Assessing the influence of upstream drainage lakes on fluvial organic carbon in a wetland-rich region

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[1] The role of aquatic ecosystems in regional and global carbon cycles is becoming increasingly apparent, and lakes and reservoirs may be particularly important to the retention and processing of organic carbon. If this is the case, then lakes and reservoirs may act as control points that decrease OC concentrations and fluxes in downstream aquatic ecosystems. We tested this hypothesis at a regional scale by comparing dissolved organic carbon (DOC) concentrations and fluxes in 52 randomly selected streams and rivers with and without upstream lakes in the water-rich Northern Highlands Lake District (NHLD), Wisconsin, USA. DOC concentrations were significantly higher ($p < 0.01$) in drainage networks that did not contain lakes (25.02 mg/L) than they were in networks with upstream lakes (10.38 mg/L). However, when accounting for differences in wetland extent between watersheds, we were unable to detect a lake effect on downstream DOC concentrations ($p > 0.49$). Likewise, there were no significant differences in DOC:DON or DOC:DOP ratios, or in yields from watersheds with and without upstream lakes after compensating for wetland influences. We suggest that lake OC storage or processing may be limited by high hydrologic flushing in lakes with stream outlets and overwhelmed by larger scale influences of landscape composition in the NHLD. Consequently, drainage lakes in carbon-rich regions like the NHLD may have limited influence on terrigenous carbon exports to the ocean.

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1. Introduction

[2] Inland aquatic ecosystems appear to play a significant role in regional and global carbon dynamics, but until recently, have been poorly integrated into our understanding of this rapidly changing cycle [*Cole et al.*, 2007; *Tranvik et al.*, 2009; *Buffam et al.*, 2011]. Consequently, there is still much to be learned about how aquatic ecosystems and the characteristics of those ecosystems embedded in the terrestrial landscape influence carbon dynamics. Although stream and river networks have the potential to process large quantities of organic carbon [*Canham et al.* 2004; *Battin et al.*, 2008; *Lauerwald et al.*, 2012], lakes and reservoirs have been identified as the aquatic sites responsible for most carbon retention [*Algesten et al.*, 2004; *Cole et al.*, 2007]. The role of these lentic systems as organic carbon (OC) sinks is supported by observations that ecosystem respiration exceeds gross primary production in most lakes (i.e., OC consumption exceeds OC production, or net heterotrophy) [*Del Giorgio et al.*, 1999; *Tranvik et al.*, 2009]; extensive processing of terrestrial DOC in lakes [*Kling et al.*, 1991; *Sobek et al.*, 2005; *Karlsson et al.*, 2010]; and positive rates of OC accumulation in sediments (i.e., OC storage; [*Stallard*, 1998; *Kastowski et al.*, 2011]. These ecosystem-scale observations have also been reproduced during experiments [*Tranvik*, 1988; *Pace et al.*, 2004]. This sink function means that lakes have the potential to reduce OC loads and concentrations and affect the metabolic balance of downstream aquatic ecosystems, including marine environments [*Algesten et al.*, 2004]. Indeed, several investigators have reported reduced dissolved organic carbon (DOC) concentrations or fluxes in watersheds containing upstream lakes relative to lake-free drainages [*Mattsson et al.*, 2005; *Larson et al.*, 2007], and higher DOC concentrations in streams flowing into lakes than in the recipient lakes [*Meili*, 1992]. Consequently, there is increasing support for the position that carbon processing in upstream lakes reducing outputs to downstream aquatic systems.

[3] The view of lakes as OC sinks is not, however, universally supported. Although large-scale studies that include multiple lakes point to lakes as OC sinks [*Tranvik et al.*, 2009], other site-specific studies have demonstrated that individual lakes can be sources of OC or have no net effect on these downstream fluxes. Potential causes for these

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departures include relatively high rates of in-lake productivity in C-poor settings [*Hood et al.*, 2003; *Goodman et al.*, 2011] or short water residence times limiting the opportunity for OC processing within a particular lake [*Kling et al.*, 2000; *Stets et al.*, 2010]. To begin reconciling the disparate roles that individual lakes may have on carbon export at larger spatial scales, the goals of this study were (1) to determine the influence of lakes embedded in stream networks on DOC concentrations and fluxes in downstream aquatic ecosystems at a regional scale, and (2) to identify lake and landscape attributes that may contribute to variability in the magnitude and direction of lake influence on downstream DOC in the Northern Highlands Lake District (NHLD), situated at the southern extent of the boreal peatlands in northern Wisconsin (USA). Our strategy for addressing these objectives was to compare DOC concentrations, stoichiometric ratios, and yields in randomly selected streams with and without upstream lakes in a lake-rich landscape.

2. Methods

2.1. Study Area

[4] Wisconsin's NHLD (ca. 5,000 km^2) contains more than 7,500 lakes and 1,500 streams and rivers. Land cover is predominantly a mix of deciduous and coniferous forest (52%), lakes (13%), and wetlands (28%) [*Homer et al.*, 2004], and over 70% of wetlands in the region are peat forming [*Buffam et al.*, 2011]. Summertime DOC concentrations in streams and lakes vary substantially across the region, ranging from 0.80 to 62.95 mg/L [*Lottig et al.*, 2011]. Regional surface water hydrology is driven by groundwater discharge [*Hunt et al.*, 1998] and overland flow is extremely rare because of the presence of extensive wetlands and high hydraulic conductivity of glacial till [e.g., see *Peters et al.*, 2006]. Consequently, temporal variability in discharge is low and overbank flooding is rare [*Watters and Stanley*, 2007]. A more detailed description of the region, including physical and biogeochemical characteristics of lakes and streams is provided by *Hanson et al.* [2007] and *Lottig et al.* [2011].

2.2. Site Selection and Sample Collection

[5] To assess lake influences on downstream DOC, we categorized streams and rivers in the NHLD based on the presence or absence of lakes in the upstream drainage network. All streams and rivers identified on U.S. Geological Survey 7.5-min topographic maps that crossed access points (hiking trails to major highways) were selected as potential sampling locations and assigned to one of the two categories based on the presence or absence of upstream lakes in the drainage network (hereafter, +Lake and −Lake sites). Each sampling location was situated in a separate drainage network to ensure observational independence. Of the ~500 possible sampling locations, 52 sites (+Lake = 29, −Lake = 23) were randomly selected based on the regional distribution of +Lake and –Lake sites and sampled during base flow conditions (June–August 2006). Of the 29 +Lake sites, three contained upstream tributary channels between the sampling location and the outlet of the upstream drainage lake, while the remaining 26 +Lake sites had no tributary channels entering the stream between the sampling location and upstream lake outlet. Two of the three tributary channels were small first order streams and the third was a second order stream.

[6] To reduce correlation between stream type and sampling time, the order in which streams were sampled was randomized to the extent possible. Because of logistical issues in traveling to many streams scattered over a wide area, on any given sampling trip, a single unsampled stream was randomly selected for sampling along with any streams that were in close proximity to the randomly selected stream. In order to limit the potential effects of events (e.g., storms), no sampling occurred during, or on the day following a storm event.

[7] Watershed boundaries were determined for each sampling location from a ~30 m digital elevation model and ArcGIS version 9.1 (Environmental Systems Research Institute, Inc., Redlands, California, USA). Percentages of forest, wetland, and open water (hereafter referred to as lakes) in each watershed were calculated from the 2001 National Land Cover Data set [*Homer et al.*, 2004]. We also quantified lake and landscape attributes that could potentially modulate the lake effect on DOC. These include indicators of water residence time in upstream lakes (surface area of lakes embedded in the drainage upstream from sampling sites and lake watershed area:lake area ratios), the fraction of runoff at a site estimated to have traveled through a lake (i.e., watershed area of upstream lake:total watershed area), and the distance upstream to the nearest lake.

[8] All sites were sampled at least 7 channel widths upstream of the access point to minimize any influences caused by culverts or other features [*Fitzpatrick et al.*, 1998]. Discharge was measured using cross-sectional area and water velocity (Marsh-McBirney Model 2000 Portable Flowmeter). Filtering was done in the field using an in-line 0.45 μm membrane filter. Samples were stored on ice and returned to the laboratory where they were preserved and analyzed according to North Temperate Long-Term Ecological Research (NTL-LTER) protocols (http://lter.limnology.wisc.edu). DOC was measured on a Shimadzu TOC-V carbon analyzer. Dissolved organic nitrogen and phosphorus (DON and DOP, respectively) were determined by the difference between total dissolved and inorganic nutrients using data from *Lottig et al.* [2011] and instantaneous DOC yields (mg DOC s^{-1} km^{-2}) were calculated from concentration (mg/L), discharge (L/s), and watershed area (km^2).

2.3. Data Analysis

[9] We used three different strategies to identify an effect of upstream lakes on DOC in NHLD streams and rivers. Our goal was to use multiple approaches, with each analysis building on the prior approach and addressing additional factors that could influence regional-scale patterns and/or confound interpretation of a lake effect. First, watershed characteristics and stream chemistry of +Lake and –Lake sites were simply compared using a two-sample *t*-test. In addition to potentially influencing concentrations and yields, upstream lakes may also alter the quality of DOC exported to downstream aquatic systems [*Goodman et al.*, 2011]. Hence, we compared differences in composition using the stoichiometric ratios [*Joffre et al.*, 2001] of DOC, dissolved organic nitrogen (DON), and dissolved organic phosphorus (DOP) with a two-sample *t*-test.

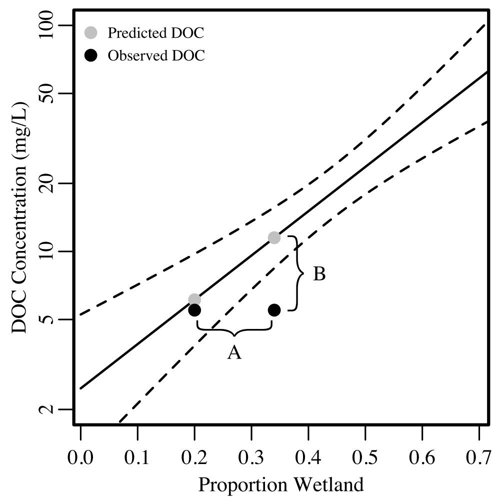

Figure 1. Example landcover adjustments and estimating DOC concentrations +Lake drainage networks if lakes were not present. Relationship between DOC concentration and wetlands in –Lake sites indicated by regression line ($F = 41.37$; $df_{1,2} = 1,21$; $r^2 = 0.66$, $p < 0.001$) and 95% confidence intervals. Theoretical observed (black circles) and predicted (gray circles) DOC concentrations in +Lake sites based on actual observations and predictions using –Lake wetland/DOC relationship. Shift in wetland extent (A) due to recalculated landcover after removing lake extent for watershed landcover calculations and difference in observed versus predicted DOC concentrations (B) due to increased wetland extent estimates. See text for more details.

[10] Next, because DOC loads and concentration can be influenced by land cover composition, and in particular, by wetland extent [*Aitkenhead et al.*, 1999; *Gergel et al.*, 1999; *Mulholland*, 2003], the second set of analyses incorporated watershed land cover effects. The first and most basic test in this category was to evaluate relationships between land cover and DOC concentrations and yields for all sites using Spearman's ρ. We next used a partial correlation test to factor out the effect of wetlands and test for independent correlations between lake extent and DOC concentrations and/or yields [e.g., *King et al.*, 2005]. We also compared DOC concentrations and yields between +Lake and –Lake watersheds using an Analysis of Covariance (ANCOVA) to determine if the presence of drainage lakes altered the magnitude of DOC concentrations and fluxes [e.g., *Mattsson et al.*, 2005]. Wetland extent was treated as a continuous covariate and the two drainage types were treated as factors in the analysis. As the final test in this category, we addressed the possibility that characteristics of lakes such as residence time or their distance upstream can also influence the biogeochemistry of streams draining lakes [*Algesten et al.*, 2004; *Arp and Baker*, 2007]. Thus, we assessed how distance to nearest upstream lake, percent of runoff routed through lakes, lake residence time (indicated by lake area and the watershed area:lake area ratio [after *Sobek et al.*, 2003]), and land cover, including lake extent, influenced DOC concentrations using multiple linear regression (MLR) analysis and Akaike's information criterion (AIC) to select the variables that best predicted DOC concentrations.

[11] Our final group of analyses was intended to address the problem that in water-rich landscapes, landcover variables such as wetland and lake extents are often correlated [*Van Sickle*, 2003; *King et al.*, 2005], potentially confounding the apparent influence of lakes on downstream DOC [*sensu King et al.*, 2005]. Different approaches can be taken to isolate the effect of lakes on DOC. A first approach could be to select several watersheds with identical land cover characteristics aside from the presence/absence of upstream lakes [e.g., *Larson et al.*, 2007], recognizing that this approach does not represent the range of watershed conditions within a region. Hence, conclusions drawn from only one level of wetland cover may or may not apply to other watersheds in the region with significantly different amounts of wetland cover. Another approach is to quantify carbon budgets of individual lakes drained by streams to determine if they are a net sink or source for DOC [*Dillon and Molot*, 1997; *Stets et al.*, 2010]. However, this approach is labor intensive and impractical to implement at regional scales, especially in water-rich landscapes such as the NHLD. A third approach, and the one used in this study, is to estimate the effect of upstream lakes by comparing observed DOC values in drainages with lakes to those predicted from drainages that have a similar landcover but do not contain lakes.

[12] To compare actual (observed +Lake) and predicted DOC (i.e., DOC predicted from –Lake drainages with similar landcover), we first established the relationship between wetland cover and DOC concentration for –Lake sites ($F = 41.37$; $df_{1,2} = 1,21$; $r^2 = 0.66$, $p < 0.001$; Figure 1 and Figure 5a). In order to estimate DOC concentrations in +Lake sites in the absence of lakes, we assumed that upstream lakes were not present and replaced the existing lake area with a weighted average of the other landcover types within the watershed. For example, in a simplified watershed containing three land cover types (40% forest, 20% wetland, and 40% lake), we would remove the lake from the land cover data and recalculate wetland extent using the No Lake scenario, which results in a watershed with 33% wetland cover and 67% forest (average of the non-lake landcover and expected landcover if lake was not present). This elevated wetland extent (A in Figure 1) would then be used to predict predicted DOC from the regional wetland-DOC relationship ($\log[DOC] = 0.99 + 4.31 * \text{wetland extent}$; Figure 1) from watersheds without lakes. The difference between the actual and predicted DOC is, effectively, a regression residual (hereafter Residual DOC) and was used as an estimate of the effect of an upstream lake on stream DOC (B in Figure 1). Similar to residuals of the –Lake versus wetland DOC regression, negative Residual DOC values indicate that actual DOC concentrations are lower than predicted from wetlands alone (lakes are sinks), while positive values occur when downstream DOC concentrations are higher than anticipated (lakes are sources). This approach maximizes the likelihood of identifying a DOC decline due to lakes because it overestimates existing wetland extent and thus predicted DOC concentrations, which may increase our Type I error. In this context, if we fail to detect a difference between predicted DOC and actual DOC in streams with upstream lakes, it suggests that lakes have little or no influence on the movement of fluvial DOC across the landscape. While this approach maximizes our ability to detect if lakes are acting as DOC sinks in this analysis, it reduces our

Table 1. Mean (Range) Watershed and Biogeochemical Characteristics in Streams With (+Lake) and Without (−Lake) Upstream Lakes[a]

Variable	−Lake Streams	+Lake Streams	t	*p* Value
Watershed Area (km^2)	4.25[a] (0.48–16.73)	11.65 (0.32–189.48)	2.47	**0.02**
Discharge (L/s)	8 (<1–461)	25 (<1–1006)	1.76	0.09
Water (%)	0.27 (0.00–7.24)	9.00 (0.21–26.7)	8.54	**<0.01**
Forest (%)	50.6 (28.5–76.9)	58.4 (25.2–79.1)	1.81	0.08
Wetland (%)	43.6 (11.1–69.0)	21.7 (9.48–53.9)	4.61	**<0.01**
DOC (mg/L)	25.02 (3.13–62.95)	10.38 (2.53–41.92)	3.00	**0.01**
DON (mg/L)	0.830 (0.114–1.587)	0.405 (0.108–1.073)	2.69	**0.01**
DOP (mg/L)	0.019 (0.007–0.051)	0.011 (0.005–0.033)	2.84	**0.01**
DOC:DON	25 (7–38)	21 (7–42)	1.95	0.06
DOC yield (mg DOC s^{-1} km^{-2})	37.6 (2.9–780.2)	27.0 (0.4–846.6)	0.72	0.48

[a]Values presented are calculated using untransformed data. Water, forest, and wetland refer to designations used in the National Landcover Database. Bold values indicate statistically significant difference (ANOVA; α = 0.05).

ability to determine if lakes are sources of DOC to downstream ecosystems [e.g., *Goodman et al.*, 2011] because the actual wetland landcover extent is lower than the overestimated extent used here. While this analysis is specifically tailored to identify potential declines in DOC downstream of lakes, the ANCOVA outlined above does not use altered watershed characteristics and is not biased in a single direction with respect to identifying if lakes were sources or sinks of DOC to downstream ecosystems

[13] Regression residuals extracted from the DOC-wetland relationship of –Lake sites and compared to +Lake Residual DOC values with a two-sample *t*-test. Levene's test was used to assess differences in the variance between residuals groups. Similar to our prior analyses of DOC concentrations, we also assessed how drainage network (i.e., distance to nearest upstream lake), lake residence time (lake area, watershed area: lake area ratio), and land cover influenced Residual DOC using MLR analysis and AIC to select the variables that best predicted Residual DOC.

[14] Finally, we quantified the uncertainty in DOC concentration measurements and landcover to assess the sensitivity of our results to wetland extent corrections and the sampling strategies employed in this study. One of our largest uncertainties is how representative a single sample taken during summer base flow is of the entire period that sampling took place (June–August). Because none of the streams were sampled repeatedly over the course of the study, we cannot estimate temporal uncertainty for the exact sampling time. However, we collected weekly data from four similar streams that spanned a gradient in ~3 mg/L to 45 mg/L DOC over the same period in 2007 (N. R. Lottig, unpublished data, 2007). We identify three major sources of variation in these estimates. First is analytical variation observed between samples analyzed at different points in time (determined using repeated measurements of a 10 mg/L DOC check standard; effectively variation in standard curves between analytical runs). The second source is uncertainty introduced from field sampling protocols (determined using the four replicate DOC samples at every site in this study). Our final source of temporal variation is the actual variation in stream DOC concentrations over the sampling period. Using these data we estimated the variation in base flow DOC concentrations as the standard deviation in stream DOC concentration (mg/L) from weekly (June–August) measurements and as the relative standard uncertainty for DOC concentrations (as percent of observed DOC concentration) as well. We estimate that summer base flow variation (±1 standard deviation) is approximately ± 5.5 mg/L, which corresponds with a relative standard uncertainty of ±6.8% observed mean DOC concentration. Approximately 25% of our uncertainty is associated with analytical uncertainty (±1.2%) and sampling protocols (±0.6%). Uncertainty in landcover the region was small (±1.5%) [*Wickham et al.*, 2010]. We further estimated that our minimal two sided detectable difference in wetland-corrected DOC (i.e., residual DOC) is approximately 3.5 mg/L DOC at power = 0.8 and alpha = 0.05. The minimal detectable difference to quantify if lakes have lower (one sided) than predicted DOC concentrations is 3.0 mg/L DOC.

[15] Mean values reported in the text are estimated using nontransformed values to aid in readability and to avoid biases back-transformations can introduce [*Helsel and Hirsch*, 2002]. Aside from reported mean values, all data were appropriately transformed prior to any statistical analysis to meet normality assumptions and back-transformed values are reported in the text for clarity when necessary. DOC:DON and DON:DOP ratios were square root-transformed, all other C, N, P constituents along with DOC yields were log-transformed, and land cover data were arcsine square root-transformed. We assumed that MLR models with ΔAIC < 2 were not significantly different [*Burnham and Anderson*, 2002]. Statistical analyses were conducted with the (R) Statistical Package (http://www.r-project.org).

3. Results

[16] Forests, wetlands, and open water covered 69%–100% (median 94%) of the watershed areas of the streams sampled in this study (Table 1). Wetlands were negatively correlated with both forests and lakes (Spearman's ρ = −0.74, p < 0.01 and ρ = −0.64, p < 0.01, respectively; Figure 2) while no correlation was observed between lakes and forests (p = 0.33). Total lake area in +Lake drainages composed, on average, 9% of the watershed area, ranging from <1% to 27%. Wetland cover was highest in –Lake drainage networks (mean 44%) and was significantly lower (22%) in +Lake networks, although substantial overlap existed between to the two network types (p < 0.01; Table 1).

[17] We observed substantial differences in DOC, DON, and DOP between sites with and without upstream lakes (Table 1). Concentrations of DOC in –Lake sites ranged from 3–63 mg/L and were significantly higher than +Lake sites where the maximum DOC concentration was 42 mg/L

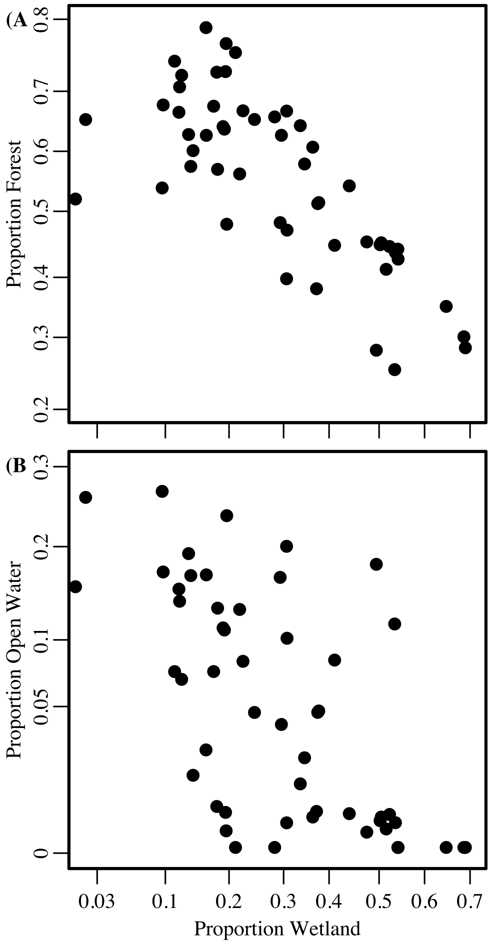

Figure 2. Significant landcover correlations between (a) wetland and forest ($\rho = -0.74$, $p < 0.01$) and (b) open water ($\rho = -0.64$, $p < 0.01$). *X*-axis and *y*-axis scales are arcsine square root-transformed; axis labels are actual proportions.

($p = 0.01$; Table 1). Although the concentration of DOC and other organic constituents were significantly different between drainage types, we observed no difference in yields, nor in the DOC:DON (regional mean = 22) and DON:DOP (regional mean = 426) ratios between the two network types (Table 1).

[18] DOC concentrations were negatively correlated with upstream lake area ($\rho = -0.50$, $p < 0.001$; Figure 3A) and positively correlated with upstream wetlands ($\rho = 0.64$, $p < 0.001$; Figure 3B). Unlike DOC concentrations, estimates of DOC yields were not correlated with any landcover variable. A partial correlation test for an independent relationship between upstream lake area and DOC concentration indicated no significant relationship after accounting for wetland area ($p = 0.508$). Similarly, we found no differences in DOC concentrations or yields between +Lake and –Lake sites when wetland extent was used as a covariate (ANCOVA, $p = 0.15$, $p = 0.54$ respectively). The best model predicting DOC concentrations in streams and rivers contained the single variable of wetland extent (Figure 4; $F = 48.46$, $df_{1,2} = 1,50$, $p < 0.01$, $r^2 = 0.49$, $\Delta AIC = 0$), although a model that also included upstream lake area performed equally as well ($p < 0.01$, $r^2 = 0.50$, $\Delta AIC = 1.58$). However, in this case, including lakes did not significantly increase the explanatory power of the model ($p = 0.53$). Residual values resulting from this analysis were greater (6.8 mg/L) than our estimates of temporal variation in summer stream DOC concentrations (5.5 mg/L) and approximately 2× greater than our minimal detectable difference between –Lake and +Lake sites. Landscape variables such as distance from the upstream lake, lake area, or the ratio of watershed area: lake area (Table 2) did not help explain observed DOC patterns.

[19] Our final set of analyses attempted to maximize our ability to detected potential downstream declines in DOC concentrations below drainage lakes (Figure 5). After amplifying the difference between predicted DOC concentrations and observed DOC concentrations, Residual

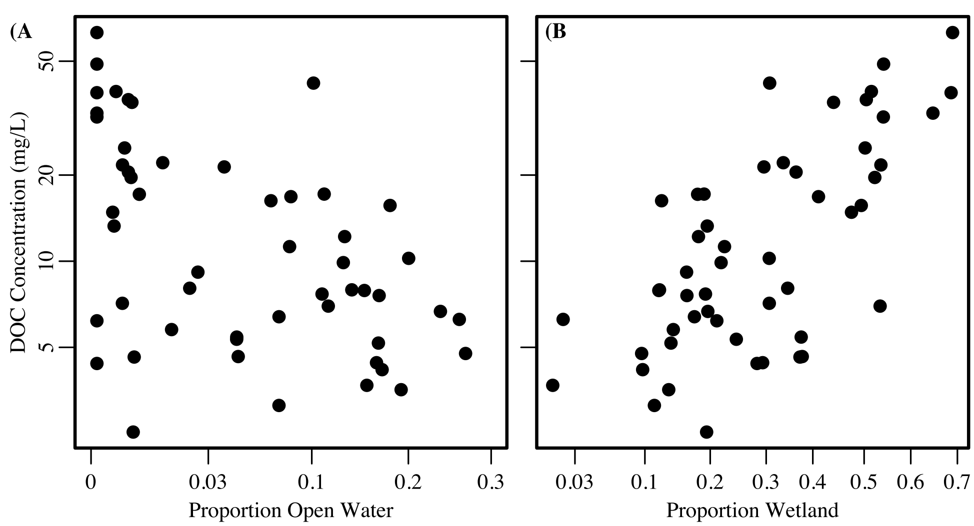

Figure 3. Correlations between DOC concentrations and (a) open water ($\rho = -0.50$, $p < 0.001$) and (b) wetlands ($\rho = -0.64$, $p < 0.001$). *Y*-axis scale is log-transformed, and *x*-axis scale is arcsine square root-transformed; axis labels are actual values.

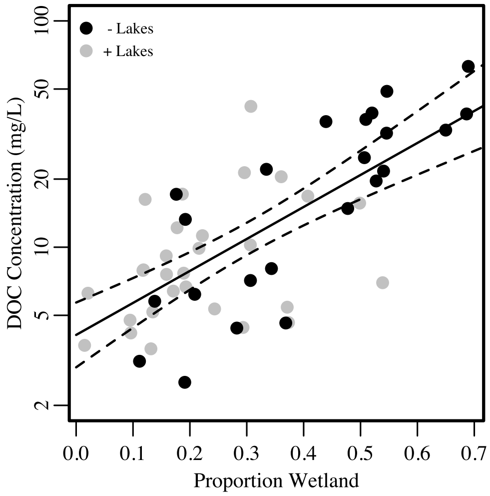

Figure 4. Combined regional wetland/DOC relationship in –Lake (black), +Lake (gray) streams, and 95% confidence interval. The best model predicting DOC concentrations in streams and rivers contained the single variable of wetland extent ($F = 48.46$, $df_{1,2} = 1,50$, $p < 0.01$, $r^2 = 0.49$).

DOC was slightly positive (Figure 5b), indicating that DOC concentrations in streams with upstream lakes tended to be higher than would be predicted if upstream lakes were absent. Because of the bias that this analysis introduces, Residual DOC in +Lake sites would be even more positive (e.g., Lakes are DOC sources) for data calculated using unaltered landscape covariates (e.g., ANCOVA above). We also observed a small increase in the range of Residual DOC in +Lake sites relative to –Lake streams (Figure 5b). However, there were no significant differences in the means (t-test, $p = 0.58$) or variances (Levene's test, $p = 0.51$) for Residual DOC and the regression residuals in −Lake sites. Additionally, no characteristics of the drainage network or lakes embedded in the network (Table 2) explained Residual DOC in this analysis (MLR; $p = 0.99$). Finally, examination of plots of residuals from the DOC-wetland regression versus lake attributes failed to reveal any consistent effect of lake extent or area, distance from lake, or percent of runoff at each site that had passed through an upstream lake (Figure 6).

4. Discussion

[20] As with many studies [e.g., *Rasmussen et al.*, 1989; *Kortelainen*, 1993; *Mulholland*, 2003], we found wetlands to be a strong predictor of regional stream and river DOC concentrations. However, unlike other empirical and model-based studies from this and other regions [e.g., *Mattsson et al.*, 2005; *Cardille et al.*, 2007; *Larson et al.*, 2007; *Hanson et al.*, 2011] and counter to our initial expectation, we failed to detect an effect of lakes on downstream DOC concentrations, stoichiometry, or yields in NHLD streams. Further, we were unable to identify lake or landscape features that may be associated with downstream DOC status other than wetland cover (e.g., upstream lake area, distance from lake, WA:LA ratio). A straightforward comparison of sites with and without upstream lakes would have led to the conclusion that lakes reduce downstream DOC, but this interpretation is confounded by the correlation between lake and wetland cover in the NHLD. Accounting for variation in wetland cover, even using an approach susceptible to overestimating a lake effect, revealed no differences between streams with and without upstream lakes. This result suggests that NHLD lakes embedded in aquatic networks do not transmit detectable effects on regional-scale stream organic carbon concentrations and yields. This is not evidence that these systems do not process or store carbon [see *Cardille et al.*, 2007; *Buffam et al.*, 2011; *Hanson et al.*, 2011], but rather that processing signals are not visible downstream.

[21] Our study design involved a spatially extensive but temporally limited approach, focusing on summertime base flow conditions, similar to other studies that have examined the effect of lakes on stream DOC [*Mattsson et al.*, 2005; *Larson et al.*, 2007; *Goodman et al.*, 2011]. Because of the spatial scale of the study, every stream could not be sampled on the same day and as a result we observed greater temporal uncertainty in our data than if we would have been able to sample on a single day. However, given that sites were randomly sampled through time, both populations have similar uncertainties (no bias between +Lake and –Lake streams groups) and even with the increased temporal uncertainty, the variation in DOC concentrations after accounting for differences in wetland extent among watersheds was greater than both the uncertainty in the data and our minimal detectable differences between +Lake and –Lake sites. We would be significantly concerned about the affects of temporal uncertainty if our uncertainty estimates in this study were greater than the variation observed in the data, which is not the case. Consequently, while temporal uncertainty could contribute to our lack of detectable lake influences, we believe that it has not altered the statistical results in this study.

[22] While the observation of limited/no lake influence on DOC stoichiometry, concentrations, and yields are applicable for the spatial and temporal scales addressed here, it may not be characteristic of annual or interannual behaviors. For example, lakes may shift from DOC sources to sinks to recipient streams from spring to summer [*Goodman et al.*, 2011] or between dry and wet years [*Einola et al.*, 2011]. However, one might anticipate the greatest potential for DOC retention in lakes to occur during this time period because of increased water temperature and solar radiation, factors influencing respiration and photodegradation. In addition to the temporal scale of the study, the spatial resolution of land cover data has the potential to introduce errors in watershed landcover estimates for this study and any study that relies on national land cover databases [*Wickham et al.*, 2010]. However, open water identification accuracy

Table 2. Mean (Range) Aquatic Landscape Characteristics for Streams That Have Upstream Drainage Lakes Embedded in the Surface Water Network (+Lake)[a]

Variable	Value
Lake area (LA) (km^2)	0.69 (0.02–3.62)
Lake Watershed Area (LW) (km^2)	1.82 (0.14–5.20)
Distance to upstream lake (km)	1.8 (0.03–17)
Runoff routed through lake (LW:WA) (%)	0.73 (0.12–1.00)
Drainage Ratio (LW:LA)	27.5 (4.4–116.2)

[a]Values presented are calculated using untransformed data.

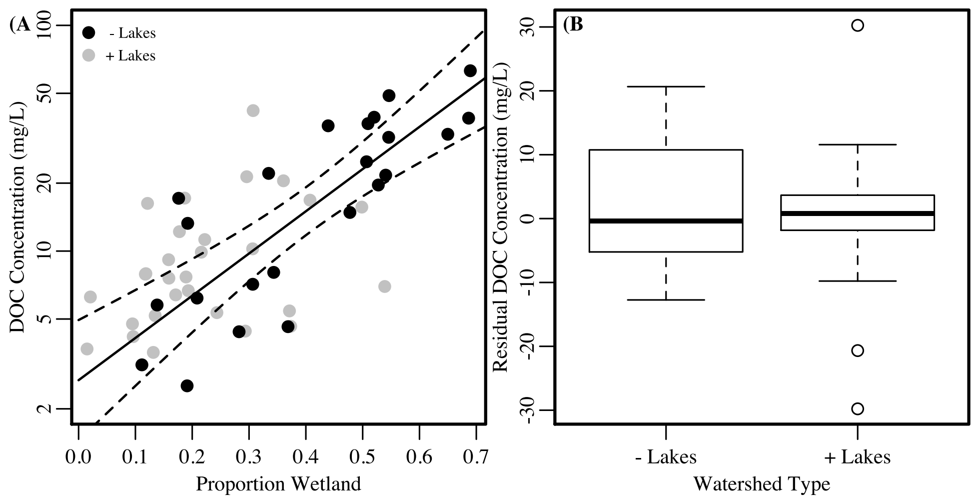

Figure 5. (a) Relationship between wetlands (as percent landcover) and dissolved organic carbon (DOC) concentrations ($F = 41.37$; $df_{1,2} = 1,21$; $r^2 = 0.66$, $p < 0.001$) in –Lake sites. (b) Box plots of residual DOC concentrations after accounting for wetland extent in sites with and without upstream lakes. Box plots show the median, first and third quartiles, whiskers equalling 1.5× interquartile range, and outliers. See text for explanation of residual DOC calculations.

for the 2001 landcover database [*Homer et al.*, 2004] was 98.0% and 84.5% for wetlands [*Wickham et al.*, 2010], suggesting that this was a minor source of uncertainty in the analysis.

[23] If the patterns observed here are representative of other time periods as well, we suggest three possible explanations for the absence of a measurable influence of upstream lakes. First, DOC loading to lakes is a critical, but poorly known component of lake budgets [*Hanson et al.*, 2011] and the amount of carbon processed (e.g., microbial, photo-degredation, sedimentation) by lakes may be offset by additional carbon inputs that are currently unaccounted for. The potential for such inputs into lakes in the region was identified by *Buffam et al.* [2011] in constructing a carbon budget for the NHLD region. Although uncertaintity is high, carbon processing in lakes was estimated to be subtantially greater than the difference between carbon inputs to aquatic ecosystems and hydrologic export out of the region, leading to an apparent imbalance in the current regional carbon budget. This disparity could be explained if critical OC inputs to lakes from either autochthonous or allochthonous sources were excluded or underestimated in the budget. A comparison of the chemistry of lakes and streams in the region indicated that lakes are dominated by precipitation and short flowpaths that may intercept riparian wetlands, which are important sources of DOC to these systems

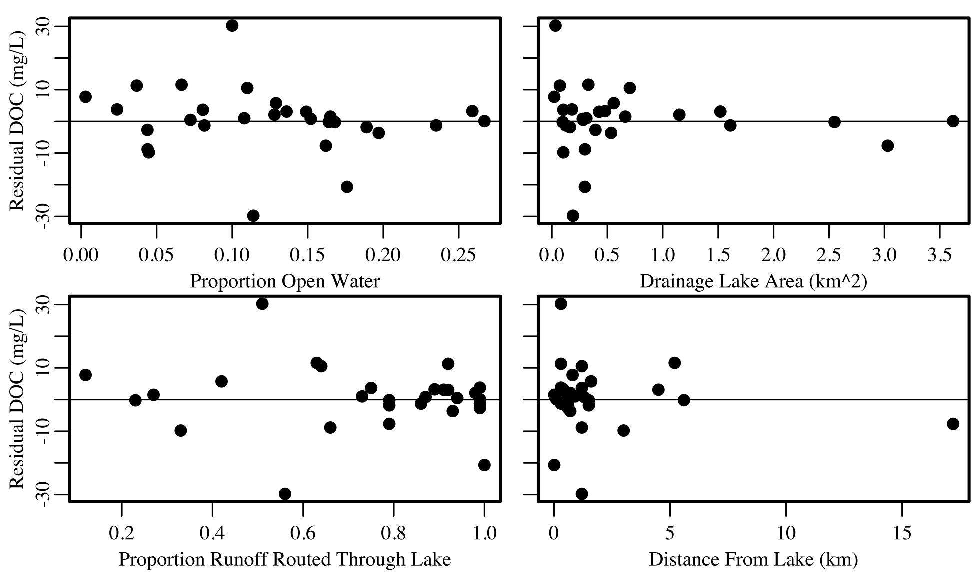

Figure 6. Residuals from the regression of DOC concentration versus percent wetland cover for sites with lakes (+Lake) as a function of the watershed lake extent (%), area of lakes embedded in the upstream drainage (km^2), the fraction of runoff at each site estimated to have passed through an upstream lake (%), and distance to upstream lake from each sampling site (km).

[*Gergel et al.*, 1999; *Hanson et al.*, 2007; *Lottig et al.*, 2011]. On the other hand, streams are dominated by longer groundwater flowpaths that can bypass or short-circuit organic matter-rich wetland soils [*Lowry et al.*, 2007; *Lottig et al.*, 2011]. If riparian wetlands contribute more DOC to adjacent lakes relative to streams, the well-documented carbon processing capacity of lakes may be offset by this additional source of DOC, leading to similar exports of terrigenous carbon from drainage networks with and without lakes.

[24] A second contributor to the apparent lack of evident lake effects of upstream lakes on stream DOC may be related to water residence time in these lakes. Even though previous studies have suggested that drainage lakes have the potential to reduce downstream yields of carbon [*Larson et al.*, 2007], high rates of hydrologic flushing often limit retention opportunities in drainage systems [*Canham et al.*, 2004; *Stets et al.*, 2010]. Using empirically based estimates of OC processing rates, *Hanson et al.* [2011] estimated that the fate of allochthonous OC in lakes would be evenly balanced between retention and export for lakes with an RT of ~2–4 yrs. Similarly, *Weyhenmeyer et al.* [2012] calculated a half-life of 12 yrs for terrestrial OC once it enters the aquatic environment. These findings suggest that a lake signal on downstream DOC would be evident only for lakes with relatively long RTs (e.g., ≥2 yrs). In contrast, the median RT for lakes with outlet streams (i.e., drainage lakes) in the NHLD has been estimated at only 0.77 yrs [*Linthurst et al.*, 1986]. This residence time translates to an estimated reduction of approximately 20% of allochthonous DOC loads [*Hanson et al.*, 2011], which may be too small to detect a lake effect signal at the heterogeneous regional scale. Consequently, if RTs of lakes embedded in drainage networks are in fact too short to exert a substantial influence on downstream DOC, regional patterns in these systems are expected to be driven by loading, as we observed.

[25] Water residence time differences in lakes with and without stream outlets (i.e., drainage and seepage lakes) combined with their regional distribution (36% drainage lakes, 64% seepage lakes; [*Linthurst et al.*, 1986]) suggest a reduced role for drainage lakes in regional aquatic C retention in the NHLD. Fluvial exports of carbon out of the region represent approximately 71% of allochthonous carbon inputs to all surface water bodies, not just inputs to drainage lakes and connecting streams and rivers [*Buffam et al.*, 2011]. On the other hand, seepage lakes may exert a larger influence on this regional carbon retention than drainage lakes because of their greater abundance and expectation of a longer RT due to lack of surface water connections. Assuming regional estimates of an average seepage lake depth of 6 m [*Linthurst et al.*, 1986], precipitation of 0.8 m/yr (based on unpublished data from the National Atmospheric Deposition Program), an evaporation rate of approximately 0.54 m/yr [*Woo and Winter*, 1990], and a water yield of 0.35 m/yr [*Van der Leeden et al.*, 1990], a crude average estimate of RT in these systems would be approximately 3.6 yrs, which would correlate with more than double (50%) the estimated retention capacity (i.e., inputs and outputs of OC) of lakes with stream outlets (20%) [*Hanson et al.*, 2011]. Given that seepage lakes occur twice as frequently in the region and may have double the retention capacity of drainage lakes, a majority of the regional DOC retention could occur in these lakes, and not in drainage lakes examined in this study. However, it is important to note that because a majority of DOC transported out of the region occurs in fluvial networks [*Buffam et al.*, 2011], there may be little opportunity for lakes disconnected from the surface water networks to intercept and process carbon as it is exported out of the region.

[26] Finally, the lack of a measurable influence of lakes on downstream organic carbon in the NHLD may be a function of the scale of this study. Prior studies in the region have been able to identify decreases in DOC concentrations and changes in quality when watershed characteristics were consistent among sites [*Larson et al.*, 2007]. Similar results have also been seen when lake budgets are quantified for individual lakes [*Curtis and Schindler*, 1997]. On the other hand, there is a growing body of literature that suggests, similar to our results, lakes may not always decrease downstream DOC [*Stets et al.*, 2010; *Goodman et al.*, 2011] and results like these may be more common than previously thought. Here, substantial variation in landcover, watershed size, and runoff— regardless of the presence or absence of lakes in drainage networks—likely contributes to the large variation in DOC concentrations and yields. Thus, while a lake effect may be present at a local (i.e., individual-lake) scale or among sites with similar land cover, its absence at the regional scale demonstrates that in the NHLD other factors are more important than lakes for understanding the movement of organic carbon across the landscape at this scale [e.g., *Sobek et al.*, 2007].

[27] Lakes have been emphasized in the global carbon cycle in part because they have the capacity to intercept and process terrigenous OC and ultimately influence export to the world's oceans [*Cole et al.*, 2007; *Downing et al.*, 2006]. However, our results suggest that in a region with substantial OC stores locked in peat and wetland soils (40% of the regional carbon pool; *Buffam et al.* [2011]), lakes with the capacity to intercept and decrease fluvial terrigenous OC exports have no regional effect on base flow DOC stoichiometry, concentration, or yields—at least during summertime base flow conditions, when biogeochemical activities are maximized in aquatic systems. If climate and land-use changes destabilize peatland OC stores [*Limpens et al.*, 2008], drainage lakes situated in OC-rich regions, such as the NHLD, may only minimally reduce the increased terrigenous OC exports to the ocean.

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