

## What role does UV-B radiation play in freshwater ecosystems?

*Craig E. Williamson*

Department of Earth and Environmental Sciences, 31 Williams Drive, Lehigh University, Bethlehem, Pennsylvania 18015-3188

### *Abstract*

Increases in incident UV-B radiation (280–320 nm) have been observed at temperate as well as polar latitudes in recent decades. Although UV-B radiation makes up only a small portion of the total energy of solar radiation and attenuates rapidly in the water column, the high sensitivity of living organisms to UV-B radiation makes the observed increases potentially important in aquatic ecosystems. To date, research has focused largely on the primary producers in marine ecosystems in Antarctica where ozone depletion and subsequent increases in UV-B radiation have been most pronounced. This review addresses the potential role of UV-B radiation in freshwaters by taking into account some of the information available in marine systems and applying some of the recent advances in our understanding of the ecology of freshwaters. The potential for complex rather than simple responses of freshwater ecosystems to UV-B radiation is emphasized.

Environmental exposure to UV-B radiation (280–320 nm) has been an integral part of the evolution of aquatic organisms. For most of their evolutionary history, organisms have been constrained to aquatic habitats where water offers some protection from damaging levels of ambient UV-B radiation. Although life has existed on our planet for  $>3 \times 10^9$  yr it was not until  $400\text{--}450 \times 10^6$  yr ago that ozone became abundant enough in the atmosphere to shield life from UV-B radiation, permitting aquatic organisms to make the transition to terrestrial habitats (Fischer 1965; Cloud 1968; Schlesinger 1991).

Recently, interest in the role of UV-B radiation in aquatic and terrestrial ecosystems has grown due to evidence that levels of ambient UV-B radiation are increasing in response to stratospheric ozone depletion (Tevini 1993; Young et al. 1993). Since the initial report of the “ozone hole” in Antarctica (Farman et al. 1985), research has focused on marine ecosystems in the Southern Ocean (Weiler and Penhale 1994) where UV-B radiation has been detected at depths of 60–70 m and inhibition of biological processes by UV-B radiation has been detected to depths of 20–30 m (Smith et al. 1992; Karentz and Lutze 1990). One of the primary concerns has been that inhibition of primary productivity related to elevated UV-B radiation will decrease global rates of carbon fixation and lead to an increase in atmospheric  $\text{CO}_2$  and a consequent acceleration of global warming trends. Independent of any future increases in UV-B radiation, many studies have demonstrated that short-wavelength solar radiation at current levels is damaging to a wide variety of aquatic organisms (Smith 1989; Häder and Worrest 1991; Häder 1993; Holm-Hansen et al. 1993).

The Southern Ocean is not the only aquatic ecosystem exposed to increased levels of UV-B radiation. Significant

increases in UV-B radiation of up to 10–20% per decade have recently been reported for both north and south temperate latitudes where freshwater ecosystems are abundant (Madronich 1992; Stolarski et al. 1992; Kerr and McElroy 1993). Less information is available on the role of UV-B radiation in freshwater than in marine ecosystems (Williamson and Zagarese 1994). Published data on depth profiles of UV-B radiation in lakes are extremely rare, and few experiments have been performed on the vulnerability of freshwater organisms to natural levels of UV-B radiation. The generally much higher concentrations of UV-B-absorbing dissolved humic substances in lakes vs. oceans (Kirk 1994) suggest that UV-B radiation will generally be attenuated more rapidly with depth in lakes than in oceans. Data that my colleagues and I recently collected on a variety of lakes from Pennsylvania, Colorado, Alaska, and Argentina suggest that the depth to which 10% of surface UV-B radiation penetrates is usually less than a few meters in all but the clearest lakes. On the other hand, the average depth of lakes worldwide is  $<10$  m (Wetzel 1990), and the warm mixed surface layers that provide favorable growth conditions for many freshwater organisms may be only a few meters thick. The lotic ecosystems of streams and rivers generally have higher dissolved and particulate loads than lakes, but they are also much shallower and thus also potentially vulnerable to damage by UV-B radiation.

### Role of UV-B radiation: Four hypotheses

In some of the clearest lakes of the world, 10% of incident UV-B radiation is still present at substantial depths: 7.7 m in Lake Tahoe, 10.8 m in Bessvatn (Norway), and 12.8 m in Laguna Negra (Chile) vs. 9 m in the Bellingshausen Sea of the Southern Ocean and up to 19.8 m in the clearest waters of the Sargasso Sea (Smith and Baker 1981; Kirk 1994). However, these lakes are exceptions, and when they are compared to marine ecosystems, lakes are likely to have steeper vertical gradients in light (UV and visible), temperature, oxygen, predators, food quality and quantity, and other habitat characteristics that influ-

### *Acknowledgments*

I thank Bruce Hargreaves, Robert Moeller, and two anonymous reviewers for their comments on the manuscript.

Supported in part by a grant from the A. W. Mellon Foundation and NSF grants DEB 93-06978, OPP 93-16534, and INT 93-14421.

ence fitness. These steep habitat gradients in lakes suggest that strong selective pressures exist in lacustrine environments for organisms to be finely tuned to changes in UV-B radiation, that it will interact with other environmental variables, and that it influences not only the primary producers, but also many trophic levels simultaneously, often with unexpected consequences (Bothwell et al. 1994). Here, four hypotheses illustrate this potentially complex role of UV-B radiation in freshwater ecosystems.

*Solar ambush hypothesis*—Aquatic organisms that cannot detect and respond to changes in UV-B radiation are especially vulnerable to damage from its natural fluctuations.

Solar radiation is highly variable over a range of scales from minutes and hours to days and weeks. In aquatic ecosystems, these fluctuations are due to changes in a variety of factors, including solar zenith angle, atmospheric aerosols, water vapor, height and density of cloud cover, elevation, and, in the water column, absorption and scattering by dissolved and particulate substances and water itself (Caldwell et al. 1980; Sullivan et al. 1992; Madronich 1994; Kirk 1994). UV-B radiation also tends to increase on the order of 6–8% per 1,000 m of elevation (Caldwell et al. 1980; Diffey 1991)—an important consideration for lakes but not for oceans. At higher elevations, increases in cloud cover may decrease the mean levels of UV-B radiation but increase the amplitude of its fluctuations, substantially changing the ratio of UV radiation to visible light. This change thus creates fundamental differences in UV-B environments in high- vs. low-elevation lakes and streams. Stratospheric ozone depletion results in a strong, selective increase in UV-B radiation, with little or no change in visible solar radiation (Molina and Molina 1986).

The importance of these wavelength-selective changes in solar radiation with ozone depletion is accentuated within the range of UV-B wavelengths (280–320 nm), where short-wavelength radiation can be several orders of magnitude more damaging per photon to biological systems than longer wavelengths (Setlow 1974; Cullen et al. 1992). Although UV-B radiation is <1% of the total energy irradiance of the sun reaching the surface of the earth, even small changes in fluxes of UV-B radiation have the potential to impact biological systems. In addition, the longer wavelength UV-A (320–400 nm) and even blue light may be either damaging or beneficial in stimulating photorepair (Hairston 1976; Siebeck 1978; Häder and Tevini 1987; Siebeck and Böhm 1994).

Thus, organisms that detect and respond to UV-A or visible light but not to UV-B can be “ambushed” and damaged by wavelength-selective changes in solar radiation. If effect, they will remain in habitats that they perceive as benign while UV-B radiation inflicts its damage. Although some invertebrates, such as the freshwater cladoceran *Daphnia* (Smith and Macagno 1990) and larvae of the sand dollar *Dendraster* (Pennington and Emlet 1986), have UV-B-sensitive photoreceptors and respond appropriately to selective increases in UV-B radiation,

other invertebrates such as the cuphausiid *Thysanoessa* (Damkaer and Dey 1983) and the freshwater midge *Cricotopus* (Bothwell et al. 1994), are unable to detect UV-B radiation and may be vulnerable to solar ambush.

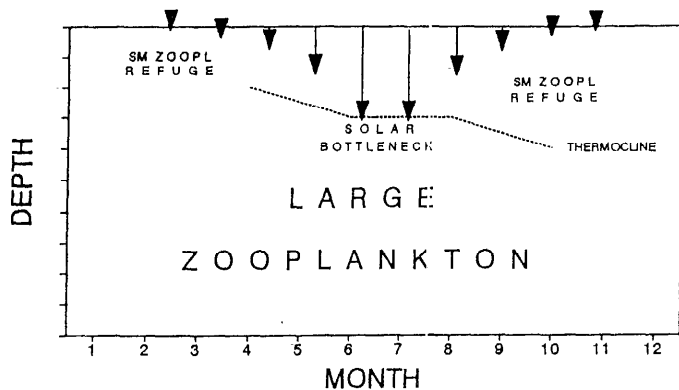
Sessile organisms may be particularly vulnerable to solar ambush because they cannot respond behaviorally to fluctuations in UV-B radiation as in, for example, the hypothesized coral bleaching by UV-B in marine ecosystems during calm, sunny periods (Gleason and Wellington 1993). Similarly, organisms that live in clear, shallow high-elevation lakes where fluctuation in UV-B radiation may be particularly severe could be vulnerable because the water is neither deep nor absorptive enough to offer refuge from damaging solar radiation. Interestingly, zooplankton in these high-elevation habitats are often highly pigmented (Siebeck 1978; Byron 1982; Modenutti 1992; Hessen 1994). The sensitivity of most vertebrate photoreceptors does not extend below the region of UV-A radiation (Siebeck et al. 1994), so they are also likely to be vulnerable to solar ambush.

*Solar bottleneck hypothesis*—Small zooplankton encounter a population bottleneck near the summer solstice in oligotrophic lakes due to two conflicting selective pressures: the diurnal vertical migration of predatory invertebrates and other large zooplankton downward during the day makes the warm epilimnetic waters a good refuge for small zooplankton; the high water clarity permits damaging levels of solar radiation to permeate these surface layers that would otherwise act as a refuge from large zooplankton. The population bottleneck occurs during the annual period of peak solar radiation and only in oligotrophic lakes where clear waters maximize penetration of damaging short-wavelength radiation (Fig. 1). In eutrophic lakes, solar radiation attenuates rapidly enough that levels of UV-B radiation are very low and the epilimnion remains an effective refuge from large zooplankton.

This hypothesis is based on two major premises. First, in situ levels of solar radiation in the epilimnion of lakes can damage zooplankton in oligotrophic but not in eutrophic lakes. Second, small zooplankton exhibit reverse vertical migration upward into the epilimnion during the day to avoid predation by large zooplankton. Damage from sunlight was one of the first hypotheses put forth to explain the adaptive significance of diel vertical migration (Huntsman 1924; Forward 1988), and solar radiation is harmful to many freshwater zooplankton (Hairston 1976; Siebeck 1978; Byron 1982; Ringelberg et al. 1984). In situ levels of the UV-B component of solar radiation within the surface waters of clear oligotrophic lakes killed zooplankton held in the top few meters of the water column and depressed reproduction to depths of 6 m, whereas zooplankton incubated simultaneously in a eutrophic lake were not harmed (Williamson et al. 1994; Zagarese et al. 1994). These experiments suggest that harmful levels of sunlight exist in the surface waters of oligotrophic lakes but not of eutrophic lakes.

Predation is well recognized as an important factor regulating the distribution and abundance of species in

## A. OLIGOTROPHIC LAKE



## B. EUTROPHIC LAKE

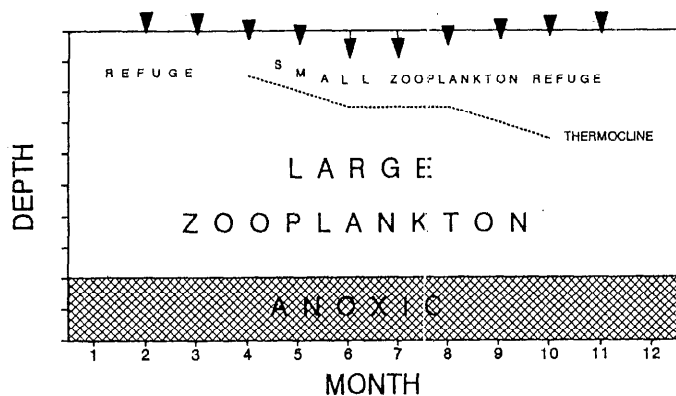


Fig. 1. Conceptual model illustrating the presence of a "solar bottleneck" for small zooplankton in clear oligotrophic lakes (A) but not in eutrophic lakes (B). Large zooplankton make the deeper strata of both types of lakes inhospitable for small zooplankton during the day. In oligotrophic lakes, deeper penetration of damaging solar radiation (arrows) creates an inhospitable environment in the warm surface waters during the summer solstice. In eutrophic lakes, the rapid attenuation of damaging solar radiation creates a persistent refuge for small zooplankton in the epilimnion.

the freshwater plankton and contributes an essential component to the "trophic cascade" (Carpenter et al. 1985; Carpenter and Kitchell 1993). Zooplanktivorous fish require light to feed and prefer to eat larger zooplankton prey (Zaret 1980). Thus, the presence of fish predators often induces strong migrations of larger zooplankton species into the deeper, darker layers of lakes during daylight hours (Kerfoot 1985; Haney 1988; Lampert 1989). These large zooplankton, in turn, can have a substantial negative impact on smaller zooplankton, such as rotifers. Some large zooplankton are tactile invertebrate predators that prey heavily on rotifers (Williamson 1983, 1993; Stemberger 1986; Moore and Gilbert 1987). Even large omnivorous and herbivorous zooplankton may damage ro-

tifers through predation or interference (Williamson and Butler 1986; Williamson 1987; Gilbert 1988; MacIsaac and Gilbert 1989; Arnott and Vanni 1993). As a consequence, rotifers and other small zooplankton often exhibit a reverse migration upward during the day and downward at night, thereby minimizing overlap in space and time with large zooplankton (Dumont 1972; Hairston 1980; Neill 1990; Ohman 1990; Williamson and Stoeckel 1990; Williamson 1993).

Two predictions arise from this population bottleneck hypothesis. First, the abundance of small zooplankton would be suppressed near the summer solstice in oligotrophic but not in eutrophic lakes. Second, reverse vertical migration into and out of the epilimnion by small zooplankton would be more intense in eutrophic lakes, where a safe refuge from large zooplankton exists, than in oligotrophic lakes, where high levels of damaging sunlight permeate the surface of this potential refuge.

*Solar cascade hypothesis*—In addition to causing direct damage to individual organisms, UV-B radiation can have a strong effect on organisms by influencing the abundance of their food resources or predators.

This hypothesis is a simple extension of the widely recognized concepts of cascading trophic interactions (Carpenter et al. 1985; McQueen et al. 1989; Carpenter and Kitchell 1993) and indirect effects (Kerfoot and Sih 1987) in freshwater communities, wherein predators (more generally, consumers) regulate the abundance of their resources and resource limitation similarly regulates the abundance of consumers. Thus, if adjacent trophic levels of a given population are more negatively influenced by direct effects of UV radiation than the population itself, the indirect response of that population to UV radiation may be stronger than the direct response. Indirect effects that are "bottom-up" will have the same positive or negative influence that direct effects have on a given population, while "top-down" effects will have the opposite influence.

Abundant evidence exists for the direct depression of phytoplankton productivity by UV radiation (Karentz et al. 1994; Vincent and Roy 1993), and this effect may be aggravated by nutrient limitation (Moeller 1994). Zooplankton, which graze on phytoplankton, are also vulnerable to UV radiation (Siebeck 1978; Ringelberg et al. 1984; Williamson et al. 1994). If the negative impact of UV radiation on these grazers is greater than the direct effect on the phytoplankton, and if the phytoplankton are grazer limited, then the net effect of increased UV radiation on the ecosystem may be an increase rather than a decrease in primary productivity and/or biomass accumulation. Such an effect has already been demonstrated for benthic stream diatom communities that showed a greater accumulation of biomass when exposed to UV radiation than diatom communities shielded from it (Bothwell et al. 1993, 1994). These studies clearly demonstrate the need for longer term mesocosm experiments that include multiple trophic level or even whole ecosystem responses to UV radiation.

Similarly complex interactions are present in microbial

communities. For example, in situ levels of UV radiation can directly inhibit heterotrophic C fixation in natural bacteria communities (Herndl et al. 1993); however, UV radiation can indirectly stimulate increased bacterial productivity by breaking down recalcitrant humic substances into low-molecular-weight organic compounds that are more available to heterotrophic bacteria (Kieber et al. 1989; Mopper et al. 1991; DeHaan 1993). This photodegradation of humic substances can also reduce oxygen levels in humic lakes (Lindell and Rai 1994) and produce toxic by-products, such as hydroxyl radicals, singlet oxygen, and hydrogen peroxide in surface waters (Cooper and Lean 1989; Mopper and Zhou 1990; Cooper et al. 1994; Lean et al. 1994). The effects of these photochemicals on aquatic organisms are largely unknown.

These indirect effects of UV-B radiation on bacteria and phytoplankton, combined with the fact that humic substances are a major regulator of UV-B attenuation in lakes, suggest that complex feedback loops exist between UV-B radiation and aquatic primary productivity. The net effect of increased UV-B radiation on aquatic ecosystems thus might be to decrease or increase net primary productivity, depending on the relative strength of these feedback loops and on whether primary productivity is grazer or nutrient limited (e.g. Banse 1990; Martin et al. 1990).

Other feedback loops may exist with higher trophic levels as well. For example, in many lakes, a spring clear-water phase of an abrupt increase in water transparency is often induced by zooplankton grazing on phytoplankton (Lampert et al. 1986; Sommer et al. 1986; Luecke et al. 1990; Mazumder et al. 1990). These clear-water periods usually occur in mid- to late May, when solar radiation is increasing and approaching its highest levels at the summer solstice. The implications of increased penetration of UV-B radiation during these periods of shifting community structure are unknown.

Related issues are that food quality is frequently important in limiting zooplankton population densities and that the nutritional quality of phytoplankton changes with light levels and nutrient availability (Rothhaupt 1991; Smith 1991). In the presence of UV light, secondary compounds, such as xanthotoxin in terrestrial plants, may show an increase in toxicity to herbivorous insects (Berenbaum 1978). Whether photoprotective pigments, such as carotenoids and mycosporine like amino acids synthesized by phytoplankton and ingested by zooplankton (Hairston 1976; Dunlap et al. 1986; Karentz et al. 1991), can change the nutritional quality of phytoplankton is an open question. Zooplankton can sequester and alter these pigments for their own photoprotection (Hairston 1976; Karentz et al. 1991), but these pigments also make them more vulnerable to visual predators (Hairston 1976; Luecke and O'Brien 1981; Byron 1982).

Fish and amphibian predators, in turn, may regulate the distribution, size structure, and species composition of zooplankton communities (Kerfoot and Sih 1987) and may themselves be vulnerable to UV radiation (Little and Fabacher 1994; Siebeck et al. 1994). Many vertebrates lay highly transparent eggs in shallow water during pe-

riods of high solar radiation, rendering the eggs potentially vulnerable to UV damage. Recent experimental and observational data suggest that UV-B radiation is a contributing factor in the widespread decline of amphibian populations (Blaustein et al. 1994). Collectively, these observations suggest that the indirect effects of UV-B radiation and corresponding feedback loops may extend all the way from water transparency to bacteria, phytoplankton, zooplankton, and vertebrate predators.

*Acid transparency hypothesis* — Anthropogenically acidified lakes are harsher UV-B environments than naturally acidified lakes.

Acidification from the burning of fossil fuels has been an important anthropogenically induced disturbance in lakes in recent decades (Likens and Bormann 1974; Hendrey 1984; Charles 1991; Schindler et al. 1991). Although data on the factors controlling UV-B radiation in freshwaters are scant, dissolved organic C and humic substances in particular seem to be important in controlling attenuation of UV-B radiation (DeHaan 1993; Kirk 1994; Scully and Lean 1994). Lakes that are naturally acidic often have high concentrations of humic substances and are therefore likely to attenuate UV-B radiation within only a few centimeters of the surface (DeHaan 1993; Kirk 1994). Anthropogenically acidified lakes, on the other hand, tend to have reduced levels of humic materials and greater water transparency (Yan and Miller 1984; Baker et al. 1991; Schindler et al. 1991). The lower levels of humic materials in anthropogenically acidified lakes suggest that these lakes are likely harsher UV-B environments than naturally acidic lakes and that UV-B radiation may even play some role in the changes in species diversity that are observed during lake acidification (Baker and Christensen 1991; Schindler et al. 1991). It is generally thought that these changes are not due exclusively to changes in pH and that other factors, such as indirect food-web effects, may be important (Yan and Geiling 1985; Yan et al. 1991; Schindler et al. 1991; Webster et al. 1992).

## Conclusions

One of the most important caveats to working with the impact of UV-B radiation on freshwater ecosystems is that complex rather than simple responses are likely to be the rule. Most of the existing information on the role of UV-B radiation in aquatic ecosystems is at the organismal or suborganismal level, but the responses we ultimately need to understand are at the community and ecosystem levels and are a function of responses at multiple trophic levels. The responses of freshwater ecosystems to UV-B radiation are not likely to be limited to simple decreases in primary productivity (Vincent and Roy 1993). Individuals, populations, and species on different trophic levels vary in their sensitivity to UV-B radiation, suggesting that more subtle shifts in community structure at multiple trophic levels may be common (Bothwell et al. 1994). This scenario is similar to the

response of freshwater ecosystems to other anthropogenic disturbances such as acid precipitation: Indirect responses as well as direct responses to disturbance are important (Schindler et al. 1991; Webster et al. 1992) and shifts in community structure are common, but *net* ecosystem processes such as primary productivity, decomposition, and nutrient cycling are largely unaffected (Baker and Christensen 1991).

The response of freshwater ecosystems to UV-B radiation is also likely to be related to other important environmental changes. For example, recent evidence suggests that climate change has altered the hydrology of the Canadian shield lakes and led to reductions in humic substances with consequent increases in water clarity and thermocline depth (Schindler et al. 1990). UV-B radiation levels likely have increased in these lakes, but no data are available. More generally, the interactions between physical and biotic factors in ecological systems (Dunson and Travis 1991) make the ecology of UV-B radiation in freshwaters a fertile area for research regardless of future changes in UV-B radiation. If the trend of increasing UV-B radiation does continue, research in this area is even more critical.

## References

- ARNOTT, S. E., AND M. J. VANNI. 1993. Zooplankton assemblages in fishless bog lakes: Influence of biotic and abiotic factors. *Ecology* 74: 2361–2380.
- BAKER, J. P., AND S. W. CHRISTENSEN. 1991. Effects of acidification on biological communities in aquatic ecosystems, p. 83–105. *In* D. F. Charles [ed.], *Acidic deposition and aquatic ecosystems*. Springer.
- BAKER, L. A., A. T. HERLIHY, P. R. KAUFMANN, AND J. M. EILERS. 1991. Acidic lakes and streams in the United States: The role of acidic deposition. *Science* 252: 1151–1154.
- BANSE, K. 1990. Does iron really limit phytoplankton production in the offshore subarctic Pacific? *Limnol. Oceanogr.* 35: 772–775.
- BERENBAUM, M. 1978. Toxicity of a furanocoumarin to armyworms: A case of biosynthetic escape from insect herbivores. *Science* 201: 532–534.
- BLAUSTEIN, A. R., AND OTHERS. 1994. UV repair and resistance to solar UV-B in amphibian eggs: A link to population declines? *Proc. Natl. Acad. Sci.* 91: 1791–1795.
- BOTHWELL, M. L., D. M. SHERBOT, AND C. M. POLLOCK. 1994. Ecosystem response to solar ultraviolet-B radiation: Influence of trophic-level interactions. *Science* 265: 97–100.
- , ———, A. C. ROBERGE, AND R. J. DALEY. 1993. Influence of natural ultraviolet radiation on lotic periphytic diatom community growth, biomass accrual, and species composition: Short-term versus long-term effects. *J. Phycol.* 29: 24–35.
- BYRON, E. R. 1982. The adaptive significance of calanoid copepod pigmentation: A comparative and experimental analysis. *Ecology* 63: 1871–1886.
- CALDWELL, M. M., R. ROBERG, AND W. D. BILLINGS. 1980. A steep latitudinal gradient of solar ultraviolet-B radiation in the arctic-alpine life zone. *Ecology* 61: 600–611.
- CARPENTER, S. R., AND J. F. KITCHELL [EDS.]. 1993. *The trophic cascade in lakes*. Cambridge.
- , ———, AND J. R. HODGSON. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35: 634–639.
- CHARLES, D. F. [ED.]. 1991. *Acidic deposition and aquatic ecosystems*. Springer.
- CLOUD, P. E. 1968. Atmospheric and hydrospheric evolution of primitive earth. *Science* 160: 729–736.
- COOPER, W. J., AND D. R. S. LEAN. 1989. Hydrogen peroxide concentration in a northern lake: Photochemical formation and diel variability. *Environ. Sci. Technol.* 23: 1425–1428.
- , C. SHAO, D. R. S. LEAN, A. S. GORDON, AND F. E. SCULLY, JR. 1994. Factors affecting the distribution of H<sub>2</sub>O<sub>2</sub> in surface waters, p. 391–422. *In* L. A. Baker [ed.], *Environmental chemistry of lakes and reservoirs*. Am. Chem. Soc.
- CULLEN, J. J., P. J. NEALE, AND M. P. LESSER. 1992. Biological weighting function for the inhibition of phytoplankton photosynthesis by ultraviolet radiation. *Science* 258: 646–650.
- DAMKAER, D. M., AND D. B. DEY. 1983. UV damage and photoreactivation potentials of larval shrimp, *Pandalus platyceros*, and adult euphausiids, *Thysanoessa raschii*. *Oecologia* 60: 169–175.
- DEHAAN, H. 1993. Solar UV-light penetration and photodegradation of humic substances in peaty lake water. *Limnol. Oceanogr.* 38: 1072–1076.
- DIFFEY, B. L. 1991. Solar ultraviolet radiation effects on biological systems. *Phys. Med. Biol.* 36: 299–328.
- DUMONT, H. J. 1972. A competition-based approach of the reverse vertical migration in zooplankton and its implications, chiefly based on a study of the interactions of the rotifer *Asplanchna priodonta* (Gosse) with several crustacea Entomostraca. *Int. Rev. Gesamten Hydrobiol.* 57: 1–38.
- DUNLAP, W. C., B. E. CHALKER, AND J. K. OLIVER. 1986. Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. 3. UV-B absorbing compounds. *J. Exp. Mar. Biol. Ecol.* 104: 239–248.
- DUNSON, W. A., AND J. TRAVIS. 1991. The role of abiotic factors in community organization. *Am. Nat.* 138: 1067–1091.
- FARMAN, J. C., B. G. GARDINER, AND J. D. SHANKLIN. 1985. Large losses of total ozone in Antarctica reveal seasonal CO<sub>x</sub>/NO<sub>x</sub> interaction. *Nature* 315: 207–210.
- FISCHER, A. G. 1965. Fossils, early life, and atmospheric history. *Proc. Natl. Acad. Sci.* 53: 1205–1215.
- FORWARD, R. B. 1988. Diel vertical migration: Zooplankton photobiology and behaviour. *Oceanogr. Mar. Biol. Annu. Rev.* 26: 361–393.
- GILBERT, J. J. 1988. Suppression of rotifer populations by *Daphnia*: A review of the evidence, the mechanisms, and the effects on zooplankton community structure. *Limnol. Oceanogr.* 33: 1286–1303.
- GLEASON, D. F., AND G. M. WELLINGTON. 1993. Ultraviolet radiation and coral bleaching. *Nature* 365: 836–838.
- HÄDER, D. 1993. Effects of enhanced solar ultraviolet radiation on aquatic ecosystems, p. 155–192. *In* M. Tevini [ed.], *UV-B radiation and ozone depletion*. Lewis.
- , AND M. TEVINI. 1987. *General photobiology*. Pergamon.
- , AND R. C. WORREST. 1991. Effects of enhanced solar ultraviolet radiation on aquatic ecosystems. *Photochem. Photobiol.* 53: 717–725.
- HAIRSTON, N. G., JR. 1976. Photoprotection by carotenoid pigments in the copepod *Diaptomus nevadensis*. *Proc. Natl. Acad. Sci.* 73: 971–974.
- . 1980. The vertical distribution of diaptomid copepods in relation to body pigmentation. *Am. Soc. Limnol. Oceanogr. Spec. Symp.* 3: 98–110. New England.

- HANEY, J. F. 1988. Diel patterns of zooplankton behavior. *Bull. Mar. Sci.* **43**: 583–603.
- HENDREY, G. R. [ED.]. 1984. Early biotic responses to advancing lake acidification. Butterworth.
- HERNDL, G. J., G. MÜLLER-NIKLAS, AND J. FRICK. 1993. Major role of ultraviolet-B in controlling bacterioplankton growth in the surface layer of the ocean. *Nature* **361**: 717–719.
- HESSEN, D. 1994. *Daphnia* responses to UV-light. *Ergeb. Limnol.* **43**: 185–195.
- HOLM-HANSEN, O., D. LUBIN, AND E. W. HELBLING. 1993. Ultraviolet radiation and its effects on organisms in aquatic environments, p. 379–425. In A. R. Young et al. [eds.], *Environmental UV photobiology*. Plenum.
- HUNTSMAN, A. G. 1924. Limiting factors for marine animals. 1. The lethal effect of sunlight. *Contrib. Can. Biol.* **2**: 83–88.
- KARENTZ, D., AND OTHERS. 1994. Impact of UV-B radiation on pelagic freshwater ecosystems: Report of working group on bacteria and phytoplankton. *Ergeb. Limnol.* **43**: 31–69.
- , AND L. H. LUTZE. 1990. Evaluation of biologically harmful ultraviolet radiation in Antarctica with a biological dosimeter designed for aquatic environments. *Limnol. Oceanogr.* **35**: 549–561.
- , F. S. MCEUEN, M. C. LAND, AND W. C. DUNLAP. 1991. Survey of mycosporine-like amino acid compounds in Antarctic marine organisms: Potential protection from ultraviolet exposure. *Mar. Biol.* **108**: 157–166.
- KERFOOT, W. C. 1985. Adaptive value of vertical migration: Comments on the predation hypothesis and some alternatives. *Contrib. Mar. Sci.* **27**: 91–113.
- , AND A. SIH. 1987. Predation: Direct and indirect impacts on aquatic communities. New England.
- KERR, J. B., AND C. T. MCELROY. 1993. Evidence for large upward trends of ultraviolet-B radiation linked to ozone depletion. *Science* **262**: 1032–1034.
- KIEBER, D. J., J. MCDANIEL, AND K. MOPPER. 1989. Photochemical source of biological substrates in sea water: Implications for carbon cycling. *Nature* **341**: 637–639.
- KIRK, J. T. O. 1994. Optics of UV-B radiation in natural waters. *Ergeb. Limnol.* **43**: 1–16.
- LAMPERT, W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.* **3**: 21–27.
- , W. FLECKNER, H. RAI, AND B. E. TAYLOR. 1986. Phytoplankton control by grazing zooplankton: A study on the spring clear-water phase. *Limnol. Oceanogr.* **31**: 478–490.
- LEAN, D. R. S., W. J. COOPER, AND F. R. PICK. 1994. Hydrogen peroxide formation and decay in lake waters, p. 207–214. In G. Helz et al. [eds.], *Aquatic and surface photochemistry*. CRC.
- LIKENS, G. E., AND F. H. BORMANN. 1974. Acid rain: A serious regional environmental problem. *Science* **184**: 1176–1179.
- LINDELL, M. J., AND H. RAI. 1994. Photochemical oxygen consumption in humic waters. *Ergeb. Limnol.* **43**: 145–155.
- LITTLE, E. E., AND D. L. FABACHER. 1994. Comparative sensitivity of rainbow trout and two threatened salmonids, Apache trout and Lahontan cutthroat trout, to ultraviolet-B radiation. *Ergeb. Limnol.* **43**: 217–226.
- LUECKE, C., AND W. J. O'BRIEN. 1981. Phototoxicity and fish predation: Selective factors in color morphs in *Heterocope*. *Limnol. Oceanogr.* **26**: 454–460.
- , M. J. VANNI, J. J. MAGNUSON, J. F. KITCHELL, AND P. T. JACOBSON. 1990. Seasonal regulation of *Daphnia* populations by planktivorous fish: Implications for the spring clear-water phase. *Limnol. Oceanogr.* **35**: 1718–1733.
- MACISAAC, H. J., AND J. J. GILBERT. 1989. Competition between rotifers and cladocerans of different body sizes. *Oecologia* **81**: 295–301.
- MCQUEEN, D. J., M. R. S. JOHANNES, J. R. POST, T. STEWART, AND D. R. S. LEAN. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecol. Monogr.* **59**: 289–309.
- MADRONICH, S. 1992. Implications of recent total atmospheric ozone measurements for biologically active ultraviolet radiation reaching the earth's surface. *Geophys. Res. Lett.* **19**: 37–40.
- . 1994. Increases in biologically damaging UV-B radiation due to stratospheric ozone reductions: A brief review. *Ergeb. Limnol.* **43**: 17–30.
- MARTIN, J. H., W. W. BROENKOW, S. E. FITZWATER, AND R. M. GORDON. 1990. Yes, it does: A reply to the comment by Banse. *Limnol. Oceanogr.* **35**: 775–777.
- MAZUMDER, A., W. D. TAYLOR, D. J. MCQUEEN, AND D. R. S. LEAN. 1990. Effects of fish and plankton on lake temperature and mixing depth. *Science* **247**: 312–315.
- MODENUTTI, B. 1992. Summer population of *Hexarthra bulgarica* in a high altitude lake of South Andes. *Hydrobiologia* **259**: 33–37.
- MOELLER, R. E. 1994. Contribution of ultraviolet radiation (UV-A, UV-B) to photoinhibition of epilimnetic phytoplankton in lakes of differing UV transparency. *Ergeb. Limnol.* **43**: 157–170.
- MOLINA, L. T., AND M. J. MOLINA. 1986. Absolute absorption cross sections of ozone in the 185–350-nm wavelength range. *J. Geophys. Res.* **91**: 14501–14508.
- MOORE, M. V., AND J. J. GILBERT. 1987. Age-specific *Chaoborus* predation on rotifer prey. *Freshwater Biol.* **17**: 223–236.
- MOPPER, K., AND X. ZHOU. 1990. Hydroxyl radical photo-production in the sea and its potential impact on marine processes. *Science* **250**: 661–664.
- , AND OTHERS. 1991. Photochemical degradation of dissolved organic carbon and its impact on the oceanic carbon cycle. *Nature* **353**: 60–62.
- NEILL, W. E. 1990. Induced vertical migration in copepods as a defence against invertebrate predation. *Nature* **345**: 524–526.
- OHMAN, M. D. 1990. The demographic benefits of diel vertical migration by zooplankton. *Ecol. Monogr.* **60**: 257–281.
- PENNINGTON, J. T., AND R. B. EMLET. 1986. Ontogenetic and diel migration of a planktonic echinoid larva, *Dendraster excentricus* (Eschscholtz): Occurrence, causes, and probable consequences. *J. Exp. Mar. Biol. Ecol.* **104**: 69–95.
- RINGELBERG, J., A. L. KEYSER, AND B. J. G. FLIK. 1984. The mortality effect of ultraviolet radiation in a translucent and in a red morph of *Acanthodiptomus denticornis* (Crustacea, Copepoda) and its possible ecological relevance. *Hydrobiologia* **112**: 217–222.
- ROTHHAUPT, K. O. 1991. Variations on the zooplankton menu: A reply to the comment by Smith. *Limnol. Oceanogr.* **36**: 824–827.
- SCHINDLER, D. W., AND OTHERS. 1990. Effects of climatic warming on lakes of the central boreal forest. *Science* **250**: 967–970.
- , AND OTHERS. 1991. Comparisons between experimentally- and atmospherically-acidified lakes during stress and recovery. *Proc. R. Soc. Edinb.* **97B**: 193–226.
- SCHLESINGER, W. H. 1991. Biogeochemistry, an analysis of global change. Academic.
- SCULLY, N. M., AND D. R. S. LEAN. 1994. The attenuation of ultraviolet radiation in temperate lakes. *Ergeb. Limnol.* **43**: 135–144.

- SETLOW, R. B. 1974. The wavelengths in sunlight effective in producing skin cancer: A theoretical analysis. *Proc. Natl. Acad. Sci.* **71**: 3363–3366.
- SIEBECK, O. 1978. Ultraviolet tolerance of planktonic crustaceans. *Int. Ver. Theor. Angew. Limnol. Verh.* **20**: 2469–2473.
- , AND U. BÖHM. 1994. Challenges for an appraisal of UV-B effects upon planktonic crustaceans under natural radiation conditions with a non-migrating (*Daphnia pulex obtusa*) and a migrating cladoceran (*Daphnia galeata*). *Ergeb. Limnol.* **43**: 197–206.
- , AND OTHERS. 1994. Impact of UV-B radiation on zooplankton and fish in pelagic freshwater ecosystems. *Ergeb. Limnol.* **43**: 101–114.
- SMITH, K. C., AND E. R. MACAGNO. 1990. UV photoreceptors in the compound eye of *Daphnia magna* (Crustacea, Branchiopoda). A fourth spectral class in single ommatidia. *J. Comp. Physiol. Ser. A* **166**: 597–606.
- SMITH, R. C. 1989. Ozone, middle ultraviolet radiation and the aquatic environment. *Photochem. Photobiol.* **50**: 459–468.
- , AND K. S. BAKER. 1981. Optical properties of the clearest natural waters (200–800 nm). *Appl. Opt.* **20**: 177–184.
- , AND OTHERS. 1992. Ozone depletion: Ultraviolet radiation and phytoplankton biology in antarctic waters. *Science* **255**: 952–959.
- SMITH, V. H. 1991. Competition between consumers. *Limnol. Oceanogr.* **36**: 820–823.
- SOMMER, U., Z. M. GLIWICZ, W. LAMPERT, AND A. DUNCAN. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.* **106**: 433–471.
- STEMBERGER, R. S. 1986. The effects of food deprivation, prey density and volume on clearance rates and ingestion rates of *Diacyclops thomasi*. *J. Plankton Res.* **8**: 243–251.
- STOLARSKI, R., AND OTHERS. 1992. Measured trends in stratospheric ozone. *Science* **256**: 342–349.
- SULLIVAN, J. H., A. H. TERAMURA, AND L. II. ZISKA. 1992. Variation in UV-B sensitivity in plants from a 3,000-m elevational gradient in Hawaii. *Am. J. Bot.* **79**: 737–743.
- TEVINI, M. [ED.]. 1993. UV-B radiation and ozone depletion. Lewis.
- VINCENT, W. F., AND S. ROY. 1993. Solar ultraviolet-B radiation and aquatic primary production: Damage, protection, and recovery. *Environ. Rev.* **1**: 1–12.
- WEBSTER, K. E., AND OTHERS. 1992. Complex biological responses to the experimental acidification of Little Rock Lake, Wisconsin, USA. *Environ. Pollut.* **78**: 73–78.
- WEILER, C. S., AND P. A. PENHALE [EDS.]. 1994. Ultraviolet radiation in Antarctica: Measurements and biological effects. *Antarc. Res. Ser. V. 62*. Am. Geophys. Union.
- WETZEL, R. G. 1990. Land-water interfaces: Metabolic and limnological regulators. *Int. Ver. Theor. Angew. Limnol. Verh.* **24**: 6–24.
- WILLIAMSON, C. E. 1983. Invertebrate predation on planktonic rotifers. *Hydrobiologia* **104**: 385–396.
- . 1987. Predator-prey interactions between omnivorous diaptomid copepods and rotifers: The role of prey morphology and behavior. *Limnol. Oceanogr.* **32**: 167–177.
- . 1993. Linking predation risk models with behavioral mechanisms: Identifying population bottlenecks. *Ecology* **74**: 320–331.
- , AND N. M. BUTLER. 1986. Predation on rotifers by the suspension-feeding calanoid copepod *Diaptomus pallidus*. *Limnol. Oceanogr.* **31**: 393–402.
- , AND M. E. STOECKEL. 1990. Estimating predation risk in zooplankton communities: The importance of vertical overlap. *Hydrobiologia* **198**: 125–131.
- , AND H. E. ZAGARESE [EDS.]. 1994. The impact of UV-B radiation on pelagic freshwater ecosystems. *Ergeb. Limnol.* **43**: 225 p.
- , P. C. SCHULZE, B. R. HARGREAVES, AND J. SEVA. 1994. The impact of short-term exposure to UV-B radiation on zooplankton communities in north temperate lakes. *J. Plankton Res.* **16**: 205–218.
- YAN, N. D., AND W. GEILING. 1985. Elevated planktonic rotifer biomass in acidified metal-contaminated lakes near Sudbury, Ontario. *Hydrobiologia* **120**: 199–205.
- , W. KELLER, H. J. MACISAAC, AND L. J. MCEACHERN. 1991. Regulation of zooplankton community structure of an acidified lake by *Chaoborus*. *Ecol. Appl.* **1**: 52–65.
- , AND G. E. MILLER. 1984. Effects of deposition of acids and metals on chemistry and biology of lakes near Sudbury, Ontario, p. 243–282. *In* J. Nriagu [ed.], *Environmental impacts of smelters*. Wiley.
- YOUNG, A. R., L. O. BJORN, J. MOAN, AND W. NULTSCH [EDS.]. 1993. *Environmental UV photobiology*. Plenum.
- ZAGARESE, H. E., C. E. WILLIAMSON, M. MISLIVETS, AND P. ORR. 1994. The vulnerability of *Daphnia* to UV-B radiation in the northeastern United States. *Ergeb. Limnol.* **43**: 207–216.
- ZARET, T. M. 1980. *Predation and freshwater communities*. Yale.

Submitted: 18 April 1994

Accepted: 12 July 1994

Amended: 16 November 1994