

Responses of phytoplankton to varied resource availability in large lakes of the Greater Yellowstone Ecosystem

Sebastian J. Interlandi and Susan S. Kilham

School of Environmental Science, Engineering, and Policy, Drexel University, Philadelphia, Pennsylvania 19104

Edward C. Theriot

Texas Memorial Museum, University of Texas, Austin, Texas 78705

Abstract

We assessed phytoplankton dynamics in three lakes in the Greater Yellowstone Ecosystem to better understand the connections between changing environmental conditions and aquatic communities. This work primarily describes the connections between resource availability and phytoplankton seasonal succession in these lakes. We hypothesized that algal species efficient at utilizing a given resource (including N, P, Si, and light) would be correlated with low relative concentrations of those resources. The lakes generally exhibited moderate resource limitation, which is characteristic of lakes in subalpine and subarctic regions. Although in proximity, the lakes all exhibited different resource relationships: Lewis Lake was most P limited, Jackson Lake was most N limited, and Yellowstone Lake exhibited a moderate degree of N limitation along with periodic Si limitation. Mixing depths and light penetration were also variable among lakes. In 1996, spring diatom biomass was dominated by *Stephanodiscus minutulus*, *Asterionella formosa*, *Aulacoseira subarctica*, and *Synedra* sp. Relative abundances and dominance varied among the lakes. *A. formosa* and *Synedra* sp. abundances were positively correlated with total N:total P (TN:TP) levels in an analysis of data from all three lakes. *A. subarctica* was negatively correlated with TN:TP and all light:nutrient ratios. Species exhibiting late season maxima included *Cyclotella bodanica*, *Fragilaria crotonensis*, and *Stephanodiscus niagarae*. *C. bodanica* abundances corresponded to high-light/low-N situations, whereas *S. niagarae* maxima were found in high-TN:TP/low-light conditions. *F. crotonensis* abundances were most strongly positively correlated with total Si:TP and TN:TP. Environmental correlations were generally in good agreement with the measured physiological requirements of these species. Additionally, local population maxima of major species of diatoms never coincided.

Seasonal succession of phytoplankton has been extensively studied and is generally assumed to be a function of changing environmental variables, including but not limited to temperature, light, nutrients, mixing, and herbivory. A number of investigators have attempted to quantitatively correlate these environmental factors with individual species' abundance and relative dominance with a modest degree of success (Lund 1954; Reynolds 1976; Tilman 1977, 1982; Talling 1987; Sommer 1993). Following these and other examples, we analyzed phytoplankton dynamics over one season in three lakes in the Greater Yellowstone Ecosystem (GYE) to determine whether species-specific patterns could be correlated with measured environmental parameters and whether these patterns were consistent with experimental observations of the physiology of particular species of phytoplankton.

Mechanistic resource competition theory (Tilman 1982)

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has been a major paradigm in research attempting to explain the patterns of distribution and succession seen in phytoplankton (Kilham 1986; Sommer 1993, 1994). Both experimental and field data have been used in tests of the importance of these mechanisms, but there is a lack of concurrent research that looks at both field and experimental data on individual species and assemblages from the same system. Tilman (1977) demonstrated a link between experimental observations of clonal cultures and field observations with two species of diatoms along an Si:P gradient. Similarly, Kilham (1986) demonstrated that patterns seen in Lake Michigan phytoplankton could be duplicated in laboratory experiments by varying the Si:P gradient for natural communities in chemostats. Sommer (1993) expanded the empirical approach by finding connections between a wide range of species and several resource ratios under limiting conditions but did not attempt to make connections between species- or group-specific physiology and field observations.

The limitations of using field measurements of resource ratios as evidence for control of phytoplankton community structure are outlined by Sommer (1993). Problems include skewed or otherwise nonnormal data distributions and the need to demonstrate that competition for the measured resources has occurred in the system. The latter requirement calls for at least a general understanding of the physiology of the organisms in terms of knowing the upper range of limiting concentrations of individual resources. A fair understanding of the resource physiology of the major diatom

species discussed in this article has developed through numerous laboratory experiments (Tilman and Kilham 1976; Kilham 1984; Mechling and Kilham 1982; van Donk and Kilham 1990; and others). Although current knowledge of N physiology of these diatoms is limited, recent studies have shed some light on N requirements (Taylor 1994; H. Roh pers. comm.). As a result, it is apparent that inorganic N concentrations of $<10 \mu\text{M}$ are at potentially limiting levels for phytoplankton.

The three lakes studied were Yellowstone and Lewis Lakes in Yellowstone National Park and Jackson Lake in Grand Teton National Park, all large, subalpine, temperate lakes (Kilham et al. 1996). Species assemblages are similar among lakes, although abundances and relative dominance vary. Although the focus of the analysis here is on the diatom species, the ecology of other planktonic species is considered as well.

Kilham et al. (1996) described these lakes as high-Si, high-P, and N-limited systems. The watersheds of the three lakes are geologically similar and primarily composed of rhyolite and other Si- and P-rich volcanic deposits. Although Jackson Lake sits at the base of the metamorphic Teton Range, its water chemistry is driven by flows originating in the upper Snake River basin on the Yellowstone Plateau. Concentrations of N in these mountain lakes are much lower than in most North American temperate lakes for a variety of reasons, including regionally low levels of atmospheric N deposition and nutrient-poor soils within the lake basins. The climate in the region is more subarctic than temperate because of the elevation. As a result, the water chemistry and temperature profiles of these lakes are generally more similar to those of subarctic lakes (Hecky et al. 1993) than to more-often-studied temperate lakes.

Kilham et al. (1996) presented general hypotheses concerning the links between the physicochemical environments and the observed phytoplankton distributions in these lakes. They suggested that N, Si, and light are all major factors that directly drive species assemblages. They further suggested that it might be possible to link seasonal and inter-annual variability in the aquatic environment to regional climatology with the ultimate goal of reconstructing long-term climate variability through correlations between the diatom fossil record and current phytoplankton populations. Toward this goal, we have attempted to test some phytoplankton–resource connections. We tested these hypotheses by obtaining and analyzing fine-scale data in time and vertical space for both chemical parameters and phytoplankton abundances.

The approach taken here is first to describe the physical and chemical dynamics within the lakes. Elemental stoichiometry of the seston is given the broadest treatment, because Kilham (1990), Hecky et al. (1993), and Lampert and Sommer (1997) all contend that planktonic elemental ratios are good metrics for understanding relative degrees of resource limitation in natural phytoplankton communities. Next, species distributions are illustrated and considered in terms of general limnological patterns in the lakes. Lastly, empirical relationships between resource availability and species and group abundances are sought, and the causal factors behind correlations are considered in terms of the experimental

physiological ecology of the species and groups. Physiological arguments are used when possible to explain field observations. Patterns that do not seem to follow prior experimental evidence are discussed in terms of alternate mechanisms. We do not suppose that resource competition is the only mechanism occurring. Among other processes, size selection and food quality selection by zooplankton are bound to occur. Additionally, it is understood that parasites and protozoans can significantly decrease an individual species' ability to grow in the natural environment (Reynolds 1984). Regrettably, there was no way to quantify these other factors in this analysis.

Methods

Field collection—In 1996, field samples were collected at weekly intervals in Jackson and Yellowstone Lakes. Samples were taken somewhat less frequently (every 10–12 d) in Lewis Lake. One main pelagic station was sampled in each lake during every outing. Additional sites were sampled occasionally in Yellowstone and Jackson Lakes to assess spatial heterogeneity within the lakes. Temperature, dissolved oxygen, and pH were measured via a multiparameter sonde (Hydrolab Surveyor II) at 1-m intervals down to 30 m in all lakes. Additional measurements were made to 50 m in Yellowstone Lake. Samples for phytoplankton counts were taken at 5-m intervals from the surface to 50 m in Yellowstone Lake, to 30 m in Jackson Lake, and to 25 m in Lewis Lake. Samples for nutrient chemistry were taken at 5 and 25 m in all lakes and at 45 m in Yellowstone Lake. Midsummer samples at 15 m were taken in Jackson Lake (five samples) and Lewis Lake (three samples). Chemistry samples were collected in 4-liter polypropylene bottles and stored in a cooler on board before processing. Water was sampled by means of a nondestructive peristaltic pump mounted on deck. The submerged end of the pump hose was fastened to the sonde (with depth sensor) to maintain accurate and consistent collection depths. Samples were taken at the main stations from ice-out (late May to early June) through mid-October. Before ice-out, samples were collected at the outlets of the lakes beginning in early May. Secchi depths were measured on all excursions, and light was measured with a photosynthetically active radiation (PAR) meter (LICOR LI-1000, Quantum Sensors) from midsummer through fall.

Our intensive sampling scheme was used to ensure that no “inflection points” were missed in either phytoplankton abundances or nutrient concentrations. Knowing when peaks in particular species abundances and rates of increase are occurring is crucial to our understanding of how these organisms are reacting to changing environmental conditions throughout the summer. Samples were taken at discrete intervals and not at points around the thermocline or other critical regions because such a process-based sampling strategy would tend to bias results in favor of high abundance counts for species that reside in these critical regions.

Sample processing and analysis—Phytoplankton samples were immediately fixed with Lugol's solution. Phytoplankton counts were performed using the inverted-microscope technique. Fixed whole-water samples, 25 ml from Lewis

and Yellowstone Lakes and 10 ml from Jackson Lake, were allowed to settle. Small coccoid cyanobacteria abundances were estimated at a magnification of $\times 400$ by counting several random view fields in the chamber. Other small algae, including *Stephanodiscus minutulus*, and small flagellates were counted at $\times 400$ over one viewing strip of the chamber. Larger phytoplankton were counted at $\times 100$ by scanning the entire chamber to count all organisms in the subsample. Once counts for a set of samples (1 d, one location) were completed, aliquots of preserved samples from all depths were pooled and preserved in Lugol's solution for later checks of taxonomic identification and cell size estimates.

Samples for chemical analysis were filtered and frozen within a few hours of collection. Samples for dissolved nutrient analyses were filtered by means of syringe filtration through 0.4- μm polycarbonate filters and frozen in 125-ml polypropylene bottles. Triplicate polycarbonate filters were saved for analysis of particulate P and particulate Si. Samples for particulate C and N analysis were filtered onto preashed GF/F filters by vacuum filtration. All filters were visually examined before freezing, and all visible zooplankton were removed. The zooplankton in these lakes are generally large, including *Daphnia magna* and *Diatomus shoshone*, so it is likely that manual removal is better in this case than prescreening, because many of the phytoplankton in these lakes are colonial forms of diatoms and cyanobacteria that would be partially removed by screening.

Samples for dissolved N (nitrate plus nitrite) were analyzed with cadmium reduction followed by colorimetric determination of nitrite. Ammonia was not measured, because previous analyses showed these lakes to have concentrations at or below detection limits. Inorganic N in early spring samples may be slightly underestimated as a result. Dissolved P was measured as soluble reactive phosphorus (SRP) by the ascorbic acid method. Dissolved Si was measured after sample dilution by the molybdosilicate method (APHA 1995). Particulate N and C were measured by combustion and gas chromatography on a Carlo Erba 1106 elemental analyzer (Stainton et al. 1977). Subsamples were punched from three GF/F filters for each C:N sample, and each subsample was run separately on the analyzer, so measurements are in triplicate for each sample. Particulate P was converted to reactive P by permanganate oxidation and then analyzed as dissolved P (American Public Health Association (APHA) 1995). Particulate Si was digested with a 5% sodium carbonate (w/w) solution, followed by acidification and analysis as dissolved Si (Conway et al. 1977). Biogenic silica is not reported because only total particulate Si was measured. Both rhyolite (the dominant source of nonbiogenic Si in these lakes) and diatom frustules are made of amorphous silicate, so it is unlikely that the two can be accurately separated by standard methods, which rely on differing rates of dissolution for the different sources of Si. Furthermore, sample sites were far (>2 km) from terrestrial inputs, so mineral interference is a small concern.

Total nutrient levels reported are dissolved plus particulate values. As such, total N (TN) is nitrate plus nitrite plus particulate N and does not include ammonia N or dissolved organic N, which were not measured. Total P is SRP plus

particulate P. Total Si (TSi) is soluble reactive silica (SRSi) plus particulate Si.

Data analysis—Statistical analyses were performed using JMP for the Macintosh (SAS Institute). Standard errors reported were calculated using a pooled error variance through an analysis of variance comparing the parameter of interest among lakes. Care was taken to use nonparametric tests when others were not appropriate for the data, and all data were examined for skewed distribution patterns, such as unimodality and bimodality.

False-color figures were prepared by combining all data for a given set in a matrix, followed by interpolation among all adjacent points. Typical phytoplankton abundance data panels (one species in one lake) contain between 100 and 200 actual data points depending on maximum sample depth and total sample dates. Elemental ratio figures contain fewer points (40–75) because particulate chemistry was sampled on a coarser scale than phytoplankton. Computation and image generation for these figures were performed using MATLAB (Mathworks).

For correlation analyses, available light was estimated using monthly averages of daily surface values for irradiance modeled for sites in Billings, Montana, and Pocatello, Idaho. Finer-scale modeled averages were not available. Yellowstone lies directly between these two cities, which are the nearest points included in available data sets. Because direct measurements of irradiance were not taken throughout the summer, this provides the only measure that can be used for all sample dates. Average surface irradiance was estimated from a 30-yr regional average (1961–1990) and was measured as “average direct normal total solar radiation” in units of $\text{W h m}^{-2} \text{d}^{-1}$. Light data were obtained from the National Solar Radiation Database maintained by the National Renewable Energy Laboratory in Golden, Colorado (<http://rredc.nrel.gov/solar/>). Extinction coefficients were estimated from an empirical logarithmic regression developed from our available data on the relationship between Secchi depth and light extinction in these lakes. Although others have found it convenient to use a scalar factor to convert Secchi depth to light extinction (Wetzel 1983), our large range of measured Secchi depths (0.20 to >11 m) forced us to use a nonlinear factor that better fit the data ($n = 27$, $r = 0.84$, $P < 0.001$). The light measure developed here is represented by the equation

$$\text{Light} = \text{IRR} \cdot \exp\{[0.979 - 0.342 \cdot \ln(\text{Secchi})] \cdot (z)\} \quad (1)$$

where z is the sample depth in meters, Secchi is Secchi transparency in meters, and IRR is a monthly averaged measure of the daily surface irradiance. Therefore, in our approach, a sample taken at the beginning of June has the same IRR as a sample taken at the end of June. Although this is a rather rough approximation of available light at the surface, Secchi depth is considerably more variable and tends to dominate the dynamics of light modeled by this equation. It is important to note that this light factor does not take into account mixing depth. As a result, analyses of correlations with this parameter will assume that distributions are not homogeneous in the epilimnion in the vertical direction.

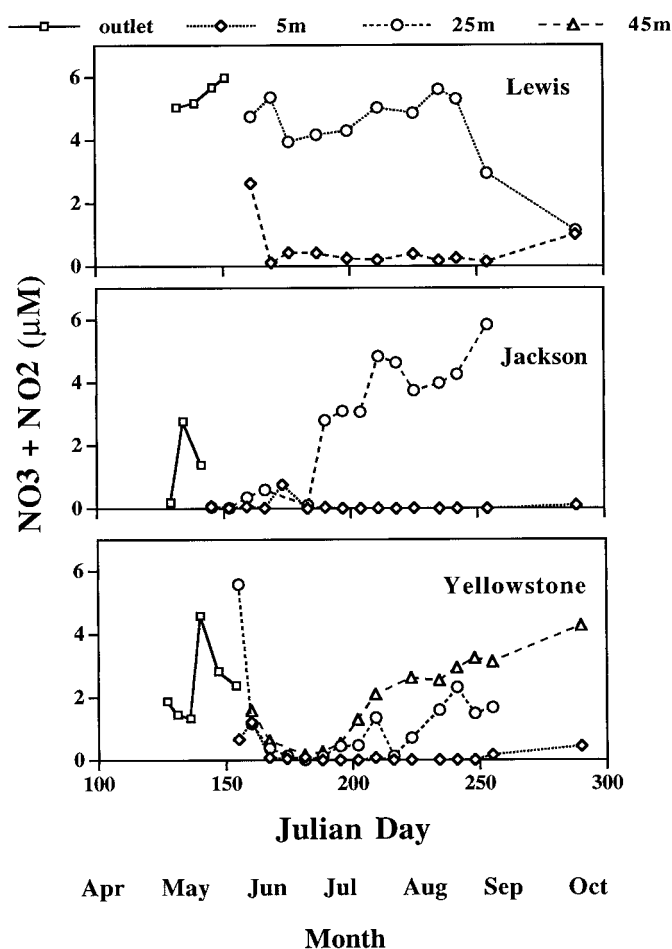


Fig. 1. Dissolved inorganic N (nitrate plus nitrite) concentrations from May through October 1996 for three lakes in the GYE. Measurements from 5, 25, and 45 m were taken from one main pelagic station in each lake. Outlet samples were surface samples taken before ice-out.

Results

Physical and chemical parameters—Precipitation, particularly in the winter, appears to drive N loading in these systems (Theriot et al. 1997; Interlandi and Kilham 1998), so it is important to characterize the regional weather when assessing the chemical and phytoplankton dynamics of these lakes. The winter of 1995–1996 had a heavy snow pack with snowfall lasting through May. This resulted in late times of ice-out in all lakes. Ice went out in Jackson Lake on 22 May (Julian day 143), in Yellowstone Lake on 3 June (day 155), and in Lewis Lake on 9 June (day 161). Heavy snow pack on the ice significantly diminished light penetration into the water and effectively prevented phytoplankton growth under the ice in 1996, particularly in Lewis and Yellowstone Lakes. Furthermore, the ice-out events in 1996 were caused by heavy winds, which quickly blew the thick ice off the lakes, resulting in a dramatic change in light climate. Other years (including 1995 and 1997) had more subtle ice-out events during which the ice melted slowly, resulting in a more gradual transition from low to high light.

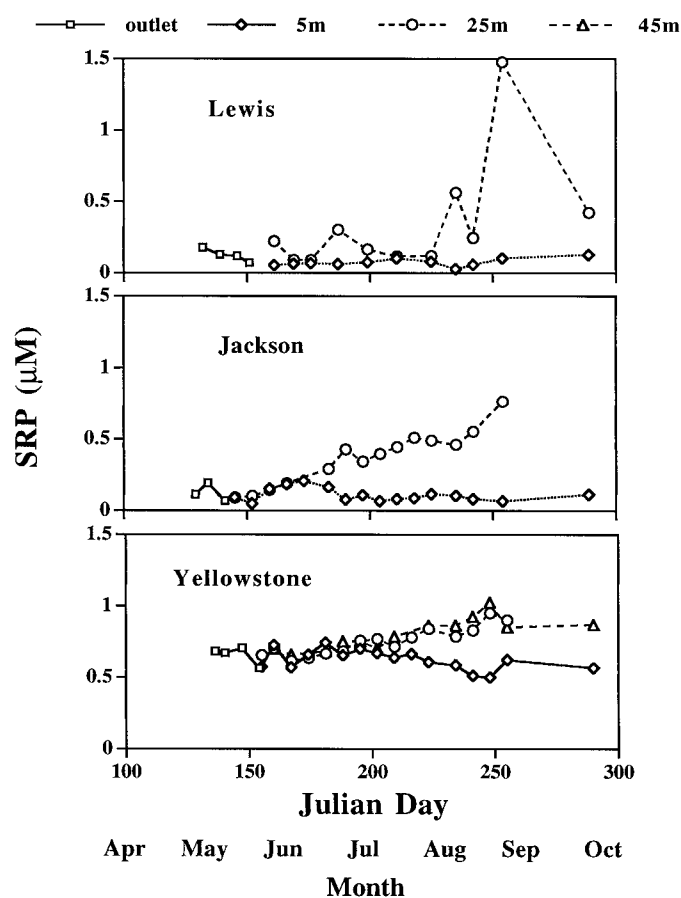


Fig. 2. SRP concentrations from May through October 1996 for three lakes in the GYE. Measurements from 5, 25, and 45 m were taken from one main pelagic station in each lake. Outlet samples were surface samples taken before ice-out.

Ice-out in all lakes came after the first snow melt had begun, so N and other nutrients that were coming into the lakes through May were essentially washed out the outlets during the period of thick ice and snow cover. Concentrations of dissolved nitrogen (DN) at the outlets in the spring were higher than any measured in the epilimnion through the summer, as expected under such circumstances (Fig. 1). In years with little snow pack and favorable light conditions, early N loads are probably used by phytoplankton under the ice, resulting in higher levels of spring phytoplankton biomass in the lake (Interlandi et al. unpubl. data).

After ice-out, nutrient depletion as a result of phytoplankton growth was immediately evident in all the lakes. DN disappeared from the euphotic zone in all lakes immediately after ice-out but was detectable in Lewis Lake soon after this initial depletion and for the remainder of the summer (Fig. 1). SRP was depleted in Lewis and Jackson Lakes and decreased gradually in the epilimnion throughout the summer in Yellowstone Lake (Fig. 2). Some SRP depletion took place in Yellowstone Lake, but data were highly variable. Thus, it is likely that some degree of Si limitation was occurring in Yellowstone Lake, but Si does not seem to be a factor in the other lakes. Average dissolved nutrient concen-

Table 1. Mean dissolved nutrient concentrations for May–October, 1996, in three lakes in the GYE.

Lake	N	Concentration (μM)		
		$\text{NO}_3 + \text{NO}_2$	SRP	SRSi
Lewis	26	2.90	0.221	127
Jackson	33	1.30	0.198	120
Yellowstone				
Excluding 45 m	37	0.94	0.697	92.0
Including 45 m	50	1.20	0.717	92.0
All lakes	109	1.64	0.443	108

trations (Table 1) illustrate the interlake variability in resource availability, particularly for N and P.

In 1996, stratification in Jackson Lake developed slowly but was strong by mid-July, with a shallow thermocline established at 6 m (Fig. 3). In Lewis Lake, the shallowest and smallest of the three, an intense stratification developed in late June at 7 m. By late August, Secchi transparencies increased to 9 m when cooler temperatures weakened the stratification. In Yellowstone Lake, stratification developed in mid-July with a thermocline established at 10 m and a Secchi transparency of 7 m. The thermal structure of Yellow-

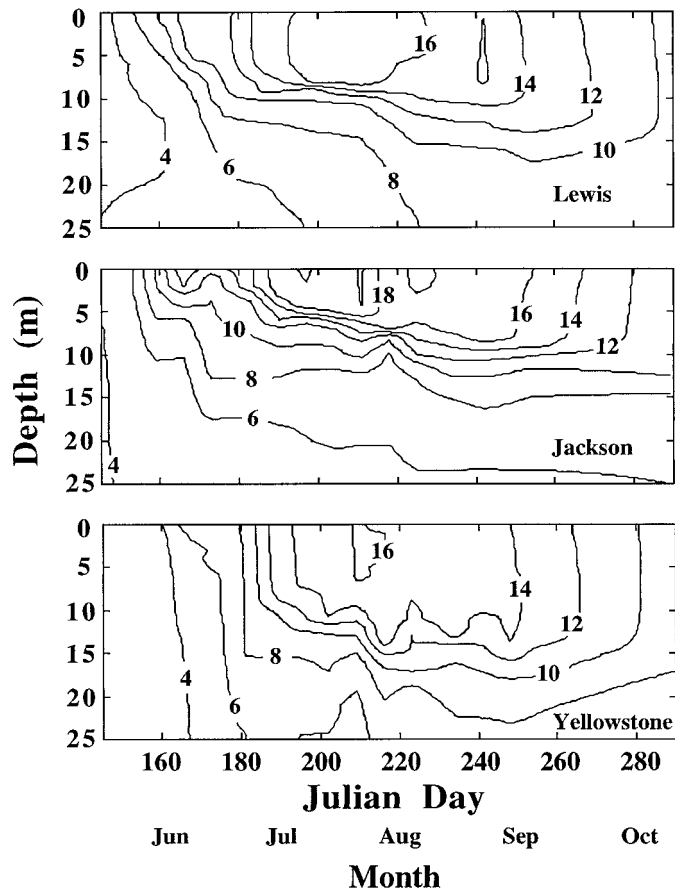


Fig. 3. Isotherms ($^{\circ}\text{C}$) for 1996 at main pelagic sampling stations in three GYE lakes.

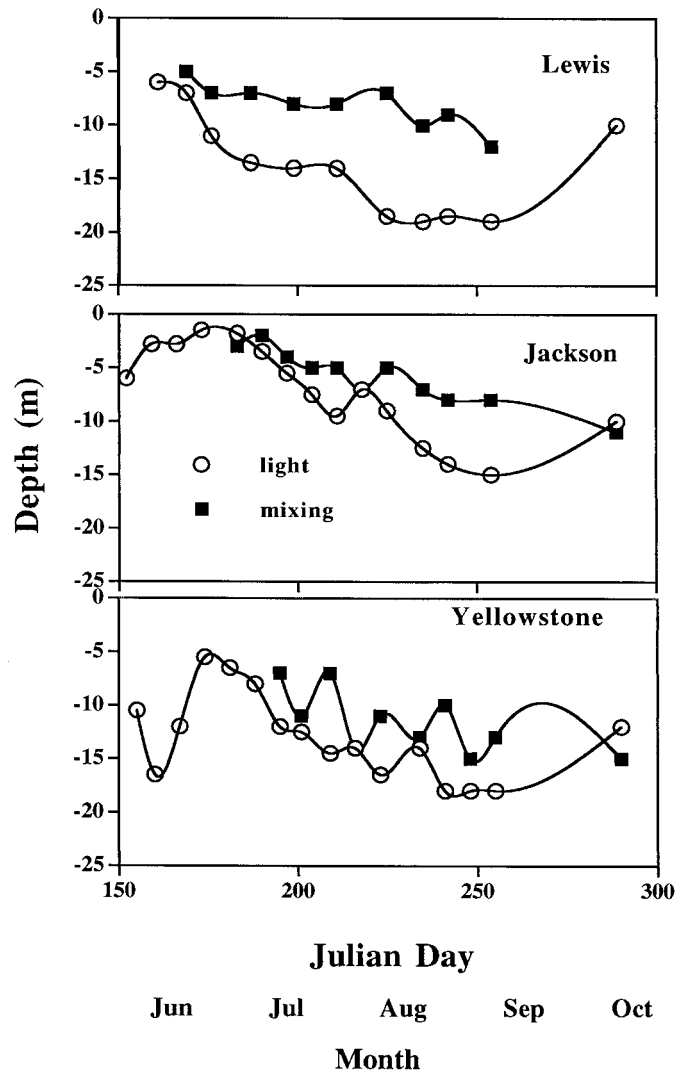


Fig. 4. Euphotic zone depths and mixing depths through the summer of 1996 in three lakes in the GYE. Light penetration is assumed to be twice the measured Secchi depth. Variability in Yellowstone Lake mixing depth is the result of seiches and thermal instability.

stone Lake was unstable, with a relatively weak and variable thermocline throughout the summer.

The euphotic zone extended into the metalimnion in all lakes in midsummer, whereas light penetration was well into the hypolimnion of Lewis Lake through August and September (Fig. 4). This allowed for the growth of a number of species in the metalimnion and hypolimnion of these lakes and suggests that solely epilimnetic considerations of phytoplankton distributions would be incomplete.

Seston elemental stoichiometry—An analysis of the linear relationships (Table 2) between pairs of elements for all particulate samples from the GYE lakes showed the strongest correlation between C and N ($r = 0.893$), with a slope of 8.62, which is above the Redfield ratio (6.6). The relationship between C and P had a slope of 54.3, well below the

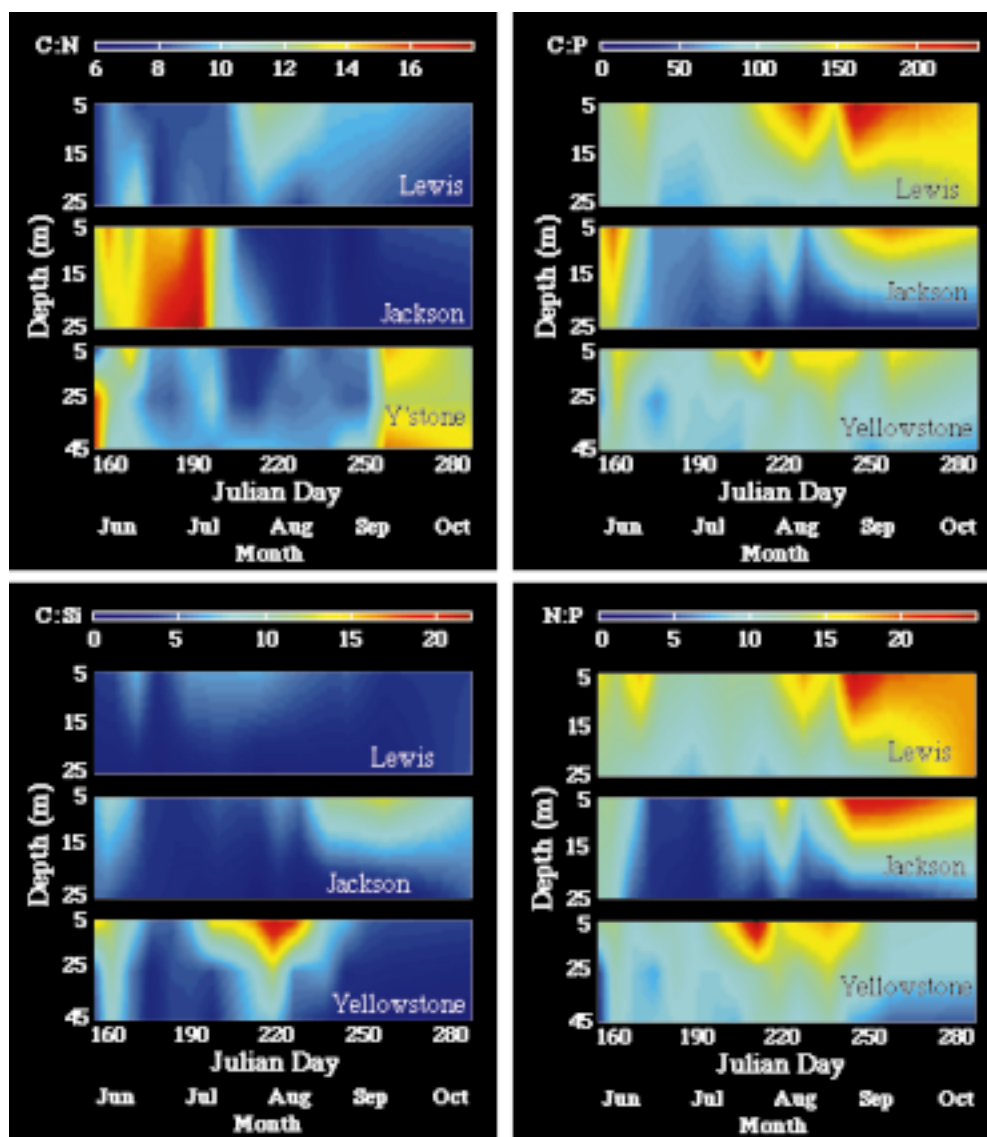


Fig. 5. Particulate (phytoplankton) elemental ratios (molar basis) versus depth and time of year in three lakes in the GYE. High values (red) generally indicate deficiencies in the latter element or the denominator in the ratio. Low values (blue) generally indicate a lack of nutrient limitation in ratios involving C. Note differences in depth scales among lakes.

Redfield ratio (106). The seston Si and P levels were also highly correlated.

There were significant differences both among lakes and within lakes temporally and vertically in particulate elemental ratios (Table 3). The average particulate C:N ratio was highest in Jackson Lake, followed by Yellowstone and Lewis Lakes. Despite the control that N exhibited in these lakes, there was considerable variability in ratios of other elements in the plankton as well. C:P ratios decreased from Lewis to Yellowstone to Jackson. C:Si ratios decreased from Lewis to Jackson to Yellowstone. According to these gross measures, Yellowstone was the most Si limited of the lakes, Jackson was most N limited, and Lewis was most P limited. Conditions changed throughout the year, however, as seen in the false-color diagrams of particulate ratios versus time and depth (Fig. 5). N deficiency (C:N above the Redfield ratio)

occurred in all lakes in the spring (most severely in Jackson), and P deficiency occurred primarily in the epilimnion of Lewis and Jackson in the summer.

Phytoplankton dynamics—The phytoplankton in these lakes (Table 4) were typically dominated by only a few species of diatoms and small coccoid cyanobacteria. Chlorophytes, chrysophytes, and small flagellated algae were also present in smaller quantities (Table 5). Most of the nondiatoms were identified only to genus, but organisms from the same genera with distinctly different morphological characteristics were counted separately.

The seasonal distribution patterns of major diatom species in the three lakes are illustrated in Fig. 6. *Stephanodiscus yellowstonensis* is left out of the Yellowstone Lake subfigure because of extremely low abundances. *Synedra* sp. is not

Table 2. Correlations and linear regressions between pairs of elements in lake seston. Data for May–October, 1996, from all depths in all three GYE lakes are included. Subarctic lakes and all lakes regressions (data from Hecky et al. 1993) include only annual averages and not individual sample values. N/R = not reported.

System	Linear regression equations	<i>r</i>	<i>N</i>	<i>P</i>
GYE lakes	C = 8.62N + 1.81	0.893	109	<0.0001
	C = 54.3P + 7.69	0.680	109	<0.0001
	C = 2.22Si + 9.43	0.561	106	<0.0001
	N = 4.79P + 0.99	0.580	109	<0.0001
	N = 0.190Si + 1.18	0.468	106	<0.0001
	Si = 16.4P + 0.872	0.816	106	<0.0001
Subarctic lakes	C = 5.70N + 6.43	0.859	12	0.0003
	C = 131P + 4.42	0.902	12	<0.0001
	N = 19.5P + 0.080	0.810	12	0.0014
All lakes	C = 9.5N + 2.1	0.796	44	N/R
	C = 166P + 11.3	0.359	44	N/R
	N = 19.0P + 0.72	0.542	44	N/R

included in the Lewis Lake subfigure because of space limitations.

One striking aspect of the phytoplankton abundance data is that the local maxima of individual species in time and vertical space never overlap with the peaks of other species. *S. minutulus* peaked just after ice-out in Jackson and Yellowstone Lakes but did not appear in Lewis Lake. Immediately after this, *Asterionella formosa* peaked in the epilimnion of all lakes. Simultaneously but slightly deeper in the water column, *Aulacoseira subarctica* had a local abundance maximum. In Yellowstone Lake, there was a midsummer peak of *Cyclotella bodanica* in the epilimnion that immediately followed a small local maximum of *A. formosa*. In Jackson Lake, *C. bodanica* peaked in late summer/early fall in the epilimnion. *Fragilaria crotonensis* is a midsummer diatom in Lewis Lake and reached its maximum at ~15 m in August. At the same time, even deeper in Lewis, we saw a maximum in the abundance of *Stephanodiscus niagarae*.

Species–resource correlations—The absolute abundances of eight major species of diatoms were significantly correlated with resource ratios (Table 6). None of the ratios or species abundances were normally distributed. Log transformations normalized some of the data, but in general transformations did not help. Therefore, the only analysis used was a nonparametric evaluation using Spearman's rank cor-

relation coefficient as a test statistic in place of a standard correlation analysis. Because there were 12 correlations attempted per species (96 cases), a level of significance of $P < 0.01$ was used as a test criterion. Correlations meeting the very strict criterion of $P < 0.0001$ are also noted in Table 6. A large number of the correlations were found to be significant (31 of 96), but we cannot assume causation, because many of the ratios will be simultaneously correlated with other important variables that could be hidden driving forces (e.g., temperature). It is better to consider all the significant findings in the context of prior knowledge of the general physiological ecology of the species considered.

Group–resource correlations—Group level analyses were performed on relative abundance values because of large differences in group-specific biomass levels. Measures of central tendencies for peak abundances were made by visually fitting a generalized nonnormal unimodal probability distribution function through the plot of resource ratio (*x*) versus relative abundance data (*y*). The peak was interpreted as the optimum ratio for a given group (Table 7). For the GYE lakes, diatoms as a group had the highest Si:P optimum, followed by green algae, cyanobacteria, chrysophytes, and dinoflagellates. Along a particulate N:P gradient, dinoflagellates exhibited the highest N:P optimum, followed by green algae, chrysophytes, diatoms, and cyanobacteria. There was considerable variability around the optimum values, but the central tendencies were partitioned well enough to discern from the data.

Discussion

Physical and chemical parameters—All three lakes, although in geographical proximity, exhibited considerable differences in water chemistry and physical structure. Yellowstone Lake had the highest SRP and lowest SRSi levels of all three lakes by a wide margin. In contrast, Lewis Lake had the highest levels of SRSi and the lowest levels of SRP. Jackson Lake had moderate levels of both SRSi and SRP (Table 1). Historically, temperatures in Yellowstone and Lewis Lakes rarely exceeded 15°C at the surface (Benson 1961). As a result, the thermal structures of these systems, particularly in Yellowstone Lake, are often unstable throughout the summer. Jackson Lake, which is at a lower elevation, has warmer midsummer temperatures and greater stability. These differences appear to drive the variability in phytoplankton species composition among lakes in the region.

Table 3. Mean particulate C, N, P, and Si concentrations for May–October, 1996, in three lakes in the GYE.

Lake	Concentration (μM)										
	<i>N</i>	<i>C</i>	<i>N</i>	<i>P</i>	<i>Si</i>	<i>C:N</i>	<i>C:P</i>	<i>C:Si</i>	<i>N:P</i>	<i>Si:N</i>	<i>Si:P</i>
Lewis	26	13.3	1.54	0.116	4.00	8.75	117	3.5	13.4	3.0	37
Jackson	33	23.6	2.24	0.294	5.59	10.5	92.6	5.3	9.50	3.3	19
Yellowstone											
Excluding 45 m	37	20.4	2.27	0.202	3.48	9.49	112	8.9	12.2	1.5	17
Including 45 m	50	18.1	1.98	0.185	3.44	9.79	105	7.7	11.2	2.0	19
All lakes	109	18.6	1.95	0.202	4.25	9.75	104	5.9	11.7	2.6	23

Table 4. Species found in the large lakes of the GYE. Most species constituted >1% of biomass in at least one sample.*

Species	Lake		
	Lewis	Jackson	Yellowstone
Diatoms			
<i>Stephanodiscus minutulus</i>	r	+	+
<i>Asterionella formosa</i>	+	+	+
<i>Aulacoseira subarctica</i>	+	+	+
<i>Fragilaria crotonensis</i>	+	+	o
<i>Diatoma elongatum</i> var. <i>tenuis</i>	r	r	+
<i>Synedra</i> sp.	+	+	r
<i>Stephanodiscus niagarae</i>	+	+	o
<i>Stephanodiscus yellowstonensis</i>	o	o	+
<i>Cyclotella bodanica</i>	r	+	+
<i>Cyclotella ocellata</i>	+	o	o
<i>Rhizosolenia eriensis</i>	+	o	+
<i>Stephanodiscus oregonica</i>	o	o	+
Cyanobacteria			
<i>Anabaena</i> spp.	r	+	+
<i>Synechococcus</i> sp.	+	+	+
<i>Aphanacapsa</i> sp.	+	+	+
<i>Dactylococcopsis</i> sp.	o	o	+
Green algae			
<i>Eudorina</i> sp.	+	+	+
<i>Oocystis</i> sp.	+	r	+
<i>Closterium</i> sp.	r	o	+
Chrysophytes			
<i>Dinobryon</i> spp.	+	+	+
<i>Synura</i> sp.	+	r	+
<i>Mallomonas</i> spp.	+	r	+
<i>Rhizochrysis</i> sp.	r	o	+
Dinoflagellates			
Two unidentified species	+	+	+
Others			
<i>Cryptomonas</i> spp.	+	+	+
<i>Euglena</i> sp.	o	o	+
<i>Rhodomonas minuta</i>	+	+	+
Various unidentified small flagellates	+	+	+

* + = common; o = absent; r = rare.

Most of the dynamics in these lakes occurred as a result of only a few early factors, such as snow melt, ice-out, and stratification. These physical events altered the light climate, nutrient chemistry, and mixing regime, which all set up the resource space in which phytoplankton grew.

The most dynamic aspect of the water chemistry and the most important in terms of understanding phytoplankton ecology in these systems was N. Lewis Lake was apparently the least productive by measures of water transparency, phytoplankton standing crop, and particulate C, N, and P concentrations, yet it had the highest levels of both DN and TN of all lakes. In both Yellowstone and Jackson Lakes, DN was below detection limits (<10 nM) in the epilimnion through much of the summer (Fig. 1). This finding suggests that something other than N limitation was occurring in Lewis Lake. Subsequent bioassay experiments (Kilham unpubl. data) support the conclusion that P limitation was oc-

Table 5. Mean biovolume and percentage of relative abundance by class with species diversity (\pm SE) for all 1996 phytoplankton samples from GYE lakes. Green algae data include solitary flagellates such as *Rhodomonas minuta* and *Cryptomonas* spp.

Group	Lake		
	Lewis N = 70	Jackson N = 112	Yellowstone N = 167
Diatoms			
Biovolume	75,661	193,480	106,330
($\mu\text{m}^3 \text{ liter}^{-1}$)	(14,718)	(11,635)	(9,529.0)
Abundance (%)	46.0	22.2	39.8
	(2.45)	(1.94)	(1.56)
Cyanobacteria			
Biovolume	49,991	641,640	107,070
($\mu\text{m}^3 \text{ liter}^{-1}$)	(26,282)	(20,778)	(17,016)
Abundance (%)	35.6	68.4	49.4
	(2.59)	(2.05)	(1.68)
Green algae			
Biovolume	29,300	76,628	23,478
($\mu\text{m}^3 \text{ liter}^{-1}$)	(5,452.7)	(4,310.9)	(3,531.3)
Abundance (%)	18.1	9.40	10.4
	(1.26)	(1.00)	(0.82)
Chrysophytes			
Biovolume	180	23.9	548
($\mu\text{m}^3 \text{ liter}^{-1}$)	(91.0)	(72.0)	(58.9)
Abundance (%)	0.23	0.00	0.24
	(0.07)	(0.05)	(0.03)
Dinoflagellates			
Biovolume	147	104	759
($\mu\text{m}^3 \text{ liter}^{-1}$)	(212)	(168)	(137)
Abundance (%)	0.10	0.01	0.34
	(0.09)	(0.07)	(0.06)
Total biovolume	155,278	911,872	238,183
($\mu\text{m}^3 \text{ liter}^{-1}$)	(27,910)	(22,065)	(18,070)
Species diversity	3.65	2.22	2.85
(ungrouped)	(0.13)	(0.10)	(0.09)

curing in conjunction with N limitation in Lewis Lake in the summer. This was particularly surprising considering the high levels of P in the bedrock of the lake basin and was thought to be in part due to rising levels of N deposition in the region (Interlandi and Kilham 1998).

Seston elemental stoichiometry—In considering how phytoplankton are affected by changes in resources, it is not enough to look at absolute measures of resources, either chemical (N, P, Si) or physical (light energy, heat energy). Some studies have attempted to do this, particularly with P or temperature, but the approach will work well only if there is one major limiting factor in the system. In the case of these mountain lakes, there appear to be three major limiting resources: N, light, and P. There are also minor ones, including Si. In such a situation, one approach is to look at the relationships among these resources in terms of ratios. Although it is difficult to directly measure the amount of light energy stored within algae, it is relatively simple to measure the absolute and relative amounts of C, N, P, and

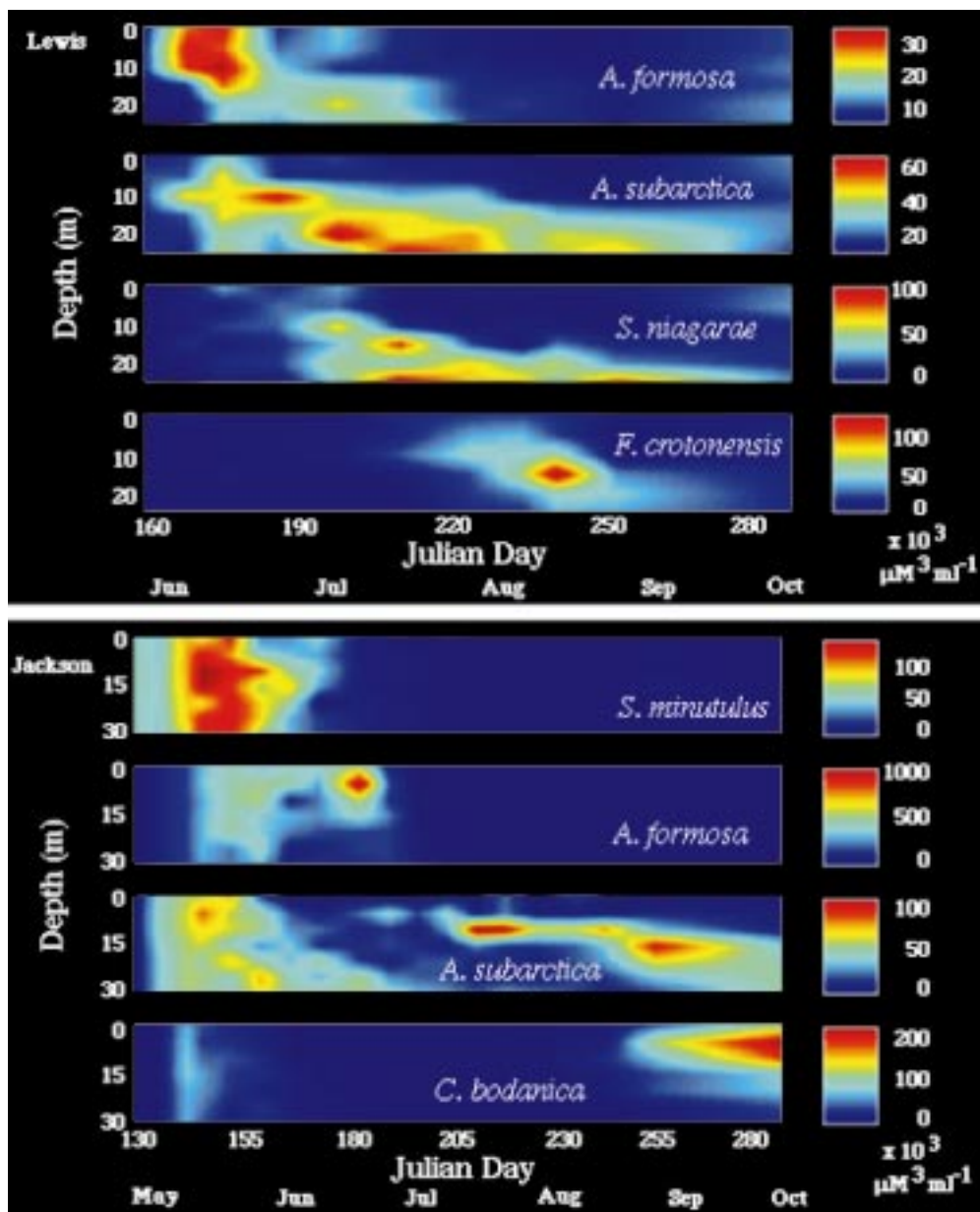


Fig. 6. Absolute abundances ($\mu\text{M}^3 \text{ml}^{-1}$) of major diatom species versus depth and time of year in three lakes in the GYE. Note differences in axes among figures. Samples in Yellowstone Lake were taken deeper (to 50 m) than in other lakes. Measurements began earlier in Jackson Lake than in the others.

Si within particulate material. Because dissolved inorganic carbon is not likely to limit algae in these lakes, particulate C may be a reasonable proxy for stored light energy.

Unfortunately, few data sets containing all the particulate analyses needed for this elemental approach have been produced for freshwater systems, and even fewer are available in the literature. Furthermore, although Hecky et al. (1993) discussed variability in plankton ratios among lakes, very little has been presented concerning variability of these parameters within lake systems (Kilham 1990). A comparison of our data to seston stoichiometry data presented by Hecky et al. (1993) illustrates the differing N-limited character of

the GYE lakes, which may actually be typical of many lakes in the larger Rocky Mountain region. The steep slope in the C:N relationship would indicate that N often limits production in these systems. The slope for C versus P is much less steep for the GYE samples (Table 2) than for either the subarctic lakes or all lakes combined in the earlier analysis of Hecky et al. (1993), suggesting that P is less limiting in this region than in most lacustrine systems.

Sterner (1994) noted that seasonal and temporal patterns in resource limitation, although known to exist, are often obscure. He suggested that studies on more kinds of lake systems, with better temporal resolution, and relevant mea-

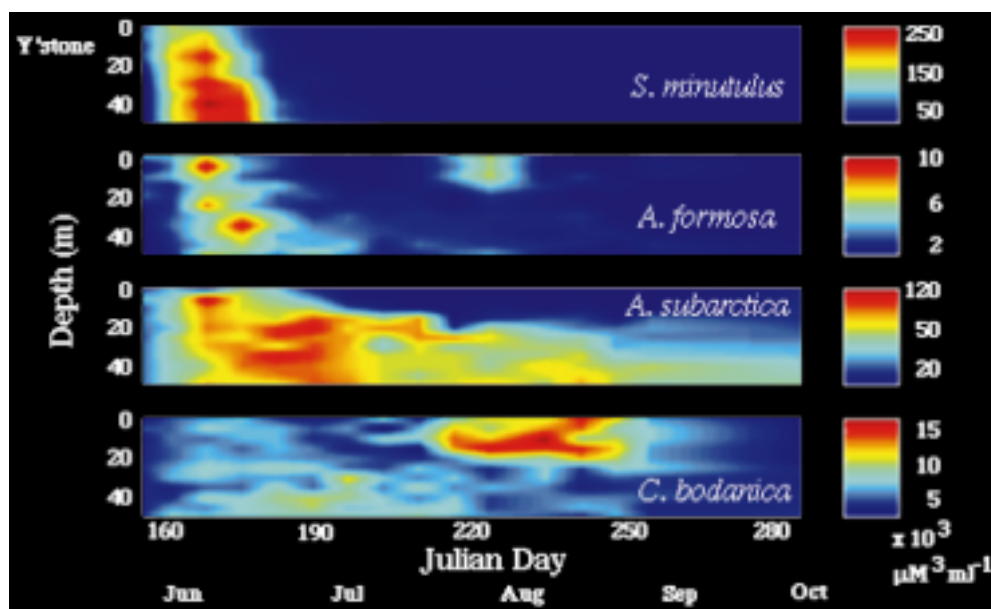


Fig. 6. Continued

tures of physical and chemical parameters are needed to improve interpretations based on elemental stoichiometry. To address this issue, we looked at temporal patterns in the GYE lakes, which are quite different from those of most P-limited temperate lakes.

Seasonal variation in resource limitation within the GYE lakes was significant (Fig. 5). Vertical variation was also apparent during periods of stratification. Much of the phytoplankton growth occurred below the thermocline in these lakes, which is an important consideration for ecological interpretation and supports arguments against the limited focus on epilimnetic populations typical in assessments of phytoplankton ecology. Jackson Lake was severely N deficient ($C:N = 2 \times$ Redfield ratio) in late June at all depths. N deficiency occurred in Yellowstone Lake immediately after ice-out in deeper waters and then again in late summer

throughout the water column. Lewis Lake, which had the lowest relative amount of cyanobacteria in the summer, actually had its highest C:N levels in midsummer, although these levels were never indicative of severe limitation. The C:Si trends suggested that the only severe Si deficiency occurred in Yellowstone Lake in late July, primarily in the epilimnion. Jackson Lake had a slight Si deficiency occurring in late summer. C:P levels indicated periodic P deficiency in the epilimnion in all lakes, most severely in Lewis Lake. Very low C:P values in Jackson Lake in the hypolimnion are probably the result of high levels of cyanobacterial biomass. This seasonal variation in algal elemental ratios must certainly have significant food quality implications (Sterner and Hessen 1994; Hassett et al. 1997; Kreeger et al. 1997), but such considerations are beyond the scope of our analysis.

Table 6. Rank correlation coefficients between absolute abundance of major diatom species and concurrent resource ratios for samples from GYE lakes.†

	SM	AF	AS	FC	SN	SY	CB	Syn
TSi:TN	-0.19	0.09	-0.03	0.28*	0.11	0.04	0.15	0.02
TSi:TP	-0.28*	0.27*	-0.27*	0.52**	0.43**	-0.21	0.33*	-0.13
TN:TP	-0.15	0.28*	-0.34*	0.43**	0.30*	-0.20	-0.41**	0.53**
Li:TN	-0.32*	-0.21	-0.56**	0.21	-0.06	0.05	-0.05	0.02
Li:TP	-0.31*	-0.03	-0.57**	0.30*	0.02	0.00	-0.12	0.13
Li:TSi	-0.12	-0.10	-0.52**	0.15	-0.09	0.08	-0.03	0.00
PSi:PN	-0.11	0.15	0.15	0.22	0.35*	-0.18	-0.30*	0.17
PSi:PP	-0.29*	0.09	0.00	0.26*	0.22	-0.13	-0.23	0.23
PN:PP	-0.18	-0.14	-0.40**	0.05	-0.22	0.15	-0.10	0.04
PC:PSi	0.22	-0.05	-0.07	-0.21	-0.35*	0.18	0.37**	-0.17
PC:PN	0.28*	0.27*	0.36**	-0.06	0.00	0.02	0.17	-0.10
PC:PP	-0.04	-0.04	-0.23	0.03	-0.25*	0.15	0.27*	-0.02

* $P < 0.01$.

** $P < 0.0001$.

† For ratios, T, total; P, particulate. Number of data per correlation, 106. SM, *S. minutulus*; AF, *A. formosa*; AS, *A. subarctica*; FC, *F. crotonensis*; SN, *S. niagarae*; SY, *S. yellowstonensis*; CB, *C. bodanica*; Syn, *Synedra* sp.

Table 7. Relative abundance optima along particulate elemental ratio gradients for algal groups in 1996 in GYE lakes.

Algal group	Si:P	N:P	Si:N
Diatoms	40:1	9:1	3:1
Green algae	24:1	14:1	4:1
Cyanobacteria	20:1	3:1	2:1
Chrysophytes	16:1	11:1	1:1
Dinoflagellates	6:1	15:1	0.5:1

The mean annual particulate C:P ratios in all lakes (Table 3) were very close to Redfield C:P ratios and were much lower than those reported for most freshwater samples (Hecky et al. 1993). The mean C:N values for these lakes were well above the Redfield ratio but were representative of moderately rather than severely N-limited plankton. Considering the low DN levels measured in these lakes, it is likely that N turnover and cycling is relatively fast. Si:N ratios of 1:1 are considered ideal in ocean systems (Dugdale and Wilkerson 1998), and although not as strongly supported as C:N:P ratios, this is a generally accepted measure (Brezinski 1985). We are aware of no such data available for freshwater ratios involving Si, but the data from the GYE lakes suggest that the optimum Si:N may be somewhat higher in freshwater. Additionally, the optimal C:Si ratios in freshwater may be lower than in the ocean (C:Si = 6.6). This is supported by Conley et al. (1989), who found that freshwater diatoms contained higher levels of Si per unit of biovolume than did their oceanic counterparts. The average of all samples in the GYE lakes was C:Si = 5.9. Although overall production of particulate C is controlled by N, it is clear that the plankton were subjected to stresses from episodic limitation by other factors throughout the summer.

Phytoplankton dynamics and species–resource correlations—Hutchinson's (1961) paradox of the plankton has been explored extensively, with the result being that species diversity is thought to exist within the plankton because of contemporaneous disequilibrium, resource variability, spatial heterogeneity, and multiple limiting conditions (Reynolds 1984). The phytoplankton distribution patterns presented here can be interpreted in a different way. Our conclusion is that there is not much of a paradox at all. The population maxima of two species never coincided in a spatiotemporal regime. This distinct separation of optima is best seen in high resolution distribution data, which are surprisingly sparse in the literature. Talling (1987) presented isographs of phytoplankton distribution versus time and depth for phytoplankton in Lake Victoria (East Africa) that clearly demonstrated this separation for two major species in the system. Similarly, Reynolds (1976) presented data for 10 species in Crose Mere (Shropshire, U.K.), including chlorophytes, diatoms, cyanophytes, dinoflagellates, and cryptomonads. Only the cyanophyte species *Anabaena circinalis* and *Aphanizomion flos-aquae* had overlapping population maxima, occurring at the surface in mid-August. The strikingly clear separation of species maxima in time and space has not been emphasized by previous observers, but we argue that it is the strongest empirical evidence that physiological

differences among species lead to ecological differentiation of community structure.

The question of why coexistence occurs, then, may not be most important, because we can come up with a number of plausible reasons for coexistence simply by saying that either equilibrium conditions do not exist or that multiple limiting effects do. The more interesting problem that our data present is twofold. First, how do we explain the separation of seasonal optima in ecological terms? Second, if resource competition is a primary mechanism, can resource ratio theory adequately explain the observed patterns?

Variations in resource levels and particulate elemental ratios (as measures of relative resource levels) would lead us to expect differences in phytoplankton community assemblages both among lakes and within lakes over the growing season (Fig. 6). Species good at utilizing P, for instance, would be expected in Lewis Lake in the summer, and those poor at P but good at N utilization would be favored in Jackson and Yellowstone Lakes. Relative abundances of major diatom species in these lakes fit as expected (Kilham et al. 1996) with these resource relationships.

S. minutulus is found in Jackson and Yellowstone lakes and not in Lewis Lake. Its abundance was negatively correlated with both total and particulate Si:P ratios in the field data. Physiological assays have previously demonstrated this species and other small members of the genus *Stephanodiscus* to have a very low Si requirement and a relatively high P requirement, making this a low Si:P specialist (Kilham 1984; Mechling and Kilham 1982; van Donk and Kilham 1990). The negative correlation with Si:P in the field samples matched the general species-specific physiological characteristics measured in the laboratory. A strong positive correlation with particulate C:N ratios was also observed. This could be interpreted as evidence of low N requirements for this species. The correlation was more likely due to the fact that most measures of biomass in the lake exhibit this relationship. High C:N levels could be the result of prior situations in which growth was sustained at high levels for a time with severe N limitation as the result. Although these measured conditions were no longer ideal for growth, they were correlated with the end result of that growth, high abundances. As a result, several diatom species showed strong positive correlations with C:N, but none showed negative correlations with this ratio.

A. formosa occurs in all three lakes. Consistent with the known physiology of the species, it was positively correlated with both TSi:TP and TN:TP. *A. formosa* has been characterized as a good competitor for P and a moderate competitor for Si (Tilman and Kilham 1976; van Donk and Kilham 1990), making it a moderate to high Si:P specialist. Not much is known about N requirements for *A. formosa*, but recent experiments have shown it to be quite good at nitrate utilization (Roh pers. comm.). In light of this, we consider the N:P correlation with this species to be dominated by the P component of the ratio, which was extremely low in Lewis Lake, where *A. formosa* was most abundant in 1996. Positive correlations of this species with N:P and Si:P have been found in other studies that considered primarily P-limited systems (Tilman 1982). Our findings in N-limited systems provide further evidence that resource ratios are a

more universal component of ecosystem function than has previously been appreciated. If these relationships hold across different types of lakes, then it is reasonable to argue that there are species-specific ratio driven niches across aquatic ecosystems.

A. subarctica exhibited an abundance pattern that was distinct from those of all other diatoms in these lakes and was similar only to *Closterium* sp., a chlorophyte, in Yellowstone Lake. *A. subarctica* reached an early spring maximum before the onset of stratification and then quickly sank out of the epilimnion as stratification developed. It then reached a second local maximum below the thermocline in all lakes. It persisted in the metalimnion in the three lakes throughout the summer. The abundance of this species was positively correlated with dissolved P ($r_s = 0.33$, $P = 0.0004$) and negatively correlated with light ($r_s = -0.50$, $P < 0.0001$). In Yellowstone Lake, it remained in very high abundances down to 50 m, which was the maximum depth of the sampling regime.

A. subarctica was strongly negatively correlated with all light:nutrient ratios. These relationships were the result of the tendency of this species to grow in the metalimnion in all lakes. As such, the correlations were driven by the direct negative correlation between light and abundance. Abundances of this diatom were also negatively correlated with TSi:TP and TN:TP ratios, suggesting a high P requirement for the species. Particulate N:P also showed a strong negative correlation, suggesting again that the cellular requirements of P are high for *A. subarctica*. A very strong positive correlation with particulate C:N suggests a low physiological requirement for N in relation to other phytoplankton species. This species certainly grows in low light conditions. The nature of this alternate strategy, for instance, the capacity to take up dissolved organic carbon as an energy source, is not known.

The unusual seasonal pattern of *A. subarctica* was previously reported by Lund (1954), who suggested that high abundances in deeper water are the result of resuspension of live cells from the sediments. It was noted at the time that *A. subarctica* cells remained viable in sediments many times longer (years) than did other species of diatoms. This explanation does not fit with the patterns from these lakes, however, because distribution maxima occurred in midsummer just below the thermocline, which is >85 m from the bottom in Yellowstone Lake.

F. crotonensis abundances generally followed expected trends of positive correlations with Si:P and N:P ratios. Physiological evaluations and multiple species competition experiments involving this diatom have shown it to be a good P competitor, a fair Si competitor, and a poor N competitor (Tilman 1981; Interlandi and Kilham 1998). Additionally, experiments by Rhee and Gotham (1981) showed that *F. crotonensis* had a high light requirement. In the field data, this species was the only one that had a strong positive correlation with any light:nutrient ratio. Its abundance was strongly positively correlated with light:P and weakly correlated with light:Si and light:N.

Correlations of *S. niagarae* and *S. yellowstonensis* were difficult to evaluate, because they were based on counts of very few cells. Abundances in 1996 were always <2 cells

ml⁻¹ for *S. niagarae*, and <0.2 cells ml⁻¹ for *S. yellowstonensis*. As a result, error in estimated abundances tends to be high, especially for *S. yellowstonensis*. Physiological studies (Taylor 1994) showed *S. niagarae* to have an optimum cellular Si:N ratio of about 2.5:1. *S. yellowstonensis*, on the other hand, has a better capacity for N utilization, with an optimum cellular ratio of 20:1 (Taylor 1994). The strong positive relationship between *S. niagarae* and TSi:TP may indicate a low P requirement, but no P physiology data are available. The inverse relationships between the two closely related species may just be a noncausal result of the fact that *S. yellowstonensis* is found only in Yellowstone Lake, where Si:P and N:P ratios are low relative to Lewis Lake, where *S. niagarae* is found.

C. bodanica, characterized as a "eutrophic" species in temperate lakes by some investigators, becomes abundant in mid to late summer in both Yellowstone and Jackson Lakes. Because these lakes typically have low N:P ratios, *C. bodanica* may be better characterized as a low N specialist rather than a high nutrient alga. Indeed, most eutrophic temperate lakes are P-rich systems with the potential for being N limited through the summer. This characterization is further supported by the presence of N-fixing *Anabaena* spp. during the period of maximum abundance of *C. bodanica* in both Yellowstone and Jackson Lakes. Furthermore, the *C. bodanica* maxima occur during periods of relatively high light penetration (Secchi depths of 9 m in Yellowstone and 5 m in Jackson) and low phytoplankton biomass, which could not be characterized as eutrophic conditions. *C. bodanica* abundances were most highly negatively correlated with total N:P, which is consistent with past observations of this species as a good N competitor and a relatively poor P competitor. Although no experimental data on *C. bodanica* are available, a congener, *Cyclotella meneghiniana*, was found to be a low Si:P specialist as a result of its poor capacity to utilize P and good efficiency for Si utilization (Tilman and Kilham 1976).

Synedra sp. is most abundant in early summer in Lewis Lake. *Synedra* spp. have consistently been found to be extremely good P competitors. In all experiments to date, no alga has been reported to outcompete a *Synedra* sp. under P limitation (Tilman 1981; Kilham 1984, 1986; Sommer 1985). Our field data were in excellent agreement with these experimental observations, because *Synedra* sp. was strongly positively correlated with TN:TP ratios. That there was no such correlation between this species and Si:P ratios may appear contradictory to former evidence showing *Synedra* sp. to dominate at high Si:P ratios. The explanation for the apparent discrepancy is rather simple. In previous experiments, the Si:P ratio was varied and conditions were set so that Si and P were always the only two possible limiting factors. In the GYE lakes, however, Si is relatively high and rarely limiting. In this case, we would not expect Si levels to affect phytoplankton growth. Si:resource ratio effects will be dominated in these systems by the other resource that actually limits the growth of some species. In these lakes, N was often that limiting factor. In general, when both N and P are at limiting levels (e.g., most of the time in Lewis Lake), the N:P ratio becomes much more important in determining species abundances. Likewise, when Si:P ratios

are correlated with species abundances in situations in which Si is high, we can almost always be sure that competition for P is occurring among the plankton. *F. crotonensis* becomes dominant and reaches its highest abundances in Lewis Lake, where N:P is highest. Similarly, *Synedra* sp., which is generally considered a specialist at low P, is most abundant in early summer in Lewis Lake, when P is low. *S. minutulus*, a poor competitor for P but an excellent competitor for Si (Kilham 1984), is found only in Jackson and Yellowstone Lakes, where Si:P is low, and not in Lewis Lake, where Si:P is high.

The differences in the individual species–resource correlations and the clear separation of species maxima are interpreted here as evidence that species do exhibit differences in their environmental optima. Additionally, low summer-time levels of resources that are depleted by phytoplankton from high spring levels indicate the presence of resource competition. Although *S. minutulus* is susceptible to grazing and its fast disappearance from Yellowstone and Jackson Lakes in the spring could be partly attributed to selective pressures from zooplankton, none of the other species distributions can be explained thusly.

Some studies have attempted to use time lags to show relationships between species and resources in aquatic systems (Sommer 1993), yet it is more mechanistically precise to look at simple species abundances, rates of increase (the first derivative of abundance), and in situ growth rates when attempting to draw connections between species and resources in natural systems (Reynolds 1984). Although the added data manipulation used to find rates of increase might yield more meaningful correlations with resource availability, the simpler approach of correlating direct abundance with resource ratios was taken here. Searching for linear relationships with simple statistical regressions may also miss the mark. Often, relationships between resources and species show strong log–log relationships that do not fall out of linear regressions. Additionally, individual species may have an optimum growth response somewhere in the middle of a concentration range for a particular resource ratio that will not be evident from simple regression analyses. Despite these considerations, direct correlations of abundance versus resource ratio can still generate important evidence of connections when considered in light of physiological ecology.

Kilham et al. (1996) made predictions about how the GYE diatom species could be expected to align themselves along resource ratio gradients. Predictions were based on known physiology and previous empirical observations from these and other lakes and not on prior statistical analyses. Hypotheses were originally developed from general observations of seasonal and interannual trends in conjunction with experimental evidence to explain how these species might divide resource space. A comparison of field correlations and the hypothesized resource ratio rankings can be made to test those predictions. Along a Si:N gradient, which was first hypothesized to be most important, Kilham et al. (1996) ranked the species from high to low Si:N as follows (see Table 6 for key to abbreviations): FC, CB > AF, AS, SY > SN > SM. *Synedra* sp. was not included, but given its reputation as a poor Si competitor, it might have been ranked on the high Si:N end. Empirical rankings from the 1996

data for GYE lakes from highest positive rank correlation coefficient with Si:N to lowest were as follows: FC > CB > SN > AF > SY > Syn > AS > SM. The extreme ends were the easiest to predict, and in this case the empirical observations matched the theory. *Synedra* sp. did not fall at the high Si:N end as might have been expected. Without an understanding of N physiology of this alga, it is difficult to know whether this result is consistent with ratio-driven dynamics or whether something else was coming into play. *S. yellowstonensis* and *S. niagarae* were opposite of what might have been expected, so we could speculate that light and P may be important in determining the dynamics of these species.

Along an N:P gradient, the hypothesized resource relationships were as follows: AF > FC, SN > SM, AS > CB, SY. The correlations from 1996 data in the GYE lakes rank the species as follows: Syn > FC > SN > AF > SM > SY > AS > CB. Again, most of the observed patterns match predictions. *F. crotonensis*, *S. niagarae*, and *A. formosa* are relatively high N:P species, whereas *C. bodanica*, *A. subarctica*, and *S. yellowstonensis* are on the low end. *S. minutulus* seems to fall in the middle. The rankings of Kilham et al. (1996) included species that were hypothetical equals along the gradients, so there is no statistical test to compare these patterns. As such, a certain amount of subjectivity is involved when these general predictions are compared with field data. Knowing the exact physiological requirements of all species would provide specific predictions, but the interpretation here is that hypotheses and subsequent field observations were well matched.

Comparison of individual species abundances and elemental stoichiometry in the natural system can help to establish a critical link between species-specific traits and functional ecosystem properties. When observed distributions of organisms are correlated with the elemental composition of the biomass and are in agreement with experimentally derived physiological properties as they are here, the approach is all the more useful. Such connections are important to establish when an explicit goal of ecological research is to develop an understanding of the roles of individual species or groups of organisms in the framework of ecosystems at large (Grimm 1995). Our analyses demonstrate that ecology can be approached from both the organismal and ecosystem levels at once. Ultimately, these connections suggest that we can use ecological stoichiometry to predict species-level changes from ecosystem-level properties and vice versa.

Group–resource correlations—Resource competition theory is only mechanistically predictive at the species level. Analysis of the diatom assemblages, then, is a direct test of this theory with empirical data. Ratios of resources have been shown, however, to drive assemblages at other taxonomic levels as well (Kilham 1986; Tilman et al. 1986). The lack of a theoretical description of this phenomenon is primarily derived from the fact that less is known about the resource physiology of these other groups in general and species within these groups in particular. Despite the lack of a mechanistic understanding here, we saw that groups of phytoplankton also demonstrated significant correlations

with resource ratios. The abundance of cyanobacteria, a major biomass component of the phytoplankton, was highly negatively correlated with particulate C:P ($r_s = -0.26$, $P = 0.0054$) and N:P ($r_s = -0.35$, $P = 0.0002$) ratios. This is in good agreement with the perception of cyanobacteria in physiological terms as having higher P requirements than diatoms (Tilman et al. 1986). Prior analyses of field observations have shown cyanobacteria to dominate at low N:P ratios, whereas diatoms and green algae dominate at higher N:P levels (Tilman 1981; Kilham 1986; Sommer 1993). The dominance of diatoms at high Si:P is also in agreement with patterns observed in many lakes in previous studies. Non-linear relationships between groups and resource ratios have also been demonstrated in prior work. Some evidence of multiple switches, meaning relative abundance optima in the middle range of the Si:P gradient, has been presented by Tilman (1982) for diatom species in Lake Michigan. Multiple partitioning of the N:P gradient among cyanobacteria, diatoms, and green algae was demonstrated by Tilman et al. (1986), who suggested that temperature was also a factor affecting taxonomic differences in optima among algal groups. In our case, we found that several groups seemed to exhibit distinct and different optima along resource ratio gradients (Table 7).

By assessing relative abundances by algal group in this data set, partitioning along Si:P and N:P gradients was apparent, generally in expected patterns. The most obvious examples are drawn by comparing abundances to particulate elemental ratios that are inherently tied to the type of biomass in the system. Although this connection is not as mechanistically rigorous as one that ties supply rates to optima, it is an important observation nonetheless. Actually, when recycling rates are unknown, the assumption that total nutrient concentrations are good estimates of supply rates may not hold (Tilman 1982), so particulate ratios may actually yield relationships that are more directly comparable to experimental observations.

Conclusions

In our study, a fine-scale analysis of the environmental distribution of some well-studied species of algae has led to a greater appreciation for and understanding of the driving forces behind phytoplankton community structure and seasonal patterns of succession. Both observational and statistical descriptions demonstrate the strong links between limiting conditions in general and relative resource variability in particular in regulating phytoplankton community structure. A high degree of seasonal and vertical variation in resource limitation is the result of physical and biological processes within the lake systems. Seasonal population maxima of phytoplankton species never coincided, supporting the conclusion that physiological differences among species lead to community differentiation on broad scales.

By considering environmental observations in light of the experimental understanding of the physiological ecology of species, we come closer to mechanistic connections between the capabilities of individual species and functional community structure in the natural environment. Use of stoi-

chiometric analyses further allows us to draw broader conclusions about the ties between ecosystem-level properties and community assemblages. The distributions of both diatom species and algal groups conform to the patterns known from both laboratory experiments and from observations in other systems (Kilham et al. 1996), which allows for the generalization of these relationships. The phytoplankton distribution patterns in the lakes of the GYE can be explained in terms that are applicable to many systems with a minimum of underlying assumptions.

Although much of the variance in succession and community structure remains derived from other unmeasured factors and even errors in the measured values of the factors considered here, the relationship between resource availability and community structure in these lake systems appears reliably interpretable.

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