S. Jones, B. J. MacFadden, Eds. (Plenum, New York, 1985), pp. 385–406.
25. J. L. Kirschvink and J. L. Gould, *Biosystems* **13**, 181 (1981).
26. A. Sievers, S. Kruse, L.-L. Kuo-Huang, M. Wendt, *Planta* **172**, 321 (1989).
27. D. A. Kuterbach and B. Walcott, *J. Exp. Biol.* **126**, 375 (1986).
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Ecosystem Response to Solar Ultraviolet-B Radiation: Influence of Trophic-Level Interactions

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Solar ultraviolet radiation (UVR) can reduce the photosynthesis and growth of benthic diatom communities in shallow freshwater. Nevertheless, greater amounts of algae accumulate in UVR-exposed habitats than in UVR-protected environments. Near-ultraviolet (UVA wavelengths of 320 to 400 nanometers) and mid-ultraviolet (UVB, wavelengths of 280 to 320 nanometers) radiation also inhibit algal consumers (Diptera: Chironomidae). Larval chironomids are more sensitive to UVB than sympatric algae. Differential sensitivity to UVB between algae and herbivores contributes to counterintuitive increases in algae in habitats exposed to UVB. These mesocosm experiments illustrate that predictions of the response of entire ecosystems to elevated UVB cannot be made on single trophic-level assessments.

Solar ultraviolet radiation (UVR: 280 to 400 nm) at mid-latitudes during the summer can inhibit algal photosynthesis in oceans and lakes (*1–5*). Middle ultraviolet radiation (UVB: 280 to 320 nm) disrupts many photosynthetic processes including the electron transport system (*6*), photosystem II reaction centers (*7*), and pigment stability (*8*). It also damages algal DNA (*9, 10*), and both UVB and near-ultraviolet radiation (UVA: 320 to 400 nm) reduce algal growth rates (*11, 12*). Short-term UVR-screening experiments confirm the UVR inhibition of attached diatom growth rates during the summer at mid-northern latitudes (*13*). Paradoxically, extended exposure to UVR substantially increased the diatom biomass (*13*). Furthermore, lower intensities of UVR, non-inhibiting to the algal accrual rate, also augmented autotrophic biomass accumulation when compared to habitats completely shielded from UVR (*13*).

Algae can increase their tolerance of UVR by synthesizing protective UVR-absorbing compounds (*14*) and by repairing damaged DNA (*9, 10*). A wide range in sensitivity to UVR exists among algal taxa (*9, 11*). Succession to algal species presumed to be more UVR-tolerant has been documented in longer experiments (*13, 15*). However, succession, physiological adaptation, or both could not explain the more than doubling of algal biomass in response to UVR exposure observed in our earlier experiments (*13*). Discrepancies between short- and long-term effects of UVR on algae have been observed and reported (*16, 17*). Severe photosynthetic inhibition and DNA damage documented in short-term exposures of Antarctic phytoplankton to near-surface levels of UVB did not lower algal growth rates or reduce algal accumulation over extended periods of time (*16, 17*). Mesocosms with freshwater plankton communities in Lake Negra (Chile) exposed to near-surface, full-spectrum sunlight for 20 days supported greater algal biomass than communities protected from UVR (*18*). Similar observations of elevated phytoplankton in mesocosms exposed to UVR have recently been made in North America (*19*).

Middle ultraviolet radiation can affect organisms at all trophic levels, both directly and indirectly (*1, 20*). Thus, compounding

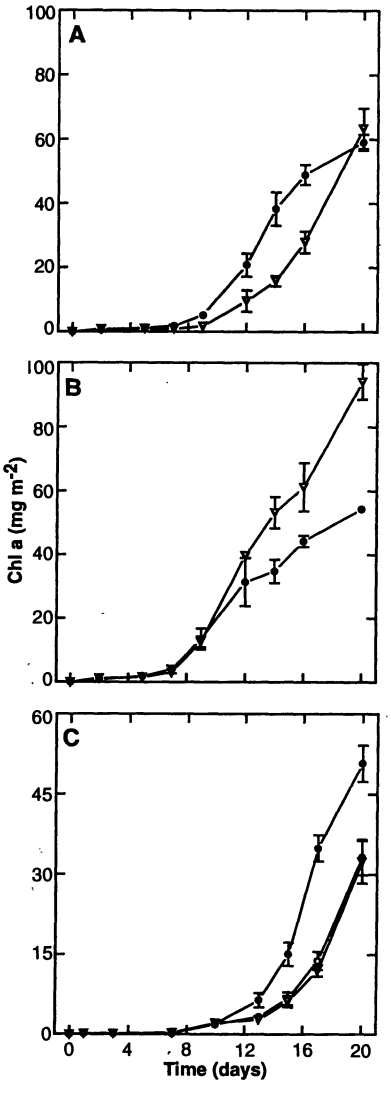

Fig. 1. (**A**) UVR inhibition of algal (Chl a) community growth and accrual by 90% PAR+UVA+UVB (PVI, inverted triangles) compared to growth under 90% PAR (UF-1, closed circles). During the initial 1 to 2 weeks, specific growth rates were lowered by UVR (*13*) (ANCOVA, $P < 0.01$). Reduced growth rates resulted in lower accrued Chl a and algal biomass (cell volumes) during this initial phase (*13*) (ANOVA, $P < 0.05$). After 3 weeks, algal biomass (Chl *a* and cell volume) in PAR+UVA+UVB exceeded that under PAR two- to fourfold (*13*). Initial UVR growth inhibition was eliminated by either (**B**) a reduction in ambient sunlight by 50% with neutral density screens [under 10 days, 50% (UF-1) PAR = 50% PAR+UVA+UVB (PVI) (ANCOVA, $P > 0.05$) or (**C**) the selective screening out of UVA [90% PAR (UF-4, closed circles) 90% PAR+UVA (Mylar, open circles) (ANCOVA, $P < 0.05$) (PAR+UVA+UVB: OP-4, inverted triangles)]. Removal of UVB had no effect on algal accrual rate [90% PAR+UVA+UVB = 90% PAR+UVA (ANCOVA, $P >> 0.05$)]. The 50% reduction in ambient sunlight intensity (B) also eventually resulted in higher algal biomass under PAR+UVA+UVB than under PAR. Mean incident UVB levels were 48.8 kJ m^{-2} d^{-1} (A and B) and 53 kJ m^{-2} d^{-1} (C). Mean incident UVA was 888 kJ m^{-2} d^{-1} during the 1992 trial. Mean daily PAR levels during the trials were 39.8 E m^{-2} d^{-1} and 36.3 E m^{-2} d^{-1} for 1991 and 1992, respectively. Error bars are ±SEM.

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or counterbalancing effects of UVB at the ecosystem level are likely. Autecological studies have demonstrated the direct deleterious effects of natural UVB on many freshwater and marine invertebrates (*21, 22*). Altered food web structure and function may be one important effect of increased UVB on aquatic ecosystems (*2, 20*). We addressed the discrepancy between short- and long-term impacts of UVR on freshwater benthic algal communities by comparing the response of algae and algal grazers to the presence and absence of solar UVA and UVB.

Ultraviolet radiation–screening experiments were conducted during July and August of 1991, 1992, and 1993 at Environment Canada's experimental river flume facility on the South Thompson River (50°49′35″N, 119°41′5″W) in British Columbia (*23*). The time-course development of algal and invertebrate communities was compared in flumes exposed to full spectrum sunlight and in flumes shielded from UVB and UVA+UVB by long-pass filters (*24*). Two levels of overall solar isolation (90% ambient and 50% ambient) were tested. Experiments commenced with the flow of unfiltered river water (*25*). Colonization by algae and insect larvae occurred naturally from populations suspended in the river. Chironomid presence was monitored in situ by enumeration of chironomid tubes (*26*) and algal abundance was monitored by chlorophyll a (Chl a) (*27*). Attached communities were collected for invertebrate counts and algal enumeration. In 1993, we also compared the impact of grazer exclusion using an insecticide with the effects of UVB on long-term algal accrual (*28*).

Under total column ozone levels of 310 to 340 DU and incident UVB and UVA levels ranging between 30 to 70 and 700 to 1200 kJ m^{-2} d^{-1}, respectively (*29*), UVR inhibited algal growth and accrual rate in shallow freshwater communities (Fig. 1A). The reduction of incident solar intensity by 50% eliminated UVR inhibition (Fig. 1B). The UVR inhibition of algal community growth was mostly attributable to UVA, because algal accrual rate increased greatly when UVA was removed from the spectrum (Fig. 1C). Screening out UVB had no effect (Fig. 1C). That UVR inhibition of algal accrual in shallow freshwater environments results largely from UVA corroborates other studies on the UVR inhibition of carbon fixation in freshwater (*30*) and marine (*16, 31, 32*) phytoplankton communities. Action spectra for the UVR inhibition of phytoplankton photosynthesis show that, per photon, shorter wavelengths (UVB) are more disruptive than longer wavelengths (UVA) (*16, 32, 33*). Nevertheless, higher photon fluence in UVA usually produces the majority of water-column UVR inhibition of photosynthesis (*4, 5*). Measurements in the Southern Ocean under the Antarctic ozone hole have shown (*4, 34*) and models predict (*32, 34*) that, whereas UVB becomes a more significant contributor to photoinhibition with ozone depletion, UVA remains important.

Near-ultraviolet radiation significantly inhibited colonization by chironomid larvae (*35*) (Fig. 2). Beginning in the second week of experiments, tube numbers under photosynthetically active radiation (PAR) alone were higher than either PAR+UVA or PAR+UVA+UVB (*36*) (Fig. 2, inset). Effects from UVB on the other hand, did not become apparent until a week later (Fig. 2). Chironomid numbers under all

Table 1. Chironomid (Orthocladiinae) abundance ($\times 10^4$ m^{-2}) ±SEM in the 1993 experiment. On each day, densities of larvae under spectral treatment regimes (except that denoted by an asterisk) significantly differed from one another ($P < 0.05$, Tukey test on log-transformed data). Day 22: 90% ambient solar intensity; day 17: 50% ambient solar intensity.

Day	PAR	PAR+UVA	PAR+UVA +UVB
22	2.35 ± 0.10	1.17 ± 0.04	0.49 ± 0.05
17	5.82 ± 1.2	2.73 ± 0.9*	1.0 ± 0.3

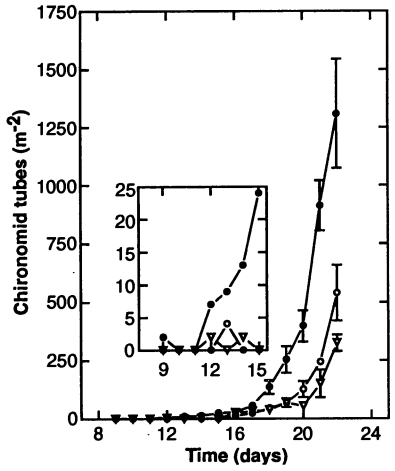

Fig. 2. Chironomid tube densities in the 1993 experiment under 90% PAR (closed circles), PAR+UVA (open circles) and PAR+UVA+UVB (inverted triangles). Inset is an enlargement of the ordinate scale for data up to day 15 to illustrate that higher tube numbers in flumes protected from UVA were first apparent within 2 weeks. Effects of UVB took longer to appear. Error bars are ±SEM. Mean daily UVB and PAR during this trial were 48.3 kJ m^{-2} d^{-1} and 35.5 einsteins (E) m^{-2} d^{-1}, respectively. No tubes were visible in flumes treated with malathion.

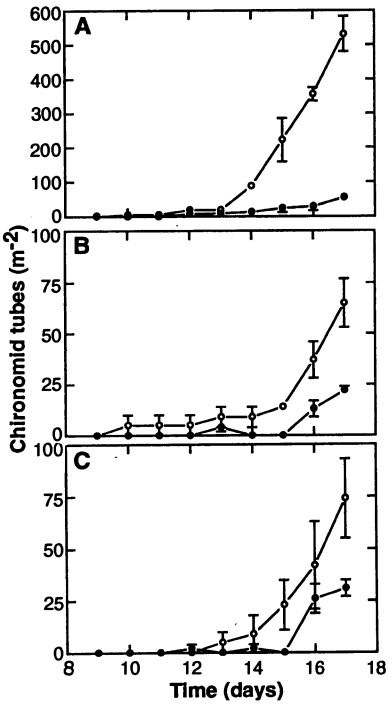

Fig. 3. Chironomid tube densities in the 1993 experiment comparing 90% (closed circles) and 50% (open circles) ambient solar intensity for (**A**) PAR, (**B**) PAR+UVA, and (**C**) PAR+UVA+UVB. Error bars are ±SEM. Higher colonization rates at lower light intensities in all spectral regimes indicated avoidance of PAR. Mean daily UVB and PAR during this trial were 48.3 kJ m^{-2} d^{-1} and 35.5 E m^{-2} d^{-1}, respectively.

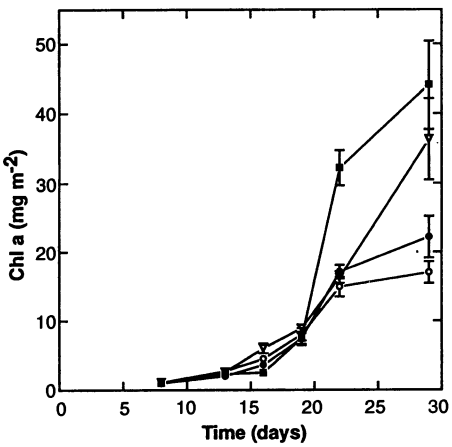

Fig. 4. Algal (Chl a) community accrual during the 1993 experiment under 90% PAR (closed circles), 90% PAR+UVA (open circles), 90% PAR+UVA+UVB (inverted triangles), and 90% PAR+malathion (squares). Chironomid densities were an order of magnitude greater during the 1993 trial than in 1992, and the intense grazing pressure in PAR relative to PAR+UVR exposures masked UVR inhibition of algal growth normally seen in the initial week of experiments. By the end of the trial, the effect of UVB on algal accrual was similar to the effect of the malathion (PAR+UVA+UVB = PAR+malathion; SNK, $P = 0.247$). Significantly higher Chl a in PAR+UVA+UVB than that in PAR+UVA (SNK, $P < 0.05$) suggested that UVB was the component of UVR that resulted in long-term reduction in chironomid grazing.

three spectral quality regimes differed by day 22 (Table 1). Even with a 50% reduction in overall solar intensity, the presence of UVA+UVB exerted a negative effect on the number of chironomids (Table 1).

A reduction of solar intensity by 50% increased chironomid colonization under all three spectral regimes (Fig. 3). Together with inhibition by UVA, these data demonstrate that colonization behavior is strongly affected by both UVA and PAR. Visual sensitivity and response to UVA by many adult insects is well known (*37*), and the avoidance of UVA (350 to 400 nm) by third and fourth instars of *Chaoborus* sp. (Diptera: Chaoboridae) has been shown (*38*). While UV photoreceptors that respond to wavelengths below 300 nm have been identified in the freshwater cladoceran *Daphnia magna* (*39*), many important species of marine zooplankton are unable to detect and avoid UVB (*40*).

The visual detection of UVA-PAR by animals as a cue to avoid UVB damage is supported by empirical and experimental evidence (*41*). Our data confirm that chironomids avoid colonization in the presence of UVA or high levels of PAR. The delayed reduction in chironomid abundance under PAR+UVA+UVB compared to PAR+UVA indicates that the larvae may be unable to detect UVB and thereby avoid exposure. The role played by UVA-PAR in UVB avoidance by animals is one of the worrisome aspects of stratospheric ozone depletion. Because ozone is a highly selective absorber of UVB, ozone decreases will not only increase UVB but will also elevate the ratio of UVB to longer wavelengths, depriving animals of their natural environmental cue to the presence of harmful levels of UVB.

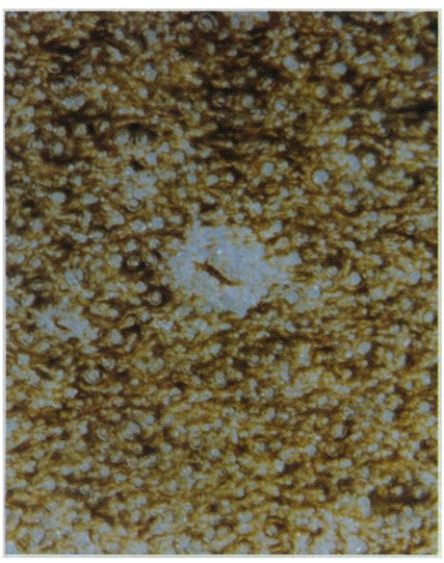

Fig. 5. Tube formed by late instar *Cricotopus bicinctus* (Meigen) in grazing scar with diameter of 1.25 cm. Chironomids graze extensively on freshwater benthic diatom communities and are inhibited by UVB radiation.

Our suggestion that UVB had a deleterious effect on chironomids eventually colonizing PAR+UVA+UVB flumes is based on two observations. First, the length of time required for the number of tubes and individual animals under PAR+UVA+UVB to decline below those in PAR+UVA indicates that although UVB is not avoided, chironomids are eventually affected by the exposure. The lag we observed was reminiscent of delayed mortality found in shrimp larvae exposed to doses of UVB exceeding their tolerance threshold (*22*). Second, UVB was the component of UVR responsible for increased algal biomass over longer periods of time (Fig. 4). Although UVA delayed chironomid colonization, the larvae kept significant grazing pressure on algal accrual relative to PAR+UVA+UVB (*42*). In contrast, the impact of UVB on chironomids, as evidenced by sharply increased Chl a accumulation at the end of the trial, was similar to the effect of insecticide (*42*) (Fig. 4).

Chironomids are important algal grazers in many freshwaters, and in some rivers and streams they are the dominant herbivore (*43*). The most conspicuous result of UVR exclusion of chironomids in our experiments was an increase in the amount of accumulated diatom biomass. Algal consumption by chironomids was visible as grazing-cleared areas on the flume bottoms (Figs. 5 and 6). The effects of UVB on chironomid grazing became evident after 3 weeks (Figs. 4 and 6). Decreased herbivory in flumes either exposed to UVB or treated with the insecticide malathion allowed algal biomass to continue accumulating through the fourth week of experiments, while grazers in UVB-protected flumes kept algae in check (Fig. 4) (*13*).

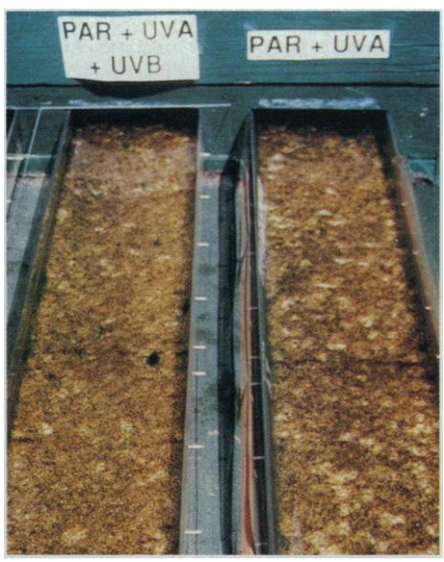

Fig. 6. Effect of UVB on chironomid grazing activity. The left-hand flume was covered with UV-transparent acrylic (OP-4). The exclusion of chironomids by UVB results in a more uniform diatom community and permits the accumulation of greater algal biomass. The right-hand flume was covered UVB-opaque Mylar. Higher grazing pressure from chironomids in the absence of UVB produces the mottled appearance of the diatom community. The photograph was taken on day 28 of the trial in August 1992.

Chironomid exclusion by UVA+UVB persisted when incident solar intensity was reduced 50% (Table 1). Inhibition by UVR of the diatom accumulation rate, on the other hand, was eliminated by the same level of attenuation (Fig. 1B). This contrast suggests that chironomids are more sensitive to UVR, especially UVB, than are the diatoms they feed on. Sensitivity of UVB that is higher in grazers than in algae could have profound significance for the functioning of aquatic ecosystems under a scenario of globally increasing levels of UVB radiation (*44*). Our experiments indicate that present-day UVB levels affect the balance between primary producers and consumers in shallow water benthic communities. Elevated levels of UVB could augment these impacts by increasing depths at which benthic grazer communities are exposed to deleterious UVB irradiance without a corresponding increase in the UVA-PAR avoidance signal. Because a large fraction of autochthonous primary production in freshwater benthic communities passes through primary consumers (*45*), the deleterious effects of UVB on herbivores might exert a stronger influence on carbon flow to higher trophic levels than the direct effects of UVB on algae. If differential sensitivity to UVB between algae and herbivores is a generalizable phenomenon, short-term measurements of UVB inhibition of algal photosynthesis, which have been the focus of much research during recent years, may not be addressing the most critical element of aquatic ecosystem sensitivity to elevations in UVB irradiance.

REFERENCES AND NOTES

1. R. C. Worrest, in *The Role of Solar Ultraviolet Radiation in Marine Ecosystems*, J. Calkins, Ed. (Plenum, New York, 1982), pp. 429–475; O. Holm-Hansen, D. Lubin, E. W. Helbling, in *Environmental UV Photobiology*, A. R. Young, L. O. Björn, J. Moan, W. Nultsch, Eds. (Plenum, New York, 1993), pp. 379–425.
2. R. C. Worrest, *Physiol. Plant.* **58**, 428 (1983).
3. R. C. Smith and K. S. Baker, *Oceanography* **20**, 4 (1989); W. F. Vincent and S. Roy, *Environ. Rev.* **1**, 1 (1993).
4. R. C. Smith *et al.*, *Science* **255**, 952 (1992).
5. J. J. Gullen and P. J. Neale, *Photosyn. Res.*, in press.
6. L. W. Jones and B. Kok, *Plant Physiol.* **14**, 1037 (1966); A. M. Noorudeen and G. Kulandaivelu, *Physiol. Plant.* **55**, 161 (1982).

7. W. Iwanzik *et al.*, *Physiol. Plant.* **58**, 401 (1983); B. M. Greenberg *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **86**, 6617 (1989); G. Renger *et al.*, *Photochem. Photobiol.* **49**, 97 (1989).
8. G. Döhler, *Mar. Biol.* **83**, 247 (1984); W. Nultsch and G. Agel, *Arch. Microbiol.* **144**, 268 (1986); D.-P. Häder, E. Rhiel, W. Wehrmeyer, *FEMS Microbiol. Ecol.* **53**, 9 (1988).
9. D. Karentz, J. E. Cleaver, D. L. Mitchell, *J. Phycol.* **27**, 326 (1991).
10. D. L. Mitchell and D. Karentz, in *Environmental UV Photobiology*, A. R. Young, L. O. Björn, J. Moan, W. Nulsch, Eds. (Plenum, New York, 1993), pp. 345–377.
11. J. Calkins and T. Thordardottir, *Nature* **283**, 563 (1980); P. L. Jokiel and R. H. York, *Limnol. Oceanogr.* **29**, 192 (1984).
12. B. E. Thomson, R. C. Worrest, H. Van Dyke, *Estuaries* **3**, 69 (1980); N. G. A. Ekelund, *Physiol. Plant.* **78**, 590 (1990); M. J. Behrenfeld, J. T. Hardy, H. Lee II, *J. Phycol.* **28**, 757 (1992).
13. M. L. Bothwell, D. Sherbot, A. C. Roberge, R. J. Daley, *ibid.* **29**, 24 (1993).
14. P. M. Sivalingam, T. Ikawa, Y. Yokohama, K. Nisizawa, *Bot. Mar.* **17**, 23 (1974); J. I. Carreto, M. O. Carignan, G. Daleo, S. G. De Marco, *J. Plankton Res.* **12**, 909 (1990); D. Karentz, F. S. Mceuen, M. C. Land, W. C. Dunlap, *Mar. Biol.* **108**, 157 (1991).
15. R. C. Worrest, H. Van Dyke, B. E. Thomson, *Photochem. Photobiol.* **27**, 471 (1978); R. C. Worrest, B. E. Thomson, H. Van Dyke, *ibid.* **33**, 861 (1981).
16. E. W. Helbling, V. Villafane, M. Ferrario, O. Holm-Hansen, *Mar. Ecol. Prog. Ser.* **80**, 89 (1992).
17. D. Karentz, in *Ultraviolet Radiation in Antarctica: Measurements and Biological Effects*, vol. 62 of *Antarctic Research Series*, C. S. Weiler and P. A. Penhale, Eds. (American Geophysical Union, Washington, DC, 1994), pp. 93–110.
18. S. Cabrera, personal communication.
19. S. Demers, personal communication. UVR-mediated increases in algal biomass have been observed in outdoor experimental tanks at the Maurice Lamontagne Institute, Quebec, and were found during a short mesocosm trial at the 1993 Group for Aquatic Primary Productivity workshop in Saskatoon, Canada, 7 to 15 June 1993.
20. R. C. Worrest, in *Overview*, vol. 1 of *Effects of Changes in Stratospheric Ozone and Global Climate*, J. G. Titus, Ed. (U.S. Environmental Protection Agency and United Nations Environmental Program, New York, 1986), pp. 175–191; D.-P. Häder and R. C. Worrest, *Photochem. Photobiol.* **53**, 717 (1991).
21. J. J. Karanas, R. C. Worrest, H. Van Dyke, *Mar. Biol.* **65**, 125 (1981); P. L. Jokiel, *Science* **207**, 1069 (1980); J. Ringelberg, A. L. Keyser, B. J. G. Flik, *Hydrobiologia* **112**, 217 (1984); C. E. Williamson, H. E. Zagarese, P. C. Schulze, B. R. Hargreaves, J. Seva, *J. Plankton Res.* **16**, 205 (1994).
22. D. M. Damkaer, D. B. Dey, G. A. Heron, *Oceologia* **48**, 178 (1981).
23. The outdoor flume facility is described by M. L. Bothwell [*Can. J. Fish. Aquat. Sci.* **45**, 261 (1988)]. The plexiglass flumes used in the trials were 2 m long by 19 cm wide and lined with open-cell styrofoam-DB (Flora Craft, Pomona, CA) as a substratum for microalgal and grazer communities.
24. All flume covers transmit ~90% of the photosynthetically active radiation (PAR; 400 to 700 nm). Flumes exposed to full-spectrum sunlight (PAR+UVA+UVB) were covered with either a film of UV-transparent polyvinylidine (PVI) (1991) or UV-transparent acrylic sheets, type OP-4 (CYRO, Toronto, Canada; 4.7 mm thick; 70 to 90% transmittance throughout the UVB and UVA) (1992 to 1993). Flumes protected from UVB were covered with Mylar-D (Du Pont, Wilmington, DE; (0.1 mm thick; 50% transmission at 318 nm) (1992 and 1993). Flumes shielded from both UVA and UVB were covered with UV-opaque acrylic sheets, type UF-1 (Rohm and Hass, West Hill Ontario, Canada; 6.4 mm thick; 50% transmission at 380 nm) (1991); or type UF-4 (Rohm and Hass; 6.4 mm thick; 50% transmission at 398 nm) (1992 and 1993). Neutral-density window screen placed over sections of flumes was used to reduce total incident solar insolation by 50%. All photo treatments were run in triplicate.
25. Discharge to troughs of 50 liters per minute produced supercritical flow conditions with water velocity, depth, and hydraulic residence time of ~50 cm s^{-1}, 1 cm, and ~4 s, respectively.
26. Areas cleared of diatoms by chironomid grazing activity (grazing scars) were readily visible. Chironomid tubes, formed by the adhesion of a diatom-detritus matrix around the larvae, were also visible (Fig. 5). Tubes were counted each day and used as an index of chironomid abundance in situ. Although the tubes visible to the unaided eye were only a fraction of the number of chironomids present, microscopic enumeration confirmed the relative chironomid abundances among treatments indicated by in situ tube counts.
27. Time course patterns in Chl a were also usually seen in algal cell numbers and biovolumes (*13*).
28. Three additional flumes exposed to 90% PAR were treated with the insecticide malathion (Dimethoxyphosphinothioyl thiobutanedioic acid diethyl ester), to exclude insect grazers chemically. Starting in the second week, 5-min pulses (final concentration of 2×10^{-3} % v/v) were metered into the flumes each day. This mild treatment retarded development of the chironomid community.
29. In 1991 and 1993, global UVB radiation and total-column ozone were measured with a Brewer Ozone Spectrophotometer (SCI-TEC Instruments, Saskatoon, Saskatchewan, Canada). During the daylight hours, automated scans were made at 30-min intervals forward and backward between 290 and 320 nm, and energy was recorded at 0.5-nm intervals. Daily ozone determinations were made with procedures outlined by J. B. Kerr, C. T. McElroy, R. A. Olafson, in *Proceedings of the International Quadrennial Ozone Symposium*, J. London, Ed., Boulder, CO, 4 to 9 August 1980 (International Ozone Commission, Boulder, CO, 1980), pp. 74–79. During 1992, global UVB, UVA, and PAR radiation were measured with an Optronics OL-752 spectroradiometer (Optronics Laboratories, Orlando, FL). Scans from 280 to 700 nm were made every 30 min during the daylight period, and readings were recorded at 2-nm intervals. In all three years, integrated PAR (400 to 700 nm) was continuously measured with a Li-Cor (Lincoln, NE) quantum cosine sensor (LI 190SA).
30. B. Bühlmann, P. Bossard, U. Uehlinger, *J. Plankton Res.* **9**, 935 (1987); D. S. Kim and Y. Watanabe, *Ecol. Res.* **8**, 225 (1993).
31. H. Maske, *J. Plankton Res.* **6**, 351 (1984).
32. J. J. Cullen, P. J. Neale, M. P. Lesser, *Science* **258**, 646 (1992).
33. B. G. Mitchell, in *Response of Marine Phytoplankton to Natural Variations in UV-B Flux*, B. G. Mitchell, O. Holm-Hansen, I. Sobolev Eds. (Chemical Manufacturers Association, Washington, DC, 1990); D. Lubin *et al.*, *J. Geophys. Res.* **97**, 7817 (1992); P. J. Neale, M. P. Lesser, J. J. Cullen, in (*17*), pp. 125–142.
34. O. Holm-Hansen, E. W. Helbling, D. Lubin, *Photochem. Photobiol.* **58**, 567 (1993).
35. Chironomid larvae were all from the subfamily Orthocladiinae: *Cricotopus* and *Orthocladius*. The majority were *Cricotopus bicinctus* (Meigen).
36. Analysis of variance on log-transformed data; Tukey test, $P < 0.05$.
37. T. H. Goldsmith, in *Handbook of Sensory Physiology*, H. J. A. Dartnall, Ed. (Springer-Verlag, New York 1972, vol. 7, chap. 17; W. S. Stark and K. E. W. P. Tan, *Photochem. Photobiol.* **36**, 371 (1982).
38. E. J. LaRow, *Ann. Entomol. Soc. Am.* **64**, 461 (1971).
39. K. C. Smith and E. R. Macagno, *J. Comp. Physiol. A.* **166**, 597 (1990).
40. D. M. Damkaer and D. B. Dey, in *The Role of Solar Ultraviolet Radiation in Marine Ecosystems*, J. Calkins, Ed. (Plenum, New York, 1982), pp. 417–428; D. M. Damkaer and D. B. Dey, *Oecologia* **60**, 169 (1983).
41. D. J. Kimeldorf and D. F. Fontanini, *Environ. Physiol. Biochem.* **4**, 40 (1974); J. A. Barcelo and J. Calkins, *Photochem. Photobiol.* **29**, 75 (1979); J. A. Barcelo and J. Calkins, *ibid.* **31**, 67 (1980).
42. On day 29, Chl a in PAR+UVA was lower than under PAR+UVA+UVB [Student-Newman-Keuls (SNK) $P < 0.05$]. However, PAR+UVA+UVB and PAR+malathion were similar (SNK, $P = 0.247$).
43. E. Eichenberger and A. Schlatter, *Verh. Int. Ver. Angew. Limnol.* **20**, 1806 (1978); M. E. Power, *Science* **250**, 811 (1990).
44. J. B. Kerr and C. T. McElroy, *Science* **262**, 1032 (1993).
45. G. A. Lamberti, S. V. Gregory, L. R. Ashkenas, A. D. Steinman, C. D. McIntire, *Ecology* **70**, 1840 (1989).
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Temperature and Water Viscosity: Physiological Versus Mechanical Effects on Suspension Feeding

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Water viscosity is inversely related to temperature. This simple physical relation couples two potential influences on organism performance. Seawater viscosity was manipulated, with and without temperature, to distinguish the physiological and mechanical effects of temperature on suspension feeding by ciliated echinoderm larvae. Change in viscosity alone accounted for half of the decline in the feeding rate at lower temperature. High viscosity shifted ingestion toward larger particles, which suggests that viscosity affects particle capture as well as rates of water processing. Temperature-induced change in viscosity, therefore, impacts suspension feeding independently of physiology and has implications for many small-scale biological processes.

Understanding the effects of temperature on biological activity and adaptation (*1*) requires the discrimination of temperature-dependent processes that underlie performance. Thermal biology has focused on physiological (biochemical) processes (*2*), but temperature can impact mechanical processes as well by influencing the viscosity (μ) of the ambient fluid (Fig. 1) (*3*).

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