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Landscape-scale regulators of water transparency in mountain lakes: implications of
projected glacial loss

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ABSTRACT

We examined factors regulating water transparency in a set of 33 lakes located in the Canadian Rocky Mountains. Eighteen lakes had catchments that included glaciers and 15 did not. In each lake, we quantified mid-summer attenuation rates for three ultraviolet wavelengths and photosynthetically active radiation, and measured chromophoric dissolved organic matter (CDOM) absorbance, turbidity, and chlorophyll *a* fluorescence. We also used GIS to quantify characteristics of lake catchments. Across lakes, turbidity and CDOM absorbance were arrayed on orthogonal gradients that intersected in a region of low turbidity and low CDOM absorbance. Nonglacially-fed lakes had low turbidity and attenuation rates were regulated by CDOM absorbance, which increased with the percentage of the catchment covered by vegetation. Glacially-fed lakes had low CDOM absorbance and attenuation rates increased with turbidity, which increased with the percentage of the catchment covered by permanent ice. Glaciers are retreating rapidly in the Canadian Rockies. As catchments become deglaciated, turbidity will likely decrease and the regulator of lake transparency is likely to switch to CDOM, which will have broad implications for lake ecosystems.

INTRODUCTION

Water transparency has important physical, chemical, and biological effects on lake ecosystems. Transparency influences lake thermal structure, vertical distributions of phytoplankton and zooplankton, foraging rates of top predators, and ultimately lake productivity (reviewed by Williamson et al. 2009). In turn, transparency reflects the connection between lakes and their catchments because it is largely determined by inputs of terrestrially-derived material (Belzile et al. 2002; Gallegos et al. 2008; Rose et al. 2014). One consequence of this aquatic-terrestrial linkage is that transparency, particularly within the UV range, is highly sensitive to environmental conditions that vary across both space and time. Specifically, climatic conditions such as precipitation interact with characteristics of lake catchments to affect inputs of material that influence transparency. Thus water transparency is a powerful sentinel of environmental change (Adrian et al. 2009; Williamson et al. 2014).

In most temperate lakes, transparency is regulated primarily by the concentration of chromophoric dissolved organic matter (CDOM: Morris et al. 1995; Arts et al. 2000; Read and Rose 2013). CDOM is derived from terrestrial vegetation in the surrounding catchment and affects transparency by absorbing incoming radiation as a decreasing function of wavelength (Williamson et al. 1996; Rae et al. 2001). Absorbance also decreases with CDOM age as a result of photobleaching (Morris and Hargreaves 1997; Del Vecchio and Blough 2002). Another factor that can influence transparency in some lakes is the presence of suspended inorganic particles, particularly sediments that affect turbidity (Hylander et al. 2011; Rose et al. 2014). These particles are brought in from sources within the catchment through erosion and reduce transparency by scattering

incoming radiation rather than absorbing it (Gallegos et al. 1990). Unlike patterns of light absorption by CDOM, the scattering by inorganic particles is not as strongly wavelength-dependent (Belzile et al. 2002).

Mountain lakes offer an ideal opportunity to examine landscape-scale factors that influence water transparency. Over small spatial scales, mountain lake catchments can vary widely in vegetation coverage and may also include glaciers that serve as an important source of suspended particles in the form of fine rock flour delivered to lakes through meltwater streams (Clifford et al. 1995). In addition, mountain lakes vary widely in transparency and include some of the most transparent lakes in the world (Laurion et al. 2000; Rose et al. 2009a; Gall et al. 2013). To date, much of the research regarding effects of CDOM and turbidity on the transparency of mountain lakes has emphasized the importance of one main regulator for a given lake or set of similar lakes. For example, CDOM absorbance was the best predictor of UVR transparency in 26 lakes in the Alps and Pyrenees (Laurion et al. 2000). In contrast, Rose et al.'s (2014) study indicated that turbidity was the main regulator of water transparency in 18 lakes glacially-fed lakes in Chile, New Zealand, and the U.S. and Canadian Rocky Mountains. Because these previous studies have focused on lakes within a single catchment type, little is known about the nature of the relationships between CDOM, turbidity, and transparency across lake types, or how these potential transparency regulators are influenced by the presence of glaciers in the catchment. Quantifying these relationships within a single region in both glacially and nonglacially-fed lakes will provide important insights into potential consequences of climate change on mountain lake ecosystems, particularly the projected

loss of glaciers and advance of vegetation (Vinebrooke and Leavitt 2005; Vinebrooke et al. 2010; Sommaruga 2015).

In this study, we examined spatial variation in transparency across a set of 33 lakes in the Canadian Rockies that were selected to include roughly equal numbers of lakes with and without glaciers in their catchments. We measured light attenuation for three ultraviolet wavelengths (305, 320, and 380 nm) and photosynthetically active radiation (PAR) in each lake, and related attenuation rates to measures of CDOM absorbance in filtered lake water, turbidity, and chlorophyll *a* fluorescence. To better understand regulators of variation in these measures, we also quantified characteristics of lake catchments using GIS. Our objective was to examine the relationships between land cover characteristics, CDOM absorbance, turbidity, and ultimately water transparency.

METHODS

Study Sites

The 33 lakes in our study were located within the boundaries of Banff and Yoho National Parks, in Alberta and British Columbia, Canada, respectively (Table S1). Fifteen of the lakes were classified as nonglacially-fed and 18 lakes were classified as glacially-fed based on the presence or absence of a glacier in the catchment (assessed by catchment characterization as described below). Lakes were located across montane, subalpine and alpine zones over an elevation range of 1300 to 2423 m asl. Physical characteristics also varied widely with a surface area range of 1.5 - 275 ha and maximum depth range of 2.4 - 84.0 m. Glacially- and nonglacially-fed lakes did not differ in elevation ($\bar{X} \pm 1$ SE: glacially-fed = 1995 ± 64 m, nonglacially-fed = 2103 ± 80 m, t-test:

$t_{31} = 1.06$, $p = 0.29$), but glacially-fed lakes were larger (glacially-fed = 60.0 ± 16.4 ha, nonglacially-fed = 11.8 ± 12.9 ha: t-test with unequal variance: $t_{18} = 2.87$, $p = 0.01$) and deeper (glacially-fed = 32.7 ± 5.7 m, nonglacially-fed = 14.7 ± 10.6 m: t-test: $t_{31} = 2.83$, $p = 0.008$). Bow, O'Hara, Louise, Moraine, Herbert, and Waterfowl had low levels of development within their catchments (e.g. lodges, hotels, picnic areas, or campgrounds) and all other lakes had undeveloped catchments.

Lake Sampling

All lakes were sampled during the ice-free season between late June and early September in 2013 or 2014. Nineteen of the lakes were sampled in 2013. In 2014, we sampled 14 additional lakes along with six of the 19 lakes that had been sampled the year before. Samples and measurements were collected between 1000 and 1400 from a boat anchored at or near the deepest part of the lake. We quantified water transparency using a cosine corrected submersible radiometer (Biospherical Instruments Inc., San Diego, CA). While being lowered slowly through the water column from the surface to the bottom or a depth of 20 m, this instrument simultaneously measured depth and downwelling irradiance of three UVR wavelengths (305, 320, and 380 nm, measured as midpoint of 8-10 nm wide bands encompassing >50% peak response within the band) as well as photosynthetically active radiation (PAR: 400 - 700 nm) at approximately 0.25 second intervals. Diffuse attenuation coefficients (K_d) were estimated for each wavelength as the slope of the log-linear portion of the irradiance vs. depth relationship.

In each lake, we also measured turbidity and chlorophyll *a* fluorescence as a function of depth using an EXO2 multiparameter sonde (YSI Inc., Yellow Springs OH).

Chlorophyll *a* was measured at 1-second intervals in relative fluorescence units (RFU) from the surface to the bottom or to a depth of 50 m. To correct for temperature-dependence of chlorophyll *a* fluorescence, we followed YSI's recommendation to increase raw fluorescence values by 1.1% per °C using temperatures measured simultaneously with the sonde. Turbidity was quantified optically with a nephelometric turbidity sensor calibrated at standards of 0 and 100 nephelometric turbidity units (NTU). For both turbidity and chlorophyll *a*, measurements were averaged for each 0.5 m depth interval. For comparisons across lakes, we calculated the average of these depth intervals from the surface to the interval that included the depth at which 1% of surface UV_{320} remained (which was estimated from K_{d320} as described above). By restricting our estimates to the 1% depth for 320 nm, each lake's chlorophyll *a* and turbidity was estimated for that portion of the water column that most influenced transparency.

To quantify CDOM absorbance, we collected 500 ml water samples from a depth of 0.5 m. Within 24 hours, samples were filtered through pre-ashed Whatman GF/F filters, wrapped in foil and stored in a refrigerator until shipment. At the end of the sampling season, samples were shipped overnight on ice to an analytical laboratory at Miami University. Following Williamson et al. (1999), we used dissolved absorbance (m^{-1}) at 320 nm (a_{320}) as an indicator of CDOM concentration. We chose this measure to represent terrestrial carbon inputs over direct quantification of dissolved organic carbon (DOC) concentration because a prior study of alpine lakes in the region indicated that DOC can include a substantial nonchromophoric component of autochthonous carbon (Parker et al. 2008). Furthermore, the relative contribution of autochthonous vs. allochthonous carbon to DOC varies as a function of elevation in mountain lakes (Rose et

al. 2015). Using a Shimadzu UV/Visible UV-1650 PC spectrophotometer, we calculated corrected dissolved absorbance values by subtracting a Milli-Q water blank and the average absorption from 775 to 800 nm from raw absorbance values for a given water sample. Napierian dissolved absorption coefficients were then calculated as $a_{320} = (2.303 * D) / r$, where D is the decadal optical density value from the spectrophotometer and r (m) is the path length of the quartz cuvette.

We did not collect water samples for CDOM analysis in four of the lakes sampled in 2013. For these lakes, we were able to estimate CDOM absorbance (a_{320}) indirectly because we used the EXO 2 sonde to collect depth profiles of fluorescing dissolved organic matter (fDOM) and relative fluorescence in all 19 lakes concurrently with turbidity and chlorophyll a . Single fDOM values for each lake were calculated using the same approach as described above for turbidity and chlorophyll a . We then regressed CDOM absorbance as a function of fDOM relative fluorescence using the 15 lakes for which we had both measures in 2013 ($F_{1,13} = 83.58$, $p < 0.0001$, $r^2 = 0.87$). The resulting best-fit regression equation was then used to predict CDOM absorbance from fDOM values in the remaining four lakes.

Catchment Characterization

We used GIS-based mapping to relate characteristics of catchments to patterns of turbidity, CDOM absorbance, and transparency of lakes. Catchments were delineated in ArcMap 10.3 using Canadian Digital Elevation Data with a 30 m (1:50000) resolution (<http://geogratis.gc.ca>). To ensure that lake shorelines were entirely included within catchments, we used a snap distance of 60 m to define pour points for all lakes. Catchments were saved as polygons and overlain with 2009 land cover data with a 30 m

resolution from the CSC2000v database (Center for Topographic Information, Earth Sciences Sector and Natural Resources Canada 2009). Within each catchment, we quantified areas covered by permanent ice (predominantly glaciers), and by vegetation. Vegetation coverage represented the combined categories of grasslands, scrub, deciduous forest, evergreen forest, mixed forest, woody wetlands, and emergent wetlands. Across our study lakes, catchment area was positively correlated with lake surface area ($r=0.41$, $n=33$, $p=0.018$), particularly for nonglacially-fed lakes ($r=0.83$, $n=15$, $p<0.001$). Therefore, we converted areas of ice and vegetation coverage to percentages of each catchment to facilitate comparisons among lakes.

Analyses

In our analyses, each lake was represented by a single set of observations. We used regression analyses to examine relationships between attenuation coefficients (K_d) of each wavelength (305, 320, 380 nm, and PAR) and the potential transparency regulators, CDOM absorbance, turbidity, and chlorophyll *a* fluorescence. Analyses were conducted for all lakes together, and for glacially- and nonglacially-fed lakes separately to determine if the effect of different regulators depended on the presence of a glacier in the catchment. We used linear and multiple regressions to examine of the relationship between potential transparency regulators individually and together, respectively, on attenuation coefficients of each wavelength. Both forward selection and backward elimination regressions produced the same final models in all analyses. For the six lakes that were sampled in both 2013 and 2014, we found very small quantitative changes in

results but no changes in statistical conclusions depending on which sample year we used. For these lakes, we only report analyses based on 2014 samples.

We also used linear regressions to examine changes in CDOM absorbance and turbidity as a function of percent ice coverage and percent vegetation coverage in the catchment across all 33 lakes, and for glacially- and nonglacially-fed lakes separately (percent ice coverage was not analyzed for nonglacially-fed lakes because all values were 0). To further explore the relationship between catchment characteristics and transparency regulators in mountain lakes, we also ran two separate Principle Components Analyses (PCA). The first analysis combined percent ice cover and percent vegetation cover and the second combined turbidity and CDOM absorbance. The association between individual lake scores on the first axes of each PCA was then analyzed by correlation.

RESULTS

Patterns of turbidity, CDOM absorbance, and transparency across lakes

Across our 33 study lakes, we observed wide variation in both turbidity (Range: 0.09 - 13.41 NTU) and CDOM absorbance as measured by a_{320} (Range: 0.02 - 4.01 m^{-1}). However, the 15 nonglacially-fed lakes all had low turbidity (≤ 1.34 NTU) and varied widely in a_{320} whereas the 18 glacially-fed lakes varied primarily in turbidity and had uniformly low CDOM absorbances ($a_{320} \leq 0.82 \text{ m}^{-1}$). Consequently, gradients of these two variables were arrayed orthogonally to one another and intersected in a region with turbidity ≤ 1.34 NTU and $a_{320} \leq 0.82 \text{ m}^{-1}$ (Figure 1). Of the 11 lakes with these low

turbidity and low CDOM characteristics, six had glaciers in their catchments and five did not.

Both turbidity and CDOM absorbance affected water transparency in our study lakes. For all study lakes combined, multiple regressions included both transparency regulators as significant predictors of attenuation coefficients for all three UV wavelengths as well as PAR (Table 1). Furthermore, the magnitude of standardized regression coefficients for turbidity and CDOM absorbance depended on wavelength. The standardized coefficient for CDOM absorbance was largest for K_{d305} and decreased with increasing wavelength. In contrast, standardized coefficients for turbidity increased with wavelength and was largest for K_{dPAR} . Unlike turbidity and CDOM absorbance, chlorophyll *a* fluorescence was not a significant predictor for any wavelength.

The relative importance of turbidity and CDOM as transparency regulators also depended on whether a glacier was present in the lake catchment. In nonglacially-fed lakes, attenuation rates of 305, 320, and 380 nm increased as a function of CDOM absorbance (Figure 2 a-c). Linear regressions of K_d as a function of a_{320} were highly significant for these ultraviolet wavelengths, and slopes decreased strongly as wavelength increased (Table 2). For PAR, attenuation rates were low ($< 0.70 \text{ m}^{-1}$) and independent of CDOM absorbance (Figure 2 d). In contrast to CDOM absorbance, there was no relationship between transparency and turbidity in nonglacially-fed lakes (Figure 2 e-h). Linear regressions of K_d as a function of turbidity were non-significant for all four wavelengths (Table 2) and turbidity was not a significant predictor in any multiple regression. Similarly, chlorophyll *a* fluorescence was not included in multiple regression models for any wavelength in nonglacially-fed lakes. Linear regressions of K_d as a

function of chlorophyll *a* fluorescence were marginally significant for 305, 320, and 380 nm ($F_{1,1} < 4.35$, $r^2 < 0.25$, $0.10 > p \geq 0.057$ for all three wavelengths). However, in each case the slope of the relationship was negative, indicating that transparency increased as a function of chlorophyll *a* fluorescence.

In the 18 glacially-fed lakes, attenuation rates of all four wavelengths increased as a function of turbidity (Figure 2 e-h). Linear regressions of K_d as a function of turbidity were highly significant for each wavelength, with r^2 values ≥ 0.90 and slopes that ranged from 0.24 for 305 nm to 0.07 for PAR (Table 3). Attenuation rates for glacially-fed lakes also increased as a function of CDOM absorbance for 305 and 320 nm, but not 380 or PAR (Table 3). However, these relationships were not as strong than those for turbidity, with $r^2 \leq 0.31$. In addition, turbidity was the only significant predictor variable of K_{d320} , K_{d380} , and K_{dPAR} in multiple regressions. For K_{d305} , turbidity was a significant predictor ($p < 0.001$) and CDOM absorbance was marginally significant ($p = 0.05$) but the multiple regression only increased r^2 by 0.02 compared to a linear regression with turbidity as the only predictor variable. Chlorophyll *a* was not included as a significant predictor in multiple regressions for any wavelength, and linear regressions were all non-significant ($F_{1,16} < 0.03$, $r^2 < 0.03$, $p > 0.80$ for all four regressions).

Associations between catchment characteristics and transparency regulators

Our study lakes varied widely in catchment characteristics. Barren rock covered between 0 and 81.8% of catchments, whereas vegetation cover ranged from 3.5 to 92.4%, and percent permanent ice cover varied from 0 to 36.2%. Wetlands covered $\leq 1.2\%$ of catchments, and 26 lakes had no defined wetlands. Vegetation and barren rock cover

were negatively correlated ($r = -0.63$, $p < 0.001$), but percent ice cover was not correlated with either barren rock ($r = -0.17$, $p = 0.36$) or vegetation ($r = -0.28$, $p = 0.11$) coverage. Percent vegetation cover decreased with elevation ($r = -0.59$, $p < 0.001$), as did the proportion of vegetation coverage composed of evergreen forest ($r = -0.85$, $p < 0.001$). In contrast, percent ice cover was independent of elevation ($r = -0.22$, $p = 0.37$).

For the combined set of 33 lakes, we observed significant positive relationships between CDOM absorbance and percent vegetation cover in the catchment ($F_{1,31} = 78.77$, $r^2 = 0.72$, $p < 0.001$) and between turbidity and percent ice cover in the catchment ($F_{1,31} = 41.89$, $r^2 = 0.58$, $p < 0.001$). These relationships were also observed when glacially- and nonglacially-fed lakes were analyzed separately. For the 15 nonglacially-fed lakes, CDOM absorbance increased as a function of percent vegetation cover (Figure 3a: $F_{1,13} = 45.39$, $r^2 = 0.78$, $p < 0.001$) and decreased with elevation ($F_{1,13} = 9.98$, $r^2 = 0.43$, $p = 0.008$). In these lakes, turbidity was independent of percent vegetation cover ($F_{1,13} = 1.29$, $r^2 < 0.09$, $p = 0.28$).

For the 18 glacially-fed lakes, turbidity increased with permanent ice cover (Figure 3b: $F_{1,16} = 12.40$, $r^2 = 0.44$, $p = 0.003$), indicating that the pattern observed across all 33 lakes was not driven by the low turbidities of nonglacially-fed lakes. However, turbidity was not associated with elevation ($r = -0.31$, $p = 0.21$). CDOM absorbance in glacially-fed lakes was not related to percent ice cover ($F_{1,16} = 0.32$, $r^2 = 0.02$, $p = 0.58$) but did increase with percent vegetation cover (Figure 3a: $F_{1,16} = 5.30$, $r^2 = 0.24$, $p = 0.035$), although the association was much weaker than for the entire lake dataset or for nonglacially-fed lakes. More importantly, the rate of increase in CDOM absorbance with percent vegetation cover was lower in glacially-fed lakes than nonglacially-fed lakes

(Figure 3a). Analysis of Covariance with CDOM absorbance as the dependent variable, presence/absence of a glacier in the catchment as a categorical variable and percent vegetation coverage as the covariate was highly significant ($F_{1,31} = 53.66$, $p < 0.001$) and included significant effects of percent vegetation coverage ($F_{1,31} = 24.83$, $p < 0.001$) and a significant interaction term ($F_{1,31} = 9.47$, $p = 0.005$), but main effect of glacial presence was not significant ($F_{1,31} = 0.02$, $p = 0.88$).

Across all study lakes combined, the first axis of the catchment characteristics PCA and the first axis of the transparency regulators PCA explained 64.1% and 62.9% of the variation among our 33 study lakes, respectively. Furthermore, individual lake scores on these two axes were negatively correlated with each other (Figure 4: $r = -0.88$, $n = 33$, $p < 0.001$). Negative values for the catchment characteristics axis and positive values for the transparency regulators axis were strongly associated with the presence of a glacier in the catchment.

DISCUSSION

Glaciers played a key role in determining whether CDOM or turbidity regulated water transparency in lakes of the Canadian Rocky Mountains. In glacially-fed lakes, transparency was driven primarily by turbidity and measures of CDOM absorbance (an indicator of CDOM concentration) were relatively low. In contrast, nonglacially-fed lakes had low turbidity and transparency was most strongly affected by CDOM absorbance. Consequently, gradients of CDOM absorbance and turbidity were orthogonal to each other. The two gradients intersected in a region of phase space represented by lakes with both low turbidity and low CDOM absorbance. Lakes in this

region are characterized by extremely high transparency, with attenuation coefficients in some lakes (e.g. Eiffel, Lower Consolation) $<0.10 \text{ m}^{-1}$ for 380 nm and $<0.12 \text{ m}^{-1}$ for PAR. These values are similar to those observed in some of the most transparent lakes in the world such as Crater Lake in Oregon, USA (Hargreaves et al. 2007), Lake Tahoe in California-Nevada, USA (Rose et al. 2009b), and Blue Lake in New Zealand (Gall et al. 2013).

In nonglacially-fed lakes, CDOM absorbance increased as a function of the percentage of the catchment that was vegetated. Other studies have also found strong associations between CDOM and characteristics of lake catchments, including both the type and amount of vegetation coverage (Pienitz and Vincent 2000; Rae et al. 2001; Sadro et al. 2012; Forsstrom et al. 2015). In part, the nonglacially-fed lakes in our study varied in vegetation coverage due to differences in elevation. Vegetation coverage was highly correlated with coniferous forest coverage, which itself decreased with increasing elevation. However, CDOM absorbance was more strongly related to coverage of all types of vegetation than just coniferous forest ($r^2 = 0.78$ for all types of vegetation vs. $r = 0.54$ for evergreen forest alone), possibly due to the presence of cryptic wetlands (Winn et al. 2009). Altitudinal changes in CDOM-driven transparency have also been observed in mountain lakes of the Alps and Pyrenees (Laurion et al. 2000), the Sierra Nevadas of Spain (Mladenov et al. 2008), the Patagonian Andes (Garcia et al. 2015), and the Yunnan Plateau of China (Zhang et al. 2007). Additionally, lake catchments may have varied in vegetation coverage as a function of time since deglaciation. Engstrom et al. (2000) found an increase in DOC concentrations as a function of time since glacial retreat in a

10,000 year chronosequence in Glacier Bay, Alaska. This increase was strongly associated with successional changes in catchment vegetation.

In glacially-fed lakes, attenuation rates increased as a function of turbidity caused by suspended inorganic particles in the form of glacial flour. For these lakes, variation in turbidity was strongly associated with the percent coverage of glaciers and permanent ice in the catchment. Originally created by glacial abrasion of underlying bedrock, fine sedimentary particles can be transported to lakes by inflowing meltwater streams (Smith 1978). These particles can then stay suspended in the water column for extended periods of time due to water column mixing and thermal density gradients (Sommaruga 2015). Although the relationship between percent ice cover in the catchment and turbidity was significant, the r^2 was only 0.44. Some of the scatter is likely due to the presence or absence of lakes upstream of our study lakes that act as settling ponds for suspended sediments (Bogen et al. 2015). For example, Myosotis Lake is downstream from Zigadenus Lake and has a lower turbidity despite having similar percent ice coverage (from the same glaciers) in their catchments. In addition, variation in catchment slopes in surrounding moraines can strongly influence sediment mobilization and transport to lakes (Theler et al. 2010). Finally, differences in local mineralogy among lake catchments can affect the composition and size distribution of glacial flour (Chanudet and Filella 2008), which in turn influences scattering of incoming radiation to lakes (Jonasz and Fournier 2007).

We also observed a relationship between vegetation coverage and CDOM absorbance in glacially-fed lakes. However, the CDOM absorbance for a given level of vegetation coverage was lower than for nonglacially-fed lakes. The reduced effect of

vegetation on CDOM absorbance in glacial lakes may be due to an interaction between glacial flour and CDOM. Specifically, CDOM may be adsorbed on to inorganic particles suspended in the water column. Tietjen et al. (2005) found strong adsorption of CDOM derived from terrestrial vegetation on to inorganic particles, particularly clay. As these CDOM-particle aggregates settle out, they would reduce CDOM absorbance in the water column. Leavitt et al. (2003) also proposed CDOM adsorption to explain the low UVR absorbance of filtered water samples from glacially-fed Sunwapta Lake in the Canadian Rockies. This interaction between glacial flour and CDOM would be consistent with the orthogonal gradient observed across our 33 study lakes. None of the lakes had a combination of both high turbidity and high CDOM, despite glacial lakes having up to 36% vegetation coverage in their catchments.

Our estimates of CDOM absorbance and turbidity are based on single measurements collected mid-summer in each lake. Both of these transparency regulators can change over daily and seasonal time scales in response to hydrological events associated with spring snowmelt or summer rainfall that deliver material from the surrounding catchment (Halder et al. 2012; Sadro and Melack 2012; Williamson et al. 2014). Consequently, the timing of sampling relative to hydrological events could affect the measurement's magnitude. Although these shorter-term dynamics would not influence the relationships between either CDOM absorbance or turbidity and transparency presented in Figure 2, the relationships between transparency regulators and catchment characteristics in Figure 3 could be affected. However, lakes with the most material (CDOM or glacial flour) in their catchments would likely have the strongest responses to hydrological events. In contrast, lakes with little vegetation or ice coverage

would have minimal inputs of transparency-regulating material and thus would show less variation over shorter time-scales. Therefore, the landscape-scale regulation of water transparency may be even stronger than reported here.

Chlorophyll *a* fluorescence was not an important regulator of transparency in our study lakes. No significant effects of fluorescence on transparency were observed for any wavelength in glacially-fed lakes, and UV transparency in nonglacially-fed lakes showed a marginally significant increase with chlorophyll *a* fluorescence. Rose et al. (2014) also concluded that chlorophyll was minimally related to attenuation in glacially-fed lakes, and Laurion et al. (2000) found no relationship between chlorophyll *a* concentration and K_{d320} , and only a weak relationship with K_{dPAR} in lakes with vegetated or barren catchments. The lack of a relationship between chlorophyll *a* fluorescence and transparency in our study lakes should be interpreted with some caution due to environmental influences on *in situ* fluorescence measurements, particularly photochemical quenching, that confound relationships between fluorescence and chlorophyll *a* concentration (Falkowski and Kiefer 1985). Nevertheless, we are confident that phytoplankton play a minimal role in regulating transparency due to their low abundance in these cold, nutrient-poor, and unproductive systems (Vinebrooke and Leavitt 1999; Murphy et al. 2010). In addition, chlorophyll *a* fluorescence in many of our study lakes peaked below the depths reached by 1% of surface UVR and thus phytoplankton did not have the potential to play a strong role in affecting our measures of transparency (see also Saros et al. 2005). Although chlorophyll *a* concentration does not appear to be closely related to variation in transparency among mountain lakes, Belzile et al. (2002) and Sommaruga and Augustin (2006) both found that seasonal changes in

transparency within individual lakes with low DOC concentrations was related to changes in chlorophyll *a* concentration.

Although increases in CDOM absorbance and turbidity both affected transparency, they had different wavelength-specific effects. CDOM absorbance of incoming solar radiation is inversely proportional to wavelength. Consequently, attenuation rates increased as a function of CDOM most rapidly for 305 nm and 320 nm whereas attenuation of PAR did not change. In contrast, inorganic particles reduce transparency primarily by scattering incoming solar radiation (Gallegos et al. 2008). Because this effect is less wavelength-specific than CDOM absorbance, attenuation rates of all measured wavelengths decreased with increasing turbidity. These contrasting wavelength-specific effects may have important implications for aquatic organisms. For example, phytoplankton in nonglacially-fed lakes where CDOM drives transparency can potentially occupy depths for which UVR exposure is low but PAR is sufficient for primary production. Phytoplankton in these lakes may therefore experience relatively little photoinhibition, particularly if their vertical distribution is concentrated in a deep chlorophyll maximum (Saros et al. 2005). In contrast, phytoplankton in glacially-fed lakes where turbidity drives transparency may experience higher UVR exposure because UVR and PAR attenuate at more similar rates. These lakes may also have less pronounced deep chlorophyll maxima (Hylander et al. 2011).

Because glaciers play a key role in determining the regulation of transparency, mountain lakes may be highly sensitive to climate change. Temperature and precipitation are both changing rapidly at high elevations (Beniston et al. 1997; Sala et al. 2000; Bradley et al. 2004). Furthermore, few glaciers are predicted to remain by 2100 and total

glacial volume in the region is projected to decrease by 90% compared to 2005 (Clarke et al. 2015). As glaciers melt, inputs of glacial flour to lakes may first increase but ultimately will decrease and eventually subside. Without these inputs, glacially-fed lakes will likely change position along the orthogonal gradient in Figure 1. Over time, higher turbidity lakes would shift position into the region of low turbidity and low CDOM and would become highly transparent (see Sommaruga 2015). More importantly, the regulator of transparency would switch from turbidity to CDOM. Depending on vegetation coverage in the catchment, this switch could result in either increases or decreases in transparency compared to current levels. For example, 10 of our 18 glacially-fed study lakes would be predicted to have higher K_{d320} and eight would be predicted to have lower K_{d320} values if glaciers were absent and transparency was driven by CDOM alone (based on a regression of K_{d320} vs. percent vegetation in the catchment for our 15 non-glacial lakes: $r^2 = 0.79$). The magnitude of this predicted change is negatively correlated with current turbidity ($r = -0.91$, $n = 18$, $p < 0.001$), with the most turbid lakes becoming more transparent and the most transparent lakes becoming less so. Furthermore, this change in transparency could occur quickly as CDOM absorbance would more closely reflect vegetation coverage in the catchment. Over longer time scales, CDOM absorbance would likely increase further as successional processes increase vegetation coverage (Engstrom et al. 2000). These increases in CDOM could be further enhanced with climate-induced increases in growing season length (Rammig et al. 2010) or treeline advance (Luckman and Kavanaugh 2000; Harsch et al. 2009). The interactive effects of these changes in catchment structure and climatic forcing have the potential to dramatically alter these aesthetically and ecologically important systems.

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Draft

Table 1: Results of multiple regressions with attenuation coefficients of 305, 320, and 380 nm and PAR as dependent variables and CDOM absorbance (a_{320}), turbidity (NTU), and temperature-corrected chlorophyll *a* fluorescence (RFU) as potential predictor variables for the 33 study lakes. Standardized coefficients are listed for variables that were significant. Forward selection and backward elimination multiple regressions produced identical final models. All regressions had 2 numerator degrees of freedom and 31 denominator degrees of freedom.

K_d	F	p -value	r^2	Standardized CDOM Coefficient	Standardized Turbidity Coefficient	Chlorophyll <i>a</i>
305	105.96	<0.001	0.88	0.924	0.520	ns
320	91.28	<0.001	0.86	0.876	0.604	ns
380	83.69	<0.001	0.85	0.573	0.884	ns
PAR	70.40	<0.001	0.82	0.259	0.940	ns

Table 2: Least squares linear regression results for attenuation coefficients as a function of turbidity (NTU) or CDOM absorbance (a_{320}) in 15 nonglacially-fed lakes. Significant regressions are in bold. Coefficients are only reported for significant regressions.

K_d	F	p -value	r^2	Slope	Intercept
Turbidity (NTU)					
305	0.98	0.34	0.07	-	-
320	0.82	0.38	0.06	-	-
380	0.36	0.56	0.03	-	-
PAR	0.06	0.81	0.01	-	-
CDOM Absorbance (a_{320})					
305	66.86	<0.001	0.84	1.38	0.11
320	50.82	<0.001	0.80	0.97	0.21
380	26.34	<0.001	0.67	0.29	0.26
PAR	2.77	0.12	0.18	-	-

Table 3: Least squares linear regression results for attenuation coefficients as a function of turbidity (NTU) or CDOM absorbance (a_{320}) in 18 glacially-fed lakes. Significant regressions are in bold. Coefficients are only reported for significant regressions.

K_d	F	p -value	r^2	Slope	Intercept
Turbidity (NTU)					
305	138.52	<0.001	0.90	0.24	0.39
320	158.23	<0.001	0.91	0.21	0.33
380	159.39	<0.001	0.91	0.15	0.16
PAR	144.37	<0.001	0.90	0.07	0.12
CDOM Absorbance (a_{320})					
305	7.34	0.016	0.31	2.98	0.22
320	6.90	0.018	0.30	2.51	0.21
380	4.04	0.06	0.20	-	-
PAR	3.07	0.10	0.11	-	-

FIGURE LEGENDS

Figure 1. Scatter plot of turbidity (NTU) vs. CDOM absorbance (a_{320}) for 33 lakes. Open squares represent 18 glacially-fed lakes. Filled circles represent 15 nonglacially-fed lakes.

Figure 2 a-d. Scatter plots of attenuation coefficients (K_d : m^{-1}) vs. CDOM absorbance (a_{320}) for a) 305 nm, b) 320 nm, c) 380 nm, and d) PAR. Figure 2 e-h: Scatter plots of attenuation coefficients (K_d : m^{-1}) vs. turbidity (NTU) e) 305 nm, f) 320 nm, g) 380 nm, and h) PAR. Symbols are as in Figure 1, and dashed lines represent significant linear regressions.

Figure 3. a) Scatter plot of CDOM absorbance (a_{320}) vs. percent vegetation coverage in catchment. Lines represent separate relationships for glacially- and nonglacially-fed lakes. Symbols are as in Figure 1. b) Scatter plot of turbidity (NTU) vs. percent ice coverage in catchment for 18 glacially-fed lakes.

Figure 4. Scatter plot of Principal Components Analysis loadings on the first axis for 33 lakes based on catchment characteristics (X axis) and transparency regulators (Y axis). The catchment characteristic PCA score is based on two variables, percent ice coverage and percent vegetation coverage, and explained 64.1% of the variation among lakes in these two variables. The transparency regulator PCA score is based on two variables, turbidity (NTU) and CDOM absorbance (a_{320}) and explained 62.9% of the variation among lakes in these two variables. Symbols are as in Figure 1.

Figure 1. Scatter plot of turbidity (NTU) vs. CDOM absorbance (a_{320}) for 33 lakes. Open squares represent 18 glacially-fed lakes. Filled circles represent 15 nonglacially-fed lakes.

254x190mm (72 x 72 DPI)

Figure 2 a-d. Scatter plots of attenuation coefficients (K_d : m⁻¹) vs. CDOM absorbance (a_{320}) for a) 305 nm, b) 320 nm, c) 380 nm, and d) PAR. Figure 2 e-h. Scatter plots of attenuation coefficients (K_d : m⁻¹) vs. turbidity (NTU) e) 305 nm, f) 320 nm, g) 380 nm, and h) PAR. Symbols are as in Figure 1, and dashed lines represent significant linear regressions.

254x338mm (72 x 72 DPI)

Figure 3. a) Scatter plot of CDOM absorbance (a_{320}) vs. percent vegetation coverage in catchment. Lines represent separate relationships for glacially- and nonglacially-fed lakes. Symbols are as in Figure 1. b) Scatter plot of turbidity (NTU) vs. percent ice coverage in catchment for 18 glacially-fed lakes.

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