Responses of Diatom Communities to Changes in Climate and Terrestrial Vegetation in a Subarctic Lake, Northern Sweden

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Abstract:

Climate change is a major societal concern, but relatively little is known about the ecological effects of climate variability due to insufficient long-term records. The lack of direct historical measurements necessitates use of indirect records contained in aquatic sediments and other sources (e.g., tree-rings, glaciers). Among the biota preserved in lake sediments, diatom algae (Class Bacillariophyceae) provide a rich source of information about past aquatic conditions and climatic change. Areas near major ecotonal boundaries are the most responsive to shifts in climate because small changes can lead to major shifts in community composition. Lake Tibetanus is located close to the present tree line in the Abisko valley of northern Sweden. A variety of scientific studies have produced a detailed knowledge of local climate fluctuations since deglaciation, making it an ideal site to study how changes in climatic conditions and terrestrial vegetation affect aquatic communities.

The objective of this study was to measure responses of the diatom communities in Lake Tibetanus to periods of climate warming and cooling and to assess if changes in the diatom community composition correlate with changes in the surrounding terrestrial vegetation, temperature and hydrological regime. Overall, results of variance partitioning analysis indicated that the major shift in diatom community composition coincided with changes in pollen inferred temperature. A total of 27.6% of the total variation observed in the diatom assemblages was explained by changes in mean July air temperature, as inferred from sedimentary pollen analysis. In contrast hydrological regime, as reflected by the sedimentary 'non-Dansgaard' oxygen stable isotope signature, was not as strongly

correlated and explained only 5.5% of the variation in diatom assemblages. The exact nature of the relationship between the aquatic and terrestrial communities remains unclear, as there did not appear to be a direct correlation. Further study is required to investigate the evidence suggesting that diatom communities exhibited a delayed response (500 years) to changes in the surrounding terrestrial vegetation.

Introduction:

Global warming and other consequences of climate change are major societal and environmental concerns, but it is difficult to quantify changes in the Earth's climate and relatively little is known about the ecological effects of climate variability. This is due to a lack of sufficient long-term climatic and ecological records. Most existing climate records date back no more than a century, a time span too short to produce accurate models for predicting future climate change. Ecological studies have taken place on even shorter time scales with very few studies covering more than 20 years. This difficulty in distinguishing between long-term trends and natural variation continues to hamper the efforts of scientists and natural resource managers (Lotter et al., 1997). The lack of direct historical measurements requires that we must turn to indirect methods to examine past climatic and ecological changes, in order to better predict our future.

Lake sediments are an important source of information about long-term change in past climatic and ecological conditions. Undisturbed sediments can provide a quantifiable record of local environmental change. For example, fossilised remains of chironimids are useful indicators of mean July air temperatures, because their life-cycles are directly affected by air temperature (Olander et al., 1999), meanwhile an area's vegetative history is recorded in preserved pollen grains (Barnekow, 1999A). The most useful indicators of climate change are those able to respond both directly and sensitively to the many physical, chemical and biological factors that can have an impact on ecological systems (Stevenson and Pan, 1999).

Diatoms are a diverse group of unicellular microscopic algae (Class Bacillariophyceae) that are prevalent in most aquatic environments (Stoermer and Smol, 1999). They are very useful in paleolimnological studies because each diatom possesses a cell wall (frustule) made of silica, which preserves well in most aquatic sediments and is used in taxonomic identification. When cells die, frustules settle to the bottom and are incorporated into the sediment record. In aquatic environments where the bottom sediments are relatively undisturbed (e.g. lakes) sedimentary diatom assemblages can be used to reconstruct the diatom communities that were present at a particular time (Hall and Smol, 1996). This allows studies of the changes in the communities and also of the environmental conditions causing those changes. Analysis of diatoms contained in a sediment core taken from a lake allows recognition of changes in the distribution and abundance of individual species with depth. Using carbon dating techniques these changes can be related back to the time at which they occurred with some degree of accuracy. With knowledge of individual species' optima and tolerance for pH, air temperature, nutrient levels and many other variables, diatoms can be used to quantify past changes in environmental conditions (Stevenson and Pan, 1999). The ability to reflect local environmental change coupled with short generation times and relatively few barriers to dispersal make diatoms excellent ecological indicators.

The environments most responsive to changes in climate are those that lie in areas with steep climatic gradients (Weckstrom et al., 1997). This is especially true of areas near major ecotonal boundaries such as treelines, because along these boundaries small changes in climate can lead to major shifts in biotic composition of communities (Weckstrom et al., 1997). Also, arctic and subarctic regions are extremely fragile and sensitive to change, due to slow growth rates and low species diversity (Korhola et al., 1999). The Abisko valley region of northern Sweden exhibits these features and has been the site of a large number of scientific studies, including investigations of glacial advances, tree-limit oscillations, pine dendrochronology (Karlen et al., 1999), and corresponding vegetation changes (Barnekow, 1999A). Consequently, a detailed knowledge of climate fluctuation since the last glacial period has been produced. This research has shown that local conditions have varied considerably. For example, the Abisko valley was dominated by birch woodlands upon deglaciation approximately 10,000 years ago, that was subsequently replaced by boreal pine-birch forest as temperatures warmed and climatic conditions became more continental (Barnekow, 1999A). When conditions were optimal for pine (6,300-4,500 cal BP) the pine tree limit extended 175 m above its present boundary, however during the past 4,000 years the pine forest has receded and birch now forms the tree limit once more (Barnekow, 1999A).

Very little research has addressed how changes in climatic (temperature, hydrology) conditions and terrestrial vegetation affect aquatic communities, yet there are definite limnological differences between lakes that differ in their catchment vegetation and soil type (Seppa and Weckstrom, 1999). The volume of knowledge that exists regarding climate change in northern Sweden provides a unique opportunity to examine and quantify how diatom communities have responded to the direct influences of climate and hydrology.

The objective of this study is to analyze the sedimentary diatom assemblages of a single lake within northern Sweden's Abisko region and determine if changes in diatom community composition are correlated with terrestrial vegetation changes in the surrounding catchment (as assessed by pollen records). If there is no direct correlation between diatom and pollen assemblages, is there instead any evidence that change in local hydrology (inferred from stable isotope records) is the principle factor responsible for variation within the diatom community.

Site Description:

This project is focused on one lake (Lake Tibetanus) within the Abisko valley of northern Sweden (see Figure 1), an area that has already been the site of a significant amount of paleoclimatic studies. In fact, the sediments from Lake Tibetanus have already been analysed for pollen content (Barnekow, 1999A) and stable oxygen isotopes (Hammarlund and Edwards, 1998; Hammarlund et al., In Press), providing a detailed vegetation and climatic history of the past 10,000 years.

Tibetanus is a small lake, approximately 3.9 m deep and 100 m in diameter. The lake is situated on a south-facing slope surrounded by sparse birch forest at an elevation of 560 m above sea level, very close to the present tree-line of 600-700 m (Barnekow et al, 1998). Previous paleoecological studies have shown that the tree line has undergone major changes since the last glaciation period, moving up and down the mountain in response to local climate changes (Barnekow, 1999A). Due to the local geology, specifically the surrounding calcite marble bedrock, Tibetanus has a high carbonate content and its water has a pH of 7.7 (Barnekow et al., 1998). There are no permanent surface tributaries; it is instead fed by groundwater and limited local precipitation runoff, with a residence time of three-four weeks that appears to have been stable over the entire Holocene (Hammarlund et al., In Press).

The geographic location of Lake Tibetanus makes it particularly interesting. It is situated along a steep climatic gradient with the climate becoming increasingly oceanic to the west and increasingly continental to the east, due to a steep precipitation gradient

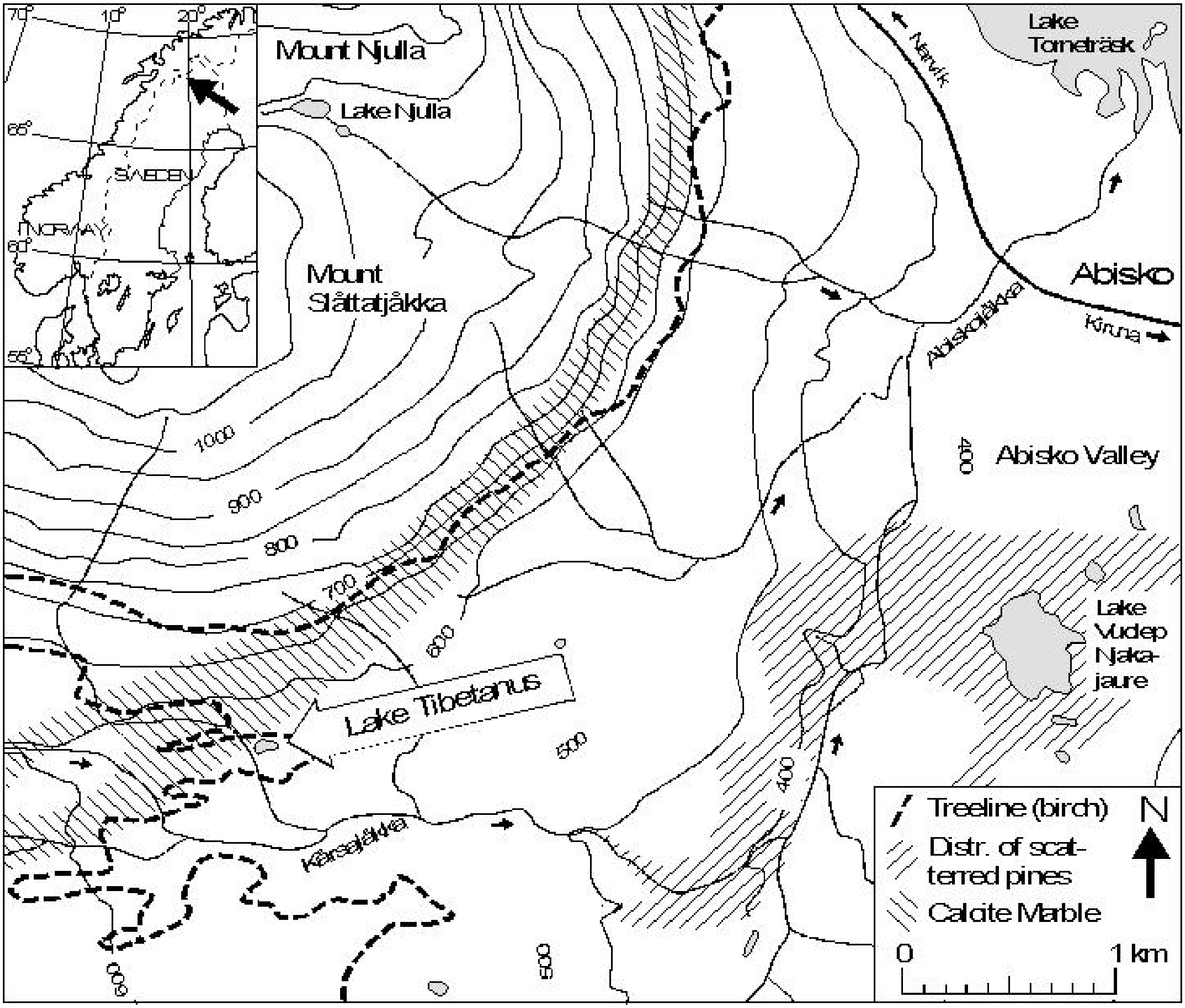

Figure 1. Map of the Abisko area showing the study site, Lake Tibetanus and its position relative to the present treeline. The inserted map shows the location of the study area in northern Sweden. (from Hammarlund et al. In Press)

imposed by the Scandes mountains (Barnekow, 1999B). The pronounced fluctuations in the surrounding vegetation have been due to local shifts in climate (Hammarlund et al., In Press) making it an excellent site to study the effects of terrestrial vegetation on aquatic communities.

Methods and Materials:

Diatoms were analysed in a sediment core that was obtained in March 1995 as a number of overlapping 1-m long core sections. The core was taken from the deepest part of Lake Tibetanus using a Russian coring device (10-cm diameter) and subsequently divided into one-centimetre thick slices for analysis (Barnekow et al., 1998).

Radiocarbon dates were obtained using both bulk sediment and terrestrial plant macrofossils (Barnekow et al., 1998). Material from twelve levels was dated using mainly delicate items such as leaves and pine needles for the macrofossil analysis. Calibration of the obtained radiocarbon ages in calendar years before present (cal BP) was performed by means of the Calibeth 1.5b computer code (Barnekow et al., 1998). This study analyses diatoms present in the same core as was used in the studies of plant pollen and macrofossils by Lena Barnekow (Barnekow et al., 1998; Barnekow, 1999A) and stable oxygen isotopes by Dan Hammarlund et al. (Hammarlund and Edwards, 1998; Hammarlund et al., In Press).

Diatom samples were prepared by treating wet sediment (~0.2g) with 10% HCl to remove carbonates and then digesting with strong acids (30%H_20_2 at 100^{o}C for 1 hour, followed by a mixture of H2SO4/HNO_3 (1:1 by volume) at 85^{o}C for 3 hours) in order to remove any remaining organic material (Hall and Smol, 1996). After settling for 24 hours acid residue was removed from the cleaned diatom slurries through repeated washings.

The washing procedure involved siphoning off excess remaining liquid, rehomogenizing the diatom pellet in diatom-free, deionized water, and finally allowing it to settle for a 24-hour period before siphoning again. This washing procedure was repeated twelve times.

Diatom suspensions were serially diluted to approximately one half, one quarter, and one eighth of the original concentration of the slurries, creating four dilutions for each sample (1:1, 1:2, 1:4, 1:8). Approximately 1.5ml of each well-mixed suspension was placed onto individual coverslips (22x22 mm). Coverslips were allowed to dry completely at room temperature. Naphrax was used to mount the cover slips onto microscope slides (two cover slips per slide).

For each sample, a minimum of 300 diatom frustules were identified and enumerated along transects using a Zeiss compound microscope with differential interference contrast optics (1000X magnification, numerical aperture = 1.30). Diatom taxonomy followed Krammer and Lange-Bertalot (1986-1991), Camburn and Charles (2000), and Patrick and Reimer (1966,1975).

Data Analysis

Diatom taxa enumerated for each lake were converted to percent abundances (i.e. a percent of the total diatom sum) and all taxa were included in numerical analyses.

Zonal boundaries separating periods of distinct diatom assemblages over time were identified using stratigraphically constrained cluster analysis available within the CONISS subroutine of Tilia version 2.0.b.4.

Rates of change in diatom community composition can be estimated by measuring the amount of change per unit time between percent abundances of all diatom taxa in adjacent sediment samples. This is most conveniently done by computing dissimilarity coefficients and standardizing them to a uniform age unit (e.g., 200 yr; Lotter et al., 1992). The chord distance was used as a dissimilarity coefficient in this study because it provides good signal-to-noise performance for diatom percentage data (Lotter et al., 1992). Rate of change computations were performed using the program RATEPOL (Birks and Line, unpublished program) and a time standardization unit (TSU) of 200 years on 31 samples spanning the period 7,490 to 30 cal BP.

Variance partitioning analysis (VPA; *sensu* Borcard et al., 1992) was used in order to quantify the relative influences of pollen-inferred temperature and isotope hydrology on changes in the diatom communities over the past 7,500 years. The two-category VPA used in this study employed redundancy analysis (RDA: a direct gradient ordination technique) to quantify the proportion of total variation in diatom communities during the past 7,500 years that could be explained; by the unique effects of each category of supplied explanatory variable (pollen-inferred mean July air temperature (T) and stable oxygen isotope inferred hydrology (H)), the interactive effects of both categories of explanatory variables (T+H), and unexplained variation that was due to other unmeasured factors (Hall et al., 1999). The variable used to quantify changes in the temperature was the mean July air temperature as inferred from a pollen analysis of Lake Tibetanus's sediments. To quantify the effects of local hydrology, the 'non-Dansgaard' stable oxygen isotope data from Tibetanus'sediments was used as an indicator of the processes involved in the transportation of moisture over the nearby Scandes mountains (Hammarlund et al., In Press). Basically, the 'non-Dansgaard' $\delta^{18}O$ record provides an index of changes in the prevailing atmospheric moisture circulation system.

Diatom percent abundances were square-root transformed for the variance partitioning analysis. Three steps were taken in partitioning variation in the fossil diatom data between pollen-inferred mean July air temperature (T) and stable oxygen isotope-inferred hydrology (H). First, an RDA without covariables was used to determine the total amount of variation (sum of canonical eigenvalues) in diatom assemblage composition that was attributable to both explanatory variables (T + H) and the total unexplained variation (100 - (T + H)). Second, a series of partial RDAs (i.e., RDAs with covariables) were used to calculate the variance explained by the unique effects of each category (T alone or H alone; Hall et al., 1999). Third, the joint-effects of both categories of variables on diatom assemblages (TH) were determined by the difference between the eigenvalues derived from the constrained and partial ordinations (total explained variance – T alone – H alone). The joint-effects measured variation in diatom assemblages which were attributable to changes in pollen-inferred temperature and stable oxygen isotope-inferred hydrology, but could not be assigned uniquely to either factor (Hall et al., 1999).

Two explanatory variables were used in the VPA to quantify the relative roles of temperature and hydrology on changes in Lake Tibetanus' diatom communities over the past 7,500 years. The effects of temperature were quantified using a five-point smoothed record of mean July air temperature as inferred from sedimentary pollen analyses (as described in Hammarlund et al., In Press). The effects of hydrological changes (i.e., shifts in the effective transport of moisture due to the position and movement of major air masses; Hammarlund et al., In Press) were quantified using the 'non-Dansgaard' oxygen stable isotope record from the sediments of Lake Tibetanus (i.e., $\delta^{18}O$ signature of bulk carbonate sediment after effects of temperature were removed; details in Hammarlund et al., In Press).

Results:

Although dating showed the entire 295 cm core to represent ~10,000 years of sedimentation (Barnekow et al., 1998), below 230.5 cm (7,490 cal BP) samples did not contain enough diatoms to reliably estimate percent abundances. The inability to make use of samples from below 230.5 cm was predominantly due to a sharp decline in diatom abundance. Difficulty in performing counts was compounded by an increase in the minerogenic content of the samples, which reduced visibility of diatoms considerably.

A total of 47 different taxa were observed in the Holocene sediment core taken from Lake Tibetanus. Throughout the Holocene, diatom diversity was low, dominated by only two species *Amphora libyca* and *Navicula jaagi*. Together, these two taxa comprised 52-99% of the assemblages at all depths in the core (Figure 2). Additionally, diatom assemblages consisted entirely of benthic or littoral species. Over the last 5,500 years the number of species present has increased somewhat, although planktonic taxa remained absent.

Constrained cluster analysis of diatom assemblages identified two main zones of distinct diatom assemblages (Figure 2). The earliest assemblage zone occurred between ~7,500-3,300 cal BP. The more recent diatom assemblage (Zone 1) encompasses from 3,300 cal BP to the present and contains several species not found in earlier samples (most notably *Navicula laevissima* and *Navicula pupula*). The older of the two zones was further divided into subzones at ~5,500 cal BP, which marks a point where a few new species (*Pinnularia interrupta* and *Neidium bisculatum*) appear in a community composed entirely (99%) of *A. libyca* and *N. jaagi*. This zonation pattern is shown in

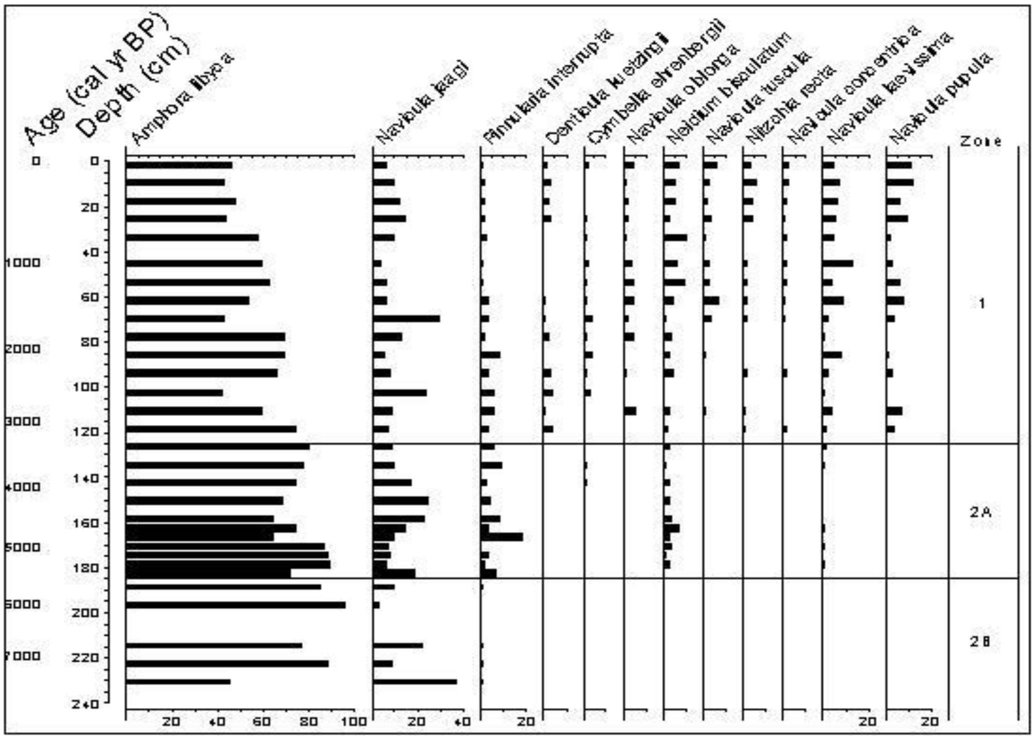

Figure 2 - Stratigraphic changes of the dominant diatom taxa present in sediments from Lake Tibetanus during the past 7,500 years.

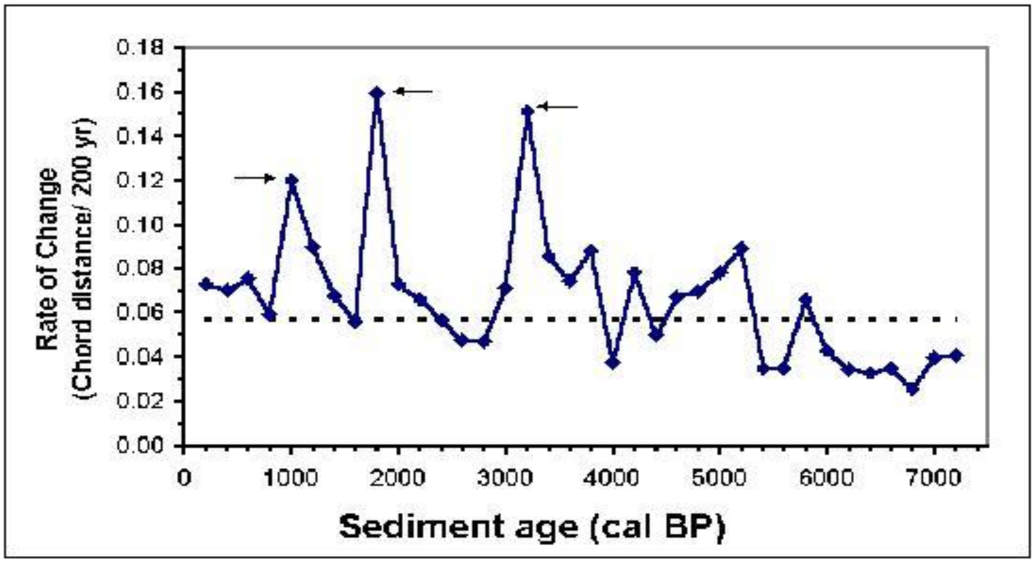

Figure 3 - Rate of change of diatom assemblages from Lake Tibetanus. Arrows indicate periods of maximum change and correspond with arrows presented in Figure 4.

Figure 2 and appears to indicate events occurred which allowed sudden increases in diversity within the diatom community.

Rate of change analysis identified 1,000, 1,800 and 3,200 cal BP as the periods of the most rapid change in the diatom community composition (Figure 3). The earliest of these periods (~3,200 cal BP) roughly coincides with the boundary between zones 1 and 2, and was characterised by increasing species diversity (~3,300 BP; Figure 2). However, the remaining two periods of rapid change also occur within the most recent assemblage zone.

After determining the major zones in Lake Tibetanus' diatom community composition, the results of the cluster and rate of change analyses were compared to equivalent patterns in the surrounding terrestrial vegetation communities (pollen analysis; Barnekow, 1999A) and moisture circulation regimes ($\delta^{18}O$ "non-Dansgaard" isotopic signature of bulk sediments; Hammarlund et al., In Press). The purpose of this was to see if there were any prominent similarities between zonation in the diatom community, changes in terrestrial vegetation as the treeline migrated up and down the mountain, and the changes in the prevalent moisture circulation pattern. This comparison is illustrated in Figure 4, with arrows indicating the points where maximum change was occurring within the diatoms. The diagram does not appear to show a direct relationship between the diatom community and either of the explanatory variables. Zonal changes indicating major shifts in the diatom assemblage do not coincide with major changes in terrestrial vegetation composition or isotopic composition of prevailing precipitation. Moreover, the periods of maximum change in diatom communities all occur in the most recent zone and do not appear to correlate with major changes in vegetation or isotopic composition

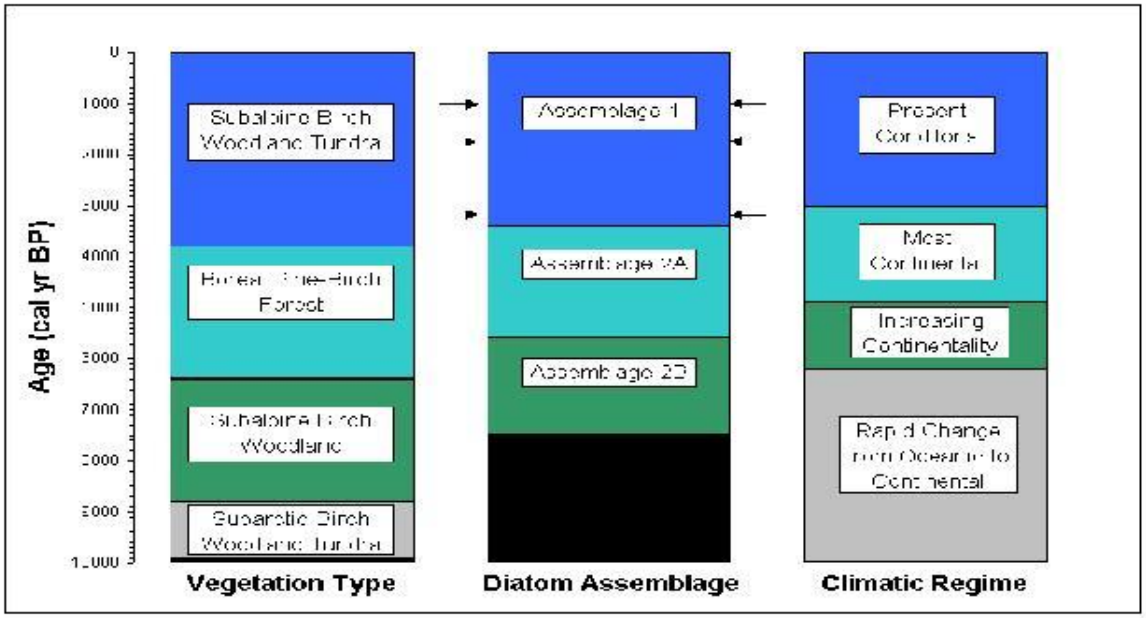

Figure 4 - Comparison of major zones of diatom assemblages, surrounding terrestrial vegetation and predominant climatic regime of Lake Tibetanus during the Holocene. Diatom and vegetation (inferred from pollen analysis) zones determined by constrained cluster analysis. Climatic regimes were reconstructed using hydrologically sensitive oxygen isotopes. Arrows indicate episodes of most rapid change in diatoms, as determined by rate-of-change analysis. Unlabeled blocks indicate sediment depths for which data was unavailable.

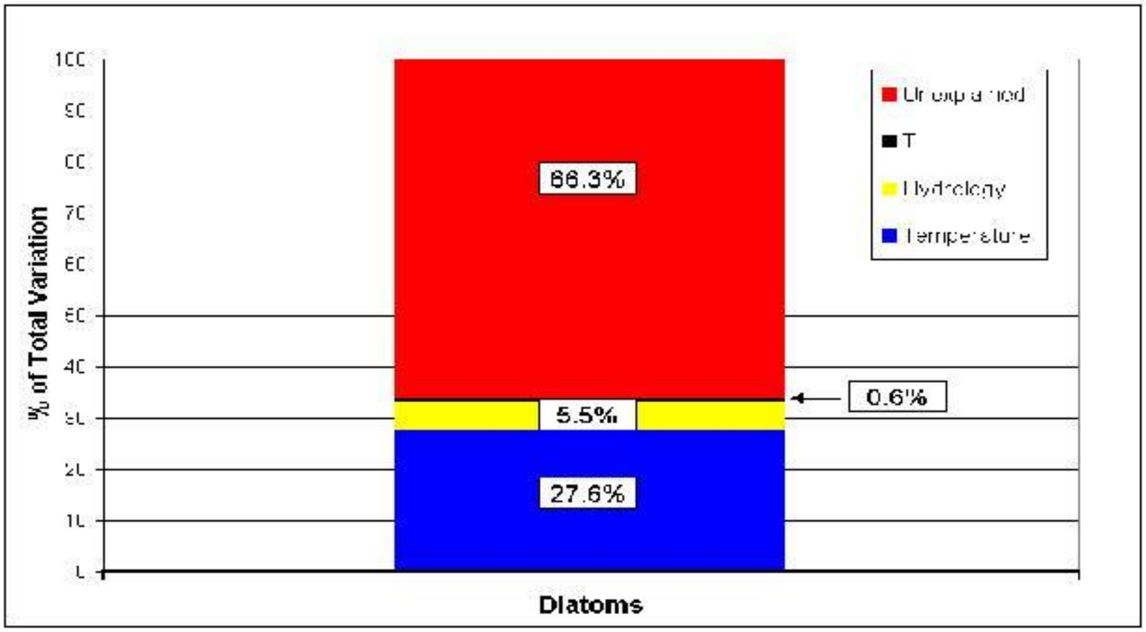

Figure 5 - Results of partitioning variation in diatom assemblages of Lake Tibetanus between vegetation (pollen inferred mean July air temperature)and hydrology (inferred from the 'non-Dansgaard' oxygen stable isotope record of bulk sediments).

either. Interestingly, there does appear to be a time-lag relationship of several hundred years between diatom assemblage and vegetation type, which differs at different periods of the Holocene. The transition from subalpine birch woodland to boreal pine forest (~6,400 cal BP) occurs about 700 years before the transition between diatom assemblages 2A and 2B. Also, the transition from boreal pine forest back to subalpine birch woodland (~3,800 cal BP) was followed 500 years later by the transition between diatom assemblages 1 and 2A. Whether this is the same lag can not be determined at this point.

In addition to a visual comparison between changes in vegetation type, diatoms and the moisture regime, the sources of variation within the diatom community were quantified through the VPA computations. Figure 5 illustrates the amount of variation in the diatom community that is explained by either temperature, the moisture regime, or a combination of both. Of the total variation in the diatom assemblages, 27.6% was explained by the pollen-inferred temperature, 5.5% was explained by oxygen stable isotope inferred hydrology (much less, but still statistically significant), and only 0.6% was explained by interactions of the two variables.

Discussion:

Lake Tibetanus' diatom communities of the past ~7,500 years were characterised by exceptionally low diversity. In fact, assemblages were dominated at all times by two main taxa (*Amphora libyca* and *Navicula jaagi*, 52-99%; Figure 2). The low diversity may be attributable to rapid flushing of the lake and restricted habitat availability, rather than to cold climatic conditions. This is because high-elevation lakes in the region with colder climatic conditions tend to have markedly higher species diversity (Bigler and Hall, In Press) than was observed in Lake Tibetanus. Interestingly, planktonic diatoms were absent from Lake Tibetanus throughout the Holocene. The extremely rapid flushing rate (every 3-4 weeks) may prevent development of planktonic non-motile algal (i.e., diatom) communities because loss rates could exceed growth rates. Benthic and littoral habitats in Lake Tibetanus consist almost entirely of marl sediments covered by calcareous charophyte macrophyte algae. Thus, periphytic habitats are rather uniform. Moreover, the lake is a small, shallow (100 m diameter, 4 m max. depth) and simple basin with no disctintion between littoral and profundal habitats. The water is so clear that light penetrates easily to the entire lake bottom. This rather uniform habitat type, combined with the rapid flushing rate, may have contributed to the observed low diversity in diatom assemblages.

Despite the relative uniformity of diatom communities and their domination *by A. libyca* and *N. jaagi*, diversity increased markedly over the last 5,500 years. In the oldest samples examined, only a few species other than the two dominants contributed more than 1% to the total population. However around 5,500 and 3,300 cal BP several new diatom species became simultaneously established in the lake community (Figure 2). The more recent event (3,300 cal BP), showed the greatest increase in diversity with many more new species appearing. These episodes of increased diversity correspond with the zonal boundaries identified by cluster analysis.

The cause of the abrupt increases in diversity is unclear, because there doesn't appear to be any direct correlation with equivalent changes in the surrounding terrestrial vegetation, or isotope-inferred hydrology, when assessed qualitatively (Figure 4). Upon visual inspection, if there is any direct relationship between transitions in terrestrial and aquatic communities there seems to be a considerable time-lag (on the order of 500 years). Given Tibetanus' unusual hydrological situation (entirely groundwater fed, highly alkaline, and with a rapid turnover) it is entirely possibility that the apparent delayed response is because the lake's catchment characteristics, elevation and water source buffers the aquatic community from terrestrial changes. It may be that in order for changes in the surrounding foliage to affect Lake Tibetanus'water chemistry to a point where it is reflected in aquatic biota, the new vegetation type needs to migrate a significant distance above the lake's position. The inflow is entirely via groundwater, and so to a large extent bypasses the surface effects of vegetation on soil chemistry. This could mean that invading vegetation has to have a significant presence throughout the entire catchment in order for the groundwater composition to be changed sufficently to overpower the stabilizing effect of the lake and its surrounding bedrock. The observed time difference between terrestrial and aquatic changes could then be explained as the time between a new type of vegetation first appearing in the proximity of the lake and it becoming prominent throughout the catchment.

Changes in the diatom assemblages don't seem to correlate directly with local hydrology shifts either (Figure 4). Again there seems to be a large time difference between transitions in the diatoms and the climate shifts between wetter, oceanic/maritime conditions and those more indicative of a continental environment (e.g. more pronouced seasonality). The ground water inflows of Tibetanus could again be an important factor. However, the relationship between diatoms and the hydrology regime appears to be much weaker than that with the vegetation type. This is because of the greater number of observed precipitation pattern zones than diatom assemblages. It is very difficult to draw strong conclusions from the qualitative analysis, especially considering that the points of maximum change within the diatom community (Figure 3) all occur during the most recent diatom assemblage. It is also important to note that the zonal boundaries are artificial constructions, using one particular point in a data set as the best representative of what is actually a slow transition, or continuum of change in environmental conditons. The ambiguity this procedure creates necessitates the use of quantitative methods such as variance partitioning analysis to elucidate the true relationships between the responses of the diatoms and the possible control factors (vegetation, temperature, and hydrology).

Variance partitioning analysis showed that a large and statistically significant amount of variation in the diatom community composition was accounted for by the pollen-inferred temperature and isotope-inferred hydrology (33.7%). The majority of this explained variation was attributable to the effects of mean July air temperature (as inferred from pollen) independent of isotope-inferred hydrological shifts (27.6%). A much smaller, but statistically significant (P, 0.05) amount of variation was attributable to changes in hydrology (as inferred from the non-Dansgaard stable isotopic signature; 5.5%). Almost none of the variation could be attributed to the interactions of these two variables (0.6%). This extremely low value is most likely due to the fact that the non-Dansgaard oxygen stable isotope record reflects the hydrological signature after the influence of temperature has been removed (Hammarlund et al., In Press). The majority of variance remained unexplained (66.3%), but this was to be expected as aquatic communities are complex structures influenced by a host of factors (sunlight, predation, competition, etc.) but only two variables (vegetation and moisture patterns) were examined through our analysis. This large amount of variation in Tibetanus' aquatic community explained by temperature, indicates that temperature is an important factor structuring diatom communities, even in a rapidly-flushing groundwater-fed lake.

Conclusions:

Over the course of this study it was shown that changes in aquatic diatom communities over the last 7,500 years in Lake Tibetanus (located in the Abisko region of northern Sweden) could be explained to a large extent by changes in the pollen-inferred mean July air temperature. Conversely, our analyses indicated that changes in the character of the moisture circulation processes of the region (shifts in moisture sources, transport and major climate systems) had less of a direct impact on the diatom communities, explaining a much lower proportion of variation within the diatoms.

This analysis was made possible by Lake Tibetanus' unique character. Pollen data (used to quantify the terrestrial vegetation) was available due to the lakes position upon an ecotonal boundary that is known to have varied significantly since the last glaciation period. The stable oxygen isotope information (used to quantify changes in local moisture circulation patterns) existed because of the lake's unusual hydrological character. The unusual hydrological setting necessitates that further study is required in order to determine whether the strong relationship between aquatic and temperature, and the weak relationship between diatom communites and hydrological changes is a general rule that can be extrapolated to other limnological systems, or is a trait peculiar to Lake Tibetanus.

A possible avenue of future research is to identify the exact nature of this relationship between the aquatic and terrestrial ecosystems. Although statistical tests showed there to be a strong relationship between the two, qualtitative analysis indicated that the relationship is not a direct one. Instead analyses point towards the possibility of a delayed response before terrestrial changes were felt by the lake. Some interesting paleoecological questions could be answered through an investigation of whether the apparent time lag between vegetative changes in a catchment and corresponding changes within the lake is a characteristic relationship, or an artifact due to compounded error in zone definitions. Additional work could also be performed in determining the reasons behind the apparent lack of impact that changes in moisture regimes has upon the diatom communities.

References:

Barnekow, L., G. Possnert, and P. Sandgren. 1998: AMS 14C chronologies of Holocene lake sediments in the Abisko area, northern Seden – a comparison between bulk sediment samples and macrofossil samples. GFF 120: 59-67.

Barnekow, L., 1999A: Holocene tree-line dynamics and inferred climatic changes in the Abisko area, northern Sweden, based on macrofossil and pollen records. The Holocene 9:253-256.

Barnekow, L. 1999B: Holocene vegetation dynamics and climate changes in the Tornetrask area, northern Sweden. Department of Quaternary Geology, Lund University, Lund, Sweden.

Bocard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045-1055.

Bigler, C., and R.I. Hall. In Press: Diatoms as indicators of climatic and limnological change in Swedish Lapland: A 100-lake calibration set and its validation for paleoecological reconstructions. Journal of Paleolimnology.

Hall, R.I., and J.P. Smol. 1996: Paleolimnological assessment of long-term water-wuality changes in south-central Ontario lakes affected by cottage development aand acidification. Canadian Journal of Fisheries and Aquatic Sciences 53: 1-17.

Hall, R.I., P.R. Leavitt, R. Quinlan, A.S. Dixit, and J.P. Smol. 1999: Effects of agriculture, urbanization and climate on water quality in the northern great plains. Limnology and Oceanography 44(3, part 2): 739-756.

Hammarlund, D., B. Buchardt, T.W.D. Edwards, L. Barnekow and H.J.B. Birks. In Press: Expression of changing Holocene atmospheric circulation in oxygen-isotope records from lacustrine carbonates in northern Scandinavia. The Holcene.

Hammarlund, D., and T.W.D. Edwards. 1998: Evidence of changes in moisture transport efficiency across the Scandes Mountains in northern Sweden during the Holocene, inferred from lacustrine oxygen isotope records. Symposium on Isotope Techniques in the Study of Past and Current Environmental Changes in the Hydrosphere and in the Atmosphere. International Atomic Energy Agency, Vienna 14-18 April 1997, IAEA-SM-349/40, 573-580.

Karlen, K., A. Bodin, J. Kuylenstierna, and J. Naslund. 1999: Climate of northern Sweden during the Holocene. Journal of Coastal Research Special Issue No. 17: 49-54.

Korhola, A., J. Weckstrom, and M. Nyman. 1999: Predicting the long-term acidification trends in small subarctic lakes using diatoms. Journal of Applied Ecology 36: 1021-1034.

Lotter, A.F., B. Ammann, and M. Sturm. 1992: Rates of change and chronological problems during the late-glacial period. Climate Dynamics 6: 233-239.

Lotter, A.F., H.J.B. Birks, W. Hoffmann, and A. Marchetto. 1997: Modern diatom, cladocera, chironimid, and chyrsophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditons in the Alps. I. Climate. Journal of Paleolimnology 18: 395-420.

Olander, H., H. J. B. Birks, et al. 1999: An expanded calibration model for inferring lakewater and air temperatures from fossil chironimd assemblages in northern Fennoscandia. The Holocene 9: 279-294.

Weckstrom, J., A. Korhola, and T. Blom. 1997: The relationship between diatoms and water temperature in thirty subarctic Fennoscandian lakes. Arctic and Alpine Research 29: 75-92.

Rosen, P., R.I. Hall, T. Korsman, and I. Renberg. 2000. Diatom transfer functions for quantifying past air temperature, pH and total organic carbon concentration from lakes in northern Sweden. Journal of Paleolimnology 24: 109-123.

Seppa, H. and J. Weckstrom. 1999: Holocene vegetational and limnological changes in the Fennoscandian tree-line area as documented by pollen and diatom records from Lack Tsuolbmajavri, Finland. Ecoscience 6: 621-635.

Stoermer, E.F., and J.P. Smol. 1999: Applications and uses of diatoms: prologue. In – Stoermer, E.F. and J.P. Smol (eds.), The Diatoms: Applications for the Environmental and Earth Sciences. Cambridge University Press, UK. pp. 3-8.

Stevenson, R.J., and Y. Pan. 1999: Assessing environmental conditions in rivers and streams with diatoms. In – Stoermer, E.F. and J.P. Smol (eds.), The Diatoms: Applications for the Environmental and Earth Sciences. Cambridge University Press, UK. pp. 11-40.