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Aquatic Insect Community Structure and Secondary Production in Coastal Wetland Ponds of the Copper River Delta, Alaska: Influence of Water Temperature and Macrophyte Community Structure

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LOYOLA UNIVERSITY CHICAGO

AQUATIC INSECT COMMUNITY STRUCTURE AND SECONDARY PRODUCTION IN COASTAL WETLAND PONDS OF THE COPPER RIVER DELTA, ALASKA: INFLUENCE OF WATER TEMPERATURE AND MACROPHYTE COMMUNITY STRUCTURE

A THESIS SUBMITTED TO
THE FACULTY OF THE GRADUATE SCHOOL
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MASTER OF SCIENCE

PROGRAM IN BIOLOGY

BY
CHANTEL CALDWELL
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ABSTRACT

The Copper River Delta (CRD), southcentral Alaska, is one of the world's largest continuous coastal wetlands and is largely composed of sloughs, lakes, and ponds. Due to coastal topography the east side of the Copper River (East Delta) is disproportionately impacted by a cold continental air mass. Wetland communities of the CRD were also impacted by a 9.2 magnitude earthquake in 1964 that shifted the more coastal portion of the CRD from tidally influenced ponds to freshwater ponds.

The West-East temperature gradient across the CRD coupled with landscape type (uplifted marsh (UM) and outwash plain (OP)) creates four regions (West-UM, West-OP, East-UM, and East-OP). The goal of this study was to assess the impact of water temperature, landscape type, and macrophyte community structure on aquatic insect community structure and secondary production. Mean water temperatures during the study were higher in uplifted marsh ponds than in outwash plain ponds. The warmer, geologically younger UM ponds were dominated by submerged macrophytes, while the colder, later successional OP ponds were dominated by long-lived perennial emergent macrophytes.

Taxa richness was highest in West-UM ponds and lowest in East-OP ponds. West-UM ponds had the second highest aquatic insect densities of the regions, and relative abundance of Odonata, Hemiptera, Trichoptera, and Diptera each comprised 20-35% of the aquatic insect communities. Predator-engulfers, a functional feeding group (FFG) with significantly higher densities in West-UM ponds than in OP ponds, had three times higher annual secondary production in West-UM ponds than in other regions. East-OP ponds had the lowest mean diversity and highest mean density of all four regions. Hemiptera relative abundance in East-OP ponds was 49.3% followed by Diptera relative abundance of 35.5%, all other remaining orders were below 11% relative abundance. Predator-piercers, an FFG composed mainly of hemipterans and coleopterans, had densities four times higher and annual secondary production rates two times higher in East-OP ponds than in other regions. Results from this study revealed significant differences in aquatic insect community structure and secondary production between the four regions of the CRD. These results have strong implications for the potential impacts of climate change in both early successional and late successional northern latitude coastal wetlands.

INTRODUCTION

Coastal wetlands are biologically diverse ecosystems (Mortsch 1998) that provide a range of critical ecosystem functions (e.g., water filtration and nitrogen cycling). More than 50% of historical wetlands in the contiguous United States have been destroyed due to direct and indirect human modification, which has led to increased efforts to conserve remaining wetlands (Whiles and Goldowitz 2005). One threat that has received increased attention is global climate change. An important component of climate change is an alteration in temperature regimes. Specifically, northern latitudes are projected to have more pronounced increases in atmospheric temperatures (Hall 1988). Warming air temperatures are predicted to dramatically increase surface water temperatures, lengthen growing seasons, and shorten the duration of seasonal ice cover (Heino et al. 2009, Woodward et al. 2010). These projected changes will alter the structure and function of wetlands with potentially profound effects on macrophyte community composition and associated aquatic insect assemblages because of their strong link to plant phenology and succession.

Aquatic insect diversity is generally higher in macrophyte beds than in open water or in minimally vegetated areas (Thorp et al. 1997, de Szalay and Resh 2000) because macrophytes provide increased habitat complexity (Rosine 1955, Brown and Lodge 1993), potential protection from predators, and food resources, mainly periphyton on plant surfaces (Rosine 1955, Thorp et al. 1997). Wetlands further north from the equator experience longer periods of ice cover (Hall 1988) and shorter growing seasons, thereby decreasing the period of time when abundant food resources and habitat are available for aquatic insects.

The Copper River Delta (CRD), located in southcentral Alaska, is one of the world's largest continuous coastal wetlands encompassing 283,300 hectares (Thilenius 1995). The CRD extends approximately 121 km along the Gulf of Alaska (Christensen et al. 2000) and is largely composed of sloughs, lakes and ponds (Boggs 2000) that have a variety of hydrologic sources. The influence of hydrologic sources, such as groundwater, precipitation, and glacial meltwater, differs in ponds depending on location on the delta.

The CRD provides habitat for a large variety of mammals, birds, and fish and is managed as "critical habitat" for fish and wildlife by the USDA Forest Service (Chugach National Forest) (Thilenius 1995, Boggs 2000). Over 200 species of resident and migratory birds use the marshes and mudflats of the CRD (Christensen et al. 2000). The delta provides important habitat and food resources for nesting and migrating waterfowl with many of these species relying on insects as a main food resource. Climate models predict increasing air temperatures in southcentral Alaska (Hall 1988, University of Alaska 2015) that will strongly influence the shallow pond habitats of CRD aquatic insects. Changes in aquatic insect species distributions due to increased temperatures will affect community structure, food web dynamics, and ecosystem characteristics at the local level (Schindler 1997, Heino et al. 2009). This could cause temporal disconnections in CRD food webs, such as migratory birds feeding on newly emerged aquatic insects (Loomis 2013).

A substantial temperature gradient occurs across the CRD due to a prevailing gap wind during autumn, winter, and spring. Pressure and gravity-induced winds advect cold continental air down the Copper River Canyon (Boggs 2000). When these gap flows are occurring, air temperatures on the eastern portion of the CRD, i.e., in the vicinity of the river mouth ("East Delta"), are considerably cooler than air temperatures on the western portions of the CRD ("West Delta"). Local temperature impacts are substantial enough to lower monthly average temperatures during autumn, winter, and spring on the East Delta, resulting in increased duration of ice cover, more sparse vegetation growth, and a shorter growing season.

In 1964, the CRD experienced a 9.2 magnitude earthquake that raised two-thirds of the delta as much as 3.4 meters (Boggs 2000, Christensen et al. 2000) resulting in two landscape types. The more coastal uplifted portion of the Delta, uplifted marsh (UM), is composed of ponds relatively uniform in size with similar aquatic macrophyte communities (Boggs 2000, Van Duzor 2011). The uplift resulted in a shift from tidally influenced ponds to freshwater ponds causing a change in pond communities (Boggs 2000). Due to this shift, macrophyte communities of UM ponds are relatively young and in early stages of plant succession. The remaining one-third of the delta, the outwash plain (OP), is located further inland than the UM and was minimally affected by the earthquake (Boggs 2000, Christensen et al. 2000). Outwash plain ponds tend to be more variable in size than UM ponds, which could be caused by geomorphology, beaver activity, and/or late stages of plant succession (Boggs 2000). Outwash plain ponds are heavily influenced by groundwater and glacial meltwater (Boggs 2000), which is high in iron resulting in the accumulation of iron flocculent on benthic substrates. Van Duzor (2011) studied ponds on the West Delta and found that West UM and OP ponds had similar water chemistry, but had substantially different aquatic insect community structure and secondary production.

Aquatic insect community composition in West CRD ponds is composed of mayflies (Ephemeroptera), dragonflies (Odonata), true bugs (Hemiptera), beetles (Coleoptera), caddisflies

(Trichoptera), and true flies (Diptera) (Van Duzor 2011; Tiegs et al. 2013). Only one fish species, the threespine stickleback (*Gasterosteus aculeatus*), has been recorded from CRD ponds. East Delta aquatic insect and macrophyte communities have not been well studied. Differences in macrophyte community structure have been documented between landscape types, i.e., OP ponds compared to UM ponds (Tiegs et al. 2013), but the west to east temperature gradient could also result in differences in macrophyte communities across the delta. Copper River Delta ponds are relatively shallow (0.7 – 1.1 m) (Thilenius 1995), which could make them highly susceptible to atmospheric temperature changes (Meerhoff et al. 2007). The CRD temperature gradient coupled with landscape type results in four recognizable regions of the CRD: West-UM, West-OP, East-UM, and East-OP. The four regions could be differentially impacted by projected climate changes, thus, empirical research comparing aquatic insect and macrophyte communities among regions may help land managers anticipate future changes on the CRD.

Study Question

The goal of this study is to assess aquatic insect community structure and secondary production across the four regions (West-UM, West-OP, East-UM, and East-OP) of the CRD to provide insights on the influence of water temperature, landscape type, and macrophyte community structure.

Hypotheses:

Influence of water temperature on aquatic insect communities:

Aquatic insect density and diversity will be lower in East CRD ponds due to lower water temperatures and a shorter growing season.

Influence of temperature on secondary production:

Due to higher temperatures, secondary production will be greater on the West CRD. Body sizes will be larger in West CRD ponds due to a longer growing season and associated food resources.

Influence of macrophyte beds on aquatic insect communities:

Aquatic insect density and diversity will be greater in West CRD ponds because macrophyte beds are more complex. The West CRD experiences warmer temperatures, resulting in well-developed macrophyte beds earlier in the season.

MATERIALS AND METHODS

Study Site

This study was conducted on the Copper River Delta (CRD), a coastal wetland complex in southcentral Alaska (Figure 1). The region is a temperate rainforest characterized by high precipitation and moderate temperatures throughout the year. The CRD is situated with the Gulf of Alaska to the south, Prince William Sound to the west, and the Chugach Mountains to the north. A strong temperature gradient occurs in an East-West direction across the CRD with temperatures east of the Copper River (East Delta) considerably cooler than those on the West Delta (Figure 2). This gradient is due to the presence of a cold continental air mass over the upper river basin that only affects the eastern half of the delta.

The CRD ecosystem is characterized by spruce and hemlock forests, bogs, and fens located closer to the mountains, whereas alder and willow stands, numerous ponds, and tidal sloughs occur closer to the Gulf. The transition in habitat is the result of a 9.2 magnitude earthquake in 1964 that raised 2/3 of the delta as much as 3.4 meters (Boggs 2000, Christensen et al. 2000). The more coastal uplifted portion of the Delta, uplifted marsh (UM), is composed of ponds relatively uniform in size with similar aquatic macrophyte communities (Boggs 2000, Van Duzor 2011). The remaining 1/3 of the delta, the outwash plain (OP), is located further inland than the UM and was minimally affected by the earthquake. Outwash plain ponds tend to have a high abundance of iron flocculent and lower aquatic macrophyte diversity compared to UM ponds. Uplifted marsh and OP landscapes are characterized by freshwater wetlands containing ponds that range in depth from 0.7-1.1 m (Thilenius 1995), creating habitat for macrophytes and aquatic invertebrates.

Sixteen ponds were studied across the West to East temperature gradient (Table 1). Four UM and four OP ponds on each side of the delta (West and East) were selected based on accessibility and their location along the West to East gradient. Thus, ponds were classified in one of four regions: West Delta uplifted marsh (West-UM), West Delta outwash plain (West-OP), East Delta uplifted marsh (East-UM), and East Delta outwash plain (East-OP). Ponds were sampled bimonthly during the macrophyte growing season (early May through late September, 2011), yielding a total of 9 sampling periods.

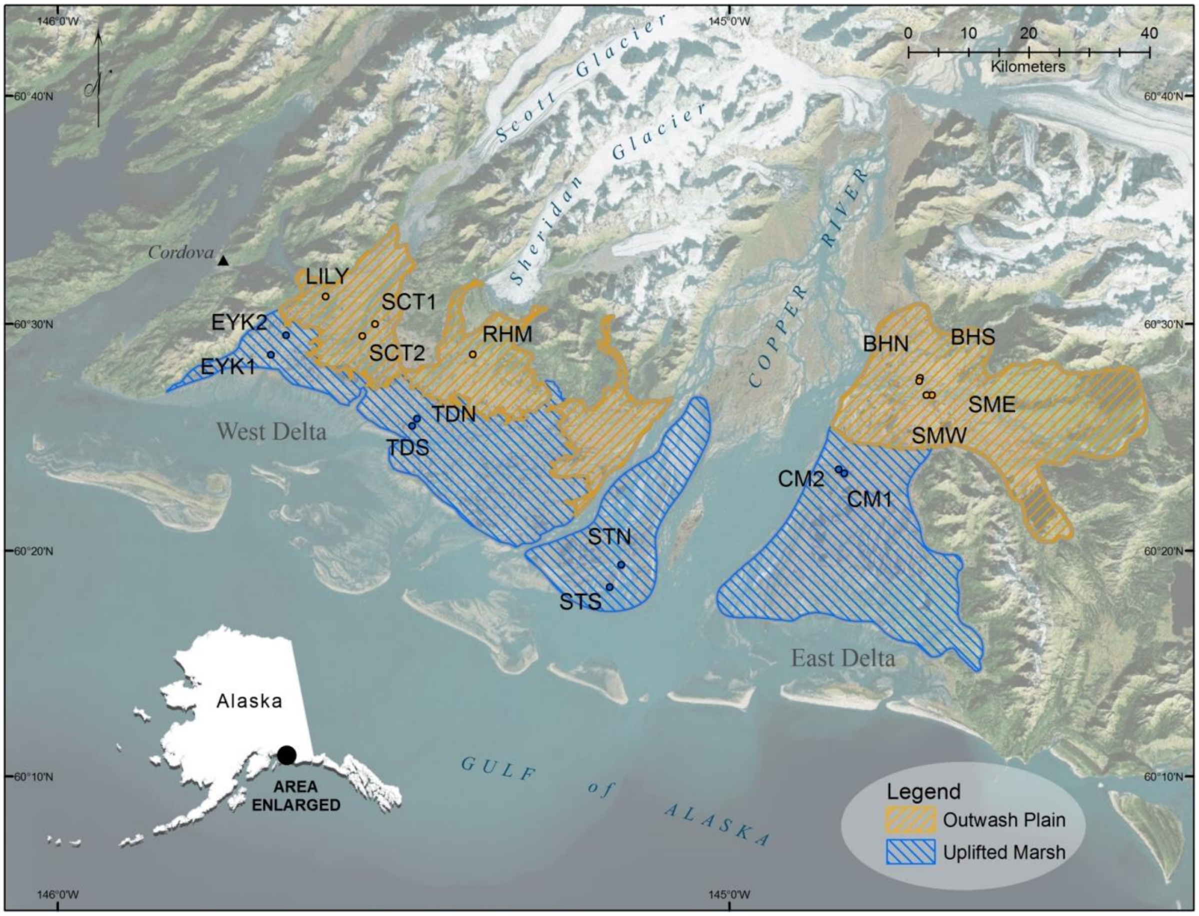


Figure 1. Study pond locations on the Copper River Delta, Alaska. Borders indicate landscape type, outwash plain and uplifted marsh, on the West and East Delta. Created by: Kelly Christansen, U.S.F.S. Pacific Northwest Research Station. See Table1 for pond abbreviations.

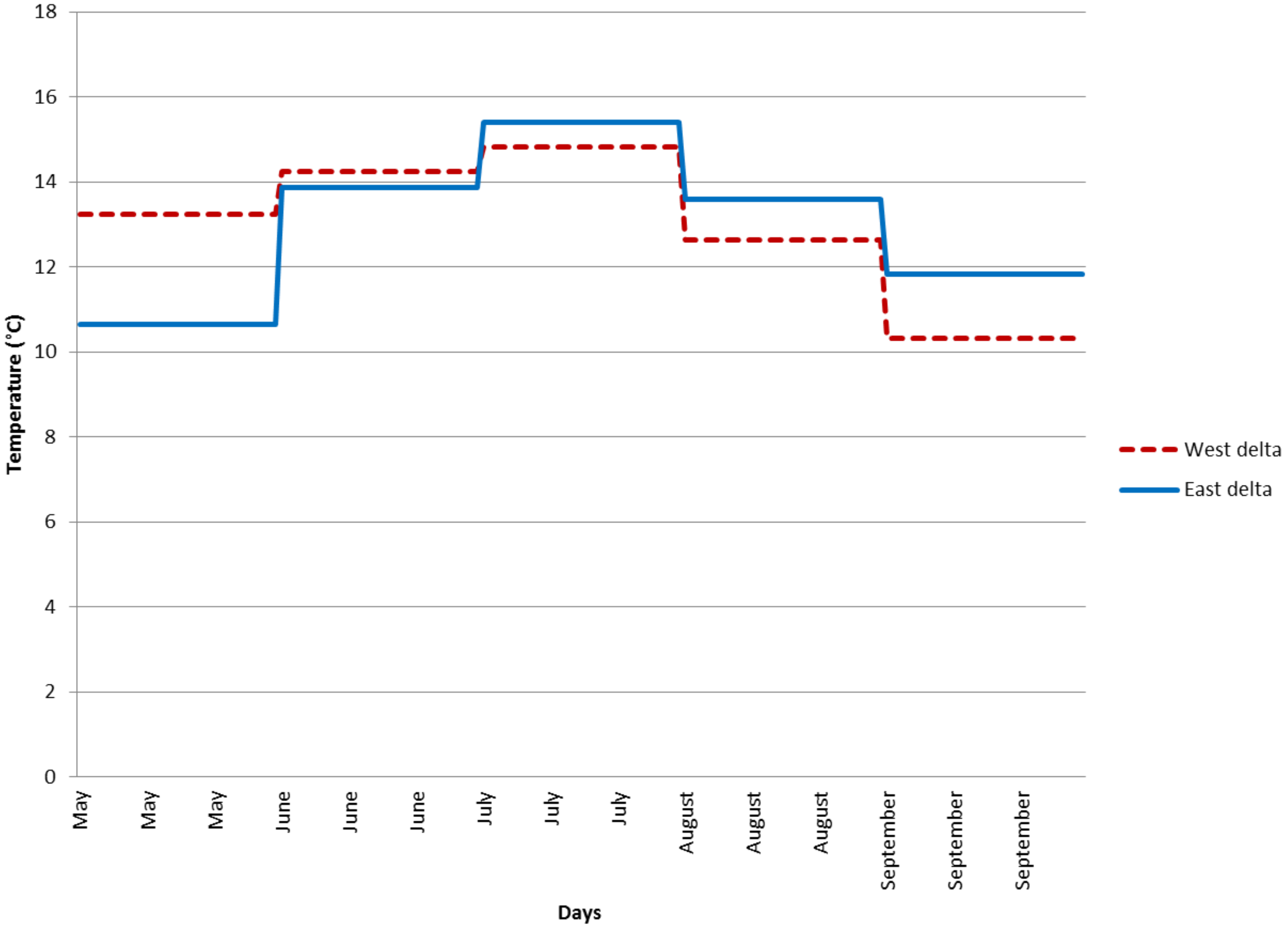
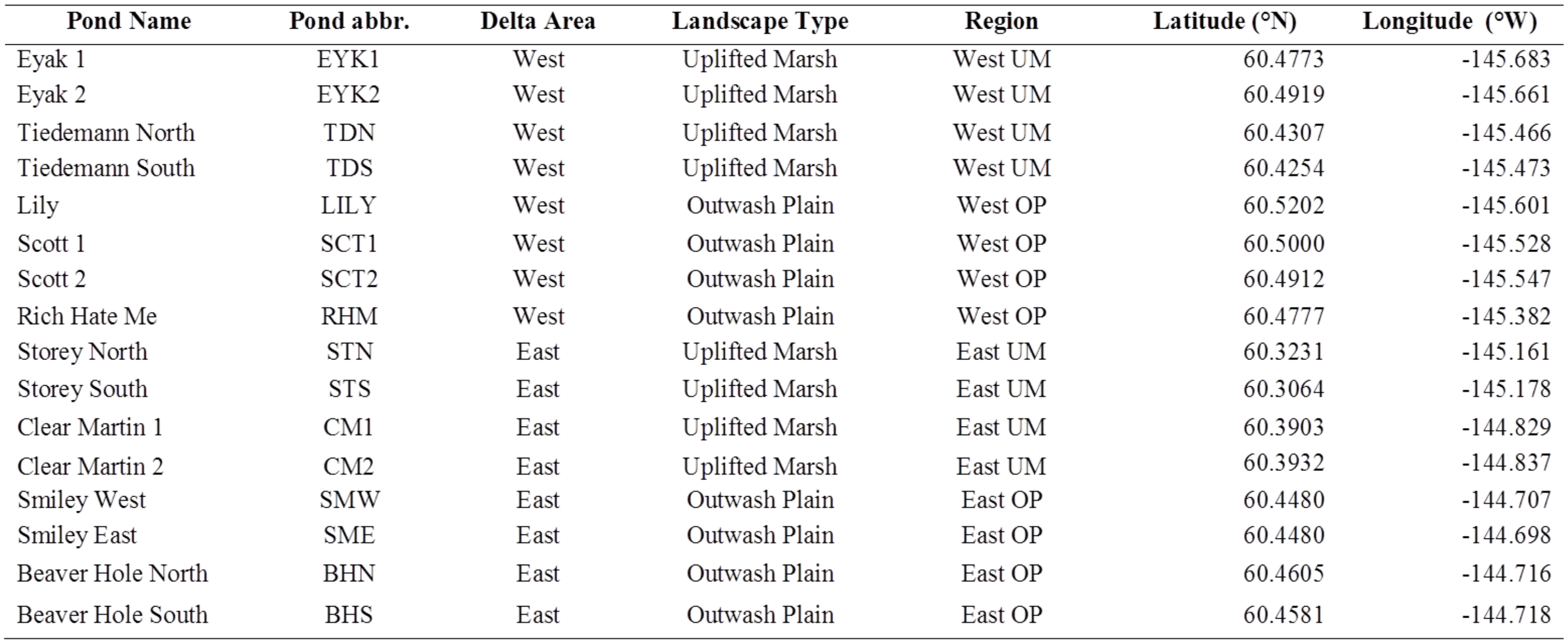


Figure 2. 30-day mean water temperatures (°C) on the West and East Copper River Delta, Alaska, May-September 2011.

Table 1. Study ponds sampled in 2011 on the Copper River Delta, AK.



Pond Name	Pond abbr.	Delta Area	Landscape Type	Region	Latitude (°N)	Longitude (°W)
Eyak 1	EYK1	West	Uplifted Marsh	West UM	60.4773	-145.683
Eyak 2	EYK2	West	Uplifted Marsh	West UM	60.4919	-145.661
Tiedemann North	TDN	West	Uplifted Marsh	West UM	60.4307	-145.466
Tiedemann South	TDS	West	Uplifted Marsh	West UM	60.4254	-145.473
Lily	LILY	West	Outwash Plain	West OP	60.5202	-145.601
Scott 1	SCT1	West	Outwash Plain	West OP	60.5000	-145.528
Scott 2	SCT2	West	Outwash Plain	West OP	60.4912	-145.547
Rich Hate Me	RHM	West	Outwash Plain	West OP	60.4777	-145.382
Storey North	STN	East	Uplifted Marsh	East UM	60.3231	-145.161
Storey South	STS	East	Uplifted Marsh	East UM	60.3064	-145.178
Clear Martin 1	CM1	East	Uplifted Marsh	East UM	60.3903	-144.829
Clear Martin 2	CM2	East	Uplifted Marsh	East UM	60.3932	-144.837
Smiley West	SMW	East	Outwash Plain	East OP	60.4480	-144.707
Smiley East	SME	East	Outwash Plain	East OP	60.4480	-144.698
Beaver Hole North	BHN	East	Outwash Plain	East OP	60.4605	-144.716
Beaver Hole South	BHS	East	Outwash Plain	East OP	60.4581	-144.718

Physicochemical Parameters

HOBO® temperature loggers were deployed in all ponds in early May 2011, and programmed to record at two hour intervals. Temperature loggers could not be retrieved for downloading during winter due to inclement winter conditions and ice cover. In addition, no loggers were recovered the following spring (2012) and were likely lost due to ice-out. Thus, temperature data were not available after mid-September 2011. Temperature data for one of the East Delta ponds, SMW, were not collected due to the logger being lost in early June. Water temperatures in each pond were calculated as 30-day averages (HOBOware Pro software) because of high daily temperature fluctuations. Thus, 4-5 30-day temperature values per pond are reported.

A YSI 556 MPS multiparameter meter was used to measure a suite of physicochemical parameters in each pond including: water temperature, specific conductance, total dissolved solids (TDS), dissolved oxygen (DO), pH, salinity and oxygen reduction potential (ORP). Physicochemical parameters were measured on all 9 sampling dates near the center of each pond or at maximum wading depth. Physicochemical measurements were recorded from three depths: just above benthic substrates, mid-water column, and water surface.

Three 60 mL water samples for nutrient analyses were collected monthly from each pond with a 60 mL Luer-Lok tip syringe (BD, Franklin Lakes, NJ) and filtered through a 25mm diameter Pall Type A/E Glass Fiber Filter (1µm pore size). Filtered samples were stored and frozen in 60 mL clear polyethylene bottles (Nalgene®) until analysis. Water samples were analyzed for soluble reactive phosphorus, nitrate, and ammonium using an AA3 Segmented Flow Multi-Chemistry Analyzer (SEAL Analytical).

Aquatic Invertebrate Sampling

Aquatic invertebrates were sampled quantitatively from each pond using a 250 µm D-net with a detachable bucket (Wildlife Supply Company). A $1m^2$ PVC frame was randomly placed in each macrophyte bed and the D-net was swept for 30 seconds inside the frame from the top layers of the benthic substrate to the water surface. Net contents were transferred to a 250 µm sieve, drained of excess water, stored in a 15cm x 21cm, 6 mil poly plastic bag, transported to the laboratory and preserved in 70% ethanol before processing and sorting. Four replicate samples were collected from monotypic beds of dominant macrophyte species in each pond. Dominant macrophytes were defined as a species comprising at least 5% of the pond surface area. The number of macrophyte beds sampled ranged from 1 to 5 beds per pond. The types of dominant monotypic macrophyte beds were noted throughout the season (Table 2).

Table 2. Presence (X) of dominant monotypic macrophyte beds in study ponds across the Copper River Delta, AK, May-September. 2011. Pond abbreviations as in Table 1.

Delta Area	**Pond**	**Buckbean** (*Menyanthes*)	**Marsh Fivefinger** (*Potentilla*)	**Marestail** (*Hippuris*)	**Pendant Grass** (*Arctophila*)	**Tufted Loosestrife** (*Lysimachia*)	**Horsetail** (*Equisetum*)	**Sedges** (*Carex*)	***Floating Pondweed*** (*Potamogeton natans*)
West	**EYK1**	X	X	X					
	EYK2	X	X	X					
	TDN	X	X	X		X			
	TDS	X	X	X					
	LILY	X		X			X		
	SCT1	X							
	SCT2			X			X		X
	RHM						X	X	
East	**STN**	X					X		
	STS	X			X		X		
	CM1			X			X		X
	CM2	X					X		
	SMW						X		
	SME						X		
	BHN						X		
	BHS						X		

Aquatic Invertebrate Processing

Initial laboratory processing of aquatic invertebrate samples occurred on the day of collection and involved washing samples in a 250μm sieve to dislodge aquatic invertebrates from large pieces of macrophytes. Samples were preserved in 70% ethanol and bags were sealed for later sorting. The majority of invertebrates collected were aquatic insects, and thus are the focus of this study. Each sample was sorted under a dissecting microscope (Leica 6.3-50X stereomicroscope) and all aquatic insects were removed and placed in 60 ml screw top scintillation vials (Wheaton Science No.:W216903) with 70% ethanol as a preservative. Large samples were split using a Folsom Plankton Splitter (Wildlife Supply Company) prior to sorting. Aquatic insects larger than 20mm were removed prior to splitting. All split samples were recorded and densities were multiplied by the appropriate number of splits performed. Aquatic insects, excluding chironomids (Diptera: Chironomidae), were identified to the lowest possible taxonomic level, usually genus, using keys from Merritt et al. (2008), Wiggins (1996; Trichoptera), and Larson et al. (2000; Dytiscidae) and counted. Chironomids were analyzed as part of a tandem study. All non-insect taxa were identified to the family-level and recorded as present/absent.

Aquatic Insect Secondary Production

Secondary production rates of aquatic insects were calculated using the size-frequency method adjusted for cohort production interval (CPI) (Hynes & Coleman 1968, Hamilton 1969, Benke 1979, Benke and Huryn 2006). Numerically dominant insect taxa were selected for secondary production analysis based on a minimum of four size classes represented in samples and densities > $0.1/m^2$. Of the 35 insect taxa collected during this study, secondary production estimates could be calculated for 14 taxa, 3 of which (Odonata) were reported by Furlan (2014).

Total body lengths of individuals were measured to the nearest 0.1 mm with an ocular micrometer. Measured individuals were then dried for 24 hours at 60°C, cooled in a desiccator, and weighed to determine dry mass. Insects were then ashed in a muffle furnace at 500°C and weighed to determine ash mass. Ash mass was then subtracted from dry mass to determine ash-free dry mass (AFDM) (Fisher and Gray 1983, Benke and Huryn 2006).

Length/mass regressions were constructed for 11 non-odonate taxa using either exponential or power models. Models with the highest R^2 values were used to determine biomass (Table 3). Exponential regressions provided the highest R^2 values for *Caenis* spp. (Ephemeroptera: Caenidae), *Callicorixa vulnerata* (Hemiptera: Corixidae), *Agabus* spp. (Coleoptera: Dytiscidae), *Agrypnia* spp. (Trichoptera: Phryganeidae), *Polycentropus* spp. (Trichoptera: Polycentropodidae), *Chaoborus* spp. (Diptera: Chaoboridae), and *Dixella* spp. (Diptera: Dixidae). Power regressions provided better fits for *Siphlonurus* spp. (Ephemeroptera: Siphlonuridae), *Oxyethira* spp. (Trichoptera: Hydroptilidae), *Nemotaulius hostilis* (Trichoptera: Limnephilidae), and *Bezzia*/*Palpomyia* spp. (Diptera: Ceratopogonidae). All cohort production intervals for non-odonate taxa were determined by examining the distribution of size classes throughout the study period.

Table 3. Regression equations for calculating ash-free dry mass (AFDM), and corresponding R^2 value for numerically dominant taxa in the Copper River Delta, AK. For regression equations: minimum number of 4 size classes, x = total body length (mm) and AFDM = ash-free dry mass (mg). Regression equations for *C. vulnerata*, *Agrypnia*, and *Nemotaulius hostilis* taken from Van Duzor (2011).

	Regression Equation	**R^2**
Caenis sp.	$AFDM = 0.012e^{0.525 x}$	0.99
Siphlonurus sp.	$AFDM = 0.0013x^{2.7233}$	0.99
Callicorixa vulnerata	$AFDM = 2E\text{-}05e^{0.6842 x}$	0.98
Agabus spp.	$AFDM = 0.0176e^{0.3257 x}$	0.99
Oxyethira sp.	$AFDM = 0.0055x^{1.8978}$	0.99
Nemotaulius hostilis	$AFDM = 1E\text{-}06x^{2.5531}$	0.99
Agrypnia spp.	$AFDM = 6E\text{-}05e^{0.2176 x}$	0.99
Polycentropus spp.	$AFDM = 0.0046e^{0.3573 x}$	0.94
Bezzia/Palpomyia	$AFDM = 0.0004x^{2.5891}$	0.99
Chaoborus spp.	$AFDM = 0.0014e^{0.4551 x}$	0.97
Dixella spp.	$AFDM = 0.0091e^{0.3995 x}$	0.98

Data Analysis

Aquatic insect community analyses and Shannon-Weiner diversity were conducted using Primer 6 (Primer-E Ltd.). One-way and two-way analysis of variance (ANOVA) were run in R (© The R Foundation) on log transformed data to examine community diversity, densities, and secondary production rates among ponds. Significant ANOVA's were followed by a Tukey post hoc test in R (© The R Foundation) to examine differences among regions. Principal components analysis (PCA) was used to compare aquatic insect taxonomic and functional feeding group (FFG) community composition among ponds. Taxa were assigned to one of the following FFGs: collector-gatherers, piercers, predator-engulfers, predator-piercers, predator-other (mainly Diptera), and shredders based on Merritt et al. (2008). Primer BEST analysis was used to rank environmental variables, singly or in combination, that best match community structure. Mean values of these parameters were calculated for all CRD regions. Non-metric multidimensional scaling (nMDS) was used to ordinate regions (West-UM, West-OP, East-UM, East-OP) with respect to square-root transformed biotic data using Bray-Curtis similarities, and then compared to all possible abiotic matrices. However, no patterns were detected with the use of nMDS.

RESULTS

Pond Physicochemical Parameters

Water temperatures (30-d averages) across all ponds ranged from 6.5°C in May to 18.6°C in July (Table 4) with temperatures increasing from May to July and then decreasing into September. Temperatures in individual ponds differed depending on depth, water source and canopy cover, however uplifted marsh (UM) ponds were generally warmer than outwash plain (OP) ponds. Temperature trends were more revealing when compared between the 4 regions, a combination of delta area and landscape type (West-UM, West-OP, East-UM, and East-OP). West uplifted marsh (West-UM) ponds had the highest 30-day average temperatures throughout the sampling period (May: 15.1°C; July: 17.1°C; September: 11.6°C) with the second highest 30-d averages found in East-UM ponds (May: 12.1°C; July: 16.7°C; September: 11.8°C) (Figure 3). East outwash plain (East-OP) ponds were warmer than West-OP ponds in July and August (September data for East-OP ponds not available).

Mean water temperatures and dissolved oxygen of the four regions were not significantly different, however mean (± SE) water temperatures during the study were higher in uplifted marsh ponds (West-UM: 15.1 ± 0.3, East-UM: 14.5 ± 0.8) compared to outwash plain ponds (West-OP: 12.8 ± 0.8; East-OP: 13.4 ± 0.2) (Table 5). Dissolved oxygen concentrations were higher in West-UM ponds compared to West-OP ponds (9.0 ±0.4 mg/L and 6.6 ± 0.9 mg/L, respectively). Total dissolved solids (TDS) were significantly lower in West-UM ponds (0.01

±0.001 g/L) than in West-OP (0.05 ± 0.01 g/L) and East-UM (0.05 ± 0.01 g/L) ponds (one-way ANOVA, $F_{3,12} = 10.3$, $p<0.01$, Tukey post hoc, $p < 0.01$)). Specific conductivity was also significantly lower in West-UM ponds (0.01 ± 0.002 µS/cm) than in West-OP (0.04 ± 0.007 µS/cm) and East-UM (0.03 ± 0.003) ponds (one-way ANOVA, $F_{3,12} = 11.3$, $p < 0.01$, Tukey post hoc, $p<0.01$).

Table 4. 30-day mean water temperatures (°C) in Copper River Delta, Alaska study ponds, May-September 2011. Pond abbreviations as in Table 1.

Delta Area	West								East							
Landscape Type	UM				OP				UM				OP			
Pond	EYK1	EYK2	TDN	TDS	LILY	SCT1	SCT2	RHM	STN	STS	CM1	CM2	SME	SMW[a]	BHN	BHS
May	15.19	15.11	15.34	14.78	14.49	6.66	14.30	10.07	14.73	14.51	12.73	6.45	12.96		6.46	6.70
June	16.44	15.88	16.83	16.54	14.40	9.04	14.67	10.19	17.64	17.60	16.23	9.06	14.99		10.41	11.17
July	16.97	16.10	17.71	17.46	14.95	10.09	14.03	11.36	18.44	18.64	18.12	11.45	15.21		12.61	13.39
Aug.	14.52	13.72	14.67	14.49	13.19	10.19	9.55	10.85	15.05	15.09	15.06	11.75	13.19		12.26	12.68
Sept.	11.96	11.45	11.57	11.61		9.09	7.31	9.36	11.92	11.75						

a - Data from SMW missing due to temperature logger not being recovered

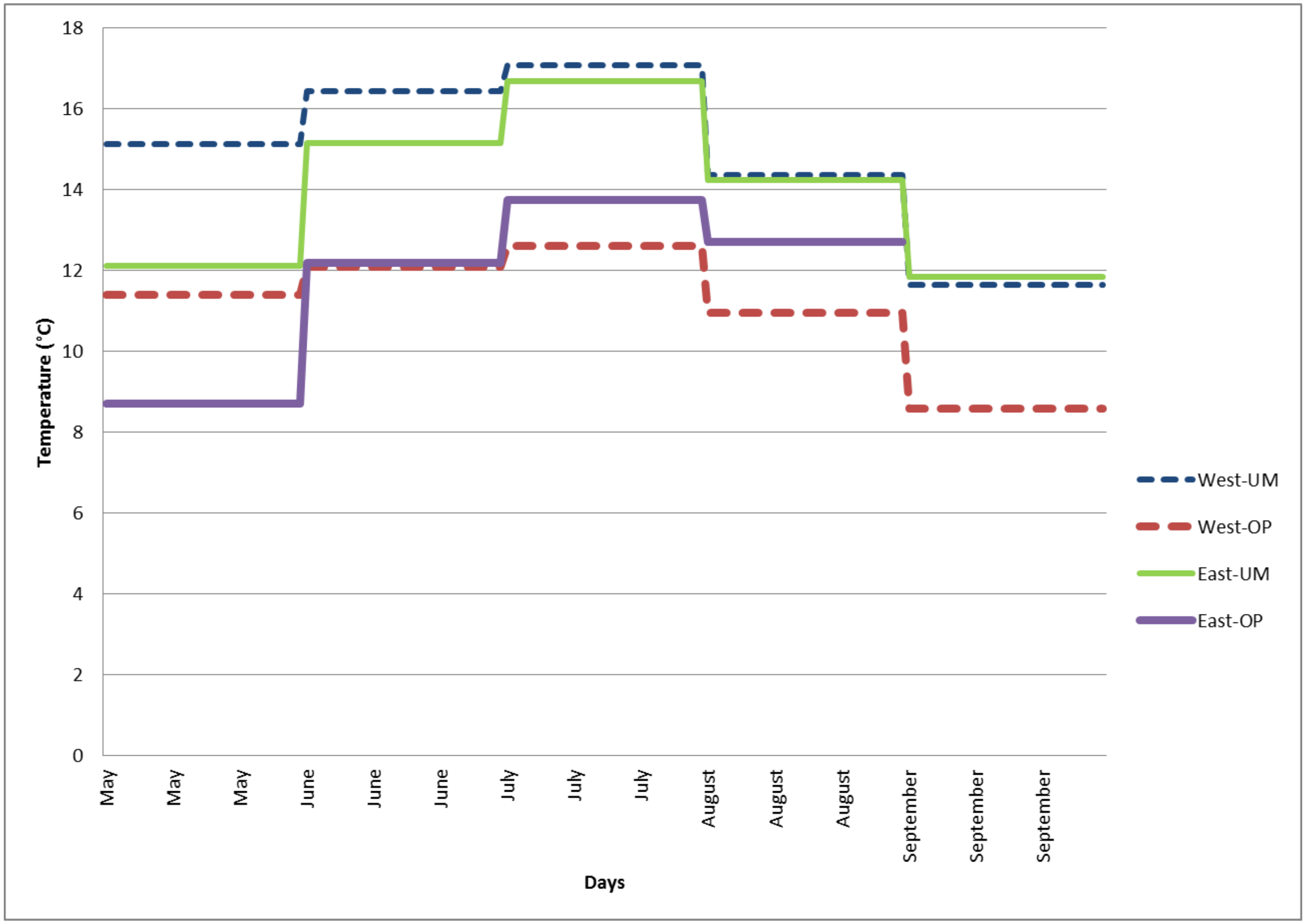
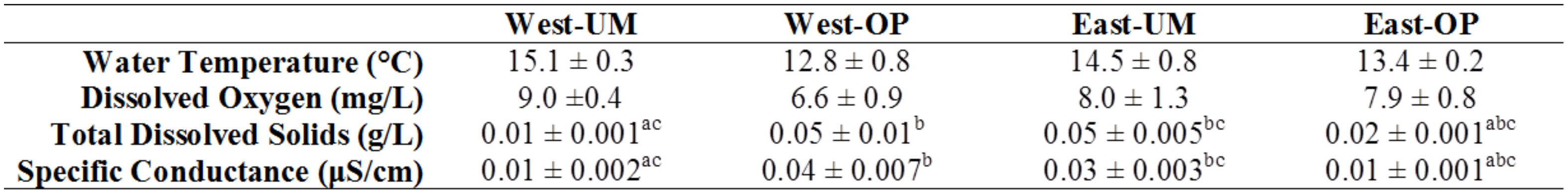


Figure 3. 30-day mean water temperatures (°C) in 4 regions of the Copper River Delta, Alaska, May-September 2011. Region abbreviations as in Table 1.

Table 5. Mean (±SE) pond physicochemical parameters in regions on the Copper River Delta, Alaska, May-September 2011. Region abbreviations as in Table 1.



	West-UM	**West-OP**	**East-UM**	**East-OP**
Water Temperature (°C)	15.1 ± 0.3	12.8 ± 0.8	14.5 ± 0.8	13.4 ± 0.2
Dissolved Oxygen (mg/L)	9.0 ±0.4	6.6 ± 0.9	8.0 ± 1.3	7.9 ± 0.8
Total Dissolved Solids (g/L)	0.01 ± 0.001^{ac}	0.05 ± 0.01^{b}	0.05 ± 0.005^{bc}	0.02 ± 0.001^{abc}
Specific Conductance (µS/cm)	0.01 ± 0.002^{ac}	0.04 ± 0.007^{b}	0.03 ± 0.003^{bc}	0.01 ± 0.001^{abc}

[a] - Statistically significant differences (Tukey post hoc test, $p < 0.01$) across pond regions denoted with different superscripts

Aquatic Insect Community Composition

A total of 15,417 non-chironomid insects from 396 macroinvertebrate samples were collected, sorted, and identified. These taxa represented 6 orders, 23 families, and 34 genera (Table 6). Taxa richness was highest in West-UM ponds (32 taxa) and lowest in East-OP ponds (25 taxa) (Table 7).

Two-way ANOVA of total aquatic insect densities revealed a significant interaction between landscape type and delta area (Two-way ANOVA interaction $F_{1,4} = 21.1$, $p = 0.001$) (Figure 4). Aquatic insect densities (mean ±SE) in West Delta ponds were significantly higher in UM than in OP ponds (West-UM: 39.2 ± 3.2 / m^2, West-OP: 21.1 ± 3.8 / m^2) (Tukey post hoc, $p = 0.03$), whereas densities in East Delta ponds were significantly higher in OP ponds than in UM ponds (East-UM: 27.8 ± 6.2 /m^2, East-OP: 82.1 ± 13.4 / m^2) (Tukey post hoc, $p < 0.01$). Across the CRD, aquatic insect densities were significantly higher in East-OP ponds compared to West-OP ponds (Tukey post hoc, $p < 0.001$).

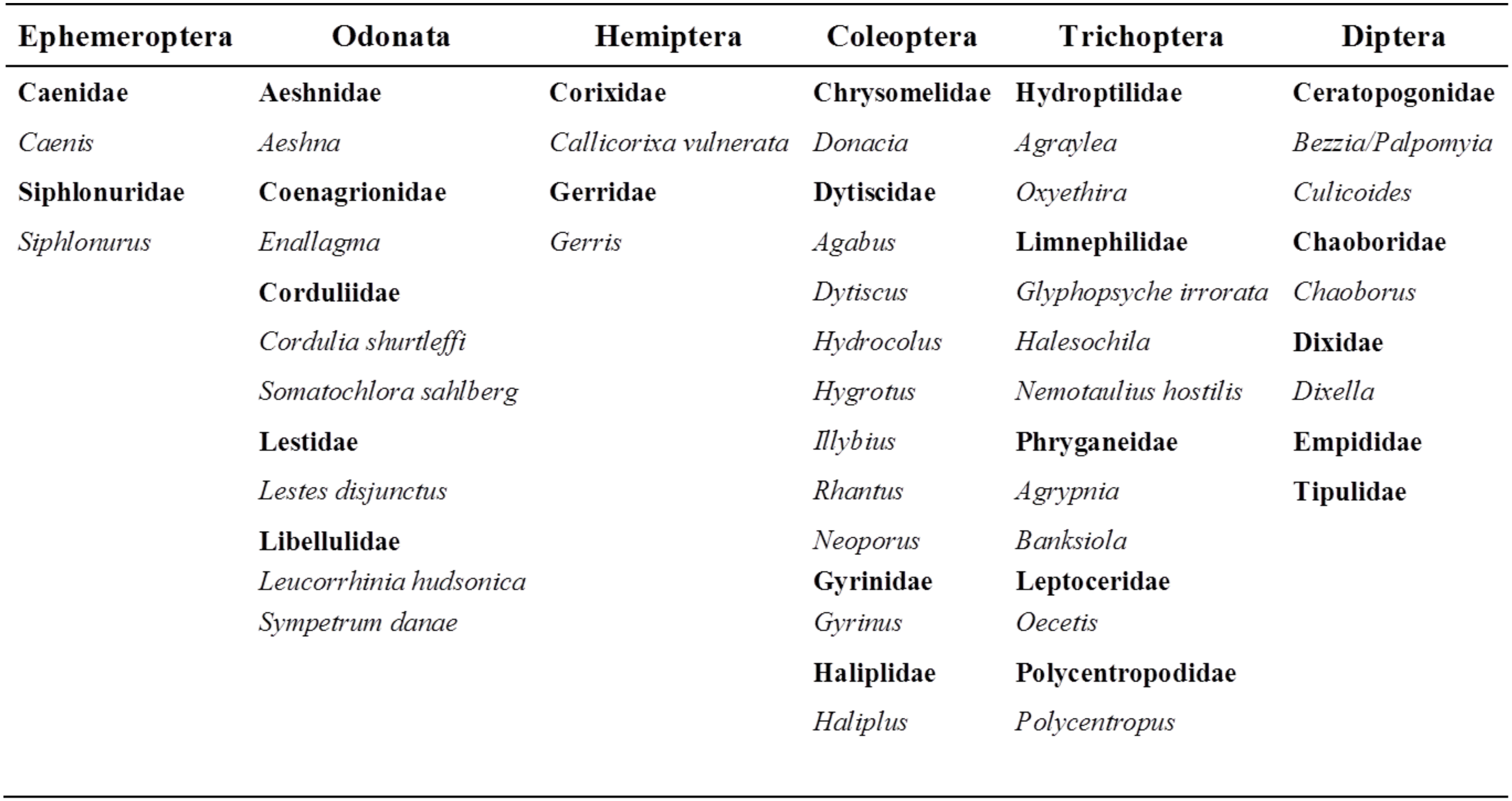
Densities (Table 8) and relative abundance (Table 7) of aquatic insect orders differed across regions of the CRD. Odonata densities and relative abundance were significantly different among the four regions (one-way ANOVA, density: $F_{3,12} = 13.9$, $p < 0.01$; relative abundance: $F_{3,12} = 9.2$, $p < 0.01$). Odonate densities were higher in West-UM ponds (7.8 ± 2.1 /m^2) compared to all other regions (West-OP: 0.9 ± 0.2 /m^2; East-UM: 1.9 ± 0.4 /m^2; East-OP: 1.5 ± 0.6 /m^2) (Tukey post hoc, $p< 0.05$), whereas odonate relative abundance was higher in West-UM ponds (19.7 ± 4.9%) than in only OP ponds (West-OP: 5.3 ± 1.7%, Tukey post hoc, $p = 0.01$; East-OP: 2.2 ± 1.1%, Tukey post hoc, $p < 0.01$). Trichoptera densities and relative abundance also were significantly different across regions (one-way ANOVA, density: $F_{3,12} = 4.0$, $p = 0.03$; relative abundance: $F_{3,12} = 4.5$, $p = 0.02$). West Delta Trichoptera densities were higher in UM ponds (14.4 ± 2.1 /m^2) than in OP ponds (2.7 ± 0.7 /m^2) (Tukey post hoc, $p = 0.02$). Relative abundance of trichopterans was higher in West-UM ponds (35.9 ± 3.7%) compared to East-OP ponds (11.4 ± 8.1%) (Tukey post hoc, $p = 0.02$). Overall, Trichoptera relative abundance was highest in UM ponds (West: 36.6 ± 3.9%; East: 27.1 ± 7.6%) and lowest in OP ponds (West: 12.1 ± 1.8%; East: 11.4 ± 8.1%).

Hemiptera densities were significantly different across regions (one-way ANOVA, $F_{3,12} = 4.1$, $p = 0.03$), where densities were higher in East-OP ponds (41.9 ± 10.5 /m^2) compared to West-OP ponds (5.2 ± 2.7 /m^2) (Tukey post hoc, $p = 0.03$). Relative abundance of Hemiptera was not significantly different among the regions, however relative abundance in East-OP ponds (49.3 ± 9.1%) was almost two-fold higher than in other regions (West-UM: 20.5 ± 4.9%, West-OP: 28.7 ± 13.0%, East-UM: 25.4 ± 7.2%). Similarly, mean Diptera density was significantly different across the regions (one-way ANOVA, $F_{3,12} = 4.1$, $p = 0.03$), whereas relative abundance of dipterans was not significantly different. Dipteran densities were higher in East-OP ponds (31.1 ± 11.2 /m^2) than in East-UM ponds (7.6 ± 0.9 /m^2) (Tukey post hoc, $p = 0.04$). Relative abundance of dipterans was higher in the OP ponds (West-OP: 47.1 ± 12.0% and East-OP: 35.5 ± 8.2%) compared to the UM ponds (West-UM: 20.9 ± 3.0% and East-UM: 30.7 ± 5.8%).

Diversity (H') across the four regions was significantly different and influenced by delta area and landscape type (Two-way ANOVA interaction: $F_{1,4}= 8.27$, $p = 0.014$) (Figure 5). Diversity (mean ±SE) was significantly lower in East-OP (1.4 ± 0.1) compared to East-UM (2.1 ± 0.1) and West-OP (1.9 ± 0.1) (Tukey post hoc, $p < 0.01$). East-OP ponds had the lowest mean diversity and highest mean density among all regions. This can be attributed to high densities of two hemipteran taxa, *Callicorixa vulnerata* and *Gerris* sp., which accounted for 49.3 ± 9.1% of all taxa collected from East-OP ponds, thus decreasing the evenness component of diversity.

Principal components analysis (PCA) was used to examine aquatic insect community structure across ponds on the basis of taxa and functional feeding groups (FFGs) (Table 9). The first principal component (PC1) for taxa analysis accounted for 41.5% of the variation and was strongly influenced by *C. vulnerata* (Figure 6), which was 1 of 10 taxa in the predator-piercers FFGs. Predator-piercers strongly influenced the FFG PCA and accounted for 45.4% of the variation in PC1 (Figure 7). East-OP ponds, excluding SMW, are tightly grouped and had the highest mean density of predator-piercers among all regions (43.0 ± 10.9 /m^2) (Table 9). Predator-piercer densities in East-OP ponds were significantly higher (one-way ANOVA, $F_{3,12} = 4.4$, $p < 0.05$) than in West-OP (6.6 ± 2.6 /m^2) and East-UM ponds (9.3 ± 4.2 /m^2) (Tukey post hoc, $p < 0.05$). West-UM ponds are clustered in the FFG PCA and differences in community structure are due to predator-engulfers and piercers (herbivores), which strongly influenced PC2 and accounted for 30.5% of the variability of PC2. Predator-engulfer mean densities in West-UM ponds (10.0 ± 2.3 /m^2) were significantly higher (one-way ANOVA, $F_{3,12} = 6.4$, $p < 0.01$) than in West-OP (1.3 ± 0.2 /m^2) and East-OP ponds (1.8 ± 0.6 /m^2) (Tukey post hoc, $p = 0.01$). Piercers densities were not significantly different among regions, however West-UM ponds had two-fold higher mean densities (10.8 ± 1.6 /m^2) than in other regions (Table 9). Overall, 75.8% of the variation in the FFG PCA can be accounted for by the first two principal components.

Table 6. Aquatic insects collected, excluding chironomids (Diptera: Chironomidae), from Copper River Delta, Alaska, ponds, May-September 2011.



Ephemeroptera	Odonata	Hemiptera	Coleoptera	Trichoptera	Diptera
Caenidae	**Aeshnidae**	**Corixidae**	**Chrysomelidae**	**Hydroptilidae**	**Ceratopogonidae**
Caenis	*Aeshna*	*Callicorixa vulnerata*	*Donacia*	*Agraylea*	*Bezzia/Palpomyia*
Siphlonuridae	**Coenagrionidae**	**Gerridae**	**Dytiscidae**	*Oxyethira*	*Culicoides*
Siphlonurus	*Enallagma*	*Gerris*	*Agabus*	**Limnephilidae**	**Chaoboridae**
	Corduliidae		*Dytiscus*	*Glyphopsyche irrorata*	*Chaoborus*
	Cordulia shurtleffi		*Hydrocolus*	*Halesochila*	**Dixidae**
	Somatochlora sahlberg		*Hygrotus*	*Nemotaulius hostilis*	*Dixella*
	Lestidae		*Illybius*	**Phryganeidae**	**Empididae**
	Lestes disjunctus		*Rhantus*	*Agrypnia*	**Tipulidae**
	Libellulidae		*Neoporus*	*Banksiola*	
	Leucorrhinia hudsonica		**Gyrinidae**	**Leptoceridae**	
	Sympetrum danae		*Gyrinus*	*Oecetis*	
			Haliplidae	**Polycentropodidae**	
			Haliplus	*Polycentropus*	

Table 7. Ordinal taxa richness (#) and percent total abundance (%) of non-chironomid aquatic insects in Copper River Delta, Alaska, ponds and regions, May-September 2011. Regions presented with total taxa richness and mean (±SE) relative abundance (%) of aquatic insects. Pond abbreviations as in Table 1.

			Ephemeroptera		Odonata		Hemiptera		Coleoptera		Trichoptera		Diptera	
Pond	**Region**	**Total #**	**#**	**%**	**#**	**%**	**#**	**%**	**#**	**%**	**#**	**%**	**#**	**%**
EYK1		20	0	0.0	5	33.5	2	6.2	2	3.4	6	28.8	5	28.1
EYK2		24	0	0.0	5	19.8	2	13.3	6	4.1	6	45.6	5	17.2
TDN		24	1	0.1	4	14.9	1	24.5	7	4.7	6	37.5	5	18.4
TDS		19	2	0.9	3	10.7	1	37.9	3	0.9	7	31.7	3	18.0
	West-UM	**32**	**2**	**0.3 ± 0.2**	**6**	**19.7 ± 4.9^{a}**	**2**	**20.5 ± 6.9**	**9**	**3.3 ± 0.8^{ab}**	**7**	**35.9 ± 3.7^{a}**	**6**	**20.4 ± 2.6**
LILY		18	2	1.3	4	10.2	1	52.2	5	8.9	4	8.0	2	19.4
SCT1		18	1	0.3	1	2.2	2	11.2	4	14.3	5	11.5	5	60.6
SCT2		20	1	0.2	2	4.1	1	49.8	5	8.5	7	11.5	4	25.9
RHM		21	2	0.3	3	4.8	2	1.5	4	5.2	6	19.5	4	68.7
	West-OP	**28**	**2**	**0.5 ± 0.3**	**4**	**5.3 ± 1.7^{b}**	**2**	**28.7 ± 13.0**	**6**	**9.2 ± 1.9^{a}**	**8**	**12.6 ± 2.4^{ab}**	**6**	**43.7 ± 12.3**
STN		20	2	1.9	4	5.6	2	39.9	3	6.5	4	20.9	5	25.3
STS		23	1	11.5	4	8.1	2	35.7	5	4.4	8	18.0	3	22.2
CM1		21	2	9.0	4	8.7	1	12.7	4	7.9	6	20.4	4	41.3
CM2		16	1	0.3	4	7.3	1	13.1	1	1.1	5	49.9	4	28.3
	East-UM	**28**	**1**	**5.7 ± 2.7**	**6**	**7.4 ± 0.7^{ab}**	**2**	**25.4 ± 7.2**	**6**	**5.0 ± 1.5^{ab}**	**8**	**27.3 ± 7.6^{ab}**	**5**	**29.3 ± 4.2**
SMW		19	0	<0.1	4	5.3	2	31.6	3	0.8	6	35.4	4	27.0
SME		15	0	<0.1	0	0.0	2	69.4	3	1.6	4	5.8	6	23.3
BHN		19	1	0.1	4	1.3	2	59.8	4	3.0	4	3.4	4	32.3
BHS		15	0	<0.1	4	2.5	2	36.5	2	0.8	3	0.9	4	59.3
	East-OP	**25**	**1**	**<0.1 ± 0.02**	**5**	**2.2 ± 1.1^{b}**	**2**	**49.3 ± 9.1**	**5**	**1.6 ± 0.5^{b}**	**6**	**11.4 ± 8.1^{b}**	**6**	**35.5 ± 8.2**
Total Taxa Richness		**36**	**2**		**7**		**2**		**10**		**9**		**6**	

[a] - Statistically significant differences (Tukey post hoc test, $p < 0.05$) across delta regions denoted with different superscripts

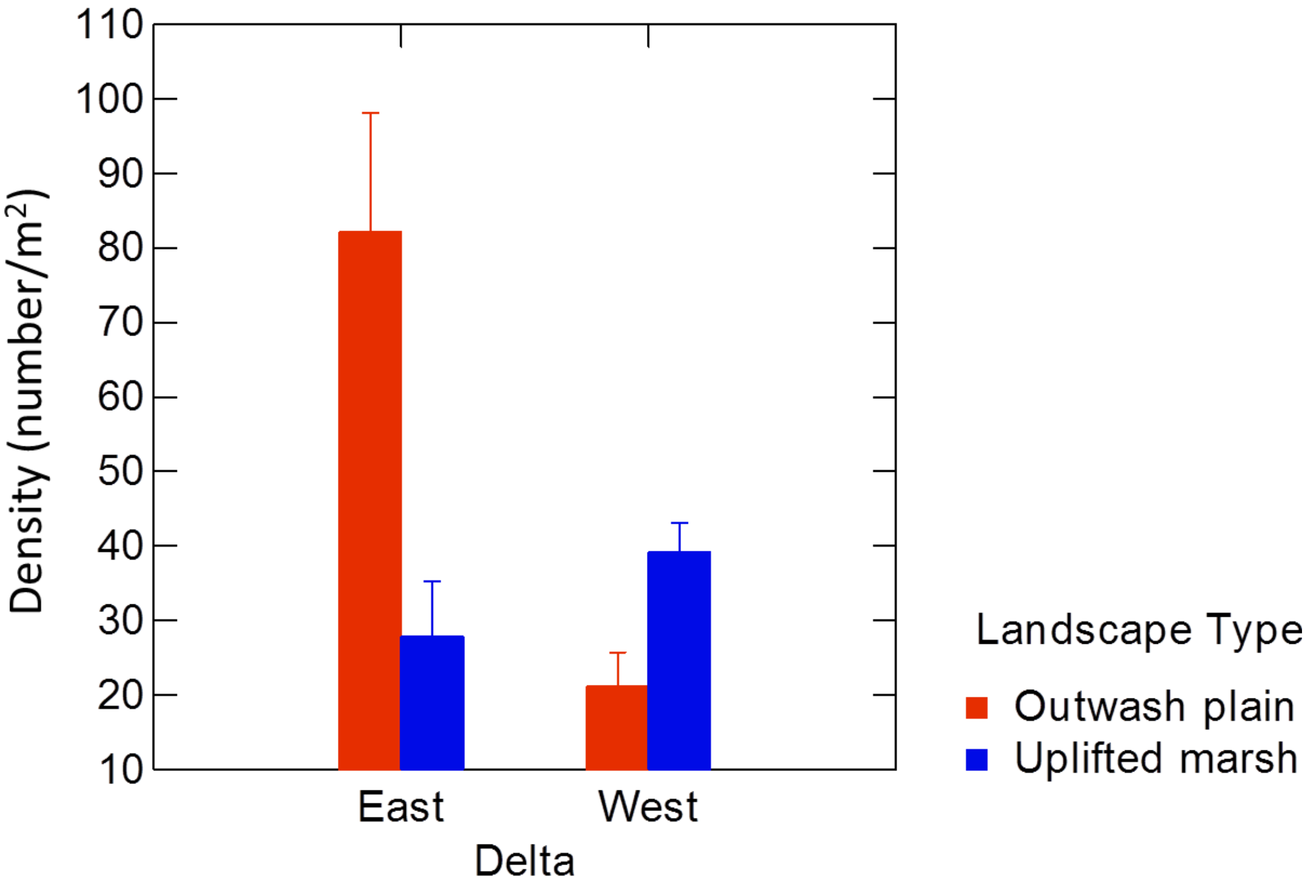


Figure 4. Density (number/m^2; mean + 1 SE) of aquatic insects in four regions of the Copper River Delta, Alaska, collected May-September 2011. There was a significant interaction between delta area and landscape type (Two-way ANOVA: $F_{1,4} = 21.1$, $p = 0.001$).

Table 8. Mean density (number/m^2) of non-chironomid aquatic insects in Copper River Delta, Alaska, ponds and regions, May-September 2011. Regions presented with mean (±SE) density of aquatic insects. Pond abbreviations as in Table 1.

Pond	Region	Ephemeroptera	Odonata	Hemiptera	Coleoptera	Trichoptera	Diptera
EYK1		0.0	13.7	2.5	1.3	12.4	12.6
EYK2		0.0	6.6	5.9	1.6	16.2	5.9
TDN		0.0	7.0	9.9	2.1	19.3	7.9
TDS		0.3	3.8	11.1	0.3	9.7	6.6
	West-UM	**0.1 ± 0.1**	**7.8 ± 2.1^{a}**	**7.4 ± 2.0^{ab}**	**1.3 ± 0.4**	**14.4 ± 2.1^{a}**	**8.2 ± 1.5^{ab}**
LILY		0.1	1.2	5.4	0.9	0.9	2.6
SCT1		0.1	0.4	2.2	2.8	2.3	12.1
SCT2		0.0	1.1	12.8	2.5	3.8	8.7
RHM		0.1	0.9	0.4	1.0	4.0	18.3
	West-OP	**0.1 ± 0.01**	**0.9 ± 0.2^{b}**	**5.2 ± 2.7^{a}**	**1.8 ± 0.5**	**2.7 ± 0.7^{b}**	**10.4 ± 3.3^{ab}**
STN		0.7	2.2	15.4	2.5	8.1	9.8
STS		4.1	2.9	14.1	1.6	7.5	8.2
CM1		1.1	1.1	1.1	1.7	2.6	6.9
CM2		0.1	1.4	2.6	0.2	9.9	5.6
	East-UM	**1.5 ± 0.9**	**1.9 ± 0.4^{b}**	**8.3 ± 3.7^{ab}**	**1.5 ± 0.5**	**7.0 ± 1.6^{ab}**	**7.6 ± 0.9^{a}**
SMW		0.0	2.3	13.7	0.3	15.4	11.8
SME		0.0	0.0	61.7	1.4	5.1	20.7
BHN		0.1	1.2	53.4	2.7	3.1	28.8
BHS		0.0	2.6	38.9	0.9	0.9	63.1
	East-OP	**$< 0.1 \pm 0.03$**	**1.5 ± 0.6^{b}**	**41.9 ± 10.5^{b}**	**1.3 ± 0.5**	**6.1 ± 3.2^{ab}**	**31.1 ± 11.2^{b}**

[a] - Statistically significant differences (Tukey post hoc test, $p < 0.04$) denoted with different superscripts

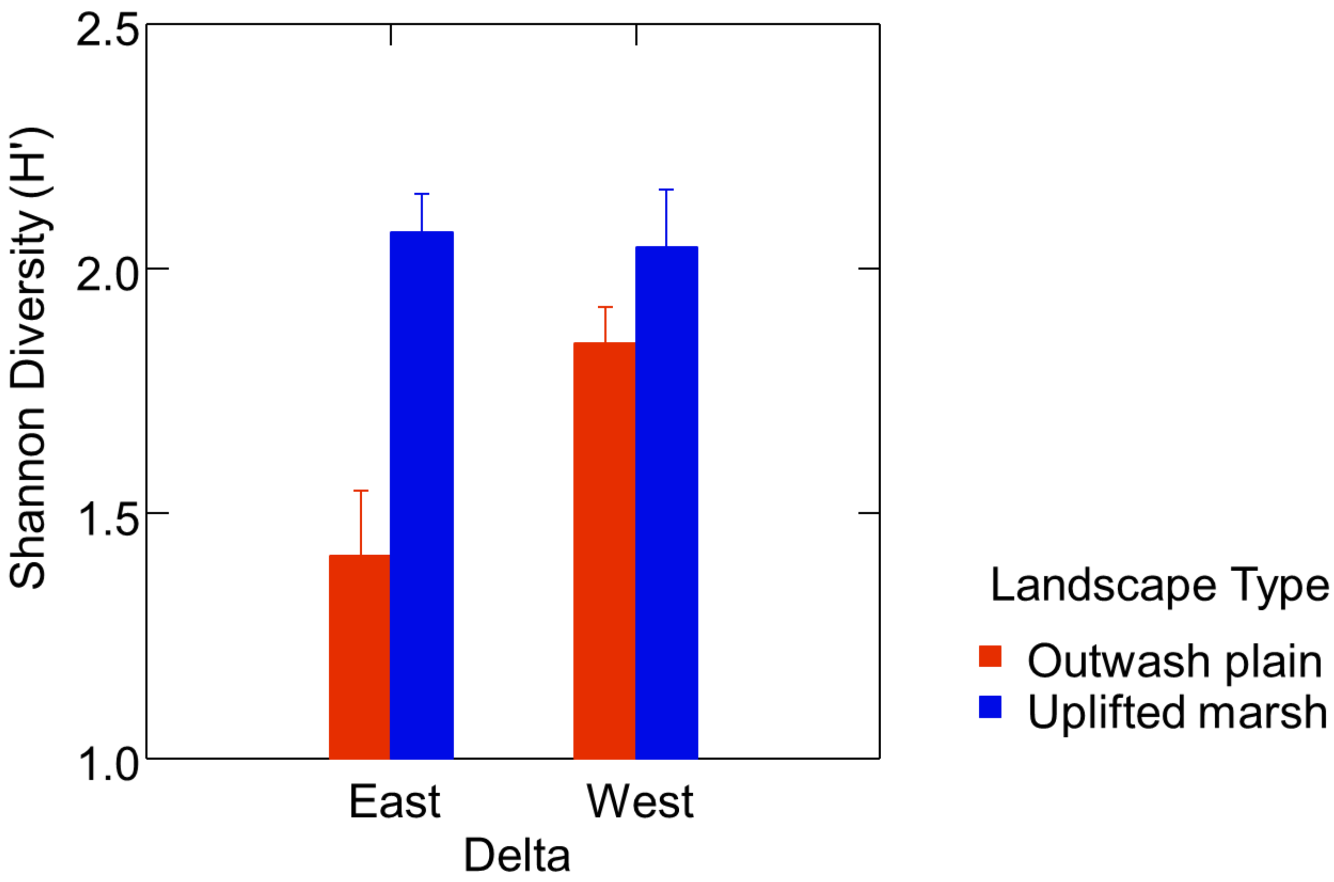


Figure 5. Shannon Diversity (H’; mean + 1 SE) of aquatic insects from ponds in four regions of the Copper River Delta, Alaska, May –September 2011. There was a significant interaction between delta area and landscape type (Two-way ANOVA: $F_{1,4} = 8.3$, p = 0.014).

Table 9. Densities (mean number/m^2 ±SE) of aquatic insect functional feeding groups (FFGs) in Copper River Delta, Alaska, regions, May-September 2011. Pond abbreviations as in Table 1.

FFGs*	**West-UM**	**West-OP**	**East-UM**	**East-OP**
Collector-gatherers	0.7 ± 0.2	2.6 ± 1.2	2.8 ± 1.3	3.2 ± 1.4
Piercers	10.8 ± 1.6	2.0 ± 0.7	4.5 ± 1.1	3.8 ± 3.4
Predator-engulfers	10.0 ± 2.3^{a}	1.3 ± 0.2^{b}	2.4 ± 0.5^{ab}	1.8 ± 0.6^{b}
Predators-other	7.5 ± 1.4	7.8 ± 3.1	6.3 ± 1.0	27.7 ± 11.6
Predator-piercers	8.6 ± 1.8^{ab}	6.6 ± 2.6^{a}	9.3 ± 4.2^{a}	43.0 ± 10.9^{b}
Shredders	1.7 ± 0.2	0.8 ± 0.4	2.4 ± 0.7	2.6 ± 0.9

* - Taxa were placed in the following FFGs: piercers (*Agraylea*, *Haliplus*, and *Oxyethira*), shredders (*Agrypnia*, *Banksiola*, *Glyphopsyche*, *Nemotaulius*, and *Tipulidae*), collector-gatherers (*Caenis*, *Dixella*, *Halesochila*, and *Siphlonurus*), predator-engulfers (*Aeshna*, *Cordulia shurtleffii*, *Enallagma*, *Gyrinus*, *Lestes disjunctus*, *Leucorrhinia hudsonica*, *Oecetis*, and *Polycentropus*), predator-piercers (*Agabus*, *Callicorixa vulnerata*, *Dytiscus*, *Empididae*, *Gerris*, *Hydrocolus*, *Hygrotus*, *Ilybius*, *Neoporus*, and *Rhantus*) and predators-other (*Bezzia/Palpomyia*, *Chaoborus*, and *Culicoides*).

[a] – Statistically significant differences (Tukey post hoc test, $p < 0.05$) denoted with superscript letters

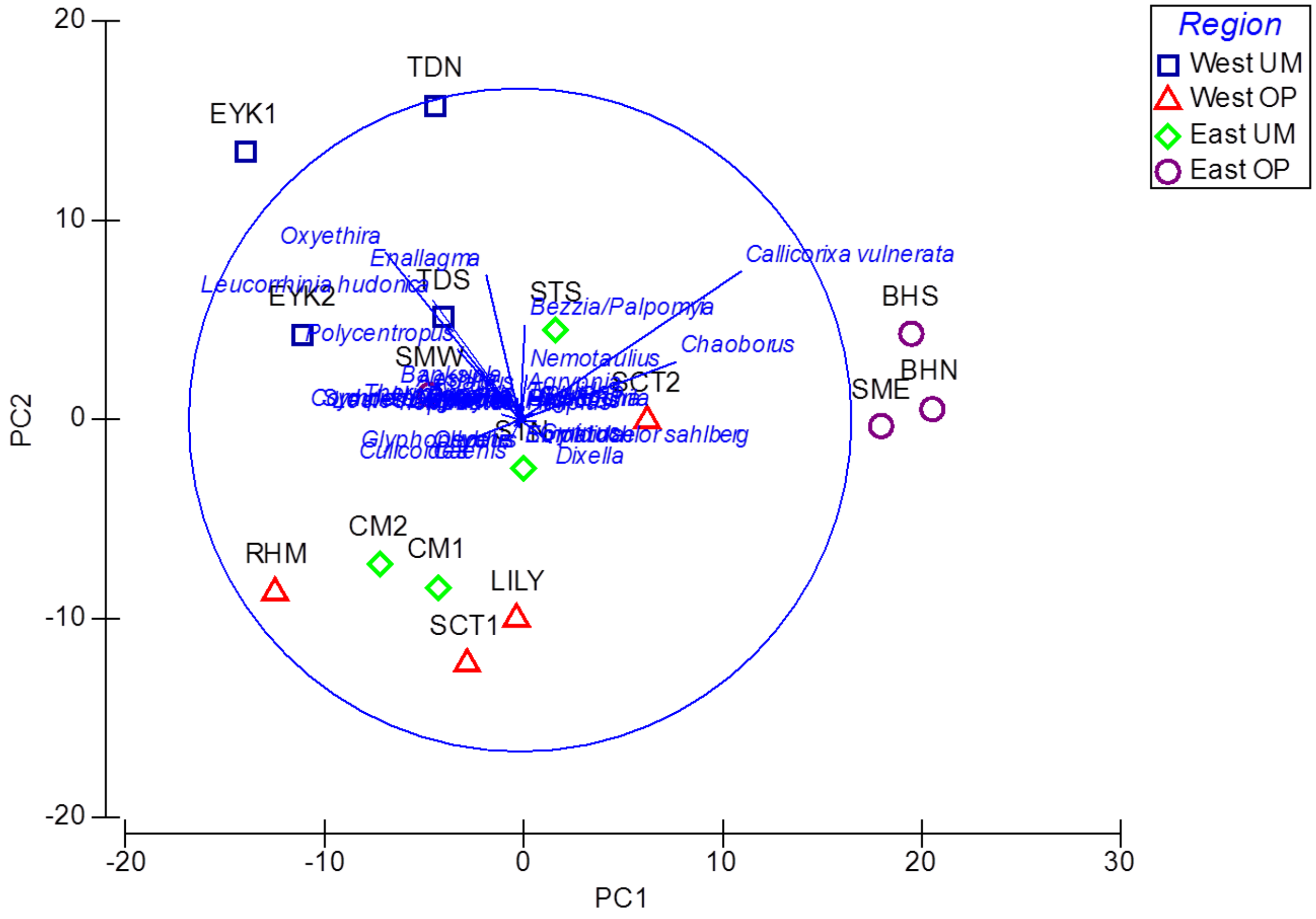


Figure 6. Principal components analysis of aquatic insect taxa from 16 ponds on the Copper River Delta, Alaska. Symbols represent the 4 regions. PC1 and PC2 account for 64.1% of the variation.

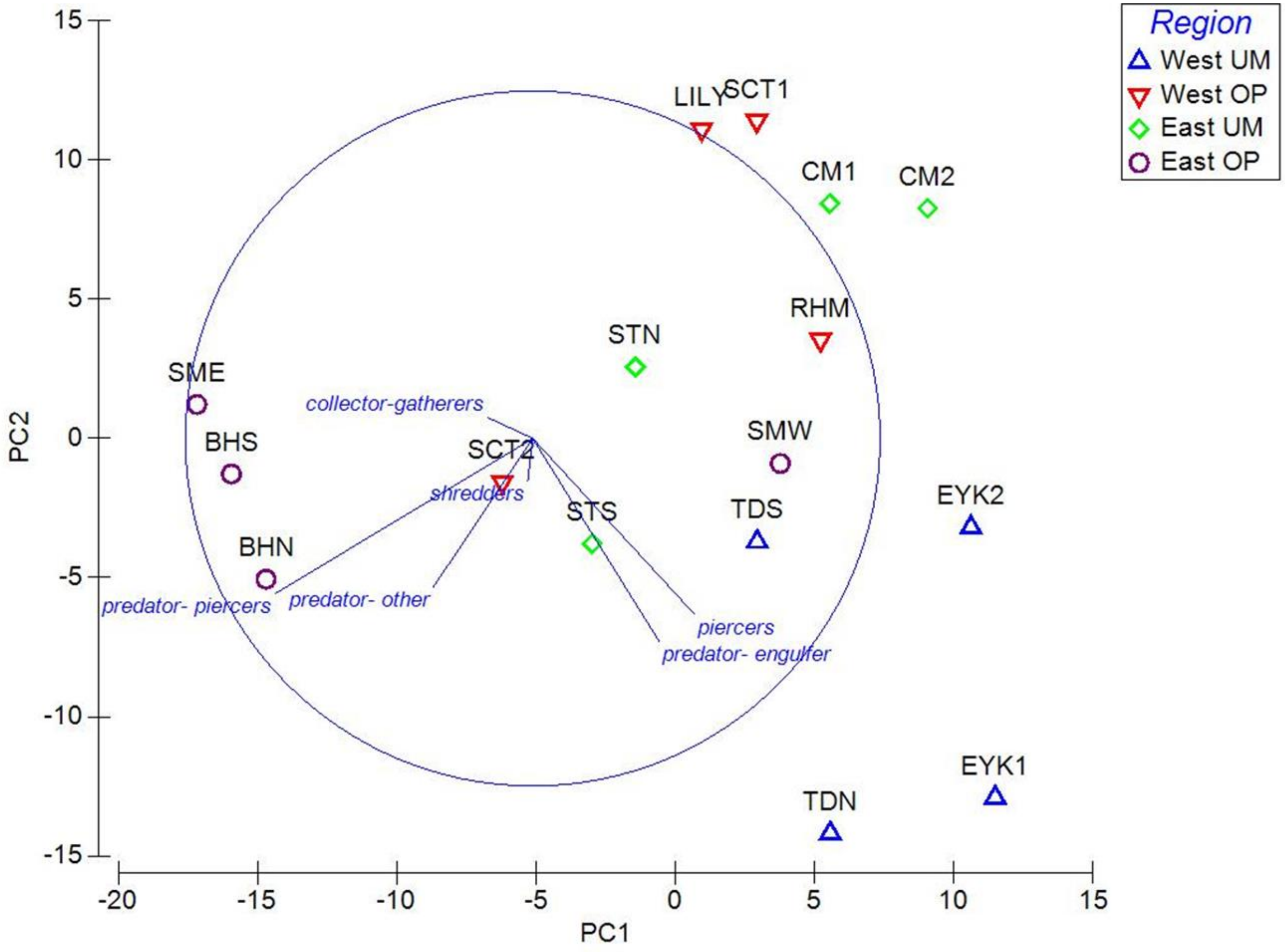


Figure 7. Principal components analysis of aquatic insect functional feeding group densities from16 ponds on the Copper River Delta, Alaska. Symbols represent the 4 regions. PC1 and PC2 account for 75.8% of the variation.

Secondary Production of Numerically Dominant Aquatic Insect Taxa

Annual secondary production was calculated for 11 taxa across pond regions on the CRD by using ponds within a region as replicates. Secondary production was not significantly different across regions for any taxa except odonates; however trends in production were apparent. *Callicorixa vulnerata* production was higher in East-OP ponds (88.0 ± 21.8 mg AFDM/m^2/yr) than in any other region (Table 10). Dipterans in East-OP ponds had relatively high secondary production rates compared to other regions. Outwash plain ponds had higher secondary production rates for *Dixella* (East-OP: 1.4 ± 0.7 mg AFDM/m^2/yr; West-OP: 0.9 ± 0.6 mg AFDM/m^2/yr) compared to UM ponds (West-UM: 0.1 ± 0.1 mg AFDM/m^2/yr; East-UM: 0.4 ± 0.2 mg AFDM/m^2/yr). The highest mean secondary production rate for *Oxyethira* was 1.2 ± 0.4 mg AFDM/m^2/yr in West-UM ponds. *Nemotaulius* was numerically dominant in only two East-OP ponds with secondary production rates of 1.8 mg AFDM/m^2/yr (SMW) and 7.2 mg AFDM/m^2/yr (SME). *Siphlonurus* was numerically dominant in one East-UM pond, STS, and had relatively high secondary production rates (13.1 mg AFDM/m^2/yr) compared to other CRD taxa.

Secondary production estimates for three odonate taxa were calculated and provided by Furlan (2014) (Table 11). Overall, Odonata secondary production rates were high across the Delta, compared to non-odonate taxa. *Leucorrhinia hudsonica* secondary production was significantly higher (one-way ANOVA, $F_{3,12} = 9.6$, $p < 0.01$) in West-UM ponds (50.1± 14.9 mg AFDM/m^2/yr) than in other regions (Tukey post hoc, $p < 0.05$) (Table 11). Secondary production of the remaining Odonata taxa were not significantly different across regions, however some trends were apparent. *Enallagma* secondary production was highest in UM ponds (West-UM:

25.5 mg ± 8.7 AFDM/m^2/yr; East-UM: 15.4 mg ± 7.6 AFDM/m^2/yr), and lowest in West-OP ponds (1.5 ± 1.0 mg AFDM/m^2/yr). *Aeshna* secondary production was similar across regions.

All 14 genera (11 non-odonate and 3 odonate) were used in calculating FFG secondary production. Evidence of cannibalism was found in CRD *Aeshna*, however the incidence of cannibalism was low (<9% of *Aeshna* foreguts contained odonate prey) (Furlan, 2014), so secondary production calculations for predator-engulfers and predator community production were not adjusted to account for cannibalism. Overall, predator-engulfers and predator-piercers had high production values across the Delta (Table 12).

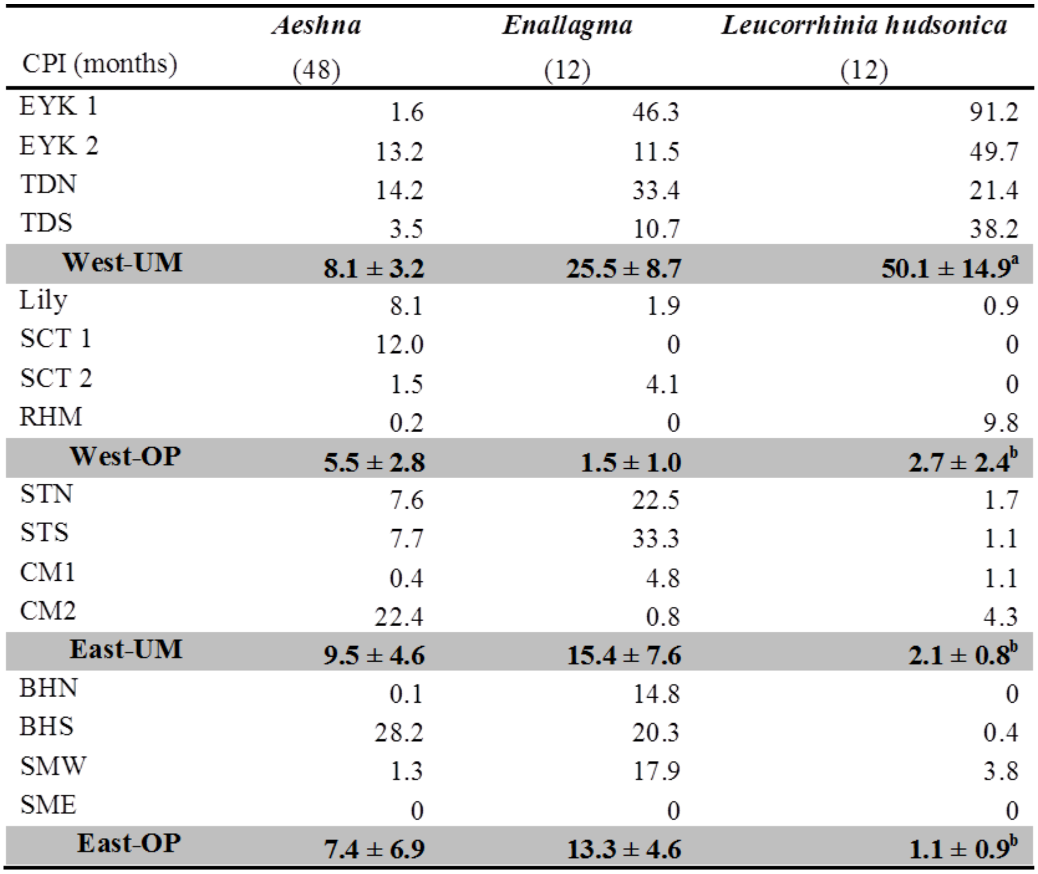
Secondary production of predator-engulfers and predator-other were significantly different in some CRD regions (predator-engulfers: one-way ANOVA, $F_{3,12} = 9.1$, $p < 0.01$; predator-other: one-way ANOVA, $F_{3,12} = 6.8$, $p < 0.01$). Secondary production of predator-engulfers was significantly higher in West-UM ponds (85.5 ± 19.5 mg AFDM/m^2/yr) than in West-OP ponds (9.6 ± 1.4 mg AFDM/m^2/yr, Tukey post hoc, $p < 0.01$) and East-UM ponds (27.3 ± 7.6 mg AFDM/m^2/yr, Tukey post hoc, $p = 0.04$). Predator-others production was higher in East-OP ponds (13.5 ± 6.3 mg AFDM/m^2/yr) than in West-OP ponds (1.9 ± 0.5 mg AFDM/m^2/yr, Tukey post hoc, $p < 0.01$) and East-UM ponds (2.7 ± 0.3 mg AFDM/m^2/yr, Tukey post hoc, $p = 0.02$). Mean secondary production of predator-piercers was higher in East-OP ponds (88.8 ± 22.0 mg AFDM/m^2/yr) than in other regions (Table 12), however these differences were not statistically significant. High secondary production of predator-piercers in East-OP ponds can be attributed to *C. vulnerata.* Overall, secondary production of predator-piercers was the highest for any FFG in three of the four regions, whereas predator-engulfer production was highest in West-UM ponds (Table 12).

Mean community secondary production was calculated for all regions with and without corixids (Table 13) because they are a seasonal component in CRD ponds with swarms of migrating *C. vulnerata* moving from ponds to streams in September. Aquatic insect community production was assessed by categorizing taxa into three groups (herbivores, predators, and predators without corixids), calculating secondary production of each group separately, and then summing those values to yield total community secondary production. Predator community production was significantly different in some regions when excluding corixids (one-way ANOVA, $F_{6,21} = 5.9$, $p = 0.01$) (Table 13). Non-corixid predator production was significantly higher in West-UM ponds (89.6 ± 19.8 mg AFDM/m^2/yr) than in West-OP ponds, which had the lowest non-corixid predator production (12.3 ± 1.4 mg AFDM/m^2/yr) (Tukey post hoc, $p < 0.01$). East-OP ponds had the second highest non-corixid predator production (36.0 ± 15.6 mg AFDM/m^2/yr), however this was three-fold less than East-OP mean community production with corixids. There were no significant differences in predator community production where corixids were included. The highest mean predator community production including corixids was East-OP (124.0 ± 28.4 mg AFDM/m^2/yr), followed by West-UM (118.4 ± 14.2 mg AFDM/m^2/yr) (Table 13). The lowest mean predator community production with corixids was West-OP ponds (38.5 ± 15.7 mg AFDM/m^2/yr). Similar trends were present in herbivore community production. No significant differences were found across the regions, however the highest herbivore production was in East-OP ponds (8.4 ± 4.9 mg AFDM/m^2/yr) and the lowest in West-OP ponds (1.1 ± 0.6 mg AFDM/m^2/yr).

Table 10. Annual secondary production (mg AFDM/m^2/yr) and cohort production intervals (CPI) (WD: West Delta, ED: East Delta) of numerically dominant non-Odonata taxa sampled from the Copper River Delta, Alaska in May-September of 2011. Secondary production values presented as means (±SE) in the four regions. Values of zero represent ponds which had low densities or absence of taxa and secondary production was not calculated. Pond abbreviations as in Table 1.

	Ephemeroptera		**Hemiptera**	**Coleoptera**	**Trichoptera**				**Diptera**		
	Caenis	***Siphlonurus***	***C. vulnerata***	***Agabus***	***Oxyethira***	***N. hostilis***	***Agrypnia***	***Polycentropus***	***Bezzia/Palpomyia***	***Chaoborus***	***Dixella***
CPI (months) WD / ED	(NA) / (3.5)	(NA) / (3.5)	(12) / (13)	(12) / (12)	(12) / (10.5)	(NA) / (3)	(11) / (12)	(12) / (12)	(12) / (12)	(11) / (12)	(12) / (12)
EYK 1			11.7	2.2	1.4		2.7	2.8	3.2	0	0
EYK 2			34.3	0	2.1		9.5	1.1	2.6	0	0
TDN			32.6	1.3	1.6		0	3.2	2.6	1.1	0.5
TDS			36.5	0	0		0	0	3.5	0	0
West-UM			**28.8 ± 5.7**	**0.9 ± 0.5**	**1.2 ± 0.4**		**3.1 ± 2.2**	**1.8 ± 0.7**	**3.0 ± 0.2**	**0.3 ± 0.3**	**0.1 ± 0.1**
Lily			34.0	0.5			0		0.7		0
SCT 1			0	2.3			0		1.6		2.7
SCT 2			70.6	0.5			0.7		3.0		0.2
RHM			0	0			0		2.3		0.8
West-OP			**26.2 ± 16.8**	**0.8 ± 0.5**			**0.2 ± 0.2**		**1.9 ± 0.5**		**0.9 ± 0.6**
STN	0	0	83.5	2.2	0.5		6.4	1.0	3.6		0.2
STS	0	13.1	48.2	1.1	0		2.7	0	2.4		0.7
CM1	3.1	0	0	0	0		0	0	2.6		0
CM2	0	0	6.7	0	0		3.2	0.3	2.0		0.5
East-UM	**0.8 ± 0.8**	**3.3 ± 3.3**	**34.6 ± 19.5**	**0.8 ± 0.5**	**0.1 ± 0.1**		**3.1 ± 1.3**	**0.3 ± 0.2**	**2.6 ± 0.3**		**0.4 ± 0.2**
BHN			131.0	1.8	0	0	3.8		1.6	10.7	2.6
BHS			99.0	0	0	0	0		8.7	23.0	0.5
SMW			27.4	0	2.2	1.8	0		3.9	0	0
SME			94.7	1.3	0	7.2	13.1		4.3	1.7	2.4
East-OP			**88.0 ± 21.8**	**0.8 ± 0.5**	**0.6 ± 0.6**	**2.3 ± 1.7**	**4.2 ± 3.1**		**4.6 ± 1.5**	**8.9 ± 5.3**	**1.4 ± 0.7**

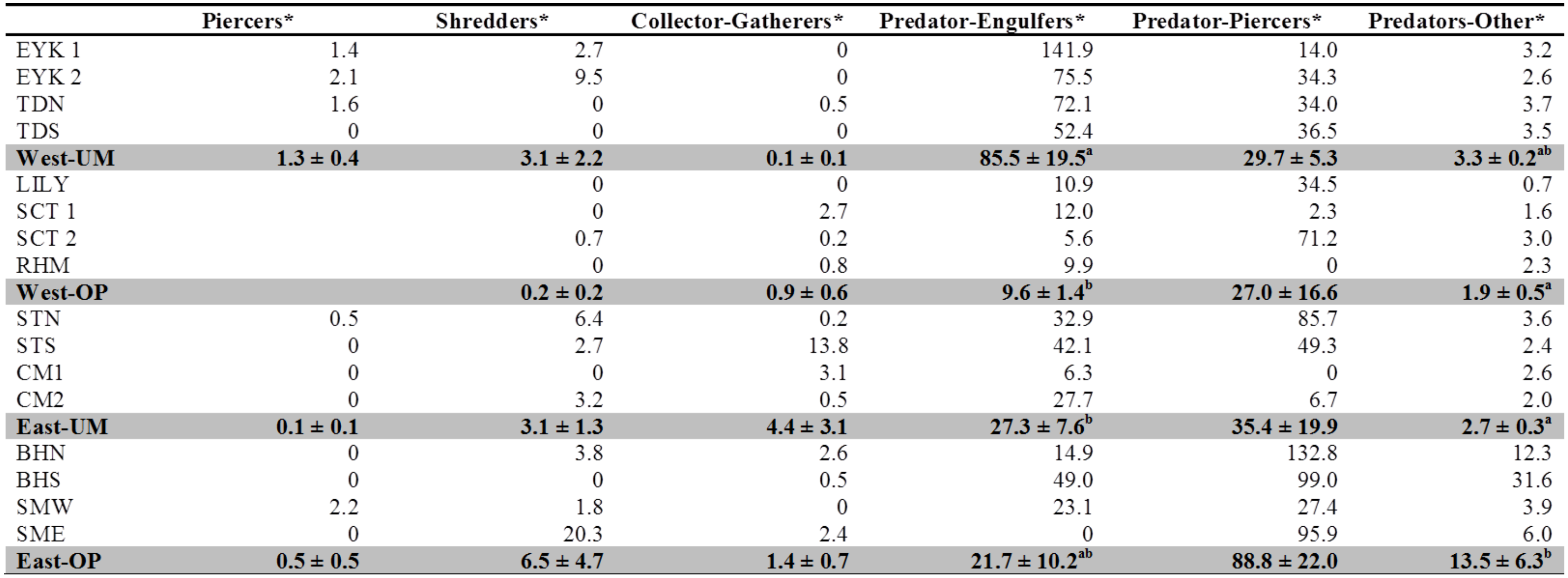
Table 11. Annual secondary production (mg AFDM/m^2/yr) and cohort production intervals (CPI) of numerically dominant Odonata taxa sampled from the Copper River Delta, Alaska, May-September of 2011. Secondary production values presented as means (± SE) in the four regions (Furlan, 2014). Pond abbreviations as in Table 1.



	Aeshna	*Enallagma*	*Leucorrhinia hudsonica*
CPI (months)	(48)	(12)	(12)
EYK 1	1.6	46.3	91.2
EYK 2	13.2	11.5	49.7
TDN	14.2	33.4	21.4
TDS	3.5	10.7	38.2
West-UM	**8.1 ± 3.2**	**25.5 ± 8.7**	**50.1 ± 14.9**[a]
Lily	8.1	1.9	0.9
SCT 1	12.0	0	0
SCT 2	1.5	4.1	0
RHM	0.2	0	9.8
West-OP	**5.5 ± 2.8**	**1.5 ± 1.0**	**2.7 ± 2.4**[b]
STN	7.6	22.5	1.7
STS	7.7	33.3	1.1
CM1	0.4	4.8	1.1
CM2	22.4	0.8	4.3
East-UM	**9.5 ± 4.6**	**15.4 ± 7.6**	**2.1 ± 0.8**[b]
BHN	0.1	14.8	0
BHS	28.2	20.3	0.4
SMW	1.3	17.9	3.8
SME	0	0	0
East-OP	**7.4 ± 6.9**	**13.3 ± 4.6**	**1.1 ± 0.9**[b]

[a] - Statistically significant differences (Tukey post hoc test, $p < 0.05$) denoted with different superscripts

Table 12. Annual secondary production (mg AFDM/m^2/yr) of functional feeding groups (FFGs) from Copper River Delta, Alaska, ponds and regions, May-September of 2011. Secondary production values presented as means (± SE) in the four regions. Pond abbreviations as in Table 1.



	Piercers*	**Shredders***	**Collector-Gatherers***	**Predator-Engulfers***	**Predator-Piercers***	**Predators-Other***
EYK 1	1.4	2.7	0	141.9	14.0	3.2
EYK 2	2.1	9.5	0	75.5	34.3	2.6
TDN	1.6	0	0.5	72.1	34.0	3.7
TDS	0	0	0	52.4	36.5	3.5
West-UM	**1.3 ± 0.4**	**3.1 ± 2.2**	**0.1 ± 0.1**	**85.5 ± 19.5^{a}**	**29.7 ± 5.3**	**3.3 ± 0.2^{ab}**
LILY		0	0	10.9	34.5	0.7
SCT 1		0	2.7	12.0	2.3	1.6
SCT 2		0.7	0.2	5.6	71.2	3.0
RHM		0	0.8	9.9	0	2.3
West-OP		**0.2 ± 0.2**	**0.9 ± 0.6**	**9.6 ± 1.4^{b}**	**27.0 ± 16.6**	**1.9 ± 0.5^{a}**
STN	0.5	6.4	0.2	32.9	85.7	3.6
STS	0	2.7	13.8	42.1	49.3	2.4
CM1	0	0	3.1	6.3	0	2.6
CM2	0	3.2	0.5	27.7	6.7	2.0
East-UM	**0.1 ± 0.1**	**3.1 ± 1.3**	**4.4 ± 3.1**	**27.3 ± 7.6^{b}**	**35.4 ± 19.9**	**2.7 ± 0.3^{a}**
BHN	0	3.8	2.6	14.9	132.8	12.3
BHS	0	0	0.5	49.0	99.0	31.6
SMW	2.2	1.8	0	23.1	27.4	3.9
SME	0	20.3	2.4	0	95.9	6.0
East-OP	**0.5 ± 0.5**	**6.5 ± 4.7**	**1.4 ± 0.7**	**21.7 ± 10.2^{ab}**	**88.8 ± 22.0**	**13.5 ± 6.3^{b}**

* - Taxa were placed in the following FFGs: piercers (*Oxyethira*), shredders (*Agrypnia* and *Nemotaulius*), collector-gatherers (*Caenis*, *Dixella*, and *Siphlonurus*), predator-engulfers (*Aeshna*, *Enallagma*, *Leucorrhinia*, and *Polycentropus*), predator-piercers (*Agabus* and *C. vulnerata*) and predators-other (*Bezzia/Palpomyia* and *Chaoborus*).

[a] - Statistically significant differences (Tukey post hoc test, $p < 0.03$) denoted with different superscripts

Table 13. Mean (±SE) annual secondary production (mg AFDM/m^2/yr) of aquatic insect communities with and without *Callicorixa vulnerata* from Copper River Delta, Alaska, regions, May-September of 2011. Pond abbreviations as in Table 1.

Region	**Herbivore Community Production**	**Predator Community Production**	**Predator Community Production without *C. vulnerata***
West-UM	4.5 ± 2.5	118.4 ± 14.2	89.6 ± 19.8^{a}
West-OP	1.1 ± 0.6	38.5 ± 15.7	12.3 ± 1.4^{b}
East-UM	7.6 ± 3.1	65.3 ± 25.9	30.7 ± 7.9^{ab}
East-OP	8.4 ± 4.9	124.0 ± 28.4	36.0 ± 15.6^{ab}

[a] - Statistically significant differences (Tukey post hoc test, p = 0.01) denoted with different superscripts

DISCUSSION

Physicochemical Parameters

Aquatic macroinvertebrate communities in wetlands are strongly influenced by a suite of abiotic parameters (Sharitz and Batzer 2009) including habitat size, water temperature, dissolved oxygen (Batzer and Wissinger 1996, Larson and House 1990), hydrological conditions, nutrients, and environmental stress and disturbance (Sharitz and Batzer 2009). A subset of these factors were examined in Copper River Delta (CRD), Alaska, ponds in an attempt to explain differences in aquatic insect communities across wetland ponds. Although no significant differences in temperature were found among ponds or regions (West-UM, West-OP, East-UM, East-OP), trends in habitat size and water temperature were apparent and could be used to explain variation between regions. Habitat size, such as pond surface area and depth, differed between pond regions. Pond surface areas increased during the study due to precipitation, and expanded laterally over surrounding vegetation. Uplifted marsh (UM) ponds were generally larger in surface area and shallower than outwash plains (OP) ponds, however the depth of most OP ponds was not measured because they were too deep for wading.

Pond temperatures across the CRD increase from May to July and begin decreasing in late August. This trend is common in shallow ponds and is a result of increased air temperatures and solar radiation (Ward and Stanford 1982). Temperate aquatic habitats at high latitudes have an annual minimum temperature of 0°C, representing the period of ice cover (Ward and Stanford

1982). The duration of this period impacts aquatic insect development because these temperatures are below the developmental threshold (Ward and Stanford 1982). Temperatures were not recorded throughout the year because loggers were lost due to heavy ice cover on ponds. Therefore it is not known how long temperatures were below the developmental threshold in CRD ponds. Despite an average day length of 18 h. 45 min across the Delta (Thilenius 1995) during the growing season (mid-May – late August), there are substantial differences between temperatures on the West and East Delta. Water temperature differences (30-day average) between the West and East Delta were greatest in May, with the East Delta about 2.5°C cooler (West Delta: 13.2°C and East Delta: 10.7°C). East Delta ponds are exposed to cold air masses, often reaching -40°C, which travel down the Copper River canyon during winter (Thilenius 1995). The West Delta is relatively protected from these cold air masses due to the Chugach Mountains along the west side of the Copper River (Thilenius 1995). Colder temperatures cause a delay in the East Delta growing season; while plants on the West Delta are in full leaf, plants on the East Delta are dormant or still buried under snow (Thilenius 1995). Thus, the East Delta growing season starts later and is shorter due to a longer period of ice cover.

Uplifted marsh ponds were consistently warmer than OP ponds, regardless of delta area. Outwash plain ponds had more extensive beds of emergent vegetation in the pond and along shorelines, and the riparian zone tended to be more tree-dominated compared to UM ponds. These characteristics of OP ponds could lead to increased shading causing the overall cooler water temperatures compared to UM ponds. Landscape position may also influence water temperature in UM ponds as they are further from the mountains than OP ponds, and cloud cover tends to be more prevalent closer to mountain ranges (Wylie et al. 2005). This may allow for higher solar radiation and therefore higher temperatures in UM ponds. An additional factor affecting pond water temperatures is water source for CRD ponds. Three primary sources of water for wetlands are precipitation, groundwater discharge, and surface water inflows (Sharitz and Batzer 2009). Although the source of water in CRD ponds is strongly influenced by their position in the landscape, this has not been extensively studied on the CRD. Outwash landscape ponds have been reported to be strongly influenced by both groundwater and precipitation (Marsh et al. 2000, Thilenius 1995), resulting in lower temperatures, whereas UM ponds are generally more heavily influenced by precipitation, with minimal groundwater discharge (Boggs 2000), although further research is needed.

Community Composition of CRD Ponds

Non-chironomid aquatic insect taxa richness across the CRD was low, with only 34 taxa present. Low diversity was also noted in previous studies of CRD ponds (Tiegs et al. 2013, Van Duzor et al. 2011). Low aquatic insect diversity could be due to a relatively short growing season, lower temperatures (Thilenius 1995), and/or the unique location of the CRD. Tiegs et al. (2013) suggest that the location of the CRD, surrounded by the Chugach Mountain range, could limit the immigration of aquatic macroinvertebrate species from surrounding areas. Although aquatic insect diversity on the CRD is relatively low, significant differences were found between the four regions.

Uplifted marsh ponds had high aquatic insect diversity compared to OP ponds. Several factors associated with macrophyte communities could account for differences in aquatic insect communities; including macrophyte diversity, geologic history, temperature, and length of growing season. Aquatic insect diversity has been shown to be strongly associated with macrophyte diversity and cover (De Szalay and Resh 2000, Kratzer and Batzer 2007, Sharitz and Batzer 2009) and across the delta UM ponds had higher macrophyte diversity than OP ponds.

Uplifted marsh ponds had 2-4 types of monoculture beds and numerous mixed beds at the peak of growing season, whereas OP ponds had 1-3 types of monoculture beds with only one type of mixed bed at the peak of growing season.

Macrophyte Community Composition

Differences in macrophyte beds between landscape types were likely due to UM ponds being geologically younger than OP ponds. The 1964 earthquake raised part of the delta, the uplifted marsh, and transformed tidally influenced wetlands into non-tidal systems (Boggs 2000; Christensen et al. 2000), eventually creating new freshwater habitats available for colonization. The further inland outwash plain was minimally affected by the earthquake. Therefore, macrophyte succession has occurred for a longer period of time in OP ponds. Changes in dominance within macrophyte communities have been documented to occur over time resulting in late-successional species out-competing and replacing early-successional species (Connell and Slatyer 1977, Milner et al. 2008). Macrophyte communities in OP ponds were numerically dominated by long-lived perennials with *Equisetum spp.* occurring in open water areas and *Carex spp.* along shorelines. *Equisetum* is capable of reproducing by rhizome growth, and can establish dense beds in locations despite dense cover of other species (Odland and Del Moral 2002). Additionally, *Equisetum* is capable of extending roots and rhizomes deeper than most macrophytes allowing access to nutrients that may be limited in shallow soils (Marsh et al. 2000). These attributes allow *Equisetum* to form dense stands and exclude less competitive taxa through nutrient uptake and shading (Sharitz and Batzer 2009), leading to its dominance in later successional ponds (e.g., OP ponds). Few UM ponds had dominant beds of *Equisetum*. The geologically younger UM ponds were dominated by a diverse community of submerged and emergent macrophytes. These macrophytes, such as buckbean (*Menyanthes*), have higher structural complexity and larger leaves than *Equisetum*.

Although differences in macrophyte communities of UM and OP ponds can be explained by vegetation succession, differences in temperature and length of growing season also impact macrophyte communities. Differences in macrophyte communities were observed between regions. All OP ponds contain *Equisetum* and *Carex*, however unlike other East-OP ponds LILY and SCT2 (West-OP ponds) also contain buckbean and marestail (*Hippuris*), two species common in West-UM ponds. Warmer water temperatures coupled with a longer growing season in LILY and SCT2 could account for similar macrophyte taxa as found in West-UM ponds. East-UM ponds contain numerically dominant beds of *Equisetum* and fewer beds of buckbean and marsh-five-finger (*Potentilla*), whereas West-UM ponds had no dominant beds of *Equisetum*. The greater abundance of *Equisetum* in East-UM ponds was likely due to colder winter temperatures and a shorter growing season, which limits the number of macrophyte taxa capable of colonizing and competing for resources.

Aquatic Insect Community Composition

The interacting effects of delta area and landscape type prohibit generalizations of aquatic insect communities across the CRD; however patterns within regions provide insights into the dynamics of aquatic insect community structure. Aquatic insect community structure among bed types within ponds was not significantly different. Because ponds are relatively small in size, plant beds are not widely separated, and insects can easily move from one plant type to another resulting in similar insect assemblages. Because of differences in macrophyte community composition among the four regions, significant differences in aquatic insect community composition and diversity are related to macrophyte communities. Macrophytes provide habitat, food resources, refuge from predators, and structures for mating and emergence of aquatic insects (Batzer and Wissinger 1996, Remsburg and Turner 2009). Overall, UM ponds had higher macrophyte diversity than OP ponds.

Higher macrophyte diversity in UM ponds resulted in greater diversity of aquatic insects and differences in aquatic insect community structure between UM and OP ponds. Large-bodied aquatic insect predators, such as odonates, are top invertebrate predators in wetlands without fish (Blois-Heulin et al. 1990, Batzer and Wissinger 1996). Copper River Delta ponds are not fishless, however, the only fish present in CRD ponds, three-spine stickleback (*Gasterosteus aculeatus*), are small and preyed upon by odonates (Furlan et al. 2014), which are top predators in CRD ponds. Thus, PCA ordinations of invertebrate functional feeding groups (FFGs) showed that UM ponds, especially West-UM ponds, were different from ponds in other regions due to the presence of predator-engulfers and piercers. Predator-engulfer density was significantly higher in West-UM ponds compared to OP ponds. Predator-engulfers in West-UM ponds are mainly comprised of odonates and several Trichoptera taxa, both of which were significantly higher in percent abundance and densities in West-UM compared to OP ponds. Uplifted marsh ponds were characterized by greater habitat complexity than OP ponds. Mixed habitats of emergent and submerged macrophytes are productive areas for a variety of aquatic insects due to increased habitat heterogeneity provided by submerged macrophytes (Batzer and Wissinger 1996, Thorp et al. 1997). These highly protective submerged macrophyte beds supply predator-engulfers with a diverse prey base in West-UM ponds. In contrast, East-UM ponds had a relatively high abundance of Trichoptera but not Odonata. The lower abundance of Odonata in East-UM ponds is likely due to decreased macrophyte structure, the predominance of structurally simple macrophytes such as *Equisetum*, and a shorter growing season than in West-UM ponds, thereby limiting the amount of time that appropriate habitat and food resources are available. Overall, greater habitat complexity in UM ponds than in OP ponds leads to increased insect diversity and therefore a wider range of prey available for higher trophic level organisms. This diverse prey base accounts for the presence of predatory taxa (Odonata and Trichoptera) in the more macrophyte-diverse UM ponds. These results are consistent with previous studies that show an increase in predator densities in macrophyte beds where prey are more abundant (Remsburg and Turner 2009).

West-UM ponds had two-fold higher densities of piercers, particularly *Oxyethira* (Trichoptera: Hydroptilidae), than in other regions, and is reflected in the FFG PCA. Hydroptilid larvae are climbers or free-living until the final instar when a case is constructed (Merritt et al. 2008). Larvae are predominately piercers and the primary food resource is algae (Keiper et al. 1998). In general, larvae feed mainly on the cellular contents of filamentous algae and some sessile diatoms (Merritt et al. 2008). Algal communities were not examined in the present study; therefore no direct connection can be made between availability of algal food resources and the high abundance of *Oxyethira* in West-UM ponds. Nevertheless, the absence of tall emergent macrophytes in West-UM ponds would allow for higher light levels than in ponds in other regions. Thus, epiphytic algal populations in West-UM ponds, and in turn hydroptilid densities, may be influenced by increased light availability via decreased shading compared to other regions. An exception to this trend is SMW, an East-OP pond with stands of tall emergent macrophytes similar to other East-OP ponds, but with high densities of *Oxyethira*. The ordination of SMW with West-UM ponds in the PCA is due to high densities of *Oxyethira*. Large accumulations of algae were abundant throughout the sampling period in SMW and were not observed in other East-OP ponds. This food resource could explain the high densities of

Oxyethira and the differences in community composition indicated by PCA in SMW. Further research on algal communities in CRD ponds may provide insights into differences in community composition among the four regions.

Aquatic insect diversity was lower in OP ponds compared to UM ponds. Low macrophyte diversity and the simple structure of *Equisetum* in OP ponds provide a low diversity of habitats and/or decreased protection from predators. Thus, insect communities in OP ponds, particularly East-OP, had decreased species richness and were characterized by only a few taxa that were numerically abundant. With the exception of SMW, PCA indicates the grouping of East-OP ponds was due to predator-piercers and predator-other, specifically *Callicorixa vulnerata* (Hemiptera: Corixidae) and *Chaoborus* (Diptera: Chaoboridae), respectively. The predator-other FFG is represented by three Diptera taxa (*Bezzia/Palpomyia*, *Chaoborus*, *Culicoides*), which generally prey on small animals including other dipterans (Merritt et al. 2008). East-OP ponds had significantly higher mean densities of dipterans compared to East-UM ponds. The predator-piercer FFG is composed of hemipterans, mainly *C. vulnerata*, and several Coleoptera taxa. East-OP ponds had significantly higher densities of predator-piercers than West-OP and East-UM ponds. Predator-piercers are active swimmers and have been found to be negatively correlated with plant cover (De Szalay and Resh 2000). Coleoptera, specifically Dytiscidae, are active predators that feed on corixids and substrate-associated prey such as chironomids (Yee et al. 2013). Corixids are cold-adapted, active swimmers (Merritt et al. 2008), and have been shown to prey on chironomids, oligochaetes, zooplankton and fish fry (Popham et al. 1984). Many corixid taxa feed near the bottom of ponds (Popham et al. 1984) and surface periodically for air. East-OP ponds have less submerged vegetation compared to other regions leading to a less vegetated water column. Less vegetation in the water column supplies habitat for swimming predators in East-OP ponds and could supply a high density of non-insect prey associated with decomposing litter on the open benthic substrate.

High densities of macroinvertebrates are rarely supported on emergent macrophytes, although high densities are found in benthic litter associated with macrophytes (Tiegs et al. 2013). East-OP ponds are suitable for high densities of predator-piercer and predator-other due to bottom-up controls resulting from decomposing *Equisetum*. Tiegs et al. (2013) studied decomposition of CRD macrophytes on the West Delta and reported high abundances of macroinvertebrate scrapers and shredders in OP ponds. Decomposition, however, was primarily attributed to phosphorus-limited microbial communities. Contrary to Tiegs et al. (2013), Marsh et al. (2000) found *Equisetum* on the CRD had high phosphorus content due to rhizomes reaching the C soil horizon, a phosphorus-rich area. *Equisetum* decomposes rapidly and releases phosphorus to surficial benthic sediments (Marsh et al. 2000), making phosphorus available to microbial communities during decomposition. The phosphorus-rich litter colonized by phosphorus-limited microbes could create a bottom-up control, supplying increased food resources to macroinvertebrates associated with decomposing litter. Many macroinvertebrates feed on decomposing plant material, and can include oligochaetes, amphipods, chironomids, and various scrapers directly targeting microbes (Tiegs et al. 2013). A majority of these macroinvertebrates are not insects and therefore were not examined in this study. However, it is likely that the abundance of these macroinvertebrates would increase with greater quality and/or abundance of decomposing litter and associated microbes resulting in increased prey abundance associated with benthic litter. These prey are consumed by predatory-piercers and dipterans (Yee et al. 2013), which explains the high abundance of predators in East-OP ponds.

Similar to East-OP ponds, West-OP ponds had relatively high densities and relative abundance of Hemiptera and Diptera. Dipteran densities in West-OP ponds, however, were three-fold lower than in East-OP ponds. West-OP ponds had the lowest densities of Hemiptera compared to other regions, with densities of predator-piercers almost seven-fold lower in West-OP compared to East-OP ponds. The low abundance of hemipterans and dipterans in West-OP ponds could be explained by the macrophyte community. Macrophyte beds in West-OP ponds were comprised of macrophytes typical of OP ponds (e.g. *Equisetum*) and macrophyte species more often present in UM ponds (e.g. buckbean and marestail). This higher macrophyte diversity in West-OP compared to East-OP could explain the higher diversity of aquatic insects in West-OP compared to East-OP ponds. The lower densities of hemipterans and dipterans in West-OP ponds could be due to the decreased abundance of *Equisetum*. Decreases in *Equisetum* could lead to decreased densities of benthic macroinvertebrates, which are common food resources for corixids (Yee et al. 2013), an abundant hemipteran in CRD ponds.

Aquatic Insect Secondary Production

Densities and annual secondary production of non-chironomid aquatic insects were low across the CRD. Mean densities of taxa in the four CRD regions ranged from 0.2 - 41.6 individuals/m^2, with 70% of taxa having mean densities less than 5.0 individuals/m^2. Secondary production values of CRD taxa, excluding odonates and corixids, were less than 10 mg AFDM/m^2/yr. Several factors can cause low annual production of aquatic insects, including low seasonal temperatures, nutrient limitation (Huryn and Wallace 2000), and a short growing season (Fisher and Gray 1983).

Mixed habitats of emergent and submerged macrophytes are productive areas for a wide range of aquatic insects, due to increased habitat (Batzer and Wissinger 1996, Thorp et al. 1997).

Uplifted marsh ponds had higher macrophyte and aquatic insect diversity compared to OP ponds. Caddisfly and odonate densities were highest in West-UM ponds and resulted in the highest production of piercers among regions and significantly higher production rates of predator-engulfers compared to West-OP and East-UM ponds. A longer growing season on the West delta and increased habitat heterogeneity of UM ponds could explain the higher production of predator-engulfers and piercers in West-UM ponds. High aquatic insect diversity due to increased habitat in UM ponds compared to OP ponds, provide a large prey base for odonates, leading to high densities of odonates in West-UM ponds. The longer growing season also could lead to higher algal abundance resulting in high *Oxyethira* production, however more research in needed on algae communities in the CRD ponds.

Predator-engulfers prey on other aquatic insects (Merritt et al. 2008), and a larger prey base for predator-engulfers is present in UM ponds compared to OP ponds due to a higher diversity of aquatic insects in UM ponds. In addition, increased prey resources in West-UM ponds could explain high *Enallagma* production and significantly higher *L. hudsonica* production in West-UM ponds compared to other regions. Secondary production rates of *Aeshna* were relatively high in East-UM ponds compared to the remaining regions. Furlan et al. (2014) reported diets of *Aeshna* from East-UM ponds in early summer dominated by dipterans, whereas terrestrial insects and crustaceans dominated in late summer and early fall. In contrast to West-UM ponds, East-UM ponds had stands of *Equisetum*, a tall emergent macrophyte. The presence of *Equisetum* provides resting and mating substrate for terrestrial insects (e.g. adult odonates), and contribute terrestrial subsidies to ponds (Nakano et al. 1999). *Siphlonurus* (Ephemeroptera: Siphlonuridae), a collector-gatherer, was found in high densities only in East-UM ponds and had relatively high production rates in STS, an East-UM pond. *Siphlonurus* was commonly associated with pendant grass (*Arctophila*), a macrophyte with large leaves along a tall stem. Detritus tends to accumulate in pendant grass beds, and may explain the high production of this collector-gatherer in STS.

Outwash plain ponds had less habitat heterogeneity and lower diversity of aquatic insects than UM ponds. Coleopterans, corixids and dipterans numerically dominated aquatic insect communities in OP ponds. Outwash plain ponds had the highest density and production of *Dixella* (Diptera: Dixidae), an abundant collector-gatherer. *Dixella* are swimmers that usually inhabit vegetated margins of standing water and feed on organic matter and associated microorganisms, algae, and aquatic micro-annelids (Haland 2009, Merritt et al. 2008). Studies conducted on stream macroinvertebrates found that bottom-up control has a strong influence on production (Huryn and Wallace 2000). Unlike UM ponds, OP ponds are influenced by groundwater sources that have high iron content and result in high amounts of iron flocculent (Marsh et al. 2000, Thilenius 1995). This flocculent is composed of microbial communities (Kato et al. 2013) and could serve as a food resource for *Dixella*. East-OP and West-OP ponds had the highest and second highest densities and production of *Dixella*, respectively. However, compared to other regions, West-OP had the lowest densities and production rates for most other aquatic insect taxa.

East-OP ponds had the highest densities and production of *C. vulnerata*, *Bezzia/Palpomyia* (Diptera: Ceratopogonidae), and *Chaoborus*. Mean production rates of East-OP predator-others (*Bezzia/Palpomyia* and *Chaoborus*) were significantly higher than in East-UM and West-OP ponds. Predator-others are typically associated with sediments and detritus and feed on micro-crustaceans (Merritt eta al. 2008). Additionally, some predator-others, like *Chaoborus*, move throughout the water column (Merritt et al. 2008). Outwash plain ponds have more open water compared to UM ponds and higher amounts of iron flocculent, which provides a food resource to other non-predatory dipterans. These characteristics of OP ponds provide habitat to predator-others, which facilitates their movement through the water column and supplies an abundant food resource of non-predatory dipteran prey. This leads to greater densities and production of dipterans in East-OP ponds.

East-OP pond predator-piercers (*Agabus* and *C. vulnerata*) had three-fold higher mean production rates than in other regions. East-OP ponds provide an ideal habitat for *C. vulnerata* and increased food resources, due to decomposing *Equisetum*, compared to other regions. The high abundance of phosphorus-limited microbes found on decomposing *Equisetum* (Tiegs et al. 2013) would cause a bottom-up control of the aquatic insect community by increasing the abundance of invertebrate prey items, known to feed on decomposing plant litter. An increase in invertebrate prey could result in higher densities and production rates of corixids in East-OP ponds. Mean secondary production of *C. vulnerata* was lower in West-OP ponds than in other regions, however within the West-OP region corixids had the highest mean secondary production of all taxa present. West-OP ponds had a mixture of *Equisetum* (common in OP ponds) and buckbean (common in UM ponds) and is likely a result of higher temperatures and a longer growing season on the West delta. The lower abundance in *Equisetum* in West-OP ponds compared to East-OP ponds could result in lower abundance of invertebrate prey for corixids and a concomitant decrease in corixid production in West-OP ponds. Well-developed microbial communities on decomposing *Equisetum* could also contribute to the high production of *Agrypnia* and *N. hostilis* (Trichoptera: Limnephilidae) in East-OP ponds. Both taxa are shredders typically found on benthic substrates or associated with detritus (Merritt et al. 2008). Many shredders feed extensively on detritus and associated microbes. Cummins (1973) compared a microbial covered leaf to peanut butter and crackers, where the protein-rich peanut butter is the microbes and the nutritionally poor cracker is the leaf. Thus, increased food quality and quantity provided by the microbially-rich *Equisetum* could lead to higher production of shredders in East-OP ponds.

Overall, outwash plain ponds had lower secondary production of all odonate taxa compared to UM ponds, however East-OP ponds had relatively high predator-engulfer production associated with *Aeshna* and *Enallagma*. Furlan et al. (2014) found East-OP *Aeshna* diets were dominated by dipterans in early summer and corixids in late summer. Corixids on the CRD presumably migrate between ponds (summer habitat: nymphs and adults) and streams (overwintering habitat: adults) and an ongoing study is investigating this behavior (M. Berg, pers. comm.). It is currently hypothesized that corixids move to CRD streams in September to feed on salmon eggs and carcasses. Preliminary samples showed the presence of corixids in CRD streams during winter months and grab samples from West delta ponds showed an absence of corixids during winter ice cover. The seasonal input of corixids can impact both predators and prey in CRD ponds. Furlan (2014) showed that diets of predators, such as odonates, are seasonally adjusted to take advantage of changing prey availability. High corixid densities would apply a seasonal pressure to prey items thereby reducing prey availability. High densities of corixids, especially on the East Delta, could exert a top-down control during the growing season with an increase in their abundance. Corixid influence on prey items as well as additional food resources for odonates has the potential to impact secondary production of aquatic insect communities across the CRD. This has not been studied and is a promising area for future research.

Conclusion

The Copper River Delta (CRD) provides habitat for a diversity of mammals, birds, and fish and is managed as “critical habitat” for fish and wildlife by the USDA Forest Service (Chugach National Forest) (Thilenius 1995, Boggs 2000). Climate models predict increasing air temperatures over the next 100 years in southcentral Alaska (Hall 1988, University of Alaska 2015), which will strongly influence the shallow pond habitats of CRD aquatic insects. Understanding the response of aquatic insect communities to changes in water temperature, growing season, and macrophyte community structure provides insight as to how climate change will impact northern coastal wetland ecosystems.

Projected air temperature increases in Southcentral Alaska will increase water temperatures and result in a longer ice-free season on the CRD. These changes will have substantial effects on CRD wetlands; however, these impacts will not be uniform across the landscape due to variation in successional stage (landscape type) and delta area (east vs. west). In early successional wetlands, such as those on the uplifted marsh, higher water temperatures will lead to rapid rates of insect development and increases in aquatic insect secondary production. In late successional wetlands, including those on the glacial outwash plains, secondary production of free-swimming and benthic associated aquatic insects will decrease due to a change in macrophyte communities from simple emergent vegetation to diverse communities of submergent and emergent vegetation. Despite a reduction in annual secondary production in these ponds, community secondary production and species diversity will increase due to increased diversity of macrophyte communities and available habitat.

Ponds presently exhibit water temperature differences due to an east-to-west temperature gradient. As surface air temperatures increase, the cooler East delta ponds will develop similar aquatic insect communities, and exhibit similar rates of secondary production and emergence times as presently observed on the West delta. West delta ponds will continue to have warmer water temperatures than the East delta, and insect growth rates and emergence times will continue to be earlier than East delta ponds.

Changes in aquatic insect communities due to water temperature will impact non-aquatic species, such as migrating birds, in both early and late successional wetlands. Northern migrating birds rely on delta habitats for nesting and on aquatic insect emergence as a predictable food resource. Photoperiod determines the start of migration for birds and water temperature determines development rates and emergence of aquatic insects. Increased temperatures will cause an earlier emergence of aquatic insects, which will decrease available food resources for migrating and nesting birds. A disconnect in the arrival of migrating birds and emergence of aquatic insects could lead to a shift in seasonal distribution of migratory bird populations or a decrease in juvenile survival. Changes to macrophyte and aquatic insect communities, resulting from global climate change, will impact coastal wetland aquatic community structures and the critical ecosystem functions they provide.

REFERENCES

Batzer, D. P., & Wissinger, S. A. (1996). Ecology of insect communities in nontidal wetlands. *Annual Review of Entomology*, *41*(1), 75-100.

Benke, A. C. (1979). A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. Limnology and Oceanography, 24(1), 168-171.

Benke, A.C. and A.D. Huryn. (2006). Secondary production of macroinvertebrates. In: Hauer RF, Lamberti GA, editors. Methods in Stream Ecology. New York: Elsevier. p 691-710.

Blois-Heulin, C., Crowley, P. H., Arrington, M., & Johnson, D. M. (1990). Direct and indirect effects of predators on the dominant invertebrates of two freshwater littoral communities. *Oecologia*, *84*(3), 295-306.

Boggs, K. (2000). Classification of community types, successional sequences, and landscapes of the Copper River Delta, Alaska. Alaska Gen. Tech. Re. PNW-GTR-469, Portland OR, US Department of Agriculture, Forest Service, Pacific Northwest Research Station. 244 p.

Brown, K. M., & Lodge, D. M. (1993). Gastropod abundance in vegetated habitats: the importance of specifying null models. *Limnology and Oceanography*, *38*(1), 217 225.

Christensen, H.H., Mastrantonio, L., Gordon, J.C., Bormann, B.T., tech eds. (2000). Alaska's Copper River: humankind in a changing world. Gen. Tech. Rep. PNW GTR-480. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 20 p.

Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, 111, 1119-1144.

Cummins, K. W. (1973). Trophic relations of aquatic insects. *Annual Review of Entomology*, *18*(1), 183-206.

De Szalay, F. A., & Resh, V. H. (2000). Factors influencing macroinvertebrate colonization of seasonal wetlands: responses to emergent plant cover. *Freshwater Biology*, *45*(3), 295-308.

Fisher, S. G., & Gray, L. J. (1983). Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. *Ecology*, 64(5), 1217-1224.

Furlan, N. (2014). Life histories, diets, and secondary production of odonata along a temperature gradient on the Copper River Delta, Alaska. Master's Thesis, Loyola University Chicago.

Haland, Ø. (2009). Notes on the life cycles of Norwegian *Dixella* species (Diptera, Nematocera, Dixidae). *Norwegian Journal of Entomology*, *56*, 37-43.

Hall, D. K. (1988). Assessment of polar climate change using satellite technology. *Reviews of Geophysics*, *26*(1), 26-39.

Hamilton, A.L. (1969). On estimating secondary production. *Limnology and Oceanography*, 14(5), 771-781.

Heino, J., Virkkala, R., & Toivonen, H. (2009). Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews*, *84*(1), 39-54.

Huryn, A. D., & Wallace, J. B. (2000). Life history and production of stream insects. *Annual Review of Entomology*, *45*(1), 83-110.

Hynes, H. B. N., & Coleman, M. J. (1968). A simple method of assessing the annual production of stream benthos. *Limnology and Oceanography*, *13*(4), 569-573.

Kato, S., Chan, C., Itoh, T., & Ohkuma, M. (2013). Functional gene analysis of freshwater iron-rich flocs at circumneutral pH and isolation of a stalk-forming microaerophilic iron-oxidizing bacterium. *Applied and Environmental Microbiology*, *79*(17), 5283-5290.

Keiper, J. B., Casamatta, D. A., & Foote, B. A. (1998). Use of algal monocultures by larvae of *Hydroptila waubesiana* and *Oxyethira pallida* (Trichoptera: Hydroptilidae). *Hydrobiologia*, *380*(1-3), 87-91.

Kratzer, E. B., & Batzer, D. P. (2007). Spatial and temporal variation in aquatic macroinvertebrates in the Okefenokee Swamp, Georgia, USA. *Wetlands*, *27*(1), 127-140.

Larson, D. J., and House, N. L. (1990). Insect communities of Newfoundland bog pools with emphasis on the Odonata. *The Canadian Entomologist*, *122*(03), 469-501.

Larson, D. J., Alarie, Y., & Roughley, R. E. (2000). *Predaceous diving beetles (Coleoptera: Dytiscidae) of the Nearctic Region, with emphasis on the fauna of Canada and Alaska* (p. 982). Ottawa: NRC Research Press.

Loomis, D. M. (2013). Reproductive success and foraging ecology of the rusty blackbird on the Copper River Delta, Alaska. Master's Thesis, Oregon State University, Corvallis, OR.

Marsh, A. S., Arnone, J. A., Bormann, B. T., & Gordon, J. C. (2000). The role of Equisetum in nutrient cycling in an Alaskan shrub wetland. *Journal of Ecology*, *88*(6), 999-1011.

Meerhoff, M., Clemente, J. M., Mello, D., Teixeira, F., Iglesias, C., Pedersen, A. R., & Jeppesen, E. (2007). Can warm climate-related structure of littoral predator assemblies weaken the clear water state in shallow lakes?. *Global Change Biology*, 13(9), 1888-1897.

Merritt, R.W., Cummins, K.W, Berg, M.B., eds. (2008). An Introduction to the Aquatic Insects of North America, 4th ed., Kendall/Hunt Publishing Co., Dubuque, IA: 862 p.

Milner, A. M., Robertson, A. L., Monaghan, K. A., Veal, A. J., & Flory, E. A. (2008). Colonization and development of an Alaskan stream community over 28 years. *Frontiers in Ecology and the Environment*, *6*(8), 413-419.

Mortsch, L. D. (1998). Assessing the impact of climate change on the Great Lakes shoreline wetlands. *Climatic Change*, *40*(2), 391-416.

Nakano, S., Miyasaka, H., & Kuhara, N. (1999). Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology*, *80*(7), 2435-2441.

Odland, A., & Del Moral, R. (2002). Thirteen years of wetland vegetation succession following a permanent drawdown, Myrkdalen Lake, Norway. *Plant Ecology*, 162(2), 185-198.

Popham, E. J., Bryant, M. T., & Savage, A. A. (1984). The role of front legs of British corixid bugs in feeding and mating. *Journal of Natural History*, *18*(3), 445-464.

Rosine, W. N. (1955). The distribution of invertebrates on submerged aquatic plant surfaces in Muskee Lake, Colorado. *Ecology*, *36*(2), 308-314.

Remsburg, A. J., & Turner, M. G. (2009). Aquatic and terrestrial drivers of dragonfly (Odonata) assemblages within and among north-temperate lakes. *Journal of the North American Benthological Society*, *28*(1), 44-56.

Schindler, D. W. (1997). Widespread effects of climatic warming on freshwater ecosystems in North America. *Hydrological Processes*, *11*(8), 1043-1067.

Sharitz, R. R., & Batzer, D. P. (2009). Wetland Communities. *Encyclopedia of Life Sciences*. John Wiley & Sons, Ltd.

Tiegs, S. D., Entrekin, S. A., Reeves, G. H., Kuntzsch, D., & Merritt, R. W. (2013). Litter decomposition, and associated invertebrate communities, in wetland ponds of the Copper River Delta, Alaska (USA). *Wetlands*, 33(6), 1151-1163.

Thilenius, J.F. (1995). Phytosociology and succession on earthquake-uplifted coastal wetlands, Copper River Delta, Alaska. Gen. Tech. Rep. PNWGTR-346. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 58 p.

Thorp, A. G., Jones, R. C., & Kelso, D. P. (1997). A comparison of water-column macroinvertebrate communities in beds of differing submersed aquatic vegetation in the tidal freshwater Potomac River. *Estuaries*, *20*(1), 86-95.

University of Alaska, Scenarios Network for Alaska and Arctic Planning. (2015). Community Charts. Retrieved (1/29/15) from www.snap.uaf.edu.

Van Duzor, R.G. (2011). Community structure and secondary production of aquatic macroinvertebrates in coastal wetland ponds of the west Copper River Delta, Alaska, following tectonic uplift. Master's Thesis, Loyola University Chicago.

Ward, J. V., & Stanford, J. A. (1982). Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology*, *27*(1), 97-117.

Wiggins, G. B. (1996). Larvae of the North American caddisfly genera (Trichoptera) (2nd ed., p. 457). Toronto: University of Toronto Press.

Whiles, M. R., & Goldowitz, B. S. (2005). Macroinvertebrate communities in central Platte River wetlands: patterns across a hydrologic gradient. *Wetlands*, *25*(2), 462 472.

Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*(1549), 2093-2106.

Wylie, D., Jackson, D. L., Menzel, W. P., & Bates, J. J. (2005). Trends in global cloud cover in two decades of HIRS observations. *Journal of Climate*, *18*(15), 3021 3031.

Yee, D. A., O’Regan, S. M., Wohlfahrt, B., & Vamosi, S. M. (2013). Variation in prey specific consumption rates and patterns of field co-occurrence for two larval predaceous diving beetles. *Hydrobiologia*, *718*(1), 17-25.

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