

# The role of solar radiation in structuring the shallow benthic communities of boreal forest lakes

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## *Abstract*

We have attempted to quantify the roles of physical, chemical, and biological interactions structuring the attached algal and invertebrate communities in eight boreal lakes at the Experimental Lakes Area, northwestern Ontario, varying in dissolved organic carbon (DOC) concentrations (3–9 mg L<sup>-1</sup>). Attached benthic communities on rocky, south-facing shores were sampled at 0.1, 0.3, 0.7, and 1.5 m depths. Multivariate redundancy analysis explained 58% of the variance in algal communities and 75% of the variance in invertebrate communities. Algal composition was determined most by photosynthetically active radiation (PAR) and ultraviolet radiation (UVR) fluxes, whereas the composition of associated invertebrates was driven by a combination of exposure to solar radiation and food quality and quantity. Communities on rock surfaces exposed to high solar fluxes in these lakes had very high concentrations of a photoprotective scytonemin-like pigment (SLP-A), and were dominated by filamentous green algae. Conversely, deeper, more shielded communities were dominated by diatoms and had low concentrations of SLP-A. This suggests that previous paleolimnological evidence of SLP-A increases might reflect changes in littoral attached algal communities rather than planktonic ones. Decreases in DOC concentrations as a result of climate warming will result in increased penetration of solar radiation in boreal lakes. As a result, in the event of decreased precipitation, we predict that the dominance of UVR-resistant epilithic algae in littoral zones will occur in deeper waters than before, with coincident reductions in densities of many invertebrate taxa in algal biofilms increasingly exposed to high solar fluxes.

Discussions of ecological limitations in lakes usually refer to nutrient limitation and biological or trophic limitation (competition/predation, e.g., Schindler et al. 1971; Carpenter et al. 1985). Studies of physical limitation of aquatic communities often have focused on the roles of temperature (Graham et al. 1996) and solar radiation (Schindler and Fee 1975; Graham and Turner 1987). More recently, ultraviolet radiation (UVR) has been recognized as both a direct and indirect mediator of change in aquatic communities (Bothwell et al. 1994; Vinebrooke and Leavitt 1999). However, studies usually have been limited to small-scale, short-term experiments, often utilizing monocultures or very simple communities.

The role of UVR in the structuring of lentic communities has been deduced by piecing together the results of many

studies; however, few experimental or descriptive investigations have addressed these hypotheses in whole lakes. During experimental acidification of Lake 302S at the Experimental Lakes Area (ELA), northwestern Ontario, there was a dramatic shift in benthic algal dominance from attached diatoms and filamentous cyanophytes to filamentous green algae as metaphyton. This was a “new” form of semi-detached growth in upper littoral zones dominated by such algae as *Spirogyra*, *Mougeotia*, and *Zygogonium* spp. (Turner et al. 1995). Acidification also caused decreased concentrations of dissolved organic carbon (DOC). DOC is the primary attenuator of solar radiation in many lakes (Kirk 1976; Scully and Lean 1994), and acidification hence led to large in-lake increases in UVR fluxes, especially in the shallows (Schindler et al. 1996). More recently, analysis of sedimentary deposits in L302S has revealed that large increases in the concentrations of algal degradation products of photoprotective scytonemin-like pigments accompanied acidification. These pigment changes were attributed to changes in the phytoplankton community in response to increased exposure to UVR (Leavitt et al. 1997). However, there was no evidence linking the pigment to a pelagic source.

Although pelagic communities have been studied a great deal, less attention has been paid to factors that structure benthic algal associations such as epilithon. There have been few efforts to compare epilithic algal and invertebrate com-

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Table 1. Water chemistry from eight lakes sampled at the Experimental Lakes Area. TDP, total dissolved phosphorus; TDN, total dissolved nitrogen; DIC, dissolved inorganic carbon.

Site	Nutrient concentrations ( $\mu\text{mol L}^{-1}$ )												
	NO <sub>3</sub>	NO <sub>2</sub>	NH <sub>4</sub>	TDP	TDN	Suspended particulate					DIC ( $\mu\text{mol L}^{-1}$ )	Chl <i>a</i> ( $\mu\text{g L}^{-1}$ )	pH
						C	N	P	C:N	N:P			
223*	3	<1	19	2	255	490	51	3	9.6	17	74	1.07	6.52
224	1	<1	13	2	170	450	41	2	11.0	20.5	91	1.10	7.19
239	<1	1	22	1	285	500	38	3	13.2	12.7	153	1.76	7.43
260	<1	<1	4.5	2.5	313	500	44	2	11.5	22	158	1.07	7.35
302S†	<1	1	11	3	260	1,110	98	5.6	11.3	19.6	27	1.96	5.56
373	1	<1	9	4	185	410	60	1	6.8	60	200	1.22	7.55
468	4.5	<1	9	3	233	550	46	3	12.0	15.3	130	0.58	7.35
979‡	<1	1	15	6	348	695	67	6	10.4	11.2	144	2.53	6.64

\* Previously experimentally acidified.

† Currently experimentally acidified.

‡ Experimentally flooded peat bog.

munities between and within lakes, and no attempt has been made to connect broad-scale natural epilithic composition with environmental physical, chemical, and biological conditions. Our objective was to identify the potential roles of solar radiation in the context of such environmental factors in the structuring of shallow-water epilithic communities in boreal lakes at the ELA.

## Methods

*Sampling*—Between 24 July and 1 August 1996, we sampled eight lakes at the ELA (49°40'N, 93°44'W) for water chemistry (Table 1), transparency to solar radiation (Table 2), and epilithic algal and invertebrate assemblages. Lakes were selected to represent a range of DOC concentrations and UV transmittance (Fig. 1) and included reference systems, lakes that were previously experimentally acidified (L223 and L302S, Schindler 1994), and an experimentally flooded peat bog (L979, Kelly et al. 1997).

Table 2. DOC quality and visible optics in eight lakes sampled at the Experimental Lakes Area. Water colors were noted as green (gr), brown (br), or orange (or). Peak fluorescence was measured at an excitation wavelength of 354 nm and emission wavelength of 496 nm and reported as quinine sulfate units (QSU). DOC ratio is the fluorescence emission ratio of 450- and 500-nm emission intensities, with excitation at 370 nm. PAR measurements were taken spectroradiometrically.

Lake	Water color	DOC fluorescence (QSU)		Visible radiation	
		Peak	Ratio	Secchi (m)	1% PAR (m)
223	gr-br	5.32	1.49	7.2	11.0
224	gr-br	1.73	1.48	7.4	15.4
239	br-or	17.17	1.40	4.55	6.3
260	gr-br	10.32	1.47	5.25	8.5*
302S	gr	7.72	1.53	4.15	5.8
373	gr	3.54	1.47	7.9	12.1
468	gr	6.59	1.45	5.5	10.2
979	br	47.96	1.39	1.65	1.6*

\* Calculated from vertical profiles of PAR flux measured with a Li-Cor light meter.

We selected biological sampling sites in the eight lakes on south-facing, rocky (bedrock or boulder) shorelines. We chose two sites within each lake sampled, and sampled four depths at each site: 0.1, 0.3, 0.7, and 1.5 m. At each depth, we collected four epilithic samples (5 cm<sup>2</sup> each) from either bedrock or large boulders using a syringe-scraper (Turner et al. 1991). We made no effort to prevent the escape of mobile macroinvertebrates, and it can be assumed that their densities in samples were lower than in situ, given their mobility, our sampling technique, and the small area sampled. We pooled samples from each depth at each site immediately after sampling and stored them on ice and in the dark. In the lab, we resuspended and subsampled these composite collections for algal and invertebrate enumeration and identification and for pigment samples. In this way, we characterized assemblages specific to each depth within each lake. We immediately froze subsamples to be analyzed later for pigments; we preserved subsamples for algal enumeration in acid Lugol's and FAA solution (4% final volume), and we preserved subsamples for invertebrate enumeration with 80% ethanol. Our subsampling procedure allowed us to express measured values as areal densities or concentrations.

*Water transparency and DOC quality*—Within a few days of epilithic sampling, we measured penetration of ultraviolet (UV-B, 300–320 nm; UV-A, 320–400 nm) and photosynthetically active radiation (PAR) spectra at 1-nm intervals using a Licor Model LI-1800UM underwater spectroradiometer that was angle-corrected (Table 2). These spectra were measured during the 2 h bracketing solar noon. The instrument has a response range of 300 to 850 nm with a half-power bandwidth of 8 nm and a total bandwidth of 16 nm. The instrument uses a standard cosine receptor, allowing for the measurement of flux densities in diffuse light (at depth) or at low sun angles. We averaged several scans at the surface and at various depths in order to diminish the variability in subsurface flux caused by surface waves. The instrument used two calibration files to process raw data—one for measurements made in air and one for those made in water—and is calibrated in air and water by Licor. We also measured Secchi depth and described water color.

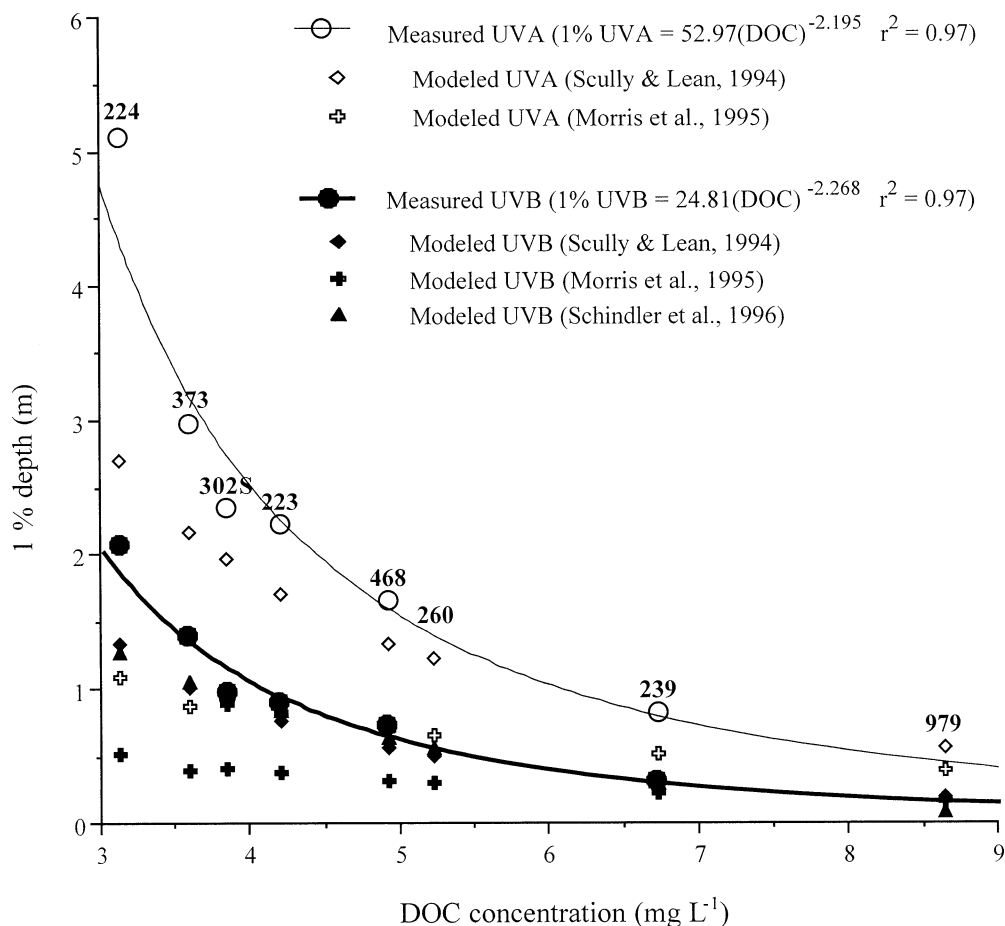


Fig. 1. DOC concentrations and corresponding 1% depths for UV-A and UV-B in a suite of eight lakes sampled at the ELA. Modeled values are from Scully and Lean (1994), Morris et al. (1995), and Schindler et al. (1996). In situ measurements were performed using a Licor Model LI-1800UM underwater spectroradiometer, and mid-July, cloudless solar fluxes were integrated over the ultraviolet spectra. Scully and Lean's and Schindler et al.'s UV-B models agree well with each other over the range of DOC concentrations covered by this survey. However, they both increasingly deviated from observed UV-B penetration for lakes with  $<4 \text{ mg L}^{-1}$  DOC. Similarly, Scully and Lean's UV-A model underestimated UV-A penetration in ELA lakes with  $<5 \text{ mg L}^{-1}$  DOC. Morris et al.'s model deviated increasingly from measured fluxes in ELA lakes with  $<7 \text{ mg L}^{-1}$  DOC.

We then used existing models to make comparative UV-A and -B predictions, as shown in Fig. 1 (DOC,  $\text{mg L}^{-1}$ ):

$$K_{d \text{ UV-B}} = 0.415 \text{DOC}^{1.86} \quad (\text{Scully and Lean 1994}) \quad (1)$$

$$1\% \text{ UV-B} = 5.173 \text{DOC}^{-0.706} - 1.029 \quad (\text{Schindler et al. 1996}) \quad (2)$$

$$K_{d \text{ UV-A}} = 0.299 \text{DOC}^{1.53} \quad (\text{Scully and Lean 1994}) \quad (3)$$

$$K_{d\lambda} = \exp(-0.01347\lambda + 5.36[\text{DOC}]^{0.157}) \quad (\text{Morris et al. 1995}) \quad (4)$$

Integrated values of solar flux were calculated from Morris et al.'s model by calculating  $K_{d\lambda}$  for  $\lambda = 300\text{--}320 \text{ nm}$  (UV-B), and  $320\text{--}400 \text{ nm}$  (UV-A). These  $K_d$  values were then used to calculate  $\lambda$ -specific flux at 50-cm depth, and these fluxes were integrated for each spectrum. The 1%

depth was then calculated according to the following equation.

$$\begin{aligned} \text{Spectral 1\% depth (cm)} \\ = 50 \{ -2 \log[\text{flux}_{50 \text{ cm}}(\text{flux}_{\text{surface}})^{-1}] \}^{-1} \end{aligned}$$

Fluxes incident on epilithon at each of the four depths (0.1, 0.3, 0.7, and 1.5 m) in the eight lakes were calculated and used in subsequent analyses.

We performed uncorrected fluorescence scans of DOC on a Shimadzu RF-1501 scanning spectrofluorometer with a xenon lamp using optically clear quartz cuvettes (pathlength = 1 cm). Specifications included: concave, nonaberration excitation/emission monochromators with blazed holographic grating, F/2.4, 900 grooves  $\text{mm}^{-1}$ ; dynode-feedback light source compensation system with monochromatic light monitoring function; and photomultiplier tubes for both excitation and emission side detection (Mandel Scientific).

These spectrofluorometric analyses of DOC quality were performed according to McKnight et al. (2001). We also performed scans of sample blanks of distilled, deionized water (distillation/deionization/activated carbon adsorption system; Milli-Q System, Millipore) to remove the effects of Raman scattering in water. Variations in lamp spectral intensities were corrected using scans of a standard  $1 \mu\text{g L}^{-1}$  quinine sulfate solution in  $0.1 \text{ N H}_2\text{SO}_4$  (Scully and Lean 1994). Absolute fluorescence values are reported in quinine sulfate units (QSU), where: 1 QSU is fluorescence at a given excitation and emission wavelength of the standard quinine sulfate solution. Excitation radiation was fixed at 370 nm, and scans of emission intensities were performed from 370 to 650 nm. A range of the ratio of the emission intensities at 450 and 500 nm was used to indicate qualitative characteristics of DOC.

**Pigments**—We extracted, isolated, identified, and quantified algal pigments, including the photoprotective scytonemin-like pigment, SLP-A (Vincent and Roy 1993; Leavitt et al. 1997). Recently, interlab comparisons have determined that SLP-A is optically identical to scytonemin in both oxidized and reduced forms, and it also is produced by benthic algae in response to UV radiation (Leavitt unpubl. data). We used standard procedures, involving high-performance liquid chromatography (HPLC, Mantoura and Llewellyn 1983). Extractions used acetone, methanol, and water (80:15:5, v/v/v) for 24 h in darkness at  $10^\circ\text{C}$ . Extracts were then filtered through  $0.2\text{-}\mu\text{m}$  Acropore membrane filters, dried, and stored under nitrogen gas in the dark at  $-20^\circ\text{C}$ . Dried extracts were dissolved in a precise volume of injection solvent (70% acetone, 25% ion-pairing reagent, 5% methanol), in which Sudan II dye ( $3.2 \text{ mg L}^{-1}$ ) served as an internal reference. Pigments were separated on a Hewlett-Packard 1050 HPLC with a Rainin 200 C-18 column ( $5 \mu\text{m}$  particle) and were detected with in-line Hewlett-Packard 1046A fluorometer and 1050PDA spectrophotometer detectors. Pigment concentrations were quantified using HPLC calibration equations that were determined using authentic standards supplied by the U.S. Environmental Protection Agency.

**Communities**—Algal counts were performed on an inverted microscope at magnifications of  $\times 125$  and  $\times 400$  with phase contrast illumination. All counts were done by a modified Utermöhl technique (Nauwerck 1963). Wet biomass estimates were made from approximations of cell volumes of each species according to best-fit formulae for different taxa (Vollenweider 1968).

Invertebrates were hand-picked using a dissecting microscope and identified on dissecting and compound microscopes at up to  $\times 400$  magnification using standard keys (organisms  $\text{m}^{-2}$ , Ward and Whipple 1959; Pennak 1989; Clifford 1991; Thorp and Covich 1991).

**Data analyses**—With the advent of analytical techniques such as redundancy or ordination analyses, complex interactions between community structure and environmental factors can be inferred from what otherwise are cumbersome datasets of descriptive spatial studies, providing the foundation for further experimental probing. We have therefore

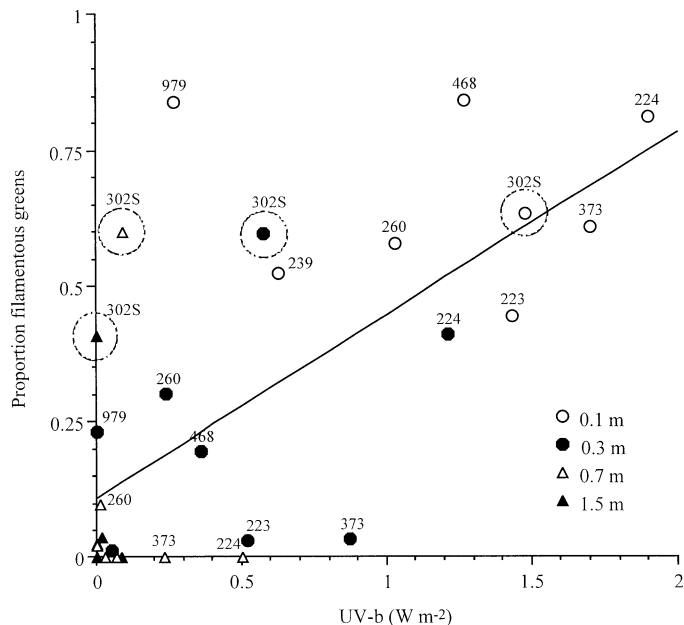


Fig. 2. Filamentous green algae dominance in epilithon exposed to a gradient of solar UV-B fluxes in eight ELA lakes. Depths are 0.1, 0.3, 0.7, and 1.5 m, and fluxes are typical of a cloudless day in mid-July 1996 (proportion filamentous greens =  $0.338(\text{UV-B}) + 0.111$ ;  $r^2 = 0.444$ ;  $F_{1,28} = 22.3$ ,  $p = 0.0001$ ). The circled data points represent algal assemblages in experimentally acidified L302S at pH 5.6 at the time of sampling.

identified potential community relationships using stepwise forward redundancy analysis (RDA, ter Braak 1988), in which environmental variables and algal and invertebrate community structure were examined to infer qualitative relationships. The length of an environmental variable arrow in the ordination plots corresponds to the variable's importance in explaining the variance in the community data. The proximity of points representing taxa corresponds to the similarity of their habitats; two taxa that are close together appear under more similar conditions than two taxa that are further apart on the ordination diagram. Based on these qualitative inferences, further examination of patterns of community and environmental variable interactions were investigated using analysis of variance (ANOVA; SPSS 6.1.1).

## Results

**Structuring of algal communities**—Perhaps surprisingly, PAR flux at the different sampling sites had no discernible effect on total algal biomass ( $F_{1,28} = 0.031$ ,  $p = 0.861$ ; ANOVA, not shown). However, filamentous green algal taxa (FGA), including *Spondylosium planum*, *Mougeotia* spp., *Zygnema* spp., *Bambusina brebissonii*, *Oedogonium* spp., and *Bulbochaete* spp., accounted for the majority of green algae at sites exposed to high PAR and UV-B fluxes. The majority of chlorophytes in the lakes were found at sites that were exposed to UV-B flux greater than  $\sim 0.5 \text{ W m}^{-2}$  (not shown). FGA dominated those sites that were exposed to the highest UV-B flux (Fig. 2;  $p < 0.001$ ). One exception was acidified L302S, which had high proportions of FGA in epi-

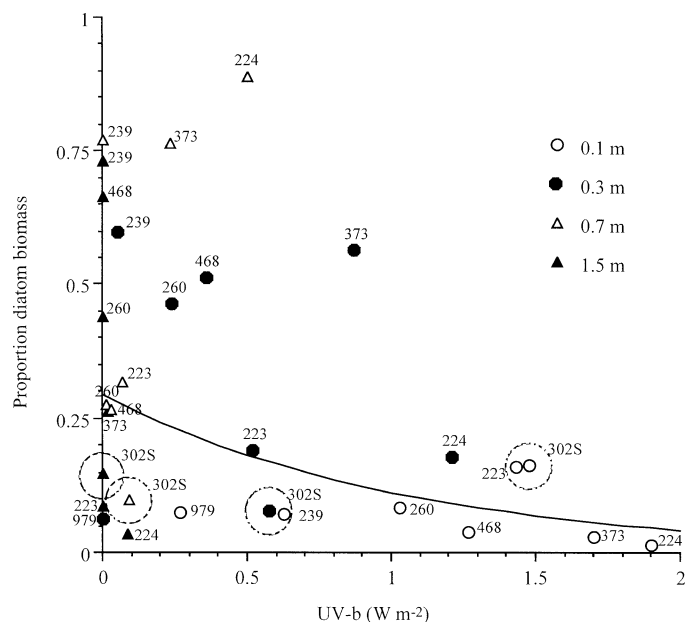


Fig. 3. Patterns of diatom dominance in epilithon from sites exposed to different incident solar UV-B fluxes in eight ELA lakes. Diatoms comprised the greatest portion of algal biomass at sites exposed to low UV-B fluxes (proportion diatoms =  $0.2957e^{(-0.953UV-B)}$ ;  $r^2 = 0.259$ ;  $F_{1,28} = 9.77$ ,  $p = 0.0041$ ).

lithon at all four depths, irrespective of UV-B flux. However, the relationship between FGA dominance and UV-B flux was positive whether or not L302S was included in the analyses. Complementary to the patterns of chlorophyte dominance was the decline of diatom dominance as UV-B exposure increased (Fig. 3;  $p = 0.0041$ ). Other algal classes showed no strong relationships with environmental variables.

In the shallow littoral zones of the lakes, 60% of the variation in biomass of algal classes was explained by the combination of environmental variables we measured in this study. Incident UV-B and PAR fluxes and DOC concentration accounted for 28% of the total variance (21% by UV-B alone) based on stepwise, forward-selection redundancy analysis and its ordination (Monte Carlo permutations,  $p < 0.01$ ; Table 3; Fig. 4). Measures of nitrogen concentrations (water column total dissolved nitrogen [TDN];  $NO_3$ ;  $NH_4$ ) accounted for 13% of total variance. C and P concentrations in the epilithon itself accounted for 17% of algal class variance. Chironomid density accounted for 2% of variance observed. All other factors measured either were colinear with one or more of the listed factors or did not explain more of the data variance, thus not meeting the selection criteria of CANOCO (a FORTRAN program for canonical community ordination). For example, UV-A flux was excluded by the model because it was colinear to fluxes of both UV-B and PAR over the range of depths in this study. However, UV-B and PAR fluxes were not sufficiently colinear to each other to dictate exclusion of either. As a result, excluded variables may share relationships to community structure that are demonstrated by those environmental variables to which they are colinear.

Table 3. Intersite, interlake variance in biomass of classes of epilithic algae explained by environmental variables (stepwise forward-redundancy analysis). Monte Carlo permutation of first canonical axis:  $F$ -ratio = 19.25,  $p < 0.01$ ; overall test:  $F$ -ratio = 3.26,  $p < 0.01$ .

Environmental variable	Variance explained (0.60 total)
UV-B flux ( $W m^{-2}$ )	0.21
Epilithon C	0.12
TDN	0.10
Epilithon P	0.05
DOC	0.04
PAR flux ( $\mu mol photons m^{-2} s^{-1}$ )	0.03
$NO_3$	0.02
Chironomid density ( $m^{-2}$ )	0.02
$NH_4$	0.01

A combination of environmental variables explained 58% of the variation in biomass of algal species found in shallow littoral communities (Table 4; Fig. 5). PAR, UV-B, and DOC concentration explained 18% of the total variance. As with algal classes, measures of nitrogen concentrations (water column-suspended N, TDN,  $NO_3$ ,  $NH_4$ ) explained less variance in algal species (17% of total). C and P concentrations in epilithon were less important in explaining variance in algal species than classes, accounting for only 6% of total variance. As before, chironomid density explained only 2% of algal species variance, suggesting they were not overly important in determining algal community structure.

The clearest pattern we observed in the study was the power function ( $r^2 = 0.709$ ) between the portion of total algal pigments formed by SLP-A and incident PAR exposure of shallow-water communities. Communities exposed to the highest PAR fluxes had the highest SLP-A dominance (Fig. 6A;  $p < 0.0001$ ). An inflection point in the relationship between proportion of SLP-A and midday PAR flux occurs at  $\sim 1,100$ – $1,400 \mu mol photons m^{-2} s^{-1}$  exposure. Algae in epilithon of lakes exposed to PAR intensities greater than this might exhibit increased SLP-A concentrations. Sites with the lowest PAR exposure had  $< 10\%$  of their pigment complements as SLP-A. Two exceptions occurred in the clearest lakes, L224 and previously acidified L223, where SLP-A still composed  $\sim 30$ – $40\%$  of the total pigment mass under exposure to PAR fluxes of  $1,100$ – $1,300 \mu mol photons m^{-2} s^{-1}$  at a depth of 1.5 m. Similarly, correlations were found between high UV-B fluxes and SLP-A dominance (Fig. 6B;  $p = 0.0015$ ). Unlike its relationship with PAR, SLP-A still accounted for the majority of algal pigments under relatively low incident UV-B exposure. At exposures of  $\sim 10\%$  of surface flux of UV-B, approximately half of the total mass of all pigments was still SLP-A. In contrast, sites with 50% of surface PAR exposure had  $< 10\%$  of the total mass of algal pigments as SLP-A. Large increases in SLP-A dominance, from 10 to 75%, coincided with small increases of UV-B at very low fluxes (from 0.05 to 0.2  $W m^{-2}$ ). At UV-B fluxes  $> 0.2 W m^{-2}$ , SLP-A concentrations increased more slowly.

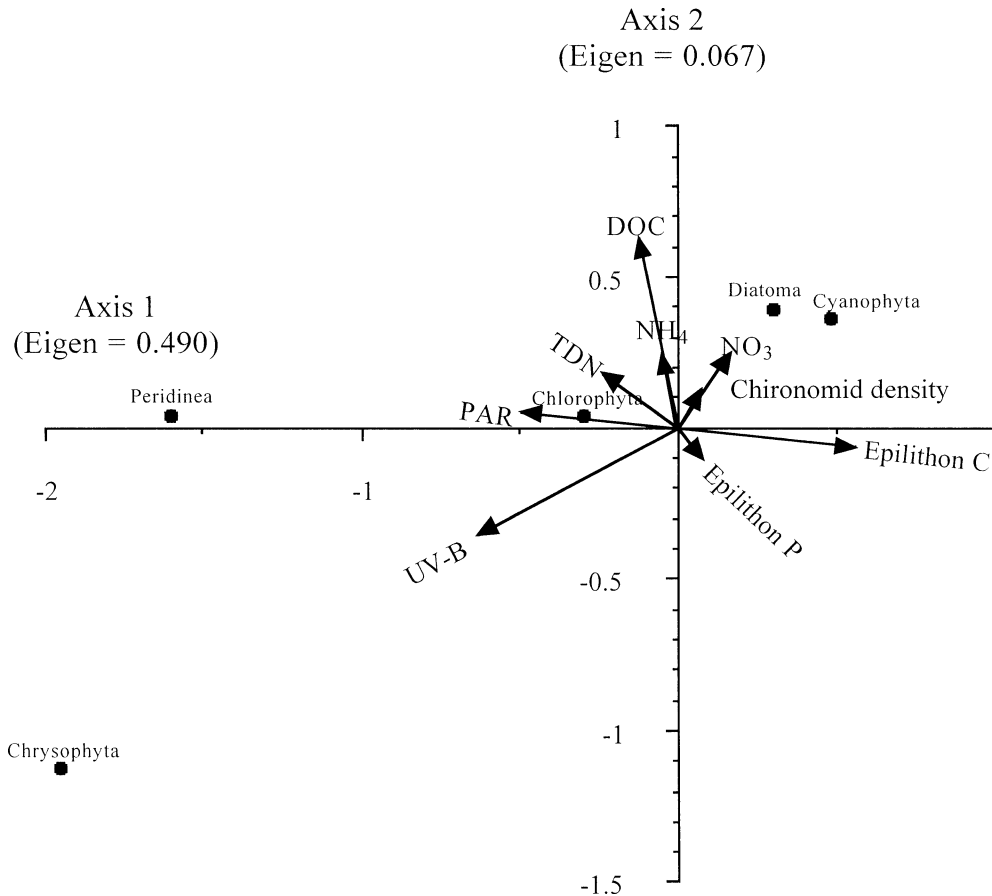


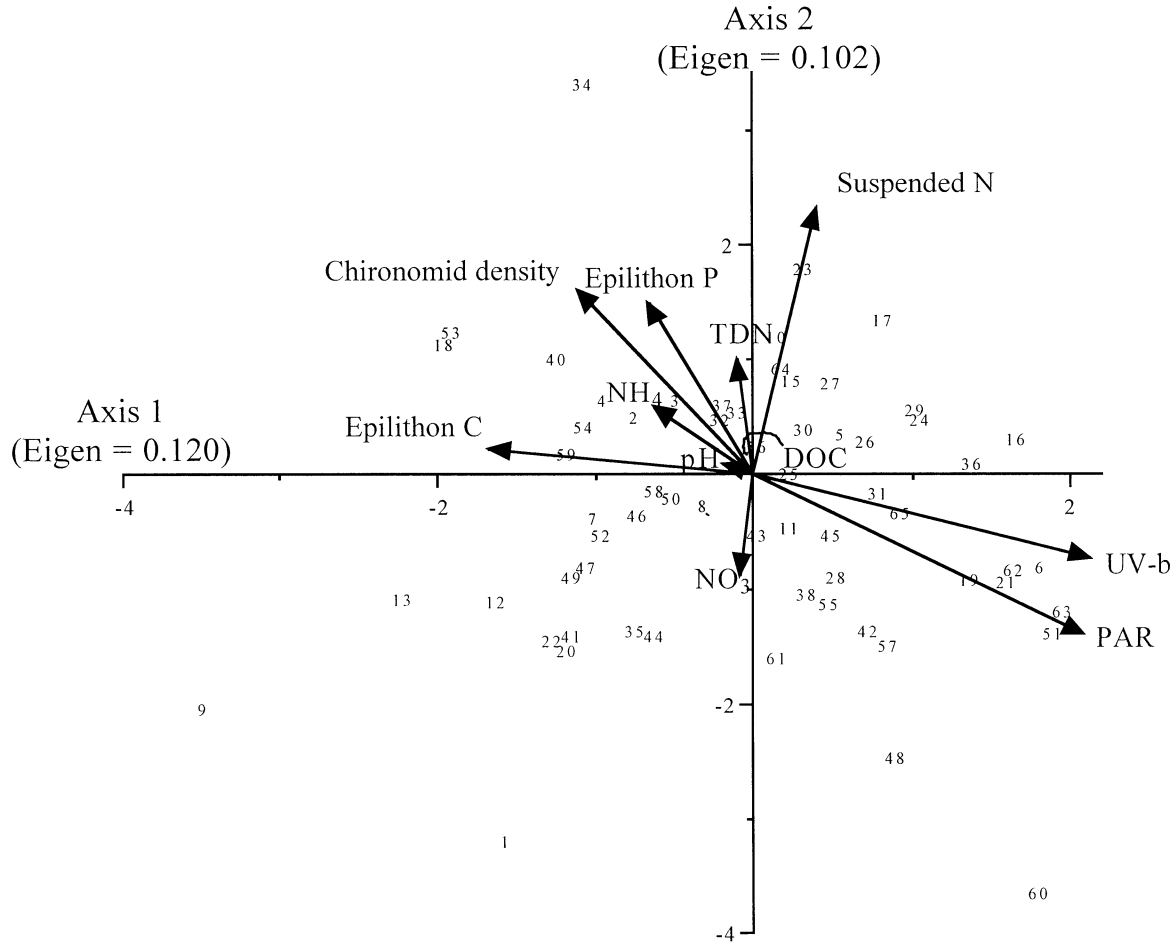
Fig. 4. Ordination plot of redundancy analysis (RDA) of algal classes and environmental variables in epilithon of eight lakes of the ELA. Epilithon was sampled in quadruplicate at 0.1, 0.3, 0.7, and 1.5 m in two sites in each lake. The relative length of arrows indicates the relative strength of environmental factors in determining algal assemblages. The relative position of classes along a line parallel to the direction of any environmental variable's arrow indicates alignment of the taxa along a gradient of that variable. The head of any arrow indicates the direction of a positive increase in that variable.

Table 4. Intersite, interlake variance in biomass of species of epilithic algae explained by environmental variables (stepwise forward-redundancy analysis). Monte Carlo permutation of first canonical axis:  $F$ -ratio = 2.74,  $p < 0.01$ ; overall test:  $F$ -ratio = 1.46,  $p < 0.01$ .

Environmental variable	Variance explained (0.58 total)
PAR ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ )	0.09
Suspended N	0.06
UV-B ( $\text{W m}^{-2}$ )	0.05
DOC ( $\text{mg L}^{-1}$ )	0.04
TDN	0.04
$\text{NO}_3$	0.04
$\text{NH}_4$	0.03
pH	0.03
Epilithon C	0.03
Epilithon P	0.03
Chironomid density ( $\text{m}^{-2}$ )	0.02

*Structuring of invertebrate communities*—Among invertebrate taxa that appear to be sensitive to solar radiation, areal densities of ostracods, the cladocerans *Latona setifera* and *Ophryoxus gracilis*, larval and naupliar cyclopoid copepods, nematodes, total Sididae, and oligochaetes were all negative functions of PAR flux (Table 5). Only densities of water mites were a positive function of PAR fluxes to epilithon. Chironomids were strongly negatively related to PAR flux (Table 5; Fig. 7A;  $p = 0.0003$ ). There was also a strongly negative relationship with UV-B flux (Fig. 7B;  $p = 0.0003$ ). However, larger relative decreases in chironomid densities even at low fluxes of UV-B suggest a greater sensitivity to variation in UV-B than PAR for chironomid larvae. All other invertebrate taxa that demonstrated negative relationships with PAR flux (except for total Sididae) also demonstrated negative relationships with UV-B flux (Table 5).

In addition to radiative flux, algal classes were important determinants of invertebrate community structure. Nematode, oligochaete, *Alluaudomyia* spp. (biting midge), chiron-



- |   |   |   |
|---|---|---|
| 1 <i>Aphanothece</i> sp.                                  | 22 <i>Micrasterias</i> sp.                          | 44 <i>Cymbella</i> sp.  |
| 2 <i>Chroococcus limneticus</i> (Lemmermann)              | 23 <i>Staurodesmus paradoxus</i> (Meyen)            | 45 <i>Cyclotella bodanica</i> (Eulenst)                       |
| 3 <i>Gomphosphaeria</i> sp.                               | 24 <i>Spondylostium planum</i> (Wolle)              | 46 <i>Epithemia argus</i> (Kutzing)                           |
| 4 <i>Merismopedia tenuissima</i> (Lemmermann)             | 25 <i>Mougeotia</i> sp.                             | 47 <i>Eunotia pectinalis</i> (Kutzing) Rabenhorst             |
| 5 <i>Synechococcus</i> sp.                                | 26 <i>Mougeotia</i> sp.                             | 48 <i>Gomphonema acuminatum</i> v. <i>coronata</i>            |
| 6 <i>Rhabdogloea</i> sp.                                  | 27 <i>Mougeotia</i> sp.                             | 49 <i>Navicula subtilissima</i> (Cleve)                       |
| 7 <i>Anabaena</i> sp.                                     | 28 <i>Zygnema</i> sp.                               | 50 <i>Navicula incerta</i> (Grunow)                           |
| 8 <i>Lyngbya</i> sp.                                      | 29 <i>Bambusina brebissonii</i> (Kutzing)           | 51 <i>Navicula pupula</i> (Kutzing)                           |
| 9 <i>Snowella</i> sp.                                     | 30 <i>Oedogonium</i> sp.                            | 52 <i>Navicula</i> sp.  |
| 10 <i>Tolypothrix</i> sp.                                 | 31 <i>Bulbochaete</i> sp.                           | 53 <i>Navicula</i> sp.  |
| 11 <i>Rivularia</i> sp.                                   | 32 <i>Dinobryon sertularia</i> (Ehrenberg)          | 54 <i>Neidium</i> sp.   |
| 12 <i>Gloeotheca</i> sp.                                  | 33 <i>Aulacoseira granulata</i> (Ehrenberg) Simonse | 55 <i>Anomoeonies serians</i> (Breb.) Cleve                   |
| 13 <i>Scytonema</i> sp.                                   | 34 <i>Cyclotella stelligera</i> (Cleve and Grunow)  | 56 <i>Anomoeonies serians</i> v. <i>brachysira</i> (Brebisso) |
| 14 <i>Chlamydomonas</i> spp.                              | 35 <i>Tabellaria fenestrata</i> (Lyngbye) Kutzing   | 57 <i>Pinnularia flexuosa</i> (Cleve)                         |
| 15 <i>Pediastrum tetras</i> (Ehrenberg) Ralfs             | 36 <i>Tabellaria floccuolsa</i> (Roth) Kutzing      | 58 <i>Pinnularia maior</i> (Kutzing)                          |
| 16 <i>Oocystis borgei</i> (Snow)                          | 37 <i>Fragilaria construens</i> (Ehrenberg) Grunow  | 59 <i>Anomoeonies exilis</i> (Kutz.) Cleve                    |
| 17 <i>Scenedesmus</i> sp.                                 | 38 <i>Synedra acus</i> (Kutzing)                    | 60 <i>Fragilaria pinata</i> (Ehrenberg)                       |
| 18 <i>Dictyosphaerium pulchellum</i> (Wood)               | 39 <i>Gomphonema</i> sp.                            | 61 <i>Cymbella gracilis</i> (Rabhorst) Cleve                  |
| 19 <i>Elakatothrix gelatinosa</i> (Willen)                | 40 <i>Aulacoseira italica</i> v. <i>subarctica</i>  | 62 <i>Pinnularia borealis</i> (Ehrenberg)                     |
| 20 <i>Cosmarium depressum</i> v. <i>achondrum</i> (Boldt) | 41 <i>Pinnularia</i> sp.                            | 63 <i>Neidium</i> sp. a                                       |
| 21 <i>Euastrum</i> spp.                                   | 42 <i>Nitzschia</i> sp.                             | 64 <i>Peridinium inconspicuum</i> (Lemmermann)                |
|   | 43 <i>Achnanthes minutissima</i> (Kutzing)          | 65 <i>Peridinium pusillum</i> (Penard) Lemmermann             |

Fig. 5. Ordination plot of redundancy analysis (RDA) of algal species and environmental variables in epilithon of eight lakes of the ELA. Epilithon was sampled in quadruplicate at 0.1, 0.3, 0.7, and 1.5 m in two sites in each lake.

omid, and larval cyclopoid copepod densities were negative functions of chlorophyte biomass. Conversely, *Ilyocryptus* spp. and *Diaphanosoma* spp. (cladocerans) densities were positive functions of chlorophyte biomass (Table 6;  $p <$

0.05). Reflecting the previously described trade-off of chlorophyte and diatom dominance along a radiative flux gradient, larval cyclopoid, nematode, oligochaete, chironomid, and *Alluaudomyia* spp. densities were positive functions of

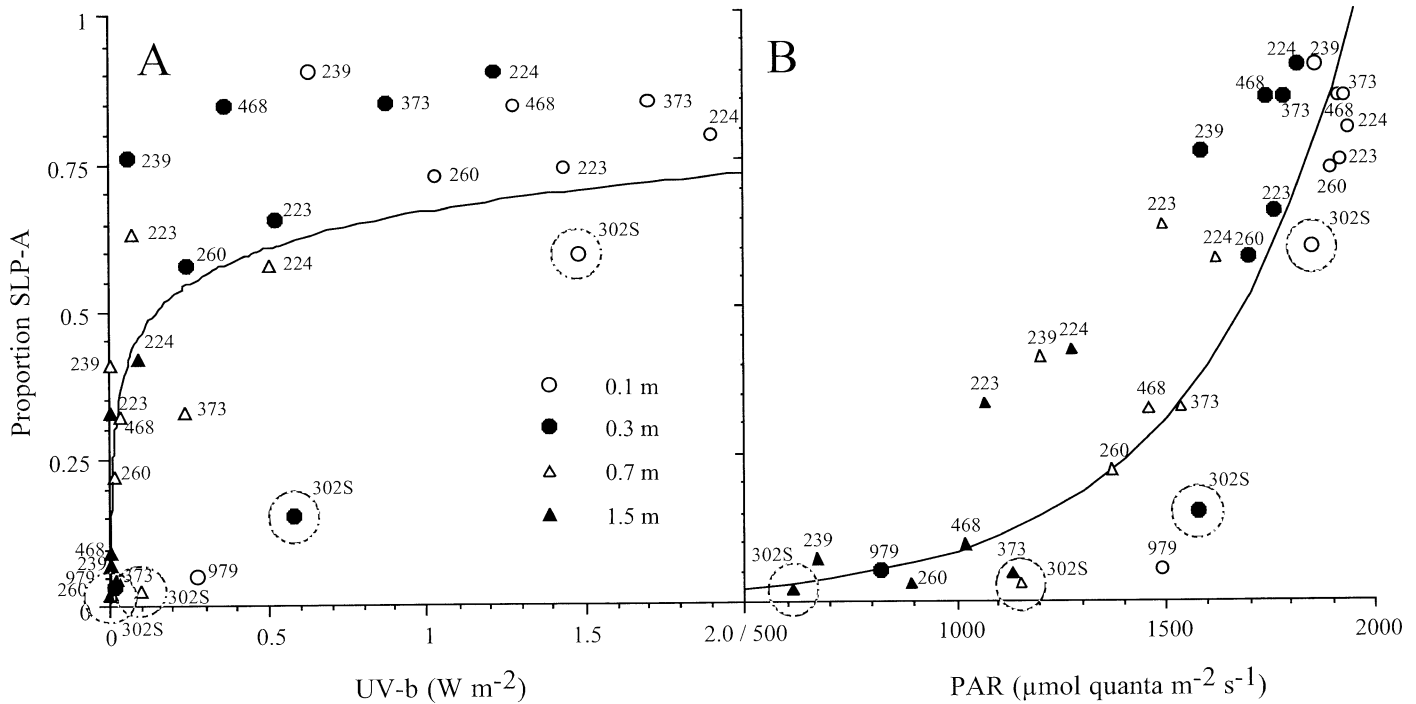


Fig. 6. Dominance of the total pigment complement in epilithon by SLP-A, a scytonemin-like photoprotective pigment, under various exposures to (A) UV-B radiation and (B) PAR in eight ELA lakes. Epilithon from sites exposed to even moderate UV-B fluxes contained high concentrations of SLP-A. However, only epilithon from sites with the greatest PAR exposure contained SLP-A comprising 80–90% of the total pigment mass (proportion SLP-A =  $0.200 \log(\text{UV-B}) + 0.672$ ,  $F_{1,28} = 13.16$ ,  $p = 0.0015$ ; proportion SLP-A =  $0.00644e^{0.00258\text{PAR}}$ ,  $r^2 = 0.709$ ,  $F_{1,28} = 68.27$ ,  $p < 0.0001$ ).

Table 5. Densities of invertebrate taxa in epilithon from four depths in eight ELA lakes as a function of PAR and UV-B exposure (July 1996).

Invertebrate taxa density ( $\text{m}^{-2}$ )	Relationship with environmental variable	$r^2$	$F_{1,28}$	$p$
PAR ( $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ )				
Ostracoda	$9,173,000e^{-0.00839(\text{PAR})}$	0.677	50.23	<0.0001
Chironomidae	$90,040e^{-0.00141(\text{PAR})}$	0.433	18.33	0.0003
<i>Latona setifera</i>	$7,410 - 1,020 \ln(\text{PAR})$	0.419	17.33	0.0003
Total mites (Hydrachnidia)	$5.38(\text{PAR}) - 4,290$	0.396	15.71	0.0006
Larval Cyclopoida	$217,000 - 28,800 \ln(\text{PAR})$	0.323	11.45	0.0025
Nematoda	$138,000 - 17,600 \ln(\text{PAR})$	0.263	8.56	0.0074
<i>Ophryoxus gracilis</i>	$8,290e^{-0.00477(\text{PAR})}$	0.263	8.55	0.0074
Naupliar Cyclopoida	$15,100e^{-0.00425(\text{PAR})}$	0.233	7.28	0.013
Sididae	$71,500 - 9,530 \ln(\text{PAR})$	0.186	5.50	0.028
Oligochaeta	$62,100e^{-0.00360(\text{PAR})}$	0.149	4.19	0.052
UV-B flux ( $\text{W m}^{-2}$ )				
Larval Cyclopoida	$-1,040 - 2,680 \ln(\text{UV-B})$	0.562	30.82	<0.0001
Ostracods	$4.09(\text{UV-B})^{-0.667}$	0.515	25.45	<0.0001
Nematodes	$4,070 - 1,680 \ln(\text{UV-B})$	0.480	22.17	0.0001
Chironomidae	$16,800e^{-0.899(\text{UV-B})}$	0.424	17.64	0.0003
Oligochaetes	$1,640e^{-3.66(\text{UV-B})}$	0.371	14.13	0.0010
<i>Latona setifera</i>	$0.950(\text{UV-B})^{-0.3578}$	0.346	12.68	0.0016
Total mites (Hydrachnidia)	$5,160 + 451 \ln(\text{UV-B})$	0.335	12.07	0.0020
<i>Ophryoxus gracilis</i>	$2.12(\text{UV-B})^{-0.363}$	0.183	5.39	0.029
Naupliar Cyclopoida	$80.0e^{-2.34(\text{UV-B})}$	0.170	4.92	0.036

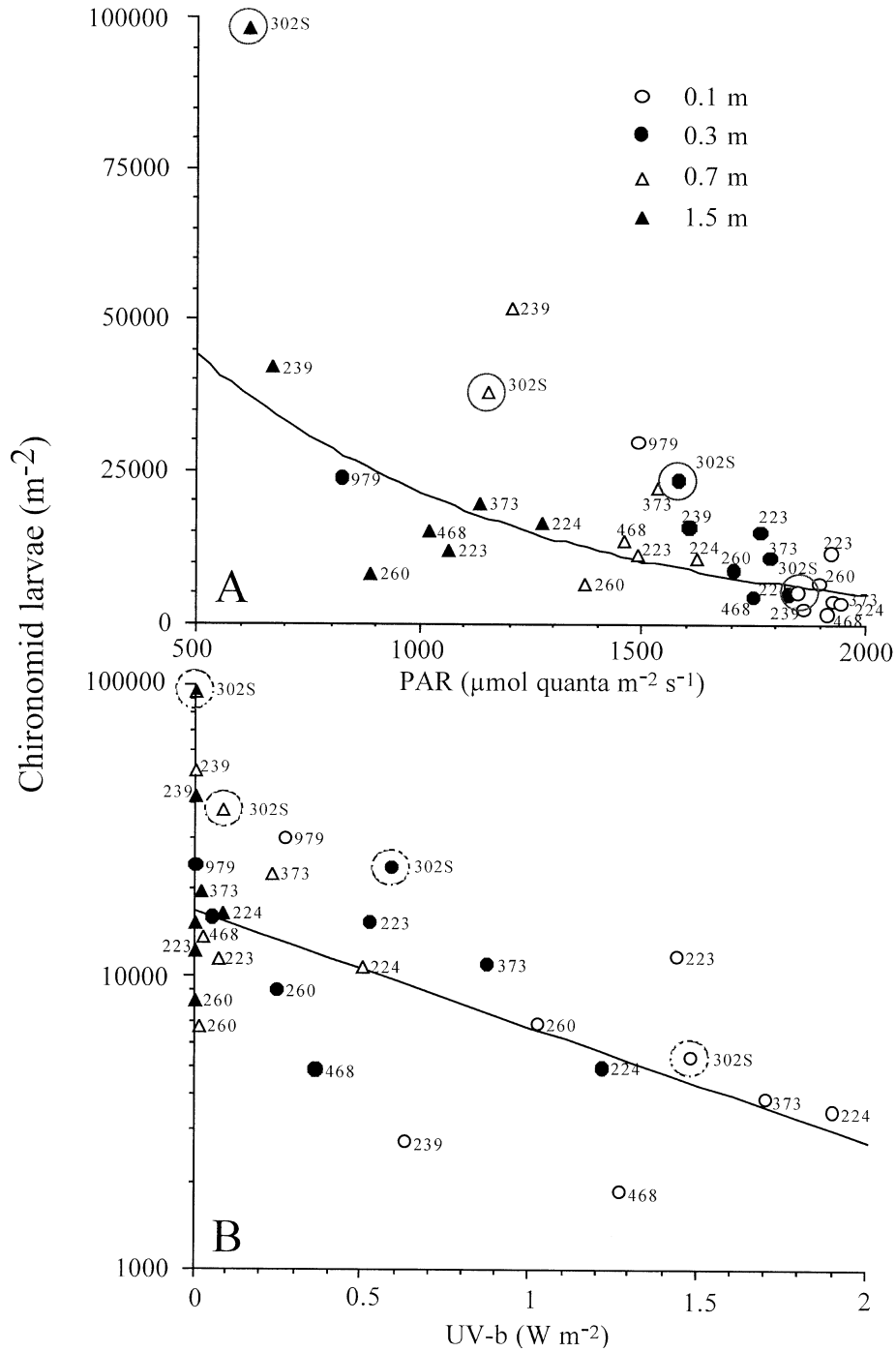


Fig. 7. Trend in chironomid larva densities in epilithon along a gradient of exposures of (A) PAR and (B) solar UV-B in eight ELA lakes. Those sites exposed to the greatest noon PAR and UV-B fluxes on a typical July day had the lowest densities of chironomids (chironomid density =  $90,040(e^{-0.00141PAR})$ ,  $r^2 = 0.433$ ,  $F_{1,28} = 18.3$ ,  $p = 0.0003$ ; chironomid density =  $16,800(e^{-0.899UVB})$ ,  $r^2 = 0.424$ ,  $F_{1,28} = 17.6$ ,  $p = 0.0003$ ). Densities of larvae in previously acidified L302S (circled) were extremely high at low UV-B fluxes (1.5 m) and were still relatively high at intermediate fluxes (0.7 and 0.3 m) compared to other lakes, perhaps as a result of extirpation of benthivorous minnows in L302S after experimental acidification.

Table 6. Densities of invertebrate taxa as a function of algal biomass in epilithon from four depths in eight ELA lakes (July 1996).

Invertebrate taxa density ( $m^{-2}$ )	Relationship with environmental variable	$r^2$	$F_{1,28}$	$p$
Chlorophyte biomass ( $\mu g m^{-2}$ )				
Nematoda	$4,670e^{-0.00551(\text{chlorophytes})}$	0.300	10.29	0.0038
<i>Ilyocypris</i> spp.	$0.801e^{0.00217(\text{chlorophytes})}$	0.292	9.92	0.0043
Oligochaeta	$853e^{-0.00463(\text{chlorophytes})}$	0.233	7.29	0.013
<i>Alluaudomyia</i> spp.	$866e^{-0.00423(\text{chlorophytes})}$	0.214	6.54	0.017
Chironomidae	$13,800e^{-0.00101(\text{chlorophytes})}$	0.208	6.30	0.019
<i>Diaphanosoma</i> spp.	$7.72e^{0.00383(\text{chlorophytes})}$	0.158	4.49	0.045
Larval Cyclopoida	$215e^{-0.00492(\text{chlorophytes})}$	0.151	4.28	0.050
Diatom biomass ( $\mu g m^{-2}$ )				
Larval Cyclopoida	$7.33e^{0.00718(\text{diatoms})}$	0.278	9.23	0.0057
Nematoda	$3,890 \ln(\text{diatoms}) - 10,200$	0.263	8.58	0.0073
Oligochaeta	$0.663(\text{diatoms})^{1.21}$	0.208	6.29	0.019
Chironomidae	$2,810(\text{diatoms})^{0.271}$	0.196	5.86	0.023
<i>Alluaudomyia</i> spp.	$2.13(\text{diatoms})^{0.991}$	0.156	4.42	0.046
Total algal biomass ( $\mu g m^{-2}$ )				
<i>Diaphanosoma</i> spp.	$0.271e^{0.00492(\text{total algae})}$	0.309	10.74	0.0032
Sididae	$0.723e^{0.00379(\text{total algae})}$	0.154	4.36	0.048

diatom biomass in epilithon samples from the eight lakes (Table 6;  $p < 0.05$ ).

Considering that most of the algal classes explained some variance in invertebrate communities in the redundancy analysis, we also related invertebrate densities to total algal biomass and chlorophyll *a* (Chl *a*). Only *Diaphanosoma* spp. and total Sididae were positive functions of total algal biomass (Table 6;  $p < 0.05$ ). However, densities of nematodes, chironomids, oligochaetes, ostracods, *Latona setifera*, cyclopoid copepods (naupliar, larval, and total densities), and *Alluaudomyia* spp. were positive functions of concentration of Chl *a* in the epilithon (Table 7;  $p \leq 0.024$ ). Only total mite densities were a negative function of epilithic Chl *a* concentration.

Potential trade-offs between biological and chemical interactions can be illustrated by determining patterns of change of a response variable normalized to another variable. We compared differences in the number of chironomids per unit of total algal biomass to infer a potential for change

in the relationship between algae and an invertebrate grazer as a function of radiative exposure of the benthic algal associations. There were fewer chironomid larvae per microgram of total algal biomass exposed to high fluxes of PAR than in epilithon exposed to low fluxes (Fig. 8). There was also a negative relationship between chironomids per microgram of filamentous algal biomass and UV-B flux (not shown); as UV-B flux increased from 0 to 2  $W m^{-2}$ , chironomid densities decreased from 500 to 20 organisms  $\mu g^{-1}$  of algal biomass. At the same time, diatom-normalized densities of chironomids in the clearest lakes with the greatest UV-B fluxes (more than  $\sim 0.9 W m^{-2}$ ) increased from  $\sim 50$  organisms  $\mu g^{-1}$  at 0.3 m to 300 organisms  $\mu g^{-1}$  at 0.1 m (in L224, the clearest lake).

The ordination plot of invertebrate communities and environmental variables illustrates that optical and algal factors were the most important determinants of invertebrate patterns (Table 8; Figs. 9, 10). According to stepwise, forward-selection redundancy analysis, PAR was the single most im-

Table 7. Densities of invertebrate taxa as a function of Chl *a* concentrations in epilithon from four depths in eight ELA lakes (July 1996).

Invertebrate taxa density ( $m^{-2}$ )	Relationship with environmental variable	$r^2$	$F_{1,28}$	$p$
[Chl <i>a</i> ] ( $mg m^{-2}$ )				
Nematoda	$6,510(\text{Chl } a) + 226$	0.587	34.15	$<0.0001$
Chironomidae	$11,200(\text{Chl } a)^{0.631}$	0.520	25.95	$<0.0001$
Oligochaeta	$320(\text{Chl } a)^{2.640}$	0.481	22.26	0.0001
Ostracoda	$36.6(\text{Chl } a)^{2.75}$	0.436	18.57	0.0002
<i>Latona setifera</i>	$0.498e^{(1.262\text{Chl } a)}$	0.350	12.92	0.0015
Total mites (Hydrachnidia)	$7,230e^{(-1.282\text{Chl } a)}$	0.309	10.72	0.0032
Larval Cyclopoida	$74.8(\text{Chl } a)^{2.53}$	0.253	8.132	0.0088
Cyclopoida	$576[\text{Chl } a]^2 - 1,280[\text{Chl } a] - 486$	0.326	5.55*	0.011
<i>Alluaudomyia</i> spp.	$342(\text{Chl } a)^{1.66}$	0.210	6.39	0.019
Naupliar Cyclopoida	$27.9(\text{Chl } a)^{1.59}$	0.195	5.82	0.024

\*  $F_{1,27}$ .

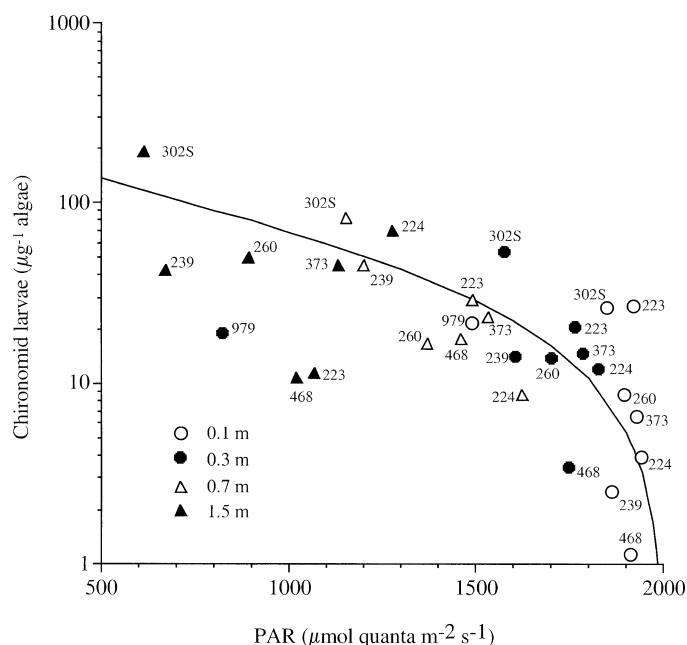


Fig. 8. Chironomid larvae per total algal biomass in epilithon from four depths exposed to different solar PAR fluxes in littoral zones of eight ELA lakes (chironomids  $\mu\text{g}^{-1}$  algae =  $-99.7 \ln(\text{PAR}) + 758$ ,  $r^2 = 0.544$ ,  $F_{1,28} = 23.82$ ,  $p = 0.0001$ ). At sites exposed to high fluxes of PAR, there were far fewer chironomid larvae per unit algae, perhaps indicating sensitivity to high fluxes of solar radiation, changes in food quality, or both.

portant environmental variable, accounting for 14–15% of the variance observed in invertebrate communities in the ELA lake samples; UV-B accounted for 4–5%. These ranges reflect the inclusion (Fig. 9) or exclusion (Fig. 10) of experimentally acidified Lake 302S, in which fish populations had been extirpated previously by experimental acidification, and vertebrate predatory pressure on invertebrate communities was removed. Biomass of algal classes accounted for 19–20% of the variance in invertebrate communities, where 8–10% of community variance was determined by chlorophyte biomass alone. Five percent of invertebrate community variance was accounted for by pH when L302S was included in the analyses (Table 8). However, when L302S was excluded, pH ceased to explain any additional variance in invertebrate communities. In general, it appears that invertebrate community patterns were reflective of variation in optical exposure, and perhaps shelter and food quality, determined by algal taxa and nutrient availability.

## Discussion

**DOC absorbance of ultraviolet radiation**—The optical properties and mixed-layer depths of most lakes are closely tied to the amount and color of DOC (Mazumder and Taylor 1994; Fee et al. 1996; Schindler et al. 1996). Ultraviolet radiation spectral intensities (UV-A and UV-B) predicted from DOC concentrations using four existing models (Scully and Lean 1994; Morris et al. 1995; Schindler et al. 1996) were less than spectroradiometrically measured intensities.

Table 8. Intersite, interlake variance in invertebrate density explained by environmental variables (stepwise forward-redundancy analysis). Monte Carlo permutation of first canonical axis (all lakes):  $F$ -ratio = 3.28,  $p = 0.02$ ; overall test:  $F$ -ratio = 2.77,  $p < 0.01$ . Monte Carlo permutation of first canonical axis (302S excluded):  $F$ -ratio = 3.28,  $p = 0.02$ ; overall test:  $F$ -ratio = 2.77,  $p < 0.01$ .

Environmental variable	Sample invertebrate variance explained	
	All lakes (0.75 total)	302S excluded (0.74 total)
PAR ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ )	0.14	0.15
NH <sub>4</sub>	0.09	0.04
Chlorophyte biomass	0.08	0.1
Suspended N	0.07	—
TDP	0.05	—
pH	0.05	—
UV-B ( $\text{W m}^{-2}$ )	0.04	0.05
Chrysophyte biomass	0.04	—
NO <sub>3</sub>	0.03	0.04
Diatom biomass	0.03	0.03
Epilithon C	0.03	0.06
Epilithon P	0.03	0.05
TDN	0.03	0.05
Cyanophyte biomass	0.02	0.04
Peridinea biomass	0.02	0.03
DOC	—	0.06
Suspended P	—	0.04

This discrepancy between modeled and observed values increased in the surveyed lakes as DOC concentrations decreased below 4–5  $\text{mg L}^{-1}$ . These models calculate UV intensities from DOC concentration without considering changes in the DOC's optical quality. The water residence time, catchment size, area of wetlands in a catchment, and productivity of a lake can all contribute to altering the optical quality of DOC within boreal lakes. As a result of interactions between these factors, DOC in low-DOC lakes of the ELA area tends to be of lower aromaticity and undergoes higher photochemical bleaching than in higher DOC lakes (Donahue et al. 1998). These low-DOC lakes thus have lower carbon-specific UV attenuation, and as a result, UV penetration is often greater in these lakes than predicted from [DOC]-based models.

Morris et al (1995) incorporated a greater range of lake types (low- to high-DOC lakes from Alaska to Argentina) into their model than the other models used here. However, this more general model was less accurate at predicting UV fluxes in our ELA lakes than either the Scully and Lean (1994) or Schindler et al. (1996) models. Although perhaps more suited for broad comparisons of very different lakes and especially those with  $\text{DOC} < 2 \text{ mg L}^{-1}$ , the model of Morris et al. (1995) likely is less able to account for high variation in optical environments within boreal oligomesotrophic lakes. In addition, the Scully and Lean (1994) and Schindler et al. (1996) models included both lakes from smaller geographic regions and ELA lakes in their development. As such, general models might therefore overestimate UV attenuation in the more dilute of these lakes be-

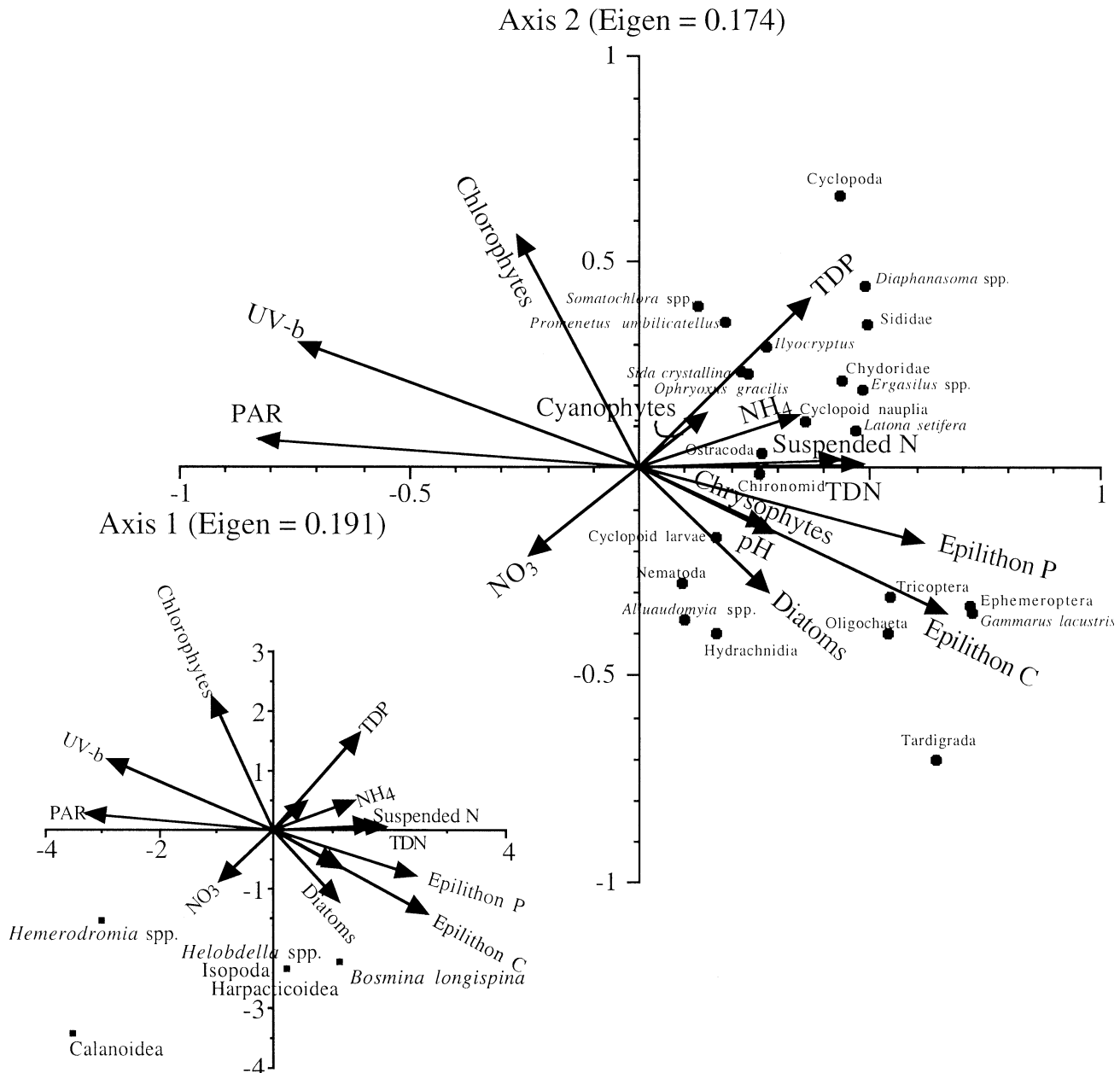


Fig. 9. Ordination plot of the redundancy analysis (RDA) of epilithon invertebrate assemblages and environmental variables in eight ELA lakes, including experimentally acidified L302S. Epilithon was sampled on south-facing shores at 0.1, 0.3, 0.7, and 1.5 m in each lake.

cause the models are constructed using optical properties of DOC from lakes covering large ranges of trophic status, latitude, and altitude. General models that use the peak fluorescence of colored dissolved organic matter for predicting UV transmittance would be more accurate than those based on DOC concentration alone. In the absence of optical or fluorescence data, however, one is limited to using historical DOC concentrations in reconstructing past UV transmissivity. DOC concentration and solar attenuation characteristics determine the penetration of PAR and UV-B in many lakes. For the lakes of the ELA, we provide two models for predicting UV-A and UV-B penetration from DOC concentra-

tion that inherently account for qualitative differences in DOC in oligo- and mesotrophic lakes in northern Ontario. These models provide more accurate predictions in ELA lakes with DOC from 3 to 9 mg L<sup>-1</sup> than existing models of UV penetration.

*Algal responses*—Taxa and biomass: Based on our lake survey, the degree of exposure to PAR and UVR is very important in structuring epilithon in the shallow littoral zone of boreal lakes. Dissolved and particulate nutrient concentrations in water and nutrient content of the biofilms themselves are less important. Similarly, Maltais and Vincent

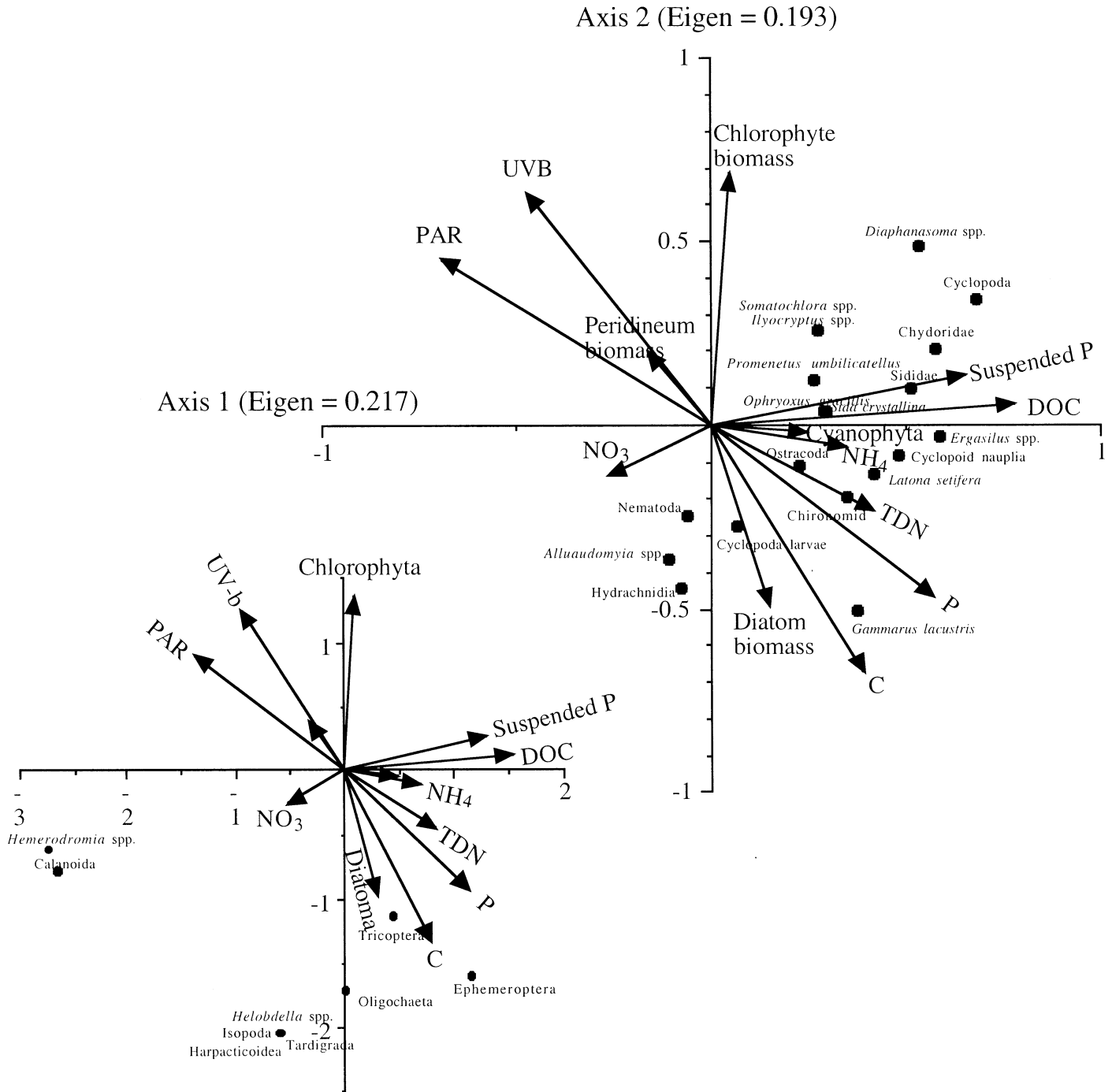


Fig. 10. Ordination plot of invertebrate communities in epilithon of seven ELA lakes after exclusion of previously experimentally acidified L302S. Epilithon was sampled on south-facing shores at 0.1, 0.3, 0.7, and 1.5 m depths in each lake.

(1997) found filamentous green algae dominating at shallow south-facing sites in a subarctic lake, but completely absent at north facing sites within the same lake; they attributed these patterns to a preference for high-light environments by FGA. Others have suggested that among-lake differences in epilithon might partly result from differences in nutrient concentrations (Sand-Jensen 1983). In our study, chlorophytes appeared to be less dominant at any given radiative flux in ultraoligotrophic lakes (223, 224, 373) than in oligotrophic

or mesotrophic lakes (239, 240, 468, 302S) or in L979, the experimentally flooded peatland with the highest phosphorus concentrations of all eight lakes. Among-lake differences in degree of dominance of filamentous green algae therefore could be in part a function of nutrient availability. Generally high densities of FGA in recovering 302S (pH 5.56) could be a residual of previous experimental acidification, where during acidification, FGA were seen to increase in abundance below pH 6 and bloom at pH 5.5 and below as a result

of more efficient dissolved inorganic carbon (DIC) utilization and the ability to withstand high light intensities (Turner et al. 1995). Unfortunately, we are unable to generalize the role of interlake differences of nutrient concentrations in determining differences in epilithon because all lakes in this study were ultra- to meso-oligotrophic. It is advisable that future studies of nutrient limitation in epilithon include comparisons of communities in lakes covering a wider range of trophic status.

We found no evidence of light limitation (PAR) of total epilithic algal biomass in ELA lakes. In contrast, positive correlations between algal ash-free dry mass and light exposure have been demonstrated in experimental troughs (Steinman and McIntire 1986; DeNicola and McIntire 1990). Turner et al. (1983) concluded that half-saturation constants for photosynthetic rates of epilithon in ELA lakes were quite low ( $10\text{--}46 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ). This suggests that shallow lentic epilithon is easily light saturated, thereby alleviating light limitation of photosynthesis or growth. This is further supported by our finding that photoprotective SLP-A formed the bulk of algal pigments at the shallowest sites, rather than pigments that maximize photosynthesis. Although total algal biomass was unrelated to light intensities, differences in proportions of algal taxa in epilithon were closely tied to irradiance. An earlier survey of ELA periphyton communities (Stockner and Armstrong 1971) integrated samples from between 0 and 5 m, preventing exact comparisons with our study. Despite this, the higher dominance of diatoms (60–70% of biomass) in these integrated samples, largely representing 1–5 m, is consistent with our observations of diatom dominance at sites with low PAR and UVR and of chlorophyte dominance at sites with high solar flux. Because epilithic algae are stationary and thus often exposed to very high solar fluxes, it is logical that solar radiation is very important in determining their community structure. Although we did not infer any discernible limitation of total epilithon algal biomass by solar radiation, it is possible that long-term increases in in-lake solar fluxes could lead to reduced benthic algal productivity and standing crop (Pienitz and Vincent 2000).

**Photoprotection:** Unlike planktonic communities, epilithon are exposed to intensities of solar radiation that change significantly and over the short term only as a result of cloud cover and sun angle. Algal community structure and function in shallow epilithon thus might rely more on adaptive or evolutionary changes that enable algae to withstand higher cumulative exposure to solar radiation. The production of UV-absorbing pigments, including SLPs, is an important adaptive photoprotective mechanism in epilithic algae (Garcia-Pichel and Castenholz 1991). The dominance of SLP-A (~75–90% of all pigments in epilithon from the 0.1-m sites in most of our lakes) suggests that an energetic priority for photoprotection exists in these communities. Only in L979, the experimentally flooded peat bog in which DOC aromaticity and concentration and attenuation of solar radiation are very high, was the proportion of SLP-A low in the shallowest epilithon. In all lakes, there were large decreases in SLP-A dominance of pigment complexes between 0.1- and 1.5-m sites as UVR exposure declined, consistent

with deeper communities needing less pigment for protection from high-energy UVR or excessive PAR.

Large increases in percent SLP-A were seen at much lower relative UV-B exposures than for PAR exposures, suggesting that this compound could be produced in response to low-wavelength solar radiation. Contrary to earlier assumptions that increases in SLP-A were linked to development of UV-resistant phytoplankton communities, SLP-A is not present in phytoplankton in ELA lakes (P. R. Leavitt unpubl. data). We propose that sedimentary degradation products of SLP-A that have been used to identify historical increases in UV environments of alpine and acidified lakes (Leavitt et al. 1997) are a record of changes in shallow attached algal communities, rather than in phytoplankton, or perhaps shifts between phytoplankton and benthic dominance.

Relationships between solar fluxes and filamentous forms of green algae were stronger than with chlorophytes as a whole, suggesting that filamentous taxa could have some competitive advantage over others in their tolerance of high-intensity UV radiation. In addition to taxonomic changes in benthic algal communities as a result of acidification, changes in primary productivity have also been observed. During experimental acidification of L302S, net photosynthesis of epilithon declined, perhaps as a result of DIC limitation as bicarbonate was eliminated (Turner et al. 1994). Seasonally, net photosynthesis reached its minimum in midsummer—coincident with high-water temperatures, low solubility of  $\text{CO}_2$ , and minimal DIC concentrations (Turner et al. 1995). One potential reason for domination of epilithon by filamentous green algae in high-light sites could be an increased photorespiratory capacity in these taxa. Along with declines in rates of photosynthesis during acidification, there were coincident increases in dark respiration rates (Turner et al. 1987), and photorespiration rates were ~40% of dark respiration rates (Graham and Turner 1987). Algae inhabiting shallow waters might have developed photorespiration as a protective mechanism to reduce photochemically induced internal production of reactive oxygen species, thus minimizing their potential to damage the photosynthetic apparatus (Kozaki and Takeba 1996). This mechanistic photorespiratory response to increased UVR fluxes also could have contributed to some of the species and metabolic changes in attached communities observed during experimental acidification (Turner et al. 1987, 1995).

**Invertebrate responses**—Direct and indirect effects of solar radiation: Bothwell et al. (1994) found that chironomid grazers were more sensitive to UVR than the algae on which they fed. In addition to chironomid sensitivity, we found that ostracods, *Latona setifera*, naupliar and larval cyclopoid copepods, nematodes, *Ophryoxus gracilis*, total Sididae, and oligochaetes decreased in densities with increasing exposure to PAR and UV-B. Many invertebrate taxa and communities exhibit sensitivity or physiological or behavioral adaptations to UVR exposure, including pleurocerid snails (*Elimia* spp., Johnson and Brown 1997), black fly larvae (Kiffney et al. 1997), caddis-fly larvae (Kelly 2001), and zooplankton, including *Daphnia* spp. (Hessen 1994), copepods (Ringelberg

et al. 1984), and rotifers (Vinebrooke and Leavitt 1999); thus, our results are not surprising.

Contrary to the strong UVR sensitivity exhibited by invertebrates in experimental stream studies (e.g., Bothwell et al. 1994; Donahue and Schindler 1998), chironomids in our study lakes appeared less sensitive to UVR, even relative to PAR. It is possible that inter- and intralake taxonomic differences exist that confer a general reduction in UV sensitivity of chironomid communities at exposed sites in ELA lakes. In addition, shallow, highly exposed artificial streams are often colonized with water pumped from deeper, more optically sheltered habitats, resulting in a potential translocation of species from low-light sites to high-light experimental conditions. It is possible that such studies represent a worst-case scenario for invertebrate responses to UVR. Patterns we observed in our lakes are undoubtedly a result of a number of complex interactions that are removed or minimized in shallow experimental streams.

Shielding by algae could be another possible explanation for the relatively weak link between UVR and invertebrate communities in our study. The higher algae-normalized chironomid larvae densities in epilithon exposed to lower fluxes than when exposed to high fluxes suggests partial limitation by radiative exposure at the shallower sites. It is possible that the increase in chironomid density in the clearest lake might have been a result of increased refuge from solar radiation for chironomids in relatively thick biofilms of filamentous green algae at the shallowest sites, which increased from  $\sim 50$  to  $750 \mu\text{g m}^{-2}$  at the same sites (0.3 and 0.1 m, respectively). Thus, our observation of reduced algae-normalized chironomid densities under high solar fluxes might be consistent with the observations of Bothwell et al. (1994) of UV-sensitivity in chironomids. It is possible we did not see increased algal biomass in response to any potential reduction in grazing because of the dominance of filamentous green algae in our systems, rather than the early successional diatom-dominated communities that tend to colonize experimental troughs.

Thicker algal biofilms present at the deeper sites also could have shielded invertebrates from benthivorous fish or macrobenthic invertebrate predators, resulting in higher invertebrate densities. For example, in 1996, very high algal biomass-normalized densities of chironomid larvae occurred at all four depths in previously acidified L302S. At the time, minnow populations in L302S were in the early stages of recovery. The difference we observed in invertebrate densities from other nearby lakes could have been a result of reduced predation by fish in L302S. Support for this conclusion was found in 1998 when, after minnow populations had become reestablished, chironomid densities in L302S were depressed to levels more similar to surrounding unacidified lakes ( $\sim 2,000$  organisms  $\text{m}^{-2}$ , Vinebrooke et al. 2001). In addition to direct sensitivities to high solar flux, it is evident that invertebrate densities respond dramatically to the presence or absence of predation. The recovery of littoral epilithic invertebrate communities in previously acidified lakes is complicated and can remain impaired despite chemical recovery, and extirpation of benthivorous fish might play a role in this persistent impairment.

Invertebrate densities and potential quality of algae as food: Many invertebrates in epilithon depend on algae and bacteria for food. Intra- and interlake differences in algal class dominance might contribute to differences in food quality for invertebrates and thus work to affect invertebrate community structure. Diatoms might be of higher food quality than other algal groups because they often contain higher concentrations of essential polyunsaturated fatty acids (PUFAs), saturated fatty acids, and total lipids, especially compared to green algae such as *Chlorella* and *Scenedesmus* spp. (Volkman et al. 1989; Brown et al. 1996). In addition, the relative production of the essential PUFAs increase as light intensity decreases (Thompson et al. 1990), suggesting that algae growing at a greater depth could be of higher food quality than in shallow depths exposed to higher radiative fluxes. These factors, combined with the sensitivity of diatoms to UVR, suggest that a gradient of food quality might exist from low food-quality, high-chlorophyte assemblages at the shallowest sites of lakes to higher food quality, high-diatom assemblages deeper in the littoral zones.

Under lower solar fluxes, chironomids might be limited by other factors, including food quality and quantity and predation. However, diatom-normalized chironomid densities were not significantly different among depths, except in the clearest lakes. Because diatom densities increased as UVR decreased, the densities of chironomids per microgram of total algae (of which diatoms comprised an increasing portion) should be greater under lower UVR exposures, even when the chironomid: diatom relationship does not change. An unchanging chironomid: diatom relationship might indicate that herbivorous chironomid larvae were food-limited at most sites, if they were feeding primarily on diatoms. In summary, densities of invertebrate grazers could be affected by a combination of several factors, including the quality and quantity of food, exposure to UVR, and the availability of refugia from UVR and predation within an overstory of algae.

Patterns of distribution of ostracods, nematodes, and oligochaetes in our lakes were consistent with those previously reported. Because they are detritivores, omnivores, or microbrotrophs, nematodes and oligochaetes tend to be less abundant in shallow, highly scoured sites because of lack of food (Brinkhurst and Gelder 1991; Poinar 1991). In addition, oligochaetes are sensitive to changes in light and physical disturbance. Finally, ostracods might feed on diatoms (De-lorme 1991), in addition to organic detritus, explaining their apparent preference for deeper sites in our study lakes.

Our analyses do not consider either the effects of hydrodynamic energy in shallower waters or short-term variations in lake levels on algal associations. However, lake levels at the ELA are relatively constant, fluctuating  $<0.2$  m between minimum and maximum depth during the open-water season (Ken Beaty pers. comm.). Gross differences in nutrient availability within the biofilm and in overlying water might also affect algal densities and dominance. None of these potentially confounding mechanisms can be accounted for in our descriptive study, which is essentially a snapshot in time and space. Further experiments are necessary to determine which environmental factors are the proximal causes for patterns we have observed, including direct algal and invertebrate

responses to UVR and PAR, the potential for interactions between sensitivities to solar radiation and foodweb dynamics, and the role of physical refugia for invertebrate grazers in the mediation of trophic or “solar” cascades.

Despite the forgoing, our results suggest that solar radiation is an important factor in structuring of littoral epilithon in boreal lakes. Shallow littoral algal communities had very high concentrations of photoprotective pigments and were dominated by filamentous green algae, likely as a result of exposure to high fluxes of solar radiation. The structure of littoral epilithic invertebrate communities appeared to be most affected by a combination of direct negative sensitivity to high solar flux, differences in food quality as a result of algal community responses to high solar fluxes, and availability of shelter within the algal biofilms from high solar fluxes and predation. Our findings also suggest that some of the changes observed in benthic communities during experimental acidification of L302S could have been contributed to by increased UVR and extirpation of benthivorous fish, as “hidden” treatments coincident with acidification.

Fluxes of UV radiation are increasing in many lakes, as DOC decreases as a result of combinations of stratospheric ozone depletion, climate change, and acidification (Schindler et al. 1996). Although increases in UVR fluxes are global, its in-lake effects are largely determined by its attenuation by DOC. In addition to shielding by DOC, physiological and behavioral adaptations of organisms make the effects of UVR on littoral communities difficult to predict. Communities that have evolved in high-UV waters usually exhibit evidence of physiological resistance or recovery mechanisms and behaviors that enable them to function in a high-UVR environment. In general, as in-lake fluxes of UVR increase, it is likely that the depth to which UVR-resistant epilithon occur will increase, and as a result, filamentous green algae could become more dominant. Furthermore, changes in invertebrate communities will likely result in response to increased in-lake UVR exposure, changes in algal taxa, and the coincident changes in food quality.

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