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Authors: Moraska Lafrancois, Brenda, Nydick, Koren R., and Caruso, Bethany

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Influence of Nitrogen on Phytoplankton Biomass and Community Composition in Fifteen Snowy Range Lakes (Wyoming, U.S.A.)

Brenda Moraska Lafrancois

Department of Fishery and Wildlife
Biology, Colorado State University,
Fort Collins, CO 80523, U.S.A.
Current address: St. Croix Watershed
Research Station, 16910 152nd St. N,
Marine on St. Croix, MN 55047, U.S.A.
brenda_moraska_lafrancois@nps.gov.

Koren R. Nydick

Natural Resource Ecology Laboratory,
Colorado State University, Fort Collins,
CO 80523, U.S.A. Current address:
Department of Aquatic, Watershed and
Earth Resources, Utah State University,
Logan, UT 84322-5210, U.S.A.

Bethany Caruso

Science and Society Program, Wesleyan
University, Middletown, CT 06459, U.S.A.

Abstract

Nitrogen (N) deposition has been implicated in changes in surface water chemistry and algal composition in several dilute mountain lakes of the western United States. Lakes of the Snowy Range (Medicine Bow National Forest, Wyoming) appear to have low nitrate concentrations currently, and 2 Snowy Range lakes showed strong eutrophication responses to N or N + phosphorus (P) additions in previous enclosure experiments. In this study, we explored the regional extent of phytoplankton N limitation by examining a nutrient ratio index (dissolved inorganic nitrogen:total phosphorus) and phytoplankton species-environment relationships across 15 Snowy Range lakes. Based on this index, we estimate that phytoplankton biomass in the study lakes is largely N limited or N + P colimited. In addition, redundancy analysis demonstrated strong relationships between phytoplankton species composition and N gradients, with chrysophyte taxa favored in low-N lakes and cyanophytes and chlorophytes favored in higher-N lakes. We conclude that both phytoplankton biomass and community structure are sensitive indicators of N gradients in lakes of the Snowy Range, and that eutrophication responses to future increases in N loading could be widespread in these and other low-N lakes.

Introduction

Mountain ecosystems are thought to be especially sensitive to atmospheric nitrogen (N) deposition due to steep, sparsely vegetated watersheds, thin soils, short growing seasons, and dilute waters with low acid-neutralizing capacity (Eilers et al., 1988; Marchetto et al., 1995; Baron et al., 2000). Nitrogen deposition is currently implicated in high surface water nitrate levels and altered diatom composition in Colorado Front Range lakes (Baron et al., 2000; Wolfe et al., 2001) and in shifts in the water clarity and nutrient status of oligotrophic Lake Tahoe (Goldman et al., 1993). The Wyoming Snowy Range receives levels of N deposition similar to the Colorado Front Range (Williams et al., 1996), but lakes in the area generally have low nitrate concentrations (Musselman, 1994), suggesting that the capacity for watershed and in-lake N uptake in the Snowy Range has not been exceeded (Aber et al., 1989).

Nutrient addition experiments in 2 remote, low-nitrate Snowy Range lakes documented significant increases in phytoplankton biomass and productivity as well as marked changes in species composition in response to N or N + phosphorus (P), indicating that N may regulate phytoplankton growth and composition in Snowy Range lakes (Lafrancois, 2002). N limitation of freshwater ecosystems has received increasing attention in recent years (Elser et al., 1990; Axler et al., 1994) and has been noted in other mountain lakes (Axler and Reuter, 1996; Kilham et al., 1996); however, the extent of phytoplankton N limitation among lakes of the Snowy Range is unknown. In addition, examples of phytoplankton N limitation have rarely been integrated with community-level data, so relationships between N and phytoplankton composition across lakes are unclear.

We examined nutrient limitation patterns and phytoplankton species-environment relationships in Snowy Range lakes by conduct-

ing a lake survey soon after spring ice-out in 2001. Previous sampling efforts in Snowy Range lakes have focused on basic limnological parameters (Secchi depth, water temperature, dissolved oxygen, pH, alkalinity, turbidity, hardness) and physical habitat characteristics for fisheries management (Snigg, 1989). Our survey extends this data set by incorporating several chemical and biological characteristics that have not been measured previously (including silica concentrations, chemical fractions of N, P, and carbon, and phytoplankton chlorophyll *a*, species richness, diversity, and composition). We applied an index of phytoplankton nutrient limitation (dissolved inorganic nitrogen:total phosphorus) to the survey data to predict whether phytoplankton biomass of Snowy Range Lakes was N or P limited and examined relationships between phytoplankton composition and environmental characteristics. Based on results from previous enclosure experiments (Nydick, 2002; Lafrancois, 2002), we expected that phytoplankton growth and composition would be strongly affected by N gradients among Snowy Range lakes, with chrysophyte taxa favored in low-N lakes and chlorophytes and cyanobacteria more common in higher-N lakes.

Study Site

The Snowy Range is a broad quartzite massif situated east of Laramie, Wyoming, in the Medicine Bow National Forest (Fig. 1). Catchments are composed of rocks, krummholz conifers, tundra, and wet meadow vegetation (Musselman, 1994). Ice cover typically lasts from late October through mid-June; annual hydrology is driven by spring snowmelt. We selected study lakes from a set of 99 lakes sampled during a previous Snowy Range fishery survey (Snigg, 1989). In order to focus on high-elevation lakes with low productivity, we eliminated from the selection pool all lakes <3100 m in elevation and

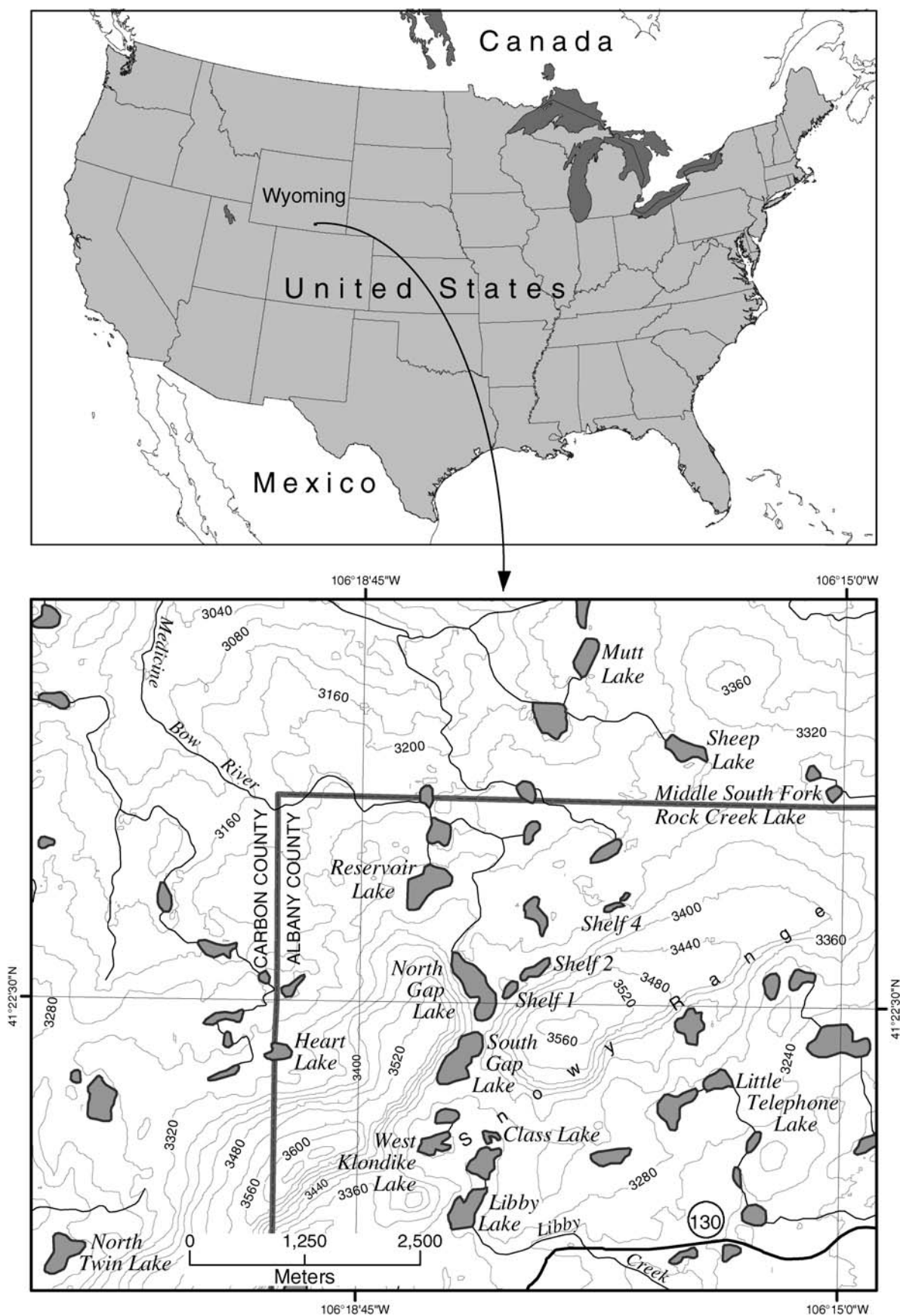


FIGURE 1. Study area for a survey of phytoplankton nutrient limitation and species composition in 15 lakes of the Snowy Range in Wyoming, U.S.A. The enlarged portion indicates lake locations and topographic features.

TABLE 1

Mean (± 1 standard deviation), minimum and maximum values for environmental variables measured in lakes of the Wyoming Snowy Range ($n = 15$). Variables selected in the redundancy analysis (RDA) data screening procedure are denoted (*). Min. = minimum; Max. = maximum

Variable	Abbreviation	Unit	Mean	Min.	Max.
Elevation*	ELEV	m	3284 \pm 47	3159	3345
Surface area*	SA	ha	6.40 \pm 5.16	1.15	17.94
Maximum depth	D _{max}	m	9.5 \pm 7.8	0.9	25.0
Mean depth	D _{mean}	m	3.7 \pm 2.9	0.4	9.0
Volume	VOL	m ³ $\times 10^5$	2.96 \pm 4.09	0.11	12.10
Surface area:volume	SA:VOL		0.84 \pm 1.08	0.11	4.13
Conductivity*	COND	$\mu\text{S cm}^{-1}$	11.33 \pm 6.16	6.10	28.50
Alkalinity*	ALK	$\mu\text{eq L}^{-1}$	94.18 \pm 59.82	28.25	257.74
pH*	pH		7.40 \pm 0.46	6.78	8.35
Temperature*	TEMP	$^{\circ}\text{C}$	13.8 \pm 3.6	5.5	20.4
Dissolved organic carbon*	DOC	mg L ⁻¹	1.86 \pm 1.20	0.50	4.66
Particulate carbon	PC	$\mu\text{g L}^{-1}$	627 \pm 293	189	1212
Silica	Si	mg L ⁻¹	1.30 \pm 0.85	0.06	2.78
Ammonium*	NH ₄ -N	$\mu\text{g L}^{-1}$	18 \pm 12	3	47
Nitrate-N	NO ₃ -N	$\mu\text{g L}^{-1}$	11 \pm 22	0	84
Dissolved inorganic nitrogen*	DIN	$\mu\text{g L}^{-1}$	29 \pm 26	0	101
Particulate nitrogen*	PN	$\mu\text{g L}^{-1}$	108 \pm 62	36	262
Phosphate-P	PO ₄ -P	$\mu\text{g L}^{-1}$	4 \pm 8	0	28
Dissolved organic phosphorus	DOP	$\mu\text{g L}^{-1}$	8 \pm 11	0	45
Total dissolved phosphorus	TDP	$\mu\text{g L}^{-1}$	12 \pm 19	1	73
Particulate phosphorus	PP	$\mu\text{g L}^{-1}$	18 \pm 10	7	40
Total phosphorus	TP	$\mu\text{g L}^{-1}$	30 \pm 20	8	86
DIN:TP*	DIN:TP		1.19 \pm 1.11	0.14	4.39
PN:PP	PN:PP		6.21 \pm 2.23	2.85	10.03
Chlorophyll <i>a</i>	CHL- <i>a</i>	$\mu\text{g L}^{-1}$	6.24 \pm 5.25	0.89	16.57
Species richness	Rich		27 \pm 8	15	41
Simpson's <i>D</i>	<i>D</i>		0.75 \pm 0.15	0.37	0.90

lakes with relatively high alkalinity ($>300 \mu\text{eq L}^{-1}$) and/or rooted macrophytes. From the remaining pool of 75 lakes, 14 were randomly selected for our survey. Shelf Lake 4, the site of previous nutrient enrichment experiments (Lafrancois, 2002), was also included in the survey for comparative purposes.

Methods

FIELD METHODS AND LABORATORY ANALYSIS

Chemistry and phytoplankton were sampled once from each lake soon after spring ice-out in 2001, from 1 through 6 July. Measurements of lake physical characteristics (elevation, surface area, mean depth, maximum depth, and volume) were derived from Snigg (1989). Depth-integrated water chemistry samples were collected from depths of 1–4 m over the deepest part of each lake and processed using standard Loch Vale Watershed project methods (Allstott et al., 1999). Nitrate (NO₃-N), ammonium (NH₄-N), and phosphate (PO₄-P) were determined colorimetrically with a Perstorp Analytical Alpkem Spectrophotometer (Model 3590) using the cadmium reduction, salicylate, and ascorbic acid methods, respectively. Dissolved organic P (DOP) was oxidized to orthophosphate with a potassium persulfate digest and analyzed as described earlier for PO₄-P. Dissolved organic carbon (DOC) was analyzed on an Oceanographics International Model 700 Carbon Analyzer (U.S. Geological Survey, Boulder, CO). Silica was analyzed colorimetrically with the molybdate method modified by Hach, Inc. Alkalinity was measured by titration (APHA [American Public Health Association], 1995). Temperature, specific conductance, and pH were measured with meters (Orion Model 128, VWR Model 8000). Particulate N (PN), particulate P (PP), and particulate carbon (PC) were collected on precombusted Whatman GF/F filters and oxidized with a potassium persulfate digest (Lampman et al., 2001). NO₃-N and

PO₄-P in the digest were determined colorimetrically as described for water samples, and PC was measured with a LI-COR Model LI-6252 CO₂ Analyzer.

Phytoplankton nutrient limitation was estimated using the ratio of dissolved inorganic N (DIN) to total phosphorus (TP) in ambient water, which has been shown to reliably predict the nature of nutrient limitation in mountain lakes (Morris and Lewis, 1988; Axler et al., 1994; Sickman, 2001). DIN:TP ratios ranging from 0.56 to 1.61 were found during the summer of 2000 in two Snowy Range lakes, indicative of N limitation or N + P colimitation (K. Nydick, unpublished data), and concurrent nutrient enrichment experiments in the same lakes corroborated these predictions (Lafrancois, 2002). Unlike the Redfield Ratio (PN:PP), which measures internal stores of N and P, DIN:TP approximates the supply of N and P available to phytoplankton. In the case of N, the largest bioavailable pool is typically dissolved inorganic N (DIN), although recent studies have shown that a small portion of dissolved organic N (DON) may supplement phytoplankton growth via its microbial transformation to ammonium or urea (Berman et al., 1999; Stepanauskas et al., 2000). In the case of P, the best index of bioavailability is TP, since this fraction encompasses both externally available dissolved phosphorus and internal reserves of PP derived from luxury consumption. For the purposes of this study, DIN:TP ratios ≤ 0.5 predicted N limitation, DIN:TP ratios ≥ 4.0 predicted P limitation, and intermediate DIN:TP ratios predicted colimitation by both N and P (Sickman, 2001). The timing of the survey was chosen conservatively; lake nitrate concentrations generally reach their annual peak during snowmelt (Baron, 1992). N limitation was least likely at this time, and our estimates of N limitation were expected to underestimate the actual occurrence of N limitation during later periods of the ice-free season.

Depth-integrated phytoplankton samples were collected from depths of 1–4 m over the deepest part of each lake for analysis of

TABLE 2

Pearson correlation matrix for all environmental variables measured in lakes ($n = 15$) of the Wyoming Snowy Range during early summer 2001. Bonferroni-corrected P -values < 0.05 are noted in boldface. See Table 1 for variable abbreviations

	ELEV	SA	D _{max}	D _{mean}	VOL	SA:VOL	COND	ALK	pH	TEMP	DOC	PC
ELEV	1.000											
SA	0.257	1.000										
D _{max}	0.166	0.683	1.000									
D _{mean}	-0.108	0.522	0.939	1.000								
VOL	0.242	0.843	0.920	0.794	1.000							
SAVOL	-0.058	-0.024	-0.516	-0.535	-0.464	1.000						
COND	-0.765	-0.309	-0.069	0.193	-0.139	-0.235	1.000					
ALK	-0.672	-0.377	-0.074	0.185	-0.185	-0.199	0.961	1.000				
pH	-0.464	-0.378	0.004	0.223	-0.214	-0.410	0.559	0.519	1.000			
TEMP	-0.430	-0.475	-0.538	-0.374	-0.556	0.096	0.363	0.336	0.243	1.000		
DOC	-0.127	-0.294	-0.563	-0.494	-0.457	0.161	0.065	0.000	-0.013	0.807	1.000	
PC	0.341	0.176	0.323	0.295	0.284	-0.453	-0.055	-0.072	0.073	-0.450	-0.245	1.000
Si	-0.714	-0.321	-0.330	-0.101	-0.343	0.288	0.425	0.404	0.266	0.380	0.285	-0.603
NH ₄ -N	0.374	0.018	-0.255	-0.349	-0.264	0.769	-0.472	-0.336	-0.584	-0.163	0.078	-0.088
NO ₃ -N	0.289	0.414	0.245	0.107	0.440	-0.067	-0.273	-0.311	-0.420	-0.741	-0.444	0.407
DIN	0.419	0.365	0.097	-0.065	0.261	0.289	-0.449	-0.421	-0.627	-0.714	-0.348	0.312
PN	0.769	0.007	0.055	-0.092	0.015	-0.215	-0.551	-0.468	-0.107	-0.143	0.186	0.574
PO ₄ -P	-0.067	-0.117	-0.524	-0.528	-0.325	0.379	-0.049	-0.064	-0.225	0.530	0.712	-0.546
DOP	0.005	-0.133	-0.554	-0.579	-0.359	0.348	-0.093	-0.107	-0.216	0.552	0.745	-0.449
TDP	-0.025	-0.127	-0.544	-0.560	-0.346	0.362	-0.075	-0.090	-0.221	0.546	0.735	-0.491
PP	0.688	0.394	0.288	0.071	0.402	-0.281	-0.523	-0.528	-0.414	-0.542	-0.163	0.752
TP	0.303	0.066	-0.383	-0.502	-0.140	0.213	-0.320	-0.337	-0.408	0.264	0.625	-0.112
DINTP	0.075	0.257	0.144	0.092	0.091	0.591	-0.292	-0.232	-0.412	-0.577	-0.532	0.005
CHL-a	0.618	0.160	0.261	0.126	0.181	-0.281	-0.606	-0.592	0.089	-0.415	-0.083	0.608
Rich	0.041	-0.235	-0.321	-0.321	-0.347	-0.019	0.292	0.321	0.419	0.361	0.147	-0.043
D	-0.450	-0.400	-0.449	-0.330	-0.564	0.294	0.511	0.522	0.425	0.584	0.299	-0.321

chlorophyll *a* and species composition. Samples for chlorophyll *a* were immediately filtered through Whatman GF/C filters in the field. Filters were frozen in dark containers, and chlorophyll was extracted with methanol (Reimann, 1980). Chlorophyll *a* corrected for phaeophytin was determined with a Sequoia-Turner Model 450 Digital Fluorometer. Samples for phytoplankton taxonomic analyses were preserved with Lugol's Iodine in a 1:100 ratio and settled in Utermöhl chambers for identification (Utermöhl, 1958). Several transects were counted under low magnification (150× or 480×) and high magnification (1500×) using a Leitz Diavert inverted microscope. Biovolume was not calculated due to concerns about species-specific distortion of cell sizes and shapes induced by the fixative (Jerome et al., 1993; Zinabu and Bott, 2000; Menden-Deuer et al., 2001) and growth condition-related variability in cell volumes (Sicko-Goad et al., 1977; Hillebrand et al., 1999). A minimum of 400 cells was enumerated per sample and identified to genus and species level where possible. Species richness and diversity (Simpson's *D* [Washington, 1984]) were calculated for each sample.

STATISTICAL ANALYSIS

Pearson correlations were calculated for environmental variables using SYSTAT version 9, 1999. The resulting matrix was used to identify patterns in the environmental data and to evaluate which environmental characteristics were most strongly correlated with DIN:TP ratios (i.e., nutrient limitation). Bonferroni-corrected P -values identified statistically significant correlations ($P < 0.05$) between environmental variables. Correlations 0.5 were used to explore relationships with potential biological significance.

Relationships between phytoplankton composition and environmental variables were assessed using redundancy analysis (RDA, CANOCO version 4, ter Braak and Smilauer, 1998), a constrained

linear ordination method appropriate for graphically describing species-environment relationships and analyzing data with relatively short gradient lengths (ter Braak and Smilauer, 1998). The taxonomic data set consisted of phytoplankton cell densities from each lake, identified to species level when possible. Phytoplankton $< 2\text{--}3\ \mu\text{m}$ in greatest linear dimension were eliminated from the analysis because of taxonomic ambiguity. Total densities for each algal division (Chlorophyta, Cyanophyta, Chrysophyta, Dinophyta, Bacillariophyta, and Cryptophyta) were included as supplementary taxonomic variables (i.e., no influence on the ordination plot), and all taxonomic data were log-transformed to stabilize variance and reduce the influence of dominant taxa on the ordination (ter Braak, 1995).

The full environmental data set included physical and water chemistry variables listed in Table 1. Species richness, diversity, PN:PP, and chlorophyll *a* were excluded from the environmental data set. Additionally, PC and silica were unavailable for one lake and could not be used in the RDA. The remaining variables were standardized (mean = 0, standard deviation = 1) and subjected to a data screening procedure in order to reduce the number of environmental variables and minimize redundancy within the environmental data set (Hall and Smol, 1992). This screening procedure identified groups of correlated variables, tested which variable(s) from each group explained significant variation in species composition, and generated a modified environmental data set (see Table 1). An RDA of the modified environmental data set was performed using forward selection to identify the variables that best explained phytoplankton species composition. Variables with P -values > 0.1 were excluded from the model. A final RDA was conducted using environmental variables selected during forward selection, and the significance of the first ordination axis was determined using Monte Carlo permutation testing (199 permutations). An ordination triplot was generated and included taxa for which at least 25% of the variation was explained by the ordination.

TABLE 2
(Extd.)

Si	NH ₄ -N	NO ₃ -N	DIN	PN	PO ₄ -P	DOP	TDP	PP	TP	DINTP	CHL-a	Rich	D
1.000													
-0.041	1.000												
-0.136	0.065	1.000											
-0.136	0.507	0.893	1.000										
-0.625	0.304	0.027	0.160	1.000									
0.530	0.210	-0.096	0.012	-0.097	1.000								
0.410	0.212	-0.110	0.001	0.026	0.982	1.000							
0.461	0.212	-0.105	0.005	-0.024	0.994	0.997	1.000						
-0.707	0.141	0.538	0.529	0.672	-0.210	-0.112	-0.153	1.000					
0.104	0.270	0.156	0.256	0.296	0.850	0.899	0.883	0.329	1.000				
-0.008	0.633	0.418	0.647	-0.147	-0.316	-0.366	-0.347	-0.008	-0.335	1.000			
-0.495	0.133	0.213	0.244	0.840	-0.267	-0.171	-0.211	0.666	0.115	0.000	1.000		
-0.266	-0.182	-0.528	-0.538	0.106	0.039	0.127	0.091	-0.145	0.018	-0.458	-0.103	1.000	
0.157	0.020	-0.683	-0.580	-0.201	0.128	0.180	0.160	-0.546	-0.107	-0.166	-0.363	0.720	1.000

Results

ENVIRONMENTAL VARIABLES

The study lakes showed considerable variation in physical characteristics but tended to be small and shallow, averaging 6.40 ± 5.16 ha in surface area and 3.7 ± 2.9 m in mean depth (Table 1). The lakes were all situated above 3100 m and spanned an elevation gradient of <200 m. Elevation was not significantly correlated with any lake physical characteristics (Table 2).

The survey lakes were cold and relatively dilute, as is typical of mountain lakes. Epilimnetic water temperature averaged $13.8 \pm 3.6^\circ\text{C}$, and conductivity and alkalinity averaged $11.33 \pm 6.16 \mu\text{S cm}^{-1}$ and $94.18 \pm 59.82 \mu\text{eq L}^{-1}$, respectively (Table 1). pH was neutral or slightly basic in most lakes (Tables 1 and 3, Appendix A). DOC values were generally low, averaging $1.86 \pm 1.20 \text{ mg L}^{-1}$. Chlorophyll *a* was variable across the study lakes, averaging $6.24 \pm 5.25 \mu\text{g L}^{-1}$ and ranging from 0.89–16.57 $\mu\text{g L}^{-1}$. Inorganic N concentrations, including NH₄-N, NO₃-N, and total dissolved inorganic nitrogen (DIN), were generally low, and NO₃-N was below detection in several lakes (Appendix A). PO₄-P and DOP varied greatly and were occasionally below detection limit (Table 1, Appendix A). Total phosphorus (TP) was moderately high (Wetzel, 2001), averaging $30 \pm 20 \mu\text{g L}^{-1}$ across the study lakes.

Several groups of related variables were identified from the correlation matrix (Table 2). Physical and morphometric characteristics were positively and significantly correlated among the study lakes. Conductivity, alkalinity, and pH were all positively correlated and were generally higher at lower elevations. Inorganic N components were positively correlated with one another and did not relate significantly to elevation. Total DIN was more strongly correlated with NO₃-N than with NH₄-N. Both DIN and NH₄-N were negatively associated with pH. Components of phosphorus chemistry (PO₄-P, DOP, TDP, TP) and DOC were positively correlated with one another.

Chlorophyll *a* was positively associated with PN, PP, and PC but was unrelated to dissolved forms of N or P. Chlorophyll *a*, PN, and PP tended to be higher in higher-elevation lakes.

NUTRIENT LIMITATION

Based on DIN:TP ratios, we estimate that phytoplankton growth in all but 1 of the 15 study lakes was either N limited or N + P colimited. Phytoplankton growth in 5 lakes was primarily N limited (DIN:TP ratios ≤ 0.5), and only one lake had a DIN:TP ratio predictive of P limitation (DIN:TP ratio ≥ 4.0) (Fig. 2). Phytoplankton growth in 9 lakes was colimited by both N and P (intermediate DIN:TP ratios). DIN:TP was not significantly correlated with other environmental variables (Table 2); however, in many cases DIN:TP was positively related to both forms of inorganic nitrogen (NH₄-N and NO₃-N) and negatively correlated with temperature and DOC. Redfield Ratios (PN:PP), calculated for comparison, were indicative of N limitation for all 15 study lakes (Appendix A).

PHYTOPLANKTON COMPOSITION

A total of 96 phytoplankton taxa were encountered in the study lakes (Appendix B). The majority of phytoplankton taxa belonged to the divisions Chlorophyta and Chrysophyta; fewer representatives were identified from Bacillariophyta and Cyanophyta, and very few cryptophytes or dinoflagellates were encountered. Species richness and Simpson's *D* averaged 27 ± 8 and 0.75 ± 0.15 , respectively, across the study lakes (Table 1). Neither measure was significantly correlated with any environmental variable; however, both showed weakly negative relationships with NO₃-N, DIN, and DIN:TP (Table 2).

The RDA using forward selection and the screened environmental data yielded two significant environmental variables, DIN ($F = 1.974$, $P = 0.010$) and PN ($F = 2.010$, $P = 0.005$). Together, these two

TABLE 3

Names and abbreviations for lakes of the Wyoming Snowy Range ($n = 15$) sampled once for chemistry and phytoplankton during early summer 2001. Refer to Figure 1 for study lake locations

Lake abbreviation	Lake name
CLA	Class
HRT	Heart
LIB	Libby
LTL	Little Telephone
MSFC	Middle South Fork Rock Creek
MUT	Mutt
NGAP	North Gap
RES	Reservoir
SGAP	South Gap
SH1	Shelf 1
SH2	Shelf 2
SH4	Shelf 4
SHP	Sheep
TLN	Twin Lake North
WKL	West Klondike

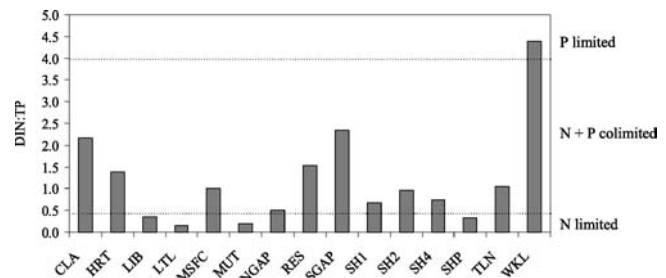


FIGURE 2. DIN:TP ratios measured from the water column of 15 Wyoming Snowy Range lakes soon after ice-out in spring 2001. Dotted lines delineate phytoplankton nutrient limitation delineations (Sickman, 2001). DIN:TP ratios ≤ 0.5 predicted N limitation, whereas DIN:TP ratios ≥ 4.0 predicted P limitation. Intermediate DIN:TP ratios predicted colimitation by both N and P. Lake abbreviations are found in Table 3.

cyanophyte *Anabaena* sp. Bory (Fig. 3). N-limited lakes tended to be chrysophyte-cryptophyte dominated (Fig. 3); P-limited and N + P colimited lakes had less distinct assemblage types.

variables accounted for 31% of the variation in the phytoplankton species data. The first RDA axis ($\lambda_1 = 0.148$) was significant ($P = 0.005$) and described a gradient of N concentration (both DIN and PN) (Fig. 3). Taxa associated with high concentrations of DIN and PN were primarily cyanophytes and chlorophytes, whereas taxa associated with low N concentrations were almost exclusively chrysophytes (Fig. 3, Table 4). The second RDA axis ($\lambda_2 = 0.108$) accounted for slightly less of the variation in species data and contrasted taxa in high-PN lakes with taxa in high-DIN lakes. Taxa associated with high DIN but relatively lower PN included the snow alga *Chlamydomonas nivalis* Wille, the cryptophyte *Chroomonas* sp. Ehrenberg, and a small chrysophyte flagellate. Conversely, taxa associated with low DIN but higher PN included several cryptophytes, a centric diatom, and the

Discussion

Our analysis of nutrient ratios (DIN:TP) supported experimental findings that phytoplankton biomass is regulated by N or N + P in many Snowy Range lakes (Lafrancois, 2002). We found DIN:TP ratios predictive of N limitation in one-third of the surveyed lakes and ratios predictive of P limitation in only 1 lake. The majority of the lakes surveyed exhibited DIN:TP ratios indicative of N + P colimitation. In this survey Shelf Lake 4 had a DIN:TP ratio indicative of N + P colimitation, but nutrient enrichment experiments in July and August 2000 provided strong evidence of limitation by N alone in this lake. This slight dissimilarity between nutrient limitation as assessed by summer nutrient

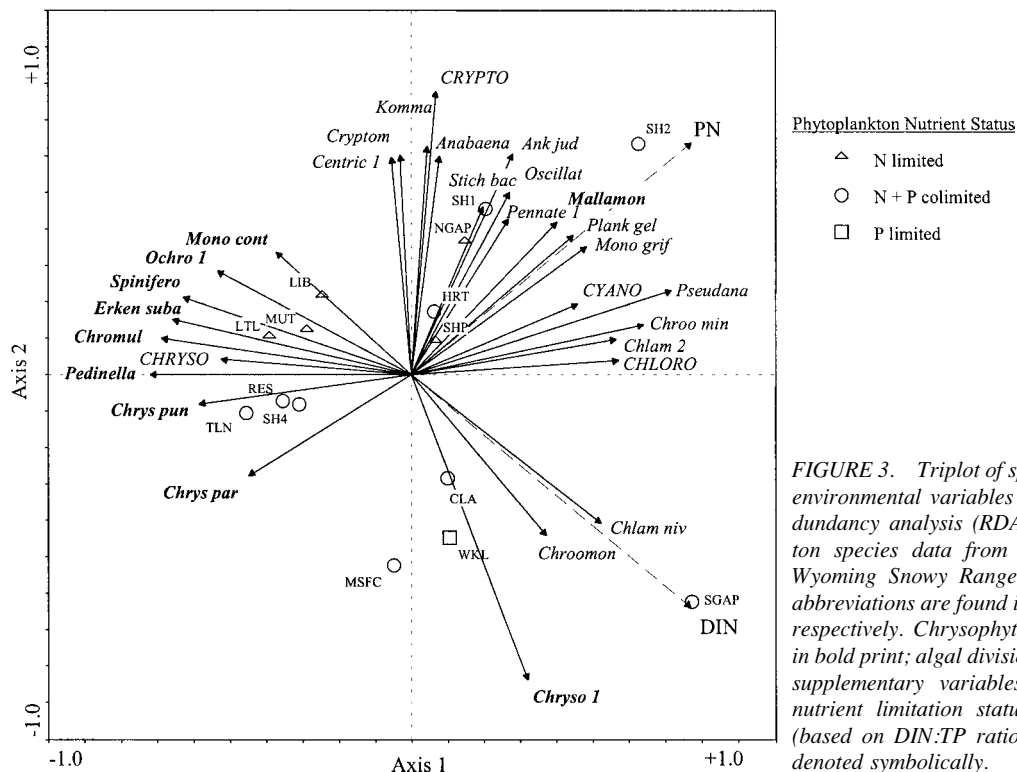


FIGURE 3. Triplot of species, lakes, and environmental variables derived from redundancy analysis (RDA) of phytoplankton species data from 15 lakes in the Wyoming Snowy Range. Lake and taxa abbreviations are found in Tables 3 and 4, respectively. Chrysophyte taxa are noted in bold print; algal divisions are plotted as supplementary variables. Phytoplankton nutrient limitation status for each lake (based on DIN:TP ratios; see Fig. 2) is denoted symbolically.

enrichment experiments versus spring DIN:TP ratios supports our assertion that spring DIN:TP ratios conservatively estimate N limitation for the entire ice-free season, and also suggests that N limitation in Snowy Range lakes may increase throughout the summer months.

Other cases of phytoplankton N limitation in western mountain lakes have been reported from Yellowstone National Park, Wyoming (Kilham et al., 1996), the Sawtooth Mountains, Idaho (Wurtsbaugh et al., 1997), the Sierra Nevada Mountains, California (Axler et al., 1981; Goldman et al., 1993), and the western slope of the Colorado Front Range (Morris and Lewis, 1988). Subalpine lakes on the eastern slope of the Colorado Front Range, however, appear to have a lower incidence N limitation (Nydick, 2002). Further, Snowy Range lakes showed a gradient of nutrient limitation, from highly N limited to N + P or slightly P limited in our early summer survey.

Variation in phytoplankton nutrient limitation among mountain lakes may be linked to regional atmospheric deposition as well as localized watershed characteristics. Deposition of atmospheric N, for example, is implicated in a gradual shift from N limitation toward P limitation in Lake Tahoe (Goldman et al., 1993), and a similar process may be responsible for the P and N + P limitation found in lakes on the eastern slope of the Colorado Front Range (Nydick, 2002). Sickman et al. (2003) suggest that P deposition at Emerald Lake, Sierra Nevada, has caused a shift toward more frequent N limitation and greater phytoplankton biomass. Variation in N and P deposition among Snowy Range lakes, however, has never been addressed, and the role of nutrient deposition in determining phytoplankton nutrient limitation of these waters is unclear.

Watershed characteristics, particularly slope and vegetation cover, have also been used effectively to explain nutrient limitation in mountain lakes. Lakes with steep, rocky watersheds tend to have higher N concentrations and higher proportions of nitrate-N than lakes with gently sloping, vegetated watersheds (Marchetto et al., 1995; Clow and Sueker, 2000; Kamenik et al., 2001; Sickman et al., 2002), and are unlikely to be N limited (Kopáček et al., 2000). Conversely, lakes with vegetated catchments tend to have higher organic carbon and TP concentrations and lower nitrate levels (Clow and Sueker, 2000; Sickman et al., 2002); these are more likely to be N limited (Kopáček et al., 2000). In our study, higher DOC and dissolved P concentrations, typical of lakes with vegetated watersheds, corresponded with low DIN:TP ratios and N limitation, offering indirect evidence that watershed characteristics affected nutrient limitation in our study.

Consistent with our initial hypotheses, RDA analysis indicated that phytoplankton composition was closely associated with N availability across Snowy Range lakes. PN and DIN accounted for more of the variation in species composition than any other environmental characteristic. Further, phytoplankton taxa were distributed predictably across N gradients, with higher relative abundance of chrysophytes occurring in low N conditions and higher relative abundance of chlorophytes and cyanophytes at higher N levels. Such taxa distributions are similar to composition changes noted in N-addition enclosure experiments in two Snowy Range lakes (Lafrancois, 2002) and whole-lake fertilization experiments in other areas (Schindler, 1975; Findlay and Kasian, 1987; Cottingham et al., 1998). These patterns are generally attributed to differences in nutrient physiology; chrysophytes commonly dominate in nutrient-poor conditions due to their small size and large surface area:volume ratios (Sandgren, 1988), whereas many cyanophytes and chlorophytes have higher N optima and thrive in higher nutrient conditions (Reynolds, 1984).

Our analysis also demonstrated a difference in how phytoplankton composition was related to two forms of N (DIN versus PN) across lakes. In general, high DIN was associated with isolated

TABLE 4

Abbreviations and full taxonomic names for phytoplankton taxa and groups included in the redundancy analysis (RDA) triplot (Fig. 3) generated from a survey of Wyoming Snowy Range lakes ($n = 15$). At least 25% of the variation in distribution of these taxa among the study lakes was explained by the ordination. Division-level taxonomic variables were included as supplementary variables and had no influence on the ordination

Taxon abbreviation	Taxon
<i>Anabaena</i>	<i>Anabaena</i> spp.
<i>Ank jud</i>	<i>Ankara judayi</i>
<i>Centric 1</i>	Indeterminate Centrales 1
<i>Chlam 2</i>	<i>Chlamydomonas</i> sp. 2
<i>Chlam niv</i>	<i>Chlamydomonas nivalis</i>
<i>Chromul</i>	<i>Chromulina</i> sp.
<i>Chroo min</i>	<i>Chroococcus minimus</i>
<i>Chroomon</i>	<i>Chroomonas</i> sp.
<i>Chrys par</i>	<i>Chrysoschromulina parva</i>
<i>Chrys pun</i>	<i>Chrysococcus punctiformis</i>
<i>Chryso 1</i>	Indeterminate Chrysophyte 1
<i>Cryptom</i>	<i>Cryptomonas</i> sp.
<i>Erken sub</i>	<i>Erkenia subaequiciliata</i>
<i>Komma</i>	<i>Komma</i> sp.
<i>Mallamon</i>	<i>Mallomonas</i> sp. 3
<i>Mono cont</i>	<i>Monoraphidium contortum</i>
<i>Mono grif</i>	<i>Monoraphidium griffithii</i>
<i>Ochro 1</i>	<i>Ochromonas</i> sp. 1
<i>Oscillat</i>	<i>Oscillatoria</i> spp.
<i>Pedinella</i>	<i>Pedinella</i> spp.
<i>Pennate 1</i>	Indeterminate Pennales 1
<i>Plank gel</i>	<i>Planktosphaeria gelatinosa</i>
<i>Pseudana</i>	<i>Pseudanabaena</i> spp.
<i>Spinifero</i>	<i>Spiniferomonas</i> sp.
<i>Stich bac</i>	<i>Stichococcus bacillaris</i>
CHRYSO	Chrysophytes (total)
CYANO	Cyanophytes (total)
CHLORO	Chlorophytes (total)

chrysophyte and cryptophyte taxa and the snow alga *Chlamydomonas nivalis* Wille. DIN likely affected phytoplankton composition directly, via N uptake and increased abundance of taxa with high N requirements as described above. Alternatively, high DIN was also associated with low water temperatures and characteristically cold-water algal taxa among our study lakes. The close association between DIN, South Gap Lake, and the snow alga *Chlamydomonas nivalis* Wille, for example, points toward recent hydrologic inputs from nearby persistent snow and ice fields and suggests that the strong relationship of DIN to phytoplankton composition may be partially attributable to corresponding low water temperatures and early snowmelt stage.

High PN, on the other hand, was associated with a suite of taxa overwhelmingly similar to those that responded positively to nitrate enrichment in previous enclosure experiments (Lafrancois, 2002). Since algae are not thought to utilize PN as a source of N (Morris and Lewis, 1988), the link between phytoplankton composition and PN was most likely indirect. Positive correlations between PN, PP, PC, and algal biomass (as chlorophyll *a*) suggest that high availability of DIN prior to our survey increased the accumulation of phytoplankton biomass and favored shifts in phytoplankton composition toward dominance by chlorophytes and cyanophytes. Similarly, nutrient enrichment/acidification experiments in Snowy Range lakes showed greater algal biomass accumulation, higher PN, and more pronounced species shifts in N-treated enclosures versus control and P-treated enclosures (Nydick, 2002).

In summary, this survey indicates that N and N + P limitation are likely prevalent among Snowy Range lakes and reveals close relationships between N chemistry and phytoplankton species composition. These findings corroborate results from previous nutrient addition experiments in the Snowy Range and suggest that increases in N deposition would have significant effects on phytoplankton biomass and community structure in the Snowy Range. Further, our experimental and survey work in the Snowy Range has spanned time periods ranging from early to late summer, indicating that phytoplankton N limitation and strong species-N relationships may persist and/or increase throughout the ice-free season. Given the predominance of N limitation, the relatively high ambient levels of available P, and the potential for strong N + P interactions in remote and sensitive lakes of the Snowy Range, future trends in N deposition and watershed N retention in the region should be closely monitored.

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APPENDIX A

Characteristics of Wyoming Snowy Range lakes (n = 15) surveyed for water chemistry and phytoplankton in early July 2001. Abbreviations for environmental variables and lakes are found in Tables 1 and 3, respectively

Variable	ELEV	SA	D _{max}	D _{mean}	VOL	SA:VOL	COND	ALK	pH	TEMP	DOC	PC	Silica	NH4-N	NO3-N	DIN	PN	PO4-P	DOP	TDP	PP	TP	DIN:TP	PN:PP	CHL-a	Richness	Simpson's
units	m	ha	m	m	m ³		µS cm ⁻¹	µeq L ⁻¹		°C	mg L ⁻¹	µg L ⁻¹	mg L ⁻¹	µg L ⁻¹	µg L ⁻¹	µg L ⁻¹	µg L ⁻¹	µg L ⁻¹	µg L ⁻¹	µg L ⁻¹	µg L ⁻¹	µg L ⁻¹		µg L ⁻¹		D	
CLA	3273	1.42	4.57	1.02	14358	0.99	12.90	125.12	7.15	12.50	0.70	543	0.89	21	27	48	90	0	5	5	17	22	2.16	5.21	3.26	28	0.88
HRT	3274	4.90	13.72	5.50	269476	0.18	6.70	39.21	8.35	11.00	1.00	644	1.88	9	16	25	136	0	3	3	15	18	1.38	8.93	16.57	23	0.69
LIB	3277	10.32	12.20	4.85	500665	0.21	17.40	168.08	8.02	13.90	1.16	581	1.08	6	0	6	99	1	4	5	12	17	0.35	7.95	4.61	41	0.88
LTL	3262	3.40	3.66	1.65	58837	0.58	18.70	129.62	7.85	15.70	2.30	682	0.78	3	0	3	67	1	5	6	15	21	0.14	4.58	2.36	38	0.90
MSFC	3270	1.57	0.91	0.70	10990	1.43	12.10	112.66	7.18	12.20	1.81	265	2.78	22	29	51	44	15	20	35	15	50	1.01	2.85	1.39	21	0.58
MUT	3241	6.52	2.13	1.14	74440	0.88	7.60	35.41	7.21	19.40	3.57	474	1.56	7	1	8	83	8	15	23	17	40	0.20	4.82	4.66	22	0.68
NGAP	3317	13.04	20.43	6.32	823058	0.16	6.90	52.77	7.21	11.10	1.32	842	0.06	20	1	21	168	0	5	5	36	41	0.52	4.71	12.19	30	0.74
RES	3284	11.70	25.00	9.03	1054666	0.11	10.60	89.16	7.14	13.70	1.20	189	1.42	12	1	13	53	1	0	1	7	8	1.54	7.07	1.34	18	0.61
SGAP	3338	17.94	21.34	6.75	1210281	0.15	6.10	28.25	6.78	5.50	0.50	1212	0.41	17	84	101	143	0	3	3	40	43	2.34	3.58	11.44	15	0.37
SH1	3345	1.15	8.84	3.66	42172	0.27	7.60	88.74	7.46	15.00	1.38	880	0.44	20	0	20	186	0	5	5	24	29	0.68	7.62	9.15	31	0.66
SH2	3345	2.35	5.49	1.90	44676	0.53	7.10	65.68	7.32	14.30	3.53	940	0.54	32	3	35	262	2	7	9	27	36	0.97	9.72	15.08	25	0.71
SH4	3313	1.17	3.35	1.49	17417	0.67	11.00	80.55	7.04	14.10	1.70	—	—	15	1	16	58	2	8	10	11	21	0.75	5.14	2.06	40	0.89
SHP	3284	7.49	1.22	0.45	33526	2.23	10.70	86.44	7.20	20.40	4.66	253	2.20	29	0	29	127	28	45	73	13	86	0.34	10.03	4.28	31	0.90
TLN	3159	3.28	13.41	8.08	264863	0.12	28.50	257.74	8.11	16.80	2.10	817	2.65	9	0	9	36	0	1	1	8	9	1.05	4.73	0.89	22	0.86
WKL	3277	9.72	6.10	2.41	23547	4.13	6.10	53.20	6.96	11.10	0.92	450	1.45	47	9	56	73	0	1	1	12	13	4.39	6.22	4.34	24	0.83

Taxa list, categorized according to algal Division, generated from
a survey of Wyoming Snowy Range lakes (n = 15) conducted in early
July 2001

Chlorophytes

Ankistrodesmus falcatus (Corda) Ralfs
Ankyra judayi (G.M. Smith) Fott
Carteria sp. Diesing
Chlamydomonas nivalis Wille
Chlamydomonas sp.1 Ehrenberg
Chlamydomonas sp.2 Ehrenberg
Chlamydomonas sp.3 Ehrenberg
Chlorella sp. Beijerinck
Chlorella vulgaris Beijerinck
Coelastrum astroideum de Notaris
Cosmarium bioculatum Brébisson
Cosmarium spp. Corda
Dictyosphaerium spp. Nägeli
Dictyosphaerium subsolitarium Van Goor
Elakotrix genevensis (Reverdin) Hindák
Eudorina elegans Ehrenberg
Franceia droescheri (Lemmermann) G. M. Smith
Gonium sociale (Dujardin) Warming
Kirchneriella sp. Schmidle
Lagerheimia genevensis Chodat
Micractinium pusillum Fresenius
Monoraphidium contortum (Thuret) Komárková-Legenerová
Monoraphidium griffithii (Berkeley) Komárková-Legenerová
Oocystis sp. Nägeli
Planktosphaeria gelatinosa G. M. Smith
Quadrigula sp. Printz
Scenedesmus bicellularis Chodat
Scenedesmus spp. Meyen
Selenastrum capricornutum Printz
Sphaerocystis Schroeteri Chodat
Spondylosium planum (Wolle) W. & G. S. West
Staurastrum sp. Meyen
Stichococcus bacillaris Nägeli
Tetraspora lemmermannii Fott
Westella sp. de Wildeman

Chrysophytes

Chromulina sp. Cienkowski
Chrysamoeba sp. Klebs
Chrysochromulina parva Lackey
Chrysococcus punctiformis Pascher
Chrysococcus spp. Klebs
Chrysolykos sp. Mack
Diacronema spp. Prauser
Diceras sp. Reverdin
Dinobryon cylindricum Imhof
Dinobryon divergens Imhof
Epipyxis sp. Ehrenberg
Erkenia subaequiciliata Skuja
Kephyrion boreale Skuja
Mallomonas akrokomos Ruttner
Mallomonas sp. 1 Perty
Mallomonas sp. 2 Perty
Mallomonas sp. 3 Perty
Ochromonas miniscula Conrad
Ochromonas sp. 1 Wyssotzki
Ochromonas sp. 2 Wyssotzki
Pedinella spp. Wyssotzki
Pseudokephyrion ellipsoideum (Pascher) Schmid
Spiniferomonas sp. Takahashi
Synura sp. Ehrenberg
Indeterminate Chrysophyte 1
Indeterminate Chrysophyte 2

(Cont.)

Cryptophytes

Chroomonas sp. Hansgirg
Cryptomonas sp. Ehrenberg
Komma sp. Hill

Cyanophytes

Anabaena spp. Bory
Aphanothece sp. Nägeli
Aphanocapsa sp. Nägeli
Chroococcus distans (G. M. Smith) Komárková-Legenerová
Chroococcus minimus (Kiessler) Lemmermann
Microcystis sp. Kützing
Nostoc sp. Vaucher
Oscillatoria spp. Vaucher
Pseudanabaena spp. Lauterborn
Rhabdoderma spp. Schmidle et Lauterborn
Spirulina spp. Turpin
Synechococcus sp. Nägeli

Diatoms (Bacillariophytes)

Asterionella formosa Hassall
Cocconeis sp. Ehrenberg
Cymbella sp. Agardh
Diatoma sp. Bory de St. Vincent
Fragilaria spp. Lyngbye
Gomphonema sp. Ehrenberg
Meridion sp. Agardh
Nitzschia sp. Hassall
Rhizosolenia sp. Ehrenberg
Surirella sp. Turpin
Synedra sp. Ehrenberg
Tabellaria sp. Ehrenberg ex Kützing
Indeterminate Centrales 1
Indeterminate Centrales 2
Indeterminate Pennales 1
Indeterminate Pennales 2

Dinoflagellates (Dinophytes)

Gymnodinium sp. 1 Stein
Gymnodinium sp. 2 Stein