Timescales of hydrolimnological change in floodplain lakes of the Peace-Athabasca Delta, northern Alberta, Canada

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ABSTRACT

Repeated measurements over 3 years (2003–2005) were made on a series of lakes along a hydrological gradient in the Peace-Athabasca Delta (PAD), Canada, to characterize the role of river flooding on limnological conditions of northern floodplain lakes and to identify the patterns and timescales of limnological change after flooding. River floodwaters elevate concentrations of suspended sediment, total phosphorus (TP), SO4 and dissolved silica (DSi) and reduce concentrations of total Kjeldahl nitrogen (TKN), dissolved organic carbon (DOC) and most ions, which leads to increased limnological homogeneity among lakes. After flooding, limnological changes occur at two distinct timescales. In the weeks to months after flooding, water clarity increases as suspended sediments and TP settle out of the water column, but concentrations of DOC, SO4, TKN and ions do not change appreciably. However, in the absence of flooding for many years to decades, evaporative concentration leads to an increase in most nutrients, DOC and ions. Contrary to a prevailing paradigm, these results suggest that regular flooding is not required to maintain high nutrient concentrations. In light of anticipated declines in river discharge, we predict that limnological conditions in the southern Athabasca sector will become increasingly less dominated by the short-term effects of flooding, and resemble nutrient- and solute-rich lakes in the northern Peace sector that are infrequently flooded. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS Peace-Athabasca Delta; flooding; floodplain lakes; hydroecology; nutrients; water transparency; lake ontogeny; pulse disturbance

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INTRODUCTION

Northern river floodplains are ecologically and culturally important freshwater landscapes that are strongly regulated by floods and variations in river flow (Marsh and Hey, 1989; English et al., 1997; Prowse and Conly, 1998; Schindler and Smol, 2006; Wolfe et al., 2007a). Seasonal and periodic flood pulses have been shown to play an important role on the water balance, light environment, habitat availability, nutrient supply, productivity and community composition of receiving water bodies (van der Valk and Bliss, 1971; Squires and Lesack, 2002, 2003a; Squires et al., 2002, 2009; Junk and Wantzen, 2004; Wolfe et al., 2007b; Brock et al., 2008; Wantzen et al., 2008; Sokal et al., 2010). Flooding has been recognized as a major hydrological vector for the transport of particulate matter, dissolved organic carbon (DOC), nutrients and biota within river floodplain systems (Tockner et al., 1999; Emmerton et al., 2007, 2008; Wantzen et al., 2008). Alterations to river discharge and flood events due to changing climatic conditions and human activities are, thus, expected to exert strong influence on high-latitude river floodplain systems (Marsh and Lesack, 1996; Rouse et al., 1997; Prowse et al., 2006; Schindler and Smol, 2006). Our understanding of the effects of both short- and long-term changes in the frequency, magnitude and timing of the flood pulse on biological communities and biogeochemical processes requires further investigation (Junk and Wantzen, 2004), as does our understanding of flood pulses in lake ecosystems (Wantzen et al., 2008). This knowledge is crucial to formulate sound strategies for effective stewardship of water resources and aquatic ecosystems.

The Mackenzie River Basin covers 20% of Canada’s land mass and is the largest source of freshwater flow from North America to the Arctic Ocean (Rouse et al., 2003; Woo and Thorne, 2003). The Mackenzie River drainage basin includes three major floodplains: the Mackenzie Delta (~68°30’N), the Slave Delta (~61°20’N) and the Peace-Athabasca Delta (PAD, ~58°40’N). A dominant feature of all three deltas is an abundance of shallow, productive, macrophyte-dominated lakes with low to moderate phytoplankton abundance that experience varying degrees of hydrologic connectivity and regularity of river flooding (Marsh and Hey, 1989; Wolfe et al., 2007b; Brock et al., 2008; Sokal et al., 2008; Squires et al., 2009). Limnological conditions of floodplain lakes have been examined at the Mackenzie Delta (Fee et al., 1988; Squires and Lesack, 2002; 2003a,b; Squires et al., 2002; 2009), the Slave Delta (Brock et al., 2007, 2008; 2009; Sokal et al., 2008; 2010) and the PAD (Wolfe et al., 2007b). Studies of lakes in the Mackenzie and Slave deltas have found that...
flooding reduces water clarity, concentrations of most nutrients in the water column and macrophyte biomass (Squires et al., 2002; 2009; Squires and Lesack, 2003a,b; Sokal et al., 2010). Interestingly, the role of flooding on phytoplankton seems to diverge in lakes of these two deltas. In the Slave Delta, phytoplankton standing crop, measured as chlorophyll a concentration (Chl a), was highest in lakes that did not flood because water column nutrient concentrations were highest in these lakes (Sokal et al., 2008; 2010). In contrast, phytoplankton standing crop in the Mackenzie Delta was highest in lakes characterized by intermediate levels of river connectivity (Fee et al., 1988; Squires and Lesack, 2002). In the Mackenzie Delta, Fee et al. (1988) proposed that light limited phytoplankton production in lakes with high river connectivity, whereas low nutrient availability reduced growth in lakes with low river connectivity. Subsequent studies by Squires and Lesack (2002) found modest support for this hypothesis, although they suggested that grazing by zooplankton and competition with macrophytes may be the dominant influences on phytoplankton standing crops.

For the PAD in northern Alberta, reduction of river flow due to climate change and human consumptive water uses has the potential to alter the delta’s aquatic ecosystems (Prowse and Conly, 1998; Wolfe et al., 2008a,b; Johnston et al., 2010). On the basis of a regional survey of water chemistry and water isotope composition in 61 lakes conducted in October 2000, closed-drainage lakes (i.e. without river connectivity) have high concentrations of many dissolved ions, DOC and dissolved nitrogen and phosphorous compared with open-drainage lakes (i.e. with continuous river connection), whereas restricted-drainage lakes (i.e. with periodic river connectivity) have intermediate concentrations (Wolfe et al., 2007b). Consistent with this pattern, analysis of photosynthetic pigment concentrations in the surface sediments found that closed-drainage lakes have higher algal production than lakes that flood more frequently (McGowan et al., 2011). Wolfe et al.’s (2007b) one-time regional survey was conducted at the end of the ice-free season, which likely under-represents the influence of important hydrological processes that occur during the spring freshet (i.e. snowmelt and river flooding) on limnological conditions. Previous studies have not yet identified the timescales under which limnological conditions respond to hydrological change. To improve our ability to anticipate limnological changes to climate- and human-mediated changes in river hydrology, knowledge of linkages between hydrological processes and limnological conditions is required over seasonal and inter-annual timescales.

In this article, we compare repeated hydrolimnological measurements over 3 years (2003–2005) at lakes and rivers in the PAD to examine the role of flooding on seasonal- and inter-annual variations in physical and chemical conditions and phytoplankton standing crop. The lakes differ widely in the frequency of river flooding, from continuous flooding to an absence of floods for at least the preceding 15 years. Reports by Fuller and LaRoi (1971) and MRBC (1981) have suggested that river flooding stimulates productivity of lakes in the PAD, although they presented no data from measurements of nutrients or aquatic productivity. More recently, Prowse et al. (2006) reviewed ongoing and anticipated climate alterations to the hydroecology of high-latitude freshwater ecosystems and concluded that reductions in ice-jam flooding will reduce overall biological diversity and productivity, with the most pronounced effects on floodplain and delta systems. The paradigm that river flooding of PAD lakes is important for maintaining nutrients and aquatic productivity has been often repeated but is lacking verification (Fuller and La Roi, 1971; MRBC, 1981; Prowse et al., 2006; Anisimov et al., 2007). Thus, our study seeks to test if river flooding elevates water column nutrient concentrations and phytoplankton standing crop in flooded lakes compared with lakes that have not flooded for many years to decades. Given the likelihood of reduced flooding and increasing water scarcity in the PAD (Wolfe et al., 2008a), this knowledge is critical to anticipate limnological changes. Ultimately, our findings provide the basis for identifying timescales of limnological trajectories that can be expected under different flood regimes.

THE PEACE-ATHABASCA DELTA

The PAD is situated in northern Alberta, Canada, at the confluence of the Peace, Athabasca and Birch rivers (Figure 1). The PAD is the world’s largest freshwater boreal delta and covers an area of approximately 6000 km² (Peters et al., 2006). The landscape is recognized as a UNESCO World Heritage Site and a Ramsar Wetland of International Importance for its ecological and cultural significance, including that it serves as a key node for four North American flyways used by waterfowl (MRBC, 1981; Prowse and Conly, 2000).

The PAD includes the Peace Delta in the north, the Athabasca Delta in the south and a central sector dominated by large, shallow, open-drainage lakes that are in continuous or near-continuous connection with rivers (e.g. lakes Claire, Mamawi, Richardson; Figure 1). Except for the elevated river levees, the Athabasca sector has very low topographic relief and floods frequently. In contrast, the Peace sector is a relic delta that has greater topographic relief than the Athabasca sector, with numerous inliers of Precambrian Shield protruding above the fluviodeltaic plain. This feature contrasts with the generally active floodplain landscapes of the Athabasca sector and the Slave and the Mackenzie deltas. Consequently, lakes in the northern Peace sector receive river floodwaters only during ice-jams that occasionally form on the Peace River (Prowse and Conly, 2000).

The low relief and countless meander scars within the delta have given rise to hundreds of shallow water bodies (hereafter we refer to all water bodies as lakes). The lakes span a broad range of hydrological conditions largely related to the role of river flooding on lake water
TIMESCALES OF HYDROLOGICAL CHANGE IN PEACE-ATHABASCA DELTA LAKES

Figure 1. Maps showing locations of the Peace-Athabasca Delta (Alberta, Canada) and the study sites.

Study lakes

Nine lakes were selected from a set of 61 lakes originally sampled for water chemistry and isotope composition in October 2000, and they include lakes in the open- (PAD 45), restricted- (PAD 8, 15, 31, 54) and closed-drainage (PAD 1, 5, 9, 23) hydrological categories as defined by Wolfe et al. (2007b) (Figure 1, Table I). A total of nine lakes were included in this study because this was the maximum number that our field sampling team and research budget could manage to sample repeatedly over the course of three seasons using boat transportation in a large and remote landscape. The nine lakes were chosen to represent the complete hydrological gradient of lakes in the PAD based on data presented in Wolfe et al. (2007b). The lakes were sampled three to six times per year for their physical, chemical and biological attributes during the ice-free seasons of 2003, 2004 and 2005. The Peace River, Athabasca River and Mamawi Creek were

balance, and they have been functionally categorized as open-, restricted- or closed-drainage basins (Pietroniro et al., 1999; Wolfe et al., 2007b). Open-drainage lakes are connected to the river network, restricted-drainage lakes periodically receive river water and closed-drainage lakes do not receive any river input except during major ice-jam flood events. The restricted- and closed-drainage lakes are numerically dominant in the PAD, and most of them are small ponds (≈5–50 ha). In contrast, there are only a few open-drainage lakes located in the central region of the PAD and they tend to have very large surface area (>5000 ha). For example, of the 61 lakes surveyed by Wolfe et al. (2007b), only lakes PAD 25 (Blanche Lake), PAD 26, PAD 38 (Richardson Lake), PAD 45 (Mamawi Lake), PAD 46 (Otter Lake), and PAD 62 (Lake Claire) were classified as open-drainage lakes based on isotope-inferred evaporation to inflow ratios.

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also sampled to characterize the water isotope signatures and physical and chemical characteristics of floodwater sources.

The closed-drainage lakes did not flood during 2003–2005. To our knowledge, PAD 1 and PAD 9 have not flooded since at least the last major ice-jam flood of 1997. PAD 5 likely has not flooded since 1986 (Wiklund et al., 2010). PAD 23 did not flood during the 3 years of monitoring. A single open-drainage lake (PAD 45 or Mamawi Lake) was sampled in this study because lakes in this hydrological class are rare in the PAD and their hydrological and limnological conditions are relatively similar because of strong influence of constant river through-flow compared to restricted- and closed-drainage lakes (Wolfe et al., 2007b). Open-drainage lake PAD 45 occupies a large and complex basin. Consequently, three separate sampling sites were used to characterize spatial variability of limnological conditions due to hydrological gradients within the lake. Site PAD 45T1 is a sheltered, macrophyte-rich embayment located ~2 km south of the Mamawi Creek delta and was included to represent a region of the lake with relatively low river influence. Site PAD 45T2 is located between two of the discharge channels of the Mamawi Creek delta and was selected to represent a region of the lake with direct river influence. Site PAD 45 is located near the centre of Mamawi Lake and was selected to represent offshore lake conditions.

For each of the monitoring years, we divided lakes in the restricted-drainage category into two subcategories—those that flooded ('flooded restricted-drainage') and those that did not flood ('non-flooded restricted-drainage'). The flooded restricted-drainage lakes included PAD 8 in all years (2003–2005), PAD 15 and 54 in 2003 and 2005, and PAD 31 at all times except spring of 2004 when it did not flood. Non-flooded restricted-drainage lakes included PAD 15 and 54 in 2004 and PAD 31 in spring of 2004 (note: PAD 31 flooded later in the summer of 2004). Flooded lakes were detected by several characteristics. These included direct observation of river inflow, recently formed high water lines on shorelines and surrounding terrestrial vegetation, abrupt water-level rises recorded by water-level loggers and measurement of isotopically depleted lake water and high suspended sediment concentration.

**METHODS**

*Field methods and sample analysis*

Water chemistry analysis was conducted on samples collected from each lake and river site in the spring (mid-May to mid-June), summer (late June to early August) and fall (late August to September). Measurements included temperature, hydrogen and oxygen stable isotope composition, pH, alkalinity, specific conductivity and concentrations of total suspended sediment (TSS), inorganic suspended sediment (ISS), organic suspended sediment (OSS), dissolved oxygen (DO), Chl a, dissolved ions (Ca, Mg, Na, K, Cl, SO₄), dissolved reactive silica (DSi), total Kjeldahl nitrogen (TKN), inorganic nitrogen (NH₄, NO₂, NO₃), total phosphorous (TP), dissolved phosphorous (DP) and DOC. Water samples were collected mid-lake (or mid-channel) from a depth of ~20 cm and immediately placed in a cooler with ice and refrigerated upon returning to the field base. Oxbow lakes PAD 54 and 15 were sampled at two locations (middle of north and south arms). Water for analysis of TP and TKN was preserved by adding 1 ml of 30% H₂SO₄ to each 250 ml sample.
For Chl a analysis, water samples were refrigerated until filtration (usually the same day of collection or the following day) through a Whatman GFF filter (0.4 μm pore size). The filter was then folded in half, wrapped in aluminum foil and frozen until analysis. Chl a extraction and quantification were performed on these samples using standard fluorescence techniques described by Stainton et al. (1977).

Water chemistry analyses (ions, nutrients, DOC) were performed by Taiga Laboratory (Yellowknife, NWT) on samples collected in 2003 and 2004, and by Environment Canada’s National Laboratory for Environmental Testing (Burlington, ON) on samples collected in 2005. Because of logistical constraints, PAD 15 and 23 were not sampled in 2005 for nutrients and dissolved ions.

To determine concentrations of suspended sediment (TSS, ISS, OSS), water was filtered through pre-combusted (at 550 °C for 1 h) and pre-weighed Whatman GF/C filters (0.7 μm pore size). Filters were folded in half, wrapped in aluminum foil and kept refrigerated until analysis. The filters were dried at 90 °C (48 h) and weighed for determination of TSS concentration, then combusted at 550 °C (2 h) and weighed for determination of ISS concentration. Filters were allowed to cool in a desiccator for several hours prior to weighing. OSS concentration was calculated as the difference between concentrations of TSS and ISS.

Water samples for hydrogen and oxygen stable isotope compositions were sealed in 30 ml high-density polyethylene bottles and analyzed at the University of Waterloo Environmental Isotope Laboratory using standard methods (Epstein and Mayeda, 1953; Morrison et al., 2001). Results are reported in δ values, representing deviations in per mil (‰) from VSMOW on a scale normalized to values of Standard Light Antarctic Precipitation (−55.5‰ for δ¹⁸O; −428‰ for δ³⁴S; Coplen, 1996). Analytical uncertainties are ±0.2‰ for δ¹⁸O and ±2.0‰ for δ³⁴S.

Temperature, specific conductivity, DO and pH were measured using a YSI 600QS multi-meter (YSI Incorporated, Yellow Springs, OH) in 2005 and Hannah Instruments meters (HI 9033, HI 9143M, HI 99 101, HI 98 128) in 2003 and 2004. Measurements were taken at three locations within a lake at regular depth intervals spanning the top 1 m of the water column, and the average value was used to represent each site.

The light extinction coefficient of photosynthetically active radiation (Kd-par) was calculated from measurements taken using an Apogee Instruments Quantum meter (Model QMSS-SUN) at ~10 depth intervals per site that spanned a 90% reduction in incident light, where water column depth permitted. Three PAR values were recorded at each depth interval and the mean value was natural log-transformed and regressed versus depth (m). The resultant slope of the relationship was used to estimate Kd-par. As with other metered measurements, Kd-par values obtained from two to three locations were averaged to represent each site. Metered measurements of river sites were performed similarly, but only at one mid-channel location.

### Data analysis

Principal components analysis (PCA) was used to explore major differences in the physical and chemical conditions among lakes and the patterns of seasonal variation. The PCA was performed using the software CANOCO version 4.5 (ter Braak and Šmilauer, 2002). All lake sites with complete data were included in the PCA. This included plotting PAD 54 and 15 north- and south-arm sites individually, though for statistical comparisons between hydrological categories (see ANOVAs described below), PAD 54 and 15 were represented as an average of their respective north and south sampling locations to prevent over-representation of these lakes. Scaling focussed on inter-sample distances, and variables were divided by their standard deviation prior to ordination and centred by variables. River samples were added passively in the ordination to assess the influence of river flooding on the lakes without affecting the patterns of variation among the lakes. The ratio of TKN/TP was also added passively, because both TKN and TP were included as active variables.

The transparency of water to photosynthetically active radiation, as measured by Kd-par, can be affected by minerogenic turbidity (estimated as concentration of ISS), suspended organic matter (estimated as concentration of OSS), coloured DOC and phytoplankton (estimated as concentration of Chl a) (Cristofor et al., 1994). Consequently, we used multiple linear regression analysis (forward and backward selection of variables, performed using the software SYSTAT version 10.5) of the concentrations of ISS, OSS, Chl a and DOC to elucidate which factor(s) best explain variation in the underwater light
climate (Kd-par) of lakes (n = 98) and rivers (n = 33), with rivers and lakes analyzed separately. The regression equations (Table II) were also used to fill in missing Kd-par data for the PCA of the limnological data. TSS was the main factor used to estimate missing Kd-par values and it was highly co-linear with Kd-par, ISS and OSS. Consequently, Kd-par was retained as an active variable in the PCA.

ANOVA tests (α = 0.05) were run to test if limnological variables differed among the hydrological lake categories and among seasons (spring, summer and fall) using SPSS version 16.0. Two-way ANOVA tests were used to assess if limnological variables differed among the seasons while accounting for the influence of differences among hydrological categories. In contrast, one-way ANOVA tests were used to assess if limnological variables differed among the hydrological lake categories within an individual season. For post hoc multiple comparisons, Tukey’s tests were used, except for variables where variances remained unequal after transformation (TSS, ISS, OSS, Kd-par, Chl a, DSi and TP). In these latter cases, Dunnett’s T3 post hoc tests were used because it allows for unequal variances. For the PCA ordination and ANOVA tests, all variables, except pH, were log_(x + 1)-transformed prior to analysis to improve normalcy and equalize variances.

RESULTS AND INTERPRETATION

Water balance

Water stable isotope (δ^{18}O and δ^2H) values differed markedly among the hydrological lake categories because of differences in the relative importance of river flooding and evaporation to the lake water balances (Figure 2). The mean isotopic values of river waters showed the least amount of seasonal variation and were closest to mean annual precipitation (δ^2H), indicating that evaporation was a small component of river water balance. Mean lake water δ^{18}O and δ^2H values of the open-drainage lake (PAD 45) were very similar to those of the rivers, although slightly more isotopically enriched, indicating only a small effect of evaporation on the water balance relative to the river inputs. In spring, the mean lake water δ^{18}O and δ^2H value for flooded restricted-drainage lakes was very similar to that of the open-drainage lake and rivers, identifying the strong influence of river flooding on their water balance during and shortly after the spring freshet. As the season progressed, however, waters became more isotopically enriched in the flooded restricted-drainage lakes than in the open-drainage lake because of the greater influence of evaporation on lake water balance. In spring, mean isotope composition of non-flooded restricted-drainage lakes was enriched compared with that of the flooded restricted-drainage lakes because the former were not flooded. Isotopic signatures of non-flooded restricted-drainage lakes and closed-drainage lakes were similar in the spring and were low relative to their values later in the ice-free season, indicating influence of snowmelt on water balance early in the ice-free season. Closed-drainage lakes experienced much greater evaporative enrichment during the summer and fall compared with the non-flooded restricted-drainage lakes, and approached signatures expected for lakes approaching terminal basin steady-state conditions (i.e. δ^8S, when inputs = evaporation).

Chemical and physical differences of the Peace and Athabasca River flood waters

The source waters for floods that enter lakes in the PAD originate from either the Peace River or the Athabasca River (Figure 1). For the two rivers, mean specific conductivity [220 ± 7.8 and 227 ± 8.0 μS/cm; Peace and Athabasca rivers, respectively (as mean ± 1 S.E.)] and alkalinity (93-84 ± 1.84 and 89-96 ± 3.04 mg/l) did not differ significantly based on one-way ANOVA tests (p > 0.05, d.f. = 22). Similarly, concentrations of Mg and K did not differ significantly between the rivers (Figure 3). However, the Athabasca River was significantly higher in concentrations of dissolved sodium (p < 0.001), chloride (p < 0.001) and DSi (p = 0.03), whereas the Peace River had higher concentrations of calcium (p < 0.001) and SO4 (p = 0.009; Figure 3).

On the basis of field observations, turbidity persisted longer in lakes flooded from the Peace River than in lakes flooded by the Athabasca River. For example, PAD 54 and PAD 31 both flooded extensively with river water in the spring of 2003 by the Peace and Athabasca rivers, respectively. The water column of PAD 31 cleared within approximately 4 weeks after the flood event, but PAD 54 took approximately 2 months for the sediment load to settle out. One explanation for this observation is...
that the sediment load in the Peace River was finer-grained and, therefore, took longer to settle out of the water column. Patterns of the rate of change in TSS concentrations support this interpretation. For example, the half-life of TSS in water at PAD 31 following a summer flood event in 2004 was estimated at 2.8 days. This is approximately 50% shorter than the half-life (5.1 days) calculated for PAD 54 following the 2003 spring flood. These estimates of half-life are based on first-order kinetics, which have previously been used to model sedimentation in lakes (Frisk, 1992) and wetlands (Holland et al., 2005). Furthermore, where sufficient data exists, first-order kinetics can be shown to accurately describe the settling of TSS from the water column (Kotz and Purcell, 1991). For example, the logarithm of TSS concentration versus time at PAD 54 (2003) follows a linear decay that spans >2 orders of magnitude of TSS concentration ($R^2 = 0.9925$, $n = 4$; linear regression not shown).

**Comparison of limnological conditions among the hydrological lake categories**

The first two axes of the PCA of the physical and chemical data ($n = 153$) explained 54-6% of the variation in limnological conditions among the study lakes and identified distinct limnological differences between flooded lakes and rivers versus the lakes that did not flood (Figure 4). Sample scores from the non-flooded lakes (i.e. closed-drainage and non-flooded restricted-drainage lakes) were positioned to the left along PCA axis 1, indicative of relatively low Kd-par (= high transparency), low concentrations of DSI, Chl a and SO$_4^{2-}$, and high pH and TKN : TP ratios. Sample scores for rivers and open-drainage lakes were positioned to the right along axis 1, indicating the opposite conditions. Samples from the flooded restricted-drainage lakes showed the greatest amount of variation in the PCA ordination, indicating that they experienced the greatest seasonal limnological changes. Limnological conditions of the flooded restricted-drainage lakes overlapped with those of the rivers and open-drainage lakes during the spring period when they flooded (Figure 4b), but rapidly migrated along axis 1 during the summer and fall as they transitioned to conditions that were more typical of the non-flooded restricted-drainage basins (Figure 4c, d). Interestingly, sample scores from two of the flooded restricted-drainage lakes (PAD 8 and 31) closely matched those of the river samples throughout the summer and fall, indicating strong influence of continued flood inputs throughout the ice-free season. In contrast, sample scores for PAD 15 and 54 in spring of 2003 and 2005, when they flooded, were similar to those of the rivers, but subsequently diverged during the summer and fall after flooding ceased (Figure 4c, d). Limnological conditions at the restricted embayment of Mamawi Lake (site PAD 45T1) were more similar to the flooded restricted-drainage lakes, because of higher pH and lower Kd-par and TP and DSI concentration, than to sites in the open-drainage regions of Mamawi Lake (PAD 45, PAD 45T2). This suggests poor exchange of water between the sheltered embayment and Mamawi Lake during periods of lower river inflow, which commonly occurred during the summer and fall.

Axis 2 of the PCA separated samples from most of the closed-drainage lakes from those of all other hydrological categories (Figure 4). Closed-drainage lakes were positioned high on PCA axis 2, characterized mainly by high alkalinity and conductivity and high concentrations of TKN, DOC, and dissolved ions Mg, Na, K and CI relative to the other hydrological categories. An exception to these patterns was PAD 23, which possessed physical and chemical characteristics more typical of the non-flooded restricted-drainage lakes because of lower concentration of solutes. For this reason, as well as others discussed below, PAD 23 was categorized together with the non-flooded restricted-drainage lakes in subsequent analyses (Figures 6–8). Overall, ordination by PCA illustrates that variations in physical and chemical conditions of lakes that flooded within the previous few
Figure 4. Principal components analysis (PCA) of physical and chemical data from water samples collected from the study lakes in the Peace–Athabasca Delta in 2003–2005 ($n = 153$). Vectors of the supplied environmental variables are shown in panel (a), whereas the other panels show the sample scores for samples collected in (b) spring (mid-May to mid-June), (c) summer (late June to early August) and (d) fall (late August to September). The number within each symbol represents the lake number (i.e. $5 = PAD 5$). For rivers, the letter within the symbol represents the Peace (P), Athabasca (A) or Mamawi (M) rivers. The river samples and the nutrient ratio variable TKN : TP were included passively. All variables, except pH, were log$_e$($x + 1$)-transformed prior to analysis.

Time-ordered trajectories of PCA scores from four representative lakes were used to explore further the seasonal and inter-annual patterns of limnological changes within each hydrological category (Figure 5). Limnological characteristics of PAD 5 (a closed-drainage lake that has not flooded to our knowledge since 1986) remained distinct from the rivers and did not fluctuate much during 2003–2005, as indicated by the relatively tight clustering of sample scores compared with the other lakes and rivers (Figure 5a). The sample scores from PAD 5 were positioned in the upper left quadrant of the PCA ordination, associated with high concentrations of TKN, DOC and dissolved ions and high pH. River samples were positioned to the right along PCA axis 1, associated with high Kd-par (low clarity) and high concentrations of suspended sediment, TP, SO$_4$ and DSi. River samples were positioned to the right along PCA axis 1, associated with high Kd-par (low clarity) and high concentrations of suspended sediment, TP, SO$_4$ and DSi, but varied along axes 1 and 2 mainly in response to changes in TP concentration and Kd-par that were associated with seasonal fluctuations in river discharge (Figures 6, 7).

Limnological conditions of PAD 54, a restricted-drainage oxbow lake, were similar to those of river water during spring of 2003 and 2005 shortly after the lake flooded, as indicated by the overlap with river samples (Figure 5b). During these times, the water was turbid (high Kd-par) and had high concentrations of suspended sediment, TP, SO$_4$ and DSi. After flooding, values of Kd-par, suspended sediment, TP and DSi declined as the season progressed. Sample scores were nearly identical during summer and fall of the 2 years when the lake flooded in spring (2003, 2005), suggesting that spring flooding exerts important control on seasonal limnological patterns. During 2004, when PAD 54 did not flood, limnological conditions were less variable compared with years when the lake flooded (2003 and 2005). Interestingly, sample scores in summer and fall of the non-flood year (2004) did not differ much from those of summer and fall of years when it flooded (2003, 2005), suggesting that more than 1 year without flooding is required for limnological conditions to develop towards those of closed-drainage lakes.
Sample scores from PAD 31, a restricted-drainage lake that received pulses of floodwater during the spring of 2003 and 2005 and during the ice-free season of all years, shifted along PCA axis 1 (Figure 5c). Whenever the lake flooded, turbidity and concentrations of TP, SO$_4$ and DSi increased, as indicated by a shift of the sample scores to the right where they overlapped with river samples. After flood events, sample scores moved to the left along axis 1, associated with declines in turbidity and concentration of TP. The sample score from spring of 2004, when PAD 31 did not flood, lies in a unique position compared with all other samples from this lake and was characterized by the lowest Kd-par, TP, SO$_4$ and DSi. Later in 2004 (June, July and possibly September), PAD 31 flooded and sample scores returned to values more similar to those of the rivers. The more complex path of PAD 31 in PCA space (Figure 5c), in comparison with PAD 54, exemplifies the behaviour of a multi-modal flood pulse (Junk and Wantzen, 2004) where limnological conditions are repeatedly influenced by river water within a single ice-free season.

Sample scores from PAD 45, an open-drainage lake that receives constant river inflow, were positioned close to those of the river, indicating continuous strong influence of river water on limnological conditions characterized by high turbidity (high Kd-par) and high TP concentrations (Figure 5d). The small offset evident between sample scores from PAD 45 and river water is likely because of settling out of suspended matter between the river mouth and the centre of Mamawi Lake as water velocity declined, which generated values of Kd-par and TP concentration that were lower compared with the rivers.

Use of bar charts and ANOVA tests allowed us to further refine our understanding of the roles of flooding on physical and chemical conditions in the hydrological lake categories of the PAD, as described in the following sections.

**Suspended sediment and water clarity.** Content of suspended sediment (TSS, ISS and OSS) was highest in rivers and decreased along the hydrological gradient from open- to closed-drainage lakes (Figure 6a–c). In the lakes that flooded (open-drainage and flooded restricted-drainage), suspended sediment concentrations were highest in the spring and decreased as the ice-free season progressed. This pattern was especially apparent in the flooded restricted-drainage lakes, where TSS and ISS concentrations declined by at least an order of magnitude...
between spring and fall to values comparable to those of closed-drainage and non-flooded restricted-drainage lakes. The mineral fraction (ISS) dominated TSS in rivers and open-drainage and flooded restricted-drainage lakes at all times. In contrast, suspended sediment content did not vary appreciably over the course of the ice-free season in the non-flooded lakes (closed-drainage and non-flooded restricted-drainage). Also, TSS consisted of a more even mixture of organic (OSS) and mineral (ISS) fractions in the closed-drainage and non-flooded restricted-drainage basins compared with flooded lakes (Figure 6).

Differences in water clarity among the hydrological lake classes, as measured by Kd-par, closely followed the trends observed for TSS and ISS, including comparable patterns of seasonal variation (Figure 6d). ISS was the
dominant factor controlling the aquatic light climate (as Kd-par) in the lakes and in rivers, based on multiple linear regression analysis with ISS, OSS, Chl a and DOC concentrations as explanatory variables ($n = 98$ for lakes; $n = 33$ for rivers; Table II). Minerogenic turbidity (ISS) alone explained 66.2 and 86.7% ($R^2_{adj}$) of the variation in the light climate of lakes and rivers, respectively, similar to findings of Pavelsky and Smith (2009) for rivers of the PAD. OSS concentration was also found to account for significant additional amounts of variation in
Kd-par in both lakes and rivers, while Chl a concentration only accounted for significant additional amounts of variation in Kd-par in lakes. DOC concentration was not found to explain significant additional variation for predicting the light climate in either lakes or rivers, even though the range of DOC concentration is large (2-6 to 74-7 mg/l and 4-6 to 24-5 mg/l for lakes and rivers, respectively). In fact, DOC concentration showed patterns opposite to those of TSS and Kd-par. DOC concentrations were highest in closed-drainage lakes and comparably low in the other hydrological lake categories and rivers (Figure 6). In all lakes, DOC concentrations did not vary appreciably during the ice-free season.

**Nutrients and chlorophyll a.** Mean total phosphorous (TP) concentration was consistently higher in rivers compared with lakes (Figure 7). Seasonally, TP concentrations in river water were highest in the spring and summer, and decreased in the fall (Figure 7a). During the spring period, lakes that flooded (open-drainage and flooded restricted-drainage lakes) had elevated TP concentrations. However, this rise was transitory, and by summer, TP concentrations became comparable with those of the non-flooded lakes—a feature that persisted into the fall.

The concentration of dissolved phosphorous (DP) was often below detection limits for analysis conducted at Taiga Laboratory on samples collected during 2003 and 2004, so a complete set of results for DP is only available from 2005 (Figure 7b). These data identify that DP concentration in closed-drainage lakes was double that of the other hydrological lake categories and rivers, which all have comparable values. Also, they identify that most of the TP in river waters is in particulate form, whereas about 50% of the TP in closed-drainage lakes is in dissolved form (DP). In closed-drainage lakes, mean DP concentration ranges 30–50 µg/l, suggesting these systems are not P-limited.

The TKN concentration in closed-drainage lakes was consistently at least double that in lakes of the other hydrological categories, including the rivers (Figure 7b). The mass ratio of TKN/TP decreased with increasing river influence (Figure 7c). This gradient was most evident during the summer sampling period.

Inorganic nitrogen (NO₂⁻, NO₃⁻, NH₄⁺) concentrations were not available for samples collected during 2003 and 2004. But samples collected in 2005 allowed us to identify that total inorganic nitrogen (TIN) concentration contributes approximately 5–15% of the total nitrogen present in the lakes and rivers. TIN concentration was lowest in rivers and increased with decreasing river connectivity (Figure 8e).

Dissolved silica (DSi) concentration was consistently high in the rivers, with little seasonal variation (Figure 7d). Concentrations of DSi were higher in flooded lakes (i.e. open-drainage, flooded restricted-drainage) than in non-flooded lakes (Figure 7d). Concentrations tended to decline after spring in the flooded lakes, but remained relatively constant in non-flooded restricted-drainage lakes.
Mean water column Chl a concentration was highest in the flooded restricted-drainage lakes throughout the ice-free season but only differed significantly from mean values in the other hydrological lake categories during the spring and when values were included for the entire season (Figure 8a,b).

DISCUSSION

During the last century, climate-driven changes in meltwater contributions from glaciers and snowpacks at the headwaters of the Mackenzie River Basin have caused marked reductions in both peak and total river discharge, a pattern that is expected to continue (Wolfe et al., 2008a). Yet, the limnological consequences of reduced river flows and associated frequency and magnitude of flooding downstream in the PAD remain largely unknown. Here we show that river floodwaters exert strong influence on limnological conditions of lakes in the PAD, although their role in supporting nutrient concentrations has been overestimated, and we identify timescales of limnological trajectories under different flood regimes. As illustrated below, these findings provide knowledge to anticipate the nature of future limnological changes and the timescales at which they are likely to occur.

The effects of flooding on nutrients and phytoplankton

Nutrient concentrations are strongly associated with hydrological conditions of lakes in the PAD. Highest concentrations of several key nutrients (DP, TKN, TIN) occurred in the closed-drainage lakes (Figure 7). Rivers have the highest TP concentration, but the majority is in particulate form rather than dissolved form (TP:DP>20:1 on average, Figure 7a). Thus, river waters elevate TP concentration in lakes that are flooded, but concentrations rapidly decline as suspended sediments settle out of the water column. As a consequence, TP concentration of lakes that flooded during spring converged by summer to values typical of closed-drainage lakes. Thus, our data indicate that regular flooding is not required as a source of nutrients to lakes in the PAD because the closed-drainage lakes in our study contain the highest concentrations of bio-available nutrients despite the absence of flooding for at least 6–17 years. This finding is contrary to previously stated hypotheses (Fuller and LaRoi, 1971; MRBC, 1981; Prowse et al., 2006; Anisimov et al., 2007), which stated that river flooding is necessary to maintain high nutrient concentrations and aquatic productivity. However, our conclusion does agree with results from limnological studies at the Slave (Sokal et al., 2008) and Mackenzie deltas (Emmerton et al., 2008) downstream of the PAD.

Phytoplankton standing crop is low in lakes of the PAD (generally <4 μg/l). On the basis of standard relationships between phytoplankton standing crop and water column concentrations of TP and total N (Brown et al., 2000), Chl a content is expected to be at least 10-fold higher than we observed in the closed-drainage lakes. This feature is also evident for lakes of the Slave (Sokal et al., 2010) and Mackenzie deltas (Fee et al., 1988; Squires and Lesack, 2002). Fee et al. (1988) identified that while Chl a content was low overall, it was highest in lakes with intermediate river connectivity and hypothesized that this was due to a tradeoff between availability of light and nutrients. We investigated this hypothesis in the PAD using multiple linear regression of water column TP concentration and Kd-par on Chl a concentration. Results show that Kd-par and TP concentration explain significant amounts of variation in Chl a concentration (p < 0.0001) and predict a response surface (Figure 9, Table III) that is congruent with the light-nutrient hypothesis of Fee et al. (1988). However, the relationship has very low predictive ability (R² = 10–7%), which is also consistent with findings by Squires and Lesack (2002). The relationship was improved by also including DSi concentration (R² = 21.6%; Table III) but still fails to explain the majority of variation in Chl a concentration. Neither water temperature (range 7.05–26.30°C) nor DP (range 7–92 μg/l) explained significant (a < 0.05) additional variation in water column Chl a concentration.

Although it is attractive to explain the observed maximal Chl a concentration at intermediate hydrologic connectivity as a tradeoff between light and nutrient availability, other contributing factors are likely the dominant controls on the abundance of phytoplankton in the PAD. Interestingly, Flanagan et al. (2003) have noted that the relationship between TP and Chl a is much weaker for high-latitude (>60°N) lakes (R² = 7% for a Log–Log plot) than for mid-latitude lakes, and that nitrogen limitation did not account for this. Instead, they observed
a strong negative correlation between Chl a concentration and latitude, independent of TP concentration. To explain this, Flanagan et al. (2003) hypothesized that the influence of abiotic factors such as light and temperature exert bottom-up control on phytoplankton abundance or that gradients of biotic factors related to food-web composition exert top-down control. Our data identify weak predictive abilities for TP, Kd-par and DSi for water column Chl a (Figure 9, Table III), and non-significant predictive ability of DP and water temperature, a finding that suggests weak bottom-up control. Therefore, we suggest top-down processes are the dominant drivers. In the PAD, phytoplankton face greater competition with macrophytes for space and light and grazing pressure by zooplankton in closed- and non-flooded restricted-drainage lakes compared with flooded restricted-drainage and open-lake lakes. In short, multiple environmental factors associated with the hydrological gradient (e.g. water clarity, nutrients, macrophytes, zooplankton, and fish) likely contribute to the observed maximal phytoplankton standing crop in the flooded restricted-drainage lakes (Figure 8a, b).

**Timescales of hydrolimnological change in the PAD**

Our results identify that the responses of hydrolimnological conditions to flooding operate at two distinct timescales in lakes of the PAD. This feature is captured by PCA ordination of samples collected during ice-free seasons of three successive years from nine lakes that span the hydrological gradient in the delta (Figure 4) and is conceptualized in Figure 10.

One timescale involves the short-term responses of lakes over a period of weeks to months after flooding, which is captured by PCA axis 1 (Figure 4) and the horizontal axis of Figure 10. Floods exchange a substantial volume of water in the shallow floodplain lakes with isotopically depleted river water that is higher in content of P-rich suspended sediment and DSi, calcium and SO₄, and lower in pH. The turbid river waters reduce water clarity (increase Kd-par) of flooded lakes. In the weeks to months after a flood, lake water becomes isotopically enriched because of evaporation, and the supplied sediments settle out of the water column leading to increases in water clarity (reduced Kd-par) and a shift to limnological conditions that resemble those of non-flooded restricted-drainage lakes (Figure 5b, 10).

Restricted-drainage lakes, thus, oscillate along the horizontal axis in response to the rapid exchange with flood waters and move leftwards on the axis in response to evaporation and sedimentation processes that affect concentrations of TSS and TP, and chemical (pH) and nutrient (DSi) factors prone to rapid biological alteration.

In contrast to the relatively rapid, seasonal to inter-annual changes that follow a flood event, the limnological transition from restricted-drainage to closed-drainage hydrological conditions occurs over a much longer timescale of several years to decades, as concentrations of the more conservatively acting ions, refractory organic matter (e.g. DOC) and dissolved nutrients (DP, N) increase. In the absence of flooding, the water

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**Table III. Results of multiple linear regression of factors contributing to variation in water column chlorophyll a (Chl a) concentration.**

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Constant</th>
<th>TP</th>
<th>Kd-par</th>
<th>DSi</th>
<th>$R^2$</th>
<th>$R^2_{adj}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chl a (lakes+ rivers)</td>
<td>Coefficient 0.3411</td>
<td>0.3547</td>
<td>-0.2560</td>
<td>N.I.</td>
<td>10.68%</td>
<td>9.76%</td>
</tr>
<tr>
<td>n = 198</td>
<td>$p$ value 0.1780</td>
<td>0.0001</td>
<td>0.0310</td>
<td>N.I.</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td>Chl a (lakes+ rivers)</td>
<td>Coefficient -1.111</td>
<td>0.328</td>
<td>-0.426</td>
<td>0.238</td>
<td>21.6%</td>
<td>20.4%</td>
</tr>
<tr>
<td>n = 198</td>
<td>$p$ value 0.003</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
</tbody>
</table>

Concentrations are in ug/l and all variables were log$_e$ (x + 1)-transformed prior to performing regression. Water temperature and dissolved phosphorus (DP) concentration were also investigated as independent variables but were not found to contribute additional significant ($p < 0.05$) explanation of water column Chl a variation. N.I. = not included.

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balance of closed-drainage lakes is mainly controlled by precipitation and evaporation. Elevated concentrations of DOC, TKN, DP and many dissolved ions in the closed-drainage lakes compared with lakes which have flooded in recent years is consistent with studies of lakes in central Alberta, which show that lakes with longer water residence time have higher conductivity and concentrations of DOC and dissolved organic N because of the strong role of evaporative concentration (Curtis et al., 1995). The process of evaporative concentration operates over years to decades and causes the limnological conditions of closed-drainage lakes to develop along a different trajectory, characterized by increasing concentrations of dissolved nutrients and ions, as illustrated by PCA axis 2 in Figure 4 and the vertical axis in Figure 10. In a matter of days, a flood event will reset limnological conditions of a closed-drainage lake to that of a flooded restricted-drainage lake (Figure 10).

Fortunately, PAD 23 provides an interesting situation that helps to clarify the timescale at which the transition from restricted-drainage to closed-drainage limnological conditions occurs. The isotopically enriched lake water composition of PAD 23 is consistent with the absence of flooding for several years, but the water chemistry reveals that evaporative concentration of nutrients and ions has not yet fully developed to a limnological state characteristic of the other closed-drainage lakes. Thus, our limnological evidence suggests the lake flooded recently, but prior to the onset of our hydrolimnological monitoring in October 2000. In contrast, the other closed-drainage lakes have not flooded, to our knowledge, since 1986 (PAD 5) and 1997 (PAD 1, PAD 9). Thus, it appears that half a decade or more post-flooding is required for a lake to shift from restricted-drainage to closed-drainage limnological status in comparison with the much more rapid hydrological response which takes ~2 years. Given that the most recent large-scale flood event occurred in 1997, much of the northern Peace sector of the PAD landscape has likely transitioned to closed-drainage limnological conditions.

The broad hydrological gradient that characterizes the PAD has provided the opportunity to define the two timescales of limnological change that occur under different flood regimes. Perhaps unique to this landscape, in comparison with the other Mackenzie River Basin deltas, the relict Peace sector delta allows us to characterize limnological changes when floods recur at decadal intervals or longer. In contrast, the Slave and Mackenzie delta lakes tend to oscillate along the short-term horizontal axis of Figure 10 because they are active floodplain landscapes (Brock et al., 2009; Marsh and Lesack 1996; Lesack et al., 1998). However, if flood frequency in those landscapes were to decline, we propose that some Slave and Mackenzie Delta lakes will begin to undergo limnological changes along the long-term (vertical) axis of Figure 10. Broader transferability of the timescales of limnological change at the PAD to other floodplains is likely dependent on local climate and other factors, and deserves further study.

The variability in flooding strength and extent observed in the 3 years of our study (see PAD 54; Figure 4b) is consistent with the Flood Pulse Concept (Wantzen et al., 2008), which states that flood pulse patterns and strength vary between years on inter-annual and inter-decadal timescales. Flood pulses have been previously noted to temporally reset and homogenize limnological conditions of floodplain lakes. After flood waters subside and lakes become disconnected from the river, limnological conditions will diverge because of local differences in basin and catchment characteristics (Tockner et al., 2000; Junk and Wantzen, 2004; Thomaz et al., 2007). Improved understanding of the impacts of both short- and long-term changes in the frequency, magnitude and timing of the flood pulse on biological communities and biogeochemical processes has previously been identified as an important focus for research (Junk and Wantzen, 2004). This is particularly acute in light of current and anticipated changes in climate which are likely to lead to long-term shifts in the hydrologic regime of many river systems (Rouse et al., 1997; Prowse et al., 2006; Schindler and Smol, 2006; Wolfe et al., 2008a; Milner et al., 2009). Landscape-scale studies of delta systems can take advantage of existing hydrologic gradients to discern the role of hydro-climatic conditions on the limnological responses to changing flood regimes.

CONCLUSIONS

In a synthesis of studies of tropical and temperate floodplain systems, Thomaz et al. (2007) proposed that flooding increases the homogeneity of limnological conditions of river floodplain systems. This occurs because flooding exchanges water, dissolved substances and particulate matter between rivers and lakes, causing limnological conditions of flooded lakes to become more similar to the rivers and each other. During intervals without flooding, however, limnological conditions diverge among floodplain lakes because differences in localized (i.e. lake basin and catchment) biotic and abiotic driving forces diversify limnological and ecological conditions (Junk and Wantzen, 2004; Thomaz et al., 2007; Wantzen et al., 2008). Our findings from a northern boreal river floodplain are consistent with this concept. For example, flooded lakes in the PAD possess similar physical and chemical conditions because of strong influence of the rivers, although subtle differences between flooded lakes in the Peace and Athabasca sectors can be attributed to the different water chemistry and settling rate of suspended sediment of the Peace and Athabasca rivers. These findings are also congruent with the Flood Pulse Concept, which predicts that the nutrient status of the floodplain depends on the amount and quality of dissolved and suspended solids of the parent river (Junk and Wantzen, 2004). In the absence of flooding, limnological conditions of the closed-drainage lakes diverge from those of the flooded lakes and rivers.

Building on this conceptual model, findings of this study allow us to characterize the timescales at which
The limnological conditions of floodplain lakes change after flooding in the PAD (Figure 10). Pulse flood events raise lake water concentrations of suspended sediments, TP, SO$_4$, and DSI and reduce water clarity and concentrations of dissolved nutrients, DOC and ions. At a timescale of a few weeks to months after floodwaters subside, suspended sediments rapidly settle out of the water column leading to reduction of TP concentration and increased water clarity. At this short timescale, concentrations of DOC, SO$_4$, TKN and ions do not change appreciably. In the absence of flooding over multiple years to decades, within-basin processes dominate that lead to greater limnological heterogeneity broadly characterized by high water clarity and high concentrations of DOC, TKN, bio-available nutrients and ions and low concentrations of suspended sediments and SO$_4$. In this region of semi-arid climate, concentrations of these variables increase because of evaporation. These conditions define the current limnological status of much of the northern Peace sector of the delta. Given expected trajectories of change in river discharge (Wolfe et al., 2008b), we predict that limnological conditions in the southern Athabasca sector will become less dominated by short-term (intra-to inter-annual) oscillations along the horizontal axis of Figure 10, and become increasingly dominated by longer term unidirectional progression along the vertical axis. This transition has begun in the more elevated portions of the Athabasca sector, such as observed at PAD 23, and is likely to become more widespread (Wolfe et al., 2008a).

On the basis of our study, this transition to increasing hydrologic closure of PAD lakes will be accompanied by an increase in water transparency and bio-available forms of nutrients which will promote primary production, a finding consistent with that of McGowan et al. (2011).

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TIMESCALES OF HYDROLIMNOLOGICAL CHANGE IN PEACE-ATHABASCA DELTA LAKES


