

Do zooplankton contribute to an ultraviolet clear-water phase in lakes?

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Abstract

Seasonal increases in the ultraviolet (UV) transparency of the surface waters of an oligotrophic lake in Pennsylvania suggest that clear-water phase (CWP) events similar to those previously observed for visible light also exist for the potentially damaging UV wavelengths. Seasonal increases in zooplankton grazers indicate that they play a role in these changes in UV that is similar to the role that zooplankton play in CWP events involving longer-wavelength visible, or photosynthetically active radiation (PAR, 400–700 nm). The potential role of zooplankton and incident UV in generating UV CWP events was investigated with a set of in situ microcosm experiments that manipulated UV and zooplankton, and followed changes in particulate and dissolved absorbance in the UV (320 nm) and PAR wavelength ranges over an 8-d period in April. Nutrients were also manipulated independently to examine the potential role of nutrient regeneration by zooplankton grazing in altering water transparency. Photobleaching by incident solar UV led to a strong and significant decrease in dissolved UV and PAR absorbance. The presence of zooplankton grazers also significantly decreased dissolved UV absorbance but increased dissolved PAR absorbance. Neither zooplankton nor UV had any significant effects on UV or PAR absorbance by particulates. In contrast, nutrient additions significantly increased dissolved absorbance in both the UV and PAR wavelength ranges, indicating that regeneration of nutrients by zooplankton offsets decreases in UV absorbance and enhances increases in PAR absorbance due to grazing. While photobleaching by UV radiation is likely to make a consistent strong contribution to UV CWP events in lakes, the net effects of zooplankton on UV transparency in a given lake will depend upon multiple factors including zooplankton density and a balance between the edibility and extent of nutrient limitation of the phytoplankton.

Many temperate lakes undergo a distinct period of increased water transparency during the late spring or early summer referred to as a clear-water phase (CWP). The CWP was first described as a distinct event in the mid 1980s (Lampert et al. 1986; Sommer et al. 1986). According to the plankton ecology group (PEG) model of seasonal succession, which is based on an intercomparison of 24 different types of lakes, reservoirs, and ponds, the CWP follows the spring phytoplankton bloom and consists of a rapid decline in phytoplankton biomass accompanied by a pronounced increase in the visible transparency of the surface waters

(Secchi depth). This rapid increase in visible transparency is accompanied by an increase in herbivorous zooplankton, and often a decline in nutrients as well. Both comparative analyses of multiple lakes (Sommer et al. 1986) and enclosure experiments that specifically manipulate zooplankton (Lampert et al. 1986) have implicated zooplankton grazing in generating the CWP. The PEG model identifies the CWP as lasting only a few weeks in May in mesotrophic to eutrophic lakes, but in oligotrophic lakes investigators observed that the CWP “always extended over the summer period” (Sommer et al. 1986). The CWP has been a useful concept in numerous studies of the regulation of planktonic processes ranging from zooplankton grazing and nutrient limitation (Lampert et al. 1986; Vyhnalek et al. 1991) to food web dynamics (Elser et al. 1995; Luecke et al. 1990), pelagic carbon metabolism (Markager et al. 1994), and the effects of major climate patterns such as the North Atlantic Oscillation (Adrian et al. 1999; Scheffer et al. 2001).

In our studies of zooplankton and transparency of surface waters in oligotrophic Lake Giles in northeastern Pennsylvania, we have noted a similar seasonal increase in the visible (photosynthetically active radiation [PAR], 400–700 nm) transparency of the water in the spring subsequent to an increase in zooplankton grazers. Consistent with the PEG model for oligotrophic lakes, this period of increased transparency continues well into the summer, with a peak that occurs sometime in July. We observed similar patterns of seasonally increasing PAR transparency in two other more productive lakes in the same region (Morris and Hargreaves 1997). We have also found pronounced seasonal increases in ultraviolet (UV) transparency that parallel increases in water transparency to PAR. We refer

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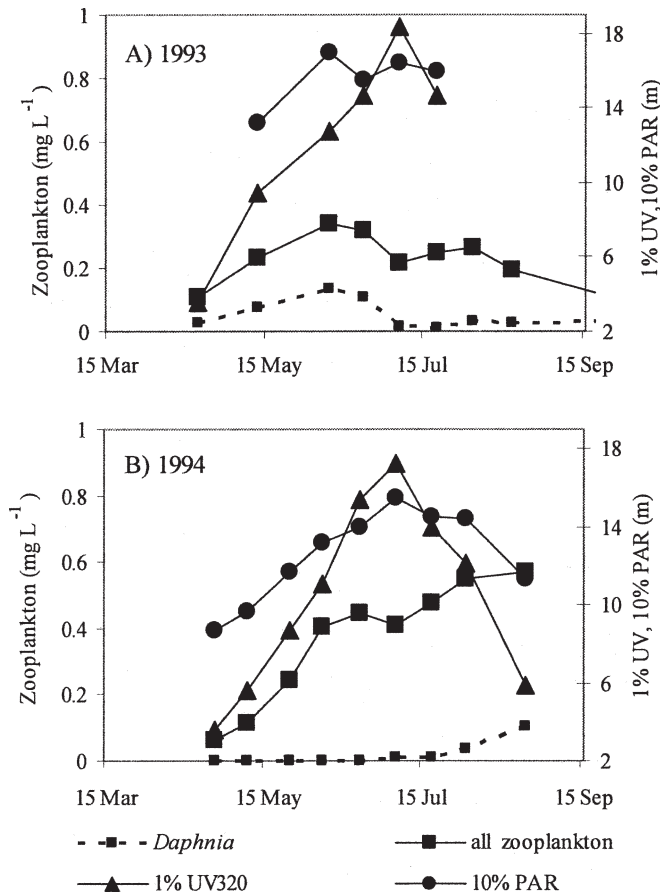


Fig. 1. Seasonal changes in zooplankton biomass and water transparency (UV and PAR) in oligotrophic Lake Giles in 1993 (A) and 1994 (B) demonstrating the seasonal development of a spring CWP coincident with an increase in the dominant crustacean zooplankton. Note the persistence of the CWP, consistent with the PEG model for oligotrophic lakes. Total zooplankton includes all life history stages of *Leptodiatomus minutus* as well as *Daphnia catawba*. Biomass of *D. catawba* alone is also shown. Zooplankton biomass estimates are from counts of vertical tow samples with a bongo net with a 48- μ m Wisconsin-type net on one side and a 202- μ m net on the other. These nets were tested to have 95–100% sampling efficiency in the study lake.

to these here as a UV CWP. In Lake Giles the 1% attenuation depth (depth to which 1% of surface irradiance potentially penetrates as estimated from an epilimnetic diffuse attenuation coefficient) for 320 nm UV may increase from about 3 m in April to 18 m or so by mid July (Fig. 1). Seasonal variation in PAR transparency varies less than for UV, with 10% attenuation depths ranging between about 8 and 15 m (Fig. 1). Actual penetration of UV and PAR in the lake is somewhat less because transparency decreases with increasing depth, but these attenuation depths are demonstrative of the dramatic changes in surface water transparency.

The relative importance of particulate and dissolved compounds in absorbing underwater solar radiation varies with wavelength. As one goes from the PAR wavelengths down into the shorter wavelength UV range (<400 nm),

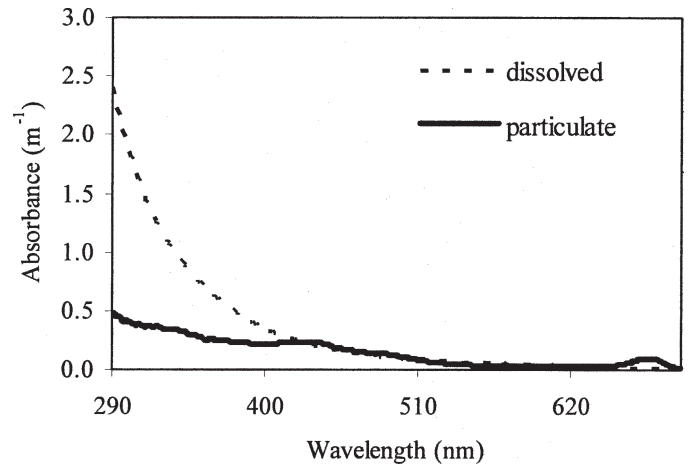


Fig. 2. Wavelength-specific changes in particulate and dissolved absorbance of a Lake Giles water sample taken at the start of the field experiment. Note the much greater absorbance of the dissolved versus particulate fraction in the short wavelength blue and UVR range and the similar contribution of these two fractions at longer PAR wavelengths.

dissolved substances account for a much greater proportion of the absorbance than do particulates (Fig. 2). This suggests that zooplankton grazing may play fundamentally different roles in altering transparency in the UV versus PAR wavelength ranges. Grazing may influence both dissolved and particulate substances through altering the size distribution of particulates as well as release of dissolved organic carbon (DOC) by both zooplankton and phytoplankton.

There are two primary mechanisms by which zooplankton could potentially influence seasonal UV CWP events. First, seasonal changes in zooplankton grazing are well known to alter the density and size distribution of phytoplankton and thought to be largely responsible for the visible CWP events. These same grazing processes may similarly increase UV transparency by reducing phytoplankton density, altering the size structure of the phytoplankton community, or decreasing the contribution of phytoplankton to the production of dissolved organic matter (DOM) pool by altering their growth rates, senescence, and proportion of “leaky” cells. Alternatively, zooplankton grazing generates both labile and refractory DOM through ‘sloppy feeding’, excretion, and leaching of DOM and nutrients from fecal matter (Markager et al. 1994; Hygum et al. 1997; Park et al. 1997; Kamjunke and Zehrer 1999). Short-term (8-h) incubation experiments with marine plankton indicate that both zooplankton and phytoplankton produce chromophoric DOM (CDOM) that decreases UV transparency (Steinberg et al. 2004). Nutrient regeneration by zooplankton grazing may also stimulate growth of phytoplankton or microbial communities that may further alter UV transparency in unknown ways.

DOC has a very similar absorption spectrum to the dissolved fraction shown in Fig. 2—selectively absorbing the shorter-wavelength UV radiation (Kirk 1994; Kirk et al. 1994). Numerous studies have clearly demonstrated that the

concentration of DOC is an important regulator of the variation in UV attenuation among lakes (Scully and Lean 1994; Morris et al. 1995; Laurion et al. 1997; Bukaveckas and Robbins-Forbes 2000). In contrast, seasonal changes in UV transparency within lakes, such as those observed in our UV CWPs, are more likely to be related to changes in the quality rather than the quantity of DOM, with the primary mechanism being the photobleaching of the chromophoric fraction of DOM by solar UV and PAR while DOC concentration stays relatively constant (Morris and Hargreaves 1997; Osburn et al. 2001). The importance of quality over quantity of DOM is also central to variations in UV attenuation in very low DOC alpine lakes, where phytoplankton play a much larger role in controlling UV attenuation (Laurion et al. 2000; Sommaruga 2001). The contribution to UV absorbance of DOM generated in situ by phytoplankton or zooplankton is likely to be less than DOM from allochthonous inputs from wetlands or terrestrial systems because DOM from the latter sources is generally more highly UV absorbing (McKnight et al. 1994).

These contrasting processes and predictions demonstrate the need to know more about the net role of both zooplankton and UV photobleaching in generating seasonal variations in UV versus PAR transparency in lakes. Here we examine the potential for zooplankton and photobleaching by UV to alter the UV and PAR transparency of lakes. The working hypothesis is that zooplankton and UV both contribute to the UV CWP observed in Lake Giles. A set of in situ experiments compared the optical properties of lake water containing natural phytoplankton in the presence and absence of zooplankton and under normal and reduced levels of solar UV radiation. A treatment with nutrient additions was also carried out to assess the potential for nutrient regeneration by zooplankton to influence the optical properties of the water. The experiment was carried out in an oligotrophic lake where the inputs of DOM from the surrounding watershed are minimal, and hence 'in-lake' processes that influence UV transparency such as zooplankton grazing and photooxidation are likely to be most apparent.

Methods

An in situ experiment was performed from 05–13 April 2000 in Lake Giles to examine the effects of the presence versus absence of zooplankton grazers as well as the presence and absence of UV radiation on the optical properties of the lake. Lake Giles is a highly transparent (summer Secchi depths 12–16 m, DOC concentration $\sim 92 \mu\text{mol L}^{-1}$) oligotrophic (total phosphorus = $0.23 \mu\text{mol L}^{-1}$) lake located on the Pocono Plateau of northeastern Pennsylvania ($41^{\circ}23'N$, $75^{\circ}06'W$). The initial experimental design was a 2×2 factorial where natural solar UV radiation and zooplankton were the factors. However, high mortality of zooplankton in the presence of UV led us to discard the +UV + zooplankton treatment and subsequently treat UV and zooplankton as independent variables in the analysis. A nutrient addition treatment was also run simultaneously in the absence of UV to assess the potential effects of nutrient regeneration by zooplankton

grazing on stimulating phytoplankton growth and consequent changes in the optical properties of the water. All treatments included four replicate 4-liter polyethylene zipper bags (Bitran) as microcosms with natural seston pumped from the surface waters and strained through a $48\text{-}\mu\text{m}$ mesh to remove the zooplankton. Polyethylene is a long-wave-pass material that transmits solar UV and has a sharp 50% transmittance cutoff at 240 nm. Microcosms were suspended at a depth of 0.5 m from buoys in racks made of 2.5-cm-diameter polyvinyl chloride pipe. The microcosms rested on netting that held the microcosms right up against an overlying acrylic filter that either transmitted (OP-4 acrylic, a long-wave-pass material with a sharp cutoff and 50% transmittance at 272 nm) or blocked (OP-2 acrylic, a long-wave-pass material with a sharp cutoff and 50% transmittance at 410 nm) UV radiation. In a separate preliminary set of experiments four replicates of deionized water were incubated to check for both leaching of organic matter from the microcosm materials (polyethylene) and leaking of lake water into the microcosms; the results demonstrated no detectable leaching or leaking.

Zooplankton for stocking the microcosms were collected on a $202\text{-}\mu\text{m}$ mesh and put in enclosures at 18 times whole water column density. When converted to biomass (2.17 mg L^{-1} total) this represents about 2.6 times the maximum summer water column biomass in Giles (0.81 mg L^{-1}), though it should be noted that the mesh size was not small enough to concentrate micrograzers as we did not want to inadvertently concentrate colonial phytoplankton. Nutrient enrichments consisted of additions of a 0.1% stock solution of modified MBL medium (Williamson 1987) plus extra N and P to bring N and P to $1.42 \mu\text{mol L}^{-1}$ N ($0.50 \mu\text{mol L}^{-1}$ N- NO_3 + $0.92 \mu\text{mol L}^{-1}$ N- NH_4) and $0.081 \mu\text{mol L}^{-1}$ P (K_2HPO_4).

Optical analyses—Subsamples of 500 mL were taken from each microcosm for optical analysis at the start of the experiment and on day 8. Following collection of water for optical analysis the samples were passed through a $48\text{-}\mu\text{m}$ mesh to remove the zooplankton, and the filtrate used for the analyses. The dissolved fractions were obtained by gentle filtration through preashed Whatman GF/F glass fiber filters with a nominal pore size = $0.7 \mu\text{m}$. Scans for dissolved absorbance (200–700 nm, 1-nm intervals) were performed using a Shimadzu UV 1601 UV-visible recording spectrophotometer in 10-cm Supersil cuvettes using low-carbon deionized water as a blank (Morris and Hargreaves 1997). Dissolved absorption coefficients (a_d) were calculated as a function of pathlength (r) and the absorbance reading in the spectrophotometer (D) from

$$a_d = 2.303D/r$$

Particulate absorbance was estimated using a modification of a filter pad method in which seston is collected onto preashed Whatman GF/C filters with a nominal pore size of $1.2 \mu\text{m}$ (Mitchell 1990). Total absorption coefficients (a_t) were estimated as the sum of a_d and a_p . This method is imperfect because absorbance of particles on a filter is not the same as absorbance of particles suspended in water, but

it is a reasonable approximation given this limitation. Our experience has shown that the amount of absorption in particulate material falling between the cutoff size of a GF/C and GF/F filter is generally only a small percentage of a_t . The use of a GF/C rather than a GF/F filter in the measurement of particulate absorbance was required because of its lower optical density. Differences in absorbance between control (phytoplankton with no UV) and experimental treatments were calculated for both PAR and UV wavelengths. We used 320 ± 5 nm (total band width of 11 nm in the spectrophotometer) to quantify UV absorbance in the microcosms since these wavelengths are both compatible with the field measurements that we get from our profiling radiometer (PUV 500, Biospherical Instruments) and relevant to the peak biologically effective incident solar damage to zooplankton when you take into account both incident wavelength-specific energy and energy-specific damage at each wavelength (Williamson et al. 2001). During the statistical analyses the residuals of the optical response data were not all normally distributed and were unresponsive to data transformation. Thus non-parametric Kruskal–Wallis rank tests were used to test for significant treatment effects. A p value of 0.05 was used to determine significance, but given that nonparametric tests have a higher chance of a type II error, marginally greater p values (0.06) are reported here.

Results

The UV exposure levels incident at the surface of the lake during the experiment were approximately 65% of the maximum potential daily values for this latitude and time of year, reflective of the mixed cloudy conditions during incubation. The cumulative incident 305- and 340-nm exposures respectively at the lake's surface during the 8-d experiment were 2.18 and 57.02 $\text{kJ m}^{-2} \text{nm}^{-1}$.

Dissolved UV absorbance decreased in response to both the addition of zooplankton and exposure to UV. Changes in water transparency due to zooplankton and UV were generally several times greater in the UV wavelength range than in the PAR wavelength range (Fig. 3, note differences in scales on y -axes). The presence of zooplankton significantly decreased dissolved UV absorbance but increased dissolved PAR absorbance (Fig. 3). The magnitude of the effect of zooplankton on UV absorbance (average decrease in a_{d320} of 0.18) was close to 10 times their effect on PAR absorbance (average increase in a_{dPAR} of 0.02, Fig. 3). UV exposure on the other hand induced a significant decrease in dissolved absorbance in the UV and PAR wavelength ranges (Fig. 3). The magnitude of the effect of UV exposure on UV absorbance was about eight times greater than its effect on PAR absorbance, with an average decrease in a_{d320} and a_{dPAR} of 0.42 and 0.05 respectively (Fig. 3). Neither zooplankton nor UV exposure induced any significant changes in particulate absorbance in either the UV or the PAR wavelength ranges (Fig. 3). In contrast, the addition of nutrients led to significant increases in dissolved absorbance and marginally significant increases ($p = 0.06$) in particulate

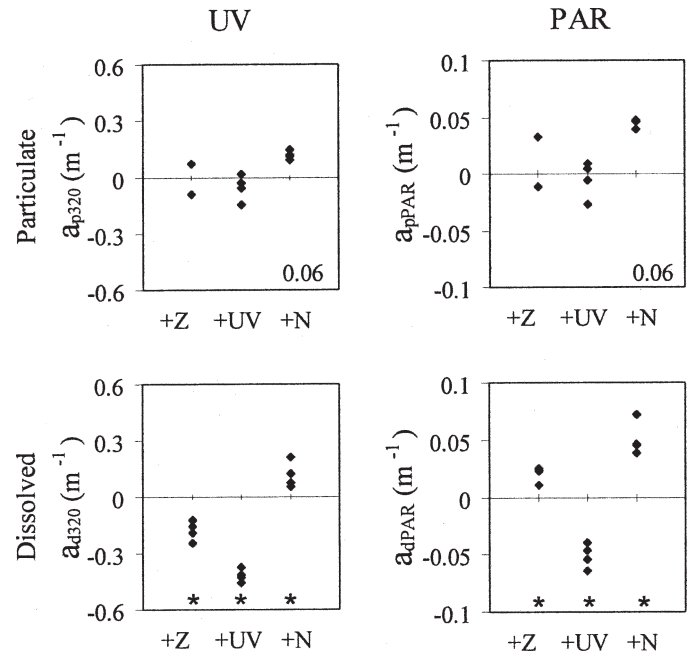


Fig. 3. Responses of particulate (a_p) and dissolved (a_d) absorbance in the UV (320 nm) and PAR (400–700 nm) wavelength regions in response to the presence of UV (+UV), zooplankton (+Z), and nutrient (+N) additions. Responses are adjusted for controls (UV-shielded with no zooplankton or nutrient additions). Asterisks (*) indicate significant treatment effects ($p < 0.05$). In two cases p values close to significant ($p = 0.06$) are given. Note that the responses in the UV wavelength range were generally much greater than for PAR wavelengths; thus the y -axis scales differ by a factor of 6.

absorbance in both the UV and PAR wavelength ranges (Fig. 3). The magnitude of the effect of nutrients on UV absorbance was about twice that on PAR absorbance for both dissolved and particulate fractions (Fig. 3).

Discussion

Evidence is presented here for a UV CWP that is similar in the timing of its development to the well-documented and widespread visible CWP events. Our experiments indicate that as with previously reported visible CWP events, zooplankton contribute to the development of the UV CWP. In Lake Giles, photobleaching by incident UV also plays a role in the development of both UV and visible (PAR) CWP events. The primary contribution of both incident UV and zooplankton to the UV CWP events in Lake Giles is through their influence on dissolved rather than particulate absorbance, with UV playing a substantially greater role than zooplankton. Support for the greater role of UV versus zooplankton in controlling UV transparency comes from both the greater magnitude of the UV effects in the experiment (Fig. 3), and the fact that UV CWP events may be pronounced even when densities of the major zooplankton grazer *Daphnia* are low (1994 data in Fig. 1).

Grazer-induced decreases in phytoplankton density are the primary mechanism by which zooplankton induce visible CWP events (Lampert et al. 1986; Sommer et al.

1986). In our experiments we found no significant response in particulate absorbance in the presence of zooplankton. This indicates that either the edibility of phytoplankton in Lake Giles at the time of the experiment was low, or that nutrient regeneration by zooplankton grazing stimulated phytoplankton growth in a way that balanced consumption. The two hypotheses are not mutually exclusive. The fact that nutrient additions alone tended to increase particulate absorbance supports the nutrient regeneration hypothesis, though these increases were only marginally significant. The decrease in dissolved UV absorbance in the presence of zooplankton indicates that either the UV absorbance of DOM produced by sloppy feeding is very low, or that production of DOM by sloppy feeding is balanced by reduced DOM release by the actively growing phytoplankton. The explanation for the increase in dissolved PAR absorbance in the presence of zooplankton is unclear, but it may be related to fewer senescent "leaky" cells or less microbial activity during more active phytoplankton growth. It is important to note that the magnitude of this increase was minimal, only about 10% of the magnitude of the decrease in dissolved UV absorbance (Fig. 3).

Earlier work on PAR CWP events describes the availability of abundant highly edible algae as a necessary precondition for the occurrence of a CWP (Lampert et al. 1986; Sommer et al. 1986). Our unpublished lab experiments support this contention by demonstrating that feeding both Diaptomid copepods and *Daphnia* with highly edible cultured algae (*Cryptomonas reflexa*) results in a decline in particulate absorbance over a period of hours. During these same experiments, however, we also observed an increase in dissolved absorbance, likely due to the high feeding rates and release of DOM from these delicate flagellates. Short-term incubations of marine zooplankton have also been shown to produce increases in dissolved absorbance in the UV wavelengths (Steinberg et al. 2004). In this same study, short-term incubation of the colonial cyanobacterium *Trichodesmium* also produced increases in UV absorbance. These short-term processes cannot be extrapolated to field conditions, but are demonstrative of how variations in the edibility of the phytoplankton and production of CDOM by both phytoplankton and zooplankton may alter the effects of zooplankton on UV CWP events. In the Lake Giles experiments the fact that particulate absorbance was not influenced by the presence of zooplankton grazers suggests that the algae present at the time were not nearly as edible as the laboratory cultures.

The observed response to nutrients suggests that UV CWP events are likely to be influenced by nutrient inputs alone in a lake. Although decreasing nutrient concentrations are not a necessary requisite for the development of PAR light CWP events (Lampert et al. 1986), low nutrient concentrations may enhance the conditions for the development of both UV and PAR CWP events. For example, in lakes like Giles, nutrient limitation of primary productivity is characteristic of the surface waters during summer stratification (Moeller unpubl. data). This nutrient limitation will reduce the growth rates of phytoplankton as well as their contribution to UV and PAR absorbance. In

low DOC lakes phytoplankton are known to play an important role in UV absorbance (Laurion et al. 2000; Sommaruga 2001).

The effects of UV and zooplankton on UV CWP events are likely to be complex and vary greatly both seasonally and from lake to lake. The importance of these variables relative to each other and to other factors will be a function of the density and species composition of zooplankton, the density and edibility of phytoplankton, levels of incident solar UV radiation, the concentrations and quality of DOM, the UV transparency of the lake, lake water temperatures and the depth of the mixed layer, and the sources and types of nutrient inputs. In addition, zooplankton and UV effects may themselves interact in several ways. For example, while both solar UV and zooplankton may contribute to a seasonal increase in UV transparency, in more transparent lakes UV may force zooplankton out of the surface waters during the day, reducing the potential effect of zooplankton grazing on UV transparency. If zooplankton are unable to detect and avoid UV, antagonistic effects between these two variables are likely due to increased zooplankton mortality and consequent reduction of the effect of zooplankton grazing in the presence of UV. In our experiments the effects of both zooplankton and UV were elevated relative to exposure levels in the lake. Zooplankton were artificially concentrated to about 2.6 times the maximum water column levels observed in Lake Giles. When extended to the 20-m-deep water column of Lake Giles, the 2.17 mg L^{-1} that we observed is equivalent to 16.2 g m^{-2} , which is about twice the peak zooplankton biomass observed by Lampert and colleagues ($\sim 8.5 \text{ g m}^{-2}$) in their experiments that demonstrated the role of zooplankton grazing in generating the CWP in Schöhsee (Lampert et al. 1986). While this zooplankton biomass is high for Lake Giles, it is only a fraction of that observed in another study of the CWP in a more productive lake where crustacean zooplankton biomass approached 20 mg L^{-1} (Luecke et al. 1990).

The incubation of the microcosms in the surface waters also exposed the UV treatments to much higher UV levels than would be experienced by water circulating in the mixed layer in Lake Giles. The mixed layer in Lake Giles varies from 2 to 6 m during the spring and summer, while the bags in this experiment were incubated at a depth of 0.5 m. Given the exponential decrease in light with depth, a static incubation at 0.5 m will give UV exposure levels that are about 2.4 times those that would be experienced in a well-mixed 4-m-deep epilimnion. These elevated treatment levels are offset to some extent, however, by the timing of the experiments. During April incident UV levels are substantially lower than during the early summer. Lake temperatures in April ($5\text{--}10^\circ\text{C}$) are also much lower than during the summer ($20\text{--}25^\circ\text{C}$), reducing the zooplankton grazing rates in April relative to later in the spring and summer. The experiments also extended over just 8 d while the surface waters of the lake are exposed to UV and zooplankton grazing throughout many months. In less UV-transparent lakes where DOM plays a greater role than phytoplankton in regulating transparency, hydrologic processes are likely to play a much greater role than

zooplankton in regulating seasonal transparency to UV and PAR.

Limnologists have relied heavily on the Secchi disk for water transparency readings for years. This has been a very simple yet powerful tool that has demonstrated the potential importance of water transparency as both a response variable and as a regulator of pelagic community and ecosystems dynamics. The extensive research on visible CWP events is a good example of this. Our data indicate that UV wavelengths are more responsive than PAR wavelengths to changes in both biotic and abiotic processes. The seasonal changes in transparency that we observed in Lake Giles were much more pronounced in the UV than in the PAR wavelengths (Fig. 1). Similarly, in the microcosm experiments the optical responses were much more pronounced in the UV wavelengths than in the PAR (Fig. 3). In contrast to the situation with PAR, dissolved absorbance plays a much greater role than particulate absorbance for UV wavelengths (Fig. 2). These relationships will vary widely depending on the relative abundance of phytoplankton, DOM, and suspended inorganic particulates across different types of lakes. More in-depth optical measurements and experiments are needed in a wider variety of lakes to help us understand the relative importance of zooplankton, UV, and other variables in the seasonal dynamics of both UV and PAR light transparency in lakes.

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