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Ultraviolet radiation in North American lakes: Attenuation estimates from DOC measurements and implications for plankton communities

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Abstract

Climate warming in North America is likely to be accompanied by changes in other environmental stresses such as UV-B radiation. We apply an empirical model to available DOC (dissolved organic C) data to estimate the depths to which 1% of surface UV-B and UV-A radiation penetrate for several major regions of North America. UV attenuation depths are also estimated from DOC data collected from treatment and reference basins during the experimental acidification of Little Rock Lake, Wisconsin.

In some regions of North America 25% of the lakes have 1% attenuation depths for UV-B radiation on the order of 4 m or more (western and northwestern U.S., Newfoundland). In other regions, 75% of the lakes have 1% attenuation depths for UV-B shallower than 0.5 m (Florida, upper midwestern U.S., northwestern Ontario, Quebec, and Nova Scotia). Attenuation depths for UV-A radiation are ~2.5 times as deep as those for UV-B. Experimental acidification approximately doubled the estimated 1% attenuation depths for UV radiation in Little Rock Lake.

The strong dependence of 1% attenuation depth on DOC below the 1–2 mg liter^{-1} DOC range suggests that UV attenuation in low DOC lakes is highly sensitive to even very small changes in DOC. We conclude that changes in climate, lake hydrology, acid deposition, and other environmental factors that alter DOC concentrations in lakes may be more important than stratospheric ozone depletion in controlling future UV environments in lakes.

Freshwater lakes provide key signals of environmental change in the terrestrial watersheds that surround them as well as in populations and in the processes that occur within them. In particular, lakes have provided substantial evidence for regional changes in climate, many examples of which are given in this issue (*see also* Schindler et al. 1990). Other important environmental stresses, however, may change along with climate, and there may be important interactions between these other forms of stress and climate change. One of these stresses about which we know very little is biologically damaging ultraviolet radiation. Interest has recently focused in particular

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on the shorter wavelength UV-B radiation (280–320 nm), which is increasing due to the destruction of stratospheric ozone. Changes in DNA-damaging UV radiation due to ozone depletion have been on the order of 10–20% in north-temperate regions from 1979 to 1992 and even higher in south-temperate and especially Antarctic regions (Madronich 1994).

There is substantial evidence that UV-B radiation may have a negative impact on many components of freshwater ecosystems ranging from bacteria and phytoplankton (Karentz et al. 1994; Vincent and Roy 1993) to zooplankton and fish (Siebeck et al. 1994; Williamson and Zagarese 1994; Williamson 1995). In addition, the impact of UV-B may not be uniform on all trophic levels within an ecosystem and may thus be difficult to predict. For example, some invertebrate grazers, such as chironomids in stream ecosystems, may be more damaged by UV-B radiation than the primary producers (Bothwell et al. 1994); primary producer biomass may actually increase over the longer term when exposure to UV-B radiation increases. Similarly, UV-B radiation may cause substantial damage to zooplankton grazers that remain in the surface waters of pelagic ecosystems during the day (Williamson et al. 1994; Zagarese et al. 1994).

Despite these trends of increasing UV-B and the demonstrated ability of UV radiation to damage living organisms, very little is known about the ecology of UV radiation in freshwaters. Interestingly, the attenuation of UV-A (320–400 nm) and UV-B radiation in freshwater ecosystems is controlled to a great extent by concentrations of dissolved organic C (DOC) in the water column (Kirk 1994*a,b*), and DOC in turn can be influenced by regional changes in climate as well as other environmental variables (Schindler et al. 1990, 1992). Empirical models have been developed to predict the attenuation of UV radiation in lakes from DOC measurements (Scully and Lean 1994; Morris et al. 1995). These models indicate that DOC is the most important variable for predicting UV attenuation in lakes without actual optical measurements. Here, we use one of these empirical models along with DOC data from the National Surface Water Survey (U.S. EPA NSWS) to estimate the depth to which 1% of surface UV-B and UV-A radiation penetrates water bodies in some of the major lake regions of North America.

In addition, we use this same approach with DOC, chlorophyll *a*, and temperature data from the 1991 pilot survey of the Environmental Monitoring and Assessment Program (U.S. EPA EMAP) to predict and compare 1% attenuation depths for UV to the mixing and maximum depths of lakes in the northeastern U.S. The fundamental concept here is that the thermocline in stratified lakes represents a critical lower habitat boundary for many planktonic organisms. Although many organisms cross this boundary, time spent below it may alter fundamental ecological interactions in detrimental or beneficial ways. For example, lower temperatures may reduce the mass-specific growth and metabolic rates of bacteria and phytoplankton (Eppley 1972; Goldman and Carpenter 1974; Morris and Lewis 1992; Fuh-Kwo and Ducklow 1994) as well as the growth and reproductive rates and hence fitness of zooplankton (Orcutt and Porter 1983; Stich and Lampert 1984; Dawidowicz and Loose 1992). Variations in resource quantity and quality as well as predation risk are also likely to occur along this vertical gradient in ways that further increase the potential for interactions between UV radiation and other important ecological variables. For this reason it is important that we know something about the depth to which UV radiation penetrates in freshwater ecosystems, how it may vary among lake regions, and how UV may interact with thermal gradients that are likely to be altered by climate change.

Because DOC plays a critical role in the attenuation of UV in lakes, any environmental change that influences DOC in turn will influence UV penetration. Although acid deposition is known to decrease DOC and increase water clarity in lakes (Yan 1983; Schindler et al. 1992; Driscoll and van Dreason 1993), no published data are available on how acidification may influence UV attenuation. Here, we use changes in DOC in response to the experimental acidification of Little Rock Lake, Wisconsin (Brezonik et al. 1993), to illustrate how environmental changes such as acid deposition may also alter UV attenuation in lakes. We argue that changes in environmental variables (such as climate and acidification) that influence changes in DOC concentrations across environmental gradients in space or time may be more important than stratospheric ozone depletion in controlling future levels of potentially damaging UV radiation in lakes.

Methods

The empirical model we use to predict 1% attenuation depths for UV was developed from UV radiation, chlorophyll, and DOC data on 65 glacial lake sites in North and South America (Morris et al. 1995). The core equations in this model are

for UV-B:

$$K_{d320} = 2.09[\mathrm{DOC}]^{1.12} \qquad (r^2 = 0.87, N = 63); \quad (1)$$

for UV-A:

$$K_{d380} = 0.83[\mathrm{DOC}]^{1.16} \qquad (r^2 = 0.92, N = 62); \quad (2)$$

for PAR:

$$K_{d\mathrm{PAR}} = 0.22[\mathrm{DOC}] + 0.07[\mathrm{Chl}\ a] - 0.05 \qquad (r^2 = 0.68, N = 63). \quad (3)$$

DOC is expressed in mg liter^{-1} and chlorophyll *a* in μg liter^{-1}. Although chlorophyll is an important predictor of PAR (photosynthetically active radiation, 400–700 nm) attenuation in this model (Eq. 3), neither chlorophyll nor particles are significant predictors of UV attenuation in this set of oligotrophic to mesotrophic lakes (Morris et al. 1995). The low r^2 (0.68) and broad waveband for PAR make predicting PAR attenuation depths from DOC and chlorophyll very crude, but they are included here to give the reader a general frame of reference within which to interpret the 1% attenuation depths for UV radiation. Because of this, the 1% attenuation depth estimates for PAR presented here should not be used in any quantitative modeling efforts or other investigations. Similarly, the modeled estimates of UV attenuation presented here are only first-order estimates and are not intended to replace the careful optical measurements that will be necessary to better understand the importance of UV radiation in aquatic ecosystems.

We estimated the depth to which 1% of surface irradiance penetrated for UV-B (320-nm band of Biospherical Instr. PUV-501) and UV-A (380-nm band of PUV-501). The 1% attenuation depths ($Z_{a\lambda}$, in m) were derived from the diffuse attenuation coefficient for downwelling radiation ($K_{d\lambda}$, in m^{-1}) according to

$$Z_{a\lambda} = 4.605\ K_{d\lambda}^{-1} \tag{4}$$

where λ is the wavelength (nm) of the light of concern. This 1% attenuation depth is equivalent to the depth (in m) at which the optical depth (a unitless number equal to $K_{d\lambda}Z$, where Z is depth in m; Kirk 1994*b*) is equal to 4.605. We use the standard exponential equation for K_d:

$$E_{dz} = E_{d0} \exp\left[-(K_d)z\right] \tag{5}$$

E_{dz} and E_{d0} are downwelling irradiance at depths z and 0 respectively (Kirk 1994*a,b*). Because of the wavelength dependency of light attenuation in the water column, it is theoretically preferable to apply K_d and related constructs only to fairly narrow-wavelength bands of light that are essentially monochromatic (Kirk 1994*a,b*). Our model was developed with a Biospherical PUV-501 profiling ultraviolet radiometer that measures radiation in four UV wavebands centered on 305, 320, 340, and 380 nm, and half bandwidths of 8–10 nm (= full width at half-maximum response), as well as PAR (400–700 nm). This instrument is identical to the PUV-500 except that it has a special 50-m depth transducer that increases the resolution of depth measurements. In detailed instrument comparisons the values of K_d estimated for UV radiation with the PUV compared favorably with those estimated for the same wavelength regions with scanning single- and double-monochromator spectroradiometers including the Optronic OL 752-PMT and the LiCor LI-1800 UW (Kirk et al. 1994).

For the more detailed analyses of the EMAP data for the northern U.S., we estimated the proportion of the mixed layer penetrated by UV-B and UV-A radiation for each lake and then expressed these data as medians and quartiles for the entire lake population using cumulative distribution functions. We defined the lower boundary of the mixed layer as the upper edge of the thermocline, where the thermocline is defined by a temperature gradient of $\geq 1°C\ m^{-1}$ (Wetzel 1983). Although we have tried to follow limnological conventions, it must be stressed that the habitat boundaries as defined here according to temperature and UV radiation are somewhat arbitrary. Their use is in their ability to help us explore the sensitivity of lakes in different regions to UV radiation and the potential for interactions between UV radiation and other relevant characteristics of the vertical habitat gradient in lakes. There is also a potential problem with relating thermocline depth to UV attenuation depth as we have done here because DOC has the potential to

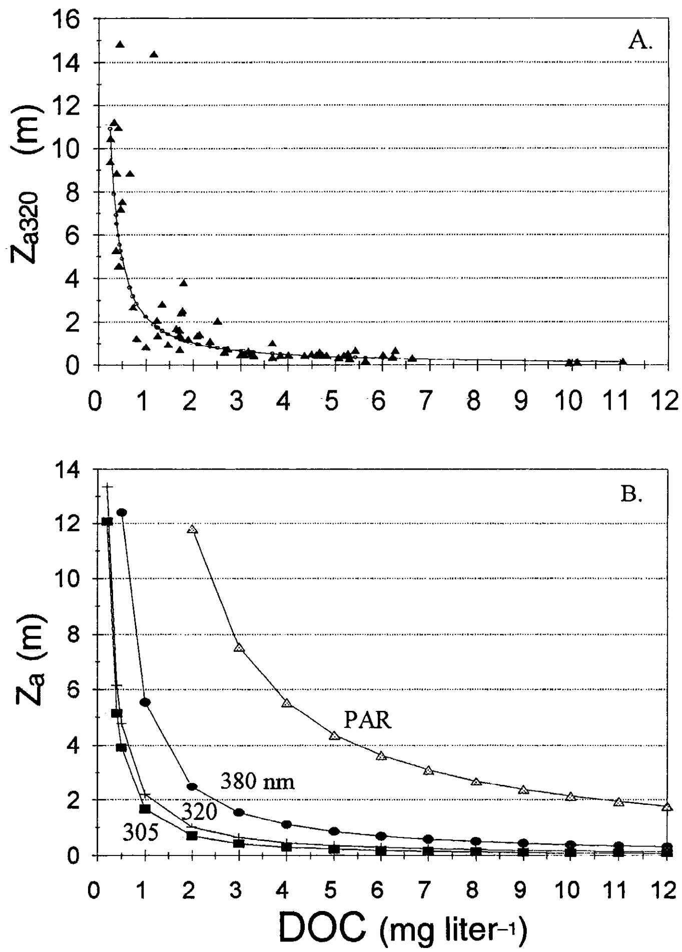

Fig. 1. Relationship between 1% attenuation depth (Z_a = 1% of surface irradiance) and dissolved organic C concentration (DOC) based on a survey of 65 glacial lakes in North and South America (Morris et al. 1995). These empirical relationships were used in the current study to estimate 1% attenuation depths for lakes in different regions of North America. A. Individual data points (▲) and model (–○–) for 320 nm. B. Model curves for 305, 320, and 380 nm and photosynthetically active radiation (PAR, 400–700 nm).

influence mixing depth by influencing PAR attenuation (e.g. Fig. 1B). However, regression analysis showed that DOC explained only a small proportion of the variance in mixing depth ($r^2 = 0.13$) for the 73 lakes in the 1991 EMAP pilot study used here, suggesting that variables other than DOC are primary in controlling mixing depth (Table 1). By using the 320-nm band of the PUV, we are estimating the maximum 1% attenuation depths for UV-B radiation. Attenuation depth estimates from our empirical UV-DOC model for the 305-nm band are somewhat less than those for the 320-nm band (Fig. 1B).

The DOC data for the major lake regions of North America were obtained from the NSWS (Charles 1991*a*), and represent 1,612 lakes sampled during the eastern lake survey (ELS) under isothermal conditions in the fall of 1984, and 720 lakes sampled during the western lakes

Table 1. Lakes, locations (lat, long in decimal notation), DOC (mg liter^{-1}) and Chl a (μg liter^{-1}) values, elevations (m asl), and mixing depths (m) for the 1991 EMAP pilot study.

Lake	Location	DOC	Chl a	Elevation	Z_{mix}	Lake	Location	DOC	Chl a	Elevation	Z_{mix}
Bissonette Pond, CT	41.92, 72.21	5.10	8.05	205	0.0	Long Pond, NY	44.65, 74.49	9.74	33.00	380	1.5
Wyassup Lake, CT	41.48, 71.87	3.59	2.51	92	3.0	Lake Kushaqua, NY	44.51, 74.11	5.39	6.10	509	4.0
Moose Pond, ME	43.58, 70.93	2.80	1.60	175	5.7	Hope Pond, NY	44.51, 74.12	7.90	7.88	515	1.5
Mountain Pond, ME	44.89, 70.64	3.86	3.15	686	5.0	Second Pond, NY	43.66, 74.08	4.61	10.20	681	4.4
Shaw Pond, ME	45.28, 70.27	7.33	4.07	385	0.0	Squaw Lake, NY	43.63, 74.73	2.91	2.13	646	6.6
Loon Lake, ME	46.14, 69.64	6.48	3.22	313	8.4	Indian Lake, NY	43.61, 74.75	3.72	2.33	654	4.0
Bear Pond, ME	45.33, 69.60	5.20	6.73	332	0.0	Middle Flow, NY	43.38, 74.02	7.04	15.30	557	0.0
Alder Brook Stream, ME	44.91, 69.25	7.47	NA	66	1.7	Big Alderbed, NY	43.32, 74.70	5.43	6.12	550	2.1
Female Pond, ME	45.74, 69.22	6.88	3.05	296	5.0	Long Lake, NY	43.31, 74.71	0.88	0.92	667	6.0
Gardner Pond, ME	46.96, 68.88	3.59	2.08	346	20.0	Schroon Lake, NY	43.81, 73.76	2.71	2.06	246	7.0
Little Black Ponds, ME	46.97, 68.85	4.79	1.61	399	3.5	Gull Pond, NY	43.83, 73.70	4.19	3.63	320	3.0
Upper Sysladobsis Lake, ME	45.30, 68.14	4.80	6.30	102	7.0	Gerlach Pond, NY	42.31, 78.97	6.22	34.90	421	0.0
East Branch, MA	42.45, 72.24	5.39	27.20	172	0.0	Mosko Pond, NY	42.45, 77.63	10.68	187.00	515	1.2
S. Ashburnham Reservoir, MA	42.59, 71.91	4.43	3.81	251	0.0	Crystal Lake, NY	43.82, 76.12	4.21	15.10	129	6.6
Muddy Pond, MA	42.60, 71.88	3.89	2.54	317	0.0	White Lake, NY	43.00, 76.04	2.54	1.73	164	11.9
Lithia Springs Reservoir, MA	42.29, 72.56	2.55	1.83	72	1.5	Hyde Lake, NY	44.24, 75.83	3.48	23.50	117	7.4
Kendall Reservoir, MA	42.34, 71.89	4.10	2.06	248	1.5	Briscoe Lake, NY	41.76, 74.87	8.38	19.70	358	2.5
Holden Reservoir, MA	42.31, 71.87	3.32	0.86	229	5.0	Little Lilly Pond, NY	43.91, 74.77	9.80	22.30	594	1.0
Upper Artichoke Reservoir, MA	42.79, 70.93	7.41	3.89	5	1.5	Upper Sister Lake, NY	43.88, 74.76	6.92	12.30	588	3.0
Savery Pond, MA	41.91, 70.84	6.41	14.70	29	1.0	Willis Pond (E), NY	44.35, 74.49	4.22	4.40	477	3.0
Lary Pond, NH	43.70, 72.00	5.98	4.42	359	1.0	Windfall Pond, NY	44.36, 74.44	3.59	3.64	503	4.0
No Name, NH	42.89, 71.94	4.77	5.05	186	0.0	Dry Channel Pond, NY	44.35, 74.43	3.04	3.12	497	2.3
Glen Lake, NH	43.01, 71.57	4.68	10.20	83	3.0	Lake Pleasant, NY	43.48, 74.42	3.34	3.67	525	5.0
Contention Pond, NH	43.16, 71.96	4.04	1.99	263	1.5	Sacandaga Lake, NY	43.48, 74.36	3.53	3.12	526	6.0
Dunklee Pond, NH	42.76, 71.58	5.66	9.41	75	0.5	Masick's Pond, NY	42.63, 74.32	4.72	5.99	210	0.0
Flints Pond, NH	42.74, 71.55	6.46	4.44	60	2.8	Oscawanna Lake, NY	41.39, 73.84	3.18	18.30	155	6.0
Two Town Pond, NH	44.87, 71.32	2.86	6.07	585	3.2	Clear Lake, NY	41.42, 73.84	1.96	2.45	271	7.0
Ivanhoe Pond, NH	43.60, 70.99	2.51	1.68	183	6.0	Wiccopee Reservoir (N), NY	41.42, 73.82	3.14	4.72	220	6.0
Waterloo Lakes, NJ	40.91, 74.74	4.43	2.13	192	0.0	Trout Lake, NY	43.54, 73.70	3.25	5.16	240	4.0
Wreck Pond (largest), NJ	40.14, 74.03	4.66	58.80	1	1.0	Snyders Lake, NY	42.66, 73.63	4.74	9.43	149	5.0
Narrow Lake, NY	44.13, 75.46	8.82	9.65	225	3.0	Arrowhead Lake, NY	41.85, 73.56	1.73	4.80	145	0.0
Indian Lake, NY	44.14, 75.45	8.69	6.17	225	5.0	Mansi's Pond, RI	41.90, 71.58	9.00	39.40	120	0.0
Barney Pond, NY	44.47, 74.80	4.84	7.45	387	3.5	Mountaindale Reservoir, RI	41.88, 71.53	2.84	3.86	66	1.0
Clear Pond, NY	44.48, 74.16	4.48	4.12	505	4.0	Watson Reservoir, RI	41.53, 71.17	4.80	9.83	14	7.9
No Name, NY	44.49, 74.13	6.28	24.6	509	1.5	Somerset Reservoir, VT	43.01, 72.94	2.93	5.51	650	7.0
Mohegan Lake, NY	44.05, 74.47	5.64	2.09	537	3.0	Sabin Pond, VT	44.40, 72.41	2.82	1.25	286	1.5
Grampus Lake, NY	44.03, 74.47	4.47	NA	532	4.0						

survey (WLS) under isothermal conditions in the fall of 1985 (Charles 1991*a,b*). Lakes with a surface area of <1 ha in the WLS and <4 ha in the ELS are not well represented (Charles 1991*b*). The DOC, chlorophyll, and temperature data for the northeastern U.S. are from 73 lakes sampled during the 1991 pilot survey of EMAP surface waters and represent ~11,500 lakes with a surface area >1 ha and minimum depth of 1 m in that region.

Both the NSWS and the EMAP studies are based on a probability sample from a defined population of lakes that permits extrapolation of results to the whole population of lakes within the given region. The NSWS lake regions were selected for their potential acid sensitivity so the results presented here are representative of each region but cannot be extrapolated to represent the general population of North American lakes.

For the more detailed 1991 EMAP data, water samples were collected with a van Dorn bottle at either 0.5-m (lakes <2 m deep) or 1.5-m depth intervals (lakes ≥2 m deep). DOC was determined in an acidified, filtered aliquot (after external sparging to remove DIC) by UV-promoted persulfate oxidation followed by infrared (IR) detection in a carbon analyzer (U.S. Environ. Prot. Agency 1987). Chlorophyll *a* was determined by filtering (glass-fiber GF/F) the lake water sample in the field (typically 500 ml). Filters were homogenized and extracted in acetone in the laboratory, and Chl *a* determined spectrophotometrically using the trichromatic equation (Am. Public Health Assoc. 1989). Temperature measurements were made with an oxygen-temperature meter at 0.5-m intervals in shallow lakes (<3 m deep), and at 1-m intervals from 0 to 15-m depths, and at 5-m intervals and 1 m above the bottom for deeper lakes (U.S. Environ. Prot. Agency 1987; Chaloud et al. 1989).

Little Rock Lake in northern Wisconsin has been the site of an experimental acidification study since 1983. The two basins of the lake were separated by a vinyl curtain and pH in the treatment basin was reduced progressively in three, 2-yr stages using sulfuric acid. Acid additions were completed in 1990 and the lake's recovery has been monitored since that time. A summary of methods and a range of limnological responses to acidification in the lake have been reported by Brezonik et al. (1993). Detailed measurements of DOC were made in both lake basins beginning in 1988 with an O.I. Corp. model 700 DIC/DOC analyzer. These values are combined here with the equations of Morris et al. (1995) to estimate the 1% attenuation depths of UV-A and UV-B light in both the treatment and reference basins of Little Rock Lake through fall 1994.

Results

When the 1% attenuation depth for UV is plotted against DOC concentration for the Morris et al. (1995) model, a striking relationship emerges: attenuation depth increases rapidly with decreasing DOC for DOC levels below the 1–2 mg liter^{-1} range (Fig. 1). Above a DOC concentration of 2 mg liter^{-1} the 1% attenuation depth for UV-B is less than 1 m and small changes in DOC have less of an effect on the 1% attenuation depth. Attenuation depths for UV-A are about 2.5 times as deep as those for UV-B, and those for PAR are about 4 times as deep as UV-A and 10 times those for UV-B (Fig. 1B).

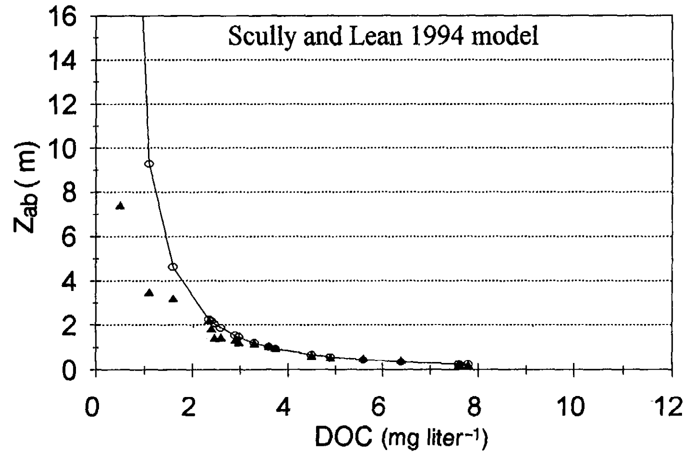

Fig. 2. Relationship between 1% attenuation depth for UV-B (Z_{ab}) and dissolved organic C (DOC) concentration based on a survey of 20 systems (lakes and enclosures) in North America. Data are from Scully and Lean (1994). Measured data (from K_d values and Eq. 4: ▲—points; ○—model.

We plotted the data and model predictions from Scully and Lean (1994) and found the same basic relationship, consisting of an increase in UV-B attenuation depth with decreasing DOC concentrations below the 1–2 mg liter^{-1} DOC range. However, we did not use their model any further in the current study because their data set had so few data points in this critical low DOC range, and because the 1% UV-B attenuation depths predicted from their model diverged substantially from their measured values in this low DOC range (Fig. 2).

In several regions of North America, 25% of the lakes had 1% attenuation depths for UV-B of close to 4 m or more. Not surprisingly, these included the lakes in the west that are some of the most dilute lakes in the U.S. (Melack and Stoddard 1991). Also included here are the lakes in the Cascades Mountains of the northwestern U.S. and in Newfoundland (Table 2). Half of the lakes in the southeastern Blue Ridge region of the U.S. had 1% attenuation depths for UV-B between 1.5 and 2.2 m, whereas all other lake regions had a very high proportion of lakes with 1% attenuation depths for UV-B of <1 m. With two exceptions (upper midwestern U.S. and northwestern Ontario), 1% attenuation depths for UV-A were >1 m for 25% or more of the lakes in each region, and in some regions these UV-A quartiles exceeded 10 m (western U.S., Cascades, and Newfoundland). Although data were not available on thermocline depth in these lakes because sampling was done under isothermal conditions in autumn (Charles 1991*b*), in several cases these 1% attenuation depths made up a substantial portion of the median lake depths for these regions (Table 2).

Table 2. UV-A and UV-B attenuation depths (1% of surface, upper and lower quartiles) estimated from DOC data for various regions in North America. All units are in meters.

Region	Median lake depth	1% UV-B (25–75%)	1% UV-A (25–75%)
United States			
Northeast (EMAP 1991)	4.5	0.28–0.61	0.67–1.47
Adirondacks, NY*	5.8	0.34–0.66	0.79–1.60
Maine*	4.9	0.22–0.59	0.51–1.41
S. Blue Ridge (SE)*	13.1	1.51–2.21	3.74–5.57
Florida*	3.0	0.12–0.47	0.27–1.13
Upper Midwest*	5.5	0.15–0.38	0.35–0.90
West†	—	1.08–4.75	2.64–12.28
Cascades (NW)‡	16.2	1.00–4.09	2.46–10.52
Canada*			
Ontario			
Northwestern	—	0.15–0.31	0.34–0.73
Northeastern	—	0.23–0.60	0.54–1.44
South central	—	0.33–0.60	0.78–1.44
Quebec	—	0.21–0.47	0.50–1.11
Labrador	—	0.27–0.54	0.63–1.30
New Brunswick	—	0.28–0.58	0.64–1.39
Nova Scotia	—	0.23–0.49	0.53–1.18
Newfoundland	—	0.18–3.99	0.41–10.27

* Baker et al. 1991.
† Melack and Stoddard 1991.
‡ Nelson 1991.

Further analysis of the EMAP lakes in the northeastern U.S. was done to assess what portion of the surface mixed layer of lakes in this region was penetrated by 1% or more of surface UV-B and UV-A radiation. These lakes were not some of the more UV-transparent lakes in the NSWS (Table 2). The median 1% attenuation depth was 0.39 m for UV-B and 0.92 m for UV-A radiation, and the median mixing depth was 2.0 m (Table 3). Thus the median 1% attenuation depth was 18% of the depth of the mixed layer for UV-B radiation and 42% for UV-A (Table 3). In 28% of the EMAP pilot survey lakes the thermocline started at the surface, so there was no surface mixed layer; consequently the Z_a/Z_{mix} values were 100% (Table 3).

During the experimental acidification of Little Rock Lake, the 1% attenuation depths for UV were generally greater in the acidified treatment basin than in the reference basin (Fig. 3). This increase was particularly pronounced during 1989 and 1990 when the pH of the treatment basin was reduced to $\lesssim$5.0, and the 1% attenuation depths for UV-A and UV-B approximately doubled (Fig. 3). During recovery (1991–1994) following acidification, the pH and 1% attenuation depths became increasingly similar in the two basins. Note also the regular pattern of annual decrease in UV attenuation depth from April to September that imparts a saw-toothed pattern to the 1% attenuation depth curves in the reference basin in particular (Fig. 3).

Table 3. Median and quartile data for UV attenuation depths and related variables in northeastern U.S. lakes (EMAP 1991 pilot survey). Attenuation depths for PAR are given for comparison, but low r^2 makes them only rough estimates.

Variable	Median	Quartiles (25–75%)
DOC (mg liter^{-1})	4.72	3.14–6.23
Mixing depth (Z_{mix}, m)	2.00	0.00–4.00
Lake depth (Z_{max}, m)	4.50	2.60–8.90
1% attenuation depth (m)		
UV-B (320 nm)	0.39	0.28–0.61
UV-A (380 nm)	0.92	0.67–1.47
PAR (400–700 nm)	3.27	2.49–4.87
Percent of mixing depth (Z_a/Z_{mix})		
UV-B (320 nm)	18	11–100
UV-A (380 nm)	42	25–100
PAR (400–700 nm)	100	90–139
Percent of maximum depth (Z_a/Z_{max})		
UV-B (320 nm)	9	7–14
UV-A (380 nm)	22	16–35
PAR (400–700 nm)	70	55–118

Discussion

Although data on the attenuation of UV radiation in freshwaters are beginning to appear in the published literature (e.g. Kirk 1994*b*; Scully and Lean 1994; Morris et al. 1995), there have not been any systematic attempts to either measure or estimate UV attenuation for entire lake regions. Here we have made such an estimation and found that 1% attenuation depths for UV-B (1% of surface) may average <0.5 m in some lake regions, and in other regions a substantial percentage of the lakes may have 1% attenuation depths for UV-B in >4 m. UV-A radiation, which has also been demonstrated to be damaging to a variety of planktonic organisms (Karentz et al. 1994; Siebeck et al. 1994) may have 1% attenuation depths that exceed 10 m for many of the lakes in some of these regions (Table 2).

The higher levels of DOC (particularly gilvin, or gelbstoff) in freshwater vs. marine environments generally will cause UV-B to attenuate more rapidly in lakes than in oceans (Kirk 1994*b*) and cause a shift in water color toward the longer wavelengths (Birge and Juday 1934; Schindler 1971; Watras and Baker 1988). Prior in situ measurements of UV in lakes have shown that 1% attenuation depths for UV-B may vary from only a few centimeters in high DOC lakes to >20 m in the very clear lakes of Argentina, Chile, and Norway (Kirk 1994*b*; Scully and Lean 1994; Morris et al. 1995). In the clearest ocean waters 1% attenuation depths for UV-B may approach 40 m (Sargasso Sea, Smith and Baker 1979), but in more coastal marine systems 1% attenuation depths of UV-B are often <20 m (Kirk 1994*b*).

Perhaps the most striking conclusion that can be drawn from this relationship between DOC and UV attenuation depth is that changes in DOC are probably more likely

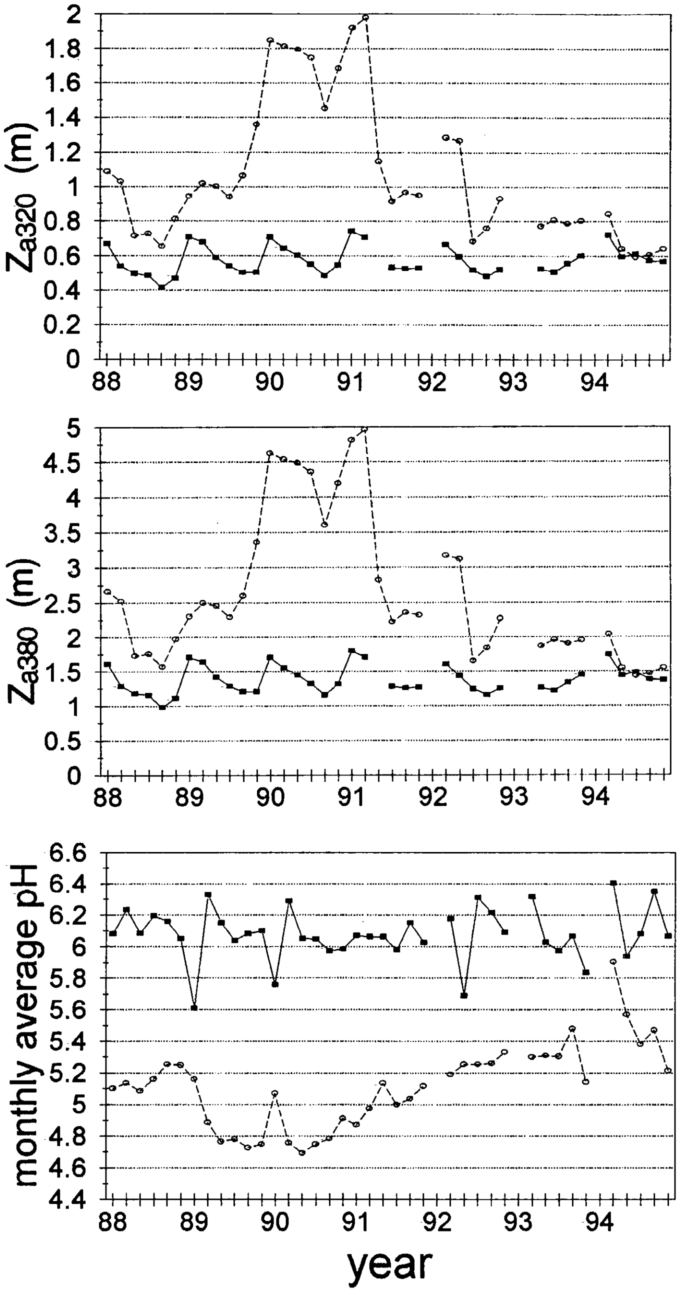

Fig. 3. Attenuation depths (1%) for UV-A (380 nm) and UV-B (320 nm) radiation, as well as pH in the experimentally acidified (○) and reference (■) basins of Little Rock Lake, April–September 1988–1994. UV attenuation depths were estimated from DOC data using the Morris et al. (1995) model, so the variation in UV attenuation depths as shown is due to changes in DOC quantity only. Year label is centered under the April data point for each year.

to alter the UV environments in lakes than are changes in stratospheric ozone. This is important because there are many environmental changes that may influence DOC concentrations in aquatic ecosystems, including changes in climate, watershed hydrology, terrestrial vegetation and land use, and anthropogenic acidification. Lakes with low levels of DOC will be most sensitive due to the pronounced increase in attenuation depths at DOC concentrations <1–2 mg liter^{-1} (Fig. 1). The central importance of DOC in regulating attenuation depth in aquatic ecosystems is largely due to the exponential increase in absorption by DOC with decreasing wavelength (Davies-Colley and Vant 1987; Kirk 1994*a,b*).

The high r^2 values of the relationship between DOC and UV attenuation (Eq. 1 and 2) support the primary importance of DOC in regulating UV attenuation (Morris et al. 1995). The scatter around the corresponding curves (Fig. 1A) may be due to either variation in DOC quality or to absorption or scattering by other substances in the water. DOC-specific absorbance in the UV range can vary by at least an order of magnitude depending on DOC composition. For example, substantial variation exists among lakes with respect to the DOC-specific absorbance in the UV range (280–400 nm, Morris et al. 1995). Published DOC-normalized spectra for fulvic, tannic, and lignosulphonic acids may show up to a 5-fold variation in the UV range (Lawrence 1980). Differences in DOC-normalized color (a_{440}) among watersheds may be attributable to differences in the relative proportions of humic and fulvic acids (Visser 1984). However, even within narrower classes of DOC compounds, such as fulvic acids, substantial differences in optical properties may exist (McKnight et al. 1994). In addition, the absorption spectra of fulvic, tannic, and lignosulphonic acids are all pH-dependent (Lawrence 1980), and these types of pH-dependent changes are not taken into account in the current study.

These considerations should make it clear that the attenuation depth estimates given here are only first-order estimates that do not take into consideration differences in the optical properties of different types of DOC. DOC comprises a very broad class of chemically and optically diverse compounds that may vary among lakes and other types of aquatic ecosystems. Although the relationship between DOC and UV attenuation is quite good as predictive ecological models go, detailed chemical and optical studies of individual lakes at particular points in time will be necessary to sort out how compositional changes in DOC either among lakes, or seasonally, or with depth within lakes will influence the underwater UV environment.

Some simple calculations based on Eq. 1, 2, 4, and 5 demonstrate how even relatively small changes in DOC quantity may substantially alter the UV environment of low DOC lakes. For example, in a lake in which the DOC concentration is reduced from 1 to 0.5 mg liter^{-1}, the 1% attenuation depth for UV-B (Z_{a320}) will increase from 2.2 m to 4.79, and the amount of UV received at a depth of 2 m would increase $\sim$10-fold. For ozone depletion to cause this same level of increase in UV at a depth of 2 m in the water column, incident UV at the surface of the lake would also have to increase by $\sim$10-fold. A 10-fold increase in DNA-damaging radiation at the lake's surface would require a drastic 70% reduction in atmospheric column ozone based on the power relationship between ozone and biologically effective UV given by Madronich (1994). These calculations are very crude and do not fully take into account potentially important changes in the spectral composition of the light—an important consideration when dealing with biological systems (Cullen et al. 1992; Cullen and Neale 1994; Madronich 1994). However, the point should be clear that small changes in DOC concentration can lead to pronounced changes in the UV environment in the water column, especially in low DOC systems. This is not to say that ozone depletion is not an important consideration in the future UV environments in aquatic ecosystems. In fact, DOC is destroyed by UV photooxidation and subsequent microbial degradation (Allard et al. 1994; Lindell et al. 1995). Thus increases in UV radiation due to stratospheric ozone depletion may decrease DOC concentrations and aggravate the vulnerability of aquatic ecosystems to UV radiation. In addition, ozone absorbs heavily in the short wavelength UV-B and UV-C regions where radiation is much more biologically active.

These calculations regarding the potential importance of DOC in regulating UV environments in lakes are not merely hypothetical because there are numerous examples of changes in DOC with changes in climate and other environmental factors. For example, substantial decreases in DOC and increases in water clarity have been observed during recent climate changes in Canadian Shield lakes (Schindler et al. 1990, 1996). Because DOC is largely a function of terrestrial vegetation and wetlands in the watershed (Engstrom 1987; Rasmussen et al. 1989: Schindler et al. 1992), changes in land-use patterns or hydrology may also alter DOC concentrations. Temporal changes in DOC of more than 2-fold are not uncommon interannually within a single lake and may correlate with precipitation, forest fires, or other environmental changes (Schindler et al. 1992; Webster et al. 1993).

Increases in water transparency to visible light have often been documented in acidified lakes, and these changes in transparency appear to be related to changes in DOC and not chlorophyll or phytoplankton biomass (Yan 1983; Bukaveckas and Driscoll 1991; Schindler et al. 1991, 1992; Driscoll and van Dreason 1993). Our estimates here suggest that changes in light fields with acidification also include substantial increases in UV penetration as influenced by shifts in DOC (Fig. 3). Such increases in UV may explain some of the indirect zooplankton community response to acidification that have been documented in Little Rock Lake (Webster et al. 1992; Gonzalez and Frost 1994). Interestingly, DOC decreases and 1% attenuation depths for UV radiation increase most dramatically only below a pH of ~5.0 (Fig. 3). Similar reductions in DOC only at a pH of <5.0 have been observed in other whole-lake acidification experiments (Shearer et al. 1987; Schindler et al. 1991, 1992), and substantial changes in underwater UV radiation have similarly been predicted from changes in DOC during drought-induced acidification (Yan et al. 1996).

The mechanism of DOC reduction during acidification is somewhat uncertain and a matter of controversy. Krug and Frink (1983) have suggested that these decreases in DOC with decreasing pH are due to a decrease in the dissociation and solubility of humic materials with the addition of H^+. Recent acidification experiments in both lakes and streams, however, suggest that this explanation is unlikely (Hedin et al. 1990; Driscoll and van Dreason 1993). Alternative explanations are that these changes in DOC may be related to increases in microbial decomposition due to increased nutrient availability (Grahn et al. 1974 *cited by* Bukaveckas and Driscoll 1991; Schindler et al. 1992; Driscoll and van Dreason 1993; *but see* Persson and Broberg 1985) or to the removal of DOC by coagulation by aluminum (Almer et al. 1978 *cited by* Bukaveckas and Driscoll 1991; Schindler et al. 1992; *but see* Driscoll and van Dreason 1993). Regardless of the mechanism, the reduction in DOC with acidification has important implications for the UV environments in lakes.

Concentrations of DOC may also be important in regulating changes in the UV environment of aquatic ecosystems along elevation gradients. For example, we applied our model to some DOC data across an elevation gradient in the Cascade Mountains (Nelson 1991). This analysis revealed that 1% attenuation depths as predicted from DOC alone would approximately double as elevation increased from <1,200 m to >2,000 m (Table 4). On the other hand, incident UV-B radiation will increase only ~6–8% per 1,000 m of elevation due to atmospheric thinning (Caldwell et al. 1980; Diffey 1991) and may actually decrease if there is an increase in cloud cover as is often observed in mountainous regions. The lower levels of DOC and consequently deeper 1% attenuation depths for lakes at higher elevations (Table 4) may reflect lower levels of terrestrial vegetation and hence reduced allochthonous inputs of DOC (Engstrom 1987; Schindler et al. 1992) at high elevations. We have estimated a 1% attenuation depth for UV-B (Z_{a320}, from measured K_{d320} values using a Biospherical Instruments PUV-501) of 33 m in a 4-m-deep lake with a barren watershed above treeline in the Argentine Andes (Morris et al. 1995).

In our analysis of the northeastern U.S. data we focused on the thermocline as a lower habitat boundary that may potentially provide important interactions with UV effects. Temperature is a critical variable in aquatic ecosystems that may be influenced by climate change. In addition to controlling the vertical stratification and mixing of nutrients, temperature plays a fundamental role in regulating rates of individual as well as ecosystem-level metabolism. By excluding some organisms from portions of the mixed layer during the day, UV radiation may

Table 4. Median UV-B and UV-A attenuation depths (m) across a range of elevations (m) in the Cascade Mts. of the Pacific Northwest estimated from DOC data (mg liter^{-1}) in the U.S. EPA NSWS (Nelson 1991).

Elevation	DOC	1% UV-B	1% UV-A
600–1,200	1.44	1.46	3.62
1,200–1,600	1.33	1.60	3.99
1,600–2,000	1.05	2.09	5.24
>2,000	0.78	2.91	7.40

force plankton populations into deeper, cooler water. This may have beneficial or detrimental effects depending on the nature of the thermal gradient and the species involved. For example, many zooplankton suffer a demographic disadvantage when forced to spend time in cooler waters (Orcutt and Porter 1983; Stich and Lampert 1984; Kerfoot 1985; Ikeda 1985; Dawidowicz and Loose 1992), yet if surface waters exceed 25°C, warmer waters may actually inhibit growth and reproduction (Moore and Folt 1993; Chen and Folt 1996; Moore et al. 1996).

In 28% of the lakes represented in the 1991 EMAP pilot survey, the thermocline started within 1 m of the surface. Some of these thermoclines may have been temporary, but the probability design of the EMAP sampling and the fact that sampling was done over a period of several weeks suggest that these conditions are not uncommon in northeastern U.S. lakes. Such near-surface thermoclines have been observed even in large oligotrophic lakes where they may trap nonmotile phytoplankton and bacterioplankton in surface waters and thus increase exposure to damaging levels of UV radiation (Milot-Roy and Vincent 1994). More motile organisms such as zooplankton may migrate down out of these surface strata but will also experience an alteration of their thermal regimes. In more productive lakes, migration down through the thermocline may also result in exposure to hypoxia, changes in pH, food quantity and quality, and in predation risk from both visual and tactile predators.

Increases in thermocline depth with climate warming might help to mitigate some of these potential interactions between damaging UV radiation and other temperature-related habitat variables. The positive relationship between DOC and PAR attenuation and therefore thermal stratification in some lakes (Schindler et al. 1990; Bukaveckas and Driscoll 1991; Driscoll and van Dreason 1993) argues for increases in thermocline depth with decreased DOC and subsequently decreased interactions between UV attenuation and thermal gradients. On the other hand, modeling efforts suggest that thermocline depth may not increase during climate warming, but rather thermal gradients will become steeper and lakes may remain stratified for longer periods of time during the ice-free season (Hondzo and Stefan 1993; De Stasio et al. 1996). This latter scenario might lead to increased rather than decreased interactions between thermal gradients and UV radiation. Clearly, the interactions among temperature, DOC, and UV attenuation during climate change events are likely to be complex.

Changes in DOC may have more severe effects on the UV environment in streams than in lakes. When our model was applied to some DOC data from Catskill streams (New York: Stoddard and Murdoch 1991), the upper and lower quartile 1% attenuation depths were 1.80–3.99 m for upstream reaches and 1.57–3.37 m for downstream reaches. Interestingly, the depth of most of these Catskill streams is substantially <1 m. The apparent lack of change in DOC with stream acidification [Hedin et al. 1990, for a high-DOC (8–9 mg liter^{-1}) acid (pH 4.2–4.6) stream] may mitigate the effects of acidification on potentially increased 1% attenuation depths for UV in some streams.

The implications of the above variations in UV attenuation depths relative to temperature and other environmental variables is unclear because so little is known about the effects of UV radiation on freshwater ecosystems. Some planktonic organisms are much more sensitive to damage by UV radiation than others, and both UV-B and UV-A radiation as well as blue light may cause photodamage in some organisms but not others (Karentz et al. 1994; Milot-Roy and Vincent 1994; Moeller 1994; Siebeck et al. 1994; Williamson et al. 1994). These attenuation data do suggest that future changes in UV radiation will be more important in low DOC lakes than in moderate-to-high DOC lakes and that variations in thermal structure, including surface thermoclines, may accentuate interactions between UV damage related to ozone depletion, climate change, anthropogenic acidification, and other important environmental variables in aquatic ecosystems.

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