

LANDSCAPE EVOLUTION AND A RELICT FISH COMMUNITY,
NORTH SLOPE, ALASKA

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Abstract

The North Slope of the Brooks Range in arctic Alaska has a complex glacial history, having been glaciated several times since the late Tertiary. As a result of these glaciations, a complex arrangement of glacial sediments is exposed on the tundra. It is the presence of the youngest glacial sediments, and their abundant lakes, which allows communities of fish to persist in this harsh environment. Although the importance of the lakes is known, the timing at which fish entered and become land-locked in specific lakes is not. The purpose of this study was to use paleolimnological information in an arctic lake, Fog Lake 3, to reconstruct the fish community dynamics in the lake, resulting from glacial and geomorphic processes on the landscape.

Information about past conditions in the lake was inferred from biotic evidence and sediment characteristics in a lake sediment core. Grain size, lithology, and carbon chemistry were used as proxies for processes occurring in the lake and its watershed. The chironomid community structure was recreated throughout the length of the core by identification of fossil remains. The core was dated using ^{14}C techniques to determine total age and sedimentation rates throughout the length of the core.

The core was divided into two zones based on constrained incremental sum of squares cluster (CONISS) analysis of the grain size data. Although the CONISS analysis created zones, the only differences in grain size characteristics between zones were marginally significant. There was little difference in the carbon chemistry in the two zones. There appeared to be a significant decrease in the mass lost on ignition at 1000°C , but that mass is likely related to water in the mineral structure of clays and not proportion of carbonate rock.

Zones in the core were also developed using the CONISS method on the chironomid community composition data. While Tanytarsini (*Tanytarsus* and *Paratanytarsus*) dominated the chironomid community throughout the core, the upper zone had higher community diversity, as determined using the Shannon index. The upper zone (Zone 2) was further broken down using the CONISS results into Zones 2a and 2b. Comparison of the two zones showed an increase in chironomid diversity, an increase in *Heterotrissocladius* relative abundance, and a decrease in the proportion Tanytarsini through time.

The evidence presented by this study suggests that the chironomid community composition was controlled by some factor or factors, possibly including fish community structure, which changed through time. The changes seen in the chironomid community are inconsistent with those expected if they were due to climate dynamics or major changes in lake levels. Increasing diversity of the chironomid community would be expected with increased predation pressures, such as those imposed on invertebrates by fish or with increased organic matter input to the lake sediments.

The initial presence of fish in the lake possibly are related to changes in the diversity of the chironomid community which occurred between 7973 ± 50 ^{14}C YBP and 7344 ± 45 ^{14}C YBP. Based on an increase in the chironomid community diversity, the best estimate of fish becoming landlocked in Fog Lake 3 is between 4230 and 4600 ^{14}C YBP.

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Introduction

Fish distributions in regions with complex glacial histories are often a result of drainage patterns formed during or after those glaciations (Hocutt and Wiley 1986, Mayden 1988, Pielou 1991, Power 2002). Determining historical fish distributions using fossil remains is challenging, as preservation of fish remains is rare in lake sediments. Using paleolimnological techniques, however, the historical distribution of fishes can be inferred using invertebrate remains as proxies for the presence or absence of fish (Lamontagne and Schindler 1994, Uutala and Smol 1996, Walker 2001, Sweetman and Finney 2003), fish population density (Kingston et al. 1992, Finney et al. 2000, Jeppesen et al. 2002, Sweetman and Finney 2003), or a change in the fish community structure (Kerfoot 1974, Kitchell and Kitchell 1980, Kerfoot 1981, Leavitt et al. 1989, Miskimmin and Schindler 1994).

Fish populations on the North Slope of Alaska's Brooks Range have been dynamic through time with community distributions resulting from the complex glacial history of the region (Johnson 1980) and the geomorphic features of the lakes (Hershey et al. 1999). Lake fish communities in this region have been studied with regards to their distribution (Reynolds 1997, Hershey et al. 1999), diet (Goyke and Hershey 1992, Hanson et al. 1992), and trophic interactions (Hershey 1985a, 1992, McDonald and Hershey 1989). Although it is known that glacial and geomorphic processes have resulted in distinct community assemblages (Reynolds 1997, Klemetson et al. 2003), as is observed in land-locked populations of anadromous fish, the timing of these events has not been determined.

The arctic tundra on the North Slope of the Brooks Range in Alaska is an active landscape, having undergone several glaciations and continuing periglacial processes. There is evidence of four major glaciations and several smaller glacial events in the Itkillik River and Sagavanirktok River valleys (Hamilton 2002, 1978, 1979). The resulting complex glacial landscape is a result of multiple sources of glacier ice and repeated glacial advances. Periglacial processes include solifluction, thermokarst, and active freeze thaw (Hamilton 2002).

Plant and animal remains, as well as inorganic sediment deposited in lake sediments, record the biotic and abiotic activity in the lake basin through time. Study of this sediment record is useful in reconstructing the history of the watershed by observing physical, biological and chemical changes. Lake sediments reflect the chemical and physical conditions in the catchment at the time of deposition. Biological or geological activity in a watershed can influence the lake sediments including the type and amount of sediment deposited (Birks and Birks 1980).

Changes in the sediments themselves reveal the history of the lake and surrounding basin. Sediment size, shape, sorting, and composition are changes in the sediment that can be noted by analyzing lake sediment cores. They can reflect both allochthonous and autochthonous changes in primary productivity, lake energy, and residence time of water in the lake (Birks and Birks 1980).

Particle size is indicative of the amount of water movement in the system (both in the lake and watershed) at the time of deposition. Inorganic sediments can reflect the amount of erosion in the watershed due to both anthropogenic and climatic events. The

proportion of inorganic sediments is also influenced by the amount of vegetation in the catchment (Birks and Birks 1980).

Chironomids and their use in paleolimnological studies

Remains of invertebrates, vertebrates, pollen, and woody plant material may be preserved in lacustrine sediment. The insect family Chironomidae (Order Diptera) is useful in the study of lake paleoecology for several reasons. Chironomidae is among the most diverse and widely distributed free-living insect family; it is estimated that there are about 15,000 species worldwide (Cranston et al. 1983, Fittkau and Roback 1983, Pinder and Reiss 1983, Epler 1995). Chironomids are usually abundant, and the family includes species that are able to exploit extreme conditions including wide ranges of salinity, pH, temperature, depth, velocities, and oxygen concentrations (Armitage et al. 1995). Many individual species of chironomids are adapted to specific niches, such as hot springs, thin films of water, the hyporheic zone, phytotelmata, soils, and brackish water (Oliver 1971, Pinder 1986, Pinder 1995). The remains of chironomid larvae preserve well in sediment and are identifiable (Hofmann 1988). The short life span of chironomids results in high resolution in the fossil record as they respond quickly to environmental change relative to other insects due to their ability to disperse as flying adults (Walker et al. 1991).

Because chironomids are adapted to specific environmental conditions, the composition of the chironomid community can be used to reconstruct the ecological conditions at the time of sedimentation (Walker 2001). Changes in the sediment fossil record reflect changes in the ecology of the lake. Likewise, lack of change in the fossil record reflects stability in the lake ecosystem (Hofmann 1988).

Chironomids have been widely used in lake typology studies. The first use of chironomids in lake type classification studies were by Brundin (1958) and Saether (1975). In these studies the chironomid community compositions were used as indicators of oxygen availability and lake trophic conditions. Saether (1979) later constructed fifteen profundal chironomid communities that could be used to classify lake trophic state, and found that classifications based on these community structures corresponded well with total phosphorus and total chlorophyll-a in the lakes.

Since these studies, chironomids have been used as indicators of organic enrichment (Davies and Hawkes 1989, Pinder and Farr 1987, Quinlan et al. 1998, Francis 2001, Little and Smol 2001, Amsinck et al. 2003, Meriläinen et al. 2000) and acidification of aquatic systems (Wiederholm and Erikson 1977, Walker et al. 1985), to describe the pollution history of lakes (Wiederholm 1984, Ilyashuk and Ilyashuk 2001), and in climate studies (Walker and Paterson 1983, Schakau 1986, Lotter et al. 1999, Battarbee 2000, Larocque et al. 2001, Palmer et al. 2002, Porinchu and Cwynar 2002). Several studies have used invertebrate subfossils as proxies for vertebrate community structure (Jones and Juggins 1995, Sun et al. 2000, Sweetman and Finney 2003), including indicators of fish presence/absence (Uutala 1990, Kingston et al. 1992, Uutala et al. 1994, Uutala and Smol 1996). Chironomid community structure has been used as indication of air and water temperatures (Walker et al. 1997, Lotter et al. 1997, Olander et al. 1997, Brooks and Birks 2000), lake succession following glaciation (Cwynar and Levesque 1994, Hofmann 2001), and lake level changes (Hofmann 1998). Presence and absence of specific species have been used to indicate climatic conditions and organic

matter content of sediments (Larocque et al. 2001), temperature and depth (Walker et al. 1991), trophic state (Saether 1975), and sedimentation (Meriläinen et al. 2000).

This study uses historical chironomid community assemblages to reconstruct the fish community dynamics in an arctic lake having a land-locked population of arctic char (*Salvelinus alpinus*) and slimy sculpin (*Cottus cognatus*) as a result of the glacial history and geomorphic processes on the landscape. Biological, physical and chemical parameters will be examined. I will use modern comparisons of fishless and char/sculpin lakes, changes in the chironomid community structure, and sedimentary features to understand the history of the lake.

Setting

North Slope Fishes

Six species of fish are found in lakes in the vicinity of the Toolik Lake Field Station and include lake trout (*Salvelinus namaycush*), arctic char (*S. alpinus*), burbot (*Lota lota*), slimy sculpin (*C. cognatus*), arctic grayling (*Thymallus arcticus*), and round whitefish (*Prosopium cylindraceum*) (Hanson et al. 1992). Of these, only grayling, sculpin, and whitefish are found in streams and rivers (Reynolds 1997). Typically arctic char are anadromous, overwintering in lakes (Johnson 1980, Parker and Johnson 1991). Char found in North Slope lakes are typically land-locked populations of *Salvelinus alpinus*, a taxon morphologically similar to *Salvelinus malma* (dolly varden char) found in rivers. Dolly varden char appear to have displaced *S. alpinus* in North Slope streams (Bahr et al. 2003). Where land-locked populations of the formerly anadromous arctic char are found in North Slope lakes they are considered glacial relicts (Reist et al. 1997).

Arctic lake fish and invertebrate populations are depauperate; however, their trophic structure is similar to temperate lakes (Hershey et al. 1999). Lake community structure is related to the interactions between organisms and their food sources. The effects are a result of bottom-up influences, such as amount of primary production (Schindler 1987), and top-down controls on the food web (Shapiro 1980, Carpenter et al. 1985). The most important interactions in arctic lakes are between benthic and pelagic species (Hershey 1985a, 1992) with aspects of community structure being controlled by the top predators. Lakes with lake trout and possibly arctic char as the top predator are known to influence the chironomid community structure by increasing chironomid density, biomass, species richness, and Shannon index (H') (Goyke and Hershey 1992, Hershey et al. 1999). Many of the lake systems have just two species of fish and are lacking large invertebrates commonly found in lakes. In these lakes chironomid larvae become especially important in trophic structure, and they may dominate benthic communities (Hershey 1985b).

Glacial and Postglacial History

On the north slope of the Brooks Range there is evidence of four major glaciations. In the late Tertiary to early Pleistocene there were two glacial periods, the Gunsight Mountain and Anaktuvuk River Glaciations (Hamilton 1978, 1986, 1994, 2002). Deposits of these early glaciations are overlain by sediments of the Sagavanirktok River Glaciation, which occurred at some time in middle Pleistocene (about 780,000 to 125,000 ybp). These sediments, in turn, are overlain by sediments of the Late Pleistocene Itkillik glacial sequence (Hamilton and Porter 1975). Each successively younger glaciation is less extensive, extending shorter distances from the Brooks Range.

Sediments and landforms of all four glaciations are therefore exposed on the North Slope (Hamilton 1978).

Itkillik glaciation is characterized by two major glacial advances. The Itkillik I phase is beyond the limit of ^{14}C dating. At their maximum, ice of the Itkillik I glaciations filled the present-day Itkillik, Atigun, and Sagavanirktok River valleys. In the Sagavanirktok River valley the glacial lobe was 14 km wide and extended 40-50 km north of the Brooks Range. The Itkillik II glaciation is of Late Wisconsin age and is characterized by two advances between 25-11.5 ka. The younger readvance is dated between 12.8 and 11.4 ka (Hamilton 2002). The younger Itkillik II glaciation had similar glacial flow pattern into the Itkillik, Sagavanirktok and Atigun River Valleys (Hamilton 1978, 2002).

Geomorphic differences have been observed by Hamilton (2002) in glacial landscapes of Itkillik I and Itkillik II ages. Sediments of Itkillik I age have undergone some post-glacial modifications including slight flattening of moraine crests, developments of frost hummocks and frost boils, secondary and tertiary polygons, and erratic boulders showing various degrees of weathering. Moraines typically have patchy heath plants on crests along with bare gravel. Slopes have silty solifluction deposits. Kettles are usually present, have wet, marshy banks, and are usually connected by small streams with well developed drainage networks.

Sharp moraine fronts delineate the boundary between Itkillik I and II glaciations. Moraines of Itkillik II age are rockier, less vegetated, and more irregular than Itkillik I moraines. They have retained surface features such as meltwater channels, multiple crests and ridges along their edges, and primary ice polygons. Soils are not as well

developed. Solifluction is not as common, drainage patterns are poorly developed and kettles are isolated. Lakes have steep slopes, irregular outlines, and lack much of the shoreline vegetation of older kettles. Some kettles are still forming.

Fog Lake 3 (UTM T6 7620400N 415500E) is one in a group of five high-elevation lakes in a lake district on the north slope of the Brooks Range on the arctic tundra near the Toolik Lake Long Term Ecological Research site (Figure 1). Fog Lake 3 has an area of $3.8 \times 10^4 \text{ m}^2$ and a watershed area of $3.9 \times 10^5 \text{ m}^2$ (including the lake).

Located within the limit of Itkillik II glaciation (Late Wisconsin age, 25,000-11,000 ybp, Hamilton 1978), the lakes are glacial kettles underlain by a continuous zone of permafrost (Ferrians 1994). Interpretation of topographic maps and aerial photos show evidence of changes in the drainage scheme of the lakes due to stream piracy and other geomorphic processes (Hershey et al. 1999). Stream piracy is the process of diversion of rivers from one drainage into an adjacent catchment due to the headward erosion of small streams in the adjacent catchment (Mackin 1936, Easterbrook 1993). Located on the lateral moraine of Itkillik II age glacial till, Fog Lake 3 would have only been able to drain to the northwest into Oksrukuyik Creek when ice of Itkillik II age filled the current Sagavanirktok River valley (Figure 2). As the glacier retreated into the Brooks Range to the south, meltwater streams in the valley eroded headward intersecting the Fog Lakes. This altered the drainage pattern of the Fog Lakes, capturing them into a higher gradient watershed. Ultimately, the glacial retreat resulted in the disappearance of paleooutlet streams and the isolation of the lakes from rivers. The current outlet of the Fog Lakes is to the east, into the Sagavanirktok River basin (Figure 2).

The fish community in Fog Lake 3 includes arctic char and slimy sculpin. The current outlets of the lakes, and the only accesses into the lakes, have gradients too steep to allow char and sculpin to ascend into the lakes from the Sagavanirktok River below. Therefore, it is assumed that the land-locked populations of char and sculpin in some of the Fog Lakes are relicts of the former geomorphologic configuration of the lakes with outlets to the north along Oksrukuyik Creek into the Sagavanirktok River (Hershey et al., 1999).

Community dynamics

Hershey et al. (1999) found that arctic lake communities could be characterized using geomorphic characteristics of the lake basin including parameters such as lake area, maximum lake depth, and outlet gradient. The geomorphic characteristics limit which fish species may inhabit a lake. For example, slimy sculpin are poor swimmers and lack swim bladders (Scott and Crosman 1973). They are not able to jump even small waterfalls or migrate long distances, and they are not found in streams that freeze solid. Lakes may be fishless if the right combination of geomorphic constraints apply to the lake basin (i.e. the gradient of the outlet is too steep for fish to ascend, lake depth is not sufficient to allow overwintering, and the lake is not connected to other lakes).

In turn, the fish species control the trophic structure of lakes (McDonald and Hershey 1989, Hershey et al. 1999, Jeppesen et al. 2001). On the north slope of the Brooks Range, where lake trout and arctic char are the top predators, other fish in the lake (slimy sculpin) are forced to the littoral zone to reduce the risk of predation where there is lower food quality and therefore lower growth rates (McDonald and Hershey 1989, Hanson et al. 1992).

Large, predatory chironomids are more abundant in fishless lakes than in lakes having a community of predaceous fish (Goyke and Hershey 1992, Hanson et al. 1992). However, the diversity of the chironomid community is greater in lakes having fish, but chironomid density was reduced up to 20 times (Goyke and Hershey 1992). No predatory chironomids were found five years after slimy sculpin were introduced to a fishless tundra lake (Hershey et al. 1999).

Methods

Coring and core analysis

Fog Lake 3 was cored in the summer of 1998 using a modified piston corer (Livingstone, 1955) that was manufactured in the lab of Dr. Michael Miller at the University of Cincinnati. The corer was suspended from a plywood platform supported by two rubber rafts. The lake was cored at its maximum depth of 21 meters, as determined using a handheld diving sonar apparatus (Hondex brand). The corer was suspended just above the lake floor when coring was started to preserve the upper most layer of sediment. The corer was driven into the sediment until hammering did not result in further driving of the corer. The resulting core had a length of 1.28 meters. The core was then brought to the surface and immediately sealed at the bottom using custom fitted rubber stoppers. The water at the top of the core was drained off, and the top of the core was sealed.

In the lab, the core was cut into two sections, 0.54 and 0.74 meters in length. The cores were then transported to the Limnological Research Center on the Twin Cities Campus of The University of Minnesota, where they were run through a magnetic susceptibility bridge and densitometer. The cores were then split longitudinally and the

sedimentary structures including grain size, layering, and color (Munsell 1944) were recorded.

Percent water, organic carbon, and inorganic carbon were determined by loss on ignition (Dean 1974, Bengtsson and Enell 1986). One cubic centimeter subsamples were taken at five-centimeter intervals down the core. The subsamples were heated at 110⁰C overnight, and then at 550⁰ and 1000⁰ C for at least an hour at each temperature. Mass lost at each temperature recorded.

Additional subsamples of 1.5 cm³ were recovered at five-centimeter intervals for grain size analysis using settling sediment grains through a water column (Folk 1974). The samples were processed in the sediment lab in the Department of Geological Sciences at the University of Minnesota-Duluth.

The core was subsampled every 5 cm for chironomids. A 0.5 centimeter slice of the core was removed and processed using the method of Hoffman (1986). The sediment was deflocculated in a warm solution of 10% KOH for 30 minutes, and centrifuged for ten minutes. The supernate was removed and the sediment was rinsed with distilled water and centrifuged again for ten minutes. The supernate was again removed and passed through two sieves with openings of 250 micrometers and 106 micrometers. Samples were stored in 90% ethanol until they were examined under a dissecting microscope. Chironomid headcapsules were picked out of the remaining sediment and mounted on microscope slides using Hoyer's mounting medium (Borror et al. 1989). Headcapsules were identified to genus under 100X power on a compound scope. The keys of Merritt and Cummins (1996) and Wiederholm (1983) were used for identification. For each sample at least 50 headcapsules were identified.

Three layers in the core were ^{14}C dated using ASM radiocarbon analysis at the National Ocean Sciences AMS Facility at the Woods Hole Oceanographic Institution in Woods Hole, Massachusetts, using bulk sediment. The bottom layer was dated to obtain lake age. The core was also dated at 85.25 cm and 100.25 cm, as those layers were located at the boundaries of obvious changes in the chironomid community structure.

The Shannon index (H') was calculated for each chironomid subsample. The Shannon index is a relative measure of species richness and is calculated as follows:

$$H' = -\sum p_i (\log p_i),$$

where p_i is the proportion of the total number of individuals in the i th genus (Hauer and Resh 1996).

The stratigraphic data were plotted using Tilia 2.0 (Grimm 1987). Zonation of the chironomids and grain size analysis data was performed using constrained incremental sum of squares cluster analysis (CONISS for Windows). CONISS is a multivariate technique for quantitatively defining stratigraphic zones in sediment cores. The creation of zones using the method is based on minimizing the within-zone dispersion of the data (Grimm 1987).

Zonation based on chironomid data used only taxa found to be significantly different in modern fishless and char/sculpin lakes based on step-wise functional analysis (Gretchen Gettel, Cornell University, personal communication). All data were tested for autocorrelation using time series analysis. Significant differences between zones in the core were determined by a two-tailed Mann-Whitney test. All p-values less than or equal to 0.10 are reported, although those between 0.05 and 0.10 will be considered marginally significant.

Results

Sediment Lithology

About 128 cm of sediment was recovered in Fog Lake 3 from a depth of 21 meters, with the water-sediment boundary preserved at the top of the core. The sediments ranged from light to dark gyttia throughout the core, punctuated with layers of clay and organic silt in the top 90 cm (Table 1). There were two thin layers of dark silt containing nodules near the base of the core.

Carbon Chemistry

The loss on ignition (LOI) at 550⁰C ranged from 3.2% to 4.9% of the dry mass of the subsamples (mean=3.9%, SD=0.003) in the entire core length (Table 2, Figure 3). The LOI of the subsamples ranged from 0.10% to 0.48% of dry weight (mean=0.28%, SD=0.0011) at 1000⁰C. Percent of dry mass lost at 550 and 1000⁰C was 3.9% and 0.3% in Zone 2 and 3.8% and 0.4% in Zone 1 (Figure 4, Table 3). When Zone 2 was further separated into two subsections loss at 550 and 1000⁰C were 4.2% and 0.4% in Zone 2a and 3.8% and 0.2% in Zone 2b (Table 3).

Grain Size Analysis

All of the subsamples were predominately silt, ranging from about 78 to 100% (Table 3). Only 7 of the subsamples had sand present. Mean size ranged from 5.4 phi to 7.1 phi. Standard deviation (which can be interpreted as sorting, Folk 1974) ranged from 1.2 to 2.0 phi. The CONISS invertebrate and grain size cluster analysis resulted in a zonation of the core into two main sections or zones (Figure 4). The boundary between Zone 1 and Zone 2 based on grain size analysis lies between 99.5 and 100.25 cm depth (Figure 4).

Zones 1 and 2 have an average of 88.3% and 91.6% silt, respectively (Table 3). Sand and clay averaged 0.7 % and 11.1% and 0.5% and 7.9% respectively. Mean grain size was 6.5 phi in Zone 1 and 5.9 phi in Zone 2 (SD 1.7 phi in both zones).

Zone 2 can further be divided into 2 subzones based on the chironomid community cluster analysis discussed below, with Zone 2a between 53-100.25 cm depth and Zone 2b all data above 53 cm depth in the core. Zone 2a was 0.2% sand, 91.7% silt, 8.2% clay, and had a mean size of 5.8 phi. Zone 2b was 0.7% sand, 91.6% silt, 7.8% clay, and had a mean size of 5.9 phi. (Table 4). Mass lost at 1000°C comprised 0.35% of the dry mass in zone 2a and only 0.18% in zone 2b (Table 3). The percent clay in the whole core is variable through time, erratic in the bottom meter and consistently low in the top 30 cm (Figure 4).

Chironomid Community

Throughout the core the lake is dominated by Tanytarsini (*Tanytarsus* and *Paratanytarsus*), with the tribe contributing at least 50 percent of the individuals through time (Figure 5). The genera *Tanytarsus* and *Paratanytarsus* are grouped together as Tanytarsini here, as identification to a lower level was not possible for most of the subfossil Tanytarsini in the core.

CONISS results showed two major groupings of Chironomidae, with the boundary between 94.25 cm and 105.25 cm (Figure 6). The lowermost zone (Zone 1) was made up of the three subsamples found at the base of the core. The remaining subsamples grouped together to form a larger second zone, which was separated into two smaller zones (Zones 2a and 2b).

Zone 1 was dominated by Tanytarsini (Table 4, Figure 5). None of the three predatory chironomid taxa found in the lake (*Procladius*, *Protanypus*, and *Monodiamesa*) were present in Zone 1. *Heterotrissocladius spp.* made up less than 4 percent of the total individuals in Zone 1. The mean Shannon index of the zone (Figure 7, Table 4) was < 1.

Zone 2 was also dominated by the tribe Tanytarsini. However, the overall diversity as measured using the Shannon index was higher in Zone 2, with a mean diversity of > 1.7 (Table 4). The predatory chironomid *Procladius sp.* was found at 4 intervals in Zone 2, while *Protanypus* and *Monodiamesa* were both found at one interval (Figure 4). *Heterotrissocladius* relative abundance increased in Zone 2 to 4.5 percent.

Based on the cluster analysis results, Zone 2 was further broken down into two subzones (Figure 6). The Shannon diversity was 1.64 and 1.75 in zones 2a and 2b respectively. Breaking Zone 2 into subzones showed trends of increasing *Heterotrissocladius*, increasing H' diversity, and decreasing *Tanytarsini* through time (Table 5).

Radiocarbon Dating

The core was radiocarbon dated at three depths (Table 6). A date of 9440 years ± 50 years was obtained at the base (128.15-128.65 cm), 7660 years ± 45 years at 100.0-100.5 cm, and 6870 years ± 40 years at a depth of 85.0-85.5 cm from the surface (Schneider, 2000). Based on the radiocarbon dates, I was able to interpolate sedimentation rates of 0.012 cm/yr between 0-85.25 cm, 0.019 cm/yr between 85.25-100.25 cm and 0.016 cm/yr between 100.25 and 128.40 cm (Table 7).

Discussion

The paleolimnological data collected in Fog Lake 3 indicates there are two major zones into which the sediment (i.e., the lake history) can be separated. The lithology of the lake sediment core suggests there are differences in sediment composition in Zones 1 and 2. Smaller mean sediment size and higher % clay in Zone 1 may represent a period of fewer storm events in the region, a larger lake basin, or more fine sediments available in the watershed. As you go from the littoral zone to the center of a lake basin mean sediment size decreases (Digerfeldt 1986). It would be expected that there would be some change in the physical properties of the sediments related to the change in outlets. One possibility is that the lake level dropped when the current outlet of the lake was established, as the lake outlet would only change if a new, lower outlet to the lake were formed. This drop in lake level would also result in a change in surface area of the lake and the distribution of sediments in the lake. When lake level drops, any given point in the lake basin becomes closer to the lake margin, where the coarsest sediments are deposited. This may result in a coarsening of sediments deposited in all areas of the lake (Digerfeldt 1986). The source of sediments to the lake is glacial till within the active layer of permafrost. Through time, it is likely the fine sediments (ie. clays) weathered out of the sediments (Hamilton 2002). This weathering would decrease the proportion of clay in the watershed, which is the source of sediments in the lake. It is likely that weathering of sediments in the watershed resulted in the observed lower percent clay in the more recent sediments.

There was no significant change in the carbon chemistry (Meyers and Ishiwatari 1995, Meyers and Teranes 2002) of the lake through time in Fog Lake 3. Although there appears to be a significant decrease in mass lost at 1000 °C through time, it is likely due

to dehydration of clays in the sediments and should not be interpreted as a change in the proportion of carbonate minerals (Dean 1974). As a lake ages, the relative amount of total inorganic carbon is expected to decrease, due to increased primary productivity and organic acids, decreased weathering of the carbonate rocks in the watershed, and lower pH (Engstrom et al. 2000). Total organic carbon would proportionally increase with lake age because of the increase in primary production. The carbon chemistry does not reflect eutrophication of the lake.

Based on top-down control of the food web, we would expect to see a decrease in primary production related to the presence of piscivorous fish in the lake which depress the primary consumer populations through the trophic cascade (Shapiro 1980, Carpenter et al. 1985, Leibold 1989, Jeppesen et al. 1997). However, several researchers have found that there is a decoupling of the trophic cascade in oligotrophic lakes, with effects of fish predation on planktivores and zooplankton not cascading to the phytoplankton (McQueen et al. 1986, Currie et al. 1990, Jeppesen et al. 2001). In Fog Lake 3 we see no decrease in the total organic carbon concentration. Increased chironomid biomass or production (associated with the presence of piscivorous fish) might be assumed to decrease the amount of benthic carbon by reduction of benthic algal biomass through top-down control of the food web, as has been shown in studies of snails in littoral habitats (Brömark et al. 1992, Martin et al. 1992, Brömark 1994, Walker McCollum et al. 1998). No studies, however, have shown the effects of predatory fish cascading down to the benthic primary producers through chironomids. Conversely, benthic organic carbon may exert bottom-up control on the chironomid community (Hirabayashi and Wotton 1999, Vos et al. 2002). Neither chironomid biomass nor production was calculated as

part of this study, so the effect of changes in fish community structure are not obvious by looking at the organic carbon content of the sediments. Additionally, there may be a decoupling of the food web between primary consumers and their food source, resulting in no change in total organic carbon in the sediments as related to interactions with higher trophic levels. This decoupling may be the result of nutrient limitation being stronger than the effects of low grazing on primary producers.

The increased organic carbon content of the sediments in the upper zone of the core also could reflect decreased dilution of nutrients related to a decrease in residence time of water in the lake (Whiteside 1983). With a new outlet and larger watershed area (due to lower lake level) and assuming that all inputs and outputs of water in Fog Lake 3 remain equal, the residence time of water in the lake would decrease, resulting in a decrease in nutrient dilution. If summer temperatures in the vicinity of Fog Lake 3 were to decrease, the active layer of the permafrost would become smaller, reducing the amount of water available in the catchment, which would also reduce lake volume (Young 1994).

The zonation of the core based on the cluster analysis of the chironomid community assemblage correlates well with the zonation based on the cluster analysis of the grain size analysis of the core. *Heterotrissocladius* sp. and *Tanystarsus* spp. were the only two taxa showing significant differences between Zones 1 and 2.

Heterotrissocladius is associated with very cold waters and the earliest development of lakes. It is often used as an indicator of climatic change, being more abundant in colder climates. Used as an indicator of deglaciation in north temperate lakes, the relative abundance of *Heterotrissocladius* typically declines sharply with deglaciation (Walker et

al. 1991). *Heterotrissocladius* showed the opposite trend, being less abundant in the time period directly following deglaciation and increasing in abundance through time.

In a comparison of lakes above and below tree line in subarctic Sweden, Larocque et al. (2001), found that *Tanytarsus* was only found at warmer, forested sites, while other taxa (including *Abiskomyia*, *Diamesa*, *Corynoneura*, and *Heterotrissocladius*) were indicative of colder, more oligotrophic lakes. Korhola et al. (2000) found that variance in chironomid communities in subarctic Fennoscandian lakes could best be described by sediment organic content, water temperature, and maximum lake depth, with *Heterotrissocladius* found in the deepest, coldest lakes.

The oldest part of the Fog Lake core is dominated by Tanytarsini. At the time the lake formed, about 9500 ybp, the North Slope was undergoing a period of warmer than present temperatures. By 6000-4000 years ago, the arctic reached modern climatic conditions (Brubaker et al. 1995, Anderson et al. 2001). There was a shift in chironomid community structure from Tanytarsini to taxa that are more indicative of older, deeper lakes, including *Stictochironomus* and *Heterotrissocladius*. It appears that the chironomid community of Fog Lake 3 may be responding to this cooling climate since the formation of the lake.

Tanytarsus sp. is often used as an indicator of an oxygen-rich hypolimneon in temperate lakes (Hoffman 1988). Fog Lake 3 has significantly more *Tanytarsus* in the lower zone than the upper zone. It should not be assumed, however, that this is the result of eutrophication of the lake. Hoffman (1988) warns against using *Tanytarsus* to determine trophic state of lakes, as they are found in both eutrophic and oligotrophic waters. This is true in the Fog Lake 3 core as well, since other taxa indicative of

oligotrophy (Saether 1975) (*Heterotrissocladius*, *Protanypus*, *Monodiamesa*) are found throughout the lake core.

Hofmann (1998) used the chironomid community of the Belauer See, Germany, to infer lake level changes in sediment cores. He found a shift from sublittoral taxa (*Tanytarsus*) to upper littoral taxa (*Limnophyes*, *Microspectra*, *Pentaneurini*, and *Polypedilum*) and *Chironomus* corresponding to water level lowering. In Fog Lake 3 there is not as dramatic a change in the community composition, as *Tanytarsus* never disappears from the core, although its relative abundance decreases at the top of the core. There is a trend of increasing richness in the upper part of the core, including the increase in relative abundance of littoral zone chironomids (*Polypedilum*, *Chironomus*, and *Abiskomyia*). Because the area of Fog Lake 3 is small, it is possible that changes in lake volume would not change the community composition as profoundly as Hoffman found, or that the part of the lake sampled by the core was profundal throughout the lake history.

The change in the Shannon Diversity of the chironomid community can not be explained by climate dynamics. It would be expected that the highest diversity would be during the warmer period. However, the Shannon-Wiener diversity index of the lake is significantly higher in the upper zone of the core, which was deposited after the warmer climatic period in the lake's early history (Brubaker et al. 1995). Thus, some factor or factors other than climate appeared to be regulating the chironomid community diversity.

Hershey et al. (1999) found that lake-trout dominated-lakes, which may be similar to arctic char/slimy sculpin lakes, have higher chironomid density, biomass, species richness, and H' than present day fishless lakes. McDonald and Hershey (1992) and Hanson et al. (1992) found that in lake trout/slimy sculpin lakes, the trout determine the

distribution of the sculpin by forcing the sculpin into the near shore habitat, where risk of predation is low (McDonald and Hershey 1989). The sculpin, in turn, control the abundance, biomass and diversity of chironomid larvae on the bare substrate (Hershey 1985, Goyke and Hershey 1992). In addition, the chironomid community diversity increases in each subsequent zone of the core. Increased chironomid diversity would also reflect increased organic matter input to the lake.

Presumably Fog Lake 3 was fishless when it formed. Fish would not have been able to enter the lake until a drainage pattern was established that provided access (low gradient streams, connected to streams used by the fish). Once a passage to the lake was established anadromous char may have used the lake freely as an overwintering site until the drainage pattern of the lake changed, restricting movement into and out of the lake. During the period of free char movement into and out of the lake, adult char would have been residents for part of the year, while juveniles would not migrate out of the lake for the first time until the age of 3-7 years (Klemetsen et al. 2003).

Based on the evidence in the chironomid community diversity, changes that are best explain the initial presence of fish in Fog Lake 3 occur between 94.25 cm and 105.25 cm depth. If we use the known date of the core at 100.25 cm and sedimentation rates based on other radiocarbon dates (Table 7) we can date the boundary of diversity change, and presumably arrival of fish in the lake, between 7973 ± 50 ^{14}C YBP and 7344 ± 45 ^{14}C YBP.

Based on grain size analysis data (Tables 2 and 3) changes in sediment characteristics occurred between the depths of 95 cm and 101 cm. Using the same interpolation technique described above for the chironomid diversity, the age of the

boundary layer for outlet change occurred between 7707 ± 50 ^{14}C YBP and 7384 ± 45 ^{14}C YBP. Because the cluster analysis does not show a strong grouping of the point at 89.5 cm in the grain size analysis (Figure 4) to either Zone 1 or 2, that point could be included in Zone 1. This would date the upper limit of Zone 1 at 7094 ± 45 ^{14}C YBP. The differences in the zones created by the CONISS analysis of the grain size characteristics are not as large as those between zones in the chironomid community cluster analysis based on the total sum of squares of both analyses (Figure 4 and Figure 6)

The chironomid community data show a trend of increasing diversity and relative abundance of *Heterotrissocladius* through time, indicating influences other than climate cooling are affecting the chironomid community composition. The significantly higher H' diversity of the chironomid community would be an expected result of increased predation pressure due to anadromous fish becoming landlocked. This increases the predation pressure on invertebrates, as adult char occupy the lake for the entire year. Based on the chironomid community cluster analysis, radiocarbon dates, and sedimentation rates calculated between 0 and 85.25 cm (Table 7), the best estimate of the time when the fish became land-locked due to loss of the low gradient outlet of Fog Lake 3 is between 4230 and 4600 ^{14}C YBP.

The evidence from the core suggests there have been major changes in the chironomid community composition in Fog Lake 3 since its formation about 9500 years before the present. These changes are likely a result of a combination of lake succession, climate dynamics, and changes in fish community structure.

Literature Cited

- Amsinch, S. L., E. Jeppesen, and D. Ryves. 2003. Cladoceran stratigraphy in two shallow brackish lakes with special reference to changes in salinity, macrophyte abundance and fish predation. *Journal of Paleolimnology* 29:495-507.
- Armitage, P. C., P. S. Cranston, and L. C. V. Pinder. 1995. *The Chironomidae*. Chapman and Hall, New York.
- Bahr, M., B. Bowden, L. Gough, A. Hershey, J. E. Hobbie, G. W. Kling, M. McDonald, W. J. O'Brien, P. Rublee, G. Shaver, and M. Walker. Biodiversity at the ARC long-term ecological research site. www.vcrlter.virginia.edu/LTER_biod/arc.html
- Battarbee, R. W. 2000. Palaeolimnological approaches to climate change, with special regard to the biological record. *Quaternary Science Review* 19:107-124.
- Bengtsson L. and M. Enell. 1986. Chemical analysis. Pages 423-451 *in* B. E. Berglund (editor). *Handbook of Holocene Palaeoecology and Palaeohydrology*. John Wiley and Sons Ltd., New York, NY.
- Birks, H. J. B. and H. H. Birks. 1980. *Quaternary Palaeoecology*. University Park Press, Baltimore.
- Borror, D. J., C. A. Triplehorn and N. F. Johnson. 1989. *An Introduction to the Study of Insects*. Sixth edition. Saunders College Publishing: Austin.
- Brönmark, C. 1994. Effects of tench and perch on interactions in a freshwater, benthic food chain. *Ecology* 75:1818-1824.
- Brönmark, C., S. P. Klosiewski, and R. A. Stein. 1992. Indirect effects of predation in a freshwater, benthic food chain. *Ecology* 73:1662-1674.
- Brooks, S. J. and H. J. B. Birks. 2000. Chironomid-inferred late-glacial and early-Holocene mean July air temperatures for Krakenes Lake, western Norway. *Journal of Paleoclimate* 23:77-89.
- Brubaker, L. B., P. M. Anderson, and F. S. Hu. 1995. Arctic Tundra Biodiversity: A Temporal Perspective from Late Quaternary Pollen Records in F. S. Chapin and C. Körner, (eds). *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*. Springer-Verlag, New York, NY.
- Brundin, L. 1958. The bottom faunistic lake type system and its application to the southern hemisphere. Moreover a theory of glacial erosion as a factor of productivity in lakes and oceans. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 13:288-297.

- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading Trophic Interactions and Lake Productivity. *Bioscience* 35(10):634-639.
- Cranston, P. S., D. R. Oliver and O. A. Saether. 1983. The larvae of Orthocladiinae (Diptera: Chironomidae) of the Holarctic region-Keys and diagnoses. *Ent. Scand. Suppl.* 19:149-291.
- Currie, D. J., P. Dilworth-Christie, and F. Chapleau. 1990. Assessing the strength of top-down influences on plankton abundance in unmanipulated lakes. *Canadian Journal of Fisheries and Aquatic Science* 56:427-436.
- Cwynar, L. C. and A. J. Levesque. 1995. Chironomid evidence for late-glacial climatic reversals in Maine. *Quaternary Research* 43:405-413.
- Dahl, J. 1998. Effects of a benthivorous and a drift-feeding fish on a benthic stream assemblage. *Oecologia* 116:426-432.
- Davies, L. J. and H. A. Hawkes. 1981. Some effects of organic pollution on the distribution and seasonal incidence of Chironomidae in riffles in the River Cole. *Freshwater Biology* 11:549-59.
- Dean, W. E. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *Journal of Sedimentary Petrology* 44:242-248.
- Digerfeldt, G. 1986. Studies on past lake-level fluctuations. Pages 127-143 in B. E. Berglund (editor). *Handbook of Holocene Palaeoecology and Paleohydrology*. John Wiley and Sons Ltd., New York, NY.
- Easterbrook, D. J. 1993. *Surface Processes and Landforms*. Macmillan, New York.
- Engstrom, D. R., S. C. Fritz, J. E. Almendinger, and S. Juggins. 2000. Chemical and biological trends during lake evolution in recently deglaciated terrain. *Nature* 408:161-166.
- Epler, J. H. 1995. Identification manual of the larval Chironomidae (Diptera) of Florida, revised edition. Florida Department of Environmental Protection.
- Finney, B. P., I. Gregory-Eaves, J. Sweetman, M. S. V. Douglas, and J. P. Smol. 2000. Impacts of Climatic Change and Fishing on Pacific Salmon Abundance Over the Past 300 Years. *Science* 290:795-799.
- Ferrians, O. J. 1994. Permafrost in Alaska. Pages 845-854 in G. Plafker and H. C. Berg, (editors). *The Geology of Alaska*. The Geology of North America, v. G-1. Geologic Society of America, Boulder, CO.

- Fittkau, E. J. and S. S. Roback. 1983. The larvae of Tanypodinae (Diptera: Chironomidae) of the Holarctic region—Keys and Diagnoses. *Ent. Scand. Suppl.* 19:22-110.
- Folk, R. L. 1974. *Petrology of Sedimentary Rocks*. Hemphill Publishing Company, Austin.
- Francis, D. R. 2001. A record of hypolimnetic oxygen conditions in a temperate multi-depression lake from chemical evidence and chironomid remains. *Journal of Paleolimnology* 25:351-365.
- Goyke, A. P. and A. E. Hershey. 1992. Effects of fish predation on larval chironomid (Diptera: Chironomidae) communities in an arctic ecosystem. *Hydrobiologia* 240:203-211.
- Grimm, E. 1987. CONISS: A fortran 77 program for the stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & Geosciences* 13(1):13-35.
- Hanson, K. L., A. E. Hershey, and M. E. McDonald. 1992. A comparison of slimy sculpin (*Cottus cognatus*) populations in arctic lakes with and without piscivorous predators. *Hydrobiologia* 240:189-201.
- Hamilton, T. D. 1978. *Surficial Geologic Map of the Phillip Smith Mountains Quadrangle, Alaska*. Department of the Interior Miscellaneous Field Studies Map MF-879A.
- Hamilton, T. D. 1982. A late Pleistocene glacial chronology for the southern Brooks Range: Stratigraphic record and regional significance. *Geological Society of America Bulletin* 93:700-716.
- Hamilton, T. D. 1986. Late Cenozoic glaciation of the central Brooks Range. Pages 9-49 in Hamilton, T.D., Reed, K.M., and Thorson, R.M. (editors.). *Glaciation in Alaska—The Geological Record*. Alaska Geological Society, Anchorage, AK.
- Hamilton, T. D. 1994. Lake Cenozoic glaciation on Alaska. Pages 813-844 in Plafker, G. and Berg, H.C. (editors). *The Geology of Alaska*. Geological Society of America, Boulder, CO.
- Hamilton, T. D., 2002. *Glacial Geology of Toolik Lake and the Upper Kuparuk River Region*. Biological Papers of the University of Alaska, Institute of Arctic Biology, Fairbanks, AK.
- Hamilton, T. D. and S. C. Porter. 1975: Itkillik glaciation in the Brooks Range, northern Alaska. *Quaternary Research* 5:471-497.

- Hauer, F. R. and V. H. Resh. 1996. Benthic Macroinvertebrates. Page 351 in F. R. Hauer and G. A. Lamberti (editors.). *Methods in Stream Ecology*. Academic Press, Boston, MA.
- Hershey, A. E. 1985a. Effects of Predatory Sculpin on the Chironomid Communities in an Arctic Lake. *Ecology* 66(4):1131-1138.
- Hershey, A. E. 1985b. Littoral chironomid communities in an arctic Alaskan lake. *Holarctic Ecology* 8:39-48.
- Hershey, A. E. 1992. Effects of experimental fertilization on the benthic macroinvertebrate community of an arctic lake. *Journal of the North American Benthological Society* 11:204-217.
- Hershey, A. E., G. M. Gettel, M. E. McDonald, M. C. Miller, H. Mooers, W. J. O'Brien, J. Pastor, C. Richards and J. A. Schuldt. 1999. A Geomorphic-Trophic Model for Landscape Control of Arctic Lake Food Webs. *Bioscience* 49:887-897.
- Hirabayashi, K. and R. Wotten. 1999. Organic matter processing by chironomid larvae (Diptera: Chironomidae). *Hydrobiologia* 382:151-159.
- Hocutt, C.H. and E. O. Wiley (eds). 1986. *The zoogeography of North American freshwater fishes*. John Wiley and Sons, New York, New York.
- Hofmann, W. 1986. Chironomid analysis. Pages 715-727 in B. E. Berglund (editor). *Handbook on Holocene Palaeoecology and Palaeohydrology*. Wiley, Chichester, UK.
- Hofmann, W. 1988. The significance of chironomid analysis (Insecta; Diptera) for paleolimnological research. *Palaeogeography, Palaeoclimatology, Palaeoecology* 62:501-509.
- Hofmann, W. 1998. Cladocerans and chironomids as indicators of lake level changes in north temperate lakes. *Journal of Paleolimnology* 19:55-62.
- Hofmann, W. 2001. Late-Glacial/Holocene succession of the chironomid and cladoceran fauna of the Soppensee (Central Switzerland). *Journal of Paleolimnology* 25:411-420.
- Ilyashuk, B. P. and E. A. Ilyashuk. 2001. Response of alpine chironomid communities (Lake Chuna, Kola Peninsula, northwestern Russia) to atmospheric contamination. *Journal of Paleolimnology* 25:465-475.
- Jeppesen, E., J. P. Jensen, S. Amsinck, F. Landkildehus, T. Lauridsen, and S. F. Mitchell. 2002. Reconstruction the historical changes in *Daphnia* mean size and

- planktivorous fish abundance in lakes from the size of *Daphnia ephippia* in the sediment. *Journal of Paleolimnology* 27:133-143
- Jeppesen, E., J. P. Jensen, M. Søndergaard, T. L. Lauridsen, L. J. Pedersen, and L. Jensen. 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* 342/343:151-164.
- Jeppesen, E., K. Christoffersen, F. Lankildehus, T. Lauridsen, S. L. Amsinck, F. Riget, and M. Søndergaard. 2001. Fish and crustaceans in northeast Greenland lakes with special emphasis on interactions between Arctic charr (*Salvelinus alpinus*), *Lepidurus arcticus* and benthic chydorids. *Hydrobiologia* 442:329-337.
- Johnson, L. 1980. The arctic char, *Salvelinus alpinus*. Pages 15-98 in E. K. Balon (editor). *Charrs, Salmonid Fishes of the Genus Salvelinus*. Dr. W. Junk Publishers, The Hague, Netherlands.
- Jones, V. J. and S. Juggins. 1995. The construction of a diatom-based chlorophyll *a* transfer function and its application at three lakes on Signey Island (maritime Antarctic) subject to differing degrees of nutrient enrichment. *Freshwater Biology* 34:433-445.
- Kerfoot, W. C. 1974. Net accumulation rates and the history of cladoceran communities. *Ecology* 55:51-61.
- Kerfoot, W.C. 1981. Long-term replacement cycles in cladoceran communities: a history of predation. *Ecology* 62:216-233.
- Kingston, J. C., H. J. B. Birks, A. J. Uutala, B. F. Cumming, and J. P. Smol. 1992. Assessing trends in fishery resources and lake water aluminum from paleolimnological analyses of siliceous algae. *Canadian Journal of Fisheries and Aquatic Science* 49:116-127.
- Kitchell, J. A. and J. F. Kitchell. 1980. Size-selected predation, light transmission, and oxygen stratification: Evidence from the recent sediments of manipulated lakes. *Limnology and Oceanography* 25:389-402.
- Klemetsen, A., P. A. Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. F. O'Connell, and E. Mortensen. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of freshwater fishes* 12:1-59.
- Lamontagne, S. and D. W. Schindler. 1994. Historical status of fish populations in Canadian Rocky Mountain lakes inferred from subfossil *Chaoborus* (Diptera: Chaoboridae) mandibles. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1376-1383.

- Larocque, L., R. I. Hall, and E. Grahn. 2001. Chironomids as indicators of climate change: a 100-lake training set from a subarctic region of northern Sweden (Lapland). *Journal of Paleolimnology* 26:307-322.
- Leavitt, P. R., S. R. Carpenter, and J. F. Kitchell. 1989. Whole-lake experiments: The annual record of fossil pigments and zooplankton. *Limnology and Oceanography* 34:700-717.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* 134:922-949.
- Little, J. and J. P. Smol. 2001. A chironomid-based model for inferring late-summer hypolimnetic oxygen in southeastern Ontario lakes. *Journal of Paleolimnology* 26:259-279.
- Livingstone, D. A. 1955. A lightweight piston sampler for lake deposits. *Ecology* 36: 137-139.
- Lotter, A. F., H. J. B. Birks, W. Hofmann, and A. Marchetto. 1997. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I: Climate. *Journal of Paleolimnology* 18:395-420.
- Mackin, J. H. 1936. Capture of the Greybull River. *American Journal of Science* 31:813-893.
- Martin, T. H., I. B. Crowder, C. F. Dumas, and J. M. Burkholder. 1992. Indirect effects of fish on macrophytes in Bays Mountain Lake: evidence for a littoral trophic cascade. *Oecologia* 89:476-481.
- Mayden, R.L. 1988. Vicariance biogeography, parsimony, and evolution in North American freshwater fishes. *Systematic Zoology* 37:329-355.
- McDonald, M. E. and A. E. Hershey. 1989. Size structure of a lake trout (*Salvelinus namaycush*) populations in an Arctic lake: influence of angling and implications for fish community structure. *Canadian Journal of Fisheries and Aquatic Science* 46:2153-2156.
- McDonald, M. E. and A. E. Hershey. 1992. Shifts in abundance and growth of slimy sculpin in response to changes in the predator population in an arctic Alaskan lake. *Hydrobiologia* 240:219-223.
- McQueen, D. J., J. R. Post, and E. L. Mills. 1989. Trophic relationships in freshwater pelagic ecosystems. *Canadian Journal of Fisheries and Aquatic Science* 43:1571-1581.

- Meriläinen, J. J., J. Hynynen, A. Teppo, A. Palomäki, K. Granberg, and P. Reinikainen. 2000. Importance of diffuse nutrient loading and lake level changes to the eutrophication of an originally oligotrophic boreal lake: a palaeolimnological diatom and chironomid analysis. *Journal of Paleolimnology* 24:251-270.
- Merrick, G. W., A. E. Hershey, and M. E. McDonald. 1992. Salmonid diet and the distribution, size, and density on invertebrates in an arctic lake. *Hydrobiologia* 240:225-233.
- Merritt, R. W. and K. W. Cummins. 1996. *An Introduction to the Aquatic Insects of North America*. Third edition. Kendall/Hunt Publishing Company. Dubuque, Iowa.
- Meyers, P. A. and R. Ishiwatari. 1995. Organic matter accumulation records in lake sediments. Pages 279-328 *in* A. Lerman, S. Imboden, and J. Gat (editors). *Physics and Chemistry of Lakes* (2nd edition). Springer Verlag, Berlin.
- Meyers, P. A. and J. L. Teranes. 2002. Sediment organic matter. Pages 229-269 *in* W. M. Last and J. P. Smol (eds). *Tracking Environmental Change Using Lake Sediments. Volume 2: Physical and Geochemical Methods*. Kluwer Academic Publishers, Boston, MA.
- Miskimmin, B. M. and D. W. Schindler. 1994. Long-term invertebrate community response to toxaphene treatment in two lakes: 50-yr records reconstructed from lake sediments. *Canadian Journal of Fisheries and Aquatic Sciences* 51:923-932.
- Olander, H., A. Korhola, and T. Blom. 1997. Surface sediment Chironomidae (Insecta: Diptera) distributions along an ecotonal transect in subarctic Fennoscandia: developing a tool for palaeotemperature reconstructions. *Journal of Paleolimnology* 18:45-59.
- Olander, H., H. J. B. Birks, A. Korhola, and T. Blom. 1999. An expanded calibration model for inferring lake water and air temperatures from fossil chironomid assemblages in northern Fennoscandia. *The Holocene* 9:279-294.
- Oliver, D. R. 1971. Life history of Chironomidae. *Annual Rev. Ent.* 16:211-230.
- Palmer, S., I. Walker, M. Heinrichs, R. Hebda, and G. Scudder. 2002. Postglacial midge community change and Holocene palaeotemperature reconstructions near treeline, southern British Columbia (Canada). *Journal of Paleolimnology* 28:469-490.
- Parker, H. H. and L. Johnson. 1991. Population structure, ecological segregation and reproduction in non-anadromous Arctic charr, *Salvelinus alpinus* (L), in four unexploited lakes in the Canadian high Arctic. *Journal of Fish Biology* 38:123-147.

- Pielou, E. C. 1991. *After the Ice Age: The return of life to glaciated North America*. The University of Chicago Press, Chicago, Illinois.
- Pinder, L. C. V. 1986. Biology of freshwater Chironomidae. *Ann Rev. Ent.* 31:1-23.
- Pinder, L. C. V. 1995. The habitats of chironomid larvae. Pages 107-133 *in* P. C. Armitage, P.S. Cranston, and L.C.V. Pinder (editors). *The Chironomidae*. Chapman and Hall, New York.
- Pinder, L. C. V. and I. S. Farr. 1987. Biological surveillance of water quality-3. The influence of organic matter enrichment on the macroinvertebrate fauna of small chalk streams. *Archiv fur Hydrobiologie* 109:619-637.
- Pinder, L. C. V. and F. Reiss. 1983. The larvae of Chironominae (Diptera: Chironomidae) of the Holarctic region-Keys and diagnoses. *Ent. Scand. Suppl.* 19:293-435.
- Porinchu, D. F. and L. Cwynar. 2002. Late-Quaternary history of midge communities and climate from a tundra site near the lower Lena River, Northeast Siberia. *Journal of Paleolimnology* 27:59-69.
- Power, G. Charrs, glaciations and seasonal ice. *Environmental Biology of Fishes* 64:17-35.
- Quinlan, R., J. P. Smol, and R. I. Hall. 1998. Quantitative inferences of past hypolimnetic anoxia in south-central Ontario lakes using fossil midges (Diptera: Chironomidae). *Canadian Journal of Fisheries and Aquatic Science* 55:587-596.
- Reist, J. D., T. D. Johnson, and T. J. Carmichael. 1997. Variation and specific identity of char from northwestern Arctic Canada and Alaska. *American Fisheries Society Symposium* 19:250-261.
- Reynolds, J. B. 1997. Ecology of overwintering fishes in Alaskan Freshwaters. Pages 281-302 *in* A. M. Milner and M. W. Oswood (editors). *Freshwaters of Alaska*, Springer, New York, NY.
- Saether, O. A. 1975. Nearctic chironomids as indicators of lake typology. *Verh. Internat. Verein. Limnol.* 19:3127-3133.
- Saether, O. A. 1979. Chironomid communities as water quality indicators. *Holarctic Ecology* 2:65-74.
- Schakau, B. 1986. Preliminary study of the development of the subfossil chironomid fauna (Diptera) of Lake Taylor, South Island, New Zealand, during the younger Holocene. *Hydrobiologia* 143:287-291.

- Schindler, D. W. 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. *Limnology and Oceanography* 23(3):478-486.
- Schneider, R. J. 2000. Data Report #00-080. National Ocean Sciences AMS Facility. Woods Hole Oceanographic Institution. Woods Hole, MA.
- Sharpiro, J. 1980. The importance of Trophic-Level Interactions to the Abundance and Species Composition of Algae in Lakes in Hypertrophic Ecosystems SIL Workshop on Hypertrophic ecosystems held at Vaxjo, September 10-14, 1979, Barcia, J and LR Mur, eds. Dr. W. Junk BV Publishers, The Hague.
- Sun, L., Z. Xie, and J. Zhao. 2000. A 3,000 year record of penguin populations. *Nature* 405:858.
- Sweetman, J. N. and B. P. Finney. 2003. Differential responses of zooplankton populations (*Bosmina longirostris*) to fish predation and nutrient-loading in an introduced and a natural sockeye salmon nursery lake on Kodiak Island, Alaska, USA. *Journal of Paleolimnology* 30:183-193.
- Uutala, A. J. 1990. *Chaoborus* (Diptera: Chaoboridae) mandibles-paleolimnological indicators of historical status of fish populations in acid-sensitive lakes. *Journal of Paleolimnology* 4:139-151.
- Uutala, A. J. and J. P. Smol. 1996. Paleolimnological reconstructions of long-term changes in fisheries status in Sudbury area lakes. *Canadian Journal of Fisheries and Aquatic Science* 53:174-180.
- Uutala, A. J., N. D. Yan, A. S. Dixit, S. S. Dixit, and J. P. Smol. 1994. Paleolimnological assessment to damage to fish communities in three acidic, Canadian Shield lakes. *Fisheries Research* 19:157-177.
- Vos, J. H., P. J. Van Den Brink, F. P. Van Den Ende, M. A. G. Ooijevaar, A. J. P. Oosthoek, J. F. Postma, and W. Admiraal. 2002. Growth response of a benthic detritivore to organic matter composition in sediments. *Journal of the North American Benthological Society* 21:443-456.
- Walker, I. R. 2001. Midges: Chironomidae and related Diptera. Pages 43-66 in J. P. Smol, H. J. B. Birks, and W. M. last (eds). *Tracking Environmental Change Using Lake Sediments. Volume 4: Zoological Indicators*. Kluwer Academic Publishers, Boston, MA.
- Walker, I. R. and C. G. Paterson. 1983. Post-glacial chironomid succession in two small, humic lakes in the New Brunswick-Nova Scotia (Canada) border area. *Freshwater Invertebrate Biology* 2:61-80.

- Walker, I. R., C. H. Fernando, and C. G. Paterson. 1985. Associations of Chironomidae (Diptera) of shallow, acid, humic lakes and bog pools in Atlantic Canada, and a comparison with an earlier paleoecological investigation. *Hydrobiologia* 120:11-22.
- Walker, I. R., J. P. Smol, D. R. Engstrom, and H. J. B. Birks. 1991. An assessment of Chironomidae as quantitative indicators of past climatic change. *Canadian Journal of Fisheries and Aquatic Sciences* 48:975-987.
- Walker, I. R., A. J. Levesque, L. C. Cwynar, and A. F. Lotter. 1997. An expanded surface-water palaeotemperature inference model for use with fossil midges from eastern Canada. *Journal of Paleolimnology* 18:165-178.
- Walker McCollum, E., L. B. Crowder, and S. A. McCollum. 1998. Complex interactions of fish, snails, and littoral zone periphyton. *Ecology* 79:1980-1994.
- Whiteside, M. C. 1983. The mythical concept of eutrophication. *Hydrobiologia* 103:107-111.
- Wiederholm, T. 1983. Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. *Entomologica Scandinavica Supplement No. 19*.
- Wiederholm, R. 1984. Responses of aquatic insects to environmental pollution. Pages 508-557 in V. H. Resh and D. M. Rosenberg (editors). *The Ecology of Aquatic Insects*. Praeger Publishers, New York.
- Wiederholm, T. and L. Eriksson. 1977. Benthos of an acid lake. *Oikos* 29:261-267.
- Young, S. B. 1994. *To the arctic*. Wiley Popular Science, New York.

Table 1. Lithology of Sediments Retrieved from Fog Lake 3

Zone	Depth Interval (cm)	Description
2b	0-23.5	Organic rich, gyttia
	23.5-35.5	Light brown, organic silt
	35.5-54.5	Organic silt and clay
2a	54.5-70.0	Dark brown, organic silt
	70.0-87.5	Very dark brown, organic silt
	87.5-93	Irregular layer of light and dark gyttia
	93-93.5	Thin layer of clay
	93.5-103	Irregular layer of light and dark gyttia
1	103-104	Dark layer of silt with nodules
	104-107	Irregular layer of light and dark gyttia
	107-110.5	Dark layer of silt with nodules
	110.5-128.5	Irregular layer of light and dark gyttia

Table 2. Loss-on-ignition at 550 and 1000 °C data for the entire length of the core.

	LOI ₅₅₀	LOI ₁₀₀₀
range	3.2-4.9%	0.10-0.48%
mean	3.9	0.28
SD	0.003	0.0011

Table 3. Grain size analysis and loss-on-ignition data averaged for the three zones (± 1 SD). Zone 1 is data below 100 cm, zone 2a is data between 53-100 cm, and zone 2b is data above 53 cm.

	Zone 1	Zone 2a	Zone 2b
% sand	0.69 (1.37)	0.19(0.39)	0.65 (1.44)
% silt	88.26 (4.92)	91.66 (5.46)	91.57 (5.55)
% clay	11.06 (4.74)	8.15 (5.54)	7.78 (5.61)
Mean size (phi)	6.47 (0.64) ^{cd}	5.83 (0.23) ^c	5.91 (0.46) ^d
Sorting	1.65 (0.23)	1.66 (0.13)	1.71 (0.23)
% H ₂ O	65.29 (4.62) ^a	64.83 (3.22) ^b	70.76 (5.26) ^{ab}
% LOI _{550°C}	3.74 (0.39)	4.18 (0.41)	3.80 (0.20)
% LOI _{1000°C}	0.38 (0.06)	0.35 (0.03)	0.18 (0.06)

a and b, $p \leq 0.05$

c and d, $p \leq 0.10$

Mann-Whitney U-test

Table 4. Relative abundance and Shannon Diversity (H') for chironomid data averaged for the two zones (± 1 SD). Zone 1 is data below 100.25 cm. Zone 2 is data above 100.25 cm in depth.

	Zone 1	Zone 2
Chironomus	0.016 (± 0.016)	0.015 (± 0.092)
Corynoneura	0 (± 0)	0.026 (± 0.041)
Heterotrissocladius*	0.015 (± 0.016)	0.045 (± 0.026)
Parakiefferiella	0 (± 0)	0.007 (± 0.011)
Polypedilum	0.005 (± 0.009)	0.066 (± 0.205)
Procladius*	0 (± 0)	0.003 (± 0.041)
Tanytarsini**	0.843 (± 0.032)	0.615 (± 0.065)
Shannon Diversity**	0.968 (± 0.051)	1.680 (± 0.192)

* $p < 0.10$

** $p < 0.05$

Mann-Whitney U-test

Table 5. Relative abundance and Shannon Diversity (H') for chironomid data averaged for the three zones (± 1 SD). Zone 1 is data below 100.25 cm. Zone 2a is data between 53-100.25 cm and Zone 2b is data above 53 cm in depth.

	Zone 1	Zone 2a	Zone 2b
Chironomus	0.02 (0.02) ^a	0.04 (0.03)	0.05 (0.03) ^a
Corynoneura	0 (0)	0.02 (0.02)	0.03 (0.05)
Heterotrissocladius	0.02 (0.02) ^a	0.03 (0.02) ^c	0.06 (0.03) ^{ac}
Parakiefferiella	0 (0)	0.09 (0.01)	0.03 (0.01)
Polypedilum	0.01 (0.01)	0.00 (0.00)	0 (0)
Procladius	0 (0)	0.02 (0.01)	0.01 (0.01)
Tanytarsini	0.84 (0.03) ^{ab}	0.63 (.08) ^b	0.59 (0.03) ^a
Shannon Diversity	0.97 (0.05) ^{ab}	1.64 (0.26) ^b	1.75 (0.04) ^a

a and b, $p \leq 0.05$

c, $p \leq 0.10$

Mann-Whitney U-test

Table 6. Radiocarbon dates of organic matter from Fog Lake 3

Lab number	Depth (cm)	Material	Ages (¹⁴ C yr BP)	Accumulation Rate (cm/yr)
OS-24714	85-85.5	Sediment	6870 ±40	0.012
OS-24715	100.0-100.5	Sediment	7660 ±45	0.019
OS-24713	128.15-128.65	Sediment	9440 ±50	0.016

Lab-National Ocean Sciences AMS Facility, Woods Hole Oceanographic Institution

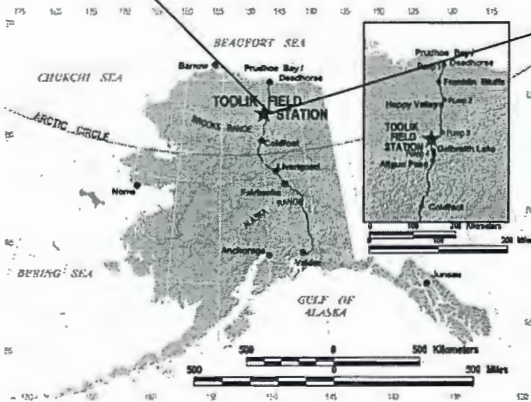
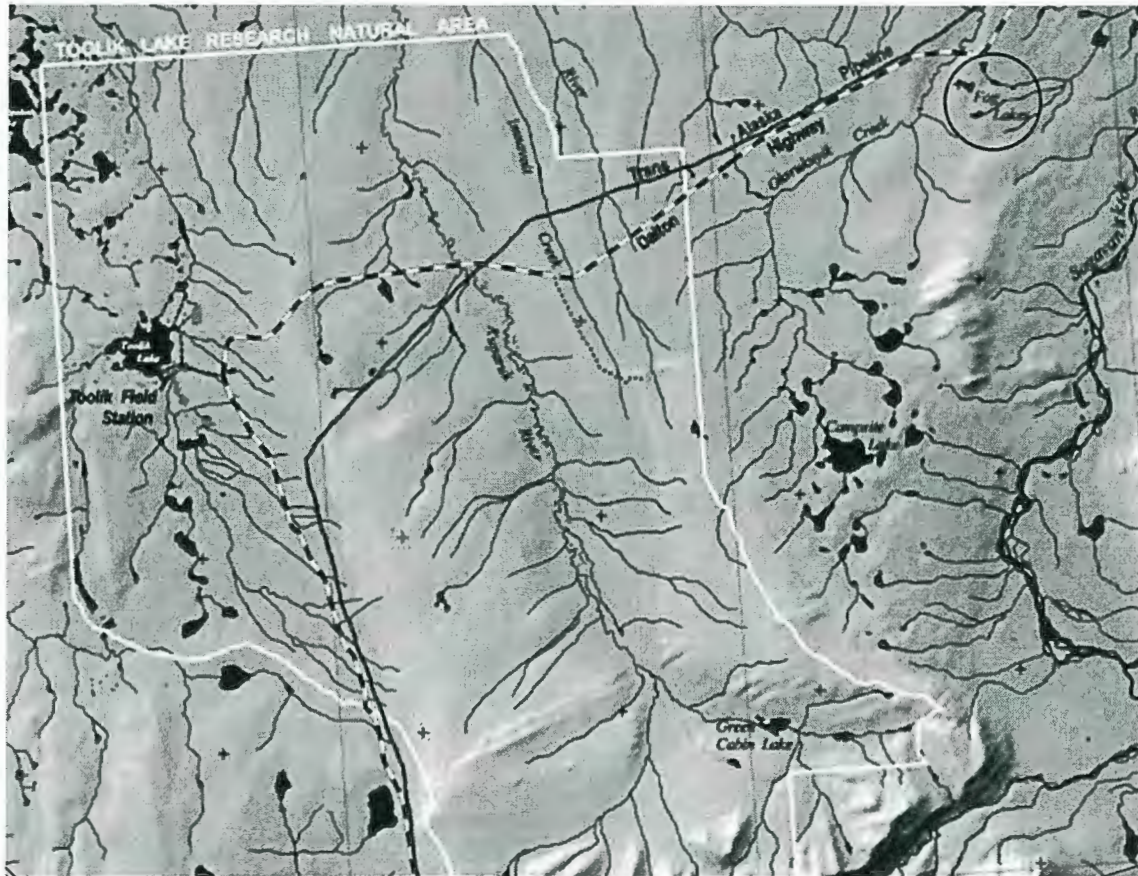


Figure 1. Location of Toolik Field Station in Alaska, with the inset showing the location of the Fog Lakes (enclosed in a circle in the upper right hand corner) relative to the Trans-Alaskan Pipeline (labeled as such), the Dalton Highway, depicted as a black and white line, and Toolik Lake Field Station. (From www.uaf.edu/toolik/maps/akmap.html).

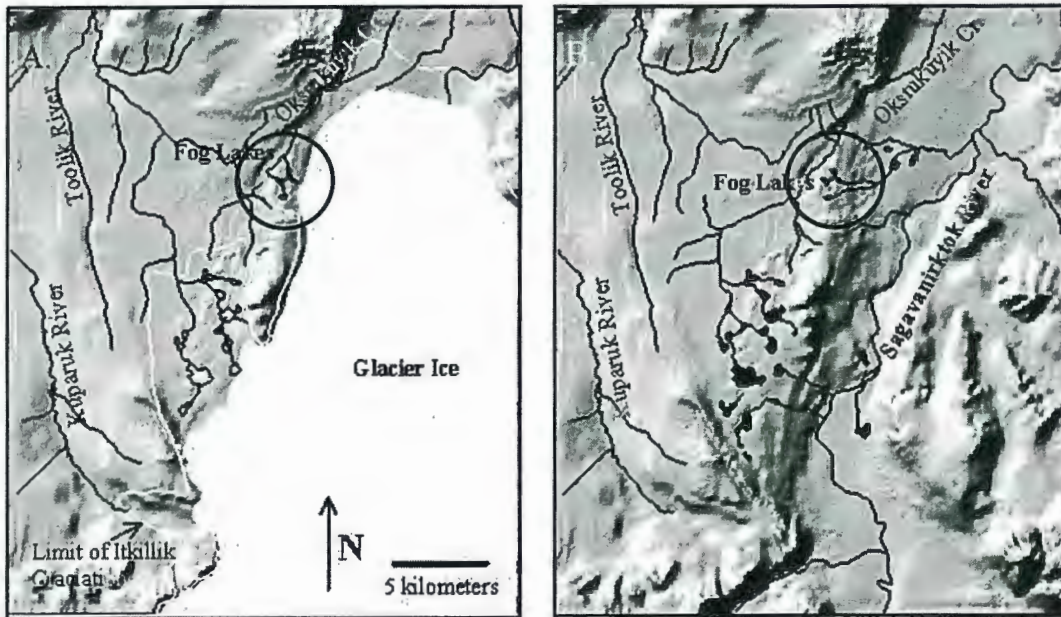


Figure 2: Position of glacial ice and the Fog Lakes during Itkillik glaciation (left panel) and after deglaciation (right panel). Note that the Sagavanirktok River fills the valley which the glacier retreated from in post-glacial times, with the Fog Lakes altering their drainage pattern. Fog Lake 3 is the southernmost of the three lakes enclosed in the circle. From <http://www.nrri.umn.edu/toolik/moers.html>.

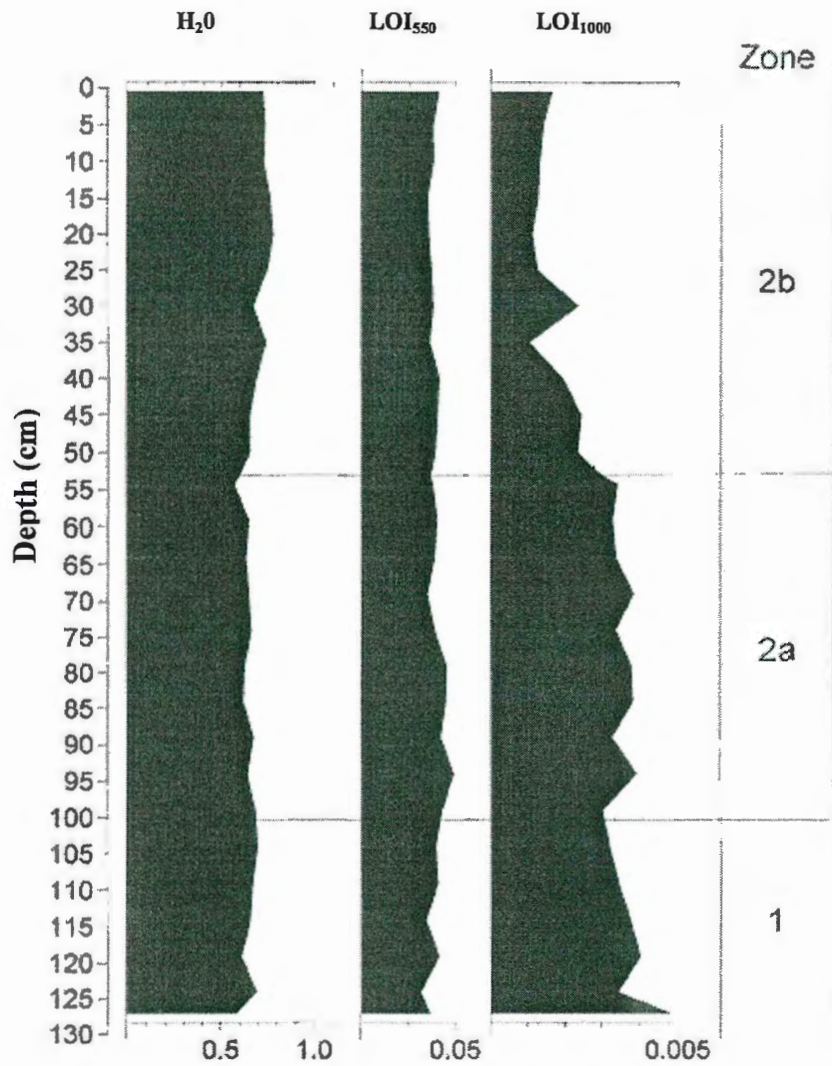


Figure 3: Proportion of water, dry mass lost at ignition at 550°C, and dry mass lost at 1000°C versus depth in the core. The zones are based on CONISS analysis of chironomid community.

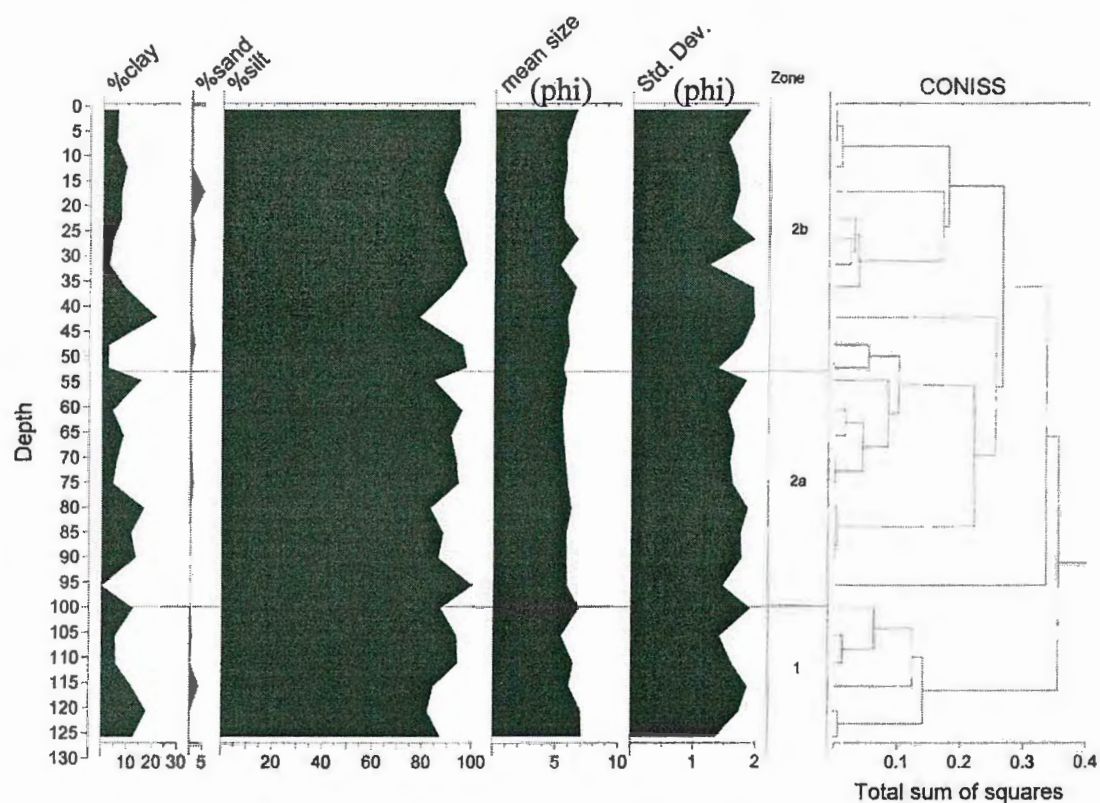


Figure 4: Results of grain size analysis versus depth. Units for mean size and standard deviation are phi. Standard deviation can be interpreted as sorting of sediment. Note the CONISS results and the boundary between the two major zones at approximately 97 cm depth. The zones are based on the chironomid community analysis.

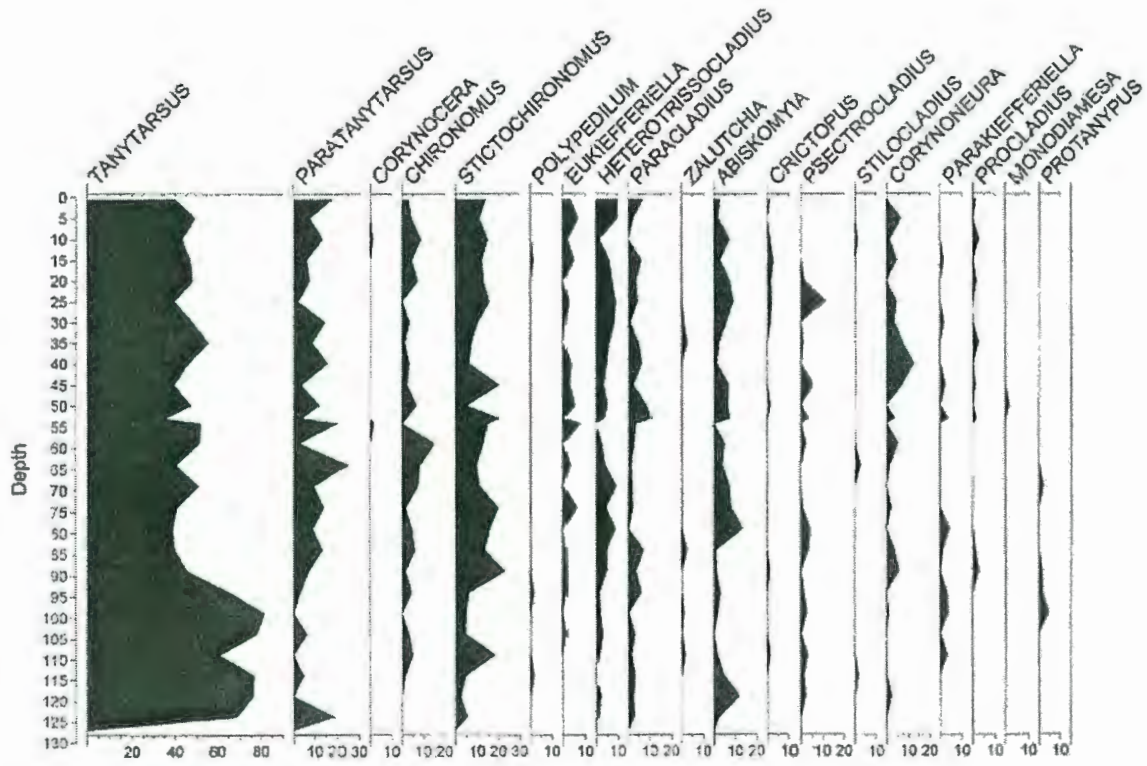


Figure 5: Percent relative abundance diagram for all taxa of Chironomidae in Fog Lake 3 core. Tanytarsus plot includes *Tanytarsus* and *Paratanytarsus* spp.

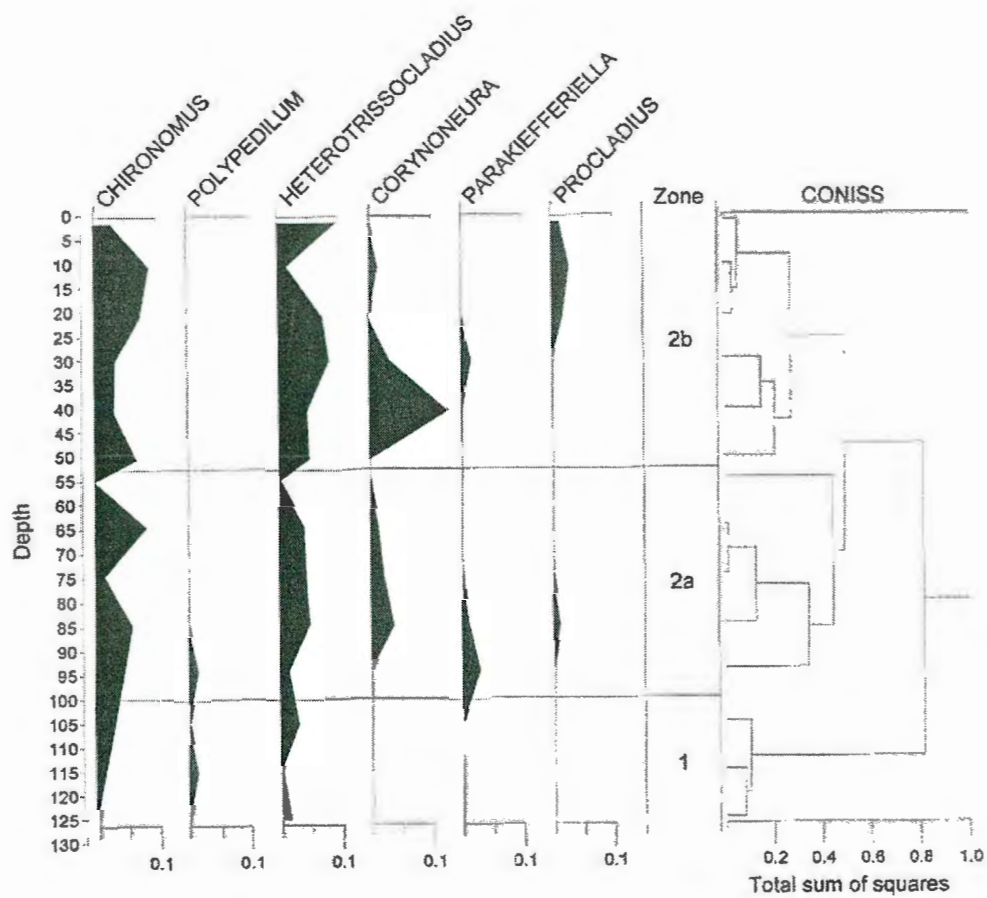


Figure 6: Relative abundance of Chironomidae Genera used to create zones in the core. Note the CONISS cluster analysis results, with the two major zones having a boundary around a depth of 100 cm and a second boundary separates Zone 2 around 53 cm depth.

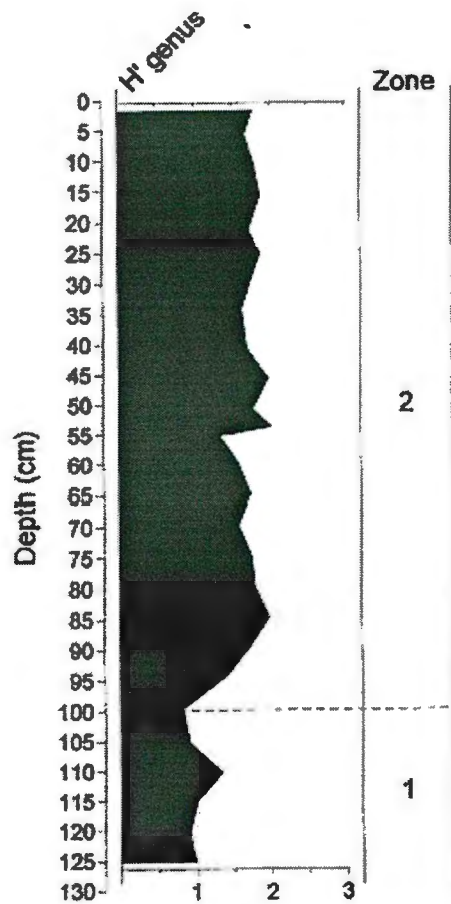


Figure 7: Shannon diversity (H') versus depth for Fog Lake 3 based on the chironomid community structure. The zones are delineated based on the chironomid community structure of taxa found to be significantly different in modern fishless versus char/sculpin lakes (Figure 6).

Appendix A. Results of Loss on Ignition Analyses for Fog Lake 3 lake sediment core.

Subsample depth (cm)	% water	%LOI ₅₅₀	%LOI ₁₀₀₀
0.5	72.6	4.1	0.2
5	73.5	3.8	0.1
10	72.9	3.8	0.1
15	76.2	3.5	0.1
20	77.8	3.6	0.1
25	74.6	3.7	0.1
30	67.2	3.8	0.2
35	74.2	3.6	0.1
40	68.8	4.1	0.2
45	65.6	4.0	0.2
50	65.5	3.9	0.2
53	60.1	3.7	0.3
54.25	57.1	3.8	0.3
59	64.9	4.0	0.3
64	63.2	3.9	0.3
69	64.8	3.5	0.4
74	66.4	3.9	0.3
79	62.6	4.5	0.4
84	61.8	4.4	0.4
89	67.4	4.2	0.3
94	64.0	4.9	0.4
99	68.4	4.3	0.3
104	69.7	4.0	0.3
109	67.2	4.1	0.3
114	65.9	3.4	0.4
119	61.1	4.1	0.4
124	69.4	3.2	0.3
127	58.3	3.7	0.5

Appendix B. Results of Grain Size Analysis for Fog Lake 3 lake sediment core.

Subsample depth (cm)	% clay	% sand	% silt	Mean Size (phi)	Standard Deviation (phi)	Skewness	Kurtosis
0.0-1.5	6.00	0.00	94.00	6.57	1.88	0.09	-1.72
6.5-8.0	5.52	0.00	94.48	5.73	1.54	1.06	-0.01
11.5-13.0	9.39	0.00	90.61	5.78	1.68	1.06	-0.22
16.5-18.0	7.34	4.86	87.80	5.47	1.72	0.75	0.40
22.0-23.5	7.35	0.00	92.65	5.55	1.60	1.35	0.49
26.0-27.5	4.13	1.27	94.61	6.67	1.97	-0.17	-1.64
31.0-32.5	2.72	0.00	97.28	5.28	1.25	1.68	2.11
35.5-37.0	8.97	0.00	91.03	6.56	1.94	0.14	-1.71
41.5-43.0	21.38	0.00	78.62	5.86	1.97	1.14	-0.41
47.0-48.5	2.64	1.67	95.69	6.03	1.78	0.19	-1.00
51.5-53.0	2.61	0.00	97.39	5.56	1.39	1.20	0.44
54.0-55.5	15.32	0.00	84.68	5.84	1.84	1.07	-0.37
60.0-61.5	4.25	0.00	95.75	5.47	1.55	1.40	0.53
65.0-66.5	8.57	0.00	91.43	5.58	1.66	1.31	0.31
70.0-71.5	5.91	0.48	93.61	5.77	1.59	0.81	-0.27
74.5-76.0	4.51	1.07	94.42	5.94	1.63	0.36	-0.45
79.5-81.0	16.70	0.00	83.30	6.23	1.87	0.66	-1.04
84.5-86.0	11.73	0.00	88.27	5.84	1.76	1.03	-0.35
89.5-91.0	13.50	0.00	86.50	5.86	1.77	1.06	-0.27
95.0-96.5	0.00	0.00	100.00	5.91	1.47	0.62	-1.07
99.5-101.0	12.60	0.00	87.40	6.86	1.92	-0.10	-1.61
105.0-106.5	5.48	0.68	93.83	5.44	1.42	1.39	1.48
110.2-112.0	5.71	0.00	94.29	6.39	1.63	0.35	-1.18
115.0-116.5	12.09	3.43	84.48	6.06	1.87	0.37	-0.46
120.0-121.5	17.90	0.00	82.10	7.01	1.74	0.02	-1.32
125.0-126.5	12.58	0.00	87.42	7.05	1.35	0.71	-1.50

Appendix C: Relative abundances of Chironomidae genera at each sub-sampling depth (cm).

	1.75	10.75	21.25	30.25	40.75	50.75	55.25	64.75	74.75
CORYNOCERA	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.00	0.00
CHIRONOMUS	0.03	0.09	0.07	0.03	0.03	0.07	0.00	0.08	0.01
STICTOCHIRONOMUS	0.14	0.15	0.13	0.10	0.06	0.05	0.15	0.10	0.20
POLYPEDILUM	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
EUKIEFFERIELLA	0.03	0.01	0.00	0.01	0.03	0.05	0.07	0.03	0.06
HETEROTRISSOCLADIUS	0.10	0.01	0.07	0.08	0.05	0.05	0.00	0.04	0.04
PARACLADIUS	0.07	0.00	0.04	0.01	0.06	0.08	0.04	0.01	0.02
ZALUTCHIA	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
ABISKOMYIA	0.03	0.07	0.07	0.06	0.02	0.07	0.00	0.04	0.08
CRICTOPUS	0.01	0.01	0.02	0.02	0.00	0.02	0.00	0.00	0.00
PSECTROCLADIUS	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.01
STILOCLADIUS	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.03	0.00
CORYNONEURA	0.00	0.01	0.00	0.03	0.13	0.00	0.00	0.01	0.02
PARAKIEFFERIELLA	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00
PROCLADIUS	0.01	0.03	0.02	0.00	0.00	0.00	0.00	0.00	0.00
MONODIAMESA	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00
PROTANYPUS	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

	84.75	94.25	105.25	115.25	125.25
CORYNOCERA	0.00	0.00	0.00	0.00	0.00
CHIRONOMUS	0.06	0.05	0.03	0.02	0.00
STICTOCHIRONOMUS	0.14	0.06	0.05	0.05	0.05
POLYPEDILUM	0.00	0.02	0.00	0.02	0.00
EUKIEFFERIELLA	0.01	0.02	0.02	0.00	0.00
HETEROTRISSOCLADIUS	0.05	0.02	0.03	0.00	0.01
PARACLADIUS	0.07	0.06	0.03	0.03	0.03
ZALUTCHIA	0.02	0.00	0.00	0.00	0.00
ABISKOMYIA	0.01	0.03	0.00	0.05	0.03
CRICTOPUS	0.00	0.00	0.00	0.00	0.00
PSECTROCLADIUS	0.04	0.02	0.00	0.02	0.00
STILOCLADIUS	0.00	0.00	0.00	0.02	0.00
CORYNONEURA	0.04	0.00	0.00	0.00	0.00
PARAKIEFFERIELLA	0.01	0.03	0.00	0.00	0.00
PROCLADIUS	0.01	0.00	0.00	0.00	0.00
MONODIAMESA	0.00	0.00	0.00	0.00	0.00
PROTANYPUS	0.00	0.02	0.00	0.00	0.00