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Modern Chironomid Assemblages and Their Relationship to Physical and Chemical Variables in Southwest Yukon and Northern British Columbia Lakes

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Abstract

Modern chironomid assemblages consisting of 68 taxa were extracted from the sediments of 39 lakes in southwest Yukon and northern British Columbia, Canada. Important factors accounting for the distribution of the chironomid taxa include sediment organic matter (LOI; weight-loss-on-ignition), total phosphorus, bottom water temperature, and lake alkalinity. The results show the importance of organic matter, which is associated with water depth and lake productivity, in affecting chironomid community composition. *Tanytarsus* sp. C, *Tanytarsus pallidicornis* type, *Allo/Mesopsectrocladius*, *Polypedilum*, and *Procladius* were associated with lakes having high LOI values and shallow lake depths, while *Paratanytarsus*, *Sergentia*, and *Corynocera oliveri* type were more prevalent in deeper lakes with more minerogenic sediments. Surprisingly, *Chironomus* was most abundant in deeper lakes with low LOI values, which might be partially explained by low oxygen levels. Contrary to some findings, *Tanytarsus lugens* group was common in shallow, productive lakes in this region.

Introduction

The distribution and abundance of aquatic organisms are influenced by numerous environmental factors. Aquatic organisms are influenced by the physical and chemical environment as well as by other organisms, and these in turn are affected by the conditions in the watershed. These factors vary in time and in space (Pourriot and Meybeck, 1995). Identifying the relative importance of various abiotic and biotic factors influencing a particular community in a lake system remains a challenge. Biogeographic and paleolimnological analyses contribute to this research effort by documenting population distributions and community patterns and relating these to environmental variability.

Chironomids are major components of the benthic fauna of lakes, especially in northern latitudes (Pourriot and Meybeck, 1995; Brinkhurst, 2002). As with any organism, the distribution and abundance of chironomids are influenced by environmental factors. Several aspects of the environment that influence chironomid communities include lake productivity, oxygen content of the hypolimnion and sediments, water properties including salinity, and water temperature (Walker, 1987). Because of the covariance of these parameters, determining the limiting factors is not always straightforward.

Chironomid taxa are used in paleoenvironmental studies because their remains are preserved in lake sediments. Many studies have reported chironomid taxa from lake sediment cores (Porinchu and MacDonald, 2003). Interpreting paleoenvironmental records relies on an understanding of the ecology of the organism in question. In the absence of extensive information about the biology of many chironomid taxa, particularly of North American species (Walker, 1987), geographical studies can provide data about species ranges and the conditions within the lakes that are correlated with community composition. These studies rely on the analysis of chironomid assemblages and water characteristics from a series of lakes and use various statistical methods to determine environmental factors most highly correlated with the abundance of the species in the community.

Several studies have documented the distribution of chironomids in relation to environmental variables in northern regions. Walker and MacDonald (1995) and Porinchu and Cwynar (2000) showed that chironomid communities differed across treeline in Canada and Siberia. Walker et al. (1991) and Walker et al. (2003) reported chironomid assemblages along transects in Labrador and in the Yukon and Northwest Territories, respectively. Lake depth, water chemistry, and surface-water temperature all influenced chironomid community composition. In Labrador lakes, sediment organic matter was not found to be a critical factor in chironomid community composition, although this may have been expected based on previous studies (Walker et al., 1991). July air temperature was also identified as a key factor explaining chironomid distributions in lakes of northern Sweden (Larocque et al., 2001) and western Norway (Brooks and Birks, 2000).

In this study, we analyze the relationship between water chemistry, physical variables, and chironomid assemblages from the surface sediment of a series of lakes in southwest Yukon Territory and northern British Columbia. The purpose of this study is to identify the factors influencing chironomid distributions and abundance in this region. We previously analyzed the diatoms in these lakes (Wilson and Gajewski, 2002). Lake size (depth and area), in addition to water chemistry, was an important factor affecting diatom distributions. We here report on another group of benthic organisms to gain a better understanding of the dynamics of these lake systems.

Study Area

Southwest Yukon is in the boreal biome, which is a dominant landscape of the Northern Hemisphere. The majority of lakes analyzed in this study are located along the Alaska Highway between Whitehorse and Beaver Creek, with a few located along the Haines Road in northern British Columbia (Fig. 1). Many sites are concentrated along the Shakwak Trench, which contains Kluane Lake. In addition to some mining, human activity in the region is concentrated in several small towns and along the major roads. There has been little human impact on most of these lakes (personal observation).

The dominant landforms of the southwest Yukon and northern British Columbia are a series of northwest-southeast–trending mountain chains and valleys. The geology is complex and varied but consists largely of metamorphic bedrock and large intrusive bodies composed of granodiorite and quartz diorite (Gabrielse et al., 1977; Oswald and Senyk, 1977). Much of the area is underlain with extensive glacial and surficial deposits (Gabrielse et al., 1977) and is located within the discontinuous scattered permafrost zone. The region lies
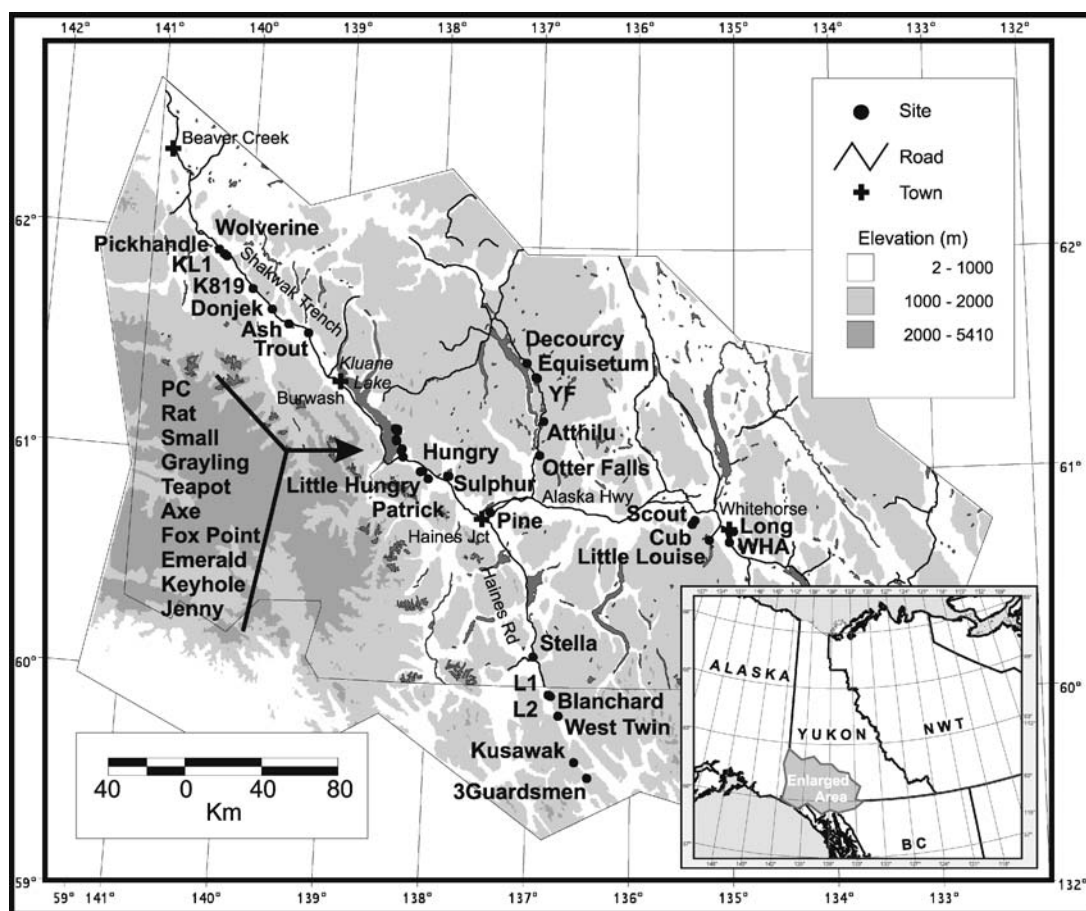
FIGURE 1.   Map of study site in southwest Yukon and northern British Columbia showing location of study lakes.

within the rainshadow of the St. Elias Mountains, resulting in precipitation less than 300 mm per year (Wahl et al., 1987). Mean July air temperature in the study region is 12°C and mean January temperature ranges from −21 to −30°C (Oswald and Senyk, 1977).

The common tree species in the study area include white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*), and trembling aspen (*Populus tremuloides*) (Johnson and Raup, 1964). Toward the eastern and southern portion of the study area the forests become more diverse, including paper birch (*Betula papyrifera*) and pine (*Pinus* spp.). There is a noticeable absence of black spruce (*Picea mariana*) in the study area and a lack of alder (*Alnus* spp.) in the region surrounding Kluane Lake. A significant aspect of the vegetation is the presence of natural grasslands, found in association with open forest stands, mainly on warm and dry, south-facing slopes. Many of the sites clustered at the south end of Kluane Lake, in addition to a few others, had catchments with substantial grassland vegetation. Although most of our sites are within the boreal forest, those in British Columbia are located at treeline, with the southernmost sites located in lichen heath tundra (Fig. 1).

Methods

FIELD METHODS AND WATER CHEMISTRY ANALYSES

Lake water and sediment samples were collected from 34 lakes between 11 and 22 July 2000. An additional 5 lakes were sampled in July or early August in 1996, 1997, or 1998 (Ash, Trout, Patrick, Hungry, and K819). Chironomid analyses were performed on sediment samples that were collected from near the center of the lake using a gravity corer (Glew, 1991), with the exception of the 1998 samples, which were collected with an Ekman Dredge (Hungry and K819) or

clear plastic tube fitted with a piston. The upper 1 to 2 cm were extruded at 0.5 cm or 1 cm intervals using a vertical extruder (Glew, 1988).

Conductivity (Cond) and temperature (T) profiles were recorded using a YSI model 33 SCT meter, and oxygen profiles were taken with a YSI model 51B oxygen meter, measured at 0.5 m intervals. Surface-water pH was averaged from 2 or 3 different handheld pH meters (Oakton pHTestr™ 2 and 3) that were calibrated daily to standard buffer solutions. Water transparency (Secchi) was measured using a standard 22-cm-diameter Secchi disc. Water collection, filtering, and sample storage protocols followed Environment Canada (1983). Details of the filtering and preparation of water samples for chemistry analyses are given in Wilson and Gajewski (2002). Loss-on-ignition (organic matter content) and carbonate content of the sediment were determined by drying 2-cm^3 samples overnight at 95°C and then igniting in a muffle furnace at 500°C for 3 h and 925°C for 4 h, respectively (Bengtsson and Enell, 1986).

CHIRONOMID ANALYSES

Samples were processed by deflocculating the sediment in hot 10% KOH for 30 min and sieving on a 90 μm mesh. Head capsules were hand sorted with forceps, from a Bogorov counting tray, under a 40× magnification using a stereo microscope, and placed on cover slips to dry. Cover slips were later mounted on slides using Entellan®. Head capsules were extracted from the uppermost 1 cm first, followed by the 1 to 2 cm sample if necessary to obtain a minimum of 50 head capsules (Heiri and Lotter, 2001; Quinlan and Smol, 2001).

Taxonomic identifications were performed at 100× to 400× magnification under bright-field illumination and were based on

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TABLE 1

Water chemistry and physical variables from 39 lakes in southwest Yukon and northern British Columbia. Alkalinity (Alk) was measured as mg/L CaCO₃, and conductivity was corrected to 25°C. Lake area was calculated manually from 1:50,000 maps (Energy, Mines and Resources, Canada). "NA" indicates data were not available and, therefore, mean values for that variable were substituted. The variables total phosphours (TP), filtered phosphorus (TP-F), Al, and Mo had detection limit values substituted in some cases (see explanation in text). These were 4 µg/L, 4 µg/L, 0.001 mg/L, and 0.0005 mg/L, respectively. In the case of bottom oxygen for Patrick Lake and K819, these values were assumed to be the same as surface oxygen because both lakes were less than 2 m deep. Elev. = elevation, T = surface water temperature, T_b = bottom water temperature, DO_s = surface oxygen, DO_b = bottom oxygen, Cond = conductivity, Alk = alkalinity, DOC = dissolved organic carbon, TKN = total Kjeldahl nitrogen, Chla = chlorophyll a, LOI = loss-on-ignition

Lake	Elev. (m)	Area (km²)	T_s (°C)	T_b (°C)	DO_s (mg/L)	DO_b (mg/L)	pH	Depth (m)	Secchi (m)	Cond (µS/cm)	Ca (mg/L)	K (mg/L)	Mg (mg/L)	Na (mg/L)	CI (mg/L)
Jenny	817	0.1990	19.5	19.3	10.4	10.4	8.9	2.5	2.5	728	20.10	10.80	81.10	13.20	1.65
Emerald	820	0.0838	17.0	15.5	8.9	8.5	8.8	8.0	5.3	702	11.80	7.12	96.90	17.30	1.50
Keyhole	826	0.0406	16.0	16.0	8.6	8.3	8.7	4.0	4.0	605	16.40	5.78	74.20	7.45	1.10
Fox Point	790	0.0375	15.0	7.0	9.6	0.2	8.5	10.5	3.5	1270	85.20	14.10	134.00	14.20	3.11
Ash	808	0.0075	14.5	14.5	8.6	8.3	8.2	0.8	0.8	152	24.10	1.30	5.90	2.10	2.24
Sulphur	854	1.4256	13.0	14.0	8.4	8.3	8.9	2.0	1.6	1040	19.70	10.20	75.40	19.90	2.50
Trout	727	0.5553	17.0	17.0	8.3	8.2	9.0	2.0	1.5	218	17.20	2.50	10.80	15.10	1.73
Donjek	732	0.0063	18.0	14.0	8.6	1.2	8.3	6.0	5.6	311	40.80	4.65	16.20	2.06	7.50
Rat	790	0.0575	16.0	15.0	8.3	5.0	8.7	7.0	4.8	333	34.30	4.76	20.80	5.32	1.00
Small	799	0.0063	17.5	14.0	8.8	6.0	8.8	6.0	5.0	440	26.90	10.80	39.90	6.52	1.20
West Twin	914	0.0813	12.0	12.0	8.6	8.0	8.3	2.6	2.6	229	29.40	0.60	9.51	2.59	0.10
Blanchard	914	0.0244	15.0	15.0	8.8	8.8	8.9	1.2	1.2	139	25.90	0.44	1.83	1.09	4.40
Pine	671	5.9750	15.0	5.5	8.8	9.2	8.5	12.0	8.8	285	32.10	2.66	14.40	3.72	0.50
KL1	686	0.0093	20.0	19.0	7.8	7.4	8.1	1.6	1.6	666	103.00	6.88	26.70	6.12	12.17
Three Guardsmen	940	0.1723	11.0	5.0	8.6	9.9	7.5	14.0	8.2	27	4.54	0.22	0.28	1.51	0.30
Kusawak	1000	0.0613	12.0	12.0	8.6	8.2	8.2	1.0	1.0	67	10.40	0.20	1.37	1.87	1.00
PC	799	0.0200	17.0	13.0	8.6	4.6	8.5	14.0	8.0	354	30.70	5.51	25.20	5.76	1.00
Grayling Bay	790	0.0491	14.8	5.8	8.5	0.5	8.7	14.0	5.5	397	21.90	6.49	35.50	7.52	1.30
Patrick	950	0.0769	14.0	14.0	NA	NA	8.1	2.0	2.0	470	38.03	2.40	33.76	4.42	0.80
Hungry	920	0.4469	15.0	15.0	8.5	9.2	8.7	6.5	NA	335	21.75	2.33	26.25	4.72	0.60
Scout	880	0.2356	15.0	11.8	9.0	11.0	8.8	9.0	7.0	332	22.40	4.85	21.60	15.50	1.70
WHA	753	0.0685	16.8	16.8	8.4	8.3	8.9	2.0	0.5	572	28.60	9.41	45.20	29.70	27.00
Long	680	0.1594	15.2	5.0	9.0	0.5	8.7	15.0	4.0	593	24.80	4.54	54.50	17.20	1.90
Little Louise	1021	0.0956	13.0	10.0	8.2	5.0	8.2	4.0	3.2	129	17.70	0.62	4.30	2.39	0.20
Pickhandle	686	1.6205	17.5	16.5	8.2	8.5	8.8	5.0	4.7	267	31.10	2.74	12.90	5.83	5.00
K819	747	0.7969	20.5	20.5	NA	NA	9.3	0.5	0.5	318	30.70	1.23	12.45	3.81	0.70
L1	838	0.0150	14.0	14.0	8.8	9.1	7.8	1.9	1.9	102	16.80	0.72	2.16	0.97	0.80
Stella	787	0.2356	14.0	14.0	8.1	8.0	8.5	5.0	4.5	165	30.10	0.41	2.73	1.88	0.50
Wolverine	686	0.2981	16.8	5.5	9.0	1.0	8.5	12.5	3.7	295	45.00	1.75	10.20	2.33	8.80
Little Hungry	990	0.0600	14.0	13.8	8.6	8.8	9.2	1.5	1.5	470	34.60	2.96	47.80	4.72	6.50
L2	878	0.0300	14.0	13.8	9.2	9.3	9.4	2.2	2.2	122	22.90	0.35	2.20	1.20	0.50
Axe	787	0.0100	16.0	15.5	8.8	9.0	8.8	2.0	2.0	442	22.20	6.38	38.80	3.77	0.80
Cub	880	0.0670	15.3	14.1	8.0	0.8	8.6	6.5	1.0	315	32.20	3.46	15.60	12.50	1.40
Teapot	808	0.0065	17.0	5.0	7.9	0.2	8.6	11.0	3.3	616	48.80	7.86	54.20	5.77	1.20
Atthilu	942	0.3643	13.0	13.0	9.6	9.3	9.0	1.3	1.3	169	28.70	0.72	4.77	3.39	0.30
Equisetum	991	0.0540	16.0	16.5	8.9	8.3	7.8	1.5	1.5	218	35.00	4.48	6.81	4.35	1.30
Decourcy	966	0.0175	15.0	15.0	8.8	8.6	8.1	1.0	1.0	273	23.80	0.79	8.40	31.30	0.50
YF	1021	0.0425	17.0	17.0	9.4	9.0	8.7	1.5	1.0	590	102.00	6.06	17.70	5.36	1.56
Otter Falls	899	0.1353	16.0	16.0	8.0	8.0	8.3	1.0	1.0	127	20.20	1.26	2.87	2.34	0.40
MEAN	841	0.3499	15.5	13.2	8.7	6.8	8.6	5.2	3.1	382	31.59	4.11	28.08	7.61	2.74
MEDIAN	820	0.0670	15.2	14.0	8.6	8.3	8.7	2.6	2.4	318	26.90	2.96	16.20	4.72	1.20
MINIMUM	671	0.0063	11.0	5.0	7.8	0.2	7.5	0.5	0.5	27	4.54	0.20	0.28	0.97	0.10
MAXIMUM	1021	5.9750	20.5	20.5	10.4	11.0	9.4	15.0	8.8	1270	103.00	14.10	134.00	31.30	27.00

Wiederholm (1983), Oliver and Roussel (1983), and Walker (1988, 2000). Taxonomy within the subtribe Tanytarsina followed Walker (2000). A number of specimens were encountered that bore a likeness to both the *Tanytarsus lugens* group and *Corynocera oliveri* type (both mentum and mandible features) and could not be placed reliably in either category. These were put in a separate grouping designated *T. lugens/C. oliveri* type. *Corynoneura* was separated from *Corynoneura/Thienemanniella* when sculpturing was visible on the head capsule surface (Wiederholm 1983), while *Cricotopus* and *Orthocladius* were largely indistinguishable and therefore grouped in many cases. The Figure 3 caption also refers to specific figures and their sources for the identification of some taxa (e.g., *Parakiefferiella* cf. sp. B, *Parakiefferiella* Fig. 367, and various *Psectrocladius* taxa).

DATA ANALYSIS

A few of the sites sampled in 1996 to 1998 were without dissolved organic carbon, transparency (Secchi), oxygen, and chlorophyll a (Chla) data. Mean values were substituted in each case (Tabachnick and Fidell, 1989) (Table 1). Chemical variables that had values below the detection limit in more than half of the study lakes were eliminated from all statistical analyses. This was the case for many of the metals,

TABLE 1
(Ext.)

SO$_4$ (mg/L)	Alk (mg/L)	DOC (mg/L)	TP (µg/L)	TP-F (µg/L)	TKN (µg/L)	Chla (µg/L)	Si (mg/L)	Al (mg/L)	Fe (mg/L)	Mn (mg/L)	Mo (mg/L)	LOI (%)	Carbonate (%)	# head capsules
212.73	210	24.0	8.0	6.0	2.10	0.81	3.6	0.002	0.1130	0.0053	0.0032	33.4	21.3	82
79.00	370	6.2	4.0	4.0	0.52	1.80	9.1	0.012	0.0131	0.0021	0.0053	22.2	23.5	123
81.00	280	5.7	5.0	4.0	0.41	0.62	9.6	0.001	0.0099	0.0039	0.0019	29.9	33.9	73
547.06	230	3.1	8.0	4.0	0.26	1.90	4.1	0.015	0.0596	0.0100	0.0046	11.8	9.2	62.5
6.90	70	19.4	16.6	4.0	1.02	NA	2.1	0.020	0.1770	0.0193	0.0005	29.3	4.7	75
88.00	340	18.8	20.0	8.0	1.22	6.77	6.1	0.006	0.0227	0.0131	0.0008	48.4	24.8	62.5
3.20	122	18.3	19.5	4.5	0.93	NA	3.9	0.010	0.1610	0.0456	0.0006	34.8	4.8	83.5
5.40	150	16.2	9.0	5.0	0.80	1.46	2.5	0.003	0.0247	0.0042	0.0009	10.7	8.2	83.5
12.80	170	5.4	9.0	8.0	0.43	2.06	1.4	0.012	0.0179	0.0107	0.0010	11.5	7.4	76.5
29.00	230	5.3	9.0	7.0	0.44	1.51	3.4	0.007	0.0199	0.0146	0.0014	14.0	27.4	93.5
30.00	89	2.2	7.0	4.0	0.25	1.66	1.7	0.001	0.2430	0.0218	0.0023	34.7	12.5	343.5
1.90	63	8.4	11.0	7.0	0.69	2.38	1.1	0.032	0.1260	0.0044	0.0017	64.9	19.2	78.5
7.80	145	3.9	6.0	5.0	0.25	0.87	3.3	0.004	0.0027	0.0009	0.0014	19.7	4.8	160
202.39	141	24.0	16.0	8.0	1.27	3.90	1.4	0.015	0.0716	0.0348	0.0005	21.3	4.2	130
1.10	14	0.8	4.0	4.0	0.10	0.71	1.4	0.015	0.0087	0.0040	0.0073	18.3	4.8	122.5
3.10	31	1.3	4.0	4.0	0.07	0.33	1.9	0.008	0.0272	0.0017	0.0013	45.5	8.9	141
23.00	174	2.5	4.0	4.0	0.27	0.91	4.6	0.026	0.0228	0.0063	0.0011	11.9	9.0	164.5
16.80	210	2.2	4.0	4.0	0.21	1.02	4.7	0.224	0.0392	0.0044	0.0011	8.7	5.9	92.5
38.00	220	NA	15.5	9.5	0.56	0.31	2.2	0.019	0.0400	0.0070	NA	27.7	22.4	115
29.00	154	NA	14.0	7.0	0.32	1.54	2.4	0.009	0.0090	0.0074	NA	25.2	18.9	196.5
5.30	171	7.0	7.0	4.0	0.50	1.14	2.1	0.021	0.0008	0.0038	0.0012	35.6	23.1	241.5
70.00	210	24.0	59.0	8.0	2.00	23.63	1.4	0.043	0.1200	0.0398	0.0037	34.8	16.1	143.5
85.00	240	6.0	4.0	4.0	0.53	2.09	6.1	0.115	0.0090	0.0031	0.0011	24.1	11.0	146.5
6.90	56	6.5	4.0	4.0	0.20	1.09	4.1	0.037	0.0565	0.0032	0.0005	12.6	2.2	163
21.00	112	11.4	36.0	24.0	0.73	2.03	0.4	0.005	0.0546	0.0510	0.0005	38.2	9.1	110
61.00	89	15.6	23.0	17.5	0.42	1.70	3.8	0.009	0.0507	0.0168	0.0009	14.5	22.5	167.5
1.40	50	9.0	15.0	10.0	0.53	1.62	1.1	0.013	0.0447	0.0130	0.0005	73.2	10.2	73
2.40	85	5.4	12.0	4.0	0.48	2.25	1.6	0.002	0.0255	0.0251	0.0005	79.9	15.9	103.5
28.00	109	16.4	13.0	6.0	0.73	4.56	0.3	0.008	0.0212	0.0156	0.0013	29.8	7.5	100
48.00	220	22.0	18.0	11.0	1.18	0.80	0.7	0.020	0.0342	0.0049	0.0009	33.0	27.0	290.5
2.20	63	12.1	8.0	4.0	0.55	0.96	2.9	0.007	0.0322	0.0030	0.0005	78.0	17.6	72.5
31.00	200	2.2	7.0	4.0	0.23	1.80	4.2	0.004	0.0383	0.0129	0.0025	18.9	25.5	72.5
14.00	152	10.8	23.0	4.0	1.04	7.25	2.4	0.017	0.0048	0.0063	0.0048	35.9	28.1	58
149.71	210	2.6	9.0	4.0	0.27	1.58	3.7	0.031	0.0311	0.0051	0.0043	22.3	24.5	98
3.60	89	10.7	17.0	4.0	0.50	3.11	3.5	0.019	0.1030	0.0157	0.0005	21.9	11.2	318.5
1.40	110	33.0	21.0	13.0	1.43	4.50	3.8	0.012	0.2580	0.0188	0.0012	58.0	8.2	75.5
14.80	124	43.0	7.0	9.0	1.02	0.69	4.1	0.024	0.0831	0.0030	0.0005	60.0	11.6	137.5
192.47	125	30.0	56.0	22.0	1.82	11.57	3.5	0.024	0.0826	0.0415	0.0036	45.3	6.2	306
3.90	60	6.4	6.0	4.0	0.28	1.18	2.2	0.038	0.0552	0.0057	0.0009	23.1	3.7	319
55.39	151	11.9	13.8	7.0	0.68	2.81	3.1	0.023	0.0593	0.0131	0.0018	32.4	14.3	137
21.00	145	8.4	9.0	4.5	0.52	1.62	2.9	0.013	0.0383	0.0070	0.0011	29.3	11.2	110
1.10	14	0.8	4.0	4.0	0.07	0.31	0.3	0.001	0.0008	0.0009	0.0005	8.7	2.2	58
547.06	370	43.0	59.0	24.0	2.10	23.63	9.6	0.224	0.2580	0.0510	0.0073	79.9	33.9	343.5

with the exception of Al, Fe, Mn, and Mo (Table 1). In other cases where values were below the limit of detection, the detection limit value was substituted. Environmental variables were tested for non-normal distributions using CALIBRATE version 0.70 (Juggins and ter Braak, 1997). All variables were log-transformed with the exception of surface and bottom-water temperature, pH, conductivity, alkalinity, dissolved organic carbon, and silicon, which were square-root-transformed. Total phosphorus and total filtered phosphorus remained highly skewed after transformation.

Ordinations were performed using CANOCO version 4.0 (ter Braak and Šmilauer, 1998). Both canonical correspondence analysis (CCA) and redundancy analysis (RDA) were used to assess the relationship between the chironomid assemblages and the measured physical and environmental variables because the length of the gradient of the first axis in a detrended correspondence analysis (DCA) was relatively small (2.2 standard deviation units) (ter Braak and Šmilauer, 1998). Taxon abundances were square-root-transformed for all ordinations, and rare species downweighted in DCA and CCA. RDA was performed with species centering and without standardization. A principal components analysis (PCA) of the environmental data, a DCA of the taxon data, and leverage diagnostics in CANOCO were used to check for outliers.

To reduce the presence of correlated environmental variables, we

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performed a series of constrained CCAs and RDAs where each environmental variable was selected as the sole variable, and the significance of the first axis tested using a Monte Carlo Permutation test. Only significant ($P < 0.05$, 500 permutations) variables were retained. Following this, variables were checked for high variance inflation factors (a VIF > 20 indicates that a variable is almost perfectly correlated with another [ter Braak and Šmilauer, 1998]) and eliminated sequentially, beginning with the variable having the highest VIF. This proceeded until all VIFs were below five. Forward selection was then used to identify those variables that explained most of the variance in the data. Variance partitioning (Borcard et al., 1992) was used to assess the strength and independence of those variables that explained the majority of the variance in the data, as determined by the series of constrained RDAs, as some of these variables were highly correlated with each other.

Results and Discussion

WATER CHEMISTRY

A summary of lake chemistry and physical properties is given in Table 1. More detailed descriptions are provided in Wilson and Gajewski (2002). In general the lakes are mostly shallow (mean depth = 5.2 m; maximum depth = 15 m) with nearly half (43%) having a maximum depth of 2 m or less (Table 1). Many of the lakes are closed basin, while a few have significant stream inflow (Hungry, Otter Falls, and Little Louise). Surface-water temperatures measured at the time of sampling ranged from 11°C to 20.5°C, although temperatures were rarely above 17°C. The lowest surface-water temperatures were recorded in the northern British Columbia lakes that are located in subalpine tundra (e.g., West Twin, Kusawak, and Three Guardsmen). Temperature profiles were uniform in all of the shallow (<5 m deep) lakes, while lakes of intermediate depth (5–10 m) had either isothermal or weakly stratified water columns by mid-July. Lakes that were >10 m deep had well-developed thermal stratification with epilimnion thickness of 6 to 7 m (not shown).

Alkalinity of the lakes was high compared to many boreal and subarctic regions (mean Alk = 147 mg L^{-1}; median pH = 8.7), and only 2 lakes had a specific conductance less than 100 μS cm^{-1}. This may be due to the presence of abundant glacial till in this part of the Yukon and to the evaporative enrichment associated with closed basin lakes, particularly those near Kluane Lake. Overall, the variability in conductivities among the lakes appears to be related to regional differences in geology, as well as differences in vegetation and the amount of stream inflow to lakes.

Most of the lakes are in the oligotrophic (<10 μg L^{-1}) (52%) and meso-eutrophic (10–30 μg L^{-1}) (40%) ranges, based on epilimnetic total phosphorus (TP) values (Table 1). Dissolved organic carbon (DOC) is variable as well (0.8–43 mg L^{-1}) and appears to be related to the relative abundance of grassland or tundra versus forest in the immediate vicinity of the lake, and possibly catchment area as well (Wilson and Gajewski, 2002). Sediment organic content (as determined by LOI) ranged from 9% to 80% with a mean of 32% (Table 1). LOI was negatively correlated with depth and highly correlated with bottom oxygen (not shown).

CHIRONOMIDS

A total of 5356 head capsules were enumerated from all lakes (mean per sample = 137; minimum = 58; maximum = 344), including those lakes that were later eliminated from the statistical analysis as outliers. Sixty-eight chironomid taxa were identified from the lakes, but only those present at $\geqslant 2\%$ abundance in at least 2 lakes were included in the statistical analyses (Quinlan and Smol, 2001), leaving 38 taxa in
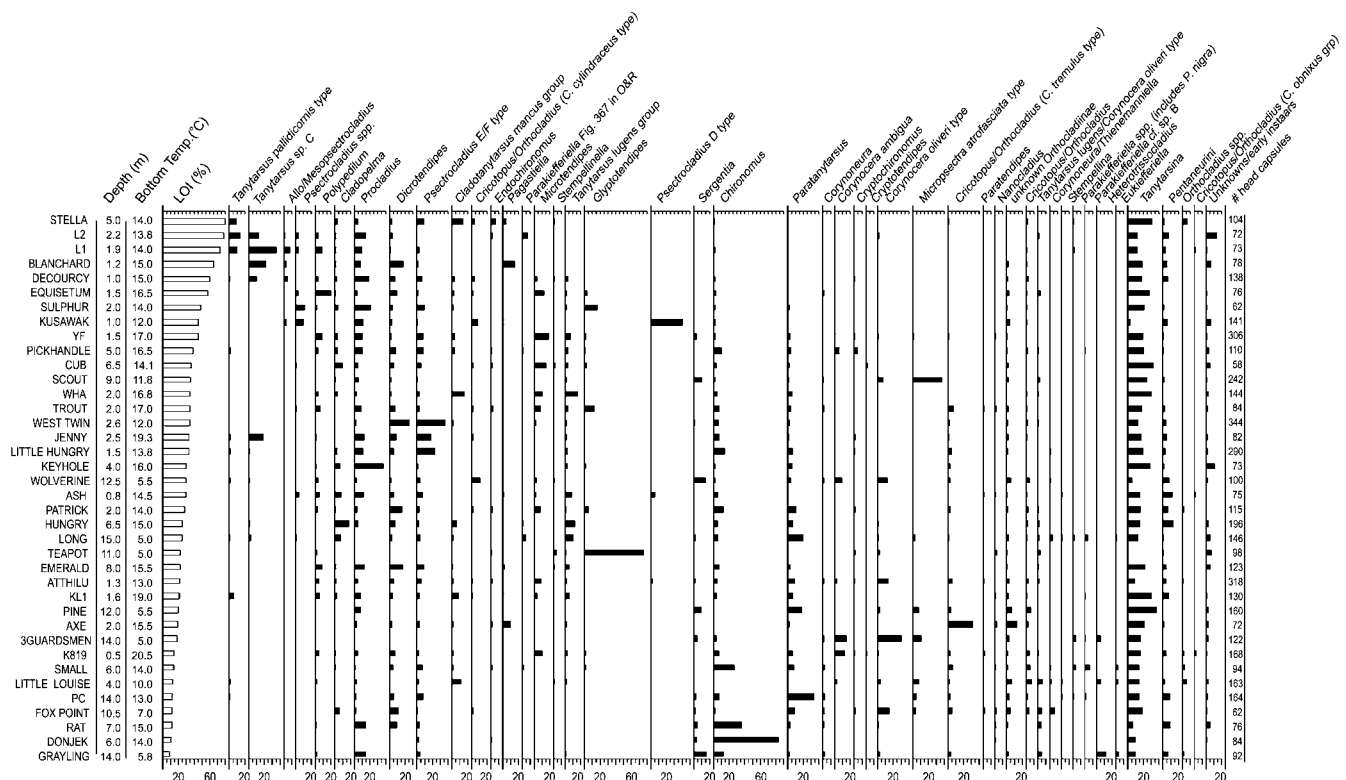
total. A few lakes had chironomid populations overwhelmingly dominated by a single genus, such as Donjek Kettle (*Chironomus* $>$ 80%) and Teapot Lake (*Glyptotendipes* $>$ 70%) (Fig. 2). *Psectrocladius* D type was abundant only in Kusawak Lake (40% relative abundance), a shallow, low alkalinity, ultra-oligotrophic lake. A number of rheophilic genera including *Rheocricotopus*, *Brillia*, *Euorthocladius*, and *Thienemanniella*? were present only in Little Louise and Otter Falls lakes, at low relative abundance (each $< 1.5\%$; not shown). These 2 lakes also had the only occurrences of Simuliidae (black fly) larval head capsules in their surface sediments, indicating stream or river influence (Currie and Walker, 1992).

The dominance of *Glyptotendipes* in Teapot Lake might be explained by a number of factors. First, Teapot Lake is relatively deep (12 m) with a very small surface area (6500 m^2), where metalimnetic oxygen maxima of 150% to 200% and a very shallow (2–3 m), mostly anoxic ($O_2 < 2$ mg L^{-1}) hypolimnion have been observed over the past 2 summers (unpublished data). Total phosphorus is much higher in the metalimnion and hypolimnion (summer averages were approximately 23 and 100 μg L^{-1}, respectively) compared to the epilimnion (9 μg L^{-1}). The small volume of oxygenated hypolimnion that the above conditions allow would explain the near absence of profundal chironomids in the surface sediments compared to lakes of similar depth, and the dominance of littoral taxa. Chironomids living in the littoral zone of the lake could easily be transported down slope (e.g., Schmäh, 1993; Walker et al., 1993), especially given the small diameter and steep sides. Second, *Glyptotendipes* is known to thrive in mesotrophic-eutrophic and highly conductive environments (Saether, 1979; Walker, 1987; Walker et al., 1995; Lotter et al., 1998), which describes well the littoral environment of Teapot Lake (specific conductance = 616 μS cm^{-1}). Furthermore, the abundance of macrophyte remains in the anoxic, deep-water sediments of Teapot Lake suggests that these are plentiful in the littoral zone, providing a substrate for the many species of *Glyptotendipes* that mine the leaves and stems of aquatic plants (Weiderholm, 1983). Based on Weiderholm (1983), the head capsules found in the surface sediments probably belong to species group A, which includes *G. barbipes*, *G. pallens*, and *G. paripes*. Lods-Crozet and Lachavanne (1994) found the *G. paripes/G. pallens* group exclusively in the submerged macrophyte zone of Lake Geneva, and *G. barbipes* is characteristic of high conductivity lakes (Wiederholm, 1983). Anoxic conditions in much of the water column of Donjek Kettle might explain the dominance of *Chironomus* in this lake, as members of the genus are known to thrive in low-oxygen environments (e.g., Hofmann, 1988; Quinlan et al., 1998).

RELATIONSHIP BETWEEN CHIRONOMIDS AND LIMNOLOGICAL VARIABLES

The Otter Falls sample was eliminated from analysis because of significant river/stream inflow from a much larger, deeper lake; Otter Falls is actually a wide area of a river. Three Guardsmen Lake was eliminated because its sample scores were outside the 95% confidence limits in both the PCA and DCA. The variables Fe and Chla were eliminated from the final ordination analyses because of extreme influence (6.9× and 5.9×, respectively) in some lakes, as revealed with leverage diagnostics (ter Braak and Šmilauer, 1998). Because we had relatively few sites, we thought it preferable to eliminate these variables rather than the lakes from the ordination. Secchi depth was also eliminated from the final ordination because these measurements were often constrained by shallow lake depths, yielding inaccurate measures of transparency (Table 1).

The series of constrained CCAs and RDAs and forward selection with both ordination methods produced similar results (not shown). However, because the percentage of the total variance in the chironomid data explained by the first 2 axes and the explained

FIGURE 2. *Chironomid assemblages from lakes in southwest Yukon and northern British Columbia arranged by weight-loss-on-ignition (%LOI) values. Weight-loss-on-ignition, bottom water temperature, lake depth, and number of head capsules shown for these sites. Three Guardsmen Lake is included to show chironomid fauna even though it was eliminated from the ordinations.*

variance of individual variables when constrained to axis 1 in RDA was slightly higher than with CCA (21% versus 20% using the 14 variables in Table 3), we present only the results for the RDA.

Of the 14 variables identified as statistically significant in the constrained RDAs, eight remained after elimination of those with the highest variance inflation factors—bottom water temperature (T_b), bottom oxygen (DO_b), depth, alkalinity (Alk), dissolved organic carbon (DOC), total phosphorus (TP), Mn, and loss-on-ignition (LOI) (Fig 3). The forward selection procedure identified LOI, TP, bottom water temperature, and alkalinity as the variables that could explain most of the variation in the chironomid data.

The first 2 axes of the RDA, consisting of the above 8 variables, were identified as statistically significant using Monte Carlo Permutation testing (P < 0.05, 500 permutations). These 2 axes explain 19.5% of the variation in the chironomid data (eigenvalues of 0.12 and 0.08, respectively). Loss-on-ignition, depth, and bottom water temperature were significantly correlated with axis 1, based on the t-values of the canonical coefficients (significant at P < 0.05), while TP and Mn were highly correlated with axis 2 (Table 2). LOI explained the majority of the variance in the data (9.8%), followed by bottom water temperature (7.7%), Secchi depth (7.5%), which was later eliminated, and depth (7.4%) (Table 3).

The results of variance partitioning between the three most significant environmental variables (as determined by constrained RDAs, but excluding Secchi depth) indicate that LOI and bottom water temperature can be considered statistically independent, as each variable captures a significant amount of variation regardless of the covariables used in the analysis (Table 4). By contrast, lake depth covaried with LOI and bottom water temperature when entered together as covariables. However, lake depth did contribute independently to the overall variance when LOI and bottom temperature were entered as single covariables (Table 4). LOI proved to be the strongest variable of the four, explaining greater than 7% of the total variance regardless of the covariables used.

These results are comparable to Olander et al. (1999) and Larocque et al. (2001), who also found sediment organic content (as measured by LOI) to be the chief explanatory variable of chironomid assemblages in subarctic lakes of northern Fennoscandia and northern Sweden, respectively. The LOI gradient represented by our Yukon lakes was relatively long (9% to 80%; Table 1) as was that of Olander et al. (17% to 88%) and Larocque et al. (3% to 87%). This may explain why Walker et al. (1991) did not find sediment organic content to be a factor determining the distribution of chironomids across treeline in Labrador, where the LOI gradient was much shorter (6.5% to 40.5%). A number of studies on chironomid ecology have pointed to the importance of substrate in determining species composition and abundance (e.g., McGarrigle, 1980; Pinder, 1986). However, the *relative* importance of sediment type versus other limnological variables in determining chironomid community composition has been the focus of debate (e.g., Warwick, 1989; Walker and Mathewes, 1989a; Walker et al., 1992). Often, sediment organic content is highly correlated with lake depth and surface water temperature as well, when lakes are sampled along strong latitudinal and altitudinal gradients (Walker et al., 1991; Lotter et al., 1997; Olander et al., 1999), making it difficult to separate the effects of these variables on chironomid communities. Surface water temperature was not a factor in determining chironomid assemblages in this study largely because lakes were not sampled along a strong climatic gradient. LOI was negatively correlated with depth (Fig. 3), although the results of the variance partitioning indicate that LOI contributed a large and statistically significant independent contribution to the overall variance when the effects of lake depth and bottom water temperature were partialled out. Olander et al. (1999) and Larocque et al. (2001) also found LOI to vary independently from both surface-water and/or air temperature and lake depth.

Other variables that were important in influencing chironomid composition in these lakes, as determined by forward selection, included

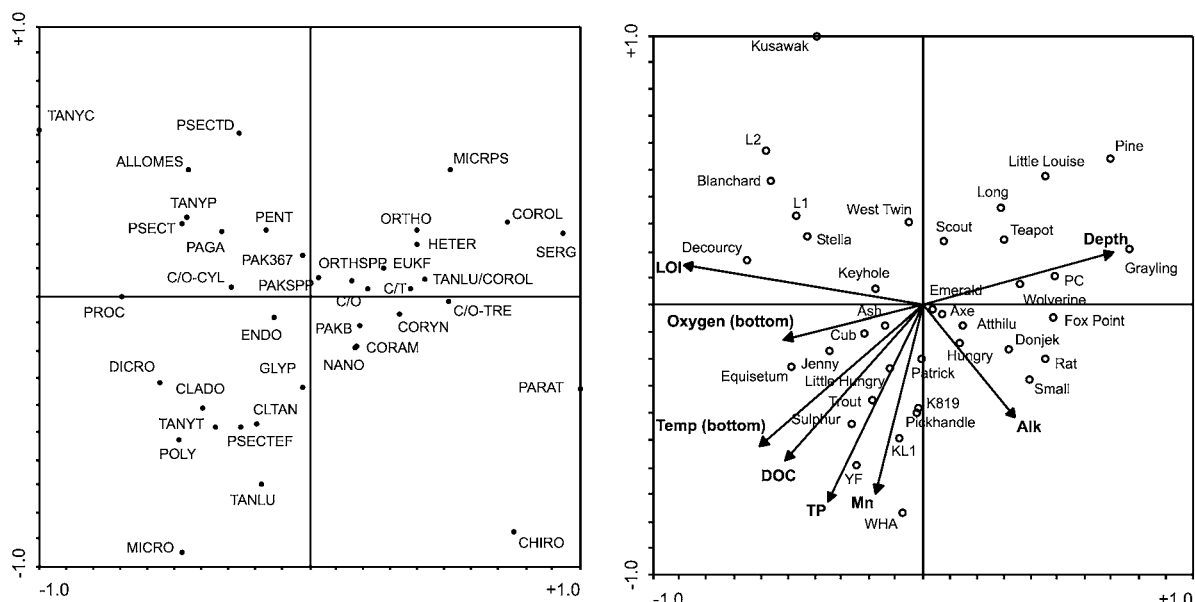S. E. WILSON AND K. GAJEWSKI / 451

FIGURE 3. Redundancy analysis (RDA) covariance biplots showing the relationship between the 8 measured environmental variables with a statistically significant relationship to chironomid distributions and the 37 lakes (A) and the 38 chironomid taxa (B). Abbreviations for the chironomid taxa are: CHIRO—Chironomus; CLADO—Cladopelma; CLTAN—Cladotanytarsus mancus group; CORAM—Corynocera ambigua; COROL—Corynocera oliveri type, CORYN—Corynoneura; C/T—Corynoneura/Thienemanniella; C/O–CYL—Cricotopus/Orthocladius (C. cylindraceus type); C/O–TRE—Cricotopus/Orthocladius (C. tremulus type); C/O—Cricotopus/Orthocladius; DICRO—Dicrotendipes; ENDO—Endochironomus; EUKF—Eukiefferiella; GLYP—Glyptotendipes; HETER—Heterotrissocladius; MICRPS—Micropsectra atrofasciata type; MICRO—Microtendipes; NANO—Nanocladius; ORTHO—unknown Orthocladiinae; ORTHSPP—Orthocladius spp.; PAGA—Pagastiella; PAKB—Parakiefferiella cf. sp. B (Walker, 1988); PAK367—Parakiefferiella Fig. 367 in Oliver and Roussel; PAKSPP—Parakiefferiella spp. (including P. nigra); PARAT—Paratanytarsus; PENT—Pentaneurini; POLY—Polypedilum; PROC—Procladius; PSECTEF—Psectrocladius E/F type (Fig. 9.61 E/F in Wiederholm); PSECTD—Psectrocladius D type (Fig. 9.61 D in Wiederholm); ALLOMES—Allo/Mesopsectrocladius; PSECT—Psectrocladius spp.; SERG—Sergentia; TANYT—Tanytarsina; TANYC—Tanytarsus sp. C; TANLU—Tanytarsus lugens group; TANLU/COROL—Tanytarsus lugens/Corynocera oliveri type; TANYP—Tanytarsus pallidicornis type.

total phosphorus, bottom water temperature, and alkalinity. Ion strength and composition are known to affect chironomid distributions (Pinder, 1986; Walker et al., 1995). Bottom water temperature is usually a measure of water depth and the degree of thermocline development, with the deepest lakes having the lowest bottom temperatures. Lake depth and bottom temperature were negatively correlated in this study (Fig. 3); however, T_b did have an independent influence on chironomid distributions that was unrelated to lake depth (Table 4). Water temperature has been shown to have a strong influence on chironomid communities (Walker et al., 1991; Olander et al., 1999), mostly through its effects on the growth and development of larvae (Oliver, 1971;

Walker and Mathewes, 1989b). Numerous studies have shown that chironomids respond to changes in the availability of hypolimnetic oxygen caused by changes in the trophic conditions of lakes (e.g., Merilainen et al., 2000; Little et al., 2000; Francis, 2001). Few studies have identified TP as a strong variable for identifying these changes (e.g., Clerk et al., 2000), although Brodersen and Lindegaard (1997) show TP to be important in determining chironomid communities in shallow lakes where hypolimnetic oxygen is not a factor. Similarly, many of our sites were shallow with uniform oxygen profiles, although the TP values for our study lakes were much smaller than those of Broderson and Lindegaard (1997).

Although LOI seems to be a major determinant of the chironomid assemblages in these lakes, a large number of environmental variables control the distribution of larval chironomids, and some of these factors determine the nature of the sediment organic matter itself. The study of sediment type appears to be an efficient means to study the joint impact of many of the above variables, as the sediments reflect the interactions of nutrient levels, light penetration, aquatic productivity, wind and wave action, distance from shore, and vegetation type (McGarrigle, 1980).

ECOLOGY OF CHIRONOMID TAXA AND COMPARISON WITH OTHER REGIONS

The RDA biplot placed chironomids indicative of high sediment organic content (LOI) on the far left side of the diagram (e.g., *Tanytarsus* sp. C, *Procladius*, *Tanytarsus pallidicornis* type, *Allo/Mesopsectrocladius*, *Psectrocladius* spp., *Microtendipes*, *Dicrotendipes*, and *Polypedilum*), and taxa indicative of more minerogenic sediments on the far right (e.g., *Chironomus*, *Paratanytarsus*, *Sergentia*,

TABLE 2

Canonical coefficients, t values, and intra-set correlations for the subset of eight environmental variables for redundancy analysis axes 1 and 2. DOC = dissolved organic carbon, TP = total phosphorus, LOI = loss-on-ignition

	Canonical coefficients		t values		Intra-set correlations	
Variable	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Bottom water temperature (T_b)	−0.52	−0.22	−3.55	−1.00	−0.60	−0.52
Bottom Oxygen (DO_b)	0.34	−0.02	2.74	−0.09	−0.51	−0.13
Depth	0.30	0.06	2.25	−2.28	0.70	0.20
Alkalinity	−0.01	−0.40	−0.15	−2.69	0.34	−0.42
DOC	−0.04	−0.27	−0.32	−1.54	−0.50	−0.57
TP	0.22	−0.41	1.48	−1.79	−0.14	−0.73
Mn	−0.04	−0.31	−0.34	−1.60	−0.18	−0.70
LOI	−0.82	0.35	−8.31	2.27	−0.88	0.15

TABLE 3

The ratio of the first constrained eigenvalue to the second unconstrained eigenvalue, percentage variance explained by the environmental variables, and results of the Monte Carlo Permutation tests (500 unrestricted permutations) in a constrained redundancy analysis where each variable is used as the sole constraining variable at a time. DOC = dissolved organic carbon, TP = total phosphorus TKN = total Kjeldahl nitrogen, Chla = chlorophyll a, LOI = loss-on-ignition

Variable	λ_1/λ_2	% Variance explained	P
Bottom temperature	0.59	7.7	0.002
Bottom oxygen	0.45	5.7	0.002
Depth	0.61	7.4	0.002
Secchi	0.59	7.5	0.002
K	0.44	5.7	0.002
Mg	0.44	5.7	0.004
Alkalinity	0.37	5.0	0.010
DOC	0.51	6.8	0.002
TP	0.47	6.5	0.002
TKN	0.50	6.8	0.002
Chla	0.34	4.8	0.012
Fe	0.42	5.5	0.010
Mn	0.38	5.3	0.014
LOI	0.85	9.8	0.002

TABLE 4

Summary of partial redundancy analysis of modern chironomid assemblages in the 37 lakes. P = significance level of Monte Carlo permutation test (500 unrestricted permutations). LOI = loss-on-ignition, T_{bot} = bottom temperature

Variable	Covariable(s)	% Variance explained	P
LOI	None	9.8	0.002
LOI	Depth	7.1	0.002
LOI	T_{bot}	8.9	0.002
LOI	Depth, T_{bot}	7.5	0.002
Depth	None	7.4	0.002
Depth	LOI	4.8	0.014
Depth	T_{bot}	5.1	0.012
Depth	LOI, T_{bot}	3.8	0.130
T_{bot}	None	7.7	0.002
T_{bot}	LOI	6.8	0.002
T_{bot}	Depth	5.4	0.006
T_{bot}	LOI, Depth	5.8	0.004

Corynocera oliveri type, *Cricotopus/Orthocladius* [*C. tremulus* type], and *Micropsectra atrofasciata* type) (Fig. 3). The first axis also represents a gradient of lake depth, with shallow lakes occurring on the left and deeper lakes on the right. Chironomids characteristic of the deepest lakes with cold hypolimnetic or bottom waters are positioned in the upper right quadrant (e.g., *Sergentia*, *Corynocera oliveri* type, *Micropsectra atrofasciata* type, *Heterotrissocladius*, *Eukiefferiella*, *Tanytarsus lugens/C. oliveri* type) while chironomids typical of the shallow lakes with higher bottom water temperatures are positioned in the lower left quadrant (e.g., *Microtendipes*, *Polypedilum*, *Cladopelma*, *Dicrotendipes*, *Tanytarsus lugens* group, *Cladotanytarsus mancus* group, and *Psectrocladius* E/F type). This latter group of taxa is also characteristic of high nutrient (TP and DOC) lakes (Fig. 3). Shallow lakes with warm bottom temperatures are typically more productive, having an abundance of algae and aquatic plants that yield higher organic sedimentation—hence, the position of these lakes on the left side of the ordination in the direction of increasing LOI.

The above trends are comparable to other studies of modern chironomid assemblages. *Heterotrissocladius*, *Sergentia*, and *Micropsectra* are common in the profundal zone of deep, thermally stratified lakes in temperate regions (Walker, 1991). *Heterotrissocladius* and *Micropsectra* are more typical of oligotrophic lakes (Saether, 1979), although *Micropsectra* has been known to occur across a trophic gradient (Lods-Crozet and Lachavanne, 1994) and was common in mesotrophic lakes in the Swiss Alps (Lotter et al., 1998). *Sergentia* was most abundant in oligotrophic (<10 μg L^{-1} TP) lakes in our data (Table 1, Fig. 3), although it commonly thrives under mesotrophic conditions (moderate oxygen depletion) (Walker, 1991; Quinlan et al., 1998). However, as very few deep, mesotrophic lakes were sampled in this study, we may simply have missed the preferred niche of this genus. The shallow-water/littoral taxa observed in our lakes are also typical of other regions (e.g., Schmäh, 1993; Walker and MacDonald, 1995; Korhola et al., 2000). One exception may be the *Tanytarsus lugens* group, which in our data was common in shallow, productive lakes (Figs 2 and 3), but is considered an oligotrophic taxon (e.g., Saether, 1979; Brundin, 1956, *in* Hofmann, 1986), and a cold stenotherm (Hofmann, 1988). *T. lugens* was also present in many

oligotrophic lakes of northern Fennoscandia (Korhola et al., 2000). However, Lotter et al. (1998) show that *T. lugens* group is common in mesotrophic lakes from the Alps, and it was a dominant taxon in the mesotrophic profundal zone of Lake Geneva (Lods-Crozet and Lachavanne, 1994). Alm and Willassen (1993) and Hofmann (1988) also note that it occurs as a profundal species in oligotrophic to weakly eutrophic lakes of middle Europe but can occur in the littoral zone of subarctic lakes where temperatures are lower. These apparent differences in ecology may be related in part to taxonomic uncertainties. Difficulties can arise in distinguishing *C. oliveri* and *T. lugens* as noted above (*T. lugens* group and *C. oliveri* type grouped in some cases) and by Alm and Willassen (1993). *C. oliveri* is considered a cold stenotherm (Pinder and Reiss *in* Olander et al., 1999) and did occur in the deepest lakes with the lowest bottom water temperatures in our sites (Figs. 2 and 3). However, given the lack of ecological information on littoral chironomid communities (Hofmann, 1986), it is possible that *T. lugens* has a more widespread trophic and bathymetric distribution than previously documented.

The chironomid distribution with respect to LOI in our data compares well with Olander et al. (1999). *Dicrotendipes*, *Psectrocladius*, *Allo/Mesopsectrocladius*, *Microtendipes*, and *Polypedilum* occur in highly organic sediments, and *Heterotrissocladius*, *Micropsectra*, and *Corynocera oliveri* type occur in more minerogenic sediments in both regions. Similarly, Larocque et al. (2001) found *Dicrotendipes*, *Polypedilum*, and *Microtendipes* in more organic sediments, as well as *Tanytarsus* sp. C and *Tanytarsus pallidicornis* type, which were prominent in the most organic-rich sediments in our study lakes (Figs. 2 and 3). *Heterotrissocladius* and *Micropsectra* were also more abundant in Swedish lakes with lower LOI values. One major difference was the dominance of *Chironomus* in Yukon lakes with the least organic sediment, compared to the Fennoscandian and Swedish lakes, where it was most abundant in highly organic lake bottoms. McGarrigle (1980) also found species of *Chironomus* to be more abundant in sediment with high organic content. The three Yukon lakes where *Chironomus* is most abundant (Donjek, Rat, and Small) have low to moderate oxygen concentrations near the lake bottom (Table 1), and in the case of Small Lake, stable oxygen readings were difficult to obtain. It is possible that low oxygen is responsible for their success in these lakes and that the low organic matter content is simply a coincidence. *Chironomus* was dominant in Donjek Kettle, and this site undoubtedly has a large influence on the relationship of LOI with *Chironomus* abundance. Donjek Kettle receives large inputs of loess from the Donjek River valley. Perhaps the loess input dilutes the

organic matter in the sediment, while the lake otherwise has conditions suitable for *Chironomus* survival.

This study confirms the importance of sediment organic matter in determining the distribution of chironomid populations in lakes from the southwest Yukon. Sediment organic matter in turn depends on the productivity of the lake in addition to watershed conditions. Future work will investigate the coupling of these ecosystems and the factors causing them to change in time and space.

Acknowledgments

References Cited

Alm, T., and Willassen, E., 1993: Late Weichselian Chironomidae (Diptera) stratigraphy of Lake Nedre Æråsvatn, Andøya, northern Norway. *Hydrobiologia,* 264: 21–32.

Bengtsson, L., and Enell, M., 1986: Chemical analysis. *In*: Berglund, B. E. (ed.), *Handbook of Holocene palaeoecology and palaeohydrology.* New York, John Wiley and Sons, 423–454.

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

Brinkhurst, R. O., 2002. *The benthos of lakes.* New Jersey, Blackburn Press, 190 pp.

Brodersen, K. P., and Lindegaard, C., 1997: Significance of subfossil chironomid remains in classification of shallow lakes. *Hydrobiologia,* 342/343: 125–132.

Brooks, S. J., and Birks, H. J. B., 2000: Chironomid-inferred late-glacial and early-Holocene mean July air temperatures for Kråkenes Lake, western Norway. *Journal of Paleolimnology,* 23: 77–89.

Clerk, S., Hall, R., Quinlan, R., and Smol, J. P., 2000: Quantitative inferences of past hypolimnetic anoxia and nutrient levels from a Canadian Precambrian shield lake. *Journal of Paleolimnology,* 23: 319–336.

Currie, D. C., and Walker, I. R., 1992: Recognition and palaeohydrologic significance of fossil black fly larvae, with a key to the Nearctic genera (Diptera: Simuliidae). *Journal of Paleolimnology,* 7: 37–54.

Environment Canada, 1983: *Sampling for Water Quality.* Water Quality Branch, Inland Waters Directorate, Ottawa, Ontario, 55 pp.

Francis, D., 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.

Gabrielse, H., Tempelman-Kluit, D. J., Blusson, S. L., and Campbell, R. B., 1977: *Geological Survey of Canada Map 1398A*, scale = 1:1,000,000.

Glew, J. R., 1988: A portable extruding device for close interval sectioning of unconsolidated core samples. *Journal of Paleolimnology,* 1: 235–239.

Glew, J. R., 1991: Miniature gravity corer for recovering short sediment cores. *Journal of Paleolimnology,* 5: 285–287.

Heiri, O., and Lotter, A., 2001: Effect of low sum counts on quantitative environmental reconstructions: an example using subfossil chironomids. *Journal of Paleolimnology,* 26: 343–350.

Hofmann, W., 1986: Chironomid analysis. *In* Berglund, B.E. (ed.), *Handbook of Holocene palaeoecology and palaeohydrology.* New York, John Wiley and Sons, 715–726.

Hofmann, W., 1988: The significance of chironomid analysis (Insecta: Diptera) for paleolimnological research. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 62: 501–509.

Johnson, F., and Raup, H. M., 1964: *Investigations in southwest Yukon: geobotanical and archaeological reconnaisance.* Andover,

Massachusetts, Papers of the Robert S. Peabody Foundation for Archaeology, 6, 488 pp.

Juggins, S., and ter Braak, C. J. F., 1997: CALIBRATE version 0.70: a C++ program for analysing and visualising species environment relationships and for predicting environmental values from species assemblages. Steve Juggins, Department of Geography, University of Newcastle, Newcastle upon Tyne, UK NE1 7RU. Stephen.Juggins@ncl.ac.uk

Korhola, A., Olander, H., and Blom, T., 2000: Cladoceran and chironomid assemblages as quantitative indicators of water depth in subarctic Fennoscandian lakes. *Journal of Paleolimnology,* 24: 43–54.

Larocque, I., Hall, R. I., and Grahn, E., 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.

Little, J. L., Hall, R. I., Quinlan, R., and Smol, J. P., 2000: Past trophic status and hypolimnetic anoxia during eutrophication and remediation of Gravenhurst Bay, Ontario: comparison of diatoms, chironomids, and historical records. *Canadian Journal of Fisheries and Aquatic Sciences,* 57: 333–341.

Lods-Crozet, B., and Lachavanne, J.-B., 1994: Changes in the chironomid communities in Lake Geneva in relation with eutrophication, over a period of 60 years. *Archiv für Hydrobiologia,* 130: 453–471.

Lotter, A. F., Birks, H. J. B., Hofmann, W., and Marchetto, A., 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.

Lotter, A. F., Birks, H. J. B., Hofmann, W., and Marchetto, A., 1998: Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. *Journal of Paleolimnology,* 19: 443–463.

McGarrigle, M. L., 1980: The distribution of chironomid communities and controlling sediment parameters in L. Derravaragh, Ireland. *In* Murray, D. A. (ed.), *Chironomidae: ecology, systematics, cytology and physiology.* Toronto, Pergamon Press, 275–282.

Merilainen, J. J., Hynynen, J., Teppo, A., Palomaki, A., Granberg, K., and Reinikainen, P., 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.

Olander, H., Birks, H. J. B., Korhola, A., and Blom, T., 1999: An expanded calibration model for inferring lakewater and air temperatures from fossil chironomid assemblages in northern Fennoscandia. *The Holocene,* 9: 279–294.

Oliver, D. R., 1971: Life history of the Chironomidae. *Annual Review of Entomology,* 16: 211–230.

Oliver, D. R., and Roussel, M. E., 1983: *The insects and arachnids of Canada. Part 11: the genera of larval midges of Canada, Diptera: Chironomidae.* Ottawa, Agriculture Canada Publication No. 1746, 263 p.

Oswald, E. T., and Senyk, J. P., 1977: *Ecoregions of Yukon Territory.* Victoria, British Columbia, Canadian Forestry Service, Environment Canada, 115 pp.

Pinder, L. C. V., 1986: Biology of freshwater Chironomidae. *Annual Review of Entomology,* 31: 1–23.

Porinchu, D., and Cwynar, L., 2000: The distribution of freshwater Chironomidae (Insecta: Diptera) across treeline near the lower Lena River, northeast Siberia, Russia. *Arctic, Antarctic, and Alpine Research,* 32: 429–437.

Porinchu, D., and MacDonald, G., 2003. The use and application of freshwater midges (Chironomidae: Insecta: Diptera) in geographical research. *Progress in Physical Geography,* 27: 378–422.

Pourriot, R., and Meybeck, M., 1995: *Limnologie générale.* Paris, Masson, 956 pp.

Quinlan, R., and Smol, J. P., 2001: Setting minimum head capsule abundance and taxa deletion criteria in chironomids-based inference models. *Journal of Paleolimnology,* 26: 327–342.

Quinlan, R., Smol, J. P., and Hall, R. I., 1998: Quantitative inferences of past hypolimnetic anoxia in south-central Ontario lakes using fossil midges (Diptera: Chironomidae). *Canadian Journal of Fisheries and Aquatic Sciences,* 55: 587–596.

Saether, O. A., 1979: Chironomid communities as water quality indicators. *Holarctic Ecology,* 2: 65–74.

Schmäh, A., 1993: Variation among fossil chironomid assemblages in surficial sediments of Bodensee-Untersee (SW-Germany): implications for paleolimnological interpretation. *Journal of Paleolimnology,* 9: 99–108.

Tabachnick, B. G., and Fidell, L. S., 1989, *Using multivariate statistics (second edition).* New York, Harper Collins, 746 pp.

ter Braak, C. J. F., and Šmilauer, P., 1998: *CANOCO for Windows: software for canonical community ordination (version 4).* Ithaca, New York, Microcomputer Power.

Wahl, H. E., Fraser, D. B., Harvey, R. C., and Maxwell, J. B., 1987: *Climate of Yukon.* Ottawa, Ontario, Climatological Studies Number 40, Environment Canada, 323 pp.

Walker, I. R., 1987: Chironomidae (Diptera) in paleoecology. *Quaternary Science Reviews,* 6: 29–40.

Walker, I. R., 1988: Late-Quaternary palaeoecology of Chironomidae (Diptera: Insecta) from lake sediments in British Columbia. Ph.D. dissertation. Burnaby, British Columbia, Simon Fraser University, 204 pp.

Walker, I. R., 1991: Modern assemblages of arctic and alpine Chironomidae as analogues for late-glacial communities. *Hydrobiologia,* 214: 223–227.

Walker, I. R., 2000. *The www field guide to subfossil midges.* http://www.ouc.bc.ca/eesc/iwalker/wwwguide/ (last accessed November 2004).

Walker, I. R., and MacDonald, G. M., 1995: Distributions of Chironomidae (Insecta: Diptera) and other freshwater midges with respect to treeline, Northwest Territories, Canada. *Arctic and Alpine Research,* 27: 258–263.

Walker, I. R., and Mathewes, R. W., 1989a: Much ado about dead Diptera. *Journal of Paleolimnology,* 2: 19–22.

Walker, I. R., and Mathewes, R. W., 1989b: Chironomidae (Diptera) remains in surficial lake sediments from the Canadian Cordillera: analysis of the fauna across an altitudinal gradient. *Journal of Paleolimnology,* 2: 61–80.

Walker, I. R., Levesque, A. J., Pienitz, R., and Smol, J. P., 2003: Freshwater midges of the Yukon and adjacent Northwest Territories: a new tool for reconstructing Beringian paleoenvironments? *Journal of the North American Benthological Society,* 22: 323–337.

Walker, I. R., Reavie, E. D., Palmer, S., and Nordin, R. N., 1993: A palaeoenvironmental assessment of human impact on Wood Lake, Okanagan Valley, British Columbia, Canada. *Quaternary International,* 20: 51–70.

Walker, I. R., Smol, J. P., Engstrom, D. R., and Birks, H. J. B., 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., Smol, J. P., Engstrom, D. R., and Birks, H. J. B., 1992: Aquatic invertebrates, climate, scale, and statistical hypothesis testing: a response to Hann, Warner, and Warwick. *Canadian Journal of Fisheries and Aquatic Sciences,* 49: 1276–1280.

Walker, I. R., Wilson, S. E., and Smol, J. P., 1995: Chironomidae (Diptera): quantitative palaeosalinity indicators for lakes of western Canada. *Canadian Journal of Fisheries and Aquatic Sciences,* 52: 950–960.

Warwick, W. F., 1989: Chironomids, lake development and climate: a commentary. *Journal of Paleolimnology,* 2: 15–17.

Wiederholm, T. (ed.), 1983: *Chironomidae of the Holarctic region. Keys and diagnoses. Part 1—Larvae.* Entomologica Scandinavica, Supplement 19, 457 pp.

Wilson, S. E., and Gajewski, K., 2002: Surface sediment diatom assemblages and water chemistry from 42 subarctic lakes in the southwestern Yukon and northern British Columbia, Canada. *Ecoscience,* 9: 256–270.