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Susan S. Kilham
Drexel University, kilhams@drexel.edu

Edward C. Theriot
Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania

Sherilyn C. Fritz
University of Nebraska-Lincoln, sfritz2@unl.edu

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Susan S. Kilham
Department of Bioscience and Biotechnology, Drexel University, Philadelphia, Pennsylvania 19104-2875

Edward C. Theriot
Academy of Natural Sciences of Philadelphia, 1900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103-1195

Sherilyn C. Fritz
Department of Earth and Environmental Sciences, 31 Williams Drive, Lehigh University, Bethlehem, Pennsylvania 18015-3188

Abstract

Resource-based physiology of the eight important planktonic diatom species in the large lakes of the Yellowstone region can be used to explain their relative abundances and seasonal changes. The diatoms are ranked along resource ratio gradients according to their relative abilities to grow under limitation by Si, N, P, and light. Hypotheses based on resource physiology can be integrated with observations on seasonal changes in diatom assemblages to explain the present distributions of diatoms and to test the causal factors proposed to explain diatom distributions over the Holocene. Knowledge of the limnology of these lakes and process-oriented physiology provide the basis for a more detailed interpretation of the paleorecord and a firmer basis for landscape-level transfer functions for fine-scale climate reconstruction.

Among biological indicators of climate change in lacustrine sediments, diatoms have highly resolved temporal sensitivity (on the scale of seasons, years, and decades) because of their relatively short generation time. Although land plants experience climate more directly, pollen records have some degree of temporal inertia because many land plants have lifespans of decades or more. In contrast, diatoms experience climate change indirectly through changes in lake level, time of ice-out, stratification, and nutrient inputs (*see* Smol 1990; Lamb et al. 1995). To date, most climate reconstructions using diatom assemblages rely on establishing correlations between diatom distributions and climate-related variables (Pienitz and Smol 1993; Pienitz et al. 1995; Dixit et al. 1992; Fritz 1990). Such an approach cannot address the basic ecological processes involved in cause and effect.

We propose a hypothetical framework designed to better understand the links between climate change, limnological change, and diatom assemblages by examining cause and effect processes. Our focus is on the large lakes in the vicinity of Yellowstone National Park, which have been the subject of intense investigations on landscape

(Hamilton 1987; Whitlock et al. 1991), climate (Barnosky et al. 1987; Waddington and Wright 1974; Whitlock and Bartlein 1993), and limnological (Theriot et al. in prep.) change.

Climate-lake-diatom links

The single most studied variable in climate research is probably temperature. Smol (1990) argued for the use of diatoms in paleoclimatic reconstruction, suggesting that temperature optima for diatom species might be an appropriate indicator of climate. Of all of the environmental variables, temperature captured most of the variation in diatom species distributions, even if it was not necessarily a direct mechanism. Pienitz et al. (1995) used this approach to study climate change across the treeline in Canada. We believe that temperature is likely to be only a proxy for factors affecting changes in diatom assemblages because of numerous observations of temperature anomalies in diatom distributions. On the other hand, a number of studies indicate that resource-related competitive interactions are a major component underlying the distribution of diatom species (e.g. Sommer 1994). Additionally, diatoms show little variation in ability to compete for nutrients across temperature gradients from 5 to 20°C (van Donk and Kilham 1990).

Lakes are primarily linked to climate through ambient temperature, solar radiation, wind (Hostetler and Bartlein 1990), rainfall directly on the lake, and terrestrial runoff. Stratification changes and timing of ice formation and loss are driven by wind energy and solar inputs, which affect mixing depth, which in turn affects the available light and redistributes nutrients from direct rainfall and

runoff. Variation in terrestrial runoff itself has several climate-linked components, including vegetation, frequency of forest fires, and patterns of surface and groundwater hydrology. All of these factors—nutrient concentrations, lake level, and thermal dynamics—directly affect algal abundance and community dynamics; these direct linkages can be inferred from the diatom record of a sediment core.

Water-column mixing processes are undoubtedly one of the dominant controls on algal community structure and succession (Reynolds 1980, 1984). The date of ice-out and duration of spring overturn, for example, control the delivery of nutrients from the hypolimnion to the epilimnion by deep-water mixing. Years of early ice-out and prolonged spring overturn should be characterized by diatom species typical of higher ambient nutrient concentrations, but with low light and low temperature requirements. These climatic conditions might also favor large, heavily silicified diatoms that can survive only during periods of increased turbulence. The relationships between lake circulation patterns and diatom community structure have been used successfully in northwestern Minnesota to reconstruct climatic change from sedimentary diatom assemblages (Bradbury and Dean 1993).

Investigations in saline and subsaline lakes have used diatoms to reconstruct patterns of midcontinent aridity (Fritz et al. 1991, 1993; Radle et al. 1989). Surface sediment diatom assemblages from a variety of habitats are correlated with ionic concentrations. In a closed basin, ionic concentration varies with water-level changes driven primarily by fluctuations in precipitation minus evaporation. Diatom assemblages are then linked statistically by a transfer function to ionic concentrations and climate change. Although the transfer functions are mathematically rigorous and have been empirically tested (Fritz 1990), deviations from expected values in empirical tests could be explained by a better understanding of diatom physiological ecology. There are many observations on changes in diatom assemblages and environment, but there are few tests of the hypotheses proposed to link observations and processes.

In saline lakes, climate-driven changes in ionic concentration are sufficiently great to cause changes in the species assemblage of biological organisms. In freshwater and hydrologically open lakes, however, water chemistry typically does not change sufficiently to exceed the ecological thresholds of most diatom species; thus a more subtle and refined approach is necessary to obtain clear climatic information from changes in diatom assemblages. In particular we argue that a knowledge of diatom resource physiology will allow us to better utilize diatoms as tools for climatic reconstruction, especially in freshwater.

One of the striking features of lacustrine records is that there are relatively few species of dominant planktonic diatoms, and these are mainly in the genera *Aulacoseira*, *Stephanodiscus*, *Cyclotella*, and *Fragilaria*. Species in these genera are important indicators of climatic change in African lakes (Kilham et al. 1986; Gasse et al. 1983; Kilham 1990; Lamb et al. 1995). A number of hypotheses have been suggested (Kilham et al. 1986; Kilham 1990) to link specific physiological characteristics of species to climate-related limnological features, including major ion and nutrient chemistry, depth, surface area, turbulence, water-column temperature and mixing, and food-web structure, most of which are correlated with climate.

Hostetler and Giorgi (in press) modeled the thermal structure of Yellowstone Lake and suggested that a doubling of atmospheric CO_2 might simultaneously produce earlier ice-off, later ice-on, and warmer summer temperatures in surface waters. Phytoplankton production rates would undoubtedly increase, and with no increase in external nutrient loadings, we speculate that the summer phytoplankton would become dominated by cyanobacteria and (or) green algae; however, Hostetler and Giorgi predicted an increase in local rainfall, which could increase nutrient loadings, particularly of silicon and perhaps nitrogen. We argue that nitrogen may be limiting to certain diatom species in these systems, and thus increased rainfall may increase diatom production. It is beyond the scope of this paper to investigate all the possible outcomes of climate change on nutrient loadings. Rather, we present hypotheses concerning the relationship of diatoms to those parameters that might be affected by climatic variation in the Yellowstone Lake area.

Methods

General limnological measurements were made periodically on five lakes of Yellowstone and Grand Teton National Parks (*see below*) for the period May–September 1992 and 1993. Measurements included temperature, oxygen and conductivity profiles and Secchi depth. Whole-water samples were collected from the lakes, with one portion filtered for dissolved and particulate N, P, and Si. Samples were frozen and shipped to D. Conley (Univ. Maryland Horn Point Lab.) for analyses. In 1992, we made 30-m, vertical, 10-μm-mesh net hauls at each sampling, but on 8 August 1992 and through 1993, a second portion of the water was preserved with Lugol's solution. Phytoplankton were determined, usually within a week of collection, on settled samples using an inverted microscope. Net hauls were enumerated for relative abundance. Whole-water samples were settled in 10-ml Utermöhl chambers and a stratified counting effort was used to improve efficiency in enumerating the eight diatom taxa of primary interest. Cyanobacteria, small flagellates (e.g. *Rhodomonas minuta*), and other small nondiatomaceous algae were enumerated over 10–20 fields at a magnification of 625×. Small diatoms (e.g. *Stephanodiscus minutulus*) were enumerated over one or more strips across the chamber at 625×. Larger diatoms and flagellates (particularly dinoflagellates, *Eudorina* sp., *Cryptomonas* spp., *Stephanodiscus yellowstonensis*, *Stephanodiscus niagarae*, *Asterionella formosa*, *Aulacoseira subarctica*, *Fragilaria crotonensis*) were enumerated over the whole chamber at 156×. Primary productivity was estimated from light-dark bottle oxygen measurements on triplicate epilimnion samples on 8 August 1992.
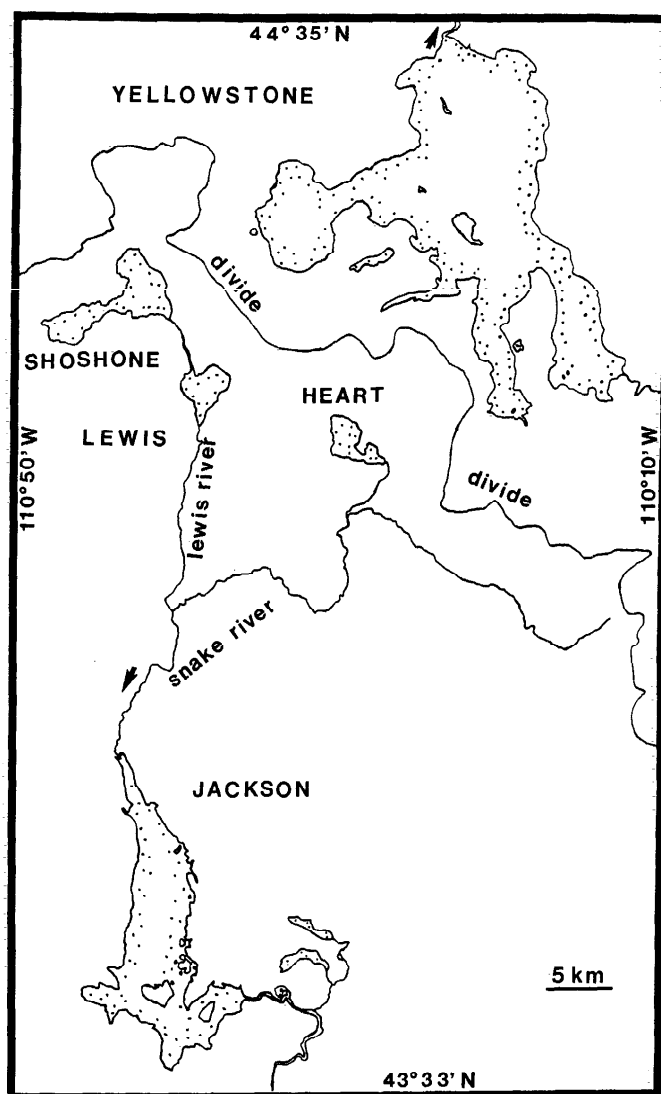
Fig. 1. The five large lakes of the Yellowstone region. Arrows indicate the direction of drainage. The divide is the Continental Divide between the Atlantic and Pacific drainages.

Limnology of the Yellowstone area lakes

The large lakes we considered are Yellowstone, Shoshone, Lewis, and Heart in Yellowstone National Park and Jackson Lake in Grand Teton National Park (Fig. 1).

All are postglacial lakes, spanning a range of size and nutrient chemistry (Tables 1, 2). The bedrock of the basins consists primarily of rhyolite, with some andesite and glacial till (Taylor et al. 1989). The volcanic rocks are rich in silicon and phosphorus; these elements are more readily leached from rhyolite in comparison with andesite. The vegetation is predominately lodgepole pine (*Pinus contorta*), and there has been little anthropogenic impact on the watersheds, except perhaps for fire suppression in the last century, which can affect nutrients released from terrestrial systems.

These particular lakes have been studied because of the fisheries they provide (Gresswell and Varley 1988) and because of unique evolutionary events within these systems (Theriot 1992). Nearly a two-decade record of some limnological variables is available through the U.S. Fish and Wildlife Service. These physical-chemical data have been analyzed for long-term trends and differences among sampling locations (Theriot et al. in prep.). Heart Lake is distinctive (Table 1), with the highest conductivity, probably because it receives more geothermal spring water than the other lakes. Shoshone and the downstream Lewis Lake are similar in water chemistry and have by far the highest silica levels (Table 2), presumably because their drainage basin is dominated by rhyolite. In contrast, roughly half of the Yellowstone drainage is underlain by the less easily weathered andesite. The remainder is rhyolite and welded tuff. The Heart Lake bedrock is welded tuffs and glacial till presumably weathered from these tuffs (Taylor et al. 1989).

Although high-mountain lakes with little anthropogenic impact are typically presumed to be oligotrophic, the algal assemblages in all five lakes (all above 2,200-m elevation) indicate mesotrophic to moderately eutrophic conditions (*discussed below*). Limnological data from 1992 indicate that Jackson is perhaps the most eutrophic of the lakes based on vertical oxygen profiles and Secchi transparency (Table 1). Primary productivity measurements in Yellowstone Lake (gross production, 240–480 mg C m^{-3} d^{-1}) are also consistent with a mesotrophic condition.

All of the lakes have a trend of increasing Secchi transparency from spring to fall (Fig. 2), which is the result of a decrease in diatom biomass from the spring bloom to fall overturn. Total silica concentrations also decrease seasonally (Theriot et al. in prep.). There is a trend in Yellowstone Lake of decreasing total silica (Fig. 3) and total dissolved solids for the period 1976–1986, perhaps

Table 1. Morphological and chemical characteristics of the five large lakes of Yellowstone and Grand Teton National Parks. Data are from Theriot et al. (in prep.) and from unpublished sources.

Lake	Area (km²)	Z_{max} (m)	Secchi (m)	Cond. (μmhos)	HCO$_3$ (ppm)	TDS (ppm)	SO$_4$ (ppm)
Yellowstone	340	107	8	86	37	64	1.3
Shoshone	28	63	12	77	30	64	<1
Lewis	11	33	9	96	32	32	<1
Heart	8.7	55	7	195	52	130	2
Jackson	77	137	4	171	—	—	—

Table 2. Nutrient data for the Yellowstone region for May–September for five lakes in 1992 and four in 1993. Concentrations (μM) are dissolved plus particulate. In parentheses—SD.

Lake	N	TSi	TN	TP	Si:N	Si:P	N:P
1992							
Yellowstone	16	177 (5.16)	9.23 (2.67)	0.95 (0.21)	20	195	10
Shoshone	3	587 (11.7)	6.12 (1.27)	0.78 (0.10)	99	759	8.0
Lewis	8	631 (26.1)	7.68 (1.89)	0.83 (0.08)	86	770	9.3
Heart	1	146 —	11.2 —	1.21 —	13	121	9.2
Jackson	6	222 (17.6)	10.1 (2.15)	0.65 (0.12)	23	351	16
1993							
Yellowstone	26	267 (22.4)	6.6 (1.3)	0.60 (0.14)	41	424	11.5
Shoshone	3	935 (115)	5.4 (1.5)	0.29 (0.04)	185	3,266	20.6
Lewis	5	1,244 (196)	6.0 (1.9)	0.43 (0.02)	264	2,910	13.9
Jackson	7	345 (37.9)	7.8 (1.6)	0.44 (0.16)	45	885	19.4

related to winter drought and lowered spring runoff (Romme and Despain 1989). Higher values of both variables were recorded for the post-1988 years, after massive fires in the basin, but those years were also postdrought. Much lower total and dissolved silica concentrations in 1992 (a dry year with no major fires in the basin) compared with 1993 (a wet year) suggest that runoff may be more important than fires.

Nutrient chemistry data for 1992 and 1993 (Table 2) show clearly that silicon and phosphorus are in excess for diatoms in all lakes, with Si:P and Si:N ratios always far above the Redfield ratios (Si:P = 16:1; Si:N = 1:1). N:P ratios are below the Redfield ratio of 16:1 in all lakes except Jackson, indicating general nitrogen limitation. The importance of N-fixing cyanobacteria in Jackson Lake may be part of the explanation for the more balanced N:P ratio.

The Si:N and Si:P ratios for the five lakes are significantly different, and the lakes can be ranked along these gradients: Si:N—Heart < Yellowstone, Jackson < Lewis < Shoshone; Si:P—Heart < Yellowstone < Jackson < Shoshone, Lewis. Even though the concentrations of Si, N, and P are relatively high, species distributions along the gradients may still be a function of nutrient ratios, as has been found in African lakes (Kilham et al. 1986).

There are sufficient seasonal data on nutrients in the epilimnia of four of the lakes in 1992 and three of the lakes in 1993 to show a general pattern of increasing N:P ratio as the diatom bloom develops, followed by a decline in both N and P (Fig. 4). In 1992, the maximum peak of the N:P ratio for all of the lakes, except Shoshone, was in early August. The trends were different in 1993, which was cooler, wetter, and cloudier, with stratification delayed >30 d compared to 1992. In Yellowstone Lake in 1993, the diatom bloom was well developed by 24 June,

day 175 (prior to stratification), and biomass generally decreased thereafter, as did the N:P ratio. In Jackson Lake in 1993, the cyanobacteria biomass increased 5-fold between 18 May and 10 September (days 139 and 253), with the diatom peak on 3 July (day 184). Diatoms continued to dominate the phytoplankton biomass throughout summer. These trends indicate that even though N is in lowest supply, demand for P exceeds that for N during the phytoplankton maxima. The sustained diatom bloom before stratification in 1993 lowered the overall amounts of both dissolved inorganic N and dissolved inorganic P, but especially P in the epilimnion of Yellowstone Lake compared to 1992.

The interpretations presented here do not address the possible influences of food web interactions on diatom community structure. A consensus is growing among food-web researchers that different systems may have different levels of influence on primary producers of resources or consumers. Without entering the wider debate, it seemed reasonable to make a first assumption that consumer influences have a small impact relative to mixing and nutrients on the general patterns of change in the diatom assemblages in the Yellowstone area lakes. Patterns of fish distribution are different among the lakes. At least two lakes, Shoshone and Lewis, were completely barren of fish until European settlement (Pierce 1987) and how have identical fish assemblages but different diatom assemblages. No data exist for zooplankton.

Distribution and seasonality of the diatoms

There are eight predominant diatom species in the modern lake assemblages: *S. yellowstonensis* Theriot and Stoermer, *S. niagarae* Ehrenb., *S. minutulus* (Kützing)
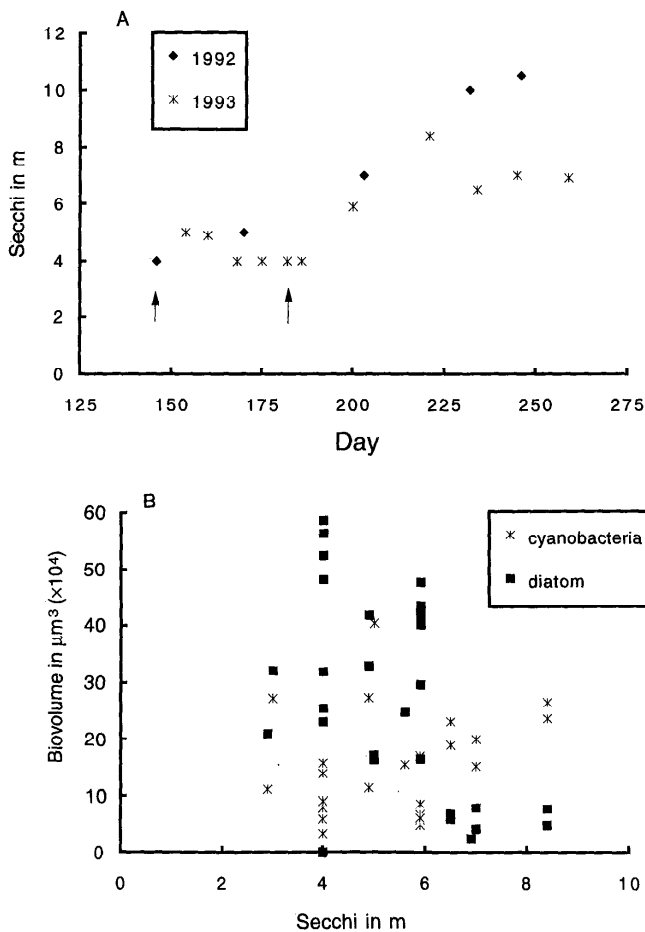
Fig. 2. Secchi transparency in Yellowstone Lake and its relation to biomass of algae. A. Transparency in 1922 and 1993. Arrows indicate the onset of stratification in the lake, which was earlier in 1992. In 1993, there was a long delay before stratification and the diatom bloom actually increased (decreasing Secchi transparency) before that time. Also in 1993, the lake started to cool earlier (peak transparency was on the warmest sampling date), and a diatom bloom started to decrease the Secchi transparency. B. Secchi transparency vs. algal biovolume of diatoms and cyanobacteria for 1993. Note the clear negative relationship for diatoms but not for cyanobacteria.

Fig. 3. Measured concentrations of total silica (all forms including mineral) in Yellowstone Lake over a period of 17 yr (*see* Theriot et al. in prep.). Data were not collected from 1987 to 1989. There was a 7-yr period of winter drought prior to the large fires of 1988. The silica concentrations decreased during the drought years and then returned to predrought levels after the fires.

Round, *Cyclotella bodanica* Eulenstein, *A. subarctica* (O. Müll.) Haworth, *A. formosa* Hassall, *F. crotonensis* Kitton, and *Rhizosolenia eriensis* H. L. Smith. Except for *S. yellowstonensis*, which appears always to have been allopatric with respect to *S. niagarae*, all species have historically occurred in all lakes (Fritz and Theriot unpubl. data). With the exception of *R. eriensis*, which is very lightly silicified, all species are very well preserved in abundance in lake sediments. This abundance is not surprising because primary production (mainly diatoms) is high (epilimnetic rates >200 mg C fixed m^{-3} d^{-1}), dissolved hypolimnetic silica concentrations are high (>200 μM), and pH is circumneutral. *S. niagarae* does not appear in the diatom stratigraphy until about 12,500 B.P., after other diatoms have become established in the sys-
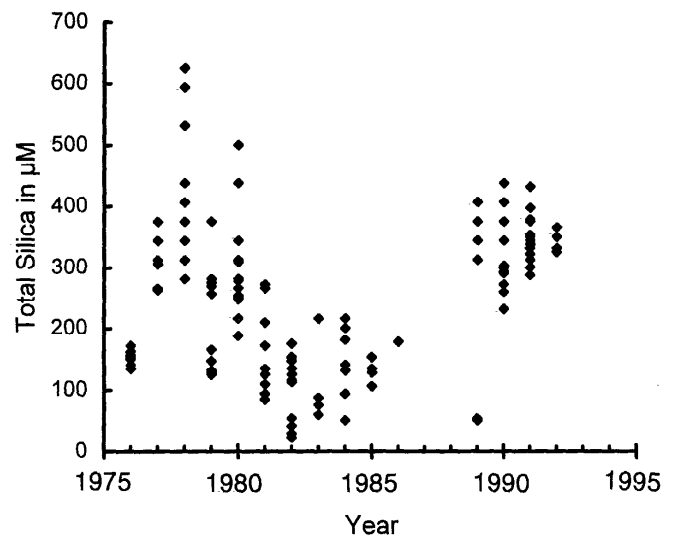
tem. *C. bodanica* is particularly abundant in the early record (13,000 B.P.). *S. niagarae* has dropped below detection level in Shoshone Lake in the modern assemblage, and *C. bodanica* has become dominant.

Yellowstone Lake—The patterns in modern limnological data (Tables 1, 2) give clues to factors that influence the annual waxing and waning of several diatom species. Secchi transparencies are shallowest (~3–4 m) in spring and generally deepen (~10 m) throughout summer and are correlated primarily with diatom biomass (Fig. 2). This lake has no carbonate precipitation and great depth (preventing resuspension of sediments). Although the Yellowstone River flows into the lake, its influence on transparency apparently is limited to the southeast arm of the lake in early spring (Theriot et al. in prep.).

In Yellowstone Lake, *S. yellowstonensis* is endemic and *S. niagarae* is absent from the modern assemblage (Theriot 1992). The dominant species in numerical abundance are *A. subarctica, A. formosa, S. minutulus,* and *R. eriensis. S. yellowstonensis* and *C. bodanica* are less abundant, and *F. crotonensis* is rarely observed. We have studied the seasonality of the plankton for 2 yr. The spring bloom is dominated by diatoms and small cyanobacteria. In 1993, the chlorophyll concentration was highly correlated ($P = 0.019$) with diatom abundance but not with cyanobacteria abundance ($P = 0.445$). Similarly, Secchi transparency corresponded closely to diatom abundance; values (~4.0 m) were lowest during the diatom maximum (Fig. 2).

The relative abundances by biovolume of the major diatom species are shown in Fig. 5 for 1993. In the early mixing period, *A. subarctica, R. eriensis, S. minutulus,*

and *A. formosa* predominated. *A. subarctica* and *S. minutulus* are typically springtime species, suggesting a general need for high nutrient concentrations, particularly silica, which is reduced in the epilimnion throughout summer. This scenario is further supported by the fact that *A. subarctica* maintains a high population level all summer in the hypolimnion where nutrient levels are high but light is low. The late mixing period into the early stratification was characterized by decreasing populations of *A. subarctica*, *A. formosa*, and *R. eriensis*, with *S. minutulus* maintaining its population well into stratification. *S. yellowstonensis* and *C. bodanica* are characteristic summer diatoms, suggesting tolerance for low nutrient concentrations. *C. bodanica* occurs at times of low N:P ratios in all lakes in the system regardless of absolute concentrations. In fall, summer populations generally declined but the relative abundances were similar, except that cyanobacteria were reduced in importance and the chlorophyte *Eudorina* sp. was abundant.

In 1993, *A. subarctica* and *A. formosa* were more abundant at depth (>20 m) than in the surface (<20 m), both before and after stratification began (Fig. 5). *S. minutulus* and *R. eriensis* were more abundant in the surface early in spring and at depth after stratification. The cyanobacteria tended to be more abundant at the surface than at depth, particularly poststratification. On 19 July 1993 (day 200), algae showed distinct depth distributions. The two cyanobacteria species had peaks at 5 (*Dactylococcopsis* sp.) and 15 m (*Chroococcus* sp.), and the diatoms had peaks at 25 (*A. subarctica*), 35 (*A. formosa*), and 40 m (*S. minutulus*, *R. eriensis*). There was a poorly demarcated mixing zone (epilimnion plus metalimnion) down to ~30 m.

Based on the available seasonal data, we present a general scheme for the relative abundances of the major species in Yellowstone Lake related to environmental variables for the mixing layer and for the upper hypolimnion (Fig. 6). The patterns of abundance are generalized from the data for 1992 and 1993. Some features of the model will likely apply to the other lakes as well.

Shoshone Lake—Shoshone and Lewis Lakes are similar in chemistry (they are connected), but their planktonic diatom floras are quite different. Shoshone Lake is the most oligotrophic of the five lakes, and the dominant diatoms are *A. subarctica* (especially before stratification) and small centric diatoms, including *Cyclotella ocellata* (Pant.) and *Cyclotella stelligera* (Cl. & Grun.) V.H. *C. bodanica* and *A. formosa* are present before stratification. *S. niagarae*, although abundant in recent sediments, has been absent from the plankton during the last few years.

Lewis Lake—Immediately downstream from Shoshone, Lewis Lake has *S. niagarae*. Before stratification, the lake is dominated by *R. eriensis* and then by *A. formosa*. *S. niagarae* becomes abundant in the stratification period and then dominates the hypolimnion assemblage in summer and fall. *F. crotonensis* is the most abundant diatom in the epilimnion in summer and declines in fall. There are abundant small coccoid cyanobacteria, especially dur-
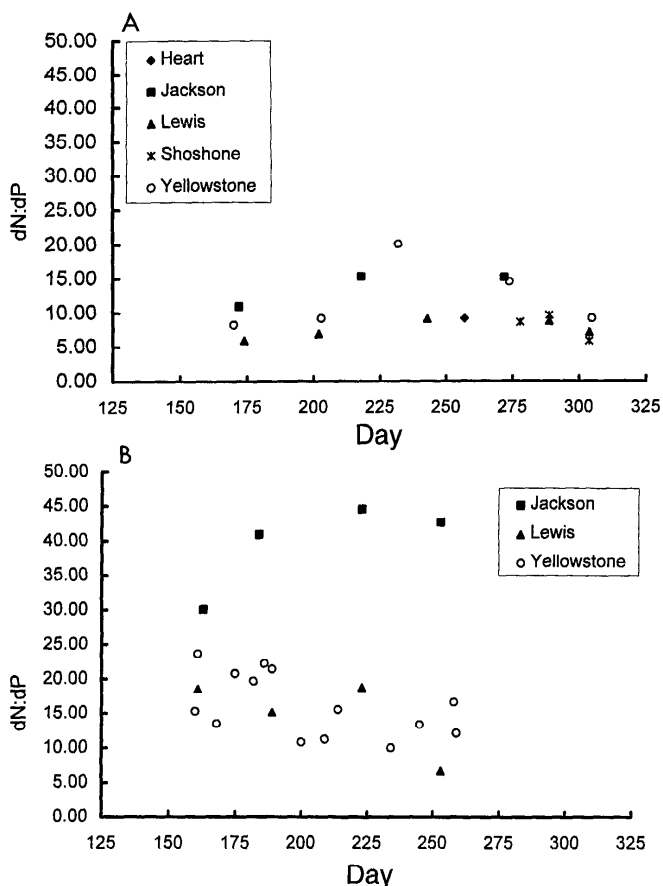

Fig. 4. N:P atomic ratios of dissolved inorganic nutrients during the growing season in 1992 (A) and 1993 (B) in the Yellowstone lakes. Note that 1993 was cooler, wetter, and cloudier.

ing stratification. In 1993, there were abundant *Synedra* sp. and *C. ocellata* also present during stratification. No *S. minutulus* has been observed in the plankton samples of either Lewis or Shoshone.

Heart Lake—The diatom flora of Heart Lake is known from only a few samples. The lake contains *S. niagarae*, *A. formosa*, *F. crotonensis*, and *Tabellaria fenestrata* (Lyngb.) Kütz. The cyanobacteria *Anabaena* sp. is also present.

Jackson Lake—Jackson Lake is the most eutrophic of the lakes and has N-fixing cyanobacteria in summer, and small coccoid cyanobacteria are abundant after stratification. In 1992, the dominant diatoms were *F. crotonensis* and *A. formosa*, with lower numbers of *A. subarctica* and *C. bodanica*. In 1993, there was a clear succession from dominance by *A. formosa* during mixing and early stratification to dominance by *C. bodanica* for the remainder of the stratified period. Small centric diatoms (including *S. minutulus*) were also abundant before stratification. During stratification, *C. bodanica* was the clear dominant, with abundant *F. crotonensis* and a *Synedra*
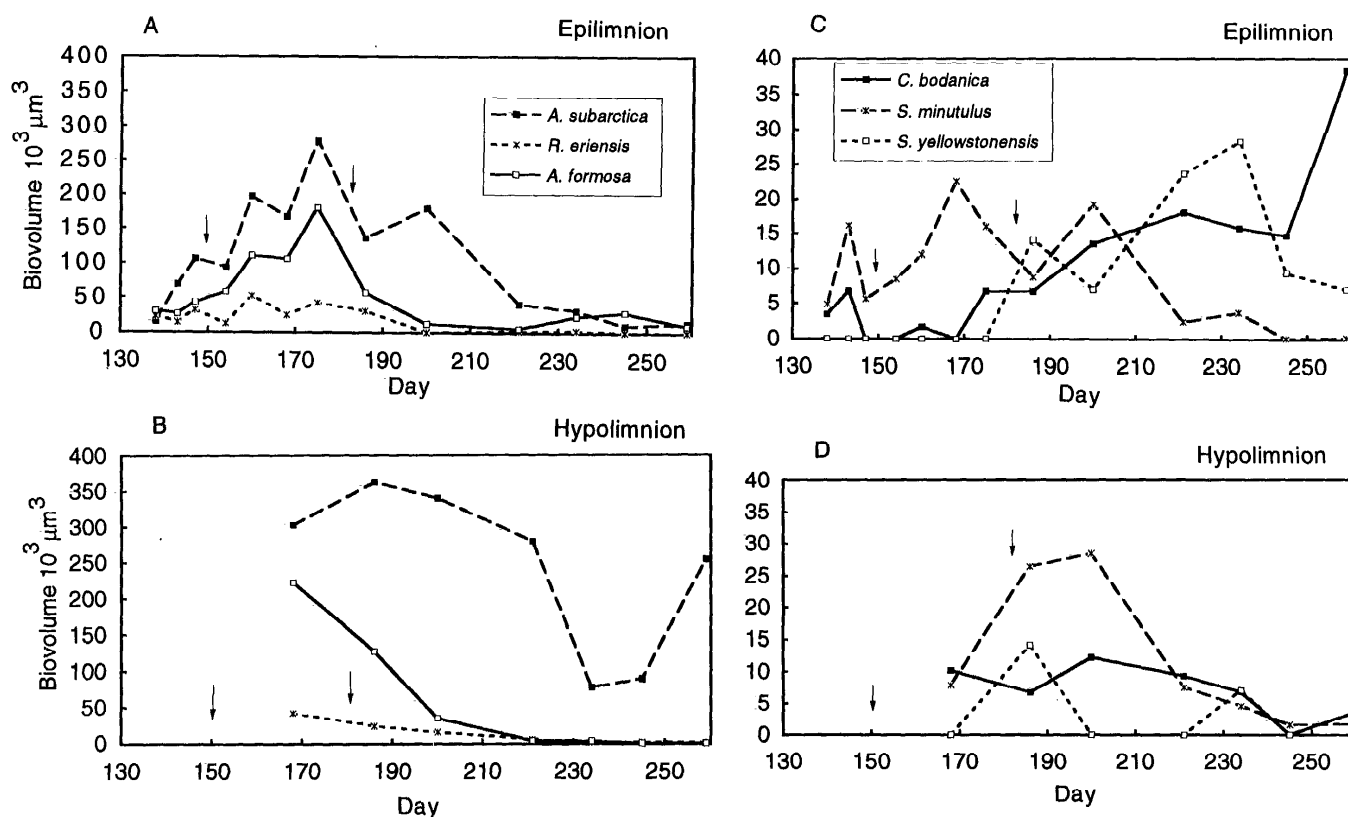
Fig. 5. Abundances by biovolume for six major diatoms in the epilimnion and the upper hypolimnion of Yellowstone Lake in 1993. The values are averages for depths <20 m (A, C) and depths ≥20 m (B, D). The species identifications in panel A apply to panel B, and those in panel C apply to panel D. Note the order of magnitude change in scale between panels A, B and C, D. Ice-out on the lake was 29 May (day 150) and onset of stratification was on 1 July (day 182, arrows).

sp. The colonial green alga, *Eudorina* sp., was abundant in the early spring sample.

Hypothesized resource physiology

Resource competition theory (Tilman 1982; Tilman et al. 1982) can be used to predict relative abilities of species to use resources (which are to a large degree climatically controlled). This theory can be used not only to explain present distributions of diatoms, but also to propose hypotheses on the proximate and climatic controls on diatom distributions during the Holocene. The reliability of the resource/diatom/climate hypotheses based on modern experiments can be tested to some degree or at least corroborated by comparing climatic inferences based on diatom distributions with those reached by analysis of other climatic proxies in the sediment record.

The information needed to make these important causative links is how the diatoms are arrayed in multidimensional resource space. Very little is actually known about the resource needs of these species. Some data are available for clones of three of the species from the Laurentian Great Lakes (Tilman et al. 1982; Mechling and Kilham 1982; Kilham 1984). We know, for example, that *A. formosa* and *F. crotonensis* have similar and relatively

high (60–100) optimum Si:P ratios (they are good competitors for P but need moderately high Si; van Donk and Kilham 1990) and moderate N:P ratios (*A. formosa* = 12, *F. crotonensis* = 25; Rhee and Gotham 1980). *S. minutulus* has a very low optimum Si:P ratio (Si:P = 1). Little additional data exist for the resource physiology of any of these species.

Because so little is actually known about resource needs for these species, specific predictions are difficult to make. However, the hypothesis that diatoms are distributed along resource ratio gradients has proven to be robust whenever it has been experimentally tested (e.g. Kilham 1986; Sommer 1993, 1994). Linking that result with field distributions has been difficult (Tilman et al. 1984; Sommer 1989, 1993). The reverse approach of hypothesizing resource ratio tradeoffs from field observations, including the paleorecord (Kilham et al. 1986) has proven to be quite useful. It is the approach we take here. Despite the fact that the Yellowstone area lakes are more similar to each other than are the African lakes, the diatoms themselves still have very distinctive geographic and ecological distributions.

Hypotheses along single gradients—We have developed a series of hypotheses of the rankings of the eight important species of diatoms in the Yellowstone ecosystem:

A. subarctica (AU), *S. yellowstonensis* (SY), *S. niagarae* (SN), *S. minutulus* (SM), *A. formosa* (AF), *F. crotonensis* (FC), *C. bodanica* (CB), and *R. eriensis* (RE).

The early-spring species (AU, RE) and the species that grow at depth in summer (SY, SN) are likely to have lower light requirements than summer epilimnetic species. One study of light-limited growth of FC showed that it had quite a high light requirement (Rhee and Gotham 1981): AU, SY, RE < SN, AF, SM < FC, CB.

Species that occur in greatest abundance in summer (CB) with N-fixing cyanobacteria are likely to have lower N requirements than species that occur in early spring under higher N conditions. The distributional data of diatoms related to total nitrogen in lakes of Ontario (Christie and Smol 1993) provide a hypothesis that is generally consistent with six of the species in the Yellowstone lakes (we rank AU as having a higher N requirement): CB < SY, FC < RE, SN, AF < AU, SM.

Phosphorus is less important than N in these lakes, but there are some data available for a few of the species (Tilman et al. 1982): AF, FC, RE < SN, CB < SM, SY < AU.

Silicon is generally high in these lakes, coming within limiting levels only in Yellowstone Lake in summer. The available data on silicon limitation (*see* van Donk and Kilham 1990) are consistent with the following rankings: SM, RE < CB, SN, SY < AF, FC < AU.

These are hypothesized relationships that serve as an initial guide for determining the relative resource relationships among these eight species.

Hypotheses along resource ratio gradients—These predictions are based primarily on the rankings given above for the individual resources. Firm predictions are possible only with physiological data, but preliminary evidence would suggest the following rankings.

Si:N will likely be the most important ratio gradient for the Yellowstone area lakes, given the low N and generally abundant Si: SM, RE < SN < SY, AF, AU < FC, CB.

For Si:P, given the distributions of the species in the lakes, the suggested ranking is SM, SY < RE, CB, SN, AU < AF, FC.

The lakes are quite similar in N:P ratios, but a suggested ranking based on the N and P rankings is CB, SY < AU, SM < SN, FC < RE, AF.

The light:N ratio is an important gradient in these lakes, but few data exist on the species on which to base it. A suggested ranking is AU, RE < SY, SM < AF, SN < FC < CB.

Do these hypotheses help us understand Yellowstone Lake biostratigraphy?

A detailed record from a surface core from West Thumb in Yellowstone Lake (Fig. 7) has four predominant species of planktonic diatoms: *A. subarctica, A. formosa, S. minutulus,* and *S. yellowstonensis* and shows significant short-term variability in the relative and absolute abundance of these taxa. The two congeners *S. minutulus* and *S.*
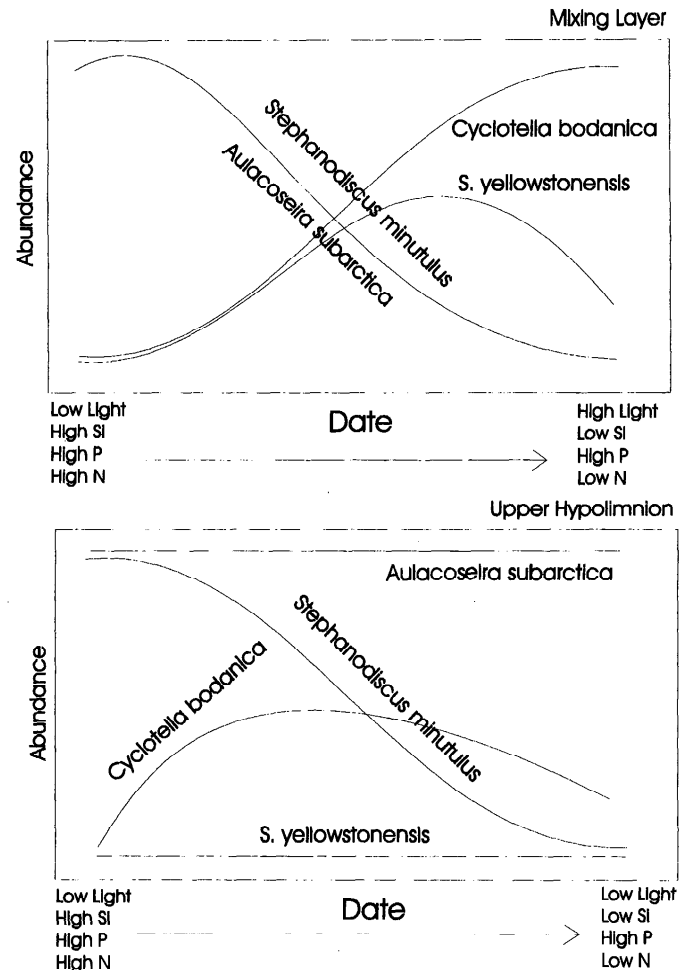

Fig. 6. Schematic representation of observed temporal and vertical distributions of four major diatoms of Yellowstone Lake and selected environmental variables. *S. minutulus* and *A. subarctica* are springtime species found in the whole-water column. *C. bodanica* and *S. yellowstonensis* are characteristic summer diatoms, suggesting tolerance for low nutrient concentrations.

yellowstonensis have opposite patterns of relative and absolute abundance, which we will try to explain using our hypotheses of resource competitiveness and effects of climate on the lake.

Our hypotheses of resource competition were based primarily on field observations on species abundance and resource variation over seasons. Although climate may be the ultimate driver of many of these changes, the proximate causes are the resources and mixing characteristics that control algal growth rates, including nutrients, light, and temperature. The hypothesized resource physiology for the dominant planktonic diatom species in Yellowstone and the other large lakes of the Yellowstone region was tested and then used as a tool to interpret the paleorecord.

We have developed a broad working hypothesis for Yellowstone Lake based on a few generalizations (Fig. 8). We are aware of, but do not specify, certain feedbacks
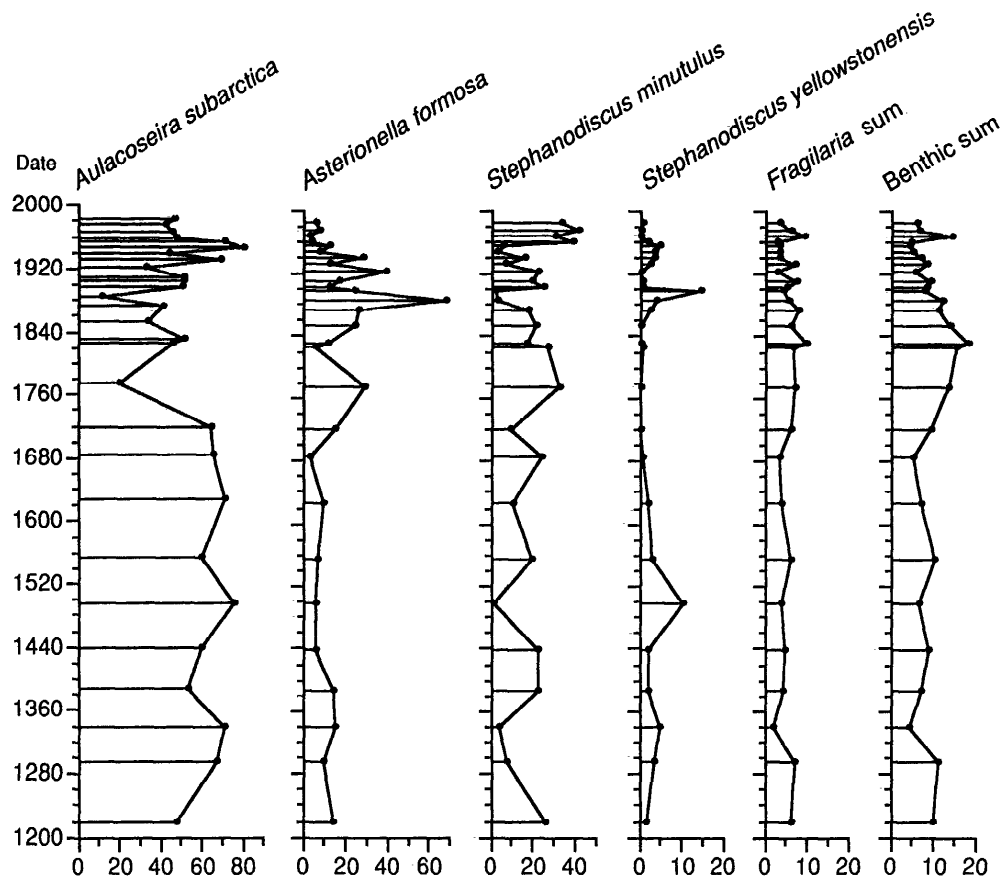
Fig. 7. Relative abundance (%) of the dominant diatoms in a short core taken in 84-m water depth in September 1991 from West Thumb, Yellowstone Lake. ^{210}Pb dates are calculated with the constant rate of supply model (Appleby and Oldfield 1978). Dates beyond the range of ^{210}Pb are extrapolated based on dry mass for each interval and the mean sediment accumulation rate of the ^{210}Pb-dated sequence.

including those predicted by resource competition theory (i.e. that the diatoms themselves affect the nutrient concentrations through demand), temperature effects on nutrient recycling, zooplankton grazing, etc. We believe our hypothesis to be appropriate as a first-order approximation of Yellowstone Lake dynamics. First, a major effect of climate will be to change internal nutrient cycling for reasons outlined above. Due to the massive volume of the lake in relation to its relatively small watershed, this may be a predominant effect on nutrient supply rates to the phytoplankton. Extended mixing periods will deliver hypolimnetic pools of nutrients to the surface waters, but light levels will be low. Shortened mixing periods will likely reduce Si and N relative to P and keep phytoplankton in the upper water column (= higher levels of light).

Second, external loading of nutrients is likely to be a correlated set of conditions related to cloud cover and precipitation on an annual basis. Our 1992–1993 data and the long-term chemistry data (Theriot et al. in prep.) show that Si levels in Yellowstone Lake (Fig. 3) decline during winter drought and rebound in years of heavy

snowpack. Wetter summers should generally result in lower light levels because of cloud cover, but with increased runoff and nutrient loadings, particularly Si, favoring high Si and low light species. Direct rainfall contributions to N loading may also be important and produce summers of high N:P ratios and high Si:P ratios. Drought summers would produce the opposite. Given our hypothesized resource physiology, we show how these hypotheses can be linked to give an interpretation of the paleodiatom record.

The least speculative case involves that of the summer diatom S. yellowstonensis, which is most abundant in sediments representing two major historical droughts— the late 19th century and the 1930s (see Fig. 7). Our hypothesized resource physiology suggests that S. yellowstonensis will be a superior competitor relative to S. minutulus under high light and low N:P conditions and possibly lower Si:P ratios, the type of conditions likely to occur during droughts.

Abundances of A. subarctica and A. formosa are not so clearly correlated with one another or with those of other

DIATOM RESULTS

GENERALIZED LIMNOLOGIC EFFECTS

Aulacoseira subarctica favored by high Si:P and low light
Stephanodiscus minutulus favored by high Si:P, reduced by low light
S. yellowstonensis and *Cyclotella bodanica* reduced by high Si:P and by low light

CLIMATE EFFECTS

low temp / cloudy / high precip

late/weak stratification
low light throughout column
cold water temp
high external nutrient loading
high Si:P

temperature
cloud cover
precipitation/runoff

high temp
sunny
low precip
no fires

early/strong stratification
high mixing-layer light
low hypolimnetic light
warm epilimnetic temp
low external nutrient loading
low summer Si:P
low summer N:P

S. yellowstonensis favored by low Si:P, higher light
C. bodanica favored by low N:P

high temp
sunny
low precip
post-fire, pre-recovery

early/strong stratification
high mixing-layer light
low hypolimnetic light
warm epilimnetic temp
high spring external nutrient loading

In early stratification:
higher Si:P favoring *S. minutulus* and *Asterionella formosa*
higher N loadings reducing *C. bodanica*

post stratification:
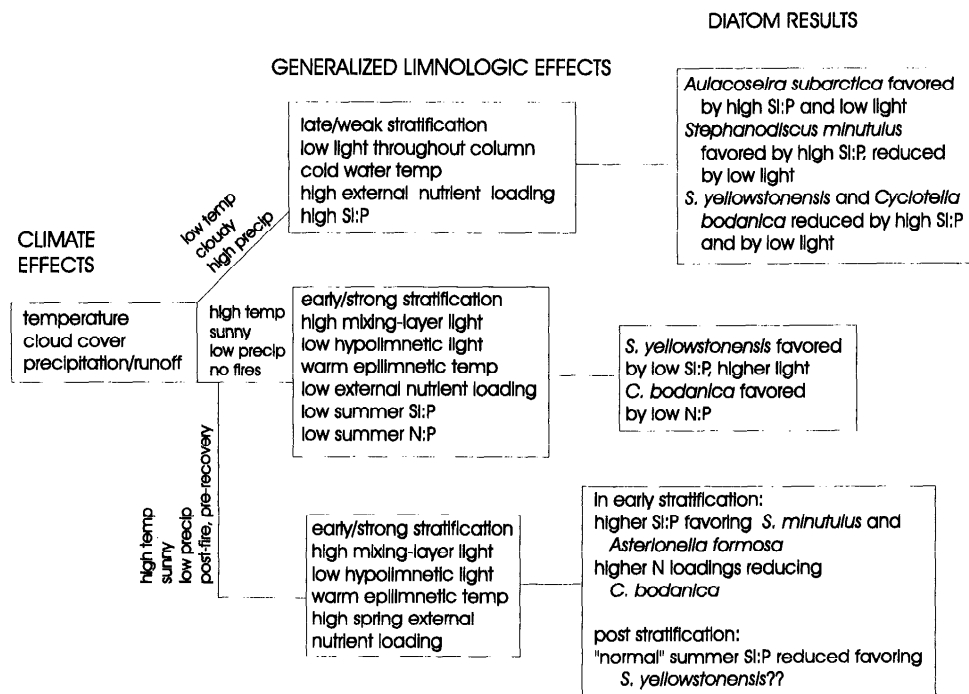"normal" summer Si:P reduced favoring *S. yellowstonensis*??

Fig. 8. Schematic diagram of some possible links between climate and diatom change in Yellowstone Lake.

species. *A. subarctica* should respond positively to low N:P ratios, but *A. formosa* should respond poorly. Indeed, *A. subarctica* reaches local maxima during the same drought periods where *S. yellowstonensis* reaches local maxima (Fig. 7). Presumably, the high abundance is partly due to hypolimnetic populations of *A. subarctica* growing in summer along with *S. yellowstonensis*; however, *A. formosa* reaches low abundances at those times predicted by its ranking on the N:P scale. On the other hand, there is a peak of *A. formosa* preceding the late 1800s *S. yellowstonensis* peak. Correspondingly, this is equivalent to the prehistoric low for *A. subarctica* and a minimum for *S. minutulus*, suggesting a time of higher N:P and higher Si:P ratios similar to what we have speculated would occur during wet summers.

Conclusions

We have attempted to address a major concern of the ecological agenda: the relationship of climate change to the structure, function, and survival of ecological communities. Resource ratio theory is used to predict relative abilities of species to use resources that are to some degree linked to the climate with transfer functions. This approach is enhanced by our use of species that fossilize well and, therefore, the paleorecord can extend the time scale under consideration.

Resource competition theory can be used not only to explain present distributions of diatoms but also to test the causal factors proposed to explain diatom distributions during the Holocene. This information is relevant

to both basic and applied questions. Diatom species have dropped below detectable levels in lakes experiencing no obvious perturbation (*S. niagarae* in Shoshone Lake) but thrive in other regional lakes (even those in the same drainage basin, such as Lewis Lake). At least one new species (*S. yellowstonensis*) has evolved in Yellowstone Lake (Theriot 1992).

Diatoms are important indicators of climate change on a scale relevant to human population response. Identification of causal links between climate change, lake dynamics, and diatom distributions increases the utility of diatoms in studies of paleoclimate reconstruction (Bradbury and Dean 1993). The combination of thorough limnology and process-oriented physiology provides a firm basis for landscape-level transfer functions that will permit climate reconstructions on a fine scale. A significant missing biological link is data on the physiological resource needs of individual diatom species.

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