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Aquatic Insect Community Structure and Secondary Production in Southcentral Alaska Streams with Contrasting Thermal and Hydrologic Regimes

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LOYOLA UNIVERSITY CHICAGO

AQUATIC INSECT COMMUNITY STRUCTURE AND SECONDARY PRODUCTION IN SOUTHCENTRAL ALASKA STREAMS WITH CONTRASTING THERMAL AND HYDROLOGIC REGIMES

A THESIS SUBMITTED TO
THE FACULTY OF THE GRADUATE SCHOOL
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To Team Science, may our bond be unbreakable.

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CHAPTER I: INTRODUCTION

Streams are naturally dynamic systems with most physical aspects exhibiting spatial and temporal heterogeneity that influence lotic macroinvertebrates. Differences in stream substrates (Minshall 1977), vegetation (Vincent 1983), discharge and temperature (Townsend et al. 1983, Bourhard et al. 1987) and channel morphology (Ward 1998, Wesche 1985) lead to variations in macroinvertebrate distribution and abundances.

Water temperature plays an integral role in the growth and development times of stream macroinvertebrates (Anderson and Cummins 1979, Vannote and Sweeney 1980). Adult size is maximized at an optimal temperature, but at nonoptimal temperatures, insects mature at smaller body sizes (Vannote and Sweeney 1980). Merritt et al. (1982) showed that an increase in stream temperatures reduced larval development time and final larval body size in blackflies (Diptera: Simuliidae), which optimally develops at a narrow range of cold temperatures.

Aquatic insect growth and development can differ appreciably in streams in close geographic proximity because of differences in water source, such as in groundwater-fed (GWF) and surface water-fed (SWF) streams. Groundwater-fed streams experience few flooding and disturbance events due to the constant flow from their water source (Gordon 2004). Temperatures in GWF streams exhibit little temporal variation (Vannote and Sweeney1980) due to the relative stability of groundwater temperatures. Macroinvertebrate community diversity in GWF streams is typically low because species composition is restricted to taxa adapted to a narrow temperature range (Vannote and Sweeney 1980).

In contrast, SWF streams, experience frequent flooding and disturbance events, and temperatures are more variable with a higher daily range than in GWF streams. Water temperatures in SWF streams are strongly influenced by the temperature of major inputs, such as precipitation and glacial melt. Macroinvertebrate diversity is generally higher in SWF streams due to the greater temperature range, which would favor a larger number of taxa (Vannote and Sweeney 1980).

In addition to groundwater or surface water inputs, channel morphology and water depth can strongly influence water temperatures (Gordon 2004). Side channels in streams are shallow with reduced current velocity. These channels are more readily warmed by solar radiation than main channel areas due to their reduced depth and increased residence time of the water (McRae and Edwards 1994, Hawkins et al. 1997). Understanding how aquatic insect community structure and function differs in areas of contrasting thermal regimes provides insights on the impact of climate change.

Effects of climate change will be most pronounced in northern latitude streams as they are expected to experience the greatest change and show effects of climate change the earliest (IPCC 2007). Northern latitude streams are predicted to have increased winter flow and more unpredictable and frequent flooding (Elsner et al. 2010). Although stream temperatures will increase with rising air temperatures, local geomorphic and hydrologic factors such as the presence of shallow side channels and the relative contribution of groundwater and surface water inputs can modify these effects (Arismendi et al. 2012). These areas may serve as early sentinels for climate change since northern latitudes are projected to experience greater temperature changes than lower latitudes.

Copper River Delta

Groundwater-fed streams along the Copper River Delta (CRD) in southcentral Alaska are stable both thermally and hydrologically year round, whereas SWF streams exhibit more variable temperatures and hydrology. Within each hydrologic type, GWF and SWF, water temperature can differ substantially in the main channel and side channels. Side channels of SWF streams on the CRD can be as much as 5°C warmer than the main channel early in the growing season (May), however differences in water temperature dissipate as the growing season progresses due to warming of the main channel. In contrast, side channel water temperatures in GWF streams are typically > 5°C warmer than the main channel and these differences are maintained throughout the growing season (G. Reeves, pers. comm.).

Groundwater and surface water- fed streams of the CRD sustain healthy populations of salmon, which are important for commercial and sport fishing along the CRD (Christensen et al. 2000). Aquatic insects are an integral component of salmon diets prior to their migration from freshwater to the marine environment (Burgner 1991). Data from previous work on coho salmon (*Oncorhynchus kisutch*) have shown higher total salmon biomass of 0+ fish in GWF than in SWF streams (G. Reeves, pers. comm.). These data also indicate that 0+ salmon are more abundant in side channels than in main channel areas (G. Reeves, pers. comm.). Although juvenile salmonid distribution can be dependent on stream velocity and channel morphology (Quinn 2005), higher densities and/or biomass of insects in side channels could also be an explanation for salmon fry congregating in these warm, calm, backwater areas, although this has not been previously studied.

The Copper River Delta (CRD), Alaska, is an ideal location to study the effects of contrasting thermal and hydrologic regimes on aquatic insect communities in vulnerable northern latitudes. The CRD is the largest contiguous wetland on the Pacific coast of North America (Thilenius 1990) and encompasses braided streams from the Copper River, glacial melt-waters and groundwater inputs. Streams on the delta are relatively pristine, have numerous side channels (Kruger & Tyler 1995), and streams in the same vicinity can have contrasting thermal and hydrologic regimes associated with being primarily GWF or SWF. These combinations of characteristics provide an opportunity to examine the effects of thermal heterogeneity (i.e. across hydrologic regimes and within streams - main channels vs. side channels) and hydrologic regimes (GWF vs. SWF) on aquatic insect community structure and secondary production.

CHAPTER II: AQUATIC INSECT COMMUNITY STRUCTURE

Introduction

Stream insect community structure is strongly influenced by a variety of regional and local environmental factors including flow permanency, substrate types (Minshall 1977), discharge and temperature regimes (Townsend et al. 1983, Bourhard et al. 1987). Milner et al. (2001) compiled a synthesis of studies examining macroinvertebrate community structure in glacier-fed streams along a temperature gradient. Results showed Baetidae (Ephemeroptera) were present in high densities at temperatures >12 °C, whereas Simuliidae (Diptera) were present in high densities > 6°C, indicating different thermal ranges. Subfamilies of Chironomidae are also known to have thermal ranges. Chironominae and Tanypodinae are prevalent in warm streams, whereas Diamesinae, Prodiamesinae and Orthocladiinae are commonly found in cooler temperatures (Beckett 1992; Coffman and de la Rosa 1998). Within cool streams, Milner et al. (2001) found that Diamesinae occurred at high densities < 6 °C, whereas Orthocladiinae was more prevalent at temperatures > 6°C.

Streams in close geographic proximity can have contrasting aquatic insect communities because of differences in water source (Friberg et al. 2001). Streams can be fed by groundwater or surface water. Groundwater-fed (GWF) streams exhibit little thermal variation (Vannote and Sweeney 1980). Macroinvertebrate community diversity in GWF streams is typically low because species composition is restricted to taxa adapted to a narrow temperature range (Vannote and Sweeney 1980). In contrast, surface water-fed (SWF) streams are more thermally variable due to the influence of temperature of major inputs such as precipitation and glacial melt. Macroinvertebrate diversity is generally higher in SWF streams due to the greater temperature range, which would favor a larger number of taxa (Vannote and Sweeney 1980).

Channel morphology and water depth can also strongly influence water temperatures (Gordon 2004). Shallow side channels are more readily warmed by solar radiation than main channel areas due to reduced depth and longer residence time of water (McRae and Edwards 1994, Hawkins et al. 1997). The effect of thermal regime on macroinvertebrate communities in streams in close geographic proximity has not been extensively studied.

Study Objectives

The goal of this project was to examine the influence of thermal and spatial heterogeneity (i.e. across hydrologic regimes and within streams) on aquatic insect community structure. These results can be expanded beyond the study region to other systems and ecological habitats, and provide a baseline for the community structure and diversity that can potentially be expected. Results from this study will provide insights as to how streams in close geographic proximity with differing thermal regimes can have different aquatic insect community structure.

Methods

Study Site

This study was conducted along the Copper River Delta (CRD) in southcentral Alaska (Figure 1). The CRD, located in the Chugach National Forest, is the largest contiguous wetland on the Pacific coast of North America extending 120 km along the

Gulf of Alaska (Christensen et al. 2000). The CRD is a diverse landscape comprised of streams, sloughs, marshlands and tidal flats with the present study focusing on the wetlands tundra ecosystem. Heavy summer rainfall and seasonal melt of glaciers and snowfields contribute to the varying hydrologic conditions on the delta. Streams on the delta are relatively pristine, have numerous side channels (Kruger & Tyler 1995), and exhibit thermal variability and contrasting hydrologic types associated with being either groundwater-fed (GWF) or surface water-fed (SWF).

Four streams (two GWF and two SWF) west of the Copper River were studied that exhibited contrasting thermal and hydrologic regimes. Groundwater-fed streams are were thermally and hydrologically stable year round, whereas SWF streams exhibited greater thermal and hydrologic variability compared to GWF streams.

The GWF streams in this study were 25 Mile and Hatchery Creeks. (Figure 1, Table 1). 25 Mile is located at mile marker 25 (40km) on the Copper River Highway and has an open canopy with the riparian zone consisting of primarily grasses and sedges. Sitka spruce (*Picea sitchensis)* and alder (*Alnus* spp.) are scattered throughout the riparian zone. The main channel, on average, is deeper than side channel areas and consists of runs, riffles and pools with a substrate comprised of cobble, pebble and fine sand. Side channels consist of shallow pools with substrates of primarily fine organic material and silt. The study site at Hatchery Creek is located 8km from the town of Cordova, AK on Power Creek Rd and has a closed canopy with a riparian zone of dense Sitka spruce, alder, devil’s club (*Oplopanax horridus*) and ferns. The main and side channels are similar to those in 25 Mile with respect to habitats (runs, riffles, pools) and substrate type.

Surface water-fed streams were 18 Mile and Blackhole Creek. 18 Mile is located at mile marker 18 (29km) on the Copper River Highway and has an open canopy (sparse

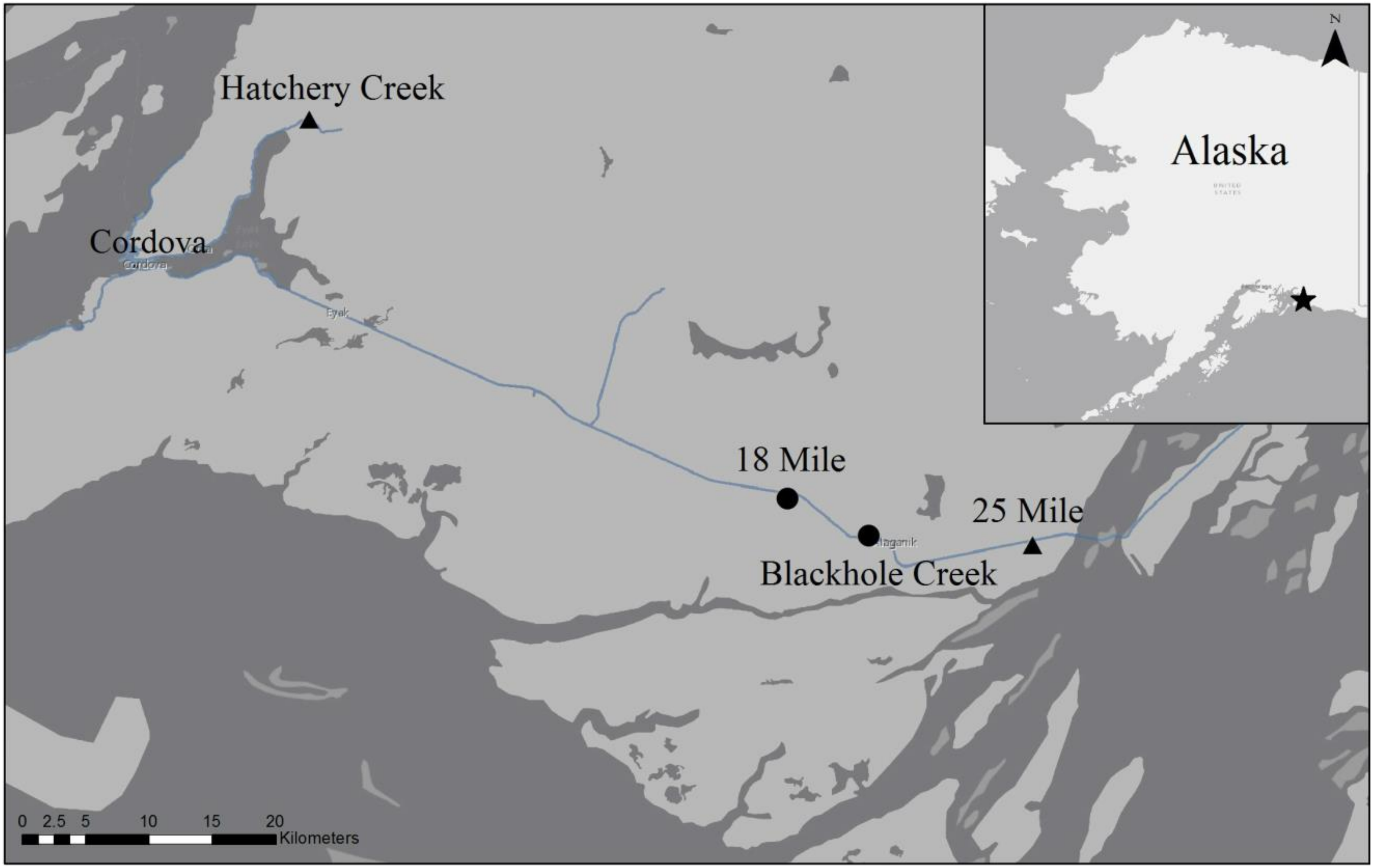

Figure 1. Map of Copper River Delta, AK, study area showing replicate streams with the two hydrologic types, triangle = groundwater-fed and circle = surface water-fed.

Sitka spruce and alder) with numerous runs, riffles and pools. Substrate type in the main channel consists of cobble, pebbles and fine sand, and a thin layer of iron precipitate covers the substrate. Side channels consist of backwater pool areas with a substrate of primarily fine organic material, however some pool areas also had fine sand and pebbles with iron precipitate. Blackhole Creek is located at mile marker 21 (34km) on the Copper River Highway and has a closed canopy with the riparian zone comprised of Sitka spruce, alder, salmonberry (*Rubus spectabilius*) and ferns. The main channel consists of runs, riffles and pools with similar substrate types as in the other three streams. Side channels consisted of fine organic material found in the backwater pools.

Sampling Regime

Each stream was sampled bimonthly from late April 2013 to August 2013 and once in September (fall) and November (early winter). Sampling in each stream occurred along a 300-meter reach in the main channel and side channel areas, the latter are shallow with little to no current.

Hobo® temperature loggers were deployed in all study reaches to track thermal variation within each stream. Two temperature loggers were placed in the main channel, two in the side channel, and one attached to a nearby tree to record air temperature. In-stream temperature loggers were submerged and attached to logs with wire. Air temperature loggers were placed in a Hobo® RS-1 Solar Radiation Shield. Temperature loggers were set to record every two hours from spring through summer because a return to the study sites after August was uncertain. Additional water temperature data from main and side channel areas for the period early May 2013 to early March 2014 were

Table 1. Descripton of study sites of streams on the Copper River Delta, Alaska, April - November 2013. GWF = groundwater-fed, SWF = surface water-fed, Main = main channel, Side = side channel.

Hydrologic Type	Stream	Channel	Abbreviation	Latitude (°N)	Longitude (°W)	Canopy	Substrate
GWF	25 Mile	Main	25mi-M	60.44234	-145.11804	Open	Cobble, pebble, fine sand
		Side	25mi-S				Fine organic material, slit
	Hatchery Creek	Main	Hat-M	60.591126	-145.631869	Closed	Cobble, pebble, fine sand
		Side	Hat-S				Fine organic material, slit
SWF	18 Mile	Main	18mi-M	60.463259	-145.309639	Open	Cobble, pebble, iron precipitate
		Side	18mi-S				Fine organic, iron precipitate
	Blackhole Creek	Main	Blk-M	60.460497	-145.356674	Closed	Cobble, pebble, fine sand
		Side	Blk-S				Fine organic material, slit

provided by collaborators (E. Campbell, pers. comm.). These loggers recorded temperature every 30 minutes.

On each sampling date, three replicate benthic samples were collected from main and side channel areas of each stream using a 0.1m Hess sampler (mesh size = 250μm). Benthic samples were collected from three randomly selected locations in each stream area and the enclosed substrate was agitated for 30 seconds. In side channel areas with little water current, a current was manually created within the Hess sampler to ensure organisms were swept into the net. Samples were transferred to Uline® poly bags, preserved with 70% ethanol and transported to the laboratory for sorting.

Aquatic Insect Sample Processing

The contents of each poly bag were elutriated to separate aquatic insects from fine sand substrate before being sorted under a Leica dissecting microscope at 6.3 – 50X magnification. Aquatic insects from each replicate sample were sorted into 30 ml scintillation vials and preserved in 70% ethanol. Chironomidae from each replicate sample were placed into separate vials. Chironomid samples with high numbers of organisms were split using a Folsom Plankton Splitter (Wildlife Supply Company, Florida, USA) to facilitate counting. A subset of three sampling dates (May, July and September) was used for community structure analysis of all aquatic insects.

Once sorted, aquatic insects were measured to the nearest millimeter (body length) and identified to the lowest possible taxonomic level, usually genus using Merritt *et al.* (2008). Chironomids in only two of the three replicates were used in analyses because of logistical constraints associated with identifying the high number of larvae collected. Aquatic insects from benthic samples were used to examine aquatic insect community structure and to quantify insect densities.

Stream Physicochemical Parameters

General physicochemical parameters of the study reaches were recorded during each sampling period. Water temperature, pH, dissolved oxygen, conductivity, salinity, and total dissolved solids were measured with a YSI 556 MPS multimeter. Stream discharge data were provided by collaborators (E. Campbell, pers. comm.). Substrate type at each site was visually assessed during spring.

Water samples for nutrient analyses (soluble reactive phosphorus, ammonium, and nitrate) were collected monthly from main and side channel areas of each stream. Water was collected with a 60ml Luer-Lok tip syringe (BD, Franklin Lakes, NJ) in 15 ml increments and filtered using a 25mm diameter Pall Type A/E Glass Fiber Filter (pore size 1 um) held into place by a Pall 25mm Syringe Filter holder. Filtered water was placed into 15 ml centrifuge tubes and frozen for later analysis using an Auto Analyzer 3 (Seal Analytical, Inc., Mequoun, WI, USA).

Benthic algal samples were collected monthly for chlorophyll *a* analyses. Replicate algal samples were collected by scrubbing a 5cm area from each of three rocks collected from the main and side channel areas in each stream. The algal slurry was filtered through 25mm diameter Pall Type A/E Glass Fiber Filter (pore size 1 um) and the filter was placed in a black 15 ml centrifuge film canister and frozen for later analysis. Chlorophyll *a* analysis and extraction was conducted in the laboratory according to Steinman et al. (2006). Extractant was analyzed with a UV-1700 spectrophotometer (Shimadzu Corp., Kyoto, Japan) at 750 nm and after acidification at 665nm. Calculations based on absorbance yielded chlorophyll *a* concentration.

Data Analyses

Non-metric multidimensional scaling (nMDS) was used to compare aquatic insect community composition for three months (May, July and September) based on taxa and functional feeding group relative abundances among hydrologic types (GWF vs. SWF) and within streams (main vs. side channels) (Primer 6, PRIMER-E Ltd, Plymouth). Non-metric multidimensional scaling (nMDS) is an ordination method that characterizes objects (i.e., streams) by multiple variables so that in a graphical representation similar communities are clustered close together and dissimilar communities are far apart. Community composition values based on taxa and functional feeding group relative abundances were square root transformed and similarity matrices were created using Bray-Curtis, which were then analyzed with nMDS. Non-metric multidimensional scaling can be graphically represented in 2- or 3-dimensions, and the 2-dimensional representation of nMDS was used for this study. Analysis of variance (ANOVA) was used for all statistical comparisons. Aquatic insect abundance data were square root transformed to meet the assumptions of ANOVA and Shannon-Wiener diversity values were also analyzed with t-tests using SYSTAT 13 (SYSTAT Vers. 13 Software, San Jose, CA).

Results

Physicochemical Parameters

Physicochemical parameters of channel types (main and side) in each stream were measured from late April through August 2013. Average stream temperature and ranges differed between hydrologic types. Mean water temperature in groundwater-fed (GWF) streams (4.6 ^{o}C) was lower than in surface water-fed (SWF) streams (7.5 ^{o}C). Water temperatures in GWF streams ranged from 0.8^{o}C in May to 9.7^{o}C in August, whereas temperatures in SWF streams ranged from 0.3°C (May) to 18.8°C in August. Mean daily temperatures in GWF streams increased slightly over the sampling period but were relatively consistent in comparison to SWF stream daily mean temperatures, which increased at a faster rate and reached higher temperatures (Figure 2).

Mean daily temperatures in 25 Mile (GWF) were consistently warmer in side channels than in the main channel throughout the study, whereas in Hatchery Creek, the other GWF stream, mean daily temperatures were similar in both channel areas (Table 2). In contrast, temperatures in both SWF streams were consistently higher in main channels than in side channels during the study (Figure 2). In both hydrologic types, however, side channels were more thermally variable such that their monthly temperature range was greater than in the main channel. For example, water temperatures in 18 Mile main channel during August ranged from 9.3 ^{o}C – 13.8 ^{o}C, whereas the side channel range was exhibited cooler low temperatures and warmer high temperatures (4.2 ^{o}C – 18.8 ^{o}C) (Table 2).

Physicochemical parameters of the streams and channels were variable or low throughout the sampling period. Dissolved oxygen (DO), pH, and oxidation-reduction

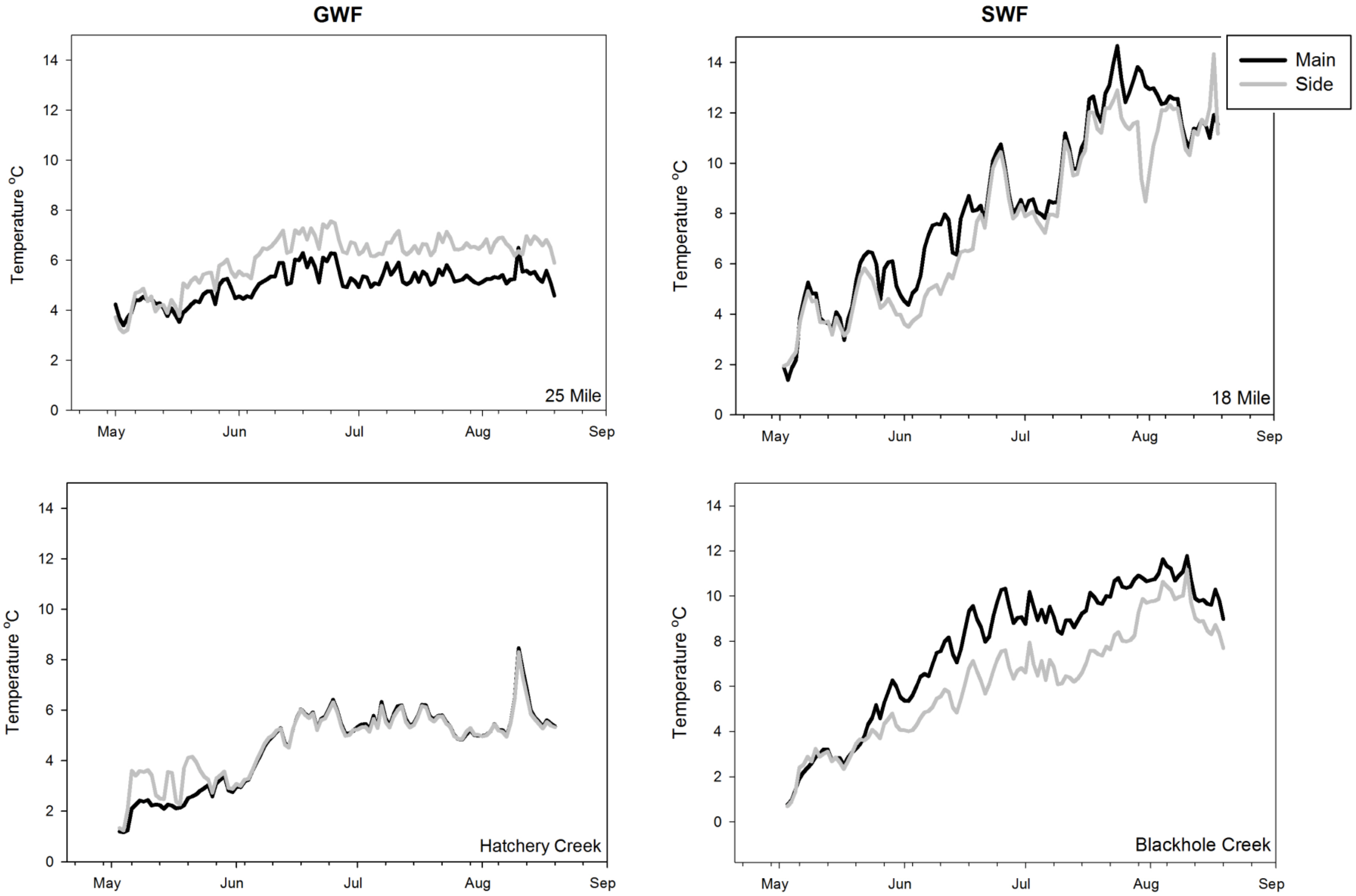

Figure 2. Mean daily water temperatures (°C) from study streams on the Copper River Delta, AK, April – August 2013. GWF = groundwater-fed, SWF = surface water-fed, Main = main channel, Side = side channel.

Table 2. Physicochemical parameters of four study streams on the Copper River Delta, AK, April - November 2013, presented as sampling period means. Variation in physicochemical parameters presented as coefficient of variation (CV, %). GWF = groundwater-fed, SWF = surface water-fed. Site abbreviations as in Table 1.

	GWF					SWF				
	25mi-*M*	25mi-*S*	Hat-*M*	Hat-*S*	**CV**	18mi-*M*	18mi-*S*	Blk-*M*	Blk-*S*	**CV**
Maximum Depth (cm)	40	20	50	30		60	30	30	25	
Temperature (°C)	4.9	5.6	4.0	4.1	**34.7**	8.4	7.7	7.7	6.2	**55.4**
Range	2.7 - 9.4	2.5 - 10.4	0.8 – 9.7	0.8 – 9.4		0.9 - 16.4	1.3 - 18.8	0.3 - 12.2	0.5 - 11.7	
pH	6.6	6.3	5.3	6.0	**16.6**	6.5	6.5	7.2	7.6	**17.1**
Dissolved Oxygen (mg/L)	9.3	8.7	8.5	8.8	**13.9**	8.3	6.7	9.2	8.4	**24.5**
Conductivity (µS/cm)	0.05	0.05	0.06	0.06	**10.4**	0.02	0.04	0.02	0.03	**51.5**
Salinity (ppt)	0.02	0.03	0.03	0.03	**17.2**	0.01	0.02	0.01	0.01	**63.2**
Total Dissolved Solids (g/L)	0.03	0.04	0.04	0.04	**9.2**	0.01	0.03	0.02	0.02	**50.6**
Oxidation Reduction Potential (mV)	63.3	60.5	58.5	51.1	**41.5**	68.2	53.7	72.5	45.7	**55.6**
Chlorophyll *a* (µg/cm^2)	0.07	0.9	0.5	1.8	**140**	0.6	0.8	0.1	0.2	**154**
Soluble reactive phosphorous (µg/L)	2.4	4.9	2.6	2.3	**105**	2.5	2.9	5.3	8.3	**152**
Ammonium (µg/L)	11.9	25.1	19.8	19.5	**71.7**	24.3	69.6	32.3	53.0	**94.4**
Nitrate (µg/L)	91.5	97.4	66.6	54.0	**44.9**	74.4	42.5	42.2	37.8	**50.7**

potential (ORP) were variable throughout the sampling period in the streams and channel types (Table 2). Conductivity, salinity, and total dissolved solids (TDS) were consistently low in all study sites (Table 2). Chlorophyll *a* and soluble reactive phosphorus (SRP) levels were relatively low in all streams and channel types throughout the sampling period with no obvious patterns between hydrologic type or channel type (Table 2). Ammonium concentrations in SWF streams were significantly higher than in GWF streams over the study period (one-way ANOVA, df=1,30; F= 5.4, p=0.02), whereas nitrate concentrations were significantly higher in GWF streams than in SWF streams (one-way ANOVA, df=1,30; F=7.3, p=0.01).

Variation (coefficient of variation, % CV) in physicochemical parameters between hydrologic type was uniformly higher for all parameters in SWF streams than in GWF streams (Table 2).

Taxonomic Composition

A total of 35,665 aquatic insects representing six orders, 18 families, and 60 genera were collected from the four study streams (Table 3, Appendix Table 14). Chironomids comprised 93.6% of all aquatic insects collected in GWF streams followed by non-chironomid Diptera (2.8%), Plecoptera (1.6%), and Ephemeroptera (1.3%) (Table 3). In SWF streams, chironomids represented 81% of aquatic insects collected followed by non-chironomid Diptera (8.2%), Ephemeroptera (4.5%), Plecoptera (3.7%), and Hemiptera (1.5%) (Table 3).

Although non-biting midges (Diptera: Chironomidae) were numerically dominant in all streams and accounted for 89.6% of all aquatic insects collected, there was a significant difference in relative abundance between hydrologic types. Chironomid

Table 3. Aquatic insect abundance (% total abundance in each stream) in groundwater-fed (GWF) and surface water-fed (SWF) study streams on the Copper River Delta, Alaska, April – November 2013. Taxa grouped by order (family for Chironomidae). Main = main channel, Side = side channel.

	Total	Chironomidae	Other Diptera	Plecoptera	Ephemeroptera	Trichoptera	Hemiptera	Coleoptera
25 Mile Main	4074	3748 (92%)	166 (4%)	31 (<1%)	107 (<1%)	22 (<1%)	0	0
25 Mile Side	5180	4857 (94%)	255 (5%)	3 (<1%)	0	35 (<1%)	24 (<1%)	6 (<1%)
Hatchery Creek Main	9197	8560 (93%)	132 (1%)	301 (3%)	195 (2%)	9 (<1%)	0	0
Hatchery Creek Side	5517	5307 (96%)	128 (2%)	56 (1%)	5 (<1%)	21 (<1%)	0	0
GWF Streams	**23968**	**22472 (94%)**	**681 (3%)**	**391 (2%)**	**307 (1%)**	**87 (<1%)**	**24 (<1%)**	**6 (<1%)**
18 Mile Main	3885	3059 (79%)	504 (13%)	81 (2%)	171 (4%)	2 (<1%)	3 (<1%)	0
18 Mile Side	1970	1742 (88%)	65 (3%)	2 (<1%)	7 (<1%)	6 (<1%)	144 (7%)	4 (<1%)
Blackhole Creek Main	3167	2262 (71%)	236 (7%)	309 (10%)	328 (10%)	32 (1%)	0	0
Blackhole Creek Side	2675	2429 (90%)	134 (5%)	46 (2%)	19 (<1%)	11 (<1%)	34 (1%)	2 (<1%)
SWF Streams	**11697**	**9492 (81%)**	**939 (8%)**	**438 (4%)**	**525 (4%)**	**51 (<1%)**	**181 (2%)**	**6 (<1%)**
Total	35665	31964 (90%)	1620 (5%)	829 (2%)	832 (2%)	138 (<1%)	205 (<1%)	12 (<1%)

relative abundance was significantly higher in GWF streams than in SWF (one-way ANOVA, hydrologic type main effect, df=1,6; F=6.6, p=0.04) (Table 3).

Within the Chironomidae, the subfamilies Orthocladiinae and Chironominae were numerically dominant and accounted for 76.1% and 18.6% of all chironomids, respectively. In GWF streams, Orthocladiinae comprised 87% of chironomids collected followed by Chironominae (8.6%), with the remaining 4% represented by Prodiamesinae, Diamesinae and Tanypodinae (Table 4). Orthocladiinae comprised 50% of chironomids collected in SWF streams followed by Chironominae (42.4%), with the remaining 8% comprised of Prodiamesinae, Diamesinae, Tanypodinae and Podonominae (Table 4).

Chironomids were more abundant in side channels than in main channels for both hydrologic types, however this difference was significant only in SWF streams (one-way ANOVA, channel main effect, df=2,5; F=26.1, p=0.002). Chironomid abundance at the subfamily level, however, revealed a different pattern. Orthocladiinae were more abundant in main channels than side channels in both GWF and SWF streams, although this difference was not significant (Table 4). Chironominae and Prodiamesinae followed the general chironomid pattern of higher abundance in the side channels than in main channels, but this was only significant for Prodiamesinae (one-way ANOVA, Channel main effect, df=1,6; F = 13.6, p=0.01) (Table 4).

The numerically dominant non-chironomid taxon in GWF streams was *Baetis* spp. (Ephemeroptera: Baetidae), although six additional taxa occurred in high abundance: *Dicranota* spp. and *Hexatoma* spp. (Diptera: Tipulidae), *Bezzia* spp. (Diptera: Ceratopogonidae), *Capnia* spp. (Plecoptera: Capniidae), *Suwallia* spp. (Plecoptera:

Table 4. Chironomidae abundance (% total abundance) by subfamily in groundwater-fed (GWF) and surface water-fed (SWF) study streams on the Copper River Delta, Alaska, April – November 2013. Main = main channel, Side = side channel.

	Total	Orthocladiinae	Chironominae	Prodiamesinae	Diamesinae	Tanypodinae	Podonominae
25 Mile Main	3748	3589 (96%)	35 (<1%)	28 (<1%)	97 (<3%)	0	0
25 Mile Side	4857	4294 (88%)	153 (3%)	383 (8%)	12 (<1%)	19 (1%)	0
Hatchery Creek Main	8560	7504 (88%)	952 (11%)	0	105 (1%)	0	0
Hatchery Creek Side	5307	4173 (79%)	792 (15%)	95 (2%)	247 (5%)	0	0
GWF Streams	**22472**	**19560 (87%)**	**1932 (9%)**	**506 (2%)**	**461 (2%)**	**19 (<1%)**	**0**
18 Mile Main	3059	2051 (67%)	932 (30%)	12 (<1%)	12 (<1%)	51 (2%)	0
18 Mile Side	1742	937 (54%)	649 (37%)	125 (7%)	3 (<1%)	28 (2%)	0
Blackhole Creek Main	2262	1211 (54%)	958 (42%)	0	0	78 (3%)	16 (<1%)
Blackhole Creek Side	2429	566 (23%)	1484 (61%)	125 (5%)	0	254 (10%)	0
SWF Streams	**9492**	**4765 (50%)**	**4023 (42%)**	**262 (3%)**	**15 (<1%)**	**411 (4%)**	**16 (<1%)**
Total Chironomidae	31964	24325 (76%)	5955 (19%)	768 (2%)	476 (1%)	430 (1%)	16 (<1%)

Chloroperlidae), and *Ecclisomyia* spp. (Trichoptera: Limnephilidae). The numerically dominant taxon in SWF streams was *Probezzia* spp. (Diptera: Ceratopogonidae) with the following taxa occurring in high abundance: *Baetis* spp., *Simulium* spp. (Diptera: Simuliidae), *Callicorixa vulnerata* (Hemiptera: Corixidae), *Capnia* spp. (Plecoptera: Capniidae), *Suwallia* spp. (Plecoptera: Chloroperlidae), and *Zapada cinctipes* (Plecoptera: Nemouridae) (Appendix Table 14).

Taxa richness among streams ranged from 31 in the GWF Hatchery Creek to 43 in the SWF Blackhole Creek (Table 5). Taxa richness was significantly higher in SWF than in GWF streams (two-way ANOVA, hydrologic type main effect, df = 1,4; F-value = 8.3, p = 0.04) (Table 5).

Taxa richness in main channels ranged from 24 in Hatchery Creek (GWF) to 28 in Blackhole Creek (SWF), whereas side channel taxa richness ranged from 25 in 25 Mile (GWF) and Hatchery Creek to 34 in Blackhole Creek. There was no significant difference between main and side channel taxa richness or the interaction of hydrologic type and channel (Table 5). Non-chironomid taxa richness among streams ranged from 14 in Hatchery Creek (GWF) to 22 in Blackhole Creek (SWF) (Table 5); there was no significant difference between hydrologic types.

Community structure

Aquatic insect diversity (chironomid and non-chironomid diversity) (H') was higher in SWF streams (18 Mile H'=2.56; Blackhole Creek H'=2.64) than in GWF streams (25 Mile H'=2.27; Hatchery Creek H'=2.04), however these differences were not significant (Table 6). Main channel diversity ranged from 1.53 in Hatchery Creek (GWF) to 2.48 in Blackhole Creek (SWF), whereas side channel diversity ranged from

Table 5. Aquatic insect taxa richness and non-chironomid taxa richness for study streams on the Copper River Delta, Alaska, April – November 2013. GWF = groundwater-fed, SWF = surface water-fed, Main = main channel, Side = side channel. Stream abbreviations as in Table 1. Values with different superscripts are significantly different.

Hydrologic Type	Stream		Stream Taxa Richness	Non-chironomid Stream Taxa Richness	Channel	Taxa Richness	Non-chironomid Taxa Richness
GWF	25mi		36	17	Main	27	13
					Side	25	14
	Hat		31	14	Main	24	13
					Side	25	11
		Mean	**34^a**	16			
SWF	18mi		39	17	Main	27	13
					Side	29	14
	Blk		43	22	Main	28	16
					Side	34	22
		Mean	**41^b**	20			

Stream taxa richness significantly higher in SWF (b) than in GWF streams (a) (Two-way ANOVA, p=0.04)

Table 6. Aquatic insect diversity (H') and non-chironomid diversity for study streams on the Copper River Delta, Alaska, April – November 2013. GWF = groundwater-fed, SWF = surface water-fed, Main = main channel, Side = side channel. Site abbreviations as in Table 1. Values with different superscripts are significantly different.

Hydrologic Type	Stream		Stream Diversity (H')	Non-chironomid Stream Diversity (H')	Channel	Diversity (H')	Non-chironomid Diversity (H')
GWF	25 Mile		2.3	0.41	Main	2.13	0.44
					Side	1.77	0.34
	Hatchery Creek		2.0	0.32	Main	1.53	0.37
					Side	2.23	0.23
		Mean	2.2	**0.36**^{a}			-
SWF	18 Mile		2.56	0.83	Main	2.32	0.89
					Side	2.22	0.51
	Blackhole Creek		2.64	0.96	Main	2.48	0.85
					Side	2.34	0.50
		Mean		**0.89**^{b}			Main = **0.87**^{c}, Side = **0.51**^{d}

Non-chironomid stream diversity significantly higher in SWF (b) than in GWF streams (a) (t-test, p=0.03).
SWF non-chironomid diversity significantly greater in main (c) than in side channel (d) (t-test, p=0.03).

1.77 in 25 Mile (GWF) to 2.34 in Blackhole Creek (SWF). There was no significant difference between main and side channel diversity or the interaction of hydrologic type and channel (Table 6).

Aquatic insect diversity excluding chironomids was analyzed to reveal patterns that may have been not apparent due to their strong influence on diversity. Non-chironomid diversity was significantly higher in SWF streams (Blackhole Creek H'=0.96; 18 Mile H'=0.83) than in GWF streams (25 Mile H'=0.41; Hatchery Creek H'=0.32)(t-test, df = 1,2; p = 0.03)(Table 6). Diversity in main channels of SWF streams was significantly higher (mean main channel H'=0.87) than in side channels (mean side channel H'=0.51)(t-test, df = 1,2; p = 0.03) (Table 6). Non-chironomid diversity in main and side channels of GWF streams was low and ranged from (0.23 to 0.44) (Table 6).

Non-metric multidimensional scaling (nMDS) using aquatic insect taxa relative abundance indicated that community structure within SWF and GWF streams was similar but differed between hydrologic types (Figure 3). Two distinct groups are evident on opposite sides of the plot and correspond to aquatic insect communities in GWF and SWF streams, indicating that streams in the same hydrologic type are relatively similar to each other. Channel types in SWF streams also ordinated separately indicating that aquatic insect community structure in main channels was distinct from those in side channels. In contrast, main and side channel community structure in GWF streams was similar in Hatchery Creek, whereas community structure in 25 Mile channel types was distinct (Figure 3).

Most of the dissimilarity between hydrologic groups was due to chironomids, which accounted for 78% of the total dissimilarity. The chironomid subfamilies

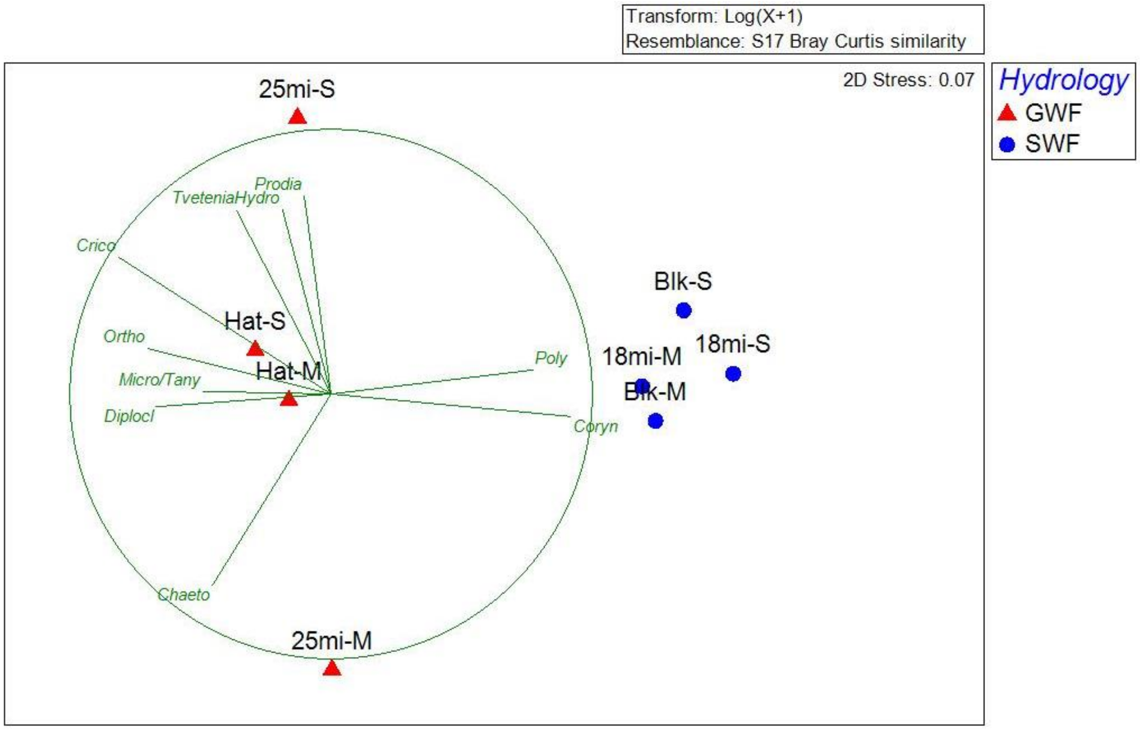

Figure 3. Non-metric multidimensional scaling of aquatic insect taxa relative abundance for four study streams on the Copper River Delta, AK, on the basis of hydrologic type (GWF = groundwater-fed, SWF = surface water-fed) and channel type (M = main channel, S = side channel) (April – November 2013). Site abbreviations as in Table 1.

Orthocladiinae and Chironominae contributed most to the dissimilarity and accounted for 44% and 13% of the total dissimilarity, respectively. Orthoclads comprised the majority of chironomids in both GWF and SWF streams; however, they were present in higher relative abundances in GWF (87% chironomid relative abundance) than in SWF (50%) streams (Table 4). The relative abundance of the subfamily Chironominae was higher in SWF (42% chironomid relative abundance) than in GWF (9%) streams (Table 4).

An nMDS incorporating the relative abundance of aquatic insect functional feeding groups (FFG) was also used to compare communities in streams of different hydrologic regimes by channel type. Relative abundances of FFGs were dissimilar in GWF and SWF streams, however channel types could not be distinguished on the basis of functional feeding groups (Figure 4). The major contributors to the dissimilarity between hydrologic groups were collector-gatherers and shredders. Collector-gatherers contributed to 37.8% of the dissimilarity and shredders contributed to 22% of the dissimilarity between GWF and SWF streams.

Collector – gatherers had the highest relative abundance of FFGs in both GWF and SWF streams; however, they were present in higher relative abundances in GWF (73% relative abundance) than in SWF (50%) streams (Table 7). Shredders had higher relative abundance in SWF (24% relative abundance) streams than in GWF (21%) streams, and scrapers (SWF: 10%, GWF 1%) and predator-engulfers (SWF: 14%, GWF: 3%) were also higher in SWF than in GWF streams (Table 7).

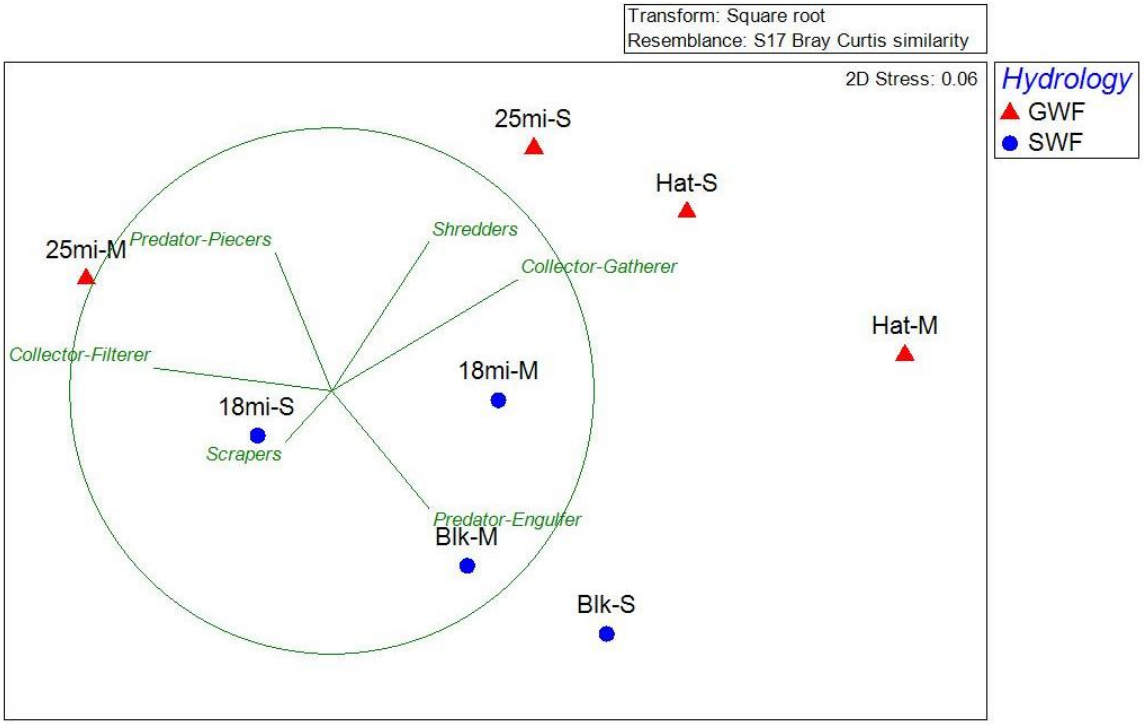

Figure 4. Non-metric multidimensional scaling of aquatic insect functional feeding group relative abundance for four study streams on the Copper River Delta, AK, on the basis of hydrologic type (GWF = groundwater-fed, SWF = surface water-fed) and channel type (M = main channel, S = side channel) (April – November 2013). Site abbreviations as in Table 1.

Table 7. Functional feeding group abundance (% total abundance) in groundwater-fed (GWF) and surface water-fed (SWF) study streams on the Copper River Delta, Alaska; May, July, September 2013. Main = main channel, Side = side channel.

	Total	Collector-Gatherer	Collector-Filterer	Shredder	Scraper	Predator-Engulfer	Predator-Piercer
25 Mile Main	678	535 (79%)	59 (9%)	62 (9%)	2 (<1%)	12 (<2%)	8 (1%)
25 Mile Side	1661	857 (52%)	0	746 (45%)	4 (<1%)	43 (<3%)	11 (<1%)
Hatchery Creek Main	2689	2408 (90%)	1 (<1%)	162 (6%)	26 (1%)	90 (3%)	2 (<1%)
Hatchery Creek Side	1892	1254 (66%)	0	509 (27%)	52 (3%)	61 (3%)	16 (<1%)
GWF Streams	**6920**	**5054 (73%)**	**60 (1%)**	**1479 (21%)**	**84 (1%)**	**206 (3%)**	**37 (<1%)**
18 Mile Main	1370	681 (50%)	25 (2%)	302 (22%)	126 (9%)	233 (17%)	3 (<1%)
18 Mile Side	705	470 (67%)	0	60 (9%)	145 (21%)	18 (<3%)	12 (<2%)
Blackhole Creek Main	694	342 (49%)	16 (2%)	195 (28%)	38 (5%)	99 (14%)	4 (<1%)
Blackhole Creek Side	667	242 (36%)	1 (<1%)	252 (38%)	19 (3%)	147 (22%)	6 (<1%)
SWF Streams	**3436**	**1735 (50%)**	**42 (1%)**	**809 (24%)**	**328 (10%)**	**497 (14%)**	**25 (<1%)**
Total	10356	6789 (66%)	102 (1%)	2288 (22%)	412 (4%)	703 (7%)	62 (<1%)

Discussion

Physicochemical Parameters

Aquatic insect community structure can be influenced by a suite of physicochemical variables including water temperature, pH, and nutrient concentrations (Lemly 1982, Jacobsen 1997), however most parameters did not reveal any consistent significant pattern in the Copper River Delta (CRD) streams examined in this study. Water temperature did exhibit patterns and can be used to explain trends across hydrologic and channel types.

Water temperature in the four study streams exhibited expected patterns based on hydrologic type. Groundwater-fed (GWF) stream temperatures were relatively stable during the growing season, whereas temperatures in surface water-fed (SWF) streams increased substantially during summer and reflected ambient air temperatures. Although water temperatures in side channels are expected to be warmer than in main channels due to reduced water depth and, as a result, more readily warmed by solar radiation (McRae and Edwards 1994), this only occurred in mean daily temperatures of GWF streams.

Mean daily temperatures in side channels of 25 Mile (GWF stream) were consistently higher than in the main channel throughout the study. Although Hatchery Creek (GWF) side channels had slightly warmer mean daily high temperatures compared to the main channel, mean daily temperatures in side channel and main channel areas were similar. These differences can be due to the extent of canopy cover, which influences stream water temperatures (Macdonald et al. 2003), as 25 Mile has an open canopy and Hatchery Creek has a closed canopy.

Mean daily temperatures of side channels in SWF streams were consistently lower than in the main channel throughout the study. Side channel temperature ranges, however, were generally greater than those in main channels. The greater temperature range in side channels is likely due to shallower water allowing for these areas to be more readily cooled and warmed than the deeper main channel. Temperature ranges in main and side channel areas of Blackhole Creek were not as large as in 18 Mile and is likely due to shading from the closed canopy.

Aquatic insect distribution and abundance is strongly influenced by the annual thermal regime (Merritt et al. 2006) and corresponds to different assemblages of aquatic insects in GWF and SWF streams examined in this study. The abundance of aquatic insects with optimal thermal regimes in cool water was greater in GWF than in SWF streams. For example, Orthocladiinae prefer cooler temperatures (Beckett 1992, Coffman and de la Rosa 1998), and are often reported as a dominant insect in springs and groundwater-fed systems (Lindegaard 1995). In contrast, aquatic insects with wider temperature ranges and preferring warmer temperatures are expected to occur in higher abundances in SWF streams than in more temperature-restricted GWF streams.

While nutrient availability also can influence aquatic insect assemblages (Lemly 1982) however; streams along the CRD are relatively nutrient poor systems (Boggs 2000) and likely does not explain differences in aquatic insect communities. These study streams are consistent with the characterization of Alaskan coastal systems to be oligotrophic (Kyle et al. 1997). Ammonium and nitrate concentrations were low in all study streams and channel types

Community Composition

Stream hydrologic type had a strong influence on aquatic insect community composition with differences in Chironomidae (Diptera) abundance and taxonomy between GWF and SWF streams. Chironomidae (Diptera) are commonly the numerically dominant and most taxonomically rich aquatic insects found in lotic systems (Ferrington et al. 2008) and comprised 94% and 81% of aquatic insects in GWF and SWF streams, respectively. Midges in the subfamily Orthocladiinae comprised 87% of chironomids in GWF streams, whereas the Chironominae comprised 9%. The high percentage of Orthocladiinae in CRD streams is consistent with values reported in other studies (Stur et al. 2005, Lencioni 2011). Orthoclads are generally cold-stenotherms (Lindegaard 1995), and their numerical dominance in these cold GWF streams (mean temperature = 4.6 ^{o}C) is expected. Orthocladiinae was also one of the numerically dominant chironomid subfamilies in SWF streams, comprising 50% of chironomids, whereas Chironominae accounted for 42% of midges collected. Water temperatures in SWF streams are at or near freezing in winter and are cold in early spring (mean temperature in April = 1.3 ^{o}C, May = 3.8 ^{o}C). These temperatures are consistent with the cold-stenothermic characteristic of orthoclads. Higher water temperatures in late spring and summer, however, would facilitate the presence of Chironominae in SWF streams, as taxa within this subfamily are more abundant in warmer habitats (Lindegaard 1995).

The relative abundance of non-chironomid Diptera, Plecoptera, and Ephemeroptera was higher in SWF streams than in GWF streams, however this difference may be due to the very large contribution of chironomids in GWF streams, thereby reducing the relative abundance of other taxonomic groups.

Community Structure

Chironomid taxa in both stream hydrologic types comprised at least 50% of taxa richness and supports the findings of Oswood et al. (1992, 2006) that Chironomidae are often numerically dominant in high-latitude lotic systems (Oswood et al. 1992, 2006). Aquatic insect taxa richness and diversity are relatively low in CRD streams (taxa richness ranged from 31 to 43, diversity (H') ranged from 2.0 to 2.6. This is consistent with studies conducted in other Alaska and northern latitude streams. Lessard and Merritt (2006) reported taxa richness of 25 – 30 in Alaskan streams while Kubo et al. (2013) reported taxa richness of 8 -28 and diversity of 1.7 – 2.7 in streams of Washington near Mt. Rainier. Despite these overall low values, taxa richness and diversity differed across hydrologic groups in our study streams. Surface water-fed streams had higher diversity and significantly higher taxa richness than GWF streams and likely results from higher thermal variability in SWF streams. The broader range of annual water temperatures in SWF streams (0.3°C – 18.8°C) will allow for taxa with differing optimal thermal preferences to predominate at different times of the year. Groundwater-fed streams were expected to have relatively low taxa richness and diversity due to relatively stable, but low, water temperatures (~4ºC) throughout the year. Taxa richness or diversity did not differ between main and side channels due to the considerable predominance of chironomids in both channel types.

Non-chironomid diversity was significantly higher in SWF streams than in GWF streams. This is consistent with Vannote and Sweeney's (1980) description of higher macroinvertebrate diversity in SWF streams. This is due to a greater temperature range, which favors a larger number of taxa compared to GWF streams. The narrow temperature range in GWF streams restricts the taxa composition. In addition, main channel diversity was significantly higher than side channel diversity in SWF streams. These differences can be explained by habitat heterogeneity and substrate type. Hynes (1970) described that high insect diversity would be expected with more complex microhabitats such as those with differing substrates. Substrates in side channel areas were primarily fine organic material, whereas the main channel was heterogeneous with cobble, pebbles, sand and woody debris.

Non-metric Multi-Dimensional Scaling

Aquatic insect community structure in GWF streams was distinctly different than in SWF streams as reflected in the relative abundance nMDS ordination. The difference in community structure, associated with temperature is consistent with other studies, (Vannote and Sweeney 1980, Ward and Stanford 1982). Groundwater-fed streams had lower diversity and taxa richness compared to SWF streams. While chironomids accounted for 94% of all insects collected from our study streams, the relative abundance of Orthocladiinae and Chironominae accounted for much of the difference in community structure between GWF and SWF streams. Orthocladiinae were abundant in both GWF and SWF streams, though their relative abundance was higher in GWF streams (87%) than in SWF streams (50%) as previously stated. Once again, Chironominae comprised of 9% relative abundance in GWF streams and 42% in SWF streams. These differences accounted for the divided community structure along hydrologic type in the nMDS plot.

Looking within the SWF grouping on the nMDS plot, aquatic insect community structure in main and side channels was distinct and was due primarily to the presence of *Corynoneura* sp. (Orthocladiinae) and *Polypedilum* sp. (Chironominae). These taxa are numerically dominant in both SWF streams and in each channel type, however higher non-chironomid diversity and taxa abundances in main channels resulted in distinct community structures in main and side channels.

Within GWF cluster on the nMDS, Hatchery Creek channels were similar to each other while 25 Mile channel types are distinctly dissimilar. Two taxa, *Cricotopus* sp. (Chironomidae: Orthocladiinae) and *Orthocladius* sp. (Chironomidae: Orthocladiinae) are found in all GWF streams but are present in higher densities in both Hatchery Creek channel types than in 25 mile channel types which accounts the tight clustering of those sites. *Cricotopus* sp.and *Orthocladius* sp. are both cold stenotherm orthoclads and are probably found in high densities in Hatchery Creek due to its cold temperatures. Furthermore, there was little to no difference of mean daily water temperature between the main and side channel of Hatchery Creek throughout the growing season.

Differences in community structure between main and side channel areas of 25 Mile are due to the numerical dominance of different taxa in each channel type. The main channel has one numerically dominant taxon whereas the side channel has five dominant taxa. One explanation for the difference in the number of dominant taxa could be due to the habitat preference of chironomids. Jowett (1991) reported that some chironomid taxa prefer habitats with low stream velocity and finer substrates, which would coincide with characteristics of the side channels in this study. Another explanation could be the difference in temperature range between main and side channels of 25 mile. Side channels have a larger temperature range than the main channels throughout the growing season. Vannote and Sweeney (1982) showed that streams with larger temperature ranges tend to have higher number of taxa then those with a narrower temperature range, which could account for the five dominant taxa present in side channels and one taxon in the main channel.

Implications

Aquatic insect communities of GWF and SWF streams were numerically dominated by chironomids. However, overall community structure differed between GWF and SWF streams, based on two subfamilies of Chironomidae. Orthocladiinae (87% relative abundance) dominated GWF streams where as Orthocladiinae (50%) and Chironominae (42%) both dominated SWF streams. Aquatic insects are an essential component to salmon diets during their first years of development. Current salmon research on these streams indicate that the majority of 0+ salmon diet consists of chironomids (E. Campbell, pers. comm.), which is consistent with the community composition data from this study. Salmon in streams along the Copper River Delta (CRD) are economically vital for the commercial and sport fishing industries in Cordova, AK.

Alaskan streams are highly valued ecosystems that provide a suite of ecosystem services, including recreational and economic opportunities. These ecosystems, however, are particularly vulnerable to the effects of climate change because these effects will be experienced earliest in northern latitudes. Understanding how northern latitude streams with contrasting thermal regimes will respond to changes in climate has implications for aquatic insect community structure, and ultimately, food resources for salmon. Results from this study provide insights that can inform management decisions concerning these critically important CRD salmon habitats and the ecosystem services they provide.

CHAPTER III: AQUATIC INSECT SECONDARY PRODUCTION

Introduction

Aquatic insects are integral components in stream energy flow because they provide a link between lower and higher trophic levels (Benke et al. 1984). One of the most common approaches used to understand energy flow is by quantifying secondary production, which is the rate of biomass accumulation over time (Huryn and Wallace 2000). Water temperature has a strong influence on secondary production of aquatic insects (Wallace and Anderson 1996, Sweeney 1984) through its effects on growth and development (Anderson and Cummins 1979, Vannote and Sweeney 1980, Sweeney 1984).

Streams in close geographic proximity can have contrasting thermal regimes because of differences in hydrologic type. Groundwater-fed (GWF) streams exhibit little thermal variation due to the stability of groundwater temperatures (Vannote and Sweeney 1980); whereas surface water-fed (SWF) streams are more thermally variable due to the influence of major inputs such as precipitation and glacial melt. In addition, channel depth also can strongly influence water temperatures (Gordon 2004). Shallow side channels are more readily warmed by solar radiation than main channels due to reduced depth and increased residence time of water (McRae and Edwards 1994, Hawkins et al. 1997).

Aquatic insects within streams of different hydrologic types, and subsequently different temperatures, would have different growth rates and secondary production

(Vannote and Sweeney 1980, Merritt et al. 1982). Huryn and Wallace (2000) reviewed systems around the world with aquatic insect taxa that have low and high growth rates as well as low and high secondary production rates. Aquatic insects with low growth and secondary production rates tended to be indicative of streams in more northern locations with cooler temperatures, whereas insects with high growth and secondary production rates were associated with streams in warmer climates (Huryn and Wallace 2000). Optimal temperature regimes exist for insects where adult size is maximized. However, at nonoptimal temperatures, whether warmer or cooler, insects mature at smaller body sizes (Vannote and Sweeney 1980). Merritt et al. (1982) showed that an increase in stream temperatures reduced larval development time and final larval body size in blackflies (Diptera: Simuliidae), which optimally develops at cold temperatures.

Study Objective

The goal of this research was to understand the influences of thermal heterogeneity (i.e. across hydrologic regimes and within streams) on aquatic insect growth and secondary production rates. Results from this study will provide insights as to how contrasting thermal and hydrologic regimes influence aquatic insect secondary production in critically important salmonid streams along the Copper River Delta.

Methods

The Copper River Delta (CRD) in south central Alaska is an ideal location to study the effects of thermal variability and hydrologic types on aquatic insect secondary production. Streams on the delta are relatively pristine, have numerous side channels (Kruger & Tyler 1995), and exhibit contrasting thermal and hydrologic types associated with being primarily groundwater-fed (GWF) or surface water-fed (SWF).

Four streams, two groundwater-fed (GWF; 25 Mile and Hatchery Creek) and two surface water-fed (SWF; 18 Mile and Blackhole Creek), were used in this study. 25 Mile is located at mile marker 25 (40 km) on the Copper River Highway and Hatchery Creek is located 8 km from the town of Cordova, AK on Power Creek Rd. 18 Mile and Blackhole Creek are located mile marker 18 (29 km) and mile marker 21 (34 km) on the Copper River Highway, respectively. A more detailed description of sites is provided in Chapter 2.

Streams were sampled bimonthly in spring and summer (late April 2013 through August 2013) and once seasonally in fall (September) and early winter (November). Sampling in each stream occurred along a 300-meter reach in the main channel, which is deeper with a more rapid current than side channel areas, which are shallow with little to no current. Aquatic insect growth and secondary production were quantified by sampling benthic substrates using a 0.1m Hess sampler (mesh size = 250 μm). Three replicate benthic samples were collected from both areas in each stream on each sampling date. The Hess sampler was randomly placed in each stream area and the enclosed substrate was agitated for 30 seconds. If there was little or no current in the side channel areas, a current was manually created within the Hess Sampler to ensure organisms were swept into the collection net. Samples were transferred to Uline® poly bags, preserved with 70% ethanol and transported to the laboratory for sorting and identification. The high numbers of chironomids (Diptera: Chironomidae) collected required subsampling using a Folsom Plankton Splitter (Wildlife Supply Company, Florida, USA). A more detailed description of chironomid sample processing is provided in Chapter 2. Aquatic insects were identified to the lowest possible taxonomic level, usually genus, using Merritt *et al.*

(2008) and were measured to the nearest millimeter under a Leica dissecting microscope at 6.3 - 50X magnification.

Growth Rates

Growth rates were calculated for five aquatic insect taxa present in all four streams (Table 8). Growth rates of congeneric taxa occurring in both channel types (main and side channels) within a stream were calculated separately. Only insect growth rates in main channels were compared across hydrologic types (groundwater-fed (GWF) vs. surface water-fed (SWF)), as no single taxon was present in side channels of all four streams (Table 8). There were insufficient data for comparing chironomid growth rates at the genera level because only three sampling dates (May, July, September) were used for chironomid identification and subsequent analyses due to logistical constraints associated with identifying the high number of chironomid larvae collected. Growth rates were calculated for the following taxa: *Dicranota* spp. (Diptera: Tipulidae), *Baetis* spp. (Ephemeroptera: Baetidae), *Suwallia* spp. (Plecoptera: Chloroperlidae), *Capnia* spp. (Plecoptera: Capniidae) and *Ecclisomyia* spp. (Trichoptera: Limnephilidae). Instantaneous growth rates (Waters 1977, 1979) were calculated as mg ash-free dry mass (AFDM)mg/d. Growth rates of taxa with multiple cohorts were calculated as a mean growth rate of all cohorts, and was used in subsequent analyses. One-way analysis of variance was used to compare mean growth rates across hydrologic types for each taxon (SYSTAT Software Vers. 13, San Jose, CA).

Secondary Production

Secondary production was estimated for the most abundant aquatic insect taxa using the size-frequency method adjusted for cohort production interval (CPI) (Hynes &

Table 8. Growth rates (mg AFDM/mg/d) of aquatic insect taxa across hydrologic types (groundwater-fed (GWF) vs. surface water-fed (SWF)) from study streams on the Copper River Delta, AK, April-November 2013.

			Growth Rates				
			Dicranota spp.	*Baetis* spp.	*Capnia* spp.	*Suwallia* spp.	*Ecclisomyia* spp.
GWF	25 Mile	Main	0.003	0.003	0.004	0.002	0.001
		Side	0.004	-	-	-	0.01
	Hatchery	Main	0.003	0.003	0.02	0.002	0.004
		Side	0.003	0.01	0.004	0.002	0.005
	Mean (±SE)		0.003 (0.0003)	0.005 (0.002) ^{a}	0.008 (0.004)	0.002 (0.0002)	0.005 (0.002)
SWF	18 Mile	Main	0.002	0.04	0.002	0.01	0.003
		Side	-	-	-	-	-
	Blackhole	Main	0.007	0.05	0.004	0.0009	0.001
		Side	0.008	0.007	0.01	-	0.004
	Mean (±SE)		0.006 (0.002)	0.03 (0.01) ^{b}	0.005 (0.003)	0.005 (0.004)	0.003 (0.0009)

Different superscripts indicate significant differences in mean growth rates (one-way ANOVA, p=0.03)

Coleman, 1968; Benke 1979, 1984). Secondary production was estimated for 17 taxa: five chironomid subfamilies, six non-chironomid dipterans, and six non-dipterans (Table 9).

Insects in each taxon were sorted into size classes and placed on pre-weighed aluminum weigh boats. Insects were dried at a constant 60 ºC for 6 hours in a drying oven. Samples were then reweighed with a Kern & Sohn GmbH analytical balance, placed in a muffle furnace at 550 ºC for 12 hours and reweighed to calculate ash-free dry mass by subtracting ash weight from dry weight. Size class-specific AFDM of congeneric taxa were determined separately in each hydrologic type (GWF or SWF).

Cohort production interval (CPI) for each taxon was determined by interpreting size-frequency graphs of taxa collected throughout the study period. Cohort production intervals for congeneric taxa occurring in both GWF and SWF streams were assigned separate CPI values (e.g., *Baetis* spp.: GWF CPI = 6, SWF CPI = 4) based on taxon-specific size class distributions within each hydrologic regime. A mean CPI was used for taxa with multiple cohorts within a given hydrologic regime. Secondary production values were calculated as mg AFDM/m^2/yr.

Total secondary production values were square root transformed to meet the assumptions of ANOVA and compared across hydrologic and channel type with a two-way analysis of variance. Secondary production of trophic levels, i.e., predators and non-predators, and functional feeding groups (FFGs) were also estimated separately, square root transformed, and analyzed with a three-way ANOVA comparing hydrologic type, channel type, and trophic level or FFG. All statistical analyses were conducted using SYSTAT Ver. 13 (SYSTAT Software, San Jose, CA).

Table 9. Aquatic insect taxa classified[*] into trophic guilds and functional feeding groups from study streams on the Copper River Delta, AK, April - November 2013. Abbreviations as listed: Non-predator (N), predator (P), collector-gatherer (C-G), collector-filterer (C-F), shredder (Sdr), scraper (Spr), engulfer (Eng), and piercer (Pcr).

Taxa	Trophic Guild	Functional Feeding Group
Ephemeroptera		
Baetidae		
Baetis spp.	N	C-G
Heptageniidae		
Cinygmula spp.	N	Spr
Plecoptera		
Capniidae		
Capnia spp.	N	Sdr
Chloroperlidae		
Suwallia spp.	P	Eng
Nemouridae		
Zapada cinctipes	N	Sdr
Trichoptera		
Limnephilidae		
Ecclisomyia spp.	N	C-G
Diptera		
Ceratopogonidae		
Bezzia spp.	P	Eng
Probezzia spp.	P	Eng
Chironomidae		
Chironominae	N	C-G
Diamesinae	N	C-G
Prodiamesinae	N	C-G
Orthocladiinae	N	C-G
Tanypodinae	P	Eng
Empididae		
Chelifera spp.	P	Pcr
Simuliidae		
Prosimulium spp.	N	C-F
Simulium spp.	N	C-F
Tipulidae		
Dicranota spp.	P	Eng

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[*] Taxa classified into trophic guilds and function feeding groups based on classifications from Merritt et al. 2008.

Results

Growth Rates

Aquatic insect growth rates in GWF streams were highest for *Capnia* spp. and lowest for *Suwallia* spp., whereas in SWF streams growth rates were highest for *Baetis* spp. and lowest for *Ecclisomyia* spp. (Table 8). *Dicranota* spp. and *Suwallia* spp. growth rates were low in GWF and SWF streams with no significant difference between hydrologic types for each taxa (Table 8). Growth rates of *Capnia* spp. were not significantly different between hydrologic types and were highly variable within GWF and SWF streams. Growth rates of *Baetis* spp. in main channels of SWF streams were significantly higher (mean = 0.04 ± 0.008 mg/mg/d) than in GWF streams (0.003 ± 0.0002 mg /mg/d; one-way ANOVA, df=1,2; F=27.1, p = 0.03) (Table 8).

While growth rates of chironomid subfamilies were not calculated, there were differences in mean individual biomass of two chironomid subfamilies between hydrologic types. Mean individual biomass (mg AFDM) of Orthocladiinae and Chironominae differed between GWF and SWF streams. Orthocladiinae mean individual biomass was relatively high in GWF streams compared to SWF streams (GWF: 0.11 mg, SWF: 0.02 mg). In contrast, mean individual biomass of Chironominae was relatively low in GWF streams compared to SWF streams (GWF: 0.07 mg, SWF: 0.20 mg).

Secondary Production

I examined the influence of hydrologic and channel type on total secondary production, trophic guild secondary production and functional feeding group secondary production. Secondary production rates were calculated for the most abundant taxa collected in a range of size categories (Tables 10 and 11). These taxa included five

Table 10. Densities (no./m^2) and secondary production rates (mg AFDM /m^2/yr) of taxa from groundwater-fed (GWF) study streams on the Copper River Delta, AK, April – November 2013. The contribution of each taxon to total density (% Density) and total secondary production (% Sec. Prod.) are presented. Maximum body lengths (Max BL; mm) also are presented and were similar in main and side channels and between streams.

25 Mile					**Hatchery Creek**						
	Main Channel		**Side Channel**		**Main Channel**		**Side Channel**				
	Density	Sec. Prod.	Density	Sec. Prod.	Density	Sec. Prod.	Density	Sec. Prod.	% Density	% Sec. Prod.	Max BL
Ephemeroptera											
Baetis spp.	356.7	1312.6	-	-	630.0	1440.6	20.0	59.7	4	16.4	9
Plecoptera											
Capnia spp.	66.7	23.3	-	-	426.7	164.9	163.3	69.2	2.6	1.5	8
Suwallia spp.	43.3	52.8	-	-	556.7	697.4	83.3	110.9	2.7	5	11
Trichoptera											
Ecclisomyia spp.	56.7	80.7	46.7	125.8	30.0	17.2	53.3	103.5	<1	1.9	14
Diptera											
Chironominae	16.7	1.5	166.7	41.3	910.0	311.1	886.7	388.7	7.8	4.3	9
Diamesinae	46.7	0.3	13.3	1.8	100.0	218.0	276.7	663.7	1.7	5.1	15
Orthocladiinae	1733.3	1310.3	4673.3	3367.2	7173.3	3112.1	4673.3	1854.4	71.8	56.1	10
Prodiamesinae	13.3	1.4	416.7	207.1	-	-	106.7	14.5	2.1	1.3	12
Tanypodinae	-	-	30.0	32.5	-	-	-	-	<1	<1	10
Bezzia spp.	13.3	0.7	486.7	23.3	-	-	-	-	1.9	<1	5
Chelifera spp.	103.3	14.4	63.3	8.9	16.7	5.8	33.3	14.0	<1	<1	7
Prosimulium spp.	233.3	222.1	-	-	-	-	-	-	<1	1.3	7
Dicranota spp.	100.0	149.1	80.0	114.9	316.7	547.8	210.0	312.6	2.8	6.5	16

Table 11. Densities (no./m^2) and secondary production rates (mg AFDM /m^2/yr) of taxa from surface water-fed (SWF) study streams on the Copper River Delta, AK, April – November 2013. The contribution of each taxon to total density (% Density) and total secondary production (% Sec. Prod.) are presented. Maximum body lengths (Max BL; mm) also are presented and were similar in main and side channels and between streams.

18 Mile					**Blackhole Creek**						
	Main Channel		**Side Channel**		**Main Channel**		**Side Channel**				
	Density	Sec. Prod.	Density	Sec. Prod.	Density	Sec. Prod.	Density	Sec. Prod.	% Density	% Sec. Prod	Max BL
Ephemeroptera											
Baetis spp.	500.0	598.8	-	-	753.3	396.9	43.3	22.7	8.6	18	7
Cinygmula spp.	90.0	74.9	-	-	336.7	201.9	20.0	16.2	3	4.1	7
Plecoptera											
Capnia spp.	303.3	73.0	-	-	246.9	28.6	-	-	3.7	1.8	6
Suwallia spp.	-	-	-	-	246.9	96.5	56.7	41.4	2	2.4	8
Zapada cinctipes	146.7	46.6	-	-	320.0	45.9	33.3	3.8	3.3	1.7	4
Trichoptera											
Ecclisomyia spp.	-	-	-	-	106.7	42.7	20.0	12.2	<1	1	14
Diptera											
Chironominae	1030.0	460.6	846.7	595.6	616.7	217.3	1110.0	770.7	23.9	36.2	14
Diamesinae	13.3	1.8	3.3	0.1	-	-	-	-	<1	<1	4
Orthocladiinae	2266.7	342.7	1223.3	96.6	780.0	64.1	423.3	33.9	31.1	9.5	6
Prodiamesinae	13.3	3.4	163.3	35.1	-	-	93.3	90.9	1.8	2.3	9
Tanypodinae	56.7	53.5	36.7	62.0	50.0	20.8	190.0	258.2	2.2	7	13
Probezzia spp.	1150.0	364.6	206.7	47.0	263.3	76.1	333.3	102.1	13	10.4	11
Prosimulium spp.	-	-	-	-	86.7	11.7	-	-	<1	<1	5
Simulium spp.	420.0	112.7	-	-	220.0	128.3	13.3	3.8	4.3	4.3	7
Dicranota spp.	30.0	5.1	-	-	166.7	41.4	40.0	12.0	1.6	1	12

chironomid subfamilies and twelve non-chironomid genera, however not all taxa were present or had sufficient densities within each of the four streams and/or channel types to estimate production. Therefore, patterns in secondary production were analyzed as total secondary production (summing separate estimates of predator and non-predator production), and by trophic guild (predator and non-predator), and functional feeding groups (FFGs)(Table 9).

Total Secondary Production

There was no significant effect of channel type or interaction between hydrologic and channel type on total secondary production (two-way ANOVA), however there was a significant difference between hydrologic types. Total secondary production (mean ± SE) was significantly higher in GWF (4369 ± 738 mg/m^2/yr) than in SWF streams (1412 ± 268 mg/m^2/yr) (two-way ANOVA, df = 1,4; F = 17.3 p = 0.01) (Figure 5).

Trophic Guild Secondary Production

Two-way ANOVA was used to examine differences in secondary production between hydrologic type and trophic guilds (predator vs. non-predator). There were significant differences in hydrologic type and in trophic guilds (two-way ANOVA, hydrologic type main effect, df=1,12; F=18.4, p =0.001; two-way ANOVA trophic guild main effect, df=1,12; F= 55.4, $p<0.001$). However, there was a significant interaction between hydrologic type and trophic guild, (two-way ANOVA, df=1,12; F=9.7, p= 0.008) indicating that hydrologic type was influencing trophic guild secondary production.

To explore this interaction two separate one-way ANOVAs were used to examine

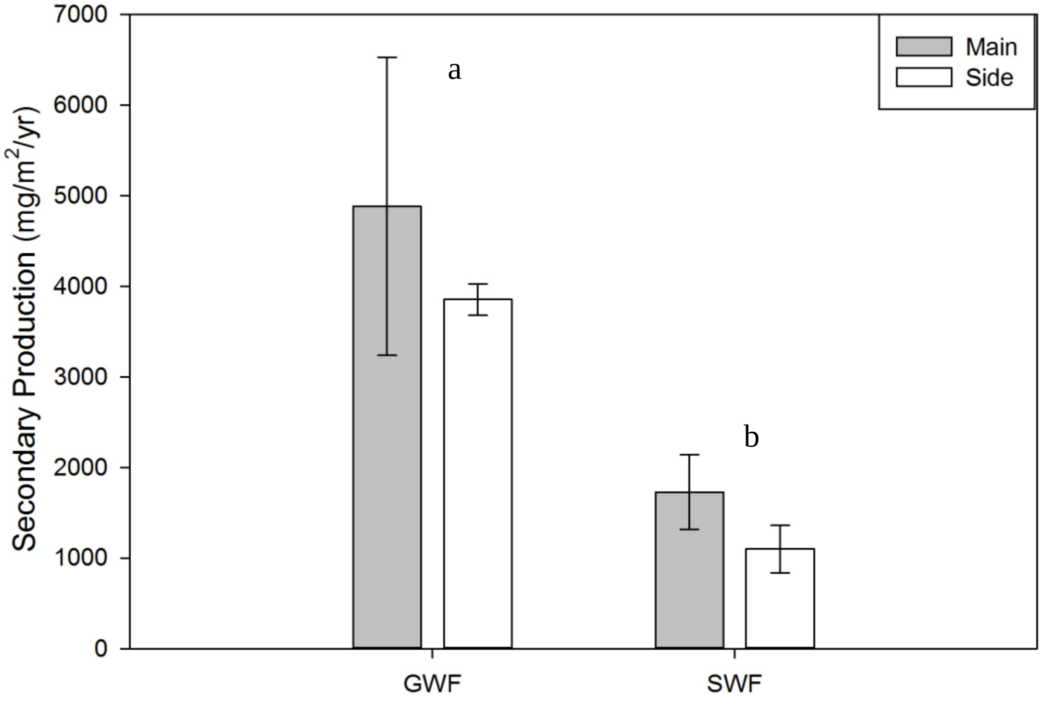

Figure 5. Mean (± SE) aquatic insect secondary production (mg AFDM/m^2/yr) from two groundwater-fed (GWF) and two surface water-fed (SWF) streams on the Copper River Delta, AK, April-November 2013. Bars with different letters are significantly different (two-way ANOVA; p=0.01).

the differences in hydrologic type for each trophic guild. There was no significant difference between GWF and SWF predator secondary production. Non-predator secondary production was significantly higher in GWF streams (one-way ANOVA, df=1,6; F=22.2, p=0.003).

To examine the differences in secondary production between channel type and trophic guilds, a two-way ANOVA was used. There was no significant difference between channel types or the interaction between channel types and trophic guilds. There was a significant difference between trophic guilds (two-way ANOVA, df=1,12; F=17.6, p=0.001). As there was no interaction between channel types and trophic guild, a one-way ANOVA was used to examine differences in secondary production based on trophic guild. Non-predator secondary production was significantly higher than predator secondary production (one-way ANOVA, df=1,14; F=19.3, p <0.001) (Table 12).

Functional Feeding Group Secondary Production

There were six functional feeding groups, collect-gatherer, shredders, engulfers, scrapers, collector-filterers and piercers. Collector-gatherers had the highest secondary production regardless of hydrologic or channel types, compared to the other five functional feeding groups (Figure 6). Secondary production rates were analyzed using two-way ANOVA to examine the differences between hydrologic type and functional feeding groups. There were significant differences in hydrologic type and in functional feeding group (two-way ANOVA, hydrologic type main effect, df=1,36; F=21.9, p<0.001; two-way ANOVA functional feeding group main effect, df=5,36; F= 53.4, p<0.001). The interaction between hydrologic type and functional feeding group was also significant (two-way ANOVA, df=5,36; F=7.9, p<0.001). Separate one-way ANOVAs

Table 12. Secondary production (mg AFDM/m^2/yr) of aquatic insect trophic guilds (predator and non-predator) in main and side channel areas of two groundwater-fed (GWF) and two surface water-fed (SWF) streams on the Copper River Delta, AK, April-November 2013. Different superscripts denote significant differences in trophic guild production (one-way ANOVA, p<0.001).

	GWF				**SWF**			
	25 Mile		**Hatchery Creek**		**18 Mile**		**Blackhole Creek**	
	Main	**Side**	**Main**	**Side**	**Main**	**Side**	**Main**	**Side**
Non-Predator	2951.5	3741.7	5262.6	3152.7	1714.5	727.4	1081.5	948.8
Mean (± SE)	3447.6 ± 801 ^{a}							
Predator	217.0	179.5	1251.0	437.5	423.1	109.0	234.7	413.7
Mean (± SE)	408.2 ± 181 ^{b}							
Total Channel	3168.5	3921.2	6513.6	3589.8	2137.6	836.4	1316.2	1362.6
Total Stream	7089.7		10103.5		2974.1		2678.8	

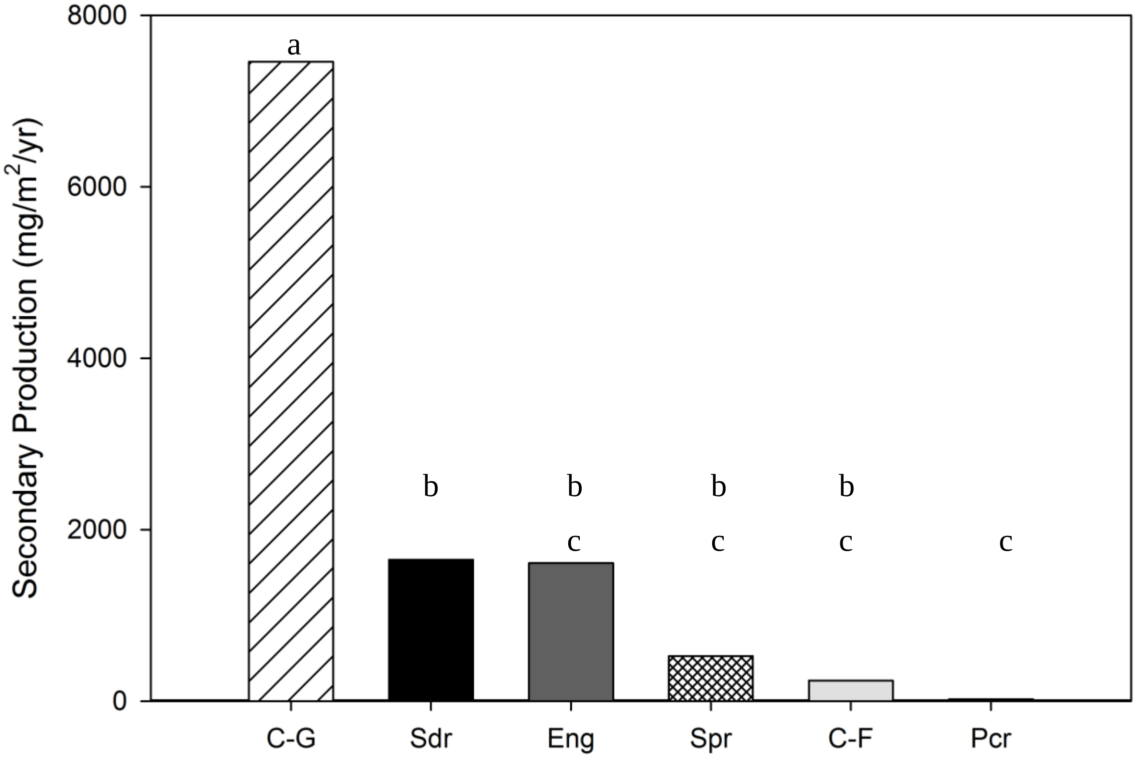

Figure 6. Overall functional feeding group secondary production across study streams. Functional feeding group abbreviations as in Table 9. Bars with different letters indicate significant differences yielded from Tukey's multiple comparison's test.

were used to examine the differences in hydrologic type for each functional feeding group to further examine the interaction between hydrologic type and functional feeding group. Secondary production was significantly higher in GWF than in SWF streams for following three functional feeding groups: collector-gatherer (one-way ANOVA, df=1,6; F=36.7, $p<0.001$), shredder (one-way ANOVA, df=1,6; F=10.9, p=0.01) and piercer (one-way ANOVA, df=1,6; F=93.9, $p<0.001$).

Differences in secondary production between channel type and functional feeding group were analyzed using a two-way ANOVA. There was no significant difference between channel types or the interaction between channel types and functional feeding groups. There was a significant difference between functional feeding groups (two-way ANOVA, df=5,42; F=22.9, $p<0.001$). A Tukey's multiple comparisons test was then conducted to determine which FFGs were different from one another (Figure 7). Collector-gatherer secondary production was significantly higher than any other FFG. Two chironomid subfamilies accounted for 69% of collector-gatherer secondary production: Orthocladiinae (54.5%) and Chironominae (14.9%). Piercer secondary production was significantly lower than all other FFGs except for collector-filters.

The effect of hydrologic and channel type, and their interaction on secondary production of FFGs, excluding piercers (no secondary production values from SWF streams), was examined using two-way ANOVAs, only collector-gatherers yielded significant results. Collector-gatherers was significantly higher in GWF (2965 $mg/m^2/yr$) than in SWF (724 $mg/m^2/yr$) streams (two-way ANOVA, df=1,4; F=33.7, p = 0.004). Channel type and the interaction of hydrologic and channel type had no significant effect on FFG secondary production.

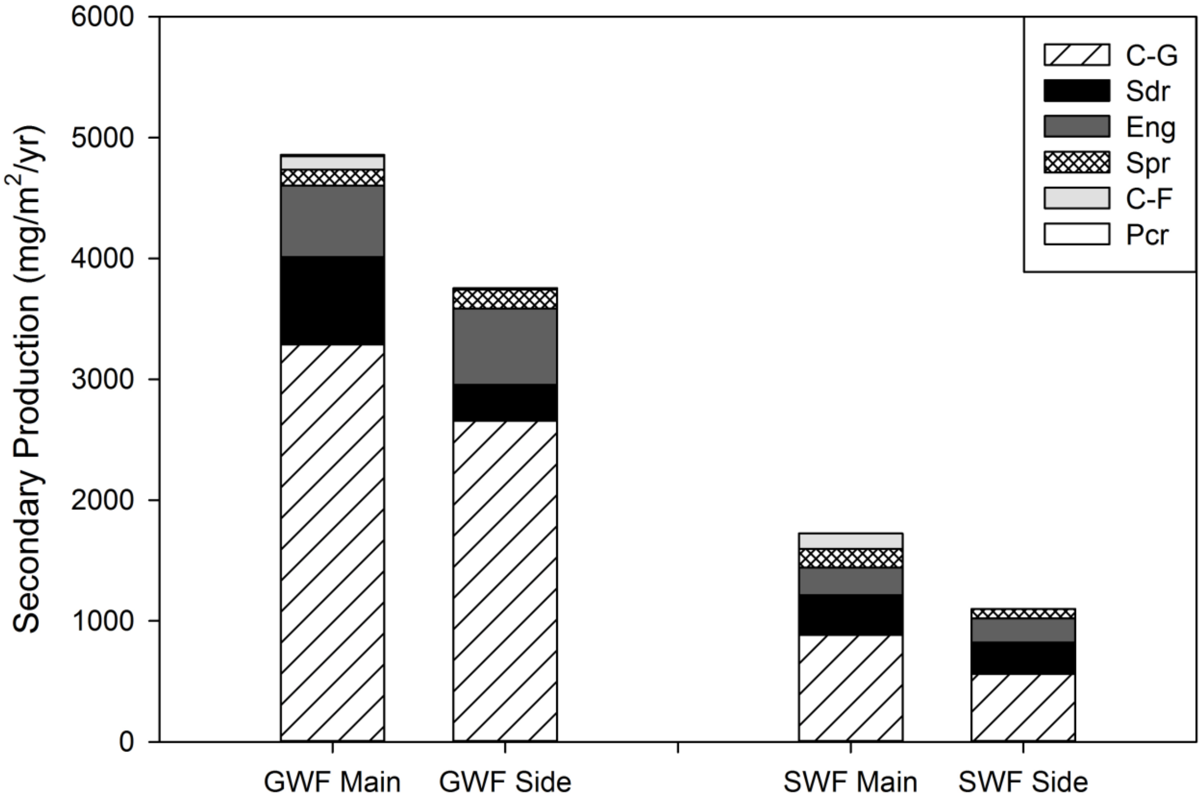

Figure 7. Secondary production (mg AFDM /m^2/yr) of aquatic insect functional feeding groups by channel type (main and side channels) from two groundwater-fed (GWF) and two surface water-fed (SWF) streams on the Copper River Delta, AK, April-November 2013. Functional feeding group abbreviations as in Table 9.

Groundwater-fed Streams

Main Channels

Orthocladiinae dominated secondary production in main channels of both GWF streams, with the highest densities and secondary production occurring in Hatchery Creek, 7173 /m^2 and 4673 mg/m^2/yr, respectively (Table 10). *Baetis* spp. secondary production was also high in main channels of GWF streams (25 Mile: 1312 mg/m^2/yr, Hatchery Creek: 1440 mg/m^2/yr). Although secondary production rates of Orthocladiinae and *Baetis* spp. were similar in 25 Mile main channels, 1310 mg/m^2/yr and 1312 mg/m^2/yr, respectively, Orthocladiinae densities (1733 /m^2) were greater than *Baetis* spp (357 /m^2).

Side Channels

Orthocladiinae had the highest secondary production in side channels of both GWF streams. Orthoclad densities were identical in both streams (4673 /m^2), however secondary production values were greater in 25 Mile (3367 mg/m^2/yr) than in Hatchery Creek (1854 mg/m^2/yr) (Table 10). Secondary production of *Ecclisomyia* spp. in both GWF streams was higher in side channel areas than in the main channel although this difference was not significant (side channel mean: 115 ± 11 mg/m^2/yr; main channel mean: 49 ± 32 mg/m^2/yr). Orthocladiinae secondary production was higher in main channels (mean: 2991 ± 1681 mg/m^2/yr) than in side channels (mean: 2610 ± 756 mg/m^2/yr), although this difference was not significant.

Surface water-fed Streams

Main Channels

Baetis spp. and Chironominae dominated secondary production in main channel areas of both SWF streams. *Baetis* spp. secondary production was 599 mg/m^2/yr and 397 mg/m^2/yr in 18 Mile and Blackhole, respectively. Chironominae secondary production was 461 mg/m^2/yr and 217 mg/m^2/yr in 18 Mile and Blackhole, respectively. Although Orthocladiinae had the highest densities in main channels of both SWF streams (18 Mile: 2266 /m^2, Blackhole Creek: 780 /m^2), secondary production (18 Mile: 343 mg/m^2/yr, Blackhole: 64 mg/m^2/yr) did not reflect these high densities (Table 11).

Side Channels

Chironominae dominated secondary production in both SWF streams in the side channels (18 Mile: 596 mg/m^2/yr, Blackhole Creek: 771 mg/m^2/yr) (Table 11). Orthocladiinae density (1223 /m^2) was highest in 18 Mile side channels, however secondary production was relatively low (97 mg/m^2/yr). Chironominae density was highest in the side channels of Blackhole Creek (1110/m^2). Chironominae secondary production was higher in side channels (mean: 683 ± 124 mg/m^2/yr) than in main channels (mean: 339 ± 122 mg/m^2/yr) although this difference was not significant.

GWF vs. SWF

The subfamilies Orthocladiinae and Chironominae had the highest secondary production rates in GWF and SWF streams, respectively and represent a substantial proportion of total secondary production.. The subfamily Orthocladiinae accounted for 72% of total insect density and 56% of total secondary production in GWF streams, whereas in SWF streams orthoclads represented 31% of total insect density and 9% of total secondary production. Orthocladiinae secondary production was significantly higher in GWF (2411 ± mg/m^2/yr) than in SWF (134 ± mg/m^2/yr) streams (two-way ANOVA, df=1,4; F=31.7, p = 0.004) (Figure 8), there was no significant effect of channel type or

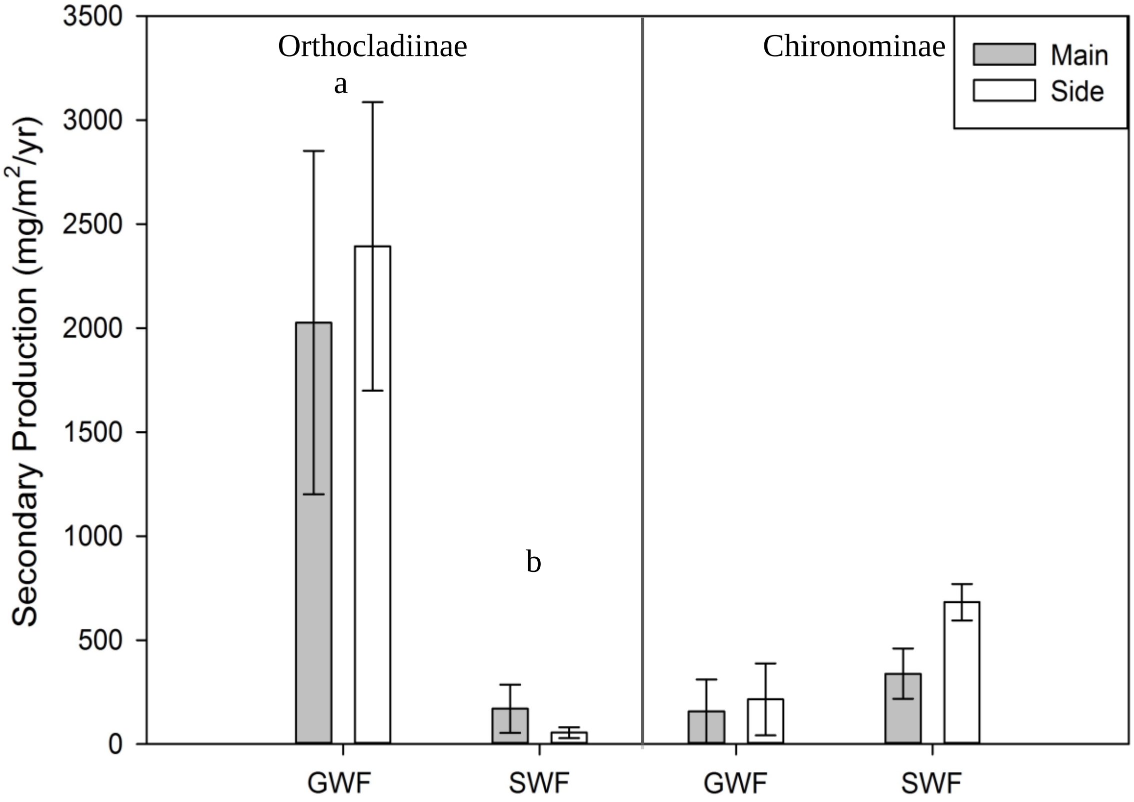

Figure 8. Mean secondary production (mg AFDM /m^2/yr) of Orthocladiinae and Chironominae in two groundwater-fed (GWF) and two surface water-fed (SWF) streams along the Copper River Delta, AK, April-November 2013. Grey bars = main channels; white bars = side channels. Error bars are ± 1 SE. Hydrologic types with different letters are significantly different (two-way ANOVA; p=0.004).

interaction between hydrologic and channel type. The subfamily Chironomidae accounted for 8% of total density and 4% of total secondary production in GWF streams, and 23% of total insect density and 36% of the total secondary in SWF streams.

Main channel vs. Side channel

There was no significant difference in Orthocladiinae secondary production in main and side channels within hydrologic type. There was no significant difference between Chironominae secondary production in GWF and SWF streams or between main and side channel areas within both hydrologic types.

Discussion

Growth Rates

Aquatic insect growth rates are strongly influenced by water temperature, which increases or decreases developmental times (Humpesch 1979, Sweeney 1984). Differences in mean water temperature of groundwater-fed (GWF) and surface water-fed (SWF) streams in this study provide an explanation for differences observed in growth rates of *Baetis* spp. between the hydrologic types. Growth rates of *Baetis* spp. were significantly higher in SWF streams than in GWF streams. During the study, mean water temperature in SWF streams was 2.9°C warmer than in GWF streams (SWF: 7.5°C; GWF: 4.6°C). High growth rates of *Baetis* spp. during the growing season, in warmer streams such as the SWF streams of this study, are consistent with those reported in other studies (Huryn and Wallace 2000). Higher mean temperatures in SWF streams increase growth rates of aquatic insects due to the accumulation of more degree-days over a shorter period of time. Merritt et al. (1982) reported similar results for blackflies, where an increase in stream temperature decreased in larval development time.

Baetis spp. were smaller in SWF streams than in GWF streams (maximum body length; SWF: 7 mm; GWF: 9 mm). Higher growth rates of *Baetis* spp. in SWF streams would result in less time for biomass accumulation(i.e., a smaller body size). Vannote and Sweeney (1980) noted that insects growing at temperatures other than their thermal optimum, whether warmer or cooler, would result in smaller body size. The smaller body size of *Baetis* spp. observed in SWF streams is consistent with Vannote and Sweeney (1980). As indicated by the larger body size, GWF stream temperature is closer to the thermal optimum range for *Baetis* spp., than is SWF stream temperature.

Secondary production

Aquatic insect secondary production in GWF streams was significantly higher than in SWF streams. Stream water temperature affects secondary production of aquatic insects (Wallace and Anderson 1996) through its effects on developmental time, which influences biomass accumulation. High Chironomidae (Diptera) secondary production, resulting from either high densities (Smock 1985) or high mean individual biomass (Benke 1984), also contributed to differences in secondary production in these study streams.

Although chironomids are ubiquitously distributed (Ferrington 2008), subfamilies can generally be considered either cold- or warm-adapted (Ward and Stanford 1982, Lindegaard 1995) and could be expected to have higher secondary production rates consistent with their thermal preferences. Cold adapted taxa such as Orthocladiinae and Diamesinae had higher secondary production rates in GWF streams, whereas warm adapted taxa such as Chironominae and Tanypodinae had higher secondary production rates in SWF streams. In this study total secondary production, trophic guild secondary production, and functional feeding group secondary production were compared across hydrologic types (GWF vs. SWF) and channel types (main channel vs. side channel).

Total Secondary Production

Significantly higher total secondary production in GWF streams compared to SWF streams is primarily due to the high secondary production rates of the chironomid subfamily Orthocladiinae in GWF streams. Orthocladiinae secondary production was significantly higher in GWF than in SWF streams and represented 55% of total secondary production in GWF streams. The substantial contribution of orthoclads to secondary production was a result of higher mean individual biomass and higher densities (mean GWF density 4563 /m^2; 72% of total density) in GWF streams (biomass: 0.11mg) than in SWF streams (biomass: 0.02 mg). Orthoclad densities in the study streams are comparable to those reported in other Alaskan streams (Lessard et al. 2009). Orthocladiinae are commonly found in cool waters (4ºC - 6ºC) (Milner 2001), and water temperatures of GWF streams in this study are within this range (Chapter 2).

Secondary production in SWF streams was dominated by the chironomid subfamily Chironominae, which accounted for 36% of total secondary production. Although Chironominae was not the most abundant taxon in SWF streams, accounting for 23% of total aquatic insect density, the high contribution of Chironominae to total secondary production suggests that this was due to high mean individual biomass. Chironominae mean individual biomass was higher in SWF than in GWF streams (SWF: 0.20 mg, GWF: 0.07mg). In contrast, Orthocladiinae was the most abundant taxon in SWF streams (31% of total insect density), however, orthoclads only accounted for 9% of the total secondary production in SWF streams. This suggests that low secondary production was due to relatively low mean individual biomass (SWF: 0.02 mg, GWF: 0.10 mg). Thus, higher Chironominae secondary production in SWF streams, despite higher orthoclad densities, was likely due to the higher mean individual biomass of Chironominae (0.20 mg) than Orthocladiinae (0.02 mg).

Total secondary production in main and side channels across both hydrologic types were not significantly different due to high densities and secondary production of Orthocladiinae in both channel types. This influence of high orthoclad secondary production potentially conceals any additional secondary production patterns. For example, *Baetis* spp. secondary production across GWF and SWF streams was higher in main channel areas than in the side channels. *Baetis* is a rheophilic insect common in riffles (Wingfield 1939), which primarily occur in main channels of the study streams.

Functional Feeding Group Secondary Production

Among the six functional feeding groups, collector-gatherers had the highest secondary production across all hydrologic types, and was also higher in GWF than in SWF streams. Other studies in groundwater streams also reported high collector-gatherer secondary production compared to other FFGs. Dobrin (2002) and Iversen (1988) found high collector-gatherer secondary production in streams in Canada and Denmark, respectively. While Krueger et al. (1983) reported similar results in cool water streams of Minnesota. A likely explanation for high collector-gatherer secondary production in this study is the high number of taxa comprising the FFG. Six taxa were categorized as collector-gatherers, whereas most other FFGs were represented by only two taxa, except for engulfers, which included five taxa. Of the six collector-gatherer taxa, four were Chironomidae subfamilies, however, high collector-gatherer production is primarily associated with two subfamilies, Orthocladiinae and Chironominae. These subfamilies collectively represented 69% of collector-gatherer secondary production.

Implications

Alaskan streams are particularly vulnerable to the effects of climate change because these effects will be more pronounced in northern latitudes (Hinzman et al. 2005). Although streams in high latitudes are expected to experience increased water temperatures as a result of climate change, local hydrologic type, such as groundwater inputs, may mediate rising stream temperatures (Arismendi et al. 2012). Thus, streams with contrasting hydrologic types, i.e., GWF vs. SWF, will respond differently to climate change. Energy flow in more vulnerable systems will be substantially altered, which will have broad ranging impacts on the ecosystem services provided by these streams.

In this study, higher aquatic insect secondary production in GWF than in SWF streams indicates more energy is potentially available to higher trophic level organisms such as coho salmon (*Oncorhynchus kisutch*), an important economic and recreational resource throughout streams on the Copper River Delta (CRD). Aquatic insects, particularly chironomids, are important food resources for larval salmonids with midges often comprising the majority of their aquatic insect diet (E. Campbell, pers. comm.). Groundwater-fed streams have been shown to provide juvenile coho salmon refuge from ice as they overwinter in streams (Woody and Higman 2011).

The protection of salmonid habitats is a major issue in the Pacific Northwest where many salmon populations have declined over the past several decades causing a nutrient deficit in those systems (Gresh et al. 2000). Migratory salmon introduce marine-derived nutrients into freshwater systems via eggs, sperm, and adult carcasses. Aquatic insects uptake marine-derived nutrients during decomposition of carcasses and aid in the transfer of these nutrients throughout the stream (Cederholm 1999). These nutrients are an important component in sustaining healthy ecosystems and food webs (Lessard et al. 2006, 2009, Cederholm 1999). Results from this study have important implications for the management of these critical habitats.

APPENDIX A: SUPPLEMENTAL TABLES

Table 13. Physicochemical parameters of four study streams on the Copper River Delta, AK, April – November 2013, presented as monthly means. Temperature includes (range) to show max and minimum temperatures. Variation in physicochemical parameters presented as coefficient of variation (CV, %). GWF = groundwater-fed, SWF = surface water-fed. Site abbreviations as in Table 1.

	GWF					SWF				
	25mi-*M*	25mi-*S*	Hat-*M*	Hat-*S*	CV	18mi-*M*	18mi-*S*	Blk-*M*	Blk-*S*	CV
Maximum Depth (cm)	40	20	50	30		60	30	30	25	
Temperature °C					34.7					55.4
Apr	4.2 (3.7-5.5)	3.7 (2.8-5.1)	1.2 (1.1-1.3)	1.3 (1.1-1.8)		1.9 (1.2-2.3)	1.9 (1.8-2.3)	0.8 (0.3-1.1)	0.7 (0.5-0.9)	
May	4.3 (2.7-7.1)	4.7 (2.5-9.1)	2.4 (0.8-4.9)	3.2 (0.8-5.2)		4.5 (0.9-9.5)	4.1 (1.3-8.6)	3.5 (0.6-8.2)	3.2 (0.56-7.98)	
June	5.4 (4.0-9.4)	6.6 (4.8-10.4)	5.0 (2.6-8.0)	5.0 (2.7-8.0)		7.7 (3.9-13.4)	6.5 (3.3-13.1)	8.0 (4.9-11.9)	5.8 (3.8-9.6)	
July	5.3 (4.5-9.0)	6.5 (5.8-9.8)	5.5 (4.1-7.5)	5.5 (4.2-7.7)		11.0 (7.3-16.4)	10.1 (6.5-14.8)	9.7 (7.3-11.9)	7.4 (5.5-10.5)	
Aug	5.3 (4.4-7.5)	6.6 (5.7-9.5)	5.8 (4.6-9.7)	5.0 (4.6-9.4)		11.9 (9.3-13.9)	11.6 (4.2-18.8)	10.5 (8.3-12.2)	9.5 (7.2-11.7)	
Sampling period Mean	4.9	5.6	4.0	4.1		8.4	7.7	7.7	6.2	
pH					16.6					17.1
Apr	6.0	5.8	4.6	5.3		5.9	6.0	8.8	9.6	
May	7.9	8.0	9.1	9.0		6.7	6.7	7.9	8.0	
June	6.8	6.9	7.0	7.2		6.7	6.9	6.5	7.0	
July	6.9	6.1	7.6	7.7		6.9	7.0	8.4	8.3	
Aug	7.1	6.8	8.3	8.2		10.5	10.2	8.0	8.1	
Mean	6.6	6.3	5.3	6.0		6.5	6.5	7.2	7.6	
Dissolved Oxygen mg/L					13.9					24.5
Apr	9.9	8.6	8.7	9.8		9.8	9.7	11.7	12.2	
May	7.6	7.0	8.0	8.5		8.8	7.6	7.9	7.9	
June	7.6	7.3	8.0	7.9		7.1	6.5	6.8	7.1	
July	10.0	9.1	8.6	8.2		7.5	4.4	8.3	6.7	
Aug	11.4	11.5	9.0	9.4		8.2	5.3	11.2	8.0	
Mean	9.3	8.7	8.5	8.8		8.3	6.7	9.2	8.4	

Table 13 Cont.

	GWF					SWF				
	25mi-*M*	25mi-*S*	Hat-*M*	Hat-*S*	CV	18mi-*M*	18mi-*S*	Blk-*M*	Blk-*S*	CV
Conductivity µS/cm					10.4					51.5
Apr	0.06	0.06	0.06	0.06		0.03	0.03	0.01	0.02	
May	0.05	0.05	0.05	0.05		0.02	0.02	0.02	0.02	
June	0.05	0.06	0.06	0.06		0.02	0.03	0.03	0.03	
July	0.05	0.06	0.06	0.06		0.02	0.07	0.03	0.03	
Aug	0.05	0.05	0.06	0.06		0.02	0.07	0.03	0.03	
Mean	0.05	0.05	0.06	0.06		0.02	0.04	0.02	0.03	
Salinity ppt					17.2					63.2
Apr	0.03	0.03	0.03	0.03		0.01	0.01	0.01	0.01	
May	0.02	0.03	0.02	0.02		0.01	0.01	0.01	0.01	
June	0.02	0.03	0.03	0.03		0.01	0.01	0.01	0.01	
July	0.02	0.03	0.03	0.03		0.01	0.03	0.01	0.01	
Aug	0.02	0.03	0.03	0.03		0.01	0.04	0.01	0.01	
Mean	0.02	0.03	0.03	0.03		0.01	0.02	0.01	0.01	
Total Dissolved Solids g/L					9.2					50.6
Apr	0.04	0.04	0.04	0.04		0.02	0.02	0.01	0.01	
May	0.03	0.03	0.03	0.03		0.01	0.01	0.01	0.02	
June	0.03	0.04	0.04	0.04		0.01	0.02	0.02	0.02	
July	0.03	0.04	0.04	0.04		0.01	0.05	0.02	0.02	
Aug	0.03	0.04	0.04	0.04		0.01	0.04	0.02	0.02	
Mean	0.03	0.04	0.04	0.04		0.01	0.03	0.02	0.02	
Oxidation Reduction Potential mV					41.5					55.6
Apr	89.7	103.0	61.7	39.7		78.8	44.6	69.6	20.0	
May	69.5	46.2	76.1	60.4		122.1	94.4	77.1	69.5	
June	63.0	57.3	79.6	62.1		75.8	80.5	100.7	59.9	
July	37.9	29.6	55.8	42.3		41.5	24.8	88.8	68.9	
Aug	56.5	66.5	19.4	NA		22.7	24.0	26.5	10.0	
Mean	63.3	60.5	58.5	51.1		68.2	53.7	72.5	45.7	

Table 13 Cont.	GWF					SWF				
	25mi-*M*	25mi-*S*	Hat-*M*	Hat-*S*	CV	18mi-*M*	18mi-*S*	Blk-*M*	Blk-*S*	CV
Chlorophyll *a* µg/cm^2					140					154
Apr	0.0	1.4	1.1	0.0		0.1	1.2	0.0	0.0	
May	0.0	0.0	1.4	3.2		0.0	0.0	0.0	0.0	
June	0.0	0.4	0.0	0.5		2.4	1.2	0.0	0.6	
July	0.3	2.6	0.0	1.8		0.0	1.4	0.6	0.4	
Aug	0.0	0.0	0.0	3.3		0.3	0.0	0.1	0.3	
Mean	0.1	0.9	0.5	1.8		0.6	0.8	0.1	0.2	
Soluble reactive phosphorus µg/L					105					152
May	1.1	2.8	1.1	0.5		0.0	0.0	0.2	0.3	
June	2.6	0.0	0.1	0.0		0.4	0.0	0.7	0.0	
July	3.0	11.3	1.1	2.8		6.0	3.1	1.2	9.3	
Aug	3.1	5.4	8.0	5.9		3.7	8.6	19.3	23.6	
Mean	2.4	4.9	2.6	2.3		2.5	2.9	5.3	8.3	
Ammonium µg/L					71.7					94.4
May	5.0	7.0	15.1	16.7		16.6	33.9	12.4	26.9	
June	6.5	12.5	15.2	8.4		13.9	10.1	13.3	12.6	
July	15.3	57.3	10.1	23.0		35.4	123.3	18.9	42.8	
Aug	21.0	23.7	39.0	29.9		31.3	110.9	84.8	129.9	
Mean	11.9	25.1	19.8	19.5		24.3	69.6	32.3	53.0	
Nitrate µg/L					44.9					50.7
May	89.9	90.0	84.4	86.5		108.1	46.6	13.2	19.2	
June	86.0	143.1	92.7	63.5		58.8	38.7	70.1	66.3	
July	131.8	106.8	69.6	51.0		86.8	48.6	58.4	35.1	
Aug	58.4	49.7	19.9	15.3		44.0	35.9	27.2	30.7	
Mean	91.5	97.4	66.6	54.0		74.4	42.5	42.2	37.8	

Table 14. Aquatic insect taxa and mean densities (no./m^2) in main and side channel areas of study streams on the Copper River Delta, AK, April – November 2013. Taxa with SE = 0 were only collected on one occasion; therefore means could not be calculated.

	GWF				**SWF**			
	25 Mile		**Hatchery Creek**		**18 Mile**		**Blackhole Creek**	
	Main	Side	Main	Side	Main	Side	Main	Side
Ephemeroptera								
Baetidae								
Baetis	44 (17)	-	69 (24)	4 (1)	53 (17)	7 (3)	84 (40)	11 (15)
Heptageniidae								
Cinygmula	-	-	5 (1)	-	18 (9)	-	34 (9)	5 (2)
Epeorus	-	-	-	-	-	-	3 (0)	-
Plecoptera								
Capniidae								
Capnia	10 (4)	3 (0)	67 (25)	14 (8)	21 (12)	3 (0)	40 (11)	8 (6)
Chloroperlidae								
Suwallia	9 (2)	7 (0)	38 (9)	10 (3)	108 (105)	-	44 (18)	22 (32)
Nemouridae								
Zapada cinctipes	-	-	4 (1)	3 (0)	29 (15)	3 (0)	40 (16)	8 (4)
Perlodidae								
Isoperla katmaiensis	-	-	3 (0)	-	-	-	-	-
Hemiptera								
Corixidae								
Callicorixa vulnerata	-	20 (13)	-	-	7 (3)	96 (84)	-	57 (61)
Trichoptera	-	13 (10)	-	-	-	-	-	-
Limnephilidae								
Ecclisomyia	11 (3)	12 (5)	6 (2)	11 (2)	3 (0)	3 (0)	13 (5)	5 (3)
Lenarchus	-	-	-	-	-	3 (0)	-	3 (0)
Limnephilus	-	13 (10)	-	-	-	-	-	-
Onocosmoecus	-	-	-	-	-	-	-	3 (0)
Psychoglypha	5 (2)	14 (6)	-	4 (1)	-	10 (0)	-	3 (0)
Coleoptera								
Dytiscidae								
Agabus	-	7 (3)	-	-	-	3 (0)	-	3 (0)

Table 14 Cont.

	GWF				**SWF**			
	25 Mile		**Hatchery Creek**		**18 Mile**		**Blackhole Creek**	
	Main	Side	Main	Side	Main	Side	Main	Side
Diptera								
Athericidae								
Atherix	-	-	-	-	-	-	5 (1)	3 (0)
Chironomidae								
Tanypodinae								
Derotanypus	-	-	-	-	-	7 (0)	-	-
Larsia	-	-	-	-	40 (0)	-	-	-
Macropelopia	-	13 (0)	-	-	-	-	-	40 (0)
Monopelopia	-	-	-	-	13 (0)	-	12 (4)	15 (5)
Psectrotanypus	-	23 (0)	-	-	-	3 (0)	-	133 (0)
Thienemannimyia grp.	-	-	-	-	3 (0)	27 (0)	-	-
Podonominae								
Paraboreochlus	-	-	-	-	-	-	10 (0)	-
Diamesinae								
Diamesa	10 (3)	-	7 (0)	-	-	-	-	-
Pagastia	-	-	15 (8)	37 (0)	13 (0)	-	-	-
Potthastia	-	-	27 (0)	-	-	3 (0)	-	-
Protanypus	-	13 (0)	-	-	-	-	-	-
Pseudodiamesa	-	-	18 (8)	81 (27)	-	-	-	-
Prodiamesinae								
Prodiamesa	13(0)	121 (73)	-	13 (0)	-	83 (0)	-	120 (0)
Odontomesa	-	53 (0)	-	93 (0)	13 (0)	80 (0)	-	13 (0)
Orthocladiinae								
Chaetocladius	482 (465)	27 (0)	-	87 (70)	-	-	3 (0)	-
Corynoneura	22 (12)	-	40 (33)	13 (0)	152 (98)	427 (80)	186 (90)	128 (48)
Cricotopus	61 (28)	821 (738)	373 (0)	1493 (0)	13 (0)	-	5 (2)	-
Diplocladius	67 (0)	-	278 (140)	454 (317)	-	3 (0)	-	-
Eukiefferiella	33 (3)	-	30 (0)	17 (0)	368 (363)	68 (65)	7 (0)	27 (0)
Heterotanytarsus	-	-	-	-	-	-	3 (0)	3 (0)
Hydrobaenus	7 (0)	328 (290)	43 (18)	27 (0)	177 (163)	80 (0)	33 (0)	27 (0)

Table 14 Cont.

	GWF				SWF			
	25 Mile		**Hatchery Creek**		**18 Mile**		**Blackhole Creek**	
	Main	Side	Main	Side	Main	Side	Main	Side
Nanocladius	-	-	-	-	-	40 (0)	-	30 (0)
Orthocladius	13 (10)	159 (61)	1734 (1719)	509 (424)	33 (0)	-	-	-
Orthocladius/Cricotopus	-	-	267 (0)	-	7 (0)	3 (0)	120 (0)	7 (0)
Parorthocladius	79 (1)	-	8 (5)	27 (0)	-	-	-	-
Psectrocladius	-	15 (8)	-	-	-	3 (0)	-	-
Rheocricotopus	-	-	-	-	47 (0)	40 (0)	7 (0)	-
Thienemanniella	-	-	347 (0)	-	53 (31)	40 (0)	27 (0)	3 (0)
Tvetenia	163 (0)	747 (0)	-	-	-	-	3 (0)	-
Unidentified genus A	-	-	-	159 (139)	-	-	-	3 (0)
Unidentified genus B	-	3 (0)	-	13 (0)	-	-	-	67 (0)
Unidentified genus C	3 (0)	-	-	-	93 (0)	3 (0)	-	-
Unidentified genus D	-	-	-	187 (0)	-	-	-	-
Chironominae								
Chironomini								
Chironomus	-	-	-	-	-	102 (32)	-	53 (0)
Phaenopsectra	-	13 (0)	-	73 (47)	10 (0)	200 (173)	-	27 (0)
Polypedilum	3 (0)	-	3 (0)	177 (0)	280 (179)	66 (31)	453 (0)	413 (387)
Unidentified genus A	-	-	-	27 (0)	-	-	-	-
Tanytarsini								
Micropsectra	-	17 (0)	-	32 (22)	13 (0)	3 (0)	22 (18)	47 (25)
Micropsectra/Tanytarsus	3 (0)	13 (0)	907 (0)	189 (172)	70 (63)	3 (0)	60 (40)	35 (18)
Paratanytarsus	10 (0)	41 (33)	-	-	27 (0)	47 (0)	-	-
Tanytarsus	-	-	-	-	-	-	-	3 (0)
Ceratopogonidae								
Bezzia/Palpomyia	6 (1)	76 (31)	-	-	-	13 (10)	8 (2)	10 (7)
Probezzia	7 (3)	18 (6)	-	3 (0)	131 (38)	42 (22)	44 (14)	67 (39)
Dolichopodidae	-	-	-	-	-	-	-	3 (0)
Empididae								
Chelifera/Metachela	15 (3)	13 (8)	3 (0)	14 (10)	-	3 (0)	3 (0)	3 (0)
Ephydridae	-	-	-	-	-	-	3 (0)	7 (0)

Table 14 Cont.

	GWF				**SWF**			
	25 Mile		**Hatchery Creek**		**18 Mile**		**Blackhole Creek**	
	Main	Side	Main	Side	Main	Side	Main	Side
Psychodidae								
Pericoma/Telmatoscopus	-	-	-	-	-	-	-	3 (0)
Simuliidae								
Prosimulium	47 (38)	-	5 (2)	-	15 (6)	-	22 (14)	3 (0)
Simulium	8 (5)	-	3 (0)	-	85 (41)	-	32 (18)	6 (0)
Tipulidae								
Dicranota	14 (4)	11 (5)	30 (8)	23 (5)	8 (1)	3 (0)	19 (5)	7 (4)
Hexatoma	16 (11)	7 (2)	28 (9)	47 (33)	-	-	-	3 (0)
Molophilus	3 (0)	-	-	-	-	-	-	-
Pedicia	-	-	-	-	3 (0)	-	-	-
Tipula	-	7 (0)	-	-	-	-	-	-

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VITA

Samantha Hertel was born and raised in the Northwest suburbs of Chicago, enjoying her childhood in the outdoors knee deep in the local ponds. This passion for nature continued as she attended Loyola University Chicago and earned a Bachelor of Arts degree in Environmental Studies in the spring of 2012 with a minor in Biology. She started her Masters of Science in Biology in the fall of 2012 focusing on aquatic ecology. Samantha has presented her research at the Society of Freshwater Science conference in Milwaukee in 2015. Currently, Samantha hopes to continue her passion for the outdoors in a future career in ecology.