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Paleolimnological evidence of change in a shallow, hypereutrophic lake: Upper Klamath Lake, Oregon, USA

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Abstract

Sediment cores were collected from Upper Klamath Lake in October, 1998 and analyzed for ^{210}Pb, ^{14}C, ^{15}N, N, P, C, Ti, Al, diatoms, *Pediastrum*, and cyanobacterial akinetes. These results were used to reconstruct changes in water quality in Upper Klamath Lake over the last 150 years. The results showed that there was substantial mixing of the upper 10 cm of sediment, representing the previous 20 to 30 years. However, below that, ^{210}Pb activity declined monotonically, allowing reasonable dating for the period from about 1850 to 1970. The sediment accumulation rates (SAR) showed a substantial increase in the 20th century. The increase in SAR corresponded with increases in erosional input from the watershed as represented by the increases in sediment concentrations of Ti and Al. The upper 20 cm of sediment, representing the last 150 years, also showed increases in C, N, P, and ^{15}N. The increases in nutrient concentrations may be affected to various degrees by diagenetic reactions within the sediments, although the changes in concentrations also were marked by changes in the N:P ratio and in a qualitative change in the source of N as reflected in increasing δ^{15}N. The diatoms showed modest changes in the 20th century, with increases in *Asterionella formosa, Stephanodiscus hantzschii*, and *S. parvus. Pediastrum*, a green alga, was well-preserved in the sediments and exhibited a sharp decline in relative abundance in the upper sediments. Total cyanobacteria, as represented by preserved akinetes, exhibited only minor changes in the last 1000 years. However, *Aphanizomenon flos-aquae,* a taxon which was formerly not present in the lake 150 years ago, but that now dominates the summer phytoplankton, has shown major increases over the past 100 years. The changes in sediment composition are consistent with activities including timber harvest, drainage of wetlands, and agricultural activities associated with livestock grazing, irrigated cropland, and hydrologic modifications.

Introduction

Upper Klamath Lake is an hypereutrophic lake in southern Oregon, USA. This is the largest natural lake in the state (~275 km^2) and has been monitored and investigated numerous times over the last three decades (Kier Associates 2000; Brownell and Rinallo 1995). The lake is located in a graben on the east side of the Cascade Range east of Mt. McLoughlin and south of Crater Lake. Upper Klamath Lake is shallow with a maximum depth of 15.2 m (Johnson et al., 1985) and an average depth of 2.2 m (USBR, 1997).

Although currently classified as hypereutrophic, there is considerable controversy regarding the historical condition of the lake prior to watershed development activities initiated by Euro-Americans beginning in the mid- to late 1800s. Previous investigations have shown that the lake has been productive for thousands of years (Sanville et al., 1974). This view of the lake as a naturally hypereutrophic system (Johnson et al., 1985) is consistent with its shallow morphometry, deep organic-rich sediments, and a large watershed with phosphorus-enriched soils. However watershed activities, beginning in the late-1800s and accelerating through the 1900s, are strongly implicated as the cause of its current hypereutrophic character (Bortleson & Fretwell, 1993).

Under current conditions, the lake exhibits many water quality problems typically associated with excessive algal production. These include extended periods of low dissolved oxygen, elevated pH, and toxic levels of un-ionized ammonia, and previously productive fisheries are now subject to fish kills and water quality stress (Kann & Smith, 1999; Perkins et al., 1999). Two fish species, the shortnose sucker (*Chasmistes brevirostris*) and Lost River sucker (*Deltistes luxatus*) were listed as endangered under the Endangered Species Act in 1988. Moreover, based on harmful levels of dissolved oxygen, pH, and chlorophyll (algal biomass), the lake has been designated as water quality limited for resident fish and aquatic life (ODEQ 303(d) List 1998). Algal production in Upper Klamath Lake is now dominated by *Aphanizomenon flos-aquae,* which can account for more than 95% of the phytoplankton biomass during June through October (Kann, 1998).

Despite relatively low precipitation for the area (the watershed for Upper Klamath Lake lies in the rain-shadow of the Cascade Range), early Euro-American settlers took advantage of the rivers supplied by snow-melt and groundwater to provide irrigation water for livestock and crops, as well as of the extensive forests in the surrounding mountains to provide abundant supplies of timber to local mills. Timber harvest in the area was most active from 1925 to 1945, and has stabilized at values near one-half maximum harvest rate (Fig. 1). Extensive wetlands, many adjacent to Upper Klamath Lake and Agency Lake, were drained to provide cropland and pasture. Cattle production in the area reached a peak near 1960 with a total of about 140 000 head of livestock in the area (Fig. 1). The Environmental Protection Agency (EPA Index of Watershed Indicators, 1998) indicates that at least 44,500 ha of the watershed have been converted to irrigated pasture or other agricultural activities, and Risley & Laenen (1999) show an 11-fold increase in permitted irrigated land acreage between 1900 and the present. Drainage of wetlands has been relatively steady throughout the first 80 years of the 20th century (Fig. 1), and large quantities of nutrients were released from the former wetlands and subsequently pumped to the lake or its tributaries (Snyder & Morace 1997).

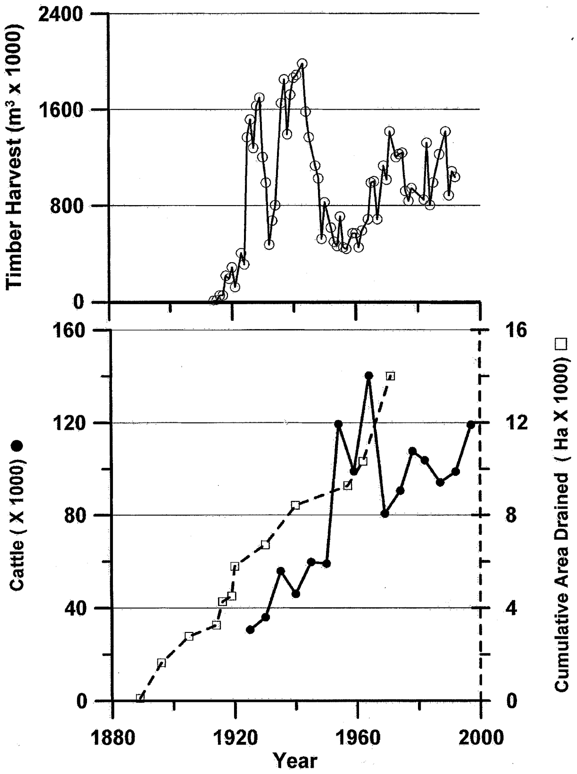

Figure 1. (a) Timber harvest (○) in Klamath County, Oregon. Values represent the sum of production from public (Winema National Forest), private, and Klamath Tribes domains. Redrawn from Risley & Laenen (1999). (b) Cattle production (●) in Klamath County, Oregon derived from U.S Dept. Commerce. Values represent the sum of both dairy and non-dairy cattle production. Cumulative acres of wetlands drained (□) in Klamath County. Data regarding wetlands compiled by Gearheart et al. (1995) and Snyder & Morace (1997).

Additional modifications to the lake hydrology include diversions of tributaries entering the lake, diversion of water out of the lake, and the construction of the Link River Dam at the lake's outlet in 1921. As a result, both the timing and quantity of lake flushing flows and nutrient retention dynamics have been altered, and lake surface elevation and volume are reduced below the historical minimum pool level.

The current sediment study was initiated to assist in better understanding the historical conditions in Upper Klamath Lake through application of more recent advances in paleolimnological techniques. The purpose of this study was to determine if water quality in Upper Klamath Lake has changed in the last century, and to determine the magnitude and timing of any possible change.

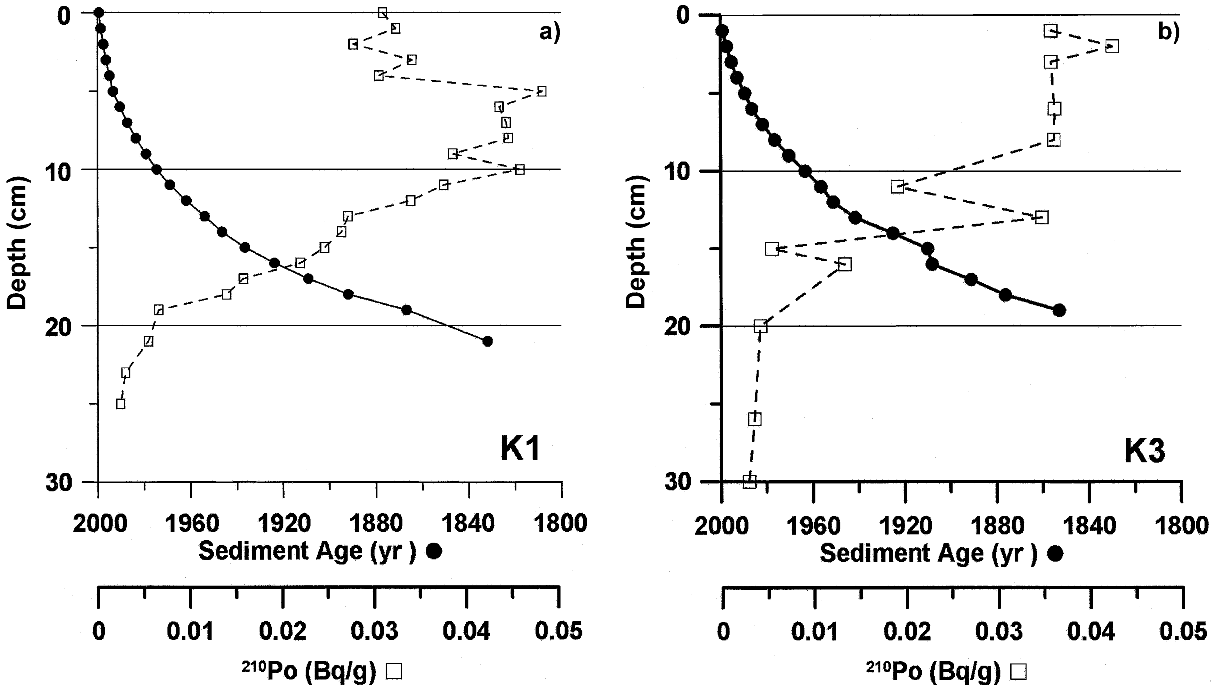

Figure 2. (a) Measured ^{210}Po activity reported in Bq/g (□) in Core K1, Upper Klamath Lake versus sediment depth. Modeled age of sediments (●) using the CRS model (Appleby & Oldfield, 1978). (b) Measured ^{210}Po activity (□) in Core K3, Upper Klamath Lake versus sediment depth. Modeled age of sediments (●) using the CRS model (Appleby & Oldfield, 1978).

Methods

Upper Klamath Lake sediments were collected on October 21, 1998. Three sediment cores were collected, two with a 10 cm diameter gravity corer and one with a 5 cm diameter piston corer. Coring locations were chosen, in part, to minimize the effects of wind-induced resuspension of sediments (Laenen & Le Tourneau, 1996). One site was located north of Shoalwater Bay (N42° 25.63′; W121° 59.02′) and two sites were located south of Bare Island (N42° 24.09′; W121° 55.14′). All cores were collected from lake depths of about 4m. A 10 cm-diameter corer, equipped with a sphincter device to close the base of the core, was slowly lowered into the sediments using a hydraulic winch mounted on a crane attached to the boat. The piston corer has the potential to retrieve a less disturbed sediment core, although in this case we observed no difference in degree of disturbance between core K1, collected with the sphincter corer, and core K3, collected with the piston corer. Core K2, which was also collected with the sphincter corer, exhibited some degree of side-wall disturbance and consequently was retained as a duplicate core. Only ^{14}C measurements were conducted on core K2.

Sediment samples were extruded and placed in Whirlpac® bags and refrigerated. Subsamples of the sediment were analyzed for ^{14}C, ^{210}Pb, percent water, C, N, S, P, Ti, Al, diatoms, *Pediastrum*, and cyanobacterial akinetes. Carbon, nitrogen, and sulfur were analyzed using a Leco model CNS-2000 elemental analyzer. Standard Leco operating procedures were followed using sulfamethazine for standardization and a combustion temperature of 1350 °C. Other elements were analyzed with a Perkin Elmer Optima 3000 DV ICP spectrometer using the radial view. Samples were first digested in a CEM Corporation model MDS-2000 microwave digestion oven. A total digest of the sediment (CEM Corp., 1991) using HNO_3, HF, HCl, and H_3BO_4 was used for the analysis of P, Ti, and Al. All chemical results are reported as dry weight.

Isotopic analysis of sediments for ^{15}N was conducted at the Stable Isotope Research Unit at Oregon State University, Corvallis, OR. The sediment samples were analyzed with a Roboprep C/N analyzer linked to a 20-20 Isotope Ratio Mass Spectrometer. The system utilizes a Dumas combustion/reduction apparatus. The reported precision for this unit is ± 0.3 parts per thousand.

Sediment samples were dated using ^{14}C and ^{210}Pb isotopes. ^{14}C was analyzed using accelerator mass spectrometry (AMS) by Lawrence Livermore Nuclear Laboratory through Beta Analytic, Inc. The material was pre-treated with HCl washes to strip the sediments of carbonates. ^{210}Pb was analyzed using alpha spectroscopy (Eakins & Morrison, 1978), which involves distillation of the sample, HNO_3 and HCl digestion, and plating onto silver prior to counting. Analytical details are presented in Flynn (1968) and Evans & Rigler (1980) with modifications described in Cornett et al. (1984) and Rowan et al. (1995). The sediment ages and accumulation rates (also reported as dry weight) were calculated using the constant-rate-of-supply (CRS) model of Appleby & Oldfield (1978) with old age dates using the method described by Binford (1990).

Preparation of diatom samples followed standard procedures outlined by Battarbee (1986). Briefly, between 2.00 to 4.83g of sediment were mixed with concentrated sulphuric and nitric (50:50 molar) acid. After washing, an aliquot of the remaining slurry was evaporated onto cover slips. Cover slips were then permanently mounted onto glass slides with Naphrax®. Approximately 600 (595–1068) diatom valves were identified and enumerated along transects. Total numbers of diatoms counted varied because counting was usually completed at the end of a transect or halfway through a transect. Counting was done under oil immersion using a Nikon Eclipse E600 microscope equipped with differential interference contrast optics (1250× magnification; N.A. = 1.4). The taxonomy and nomenclature follows: Patrick & Reimer (1966, 1975), Krammer & Lange-Bertalot (1986–1991) and Cumming et al. (1995).

Slides for enumeration of akinete and *Pediastrum* counts were prepared by diluting a 1 ml subsample of the lake sediments to 20 ml. From this diluted subsample, 0.25 ml was permanently mounted in HPMA using a modification of Crumpton (1987) and St. Amand (1990). Cyanobacterial akinetes, pollen grains, and *Pediastrum* colony remnants were counted on an Olympus BH-2 research grade compound microscope equipped with Nomarski optics and epifluorescence and a 1.25 multiplier. Cells, grains, and colony remnants were visualized using blue-light epifluorescence at 400×. Between 300 to 400 random fields were spread evenly over three slide mounts per sample. In the case of colony remnants, cells per colony were also tabulated.

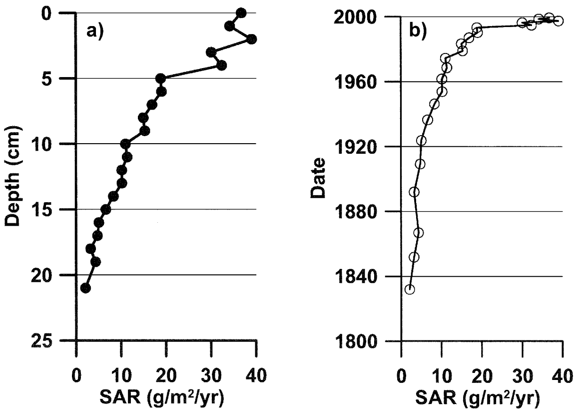

Figure 3. (a) Calculated sediment accumulation rates (SAR) for Core K1 plotted versus sediment depth (●) and (b) date (○).

Results

Sediment dating and sediment accumulation rates

Sediment from the base of two of the three cores was aged using ^{14}C methodology. The measured ^{14}C age was 1420 (± 40) YBP in core K1 for interval 65–66 cm. This corresponds to a calibrated radiocarbon date of 550 to 665 AD. For core K2 at interval 64–66 cm, the measured age was 1460 (±) 40 YBP. This corresponds to a calibrated radiocarbon date of 530 to 650 AD. The ^{14}C results for the two separate cores are not significantly ($P = 0.05$) different from one another. Core K2 was retained for duplicate analysis, although no further use of this core was made in this study.

The primary focus of this project was to assess changes in Upper Klamath Lake that may have occurred in the last 100 to 150 years. The sediment in core K1 and K3 was dated using ^{210}Pb methodology, which provides information on sediment age for the period of interest. The measured ^{210}Pb concentrations in the two cores agree closely (Fig. 2). The supported concentrations are noteworthy because of the extremely low values at about 0.003 Bq/g. However, because of the variability in core K3, the remainder of the results are presented for core K1.

Sediment accumulation rates (SAR) calculated from the ^{210}Pb measurements are presented in Figure 3. The rates of accumulation in core K1 range from about 2 to 39 g/m^2/yr. The rate of sediment accumulation appears to increase throughout the period datable with ^{210}Pb. Accumulation rates increase at a lower rate in the lower sediments and accelerate to substantially greater values in the upper sediments. The overall rate

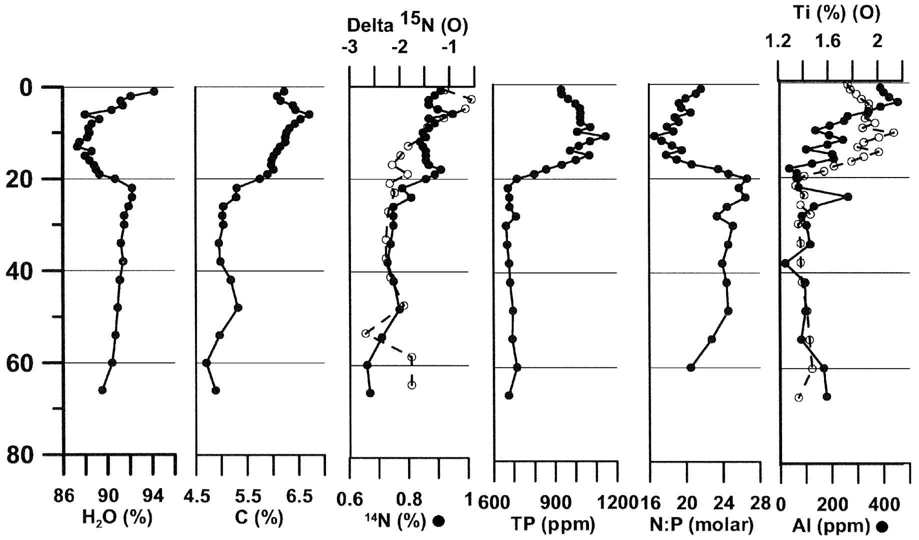

Figure 4. Sediment composition for core K1, Upper Klamath Lake. Water content is expressed as a percent of total weight. Concentrations of carbon and nitrogen, for sediments are expressed as a percent dry weight. Carbon and nitrogen are expressed as percent dry weight. ^{15}N is expressed as delta (‰) and phosphorus is expressed as parts per million dry weight. The N:P ratio is expressed in molar units. Titanium concentrations are expressed as percent dry weight and aluminum concentrations are expressed as parts per million dry weight.

of sediment accumulation appears to have increased about seven-fold, using a baseline rate of 3 g/m^2/yr at 20 cm to 22 g/m^2/yr as an average rate for the upper 10 cm.

Sediment composition

Water content in the sediment was high ranging from 87% to over 94% at the sediment–water interface (Fig. 4). However, unlike many lake sediments which exhibit a monotonic decline in water content, the sediment in Upper Klamath Lake displays a rapid initial decline in water content, followed by an increase for several centimeters before again resuming a relatively continuous decline.

The sediment was analyzed for carbon (C), nitrogen (^{14}N, ^{15}N), and total phosphorus (P). The results shown in Figure 4 illustrate that the upper sediments are enriched in C, N, and P relative to concentrations measured in the lower sediment. The enrichment of the upper sediments ranged from about 20% for nitrogen to approximately 50% for phosphorus. Although both N and P increase in the upper sediments, the differences in the rates of enrichment result in a significant alteration in the N:P molar ratio where the ratio is generally above 20 in the sediment below 17 cm and is less than 20 in the upper sediments. The heavier isotope of nitrogen (^{15}N) also was measured to assist in determining possible factors associated with changes in total nitrogen. The results show a significant change in the proportion of ^{15}N in the upper sediments. Thus, there has been both an increase in the overall concentration of N in the upper sediments and a qualitative change in the source of nitrogen being deposited in the lake.

Titanium (Ti) and aluminum (Al) were measured in the sediments to assess possible changes in the source material being deposited. Ti and Al are both used as indicators of erosional inputs from the watershed. Ti is particularly useful for this application because it is neither sensitive to redox conditions in the sediment nor is it incorporated into biological processes. Ti shows a 40% increase in the upper sediments, whereas Al exhibits an increase over 200% (Fig. 4). The increase in Ti occurs from 20 to 10 cm, whereas the increase in Al occurs largely above 10 cm.

Algal remains

Several biological indicators of water quality in Upper Klamath Lake were analyzed to assess possible changes in the lake. The first group of organisms presented here is the diatoms. The dominant diatom taxa are illustrated in Figure 5. Three principal zones have been identified in the core: (1) Zone 1 (66–59.5 cm); (2) Zone 2 (59.5–19 cm), and (3) Zone 3 (19–0 cm). Zone 3 has been further partitioned into two subsets.

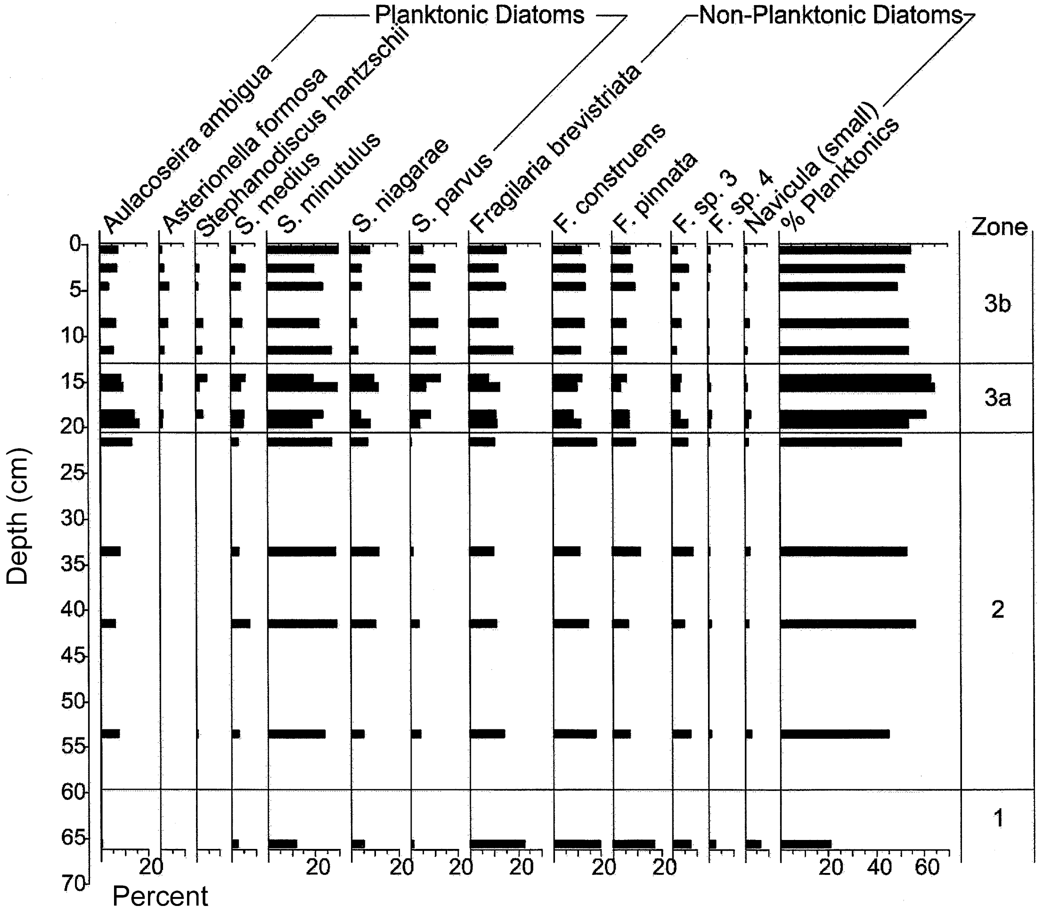

Figure 5. Dominant diatom taxa in the sediment for Upper Klamath Lake.

Zone 1 (66–59.5 cm) is dominated by small benthic *Fragilaria* (~71%), including mainly *F. brevistriata* (~23%), *F. construens* (~19%), *F. pinnata* (~17%) and *F.* sp. KL 3 (~7%). This zone also includes the highest abundance (~6%) of small *Navicula* diatoms (also non-planktonic), such as *N. absoluta*, *N. modica*, *N. minima*, *N. pseudoventralis*, small *N. pupula*, *N. submuralis* and *N.* sp. KL 1 in this core. Planktonic diatoms only make up approximately 20% of zone 1. Zone 2 (59.5–20 cm) is delineated by a sharp increase in planktonic diatoms from ~20% to ~51%. *Stephanodiscus minutulus*, *S. niagarae* and *S. parvus* increase (24%, ~9% and 4.2%, respectively) and *Aulacoseira ambigua* (~9%) appears for the first time. *Fragilaria brevistriata*, *F. construens* and *F. pinnata* all decrease at this time (~11%, ~16% and 9%, respectively). Zone 3 (20–0 cm) has been subdivided into two subzones – Zone 3a and 3b. Zone 3a extends from 20–13 cm, and is differentiated from Zone 2 by the first appearance of *Asterionella formosa* (~0.9%) and increases of *Stephanodiscus hantzschii* (~2%: Fig. 16) and *S. parvus* (~8%) from close to 0% in zone 2. The percentage of planktonic diatoms increases to ~56% in this zone. Zone 3b extends from 13–0 cm, and is differentiated from Zone 3a primarily by decreasing *Aulacoseira ambigua* (~6%) and *S. niagarae* (~5%).

Pediastrum is a genus of green (Chlorophyta) algae that leaves fossilized coenobia in lake sediments (Zippi, 1998). The relative abundance of *Pediastrum* declined from about 95% (relative to akinete counts; although *Aphanizomenon* is the current dominant phytoplankton taxa in the surface waters, not all *Aphanizomenon* individuals form akinetes thus accounting for the difference in the relative abundances of the *Pediastrum* and *Aphanizomenon* in the sediments) in the lower sediments to below 80% in the surface sediments (Fig. 6). Because the upper sediments have

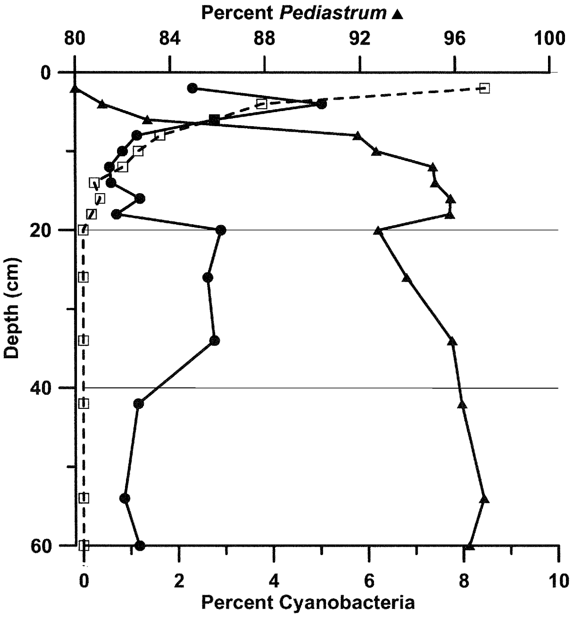

Figure 6. Relative abundance of *Aphanizomenon* (□), non-*Aphanizomenon* cyanobacterial akinetes (●), and *Pediastrum* (▲) in Upper Klamath Lake.

shown a major increase in SAR, the absolute counts of *Pediastrum* have increased overall but their proportion relative to other reference taxa has decreased significantly.

The cyanobacterium, *Aphanizomenon flos-aquae,* is the dominant phytoplankton species in Upper Klamath Lake during the summer growing season (Kann, 1998), and biomass levels are such that they support a major harvesting program used to manufacture food supplements (Carmichael et al., 2000). Although cyanobacteria normally decompose within the lake or the sediments, some species produce resting cysts, termed akinetes, which can remain preserved for thousands of years, cf. van Geel et al., 1994). Two types of akinete counts were conducted: total cyanobacterial akinetes and *Aphanizomenon* akinetes. The results show relatively small changes in the total abundance of preserved akinetes in Upper Klamath Lake, but *Aphanizomenon* akinete abundance has increased from apparent absence in the sediments below 20 cm to over 8% (Fig. 6).

Discussion

The dating of sediments in a shallow, productive system such as Upper Klamath Lake can be highly problematic due to wind-induced resuspension of sediments, diagenetic reactions causing gas generation, bioturbation from benthivorous fish, burrowing insect larvae, and detachment of surface sediment from the lake bottom by algal mats. Several previous attempts at dating the sediments in Upper Klamath Lake have yielded some useful results, although all investigators noted the existence of various degrees of mixing in the upper sediments. Sanville et al. (1974) measured ^{14}C in eight sediment intervals distributed among three different cores and concluded that sediment accumulation rates (SAR) had increased greatly in recent times. Martin & Rice (1981) measured ^{210}Pb activity in eight sediment cores collected from throughout Upper Klamath Lake and also concluded that SAR had increased in modern times.

The most recent study of the lake sediment, prior to our effort, was an extensive study of long-term rates of sediment chemistry and diatom stratigraphy conducted by the U.S. Geological Survey as part of larger effort to better understand climate change. Colman et al. (2004) measured ^{137}Cs, ^{210}Pb, and ^{14}C in three cores collected in various locations in the lake. Although the major focus of their effort was to construct a long-term chronology for evaluation of climatic changes, they measured ^{137}Cs and ^{210}Pb to constrain the uncertainty in the ^{14}C dating. The extensive downcore analysis of ^{14}C by Colman et al. (2004) indicated that the carbon dating exhibited a positive bias of about 400 years. They attributed this to inputs of older organic material. The results for both cesium and lead showed that there was mixing of the upper sediments and mobilization of the cesium downcore. Similar to Martin & Rice (1981), Colman et al. (2004) presented the results as an average sedimentation rate (SR) for the surficial sediments (upper 20–25 cm). When we compare the results from Martin & Rice (1981) [median SR = 1.70 mm/yr] and Colman et al. (2004) expressed as an average rate of sedimentation for the upper sediments (<25 cm) [median SR = 1.72 mm/yr for CIC model; SR = 1.81 mm/yr for CRS model], we observe reasonable similarity with our results [SR = 1.25 mm/yr with CRS model].

Thus, all three studies show that the upper 20 to 25 cm of sediment represent the most recent 150 years of accumulation. However, it is uncertain the degree to which the upper sediments can be distinguished with respect to specific dates or ranges of dates. Colman et al. (2004) reported a mixing zone of about 8 cm thick. Our observations are consistent with this at about 10 cm thick. The measured ^{210}Pb in the upper

10 cm corresponds with an activity level representing 20 to 30 years of ^{210}Pb. Therefore, if the mixing is instantaneous (i.e., associated with wind-induced mixing episodes) all of the reported ages in our cores are about 25 years too old. However, it is unlikely that the mixing is instantaneous which is supported by the results of other constituents such as the *Aphanizomenon* akinetes. Because other sediment constituents are not homogenously mixed, the time constant for the mixing must be finite. Although the mixing characteristics of Upper Klamath Lake contribute to uncertainty in the dating of recent sediments, the results show that the upper sediments can be partitioned into zones representing different periods of recent history. Under the most conservative of interpretations, the results demonstrate a major change from pre-development water quality to current conditions. However, we show that in the case of core K1, a more refined partitioning is supportable in which the 20th century can be distinguished as several zones of about 25 to 30 years in duration.

The sediment chemistry of Upper Klamath Lake, as characterized by core K1, shows an abundance of nutrients. The composition of the modern sediments (20th century) is enriched in both N and P compared to pre-settlement sediment. However, whether this pattern reflects differences in depositional history is uncertain. Upper Klamath Lake is subject to a high degree of physical mixing as previously described. In addition, diffusion and diagenetic reactions make it highly likely that redox-sensitive constituents move rapidly through these sediments. For example, Colman et al. (2004) attributed the peak of ^{137}Cs in the sediments at a depth of 19 cm to chemical mobilization downcore rather than a simple physical mixing process.

Despite the likelihood that considerable physical mixing and chemical transport occurs in the sediments, there are some intriguing patterns with respect to nitrogen and phosphorus in the sediments that warrant examination. As noted in the results, both N and P increase in the modern sediments. However, the rates of increase are quite different, resulting in a significant decrease in the N:P ratio in the upper sediments (Fig. 4). If this pattern is not an artifact of post-depositional processes, then either the phosphorus loading to the lake has increased relative to the nitrogen loading, or the degree of N fixation from sources such as cyanobacteria has declined. Given the abundance of N-fixing cyanobacteria present in Upper Klamath Lake, it would appear more likely that the P loading has increased relative to N loading. A third possibility for altering the N:P ratio in the sediments is that conditions favorable for volatilization of nitrogen in the lake have increased. Nitrogen volatilization could occur through denitrification ($NO_2^- \rightarrow N_2\uparrow$) or through ammonification ($N_{org} \rightarrow NH_4 \leftrightarrow NH_3\uparrow$), the latter of which is favored under high pH conditions (Chapra, 1997). Elevated pH conditions are well documented in Upper Klamath Lake (Kann & Smith, 1999) and have been implicated as a contributing factor in the loss of fish (Perkins et al., 2000).

The apparent decrease in the N:P ratio in the upper sediments may have important effects on community composition of phytoplankton, especially on the cyanobacteria. The greater increase of P in the surficial sediments may lend competitive advantage to various taxa and alter the phytoplankton community composition. Based on the data presented here, *Aphanizomenon* was apparently not present in Upper Klamath Lake in the 19th century. It is remotely possible that they were present, but the conditions changed and they began to form akinetes in the 20th century, or that the akinetes exhibit very rapid decomposition rates in these sediments. However, akinetes from a nearby lake show a bimodal distribution in akinetes during the last century which would suggest that the observed pattern of akinetes in Upper Klamath Lake is not an artifact (Eilers et al., 2001). It is conceivable that the increasing dominance of *Aphanizomenon* in the 20th century may be a consequence of either the increase in P loading or a change in the ratio of N:P. Naturally high concentrations of phosphorus in the major tributaries would suggest that changes in nitrogen inputs would be important to the phytoplankton composition. However, *Aphanizomenon flos-aquae* is capable of fixing nitrogen and presumably would be less affected by direct changes in N availability than taxa such as *Microcystis* which is not capable of fixing nitrogen (Paerl, 1988).

Another issue relative to nutrients in the sediments that we explored in this study was the concentration of ^{15}N in sediments. This stable isotope of nitrogen has been used to investigate a variety of ecological processes, perhaps most notably as a tracer in freshwater systems for marine-derived N from anadromous fish (cf. Bilby et al., 1996). In these applications, the marine-derived N is recognized by a much higher proportion of $^{15}N/^{14}N$. In studies of freshwater systems impacted by large inputs of nonpoint sources of pollution from watershed sources and wastewater, the proportion of ^{15}N is also often elevated (Fry, 1999). Denitrification can contribute to substantial enrichment of $\delta^{15}N$ (Clark & Fritz, 1997) as shown in studies of septic tanks (Aravena et al., 1996) and agricultural sources (Böttcher et al., 1990). Increased nitrogen fixation in the lake also could alter the isotopic ratio of nitrogen in the sediments. Although anadromous fish historically passed through Upper Klamath Lake, the magnitude of the runs relative to the size of the lake were far smaller than experienced by systems in Alaska where marine-derived nitrogen can be a significant component of the nutrient budget (Kline et al., 1993). In Upper Klamath Lake, the large nutrient contributions from the watershed and the nitrogen fixation derived from cyanobacteria would probably greatly overshadow any historical contributions from anadromous fisheries. The ^{15}N results for Upper Klamath Lake indicate a significant increase in the later part of the 20th century. If salmonids had played a significant role in the nitrogen budget of Upper Klamath Lake, we would have expected to see a decrease in the proportion of ^{15}N corresponding to 1921 when the Copco Dam on the Klamath River prevented salmon from reaching Upper Klamath Lake (KRBFTF, 1991). Instead, the proportion of ^{15}N has increased during this period. These results are consistent with an increase in watershed loading of nonpoint sources of nitrogen (Clark & Fritz, 1997). An alternative interpretation is that nitrogen fixation from heterocystous cyanobacteria such as *Aphanizomenon flos-aquae* is causing more atmospheric nitrogen to be fixed, which would cause the expected ^{15}N ratio in the sediments to decline. The potential role of other factors, such as changing water temperatures or selective uptake of heavy nitrogen by aquatic organisms (Adams & Sterner, 2000) in altering the sediment ^{15}N cannot be excluded here. A number of other factors operating at different scales of time, space, and species can alter the nutrient ratios in ways that make it difficult to unequivocally link the changing C:N:P ratios to eutrophication processes alone (cf. Sterner & Elser, 2002).

A less ambiguous signal of watershed disturbance is derived from the results of Ti and Al, both of which indicate major increases in erosional inputs to Upper Klamath Lake in the 20th century (Fig. 4). Both metals show major increases above 18 cm in the sediment, with Ti peaking at 10 cm and Al peaking at 4 cm. The only explanation for these distributions, other than accelerated erosional inputs from the watershed, is that there has been a rapid decrease in deposition of plankton in the 20th century, which would cause the allocthonous inputs to be proportionally greater than the autochthonous inputs. This latter explanation seems highly unlikely given the history of the watershed and the current levels of primary production. We believe that the increase in Ti and Al provide strong evidence of erosional inputs associated with disturbance of the watershed in the 20th century.

Three components of the plankton history in Upper Klamath Lake were investigated: (1) diatoms, (2*)* *Pediastrum*, and (3) cyanobacteria akinetes. The stratigraphy from Upper Klamath Lake shows changes in the diatom community that can be divided into several zones. Although subtle, these changes may represent important changes in environmental conditions.

Zone 1 is dominated by small, primarily benthic *Fragilaria* species. The greater abundance of small benthic *Fragilaria* at the bottom of the core may reflect more wetlands adjacent to or upstream of Upper Klamath Lake at this time. The decrease in small, benthic *Fragilaria*, Zone 2 is also marked by the appearance of *Aulacoseira ambigua. Aulacoseira ambigua* is a heavily silicified diatom that requires turbulence to remain in the photic zone. It is unclear whether the turbulence of the lake has increased in response to greater fluctuations in lake stage following construction of the Link Dam or whether this taxon is responding to other changes in the lake. The appearance of *Asterionella formosa* and *Stephanodiscus hantzschii* at the start of Zone 3 likely indicates increased human activity and increased nutrient availability. Current diatom seasonality is characterized by spring dominance of small and intermediate-sized *Stephanodiscus* species (*S. parvus*, *S. oregonicus*, and *S. hantzschii*) along with *A. formosa* and occasional *Aulacoseira*, whereas *S. niagarae* increases in the fall (Kann, 1988). Such changes in response to the arrival of Europeans have been noted by others (cf. Hall et al., 1999). The increase in *S. parvus* may also be related to increased nutrients. The slight decreases in small, benthic *Fragilaria* species may indicate a corresponding decrease in wetlands within the drainage basin of Upper Klamath Lake. The slight decrease in *A. ambigua* and *S. niagare* and coincident increase in *Asterionella formosa* in Zone 3b could indicate: (1) a decrease in available silicon (Si) and/or (2) a decrease in transparency. *Aulacoseira* are heavily silicified diatoms and have high growth requirements for silicon (Kilham et al., 1986). It is expected that *S. niagarae*, also a heavily silicified diatom, would have high silicon requirements. *Asterionella formosa* also require relatively high amounts of silicon for growth (Kilham & Kilham, 1978), although their requirements would be expected to be lower than those of *Aulacoseira*. Silicon can become limiting with an increase in phosphorus availability, which can result in decreased diatom production (Schelske & Stoermer, 1971). Increased phosphorus concentration in the upper sediments along with increased erosional inputs as indicated by Al and Ti during this same period may reflect such an increase in P availability.

In addition to the diatoms, one genus of Chlorococcales, *Pediastrum*, is well represented in lake sediments (Hutchinson, 1967; Zippi, 1998). *Pediastrum* is generally present in nutrient-rich lakes and is often associated with other taxa such as *Anacystis, Anabaena, Melosira, and Fragilaria crotenensis* (Hutchinson, 1967). The abundance of *Pediastrum* remains in the sediments of Upper Klamath Lake support the view that the lake has been highly productive for a long period. However, a decrease in the relative proportion of *Pediastrum* does not indicate a decrease in productivity of the system, but likely indicates a decrease in competitive advantage relative to *Aphanizomenon*. Moreover, since the increase in lake sediment nutrients shows that the lake has not become less productive, the decrease in relative abundance of *Pediastrum* is likely the consequence of a further advancement in the productivity of the lake.

Although some diatom taxa have made new appearances (*A. formosa*) or notable increases (*S. parvus*; *S. hantzschii*) in Upper Klamath Lake, the most noteworthy change in phytoplankton composition is the appearance and current dominance of the cyanobacterium, *Aphanizomenon flos-aquae*. During the summer, biomass of the organism typically reaches 50 mg l^{-1} wet wt. or >250 μg l^{-1} chlorophyll *a* (Kann, 1998). Because *Aphanizomenon* generally requires high P levels to dominate (Sommer, 1989; Pechar, 1992), and has a competitive advantage at lower N:P ratios (cf. Smith, 1983), the apparent absence of *Aphanizomenon* akinetes in sediments deeper than 20 cm and its transition to become the dominant phytoplankton taxon is indicative of a transition to a hypereutrophic system in the 20th century.

There is often concern that when most of the sediment analysis is based primarily on one core, the results could be an artifact of atypical patterns from that specific sediment sample. There are several lines of evidence indicating that the patterns we observed in core K1 are representative of lake-wide responses to watershed changes. First, is that the dating sequence we observed in core K1 was repeated elsewhere in core K3 located several kilometers from the location of core K1. Second, the dating sequences we observed in both cores were similar to the results obtained by Bradbury et al. (2004) and consistent with general rates of sediment accumulation measured by other investigators in Upper Klamath Lake. Third, the patterns we observed for *Pediastrum*, the *Aphanizomenon* akinetes, and erosional inputs (we measured Ti, whereas they measured tephra) agreed closely to those observed by Bradbury et al. (2004).

Conclusions

Upper Klamath Lake, for at least the period of record represented by this study (~1000 yr), has been a very productive lake. The diatom stratigraphy shows a diverse assemblage of taxa typically found in eutrophic and hypereutrophic lakes. Cyanobacteria have been present throughout this period and nutrient concentrations in the sediment have been high. Nevertheless, the recent sediments show a coherent record of higher nutrient concentrations, decreased ratios of N:P, elevated erosional inputs, higher rates of sediment accumulation, and appearance of phytoplankton taxa previously unseen in the lake. The new phytoplankton taxa are without exception indicative of extremely productive waters. The evidence indicates that Upper Klamath Lake has experienced a substantial increases in erosional inputs, nutrients, and *Aphanizomenon flos-aquae* – all consistent with changes in the watershed during the 20th century.

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