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Effects of upstream lakes on dissolved organic matter in streams

James H. Larson and Paul C. Frost
Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana, 46556

Zhiyu Zheng and Carol A. Johnston
Center for Biocomplexity Studies, South Dakota State University, Brookings, South Dakota, 57007

Scott D. Bridgham
Center for Ecology and Evolutionary Biology and Environmental Studies Program, University of Oregon, Eugene, Oregon 97403

David M. Lodge and Gary A. Lamberti
Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana, 46556

Abstract

We examined the effects of upstream lakes on dissolved organic matter (DOM) quantity and the absorbance of ultraviolet (UV) radiation in the streams of northern Michigan. We assessed DOM concentration and absorbance in 15 streams with upstream lakes and 17 streams without upstream lakes located in the same geographic region in May and August 2003. In addition, we estimated watershed land cover and morphology to assess the possibility that other landscape variables could account for DOM differences between the two stream types. The concentration of dissolved organic carbon, its UVB absorbance, and its molar absorbtivity (absorbance per unit carbon) were all significantly lower in streams with upstream lakes than in streams with no lakes. Strong predictive relationships existed between upstream watershed metrics and stream DOM properties, but varied by season and the presence of upstream lakes. DOM quantity and UV-absorbing ability were related to different watershed metrics, with DOM quantity being strongly related to terrestrial watershed metrics, whereas UV-absorbing ability was most strongly related to percent water surface area. Upstream lakes strongly influence downstream DOM potentially because of their long water residence times, which could increase opportunities for DOM processing. Upstream lakes represent a strong landscape predictor of stream DOM properties that is not directly tied to terrestrial DOM sources and processing.

Dissolved organic matter (DOM) in aquatic ecosystems contains a remarkable diversity of organic molecules, ranging from simple carbohydrates to complex chains of aromatic rings (Wetzel 2001). These DOM constituents exhibit a range of physical and chemical properties that vary predictably across a size spectrum of organic molecules (Cabiniss et al. 2000). DOM heterogeneity affects many ecological properties, including physical (absorbance of light; Kirk 1991), chemical (binding of pollutants; Voets et al. 2004), and biological (microbial substrate; Bernhardt and Likens 2002) processes. As a result, DOM properties, including its concentration, are important drivers of aquatic communities (Williamson et al. 1999).

From a landscape perspective, stream DOM concentration (usually expressed as concentration of dissolved organic carbon [DOC]) is generally considered to reflect terrestrial landscape sources of DOM (Gergel et al. 1999; Mulholland 2003), autochthonous production of DOM (Kaplan and Bott 1982), and the diluting effects of low-DOM groundwater (Kaplan and Newbold 1992; Maurice et al. 2002). At broad scales, watershed controls of DOM in aquatic systems have been demonstrated for lakes (e.g., Xenopoulos et al. 2003) and streams (e.g., Mulholland 2003). For example, the proportion of watershed area in wetlands and the watershed slope can explain >50% of the variation in stream [DOC] (Gergel et al. 1999; Mulholland 2003). Such relationships seem mechanistically linked to terrestrial, rather than aquatic, sources and DOM processing (Gergel et al. 1999; Mulholland 2003; Xenopoulos et al. 2003).

Whereas much work has examined how DOM concentration relates to watershed characteristics, little is known about how watershed characteristics relate to other properties of DOM. Stream DOM from terrestrial sources tends to absorb light strongly (Wetzel 2001), suggesting watershed characteristics that predict [DOC] should also predict absorbance. However, photodegradation (Kohler et al. 2002), microbial processing (Qualls et al. 2002), and other factors may significantly reduce the ability of

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DOM to absorb light without significantly changing its concentration. Processes that alter the ability of DOM to absorb light may not be well represented by landscape metrics that describe the source–dilution relationship of DOM quantity. Landscape metrics that reflect aquatic processing may be needed to explain ecologically relevant DOM properties other than concentration, such as light-absorbing ability. For example, streams that originate as outflows from lakes are common in certain regions, but most analyses of watershed controls over DOM properties have not considered this potentially important connection in the landscape (but *see* Frost et al. 2006).

The residence time of the water within an aquatic ecosystem may be a critical determinant of DOM properties (Lindell et al. 1996), because processing agents (e.g., light or microbes) may require considerable time to cause significant changes (days to weeks; Osburn et al 2001; Kohler et al. 2002). Watershed features that slow the passage of water downstream thus increase the potential for DOM to be broken down by those processes. We hypothesize that lakes, by slowing the longitudinal movement of water, act as spatially abrupt transformers of DOM. Compared to free-flowing systems, water emanating from upstream lakes has experienced much greater residence time and, consequently, exposure to processing agents that can influence DOM properties. Autochthonous production of algal and macrophyte DOM also is likely to be greater in lakes because of their lack of vegetative canopies and long residence times (Martin et al. 2005). Such DOM is likely to have lower molecular weight, be less absorptive of light, and have different biodegradability than terrestrially derived humic matter (Kreutzweiser and Capell 2003; Mash et al. 2004). If so, we would predict that DOM concentration and light-absorbing ability would be lower in streams with upstream lakes because of in-lake production and processing of terrestrial DOM. We would also predict that streams with upstream lakes would have weaker relationships between terrestrial watershed properties and stream DOM properties because of (1) a reduction in the amount and quality of terrestrial DOM present because of selective processing within the lake and (2) an increase in the algal and macrophyte DOM component.

The primary objective of this study was to assess whether upstream lakes alter DOM properties in streams. We conducted a survey of streams with and without upstream lakes and compared DOM properties between those stream categories. We also calculated upstream watershed characteristics for both stream categories and related them statistically to stream DOM properties. Our results indicate that stream DOM is strongly influenced by upstream lakes and suggest that the causes and consequences of these effects warrant further study.

Methods

Sampling locations—We sampled DOM in 32 small streams (15 with and 17 without upstream lakes; *see* Table 1, Fig. 1) located in northern Wisconsin and the upper peninsula of Michigan during two periods: 12–15 May and 4–8 August 2003. These streams primarily drain low-gradient watersheds covered by mixed coniferous and deciduous forest. Stream flow in this region typically peaks in April (driven by snowmelt), declines to ~60% of that flow in May, and then to ~15% of April flow by August (Holtschlag and Nicholas 1998). Sampling locations were selected based on the presence or absence of an upstream lake (with a surface-water connection to the stream) and secondarily on accessibility (e.g., near a road crossing). Our criterion for an upstream lake was a permanent body of water with a surface area of >500 m^2 (with most lakes being $>>500$ m^2). Streams with upstream lakes were sampled near the lake outflow (generally <1 km downstream) to ensure that the lake was a significant portion of the upstream watershed (*see* Table 1 for exact distances).

Water analysis—Streamwater was sampled from the middle of the water column at a midstream location. At each site ~100 mL of streamwater was either filtered streamside (May sampling) or stored in coolers and then filtered within 6 h at the University of Notre Dame Environmental Research Center (August sampling). Water was sequentially filtered through a pre-ashed Whatman GF/F filter and a 0.2-μm polycarbonate filter. Polycarbonate filters were rinsed with >50 mL of distilled water before use to remove potential organic contaminants (Yoro et al. 1999). Approximately 50 mL of filtered streamwater for DOM analysis was then stored in amber bottles at 4°C until analyzed.

Dissolved organic carbon (in mg C L^{-1}; [DOC]) of streamwater was measured using a Shimadzu TOC 5000 analyzer. Samples were acidified before analysis using concentrated nitric acid and purged of inorganic carbon. Ultraviolet (UV) radiation Absorbance was measured using an Ocean Optics S2000 UV-VIS spectrometer at ~100 evenly distributed wavelengths between 280 nm and 320 nm. The UV spectrum can be separated into different bands based on energetic quality and biological relevance (e.g., Morris and Hargreaves 1997; Madronich et al. 1998). Here, the UVB band refers to all wavelengths between 280 nm and 320 nm. We averaged the absorbance of wavelengths in the UVB band, which will be referred to hereafter as UVB absorbance. Here and elsewhere in this article we treat UVB absorbance as an index of DOM quantity, both because it has often been used as a metric of colored DOM (Kirk 1994; CDOM) and because the UVB absorbance patterns we observed were similar to our other index of DOM quantity ([DOC]). Furthermore, UVB absorbance was strongly related to [DOC] in our samples (simple linear regression $R^2 = 0.85$, $p < 0.005$).

Molar absorbtivity, defined as UV absorbance per mole carbon (C) (Chin et al. 1994), was calculated by dividing the UV absorbance at a particular wavelength by the concentration of DOM (moles DOC L^{-1}). Molar absorbtivity for each wavelength in the UVB band was then averaged to give a UVB molar absorbtivity for each stream.

Table 1. Coordinates (degrees, minutes, seconds) of streams in northern Wisconsin and Michigan sampled in May and August of 2003. Streams with upstream lakes contain one or more lakes upstream of the sampling location. All streams are first to third order streams at the sampling location.

Stream	Latitude (N)	Longitude (W)	Stream order	Upstream lake	Distance from upstream lake (km)
Baltimore	46°28′44.0″	89°12′06.1″	2	Absent	na
Banner	46°21′41.8″	89°35′50.3″	1	Absent	na
Grosbeck	46°20′10.1″	89°27′51.8″	1	Absent	na
Imp	46°14′10.0″	89°05′12.7″	1	Absent	na
Jackson	46°26′49.4″	89°51′53.7″	1	Absent	na
Marsh Bay	46°08′59.1″	89°02′18.5″	1	Absent	na
Marshall	46°24′29.3″	89°34′06.5″	2	Absent	na
Matheson	46°21′49.5″	89°10′09.0″	1	Absent	na
McGinty	46°19′22.6″	89°01′33.9″	1	Absent	na
Meander Tributary	46°16′59.6″	89°39′56.9″	1	Absent	na
Merriweather	46°34′05.6″	89°39′04.1″	1	Absent	na
Monarch Tributary	46°23′25.0″	89°44′46.8″	1	Absent	na
Morrison	46°17′39.6″	89°04′09.5″	1	Absent	na
Nelson	46°23′51.4″	89°37′48.1″	1	Absent	na
Ontonagon Tributary	46°16′52.6″	89°08′53.5″	3	Absent	na
Presque Isle Tributary	46°22′45.5″	89°46′47.9″	2	Absent	na
Rolston	46°28′40.0″	89°00′28.5″	2	Absent	na
Bass	46°17′56.7″	89°10′16.6″	1	Present	<0.1
Birch	46°08′36.0″	89°09′34.3″	1	Present	1.0
Bluebill	46°18′06.8″	89°34′14.5″	1	Present	<0.1
Buckatabon	46°01′14.6″	89°18′40.8″	2	Present	<0.1
Heart	46°20′58.5″	89°44′05.4″	1	Present	0.63
Kenu	46°08′01.3″	89°18′16.4″	2	Present	0.64
Kildare	46°07′10.3″	89°09′21.8″	1	Present	0.43
Lac Vieux	46°07′19.7″	89°09′18.1″	2	Present	0.39
Morris	46°15′45.0″	89°31′46.1″	1	Present	0.38
Pomeroy	46°17′15.7″	89°34′54.7″	1	Present	0.79
Summit Chain	46°15′42.3″	89°36′44.5″	1	Present	1.3
Tenderfoot	46°15′33.7″	89°32′02.6″	2	Present	3.9
Unnamed Lake Outflow	46°07′38.1″	89°20′52.2″	1	Present	0.25
White Birch	46°05′24.3″	89°18′42.9″	2	Present	<0.1
White Sands	46°05′52.4″	89°36′43.6″	2	Present	0.45

na, not applicable.

Watershed characteristics—Digital basin boundaries were downloaded from the Elevation Derivations for National Applications Viewer (http://gisdata.usgs.net/website/EDNA/viewer.php) to delineate the watershed for sampling locations. Manual editing using a digital topographic map background was used to adjust watershed boundaries in areas where subtle topography confused the automated delineation application. The area and perimeter for each basin were calculated with ESRI ArcGIS 8.3. The elevation layer from the National Elevation Dataset (http://seamless.usgs.gov/) was clipped with the basin boundary to obtain the minimum, maximum, average, and standard deviation of the elevation and slope of the basin.

To determine watershed land cover, we downloaded a national land cover dataset (NLCD) map from the U.S. Geological Survey (http://landcover.usgs.gov/natllandcover.asp). Using ArcGIS 8.3, the NLCD map was clipped with the basin boundary to calculate the areas for each land use. Areas of water (including streams, lakes, and any other water bodies with <25% vegetative cover), evergreen forest, woody wetlands, and emergent herbaceous wetlands for each basin were calculated as percentages of total watershed area (additional descriptions of these categories are available in Cowardin et al. 1979). Watershed morphology was determined using national hydrography dataset (NHD) maps (http://nhd.usgs.gov/). The NHD route drain layer was clipped with the basin boundary, the length for the stream/river and the artificial path (in the lake) in each basin were calculated, and then drainage densities were calculated based on NHD.

Data analysis—We analyzed the differences in DOM properties between the stream categories across time using a repeated-measures analysis of variance (ANOVA), with a factor of upstream lake presence (lakes or no lakes) sampled through time (May and August). To meet ANOVA assumptions, we natural log-transformed DOM concentration and arc-sine square-root transformed UVB absorbance (Zar 1999). We also performed a multiple analysis of variance (MANOVA) comparing all of our watershed properties between categories. To meet assumptions, we natural-log transformed morphological data and arc-sine square-root transformed landcover variables measured as proportions (Zar 1999). Because the MANOVA

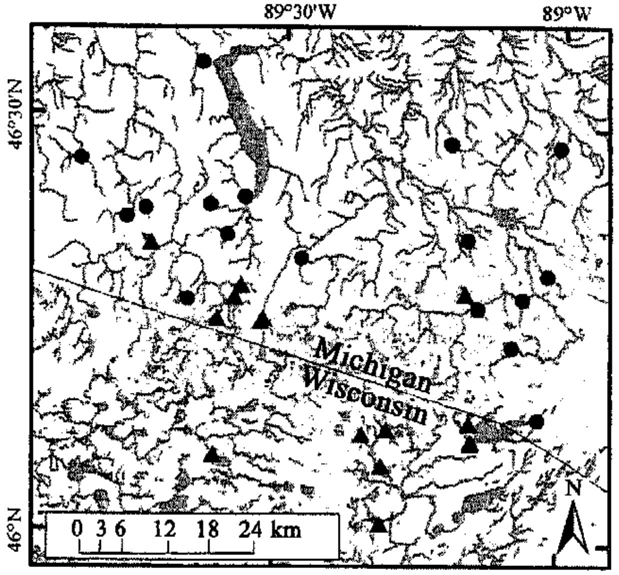

Fig. 1. Map of stream sites used in this study. Grey represents water bodies (streams and lakes). Triangles represent streams with upstream lakes, and circles are those without upstream lakes. Streams are identified in Table 1.

was significant, we ran univariate ANOVAs on each watershed characteristic. ANOVA and MANOVA were conducted using SYSTAT version 10 (SPSS 2000).

We further examined the effect of lakes relative to other watershed metrics by using Akaike's corrected information criterion (AIC_c; used instead of AIC for analyses with low data point-to-variable ratios; Burnham and Anderson 1998) to find the best models from among all candidate models. AIC (and AIC_c) are model selection tools with substantial benefits as compared with the more traditional multiple regression approaches (*see* Burnham and Anderson 1998). Whereas multiple regression attempts to find the best fit between an assumed model and data by adjusting coefficients, AIC selects from among numerous models those few that best fit the data with the fewest number of variables (Burnham and Anderson 1998). We included, as candidate models, all possible linear combinations of our transformed watershed metrics. AIC values were calculated using SAS 8.2 (SAS Institute) and then transformed to AIC_c values as described by Burnham and Anderson (1998). We then calculated the AIC_c differences (ΔAIC_c) across all of the candidate models (Burnham and Anderson 1998). After convention, we considered all models with a ΔAIC_c value of <2 to have substantial support (Burnham and Anderson 1998) and then considered them in greater detail. This procedure was done three times for each DOM property: (1) for all streams, (2) for streams without upstream lakes, and (3) for streams with upstream lakes.

To test whether lake area was a significant predictor of [DOC] (relative to other potentially important landscape predictors), we first conducted our model selection procedure with all streams included. We used this all-stream inclusive analysis to assess how much variation in DOM properties was explained by each of the categorically different watershed metrics. To do this, we calculated the partial R^2 of each watershed metric when it appeared in the supported models for all of the streams combined.

We repeated our model selection procedure for each stream category separately (with and without upstream lakes) to assess whether upstream lakes altered the ability of watershed metrics to explain DOM properties. We calculated the mean total R^2 values for all of the supported models from each category as well as the mean partial R^2 values for each watershed metric.

Results

Categorical DOM differences—DOM properties measured in May and August varied broadly within stream categories, but also revealed statistical differences between categories and dates (Fig. 2). Stream categories (upstream lakes or no upstream lakes) differed for [DOC], UVB absorbance, and UVB molar absorbtivity, with all measured DOM concentrations and molar absorbtivities being lower in streams with upstream lakes. In addition, we found significant differences between sampling dates for [DOC], UVB absorbance, and UVB molar absorbtivity, which appear to be a result of a systemwide decline in DOM concentrations and absorbance from May to August. We found a significant interaction between stream category and sampling date for UVB absorbance caused by much greater declines in streams without upstream lakes than in streams with upstream lakes during the summer (Fig. 2, *see* Web Appendix 1: http://www.aslo.org/lo/toc/vol_52/issue_1/0060a1.pdf for raw data).

Categorical watershed differences—Of our eight watershed metrics, three (percent surface water, percent evergreen forest, and watershed area) differed significantly between stream categories (Table 2). The first of these, percent surface water, was related to the defining characteristic of our survey and was the presumed cause of the DOM differences between categories. Categorical differences in percent evergreen and watershed area are potentially confounding if these watershed properties are also important predictors of DOM properties. Alternatively, if percent evergreen and watershed area are not strongly related to DOM properties, then the observed categorical differences (as documented) can be more confidently attributed to percent surface water (i.e., the effect of lakes).

The frequency with which these three factors (percent surface water, percent evergreen forest, and watershed area) appear in the AIC_c-supported models in the analysis involving all streams varied by season (Table 3). In our May sampling, surface water was by far the more important explanatory variable of the three that differed between categories. Surface water appeared in all models for all DOM properties and explained a considerable amount of variation in these models (mean partial R^2 between 0.16 and 0.39). However, in August, percent evergreen forest also was important in predicting [DOC] (all five models) and UVB absorbance (9 of 16 models), whereas surface water and watershed area were important in UVB absorbance models (7 and 10 of 16 models, respectively). Overall the ability of surface water to explain

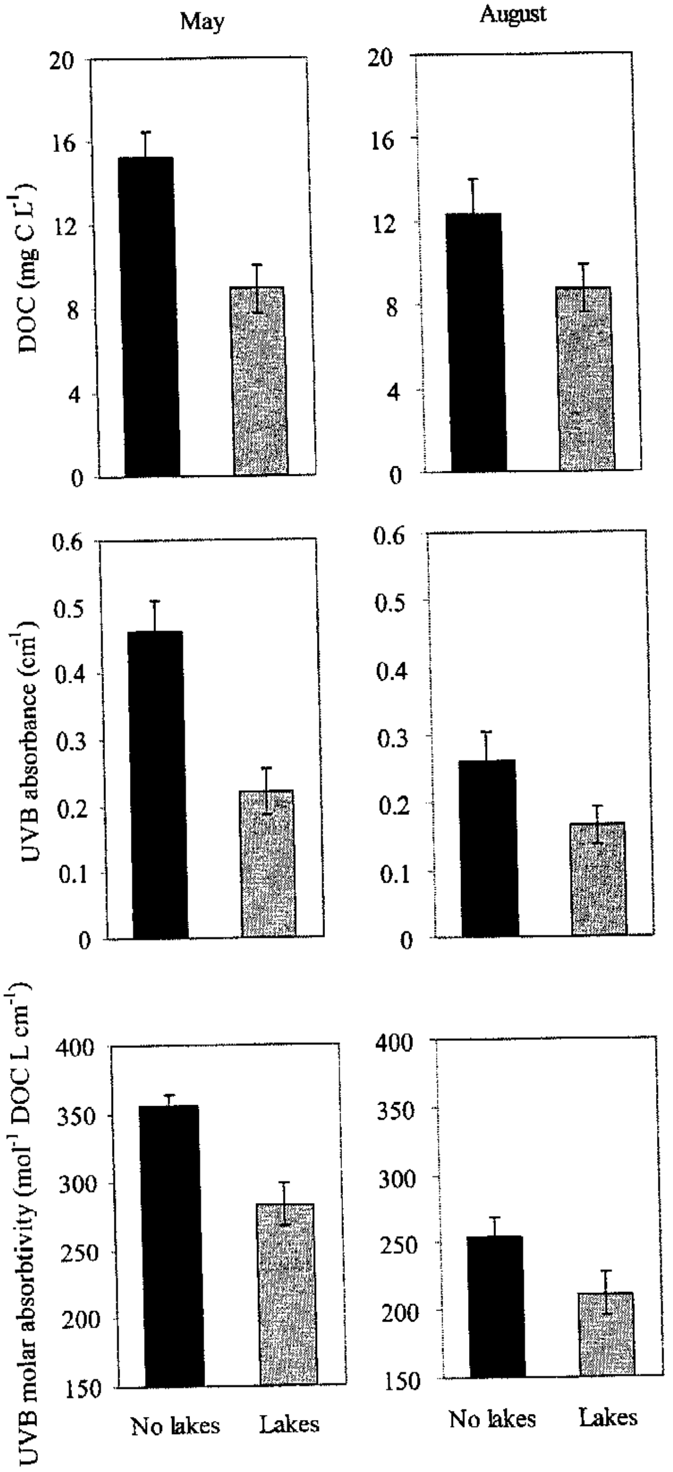

Fig. 2. Mean values (±SE) for DOM properties in streams with lakes (n = 15) and without upstream lakes (n = 17) located near the Michigan–Wisconsin border. Repeated-measure ANOVAs revealed significant differences between stream categories for [DOC] ($p = 0.014$), UVB absorbance ($p = 0.002$), and UVB molar absorbtivity ($p = 0.014$). The effect of sampling date was also significant for these variables ($p = 0.04$, <0.0005, and <0.005, respectively), with a significant interaction occurring for UVB absorbance ($p = 0.001$).

Table 2. Mean (SE) watershed characteristics for streams with upstream lakes and without upstream lakes. Surface water, evergreen, woody wetlands, and herbaceous wetlands refer to designations used in the NLCD. Bold denotes statistically significant differences.

Variable	No lakes	Lakes	p value (ANOVA)
Watershed area (km^2)	90.50 (22.69)	202.92 (47.91)	**0.046**
Drainage density (km^{-1})	0.22 (0.05)	0.17 (0.09)	0.176
Watershed slope (degrees)	2.75 (0.29)	2.42 (0.15)	0.335
Percent surface water	1.59 (0.498)	12.39 (1.44)	**<0.005**
Percent evergreen forest	7.90 (1.69)	12.93 (1.61)	**0.005**
Percent woody wetlands	17.53 (2.72)	16.88 (2.15)	0.734
Percent herbaceous wetlands	2.78 (0.43)	4.00 (0.62)	0.342
Percent agriculture	4.45 (1.86)	1.45 (0.22)	0.614

variation in DOM properties greatly declined in August (mean partial R^2 between 0.02 and 0.20).

Watershed models of [DOC] and UVB absorbance—Results from our categorical analysis demonstrated that streams with upstream lakes had significantly less [DOC] and lower UVB absorbance. This indicates that the presence of upstream lakes reduced the quantity of DOM in outflowing streams. With our second AIC$_c$ analysis, we separately examined the relationships between landscape variables and DOM in streams with upstream lakes and in streams without upstream lakes. This analysis had two primary implications. First, the variation in upstream surface water for streams without upstream lakes was drastically reduced (because no lakes were present). Second, the effect of variation in lake presence was removed for our streams with upstream lakes (because all streams had upstream lakes). Therefore, in streams without upstream lakes, we would expect to find no effect of surface water (because no upstream lakes were present). In streams with upstream lakes, the effect of water surface area should reflect relative lake size (because upstream lake presence/absence is no longer variable).

Upstream lakes did not appear to strongly affect relationships between watershed characteristics and DOM concentration. In May, strongly supported models (with a ΔAIC$_c$ of <2) explained an average of 59.2% (± 0.7% SE) of the variation for streams with lakes and 57.3% (± 2.9%) of the variation in [DOC] in streams without upstream lakes (Fig. 3). Percentage woody wetlands was the most commonly occurring predictor variable for [DOC], occurring in all models for both stream categories. Woody wetlands also appeared in all models relating UVB absorbance to watershed metrics in May, and those models explained 62.7% (±0.7%) and 71.2% (±0.8%) of variation in streams with and without lakes, respectively (Fig. 3).

Table 3. Information on the likelihood that three variables caused the observed differences in DOM properties between streams with or without upstream lakes. Listed are the number of models with a ΔAIC_c of <2 (and average R^2), below which is the number of those models that included the individual variable (and its average partial R^2). All three variables differed between categories and had a negative relationship to all measured DOM properties when significant. Much of the variation in DOM properties was explained by variables that did not differ between stream categories. Note that in May both evergreen forest and watershed area do not appear to influence DOM properties and so are unlikely to cause categorical differences in those properties. In August, the percent evergreen forest and watershed area do appear to be influencing DOM quantity and may be driving categorical differences in those properties.

	May			August		
Watershed metric	[DOC]	UVB absorbance	UVB molar absorbtivity	[DOC]	UVB absorbance	UVB molar absorbtivity
Number of models	6 (0.61)	4 (0.66)	5 (0.59)	5 (0.52)	16 (0.38)	9 (0.34)
Surface-water area	6 (0.16)	4 (0.21)	5 (0.39)	2 (0.02)	7 (0.07)	9 (0.20)
% Evergreen forest	2 (0.01)	1 (0.02)	0	5 (0.27)	9 (0.15)	4 (0.04)
Watershed area	0	0	1 (0.02)	5 (0.10)	10 (0.10)	1 (0.03)

In August, the variation in [DOC] and UVB absorbance explained by the best models generally declined, and different watershed metrics were important. In streams with no lakes, [DOC] was most influenced by percent evergreen forest (in all models) and was also strongly influenced by percent herbaceous wetlands (a positive relationship in all models). In streams with lakes, [DOC] was positively affected by the presence of herbaceous and woody wetlands. Watershed metrics explaining UVB absorbance also differed between categories. Percent herbaceous wetlands appeared in all four supported models for streams with upstream lakes, whereas percent woody wetlands and watershed area were present in all five supported models describing UVB absorbance in streams without upstream lakes.

Watershed models of UVB molar absorbtivity—As with DOM quantity, we saw significant categorical differences in UVB molar absorbtivity. Although this effect can be attributed to the presence of upstream lakes, we were also interested in (1) how upstream lakes altered the relationship between UVB molar absorbtivity and other watershed characteristics and (2) how differences in the relative size of upstream lakes altered UVB molar absorbtivity.

Models relating watershed characteristics to UVB molar absorbtivity in May were different between streams with and without upstream lakes (Fig. 3). The most important predictor variable for streams with upstream lakes was the percent surface water in the watershed (i.e., the relative lake surface area), which was present in all of the strongly supported models. In streams without upstream lakes, the percent woody wetlands was the most important variable (present in all models). The variation explained by these models differed considerably as well, with more variation explained in streams without upstream lakes ($R^2 = 0.67 \pm 0.02$) than in streams with upstream lakes ($R^2 = 0.42 \pm 0.08$).

We found different relationships between UVB molar absorbtivity and watershed characteristics in our data from the August sampling. The watershed metrics that explained the most variation remained the same for streams with upstream lakes (percent surface water appears in all models) but the most important watershed metrics describing UVB molar absorbtivity in streams without upstream lakes were the percent woody wetlands (appearing in all models) and the percent agriculture (appearing in three of four models). However, the ability of all the August models to explain variation in UVB molar absorbtivity greatly declined as compared to May, and no categorical differences were apparent in mean total R^2.

Discussion

We found strong evidence that DOM properties differed between streams with and without upstream lakes in their watershed. Specifically, the quantity (as [DOC]) and light-absorbing capacity of DOM was lower in streams with upstream lakes than in streams lacking upstream lakes. An initial question to consider is why DOM properties might differ between stream categories. Two nonexclusive possibilities exist: (1) upstream processing of DOM differs between categories and (2) sources of DOM differ between categories. DOM processing occurs via a variety of biotic and abiotic mechanisms, many influenced by water (and thus DOM) residence time (Tranvik and Bertlisson 2001). For streams of comparable size, water in streams with upstream lakes will have longer upstream residence times in the watershed than water in streams without lakes. Consequently, DOM would presumably experience more processing in streams having greater areas of surface water in their watersheds. The sources of DOM will likely also differ between streams with and without upstream lakes. Organic matter entering north temperate forested streams is often dominated by terrestrial inputs (Hinton et al. 1998; Elder et al. 2000) but lake algal or macrophyte production in upstream lakes may contribute significant quantities of DOM to outflowing streams (Martin et al. 2005). Upstream algal blooms have previously been observed to contribute significant quantities of DOM to streams (Kaplan and Bott 1982), but we are unaware of any study that has linked upstream lake productivity with DOM quantity in outflowing streams. In addition, there are other explanations for these observed differences. For one, lakes may collect low DOM snowmelt during spring months and release this

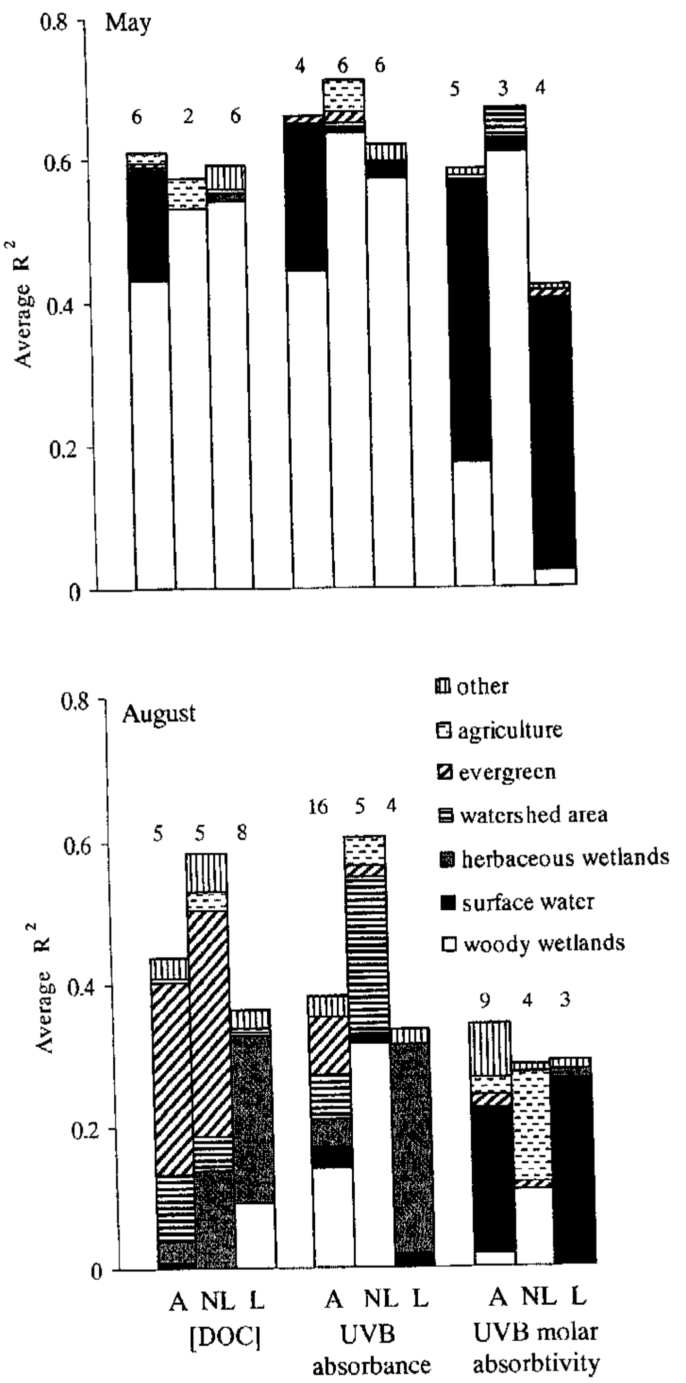

Fig. 3. The average variation in DOM properties explained (R^2) by models with $\Delta AIC_c < 2$ for streams with lakes (L), with no lakes (NL), or with all streams together (A). Numbers over bars refer to the number of strongly supported AIC_c models. Partial R^2 was calculated by averaging the variation explained by each variable. All correlations were negative except for herbaceous and woody wetlands. The Other category includes drainage density and slope, which never explained >5% of the variation in any model.

water throughout the summer. Outflowing streams would thus potentially have lower DOM than nonoutflow streams that would be receiving water passing through shallow and organic rich soils. Lakes in this region could also receive a greater proportion of their incoming water from deep groundwater known for low DOM (Kaplan and Newbold 1992). Another possibility is that there are other unmeasured differences in the watersheds of streams with and without upstream lakes (e.g., categorical differences in soil carbon : nitrogen ratio).

The importance of upstream lakes on watershed-level DOM relationships may be accentuated in our study because our streams with upstream lakes were sampled close to the lake outflow (most <1 km). In other words, if upstream lakes have a relatively small capacity to influence DOM properties compared to other watershed variables, then detecting it over larger spatial scales may be difficult. Although we found categorical differences in DOM properties, lake surface area was generally not the most important predictor of DOM quantity, but was a strong predictor of UVB molar absorbtivity. We are unaware of any other landscape-DOM studies that have identified upstream lakes as a significant predictor of DOM quantity. However, Frost et al. (2006) found a significant relationship between upstream lakes and UV molar absorbtivity in the same region as this study. The inability of that study to detect an effect of lake area on DOM quantity may have resulted from lower variability in percent surface water. Our study was explicitly designed to assess the effect of upstream lakes and included greater contrasts in percent surface water, which enabled us to detect the effect of upstream lakes on DOM quantity and absorbtivity.

Effect of upstream lakes on DOM quantity—We hypothesized that upstream lakes would act as a location of aquatic breakdown of DOM. The results of our categorical comparison are consistent with this hypothesis, but we cannot rule out other possible watershed factors that might differ categorically. We identified two such factors (percent evergreen forest and watershed area) within our watershed data. If these variables never appeared prominently in models relating upstream watershed characteristics to DOM quantity, then we could reasonably (but not conclusively) dismiss those variables as unimportant to categorical differences in DOM. In May, such a dismissal appears justifiable because these variables minimally contributed to the best models. In August, however, these variables emerge as significant predictors, although the amount of variation explained is relatively low. Why should these relationships change so markedly with season? We can think of at least two important attributes of this system that likely changed from May to August—discharge and biotic activity. In May, streamflow was relatively high and likely included substantial surface-water inputs as overland flow from the surrounding forest. In August, streams were at or near baseflow, suggesting that flow was dominated by deep groundwater inputs (Allan 1995; Holtschlag and Nicholas 1998). Near-surface flowpaths, which likely were more prominent in the much wetter May, are probably a much greater source of DOM to streams than is groundwater (Kaplan and Newbold 1992; Elder et al. 2000). The reduction (or elimination) of these near-surface flowpaths by August could have reduced DOM moving from woody wetlands to streams, thus reducing the importance of wetlands as a source of DOM.

Whereas the water flow diminished from May to August, the biotic activity of forests probably increased from May to August, which could have had several effects. One possibility is that evergreen forests have higher water use in August, exacerbating already low flow through near-surface pathways. Wei et al. (2005 and citations therein) reviewed the effects of forests on streamflow, demonstrating that forests can significantly reduce stream and overland flow. The diminishing streamflow could be reflected in the landscape variable of percent evergreen forest, which became increasingly important in predicting DOM quantity in August.

Interestingly, when our categories were analyzed separately, DOM quantity was not strongly related to percent surface water. This is not entirely unexpected for streams without upstream lakes because, without upstream lakes, the remaining variation in percent surface water is low. However, we also saw no relationship between DOM quantity and percent surface water in streams with upstream lakes, despite a range of lake sizes. Clearly this suggests that it is the presence of lakes, and not the surface area, that is important in determining DOM quantity. One explanation is that the difference between water residence time in small lakes and streams is significant, but that the removable DOM is then exhausted, and subsequent increases in water residence time are unimportant. Yet molar absorbtivity was strongly related to lake surface area, suggesting the DOM pool remains reactive.

Another explanation is that variation in water residence time between lakes may not be strongly correlated to lake surface area. Other factors (i.e., volume or morphology) can also strongly influence water residence times. Molar absorbtivity, on the other hand, may be strongly related to lake surface area because its variation is driven by photodegradation. Lake surface area would then be linked to light exposure. This indicates a difference between the controls over DOM quantity and absorbing ability.

Effect of upstream lakes on UVB molar absorbtivity— Differences between the controls of DOM concentration and its ability to absorb light have been hypothesized previously (Curtis and Schindler 1997; Molot and Dillon 1997) and also documented (Reche and Pace 2002). Differences could exist because the light-absorbing capacity of DOM often declines at a faster rate than its concentration (Molot and Dillon 1997; Reche and Pace 2002). In May, the watershed metrics that predicted UVB molar absorbtivity were similar to those for DOM quantity, but by August different predictors emerged and predictive power declined. Reche and Pace (2002) found that the cumulative seasonal dose of solar radiation, by photobleaching DOM, significantly affected molar absorbtivity but not [DOC]. Similarly, watershed metrics that could reflect the dose of solar radiation entering the system, such as percent surface water, might be expected to influence molar absorbtivity but not [DOC]. In our study, percent surface water remained an important predictor of UVB molar absorbtivity from May to August. Total UVB absorbance, however, was more tightly linked to [DOC] and the variables describing its concentration.

Effects of lakes on watershed-DOM models—In addition to differences in DOM properties between streams with and without upstream lakes, we also hypothesized that the relationships between watershed characteristics and DOM properties would be affected by upstream lakes. Our categorical results demonstrated that upstream lakes reduced DOM in outflowing streams. By separately analyzing relationships between upstream watershed properties and DOM properties in streams with and without upstream lakes, we could investigate the effect of lakes on such relationships. This effect could be caused by the removal or alteration of terrestrial DOM by lakes, leading to reduced power of terrestrial watershed metrics to predict DOM properties. Lakes, by having long water residence times, also slow the movement of water through the watershed. If relationships between watershed metrics and DOM properties vary with season in streams, then lakes may temporally disrupt these connections by delaying the downstream movement of water. For example, water entering streams from flooded wetlands in spring may be retained for months or years in a lake before being released downstream.

Indices of DOM quantity ([DOC] and UVB absorbance) were best explained by watershed metrics representing terrestrial sources and processing of organic matter. Watershed metrics that distinguish among water sources that are DOM-rich or DOM-poor have been used by others to predict [DOC] (Gergel et al. 1999; Xenopoulos et al. 2003) and also appear to be useful in our models. These watershed models, however, appear to lose predictive power in streams with upstream lakes over the growing season. These patterns are consistent with our hypothesis that lakes remove or alter terrestrial DOM, because the processes that affect DOM quantity (biotic uptake and photoreactions) are likely to be more prominent in August than in May.

The ability of DOM to absorb UVB radiation appears to be dominated by a source-breakdown relationship. In streams with upstream lakes, the lakes themselves appear to be an important site of aquatic DOM breakdown. However, by late summer models explaining UVB molar absorbtivity appear to lose much of their explanatory power. This decline in explanatory power during the summer may reflect reduced terrestrial inputs of highly absorbtive DOM, increased biotic transformation, and enhanced photodegradation. Additional work is needed to assess the relative importance of these processes in determining the UVB molar absorbtivity.

We found that DOM was lower in quantity and UV-absorbing ability in streams with lakes in their watershed. Furthermore, upstream lakes appear to act as a sink for terrestrial DOM and as a reducer of the UVB molar absorbtivity of DOM in outflowing streams. Future research should address the implications of these differences to stream biota. First, how do differences in DOM properties affect downstream aquatic microbial communities? DOM that has passed through a lake may be less labile, because considerable biotic processing has already occurred. Alternatively, terrestrial DOM may be more labile if extensive photo-processing in lakes leads to greater bioavailability (Tranvik and Bertilsson 2001; Biddanda and Cotner 2003) or if algal DOM production is considerable. Second, what are the implications of reduced UVR-absorbing capacity for UVR dosage to downstream communities? DOM is one of the primary controls of UVR attenuation within lakes and streams (Xenopoulos and Schindler 2001; Frost et al. 2005), and thus reduced [DOC] or molar absorbtivity in streams with upstream lakes may significantly increase the UVR dose to benthic stream organisms, with possibly deleterious effects.

For DOM dynamics in north-temperate forested watersheds, our results suggest a complex interaction between terrestrial and aquatic environments that is mediated by lake–stream connections. If terrestrial inputs of material to streams, other than DOM, are similarly influenced by upstream lakes, then we can expect streams with and without upstream lakes to differ across a wide range of properties. Streams with upstream lakes also display unique temperature and nutrient regimes controlled by physical, chemical, and biological processes in the lake (Benenati et al. 2000; Martin et al. 2005). Our study of DOM demonstrates another system variable that can be strongly influenced by lake–stream connections in the landscape.

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