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Distribution of Midge Remains (Diptera: Chironomidae) in Surficial Lake Sediments in New England

Donna R. Francis*

Abstract - A survey of larval midge remains from surficial sediments in 37 New England lakes was undertaken in order to relate midge distributions to environmental factors. The lakes are located along a transect from northern New Hampshire to southern Connecticut. The midges proved to be a very diverse group of insects in these freshwater habitats. A total of 65 chironomid taxa were recovered. Canonical correspondence analyses indicated that the environmental variables which best explain the distribution of chironomid taxa were mean July air temperature, percent sediment organic matter, pH, and lake depth. This knowledge about the relationship between midge distribution and mean July air temperature can be applied to midge assemblages preserved in older lacustrine sequences to improve our understanding of past environmental conditions in the region.

Introduction

In most freshwater habitats, the Chironomidae (Diptera: Nematocera) are usually the most abundant macroinvertebrate group, both in terms of number of species and number of individuals (Epler 2001). Although they are an extremely important and abundant group in freshwater ecosystems, there is still much work to be done in understanding their life histories, ecology, and the factors that determine species distributions. Chironomids are one of the most widely distributed insect groups in the world, occurring on all continents, from 81°N to 68°S, and from 5600 m above sea level in the Himalayas to a depth of 1000 m below sea level in Lake Baikal (Cranston 1995).

Insects in the family Chironomidae are holometabolous, passing through egg, larval, pupal, and adult life-stages. Most larvae are aquatic, and are found in all types of fresh-water habitats worldwide (Cranston 1995). The larval stage consists of four phases, or instars, with a complete molt between each instar. The larvae have a non-retracting head capsule, consisting of sclerotized chitin, which bears opposing mandibles, antennae, eyespots, and various other sensory structures. The morphology of structures preserved on the head capsule is used in identifying the larval stage to genus (Epler 2001). These head capsules are shed with every molt in the transition to pupal stage and become part of the sediments in lakes and ponds; they are extremely resistant to decay once buried in the sediments,

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especially those of the third and fourth instars (Walker 2001). These remains can be recovered and identified, making chironomids very useful in paleoecological studies.

According to Frey (1964), chironomid remains were first identified from sediments in the early 1900s. The use of chironomid remains in paleoecological studies developed slowly at first, but recently there has been an explosion of interest in using this group as a tool for reconstructing paleoenvironments. Because of their ubiquitous and worldwide distribution, their abundance, and their sensitivity to specific environmental gradients, they have proven to be quite valuable, especially in the area of reconstructing past temperatures (Battarbee 2000). In order to use midge remains in paleoecological reconstructions, the relationship between species distributions and environmental variables must be established (Walker 2001). To this end, chironomidists have undertaken modern surveys of the midge remains deposited in surficial sediments (the most recent). Assuming that the remains in the topmost sediments represent the current or modern species assemblage in a lake, the abundances of the taxa recovered are then related to current environmental conditions, such as lake water temperature, conductivity, pH, water clarity, and so forth. Distributions of midge taxa have been found to be significantly correlated with temperature gradients in Atlantic Canada (Walker et al. 1991, 1997; Wilson et al. 1993), Switzerland (Lotter et al. 1997), Scandinavia (Brooks and Birks 2001, Larocque et al. 2001, Olander et al. 1999), British Columbia (Palmer et al. 2002), California (Porinchu et al. 2002), and Yukon and Northwest Territories (Walker et al. 2003). Distributions of midge taxa have also been related to salinity (Heinrichs et al. 2001, Walker et al. 1995) and hypolimnetic oxygen (Little and Smol 2001, Quinlan et al. 1998). Such data sets can then be used to develop mathematical transfer functions which can be applied to assemblage data from sediment cores to reconstruct past values of an environmental variable such as temperature.

In this study, midge remains from the surficial sediments of a set of small lakes and ponds were enumerated. The study sites were located on a broad north-south transect in order to capture a climatic (temperature) gradient. The midge assemblages were then related to environmental variables using ordination techniques. These data will not only be useful in understanding the basic ecology and biogeography of midges, but will also contribute to the growing training set used for paleoecological studies on the eastern coast of North America (Walker et al. 1997).

Methods

A total of 37 sites were selected on a transect from northern New Hampshire to southern Connecticut (Fig. 1, Table 1). Generally, small, shallow ponds with no inflowing streams were selected for the study.

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Surficial sediment samples were collected from the deepest point in each lake, either by coring or Ekman grab sampler. Cores were collected by piston corer, extruded in the field, and the top one or two centimeters were used for chironomid analysis. Ekman grab samples were brought into the boat and the top two centimeters of sediment were carefully scooped off and placed in plastic bags for storage. All samples were stored at 4 °C.

For chironomid analysis, 1–3 ml of wet sediment was treated with 10% HCl to remove carbonates, then warm 5% KOH, with distilled water rinses

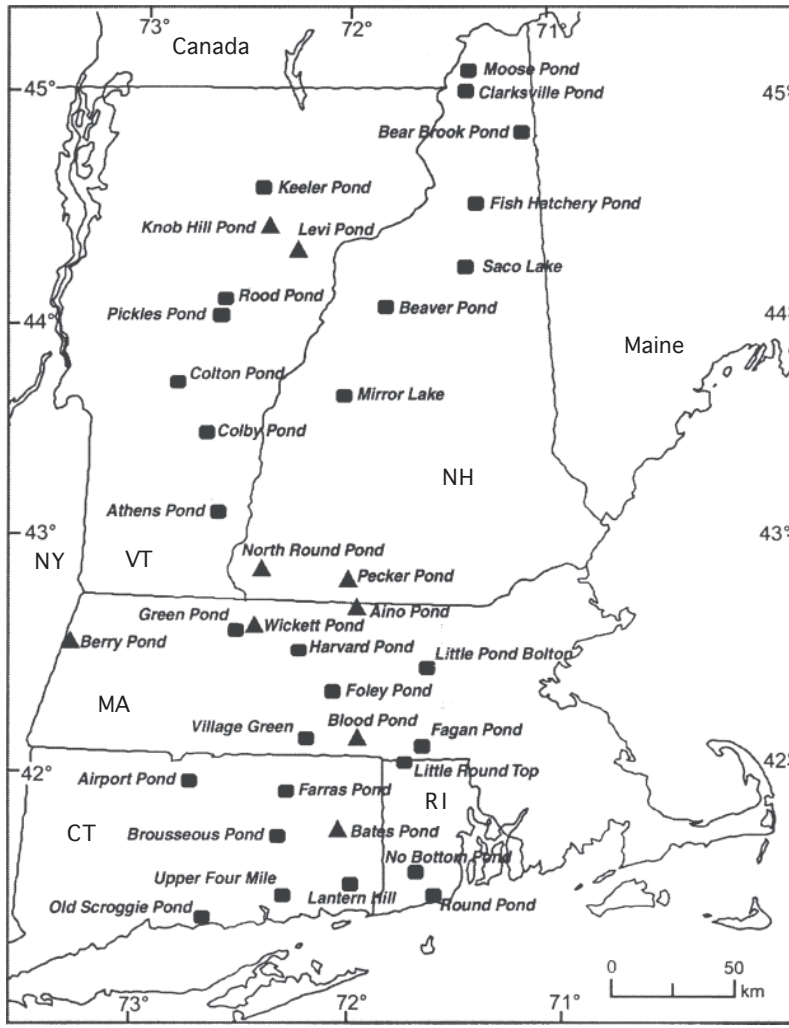

Figure 1. Location of thirty-seven surficial sediment and core sampling sites. Solid squares indicate sites at which only surficial sediments were collected. Solid triangles indicate that a sediment core was collected, but only the top 1 or 2-cm interval was analyzed for this study.

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Table 1. Location of sampling sites, elevations, and selected parameters measured at each site. July air temperature was calculated using Ollinger et al. (1995). Sites marked with an asterisk indicate that a core was collected. At all other sites surficial sediments only were collected.

Site	Latitude	Longitude	Elevation (m)	Maximum depth (m)	July water °C	Mean July air °C	pH	Conductivity (µS cm^{-1})	Secchi depth (m)	% organic matter
1 Moose Pond	45°5.8'N	71°22.8'W	420	3.4	23.3	17.67	8.0	16	2.9	65.79
2 Clarksville Pond	45°0.2'N	71°23.6'W	618	1.6	22.2	16.24	7.7	13	1.6	63.09
3 Bear Brook Pond	44°49.4'N	71°6.8'W	427	4.4	25.6	17.81	6.6	11	2.5	61.63
4 Keeler Pond	44°34.4'N	72°24.1'W	429	3.1	26.7	17.91	6.8	16	3.0	61.14
5 Fish Hatchery Pond	44°29.7'N	71°20.8'W	500	1.9	22.8	17.60	7.3	11	1.5	59.60
6 Knob Hill Pond*	44°21.6'N	72°22.4'W	371	4.6	23.3	18.64	7.7	21	2.9	39.96
7 Levi Pond*	44°15.9'N	72°13.7'W	499	7.0	25.0	17.64	5.7	15	4.0	55.00
8 Saco Lake	44°13.1'N	71°24.2'W	576	1.7	26.7	16.60	5.3	10	1.7	72.05
9 Rood Pond	44°4.4'N	72°35.2'W	398	9.5	24.4	18.46	8.3	27	4.2	82.64
10 Beaver Pond	44°2.5'N	71°47.6'W	564	2.0	26.7	17.12	6.1	10	2.0	62.32
11 Pickles Pond	44°0.0'N	72°36.5'W	451	1.3	26.1	18.28	8.1	35	1.3	42.96
12 Colton Pond	43°41.9'N	72°49.2'W	398	3.1	24.5	18.54	8.0	26	2.7	66.46
13 Mirror Lake	43°38.3'N	71°59.9'W	290	5.3	29.0	19.59	7.2	21	1.8	57.22
14 Colby Pond	43°28.3'N	72°40.0'W	479	3.5	23.0	18.34	7.9	28	2.7	72.54
15 Athens Pond	43°7.3'N	72°36.4'W	355	3.6	23.0	19.41	7.2	20	2.5	56.64
16 North Round Pond*	42°50.8'N	72°27.2'W	317	3.4	23.5	19.90	5.7	10	2.8	54.73
17 Pecker Pond*	42°42.8'N	71°57.9'W	370	4.8	24.8	19.58	6.3	14	4.2	35.82
18 Aino Pond	42°40.7'N	71°55.6'W	357	2.6	24.3	19.69	4.9	10	1.2	47.39

Table 1, continued.

Site	Latitude	Longitude	Elevation (m)	Maximum depth (m)	July water °C	Mean July air °C	pH	Conductivity (µS cm^{-1})	Secchi depth (m)	% organic matter
19 Green Pond	42°35.4'N	72°30.7'W	82	6.3	27.0	21.51	4.6	17	6.0	29.35
20 Wickett Pond*	42°34.2'N	72°25.9'W	330	2.3	26.9	20.68	5.5	11	2.3	35.41
21 Berry Pond*	42°30.3'N	73°19.2'W	631	2.5	27.0	18.22	6.4	8	2.0	43.30
22 Harvard Pond	42°30.0'N	72°12.7'W	230	2.5	26.1	20.73	5.2	20	1.3	52.26
23 Little Pond, Bolton	42°25.4'N	71°35.3'W	99	3.1	26.2	21.65	7.0	20	1.9	33.17
24 Foley Pond	42°19.1'N	72°2.4'W	222	1.2	23.8	20.93	6.2	15	1.2	34.27
25 Village Green Pond	42°6.5'N	72°9.8'W	225	1.9	25.0	21.00	6.9	30	1.8	12.16
26 Blood Pond*	42°4.8'N	71°57.7'W	214	3.6	25.0	21.14	6.8	29	0.3	48.28
27 Fagan Pond	42°4.4'N	71°36.8'W	69	1.0	25.0	22.11	6.1	11	0.7	63.10
28 Little Round Top Pond	42°0.1'N	71°41.8'W	116	2.7	25.0	21.77	6.1	18	2.7	21.73
29 Airport Pond	41°54.5'N	72°43.6'W	52	2.0	28.0	22.46	7.8	21	0.6	25.21
30 Farra's Pond	41°52.2'N	72°15.9'W	204	3.2	28.0	21.31	6.9	41	3.1	15.67
31 Brousseous Pond	41°40.3'N	72°18.1'W	168	1.2	27.0	21.66	7.1	21	1.2	36.33
32 Bates Pond*	41°39.5'N	72°0.9'W	95	3.6	28.5	22.27	6.0	20	2.0	38.10
33 No Bottom Pond	41°30.5'N	71°38.2'W	49	5.3	22.8	22.64	5.7	13	4.5	45.85
34 Lantern Hill Pond	41°27.5'N	71°56.9'W	36	13.3	25.5	22.62	6.2	12	1.5	12.19
35 Round Pond	41°24.4'N	71°33.4'W	33	9.9	26.4	22.82	4.8	12	4.5	60.86
36 Upper Four Mile Pond	41°24.3'N	72°16.3'W	49	2.2	27.0	22.70	6.8	15	2.0	11.65
37 Old Scroggie Pond	41°18.3'N	72°39.3'W	9	1.3	26.0	23.07	6.1	29	0.5	65.23

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in between steps using a 100-µm sieve (Walker 2001). Following the final rinse, the residue was examined under a dissecting microscope at 50x using a Bogorov counting chamber (Gannon 1971). Individual chironomid head capsules were removed and mounted permanently on microscope slides in Euparal®. The volume of sediment used was dependent on the concentration of head capsules. Enough sediment was processed to obtain a minimum of 50 head capsules per sample (Heiri and Lotter 2001, Quinlan and Smol 2001). Identification of chironomid remains to the lowest possible taxonomic level was done at 400x using the keys of Coffman and Ferrington (1984), Epler (1992, 2001), Oliver and Roussel (1983), Walker (1988, 2000), and Wiederholm (1983). Identification of Chaoboridae mandibles was based on Uutala (1990).

Remains of some related families of Diptera were also recovered from the sediment samples and are reported herein. These include the families Ceratopogonidae (biting midges) and Simuliidae (black flies), in which the larvae also possess sclerotized head capsules that are preserved in lake sediments; and the family Chaoboridae (phantom midges), whose larval mandibles are preserved in lake sediments.

Limnological data for each site were collected once during the month of July, either during the time the surficial sediment sample was collected or, in the case of cores which were often collected in winter, the following July. Parameters measured included maximum lake depth, pH, conductivity, secchi depth, and surface water temperature (Table 1). Water temperature and conductivity were measured in surface water (less than 0.5 m) near the sediment sampling site using a YSI model 33 S-C-T meter. pH was measured at the same site in each lake using a hand-held Oaklon pH Tertr 2 meter, or a Radiometer PHM80 portable pH meter. Sediment organic content was measured in the lab by loss-on-ignition at 550 °C (Dean 1974).

Mean July air temperatures were estimated using a GIS climate model for the northeast developed by Ollinger et al. (1995). The climate model uses 30-year means (1951–1980) from 164 weather stations in New York and New England, and takes into account latitude, longitude, and elevation.

Ordinations were performed using the computer program CANOCO v3.12 (ter Braak 1988). Taxa percentages were square-root transformed prior to analyses. Taxa that occurred in less than two sites, or whose abundance never exceeded 2% of the total identifiable chironomid remains, were deleted from the ordination analyses. Two environmental variables (lake maximum depth and conductivity) were log transformed to alleviate skewness. Screening for outlier samples was done by determining whether any sample scores fell outside the 95% confidence limits about the sample score means in both a DCA (detrended correspondence analysis) of the species data and a PCA (principal components analysis) of the environmental data (Walker et al. 2003). This

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process resulted in no samples being declared outliers, and therefore no samples were deleted prior to analysis. The main patterns of variation were analyzed using DCA with detrending by second order polynomials. CCA (canonical correspondence analysis) was used to identify which environmental variables could directly account for the observed variation in the faunal assemblages. Species scores were scaled to be weighted means of the sample scores. Monte Carlo permutation tests (with 999 unrestricted permutations) were used to test the statistical significance of forward selected variables as well as the significance of the first four canonical axes.

Results and Discussion

Locations of all sites, along with the environmental data collected, are presented in Table 1. Sites range in latitude from 41°18.1'N to 45°5.8'N. The ponds were generally shallow, with only one (Lantern Hill Pond) exceeding 10 m maximum depth. July water temperatures (taken in the top 1 m) ranged from 22.2 °C to 29.0 °C. Because water temperature data were collected on only one date for each pond, they may not be an accurate reflection of mean July water temperatures (Livingstone et al. 1999). Mean July air temperatures were also used, estimated using a GIS model (Ollinger et al. 1993). This model takes into account latitude as well as elevation of the sites. The mean July air temperatures, as inferred from the GIS model, ranged from 16.24 °C to 23.07 °C. Air temperatures and lake surface water temperatures are closely correlated even though water temperatures are 3–5 °C higher than air temperatures (Livingstone et al. 1999) Thus, mean July air temperature will reflect the lake water temperatures, and will reflect average conditions much better than single water temperature measurements (Brooks and Birks 2001).

Site elevations ranged from 9 m near the Connecticut coast, to 631 m at the only site in the Berkshires of western Massachusetts (Berry Pond). The range of pH values encountered was 4.6 to 8.3. Conductivity was very low, with no values exceeding 30 $\mu S\ cm^{-1}$. Secchi depths ranged from as little as 0.3 m to 6.0 m, but in some of the shallowest ponds, secchi depth was equal to maximum water depth. Sediment organic matter varied from 11.65% to 82.64%.

A total of 65 Chironomidae taxa were identified (Table 2). Taxonomic designations follow those of Epler (2001) and Walker (2000). In some cases differentiation between two or more genera is not possible. This is evident in Table 2 where two genera are listed together (e.g., *Cricotopus/Orthocladius*), or as larger taxonomic groupings such as Tribe Pentaneurini or Tanytarsina. Remains of Chaoboridae, Ceratopogonidae, and Simuliidae were also recovered, though in much fewer numbers than the Chironomidae. Presence of Simuliidae remains in lake sediments usually indicates stream input

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to the lake, as these larvae are restricted to flowing water (Walker 2001). Only two ponds had Simuliidae head capsules.

Table 2. Dipteran taxa recovered from surficial sediments from 37 ponds in New England. References are given for taxa with uncertain designations.

Family Chironomidae
- Subfamily Tanypodinae
  - *Clinotanypus* Kieffer
  - *Procladius* Skuse
  - *Macropelopia* Thienemann
  - *Tanypus* Meigen
  - Tribe Pentaneurini
  - *Ablabesmyia* Johannsen
  - *Guttipelopia* Fittkau
  - *Labrundinia* Fittkau
  - Pentaneurini (undifferentiated)
- Subfamily Chironominae
  - Tribe Tanytarsini
    - *Cladotanytarsus mancus* Walker group (Walker 2000)
    - *Cladotanytarsus* Kieffer group A (Walker 2000)
    - *Corynocera oliveri* Lindeberg/*Tanytarsus lugens* Kieffer type
    - *Micropsectra atrofasciata* Kieffer type (Walker 2000)
    - *Neostempellina* Reiss
    - *Paratanytarsus* Thienemann & Bause
    - *Stempellina* Thienemann & Bause
    - *Stempellinella* Brundin/*Zavrelia* Kieffer
    - *Tanytarsus chinyensis* type (Walker 2000)
    - *Tanytarsus* sp. C type (Walker 2000)
    - Tanytarsina (undifferentiated)
  - Tribe Pseudochironomini
    - *Pseudochironomus* Malloch
  - Tribe Chironomini
    - *Chironomus* Meigen
    - *Cladopelma* Kieffer
    - *Cryptochironomus* Kieffer
    - *Cryptotendipes* Beck & Beck
    - *Dicrotendipes* Kieffer
    - *Einfeldia* Kieffer
    - *Endochironomus* Keiffer
    - *Glyptotendipes* Kieffer
    - *Glyptotendipes (Caulochironomus)* (Epler 2001)
    - *Hyporhygma quadripunctatum* Malloch
    - *Lauterborniella* Thienemann & Bause/*Zavreliella* Kieffer type
    - *Microtendipes* Kieffer
    - *Nilothauma* Kieffer
    - *Pagastiella ostansa* Webb
    - *Parachironomus* Lenz
    - *Paracladopelma* Harnisch
    - *Paralauterborniella* Lenz
    - *Paratendipes* Kieffer
    - *Polypedilum* Kieffer
    - *Polypedilum* sp. A type (Epler 2001)
    - *Stenochironomus* Kieffer
    - *Tribelos* Townes
    - *Xenochironomus* Kieffer
- Subfamily Orthocladiinae
  - *Corynoneura* Winnertz/*Thienemanniella* Kieffer
  - *Cricotopus* Wulp/*Orthocladius* Wulp group
  - *Diplocladius* Kieffer
  - *Eukiefferiella* Thienemann
  - *Heterotanytarsus* Spärck
  - *Heterotrissocladius* Spärck
  - *Nanocladius* Kieffer
  - *Parakiefferiella* sp. A (Epler 2001)
  - *Parakiefferiella* sp. E (Epler 2001)
  - *Parakiefferiella* sp. F (Epler 2001)
  - *Parametriocnemus* Goetghebuer
  - *Paraphaenocladius* Thienemann
  - *Psectrocladius (*subgenus *Monopsectrocladius)* (Epler 2001)
  - *Psectrocladius sordidellus* Zetterstedt group (Epler 2001)
  - *Psectrocladius* Kieffer (undifferentiated)
  - *Psilometriocnemus* Sæther
  - *Rheocripcotopus* Thienemann & Harnisch
  - *Smittia* Holmgren
  - *Stilocladius* Rossaro
  - *Unniella* Sæther
  - *Zalutschia* Lipina
  - *Zalutschia* cf. *zalutschicola* Lipina

Family Chaoboridae (mandibles)
- *Chaoborus flavicans* Meigen
- *Chaoborus trivittatus* Loew
- *Chaoborus (*subgenus *Sayomyia)* (Uutala 1990)

Family Ceratopogonidae

Family Simuliidae

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Distributions of the most abundant taxa at all sites are shown in Figure 2. The taxa are displayed in order according to their temperature optima. Taxa with the lowest temperature optima are on the left side of the figure, with temperature optima increasing from left to right. Taxa showing a change in relative abundance over the north-south gradient include *Clinotanypus*, *Ablabesmyia*, *Tanytarsus* sp. C (sensu Walker 2000), *Glyptotendipes*, *Zalutschia* cf. *zalutschicola*, and *Chaoborus* (*Sayomyia*). These taxa were more abundant in southern sites. Taxa such as *Corynocera oliveri/Tanytarsus lugens* type, *Micropsectra* (*atrofasciata*) type, *Microtendipes*, *Eukiefferiella*, *Heterotanytarsus*, and *Heterotrissocladius* were more abundant in the northern sites. Several taxa were distributed fairly evenly over the transect, such as *Chironomus* and *Dicrotendipes*. Some sites were dominated by individual taxa, most notably Levi Pond, which was dominated by *Psectrocladius* (*Monopsectrocladius*). The possible reasons for this dominance are not clear. Interestingly, this pond has been dominated by *Monopsectrocladius* throughout the latter part of the Holocene, as shown by the downcore analysis (Francis, unpubl. data).

The Chaoboridae are identifiable to the subgenus or species level, based on the morphology of the larval mandibles (Uutala 1990). In this study, *Chaoborus trivittatus* was found mostly at the northernmost sites. This species appears to be somewhat cold-tolerant, and has been collected as far north as Baffin Island (Borkent 1981; Francis, unpubl. data). *Sayomyia* is a subgenus of *Chaoborus*, and includes *C. punctipennis* and *C. albatus* (Uutala 1990). This group was by far the most abundant of the Chaoboridae.

The 65 taxa of Chironomidae recovered in this study clearly show the great diversity of this insect group in New England, even at the genus level. The value of using one surficial sediment sample to characterize the midge fauna of a lake is that it provides a spatially integrated sample for the entire lake (Walker et al. 1984). Head capsule remains from larvae living in the littoral zones as well as deeper water zones are all entrained in the sediments that accumulate at the deepest point. By using these subfossil remains, one can avoid the notorious problem of spatial heterogeneity of lake bottom habitats. The remains deposited in the uppermost layer of sediment represent the animals that lived in the lake in the past few years, or in other words, the modern fauna.

Both DCA (detrended correspondence analysis) and CCA (canonical correspondence analysis) were performed on the midge abundance data. Members of the Chaoboridae and Ceratopogonidae were also included in these ordinations. DCA with detrending by polynomials was performed using the midge assemblage data in order to discern patterns in their distributions. The gradient length of the first DCA axis was 4.60 standard deviation units, indicating that unimodal models such as DCA and CCA

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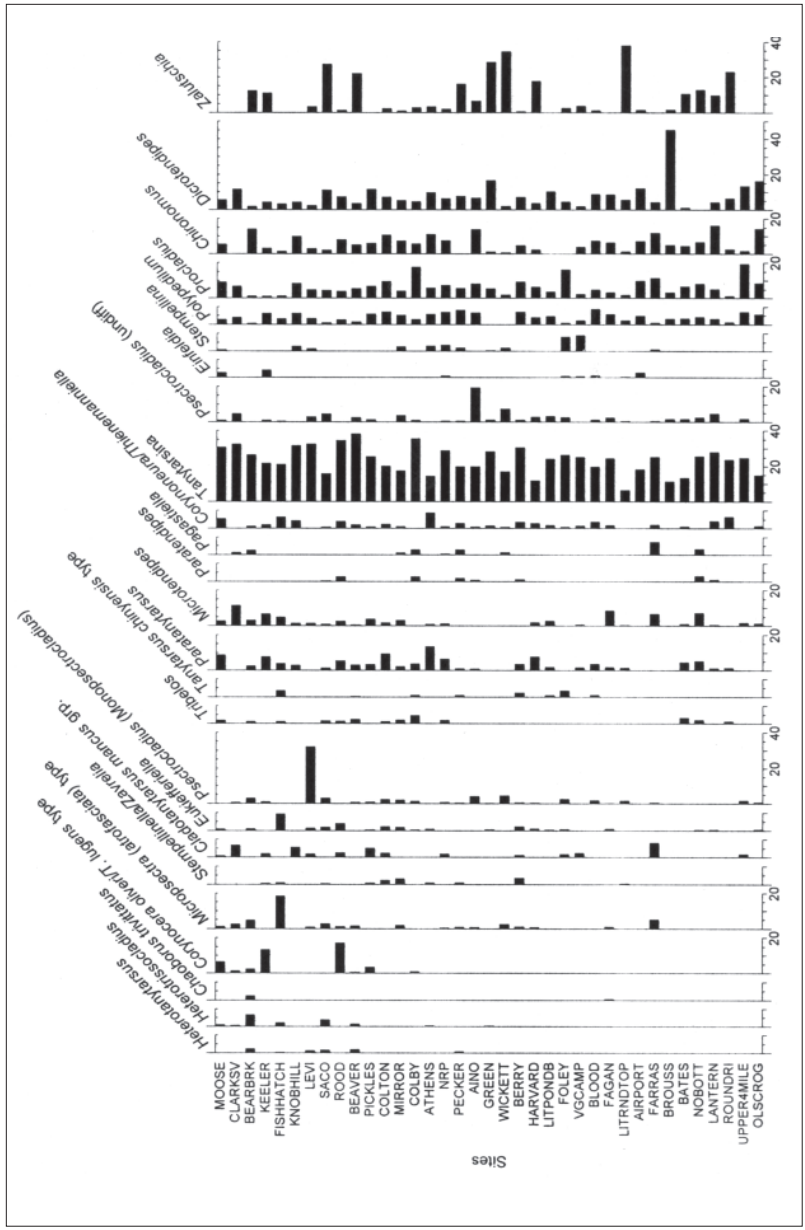

Figure 2. Relative abundances of some of the major midge taxa found at the 37 sites. The sites are arranged on the Y axis by latitude, with the northernmost sites at the top of the graph. The taxa are arranged according to their relative temperature optima (determined by weighted averaging regression), with the more cold-tolerant taxa on the left, and warm-water taxa on the right (continued on the next page).

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are appropriate for this data set (Birks 1995). DCA is a type of indirect gradient analysis which can illuminate the main patterns of variation in a complex data set. These patterns can be depicted in the axis 1 scores for both taxa and sites (Figure 3). The first axis of the ordination explains the greatest amount of the variation in the data set. The ordination axes can be interpreted as reflecting underlying environmental gradients. The DCA axis 1 scores for taxa reflect their temperature optima (Figure 3a). The more cold-tolerant fauna such as *Chaoborus trivittatus* and *Heterotrissocladius* are positioned on the positive end of the axis while warmer water taxa such as *Tanytarsus* sp. C are found at the other end of the axis. This pattern is similar to that shown in Figure 3 in which the taxa are arranged according to their temperature optima. Not all taxa are shown in all figures, for the sake of clarity.

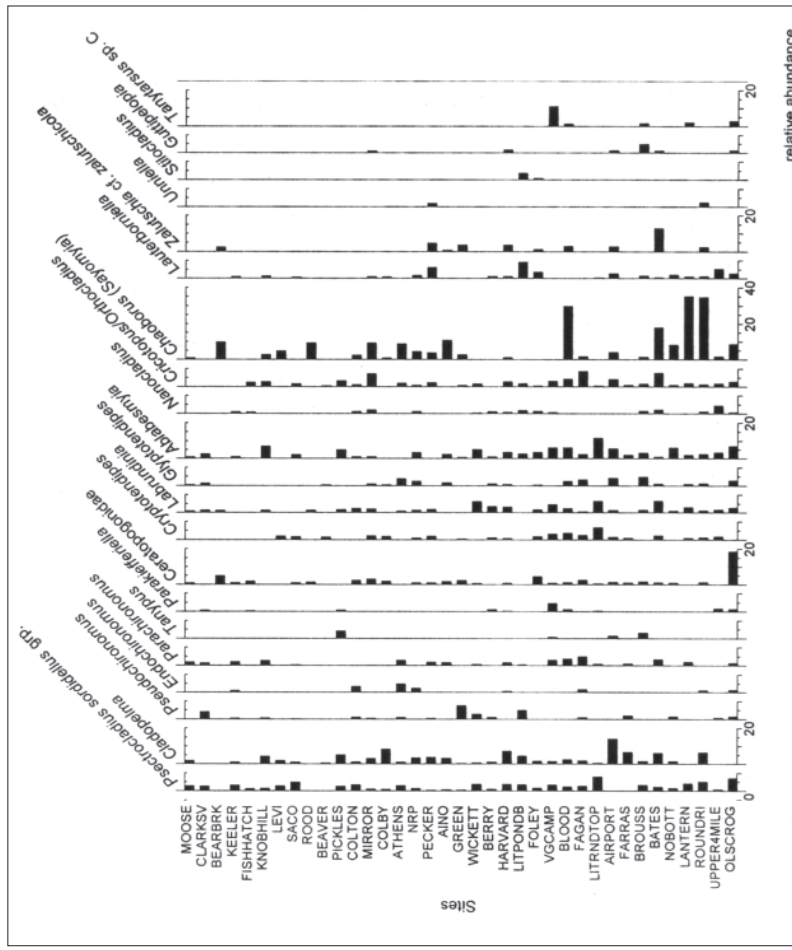

Figure 2, continued.

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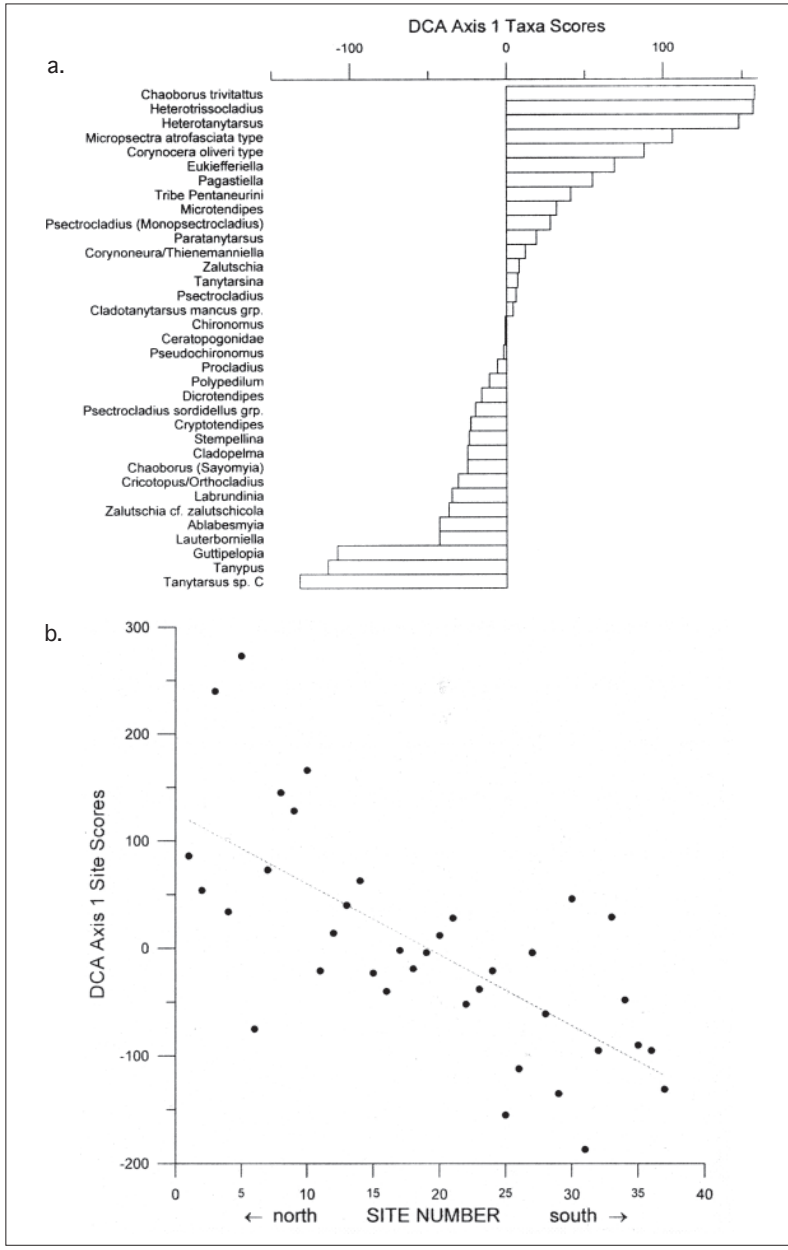

Figure 3. a. Axis 1 species scores from DCA ordination. Taxa that are more cold tolerant have high positive scores. Distribution of species scores on the first axis are roughly equivalent to their temperature optima as shown in Figure 2. In general, taxa with relative abundance greater than 5% are shown. b. Axis 1 sample (site) scores from the same DCA ordination. Sites are arranged on the X axis from north to south.

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DCA axis 1 sample or site scores are shown in Figure 3b. In this case, the sites are arranged on the X-axis according to their latitude with the northernmost site (#1 Moose Pond) on the left and the southernmost site (#37 Old Scroggie Pond) on the right. The axis 1 scores are correlated with latitude ($r^2 = 0.4892$).

CCA is a type of ordination based on direct gradient analysis. In canonical (or constrained) ordination techniques, the ordination axes are constrained to be linear combinations of environmental variables (ter Braak 1986). Variables used in the CCA included only the limnological variables (summer surface water temperature, maximum lake depth, secchi depth, % sediment organic matter, pH, and specific conductance), plus mean July air temperature. None of the environmental variables had extreme influence on the ordination (< 6×), and all variance inflation factors were < 3, indicating that no variable was highly correlated with any other variables. Monte Carlo tests showed that the overall CCA was significant ($p < 0.001$) (Table 3). The first three axes were also statistically significant (Table 3). The three axes accounted for 30.4%, 20.2%, and 17.7% of the species-environment relation (Table 3). Forward selection indicated that mean July air temperature (JULair) explained the greatest amount of the variance in the data set ($p < 0.001$). Other variables that explain a significant amount of the variation were pH ($p < 0.001$), % sediment organic matter (%ORG) ($p < .002$), and lake depth (ZMAX) ($p < 0.001$).

Table 3. Eigenvalues, species-environment correlations, cumulative % variance explained, and statistical significance of the 4 CCA axes.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.100	0.066	0.058	0.042
Species-environment correlation	0.882	0.857	0.859	0.799
Cummulative % variance				
of species data	9.4	15.6	21.1	25.1
of species-environment relation	30.4	50.6	68.3	81.2
Significance (probability)	0.001	0.002	0.004	0.125
(Overall probability = 0.001)				

Table 4. Canonical coefficients of the first 2 axes, their t-values, and inter-set correlations.

	Canonical coefficients		t-values		Inter-set correlation	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
ZMAX	-0.077	0.638	-0.58	4.30	-0.151	0.563
pH	-0.209	-0.454	-1.43	-2.76	-0.215	-0.580
COND	0.276	-0.172	2.05	-1.13	0.310	-0.337
SECCHI	-0.270	-0.105	-1.98	-0.68	-0.314	0.332
%ORG	-0.255	0.523	-2.07	3.78	-0.595	0.196
WAte	-0.590	0.110	-0.53	0.89	0.285	0.136
JULair	0.647	0.371	4.47	2.28	0.804	0.252

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Canonical coefficients, their t-values, and inter-set correlations for the first two canonical axes are presented in Table 4. These data indicate that JULair is important in defining the first axis: the canonical coefficient is the highest in absolute value (0.647), and its t-value (4.47) is greater than 2.1. If the t-value of a variable is greater than 2.1, that variable contributes uniquely to the fit of the species data (ter Braak 1988). For the second axis, ZMAX, pH, and %ORG have high absolute values of the canonical coefficients, and high t-values (Table 4).

The CCA biplot of sample scores and environmental vectors is shown in Figure 4a. The northern sites tend to be on the left of axis 1, and southern sites on the right. The environmental vectors show that JULair and %ORG are most highly correlated with axis 1 (0.804 and -0.595, respectively) (Table 4). ZMAX and pH are correlated with axis 2 (0.563 and -0.580, respectively). The direction of the arrow indicates increasing values for the variable.

The CCA biplot of species scores indicates that patterns are similar to DCA results (Figure 4b, c). The more cold-tolerant taxa such as *Heterotrissocladius* cluster at the left end of axis 1. This corresponds to the northernmost sites in the biplot of sample scores. The warm water taxa cluster towards the right on axis 1, which corresponds with southernmost sites. These results are similar to those found in other surface data sets. In both Olander et al. (1999) and Walker et al. (1991), taxa correlated with warm temperatures on the ordination axis included *Dicrotendipes*, *Polypedilum*, and *Chironomus*, while taxa correlated with colder conditions included *Heterotrissocladius*, *Heterotanytarsus*, and *Corynocera oliveri* type.

The patterns of variation revealed by DCA and CCA were quite similar, which gives added weight to the argument that the environmental variables that were measured are significant in determining the distribution of midge taxa. Of the factors included in the study, temperature proved to be the most significant explanatory variable,

Figure 4. CCA biplots. a. Sample (site) scores and environmental vectors. Solid circles represent northern sites, mostly in Vermont and New Hampshire. Solid triangles represent southern sites. JULair = mean July air temperature, WAte = summer surface water temperature, ZMAX = maximum lake depth, SECCHI = secchi depth, %ORG = % sediment organic matter, pH = pH, COND = specific conductance. b. CCA biplot of scores for all taxa. c. For the sake of clarity, the biplot of taxa scores is also shown with *Unniella* (Un) and *Tanypus* (Tanyp) removed, and environmental vectors included. Ab = *Ablabesmyia*, Cer = Ceratopogonidae, CH = *Chironomus*, Ch = *Chaoborus*, ChT = *Chaoborus trivittatus*, CL = *Cladopelma*, Cm = *Cladotanytarsus mancus* grp., co = *Corynocera oliveri/Tanytarsus lugens* type, C/O = *Cricotopus/Orthocladius*, C/T = *Corynoneura/ Theinemanniella*, CrC = *Cryptochironomus*, CrT = *Cryptotendipes*, Di = *Dicrotendipes*, Ei = *Einfeldia*, En = *Endochironomus*, Eu = *Eukiefferiella*, Gl = *Glyptotendipes*, Gu = *Guttipelopia*, HeTa =

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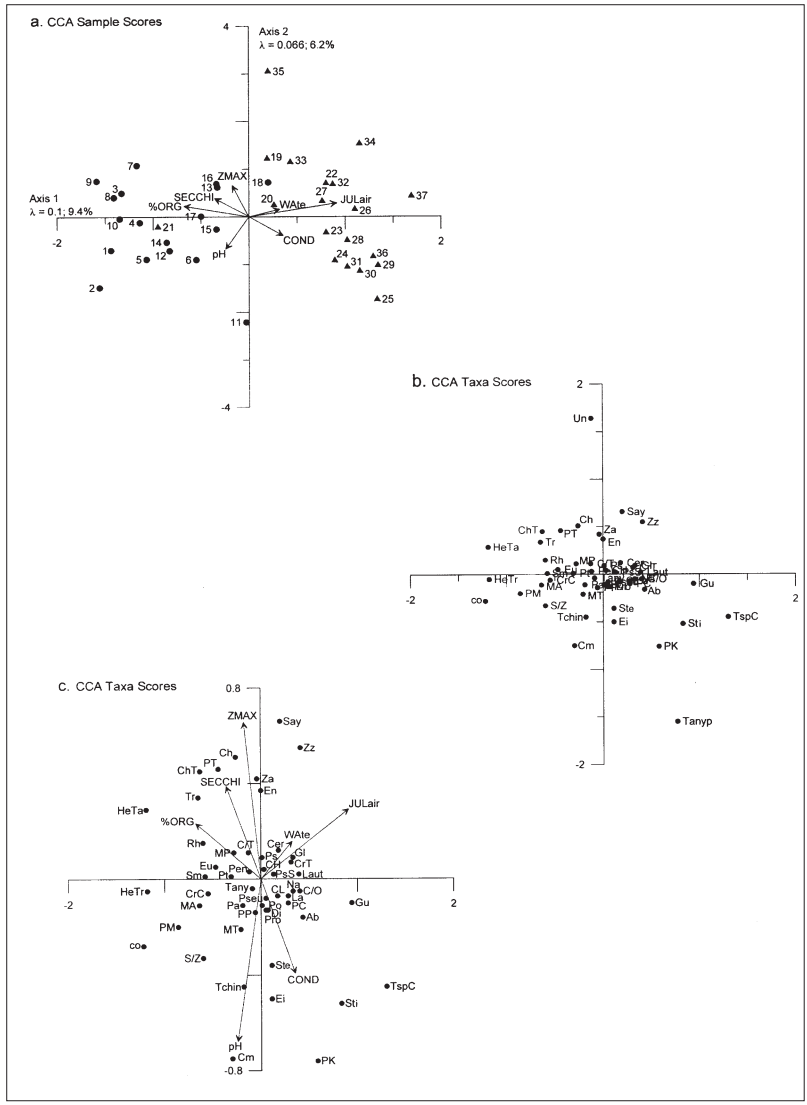

Figure 4, continued. *Heterotanytarsus*, HeTr = *Heterotrissocladius*, La = *Labrundinia*, Laut = *Lauterborniella*, MA = *Micropsectra* (*atrofasciata*) type, MP = *Psectrocladius* (*Monopsectrocladius*), MT = *Microtendipes*, Na = *Nanocladius*, Pa = *Pagastiella*, PC = *Parachironomus*, Pen = Pentaneurini, PK = *Parakiefferiella*, PM = *Parametriocnemus*, PP = *Paraphaenocladius*, Po = *Polypedilum*, Pro = *Procladius*, Pseu = *Pseudochironomus*, Ps = *Psectrocladius*, PsS = *Psectrocladius sordidellus* grp., Pt = *Paratanytarsus*, PT = *Paratendipes*, Rh = *Rheocricotopus*, Say = *Chaoborus* (*Sayomyia*), Sm = *Smittia*, S/Z = *Stempellinella/Zavrelia*, Ste = *Stempellina*, Sti = *Stilocladius*, Tany = Tanytarsina, Tchin = *Tanytarsus chinyensis* type, Tr = *Tribelos*, TspC = *Tanytarsus* sp. C type, Za = *Zalutschia*, Zz = *Zalutschia* cf. *zalutschicola*.

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followed by pH, % sediment organic matter, and lake depth. However, this is not to say that some variable that was not measured could not also influence the midges. Walker et al. (2003) found that total Kjeldahl nitrogen was a significant factor in midge distributions in the Yukon Territory. Other studies have determined dissolved oxygen (Little and Smol 2001, Quinlan et al. 1998) to be a significant contributor to midge distributions. Dissolved oxygen data were available for only about one third of the study sites, so it was not included in the analysis. Most of the ponds analyzed are quite shallow and unstratified, and dissolved oxygen may not have proved to influence midge assemblages in this study.

With the exception of dissolved oxygen, the parameters that were included in the study (temperature, pH, lake depth, and sediment organic content) are ones that have been shown to be important in other regions. Temperature, either water temperature or air temperature, is very often the factor that explains the greatest amount of variation in modern chironomid data sets. Temperature was the most significant explanatory variable in training sets from Atlantic Canada (Walker et al. 1991, 1997; Wilson et al. 1993), Switzerland (Lotter et al. 1997), Finland (Olander et al. 1999), northern Sweden (Larocque et al. 2001), Norway (Brooks and Birks 2001), British Columbia (Palmer et al. (2002), California (Porinchu et al. 2002), and the Yukon Territory (Walker et al. 2003). Temperature is a major controlling factor in larval growth and development of chironomids (Sweeney 1984, Tokeshi 1995). Temperature may affect hormone and enzyme function, digestion, and metabolic rates (Sweeney 1984). Many species appear to have temperature maxima for growth, above which the maintenance costs at higher temperatures are greater than the benefits of increased metabolic rate (Tokeshi 1995).

A survey in the Yukon Territory similar to the one conducted here determined that midge distributions were also correlated with pH (Walker et al. 2003). Many other qualitative studies have shown that pH is a significant variable in explaining midge distributions, including Charles et al. (1987), Ilyashuk and Ilyashuk (2001), Johnson and McNeil (1988), Orendt (1999), and Schnell and Willassen (1996). pH directly affects the physiology of aquatic organisms by influencing ionic balance and enzyme function (Wiederholm 1984). Chironomid taxa that are tolerant of low pH-levels tend to be large-bodied, able to maintain internal pH-balance (Wiederholm and Eriksson 1977), and possess hemoglobin which provides greater buffering capacity (Jernelöv et al. 1981).

Sediment organic matter content (LOI or loss-on-ignition) has been shown to be a significant variable in two other studies: a surface set in northern Finland (Olander et al. 1999), and in northern Sweden (Larocque et al. 2001). In northern Finland, LOI proved to have the greatest explanatory power for that data set; however, in other studies, LOI has not been an important variable in midge distributions (Walker et al. 1991). In all three cases in which LOI was significant, the sites had a very large range of LOI

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values, whereas the Walker et al. (1991) study sites had a much smaller range of LOI values. LOI may be an indicator of the productivity of a lake, and hence the available food for chironomid larvae.

Lake depth is also identified as an important variable in many training sets (Larocque et al. 2001; Little and Smol 2001; Olander et al. 1999; Porinchu et al. 2002; Walker et al. 1991, 2003). However, the contribution of lake depth is difficult to separate from water temperature, as these variables are often negatively correlated (Walker 2001). Most of the influence of lake depth is probably due to its influence on surface-water temperature: the greater the depth of water to be heated, the lower the summer surface-water temperature (Walker et al. 1991).

Patterns of chironomid distribution have also been related to salinity (Heinrichs et al. 2001), but lakes in this region of New England are strictly freshwater, so salinity would not be expected to be a factor affecting the distribution of taxa. The sites also represented a very narrow range of conductivity (a measure of the ionic content of the water), so it is not surprising that conductivity did not have much influence in this study.

Conclusions

The findings of this study support and corroborate those of similar surveys of fossil midge remains in Canada and Europe. Temperature, either of air or water, has a strong influence on the distribution of midge faunas. This relationship makes possible the use of midge remains in lake sediment cores to reconstruct past climate change. Understanding past climate variation is critical to understanding current and future climate change. Data from the current study will be used to interpret core data from New England lakes, as well as to extend the data set that exists for Atlantic Canada (Walker et al. 1997). This study also underscores the great diversity of the family Chironomidae and related Diptera in New England and their importance in aquatic systems both past and present.

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