LOYOLA UNIVERSITY CHICAGO

LIFE HISTORIES, DIETS, AND SECONDARY PRODUCTION OF ODONATA ALONG A TEMPERATURE GRADIENT ON THE COPPER RIVER DELTA, ALASKA

A THESIS SUBMITTED TO
THE FACULTY OF THE GRADUATE SCHOOL
IN CANDIDACY FOR THE DEGREE OF
MASTER OF SCIENCE

PROGRAM IN BIOLOGY

BY
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DECEMBER 2014

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ACKNOWLEDGEMENTS

Although a thesis credits only one author, this work represents the contributions and support of countless individuals, institutions, and funding agencies. First and foremost, I owe immense gratitude to Dr. Martin Berg for tirelessly providing insight, mentorship, and a healthy sense of humor. I am incredibly lucky to have worked with him for so long, and to have had the opportunity to spend my field season on Alaska's Copper River Delta. I doubt that I will ever visit another place as beautiful as the delta, and it will always hold a place in my heart. Additionally, it's often easy to lose oneself in the minutiae of research, but my committee members have always helped to reinforce the importance of perspective. Thank you to Dr. Timothy Hoellein and Dr. John Kelly for asking the difficult questions; I am a stronger researcher for it.

To Chantel Caldwell: thank you for your hard work in the field and your excellent company in the lab. This project would have been a whole lot longer and much less fun without you. I would also like to thank Emily Campbell for her willingness to donate time and energy to this study, and for her love of the delta.

Thank you to Conrad and Sarah Zack for their continual support and friendship. There are few people who are kinder or more generous than Conrad and Sarah, and I am lucky to know them.

The Cordova Ranger District was indispensible to this study and

provided transportation, logistical support, sampling assistance, and funding. Special thanks to Luca Adelfio, Erin Cooper, Jason Fode, Ken Hodges, Tim Joyce, Deyna Kuntzsch, and Sean Meade for squeezing this research into an already busy summer field season. Additional funding was also provided by the National Fish and Wildlife Federation.

Finally, thank you to Gordon Reeves for his deep commitment to all aspects of research on the Copper River Delta.

To Megan: for your love, your patience, and your support.

What would the world be, once bereft
Of wet and of wildness? Let them be left,
O let them be left, wildness and wet;
Long live the weeds and the wilderness yet.

- Gerard Manley Hopkins (1881)

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ABSTRACT

Southcentral Alaska's Copper River Delta (CRD) is the largest contiguous coastal wetland on the west coast of North America, representing a vital network of aquatic and terrestrial habitats as well as a wealth of wildlife and fisheries resources. Coastal topography drives cold air masses from Alaska's Interior through the Copper River Canyon and these masses have a disproportionate impact on the east side of the delta. The resulting east-west temperature gradient provides an ideal backdrop for testing the effects of contrasting temperature regimes on aquatic insect communities in CRD ponds, in which dragonflies (Odonata: Epiprocta) and damselflies (Odonata: Zygoptera) are often apex predators.

To compare odonate life histories, secondary production, and diets in different temperature regimes, eight ponds were chosen from the east and west sides of the delta, divided evenly between two contrasting landscape types: outwash plain (OP) and uplifted marsh (UM). Water temperatures were coldest in OP ponds on the west delta and warmest in UM ponds on the west delta. Growing degree days (GDD) accumulated most rapidly in west UM ponds (16.4 GDD/day) and least rapidly in west OP ponds (12.1 GDD/day).

Five families of odonate taxa were collected and *Enallagma boreale* (Coenagrionidae) was the numerically dominant odonate taxon in 10 of the 16 sampled ponds, comprising 48.5% of all odonates collected during the study. *Leucorrhinia hudsonica* (Libellulidae) and *Aeshna juncea* (Aeshnidae) comprised 36.6% and 10.4% of collected odonates, respectively. Odonate densities were higher in west delta ponds than in east delta ponds, and 70.3% of the odonates collected over the course of the study were taken from UM ponds on the west delta. There were no significant differences in *A. juncea* or *E. boreale* densities or secondary production between pond types, but *L. hudsonica* densities and secondary production were significantly higher ($p<0.001$) in west delta UM ponds than in any other pond type.

A. juncea diets in west OP ponds were dominated by low-quality prey such as ostracods (Ostracoda), water mites (Hydrachnidae), and water boatmen (Corixidae). Midge larvae (Chironomidae) dominated *A. juncea* diets in all other pond types, occurring in 68% of foreguts. *A. juncea* diets containing *E. boreale* and *L. hudsonica* demonstrated intraguild predation, and cannibalism was evident in 6% of foreguts. Foreguts containing threespine stickleback (*Gasterosteus aculeatus*) revealed *A. juncea's* apex predator role in CRD ponds. The phenology of odonate emergence was not assessed due to insufficient numbers of collected exuviae, but it is likely that odonates emerge earliest in UM ponds on the west delta due to rapid degree day accumulation and high densities of prey items for consumption. This study may provide valuable insights into the potential impacts of climate change on coastal wetland ecosystems, especially the role of odonates as food resources for avian taxa that nest and breed on the CRD.

CHAPTER ONE

INTRODUCTION

Coastal wetland ecosystems are valuable natural resources, providing a suite of ecosystem services including carbon sequestration (Mcleod et al. 2011), shoreline stabilization (Gedan et al. 2010) and water filtration (Carter 1997). Additionally, coastal wetlands support high animal and plant diversity (Comer et al. 2005, Gopal et al. 2009) and play a pivotal role in the productivity of commercial and recreational fisheries (Pendleton 2008). Despite comprising only 4-6% of the earth's surface (Mitsch and Gosselink 2007), these ecosystems have considerable economic importance. Costanza et al. (1998) estimated that the aggregate value of services generated by wetlands throughout the world is approximately $4.9 trillion per year. Although among the most productive ecosystems on earth (Mitsch and Gosselink 2007), wetlands are increasingly threatened by anthropogenic impacts (Crossett et al. 2004). According to a recent report, wetlands in the continental United States were lost at an average rate of 80,000 acres a year between 2004-2009 (Dahl and Stedman 2013).

Aquatic insects in coastal wetland ecosystems are important food resources for many fish, songbirds, shorebirds, and waterfowl that use these ecosystems for breeding, nesting, or as a migratory stopping point (Crow 1971, Bromley and Roth 2003, Smith et al. 2004, McDade et al. 2011). Dragonflies (Odonata: Epiprocta) and damselflies (Odonata: Zygoptera) are especially vital food resources for avian taxa, both as nymphs during emergence and as aerial adults (Kennedy 1950, Corbet 1999, Loomis 2013, Orr 2013). Odonates are ecologically important not only as prey, but also as apex predators in aquatic systems lacking vertebrate taxa such as fish or amphibians (Batzer and Wissinger 1996). Odonates also have considerable value as indicators of ecosystem quality due to their trophic position, life cycles that encompass both aquatic and terrestrial habitats (Corbet 1999), and sensitivity to environmental changes or degradation (Westfall and May 1999; Hornung and Rice 2003; Lee-Foote and Rice-Hornung 2005). Furthermore, dragonflies and damselflies often serve as flagship species due to their charismatic nature and widespread public appeal (Hornung and Rice 2003).

The Copper River Delta (CRD), located in southcentral Alaska's Chugach National Forest, is the largest contiguous coastal wetland on the west coast of North America and encompasses 2800 km^2 of wetland habitat classified into tidal flats, floodplains, marshlands, and glacial outwash plains (Thilenius 1995). These areas are intersected by braided channels of the Copper River, glacial streams, and beaver sloughs. The CRD is replete with ponds and its hydrology is impacted by groundwater inputs, glacial meltwater, tidal fluctuations, and beavers. The CRD is classified as one of Alaska's three Key Coastal Wetlands (KCWs) and is a major focus of the United States Forest Service (USFS), representing a vital network of aquatic and terrestrial habitats as well as a wealth of wildlife and fisheries resources. The delta supports a diversity of animal life, large runs of five species of Pacific salmon, and is a critical stopover for an estimated 12 million migratory shorebirds during their annual spring migration along the Pacific Flyway (Alaska Department of Fish and Game 2014). Additionally, coastal ponds on the delta serve as the sole nesting and breeding sites for the threatened dusky Canada goose (*Branta canadensis occidentalis*) as well as providing nesting habitat and food resources for the IUCN red-listed rusty blackbird (*Euphagus carolinus*) (Alaska Department of Fish and Game 2012). A recent study found that over 90% of food items provisioned to CRD *E. carolinus* nestlings were newly emerged dragonfly nymphs from nearby ponds and sloughs (Loomis 2014).

The CRD is a study in contrasts. The east and west sides of the delta, i.e., east and west of the Copper River, differ greatly in vegetation and temperature regime, due in part to the movement of cool air over the Copper River. The Chugach Mountain range of south-central Alaska shields most of the coast from continental cold air masses, but the Copper River canyon breaches the Chugach Mountains and forms a corridor through which cold air currents flow along the Copper River and out to sea (Boggs 2000). These currents have a disproportionate impact on the east side of the delta, and mean air temperature declines substantially across the CRD as one moves from west to east (M. Berg, pers. comm.). Additionally, the east delta is characterized by sparser and lower growing vegetation than the west delta, and pond vegetation assemblages are less diverse than those on the west delta.

Tectonic uplift caused by the Good Friday earthquake of 1964 (Richter magnitude 9.2) introduced an additional layer of contrast to CRD ponds. The earthquake raised coastal regions by 2-3 meters (Thilenius 1995) and divided the CRD into two distinct landscape types: the elevated and more coastal uplifted marsh (UM), and the outwash plain (OP), which comprises unaffected inland areas. Hydrological dissimilarities between the OP and UM landscape types further contribute to temperature differences between CRD pond types (east OP, east UM, west OP, and west UM) and their impact on CRD odonates.

Few aquatic vertebrates occur in CRD ponds. Only one fish species, the threespine stickleback (*Gasterosteus aculeatus*), is common. Copper River Delta pond food webs are thus dominated by aquatic insect communities comprised of true flies (Diptera), caddisflies (Trichoptera), beetles (Coleoptera), and true bugs (Hemiptera), with dragonflies (Odonata: Epiprocta) and damselflies (Odonata: Zygoptera) serving as apex predators. Although aquatic insect communities on the west side of the CRD have been investigated (Schroer 2010, VanDuzor 2011, Loomis 2013, Tiegs 2013), the east side of the delta has not been well studied and little is known about the ponds and their aquatic insect communities. Furthermore, although the effects of temperature on odonate respiration, growth rates, life cycles, and foraging have been studied in a variety of laboratory settings and natural systems (Lutz 1968, Procter 1973, Ingram and Jenner 1973, Lutz 1974, Lawton 1971, Trottier 1971, Pickup and Thompson 1990, Krishnaraj and Pritchard 1995), the impact of temperature differences across the CRD on odonate nymphs is unknown. The CRD'S west-to-east temperature gradient and history of tectonic alteration provide an ideal backdrop for testing the effects of differing temperature regimes coupled with contrasting landscape types on odonate life histories, diets, and secondary production.

Study Questions

The objective of this study was to assess differences among CRD pond types (east OP, east UM, west OP, and west UM) in regard to pond physicochemical parameters as well as the densities, secondary production, maximum body size, and diets of conspecific odonate nymphs.

CHAPTER TWO

METHODS

Study Site and Sampling Regime

This study was conducted on the east and west sides of the Copper River Delta (CRD) located in southcentral Alaska (Fig. 1). The delta’s climate is characterized as cool maritime with mild wet summers and cool wet winters. Mean monthly temperatures range from -3 °C in January to 12 °C in July (Data from the Cordova Airport; Boggs 2000). Mean monthly precipitation ranges from 12.9 centimeters in June to 32.8 centimeters in September (Boggs 2000). The growing season lasts approximately 110 days from mid-May to mid-September (Boggs 2000).

The CRD landscape is dominated by outwash plains (OP) and uplifted marshes (UM), and ponds are numerous on both (Boggs 2000). The Good Friday earthquake of 1964 (Richter magnitude 9.2) uplifted substantial areas of the coastal CRD by 2-3 meters. Subtidal areas became intertidal, and intertidal areas became supertidal, with the consequent formation of large areas of uplifted freshwater marsh no longer under tidal influence (Thilenius 1995). The OP is situated further inland and was unaffected by the earthquake. Ponds in these regions are primarily fed by groundwater inputs. Dominant emergent vegetation types in CRD ponds include horse tail (*Equisetum* spp.), mare’s tail (*Hippuris* *vulgaris* L.), buckbean (*Menyathes trifoliata* L.), yellow pond lily (*Nuphar polysepalum* Engelm) and a variety of sedges (*Carex* spp.). These plant taxa helped to control for variables that could differ among ponds that vary in vegetation.

Sixteen ponds were selected for study across the CRD: eight on the west delta, and eight on the east delta (Fig. 1). Ponds were chosen using GIS maps and selected for size, presence of emergent vegetation, and accessibility. Four OP ponds and four UM ponds were selected in each delta area, resulting in four distinct pond type classifications: east OP, east UM, west OP, and west UM. All ponds were sampled bimonthly during the growing season from May through September 2011 for a total of nine sampling periods.

Pond Physicochemical Parameters

HOBO pendant temperature loggers (Onset Computer Corporation) were deployed in each pond. Individual loggers were attached to a 1.9 x 121.9 cm hardwood dowel hammered into the pond substrate. All loggers were suspended approximately 10 to 15 cm above the benthic substrates and temperature readings were recorded every two hours. Data were downloaded monthly using a HOBO U-DTW-1 Waterproof Shuttle (Onset Computer Corporation) and uploaded to a computer for analysis. Temperature data were used to calculate the accumulation of growing degree days (GDD) for each pond using the single triangle method (Roltsch et al. 1999) with a lower developmental threshold temperature of 0 °C.

On each sampling date, a YSI 556 MPS multiparameter meter was used to record temperature, specific conductance, total dissolved solids (TDS), salinity, dissolved oxygen (DO), pH, and oxygen reduction potential (ORP) in each pond. Readings were taken at three levels in each pond: at the water surface, mid-water column, and just above the benthic substrates. These three readings were used to calculate a mean for each pond for each sampling date. The approximate maximum depth of each pond was also recorded.

Benthic Sampling for Aquatic Macroinvertebrates

Aquatic invertebrates were sampled quantitatively from each pond to assess odonate densities, as well as the diversity and abundance of potential prey items. Aquatic invertebrates were sampled from within a 1 m^2 area delineated by a floating PVC frame. Samples were collected using a 250 µm D-frame net with a detachable bucket (Wildlife Supply Company (WildCo) Yulee, FL). The PVC frame was randomly placed into beds of dominant emergent vegetation. Dominant vegetation was determined by visual assessment, with dominant vegetation types representing a minimum 10% of the pond’s surface vegetation cover. A thirty-second sweep was performed throughout the boundary of the frame, from the water surface to the benthic substrates. Net contents were transferred to a 250 µm sieve to remove excess water, and large pieces of vegetation were rinsed to dislodge aquatic macroinvertebrates and discarded. Each sample was transferred to a labeled 30 x 35 cm bag made of 6 mil poly plastic for transport to the laboratory. In the laboratory, samples were preserved with 70% ethanol and sealed until they could be sorted and processed. The number of samples collected from each pond depended upon the number of dominant vegetation types present. Four replicate samples were taken from each vegetation type, and the total number of replicates collected from each pond ranged from 4-16 (1-4 vegetation types x 4 replicates/vegetation type).

Each benthic sample was washed in a 250 μm sieve under running water to remove large pieces of vegetation and detritus. Samples larger than 2 liters were split using a Folsom Plankton Splitter (Wildlife Supply Company). Insects with a body length ≥ 20 mm were removed prior to splitting (Waters 1969). Samples were then sorted under a dissecting microscope (Leica WILD MZ8) and macroinvertebrates were removed from plant material and detritus using forceps. Sorted material was placed in 20 mL scintillation vials (WHEATON) with 70% ethanol for later identification. Prior to any calculations, densities of all other taxa in split samples were multiplied by 2. Potential prey items were identified to genus using Merritt et al. (2008), Wiggins (1996; Trichoptera), and Larson el al. (2000; Dytiscidae). Odonates were identified to species using Merritt et al. (2008), Walker (1953) and Needham et al. (2014).

Secondary Production

Secondary production was calculated using the size-frequency method adjusted for the cohort production interval (CPI) (Hynes and Coleman 1968; Hamilton 1969; Waters 1977; Benke 1979, 1984). Secondary production of the odonate taxa *Aeshna juncea* (Aeshnidae), *Enallagma boreale* (Coenagrionidae), and *Leucorrhinia hudsonica* (Libellulidae) was calculated. The odonate taxa *Cordulia shurtleffi* (Corduliidae), *Lestes disjunctus* (Lestidae) and *Sympetrum danae* (Libellulidae) were excluded due to insufficient densities. Total body length measurements were recorded and individual masses for *A. juncea* and *E. boreale* were taken from length-mass regressions calculated by VanDuzor (2011). Individual mass values for *L. hudsonica* were calculated using the dry weight literature value in Benke et. al (1999) and converting to AFDM using dry weight x 0.9 in Waters (1977).

Cohort production intervals were determined by analyzing the size frequency distribution for each taxon. *E. boreale* and *L. hudsonica* were determined to have a CPI of 12 months. Due to low abundance, the CPI for *A. juncea* was estimated as 48 months using literature values (Walker 1953, Corbet 1999). Secondary production for these three taxa was calculated as mg AFDM/m^2/yr.

Diet Sampling

Quantitative collections of odonates were supplemented with qualitative collections to provide sufficient numbers of organisms for diet analysis. Qualitative collections involved sweeping areas of near-shore emergent vegetation using a 250 μm D-frame net. Sampling continued until at least five large-bodied (≥15 mm long) odonates were collected. Specimens were stored individually in resealable bags to account for regurgitation of gut contents. In the laboratory, odonates and bag contents were preserved with 70% ethanol, labeled, and sealed into individual 15 x 20 cm bags made of 6 mil poly plastic until dissection and analysis of gut contents could be performed.

In the laboratory, odonate nymphs were dissected and the foregut removed. Full guts were further dissected to remove gut tissue, leaving only gut contents. Foregut contents were preserved with 70% ethanol and stored in 0.5 ml PCR tubes (MIDSCI, St. Louis, MO, USA). Analysis was performed using Image-Pro Premier (Media Cybernetics Inc., Rockville, MD). Prey items were identified to family level when possible and counted. Additionally, area measurements were taken to calculate the relative proportion of prey items in the diets by volume. Odonates are swallowers and prey items found in the foregut have been macerated by the mandibles (Corbet 1999). Areal measurements alone may underestimate the importance of small prey items with limited sclerotization, such as midge larvae (Chironomidae). Conversely, prey counts may underestimate the contribution of larger prey items such as caddisfly larvae (Trichoptera), which appear less frequently in the diet, but likely represent a higher quality food resource (Cummins and Wuycheck 1971). Both areal measurements and prey counts were employed to provide a more complete picture of odonate diets in CRD ponds.

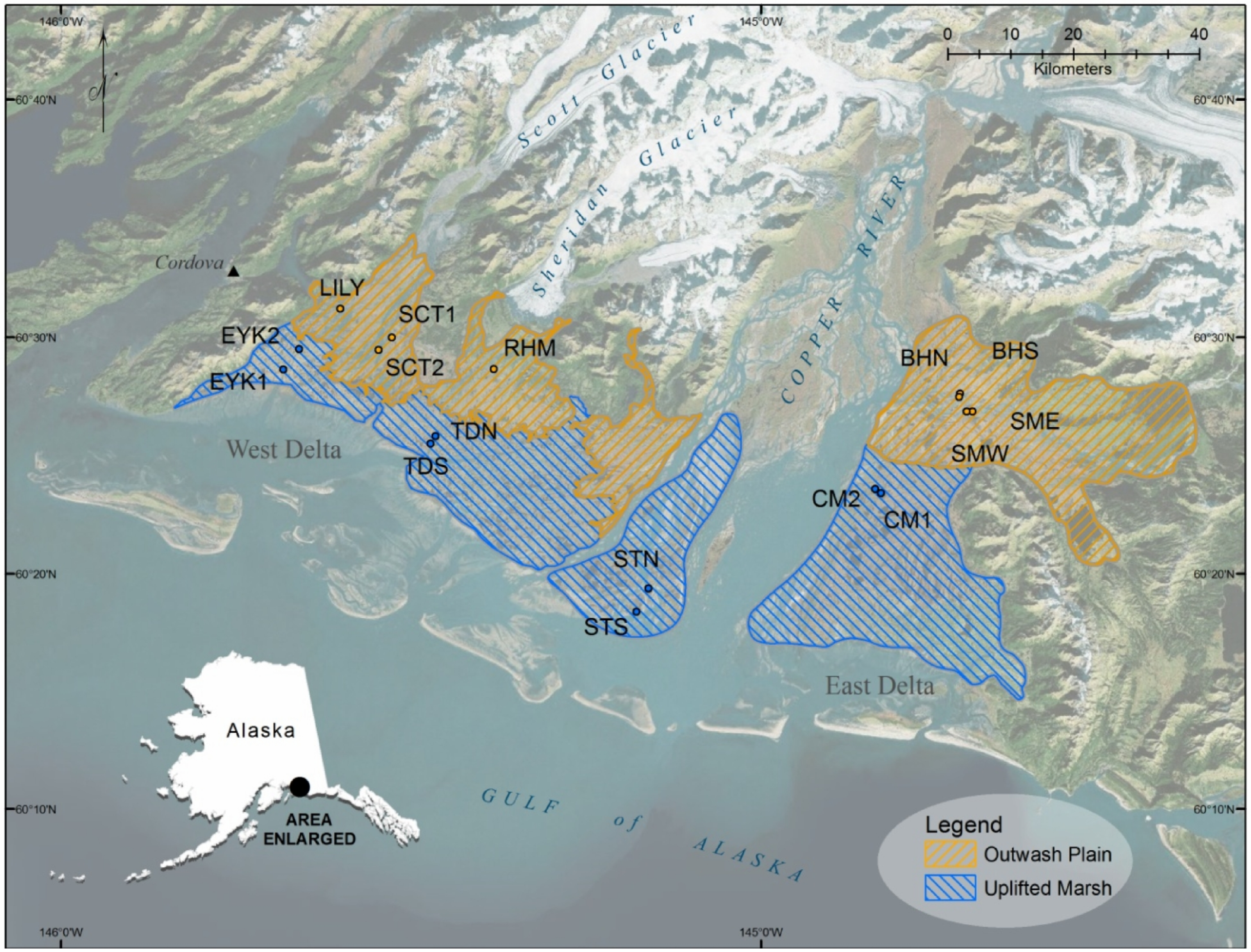
Exuviae Collection

To assess the phenology of odonate emergence from CRD ponds, odonate exuviae were qualitatively collected from emergent vegetation at each pond. Collection was restricted to the Epiprocta, as the small size of Zygopteran exuviae increases the chance that they will be overlooked. Approximately ten minutes were spent on exuviae surveys; all exuviae were stored in airtight 20 mL scintillation vials (WHEATON) and returned to the lab for analysis. Species-level identification, length measurement (in mm) and sex were determined for each specimen.

Statistical Analysis

Pond physicochemical parameters, odonate densities, secondary production, and maximum body size were compared among pond types using one-way ANOVA followed by Tukey's multiple comparison test.

Figure 1. Sampling sites across the Copper River Delta, May-September 2011.



BHN = Beaver Hole North; BHS = Beaver Hole South; CM1 = Clear Martin #1; CM2 = Clear Martin #2; EYK1 = Eyak Uplift #1; EYK2 = Eyak Uplift #2; LILY = Lily Pond; RHM = Rich Hate Me; SCT1 = Scott Outwash #1; SCT2 = Scott Outwash #2; SME = Smiley East; SMW = Smiley West; STN = Storey North; STS = Storey South; TDN = Tiedeman North; TDS = Tiedeman South

CHAPTER THREE

RESULTS

Pond Physicochemical Parameters

Physical and chemical properties of Copper River Delta (CRD) ponds were recorded from May-September 2011. Mean daily temperatures in east delta (ED) ponds ranged from 7 °C in May to 18.7 °C in late July (Fig. 2), whereas temperatures in west delta (WD) ponds ranged from 8.6 °C in May to 19.7 °C in late July (Fig. 2). Differences in pond size, depth, vegetation cover, and landscape type influenced temperature regimes of CRD ponds, with greater differences in mean daily temperature associated with landscape type (outwash plain (OP) vs. uplifted marsh (UM)) than delta region (east delta vs. west delta), particularly on the west delta. UM ponds were warmer than OP ponds on both the east and west delta. On average, mean daily temperature in west UM ponds was generally 4 °C warmer than in west OP ponds, and mean daily temperature in east UM ponds was 2.7 °C warmer than in east OP ponds (Fig. 2). Overall, mean temperature over the course of the sampling season was warmest in west UM ponds (16.1°C), coldest in west OP ponds (11.9 °C), and intermediate in east UM and OP ponds (15.1 and 12.3 °C, respectively).

Temperature differences in CRD ponds influenced the accumulation of growing degree days (GDD) across the delta (Fig. 3). Between May and August, GDD accumulated most rapidly in west UM ponds (16.4 GDD/day), and least rapidly in west OP ponds (12.1 GDD/day). Consequently, total accumulated degree days were lowest in west OP ponds (1,075 GDD) and highest in west UM ponds (1,455 GDD) by the end of August 2011 (Fig. 3).

Mean dissolved oxygen (DO) concentration in west OP ponds was significantly lower than all other pond types, and there were no significant differences in mean DO between OP and UM ponds on the east delta (Table 1). Mean pH in east UM ponds was significantly higher than all other pond types (Table 1). Mean total dissolved solids (TDS), salinity, and conductivity were highest in west OP ponds, lowest in west UM ponds and intermediate in east delta ponds. East delta UM ponds exhibited higher mean TDS, salinity, and conductivity than east OP ponds (Table 1). Remaining water quality data were highly variable with no obvious patterns between delta or pond type.

Figure 2. Mean daily temperature (°C) in Copper River Delta ponds, May-August 2011. Ponds are grouped by delta and landscape type.

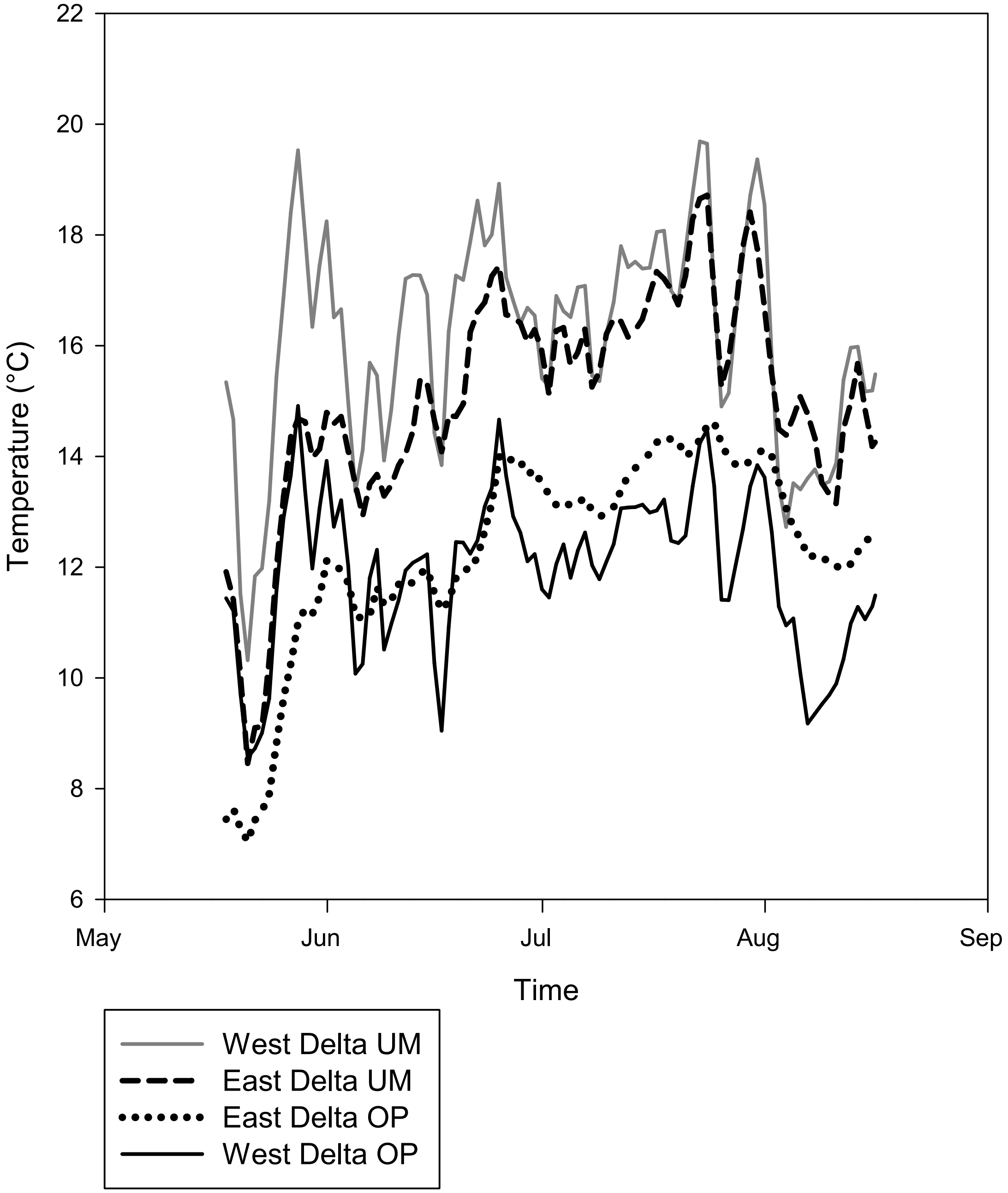


Figure 3. Growing degree day (GDD) accumulation in Copper River Delta ponds, Alaska, May-August 2011. Ponds are grouped by delta and landscape type.

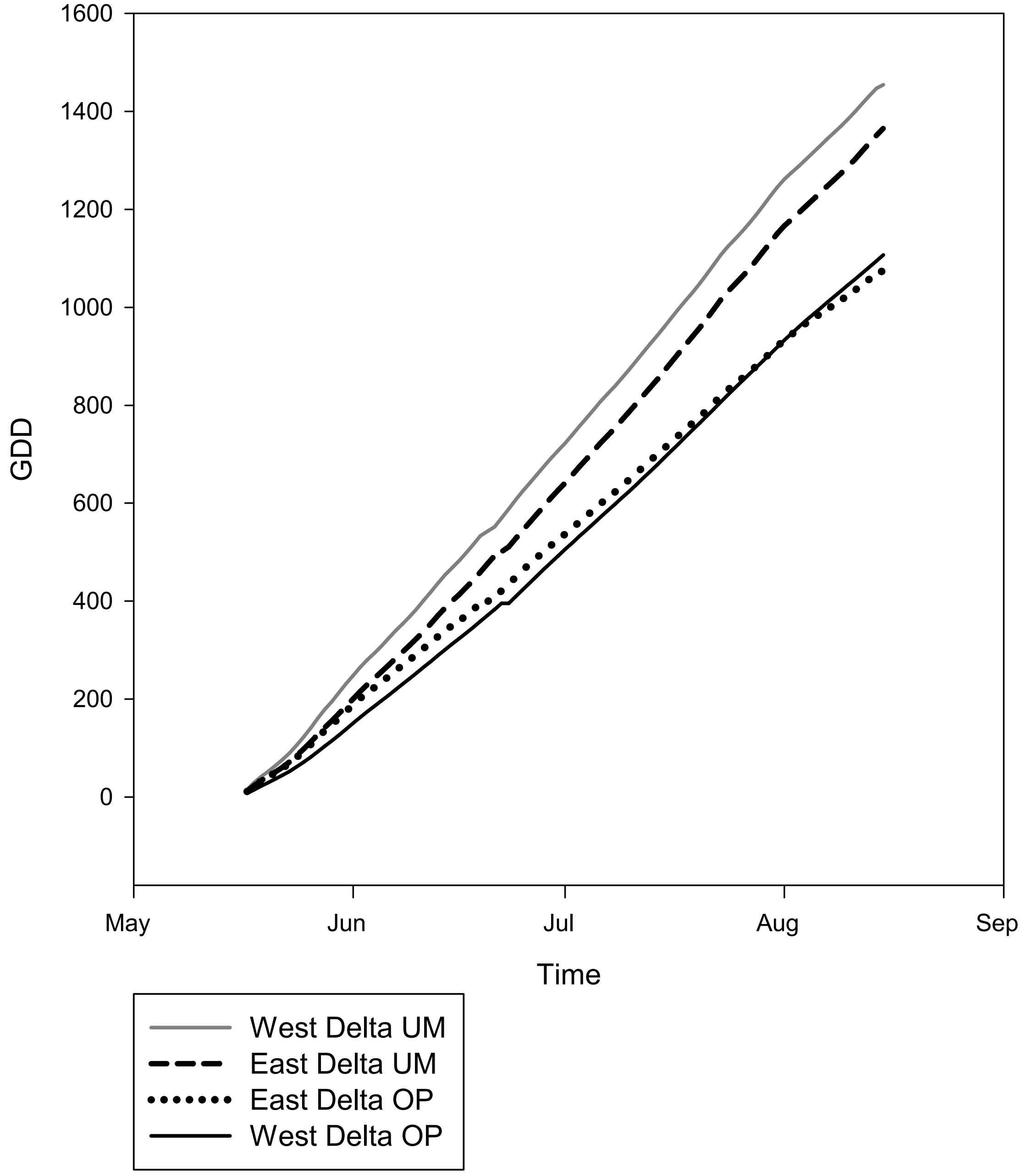


Table 1. Physicochemical parameters of sixteen study ponds across the Copper River Delta, AK (May-September 2011). Pond name abbreviations taken from Figure 1.

	East Delta								West Delta							
	Outwash Plain				Uplifted Marsh				Outwash Plain				Uplifted Marsh			
	BHN	**BHS**	**SME**	**SMW**	**CM1**	**CM2**	**STN**	**STS**	**LILY**	**RHM**	**SCT1**	**SCT2**	**EYK1**	**EYK2**	**TDN**	**TDS**
Maximum Depth- cm	90	120	60	90	50	60	50	60	70	60	75	90	50	60	70	70
Minimum Conductivity- mS/cm	0.02	0.02	0.02	0.03	0.04	0.04	0.04	0.07	0.05	0.02	0.06	0.04	0.01	0.01	0.01	0.01
Maximum Conductivity- mS/cm	0.05	0.06	0.04	0.06	0.07	0.09	0.07	0.10	0.21	0.07	0.12	0.09	0.01	0.02	0.02	0.02
Mean Conductivity- mS/cm	0.03	0.03	0.03	0.04	0.06	0.05	0.06	0.09	0.12	0.06	0.09	0.05	0.01	0.02	0.01	0.01
MEAN BY POND TYPE	**0.03 (±0.002)^{a}**				**0.06 (±0.003)^{b}**				**0.08 (±0.007)^{b}**				**0.01 (±0.0006)^{c}**			
Minimum TDS- g/L	0.01	0.02	0.02	0.02	0.03	0.02	0.03	0.05	0.03	0.02	0.04	0.03	0.00	0.01	0.01	0.01
Maximum TDS- g/L	0.05	0.04	0.02	0.04	0.05	0.06	0.15	0.07	0.14	0.05	0.08	0.06	0.01	0.02	0.04	0.03
Mean TDS- g/L	0.02	0.02	0.02	0.02	0.04	0.03	0.05	0.06	0.08	0.04	0.06	0.04	0.01	0.01	0.01	0.01
MEAN BY POND TYPE	**0.02 (±0.001)^{a}**				**0.04 (±0.003)^{b}**				**0.05 (±0.005)^{b}**				**0.01 (±0.001)^{a}**			
Minimum Salinity- ppt	0.00	0.01	0.01	0.01	0.02	0.02	0.02	0.03	0.02	0.01	0.02	0.02	0.00	0.01	0.00	0.00
Maximum Salinity- ppt	0.02	0.02	0.02	0.02	0.04	0.04	0.03	0.05	0.10	0.04	0.06	0.04	0.01	0.01	0.01	0.01
Mean Salinity- ppt	0.01	0.01	0.01	0.02	0.03	0.02	0.03	0.04	0.06	0.03	0.04	0.02	0.00	0.01	0.01	0.00
MEAN BY POND TYPE	**0.014 (±0.0008)^{a}**				**0.03 (±0.001)^{b}**				**0.04 (±0.003)^{b}**				**0.005 (±0.0009)^{c}**			
Minimum DO- mg/L	6.15	3.79	6.54	6.37	7.87	2.54	6.89	8.72	2.62	5.27	3.29	5.73	5.36	5.65	7.26	8.52
Maximum DO- mg/L	8.29	10.63	11.87	11.58	11.24	5.94	10.08	13.43	9.48	9.60	5.72	10.57	11.56	11.36	9.88	10.83
Mean DO- mg/L	6.97	6.13	9.17	9.47	9.08	4.18	8.35	10.34	5.44	7.50	4.51	8.41	8.97	7.74	8.57	9.62
MEAN BY POND TYPE	**7.98 (±0.39)^{a}**				**7.98 (±0.44)^{a}**				**6.46 (±0.39)^{b}**				**8.77 (±0.30)^{a}**			
Minimum pH	4.69	4.69	5.34	4.91	6.77	5.67	7.22	7.17	6.25	5.85	5.65	6.54	5.11	5.10	5.74	5.69
Maximum pH	6.37	6.45	6.64	7.07	7.63	6.48	8.31	8.81	7.08	7.24	6.82	6.95	7.93	6.81	6.94	6.71
Mean pH	5.71	5.90	6.22	6.49	7.12	5.99	7.56	7.96	6.63	6.47	6.45	6.72	6.34	6.06	6.30	6.17
MEAN BY POND TYPE	**6.09 (±0.11)^{a}**				**7.16 (±0.14)^{b}**				**6.57 (±0.05)^{a,c}**				**6.22 (±0.10)^{a}**			
Minimum ORP- mV	26.70	-7.73	56.37	-58.43	-33.40	43.40	9.03	-28.77	-113.67	-74.20	-42.10	-57.43	75.13	112.17	27.37	74.17
Maximum ORP- mV	168.43	135.23	172.50	203.60	105.10	131.50	107.67	66.10	79.23	135.73	81.30	173.77	197.80	190.90	174.07	184.03
Mean ORP- mV	130.63	85.49	132.01	79.92	34.64	97.44	59.90	19.38	-1.58	56.77	7.00	55.27	141.59	144.73	112.39	128.97
MEAN BY POND TYPE	**106.19 (±10.06)^{a}**				**52.84 (±7.47)^{b}**				**29.26 (±10.64)^{b}**				**130.51 (±7.62)^{a}**			
Growing Degree Days - GDD (May-August)	982	1040.2	1299.1	*	1452.7	896.42	1554.5	1558	1307.56	967.47	826.2	1198.87	1461.24	1405.16	1496.49	1455.54

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[a] - Statistically significant (One Way ANOVA, p<0.05, df = 134) differences for each parameter are denoted by superscript letters

* - Temperature readings were not recorded due to loss of temperature logger.

Odonate Taxa

A total of 408 benthic macroinvertebrate samples were collected from May-September 2011 and all Odonata were identified to the species level. Five families of odonates were collected, totaling 1459 individuals (Table 2). *Enallagma boreale* (Zygoptera: Coenagrionidae) was the numerically dominant odonate taxon, comprising 48.5% of all odonates collected during the study, followed by *Leucorrhinia hudsonica* (Epiprocta: Libellulidae) (36.6%) and *Aeshna juncea* (Epiprocta: Aeshnidae) (10.4%). *Cordulia shurtleffi* (Epiprocta: Corduliidae), *Sympetrum danae* (Epiprocta: Libellulidae), and *Lestes disjunctus* (Zygoptera: Lestidae) were collected less frequently and comprised the remaining 5% (Table 2). Odonate assemblages in 10 of the 16 ponds were numerically dominated by *E. boreale*, which comprised 34-84% of odonate taxa collected from each pond (Table 2). Exceptions were CM2 (east UM) and SCT1 (west OP), with odonate assemblages numerically dominated by *A. juncea*, and EYK2 (west UM), RHM (west OP), and TDS (west UM), which were dominated by *L. hudsonica*.

With the exception of *L. disjunctus*, odonate densities were higher in west delta ponds than in east delta ponds. Furthermore, densities were greatest in UM ponds on the west delta. Of the 1459 total odonates collected, 70.3% were collected from west UM ponds (Table 2), and was strongly influenced by odonate densities in EYK1. Densities of *E. boreale* and *L. hudsonica* in EYK1 were very high and accounted for 94.6% of all odonates collected in the pond and 47.7% of all odonates collected from west delta UM ponds (Table 2).

Densities and Secondary Production

Of the six odonate taxa collected from CRD ponds, only *A. juncea*, E. *boreale*, and *L. hudsonica* were collected in densities sufficient for estimating secondary production. Densities and secondary production estimates varied greatly among ponds (Table 3).

A. juncea was collected in all but one pond, and densities were generally low (0.06-0.94 individuals/m^2) (Fig. 4, Table 3). Mean density and secondary production of *A. juncea* were similar between the east and west delta, and although mean secondary production was lowest in OP ponds on the west delta, high variation among ponds precluded clear interpretation (Fig. 5, Table 3). Secondary production of *A. juncea* was highest in BHS (east OP: 28.24 mg AFDM/m^2/y), despite lower densities than in CM2 (east UM) and TDN (west UM) (Table 3).

E. boreale was collected in all but three ponds, and densities were low (>1-6.5/m^2) (Fig. 4, Table 3). Although mean density and secondary production of *E. boreale* were similar in both delta regions, there was a striking difference in mean secondary production between OP and UM ponds on the west delta (Fig. 5, Table 3). Mean secondary production of *E. boreale* in west delta UM ponds was 17-fold greater in west delta OP ponds (Table 3). This difference was primarily due to EYK1, a west delta UM pond, which not only had the highest density (6.46 individuals/m^2), but also the highest secondary production (46.29 mg AFDM/m2/y) of *E. boreale*. Low secondary production of *E. boreale* in west OP ponds was likely due to low densities.

L. hudsonica densities were significantly higher in west delta ponds ($p < 0.01$), resulting in higher mean secondary production (26.4 ± 11.4 mg AFDM/m^2/y) than in east delta ponds (1.56 ± 0.6 mg AFDM/m^2/y) (Fig. 5, Table 3). This trend was driven by the UM ponds, in which 90.3% of all west delta *L. hudsonica* were collected (Table 2). EYK1 had nearly twice the secondary production (91.2 mg AFDM/m2/yr) of *L. hudsonica* than the pond with the next highest value (EYK2: 49.7 mg AFDM/m2/yr) (Table 3). *Leucorrhinia hudsonica* production was lowest in OP ponds on the east delta (0-3.8 mg AFDM/m^2/yr), and highest in UM ponds on the west delta (21.4-91.2 mg AFDM/m^2/yr) (Fig. 5, Table 3).

Odonate Maximum Body Size

Odonate body length data from benthic and diet samples were combined to provide sufficient numbers of specimens, particularly in ponds with low odonate densities. Only *A. juncea*, *E. boreale*, and *L. hudsonica* were collected in densities sufficient for maximum body size comparisons. Mean maximum body length for all three taxa was lowest in OP ponds on the west delta, although differences in mean maximum body length among the four pond types were not statistically significant (Fig. 6, Table 3). *A. juncea* and E. *boreale* reached the largest sizes in east OP ponds, whereas *L. hudsonica* were largest in west UM ponds (Fig. 6, Table 3). Mean maximum body length was greater on the east delta than the west delta for all major odonate taxa except for *L. hudsonica*, although these differences were not statistically significant (Fig. 6, Table 3).

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Table 2. Odonate taxa collected from Copper River Delta ponds, May-September 2011. Percentages calculated by pond, delta area, and pond type. Pond name abbreviations taken from Figure 1.

			Suborder Epiprocta				**Suborder Zygoptera**	
		Total	*Aeshna juncea*	*Cordulia shurtleffi*	*Leucorrhinia hudsonica*	*Sympetrum danae*	*Enallagma boreale*	*Lestes disjunctus*
East Delta Ponds	BHN	19	1 (5.26%)	2 (10.53%)	0	0	16 (84.21%)	0
	BHS	43	10 (23.26%)	1 (2.33%)	2 (4.65%)	0	30 (69.7%)	0
	SME	0	0	0	0	0	0	0
	SMW	46	2 (4.35%)	8 (17.39%)	6 (13.04%)	0	30 (65.22%)	0
	CM1	37	2 (5.41%)	13 (35.14%)	2 (5.41%)	0	20 (54.05%)	0
	CM2	26	17 (65.38%)	1 (3.85%)	5 (19.23%)	0	3 (11.54%)	0
	STN	39	9 (23.08%)	0	2 (5.13%)	0	27 (69.23%)	1 (2.56%)
	STS	106	12 (11.32%)	0	2 (1.89%)	0	86 (81.13%)	6 (5.66%)
West Delta Ponds	LILY	32	10 (31.25%)	5 (15.63%)	6 (18.75%)	0	11 (34.38%)	0
	RHM	34	3 (8.82%)	4 (11.76%)	27 (79.41%)	0	0	0
	SCT1	8	8 (100%)	0	0	0	0	0
	SCT2	44	7 (15.91%)	0	0	0	37 (84.09%)	0
	EYK1	517	16 (3.09%)	10 (1.93%)	234 (45.26%)	2 (0.39%)	255 (49.32%)	0
	EYK2	164	13 (7.93%)	9 (5.49%)	102 (62.2%)	0	39 (23.78%)	1 (0.61%)
	TDN	245	29 (11.84%)	2 (0.82%)	87 (35.51%)	0	127 (51.84%)	0
	TDS	99	13 (13.13%)	0	59 (59.6%)	0	27 (27.27%)	0
Delta	ED	316	53 (16.78%)	25 (7.91%)	19 (6.01%)	0	212 (67.1%)	7 (2.22%)
	WD	1143	99 (8.66%)	30 (2.62%)	515 (45.06%)	2 (>1%)	496 (43.39%)	1 (>1%)
Pond Type	ED_OP	108	13 (12.04%)	11 (10.58%)	8 (7.69%)	0	76 (73.08%)	0
	ED_UM	208	40 (19.23%)	14 (6.73%)	11 (5.29%)	0	136 (65.38%)	7 (3.37%)
	WD_OP	118	28 (23.73%)	9 (7.63%)	33 (30.56%)	0	48 (40.68%)	0
	WD_UM	1025	71 (6.93%)	21 (2.05%)	482 (47.02%)	2 (>1%)	448 (43.70%)	1 (>1%)
Total		1459	152 (10.4%)	55 (3.77%)	534 (36.6%)	2 (0.14%)	708 (48.53%)	8 (0.55%)

Table 3. Cohort production intervals (CPI), annual secondary production (P- mg AFDM/m^2), mean densities (#/m^2), and maximum body length (mm) of three odonate taxa in Copper River Delta ponds, May-September 2011. Mean secondary production, densities and maximum body lengths are provided for delta area and pond type with accompanying standard error in parentheses. Pond name abbreviations taken from Figure 1.

		Aeshna juncea			***Enallagma boreale***			***Leucorrhinia hudsonica***		
	CPI (months)	(48)			(12)			(12)		
		Density	P	Max Length	Density	P	Max Length	Density	P	Max Length
East Delta Ponds	BHN	0.06	0.10	48	1.94	14.81	23	0.00	0.00	19
	BHS	0.63	28.24	50	1.00	20.31	22	0.13	0.40	5
	SME	0.00	0.00	46	0.00	0.00	*	0.00	0.00	*
	SMW	0.11	1.28	50	1.67	17.95	27	0.33	3.84	19
	CM1	0.08	0.38	40	0.67	4.82	20	0.08	1.10	9
	CM2	0.94	22.41	50	0.17	0.77	19	0.28	4.30	16
	STN	0.50	7.62	49	1.50	22.52	22	0.11	1.73	19
	STS	0.39	7.73	53	2.39	33.33	22	0.06	1.08	15
West Delta Ponds	LILY	0.50	8.07	49	0.31	1.90	17	0.17	0.88	7
	RHM	0.08	0.18	37	0.00	0.00	*	0.75	9.76	18
	SCT1	0.44	12.04	47	0.00	0.00	*	0.00	0.00	*
	SCT2	0.19	1.53	49	0.96	4.05	19	0.00	0.00	*
	EYK1	0.38	1.57	44	6.46	46.29	22	5.97	91.18	20
	EYK2	0.58	13.18	48	1.47	11.50	19	3.94	49.72	19
	TDN	0.81	14.15	48	3.67	33.35	25	2.43	21.41	20
	TDS	0.53	3.51	50	0.86	10.69	21	2.39	38.25	18
Mean by Delta	ED	0.34 (±0.12)^a	7.62 (±3.89)^a	48.25 (±1.37)^a	1.17 (±0.30)^a	14.31 (±4.13)^a	22.14 (±0.96)^a	0.12 (±0.04)^a	1.56 (±0.59)^a	14.57 (±2.09)^a
	WD	0.44 (±0.08)^a	6.78 (±2.04)^a	46.5 (±1.5)^a	1.72 (±0.80)^a	13.47 (±6.08)^a	20.5 (±1.15)^a	1.96 (±0.77)^b	26.40 (±11.36)^b	17 (±2.03)^a
Mean by Pond Type	E OP	0.20 (±0.15)^a	7.41 (±6.95)^a	48.5 (±0.96)^a	1.15 (±0.43)^a	13.27 (±4.56)^a	24.00 (±1.53)^a	0.12 (±0.08)^a	1.06 (±0.93)^a	14.33 (±4.67)^a
	E UM	0.48 (±0.18)^a	9.54 (±4.62)^a	48 (±2.80)^a	1.18 (±0.49)^a	15.36 (±7.63)^a	20.75 (±0.75)^a	0.13 (±0.05)^a	2.05 (±0.77)^a	14.75 (±2.10)^a
	W OP	0.30 (±0.10)^a	5.46 (±2.79)^a	45.5 (±2.87)^a	0.32 (±0.23)^a	1.49 (±0.96)^a	18 (±1.00)^a	0.23 (±0.18)^a	2.66 (±2.37)^a	12.5 (±5.50)^a
	W UM	0.58 (±0.09)^a	8.10 (±3.24)^a	47.5 (±1.26)^a	3.12 (±1.27)^a	25.46 (±8.70)^a	21.75 (±1.25)^a	3.68 (±0.85)^b	50.14 (±14.86)^b	19.25 (±0.48)^a

*- Taxon not collected

^{a}- Statistically significant differences (One Way ANOVA, $p<0.05$, df = 15) denoted with superscript letters

Figure 4. Mean densities of three odonate taxa in Copper River Delta Ponds, Alaska, May-September 2011. Bars denote standard error.

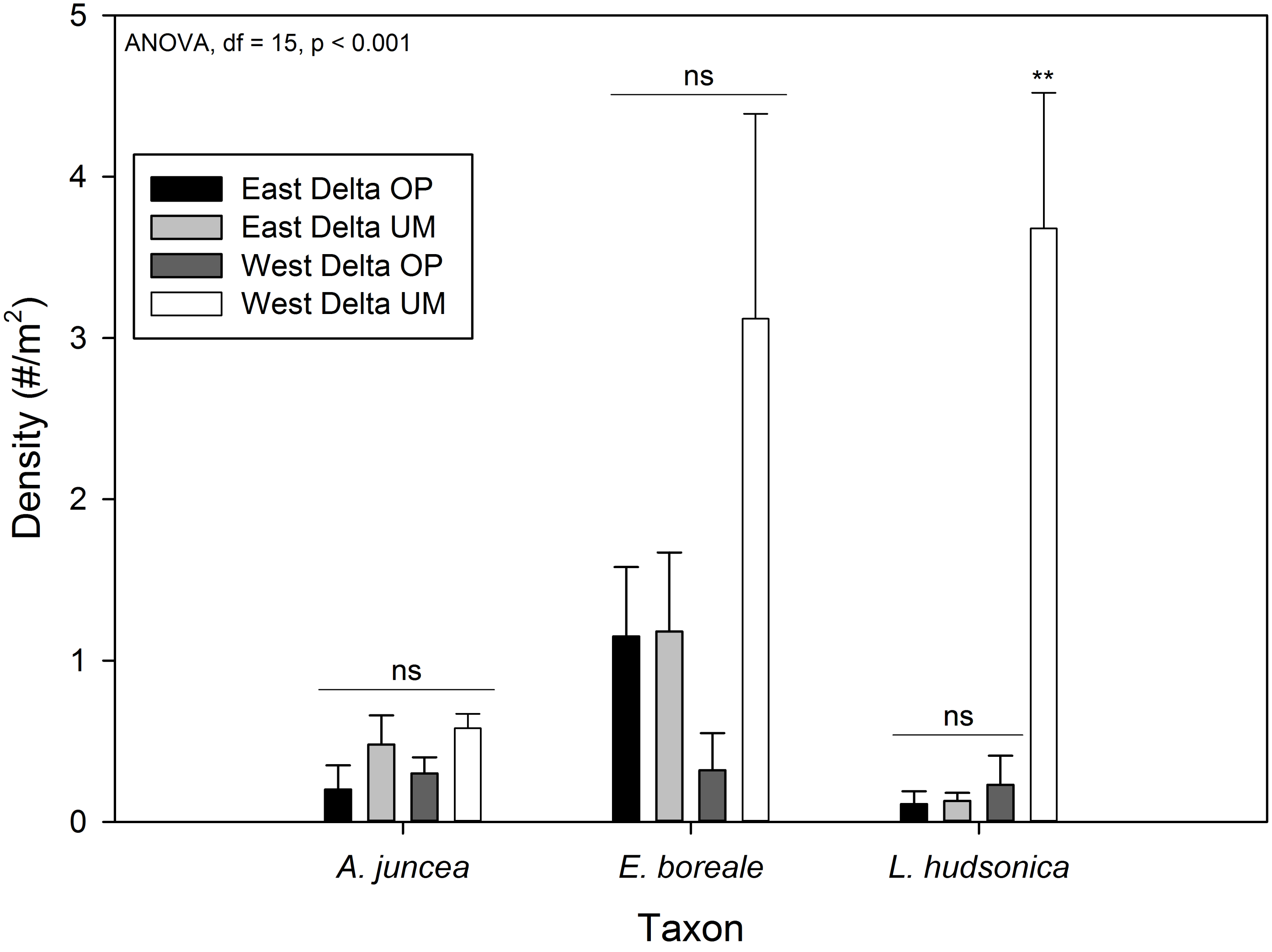


Figure 5. Mean secondary production of three odonate taxa in Copper River Delta Ponds, Alaska, May-September 2011. Bars denote standard error.

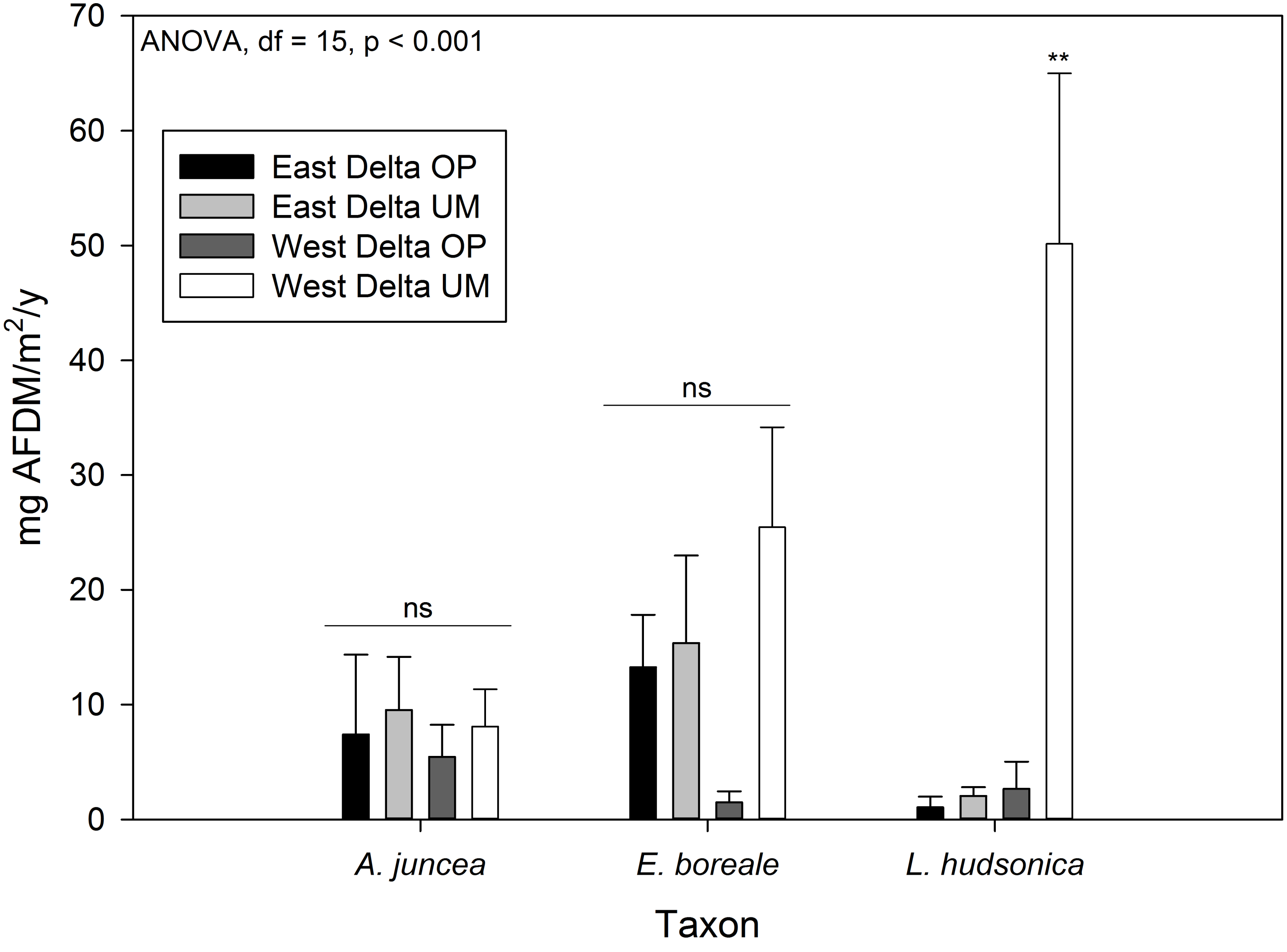
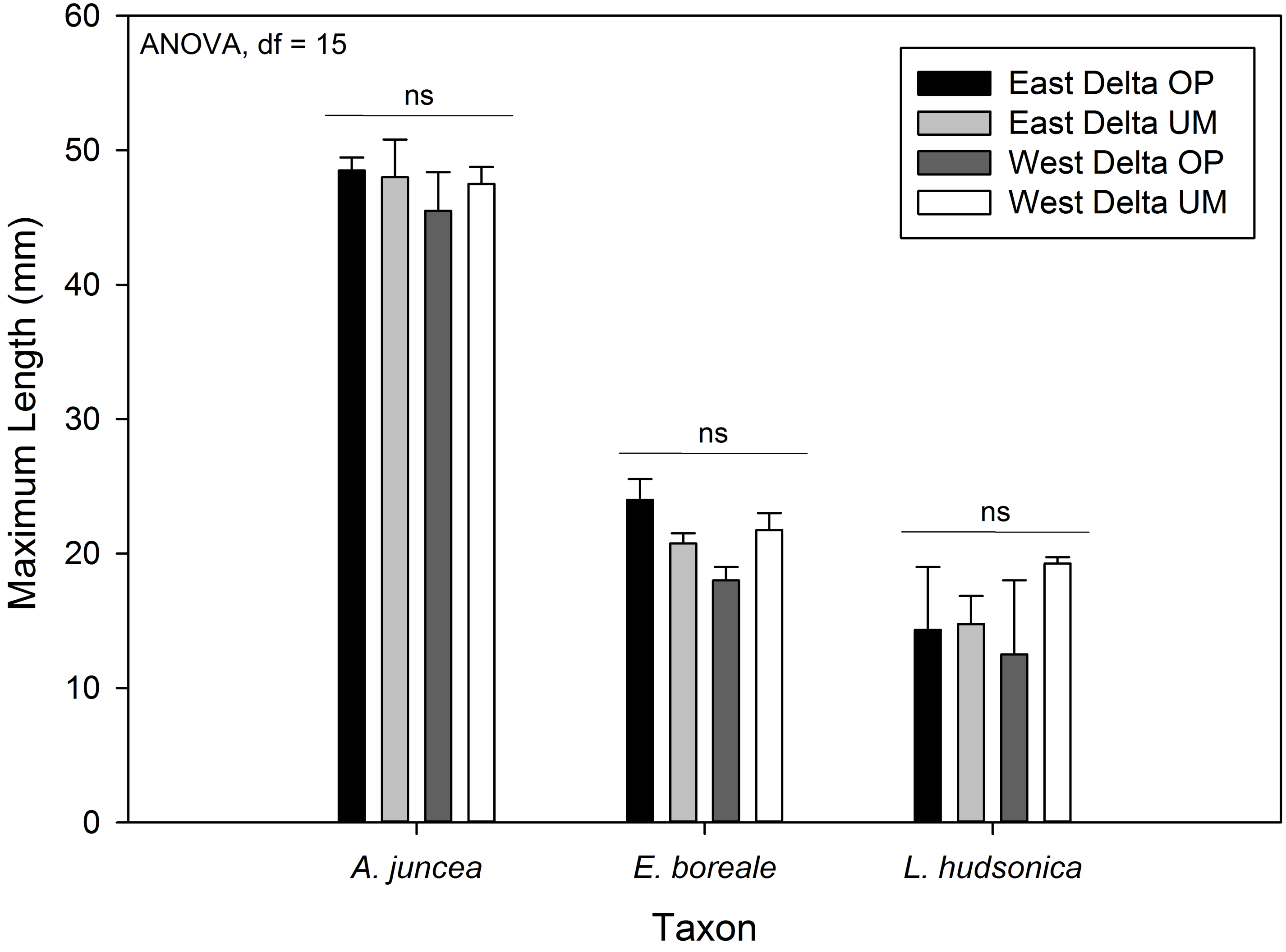


Figure 6. Mean maximum length of three odonate taxa in Copper River Delta ponds, May-September 2011. Bars denote standard error.



Diet Analysis

A total of 167 *A. juncea* foreguts contained sufficient material for diet analysis. Twenty-eight prey families were found; 20 aquatic insect taxa and 8 non-insect taxa (Tables 4A and 4B). Gut content data were pooled by pond type, and prey families were grouped into higher taxonomic group categories for analysis (Tables 4A and 4B). *A. juncea* diets were evaluated over the length of the study and on a monthly basis.

Aeshna juncea diets were highly variable on a temporal scale. Diets from east OP specimens were numerically dominated by dipterans early in summer, but shifted to hemipterans and other odonates in August (Fig. 10A). Diets of east UM *A. juncea* were also dominated by dipterans early in the summer, but contained terrestrial prey items in June (Fig. 8A) and high numbers of crustaceans in September (Fig. 11A). Diets of *A. juncea* from east UM ponds were highly diverse in August and consisted of 9 prey families (Fig. 10A).

Early season west OP diets were dominated by crustaceans such as ostracods, and chironomids were not ingested as extensively as in other pond types until June (Fig. 8A). The occurrence of chironomids in diets of west OP *A. juncea* decreased in July when hemipterans became the numerically dominant prey item (Fig. 9A). *Aeshna juncea* diets in west UM diets were numerically dominated by dipterans during the entire summer (Figs. 7A-11A). Trichopterans comprised <20% of the prey items consumed by *A. juncea* in west UM ponds until September, when their contribution rose to about 33% of all prey items consumed (Fig. 11A).

Analysis of food items on an areal basis provided a slightly different picture of *A. juncea* diets. Prey families whose numerical contributions to diets were modest, primarily trichopterans and hemipterans, represented large areal percentages of foregut contents. Conversely, small prey items such as chironomid larvae, hydrachnid mites and ostracods contributed little to the diets in terms of area despite being present in high numbers.

According to overall prey count analysis, dipterans, primarily chironomid larvae, were the numerically dominant prey item ingested by *A. juncea* in all pond types except for west OP ponds, comprising 65-71% of all consumed prey (Fig. 12A). In contrast, diets in west OP ponds were numerically dominated by crustaceans such as ostracods, which accounted for 43% of consumed prey during the sampling period (Fig. 12A). Hemiptera and Coleoptera were consumed most frequently in west OP ponds, where they comprised 13% and 7% of consumed prey, respectively (Fig. 12A).

By overall area analysis, dipterans also comprised the largest percentage of *A. juncea* gut contents in east delta ponds, accounting for 27-33% of food items by area (Fig. 12B). Diets in west UM ponds were dominated by trichopterans (37%) and odonates (30%) (Fig. 12B). *Aeshna juncea* diets in west OP ponds were dominated by hemipterans (39%) and coleopterans (21%) (Fig. 12B). Threespine stickleback (*Gasterosteus aculeatus*) were consumed in all pond types except for east OP, but were a minor component of *A. juncea* diets (1.5-6% of total food item area) (Fig. 12B).

Prey Density

Mean densites of six aquatic insect families commonly found in *A. juncea* foreguts were calculated in eight CRD ponds, May-September 2011. Data were pooled by pond type. Overall insect prey densities were significantly higher in west UM and east OP ponds than in any other pond type (Table 6). In west UM ponds, this trend was primarily due to chironomids (440.7 ± 39.8 individuals/m^2), with densities significantly higher than in any other pond type and nearly 1.5 times higher than the pond type with the next highest mean chironomid density (east OP: 268.2 ± 46.2 individuals/m^2). In east OP ponds, this trend was primarily driven by high corixid densities (24.9 ± 5.3 individuals/m^2), which were over 2 times higher than the densities in the pond type with the next highest mean corixid density (east UM: 9.4 ± 1.8 individuals/m^2). Trichopteran densities tended to be highest in west UM ponds, although mean Phryganeidae density was highest in east UM ponds (Table 6). Mean corixid densities were highest in east delta ponds, whereas mean dytiscid densities were highest on the west delta, particularly in OP ponds (Table 6).

Table 4. Insect (A) and non-insect (B) prey items found in foreguts (n=167) of *Aeshna juncea* collected from Copper River Delta ponds, May-September 2011. Numbers denote the total number of foreguts containing each prey taxon with overall percentage of foreguts containing each prey family in parentheses.

A

PREY FAMILY	# OF FOREGUTS
COLEOPTERA	
Chrysomelidae	1 (0.60%)
Dytiscidae	30 (17.96%)
Gyrinidae	2 (1.20%)
Haliplidae	1 (0.60%)
DIPTERA	
Ceratopogonidae	4 (2.40%)
Chironomidae	114 (68.26%)
Dixidae	7 (4.19%)
Tipulidae	1 (0.60%)
EPHEMEROPTERA	
Siphlonuridae	1 (0.60%)
HEMIPTERA	
Corixidae	24 (14.37%)
Gerridae	2 (1.20%)
Homoptera	1 (0.60%)
ODONATA	
Aeshnidae	10 (5.99%)
Coenagrionidae	4 (2.40%)
Libellulidae	1 (0.60%)
TRICHOPTERA	
Hydroptilidae	4 (2.40%)
Limnephilidae	3 (1.80%)
Phryganeidae	14 (8.38%)
Polycentropodidae	8 (4.79%)
TERRESTRIAL	
Terrestrial Adult	3 (1.80%)

B

PREY FAMILY	# OF FOREGUTS
CRUSTACEA	
Daphniidae	3 (1.80%)
Hyallelidae	1 (0.60%)
Ostracoda	26 (15.57%)
TRICLADIDA	
Planariidae	2 (1.20%)
MOLLUSCA	
Planorbidae	3 (1.80%)
Sphaeriidae	9 (5.39%)
GASTEROSTEIDAE	
Gasterosteus aculeatus	4 (2.40%)
HYDRACHNIDAE	
Hydrachna	24 (14.37%)

Figure 7. *Aeshna juncea* diets by prey count (A) and area (B), May 2011. Numbers above stacked bars denote the number of pooled foreguts. E = East Delta, W = West Delta; OP = Outwash Plain, UM = Uplifted Marsh.

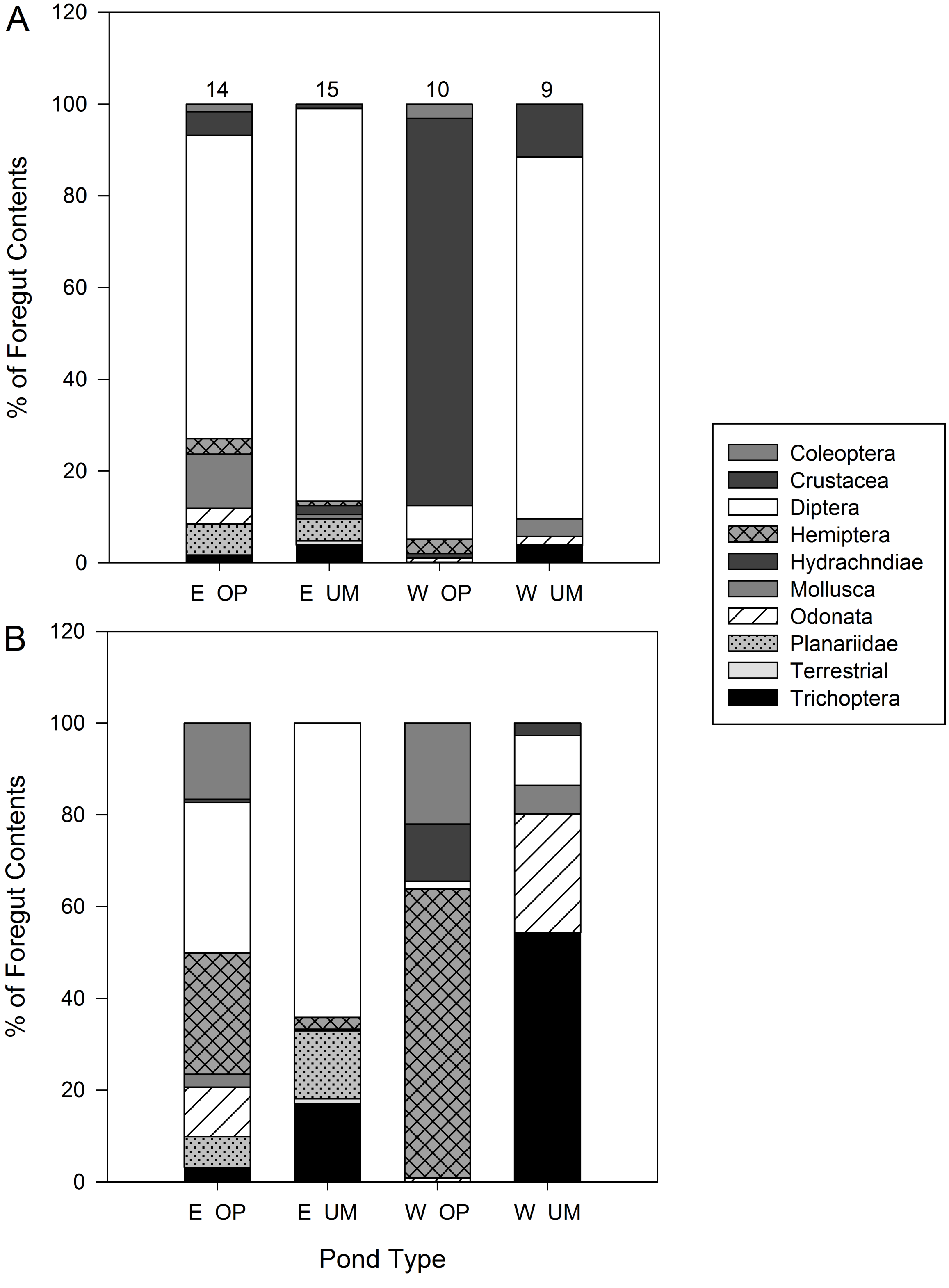


Figure 8. *Aeshna juncea* diets by prey count (A) and area (B), June 2011. Numbers above stacked bars denote the number of pooled foreguts.
E = East Delta, W = West Delta; OP = Outwash Plain, UM = Uplifted Marsh.

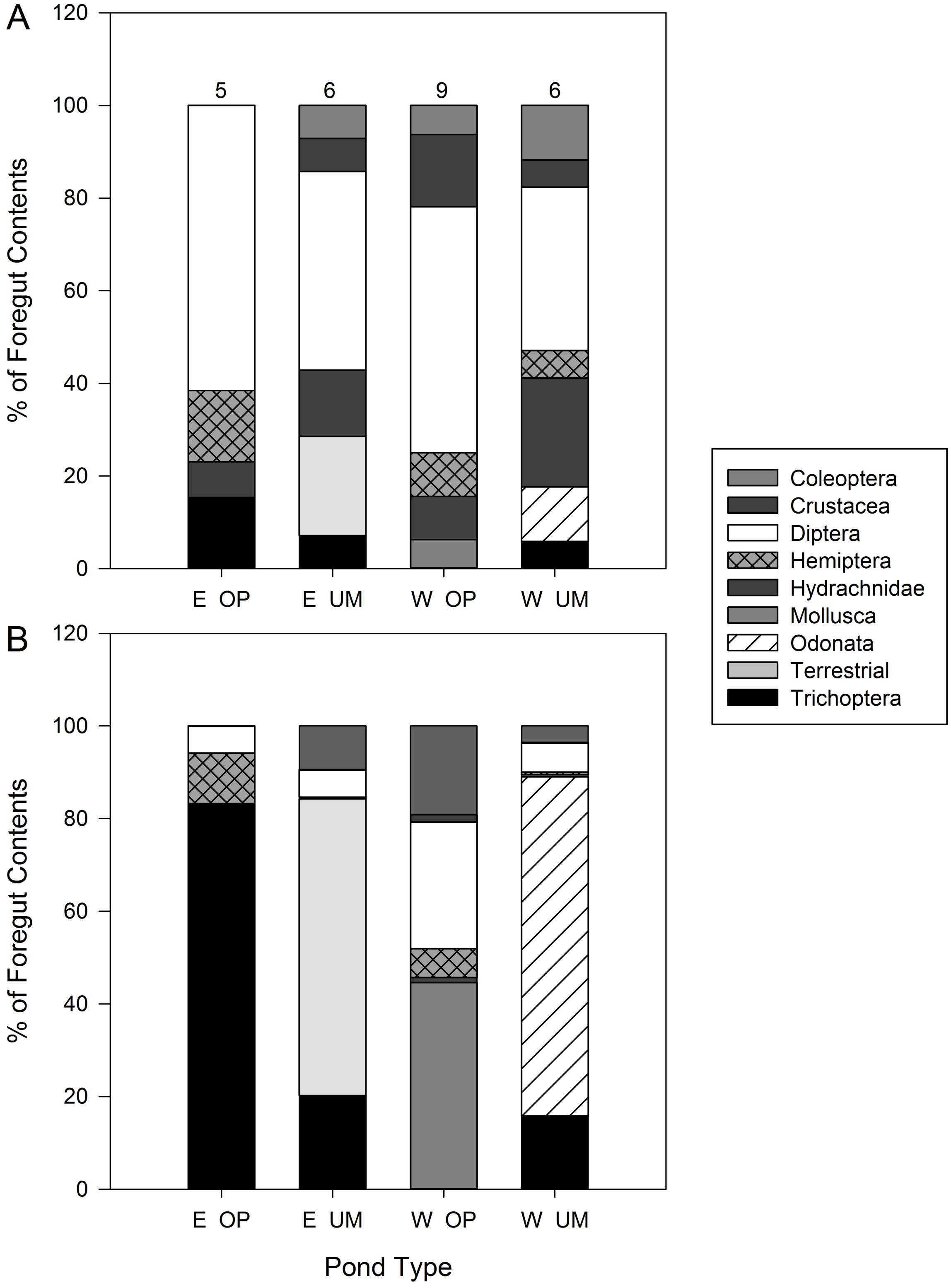


Figure 9. *Aeshna juncea* diets by prey count (A) and area (B), July 2011. Numbers above stacked bars denote the number of pooled foreguts. E = East Delta, W = West Delta; OP = Outwash Plain, UM = Uplifted Marsh.

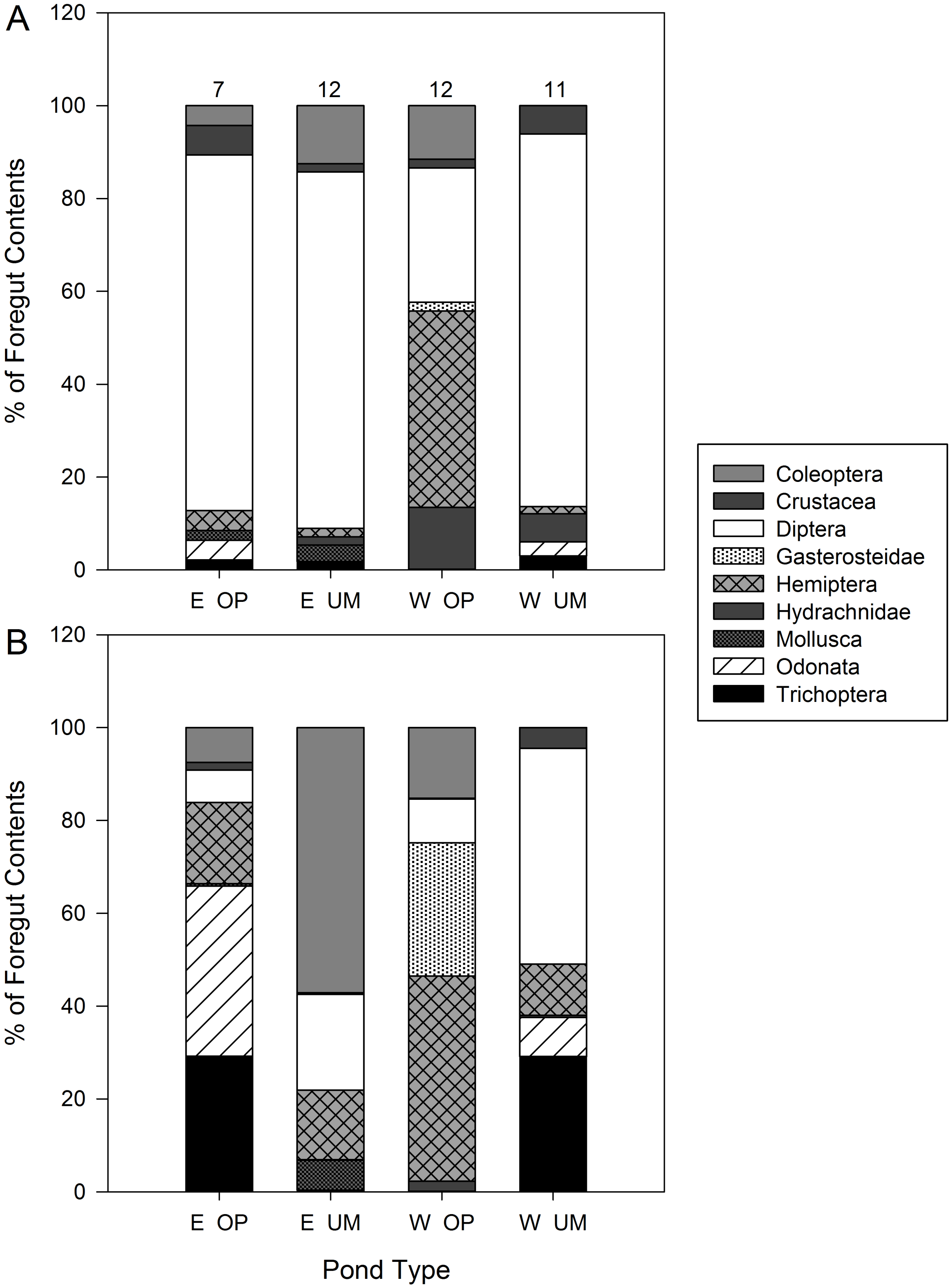


Figure 10. *Aeshna juncea* diets by prey count (A) and area (B), August 2011. Numbers above stacked bars denote the number of pooled foreguts. E = East Delta, W = West Delta; OP = Outwash Plain, UM = Uplifted Marsh.

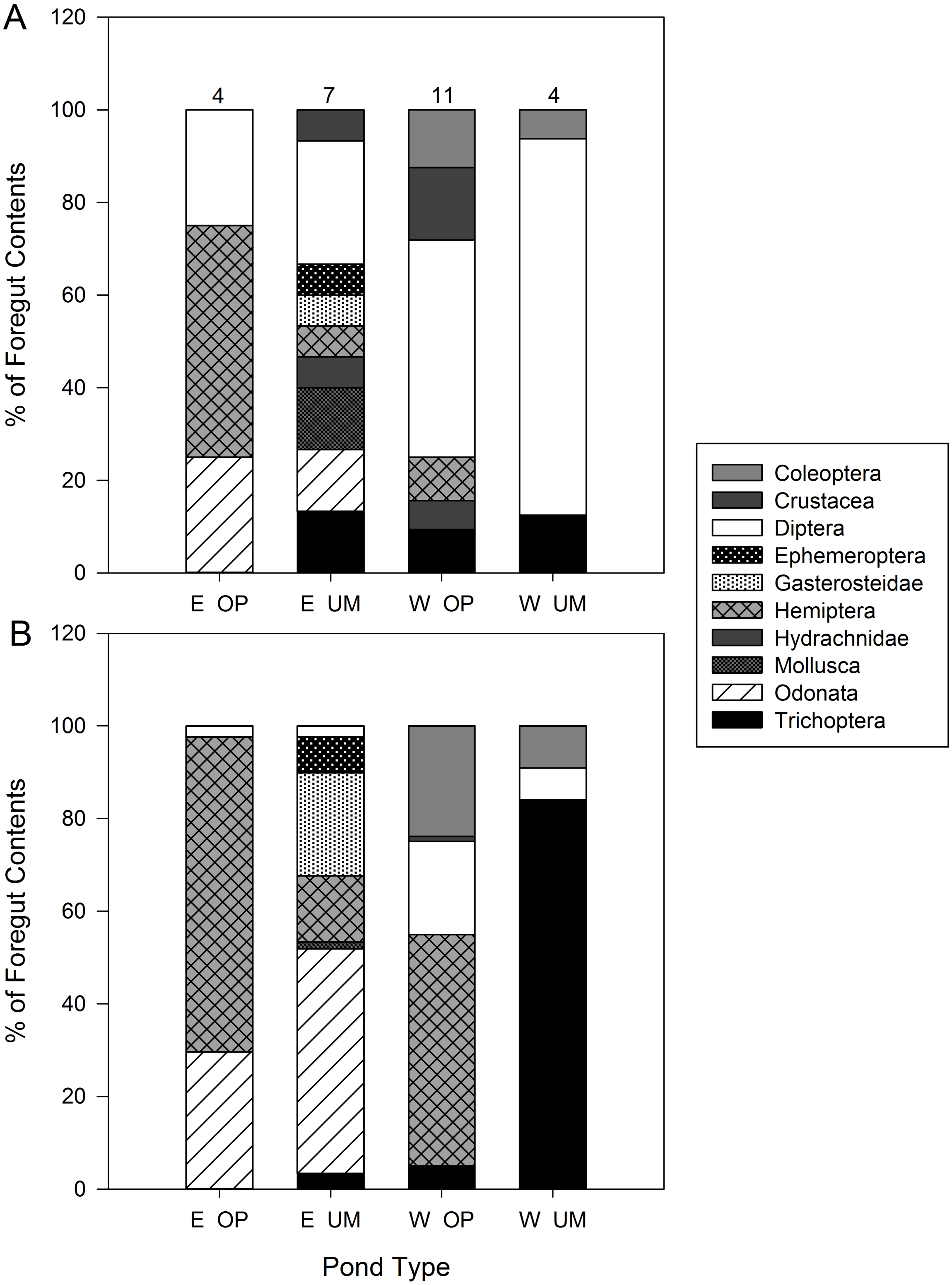


Figure 11. *Aeshna juncea* diets by prey count (A) and area (B), September 2011. Numbers above stacked bars denote the number of pooled foreguts. E = East Delta, W = West Delta; OP = Outwash Plain, UM = Uplifted Marsh.

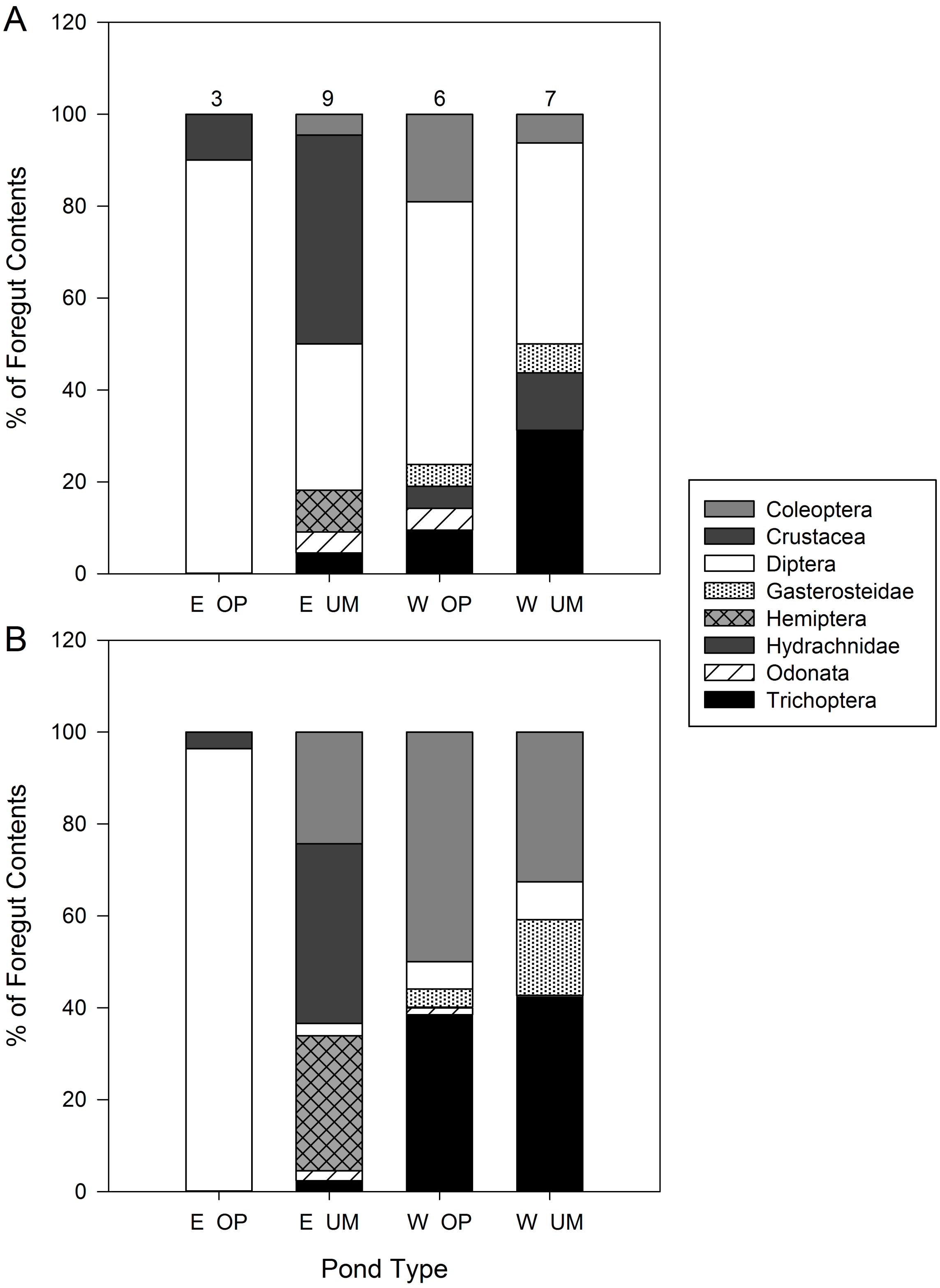


Figure 12. *Aeshna juncea* diets by prey count (A) and area (B), May through September 2011. Numbers above stacked bars denote the number of pooled foreguts. E = East Delta, W = West Delta; OP = Outwash Plain, UM = Uplifted Marsh.

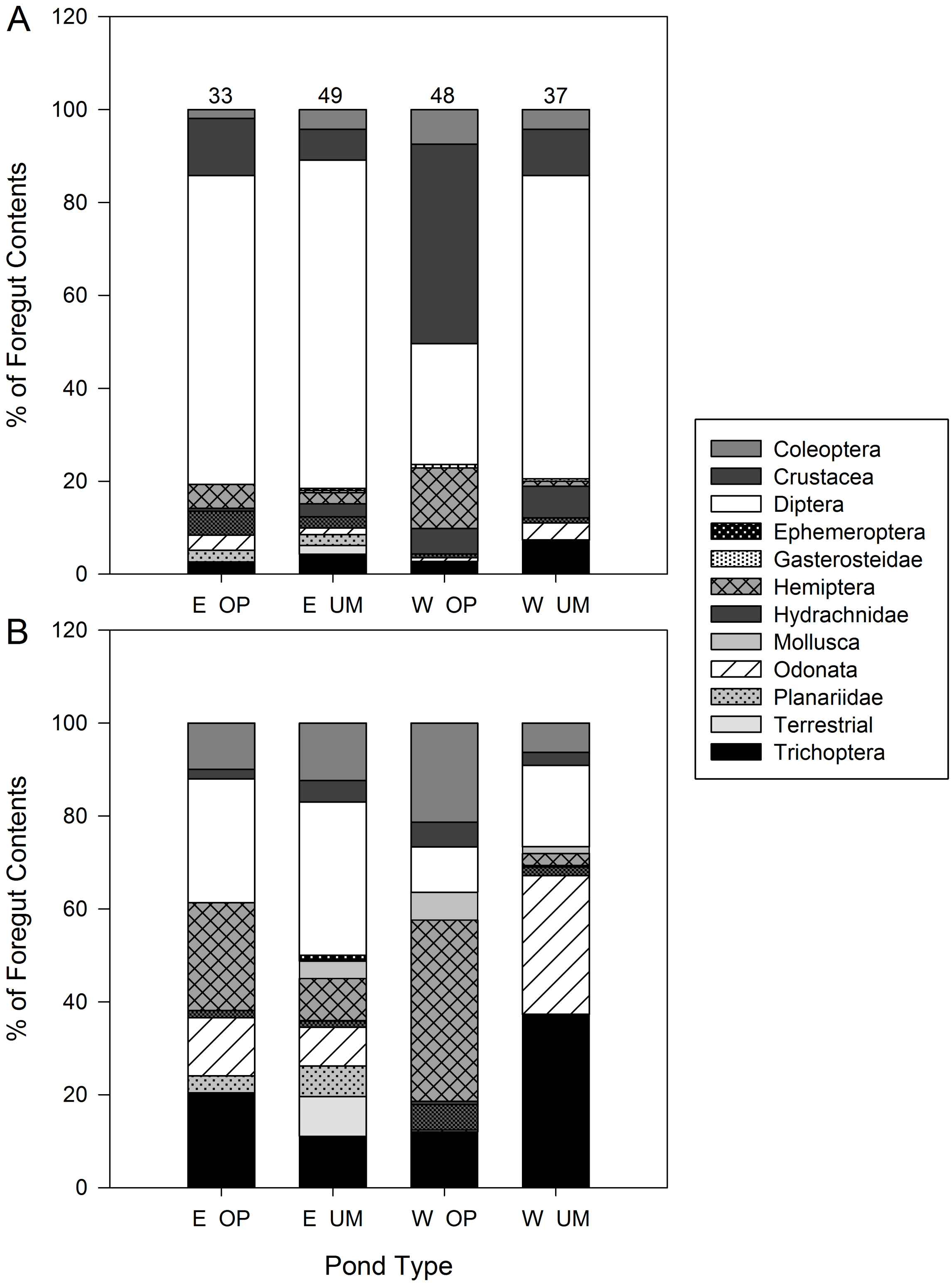


Table 5. Mean density (#/m^2) of six aquatic insect families commonly found in *Aeshna juncea* foreguts with standard error in parentheses, May-September 2011. Data collected from eight representative Copper River Delta ponds and pooled by pond type.

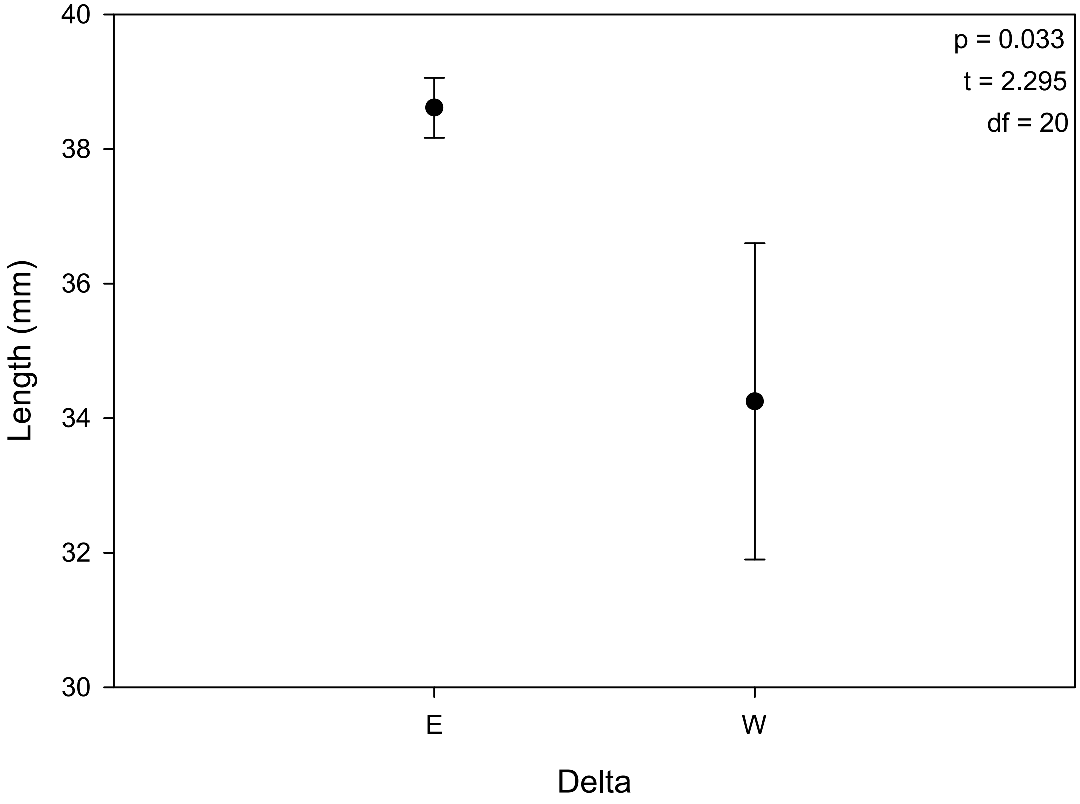
	E OP	E UM	W OP	W UM
Chironomidae	268.21 (±46.18)^{a}	204.40 (±21.28)^{a}	205.34 (±34.22)^{a}	440.66 (±39.77)^{b}
Corixidae	24.85 (±5.29)^{a}	9.42 (±1.82)^{b}	4.55 (±0.79)^{b}	8.32 (±1.38)^{b}
Dytiscidae	0.27 (±0.10)^{a}	0.89 (±0.27)^{a,b}	1.64 (±0.38)^{b}	1.61 (±0.23)^{b}
Limnephilidae	0.77 (±0.25)	0.79 (±0.17)	0.25 (±0.10)	0.84 (±0.32)
Phryganeidae	0.35 (±0.12)^{a}	1.39 (±0.27)^{b}	0.05 (±0.05)^{a}	0.71 (±0.24)^{a,b}
Polycentropodidae	0.03 (±0.03)^{a}	0.25 (±0.10)^{a}	0.48 (±0.15)^{a}	3.52 (±0.73)^{b}
TOTAL INSECT PREY	351.21 (±50.60)^{a,b}	237.23 (±21.10)^{b}	221.32 (±35.63)^{b}	485.48 (±41.13)^{a}

[a] – Statistically significant differences (One-Way ANOVA, df = 3, $p < 0.05$) denoted with superscript letters

Exuviae

A total of 35 odonate exuviae were collected from emergent vegetation in CRD ponds between May and September 2011. *Aeshna juncea* exuviae accounted for 88.6% of exuviae collected with 67.7% of those collected from east delta ponds. Female exuviae were collected more frequently than male exuviae (female:male ratio = 2.1), and the mean body length of female exuviae was significantly larger ($p = 0.033$) on the east delta (38.6 ± 0.45 mm) than on the west delta (34.3 ± 2.4 mm) (Fig. 13). High numbers of *A. juncea* exuviae collected on the east delta during sampling period 5 (July 5-8) indicate that an emergence had occurred since the previous sampling period (June 20-23). However, due to low numbers of exuviae collected, odonate emergence phenology could not be definitively assessed.

Figure 13. Mean length of female *Aeshna juncea* exuviae (n=21) collected from Copper River Delta ponds, May-September 2011. Bars denote standard error. E = east delta, W = west delta.



CHAPTER FOUR

DISCUSSION

Pond Physicochemical Parameters

Wetland insect communities are influenced by abiotic factors such as pond depth, water temperature, and dissolved oxygen (Batzer and Wissinger 1996), and differences in these parameters may impact Copper River Delta (CRD) odonates.

Structural and hydrological dissimilarities likely account for differences in water temperature between CRD pond types. Outwash plain (OP) ponds on the west delta are deep and receive cold groundwater inputs from several nearby glaciers, especially during warm summer months when increased melting and calving occur due to higher temperatures and sun exposure (Nye 1960). Uplifted marsh (UM) ponds on the west delta tend to have large surface areas, shallow depths due to tectonic uplift (Boggs 2000), and limited groundwater upwelling due to a thick silt layer sealing the pond substrate (Davidson and Klinge 1992). The 2011 sampling season was particularly warm and sunny compared to previous sampling seasons on the CRD. Van Duzor (2011) reported only 7 days of sun or mostly sun occurring between June and September 2008, whereas 37 days of sun or mostly sun occurred between May and September 2011 (Merle K "Mudhole" Smith Airport (CDV), Cordova, AK). As such, glacial influence on OP ponds was likely substantial during this study. Warmer water temperatures in UM ponds compared to OP ponds may also be due to pond surface sun exposure, which has been shown to cause significant temperature increases in ponds ≤ 1 m deep (Weinberger 1964), particularly in conjunction with high surface area.

Warmer water temperatures and more rapid accumulation of degree days in UM ponds would likely lead to faster odonate development and earlier emergence as terrestrial adults than in OP ponds. Aquatic insect development is closely tied to temperature (Hynes 1970; Precht et al. 1973; Wieser 1973), with more rapid insect growth and development occurring at higher temperatures. Lutz (1968) noted that on a 14-hr photoperiod, nymphal development of the damselfly *Lestes eurinus* (Lestidae) proceeded almost four times faster at 20 °C than at 15 °C, Pickup and Thompson (1990) found that *Lestes sponsa* Hansemann developed more quickly when reared at 20 °C than at 12 or 16 °C, and *Lestes disjunctus* growth rates were positively correlated with rearing temperature in a study conducted by Krishnaraj and Pritchard (1995). Finally, increasing the average daily temperature by 6 °C during egg hatching and immature development can decrease the nymphal period of grasshoppers by 17 days, nearly 3 days per °C (Logan, et al. 2006).

Temperatures optimal for high growth rates may be suboptimal for growth efficiency, emergence success, or adult longevity (Heiman et al. 1975). From a metabolic standpoint, maintenance costs (assimilated energy needed for respiration and other non-trophic growth) increase with temperature; Lawton (1971) found that the Q_{10} for respiration of the damselfly *Pyrrhosoma nymphula*

(Coenagrionidae) rose from 2.20 at 5-10 °C to 3.12 at 10-16 °C. As a result, the growth potential of immatures may be reduced at high temperatures due to insufficient energy remaining for growth after allocation for maintenance costs (Vannote and Sweeney 1980). Thus, higher temperatures cause most ectotherms to metamorphose or mature at a smaller size (Precht et al. 1973, Krishnaraj and Pritchard 1995, Atkinson 1996), potentially reducing reproductive potential.

For most odonates, size attained during the immature growth period is directly related to adult reproductive success. Large females generally produce more or larger eggs than smaller females, and large males often gain access to more females than do smaller males (Hinton 1981, Thornhill and Alcock 1983). Odonate size will also have an effect on the food resources it can exploit, what predators it must avoid, and its physiology and energetics (Peters 1986). It has been posited that because emerging odonates feed for 1-3 weeks and roughly double in body mass before initiating mating (Anholt et al. 1991), size at emergence is of minor importance for fitness (Anholt 1991, Richardson and Baker 1997, McPeek and Peckarsky 1998). Yet emergence size, which determines exoskeletal characteristics, may strongly constrain subsequent weight gain and flight performance, thereby influencing survival and reproductive success (Crowley and Johansson 2002).

Mean dissolved oxygen (DO) concentrations were lowest in west OP ponds (6.5 ± 0.4 mg/L), potentially caused by limited surface water oxygenation due to low surface area and extensive sheltering vegetation (Gullan and

Cranston 1994), as well as oxygen demand from benthic decomposition of organic matter. Tiegs et al. (2013) found that temperature-corrected decomposition rates were significantly higher in west OP ponds than in west UM ponds ($p < 0.0001$) on the CRD. Furthermore, increased water depth diminishes primary production (and therefore oxygen generation) due to the limited ability of light to penetrate the entirety of the water column (Verduin 1956, Hepher 1962). Photosynthetic activity in west OP ponds may therefore be limited by increased depth compared to west UM ponds. Primary production and periphyton have also been shown to be decreased by the presence of dissolved iron (Rasmussen and Lindegaard 1988), which is a factor in OP ponds on the west delta as evidenced by the presence of ochreous colloidal iron precipitates.

Aquatic insect growth and development are positively related to DO concentrations (Dermott et al. 1977, Butler and Anderson 1990), with evidence of enhanced growth and development at higher DO levels. Overall, low DO levels in west OP ponds may impede the growth and development of odonates, resulting in longer life cycles (Butler and Anderson 1990) and delayed emergence, particularly when combined with low water temperatures (Fig. 2) and slow accumulation of GDD (Fig. 3).

pH has been demonstrated to have little influence on insect taxa in wetland habitats (Batzer and Wissinger 1996). The majority of CRD ponds were slightly acidic (~6) with the exception of UM ponds on the east delta, with pH levels closer to neutral (~7). Slightly acidic pH levels are not surprising in CRD ponds due to high amounts of decomposing vegetation.

As expected, there was a strong correlation between salinity, conductivity, and total dissolved solids (TDS) in CRD ponds, with the highest levels found in west OP ponds (Table 1), likely due to strong groundwater influence. Conversely, levels were lowest in west UM ponds (Table 1). Although these parameters were higher in OP ponds than in UM ponds on the west delta, this pattern was reversed on the east delta (Table 1), suggesting that the impacts of tectonic uplift and landscape type are more pronounced on the west delta than on the east delta.

Although turbidity (total suspended solids, or TSS) was not directly assessed in this study, TSS is positively correlated with TDS (Bhandari et al. 2008), suggesting high turbidity in west OP ponds. The most ecologically significant impact of suspended sediment is an increase in light attenuation (Davies-Colley and Smith 2001), which decreases light penetration for photosynthesis (Kirk 1994) and reduces visibility for visual predators, especially when combined with high densities of submerged vegetation (Van de Meutter et al. 2005). Odonate nymphs require visual cues to stalk and capture prey (Corbet 1999), and numerous studies have documented positive correlations between prey activity level and capture by odonate predators (Lawton et al. 1974, Crowley 1979, Folsom and Collins 1984, Chovanec 1992). Therefore, it is likely that prey detection in west OP ponds relies more heavily on highly active taxa such as corixids, which provide visual cues for odonate predators despite reduced visibility in these habitats.

Outwash plain ponds receive the majority of their groundwater from nearby glaciers, and glacial meltwater provides ecologically significant amounts of dissolved and particulate iron to watersheds throughout the world (Bhatia et al 2011, Schroth et al 2011, Zhang et al 2013), including the CRD and Gulf of Alaska (Crusius et al 2010, Crusius et al 2011). Although the iron concentrations in CRD ponds were not assessed, west OP ponds are characterized by high amounts of ochreous colloidal iron precipitates, caused by the oxidation of groundwater Fe (II) to Fe (III) (Scroth et al. 2011). These precipitates settle on the benthic substrates and may increase the turbidity of aquatic habitats when resuspended in the water column by turbulence. Furthermore, iron precipitates may reduce pond photosynthesis by sequestering phosphorous in pond sediments (Rosenberry et al. 2011) as well as limiting oxygen and periphyton availability for aquatic invertebrate grazers (Warnick and Bell 1969, Rasmussen and Lindegaard 1988). Grazers serve as a food resource for higher trophic level predators such as odonate nymphs, and decreased periphyton availability may impose bottom-up control on CRD pond communities. While there is evidence of iron in OP ponds on the east side of the delta, colloidal iron precipitates occur less frequently and suggest lower iron concentrations.

Odonate Taxa and Densities

Odonate taxa richness (6 taxa) on the CRD is low compared to other pond ecosystems (Benke and Benke 1975, Benke 1976, Braccia et al. 2007). The lack of significant differences in densities of *Aeshna juncea* and *Enallagma boreale* among pond types may indicate that these two taxa are cosmopolitan in CRD ponds. However, high densities of *Leucorrhinia hudsonica* in west UM ponds (specifically EYK1), may be due to the absence or low densities of threespine stickleback (*Gasterosteus aculeatus*), as none were collected from this pond during the sampling season. Evans (1989) noted that *Leucorrhinia*, which dominate the benthos of acidified, fishless lakes, may be a reliable indicator of fish absence.

Lestes disjunctus was present only in UM ponds and collected in low numbers. Of the eight individuals collected between May and September 2011, 7 were collected from ponds STN and STS (Table 2). These ponds are located on Storey Island, a land mass in the Copper River, and this may represent a habitat unique from other CRD ponds on the mainland.

Sympetrum danae occurred less frequently than *L. disjunctus*, and only in one pond: EYK1 on the west delta (Table 2). While low densities may have precluded detection in other CRD ponds, EYK1 might be an ideal oviposition site for adult *S. danae* due to high amounts of submerged *Sphagnum* moss (Michiels and Dondt 1990).

Odonate Secondary Production

Secondary production estimates for *A. juncea*, *E. boreale*, and *L. hudsonica* in CRD ponds were low in comparison to published literature values (Braccia et al. 2007). Contributing factors may be low densities, low prey availability, and a short growing season on the CRD.

Trends in secondary production followed an identical pattern to that of odonate density. There were no significant differences in secondary production among pond types for *A. juncea* or *E. boreale* (Fig. 5, Table 3). *Leucorrhinia* *hudsonica*, however, had significantly higher secondary production in west UM ponds, likely due to high densities (Fig. 5, Table 3). Although differences in secondary production among pond types were not significant due to high variability, mean secondary production estimates were uniformly higher in UM ponds than in OP ponds for all three dominant odonate taxa (Fig. 5, Table 3), potentially due to significantly higher prey density in UM ponds, especially on the west delta. Furthermore, UM ponds tended to have higher densities of trichopterans (Table 5), which likely represent a high quality food resource (Cummins and Wuychek 1971) and may contribute to increased odonate biomass accrual. Despite studies demonstrating smaller body size at increased temperatures (Krishnaraj and Pritchard 1995, Atkinson 1996), diet quality may be a major factor in secondary production differences in CRD ponds.

Aeshna juncea secondary production was highest in the east OP pond BHS (28.2 mg AFDM/m^2/yr), despite lower density in this pond (0.63 individuals/m^2) compared to two other ponds, CM2 (east UM) and TDN (west UM) (Table 3). This may indicate that although fewer *A. juncea* were collected from BHS, they were larger in size; this is likely a function of more late-instar nymphs in BHS (east OP) than in CM2 or TDN.

Diets

Although food quality for predators is relatively high and odonate assimilation efficiency (AE) ranges from 75-92% (McAleer 1973, Minshall et al. 1975), prey density can have an effect on the population size, biomass, and generation time of predators (Anderson and Cummins 1974). Furthermore, certain prey items may be preferentially selected or avoided due to morphological, behavioral, or biochemical characteristics (Peckarsky 1982).

Odonate diets are typically assessed either through fecal pellet analysis (Pritchard 1964, Thompson 1978, Folsom and Collins 1984, Merrill and Johnson 1984, Blois 1985, Johnson et al. 1985, Van Buskirk 1992) or through dissection of the foregut (Cloarec 1977, Lamoot 1977, Burcher and Smock 2002), as in this study. Both methods rely on the presence of large sclerotized prey body parts such as mandibles, head capsules, abdominal hooks, and legs (Pritchard 1964, Kime 1974) for prey identification. Foregut analysis, however, has the advantage of detecting soft-bodied prey such as annelids, leeches, and mollusks that are not detectable in fecal pellets (Pritchard 1964). Additionally, foregut dissection allows for the estimation of gut content area, as consumed prey have not yet been ground by the gizzard (Gullan and Cranston 1994).

Odonate nymphs are generalist predators and with the exception of exhibiting preference or aversion to some prey, their diets typically reflect prey availability in the habitat (Corbet 1999). The most abundant prey of *A. juncea* in CRD ponds were chironomid larvae (found in 114 of 167 foreguts, 68%). The importance of larval chironomids in aeshnid diets has been well documented (Pritchard 1964, Blois 1985, Blois 1985a, Van Buskirk 1992), and it is thought that despite their small size, they represent a significant quantitative contribution to diets (Pritchard 1964). Furthermore, chironomids are vulnerable to odonate predation due to their conspicuous wriggling movements, soft bodies, and ease of capture (Pritchard 1964). Chironomids were underrepresented in west OP *A.*

juncea diets early in the sampling season (Fig. 7A), as well as in overall prey count analysis from May to September (Fig. 12A). However, mean chironomid density in these ponds was similar to densities in east OP and UM ponds (Table 5), suggesting that chironomids in west OP ponds are avoiding predation. Benke (1976) observed that prey elude odonate predation mainly through refugia, which may be provided by iron precipitates present on benthic substrates of west OP ponds. Chironomid larvae have been observed to burrow up to 10 cm below the sediment-water interface (Matisoff and Wang 2000) and are adapted to the hypoxic or anoxic conditions in these regions through behavioral adaptations such as burrow wiggling or the presence of high-affinity hemoglobin (Gullan and Cranston 1994).

Odonate consumption of corixids has been documented (Pritchard 1964, Staddon and Griffiths 1967, Folsom and Collins 1984, Blois 1985, Van Buskirk 1992, Coccia et al. 2014), despite their heavy sclerotization and vigorous escape response. Corixids occurred in *A. juncea* diets most frequently during August and September, when corixid densities in CRD ponds were highest. Additionally, west OP aeshnids consumed corixids more often than aeshnids in any other pond type (Fig. 12A), despite lower mean densities of corixids than in the other three pond types (Table 5). This may be due to their high activity level providing visual cues in a low visibility environment, combined with the low densities of higher quality prey items such as trichopterans.

Trichopterans occurred in *A. juncea* diets most frequently in August and September due to high trichopteran densities late in the sampling season. The preference for trichopteran larvae by aeshnids is well documented (Pritchard 1964, Cloarec 1977, Blois 1985), and caddisfly larvae likely represent a high quality food resource for odonate predators in CRD ponds. Trichopteran larvae, which occurred in nearly 15% of *A. juncea* foreguts (Table 4A), are slow-moving (Pritchard 1964), and can reach large sizes with relatively little sclerotization to deter predators (Wiggins 1996). Although many caddisfly taxa may attempt to retreat into their cases for protection upon capture, the piercing labial palps of aeshnids typically prevent this behavior (Pritchard 1964).

Erratic movement of microcrustaceans attracts visual predators and these prey figured prominently in early season west OP *A. juncea* diets (Fig. 7A). Although they are often preyed upon because of their high densities and relatively low handling time (Lawton 1970, Benke 1976), their small size ensures that odonate predators must consume many individuals to reach the same level of satiation and energy intake achieved by eating a single, larger prey item. Benke (1976) found that microcrustacean consumption generated no more than 5% of odonate energy intake, despite comprising 24-55% of prey by number. Early season *A. juncea* diets in west OP ponds could be considered less energetically beneficial than the diets in other CRD pond types, with accompanying differences in growth potential and secondary production.

Despite published literature reporting high numbers of damselflies in dragonfly diets (Pritchard 1964, Cloarec 1977, Blois 1985) and high densities in west UM ponds (Fig. 4, Table 3), Coenagrionidae only occurred in 2.4% of *A. juncea* foreguts on the CRD. It is unclear what caused this low representation, although Van Duzor (2011) noted that CRD ponds with high densities of large-bodied Epiprocta (*A. juncea*) typically did not support high densities of Zygoptera (*E. boreale* or *L. disjunctus).*

Cannibalism occurred in 6% of *A. juncea* foreguts, a frequency similar to published literature values (Pritchard 1964, Van Buskirk 1992). Furthermore, cannibalism occurred most frequently in west UM ponds, likely due to high conspecific density (Hopper et al. 1996) and warmer water temperatures (Crumrine 2010). Asynchronous oviposition or semivoltine life histories result in the presence of numerous coexisting odonate size classes (Corbet 1957, Eller 1963), and as a consequence of large size differences between early and late-instar nymphs and generalist diets, odonates engage in strong competition and cannibalism among instars (Wissinger 1987, Van Buskirk 1992, Johansson 1993). Additionally, odonate cannibalism in CRD ponds is likely due to the 48 month CPI of *A. juncea* at high northern latitudes (Walker 1953), which explains the coexistence of early and late-instar nymphs in our benthic samples.

The role of *A. juncea* as an apex predator in CRD ponds was supported by the presence of threespine stickleback in 2.4% of foreguts (Table 4B). Despite their classification as predatory vertebrates, threespine sticklebacks are small in size (~5 cm in length) and feed primarily on small benthic prey such as chironomids (Becker 1983). Furthermore, as evidenced by this study and others, late-instar odonates actively pursue prey items of their own size or slightly larger, such as small fish (Warren 1915, Reimchen 1994) and larval amphibians (Cloarec 1977, Caldwell et al. 1980, Crump 1984, Van Buskirk 1988).

Prey Density

Mean densities of six prey families commonly found in *A. juncea* foreguts were calculated in eight representative CRD ponds. Greater prey density is likely to increase odonate growth rates (Pickup and Thompson 1990) and decrease odonate instar duration (Hassan 1976, Lawton et al. 1980, Baker 1982, Wissinger 1988) in CRD ponds. Higher prey densities in west UM ponds, when combined with higher temperatures, may lead to the earlier emergence of odonates from UM ponds on the west delta. Furthermore, studies have found positive correlation between warmer temperatures and the number of prey consumed by predatory aquatic insects (Thompson 1978a, Jamieson and Scudder 1979), indicating that west UM odonates not only experience increased densities of available prey items, but also may consume more prey than odonates in other pond types on the CRD.

Exuviae

The large size and persistence of odonate exuviae facilitate the quantitative study of emergence (Corbet 1957); molted exoskeletons tend to remain on emergence supports for several days. The sex ratio of exuviae collected from CRD ponds was female-biased, which, according to the model suggested by Crowley and Johansson (2002), would be expected for odonate taxa demonstrating high territoriality. Low overall odonate densities prevented definitive determination of emergence phenology. The mean length of female *A. juncea* exuviae was significantly larger on the east delta than on the west delta (p

= 0.033). As stated previously, size differences in odonate nymphs are often tied to environmental factors such as temperature, dissolved oxygen concentration, and diet quality.

Understanding CRD odonate responses to the different thermal regimes across the CRD may shed light on the potential consequences of climate change in northern coastal wetland ecosystems. Although the phenology of odonate emergence from CRD ponds could not be definitively assessed due to low numbers of collected exuviae, differences in pond temperature and prey density may forecast differences in emergence phenologies from different pond types. The timing of odonate emergences are of particular importance to avian species that rely heavily on these taxa to provision their young while nesting on the CRD (Loomis 2013) and whose migrations coincide with high densities of emerging insects. With climate change likely to impact coastal wetland ecosystems of southcentral Alaska by increasing temperatures, temporal decoupling between insect development and bird migration may lead to birds failing to breed at the time of maximal food abundance (Visser et al. 1998, Visser et al. 2004, Visser and Both 2005), which can in turn lead to avian population declines (Both et al. 2006).

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