CHAPTER 1

INTRODUCTION[1]

The Chironomidae compose a family of true flies (Diptera) which as larvae constitute the most abundant bottom–dwelling macro–invertebrates of freshwater aquatic systems. Long viewed with importance by limnologists, they have proven valuable as indicators of lake productivity, and have been instrumental in the development of modern lake trophic classification (Brinkhurst, 1974; Sæther, 1979). Remains of dead larvae, and exuviae produced during each of four larval moults, occur abundantly as fossils in lake sediments, and are recognized as important palaeoecological tools (Crisman, 1978; Frey, 1964, 1976; Hofmann, 1986; Walker, 1987).

The influence of lake productivity, acidity, and salinity upon chironomid faunas has already proven useful in palaeolimnological research (Walker, 1987). As yet, little work has focused upon the direct and indirect effects of climate on chironomids (Danks, 1971a, b, c, 1981; Oliver, 1968). However, the direct influence of temperature, and indirect climatic regulation of lake productivity may have important consequences for chironomid faunal composition. Indeed, Andersen's (1938) pioneering results in this area depict the ability of midge communities to respond rapidly to known Danish late–Pleistocene climatic variations.

Little research regarding either the ecology, or palaeoecology, of these invertebrates has been conducted in the Pacific Northwest of North America. Garrett's (1925) Dipteran studies may be the earliest investigation of British Columbia Chironomidae. Rawson (1942, 1955) and Ricker's (1952) surveys of benthos in large Cordilleran lakes suffer from poor taxonomic resolution. More recently, Hamilton (1965) has provided a detailed account of

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[1] This chapter is partially adapted from three published articles (Walker, 1987; Walker and Mathewes, 1987a, b).

Chironomidae inhabiting Marion Lake, near Maple Ridge, British Columbia. Similarly Sæther (1970) and Sæther and McLean (1972) have conducted several recent surveys of large lakes occupying the Okanagan Valley. The littoral faunas of both saline lakes (Cannings, 1975a, b; Cannings and Scudder, 1978; Topping, 1969, 1971; Wiederholm, 1980) and marine (Morley and Ring, 1972a, b; Parkinson and Ring, 1983) habitats have been addressed. In addition, the present and very recent fossil faunas of Lakes Washington, and Sammamish, near Seattle, Washington were described by Thut (1969) and Wiederholm (1976, 1979). Most recently, Roback (1984) has examined the Tanypodinae of Afognak and Kodiak Islands, Alaska. Many other records are scattered through the literature (e.g. Cranston, 1982a; Hansen and Cook, 1976; Kangasniemi and Oliver, 1983; Sæther, 1969, 1976, 1977).

Consequently, the investigations reported in this manuscript contribute to the limited, but growing knowledge of Pacific Northwest Chironomidae. Three questions fundamental to chironomid biology are addressed: 1) Which genera are represented in lacustrine sediments of the Pacific Northwest?; 2) How are these taxa distributed in space and time?; 3) How did their present patterns of distribution originate?

Literature Review

Chironomids and lake classification

The roots of limnology as a modern science may be traced to the work of August Thienemann and Einar Naumann, contemporaries who both sought to develop a classification for lakes (Sæther, 1979). Borrowing terms which Weber (1907) had coined for nutrient supply to bogs, Naumann (1919) categorized lakes according to their phytoplankton productivity, providing the basis for our present lake trophic classification. Naumann (1919) described two basic lake types, the highly productive or "eutrophic"

Baltic lakes and the unproductive or "oligotrophic" north European lakes. Hansen (1962) also credits Naumann (1917, 1918, 1920) with introducing the "dystrophic", humic or brown-water lake as a sub-type of the north European lakes.

Thienemann (1918, 1921) derived similar conclusions through his attempts to classify lakes on the basis of dominant components in their benthic fauna. Thienemann (1921), accepting Naumann's (1919) terminology, described oligotrophic *Tanytarsus* v.d.Wulp lakes, eutrophic *Chironomus* Meigen lakes, and humic lakes in which both *Chironomus* and *Corethra* Meigen (=*Chaoborus* Lichtenstein, Chaoboridae) were prominent.

Brinkhurst (1974) provides an excellent review of subsequent attempts to refine Thienemann's typology. The scheme of Brundin (1949, 1956, 1958) describes several classes of temperature stratified lakes: arctic *Heterotrissocladius subpilosus* (Kieffer) lakes (ultraoligotrophic), subarctic and high boreal *Tanytarsus- Heterotrissocladius* Spärck lakes, boreal and montane *Tanytarsus lugens* Kieffer lakes (oligotrophic), *Stictochironomus rosenscholdi* (Zetterstedt)-*Sergentia coracina* (Zetterstedt) lakes (a transitional "mesotrophic" type between oligotrophy and eutrophy), *Chironomus anthracinus* Zetterstedt and *C. plumosus* (Linnaeus) lakes (eutrophic), and *C. tenuistylus* Brundin (dystrophic) lakes. Furthermore, Brundin (1951) argued that oxygen microstratification at the mud-water interface was a major determinant of the profundal fauna. Larger chironomid taxa, commonly associated with more productive lakes, could better cope with a micro-layer of O_2-depleted water at the mud-water interface. Also, such larvae (e.g. *Chironomus*) frequently possess hemoglobin. Because lakes with higher productivity generally display greater profundal oxygen deficiencies, a correlation was perceived among lake productivity, oxygen deficit, and benthic fauna.

As Rodhe (1969) has emphasized, trophic categories are abstract entities with overlapping ranges. A continuum of lakes among all of those described probably exists.

This is apparent in Sæther's (1975a, 1979, 1980a) recent re–evaluation of benthic lake typology. He describes 15 trophic categories, ranging from ultra–oligotrophy to extreme eutrophy, in addition to the mesohumic and polyhumic types. Sæther's (1975a, 1979) analysis extends European benthic lake typology to North America. He also describes a trophic range for each of many chironomid taxa. Warwick (1975) and Sæther (1979) suggest that apart from the more eutrophic lakes, food may be more critical than oxygen microstratification in determining the profundal fauna of lakes.

Sæther's studies (1975a, 1979, 1980a) correlate the occurrence of characteristic benthic faunas with total phosphorous, epilimnetic chlorophyll *a*, and lake depth. The total phosphorous and chlorophyll *a* relationships with benthic fauna confirms the importance of chironomids as indicators of lake productivity. This relationship however varies with lake depth (Sæther, 1980a) such that an increase in lake productivity would have to be much greater in a deep lake, than a shallow lake to yield a similar change in profundal fauna. Thus, the faunas of shallow stratified lakes are much more responsive to productivity changes than those of deep lakes.

Chironomids and palaeoecology

The attribute of chironomids as lake trophic indicators, and the abundance of chironomid remains in lake sediments has stimulated much palaeolimnological research (Walker, 1987). Although some investigations have dealt with the response of chironomids to changes in salinity or lake acidity (e.g. Brodin, 1986; Paterson and Walker, 1974), most have addressed natural and man–induced variations in lake productivity.

According to Frey (1964), the earliest report of the chitinous sedimentary remains of Chironomidae may be attributed to Ekman (1915). Numerous subsequent reports (e.g. Lundbeck, 1926; Gross, 1937; Brehm *et al.*, 1948) have since been compiled by Frey (1964) who considers the earliest attempt to interpret such remains in terms of past conditions to be that of Gams (1927). Gams (1927) was able to demonstrate that *Eutanytarsus* Thienemann & Bause, abundant in interstadial sediments of Lunzer Obersee, was later replaced by *Bezzia* Kieffer (Ceratopogonidae) and *Chironomus*. Such a sequence could be interpreted as indicating a natural increase in lake productivity. This was contrary to the original speculation of Naumann (1919) that lakes should gradually become less productive as a consequence of constant leaching of catchment soils.

Deevey (1942) described evidence that an early *Tanytarsus* fauna at Linsley Pond was first succeeded by *Endochironomus* Kieffer and *Glyptotendipes* Kieffer, and subsequently by *Chironomus*. Frey (1955) reported *Eutanytarsus* as initially abundant in Längsee, Austria, but with *Chaoborus* (Chaoboridae) arriving later. In contrast to Naumann's (1919) concept, these results contributed to the perception that "eutrophication", a gradual increase in lake productivity, was a dominant, if not universal process (Whiteside, 1983).

However, Livingstone *et al.* (1958) suggested, on the basis of large concentrations of chironomid remains [principally Tanytarsini, including *Corynocera* Zetterstedt (as *Dryadotanytarsus* Andersen)] and other microfossils, that Eight Lake in arctic Alaska may have experienced an early eutrophic stage, becoming less productive as the lake tended to dystrophy. At Myers Lake, Indiana (Stahl, 1959), an early *Sergentia* Kieffer dominated fauna declined as *Chaoborus* increased. Stahl (1959) argued that even in its early stages this lake may have experienced "moderate severe oxygen depletion", and that subsequent changes arose from a reduction in hypolimnetic volume rather than an increase in productivity.

Bryce (1962) also presented contrary results, indicating an early dominance by *Chironomus* at his Malham Tarn Moss site. Bryce (1962) argued that marl deposition may have reversed the ontogenetic process, causing the site to become more oligotrophic. Stahl

(1969) finds this conclusion unsubstantiated.

In southern Finland, Alhonen and Haavisto (1969) noted an early eutrophic stage subsequent to a lake's isolation from the sea. Hofmann (1971a, 1979) indicates that the eutrophic north German *Chironomus* lakes were formerly oligotrophic *Tanytarsus lugens* lakes. Lawrenz (1975) suggested that Green Lake, Michigan, had always remained oligotrophic, although the fauna did respond to a variety of factors including changes in sediment type, water level, and climate. Stark's (1976) results imply an early oligotrophic phase, but eutrophic conditions thereafter.

The above results suggest that broad generalizations regarding lake ontogenetic patterns may be unwarranted. The oligotrophic phase suggested in early lake sediments often relates to cold climatic conditions prevailing during the late–Pleistocene. Indeed, if the timing of the described changes is considered, the relevance of climate is readily apparent.

In addition, Hofmann (1971a: p.55, 1980) notes that Thienemann's (1915) *Tanytarsus* lakes were originally characterized by a misidentified species, later placed in *Lauterbornia* Kieffer, and now recognized to belong to *Micropsectra* Kieffer. Since few palaeoecologists have been able to distinguish among several Tanytarsini genera (including *Micropsectra*), the genus *Tanytarsus* has been employed in a broad sense incorporating taxa not characteristic of profundal oligotrophic environments. Similarly, although *Chironomus anthracinus* and *C. plumosus* are important indicators of eutrophy, some *Chironomus* species may be abundant in dystrophic, or even oligotrophic situations.

Stahl (1969) has noted that chironomid palaeoecological investigation sites have included unstratified lakes. The system of benthic lake typology conceived by Thienemann (1915, 1918, 1921) and Brundin (1956) was intended only for stratified lake environments. Nevertheless, Warwick (1975) and Sæther (1979) have argued that, apart from the more eutrophic lakes, food may be more important than O_2 microstratification in determining the benthic fauna. If true, benthic lake typology may be applicable to shallow polymictic lakes. Unfortunately, many of the best oligotrophic and mesotrophic indicators are cold stenotherms restricted to profundal habitats at temperate latitudes.

Chironomids, trophic status, and climate

Climate has had a tremendous impact upon the development of lakes. This point is not obvious within a small geographical area (the "local scale" at which most limnologists conduct their work). At this scale differences in geology of catchments, and size of lakes and watersheds are more important. However, on a continental scale the role of climate dominates (Brylinsky and Mann, 1973). This is dramatically depicted by the distribution of lake types in western Canada (Northcote and Larkin, 1963). In British Columbia the dilute unproductive ("oligotrophic") lakes of the humid coast contrast with the more saline and often more productive ("mesotrophic" to "eutrophic") lakes of the dry interior. Similarly, the saline lakes of southern Alberta and Saskatchewan share few characteristics with those present on similar bedrock in northern Alberta. Differences in nutrient concentrations, temperature, and phytoplankton density are also readily apparent in Moore's (1978) survey of benthos across the arctic – subarctic transition.

Although the relationships between chironomids, lake trophic state, and climate have attracted little recognition, these effects are implicit in the early benthic lake classifications. Thienemann's (1918) *Chironomus* lakes were low elevation Baltic sites, but his *Tanytarsus* lakes are described as sub-Alpine. Similarly, Brundin (1949, 1956, 1958) described the ultraoligotrophic *Heterotrissocladius* lakes as principally arctic whereas *Tanytarsus lugens* lakes were common in boreal and montane climates. In warmer climates, *Chironomus* lakes are common. Furthermore, Brundin states (1958: p.289), "In a lake type system of the world the ultraoligotrophic lake indicates one extreme of a climatically based type–series, where the ultraeutrophic equatorial lowland lake forms the other extreme." *Heterotrissocladius* is a characteristic taxon of the cold, ultraoligotrophic lakes, whereas *Chironomus* prevails in eutrophic lakes. Brundin's (1958) views portray the fact that climate, lake trophic state, and chironomid faunas are related. Lakes in warm climates have higher temperatures in both epilimnetic and hypolimnetic regions (Barton and Smith, 1984), receive more radiant energy, and via chemical weathering profit from a greater nutrient supply. Thus, "all low–altitude tropical lakes are eutrophic and all arctic lakes are oligotrophic by accepted standards regardless of basin morphometry" (Lawrenz, 1975).

Chironomids have evolved adaptations necessary to cope with the full range of conditions prevailing across this gradient. Arctic lacustrine chironomids must cope with very low temperatures, short emergence periods, silty substrata, and low "food" supplies, but benefit from abundant oxygen in all lakes of moderate or greater depth. Chironomids adapted to conditions prevailing in warm climates may benefit from abundant food, but must cope with higher water temperatures as larvae, higher air temperatures during emergence, and the extremely low oxygen concentrations prevalent in hypolimnetic sediments of eutrophic lakes. It is therefore not surprising that the factors influencing chironomid faunal changes frequently escape simple explanations.

In general terms, the chironomid subfamilies Podonominae, Diamesinae, Prodiamesinae, and Orthocladiinae are cold–stenothermous oligotrophic taxa with distributions centred in temperate and montane to polar and alpine climatic regions (Oliver, 1971). In contrast, the Tanypodinae and Chironominae tend to be most abundant at low elevation and latitude (Oliver, 1971).

The preceding discussion indicates that a relation between chironomids, lake trophic state, and climate exists. Thus the Chironomidae may have potential, as yet little exploited, for indicating rapid climatic changes such as those conceived for the late–Pleistocene. Although the climatic control of chironomid faunas is unlikely to be as closely defined as that regulating terrestrial vegetation, chironomid palaeoecological studies might prove useful where equivocal climatic interpretations exist. Thus, in addressing the ecology and palaeoecology of Pacific Northwest Chironomidae, I shall focus particularly on this possibility.

The main text of this thesis is arranged into 5 chapters. This introduction and literature review, the first chapter, have introduced several major concepts which are central to subsequent discussions. Chapter 2 reports a first exploratory look at chironomid stratigraphy in one British Columbia lake, Marion Lake, in the University of British Columbia Research Forest. Ideas developed during the Marion Lake research, regarding the influence of climate upon postglacial chironomid succession, were tested with subsequent cores from Mike and Misty Lakes (Chapter 3). Chapter 4 reports exploratory chironomid stratigraphic work at Hippa Lake, on the biogeographically intriguing Queen Charlotte Islands. Finally, to better appreciate the role of climate in shaping chironomid faunas, fossil head capsules were analyzed from surficial sediment of a lake series, spanning an altitude gradient. This study is reported in Chapter 5. These chapters are arranged in chronological order, which best reflects the progression of thought through my studies. As much as possible each chapter is arranged as an independent paper.