than the proportion of either available in the drift. This higher consumption suggests a possible preference for these taxa. Juvenile Chinook also capitalized on the increased availability of aphids in 2009. Furthermore, this project observed an increase in terrestrial invertebrate consumption after a 60-year flood. One of the companion studies to this project found that benthic invertebrates were negatively associated with discharge (Benson, 2010). This finding supports our conclusion that terrestrial invertebrate taxa may be particularly important after periods of high discharge when benthic and aquatic invertebrate levels may be low. This finding is not unique to our study, as several other studies have suggested that fish may switch to terrestrial invertebrates when aquatic invertebrates are less available (Cloe & Garman, 1996; Nakano & Murakami, 2001; Romero *et al.*, 2005).

Tree and plant type have been known to influence terrestrial invertebrate quantities and communities which may thereby influence food resources for fish and other species that prey upon these invertebrates (Wipfli, 1997; Allan *et al.*, 2003). Thus riparian forest management likely plays a role in regulating food resources for fish. Due to its proximity to the city of Fairbanks, there has been and will continue to be development near the Chena River. As development continues, the effects on food sources for juvenile Chinook diet should be considered.

For aquatic invertebrates, Dipteran chironomids in all their life stages were important prey in the juvenile Chinook diet. A concurrent benthic study on the Chena River found larval chironomids to be the most common taxons in 3 out of 4 study sites (Benson, 2010). The importance of chironomids for juvenile Chinook has been documented in several other lotic systems (Loftus & Lenon, 1977; Kolok & Rondorf, 1987; Miller & Simenstad, 1997). One thing to note is that this study examined juvenile Chinook diet in only one river. A study comparing the diet of juvenile Chinook in two or more mid-size rivers in Alaska or at such northern latitudes would help to further our understanding juvenile Chinook diet as well as the importance of terrestrial invertebrates in their diet.

As this project's larger goal was to improve the understanding of environmental processes that may regulate the abundance of Chinook salmon in the Chena River, this study showed that total invertebrate consumption was negatively affected by high discharge. Decreased prey consumption by juvenile fish could lead to greater mortality and eventually fewer returning adult salmon (Grant, 1993; Elliott, 1994; Milner *et al.*, 2003). Since salmon are important for fisheries users, understanding factors that control food availability for fishes and its consequential effects will aid natural resource management.

References

Allan, J.D., Wipfli, M.S., Caouette, J.P., Prussian, A. & 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.

Bale, J.S., Hodkinson, I.D., Block, W., Weeb, N.R., Coulson, S.C. & Strathdee, A.T. (1997) Life strategies of arctic terrestrial arthropods In: *Ecology of Arctic Environments.* (Ed^Eds S.J. Woodin & M. Marquiss), pp. 137-165. Blackwell Sciences Ltd, Osney Mead, Oxford.

Baxter, C.V., Fausch, K.D. & Saunders, C.W. (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology,* **50,** 201-220.

Benson, E. (2010) *Relationships between ecosystem metabolism, benthic macroinvertebrate densities, and environmental variables in a sub-arctic Alaskan river.* M.S. , University of Alaska Fairbanks, Fairbanks, Alaska.

Cloe, W.W. & Garman, G.C. (1996) The energetic importance of terrestrial arthropod inputs to three warm-water streams. *Freshwater Biology,* **36,** 104-114.

Elliott, J.M. (1994) *Quantitative ecology of the brown trout,* Oxford University Press.

Grant, J.W.A. (1993) Self-thinning in stream-dwelling salmonids. *Canadian Special Publication of Journal of Fisheries and Aquatic Sciences,* **118,** 99-102.

Kolok, A.S. & Rondorf, D.W. (1987) Effect of differential gastric evacuation and multispecies prey items on estimates of daily energy intake in juvenile Chinook salmon. *Environmental biology of fishes,* **19,** 131-137.

Loftus, W.F. & Lenon, H.L. (1977) Food habits of the salmon smolts, *Oncorhynchus tshawytscha* and *O. keta*, from the Salcha River, Alaska. *Transactions of the American Fisheries Society,* **106,** 235 - 240.

Miller, J.A. & Simenstad, C.A. (1997) A comparative assessment of a natural and created estuarine slough as rearing habitat for juvenile Chinook and Coho salmon. *Estuaries,* **20,** 792-806.

Milner, N.J., J.M. Elliott, J.D. Armstrong, R. Gardiner, J.S. Welton & Ladle, M. (2003) The natural control of salmon and trout populations in streams. *Fisheries Research,* **62,** 111-125.

Nakano, S. & 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.

Romero, N., Gresswell, R.E. & 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.

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.