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Sun angle, site selection, parameter choice, and generalizing UV effects in freshwater benthic ecosystems (Reply to the comment by Donahue and Clare)¹

Donahue and Clare (1999) provide a number of criticisms of our study of the ecological effects of ultraviolet (UV) light in a Tennessee stream (Hill et al. 1997), asserting that errors in experimental design, site selection, and parameter choice prevented us from detecting potential UV effects on periphyton and grazers. Here, we examine the merit of these criticisms and reemphasize the potential variability of UV effects in freshwater benthic communities.

In their first criticism, Donahue and Clare question the efficacy of the Plexiglas shields at low sun angles. They calculate the horizontal displacement of the UV shadow on the streambed from the Plexiglas (resulting from seasonal or daily variation in solar azimuth and elevation), arguing that this displacement would have caused significant exposure of substrates directly below the Plexiglas and significant shadow effects on adjacent control areas. We agree that the UV shadow would have been displaced at low sun angles. However, this displacement was inconsequential for two reasons. First, we countered the northerly displacement of the UV shadow that occurred during the autumn experiments when the sun was low in the south by simply placing the experimental substrates in a northerly direction on the streambed, using the visible shadow of the Plexiglas-supporting steel rods as a guide to the northerly displacement of the UV shadow. Second, the daily west-to-east movement of the UV shadow would have had little effect because the experimental substrates were much narrower than the UV shadows. All periphyton and snail response variables were measured on these substrates, which consisted of groups of tiles 10 cm wide (16 tiles, each 2.5×2.5 cm, arranged 4×4) centered at the east-west midpoint of the Plexiglas shields. Using relevant angles of solar altitude and azimuth and a refractive index of 1.358 for UV (specifically, that of 303 nm), we calculate that on 11 November, when the potential effect of hourly changes in sun angle is greatest in this study, the 10-cm-wide groups of tiles 15 cm below 40- \times 40-cm Plexiglas shields would have been completely shaded from UV during the 6-h period surrounding solar noon. This is the period when direct sunlight fell on the stream in autumn; direct sunlight was blocked by adjacent trees and the streambank earlier and later in the day. Moreover, it is the period during which >90% of the potential daily UV-B irradiance occurs on any day of the year. Tiles were 15 cm below the Plexiglas in three of the four blocks in our experiments. The group of tiles 35 cm below the shield in the remaining block would have been shaded 75% of this time.

The percent UV-B screened out by the Plexiglas shields can be calculated with time-specific UV-B irradiances obtained from *UV-B: Version 3.00* (Fiscus and Booker 1994): 78% of the potential UV-B radiation impinging upon sub-

strates 35 cm below the Plexiglas shield during the 6 h surrounding solar noon on 11 November would have been intercepted by the shields. Similar calculations performed for the beginning and ending dates of the other experiments showed that shielding was even more effective (>78%) in the one block where substrates were 35 cm below the Plexiglas and was 100% effective in the other three blocks. Our field notes show that Plexiglas shields used in the midsummer experiment were actually 55 cm wide and 80 cm long (as were the adjacent polyvinylidene controls), so even the group of tiles in the one block that was 35 cm below the Plexiglas was 100% shielded from UV-B in this experiment. Shadow effects on adjacent control (ambient UV) substrates at low sun angles would also have had negligible effects on treatment efficacy because of the narrowness of the substrates. Substrates below the polyvinylidene were the same as those below Plexiglas: 10-cm-wide groups of tiles centered on an east-west midpoint. They would have been shaded by the displaced UV shadow only in the block where the substrates were 35 mm below the polyvinylidene, and the UV shadow would have fallen on the substrates for <1 h either in the morning or in the afternoon, when UV intensities were relatively low. Control substrates 35 cm below the polyvinylidene would have had their maximum potential daily UV dose reduced by <14% on 11 November, when shadow displacement would have been greatest. We believe that treatment efficiencies that were reduced by <14% (control) and 22% (UV-shielded) by low sun angles in only one of four blocks do not seriously compromise our results.

In a second criticism, Donahue and Clare argue that our study was biased against detecting UV effects because all the biota at our research site were “adapted” to high levels of UV. White Oak Creek, like most streams, offers a variety of UV environments on a variety of scales. On a small scale, shaded microhabitats should be abundant on the sides of stream cobbles and elsewhere, even within high light sites. On a larger scale, our high light site is relatively uncommon in upper White Oak Creek, which is extensively shaded by terrestrial vegetation for the 6 months of the year that leaves are present (Hill et al. 1995). The tree canopy overhangs the stream only 20 m upstream from our site. Given the vast numbers of microalgae that drift downstream over the course of a day, it seems very unlikely that there was no pool of algae from shaded micro- or macrohabitats available to colonize the experimental substrates. In addition, the tiles with attached periphyton that we used for the experiments were taken from a shaded site upstream, so if there was a bias, it was that the periphyton communities beginning the experiments were shade adapted, a preconditioning state that Donahue and Clare recommend.

The pool of potential grazers available to colonize the UV-shielded substrates may have been more limited than that of

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Table 1. Relative abundance of attached algae on substrates exposed to and shielded from ambient UV radiation in White Oak Creek, autumn experiment 1993. Samples were taken at the end of the experiment. Values are mean percentages \pm standard errors, $n = 4$.

Genus	Ambient UV	UV shielded
<i>Stigeoclonium</i>	94.5 \pm 2.7	90.5 \pm 3.2
<i>Phormidium</i>	3.2 \pm 1.8	1.5 \pm 0.9
<i>Cymbella</i>	0.9 \pm 0.8	0.2 \pm 0.1
<i>Gomphonema</i>	0.6 \pm 0.4	0.2 \pm 0.2
<i>Cocconeis</i>	0.5 \pm 0.3	0.4 \pm 0.2
<i>Navicula</i>	0.2 \pm 0.2	0.7 \pm 0.4
<i>Achnanthydium</i>	0.1 \pm 0.1	4.9 \pm 2.4

the algae, as chironomids and mayflies are relatively scarce in White Oak Creek. Nonetheless, it certainly was not obvious beforehand that *Elimia clavaeformis* would not respond to UV manipulations. The snail's resistance to UV is something we now deduce from the results of our in situ experiments and from controlled dose-response experiments recently performed in our laboratory (McNamara et al. submitted), not from the ostensible habitat preference of a congener.

In a third criticism, Donahue and Clare express their concern over the lack of detailed taxonomic data in our study. We agree that detailed taxonomic analyses are necessary to carefully examine potential UV effects on algal assemblage structure, and we do not rule out the possibility that the relative abundance of algal species changed in response to our UV treatments. However, it would be unusual if significant taxonomic change occurred in periphyton without parallel changes in ash-free dry mass (AFDM), chlorophyll *a* (Chl *a*), or productivity. Previous experiments showing UV effects on periphyton assemblage structure also demonstrated very clear effects on AFDM and Chl *a* (Bothwell et al. 1993, 1994; Vinebrooke and Leavitt 1996). If changes in food quality or availability to grazers occurred as a result of UV-induced alterations in assemblage structure in our study, these changes were not reflected in *Elimia* densities, which were not significantly altered by our UV treatments.

A long list of parameters exists for characterizing periphyton communities. No study includes them all. Donahue and Clare characterize measurements of AFDM, Chl *a*, and photosynthesis as crude and potentially misleading, but these parameters are important ecological measurements with a long history of use in quantifying the importance of environmental factors in aquatic studies. Their significance as descriptors of periphyton should not be lightly dismissed. This is not to say that we were uninterested in the potential shift in microalgal assemblage composition if UV effects were significant. Samples of the periphyton from the last two experiments were collected for microscopic analysis, but the analyses were not reported in the original note because the summer samples were improperly preserved and the late fall samples were identified to genus level only (Table 1). Although these analyses did not identify algae to the species level and are from the experiment with the lowest ambient UV levels, they do not suggest a significant assemblage re-

sponse at the generic level: no statistically significant difference existed between UV treatments for any individual taxon. As for carbon uptake measurements made under metal halide lamps in the laboratory, transient UV effects on photosynthesis would undoubtedly have been underestimated if they occurred, but these putative effects must have been very small if they were not reflected in biomass accrual on the ungrazed substrates or in snail densities on the grazed substrates in the summer experiment.

Finally, Donahue and Clare suggest that we were interested in "making general claims about lack of sensitivity of stream systems to UV radiation." Our intent was exactly the opposite. We believe that generalizations about current and future UV effects will be difficult to make because of the inherent variability in exposure and organism sensitivity. A range of UV effects on benthic communities is expected, given the taxonomic variety, range of incident UV irradiances, substrate depths, and concentrations of UV-attenuating substances (e.g., dissolved organic carbon) that occur in shallow-water ecosystems. The periphyton-grazer system in White Oak Creek appears to be an example of a community little affected by UV. While other communities may be more sensitive (e.g., Bothwell et al. 1994), we feel it is important to identify nonsensitive systems as well as sensitive systems in order to provide an unbiased view of the overall impact of UV.

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