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Are the Deep Chlorophyll Maxima in Alpine Lakes Primarily Induced by Nutrient Availability, not UV Avoidance?

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Abstract

Alpine lakes are often highly transparent to ultraviolet (UV) wavelengths, which has led to the suggestion that a deep chlorophyll maximum (DCM) results in these systems from UV avoidance by phytoplankton. However, an alternative explanation is that the formation of the DCM is primarily driven by greater nutrient availability below the thermocline in these oligotrophic systems. We investigated the location of the chlorophyll maximum over spatial and temporal scales in a set of high-elevation lakes in the Beartooth Mountains (Montana/Wyoming). The position of the DCM was compared to a suite of physical and chemical variables across systems. Chlorophyll was strongly correlated to a suite of nitrogen variables, whereas correlations with UV parameters were not consistently observed. We also conducted an experiment with the natural phytoplankton assemblage from the DCM in Beartooth Lake; both UV exposure and nutrient additions were tested in a factorial design. The UV-exposed treatment and the control had the same final total phytoplankton biovolume, while the nutrient addition treatment had a final biovolume ten times as great. These results suggest that, as in other oligotrophic aquatic systems, greater nutrient availability in the hypolimnion leads to the development of the DCM in alpine lakes.

Introduction

Deep chlorophyll maxima are often found in large, oligotrophic systems, such as the Great Lakes (Brooks and Torke, 1977; Moll and Stoermer, 1982) and marine systems, as well as some small lakes (Fee, 1976; Williamson et al., 1996). The deep chlorophyll maximum (DCM) occurs in or below the thermocline, where light and temperature are relatively low but the availability of nutrients is often greater than in the epilimnion. Some studies suggest that the DCM is generated in situ (Fee, 1976), whereas others suggest that it is primarily formed by sinking cells, with only occasional active photosynthesis occurring here (Shortreed and Stockner, 1990). The chlorophyll *a*:carbon ratio must be considered when determining the ecological significance of the DCM, as phytoplankton will increase production of this pigment under low light levels.

The presence of a DCM is also characteristic of many alpine lakes, but the mechanisms that lead to its development and maintenance in these systems are still unclear. UV avoidance has been proposed as one such mechanism, as many alpine lakes have low dissolved organic carbon (DOC) concentrations (<1 mg L^{-1}) and thus are highly transparent to UV wavelengths. In alpine lakes dominated by flagellates, such as those in the Austrian Alps, Rott (1988) and Sommaruga and Psenner (1997) have proposed that UV avoidance causes the formation of the DCM, as these motile phytoplankton move to lower depths to escape the high UV radiation at the surface. However, many alpine lakes, such as those in the southern and central Rocky Mountains of North America, are dominated by non-flagellated forms such as diatoms for much of the year and still develop DCM. While several studies indicate that UV radiation can inhibit algal photosynthesis in alpine lakes (Montesinos et al., 1997; Villafañe et al., 1999), others reveal little to no effect of UV on phytoplankton photosynthesis or species composition (Halac et al., 1997; Vinebrooke and Leavitt, 1999). Experiments by Cabrera et al. (1997) in an alpine lake in Chile revealed a greater effect of UVB radiation on phytoplankton species composition than on overall production.

Alternatively, the development of the DCM in alpine lakes may be driven by greater nutrient availability below the thermocline. This has been suggested as the driving factor for DCM development in other systems as well. In Lake Michigan, the location of the deep chlorophyll layer was linked to greater ammonium availability below the epilimnion (Moll and Stoermer, 1982). In mesocosm experiments conducted in oligotrophic Redfish Lake, which develops a DCM, Gross et al. (1997) found that nutrient additions increased primary production in the epilimnion. The development of the DCM in this and other lakes in the Sawtooth Valley was partly attributed to the delivery of nutrients to the meta- and hypolimnia via cold stream water inflows.

To investigate the mechanisms that lead to the development of the DCM in alpine lakes, we examined the location of the chlorophyll maximum over spatial and temporal scales in a set of high-elevation lakes in the Beartooth Mountains (Montana/Wyoming). The relationship between chlorophyll and a suite of physicochemical parameters was explored to assess which factors play a role in structuring chlorophyll profiles in these systems. We also conducted an experiment with the natural phytoplankton assemblage in the DCM of Beartooth Lake and investigated the effects of UV and nutrient manipulations on chlorophyll concentrations.

Methods

The vertical chlorophyll profiles of a set of lakes in the Beartooth Mountains were collected in July of 2001 and 2002 (Table 1), and the experiment with the phytoplankton assemblage from the DCM of Beartooth Lake was conducted in July 2003. The Beartooth Mountains lie to the northeast of Yellowstone National Park, along the border of Montana and Wyoming, and comprise a large section of the Absaroka-Beartooth Wilderness Area. Over 600 permanent lakes have been identified in the 900 km^2 Beartooth primitive area. As a result of the slow-weathering bedrock, lakes in the region generally have low

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TABLE 1

Characteristics of the four study lakes, along with measured parameters and their ranges during the study period. Seston nutrient ratios are on a molar basis.

	Kersey	Beartooth		Island	Fossil
Year sampled	2001	2001	2002	2002	2001
Elevation (m a.s.l.)	2690	2967	2967	3172	3300
Max. depth (m)	22	28	28	33	50
Surface area (ha)	47	44	44	58	66
Temperature (°C)	4–18	4–15	4–15	4–15	5.1–12.0
pH	6.3–7.5	7.2–7.9	7.1–7.9	6.3–7.4	6.5–7.1
Conductivity ($\mu S \cdot cm^{-1}$)	13–16	26–34	15–34	6–7	1–2
TN ($\mu mol\ L^{-1}$)	1.7–5.4	2.4–9.3	1.3–5.7	2.0–4.9	2.5–3.8
TP ($\mu mol\ L^{-1}$)	0.08–0.25	0.10–0.24	0.02–0.26	0.05–0.64	0.10–0.17
NO_3^- ($\mu mol\ L^{-1}$ N)	0.27–3.3	0.50–6.9	0–4.7	0–1.9	0.05–0.55
SRP ($\mu mol\ L^{-1}$ P)	0.01–0.19	0.01–0.15	0.03–0.06	0.02–0.07	0–0.08
Silica ($\mu mol\ L^{-1}$ Si)	52.6–57.4	24.8–29.7	32.3–44.0	25.6–32.3	16.2–17.2
Seston					
C:N	7.6–8.9	5.4–6.2	7.0–15.0	7.5–12.3	6.0–8.5
C:P	168–225	124–147	96–289	43–269	121–236
N:P	20.0–30.5	21.2–25.6	8.0–31.0	4.5–32.5	18.3–27.7
Si:N	0.30–0.39	0.37–0.61	0.46–1.3	0.25–0.98	0.09–0.15
Si:P	7.0–12.9	8.4–12.8	7.8–17.5	1.9–19.2	1.7–4.2

silica and phosphorus levels. Nitrate concentrations are also low in these lakes (Table 1). Many of the lakes in the Beartooth area lie above 2500 m, with treeline ranging between 2750 and 3000 m.

CHLOROPHYLL PROFILES

In 2001, three lakes (Fossil, Beartooth, and Kersey) situated along an elevational gradient were profiled once during the second week of July. In 2002, Island and Beartooth Lakes were profiled every three days during a three-week period starting at the end of June, which was approximately 10 days after ice-off and at the onset of thermal stratification. We sampled these two lakes repeatedly because they have representative nutrient chemistries for lakes in the area and several parameters, including nutrient concentrations, were rapidly changing over this period. This was also shortly after summer solstice, hence UV exposure was near its peak for the year.

For each profile, samples were collected with a horizontal van Dorn bottle from a depth of 3 m to below the DCM. Samples were split for chlorophyll analysis and phytoplankton enumeration to determine which taxa comprised the chlorophyll maximum in each lake and to compare cell concentrations to chlorophyll values. In addition, a suite of physical and chemical variables were measured: temperature, pH, conductivity, light (including 320 nm [UV-B], 380 nm [UV-A], and photosynthetically active radiation [PAR]), total nitrogen (TN), total phosphorus (TP), nitrate, soluble reactive phosphorus (SRP), dissolved silica, and particulate C, N, Si, and P. These particulate data were used to calculate C:N, C:P, N:P, Si:N, and Si:P seston ratios.

In the 2001 samples, chlorophyll *a* was measured by immediately filtering 1.0–1.5 L of lake water through a Whatman GF/F filter for each sample depth. Filters were placed in petri dishes, wrapped in foil, and stored in a freezer until analysis. All samples were analyzed within three weeks of collection. Chlorophyll was extracted in 90% acetone; the extract was clarified by centrifugation. Chlorophyll *a* concentrations were determined spectrophotometrically, as described in APHA et al. (2000). In 2002, chlorophyll *a* was measured in Island Lake samples as described above, as well as in vivo with a field fluorometer (Turner Designs 10-AU). Samples from Beartooth Lake in 2002 were only measured on the fluorometer. A linear regression comparing measurements from both methods for all Island Lake samples yielded an $r^2 = 0.743$, indicating similar trends in values obtained from both methods.

Temperature, pH, conductivity, and PAR were measured with a Hydrolab® multiparameter probe. Water column profiles for UV were taken with either a PUV-501B or a BIC submersible profiling radiometer (Biospherical Instruments Inc., San Diego, California, U.S.A.). Dissolved nutrient samples were collected by filtering through pre-rinsed 0.4-μm polycarbonate filters and analyzed by standard methods (APHA et al., 2000). Nitrate plus nitrite was measured by the cadmium reduction method, and SRP by the ascorbic acid method. Dissolved Si was measured by the heteropoly blue method. Material retained on the polycarbonate filters was analyzed for particulate P by persulfate digestion followed by measurement of SRP, and for particulate Si by sodium carbonate digestion followed by measurement of soluble reactive Si. Particulate C and N were collected on 0.45 μm Whatman GF/F filters and measured via combustion and gas chromatography with a Carlo Erba 1106 elemental analyzer. TP and TN were estimated by adding the dissolved and particulate measurements of each nutrient (in $\mu mol\ L^{-1}$), thus the dissolved organic pool of these nutrients is not represented in this value. DOC was measured in water samples collected at a depth of 2 m, using a Shimadzu TOC-5000 Analyzer as described in Morris et al. (1995).

DATA ANALYSIS OF CHLOROPHYLL PROFILES

Chlorophyll profiles were related to physicochemical parameters by two different approaches: (1) for the samples in which chlorophyll was measured by extraction ($n = 31$), correlations were explored between chlorophyll concentration and measured parameters by either pairwise correlations or Spearman's rank correlation, depending upon the distribution of the data; (2) to expand the data set (to include chlorophyll samples measured by fluorometry) and standardize values across systems, ranks were assigned within each profile. For each sample date at a particular lake, chlorophyll values were assigned ranks in ascending order, such that the lowest chlorophyll value in the water column on a given date was ranked "1". Thus, the depth of the chlorophyll maximum had the highest rank value. Using Spearman's rank correlation analysis, relationships were explored in the entire data set ($n = 55$) between chlorophyll rank and the suite of measured physical and chemical variables. The software JMP (SAS Institute) was used for all correlation analyses. The relationship between the chlorophyll rank of samples and the environmental variables was also explored using principal components analysis (PCA). Ordination analyses were performed with Canoco version 4.5 (ter Braak and Smilauer, 2002).

For all UV and PAR parameters the irradiance values at each depth were adjusted for attenuation in the water column using the diffuse attenuation coefficient for downwelling irradiance (K_d) estimated by linear regression analysis to determine the slope of the relationship between the natural log of irradiance and depth.

UV irradiance values were also adjusted for ozone and aerosol-related elevation differences before they were entered into the among-lake statistical analyses. Incident daily irradiance was measured at 320 and 380 nm on the shores of Beartooth Lake with the deck cell of a BIC UV radiometer system to enable estimation of a standard UV exposure day for 320 and 380 nm irradiance. UV data were collected continuously at 1-min intervals from dawn to solar noon on 3 July 2003. There were no clouds or haze during the entire measurement period. Irradiance for the second half of the day was extrapolated in a mirrored fashion from the morning data and all values multiplied by 60 s and summed over the entire day to estimate a full exposure day in $KJ\ m^{-2}\ nm^{-1}$. One exposure day is defined as the ambient UV exposure at a given wavelength on a bright sunny day near summer solstice (Williamson et al., 2001). An exposure day thus represents the maximum potential solar irradiance for a single day at a given location and was used as the

standard unit of exposure. For the Beartooth Lake location the exposure day values were 9.06 KJ m^{-2} nm^{-1} at 320 nm and 22.43 KJ m^{-2} nm^{-1} at 380 nm. These values were adjusted for elevation-related changes of 11% and 9% per 1000 m for 320 and 380 nm global irradiance, respectively (Blumthaler et al., 1997). PAR values tend to change less with elevation and were thus not adjusted for elevation differences.

FIELD EXPERIMENT

In addition to the chlorophyll profiles, we conducted a set of bag experiments in which UV and nutrients were manipulated and the effects on phytoplankton abundance were investigated. UV was manipulated with UV-blocking (Cortguard) and UV-transmitting (Aclar) acrylic sheets. Cortguard blocks most UVR (transmits no UV-B, 295–319 nm, and only 9% of UV-A, 320–400 nm with a sharp wavelength cutoff and a 50% transmittance point at 400 nm) and transmits 95% of PAR (400–800 nm) in water. Aclar transmits both PAR (100% 400–800 nm) and most UVR (98% of UV-B, 295–319 nm, 99% UV-A, 320–399 nm). Lake water was collected from the depth of the chlorophyll maximum (8 m) in Beartooth Lake in July 2003 and filtered through a 153-μm mesh to remove large grazers. Triplicate sub-samples of 50 mL each of this water were collected and preserved to determine the initial total phytoplankton biovolume. Initial nutrient concentrations at this depth were 3.66 μM TN, 0.08 μM TP, and 36.0 μM dissolved Si. Four nutrient treatments were created: no added nutrients (control), N enrichment (18 μM N), P enrichment (5 μM P), and N+P enrichment (18 μM N + 5 μM P). Nitrogen was added in the form of $NaNO_3$; P was added in the form of NaH_2PO_4. The amended water was added to 500-mL Bitran bags made of UV-transmitting polyethylene (50% transmittance at 234 nm, transmits 94% PAR, 400–800 nm, and 86% of solar UV, 295–399 nm).

Bags were incubated at the surface of Chain Meadow Pond (Park County, Wyoming), which was chosen for incubation due to its remote location (i.e., no boat traffic). Bags were suspended on racks constructed of 2.5-cm PVC pipe, with bags sandwiched between bird netting (underneath) and either Cortguard or Aclar (on top). A small piece of rope with an attached carabineer was fastened to the middle of each rack and secured the rack to a buoy attached to an anchored rope. This design allowed the racks to float at the very surface of the water, prevented shading of the rack by the buoy, and eliminated problems with attenuation of light by lake water. To compensate for the high light levels at the surface, a layer of window-screen mesh was placed over every bag to act as a neutral density filter and further reduce incident levels of light to 62% of ambient levels. In total, there were 2 UV × 4 nutrient treatments, each with 4 replicates.

The experiment was incubated at about 14°C for seven days. At the end of the experiment, triplicate 50-mL sub-samples were collected from each bag and preserved with Lugol's iodine solution for enumeration of phytoplankton. The entire 50-mL sub-sample was settled in an Utermöhl-style chamber and counted with a Nikon TS-100 inverted microscope at a magnification of 400×. Four transects were counted for each sample; additional transects were added if needed until a minimum of 500 individuals were counted. Biovolumes were calculated by using an approximate volume for each species based on a geometric shape. The dimensions of twenty different individuals of the same species (taken randomly from at least four separate slides) were measured, and the cell volume was calculated. Biovolumes were determined by multiplying cell volume by total cell number for each taxon.

To assess the effects of nutrients and UV on phytoplankton abundance, each treatment was compared to the control (UV, no nutrients) using a one-way analysis of variance (ANOVA) with Tukey's honestly significant difference (HSD) post-hoc test ($p \leq 0.05$). Data were log transformed to meet the assumptions of normality and homogeneity of variance.

TABLE 2

Optical properties of the four lakes, with 1% depths for 320 nm, 380 nm, and PAR determined from K_d values ($z_{1\%} = 4.6/K_d$). These values were measured in July 2001 (unless otherwise noted), while DOC was measured in samples collected in July 2000.

	Kersey	Beartooth	Island	Fossil
Elevation (m)	2690	2967	3172	3300
DOC (mg/L)	2.1	1.1	1.4	0.5
1% depth (m)				
320 nm	0.54	1.26	0.91	7.03‡
380 nm	1.39	3.23	2.26	15.64‡
PAR	8.2	14.6	11.0	20.5

‡ = values based on attenuation coefficients measured in August 2003. Note that the 1% PAR depth at that time was 28.5 m.

Results

CHLOROPHYLL PROFILES

In general, we found a positive linear relationship between chlorophyll values and the total number of cells mL^{-1} in the samples ($r^2 = 0.787$). The ratio of chlorophyll to particulate C increased slightly with depth ($r^2 = 0.127$), indicating that shade adaptation was occurring to some extent, but again the total number of cells mL^{-1} did increase concurrently with chlorophyll.

Phytoplankton assemblages mainly consisted of a species of *Dinobryon* as well as several diatoms, including *Asterionella formosa* Hassall, *Fragilaria crotonensis* Kitton, *Tabellaria flocculosa* (Roth) Kutzing, and *Aulacoseira distans* (Ehr.) Simons. *Dinobryon* sp. was abundant throughout the water column in Beartooth and Island Lakes at the end of June, and comprised the DCM in all lakes. *F. crotonensis* and *A. formosa* were also abundant during the sampling period and typically dominated samples with the second highest chlorophyll values in the water column, which were situated above the depth of the DCM.

Light measurements indicated that the 1% depths for the various wavelengths followed trends in DOC concentrations (Table 2), such that light penetrated to greater depths in systems with lower DOC. DOC concentrations generally declined with increasing elevation, as watershed vegetation became sparser.

In Kersey, Beartooth, and Fossil Lakes in 2001, thermoclines were shallow and typically occurred between 4 and 6 m. The depth of the chlorophyll maximum deepened with increasing elevation (Fig. 1), thus the chlorophyll maximum at 16 m in Fossil (the highest elevation system, 3300 m a.s.l.) was the deepest. In all cases, the peak in chlorophyll occurred just above the limit of the euphotic zone as defined by the 1% attenuation depth for PAR.

In Beartooth and Island Lakes in 2002, the first sample date coincided with the end of the mixing period, after which thermal stratification was established and intensified during the three-week sampling period. Again, thermoclines were situated between about 4 and 6 m. In late June in both lakes, chlorophyll profiles indicated relatively low concentrations throughout the water column, with slightly higher values in the upper 6 m. This was followed by the development of chlorophyll maxima at 9–12 m in both lakes shortly after thermal stratification became established (Fig. 2, data shown only for Island Lake). The depth of the chlorophyll maximum stayed above the 1% PAR depths in both lakes (Table 2). Nitrate concentrations varied spatially and temporally in both lakes, with lower concentrations (often below the detection limit of 0.01 μM) frequently found in areas with higher chlorophyll (Fig. 2, data shown only for Island Lake).

Most of the measured parameters showed a fair amount of variation in the water column as well as over the course of sampling

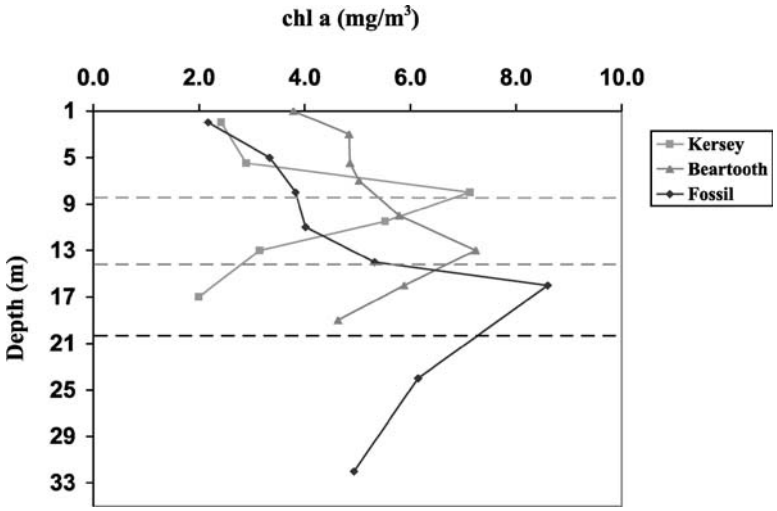

FIGURE 1. Chlorophyll profiles for three lakes in the Beartooth Mountains situated along an elevational gradient: Kersey, 2690 m a.s.l.; Beartooth, 2967 m a.s.l.; and Fossil, 3300 m a.s.l. The 1% PAR attenuation depth is indicated with corresponding dashed lines for each lake. Lakes were profiled during July 2001, which was within four weeks after ice-off for all lakes. The depth of the chlorophyll maximum increases with elevation and is situated above the limit of the euphotic zone in each case.

(Table 1). The data for all parameters except PAR, 380 nm, 320 nm, SRP, and nitrate were normally distributed. Log transformations of these parameters did not alter their distribution. For nitrate, this was largely due to the high proportion of samples that were below our detection limit, resulting in several zero values. There were also several zero values in the 320 and 380 nm data set. Thus, Spearman's rank correlation analysis was used to compare these parameters to chlorophyll concentrations.

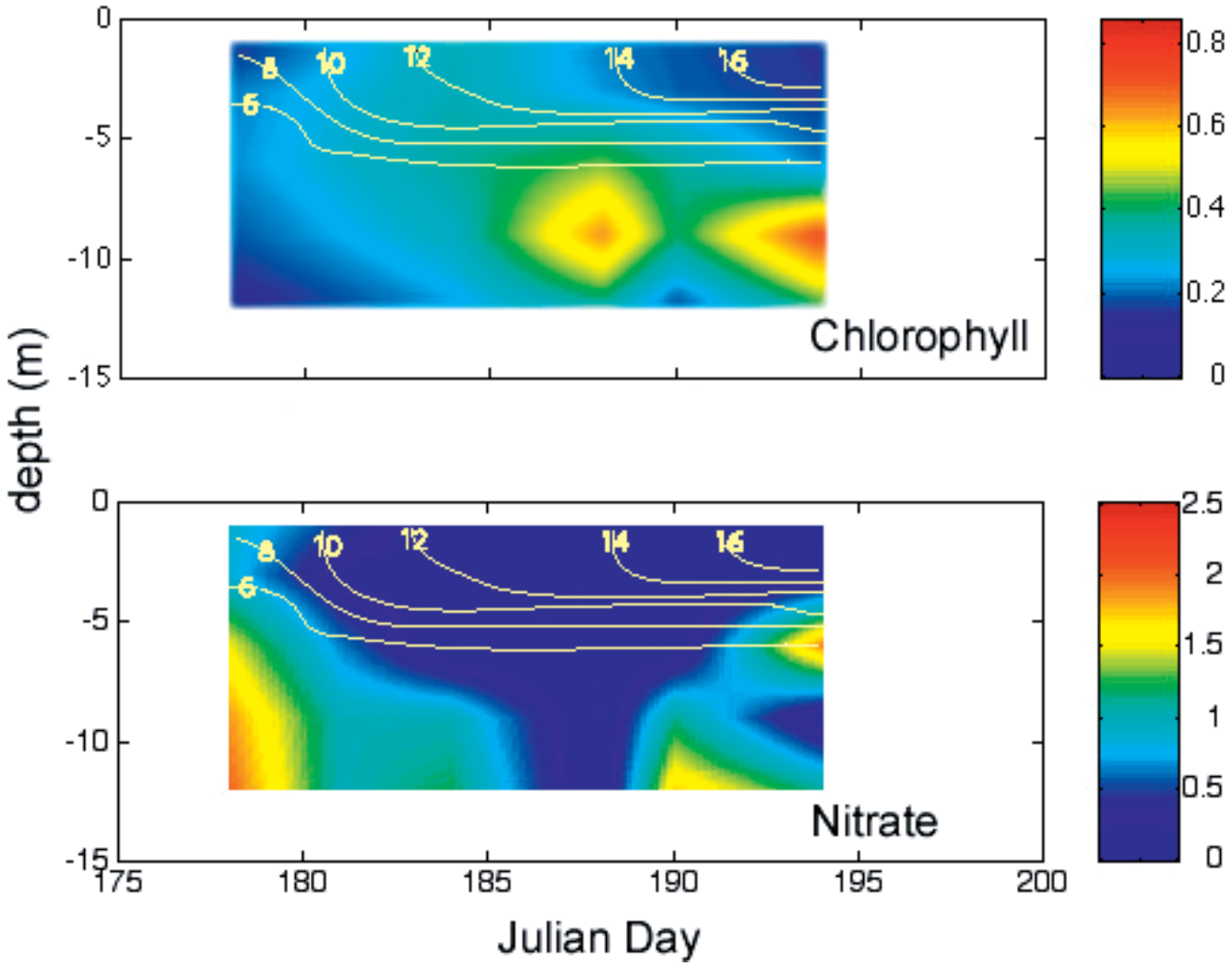

FIGURE 2. Chlorophyll and nitrate profiles in Island Lake during three weeks in late June to early July 2002, with temperature (°C) isolines indicated. Temperatures below the 6°C isoline were between 4 and 6°C. Chlorophyll values were measured in vivo with a fluorometer and are reported as relative fluorescence units (r.f.u.). Nitrate values are in μM, with values below the detection limit of 0.01 μM reported as zero.

TABLE 3

Correlation coefficients between chlorophyll concentration (measured by extraction and spectrophotometric determination) and various parameters from four lakes in the Beartooth Mountain region, with significant parameters indicated in bold. Spearman's rank correlation coefficient was used when the data had non-normal distributions.

Parameter	Correlation coefficient	*p*-value
Pairwise		
C:N	**−0.57**	**0.0009**
Si:N	**−0.44**	**0.013**
N:P	**0.43**	**0.017**
TN	**0.43**	**0.015**
Conductivity	**0.41**	**0.024**
C:P	0.05	0.78
Si:P	−0.17	0.35
Dissolved Si	−0.13	0.49
TP	−0.16	0.38
Temperature	−0.14	0.46
pH	0.09	0.64
Spearman's rank		
PAR	−0.11	0.54
380 nm	0.07	0.72
320 nm	0.27	0.14
Nitrate	0.12	0.51
SRP	0.02	0.93

Correlations between chlorophyll concentrations and the measured parameters revealed strong associations with a suite of nitrogen variables (Table 3). Positive correlations were observed with TN ($r^2 = 0.43$) and seston N:P ($r^2 = 0.43$), and negative correlations with seston C:N ($r^2 = –0.57$) and Si:N ($r^2 = –0.44$). A positive correlation was also found with conductivity ($r^2 = 0.41$). Associations with P or Si parameters, as well as any UV parameters, were not apparent.

Spearman's rank correlation analysis between these parameters and chlorophyll ranks for all profiles (2001 and 2002 data) are indicated in Table 4 and reveal the strongest relationships between chlorophyll rank and TN ($\rho = 0.52$), temperature ($\rho = –0.46$), and 380 nm UV ($\rho = –0.46$). Negative associations with PAR ($\rho = –0.42$) and 320 nm UV ($\rho = –0.40$) were also found. The results of correlation analyses between temperature and a suite of other variables are also provided in Table 4 as an indication of how these parameters co-varied with depth.

We also analyzed the June data separately from the July samples to determine whether a stronger UV effect was apparent earlier in the season. No significant associations between chlorophyll rank and any parameters were found in the June data set alone.

The results of the PCA (Fig. 3) revealed that the first principal component explained 22.6% of the variance in the data and was strongly correlated to PAR (0.87), temperature (0.80), 380 nm (0.72), and TN (–0.69). The second PCA axis accounted for an additional 21.1% of the variance and was correlated to Si:N (–0.87), pH (–0.72), conductivity (–0.72), and C:N (–0.60). Several of the high-ranking chlorophyll samples are located in the upper left quadrant of the biplot and plot near the TN vector, revealing a correlation with this parameter (Fig. 3). The orthogonal position of these samples to the 320 and 380 nm vectors also indicates that their position on the biplot is essentially independent of these variables. Another cluster of high-ranking chlorophyll samples plot opposite the UV vectors (i.e., in the lower left quadrant of the biplot). These samples are a sub-set from Beartooth Lake that have higher Si:N seston ratios, hence their location in this quadrant is at least partly due to their positive relationship with the Si:N vector.

TABLE 4

Results of Spearman's rank correlation analyses with a *p*-value < 0.10 for all samples between (1) chlorophyll rank and various parameters; and (2) temperature and various parameters, to illustrate covariation between temperature and several variables.

Parameter	Spearman's ρ	*p*-value
Chlorophyll rank		
TN	0.52	0.0002
Temperature	−0.46	0.0010
380 nm	−0.46	0.0011
PAR	−0.42	0.0032
320 nm	−0.40	0.0053
pH	−0.25	0.0817
TP	−0.25	0.0866
Temperature		
PAR	0.88	<0.0001
380 nm	0.81	<0.0001
pH	0.71	<0.0001
TN	−0.67	<0.0001
380 nm	0.45	0.0013
TP	−0.32	0.0254

FIELD EXPERIMENT

The total biovolume of phytoplankton cells among all eight treatments are displayed in Figure 4. Phytoplankton assemblages were dominated by *Dinobryon* sp., with diatoms such as *F. crotonensis* and *A. formosa* also abundant. Total phytoplankton biovolume increased in all treatments over the course of the experiment, as indicated by comparison with the initial total biovolume (Fig. 4).

In the treatments without nutrient additions, UV exposure had no effect on total phytoplankton biovolume ($p = 0.33$), which increased approximately 2.5-fold over initial values in both the + and − UV treatments. In contrast, the addition of N+P resulted in approximately 10- and 20-fold increases in total biovolume in the +UV and −UV treatments, respectively ($p < 0.001$ for both comparisons with Tukey's HSD). The difference between the +UV and −UV treatments with nutrients was significant ($p < 0.001$), with lower total biovolume in the +UV treatment.

Discussion

Our results suggest that greater nutrient availability (particularly of N) and adequate PAR below the thermocline allow the DCM to form in these alpine lakes. Chlorophyll concentrations were consistently correlated to seston ratios indicative of higher N content. The experiment presented here, as well as other enrichment experiments conducted in the area (Saros, unpublished), indicates co-limitation of primary production by N and P, as total phytoplankton biovolume was higher in treatments with N+P added. Thus, a correlation between chlorophyll and N, rather than P, is not surprising in these systems. These lakes generally experience their maximum dissolved nutrient concentrations during spring turnover, as snowmelt typically provides the biggest pulse of nutrients to alpine lakes. We found that dissolved nutrient concentrations were rapidly depleted in the epi- and metalimnia of these lakes as thermal stratification became established, leading to the development of the DCM.

A number of mechanisms can explain how this chlorophyll layer can persist below the mixed layer. Flagellated chrysophytes, such as *Dinobryon*, can maintain populations at particular depths in poorly mixed areas of the euphotic zone (Nichols, 1995). Non-motile pennate diatoms, such as *A. formosa* and *F. crotonensis*, inherently have slower settling rates than centric diatoms (Bienfang and Harrison, 1984). Sinking rates are also regulated by nutrient and light conditions, with

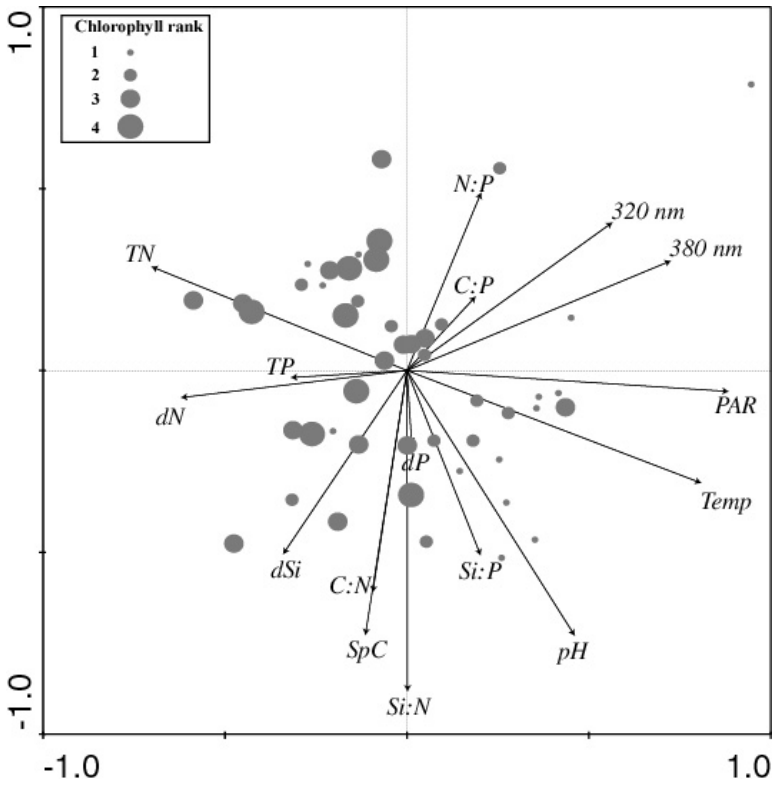

FIGURE 3. Principal components analysis to explore the relationship between the chlorophyll rank of samples and the measured environmental variables. Positions of the samples on the biplot are indicated by circles, with larger circles indicating a higher chlorophyll rank in that sample (i.e., the highest chlorophyll concentration for that profile). The conductivity vector is denoted as SpC; the dissolved nutrient vectors are dN, dP, and dSi.

slower rates observed under nutrient-replete (Bienfang and Harrison, 1984) and/or low light (Bienfang et al., 1983) conditions. Hence, the low light and relatively greater nutrient availability in the hypolimnia of these lakes would allow phytoplankton to reduce their settling rates. Bienfang et al. (1983) suggested that, while settling rate deceleration may not be an important factor in DCM formation in warm marine waters, it would likely play an important role in the development of the DCM in temperate waters with a shallow mixed layer, a well-developed pycnocline, and a phytoplankton population comprised of large-celled species—all of which are found in these alpine lakes.

The DCM in these lakes were shallower than those in large, oligotrophic systems, where the DCM are typically situated around 20–25 m, but were similarly located at the margin of the euphotic zone and in the hypolimnion. While Fennel and Boss (2003) found that the maxima in chlorophyll and particulate organic carbon were vertically separated in some systems, we did not find this to be the case in these lakes, as a positive correlation was found between chlorophyll values and the total number of cells mL^{-1} in the profiling samples.

While the position of the DCM was correlated with various N parameters, we found little evidence to support UV as the main factor inducing DCM formation in these lakes. Although a strong negative correlation was found between chlorophyll rank and 380 nm, no relationship between UV parameters and chlorophyll concentration was found, and the DCM was always located well below the 1% attenuation depths for 380 nm. Further support for this conclusion is provided by the results of the experiment—under ambient nutrient conditions, UV exposure had no effect on total phytoplankton biovolume. Even though total phytoplankton biovolume was lower in the +UV versus –UV treatments under nutrient replete conditions, it still represented a ten-fold increase over initial biovolume. A lack of UV inhibition of phytoplankton growth has been observed in other alpine lakes (Halac et al., 1997; Bertoni and Callieri, 1999; Vinebrooke and Leavitt, 1999). Phytoplankton from high-elevation lakes may be well adapted to high UV radiation (Moeller, 1994; Halac et al., 1997), thus for several alpine taxa this factor may not strongly influence productivity.

In alpine lakes for which data are available, chrysophytes, diatoms, dinoflagellates, and cryptophytes are typically the most abundant phytoplankton. In high-elevation lakes of the Alps, motile species of chrysophytes, dinoflagellates, and cryptophytes dominate phytoplankton assemblages, with diatoms dominant in 13% of the 48 lakes considered (as reviewed by Sommaruga, 2001). Cabrera et al. (1997) reveal that the phytoplankton assemblages of the Andean Laguna Negra were dominated by diatoms such as *F. crotonensis* and *Fragilaria construens* as well as a chlorophyte. In lakes of the southern Rocky

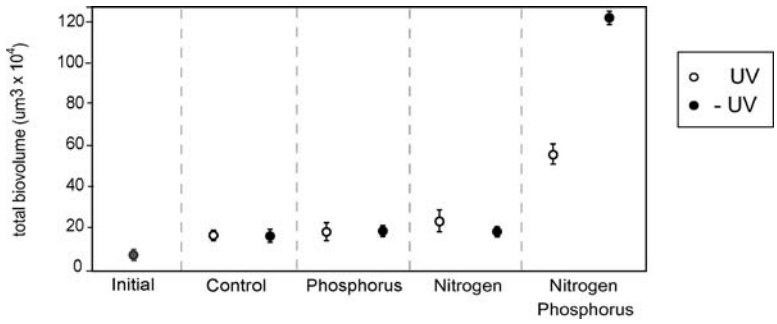

FIGURE 4. Total phytoplankton biovolume measurements (with standard error estimates indicated) from the field experiment in which nutrients and UV exposure were manipulated in a factorial design. The UV treatments consisted of +UV or –UV and are indicated in the legend. Nutrient treatments are indicated on the x-axes, with the control representing no nutrient additions.

Mountains of North America (e.g., the Colorado Front Range), the phytoplankton are frequently dominated by diatoms such as *A. formosa* (Olive, 1953; Keefer and Pennak, 1977; McKnight et al., 1990), with fall blooms of cyanobacteria also observed (McKnight et al., 1990). In lakes of the Beartooth Mountains, which are part of the central Rocky Mountains, we found that a motile chrysophyte, *Dinobryon* sp., dominated phytoplankton assemblages in late June to early July, and the diatoms *F. crotonensis* and *A. formosa* were also abundant at this time. These assemblages share common taxa with other alpine systems around the world, thus similar mechanisms driving the formation of the DCM may be expected in alpine lakes from other regions.

The results presented here suggest that the combination of high transparency to PAR and greater availability of nutrients in the hypolimnion leads to the development of the DCM in alpine lakes, much like other studies indicate for large, oligotrophic lakes in temperate areas. While several studies reveal that UV can influence the composition of phytoplankton assemblages in alpine lakes, our results indicate that nutrient availability may play a more important role than UV in inducing the formation of the DCM in these lakes.

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