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Avian-Driven Modification of Seasonal Carbon Cycling at a Tundra Pond in the Hudson Bay Lowlands (Northern Manitoba, Canada)

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Abstract

The past ~40 years have seen a geometric increase (5–7% per year) in the size of the lesser snow goose (LSG; *Chen caerulescens caerulescens*) population and marked spatial expansion of the area they inhabit within the coastal fen ecotype of Wapusk National Park (Hudson Bay Lowlands, northern Canada), raising concerns and uncertainty about the environmental effects of their activities (grubbing of vegetation, soil disturbance, deposition of feces) on the abundant shallow tundra ponds. In this study, we use conventional limnological measurements as well as water and carbon (C) isotope tracers to explore similarities and differences in seasonal patterns of hydrological, limnological, and biogeochemical conditions of 15 shallow coastal fen ponds that currently have minimal (if any) disturbance from the LSG population with one pond (WAP 20) that is subject to substantial LSG activity. Carbon isotope measurements reveal that C cycling at WAP 20 (LSG-disturbed site) is markedly different compared to the other ponds, whereas only small differences were observed in hydrological conditions and concentrations of major nutrients and chlorophyll *a* of pond water. A mid-summer decrease in C isotope composition of dissolved inorganic carbon (DIC) occurred at WAP 20, likely as a consequence of high pond-water pH and intense C demand by aquatic productivity. These conditions appear to have promoted “chemically enhanced CO_2 invasion,” which causes strong kinetic C isotope fractionation. High C demand at WAP 20 is also suggested by mid-summer ^{13}C enrichment in particulate organic matter. In contrast, the ponds with little to no LSG activity exhibited expected seasonal C isotope behavior (i.e., ^{13}C enrichment of DIC) under conditions of increasing productivity when C is in relatively low demand. Small differences in nutrient concentrations may be due to rapid uptake by the benthic mat at WAP 20. Data from the low disturbance ponds also provide baseline information for future studies assessing potential effects of LSG.

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Introduction

Shallow lakes and ponds are a dominant feature of tundra landscapes in the Arctic and subarctic, and they provide important habitat and resources for abundant waterfowl populations. These relatively pristine freshwater ecosystems are particularly responsive to environmental stressors because they possess small water volumes and high surface area to volume ratios (e.g., Rouse et al., 1997; Prowse et al., 2006; Schindler and Smol, 2006; Smol and Douglas, 2007a, 2007b; Rowland et al., 2010). For over 20 years, concerns have been mounting about the environmental effects of increased waterfowl populations and how changes in their geographic distribution may alter the structure and function of Arctic and subarctic freshwater ecosystems. Consequences may include eutrophication, changes in nutrient cycling, and destruction of vegetation and available habitat (e.g., Handa et al., 2002; Gregory-Eaves et al., 2004; Lim et al., 2005; Van Geest et al., 2007; Côté et al., 2010; Sun et al., 2013).

Limnological and paleolimnological approaches have been utilized to assess the effects of fluctuations in waterfowl populations on Arctic and subarctic lakes and ponds. For example, Côté et al. (2010) used measurements of several physical and chemical variables, including water-column concentrations of dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total phosphorus (TP), and total Kjeldahl nitrogen (TKN) to assess the influence of greater snow goose (*Chen caerulescens atlantica*) activity on lakes and ponds on Bylot Island, Nunavut, Canada. Based on a single sampling episode during the summer (July–August), they found no significant difference in DOC and DIC concentrations in lakes and ponds with and without geese. Concentrations of TP were generally low (mean: 13.8 μg L^{-1}, range: 3.9–37.4 μg L^{-1}), and were significantly elevated in lakes with geese. Keatley et al. (2009) combined measurements of limnological variables (e.g., pH, concentration of P and N) with the analysis of diatoms in surface sediments of ponds on Devon Island (Nunavut, Canada) to determine that influence of seabirds (northern fulmars, *Fulmarus glacialis*) significantly elevated pH and concentrations of P and N and altered diatom community composition. Additional contemporary and paleolimnological studies, including work from Devon Island, Cape Vera, and Cornwallis Island, have also found increases in productivity and nutrient concentrations in response to seabird populations (e.g., Michelutti et al., 2009, 2010; Keatley et al., 2011; Sun et al., 2013).

To date, limnological studies in Arctic locations have focused almost exclusively on assessing whether waterfowl population expansion modifies nutrient (mainly P and N) concentrations in the water column. Considerably less research has been conducted

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to assess the influence of waterfowl population expansion on C cycling. Moreover, previous studies of the influence of waterfowl on biogeochemical cycles and productivity of Arctic lakes have used conventional limnological measurements of C (e.g., concentrations of DOC and DIC; Côté et al., 2010), but as far as we are aware have yet to incorporate measurements of C isotope composition of dissolved and particulate fractions. Carbon isotopes have been used successfully in temperate lakes to assess productivity and track C cycling (e.g., Rau, 1978; Quay et al., 1986; Takahashi et al., 1990, Bade et al., 2004), and so may be useful to assess effects of waterfowl disturbance in Arctic and subarctic ponds.

Most of the limnological studies that have examined the influence of waterfowl on Arctic lakes have relied on single, point-in-time water chemistry measurements. This is often a consequence of logistical constraints and high costs associated with sampling in remote northern locations. For example, Côté et al. (2010) sampled lakes once (in July or August) to provide a "snapshot" of the differences in limnological conditions between lakes with and without substantial waterfowl populations. And, Keatley et al. (2009) sampled sites once per year during July for three years, although not every site was sampled each year. An exception is a study by Mallory et al. (2006), which involved a nine-week sampling period to track changes in limnological conditions of a single pond in Nunavut located adjacent to an eider colony. They documented a decrease of pH and increase of P and N concentrations by the end of the ice-free season compared to lakes uninfluenced by the eider colony. Mallory et al. (2006) demonstrated that multiple limnological measurements over seasonal timescales may be important to quantify the influence of waterfowl populations on limnological conditions in some situations. Furthermore, findings illustrated that trends and differences may be missed by studies that rely on single, point-in-time sample collection.

Shallow lakes and ponds of Wapusk National Park (WNP; northeastern Manitoba, Canada) offer an opportunity to examine the influence of changes in waterfowl populations on the hydrolimnological and biogeochemical conditions in a subarctic

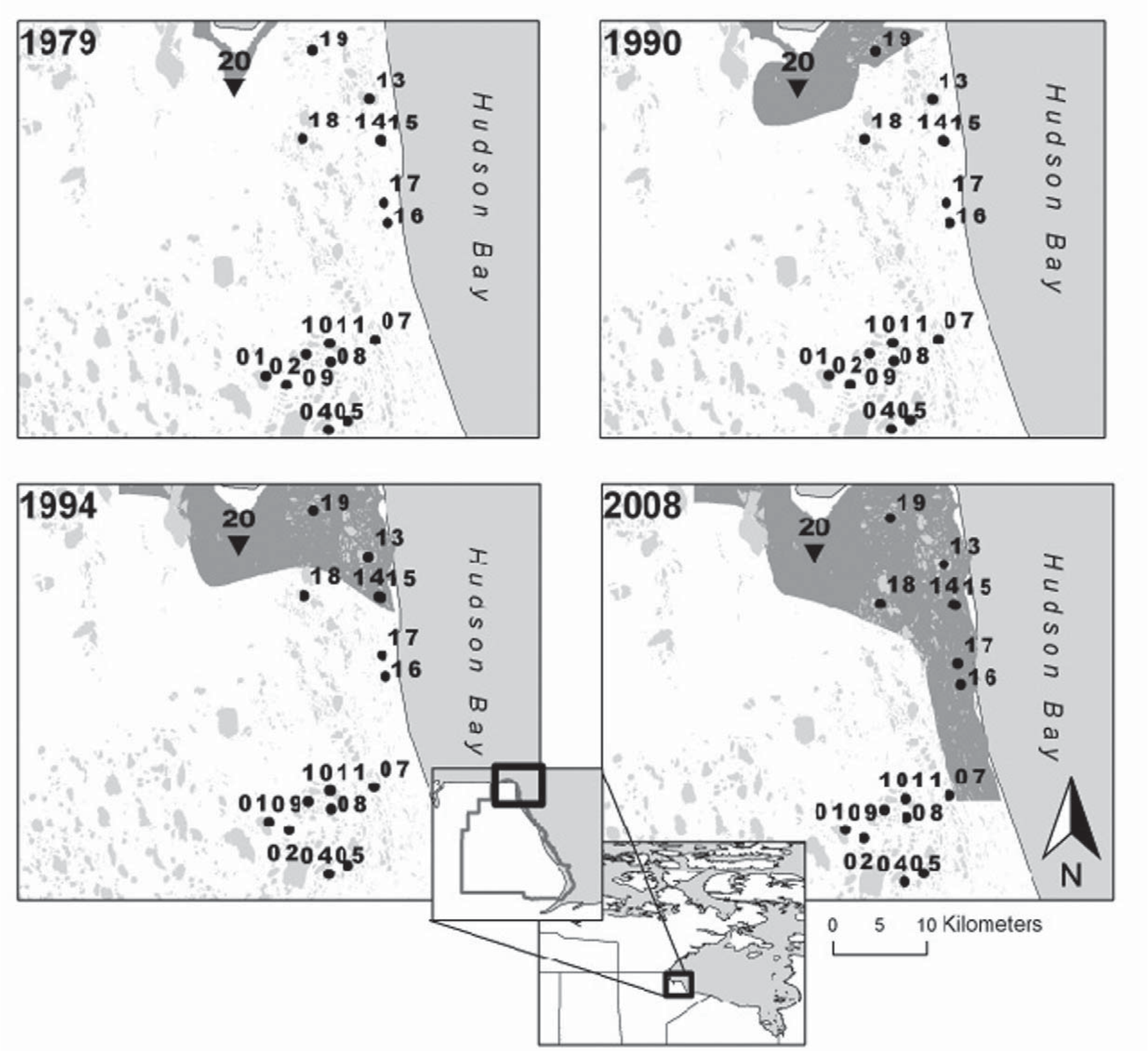

FIGURE 1. Location of Wapusk National Park (Manitoba, Canada) and the distribution of the 16 ponds sampled for this study. Sampled pond "20" (referred to as WAP 20 in the text, 58.6700°N, 93.4437°W) is situated in an area of high disturbance by lesser snow geese (LSG). Gray regions in the four panels on the map depict the geographic limits of the LSG population distribution (data from Parks Canada, 2010).

setting (Figs. 1, 2). WNP, located in the Hudson Bay Lowlands (HBL), contains abundant shallow lakes and ponds and is internationally renowned for its biodiversity and vital habitat for polar bears (*Ursus maritimus*) and migratory birds. Coastal regions of WNP have experienced a rapid increase in the lesser snow goose (LSG; *Chen caerulescens caerulescens*) population. A geometric increase of 5–7% per year has occurred since the 1960s (Batt, 1997; Jefferies et al., 2006), which has disturbed the landscape and caused substantial changes in vegetation and habitat (Fig. 2). For example, extensive grubbing by the LSG population in the soil to obtain roots and shoots of plants for nutrition has denuded vegetation in areas of coastal salt marshes and increased salinity and humidity in the soils (Fig. 2; e.g., Srivastava and Jefferies, 1996; Parks Canada, 2000; Handa et al., 2002; Jefferies and Rockwell, 2002). As the LSG have moved farther inland, grubbing for nutrition, removal of grasses for manufacture of nests and substantial deposits of feces have been observed. As the number of geese has grown, the spatial extent of the limit of their breeding grounds has also increased markedly, from <5 km^2 in 1969 to >300 km^2 as of 2008 (Fig. 1). These increases have been attributed to a combination of agricultural food subsidies in their wintering grounds, creation of conservation refuges along migration flyways, and warmer nesting locations, all of which increased energy allocated to reproduction and survival rates (Batt, 1997; Abraham et al., 2005b; Jefferies et al., 2006). At present, little is known about the consequences of the increased LSG population on the hydrolimnological and biogeochemical conditions of the coastal ponds of WNP. This information is required to predict the potential effects of further expansion of waterfowl populations in WNP and inform effective ecosystem stewardship decisions.

In this paper, we present a pilot study that characterizes the water chemistry and biogeochemical conditions of 16 shallow ponds located in the coastal fen ecotype within WNP and that assesses influences of LSG activities on carbon cycling and trophic status. Fifteen ponds that span the coastal fen ecotype and that currently have only low (if any) disturbance from the LSG population were sampled to provide insight into the range of hydrolimnological variability for ponds unaffected by the LSG population expansion. Results are compared with analyses from pond WAP 20, which receives heavy use by LSG—its catchment is strongly disturbed by their activities during the breeding season (late May to late August; Jefferies et al., 2003). Our intent was to expand on methods employed in previous limnological studies of waterfowl disturbance. We used conventional water chemistry (e.g., nutrients, ions, and alkalinity) and water isotope (e.g., δ^{18}O and δ^{2}H) and C isotope (e.g., $\delta^{13}C_{DIC}$ and $\delta^{13}C_{POM}$) measurements to compare seasonal changes and patterns of hydrological, limnological, and biogeochemical conditions between the 15 low-disturbance ponds and one highly disturbed pond. From these data, we explore potential hydrological, limnological, and biogeochemical effects of disturbance by the LSG population on a tundra pond in WNP. Data from the low disturbance ponds also provide baseline information for future studies assessing potential effects of LSG.

Study Area

WAPUSK NATIONAL PARK

WNP was established in 1996 to protect a representative section of the northwestern HBL. WNP is underlain by continuous permafrost in northern sections and discontinuous permafrost in the far south end of the park. Vegetation spans the transition between Arctic tundra and boreal forest (Parks Canada, 2000). Wetlands cover approximately 80% of the surface area of the park, with fens and bogs located along the coast and polygonal peat plateaus located farther inland (Parks Canada, 2008). In this study, we focus on ponds located within the coastal fen of WNP because it is the ecotype selected by LSG for their breeding grounds (Fig. 1). The coastal fen region comprises approximately 11% of the park (Parks Canada, 2000). Within this area, vegetation includes mainly sedges (*Carex aquatilis*) and rushes (*Scorpidium scorpoides* and *Scirpus caespitosus*), and terrestrial plant cover is sparse. During the past ~40 years, the LSG population has expanded dramatically throughout the coastal fen ecotype in population size, density, and geographic distribution (Figs. 1, 2). The LSG population typically arrives in the HBL in late May and begins the southward migration at the end of August (Jefferies et al., 2003). Terrestrial areas with the highest disturbance show evidence of substantial grubbing activity and vegetation loss, and contain abundant deposits of feces. However, based on our field observations, the influence of LSG within the mapped geographic limits of Figure 1 is patchy, and substantial areas remain relatively undisturbed.

STUDY SITES

The original intent of this study was to characterize seasonal hydrolimnological and biogeochemical behavior in coastal fen ponds. However, following conversations with wildlife ecologists at the Churchill Northern Studies Centre (CNSC) and assessment of our data and field observations, we recognized an opportunity to explore differences in hydrolimnological and biogeochemical conditions between a highly LSG-disturbed pond (WAP 20) in our data set and 15 other low-disturbance ponds (note that WAP 3, 10, 11, and 12 were removed from the data set because they desiccated during mid-summer of the sampling year (2010); Fig. 1). These ponds are all small (average area = 0.29 km^2) and shallow (<0.5 m), and were selected under the assumption that they are representative of ponds within the coastal fen ecotype. Based on observations made during our field campaigns, ponds WAP 1–19 had little to no visual evidence of disturbance by geese within their catchments even though several are located within the mapped area of the LSG breeding grounds (Fig. 1). Catchments of these ponds contained few deposits of feces and only small, if any, amounts of grubbing (hereafter termed low-disturbance coastal fen ponds, or LDCF ponds). In contrast, LSG have substantially disturbed the catchment of pond WAP 20 by depositing high densities of feces, establishing nests with eggs along the pond shoreline, and removing the terrestrial vegetation by grubbing (Fig. 2, parts c and d). WAP 20 is located in the area that has been longest disturbed by the LSG (e.g., Batt, 1997; Lacobelli and Jefferies, 1991; Abraham et al., 2005a, 2005b; Jefferies et al., 2006; Fig. 1).

CLIMATE

Meteorological conditions monitored at the Churchill airport show marked seasonal variations in temperature and precipitation (Fig. 3, parts a and b; Environment Canada, 2010). Based on 1971–2000 climate normals, average annual temperature is –6.9 °C, and average annual precipitation is 431.6 mm (rain = 264.4 mm, snow = 167.2 mm). During the sampling season of 2010, temperature was similar to climate normals in May, June, and August but slightly elevated in July and September. Rainfall was lower in June but markedly higher in late August (Fig. 3). Snow accumulation during the preceding winter (2009–2010) was considerably lower than the climate normal.

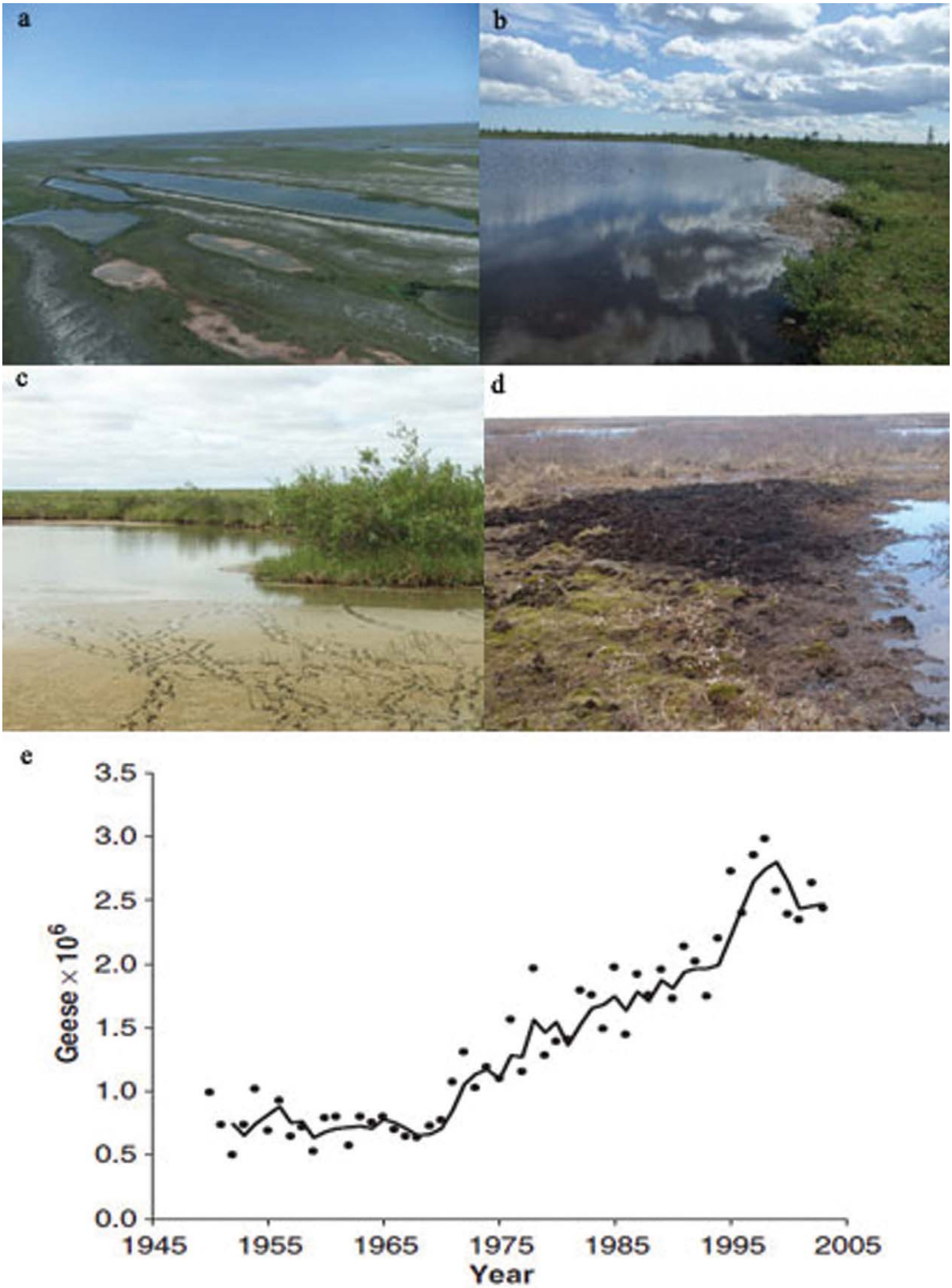

FIGURE 2. (a, b) Top photographs depict ponds from the coastal fen ecotype of Wapusk National Park with low disturbance from the lesser snow goose (LSG) population. (c, d) Bottom photographs are from pond WAP 20, which has evidence of high disturbance from the LSG population. (e) Graph was taken from data available in Abraham et al. (2005b) on the mid-winter index of LSG and Ross's geese from 1950 to 2003. The solid line is a 3-year running average.

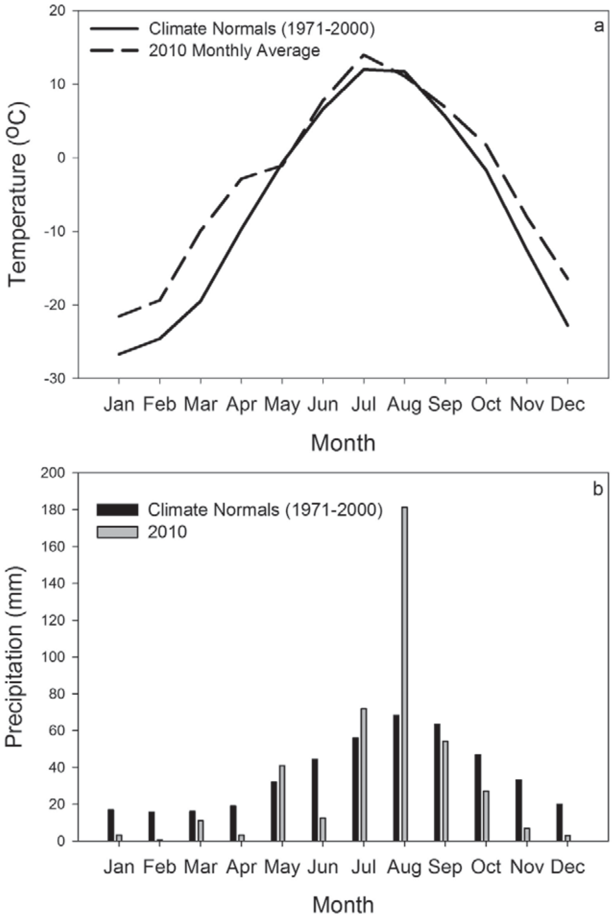

FIGURE 3. Comparison of average monthly (a) temperature and (b) precipitation at Churchill, Manitoba (1971–2000) (Environment Canada, 2010).

Methods

To characterize seasonal variations in hydrology, water chemistry, and C dynamics of the study ponds, surface water samples were collected at approximately 10- to 15-cm depth from all ponds on 8 June (soon after ice-off), 31 July (mid-summer) and 23 September (before ice-on) of 2010. The sampling dates were selected to encompass the early ice-free season (snow and ice melt), mid-summer (growth season), and autumn periods.

ISOTOPE HYDROLOGY

Pond water samples for analysis of water isotope composition were stored in tightly sealed 30-mL high density polyethylene bottles until analysis following standard methods (Epstein and Mayeda, 1953; Morrison et al., 2001) at the University of Waterloo Environmental Isotope Laboratory (UW-EIL). Isotopic compositions are reported as δ^{18}O (‰) and δ^2H (‰) relative to the Vienna Standard Mean Ocean Water (VSMOW) standard. δ^{18}O and δ^2H results are normalized to –55‰ and –428‰, respectively, for Standard Light Antarctic Precipitation (Coplen, 1996). The analytical uncertainty was ±0.2‰ and ±2.0‰ for δ^{18}O and δ^2H, respectively.

WATER CHEMISTRY

Surface water samples and limnological measurements were collected from all the ponds during the three field visits. *In situ* measurements for pH were also conducted at approximately 10- to 15-cm depth using a YSI 600QS multimeter. Following collection, all water samples were stored at 4 °C until analysis. Immediately following collection, the pond water was passed through a screen (80-μm mesh) to remove large particles that can affect estimates of concentrations in the pond water. For determination of DIC and DOC, water was filtered within 12 hours of collection (cellulose acetate filters: 0.45-μm pore size, 47-mm diameter) and stored in the dark at 4 °C until analysis at Environment Canada's National Laboratory for Environmental Testing (Burlington, Ontario) following their standard methods (Environment Canada, 1994). Samples for determination of TP and TKN were acidified (held at 0.02% H_2SO_4) and analyzed at the Biogeochemistry Lab at the University of Waterloo (TKN = Bran Luebbe, Method No. G-189-097; TKP = Bran Luebbe, Method No. G-188-097; Seal Analytical, Seattle, U.S.A.). Chlorophyll *a* concentrations were determined by filtering measured volumes of water onto Whatman® GF/F filters at the CNSC, and the filters were stored frozen and in the dark until chlorophyll *a* concentration was determined using standard fluorometric techniques (Parsons and Strickland, 1963; SCOR/UNESCO, 1966) at the Aquatic Ecology Group Analytical Laboratory at the University of Waterloo.

CARBON ISOTOPE ANALYSES

Water samples were collected from all ponds during the three field visits in 2010 for the analysis of C isotope composition of DIC ($\delta^{13}C_{DIC}$) using 125 mL glass serum bottles, with rubber stoppers and syringe needles that were used to expel excess air. Samples were stored at 4 °C until analysis. Samples for the C isotope analysis of suspended particulate organic matter ($\delta^{13}C_{POM}$) were collected using multiple horizontal tows with a phytoplankton net (mesh size = 25 μm). Upon return to the field base (CNSC), samples were passed through a 63-μm mesh net to remove zooplankton and other large particles, filtered onto pre-ashed Whatman® quartz filters (0.45-μm pore size), and dried at 60 °C for 24 hours in a drying oven. Filters were then exposed to 12 N HCl fumes in an air-tight vessel for 4 hours to remove carbonates, following the methods of Lorrain et al. (2003). Water samples were analyzed for $\delta^{13}C_{DIC}$ and acidified filters were analyzed for $\delta^{13}C_{POM}$ at the UW-EIL. Stable C isotope ratios are reported as δ^{13}C (‰) relative to the Vienna-PeeDee Belemnite (VPDB) standard. The analytical uncertainty was ±0.05‰ and ±0.01‰ for $\delta^{13}C_{DIC}$ and $\delta^{13}C_{POM}$, respectively. The C isotope fractionation factor was estimated from the difference between $\delta^{13}C_{DIC}$ and $\delta^{13}C_{POM}$ (i.e., $\Delta^{13}C_{DIC\text{-}POM}$; Fry 2006). To supplement C isotope measurements, dissolved CO_2 concentration and saturation values in the ponds were calculated based on methods outlined by Stumm and Morgan (1981) and Macrae et al. (2004), which determines the ratio of pond dissolved CO_2 concentration to equilibrium pond CO_2 concentration. A partial pressure of atmospheric CO_2 of 393 ppm was used for calculations (representative value for 2010 conditions; M. Macrae and R. Bourbonniere, unpublished data). Values of CO_2 saturation <1 indicate waters are under-saturated in dissolved CO_2, whereas values >1 indicate waters are over-saturated in dissolved CO_2.

NUMERICAL AND STATISTICAL ANALYSES

Principal components analysis (PCA) was used to explore patterns of variation in limnological and biogeochemical conditions among ponds over the course of the ice-free season. Only ponds that had a complete data set for all three sampling episodes were included in the PCA (i.e., ponds WAP 1 and 2 were not included in the PCA due to loss of the July $\delta^{13}C_{DIC}$ sample). The median value for the sample scores of the LDCF ponds was added in the ordination plot to assess the typical pattern of seasonal change for the undisturbed ponds. The values for CO_2 saturation were added passively to the PCA to avoid over-representation, as it was calculated based on other variables included in the PCA. The PCA was performed using CANOCO version 4.5 software (ter Braak and Šmilauer, 2002).

To further compare limnological and biogeochemical conditions between the highly disturbed WAP 20 and the LDCF ponds (WAP 1–19), the distribution of values for the LDCF ponds was compared using boxplots with values from WAP 20 for the three sampling periods. One-sample *t*-tests were used to determine if the mean value of each variable in the LDCF ponds differs from the value obtained at WAP 20. These tests were performed for each of the three sampling periods using SPSS version 20, and alpha was set at 0.05. Interquartile ranges (IQR) were also calculated using SPSS version 20 in order to provide information on the variability of data. Spearman Rank correlations were used to assess trends over time for pH and DIC.

Results

ISOTOPE HYDROLOGY

During the ice-free season of 2010, seasonal variations in pond water balances did not differ substantially between WAP 20 and the LDCF ponds based on water isotope values (Fig. 4). Pond water isotope composition at WAP 20 plots in similar $\delta^{18}O$-$\delta^{2}H$ space as the median values for the LDCF ponds during each of the corresponding three sampling periods in 2010 (June $\delta^{18}O$: –10.1‰ and –10.4‰, $\delta^{2}H$: –87.6‰ and –82.7‰; July $\delta^{18}O$: –6.2‰ and –6.2‰, $\delta^{2}H$: –66.7‰ and –67.1‰; September $\delta^{18}O$: –12.6‰ and –11.1‰, $\delta^{2}H$: –94.5‰ and –89.2‰; WAP 20 and LDCF, respectively). Pond waters were more isotopically depleted in the spring and fall, compared to summer values, and mostly plotted above the Local Evaporation Line (LEL), likely owing to the influence of rainfall. During the summer, waters became more isotopically enriched in the LDCF ponds and WAP 20 and exceeded δ_{SSL}, the terminal basin steady-state value, indicating marked mid-summer evaporation and pond-level drawdown. Substantial evaporation was noted throughout the coastal fen ecotype between June and July, and four ponds within our original study set (WAP 3, 10, 11, and 12) desiccated during this time.

MULTIVARIATE ANALYSIS: LIMNOLOGY AND CARBON ISOTOPE MEASUREMENTS

Multivariate ordination by PCA was used to assess similarities and differences in seasonal patterns of variation in limnological conditions and C isotope biogeochemistry between WAP 20 and the LDCF ponds (Fig. 5). The first two PCA axes explained 59.9% of the total variation in the measured limnological variables and C biogeochemistry. Axis 1 explained 34.8% and separated sample scores mainly based on seasonal changes in C biogeochemistry ($\delta^{13}C_{DIC}$, DIC concentration), pH, and alkalinity. Axis 2 captured 25.1% of the variation and separated samples mainly based on variations in concentrations of nutrients (TP, TKN) and chlorophyll *a*. For the LDCF ponds, sample scores in June generally clustered in the lower left quadrant, associated with relatively high pH, low concentrations of DIC, DOC and TKN, and low values of alkalinity, CO_2 saturation, and $\delta^{13}C_{DIC}$. In June, limnological conditions of LDCF ponds differed markedly from those at WAP 20, based on clear separation of the sample score for WAP 20 from the median of the sample scores for the LDCF ponds. The sample score for WAP 20 was positioned centrally within the ordination plot, representing more moderate values of all the variables relative to the LDCF ponds. In July, even greater limnological differences occurred between WAP 20 and the LDCF ponds. At this time, WAP 20 possessed higher concentrations of nutrients (TP, TKN), chlorophyll *a*, and $\delta^{13}C_{POM}$ than all but one of the LDCF ponds (WAP 8, which had high [13.9 μg L^{-1}] chlorophyll *a* values compared

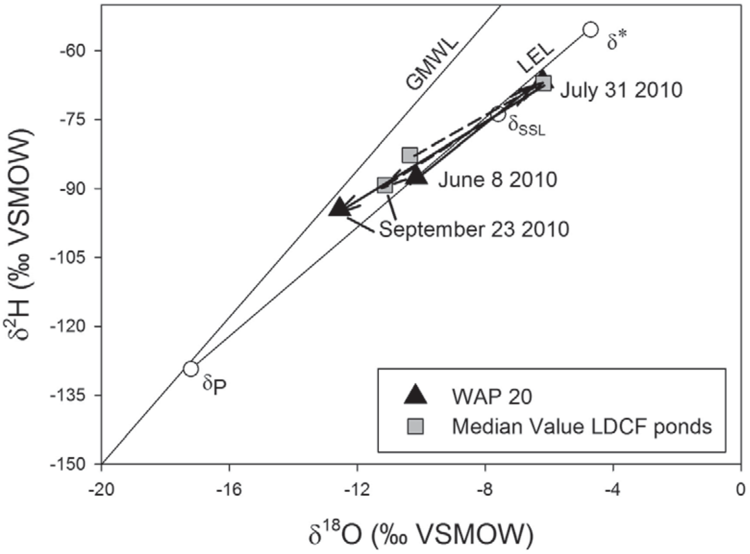

FIGURE 4. $\delta^{18}O$-$\delta^{2}H$ graph showing the seasonal trajectory of median water isotope compositions for the low-disturbance coastal fen (LDCF) ponds (gray squares, dashed line) and WAP 20 (black triangles, solid line) with respect to the Global Meteoric Water Line (GMWL; Craig, 1961) and the Local Evaporation Line for the Churchill region as reported in Wolfe et al. (2011).

to other ponds). The highest amount of variability among LDCF ponds occurred in July, as illustrated by the wide dispersal of sample scores along PCA axes 1 and 2. By September, differences in the distribution of limnological and biogeochemical variables between WAP 20 and the LDCF ponds lessened considerably, as indicated by the relatively close positioning of sample scores for most of the ponds (including WAP 20) towards the lower right quadrant. Sample scores during this time were associated with lower nutrient concentrations, pH, and $\delta^{13}C_{POM}$, and higher DIC concentrations, alkalinity, CO_2 saturation, and $\delta^{13}C_{DIC}$ compared to July. Overall, the position of the sample scores identified that both differences and similarities existed in the seasonal progression of limnological and biogeochemical conditions between WAP 20 and the LDCF ponds.

UNIVARIATE ANALYSES: WATER-CHEMISTRY VARIABLES

Use of boxplots (Fig. 6) and one-sample *t*-tests (Table 1) allowed more detailed assessment of the similarities and differences in the values and seasonal patterns of variation in water chemistry variables between WAP 20 and the LDCF ponds. Generally, the boxplots illustrate that concentrations of TKN, TP, DOC (except September), and chlorophyll *a* at WAP 20 were within the range of values at the LDCF ponds (Fig. 6, parts a–d). However, two interesting patterns were observed. First, concentrations of TKN and DOC at WAP 20 were near the upper range of the LDCF ponds, but chlorophyll *a* concentrations at WAP 20 were not elevated. In fact, chlorophyll *a* was near the lower range for the LDCF ponds in June and September of 2010. Second, WAP 20 and the LDCF ponds had different seasonal patterns of variation in TP concentration. Additional details are presented below.

In June, the range of TKN concentrations in the LDCF ponds was relatively small (IQR: 0.4 mg L^{-1}), and the median concentration (0.54 mg L^{-1}) was low (Fig. 6, part a). At WAP 20, TKN concentration was 1.01 mg L^{-1}, which approached the 90th percentile of the LDCF ponds and differs significantly from the mean of the LDCF ponds (Table 1). Between June and July, TKN concentration increased (median = 1.32 mg L^{-1}) in the LDCF ponds and variability rose as shown by a larger interquartile range (0.8 mg L^{-1}). TKN concentration also rose at WAP 20 (2.28 mg L^{-1}), to a value slightly above the 75th percentile of the LDCF ponds. By September, TKN concentrations declined, the IQR remained similar (0.9 mg L^{-1}), and the concentration at WAP 20 (0.69 mg L^{-1}) was close to the median of the LDCF ponds (0.64 mg L^{-1}).

Seasonal patterns of DOC concentration were similar to the patterns for TKN concentration for both WAP 20 and the LDCF ponds, with lower concentrations in June followed by increased values in July and declines between July and September (Fig. 6, part b). However, mean DOC concentrations for the LDCF ponds were significantly lower than the values at WAP 20 for all three sampling periods (Table 1; Fig. 6, part b). In June, both WAP 20 (11.0 mg L^{-1}) and the LDCF ponds (median: 6.0 mg L^{-1}) had low concentrations compared to the rest of the season. Variability of DOC concentrations among the LDCF ponds was small in June (IQR: 4.7 mg L^{-1}), and the concentration at WAP 20 was close to the 90th percentile of the LDCF ponds. Increased concentrations were observed for both WAP 20 (21.6 mg L^{-1}) and the LDCF ponds (median 11.1 mg L^{-1}) in July. Also in July,

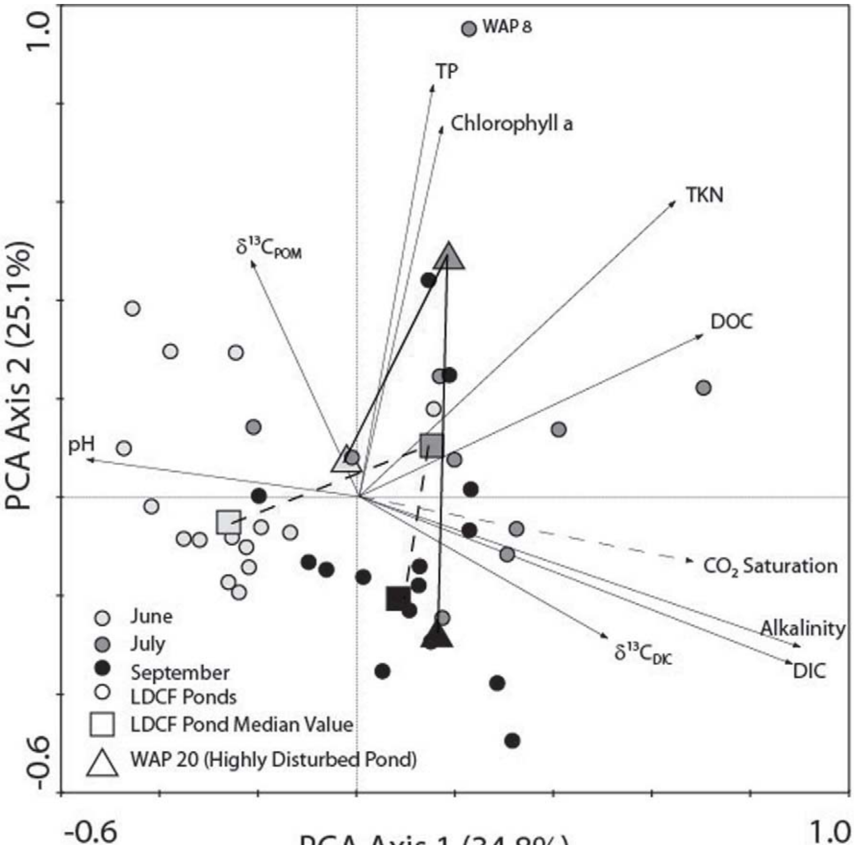

FIGURE 5. Principal components analysis (PCA) ordination biplot comparing limnological and biogeochemical conditions in WAP 20 (triangles) and the LDCF ponds (small circles) from the three sample periods in 2010. Vectors with solid lines represent active variables in the PCA, whereas vectors with dashed lines represent variables added passively. Lines connect sample scores for WAP 20 (triangles and solid line) and the median for the 15 LDCF ponds (squares, dashed lined) to assess seasonal patterns of change in the limnological variables with and without extensive lesser snow goose activity, respectively.

TABLE 1

Results of one-sample t-tests, which compare the mean value of water chemistry variables from the low-disturbance coastal fen (LDCF) ponds with the value obtained at WAP 20. Comparisons are presented for all three sampling episodes (June, July, September).

	June		July		September	
	t–statistic	*P* value	*t*–statistic	*P* value	*t*–statistic	*P* value
TKN (mg L^{-1})	–2.551	0.023	–1.810	0.092	1.658	0.121
DOC (mg L^{-1})	–5.938	3.621×10^{-5}	–3.621	0.003	–9.317	2.228×10^{-7}
Chl *a* (μg L^{-1})	3.513	0.003	1.406	0.181	3.429	0.004
TP (μg L^{-1})	–3.797	0.002	2.001	0.065	1.389	0.188
DIC (mg L^{-1})	–6.483	1.443×10^{-5}	1.702	0.111	–1.909	0.077
pH	–1.849	0.086	–9.041	3.208×10^{-7}	–1.707	0.11
$\delta^{13}C_{DIC}$ (‰VPDB)	–0.885	0.391	6.979	6.471×10^{-5}	9.055	3.148×10^{-7}
$\delta^{13}C_{POM}$ (‰VPDB)	–1.669	0.117	–4.954	3.343×10^{-4}	13.305	-2.458×10^{-9}
$\Delta^{13}C_{DIC-POM}$ (‰VPDB)	0.899	0.384	12.016	7.614×10^{-7}	–3.908	0.002
CO_2 Saturation	–3.310	0.05	3.590	0.003	1.108	0.286

a larger range of concentrations was observed for the LDCF ponds (IQR: 6.4 mg L^{-1}), and the DOC concentration at WAP 20 again approached the 90th percentile of the LDCF ponds. In September, DOC concentrations declined to values similar to those in June (13.6 mg L^{-1} and 9.8 mg L^{-1}; WAP 20 and LDCF medians, respectively). Additionally, the LDCF ponds had a narrower range of DOC concentrations in September (IQR: 1.8 mg L^{-1}), and the concentration at WAP 20 was slightly above the maximum value of the LDCF ponds.

In contrast to TKN and DOC, water-column concentrations of chlorophyll *a* were not elevated in WAP 20 compared to the LDCF ponds throughout the ice-free season (Fig. 6, part c). In June and September, chlorophyll *a* concentrations were low in the LDCF ponds (median: 1.9 μg L^{-1} and 1.6 μg L^{-1}, respectively) and spanned a relatively narrow range (June IQR: 1.8 μg L^{-1}; September IQR: 2.2 μg L^{-1}). At these times, chlorophyll *a* concentrations at WAP 20 (1.1 μg L^{-1} and 0.7 μg L^{-1}, respectively) were near the 10th percentile and significantly lower than the mean of the LDCF ponds (Table 1). Maximum chlorophyll *a* values occurred in July for both WAP 20 and the LDCF ponds, and the value at WAP 20 was close to the median value for the LDCF ponds (3.2 μg L^{-1} and 3.0 μg L^{-1}, respectively), while the IQR remained similar (2.2 μg L^{-1}).

For the LDCF ponds, relatively low TP concentrations in June (median: 4.0 μg L^{-1}; IQR: 9.0 μg L^{-1}) were followed by an increase in July (median: 12.0 μg L^{-1}), with a marked increase in range (from <0.5 μg L^{-1} to 69.0 μg L^{-1}; IQR: 18.0 μg L^{-1}; Fig. 6, part d). In September, TP concentrations declined in the LDCF ponds (median: <0.5 μg L^{-1}), and there was a much narrower range of values (IQR: 0.0 μg L^{-1}). In contrast, TP concentration decreased from June to July (13.0 μg L^{-1} and 10.0 μg L^{-1}, respectively) at WAP 20, corresponding to a decline from the 75th percentile of the LDCF ponds in June to the 25th percentile in July, and then declined more substantially between July and September (to <0.5 μg L^{-1}, a value similar to the median of the LDCF ponds). Although seasonal patterns in TP differed, one-sample *t*-tests indicate a significant difference only in June between the mean of the LDCF ponds and the value for WAP 20 (Table 1).

UNIVARIATE ANALYSIS: VARIABLES RELATED TO CARBON ISOTOPE BEHAVIOR

In contrast to broadly similar patterns of seasonal variation in pond-water concentrations of TKN, DOC, and chlorophyll *a*, seasonal behavior of variables associated with C biogeochemistry differed markedly between WAP 20 and the median of the LDCF ponds. For example, seasonal trajectories of change in DIC concentration differed between WAP 20 and the LDCF ponds (Fig. 6, part e). Although values at WAP 20 were within the range of the LDCF ponds for all three sampling periods, WAP 20 was the only pond where DIC concentrations did not increase between June and July, as demonstrated by a strong rise of DIC between June and July for the LDCF ponds ($r_s = 0.697$, $p = 1.870 \times 10^{-5}$, d.f. = 28). In June, WAP 20 had a higher DIC concentration than the 90th percentile of the LDCF ponds (WAP 20: 20.1 mg L^{-1} and LDCF median: 13.2 mg L^{-1}; IQR: 6.9 mg L^{-1}) and this value is significantly different from the mean of the LDCF ponds (Table 1). In July, the median DIC concentration in the LDCF ponds increased by ~7.8 mg L^{-1} (range 3.6–15.6 mg L^{-1}; IQR: 8.4 mg L^{-1}), whereas the DIC concentration remained relatively constant (19.8 mg L^{-1}) at WAP 20 and fell within the 25th and 50th percentile of values for the LDCF ponds. Between July and September, both the range (IQR: 6.7 mg L^{-1}) of DIC concentrations and the median value (21.3 mg L^{-1}) remained similar at the LDCF ponds. In contrast, DIC concentration increased at WAP 20 between July and September, to 25.8 mg L^{-1}, a value near the 75th percentile of the LDCF ponds.

From June to July, pH declined in all the LDCF ponds that are supported by a significant negative trend (r_s (45) = –0.805, $p = 2.671 \times 10^{-11}$), but in July, pH was significantly higher in WAP 20 compared to the mean for the LDCF ponds (Fig. 6, part f; Table 1). In June, both WAP 20 and the LDCF ponds possessed similar pH values (9.2 and 9.1; WAP 20 and LDCF median, respectively). Between June and July, pH declined only slightly at WAP 20 (9.2 to 9.0, respectively), whereas median pH declined more strongly in the LDCF ponds (9.2 to 8.5). In the LDCF ponds, the range of pH values in July declined to below the 25th percentile of the values measured in June. In the

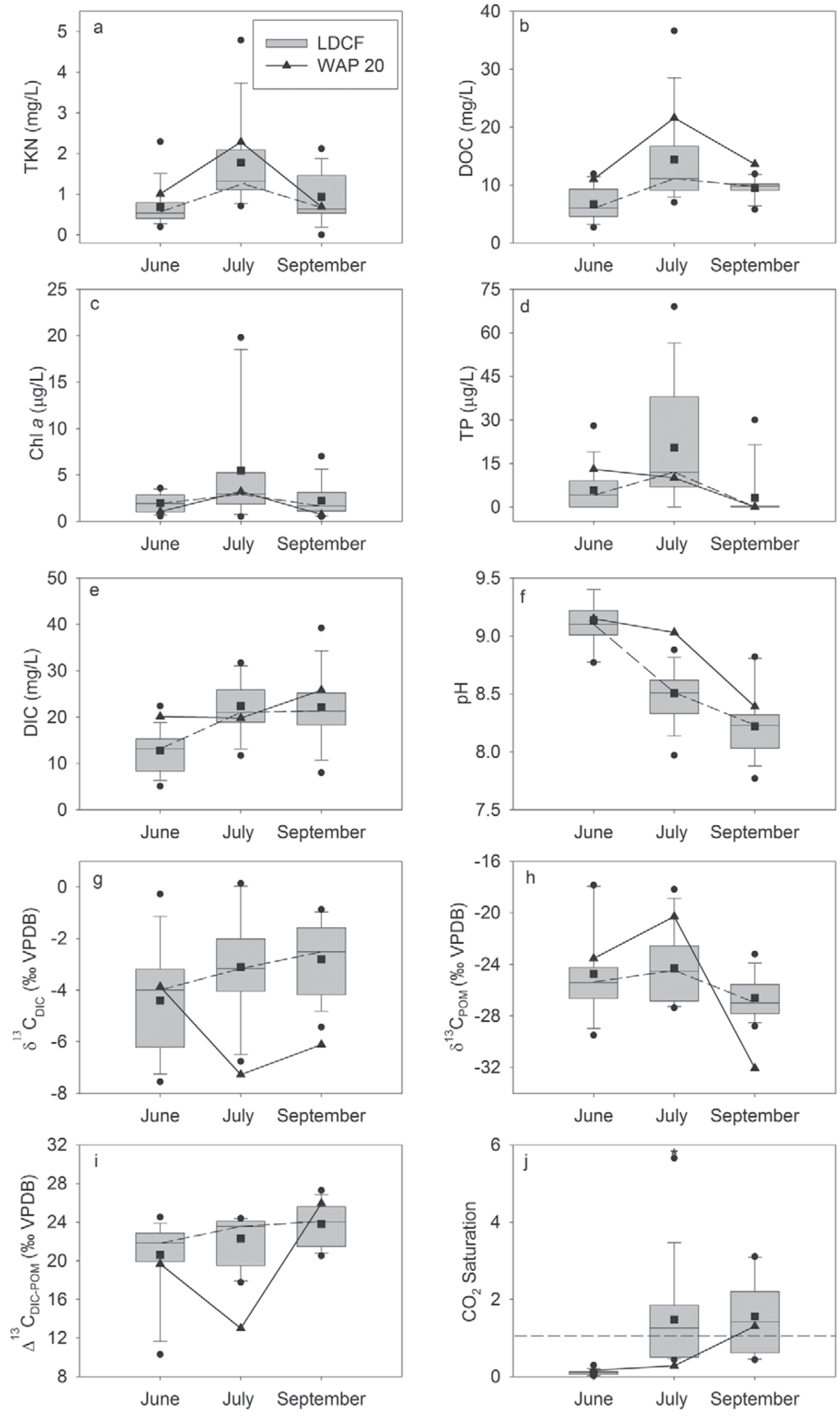

FIGURE 6. **Boxplots depicting seasonal changes in (a) TKN concentration, (b) DOC concentration, (c) Chlorophyll a concentration, (d) TP concentration, (e) DIC concentration, (f) pH, (g) $\delta^{13}C_{DIC}$, (h) $\delta^{13}C_{POM}$, (i) $\Delta^{13}C_{DIC\text{-}POM}$, and (j) CO_2 saturation. The boxes identify the 25th percentile, median value, and 75th percentiles for the low disturbance coastal fen (LDCF) ponds. The whisker bars represent the 10th and 90th percentile, the solid black circles represent the maximum and minimum values observed for the LDCF ponds, and asterisks represent outliers. Black squares represent the mean seasonal value for the LDCF ponds. Black triangles joined by the solid line represent the values for WAP 20.**

LDCF ponds, pH continued to decline between July and September (median 8.2), with the 75th percentile value in September falling below the 25th percentile from July. At WAP 20, pH declined to 8.4 in September, which was slightly above the 75th percentile of the LDCF ponds. The variability of pH in the LDCF ponds was similar in June, July, and September (IQR: 0.2, 0.2, and 0.3, respectively).

Measurements of the C isotope composition of DIC revealed unique seasonal C behavior in WAP 20 compared to the LDCF ponds (Fig. 6, part g). In June, the $\delta^{13}C_{DIC}$ value at WAP 20 was similar to the median value for the LDCF ponds (–3.9 and –4.0‰, respectively). At this time, the LDCF ponds spanned a relatively broad range of $\delta^{13}C_{DIC}$ values, (–7.6 to –0.3‰; IQR: 3.0‰). In July and September, there was a large divergence in the seasonal pattern of change in $\delta^{13}C_{DIC}$ between WAP 20 and the LDCF ponds, and the mean for the LDCF ponds differed significantly from the value at WAP 20 (Table 1). Median $\delta^{13}C_{DIC}$ values of the LDCF ponds increased throughout the ice-free season (July: –3.2‰ and September: –2.5‰). All but three of the LDCF ponds showed this pattern. Those three LDCF ponds showed only small decreases between June and July (0.4 to 1.1‰). In contrast, the $\delta^{13}C_{DIC}$ of WAP 20 decreased sharply between June and July (to –7.3‰). The $\delta^{13}C_{DIC}$ increased between July and September (to –6.1‰) as was observed in the LDCF ponds. In July, the interquartile range of $\delta^{13}C_{DIC}$ values in the LDCF ponds was more narrow (IQR: 2.0‰), but the overall range was large due to occurrence of ponds with more extreme minimum (WAP 13: –6.8‰) and maximum (WAP 9: 0.1‰) values. Despite the large range, the July $\delta^{13}C_{DIC}$ value for WAP 20 fell below the minimum value for the LDCF ponds. And, $\delta^{13}C_{DIC}$ at WAP 20 remained below the range of the LDCF ponds in September (IQR: 2.6‰).

Seasonal patterns for $\delta^{13}C_{POM}$ were similar at WAP 20 and the LDCF ponds, but larger changes occurred between sampling episodes for WAP 20 (Fig. 6, part h). In June, $\delta^{13}C_{POM}$ at WAP 20 fell within the range of LDCF ponds (–23.5 and –25.4‰, respectively). Between June and July, $\delta^{13}C_{POM}$ increased by 3.3‰ to –20.3‰ in WAP 20. In contrast, the median value of the LDCF ponds increased only slightly. Also, the range of values for the LDCF ponds was wider in July (IQR: 3.4‰) than in June (IQR: 2.4‰), and $\delta^{13}C_{POM}$ at WAP 20 was near the 90th percentile of the LDCF ponds. The mean for the LDCF ponds was significantly lower than the value at WAP 20 in July (Table 1). In September, $\delta^{13}C_{POM}$ decreased substantially (to –32.1‰) in WAP 20, whereas the decline was more muted at the LCDF ponds (median: –27.0‰). In September, the range of $\delta^{13}C_{POM}$ values declined in the LDCF ponds (IQR: 1.8‰), and $\delta^{13}C_{POM}$ at WAP 20 fell well below the minimum value of the LDCF ponds.

The patterns of seasonal change in C isotope fractionation ($\Delta^{13}C_{DIC\text{-}POM}$; Fig. 6, part i) also differed markedly between WAP 20 and the LDCF ponds. C isotope fractionation did not change appreciably for most of the LDCF ponds during the 2010 sampling season, as evidenced by the large amount of overlap among interquartile ranges in June, July, and September, and the comparable amount of variation (3.0, 4.6, and 3.3‰, respectively) and median values (21.8, 23.5, and 24.0‰, respectively). In contrast, $\Delta^{13}C_{DIC\text{-}POM}$ declined significantly in July at WAP 20 (June: 19.7‰, July: 13.0‰, and September: 25.9‰; Table 1) to well below the minimum value in July at the LDCF ponds.

In June, all ponds were under-saturated for CO_2 with little variability (CO_2 saturation = 0.2 and 0.1 for WAP 20 and median LDCF ponds, respectively; IQR: 0.1; Fig. 6, part j). In July, all of the LDCF ponds had increased values for CO_2 saturation, and the majority (9 out of 15) were supersaturated in CO_2 (median value 1.3). The range of values also increased (0.5 at WAP 13, to 5.7 at WAP 2; IQR: 0.8). In contrast, WAP 20 remained under-saturated in CO_2 in July and its value was significantly different from the mean of the LDCF ponds (Table 1) with a CO_2 saturation value (0.3) similar to that measured in June. In September, the majority (11 out of 15) of the LDCF ponds were supersaturated in CO_2 (median value 1.4; IQR: 1.4) and CO_2 saturation in WAP 20 increased to a value similar to the LDCF ponds (1.3).

Discussion

During the past ~40 years, WNP has witnessed a rapid increase in the LSG population and an expansion of the geographic region they inhabit within the coastal fen ecotype (Figs. 1, 2). Their activities have disturbed vegetation and soils (e.g., Srivastava and Jefferies, 1996; Jefferies et al., 2004, 2006; Abraham et al., 2005a, 2005b). Knowledge of their effects on coastal ponds within WNP is lacking, but is important for determining the consequences of this changing wildlife population. Previous limnological studies of waterfowl disturbance in Arctic freshwater ecosystems have relied mainly on single, point-in-time or "snapshot" sampling, or paleolimnological records to characterize their effects on the concentration of major nutrients and phytoplankton biomass (e.g., P, N, chlorophyll *a*; Mallory et al., 2006; Keatley et al., 2009, 2011; Côté et al., 2010; Sun et al., 2013). To date, few, if any, studies have employed multiple sampling over seasonal timescales or C isotope measurements. As we discuss below, C isotope measurements were in fact more informative than standard limnological measurements, because they effectively capture marked differences in C behavior in the pond affected by LSG activities compared to those with little to no LSG activity. We also demonstrate that it is important to track seasonal changes in pond hydrology, nutrient concentrations, and C isotope behavior in order to disentangle effects of LSG activity from those caused by seasonally fluctuating meteorological and hydrological changes, because LSG activity exerted the strongest influence on limnological and biogeochemical conditions in mid-summer, whereas hydroclimatic controls were more prevalent during June (due to snowmelt) and September (due to late summer rain). Notably, concentrations of major nutrients (TKN, TP, DOC) at WAP 20, the pond with extensive LSG activity, were not outside the range of values measured at the LDCF ponds during the ice-free season of 2010 (except for DOC in September). Instead, LSG activities affected most strongly patterns of change in C cycling, pH, and TP concentrations between early June and late July, when biological activity increased between ice-off and mid-summer. Thus, a key recommendation is that detection of differences between ponds with and without extensive LSG activity requires a sampling regime that captures temporal variations of both limnological and biogeochemical conditions over the course of the ice-free season.

CARBON ISOTOPE DYNAMICS

At the 15 ponds with little to no LSG activity, $\delta^{13}C_{DIC}$ values increased over the course of the ice-free season (Fig. 6, part g). As summer progressed, aquatic primary productivity increased, which caused an increase in the $\delta^{13}C_{DIC}$ due to preferential use of ^{12}C by algae during photosynthesis (e.g., Quay et al., 1986; Keeley and Sandquist, 1992; Wachniew and Różański, 1997). Thus, the increase in $\delta^{13}C_{DIC}$ values that occurred between June and July in the LDCF ponds likely reflects an increase in primary productivity under conditions where C supply exceeded C demand. This is supported by the increase in DIC concentrations that occurred between June and July in the LDCF ponds, which indicate ample supply of DIC to meet demands by photosynthesis. And, it is consistent with the modest rise in phytoplankton biomass in the ponds between June and July, as estimated by pond water chlorophyll *a* concentration. The source of the DIC to the ponds is not clear, but likely came from decomposition in the pond sediments, which would have been warmer in July compared to June. The import of DIC from the catchment is unlikely as the ponds were drying and no surface inflow was observed at that time. Additionally, C isotope fractionation values were consistently around –20‰ throughout the ice-free season in the LDCF ponds, which are expected when there is sufficient dissolved CO_2 to support aquatic photosynthesis (e.g., Rau, 1978; Herczeg and Fairbanks, 1987; Bade et al., 2004).

In sharp contrast to the rise in $\delta^{13}C_{DIC}$ values in the LDCF ponds between June and July, driven by seasonally increasing aquatic productivity under conditions of adequate C supply, $\delta^{13}C_{DIC}$ declined sharply between June and July at WAP 20 (Fig. 6, part g). This feature suggests substantially different behavior of dissolved C cycling at the pond affected by marked LSG activity. Such deviation from the characteristic seasonal pattern of ^{13}C-enrichment of DIC under conditions of increasing productivity can occur in certain situations. For example, elevated supply of soil-derived isotopically depleted DIC from the catchment can lower $\delta^{13}C_{DIC}$ values (Wachniew and Różański, 1997). Also, increased net respiration of particulate organic carbon can result in increased DIC concentrations, decreased pH, and consequently a decline in $\delta^{13}C_{DIC}$ (Quay et al., 1986; Wachniew and Różański, 1997). However, elevated supply of soil-derived isotopically depleted DIC was unlikely at WAP 20, because as stated above, the ponds were drying and no surface inflow was observed at that time. We note that approximately 90% of rainfall in July occurred prior to July 11 and is unlikely to account for the decline in $\delta^{13}C_{DIC}$ as this would have probably influenced all of the ponds. Additionally, because pond water levels were lower in July, they were likely not receiving substantial input from permafrost thaw. Indeed, 4 of our 20 study ponds desiccated in July. Increased net respiration is also an unlikely explanation as this would result in a corresponding increase in DIC concentration, which was not observed in this pond (Fig. 6, part e).

We propose an alternative mechanism to explain the sharp decline in $\delta^{13}C_{DIC}$ values between June and July at WAP 20. Under conditions of high algal production, high C demand, and high pH, previous studies have identified that strong kinetic C isotope fractionation can occur during CO_2 invasion from the atmosphere, which causes a decline in $\delta^{13}C_{DIC}$ (Herczeg and Fairbanks, 1987; Takahashi et al., 1990; Bade et al., 2004). Under these conditions, C isotope fractionation will decline substantially from ~20‰ (Rau, 1978; Herczeg and Fairbanks, 1987), as was observed in WAP 20 (13.0‰; Fig. 6, part i). This process, previously termed "chemically enhanced CO_2 invasion," was initially described by Herczeg and Fairbanks (1987) in their isotope study of Mohonk Lake during a cyanobacterial bloom. This phenomenon has also been observed in other highly productive temperate lakes and ponds (e.g., Emerson, 1975; Takahashi et al., 1990, Bade et al., 2004) and represents a plausible explanation for the $\delta^{13}C_{DIC}$ decline that occurred between June and July at WAP 20. We propose that increased photosynthesis due to the LSG activity generated substantial C demand that exceeded dissolved CO_2 availability, which subsequently led to strong kinetic C isotope fractionation during CO_2 invasion. The increased C uptake is likely a consequence of high photosynthetic demand by benthic algae (not measured in our study) rather than phytoplankton, because phytoplankton biomass (as chlorophyll *a* concentration) was similar in ponds with and without the waterfowl activity and increased only modestly between June and July (see also next section for further details). Also, macrophytes are extremely sparse in WAP 20, and cannot account for the C demand. This description of C behavior implies that WAP 20 was a net C sink during mid-summer, which is further supported by low values of CO_2 saturation in July indicative of CO_2 under-saturation (Fig. 6, part j). In contrast, the majority (9 out of 15) of the LDCF ponds (and their median value) were super-saturated with CO_2 at this time and all of the LDCF ponds had CO_2 saturation values higher than WAP 20. The super-saturated CO_2 values in the LDCF ponds may be a consequence of less intense algal productivity, sediment degassing, or higher rates of respiration than in WAP 20. We attribute the rise in $\delta^{13}C_{DIC}$ in September at WAP 20 (Fig. 6, part g) to the reduction in the intensity of this process due to lower C demand as temperatures cooled, which is consistent with the increase in C isotope fractionation (Fig. 6, part i). High amounts of rainfall and subsequent runoff of comparably isotopically enriched DIC derived from carbonate dissolution may have also contributed to the rise in $\delta^{13}C_{DIC}$ in September at WAP 20 and the LDCF ponds.

Further support for the interpretation of C isotope dynamics from the $\delta^{13}C_{DIC}$ patterns is evident in the values of $\delta^{13}C_{POM}$ and their seasonal trends (Fig. 6, part h). Both WAP 20 and the LDCF ponds depicted similar seasonal patterns of $\delta^{13}C_{POM}$, with increases between June and July, and declines between July and September. This pattern, however, was more striking at WAP 20, with both a larger increase between June and July and larger decline between July and September compared to the LDCF ponds. The C isotope composition of particulate organic matter is dependent on the concentration of dissolved CO_2, the degree of productivity within a pond, and the source of C (O'Leary, 1981; Allen and Spence, 1981; Keeley and Sandquist, 1992). In June, $\delta^{13}C_{POM}$ values were approximately –25‰ in both WAP 20 and the LDCF ponds, which are typically observed when there is high availability of dissolved CO_2 allowing ample isotopic fractionation to occur during photosynthesis (Keeley and Sandquist, 1992). By July, a large increase in $\delta^{13}C_{POM}$ occurred at WAP 20, whereas this value increased only slightly at the LDCF ponds. The larger increase in $\delta^{13}C_{POM}$ at WAP 20 can be attributed to higher C demand as evidenced by reduced C isotope fractionation (Fig. 6, part i). In contrast, ample supply of dissolved CO_2 at the LDCF ponds resulted in only slight increases in $\delta^{13}C_{POM}$. Alternatively, the increase in $\delta^{13}C_{POM}$ at WAP 20 between June and July may be due to bicarbonate uptake. Under conditions of low concentrations of DIC and high pH, as was the case for WAP 20, algae may switch from using dissolved CO_2 as their main form of C to bicarbonate (Deuser et al., 1968; Emrich et al., 1970; Allen and Spence, 1981). Bicarbonate is isotopically heavier in C, which would lead to ^{13}C-enrichment of POM. By September, $\delta^{13}C_{POM}$ values decreased in WAP 20 likely due to lower C demand, increased inputs of DIC due to large precipitation events, and/or a switch back to uptake of dissolved CO_2 to support photosynthesis.

POND HYDROLOGY AND NUTRIENT DYNAMICS

In contrast to the striking differences in the seasonal behavior of the C isotope composition of dissolved inorganic and particulate organic fractions between the LSG-disturbed pond WAP 20 and LDCF ponds unaffected by LSG population expansion, seasonal patterns of variation in basin hydrology (assessed using $\delta^{18}O$, δ^2H) and concentrations of major nutrients (except TP) and phytoplankton biomass (as chlorophyll *a*) were broadly comparable at all ponds. This finding suggests that the changes in basin hydrology are strongly regulated by a common external driver such as seasonal variations in meteorological conditions, rather than differences in the amount of disturbance by LSG populations. In northern landscapes, intense seasonality of meteorological conditions can exert strong influence on hydrology of tundra ponds, and affect seasonal patterns of change in nutrients and aquatic productivity (Sheath, 1986; Lougheed et al., 2011; White et al., 2014). For example in the HBL, snowmelt in spring increases connectivity of ponds with the surrounding catchment, and higher hydrologic inflow increases the transfer of allochthonous materials to ponds (e.g., Macrae et al., 2004; Wolfe et al., 2011; White et al., 2014). As the ice-free season progresses, these allochthonous inputs supplied in spring may lead to higher nutrient concentrations and productivity during summer. Indeed, Macrae (1998) observed that snowmelt runoff supplied nutrients to ponds. Then, hydrologic connectivity may decline as a result of drier conditions that increase evaporation and reduce overland flow (Macrae, 1998; Macrae et al., 2004), which can lead to lake-level drawdown and raise nutrient concentrations and productivity in ponds of the HBL (Macrae et al., 2004; White et al., 2014). Conversely, intense episodes of rain in late summer may result in subsequent dilution of nutrients and ions (Fig. 3; White et al., 2014). Such seasonal shifts in meteorological conditions appear to have exerted strong influence on pond water balance, nutrient concentrations, and phytoplankton biomass in all of the study ponds. For example, increasing pond-water isotope values between June and July indicate strong influence of evaporation (Fig. 4). These changes were concomitant with increases in concentrations of TKN, DOC, and chlorophyll *a* in the water column of all the study ponds (Fig. 6, parts a–c), likely due to evaporative concentration and phytoplankton growth. Increases in these variables can also be due to increased allochthonous inputs that occurred in the spring, but there was a low amount of winter snowfall observed (Fig. 3). Individual catchment characteristics may result in these processes differing among ponds (Wolfe et al., 2011) and, thus, may account for the wide range of values observed for concentrations of nutrients, DOC, and chlorophyll *a* during July in the LDCF ponds. After mid-July, the ponds experienced a decrease in water isotope compositions due to a period of heavy rainfall in August (>double the climate normal; Figs. 3, 4) and, correspondingly, concentrations of nutrients and chlorophyll *a* were diluted in all ponds (Fig. 6). Similar seasonal changes in nutrient concentrations in response to hydroclimatic conditions have also been reported for other shallow ponds in the Churchill area (Macrae et al., 2004; White et al., 2014).

In contrast to TKN, DOC, and chlorophyll *a*, seasonal variation of TP concentration differed between WAP 20 and the LDCF ponds (Fig. 6, part d). TP concentrations rose between June and July at the LDCF ponds, but declined at WAP 20 despite modest increase in water-column chlorophyll *a* concentration. A rise in chlorophyll *a* concentration in the water column is typically associated with a coincident increase in TP concentration, because phosphorus is contained within the phytoplankton (Wetzel, 2001). Consequently, the decline in TP concentration at WAP 20 between June and July, when values increased in the LDCF ponds, suggests P demand became greater at WAP 20. As described above, evidence from C isotope measurements and pond water pH indicates that the substantially greater C demand at WAP 20 in July was likely driven by higher rates of photosynthesis than occurred at the LDCF ponds. The inferred increase in P demand also is likely associated with the elevated rates of photosynthesis that produced the C demand. However, phytoplankton productivity does not appear to explain the greater demand for C and P at WAP 20, because concentrations of chlorophyll *a* in the water column were comparable at WAP 20 and the LCDF ponds throughout the ice-free season. Instead, we suggest that stimulation of photosynthesis by benthic algae at WAP 20 is a main cause of the increased C and P demand. WAP 20 is very shallow (<0.5 m), has sparse macrophytes, and so the luxuriant benthic mat along the pond bottom has potential to contribute a large fraction of the pond's total primary production. We note that lower-than-expected phytoplankton chlorophyll *a* concentrations have been found in other Arctic lakes and ponds and attributed to benthic productivity (e.g., Van Geest et al., 2007; Côté et al., 2010). Moreover, a recent nutrient enrichment experiment that used microcosms containing water from a nearby coastal fen pond, with and without surficial pond sediments and associated benthic algal mat, demonstrated that these ponds rapidly assimilate additions of dissolved inorganic N (nitrate, ammonia) and P (phosphate) when surficial sediments and associated benthic biofilm are present (Eichel et al., 2014). Phosphate was taken up more rapidly from the water than inorganic N, and benthic algal biomass (as chlorophyll *a* concentration) became elevated when inorganic N and P were co-added to the microcosms, but not when N was added alone. Collectively, results of our study and the experiment by Eichel et al. (2014) suggest that nutrients supplied by waterfowl disturbances (feces, soil erosion) are rapidly taken up by benthic algae, which leads to increased demand for C and P. Measurements of benthic chlorophyll *a* and field-intensive nutrient studies would be needed to test this hypothesis. Stimulation of zooplankton grazing is another process that may explain the low chlorophyll *a* concentrations. In temperate locations, persistent N limitation as a consequence of waterfowl disturbance has often been reported and has been attributed to the low N:P ratio of bird feces (Manny et al., 1994; Post et al., 1998; Olson et al., 2005). However, in our study the comparable seasonal changes in TKN concentration between WAP 20 and the LDCF ponds suggest that demand for N is lower than demand for P. Other studies have also found significant alteration of phosphorus dynamics by waterfowl activities in both Arctic (e.g., Keatley et al., 2009; Côté et al., 2010) and temperate locations (e.g., Manny et al., 1994; Post et al., 1998). Consequently, seasonal measurements of TP concentration appear to provide a more effective measure of the effects of the LSG disturbance on coastal fen ponds compared to measurements of TKN or chlorophyll *a* concentrations. However, based on our case study, C-isotope measurements appear to provide the clearest distinction between WAP 20 and the LDCF ponds.

Concluding Remarks

During the past ~40 years, coastal regions of WNP have witnessed exponential increases in the LSG population and the geographic range of their nesting area. Concerns have been mounting regarding their effects on the abundant shallow ponds (Parks Canada, 2000). We used hydrolimnological and C isotope measurements, as well as seasonal sampling, to evaluate the influence of LSG population on a disturbed pond. We showed that when comparing nutrient concentrations between the highly LSG-disturbed pond WAP 20 and the 15 LDCF ponds, hydrolimnological measurements can identify only small differences which are difficult to attribute conclusively to activities of LSG. In contrast, C isotope measurements reveal distinctive C dynamics over the course of the ice-free season in WAP 20 compared to the LDCF ponds. Our data suggest that increased nutrient supply from the LSG activities at WAP 20 resulted in a shift in C dynamics compared to the LDCF ponds. We propose that "chemically enhanced CO_2 invasion" occurred at WAP 20 when elevated nutrient supply was quickly assimilated, and this stimulated intense mid-summer C demand by benthic algae in the presence of high pH. Consequently, WAP 20 remained as a net sink of C during mid-summer. In contrast, at the ponds with little to no LSG activity, CO_2 saturation values increased and the majority became net sources of CO_2 to the atmosphere by mid-summer. Knowledge of patterns of seasonal change in this study was important to determine how LSG populations may alter pond ecosystems.

Further studies are required to test whether the unique C behavior at WAP 20 is evident in other LSG-affected ponds and the persistence of these patterns over multiple years under varying hydroclimatic conditions. Disentangling the roles of hydroclimatic variability and waterfowl disturbance is challenging, and future studies should employ methods that include both seasonal sampling and measurements of C isotope composition of both dissolved inorganic and particulate organic fractions. Conventional limnological measurements of nutrient concentrations on a single visit may not capture waterfowl disturbance because of the potential for rapid uptake by the benthic mat. Ongoing contemporary and paleolimnological research throughout WNP aims to further identify linkages among hydrological, limnological, and biogeochemical (C isotopic geochemistry and greenhouse gas fluxes) conditions and provide information on the expected trajectories of this dynamic landscape in the context of continued changes in climatic conditions and wildlife populations.

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References Cited

Abraham, K. F., Jefferies, R. L., and Rockwell, R. F., 2005a: Goose-induced changes in vegetation and land cover between 1976 and 1997 in an Arctic coastal marsh. *Arctic, Antarctic, and Alpine Research*, 37: 260–275.

Abraham, K. F., Jefferies, R. L., and Alisauskas, R. T., 2005b: The dynamics of landscape change and snow geese in mid-continent North America. *Global Change Biology*, 11: 841–855.

Allen, E. D., and Spence, D. H. N., 1981: The differential ability of aquatic plants to utilize the inorganic carbon supply in fresh waters. *New Phytologist*, 87: 269–283.

Bade, D. L., Carpenter, S. R., Cole, J. J., Hanson, P. C., and Hesslein, R. H., 2004: Controls of δ^{13}C-DIC in lakes: geochemistry, lake metabolism, and morphometry. *Limnology and Oceanography*, 49: 1160–1172.

Batt, B. D. J. (ed.), 1997: Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group. Washington D.C.: U.S. Fish and Wildlife Service, and Ottawa, Ontario: Canadian Wildlife Service, Arctic Goose Joint Venture Special Publication, 120 pp.

Coplen, T. B., 1996: New guidelines for reporting stable hydrogen, carbon and oxygen isotope ratio data. *Geochimica et Cosmochimica Acta,* 60: 3359–3360.

Côté, G., Pienitz, R., Velle, G., and Wang, X., 2010: Impact of geese on the limnology of lakes and ponds from Bylot Island (Nunavut, Canada). *International Review of Hydrobiology,* 95: 105–129.

Craig, H., 1961: Isotopic variations in meteoric waters. *Science,* 133: 1702–1703.

Deuser, W. G., Degens, E. T., and Guillard, R. L. L., 1968: Carbon isotope relationships between plankton and sea water. *Geochimica et Cosmochimica Acta*, 32: 657–660.

Eichel, K. A., Macrae, M. L., Hall, R. I., Fishback, L., and Wolfe, B. B., 2014: Nutrient uptake and short-term responses of phytoplankton and benthic communities from a subarctic pond to experimental nutrient enrichment in microcosms. *Arctic, Antarctic, and Alpine Research*, 46: 191–205.

Emerson, S., 1975: Chemically enhanced CO_2 gas exchange in a eutrophic lake: a general model. *Limnology and Oceanography*, 20: 743–753.

Emrich, K., Ehhalt, D. H., and Vogel, J. C., 1970: Carbon isotope fractionation during the precipitation of calcium carbonate. *Earth and Planetary Science Letters*, 8: 363–371.

Environment Canada, 1994: *Manual of Analytical Methods: Major Ions and Nutrients, Volume 1*. Burlington, Ontario: National Laboratory for Environmental Testing, Canadian Centre for Inland Waters.

Environment Canada, 2010: *National Climate Data and Information Archive*. <http://www.climate.weatheroffice.ec.ge.ca/climateData/hourlydata e.html> (accessed January 2011).

Epstein, S., and Mayeda, T. K., 1953: Variations of O^{18} contents of waters from natural sources. *Geochimica et Cosmochimica Acta*, 4: 213–224.

Fry, B., 2006: *Stable Isotope Ecology*. New York: Springer.

Gregory-Eaves, I., Finney, B. P., Douglas, M. S. V., and Smol, J. P., 2004: Inferring sockeye salmon (*Oncorhynchus nerka*) population dynamics and water quality changes in a stained nursery lake over the past similar to 500 years. *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 1235–1246.

Handa, I. T., Harmsen, R., and Jefferies, R. L., 2002: Patterns of vegetation change and the recovery potential of degraded areas in a coastal marsh system of the Hudson Bay Lowlands. *Journal of Ecology*, 90: 86–99.

Herczeg, A. L., and Fairbanks, R. G., 1987: Anomalous carbon isotope fractionation between atmospheric CO_2 and dissolved inorganic carbon induced by intense photosynthesis. *Geochimica et Cosmochimica Acta*, 5: 895–899.

Jefferies, R. L., and Rockwell, R. F., 2002: Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science*, 5: 7–16.

Jefferies, R. L., Rockwell, R. F., and Abraham, K. F., 2003: The embarrassment of riches: agricultural food subsidies, high goose numbers, and loss of Arctic wetlands—A continuing saga. *Environmental Reviews*, 11: 193–232.

Jefferies, R. L., Rockwell, R. F., and Abraham, K. F., 2004: Agricultural food subsidies, migratory connectivity and large-scale disturbance in Arctic coastal systems: a case study. *Integrative and Comparative Biology*, 44: 130–139.

Jefferies, R. L., Jano, A. P., and Abraham, K. F., 2006: A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology*, 94: 234–242.

Keatley, B. E., Douglas, M. S. V., Blais, J. M., Mallory, M. L., and Smol, J. P., 2009: Impacts of seabird-derived nutrients on water quality and diatom assemblages from Cape Vera, Devon Island, Canadian High Arctic. *Hydrobiologia,* 621: 191–205.

Keatley, B. E., Blais, J. M., Douglas, M. S. V., Gregory-Eaves, I., Mallory, M. L., and Smol, J. P., 2011: Historical seabird population dynamics and the effects on Arctic pond ecosystems: a multi-proxy paleolimnological study from Cape Vera, Devon Island, Arctic Canada. *Fundamental and Applied Limnology*, 179: 51–66.

Keeley, J. E., and Sandquist, D. R., 1992: Carbon: freshwater plants. *Plant, Cell and Environment*, 15: 1021–1035.

Lacobelli, A., and Jefferies, R. L., 1991: Inverse salinity gradients in coastal marshes and the death of *Salix*; the effects of grubbing by geese. *Journal of Ecology*, 79: 61–73.

Lim, D. S. S., Douglas, M. S. V., and Smol, J. P., 2005: Limnology of 46 lakes and ponds on Banks Island, N.W.T., Canadian Arctic Archipelago. *Hydrobiologia,* 545: 11–32.

Lorrain, A., Savoye, N., Chauvaud, L., Paulet, Y.-M., and Naulet, N., 2003: Decarbonation and preservation method for the analysis of organic C and N contents and stable isotope ratios of low-carbonated suspended particulate material. *Analytica Chimica Acta*, 491: 125–133.

Lougheed, V. L., Butler, M. G., McEwen, D. C., and Hobbie, J. E., 2011: Changes in tundra pond limnology: re-sampling Alaskan ponds after 40 years. *AMBIO*, 40: 589–599.

Macrae, M. L., 1998: Variations in organic carbon storage in shallow tundra ponds. MSc thesis, York University, Toronto, Canada.

Macrae, M. L., Bello, R. L., and Molot, L. A., 2004: Long-term carbon storage and hydrological control of CO_2 exchange in tundra ponds in the Hudson Bay Lowland. *Hydrological Processes*, 18: 2051–2069.

Mallory, M. L., Fontaine, A. J., Smith, P. A., Robertson, M. O. W., and Gilchrist, H. G., 2006: Water chemistry of ponds on Southampton Island, Nunavut, Canada: effects of habitat and ornithogenic inputs. *Archiv für Hydrobiologie*, 166: 411–432.

Manny, B. A., Johnson, W. C., and Wetzel, R. G., 1994: Nutrient additions by waterfowl to lakes and reservoirs—Predicting their effects on productivity and water quality. *Hydrobiologia*, 280: 121–132.

Michelutti, N., Keatley, B. E., Brimble, Y., Blais, J. M., Liu, H., Douglas, M. S. V., Mallory, M. L., Macdonald, R. W., and Smol, J. P., 2009: Seabird-driven shifts in Arctic pond ecosystems. *Proceedings of the Royal Society: Biological Sciences,* 276: 591–596.

Michelutti, N., Brash, J., Thienpont, J., Blais, J. M., Kimpe, L., Mallory, M. L., Douglas, M. S. V., and Smol, J. P., 2010: Trophic position influences the efficacy of seabirds as contaminant biovectors. *Proceedings of the National Academy of Sciences*, 107: 10543–10548.

Morrison, J., Brockwell, T., Merren, T., Fourel, F., and Phillips, A. M., 2001: A new on-line method for high precision stable-hydrogen isotopic analyses on nanolitre water samples. *Analytical Chemistry*, 73: 3570–3575.

O'Leary, M. H., 1981: Carbon isotope fractionation in plants. *Phytochemistry*, 20: 553–567.

Olson, M. H., Hage, M. M, Binkley, M. D., and Binder, J. R., 2005: Impact of migratory snow geese on inputs. *Archiv für Hydrobiologie,* 166: 411–432.

Parks Canada, 2000: Background information to the Wapusk Ecological Integrity Statement. Winnipeg, Manitoba: Parks Canada Agency, Western Canada Service Centre.

Parks Canada, 2008: Ecological Integrity Monitoring Action Plan for Wapusk National Park of Canada 2008–2013. Churchill, Manitoba: Parks Canada Agency, Manitoba Field Unit.

Parsons, T. R., and Strickland, J. D. H., 1963: Discussion of spectrophotometric determination of marine-plant pigments, with revised equations for ascertaining chlorophylls and carotenoids. *Journal of Marine Research*, 21: 155–163.

Post, D. M., Taylor, J. P., Kitchell, J. F., Olson, M. H., Schindler, D. E., and Herwig, B. R., 1998: The role of migratory waterfowl as nutrient vectors in a managed wetland. *Conservation Biology*, 12: 910–920.

Prowse, T. D., Wrona, F. J., Reist, J. D., Gibson, J. J., Hobbie, J. E., Lévesque, L. M. J., and Vincent, W. F., 2006: Climate change effects on hydroecology of Arctic freshwater ecosystems. *Ambio,* 35: 347–358.

Quay, P. D., Emerson, S. R., Quay, B. M., and Devol, A. H., 1986: The carbon cycle for Lake Washington—A stable isotope study. *Limnology and Oceanography*, 31: 596–611.

Rau, G., 1978: Carbon-13 depletion in a subalpine lake: carbon flow implications. *Science*, 201: 901–902.

Rouse, W. R., Douglas, M. S. V., Hecky, R. E., Hershey, A. E., Kling, G. W., Lesack, L., Marsh, P., Mcdonald, M., Nicholson, B. J., Roulet, N. T., and Smol, J. P., 1997: Effects of climate change on the freshwaters of Arctic and subarctic North America. *Hydrological Processes*, 11: 873–902.

Rowland, J. C., Jones, C. E., Altmann, G., Bryan, R., Crosby, B. T., Geernaert, G. L., Hinzman, L. D., Kane, D. L., Lawrence, D. M., Mancino, A., Marsh, P., McNamara, J. P., Romanovsky, V. E., Toniolo, H., Travis, B. J., Trochim, E., and Wilson, C. J., 2010: Arctic landscapes in transition: responses to thawing permafrost. *EOS, Transactions, American Geophysical Union,* 91(26): 229–236.

Schindler, D. W., and Smol, J. P., 2006: Cumulative effects of climate warming and other human activities on freshwaters of Arctic and subarctic North America. *Ambio*, 35: 160–168.

SCOR/UNESCO, 1966: Working group on photosynthetic pigments: monographs on oceanographic methodology. Paris: UNESCO.

Sheath, R. G., 1986: Seasonality of phytoplankton in northern tundra ponds. *Hydrobiologia*, 138: 75–83.

Smol, J. P., and Douglas, M. S. V., 2007a: Crossing the final ecological threshold in High Arctic ponds. *Proceedings of the National Academy of Sciences*, 104: 12395–12397.

Smol, J. P., and Douglas, M. S. V., 2007b: From controversy to consensus: making the case for recent climatic change in the Arctic using lake sediments. *Frontiers in Ecology and the Environment*, 5: 466–474.

Srivastava, D. S., and Jefferies, R. L., 1996: A positive feedback: herbivory, plant growth, salinity and the desertification of an Arctic salt marsh. *Journal of Ecology*, 84: 31–42.

Stumm, W., and Morgan, J., 1981: *Aquatic Chemistry: an Introduction Emphasizing Chemical Equilibria in Natural Waters*. New York: John Wiley and Sons, Inc.

Sun, L. G., Emslie, S. D., Huang, T., Blais, J. M., Xie, Z. Q., Liu, X. D., Yin, X. B., Wang, Y. H., Huang, W., Hodgson, D. A., and Smol, J. P., 2013: Vertebrate records in polar sediments: biological responses to past climate change and human activities. *Earth Science Reviews*, 126: 147–155.

Takahashi, K., Yoshioka, T., Wada, E., and Sakamoto, M., 1990: Temporal variations in carbon isotope ratio of phytoplankton in a eutrophic lake. *Journal of Plankton Research*, 12: 799–808.

ter Braak, C. J. F., and Šmilauer, P., 2002: *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5)*. Ithaca, New York: Microcomputer Power.

Van Geest, G. J., Hessen, D. O., Spierenburg, P., Dahl-Hansen, G. A. P., Christensen, G., Faerovig, P. J., Brehm, M., Loonen, M. J. J. E., and Van Donk, E., 2007: Goose-mediated nutrient enrichment and planktonic grazer control in Arctic freshwater ponds. *Oecologia*, 153: 653–662.

Wachniew, P., and Różański, K., 1997: Carbon budget of a mid-latitude, groundwater-controlled lake: isotopic evidence for the importance of dissolved inorganic carbon recycling. *Geochimica et Cosmochimica Acta*, 61: 2453–2465.

Wetzel, R. G., 2001: *Limnology: Lake and River Ecosystems.* New York: Academic Press.

White, J., Hall, R. I., Wolfe, B. B., Light, E. M., Macrae, M. L., and Fishback, L., 2014: Hydrological connectivity influences seasonal patterns of limnological conditions in shallow tundra ponds of the western Hudson Bay Lowlands. *Arctic, Antarctic, and Alpine Research*, 46: 218–235.

Wolfe, B. B., Light, E. M., Macrae, M. L, Hall, R. I., Eichel, K., Jasechko, S., White, J., Fishback, L., and Edwards, T. W. D., 2011: Divergent hydrological responses to 20th century climate change in shallow tundra ponds, western Hudson Bay Lowlands. *Geophysical Research Letters,* 38: L23402, doi: http://dx.doi.org/10.1029/2011GL049766.

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