

Influence of hydrological connectivity on winter limnology in floodplain lakes of the Saskatchewan River Delta, Saskatchewan

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Abstract: Globally, hydrological connectivity between rivers and their floodplains has been reduced by river flow management and land transformation. The Saskatchewan River Delta is North America's largest inland delta and a hub for fish and fur production. To determine the influence of connectivity on limnology within this northern floodplain, water chemistry and stable isotopes (δ^{18} O and δ^{2} H) were analyzed during the winter of 2014 in 26 shallow lakes along a hydrological gradient. A total of five lake connectivity categories were determined by optical remote sensing imagary of surface water coverage area from years of varying flood intensities. Accuracy of categories was verified by degree of ¹⁸O and ²H enrichment within lakes. Both isotopes showed marked successional enrichment between connectivity categories, with more isolated lakes exhibiting greater enrichment. Water chemistry in lakes with greater connectivity to the main channel were characterized by higher pH, dissolved oxygen, nitrates, and sulfates and lower total nitrogen, total phosphorus, and ammonium compared with more isolated lakes. These findings illustrate how connectivity influences water chemistry in northern floodplain lakes and how it might determine the suitability of these lakes as winter refuge for fishes. Additionally, our study provides supporting evidence for the effective use of optical remote sensing imagery, an inexpensive and accessible source of data for researchers, when determining connectivity characteristics of large northern floodplain systems. Additionally, this study provides further evidence that the inundation of floodplain lakes by river water during peak discharge has an impact on the conditions within the lakes long into the winter ice-cover season. Understanding the year-round influence of river-floodplain connection is imperative for assessing potential impacts of climate change and future water regulation on such ecosystems.

Résumé : À l'échelle planétaire, la gestion des débits des rivières et la transformation du territoire ont entraîné une diminution de la connectivité hydrologique entre les rivières et les plaines inondables. Le delta de la rivière Saskatchewan est le plus grand delta intérieur d'Amérique du Nord et une plaque tournante pour la production de poissons et de fourrures. Afin de déterminer l'influence de la connectivité sur la limnologie dans cette plaine inondable septentrionale, la chimie de l'eau et ses isotopes stables (δ^{18} O et δ^{2} H) ont été analysés durant l'hiver 2014 dans 26 lacs peu profonds le long d'un gradient hydrologique. Cinq catégories de connectivité des lacs ont été établies au total sur la base d'images optiques de télédétection des aires recouvertes par les eaux de surface pour des années caractérisées par différentes intensités des crues. L'exactitude des catégories a été vérifiée à la lumière du degré d'enrichissement en ¹⁸O et ²H dans les lacs. Les deux isotopes présentaient un enrichissement progressif marqué entre les catégories de connectivité, les lacs plus isolés montrant un enrichissement plus important. La chimie de l'eau dans les lacs de plus grande connectivité au chenal principal était caractérisée par un pH et des concentrations d'oxygène dissous, de nitrates et de sulfates plus élevés et des concentrations d'azote total, de phosphore total et d'ammonium plus faibles comparativement aux lacs plus isolés. Ces résultats illustrent l'influence de la connectivité sur la chimie de l'eau dans les lacs de plaines inondables septentrionales et comment elle pourrait déterminer l'adéquation de ces lacs comme refuges hivernaux pour les poissons. En outre, notre étude fournit des données témoignant de l'utilité de l'imagerie optique de télédétection, une source de données accessible et peu coûteuse, pour la détermination des caractéristiques de connectivité des grands systèmes de plaines inondables nordiques. L'étude fournit aussi de nouvelles données appuyant la thèse voulant que l'inondation des lacs de plaines inondables par l'eau de rivière en période de débits de pointe ait une incidence persistante sur les conditions dans les lacs durant la période hivernale de couverture de glace. La compréhension de l'influence tout au long de l'année de la connexion rivièreplaine inondable est nécessaire à l'évaluation des impacts potentiels des changements climatiques et de la régularisation future de l'eau sur de tels écosystèmes. [Traduit par la Rédaction]

Introduction

Floodplains are among the most productive and threatened ecosystems on earth. As a result of anthropogenic river flow management and land transformation, 90% of floodplains within North America have become functionally extinct (Tockner and Stanford 2002). The most characteristic process within a river–floodplain system, the flood pulse, is a key driver of the high biodiversity and seasonal productivity observed in these disturbance-dominated environments (Welcomme 1979; Junk et al. 1989; Tockner and Stanford 2002). Yearly and seasonal variability in river discharge

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creates a mosaic of limnological conditions throughout the floodplain (Tockner et al. 2000; Amoros and Bornette 2002). The properties of a pulse event, including amplitude, duration, frequency, and magnitude, combines with the degree of lateral connection a site has to the main channel to ultimately shape the biotic and abiotic properties within off-channel habitat (Junk et al. 1989; Wolfe et al. 2007; Sokal et al. 2008, 2010). Owing to the spatial heterogeneity and sheer breadth of floodplain valleys, connectivity classes are often created for water bodies within a riverfloodplain system, with each class possessing a characteristic set of limnological and ecological conditions (Tockner et al. 2000; Wolfe et al. 2007; Sokal et al. 2008, 2010; Brock et al. 2009). Withinclass variation also exists even in the absence of overbank flows as a result of subsurface connection by hyporheic exchange (Mertes 1997; Tockner et al. 2000) and surface connection through levee breaks and small channels (Brock et al 2007; Sokal et al. 2008) that maintain some degree of influence from the main channel on limnological conditions.

During inundation from a pulse event, floodwaters from the river overflow the banks, inundating floodplain habitat and homogenizing the limnological features of floodplain water bodies to conditions more characteristic of the main channel (Thomaz et al. 2007). River water that typically carries higher levels of sediment and greater concentrations of most nutrients mixes with flood-connected lake water that often has high concentrations of organic detritus and algal biomass, ultimately introducing nutrients into the usually autogenic system of a floodplain lake. After floodwaters begin to recede and connection to the main channel is severed, floodplain lakes begin to take on local characteristics (Junk and Wantzen 2004; Pithart et al. 2007; Thomaz et al. 2007; Wantzen et al. 2008; Wiklund et al. 2012). Local processes within individual water bodies, such as overland flow from rainfall or snowmelt, seepage from local aquifers or other subsurface water sources, and sedimentation begin to impact the physical and chemical conditions of a disconnected lake (Thomaz et al. 2007). If off-channel waterbodies become isolated from floodwaters for a substantial amount of time, the local processes mentioned above, along with evaporative enrichment, create isolated water bodies that have higher water clarity, dissolved organic carbon (DOC), total nitrogen (TN), and bioavailable nutrients (Sokal et al. 2010; Wiklund et al. 2012).

Accurately assessing the hydrological connectivity gradient of a river-floodplain system is imperative to determine its impact on off-channel limnology. More conventional methods for determining connectivity of off-channel habitats include physical assessment of floodplain topography (Gibson et al. 1996; Peters 2003) and monitoring of water balances (Mackay 1963; Marsh and Hey 1989), both heavily field-intensive methods. An alternative method, optical remote sensing, has proven successful in monitoring floodplain inundation in many tropical (Hess et al. 2003; Ward et al 2013, 2014) and temperate (Pavelsky and Smith 2009; van de Wolfshaar et al. 2011; Long and Pavelsky 2013) systems. Optical remote sensing, however, can be limited by dense vegetation, smoke, and cloud cover, as they can obscure image clarity. This limitation, along with the high cost of accessing microwave remote sensing images that can penetrate many obstructions, calls for combined approaches. On-ground spot measurements of stable isotopes of hydrogen (δ^2 H) and oxygen (δ^{18} O) have been shown to be a cost-effective and accurate method for assessing connectivity within a floodplain system because evaporative enrichment occurs in lakes less frequently inundated, leading to greater concentrations of the heavy isotopes. This method proved to be effective for two large Canadian deltaic systems (Slave River Delta and Peace-Athabasca Delta (PAD)) in classifying basin-wide, off-channel lake hydrology (Brock et al. 2007; Wolfe et al. 2007). Studies applying both remote sensing and stable isotope methods to assess connectivity classes of off-channel lakes have not been conducted within river-floodplain systems and could prove effective in evaluating the accuracy of optical remote sensing in determining river-floodplain hydrology.

In this study, we characterized connectivity and determined its influence on winter limnology within off-channel lakes and wetlands (hereinafter referred to as lakes) of the Saskatchewan River Delta (SRD), a large and productive inland delta with a flood regime that has been altered by upstream river flow management (Sagin et al. 2015). Our overall aim was to evaluate the use of combined optical remote sensing and stable isotope methods to determine hydrological connectivity of large river floodplains and better understand the influence of river flooding on limnology within these systems. First, we determined connectivity classes for SRD lakes using a series of optical remote sensing images representing different flood stages for the SRD (Sagin et al. 2015). Next, we compared these classes with stable isotope composition measured in each of the lakes during winter. Finally, we tested for differences in the winter biogeochemistry of lakes in the different classes, including measurements of dissolved oxygen (DO), nutrients, and algal biomass. We hypothesized that less-connected lakes, as indicated by optical remote sensing images, would exhibit greater stable isotope enrichment within site water samples. Additionally, we hypothesized that lakes within the same connectivity class would possess similar limnological characteristics, with classes of higher connectivity having characteristics more similar to the main channel.

Methods

Study area

The SRD is located at the Saskatchewan-Manitoba border (approximately 53°29'N, 100°37'W). The delta covers an area of 10 000 km² and is the largest active inland delta in North America, draining the North Saskatchewan River, the South Saskatchewan River, and their tributaries, an area of approximately 405 864 km². The SRD consists of two areas that are separated by The Pas Moraine: the upper delta, located primarily in Saskatchewan; and the lower delta, located in Manitoba. The delta is characterized by a mosaic of large and small river channels, fens, bogs, forests, and numerous shallow wetlands and lakes (<3 m depth). The SRD is located downstream of three large hydroelectric dams, the Gardiner Dam, Francois Finley Dam, and E.B. Campbell Dam, that impact the natural flow regime downstream (Wheater and Gober 2013). Though flood peaks are smaller than those observed prior to dam construction in the 1960s, there is still sufficient flow in many years to cause inundation and connect off-channel lakes (Smith and Perez-Arlucea 2008).

The SRD is highly seasonal in temperature, precipitation, and discharge. Temperatures reach as low as -49.4 °C in the winter (e.g., mean temperature December 2013 = -25.1 °C) and as high as 37.6 °C in the summer (e.g., mean temperature July 2013 = 17.8 °C) (World Meteorological Organization (WMO) ID: 71867; Environment Canada 2015). It receives an average of 450 mm of precipitation annually, with most rainfall occurring between June and August (peaking in July), and snowfall occurring between November and March (peaking in December) (WMO ID: 71867; Environment Canada 2015). Because of contributions from snowmelt and later runoff from the Rocky Mountain headwaters, the SRD typically experiences both a spring and a summer flood event. River discharge within the SRD increases in mid-April during spring melt, with a peak in late April to early May (historical mean spring peak discharge at station 05KD003 South Saskatchewan River below Tobin Lake = \sim 650 m³·s⁻¹; Environment Canada 2015). After spring peak, water levels continue to drop until mid-June when rain after snow events in the Rocky Mountains trigger runoff that soon reaches the SRD. Summer river discharge is often greater than spring discharge (historical mean summer peak discharge at station 05KD003 = ~870 m³·s⁻¹; Environment Canada 2015), causing more extensive flooding in the delta with a peak in late June to

Fig. 1. Location of the Saskatchewan River Delta, Canada, and sampling sites with an image of surface water coverage area for different flood categories, including drought-connected and low flood-connected (discharge < $500 \text{ m}^3 \cdot \text{s}^{-1}$; surface water coverage area (SWCA) < 70 km^2), moderate and high flood-connected ($500 \text{ m}^3 \cdot \text{s}^{-1}$ < discharge < $2000 \text{ m}^3 \cdot \text{s}^{-1}$; 70 km^2 < SWCA < 280 km^2), and extreme flood-connected (discharge > $2000 \text{ m}^3 \cdot \text{s}^{-1}$; 70 km^2 < SWCA < 280 km^2), and extreme flood-connected (discharge > $2000 \text{ m}^3 \cdot \text{s}^{-1}$; 70 km^2 < SWCA < 280 km^2). For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2015-0210.



early July. Prior to our sampling in winter 2014, a large flood event occurred within the SRD in 2013, with spring and summer river discharge much greater compared with the historical average (spring peak discharge at station 05KD003 = 1690 m³·s⁻¹; summer peak discharge at station 05KD003 = 3640 m³·s⁻¹; Environment Canada 2015). As a result of such large flood events, an extensive amount of the historically connected floodplain within the SRD was inundated (Sagin et al. 2015).

Remote sensing

Water coverage data for the SRD were obtained using optical remote sensing images as described in Sagin et al. (2015). A combination of Landsat, Spot, and RapidEye images were used to determine surface water coverage area (SWCA) during flood events of varying magnitudes. Landsat data were obtained from the United States Geological Survey (USGS) Earth Resources Observation and Science Center's (EROS) Global Visualization Viewer (GLOVIS; http://glovis.usgs.gov/), SPOT data were obtained from the Alberta Terrestrial Imaging Center (ATIC), and RapidEye data were purchased from BlackBridge Geomatics. For greater resolution, datasets during days with minimal cloud cover were targeted for map production. SWCA maps were created using a surface water extraction coverage area tool (SWECAT: Sagin et al. 2015). SWECAT was developed by extracting SWCA for flood events from Landsat and comparing them with Canadian National Hydro Network, SPOT, and RapidEye SWCA datasets during a similar timeframe to verify results. Comparison of SWCA derived from Landsat images for three flood events (moderate flood, high flood, extreme flood) with those obtained from RapidEye and SPOT showed good agreement, with less than 7% difference in SWCA (Sagin et al. 2015).

SWCA maps of flood events of varying flood frequencies were layered to produce a system-wide map displaying the connectivity gradient for a 1315 km² study area within the upper delta (Fig. 1). This map was then used to manually select connectivity categories for lakes within the delta. Only when a connection pathway of a lake to a main channel or side channel was apparent was it classified as connected. An increase in size of a lake without a clear connection pathway was insufficient to classify it as connected because of the potential influence of local precipitation, overland runoff, and groundwater infiltration. SRD lakes were classified into five categories based on their connection during different river discharges (drought = <350 m³·s⁻¹; low flood = 350-500 m³·s⁻¹; moderate flood = 500–1000 m³·s⁻¹; high flood = 1000– 2000 m³·s⁻¹; extreme flood = >2000 m³·s⁻¹). The remote sensing satellite maps obtained for different flood frequencies showed marked differences in SWCA and therefore degree of floodplain inundation and connectivity. All lakes that were connected to the river in an image from 6 August 2001 when river discharge and SWCA was lowest (discharge = $327 \text{ m}^3 \cdot \text{s}^{-1}$; SWCA = 56 km^2) were classified as drought-connected. Low flood-connected lakes were based on an image from 13 September 1990 (discharge = 422 $m^3 \cdot s^{-1}$; SWCA = 89 km²), while moderate flood-connected lakes were from 8 June 2005 (discharge = 1110 m³·s⁻¹; SWCA = 151 km²). The map for high flood-connected lakes was obtained using an image from 29 July 2011 (discharge = 1050 m³·s⁻¹; SWCA = 178 km²). The image corresponding to the largest available flood



was from 8 July 2005 (discharge = $1810 \text{ m}^3 \cdot \text{s}^{-1}$; SWCA = 289 km^2) and used to categorize extreme flood-connected lakes.

Stable isotope hydrology

Stable isotope compositions within local water bodies are generally dependent on two factors: source waters and evaporation. The local meteoric water line (LMWL) and the local evaporation line (LEL) ultimately constrain δ^2 H and δ^{18} O. LMWL is dependent on summer and winter isotopic composition of precipitation, whereas LEL is dependent on the LMWL and local atmospheric conditions. For the SRD, an LMWL of δ^2 H = 7.7 × δ^{18} O – 1.2 was used based on regional isotope composition of precipitation from 1990 to 2005 (Pham et al. 2009).

To develop an LEL for the SRD, we analyzed $\delta^2 H$ and $\delta^{18}O$ composition of floodwaters and wetlands in a spillway channel downstream of E.B. Campbell Dam from June to August 2013 (Fig. 2). During summer, when water levels in Tobin Lake reservoir (formed by E.B. Campbell Dam) begin to rise and discharge reaches the maximum capacity of the hydroelectric station, the spillway gates are opened to release excess water, inundating wetlands in the spillway channel. When the spillway is closed, these wetlands immediately drain and disconnect, leaving shallow residual pools that slowly evaporate. The spillway wetlands were sampled monthly for isotopic composition in June (disconnected), July (connected), and August (disconnected) 2013 to envelop the inundation and isolation-evaporation phases and benchmark our isotope data for lakes in the SRD that were filled by the same floodwaters. δ^{2} H and δ^{18} O values for spillway sites were plotted and a best-fit line determined to obtain an LEL for the SRD, using ordinary least squares regression (Fig. 3a).

Field sampling

From early February to late March 2014, a total of 26 SRD lakes of varying connectivity to the main channel were sampled (Fig. 1). The 26 lakes were selected to ensure wide coverage within a 1315 km² study area in the upper delta and included all five lake hydrological categories (drought-connected, n = 3; low floodconnected, n = 6; moderate flood-connected, n = 3; high floodconnected, n = 7; extreme flood-connected, n = 7). As much as possible, lakes were selected to ensure an approximately equal lake surface area distribution among the five lake categories.

At each site, holes were augured through the ice and water quality measurements were taken, including DO, pH, turbidity, and conductivity, at mid-depth using a YSI EXO2 Sonde at the center or perceived deepest part of each lake. Unfiltered surface-water samples were collected for water column chlorophyll (chl-a), TN, and total phosphorus (TP) at each site in sterile 500 ml Nalgene bottles. Filtered surface-water samples (0.45 μ m filter) for DOC, hydrogen and oxygen stable isotopes (δ^2 H, δ^{18} O), nitrate-nitrite (NO₃-NO₂), ammonia-ammonium (NH₃-NH₄), and sulfate (SO₄) were also collected at each site. All water samples were collected from 10 cm below the water surface. Filtered samples for DOC were stored in amber polyethylene bottles, while samples for δ^2 H– δ^{18} O, NO₃, NH₃-NH₄, and SO₄ were stored in 50 ml Falcon tubes. All water samples, excluding $\delta^2 H - \delta^{18} O$ samples, were frozen at -20 °C until further laboratory analysis. In addition to water samples, physical measurements including ice thickness, snow depth, and lake depth were taken.

To provide temporal information on water chemistry to complement our spatial study in winter, two of the lakes from the high flood-connected category (BMO5, Ben's Lake, 53°56'N, 103°0'W; and BMO6, Cook Lake, 53°55'N, 102°58'W) and the main channel were also sampled monthly from May to September 2014 (Fig. 2). One of these lakes (Ben's Lake) and the main channel were also sampled prior to the winter sampling in August 2013 to provide a prewinter sampling baseline immediately after the flood peak. Sampling methods for water column chl-*a*, TN, TP, DOC, NO₃-NO₂, and SO₄ and pH, conductivity, and turbidity were as previously described.

Laboratory analysis

Samples for δ^2 H and δ^{18} O were stored at room temperature in the dark until they were analysed at Environment Canada's National Hydrology Research Centre. Isotope ratios were analysed with an LGR DLT-100 OA-ICOS liquid water isotope analyzer



coupled to an LC-PAL autosampler. Each sample was injected six times; the results of the first three injections were discarded to eliminate memory effect between samples. Two reference waters that isotopically bracket the sample values were included in each sample run. These references were previously calibrated with Standard Light Antarctic Precipitation and Vienna Standard Mean Ocean Water. Results are calculated based on a rolling calibration so that each sample is calibrated by the three standards run closest in time to that of the sample.

Water samples were analyzed for TN, TP, DOC, chl-a, SO₄, NO₃-NO₂, and NH₃-NH₄ using conventional techniques. TN and TP samples were analyzed using techniques outlined by Parsons et al. (1984), Crumpton et al. (1992), and Bachmann and Canfield (1996). Following persulfate digestion, TN was measured by secondderivative spectroscopy analyses. TP samples were analyzed following treatment with a reagent containing molybic acid, ascorbic acid, and trivalent antimony; the resulting blue TP solution was measured at 885 nm. DOC was analyzed using an automated Shimadzu TOC-V C, P, and N analyzer. Water column chl-*a* samples were analysed using a Turner Trilogy fluorometer following a 7 min digestion in 90% EtOH at 80 °C. Sulfate was analyzed by Method SUL-001-A (based on American Society for Testing and Materials method D516-90, 02 and standard methods 426C 16th ed.), a turbidometric analysis where sulfate is converted to a barium sulfate suspension and turbidity determined at 420 nm (minimum detectable limit = ~1 mg·L⁻¹). Nitrate–nitrite were analysed colorometrically following reduction of nitrate to nitrite (cadmium reduction) using Smartchem method NO3-001-A (based on Environmental Protection Agency (EPA) method 353.2, rev. 2 and standard methods 4500 NO3F), with a

range of 0.02–2 mg N·L⁻¹. NH₃·NH₄ was analysed colorometrically by the phenol–hypochlorite method (EPA 350.1) with a range of 0.01–2 mg·L⁻¹. All SO₄, NO₃-NO₂, and NH₃-NH₄ samples below the detectable limit of their associated analyzer were reported as half the value of the minimum detection limit.

Data analysis

To assess the utility of remote-sensing-based classifications of connectivity, we tested for differences in $\delta^2 H$ and $\delta^{18} O$ values within different lake categories. We used a multivariate analysis of variance (MANOVA) with δ^2 H and δ^{18} O values as the dependent variables and connectivity class as the independent variable. To elucidate potential conditions that may be impacted by the degree of connectivity to the river, a MANOVA was used to compare multiple independent variables (DO, TN, TP, DOC, chl-a, SO₄, NO₃-NO₂, NH₃-NH₄ turbidity, pH, and conductivity) of the sampled lakes among connectivity categories as the independent variable. In addition to the MANOVA, a principal component analysis (PCA) was used to assess differences in limnological conditions among the five lake connectivity categories and to determine which variables were correlated. PCA was performed using the statistical program R. Prior to statistical analysis, all variables were assessed visually for normality using histograms and Q-Q plots with the computer program SPSS Statistics 22 (IBM Ireland); equal variance for variables between connectivity was assessed using Levene's test. Appropriate transformations were applied to the dataset when necessary to create normality and to equalize variance. Normality and homogeneity of variance were achieved for all variables except NO₃-NO₂ and NH₃-NH₄. This included 26 sites (drought-connected, n = 3; low flood-connected, n = 6; moderate flood-connected, n = 3; high flood-connected, n = 7; extreme floodconnected, n = 7) for TN, TP, DOC, chl-a, SO₄, NO₃-NO₂, and NH₃- NH_4 and 24 sites (drought-connected, n = 3; low flood-connected, n = 6; moderate flood-connected, n = 3; high flood-connected, n = 5; extreme flood-connected, n = 7) for DO, turbidity, pH, and conductivity. Differences among categories in the MANOVA were compared post hoc with a Tukey's HSD test. All statistical analyses were conducted using SPSS.

Results

Stable isotope hydrology

Hydrogen and oxygen stable isotope values of floodwaters from sites upstream of the SRD ranged from –17.8% to –16.5% for δ^{18} O and –144.8% to –133.3% for δ^{2} H, while those for the isolated spillway channel wetlands ranged from –17.5% to –13.9% for δ^{18} O and –139.3% to –125.0% for δ^{2} H (Fig. 3*a*). Combining these values created the LEL (eq. 1; r^2 = 0.83, p < 0.001; Fig. 3*a*).

(1)
$$\delta^2 H = 3.97 \times \delta^{18} O - 68.87$$

Isotopic values for the SRD samples collected between February and March of 2014 during the ice-covered season differed among connectivity categories (Fig. 3b). These data followed a trend line of $\delta^2 H = 5.76 \times \delta^{18} O - 39.46$ ($r^2 = 0.96$, p < 0.001; Fig. 3b), which generally followed that of the expected LEL, confirming a common water source (Saskatchewan River floodwaters) for these lakes. Lakes in the more isolated connectivity categories (high flood-connected, extreme flood-connected) were typically located further along the LEL compared with lakes that were more often connected (drought-connected, low flood-connected), suggesting greater evaporative enrichment in more isolated lakes. Comparatively, waters from drought-connected lakes were in close proximity to the LMWL, with minimal evaporative enrichment and isotopic composition more similar to that of the source water. Isotopic composition of water varied significantly between connectivity categories for both δ^2 H (p = 0.003) and δ^{18} O (p = 0.002). As shown in Table 1, δ^2 H values for drought-connected lakes had significantly lower isotopic signatures compared with high flood-connected (p = 0.005) and extreme flood-connected lakes (p = 0.010), and δ^{18} O showed similar patterns, with drought-connected lakes having significantly lower values compared with high flood-connected (p = 0.003) and extreme flood-connected lakes (p = 0.004).

Water chemistry and nutrients

Limnological conditions varied greatly among the floodplain lakes of the SRD. Turbidity (range = 1.0–39.0 NTU), pH (range = 7.04–8.77), and conductivity (range = 288–1840 μ S) all had large among-site variation. Lake DO levels varied from anoxic (0.4 mg O₂·L⁻¹) to near saturation (12.0 mg O₂·L⁻¹) depending on the lake sampled. Concentrations of all nutrients ranged from oligotrophic to eutrophic conditions, with TN (range = 446–6480 μ g·L⁻¹), TP (range = 7–874 μ g·L⁻¹), DOC (range = 0–49.1 mg·L⁻¹), NO₃-NO₂ (range = 0–0.40 mg·L⁻¹), NH₃·NH₄ (range = 0.01–3.69 mg·L⁻¹), and SO₄ (range = 6.88–72.81 mg·L⁻¹) all showing large among-lake variation. Corresponding chl-*a* levels also ranged widely from very low (0.3 μ g·L⁻¹) to very high (28.6 μ g·L⁻¹).

Limnological conditions of floodplain lakes significantly differed among the five connectivity categories (Fig. 4). DO, pH, NO₃-NO₂, and SO₄ were all significantly influenced by connectivity to the river (p < 0.05). As connectivity to the main channel decreased, we observed decreasing DO (p = 0.019), pH (p = 0.030), NO₃-NO₂ (p < 0.001), and SO₄ (p < 0.001). DO levels were highest in droughtconnected lakes (mean = 10.2 ± 2.8 mg·L⁻¹) and declined to minimal levels in all other categories, with the only exception being SRD13, which was a high flood-connected lake and possessed oxygen levels more characteristic of drought-connected lakes. As shown in Table 1, there were significantly higher DO levels within drought-connected compared with moderate flood-connected (p = 0.040) and extreme flood-connected lakes (p = 0.013). The pH was highest in drought-connected lakes (mean = 8.39 ± 0.36), with a gradual decrease in pH as connectivity declined and with droughtconnected lakes having significantly higher pH than moderate floodconnected (p = 0.032) and extreme flood-connected (p = 0.028) lakes. NO₃-NO₂ concentrations were also highest in drought-connected lakes (mean = $0.35 \pm 0.08 \text{ mg} \cdot \text{L}^{-1}$) then quickly decreased in the low flood-connected category and above. For this variable, there was significant separation between drought-connected and all other connectivity categories (p < 0.005 for all comparisons), with low flood-connected being the only other category with mean values $(0.11 \pm 0.16 \text{ mg} \cdot \text{L}^{-1})$ not bordering the minimum detection limit of 0.02 mg·L⁻¹. SO₄ concentrations were highest in droughtconnected lakes (mean = $66.37 \pm 5.63 \text{ mg} \cdot \text{L}^{-1}$) and decreased as connectivity declined. Similar to NO₃-NO₂ concentrations, there was significant separation between drought-connected lakes and all other connectivity categories for SO4 (low flood-connected, mean = 33.97 ± 22.99 mg·L⁻¹, p = 0.028; moderate flood-connected, mean = 8.20 ± 0.67 mg·L⁻¹, p < 0.001; high flood-connected, mean = $16.36 \pm 12.52 \text{ mg} \cdot \text{L}^{-1}$, p < 0.001; extreme flood-connected, mean = 17.92 \pm 9.33 mg·L⁻¹, *p* = 0.001). TN, TP, and NH₃-NH₄ tended to be higher in less-connected lakes but these differences were not significant (TN, *p* = 0.059; TP, *p* = 0.092; NH₃-NH₄, *p* = 0.096). There were no differences among connectivity categories for turbidity (p = 0.164), conductivity (p = 0.300), chl-a (p = 0.616), DOC (p = 0.277), snow depth (p = 0.123), ice thickness (p = 0.992), and lake depth (p = 0.191).

PCA for the winter limnological data indicated that water chemistry and isotopes for the lakes of the SRD differed among lake connectivity categories (Fig. 5). Eigenvalues were 51.9% for the first axis and 18.5% for the second axis and explained a large amount of variation within the dataset (70.4%). DO, pH, NO₃, and SO₄ were positively correlated to the first axis, while nutrients (TN, TP, NH₃-NH₄), chl-*a*, conductivity, and turbidity were negatively correlated to the first axis. DOC was negatively correlated with axis 2, while δ^{18} O and δ^{2} H were negatively associated with both axes 2

| Variable | Category | Drought | Low flood | Moderate flood | High flood | Extreme flood |
|----------------------------------|----------------------------|---------|-----------|----------------|------------|---------------|
| δ²H | Drought | _ | 0.525 | 0.376 | 0.005* | 0.010* |
| | Low flood | | _ | 0.981 | 0.560 | 0.109 |
| | Moderate flood | | | — | 0.400 | 0.558 |
| | High flood | | | | _ | 0.996 |
| | Extreme flood | | | | | _ |
| $\delta^{18}O$ | Drought | — | 0.288 | 0.115 | 0.003* | 0.004* |
| | Low flood | | _ | 0.882 | 0.770 | 0.123 |
| | Moderate flood | | | _ | 0.706 | 0.814 |
| | High flood | | | | _ | 0.999 |
| | Extreme flood | | | | | _ |
| DO | Drought | _ | 0.169 | 0.04* | 0.067 | 0.013* |
| | Low flood | | _ | 0.731 | 0.957 | 0.547 |
| | Moderate flood | | | _ | 0.969 | 1.000 |
| | High flood | | | | | 0.940 |
| | Extreme flood | | | | | |
| рH | Drought | | 0.077 | 0.032* | 0.077 | 0.028* |
| 1 | Low flood | | _ | 0.880 | 1.000 | 0.982 |
| | Moderate flood | | | _ | 0.922 | 0.984 |
| | High flood | | | | | 0.994 |
| | Extreme flood | | | | | _ |
| NO ₂ -NO ₂ | Drought | _ | 0.005* | 0.001* | <0.001* | <0.001* |
| 11031102 | Low flood | | | 0.447 | 0.237 | 0 292 |
| | Moderate flood | | | | 1 000 | 1 000 |
| | High flood | | | | 1.000 | 1,000 |
| | Extreme flood | | | | | 1.000 |
| 50 | Drought | _ | 0.028* | <0 001* | <0.001* | 0.001* |
| 50_4 | Low flood | | 0.020 | 0 100 | 0.202 | 0.001 |
| | Moderate flood | | | 0.109 | 0.202 | 0.279 |
| | High flood | | | _ | 0.915 | 1,000 |
| | Extreme fleed | | | | | 1.000 |
| TN | Drought | | 0.416 | 0.007* | 0.157 | 0.499 |
| IN | Low flood | — | 0.410 | 0.037 | 0.157 | 1,000 |
| | LOW HOOd Mederate fleed | | _ | 0.385 | 0.950 | 1.000 |
| | Moderate nood | | | _ | 0.695 | 0.279 |
| | Fight flood | | | | _ | 0.867 |
| TD | Extreme nood | | 0.050 | 0.051 | 0.150 | |
| TP | Drought | _ | 0.853 | 0.251 | 0.1/2 | 0.939 |
| | LOW IIOOd | | _ | 0.608 | 0.493 | 0.997 |
| | Moderate flood | | | — | 1.000 | 0.431 |
| | High flood | | | | _ | 0.282 |
| | Extreme flood | | | | 0.005 | |
| NH ₃ | Drought | | 0.645 | 0.091 | 0.206 | 0.733 |
| | Low flood | | _ | 0.448 | 0.846 | 0.999 |
| | Moderate flood | | | — | 0.880 | 0.329 |
| | High flood | | | | | 0.699 |
| | Extreme flood | | | | | — |

Table 1. Summary of MANOVA results (*p* values for post hoc comparisons) for differences in limnological variables among connectivity categories.

Note: Asterisks indicate significant differences at $\alpha = 0.05$.

and 1. All drought-connected lakes and two of the low floodconnected lakes plotted high on axis 1 characterized by high DO, pH, NO₃, and SO₄ (Fig. 5). The remaining low flood-connected lakes and moderate flood-connected lakes plotted low on axis 1 characterized by high nutrients, chl-*a*, conductivity, and turbidity. High flood and extreme flood-connected lakes had a wide range along axis 1 and were relatively low compared with the other lake categories along axis 2, indicative of greater δ^{18} O, δ^{2} H, and DOC concentrations.

TN, TP, SO₄, chl-*a*, DOC, turbidity, and conductivity all showed variation among seasons for the two high flood-connected lakes (Ben's and Cook lakes, Table 2). Highest values were observed during the winter sampling event for TN, TP, SO₄, chl-*a*, DOC, turbidity, and conductivity. The lowest levels were observed during the 2014 summer months for TN, TP, SO₄, chl-*a*, DOC, turbidity, and conductivity. pH was variable over the sampling period, with no consistent seasonal differences.

Discussion

The degree of connection to the main channel for floodplain lakes within the SRD was associated with distinct limnological conditions within lakes. Connectivity to the main channel influenced the degree of isotope enrichment as well as pH, DO, and the concentrations of many nutrients. Our findings are in agreement with similar studies done in large northern floodplain systems (Wolfe et al. 2007; Sokal et al. 2008, 2010; Wiklund et al. 2012) that show highly connected lakes possess similar characteristics as the parent river. Connected floodplain lakes are greatly influenced by the existing conditions in the main channel, whereas isolated lakes are more impacted by local precipitation, evaporation, and other environmental processes. As a result, this gradient of limnological conditions for lakes within the SRD floodplain forms the foundation of biogeochemical diversity in this important northern delta.

Determining connectivity can often involve a substantial amount of field research physically analyzing local topography

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Fig. 4. Boxplots of physical and chemical variables for drought-connected lakes (connectivity category 1; n = 3), low flood-connected lakes (connectivity category 2; n = 6), moderate flood-connected lakes (connectivity category 3; n = 3), high flood-connected lakes (connectivity category 4; n = 7), and extreme flood-connected lakes (connectivity category 5; n = 7). (Note for snow boxplot: 1 inch = 2.5 cm.)

and water balances. As a result, many researchers have begun to use a combination of desktop and on-ground methods to accurately determine the connectivity of floodplain lakes (e.g., Wolfe et al. 2007; van de Wolfshaar et al. 2011; Ward et al. 2013). Stable isotope composition of water samples from lakes within the SRD during the winter following a large summer flood event (2013– 2014) provided an effective validation of classifications based on remote sensing. Lakes with greater connection to the main channel showed minimal ²H and ¹⁸O enrichment, whereas more isolated lakes exhibited marked ²H and ¹⁸O enrichment. This pattern was also observed within the PAD (Wolfe et al. 2007), and the Slave River Delta (Brock et al 2007, 2009). The five connectivity classes determined by optical remote sensing in our study generally showed good agreement with the isotope data (Fig. *3b*), providing evidence for the effectiveness of remote sensing as a cost-effective tool for making initial classifications.

Although there was considerable agreement between isotopic enrichment and remotely sensed connectivity, not all lake categories showed clear separation isotopically because of considerable variation within categories. Lakes of the high floodconnected category ranged widely in isotopic composition compared with other lake categories, with low values neighbouring low flood-connected lakes and high values neighbouring extreme flood-connected lakes. Isotopic values outside of those expected based on their connectivity categories derived from remote sensing data could be attributed to many factors; these include overhanging vegetation that can obscure lake-river connections in remote sensing images leading to incorrect classi-

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Fig. 5. Principal component analysis (PCA) displaying the vectors of the 13 physical and chemical variables sampled from lakes of the SRD during the winter of 2014 and the distribution of lakes from the five connectivity categories with respect to the 13 variables based on individual lake limnological conditions.



fication, variation in the influence of subsurface lake-river connection leading to unexpected replenishment of isotopically depleted waters, and (or) degree of macrophyte-physical cover reducing evaporation within lakes. As previously reported by Brock et al. (2009), isotopic composition of floodplain lakes is driven by hydrology more than lake size; therefore, the deviation of isotopic values from expected values in the aforementioned sites is not likely a result of variation in lake size. Snow melt can be an important isotopic input, with the degree of snowmelt input being driven by lake catchment size and snowpack density (Brock et al. 2007). However, since our site sampling was done during winter prior to snowmelt, the impact of snowmelt on isotopic composition of lakes would be minimal. Additionally, the majority of isotope data points for the SRD plotted above the LEL. This occurs as a result of greater precipitation input, whereas data points below the LEL result from greater snowmelt input (Wolfe et al. 2007). This further reinforces our expectation that the main water input into the lakes of the SRD was floodwaters derived largely from precipitation in the basin's headwaters in 2013 (Wheater and Gober 2013).

The limnological conditions within floodplain lakes of the SRD depended on their degree of connectivity, as has been observed in both the PAD (Wolfe et al. 2007; Wiklund et al. 2012) and the Slave River Delta (Brock et al. 2007; Sokal et al. 2008, 2010). Lakes of the SRD with greater connectivity to the main channel possessed characteristics similar to that of the main channel (higher levels of DO, pH, NO_3 - NO_2 , and SO_4). The higher DO levels in lakes of greater connectivity may be attributable to permanent direct exchange with the river during the winter months. This exchange assists in maintaining oxygen levels near saturation at levels suit-

able for fish (Mathias and Barica 1980) despite the potentially high respiration rates within these lakes due to decomposition of organic matter (Molles et al. 1998). As less-connected lakes are not replenished by oxygen-rich river water, oxygen levels within such lakes become depleted during ice cover. Rates of under-ice oxygen consumption in northern lakes during winter months are a function of mean depth and nutrient levels (Barica and Mathias 1979; Mathias and Barica 1980; Babin and Prepas 1985). Our SRD lakes did not differ in depth across connectivity categories, but lakes of midrange connectivity did have higher water column nutrient levels compared with highly connected lakes. With eutrophic lakes experiencing O₂ consumption rates that are three times higher than oligotrophic lakes (Mathias and Barica 1980), the low oxygen levels within less-connected lakes could be attributed to higher nutrient concentrations. It could also be explained by their initial DO storage. Lakes of higher connectivity maintain direct exchange with oxygen-rich river water longer into the ice-free season than lakes of less connectivity, potentially resulting in greater DO concentrations at the time when ice forms on the lakes. Assuming a constant rate of DO depletion across lakes, lakes with greater oxygen concentrations prior to ice cover will maintain higher concentrations throughout the winter (Barica and Mathias 1979). Similarly, timing of ice cover formation will also influence DO concentrations into the winter. If lakes of higher connectivity remain ice-free later into the season because direct connection with the main channel slows ice formation, atmospheric oxygen exchange will also be maintained longer.

TN, TP, and NH_3 - NH_4 also appeared to be influenced by connectivity, however not to a significant degree. Highly connected lakes, with close association to river water, remained consistently

| | Variable | Date | | | | | | | | |
|--------------|---------------------------------------|--------------|-------------|-------------|--------------|--------------|--------------|---------------|--|--|
| Lake site | | 24 Aug. 2013 | 1 Feb. 2014 | 1 June 2014 | 22 June 2014 | 19 July 2014 | 28 Aug. 2014 | 22 Sept. 2014 | | |
| Ben's Lake | Turbidity (NTU) | 4.96 | 12.52 | 1.93 | 2.37 | 2.47 | 2.38 | 4.87 | | |
| | Chl-a ($\mu g \cdot L^{-1}$) | 9.61 | 5.78 | 3.78 | 4.24 | 3.00 | _ | _ | | |
| | TP (mg·L ⁻¹) | 0.13 | 0.11 | 0.04 | 0.04 | 0.04 | 0.07 | 0.04 | | |
| | TN (mg·L ^{−1}) | 1.00 | 2.00 | 0.91 | 0.73 | 0.94 | 0.77 | 1.60 | | |
| | Conductivity | 480 | 1069 | 383 | 262 | 313 | 363 | 421 | | |
| | рН | 7.70 | 7.40 | 8.04 | 8.24 | 8.14 | 7.34 | 8.15 | | |
| | DOC (mg·L ⁻¹) | 9.2 | 11.8 | 8.1 | 9.4 | _ | 13.4 | — | | |
| | SO ₄ (mg·L ^{−1}) | 37.0 | 28.2 | 15.0 | — | 6.9 | — | 9.1 | | |
| | | 24 Aug. 2013 | 1 Feb. 2014 | 2 June 2014 | 23 June 2014 | 20 July 2014 | 28 Aug. 2014 | 23 Sept. 2014 | | |
| Cook Lake | Turbidity (NTU) | _ | 70.00 | 2.39 | 1.43 | 1.43 | 1.75 | 4.63 | | |
| | Chl-a ($\mu g \cdot L^{-1}$) | _ | 7.93 | 15.14 | 3.55 | 7.90 | _ | _ | | |
| | TP (mg·L ⁻¹) | _ | 0.15 | 0.04 | 0.04 | 0.02 | 0.03 | 0.03 | | |
| | TN (mg·L ⁻¹) | _ | 2.74 | 1.00 | 0.73 | 0.90 | 0.85 | 1.20 | | |
| | Conductivity | _ | 762 | 398 | 218 | 283 | 500 | 454 | | |
| | pH | — | 7.88 | 8.09 | 9.24 | 8.19 | 7.62 | 8.03 | | |
| | DOC (mg·L ⁻¹) | — | 42.2 | _ | 9.5 | 11.5 | 14.6 | — | | |
| | SO ₄ (mg·L ⁻¹) | — | 16.8 | 13.0 | — | 8.1 | — | 6.2 | | |
| | | 22 Aug. 2013 | 1 Feb. 2014 | 1 June 2014 | 23 June 2014 | 20 July 2014 | 20 Aug. 2014 | 20 Sept. 2014 | | |
| Saskatchewan | Turbidity (NTU) | 3.02 | _ | 4.48 | 2.13 | 3.95 | 3.38 | 2.75 | | |
| River | Chl-a ($\mu g \cdot L^{-1}$) | 4.04 | _ | 4.80 | 7.45 | 1.76 | _ | _ | | |
| | TP (mg·L ^{−1}) | 0.03 | _ | 0.01 | 0.02 | 0.02 | 0.02 | 0.02 | | |
| | TN (mg·L ⁻¹) | 0.73 | _ | 0.72 | 0.49 | 0.62 | 0.19 | 0.42 | | |
| | Conductivity | 471 | _ | 473 | 323 | 495 | 461 | 499 | | |
| | pН | 8.36 | _ | 8.10 | 8.93 | 8.66 | 8.75 | 8.60 | | |
| | _ DOC (mg·L⁻¹) | 6.51 | _ | 4.39 | 4.42 | 5.04 | 5.37 | _ | | |
| | $SO_4 (mg \cdot L^{-1})$ | 94 | — | 81 | _ | 80 | _ | 78 | | |

Table 2. Summary of limnological data for two floodplain lakes from the high flood-connected category found within the Saskatchewan River Delta (Ben's Lake (SRD05) and Cook Lake (SRD06)) and the Saskatchewan River.

Note: Sites were sampled intermittently from August 2013 to September 2014.

low in TN and TP throughout the study period (Fig. 4), indicative of oligotrophic conditions (Smith et al. 1999). The higher levels of nutrients in less-connected lakes suggests nutrient flux into these lakes is not solely derived from the parent river and that flooding may not be required to maintain high nutrient levels. This is consistent with findings from the Slave River Delta and the PAD (Sokal et al. 2008; Wiklund et al. 2012), though these conclusions were based on findings from concentrations of bioavailable nutrients, not TN and TP. The floodplain itself may be a source of nutrients for the lakes. In river floodplains, leaf litter, vegetation, and sediment are capable of providing important nutrients and organic matter to adjacent aquatic systems (Fisher and Likens 1973; Cuffney 1988; Ostojić et al. 2013) and are an essential part of nutrient cycling in river floodplain systems (Baldwin 1999; Inglett et al. 2008). Although highly connected lakes inundate their surrounding terrestrial zone during times of peak river flow, nutrients that do enter the lakes have greater potential to be diluted or flushed out of the lakes by nutrient-poor river water. Additionally, as the surrounding terrestrial zones of infrequently flooded lakes have been exposed to the atmosphere for a greater amount of time and are highly organic (Molles et al. 1998; Sokal et al. 2010), we postulate that inundation of these areas releases a greater amount of nutrients compared with the terrestrial zone of more connected lakes. The peaks in TP and chlorophyll in intermediate connectivity lakes appear to imitate patterns expected for floodplain biodiversity. In riverine systems, high species diversity is expected for habitats of intermediate disturbance (Amoros and Bornette 1999; Ward et al. 1999). Additionally, the high variation in nutrient concentrations and the range of other limnological variables measured among lake connectivity categories may also contribute to the high biodiversity found within this delta as biota become adapted to exploit the various conditions found throughout the floodplain (Welcomme 1979; Junk et al. 1989; Ward et al. 1999).

Characteristics of the parent river water, as influenced by erosion and deposition occurring upstream, dictates its role in supplying sediment and associated nutrients to floodplain lakes. Relatively low TN within the river water of the SRD (420-730 mg·L⁻¹) was also observed for the PAD (240-820 µg·L⁻¹; Wolfe et al. 2007), but our TP levels (mean TP May-September 2014 = $20 \,\mu g \cdot L^{-1}$) were much lower compared with that of the delta (mean TP October 2000 = 84 μ g·L⁻¹; Wolfe et al. 2007). High TP levels within the rivers of the PAD are likely a result of the associated high suspended sediment load (mean total suspended sediments October 2000 > 150 mg·L⁻¹; Wiklund et al. 2012), while the Saskatchewan River delivers less sediment to the SRD (mean total suspended sediments May–September 2014 = 6 mg·L⁻¹). Phosphorus adsorbs to sediment particles to a larger degree compared with nitrogen (50%-70% versus 2%-3%; Olde Venterink et al. 2006), and it is sediment-bound phosphorus that makes up the major pathway of supplementation to the floodplain for deltaic systems (Forsberg et al 1988; Wolfe et al. 2007). Retention of river sediment by Tobin Lake reservoir upstream of the SRD has been recorded as significant, reducing the sediment load from 9 × 106 t-year-1 to less than 0.1 × 10⁶ t·year⁻¹ (Ashmore and Day 1988), and may explain P-depletion in downstream river water feeding the SRD. Phosphorus retention by reservoirs can be large (up to 90%), with higher retention of phosphorus than nitrogen (Kunz et al. 2011a, 2011b). Though the PAD has a large dam (Bennett Dam) in its headwaters, suspended sediments are largely derived from the lower reaches of these large continental rivers (Ashmore and Day 1988); thus, waters contained within upland reservoirs are likely sedimentand nutrient-poor, leading to limited impacts on nutrient levels downstream. Conversely, the SRD has the potential to be substantially impacted by the influence of reservoirs (Lake Diefenbaker, Codette Lake, and Tobin Lake), as they are located more immediately upstream of the delta (Ashmore and Day 1988). Low levels of phosphorus and comparatively higher levels of nitrogen in the

Time series data for the two rarely connected lakes (Ben's Lake and Cook Lake) provided insight on how limnological conditions vary from midwinter to the ice-free season and within the ice-free season (~May-September). These lakes had high concentrations of TN and TP during the winter and low levels during the spring and summer. During winter, when decomposition exceeds production, particularly for submerged macrophytes, there is little uptake of available nutrients; however, during the summer season, when productivity is very high within these disconnected lakes, there is a rapid uptake of available nutrients. High macrophyte cover is associated with decreased levels of nutrients and phytoplankton growth (Søndergaard and Moss 1998; Rooney and Kalff 2003; Norlin et al. 2005) due to increased metabolic activity of macrophytes and their inhibition of phytoplankton through competition for space and light (Søndergaard and Moss 1998; Wiklund et al. 2012). Less-connected lakes also experience greater macrophyte growth compared with highly connected lakes (Sokal et al. 2010), and we observed extensive macrophyte beds in both Ben's and Cook lakes during the summer of 2014 (B. MacKinnon, personal observation). Lake-ice formation within floodplain lakes may also contribute to greater concentrations of nutrients and ions during winter months through cryoconcentration or freezeout. As ice forms, dissolved substances are excluded with efficiencies of up to 97% for some major ions; however, exclusion is less efficient for nutrients, with TN and TP efficiencies around 53% and 60%, respectively (Welch and Legault 1986). Although less efficient compared with ions, the excluded nutrients from ice can still lead to a major increase in water column concentrations compared with levels prior to ice formation (Belzile et al. 2002). High chl-a concentrations during the low water stage for the SRD is consistent with findings within other floodplain systems (Knowlton and Jones 1997; Peršić and Horvatić 2011; Mayora et al. 2013). However, high winter chl-a concentrations are not necessarily indicative of increased phytoplankton biomass, but instead could be driven by an increase in phytoplankton cellular chlorophyll content to maximize photosynthesis under major ice-cover and low light conditions (Hunter and Laws 1981; Prézelin and Matlick 1983). Low light conditions in the lakes of the SRD are likely the limiting factor for phytoplankton during the winter months, as chlorophyll did not differ across lake connectivity categories, and all lakes were underneath 50-100 cm of ice and an additional 50-100 cm of snow.

The winter DO and ammonium levels experienced within floodplain lakes of the SRD, although nearing toxicity for many species, maintain levels capable of supporting some tolerant fish species. Since large, intolerant species are unlikely to inhabit these offchannel waterbodies during the ice-cover season, these habitats may be used as winter refuge by tolerant species, similar to what has been observed in tropical floodplain systems (Chapman et al. 1996; Robb and Abrahams 2002, 2003). Additionally, future isolation of these off-channel lakes by reduction in river discharge could ultimately lead to intermittent, or even permanent, desiccation due to lack of hydrological recharge (Brock et al. 2007) and eliminating the potential for these lakes to act as winter habitat for aquatic species.

Floodplain ecosystems provide essential habitat for a diverse array of biota and can provide critical ecological and cultural services for local peoples. Northern floodplains are known to be greatly affected by upstream river impoundments that alter the natural flow regime of the river and disrupt the connection between the river and its floodplain (Prowse et al. 2002). For the SRD, in addition to alteration of the flow regime, the close proximity of the upstream impoundments to the delta also appears to affect nutrient concentrations in downstream river water. The retention of phosphorus-rich sediment has potentially decreased phosphorus levels downstream, lowering levels entering the floodplain lakes of the SRD. In addition to river impoundment, climate change is also projected to cause a reduction in both peak and total discharge within these systems (Wolfe et al. 2008), potentially leading to further disconnection between the floodplain and the main channel. Since our findings show the large effect inundation by river water has on the limnological conditions of floodplain lakes, further reduction in the connectivity of these lakes will ultimately impact nutrient and water quality dynamics within these ecosystems.

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