

Primary Research Paper

## The effect of fish introductions on the diatom and cladoceran communities of Lake Opeongo, Ontario, Canada

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### Abstract

Fish introductions are one of the most widespread anthropogenic perturbations to aquatic ecosystems. Paradoxically, the effects of these introductions on aquatic ecosystems are typically poorly documented. This project studied the effect of fish introductions on Lake Opeongo, an oligotrophic lake in Algonquin Provincial Park, Ontario, Canada (45° 42' N, 78° 22' W), using the remains of algae (diatoms) and zooplankton (cladocerans) preserved in the sediments. It was hypothesized that the introduction of cisco or lake herring (*Coregonus artedii* Lesueur) in 1948, which filled the underutilized pelagic forage fish niche, should have altered nutrient availability for phytoplankton. Prior to cisco introduction, the diatom community of Lake Opeongo reflected a relatively stable oligotrophic state established before European settlement, and consisted of the *Cyclotella stelligera* complex with subdominants *Tabellaria flocculosa* IIIp and the *Aulacoseira distans* complex. No marked changes occurred until ca. 1962 when the diatom community shifted to an assemblage with increased total phosphorus preferences, consisting of *Asterionella formosa* and lesser amounts of *Cyclotella bodanica* var *lemanica*, the *C. stelligera* complex, *Fragilaria crotonensis* and *T. flocculosa* IIIp. The dominant cladoceran *Bosmina longirostris* increased significantly in relative abundance since the introduction of cisco. The most likely cause of this shift was increased nutrient recycling and/or trophic level changes caused by human manipulation of the fish community of the lake.

### Introduction

Fish introductions and translocations are one of the most widespread anthropogenic perturbations to aquatic ecosystems, triggering trophic cascade and nutrient recycling effects among others (Lodge et al., 1998). The distributions of many fish species have increased throughout the world as a result of intentional introductions for aquaculture and angling, as well as unintentional ballast water transfers, aquarium releases and illegal stockings. The extent of this process is poorly documented, both in the extent of the introductions and in the

effects of the introductions on the original aquatic ecosystems (Rahel, 2000; Schindler et al., 2001). While paleolimnological techniques have a long history of being used to recover missing monitoring data in anthropogenic global warming (e.g., Birks et al., 2004), acidification (e.g., Cattaneo et al., 2004) and eutrophication (e.g., Meriläinen et al., 2003), their use in studying the effects of fish introductions is relatively sparse, but increasing. Examples of the use of paleolimnological methods to study fish introductions include Salo et al. (1989), Schindler et al. (2001), Miskimmin et al. (1995), Leavitt et al. (1994a, b), Sweetman &

Finney (2003), Uutala et al. (1994), Heiri & Lotter (2003), Amsinck et al. (2003) and Bos (2001).

In particular, Schindler et al. (2001) and Leavitt et al. (1994b) used paleolimnological methods, bioenergetics modeling and mesocosm experiments to examine the whole lake aquatic ecosystem effects of the widespread introduction of brook (*Salvelinus fontinalis*), cutthroat (*Oncorhynchus clarkia*) and rainbow trout (*O. mykiss*) for recreational fishing in western North America. They found that these introductions of trout into naturally fishless lakes routinely increased nutrient regeneration and algal biomass. Their results indicated that introduced trout fundamentally altered nutrient cycles and stimulated primary production by accessing benthic phosphorus sources that are not normally available to pelagic communities in oligotrophic mountain lakes. They suggest that recreational trout introductions constitute a substantial biogeochemical perturbation to the thousands of formerly fishless mountain lakes throughout western North America.

The overall objective of this project was to study the effect of fish introductions in Lake Opeongo, a large soft-water Canadian Shield lake with a relatively undisturbed watershed, using diatoms and cladoceran remains preserved in the sediments. In particular, it was hypothesized that the introduction of cisco or lake herring (*Coregonus artedii* Lesueur) to serve as food for the sport-fished lake trout should have altered nutrient availability for phytoplankton. This lake has been well-studied by fisheries scientists (Martin, 1970; Shuter et al., 1987; Matuszek et al., 1990; Langeland et al., 1991), starting in 1931 with the founding of the Harkness Fisheries Laboratory; however, no long-term water chemistry data tracking the effect of the fish introductions have ever been compiled and published. Hence, we use diatom-inferred transfer functions to deduce some record of the missing water chemistry data. As well, no long-term phytoplankton or zooplankton data also tracking the effect of the fish introductions on the aquatic ecosystem have ever been published in an easily and widely accessible format. Therefore, we use a paleoecological study of the diatoms and cladoceran remains in order to infer some record of the phytoplankton and zooplankton communities of this lake before and after the fish introductions.

## Site description

### *Natural conditions*

Lake Opeongo is a multi-basin, oligotrophic lake (45° 42' N, 78° 22' W) in Algonquin Provincial Park, Ontario, lying on the Canadian Shield (Fig. 1). Physical and chemical characteristics of Lake Opeongo are provided in Table 1. Algonquin Park lies on the highest land in Southern Ontario with the lowest temperatures and shortest growing season for the area. The most important fish are lake trout (*Salvelinus namaycush* Walbaum), smallmouth bass (*Micropterus dolmieu* Lacépède), lake whitefish (*Coregonus clupeaformis* Mitchell), round whitefish (*Prosopium cylindraceum* Pallas), cisco, burbot (*Lota lota* L.) and yellow perch (*Perca flavescens* Mitchell) (Martin & Fry, 1972). Zooplanktivorous cisco is the primary prey of lake trout (Matuszek et al., 1990). Smallmouth bass and perch are restricted to the littoral zone (Martin & Fry, 1972; Vander Zanden & Vadeboncoeur, 2002). It is thought that the overall biomass tied up in the populations of whitefish (zoobenthic feeders, Vander Zanden & Vadeboncoeur, 2002), burbot (another zoobenthic feeder) and perch is significant, but likely less than that in the lake trout, cisco and bass (Dr B.J. Shuter, Ontario Ministry of Natural Resources, personal communication.). Data for the smallmouth and lake trout populations exists continuously from ca. 1930, based primarily upon fishermen's reported catches, together with occasional mark-recapture experiments (Shuter et al., 1987; Matuszek et al., 1990); only scattered population data exist for the cisco (Vascotto & Shuter, 2005).

### *Human impacts on the watershed*

Over the past 200 years the lake has been affected by Euro-Canadian settlement. Loggers built a dam at the outflow ca. 1867 which caused the water level to rise approximately 5 m, linking three previously separate lakes into one (Shaw, 1998). The watershed was logged, primarily for white pine (*Pinus strobus* L.), beginning ca. 1860; and selective logging continues today according to Ontario Ministry of Natural Resources policy. Small portions of the watershed were also cleared for farms. Algonquin Provincial Park was established in

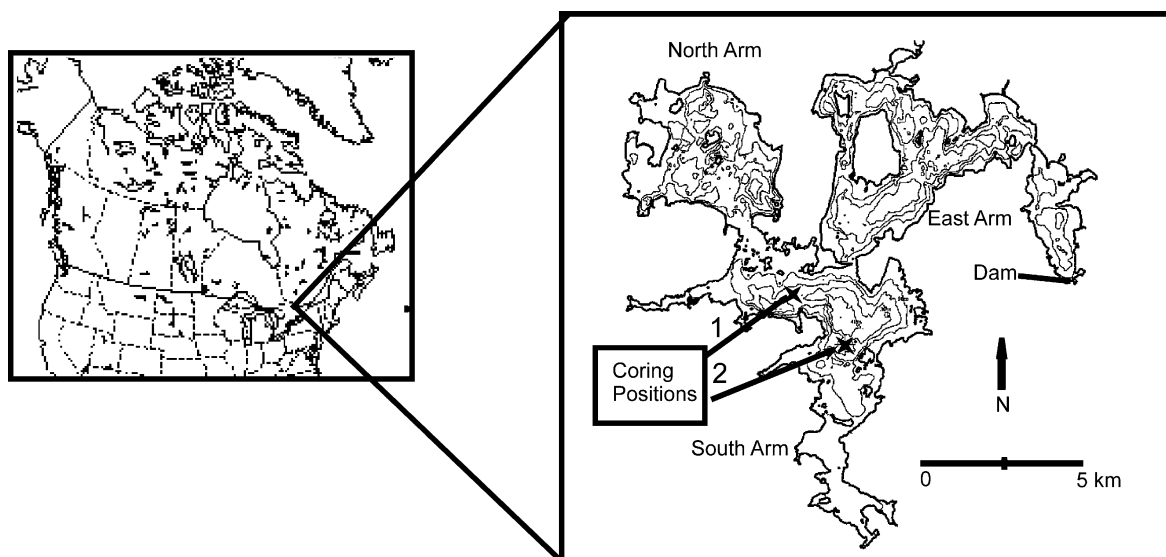


Figure 1. Bathymetric map of Lake Opeongo, Ontario showing coring sites 1 and 2. Cores 1 and 2 from site 1, cores 3 and 4 from site 2. Each contour line marks 10 m.

Table 1. Selected physical and chemical characteristics of Lake Opeongo

<i>Physical</i>	
Drainage area (km <sup>2</sup> )	189.6
Surface area (km <sup>2</sup> )	58.6
Shoreline (km) (including islands)	171
Water residence (years)	3.4
Mean depth (m)	14.8
Maximum depth (m) (in South arm)	51.8
Elevation (m) asl.	403.4
Highest relief of watershed (m) asl.	578
Secchi depth (m)	5.1
<i>Chemical</i>	
Chlorophyll a (mg/m <sup>3</sup> )	1.6
Total Kjeldahl nitrogen (mg/l)	0.29
Total phosphorus (μg/l)	8.0 ± 7.0 (38)
Alkalinity as CaCO <sub>3</sub> (mg/l)	4.60
Hardness (mg/l)	15–30
pH	6.8
Specific conductivity (μS/cm)	39
Dissolved organic carbon (DOC) (mg/l)	4.2

See St. Jacques (2000) for sources of the data. TP presented as means (1980–1989) ± standard deviation (sample size indicated in brackets).

1893, prohibiting trapping. The farms seem to have gradually disappeared as access to the lake has increased. In 1933–1936, Highway 60 was built

4 km to the south of Lake Opeongo, cutting across its watershed and greatly increasing tourist and angler use of the park. Smallmouth bass, a large piscivore, was introduced in 1900 (Shaw, 1998). Cisco, a planktivorous fish, which greatly increased the population of lake trout and filled the underutilized pelagic forage fish niche, was introduced in 1948 (Martin, 1970; Shuter et al., 1987; Matuszek et al., 1990). The lake is no longer being stocked with fish.

## Materials and methods

### Coring procedures

Locations of the coring sites are shown on the map (Fig. 1). All cores were taken with a Glew maxi corer (Glew, 1989). Cores 1 and 2 were recovered on February 14, 1999, and used for preliminary studies. On May 20, 1999, cores 3 and 4 were taken at 50 m depth from the deepest portion of the lake. Core 3 was used for diatom analysis and core 4 was used for cladoceran analysis. They both were 43.5 cm in length and 63 mm in diameter. The top 13 cm of core 3 was sampled at 0.25 cm intervals, the subsequent 7 cm at 0.5 cm intervals, and the remainder at 1 cm intervals. The top 10 cm of core 4 was sampled at 0.25 cm intervals, the subsequent

10 cm at 0.5 cm intervals, and the remainder at 1 cm intervals.

#### *Microfossil preparation and analysis*

Samples from core 3 were prepared for diatom analysis following Battarbee (1986). Strewn mounts were made and plated in Naphrax®. The slides were examined under 1000× magnification with either a Nikon Optiphot X-2 (numerical aperture = 1.25) or a Leica DMRB (numerical aperture = 1.3) compound microscope. At least 500 diatom valves per slide were identified and counted. To aid in identification, photographs were taken using black and white Kodak Techpan film (50 ASA) or using a CoolSnap digital camera (RS Photometrics, Roper Scientific Inc.). Taxonomically difficult taxa were studied using a JEOL 840 scanning-electron microscope at 15 kV. Taxonomic notes are documented in St. Jacques (2000).

Samples from core 4 were prepared for cladoceran analysis following Bos (2001) from 1 ml volumes of sediment per level. Strewn mounts were made and plated in Karo® corn syrup. The slides were examined under 200× or 400× magnification with a Leica DMRB (numerical aperture = 1.3) microscope. Each slide was enumerated entirely. To aid in identification, photographs were taken using a CoolSnap digital camera. Taxonomic identifications most closely follow Bos (2001). Cladoceran and diatom samples and slides are stored in the Paleoenvironmental Assessment Laboratory, Department of Geology, University of Toronto.

#### *Sediment chronology*

Dating of core 3 was performed using <sup>210</sup>Pb analysis by J. Cornett, MyCore Ltd. (Dunrobin, Ontario). The constant rate of supply (CRS) model (Binford, 1990) was used to determine the geochronology. Confirmatory pollen analysis was done on core 3 by J.H. McAndrews in order to determine an approximate depth in the lake sediments for the rise in ragweed (*Ambrosia* L.) pollen which signals the beginning of European forest clearance. Core 4 was recovered approximately 1 m away from core 3, hence core 3's <sup>210</sup>Pb chronology is assumed to apply to core 4 as well.

However, some error must be assumed; based upon diver's reports of the deep-basin sediments, an error of ±1 cm in matching up the cores' stratigraphy is reasonable.

#### *Statistical analysis*

Only diatom species that occurred in more than one sample and greater than 1% abundance in at least one sample were used in statistical calculations. Principal components analysis (PCA) of sub-fossil diatom assemblages was used to explore patterns of diatom community change over the entire time period included in the sediment core and to determine when change occurred (Manly, 1994; Faulkenham et al., 2003). Lake-water total phosphorus concentrations (TP) were inferred from diatom percent abundance data using a weighted averaging (WA) regression and calibration model (Hall & Smol, 1996; Wilson et al., 1996) and WACALIB v. 3.3 software (Birks et al., 1990; Line et al., 1994). In order to ensure the best nutrient reconstruction, several calibration sets were examined for close modern analogs to the Lake Opeongo assemblages of which two are reported here (St. Jacques, 2000): Hall & Smol (1996) and Wilson et al. (1996). To determine how well a calibration set of modern samples provides analogs for fossil core samples, the method of minimum dissimilarity (DC) coefficients using a squared chord distance was used (ANALOG v.1.6; H.J. Birks and J.M. Line, unpub. program; Anderson et al., 1989; Birks et al., 1990). Analog analysis using minimum squared chord dissimilarity coefficients showed that both calibration sets provided reasonable modern analogs to the fossil diatom assemblages (St. Jacques, 2000). Since Hall & Smol (1996) developed their calibration set from lakes in the same geographical and geological area as Lake Opeongo, results using this calibration set are reported in detail. For Hall & Smol's (1996) calibration set, any fossil samples with minimum dissimilarity coefficient (DC) > 0.3858 have no modern analogs (a conservative judgment according to Anderson et al. (1989)) and those samples with 0.2714 < minimum DC < 0.3858 have good modern analogs and any fossil samples with minimum DCs < 0.2714 have close modern analogs. There were good or close modern analogs for 87% of the samples using this calibration set.

With two exceptions, the samples without modern analogs were prior to 1924, well before noticeable changes started occurring in the diatom assemblages. In order to estimate the errors of the inferences, bootstrapping using WACALIB 3.3 (1000 bootstrap cycles) was used to estimate the estimated standard errors of prediction of TP for the fossil samples (Birks et al., 1990; Line et al., 1994). In order to assess whether significant changes have occurred in a time series, a modified *t*-test, the "Table-Look-Up Test" (von Storch & Zwiers, 1999), was used. This was necessary because of serial autocorrelation in the time series. A regular *t*-test assumes that a time series is independent, identical and normally distributed, and is therefore inappropriate for diatom or cladoceran abundance data.

## Results

The plot of  $\log_{10}^{210}\text{Pb}$  activity (Bq/g) against core depth (cm) for Lake Opeongo core 3 (Fig. 2) shows a linear decay  $\log_{10}^{210}\text{Pb}$  profile except in the top 4 cm. These four outlying points are not used in calculating the least-squares regression line. In core 3, the rise of the ragweed pollen, marking heavy European land clearance in the 1850s, occurs between 13 and 18 cm, which is between 1856 and 1924 according to the  $^{210}\text{Pb}$  dating.

In this study, a total of 221 taxa representing 32 genera was identified. The majority of the diatom frustules were from planktonic taxa with an average abundance of 76.0%. In all cores examined, the smaller diatoms were well preserved while the

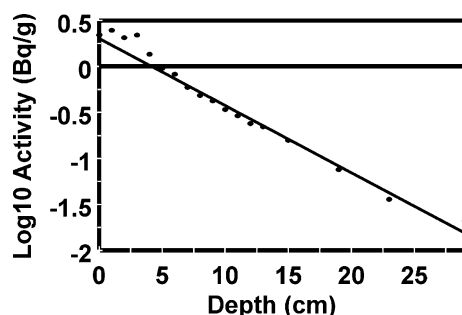


Figure 2. Plot of  $\log_{10}^{210}\text{Pb}$  activity (Bq/g) against core depth (cm) for Lake Opeongo core 3. Also shown is a least-squares regression line.

long slender diatoms from genera such as *Asterionella*, *Tabellaria*, *Fragilaria* and *Rhizosolenia* were often broken, making it necessary to count tips and adjust the counts accordingly by dividing the sum of the tips by two.

The relative abundance of the eleven common taxa (greater than or equal to 5% in at least one level) in core 3 is shown in Fig. 3. The diatom zone boundary denoting where major change in the diatom assemblages begins was drawn by using PCA ordination of the species that were present at least 1% on at least one level. All 70 diatom samples were included in the ordination. Figure 4a shows the samples plotted according to their first two PCA axes scores. The first two axes account for 91.8% of the cumulative variance in the species data ( $\gamma_1 = 0.776$ ,  $\gamma_2 = 0.142$ ). The samples clearly fall into two classes: those levels at least 7.5 cm deep in the core and dating from prior to 1962 form a relatively compact set in the left hand side of the ordination. Then starting at ca. 1962, all subsequent samples diverge from this set and move towards the right hand portion of the plot. Hence, the boundary was drawn at 7.4 cm. Because the diatom stratigraphy shows a clear transitional state, a bottom up or agglomerative constrained cluster analysis algorithm such as CONISS (Grimm, 1987) is not appropriate (Birks, 1986; Grimm, 1987).

### Zone 1: pre-1800–1962 (42–7.5 cm)

The diatom assemblage in this zone characterizes ultra-oligotrophic conditions in Lake Opeongo. The assemblage is dominated by the oligotrophic, planktonic *C. stelligera* complex which had an average abundance of 39.4% in this zone. *Tabellaria flocculosa* (Roth) Kutzing IIIp sensu Koppen and the *Aulacoseira distans* (Ehrenberg) Simonsen complex, both planktonic, were the co-dominants, with averages of 14.3 and 6.1%, respectively. (The *Aulacoseira distans* complex includes *Aulacoseira distans*, *Aulacoseira distans* var *nivaloides* (Camburn) Simonsen, *Aulacoseira tenella* (Nygaard) Simonsen, and *Aulacoseira humilis* (Cleve-Euler) Simonsen.) Benthic *Achnanthes minutissima* Kutzing and the small, benthic, alkaliphilous *Fragilaria pinnata* Ehrenberg and *Fragilaria brevistriata* Grunow were also present. The more eutrophic *A. formosa*, *C. bodanica* var

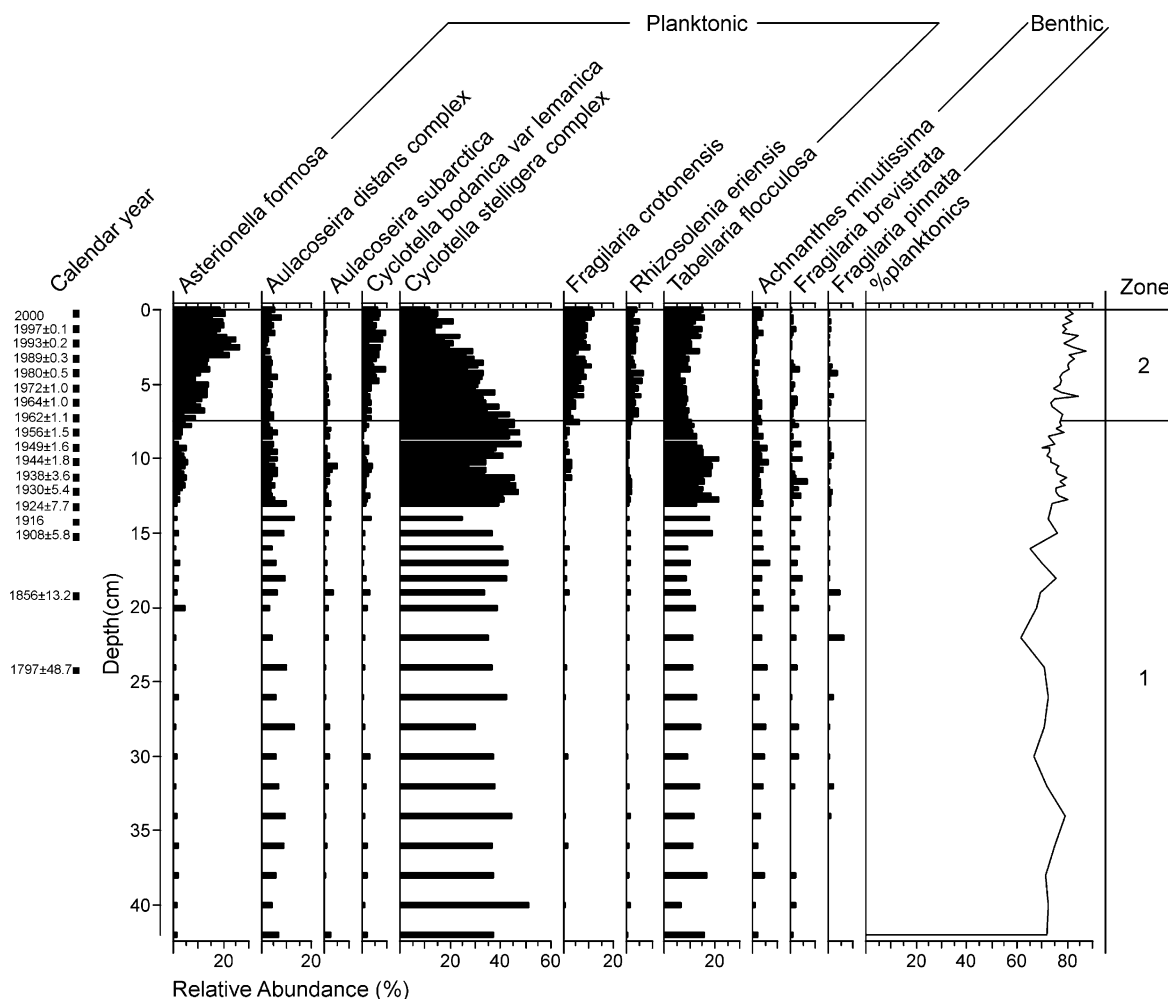


Figure 3. The relative abundance of common diatoms of Lake Opeongo core 3 plotted against core depth. Shown are the taxa with a relative abundance of at least 5% in at least one stratigraphic level. Included is the percent planktonic species. Also included are calendar year dates derived from  $^{210}\text{Pb}$  analysis together with their standard deviation.

lemanica, and *F. crotonensis* (all planktonic) were present in very low average abundances (2.8, 1.8, 1.1%, respectively) as was the planktonic *Rhizosolenia eriensis*. The relative composition of the diatom community appears relatively stable. The average percent abundance of the summed planktonic species was 73.3%.

#### Zone 2: 1962–1999 (7.25–0 cm)

The diatom assemblage in this zone indicates a transition to conditions of increased TP (but still within the oligotrophic range) in Lake Opeongo starting at ca. 1962. From the data, it is not clear if a stable community has been reached. The

ultra-oligotrophic *C. stelligera* complex declines in abundance, reaching a minimum of 12.1% in this zone. *Asterionella formosa*, *C. bodanica* var *lemanica*, and *F. crotonensis*, which have higher TP preferences, all greatly increase in abundance, reaching respective maxima of 26.2, 9.2 and 11.8%. The planktonic *R. eriensis* also increases in abundance. However, this latter increase may well be an artifact of preservation in the sediments as this diatom is extremely fragile. *Tabellaria flocculosa* IIIp first decreased in percentage, then appeared to regain its former numbers. *Aulacoseira distans* complex and *A. minutissima* declined in abundance. The average percentage of the summed planktonic diatoms increases in this

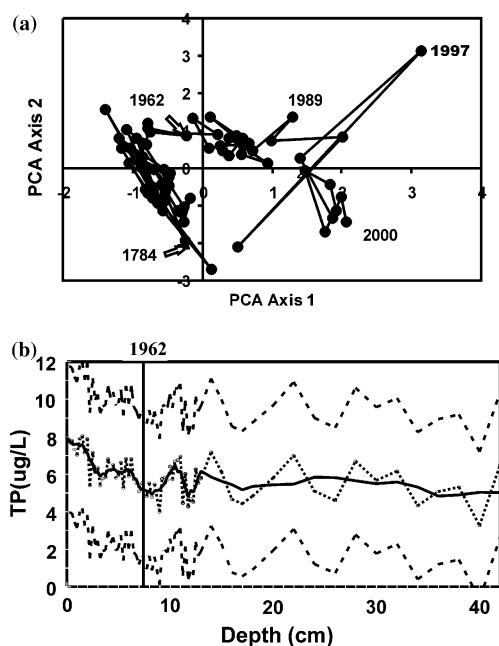


Figure 4. (a) Principal components analysis (PCA) of changes in sedimentary diatom assemblages (as % abundance) from Lake Opeongo. Sample scores are presented for the first two PCA axes because they accounted for most of the variation in diatom assemblages. The age of selected samples from  $^{210}\text{Pb}$  analysis are shown to indicate temporal trends. (b) Diatom-inferred total phosphorus ( $\mu\text{g/l}$ ) (dotted line) based upon the transfer function of Hall & Smol (1996). Also shown is a five-point running mean (solid black line). Also shown are the estimated standard errors of prediction for the WA inferences (dashed line). The vertical black line shows where 1962 occurs in the core.

zone to 79.2%. A two-tailed Table-Look-Up  $t$ -test on the combined percentages of the planktonic diatoms shows that this increase is significant at the 0.05 level ( $n = 53$ ,  $t = 4.600$ ,  $\alpha = 0.3834$ ). This test was performed on a reduced dataset of samples taken at 0.25 cm intervals, i.e. 0–13 cm, and thereby at approximately equal time intervals during 1930–1999.

The diatom-inferred TP from Hall & Smol (1996) calibration sets shows a trend of increasing TP in the upper 7 cm (Fig. 4b). The diatom-inferred TP from Wilson et al. (1996) calibration showed an identical trend (St. Jacques, 2000). Only the uppermost 2–3 cm samples of the core show a significant change in TP as measured by the transfer function approach. The  $\text{RMSE}_{\text{boot}}$  of  $4.2 \mu\text{g/l}$  for Hall & Smol's TP inference is quite large; hence the transfer function approach can

only detect relatively large shifts in TP. However, our high-resolution sampling allows us to detect the beginning of this trend at 7.5 cm when the diatom assemblage begins changing, before the transfer function is able to detect it. Note that the current measured average TP value of  $8 \mu\text{g/l}$  (Table 1) is exactly predicted by this transfer function.

In this study, a total of 28 taxa of cladocera representing 16 genera were identified in core 4. Their relative abundances are shown in Fig. 5. By far the most prominent species was planktonic *Bosmina longirostris* O.F. Muller (average abundance of 83.1%), which is represented with all body parts. After *B. longirostris*, the most abundant species are *Daphnia* spp. (including *Daphnia ambigua* Scourfield, *Daphnia dentifera* Forbes and *Daphnia longiremis* Sars), *Chydorus sphaericus* O.F. Muller, *Sida crystallina* O.F. Muller, and *Acroperus harpae* Baird with maximum abundances of 10, 9.1, 7.7 and 7.7% respectively. Other species are represented by occasional remains only scattered throughout the core and can therefore be of limited value in core analysis. For ease of comparison, the diatom zone boundary at 7.4 cm is drawn across the cladoceran stratigraphy.

The relative abundance of *B. longirostris* has been high over the past 150 years. However, the relative abundance of *B. longirostris* has further increased since the introduction of cisco from a mean of 78.9% to 90.1%. A two-tailed Table-Look-Up  $t$ -test shows that this increase is significant at the 0.05 level ( $n = 21$ ,  $t = 5.226$ ,  $\alpha = 0.3031$ ). This test was performed on a dataset of samples taken at successive 1.0 cm intervals, i.e., 0–20 cm. There was no significant change in the absolute abundance of *B. longirostris* since the introduction of cisco. The relative abundance of the planktonic *Daphnia* species declines after 1962 and even vanishes. Littoral zone *Chydorus sphaericus*, which does well under heavy fish predation, increases after cisco was introduced.

## Discussion

This study found that Lake Opeongo has shown a definite shift of increasing TP that began at approximately 1962, most likely in response to the introduction of cisco. This increased TP is shown by the sub-fossil diatom community. Prior to 1962,

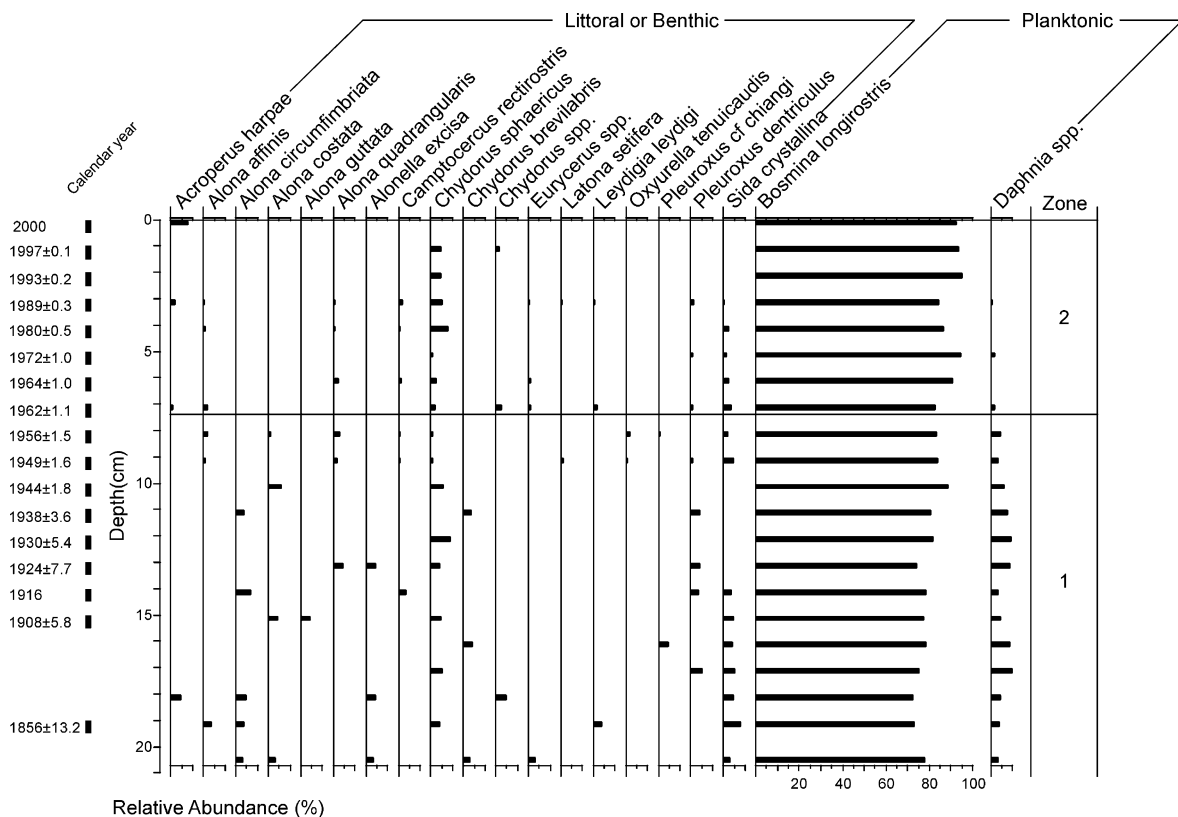


Figure 5. The relative abundances of cladocera against core depth (cm) for Lake Opeongo core 4. Included are the  $^{210}\text{Pb}$  dates from nearby core 3. 1962 is shown as a line.

the lake's diatom community was dominated by the *Cyclotella stelligera* complex with subdominants *Tabellaria flocculosa* IIIp and the *Aulacoseira distans* complex. At this time, the community began to shift to one consisting of increasing amounts of *Asterionella formosa*, *C. bodanica* var *lemanica*, *Rhizosolenia eriensis* and *Fragilaria crotonensis* and decreasing percentages of the *C. stelligera* complex and the *A. distans* complex. *Tabellaria flocculosa* IIIp remained a relative subdominant in this different community. An examination of the TP preferences of the major diatoms as published in the literature (St. Jacques, 2000) shows that this shift was towards taxa with higher TP preferences, as *A. formosa*, *C. bodanica* var *lemanica*, *F. crotonensis* and *R. eriensis* have higher TP optima than the *C. stelligera* complex and the *A. distans* complex do. The significant increase in the relative abundance of the planktonic species in Zone 2 also suggests that the lake became more nutrient-rich. Planktonic diatoms are more likely

to be limited by phosphorus than periphytic diatoms, which have access to further sources of phosphorus. Hence, an increase in the relative abundance of planktonic species versus periphytic ones suggests that the nutrient concentrations have increased in the epilimnion.

A reference site or sites in the same region is needed in order to determine the most likely cause of the increased TP. Unfortunately there are no other relatively undisturbed lakes of equal size in Algonquin Park or in the region. However, there is a much smaller lake in the park, Lake Delano (45° 30' N, 78° 36' W, surface area 0.3 km<sup>2</sup>, watershed 1.4 km<sup>2</sup>, maximum depth 20 m) that has been maintained by the Park authorities in a relatively undisturbed state as a control for fisheries studies. It is accessible solely by canoe and portage routes, and has had no cottage development or known fish stocking. It is a natural lake trout lake, also naturally without cisco or any other pelagic forage fish (personal communication:



Dr Brian Monroe, Algonquin Park Fisheries Assessment Unit). It has a logging and fire history similar to that of Lake Opeongo. This lake serves as a control site for our study. Smol & Dickman (1981) found in their short core diatom study that over the past 150 years Lake Delano has become more oligotrophic, with the ultra-oligotrophic modern dominant *C. stelligera* monotonically increasing in relative abundance, reaching its maximum at the top of the core. In comparison, the relative abundances of mesotrophic *C. bodanica* var *lemanica* (old name: *Cyclotella comta*) and mesotrophic *A. formosa*, whose increases in Lake Opeongo signify its increased nutrient status, remain constant throughout the 150 years.

As well, Hall & Smol (1996) provide a regional-scale study to serve as a reference. They surveyed 54 lakes in the nearby Muskoka-Haliburton region that mainly lay on Precambrian bedrock and inferred postindustrial pH and TP changes from paired surface and pre-1850 sediment diatom assemblages. Diatom-inferred TP suggests that in almost all lakes, present day TP is not higher than before European settlement. Only five lakes have increased their diatom-inferred TP by more than 2  $\mu\text{g/l}$  over the past 150 years. All of these five lakes are relatively small in surface area (10–100 ha) and have experienced much heavier present-day human impacts than Lake Opeongo has: moderate cottage and resort development, roads built through watersheds, etc. (Wilkinson et al., 1999; 1996 topographic maps). Hence, Opeongo's eutrophic trend is counter to regional steady-state or oligotrophic trends, including that of control Lake Delano.

The most likely cause of the increased TP in Lake Opeongo is nutrient recycling and trophic cascade effects triggered by the introduction of cisco in 1948. Introduced fish can affect algal production and standing crop by altering nutrient recycling (resource-based or bottom-up forces), and/or by trophic cascade effects (predator-based or top-down forces). Primary production can increase when size-selective predation by fish or large herbivorous zooplankton reduces grazing on phytoplankton communities (Carpenter & Kitchell, 1993). Although these effects are much debated, Brett & Goldman (1996) found in their quantitative summary of the freshwater trophic cascade mesocosm literature that planktivorous fish

treatments resulted in decreased zooplankton and increased phytoplankton biomass. Phytoplankton response to the cascade is highly variable with weak responses in two-thirds of the experiments and very strong responses in the other third. Particularly in oligotrophic lakes, overall lake productivity may be more strongly limited by nutrient supply than by herbivory (Elser et al., 1990). In such lakes, introduced fish may stimulate algal production by: (1) shifting the zooplankton community towards smaller-bodied species with resulting increases in per unit mass phosphorus excretion by zooplankton (Carpenter & Kitchell, 1993; Vanni, 1996); (2) increased abundances of fish with associated increases in fish excretion and thus increases in rates of nutrient regeneration as dissolved inorganic forms which are highly useable by phytoplankton (Brabrand et al., 1990; Vanni & Findlay, 1990; Vanni, 1996); (3) increased transport of phosphorus by fish from the benthos, littoral zone or hypolimnion to the pelagic epilimnion (Perez-Fuentetaja et al., 1996); and (4) decreased nutrient transport and/or sedimentation by small-bodied zooplankton in comparison to large-bodied zooplankton (Taylor & Carter, 1997). In addition to changes in nutrient regeneration rates and forms, the ratios in which nutrients are supplied may be altered (Tilman et al., 1982; Sterner, 1990; Vanni, 1996). Changes at the planktivore level can cascade throughout the lake's trophic levels. For instance, Harman et al. (2002) linked a change in the pelagic forage fish regime to major changes in the phytoplankton, zooplankton and piscivore communities, including a shift to a more eutrophic state, when the introduced alewife (*Alosa pseudoharengus*), a more efficient zooplanktivore, replaced cisco in Otsego Lake, New York, USA. Given Lake Opeongo's initial extreme oligotrophy and nutrient limitations, any increase in nutrient availability from increased recycling could have had a marked impact on the diatom community.

Although cisco have the reputation of being pelagic midwater foragers, from fall to spring they are not thermally isolated from the littoral zone and do move into shallower waters where they spawn (in the autumn) and consume a wide variety of foods (Scott & Crossman, 1973). Stable isotope studies (Vander Zanden & Vadeboncoeur, 2002; Vadeboncoeur et al., 2002) have shown that 15%

of their diet is actually directly from the zoobenthos (this is possibly an underestimate as stable isotope studies cannot differentiate between a pelagic and a profundal benthic food source). Hence, cisco (the only pelagic forage fish), whose numbers increased from none to an estimated 2–10 million post-larval fish (unpublished hydro-acoustic data, Dr Mark Ridgway, Director, Harkness Fisheries Laboratory, Algonquin Park, Ontario; net-sampling data, Vascotto & Shuter, 2005), could be serving as a nutrient pump from the benthic to the pelagic habitat. Lake trout numbers also increased fivefold from prior to the introduction of cisco to the mid-1970s (Shuter et al., 1987; Matuszek et al., 1990). Vander Zanden & Rasmussen (1996), Vander Zanden & Vadeboncoeur (2002) and Vadeboncoeur et al. (2002) have found that lake trout derive a substantial portion of their food from the zoobenthos both directly and indirectly and from the littoral zone. Particularly during winter, lake trout are not thermally isolated from littoral fish by the hypolimnion (Martin, 1952). (Even the relatively deepwater South Arm has a reasonable sized littoral zone; 33% of the surface area of the lake is 5 m in depth or shallower.) Hence, the increased numbers of lake trout could also be contributing to pumping an increased amount of nutrients from the littoral and benthic zones to the pelagic zone, particularly in spring when most diatoms bloom. The timing of the diatom community shift relative to the introduction of cisco is persuasive. By 1959, the cisco had become common enough to form more than 50% of sampled lake trout stomach contents (Matuszek et al., 1990). Similarly, Leavitt et al. (1994b) and Schindler et al. (2001) have shown that the introduction of salmonid fishes into naturally fishless oligotrophic lakes in western North America has caused substantial increases in algal production due to increased nutrient recycling from phosphorus excretion from the fish. They stressed that although the phosphorus regeneration rate directly attributed to the trout was low relative to estimates from invertebrates and plankton (Hudson et al., 1999), they were important because they represented a new source of phosphorus from the benthic and littoral zones for pelagic phytoplankton in these ultra-oligotrophic lakes that was unavailable when the trout were not present. In a similar manner, we suspect that the increased numbers of

cisco and lake trout are pumping new, previously largely unavailable phosphorus from the littoral and benthic zones to the pelagic zone in Lake Opeongo.

The significant increase in the relative abundance of the small cladoceran *B. longirostris* since the introduction of cisco suggests increased zooplanktivory by fish (Carpenter & Kitchell, 1993). As well, the large *Daphnia* species (Fig. 5), which are vulnerable to a visual planktivore such as cisco, decline and eventually vanish after the introduction of cisco, after having been present earlier at low abundance in the core. A detailed food study in nearby Lake Nipissing, Ontario (Langford, 1938) showed that *Daphnia* were an important food of the adult cisco in shallow water. Cisco have been found in Lake Mendota to be a strong regulator of zooplankton community structure via its being an efficient and voracious zooplanktivore (Johnson & Kitchell, 1996). Because of insufficient sediment, the core used for cladoceran analysis was not directly dated, but rather the dates from the diatom core, taken 1 m away, are assumed to be good estimates. Because of the potential error from this, the change in the cladocerans can be determined to be contemporaneous with that of the change in the diatoms, but it is not reasonable to deduce that one leads or lags the other. Given that trophic cascade effects act through a complex combination of predation and nutrient-cycling alterations, it is not necessary to prove that phytoplankton changes lead or lag zooplankton changes in order to recognize trophic cascade effects from pelagic forage fish introductions. Because the changes in the cladocerans are relatively small, we suspect the important effect of the cisco on the diatoms has been via nutrient-cycling changes directly from the presence of the fish and not via predation effects of the altered zooplankton community on the phytoplankton. Unfortunately, copepods and rotifers do not preserve well in sediments; therefore, there is no paleolimnological information about any changes in their abundances. Therefore, we do not have a complete picture of alterations (present or absent) in the zooplankton community after cisco was introduced. Cyclopoid copepods became the dominant zooplankton in two lakes in Wisconsin, USA that had been invaded by an exotic zooplanktivore, rainbow smelt (*Osmerus mordax*), and whose

zooplankton communities had been subsequently altered (Beisner et al., 2003). Cyclopoid copepods have been shown by Langeland et al. (1991) to be important constituents in Lake Opeongo's present zooplankton.

There are other possible ways that nutrient availability in Lake Opeongo could have increased, acting singly or jointly and in conjunction with the above. Among these are direct human impact on the watershed; increased North American post-war fertilizer use; global warming, including changes in the thermal conditions of the lake; and increased nutrient run-off as a result of fires in the watershed. We will explain why these latter factors are much less likely to be important.

It is possible that the lake has received a higher input of nutrients due to increased direct human impacts on the watershed. Because of the recent date of the diatom community shift, increased nutrient release into the lake resulting from the construction of the dam (ca. 1867) and from logging (Bormann & Likens, 1979), heaviest from 1860 to 1900, are unlikely main causal factors. The diatom communities of Lake Opeongo showed no changes when the dam was constructed. Intuitively, it seems that earlier logging, agriculture, and railway and road-building in Lake Opeongo's watershed would have had a greater impact than the current levels of tourism, mainly canoers and anglers.

After World War II, inorganic fertilizer use increased greatly in North America (Vitousek, 1994; Jefferies & Maron 1997). Significant proportions of these fertilizers are transported long distances in the atmosphere and redeposited (Langan, 1999). Wolfe et al. (2001) report unprecedented changes, beginning in 1950, in the diatom communities of alpine lakes in Colorado, USA, towards species with increased TP preferences (including *A. formosa* and *F. crotonensis*), due to airborne nitrogen deposition from agricultural and industrial activities in adjacent lowland regions. However, if the trend in increased nutrient availability in Lake Opeongo is due to deposition of airborne nitrogen and phosphorus, one should observe a region-wide signal, which does not exist, either in control Lake Delano (Smol & Dickman, 1981) which experiences the same climate and weather conditions as Opeongo does, or in Hall & Smol (1996) 54 lakes in the nearby

Muskoka-Haliburton region. If nutrient enrichment due to long-distance airborne transport of fertilizer were occurring, a greater number of Hall & Smol's (1996) 54 lakes and Lake Delano (all lakes much smaller than Opeongo and hence more likely to respond to a regional impact) would be expected to show increased TP.

Another possible impact on Lake Opeongo is that from global warming. Schindler et al. (1990) examined climatic, hydrologic and ecological records from 1969 to 1988 for the Experimental Lakes Area (ELA) of northwestern Ontario. They found that water renewal rates have decreased and concentrations of most chemicals, including total dissolved nitrogen and more conservative ions, but not phosphorus, increased because of decreased water renewal and forest fires in the catchments. However, in Lake Opeongo, phosphorus (or perhaps another limiting nutrient) appears to have become more, not less, abundant. In the ELA, thermoclines deepened due to increased wind velocities, increased wind exposure in burned catchments and increased transparency. In contrast, King et al. (1999) found that the average mid-summer thermocline depths for the South and East Arms of Lake Opeongo have shown a significant ( $p < 0.05$ ) shallowing trend during the time that records exist (1958–1996, with 12 missing years concentrated at the beginning of the record, sampling rate within summers not given). Unfortunately, thermocline records do not exist for the period prior to the diatom community shift, so the year of the beginning of this trend is unknown. (In fact, the only physical or chemical limnological or climatic records that exist continuously from ca. 1950 on are those of precipitation and air temperature from Madawska, Ontario, 36 km southeast, the nearest Environment Canada weather station. This paucity of records makes variance partitioning methods inapplicable.) This shift in thermal stratification could affect the nutrient dynamics of the lake as well as the light regime experienced by the epilimnetic diatoms. However, the shallowing of the epilimnion appears counter-intuitive to a trend of increased TP. Schindler et al. (1996) found that in the ELA, both climate warming and lake acidification led to declines in the dissolved organic carbon (DOC) content of lake waters, allowing increased penetration of solar radiation, including biologically harmful

ultraviolet-B radiation. Yet once again, if Lake Opeongo's TP increase is due to global warming, other relatively unsettled lakes in the region should be also showing this trend, and they are not (Smol & Dickman, 1981; Hall & Smol, 1996).

Increased nutrient run-off into the lake as a consequence of forest fires is a possible cause of a trend of increasing nutrients (Moser, 1996). However, several studies have demonstrated that fires have little effect on nutrient levels and limnic diatoms in lakes (Schindler et al., 1980; Bradbury, 1986; Bayley et al., 1992; Moser, 1996). According to various records (summarized in St. Jacques, 2000), there was only one large fire in the Lake Opeongo watershed during the period 1920–1978: a large fire in 1953 at the North Arm. However, it is unlikely that this fire served as the trigger for the change, since limnological effects from fire are not that long-lasting (Bayley et al., 1992; Korhola et al., 1996) and this change has persisted for more than 40 years.

In conclusion, before European settlement, Lake Opeongo was ultra-oligotrophic, with the diatom community consisting primarily of the *C. stelligera* complex with subdominants *T. flocculosa* IIIp and the *A. distans* complex. The diatom-inferred paleolimnological record showed no changes when the dam was built linking the three original lakes, during forest clearance or during the first half of this century. A significant change towards taxa with higher TP preferences occurs ca. 1962 when the diatom community shifted to the current one consisting of *A. formosa* with lesser amounts of *C. bodanica* var *lemanica*, the *C. stelligera* complex, *F. crotonensis* and *T. flocculosa* IIIp. The dominant cladoceran *Bosmina longirostris* increased significantly in relative abundance at the same time. This shift most likely occurred due to increased nutrient recycling and trophic level changes caused by human manipulation of the fish community of the lake. These results assert an obvious conclusion: fisheries management practices create impacts upon aquatic ecology, trophic condition and water quality. Unfortunately, during the 70 years or so of long-term fisheries management on Lake Opeongo there has not been a parallel record of water quality and/or trophic conditions. This issue appears to be extremely understudied: a search using Web of Science on cisco introduction, a commonly

introduced fish by fisheries managers, produced a single paper, Matuszek et al. (1990), which only addressed cisco's impact on lake trout and not broader aquatic ecosystem impacts. Aquatic resource managers have long endeavored to isolate and mitigate the effects from complex human impacts (acid rain, climate change, etc.) upon recipient water bodies. This paleolimnological exercise indicates that purposeful management activities (e.g. fish stocking) can create as much change in a natural system as other human activities that we aggressively seek to mitigate.

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