CHAPTER 5

SURFACE SAMPLES

One of the major impediments to palaeoecological research is the dearth of ecological information for many fossil organisms. Although "descriptive" research is no longer in vogue, palaeoecologists often wish more professional naturalists, like Darwin, Dawson, Ganong, and Richardson, were surveying our flora and fauna today. A tremendous volume of chironomid ecological data is scattered through the literature, yet isolating the pertinent facts for palaeoecological reconstructions is a laborious process. Fortunately, a few recent synthetic articles compile this information for the holistic ecologist (e.g. Brinkhurst, 1974; Danks, 1981; Fitkau and Reiss, 1978; Sæther, 1979).

This information must be used cautiously by palaeoecologists. The fossil assemblage, isolated by palaeoecologists, is not the same as the fauna perceived by ecologists. Benthic ecologists often sample the summer fauna, ignoring winter inhabitants. The methods of separating benthos vary widely (e.g. Ankar *et al.*, 1979; Flannagan, 1973). On the other hand, taphonomic (factors relating to decomposition, deposition, and preservation of fossils) processes regulate which organisms will be preserved, in what numbers, and where. Fortunately, taphonomic considerations are not as severe an influence upon chironomid fossils (Iovino, 1975; Walker *et al.*, 1984), as with some other groups of organisms.

To avoid, or at least to partially circumvent such problems, palynologists and diatomists have increasingly relied upon recent "fossil" assemblages available in the surficial sediments of lakes (e.g. Davis and Anderson, 1985; MacDonald and Ritchie, 1986). Analysis of surficial sediment samples across environmental gradients, such as pH, climate, or concentrations of specific nutrients, can reveal the influence of each factor. No comparable chironomid analyses have yet been published.

This chapter published in modified form, 1989 (Journal of Paleolimnology 2:61-80).

To examine how climate influences chironomid faunal composition, as perceived by the palaeoecologist, I have collected surficial sediments from lakes distributed across an altitudinal gradient. This gradient is not entirely comparable to a horizontal climatic gradient, but offers a first approximation.

Study sites

Thirty surface samples were collected primarily in the Pacific Northwest, from lakes near Vancouver, Canada, and the adjacent Mount Baker area of Washington State, U.S.A. Several samples were also collected in Yoho and Banff National Parks, in the Canadian Rocky Mountains. These parks straddle the British Columbia - Alberta border. Also included is one Queen Charlotte Island location, and surface records from each of my four British Columbia stratigraphic study sites (Chapters 2, 3, and 4). The locations of each of these sites are summarized in Table 5.1. Several of the lake names are informal designations (placed in quotation marks), since no formal names have yet been assigned. Some observations concerning the lakes' characteristics, at the time of sampling are summarized in Table 5.2.

The lakes are distributed from near sea level to alpine situations. Complete forest cover surrounds most of the low elevation lakes, whereas no trees are present at the highest elevations. Heikkinen (1984b, 1985) notes that the coastal timberline zone is exceptionally broad, spanning elevations from 1400 to 1750 m on Mount Baker, Washington (near Vancouver, B.C.). Although in many regions timberline is primarily regulated by temperature, the great snow accumulations in coastal British Columbia persist long into summer. Patches of persistent snow are likely responsible for the great breadth of the upper subalpine woodland-meadow mosaic (Brooke *et al.*, 1970; Heikkinen, 1984b, 1985) on Pacific coastal mountains. Although trees were common on the south side of

Table 5.1. Locations of the Cordilleran lakes sampled for surficial sediments.

Park and District Codes:
AL=Alice Lake Provincial Park
B=Banff National Park, Alberta
DL=Duffey Lake area
G^1=Garibaldi Provincial Park, near Elfin Shelter
G^2=Garibaldi Provincial Park, near the Black Tusk
G^3=Garibaldi Provincial Park, near Singing Pass
GE=Golden Ears Provincial Park
MB=Mount Baker National Forest, Washington, U.S.A.
MS=Mount Seymour Provincial Park
QCI=Queen Charlotte Islands
S=Sasquatch Provincial Park
URF=University of British Columbia Research Forest
VI=Vancouver Island
W=Whistler area
Y=Yoho National Park

	Elevation	Longitude	Latitude	Park or District
<u>Banff and Yoho Nat. Pk</u>				
Ptarmigan Lk.	2330 m	116°04.5'W	51°29.0'N	B
Hidden Lk.	2270	116°06.5'	51°29.1'	B
Opabin Lk.	2270	116°18.7'	51°20.4'	Y
Hungabee Lk.	2240	116°19.1'	51°20.5'	Y
Lk. Annette	1970	116°12.5'	51°19.3'	B
Mud Lk.	1600	116°10.5'	51°26.3'	B
<u>Southwestern B.C.</u>				
"Chlorine" Lk.	2090	122°09.2'	50°20.5'	DL
"Aqua incognito"	1970	122°10.2'	50°20.4'	DL
Russet Lake	1870	122°51.9'	50°01.4'	G^3
Black Tusk Lk.	1750	123°01.6'	49°57.6'	G^2
Helm Lk.	1720	123°01.4'	49°58.0'	G^2
Mimulus Lk.	1720	123°01.8'	49°57.5'	G^2
"Coleman Pd"	1680	121°44.0'	48°48.6'	MB
"N." Elfin Lk.	1480	122°59.2'	49°47.2'	G^1
"S." Elfin Lk.	1480	122°59.2'	49°47.1'	G^1
Hayes Lk.	1460	121°43.3'	48°51.5'	MB
Highwood Lk.	1250	121°40.5'	48°51.9'	MB
Mystery Lk.	1140	122°56.0'	49°22.5'	MS
Goldie Lk.	990	122°56.1'	49°22.3'	MS
Lost Lk.	690	122°56.1'	50°07.7'	W
Marion Lk.	300	122°33.0'	49°19.0'	URF
Mike Lk.	220	122°32.3'	49°16.5'	GE
Stump Lk.	200	123°07.3'	49°47.3'	AL
Alice Lk.	180	123°07.3'	49°46.7'	AL
Misty Lk.	70	127°15.7'	50°36.3'	VI
Hicks Lk.	60	121°42.0'	49°20.5'	S
Deer Lk.	60	121°40.5'	49°22.0'	S
Great Central Lk.	25	125°05.0'	49°20.0'	VI
<u>Queen Charlotte Islands</u>				
"Hermit Thrush Pd"	550	131°54.4'	52°41.3'	QCI
"Hippa Lk."	230	132°58.4'	53°31.9'	QCI

Table 5.2. Characteristics of lakes and ponds from which surface samples were collected for chironomid analysis. (Temperature and pH values are for surface water.)

Lake	Depth of Sample	pH	Temperature at Sampling	Date
<u>Banff and Yoho Nat. Parks</u>				
Ptarmigan	8.5 m	7.9	6°C	4/9/86
Hidden	13.5	8.2	5	4/9/86
Opabin	6.0	7.9	5	3/9/86
Hungabee	2.5	7.6	7	3/9/86
Annette	13.0	8.2	4	2/9/86
Mud	7.0	8.3	10	5/9/86
<u>Southwestern B.C.</u>				
"Chlorine"	3.5	6.6	2	3/8/86
"A. Incognito"	3.	6.9	2	3/8/86
Russet	14.5	8.4	9	13/8/86
Black tusk	13.	7.4	8	17/8/86
Helm	9.5	7.3	1	17/8/86
Mimulus	1.0	7.4	12	17/8/86
"Coleman"	12.	6.1	4	13/9/86
"N." Elfin	4.	5.5	7	27/7/86
"S." Elfin	5.5	5.5	4	27/7/86
Hayes	17.	7.3	15	24/7/86
Highwood	6.5	6.6	7	19/6/86
Mystery	6.5	-	FROZEN	2/86
Goldie	1.	-	FROZEN	2/86
Lost	11.	7.3	-	10/5/86
Marion	6.	-	-	6/82
Mike	6.5	-	-	2/86
Stump	16.	-	FROZEN	2/86
Alice	10.5	-	FROZEN	2/86
Misty	5.	-	-	18/8/86
Hicks	17.	6.5	-	5/4/86
Deer	5.	6.7	-	5/4/86
Great Central	123.	-	-	1/11/88
<u>Queen Charlotte Islands</u>				
"H. Thrush"	2.	5.7	-	20/7/84
"Hippa"	1.	-	-	14/7/83

subalpine "Hermit Thrush Pond", on the Queen Charlotte Islands, trees were scattered and stunted on adjacent, slightly higher slopes. Timberline is higher and better defined in the Rocky Mountains. The alpine–subalpine transition is evident near 2200 m in Banff National Park (Mayhood and Anderson, 1976).

Although timberline is lower on the coast, including the Queen Charlotte Islands and Coast Ranges, mean annual temperatures are lower at timberline in the Rockies. Mean annual temperatures below 0° C occur at some lower subalpine sites in the Rocky Mountains, but may exceed 0° C near coastal timberline (Heikkinen, 1984b; Prov. of B.C, 1980). However, snow accumulation is greater on the coast, and may remain longer to produce a short growing season, similar to that inland. Climatic summaries are provided in Table 5.3 for several locations near my study sites.

Most of the lakes sampled, in the Coast Mountains near Vancouver, including those in Alice, Garibaldi, Golden Ears, and Mount Seymour Provincial Parks, the Duffey Lake area, and the University of British Columbia Research Forest, are underlain by base–poor plutonic rocks of the Coast Mountain complex. However, other volcanic rocks, and some sedimentary exposures, are scattered throughout the Coast Mountains (Prov. of B.C., undated). Those lakes sampled near the Black Tusk in Garibaldi Provincial Park, and at Mount Baker in Washington, lie in areas of recent Pleistocene volcanic activity. Thus intact or finely fragmented basaltic rocks may dominate in the bedrock and derived soils. Palaeozoic and Mesozoic sedimentary rocks prevail within Sasquatch Provincial Park, and at Misty Lake on Vancouver Island.

In contrast, the Canadian Rocky Mountains are mostly composed of sedimentary materials. The main ranges, in which all of the sampled lakes lie, are composed principally of Cambrian carbonates and quartzitic sandstone (Rutter, 1972).

Table 5.3. Climatic summaries for weather stations near the surface sample collection sites. (southwestern British Columbia - Vancouver Harbour and Hollyburn Ridge; Queen Charlotte Islands - Tasu Sound; Rocky Mountains - Boulder Creek, Yoho National Park).

	Vancouver Harbour	Hollyburn Ridge	Tasu Sound	Yoho Nat. Pk (Boulder Ck)
Latitude	49°18'	49°22'	52°46'	51°23'N
Longitude	123°07'	123°12'	132°03'	116°32'W
Elevation (m)	0	951	15	1219
Mean Daily Temperature (°C)				
Coldest Month	3.4	-2.3	2.8	-10.9
Warmest Month	17.6	13.2	14.6	15.3
Annual	10.3	5.0	8.2	2.9
Precipitation				
Rain (mm):				
Annual	1482.3	2134.3	4172.7	308.6
Snow (cm):				
Annual	60.0	820.2	75.7	323.1
Frost-free Period (d)	270	126	217	90
Degree-days (d·°C)				
above 0°C	3838.3	2008.4	3039.0	2102.5
above 5°C	2092.0	919.2	1441.5	1109.4

(Environment Canada, 1982)

Intrusive Mesozoic crystalline rock, dissected by mafic dykes, is exposed at "Hermit Thrush Pond" in the Queen Charlotte Islands. Volcanic rocks, including basalt and rhyolite, are common near "Hippa Lake" (Sutherland Brown, 1968).

Methods

Surface samples were collected with an Ekman grab, deployed from a small inflatable raft. Collections were usually made near the centre of the lakes, although practical considerations including safety, winds, and sampling difficulties occasionally interfered with my best intentions. Sampling depths are summarized in Table 5.2. About 250 mL of sediment, within the top 10 cm of the grab sample, were retained. These sediments probably represent the last 50 to 100 years of deposition. These were refrigerated upon my return from field trips.

Analysis of this sediment proceeded largely as described for earlier core investigations. Head capsule concentrations usually permitted small aliquots (1 or 2 mL), to be analyzed. However, some samples, particularly those obtained from glacial lakes required more elaborate treatments. For those samples, larger aliquots, up to 93 mL, were occasionally analyzed.

To achieve acceptable head capsule "concentrates" from glacial lakes unusual chemical treatments were necessary. These frequently included the HF and HCl acid treatments commonly employed by palynologists, as well as the usual KOH and sieving techniques. Best results for clay samples were obtained using the following treatment series:

1) Sediment washed in .075 mm sieve; backwash material retained by sieve into centifuge tube.

2) Centrifugation of material at moderate speeds for about 5 minutes; decant water

3) Wash with 10% HCl

4) Centrifuge and decant acid

5) Wash with cold concentrated HF (let stand overnight)

6) Centrifuge and decant acid

7) Wash with HCl

8) Centrifuge and decant

9) Wash with warm 6% KOH

10) Collect and wash concentrate in .075 mm sieve with water

11) Backwash concentrate into 50 mL beaker for later examination in Bogorov counting cells (Gannon, 1971)

Although the HF treatment is unusual for chironomid stratigraphic work, it is commonly employed by palynologists to dissolve silicates. HF has little apparent effect on organic tissues. Palynologists regularly discover chitinous remains on their slides, including insect and fungal fragments, even where acetolysis (a more severe treatment to remove organic matter) has been employed. Without the HCl and HF treatments analysis of glacial lake sediments for chironomids would usually have been impossible.

Results

A summary of the surface sample results is presented in Figure 5.1. It was readily apparent that many species common at low elevations were absent at higher elevations, particularly in the alpine or upper subalpine. A few taxa were common at all altitudes, and another group was most abundant at the highest locations. Diversity figures (Figure

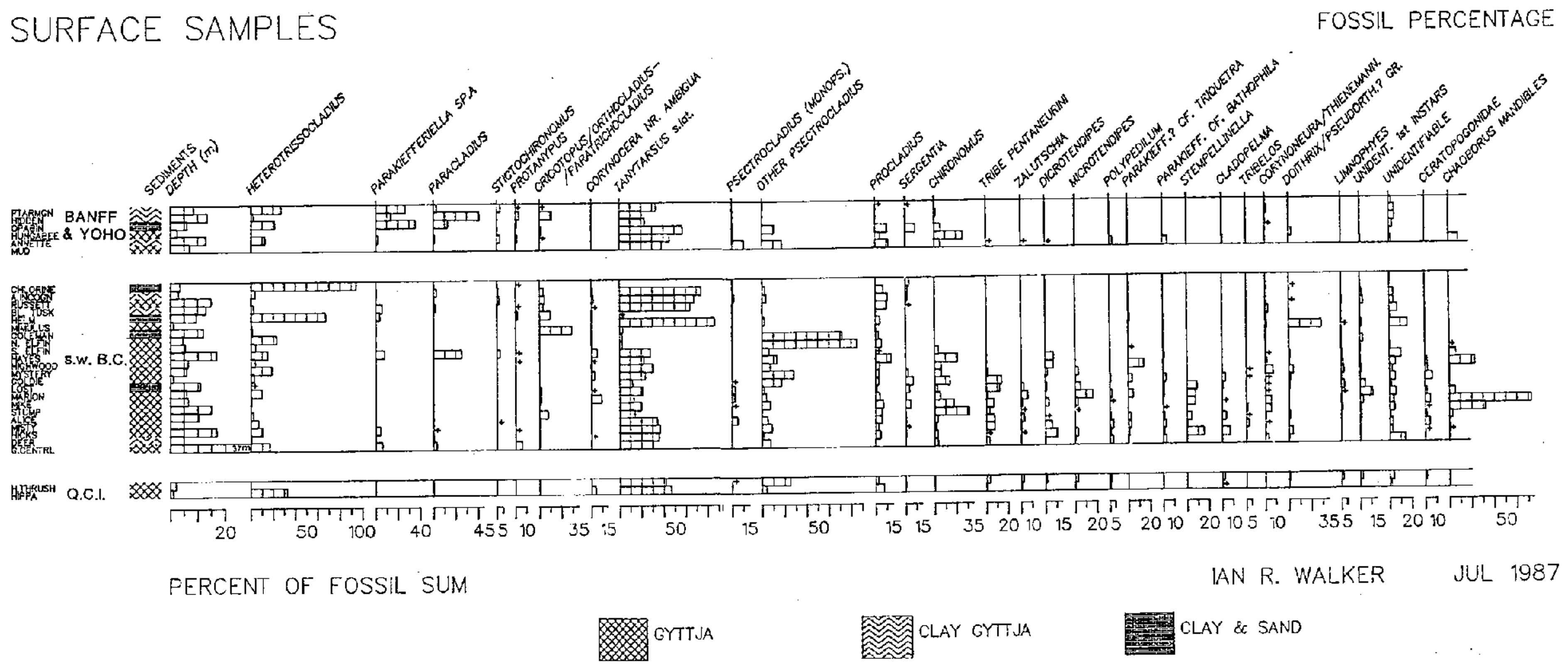

Figure 5.1 Percentage (of total number of chironomid head capsules at each sample site) diagram representing altitude distribution of common chironomid taxa from surface samples in the Cordillera of southern Canada, and adjacent United States.
(Several rare taxa, including *Pseudodiamesa* have been excluded; "+" indicates presence in small numbers). Samples are arranged as in Tables 5.1 and 5.2 – ie. 1) Samples from different regions are separated; 2) Within a region the samples are organized by altitude.

5.2) indicate complex faunas at all sites lower than the subalpine, but a sharp decrease in diversity occurs in the coastal upper subalpine zone (*ca.* 1400 to 2000 m). To effectively summarize these results, I have divided the total fauna into three groups:

1) *Low to mid-elevation taxa* - Few chironomid genera completely disappeared from the samples at elevations below the lower subalpine, however many were rare or entirely absent from higher sites, including the alpine and upper subalpine. Prominent low to mid elevation taxa included many of the Chironomini (e.g. *Cladopelma* Kieffer, *Cryptotendipes* Lenz, *Dicrotendipes*, *Lauterborniella* Thienemann & Bause/*Zavreliella* Kieffer, *Microtendipes*, *Pagastiella* cf. *ostansa*, *Paratendipes* Kieffer, *Polypedilum* Kieffer, and *Tribelos*), but some representatives of the Tanytarsini, Orthocladiinae, and Tanypodinae also fall within this category. For example, *Stempellinella*, Tanytarsini sp.A, *Parakiefferiella* cf. *bathophila* (Kieffer), *Zalutschia*, and the Pentaneurini were never recorded higher than the lower subalpine lakes. Most Ceratopogonidae and *Chaoborus* seem to be similarly distributed. In addition, several taxa common at low altitudes were much less common at the higher sites, although they did occur. *Chironomus*, *Parakiefferiella*? cf. *triquetra*, and *Psectrocladius* (including *Monopsectrocladius* Laville) clearly portray this pattern of distribution. *Psectrocladius* was exceptionally abundant in two upper subalpine lakes, but rare or absent at other high altitude stations. These two sites, "North" and "South" Elfin Lakes were the most acidic lakes sampled (pH near 5.6). *Psectrocladius* is often common in acidic conditions (e.g. Henriksson *et al.*, 1982; Mossberg and Nyberg, 1979; Walker *et al.*, 1985). *Corynocera* nr. *ambigua* could also be included with the low to mid-elevation group. However, *C.* nr. *ambigua* was most abundant at mid-elevations, and rare at the highest and lowest lakes.

2) *High elevation taxa* - None of the taxa are truly restricted to high elevation sites, since all occur either in the benthos of low-elevation arctic waters, the profundal of

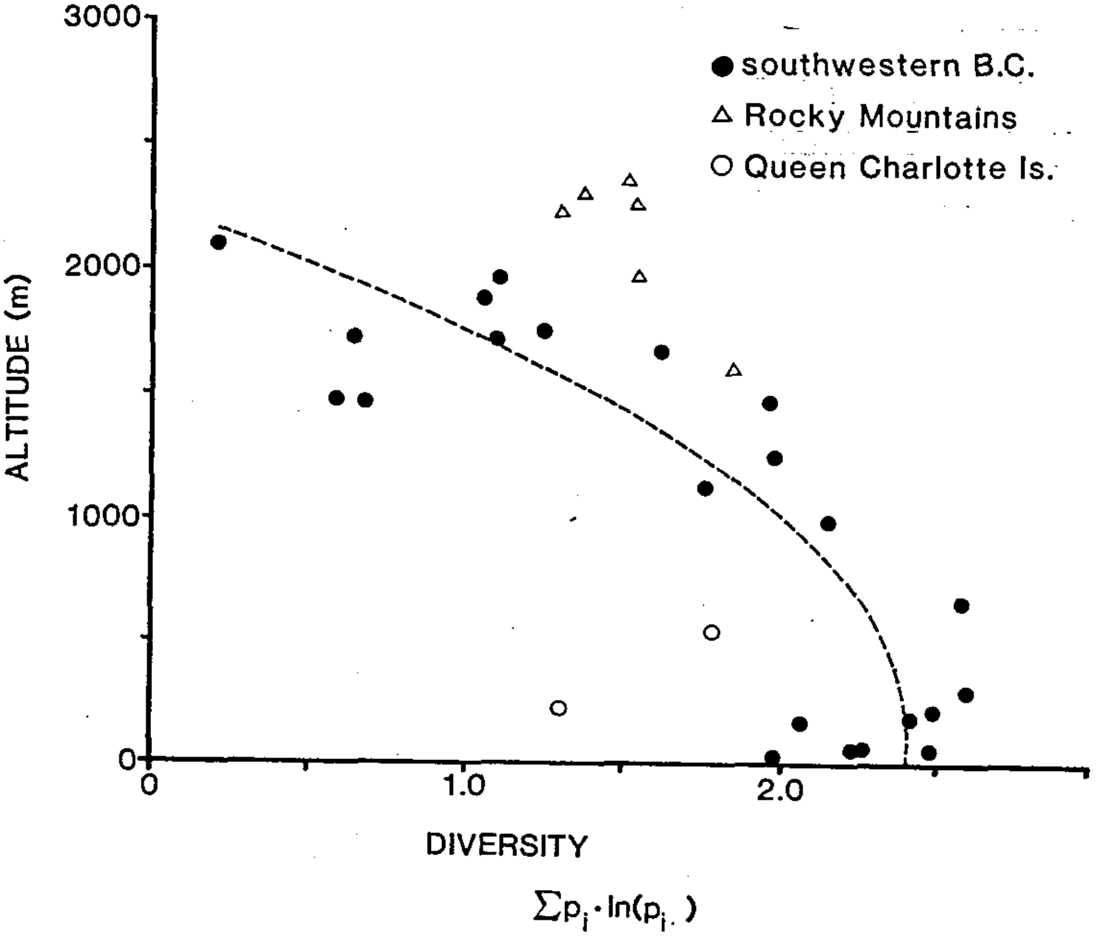

Figure 5.2 Shannon-Wiener diversity of surface-sample chironomid taxa versus elevation in the Cordillera. (Closed circles=sites in southern, coastal British Columbia; Open circles=Queen Charlotte Islands sites; Triangles=sites in Banff and Yoho National Parks). Curve is based upon data for southern, coastal British Columbia only. The transition from subalpine forest to open meadows spans ca. 1400 to 2000 m on the southern coast. Timberline is close to 600 m on the Queen Charlotte Islands, and 2250 m in Banff and Yoho National Parks.

deep, temperate, oligotrophic lakes, or both. All of the "high-elevation" taxa, except *Paracladius* Hirvenoja, have been recorded in low-elevation, late-Pleistocene sediments at Marion Lake. Thus, this "high-elevation" group is equivalent to the regional "*Heterotrissocladius*" fauna described in Chapter 2. The larvae are probably cold-stenotherms. Emergence at low-elevations and temperate latitudes probably occurs in early spring when cool weather prevails. Representatives of this group include *Heterotrissocladius*, *Parakiefferiella* sp.A, *Paracladius*, *Protanypus*, *Pseudodiamesa*, and *Stictochironomus*.

Heterotrissocladius is the most common and widely distributed of these taxa. Although it is uncommon at low elevation sites, it still occurs there, even in shallow waters. This broad range probably incorporates the distribution of several *Heterotrissocladius* species which have not been distinguished. *H. marcidus* and *H. latilaminus* may account for most of the low elevation records. *H. oliveri* may be common at the highest elevations.

The distributions of the other "high-elevation taxa" are more restricted, making them the better indicators. These were most common in the alpine samples from the Canadian Rocky Mountains. I suspect each is represented by a single species in this study. Below the subalpine *Parakiefferiella* sp.A and *Paracladius* were collected only at two sites, Hicks Lake, and Great Central Lake. These are two of the three largest and deepest low-elevation lakes sampled. *Protanypus* and *Stictochironomus* were never very common. Their remains occurred sporadically, being most frequent in lakes at lower subalpine or higher elevations.

Pseudodiamesa was a common chironomid in sediments of "Coleman Pond" and rare at Mimulus Lake. *Pseudodiamesa* may occur in either lakes or streams. I suspect most of the remains, at both locations, are derived from inflowing streams. There is little indication of a lacustrine fauna in the "Coleman Pond" sample. Ice from the previous winter was still partially covering the lake in September, 1985. The entire surrounding landscape bears little vegetation. I believe a permanent snowfield occupied "Coleman Pond" until at least this century. Very large volumes of sediment had to be sorted to find any chironomid remains. Heikkinen (1984a, b, c, 1985) reports an expansion of subalpine forest and glacial retreat on Mount Baker during the last century, probably a response to increased warmth and decreased precipitation.

Most of the "high elevation" taxa occur together in the deeper and most oligotrophic lakes of the Okanagan Valley (Sæther, 1970, Sæther and McLean, 1972), and in Parry Sound, Lake Huron (Hare, 1976). [*Paracladius* and *Parakiefferiella* sp.A are respectively reported as *Cricotopus* "*Paratrichocladius*" and "genus near *Trissocladius*" by Sæther (1970) and Sæther and McLean (1972)]. Sediment from Chilko Lake, a large oligotrophic, high–elevation lake in the coast mountains, has been collected by J. Stockner. Although this material only included 6 chironomid head capsules, both *Paracladius* and *Stictochironomus* were represented[1]. *Heterotrissocladius*, *Paracladius*, *Parakiefferiella* sp.A, and *Protanypus* also occur in Hicks and Great Central Lakes, near sea level. Thus summer air temperatures have little direct relevance to the distribution of these taxa. Cool, oligotrophic waters in the profundal of deep, low–elevation lakes offer refuge. Although they are most common at high elevations, they are mostly absent from the shallowest lakes, even at high altitudes.

3) *Widely distributed taxa* – Few taxa were widely distributed at all elevations, although rheophilous chironomids, and taxa characteristic of shallow timberline lakes and ponds appear to fall mostly within this category.

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[1] Other taxa collected from Chilko Lake, included *Corynocera* nr. *ambigua*, *Corynoneura/Thienemanniella*, *Limnophyes* Eaton, and *Tanytarsus* s.lat.

The most widely distributed group is *Tanytarsus* s.lat. This group is certain to include representatives of several genera and species which could not be reliably distinguished. The individual species would have narrower ecological ranges. The same situation may be true for other taxa within this category.

Procladius and *Sergentia* are also common in lakes at all elevations. *Procladius* may occur in both littoral and profundal regions. Although *Sergentia* is a common profundal taxon in temperate climates, at high elevations it was more common in the shallowest lakes and ponds. *Sergentia* seems to occupy similar shallow habitats in the arctic (Andersen, 1937, 1946: as *Pentapedilum coracina* Zetterstedt and *P. coracinum* Zetterstedt).

The groups *Corynoneura/Thienemanniella*, *Cricotopus/Orthocladius/Paratrichocladius*, *Doithrix* Sæther & Sublette/*Pseudorthocladius* Goetghebuer? group, and *Limnophyes* Eaton are also widely distributed. Each of these taxa may be common in soils or streams. *Corynoneura/Thienemanniella*, *Cricotopus/Orthocladius/Paratrichocladius*, and *Limnophyes* may also occur in lakes. *Cricotopus/Orthocladius/Paratrichocladius* includes three large and widely distributed genera, together including at least 150 species in the Holarctic region (Coffman *et al.*, 1986).

Discussion

The trends apparent along my altitude transect parallel the known distribution of chironomids along horizontal climatic gradients. Although most Canadian chironomid genera are present north to tree–line (Table 5.4), many Chironominae and Tanypodinae genera are not known from the Canadian arctic (Danks, 1981; Oliver and Roussel, 1983a). In contrast, at least 2/3 of the Canadian Orthocladiinae genera have been reported in the arctic.

Table 5.4. Number of chironomid taxa in major Canadian regions. HA=high arctic; LA=low arctic; Y&sNWT=Yukon and sw. Northwest Territories (north of 60°N, but south of treeline); W=sw Canada (British Columbia to Manitoba), E=se Canada (Ontario to Newfoundland).

SUBFAMILY OR TRIBE	NUMBER OF GENERA				
	HA	LA	Y&s.NWT	W	E
CHIRONOMINAE					
Chironomini	3	8	26	29	27
Pseudochironomini	-	-	1	1	1
Tanytarsini	3	6	9	10	8
DIAMESINAE	5	5	5	4	3
ORTHOCLADIINAE*	21	22	33	35	36
PODONOMINAE	1	1	1	3	3
PRODIAMESINAE	-	1	2	2	3
TANYPODINAE	1	7	16	18	22
TELMATOGETONINAE	-	-	-	1	-

Compiled with reference to Danks (1981), Oliver (1981), and Oliver and Roussel (1983a).

*-A list compiled by D.R. Oliver (pers. comm.) includes 35 arctic Orthocladiinae genera. Figures for other subfamilies and tribes differ only slightly (±1 or 2 genera).

Lakes inhabited by oligotrophic, cold-stenothermous taxa, including *Heterotrissocladius oliveri, Paracladius, Parakiefferiella* Thienemann, *Protanypus, Pseudodiamesa, Stictochironomus*, and Tanytarsini are not uncommon in the North American arctic (Bliss, 1977; de March *et al.*, 1978; Hershey, 1985a, b; Nyquist and LaPerriere, 1973; Oliver, 1963, 1964, 1968, 1976). The above taxa, however, are largely absent from the shallowest high-elevation and arctic lakes and ponds, where *Chironomus, Corynoneura, Cricotopus, Orthocladius, Procladius, Psectrocladius, Sergentia*, and Tanytarsini may be abundant (Andersen, 1946; Butler *et al.*, 1981; Danks and Oliver, 1972a, b; this study). Danks and Oliver (1972b) indicate "There is little overlap in species between the two types of habitat" (arctic lakes vs. arctic ponds). In the shallow lakes and ponds all or most of the bottom may freeze in winter. The long arctic and alpine winters also contribute to anoxia in shallow waters (Hobbie, 1973). During summer the ponds are much warmer than larger, and deeper lakes nearby. Ice scouring disrupts the littoral fauna of large arctic lakes (Andrews and Rigler, 1985).

The following taxa, recorded only at low-elevations in my southern British Columbia studies, are not known from the North American arctic (Danks, 1981; D.R. Oliver, pers. comm.) - *Labrundinia* Fittkau, *Nilotanypus* Kieffer, *Glyptotendipes, Cladopelma, Cryptotendipes, Cyphomella* Sæther/*Harnischia* Kieffer/*Paracladopelma* Harnisch, *Lauterborniella/Zavreliella*[2], *Nilothauma* Kieffer, *Omisus* Townes, *Pagastiella* cf. *ostansa, Paralauterborniella* Lenz, *Paratendipes, Stenochironomus* Kieffer, *Xenochironomus* Kieffer, *Pseudochironomus* Malloch, *Heterotanytarsus* cf. *perennis*, and *Synorthocladius* Thienemann. Several taxa which I have not collected at high elevations are recorded only as rare elements of the low-arctic tundra fauna (e.g. *Dicrotendipes, Microtendipes,*

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[2] Although *Lauterborniella* has been reported from Char Lake, N.W.T. (Welch, 1973), this record is clearly the result of confusion with *Lauterbornia sedna* Oliver (now a *Micropsectra*), which Oliver (1976) described from this lake. Welch's (1973) error has been propogated in several subsequent articles (ie. Andrews and Rigler, 1985; Davies, 1975; Rigler, 1978).

Parachironomus Lenz, *Polypedilum*, *Stempellinella*).

Ceratopogonidae have been reported from the high arctic (Danks, 1981). One *Chaoborus* record, *C.* (*Schadonophasma*) *trivittatus* (Loew), exists for Baffin Island (Danks, 1981). However, Borkent (1979) remarks, "In the Rocky Mountains, the species has not been found above treeline. The single record from Baffin Island is suspect." While many of these taxa may yet be recorded farther north, or at higher elevations, they are obviously rare in cold climatic regions.

The parallels between the chironomid response along a north-south climatic gradient, and an altitude gradient offer some assurance that climate is directly or indirectly influencing faunistic composition. Independent studies by Mayhood and Anderson (1976) for the Canadian Rockies, and by Reiss (1968) in the Alps, portray similar trends. Although Tuiskunen and Lindeberg (1986) report many of the listed genera north of 68° in Europe, their sites appear to be at, or near timberline. A study of the Saskatchewan River Chironomidae (Mason and Lehmkuhl, 1983) indicates that many Chironomini occurring upstream of a reservoir may not occur in the cooler downstream waters.

The disappearance of many chironomid genera at a major vegetation boundary raises suspicion concerning the independence of these insects from terrestrial flora. The distributions of wood-mining chironomids (e.g. *Orthocladius* (*Symposiocladius*) *lignicola*) are certainly limited by the occurrence of trees and shrubs. Also, since aquatic macrophytes are less common in arctic and alpine lakes, chironomids (e.g. *Brillia* Kieffer, *Stenochironomus*) dependent upon either these habitats, or leaves from terrestrial vegetation will be less common. However, such obligate relationships will not explain the disappearance of the majority of chironomids, including many deposit and filter feeders. If trees were important in providing habitat to chironomids, a similar reduction in generic diversity would be apparent at lakes in grassland regions. However, many of the genera absent in the arctic are abundant in grassland lakes and ponds (Driver, 1977; Cannings and Scudder, 1978; Timms *et al.*, 1986; Wiederholm, 1980).

It should be remembered that the horizontal and vertical climatic gradients are not linear functions of altitude or latitude. The Canadian northern limit of trees is defined by the mean summer position of the arctic front (Bryson, 1966). A marked difference of climate exists on either side of this narrow frontal zone. Summer temperatures, and duration of the growing season are significantly reduced north of arctic treeline. G.M. MacDonald (pers. comm.) indicated a pronounced change in ice thickness, and sedimentation rates at lakes on either side of timberline. Treeline also seems to be an important biogeographic boundary for many other insect groups, including the Odonata (Danks, 1981; Downes, 1964). These predaceous aquatic insects have no direct ties to terrestrial vegetation, yet few Odonata species occur on the southernmost arctic tundra (Danks, 1981; Downes, 1964). The Odonata are aquatic as larvae and predaceous both in mature and immature stages.

Although temperature varies gradually with elevation, distinct climatic changes are evident across the subalpine zone. Freezing levels average *ca.* 900 m during winter in southern coastal British Columbia (Peterson, 1969). Thus, snow and ice cover are ephemeral at elevations below *ca.* 900 m near Vancouver, but at higher elevations (the subalpine zone) snow accumulates to several metres depth (Brooke *et al.*, 1970; Bunnell *et al.*, 1985). This produces a sharp reduction in growing season. Lakes within the lower subalpine may thaw in early summer, but upper subalpine lakes could not be sampled before late July and early August during 1986. At this time ice partially covered many coastal upper subalpine lakes. "Coleman Pond" thawed only in September 1985, when early snow began to reappear on adjacent peaks.

With major climatic changes occurring over such short horizontal and vertical distances, it is not surprising that the northern and altitude limits of many groups of unrelated organisms should nearly coincide. Marked limnological changes may also be expected. The reduced growing season limits primary production. Low temperature also slows the chemical weathering of rocks, the ultimate source for many nutrients.

The task of determining precisely why many chironomid genera and species cannot cope with arctic conditions is not easily resolved. Danks (1981), MacLean (1975) and Oliver (1968) provide extensive reviews of physiological and behavioural adaptations which distinguish arctic insects, but the significance of these adaptations requires much further evaluation.

The harsh physical environment of arctic regions, especially in winter, would seem a likely factor. Andrews and Rigler (1985) report that temperate ice rarely exceeds 0.6 m thick, but arctic ice may reach 2.5 m. Alpine ice 1.3 m thick is also reported (Pennak, 1968). Although, by occupying lake environments most chironomids are isolated from the severity of winter, an ability to avoid or tolerate freezing would seem an important adaptation. Danks (1971a, b, c) has carefully studied the winter habits and survival of chironomids. He (Danks, 1971a) notes "... that freezing tolerance is found in nearly every major genus group (except in Tanypodinae)." Many species are noted as freezing tolerant, including an African tropical species, *Polypedilum vanderplanki* Hint. Thus, Danks (1971a) concluded "... that the Chironomidae can probably be considered preadapted to seasonally frigid habitats." However, it should be noted that prolonged freezing at temperatures below −15°C has proven lethal, even to arctic species (Baust and Edwards, 1979; Danks, 1971a, 1981: p. 278–279). Similar temperatures may exist in arctic littoral habitats (Andrews and Rigler, 1985; Danks, 1971b; Livingstone, 1963). Although arctic Chironomidae lack a "metabolic cold adaptation", polar species may have lower activation energies (Lee and Baust, 1982).

The reduced productivity at arctic and alpine sites (Brylinsky and Mann, 1973) is also a potentially important factor, determining the availability of food to benthos. Thus chironomids characteristic of strongly oligotrophic environments prevail in all arctic lakes where oxygen concentrations remain continuously high. All arctic and alpine species will have to tolerate the characteristically low food supplies of cold climates. Moore's (1978) results indicate that P, NO_3–N, and phytoplankton concentrations are all lower in arctic than subarctic environs.

Chironomus plumosus, a temperate midge of eutrophic lakes is certainly poorly adapted to the arctic food supply. Filter-feeding will require much greater effort and is probably not an effective food-gathering mechanism in dilute ultra-oligotrophic arctic lakes. The pronounced diatom blooms which provide emergence cues to *C. plumosus* (Hilsenhoff, 1967) may not occur in arctic waters.

Perhaps most important is the influence of summer temperature. Danks (1971b) notes, "Ecologically significant processes such as growth and development generally involve temperature thresholds below which the processes do not occur (Allee *et al.*, 1949: pp. 110–11)." Although the metabolism of arctic chironomid larvae is not "extraordinary" (Welch, 1976), normal larval activity may occur at lower temperatures than in temperate species. The activity threshold for arctic pond larvae is near 0° C (Welch, 1976). Apparently many Orthocladiinae larvae grow only at temperatures below 5° C (Sæther: according to Hågvar and Østbye, 1973). In contrast the temperate profundal midge *Chironomus plumosus* may not feed below 5° C (Hilsenhoff, 1966).

The pupation threshold of chironomids is generally higher than the activity threshold. For high arctic pond species, this threshold is about 5° C, with emergence occurring only in water 7° C or warmer (Danks, 1971b; Danks and Oliver, 1972b). Emergence from subarctic lakes near Inuvik, N.W.T. is restricted to temperatures greater than 9° C (Chang, 1975). Fjellberg (1972) suggests the pupation threshold of *Corynocera ambigua* to be *ca.* 8° C. One temperate midge, *Chironomus salinarius* Kieffer requires temperatures of 13° C to complete emergence at the northern limit of its range (Koskinen, 1968). Species characteristic of arctic lakes, *Heterotrissocladius subpilosus, Paracladius quadrinodosus* Hirvenoja, and *Pseudodiamesa arctica* (Malloch), emerge through candled ice at Lake Hazen, Northwest Territories (Oliver, 1968), completing their entire life cycle in temperatures near freezing. Temperatures in arctic lakes of moderate depth or deeper are too cold for development of species from adjacent ponds (Danks and Oliver, 1972a).

Flight and egg development are also temperature dependent. Eggs of *Chironomus plumosus* do not hatch below 8° C (Hilsenhoff, 1966). Arctic chironomids are capable of flight at temperatures near 3.5° C (Downes, 1964). Some arctic chironomid species are parthenogenetic, while others may swarm, copulate, or both without flight (Danks, 1981; Fjellberg, 1972; Oliver, 1968; Oliver and Danks, 1972). Thus low summer air and water temperatures may impair the ability of species to complete their life cycles.

The importance of temperature in restricting chironomid distributions has been noted by Moore (1978) across arctic treeline. *Dicrotendipes nervosus* (Staeger) is reported only from a small, warm subarctic lake. Similarly, "... many of the less common species (e.g. *Ablabesmyia janta* (Roback), *Microtendipes* sp., and *Monodiamesa bathyphila* (Kieffer)) clearly reached the northern limit of their distribution in the study area" (Moore, 1978). Other species, *Heterotrissocladius oliveri* and *Micropsectra* cf. *groenlandica* Andersen occurred only in cold water.

Danks and Oliver (1972a) note that the arctic fauna is derived from the "absolute spring species" of farther south. These species overwinter entirely as fully mature larvae, with diapause preventing emergence late in the preceding summer or autumn season

(Danks and Oliver, 1972a). Emergence begins in spring once sufficient degree–days have accumulated, and when the necessary temperature thresholds are achieved. If such conditions are not presented, the arctic species may overwinter again in the pre–pupal stage (Danks and Oliver, 1972a; Oliver, 1968).

The temperatures which restrict the distribution of chironomids will be those in the least favourable years or series of years. In this regard, it is noteworthy that this century has been warmer than the 19th century (Dunbar, 1985). Thus distributions of many arctic organisms may not be in equilibrium with present climatic conditions. According to Livingstone (1963), maximum summer temperatures at Imikpuk Lake near Point Barrow, Alaska, varied from 8 to 12° C between 1951 and 1955 (Brewer, 1958). Livingstone (1963) notes that 75% of the heat supplied to Chandler and Peters Lakes was consumed in melting the ice.

A temperature gradient similar to that evident along a north–south transect occurs in lakes and ponds along my altitude transect. High elevation lakes are much colder than low–elevation sites. Shallow alpine ponds are usually warmer in mid–summer than deeper waters nearby. In Banff National Park, alpine summer temperature for lakes and pond surfaces range from 6° C to 11° C (Mayhood and Anderson, 1976). One lower subalpine pond, 600 m below timberline, was the warmest in their study area with summer surface temperatures of 20° C (Mayhood and Anderson, 1976). Surface water temperatures of 27° C are recorded for Mike Lake, at low–elevation near Vancouver.

Water temperatures are not a simple function of air temperature (Corbet, 1972). The temperature of shallow ponds often exceeds that of the air, particularly where scant cloud cover permits insolation of the pond bottom (Danks, 1971b; Downes, 1964; Thomasson, 1956). Glacial streams often regulate the temperature of arctic and alpine lakes. Since arctic lakes seldom stratify, the great thermal inertia of deep lakes precludes high summer temperatures in littoral, as well as profundal regions.

Although the temperature and habitat requirements of chironomid larvae obviously require further study, I propose the following factors as important future hypotheses which may explain the distribution of chironomids in the arctic and at high elevations.

1) *Low summer temperatures and short growing seasons* probably prevent many temperate species and genera from permanently colonizing arctic and alpine waters. Arctic and alpine pond species also cannot cope with the lower summer temperatures in arctic lakes which either exceed a moderate depth, or receive glacial meltwater.

2) *Winter anoxia* is probably most important in preventing characteristic arctic and alpine lake species from occupying shallower waters.

3) *The availability of cold, well-oxygenated profundal environments* probably limits the southern and lower limits of arctic and alpine lake taxa (e.g. *Heterotrissocladius subpilosus, Paracladius*). A similar relationship may regulate occurrence of *Sergentia coracina.* Perhaps other arctic and alpine pond species can also find southern refuge in springs where temperatures approach the annual mean.

Much further work is necessary to examine the possible role of these factors in regulating chironomid distributions, during each life stage. Danks (1971a, b, c), Danks and Oliver (1972a, b), Oliver (1964, 1968), and Oliver and Danks (1972) provide excellent evidence of chironomid adaptations to arctic environments. However, much more comparative physiological work and experimental research is necessary to reveal how arctic and temperate species differ. Our knowledge of chironomid distributions is still poor in arctic and alpine habitats, especially in a critical region, the Canadian low arctic.

In view of these data it is interesting to re-examine the palaeoecological data from British Columbia and other North American sites. In Marion, Misty, Mike, and Hippa

Lakes, most chironomid genera arrived very quickly following deglaciation. Summer temperatures were not sufficiently low to prevent rapid colonization. Nevertheless, many chironomid taxa, presently more abundant at high elevations, were common during the late-glacial at low-elevations. This probably reflects, in part the greater water depth, but also colder and more oligotrophic conditions, related to a more severe late-glacial climate.

Elsewhere in North America, several chironomids which are or absent in the arctic occur in the early late-glacial sediments [e.g. *Dicrotendipes*, and *Glyptotendipes* at Green Lake, Michigan (Lawrenz, 1975), and *Cladopelma* and *Polypedilum* in New Brunswick, Canada (Walker and Paterson, 1983)]. Palynological evidence suggests that the late-glacial landscape at these sites was not forested, but trees may have been slow to re-colonize these areas. Thus, warm-adapted Chironomidae may have colonized these habitats before trees were able to reoccupy the same regions. The lacustrine climate is not the same as that of terrestrial habitats, but conditions may have been warmer than the tundra landscape palynological evidence implies. While it is too early to provide a precise statement of how late-glacial conditions differed from arctic environs, future chironomid analyses of surficial sediment samples across the arctic - subarctic transition, and improved knowledge of chironomid distribution limits should provide important clues.