

## Mid-Holocene hemlock decline and diatom communities in van Nostrand Lake, Ontario, Canada

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### Abstract

Terrestrial ecosystem disturbances inferred from the fossil hemlock pollen decline (ca. 4,800 BP) and recovery (ca. 3,800 BP) affected van Nostrand Lake including the diatom communities. Ecological models suggest the lake responded by eutrophying, reflecting higher nutrient influx resulting from increased erosion. A decline in lake productivity followed as the forest vegetation recovered and erosion slowed. Lastly, as the forest switched from early and middle successional species to mature species, lake productivity increased as erosion increased nutrient inflow, especially phosphorus. However, this eutrophication response was delayed or buffered, perhaps due to wetland development surrounding the lake. The lake never fully returned to its initial, pre-hemlock decline state, but oscillated between more eutrophic and more mesotrophic or oligotrophic stages, possibly reflecting other disturbances in the catchment and climatic change.

### Introduction

Pollen analysis has shown that from ca. 7,700 to ca. 4,800 BP, *Tsuga canadensis* (L.) Carrière (eastern hemlock) was a dominant conifer in eastern North American forests (Ritchie, 1987). However, at approximately 4,800 BP, over the course of roughly 60 yrs, it was decimated across its range (Davis, 1981). It is suspected that a pathogen was responsible for its decline (Davis, 1981; Allison et al., 1986), which was later supported by macrofossil evidence (Bhiry & Fillion, 1996) linking the decline with infestations of *Lambdina fiscellaria* Guen. (hemlock looper) and *Choristoneura fumiferana* Clem. (spruce budworm). Such an outbreak of phytophagous insect activity might have been triggered by a mid-Holocene warm/dry period (Yu & McAndrews, 1994; Yu, 1995; Yu et al., 1997). Whatever caused the decline, it took approximately 2000 yrs for hemlock to recover to near its previous abundance. During the hemlock minimum, the pollen percentages of successional species such as

*Betula* (birch) and *Pinus strobus* L. (eastern white pine) at first increased. Further succession in southern Ontario was signalled by increases in *Acer saccharum* Marsh. (sugar maple) and *Fagus grandifolia* Ehrh. (American beech), which are competitors of *Tsuga* in mature stands.

Such major changes in the composition of the terrestrial ecosystem would be expected to directly impact the aquatic ecosystem as well. Initially, there would be a decline in evapotranspiration (because of tree loss) resulting in an increase in runoff water and nutrients entering the aquatic ecosystem due to accelerated erosion (summarised in Bormann & Likens, 1979). This increased nutrient inflow, especially that of phosphorus and nitrogen, should cause lakes to become more eutrophic. This stage is generally very short, lasting for just 10–20 yrs (Bormann & Likens, 1979). Tests of this model have not always produced the predicted results (Whitehead et al., 1973; Likens & Davis, 1975; Smol & Boucherle, 1985; Boucherle et al., 1986; Hall, 1993; Hall & Smol, 1993; Huvane & Whitehead, 1996). For instance, Boucherle et al. (1986)

examined three southern Ontario lakes but found evidence of eutrophication after the hemlock decline in only two sites.

Ecological theory further suggests that during the beginning stages of terrestrial ecosystem recovery, nutrients should become bound up in accumulating plant biomass as the early successional species establish themselves (Vitousek & Reiners, 1975; Bormann & Likens, 1979). Hence, the initial high nutrient inflow into lakes should decrease, and the aquatic system should then return to a more oligotrophic condition (Hall & Smol, 1993). This stage can last up to 200 yrs (Hall & Smol, 1993). As the pioneer taxa are replaced by later successional species, the terrestrial ecosystem again suffers a decline in total biomass and a release of nutrients. This stage in terrestrial ecosystem development, which is of variable length, should be accompanied by increasing lake productivity, as nutrient inflow into the lake once again accelerates.

Hall & Smol (1993) tested the above model for aquatic ecosystem response to the mid-Holocene hemlock decline, a strong upland forest ecosystem disturbance, by reconstructing diatom and chrysophyte communities and diatom-inferred total phosphorus concentration in five southern Ontario lakes. The magnitude of the lake response to the hemlock decline varied along a gradient of catchment size to lake volume: the lake with the greatest relief and a relatively large catchment (Flower Round Lake) experienced the most eutrophication in response to the *Tsuga* decline. Lake trophic status increased to a lesser extent in two other lakes: Long and Singleton lakes. Flower Round Lake also showed a strong decrease in aquatic productivity as the forest reorganised and recovered from the loss of hemlock. Diatom-inferred lake water phosphorus concentrations also decreased in Long and Singleton lakes. As the hemlock pollen abundance recovered to its pre-decline levels at ca. 3,500 BP, the terrestrial ecosystem again probably suffered a decline in total biomass and a release of nutrients as the pioneer species died and were replaced by later successional species. This was mirrored by increased aquatic productivity in Flower Round, Long and Burridge lakes as nutrient inflow increased into the lakes.

The purpose of our paleolimnological study was to test this model of lake response to the mid-Holocene hemlock decline in van Nostrand Lake – a small lake with a particularly small surface area to catchment ratio. According to Hall & Smol (1993) such a lake should show a full and strong response to the hemlock decline. As well, the lake is on the Oak Ridges Moraine, a

regional aquifer for the Greater Toronto Area; there is great interest in the paleohistory of this aquifer. To our knowledge, this is the first diatom and pollen study of a long core from a lake in this aquifer.

### Site description

Van Nostrand Lake (43° 59' 50''N, 79° 23' 00''W) (297.2 m asl.) is located 30 km north of downtown Toronto, Ontario (Figure 1). In south-central Ontario, this moraine is a prominent glacial feature of approximately 1,400 km<sup>2</sup> that is located on the rapidly urbanising northern margin of the Greater Toronto Area. The moraine was formed between two lobes of a retreating glacier, and it consists of up to 160 m of drift over the bedrock. Between sand or gravel hills are fairly level tracts of sand with layers of fine porous sand which form a major regional aquifer system. The sand is fairly high in phosphorus and lime, but low in potash (Chapman & Putnam, 1984).

Van Nostrand Lake has a surface area of 2.2 ha and a catchment of approximately 5 km<sup>2</sup> containing relief up to 30 m. It has a rather large catchment for its size with a surface area/catchment area ratio of 0.4%. In comparison, Hall & Smol's (1993) two lakes with the smallest surface area/catchment ratios were Flower Round (1.8%) and Singleton (0.3%). However, Singleton Lake's actual ratio is probably much higher as the lake has a very complex catchment that is difficult to estimate. Therefore, van Nostrand Lake extends their lake set well. The lake lies along a tributary of the Holland River. Formed 12,000 yrs ago as a kettle lake, it currently has a maximum depth of 8 m. The lake presently lies along

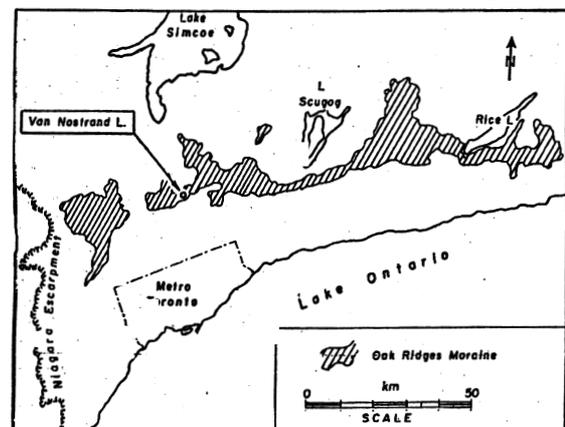


Figure 1. Location of van Nostrand Lake, Ontario, on the Oak Ridges Moraine.

the southern boundary of the white pine-hardwood forest and is surrounded by a sedge-dominated wetland. The hill above it has been inhabited for the past 500–600 years (G. Dibb, pers. commun.). Farm fields dating from the 19th century and forest woodlots occupy the catchment.

## Methods

A 970 cm long core was recovered with a modified Livingstone piston sampler from beneath eight meters of water in 1982. Organic matter, calcium carbonate and silicates were analysed by loss-on-ignition (Dean, 1974). Fossil pollen were concentrated following Cwynar et al. (1979); identifications follow McAndrews et al. (1973). Two hundred tree pollen were counted per level. Percentage calculation and graphing was done by CANPLOT (Campbell & McAndrews, 1992). Zonation and interpretation follow McAndrews (1994); the core was dated by correlation of fossil pollen zone boundaries from sediment cores from other southern Ontario lakes that have been radiocarbon dated (McAndrews, 1994).

Samples were prepared for diatom analysis from 34 levels at ca. 20 cm intervals, spanning 200–680 cm. Calcium carbonate was dissolved from the sediment with 10% HCl. To remove organic matter, the samples were then heated twice in a hot water bath for three hours in a 1:1 mixture of concentrated sulphuric and nitric acids. The samples were washed eight times with distilled water and allowed to settle 24 h between rinses. Each rinse was removed by aspiration. Strewn mounts were mounted in Naphrax. Samples and slides are stored in the Paleo-environmental Assessment Laboratory (PAL), Dept. of Geology, at the University of Toronto.

The slides were examined under 1000x magnification with a Nikon Optiphot X-2 microscope. At least 500 diatom valves per slide were identified and counted, together with chrysophyte cysts. To aid in identification, photographs were taken using black and white Kodak Techpan film (50 ASA). Taxonomically difficult species, i.e., *Cyclotella* and *Stephanodiscus* spp., were studied using a JEOL 840 scanning-electron microscope at 15 kV. Identifications follow Cumming et al. (1995) (most closely), Krammer & Lange-Bertalot (1986–1991), Moser et al. (in prep.) and Patrick & Reimer (1966, 1975). For each level, the diatom/chrysophyte cyst ratio was also used as a measure of eutrophication (Smol, 1985).

Correspondence analysis was used to ordinate the diatom data using CANOCO (Ter Braak, 1988). No horse-shoe effect was observed. Diatom species that occurred

in more than one sample and greater than 1% abundance in at least one sample were used in ordination calculations. Lake-water total phosphorus concentrations (TP) were inferred from diatom percent abundance data using a weighted averaging regression and calibration model (WACALIB v. 3.3; Line et al., 1994) developed from spring diatoms in 64 British Columbia lakes (Reavie et al., 1995). This data set includes that used by Hall & Smol (1993). As the authors recommend, we used square root species data transformation and classical deshrinking. As discussed in Reavie et al. (1995), 5 outlier lakes were dropped, leaving 59 lakes in the calibration set. TP was normalized using a  $\ln(x+1)$  transformation as it had a skewed distribution. We chose to use this particular calibration set for several reasons. All other available published calibration sets from northeastern North America did not include our two most important diatom species, *Cyclotella michiganiana* Skvortzow and *Stephanodiscus minutulus* (Kutz.) Round, (Agbeti, 1992) or are not useful for estimating spring TP (Dixit et al., 1991; Christie & Smol, 1993; Cumming et al., 1995; Dixit et al., 1999). In two instances, taxonomic uncertainty prevented direct comparisons of data sets (Christie & Smol, 1993; Fritz et al., 1993). An unpublished calibration set from southern Ontario (E. Reavie, pers. commun.) did not provide as good a fit as the B.C. set (i.e. 67% versus 78%, respectively, species in common). The species that did not occur included some of the major species (greater than 5% relative abundance on one level) and had an average abundance of 9.7% with a maximum abundance of 31.7%. In the B.C. calibration set, all of the species that did not occur had an individual relative abundance of less than 5%. Their maximum total abundance on any level was 12.5% with an average abundance of 2.0%. Analogue analysis was done according to Birks et al. (1990) using both the unpublished southern Ontario calibration set and the B. C. set together with the data from van Nostrand Lake. No level had a close modern analogue in the Ontario calibration set, whereas with the B. C. set there were close modern analogues. It is especially important to note that the taxonomy of two centric diatom genera in particular, i.e., *Stephanodiscus* and *Cyclotella*, is in a state of confusion. For this reason we reference published photographs and include two photomicrographs, for taxonomic clarity (see next sections). Paleolimnological inference reliability was assessed by bootstrapping, an iterative resampling procedure, using WACALIB 3.3 and by analogue analysis; i.e. a level was considered to have no close modern analogue in the training set if the minimum dissimilarity measure was greater than 0.45 (Birks et al., 1990).



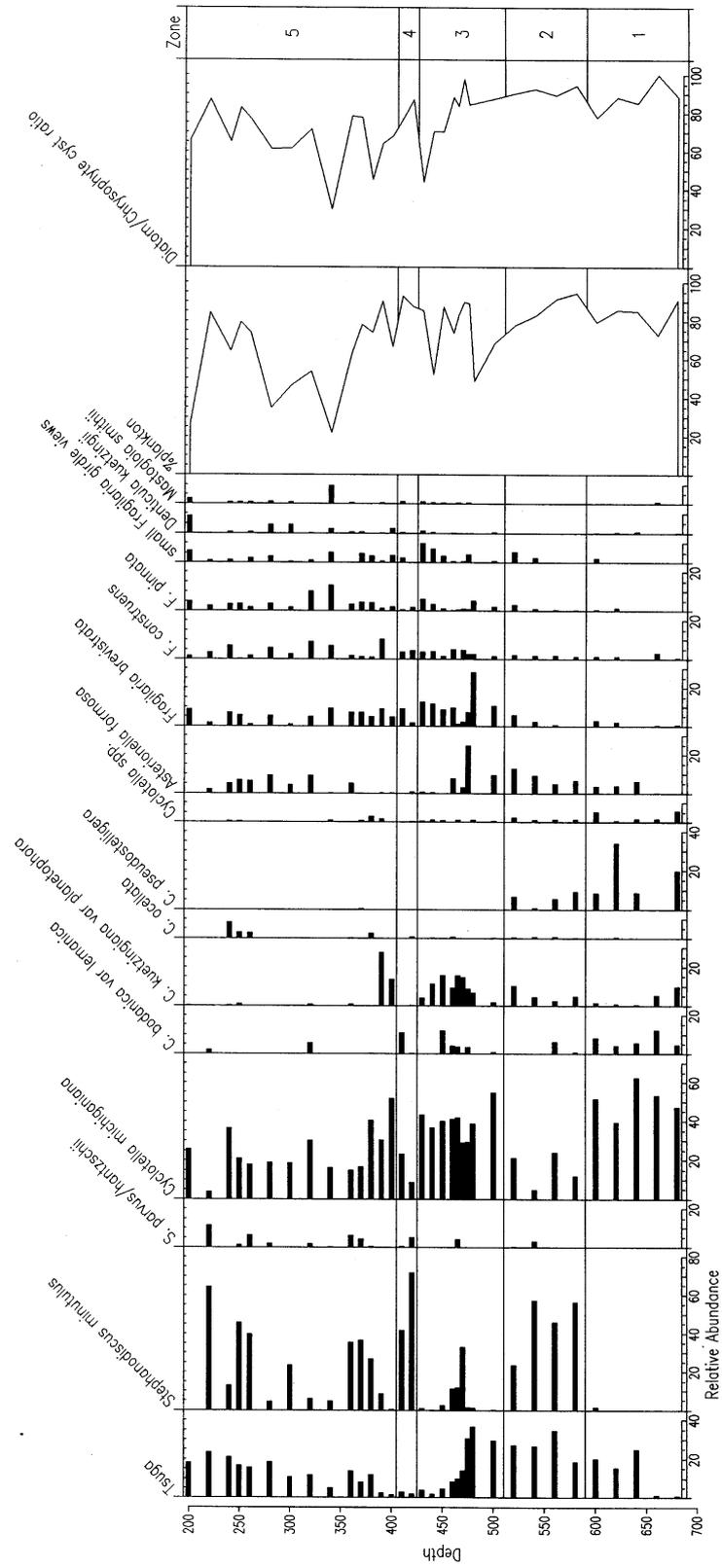


Figure 3. *Tsuga* pollen and dominant diatoms (percentages) of the van Nostrand core plotted against core depth. Shown are the taxa with relative abundance of at least 5% in at least one stratigraphic level.

tychoplanktonic diatoms *Fragilaria* and *Denticula*, peak erratically in the core, but they seldom exceed 20%. The diatom/chrysophyte cyst ratio showed a weak relationship with trophic levels, as has been found by other researchers with other cores (Duff et al., 1997).

There exists great confusion about the taxonomy of the small *Cyclotella* and *Stephanodiscus* species. Hence, we include Table 1 and Figure 4 which respectively provide references to published photomicrographs and show a photomicrograph of what we consider to be typical examples of these species in the core.

Five diatom zones were determined by visual inspection. Zone 1 (680–600 cm) has *Cyclotella michiganiana* as the dominant with *C. pseudostelligera* Hustedt, *C. bodanica* var *lemanica* (O. Muller ex Schroter) and *C. kuetzingiana* var *planetophora* Fricke as subdominants, virtually no *S. minutulus* and only few tychoplanktonic or benthic *Fragilaria*. Zone 2 (580–520 cm) has *S. minutulus* as the dominant with lesser amounts of *C. michiganiana* and *C. pseudostelligera*, an increase in *Asterionella formosa* Hasall, and few tychoplanktonic or benthic *Fragilaria*. In zone 3 (500–430 cm), *C. michiganiana* again dominates, *C. kuetzingiana* var *planetophora* becomes a subdominant, as do the tychoplanktonic *Fragilaria brevistriata* Grun. in Van Heurck, *F. construens* (Ehrenb.) Grun. and *F. pinnata* Ehrenb. Zone 4 (410 cm) consists of two levels containing a peak of *S. minutulus* (71.8%). The boundaries for zone 5 (400–200 cm) are not as sharply defined as the other zone boundaries. *Cyclotella michiganiana* maintains at least 4% relative abundance, sometimes as much as 51.6%. *Stephanodiscus minutulus* percentages range between 5–64%. This zone is dominated by both species and rapid shifts between them. Other *Cyclotella* species are rare at these levels, except for *C. ocellata* Pant.. However, *A. formosa*, the tychoplanktonic *Fragilaria* and *Denticula kuetzingii* Grun. are moderately abundant. Planktonic taxa are relatively less common than the average percentage of planktonic

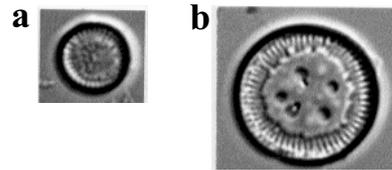


Figure 4. (a) *Cyclotella comensis*  $\times 1500$ , (b) *Cyclotella ocellata*  $\times 1500$ .

taxa in the first four zones: 80.9% versus 61.3% in the last zone. The remaining minor diatom species, those which never exceed 5% but which have a relative abundance of at least 1% on at least one stratigraphic level, are shown in Figure 5. There are a few planktonic species among them, but most are periphytic or tycho-planktonic.

Correspondence analysis of the diatom data was used to search for trends that were not obvious in the stratigraphic profiles (Ter Braak, 1988). Figure 6 shows the plot of correspondence analysis of the diatom species. Species were spread along axis 1 according to which of the two dominants they tended to co-occur with. Hence, a species co-occurring with *S. minutulus* had a high positive score on the first axis. If, on the other hand, it co-occurred with *C. michiganiana*, then it had a negative score on the first axis. Axis 2 appears to reflect a depth gradient, with most planktonic species plotting at the bottom of the axis and benthic species at the top. Axes 1 and 2 summarise a major portion of the variance in the species data set (45.3%) ( $\lambda_1 = .375$  and  $\lambda_2 = .245$  with a total sum of eigenvalues of 1.370). Correspondence analysis of the examined stratigraphic levels shows that the lake had two developmental stages (Figure 7). In the first stage, Zone 1 with abundant *C. michiganiana*, *C. bodanica* var *lemanica*, *C. kuetzingiana* var *planetophora* and *C. pseudostelligera* forms a cluster in the bottom left quadrant. The second stage is formed by the remaining stratigraphic levels occupying the other three

Table 1. Taxonomically confusing taxa

Species	Reference photomicrograph
<i>Stephanodiscus minutulus</i>	Cumming et al. (1995) pl. 4, figure 27–29
<i>Cyclotella michiganiana</i>	Cumming et al. (1995) pl. 2, figure 7–13
<i>C. bodanica</i> var <i>lemanica</i>	Cumming et al. (1995) pl. 2, figure 3–5
<i>C. comensis</i>	Figure 4a; or Cumming et al. (1995) pl. 57, figure 4
<i>C. kuetzingiana</i> var <i>planetophora</i>	Cumming et al. (1995) pl. 57, figure 2
<i>C. kuetzingiana</i> var <i>radiosa</i>	Cumming et al. (1995) pl. 57, figure 3
<i>C. ocellata</i>	Figure 4b; or Cumming et al. (1995) pl. 57, figure 10; or Krammer & Lange-Bertalot vol.3, pl. 50, figure 6
<i>C. pseudostelligera</i>	Reavie & Smol (1998) pl 2, figure 7–22

quadrants and creating a diffuse line with a negative slope. In this second stage, levels appear to be spread out along the first axis depending on the relative abundance of the dominants at a particular level. Levels with high percentages of *S. minutulus*, e.g. in zone 2 and levels 220 cm and 420 cm in which this diatom peaks, or those levels in zone 5 with high *S. minutulus* abundance, have positive first axis scores. Levels with high percentages of *C. michiganiana* have negative first axis scores.

Lake-water total phosphorus concentrations (TP) were inferred using regression and calibration of diatom abundance data from British Columbia lakes (Reavie et al., 1995). The graph of inferred lake-water total phosphorus concentrations from weighted average calibration (WA) (Birks et al., 1990) versus the stratigraphic levels is shown in Figure 8a. A plot of observed TP values against concentrations calculated by WA for the 59 calibration lakes had RMSE = 0.3757 and  $r^2 = 0.7247$ . While paleolimnological inference procedures always produce results, there are no simple methods for evaluating their trustworthiness (Birks et al., 1990). We assessed inference reliability by two methods: bootstrapping and modern analogue analysis. From bootstrapping (10,000 iterations), a  $RMSE_{boot} = 0.48$  was obtained for WA. 10 of the 34 levels had a close modern analogue in the calibration set: 220, 250, 260, 320, 340, 360, 420, 540, 580 and 620.

The WA estimate shows that: (1) TP was high throughout zone 2, (2) a spike occurred at 420 cm (zone 4) and (3) TP rose again in zone 5 with another spike at 220 cm. (For reference, the *Tsuga* pollen declines at 460 – 480 cm.) Phosphorus levels were low but rose steadily during zone 1, declined in zone 3, and had an initial low in zone 5.

Lake water pH, using the same calibration set, was inferred, but no significant trends were observed.

## Discussion

The correspondence analysis ordination of stratigraphic levels indicates two distinct lake stages: an early lake stage of zone 1 and a later lake stage of zones 2, 3, 4 & 5. The early stage was dominated by *Cyclotella* taxa with greater than 80% planktonic diatoms. The second stage was characterised by rapid shifts in dominance between *C. michiganiana* and the more eutrophic *S. minutulus*. The tycho planktonic *Fragilaria* species are abundant, as is *C. kuetzingiana* var *planetophora*, but not *C. bodanica* var *lemanica*

or *C. pseudostelligera*. The levels corresponding to this stage approximate a negatively sloped line (Figure 7). The levels shift along this line according to which taxa dominate and the presence of planktonic versus benthic taxa. As the lake matures, it becomes shallower; increased periphytics and a decrease in planktonics indicate infilling with sediment. However, water level fluctuations due to climate but independent of sediment infilling could be superposed on this trend.

Diatom zone 1 contains mostly oligotrophic taxa in the early lake stage. *Cyclotella michiganiana*, common in oligotrophic lakes (Stoermer & Yang, 1970), dominated all early lake samples. Reavie et al. (1995), in their (updated) survey of British Columbia lakes, found that *C. michiganiana* had a total phosphorus optimum of  $11.3 \mu\text{g l}^{-1}$ . This agrees with other work by Hall (1993) who found a total phosphorus optimum of  $10.1 \text{ g } \mu\text{g l}^{-1}$ , Cumming et al. (1995) who report a total phosphorus optimum of  $10.0 \mu\text{g l}^{-1}$  for this species in their survey of summer British Columbia lakes, and Hall & Smol (1996) who report a total phosphorus optimum of  $7.26 \mu\text{g l}^{-1}$  in south-central Ontario lakes. Two other oligotrophic *Cyclotella* species were also somewhat abundant during this period: *C. bodanica* var *lemanica* (Duthie & Sreenivasa, 1971; Sreenivasa & Duthie, 1973), and *C. kuetzingiana* var *planetophora*. Their peaks suggest an oligotrophic lake. However, *C. pseudostelligera* and *A. formosa*, present in some abundance, have broader tolerances for lake trophic status, and generally indicate more eutrophic conditions (Stoermer & Yang, 1968; Bradbury, 1975). The diatom assemblages and the diatom-inferred WA phosphorus levels by and large indicate that the lake was oligotrophic to mesotrophic.

Several paleolimnological studies have shown that southern Ontario lakes were oligotrophic during the *Pinus* pollen zone (Sreenivasa & Duthie, 1973; Smol, 1979; Smol, 1982; Smol & Boucherle, 1985; Hall, 1993). A number of factors may have contributed to this oligotrophy (Smol, 1982; Smol & Boucherle, 1985; and Hall, 1993). Among them was a cool, dry climate with a short growing season that inhibited microbial decay, and thereby nutrient cycling and algal growth (Terasmae, 1981; Anderson, 1987; Edwards & McAndrews, 1989). Furthermore, nutrients for aquatic and terrestrial plants might have been locked up inside mineral particles because chemical weathering was inhibited. Because immature, open forests sequester nutrients as they gain biomass (Vitousek & Reiners, 1975; Bormann & Likens, 1979), nutrient run-off from the catchment might be low. Lastly, pine litter has a low nutrient content which tends

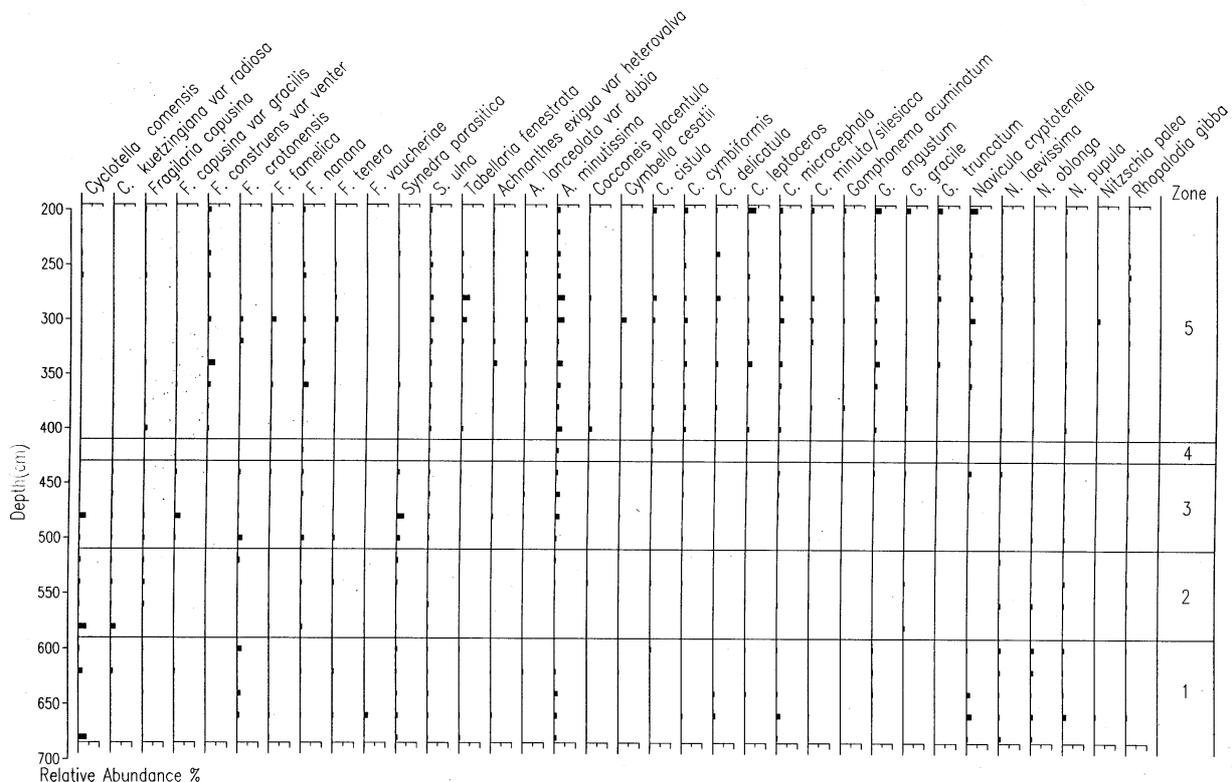


Figure 5. Minor diatoms (percentages) of the van Nostrand core plotted against core depth. Shown are the taxa 1–5% in at least one stratigraphic level. The major tic mark denotes an abundance of 10%.

to release slowly during cool climate conditions (Rodin & Bazilevich, 1967; Bell, 1974). According to the pollen record, oligotrophic zone 1 of van Nostrand Lake overlaps the pine zone and the beginning of the deciduous forest pollen zone 3a. Hence, zone 1 in the lake corresponds to the general trend of southern Ontario lakes being oligotrophic at this time (Smol & Boucherle, 1985; Hall, 1993). Van Nostrand Lake remained oligotrophic well into pollen zone 3a until the mixed deciduous forest consisting of *Fagus*, *Tsuga*, *Acer saccharum* and *Quercus* (oak) matures and *Pinus* pollen is insignificant. This occurred between 600–580 cm, when the lake switched into a second, more mesotrophic stage.

In lake stage 2, *S. minutulus*, *A. formosa* and the smaller *Fragilaria* species become important, while *C. michiganiana* and *C. kuetzingiana* var. *planetophora* remain abundant, and *C. pseudostelligera* and *C. bodanica* var. *lemanica* decline in relative frequency. *Stephanodiscus minutulus* and all the small *Stephanodiscus* species indicate more eutrophic conditions (Bradbury, 1988; Engstrom et al., 1991; Fritz et al., 1993; Reavie et al., 1995). *Stephanodiscus minutulus* competes well for silicon but needs a plentiful supply of phosphorus

and hence is more common in waters with relatively low silicon/phosphorus ratios (Kilham & Kilham, 1978). Reavie et al. (1995) (updated), in eutrophic British Columbia lakes, found that *S. minutulus* had a relatively high total phosphorus optimum of  $19.6 \mu\text{g l}^{-1}$ . This is higher than other published values of  $12.3 \mu\text{g l}^{-1}$  (Hall, 1993; Cumming et al., 1995). However, this value better agrees with Fritz et al. (1993) who found a TP optimum of  $23.09 \mu\text{g l}^{-1}$  and with the consensus in the literature that *S. minutulus* indicates more eutrophic conditions. *Asterionella formosa* is intermediate in its phosphorus and silicon demands (Kilham & Kilham, 1978; Bradbury & Dieterich-Rurup, 1993). However, Brugam (1988) views *A. formosa* as an indicator of eutrophication and warns that there are variable responses to silica and phosphorus limitations between different clones. It is unclear what the increased abundance of the small *Fragilaria* species, such as *F. brevistriata*, *F. construens*, and *F. pinnata* means, as these are species which are often considered to be eurytopic.

The WA estimate shows that TP was high throughout diatom zone 2. According to the pollen analysis, this was the time period during which the coniferous boreal forest

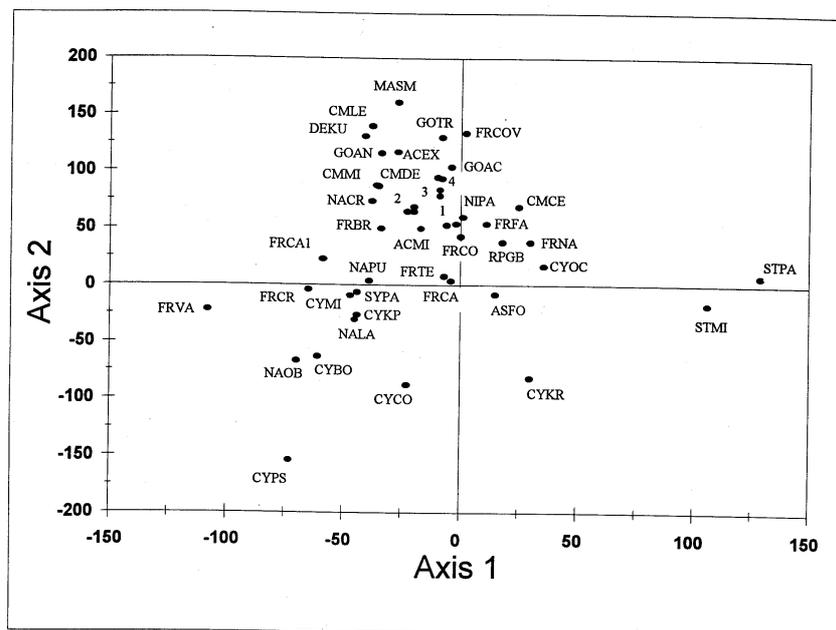


Figure 6. Plot of correspondence analysis ordination of diatom species on axes 1 and 2. The species codes are as follows: ACEX – *Achnanthes exigua* var. *heterovalva* Krasske, ACMI – *Achnanthes minutissima* Kutz., ASFO – *Asterionella formosa*, CYBO – *Cyclotella bodanica* var. *lemanica*, CYCO – *Cyclotella comensis* Grun. in Van Heurck, CYKP – *Cyclotella kuetzingiana* var. *planetophora*, CYKR – *Cyclotella kuetzingiana* var. *radiosa* Fricke, CYMI – *Cyclotella michiganiana*, CYOC – *Cyclotella ocellata*, CYPS – *Cyclotella pseudostelligera*, CMCE – *Cymbella cesatii* (Rabenh.) Grun. in A. Schmidt, CMDE – *Cymbella delicatula* Kutz., CMLE – *Cymbella leptoceros* (Ehrenb.) Kutz., CMMI – *Cymbella minuta* Hilse ex Rabenh., *Cymbella silesiaca*, DEKU – *Denticula kuetzingii*, FRBR – *Fragilaria brevistriata*, FRCA – *Fragilaria capucina* Desm., FRCA1 – *Fragilaria capucina* var. *gracilis* (Oestrup) Hustedt, FRCO – *Fragilaria construens*, FRCOV – *Fragilaria construens* var. *venter*, FRCR – *Fragilaria crotonensis*, FRFA – *Fragilaria famelica* (Kutz.) Lange-Bertalot, FRNA – *Fragilaria nanana* Lange-Bertalot, FRTE – *Fragilaria tenera* (W. Smith) Lange-Bertalot, FRVA – *Fragilaria vaucheriae* (Kutz.) J.B. Petersen, GOAN – *Gomphonema angustum* Agardh, GOTR – *Gomphonema truncatum* Ehrenb., MASM – *Mastogloia smithii* Thwaites ex W. Smith, NACR – *Navicula cryptotenella* Lange-Bertalot, NALA – *Navicula laevisissima* Kutz., NAOB – *Navicula oblonga* (Kutz.) Kutz., NAPU – *Navicula pupula* Kutz., NIPA – *Nitzschia palea* (Kutz.) W. Smith, RRGB – *Rhopalodia gibba* (Ehrenb.) O. Mull., STMI – *Stephanodiscus minutulus*, STPA – *Stephanodiscus parvus* Stoermer & Hakansson *Stephanodiscus hantzschii* Grun., SYPA – *Synedra parasitica* (W. Sm.) Grun. in Van Heurck, 1 – *Synedra ulna* (Nitzsch.) Ehrenb. and *Achnanthes lanceolata* var. *dubia* Grun. in Cleve & Grun., 2 – (*Tabellaria fenestrata* (Lyngb.) Kutz., *Cocconeis placentula* Ehrenb., *Cymbella microcephala* Grun. in Van Heurck), 3 – (*Fragilaria pinnata* and *Cymbella cistula* (Ehrenb. in Hemp and Ehrenb.) Kirchn.), and 4 – (*Gomphonema acuminatum* Ehrenb., *Gomphonema gracile* Ehrenb. and *Cymbella cymbiformis* Agardh).

was in transition to the mixed deciduous forest. In comparison, none of Hall's (1993) lakes entered into a more eutrophic phase during this time. We suggest that the peak at 420 cm was in response to the hemlock decline. Nothing in the pollen record or in the LOI immediately suggests a reason for the spike at 220 cm. The peak at 420 cm and the rise in diatom zone 2 are significant by the bootstrapped error envelope (Figure 8b). Hence, based on the diatom community composition and diatom-inferred phosphorus levels, it appears that during the second stage, particularly in zones 2, 4 and parts of 5, the lake became more eutrophic.

Changes in the van Nostrand Lake diatom communities showed the predicted response to the *Tsuga* decline, although it was delayed. From the pollen record,

the hemlock die-off occurred between 480–460 cm. From 480–430 cm, diatom-inferred phosphorus levels remain at a low level. Then at 420 cm there is a major, albeit short-lived phosphorus peak. This peak corresponds to the predicted eutrophic period with increased nutrient inflow. Then, as successional species such as *Betula* (Figure 2) replaced the hemlock in the surrounding watershed, erosion lessened, nutrient inflow decreased, and the lake became more meso- to oligotrophic again as is shown by the steep WA diatom-inferred phosphorus level decrease at 400 cm. There was perhaps a second period of erosion and increased nutrient inflow into the lake once these short-lived early successional species died-off, as is shown by the rise at 380 cm. After this time, phosphorus levels remained relatively high while the forest matured to later successional *Acer saccharum*,

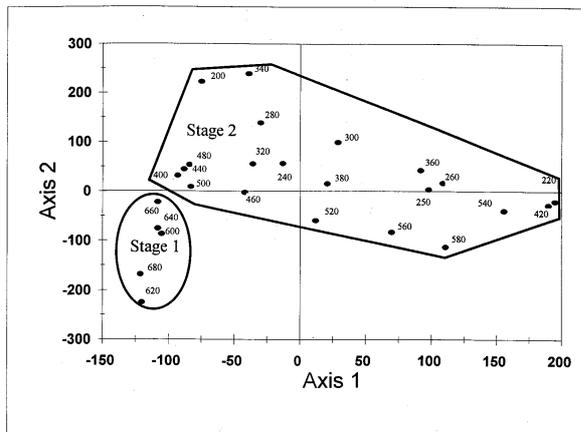


Figure 7. Plot of correspondence analysis ordination of the stratigraphic levels (in cm) on axes 1 & 2.

and *Tsuga* began its recovery. Additionally, there was a later peak in TP at 220 cm due to other unknown reasons.

The only major caveat with the above scenario and model agreement is the delayed response. A TP peak at the hemlock decline may have been missed by the 5 cm sampling interval. However, typical southern Ontario sedimentation rates at this time in comparable sites are 8 yrs per cm. Hence the time period from 460–420 cm represents roughly 300 yrs. On the other hand, the interval from 460–420 cm could represent a brief time period of 60 to 100 yrs; correspondingly, a period of high erosion-supplied sedimentation, as according

to Davis (1981) and Allison et al. (1986) the hemlock decline was catastrophic and swift throughout its range. From the increase in silicates on the loss-on-ignition profile from 460–440 cm, there is an increase in sedimentation at this time, rather than at the hemlock decline 480–460 cm. Hence, if the decline of the major dominant in the surrounding forest caused any erosional event, the effect of the erosion on the lake was delayed. There are several physical features of the landscape that could delay the pulse of erosion into the lake. Fossil pollen indicates that the lake was surrounded by a wetland and that this wetland expanded during the hemlock minimum. The wetland may well have taken up the early pulse of nutrients and delayed its effect on the lake. Furthermore, it must be remembered that the land surrounding this lake is of fairly low relief and that this would probably delay erosion. As well, the large catchment area relative to the lake’s surface area suggests that a major erosional event in the catchment could have a large effect on the lake’s nutrient status when the effect, possibly delayed, arrives and sedimentation would greatly increase. Therefore, it seems likely that van Nostrand Lake’s response followed the model, showing first a pronounced brief eutrophication, and then a return to a more mesotrophic or oligotrophic lake as the forest recovered. The lake next perhaps entered, as predicted, into another eutrophic stage.

Large shifts in diatom communities could be also explained by concurrent shifts in pH and alkalinity due to removal of the extensive hemlock forests and acidic conifer litter. However, no significant trends in inferred

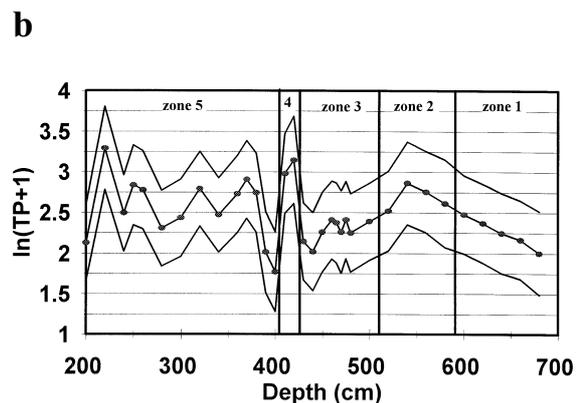
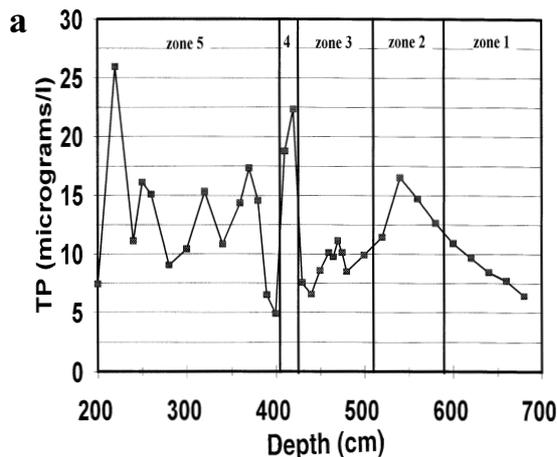


Figure 8. (a) Graph of trends in inferred lake - water total phosphorus (TP) concentrations versus stratigraphic level. Shown is the weighted average estimate (WA) (Birks et al., 1990). Included are the zones from the diatoms; (b) TP reconstructions for van Nostrand lake showing error envelope of WA. TP values are expressed on a logarithmic scale as they are transformed in the calibration set. The error envelope represents the root mean square error of the prediction from bootstrapping.

pH were observed, most likely reflecting the well-buffered nature of the system.

In van Nostrand Lake, a more eutrophic period is signalled by the abundance of *S. minutulus* and a more oligotrophic period is signalled by an increase in *C. michiganiana*. However, other southern Ontario lakes which were affected by the hemlock decline often have different species responding. In Flower Round Lake (Hall & Smol, 1993), a more productive lake was shown by an increase in *Aulacoseira ambigua* (Grun. in Van Heurck) Simonsen, *A. formosa*, and *F. crotonensis* and a decline in the smaller *Fragilaria* species: *F. construens*, *F. construens var venter* (Ehrenb.) Grun. in Van Heurck, *F. pinnata*, and *F. lapponica* Grun. in Van Heurck, which are associated with a less productive lake. In Little Round Lake (Smol & Boucherle, 1985), a more eutrophic phase was denoted by *Stephanodiscus hantzschii* Grun. in Cleve & Grun, and *F. crotonensis*, and a more oligotrophic phase was denoted by *C. stelligera*.

## Conclusions

This pollen and diatom study examined a long stratigraphic record from van Nostrand Lake, Ontario, which is located on an important regional aquifer. From the diatom record, it appears that the TP concentration has changed greatly, and hence the lake's trophic state, during the history of the lake. The lake was more oligotrophic or mesotrophic during the boreal forest; it became more eutrophic as the upland vegetation changed from coniferous to mixed deciduous; it became more oligotrophic again once the mixed deciduous forest became dominant; it then showed a eutrophic phase again after the hemlock decline and switched back to briefly being more oligotrophic as successional tree species were established; and finally shifted into a variable but more eutrophic phase.

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