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Role of dissolved organic carbon in the attenuation of photosynthetically active and ultraviolet radiation in Adirondack lakes

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SUMMARY

1. We surveyed eighty-five lakes located in the Adirondack Mountain Region of New York State, U.S.A., to characterize the attenuation of photosynthetically active (PAR) and ultraviolet radiation (UVR) in relation to dissolved organic carbon (DOC) concentrations and pH. Attenuation of PAR was quantified *in situ*. Attenuation was also inferred by measuring the light absorption of filtered lake water samples at wavelengths (300, 340 and 440 nm) representing UV-B, UV-A and PAR.
2. Substantial variation in transparency was observed among lakes in this region. Attenuation depths ($z_{1\%}$) for PAR ranged from 0.5 to greater than 20 m, while inferred values for UV-B and UV-A ranged from a few centimetres to > 5 m. Median values of UV-A penetration (0.75 m) and UV-B penetration (0.45 m) corresponded to 11% (UV-A) and 6% (UV-B) of lake maximum depth.
3. Much of the variation in PAR and UVR attenuation was explained by differences in lake DOC. Univariate power models based solely on DOC accounted for 85% (PAR), 90% (UV-A) and 91% (UV-B) of the variation in absorption.
4. Attenuation and absorption coefficients were generally lower for recently acidified lakes compared to acidic and circumneutral lakes which have not undergone recent acidification. However, differences among these three groups of lakes were not statistically significant. Our results suggest that the effects of acidification on the optical properties of a regional population of lakes, even in an area experiencing widespread acidification, are relatively subtle in comparison with other factors contributing to inter-lake variability.
5. The presence of near-shore wetlands is probably a key factor influencing regional variability in DOC and light climate among Adirondack lakes. Temporal variability in climatic factors influencing wetland DOC production and export may mask more subtle influences on lake DOC associated with anthropogenic acidification.

Keywords: acidic deposition, Adirondack Mountains, dissolved organic carbon, light attenuation, photosynthetically active radiation, ultraviolet radiation

Introduction

Lakes within a given geographical region exhibit similarities in physical, chemical and biological characteristics to varying degrees. Differences arise despite a common geohydrologic setting, local climate and shared pool of species. The extent to which characteristics of individual lakes diverge from the regional population will depend on catchment- or smaller-scale processes governing material flux (Driscoll & Newton, 1985; Kratz *et al.*, 1991) and, for biota, on historical factors such as invasion and extinction events (e.g. Tonn *et al.*, 1990). An important goal of

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limnology is to understand the mechanisms which give rise to inter-lake variation since these have been shown to determine the sensitivity of individual lakes to atmospheric pollutants, climate change and other human impacts (Webster *et al*., 1996; Stoddard *et al*., 1998). For example, Goldstein *et al*. (1985) demonstrated that sensitivity to a regional stressor (acidic deposition) could be predicted based on lake-specific differences in hydrologic flow paths which were related to the depth of till within the catchment. More recently, Saunders *et al*. (1999) showed that the occurrence of nitrogen limitation of phytoplankton growth in a region dominated by phosphorus-limited lakes could be predicted on the basis of the hydrologic setting of a lake (drainage versus seepage). These examples highlight the need for understanding the interplay between local- and regional-scale processes in order to predict rates and direction of future change.

In this paper, we examine regional variability in the attenuation of photosynthetically active and ultra-violet radiation (PAR and UVR) among lakes occurring in the Adirondack Mountains of New York State, U.S.A. Although limnologists have long recognized that human impacts within a catchment (e.g. nutrient loading and soil erosion) have direct consequences for lake transparency, few studies have attempted to assess variability in regions remote from direct human disturbance. The attenuation of solar energy within the water column is an important factor determining the depth distribution of photosynthesis (e.g. Anderson, 1993), lake mixing depth (Bukaveckas & Driscoll, 1991a; Mazumder & Taylor, 1994) and foraging efficiency of visually oriented predators (O'Brien, 1987). In recent years, attention has focused on the ecological effects of short-wavelength radiation (UV-A and UV-B) which is increasing because of the destruction of stratospheric ozone (Kerr & McElroy, 1993). Ultraviolet radiation has been shown to have negative effects on a variety of freshwater biota including plankton and fish (Williamson & Zagarese, 1994; Williamson, 1995). A number of studies have suggested that acidification is accompanied by a decrease in dissolved organic carbon (DOC) and an increase in lakewater clarity (Bukaveckas & Driscoll, 1991b; Schindler *et al*., 1991; Williamson *et al*., 1996). Increases in UVR penetration may partly account for changes in aquatic food webs associated with acidification (Frost *et al*., 1999; Williamson *et al*., 1999a).

The transmission of solar radiation through the water column is attenuated by absorption and scattering. Light is scattered by suspended particles which include living cells, minerals and detritus. Scattering increases the path length of photons through water, thereby increasing the probability that these will be absorbed. Light is absorbed by water itself and by a diverse array of chromophoric compounds, mainly humic and fulvic acids, which constitute a variable fraction of DOC in natural waters. Phytoplankton and other suspended particles contain photosynthetic pigments, and contribute to both the scattering and absorption of light. The relationship between light attenuation and phytoplankton abundance has been well documented for lakes in regions where cultural eutrophication has resulted in a wide range of trophic conditions (e.g. Carlson, 1977; Jewson, 1977). In geographic regions where surface waters are dilute and nutrient poor, lakes are typically oligotrophic and factors other than phytoplankton can regulate light attenuation. In these lakes, light absorption by DOC has been shown to be a principal factor attenuating light (Kirk, 1994a) and empirical models have been developed to predict the attenuation of PAR and UVR from DOC (Scully & Lean, 1994; Morris *et al*., 1995).

The Adirondack Mountain Region is characterized by shallow, base-poor soils which are underlain by bedrock which is highly resistant to weathering (Driscoll *et al*., 1991). As a result, lakes in this region are dilute and nutrient poor. Acidic lakes are common and many of these are thought to have acidified recently as a result of anthropogenic atmospheric inputs (Driscoll *et al*., 1991; Cumming *et al*., 1992). Site-specific studies have documented changes in transparency associated with changes in acidity for a few lakes (Bukaveckas & Driscoll, 1991b). One previous survey relied on empirical models, and measured DOC concentrations to estimate attenuation of PAR and UVR in Adirondack lakes (Williamson *et al*., 1996). In the present study, we surveyed 85 Adirondack lakes to quantify PAR attenuation *in situ* and characterize light absorption spectra for filtered lakewater samples. Light absorption was measured at wavelengths of 300, 340 and 440 nm to represent UV-B, UV-A and PAR, respectively. Our objective was a regional-scale assessment of acidification effects in the context of other lake and catchment factors influencing optical properties. We compare PAR and UVR attenuation among acidic and circumneutral lakes, and examine variability in attenuation among lakes differing in DOC, trophic state (CHLa) and hydrogeomorphic position. For a subset of lakes included in this study, paleolimnological data were available to infer historical changes in lake acidity (Cumming *et al.*, 1992). We use these data and current (measured) pH to interpret the potential effects of acidification on the light climate of lakes in this region.

Methods

Study sites

Our survey sites included thirty of the 38 lakes which were randomly selected by the U.S. EPA Direct/Delayed Response Project (Church *et al.*, 1989) from over 760 lakes sampled by the EPA Eastern Lakes Survey (Landers *et al.*, 1988). For each of the 38 lakes, a known probability of inclusion was calculated; the inverse of the inclusion probability gives the number of lakes in the target population represented by each study lake (Church *et al.*, 1989). The 30-lake subset represents a population of 619 relatively undisturbed, low alkalinity (ANC < 400 μeq L^{-1}) Adirondack lakes with maximum depths > 1.5 m, surface areas between 4 and 200 ha, and catchment areas < 3000 ha.

Additional survey data were obtained from another fifty-five lakes which were not selected at random, but were chosen to represent the diversity of lakes in the region with respect to geographic location, hydrology (drainage and seepage lakes), morphometry (surface area, depth) and water chemistry (pH and trophic state). This group of lakes had previously been sampled as part of the EPA Eastern Lakes Survey (Landers *et al.*, 1988), the Adirondack Long-Term Monitoring Project (Driscoll & van Dreason, 1993) and concurrent studies of acidification effects on plankton communities (Bukaveckas & Shaw, 1998; Saunders *et al.*, 1999).

The eighty-five lakes in our survey were distributed throughout the major drainage basins of the Adirondack region. The group included lakes at moderate to high elevations (550–700 m) in the south-western Adirondacks, and lower elevation lakes in the central and southern Adirondacks. The lakes are located in predominantly forested and unpopulated catchments, although seasonal dwellings are present on the shoreline at some sites. The majority of sites were classified as drainage lakes on the basis of having an outflow stream and one or more inlet tributaries (Table 1). Nineteen out of the 85 sites were closed-basin lakes (seepage lakes) which lacked an outflow stream, and were primarily dependent upon hydrologic inputs from groundwater and direct precipitation. The survey group was dominated by lakes of small surface area (< 10 ha) and moderate depth (maximum depth = 5–15 m). Hydrologic classifications and lake morphometric data were obtained from the Adirondack Lake Survey Corporation database (Kretser *et al.*, 1989). Survey sites included lakes which were chronically acidic (28% with pH = 4–5), moderately acidic (37% with pH = 5–6) and circumneutral (35% with pH = 6–7). Chlorophyll concentrations were < 10 μg L^{-1} in 80% of the study lakes. Only six out of the eighty-five sites exhibited depth-integrated chlorophyll concentrations over 20 μg L^{-1} (Table 1). Sixteen lakes of moderate to high DOC (6–15 mg L^{-1}) were included in the survey, but the majority of sites had low DOC (< 5 mg L^{-1}).

Lake sampling

All lakes were sampled between 20 May and 20 August within 3 h of solar noon. At each site, depth profiles of irradiance (Protomatic photometer), temperature (YSI S-C-T meter, Yellow Springs, Ohio, USA) and dissolved oxygen (Winkler titration) were obtained from a station at or near the deepest portion of the lake basin. Irradiance was measured using a photometer equipped with upward and downward spherical sensors exposed as hemispheres. The wavelength response of this meter is similar to the ideal quantum response for PAR at wavelengths of 400–625 nm (Field & Effler, 1983). However, it should be noted that this device measures a small fraction (20–40%) of the light energy in the near-UV range (350–400 nm) and underestimates by 50–80% light energy at wavelengths of 650–700 nm.

A depth-integrated water sample was collected at each site using a small-diameter tube lowered from the surface to within 1 m of the lake bottom. Chemical analyses included measurements of pH (glass electrode) and acid neutralizing capacity (Gran titration). Samples for chlorophyll analyses were filtered

Table 1 Optical, chemical and morphometric characteristics of eighty-five Adirondack lakes. Attenuation and absorption coefficients for photosynthetically active radiation (PAR) are denoted as K_d and abs; a_{440}, a_{340} and a_{300} are absorption coefficients for PAR, and ultraviolet-A and ultraviolet-B radiation, respectively, measured in filtered lakewater samples. Asterisks (*) denote sites which were a randomly selected subset from the U.S. EPA Eastern Lakes Survey

			Absorption coefficient (m^{-1})							
Lake name	K_d (m^{-1})	abs (m^{-1})	a_{440} (m^{-1})	a_{340} (m^{-1})	a_{300} (m^{-1})	DOC (mg L^{-1})	CHLa (μg L^{-1})	pH	Area (ha)	z_{max} (m)
Silver L.	0.09	0.09	0.015	0.145	0.461	1.40	0.379	4.87	21.0	18.0
Otter L.	0.15	0.14	0.028	0.542	1.209	2.79	0.707	5.30	16.0	4.0
Mays P.	0.19	0.18	0.027	0.543	1.324		0.784	5.21	13.0	4.0
Woods (EPA)*	0.21	0.20				2.01	3.387	5.91	26.0	10.0
Evergreen L.	0.23	0.21	0.132	1.712	3.512	2.44	4.335	4.66	20.0	8.0
South L.*	0.24	0.23	0.032	1.143	2.530	1.84	1.284	5.15	196.0	18.0
John P.*	0.24	0.21	0.100	0.767	1.551	1.86	2.014	5.24	6.0	8.0
L. Madeleine	0.26	0.24	0.195	1.667	3.495	2.58	1.052	6.62	122.0	21.0
Limekiln L.	0.28	0.25	0.098	1.181	2.418	2.86	1.043	5.85	187.0	21.0
Clear P.	0.28	0.27	0.302	2.722	5.732	3.84	1.414	6.32	71.0	24.0
Crystal L.	0.29	0.27	0.281	1.124	1.842	1.62	1.810	4.48	5.6	8.0
Grass (LC)	0.30	0.28	0.291	2.184	4.261	3.65	3.222	5.67	7.5	10.0
Cranberry P.	0.30	0.28	0.116	1.150	2.454	2.77	1.059	4.99	7.0	6.5
Hawk P.*			0.064	1.238	2.936	2.24	2.203	4.81	13.0	10.0
Raven L.	0.30	0.28	0.140	2.031	4.145	1.52	1.615	4.51	52.0	14.0
Mt. Arab L.*	0.31	0.29	0.135	1.426	3.096	2.70	3.652	6.08	50.0	16.0
St. John L.*	0.31	0.28	0.492	3.029	5.581	2.92	2.040	5.44	13.0	10.0
Wilmurt L.*	0.32	0.30	0.340	2.270	4.611	2.28	3.681	5.80	39.0	11.0
Queer L.	0.32	0.31	0.499	3.338	5.847	1.49	1.581	5.27	62.0	18.0
Woodhull L.*	0.32	0.30	0.242	2.149	4.088	2.60	3.529	5.45	443.0	17.0
Cascade L.	0.35	0.33	0.264	1.961	4.085	3.15	1.438	5.98	37.0	6.0
Little Long	0.36	0.30	0.024	0.379	1.036	2.26	9.228	4.78	16.0	13.0
Wolf (HF)	0.40	0.38	0.542	3.358	6.453	3.66	2.520	6.59	57.0	12.0
Trout L.*	0.44	0.42	0.479	4.412	9.289	4.72	3.155	7.02	146.0	9.0
Little Simon P.	0.44	0.43	0.631	4.720	8.815	3.29	1.026	6.40	63.0	33.0
Gull South*	0.47	0.44	0.440	2.779	5.209	4.75	0.895	4.80	10.0	4.0
EastP.	0.47	0.46	0.651	4.634	8.606	4.46	1.714	6.11	22.0	16.0
Moss L.	0.48	0.47				3.12	1.377	6.18	46.0	11.5
Rock P.	0.48	0.44	0.374	2.595	5.267	4.26	2.024	5.88	13.0	3.0
Woods (LAMP)	0.49	0.48	0.680	4.570	8.410	3.44	3.752	6.68	23.0	12.0
Heart L.	0.49	0.43	0.203	1.443	3.114	3.03	8.360	6.10	11.0	13.0
Sunday P.	0.50	0.47	0.803	3.510	6.395	3.63	5.604	5.45	4.0	8.0
Trout (PL)*	0.50	0.47	0.885	4.630	8.491	4.02	1.264	4.97	17.0	6.0
Kiwassa L.*	0.50	0.46	0.481	4.011	8.359	3.65	4.516	6.52	115.0	12.0
Long (KS)*	0.51	0.49	0.865	4.717	8.837	3.34	11.323	5.73	15.0	11.0
Big Moose L.	0.54	0.54	0.599	6.852	11.990	3.81	1.056	4.93	504.0	21.0
Thirsty P.	0.54	0.51	0.343	2.683	4.811	3.00	1.707	5.01	11.0	4.0
Buck P.	0.58	0.54	0.535	4.124	7.676	3.20	5.356	6.14	8.4	9.5
Dart's L.	0.60	0.57	0.892	6.690	11.973	2.93	0.862	5.28	52.0	14.5
Bubb Lake	0.61	0.57	0.745	4.642	8.146	4.39	2.798	6.40	20.0	3.0
L. Frances*	0.63	0.59	0.935	4.635	8.929	3.94	10.509	5.92	6.0	5.0
Sis Lake			0.981	6.415	11.525	4.39	1.026	6.79	10.0	2.0
Fourth L.*	0.65	0.62	1.711	9.239	16.568	3.95	1.820	5.52	23.0	9.0
Nicks P.*	0.66	0.63	1.491	7.108	11.865	3.01	3.454	6.07	6.0	6.0
Duck L.	0.68	0.65	0.853	6.363	11.879		2.544	6.20	137.0	3.0
Bellows L.	0.73	0.69	1.270	7.582	14.191	3.68	2.459	5.08	12.0	5.0
L. Rondaxe	0.74	0.71	0.591	4.543	8.013	2.95	2.723	5.76	92.0	11.0
Catamount P.	0.75	0.70	1.421	5.953	9.332	2.87	53.687	4.86	4.8	8.0

Table 1. Continued

			Absorption coefficient (m^{-1})							
Lake name	K_d (m^{-1})	abs (m^{-1})	a_{440} (m^{-1})	a_{340} (m^{-1})	a_{300} (m^{-1})	DOC (mg L^{-1})	CHLa (μg L^{-1})	pH	Area (ha)	z_{max} (m)
Windfall P.	0.79	0.77	1.013	7.863	13.774	5.34	9.121	6.49	1.6	6.0
Chub P.*			1.491	8.203	14.364	5.44	13.241	5.35	6.6	5.0
Partlow L.*	0.79	0.76	1.342	8.933	15.392	5.31	4.428	5.81	30.0	7.0
Heavens L.	0.80	0.78	1.558	10.630	18.789		15.090	6.51	11.0	7.0
Curtis L.*	0.84	0.80	1.304	5.525	9.156	3.18	8.380	5.20	4.0	9.0
Constable P.*	0.85	0.80	0.880	4.665	8.853	4.99	6.609	4.77	21.0	4.0
Arbutus L.	0.88	0.85	1.071	8.677	15.214	4.93	2.130	6.25	50.0	8.0
Middle P.*	0.89	0.85	1.169	6.869	12.526	6.41	6.194	6.51	24.0	2.0
Grass P.*			1.675	9.413	16.626	4.34	2.124	5.54	5.0	5.0
Unknown P.*	0.90	0.83	1.650	9.771	17.850	4.75	7.162	6.41	14.0	6.0
Barnes L.	0.91	0.88	2.439	11.079	18.154	6.86	23.907	6.48	3.0	9.0
SE Pine P.	0.91	0.88	1.953	9.605	17.862	5.52	14.299	6.45	2.0	7.0
Fish Ponds*	0.91	0.84	1.698	8.897	16.556	4.99	3.488	6.22	8.0	4.0
Nate P.*	0.91	0.87	1.386	8.305	16.413	8.16	9.404	6.26	9.0	6.0
Twitchell L.	0.92	0.90	0.908	6.620	11.299	3.14	1.140	5.14	58.0	11.0
Deer L.	0.94	0.86	1.508	9.771	17.716	3.14	3.574	6.92	39.0	3.0
Cheney P.*	0.96	0.94	1.590	8.371	15.515	5.34	3.308	6.08	7.0	3.0
Hitchcock L.*	1.00	0.98	2.067	11.876	21.644	6.69	6.703	4.92	15.0	11.0
Long (CL)	1.20	1.19	3.461	16.639	29.001	5.31	9.291	5.44	7.0	6.0
Big Chief P.	1.24	1.28	1.624	10.355	18.958	8.33	7.295	5.47	2.4	10.0
Mud (SL)*	1.30	1.20	1.620	8.962	17.096	6.06	14.955	4.65	9.0	3.0
Wolf P.*			1.443	10.255	19.248	6.80	1.528	4.49	4.3	8.0
Dianas P.	1.39	1.35	2.164	13.865	26.123		13.171	6.78	6.0	7.0
Little Clear P.	1.46	1.48	3.296	15.596	26.804	7.87	20.492	5.75	1.9	12.0
Grass (SC)			3.040	15.524	27.465	6.20	19.312	4.66	1.6	6.0
Pocket P.	1.48	1.50	4.678	34.116	56.894	11.04	8.407	4.86	2.0	9.0
Doe P.	1.48	1.50	4.024	19.238	33.924	7.87	9.920	5.35	1.2	9.0
Mud (CL)*	1.54	1.46	2.440	10.931	18.475	5.41	12.734	4.91	5.0	8.5
E Copperas P.	1.71	1.68				4.64	34.560	4.40	3.6	5.0
Twin Ponds	1.75	1.72	5.620	27.978	47.958	8.59	6.292	5.40	5.0	9.0
Buck (STL)	1.77	1.75	5.556	24.653	38.533	5.23	13.948	5.92	4.1	5.0
Silver Dollar P.	1.80	1.82	5.588	35.653	61.090	11.18	8.312	4.94	0.8	7.0
Outlet P.	1.93	1.89	1.765	10.668	18.810	8.70	4.644	6.03	5.2	2.0
Marsh P.	2.45	2.49	3.735	16.342	27.840	5.29	48.074	4.68	1.5	5.0
Squash P.	2.74	2.85	5.165	31.417	63.573	11.81	21.533	4.62	2.0	4.5
Little Echo P.	2.90	2.90	8.841	45.298	77.347	15.08	38.907	4.19	1.0	5.0
St. Huberts P.	2.91	2.87	3.424	17.274	29.151		2.409	4.92	6.0	1.0

through Gelman A/E glass fibre filters and extracted in 10 mL of aqueous acetone (90%). Filters were macerated using a Teflon tissue grinder and steeped for 12 h in the dark at 4 °C. Concentrations of chlorophyll degradation products were determined by measuring absorbance before and after acidification with 0.1 M HCl. Estimates of chlorophyll *a* corrected for phaeophytin *a* were calculated using the Lorenzen equations as modified by Speziale *et al.* (1984). The DOC was measured by persulphate digestion followed by infrared detection for samples collected at 58 of the 85 lakes included in this study. Additional DOC data were obtained from the EPA Eastern Lakes Survey (fifteen sites), the Adirondack Lake Survey (four sites) and the Adirondack Long-Term Monitoring Program (nine sites).

Dissolved colour

Samples were stored in opaque bottles at 4 °C and analysed within 24 h of collection. A dual-beam spectrophotometer (Varian DMS70) was used to derive absorption spectra by placing filtered samples (0.45 μm glass fibre filters) and blanks (low carbon distilled water) in matched quartz cuvettes (4 cm path length). Absorbance readings were recorded at 10–50-nm intervals for wavelengths from 270 to 700 nm. The apparent absorption coefficient was calculated for each wavelength as:

$$a_\lambda = \ln(10^{A/r}) \tag{1}$$

where A is the measured absorbance at that wavelength and r is the path length of the cuvette (4 cm). Calculation of the true absorption coefficient requires correction for residual scattering in the filtered water samples. Following Bricaud *et al.* (1981), we assumed that apparent absorption was caused by scattering by filter-passing colloids at a long reference wavelength (700 nm) (negligible true absorption). The equation given by Davies-Colley & Vant (1987) was used to calculate the true absorption coefficient from the apparent absorption coefficient by correcting for residual scattering:

$$a = a_\lambda - a_L{}^{L/A} \tag{2}$$

Absorption coefficients were derived for the reference wavelengths of 300, 340 and 440 nm (a_{300}, a_{340}, a_{440}) representing absorption of UV-B, UV-A and PAR, respectively. Absorption coefficients were reported for a 1-m path.

Light attenuation

Depth profiles of downwelling (E_{od}) and upwelling (E_{ou}) irradiance were analysed using the methods of Kirk (1994a) to estimate coefficients of light attenuation, absorption and scattering. The conformations of the upward and downward sensors were appropriate for measuring quantities proportional to the sum of scalar and vector irradiance (Hojerslev, 1975). Vector irradiance (E) was calculated as downwelling minus upwelling radiation; scalar irradiance (Eo) was calculated as the sum of upwelling and downwelling radiation. Coefficients of light attenuation were calculated as the slope of a line obtained by plotting the natural logarithm of irradiance against depth. The attenuation coefficient for downwelling irradiance (K_d) was determined from a linear regression of the natural logarithm of downwelling irradiance against depth. The attenuation coefficient for net downward irradiance (K_e) was estimated from a linear regression of the natural logarithm of downwelling minus upwelling irradiance against depth. Correlation coefficients derived from fitting least squares linear regressions to irradiance data were uniformly high ($R^2 > 0.98$). The standard error of the slope was less than 5% for 90% of the regressions.

The absorption coefficient (a_{PAR}) was calculated as the product of K_e and the average cosine (u). The average cosine is the ratio of vector (Ed − Eu) to scalar (Ed + Eu) irradiance which varies as a function of the amount of upwelling radiation within the water column. An increase in scattering will result in an increase in upwelling radiation and a decrease in the average cosine. The scattering coefficient (b) was estimated from K_d and a_{PAR} according to the expression developed by Kirk (1994a):

$$b = (K_d{}^2 - a^2) / 0.25a \tag{3}$$

The method by which the scattering coefficient is calculated assumes that upwelling irradiance originates entirely from the scattering of light within the water column. Light reflecting from the bottom will increase upwelling irradiance and result in overestimation of the scattering coefficient. To examine the validity of this assumption, estimates of average cosine were plotted against depth for all sites. The average cosine exhibited little variability with depth indicating that reflectance from the bottom did not contribute significantly to measurements of upwelling irradiance. Estimates of average cosine calculated for the middle of the photic zone (10% light level) were used to calculate absorption coefficients.

The mechanisms regulating light attenuation in the epilimnion and hypolimnion may differ and result in changes in both the rate of light attenuation with depth, and in the relative contributions of scattering and absorption. Optical stratification is more likely to occur in deep lakes where thermal stratification prevents mixing of the upper and lower water column. For the subset of lakes where $z_{1\%}$ (PAR) exceeded the depth of the mixed zone (29 sites), we calculated separate attenuation, absorption and scattering coefficients for the epilimnion and hypolimnion using the average cosine for that layer. Light coefficients were greater in the hypolimnion at 25 of the 29 sites, primarily because of increases in scattering. The average attenuation coefficients for the epilimnion and hypolimnion were 0.45 and 0.66 m^{-1}, respectively. Results from these analyses suggest that optical stratification is common among deep Adirondack lakes (depth > 9 m), but for the majority of these lakes, coefficients derived for the entire photic zone provided an adequate representation attenuation, absorption and scattering.

Results

Coefficients of PAR attenuation for Adirondack lakes (Table 1) range from values comparable to those for the clearest inland waters ($K_d < 0.20$ m^{-1}) to those reported for highly coloured lakes ($K_d > 2.00$ m^{-1}; Kirk, 1994a). The depth of the photic zone ($z_{1\%}$ PAR) can be approximated as $4.6/K_d$, assuming that attenuation is approximately constant with depth. Thus, the variation in K_d encountered in this survey corresponds to a range of $z_{1\%}$ from 0.5 to > 20 m. The majority of lakes (75%) exhibited attenuation coefficients in the range from 0.2 to 1.0 m^{-1} (Fig. 1) and attenuation depths ranging from 5 to 20 m. A frequency distribution of K_d values was generated from the subset of sites ($n = 30$) which were a random sample of the EPA Adirondack Regional survey. These were weighted according to their probability of occurrence and extrapolated to a target population of Adirondack lakes (see 'Methods'). This frequency distribution was generally similar to that of the eighty-five-lake data set, with lakes exhibiting K_d values between 0.2 and 1.0 m^{-1} accounting for 94% of the population (Fig. 1). The two distributions differed in that the non-random sampling included a greater proportion of lakes in which K_d exceeded 1.0 m^{-1}. These lakes were characterized by their small surface area (mean = 4 ha), shallow depth (mean = 6 m), low pH (mean = 5.13) and high DOC (mean = 7.96). This group also included a disproportionate fraction of the seepage lakes sampled in the eighty-five-lake survey.

Absorption coefficients (a_{PAR}) derived from upwelling and downwelling irradiance exhibited a range and distribution of values closely comparable to that

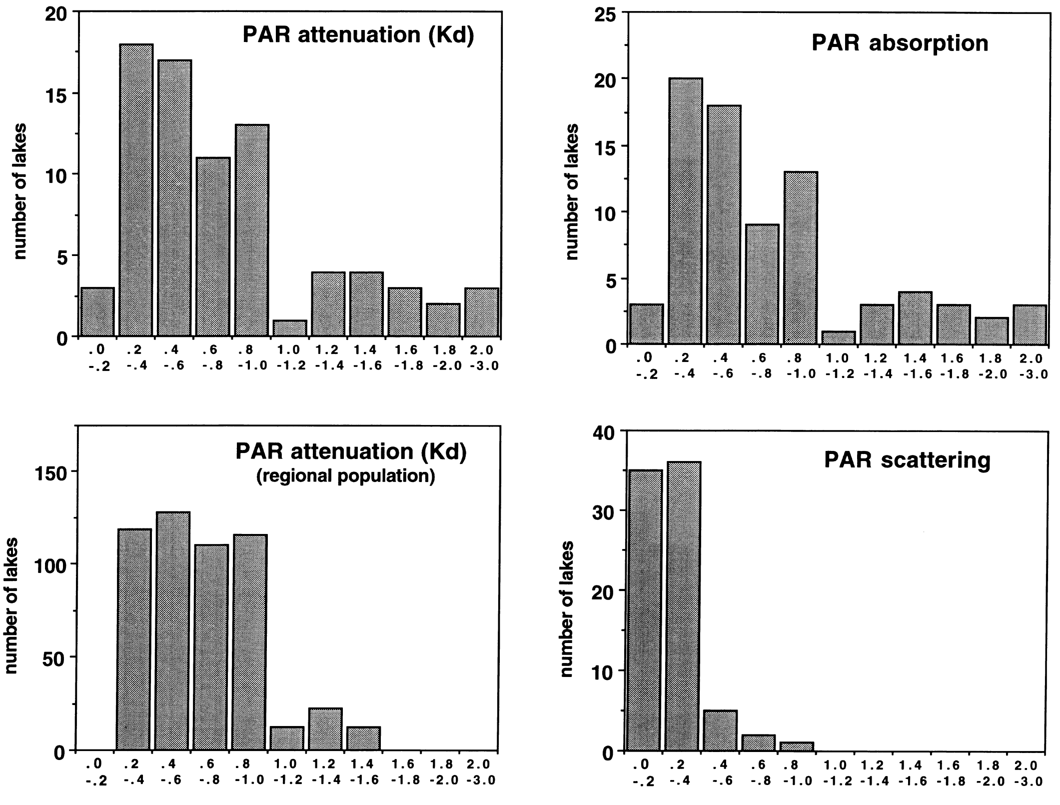

Fig. 1 Frequency distributions of attenuation (K_d), absorption and scattering coefficients (PAR m^{-1}) for 85 Adirondack lakes and an extrapolated distribution for 619 Adirondack lakes (K_d only) based on a randomly selected subset of the target population (see Methods).

Table 2 Univariate and multivariate regression models relating attenuation (K_d PAR) and absorption (a_{440}, a_{340} and a_{300}) coefficients to variation in lake dissolved organic carbon (DOC; mg L^{-1}), chlorophyll (μg L^{-1}) and pH

Predicted	Model equation	Number	R^2	*P*-value
K_d PAR	$K_d = 0.19(DOC) - 0.09$	73	0.72	0.0001
	$K_d = 0.16(DOC) + 0.02(CHL) - 0.09$	73	0.81	0.0001
	$K_d = 0.19(DOC) - 0.14(pH) - 0.14$	73	0.73	0.0001
	$K_d = 0.15(DOC)^{1.08}$	73	0.90	0.0001
a_{440}	$a_{440} = 0.55(DOC) - 1.10$	76	0.72	0.0001
	$a_{440} = 0.48(DOC) + 0.04(CHL) - 1.08$	76	0.77	0.0001
	$a_{440} = 0.53(DOC) - 0.30(pH) + 0.63$	76	0.73	0.0001
	$a_{440} = 0.11(DOC)^{1.60}$	76	0.85	0.0001
a_{340}	$a_{340} = 3.03(DOC) - 5.84$	76	0.79	0.0001
	$a_{340} = 2.83(DOC) + 0.11(CHL) - 5.76$	76	0.80	0.0001
	$a_{340} = 2.95(DOC) - 1.50(pH) + 2.85$	76	0.80	0.0001
	$a_{340} = 0.62(DOC)^{1.59}$	76	0.90	0.0001
a_{300}	$a_{300} = 5.30(DOC) - 9.94$	76	0.81	0.0001
	$a_{300} = 4.99(DOC) + 0.17(CHL) - 9.79$	76	0.82	0.0001
	$a_{300} = 5.17(DOC) - 2.55(pH) + 4.84$	76	0.82	0.0001
	$a_{300} = 1.16(DOC)^{1.57}$	76	0.91	0.0001

for attenuation coefficients (Fig. 1). By comparison, scattering coefficients were lower (seventy-one sites < 0.4 m^{-1}) and fell within a narrower range of values (0.01–0.92 m^{-1}; Fig. 1). We calculated the ratio of absorption to scattering as an index of their relative contributions to PAR attenuation. For the majority of lakes (87%), absorption was greater than scattering (ratio > 1.5) and scattering exceeded absorption at only three sites where absorption coefficients were relatively low ($a_{PAR} = 0.21–0.43\ m^{-1}$). These results suggest that absorption is the dominant mechanism attenuating PAR and that the contribution of scattering is minor in a large majority of Adirondack lakes.

Variation in PAR attenuation was largely explained by differences in lake DOC concentrations. A univariate regression model based on DOC accounted for 72% of the variance in K_d (Table 2). The linear model provided a reasonable approximation of the relationship between K_d and DOC (Fig. 2). Residuals from this model were significantly correlated with lake chlorophyll concentrations, but inclusion of a chlorophyll term in a multivariate regression accounted for only an additional 9% of the variance in K_d (Table 2). We estimated the phytoplankton component of PAR absorption as the product of measured chlorophyll concentrations and the mean spectral chlorophyll absorption coefficient. Using a value approximating the upper limit of chlorophyll absorption (Bannister & Weidemann, 1984), we estimated that the phytoplankton component of absorption was less than 0.10 m^{-1} in

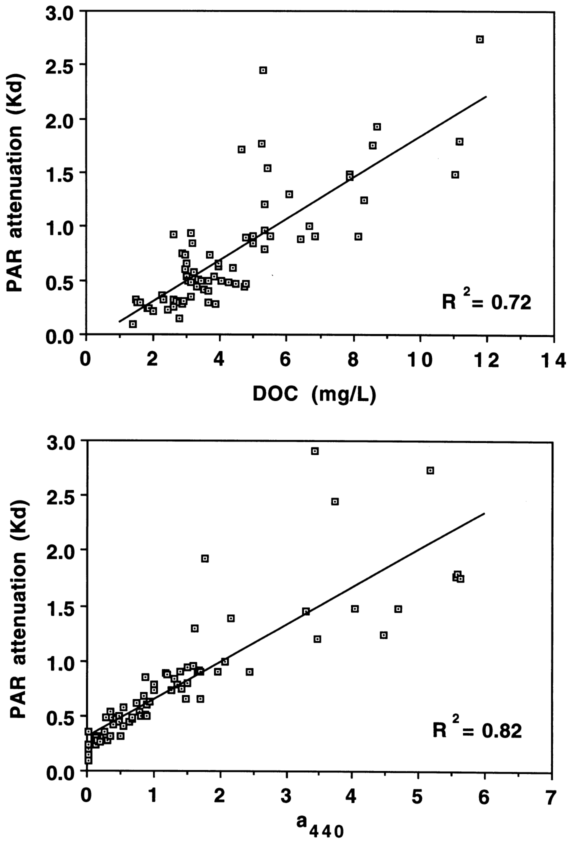

Fig. 2 Photosynthetically active radiation attenuation (K_d) as a function of (a) dissolved organic carbon concentrations (mg L^{-1}) and (b) absorption measured at 440 nm (a_{440}) for eighty-five Adirondack lakes.

80% of the surveyed lakes. Among the six lakes exhibiting chlorophyll concentrations greater than 20 μg L^{-1}, the phytoplankton component of PAR absorption was estimated to be between 0.21 and 0.53 m^{-1} and accounted for a variable proportion of a_{PAR} (mean = 28%, range = 7–76%).

To characterize the light-absorbing properties of dissolved organic compounds, we measured absorption spectra for lakewater samples collected from each site. Light absorption decreased exponentially with increasing wavelength in the UV and visible spectrum (Fig. 3). A linear regression of log-transformed absorption coefficients was used to model the absorption spectra and to calculate absorption coefficients for the reference wavelengths (300, 340 and 440 nm). The linear model provided a useful approximation for absorption spectra ($R^2 > 0.98$), although some non-linearity was evident in the range from 270 to 280 nm. Non-linearity also occurred at longer wavelengths (> 400 nm) when concentrations of dissolved pigments were low (e.g. Silver Lake, Fig. 3). The change in slope at wavelengths approaching 700 nm may result from an over-correction for scattering when absorption measurements are of low relative precision (Davies-Colley & Vant, 1987). To avoid the non-linear regions of the spectrum, regression equations were derived from absorption values measured in the range from 280 to 450 nm. The slopes of the regressions were similar among the surveyed lakes (mean = 0.0193, c.v. = 21%) and comparable to the averages for sixty-five lakes in North and South America (0.0181; Morris *et al.*, 1995) and twelve New Zealand lakes (0.0187; Davies-Colley & Vant, 1987).

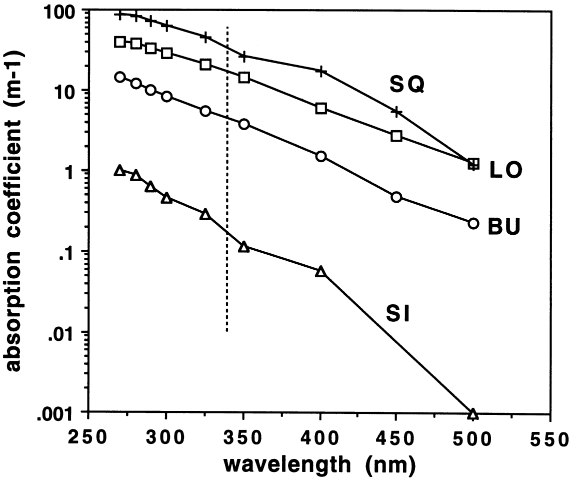

Fig. 3 Representative absorption spectra for four Adirondack lakes: (△) Silver Lake (K_d = 0.09 m^{-1}, DOC = 1.40 mg L^{-1}); (○) Bubb Lake (K_d = 0.61 m^{-1}, DOC = 4.39 mg L^{-1}); (□) Long Lake (K_d = 1.20 m^{-1}, DOC = 5.31 mg L^{-1}); and (+) Squash Pond (K_d = 2.74 m^{-1}, DOC = 11.81 mg L^{-1}).

Absorption coefficients representing PAR attenuation (a_{440}) ranged from 0.015 to 8.841 m^{-1} (mean = 1.432 m^{-1}), and showed good correspondence to a_{PAR} (R^2 = 0.75) derived from measurements of upwelling and downwelling irradiance, and to K_d (R^2 = 0.82; Fig. 2). Residual variation in the K_d-DOC relationship was partly caused by differences in the light-absorbing properties of DOC among lakes. DOC-specific rates of absorption at 440 nm were twofold higher among lakes where DOC exceeded 5 mg L^{-1} (mean = 0.406 m^{-1}/mg L^{-1}) in comparison to lakes of low DOC (mean = 0.183 m^{-1}/mg L^{-1}). As a result, the use of a power model ($K_d = X[DOC]^Y$) provided the best approximation of the K_d-DOC relationship (R^2 = 0.90; Table 2). Power models using lake DOC concentrations as a predictor also accounted for a large proportion of the variance in a_{300} (91%), a_{340} (90%) and a_{440} (85%; Table 2, Fig. 4). For the range of DOC concentrations encountered in this study, a unit increase in DOC corresponded to a mean increase (± SE) in a_{300} of 5.30 ± 0.31, an increase in a_{340} of 3.03 ± 0.19 and an increase in a_{440} of 0.55 ± 0.04.

Coefficients derived for the reference wavelengths representing UV-A (a_{340}) and UV-B (a_{300}) absorption varied by more than two orders of magnitude (Table 1). Absorption of UV-A radiation averaged 8.229 m^{-1} (range = 0.145–45.298 m^{-1}) and absorption of UV-B radiation averaged 14.712 m^{-1} (range = 0.461–77.347 m^{-1}). Median values of inferred attenuation depths were 0.75 m (UV-A) and 0.45 m (UV-B). We used the ratio of inferred attenuation depth to maximum depth ($z_{1\%}/z_{max}$) as an index of UV exposure for organisms residing in the water column (Williamson *et al.*, 1996). Frequency distributions of these values were derived from both the 85-lake survey and from the subset of sites (n = 30) which were a random sample of the EPA Adirondack Regional Survey. The two frequency distributions showed similar patterns (Fig. 5). For the large majority of lakes, $z_{1\%UV\text{-}A}$ represented less than 20% of the water column (median = 11%) and $z_{1\%UV\text{-}B}$ less than 10% of the water column (median = 6%). The two distributions differed in that the 85-lake survey group included a greater number of sites where $z_{1\%UV\text{-}A}$ (eight lakes) and $z_{1\%UV\text{-}B}$ (three lakes) accounted for

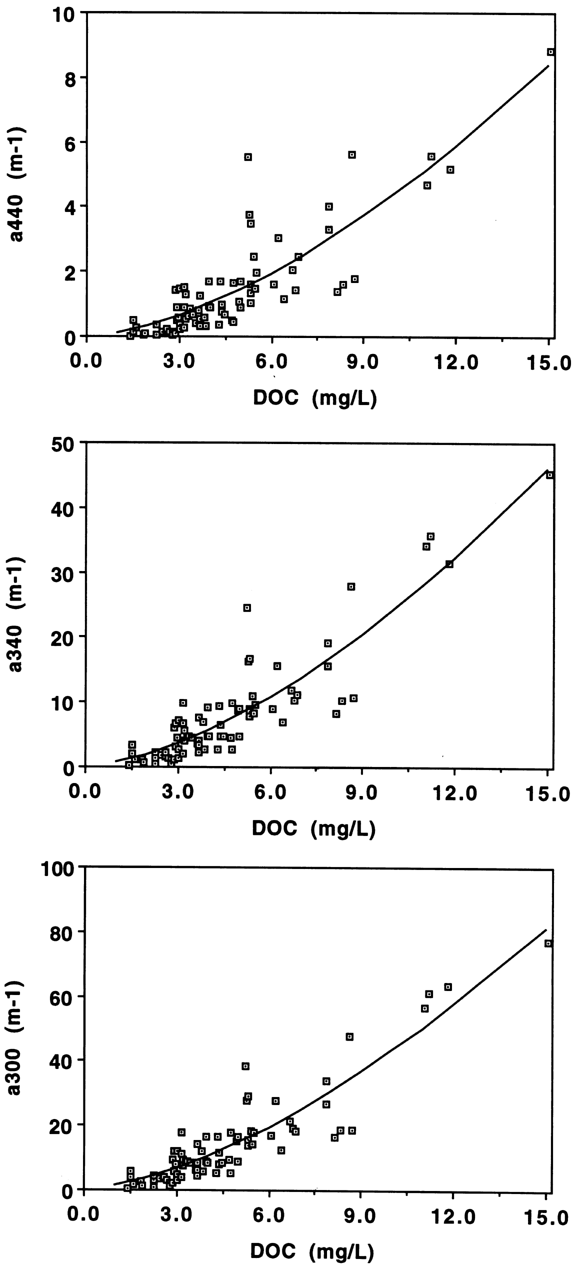

Fig. 4 Absorption at wavelengths representing (a) photosynthetically active radiation (a_{440}), and (b) ultraviolet-A (a_{340}) and (c) ultraviolet-B radiation (a_{300}) as a function of dissolved organic carbon concentrations (mg L^{-1}) in 85 Adirondack lakes. Regression lines are based on power models of the form: $a_{\lambda} = X[DOC]^{Y}$.

more than half of the water column at the deepest point of the lake. These lakes were characterized by their small surface area (mean = 12 ha), moderate depth (mean = 8 m), low pH (mean = 5.09) and low DOC (mean = 2.42).

To assess potential effects of acidification on light climate, we used lake pH as a predictor of residual variance in models relating attenuation and absorption coefficients to lake DOC. Incorporation of a term for lake pH improved all four models (K_d, a_{440}, a_{340} and a_{300}), although the additional variance explained was only 1% in each case (Table 2). The coefficient for the pH term was negative suggesting that, for lakes of comparable DOC, light coefficients tend to be higher not lower in acidic lakes. We calculated average attenuation and absorption coefficients among lakes grouped according to pH. Lakes in which DOC exceeded 5 mg L^{-1} were not included in these analyses to exclude sites which were acidic because of the

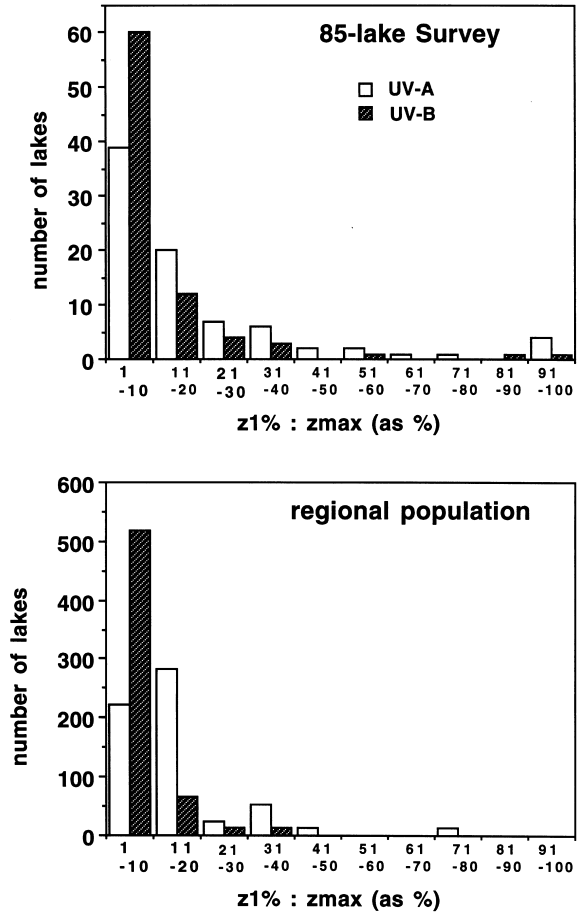

Fig. 5 The proportion of the water column (%) receiving a significant flux of ultraviolet-A and ultraviolet-B radiation calculated as the ratio of inferred attenuation depth to lake maximum depth ($z_{1\%}/z_{max}$). Frequency distributions were derived for the eighty-five-lake survey and for a regional population of 619 lakes (based on a randomly selected subset of the target population).

Table 3 Average attenuation coefficients (K_d PAR), absorption coefficients (a_{440}, a_{340} and a_{300}), dissolved organic carbon (DOC) concentrations and DOC-specific PAR absorption (a_{440}:DOC) for 58 low-DOC (< 5 mg L^{-1}) Adirondack lakes grouped according to current (measured) pH. Differences among group means were not statistically significant

		Absorption coefficient (m^{-1})					
Lake pH	K_d (m^{-1})	a_{440}	a_{340}	a_{300}	DOC (mg L^{-1})	a_{440}: DOC	Number
4–5	0.53	0.41	2.72	5.01	3.02	0.13	14
5–6	0.45	0.62	3.83	7.03	3.04	0.20	23
6–7	0.58	0.82	5.47	10.13	3.75	0.20	21

presence of organic acids. The mean attenuation coefficient for lakes exhibiting pH < 5.0 was not significantly different from the means for moderately acidic lakes (pH = 5.0–6.0) and weakly acidic lakes (pH = 6.0–7.0) based on a one-way analysis of variance (ANOVA) (Table 3). Light absorption coefficients, DOC concentrations and DOC-specific absorption were also not significantly different among the three groups of lakes (Table 3).

The survey group included thirty lakes for which historical changes in lake acidity were inferred from diatom-based estimates of pre-industrial and present-day pH (Cumming *et al*., 1992). These lakes were divided into three groups: (1) acidic lakes which have experienced recent acidification (n = 11); (2) acidic lakes in which pH has not changed since pre-industrial times (n = 10); and (3) non-acidic lakes (pH > 5.5) in which pH has not changed since pre-industrial times (n = 9). Among lakes designated as recently acidified, decreases ranged from 0.5 to 1.2 pH units relative to current pH. The optical characteristics of these lakes were compared to acidic and non-acidic lakes which had not undergone recent changes in pH (inferred historical change < 0.5 pH units). Attenuation and absorption coefficients were lower among recently acidified lakes in comparison to acidic and circumneutral lakes which have not undergone recent acidification (Table 4). However, a one-way ANOVA failed to detect significant differences in attenuation, absorption, DOC or DOC-specific absorption among the three groups of lakes.

Discussion

Absorption was the dominant mechanism attenuating PAR in Adirondack lakes. Scattering was a minor component of attenuation except in the hypolimnia of several lakes exhibiting strong thermal and chemical stratification. The relatively small contribution by scattering suggests that catchment inputs of mineral particulates and particulate organic carbon are not important factors influencing the optical properties of Adirondack lakes. Most Adirondack lakes occur in relatively undisturbed catchments where the effects of particulates on attenuation are minimal. Low scattering coefficients also suggest that autochthonous sources of particulate organic matter such as sediment resuspension and phytoplankton production are not important factors regulating attenuation. Phytoplankton were not abundant at the majority of our sites and were not important determinants of attenuation.

Substantial variation in transparency was observed among the eighty-five lakes included in this regional survey. Attenuation depths ($z_{1\%}$) for PAR ranged

Table 4 Average attenuation coefficients (K_d PAR), absorption coefficients (a_{440}, a_{340} and a_{300}), dissolved organic carbon (DOC) concentrations and DOC-specific PAR absorption (a_{440}:DOC) for 30 Adirondack lakes grouped according to current (measured) pH and inferred historical changes in lake pH (see text). Differences among group means were not statistically significant

			Absorption coefficient (m^{-1})					
Lake pH (range)	ΔpH	K_d (m^{-1})	a_{440}	a_{340}	a_{300}	DOC (mg L^{-1})	a_{440}: DOC	Number
Acidic (4.5–5.5)	Acidified (ΔpH > 0.5)	0.61	0.92	5.34	9.78	3.93	0.20	11
Acidic (4.6 – 5.8)	Non-acidified (ΔpH < 0.5)	0.65	1.14	6.29	11.39	4.08	0.25	10
Non-acidic (6.1–7.0)	Non-acidified (ΔpH < 0.5)	0.72	1.12	6.57	12.38	4.86	0.24	9

from 0.5 to > 20 m, while inferred attenuation depths for UV-B and UV-A ranged from a few centimetres to greater than 5 m. Median values of UV-A penetration (0.75 m) and UV-B penetration (0.45 m) were comparable to median values reported for lakes in the north-eastern U.S.A. (0.92 and 0.39 m, respectively; Williamson *et al.*, 1996). The latter were derived from measured lake DOC concentrations and empirical relationships relating wavelength-specific attenuation coefficients to DOC. Median values for inferred attenuation depths expressed as a proportion of lake maximum depth (UV-A = 11%, UV-B = 6%) were lower than those reported by Williamson *et al.* (1996) (22% and 9%, respectively). Differences could be accounted for by the greater median depth among lakes included in this survey (8 m) in comparison to those studied by Williamson *et al.* (1996) (5.8 m).

Ultraviolet transmission varied greatly among Adirondack lakes, but by our estimates of attenuation, UVR only rarely penetrated more than 50% of the water column. Inferred attenuation depths of UV-A and UV-B exceeded 50% of $z_{\max}$ at only three sites (Silver, Mays and Otter). Attenuation depths of UV-A exceeded 50% of $z_{\max}$ at five additional sites. Extrapolation to a target population of 608 Adirondack lakes suggests that UVR attenuation depths exceed 50% of $z_{\max}$ in less than 1% of lakes. These data support recent findings that UVR attenuation depths can represent a significant fraction of the water column in some lakes (Kirk, 1994b; Scully & Lean, 1994; Morris *et al.*, 1995), but suggest that these types of lakes are very rare in the Adirondack region. The lakes which were most impacted by incident UVR exposure were relatively small in surface area (6–21 ha), of variable depth (3–18 m) and low in DOC (1.4–4.2 mg L^{-1}). These lakes are also highly sensitive to anthropogenic acidification, as indicated by their low pH (mean = 5.1) and acid neutralizing capacity (mean = –16 μeq L^{-1}; P. Bukaveckas, unpublished data).

Much of the variation in PAR attenuation and dissolved absorbance of UVR was linked to differences in DOC concentrations. A linear, univariate model based on DOC alone accounted for 72% of the variation in K_d. For the range of DOC concentrations encountered in this survey (1–15 mg L^{-1}), one unit increase in DOC corresponded to a 0.19-m^{-1} increase in K_d (SE ± 0.02). This estimate was similar to the slope of 0.22 m^{-1} reported by Morris *et al.* (1995) for 65 lakes in North and South America. The range and distribution of K_d and DOC values for Adirondack lakes was comparable to those surveyed by Morris *et al.* (1995) in Colorado, Alaska, the north-eastern U.S.A. and Argentina. In our study, chlorophyll was positively correlated with DOC ($R^2 = 0.49$, $P = 0.0001$), as had been reported previously by Vertucci & Likens (1989). However, inclusion of a chlorophyll term in our multivariate models did not substantially improve the prediction of attenuation or absorption coefficients.

DOC concentrations were strongly correlated with absorbance values for filtered lakewater samples. Our best estimates of absorption were derived from univariate power models based solely on DOC. These models accounted for greater than 85% of the variation in PAR, UV-A and UV-B absorption and have the advantage that they account for increasing DOC-specific absorbance observed in high DOC lakes (Morris *et al.*, 1995; this study). Overall, the regression models derived from our data set were similar with respect to model coefficients and predictive power to those described in Morris *et al.* (1995).

Comparisons of acidic and circumneutral lakes in the region did not reveal consistent differences in attenuation, absorption or DOC. The optical characteristics of recently acidified lakes (based on diatom inferences) were not significantly different from acidic lakes which had not undergone recent acidification, although the sample size for this analyses was relatively small ($n = 21$). Previous support for the hypothesis that acidification is associated with increasing water transparency was based largely on site-specific studies, principally whole-lake experiments and a few lakes for which historical data were available. Almer *et al.* (1974, 1978) documented increases in transparency during acidification of some Swedish lakes which they attributed to the coagulation and removal of DOC by monomeric aluminium. Subsequently, Effler *et al.* (1985) showed that seasonal variation in K_d in an acidic Adirondack lake corresponded to changes in DOC which were coupled with the loss of aluminium from the water column. Whole-lake acidification experiments have consistently demonstrated decreases in attenuation (Shearer *et al.*, 1987; Williamson *et al.*, 1996). Bukaveckas & Driscoll (1991b) showed that changes in attenuation following lake neutralization were comparable to those observed during experimental acid-

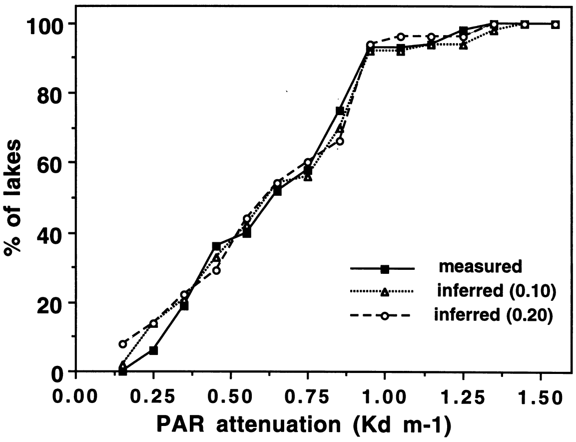

Fig. 6 Cumulative frequency distributions of current (measured; ■) and pre-1850 (inferred) K_d values of photosynthetically active radiation (PAR) for the regional population of 619 lakes. Inferred values were derived from diatom-based estimates of acidification and assuming a change in K_d PAR of 0.10 (△) or 0.20 m^{-1} (○) per unit change in pH.

ification. Changes in PAR attenuation following neutralization of an acidic Adirondack lake were sufficient to bring about changes in the depth-distribution of phytoplankton and aquatic macrophytes (Bukaveckas, 1988a,b).

To interpret potential effects of acidification in the context of other factors influencing regional variation in transparency, we attempted to infer historical (pre-acidification) K_d values using data from whole-lake experiments and diatom-based estimates of acidification. Changes in lake pH since 1850 were taken from Cumming *et al.* (1992) and we assumed a change in K_d of 0.10 m^{-1} per unit change in lake pH. The rate of change in K_d was an average based on data from six whole-lake acidification and neutralization experiments conducted over a pH range (4.8–7.1) comparable to that of the thirty lakes used in this analyses (Bukaveckas & Driscoll, 1991b). Although the observed change in K_d among various whole-lake experiments was quite consistent (range = 0.09–0.11 m^{-1} per unit pH), we also evaluated the effects of doubling this value on inferred estimates. The thirty lakes for which paleolimnological data were available include sites which have undergone increases as well as declines in pH and these were weighted according to their probabilities of occurrence and extrapolated to a target population of 619 lakes (Church *et al.*, 1989). The distribution of current (measured) K_d values follows closely with that of pre-1850 (inferred) K_d values (Fig. 6), suggesting that anthropogenic inputs have not substantially altered the optical properties of this population of lakes. Results from these analyses suggest that, while the effects of acidification on attenuation may be detectable through site-specific monitoring, the effects on a regional population of lakes, even in an area experiencing widespread acidification (Cumming *et al.*, 1992), are relatively subtle in comparison with other factors contributing to inter-lake variability in attenuation.

Empirical relationships derived from the survey data show that differences in DOC account for a large proportion of the variance in attenuation among Adirondack lakes. However, only a small percentage of the variance in DOC could be explained by lake and catchment parameters examined in this study. Lake surface area was found to be a useful predictor of DOC ($R^2 = 0.33$), whereas lake acidity and trophic state were not. Photosynthetically active radiation attenuation was significantly higher in small lakes (area < 10 ha; $K_d = 1.21\ m^{-1}$) compared to lakes with moderate (10–50 ha; $K_d = 0.53\ m^{-1}$) and large surface areas (area > 50 ha; $K_d = 0.48\ m^{-1}$). Dissolved organic carbon concentrations were two-fold higher and chlorophyll concentrations were three-fold higher among small lakes. Absorption coefficients and light absorption per unit of DOC were also highest in small lakes. The correlation between DOC and lake surface area may reflect differences in lake hydrology related to lake size since lakes grouped in the < 10 ha size class included eighteen out of the twenty seepage lakes sampled in this survey. However, a comparison of light attenuation and DOC among small seepage lakes ($n = 18$) with drainage lakes of comparable size ($n = 36$) was not statistically significant.

Lakes of small surface area have high shoreline length to lake volume ratios, and therefore, are likely to be more strongly influenced by the presence of near-shore wetlands. Adirondack lakes are often ringed by wetlands (Roy *et al.*, 1996) and these may be important source areas of DOC (Schiff *et al.*, 1990; Cirmo & Driscoll, 1993). Driscoll *et al.* (1995) reported that DOC concentrations among sixteen Adirondack lakes were strongly correlated with the presence of near-shore wetlands ($R^2 = 0.85$). Other studies have also documented the relationship between lake DOC and catchment-wetland characteristics (David & Vance, 1991; Kortelainen, 1993; Houle *et al.*, 1995).

The strong dependence of DOC on wetlands, and in turn, of PAR attenuation and UVR absorbance on DOC, suggests that even modest changes in near-shore wetlands would exert a strong influence on light climate. The Driscoll *et al*. (1995) model predicts that a decrease in near-shore wetlands by an area equivalent to 1% total catchment area would result in a decrease in lake DOC of 1.28 mg L^{-1}. For a lake with a DOC concentration of 3.8 mg L^{-1} (median value for this data set), our models predict that a decrease of 1.28 mg L^{-1} would increase the depth of the photic zone ($z_{1\%\ \mathrm{PAR}}$) from 7 to 11 m. Corresponding increases of inferred attenuation depths for UV-A (0.9–1.7 m) and UV-B (0.5–0.9 m) would increase the proportion of the water column receiving substantial UVR to 21% and 11%, respectively, for a lake of median depth (8 m). These analyses suggest that the presence of near-shore wetlands is a key factor influencing regional variability in DOC and light climate among Adirondack lakes.

It is clear from our analyses that DOC has a major influence on the underwater light-field. The amount of DOC in a lake depends on loading from the surrounding catchment and in-lake processes (e.g. photobleaching and microbial utilization) which alter concentration and optical properties. These localized and catchment-scale processes apparently mask more subtle influences on lake DOC associated with human impacts in this region (anthropogenic acidification). Inter-lake variability in light climate arising from differences in catchment DOC loading may be the key determinant of primary production in regions like the Adirondacks where direct human impacts (e.g. nutrient loading) are minimal. Carpenter *et al*. (1998) analysed changes in chlorophyll during whole-lake experiments and found that the effects of changing DOC concentrations were comparable in magnitude to those attributed to nutrient addition and grazer manipulation. Natural variation in lake DOC concentrations may be a major cause of variation in primary productivity in lake districts where cultural eutrophication is not widespread (see also Williamson *et al*., 1999b).

A systematic analyses of catchment attributes which explain variability in lake DOC among Adirondack lakes awaits further study. Spatial variability is likely to be related to the presence and extent of wetlands within the catchment, the proportion of lake inflow which is intercepted by wetlands and wetland-specific differences in DOC export. Catchment-scale information on the presence of wetlands and their hydrogeomorphic position are readily amenable to regional analyses, whereas indicators of wetland functioning which might be used to predict DOC export are more problematic. Our understanding of spatial organization in lake districts will ultimately depend on our ability to characterize the processes acting across ecotonal boundaries and the mechanisms by which these give rise to inter-lake variability.

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