

**DIVERSITY PATTERNS OF BENTHIC DIATOMS AND THEIR USE AS
POTENTIAL BIOINDICATORS IN WESTERN BOREAL WETLANDS**

by

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ABSTRACT

Widespread habitat degradation associated with resource development in Canada's boreal zone is a major and ongoing threat to biodiversity and ecological integrity. Despite the extensive and intensive development occurring in these regions, little information exists on biological diversity and the potential impacts associated with expansion in Canada's north. Wetlands are a prevalent landscape feature in the boreal zone and provide many ecosystem services currently at risk of being reduced or lost. In this thesis, diversity patterns of diatom communities in boreal wetlands in Canada's largest freshwater delta - the Peace-Athabasca Delta in northern Alberta – are examined and assessed for their potential use as indicators in a large-scale biomonitoring program for the federal government. This work has shown that the traditional bioindicator, benthic macroinvertebrates, are not always sufficient indicators of all potential impacts on their own, and that diatoms may be responding to different environmental drivers than the benthic macroinvertebrates in these wetlands. In conclusion, this thesis establishes the need for expansion of standard biomonitoring protocols to include the primary producer community in order to effectively predict future anthropogenic-induced habitat change.

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CHAPTER 1: INTRODUCTION

Introduction

Resource development in Canada

Canada's North is an area of increasing industrialisation with little information known about its ecosystems (Spencer *et al.*, 2008) despite the prevalence of natural resource development. Management and conservation of aquatic resources are dependent upon accurate knowledge of the diversity and abundance of organisms present within particular habitats (Dudgeon *et al.*, 2006); however, there is limited information in the scientific literature on the effects of anthropogenic disturbance on aquatic biodiversity (Kreutzweiser *et al.*, 2013). Additionally, reliable species richness estimates are not available for lower order organisms (primary producers and consumers) which are used as indicator taxa. Aquatic systems are ecologically linked to their surrounding terrestrial watersheds (Hynes, 1975), therefore resource development in the Canadian boreal zone has significant potential to adversely impact the aquatic ecosystems in the area, as well as the portion of terrestrial ecosystems effectively removed by the development footprint.

Resource development in the Western Plains region of the Canadian boreal zone consists mainly of mineral mining, hydroelectric dams, and gas and oil mining. Between 2006 and 2010 mineral production in Canada's north increased by approximately 53%, and the mining sector is currently the main driver of economic activity in northern Canada (House of Commons Standing Committee on Natural Resources, 2012). In 2010, Canada produced 588.9 TW hours of electricity and 59.1% of generation was from hydroelectric sources (NRCan, 2011). A total of \$2.2 billion in electricity was exported to the United States in the same year (NRCan, 2011). Currently the Peace River has one of

the largest hydroelectric schemes in North America along its headwaters – the Bennett Dam in British Columbia (Webster *et al.*, 2015) with three additional dams proposed for the Slave River, the Athabasca River and the Wabasca River, a tributary of the Peace River in Alberta (NRCan, 2003). Fossil fuels are responsible for the largest percentage of energy production in Canada. Approximately 41.4% is through crude oil, of which the oil sands represented 97% of reserves and over half of crude production in 2010 (NRCan, 2011). Production in 2011 was 1.7 million barrels per day (Alberta Energy, 2013), and is projected to increase to 4.3 million barrels per day by 2030 (Prebble *et al.*, 2009). Estimates place the industrial footprint of oil and gas at 46 million hectares (Timoney and Lee, 2001). The footprint of natural resource development in the Canadian Boreal Zone is expected to increase by 50-60% by 2030 (Webster *et al.*, 2015).

Wetlands are a dominant feature of the boreal landscape. Over 20% of the world's wetlands occur in the Canadian boreal zone (Webster *et al.*, 2015). The structure and function of these aquatic ecosystems could be directly threatened by disturbance to waterbodies or indirectly through disturbance to boreal forest watersheds (Kreutzweiser *et al.*, 2013). Economic development is one of the primary indirect drivers of wetland degradation and loss (Millennium Ecosystem Assessment, 2005a). Industrial activities include: land/wetland clearing during site preparation, road construction, diversion of natural drainage, water extraction, spills, and seepage from tailings (Kreutzweiser *et al.*, 2013) and these can result in the removal of water, alteration of hydrologic and biogeochemical flows, increase in erosion and siltation, and an increase in pollutants and contaminants (Webster *et al.*, 2015). These anthropogenic disturbances have longer impact times than natural disturbances (e.g. forest fire) and delayed recovery (Webster *et*

al., 2015). The major impacts to water quantity and quality caused by the main three resource development types are shown in Table 1.1. Specifically, dams increase lentic environments and introduce considerable amounts of terrestrially derived nutrients and organic matter. Mining activities can impact water quality directly through contamination from spills or leakage from tailings; however, effects on water quantity are more variable. Water quantity is reduced in some areas when extracted from rivers and aquifers for use in processing, but increased in others when tailings ponds are created on the landscape. The oil and gas industry uses water resources for all stages of development including exploration, drilling and production. Approximately 523 million cubic metres of water is used per year in the oil sands extraction process, and 50 – 75% of this water comes from the Athabasca River with less than 10% being returned (Webster *et al.*, 2015).

Disturbance from mining activities is often extreme with complete removal of vegetation, and a total loss of ecological function at the site level (House of Commons Standing Committee on Natural Resources, 2012). In addition to direct impacts from mining activities, there are also indirect effects caused by atmospheric deposition of chemicals and particulates. The main emissions from industry are nitrogen (NO_x) and sulphur (SO_x) based (Brandt *et al.*, 2013). These emissions are quickly spread by prevailing winds, and fall as wet or dry deposition. This acid precipitation reduces pH in soil and surface waters, and acidification can exacerbate the bioavailability and toxicity of metal contaminants (Keller and Pitblado, 1986; Schindler, 1988). Many waterbodies in the Canadian boreal zone have low buffering capacities (Hazewinkel *et al.*, 2008; Aherne and Shaw, 2010) and are therefore at risk of acidification from atmospheric deposition.

The Peace – Athabasca Delta

The Peace-Athabasca Delta (PAD) (Figure 1.1) is the largest inland river delta in North America and the largest boreal delta wetland in the world (Wolfe *et al.*, 2007). The Delta is located on the western margin of Lake Athabasca and was formed due to sediment deposition where the Athabasca and Peace Rivers flow into Lake Athabasca. In 1982, the PAD in Northern Alberta was added to the list of Ramsar sites – wetlands of international importance under the Ramsar convention (Environment Canada, 2007).

Wood Buffalo National Park (WBNP) is the largest of Canada's national parks. It covers an area of 44, 807km² which is approximately 1.47X larger than the country of Belgium. The Park was created in 1922 and provides protected habitat for many species of birds, mammals, and plants. In 1983, the United Nations Educational, Scientific and Cultural Organization (UNESCO) designated WBNP a World Heritage Site; however, the World Heritage status of WBNP was currently reviewed due to concerns about oil sands and hydroelectric development in the areas upstream of the Delta and could be added to the list of World Heritage Sites in Danger (Weber, 2017).

This area is critical habitat for migrating water fowl in North America, including the endangered Whooping Crane, and supports up to 400,000 birds in the spring and over 1 million in the fall (Environment Canada, 2007). This region also contains some of the largest undisturbed grass and sedge meadows in North America, which support a large herd of Plains and Wood Bison (Environment Canada, 2007). Monitoring of boreal forest and wetland habitats is extremely important to ensure that the ecological integrity of these protected sites is not compromised.

The need for monitoring

With current projections of climate change, expanding human populations, and increasing industrial activity, freshwater ecosystems in the Canadian boreal zone are under high stress (Schindler and Lee, 2010). Rivers, lakes and wetlands provide a source of drinking water for human populations, are necessary for large-scale agriculture, fisheries, and ecotourism, and they provide important ecosystem services, which are generally undervalued (Schindler and Lee, 2010). Biomonitoring and conservation programs are crucial in order to maintain the ecological integrity of Canada's freshwater resources.

Conservation and management strategies often speak of maintaining the biodiversity of a site. Biodiversity is the foundation of the ecosystem services that critically contribute to human well-being (Millennium Ecosystem Assessment, 2005b). High biodiversity is considered an indication of a healthy ecosystem; however, the term biodiversity is quite broad and can refer to genetic diversity (within species), taxonomic diversity (among species) and ecological diversity (of ecosystems) (Gaston, 1996; Millennium Ecosystem Assessment, 2005b). Traditional biomonitoring studies focus mainly on taxonomic diversity – the number of different species (richness) and their abundance/distribution (evenness). Taxonomic diversity is one of the main drivers of ecosystem productivity and stability (Tilman *et al.*, 2014). The loss of biodiversity (as a reduction in taxonomic and genetic diversity) decreases ecosystem resilience – the ability to maintain ecosystem services as conditions change (Millennium Ecosystem Assessment, 2005a), and this reduced resilience is of particular concern given that

human-induced biodiversity changes were more rapid in the last 50 years than at any other time in human history (Millennium Ecosystem Assessment, 2005b).

Wetlands are one of the most important aquatic habitats on the planet. Wetland habitats act as an ecotone – a transition zone between two biomes – between aquatic and terrestrial habitat. This creates a unique habitat that shares characteristics of both aquatic and terrestrial ecosystems that are highly productive and diverse supporting an abundance of aquatic and terrestrial organisms. Wetlands also act as a carbon sink making them an important part of the global carbon cycle (Millennium Ecosystem Assessment, 2005a), and provide a wide array of regulatory, cultural and supporting ecosystem services (Table 1.2). Loss and degradation of wetland ecosystem services harms the health and well-being of individuals and local communities (Millennium Ecosystem Assessment, 2005a). Without the ecosystem services provided by wetland habitats, humans, and many other organisms, could not survive.

Bioindicators in monitoring

Biomonitoring is the science of inferring the ecological condition of a habitat by examining the organisms present in the ecosystem. Freshwater biomonitoring generally includes analyses of one or more of three groups of organisms in the ecosystem: algae, benthic macroinvertebrates, and fish. These groups, also known as bioindicators, are used as surrogate taxa to replace the costly and labour intensive process of sampling all organisms in an ecosystem (Bagella *et al.*, 2011). Biggs (2000) outlined six characteristics of organisms (chosen from a larger list proposed by Cairns *et al.*, 1993) indicating their value as a bioindicator: 1) biological relevance, 2) social relevance, 3) broad applicability to many stressors and sites, 4) sensitivity to stressors, 5) it should be

measurable, operationally definable and quantifiable using an accepted procedure with known precision and accuracy, and 6) it should be interpretable (i.e. its use should permit us to distinguish 'acceptable' from 'unacceptable' conditions). Benthic macroinvertebrates are most commonly utilised because they meet these requirements, and are relatively easy to work with both in terms of field sampling and lab analyses. A number of indices have been developed based on the community assemblage of benthic macroinvertebrates including, the Family Biotic Index [FBI] (Hilsenhoff, 1988), EPT index (Lenat, 1988), and the Canadian Ecological Flow Index [CEFI] (Armanini *et al.*, 2011). However, examining more than one taxonomic group (e.g. invertebrates and diatoms) in combination can give additional insight, possibly due to: differential responses to environmental drivers and variation in reaction time, into the state of the ecosystem as a whole and allows for better management of these habitats.

Cross-taxon congruence is an observed phenomenon in which diversity patterns of species co-vary in space. Biomonitoring studies, particularly those in freshwater, often assume a high level of congruence in order to apply results from indicator taxa or taxon groups to the ecosystem as a whole (Bilton *et al.*, 2006). However, past studies have rarely tested how well an indicator reflects richness and diversity of the wider community. The level of congruence between indicators has been shown to vary with taxonomic pairings (Paavola *et al.* 2003), geographic region (Su *et al.*, 2004), and scale (Qian and Kissling, 2010). This may cause problems in applicability and reliability of biomonitoring programs as levels of congruence vary among ecosystems. For this reason, it is important to first assess the reliability (wide distribution, consistent response to stressors, etc.) of the chosen indicator, and consider the utility of additional groups (Do

they respond to different environmental variables? Do they respond to different anthropogenic stressors? Do response times vary?) before implementing a long-term monitoring program.

Objectives

Northern Alberta is the focus of the Canada-Alberta Joint Implementation Plan for Oil Sands Monitoring. As part of this large-scale monitoring program this thesis, presented in partial manuscript format, aims to examine the congruence of diversity patterns between benthic macroinvertebrates and diatoms, as well as to examine the value of diatom communities as indicators of ecosystem status. Chapter 2 will discuss the concordance of diversity patterns between these two sets of indicator taxa. Chapter 3 is an exploratory survey of diatom communities in the Peace-Athabasca Delta. It will discuss the use of diatoms as bioindicators in wetlands, and what information can be obtained from community assemblages of diatoms. Chapter 4 presents overall conclusions and implications, as well as suggesting what the next steps should be.

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Table 1.1 - Primary effects on water quantity and quality by the main resource development practices affecting the Western Plains of the Canadian Boreal Zone. Reproduced from Webster *et al.* 2015 with permission © Canadian Science Publishing or its licensors.

Development Type	Primary effects on water quantity	Primary effects on water quality	Length of effect (years)
Minerals and metal mining	Decrease in stream flow due to removals; increase where tailings ponds created; groundwater table declines due to dewatering	Contaminants and nutrients	1000+
Hydropower electricity generation	Increase upstream (flooding) and decrease downstream (lower and irregular flows)	MeHg and nutrient export; temperature alterations	100+
Oil and gas and oil sands development	Decrease in stream flow to removals; for surface extraction of oil sands end pit lakes created, but groundwater table declines due to dewatering	Contaminants and nutrients	1000+

Table 1.2 - Ecosystem services provided by wetlands in Canada's boreal zone.
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Service	Function
Regulating services	
Climate regulation	Regulation of greenhouse gases; regulation of climatic processes
Water regulation	Water storage; groundwater recharge, and discharge
Water purification and waste treatment	Retention, recovery, and removal of excess nutrients and pollutants
Cultural services	
Recreational and aesthetic	Opportunities for recreation and tourism; appreciation of nature
Spiritual and inspirational	Personal feelings and well-being; religious significance
Educational	Opportunities for education, training, and research
Supporting services	
Biodiversity	Habitats for species
Soil formation	Accumulation of organic matter
Nutrient cycling	Storage, recycling, processing, and acquisition of nutrients

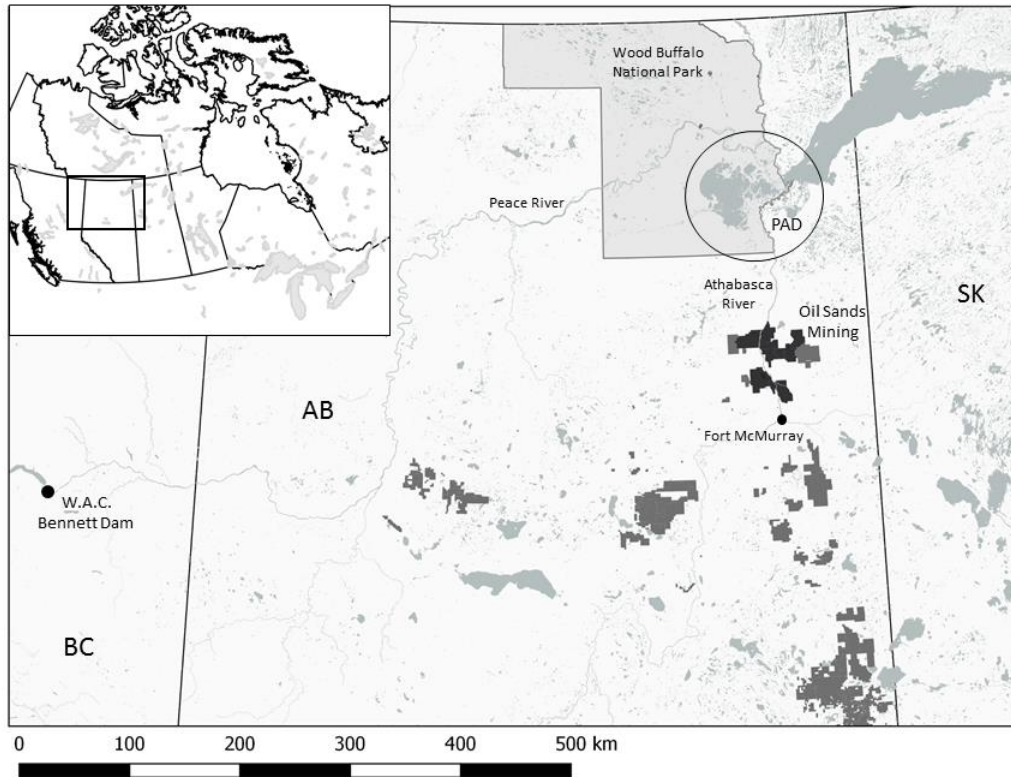


Figure 1.1 Map showing the study region in northeastern Alberta, the Peace – Athabasca Delta (PAD), and sources of potential impact due to resource development – W.A.C. Bennet Dam in British Columbia on the Peace River, and oil sands mining in Alberta along the Athabasca River. Mineable deposits are shown in black while additional *in situ* bitumen deposits are shown in dark grey. Map produced with layers produced for, and published in, Alexander and Chambers (2016).

CHAPTER 2: CONGRUENCE OF DIVERSITY PATTERNS BETWEEN BENTHIC DIATOM AND MACROINVERTEBRATE ASSEMBLAGES FROM BOREAL WETLANDS

Abstract

Despite the unclear and highly variable relationships in concordance of diversity patterns among taxa, the use of indicators in biomonitoring programs is ubiquitous. However, the choice of indicator may be inappropriate if assumptions concerning cross-taxon congruence are not tested before implementing a monitoring protocol. Diversity patterns of macroinvertebrates and benthic diatoms were examined from 12 boreal wetlands over two summers in the Peace-Athabasca Delta, Alberta, Canada to test the assumption of concordance in diversity patterns among traditional bioindicators. In two out of three periods sampled the diversity patterns were congruent and macroinvertebrates were a good indicator of diatom diversity. However, in August 2015 the diversity of macroinvertebrates and benthic diatom assemblages were incongruent likely due to a shift in the diatom community that was not reflected in the primary consumer assemblage. These results are consistent with the variability of cross-taxon congruence in the literature, and support the suggestion that samples of taxa from multiple trophic levels be used when assessing ecosystem status in biomonitoring programs.

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Introduction

Conservation strategies require accurate habitat information to support the management of ecosystems. Lack of resources and time constraints make extensive biodiversity surveys nearly impossible (Angermeier and Winston, 1997; Heino *et al.*, 2009). With each taxonomic group added to a survey there is an increase in: equipment costs, sampling effort, processing time, and expertise required. Consequently, biomonitoring studies frequently rely on the use of surrogate taxa to determine the current state of ecosystems (Angermeier and Winston, 1997). Looking at taxa or groups of taxa as bioindicators indirectly provides valuable information on habitat conditions (Bilton *et al.*, 2006) that are more difficult to assess using single time point samples of environmental variables [e.g., nutrient status (Rimet *et al.*, 2015); pollutants (Hirst *et al.*, 2002); and dissolved oxygen (Karlsen *et al.*, 2000)] However, the use of surrogate groups is a valid approach only if high cross-taxon congruence exists in the diversity patterns of target groups (Lopes *et al.*, 2011).

Cross-taxon congruence is an observed phenomenon in which diversity patterns of species co-vary in space (Gaston, 1996). This pattern has been observed in terrestrial (Su *et al.*, 2004; Qian and Kissling, 2010), and freshwater (Bilton *et al.*, 2006) ecosystems. This pattern can occur for one or more reasons including: i) similar responses to shared environmental variables, ii) shared biogeographic history, and/or iii) direct biotic interactions such as a predator- (or parasite-) prey relationships (Toranza and Arim, 2010). Biomonitoring studies, particularly those in freshwater, often assume a high level of cross-taxon congruence in order to apply results from an indicator taxon to the ecosystem as a whole (Bilton *et al.*, 2006). However, past studies have rarely tested how

well an indicator taxon reflects the richness and diversity of the wider community. This may cause problems in applicability and reliability of biomonitoring programs as levels of congruence vary among ecosystems. Congruency among taxa can vary by region, taxa studied, scale, and disturbance level. For example, a study on terrestrial organisms by Su *et al.* (2004) found positive correlation between plant species richness and butterfly richness in one study site (the Tetons), but no correlation in another study site (the Gallatins) even though both study sites occurred within Yellowstone National Park. Specifically in aquatic habitats, assemblage concordance varies by taxa studied. Grenouillet *et al.* (2008) found that while fish assemblages were concordant with both diatoms and benthic macroinvertebrates assemblages, the diatom community was not concordant with the benthic macroinvertebrate community. Additionally, Paavola *et al.* (2003) found that community classifications in headwater streams are not concordant across taxonomic groups (fish, invertebrates, and bryophytes) because different taxa respond to different environmental factors. However, Tisseuil *et al.* (2013) found that species richness and endemism patterns are significantly correlated among five freshwater taxa – aquatic mammals, aquatic birds, fishes, crayfish and aquatic amphibians – at a global scale. Qian and Kissling (2010) found that correlation of species richness is stronger at the regional scale in terrestrial systems. Disturbance level has also been shown to have inconsistent effects on congruence. A study in two ecoregions of Alberta on four terrestrial indicators (birds, vascular plants, bryophytes, and mites) found that congruence was stronger in highly disturbed sites in the Boreal ecoregion while congruence was weaker in highly disturbed sites of the Grasslands ecoregion (Rooney and Azeria, 2014). To complicate matters further, community assemblage patterns may

be concordant among sites while species richness is not (Su *et al.*, 2004). Erroneous conclusions drawn from unreliable bioindicators can potentially lead to inappropriate conservation measures (Paavola *et al.*, 2003). Cross-taxon congruence can vary with scale, habitat type, the taxa observed, geographic location, and disturbance level so it is critical to management that these relationships are determined for a specific region before biomonitoring programs are established with the testing restricted to one group of indicator taxa.

Biomonitoring of aquatic habitats in Canada generally focuses on benthic macroinvertebrates (Environment Canada, 2008). For a taxon or group of taxa to be considered an effective bioindicator it should be i) taxonomically/ecologically well-understood, ii) easily sampled, iii) easily identified, iv) present under various environmental condition, and v) show strong relationships in biodiversity with other target groups (Noss, 1990; Pearson, 1994; Heino *et al.*, 2009). Benthic macroinvertebrates are prime candidates for the first four requirements, but the status of the fifth requirement (diversity concordance) remains unclear from region to region. In particular, heterotrophic taxa may not be good indicators of responses in the photoautotrophic community. Paavola *et al.* (2003) found that benthic macroinvertebrates respond to environmental variables such as pH and stream size while photoautotrophs, like bryophytes, respond to water colour and nutrient levels. In terms of pollution sensitivity the nature of response by a bioindicator taxon can also vary among groups. In response to metal pollution in rivers, benthic macroinvertebrates show decreases in diversity, richness and total abundance while diatoms showed a shift in community assemblage, but no change in diversity, richness, or total abundance (Hirst *et al.*, 2002).

With the potential for impacts from resource development in the watershed of the Peace-Athabasca Delta, and the lack of traditional indicator taxa (e.g. Ephemeroptera, Plecoptera, and Trichoptera (EPT) are less prevalent in wetlands, and at high latitudes), the nature of these relationships needs to be determined in order to establish a successful biomonitoring program.

The aim of this study was to determine if diversity patterns of benthic diatoms and macroinvertebrate community assemblages are congruent for boreal wetlands in the Peace-Athabasca Delta in Alberta, Canada. This will be done by 1) characterizing the taxa present in the benthic diatom and macroinvertebrate communities, 2) assessing the similarity of wetland sites based on these assemblages, and 3) comparing the relationship among wetlands based on both benthic diatom and macroinvertebrate communities.

Methods

Study Sites

The study area was the Peace-Athabasca Delta (PAD) in northeastern Alberta, Canada. It is the world's largest boreal wetland, and is found in the southern range of Canada's Wood Buffalo National Park (Figure 2.1). This area is protected as a Ramsar wetland of international importance due to its status as critical habitat for migrating water fowl, including the endangered Whooping Crane (*Grus americana*). A total of 12 sites across four basins (Table 2.1) were sampled in June and August 2014, as well as in August 2015.

Periphyton

Collection of periphyton focused on the epiphytic portion (growing on plants) of the diatom community. Epipellic (growing at the sediment surface) algae have low

abundance in wetlands with extensive submerged and emergent macrophyte growth (Goldsborough and Robinson, 1996) so this form of periphyton was not sampled. Periphyton samples were collected from the biofilm of macrophyte clippings at each site. For the initial sampling trip (June 2014) a total of 10 macrophyte clippings were collected to ensure that enough diatom frustules were collected for analysis as total production in these sites was unknown. Due to the high density of material obtained from 10 clippings, the number of clippings collected in August (both 2014 and 2015) was reduced to five – the European standard for this collection method (King *et al.*, 2006). Macrophyte clippings were placed into a 1 L sampling jar with approximately 500 ml of native wetland water (June and August 2014), and shaken vigorously to dislodge the biofilm from the macrophyte; clippings were then discarded. In August 2015, native wetland water was replaced with municipal tap water to reduce the density of total suspended solids (silt, fine particulate organic matter, etc.) in the final sample because high levels of silt in August 2014 made some samples unable to be processed. The change from wetland water to tap water should not affect the community composition results because there was not a significant amount of planktonic taxa in any season sampled. Both emergent and submerged macrophytes were sampled, and the proportion of each was based on abundance and distribution at each sampling site. Diatoms were preserved using Lugol's iodine solution (5% w/v) to a final concentration of 1% by volume, and stored in a refrigerator until further processing.

Periphyton samples were gravity settled for approximately 24 hours, and the supernatant removed. A 10ml subsample was treated with 1M hydrochloric acid (HCl) to decalcify the sample. Diatom valves were cleaned using the hot hydrogen peroxide (30%

H₂O₂) method as described by Taylor *et al.* (2007). Additional digestion was required as the polysaccharide matrix of the biofilm did not decompose after the initial treatment. Addition of strong (15M) nitric acid (HNO₃) was used to oxidize any remaining organic matter (Stevenson and Bahls, 1999). After digestion, 0.5 ml of the cleaned sample was mounted in Naphrax to produce permanent slides for identification of diatom frustules (Barbour *et al.*, 1999; Taylor *et al.*, 2007).

Diatoms were identified at 400X magnification (or 1000X under oil immersion, where necessary) based on morphology of frustules, and identified to Genus level as deemed sufficient for routine biomonitoring by Kelly *et al.* (1995). Taxonomic identification mainly followed Krammer and Lange-Bertalot (1986, 1988, 1991, 1992), Krammer (2003) and Spaulding *et al.* (2010). Each sample was analysed with the use of a Leica DM2500, or an Olympus BX40 compound microscope. A minimum of 300 valves were counted, and additionally a taxa accumulation curve was generated for each slide. In order to maximize encounters of rare taxa, slides were analysed until 50 consecutive fields of view with no novel taxa were observed.

Benthic Macroinvertebrates

At each site, macroinvertebrates were sampled following a modified Canadian Aquatic Biomonitoring Network (CABIN) protocol (Environment Canada, 2008). A 400 µm kick net was swept through emergent and submerged vegetation for a total of two minutes; excess vegetation was rinsed and removed. The samples were transferred to 1 L storage containers and preserved using 95% ethanol and stored in a freezer.

Macroinvertebrate samples were processed according to the CABIN standard (Environment Canada, 2008). Samples were subsampled using a Marchant box, and a

minimum of 5% of the sample was identified to Family level with the use of a dissection microscope. Identification continued until at least 300 individuals (excluding planktonic taxa: cladocerans, copepods, etc.) were obtained.

Statistical Analysis

Each sampling period was analysed separately because this is more indicative of the sampling resolution at which biomonitoring programs function. Monitoring programs aim to produce data quickly to allow managers to make decisions about potential conservation measures, and do not regularly wait to pool data from multiple sampling trips before analysing the results. The assumptions of high cross-taxon congruence must be met consistently in each sampling period for bioindicators to be an effective tool.

Diversity patterns among benthic diatom communities, and macroinvertebrate + zooplankton communities at each site were analysed using principal coordinates analysis (PCoA; Gower, 1966). Zooplankton abundances were included in the macroinvertebrate analysis as these are a large component of the primary consumer community, and the more restrictive CABIN list of target organisms was designed for river sampling rather than wetland habitats.

Community dissimilarities were based on the Bray-Curtis dissimilarity index (Bray and Curtis, 1957; function: *vegdist*; package: *vegan*). While Bray-Curtis can be overly sensitive to datasets with highly dominant taxa, it is standard use in ecological community analyses and was determined to be useful for detecting ecological gradients (Faith *et al.*, 1987). Diatoms were identified to Genus level, while invertebrates were identified to Family level or Order for insect and non-insect taxa, respectively. Genus level identifications are standard for biomonitoring (King *et al.*, 2006) while Family and

Order level identifications for insect and non-insect taxa are standard in the CABIN protocol (Environment Canada, 2008). This disparity in taxonomic resolution should not affect analyses as separate PCoA ordinations were made for diatoms and benthic invertebrates, and Bray-Curtis dissimilarity indices for each pair of sites were calculated separately for diatoms and invertebrates. A similar study testing concordance among benthic macroinvertebrates and diatoms also used Bray-Curtis distance matrices with invertebrates at Family and diatoms at Species (Grenouillet *et al.*, 2008).

Distances were calculated using an arcsine-transformed ($p' = \arcsin[\sqrt{p}]$; Sokal and Rohlf, 1995; McCune and Grace, 2002; Whitlock and Schluter, 2009) taxon by site matrix of proportional abundances for June and August 2014. Arcsine was chosen over the logit transformation because the majority of criticism surrounding arcsine involves issues with regression analyses (see Warton and Hui, 2011). Additionally logit does not perform well when a dataset includes either extreme (0 or 1), and the included data matrix contained many zeros. Transformations were used due to a horseshoe effect in the benthic diatom community distribution, and for consistency among data sets in the macroinvertebrates + zooplankton matrix. The community distributions for August 2015 showed no evidence of horseshoe effects, however the analyses were run on both transformed and untransformed datasets with no difference in results so untransformed results were presented.

Concordance of diversity patterns between benthic diatom, and macroinvertebrate + zooplankton communities were analysed using PROTEST (Jackson and Harvey, 1993; Jackson, 1995; package: vegan) based on Procrustean matrix rotation (Gower, 1971;

1975). All statistical analyses were performed using R 3.0.3 statistical software (The R Foundation for Statistical Computing).

Results

A summary of taxon richness and Shannon diversity indices (H) for each site can be found in Table 2.2 (diatoms) and Table 2.3 (macroinvertebrates + zooplankton). The highest richness count for diatoms was found in PAD 3 with a total of 50 taxa in August 2015, while the lowest richness count was found in PAD 96 with a total of 11 taxa in August 2014. For macroinvertebrates the highest richness was found in PAD 38 in August 2014 with a total of 49 taxa, and the lowest richness was found in PAD 97 in June 2014 with a total of 26 taxa. The highest diversity of diatoms was found in PAD 1 with $H = 2.9$, while the lowest diversity index was found in PAD 97 with $H = 1.02$ both in August 2014. The highest diversity of benthic invertebrates was found in PAD 3 with $H = 2.90$, and the lowest diversity was found in PAD 97 with $H = 1.41$, both in June 2014. A list of Genus occurrence by site and sampling period for diatom taxa is available in Appendix 1.

In June 2014, 28.6% and 18.5% of the variance in the benthic diatom community was explained by the first two axes, respectively (Fig 2.2a). For the macroinvertebrate + zooplankton community, 30.4% and 13.9% of the variance was explained by the first two axes (Fig 2.2b). This represents variation among wetlands due solely to differences in community assemblages. In both the diatom ($BC = 0.29$, where 0 represents identical community composition and 1 represents no shared taxa) and macroinvertebrate ($BC = 0.22$) ordinations, sites in the Embarras sub-delta (PAD 96 and 97) plot together, and separately from sites in other sub-deltas. Similarly, the sites from Cree-Mamawi Creek

(PAD 01, 03, and 04) also plot distinctly from other sub-deltas, with more overlap between sites in the Peace and Birch sub-deltas. The PROTEST analysis found that the benthic diatom and macroinvertebrate + zooplankton communities from June 2014 were significantly more similar than due to chance (Fig 2.2c; 999 permutations; $m^2 = 0.48$; $p = 0.003$).

In August 2014, 32.8% and 22.1% of the variance in the benthic diatom community was explained by the first two axes (Fig 2.3a). For the macroinvertebrate + zooplankton community, 28.2% and 23.9% of the variance was explained by the first two axes (Fig 2.3b). This represents variation among wetlands due solely to differences in community assemblages. Similarly to the results from June, PAD 96 and 97 (Embarras) are grouping together in both the benthic diatom ($BC = 0.38$) and macroinvertebrate + zooplankton ($BC = 0.35$) communities. In the Peace sub-delta PAD 14 and 33 are dissimilar in both the diatom ordination ($BC = 0.76$) and the macroinvertebrate + zooplankton ordination ($BC = 0.51$) despite their geographic proximity. The PROTEST analysis found that the benthic diatom and macroinvertebrate + zooplankton communities from August 2014 were significantly more similar than due to chance (Fig 2.3c; 999 permutations; $m^2 = 0.58$; $p = 0.023$).

In August 2015, 45.1% and 21.9% of the variance in the benthic diatom community was explained by the first two axes, respectively (Fig 2.4a). For the macroinvertebrate + zooplankton community, 26.9% and 25.2% of the variance was explained by the first two axes (Fig 2.4b). This represents variation among wetlands due solely to differences in community assemblages. Following the pattern evident in 2014, the Embarras sites (PAD 96 and 97) have distinct communities that cause them to group

together for both benthic diatoms (BC = 0.17) and macroinvertebrates (BC = 0.38). There are distinct differences among sites in the Peace sub-delta, in particular with PAD 14 and 33, in the diatom community. In the diatom ordination, PAD 14 and 33 are highly dissimilar (BC = 0.72), while in the macroinvertebrate + zooplankton ordination the communities are very similar (BC = 0.26). The PROTEST analysis found that the benthic diatom and macroinvertebrate + zooplankton community assemblages from August 2015 were not more similar than due to chance (Fig 2.4c; 999 permutations; $m^2 = 0.79$; $p = 0.18$).

Discussion

Richness and Diversity in the Peace – Athabasca Delta

Generally speaking, species richness and diversity tend to decrease with increasing latitude, also known as the latitudinal diversity gradient (Fischer, 1960). However, despite its high latitude (~58°N), the Peace-Athabasca Delta is considered to be a diverse and productive inland delta with 219 bird species, 300+ species of invertebrates, 22 species of fish, and 43 species of mammals (Struzik, 2013). Given this, and assumptions of concordant diversity patterns, we would expect the diversity of diatoms to also be high and comparable with similar habitats at lower latitudes. Richness ranged from 11 to 50 (Table 2.2) taxa among sites, similar to the findings of Duthie (1979) with 20 – 50 found per sample for Labrador lakes in late summer. A study by Veres *et al.* (1995) on periphytic diatoms of saline subarctic lakes in the Yukon found taxon richness varied from 13 – 22 with a total of 36 taxa identified from a total of three lakes. However, most limnological studies in Canada focus on either the periphyton community of rivers or the phytoplankton community of lakes and as such, further comparisons of the diatom

communities (richness and diversity) in wetlands of the Peace-Athabasca Delta to other regions of Canada is difficult. A typical river study such as that by Hill *et al.* (2001) of Mid-Appalachian streams found as many as 72 distinct diatom taxa in a single sample and a total of 522 species, whereas in the PAD a total of 89 distinct diatom taxa were identified out of 35 samples from 12 separate wetlands.

The Peace-Athabasca Delta is characterized by a series of low lying rivers with associated perched basins. The relatively flat landscape coupled with the higher elevation of the wetlands compared to the nearby river channel may lead to low recruitment of taxa. Migration of low motility species (such as diatoms) occurs passively, and only during flood events which replenish wetlands with nutrients, and allow for connectedness among distinct basins. There is also relatively homogeneous habitat within and among wetlands. Available substrate for diatom growth includes: on the sediment (epipelonic/episammonic), on macrophytes (epiphytic), or in the water column (planktonic). The combination of low recruitment and low niche differentiation could contribute to lower diatom richness when compared to more dynamic and heterogeneous habitats such as those found in rivers.

Community Similarity

Despite being part of the relictual Athabasca sub-delta, wetland sites along the Embarras River (PAD 96 and 97) have distinct diatom and macroinvertebrate communities from other wetlands in the Athabasca sub-delta (PAD 01, 03, and 04). The major diatom Genus present in the Embarras wetlands is *Cocconeis* Ehrenberg 1837 with an average proportional abundance across sampling periods of 0.69 and 0.86 for PAD 96 and 97, respectively. This Genus is alkaliphilous and tolerant of moderate organic

pollution (Kelly *et al.*, 2005). Similar to the diatom community, the benthic invertebrate community is also dominated by more tolerant taxa with high proportional abundances of Amphipoda and Daphniidae. These two sites fall outside of the Park boundary, and the winter ice road from Fort Chipewyan to Fort McMurray is in close proximity to these wetlands. The additional impact caused by automobile pollution is a likely contributor to the distinct diatom and benthic invertebrate communities found at these sites.

Congruence of Community Ordinations

For June and August 2014, the benthic diatom and macroinvertebrate + zooplankton community ordinations were significantly more similar than due to chance. The macroinvertebrate + zooplankton community diversity is an accurate indicator of diversity in the benthic diatom community as their diversity patterns are congruent. Contrary to the results of previous sampling periods the benthic diatom and macroinvertebrate + zooplankton community ordinations were not significantly more similar than due to chance in August 2015. Therefore, these ordinations were not concordant (i.e. diversity patterns were not congruent) and the macroinvertebrate + zooplankton community assemblage was not an accurate indicator of the benthic diatom community, or vice versa.

In August 2015, PAD 14 was distinct from other sites in the Peace sub-basin (PAD 33, 37 and 38) for the benthic diatom community (Fig 2.4a) whereas all Peace wetlands grouped together based on the macroinvertebrate + zooplankton community (Fig 2.4b). In particular, PAD 14 and PAD 33 were highly dissimilar in the benthic diatom community, but were one of the most similar pairings in the macroinvertebrate + zooplankton community. This difference in community composition similarity was likely a major

factor driving the incongruence of these two ordinations. The benthic diatom communities of wetlands in August 2015 were dominated by either *Cocconeis* Ehrenberg 1837 (Birch, Peace and Embarras sites) or *Epithemia* Kützing 1844 (Mamawi and Peace sites) (Table 2.4). As mentioned previously, *Cocconeis* Ehrenberg 1837 is a Genus tolerant of moderate organic pollution (Kelly *et al.*, 2005) and *Epithemia* Kützing 1844 can dominate in nitrogen-limited conditions due to nitrogen-fixing cyanobacterial endosymbionts (Spaulding, 2010). The benthic diatom community of PAD 14 lacks either of these Genera in significant proportions, and this is likely driving the difference between PAD 14 and other wetlands in the benthic diatom ordination, particularly other sites in the Peace sub-basin.

The increase of Epithemoid taxa (*Epithemia turgida* (Ehrenberg) Kützing 1844, *E. sorex* Kützing 1844, *E. adnata* (Kützing) Brébisson 1838, and *Rhopalodia gibba* (Ehrenberg) O. Müller 1895), which possess nitrogen-fixing cyanobacteria, could suggest that nitrogen limitation is an issue in wetlands of the Athabasca and Peace (excluding PAD 14) sub-deltas. Blooms of nitrogen-fixing taxa are a common response to low nitrogen conditions (Schindler, 1977; Smith, 1983; Schindler, 1990), which may be caused by an influx of phosphorous to the system (Camarero and Catalan, 2012). This community shift due to possible eutrophication would not necessarily be detected by exclusively sampling the macroinvertebrate + zooplankton community.

Conclusion

As in previous studies, these results do not suggest a clear answer to the question of concordance of diversity patterns among bioindicator taxa. Despite the significant congruence of diversity patterns in 2014, these results alone do not support the

justification of restricting monitoring to one group of bioindicators. Generally, studies in aquatic systems that have shown significant correlation among taxa have not shown high correlation among taxa and so significantly congruent diversity patterns are not enough to predict biodiversity in other taxa (Heino, 2010). Many studies on diversity pattern congruence have found variable and inconclusive results that cannot be generalized to a wider region. Patterns of diversity may or may not be concordant based on the taxa studied, the geographic region in which a study is performed, the habitat type sampled, and the scale at which samples are collected. The most consistent pattern observed has been that richness and endemism patterns for freshwater taxa are congruent at a global scale (Tisseuil *et al.*, 2013), but this resolution is not exceedingly useful for the purposes of biomonitoring. Due to lack of consistency, cross-taxon congruence cannot be assumed to exist between particular taxa for the purpose of using a single bioindicator (e.g. benthic macroinvertebrates).

Any large-scale biomonitoring program should first test the efficacy of their chosen bioindicators before implementing a final sampling protocol. Given that autotrophs and heterotrophs generally respond to different physical and chemical variables (Paavola *et al.*, 2003), and that their responses to the same stressor can be different (Hirst *et al.*, 2002), taxa from each broad group should be analysed for the purposes of potential impact monitoring. Specifically for the Peace-Athabasca Delta, macroinvertebrates would be a useful indicator for potential pollutant impacts, but given that eutrophication could also be an issue associated with resource development and landscape changes in the watershed, the primary producer community, particularly diatom community assemblage, should continue to be monitored.

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Table 2.1 - Site identification and decimal degree coordinates for sampling sites in Fort Chipewyan, Alberta, Canada. Both Cree – Mamawi Creek and the Embarras River are part of the relictual Athabasca Delta

Site ID	Local Basin	N	W
PAD 01	Cree – Mamawi Creek	58.6028	-111.52577
PAD 03	Cree – Mamawi Creek	58.56453	-111.51126
PAD 04	Cree – Mamawi Creek	58.50785	-111.51802
PAD 14	Peace River	58.87459	-111.3247
PAD 33	Peace River	58.89661	-111.41808
PAD 37	Peace River	58.83228	-111.28118
PAD 38	Peace River	58.86371	-111.5837
PAD 92	Birch River	58.35612	-112.75845
PAD 93	Birch River	58.41061	-112.57385
PAD 94	Birch River	58.44769	-112.40499
PAD 96	Embarras River	58.4835	-111.21086
PAD 97	Embarras River	58.50724	-111.2674

Table 2.2 - Taxon richness and Shannon Diversity Index of diatom community, summarised at Species level, for each wetland for sampling periods June 2014, August 2014, and August 2015. The highest and lowest values for richness and diversity are shown in bold.

Site ID	Taxon Richness			Shannon Diversity Index		
	Jun-14	Aug-14	Aug-15	Jun-14	Aug-14	Aug-15
PAD 01	30	35	37	2.57	2.90	2.06
PAD 03	27	24	50	2.68	2.55	2.36
PAD 04	25	--	44	2.26	--	2.44
PAD 14	23	23	35	2.48	2.31	2.57
PAD 33	12	14	34	1.93	1.05	1.73
PAD 37	25	18	28	1.88	1.75	1.89
PAD 38	29	25	29	2.43	2.47	2.14
PAD 92	24	17	29	2.46	1.68	1.78
PAD 93	13	16	21	1.94	2.27	2.02
PAD 94	21	18	25	2.53	1.76	1.68
PAD 96	28	11	36	1.94	1.59	1.37
PAD 97	30	18	32	2.53	1.02	1.58

Table 2.3 – Taxon richness and Shannon Diversity Index of benthic macroinvertebrate community, summarised at Family level for insects and Order level for non-insect taxa, for each wetland for sampling periods June 2014, August 2014, and August 2015. The highest and lowest values for richness and diversity are shown in bold.

Site ID	Taxon Richness			Shannon Diversity Index		
	Jun-14	Aug-14	Aug-15	Jun-14	Aug-14	Aug-15
PAD 01	31	29	28	2.41	2.27	1.56
PAD 03	43	34	26	2.90	2.02	1.69
PAD 04	42	33	28	2.34	1.85	1.98
PAD 14	39	35	26	2.28	2.39	2.26
PAD 33	36	38	31	2.35	1.79	2.41
PAD 37	40	38	44	2.35	2.42	2.46
PAD 38	36	49	28	1.99	2.15	2.55
PAD 92	34	34	35	2.59	2.50	2.58
PAD 93	37	45	45	2.45	2.53	2.45
PAD 94	41	35	24	2.54	2.78	1.95
PAD 96	27	30	22	1.75	2.07	1.62
PAD 97	26	27	29	1.41	2.39	2.28

Table 2.4 - The top three most abundant benthic diatom taxa, summarised at Genus level, for each wetland site in August 2015 with associated proportional abundances.

Most Abundant Taxa			
	1st	2nd	3rd
PAD 1	<i>Cocconeis</i> (0.45)*	<i>Epithemia</i> (0.19)†	<i>Nitzschia</i> (0.17)◇
PAD 3	<i>Cocconeis</i> (0.52)*	<i>Epithemia</i> (0.16)†	<i>Gomphonema</i> (0.09)
PAD 4	<i>Epithemia</i> (0.41)†	<i>Navicula</i> (0.12)	<i>Nitzschia</i> (0.17)◇
PAD 14	<i>Eunotia</i> (0.28)	<i>Gomphonema</i> (0.24)	<i>Encyonema</i> (0.17)
PAD 33	<i>Epithemia</i> (0.65)†	<i>Encyonema</i> (0.08)	<i>Nitzschia</i> (0.07)◇
PAD 37	<i>Cocconeis</i> (0.47)*	<i>Epithemia</i> (0.28)†	<i>Fragilaria</i> (0.10)
PAD 38	<i>Cocconeis</i> (0.34)*	<i>Fragilaria</i> (0.18)	<i>Epithemia</i> (0.16)†
PAD 92	<i>Cocconeis</i> (0.72)*	<i>Nitzschia</i> (0.07)◇	<i>Navicula</i> (0.04)
PAD 93	<i>Nitzschia</i> (0.49)◇	<i>Cocconeis</i> (0.14)*	<i>Navicula</i> (0.11)
PAD 94	<i>Cocconeis</i> (0.76)*	<i>Gomphonema</i> (0.09)	<i>Nitzschia</i> (0.05)◇
PAD 96	<i>Cocconeis</i> (0.84)*	<i>Nitzschia</i> (0.07)◇	<i>Halamphora</i> (0.01)
PAD 97	<i>Cocconeis</i> (0.78)*	<i>Gomphonema</i> (0.10)	<i>Navicula</i> (0.05)

† Indicates taxa that harbour nitrogen-fixing cyanobacterial endosymbionts

* Indicates taxa that are tolerant of mild to moderate organic pollution

◇ Indicates taxa that are tolerant to high organic pollution

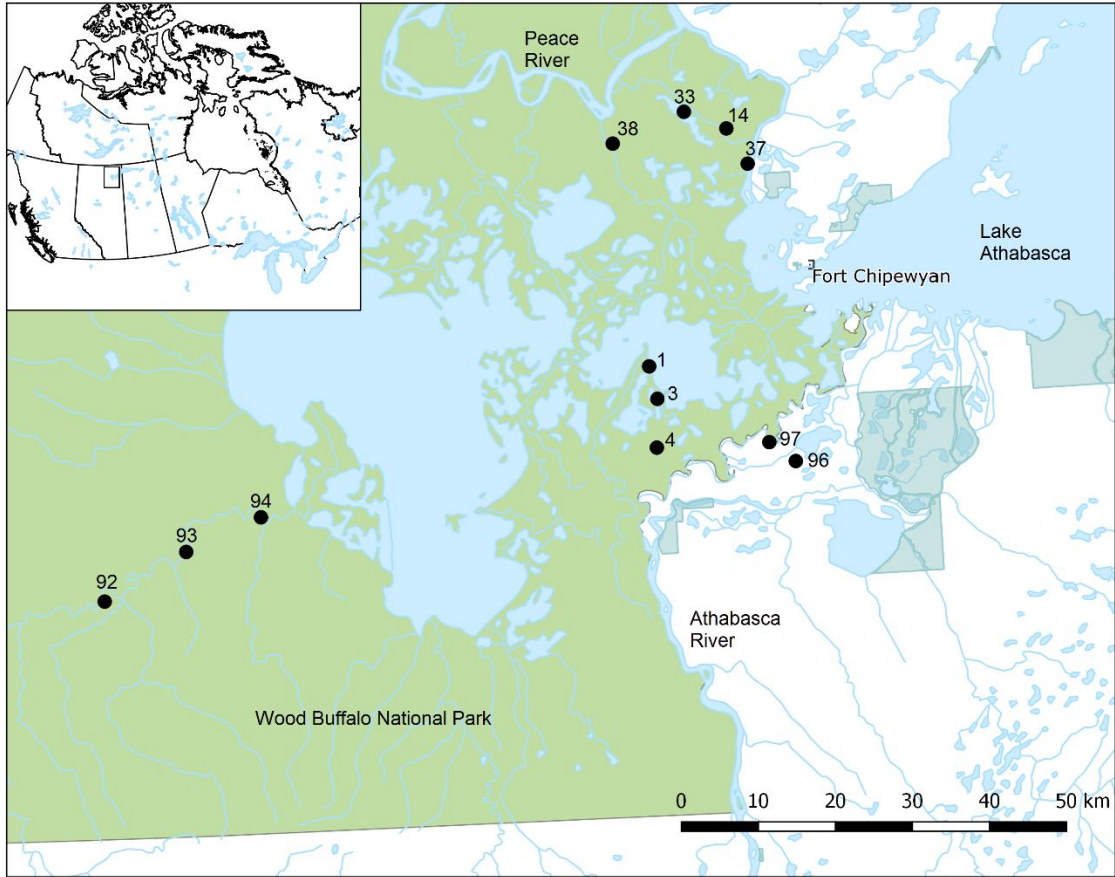


Figure 2.1 - Location of 12 study sites across four sub-basins in the Peace Athabasca Delta in northeastern Alberta, Canada.

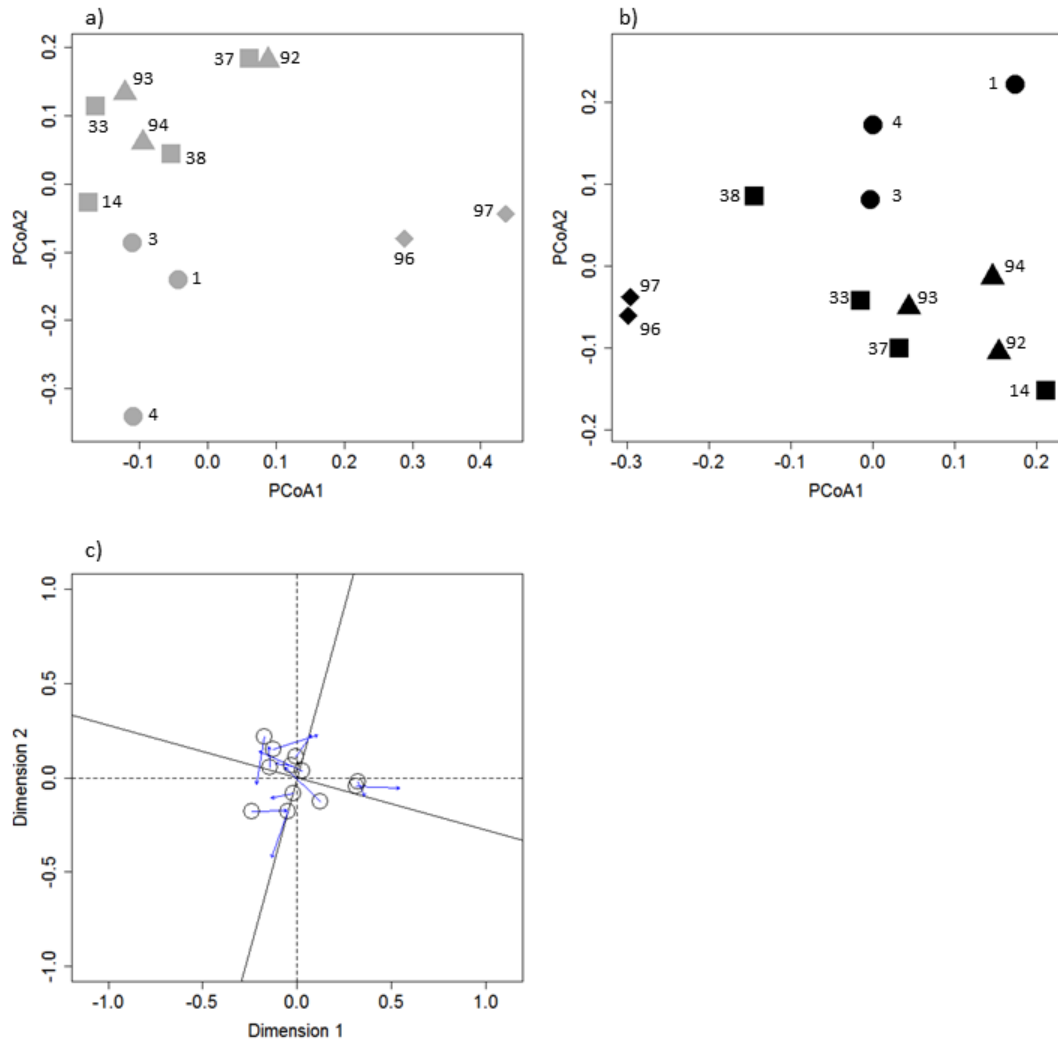


Figure 2.2 - Principal coordinates analysis (PCoA) based on arcsine squareroot-transformed Bray-Curtis distances of (a) benthic diatom community assemblages (28.6% and 18.5% variance explained by the first two axes) and (b) macroinvertebrate + zooplankton community assemblages (30.4% and 13.9% variance explained by the first two axes) of wetlands in the Peace-Athabasca Delta from June 2014; and (c) PROTEST analysis on benthic diatom and macroinvertebrate + zooplankton ordinations ($m^2 = 0.48$; $p = 0.003$, 999 permutations). Taxonomy is summarised at the Genus level for the benthic diatom community, and at Family level or Order for insects and non-insect taxa, respectively in the macroinvertebrate + zooplankton community.

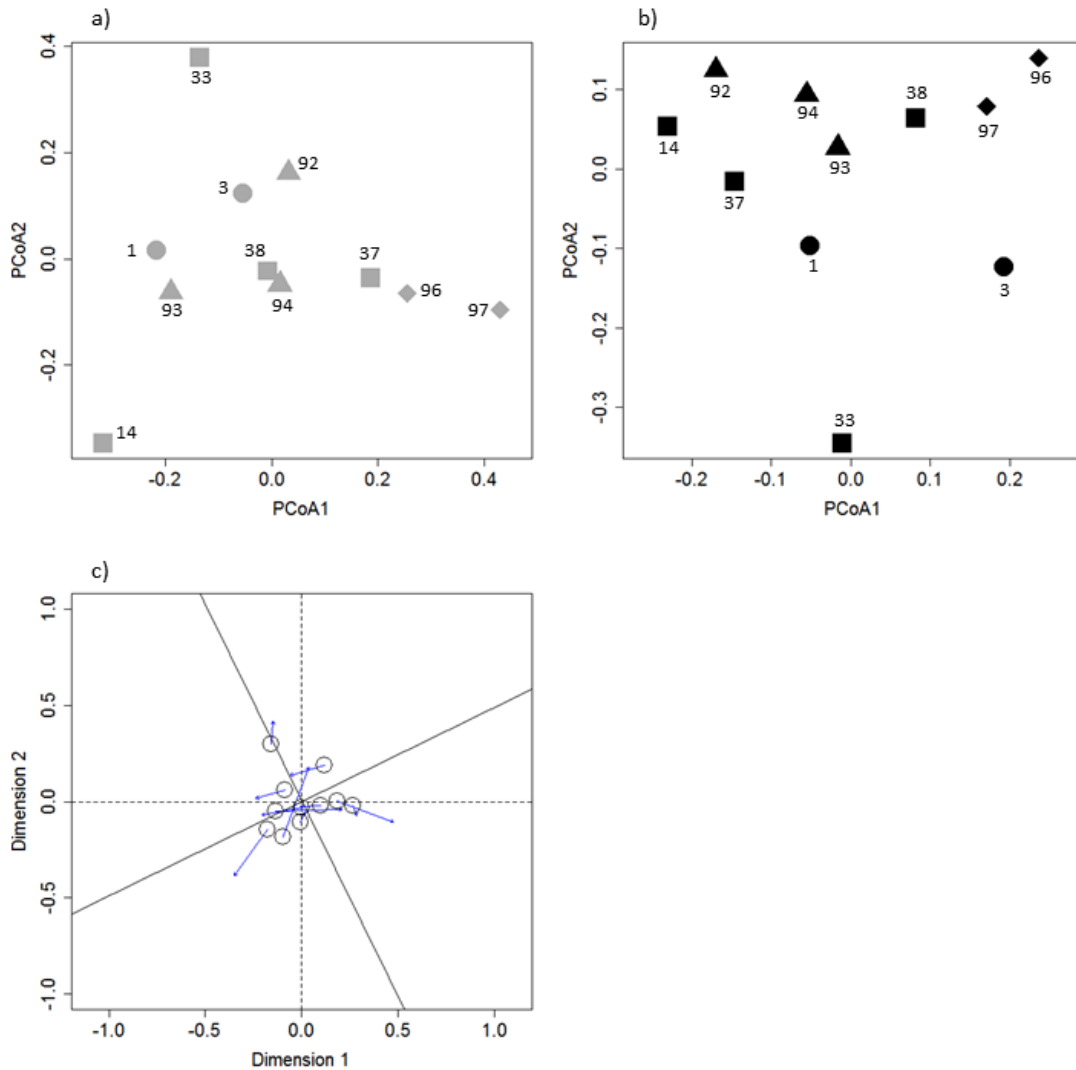


Figure 2.3 - Principal coordinates analysis (PCoA) based on arcsine squareroot-transformed Bray-Curtis distances of (a) benthic diatom community assemblages (32.8% and 22.1% variance explained by the first two axes) and (b) macroinvertebrate + zooplankton community assemblages (28.2% and 23.9% variance explained by the first two axes) of wetlands in the Peace-Athabasca Delta from August 2014; and (c) PROTEST analysis on benthic diatom and macroinvertebrate + zooplankton ordinations ($m^2 = 0.58$; $p = 0.023$, 999 permutations). Taxonomy is summarised at the Genus level for the benthic diatom community, and at Family level or Order for insect and non-insect taxa, respectively in the macroinvertebrate + zooplankton community.

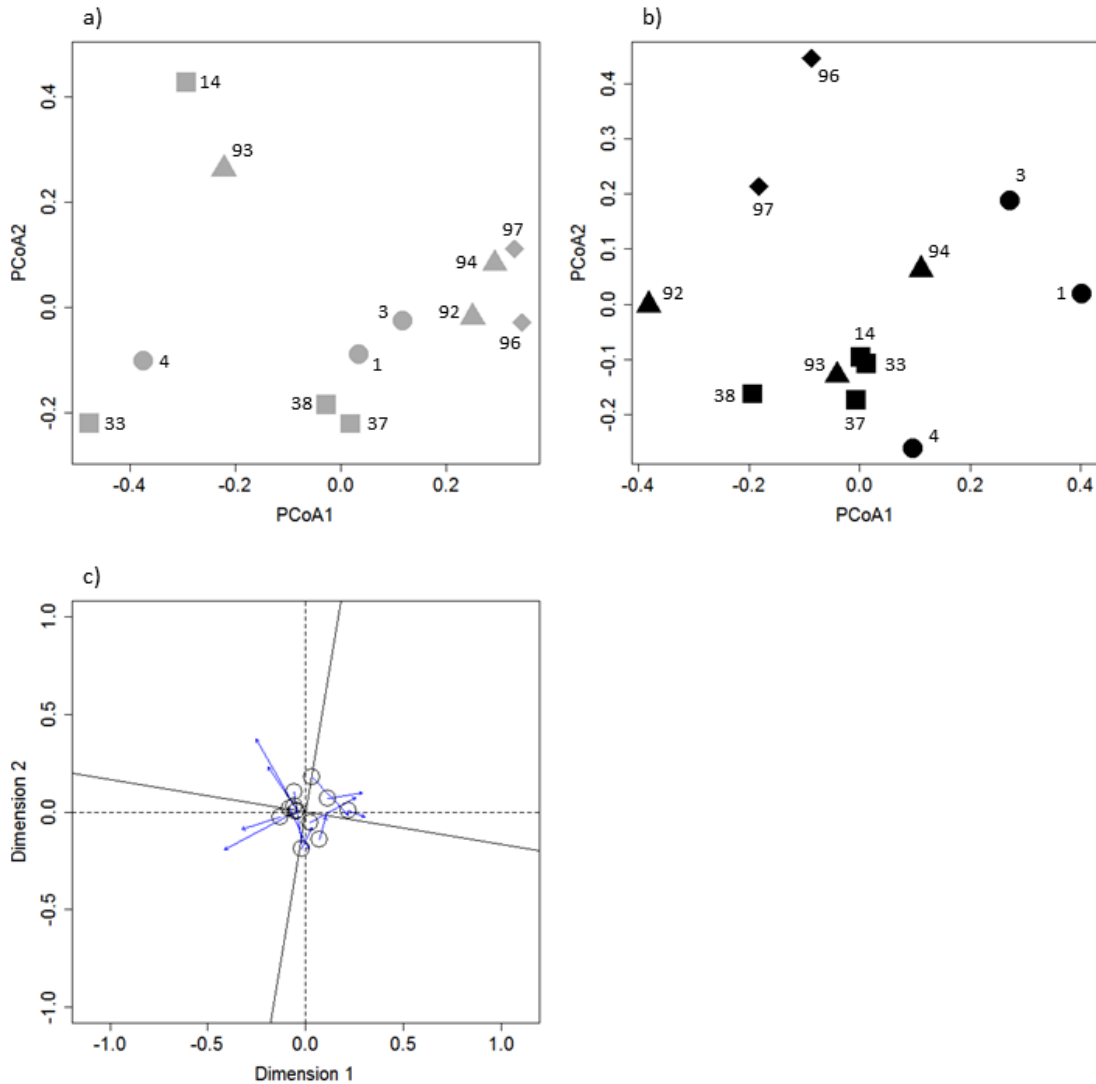


Figure 2.4 - Principal coordinates analysis (PCoA) based on Bray-Curtis distances of (a) benthic diatom community assemblages (45.1% and 21.9% variance explained by the first two axes) and (b) macroinvertebrate + zooplankton community assemblages (26.9% and 25.2% variance explained by the first two axes) of wetlands in the Peace-Athabasca Delta from August 2015; and (c) PROTEST analysis on benthic diatom and macroinvertebrate + zooplankton ordinations ($m^2 = 0.79$; $p = 0.18$, 999 permutations). Taxonomy is summarised at the Genus level for the benthic diatom community, and at Family level or Order for insects and non-insect taxa, respectively in the macroinvertebrate + zooplankton community.

CHAPTER 3: ENVIRONMENTAL DRIVERS OF DIATOM COMMUNITY DISTRIBUTION IN THE PEACE-ATHABASCA DELTA

Abstract

Habitat degradation associated with resource development is a major ecological concern, particularly in Canada's boreal zone where limited information on biodiversity is available. Habitat degradation can lead to reductions in biodiversity and ecosystem function, especially when drivers of variability and diversity patterns have not been identified for a region of interest. Spot measurements of six abiotic variables (total dissolved nitrogen, total dissolved phosphorus, dissolved iron, turbidity, pH, and specific conductance) were taken from 12 wetlands in northern Alberta's Peace-Athabasca Delta over three sampling periods, and regressed against an ordination of diatom community composition to identify key environmental drivers of diatom community variation. Indirect gradient analysis identified two major gradients among sites. First, separation of sites among sampling periods showed successional seasonal change in diatom community composition. Second, separation of sites from the Peace sub-delta and Birch sub-delta showed a gradient of geographic separation. The direct gradient analysis failed to explain the drivers of these two gradients, but did show that alkalinity is a key driver of diatom community composition in the Embarras sub-delta and that these sites could be particularly vulnerable to community changes associated with acidification.

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Introduction

Resource development can have significant impacts on the surrounding landscape. Waterbodies, such as rivers and wetlands, are particularly vulnerable to anthropogenic induced habitat loss in the associated watershed. Some of these alterations include: land use type/ land clearing (e.g. a shift from forest habitat to urban development), water extraction, and channelization/ river engineering. A shift in land use to mining activities (such as oil sands extraction) can create sulphur and nitrogen oxide emissions which may be deposited in wetlands in the form of acid precipitation (Beamish, 1976; Galloway *et al.* 1978; Cowling and Linthurst, 1981) increasing the potential for acidification. Land clearing destabilizes the soil matrix and reduces water retention (Saha and Kukal, 2013). This can lead to increased run-off of nutrients and sediment to rivers increasing the potential for eutrophication, high turbidity (due to increased total suspended solids (TSS)), and acidification in downstream waterbodies. Water extraction and river engineering may reduce the volume of receiving water in rivers and downstream wetlands which further exacerbates eutrophication as nutrients become more concentrated in the water column, as well as increasing conductivity as ions also become more concentrated. In addition to impacts from resource development, changes in receiving waters are intensified by warmer and drier conditions associated with climate change in Canada's north which also reduce water levels through higher rates of evaporation (Rouse *et al.*, 1997).

Acidification has both sub-lethal and lethal effects on biota. Cell function is reduced because proteins cannot function outside of their optimal pH range (Campbell *et*

al., 2008). Organisms only have access to a finite amount of resources and must allocate these resources among three main processes: maintenance, growth and reproduction (resource allocation theory). Acid stress causes organisms to put more effort into maintenance rather than growth or reproduction which reduces fecundity and ultimately can contribute to local extinction of taxa. At the community level this can be seen as a shift in composition. Reductions in taxon richness and diversity are possible as only the most tolerant taxa remain (Connell, 1978); however, these changes can also favour establishment of non-native or invasive taxa (Clark *et al.*, 2015) as natives become less competitive which may cause richness to stay the same or even increase.

Eutrophication of aquatic habitats increases the magnitude and frequency of harmful algal blooms (HABs) (Steffen *et al.*, 2014). Excess nutrients in the environment stimulate growth of photoautotrophs that increases the potential for toxin buildup in the water column. The boom-bust life cycle of phytoplankton and phytobenthos ultimately leads to a large die-off that creates oxygen minimum zones due to increased rates of decomposition (Chislock *et al.*, 2013). These hypoxic/anoxic conditions are unfavourable for heterotrophs and may cause fish kills.

Increased turbidity may lead to reductions in productivity by reducing light availability for photosynthesis. The photoautotrophic community will shift to taxa that are able to maintain their photosynthetic rate under low light conditions, including certain low-light adapted species of cyanobacteria (Donald *et al.*, 2011; Taranu *et al.*, 2015). If total production is reduced then a shift from autochthonous to allochthonous carbon sources is probable which would lead to a shift in the primary consumer community from taxa that feed on algae (i.e. scrapers/grazers) to taxa that feed on detritus (e.g.

collectors/shredders). This can reduce community diversity and likely results in loss of ecosystem function.

Similarly to acidification, increased specific conductance of the external environment can also reduce growth and reproduction in biota. Increased ion concentration in the water column creates osmotic stress, and more cellular resources (re: energy) are put into maintaining osmotic balance (Campbell *et al.*, 2008). In the short term, reproduction decreases and population size is lowered. If these conditions are maintained local extinctions can occur, invasion success can increase, and community composition shifts. Reductions in richness and diversity are also possible.

Objectives

The purpose of this study was to examine what physico-chemical variables are potentially driving observed differences in diatom community composition in wetlands of the Peace-Athabasca Delta. This was done by: 1) examining the differences in six variables over three sampling periods in each sub delta, and 2) regressing these variables against an ordination of community composition and abundance to identify possible drivers of variation. This also allowed us to examine which environmental factors were associated with individual sites and taxa.

Methods

Study Sites

Samples were collected from 12 wetlands in the Peace-Athabasca Delta (PAD) in northeastern Alberta, Canada (Fig 3.1). The PAD is a delta complex formed at the inland confluence of two large rivers (the Peace and the Athabasca) and a third smaller river (the Birch). It consists of a series of variably connected low-lying wetlands and their

associated rivers covering 5,674 km² west of Lake Athabasca. Approximately 80% of the delta lies within Wood Buffalo National Park. This area is protected both as a Canadian National Park and as a wetland of international importance under the Ramsar Convention (Ramsar Secretariat, 2003). It is at risk of impact from upstream development including oil sands mining in the watershed of the Athabasca River and hydroelectric dams on the Peace River. The Peace-Athabasca Delta is an ecologically important boreal wetland providing habitat to the largest free-roaming herd of bison (*Bison bison*) in the world (Timoney, 2013) and migrating water fowl, such as the endangered Whooping Crane (*Grus americana*).

Water Chemistry

Water samples, for chemical analysis, were collected as part of the Joint Canada-Alberta Implementation Plan for Oil Sands Monitoring starting in June 2012 following standard operating protocols. Samples for metals, major ions, and nutrients were analysed at Environment Canada's National Laboratory for Environmental Testing (NLET) facility using nationally recognized analytical standards and procedures (Environment Canada, 2012). See Appendix 2 for table of parameters analysed.

Periphyton

Samples for diatom community composition analysis were collected from the epiphytic biofilm community at each wetland site. These soft-bottomed wetlands lack hard substrates for traditional rock scrapes, and the density of submerged macrophytes means epipsammic diatoms are of low abundance. Both submerged and emergent macrophytes were sampled as the dominant substrate. A total of 10 clippings per site were collected for the initial June sampling to ensure an adequate density of material for

identification. After preliminary analysis, macrophyte collection was reduced to five clippings for August 2014/15 due to the excessive density of diatom valves obtained from 10 clippings. Clippings were placed into 1 L wide-mouthed sampling jars with approximately 500 ml of water and vigorously shaken to remove the biofilm. In 2014, local wetland water was used to collect samples. For 2015 sampling this was changed to municipal tap water to reduce the density of fine particulate matter (i.e. silt) in the sample which had caused processing issues in previous sampling periods. Macrophyte clippings were discarded, and the sample was preserved with 5% w/v Lugol's iodine solution to a final concentration of 1% by volume. Samples were stored in a refrigerator until further processing.

Diatom samples were settled for 24 hours and the supernatant was removed to reduce the volume of sample to approximately half (~250 ml). A 10 ml subsample was removed for digestion. Periphyton samples were treated with 1M hydrochloric acid (HCl) for decalcification, and boiled in concentrated hydrogen peroxide (30% H₂O₂) for three hours to oxidize any organic matter, and to clean diatom frustules (Stevenson and Bahls, 1999). A second round of digestion with concentrated nitric acid (16M HNO₃) (Stevenson and Bahls, 1999) was performed to further break down residual polysaccharides from the biofilm matrix. A 0.5 ml subsample of cleaned diatom valves was mounted in Naphrax to produce permanent slides for identification of diatom frustules (Stevenson and Bahls, 1999).

Diatoms were identified at 400X magnification (or 1000X under oil immersion, where necessary) based on morphology of frustules, and identified to Genus level to minimize identification errors (Kelly *et al.*, 1995). Taxonomic identification mainly

followed Krammer and Lange-Bertalot (1986, 1988, 1991, 1992), Krammer (2003) and Spaulding *et al.* (2010). Each sample was analysed with the use of a Leica DM2500, or an Olympus BX40 compound microscope. A minimum of 300 valves were counted, and additionally a taxa accumulation curve was generated for each slide. In order to maximize encounters of rare taxa, slides were analysed until 50 consecutive fields of view with no novel taxa were observed.

Statistical Analyses

Indirect and direct gradient analyses were performed in order to identify gradients in community composition among sites. Community composition data was summarised in a site by Genus matrix of proportional abundances. A Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980) was performed in order to determine if the gradient response was linear or unimodal (function: *decorana*; package: *vegan*). The results of the DCA showed that the response was linear with a first axis gradient length of 2.33 (see DCA output in Appendix 3). According to Legendre and Legendre (1998) a gradient length of < 2.5 denotes a linear gradient, so PCA (indirect) and RDA (direct) were chosen for further analyses.

Principal Components Analysis (PCA; Hotelling, 1933) was used to examine biotic variation among sites (function: *rda*; package: *vegan*). The site by Genus matrix was logit transformed as suggested by Warton and Hui (2011) to remove a minor horseshoe effect (function: *logit*; package: *car*). The initial PCA results showed four sites as outliers (PAD 4 June 2014; PAD 3, PAD 4, and PAD 14 from August 2015) leading to clumping of the remaining sites and so they were removed from the analysis. The PCA results were plotted on axes PC1 and PC3 to maximize separation of sites in

multidimensional space. After gradients among wetlands were identified using PCA a direct gradient analysis was performed to identify what variables may be driving these gradients.

Physical and chemical water quality variables were chosen *a priori* for use in a Redundancy Analysis (RDA: van den Wollenberg, 1997). An RDA performs a multiple regression with continuous response variables against a community ordination in order to identify factors that may be driving the dissimilarity among sites and which variables are associated with individual taxa (function: rda; package: vegan). These variables include: total dissolved nitrogen (mg/l), total dissolved phosphorus (mg/l), dissolved iron ($\mu\text{g/l}$), turbidity (NTU), pH, and specific conductance (SPC; $\mu\text{S/cm}$). These variables were chosen as they have been previously shown to determine diatom species occurrence: N and P are essential macronutrients, while iron is a required micronutrient (Guillard and Lorenzen, 1972), turbidity affects light availability for photosynthesis (Goldsborough and Robinson, 1996), pH (Stokes, 1987) and SPC (Potapova and Charles, 2003) affect species richness and community composition. Due to strong correlations between dissolved iron and total dissolved phosphorus ($r = 0.64$), and between dissolved iron with total dissolved nitrogen ($r = 0.79$), the RDA was run without dissolved iron (see Appendix 4 for correlation table). Similar to the PCA, the RDA was run using the logit transformed site by Genus matrix with PAD 4 June 2014, PAD 3 August 2015, PAD 4 August 2015, and PAD 14 August 2015 removed. The RDA output was plotted on axes RDA1 and RDA3 to visualise the strongest correlations with explanatory variables.

All analyses were performed using R version 3.3.2 statistical software (The R Foundation for Statistical Computing).

Results

Based on spot measurements gathered over three sampling periods, total dissolved nitrogen was seen to increase within the $n = 4$ Peace sub-basin wetlands (Fig 3.2a) while total dissolved phosphorus increased in the $n = 5$ Athabasca sub-basin wetlands (Fig 3.2b). These results are reflected in the total nitrogen: total phosphorus (TN:TP) ratios of each wetland since 2012 where sites in the Athabasca sub-delta (PAD 01, 03, and 04) have had TN:TP ratios indicative of eutrophication and nitrogen-limitation for several seasons (Table 3.1). The concentration of dissolved iron was seen to increase in wetlands of both the Peace and Athabasca sub-basins, and was also more variable in August 2015 (Fig 3.2c). The turbidity of each sub-basin was seen to increase and become more variable over the time periods sampled (Fig 3.2d). The Birch ($n = 3$) and Peace sub-basin wetlands showed decreasing pH over the three periods sampled (Fig 3.2e). While quite variable, the specific conductance of each sub-basin was seen to increase with each sampling period (Fig 3.2f).

The first three axes of the PCA explained 34.6% of the variance among samples. This represents differences among sites based on biotic variation. The first principal component explains 14.8% of the variance, the second explains 10.1% of the variance and the third principal component explains an additional 9.71% of the variance (Figure 3.3a; Figure 3.3b). PC1 shows separation of June 2014 samples from August 2015 samples (Figure 3.3b) – variation based on seasonal separation. PC2 shows some separation among sites sampled in August 2015, but there was clumping around the origin for the additional samples (Figure 3.3a). Along PC3 there is separation of the

Peace sub-delta sites from the Birch sub-delta sites (Figure 3.3b) – variation based on geographic separation.

The Redundancy Analysis (Figures 3.4; 3.5) explained 21.6% of the (constrained) variance with a residual (unconstrained) of 78.4% left unexplained. Of the portion of variance explained, RDA axis 1 explained 11.9% and was negatively correlated with pH ($r = -0.55$) and turbidity ($r = -0.53$). RDA axis 2 explained 5.3% of the variance and was positively correlated with pH ($r = 0.56$) and negatively correlated with total dissolved phosphorus ($r = -0.36$). RDA axis 3 explained only 2.3% of the variance and was positively correlated with total dissolved nitrogen ($r = 0.64$), total dissolved phosphorus ($r = 0.79$), and specific conductance ($r = 0.89$).

There is a gradient of pH along axis 1 that separates the Embarras wetland samples (PAD 96 and 97, all years) from the Peace sub-delta samples (PAD 14, 33, and 38) as well as from PAD 93 (all years) in the Birch sub-delta (Figure 3.4). Along this gradient, PAD 96 is strongly associated with high pH in all sampling periods. Also along axis 1 there is a strong association of *Cocconeis Ehrenberg 1837* with high pH (Figure 3.5).

Additionally, there is a gradient along axis 3 driven largely by nutrients/ions that separates the Embarras sites (PAD 96 and 97) from the Cree-Mamawi Creek sites (PAD 01 and 03) despite both being part of the relictual Athabasca sub-delta (Figure 3.4). Along this gradient, PAD 33 is strongly associated with high specific conductance in all sampling periods while PAD 14 and 38 are strongly associated with low nutrient concentration (both N and P) in 2014. Along the gradient of specific conductance, *Boreozonacola* Lange-Bertalot, Kulikovskiy and Witkowski 2010 and *Hippodonta* Lange-Bertalot, Witkowski and Metzeltin 1996 are associated with high ion

concentration. *Epithemia* Kützing 1844 is associated with higher than average specific conductance and is uncorrelated with nutrients. Along the nutrient gradient *Navicula* Bory de Saint-Vincent 1822, *Rhopalodia* O. Muller 1895 and *Tabellaria* Ehrenberg ex Kützing 1844 are associated with low nutrients (Figure 3.5).

Discussion

The principal components analysis showed two gradients of interest. The first gradient along PC1 explained the highest variance among sites and represented a gradient of seasonality. There was a successive change in diatom community composition along PC1 from June 2014 through August 2014 to August 2015. *Epithemia* Kützing 1844 was one Genus of diatom that increased in abundance throughout the periods sampled with it being dominant at most sites in August 2015. Given the dominance of *Epithemia* Kützing 1844 in 2015, and its ability to fix atmospheric nitrogen through cyanobacterial endosymbionts it was hypothesized that the seasonal gradient was being driven by changes in nutrient concentrations – in particular, nitrogen limitation due to an influx of phosphorus to the system. The second gradient of interest was along PC3 showing broad separation of sites in the Birch sub-delta from those in the Peace sub-delta. This gradient of geographic separation was hypothesized to be due to differences in the physical and chemical properties of receiving waters.

The highest variance among sites was explained by a gradient of pH. This finding is similar to previous studies that found pH to be a strong explanatory variable of regional community variation in lacustrine diatoms (Allen *et al.*, 1999; Bennett *et al.*, 2010). In particular, diatom communities of sites in the Embarras sub-delta (PAD 96 and 97) are being driven by a strong association with high pH and these wetlands have communities

dominated by the alkaliphilous Genus *Cocconeis* Ehrenberg 1837. This relationship could make wetlands in the Embarras sub-delta particularly vulnerable to changes in community composition via acidification associated with resource development in the area (i.e. oil sands mining in the upstream region of that Athabasca River watershed). As described above, sulphur and nitrogen oxides are produced as by-products of mining processes, and these are returned to the landscape via dry or wet deposition (i.e. acid precipitation). This phenomenon, coupled with the reduced water retention associated with land clearing, can lead to acidification of rivers, lakes, and wetlands in the affected area. Reductions in pH are very likely to result in a shift in the diatom community as the chemical conditions move outside of the pH optimum for this Genus. Given that *Cocconeis* is the dominant diatom in these wetlands, their replacement by successive taxa could have cascading effects on higher trophic levels. *Cocconeis* Ehrenberg 1837 is resistant to grazing (Pan and Lowe, 1994) so loss of this Genus may promote increased abundance of grazing macroinvertebrates (e.g. snails) if it is succeeded by more palatable taxa. This could also lead to a reduction in overall productivity if more biomass of the diatom community in the biofilm is effectively removed by grazers.

A nutrient/ion gradient was also present driving differences between the Embarras and Cree-Mamawi Creek; however, this gradient explained only a small portion of the variance. This gradient also separates Egg Lake (PAD 33) from other wetland sites in the Peace sub-delta, where PAD 33 is strongly associated with high specific conductance while PAD 14 and 38 are strongly correlated with low nutrients. Two Genera (*Hippodonta* Lange-Bertalot, Witkowski and Metzeltin 1996 and *Boreozonacola* Lange-Bertalot, Kulikovskiy et Witkowski 2010) were also strongly correlated with high SPC.

Hippodonta Lange-Bertalot, Witkowski and Metzeltin 1996 favours saline conditions and is commonly found in inland seas (Spaulding and Edlund, 2008). *Boreozonacola* Lange-Bertalot, Kulikovskiy et Witkowski 2010 is a common Genus found at northern latitudes throughout the boreal zone in both North America and Eurasia, but is most common in lakes with low electrolyte content (Kulikovskiy *et al.*, 2010). It was absent from most wetlands and had very low abundance at Egg Lake (< 1%) so it's perceived association with high specific conductance is likely driven by its absence at other sites and not a true relationship with high specific conductance.

Analysis of water chemistry has suggested that the Peace-Athabasca Delta may be becoming eutrophic. Concentrations of total dissolved phosphorus are increasing, particularly in the Athabasca sub-delta, and this can lead to eutrophication (defined by the absolute value of total phosphorus concentration; Naumann, 1929) and nitrogen limitation (defined by the relative concentrations of total nitrogen and total phosphorus; Sakamoto, 1966). Despite the presence of a nutrient gradient among sites, this gradient explains only a small portion of the variance and may not be an important driver of diatom distribution in the Peace-Athabasca Delta. PAD 14 and 38 (from the Peace sub-delta) were correlated with low nutrient concentrations in both sampling periods of 2014 which may be driven by the fact that the Peace sub-delta is not having the same influx of phosphorus that was found in the Athabasca sub-delta. Three diatom Genera were strongly correlated with lower than average nutrient concentrations: *Rhopalodia* O. Muller 1895, *Navicula* Bory de Saint-Vincent 1822, and *Tabellaria* Ehrenberg ex Kützing 1844. *Rhopalodia* O. Muller 1895 is a member of the Epithemiaceae – a Family of diatoms containing nitrogen-fixing cyanobacterial endosymbionts. This could lead to

an affinity for nutrient poor waters as the ability to fix atmospheric nitrogen would give this Genus a competitive advantage under these conditions. The valves of *Tabellaria* Ehrenberg ex Kützing 1844 present were specifically *Tabellaria flocculosa* (Roth) Kützing 1844 which is a cosmopolitan Species at northern latitudes and commonly found in peat bogs (Spaulding *et al.*, 2010). This species was likely correlated with low nutrients due to its high abundance at PAD 14 (high peat content) rather than due to a relationship with nutrients.

Overall, the variance among wetlands explained by the included environmental parameters was quite low and the seasonal separation evident from the PCA was not explained. The majority of variance among these sites is responding to some other underlying gradient. Other studies in the region have found temperature, geology and riparian vegetation to be important determinants of diatom distribution. In particular, studies further south, in the region directly surrounding the Athabasca oil sands development, have found that temperature is an important driver of change in both zooplankton community composition (Kurek *et al.*, 2012) and in primary production (Summers *et al.*, 2016). A survey of diatoms in Wood Buffalo National Park (north of the PAD) have found that underlying geology is the main driver of diatom distribution, and that sites with a riparian zone dominated by Spruce trees (*Picea*) have distinct diatom communities (Moser *et al.*, 2004).

Hydrological regime is also an important aspect to consider, including: magnitude, frequency, duration, and timing. The flow regime of a waterbody affects water quality, energy sources, physical habitat and biotic interactions, and thus contributes to the ecological integrity of the waterbody (Poff *et al.*, 1997). Habitats in the

Peace-Athabasca Delta are sensitive to water level fluctuations in the lower Athabasca River (Wolfe *et al.*, 2008; Timoney, 2009; Monk *et al.*, 2012). Flooding is particularly important in a wetland complex like the PAD as this contributes significantly to replenishment of nutrients and sediments from the river channel to the associated wetlands. The seasonal gradient from June 2014 to August 2015 shows a successional shift in diatom communities that may be driven by a gradient of drying conditions in the Peace – Athabasca Delta. An ice jam on the Peace River in May 2014 led to widespread flooding in June, and many of the affected sites had dried significantly by August 2014 (personal observation), and the following August was also dry (K. Heard, pers. comm.) Contrary to expectations, *Epithemia* Kützing 1844 showed no correlation with total dissolved nitrogen, but in addition to containing nitrogen-fixing endosymbionts this Genus is known to be tolerant of drought conditions (Timoney, 2013). Its widespread high abundance during the sampling of August 2015 could be driven by drying in the Delta rather than possible eutrophic conditions leading to the successional change across sampling periods detected by the PCA.

Of the drivers affecting diatom community composition, hydrological regime is the only variable that can be effectively controlled by managers. Increased evaporation associated with warming and a longer ice-free season cannot effectively be mitigated at this point since current projections of climate change show that widespread warming will continue (IPCC, 2014). However, moving forward managers can control the hydrological regime in the Peace-Athabasca Delta by setting minimum flow requirements for the Athabasca and Peace Rivers, restricting the total volume of water that can be extracted by industry, and setting standards for water releases from the Bennett Dam head pond to

maintain flushing flows and natural cycles of flooding to replenish wetlands in the Delta with nutrients and sediment.

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Table 3.1 - Summary of total nitrogen to total phosphorus (TN:TP) ratios for each wetland from June 2012 to August 2015. Based on Sakamoto's (1966) classification for nutrient limitation, sites shown in bold are indicative of possible nitrogen limitation, where $N:P < 10:1 = N$ limitation and $10:1 < N:P < 17:1 =$ possible N limitation.

	2012		2013		2014		2015
	June	August	June	August	June	August	August
PAD 1	3.22	N/A	9.55	3.08	7.82	7.87	19.4
PAD 3	4.65	6.66	7.65	3.69	11.66	5.49	11.42
PAD 4	13.85	14.6	7.89	14.08	8.15	10.18	12.62
PAD 14	13.21	36.55	92.67	--	71.42	37.18	46.3
PAD 33	33.71	22.45	32.85	1.04	16.57	16.32	45.06
PAD 37	53.27	33.85	31.45	26.31	25.15	45.66	16.71
PAD 38	22.77	34	10.32	23.63	12.88	21.35	21.51
PAD 92	--	--	--	--	58.83	16.53	28.12
PAD 93	--	--	--	--	12.89	6.33	11.10
PAD 94	--	--	--	14.46	15.67	16.41	3.4
PAD 96	--	--	--	5.06	16.55	19.67	11.61
PAD 97	--	--	--	8.85	20.77	18.61	13.64

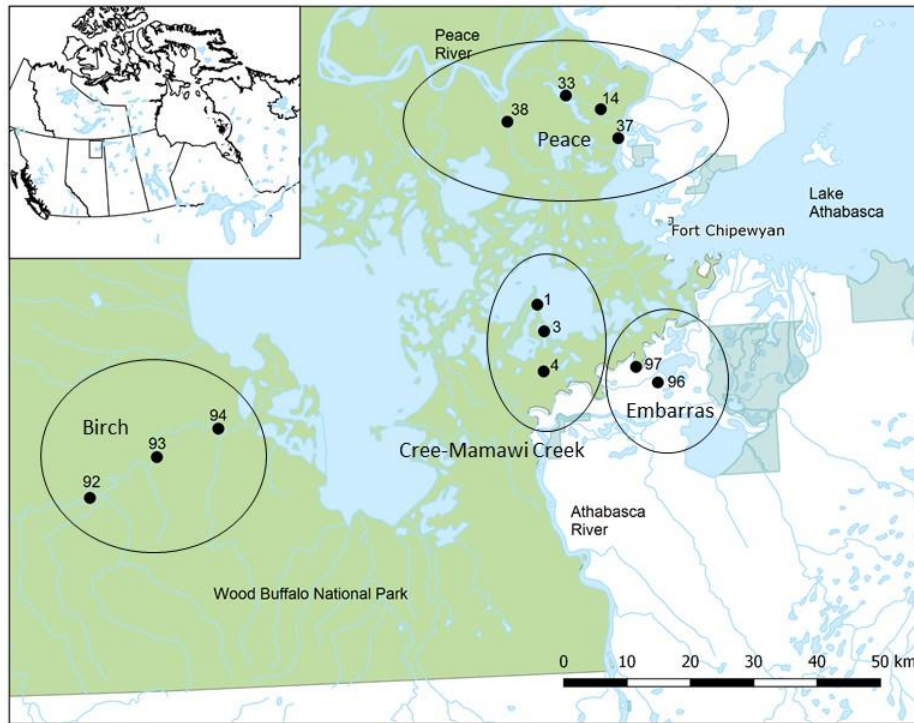


Figure 3.1 - Location of 12 study sites across four sub-basins (Peace, Birch, Cree-Mawai Creek, and Embarras) in the Peace Athabasca Delta in northeastern Alberta, Canada.

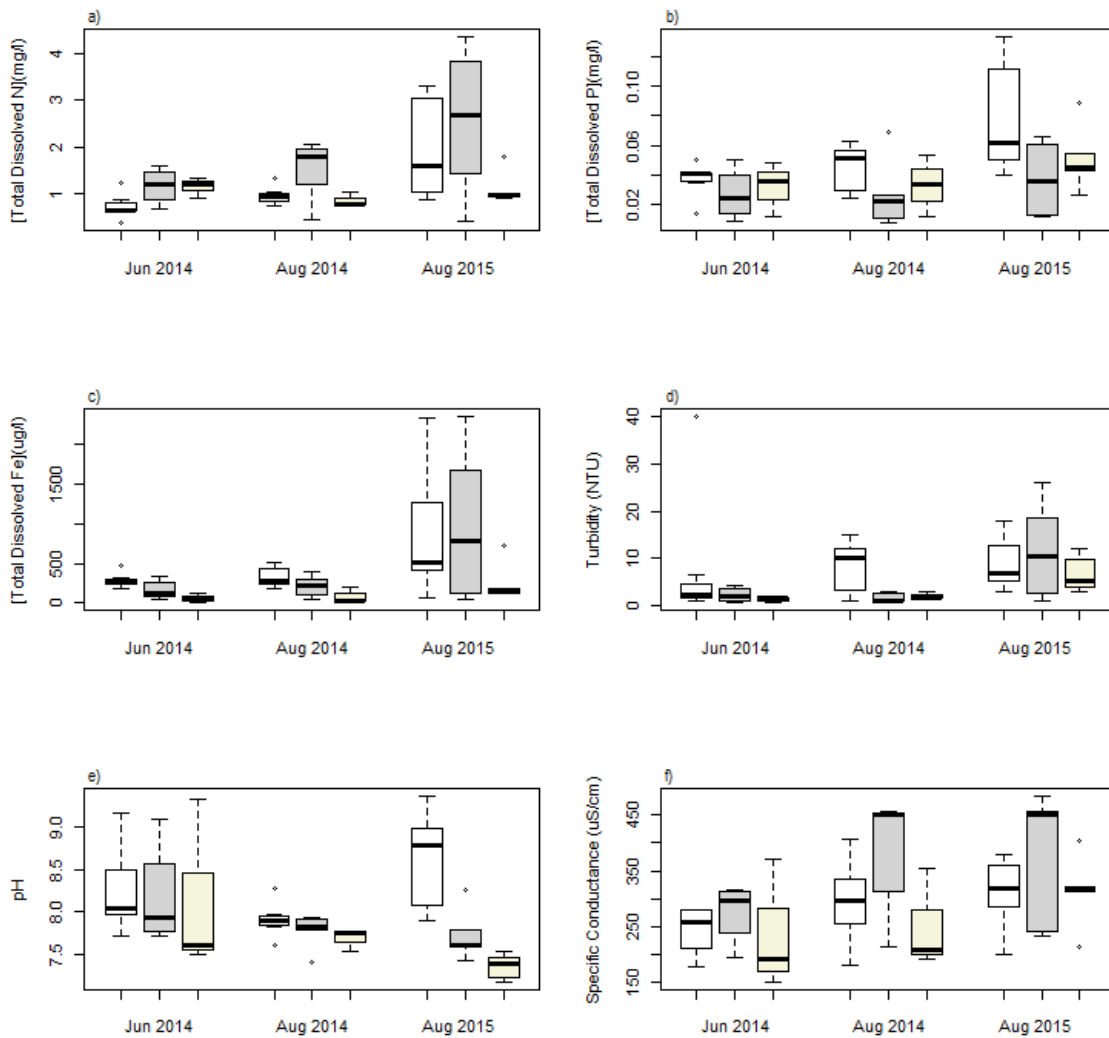


Figure 3.2 - Boxplots of various physico-chemical variables: a) Total dissolved nitrogen (mg/l), b) Total dissolved phosphorus (mg/l), c) Dissolved iron ($\mu\text{g/l}$), d) Turbidity (NTU), e) pH, and f) Specific conductance ($\mu\text{S/cm}$) over three sampling periods (June 2014, August 2014, and 2015) for wetlands in the Athabasca (white), Peace (grey), and Birch (beige) sub-basins of the Peace-Athabasca Delta, northeastern Alberta, Canada.

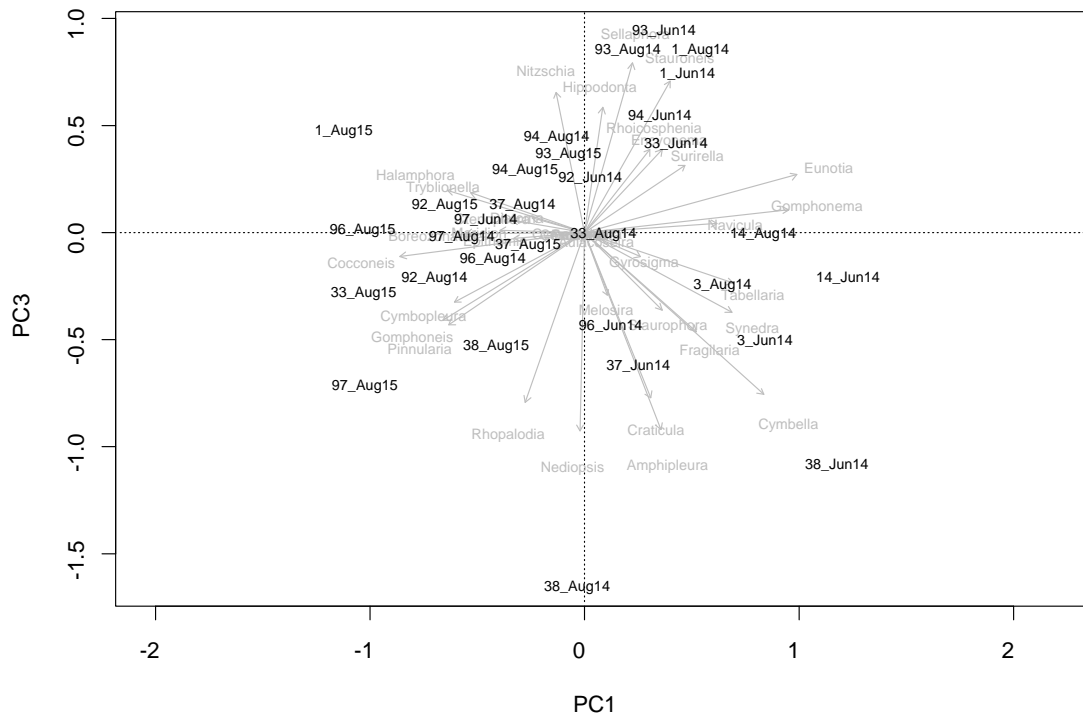


Figure 3.3b – Principal components biplot projecting axes PC1 and PC3 for diatom community composition, summarised at Genus level, and wetland sites in the Peace – Athabasca Delta for three sampling periods: June 2014, August 2014, and August 2015. Variation among sites represents variation due to biotic differences (i.e. diatom community composition). PC1 explains 14.8 % variance among sites and PC3 explains 9.71 % variance.

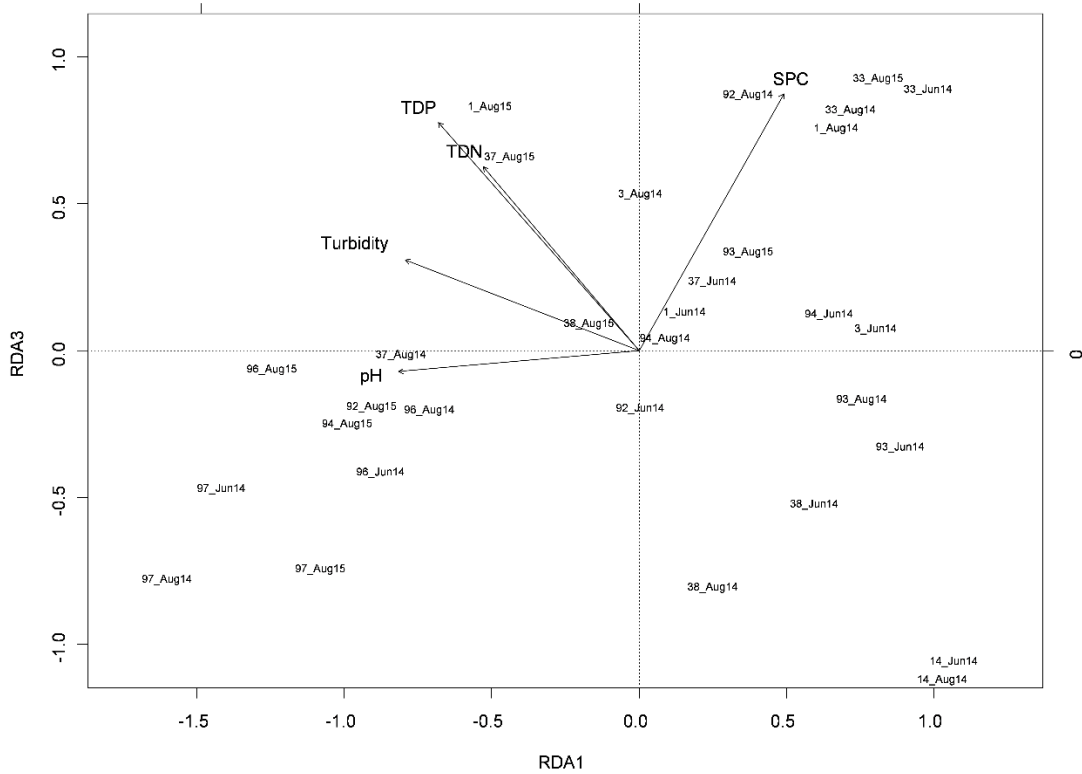


Figure 3.4 – Redundancy analysis biplot projecting RDA axes 1 and 3 showing wetland sites from the Peace-Athabasca Delta from three sampling periods – June 2014, August 2014, and August 2015 – and associated physico-chemical parameters: TDN or total dissolved nitrogen (mg/L), TDP or total dissolved phosphorus (mg/L), pH, turbidity (NTU) and SPC or specific conductance ($\mu\text{S}/\text{cm}$). The overall variance explained by the RDA was 21.6% with 11.9% explained by axis RDA axis 1 and 2.3% explained by RDA axis 3. RDA axis 1 shows a gradient of pH that separates the Embarras sub-delta from the Peace sub-delta. RDA axis 3 shows a gradient of ion content/nutrient concentration that separates the Embarras sub-delta from the Cree-Mamawi Creek sub-delta (both in the relictual Athabasca sub-delta), as well as separating Egg Lake (PAD 33) from other wetlands in the Peace sub-delta (PAD 14 and 38).

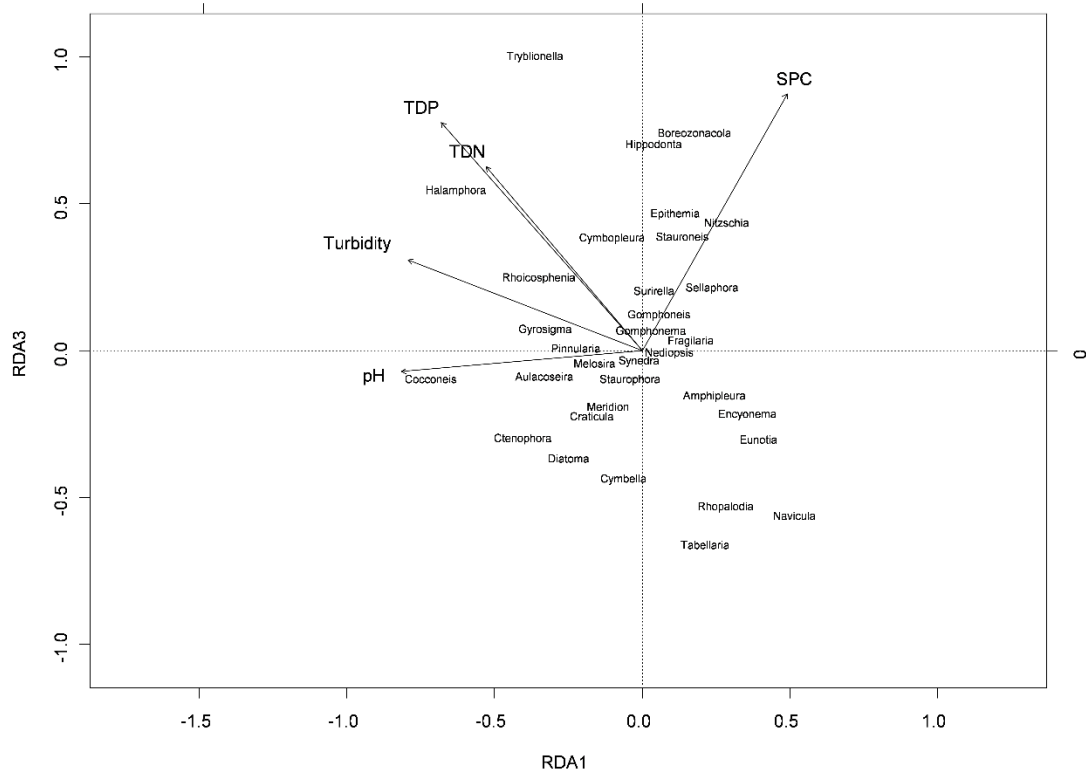


Figure 3.5 – Redundancy analysis biplot projecting RDA axes 1 and 3 showing diatom Genera from the Peace-Athabasca Delta from three sampling periods – June 2014, August 2014, and August 2015 – and associated physico-chemical parameters: TDN or total dissolved nitrogen (mg/L), TDP or total dissolved phosphorus (mg/L), pH, turbidity (NTU) and SPC or specific conductance ($\mu\text{S}/\text{cm}$). The overall variance explained by the RDA was 21.6% with 11.9% explained by axis RDA axis 1 and 2.3% explained by RDA axis 3. RDA axis 1 shows a strong correlation between high pH and *Cocconeis* Ehrenberg 1837. RDA axis 3 shows a gradient of ion content/nutrient concentration where *Hippodonta* Lange-Bertalot, Witkowski and Metzeltin 1996 and *Boreozonacola* Lange-Bertalot, Kulikovskiy et Witkowski 2010 are associated with high specific conductance while *Navicula* Bory de Saint-Vincent 1822, *Rhopalodia* O. Muller 1895 and *Tabellaria* Ehrenberg ex Kützing 1844 are associated with low nutrient concentration.

CHAPTER 4: SUMMARY AND SYNTHESIS

Anthropogenic habitat degradation associated with resource development is a major concern in Canada's North. Major types of resource development in Canada's Western boreal zone include mining, hydroelectric power generation, and oil and gas developments. In 2010, the natural resources sector generated 11.5% (or \$142.5 billion) of Canada's gross domestic product (NRCan, 2011), and these activities are expected to continue and expand. We currently know little about these northern ecosystems (Spencer *et al.*, 2008) despite the extent of resource development occurring, and this presents significant challenges to managers trying to minimize and mitigate impact in these areas.

Current biomonitoring practices rely on the use of surrogate taxa as indicators of ecosystem health. The use of these bioindicator taxa operates under the assumption that diversity patterns among taxa within a particular habitat are concordant – thus protection of one equals protection of all; however, this criterion is rarely tested for specific indicators in each region of interest. Previous studies have shown that the applicability of cross-taxon congruence can vary by geographic region (Su *et al.*, 2004), the scale at which the study is performed (Qian and Kissling, 2009; van Weerd and Udo de Haes, 2010; Tisseuil *et al.*, 2013), and the taxa studied (Paavola *et al.*, 2003). In particular, using heterotrophs as indicators of photoautotroph community health (and vice versa) are likely to be inappropriate as these two communities can show divergent responses to environmental drivers. For example, a study by Jüttner and Ormerod (2002) on impacts of mining effluent showed that in response to metal toxicity the benthic macroinvertebrate community showed reductions in richness, diversity and abundance

while the diatom community showed a shift in composition, but no significant change in richness, diversity or total abundance. The purpose of this thesis was to explore the relationship of diversity patterns between two common bioindicators (macroinvertebrates and benthic diatoms), and to examine particular environmental variables that were predicted to drive the diversity of diatom community assemblages.

In Chapter 2, the diversity patterns of benthic diatoms and macroinvertebrate community assemblages in wetlands of the Peace-Athabasca Delta were analysed for concordance. This was done by characterizing the taxa present in both the benthic diatom and macroinvertebrate communities, assessing the similarity of wetlands based on these assemblages, and comparing the relationship among wetlands based on both benthic diatom and macroinvertebrate communities. For both June and August 2014 the community ordinations for benthic diatoms and macroinvertebrates were concordant; however, for August 2015 they were incongruent. The lack of concordance between diversity patterns in 2015 was likely due to a significant shift in the community assemblage of diatoms without a similar shift in macroinvertebrates. In particular, PAD 14 and 33 had similar macroinvertebrate communities, while the diatom communities at these two sites were dissimilar due largely to one species: *Epithemia turgida* (Ehrenberg) Kützing 1844. It was hypothesized that the diatom community was responding to an environmental variable that was either not affecting the macroinvertebrate community or not affecting macroinvertebrates in a similar manner (e.g. on the same time scale). This particular case is a good example of why diversity pattern concordance cannot be assumed to exist for the purposes of simplifying a monitoring program.

In Chapter 3, the influence of predicted environmental variables on diversity patterns of diatom community assemblages in wetlands of the Peace-Athabasca Delta was explored. This was done by identifying six physico-chemical factors that vary among sites which have previously been demonstrated to affect diatom community assemblages, and subsequently regressing these variables against an ordination of community composition and abundance to identify diversity gradients. An indirect gradient analysis identified two major gradients among samples based solely on biotic variation. The strongest gradient separated sites sampled in June 2014 from those sampled in August 2015 – a seasonal gradient. The second gradient separated sites from the Birch sub-delta from those in the Peace sub-delta. The direct gradient analysis failed to identify a driver for either of these gradients, but did show that the diatom community of wetlands in the Embarras sub-delta are being driven by alkaline conditions. The strong association between the Embarras and high pH suggests that this sub-delta may be particularly vulnerable to community shifts associated with anthropogenic induced acidification. Given the high abundance of *Epithemia turgida* (Ehrenberg) Kützing 1844 in August 2015, and its known association with drying conditions, it was hypothesized that drying in the Delta may be a major driver not accounted for in the analysis which could explain the seasonal variation detected by the indirect gradient analysis. The combination of water extraction for oil sands mining, flow regulation for hydroelectric power generation, and drying associated with climate change (longer ice-free season + increased evaporation) can only exacerbate reductions in water level in future years.

For large-scale biomonitoring programs, identifying reliable bioindicators can save many resources in terms of person hours, costs, and time, as well as ensuring the

success of such programs. Diatom community assemblages possess many traits as ideal candidates for monitoring potential impact due to resource development projects including hydroelectric dams and mining. Diatoms are abundant in the environment and easy to collect with a short lifecycle and high turnover rate that contribute to quick responses to environmental change. Most importantly, the silica frustules accumulate in the sediment, and thus present day communities can be compared to those of the past. This is especially useful in areas like the Peace-Athabasca Delta where true baseline data prior to development do not exist. As a major source of fixed carbon in the environment, changes in the diatom community can have cascading effects on higher trophic levels and can act as an early warning system before more severe effects are detected. Coupling this information with what can be gathered from traditional macroinvertebrate bioindicators will give a more cohesive picture of ecosystem health and the potential for habitat degradation which will allow managers to more effectively and efficiently make decisions regarding biodiversity and conservation.

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APPENDIX 1: List of diatom genera found in wetlands of the Athabasca, Peace, and Birch deltas with occurrence in each period sampled

June 2014 - Athabasca Delta

Genera	PAD 1	PAD 3	PAD 4	PAD 96	PAD 97
<i>Amphipleura</i>	X				
<i>Aulacoseira</i>	X	X	X	X	X
<i>Cocconeis</i>	X	X	X	X	X
<i>Craticula</i>		X	X	X	X
<i>Ctenophora</i>					X
<i>Cymbella</i>		X		X	X
<i>Cymbopleura</i>			X		
<i>Encyonema</i>	X	X	X	X	
<i>Epithemia</i>	X	X	X	X	X
<i>Eunotia</i>	X	X	X	X	X
<i>Fragilaria</i>	X	X		X	X
<i>Gomphonema</i>	X	X	X	X	X
<i>Halamphora</i>					
<i>Hippodonta</i>					X
<i>Melosira</i>					
<i>Meridion</i>			X		
<i>Navicula</i>	X	X	X	X	X
<i>Nediopsis</i>			X		
<i>Nitzschia</i>	X	X	X	X	X
<i>Rhoicosphenia</i>	X	X	X	X	X
<i>Rhopalodia</i>	X	X	X	X	X
<i>Sellaphora</i>	X			X	X
<i>Stauroneis</i>	X	X	X	X	X
<i>Staurophora</i>		X			
<i>Surirella</i>	X		X	X	
<i>Synedra</i>	X	X	X	X	X
<i>Tabellaria</i>			X		

June 2014 - Peace Delta

Genera	PAD 14	PAD 33	PAD 37	PAD 38
<i>Amphipleura</i>				X
<i>Aulacoseira</i>				
<i>Cocconeis</i>	X		X	X
<i>Craticula</i>			X	X
<i>Ctenophora</i>				
<i>Cymbella</i>	X		X	X
<i>Cymbopleura</i>				
<i>Encyonema</i>	X	X	X	X
<i>Epithemia</i>	X	X	X	X
<i>Eunotia</i>	X	X	X	X
<i>Fragilaria</i>	X	X	X	X
<i>Gomphonema</i>	X	X	X	X
<i>Halamphora</i>				
<i>Hippodonta</i>				X
<i>Melosira</i>			X	
<i>Meridion</i>				
<i>Navicula</i>	X		X	X
<i>Nediopsis</i>			X	X
<i>Nitzschia</i>		X	X	X
<i>Rhoicosphenia</i>	X			X
<i>Rhopalodia</i>		X	X	
<i>Sellaphora</i>				X
<i>Stauroneis</i>	X	X		X
<i>Staurophora</i>			X	
<i>Surirella</i>				X
<i>Synedra</i>	X	X		X
<i>Tabellaria</i>	X			X

June 2014 - Birch Delta

Genera	PAD 92	PAD 93	PAD 94
<i>Amphipleura</i>			
<i>Aulacoseira</i>			X
<i>Cocconeis</i>	X	X	X
<i>Craticula</i>			
<i>Ctenophora</i>			
<i>Cymbella</i>			X
<i>Cymbopleura</i>			
<i>Encyonema</i>	X	X	X
<i>Epithemia</i>	X	X	X
<i>Eunotia</i>	X	X	X
<i>Fragilaria</i>	X	X	X
<i>Gomphonema</i>	X	X	X
<i>Halamphora</i>	X		
<i>Hippodonta</i>			
<i>Melosira</i>			
<i>Meridion</i>			
<i>Navicula</i>	X	X	X
<i>Nediopsis</i>			
<i>Nitzschia</i>	X	X	X
<i>Rhoicosphenia</i>			X
<i>Rhopalodia</i>	X		
<i>Sellaphora</i>	X	X	X
<i>Stauroneis</i>	X		X
<i>Staurophora</i>			
<i>Surirella</i>	X	X	
<i>Synedra</i>	X		
<i>Tabellaria</i>			

August 2014 - Athabasca Delta

Genera	PAD 1	PAD 3	PAD 4	PAD 96	PAD 97
<i>Amphipleura</i>					
<i>Aulacoseira</i>	X				X
<i>Cocconeis</i>	X	X		X	X
<i>Craticula</i>	X	X		X	
<i>Ctenophora</i>					X
<i>Cymbella</i>	X	X			
<i>Encyonema</i>	X	X		X	X
<i>Epithemia</i>	X	X		X	X
<i>Eunotia</i>	X	X		X	X
<i>Fragilaria</i>	X	X		X	X
<i>Gomphoneis</i>	X				
<i>Gomphonema</i>	X	X			X
<i>Gyrosigma</i>		X			
<i>Halamphora</i>					
<i>Hippodonta</i>	X				
<i>Navicula</i>	X	X		X	X
<i>Nediopsis</i>	X				
<i>Nitzschia</i>	X	X		X	X
<i>Rhoicosphenia</i>	X	X			
<i>Rhopalodia</i>		X		X	X
<i>Sellaphora</i>	X				X
<i>Stauroneis</i>	X	X		X	X
<i>Staurophora</i>		X			
<i>Surirella</i>	X	X			
<i>Synedra</i>	X	X			X
<i>Tabellaria</i>					

August 2014 - Peace Delta

Genera	PAD 14	PAD 33	PAD 37	PAD 38
<i>Amphipleura</i>				X
<i>Aulacoseira</i>				X
<i>Cocconeis</i>	X	X	X	X
<i>Craticula</i>	X			X
<i>Ctenophora</i>				
<i>Cymbella</i>	X			X
<i>Encyonema</i>	X		X	X
<i>Epithemia</i>		X	X	X
<i>Eunotia</i>	X	X	X	X
<i>Fragilaria</i>	X	X	X	X
<i>Gomphoneis</i>				X
<i>Gomphonema</i>	X	X	X	X
<i>Gyrosigma</i>				
<i>Halamphora</i>				
<i>Hippodonta</i>				
<i>Navicula</i>	X	X	X	X
<i>Nediopsis</i>	X			X
<i>Nitzschia</i>	X	X	X	X
<i>Rhoicosphenia</i>		X		
<i>Rhopalodia</i>		X	X	X
<i>Sellaphora</i>			X	
<i>Stauroneis</i>		X		X
<i>Staurophora</i>				
<i>Surirella</i>				
<i>Synedra</i>		X	X	X
<i>Tabellaria</i>	X			

August 2014 - Birch Delta

Genera	PAD 92	PAD 93	PAD 94
<i>Amphipleura</i>			
<i>Aulacoseira</i>			
<i>Cocconeis</i>	X	X	X
<i>Craticula</i>			
<i>Ctenophora</i>			
<i>Cymbella</i>			
<i>Encyonema</i>	X	X	X
<i>Epithemia</i>	X	X	X
<i>Eunotia</i>		X	X
<i>Fragilaria</i>	X	X	X
<i>Gomphoneis</i>	X		
<i>Gomphonema</i>	X	X	X
<i>Gyrosigma</i>			
<i>Halamphora</i>	X		
<i>Hippodonta</i>		X	
<i>Navicula</i>	X	X	X
<i>Nediopsis</i>			
<i>Nitzschia</i>	X	X	X
<i>Rhoicosphenia</i>	X		X
<i>Rhopalodia</i>	X		
<i>Sellaphora</i>		X	X
<i>Stauroneis</i>	X	X	X
<i>Staurophora</i>	X		
<i>Surirella</i>			
<i>Synedra</i>			X
<i>Tabellaria</i>			

August 2015 - Athabasca Delta

Genera	PAD 1	PAD 3	PAD 4	PAD 96	PAD 97
<i>Amphipleura</i>			X		
<i>Aulacoseira</i>	X	X	X	X	X
<i>Boreozonacola</i>	X		X		
<i>Caloneis</i>		X	X		
<i>Cocconeis</i>	X	X	X	X	X
<i>Cosmioneis</i>		X			
<i>Craticula</i>	X	X	X	X	X
<i>Ctenophora</i>		X	X	X	X
<i>Cymatopleura</i>		X			
<i>Cymbella</i>	X	X	X	X	
<i>Cymbopleura</i>	X	X	X		X
<i>Diatoma</i>		X			
<i>Encyonema</i>	X	X	X	X	X
<i>Epithemia</i>	X	X	X	X	X
<i>Eunotia</i>	X	X	X	X	X
<i>Fragilaria</i>	X	X	X	X	X
<i>Frustulia</i>		X			
<i>Gomphoneis</i>	X	X	X	X	X
<i>Gomphonema</i>	X	X	X	X	X
<i>Gyrosigma</i>		X			
<i>Halamphora</i>	X	X	X	X	X
<i>Hippodonta</i>	X	X	X	X	X
<i>Meridion</i>				X	
<i>Navicula</i>	X	X	X	X	X
<i>Nediopsis</i>	X	X	X	X	X
<i>Nitzschia</i>	X	X	X	X	X
<i>Pinnularia</i>			X	X	X
<i>Rhoicosphenia</i>	X	X	X	X	X
<i>Rhopalodia</i>	X	X	X	X	X
<i>Sellaphora</i>	X	X	X	X	X
<i>Stauroneis</i>	X	X	X	X	X
<i>Surirella</i>		X	X		
<i>Synedra</i>	X	X	X		
<i>Tabellaria</i>		X			
<i>Tryblionella</i>	X	X	X		

August 2015 - Peace Delta

Genera	PAD 14	PAD 33	PAD 37	PAD 38
<i>Amphipleura</i>				X
<i>Aulacoseira</i>	X	X	X	
<i>Boreozonacola</i>	X	X		
<i>Caloneis</i>				
<i>Cocconeis</i>	X	X	X	X
<i>Cosmioneis</i>				
<i>Craticula</i>	X	X	X	X
<i>Ctenophora</i>			X	
<i>Cymatopleura</i>				
<i>Cymbella</i>	X		X	X
<i>Cymbopleura</i>	X	X	X	
<i>Diatoma</i>				
<i>Encyonema</i>	X	X	X	X
<i>Epithemia</i>	X	X	X	X
<i>Eunotia</i>	X	X	X	X
<i>Fragilaria</i>	X	X	X	X
<i>Frustulia</i>	X			
<i>Gomphoneis</i>		X		
<i>Gomphonema</i>	X	X	X	X
<i>Gyrosigma</i>				
<i>Halamphora</i>		X		
<i>Hippodonta</i>	X	X		
<i>Meridion</i>				
<i>Navicula</i>	X	X	X	X
<i>Nediopsis</i>		X		
<i>Nitzschia</i>	X	X	X	X
<i>Pinnularia</i>	X	X		X
<i>Rhoicosphenia</i>		X	X	X
<i>Rhopalodia</i>	X	X	X	X
<i>Sellaphora</i>	X	X	X	X
<i>Stauroneis</i>	X	X	X	X
<i>Surirella</i>		X		
<i>Synedra</i>			X	X
<i>Tabellaria</i>	X			X
<i>Tryblionella</i>		X		

August 2015 - Birch Delta

Genera	PAD 92	PAD 93	PAD 94
<i>Amphipleura</i>	X		
<i>Aulacoseira</i>	X		
<i>Boreozonacola</i>			
<i>Caloneis</i>			
<i>Cocconeis</i>	X	X	X
<i>Cosmioneis</i>			
<i>Craticula</i>			X
<i>Ctenophora</i>	X		X
<i>Cymatopleura</i>			
<i>Cymbella</i>	X		
<i>Cymbopleura</i>			
<i>Diatoma</i>	X		
<i>Encyonema</i>	X	X	X
<i>Epithemia</i>	X	X	X
<i>Eunotia</i>	X	X	X
<i>Fragilaria</i>	X	X	X
<i>Frustulia</i>			
<i>Gomphoneis</i>			
<i>Gomphonema</i>	X	X	X
<i>Gyrosigma</i>			
<i>Halamphora</i>	X		
<i>Hippodonta</i>			X
<i>Meridion</i>			
<i>Navicula</i>	X	X	X
<i>Nediopsis</i>		X	
<i>Nitzschia</i>	X	X	X
<i>Pinnularia</i>			
<i>Rhoicosphenia</i>	X		X
<i>Rhopalodia</i>	X		
<i>Sellaphora</i>		X	X
<i>Stauroneis</i>		X	X
<i>Surirella</i>			
<i>Synedra</i>	X	X	
<i>Tabellaria</i>			
<i>Tryblionella</i>			

APPENDIX 2: Physico-chemical variables measured over three sampling periods at each wetland site and chosen *a priori* for use in a redundancy analysis

	Total Dissolved Nitrogen (mg/L)			Total Dissolved Phosphorus (mg/L)		
	Jun-14	Aug-14	Aug-15	Jun-14	Aug-14	Aug-15
PAD 1	0.614	1.34	3.31	0.041	0.063	0.13
PAD 3	0.68	0.92	3.04	0.04	0.055	0.11
PAD 4	0.382	0.757	1.04	0.014	0.025	0.04
PAD 14	1.29	1.2	1.57	0.009	0.008	0.01
PAD 33	1.11	1.67	1.44	0.051	0.069	0.02
PAD 37	1.61	1.98	3.99	0.029	0.024	0.06
PAD 38	0.665	0.439	0.43	0.02	0.011	0.01
PAD 92	1.35	0.762	0.98	0.012	0.012	0.03
PAD 93	0.907	0.762	0.95	0.036	0.054	0.05
PAD 94	1.21	1.04	1.80	0.048	0.034	0.09
PAD 96	0.878	0.768	0.86	0.041	0.026	0.05
PAD 97	1.23	1.05	1.59	0.05	0.034	0.06

	Dissolved Iron (µg/L)			Turbidity (NTU)		
	Jun-14	Aug-14	Aug-15	Jun-14	Aug-14	Aug-15
PAD 1	482	269	1260	6.5	5.3	5.12
PAD 3	277.33	400.33	2330	2.4	13	18.1
PAD 4	178	191	513	40	10	6.92
PAD 14	344	184	1680	0.8	2.6	3.82
PAD 33	104	102	127	1.4	1.1	1.03
PAD 37	162	318.00	1305	2.9	1.73	20.63
PAD 38	54.6	37.5	38.2	4.2	1.1	2.82
PAD 92	6.3	31.1	187	0.7	3	12.2
PAD 93	47.6	36	140	1.7	1.7	4.12
PAD 94	117	199	733	1.8	1.7	9.68
PAD 96	264	228	422	1.2	0.9	3.14
PAD 97	242	481	73.2	1.3	1.6	12.8

	pH			Specific Conductance ($\mu\text{S}/\text{cm}$)		
	Jun-14	Aug-14	Aug-15	Jun-14	Aug-14	Aug-15
PAD 1	7.72	7.60	9.36	257	375	378
PAD 3	8.00	7.86	8.99	280	295.67	359
PAD 4	8.05	7.94	8.78	226	407	318
PAD 14	7.83	7.41	7.61	193	214	241
PAD 33	7.72	7.78	7.62	310	448	448
PAD 37	9.09	7.86	7.60	283	454	463.33
PAD 38	8.05	7.94	8.25	316	313	233
PAD 92	9.33	7.77	7.53	150	191	214
PAD 93	7.60	7.76	7.36	372	354	317.67
PAD 94	7.49	7.53	7.17	191	208	403
PAD 96	9.16	8.28	7.89	196	181	199
PAD 97	8.92	7.97	8.08	177	215	286

APPENDIX 3: Detrended Correspondance Analysis output

	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.4329	0.3057	0.1839	0.20137
Decorana values	0.4727	0.2933	0.1545	0.08261
Axis lengths	2.3302	2.6098	2.1334	1.65234

APPENDIX 4: Correlation table of water quality measurements from June and August 2014, and August 2015.

	pH	SPC	Turbidity	TDN	TDP	Dis.Fe
pH	1					
SPC	-0.29606	1				
Turbidity	-0.23721	0.29783	1			
TDN	0.14092	0.52734	0.50928	1		
TDP	0.10302	0.42548	0.36082	0.56922	1	
Dis.Fe	0.0845	0.33861	0.55336	0.78844	0.63829	1

Curriculum Vitae

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Universities attended (with dates and degrees obtained):

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M.Sc.: Biology

Thesis title: Diversity patterns of benthic diatoms and their use as potential bioindicators in western boreal wetlands

- Best Student Presentation, UAMRICH Meeting 2015

2008 – 2013 University of British Columbia Vancouver, BC

B.Sc.: Marine Biology

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Conference Presentations:

S.J. Connor. 2016. Environmental Drivers of Diatom Community Variation. Oral Presentation presented at 13th Annual CRI Days, September 30 - October 1, 2016, Quebec City, Quebec, Canada.

S.J. Connor, D.J. Baird, J.F. Gibson, M. Hajibabaei, and S. Shokralla. 2015. Diversity patterns of benthic diatoms in wetlands of the Peace-Athabasca Delta, Alberta, Canada. Poster Presentation presented at 12th Annual CRI Days, October 30 – 21, 2015, Fredericton, New Brunswick, Canada.

S.J. Connor, D.J. Baird, J.F. Gibson, M. Hajibabaei, and S. Shokralla. 2015. Diversity patterns of benthic diatoms in wetlands of the Peace-Athabasca Delta, Alberta, Canada. Oral Presentation presented at 9th Use of Algae in Monitoring Rivers and comparable habitats meeting, June 17 - 19 2015, Trento, Italy.

S.J. Connor, D.J. Baird, C. Curry, J. Gibson, M. Hajibabaei, K. Heard, B. Hussey, I. King, W. Monk, S. Rosolen, and S. Shokralla. 2014. Applying the Biomonitoring 2.0 approach in two contrasting sub-arctic tributaries of the Slave River, NWT, Canada. Poster Presentation presented at 11th Annual CRI Days, October 3 – 4, 2014, Charlottetown, Prince Edward Island, Canada.

S.J. Connor, D.J. Baird, C. Curry, J. Gibson, M. Hajibabaei, K. Heard, B. Hussey, I. King, W. Monk, S. Rosolen, and S. Shokralla. 2014. Applying the Biomonitoring 2.0 approach in two contrasting sub-arctic tributaries of the Slave River, NWT, Canada. Poster Presentation presented at Joint Aquatic Sciences Meeting, May 17 - 21, 2014, Portland, Oregon, USA.