Diatom–chemistry relationships in Yellowstone Lake (Wyoming) sediments: Implications for climatic and aquatic processes research

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Abstract

We analyzed sediment elemental composition (C, N, P, and Si) and planktonic diatom fossils from the top 32 cm of a short core (55 cm) from Yellowstone Lake (Wyoming), tracking deposition from about 1650 to 1998. Associations between fossil communities and sediment chemistry were measured by rank-order correlation to gauge decadal scale relationships between lake chemistry and phytoplankton community composition. Strong associations were found between the abundance of individual diatom species and the chemical composition of sediments, suggesting that sediment chemistry can directly track the elemental composition of seston. Among three fossil measures (relative frustule abundance, relative biovolume, and absolute biovolume), associations between sediment chemistry and relative biovolume were strongest. We then compared measures and trends in sediment elemental composition to in-lake seston chemistry to assess transport processes that alter sediment composition relative to source material. On the basis of elemental stoichiometry, sediments were enriched in P and depleted in C and N compared with seston. Trends of increasing C and N accumulation along with decreasing Si accumulation were consistent with patterns of increasing productivity, increasing lake N levels, and decreasing dominance of diatoms, respectively. A sharp increase in sediment C:N ratio, with a decrease in diatom absolute biovolume and absolute C and N levels, was associated with a prolonged drought in the 1930s. These trends suggest alteration of ecosystem properties by a combination of climatic variation and increasing N availability, adding complexity to larger goals of climatic reconstruction by diatom–nutrient chemistry–climate transfer functions in large lakes of the region.

Lacustrine sediments hold a wealth of natural history that allows the reconstruction of changes in aquatic and ecosystem processes with both direct and indirect metrics. In particular, diatom fossil records alone are most often used to reconstruct lake chemistry. Transfer functions between diatoms and/or chrysophytes found in surface sediment communities and lake chemistry have been constructed using weighted averaging regression and calibration models that allow correlation of diatom community composition with water chemistry in a defined regional series of lakes (e.g., Dixit et al. 1992). The fossil stratigraphy in those and similar lakes can then be assessed by means of the calibration model to reconstruct historical water chemistry. These models make the general assumption that the chemistry–community relationship has remained within the range of the modern calibration set throughout the historical period recorded in the lake sediments.

The reconstructed aquatic conditions then allow us to infer environmental change on a broader scale. For instance, transfer functions developed between diatom communities and

water salinity have allowed the inference of drought conditions in prairie lakes in the midwestern U.S.A. (Fritz 1990; Laird et al. 1998). Other recent work has demonstrated the ability to reconstruct climate variables on a variety of time scales with this strategy (Bradbury et al. 1993; Battarbee 2000; Bradbury 2000).

We have been employing a similar approach to reconstruct water chemistry and ultimately climate in the Yellowstone region. In our framework for the lakes in Yellowstone, we have hypothesized that the relative availability of resources (N, P, Si, and light) regulates diatom community structure. One aspect of the original conceptual model for this reconstruction was that winter precipitation regulates nutrient loading in the lakes (Theriot et al. 1997), which in turn affects diatom species composition by altering the outcome of competition for resources among phytoplankton (Kilham et al. 1996). By a combination of approaches, we have shown that modern winter precipitation regulates nitrogen loading to the watersheds of the Greater Yellowstone Ecosystem and thus drives nitrogen concentrations in lakes (Theriot et al. 1997; Interlandi 2001). This work has also shown that stream and lake water silicate concentrations are inversely correlated with winter precipitation, possibly driven by both direct (base stream flow silicate dilution) and indirect (greater biological utilization enhanced by increased nitrogen) mechanisms.

One problem we have discovered with this approach to climate reconstruction is that the assumption of temporal independence of the climate–nutrient chemistry relationship may be invalid. To reconstruct climate through diatom–

chemistry–climate transfer functions, we would generally assume that the nutrient loading is and has been a constant function of weather. This assumption is in question, however, for several reasons. First, modern increases in acid deposition have potentially altered the process of chemical weathering of soils and bedrock, thus changing the relationship between precipitation and the loading of silicon and phosphorus. Also, human-induced increases in inorganic nitrogen deposition may have uncoupled the historical relationship between precipitation and nitrogen loading in these watersheds (Interlandi and Kilham 1998). To address this problem and to assess recent changes in loading rates of nitrogen, we have taken a closer look at the most recent lacustrine sediments in Yellowstone Lake to track patterns in the diatom assemblages and elemental stratigraphy of sediments deposited after European colonization of the Americas.

Although fossil records can remain relatively stable in lake sediments, sediment chemistry is often much more dynamic. Dissolution of inorganic materials and the degradation of organic compounds in sediments often confound the relationship between the elemental composition of sediments and that of the source material (Ostrum et al. 1998). Typically, rates of chemical fluxes are greatest in the most recent and uncompacted sediments. These processes are generally lumped under the term early diagenesis. The regeneration of individual elements also can differ depending upon properties of the overlying water. For instance, phosphorus release from sediments is enhanced under anoxic conditions (Sondergaard et al. 1996). Where the general chemical properties (i.e., pH, conductivity, dissolved oxygen) of hypolimnetic water are relatively constant, however, we expect rates of diagenesis in both recently deposited and compacted sediments to remain stable through time. Thus, by developing transfer functions between downcore sediment composition and the original seston composition, it is possible to use sediment chemistry in conjunction with fossil stratigraphy in the development of a more direct reconstruction of historical aquatic conditions.

Despite the problems related to sediment chemical transformations, a number of direct chemical metrics have been used to infer past conditions effectively in other studies. For instance, the proportion of biogenic silica in sediments is a convenient rough measure of total diatom production. Also, large variations in sediment $C:N$ ratios have been used to infer whether source organic material is primarily terrestrial (high $C:N$) or aquatic (low $C:N$) (e.g., Meyers 1997). Sediment phosphorus content has been used in some cases to directly infer phosphorus loading rates (Engstrom and Wright 1984; Anderson and Rippey 1994). Biochemical compounds, such as algal pigments, and the ratios of group-specific pigments also have been employed to reconstruct the relative abundance of diatoms and green and blue-green algae in lakes (Leavitt et al. 1994). These and other direct chemical measures may be particularly useful for reconstructing past conditions in Yellowstone Lake and other deep cold-water lakes in general because of the low level of variability in hypolimnetic conditions and sediment transport processes (Eadie et al. 1990). Variation in rates of sediment diagenesis under such conditions is likely to be regulated primarily by the concentration of individual elements and

compounds in the sediments that can affect reaction rates in sediment pore water (Hartikainen et al. 1996).

We previously demonstrated strong direct empirical relationships between the community structure of live diatoms and seston elemental composition in Yellowstone Lake and other large lakes of the Greater Yellowstone Ecosystem (Interlandi et al. 1999). If strong relationships between sediment chemistry and seston chemistry do exist, we should expect to see some direct correlation between fossil diatom communities and sediment elemental composition. In this study, we analyzed such relationships.

In this report, we focus on efforts to understand three specific links in the chain of relationships among diatom communities and regional climatic and ecological conditions. First, we assessed sediment chemistry (C, N, P, and Si) in relation to observed and suspected patterns in nutrient loading to determine whether sediment chemistry was directly consistent with the presumed qualitative nutrient loading patterns over the past several centuries in these and other lake systems. Next, we explored the direct relationships between diatom fossil communities and sediment chemistry through the same time period and considered these relationships in light of our understanding of the specific resource physiologies of the diatom species. Finally, we assessed seston chemistry data from Yellowstone Lake collected over 2 yr and qualitatively compared patterns in seston chemistry to the centuries-long record of the elemental composition of sediments.

We assessed diatom fossil abundance by several metrics, relying primarily on relative abundance on a biovolume basis (relative biovolume). Most surveys of diatoms in sediments have relied on direct cell counts to determine relative abundance, so we also measured relationships between this standard measure and sediment chemical composition. Although use of this metric is often valid and can lead to accurate historical reconstruction, it also has the tendency to overestimate the biological importance of small-celled and numerous species over large-celled ones. Because we were attempting to relate diatom community composition to nutrient chemistry, it was important to work with measures analogous to biomass that are most relevant within the framework of resource competition. We also looked at relationships between the absolute abundance of fossils (as absolute biovolume in units of cubic micrometers per microgram) and sediment chemistry and compared the statistical results among all three metrics.

In our assessment of patterns in the elemental composition of seston, we also compared results between years (1996 and 1997). We then briefly considered possible climatic drivers of interannual variability in resource availability that is hypothesized to control the longer term variation in phytoplankton communities and seston chemistry that are preserved in the lake sediments.

Site description and study methodology

Yellowstone Lake sits within the bounds of Yellowstone National Park at an elevation of 2,358 m. It is the largest lake at this (or higher) elevation in North America. The lake

has a surface area of 35,400 ha, a maximum depth of 102 m, and a mean depth of 42 m. It is generally ice covered from late December or early January through late May or early June. Although the lake is dimictic, summer stratification is often weak. Because of relatively low productivity and cold water temperatures, hypolimnetic water directly over the sediments is always well oxygenated and close to 4°C.

Modern studies of the lake have demonstrated that its phytoplankton community is primarily susceptible to nitrogen and light limitation, whereas phosphorus and silica concentrations are generally high as a result of the volcanic soils of the caldera basin in which the lake sits. Episodic silica and even phosphorus limitation are possible nevertheless for short periods during very early spring while surface ice and snow are melting, diluting mineral elements in embayments and the uppermost surface waters (Interlandi et al. 1999; Interlandi and Kilham 2001).

Diatom production through the past decade has been dominated by the centric species *Aulacoseira subarctica* (O. Mull.) Haworth, as indicated by studies of summertime plankton succession (Interlandi et al. 1999) and sediment fossil remains (Kilham et al. 1996). Although *A. subarctica* has not always dominated the diatom community structure in the lake, it has been present since the lake formed during the last glacial retreat from the Yellowstone plateau (Fritz and Theriot unpubl. data). The planktonic diatom assemblage of Yellowstone Lake has remained remarkably simple through time and is primarily composed of seven dominant species. Additionally, Yellowstone Lake holds one modern endemic planktonic diatom, *Stephanodiscus yellowstonensis* Theriot and Stoermer, which evolved from the cosmopolitan diatom *Stephanodiscus niagarae* Ehrenberg over a period of 1,500 yr approximately 9,000 yr ago (Theriot and Stoermer 1984). Previous work on sediment diatoms in Yellowstone Lake (Kilham et al. 1996) showed qualitatively an association between the abundance of *S. yellowstonensis* and drought. In particular, this species was noted in very high relative abundance through the well-documented and severe regional drought of the 1930s.

Water collection—Water samples from Yellowstone Lake were collected weekly from May through September in 1996 and 1997. Samples were generally collected for seston chemistry at a single location in the main basin of the lake at depths of 5, 25, and 45 m. Several samples included in the overall analysis were collected at the lake outlet prior to ice-off. Water was pumped from discrete depths by a peristaltic pump on board our research vessel with a hose attached to a Hydrolab sonde fitted with a depth–pressure sensor. The water was then filtered immediately upon return to the Yellowstone Park Aquatic Resources Office at Lake Village in Yellowstone. Samples for particulate carbon and nitrogen were filtered under constant vacuum through precombusted GF/F filters. Samples for particulate phosphorus and silicon were collected by syringe filtration through polycarbonate filters with a 0.4-μm pore size. All filters were stored frozen in individual containers and shipped to Drexel University for later chemical analysis. All samples for seston elemental chemistry were filtered and analyzed in triplicate, and data

reported here are based on means of the three measures. Phytoplankton samples were taken in separate 125-ml bottles at 5-m intervals from the surface down to 50 m on most dates. Adverse limnological conditions precluded collection of samples at the greatest depths only on rare occasions. Patterns in phytoplankton distribution and their relationships with seston chemistry have been reported previously (Interlandi et al. 1999).

Aquatic analyses—Samples were analyzed for particulate (seston) carbon and nitrogen via combustion and gas chromatography with a Carlo Erba 1106 elemental analyzer. Samples were processed for particulate phosphorus by autoclave persulfate digestion followed by analysis of the sample as soluble reactive phosphorus (SRP) with the ascorbic acid method. Samples were processed for particulate silicon with a sodium carbonate digestion for 2 h at 85°C followed by sample acidification and analysis as SRSi by the heteropoly blue method. Phytoplankton counts on 25-ml subsamples were made with the inverted microscope technique. All limnological methods have been described in detail previously (Interlandi et al. 1999; Interlandi and Kilham 2001).

Sediment collection—Sediments from Yellowstone Lake were collected in August 1998. A 55-cm core was taken at approximately 75 m depth in the main basin of Yellowstone Lake, north of Stevenson Island. The coring location is characterized by a wide and flat subbasin where previously collected sediment cores have shown no evidence of stratigraphic disturbance. The core was collected with a gravity-coring device approximately 35 kg in total weight that was fitted with an automatic check valve and was retrieved with a hand-turned winch aboard the research vessel. The core liners of this device have an internal diameter of 7.62 cm, and the core barrel itself has an outer diameter of 8.25 cm. The core was extruded in open air and sectioned into 0.5-cm slices through the top 10 cm and 0.33-cm slices through the remainder. Sediments were immediately frozen and later shipped to Drexel University for processing. Only the top 32 cm of the core material was processed for chemistry and diatoms, and the results we report here are based on this upper section of the core.

Sediment analyses—Prior to analytical work, all sediments were freeze dried and subsequently stored in tightly capped vials under ambient conditions at Drexel University. Sediment subsamples for carbon and nitrogen determinations were weighed and measured by elemental analyzer (Carlo Erba 1106). Phosphorus was determined by first weighing material and then combusting these subsamples for 2 h at 450°C. Next, the sediments were subjected to an overnight dilute acid digestion in 0.1 molar HCl then pulverized in a teflon-on-glass tissue grinding tube. This slurry was then diluted and processed by an autoclave persulfate digestion followed by determination of SRP. Biogenic silicon in sediments was analyzed by the same method used for seston.

Sediment subsamples for diatom counts were analyzed by first mixing a known mass of sediment into 25 ml deionized water. Several drops of Lugol's solution were added to prevent diatom frustule dissolution. This slurry was vigorously

mixed, and a 1-ml aliquot was pipetted directly into a sedimentation chamber for counting by the inverted microscope technique. Because we were only interested in the major species of planktonic diatoms from Yellowstone Lake, which are readily recognizable in these sediments, no cleaning or other treatment of the sediment was needed. Fossils were enumerated at ×100, except for small *Stephanodiscus* spp., which were counted at ×400. Previous diatom counts in Yellowstone Lake sediments (Kilham et al. 1996) conducted at higher magnification using cleaned samples had indicated that virtually all *Stephanodiscus* frustules <10 μm in diameter were *Stephanodiscus minutulus* (Kutzing) Round.

Where dates are assigned to core depths, these dates were inferred from several sources. Direct Cs-137 measurements made through the top of this core were used to estimate dates after 1958. Earlier dates were inferred from Pb-210–dated sequences and resulting sedimentation rates reported for other cores from the lake (Shero 1994; Kilham et al. 1996) and by matching diatom stratigraphy and sediment depth in this core to the fossil stratigraphies of the previously dated cores. Kilham et al. (1996) found a highly consistent rate of mass accumulation in their Pb-210–dated section of a short core from the lake and extrapolated dates further down the core assuming a constant mass accumulation rate. In particular, we compared the abundance patterns of *Stephanodiscus oregonica* between cores and concluded that the linear sedimentation rate of this core was nearly identical to that of the core described earlier.

Data analysis—Correlation among variables was generally measured using nonparametric rank order tests because the data for measured samples were not normally distributed and numerical transformations did not improve this situation. Where linear regression was used, we report goodness of fit for the linear regression and correlation statistics for the comparable nonparametric test. Comparisons among groups of samples were also made using nonparametric tests, including a median test and Van der Waerden's normal quantile test, depending upon the nature of sample distributions. All statistics were carried out using JMP (SAS Institute) for the Macintosh.

All absolute measures of elemental and fossil composition are calculated based on sediment dry mass. Earlier Pb-210 dating of sediment cores from the lake (Kilham et al. 1996) indicated relatively constant rates of total mass accumulation (even through the major drought period), indicating that allochthonous inputs to the deep sediments of the lake are not highly variable. As such, absolute metrics of biogenic elements and fossils should be indicative of in-lake trends and should not be complicated by changing rates of sedimentation of terrestrially derived inorganic material.

Fossil biovolume was calculated using an average cell volume, based on simple geometry, for each individual species. Twenty frustules of the reported diatom species were measured for each of 10 separate sediment samples spaced evenly throughout the core. No significant among-sample differences were found in cell sizes for any of the diatoms, so a single mean of all measurements for each species was used to calculate the volume per cell throughout the core.
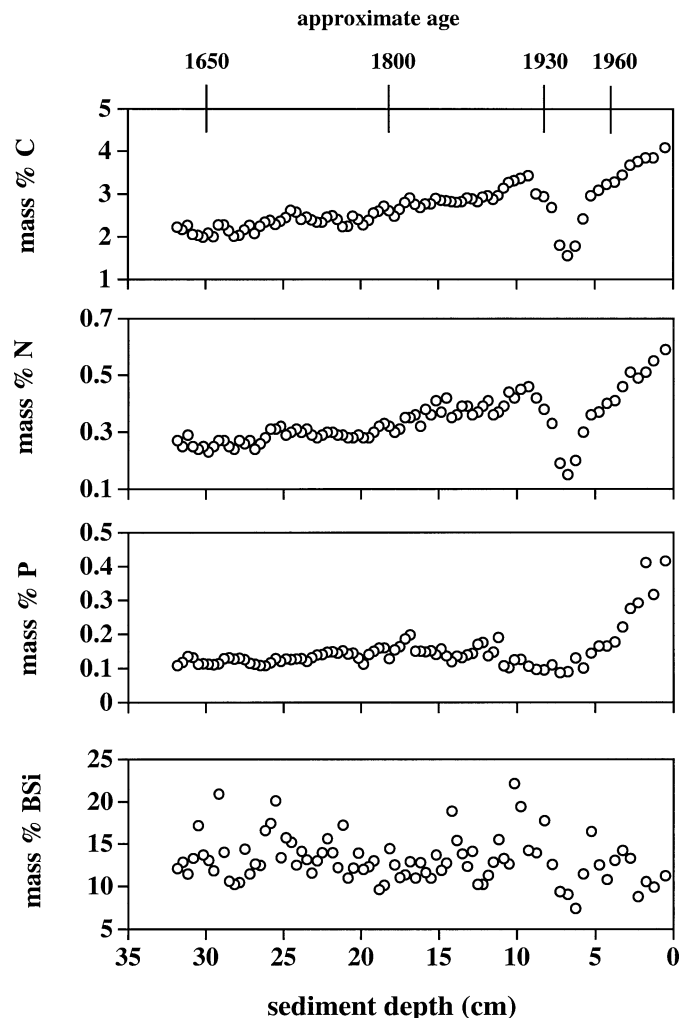

Fig. 1. Elemental composition of sediments from Yellowstone Lake. Sediment core was taken in 1998 in the north basin of the lake. Minimum levels of C and N content correspond to a period of prolonged drought associated with the dust bowl period of the 1930s.

Results

Yellowstone sediments—Sediment chemistry profiles demonstrated distinct patterns through the core in quantities (percentage of total sediment dry weight) of major nutrient elements (Fig. 1). Both C and N increased steadily from 32 cm up through the core to a depth of 10 cm. Additional variation about the main C and N trend lines occurred on a 2–3-cm scale within this section of the core, indicating potential short-term variation in source composition. Sediments immediately above 10 cm demonstrated a precipitous drop in both C and N levels through a depth of 6 cm. In the top of the core, levels of these elements increased sharply toward the surface. Levels of P in the sediment core remained remarkably stable from 32 cm through 10 cm, with slight variation about the main trend line readily apparent. Sediment P increased sharply toward the sediment surface, as did the C and N levels. Levels of Si in sediments were the most highly variable of all these major elements, but Si did not
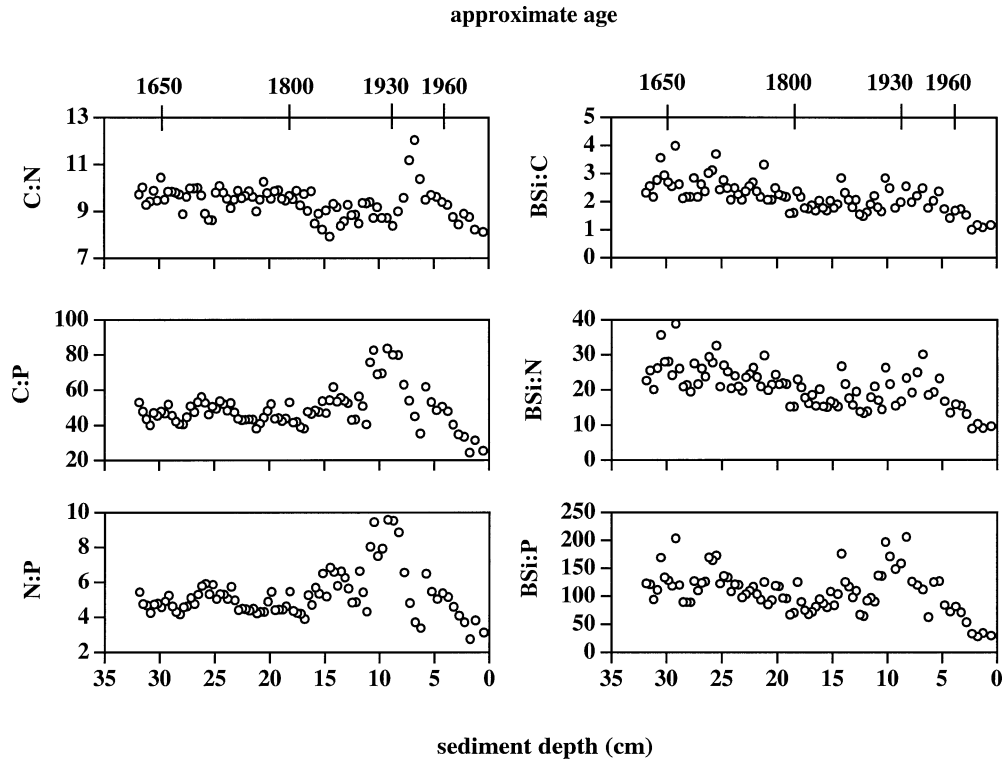
approximate age

Fig. 2.   C:N:P:BSi molar ratios in sediments from Yellowstone Lake collected in 1998.

exhibit a sharp increase toward the core surface. Si levels throughout the core actually decreased slightly from bottom to top (Spearman's $\rho = 0.177$, $P = 0.1062$).

The C:N:P molar ratios also demonstrated distinct patterns through the sediment core (Fig. 2). The C:N ratio decreased from 32 cm through 10 cm. A chemical signal corresponding to the known prolonged drought of the 1930s was readily apparent from 9 cm through 6 cm depth; the C:N ratio climbs above 12 in this section. C:P ratios elicited no particular trend in the bottom section, although sharp shorter term events appear to be traced by this measure, e.g., between 22 and 20 cm depth when the C:P ratio climbs sharply in a linear fashion for five consecutive samples. Such clear shorter term trends in sediment composition occur throughout the record, although interpretations of these subdecade scale patterns would be rather speculative, at this point. C:P ratios dropped precipitously during the drought period around the 1930s, at the same time C:N ratios increased. C:P ratios were remarkably low in general, probably because of the high levels of P in the regional volcanic rocks and the resultant high levels of dissolved P in the overlying lake water. N:P levels generally increased from 18 cm through 9 cm, where the measure became highly variable, including a sharp drop through the drought period.

The ratios of Si to nutrients all tended to decrease with time ($P < 0.001$ by rank order correlation for all cases), with the sharpest decreases occurring near the core surface, probably as a result of near-surface diagenesis of organic material (Fig. 2). The Si:P ratio peaked sharply through the drought period and may have been affected by fine mineral particles. Volcanic rhyolite, which underlies much of the

lake basin, is composed of readily dissolvable amorphous silicates, which can dissolve at the same rates as diatom frustules under the conditions of the chemical digestion.

Yellowstone fossil diatoms—Relative fossil biovolume for the seven major planktonic species is depicted in Fig. 3. *S. oregonica* (Ehrenberg) Hakansson, *Rhizosolenia eriensis* H. L. Smith, and *Cyclotella bodanica* Grunow never constituted more that 6% of diatom biovolume in this short core, but marked trends in their abundance were evident nevertheless. *S. oregonica* was most abundant from 25 cm through 15 cm in the core. This distance corresponds temporally with the period of and surrounding the 18th century, the coldest period of "the little ice age" in this region. *R. eriensis* appeared most abundant in the top of the core, but this lightly silicified species may not have been preserved well further downcore, so interpretation of this trend is problematic. *C. bodanica* was most abundant at 8 cm depth, corresponding well with the most severe drought period on record. *S. minutulus,* a major spring species in recent years, was most abundant at the top of the core, although it was eclipsed by *A. subarctica,* as were all the other species, at the very top of the core. *Asterionella formosa* Hassal did not peak sharply but was in greatest proportion from 15 cm through 10 cm. *A. subarctica,* one of the two most dominant species in the fossil record, did well throughout the core but completely dominated the assemblage in the uppermost section of the core. *S. yellowstonensis,* the other dominant species, tracked directly opposite to *A. subarctica* and virtually disappeared at the top of the core.

Absolute biovolume of all planktonic diatoms and of the

approximate age

Fig. 3. Relative biovolume of fossil planktonic diatoms from Yellowstone Lake sediments. No other species ever constituted >3% of the planktonic fossil biovolume in the core samples.

seven major species is depicted in Fig. 4. Total fossil biovolume was lowest during the drought period of the 1930s and was generally a function of the two major species, *A. subarctica* and *S. yellowstonensis.* Trends in the individual species typically mirrored the trends in relative abundance, particularly for *S. oregonica* and *A. formosa.* The absolute biovolume of *R. eriensis* was highly variable, however, whereas the absolute biovolume of *A. subarctica* (excepting the drought period and surface sediment) showed remarkably little variation.
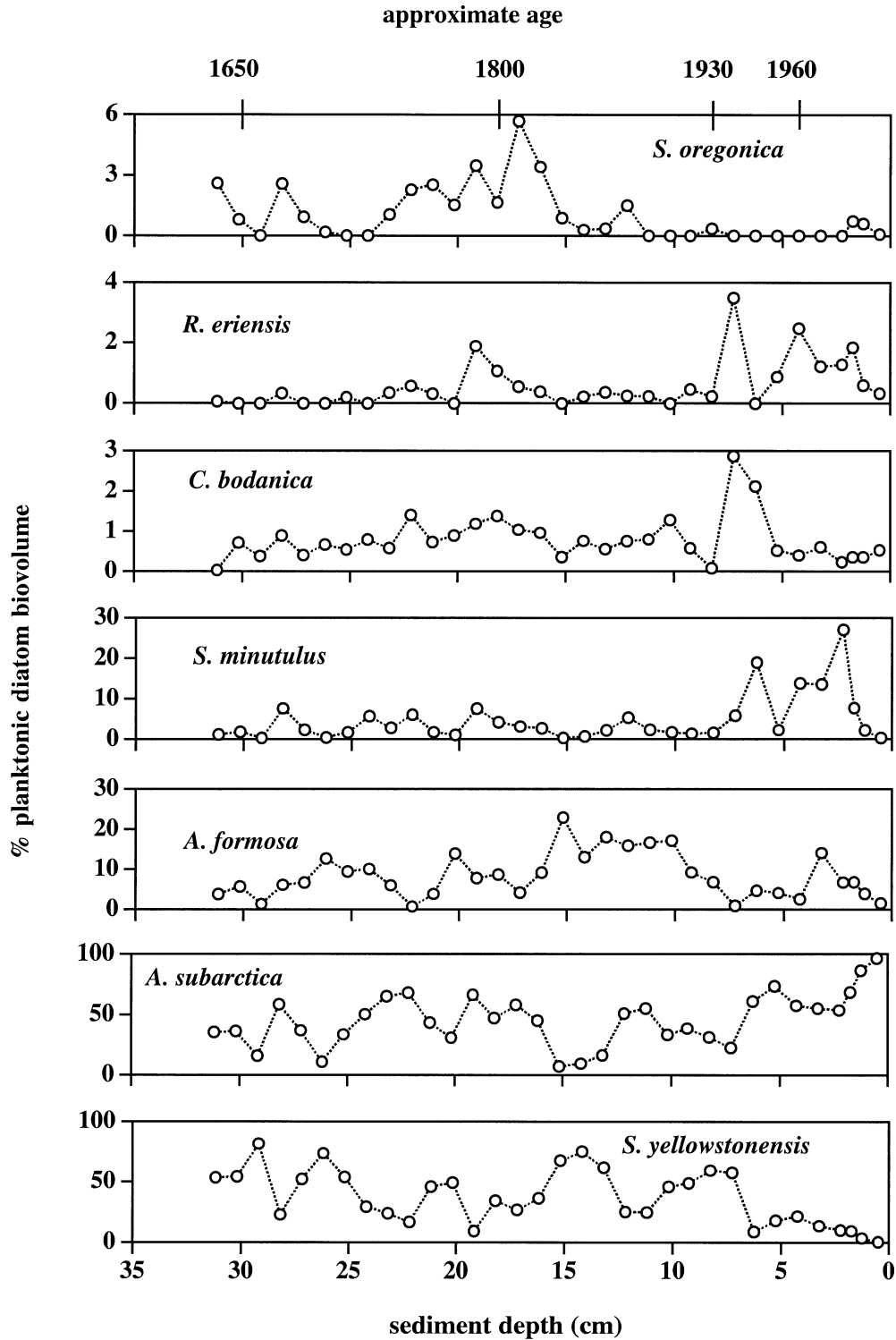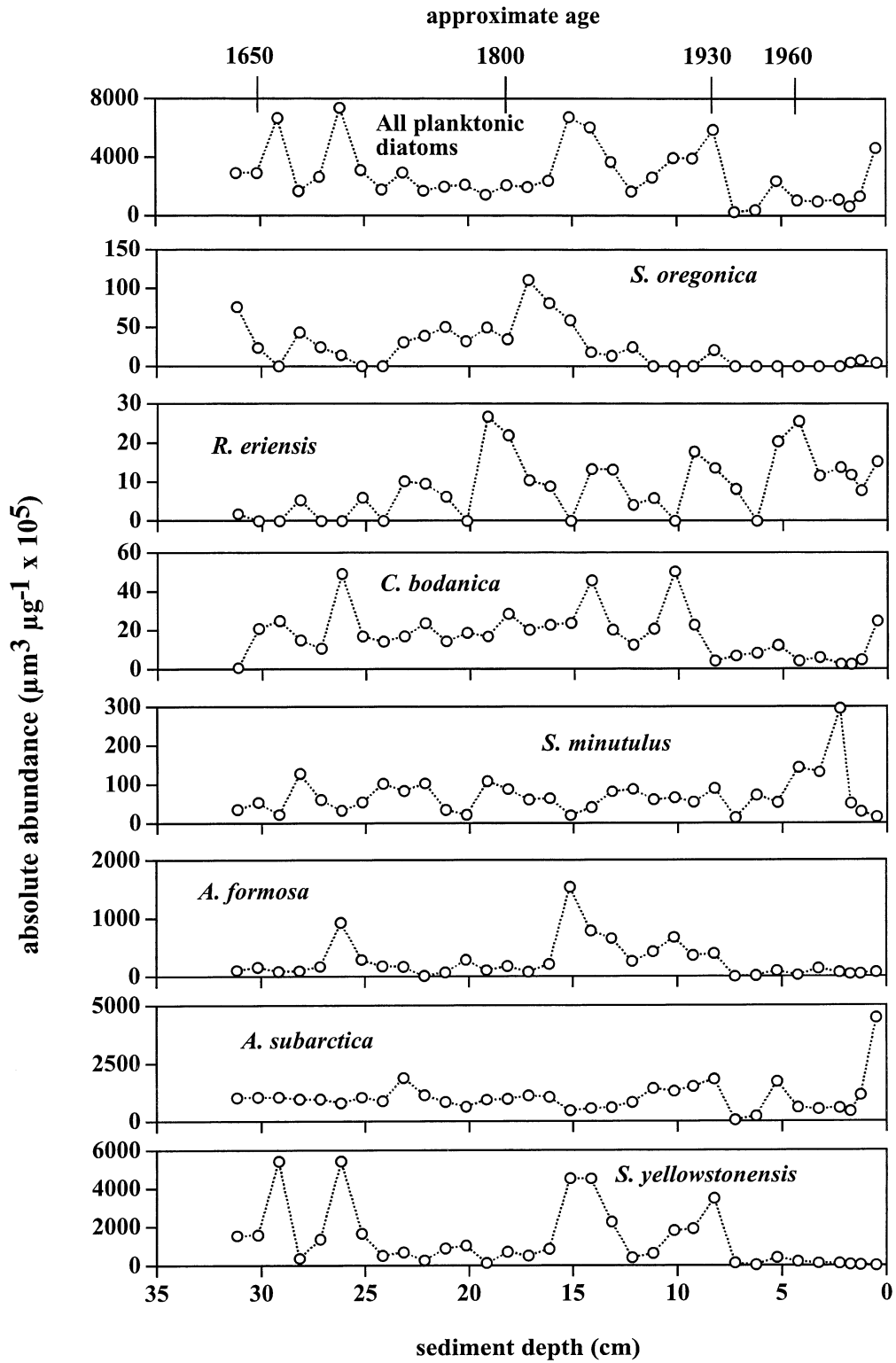
Fig. 4. Absolute biovolume of fossil diatoms in Yellowstone Lake sediments. No other species ever constituted >3% of the planktonic fossil biovolume in the core samples.

Table 1. Rank correlation coefficients between sediment elemental chemistry and the relative biovolume of planktonic diatom fossils* in Yellowstone Lake sediments.

	AS	SM	AF	FnotC	RE	SO	SY	CB	Lg Syn
% C	0.324	0.029	0.275	−0.149	0.413	−0.292	−0.397	−0.369	−0.338
% N	0.260	−0.021	0.305	−0.168	0.372	−0.251	−0.344	−0.418†	−0.331
% P	0.667†	0.369	−0.060	0.061	0.463†	0.175	−0.733†	−0.156	0.192
% Si	−0.428†	−0.546†	0.264	−0.135	−0.323	−0.089	0.485†	0.069	−0.466†
C:N	−0.037	0.271	−0.261	0.382	−0.122	0.108	0.073	0.515†	0.345
C:Si	0.533†	0.467†	0.004	0.083	0.474†	−0.047	−0.619†	−0.259	0.157
Si:N	⁻0.488†	−0.368	−0.085	0.028	−0.416†	0.081	0.572†	0.360	−0.073
C:P	−0.699†	−0.448†	0.348	−0.049	−0.260	−0.258	0.737†	0.034	−0.462†
N:P	−0.672†	−0.491†	0.446†	−0.173	−0.302	−0.268	0.708†	−0.107	−0.539†
Si:P	−0.660†	−0.566†	0.123	−0.119	−0.388	−0.145	0.745†	0.098	−0.399

* AS, *A. subarctica*; SM, *S. minutulus*; AF, *A. formosa*; FnotC, *Fragillaria* sp.; RE, *R. eriensis*; SO, *S. oregonica*; SY, *S. yellowstonensis*; CB, *C. bodanica*; Lg Syn, *Synedra* sp.
† Correlation significant $P < 0.02$.

Fossil diatom–sediment chemistry correlation—Correlation results between the relative biovolume of major individual fossil species and sediment chemistry are presented in Table 1. *A. subarctica* was strongly positively correlated with sediment P and negatively correlated with C:P, N:P, and Si:P ratios. These strong relationships appeared driven in part by the sharp increase in P toward the sediment surface, but this was not an overwhelming factor. *S. minutulus* was negatively correlated with sediment Si and weakly positively correlated with sediment P. *A. formosa* was most strongly and positively associated with the sediment N:P ratio. Although less abundant, *R. eriensis* and *S. oregonica* also showed significant associations with sediment chemistry. *R. eriensis* was positively associated with sediment C, N, and P, whereas *S. oregonica* was negatively associated with sediment C. Of all species, *S. yellowstonensis* was most strongly associated with sediment chemistry. This species was negatively correlated with P and related ratios and positively correlated with sediment Si. *C. bodanica,* although negatively associated with both sediment C and N, was strongly positively correlated with the C:N ratio.

The fossil–sediment relationships determined using relative abundance by cell counts (Table 2) were generally similar to those described above, with a few notable exceptions.

Correlation between *A. subarctica* and sediment chemistry was considerably weaker and in several cases was in the opposite direction. *C. bodanica* relative abundance by cell count was significantly positively correlated with sediment Si content and Si:P ratio.

Associations by absolute biovolume (Table 3) were quantitatively similar to those obtained using relative fossil cell number. Again, correlation between *A. subarctica* and sediment chemistry was generally weaker than when measured by relative biovolume. Correlation between *S. minutulus* absolute biovolume and sediment chemistry was also weak. *A. formosa* was most strongly positively correlated with sediment N:P by this metric, in comparison to the two other measures. Associations with *S. yellowstonensis* were strong again and similar to those measured by the other metrics.

To compare the overall results between the three diatom metrics, we looked at the relative strength of each correlation series by comparing the absolute values of all Spearman's ρ values for each case (Table 4). Correlation was strongest by the metric of relative biovolume, with a median absolute value of 0.3138 for ρ. Correlation between absolute biovolume and chemistry was weakest (median ρ of 0.2523), and the three cases were distinct as measured by a nonparametric median test of central tendencies.

Table 2. Rank correlation coefficients between sediment elemental chemistry and the relative abundance (% total cells) of planktonic diatom fossils* in Yellowstone Lake sediments.

	AS	SM	AF	FnotC	RE	SO	SY	CB	Lg Syn
% C	0.062	0.033	0.032	−0.239	0.428†	−0.189	−0.333	−0.357	−0.395
% N	0.028	0.016	0.079	−0.235	0.398	−0.116	−0.274	−0.380	−0.374
% P	0.198	0.346	−0.351	−0.087	0.378	0.163	−0.635†	−0.405†	0.049
% Si	0.132	−0.381	0.502†	0.179	−0.160	−0.002	0.608†	0.562†	−0.063
C:N	−0.089	0.163	−0.199	0.325	−0.165	−0.072	−0.013	0.323	0.263
C:Si	−0.067	0.392	−0.337	−0.194	0.371	−0.076	−0.632†	−0.643†	−0.190
Si:N	0.034	−0.340	0.231	0.260	−0.331	0.095	0.547†	0.663†	0.214
C:P	−0.299	−0.418†	0.566†	0.128	−0.130	−0.175	0.660†	0.336	−0.302
N:P	−0.245	−0.370	0.663†	0.047	−0.145	−0.145	0.703†	0.285	−0.294
Si:P	0.000	−0.477†	0.461†	0.154	−0.236	−0.064	0.735†	0.565†	−0.054

* AS, *A. subarctica*; SM, *S. minutulus*; AF, *A. formosa*; FnotC, *Fragillaria* sp.; RE, *R. eriensis*; SO, *S. oregonica*; SY, *S. yellowstonensis*; CB, *C. bodanica*; Lg Syn, *Synedra* sp.
† Correlation significant at $P < 0.02$.

Table 3. Rank correlation coefficients between sediment elemental chemistry and the absolute biovolume (μm^3 μg^{-1}) of planktonic diatom fossils* in Yellowstone Lake sediments. Results are identical to those that would be obtained if absolute abundance by cell/frustule counts had been used as a metric.

	AS	SM	AF	FnotC	RE	SO	SY	CB	Lg Syn
% C	0.181	0.139	0.087	−0.157	0.523†	−0.315	−0.254	−0.068	−0.348
% N	0.122	0.105	0.116	−0.148	0.485†	−0.254	−0.206	−0.073	−0.333
% P	−0.033	0.167	−0.379	−0.159	0.330	0.102	−0.654†	−0.293	−0.034
% Si	0.316	−0.141	0.521†	0.317	−0.047	0.001	0.633†	0.582†	−0.012
C:N	−0.112	0.096	−0.196	0.247	−0.246	0.070	−0.035	0.020	0.231
C:Si	−0.168	0.259	−0.320	−0.238	0.345	−0.111	−0.637†	−0.477†	−0.214
Si:N	0.099	−0.250	0.212	0.279	−0.343	0.134	0.546†	0.450†	0.219
C:P	0.056	−0.107	0.627†	0.306	−0.032	−0.146	0.733†	0.388	−0.170
N:P	0.098	−0.041	0.710†	0.249	−0.015	−0.148	0.775†	0.381	−0.164
Si:P	0.215	−0.238	0.485†	0.287	−0.158	−0.049	0.784†	0.499†	0.006

* AS, *A. subarctica*; SM, *S. minutulus*; AF, *A. formosa*; FnotC, *Fragillaria* sp.; RE, *R. eriensis*; SO, *S. oregonica*; SY, *S. yellowstonensis*; CB, *C. bodanica*; Lg Syn, *Synedra* sp.
† Correlation significant at $P < 0.02$.

Next, we compared the general relationships between the associations calculated by the three metrics by comparing the correlation results obtained by each measure against the other two. Correlation results between relative cell number and relative biovolume were moderately similar ($\rho = 0.7792$, $P < 0.0001$, $n = 90$). Correlation results between relative biovolume and absolute biovolume were most dissimilar ($\rho = 0.5933$, $P < 0.0001$, $n = 90$), whereas results by relative cell count and absolute biovolume were most similar ($\rho = 0.9105$, $P < 0.0001$, $n = 90$). The results suggest that these three metrics may give qualitatively similar results, but they are not interchangeable.

To assess the possible confounding effect of early diagenesis on these relationships, we repeated the correlation analyses excluding all samples from the sediment surface through 10 cm depth. In the case of P-related measures (%P, C:P, N:P, Si:P) based on relative biovolume, the correlation results were highly similar to those calculated using the entire data set ($\rho = 0.8978$, $P < 0.0001$, $n = 36$). Of all relationships based on relative biovolume that were deemed significant ($P < 0.02$) for the entire data set (Table 1), the results of correlation analyses were again highly similar when calculated on the 10–32-cm data only ($\rho = 0.9049$, $P < 0.0001$, $n = 29$). The relative biovolume correlations for 10–32 cm were again stronger (mean absolute value of $\rho = 0.3141$) than those for relative abundance data (mean abso-

lute value of $\rho = 0.2897$) and for absolute biovolume data (mean absolute value of $\rho = 0.3006$). Thus, early diagenesis did not appear to have a marked effect on the measured diatom–chemistry relationships.

Seston chemistry—All seston data for samples collected in 1996 and 1997 at a single pelagic sampling station in Yellowstone Lake were pooled, and results are presented in Table 5. Algal biomass was generally higher in 1996 (data not shown), as reflected in the tabulated results of the particulate concentrations of individual elements in the lake water. Particulate C was significantly higher in 1996 than in 1997, as was particulate N. Seston P, however, was not significantly different between the 2 years. Seston Si was significantly higher in 1997 because the heavily silicified *A. subarctica* dominated the phytoplankton in 1997. Average C:N was slightly higher in 1996, whereas in both years there was moderate N deficiency in the phytoplankton as indicated by the generally accepted metrics of Healey and Hendzel (1980). C:P ratios were much lower in 1997, whereas average values for both years were well below those found in most temperate lakes (Hecky et al. 1993). Average N:P ratios also indicated a predominance in N limitation over P limitation.

C:N ratios in lake seston were slightly higher than those in surface sediments but were well within the range of variation in the sediments downcore. C:P ratios in surface sediments and throughout the core were much lower than those for lake seston collected in 1996 and 1997 and were lower than those measured in most lake sediments. Sediment N:P ratios were also considerably lower throughout the core (except just prior to the drought period of the 1930s) than in lake seston.

Discussion

The problem of preferential elemental diagenesis in aquatic sediments has often precluded the direct use of major element composition to infer past environmental conditions. Even when these data have been available along with a biologically based transfer function, often little mention has been made of the apparent similarities between major ele-

Table 4. Comparison of absolute values of Spearman's ρ for all correlations of fossil planktonic diatoms versus sediment elemental composition. Correlation values for the three measures are illustrated in Table 1, 2, and 3. A rank-order nonparametric median test indicates that measures are distinct and that associations between fossil relative biovolume and sediment elemental composition are the strongest ($\chi^2 = 10.72$, $P = 0.0047$).

Statistic	Relative biovolume	Relative abundance	Absolute biovolume
Mean	0.3133	0.2783	0.2598
Median	0.3138	0.2523	0.2145
SD	0.2012	0.1934	0.2009
n	90	90	90

Table 5. Seston elemental composition in Yellowstone Lake over two summers. Elemental ratios are on a molar basis. Both years were preceded by higher than average winter precipitation and snowpack. However, summer was much warmer and dryer in 1996 than in 1997, which is reflected in generally higher C levels and higher ratios of C to nutrients. Higher seston Si in 1997 reflects a much larger contribution of the heavily silicified *A. subarctica* to the biomass of that year (data not shown). Differences between years were assessed by a non-parametric normal quantiles test because data were not normally distributed.

Parameter	1996			1997			Van der Waerden	
	Mean	SD	n	Mean	SD	n	χ^2	P
pC (μmol L^{-1})	18.2	9.52	50	11.6	3.21	52	16.49	<0.0001
pN (μmol L^{-1})	1.98	1.25	50	1.34	0.455	52	7.718	0.0055
pP (μmol L^{-1})	0.185	0.129	50	0.194	0.167	53	2.601	0.1068
pSi (μmol L^{-1})	3.33	2.96	50	6.04	3.01	53	24.52	<0.0001
C:N	9.79	2.05	50	8.94	1.35	52	5.028	0.0249
C:Si	7.65	5.74	47	2.64	1.70	52	37.42	<0.0001
Si:N	2.00	1.45	50	4.89	2.90	52	31.36	<0.0001
C:P	105	29.2	50	69.4	13.9	52	41.64	<0.0001
N:P	11.2	3.85	50	7.98	2.09	52	21.75	<0.0001
Si:P	18.63	8.41	50	34.3	15.7	53	27.90	<0.0001

ment composition and the inferred historical condition. Likewise, in sediment research attempting to link trends in stable isotopes of C, N, and O, often the C:N ratio is highly correlated with isotopic composition, but this is also rarely discussed (e.g., Hassan et al. 1997; Hodell and Schelske 1998; Brenner et al. 1999).

In sediments in deep, cold lakes, these associations should be strongest and most reliable because diagenetic processes are likely to have the most minimal impact on sediment composition in these types of systems (Eadie et al. 1990). For example, den Heyer and Kalff (1998) demonstrated that the rates of mineralization of organic material are functions of depth and temperature within and across lakes, with the lowest rates occurring in the deepest, coldest waters. High levels of combined Si and P in sediments, as in Yellowstone Lake, also can limit diagenetic processes by shifting equilibrium toward solid phases within sediment pore water (Hartikainen et al. 1996).

The most likely causes for temporal variation in diagenetic processes in the pelagic sediments of Yellowstone Lake would be changing rates of sediment burial and dynamic chemical equilibria driven by varying solute concentrations in overlying water. Long-term drought, for instance, would be expected to increase dissolved silicate and phosphate levels and to decrease influx of N to hypolimnetic water. Also, source particulate material would be characterized by high C:N and low N:P. Under these conditions, rates of N diagenesis in surface sediments should increase as a result of slower burial and greater N demand from consumers and bacteria. Si diagenesis should decrease as a result of higher dissolved silicate levels and a shift in silicate equilibrium toward the solid state. In essence, the primary result of these processes should be an amplification of the in-lake seston stoichiometric characteristics. High C:N seston produced during a drought should produce even more N-deficient sedimentary material. Low C:Si seston should produce sediment even further C deficient. As a result of these and other feedback mechanisms, composition of major elements in the sediment could amplify within-lake variation and make it

possible to detect variation in lacustrine processes that could not otherwise be measured directly.

In comparisons between seston and sediment stoichiometry in Yellowstone Lake, lower surface sediment C:N levels may indicate greater losses of C by diagenesis, but the differences were small enough to suggest that large changes in sediment C:N stoichiometry due to diagenesis are unlikely. Throughout the core, sediment C:P levels were considerably lower than those measured in seston, which may indicate that particulate material in Yellowstone Lake is preferentially stripped of C by bacteria and consumers (which are probably not P limited in this system) while sinking through the hypolimnion. Additionally, sediment N:P levels were also lower than those in seston samples, suggesting that N may also be removed from seston at a faster rate than P during sinking. Samples collected from sediment traps in Yellowstone Lake in 1995 and 1996 support these interpretations; C and N content of sediment tended to decrease with increasing depth ($P < 0.01$ in all cases), but levels of P remained unchanged (Eadie unpubl. data).

Trends in recently deposited sediments in Yellowstone Lake indicate consistently increasing levels of C and N through time when temporal patterns are superimposed on the core stratigraphy. Even considering the potential for early diagenetic removal of organic material (which would deplete C and N at depth in the core), it appears that overall productivity in the lake has been increasing by these combined measures. The lake is primarily N limited (Interlandi and Kilham 1998; Interlandi et al. 1999; Interlandi 2001), which suggests a trend of several centuries of steadily increasing N loading to the lake. Unfortunately, we did not measure sediment composition far enough down the core to develop baseline sediment N levels. A liberal interpretation of the N record in the sediment core might suggest that rates of N loading and system productivity began to increase rapidly at a sediment depth of 20 cm (corresponding to ca. 1780). Rates of change (slope of %N or %C vs. sediment age) in C and N content of sediment further downcore (32–20 cm), however, were still positive and significantly different from

zero ($P < 0.001$ for both cases). The sharp dip in C and N content that begins at 9 cm (ca. 1920) and results in a sharp peak in the sediment C:N ratio at 6.5 cm depth is evidence for severe effects of drought on both pelagic and sedimentary processes. This peak may be an example of the hypothesized feedback effect by which seston that is sparse and characterized by high C:N levels produces sediments that are depleted of organic matter and depleted of N to an even greater degree. This result would be a combined function of greater rates of diagenesis from slowed sediment burial and more efficient removal of N and C from sinking particles by zooplankton and bacteria. No long-term directional climatic trends are apparent in regional historical meteorological measures (precipitation or temperature) that might cause long-term changes in organic content in the lake sediments. Further, land use in the Yellowstone Lake watershed is minimal because the area is protected as part of Yellowstone National Park and surrounding wilderness areas. As such, increases in atmospheric N over the past several centuries (Vitousek et al. 1997) are a likely cause of the long-term trends in sediment C and N content.

The increases in C and N through time in the core section are small on a percentage basis, but they are large on the basis of relative mass accumulation. Given the relatively constant sedimentation rate in the lake over the past centuries (Kilham et al. 1996) and in general (Shuey et al. 1977), current rates of C and N accumulation are double the rates in the lower section of the core. A definitive test of the mechanism behind the apparent increase in C and N accumulation might be conducted using controlled experiments to assess rates of C evolution from discrete sediment layers or by resampling of sediments in decades to come. These approaches would allow exploration of the fraction of the increase attributable to century-scale diagenesis. Measures of C and N isotopic variation in sediments may also yield insight into these processes, and work along these lines will be incorporated into future work on these lake sediments.

Human-mediated increases in N loading via the atmosphere have caused changes in diatom productivity and assemblage composition in lakes in Colorado dating back about 50 yr (Wolfe et al. 2001). Severe assemblage changes have not occurred in Yellowstone Lake, however, because the volcanic soils of the lake basin yield large amounts of dissolved Si and P, allowing N limitation to continue to predominate.

The absolute levels of P and Si did not increase steadily up through the core. P increased rapidly only in the upper section, and Si exhibited a weak decreasing trend through time. These factors taken together with the C and N trends suggest a decrease in the relative dominance of Si-rich diatoms and a shift toward greater abundance of other algal groups. This shift is further supported by the long-term decreasing trends with time in the Si:C, Si:N, and Si:P ratios in lake sediments (Fig. 2). Shero (1994), who interpreted sediment silica content and diatom composition in modern submerged and older exposed sediment in the Yellowstone Lake basin, reached a similar conclusion of decreasing diatom production in the lake over the past 4,000 yr. Single-celled blue-green algae are the most common of the nondiatom algae in the lake and can make up the major fraction of the biomass during certain times (Interlandi et al. 1999). Analysis of algal pigments in short sediment cores from the lake might be useful to test the idea of a shift in algal composition, but all material from this core has been dried, making it unsuitable for such work.

The sharp increase in sediment P content through the top 10 cm of the core suggests an early diagenetic effect on the sediment stores of this element. Alternatively, the profile may indicate the occurrence of P mobilization through these most recently deposited sediments, or some combination of the two processes may be at work. A portion of the increase in sediment P toward the surface, however, would also be consistent with increasing productivity in this lake. Because the lake is primarily N limited and dissolved P levels are always above growth-saturated levels (ca. 0.3 μM; Interlandi and Kilham 2001), phytoplankton in this lake should have considerable capacity for storing excess P via luxury consumption. Thus, if productivity has increased, resulting in a greater transfer of autotrophic production to the sediments, phytoplankton P would be expected to accumulate in the sediments at a faster rate relative to other inorganic materials that make up the major fraction of sediment mass. Regardless of the mechanism behind elevated P levels in surface sediments, this trend did not significantly affect the diatom–chemistry relationships found in the sediment core, and it had little effect on our interpretations of the diatom–resource relationships in the lake.

Of the three measures of planktonic diatom abundance in the sediment core, relative biovolume produced the strongest associations with sediment chemistry. In light of the broader utility of this metric in conjunction with process-based theories of phytoplankton growth and succession, we recommend further exploration of its use and further comparison with the other more common measures of relative abundance based on cell count and absolute abundance, particularly in studies that rely on inferences from strictly planktonic diatoms. Our measure of absolute biovolume is directly interchangeable (for correlation analyses) with a measure of absolute abundance based on cell count. We urge other investigators to make the additional step of calculating frustule sizes to develop these associations, and we further recommend the use of the relative biovolume metric in the development of transfer functions and calibration models using phytoplankton to reconstruct pelagic chemistry in paleolimnological research. Although this approach would clearly be problematic when incorporating both benthic (usually larger) and planktonic (usually smaller) organisms into a single survey, it should be beneficial when one functional group of diatoms is considered on its own. Such an advance would help to bridge an unfortunate gap that exists between those primarily engaged in physiology-based limnological ecology and those relying on empirical associations of surface sediments and water chemistry in the development of models for ecological prediction and reconstruction.

Possible ecological mechanisms behind patterns in fossil diatom composition in Yellowstone Lake have been previously discussed (Shero 1994; Kilham et al. 1996), but more recent empirical and experimental work on this lake system has provided a more substantive understanding of these processes. *C. bodanica,* for instance, appears to gain advantage

from a capacity to remain positively buoyant, allowing it to remain in high-light, low-nutrient near-surface water during calm late-summer periods. This species was negatively correlated with both %C and %N in the lake sediments but was associated strongly and positively with sediment C:N levels. This is exactly the seston quality expected when *C. bodanica* is most successful: low total biomass concentrations with high-light, low-N conditions producing high C:N seston. The strong associations of *S. yellowstonensis* with sediment P (negative) and Si (positive) are driven in part by the fact that this diatom was very low in abundance in the most recent P-rich sediments. This scarcity may indicate a propensity of this diatom to grow when diatoms are most abundant and P-rich blue-green algae are not. Kilham et al. (1996) hypothesized that this diatom does best during droughts when light and Si are high and N is low. Although *S. yellowstonensis* was not strongly associated with sediment C:N, it was positively associated with Si:N. A smaller congener, *S. minutulus,* has a high P requirement and low Si requirement and is typically viewed as a low Si:P specialist (Lynn et al. 2000). These patterns were all apparent in the associations of this diatom with sediment chemistry. Although *A. subarctica* is a relatively heavily silicified diatom, its abundance was negatively correlated with sediment Si content. In general, Si content of the sediment appeared to be controlled by the abundance of *S. yellowstonensis* fossils, which are very large and even more thickly silicified than *A. subarctica. A. subarctica* typically does best when springtime stratification is delayed by cold rainy weather (Kilham et al. 1996). Its positive associations with sediment C, N, and P may be driven partly by its strong presence in the most recent sediments but might also indicate its tendency to occur when the single-celled blue-green algae are most abundant and driving sediment organic content. Because exclusion of the uppermost sediment samples had little effect on correlation results, the latter explanation would seem more reasonable.

Both the relative and absolute abundance of *S. oregonica* were elevated between 26 cm and 18.5 cm in the sediment core, which was deposited during the "little ice age," indicating a preference of this species for sustained cold and wet weather. No strong associations between this diatom and sediment chemistry were apparent. The sharp peak in absolute abundance of *A. formosa* at 15 cm was followed by a period of moderately high relative abundance through 10 cm. This abundance coupled with a strong positive association with sediment N:P levels suggests that this species benefits from a moderate climate generating high levels of winter precipitation and N loading combined with relatively warmer temperatures and early onset of summer stratification. The high abundance of *S. minutulus* in the period following the extended drought of the 1930s follows the general ecological characterization of this alga as an opportunist, or r-selected species.

Based on the low C and N levels in the core resulting from this extended drought, it appears that desertification of large lakes may occur in direct parallel to the occurrence of this phenomenon in surrounding terrestrial systems. Prolonged drought, as opposed to short-term severe drought, may force important feedback responses of internal nutrient

cycles in these lakes. In the case of the Yellowstone Lake basin, very low external N loading over decade scale periods appears to force depletion of sediment N stores, resulting in much lower internal regeneration of N. Over this time scale, the decreased diatom biomass from low total available N may result in diminished seed populations needed to inoculate the spring algal bloom. In such a scenario, when long-term drought is followed by recovery or increased winter precipitation, the most quickly growing species may have an advantage over those that are more efficient at utilizing low levels of resources but are in very low abundance. Since the end of this prolonged drought period, winter precipitation in the Yellowstone region has been higher in general, and droughts have been shorter. As a result, the extended period of high precipitation may have allowed the slowly growing but more efficient (at light and N) *A. subarctica* to catch up to *S. minutulus* and surpass it in relative dominance in the most recent decades.

Paleolimnological surveys in the midwestern U.S.A. found that lakes and their diatom communities responded very strongly to the drought of the 1980s (Laird et al. 1998), but both sediment chemistry and fossil diatoms in Yellowstone Lake were clearly affected more strongly by the earlier 1930s drought. A general survey of climatic conditions (using public data from the National Climatic Data Center) in the Yellowstone region indicates that the 1930s drought in this area was more severe and much longer. Some regional locations actually experienced lower than average (based on 1912–2000 data) winter precipitation every year from 1921 through 1941. The 1980s drought lasted about 5 yr in the region and was not apparently severe enough to affect lake processes as dramatically.

Surveys of related literature yielded only one directly comparable study (Steinberg and Trumpp 1993) in which correlation among fossil diatoms and sediment chemistry was assessed. In that study, the authors compared relative frustule abundance to sediment Si and P levels, including different operational P fractions. In that study, niches for 13 diatoms were described along the Si:P gradient, and levels of correlation (maximum $\rho = -0.721$) were similar to those found in our study. As in our study, Steinberg and Trumpp found a strong positive relationship between *A. formosa* and BSi ($\rho = 0.422$) and a strong positive relationship between *S. minutulus* and organic P ($\rho = 0.400$). The paucity of such studies is likely a result of two problems. First, there has previously been an unfortunate but well-recognized divide between those focused on paleolimnological surveys and those studying the physiological ecology of phytoplankton (Smol 1991; Kilham et al. 1996). Second, the effort required to process enough fossil assemblage and sediment chemistry samples to uncover significant relationships has been a practical limitation. Recently, physiological and paleolimnological studies have been converging (e.g., Kilham et al. 1996; Anderson et al. 1997; Saros and Fritz 2000), and faster analytical techniques such as near-infrared analysis of sediment chemistry (Malley et al. 2000) are on the horizon. Thus, the opportunities for this line of research look promising for the near future.

The relative importance of ecological mechanisms regulating algal community structure has been extensively de-

bated. Currently, there are two main lines of reasoning. First, regulation of phytoplankton community structure by resource availability and competition follows the process theory of Tilman (1982). Second, the importance of variable growth strategies after the Plankton Ecology Group (PEG) model (Reynolds 1997) generally suggests dominating roles for initial physical conditions and opportunism. Our results suggest that complex interplay between these two mechanisms may be at work in the Yellowstone pelagic system. Both short-term and long-term quasiequilibria act to regulate the seasonal and decade scale succession of phytoplankton within the aquatic system. Opportunism and variable growth strategies, however, may be more important following long-term disturbance to the system, as in the case of the prolonged drought earlier this century. Although the data supporting this hypothesis are tenuous, it is exciting to speculate that the balance between disturbance and equilibrium can be measured at both the seasonal and decadal scales within pelagic systems! Consideration of such matters of temporal scale when interpreting paleolimnological patterns is crucial to developing appropriate connections between the paleontological record and aquatic ecology (Anderson 1995).

Associations between fossil diatom abundance and sediment chemistry were not always similar to those determined previously between living communities and seston chemistry in large lakes of the Yellowstone region (Interlandi et al. 1999). Additional examinations of seston chemistry and relative abundance in Yellowstone Lake only, using 1996 and 1997 data, did not always result in relationships that were significantly similar to those measured in the lake sediments. In the case of *S. minutulus,* however, the relationships between the relative abundance of this species and particulate elemental ratios in seston from 1996 and in the sediments were nearly identical ($\rho = 0.8857$, $P = 0.0188$, $n = 6$). For *A. formosa,* the relationships between the relative abundance of this species and the particulate elemental ratios in seston (from 1996 and 1997 in Yellowstone Lake only) and in the sediments of that lake were highly similar ($\rho = 0.8256$, $P = 0.0416$, $n = 6$) Otherwise, the general lack of agreement between the two types of data is in opposition to our initial expectations, but this discrepancy can be explained in the context of the previous paragraph. Although the mechanisms regulating phytoplankton succession on the seasonal and decadal scales are the same, their relative importance varies along this scale. For example, *S. yellowstonensis* was highly correlated with sediment chemistry in accordance with its description as a drought species. In seston data from 1996 and 1997, however, this species showed no strong association with chemistry (*see* Interlandi et al. 1999, for seston associations in 1996). In these 2 years, however, *S. yellowstonensis* was extremely rare. It was encountered in only one of every few samples collected during both seasons. Under such conditions, its low numbers would preclude it from becoming dominant in a single season, even if it were growing at a faster absolute rate than other species. It might take years of ideal conditions (prolonged drought) for *S. yellowstonensis* to regain its competitive advantage in absolute numbers. Also, seasonal and interannual diatom–chemistry relationships may measure somewhat different properties. A spring diatom that grows in drought years might theoreti-

cally be expected to be negatively associated with $C:N$ in all samples collected in a given year because spring communities have access to more available dissolved N than do summer communities. This same diatom, however, would be expected to be positively associated with average lake seston $C:N$ among years because it grows in drought years, which are characterized by high $C:N$ in general. In short, sediment chemistry integrates time, and at the scale we have examined here, it preserves longer term patterns driven by interplay between resource competition and disturbance in the natural environment.

The apparent increase in total system productivity and decrease in diatom biomass over the past several centuries in Yellowstone Lake, which is supported by the sediment chemistry and diatom fossil abundance, suggests that increases in N loading independent of changes in regional precipitation are occurring in the region. This process effectively invalidates a direct assumption of our paleolimnological climatic reconstruction technique, i.e., that resource loading is a direct function of climate. The long-term increases in N loading are not in accordance with our knowledge of historical regional climatic trends and appear to be directly affected by increases in atmospheric N levels. As such, an additional time-dependant transfer function is needed to adequately reconstruct climate from diatom–resource linkages in this and other similar lake systems.

Our assessment of fossil diatom–sediment chemistry relationships suggests that sediment elemental stoichiometry may be similar to that of source seston material, with internal regeneration of limiting elements serving to amplify the time-integrated signal of sediment elemental stratigraphy. Fossil diatoms were highly associated with sediment elemental chemistry, suggesting that resource availability can regulate phytoplankton community structure at the interannual to decade scale.

The strongest associations between sediment chemistry and fossil diatom composition were found using the measure of relative biovolume. Further critical evaluations of this metric are needed alongside the measure of relative abundance by cell count because of the importance of relative biomass for community ecology and ecological processes in general and the likelihood of improved model development and reconstruction with its use.

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