

BIOGEOGRAPHY OF HEPTAGENIID MAYFLIES  
IN SASKATCHEWAN:  
A MULTIVARIATE ECOLOGICAL STUDY

A Thesis

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by

Eric Ross Whiting  
Saskatoon, Saskatchewan

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## ABSTRACT

The distributions of 22 species of heptageniid mayflies (Ephemeroptera: Heptageniidae) in Saskatchewan and west-central Manitoba are described. The distribution patterns of 16 species are examined intensively at 35 sites in central Saskatchewan, using multivariate methods and both quantitative and qualitative data.

Cluster analysis of quantitative data (using Ward's method and Euclidean distance) shows two major groups of sites or faunal zones: 1) the Saskatchewan Rivers, with seven characteristic species (Heptagenia adequata, H. elegantula, H. flavescans, Macdunnoa nipawinia, Raptoheptagenia cruentata, Rhithrogena undulata and Stenonema terminatum) and 2) boreal streams and rivers, with six characteristic species (Leucrocuta hebe, Nixe inconspicua, N. lucidipennis, N. rusticalis, N. simplicoides and Stenonema vicarium). High gradient streams form a distinct subgroup of boreal streams characterized by the presence of Nixe rusticalis and N. simplicoides.

Ordination using detrended correspondence analysis shows two major community gradients in the intensive study area. Saskatchewan River and boreal sites are separated on the first and most important community gradient; high gradient and other boreal sites are separated on the second. Both gradients are discontinuous showing the distinctness of the faunal zones. Faunal differences between zones are greatest in June and early July when larvae of species with summer life cycles are present.

Multivariate analyses of presence/absence data from 172 sites throughout Saskatchewan show similar faunal zonation, but with two additional boreal subzones (Shield and low gradient streams) and one additional Saskatchewan River subzone (large southern boreal and parkland streams that are similar to the Saskatchewan Rivers).

Environmentally, the Saskatchewan River and boreal faunal zones differ in depth, water temperature, siltation, water clarity, and type of organic matter. High gradient and other boreal streams differ in current velocity, water temperature, and type of organic matter. These environmental differences may all be due to differences in stream size and associated longitudinal gradation of physical parameters and organic matter characteristics. Although differences in feeding strategies among heptageniids are not known, longitudinal zonation of organic matter characteristics provides the best explanation of observed heptageniid distribution patterns. These effects are probably modified by streambank vegetation.

Observed heptageniid distribution patterns do not appear to be influenced by drainage basins or by historical factors associated with the Wisconsin glaciation.



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## 1 INTRODUCTION

### 1.1 Distribution Patterns

The distributions of plant and animal species are not random; they show regular patterns which are governed by environmental factors. Two basic types of distribution patterns can be recognized: 1) community gradients, in which species composition changes more or less continuously along an environmental gradient, and 2) biotic zonation, in which species composition is relatively homogenous over large areas, and large changes in species composition are restricted to small areas between adjacent biotic zones.

Zonation of terrestrial vegetation has been well described. Major vegetation zones are defined by the growth form of the dominant species (Scudder 1979), although many other species generally show similar distribution patterns. Vegetation zones are regulated primarily by climatic factors, especially temperature and precipitation (Scudder 1979, Pielou 1979). The transition between adjacent vegetation zones is generally rather abrupt, so that the zones are distinct entities rather than arbitrary parts of an ecological gradient:

Faunal distribution patterns are not as well known. Many terrestrial vertebrates, especially small mammals and birds, show zonation similar to that of terrestrial vegetation (Scudder 1979). This zonation may be regulated by changes in vegetation, or directly by changes in climate. The biogeography of terrestrial invertebrates has not been adequately studied to describe generalized distribution

patterns; however, preliminary investigations suggest that at least some groups conform to vegetation patterns (Scudder 1979).

Large-scale distribution patterns of stream organisms have not been well studied, except for the special case of longitudinal zonation. Longitudinal zonation refers to the change in physical factors (temperature, depth, current velocity, turbidity and substrate type) and fauna (especially fish and invertebrates) along the length of a stream, from the headwaters to the mouth (Hynes 1970, Hawkes 1975). Although physical factors change more or less continuously, faunal changes are usually relatively discontinuous, allowing the recognition of longitudinal faunal zones (Illies and Botosaneanu 1963, Hynes 1970). Vannote et al. (1980) suggested that such faunal discontinuities are due to discontinuous longitudinal changes in the nature of stream organic matter. The major source of stream organic matter changes from coarse particulate organic material in headwater streams, to autotrophic production in mid-reaches, to fine particulate, partially-processed material from upstream in large rivers (Vannote et al. 1980). Cushing et al. (1980), Hawkins and Sedell (1981), Culp and Davies (1982), Minshall et al. (1983), Bronmark et al. (1984), and Bruns et al. (1984) have quantitatively described longitudinal zonation of stream invertebrates and organic matter.

The potential importance of distribution patterns other than longitudinal zonation is virtually unknown. Several biogeographical studies of stream organisms in North America

have concentrated on post-Pleistocene dispersal into previously glaciated areas. These studies have generally related distribution patterns to drainage systems and watersheds. However, most of these studies have been on strictly aquatic organisms, such as fish (McPhail and Lindsay 1970) and molluscs (Clarke 1973). While watershed boundaries may present barriers to the dispersal of strictly aquatic animals, such boundaries are less likely to present barriers to the dispersal of aquatic insects, which have winged, terrestrial adults.

The distributions of stream organisms might also be related to terrestrial vegetation zones because of the importance of allochthonous organic material in stream community metabolism. Climatic factors might have some effect on stream faunal zones. Temperature, through its regulation of life cycles and organic matter processing rates, might be especially important. Precipitation could also be important because of its effect on discharge and stream permanence.

Wright et al. (1984) (see also Furse et al. 1984) have conducted the only comprehensive study of stream community zonation incorporating a broad spectrum of stream types and sizes. They related zonation of stream macroinvertebrates in Great Britain to longitudinal and altitudinal variation.

Minshall et al. (1983) studied longitudinal zonation of organic matter characteristics, community metabolism, and invertebrate functional feeding group composition in four American streams from regions with different terrestrial vegetation, geology and climate. However, macroinvertebrates

were not treated taxonomically and all four streams were from forested areas, although forest type differed. Longitudinal zonation of macroinvertebrate functional feeding group composition was similar in the four streams studied, but zonation of organic matter characteristics varied greatly among watersheds.

## 1.2 Quantitative Methods in Ecological Biogeography

Until recently, most analyses of large-scale distribution patterns were entirely subjective. Multivariate biogeographical data could not be analyzed quantitatively before the development of computers and suitable multivariate statistical techniques. Multivariate analysis of ecological and biogeographical data is especially difficult because of the large size of data sets, the large number of zeros usually present in samples x species data matrices, and the difficulty in providing environmental or other explanations for observed biotic patterns.

The lack of objective, quantitative methods does not appear to have hindered the recognition of terrestrial vegetation zones. The organisms involved are large and obvious, and their distribution patterns are primarily associated with two environmental factors, temperature and precipitation. On the other hand, stream organisms are small and difficult to observe, and their distribution patterns may be related to one or more of several environmental phenomena (including longitudinal zonation, variation in terrestrial vegetation and climate, and watershed boundaries). The

distribution patterns displayed by stream organisms are thus more difficult to recognize and require the use of objective techniques for analysis.

Multivariate statistical techniques were first used in community ecology in 1954 (Gauch 1982). However, they have been standardized, and generally applied in ecological and biogeographical studies, only within the last 5 to 10 years. In terrestrial ecological biogeography, multivariate techniques have been used primarily to study intrazonal or subzonal variation among vegetation communities (Gauch, Whittaker and Wentworth 1977, Whittaker and Gauch 1978, Gauch and Stone 1979, Hill and Gauch 1980, Gauch and Whittaker 1981, all cited from Gauch 1982) and bird communities (Anderson 1979, Holmes, Bonney and Pacala 1979, Sabo and Whittaker 1979, Sabo 1980, all cited from Gauch 1982). In stream ecology, multivariate techniques have been applied in studies of longitudinal zonation (Cushing et al. 1980, Culp and Davies 1982, Bronmark et al. 1984) and microhabitat preference (Sheldon and Haick 1981). Only Wright et al. (1984) have used multivariate statistical techniques to examine the major distribution patterns of stream organisms.

### 1.3 Scope of the Study

This study was designed to examine the regional distribution patterns of a group of stream insects, to determine what faunal zones and community gradients are present, and to associate observed distribution patterns with environmental factors.

The geographic boundaries of the study area are approximately those of the province of Saskatchewan. Saskatchewan is a good area for studying major distribution patterns of stream insects because: 1) two of the six major vegetation zones in North America (grasslands and boreal forest) are represented; 2) within each of the two major vegetation zones there is a wide diversity of stream types (including glacier, spring and lake-fed streams) and stream sizes (from small streams to large rivers, stream orders 1 to 8); 3) three of the five major drainage systems in Canada (Arctic - Mackenzie, Hudson Bay - Churchill/Nelson and Gulf of Mexico - Missouri/Mississippi) are represented; and 4) Saskatchewan's aquatic insect fauna includes a mixture of eastern and western species, facilitating an assessment of the importance of historical biogeographical factors.

The taxonomic boundaries of the study were those of the mayfly (Ephemeroptera) family Heptageniidae. Ideally, all stream invertebrates would have been included. This was not possible because: 1) many stream invertebrates (including most microinvertebrates and dipteran larvae) cannot be accurately identified to species, and 2) collection and processing of all stream invertebrates from a large study area would have required too much time and manpower. Wright et al. (1984) included all macroinvertebrates in their study of British stream faunal zones. However, the taxonomy of British stream invertebrates is well known, Britain is a smaller area to study than Saskatchewan, and a large number of researchers were available for Wright et al.'s study.

The family Heptageniidae was chosen because: 1) it is large enough to provide meaningful information about distribution patterns, but small enough to be studied with available resources, 2) heptageniid taxonomy is reasonably well known, and 3) species within the family (at least within the subfamily Heptageniinae, which includes 20 of the 23 species in the province) are very similar in microhabitat preference and feeding strategy. Larvae of all species in the family are dorso-ventrally flattened, and are more or less restricted to the surfaces of stones, or the interstitial spaces between stones, in moderate to fast currents (except Stenonema femoratum and Arthroplea bipunctata which are found primarily in lentic habitats). All species within the subfamily Heptageniinae, except Raptoheptagenia cruentata, are generalistic herbivore/detritivores, feeding primarily on fine particulate organic material and to a lesser extent on diatoms (Shapas and Hilsenhoff 1976, Merritt and Cummins 1978, Hamilton and Clifford 1983). Reducing variability in microhabitat preference and feeding strategy among species studied (by working with ecologically similar organisms, such as heptageniines) should facilitate the recognition of large scale distribution patterns. Furthermore, choosing a restricted group of organisms increases sampling efficiency, because sampling can be restricted to one microhabitat type.

Environmental factors studied included physical factors, macroscopic plant growth, and organic matter characteristics. Water chemistry was excluded because: 1) chemical factors are unlikely to be important in regulating stream insect



distributions, except in extreme circumstances (such as gross pollution) (Hynes 1970, Lehmkuhl 1979a), and 2) available time and equipment were insufficient for water chemistry analysis.

#### 1.4 Previous Studies of Stream Insects in Saskatchewan

Taxonomic studies of mayflies (Lehmkuhl 1972a, 1976a, 1976b, 1979b), stoneflies (Dosdall and Lehmkuhl 1979) and caddisflies (Smith 1975, 1984) provided preliminary information about stream habitats and heptageniids in Saskatchewan. Lehmkuhl (1976a) subjectively defined four mayfly faunal zones in Saskatchewan: 1) boreal, 2) Saskatchewan River, 3) Cypress Hills, and 4) prairie (the prairie fauna contains no heptageniids). Fourteen species of heptageniids, three of which were not named, were known from Saskatchewan prior to this study (Lehmkuhl 1976a).

#### 1.5 Objectives

The objectives of this study are to quantitatively describe and explain the distribution patterns of heptageniid mayflies in Saskatchewan. Specifically, these objectives are: 1) to describe the distributions of heptageniid species in Saskatchewan, 2) to objectively and quantitatively describe the distribution patterns of the Saskatchewan heptageniid fauna as a whole, with reference to faunal zones and community gradients, 3) to determine which environmental factors are associated with, and potentially responsible for, observed heptageniid distribution patterns, and 4) to

determine if observed heptageniid distribution patterns are associated with other biogeographical phenomena, such as terrestrial vegetation zones, longitudinal zonation, or drainage basins.

## 2 DESCRIPTION OF THE STUDY AREA

The boundaries of the study area are approximately those of the province of Saskatchewan (from 49° to 60° N latitude and from 102° to 110° W longitude). The northernmost part of the province, north of 59°30', was not included because of the absence of road access. The study area did include the Cypress Hills in Alberta, and a narrow strip (up to 40 km wide) of western Manitoba, between the TransCanada Highway and Flin Flon. These two areas were included to obtain more information about particular species and habitats that were present but rare in Saskatchewan.

In general, Saskatchewan is a province of low relief. It slopes gradually to the northeast, with altitude decreasing from almost 1400 m to just over 200 m. Much of the local topography has been produced by glacial erosion or deposition, during the Wisconsinan Glaciation. The Wisconsinan Ice Sheet covered nearly all of Saskatchewan, and only retreated from the province between 18,000 and 9,000 years ago, in the southwest and northeast respectively (Gordon 1979). Saskatchewan's climate is cold continental, with short warm summers and long cold winters. Moisture conditions range from semiarid in the south to subhumid in the north. Two of the major vegetation zones in North America, the grasslands and the boreal forest, occur in the province.

### 2.1 Geology and Physiography

Saskatchewan contains two major physiographic regions,

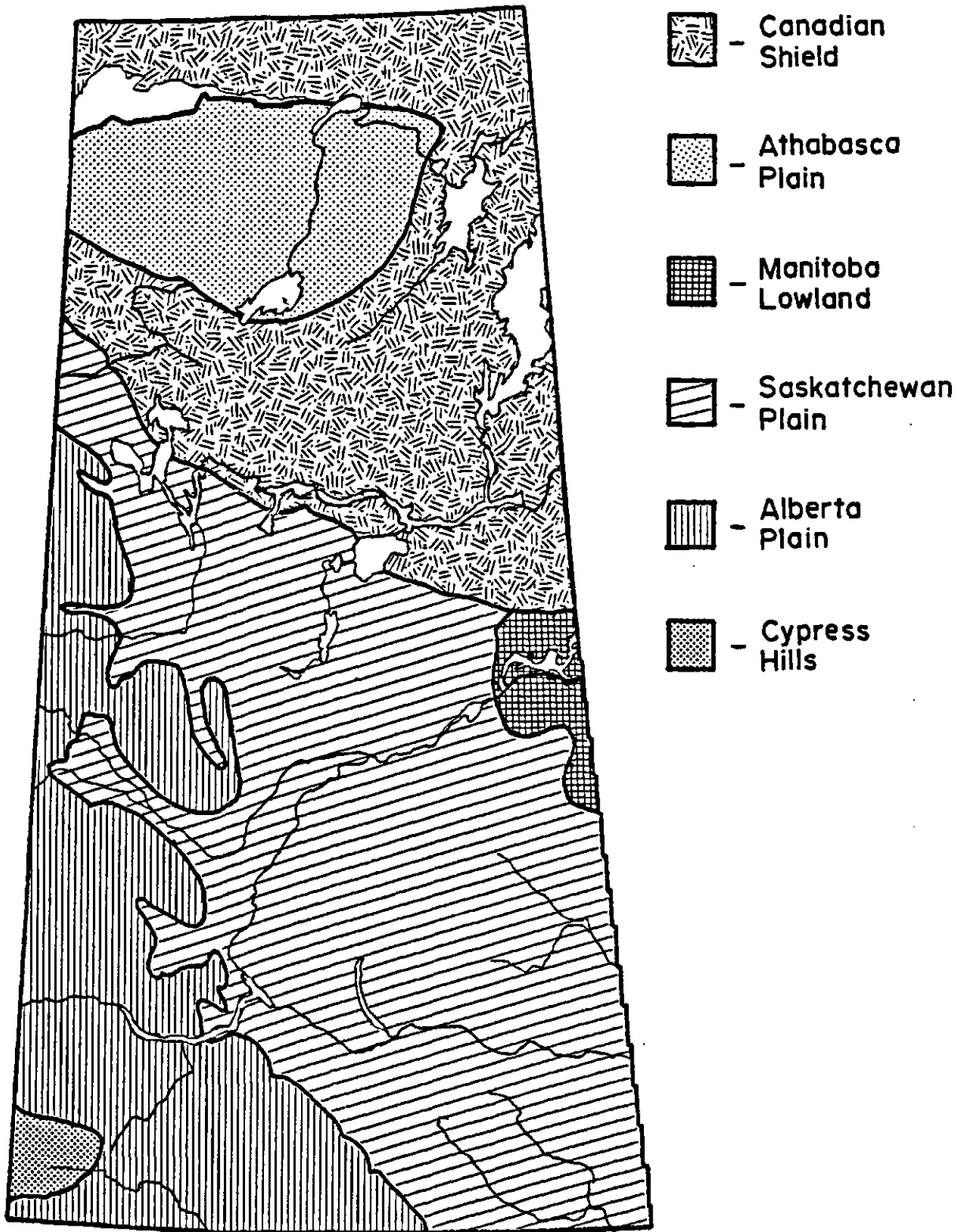


Figure 1. Physiographic regions of Saskatchewan (after Gordon 1979 and Richards and Fung 1969).

the Canadian Shield and the Central Plains (Figure 1). In the Canadian Shield, the bedrock is mostly igneous or metamorphosed igneous and sedimentary rock, and is Precambrian in age (Richards 1981). This bedrock is characteristically overlain by only a thin layer of soil, so that exposed rock outcrops are common. The Shield was primarily an area of glacial erosion, and glacial deposits are neither extensive nor deep (Richards 1981). Surficial scouring and abrasion are the most common glacial features in the area.

In the Shield, local relief is both extensive and steep. Rock ridges and knobs rise 12 to 46 m above the level of adjacent basins, producing a very rugged landscape (Richards 1969, 1981). The ridges and basins are often elongated in a northeast-southwest direction, reflecting Precambrian folds and lines of weakness in the bedrock (Richards 1981). The basins usually contain lakes or rivers. On a larger scale there is little relief, and most of the land lies between 350 and 550 m above sea level (although the Lake Athabasca basin is only a little more than 200 m above sea level in places) (Richards 1969).

Water and wetland formations are very common on the Shield. Twenty to thirty percent of the surface area is covered by water, and nearly every depression or basin contains a lake, bog, marsh or muskeg (Harris et al. 1983). Beneath the muskeg, permafrost is common, especially in the northern part of the region.

Rock knob, ridge and basin topography occupies most of

the Shield region of Saskatchewan. However, south and southeast of Lake Athabasca, the Athabasca Plains form an extensive area of continuous, sandy drift plain. This area is underlain by sandstones, siltstones and conglomerates, which are somewhat younger than the bedrock in other parts of the Shield (Richards 1969, 1981). Active and stabilized sand dunes are common in the area, especially along the south shore of Lake Athabasca. Other glacial depositional features are also more common than in other parts of the Shield, and exposed bedrock and open water are less common (Richards 1969).

South of the Shield, in the Central Plains region, the bedrock is primarily Mesozoic or Cenozoic. Most of this bedrock is Cretaceous, and was deposited from an extensive inland sea. In southern Saskatchewan there are also areas of Tertiary bedrock, which is freshwater in origin. Some Paleozoic (Cambrian, Ordovician, Silurian and Devonian) bedrock is present along the southern edge of the Shield, especially in the eastern part of the province (Byers, Caldwell and Kupsch 1969, Gordon 1979, Richards 1981).

The Central Plains was an area of extensive glacial deposition. Thus, most of the bedrock is overlain by a thick layer of glacial till, up to 300 m thick (Richards 1981). Most of the landforms in the area were formed by glacial activity, either by glacial or glacio-lacustrine deposition or by glacio-fluvial activity. Such landforms include moraines, till plains, kames, outwash plains, lake beds and meltwater channels (Gordon 1979).

Physiographically, the Central Plains can be divided into three regions, corresponding to different topographic levels: 1) the Manitoba Lowland, 2) the Saskatchewan Plain and 3) the Alberta Plain (Gordon 1979, Richards 1969, 1981) (Figure 1).

The Manitoba Lowland occupies only a small area in Saskatchewan, in the east-central part of the province. The Lowland comprises an extremely flat, featureless and poorly drained area, between 250 and 350 m above sea level, that corresponds to the floor of Glacial Lake Agassiz (Richards 1969, 1981). Surface materials are mainly deep silts and clays that were deposited on the floor of Lake Agassiz. There are also some old beach deposits, consisting of sand and gravel. Coarse outwash deposits are common in the northern part of the area.

The Manitoba Lowland is bounded to the west by the Saskatchewan Plain, which is 250 to 650 m above sea level (Figure 1). The two regions are separated by a series of steep east-facing slopes that rise as much as 120 m in a few kilometers. These slopes form the eastern faces of the Pasquia and Porcupine Hills and Duck Mountain, and are part of the Manitoba Escarpment (Richards 1981).

The Saskatchewan Plain occupies much of eastern and central Saskatchewan, south of the Shield. Local topography within the area varies greatly, depending on glacial history. Gently undulating till plains are the most common landscape. Flat clay plains, corresponding to glacial lake bottoms, are also quite common (Richards 1981). Less common, but providing

more relief, are gently rising till-covered uplands (which may be up to 50 m high), steep-walled glacial meltwater channels (up to 90 m deep), and sand hills (Richards 1981).

Open water is quite common in the northern half of this region, with small lakes, bogs, marshes and streams occupying 7 to 10% of the surface area (Harris et al. 1983, Richards 1969). In the southern half of the area, surface water is much less common and tends to be seasonal.

To the west of the Saskatchewan Plain lies the Alberta Plain (Figure 1). The two regions are separated by the Missouri Couteau, an east-facing escarpment that rises 90 to 150 m. Although it is neither as steep nor as high as the Manitoba Escarpment, the Missouri Couteau is distinct along most of its length, because of the thick layer (up to 30 m thick) of hummocky moraine deposited along its crest by the Wisconsinan Ice Sheet (Richards 1969, 1981).

The Alberta Plain is higher (550 to 1400 m above sea level) and has more local relief than the Saskatchewan Plain (Richards 1981). The local topography again varies from one area to another, depending on glacial history, and includes till plains, till-covered uplands, rolling moraines, flat glacial lake bottoms, glacial meltwater channels and sand hills. Surface water is relatively common in the north, occupying up to 10% of the surface area, and relatively uncommon in the south (Harris et al. 1983).

In the southern part of the Alberta Plain there are three distinct upland areas: the Cypress Hills, Wood Mountain and Pinto Butte. These uplands are strongly dissected



tablelands of Tertiary bedrock, which were either unglaciated or modified little by glacial activity (Richards 1981). Consequently exposed bedrock is more common here than in any other part of the Central Plains. The dominant features of local topography are due to erosion by flowing water, and include deep, steep-sided gullies and buttes (Richards 1981). Local relief is generally greater than elsewhere in the province, especially in the Cypress Hills which rise to an altitude of almost 1400 m.

## 2.2 Vegetation, Soils and Climate

Climate, soils and natural vegetation are highly interrelated and show very similar patterns of variation. Thus, they can be used together to define ecological regions. Harris et al. (1983) recognize six such ecological regions in Saskatchewan (Figure 2, Tables 1 and 2).

In the northeastern corner of the province is the Subarctic Boreal Ecoregion, an area of transition between boreal forest and tundra. The vegetation of this region is mainly lichen woodland (Coupland and Rowe 1969), consisting of semi-open stands of black spruce (Picea mariana), with a ground cover of reindeer moss (Cladonia spp.) on thin Brunisolic soils, or of peat moss (Sphagnum spp.) on Organic soils. The climate is humid (primarily because of low evapotranspiration) and very cold (Harris et al. 1983). This ecological region is not accessible by road and thus lies outside the boundaries of the study area.

To the south of the Subarctic Boreal Ecoregion is the

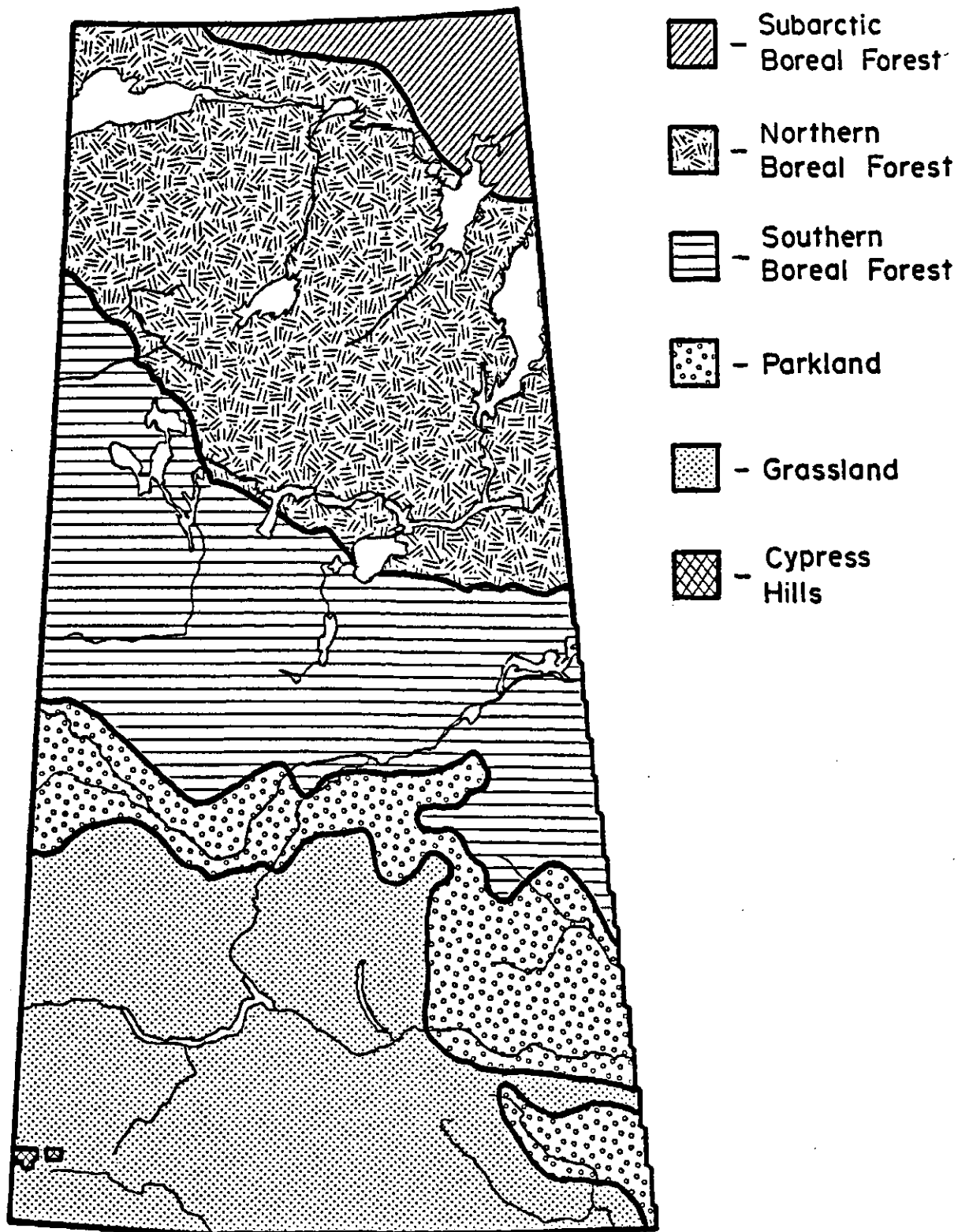


Figure 2. Ecological regions of Saskatchewan (after Harris *et al.* 1983).

Table 1. Ecological regions of Saskatchewan: Vegetation and soils  
(adapted from Harris *et al.*, 1983).

<u>Ecological Region</u>	<u>Area km<sup>2</sup>x10</u>	<u>Vegetation</u>	<u>Soil</u>
Subarctic Boreal	28	Black spruce, lichen, Sphagnum moss	Brunisolic & Crysollic
Northern Boreal	210	Black spruce, jack pine, feather moss, lichen	Brunisolic, Organic & Regosolic
Southern Boreal	159	White spruce, aspen, jack pine, balsam poplar,	Brunisolic, Luvisolic, Gleysolic & Organic
Parkland	81	Aspen, blue grass	Black Chernozemic
Grassland	174	Speargrass, wheatgrass	Brown & Dark Brown Chernozemic
Cypress Hills	0.2	Lodgepole pine, white spruce, fescue grass	Dark Brown Chernozemic & Luvisolic

Table 2. Ecological regions of Saskatchewan: Climate  
(adapted from Harris *et al.*, 1983).

<u>Ecological Region</u>	<u>Mean Temperature (°C)</u>		<u>Degree Days*</u>	<u>Total Annual Precipitation (mm)</u>
	<u>January</u>	<u>July</u>		
Subarctic Boreal	-27.4	15.0	1020	369
Northern Boreal	-23.8	15.0	1116	424
Southern Boreal	-20.7	17.1	1382	431
Parkland	-19.0	18.1	1530	412
Grasslands	-16.7	18.7	1664	370
Cypress Hills	-11.3	17.1	1330	494

\* - degrees Celsius summed daily above a base of 5°C.

Northern Boreal Ecoregion (Figure 2). Its southern limit coincides approximately with the southern limit of the Canadian Shield. The vegetation of the region is coniferous or mixedwood forest. The dominant tree species varies with local topography; jack pine (Pinus banksiana) is most common on drier upland sites or in recently burned areas, while black spruce predominates in lower moister areas. The ground cover generally consists of feather mosses (Pleurozium schreberi and Hylocomium splendens), with some low herbs and shrubs. Soils are mostly Brunisolic. In low-lying, poorly drained areas soils are Organic, and black spruce, tamarack (Larix laricina), peat moss (Sphagnum spp.) and Labrador tea (Ledum groenlandicum) comprise the dominant vegetation. White spruce (Picea glauca) and balsam fir (Abies balsamea) may be common along river valleys and lakeshores. Aspen (Populus tremuloides) and white birch (Betula papyrifera) also occur in the Northern Boreal Forest, especially along water courses, but form only a minor component of the forest. In the Athabasca Plains, jack pine forms extensive stands, with a ground cover of reindeer moss on dry, sandy Brunisolic soils. The climate of the Northern Boreal Forest is cold and humid (Table 2). The Athabasca Plains are slightly colder and drier than the rest of the Northern Boreal Forest.

The Central Plains of Saskatchewan contain three major ecological regions, the Southern Boreal, Parkland and Grassland Ecoregions (Figure 2). In addition, the Cypress Hills Ecoregion occupies a small area in the southwest corner of the province.

The Southern Boreal Ecoregion is an area of mixedwood forest, the composition of which varies locally with topography and soil conditions. On dry, well-drained uplands or sandy soils, jack pine usually predominates, often mixed with aspen, with a ground cover of reindeer moss, blueberry (Vaccinium myrtilloides), and bearberry (Arctostaphylos uva-ursi). In moister, well-drained areas, the most common tree species is white spruce, usually mixed with aspen, jack pine, white birch, and in older and more mature forests, balsam fir. The understory and ground vegetation is often very diverse, especially where the canopy is somewhat open, and consists of a number of broad-leaved herbs and shrubs. In still moister, less well-drained areas, white spruce is mixed with, or replaced by, black spruce and balsam poplar (Populus balsamifera). The wettest and most poorly drained sites support stands of black spruce, or black spruce and tamarack, with a ground cover of peat moss, and an understory of dwarf birch and Labrador tea. In the southernmost part of the region, large areas of forest have been cleared for agriculture.

Soils also vary greatly with local topography in the Southern Boreal Ecoregion. Brunisolic and Luvisolic soils are common in moderately to very well-drained areas, while Gleysolic and Organic soils predominate in poorly-drained areas. There are also some Chernozemic soils along the southern edge of this region. The Chernozemic soils were apparently formed during a past, northward extension of the grassland zone. The climate in the Southern Boreal Ecoregion

is subhumid and cool (Table 2).

The Parkland Ecoregion (Figure 2) forms an area of transition between grassland and boreal forest, south of the Southern Boreal Ecoregion and in the southeastern corner of the province. The natural vegetation of this ecoregion is a mosaic of grasslands and aspen groves. The most common tree species is trembling aspen, although balsam poplar and white birch may be locally abundant in cooler, moister areas, and cottonwood (Populus deltoides), green ash (Fraxinus pennsylvannica) and Manitoba maple (Acer negundo) are common in river valleys. Bur oak (Quercus macrocarpa) is also present, in drier areas along the Qu'Appelle River Valley. The understory in the aspen groves is composed of a variety of shrubs, including willow (Salix spp.), Saskatoon (Amelanchier alnifolia) and pincherry (Prunus pennsylvanica). The predominant ground vegetation is brome grass (Bromus spp.) and bluegrass (Poa spp.). In open areas, the dominant natural vegetation was grassland, consisting of rough fescue (Festuca scabrella), speargrass (Stipa comata) and wheatgrass (Agropyron dasystachyum), with sedges (Carex spp.) in the moister, marshy areas. Most of the native vegetation in the Parkland Ecoregion has been destroyed by cultivation, although isolated aspen groves still exist.

The soils of the Parkland Ecoregion are mainly Black and Dark Gray Chernozemic with some Gleysolic soils in low-lying areas. The climate is dry and warm (Table 2).

The Grassland Ecoregion in Saskatchewan was mostly mixedgrass prairie. The natural vegetation of this area

consisted of a mixture of grasses and herbs, including speargrasses (Stipa comata and S. spartea), wheatgrasses (Agropyron dasystachyum and A. smithii), June grass (Koeleria cristata) and pasture sage (Artemisia frigida). Blue grama (Bouteloa gracilis) and thread-leaved sedge (Carex filifolia) occurred on the driest sites, while low-lying areas contained shrubs such as willow, Saskatoon, chokecherry (Prunus virginiana), snowberry (Symphoricarpos occidentalis) and wolf willow (Eleagnus commutata). Small isolated stands of aspen were also present, and cottonwood grew in river valleys. In the southwestern corner of the province, there were about 12,000 square kilometers of shortgrass prairie, where speargrass, blue grama, wheatgrass, June grass and thread-leaved sedge were common. Most of the natural vegetation in the Grassland Ecoregion has been destroyed or greatly modified by cultivation or intensive grazing.

The soils of the Grassland Ecoregion are mostly Brown to Dark Brown Chernozemic. The climate is warm and dry to very dry (Table 2). The shortgrass prairie is slightly warmer than the mixedgrass prairie, and is the driest area in the province.

Because of high altitude, the physical environment and vegetation of the Cypress Hills Ecoregion are similar to those in the Rocky Mountains and their foothills. Vegetation consists of lodgepole pine (Pinus contorta) forest and fescue prairie. Pine forests occur mainly on the slopes of the hills, occasionally mixed with aspen, and with a ground cover of mixed grasses and herbs. White spruce and balsam poplar

are common in ravines. The dry, flat uplands are covered by fescue prairie with rough fescue, oat grass (Danthonia intermedia) and shrubby cinquefoil (Potentilla fruticosa) predominating.

The soils of the Cypress Hills are primarily Dark Brown Chernozemics, with some Luvisols on the slopes. The climate is subhumid and cool because of the altitude and relief (Table 2).

Within any ecoregion, vegetation, soils and climate show considerable local variation, primarily in association with changes in topography. Uplands tend to be warmer and drier than surrounding landscapes, and thus to have vegetation and soils resembling those of ecoregions to the south. Similarly, lowlands tend to be moister and cooler, and if they are well-drained, often have vegetation and soils that are similar to those of more northerly ecoregions. River and stream valleys, which are of particular interest in this study, often provide such moist, cool, well-drained environments. Thus, river valleys in the grasslands may support extensions of parkland vegetation, while those in the parkland may support extensions of boreal forest. River valleys may also contain specific river valley floral elements.



### 2.3 Hydrography

One eighth of the surface area of Saskatchewan is covered by water. However, this surface water is not evenly distributed within the province, and the nature of surface waters and drainage patterns is highly variable. This variability is due primarily to differences in precipitation and evapo-transpiration, but the type of surface materials also has some effect (Richards 1981).

On the Shield, precipitation is the highest and evapo-transpiration the lowest in the province (Harris et al. 1983). Hence this area has the largest amount of surface water and the largest lakes. Most of the surface water on the Shield lies in elongated basins in the bedrock. Because of this, and the absence of true valleys in the Shield, most of the drainage systems are complex and poorly defined (Richards 1981). The larger rivers, such as the Churchill, generally consist of chains of lakes connected by short stretches of fast water. Because of the large number and sizes of lakes, and the low evapo-transpiration, both lake water levels and stream flow levels tend to be relatively stable.

In the southern boreal forest and northern parkland, precipitation is lower and evapo-transpiration is higher. Thus, although surface water is moderately abundant, water bodies are smaller and fewer than on the Shield, and seasonal fluctuations in lake levels and stream flows are greater (Richards 1981).

Farther south, in the southern parkland and grassland, precipitation is the lowest and evapo-transpiration is the

highest in the province. Thus, this area has the least surface water. Seasonal fluctuations in water levels and stream flows are very large, even in the larger lakes which tend to be shallow and saline (Richards 1981). Many of the smaller water bodies and streams are temporary, and exist only for short periods following spring snowmelt or heavy summer rains (Richards 1981). In large areas of the grasslands, especially in the western half of the province, drainage is restricted to enclosed, internal basins centered on shallow saline lakes (Figure 3) (Richards 1981). These are essentially evaporation basins.

The only large rivers in southern Saskatchewan are the North and South Saskatchewan Rivers, which unite 50 kilometers east of Prince Albert to form the Saskatchewan River. Seventy-five to 90% of the water in these rivers comes from outside the province, primarily from the Rocky Mountains (Richards 1981). Only a small proportion of the province actually drains into the Saskatchewan Rivers, and this area provides little runoff. Seasonal variations in flow in the Saskatchewan Rivers are great. Peak flows occur in mid-June to mid-July, during spring snowmelt and rainfall in the mountains.

Large sections of the Saskatchewan Rivers in Saskatchewan are modified by the Gardiner and Squaw Rapids Dams. These dams reduce the seasonal variation in flow, and increase the diurnal variation. They also reduce seasonal variation in water temperature, producing cooler summer and warmer winter temperatures. In addition, the amount of

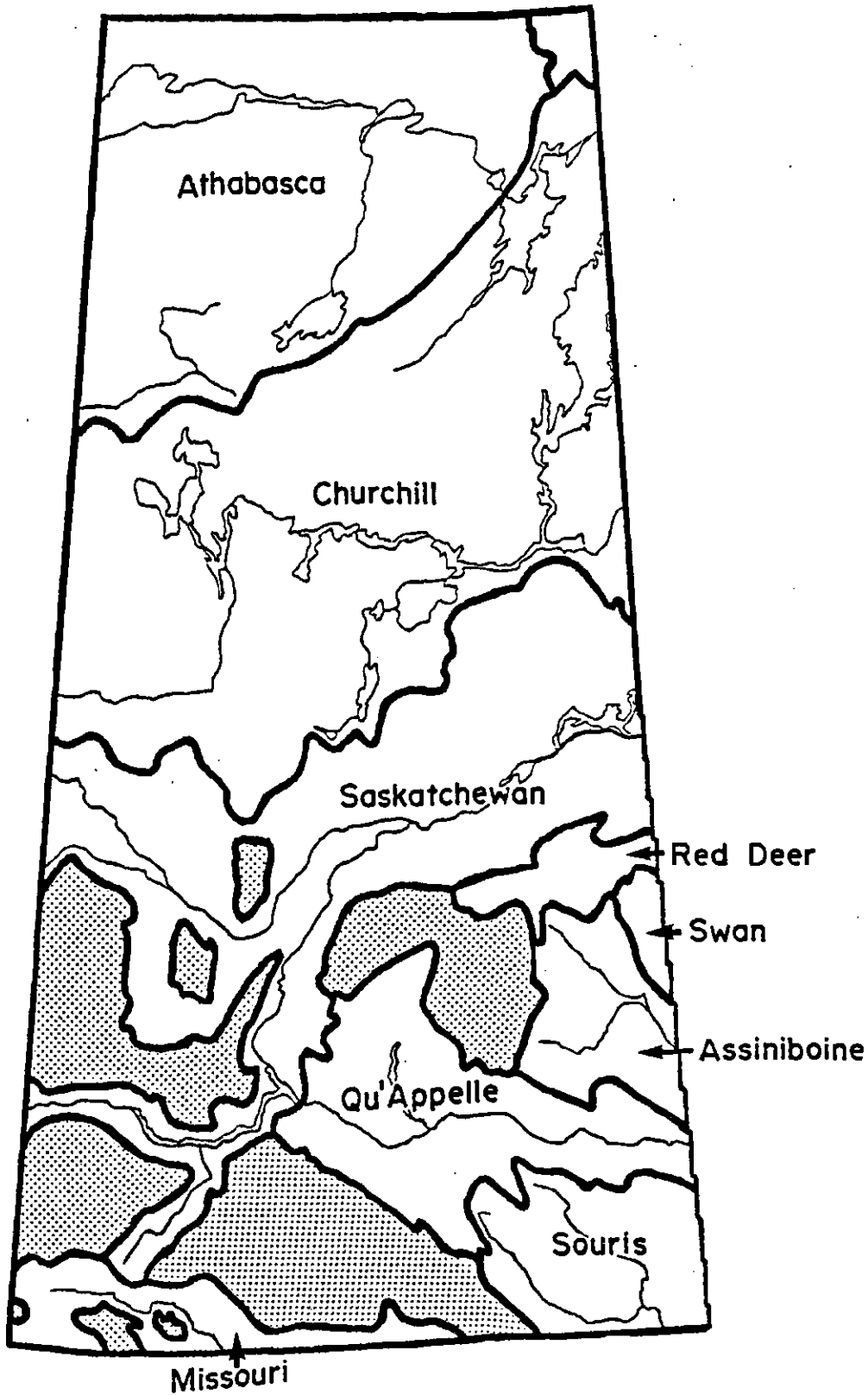


Figure 3. Drainage basins in Saskatchewan (after Danks 1979, Richards 1981 and Richards and Fung 1969). Stippled areas are endorheic drainage basins.

suspended material is greatly reduced, and water clarity is greatly increased, by the dams and their associated reservoirs. Gardiner Dam affects the South Saskatchewan River as far downstream as its confluence with the North Saskatchewan River. Squaw Rapids Dam affects the Saskatchewan River at least as far downstream as the Cumberland Delta.

Saskatchewan contains parts of three major drainage systems (Figure 3). A large area in northern and northwestern Saskatchewan drains into the Arctic Ocean via the Mackenzie River. The Clearwater and Fond du Lac Rivers and Lake Athabasca are part of this system. In the southwestern corner of Saskatchewan, parts of the Cypress Hills and Wood Mountain drain into the Gulf of Mexico, via the Frenchman River and Battle Creek, and the Missouri-Mississippi River System. The rest of the province drains eastward into Hudson Bay, through two separate drainage systems, the Churchill and the Nelson. The Churchill River drains much of the southern and eastern parts of the Shield, and the western part of the Southern Boreal Forest. The Souris, Qu'Appelle and Assiniboine Rivers, all of which empty into the Red River, the Swan River, the Red Deer River and the Saskatchewan Rivers are all part of the Nelson River System. These rivers drain most of eastern Saskatchewan south of the Shield.

#### 2.4 Intensive Study Sites

Thirty-five sites in Saskatchewan were selected for intensive study (Figure 4, Table 3). All of these sites are located in riffles or runs - areas of relatively fast current

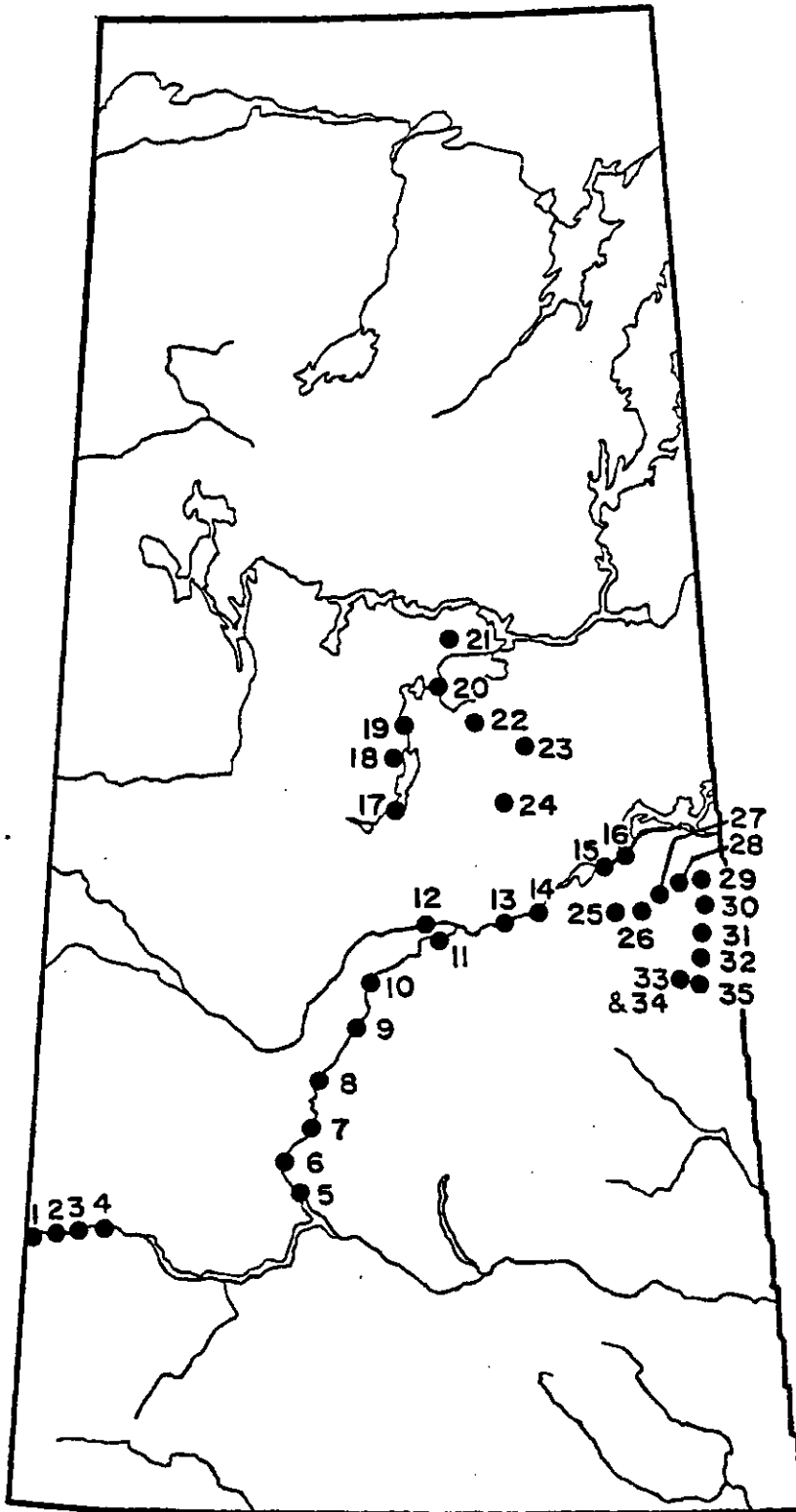


Figure 4. Locations of intensive study sites. Sites are described in the text.

Table 3. Descriptions of intensive study sites.

Site #	Stream Name	Width (m)	Depth (m)	Substrate	Current Velocity
1	South Saskatchewan R.	450	>2	Gravel & cobbles	Fast
2	"	* 300	>2	Boulders & mud	Moderate
3	"	* 250	>2	Gravel, cobbles & boulders	Moderate
4	"	* 200	>2	Gravel & cobbles	Fast
5	"	200	>2	Cobbles and sand	Slow
6	"	550	>2	Cobbles, small boulders & sand	Slow
7	"	450	2	Cobbles, small boulders & sand	Slow
8	"	400	>2	Cobbles, small boulders & sand	Moderate
9	"	250	>2	Cobbles and boulders	Moderate
10	"	200	1.5	Cobbles and small boulders	Moderate
11	"	200	1.5	Cobbles, boulders & sand	Moderate
12	North Saskatchewan R.	200	>2	Cobbles and small boulders	Fast
13	Saskatchewan R. *	250	>2	Cobbles and boulders	Fast
14	" *	250	>2	Cobbles and boulders	Fast
15	"	250	1.5	Cobbles, boulders & sand	Slow
16	"	550	1.5	Cobbles, boulders & sand	Slow
17	Waskesiu River	15	2	Cobbles, boulders & sand	Slow
18	Weyakwin River	15	0.6	Boulders	Fast
19	Montreal River	50	2	Boulders, cobbles, sand & gravel	Moderate
20	"	50	2	Boulders, cobbles & sand	Fast
21	Mackay Creek	4	0.3	Boulders	Moderate
22	Nipekamew River	15	1	Cobbles & boulders	Fast
23	unnamed stream	5	0.5	Cobbles, small boulders & sand	Moderate
24	McDougal Creek	4	0.7	Boulders, cobbles & sand	Moderate
25	Carrot River *	10	1.5	Cobbles, boulders, gravel & mud	Moderate
26	Red Earth Creek *	4	1.5	Mud and sand	Slow
27	McVey Creek	5	0.5	Cobbles and boulders	Moderate
28	Rice River	10	0.7	Boulders, cobbles & sand	Fast
29	Bainbridge River	5	0.4	Boulders, cobbles & sand	Fast
30	Waskwei River	10	0.4	Cobbles & small boulders	Moderate
31	Pasquia River	12	0.5	Cobbles, boulders & sand	Moderate
32	Overflowing River	15	0.5	Cobbles, boulders & sand	Moderate
33	Fir River	17	0.5	Cobbles and small boulders	Moderate
34	"		0.2	Cobbles & small boulders	Moderate
35	Red Deer River	50	1.5	Boulders	Moderate

\* - Turbidity very high

and stony substrate.

Sites 1 to 4 are on the South Saskatchewan River upstream from Lake Diefenbaker. Site 1 is on the south bank, 1 km downstream from the confluence of the Red Deer River. There is no mixing of Red Deer and South Saskatchewan River water at this point. Site 2 is at the bridge on Highway 21 north of Leader. Site 3 is north of Prelate, at an old ferry site, and site 4 is at Lemsford Ferry, south of Kindersley.

Sites 5 to 11 are on the South Saskatchewan River between Lake Diefenbaker and the confluence with the North Saskatchewan River. Because of Gardiner Dam, discharge and current velocity are relatively low, and water clarity is very high at all of these sites. Sites 5 to 8 are in the area that is thermally influenced by Gardiner Dam (Lehmkuhl 1972b). Site 5 is approximately 0.5 km downstream from Gardiner Dam; site 6 is just upstream from Outlook at the bridge on Highway 15; site 7 is approximately half way between Outlook and Saskatoon; and site 8 is just upstream from Saskatoon, 0.5 km upstream from the Queen Elizabeth Power Station. At site 5, water temperatures are very low, and there are large diurnal fluctuations in water level. Temperatures increase and water level fluctuations decrease moving downstream towards site 8.

Sites 9 to 11 are downstream from Saskatoon. This stretch of the South Saskatchewan River is quite eutrophic, and produces extensive growths of filamentous algae and macrophytes. Site 9 is at Hague Ferry, east of Hague; site 10 is at St Laurent Ferry, east of Duck Lake; and site 11 is

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 ... ..

0.5 km upstream from Birch Hills Ferry, north of Birch Hills.

Site 12 is on the North Saskatchewan River at Cecil Ferry, 15 km east of Prince Albert, on the south side of the river. Sites 13 to 16 are on the Saskatchewan River downstream from the confluence of the North and South Saskatchewan Rivers. Sites 13 and 14 are upstream from Tobin Lake, at the old Gronlid Ferry site north of Melfort, and 6 km upstream from Nipawin, respectively. Sites 15 and 16 are 100 m and 18 km, respectively, downstream from Squaw Rapids Power Station. Because of their proximity to the dam, both sites experience relatively low summer temperatures, very clear water, and large diurnal fluctuations in water level.

Sites 17 to 21 are on boreal streams in the Montreal Lake and Lac la Ronge areas. All of these streams were sampled where they cross Highway 2. Site 17 is on the Waskesiu River; site 18 is on the Weyakwin River; sites 19 and 20 are both on the Montreal River, 60 km south of La Ronge, and at La Ronge just upstream from where it empties into Lac la Ronge, respectively; site 21 is 60 km north of La Ronge on Mackay Creek.

Sites 22 and 23 are located along Highway 165 (between La Ronge and the Hanson Lake Road). Site 22 is on the Nipekamew River. Site 23 is on a small, unnamed stream 10 km west of the Highway 106 junction. This stream is spring-fed and very cold. Site 24 is on McDougal Creek, where it crosses a Prince Albert Pulp Company access road just northeast of Nipawin Provincial Park.

Sites 25 to 35 are all in or near the Pasquia Hills.



Site 25 is on the Carrot River, a large stream draining a large area of agricultural land to the south and southwest of the study site. In most places the Carrot River is wide, deep, and slow-flowing, with a mud bottom. However, the study site is in a shallow riffle where current velocity is moderate and the substrate is composed of cobble and boulders. Site 26 is on Red Earth Creek. The substrate here is composed of mud and sand only. However, many logs and pieces of wood are present.

Sites 27 to 31 are all on cold, spring-fed, high gradient streams along the steep northern and eastern slopes of the Pasquia Hills. The sites are on McVey Creek, Rice River, Bainbridge River, Waskwei River and Pasquia River, respectively. Gradient is especially high on the Rice and Bainbridge Rivers. At basal flow, these streams are all quite small and shallow, with moderately fast to fast current velocities. Very large increases in discharge and current velocity occur at all of these sites during spring snowmelt or heavy summer rains. During such runoff incidents, the normally clear water becomes very turbid.

Sites 32 to 35 are just southeast of the Pasquia Hills. Site 32 is on the Overflowing River; sites 33 and 34 are both on the Fir River; site 35 is on the Red Deer River. The Fir River is quite warm; however, there are several short stretches that are cooled by the influx of cold water from springs in the stream bank. Site 34 is in such a spring-cooled stretch of stream, where water temperature is 5 to 15°C cooler than in nearby stream reaches. Site 33 is in a

warmer area that is unaffected by springs.

Sites 25 to 28 are along the north side of the Pasquia Hills where their respective streams cross Highway 163. Sites 29 to 32 are along the east side of the hills, along Highway 9. Sites 33 and 34 are within Hudson Bay Regional Park, 5 km southwest of the town of Hudson Bay. Site 35 is where the Red Deer River crosses Highway 9, 5 km south of Hudson Bay.

Sites 1 to 8 on the South Saskatchewan River are in the Grassland Ecoregion. Sites 9 and 10 are in the Parkland. Site 21, on Mackay Creek, is in the Northern Boreal Forest. All other sites are in the Southern Boreal Forest.

### 3 METHODS

The study was divided into two components: 1) an extensive study of the entire province to determine the identity and range of each Saskatchewan heptageniid species, and 2) an intensive study of a smaller number of sites to determine heptageniid distribution patterns, seasonal variations in distribution patterns, and the relationship between distribution patterns and environmental parameters.

#### 3.1 Extensive Study

Streams and rivers in all parts of Saskatchewan that are accessible by road were visited and searched for heptageniid larvae (Figure 5). Some streams in western Manitoba and in the Cypress Hills in Alberta were also examined, as were a few lakes in northern Saskatchewan. Heptageniids were found at 170 of 272 stream sites examined and at four of seven lake sites. Larvae were collected by: 1) sweep netting, 2) picking larvae from stones removed from the stream substrate, and 3) picking larvae from logs removed from the stream. As many of these three methods as possible were used at each site.

The extensive study was conducted in 1979, 1981 and 1982. Each site was visited at least once between mid-May and early July, when larvae of all heptageniids known to occur in Saskatchewan are present. Many sites were also visited earlier and later in the year, to confirm that no species with different life cycles were present.

There are no comprehensive keys to species for heptageniid larvae, except in the genus Stenonema. In other

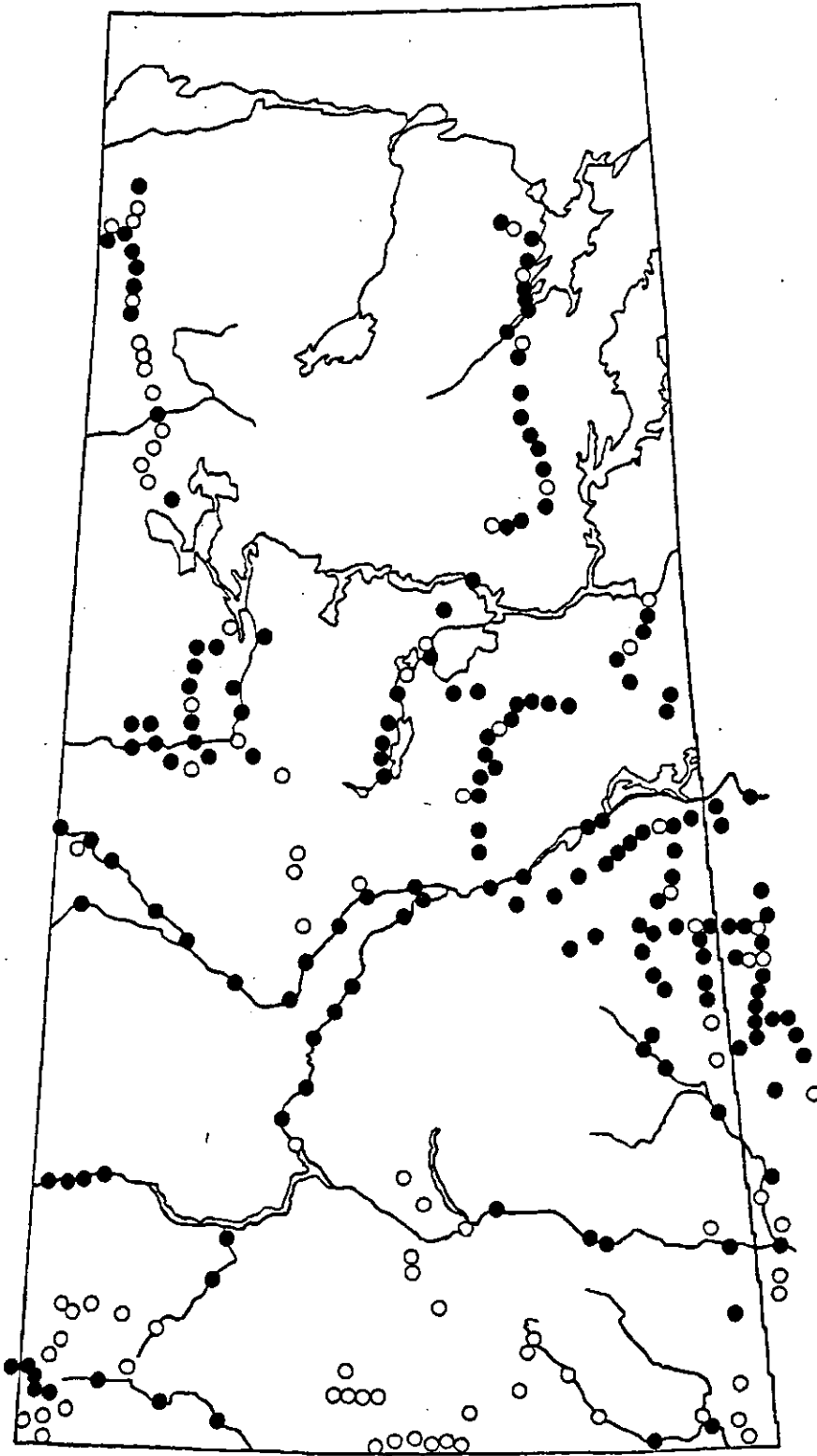


Figure 5. Locations visited during extensive study. Solid dots indicate sites where heptageniid larvae were collected. Open dots indicate sites where no heptageniid larvae were found.

genera, male imagoes are required for species identification. However, heptageniid adults are very difficult to collect in the field. Therefore, initial species identifications were based on adult males that had been reared from larvae in the laboratory. Larvae from all parts of the province were returned to the laboratory and kept in individual cages in aquaria for rearing. Subsequent examination of larval exuviae associated with reared adults led to the production of a larval key for Saskatchewan heptageniid species. Larvae were distinguished mainly by color patterns which were both reliable and easy to use. Larval keys and descriptions are being published separately.

### 3.2 Intensive Study

The 35 sites included in the intensive study (Figure 4) were chosen to maximize the diversity of sites examined within a manageable area. As wide as possible a range of temperature regimes, current velocities, stream sizes and substrate types were included. As many sites as possible were chosen from the Saskatchewan River system and the boreal forest, which appeared to be the two major heptageniid faunal areas in the province based on preliminary collections.

#### 3.2.1 Sampling frequency

Each of the 35 sites selected for intensive study was visited eight times between mid-April and mid-October, 1980. Sampling interval varied seasonally with the number of species present. Sites were visited every 3 weeks in spring,

every 2 weeks in early summer and approximately every 4 weeks in late summer and autumn. Sampling periods were in April (April 23-May 2), May (14-21), early June (2-12), late June (18-25), July (3-12), August (5-13), September (4-14) and October (September 27-October 14). During each sampling period, except the last, all sites were visited within 7 to 10 days. Sites 1-7, 15 and 16 were not visited in late June because of extremely high water levels. Sites 1, 11, 12 and 13 were not visited in April because of bank ice. Muddy roads prevented visits to site 4 in October and site 14 in July.

### 3.2.2 Sampling heptageniid larvae

Heptageniid larvae were sampled using three different semi-quantitative techniques. Three sampling methods were required because no one method alone produced adequate numbers of all species at all sites. The three sampling methods used were: 1) Sweep netting, using a standard sweep net with a 1 mm mesh bag. Samples were sorted in an enamel pan in the field and the heptageniid larvae removed were fixed in 80% ethanol. The area sampled was calculated from the length of the sweep net haul and the width of the net mouth. 2) Picking larvae from stones - heptageniid larvae were picked from 20 to 40 stones which had been removed from the stream substrate. The surface area of stone sampled was calculated from three linear measurements of each stone, assuming that all stones are rectangular in shape. 3) Picking larvae from logs - logs and other large pieces of wood were removed from the stream, and heptageniid larvae were picked

from them and preserved. The surface area of log sampled was calculated from measurements of the total length and median diameter of each log. The surface area of irregular pieces of wood was calculated from three linear measurements. Sweep net samples were taken at all sites, except site 34. Stone samples were taken at all sites, except site 26, which had a mud and sand substrate. Log samples were taken wherever and whenever possible, and were always taken at site 26.

Because of large variations in larval density, sampling area could not be standardized without causing either unmanageably large samples at some sites or inadequately small samples at others. Therefore, sampling effort was standardized instead, at approximately 1.5 hours of sampling per site. In June and early July, when the number of species present was greatest, sampling effort was increased to approximately 2 hours per site. At each site, sampling effort was divided among the three sampling methods relative to their effectiveness at collecting larvae at that site; i.e. more time was spent sampling with the more productive methods.

Samples were preserved in ethanol and returned to the laboratory, where heptageniid larvae were identified and counted with the aid of a dissecting microscope.

### 3.2.3 Measurement of environmental parameters

Several environmental parameters were measured at each intensive study site. Environmental parameters were measured during each visit to each site, except that the size

distribution of substrate particles was measured only in September.

In streams that could be waded across, stream width was measured at the study site with a tape measure. In deeper streams and rivers, except the Saskatchewan Rivers, width was measured along adjacent bridges. Width at Saskatchewan River study sites was estimated from 1:50,000 topographic maps. Stream depth was measured with a meter stick. Depths greater than 2 m were not measured, and deeper streams and rivers were all assigned maximum depths of 2 m.

Air and water temperatures were measured using an ASTM field thermometer. Daily temperature variation was measured with a maximum-minimum thermometer at sites 4, 11, 12, 20, 24, 28, 29, 33 and 35.

Current velocity was measured using the floating orange method (Welch 1948). The time taken for an orange (which floats just below the surface) to travel a measured distance was determined. At least three replicate velocity measurements were taken at each site.

Turbidity was measured using a modified Secchi disc apparatus, consisting of a weighted plastic petri dish. Because of its small size and transparency, this apparatus is much more sensitive than a standard Secchi disc. Such sensitivity is required to measure low turbidities in shallow water.

The depth of silt on the substrate was measured using a



bottomless metal cylinder, 30 cm in diameter, which was placed firmly on the substrate. The substrate within the cylinder was disturbed, and the water vigorously stirred, to suspend and evenly mix the silt. A 250 ml sample of water and suspended silt was then withdrawn from the metal cylinder, and allowed to settle for one hour in a graduated cylinder. The concentration of silt in the water enclosed by the metal cylinder is given by

$$s_1 = \frac{\text{the volume of silt on the substrate}}{\text{the volume of water in the metal cylinder}} \\ = (s \cdot a)/(d \cdot a) = s/d$$

where  $s$  is the depth of silt on the substrate,  
 $a$  is the cross sectional area of the metal cylinder,  
 and  $d$  is the depth of water in the cylinder

This is equivalent to the concentration of silt in the sample that was withdrawn from the metal cylinder,

$$s_2 = \frac{\text{the volume of silt in the graduated cylinder}}{\text{the volume of the graduated cylinder}} \\ = v \text{ (ml)}/250 \text{ ml}$$

Thus,

$$s/d = v/250$$

and the depth of silt originally on the substrate,

$$s = d \times v/250$$


The depth of silt on the substrate can thus be calculated from the volume of silt in the sample withdrawn from the metal cylinder ( $v$ ) and the depth of water where the sample was taken ( $d$ ).

The size distribution of substrate particles (stones,

gravel and sand) was analyzed by removing approximately 0.25 m<sup>2</sup> of substrate, to a depth of 10 to 15 cm, using a shovel. This sample of substrate was passed through a standard, graded Tyler series of screens, with 0.125 to 16 mm openings (Cummins 1962). Larger stones were separated into size classes (16 - 32 mm, 32 - 64 mm, 64 to 128 mm and 128 - 256 mm) by hand measurement and sorting. The volume of particles in each size class was then determined by submersing the particles and measuring the volume of water displaced. Two replicate samples of substrate were collected and analyzed at each site, except site 26, where the substrate was not analyzed.

To measure the amount of organic material on the substrate, detritus was collected in a 5 m sweep net haul. A double-bag sweep net with mesh sizes of 0.2 and 1 mm was used, to divide the detritus into coarse and fine fractions. Detrital samples were preserved in 80% ethanol and returned to the laboratory, where they were air-dried within 10 days of collection. Samples were then weighed, ashed at 560°C for 1 hour in a muffle furnace, and reweighed. The ash-free dry weight of coarse and fine detritus per square meter of substrate was then calculated.

The amount of plant growth and allochthonous organic material were assessed subjectively, by assigning one of eight abundance values (0 - 7). Seven easily recognizable types of plant growth- filamentous bacteria or fungi (probably mostly Sphaerotilus), filamentous algae (mostly Cladophora), diatoms, Nostoc, Chara, moss and macrophytes,



and three kinds of allochthonous material- grass, broad leaves and wood, were distinguished. Each of these types of plant growth and allochthonous material was assessed independently and assigned an abundance value.

### 3.3 Data Analysis

The intensive study generated four separate data sets, one from each of the three biological sampling methods (species x sites), and one of environmental data (environmental parameters x sites). Data generated by the three biological sampling methods are not strictly comparable, because of differences in sampling efficiency and species selectivity. Thus, the three sets of data could not be combined, and were analyzed separately. Another set of biological data consisting of combined species presence/absences from sweep net and stone samples was also analyzed. The rationale for combining presence/absence data from different sampling methods is presented in Section 4.2.4.

It is impossible to analyze simultaneously across both sites and sampling times, because multivariate analyses cannot be directly applied to three-dimensional matrices. Therefore, each data set was analyzed in two different ways. First, data for each site were averaged across all sampling times prior to analysis. Mean annual abundances of each species, and mean, minimum and maximum values of environmental parameters were used. Subsequently, data were analyzed treating each site-time (each sampling time at each

site), instead of each site, as a sampling unit, to examine seasonal structure in the data.

Multivariate analyses were also performed on species presence/absence data from the extensive study. For sites that had been visited more than once, data from all sampling visits were combined. Data from the 35 intensive study sites (combined across all sampling times) were also included.

### 3.3.1 Data transformation

Prior to analysis, species abundances were converted to their natural logarithms, using the formula

$$x' = \ln(x + 1)$$

where  $x$  is the raw species density,

and  $x'$  is the log transformed density

The use of raw abundances is undesirable because it excessively weights a few dominant species, which become the primary determinants of the results. Furthermore, log-transformed data are more meaningful biologically because the processes responsible for species abundances are usually of an exponential nature (Maarel 1979, cited from Gauch 1982). Log-transformed data are also more normally distributed, and thus better fit the requirements of most statistical analyses.

Species abundances were not standardized because this excessively weights rare species. Standardization involves treating all species equally so that a small change in the abundance of a rare species is given the same weight as a large change in the abundance of a more common species. As a

result, in classifications using standardized species abundances, most clusters are defined solely by the presence or absence of one or two rare species.

Sites were normalized (standardization by norm, rather than standard deviation) prior to classification to remove bias due to unequal sample sizes. If this bias is not removed, sites with low total abundances tend to be grouped together, regardless of their species compositions. Data were normalized by dividing the abundance of a species at each site by the square root of the sum of squares of all abundances at that site:

$$x_{ij}' = x_{ij} / (\sum_{i=1}^m x_{ij}^2)^{1/2}$$

where  $x_{ij}$  is the abundance of species  $i$  at site  $j$ ,

$x_{ij}'$  is the normalized abundance of species  $i$  at site  $j$ ,

Data were not normalized prior to ordination because the ordination algorithm used includes double standardization (by maximum).

Environmental data were standardized to unit mean and variance to remove bias due to different units of measurement. A mean of one, rather than zero, was required to allow weighted averages hybrid ordination. Each environmental parameter was standardized using the formula:

$$y_{ij}' = ((y_{ij} - y_i) / s_i) + 1$$

where  $y_{ij}'$  is the standardized value of parameter  $i$  at site  $j$

$y_{ij}$  is the unstandardized value,

$y_i$  is the mean raw value of parameter  $i$

and  $s_i$  is the standard deviation of parameter  $i$

### 3.3.2 Multivariate analyses

Two complementary multivariate techniques, classification and ordination, were used to examine the distribution patterns of heptageniid larvae. Multivariate analyses deal with two-dimensional data matrices, in this case species  $\times$  sites matrices (or sites  $\times$  sites resemblance matrices). Such data matrices can be described geometrically as  $m$ -dimensional clouds of points, with each species as an axis and samples plotted in  $m$ -dimensional hyperspace based on their species abundances (or with sites as axes and each site plotted in  $m$ -dimensional space based on its dissimilarity to all other sites). Multivariate techniques are used to summarize the variation in such clouds of points. Classification locates clusters of points within the cloud. Ordination reduces the dimensionality of the cloud by defining a smaller number of dimensions that contain most of the variation. This facilitates the recognition of patterns or trends in the data.

The relationship of observed species distribution patterns to environmental parameters was examined using weighted averages hybrid ordination.

#### 3.3.2.1 Classification

In classification individuals are grouped into clusters based on their overall similarity (or dissimilarity). Multivariate classification techniques were used to examine

the relationships among stream sites based on resemblances in their heptageniid faunas, and to determine whether heptageniid distribution patterns can be adequately described in terms of faunal zones (that is, by large, distinct, relatively homogenous clusters of sites). Sites were also classified by their environmental similarities.

Classification was performed using programs in the CLUSTAN package (Wishart 1978). The resemblance between a pair of sites was calculated as Euclidean distance. Euclidean distance was used because: 1) it is metric - it can be related to geometric theory and thus obeys the principles of geometry, 2) it is related to standard deviation, 3) it is the simplest and most straightforward of the metric distance coefficients, and involves no weighting, 4) it is the most commonly used dissimilarity measure, facilitating comparison with other studies and 5) it is compatible with robust clustering methods, such as Ward's method (Wishart 1978). For quantitative data (species abundances), the Euclidean distance between two sites  $j$  and  $k$  was calculated as:

$$(1/m \sum_{i=1}^m (x_{ij} - x_{ik})^2)^{1/2}$$

where  $x_{ij}$  is the abundance of species  $i$  at site  $j$ ,

$m$  is the total number of species,

and summation is over all  $m$  species,

For binary data (species presence/absences), this formula can be reduced to

$$(B + C)/m$$

where  $B$  is the number of species present in  $j$  but absent in  $k$ ,

and  $C$  is the number of species present in  $k$  but absent in  $j$

The clustering algorithm used was Ward's method. This method is sequential, agglomerative, hierarchical and non-overlapping. That is, it sequentially produces a hierarchy of clusters, starting with individuals, and grouping individuals and smaller clusters into larger and larger clusters. Clusters are not weighted and the method is combinatorial - the distances between a new cluster and all other clusters can be calculated from the distances and sizes of its component clusters. Ward's method produces minimum-variance spherical clusters (Wishart 1978).

Classification begins with the fusion of the most similar pair of individuals. In Ward's method, subsequent fusions are made so as to minimize increases in the error sum of squares. Thus, the next fusion, at any point in the hierarchical sequence, is the one that unites those two clusters (or individuals) whose fusion produces the least increase in the error sum of squares. The sum of squares is defined as the sum of the distances from each individual to the centroid of its parent cluster. Thus, both dispersion around the centroid and the absolute position of the centroid, i.e. both the within and between sums of squares, are considered.

Ward's method produces a hierarchical classification of sites. In this study the primary interest is in large, distinct, homogenous clusters of sites that may represent faunal zones. Such clusters can be found by plotting the



distance coefficient between each pair of fusing clusters against the number of clusters at that point in the fusion sequence. In this plot, a sudden, large change in slope occurs wherever a relatively homogenous cluster of sites fuses with a dissimilar cluster. Distinct clusters may occur at more than one level in the classification hierarchy, indicating the existence of distinct subgroups within one or more larger groups.

The membership of each large, distinct cluster produced by Ward's method was reexamined using procedure RELOCATE of the CLUSTAN package. RELOCATE compares each individual to the centroid of its parent cluster and to the centroids of all other clusters (at that level in the classification), to determine if that individual has been optimally classified. If necessary, individuals are reclassified, the centroids of affected clusters are recalculated, and all individuals are compared with the new centroids. The distance between an individual site,  $i$ , and the centroid of a cluster,  $p$ , was calculated as the error sum of squares,

$$1/m \sum_{j \in p} \sum_{i=1}^m (x_{ij} - U_{ip})^2$$

where  $m$  is the number of species,

$x_{ij}$  is the abundance of species  $i$  at site  $j$ ,

and  $U_{ip}$  is the mean value for species  $i$  in cluster  $p$

This procedure is comparable to using Ward's method of clustering with a Euclidean distance matrix.

### 3.3.2.2 Ordination

Ordination was performed using detrended correspondence analysis (DCA), a modification of reciprocal averaging (RA) or correspondence analysis. DCA and RA are members of a group of ordination techniques, including principal components analysis (PCA), which operate by eigenanalysis. In eigenanalysis, a series of ordination axes (components) are derived which together describe the variation present in the original data set. Each ordination axis is associated with an eigenvalue, which indicates the amount of variation described, and a vector of ordination scores for each site (or species) in the data matrix. An ordination score indicates the position of a site (or species) on the ordination axis, and is determined by dropping each point in the m-dimensional cloud orthogonally onto the axis. The first ordination axis describes as much variation as possible in any one dimension, and thus corresponds to the longest dimension in the m-dimensional cloud of points. It has the largest eigenvalue. The second axis describes as much of the remaining variation as possible, and has the second highest eigenvalue. The second axis describes only variation that has not been described by the first, and thus must be orthogonal (uncorrelated) to it. Similarly the third axis must be orthogonal to both the first and second axes. A series of axes with decreasing eigenvalues, describing decreasing amounts of variation, are thus derived. The maximum number of axes which can be derived is equivalent to the smaller

dimension of the original species x sites data matrix. However most of the variation is usually concentrated in the first few axes.

Either site or species ordinations can be derived by eigenanalysis. The two ordinations are necessarily related, and either can be derived from the other without a new eigenanalysis.

There are two problems inherent in all eigenanalysis techniques, except DCA: 1) Compression at the ends of the ordination axes. A pair of sites with a given difference in species composition tend to be separated by less distance on the axis if they occur near either end than if they occur near the middle; i.e. a given separation distance on the ordination axis does not have a consistent meaning in terms of difference in species composition. 2) Second and higher level axes may be related to the first in a non-linear way; e.g. they may be quadratic distortions of preceding axes. Interpretation of results is very difficult in such circumstances because spurious axes must be distinguished from valid ones, and because valid axes may be deferred to higher levels by spurious axes. The problem of non-linearly related higher axes is called the arch problem (Gauch 1982, Hill and Gauch 1980).

The algorithm for DCA involves iteration and matrix algebra. The first step is the assignment of arbitrary species ordination scores. Next, corresponding site ordination scores are calculated using weighted averages ordination. The previously assigned species scores are used

as weights, and the ordination score for each site  $j$  is calculated as

$$\frac{\sum_{i=1}^m (x_{ij} \cdot w_i)}{\sum_{i=1}^m x_{ij}}$$

where  $x_{ij}$  is the abundance of species  $i$  at site  $j$ ,

$w_i$  is the weight for species  $i$

= the previous ordination score for species  $i$ ,

and summation is over all  $m$  species.

Then new species scores are similarly calculated from these site scores. Iterations continue in this manner until the ordination scores stabilize. The algorithm always produces a unique solution that is unaffected by the initial choice of arbitrary species scores (Gauch 1982). Vectors of site and species ordination scores are produced simultaneously, and the correlation between site and species scores is maximized. The eigenvalue of a DCA (or RA) axis is equal to the square of the correlation coefficient between the site and species scores (before rescaling) (Pielou 1984).

The ordination axes are then rescaled to eliminate compression at the axis ends. Rescaling is accomplished by expanding or contracting short segments of an axis so that there is a uniform rate of species turnover; i.e. so that equal distances on an axis correspond to equal differences in species composition. This results in standard, meaningful units of axis length, called average standard deviations of species turnover (SD's). One SD is approximately equivalent to a 50% change in species composition, and four SD's correspond roughly to a complete turnover.

A second ordination axis can be derived in the same way

as the first, except that it must be corrected so as to be completely unrelated to the first. This is done by dividing the first axis into a number of segments, and adjusting the second axis scores within each segment so that there is no linear relationship between the axes in any segment. Third and higher level axes can be similarly "detrended" so that they are not related to any lower axis. By requiring that higher level axes be completely unrelated to lower ones, instead of just orthogonal to them, the arch problem is overcome. Second and higher level axes are rescaled, in the same way as the first. Except for rescaling and detrending, DCA is identical to RA.

In tests using both real and simulated ecological data, DCA has been shown to be superior to other ordination techniques in producing meaningful, consistent, readily interpretable ordinations (Gauch 1982, Hill and Gauch 1980). DCA is especially useful and successful in the analysis of species x samples data matrices which are very large or contain a lot of zeros, and in dealing with long community gradients (Gauch 1982, Hill 1979, Hill and Gauch 1980). The assumptions required for the use of DCA (that the data set consist of a set of records of the abundances, or presences, of a series of species within a set of samples, and that the samples can be arranged along a gradient in such a way that species can occupy only a limited extent of the gradient (Hill 1979)) are relatively simple and easily met. For these reasons, and because it overcomes the arch and end compression problems, DCA was chosen for use in this study,

in preference to PCA and other ordination techniques.

DCA was performed using the DECORANA program developed by M.O. Hill (1979) at Cornell University. This program derives the first four ordination axes, and their site and species scores. Standardized environmental parameters x sites data were also ordinated.

### 3.3.2.3 Weighted averages hybrid ordination

One of the most difficult tasks in community ordination is environmental interpretation of results. Environmental and biological data cannot be analyzed simultaneously, except using canonical correlation analysis, and reliable computer programs for canonical analysis were not available at the University of Saskatchewan at the time of this study. However, environmental parameters can be associated with observed patterns in biological data using weighted averages hybrid ordination (Gauch 1982).

In weighted averages hybrid ordination, site scores from a previous ordination of species x sites data are used as weights for weighted averages ordination of environmental parameters x sites data. Ordination scores for each environmental parameter are calculated as:

$$\frac{\sum_{j=1}^n (y_{ij} \cdot w_j)}{\sum_{j=1}^n y_{ij}}$$

where  $y_{ij}$  is the value of environmental parameter  $i$  at site  $j$ ,

and  $w_j$  is the weight for site  $j$  = the score for site  $j$  from a previous ordination

Hybrid ordination environmental parameter scores can thus be

calculated for as many previous ordination axes as desired, using the appropriate site scores. This technique ordinales environmental parameters based on their association with sites at various positions on species x sites DCA ordination axes. The resulting ordination does not necessarily indicate any inherent patterns of variation within the environmental parameters x sites data.

Weighted averages hybrid ordination was performed on standardized environmental data using site scores from DCA ordinations of three biological data sets (sweep net samples, stone samples and species presence/absence data). Environmental parameter scores were calculated for the first four DCA ordination axes from each data set. Calculations were done using programs developed from the data manipulation and arithmetic subprograms of SPSS. Details of these programs are presented in Appendix 1.

## 4 RESULTS AND DISCUSSION

## 4.1 Distributions and Biology of Saskatchewan Heptageniidae

Twenty-three species of Heptageniidae, in 14 genera and 4 subfamilies, are known to occur in Saskatchewan (Table 4). Twenty-three per cent of the species, 82% of the genera and 80% of the subfamilies occurring in North America are represented. Ten species, five genera, and one subfamily are reported from Saskatchewan for the first time; one genus and species are new to science.

Life cycles of heptageniids in Saskatchewan are of two general types (as determined by subjective examination of larvae collected from the intensive study) (Figure 6): 1) seasonal univoltine winter - eggs hatch in summer and early fall, and most of the population overwinters as larvae (some recruitment may occur in the early spring), and 2) seasonal univoltine summer - the entire population overwinters as eggs which do not hatch until spring; larval growth and development are restricted to the spring and early summer (life cycle terminology follows Clifford (1982)). In most species, emergence occurs primarily or exclusively between mid-June and early July. In general, species with summer life cycles have shorter, more discrete emergence periods than those with winter life cycles.

A brief account of the distributions and life cycles of Saskatchewan heptageniid species follows.



Table 4. Heptageniid species occurring in Saskatchewan.

## Family Heptageniidae

## Subfamily Heptageniinae

*Acanthomola pubescens* Whiting and Lehmkuhl  
*Cinygmula mimus* (Eaton)  
*Epeorus longimanus* Eaton  
*Heptagenia adequata* McDunnough  
*H. diabasia* Burks  
*H. elegantula* (Eaton)  
*H. flavescens* Walsh  
*H. pulla* (Clemens)  
*Leucrocuta hebe* (McDunnough)  
*Macdunnoa nipawinia* Lehmkuhl  
*Nixe inconspicua* (McDunnough)  
*N. lucidipennis* (Clemens)  
*N. rusticalis* (McDunnough)  
*N. simplicoides* (McDunnough)  
*Raptoheptagenia cruentata* (Walsh)  
*Rhithrogena undulata* (Banks)  
*Stenacron interpunctatum* (Say)  
*Stenonema femoratum* (Say)  
*S. terminatum* (Walsh)  
*S. vicarium* (Walker)

## Subfamily Anepeorinae

*Anepeorus rusticus* McDunnough

## Subfamily Arthropleinae

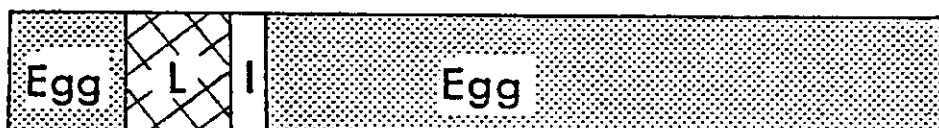
*Arthroplea bipunctata* (McDunnough)

## Subfamily Pseudironinae

*Pseudiron centralis* McDunnough



A M J J A S O N D J F M



I - Imago

E - Egg

L - Larva

Figure 6. General life cycle patterns of Saskatchewan Heptageniidae.  
 top: seasonal univoltine winter  
 bottom: seasonal univoltine summer

## Subfamily Heptageniinae

Acanthomola pubescens Whiting and Lehmkuhl

A. pubescens is a new genus and species of heptageniid known only from Saskatchewan and northern Alberta (Appendix 2). In Saskatchewan, A. pubescens has been collected only at site 4, on the South Saskatchewan River upstream from Lake Diefenbaker (Figure 7).

Because very few specimens of A. pubescens have been collected, little is known about its life cycle. It appears to have a univoltine summer life cycle, with eggs hatching in early to mid-May.

Cinygmula mimus (Eaton) 1885

C. mimus is a western North American species that has been previously reported from the western United States, British Columbia, and Alberta. The Saskatchewan record is a northeastern range extension. Within Saskatchewan, C. mimus has been collected only at one location, a small unnamed stream south of Canoe Lake in the west-central part of the province (Figure 7).

Because of its rarity, little is known about the life cycle of C. mimus in Saskatchewan. The presence of late instar and mature larvae in mid-June suggests that it emerges in mid- to late June or early July.

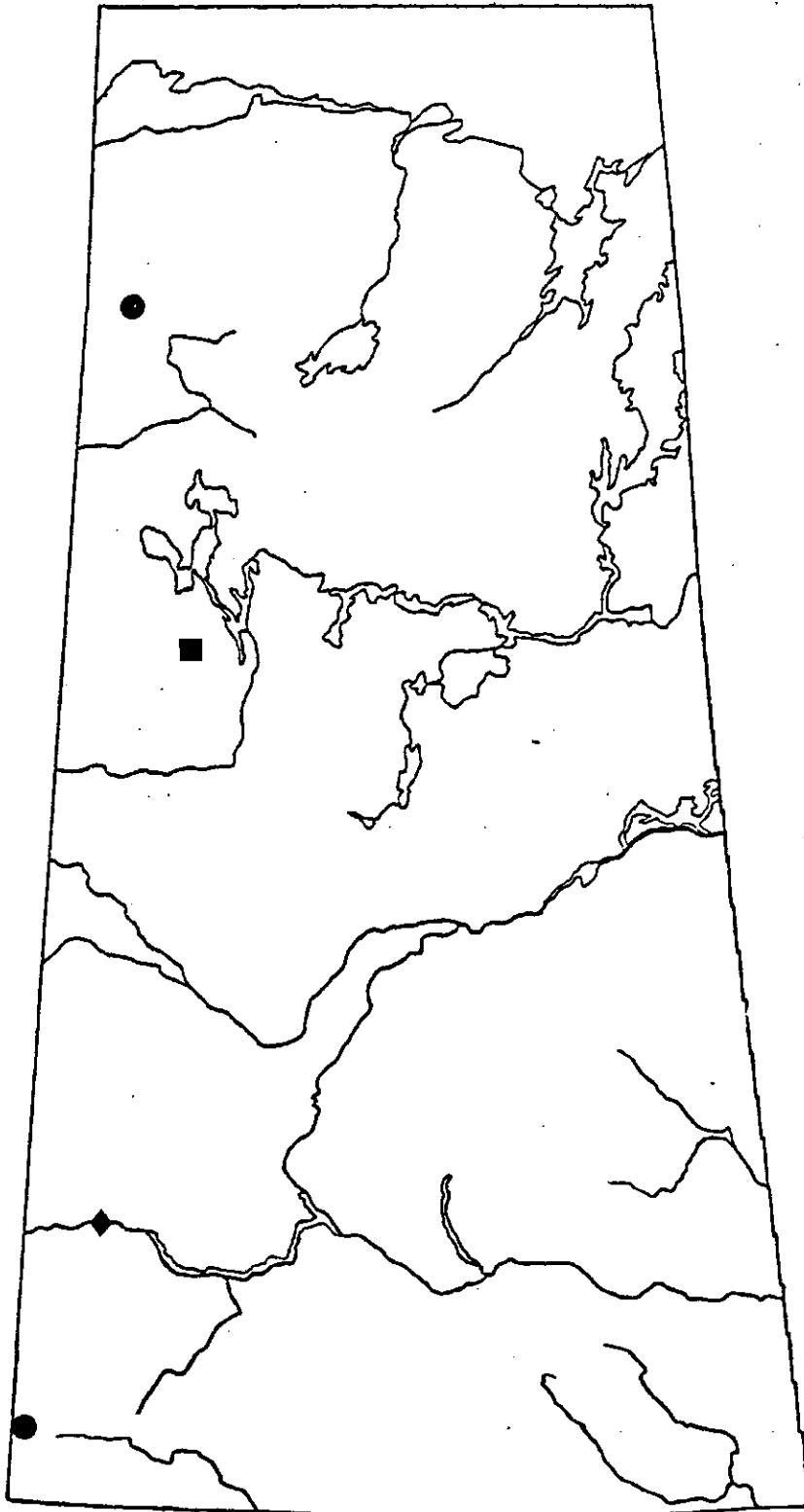


Figure 7. Map of Saskatchewan collection locations for *Acanthomola pubescens* ♦, *Cinygmula mimus* ■ and *Epeorus longimanus* ●.

Epeorus longimanus Eaton 1881

E. longimanus is a common western North American species that occurs throughout the western United States, and in Alaska, British Columbia, Alberta and Saskatchewan. E. longimanus has been collected from several small streams in the Cypress Hills, and from one small stream in northwestern Saskatchewan (Figure 7).

In the Cypress Hills, E. longimanus has a univoltine winter life cycle, with a relatively discrete emergence period in late June and early July. Larvae are absent from early July until October, suggesting a mid-summer diapause in the egg or early larval instars. Lehmkuhl (1968) reported a similar life cycle for E. longimanus in Oregon. However, in an Alberta foothills stream, E. longimanus larvae were present year-round and did not emerge until August or September (Clifford, Robertson and Zelt 1979).

Heptagenia adequata McDunnough 1924

H. adequata is known only from Alberta and Saskatchewan. In Saskatchewan, it has been collected only in the South Saskatchewan River upstream from Lake Diefenbaker (Figure 8).

H. adequata has a univoltine winter life cycle, with larvae present year-round. Emergence occurs throughout June, July and August, but is concentrated in late June and early July.

Heptagenia diabasia Burks 1946

H. diabasia is an eastern North American species that

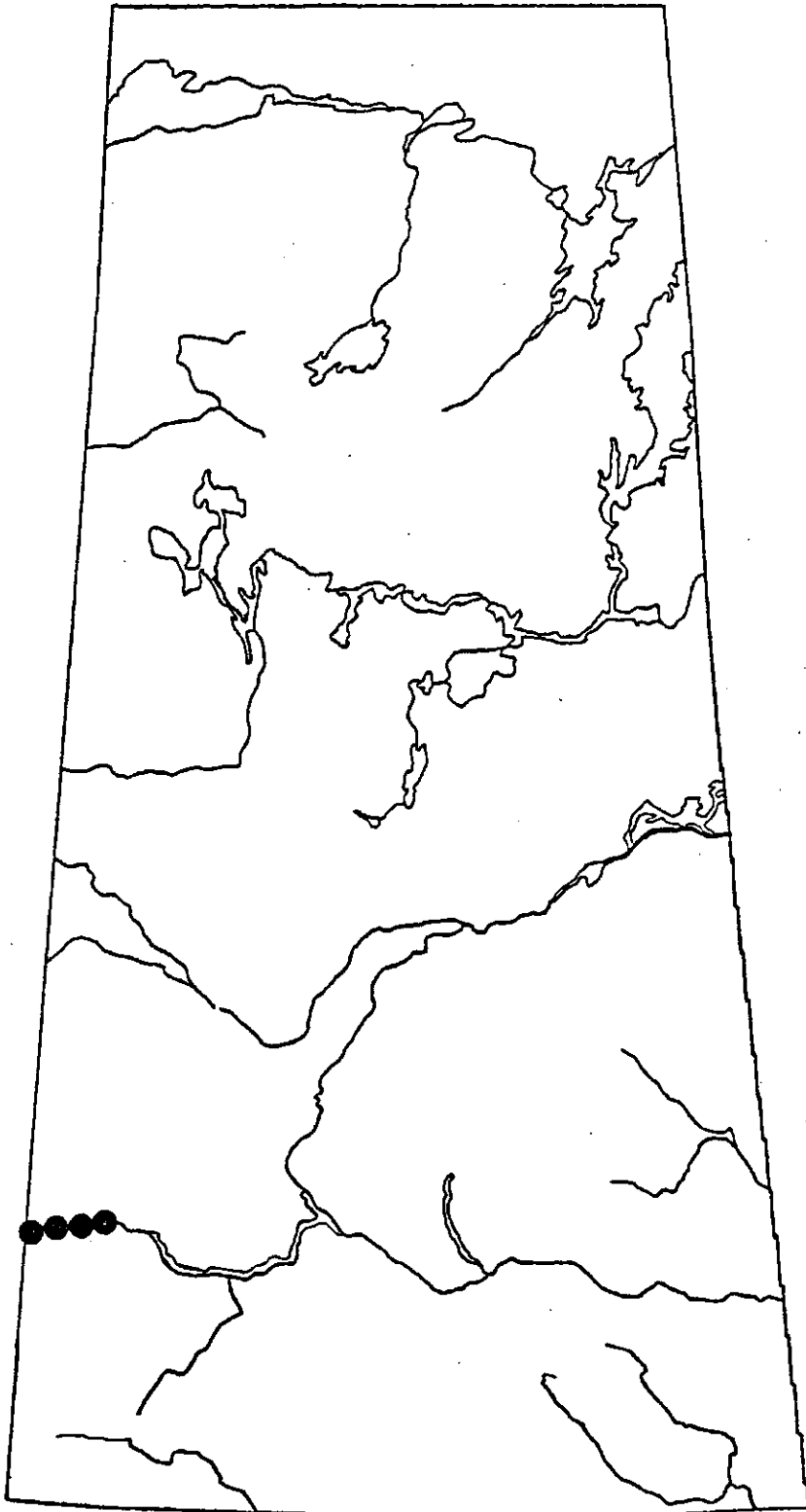


Figure 8. Map of Saskatchewan collection locations for Heptagenia adequata.

occurs in most of the Great Lakes states, Iowa, West Virginia, Maine, Quebec, Manitoba and Saskatchewan. In Saskatchewan, H. diabasia is most abundant in streams in the east-central part of the province, although it has also been collected in the Saskatchewan River system and some southern boreal streams (Figure 9).

H. diabasia has a univoltine winter life cycle. Larvae are present year-round, and emergence is concentrated in late June and early July. The life cycle of H. diabasia was similar in Wisconsin, with emergence from late June to early September (Flowers and Hilsenhoff 1978).

#### Heptagenia elegantula (Eaton) 1885

H. elegantula is a western North American species that occurs in the western United States, southern British Columbia, Alberta, Saskatchewan and Manitoba. It is found primarily in large, warm, silty rivers (Bednarik and Edmunds 1980). In Saskatchewan, H. elegantula is common throughout the Saskatchewan River system (Figure 10).

H. elegantula has a univoltine winter life cycle. Larvae are present year-round, and emergence occurs throughout the summer but is concentrated in late June and early July.

H. elegantula and H. diabasia intergrade morphologically in Saskatchewan. Several specimens which are intermediate between the two species have been collected.

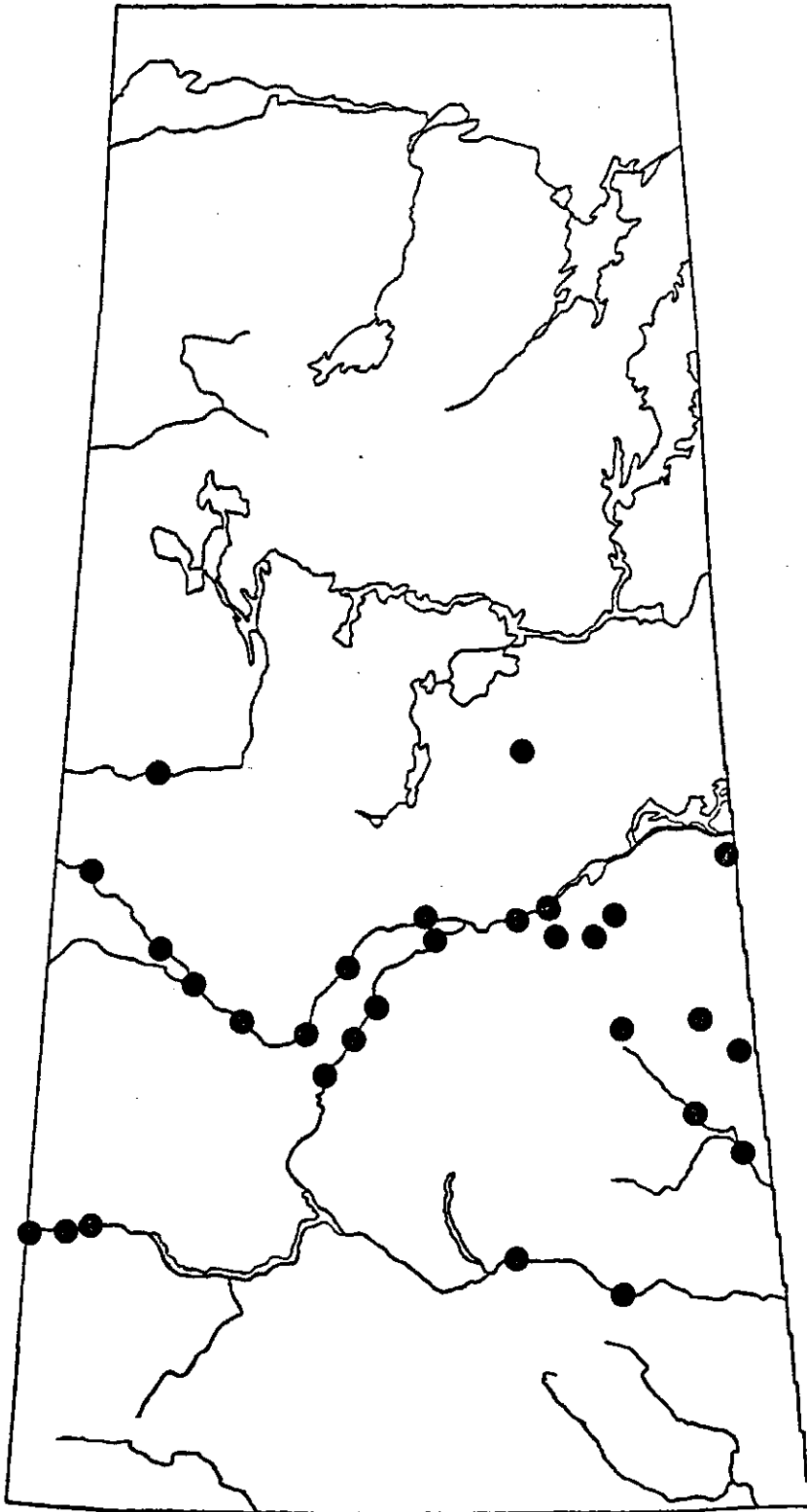


Figure 9. Map of Saskatchewan collection locations for Heptagenia diabasias.



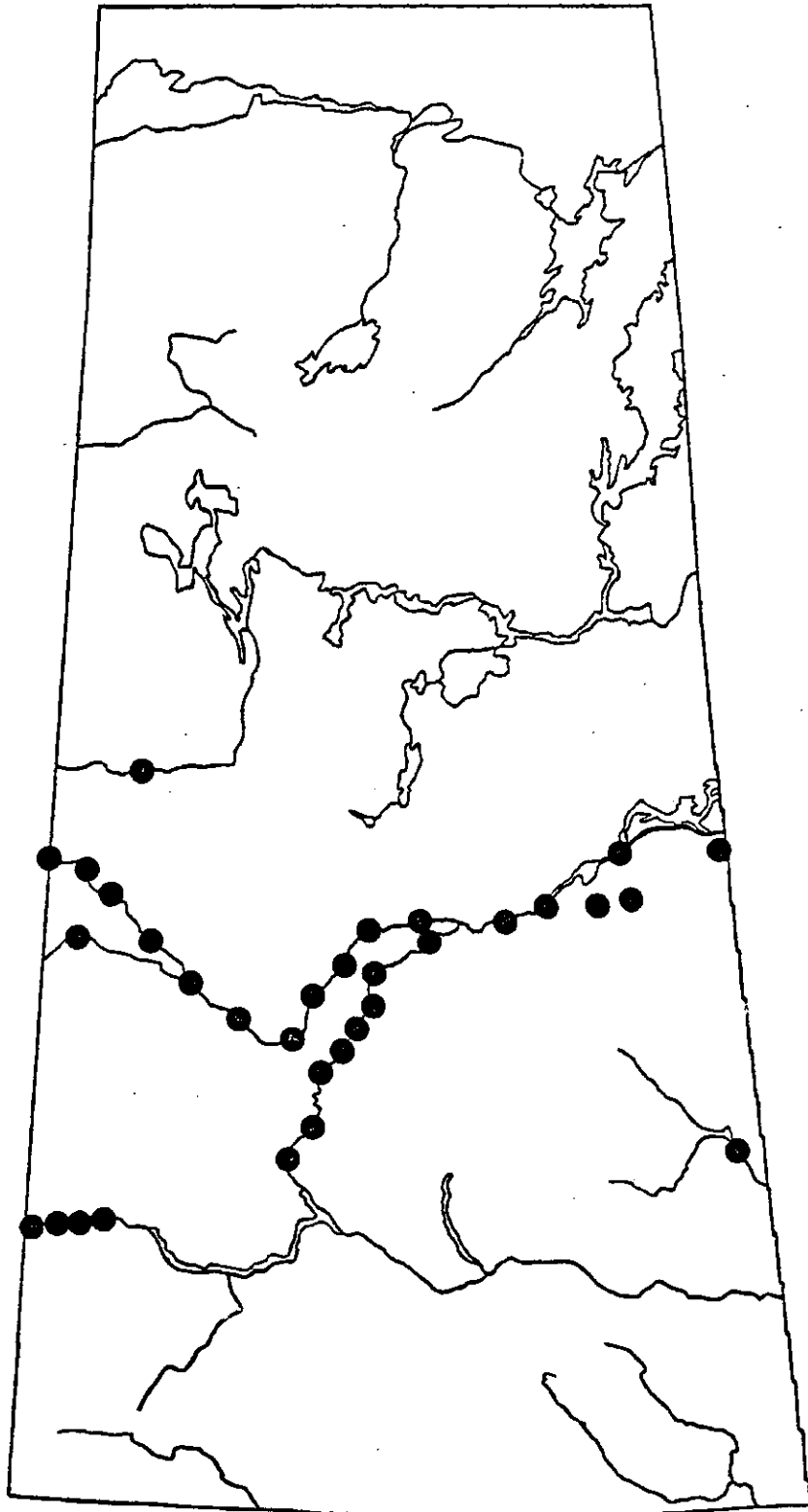


Figure 10. Map of Saskatchewan collection locations for Heptagenia elegantula.

Heptagenia flavescens Walsh 1862

H. flavescens is an eastern North American species that occurs throughout the eastern half of the United States, and in Colorado, southern Ontario, Manitoba and Saskatchewan. In Wisconsin, H. flavescens was collected mainly in large streams (Flowers and Hilsenhoff 1978). In Saskatchewan, H. flavescens has been collected from several locations on the Saskatchewan Rivers (Figure 11).

H. flavescens is not sufficiently abundant in Saskatchewan to allow a detailed description of its life cycle. However, it appears to have a univoltine winter life cycle with emergence concentrated in late June and early July, as in other Heptagenia species. Larvae are present year-round.

Heptagenia pulla (Clemens) 1913

H. pulla is a common northeastern North American species. It has been reported from most of the Great Lakes states, North Carolina, Alabama, Ontario, Quebec, Manitoba, Saskatchewan, northern Alberta and the Northwest Territories. H. pulla is the most common and widespread heptageniid in Saskatchewan (Figure 12). It has been collected from streams and rivers throughout the boreal forest and Shield, and from nearly all parts of the Saskatchewan River system.

H. pulla has a univoltine winter life cycle. Larvae are present year-round, and emergence occurs throughout the summer but is concentrated in late June and early July. In Michigan, H. pulla emerged from early June to early August,

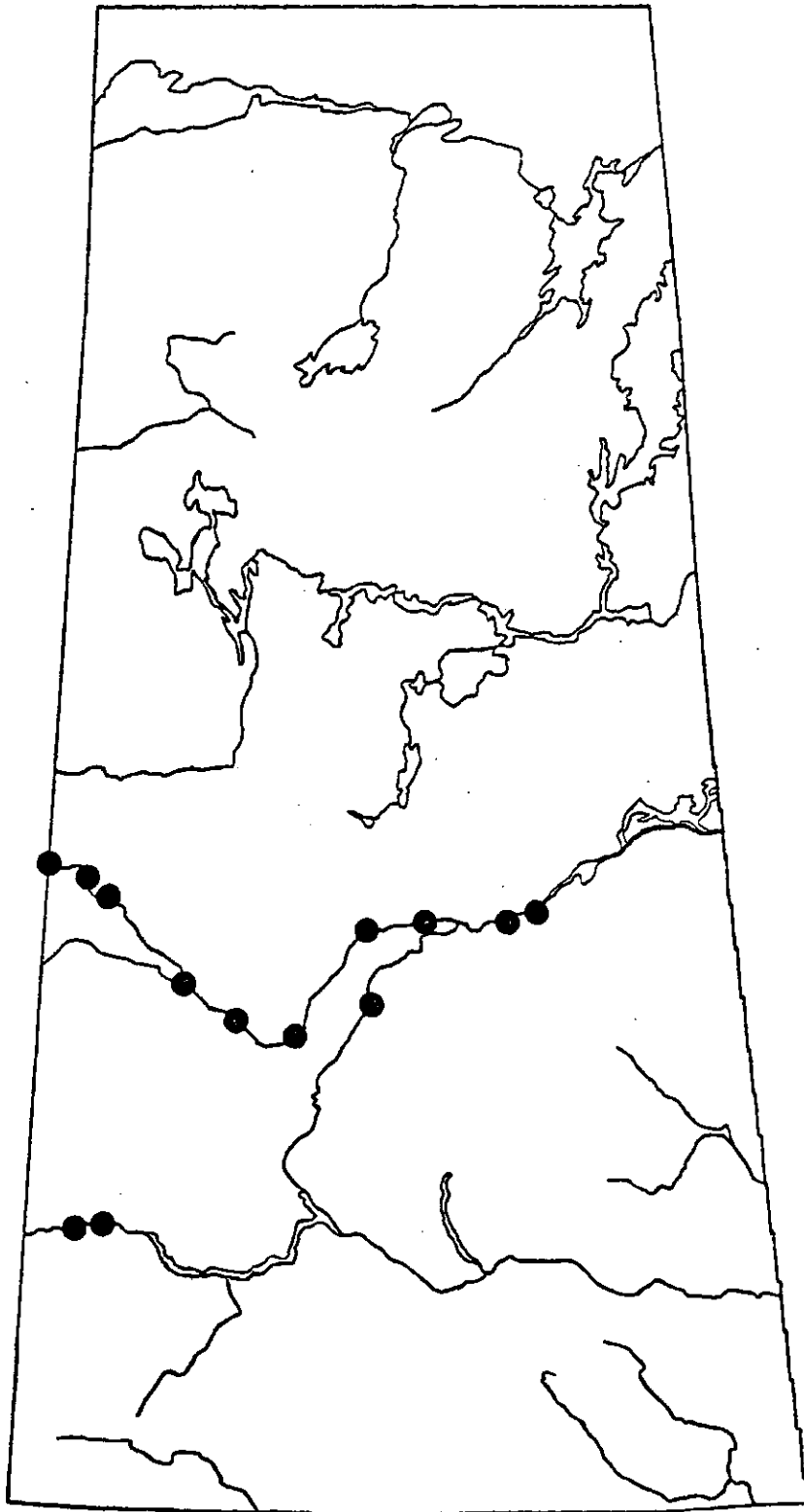


Figure 11. Map of Saskatchewan collection locations for Heptagenia flavescens.

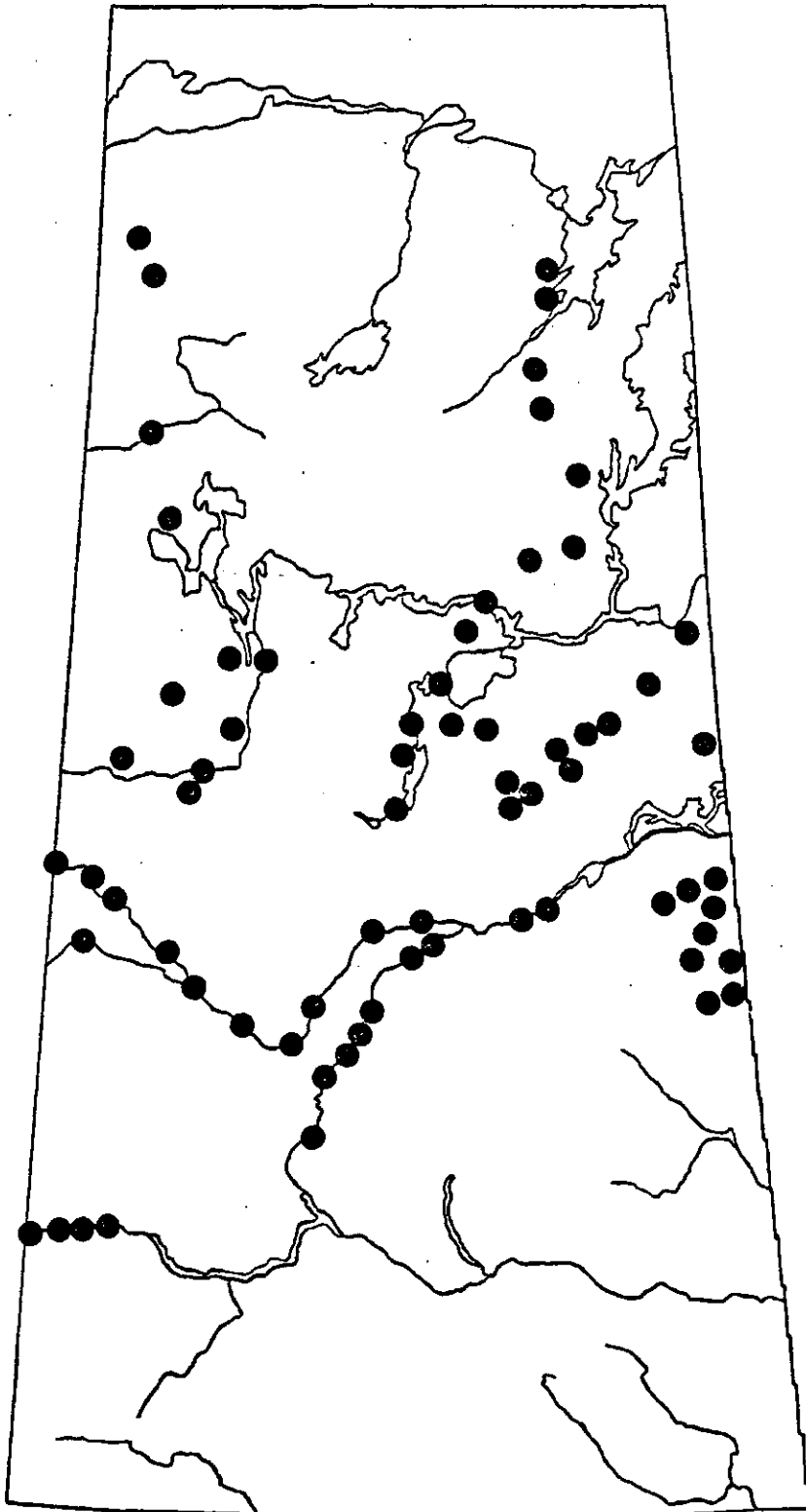


Figure 12. Map of Saskatchewan collection locations for Heptagenia pulla.

with peak emergence in June (Leonard and Leonard 1962).

Leucrocuta hebe (McDunnough) 1924

L. hebe is a common eastern North American species that occurs throughout the eastern United States, and in Quebec, southern Ontario, Manitoba, Saskatchewan and Alberta. In Saskatchewan, L. hebe is more or less restricted to streams in the southern boreal forest (Figure 13). It also occurs in the Battle River in west-central Saskatchewan and in the Cypress Hills.

L. hebe has a univoltine summer life cycle, with larvae hatching in mid-May and adults emerging in late June and early July. In some streams, small numbers of adults continue to emerge throughout July and early August. In Michigan and Wisconsin, the emergence period of L. hebe was similar but began two or three weeks earlier (Leonard and Leonard 1962, Flowers and Hilsenhoff 1978).

Macdunnoa nipawinia Lehmkuhl 1979

M. nipawinia is known only from the Saskatchewan River system in Saskatchewan. In this study M. nipawinia was collected at three locations (Figure 14); Lehmkuhl (1979b) reported it from four additional locations.

According to Lehmkuhl (1979b), M. nipawinia has a univoltine summer life cycle with emergence in late June and early July.

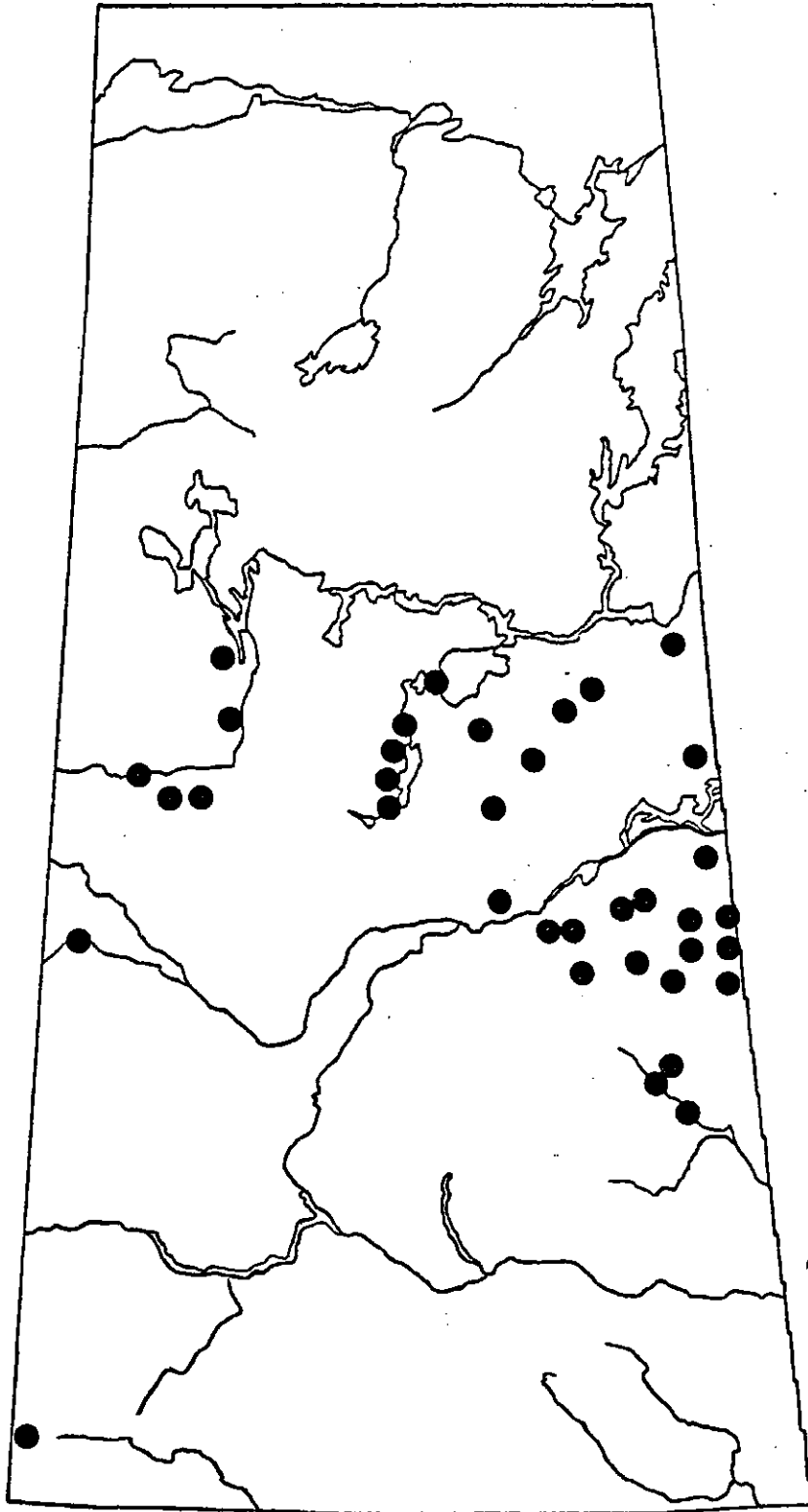


Figure 13. Map of Saskatchewan collection locations for Leucrocuta hebe.

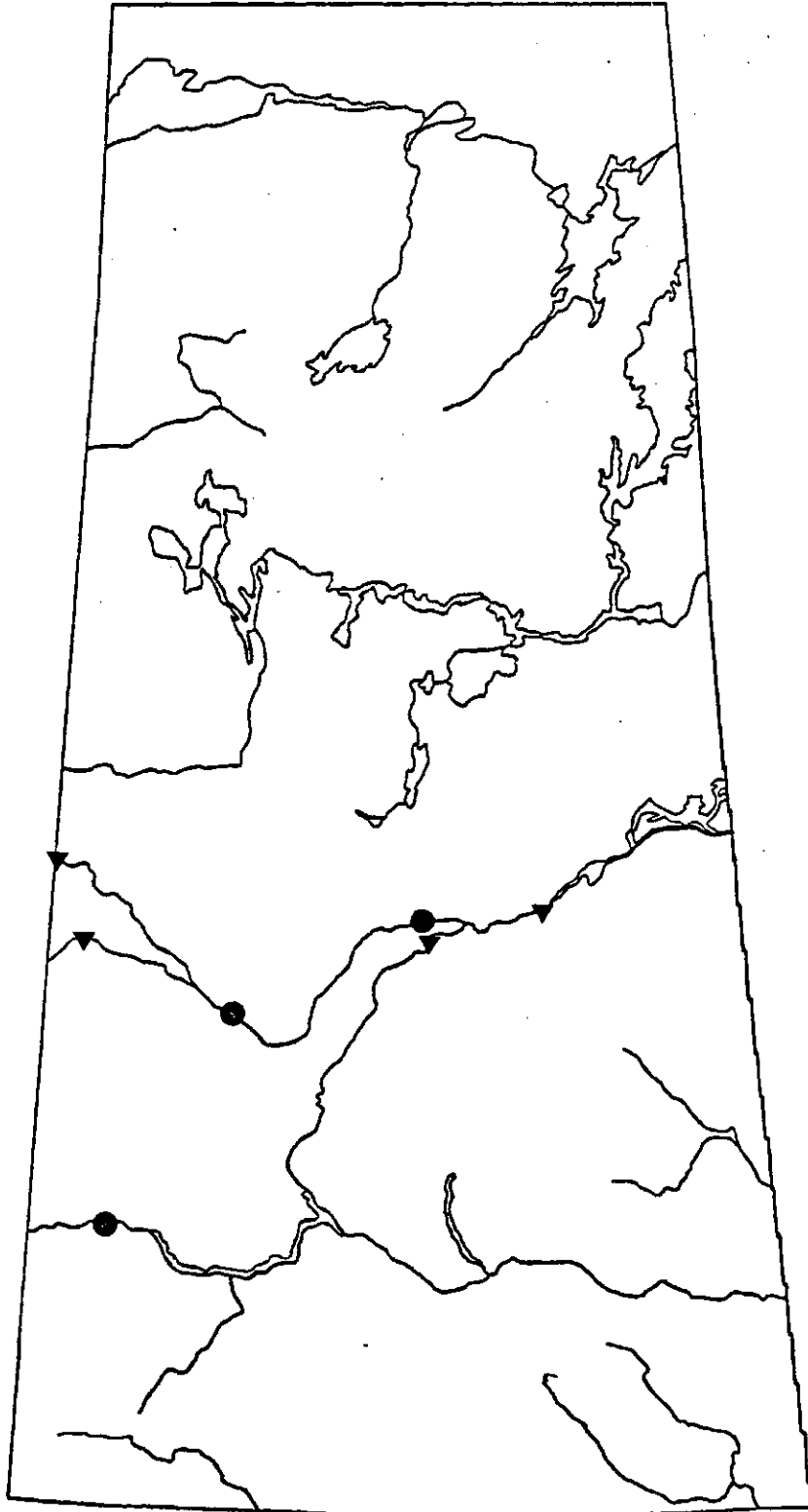


Figure 14. Map of Saskatchewan collection locations for Macdunnosa nipawinia.

- - collected during this study
- ▼ - reported by Lehmkuhl (1979b)

Nixe inconspicua (McDunnough) 1924

N. inconspicua occurs in the mid-western United States, from Arkansas north to Wisconsin and Ohio, and in southern Manitoba and east-central Saskatchewan. The Saskatchewan records are a western range extension. In Saskatchewan, N. inconspicua has been collected only in the east-central part of the province near the Pasquia and Porcupine Hills (Figure 15).

N. inconspicua has a univoltine summer life cycle, with larvae present from mid-May until early July. Emergence occurs during the last week in June or the first week in July.

Nixe lucidipennis (Clemens) 1913

N. lucidipennis is found in the Great Lakes states, southern Ontario, Quebec, and Saskatchewan. Saskatchewan records from this study are a disjunct western range extension. In Saskatchewan, N. lucidipennis has been collected from the southern boreal forest in the eastern half of the province (Figure 16).

N. lucidipennis has a univoltine summer life cycle, with larvae present from mid-May until early July and emergence occurring in the last week in June or the first week in July. The life cycle of N. lucidipennis was similar in Michigan (Lyman 1955) and Wisconsin (Flowers and Hilsenhoff 1978), although emergence was almost a month later at one Wisconsin site.



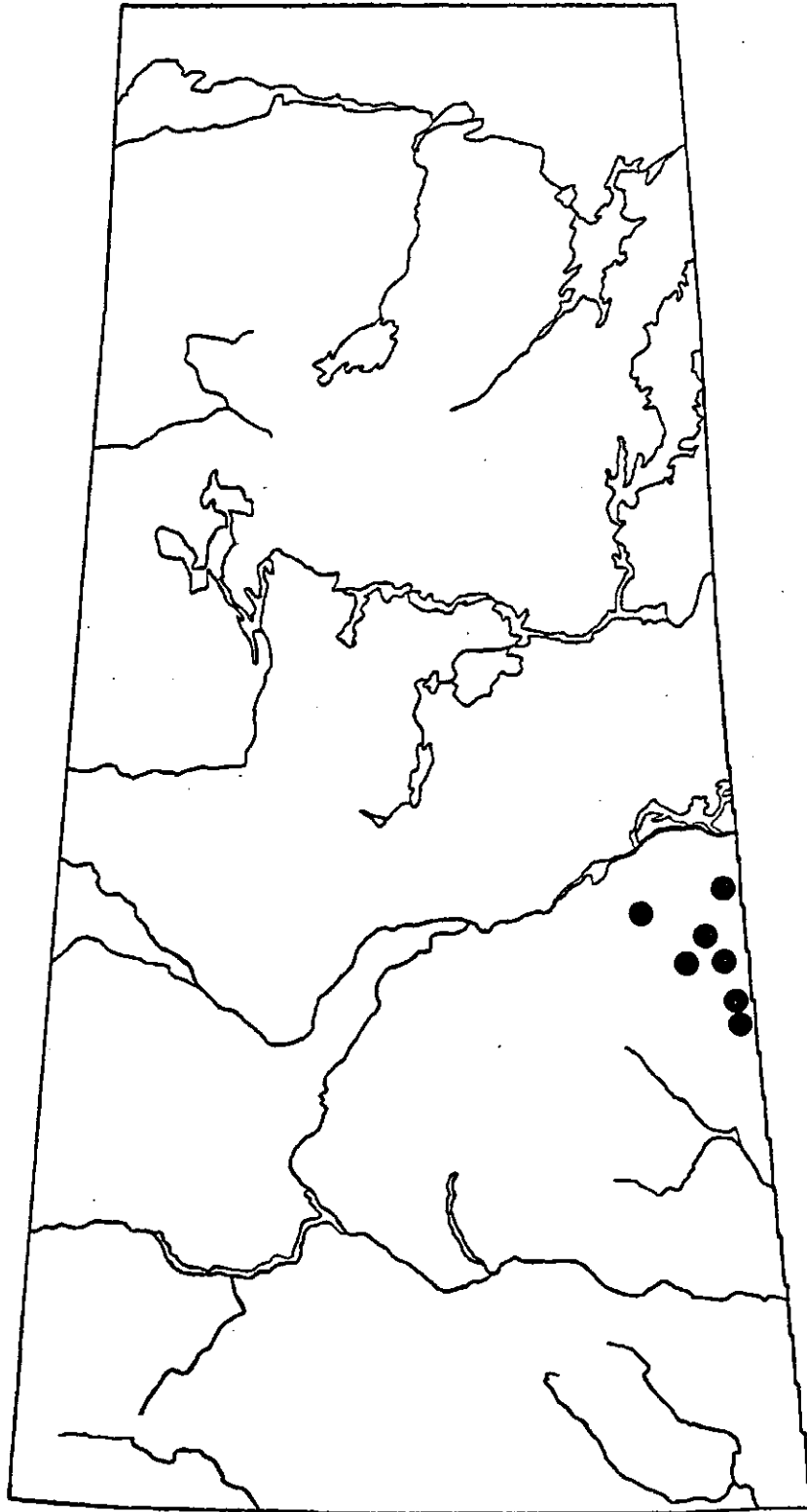


Figure 15. Map of Saskatchewan collection locations for *Nixe inconspicua*.

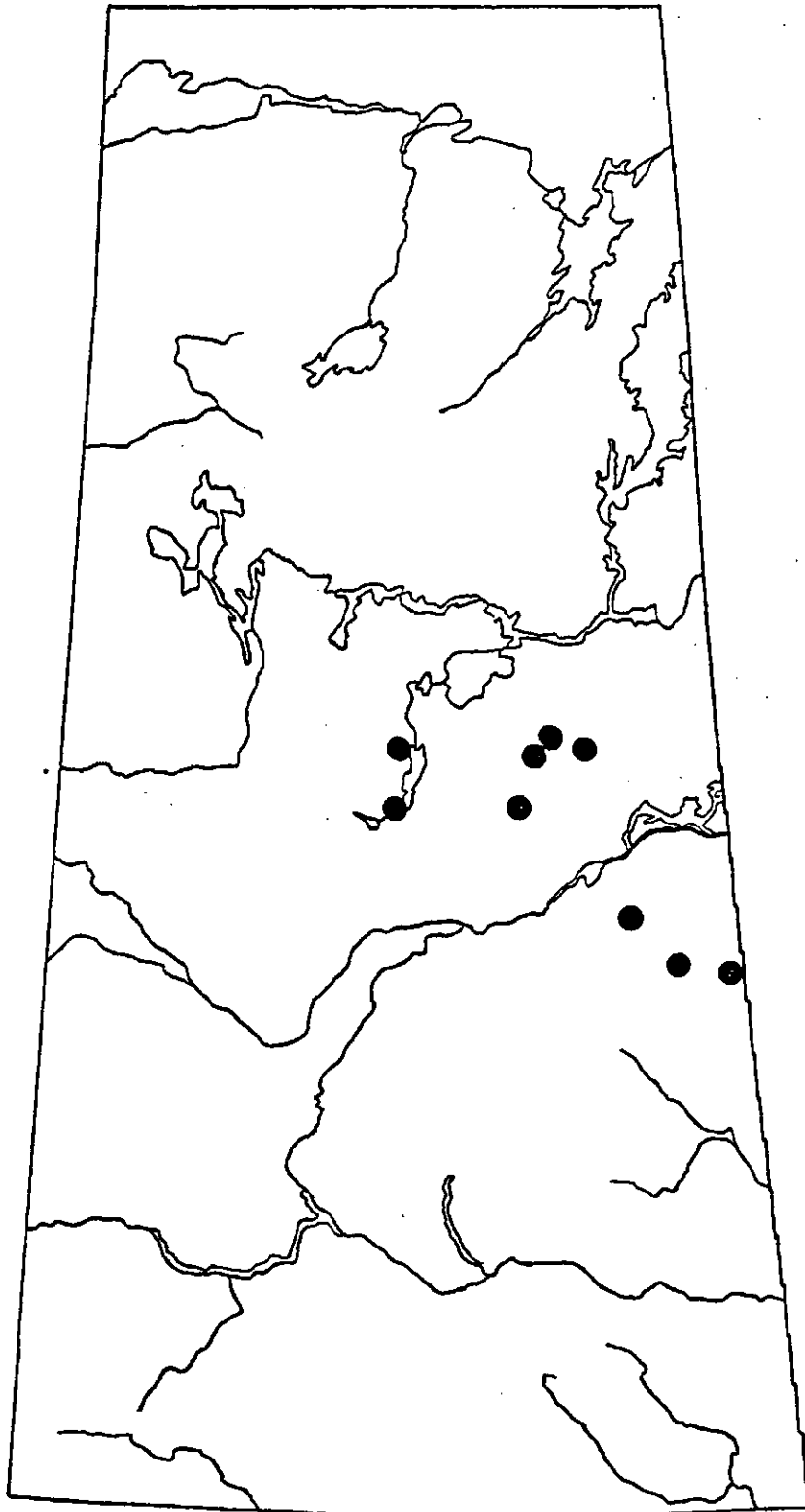


Figure 16. Map of Saskatchewan collection locations for Nixe lucidipennis.

Nixe rusticalis (McDunnough) 1931

N. rusticalis is known only from Ohio, New York, southern Quebec and Saskatchewan. Saskatchewan records from this study are a disjunct western range extension. In Saskatchewan, N. rusticalis has been collected in the east-central part of the province in the Pasquia, Porcupine and Wapawekka Hills (Figure 17).

N. rusticalis has a univoltine summer life cycle, with larvae present from mid-May until early July, and emergence occurring in the last week in June or the first week in July.

Nixe simplicoides (McDunnough) 1924

N. simplicoides is a western species that is known from the western United States, British Columbia, Alberta, Saskatchewan and west-central Manitoba. In the Rocky Mountains, N. simplicoides was found mainly in warm, silty streams and rivers (Bednarik and Edmunds 1980). In Saskatchewan, N. simplicoides has been collected from the Pasquia and Porcupine Hills in the east-central part of the province, the South Saskatchewan River upstream from Lake Diefenbaker, and the Cypress Hills (Figure 18).

N. simplicoides has a univoltine summer life cycle with larvae present from mid-May until early July, and emergence occurring in the last week in June and the first week in July.

Raptoheptagenia cruentata (Walsh) 1863

R. cruentata (previously known as the larva of Anepeorus

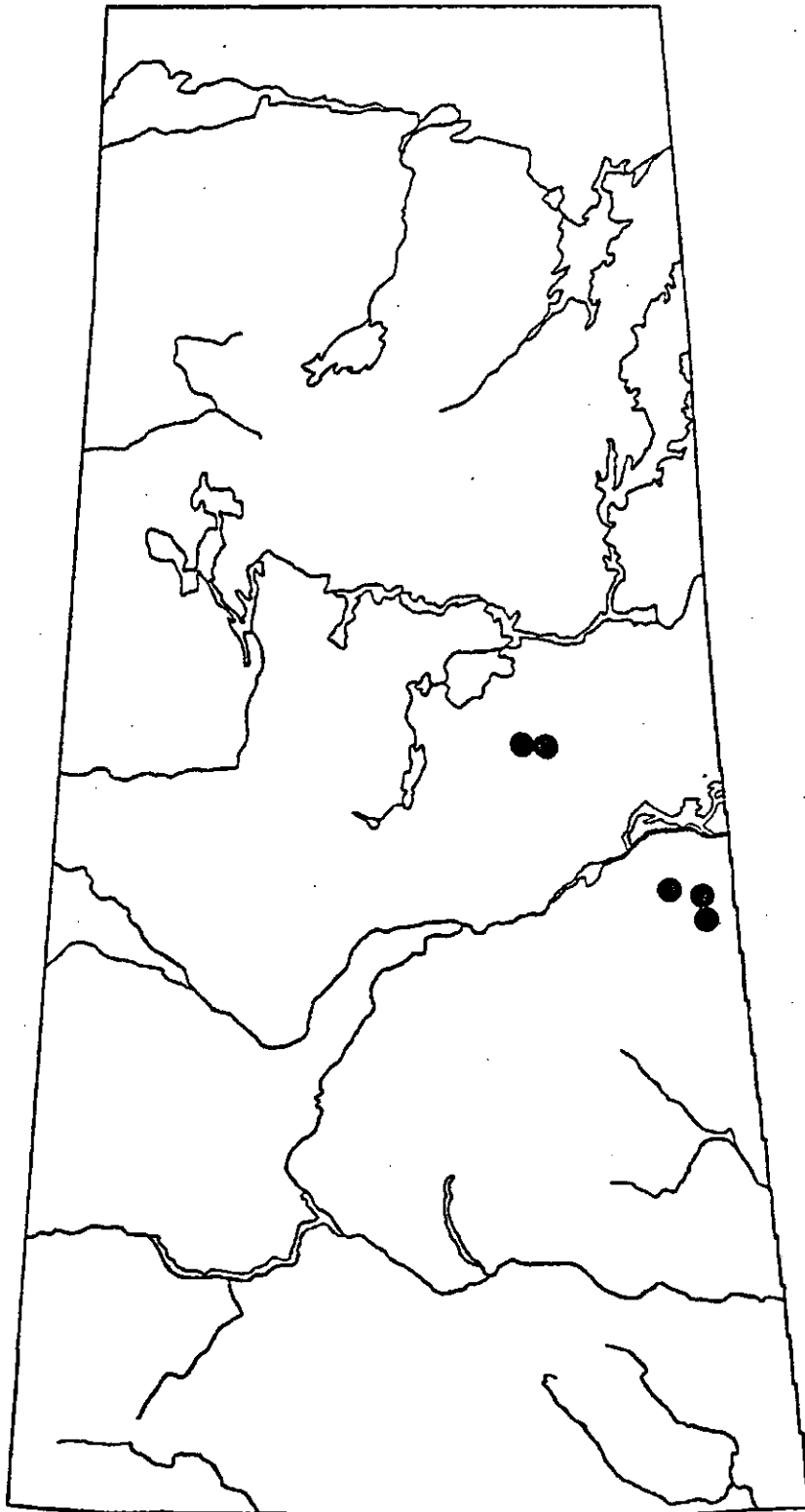


Figure 17. Map of Saskatchewan collection locations for Nixe rusticalis.

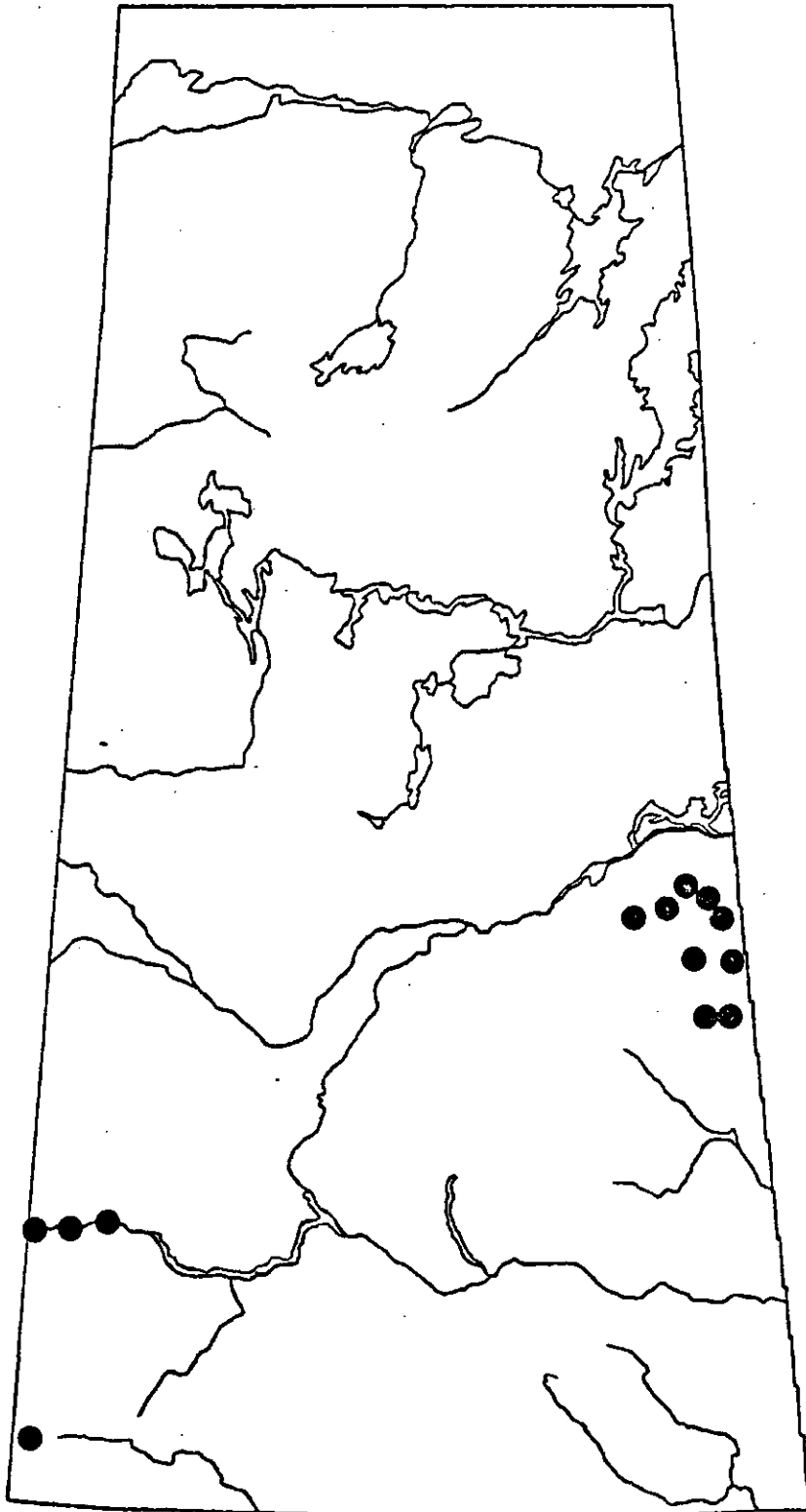


Figure 18. Map of Saskatchewan collection locations for Nixe simplicoides.

rusticus and the adult of Heptagenia cruentata; see Appendix 3) is known from the central United States, Manitoba and Saskatchewan. It is apparently restricted to big rivers (Edmunds, Jensen and Berner 1976, Beckett 1977). In Saskatchewan, R. cruentata has been collected from several isolated localities in the Saskatchewan River system, and is most common in the South Saskatchewan River upstream from Lake Diefenbaker (Figure 19).

R. cruentata has a univoltine summer life cycle, with larvae present from mid-May until early July, and emergence occurring in late June and early July.

R. cruentata larvae are predaceous (Edmunds, Jensen and Berner 1976).

#### Rhithrogena undulata (Banks) 1924

R. undulata is a western North American species that has been reported from many western states, Saskatchewan, the Yukon, and the western Northwest Territories. In Saskatchewan, R. undulata occurs in the South Saskatchewan River upstream from Lake Diefenbaker (Figure 20). Lehmkuhl (pers. comm.) has also collected R. undulata from the Saskatchewan River near Nipawin.

R. undulata emerges from mid-May until early June, earlier than any other Saskatchewan heptageniid. Larvae are apparently absent from early June until freeze-up. However, larvae collected in April are approximately half grown. It is not known whether R. undulata overwinters as larvae which hatch in very late fall (a univoltine winter life cycle with

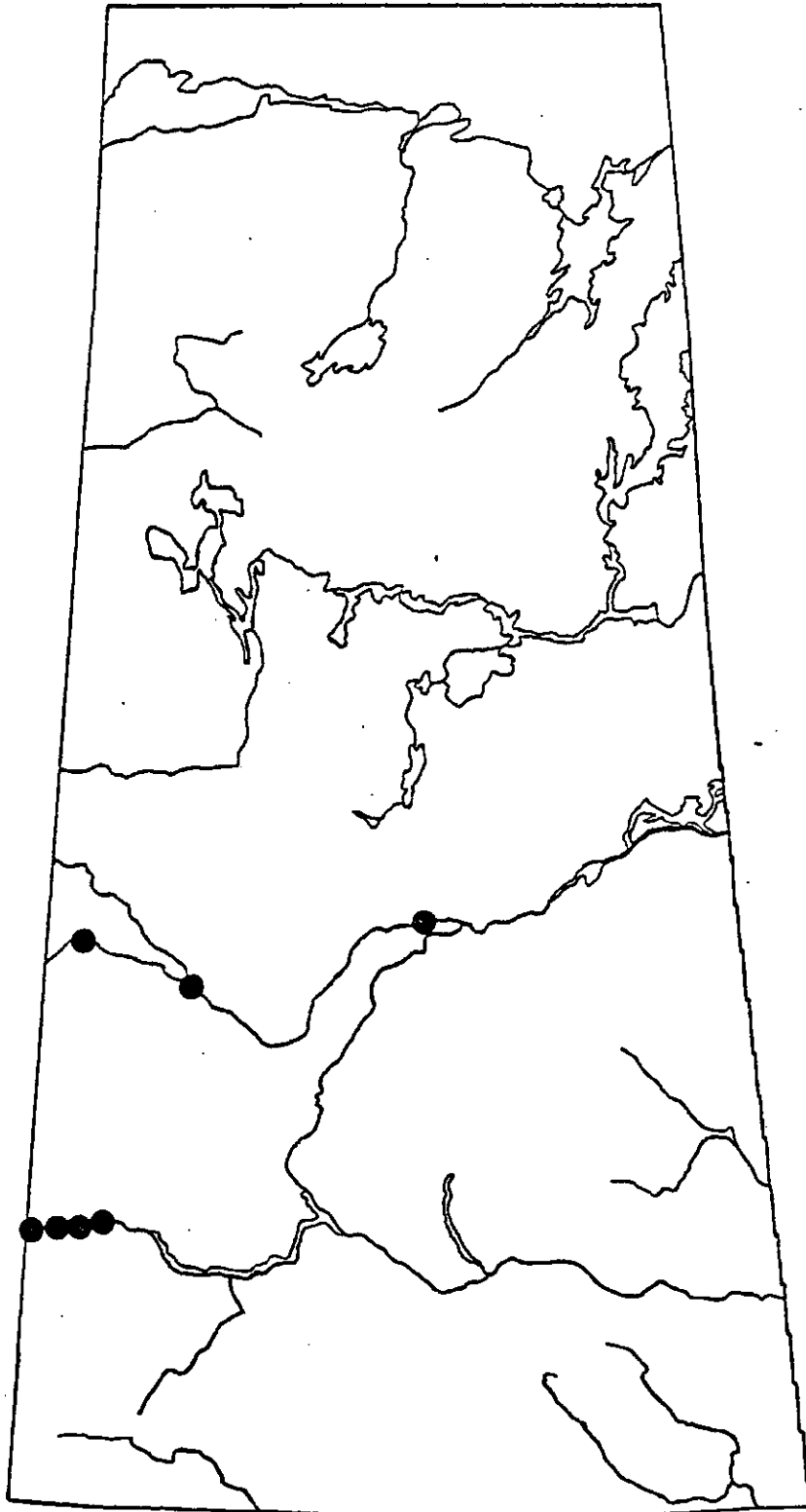


Figure 19. Map of Saskatchewan collection locations for Raptioheptagenia cruentata.

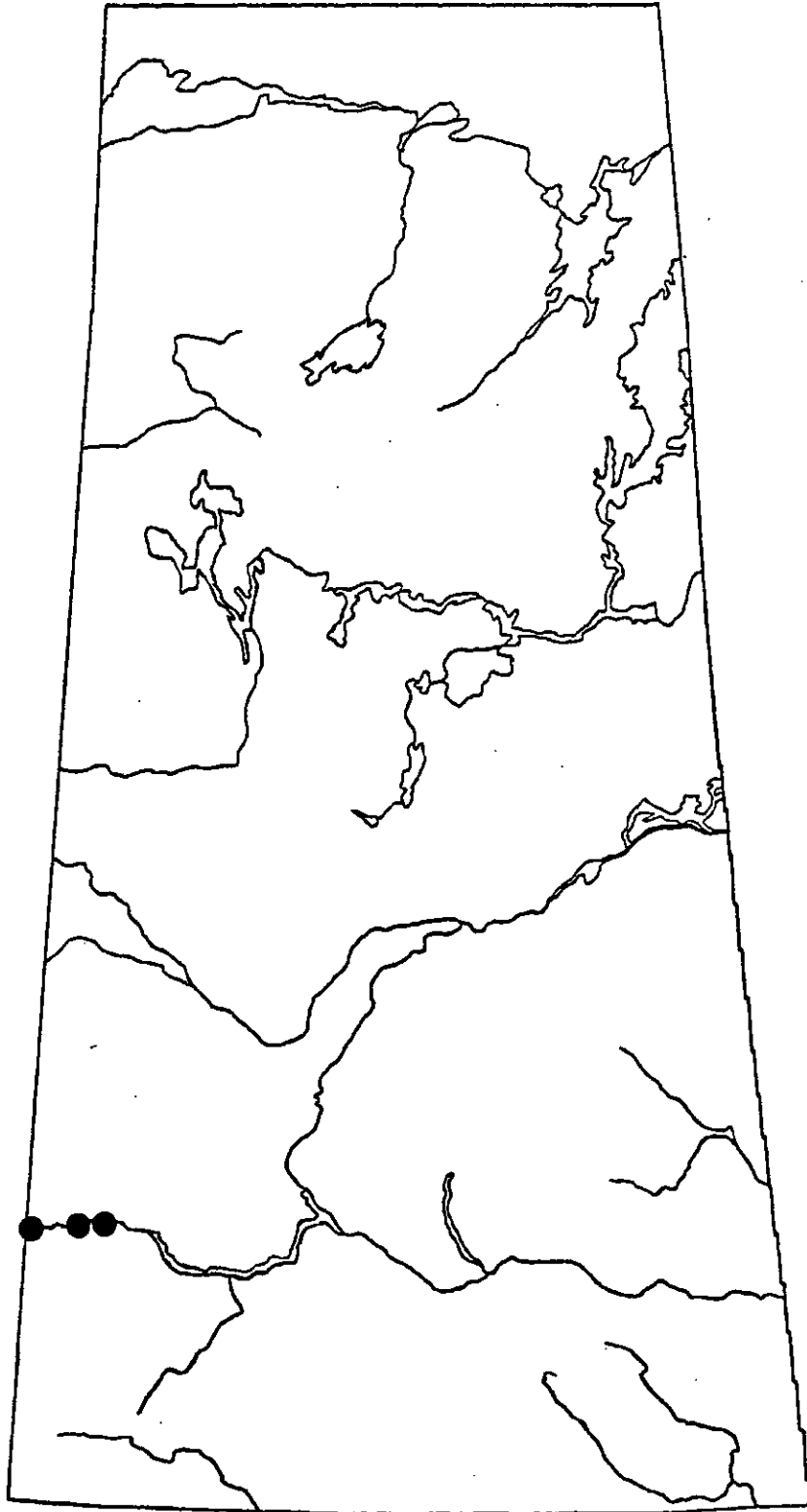


Figure 20. Map of Saskatchewan collection locations for Rhithrogena undulata.



a summer diapause), or as eggs which hatch in very early spring (a univoltine summer life cycle).

Stenacron interpunctatum (Say) 1839

S. interpunctatum is an eastern North American species that occurs throughout the eastern and mid-western United States, and in New Brunswick, Quebec, Ontario, Manitoba, Saskatchewan, and northeastern Alberta. In Wisconsin, S. interpunctatum larvae were found primarily in slow-flowing streams, and were very tolerant of eutrophication and siltation (Flowers and Hilsenhoff 1978). S. interpunctatum is one of the commonest and most widespread species in Saskatchewan. It has been collected from streams and rivers throughout the Shield, boreal forest and parkland, and from the Saskatchewan Rivers in the eastern half of the province (Figure 21).

S. interpunctatum has a univoltine winter life cycle, with larvae present year-round. The emergence period is extended, starting in mid-May at the warmest sites, and lasting until mid-August. Similar life cycles and emergence periods were reported for S. interpunctatum in Indiana (mid-May until late September (McCafferty and Huff 1978)), Michigan (June 15 to September 15 (Lyman 1955); June 5 to August 14 (Leonard and Leonard 1962)) and Wisconsin (early June to August (Flowers and Hilsenhoff 1978)). The emergence period was much shorter in northern Manitoba (July 4 to 18 (Flannagan and Lawler 1972)). In Indiana (McCafferty and Huff 1978) and Michigan (Lyman 1955), three distinct, overlapping

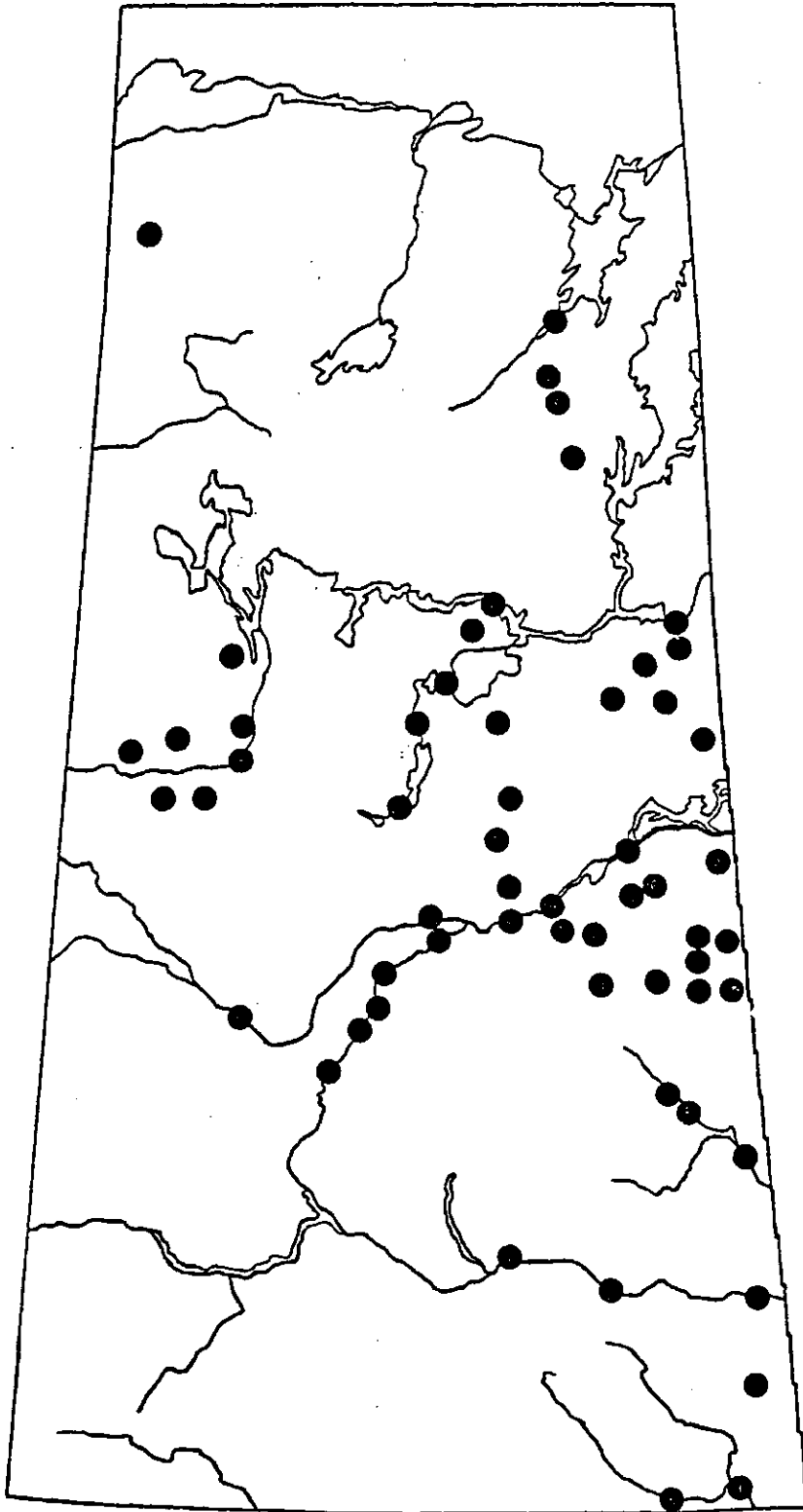


Figure 21. Map of Saskatchewan collection locations for Stenacron interpunctatum.

cohorts were present. All three cohorts were univoltine, but emerged at different times of the year. Life history data from Saskatchewan have not yet been analyzed to determine if such overlapping cohorts exist here.

Lewis (1974) recognized four subspecies of S. interpunctatum. Morphological variation among Saskatchewan S. interpunctatum larvae and adults encompasses the descriptions of two of the recognized subspecies, S. interpunctatum canadense and S. interpunctatum interpunctatum. Most specimens show a combination of characteristics from these two subspecies. Both visual inspection and multivariate analyses (cluster analysis and principal components analysis) of 27 characters from 48 specimens (adult males and associated larval exuviae) failed to locate any distinct groups among Saskatchewan S. interpunctatum. Observed morphological variation was also unrelated to collection site or emergence time. It thus appears that Saskatchewan S. interpunctatum belong to a single taxonomic entity, which probably arose from interbreeding between S. i. canadense and S. i. interpunctatum. Intermediates between these two subspecies are common in several mid-western states (Lewis 1974).

#### Stenonema femoratum (Say) 1823

S. femoratum is an eastern North American species that is common throughout the eastern and mid-western United States, southern Ontario and Quebec. It also occurs in New Brunswick, Manitoba, Saskatchewan, and the Northwest

Territories. In Saskatchewan, S. femoratum appears to be widespread in the Shield and eastern boreal forest (Figure 22). However, because it is found almost exclusively in lentic habitats, there are few collection records from this study. S. femoratum (as S. tripunctatum) was also collected mainly from lakes in Wisconsin (Flowers and Hilsenhoff 1978).

Because of the paucity of collection records, little is known about the life cycle of S. femoratum in Saskatchewan. The emergence period probably lasts from early June until late June or early July. S. femoratum emerged from mid-May to mid-August in Michigan (Lyman 1955, Leonard and Leonard 1962) and Wisconsin (Flowers and Hilsenhoff 1978). Farther south, in West Virginia, emergence lasted from late April until the end of May (Richardson and Tarter 1976). S. femoratum was univoltine in most of these areas, but was bivoltine in some Wisconsin streams.

#### Stenonema terminatum (Walsh) 1862

S. terminatum is the only North American heptageniid with a transcontinental distribution. It is common throughout the eastern and mid-western United States, southern Ontario and Quebec, Manitoba, Saskatchewan, Alberta, southern British Columbia, and the northwestern United States. S. terminatum was found primarily in large rivers in Wisconsin (Flowers and Hilsenhoff 1978). In Saskatchewan, S. terminatum is common in streams and rivers throughout the southern half of the province, and is most abundant in the Saskatchewan River system and the southwest corner of the province (Figure 23).

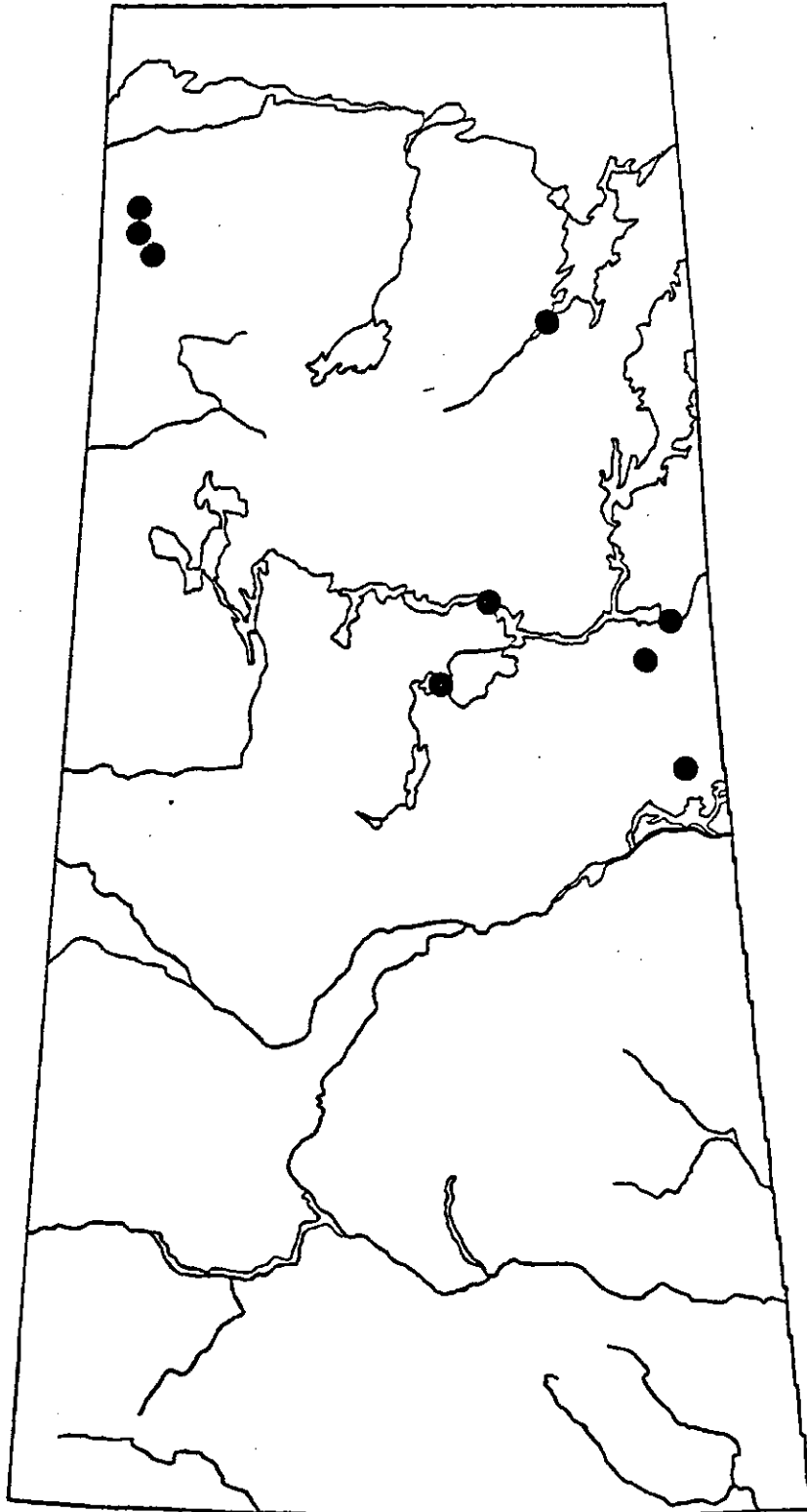


Figure 22. Map of Saskatchewan collection locations for Stenonema femoratum.

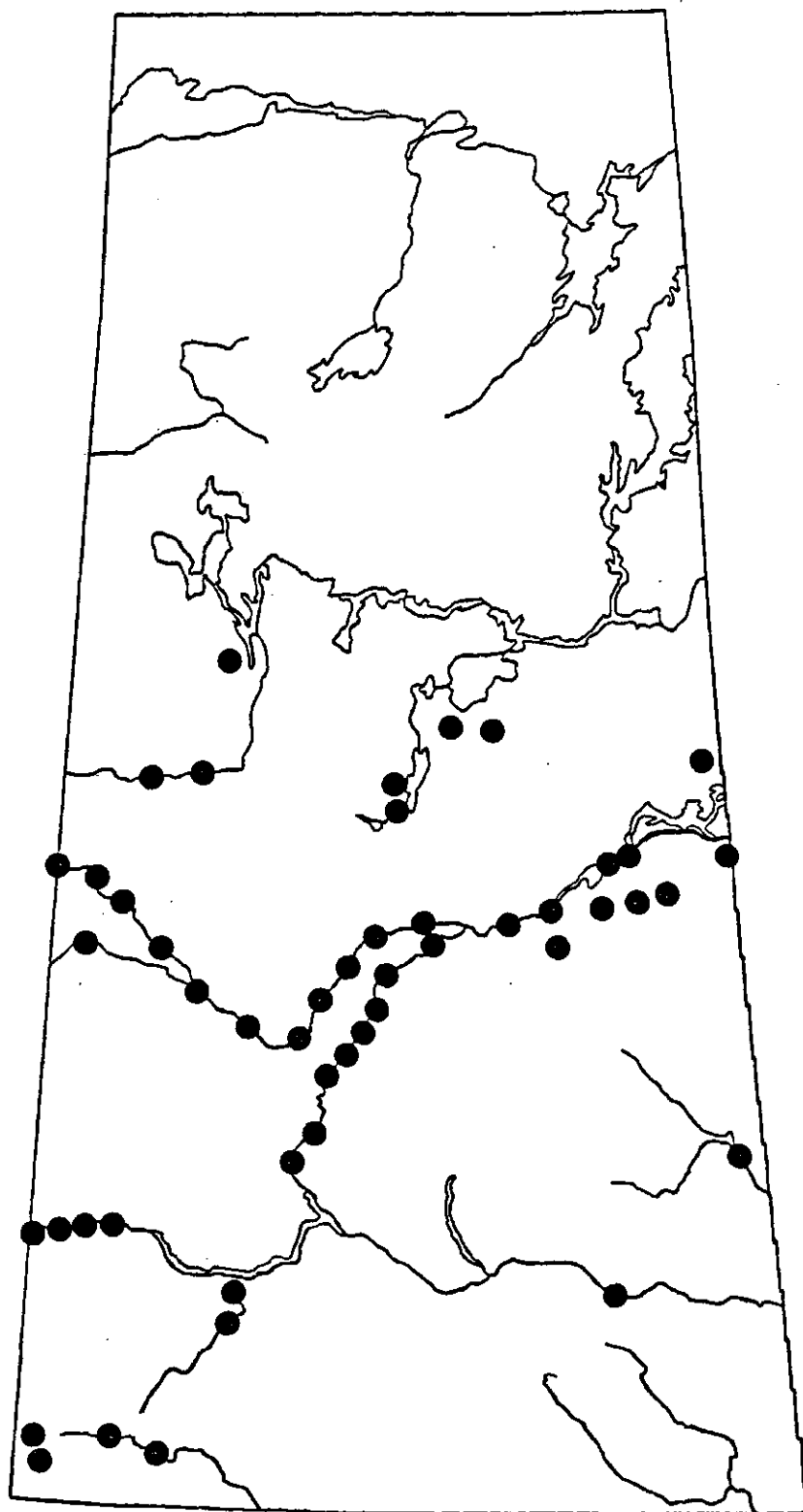


Figure 23. Map of Saskatchewan collection locations for *Stenonema terminatum*.

S. terminatum has a univoltine winter life cycle, with emergence between mid-June and early July. Larvae appear to be absent for 2 to 4 weeks in late July and early August, suggesting that eggs undergo a short, mid-summer egg diapause, or that early instar larvae are hyporheic. A similar life cycle was reported for S. terminatum in Wisconsin (Flowers and Hilsenhoff 1978).

Stenonema vicarium (Walker) 1853

S. vicarium is an eastern North American species that is common in the northeastern and Great Lakes states, southern Ontario, Quebec, Manitoba, Saskatchewan, and northern Alberta. It has also been reported from West Virginia, Tennessee, North Carolina, New Brunswick, and the Northwest Territories. In Saskatchewan, S. vicarium is common and widespread throughout the boreal forest and Shield (Figure 24).

S. vicarium has a univoltine winter life cycle, with larvae present year-round. Emergence lasts from mid-May until early July, but is usually concentrated in late May and June. A similar life cycle was reported for S. vicarium in West Virginia (Richardson and Tarter 1976) and Wisconsin (Flowers and Hilsenhoff 1978). Emergence was somewhat earlier in West Virginia (early to late May) and somewhat later in Wisconsin (June to early July).

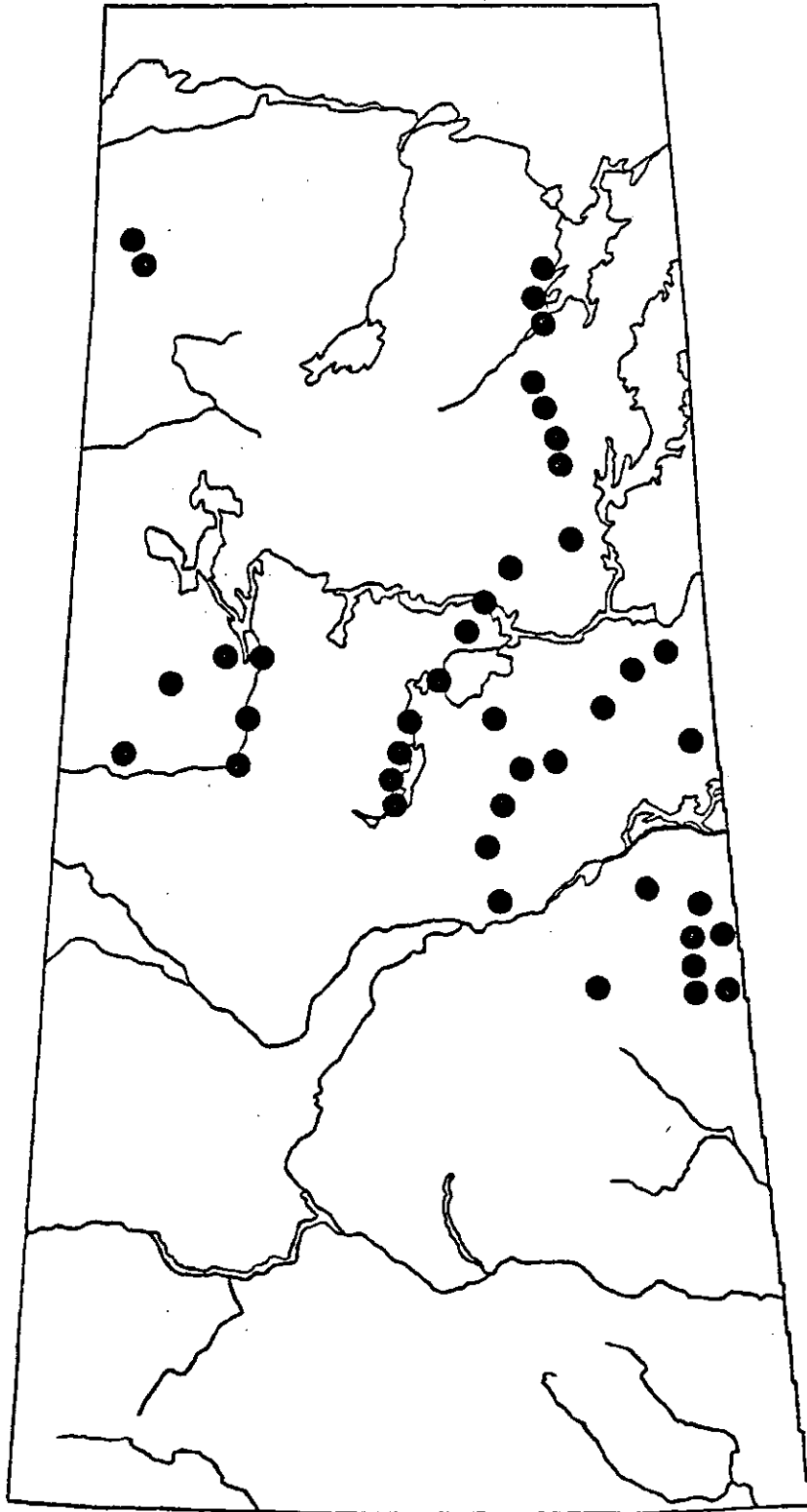


Figure 24. Map of Saskatchewan collection locations for *Stenonema vicarium*.



## Subfamily Anepeorinae

Anepeorus rusticus McDunnough 1925

A. rusticus is known only from Saskatchewan and Utah. It was described from adults collected in Saskatoon in 1924. No adults have been collected since, and the larva is unknown. Therefore, A. rusticus was not included in this study. However, Acanthomola pubescens may be the larva of A. rusticus (see Appendix 3).

## Subfamily Arthropleinae

Arthroplea bipunctata (McDunnough) 1924

A. bipunctata is an eastern North American species that occurs in the northeastern and Great Lakes states, southern Ontario, Quebec, Saskatchewan and the Northwest Territories. In Saskatchewan, A. bipunctata has been collected at only two sites in the Athabasca Plains (Figure 25). Both of these records are from collections made by the Saskatchewan Research Council; no specimens of A. bipunctata were collected during this study.

The life cycle of A. bipunctata in Saskatchewan is unknown. In Wisconsin, A. bipunctata had a univoltine summer life cycle, with eggs hatching in early May and adults emerging in late May (Flowers and Hilsenhoff 1978).

A. bipunctata larvae are filter-feeders, and usually inhabit aquatic vegetation in very slow-flowing or standing water (Edmunds, Jensen and Berner 1976, Flowers and Hilsenhoff 1978).

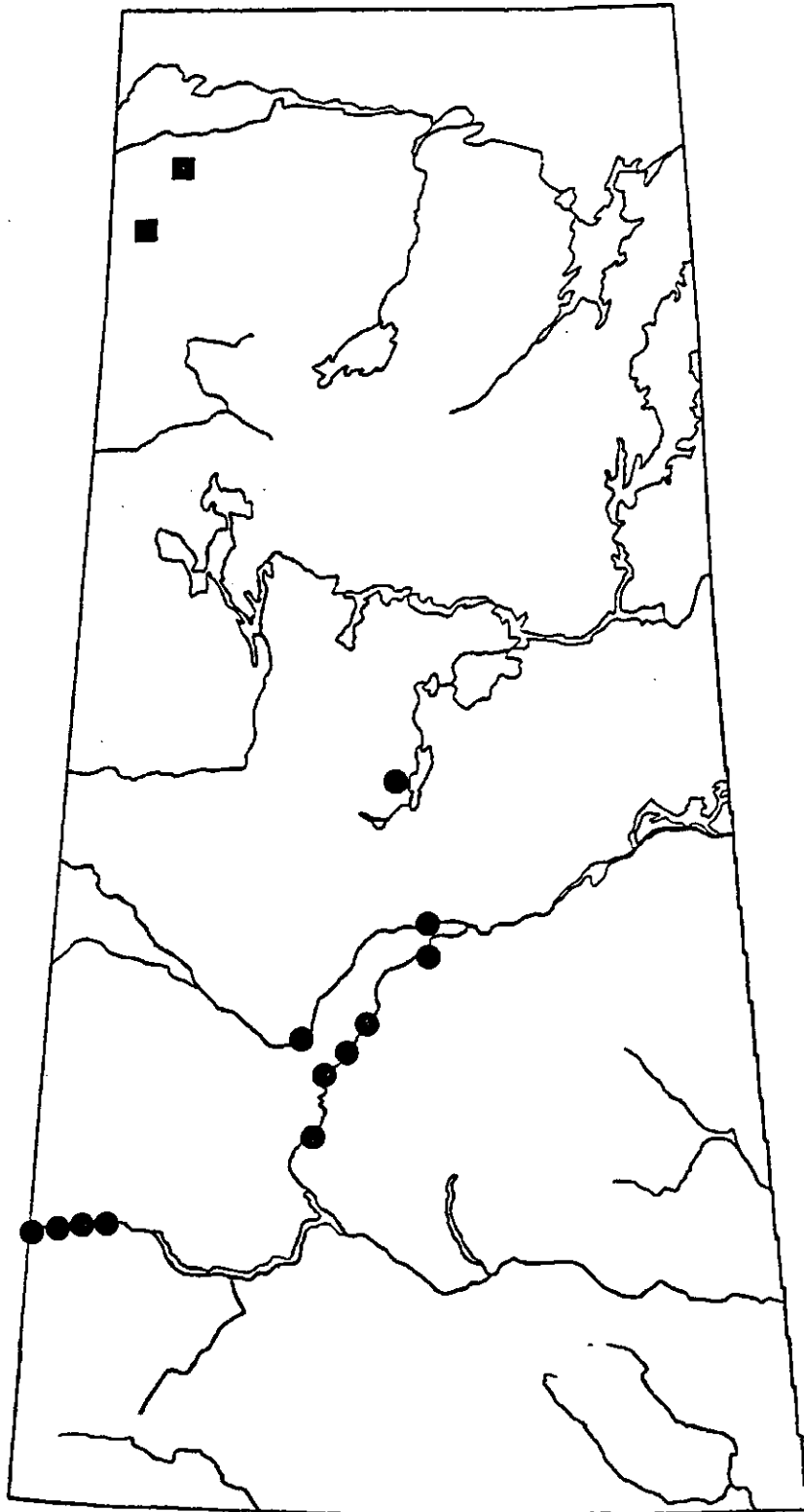


Figure 25. Map of Saskatchewan collection locations for Arthroplea bipunctata ■ and Pseudiron centralis ●.

## Subfamily Pseudironinae

Pseudiron centralis McDunnough 1931

P. centralis occurs in several mid-western states, southern Manitoba, Saskatchewan, and east-central Alberta. The larvae are restricted to sandy substrates in medium-sized to large rivers (Edmunds, Jensen and Berner 1976, Soluk and Clifford 1984). In Saskatchewan, P. centralis has been collected from several locations on the North and South Saskatchewan Rivers, and from the MacLennan River, west of Montreal Lake (Figure 25).

P. centralis has a univoltine summer life cycle, with larvae present from mid-May until early July, and emergence occurring in late June and early July. The life cycle of P. centralis was similar in Alberta, with larvae hatching in late April and adults emerging from late June until late July (Soluk and Clifford 1984).

Larvae of P. centralis are predaceous on chironomid larvae (Edmunds, Jensen and Berner 1976, Soluk and Clifford 1984).

#### 4.2 Intensive Study: Distribution Patterns

Sixteen species were included in the intensive study. Cinygmula reticulata, Epeorus longimanus and Arthroplea bipunctata were not included because they do not occur in the intensive study area; Acanthomola pubescens and Anepeorus rusticus were not collected during the intensive study period. Stenonema femoratum and Pseudiron centralis were removed from the intensive study data because they were outliers (single species with unique distribution patterns) in preliminary ordinations. These two species have unique habitat preferences: S. femoratum is found almost exclusively in standing water, and P. centralis is restricted to coarse sand substrates. Outliers should be excluded from multivariate analyses, because their presence interferes with the elucidation of other patterns in the data (Gauch 1982).

##### 4.2.1 Cluster analysis of annual species abundance data

The classification of 34 intensive study sites by annual sweep net abundance data is presented in Figure 26 (mean annual abundances of heptageniids in sweep net samples at intensive study sites are given in Appendix 4). Site 34 is not included because shallow water at this site prevented sweep net sampling. Figure 27 shows the relationship between distance between fusing clusters and the number of clusters in the classification. Large changes in slope occur at two points in this plot, at the two and seven cluster levels. Such changes in slope occur at points where clusters of similar sites fuse with relatively dissimilar ones,

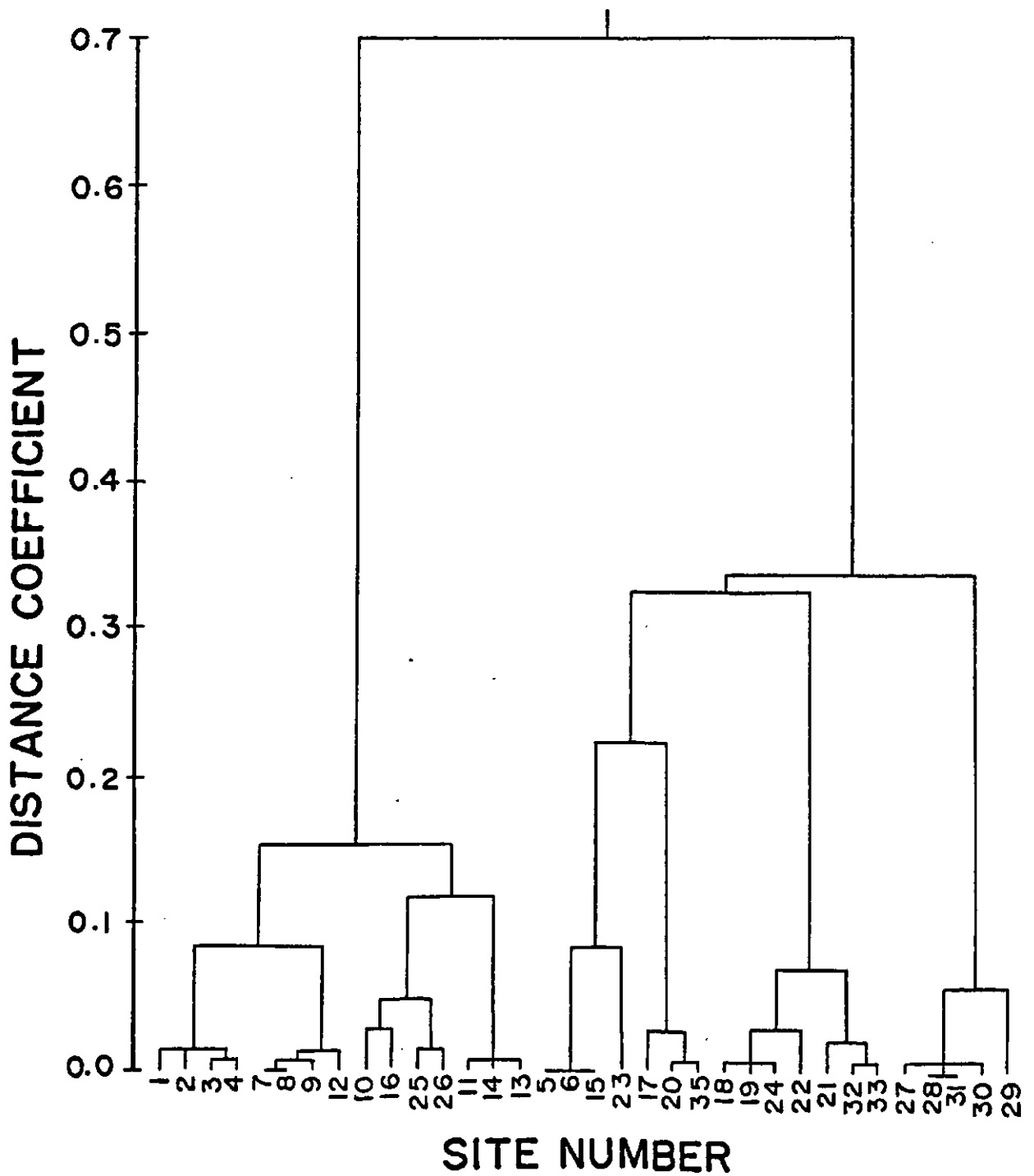


Figure 26. Classification of intensive study sites by annual sweep net data.

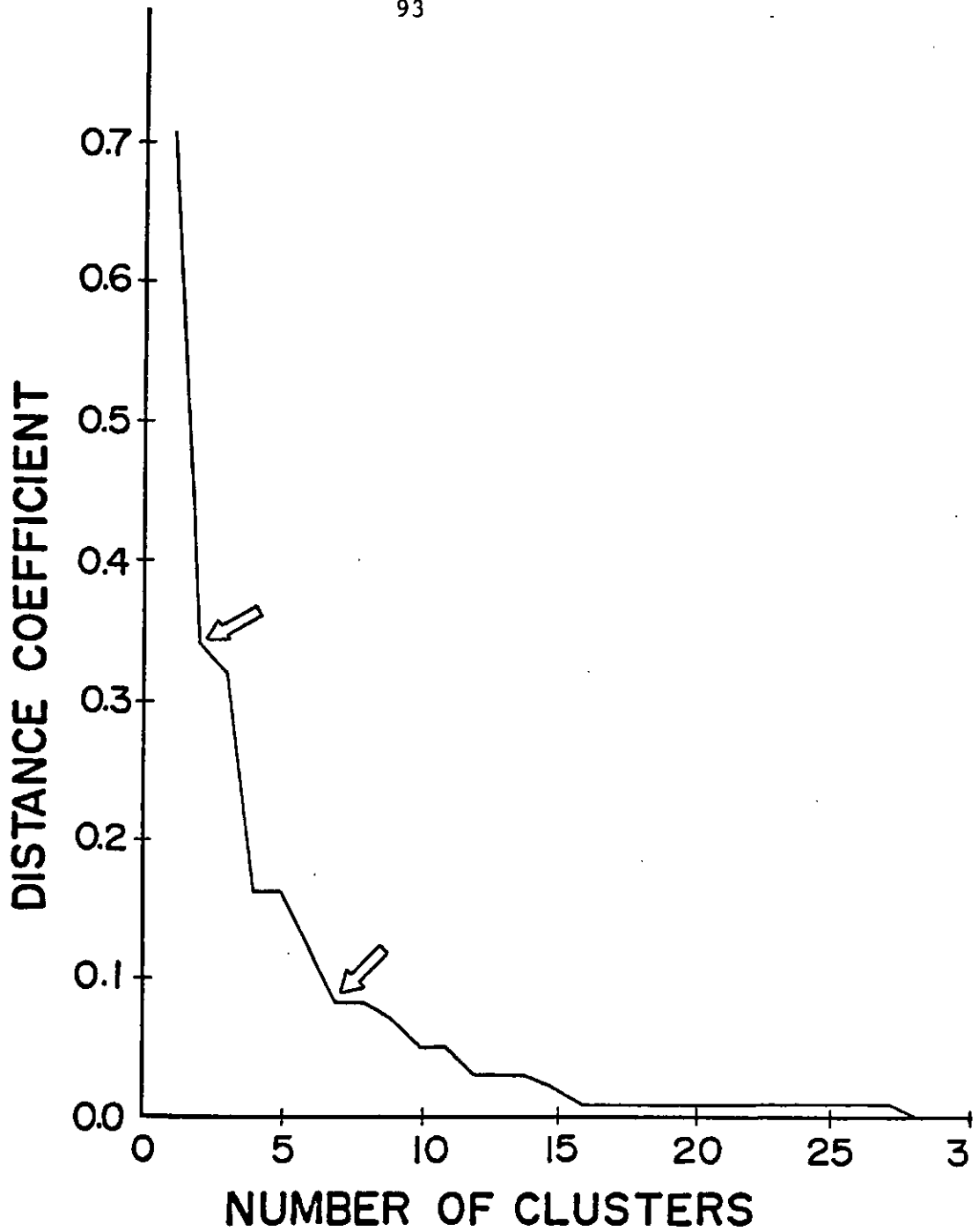


Figure 27. Relationship between distance between fusing clusters and number of clusters in the classification of intensive study sites by annual sweep net data. Changes in slope occur at the 2 and 7 cluster levels.

indicating the existence of distinct, homogenous groups of sites, or faunal zones. Thus, there appear to be two heptageniid faunal zones, and seven subzones, in the intensive study area.

One of the two large clusters contains all Saskatchewan River sites (except sites 5, 6 and 15), and two southern boreal stream sites (sites 25 and 26). The two boreal sites are part of the Saskatchewan River drainage, and possess a mixture of Saskatchewan River and boreal species.

The other large cluster contains all remaining boreal sites, and Saskatchewan River sites 5, 6 and 15. Heptageniids were never collected in sweep net samples at these Saskatchewan River sites. Their apparent similarity to boreal sites is due entirely to common low diversities and abundances (both diversity and total abundance were slightly lower at boreal than Saskatchewan River sites), and is therefore artificial.

Thus, the two major clusters apparently correspond to a Saskatchewan River and a boreal faunal zone.

The Saskatchewan River faunal zone contains three subzones (at the seven cluster level): 1) sites 1-4 and 7-9 on the South Saskatchewan River and site 12 on the North Saskatchewan River, where heptageniid faunas are dominated by Heptagenia spp. and Stenonema terminatum, and Stenacron interpunctatum is absent, 2) site 11 on the South Saskatchewan River and sites 13 and 14 on the Saskatchewan River, where S. interpunctatum, Heptagenia spp. and S. terminatum are all abundant, and 3) sites 10 on the South

Saskatchewan River, 16 on the Saskatchewan River and 25 and 26 on southern boreal streams, where the fauna is dominated by S. interpunctatum and/or S. terminatum, and Heptagenia spp. are uncommon or absent.

The boreal faunal zone contains four subzones: 1) high gradient Pasquia Hills sites (sites 27-31), where Heptagenia pulla, Nixe rusticalis and N. simplicoides are common, 2) Saskatchewan River sites where no heptageniids have been collected (sites 5, 6 and 15), and site 23 (on a high gradient stream in the Wapawekka Hills) where only N. rusticalis has been collected, 3) large boreal river sites (sites 17, 20 and 35), where Stenacron interpunctatum is the most abundant heptageniid, and H. pulla is relatively uncommon, and 4) smaller boreal stream sites (sites 18, 19, 21, 22, 24, 32 and 33), where H. pulla and Stenonema vicarium are common and S. interpunctatum is relatively uncommon.

The classification of 34 intensive study sites by annual stone abundance data (mean annual abundances of heptageniids picked from stones at intensive study sites; Appendix 5), is presented in Figure 28. Site 26 was not included because no stones were present. The plot of distance between fusing clusters vs. number of clusters (Figure 29) contains two large changes in slope, at the three and eight cluster levels. Thus, three faunal zones, and eight subzones, are indicated by this classification. The three zones are: 1) the Saskatchewan Rivers (sites 1-4, 6-16 and 25), 2) high gradient boreal streams (sites 23 and 27-31), and site 5, and 3) other boreal streams (sites 17-22, 24, and 32-35). This



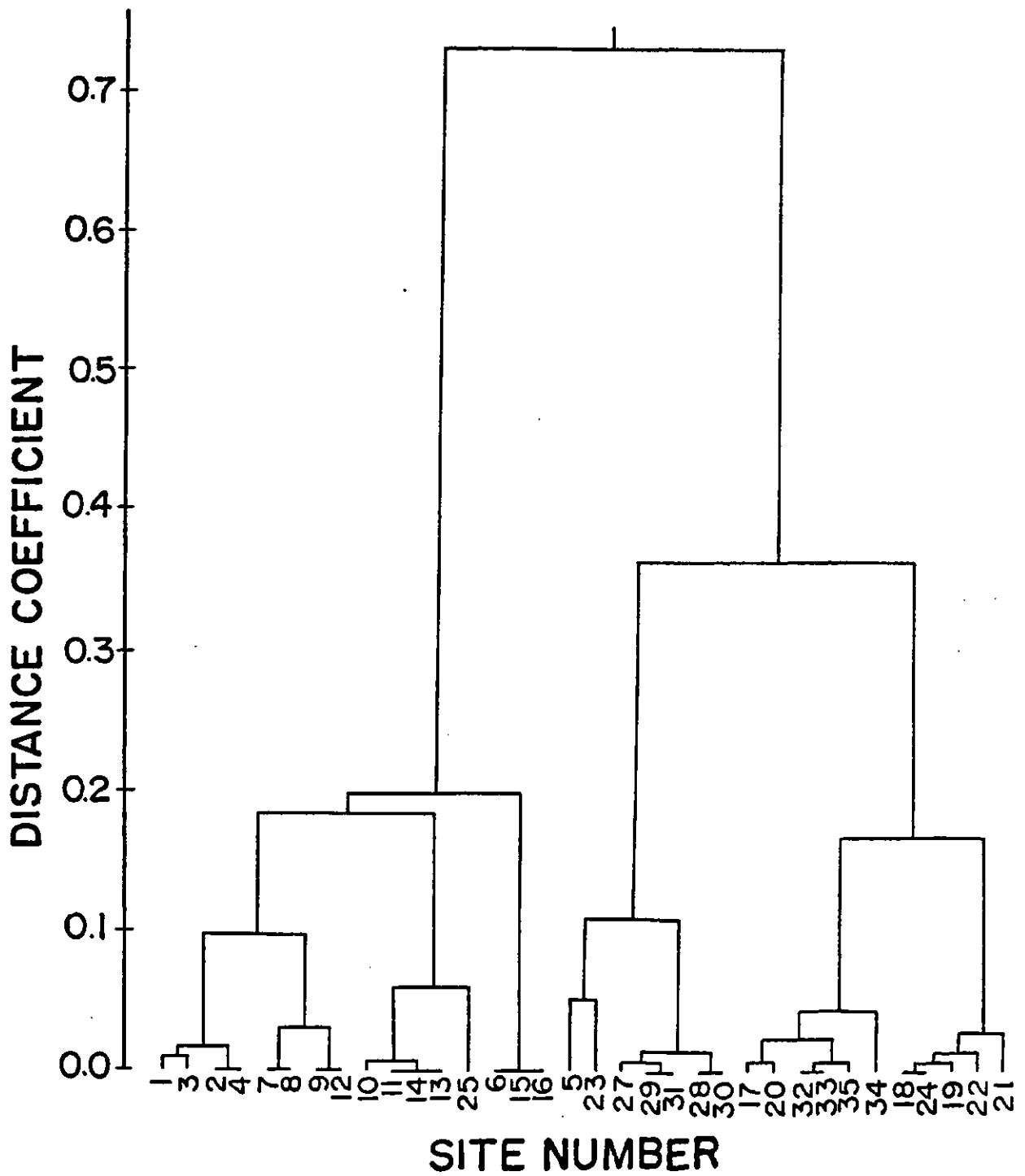


Figure 28. Classification of intensive study sites by annual stone data.

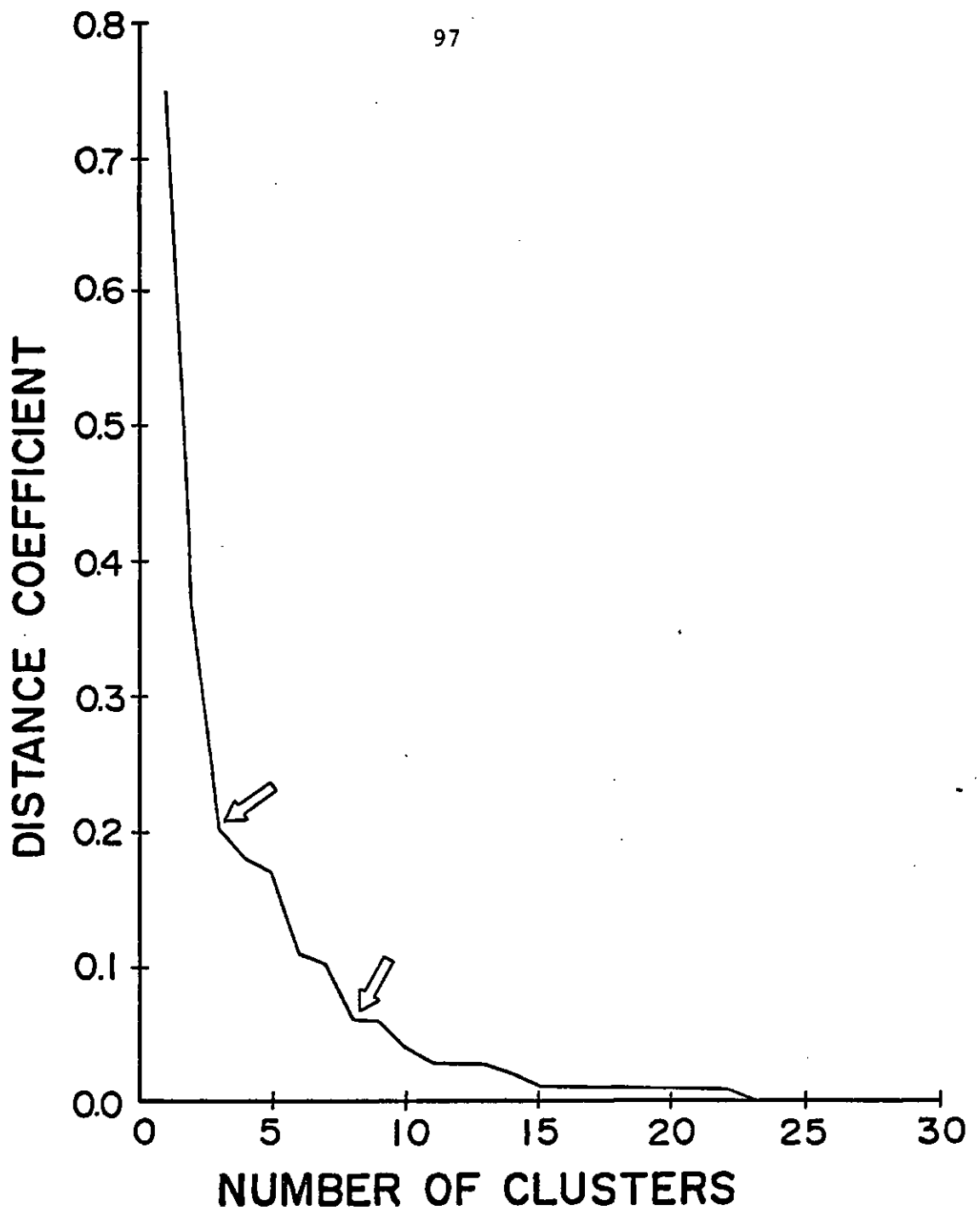


Figure 29. Relationship between distance between fusing clusters and number of clusters in the classification of intensive study sites by annual stone data. Changes in slope occur at the 3 and 8 cluster levels.

classification differs from the one based on sweep net data in that high gradient streams are a separate zone instead of a boreal subzone. This is due to differences in the apparent distinctness of the high gradient cluster which is very homogenous in both analyses. In the sweep net data classification, other boreal streams form a relatively loose and heterogenous cluster, containing sites which are almost as different from one another as from high gradient sites. In the stone data classification, other boreal streams are more similar to one another, increasing the apparent distinctness of the high gradient cluster.

The stone and sweep net data analyses also differ in the classification of sites 6 and 15, which are in the boreal zone in the sweep net classification and in the Saskatchewan River zone in the stone classification. Small numbers of Stenonema terminatum nymphs were collected from stones at these sites. The stone classification of these sites has greater biological meaning, because it is based on shared species occurrences, rather than shared absences.

Four of the eight subzones in the stone data classification are in the Saskatchewan River zone, two are in the high gradient boreal zone, and two are in the other boreal zone. The Saskatchewan River subzones are: 1) South Saskatchewan River sites upstream from Lake Diefenbaker (sites 1-4), characterized by high diversity and the presence of Heptagenia adequata, 2) sites a short distance downstream from dams (sites 6, 15 and 16), where only Stenonema terminatum has been collected, usually in low numbers, 3)

sites 7-9 and 12, where Stenacron interpunctatum is absent or rare and 4) sites 10, 11, 13, 14 and 25, where S. interpunctatum is common. This subgroup classification differs from that in sweep net data analysis, where the first and third of these subgroups are combined, and the fourth is split into two subgroups.

The high gradient boreal subzones are: 1) high gradient Pasquia Hills sites (sites 27-31), where Heptagenia pulla, and Nixe rusticalis or N. simplicoides are common, and 2) sites 5 and 23. No heptageniids were collected at site 5, and only N. rusticalis was collected at site 23. This subgroup (like the corresponding subgroup in the sweep net classification which contains sites 5, 6, 15 and 23) is probably an artificial group of low diversity sites.

The division of the remaining boreal sites into subzones is similar to that in the sweep net classification. One subzone contains sites 17, 20, and 32-35, where Stenacron interpunctatum is the most abundant heptageniid; the other contains sites 18, 19, 21, 22 and 24, where Heptagenia pulla and/or Stenonema vicarium are more abundant than S. interpunctatum. The two subzonal classifications differ only in the positions of sites 32 and 33, where S. interpunctatum was common in stone samples but uncommon in sweep net samples.

#### 4.2.2 Ordination of annual species abundance data

The eigenvalues of the first four ordination axes derived by DCA of annual sweep net data are presented in

Table 5. The first two axes have much higher eigenvalues than the third or fourth, and thus describe much more of the variation in the data. Therefore, a two-dimensional plot of sites, according to their first and second axis ordination scores (Figure 30), shows most of the important features present in the original data. Three fairly distinct clusters of sites are apparent: Saskatchewan River sites, high gradient boreal streams, and other boreal streams and rivers. The first axis separates Saskatchewan River sites from boreal sites, in opposite halves of the axis. South Saskatchewan River sites upstream from Lake Diefenbaker (sites 1 to 4) lie at the extreme Saskatchewan River end of the axis. The downstream-most South Saskatchewan and Saskatchewan River sites (sites 10, 11, 13 and 14) lie closer to the center of the axis, and are thus more similar to boreal streams. Sites 25 and 26 are intermediate between Saskatchewan River and boreal sites. High gradient boreal streams lie closer to the center of the first axis than other boreal streams, but are well separated from Saskatchewan River and other boreal sites on the second axis. Site 23 has the lowest score on the second axis.

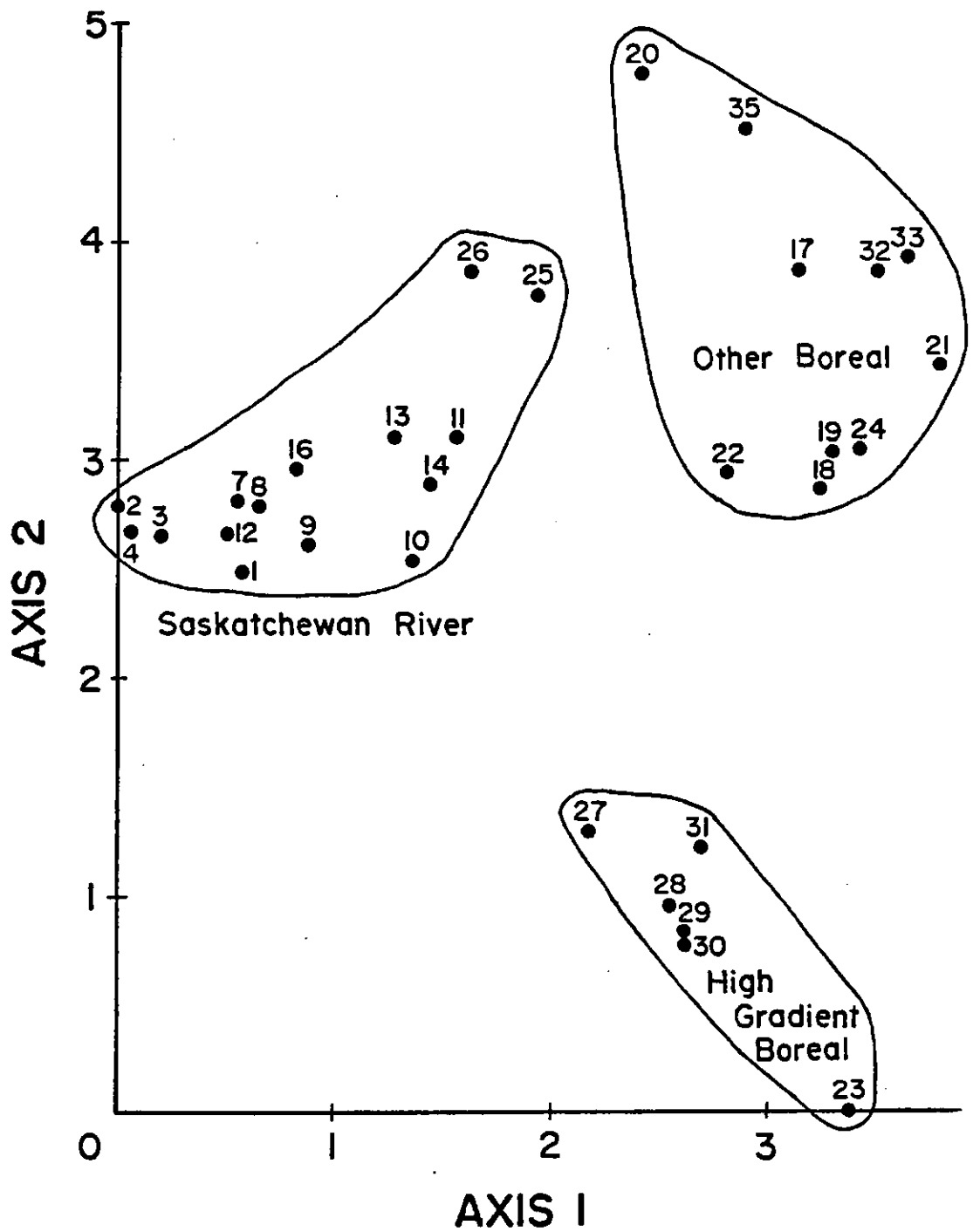


Figure 30. DCA ordination of annual sweep net data: site scores on axes 1 and 2. Site scores are represented by dots, labelled with site numbers. Enclosed areas represent major groups present in classifications.

Table 5. Eigenvalues of the first four ordination axes from DCA of four annual data sets.

<u>Data Set</u>	<u>Axis Number</u>			
	1	2	3	4
Sweep net samples	0.71	0.42	0.10	0.08
Stone samples	0.65	0.34	0.09	0.05
Log samples	0.77	0.32	0.14	0.08
Presence/absence	0.56	0.30	0.08	0.06

Species can also be plotted in two dimensions, according to their scores on the first two ordination axes.

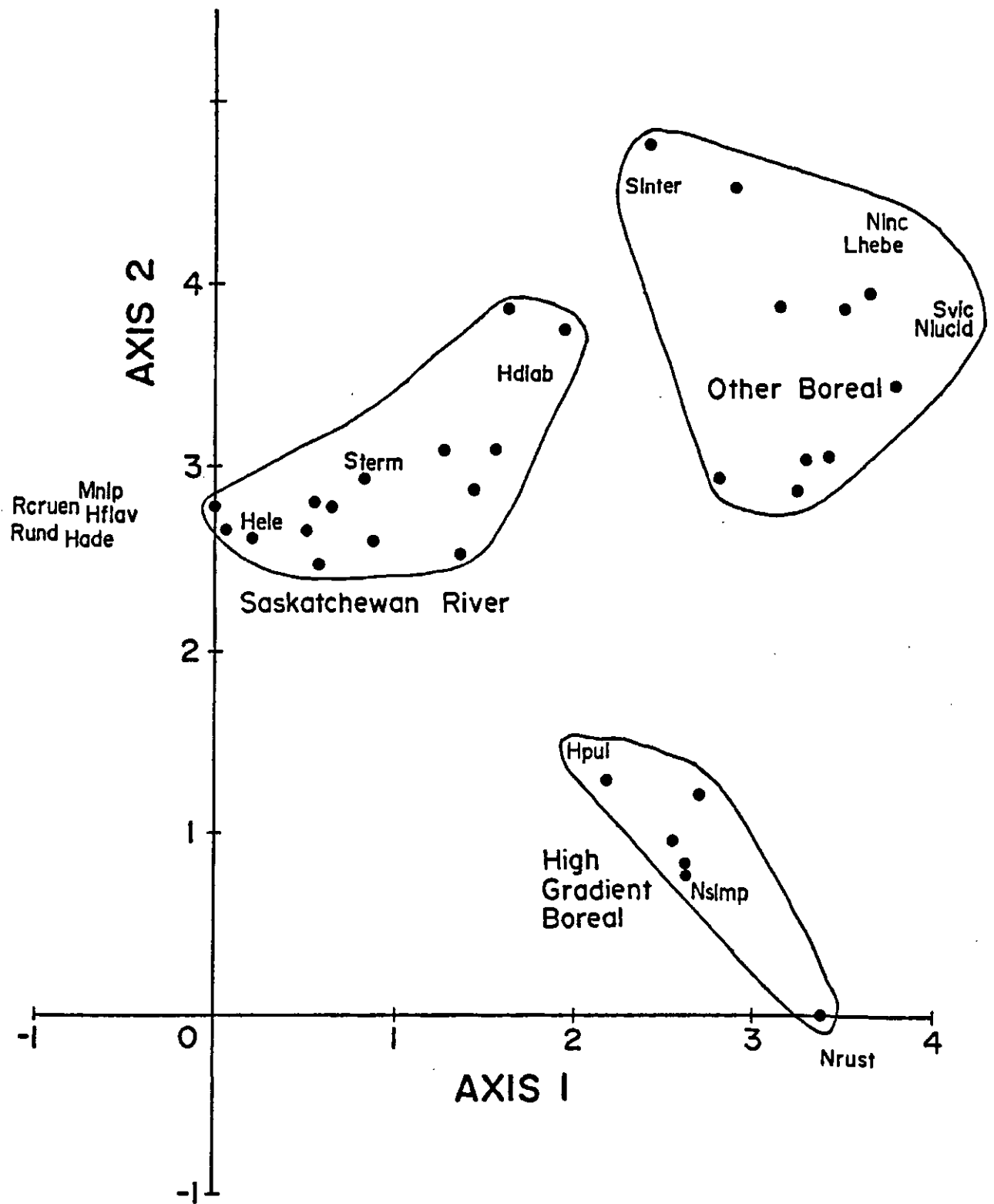
Superimposing species on the site plot (Figure 31) shows which species are associated with which groups of sites.

Heptagenia diabasica, H. elegantula and Stenonema terminatum are associated with the Saskatchewan River zone; H. pulla, Nixe rusticalis and N. simplicoides are associated with high gradient Pasquia Hills streams; and Leucrocuta hebe, N. inconspicua, N. lucidipennis, Stenacron interpunctatum and Stenonema vicarium are associated with the other boreal faunal zone.

Heptagenia adequata, H. flavescens, Macdunnoa nipawinia, Rhithrogena undulata and Raptoheptagenia cruentata have lower first axis ordination scores than any Saskatchewan River site. These species are all more or less restricted to the South Saskatchewan River upstream from Lake Diefenbaker, and most are rare. The DCA algorithm is based on a model of species showing normal.(Gaussian) abundance curves along

Figure 31. DCA ordination of annual sweep net data: species scores on axes 1 and 2. Species scores are represented by the centers of abbreviated species names, consisting of the first letter of the genus name (upper case) and the first three to five letters of the species name (lower case). Site scores are represented by dots. Enclosed areas represent major groups present in classifications.





environmental gradients (Gauch 1982). Therefore, these five species appear to be characteristic of a hypothetical habitat that is more "Saskatchewan River-like", and would have a lower first axis ordination score, than any of the sites included in the intensive study.

The second axis is longer than the first, indicating greater species turnover (change in species composition) along the second axis. However, the first axis has the highest eigenvalue and is therefore the most important. This is because the number of species associated with the first axis is greater, and hence the first axis accounts for more variation in the data, even though change in species composition is less than on the second axis.

The DCA ordination of annual stone data is very similar. Again the first two axes have much higher eigenvalues than the third or fourth, and describe most of the variation (Table 5). Two-dimensional plots of sites and species, according to their first and second axis ordination scores (Figures 32 and 33) are very similar to plots using ordination scores from sweep net data. The same three clusters of sites are apparent. The stone data ordination plots differ mainly in that: 1) Site 12 lies closer to the center of the first axis, and is not closely associated with sites 1 to 4 on the South Saskatchewan River upstream from Lake Diefenbaker. This is probably because the rare species unique to these five sites (H. flavescens, M. nipawinia and R. cruentata) are all very rare or absent in stone samples. 2) N. inconspicua lies closer to the high gradient Pasquia

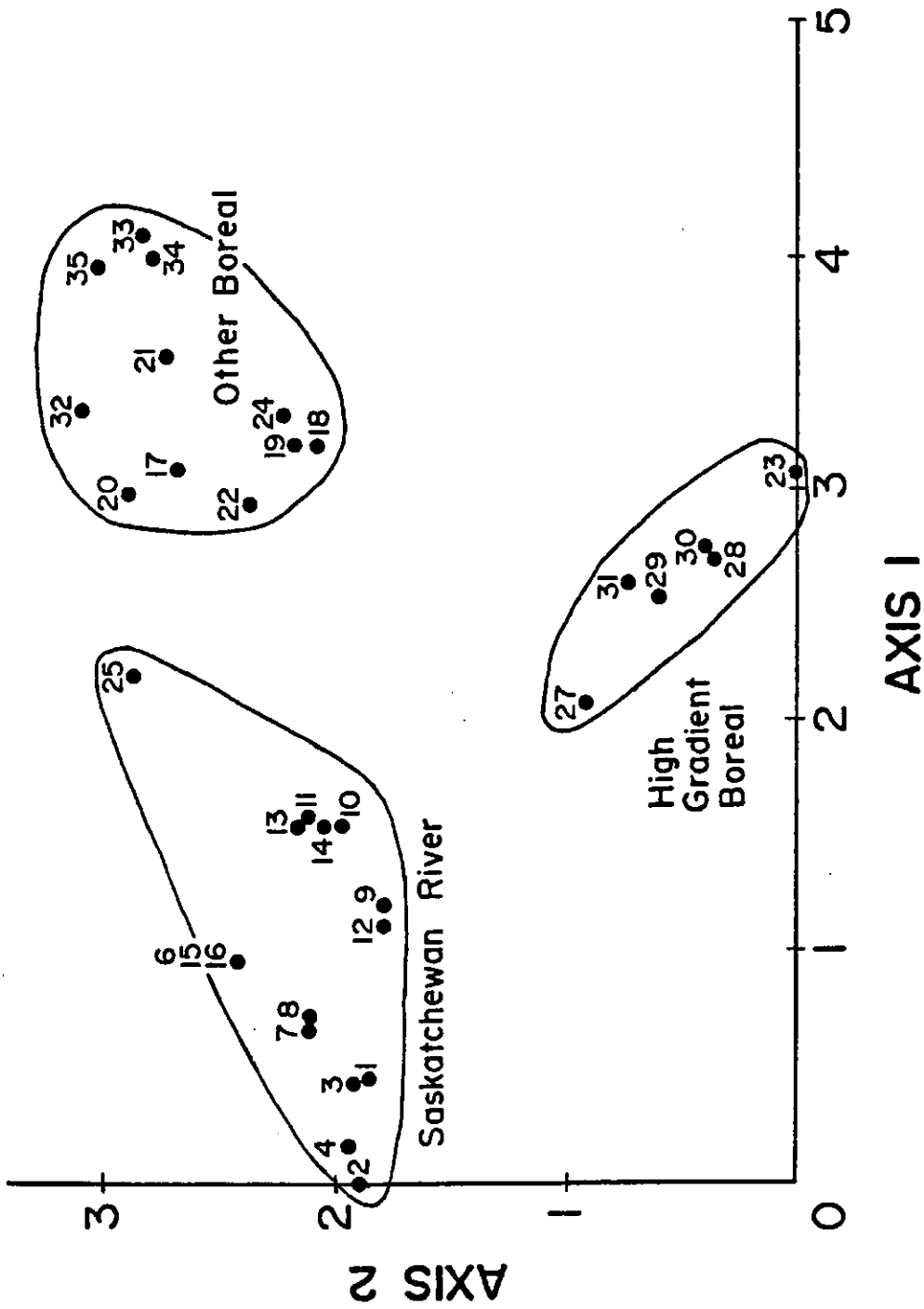
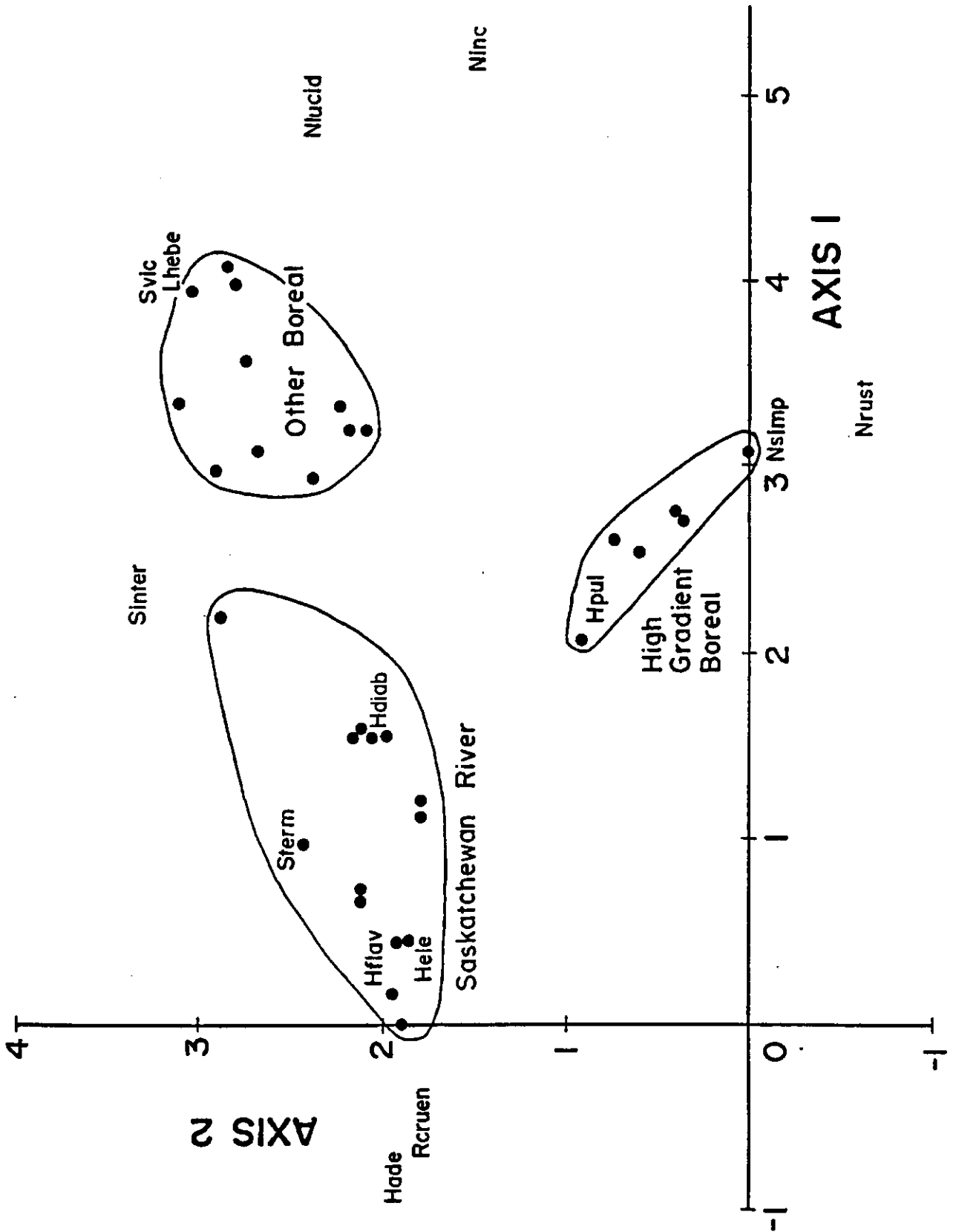


Figure 32. DCA ordination of annual stone data; site scores on axes 1 and 2. Symbols and labels are explained in Figure 30.

Figure 33. DCA ordination of annual stone data: species scores on axes 1 and 2.

Symbols and labels are explained in Figure 31.



Hills end of the second axis. However, N. inconspicua was rarely collected in stone samples; thus, stone data may be less representative than sweep net data.

The ranges of site and species scores on the first stone and sweep net axes are similar, indicating similar rates of species turnover. The range of species scores on the second axis is less in stone data ordination, indicating less species turnover. This may be due to the low numbers of Nixe species in stone samples. These species have scores at either end of the second axes, and thus are associated with much of the variation described.

The third and fourth sweep net and stone axes all have low eigenvalues, and describe little variation. Furthermore, the variation cannot be explained. The ranges of species scores are much larger than the ranges of site scores (Figures 34 and 35), and one or two species have very extreme scores on each axis. This suggests that the variation described is primarily related to the distributions of one or two species, rather than to general zoogeographical trends. The third and fourth stone data axes are completely different than the third and fourth sweep net data axes, except for a slight similarity between the third stone and fourth sweep net axes, and between the fourth stone and third sweep net axes.

Distribution patterns indicated by ordinations of sweep net and stone data are very similar to those shown in cluster analyses. In all cases, except cluster analysis of sweep net data, three distinct groups of sites are evident. The

Figure 34. DCA ordination of annual sweep net data: site and species scores on axes 3 and 4. Vertical lines represent the ranges of site and species scores. Horizontal lines represent individual scores. Abbreviated species names consist of the first letter of the genus name (upper case) and the first three to five letters of the species name (lower case).

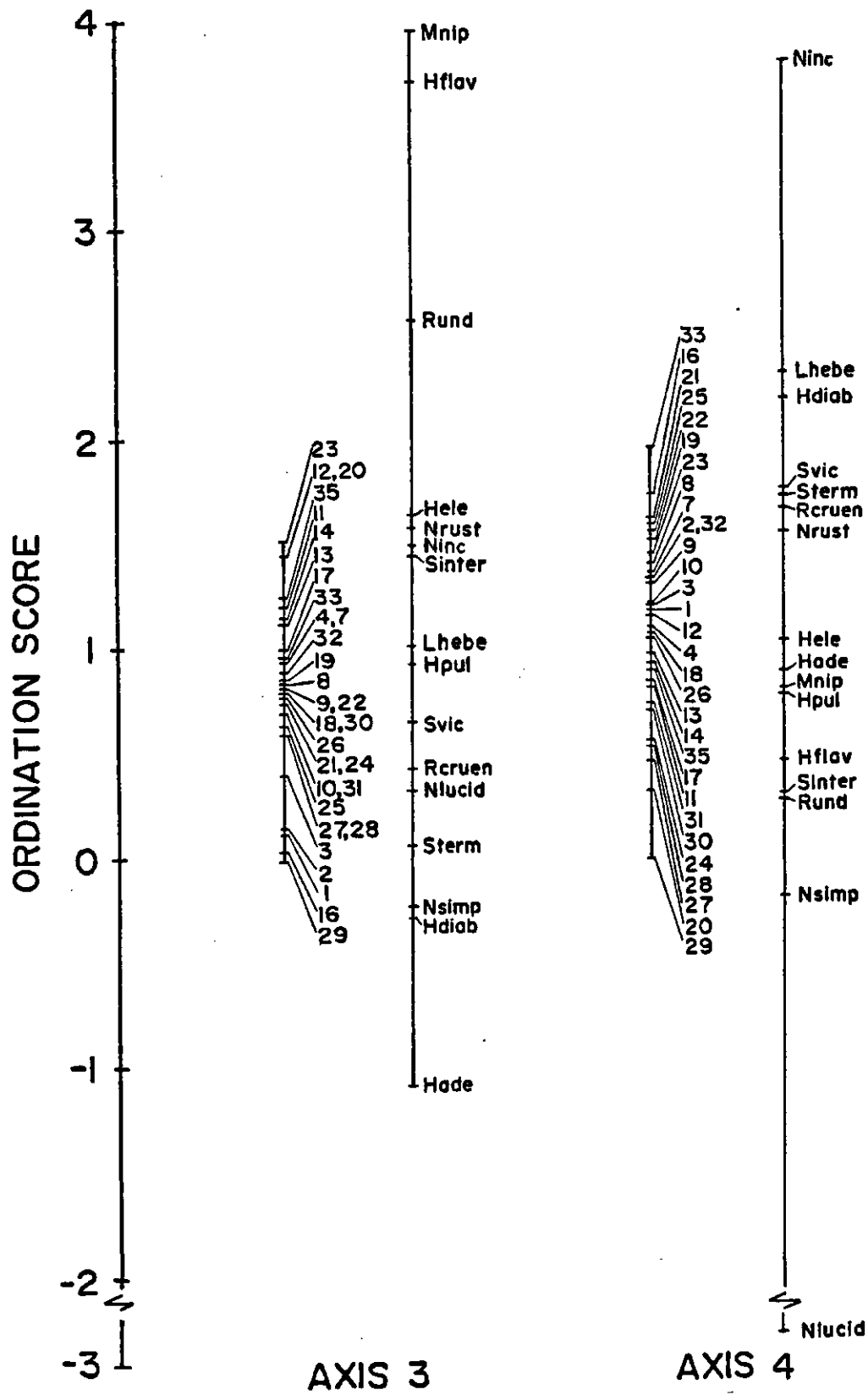
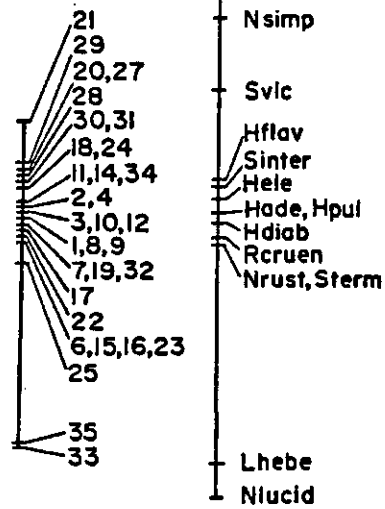
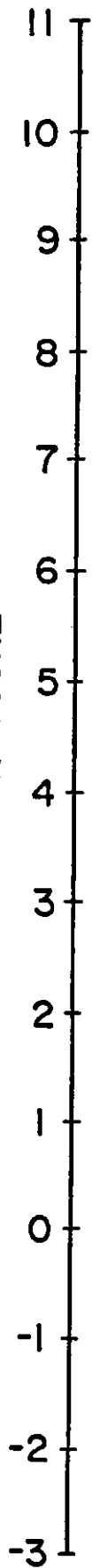


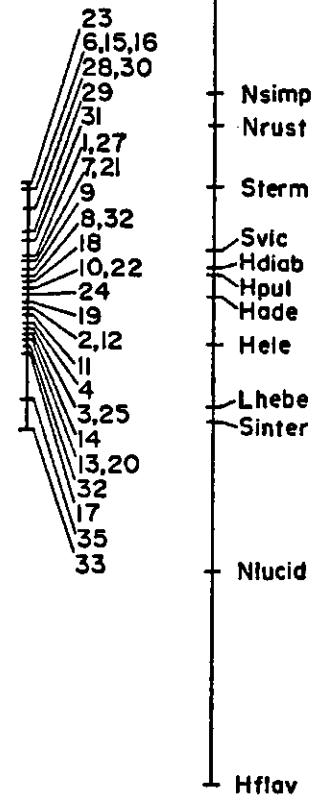


Figure 35. DCA ordination of annual stone data: site and species scores on axes 3 and 4. Lines and labels are explained in Figure 34.

ORDINATION SCORE



AXIS 3



AXIS 4

compositions of these groups are virtually identical in all analyses, except that sites 25 and 26 are intermediate between boreal and Saskatchewan River sites in ordinations, but members of the Saskatchewan River group in cluster analyses. In all cases, the high gradient boreal sites are more similar to other boreal sites than to Saskatchewan River sites, and the Saskatchewan River group is more homogenous than either of the other two groups.

#### 4.2.3 Analysis of annual log data

Log data (mean annual abundances of heptageniids picked from logs; Appendix 6) contain a relatively small subset of the sites and species included in the intensive study. Logs, or other pieces of wood suitable for colonization by heptageniids, were only present at 23 of 35 intensive study sites; and suitable pieces of wood were rare (and numbers of heptageniids collected were low) at all but 12 of these sites (sites 8, 11, 13, 14, 16, 17, 21, 22, 24, 25, 26 and 31). Only 11 species of heptageniids were found on logs (all five Saskatchewan Heptagenia species, Leucrocuta hebe, Nixe lucidipennis, N. simplicoides, Stenacron interpunctatum, Stenonema terminatum and S. vicarium). The two Nixe species were rare in log samples.

The classification of study sites by log data contains three large, distinct groups of sites (Figures 36 and 37). However, these three groups are quite different from those in classifications of sweep net and stone data. The first two groups include all Saskatchewan River sites and six boreal

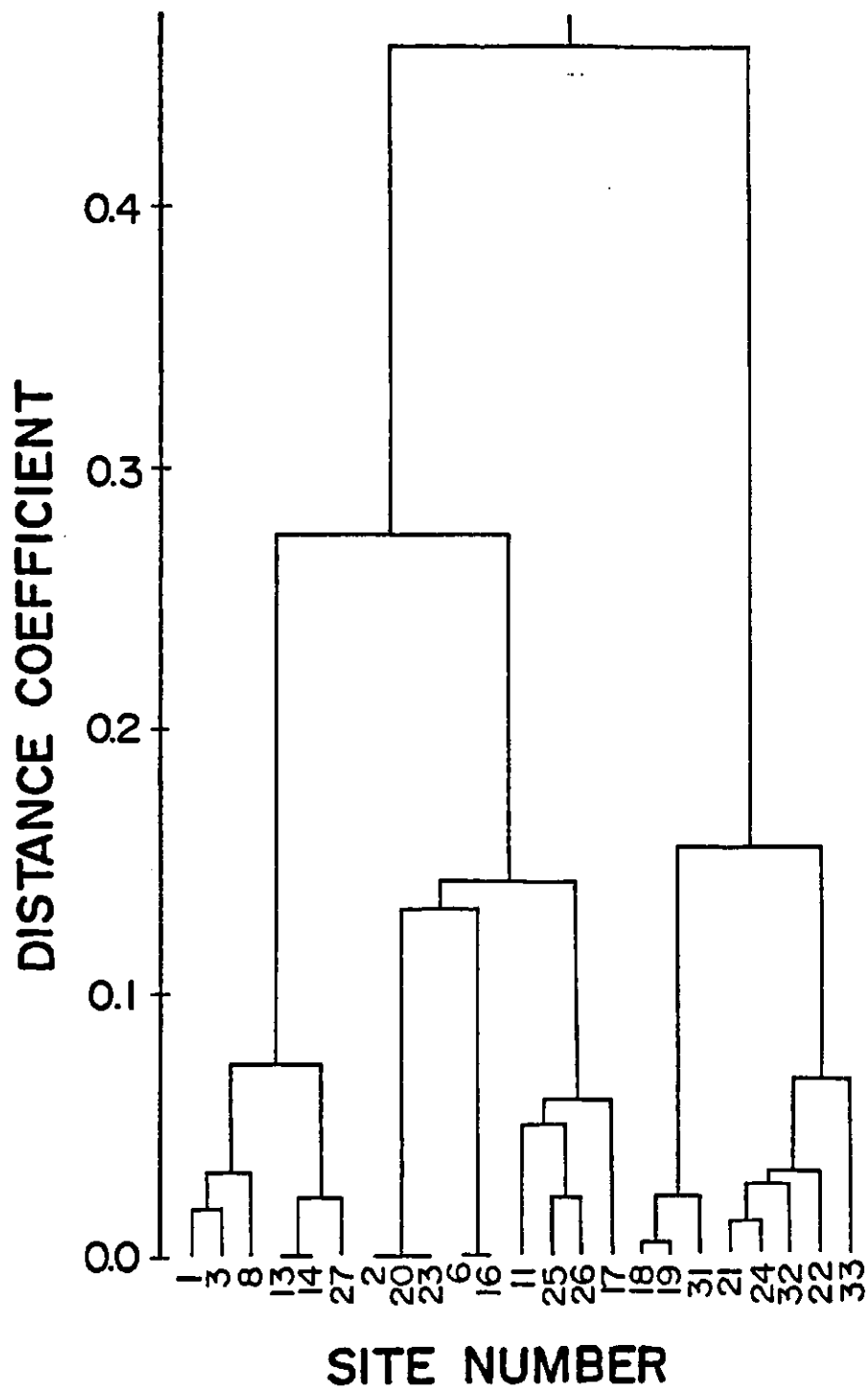


Figure 36. Classification of intensive study sites by annual log data.

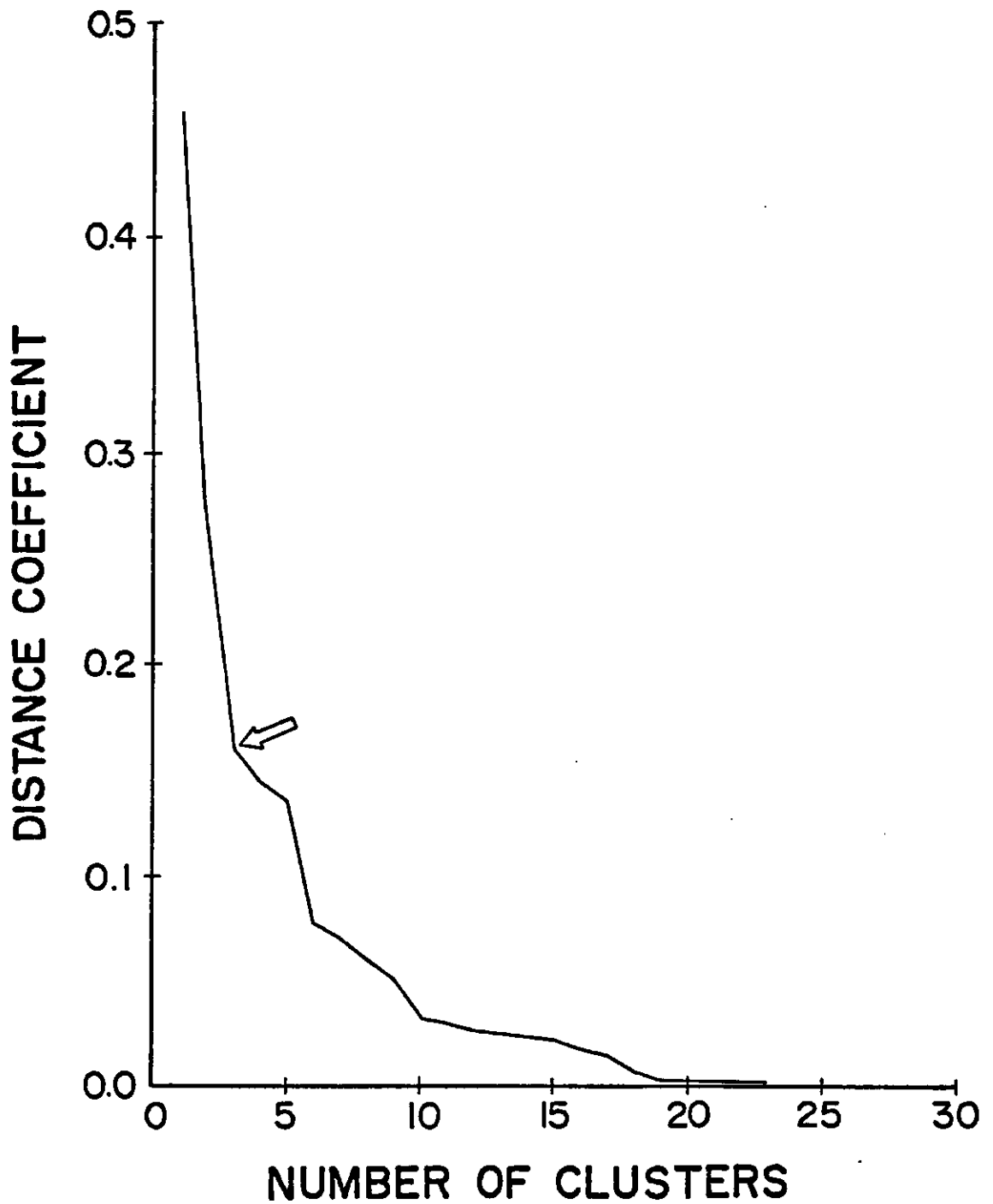


Figure 37. Relationship between distance between fusing clusters and number of clusters in the classification of intensive study sites by annual log data. Change in slope occurs at the 3 cluster level.

sites: 25 and 26 (which were classified with Saskatchewan River sites in previous cluster analyses), 23 and 27 (two of the three high gradient boreal sites included in log data), and 17 and 20 (large boreal river sites). The separation of these sites into two groups is apparently based on the presence or absence of S. interpunctatum. However, S. interpunctatum was absent in log samples at several sites where it was abundant in sweep net or stone samples. Thus, the two groups produced are very different from any major groups in the sweep net or stone data classifications. The third large group in log data classification contains the remaining boreal sites.

The high gradient boreal group is not evident in log data classification. This is probably because of the absence of N. rusticalis and low numbers of N. simplicoides (two characteristic high gradient stream species), and the inclusion of only three of seven high gradient sites in log data.

The ordination of log data is more similar to that of sweep net or stone data. Most of the variation is described by the first two axes, which have much larger eigenvalues than the third or fourth axes (Table 5). As in sweep net and stone analyses, Saskatchewan River and boreal sites are separated in opposite halves of the first axis (Figure 38). Sites 25 and 26 lie near the center of the axis, but appear to be part of the Saskatchewan River cluster rather than intermediates. However, Saskatchewan River sites 13 and 14 (which were most similar to boreal sites in analyses of sweep

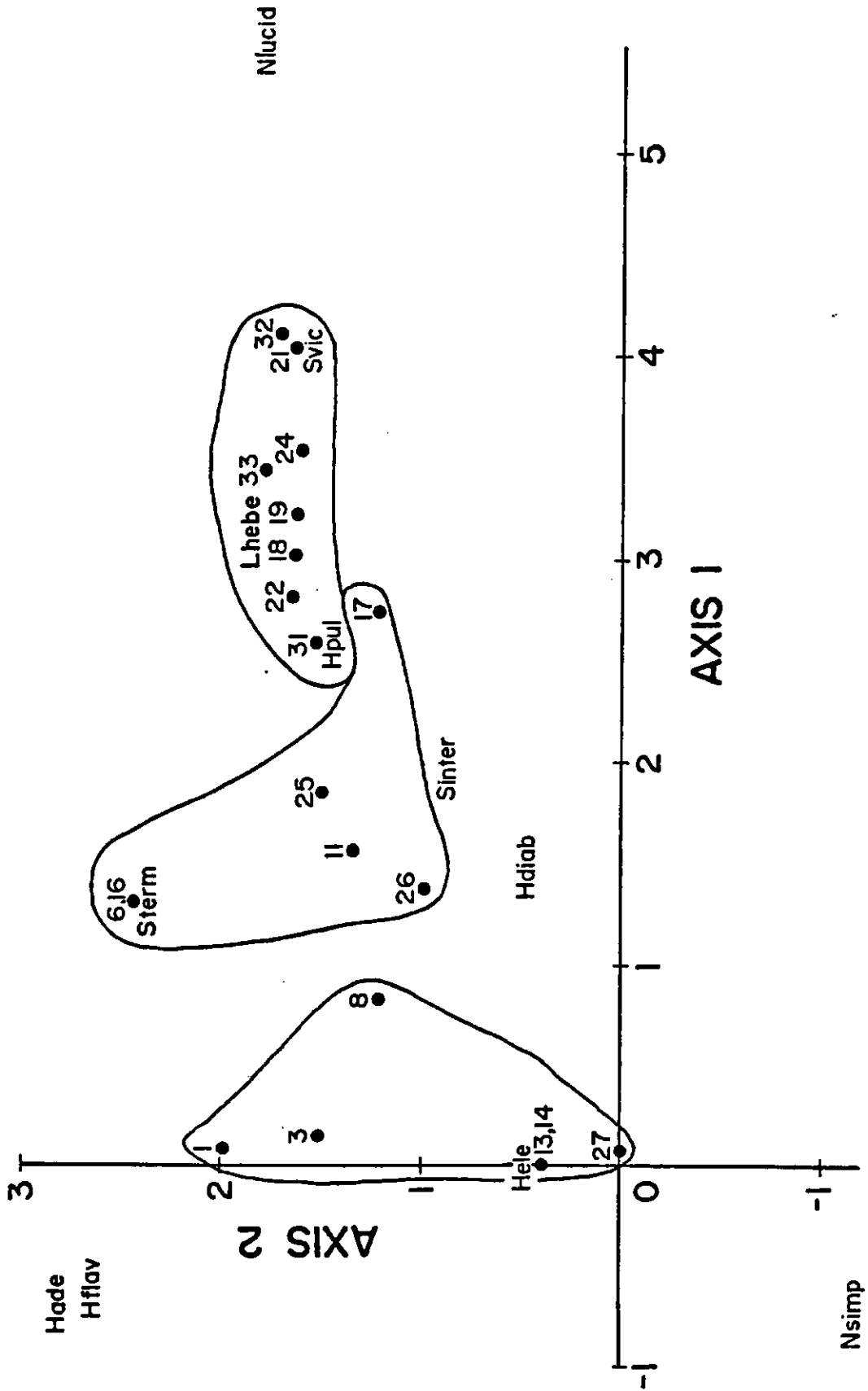


Figure 38. DCA ordination of annual log data: site and species scores on axes 1 and 2. Symbols and labels are explained in Figures 30 and 31.

net and stone data) and high gradient site 27 lie near the extreme Saskatchewan River end, with the South Saskatchewan River sites upstream from Lake Diefenbaker. Log samples from sites 13 and 14 are dominated by H. elegantula and contain low numbers of other species such as H. pulla and S. interpunctum, which are abundant in other sample types. This makes these sites more similar to upstream Saskatchewan River sites and less similar to boreal sites in log data analysis. Similarly, log samples from site 27 contain more H. elegantula than other sample types from this site. Because N. simplicoides larvae were only collected in log samples at site 27, N. simplicoides is also associated with the Saskatchewan River end of the first axis.

The second log axis describes variation among Saskatchewan River sites, separating sites where H. diabasia or H. elegantula predominate from those where other Heptagenia species or S. terminatum are also common. The second log axis is thus very different from major axes in ordinations of other data sets.

The third log axis (Figure 39), although it does not describe very much variation, is more similar to the second axes in sweep net and stone data ordinations. One of the two high-gradient streams included lies at one end of the axis, while some other boreal sites are at the other end. H. pulla lies at the high gradient end of the axis, and L. hebe and N. lucidipennis lie at the other boreal end. The low eigenvalue associated with this axis is probably due to the absence of N. rusticalis and low numbers of N. simplicoides in log



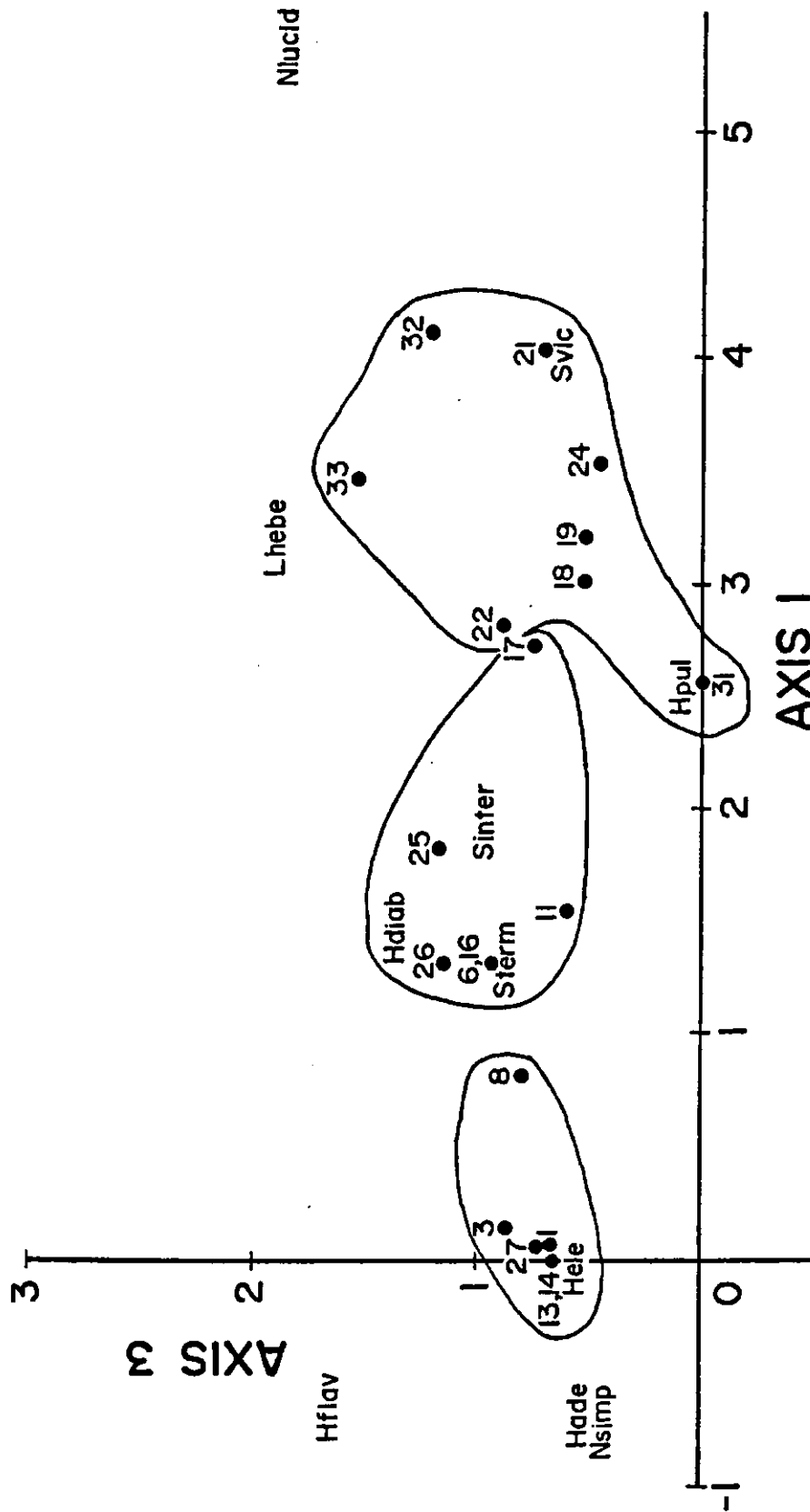


Figure 39. DCA ordination of annual log data: site and species scores on axes 1 and 3. Symbols and labels are explained in Figures 30 and 31.

samples, and the small number of high gradient sites included in the log data. Much of the variation associated with the second axes in sweep net and stone ordinations was due to these species and sites.

The fourth log axis (Figure 40) has a still lower eigenvalue, is very different than any sweep net or stone axes, and cannot be explained.

Distribution patterns shown by multivariate analyses of log data are poorly defined, difficult to interpret, and very different from those in analyses of sweep net and stone data. Therefore, the results of log data analyses will not be discussed further, or used to form conclusions about heptageniid distribution patterns.

#### 4.2.4 Analysis of annual presence/absence data

Presence/absence data from sweep net and stone samples were combined to form a single data set. Combination of data from different sampling methods is not strictly justified, because the sampling methods are differentially selective (see Section 4.5.2.). However, because the major distribution patterns indicated by multivariate analyses of the two data sets are very similar, the error produced by combining them should be small.

The classification of intensive study sites by annual combined presence/absence data is presented in Figure 41. The only large change in slope in the plot of distance between fusing clusters vs. number of clusters occurs at the six cluster level (Figure 42). This suggests that the

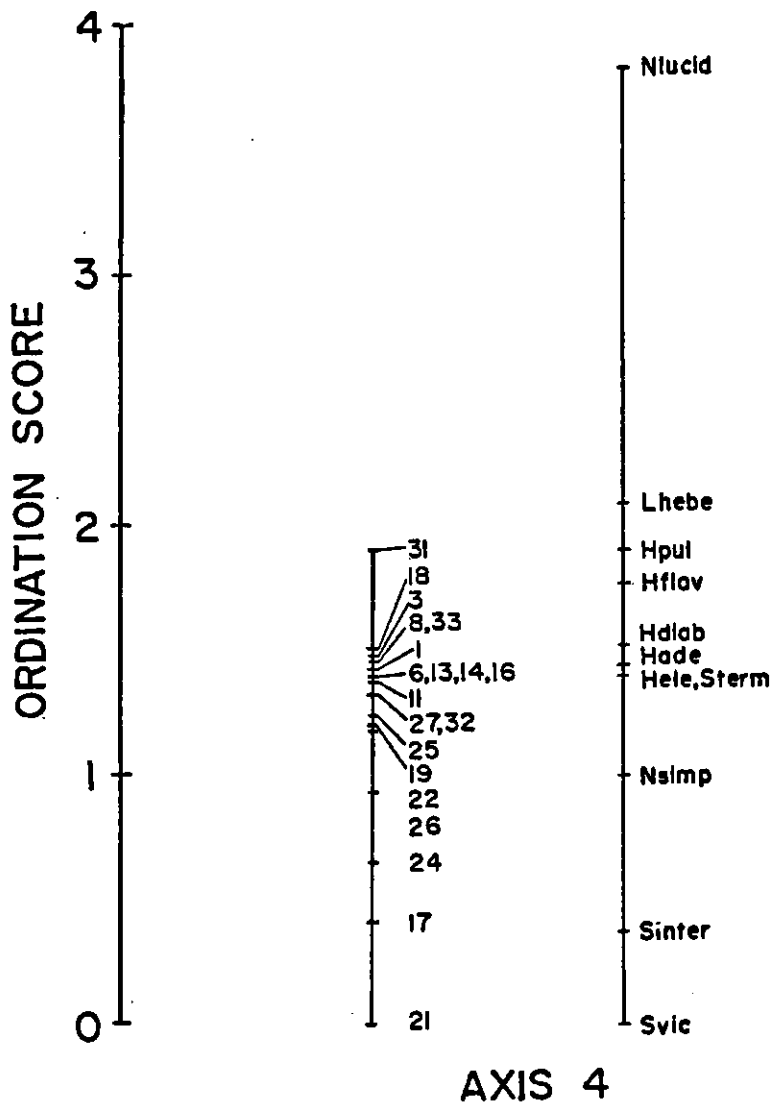


Figure 40. DCA ordination of annual log data: site and species scores on axis 4. Lines and labels are explained in Figure 34.

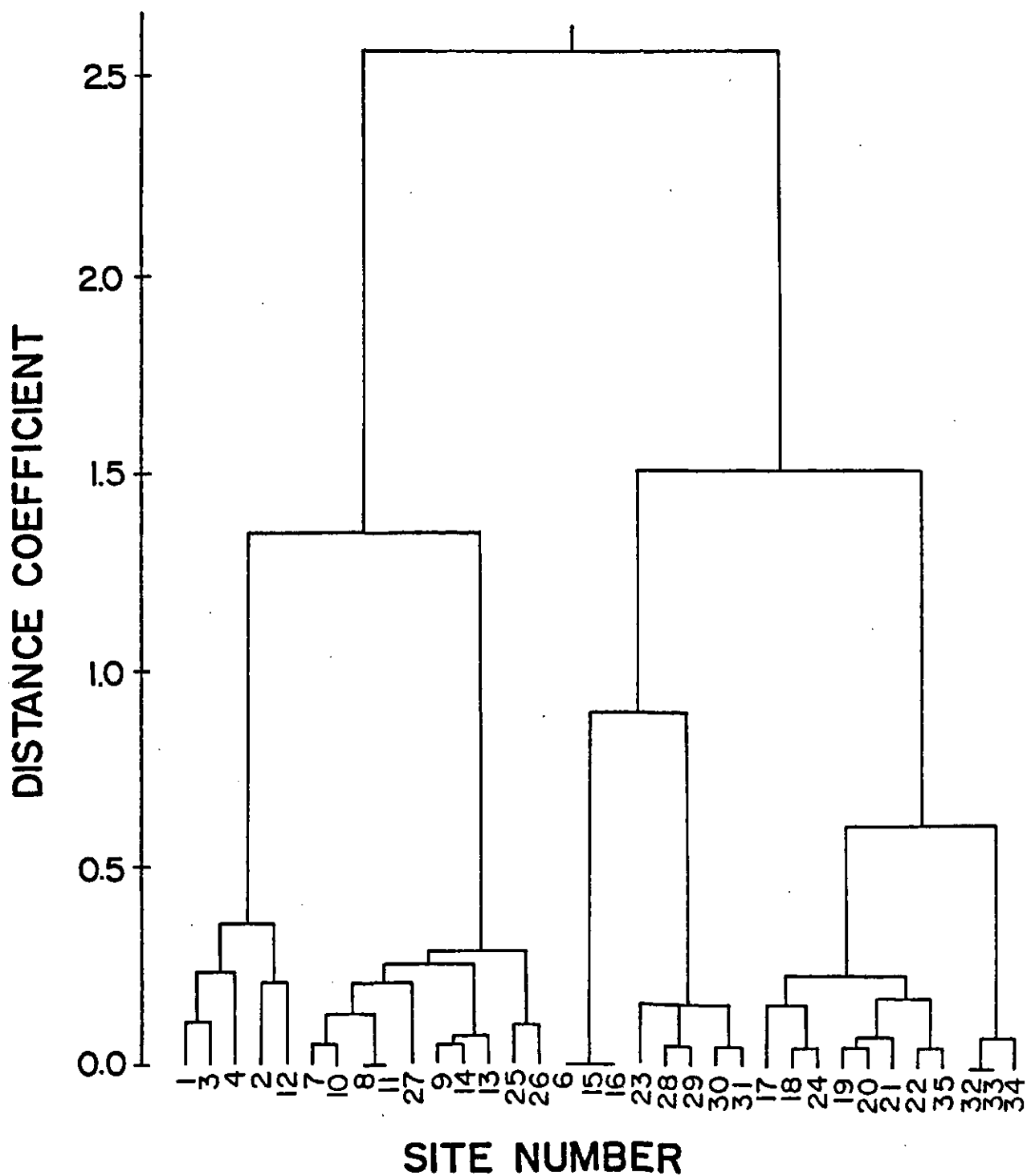


Figure 41. Classification of intensive study sites by annual presence/absence data.

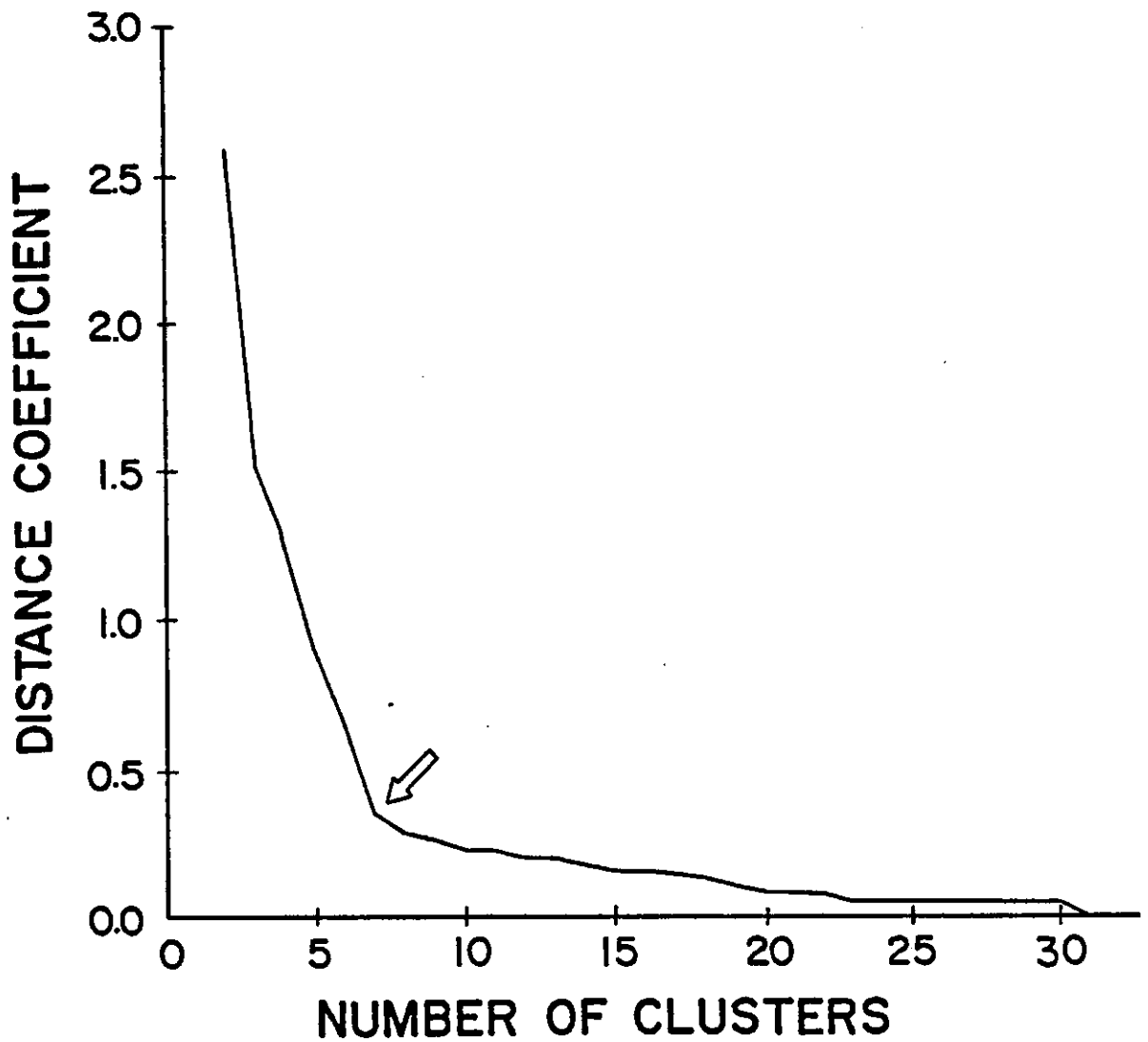


Figure 42. Relationship between distance between fusing clusters and number of clusters in the classification of intensive study sites by annual presence/absence data. Change in slope occurs at the 6 cluster level.

classification contains six groups of sites: 1) South Saskatchewan River sites upstream from Lake Diefenbaker (sites 1-4) and site 12 on the North Saskatchewan River, 2) other Saskatchewan River sites, excluding sites 6, 15 and 16, but including boreal sites 25-27, 3) Saskatchewan River sites just downstream from dams (sites 6, 15 and 16), 4) high gradient boreal sites, excluding site 27, 5) sites 32, 33 and 34, and 6) other boreal stream sites. These six groups are loosely combined into two larger clusters, containing the first two and last four groups, respectively. However, the two larger clusters are too heterogenous to be considered faunal zones.

The two Saskatchewan River groups differ in the presence or absence of Heptagenia adequata, H. flavescens, Macdunnoa nipawinia, Raptoheptagenia cruentata and Rhithrogena undulata. These species, except H. adequata, are rare. Hence their importance in defining faunal areas is greater, and the two Saskatchewan River groups are less similar, than in classifications of quantitative data. The association of site 12 with the four sites upstream from Lake Diefenbaker is likely due to the common occurrence of H. flavescens, M. nipawinia and R. cruentata at site 12 and one or more of the other four sites.

Site 27 is classified with Saskatchewan River instead of high gradient boreal sites. Three Saskatchewan River species (Heptagenia diabasias, H. elegantula and Stenonema terminatum) occur at site 27. However, these species are quite rare at site 27, and affect its classification only in the analysis

of presence/absence data.

The remaining sites are divided into four groups. Two of these, Saskatchewan River sites just downstream from dams and high gradient boreal sites, are similar to subgroups present in quantitative data classifications. However, the other two boreal groups are very different from those in quantitative data classifications; the only apparent difference between these two groups is the presence or absence of one rare species, Nixe inconspicua (which is present only at sites 32-34).

In general, differences between classifications based on presence/absence and quantitative data appear to be due to the greater importance of rare species in presence/absence data analysis. This causes greater heterogeneity among small groups of sites (which are subgroups in quantitative data analyses), and within the larger groups formed by their fusion. It also results in a different subdivision of boreal sites, and a different classification of some sites with several rare species. Otherwise, classifications based on presence/absence and quantitative data are quite similar.

As in quantitative data analyses, the first two ordination axes have much higher eigenvalues than subsequent axes (Table 5), and thus describe most of the variation in presence/absence data. Distribution patterns indicated by the first and second ordination axes (Figures 43 and 44) are similar to those indicated by the corresponding quantitative data axes, except that:

- 1) three distinct groups of Saskatchewan River sites are

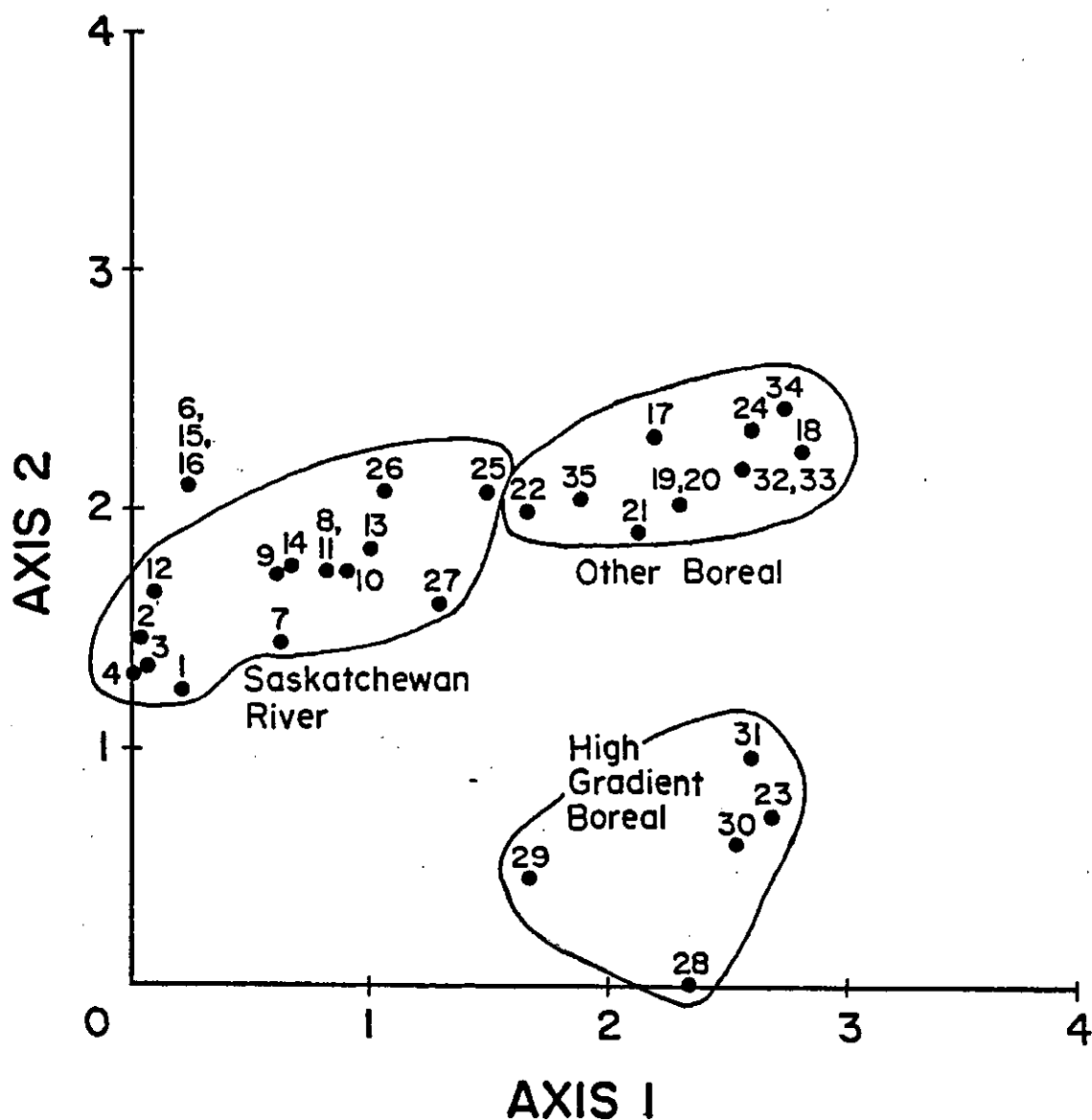
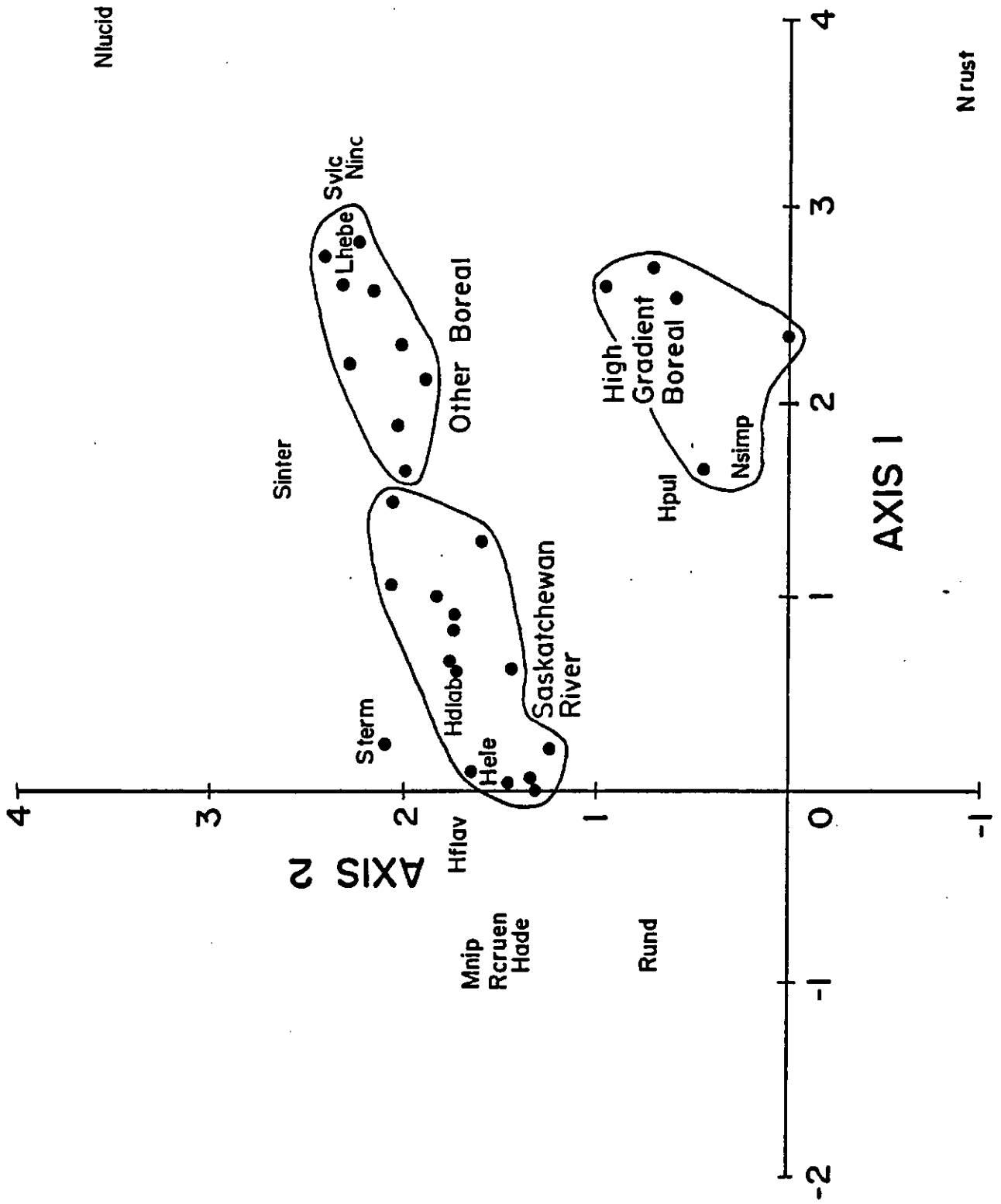


Figure 43. DCA ordination of annual presence/absence data: site scores on axes 1 and 2. Symbols and labels are explained in Figure 30.



Figure 44. DCA ordination of annual presence/absence data: species scores on axes 1 and 2.

Symbols and labels are explained in Figure 31.



present (sites 1-4 upstream from Lake Diefenbaker and site 12, the three sites just downstream from dams, and the remaining seven sites). Differences among these groups of sites are probably due to differences in rare species, which are more important in qualitative than quantitative data analyses;

2) site 27 is more similar to Saskatchewan River sites than high gradient boreal sites, probably due to the occurrence of three Saskatchewan River species at site 27;

3) site 12 is more similar to the four sites upstream from Lake Diefenbaker, probably because of the common occurrence of several rare species (Heptagenia flavescens, Macdunnoa nipawinia and Raptoheptagenia cruentata) at site 12 and one or more of the sites upstream from Lake Diefenbaker. The similarity among these sites was also apparent in cluster analysis of presence/absence data;

4) high gradient boreal sites, except sites 27 and 29, lie nearer the boreal end of the first axis. The only Nixe species collected at sites 27 and 29 was N. simplicoides, which was also found at Saskatchewan River sites 1-4. Thus sites 27 and 29 appear more similar to Saskatchewan River sites and lie near the center of the axis. N. rusticalis is present at all other high gradient sites, so that they are more different from Saskatchewan River sites and lie nearer the boreal end of the axis. N. rusticalis also lies nearer the boreal end of the first axis than in quantitative data ordinations; and

5) sites 17, 18, 24 and 34, and Nixe inconspicua and N.

lucidipennis, all lie at the extreme other boreal end of the second axis. This may be due to the greater importance of the relatively uncommon Nixe species in presence/absence data analysis, and to the absence of quantitative information about Stenacron interpunctatum (which was important in defining faunal patterns in quantitative data analyses).

The third and fourth presence/absence data ordination axes have very low eigenvalues. On both axes (Figure 45), the range of species scores is much greater than the range of site scores, and one or two species have very extreme scores. This suggests that these axes are related primarily to the distributions of one or two species, rather than to general distribution patterns. The third and fourth presence/absence data axes are different from all quantitative data axes.

Ordination and cluster analysis of presence/absence data indicate similar distribution patterns. However, in ordinations the subdivision of other boreal sites is not evident (so that there are five groups instead of six), sites 25-27 are intermediate between the Saskatchewan River and boreal groups (instead of members of the Saskatchewan River group), and sites 6, 15 and 16 are more similar to other Saskatchewan River sites than to boreal sites.

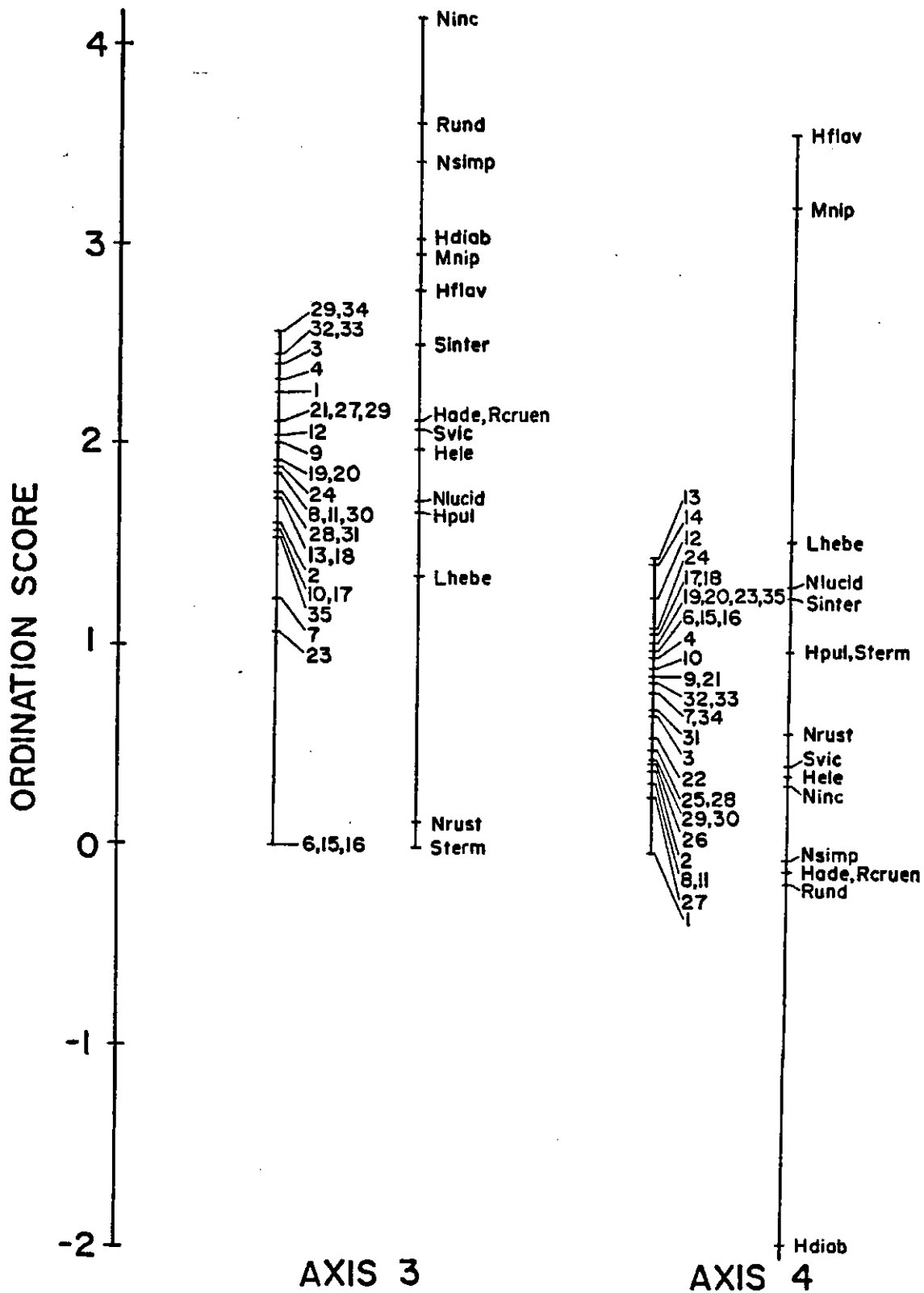


Figure 45. DCA ordination of annual presence/absence data: site and species scores on axes 3 and 4. Lines and labels are explained in Figure 34.

### 4.3 Intensive Study: Seasonal Variation in Distribution Patterns

Effects of seasonal changes in the heptageniid fauna on distribution patterns were examined by analyzing samples (site-times) x species data matrices. Elements in these data matrices are species abundances (or occurrences) at each site at each sampling time rather than mean annual abundances. The importance of seasonal variation can be assessed by comparing the results of these analyses with those obtained by analysis of annual data.

#### 4.3.1 Cluster analysis of seasonal data

##### 4.3.1.1 Analysis of seasonal sweep net data

Two large groups and eleven subgroups are present in the classification of seasonal sweep net data (Figures 46 and 47, Table 6). Group I contains most Saskatchewan River samples, and one sample each from boreal sites 22 and 25. It is relatively homogenous. Group II, which is somewhat less homogenous, contains nearly all boreal stream samples, all samples in which there were no heptageniids, and a few Saskatchewan River samples. Saskatchewan River samples included in Group II are all early or late season samples from sites 10, 11, 13 and 14 (the two downstream-most sites on the South Saskatchewan River, and the two sites upstream from Tobin Lake on the Saskatchewan River). Either Stenacron interpunctatum or Heptagenia pulla is the most abundant heptageniid species in these samples.

The first dichotomy within the boreal group (Group II)

Figure 46. Classification of intensive study sweep net samples by seasonal species abundances. The dendrogram is truncated at the 18 cluster level. Subgroups present at the 11 cluster level are labelled along the base of the dendrogram. Numbers in parentheses are the numbers of samples in each subgroup. The samples included in each subgroup are listed in Table 6.

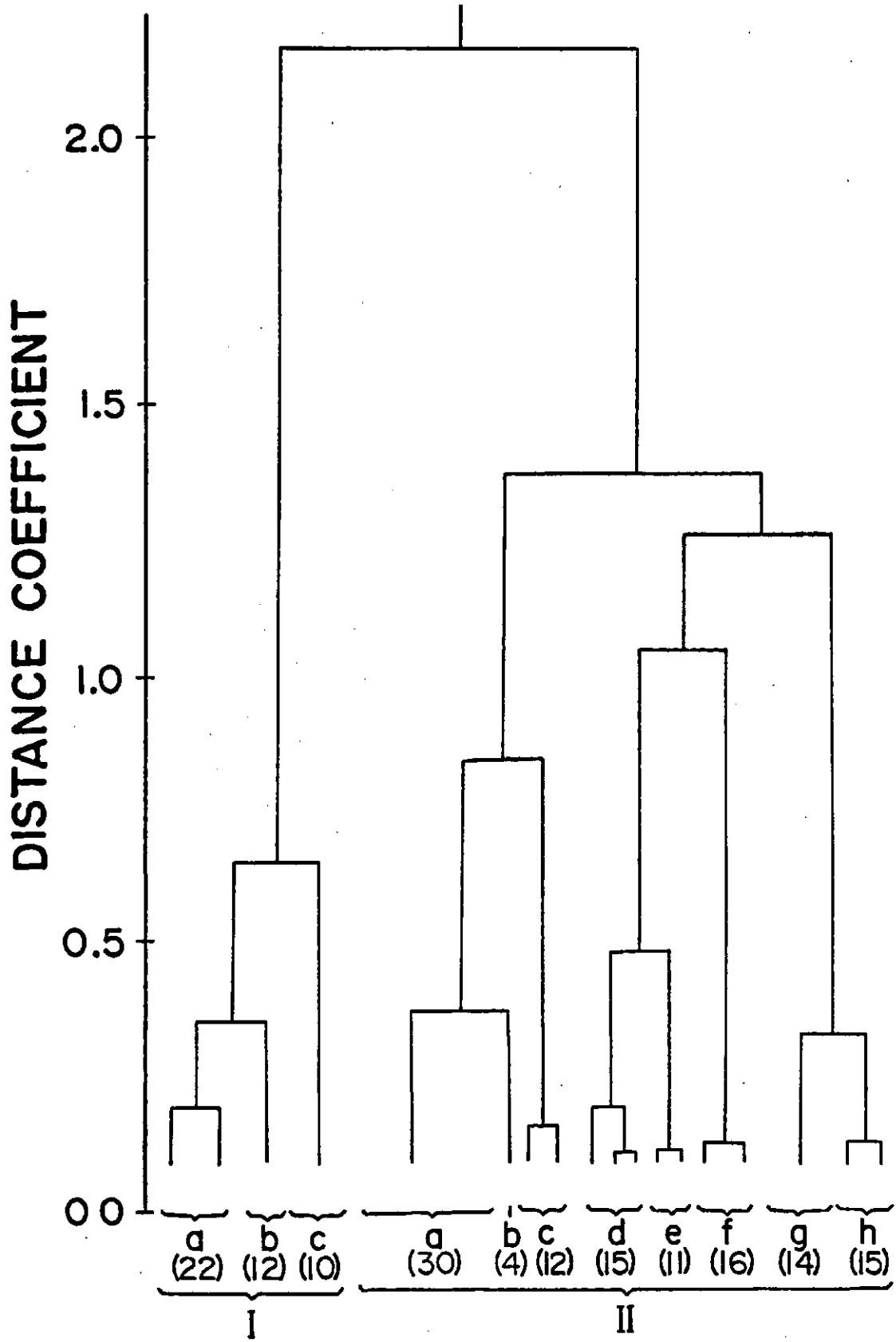




Figure 47. Relationship between distance between fusing clusters and number of clusters in the classification of seasonal sweep net samples. Large changes in slope occur at the 2 and 11 cluster levels. The plot is truncated at the 30 cluster level, where the slope is near zero.

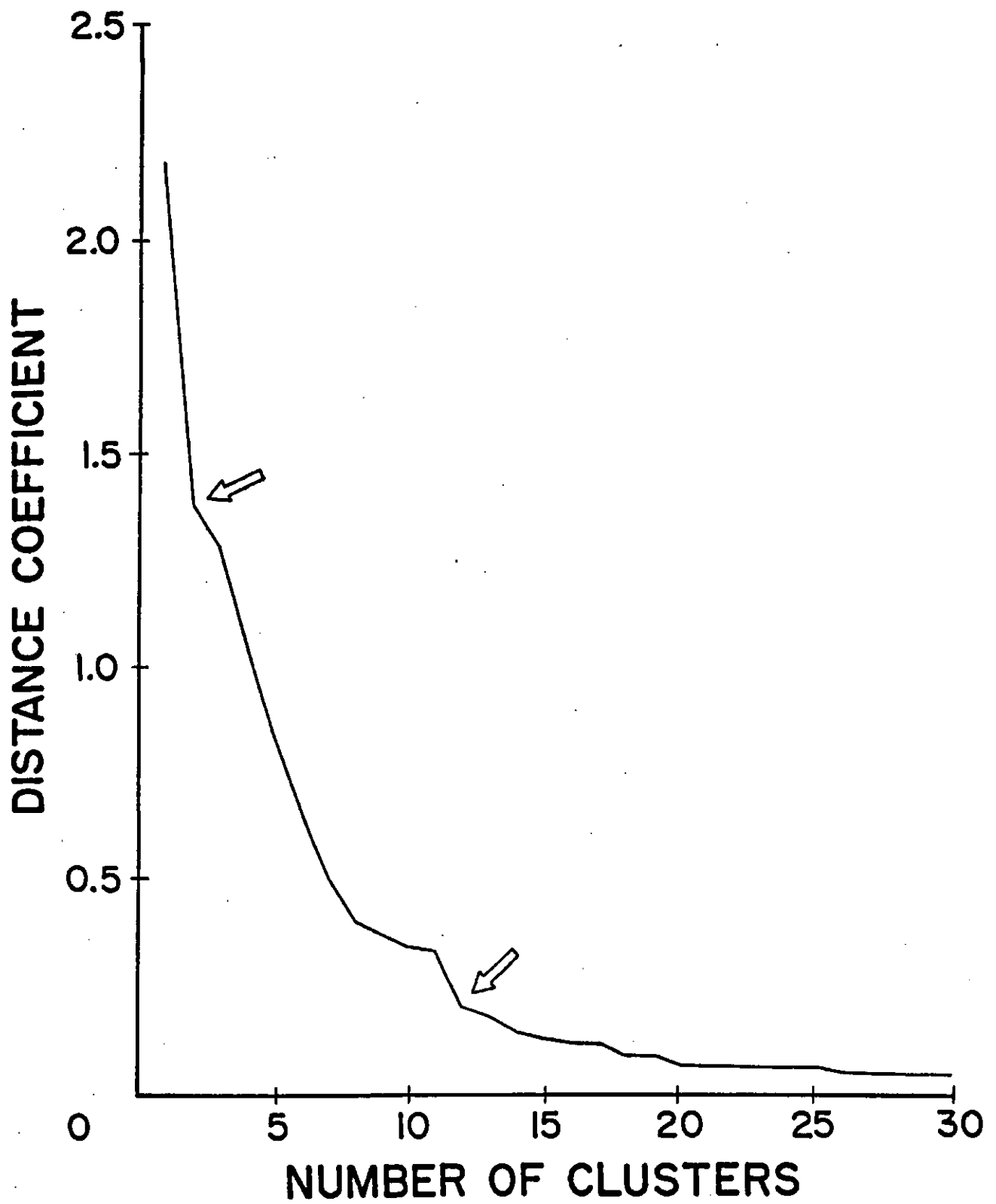


Table 6. Samples included in each subgroup in the classification of seasonal sweep net data. Sample names are in the form a-b, where a and b are the numbers of the site and time, respectively, at which the sample was collected (1 - April; 2 - May; 3 - early June; 4 - late June; 5 - July; 6 - August; 7 - September; 8 - October).

<u>Subgroup #</u>	<u>Samples Included</u>
Ia	1-3, 1-5, 1-6, 2-3, 3-3, 3-5 to 3-8, 4-3, 4-5, 4-7, 8-3, 8-5, 9-4, 9-7, 9-8, 12-3, 12-4, 12-6 to 12-8.
Ib	1-7, 1-8, 7-7, 8-7, 8-8, 9-3, 10-3, 10-4, 10-8, 16-8, 22-7, 25-3.
Ic	7-5, 8-4, 9-5, 10-5, 11-4, 11-5, 12-5, 13-4, 13-5, 14-4.
IIa	2-5, 5-3 to 5-8, 6-3 to 6-8, 7-6, 7-8, 15-4 to 15-8, 16-4, 16-6, 20-3 to 20-5, 21-3, 23-3, 23-8, 26-5, 28-7, 29-6, 29-8, 35-3.
IIb	23-4 to 23-7.
IIc	27-4, 27-5, 28-3, 28-4, 29-3, 29-4, 29-7, 30-3 to 30-5.
IId	10-7, 11-3, 11-7, 11-8, 13-7, 13-8, 14-6, 14-8, 20-8, 25-7, 25-8, 26-3, 35-6, 35-7.
IIe	17-3 to 17-5, 25-5, 32-3 to 32-5, 33-4, 33-5, 35-4, 35-5.
IIf	17-6 to 17-8, 19-6, 21-8, 22-8, 24-4, 24-8, 32-6 to 32-8, 33-3, 33-6 to 33-8, 35-8.
IIg	18-3 to 18-8, 19-3, 19-7, 19-8, 24-3, 24-6, 24-7, 31-7, 31-8.
IIh	19-4, 19-5, 22-3, 22-4, 24-5, 27-6 to 27-8, 25-5, 25-8, 29-5, 30-6 to 30-8, 31-6.

divides it into two heterogenous clusters, one containing June and July samples from high gradient boreal streams and all samples with no heptageniids (Subgroups IIa-IIc), and the other containing all other boreal samples, and Saskatchewan River samples dominated by Stenacron interpunctatum or Heptagenia pulla (Subgroups IId-IIh).

Up to this point, the classification is similar to that of annual sweep net data, except that: 1) some Saskatchewan River samples, and nearly all samples from sites 25 and 26, are in the boreal group (II), and 2) August, September and October samples from high gradient sites are classified with samples from other boreal sites. The association of late season high gradient samples with those from other boreal sites is probably due to the absence of two diagnostic high gradient species (Nixe rusticalis and N. simplicoides) in late season samples.

The remainder of the classification, and the associated subgroup structure, are very different from classifications of annual data. Only three of the eleven subgroups resemble those in annual data classifications: 1) subgroup Ia, which contains nearly all samples from the four South Saskatchewan River sites upstream from Lake Diefenbaker, in addition to some samples from other Saskatchewan River sites (8, 9 and 12), 2) subgroup IIa, which contains all samples in which there were no heptageniids, and 3) subgroup IIc, which contains all June and July samples from high gradient boreal sites. The compositions of the other eight subgroups are very different from those in any previous analysis and cannot be

meaningfully interpreted.

#### 4.3.1.2 Analysis of seasonal stone data

The classification of seasonal stone data is similar to that of annual stone data (Figure 48 and Table 7). As in the classification of annual data, three large groups are present (Figure 49): 1) Group I - all Saskatchewan River samples, and all samples from site 25, 2) Group II - high gradient boreal samples, and 3) Group III - other boreal samples. The latter two groups are more similar to one another than either is to the Saskatchewan River group. The site compositions of the three large groups are the same as in the classification of annual stone data, except that samples containing no heptageniids, and the July sample from site 27 (which contained only Heptagenia elegantula and H. pulla) are classified in the Saskatchewan River group (I) instead of the high gradient boreal group (II).

Subgroup structure in this classification is also similar to that in analysis of annual stone data, except that there are twelve subgroups instead of eight. The additional four subgroups are all equivalent to subdivisions of subgroups present in the annual data classification.

The Saskatchewan River group contains six subgroups: 1) Ia - all samples from sites upstream from Lake Diefenbaker, except July samples from sites 1 and 3. These sites, which are characterized by the presence of Heptagenia adequata and several rare heptageniids, also form a distinct subgroup in most annual data classifications. 2) Ib - some

Figure 48. Classification of intensive study stone samples by seasonal species abundances. The dendrogram is truncated at the 14 cluster level. Subgroups present at the 12 cluster level are labelled along the base of the dendrogram. Numbers in parentheses are the numbers of samples in each subgroup. The samples included in each subgroup are listed in Table 7.

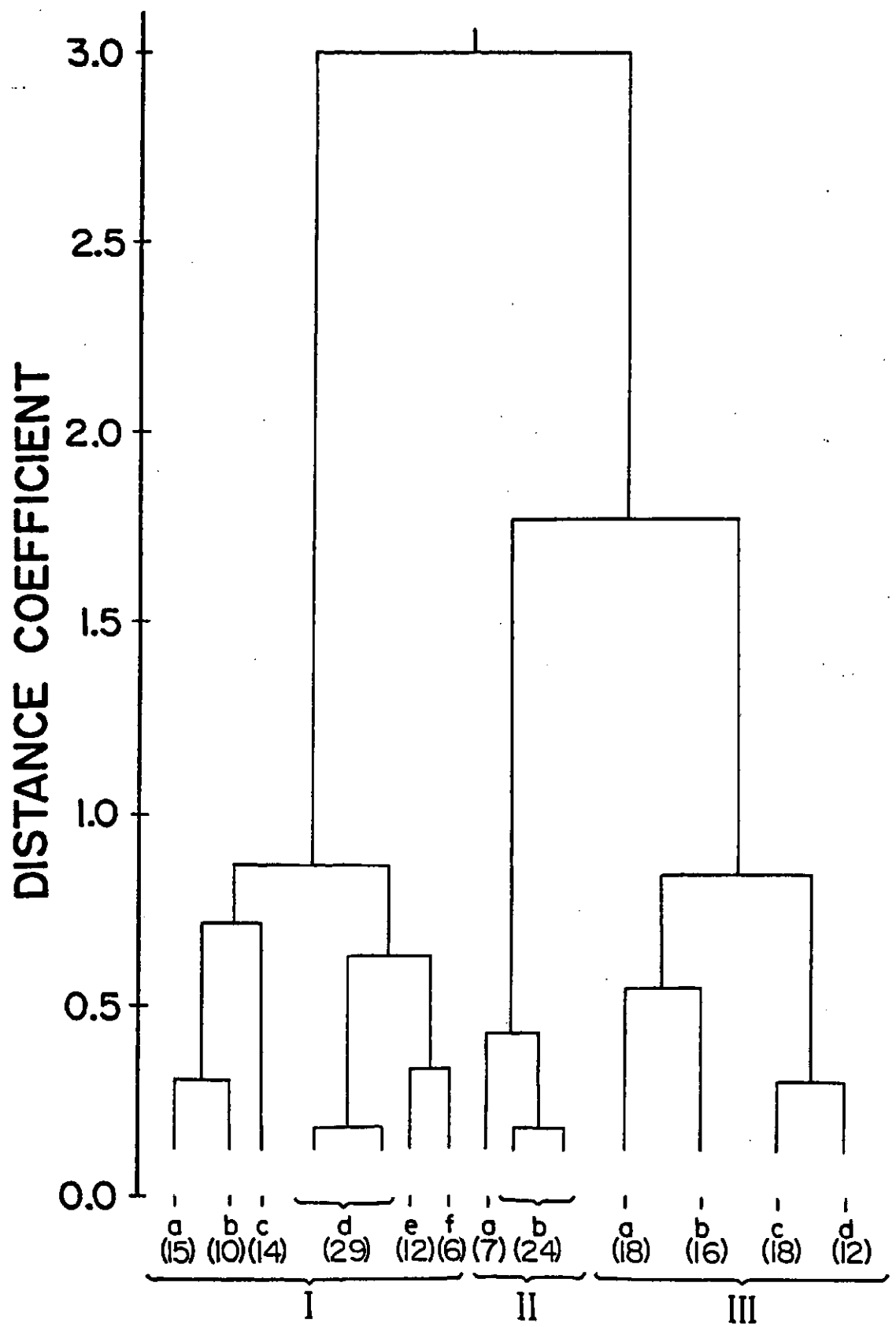


Table 7. Samples included in each subgroup in the classification of seasonal stone data. Sample names are in the form a-b, where a and b are the numbers of the site and time, respectively, at which the sample was collected (1 - April; 2 - May; 3 - early June; 4 - late June; 5 - July; 6 - August; 7 - September; 8 - October).

<u>Subgroup #</u>	<u>Samples Included</u>
Ia	1-3, 1-6 to 1-8, 2-3, 2-5 to 2-8, 3-6 to 3-8, 4-5 to 4-7.
Ib	7-3, 7-5, 8-3, 8-5, 9-5, 10-5, 12-3, 13-5, 14-4.
Ic	5-6, 5-7, 6-3, 6-8, 15-8, 16-4, 16-5, 16-8, 23-3, 23-8, 28-8, 29-3, 29-7, 29-8.
Id	1-5, 3-5, 9-3, 9-4, 9-6 to 9-8, 10-3, 10-4, 10-6 to 10-8, 11-3 to 11-8, 12-6 to 12-8, 13-3, 13-6 to 13-8, 14-3, 14-6, 14-7, 27-5.
Ie	6-5 to 6-7, 7-6 to 7-8, 8-6 to 8-8, 15-7, 16-6, 16-7.
If	25-3 to 25-8.
IIa	23-4 to 23-6, 28-4, 28-5, 30-4, 30-5.
IIb	23-7, 27-3, 27-4, 27-6 to 27-8, 28-3, 28-6, 28-7, 29-5, 29-6, 30-3, 30-6 to 30-8, 31-3 to 31-8.
IIIa	17-3 to 17-5, 20-4, 20-5, 32-3 to 32-5, 33-3 to 33-5, 34-3 to 34-5, 35-3 to 35-5.
IIIb	17-6 to 17-8, 20-3, 20-6 to 20-8, 32-6 to 32-8, 33-6 to 33-8, 35-6 to 35-8.
IIIc	18-4, 18-5, 19-3 to 19-5, 22-3 to 22-5, 24-3 to 24-5.
IIId	18-3, 18-6 to 18-8, 19-7, 19-8, 21-3 to 21-8, 22-6 to 22-8, 24-6 to 24-8.



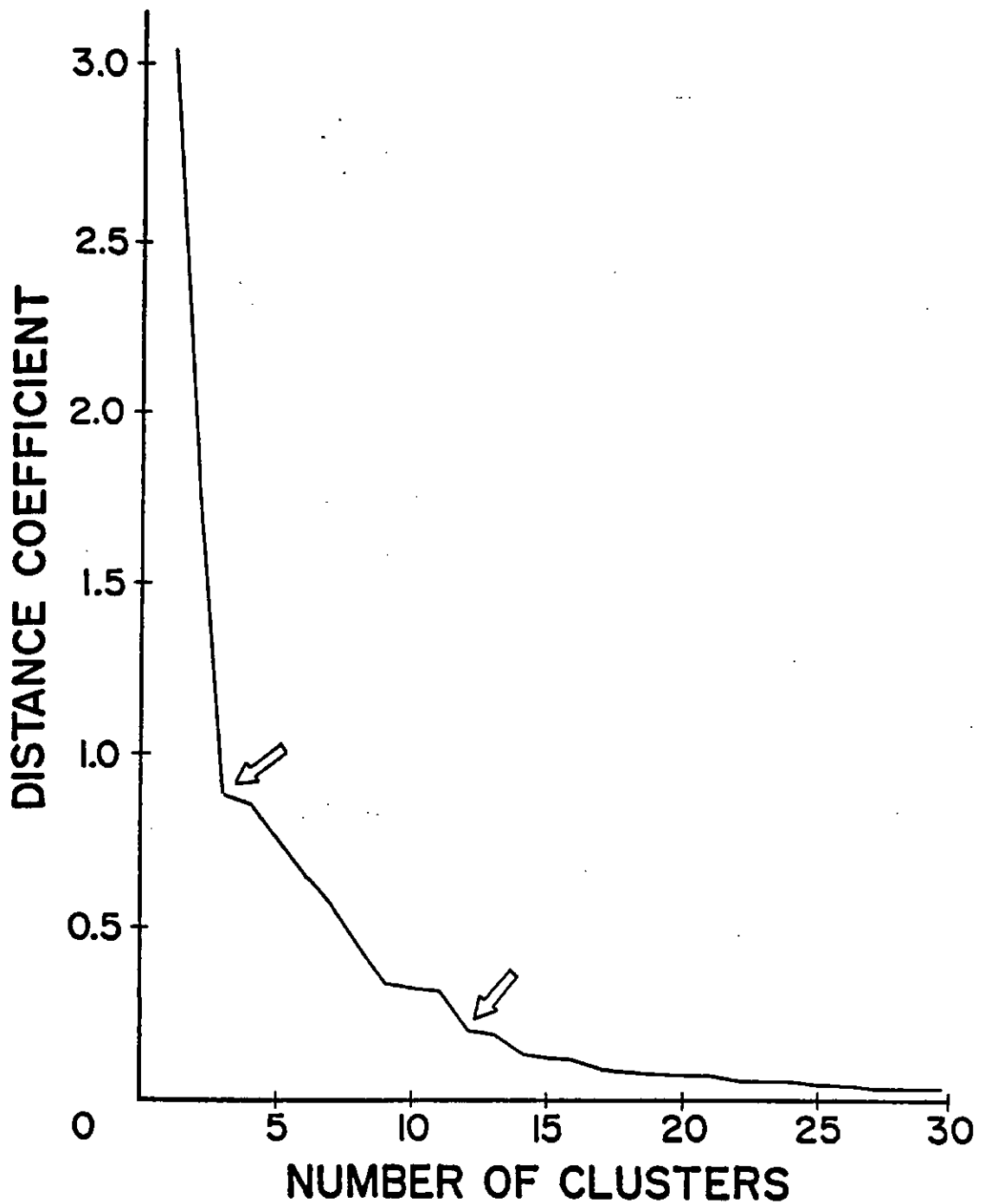


Figure 49. Relationship between distance between fusing clusters and number of clusters in the classification of seasonal stone samples. Large changes in slope occur at the 3 and 12 cluster levels. The plot is truncated at the 30 cluster level, where the slope is near zero.

June and July samples from sites 7 to 9, 10 and 12 to 14. H. elegantula is the most abundant heptageniid in these samples. 3) Ic - all samples in which no heptageniids were collected. 4) Id - July samples from sites 1 and 3, some June and July samples and all late-season (August to October) samples from sites 9 to 14, and the July sample from site 27. H. pulla and Stenonema terminatum are the most abundant heptageniids in these samples. 5) Ie - all samples (containing heptageniids) from the three sites just downstream from dams (sites 6, 15 and 16), and August to October samples from sites 7 and 8. S. terminatum is the most abundant, or only, heptageniid in these samples. 6) If - all samples from site 25 (the southern boreal stream that is classified with Saskatchewan River sites in annual data classifications). Both Saskatchewan River and boreal species were collected at this site.

Subgroups Ia and Ie are almost identical in site composition to Saskatchewan River subgroups present in the annual stone data classification (Figure 28, pg. 96). Subgroup Ic (containing samples with no heptageniids) also corresponds to a subgroup present in the annual data classification. However, in analysis of annual data, this subgroup was part of the boreal group, rather than the Saskatchewan River group. The other three Saskatchewan River subgroups are different from those in the classification of annual stone data.

Two subgroups of high gradient boreal samples are present: 1) IIa - all samples from site 23 (except those in which there were no heptageniids), and late June and July

samples from sites 28 and 30. This subgroup includes all samples containing Nixe rusticalis. 2) IIb - all other high gradient samples. Late season samples are classified with June and July samples (instead of with other boreal samples, as in the classification of seasonal sweep net data), even though the two diagnostic Nixe species are absent. This suggests an underlying similarity among high gradient sites beyond the common occurrence of N. rusticalis and N. simplicoides.

These two high gradient subgroups are similar to those in the classification of annual stone data, except that samples containing no heptageniids are not included, and some mid-summer samples from sites 28 and 30 are classified with samples from site 23.

Four subgroups of other boreal samples are present:

1) IIIa - June and July samples from large boreal stream sites 17, 20 and 32 to 35, 2) IIIb - August to October samples from these large boreal stream sites, and the early June sample from site 20, 3) IIIc - June and July samples from small boreal stream sites 18, 19, 22 and 24, and 4) IIId - August to October samples from small boreal stream sites, and all samples from site 21. Subgroups IIIa and IIIb are sister subgroups as are subgroups IIIc and IIId. Each pair of sister subgroups corresponds in site composition to one of the two boreal subgroups present in the classification of annual stone data. Each pair is subdivided into a mid-season and a late-season subgroup. June and July samples differ from late season samples because they contain larvae of species

with summer life cycles (Leucrocuta hebe and Nixe lucidipennis). Species with summer life cycles were never collected at site 21; therefore, all samples from site 21 are classified with late season samples from similar sites.

#### 4.3.1.3 Analysis of seasonal presence/absence data

Four large groups are present in the classification of seasonal presence/absence data (Figures 50 and 51, Table 8): 1) Group I - most samples from South Saskatchewan River sites upstream from Lake Diefenbaker, and some samples from site 12 on the North Saskatchewan River, 2) Group II - all other Saskatchewan River samples (except those with no heptageniids), all samples from sites 25 and 26, and one late season sample each from sites 27 and 35, 3) Group III - most high gradient boreal samples, and all samples in which there were no heptageniids, and 4) Group IV - all other boreal stream samples, and some late season samples from sites 27, 30 and 31. No distinct subgroup structure is present in this classification.

This classification is quite similar to that of annual presence/absence data, except that high gradient and low diversity samples are combined in a single group (Group III), as are all other boreal stream samples (Group IV). Thus, no important seasonal variation is evident in classification of presence/absence data.

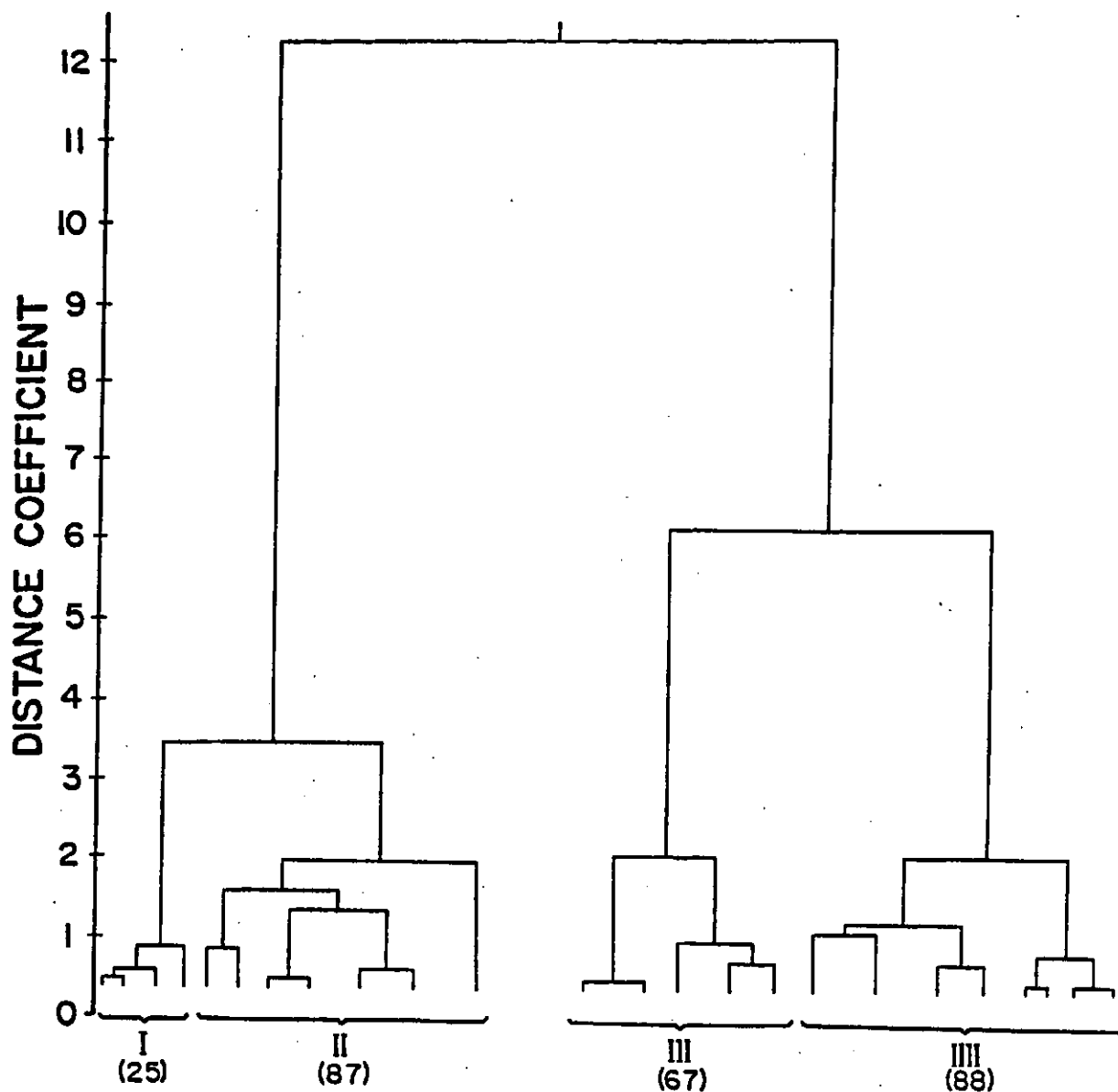


Figure 50. Classification of intensive study samples by seasonal presence/absence data. The dendrogram is truncated at the 24 cluster level. Groups present at the four cluster level are labelled along the base of the dendrogram. Numbers in parentheses are the numbers of samples in each group. The samples included in each group are listed in Table 8.

Figure 51. Relationship between distance between fusing clusters and number of clusters in the classification of seasonal presence/absence data. A large change in slope occurs at the four cluster level. The plot is truncated at the 50 cluster level, where the slope is near zero.

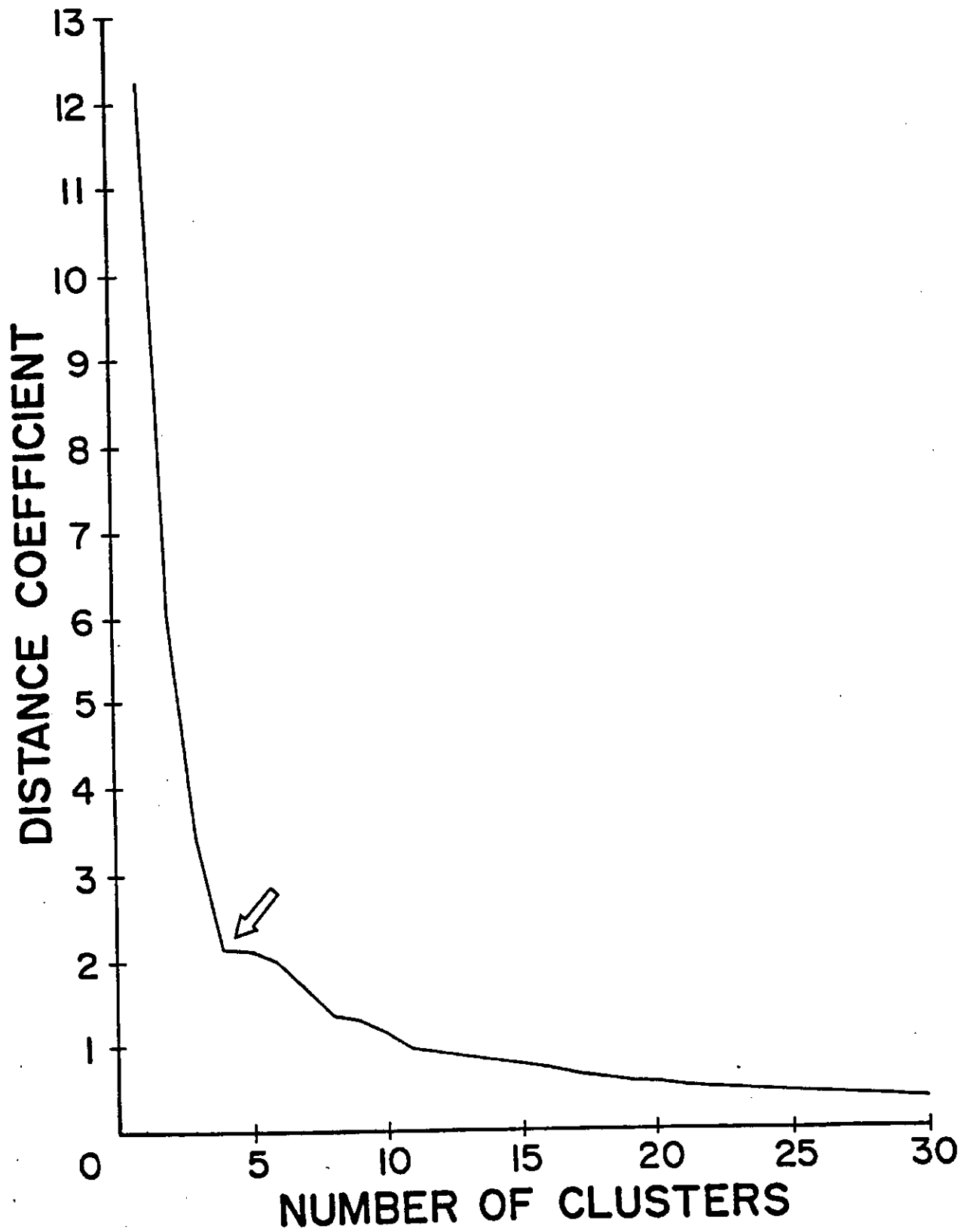


Table 8. Samples included in each group in the classification of seasonal presence/absence data. Sample names are in the form a-b, where a and b are the numbers of the site and time, respectively, at which the sample was collected

(1 - April; 2 - May; 3 - early June; 4 - late June; 5 - July; 6 - August; 7 - September; 8 - October).

<u>Group #</u>	<u>Samples Included</u>
I	1-2, 1-3, 1-5, 1-7, 1-8, 2-1 to 2-3, 2-5, 2-7, 2-8, 3-1 to 3-2, 3-5, 3-8, 4-1 to 4-3, 4-5 to 4-7, 12-3, 12-4, 12-7.
II	1-6, 2-6, 3-6, 3-7, 6-1, 6-2, 6-5 to 6-7, 7-1 to 7-3, 7-5 to 7-8, 8-1 to 8-8, 9-1 to 9-8, 10-1 to 10-8, 11-1 to 11-8, 12-2, 12-5, 12-6, 12-8, 13-2 to 13-8, 14-1 to 14-4, 14-6 to 14-8, 15-7, 16-6 to 16-8, 25-1 to 25-8, 26-1 to 26-8, 27-7, 35-6.
III	5-1 to 5-3, 5-4 to 5-8, 6-3, 6-8, 15-2, 15-4 to 15-6, 15-8, 16-1 to 16-5, 23-1 to 23-8, 27-1, 27-3 to 27-6, 27-8, 28-1 to 28-8, 29-1 to 29-8, 30-1 to 30-6, 30-8, 31-3 to 31-5.
IV	17-1 to 17-8, 18-1 to 18-8, 19-1 to 19-8, 20-1 to 20-8, 21-1 to 21-8, 22-1 to 22-8, 24-2 to 24-8, 27-2, 30-7, 31-6 to 31-8, 32-1 to 32-8, 33-1 to 33-8, 34-2 to 34-6, 35-1 to 35-4, 35-6 to 35-8.

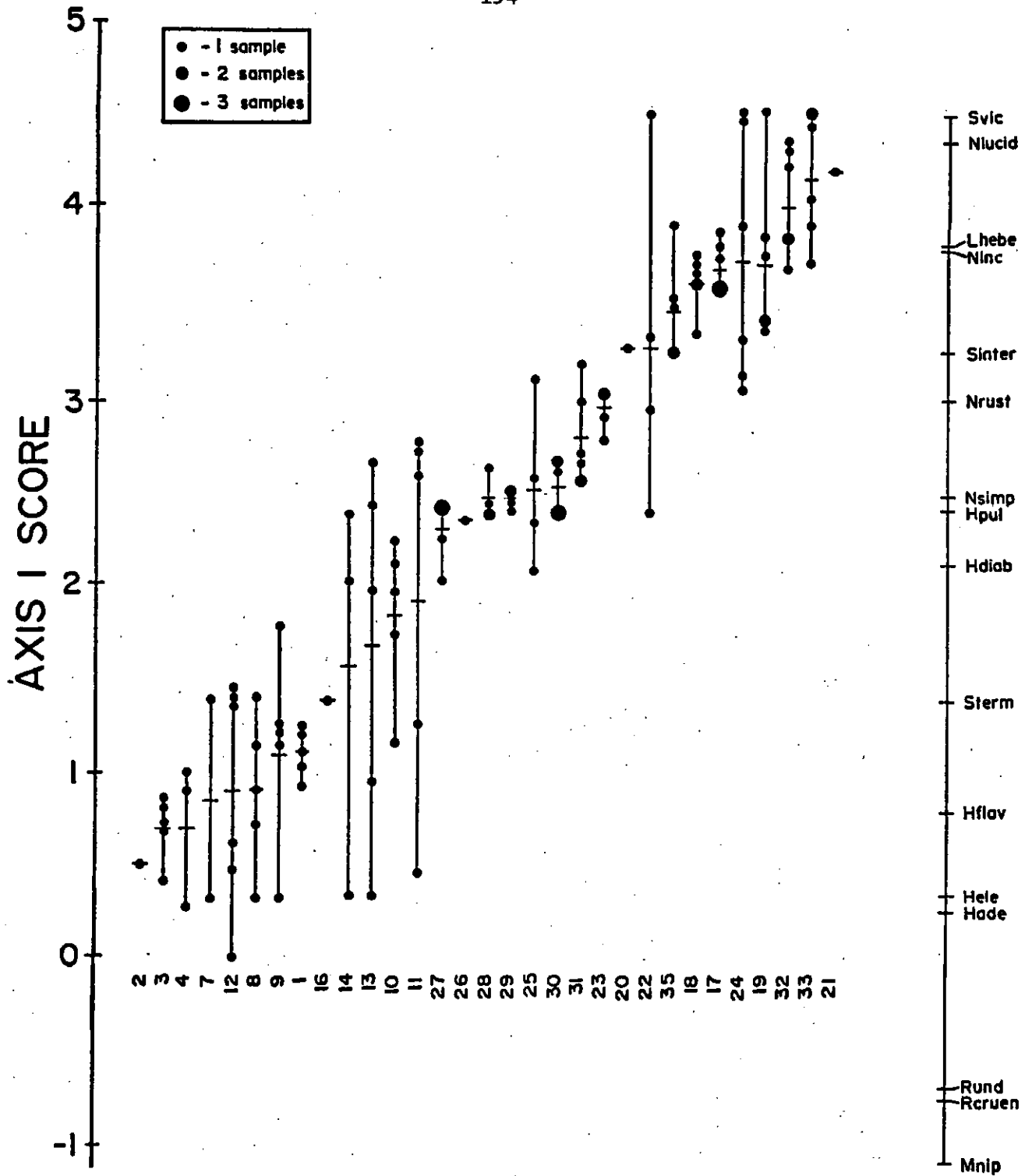


#### 4.3.2 Ordination of seasonal data

##### 4.3.2.1 Analysis of seasonal sweep net data

The major community gradients in the ordination of seasonal sweep net data are similar to those in the ordination of annual sweep net data. As in the annual data ordination, the first axis shows a community gradient extending from South Saskatchewan River sites upstream from Lake Diefenbaker, through other Saskatchewan River and high gradient boreal sites to other boreal sites (Figure 52). For most sites, samples from different sampling times have similar ordination scores. The greatest seasonal variation in ordination scores occurs at Saskatchewan River sites 9, 11, 13 and 14. The pattern of seasonal variation is similar at these and many other Saskatchewan River sites: June and July samples have relatively low scores; late season samples have higher scores which are more similar to those of boreal samples. First axis sample scores also vary seasonally at some boreal sites, especially sites 19, 22 and 24. However, the pattern of seasonal variation is different at each of these sites. Except for a few late season samples from sites 11, 13 and 14, there is no overlap in ordination scores between Saskatchewan River and other boreal samples; the two groups are clearly separated on the first axis. Samples from site 25 (which was intermediate between Saskatchewan River and boreal sites in annual data ordinations) and from high gradient boreal streams have intermediate scores that overlap with both the highest Saskatchewan River and the lowest other boreal sample scores.

Figure 52. DCA ordination of seasonal sweep net data: first axis sample and species scores. The vector of sample scores has been split into segments, with one segment for each site. The individual points on each segment represent the scores for each sample collected at that site (at different sampling times during the year). Larger dots represent two or more samples from one site which have the same first axis score. Horizontal lines represent the mean sample score for each site. Sites are arranged in order of increasing mean sample scores. Species names given are abbreviations incorporating the first letter of the genus name (upper case) and the first three to five letters of the species name (lower case).



First axis species scores are also similar to those in the ordination of annual sweep net data. The similar ranges of species scores (Table 9) indicate similar amounts of species turnover.

The second seasonal sweep net axis (Figure 53) is also similar to the corresponding annual data axis (Figure 30, pg. 101). High gradient stream samples lie in one half of the axis; other boreal and Saskatchewan River samples lie in the other. Seasonal variation in high gradient sample scores is great. June and July samples have very low scores; samples from August to October have higher scores that are more similar to those of other boreal samples. Seasonal variation among high gradient sample scores is probably due to seasonal changes in the abundances of Nixe rusticalis and N. simplicoides, which have summer life cycles.

The range of other boreal sample scores on the second axis is greater than in mean annual data analysis. Samples from sites 18, 19, 21, 22 and 24 have scores intermediate between those of high gradient and Saskatchewan River samples. Samples from these five boreal sites are similar to late season samples from high gradient sites in that Heptagenia pulla and Stenonema vicarium are the most abundant heptageniids present. Samples in which Stenacron interpunctatum is abundant, including most samples from sites 20, 25, 26 and 35, and a few samples from sites 11, 13 and 17, have the highest second axis scores. Seasonal variation in second axis scores is highest among samples from sites 11, 13 and 17, probably because of seasonal variation in the

Table 9. Ranges of site (or sample) and species scores (standard deviations of species turnover) on annual and seasonal DCA ordination axes. Four standard deviations correspond to a full turnover in species composition; 1 s.d. corresponds to a 50% change (Gauch 1982).

Range of Site or Sample Scores

<u>Data Set</u>	<u>Axis 1</u>	<u>Axis 2</u>	<u>Axis 3</u>	<u>Axis 4</u>
Annual Data				
Sweep Net	3.78	4.77	1.49	1.96
Stones	4.09	3.08	2.65	1.98
Presence/absence	2.81	2.42	2.55	1.46
Seasonal Data				
Sweep Net	4.58	4.70	3.12	2.57
Stones	4.74	4.16	2.47	2.99
Presence/absence	4.23	0.69	3.03	2.27

Range of Species Scores

<u>Data Set</u>	<u>Axis 1</u>	<u>Axis 2</u>	<u>Axis 3</u>	<u>Axis 4</u>
Annual Data				
Sweep Net	5.09	5.00	5.08	6.66
Stones	6.07	6.60	9.38	13.71
Presence/absence	4.65	4.48	4.14	5.51
Seasonal Data				
Sweep Net	5.66	6.40	4.14	4.13
Stones	5.90	5.41	5.26	4.17
Presence/absence	6.21	0.69	4.19	4.78

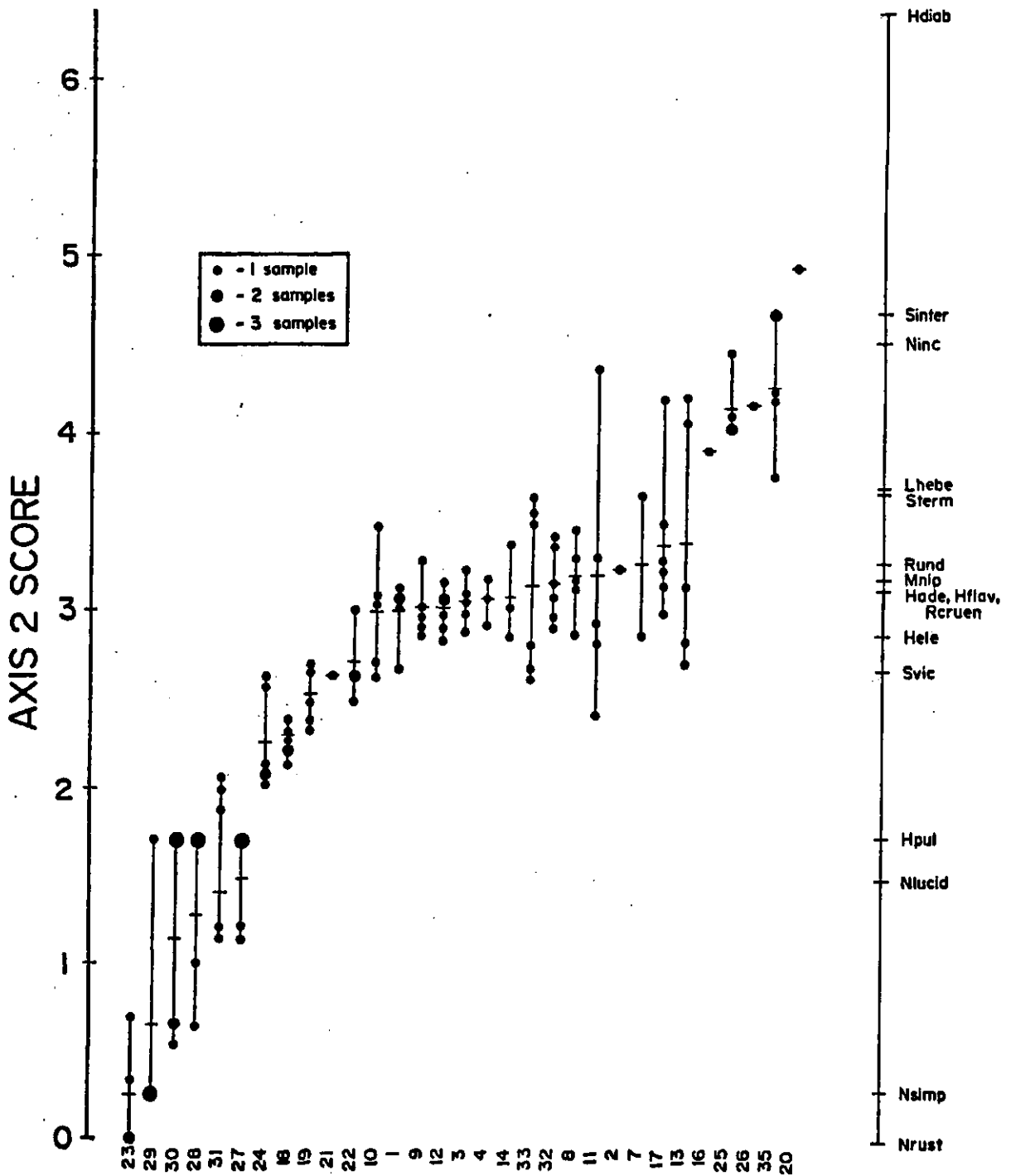


Figure 53. DCA ordination of seasonal sweep net data: second axis sample and species scores. Symbols and labels are explained in Figure 52.

abundance of S. interpunctatum at these sites.

Second axis species scores are also similar to those in the annual sweep net data ordination, except that Nixe lucidipennis and Stenonema vicarium lie near the center of the axis instead of near the other boreal end, and Heptagenia diabasias lies at the extreme other boreal end instead of near the center.

The range of second axis species scores is slightly greater in the ordination of seasonal data than in the ordination of annual data, indicating greater species turnover (Table 9). This is probably due to the importance of the two Nixe species on this axis. These species have summer life cycles and thus show seasonal as well as geographical variation, both of which are described by the seasonal second axis.

The third and fourth seasonal sweep net axes have relatively large eigenvalues (Table 10), unlike the corresponding annual data axes (Table 5, pg. 102). Most of the variation in ordination scores on these two axes is among sampling times (Figures 54 and 55); differences among sites are relatively small. Thus most of the variation described by the third and fourth axes is within-site seasonal variation, rather than geographical variation.

Figure 54. DCA ordination of seasonal sweep net data: third axis sample and species scores.

Symbols and labels are explained in Figure 52.



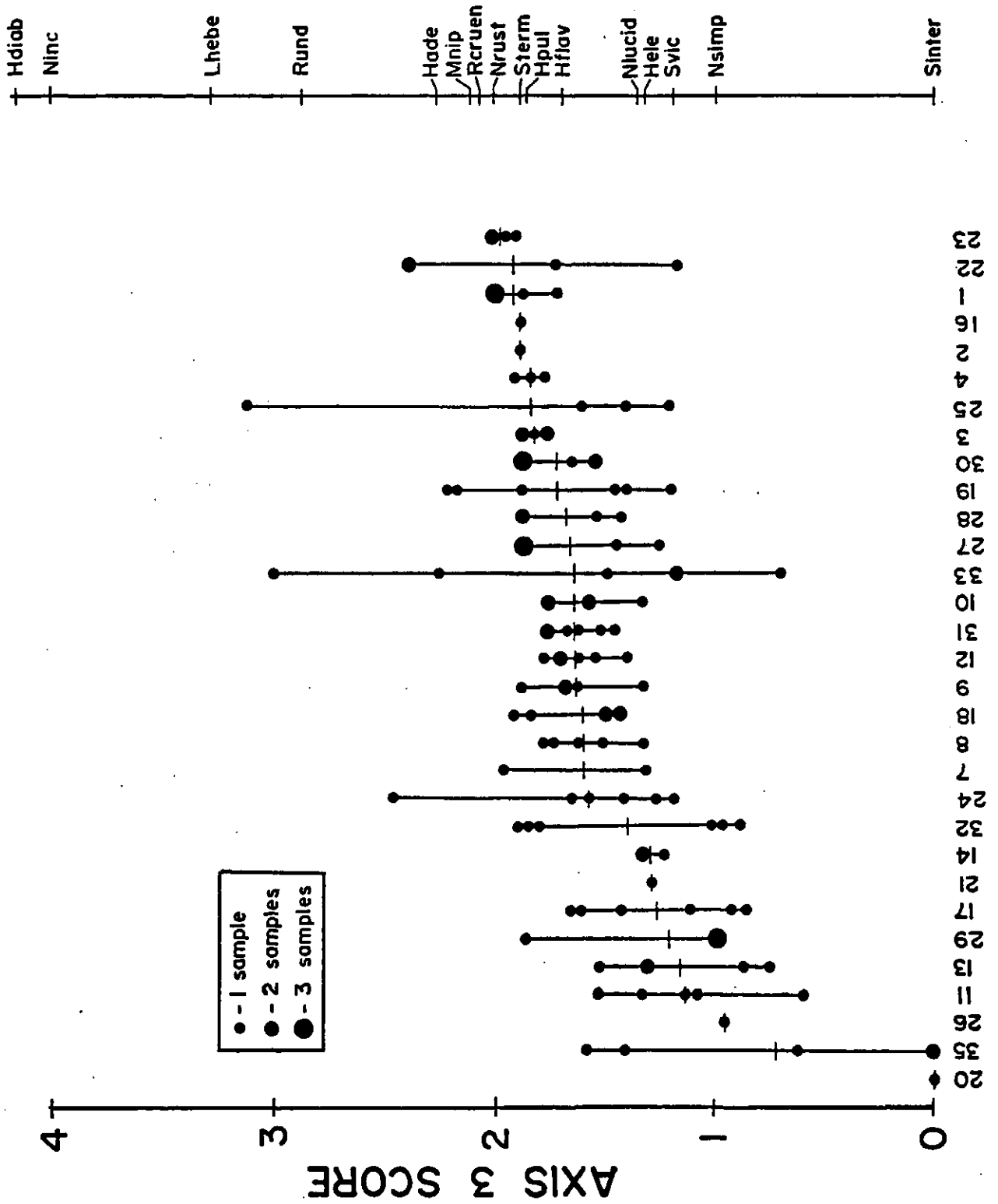


Figure 55. DCA ordination of seasonal sweep net data; fourth axis sample and species scores.

Symbols and labels are explained in Figure 52.

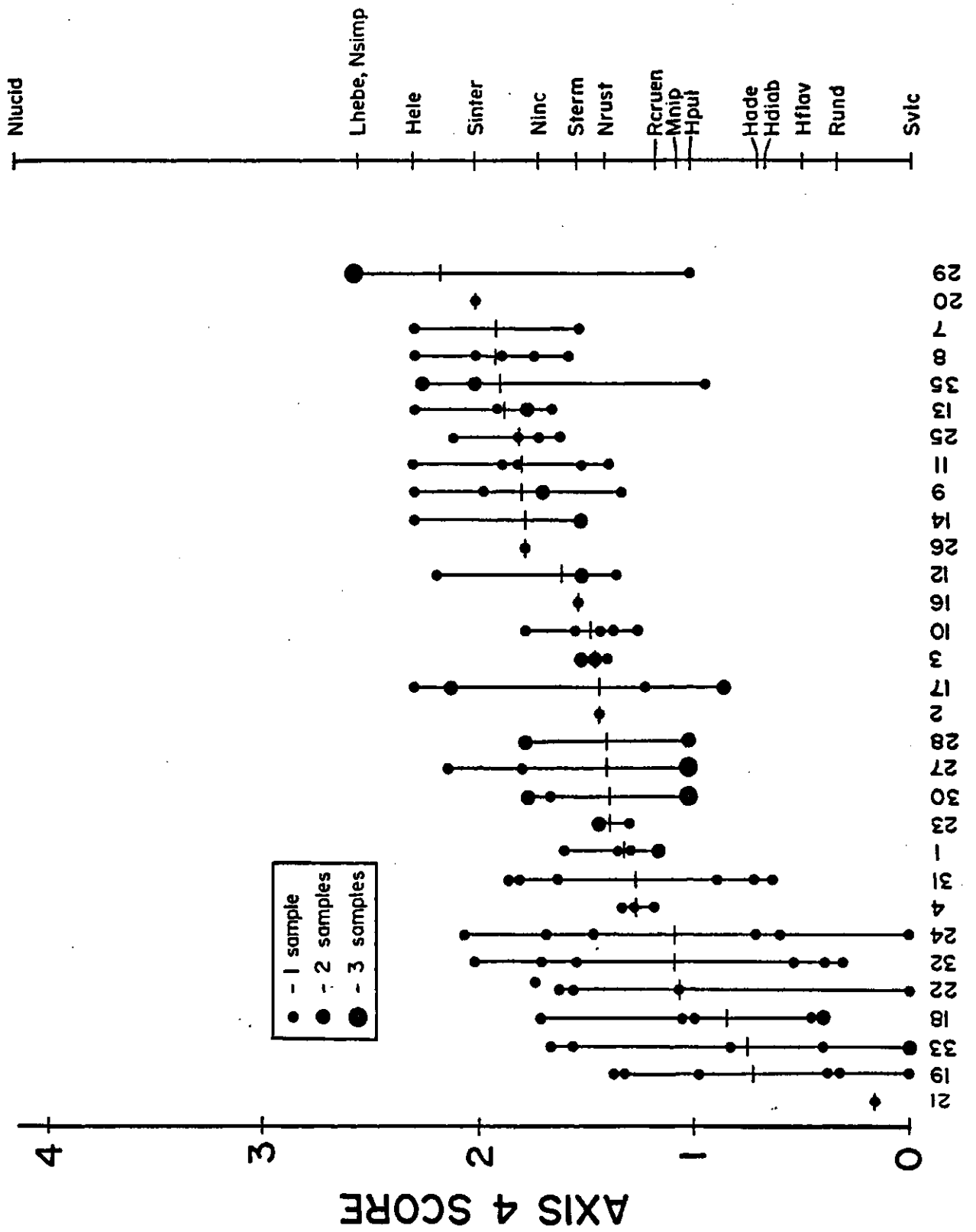


Table 10. Eigenvalues of the first four ordination axes from DCA of three seasonal data sets.

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<u>Data Set</u>	<u>Axis 1</u>	<u>Axis 2</u>	<u>Axis 3</u>	<u>Axis 4</u>
Sweep Net Sample	0.766	0.477	0.303	0.170
Stone Sample	0.650	0.473	0.222	0.128
Presence/Absence	0.618	0.470	0.227	0.143

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Variation described by the third axis is associated primarily with differences between June and July samples and late season samples at several boreal sites (especially sites 19, 22, 24, 25, 32, 33 and 35) (Figure 54). Heptagenia diabasia, Nixe inconspicua and/or Leucrocuta hebe are common at these sites in June and July; Stenacron interpunctatum is more abundant in August, September and October. These four species have the highest and lowest third axis species scores. There is little variation among Saskatchewan River samples on this axis.

On the fourth axis, June and July samples have higher scores than late season samples at nearly all sites (Figure 55). Stenonema vicarium and Nixe lucidipennis have the highest and lowest fourth axis species scores, respectively.

#### 4.3.2.2 Analysis of seasonal stone data

The ordination of seasonal stone data is similar to ordinations of seasonal sweep net data and annual quantitative data. The first axis (Figure 56) again shows a

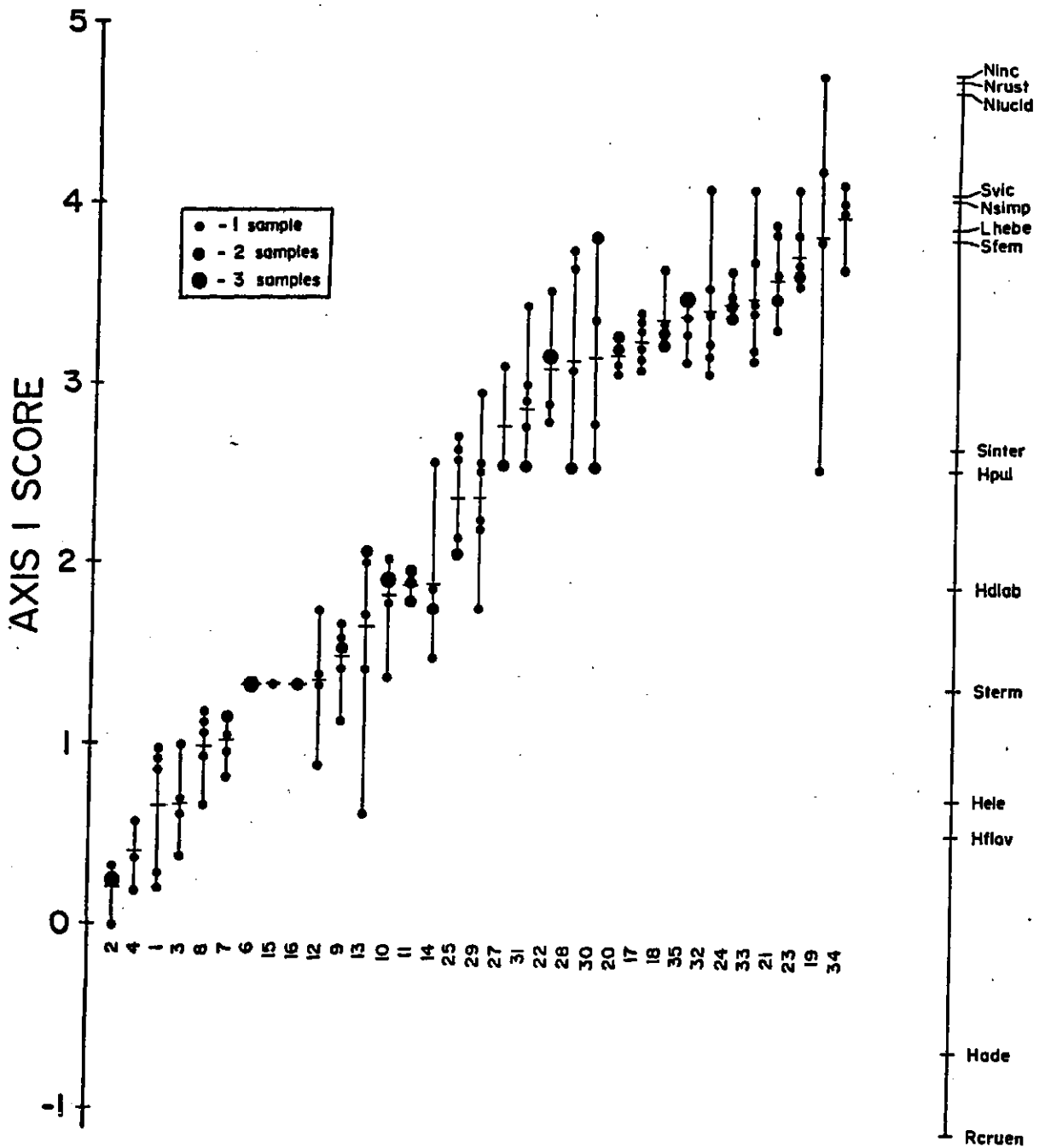


Figure 56. DCA ordination of seasonal stone data: First axis sample and species scores. Symbols and labels are explained in Figure 52.

community gradient extending from South Saskatchewan River sites upstream from Lake Diefenbaker through other Saskatchewan River and high gradient stream sites to other boreal stream sites. At most boreal and Saskatchewan River sites, except sites 12, 13 and 14, seasonal variation in sample scores is relatively small. At most Saskatchewan River sites, June and July samples have slightly lower scores than late season samples. Patterns of seasonal variation differ among boreal sites; however, at the two most variable boreal sites (19 and 24), seasonal variation is similar to that at most Saskatchewan River sites. All boreal samples (excluding high gradient stream samples) have higher ordination scores than any Saskatchewan River sample except the October sample from site 14.

Samples from site 25, and from high gradient streams other than site 23, are intermediate between Saskatchewan River and boreal samples. Seasonal variation among high gradient boreal samples is large, and June and July samples generally have higher scores than late season samples. Seasonal variation among high gradient samples is probably due to seasonal changes in the abundances of Nixe rusticalis and N. simplicoides which also have relatively high first axis scores. In ordinations of seasonal sweep net data and annual quantitative data, seasonal variation in first axis high gradient sample scores was low, and N. rusticalis and N. simplicoides had intermediate first axis scores.

The ranges of first axis sample and species scores are greater in the ordination of seasonal stone data than in the

ordination of annual stone data. As for the second seasonal sweep net axis, high species turnover is probably due to the high scores and summer life cycles of Nixe species.

The second seasonal stone axis (Figure 57) is similar to second axes in ordinations of other data sets. Samples from high gradient boreal streams, and Nixe rusticalis and N. simplicoides, lie at one end of the axis. Seasonal variation in ordination scores is high among high gradient samples, and is probably due to seasonal changes in the abundances of N. rusticalis and N. simplicoides.

Samples from other boreal sites (including site 25) lie at the opposite end of the second axis. Seasonal variation in ordination scores at these sites is quite small, except at sites 19, 20 and 24. Nixe inconspicua and N. lucidipennis, which have the highest species scores, are common at these three sites. In other ordinations (except the ordination of annual presence/absence data), Heptagenia diabasias, Stenacron interpunctatum and/or Stenonema vicarium have the highest second axis scores, and N. inconspicua and N. lucidipennis lie closer to the center of the axis. Separation of N. inconspicua and N. lucidipennis from N. rusticalis and N. simplicoides on the second seasonal stone axis may be related to their similarity on the first axis. In other ordinations, these four species were separated more on the first axis and less on the second.

Saskatchewan River samples and species lie near the center of the second axis. Seasonal variation among these samples is very low, except at site 14. Saskatchewan River

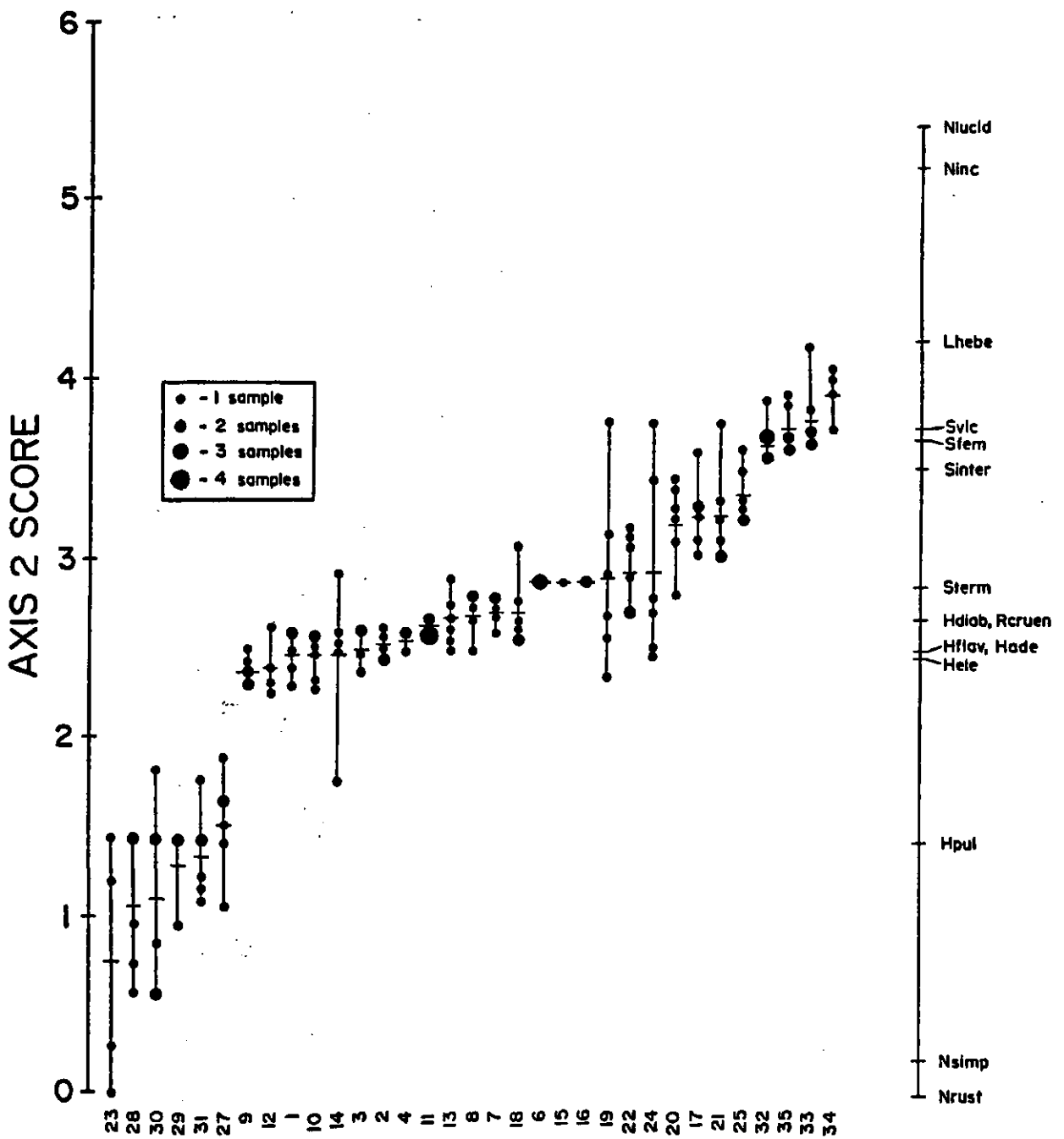


Figure 57. DCA ordination of seasonal stone data: second axis sample and species scores. Symbols and labels are explained in Figure 52.



sample scores overlap little with those from either high gradient or other boreal sites, except boreal sites 19, 20, 22 and 24.

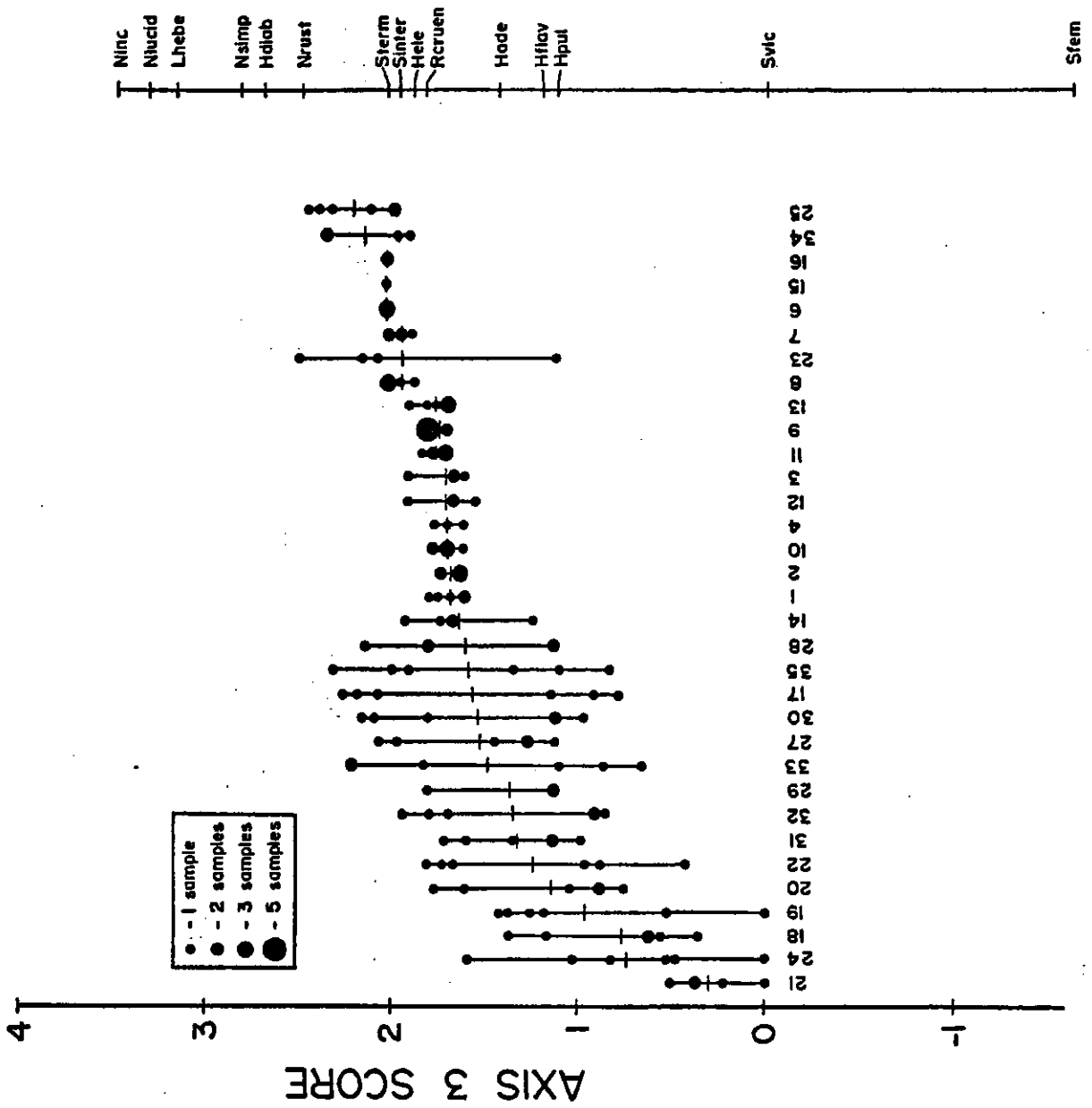
The range of sample and species scores is greater on the second seasonal stone axis than on the second annual stone axis (Table 9). This may be due to the extremely high and low scores of species with summer life cycles, especially Nixe species, on this axis.

The third and fourth seasonal stone axes have relatively large eigenvalues (Table 10) and thus appear to describe important variation in the data (as in the ordination of seasonal sweep net data).

The third axis (Figure 58) describes within-site seasonal variation at boreal and high gradient stream sites. Seasonal differences among samples from most of these sites are large, and differences among sites are small. The pattern of seasonal variation is quite consistent; June and July samples generally have higher ordination scores than August to October samples. This variation is associated with seasonal changes in the abundances of boreal species with summer life cycles (Leucrocuta hebe and all four Nixe species) which also have high scores on these axes. Boreal species with winter life cycles (Heptagenia pulla and Stenonema vicarium) have the lowest species scores and are associated with late season samples. Samples from site 21 show little seasonal variation and all have low scores. Species with summer life cycles were never collected at site 21.

Figure 58. DCA ordination of seasonal stone data: third axis sample and species scores.

Symbols and labels are explained in Figure 52.



Variation in third axis scores among Saskatchewan River samples is low, both among sites and seasonally among samples from any one site. Saskatchewan River species all have intermediate scores and lie together near the center of the axis. This axis is different from all seasonal sweep net data axes.

The fourth seasonal stone axis (Figure 59) is also related primarily to within-site seasonal variation, except that samples from site 23 and the three Saskatchewan River sites just downstream from dams (sites 6, 15 and 16) have lower ordination scores than most other samples. Other differences among sites are small, and seasonal variation among samples from most sites is relatively large. However, patterns of seasonal variation are not consistent among sites. The distribution of species scores on the fourth axis appears random.

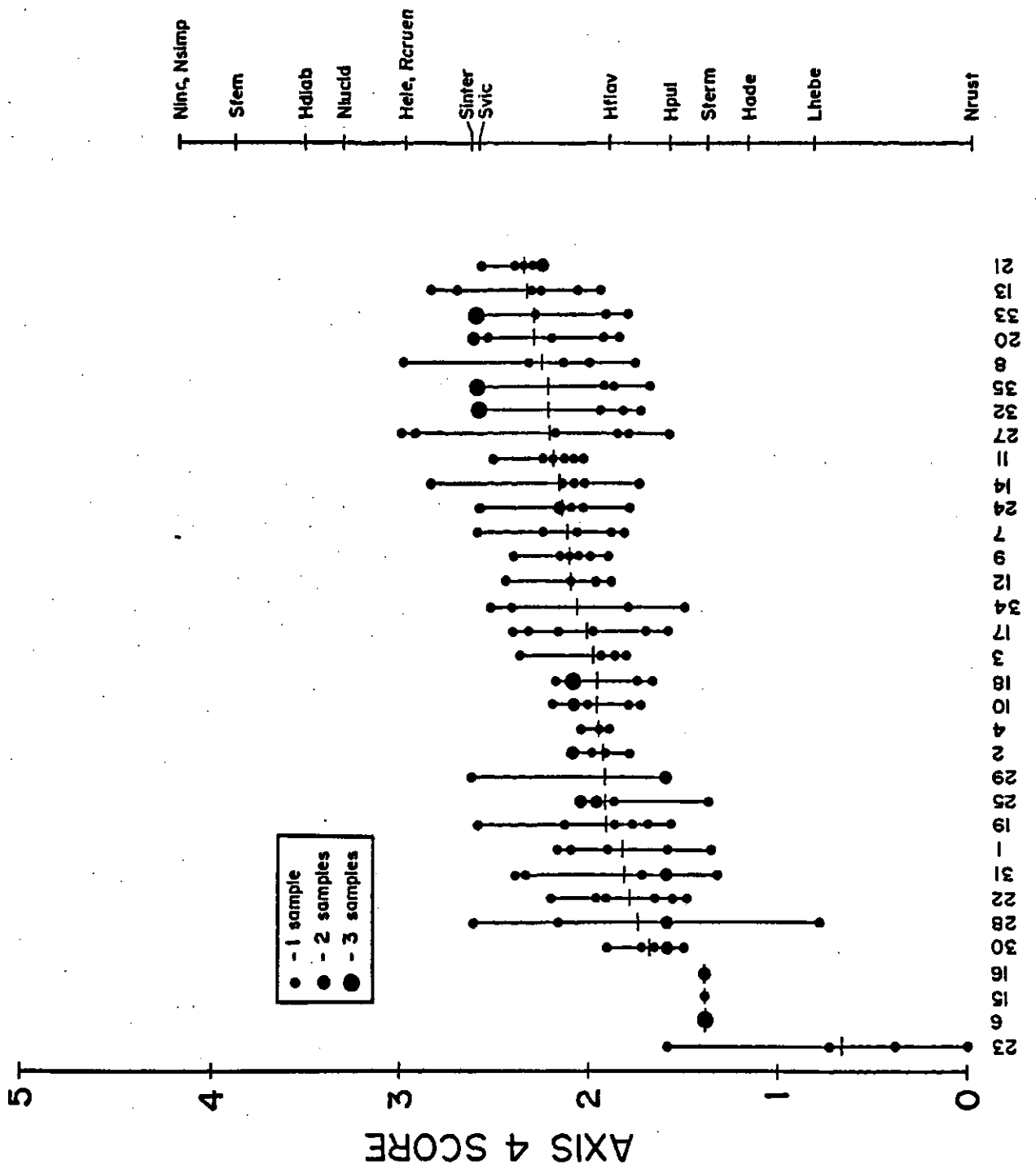
#### 4.3.2.3 Analysis of seasonal presence/absence data

The ordination of seasonal presence/absence data is similar to ordinations of other data sets. The first axis (Figure 60) again shows a community gradient from South Saskatchewan River sites upstream from Lake Diefenbaker through other Saskatchewan River and high gradient stream sites to other boreal streams sites. Most samples from site 12 (on the North Saskatchewan River) have scores similar to those from the four sites upstream from Lake Diefenbaker.

Sample scores from sites 25 and 27 overlap with both the highest Saskatchewan River and lowest boreal sample scores.

Figure 59. DCA ordination of seasonal stone data; fourth axis sample and species scores.

Symbols and labels are explained in Figure 52.



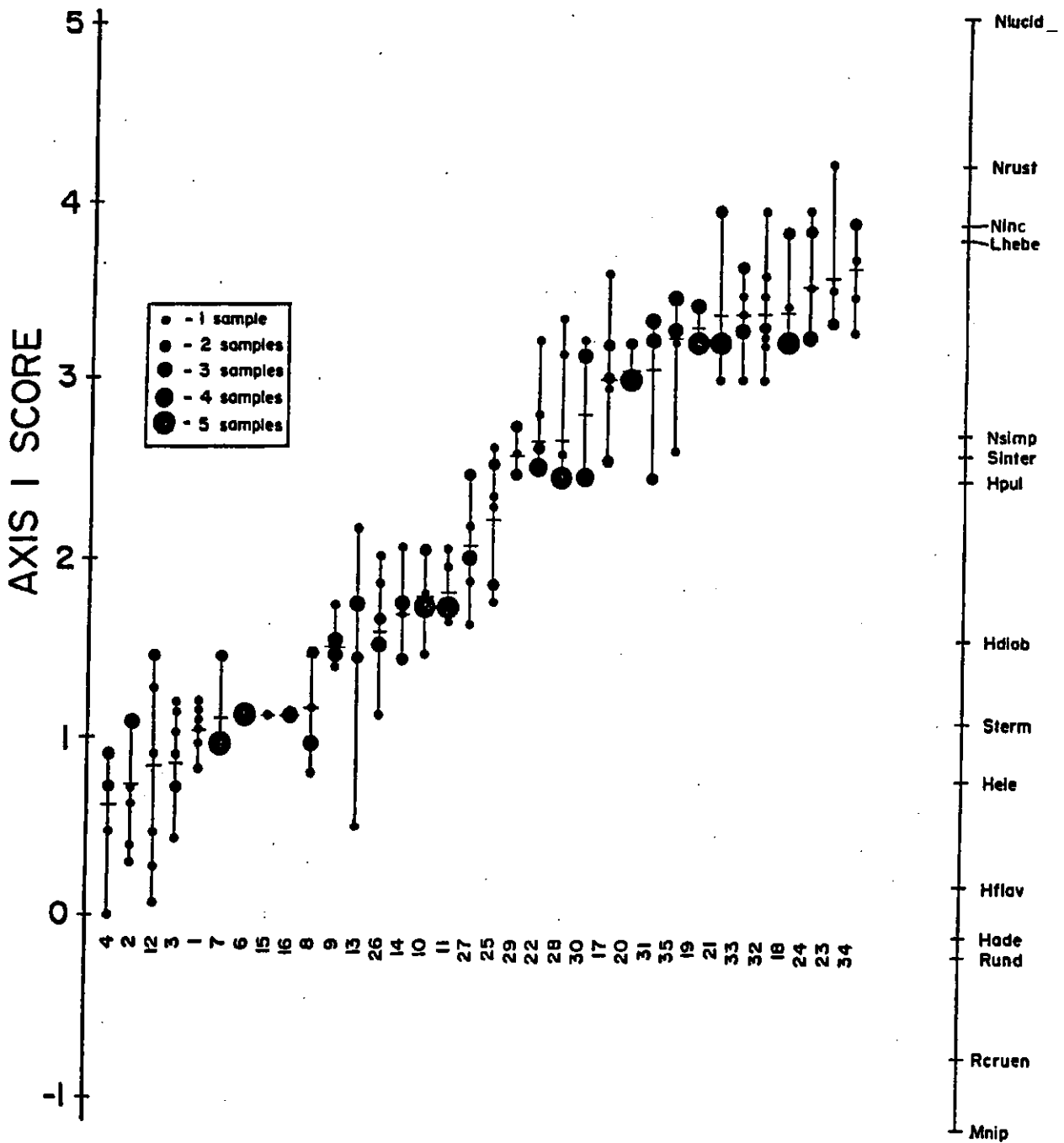


Figure 60. DCA ordination of seasonal presence/absence data: first axis sample and species scores. Symbols and labels are explained in Figure 52.

Thus, these two sites appear to be intermediate between Saskatchewan River and boreal sites. Sample scores from site 26 are all similar to those from the downstream-most Saskatchewan River sites (sites 10, 11, 13 and 14). In the ordination of annual presence/absence data, sites 25 to 27 are all intermediate between Saskatchewan River and boreal sites; only sites 25 and 26 are intermediates in quantitative data ordinations. Saskatchewan River sample scores are all lower than any boreal scores, except for some samples from sites 25 and 27.

Patterns of seasonal variation are not consistent among sites, except among South Saskatchewan River sites upstream from Lake Diefenbaker. At these sites, June samples generally have lower ordination scores than either early (April and May) or late (August to October) season samples.

Species scores on this axis are similar to those on the first axes from ordinations of other data sets. Species characteristic of the South Saskatchewan River upstream from Lake Diefenbaker (Heptagenia adequata, H. flavescens, Macdunnoa nipawinia, Raptoheptagenia cruentata and Rhithrogena undulata) have the lowest scores; Nixe lucidipennis and Nixe rusticalis have the highest scores.

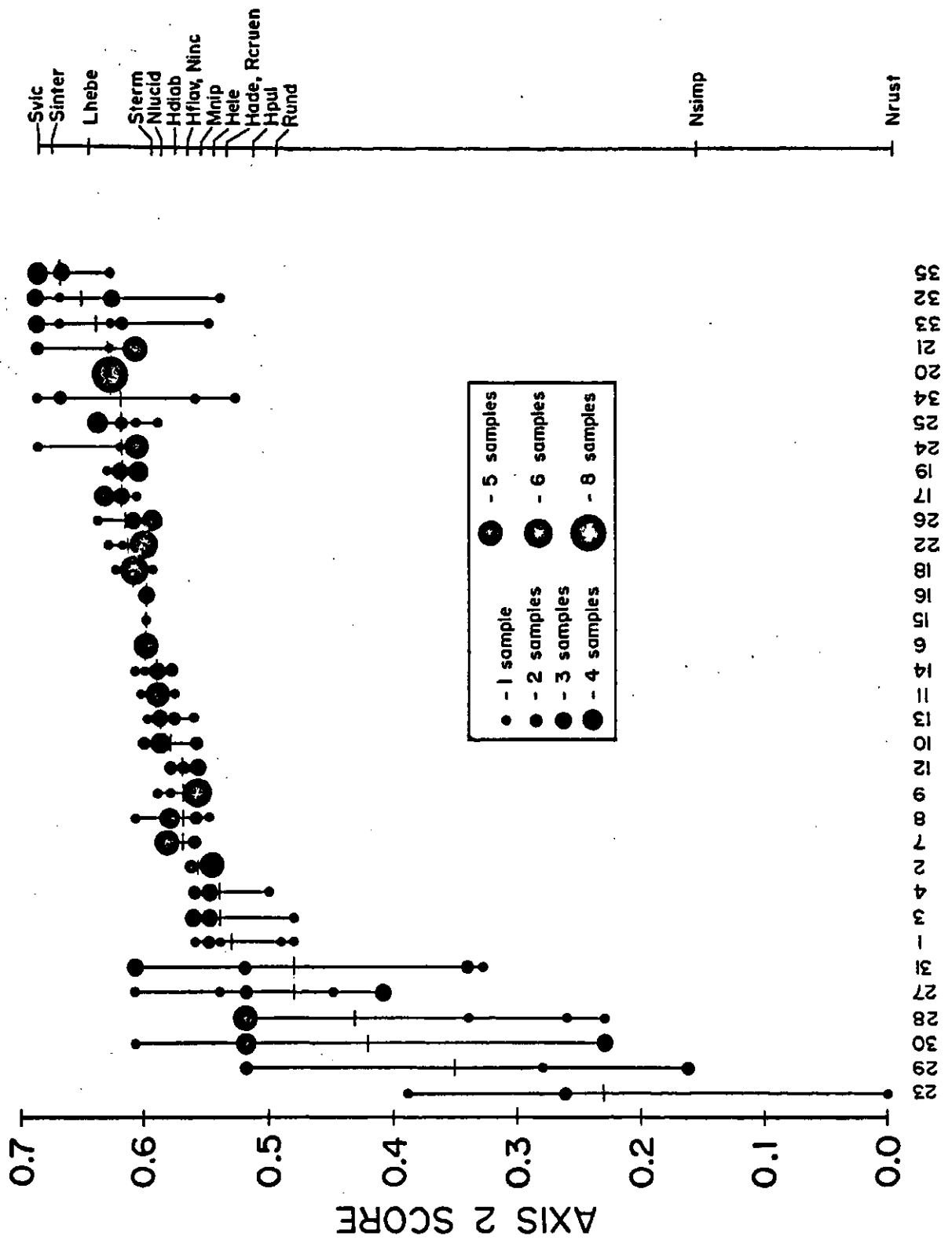
This axis has a greater range of sample and species scores than the corresponding annual presence/absence axis (Table 9).

The second seasonal presence/absence axis describes seasonal variation at high gradient sites (Figure 61). June and July samples from these sites have much lower ordination



Figure 61. DCA ordination of seasonal presence/absence data: second axis sample and species scores.

Symbols and labels are explained in Figure 52.



scores than early or late season samples. Seasonal variation in sample scores is especially high at site 23. The low scores of June and July samples is associated with the seasonal occurrences of Nixe rusticalis and N. simplicoides which also have low second axis scores.

Saskatchewan River and boreal samples have second axis scores similar to those of late season samples from high gradient streams. Both between-site geographical variation and within-site seasonal variation in second axis scores are low among Saskatchewan River and other boreal sites. May and early June samples from sites 1, 3 and 4 have slightly lower scores than other Saskatchewan River samples. June samples from boreal sites 20, 32 and 33 have lower scores, and April and August to October samples higher scores, than at most other boreal and Saskatchewan River sites.

Stenonema vicarium, Stenacron interpunctatum and Leucrocuta hebe have the highest second axis species scores. These species also have high second axis scores in annual quantitative data ordinations. However, in ordinations of annual presence/absence data and seasonal quantitative data, Nixe inconspicua, N. lucidipennis and/or Heptagenia diabasia have the highest second axis scores.

The second seasonal presence/absence axis has a much smaller range of species and sample scores than other DCA axes in this study. Thus, species turnover is low, although the variation described is important as indicated by the relatively high eigenvalue (Table 10).

The third and fourth seasonal presence/absence axes have

relatively large eigenvalues (Table 10) and thus describe important variation in the data. On both axes, within-site seasonal variation in ordination scores is greater than between-site geographical variation (Figures 62 and 63).

The third axis (Figure 62) describes seasonal variation at high gradient and other boreal sites. June and July samples from these sites, containing Leucrocuta hebe and/or Nixe species, generally have higher scores than either early or late season samples which are dominated by Heptagenia pulla and Stenonema vicarium. There is some seasonal variation at Saskatchewan River sites on this axis, but the trends are not consistent.

The fourth axis (Figure 63) describes seasonal variation at Saskatchewan River sites. However, seasonal trends are again neither consistent among sites nor readily interpretable. This axis also describes some geographical variation; samples from the three Saskatchewan River sites just downstream from dams (sites 6, 15 and 16) have lower scores than other samples (except the April sample from site 26).

Both the third and fourth axes are very different from all previously described ordination axes.

#### 4.3.3 Comparison and summary of analyses of seasonal variation

Multivariate analyses of the three seasonal data sets produced similar results. However, classifications were less similar than ordinations. The number of major groups

Figure 62. DCA ordination of seasonal presence/absence data: third axis sample and species scores.  
Symbols and labels are explained in Figure 52.

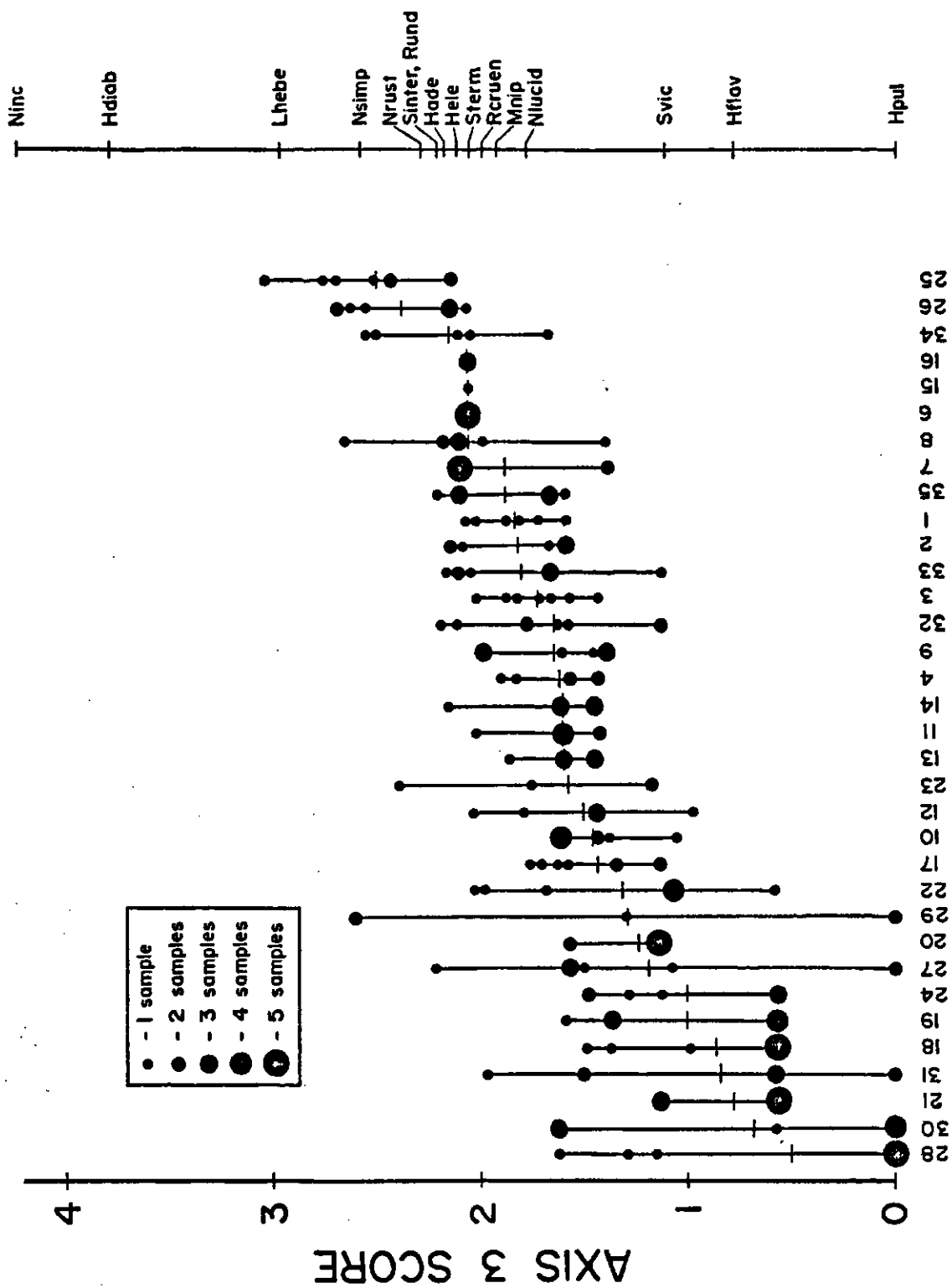
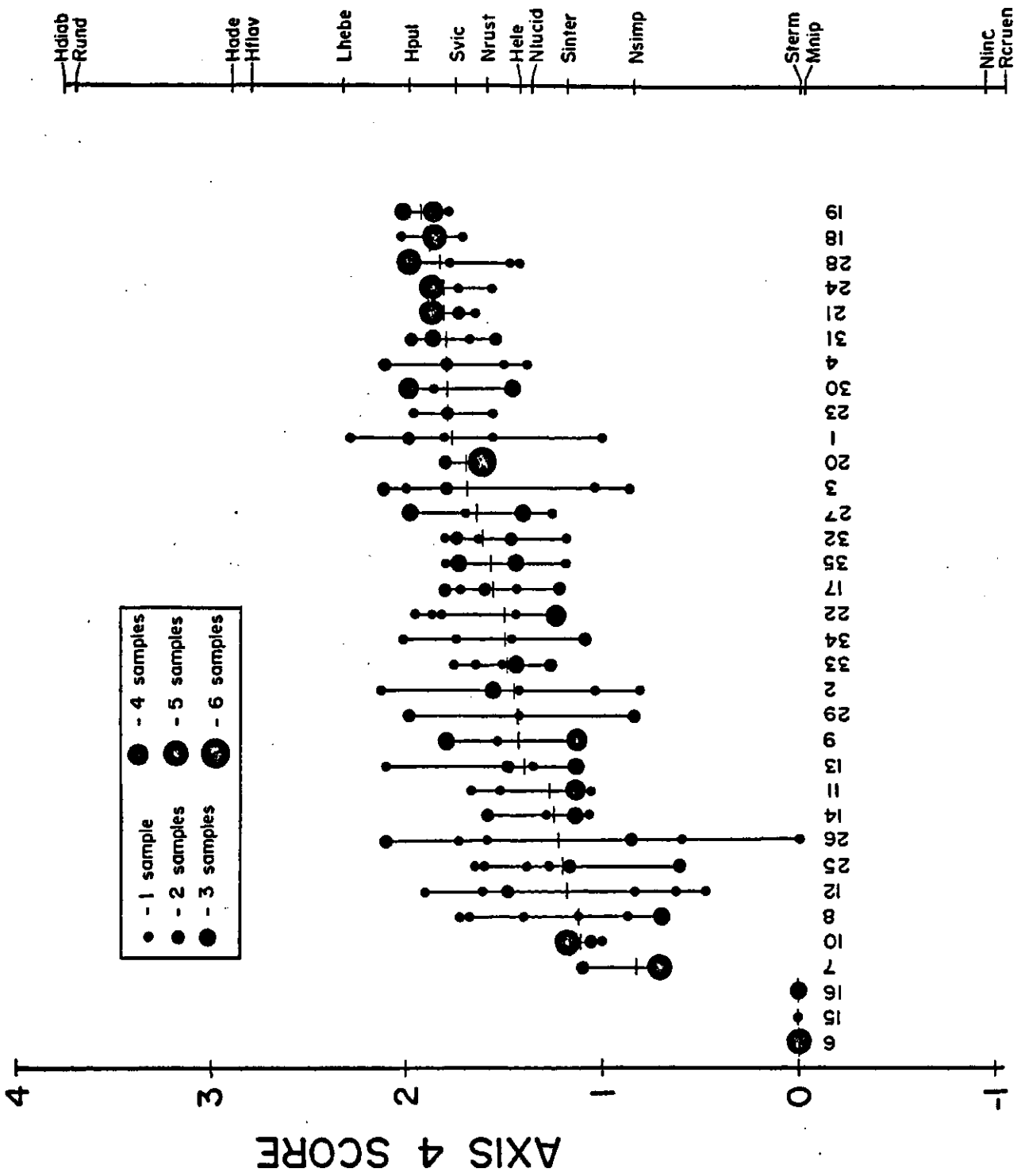


Figure 63. DCA ordination of seasonal presence/absence data: fourth axis sample and species scores.  
Symbols and labels are explained in Figure 52.





recognized ranged from two in analysis of sweep net data to four in analysis of presence/absence data. Differences in the number of major groups are due to differences in the distinctness of some clusters (such as high gradient streams and South Saskatchewan River sites upstream from Lake Diefenbaker) which are recognized as major groups in some analyses and as subgroups in others. There were similar differences in the number of major groups among the three annual data classifications.

The site compositions of large groups present in seasonal stone and presence/absence data classifications are similar to those in annual data classifications. However, in the seasonal sweep net data classification, some samples from Saskatchewan River sites 10, 11, 13 and 14, and from sites 25 and 26, were classified in the boreal group instead of the Saskatchewan River group. This is likely due to the existence of several low abundance, potentially non-representative, sweep net samples. Most of the Saskatchewan River sweep net samples that are classified in the boreal group are smaller and less diverse than stone samples collected at the same sites and times.

The division of major zones into subzones is very different in seasonal sweep net and stone data classifications and is absent in the seasonal presence/absence data classification. Subzones in the seasonal stone data classification are very similar to those in the annual stone data classification, except for the assignment of site 25 to a separate subzone and the presence

of separate mid- and late-season subzones among both high gradient and other boreal sites. The subzones in the seasonal sweep net data classification are different than those in any other classification.

Ordinations of the three seasonal data sets are more similar. The community gradient described by the first axis is basically the same in all three ordinations. Only samples from sites 12 and 23 differ greatly in first axis scores among ordinations. The amount of seasonal variation differs among the three first axes but is generally greatest at sites 12, 20 and 23. June and July samples from South Saskatchewan River sites upstream from Lake Diefenbaker generally have lower scores than other samples. Other patterns of seasonal variation are not consistent either among the sites in any group within an analysis or at any one site among the three analyses.

The three sets of species scores are highly correlated with one another ( $r = .84$  to  $.96$ ,  $p < .01$ ; Table 11).

The three second axes are also similar. On all three, samples from high gradient streams, at least from June and July, have lower scores than samples from other sites; and other boreal sites have the highest scores. In ordinations of stone and presence/absence data, all other boreal sites have higher scores than Saskatchewan River sites. In the sweep net data ordination, second axis scores are lower at some boreal sites than at Saskatchewan River sites.

Second axis seasonal variation is greatest among samples

from high gradient sites where scores are lowest in June and July and higher both earlier and later in the year. The opposite pattern occurs at most other boreal sites. Seasonal variation in second axis scores is low at Saskatchewan River sites, except in the sweep net data ordination.

Nixe rusticalis and N. simplicoides have the lowest second axis species scores in all seasonal data ordinations. However, the species with the highest second axis scores differ among the three ordinations. The highest species scores belong to Heptagenia diabasia in the sweep net data ordination, Nixe lucidipennis and N. inconspicua in the stone data ordination, and Stenonema vicarium, Stenacron interpunctatum and Leucrocuta hebe in the presence/absence data ordination.

Second axis species scores in the presence/absence data ordination are significantly correlated with species scores in the other two ordinations ( $r = .71$  to  $.77$ ,  $p < .01$ ; Table 11), although  $r$  values are lower than between pairs of first axis scores. Species scores in the sweep net and stone data ordinations are not significantly correlated.

The third and fourth axes in the three seasonal data ordinations are all different, except that they all appear to be related primarily to within-site seasonal variation rather than geographical variation.

Therefore, the major patterns present in seasonal data are related primarily to geographical rather than seasonal trends. In classifications, major groups generally contain all samples (from all sampling times) from each site

included. Major groups are thus defined by differences among sites rather than among sampling times. Similarly, differences among sites are generally greater than differences among sampling times on the first two ordination axes.

Table 11. Correlations among species scores from ordinations of three seasonal data sets.

		Sweep Net Samples			
<u>Data Type</u>	<u>Axis #</u>	<u>Axis 1</u>	<u>Axis 2</u>	<u>Axis 3</u>	<u>Axis 4</u>
Stone samples	1	0.84 **	NS	NS	NS
	2	NS	NS	NS	NS
	3	NS	NS	NS	NS
	4	NS	NS	-0.71 **	NS
Presence/absence	1	0.96 **	NS	NS	0.51 *
	2	NS	0.71 **	NS	NS
	3	NS	NS	0.60 *	NS
	4	NS	NS	NS	NS
		Stone Samples			
<u>Data Type</u>	<u>Axis #</u>	<u>Axis 1</u>	<u>Axis 2</u>	<u>Axis 3</u>	<u>Axis 4</u>
Presence/absence	1	0.90 **	NS	NS	NS
	2	NS	0.77 **	NS	NS
	3	NS	NS	-0.73 **	NS
	4	NS	NS	NS	NS

\* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; NS - Not Significant

Distribution patterns in seasonal data are very similar to those in annual data. The number of major groups present and the site compositions of these groups are similar in classifications of seasonal and annual data for all sample types (except that the classification of seasonal presence/absence data contains two fewer major groups than the classification of annual presence/absence data). The major community gradients in seasonal and annual data

ordinations are also similar.

Seasonal variation is apparent in the subgroup structure of quantitative data classifications, the within-site seasonal variation in sample scores on the first two ordination axes, and the relatively high eigenvalues of the third and fourth axes. Much of this variation appears to be due to seasonal changes in the abundances of species with summer life cycles. Such species are important in differentiating high gradient streams from other boreal streams (Leucrocuta hebe and Nixe species), and sites upstream from Lake Diefenbaker from other Saskatchewan River sites (Macdunnoa nipawinia, Rhithrogena undulata, and Raptoheptagenia cruentata). This seasonal variation is manifested in the separation of mid- (June and July) and late (August to October) season samples of high gradient and other boreal sites in the stone data classification, and in the within-site seasonal variation in first and/or second axis ordination scores at high gradient sites and South Saskatchewan River sites upstream from Lake Diefenbaker.

Some of the variation described by the third and fourth axes also appears to be related to seasonal changes in the abundances of species with summer life cycles. However, much of the variation described by these axes, as well as some of the within-site seasonal variation on the first and second axes and the subgroup structure in the sweep net data classification, cannot be meaningfully interpreted. Because the patterns associated with this unexplained variation are not consistent among samples within or between analyses, they

may be due to noise in the data.

#### 4.3.4 Analysis of seasonal variation alone

Purely seasonal trends can be examined by removing geographical variation, by averaging species abundances across all sites for each sampling time. The resulting sampling times x species data matrices are presented in Appendices 7 and 8. The first axes in ordinations of sampling times x species data have much higher eigenvalues than subsequent axes (Table 12). Therefore, there is only one important seasonal trend present. This trend is related to seasonal changes in the abundances of species with summer life cycles (Figure 64). These species, and the June and July samples in which they occur, all have higher first axis scores than species with winter life cycles, and either early or late season samples. This trend is similar to the major patterns of seasonal variation present in analyses of seasonal samples x species data.

The second sampling times x species abundance axes have very low eigenvalues (approximately 1/10 as large as the first; Table 12) and thus describe only a very small amount of seasonal variation. These second axes (Figure 65) describe differences between samples from early June and those from late June and July. These differences might be related to differences between summer species with early, discrete emergence periods and those with later or more extended emergence periods. Raptoheptagenia cruentata has the highest second axis species scores and is absent from late June and

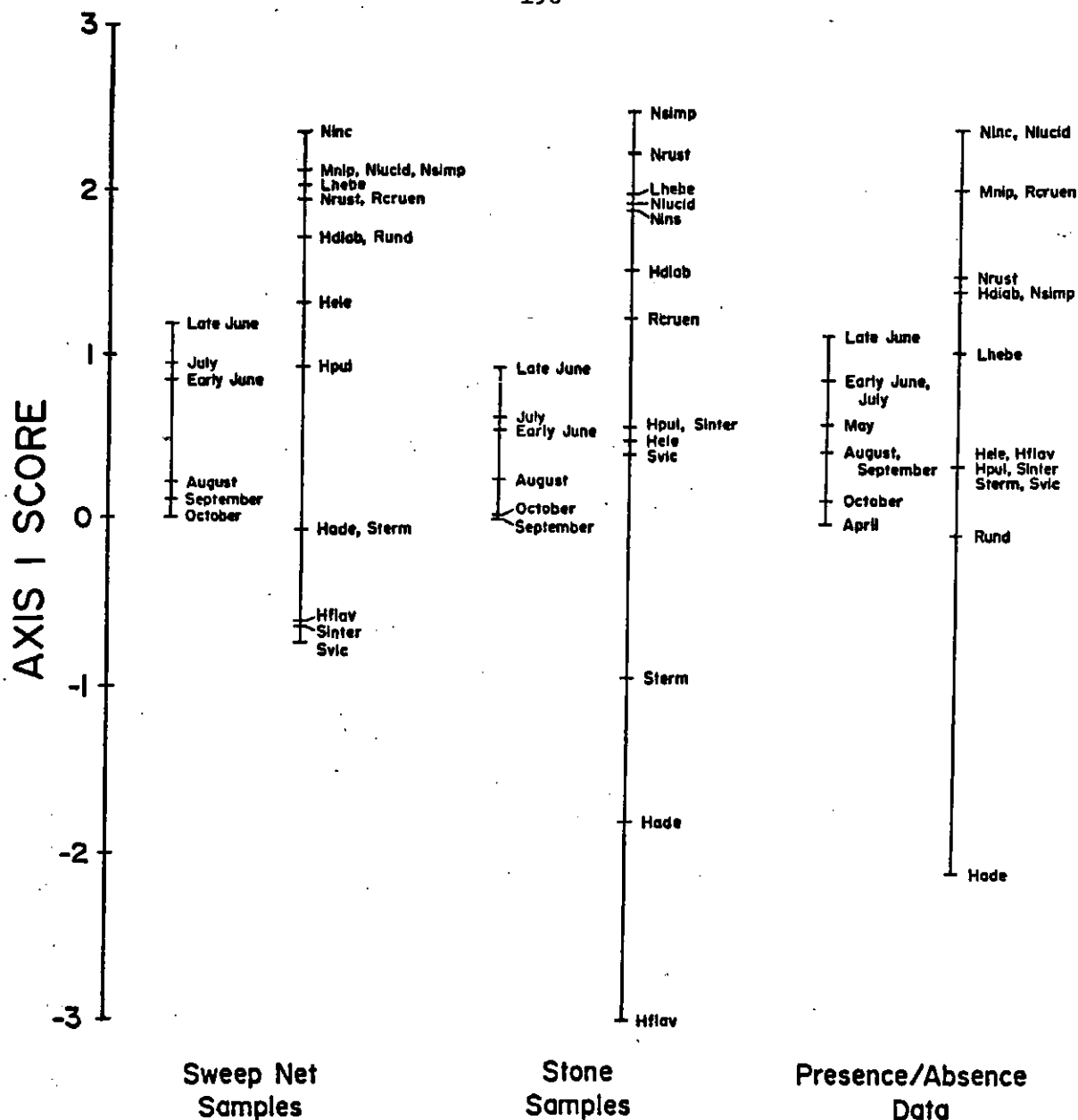


Figure 64. DCA ordinations of sampling times x species data: first axis time and species scores for ordinations of sweep net, stone and presence/absence data. Species names given are abbreviations incorporating the first letter of the genus name (upper case) and the first three to five letters of the specific name (lower case).

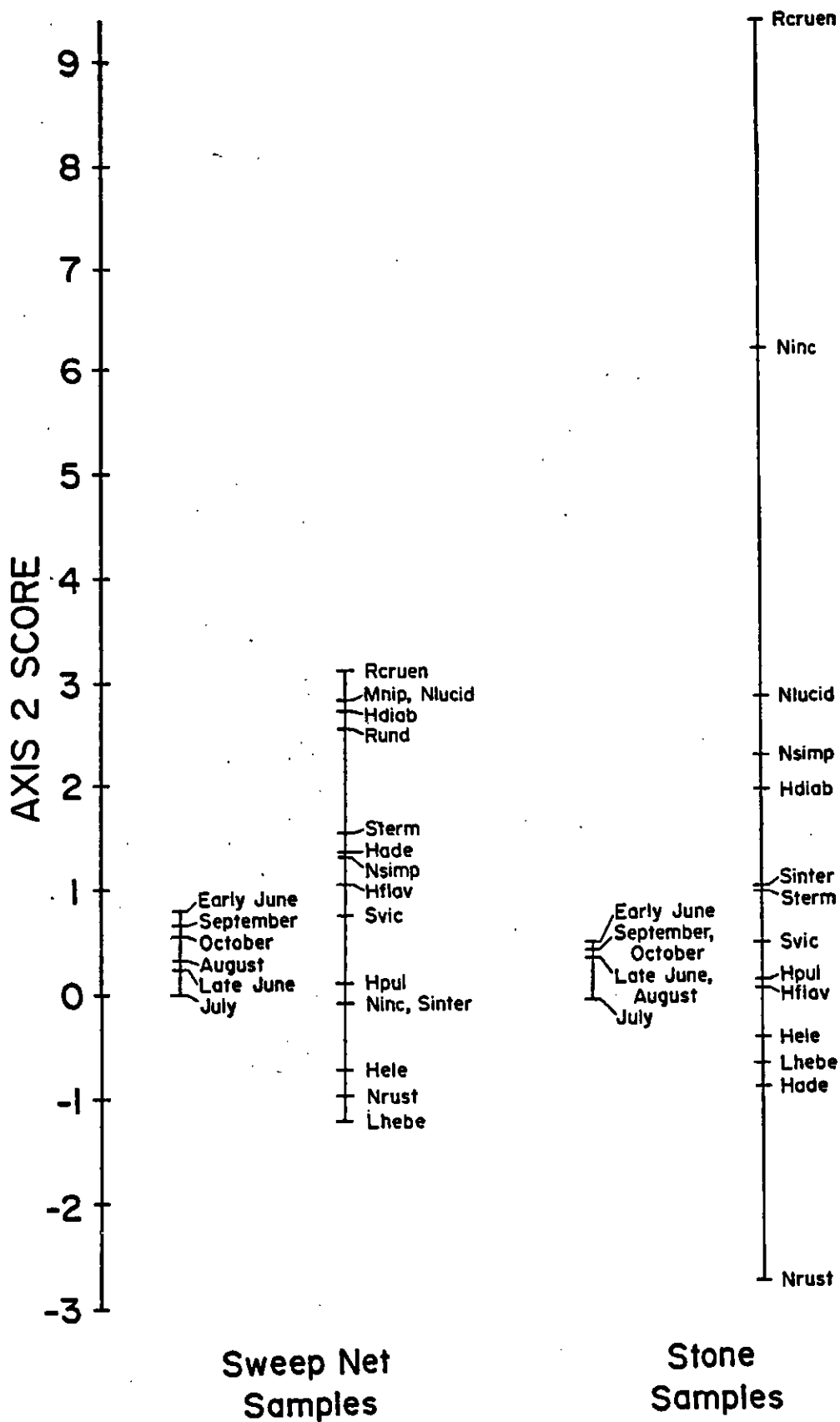


Figure 65. DCA ordinations of sampling times x species data: second axis time and species scores for ordinations of sweep net and stone data. Abbreviated species names are explained in Figure 64.



July samples. However, R. cruentata is absent from late June and July samples only because high water levels interfered with sampling at sites 1-4 and 12 at these times. Qualitative information from other years indicates that the emergence period of R. cruentata is relatively extended and lasts from late June or early July until mid- to late July. Therefore, the variation described by these second axes is at least partly an artifact of sampling difficulties associated with high water levels.

Table 12. Eigenvalues of the first four ordination axes from DCA of sampling times x species data.

<u>Data Set</u>	<u>Axis 1</u>	<u>Axis 2</u>	<u>Axis 3</u>	<u>Axis 4</u>
Sweep net samples	.217	.021	.000	.000
Stone samples	.142	.010	.000	.000
Presence/absence	.153	.000	.000	.000

The third and fourth sampling times x species abundance axes, and the second and higher sampling times x species presence/absence axes, all have eigenvalues of zero. Thus, all purely seasonal variation can be explained in one or two dimensions. Seasonal variation described by the third and fourth axes in ordinations of seasonal samples x species data must be due to interactions between seasonal and geographical factors.

Species scores on the first sampling time x species axes are not significantly correlated with species scores on either the first or second seasonal samples x species axes for any data type (Table 13), except for a correlation

Table 13. Correlations of species scores on seasonal samples  
x species axes with species scores on annual sites  
x species and sampling times x species DCA axes.

<u>Sweep Net Data</u>					
Seasonal Samples x Species Axes					
<u>Data Type</u>	<u>Axis #</u>	<u>Axis 1</u>	<u>Axis 2</u>	<u>Axis 3</u>	<u>Axis 4</u>
Sites x species	1	0.97 **	NS	NS	NS
	2	NS	0.76 **	NS	NS
	3	NS	NS	NS	NS
	4	NS	NS	0.59 *	NS
Times x species	1	NS	NS	NS	NS
	2	NS	NS	NS	NS
<u>Stone Data</u>					
Seasonal Samples x Species Axes					
<u>Data Type</u>	<u>Axis #</u>	<u>Axis 1</u>	<u>Axis 2</u>	<u>Axis 3</u>	<u>Axis 4</u>
Sites x species	1	0.97 **	NS	NS	NS
	2	NS	0.75 **	NS	NS
	3	NS	NS	NS	NS
	4	NS	NS	NS	NS
Times x species	1	0.65 *	NS	0.62 *	NS
	2	NS	NS	NS	0.67 *
<u>Presence/Absence Data</u>					
Seasonal Samples x Species Axes					
<u>Data Type</u>	<u>Axis #</u>	<u>Axis 1</u>	<u>Axis 2</u>	<u>Axis 3</u>	<u>Axis 4</u>
Sites x species	1	0.99 **	NS	NS	NS
	2	NS	0.81 **	NS	NS
	3	NS	NS	NS	NS
	4	NS	NS	NS	NS
Times x species	1	NS	NS	NS	NS
	2	NS	NS	NS	NS

\* -  $p < .05$ ; \*\* -  $p < .01$ ; NS - Not Significant

s x species axes for any data type (Table 13), except for a correlation between first axis scores in stone data ordinations ( $r = .65$ ;  $p < .05$ ). On the other hand, first and second axis annual sites x species ordination scores are highly correlated with the corresponding first and second seasonal axis samples x species scores ( $r = .97$  to  $.99$  between pairs of first axis scores, and  $.75$  to  $.81$  between pairs of second axis scores;  $p < .01$ ). This further demonstrates that geographical variation is much more important than seasonal variation (i.e. that differences among sites are much greater than differences among sampling times).

#### 4.4 Extensive Study Distribution Patterns

Extensive study data include species presence/absences from 174 sites in Saskatchewan, western Manitoba and southeastern Alberta. Annual presence/absence data from the intensive survey are included.

##### 4.4.1 Cluster analysis of extensive study data

The classification of extensive study (presence/absence) data is presented in Figure 66 and Appendix 10. Two large, distinct groups of sites, and eight subgroups, are present in this classification (Figure 67). Group I contains nearly all Saskatchewan River sites, and a few southern boreal and parkland sites. Group II contains all other parkland, southern boreal and Shield sites, and all sites where only one species of heptageniid, or no heptageniids, were collected. Thus there appear to be two faunal zones in Saskatchewan, a Saskatchewan River and a boreal faunal zone. The two zones contain a total of eight subzones.

The Saskatchewan River zone contains three subzones:

1) Subzone Ia - South Saskatchewan River sites upstream from Lake Diefenbaker, and site 12 on the North Saskatchewan River. This subzone is characterized by a very diverse heptageniid fauna that includes Heptagenia elegantula, H. flavescens, Macdunnoa nipawinia, Raptoheptagenia cruentata and Stenonema terminatum. Two additional species, H. adequata and Rhithrogena undulata are found at the four sites upstream from Lake Diefenbaker. These five sites are all included in the intensive study and form a Saskatchewan River subzone in

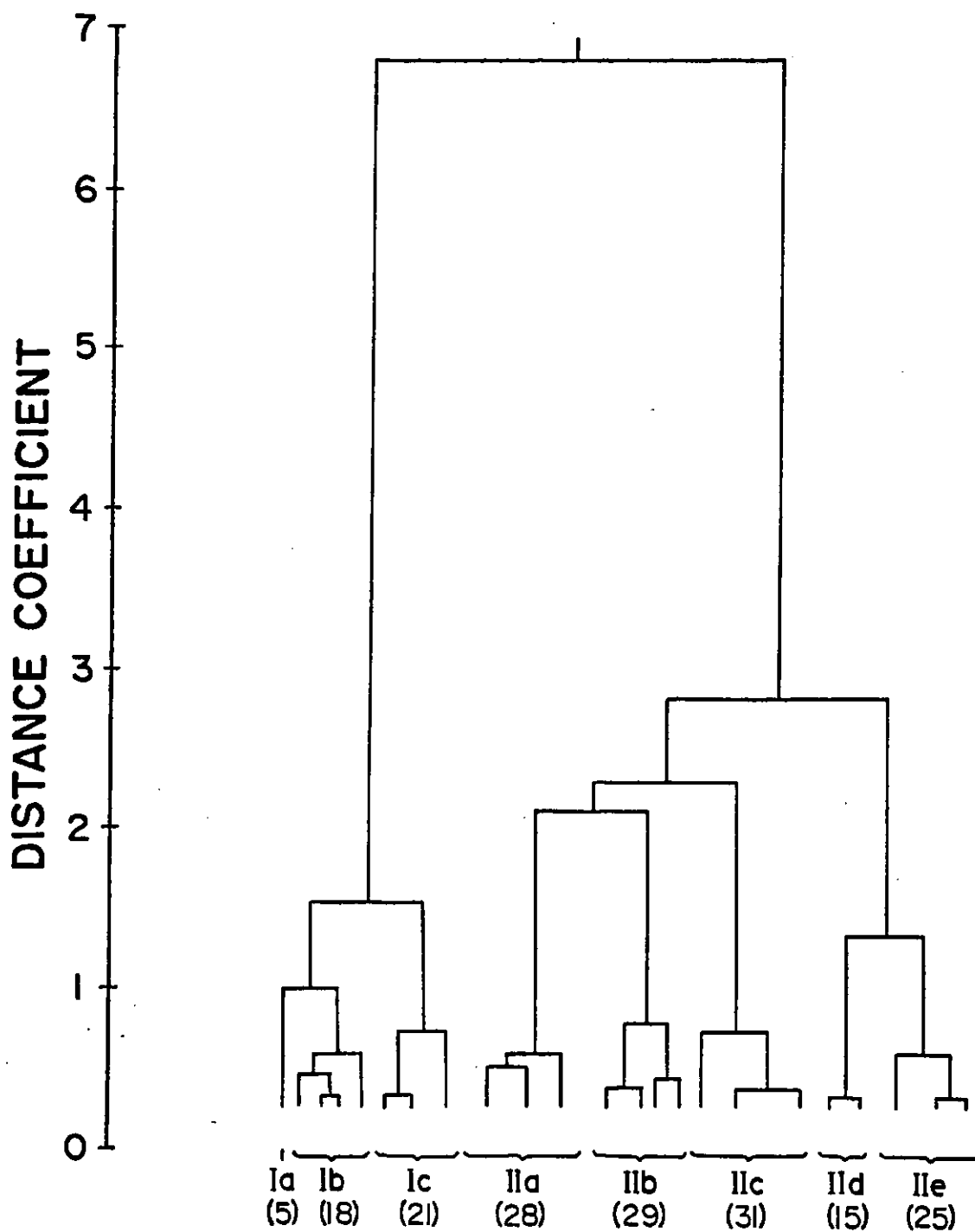
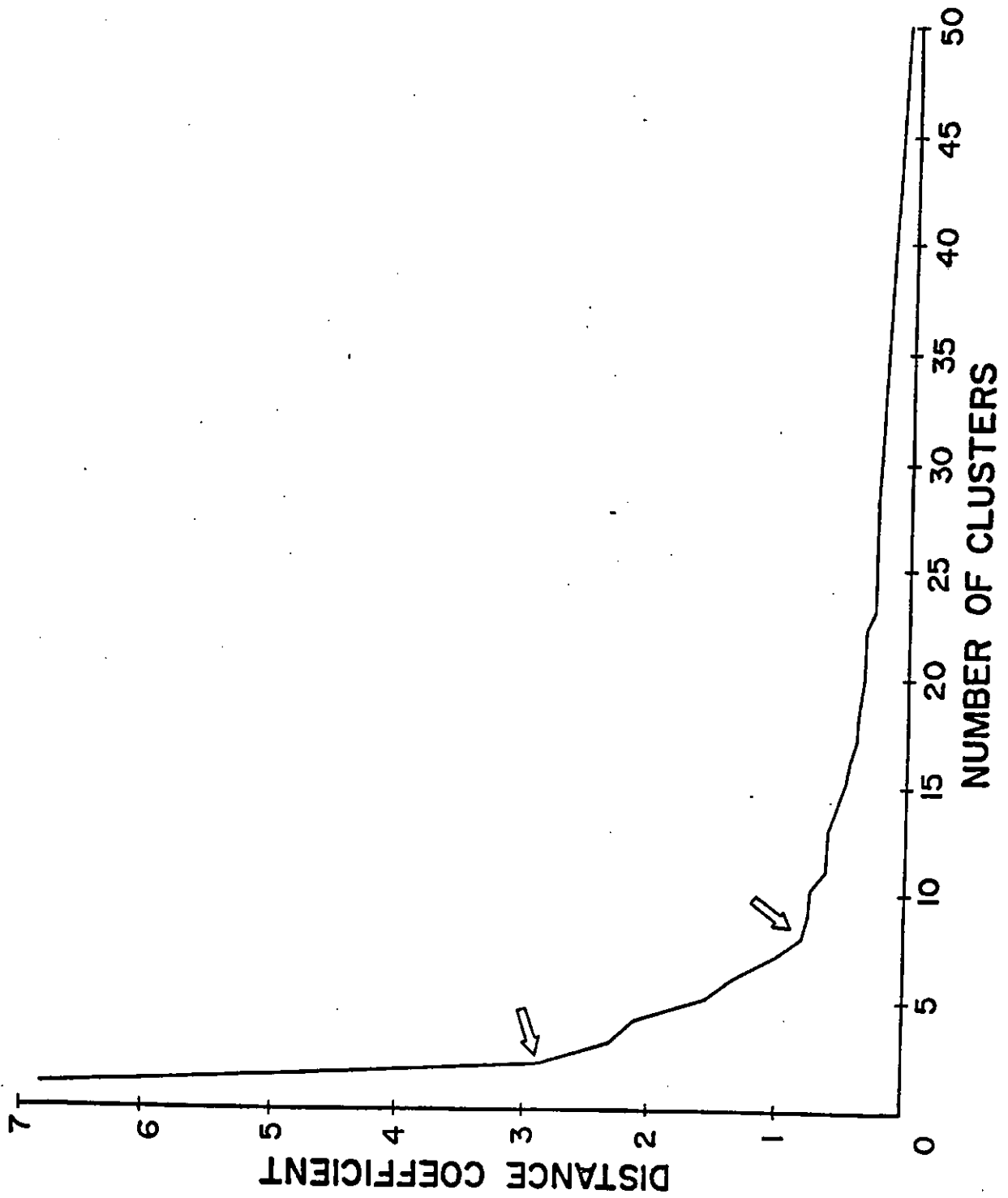


Figure 66. Classification of extensive study sites.

The dendrogram is truncated at the 23 cluster level. Subgroups present at the eight cluster level are labelled along the base of the dendrogram. Numbers in parentheses are the numbers of sites in each subgroup. The sites included in each subgroup are listed in Appendix 10.

Figure 67. Relationship between distance between fusing clusters and number of clusters in the classification of extensive study sites. Large changes in slope occur at the 2 and 8 cluster levels. The plot is truncated at the 50 cluster level, where the slope is near zero.



intensive study classifications.

2) Subzone Ib - all other Saskatchewan River sites, except the first two sites downstream from Gardiner and Squaw Rapids Dams and the site at The Pas, Manitoba. The Battle River site is also included. This subzone is characterized by the presence of Heptagenia elegantula and Stenonema terminatum, and the absence of the rare species that are characteristic of Subzone Ia. These two subzones are quite similar, and differ only in the presence or absence of rare species.

3) Subzone Ic - Saskatchewan River sites 11 miles downstream from Gardiner Dam and at The Pas, and southern boreal and parkland sites that are faunistically similar to Saskatchewan River sites. Most boreal sites included are on low gradient, larger streams or rivers that are tributaries of the Saskatchewan River. S. terminatum was collected at most sites in this subzone. Some Saskatchewan River Heptagenia spp. and/or boreal species were usually also present. The faunal distinction between this subzone and the previous one is not obvious, although the presence of one or two boreal species in addition to Saskatchewan River species may be important.

Five boreal subzones are present:

1) Subzone IIa - sites where no heptageniids, or only one species of heptageniid, were collected. The single species present differed among sites but was often one of the three Stenonema species in Saskatchewan. This subzone includes all sites from southwestern Saskatchewan and southeastern Alberta (except one Cypress Hills site) where only Stenonema terminatum was collected, several lake and stream sites in



northwestern Saskatchewan where only S. femoratum was collected, several boreal and Shield sites where only S. vicarium or Heptagenia pulla were collected, and Saskatchewan River sites just downstream from dams where no heptageniids, or only S. terminatum, were collected. Like groups of low diversity sites in intensive study classifications, this subzone is probably artificial.

2) Subzone IIb - high gradient boreal streams, including most sites from the north and east slopes of the Pasquia and Porcupine Hills, the north side of Duck Mountain, and the south side of the Wapawekka Hills, and one site from the Cypress Hills. This subzone is characterized by the presence of Nixe rusticalis and/or N. simplicoides. Heptagenia pulla, N. lucidipennis and Stenonema vicarium were also collected at some sites.

3) Subzone IIc - small to medium-sized, slow-flowing, southern boreal or parkland streams and large, slow-flowing, Shield rivers. This subzone is characterized by the presence of Stenacron interpunctatum and the absence of Heptagenia pulla. Leucrocuta hebe or Stenonema femoratum were also collected at most sites in this subzone; and Heptagenia diabasias, Nixe inconspicua and Stenonema vicarium were collected at a few sites.

4) Subzone IID - moderately fast flowing, primarily southern boreal streams and rivers. Both Heptagenia pulla and Stenonema vicarium were collected at most sites in this subzone, along with Stenacron interpunctatum, Leucrocuta hebe and/or one or more Nixe species. Species richness and

diversity are higher at sites in this subzone than at other boreal sites.

5) Subzone IIe - most lotic Shield sites and a few southern boreal stream sites. The heptageniid fauna at these sites is similar to that at sites in the previous subzone, except that Leucrocuta hebe and Nixe species are not present. These two subzones are very similar, sister subgroups in the classification.

This classification is quite similar to the classification of intensive study presence/absence data, except that many more sites are included (Table 14). Three extensive study subzones (Ia - South Saskatchewan River sites upstream from Lake Diefenbaker, IIa - low diversity sites, and IIb - high gradient boreal stream sites) correspond closely to zones present in the intensive study classification, except for the inclusion of additional sites. Most other Saskatchewan River sites are placed in a single group in both classifications. However, the Saskatchewan River site 18 km downstream from Squaw Rapids Power Station, and three Saskatchewan River-like southern boreal sites (sites 25, 26 and 27), are placed in a separate subzone (Ic) in the extensive study classification.

All boreal sites included in the intensive study, except site 21 and the high gradient stream sites, are placed in a single subzone (IIId) in the extensive study classification. Sites 32 to 35 are not separated from other boreal sites as they are in the intensive study classification. Site 21 is placed in a different subzone (IIe), along with many other

Shield sites. Neither these Shield sites nor the Shield group are present in the intensive study classification. The remaining boreal subzone in the extensive study classification (Subzone IIc), which contains low-gradient southern boreal and parkland sites, does not correspond to an intensive study group and does not contain any intensive study sites.

Table 14. Correspondence between groups present in classifications of extensive and intensive study presence/absence data.

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Corresponding Group Numbers	
<u>Intensive Study</u>	<u>Extensive Study</u>
1	Ia
2	Ib and Ic *
3	IIa *
4	IIb *
5 and 6	IIc *
(except site 21)	
5	IIe *
(site 21)	
-	IIc

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\* - includes additional sites that are not present in the intensive study.

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The classification of extensive study sites can be shown geographically on a map of Saskatchewan (Figure 68). Most subzones correspond to specific geographical regions of the province, either to parts of the Saskatchewan River system, to areas of steep hillsides, or to terrestrial ecological regions. For most subzones, only a few sites lie outside the boundaries of the corresponding geographical region (Table 15). Only subzone IIb, which contains low diversity sites,

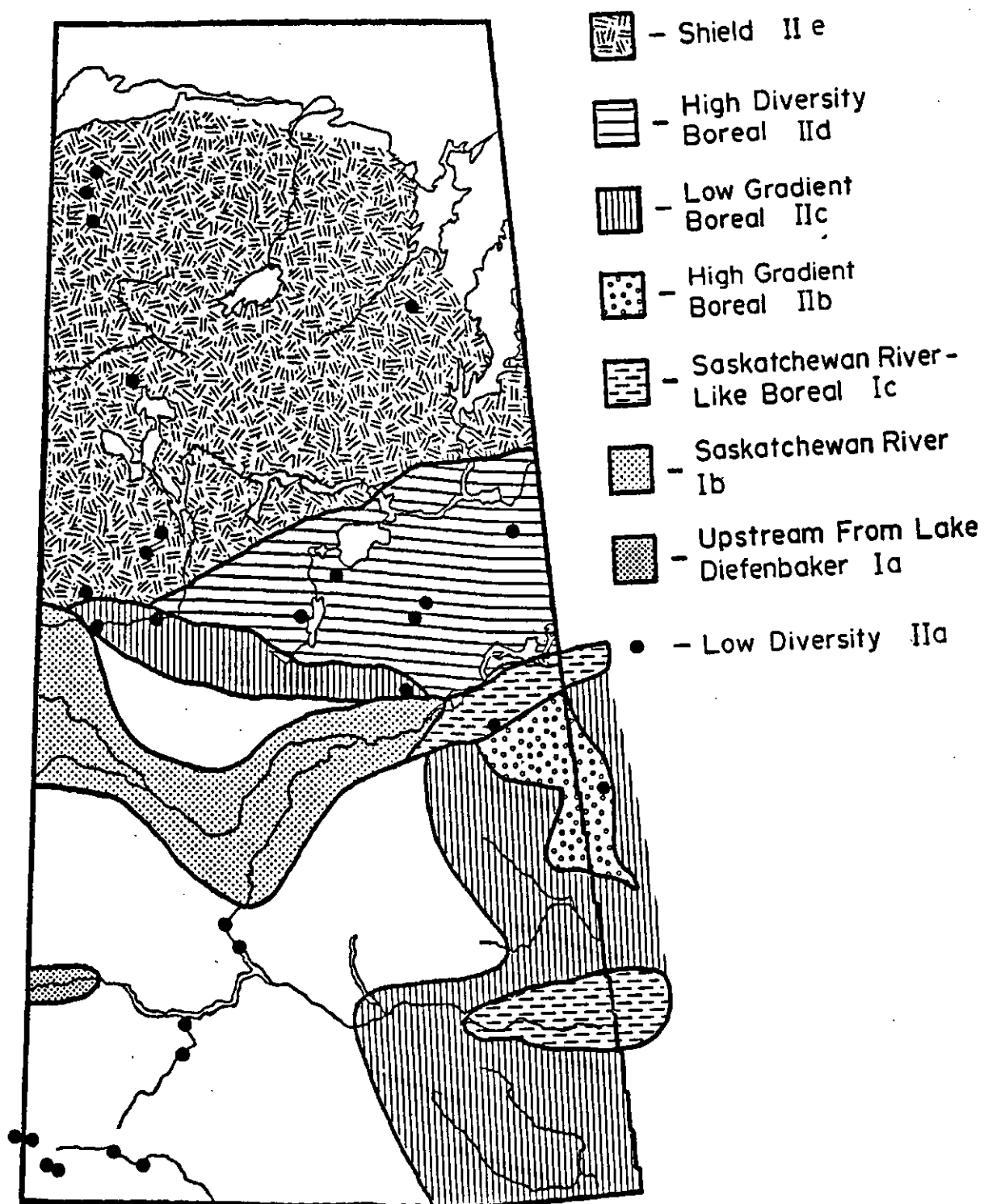


Figure 68. Approximate geographical boundaries of heptageniid faunal subzones in Saskatchewan (as indicated by cluster analysis of extensive study sites). The number of sites lying within and outside of the indicated geographical boundaries of each subzone are given in Table 15.

does not correspond to a specific geographical region, and this subzone is probably artificial.

Table 15. Correspondence of extensive study subzones to geographical areas. Approximate geographical boundaries of subzones are shown in Figure 68.

<u>Subzone #</u>	<u>Subzone Name</u>	<u># of Sites Within Area</u>	<u># of Sites Outside Area</u>
Ia	South Sask. R., upstream from L. Diefenbaker	4 (80%)	1 (20%)
Ib	Other Sask. River	18 (100%)	0 (0%)
Ic	Sask. River-Like	21 (100%)	0 (0%)
IIa	Low Diversity	-	-
IIb	High Gradient Boreal	24 (83%)	5 (17%)
IIc	Low Gradient Boreal	27 (87%)	4 (13%)
IIId	High Diversity Boreal	10 (67%)	5 (33%)
IIe	Shield	20 (80%)	5 (20%)

#### 4.4.2 Ordination of extensive study data

Figure 69 is a two-dimensional plot of site scores on the first two extensive study ordination axes. The first axis shows differences between the Saskatchewan River (I) and boreal (II) faunal zones, and among the three Saskatchewan River subzones. South Saskatchewan River sites upstream from Lake Diefenbaker (Subzone Ia) are nearest the end of the axis and are the most different from boreal streams. Saskatchewan River-like southern boreal and parkland sites (Subzone Ic) are nearest the center of the axis and are the most similar

to boreal sites. Boreal subzones are not separated on the first axis.

The second axis (Figure 69) describes variation among boreal subzones. High gradient stream sites (Subzone IIb) have the lowest ordination scores, and low gradient southern boreal and parkland streams (Subzone IIc) have the highest scores. Sites from the other two boreal subzones (Subzones IIId and IIe) lie near the center of the second axis. These two subzones are not separated on either the first or second axis. Most Saskatchewan River sites also lie near the centre of the second axis. However, South Saskatchewan River sites upstream from Lake Diefenbaker have slightly lower second axis scores than most other Saskatchewan River and boreal sites.

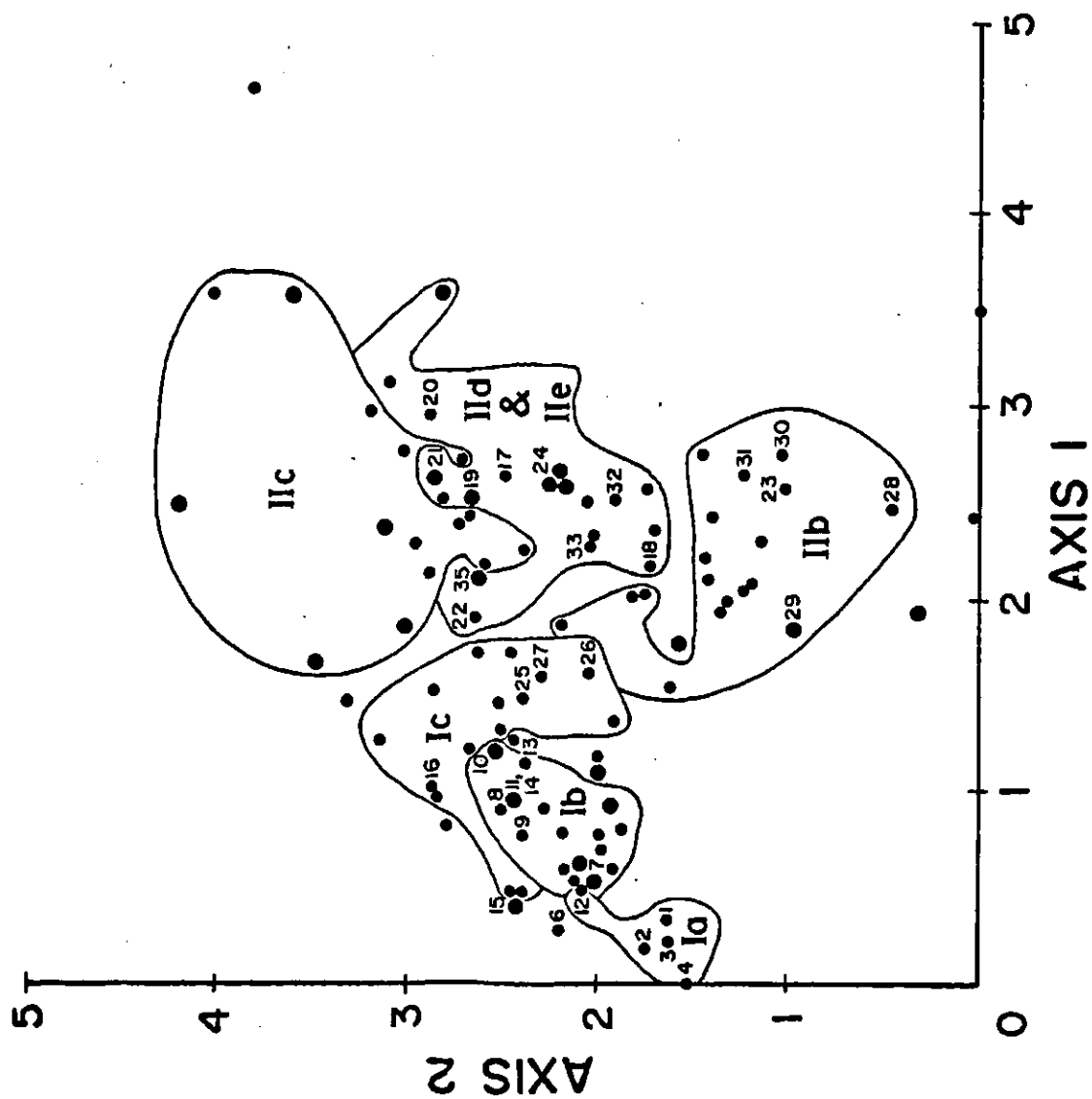
Thus, six of the eight subzones in the classification of extensive study data can be distinguished by their scores on the first two ordination axes.

Subzones IIId and IIe (high diversity southern boreal sites and Shield sites) are not separated on either the first or second DCA axis. These two subzones are very similar to one another and are the most similar pair of subzones in the classification of extensive study data.

Low diversity sites (Subzone IIa) have a wide range of ordination scores on both the first and second axes. The score assigned to each of these sites is related only to the ordination score of the single species present; no association among low diversity sites is evident. This further demonstrates the heterogeneity and artificiality of

Figure 69. DCA ordination of extensive study data: site scores on axes 1 and 2.

Larger dots represent two or more sites which have the same scores on both axes. Each enclosed area contains all the sites belonging to one of the subzones in the classification of extensive study data. Enclosed areas are labelled with a zone (Roman numeral) and subzone (lower case letter) label. Sites lying outside of the enclosed areas all belong to subzone IIa (very low diversity sites). Arabic numerals are intensive study site numbers.





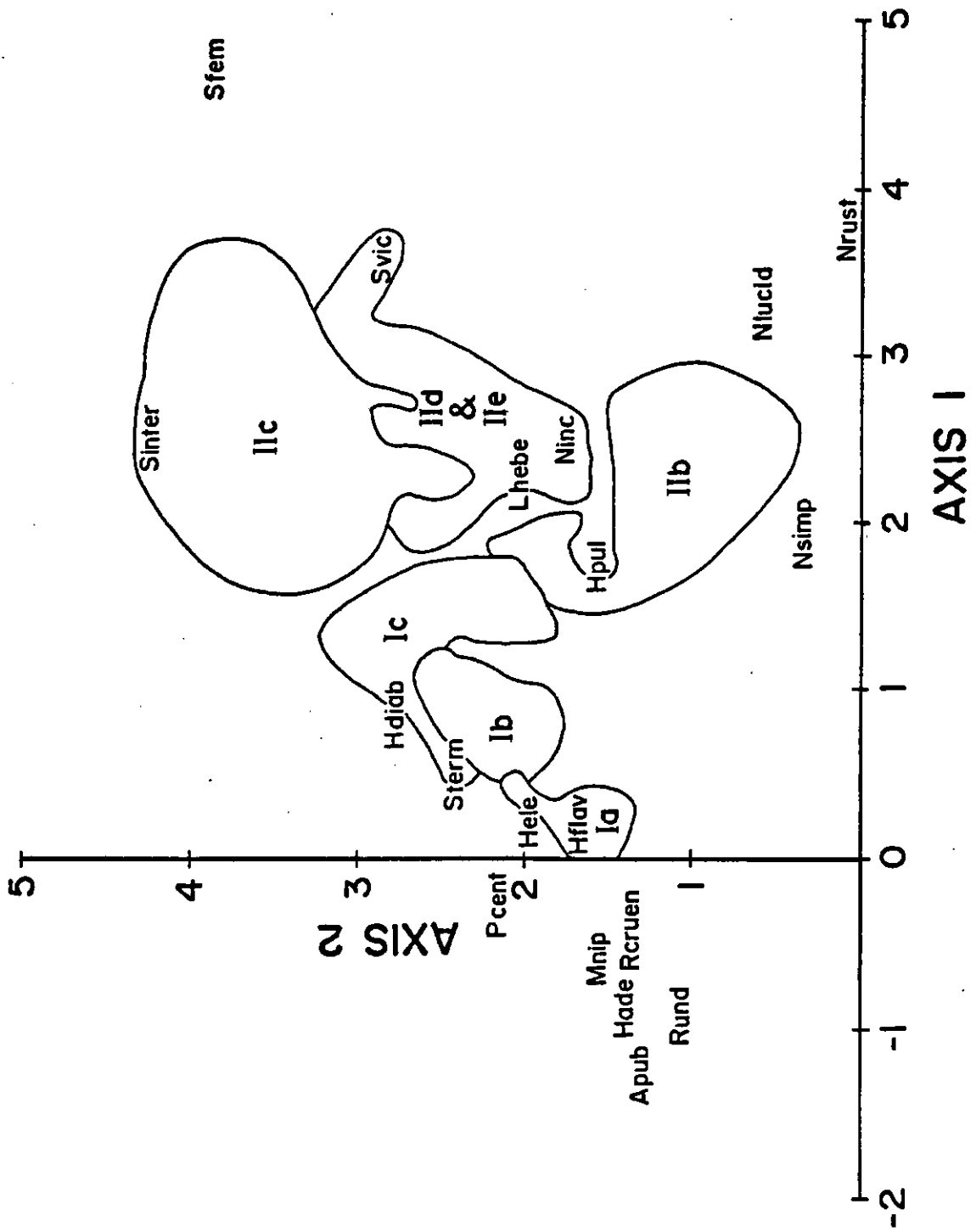
this subgroup.

The first two extensive study ordination axes are quite similar to the corresponding intensive study axes both in the general distribution patterns indicated and in the scores of the 35 intensive study sites. However, the range of site scores is greater on both extensive study axes. The greater range of site scores is due to the presence of sites from geographical areas not included in the intensive study. The sites with the highest first axis scores are nearly all Shield sites at which only Stenonema femoratum, or S. femoratum and Stenacron interpunctatum were collected. Neither S. femoratum nor any of these sites is included in the intensive study. The highest second axis scores belong to southern boreal and parkland sites at which S. interpunctatum is the dominant heptageniid. Not one of these sites is included in the intensive study. The other (lower) ends of both the first and second axes are similar to those of the corresponding intensive study axes.

Species scores on the first and second extensive study axes (Figure 70) are also similar to those on the corresponding intensive study axes. First axis species scores are especially similar, except for the inclusion of three additional species: Acanthomola pubescens, Pseudiron centralis and Stenonema femoratum (the first of these species was not collected during the intensive study; the latter two were outliers). Although A. pubescens and S. femoratum have the lowest and highest species scores, respectively, the range of first axis species scores is only slightly greater

Figure 70. DCA ordination of extensive study data; species scores on axes 1 and 2.

Species names given are abbreviations incorporating the first letter of the genus name (upper case) and the first three to five letters of the specific name (lower case). The boundaries of faunal subzones (as indicated by the range of site scores for each subzone) are indicated by solid lines, and each enclosed area is labelled with a zone and subzone number.



than in the intensive study ordination.

Most species have similar second axis scores in extensive study and intensive study ordinations. However, Nixe lucidipennis has a much lower score on the second extensive study axis and appears to be associated with high gradient streams (Subzone IIb) rather than other boreal streams. Stenacron interpunctatum has the highest second axis score, probably because of its association with low gradient southern boreal and parkland streams (Subzone IIc). In intensive study quantitative data ordinations, S. interpunctatum also has the highest, or second highest, second axis species score. However in the intensive study presence/absence data ordination, N. inconspicua and N. lucidipennis have the highest second axis scores. Stenonema femoratum also has a high second axis score in the extensive study ordination.

The eigenvalues of the third and fourth extensive study axes are not much lower than those of the first two axes (Table 16). Thus, all four axes appear to be important in describing variation in the extensive study data.

Table 16. Eigenvalues of extensive study DCA axes.

<u>Axis Number</u>	<u>Eigenvalue</u>
1	0.559
2	0.390
3	0.222
4	0.160

The third axis describes differences between the

Saskatchewan River (Ib) and Saskatchewan River-like (IIc) subzones, and between the Shield (IIe) and other boreal (IIb-IIId) subzones (Figure 71). Saskatchewan River-like sites have higher ordination scores than Saskatchewan River sites and are more clearly differentiated from Saskatchewan River sites than on the first and second axes. Shield sites have lower ordination scores than most other boreal sites and are clearly differentiated from high diversity southern boreal sites. As on the first two axes, low diversity sites (Subzone IIa) have a wide range of ordination scores. Variation in third axis scores is also high among southern boreal (Subzone IIId), parkland (Subzone IIc) and Saskatchewan River (Subzone Ib) sites.

The highest third axis species score belongs to Nixe inconspicua (Figure 72). Other southern boreal species such as Leucrocuta hebe, N. lucidipennis and N. simplicoides also have relatively high scores. None of these species has been collected in the Shield. The two commonest heptageniids in Shield streams and rivers, Heptagenia pulla and Stenonema vicarium, have very low third axis scores. N. rusticalis also has a relatively low score, probably because of its association with high gradient streams (Subzone IIb), some of which also have low third axis scores. The similarity of these high gradient sites to Shield sites (Subzone IIe) is probably due to the occurrence of H. pulla at both groups of sites.

Pseudiron centralis has the lowest third axis species score. P. centralis is the only psammophilic heptageniid in

Figure 71. DCA ordination of extensive study data: site scores on axes 1 and 3.

Symbols and labels are explained in Figure 69.

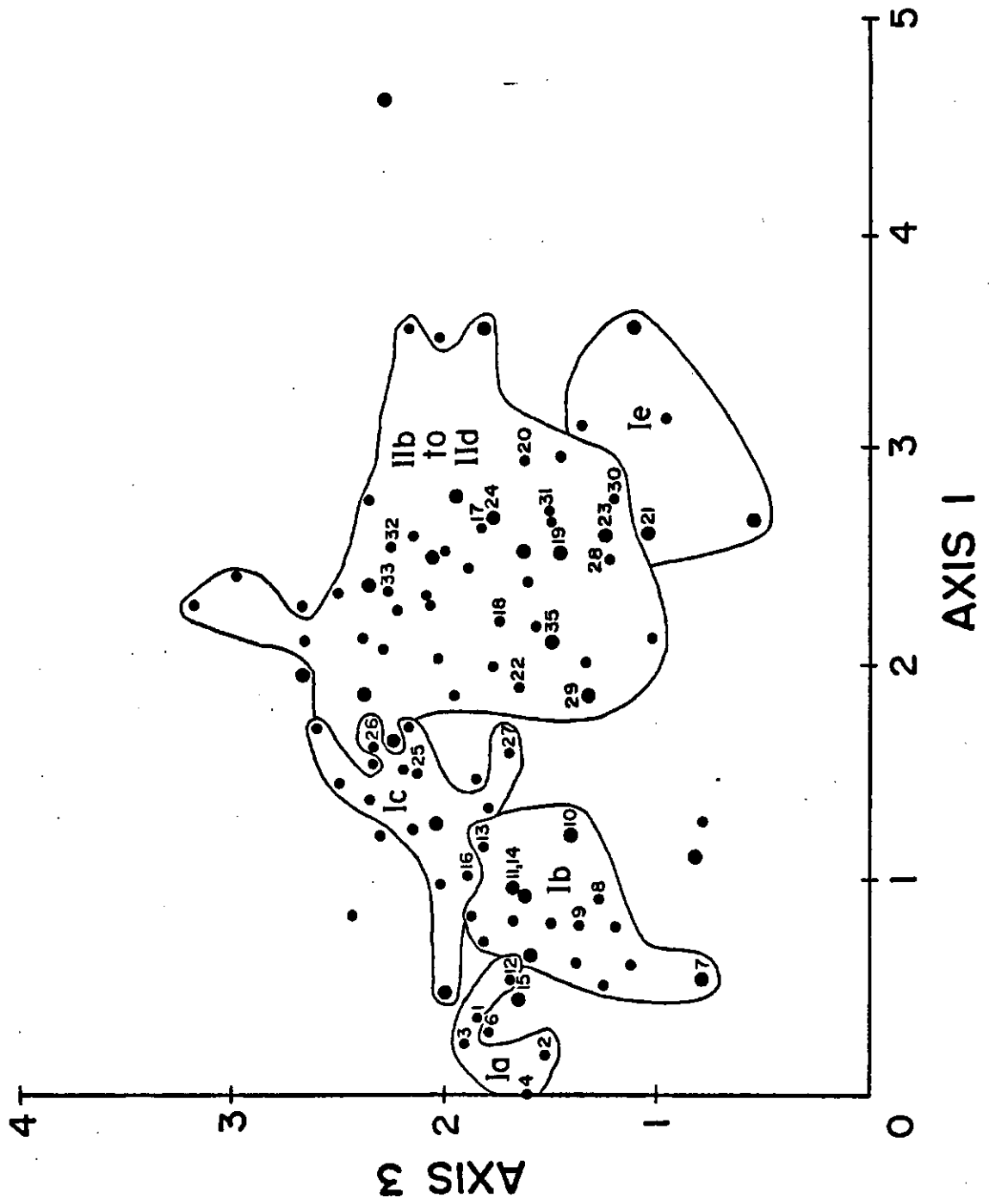
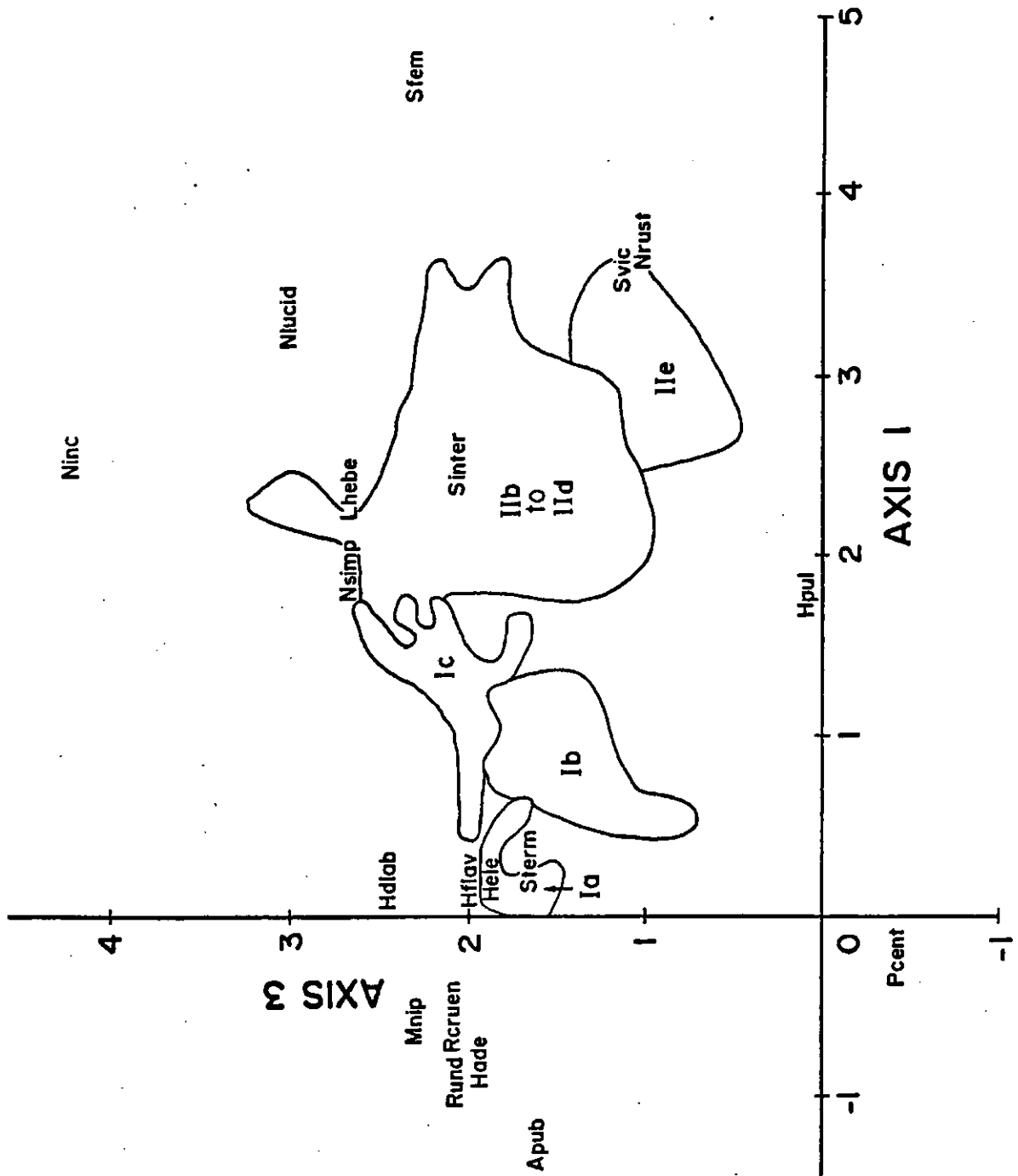


Figure 72. DCA ordination of extensive study data: species scores on axes 1 and 3.

Symbols and labels are explained in Figure 70.





Saskatchewan and has a different distribution than other Saskatchewan River species. The observed variation in Saskatchewan River site scores on the third axis may be related to the presence or absence of P. centralis. Other Saskatchewan River species all have scores near the center of the third axis.

Site scores on the fourth extensive study axis (Figure 73) do not differ much among subzones or among the sites within any subzone, except among the low diversity sites (Subzone IIa). Thus, much of the variation described by the fourth axis appears to be related to differences in the species present at low diversity sites. Sites where only Nixe rusticalis is present have the highest site scores; sites where another Nixe species or a Stenonema species is present have the lowest scores. N. rusticalis has the highest fourth axis species score, and N. lucidipennis, N. simplicoides and the three Stenonema species have the lowest scores (Figure 74).

There is some variation in fourth axis scores among boreal sites. Low gradient southern boreal and parkland sites (Subzone IIc) generally have higher scores than other boreal sites, and high gradient stream sites (Subzone IIb) are divided into two fairly distinct groups. High gradient sites where Nixe rusticalis was collected have relatively high scores, similar to those of high diversity boreal and Shield sites; high gradient sites where N. rusticalis was absent have lower scores than most other boreal sites.

Thus, some of the variation described by the fourth axis

Figure 73. DCA ordination of extensive study data: site scores on axes 1 and 4.

Symbols and labels are explained in Figure 69.

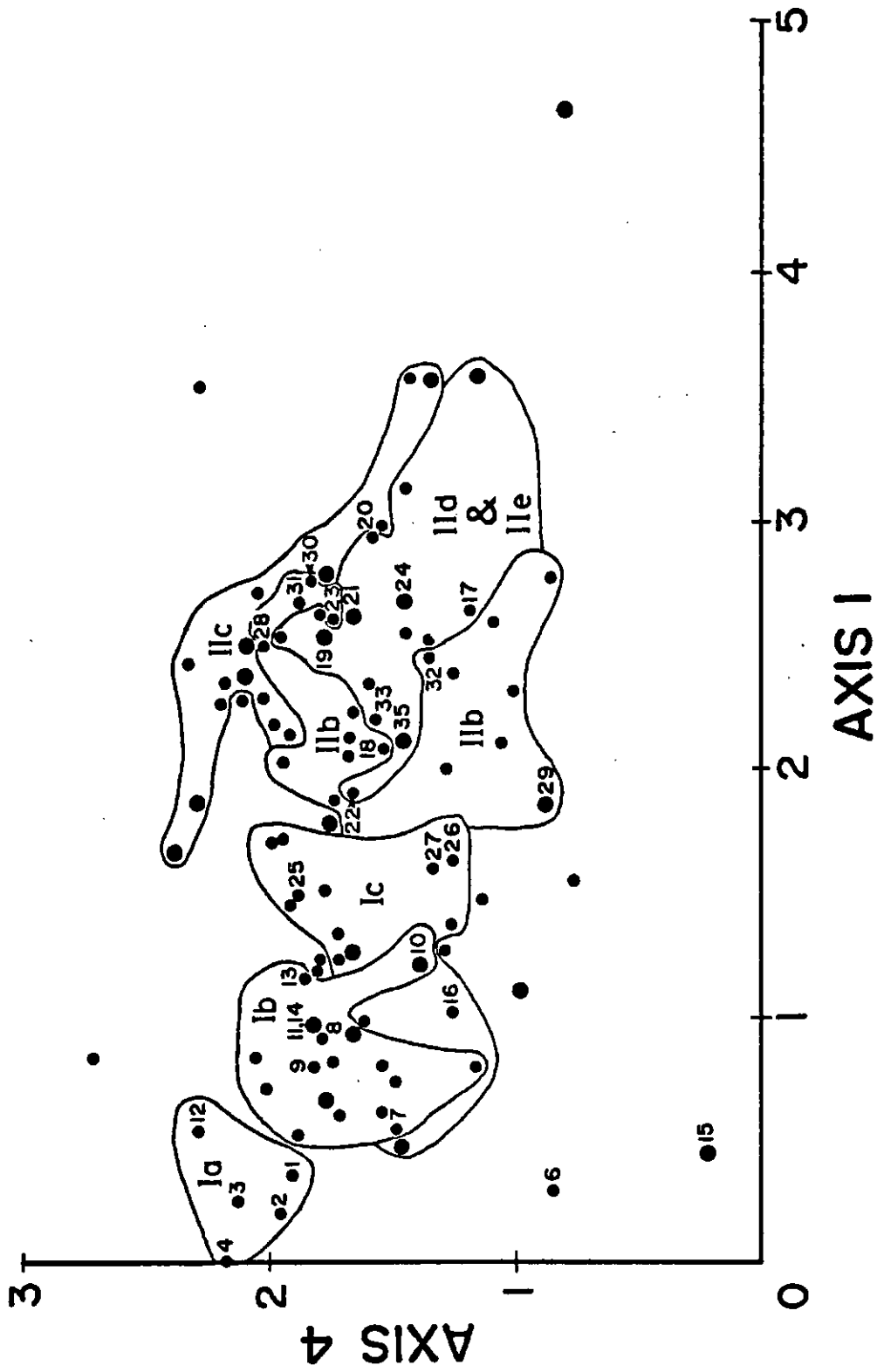
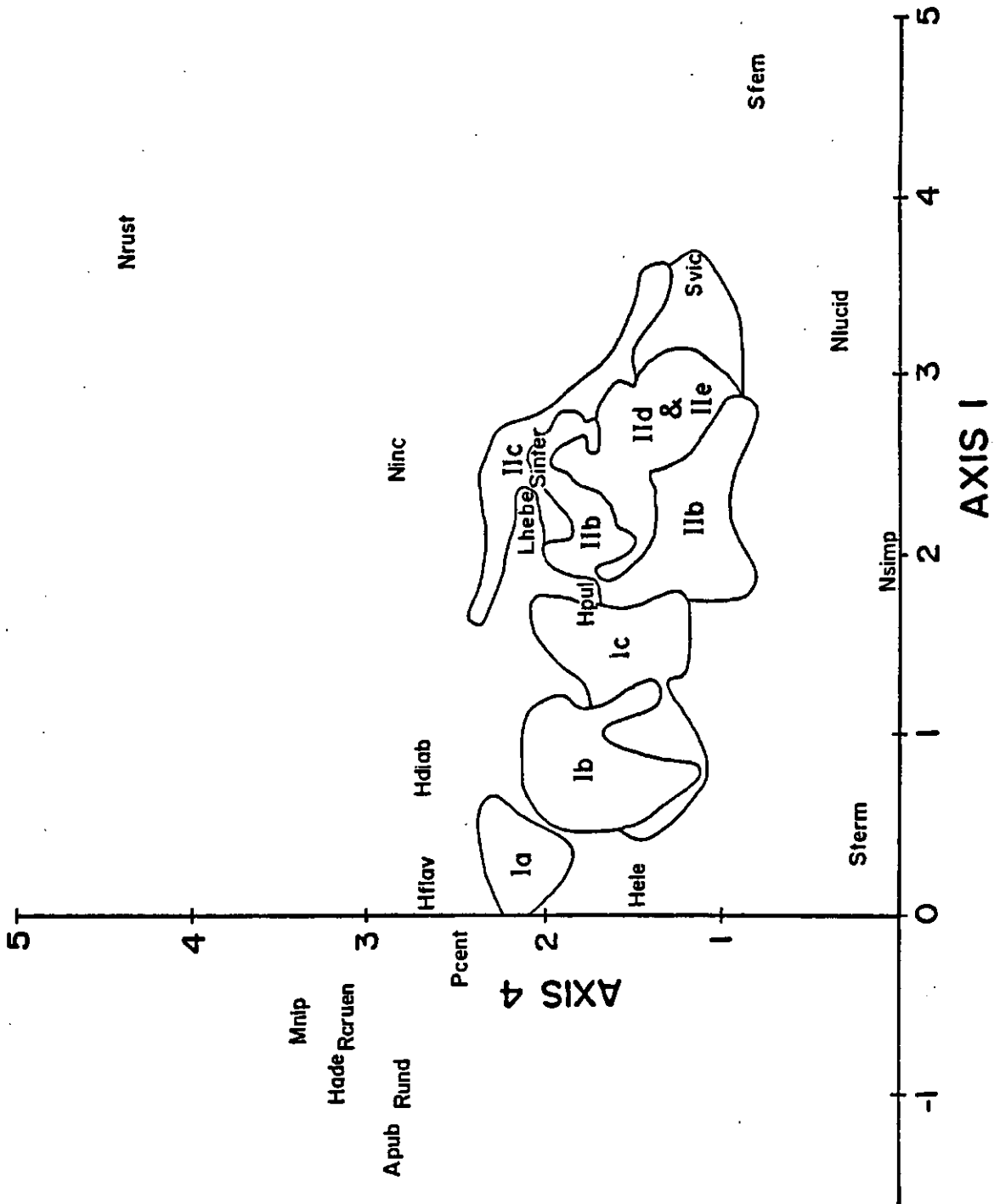


Figure 74. DCA ordination of extensive study data; species scores on axes 1 and 4.  
Symbols and labels are explained in Figure 70.



appears to be related to intrazonal differences in the distributions of Nixe species. An examination of the distributions of only Nixe species reveals niche separation among three of the four species, primarily within the high gradient stream subzone (see Section 4.10).

Saskatchewan River sites (Zone I) differ little in fourth axis ordination scores, except that the four South Saskatchewan River sites upstream from Lake Diefenbaker and site 12 on the North Saskatchewan River (Subzone Ia) have slightly higher scores than other Saskatchewan River and Saskatchewan River-like sites (Subzones Ib and Ic). Rare species associated with the sites upstream from Lake Diefenbaker and site 12 also have relatively high fourth axis scores.

The third and fourth extensive study axes are different from all intensive study axes. Most intensive study sites lie near the centers of these axes. Therefore, most of the variation described by the third and fourth extensive study axes appears to be related to differences among sites not included in the intensive study.

Groups of sites are not as clearly separated in ordination space as they are in analyses of intensive study data. This is probably because of the larger size of the extensive study data set. Large data sets contain a larger number of intermediate sites, so that clusters are separated by areas of low point density rather than by gaps. The concept of biotic zones does not preclude the existence of intermediate transition areas; it only requires that such

transition areas be small relative to the sizes of zones. The validity of the indicated zones and subzones is affirmed by their distinctness in cluster analysis. The ordination plots show the relationships among these groups along several community gradients, along which the rate of change in species composition is not constant.

Ordination and classification of extensive study data indicate similar heptageniid distribution patterns. Both major groups and seven of the eight subgroups recognized in cluster analysis can be distinguished by their scores on the first three ordination axes. The low diversity subgroup is not apparent in the ordination, but this subgroup is probably artificial.



## 4.5 Comparisons of Data Sets and Analysis Techniques

### 4.5.1 Comparison of intensive study data sets

The three sampling methods used all show species selectivity, relative to one another. Frequencies of occurrence and relative abundances of many species differ significantly among sampling methods (Tables 17 and 18).

In spite of these differences in species selectivity, ordinations and classifications of annual sweep net and stone data are very similar. Ordinations are especially similar. Classifications are also similar, but differ in the apparent distinctness of the high gradient stream cluster (whether or not this cluster should be recognized as a boreal subgroup or as a separate major group).

Multivariate analyses of log data produce results that are quite different from those of the other two sampling methods. This may be due to the small number of species and study sites included in the log data set.

Multivariate analyses of combined presence/absence data produce results similar to those from analyses of quantitative sweep net and stone data. Again, ordinations are especially similar. Classifications differ in one important feature. The six clusters recognized in the presence/absence data classification, which correspond quite closely to subgroups present in quantitative data classifications, are too different to be combined into two or three large groups. The greater heterogeneity among these clusters in presence/absence data analysis is probably due to the greater weight placed on rare species. In analysis of

Table 17. Relative abundances of Saskatchewan heptageniids in different types of samples. Values given constitute the percentage composition of each sample type, averaged across all sites and times.

<u>Species</u>	<u>Sample Type</u>		
	<u>Sweep Net</u>	<u>Stone</u>	<u>Log</u>
Heptagenia adequata	5.4	3.5	2.3
H. diabasia	0.3	1.1	8.9
H. elegantula	12.0	13.8	19.2
H. flavescens	1.5	0.9	0.8
H. pulla	20.8	23.9	15.9
Leucrocuta hebe	7.0	8.2	8.5
Macdunnoa nipawinia	1.0 a	0 b	0 b
Nixe inconspicua	0.8	0.2	0 ab
N. lucidipennis	1.9	0.7	0.7
N. rusticalis	3.6	1.6	0 ab
N. simplicoides	5.3	2.0	0.7
Raptoheptagenia cruentata	1.3 a	0.1 b	0 b
Rhithrogena undulata	0.2 a	0 b	0 b
Stenacron interpunctatum	9.8	15.7	14.6
Stenonema femoratum	0 a	0.2 b	0 a
S. terminatum	15.6	14.9	20.4
S. vicarium	12.8	13.0	16.5
Pseudiron centralis	0.8 a	0 b	0 b

a - significantly different from percent present in stone samples,  $p < .01$ ,

b - significantly different from percent present in sweep net samples,  $p < .01$ ,

significance determined by test of difference between two proportions (Walpole and Myers 1972, pp. 261).

Table 18. Frequencies of occurrence of Saskatchewan heptageniids in different types of samples. Values given are the percentages of samples, from all sites and times, in which each species was collected.

<u>Species</u>	<u>Sample Type</u>		
	<u>Sweep Net</u>	<u>Stone</u>	<u>Log</u>
Heptagenia adequata	9.1	10.1	2.0 ab
H. diabasia	0.9 a	3.9 b	15.2 ab
H. elegantula	21.1 a	32.9 b	24.2
H. flavescens	5.6	4.4	1.0
H. pulla	49.6 a	60.1 b	20.2 ab
Leucrocuta hebe	10.3	16.2	10.1
Macdunnoa nipawinia	2.2 a	0 b	0
Nixe inconspicua	1.7	0.9	0
N. lucidipennis	3.0	2.6	1.0
N. rusticalis	4.7	4.4	0 ab
N. simplicoides	7.8	5.7	1.0 b
Raptoheptagenia cruentata	3.4 a	0.4 b	0
Rhithrogena undulata	3.0 a	0 b	0
Stenacron interpunctatum	21.6 a	4.0 b	21.2 a
Stenonema femoratum	0	1.3	0
S. terminatum	34.9	38.6	29.3
S. vicarium	26.3 a	35.5 b	23.2
Pseudiron centralis	3.0 a	0 b	0

a - significantly different from percent present in stone samples,  $p < .01$ ,

b - significantly different from percent present in sweep net samples,  $p < .01$ ,

significance determined by chi-square test of independence (Walpole and Myers 1972, pp. 276)

presence/absence data all species are treated equally, and rare species are more important in defining group associations and intergroup differences than they are in quantitative data analyses. In analysis of quantitative data species are weighted relative to the logarithms of their abundances, and sites having similar complements of abundant species are likely to be grouped together regardless of differences in rare species. The greater importance of rare species in presence/absence data is probably also responsible for the assignment of some sites to different clusters than in quantitative data analyses.

Major distribution patterns present in seasonal data are very similar to those in annual data. There is some additional structure in the seasonal data associated with seasonal changes in the abundances of species with summer life cycles. This seasonal variation is reflected in the subgroup-level separation of early and late season samples in the classification of seasonal stone data, and in the greater length of the first and second axes in ordinations of all data sets. Further additional structure in the seasonal data is indicated by the high eigenvalues of the third and fourth axes. However, these axes differ among data sets, and the variation they describe is probably not meaningful. Subgroup structure in the classification of seasonal sweep net data differs greatly from that in other analyses and is probably due to several low abundance samples in the seasonal sweep net data rather than to meaningful distribution patterns.

In conclusion, sweep net and stone samples appear to be

equally useful for studying heptageniid distribution patterns. Stone data provide slightly better classifications, especially in regard to subgroup structure. However, several species were collected only in sweep net samples. Therefore, both sweep net and stone samples are useful. Log samples, however, are unsuitable for analyzing general heptageniid distribution patterns.

Species presence/absence data are also useful for analyzing heptageniid distribution patterns. Multivariate analyses of presence/absence data are similar to those of quantitative data, except for the failure of subzones to fuse into large homogenous groups in cluster analysis, and differences in the associations of several sites in both classifications and ordinations. Because of these differences, presence/absence data does not appear to be as good as quantitative data for analyzing heptageniid distribution patterns. However, presence/absence data is much easier and less expensive to collect and may be suitable for some purposes. Furthermore, differences between presence/absence and quantitative data analyses appear to be primarily due to the weight placed on rare species. Removal or downweighting of rare species might improve the quality of classifications and ordinations of presence/absence data.

#### 4.5.2 Representativeness of the intensive study sites

Distribution patterns indicated by analyses of intensive study and extensive study data are similar. Classifications of the two data sets contain the same two or three major

groups, in spite of the inclusion of 139 additional sites in the extensive study.

More subzones are recognized in the extensive study than in the intensive study. Thus, some areas in the province were not adequately sampled in the intensive study. Extensive study subzones not recognized in the intensive study include:

- 1) Subzone Ic - Saskatchewan River-like southern boreal and parkland rivers. Four sites from this subzone, sites 16, 25, 26 and 27, were included in the intensive study, where they were classified with Saskatchewan River sites. The inclusion of more sites from this subzone in the intensive study might have facilitated its recognition, but would have greatly increased travel time and expense.
- 2) Subzone IIe - Shield streams and rivers. Only one of these sites (site 21) was included in the intensive study. This subgroup is distinguished from other boreal subzones by the absence of species with summer life cycles (Leucrocuta hebe and Nixe species). These species are much more widespread in the southern boreal forest than preliminary collections indicated. Thus, the importance of including more Shield sites in the intensive study was not evident. The inclusion of more Shield sites would have been very expensive.
- 3) Subzone IIc - low gradient southern boreal and parkland streams. No sites from this subzone were included in the intensive study. This subzone is characterized by a unique combination of heptageniid species, rather than by any unique species. Because of this, its existence was not recognized either in preliminary collections or in visual inspection of

the extensive study data. Several sites from this subzone could have been included in the intensive study without a large increase in travel expense.

Most boreal stream sites included in the intensive study (other than high gradient sites) belong to one subzone in the extensive study classification. These sites were divided into two subgroups in most intensive study classifications. However, the division of boreal sites into subgroups differed among intensive study classifications and probably was artificial.

Ordinations of intensive study and extensive study data are also similar. The community gradients associated with the first two ordination axes are very similar in the two ordinations. However, the two extensive study axes are slightly longer than the corresponding intensive study axes, because of additional variation associated with Shield and low gradient southern boreal streams. Thus, while the intensive study correctly identified the two most important community gradients in Saskatchewan, it did not fully describe the extent of either gradient. Additional structure in the extensive study data, not present in the intensive study data, is described by the third and fourth extensive study axes. The third extensive study axis describes differences between Saskatchewan River and Saskatchewan River-like sites, and between Shield and southern boreal sites. Both Saskatchewan River-like and Shield sites were inadequately sampled in the intensive study. The fourth axis appears to be primarily related to intrazonal variations in

the distributions of Nixe species.

In summary, the intensive study sites provide a representative sample of heptageniid habitats in Saskatchewan, except for the low numbers of Shield, low gradient southern boreal and parkland, and Saskatchewan River-like sites included. These deficiencies do not prevent the recognition of major faunal zones or community gradients within the province. However, the extent of the two major community gradients is not fully described, and other important community gradients and some faunal subzones are missed. The inclusion of more Shield and Saskatchewan River-like sites in the intensive study probably would have been impractical.

#### 4.5.3 Comparison of classification and ordination

Comparing classifications and ordinations is difficult because the two techniques have different objectives. Nevertheless, distribution patterns indicated by cluster analysis and DCA are similar for most data sets examined in this study. The important DCA axes usually describe differences among groups of sites recognized in cluster analysis, and the first one or two DCA axes are always associated with differences among the two or three major clusters in the classification. Classifications and ordinations of annual intensive study data are especially similar in that ordinations contain recognizable clusters of sites that are very similar to groups or subgroups present in classifications. Clusters of sites are not as obvious in



ordinations of seasonal intensive study data or extensive study data because of the large number of data points.

Although cluster analysis and DCA show similar heptageniid distribution patterns, DCA appears to be superior to cluster analysis in two ways:

- 1) DCA is more robust. Ordinations vary less among data sets than do classifications. The two major community gradients (as indicated by the first two DCA axes) are very similar in all data sets. Differences among ordinations of different data sets are generally of relatively little importance, such as differences in the orientation of sites within a cluster or in the compactness of a cluster. On the other hand, differences among classifications tend to be greater, such as differences in the number of major groups recognized or in the assignment of individuals to major groups; and
- 2) ordination handles low diversity sites in a more meaningful way than does classification. In classifications, all low diversity sites are grouped together, regardless of the species present. Such associations of sites based only on the number of species present are not biogeographically meaningful. On the other hand, ordination scores assigned to low diversity sites are based on the identity of the species present.

The apparent superiority of DCA to cluster analysis may be due to the hierarchical and agglomerative nature of cluster analysis. However, performing relocation on existing classifications, which should produce global optimum classifications, does not improve consistency or the handling

of low diversity sites. The apparent superiority of DCA may also be due to the multidimensional presentation of ordination results. Although classifications are also multidimensional, their multidimensional nature cannot be adequately portrayed graphically or interpreted.

Nevertheless, cluster analysis provides useful information about the distinctness of clusters, and about the optimum locations for intercluster boundaries, which ordination cannot provide. Thus, both classification and ordination techniques are useful in the analysis of heptageniid distribution patterns.

#### 4.5.4 Synthesis of results from different analyses

The similarity among ordinations of different data sets makes it possible to draw firm conclusions about major linear trends in heptageniid distribution patterns. Only two important geographical community gradients are present in the intensive study area. Nearly all of the variation in annual data sets is described by these two gradients. Additional structure present in seasonal data is apparently related to within-site variation rather than to geographical variation. This within-site variation differs among sites and data sets and is probably due to noise in the data.

The two important intensive study gradients together define three fairly distinct clusters of sites: 1) Saskatchewan River, 2) high gradient boreal and 3) other boreal. The first community gradient distinguishes Saskatchewan River sites from boreal sites. Sites upstream

from Lake Diefenbaker are the most different from boreal streams, and the downstream-most South Saskatchewan and Saskatchewan River sites are the most similar to boreal sites. Two southern boreal stream sites, sites 25 and 26, are intermediate between Saskatchewan River and boreal sites. The second community gradient distinguishes high gradient boreal sites from other boreal sites.

If all species are weighted equally (as in analysis of species presence/absence data), South Saskatchewan River sites upstream from Lake Diefenbaker and site 12 on the North Saskatchewan River are sufficiently different from other Saskatchewan River sites to constitute a separate group. Similarly, site 27 is most similar to Saskatchewan River sites, rather than to high gradient stream sites, if all species are weighted equally.

The two most important community gradients in the entire province (as indicated by the first two extensive study DCA axes) are very similar to those in the intensive study area, but are slightly longer. The extensive study gradients are extended by the addition of Shield and low gradient southern boreal and parkland sites. Two additional community gradients are present in extensive study distribution patterns. The third community gradient describes differences between Shield and southern boreal streams, and between the Saskatchewan Rivers and Saskatchewan River-like southern boreal or parkland streams. The fourth gradient describes variation among very low diversity and high gradient stream sites, primarily related to intrazonal differences in the

distributions of Nixe species.

It is more difficult to draw conclusions about the existence or limits of faunal zones, because of differences among classifications of different data sets. There appear to be at least two faunal zones in Saskatchewan: 1) the Saskatchewan Rivers (including several southern boreal and parkland rivers with similar faunas), and 2) boreal streams and rivers (including most Shield, southern boreal and parkland streams and rivers). These two groups of sites form large, distinct clusters in classifications of all quantitative data sets and of extensive study presence/absence data. However, in the classification of intensive study presence/absence data, smaller groups are sufficiently different that they fail to form two or three large, homogenous clusters. The major difference among other classifications is whether high gradient streams are recognized as a boreal subzone or a separate major zone. In classifications of presence/absence and seasonal stone sample data, high gradient streams form a separate major zone; in classifications of extensive study and seasonal sweep net data they are a boreal subzone.

There are probably not more than three heptageniid faunal zones in Saskatchewan. Although classifications of intensive study presence/absence data contain four to six major groups, these classifications are probably less reliable than those based on quantitative data or extensive study data (in which only two or three major groups were recognized). Intensive study presence/absence data contains

less information than the other data sets.

Subzone structure varies even more among classifications and is therefore more difficult to draw conclusions about. High gradient streams certainly constitute a valid subzone, if they are not a separate major zone; a distinct high gradient stream cluster is evident in all classifications. South Saskatchewan River sites upstream from Lake Diefenbaker also form a distinct cluster in all analyses, and thus appear to constitute a valid subzone. However, it is not clear whether or not site 12 (on the North Saskatchewan River), and possibly also sites 7, 8 and 9, belong to this subzone. Low diversity sites form a distinct subgroup in all analyses. However, the similarity among these sites is only in the low numbers of species present and not in the identities of these species; thus, this subgroup is artificial. Boreal sites (other than high gradient sites) are divided into two subzones in nearly all intensive study data classifications. However, the compositions of these other boreal subzones differ greatly from one classification to the next, and no clear division of other boreal sites is evident in the classification of extensive study data or in any ordination. Therefore, intensive study boreal sites, other than high gradient stream sites, probably all belong to a single subzone.

In conclusion, the intensive study area appears to contain four subzones: South Saskatchewan River sites upstream from Lake Diefenbaker, other Saskatchewan River sites, high gradient boreal stream sites, and other boreal

sites.

Three additional subzones, which are poorly represented or absent in the intensive study area, are present in the extensive study area: Saskatchewan River-like southern boreal and parkland rivers, low gradient southern boreal and parkland streams and rivers, and Shield streams and rivers.

#### 4.6 Comparison of Heptageniid and Other Stream Insect Distribution Patterns in Saskatchewan

Faunal zones identified in this study are similar to those described by Lehmkuhl (1976a) for all mayflies in Saskatchewan (based on subjective assessment of the distributions of all mayfly species then known from Saskatchewan). Lehmkuhl recognized four mayfly faunal zones in Saskatchewan: 1) boreal, 2) Saskatchewan River, 3) Cypress Hills, and 4) prairie. The prairie mayfly fauna is very restricted and contains no heptageniid species. The Cypress Hills area contains only one characteristic heptageniid species which, because of its restricted distribution in Saskatchewan, is an outlier in this study. Thus, neither the prairie nor the Cypress Hills faunal zone is apparent in this study. Lehmkuhl's other two faunal zones are the same as the two major zones recognized in this study. Lehmkuhl did not recognize the distinctness of high gradient streams. However, the Nixe species which characterize these streams were not known from Saskatchewan in 1976.

Stonefly distribution patterns in Saskatchewan are similar to those of heptageniids. Sixteen of the 18 most common stoneflies in Saskatchewan are primarily or exclusively restricted to one of three areas: 1) the boreal forest (five species), 2) the Saskatchewan Rivers (six species), and 3) the Cypress Hills (five species) (Dosdall and Lehmkuhl 1979, L. Dosdall pers. comm.). Only two species are common in both Saskatchewan River and boreal habitats.

The major difference between heptageniid and stonefly distribution patterns is the presence of a Cypress Hills stonefly faunal zone. The evidence for a Cypress Hills zone from both stonefly and non-heptageniid mayfly distributions suggests that it is a valid stream insect faunal zone.

Among Saskatchewan stoneflies, there are several triplets of species belonging to the same genus, or to closely related genera, in which one species from each triplet is found in each faunal zone (L. Dosdall pers. comm.). Thus, interzonal differences in stonefly faunas tend to be primarily specific. On the other hand, interzonal differences in heptageniid faunas tend to be generic. A possible explanation for this difference in the level of interzonal taxonomic differences is presented in Section 4.10.

No subzone structure was evident in stonefly distribution patterns (although subzones may be difficult to detect without quantitative data and multivariate analysis). No differences in stonefly faunas were found between northern and southern boreal streams, or between high and low gradient streams (L. Dosdall pers. comm.).

Caddisfly faunas also differ between boreal streams or rivers and the Saskatchewan Rivers, although not as much as do heptageniid or stonefly faunas. One hundred and seventy-two caddisfly species are known from the boreal forest and 55 from the Saskatchewan Rivers; 40 of these species occur in both areas (Smith 1975, 1984).

Smith (1984) observed differences in the caddisfly



faunas of the Shield and southern boreal forest similar to those observed in heptageniid faunas. Only one half (79 of 157) of the caddisfly species found in the southern boreal forest were also collected in the Shield (Smith 1984). Fifteen additional caddisfly species were collected only on the Shield. However, caddisfly faunas were similar in high gradient, low gradient, and other boreal streams. The faunal peculiarity of high gradient boreal streams may be restricted to heptageniids.

Geographical variation in the caddisfly fauna within the South Saskatchewan River also resembles that displayed by heptageniids. The caddisfly fauna in the South Saskatchewan River upstream from Lake Diefenbaker is relatively rich; between Gardiner Dam and Saskatoon (in the area that is thermally influenced by Gardiner Dam), the fauna is reduced in richness and contains a number of boreal species; downstream from Saskatoon, the caddisfly fauna is richer but different in composition than that either immediately upstream or downstream from Lake Diefenbaker (Smith 1975). Heptageniid distribution patterns within the South Saskatchewan River are similar, except that: 1) no boreal heptageniids were collected between Gardiner Dam and Saskatoon, 2) the first site downstream from Saskatoon (site 9) is more similar to sites between Gardiner Dam and Saskatoon than to other sites downstream from Saskatoon, and 3) other sites downstream from Saskatoon are the most similar to boreal sites.

The caddisfly fauna of the North Saskatchewan River is

relatively depauperate, except for the two downstream-most sites (Borden Bridge and Cecil Ferry, site 12), which faunistically resemble sites upstream from Lake Diefenbaker (Smith 1975). Again, heptageniid distribution patterns are similar, except that only the downstream-most North Saskatchewan River site (site 12) resembles sites upstream from Lake Diefenbaker in heptageniid species composition.

#### 4.7 Environmental Explanation of Distribution Patterns

Associations between environmental parameters and observed heptageniid distribution patterns were identified by weighted averages hybrid ordination. Hybrid ordination scores for standardized environmental variables were calculated using site (or sample) scores from DCA ordinations of annual (or seasonal) biological data.

The absolute values of hybrid ordination environmental scores are meaningless and vary with the magnitude of the mean to which each parameter is standardized. Therefore, environmental scores were rescaled to the same range as the corresponding site scores to facilitate comparisons with faunal patterns (the range of site scores on each axis is determined during DCA rescaling as the amount of species turnover along the axis).

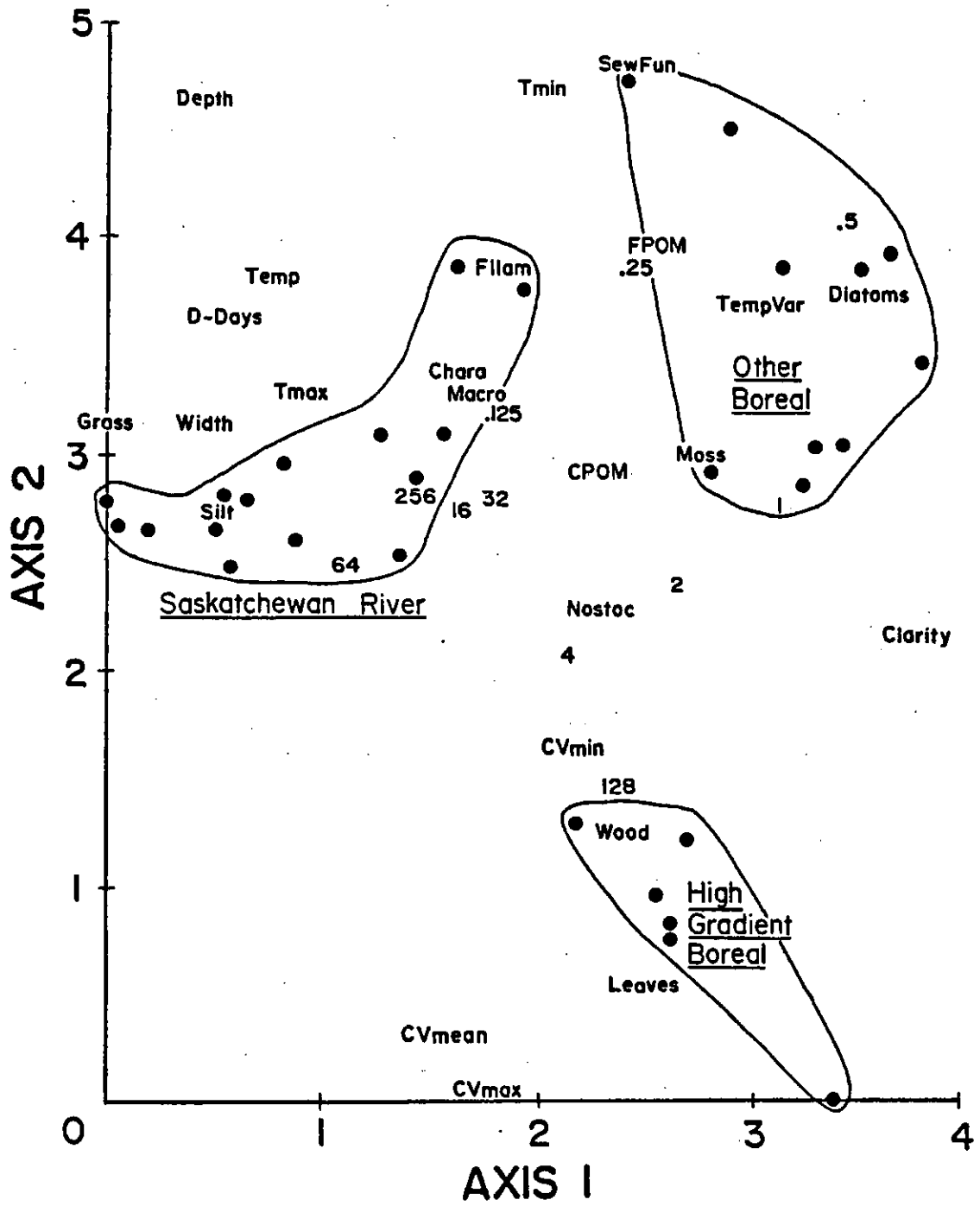
##### 4.7.1 Hybrid ordination of annual data

Annual environmental data include measurements of substrate particle size distribution (once at each site), mean, maximum and minimum annual measurements of water temperature and current velocity, and mean annual measurements of other environmental parameters (Appendix 9).

Figure 75 shows hybrid ordination environmental scores on the first and second, annual sweep net data, DCA axes. Environmental parameters with extreme scores on the first axis are important in distinguishing the Saskatchewan River and boreal faunal zones (which are separated on the first DCA axis). Stream depth and width, mean and maximum water

Figure 75. Hybrid ordination environmental scores on the first and second, annual sweep net data, DCA axes. Environmental scores on each axis have been rescaled to the same range as the site scores. First and second axis site scores are represented by dots. Enclosed areas represent the three main faunal regions in Saskatchewan, as defined in the faunal classification of intensive study sites. Environmental scores are represented by the centers of abbreviated environmental parameter names, which are explained below.

<u>Abbreviation</u>	<u>Environmental Parameter</u>
Depth	Maximum stream depth
Width	Stream width
Temp	Water temperature
Tmax	Maximum water temperature
Tmin	Minimum water temperature
D-Days	Annual number of degree-days
TempVar	Diurnal water temperature variation
CVmean	Mean current velocity
CVmax	Maximum current velocity
CVmin	Minimum current velocity
Silt	Depth of silt on the substrate
Clarity	Water clarity
CPOM	Ash-free dry weight of coarse (> 1 mm) particulate organic material
FPOM	Ash-free dry weight of fine (0.2 to 1mm) particulate organic material
SewFun	Sewage fungus
Filam	Filamentous algae
Nostoc	<u>Nostoc</u>
Diatoms	Diatom blooms
Chara	<u>Chara</u>
Moss	Moss
Macro	Macrophytes
Grass	Allochthonous grass
Leaves	Allochthonous broad leaves
Wood	Allochthonous wood fragments
256	Substrate particles > 256 mm in diameter
128	Substrate particles 128 to 256 mm in diameter
64	Substrate particles 64 to 128 mm in diameter
32	Substrate particles 32 to 64 mm in diameter
16	Substrate particles 16 to 32 mm in diameter
4	Substrate particles 4 to 16 mm in diameter
2	Substrate particles 2 to 4 mm in diameter
1	Substrate particles 1 to 2 mm in diameter
.5	Substrate particles 0.5 to 1 mm in diameter
.25	Substrate particles 0.25 to 0.5 mm in diameter
.125	Substrate particles 0.125 to 0.25 mm in diameter



temperature, annual number of degree-days, silt deposition, and allochthonous grass all have low first axis scores. Thus, these parameters characteristically have higher values at Saskatchewan River sites (which have the lowest site scores on the corresponding DCA axis) than at boreal sites. Similarly, water clarity, coarse sand (substrate particles in the 0.5 to 1, and 1 to 2 mm size classes), diatom blooms, and diurnal water temperature variation have high first axis scores and are greater at boreal sites.

Second axis hybrid scores show which environmental parameters are important in distinguishing high gradient and other boreal streams. Current velocity (especially mean and maximum annual velocity), and allochthonous leaves and wood have the lowest second axis scores and thus are characteristically greater in high gradient streams. Water depth, minimum annual water temperature and sewage fungus growth have the highest second axis scores and are thus greater at other boreal and Saskatchewan River sites.

The third and fourth axes in the DCA ordination of annual sweep net data have very low eigenvalues, do not describe important variation in the data, and cannot be interpreted meaningfully. Hybrid ordination environmental scores on these axes (Table 19) also appear to be random.

Figure 76 shows hybrid ordination environmental scores on the first and second, annual stone data, DCA axes. These scores are similar to those on the first and second sweep net axes. Faunal differences between the Saskatchewan River and boreal zones again appear to be associated with differences

Table 19. Hybrid ordination environmental scores on the third and fourth, annual sweep net data, DCA axes. Environmental scores on each axis have been rescaled to the same range as site scores. Abbreviated environmental parameter names are explained in Figure 75.

<u>Axis 3</u>		<u>Axis 4</u>	
<u>Environmental Parameter</u>	<u>Ordination Score</u>	<u>Environmental Parameter</u>	<u>Ordination Score</u>
Nostoc	1.49	Tmax	1.96
128	1.35	D-Days	1.84
.125	1.35	.125	1.61
Tmax	1.26	Temp	1.61
64	1.16	Filam	1.58
D-Days	1.16	4	1.58
32	1.12	CVmean	1.54
Diatoms	1.07	CVmin	1.54
Temp	1.07	64	1.54
2	0.98	Grass	1.50
Leaves	0.98	Diatoms	1.50
CPOM	0.98	32	1.50
Wood	0.93	CPOM	1.46
CVmax	0.88	Silt	1.46
CVmean	0.84	16	1.38
Macro	0.84	128	1.38
Tmin	0.79	256	1.38
FPOM	0.79	Macro	1.38
4	0.79	2	1.35
1	0.75	Width	1.27
Moss	0.75	Nostoc	1.23
CVmin	0.75	CVmax	1.19
TempVar	0.75	Leaves	1.15
Grass	0.65	Wood	1.11
Depth	0.61	FPOM	1.11
Clarity	0.61	Moss	1.11
Chara	0.51	Depth	1.11
256	0.47	SewFun	1.00
SewFun	0.47	Chara	1.00
16	0.37	1	1.00
Silt	0.37	Clarity	0.92
Filam	0.28	TempVar	0.88
25	0.19	Tmin	0.77
Width	0.14	.25	0.46
.5	0.00	.5	0.00

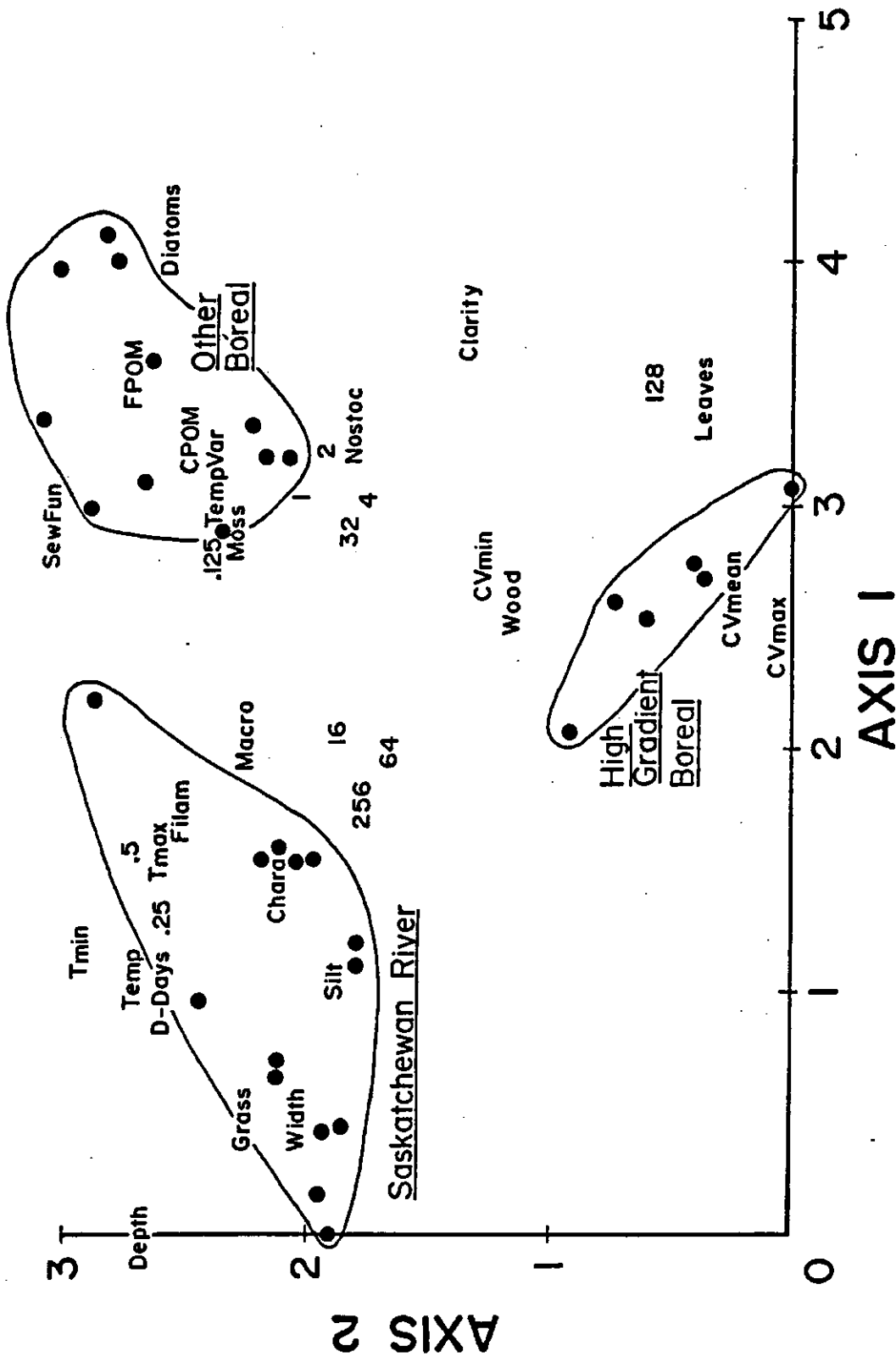


Figure 76. Hybrid ordination environmental scores on the first and second, annual stone data, DCA axes. Symbols and abbreviated environmental parameter names are explained in Figure 75.



in stream depth and width, and the amount of allochthonous grass (all of which are greater at Saskatchewan River sites), and diatom blooms and water clarity (which are greater at boreal sites). Fine particulate organic material (FPOM), stones 128 to 256 mm in diameter, and allochthonous leaves also have relatively high first axis scores, and thus also appear to be associated with boreal streams. Water temperature, silt depth, and coarse sand are less important than on the first sweep net axis.

On the second stone axis, mean and maximum annual current velocity, allochthonous leaves, and stones 128 to 256 mm in diameter have the lowest scores; and minimum annual water temperature and sewage fungus growth have the highest scores. These parameters thus appear to be characteristic of high gradient and other boreal streams, respectively. All of these parameters, except 128 to 256 mm stones, are also important in distinguishing high gradient and other boreal streams on the second sweep net axis. Water depth and allochthonous wood are less important than on the second sweep net axis.

Third and fourth axis environmental scores (Table 20) defy meaningful interpretation and are unlike the third or fourth sweep net axis hybrid scores.

Hybrid ordination environmental scores on the first and second, annual presence/absence data, DCA axes (Figure 77) are similar to those on the corresponding quantitative data axes. The Saskatchewan River and boreal zones again differ mainly in stream depth and width, allochthonous grass, water

Table 20. Hybrid ordination environmental scores on the third and fourth, annual stone data, DCA axes. Environmental scores on each axis have been rescaled to the same range as site scores. Abbreviated environmental parameter names are explained in Figure 75.

<u>Axis 3</u>		<u>Axis 4</u>	
<u>Environmental Parameter</u>	<u>Ordination Score</u>	<u>Environmental Parameter</u>	<u>Ordination Score</u>
TempVar	2.56	Width	1.98
SewFun	2.06	Filam	1.52
32	2.01	Chara	1.37
Width	1.92	TempVar	1.07
Grass	1.87	SewFun	0.99
.125	1.87	Macro	0.91
64	1.74	Clarity	0.84
FPOM	1.69	Depth	0.84
Tmax	1.64	Grass	0.76
Chara	1.55	128	0.76
256	1.46	64	0.69
D-Days	1.42	256	0.61
4	1.42	32	0.61
Depth	1.37	16	0.53
Macro	1.37	CVmean	0.53
Filam	1.33	CPOM	0.46
Nostoc	1.28	1	0.46
Silt	1.23	Silt	0.46
16	1.23	CVmin	0.46
Temp	1.23	4	0.38
2	1.14	CVmax	0.38
CPOM	1.10	Moss	0.30
1	1.10	Leaves	0.30
128	0.78	D-Days	0.30
Diatoms	0.78	Temp	0.23
CVmean	0.73	Nostoc	0.23
Moss	0.69	FPOM	0.15
Tmin	0.64	2	0.15
Leaves	0.55	.5	0.15
CVmax	0.50	.125	0.15
CVmin	0.27	.25	0.08
Clarity	0.23	Diatoms	0.08
.25	0.09	Tmax	0.08
.5	0.00	Tmin	0.00
Wood	0.00	Wood	0.00

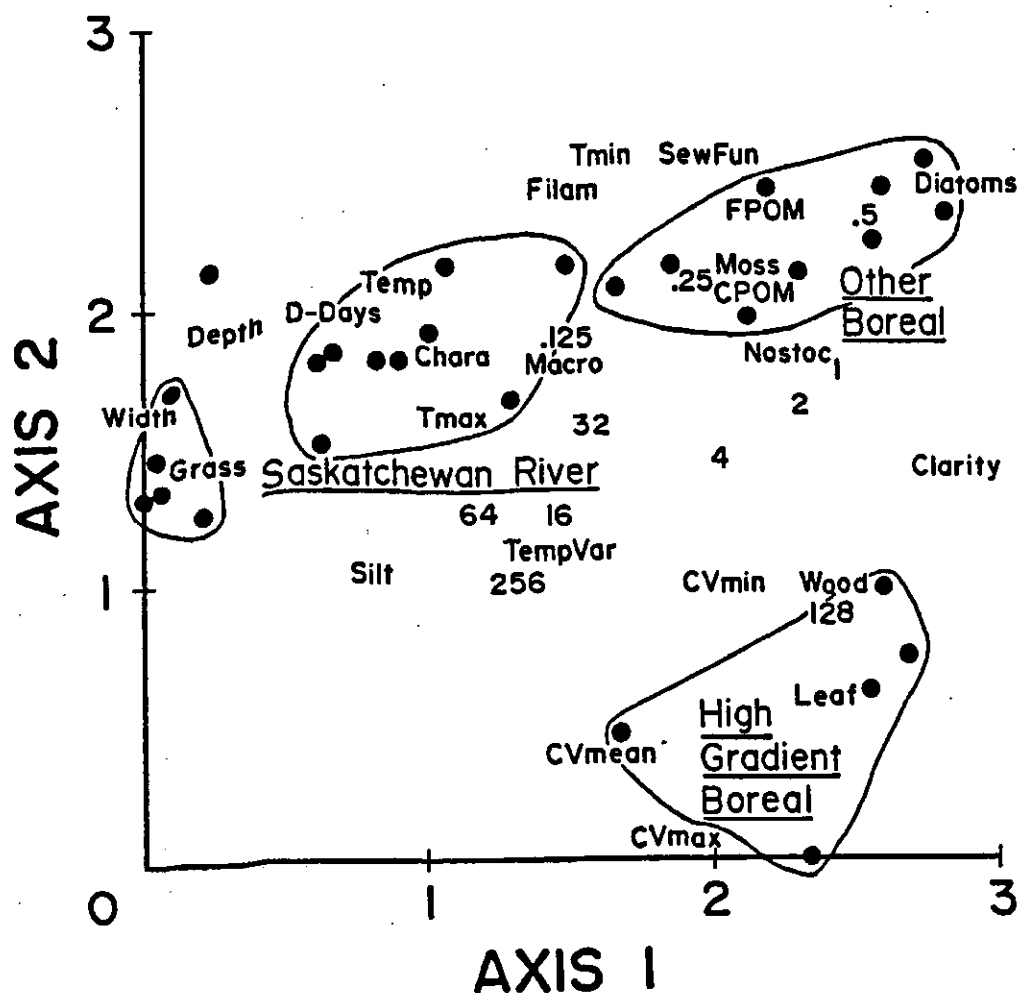


Figure 77. Hybrid ordination environmental scores on the first and second, annual presence/absence data, DCA axes. Symbols and abbreviated environmental parameter names are explained in Figure 75.

clarity and diatom blooms (all of which have extreme first axis scores). Water temperature, silt depth, and the amounts of coarse sand, allochthonous leaves and wood, and stones 128 to 256 mm in diameter, also appear to be different in the two faunal zones.

Mean and maximum annual current velocity, and allochthonous leaves have the lowest second axis scores and thus appear to be associated with high gradient streams; minimum annual water temperature and sewage fungus growth have the highest scores and appear to be associated with other boreal streams.

Third and fourth axis environmental scores (Table 21) again defy meaningful interpretation and are unlike the third or fourth axis scores on either quantitative data axis.

First and second axis environmental scores are quite similar in the three hybrid ordinations. Stream depth and width, water temperature, allochthonous grass, diatom blooms and water clarity have extreme first axis scores in all three ordinations and thus appear to be the most important environmental parameters in distinguishing the Saskatchewan River and boreal faunal zones. Silt depth, coarse sand, allochthonous leaves and FPOM also appear to differ between the two faunal zones.

Current velocity, minimum annual water temperature, and sewage fungus growth have extreme second axis scores and are most important in distinguishing high gradient and other boreal streams. Allochthonous leaves and FPOM also have relatively low second axis scores.

Table 21. Hybrid ordination environmental scores on the third and fourth, annual presence/absence data, DCA axes.  
 Environmental scores on each axis have been rescaled to the same range as site scores. Abbreviated environmental parameter names are explained in Figure 75.

<u>Axis 3</u>		<u>Axis 4</u>	
<u>Environmental Parameter</u>	<u>Ordination Score</u>	<u>Environmental Parameter</u>	<u>Ordination Score</u>
Tmin	2.67	FPOM	1.42
16	2.67	32	1.42
.25	2.56	.125	1.42
Silt	2.16	TempVar	1.37
4	2.16	Diatoms	1.37
.5	2.16	Nostoc	1.27
Temp	2.10	CPOM	1.18
D-Days	2.05	128	1.13
2	1.99	2	1.13
CVmin	1.99	4	1.03
CVmean	1.99	Grass	1.03
Tmax	1.99	SewFun	0.98
.125	1.87	Tmax	0.98
Wood	1.87	Moss	0.98
CVmax	1.87	1	0.98
Moss	1.76	D-Days	0.98
FPOM	1.76	Leaves	0.98
256	1.65	Macro	0.88
1	1.59	Temp	0.83
Diatoms	1.53	Clarity	0.78
Grass	1.53	64	0.78
Depth	1.42	CVmax	0.69
32	1.42	256	0.69
Nostoc	1.25	Wood	0.64
Leaves	1.19	Filam	0.64
Macro	1.19	Depth	0.64
CPOM	1.14	CVmean	0.59
64	1.08	Tmin	0.59
SewFun	0.62	CVmin	0.54
Filam	0.57	Width	0.54
Clarity	0.51	Silt	0.49
TempVar	0.34	Chara	0.49
128	0.17	16	0.44
Chara	0.11	.25	0.10
Width	0.00	.5	0.00

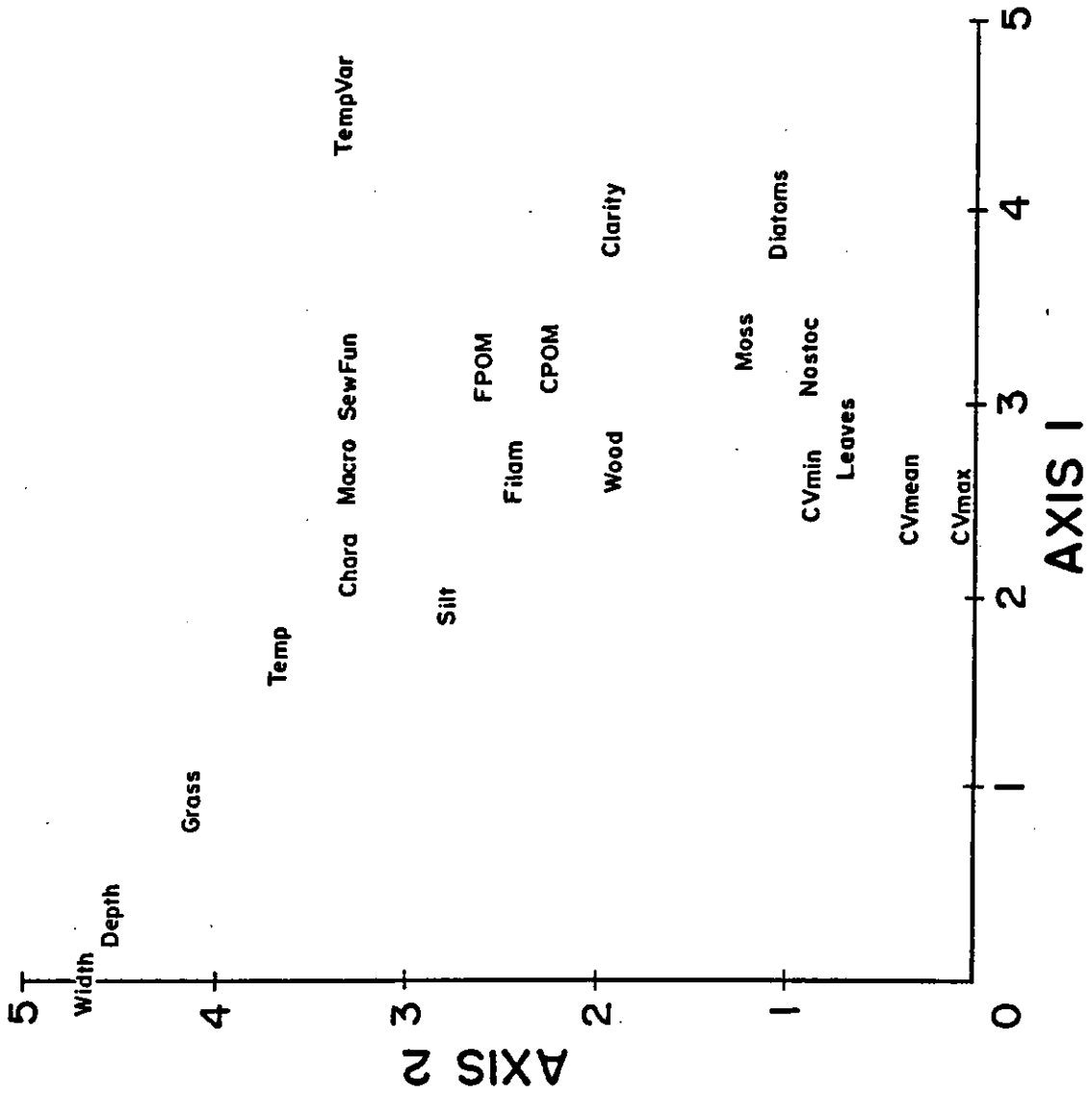
#### 4.7.2 Hybrid ordination of seasonal data

Hybrid ordinations of seasonal environmental data were performed using site scores from DCA ordinations of seasonal biological data. Seasonal environmental data include measurements of environmental parameters, including within-site minimum, maximum and mean current velocities, at each sampling site and time. Substrate particle size distribution is not included, because it was only measured once at each site.

Hybrid ordination environmental scores on the first and second, seasonal sweep net, DCA axes are presented in Figure 78. First axis scores are similar to those on the corresponding first annual DCA axes, except for the high score assigned to diurnal temperature variation. Water clarity and diatom blooms also have high first axis scores, and stream depth and width, allochthonous grass, and water temperature have low scores.

Current velocity and allochthonous leaves have the lowest second axis scores and thus appear to be characteristic of high gradient streams, as in annual data hybrid ordinations. Diatom blooms, Nostoc, and moss also have relatively low second axis scores. Environmental parameters associated with the Saskatchewan River zone (stream depth and width, allochthonous grass, and water temperature) have the highest second axis scores. The high scores assigned to these parameters, which are much higher than on other second axes, are probably due to the relatively high second axis scores

Figure 78. Hybrid ordination environmental scores on the first and second, seasonal sweep net data, DCA axes. Environmental scores on each axis have been rescaled to the same range as sample scores. Environmental scores are represented by the centers of abbreviated environmental parameter names, which are explained in Figure 75.



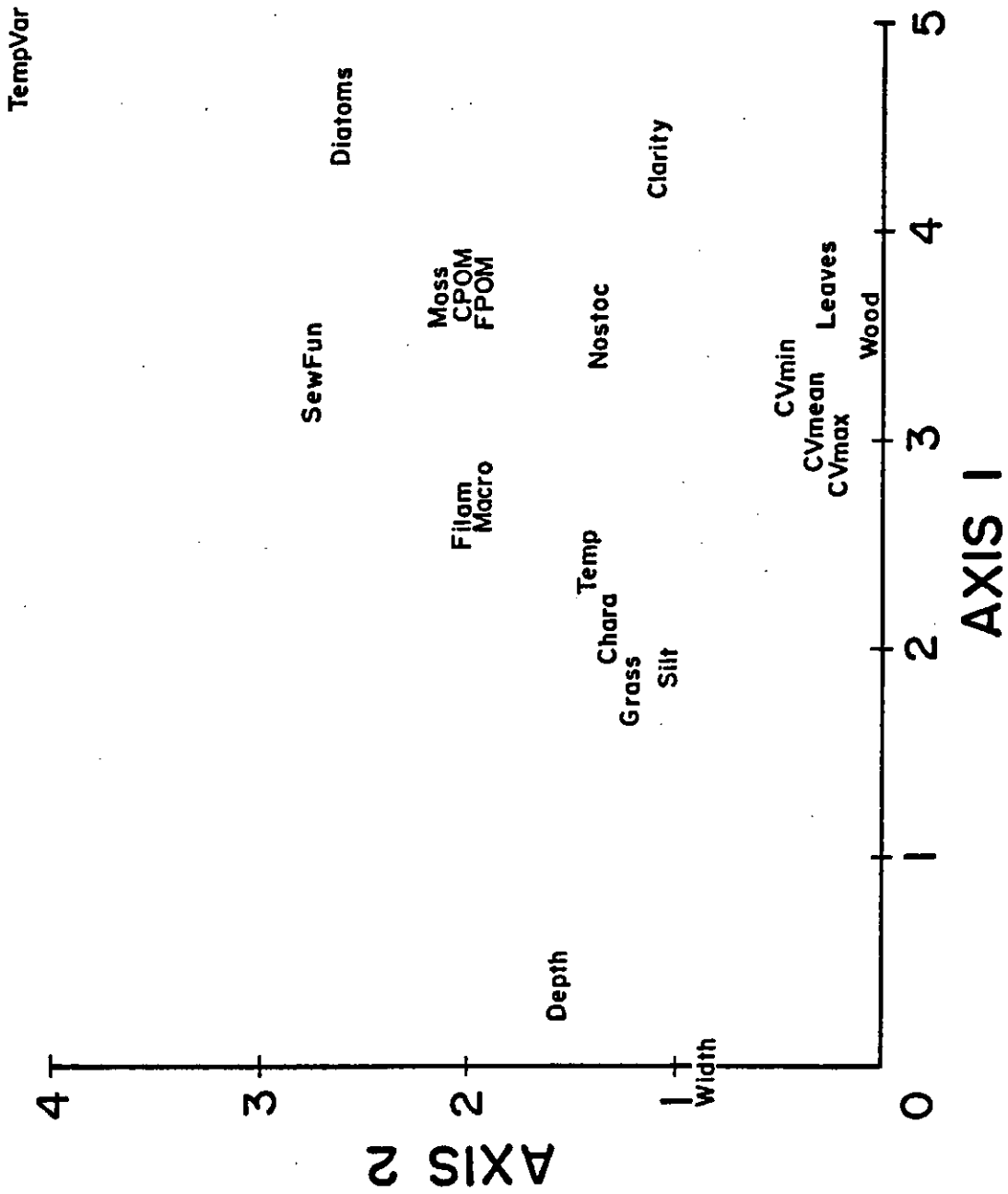


assigned to many Saskatchewan River samples. Although some boreal samples have higher scores than Saskatchewan River samples, environmental scores suggest that the second seasonal sweep net axis is related mainly to differences between high gradient and Saskatchewan River sites, rather than between high gradient and other boreal sites.

Hybrid ordination environmental scores on the first and second seasonal stone axes are presented in Figure 79. These scores are similar to those on the corresponding annual stone axes, except for the extreme position of diurnal water temperature variation on both axes. The high scores assigned to diurnal temperature variation may be related to seasonal faunal variation. Although the first and second axes describe mainly geographical variation, they also describe seasonal differences between June and July samples, which tend to have low scores on both axes, and late season samples, which tend to have higher scores (at least at some sites). Diurnal temperature variation also varies seasonally, being generally highest early and late in the year and lowest in June and July. Alternatively, the extreme scores assigned to diurnal temperature variation may be due to one or two extreme measurements. One or two very high measurements could have a large effect on the hybrid ordination score, because the number of diurnal temperature variation measurements was small (diurnal temperature variation was measured at only nine sites).

Other environmental parameters with extreme scores on the first seasonal stone axis are stream depth and width,

Figure 79. Hybrid ordination environmental scores on the first and second, seasonal stone data, DCA axes. Environmental scores on each axis have been rescaled to the same range as sample scores. Environmental scores are represented by the centers of abbreviated environmental parameter names, which are explained in Figure 75.



diatom blooms and water clarity, all of which had extreme scores on the annual first axis. Allochthonous grass, which had a low score on the first annual stone axis, has an intermediate score on the first seasonal axis.

As in hybrid ordinations of annual data, high current velocities, and allochthonous leaves and wood have low second axis scores, and thus appear to be associated with high gradient streams. Sewage fungus and diatom blooms have high second axis scores and appear to be characteristic of other boreal streams. Stream depth and water temperature, which had high annual second axis scores, are not associated with other boreal streams on the second seasonal stone axis.

Hybrid ordination environmental scores on the first and second seasonal presence/absence axes are presented in Figure 80. As in quantitative data analyses, first axis environmental scores are similar in seasonal and annual ordinations, except for the extreme score assigned to diurnal temperature variation and the intermediate score assigned to allochthonous grass in the seasonal ordination.

Second axis environmental scores, however, differ from those in other hybrid ordinations. The range of environmental scores on this axis is very low, because of the low range of sample scores from which they are calculated. Furthermore, the environmental parameters with the lowest second axis scores are diatom blooms, allochthonous wood, coarse particulate organic material, and diurnal temperature variation. Thus, these parameters, rather than current velocity, appear to be most closely associated with high

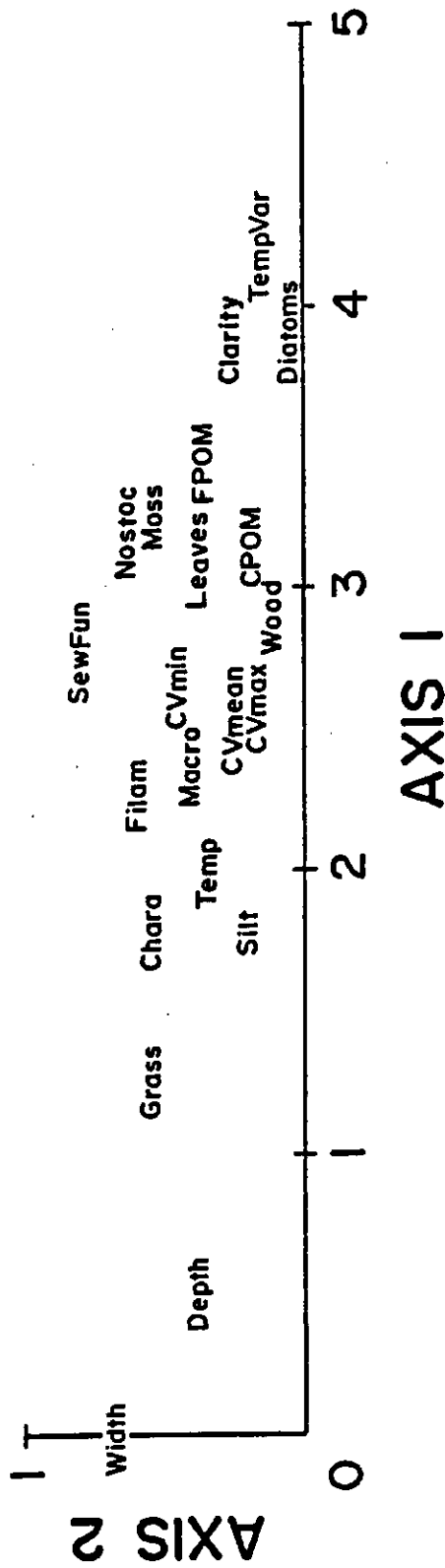


Figure 80. Hybrid ordination environmental scores on the first and second, seasonal presence/absence data, DCA axes. Environmental scores on each axis have been rescaled to the same range as sample scores. Environmental scores are represented by the centers of abbreviated environmental parameter names, which are explained in Figure 75.

gradient streams. Sewage fungus and stream width have the highest second axis environmental scores, as in seasonal quantitative data hybrid ordinations.

Diurnal water temperature variation has a very low score on the second seasonal presence/absence axis. On quantitative data axes, temperature variation had very high second axis scores. This suggests that the extreme scores assigned to temperature variation are random and do not indicate an association between temperature variation and faunal patterns (at least on the second axis).

The third and fourth seasonal DCA axes all have relatively high eigenvalues, suggesting that they describe important variation. However, these axes differ among analyses of different data sets, and defy meaningful interpretation. They may be due primarily to noise in the seasonal data. Environmental scores on these axes (Tables 22 to 24)) also differ among analyses and appear random.

In summary, the major environmental differences between the Saskatchewan River and boreal faunal zones appear to be in stream depth and width, and allochthonous grass (all of which are greater at Saskatchewan River sites), and in water clarity and diatom blooms (both of which are greater in boreal streams). Similarly, high gradient streams have higher current velocities, more allochthonous leaves and wood, and less sewage fungus growth than other boreal streams. These parameters all show consistent patterns among analyses and have extreme first or second axis scores on all, or nearly all, seasonal and annual ordination axes. Coarse sand and

Table 22. Hybrid ordination environmental scores on the third and fourth, seasonal sweep net data, DCA axes. Environmental scores on each axis have been rescaled to the same range as sample scores. Abbreviated environmental parameter names are explained in Figure 75.

<u>Axis 3</u>		<u>Axis 4</u>	
<u>Environmental Parameter</u>	<u>Ordination Score</u>	<u>Environmental Parameter</u>	<u>Ordination Score</u>
Wood	3.12	Grass	2.57
Clarity	2.98	Leaves	1.25
CVmean	1.69	CVmax	1.23
Temp	2.77	Wood	2.25
CVmax	2.77	CVmean	2.25
CVmin	2.66	CVmin	2.20
Leaves	2.66	Clarity	2.16
Moss	2.54	Temp	2.11
CPOM	2.20	Width	2.02
Silt	1.73	FPOM	1.97
Grass	1.50	Chara	1.84
FPOM	1.39	Depth	1.70
Chara	1.27	Filam	1.70
TempVar	1.27	Moss	1.65
Macro	1.04	Silt	1.65
Filam	0.92	Macro	1.65
Diatoms	0.81	Coarse	1.65
Width	0.69	Nostoc	1.51
Nostoc	0.69	Diatoms	1.47
Depth	0.12	SewFun	1.29
SewFun	0.00	TempVar	0.00

Table 23. Hybrid ordination environmental scores on the third and fourth, seasonal stone data, DCA axes. Environmental scores on each axis have been rescaled to the same range as sample scores. Abbreviated environmental parameter names are explained in Figure 75.

<u>Axis 3</u>		<u>Axis 4</u>	
<u>Environmental Parameter</u>	<u>Ordination Score</u>	<u>Environmental Parameter</u>	<u>Ordination Score</u>
Diatoms	2.47	TempVar	2.99
CVmax	2.29	Grass	2.54
CVmean	2.29	Depth	2.09
CVmin	2.23	Diatoms	1.94
Leaves	2.17	Macro	1.64
Nostoc	2.17	FPOM	1.64
Clarity	2.17	SewFun	1.50
Moss	1.93	Nostoc	1.50
CPOM	1.51	Silt	1.35
Filam	1.51	Width	1.20
Wood	1.33	CPOM	1.20
Macro	1.27	Temp	1.20
Silt	1.20	Filam	1.05
FPOM	1.08	CVmax	1.05
SewFun	1.02	CVmean	0.82
Grass	0.78	Moss	0.90
Chara	0.72	CVmin	0.75
Depth	0.48	Chara	0.75
Temp	0.30	Leaves	0.75
TempVar	0.06	Wood	0.30
Width	0.00	Clarity	0.00



Table 24. Hybrid ordination environmental scores on the third and fourth, seasonal presence/absence data, DCA axes. Environmental scores on each axis have been rescaled to the same range as sample scores. Abbreviated environmental parameter names are explained in Figure 75.

<u>Axis 3</u>		<u>Axis 4</u>	
<u>Environmental Parameter</u>	<u>Ordination Score</u>	<u>Environmental Parameter</u>	<u>Ordination Score</u>
CVmax	3.03	Width	2.27
CVmean	3.03	Chara	1.96
CVmin	2.88	Depth	1.80
Leaves	2.80	SewFun	1.72
Clarity	2.73	Filam	1.41
Nostoc	2.35	TempVar	1.33
Diatoms	2.27	Grass	1.33
Moss	1.74	Macro	1.25
Wood	1.52	Temp	0.78
CPOM	1.36	FPOM	0.69
Macro	1.21	CPOM	0.69
Filam	1.14	Clarity	0.69
SewFun	0.98	Nostoc	0.55
TempVar	0.83	Silt	0.47
Silt	0.76	Leaves	0.39
Chara	0.76	Moss	0.31
Grass	0.68	Wood	0.31
FPOM	0.53	CVmin	1.01
Depth	0.38	Diatoms	0.16
Width	0.08	CVmean	0.03
Temp	0.00	CVmax	0.00

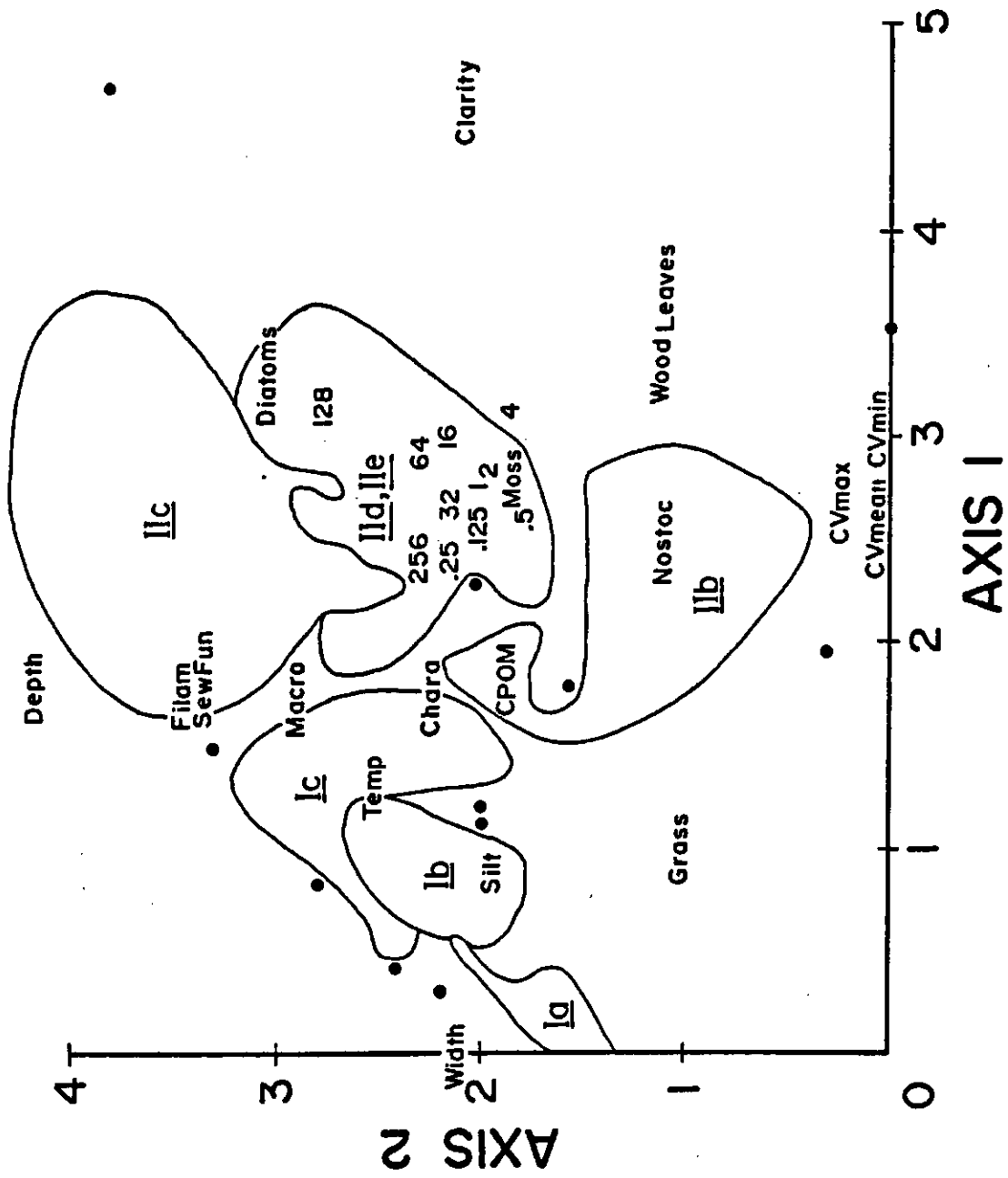
minimum annual water temperature also show consistent associations with the boreal zone and other boreal subzone, respectively, but are included only in annual data ordinations.

#### 4.7.3 Hybrid ordination of extensive study data

Extensive study environmental data include measurements of environmental parameters at 149 sites, from 1980, 1981 and 1982. All measurements were made in June and July (when all Saskatchewan heptageniids are present as larvae). Consistent methods of collecting environmental data were not employed in 1979; therefore, 1979 environmental data, and sites visited only in 1979, are not included. Environmental data from the 35 intensive study sites, from June and July, 1980, are included. Diurnal water temperature variation was measured at very few sites outside of the intensive study area and is therefore not included in the extensive study environmental data. Substrate particle size distribution was measured at only 61 sites. Therefore, ordination scores assigned to substrate particle size classes are not as reliable as those assigned to other environmental parameters.

Hybrid ordination environmental scores on the first and second extensive study DCA axes are presented in Figure 81. These scores, like the associated site and species scores, are similar to those on most first and second intensive study axes. Stream width and water clarity have the lowest and highest first axis environmental scores, respectively. Stream depth and diatom blooms have much more moderate scores than

Figure 81. Hybrid ordination environmental scores on the first and second, extensive study, DCA axes. Environmental scores on each axis have been rescaled to the same range as the site scores. Environmental scores are represented by abbreviated environmental parameter names, which are explained in Figure 75. Enclosed areas represent faunal subzones, as defined in the classification of extensive study sites (Figure 66): Ia - South Saskatchewan River upstream from Lake Diefenbaker, Ib - other Saskatchewan River, Ic - Saskatchewan River-like, IIa - low diversity, IIb - high gradient boreal, IIc - low gradient southern boreal, IId - high diversity boreal, IIe - Shield.



in intensive study ordinations. This may be due to the inclusion of Shield sites (subzone IIe) in the extensive study. Shield sites, which have very high first axis site scores, tend to be deeper than most southern boreal streams and not to have diatom blooms. Thus, stream depth and diatom blooms are less characteristic of sites at the low and high end, respectively, of the first extensive study axis. Silt depth, allochthonous grass, and water temperature also have relatively low first axis scores.

Maximum, minimum and mean current velocities have the lowest second axis scores and thus appear to be characteristic of high gradient boreal streams (subzone IIb), as in intensive study hybrid ordinations. Allochthonous leaves and wood also have relatively low scores, but are not as clearly associated with high gradient streams as in most intensive study hybrid ordinations.

Stream depth, filamentous algae, and sewage fungus have the highest second axis scores. The high scores assigned to stream depth and filamentous algal growth are probably due to their association with low gradient southern boreal and parkland sites (subzone IIc). These sites have the highest second axis site scores, and tend to have greater water depth, and more filamentous algal and fungal growth, and lower current velocities, than other boreal sites.

The third extensive study axis describes differences between Saskatchewan River (subzones Ia and Ib) and Saskatchewan River-like (subzone Ic) sites, and between Shield (subzone IIe) and other boreal sites (subzones

IIb-IIId). Water temperature has an extremely high score on this axis (Figure 82) and appears to be the most important environmental parameter in distinguishing these groups of sites. Current velocity and water clarity have relatively low third axis scores. Thus, current velocity and water clarity are higher, and water temperature is lower, at Saskatchewan River and Shield sites than at Saskatchewan River-like and other boreal sites, respectively.

The fourth extensive study axis describes differences among low diversity sites (subzone IIa), and between high gradient sites where Nixe rusticalis is present and other high gradient sites (subzone IIb). Current velocity has the highest score on this axis (Figure 83) and thus appears to be higher at N. rusticalis streams than at other high gradient sites or low diversity sites where only Stenonema terminatum was collected (which also have low fourth axis scores). A large number of environmental parameters, including water temperature, allochthonous leaves and wood, diatom blooms, silt depth, stream depth, and allochthonous grass, have low fourth axis scores.

Substrate particle size classes all lie near the centers of the extensive study axes, and there is little variation among substrate scores on any axis. Therefore, differences in substrate particle size distribution do not appear to be important in differentiating heptageniid faunal zones or subzones in Saskatchewan or in regulating the distributions of most heptageniid species. The reliability of substrate scores on extensive study axes is questionable because of the

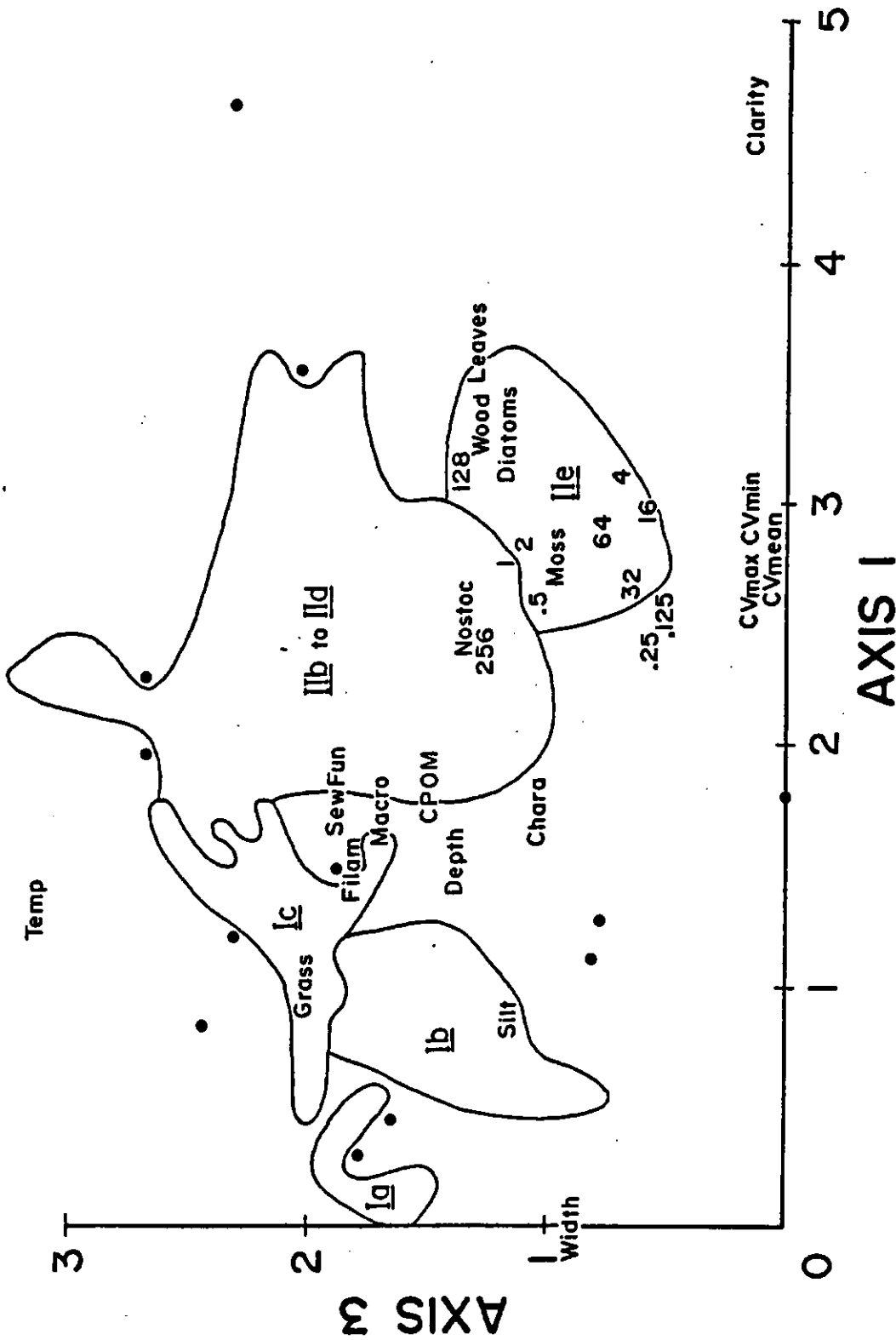


Figure 82. Hybrid ordination environmental scores on the first and third, extensive study, DCA axes. Symbols are explained in Figure 81. Abbreviated environmental parameter names are explained in Figure 75.

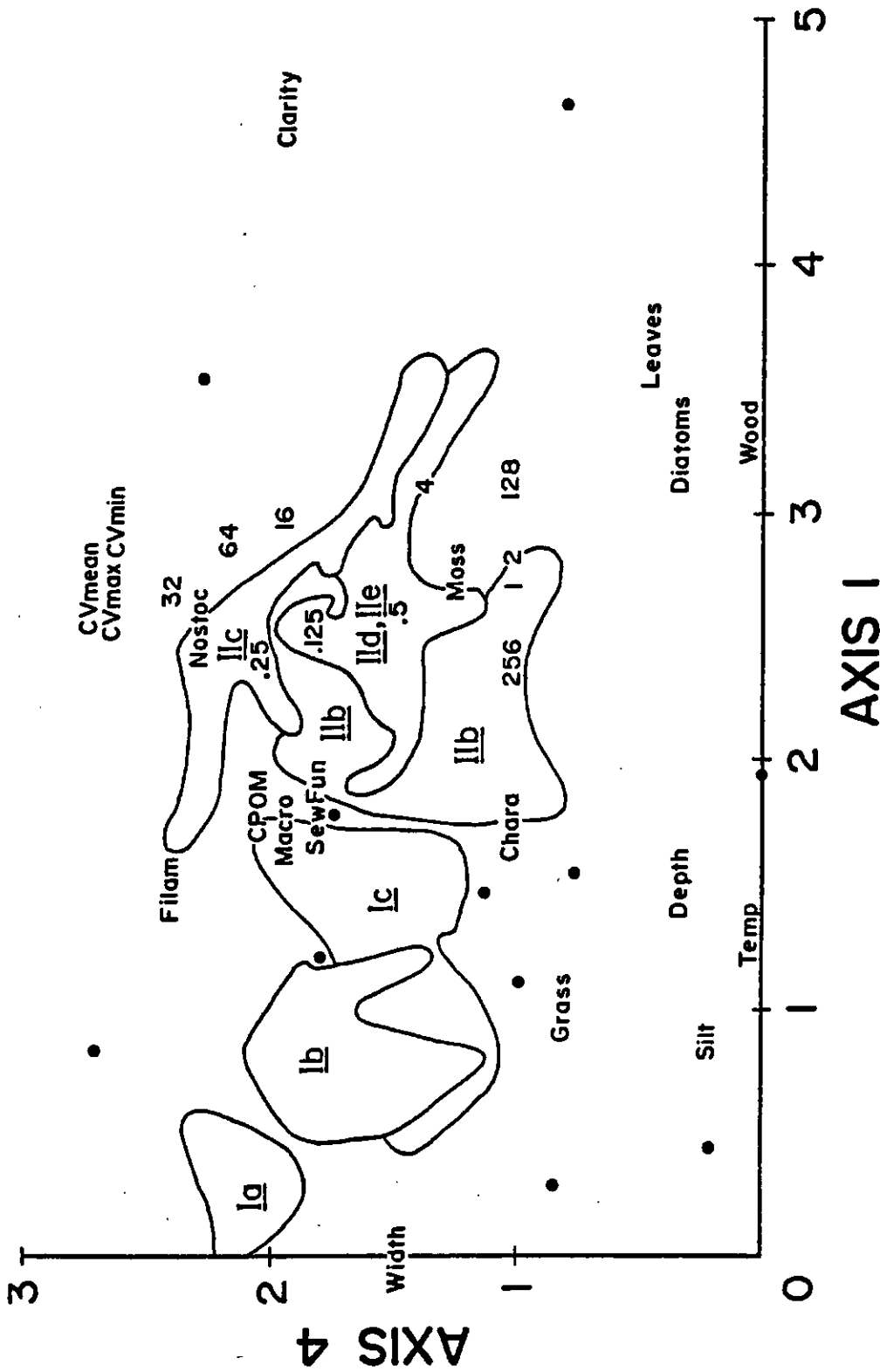


Figure 83. Hybrid ordination environmental scores on the first and fourth, extensive study, DCA axes. Symbols are explained in Figure 81. Abbreviated environmental parameter names are explained in Figure 75.



relatively small number of sites at which substrate particle size distribution was measured. However, the number of measurements included does not determine the magnitude of an ordination score, and substrate particle size distribution was measured at as great a diversity of sites as possible. Therefore, the apparent lack of importance of substrate type is probably real.

#### 4.8 Independent Analysis of Environmental Data

Standardized environmental data were analyzed independently to examine patterns of environmental variation among heptageniid habitats in Saskatchewan and to compare patterns of environmental and faunal variation. To facilitate comparison, environmental analyses were performed using the same multivariate techniques that were used in faunal analyses, cluster analysis (using Euclidean distance and Ward's method) and detrended correspondence analysis.

##### 4.8.1 Cluster analysis of annual environmental data

Annual environmental data include measurements of substrate particle size distribution, and mean annual measurements of all other environmental parameters except diurnal water temperature variation (which was excluded because it was an outlier in preliminary analyses) at each intensive study site. Annual maximum and minimum water temperature and current velocity were also included.

The environmental classification of intensive study sites is presented in Figure 84. Figure 85 indicates that there are two major groups and seven subgroups in this classification. Group I contains all Saskatchewan River sites and five boreal sites: site 25 (the southern boreal site classified with Saskatchewan River sites in most faunal analyses), sites 19 and 20 (the two Montreal River sites), site 21 (the only Shield site included in the intensive study), and site 22. Group II contains all other boreal sites.

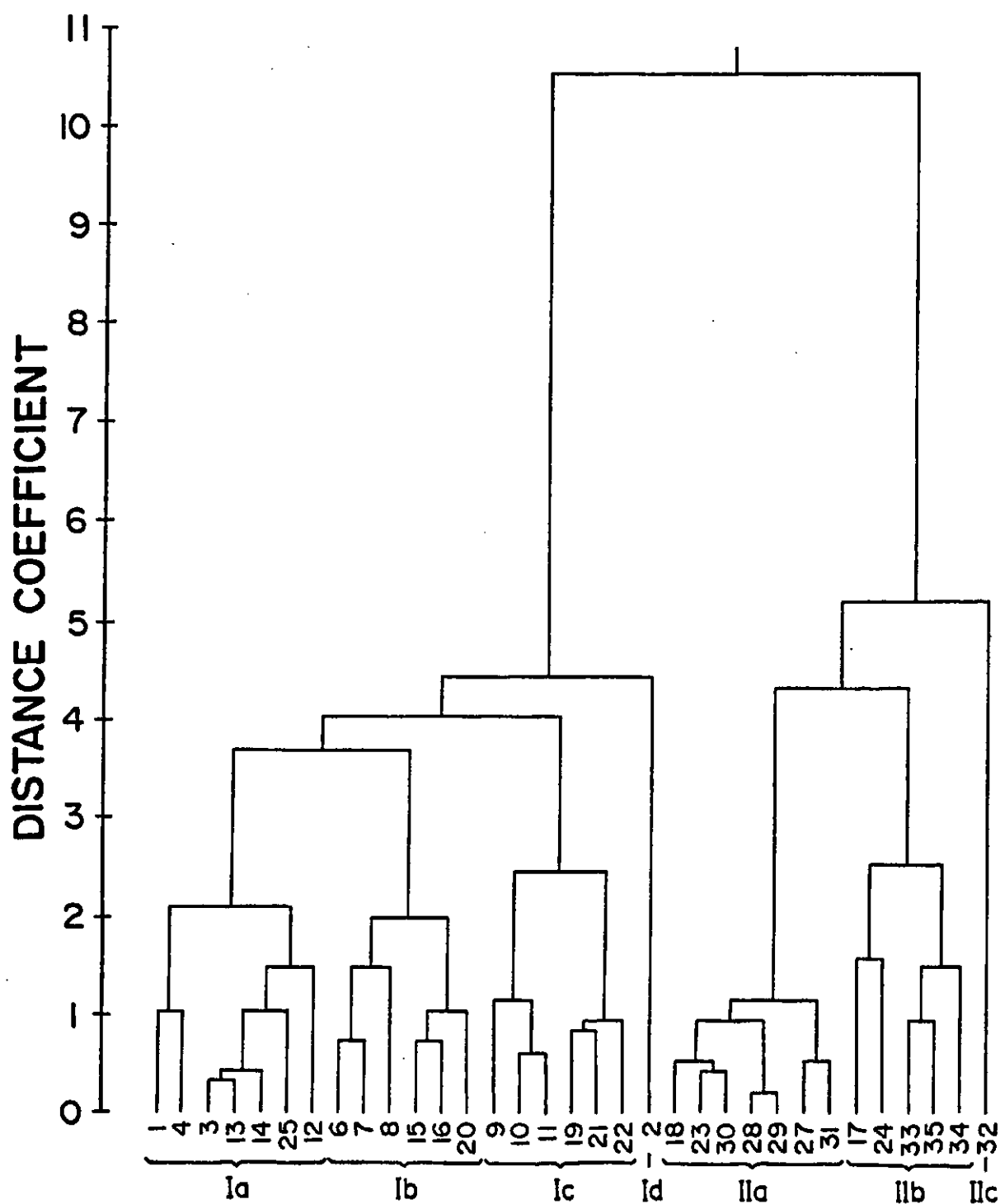


Figure 84. Classification of intensive study sites by annual environmental data. Site numbers (Arabic numerals) and group and subgroup numbers (Roman numerals and lower case letters, respectively) are indicated along the base of the dendrogram.

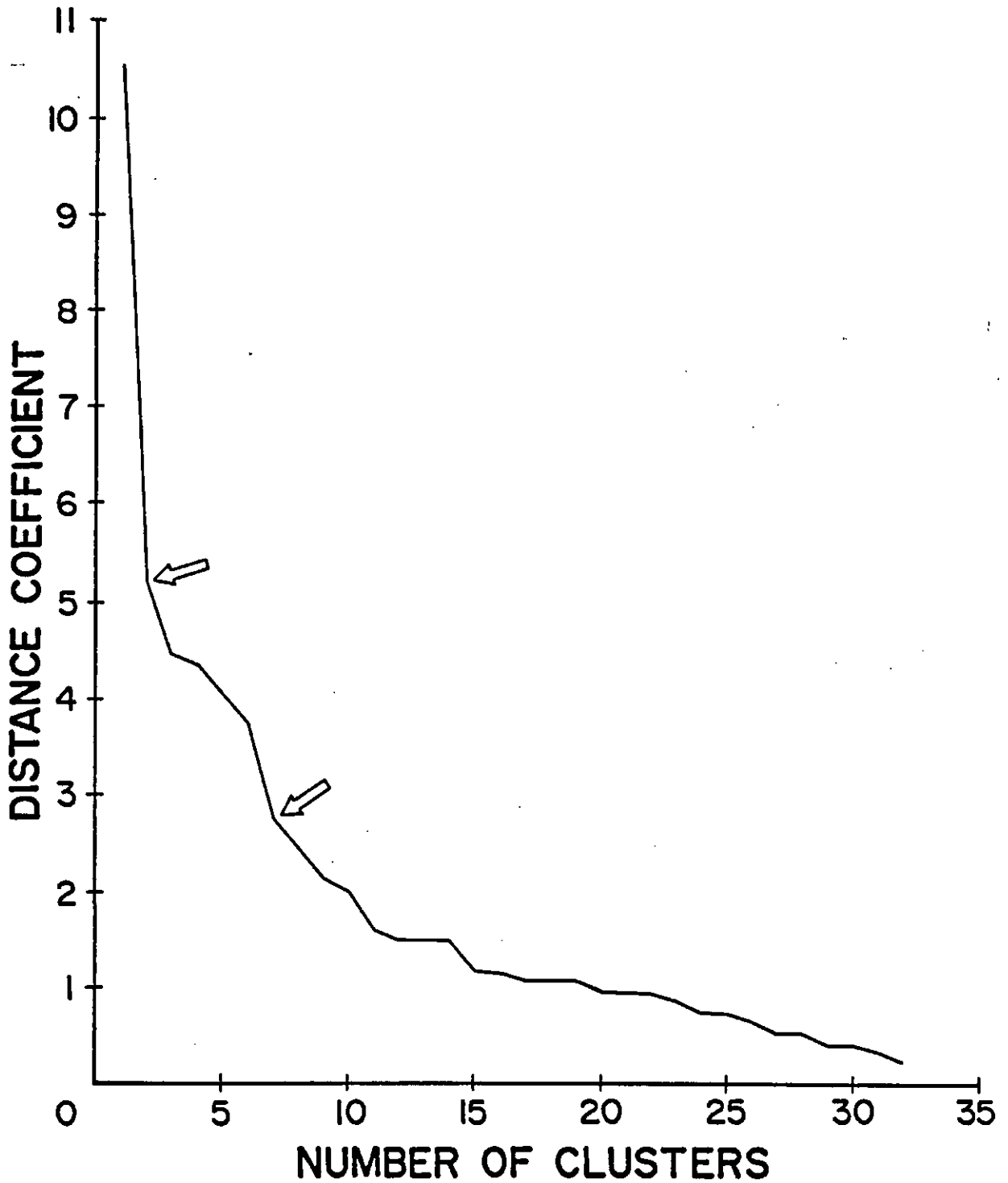


Figure 85. Relationship between distance between fusing clusters and number of clusters in the classification of intensive study sites by annual environmental data (Figure 84). Large changes in slope occur at the 2 and 7 cluster levels.

Globally optimizing this classification at the two cluster level (using procedure RELOCATE in the CLUSTAN package) shifts sites 21 and 22 from Group I to Group II, and site 35 from Group II to Group I. Thus, while sites 21 and 22 are initially most similar to some Saskatchewan River sites, their overall similarity to boreal sites is greater than to Saskatchewan River sites. Similarly, site 35 is most similar to Saskatchewan River sites.

Thus, the major environmental pattern in the intensive study area is the difference between the Saskatchewan Rivers and most boreal streams. These two groups of sites differ in several environmental parameters, including stream size, water temperature, turbidity, siltation, and the type of allochthonous organic material present. Site 25, which is included in the Saskatchewan River group (Group I) in both faunal and environmental classifications, is similar to Saskatchewan River sites in temperature, turbidity, siltation and type of allochthonous organic material, but is much smaller in size. The three other boreal sites classified in Group I (sites 19, 20 and 35) are on the two largest boreal rivers sampled. These rivers are intermediate in size between other boreal streams and the Saskatchewan Rivers and tend to be slightly warmer than most other boreal streams. However, their heptageniid faunas are distinctly boreal.

The major groups present in the globally optimized environmental classification are very similar to those in most faunal classifications, except for the assignment of sites 19, 20 and 35 to the Saskatchewan River group (Group

I). This similarity suggests that heptageniid distribution patterns in Saskatchewan are related to major environmental trends, or at least to environmental parameters associated with major environmental trends.

Seven subgroups are present in the environmental classification of intensive study sites (Figure 85), four in the Saskatchewan River zone (Group I) and three in the boreal zone (Group II). The Saskatchewan River subgroups are:

- 1) subgroup Ia - three of the four sites upstream from Lake Diefenbaker on the South Saskatchewan River (sites 1, 3 and 4), site 12 on the North Saskatchewan River, the two Saskatchewan River sites upstream from Tobin Lake (sites 13 and 14), and southern boreal site 25. All of the Saskatchewan River sites in this subgroup are upstream from dams;
- 2) subgroup Ib - sites 6 to 8 on the South Saskatchewan River, sites 15 and 16 on the Saskatchewan River, and boreal site 20. Saskatchewan River sites in this subgroup are all located a short distance downstream from dams;
- 3) Subgroup Ic - sites 9 to 11 on the South Saskatchewan River, and boreal sites 19, 21 and 22. Sites 9 to 11 are downstream from Gardiner Dam, but are further from it than sites in the previous subgroup (Ib); and
- 4) subgroup Id - site 2, on the South Saskatchewan River upstream from Lake Diefenbaker.

In the global optimum subgroup classification, site 20 is transferred from subgroup Ib to subgroup Ic, and site 21 is transferred to boreal subgroup IIa.

The environmental subgroup classification of

Saskatchewan River sites appears to be related primarily to the effects of dams and impoundments. Three of the four subgroups present correspond to sites upstream, just downstream, and further downstream from dams, respectively. Sites 13 and 14 on the Saskatchewan River are downstream from Gardiner Dam, but are classified in subgroup Ia. However, because the discharge of the North Saskatchewan River (which is unaffected by dams or impoundments) is three to four times as great as that of the South Saskatchewan River, the Saskatchewan River downstream from the confluence is virtually unaffected by Gardiner Dam. Thus, sites 13 and 14 are environmentally most similar to sites upstream from impoundments. Water temperature, turbidity and siltation are all higher upstream than downstream from impoundments.

The separation of sites downstream from dams into two subgroups (subgroups Ib and Ic) may be related to partial recovery from the effects of dams at the more downstream sites. At these sites (sites 9 to 11), water temperature is similar to that at sites unaffected by dams, but turbidity and siltation are still very low. Alternatively, sites 9 to 11 may differ from other Saskatchewan River sites because of the effects of Saskatoon sewage effluent. Extensive growths of macrophytes and filamentous algae occur in the South Saskatchewan River between Saskatoon and the confluence, probably because of nutrient enrichment associated with Saskatoon sewage effluent. Large boreal rivers, which also have low turbidity and siltation, and high filamentous algal growth, are environmentally most similar to South

Saskatchewan River sites between Saskatoon and the confluence.

Site 2 is classified in a subgroup by itself. At this site, current velocity is very low, and the substrate is dominated by large boulders and mud. Other environmental conditions, such as water temperature, turbidity and siltation, are similar to those at other sites upstream from Lake Diefenbaker (sites 1, 3 and 4). The heptageniid fauna is also similar. This suggests that current velocity and substrate type are relatively unimportant in regulating heptageniid distributions. Alternatively, site 2 may be an isolated pocket of "atypical" habitat that has been swamped by heptageniids from nearby habitats with faster current velocities and gravel and cobble substrates. The boulder and mud substrate at site 2 is a recently created habitat at the base of a bridge, and is the only such habitat observed in this part of the South Saskatchewan River.

Saskatchewan River subgroups in this classification are different from those in faunal classifications. Thus, while dams and impoundments appear to be the major factors controlling environmental zonation of the Saskatchewan River, they do not appear to have a major effect on heptageniid faunal zonation (except perhaps for the faunal distinctness of the four South Saskatchewan River sites upstream from Lake Diefenbaker). Similarly, South Saskatchewan River sites downstream from Saskatoon and large boreal rivers are environmentally similar, but faunally very different. The effects of dams and impoundments are discussed further in



#### Section 4.9.4.

Boreal subgroups in the environmental classification are:

- 1) subgroup IIa - high gradient streams (sites 23 and 27 to 31), and site 18;
- 2) subgroup IIb - most other small to medium-sized boreal streams (sites 17, 24 and 32 to 35); and
- 3) subgroup IIc - site 32.

In the global optimum subgroup classification, site 24 is transferred from subgroup IIb to IIc, and sites 21 and 22 are included in subzone IIb.

High gradient streams have higher current velocities, more allochthonous leaves and wood, lower water temperatures, and less sewage fungus than other boreal streams. Site 18 resembles high gradient streams environmentally, but has a typical "other boreal" heptageniid fauna. The environmental peculiarity of sites 24 and 32, and the nature of environmental differences between these and other boreal sites, is not apparent.

Boreal subzones are similar in environmental and faunal classifications, except for the association of site 18 with high gradient streams.

#### 4.8.2 Ordination of annual environmental data

The eigenvalues of the first four environmental DCA axes are presented in Table 25. These eigenvalues are very low relative to those of faunal ordination axes. Although this suggests that the patterns present in the environmental data

are not as well defined as those in the faunal data, the low environmental ordination eigenvalues are more likely due to standardization of the environmental data.

Table 25. Eigenvalues of the first four ordination axes from DCA of environmental data.

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<u>Axis 1</u>	<u>Axis 2</u>	<u>Axis 3</u>	<u>Axis 4</u>
.013	.005	.004	.002

---

Site scores on the first and second environmental DCA axes are presented in Figure 86. As in ordinations of faunal data, the two major groups of sites (as recognized by cluster analysis, Figure 84) are separated in opposite halves of the first axis. Boreal sites 19, 22, 25 and 35, which were classified in the Saskatchewan River group (Group I), occupy an intermediate position, near the center of the axis.

Except for the separation of Saskatchewan River and boreal sites in opposite halves of the first axis, relative first axis site scores are quite different from those in faunal ordinations. For example, sites 13 and 14 lie near the low (Saskatchewan River) end of the axis instead of near the center, and sites 1 and 4 (on the South Saskatchewan River upstream from Lake Diefenbaker) lie nearer the center of the axis. High gradient streams (sites 23 and 27-31) lie near the extreme high (boreal) end of the first environmental axis,

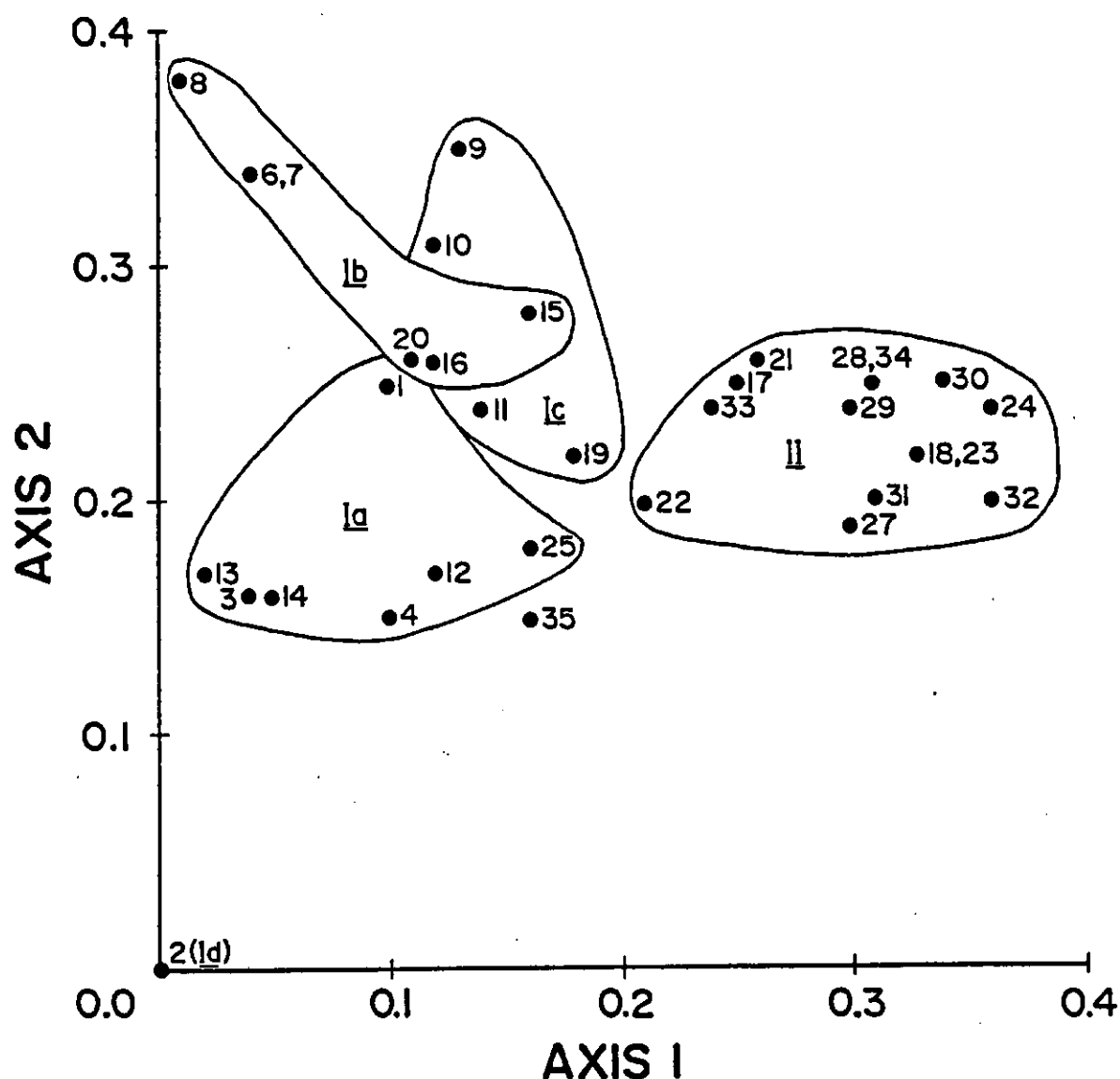


Figure 86. DCA ordination of annual environmental data: site scores on axes 1 and 2. Site scores are represented by dots and labelled with site numbers (Arabic numerals). Subgroups present in the classification of intensive study sites by annual environmental data (Figure 84) are represented by enclosed areas, which are labelled with group and subgroup numbers (Roman numerals and lower case letters, respectively).

instead of near the center. Furthermore, high gradient streams are quite clearly separated from other boreal sites, except sites 18, 24, 32 and 34. In ordinations of faunal data, high gradient and other boreal streams are separated only on the second axis. Thus, it appears that environmental differences among these three faunal areas (the Saskatchewan Rivers, high gradient streams and other boreal streams) can be described by a single ordination axis, and that the three groups represent different parts of a single environmental gradient. On the other hand, faunal separation of the three groups involves two separate community gradients.

First axis environmental scores are presented in Figure 87. Stream depth and width, water temperature, silt depth, and allochthonous grass have the lowest first axis scores; allochthonous leaves, coarse sand, and water clarity have the highest scores. These parameters thus appear to be important in environmentally distinguishing the Saskatchewan River and boreal zones. These are the same parameters that were identified as being important in distinguishing major heptageniid faunal zones in weighted averages hybrid ordination, except that diatom blooms are not as clearly associated with the boreal zone.

The eigenvalues of the second and higher axes are substantially smaller than that of the first axis (Table 25). This indicates that the second and higher axes describe little important variation in the environmental data. The apparent unimportance of these axes may be related to the separation of Saskatchewan River, high gradient and other

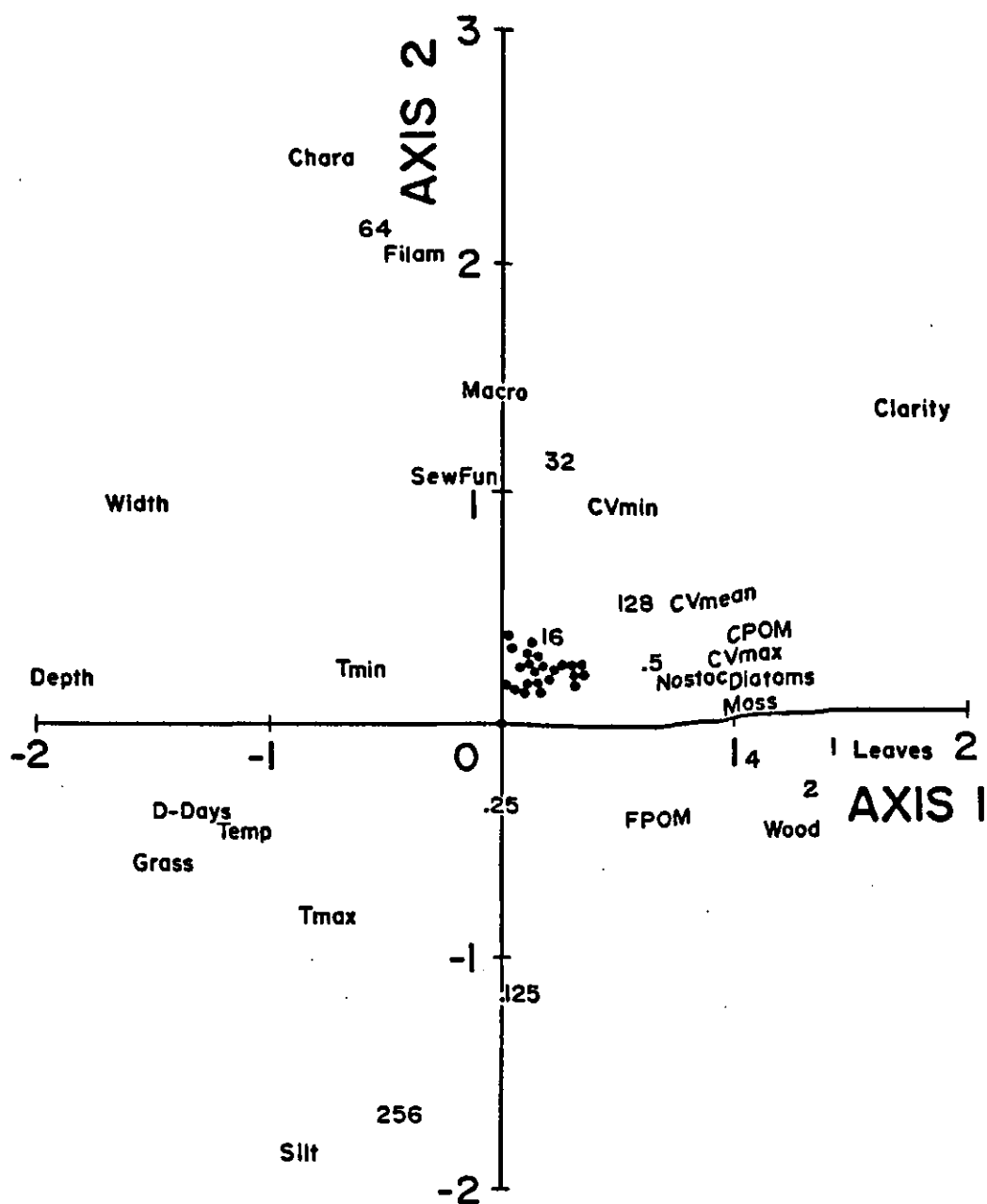


Figure 87. DCA ordination of annual environmental data: environmental scores on axes 1 and 2. Environmental scores are represented by abbreviated environmental parameter names, which are explained in Figure 75. Site scores (which are the same as in Figure 86) are represented by dots.

boreal groups of sites on the first axis (leaving little important variation to be described by higher level axes). Nevertheless, the second and third axes are similar to some previously described geographical patterns and will therefore be presented and discussed in spite of their low eigenvalues.

The second environmental DCA axis (Figure 86) describes variation primarily among Saskatchewan River sites (Group I). Sites downstream from dams, especially the first four sites downstream from Gardner Dam (sites 6-9), have the highest second axis scores, while sites upstream from reservoirs (sites 1-4, 13 and 14), and boreal sites 25 and 35, have relatively low scores. Boreal sites (Group II) differ little in second axis scores and all lie near the center of this axis.

Second axis environmental scores (Figure 87) indicate environmental differences between sites upstream and downstream from dams. Sites upstream from reservoirs (subgroup Ia) are generally warmer and have more silt, fine sand, large cobbles and boulders (substrate particles > 128 mm in diameter), and allochthonous grass and wood; sites downstream from reservoirs (subgroups Ib and Ic) generally have clearer water and more plant growth (especially Chara, filamentous algae and macrophytes) and small cobbles (substrate particles 32 to 128 mm in diameter). Differences in water temperature, water clarity, siltation, and the amount of allochthonous material can all be directly related to the presence of a reservoir. The decrease in current velocity (to near zero) in a reservoir causes sedimentation

of suspended silt, fine sand and allochthonous material, and a resulting increase in water clarity. Reservoirs are less affected by insolation than rivers, causing a reduction in water temperature in, and downstream from reservoirs. Increased plant growth below reservoirs is probably at least partly due to increased water clarity, which facilitates photosynthesis.

Site 1, which is on the South Saskatchewan River upstream from Lake Diefenbaker, has a higher second axis score than other sites upstream from reservoirs (subgroup Ia). This site is environmentally similar to sites downstream from dams in its low turbidity and siltation, and extensive growth of filamentous algae. Site 1 is apparently influenced by dams on the Oldman and Bow Rivers, which are the major tributaries of the South Saskatchewan. The other three sites upstream from Lake Diefenbaker (sites 2 to 4) are downstream from the confluence of the turbid, silty Red Deer River (which is approximately equal in size to the South Saskatchewan River upstream from their confluence) and therefore are not perceptibly influenced by dams on the Oldman and Bow Rivers. In spite of these environmental differences, the heptageniid fauna at site 1 is similar to that at sites 2 to 4.

Site scores on the third environmental axis (Figure 88) are somewhat similar to those on second faunal ordination axes. High gradient stream sites (subgroup IIb) all have relatively low third axis scores, and some other boreal sites (sites 17, 33, 34 and 35) have the highest scores. However,

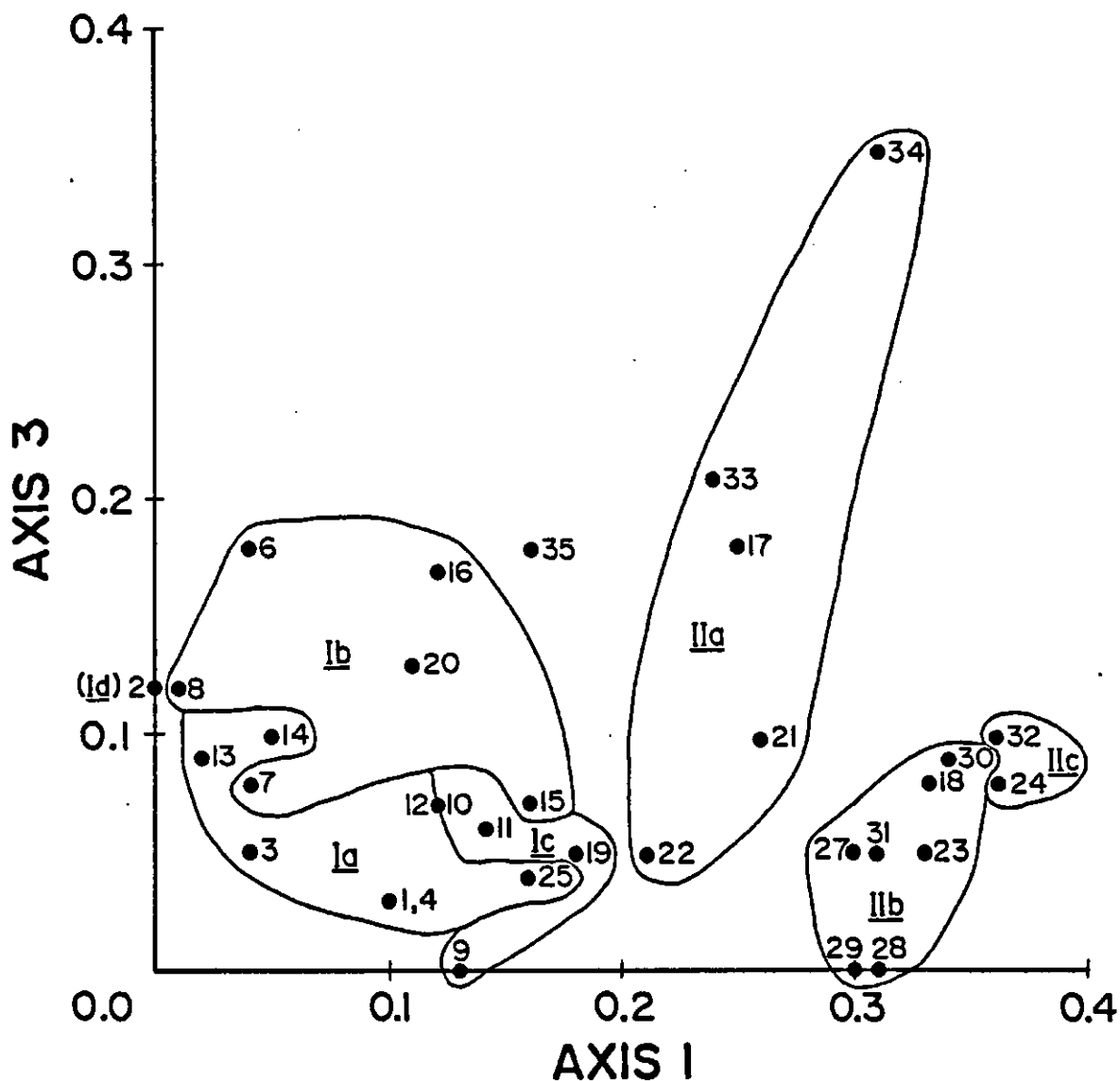


Figure 88. DCA ordination of annual environmental data: site scores on axes 1 and 3. Symbols and labels are explained in Figure 86.



site 34 has an extremely high score, and much of the variation described by the third environmental axis is apparently related to differences between site 34 and all other sites.

Environmental parameters with extreme scores on the third environmental axis (Figure 89) also have extreme second axis hybrid ordination scores. Thus, high gradient streams are associated with high current velocities and large amounts of allochthonous wood, while site 34 (and a few other boreal sites) appear to be associated with large amounts of sewage fungus and fine particulate organic matter. The relatively low score assigned to water temperature is probably related to the low scores of Saskatchewan River sites (at which water temperature tends to be higher than at boreal sites) rather than to an association between high gradient sites and high water temperatures.

Site scores on the fourth environmental DCA axis (Figure 90) are different from those on any faunal ordination axis. Site 32 has an extremely high fourth axis score, suggesting that much of the variation described by this axis is related to differences between site 32 and other boreal sites.

Fourth axis environmental scores are presented in Figure 91. Very coarse sand and gravel (substrate particles 1 to 16 mm in diameter) have very high ordination scores. Many environmental parameters, including boulders (substrate particles > 128 mm in diameter), Nostoc, diatom growth, allochthonous leaves and wood, and coarse and fine particulate organic matter, have low fourth axis scores.

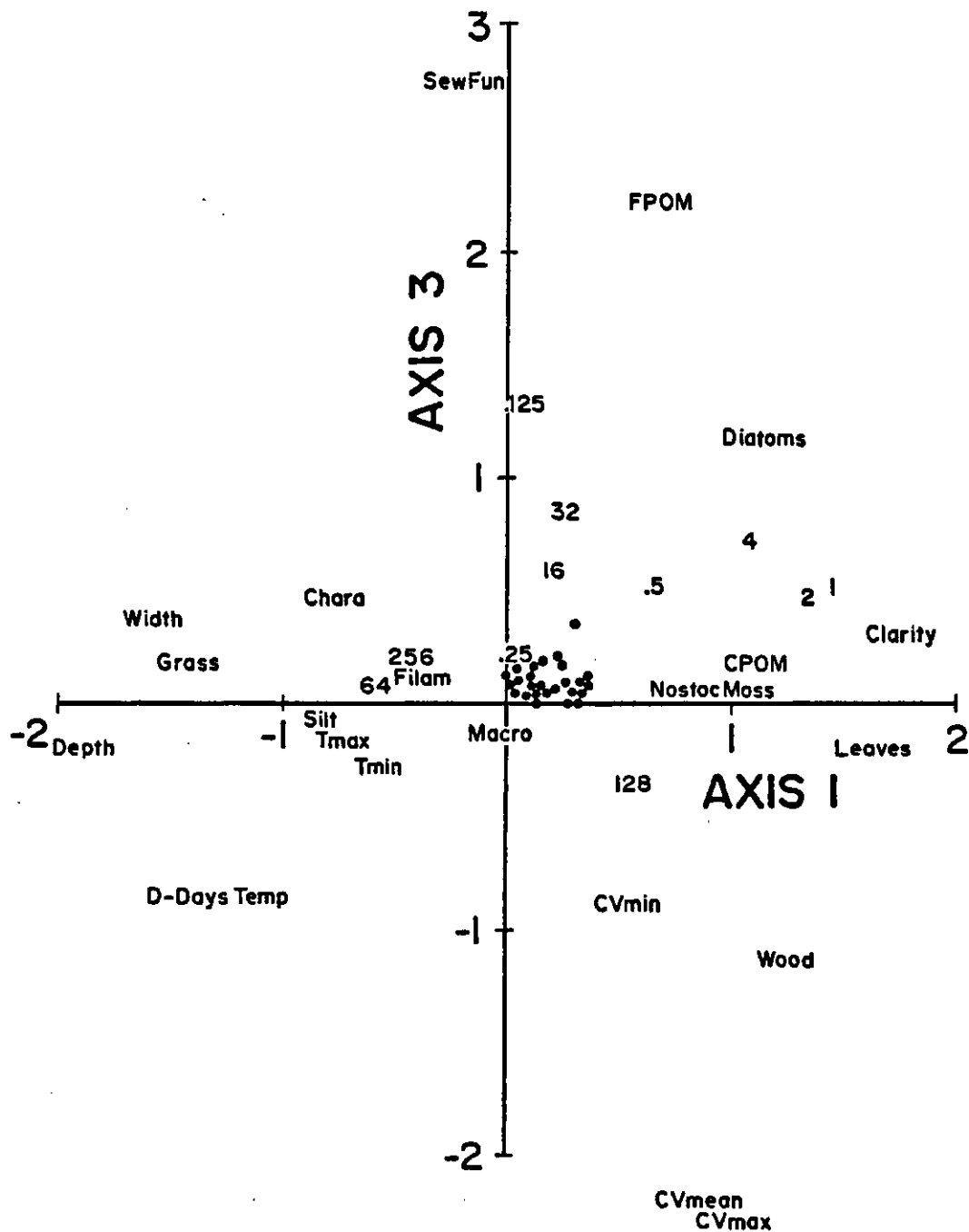


Figure 89. DCA ordination of annual environmental data: environmental scores on axes 1 and 3. Environmental scores are represented by abbreviated environmental parameter names, which are explained in Figure 75. Site scores (which are the same as in Figure 88) are represented by dots.

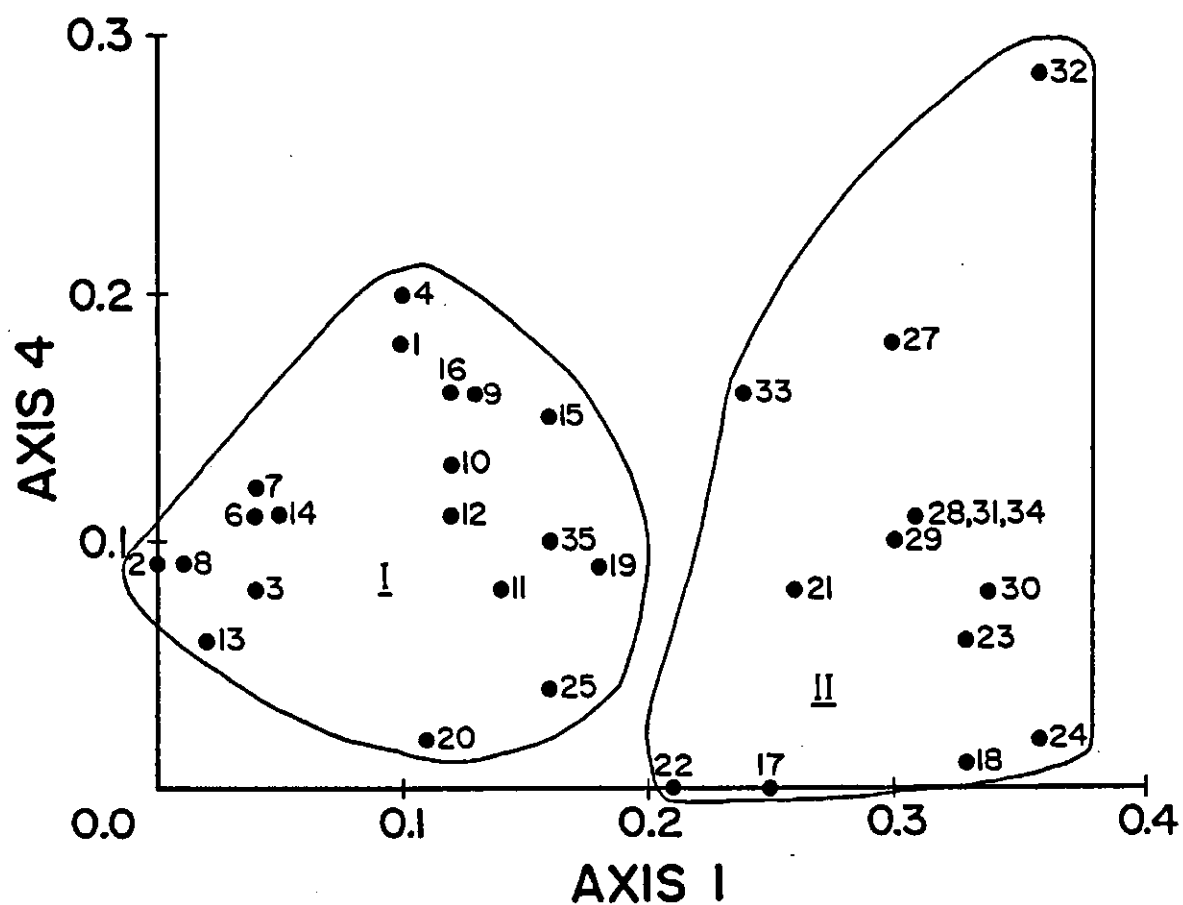


Figure 90. DCA ordination of annual environmental data: site scores on axes 1 and 4. Symbols and labels are explained in Figure 86.

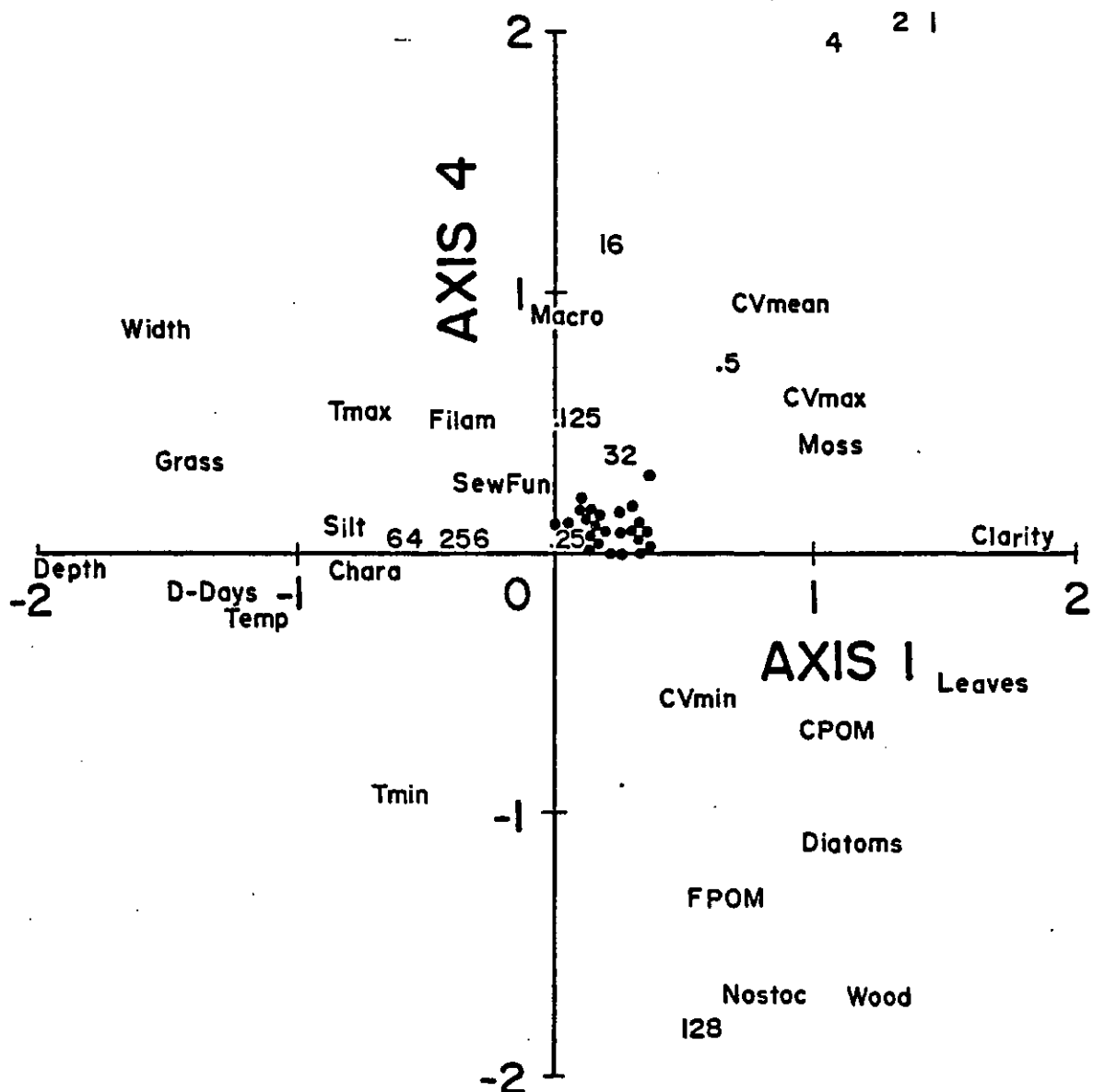


Figure 91. DCA ordination of annual environmental data: environmental scores on axes 1 and 4. Environmental scores are represented by abbreviated environmental parameter names, which are explained in Figure 75. Site scores (which are the same as in Figure 90) are represented by dots.

Thus, variation described by the fourth axis may be related to differences in substrate. Sites with predominantly coarse sand and gravel substrates have relatively high scores, and sites where boulders and particulate organic matter are abundant have relatively low scores.

The range of environmental scores is much greater than the range of site scores on all four environmental DCA axes. This suggests that the environmental gradients examined are too short for meaningful analysis, possibly because the nature of environmental variation is inconsistent with the DCA model. The DCA algorithm is based on a model of species showing Gaussian distributions along an ecological gradient (with the abundance of each species rising to a maximum and then declining again along the gradient, as it reaches and then passes its optimum habitat) (Hill 1979, Gauch 1982). However, environmental parameters, which were treated as species in this analysis, are more likely to show continual increase or decrease along an ecological gradient. The failure of environmental parameters to show Gaussian turnover along a gradient would be interpreted as an indication that the gradient is too short and would result in an artificially low range of site scores. Thus, the absolute values of the site scores and the relative ranges of site and environmental scores are meaningless in DCA ordinations of environmental data. However, only the scaling of the axes, and not the relative values of site and environmental scores, should be affected.

DCA and RA were designed originally for discrete data.

However, most of the environmental parameters measured are continuous. This may also affect the quality of DCA ordinations of environmental data.

#### 4.8.3 Independent analysis of seasonal and extensive study environmental data

Multivariate analyses of seasonal environmental data (excluding substrate particle size distribution which was measured only once at each site, and diurnal temperature which was measured at only nine sites) produce results that are very different from those of other analyses, and defy meaningful interpretation. Therefore, the results of these analyses are not presented and are discussed only very briefly.

Distinct homogenous groups are present at only one level in the classification of seasonal environmental data, at the 13 cluster level. The 13 groups present bear little resemblance to groups or subgroups present in any faunal classification or in the classification of annual environmental data.

Eigenvalues of seasonal environmental DCA axes are all extremely small (.003 to .001), suggesting that there are no important linear trends present in the seasonal environmental data. Furthermore, there is virtually no between-site variation on any axis, and the patterns of within-site variation are extremely variable. Thus, no meaningful geographical or seasonal patterns are evident.

Multivariate analyses could not be performed on

extensive study environmental data because there were too many missing data. The number of missing data for any one environmental parameter or site was very low. Thus, weighted averages hybrid ordination of extensive study data, in which missing values are ignored on a datum by datum basis, should not be significantly biased. However, in cluster analysis or DCA, missing values must be dropped on a variable by variable, and case by case basis; i.e. no sites or variables for which there are missing values can be included. This greatly reduces the number of sites and environmental parameters included, and thus severely biases the results.

#### 4.9 Relationship of Heptageniid Distribution Patterns to Broader Geographical Trends

##### 4.9.1 Stream size and the river continuum concept

###### 4.9.1.1 Longitudinal variation in physical parameters

Most environmental differences between the Saskatchewan River and boreal faunal zones, and some differences between high gradient and other boreal streams, can be related to differences in stream size and associated longitudinal variation in physical parameters.

Moving downstream from the headwaters of a stream to its mouth, there is generally a progressive increase in discharge, as the number of tributaries and the area of the watershed increase. Increase in discharge is usually associated with increases in stream depth and width. Other environmental parameters such as water temperature, current velocity and sediment load, tend to change longitudinally in a characteristic manner as stream discharge and size increase (Leopold, Wolfman and Miller 1964, Vannote et al. 1980).

Water temperature tends to increase longitudinally with increases in stream width (which reduces shading by stream banks and bankside vegetation and increases the exposure of the stream to insolation) and stream length (which increases the time of exposure to insolation) (Leopold et al. 1964). Diurnal and seasonal variation in water temperature tend to increase from headwater to medium-size streams, with increases in exposure to insolation and distance from stream sources (such as springs, groundwater



and lakes) with relatively constant temperatures (Vannote et al. 1980). Temperature variation decreases from mid-size streams to large rivers, as stream depth and discharge increase, creating a larger heat sink that is less responsive to insolation.

Current velocity tends to decrease longitudinally (Leopold et al. 1964). This decrease depends somewhat on the source and geographical location of the stream, but generally applies to streams that originate in mountains or other uplands and flow on to flatter plains at lower elevations.

Sediment load (the amount of sediment carried in the water column) tends to increase longitudinally, due to an accumulation of sediment material scoured from the stream substrate. The increase in sediment load increases turbidity and decreases clarity. Because increase in sediment load is usually associated with a decrease in current velocity, sediment deposition also tends to increase longitudinally.

The major environmental differences between the Saskatchewan River and boreal faunal zones are in stream depth and width, water temperature, turbidity and silt deposition. These differences can all be related to differences in stream size and associated longitudinal gradation of physical factors. Differences in current velocity are not evident.

The major physical environmental differences between high gradient and other boreal streams are in current velocity and water temperature. These differences may also be related to differences in stream size.

#### 4.9.1.2 Longitudinal zonation of organic matter characteristics

The type of organic material in streams (and hence the food source of stream primary consumers) also varies longitudinally (Vannote et al. 1980). Three longitudinal zones, which grade into one another, can be recognized based on the nature of organic material present:

- 1) headwater streams - stream orders 1 to 3
- 2) medium-sized streams - stream orders 4 to 6
- 3) large rivers - stream orders 7 and higher

(Stream order is a measure of the size of a stream based on the number and size of its tributaries. The smallest streams, which have no tributaries, are first order; when two first order streams join, they form a second order stream; when two second order streams join, they form a third order stream, etc. (Hynes 1970). Fusion with a lower order tributary does not change stream order.)

Headwater streams are very small and are therefore greatly influenced by streamside terrestrial vegetation. Streamside vegetation contributes large amounts of allochthonous detritus to the stream and reduces autochthonous production by shading the stream (Vannote et al. 1980). This allochthonous detritus consists primarily of large detrital fragments (such as entire leaves and branches), especially in forested areas. In deciduous forests, the quantity and quality of available organic matter varies seasonally. Allochthonous detritus is most abundant in

the autumn and early winter, following autumn leaf drop. Brief periods of autochthonous production may occur in the early spring and late fall, when the stream is not shaded by deciduous leaves.

As stream size increases, shading by streamside vegetation becomes less important, and autochthonous production by attached algae and macrophytes becomes more important (Vannote et al. 1980). Thus, in medium-sized streams, autochthonous production usually provides a major source of organic material. Streamside vegetation still provides some allochthonous detritus, but because of increased stream size, allochthonous inputs are less important than in headwater streams. Additional organic material is provided by transport from upstream headwater streams. Stream communities are very inefficient, and much of the allochthonous material entering headwater streams is transported downstream. During transport, the nature of this allochthonous material is changed by physical abrasion, leaching, and the action of stream consumers (which both physically break up, and partially digest the detrital material). Thus, both the particle size and organic content of detrital material decrease during downstream transport.

Farther downstream, in large rivers, increased depth, sediment load, and turbidity tend to inhibit or prevent autochthonous production (Vannote et al. 1980), and increased width further reduces the importance of allochthonous detrital inputs. Thus, the major source of organic matter in most large rivers is transport from upstream medium-sized and

headwater streams. This organic matter tends to be relatively small in size and low in nutritional value.

The division between headwater and medium-sized streams depends primarily on the amount of shading by bankside vegetation (Minshall 1978). In forested areas, the transition generally occurs between third and fourth order streams. In more open areas (such as the prairies), riparian vegetation has less effect, and the transition from headwater streams to medium-sized streams occurs at a lower stream order (Vannote et al. 1980). The transition from medium-sized streams to large rivers is less affected by the type of riparian vegetation.

The three main heptageniid faunal regions in the intensive study area (high gradient streams, other boreal streams, and the Saskatchewan Rivers) correspond in size and organic matter characteristics to the three longitudinal organic matter zones described by Vannote et al. (1980). High gradient boreal streams contain large quantities of large leaf and wood fragments, and are all second or third order (Table 26). High gradient streams thus fit the description of headwater streams.

Other boreal streams are characterized in part by the presence of diatom blooms. Although algal productivity was not measured, the importance of diatom blooms in characterizing other boreal streams suggests that algal productivity was higher in these streams than in other faunal subzones. All other boreal sites, except sites 18 and 21, are on fourth to sixth order streams (Table 26) and thus fall

Table 26. Stream order at intensive study sites.

<u>Site Number</u>	<u>Stream Name</u>	<u>Stream Order</u>
<u>Saskatchewan River Zone</u>		
1	South Saskatchewan River	7
2	"	8
3	"	8
4	"	8
5	"	8
6	"	8
7	"	8
8	"	8
9	"	8
10	"	8
11	"	8
12	North Saskatchewan River	7
13	Saskatchewan River	8
14	"	8
15	"	8
16	"	8
25	Carrot River	5
26	Red Earth Creek	4
<u>Other Boreal Subzone</u>		
17	Waskesiu River	5
18	Weyakwin River	3
19	Montreal River	5
20	"	5
21	Mackay Creek	3
22	Nipekamew River	4
24	McDougal Creek	4
32	Overflowing River	4
33	Fir River	4
34	"	4
35	Red Deer River	6
<u>High Gradient Boreal Subzone</u>		
23	unnamed stream	3
27	McVey Creek	3
28	Rice River	3
29	Bainbridge River	2
30	Waskwei River	3
31	Pasquia River	3

within the size range of medium-sized streams suggested by Vannote et al. (1980). Sites 18 and 21 are on third order streams. Site 18 is somewhat similar to high gradient streams in both faunal and environmental ordinations. Site 21 is located only 0.5 km downstream from a lake, and may receive large amounts of lentic algal material. Site 21 may thus resemble sites at which in-stream autochthonous production is more important.

The Saskatchewan Rivers are seventh or eighth order at all intensive study sites (Table 26) and thus fall within the size range of large rivers suggested by Vannote et al. (1980). According to Vannote et al., large rivers should be characterized by the presence of large amounts of fine particulate organic matter (FPOM). However, measured amounts of both coarse and fine particulate organic matter were similar in the Saskatchewan River and boreal zones. This may be due to inaccuracies in the measurement of FPOM. The smallest FPOM (0.05 to 0.20 mm), the amount of which was not measured, is probably the most important in determining community composition. Mayflies feeding on detritus consume mainly particles less than 0.16 mm in diameter (Hamilton and Clifford 1983). The apparent lack of importance of differences in FPOM may also be due to lumping benthic and suspended organic matter, which may have very different ecological properties (Minshall et al. 1983). Alternatively, the nutritional value of organic matter may be more important than its particle size in defining stream communities (Bruns et al. 1982). Bruns et al. (1982) and Minshall et al. (1983)

also observed that the shift from coarse to fine particulate organic matter moving from medium-sized streams to large rivers was less obvious than predicted by the river continuum concept, or was absent.

Site 25 is classified in the Saskatchewan River zone, but is on a fifth order stream, the Carrot River. The large area of agricultural, "prairie" land drained by the Carrot River upstream from the study site may cause it to shift from a medium-sized stream to a large river at a lower stream order than if it was in the boreal forest. Many Saskatchewan River-like sites in the extensive study are also on fifth or sixth order streams and drain agricultural land.

Large fifth and sixth order boreal rivers, for example, the Montreal and Churchill Rivers, have distinctly boreal heptageniid faunas. These rivers show no sign of being transitional between smaller boreal streams and the Saskatchewan Rivers. This may be at least partly because most large boreal rivers occur on the Shield, where river channels consist of a series of lakes joined by short stretches of flowing water. Sediment and particulate organic matter are lost from these rivers through deposition in the intervening lakes. Thus, Shield rivers tend to be clearer and have higher levels of autochthonous production than southern rivers of comparable size. Loss of particulate organic matter through sedimentation increases the importance of the autochthonous production. Furthermore, lentic algae may be present for several kilometers downstream from lakes. Large lakes also reduce water temperature, and water temperature variation.

Thus, these lakes lower the apparent size of large northern rivers, from physical, organic and faunistic perspectives.

Longitudinal variation of physical factors forms a single, more or less continuous gradient from headwater streams to large rivers. In DCA ordination of intensive study environmental data, the three heptageniid faunal regions are separated along the first axis with high gradient, headwater streams near one end and Saskatchewan River sites at the other. Thus, the major pattern of environmental variation within the intensive study area may be due to longitudinal gradation of physical factors.

Longitudinal zonation of organic matter characteristics consists of two separate gradients, one from large particulate organic matter in headwater streams to autotrophic production in medium-sized streams, and another from autotrophic production to fine particulate, partially processed organic material in large rivers. Faunal zonation in the intensive study also consists of two separate gradients. Observed heptageniid distribution patterns are thus more similar to expected patterns of longitudinal change in organic matter than to expected patterns of change in physical factors. Therefore, organic matter may be more important than physical factors in regulating heptageniid distribution patterns in Saskatchewan.

Longitudinal gradation of both physical and organic matter parameters should be more or less continuous. However, variation in heptageniid distribution patterns is somewhat discontinuous; two or three distinct faunal zones are evident



in both classifications and ordinations. Observed discontinuities may be due to bias in the choice or availability of sampling sites, quantum responses of the fauna to more gradual environmental changes, or discontinuities in other environmental factors affecting heptageniid distribution patterns. The discontinuity between medium-sized streams and large rivers is coincident with differences in terrestrial vegetation. Most headwater and medium-sized streams in the study area are located in the boreal forest; the Saskatchewan Rivers are located primarily on the prairie. Although the Saskatchewan Rivers flow through parkland or boreal forest in the eastern half of Saskatchewan, this vegetation probably has little impact on the Saskatchewan Rivers, because of their large size and the small amount of boreal runoff entering them (only 10 to 25% of the water in the Saskatchewan Rivers originates in Saskatchewan). The faunal similarity between high gradient, headwater streams and other, medium-sized boreal streams (which is greater than between either group and large rivers) is coincident with similarities in adjacent terrestrial vegetation.

Thus, the major heptageniid distribution patterns in Saskatchewan appear to be due to longitudinal zonation of organic matter and/or physical environmental factors, perhaps modified by the nature of terrestrial vegetation. Longitudinal zonation of organic matter and/or stream organisms in accordance with Vannote et al's. (1980) river continuum concept have also been observed by Hawkins and

Sedell (1981), Bruns et al. (1982), Culp and Davies (1982), Minshall, Brock and LaPoint (1982), Ross and Wallace (1982), Minshall et al. (1983) and Bronmark et al. (1984). Wright et al. (1984) found that the the most important trend in stream invertebrate distributions in Great Britain was related to longitudinal zonation. Culp and Davies (1982) and Minshall et al. (1983) observed an interaction between longitudinal zonation and terrestrial vegetation in regulating stream community structure.

#### 4.9.1.3 Longitudinal zonation of feeding strategies

If organic matter type is important in regulating heptageniid distribution patterns, heptageniid feeding strategies should differ among observed faunal regions. Shredders and coarse particle collectors should predominate in high gradient, headwater streams; grazers should predominate in medium-sized, other boreal streams; and fine particle collectors should predominate in the Saskatchewan Rivers (Vannote et al. 1980). However, all heptageniids that have been studied (excluding predators) have similar feeding habits. These 18 species (of which 6 occur in Saskatchewan) all feed primarily on detritus, although most species also consume some diatoms (up to 35% of their diets) (Shapas and Hilsenhoff 1976, Hamilton and Clifford 1983). Most detrital particles consumed are less than 0.16 mm in diameter (Hamilton and Clifford 1983). No heptageniids are known to be shredders.

Shapas and Hilsenhoff (1976) studied the feeding habits

of five heptageniids that occur in Saskatchewan, including two boreal species (Leucrocuta hebe and Nixe lucidipennis), one Saskatchewan River species (Stenonema terminatum), and two species that occur in both regions (Heptagenia diabasia and H. pulla). The diet of one of the boreal species, L. hebe, contained the highest proportion of diatoms reported for any heptageniid. However, the other boreal species, N. lucidipennis, consumed no diatoms. The two Heptagenia species were also exclusive detritivores, while the Saskatchewan River species, S. terminatum, consumed a small amount of diatoms (3% of its diet).

Hamilton and Clifford (1983) found no consistent differences in feeding strategy among five heptageniid species studied. All were primarily fine particle collector/gatherers that occasionally fed on diatoms (with diatoms comprising up to 25% of their diets). There were no interspecific differences in the size of detrital particles consumed. The only Saskatchewan heptageniid included, Stenacron canadense (= Stenacron interpunctatum), was almost exclusively a detritivore.

Thus, no interspecific differences in heptageniid feeding strategies are apparent. However, few species have been studied, and all but one of these are found primarily or exclusively in medium-sized boreal streams. Furthermore, particle size selection has been studied in only one geographical area. Potential effects of food quality have not been studied. Therefore, information about heptageniid feeding strategies is insufficient to support or reject the

hypothesis that heptageniid distribution patterns are regulated by organic matter.

If longitudinal zonation of stream communities is regulated primarily by organic matter, primary consumers, which feed directly on detritus and algae, should differ more between zones than predators, which are one trophic level higher and tend to be relatively unselective (Vannote et al. 1980). Observed differences in heptageniid and stonefly faunas between the Saskatchewan River and boreal zones (see Section 4.6.2) fit this pattern.

#### 4.9.2 Terrestrial vegetation, climate and physiography

Terrestrial vegetation may have some effect on heptageniid distribution patterns, in addition to or in association with the effects of stream size. The boundary between the two major faunal zones in the province coincides with the boundary between the boreal forest and prairie. High gradient and other boreal streams are all located in the boreal forest, while the Saskatchewan Rivers are primarily on the prairie. The downstream-most seven Saskatchewan River sites are located in the boreal forest. However, because of the large size of the Saskatchewan Rivers and the relatively small amount of boreal runoff, these seven sites should not be greatly affected by boreal vegetation. Nevertheless, these sites are more similar faunistically to boreal streams than are other Saskatchewan River sites.

The heptageniid faunas of high gradient, headwater

streams and other boreal, medium-sized streams are more similar to each other than either are to the Saskatchewan River fauna. This may be because both high gradient and other boreal streams are located in the boreal forest, while the Saskatchewan Rivers are located primarily on the prairie. The similarity between site 25 (on the Carrot River, which drains primarily agricultural land) and the Saskatchewan Rivers may also be due to similarities in adjacent terrestrial vegetation.

The main effects of terrestrial vegetation on stream communities are on the quantity and quality of allochthonous organic matter and on stream shading. Thus stream size and terrestrial vegetation probably interact in their effects on stream community composition. This interaction may be the cause of the apparent association of heptageniid distribution patterns in Saskatchewan with both stream size and terrestrial vegetation. Culp and Davies (1982) and Minshall et al. (1983) have also observed apparent interactions between stream size (longitudinal zonation) and terrestrial vegetation in regulating stream community structure. Hawkins, Murphy and Anderson (1982) and Molles (1982) have shown the importance of watershed vegetation alone in determining the compositions of stream macroinvertebrate communities.

The two major heptageniid faunal zones in Saskatchewan also differ climatically. However, this climatic difference is coincident with differences in stream size and terrestrial vegetation.

The two major heptageniid faunal zones show no

relationship to major physiographic regions. Current velocity, which is related to physiography, is important in distinguishing high gradient streams from other boreal streams. However, small headwater streams are generally faster-flowing than larger streams and rivers. Thus, the association between current velocity and high gradient species may be due to a common association with headwater streams rather than a direct effect of current velocity.

Boreal subzones recognized in the extensive study are associated with differences in adjacent terrestrial vegetation. Three of these subzones, Shield (IIe), southern boreal (IIId), and low gradient southern boreal and parkland (IIc), correspond approximately to floral subdivisions of the boreal forest, the northern boreal forest, southern boreal forest and parkland, respectively (see Section 2.2). However, these floral and faunal differences are also associated with coincident differences in climate and topography. The relative importances of these three sets of environmental factors cannot be directly assessed. Water temperature and current velocity are most important in distinguishing these boreal subzones in hybrid ordinations. The potential importance of differences in organic matter quality, associated with differences in terrestrial vegetation, was not assessed.

Faunal differences between small to medium-sized prairie streams (in which heptageniids are absent, or only Stenonema terminatum is present) and similar-sized boreal streams are also correlated with differences in vegetation, climate, and

topography. The impoverished heptageniid fauna of small prairie streams is probably due to climate and physiography. Low current velocities, periodic drying, and high temperatures in these streams provide unsuitable habitats for most or all heptageniids. Prairie vegetation alone is unlikely to be responsible for such a poor heptageniid fauna.

The Cypress Hills are unique in physiography, climate, and terrestrial vegetation. The stream insect fauna of this area is also unique and contains several western, montane species (Lehmkuhl 1976a, Dosdall and Lehmkuhl 1979). However, which environmental factors are most important in determining the unique fauna of the Cypress Hills is not known.

#### 4.9.3 Drainage systems

Drainage systems appear to be important in regulating the distributions of some stream organisms, especially strictly aquatic organisms such as fish (McPhail and Lindsay 1970) and molluscs (Clarke 1973). However, observed heptageniid distribution patterns in Saskatchewan do not appear to be related to drainage systems. The boundaries of heptageniid faunal zones and subzones do not coincide with those of any drainage system. The boreal zone includes sites in all three major drainage systems in Saskatchewan (the Arctic, Hudson Bay and Missouri-Mississippi systems) and in most of the individual drainage basins within the Hudson Bay system. All boreal subzones include sites from at least two different drainage basins. The Saskatchewan River faunal zone is more or less restricted to the Saskatchewan River drainage

basin; however, some Saskatchewan River-like sites are in the Qu'Appelle and Assiniboine basins. Furthermore, some tributaries of the Saskatchewan River in east-central Saskatchewan are in the boreal zone and among them contain all boreal species included in the intensive study. Only the two rarest boreal species (Arthroplea bipunctata and Cinygmula mimus) and some of the rarer Saskatchewan River species are restricted to a single drainage basin.

Drainage basins in Saskatchewan are apparently not sufficiently separated to provide a barrier to heptageniid dispersal. Within the boreal forest there is little geographical separation between the headwater streams of different drainage basins. Wollaston Lake actually drains both northwest into the Athabasca River system and east into the Churchill system. Several boreal streams are tributaries of the Saskatchewan River, providing a connection between boreal and Saskatchewan River drainage basins.

The ability of adult mayflies to disperse over long distances is probably underrated, as suggested by the presence of Leucrocuta hebe (which is otherwise strictly boreal) in the Cypress Hills. Most stream organisms with distributions that appear to be regulated by drainage basin boundaries have no terrestrial stage in their life cycles, and thus would have much more difficulty than heptageniid mayflies in dispersing between drainage basins.

#### 4.9.4 Dams and impoundments

Dams and associated reservoirs have several effects on



downstream reaches of rivers (Baxter 1977). Reservoirs act as heat sinks and thus reduce mean and maximum water temperature, and water temperature variation. Suspended silt and particulate organic matter are deposited in reservoirs, and are thus greatly reduced downstream from reservoirs. The associated increase in water clarity causes an increase in autochthonous production by algae and macrophytes, which becomes the primary source of organic matter for stream consumers. Downstream from hydroelectric dams, diurnal fluctuations in power demand and production lead to great fluctuations in water level. These fluctuations cause periodic exposure and rewetting of large areas of stream substrate, and great changes in current velocity. However, diurnal fluctuations in discharge are quickly attenuated, and have little impact farther downstream. Seasonal fluctuations in discharge, which are normally extensive in large rivers such as the Saskatchewan, are greatly reduced by dams and impoundments.

Heptageniids are absent in the South Saskatchewan River immediately downstream from Gardiner Dam, and the heptageniid fauna remains depauperate as far downstream as Saskatoon. Lehmkuhl (1972b) found that the richness of all stream insects was reduced in this stretch of the South Saskatchewan River. He attributed this faunal reduction to the reduced number of degree-days available for growth and to the disrupted annual temperature regime. Similar faunal impoverishment has been observed downstream from other dams and impoundments (Spence and Hynes 1971, Ward 1974, 1976,

Gore 1977).

Farther downstream, between Saskatoon and the confluence with the North Saskatchewan River, water temperature is normal or near normal, but turbidity and siltation remain very low. Production of macrophytes and filamentous algae in this stretch of the South Saskatchewan River is very high. This primary productivity is probably enhanced by nutrient enrichment associated with Saskatoon sewage effluent, as well as by high water clarity associated with the effects of Gardiner Dam.

If heptageniid distribution patterns are regulated by the nature of available organic matter, the high primary productivity in reaches of the South Saskatchewan River affected by Gardiner Dam should be associated with a boreal heptageniid fauna. Boreal, or small stream, species of caddisflies have been found downstream from dams on the South Saskatchewan River (Smith 1975) and in Montana (Hauer and Stanford 1982). However, the heptageniid fauna downstream from Gardiner Dam consists primarily of Saskatchewan River species and includes no distinctly boreal species.

The absence of boreal heptageniids in the South Saskatchewan River downstream from Gardiner Dam may be due to inadequate opportunities for colonization. Gardiner Dam was closed only 18 years ago. This is probably not an adequate length of time for colonization by boreal heptageniids. In comparison, the colonization of natural stream habitats in Saskatchewan has taken as long as 10,000 years. The presence of boreal caddisflies, but not mayflies, in areas affected by

dams may reflect the longer life span and greater flying ability of adult caddisflies.

The effects of Squaw Rapids Dam were studied less than those of Gardiner Dam, because fewer suitable sampling sites were available. Nevertheless, Squaw Rapids Dam appears to have a similar, although slightly less severe, effect on heptageniids. The heptageniid fauna at site 16, 18 km downstream from Squaw Rapids Dam, was slightly more diverse than that at site 6, 25 km downstream from Gardiner Dam. Lehmkuhl (unpublished data) and Mason and Lehmkuhl (1983) have found faunal reductions below Squaw Rapids Dam similar to those below Gardiner Dam.

#### 4.10 Effect of the Wisconsin Glaciation on Present-day Heptageniid Distribution Patterns

##### 4.10.1 Heptageniid refugia during the Wisconsin

The Wisconsinan glaciation is the most important recent historical event affecting the distributions of heptageniid mayflies in Saskatchewan. Seventeen thousand years B.P., the Wisconsin Ice Sheet covered nearly all of Saskatchewan (Christiansen 1979). Only parts of the Cypress Hills and Wood Mountain were free of ice (Christiansen 1979). The climate in these ice-free areas was almost certainly too cold, and possibly also too arid, to permit the survival of stream insects. It is especially unlikely that heptageniids, which are absent in Arctic Canada today (D. M. Lehmkuhl pers. comm.), could have survived the Wisconsinan glaciation in ice-free parts of Saskatchewan.

Thus, the present-day heptageniid fauna of Saskatchewan must have invaded from extra-provincial refugia after the retreat of the Wisconsin Ice Sheet, 17,000 to 8000 years ago. Three main refugia are thought to have existed in North America during the Wisconsinan glaciation: 1) Alaska-Beringia, in the northwest, 2) the western United States and 3) the eastern United States (McPhail and Lindsay 1970, Lehmkuhl 1980, Mason and Lehmkuhl 1985). At least two distinct centers of origin are present within each of the latter two refugia, the Rocky Mountains and Sonoran (or western interior basin) in the west, and the Appalachian (or boreal) region and southeastern United States in the east. Present-day distributions provide the best available clues

about which refugium, or refugia, a species occupied during the Wisconsinan glaciation (Larson 1975); i.e. if a species' present-day distribution includes only one refugium, then the species may well have spent the Wisconsin in that refugium.

The known North American distributions of Saskatchewan heptageniids are indicated in Table 27. It is unlikely that any Saskatchewan heptageniid species survived the Wisconsin in the Beringian refugium. Nearly all insect species that are thought to have utilized the Beringian refugium have present-day distributions that are primarily Arctic (Lehmkuhl 1980, Mason and Lehmkuhl 1985), and heptageniids are not found in the Arctic. Furthermore, only one Saskatchewan heptageniid, Epeorus longimanus, has been collected in Alaska, and it is widespread in western North America. Therefore, E. longimanus probably spent the Wisconsin in the western United States in addition to, or instead of, the Beringian refugium. It thus appears that Saskatchewan's heptageniid fauna originated only from southern refugia.

The two southern refugia, in the eastern and western United States, appear to have been isolated from one another during the Wisconsinan glaciation. Most Saskatchewan heptageniids, and many other North American mayflies, are restricted to either the eastern or western half of the continent (Table 27); only one Saskatchewan heptageniid, Stenonema terminatum, has a transcontinental distribution. These species include many pairs of closely related species, of which one is eastern and one is western. This suggests past separation of eastern and western populations during the

Table 27. Known distributions of Saskatchewan heptageniid species in North America.

	<u>Distribution *</u>
<u>Boreal Species</u>	
<i>Arthroplea bipunctata</i>	eastern - Great Lakes (M)
<i>Cinygmula mimus</i>	western
<i>Leucrocuta hebe</i>	eastern
<i>Nixe inconspicua</i>	eastern - Mississippi
<i>N. lucidipennis</i>	eastern - Great Lakes
<i>N. rusticalis</i>	eastern - Great Lakes
<i>N. simplicoides</i>	western
<i>Stenonema femoratum</i>	eastern (M)
<i>S. vicarium</i>	eastern (M)
<u>Boreal/Saskatchewan River Species</u>	
<i>Heptagenia diabasias</i>	eastern - Great Lakes
<i>H. pulla</i>	eastern (M)
<i>Stenacron interpunctatum</i>	eastern
<u>Saskatchewan River Species</u>	
<i>Acanthomola pubescens</i>	Saskatchewan and Alberta
<i>Anepeorus rusticus</i>	western - Sonoran
<i>Heptagenia adequata</i>	Saskatchewan and Alberta
<i>H. elegantula</i>	western
<i>H. flavescens</i>	eastern
<i>Macdunnoa nipawinia</i>	Saskatchewan
<i>Pseudiron centralis</i>	eastern - Mississippi
<i>Raptoheptagenia cruentata</i>	eastern - Mississippi
<i>Rhithrogena undulata</i>	western (M)
<i>Stenonema terminatum</i>	transcontinental
<u>Cypress Hills Species</u>	
<i>Epeorus longimanus</i>	western

\* Descriptions of distribution patterns

eastern: generally distributed in eastern and southeastern North America.

eastern - Great Lakes: found primarily in states or provinces on or near the Great Lakes (and in Saskatchewan).

eastern - Mississippi: found only in the Mississippi River and its tributaries (and in Saskatchewan).

western: generally distributed in western North America.

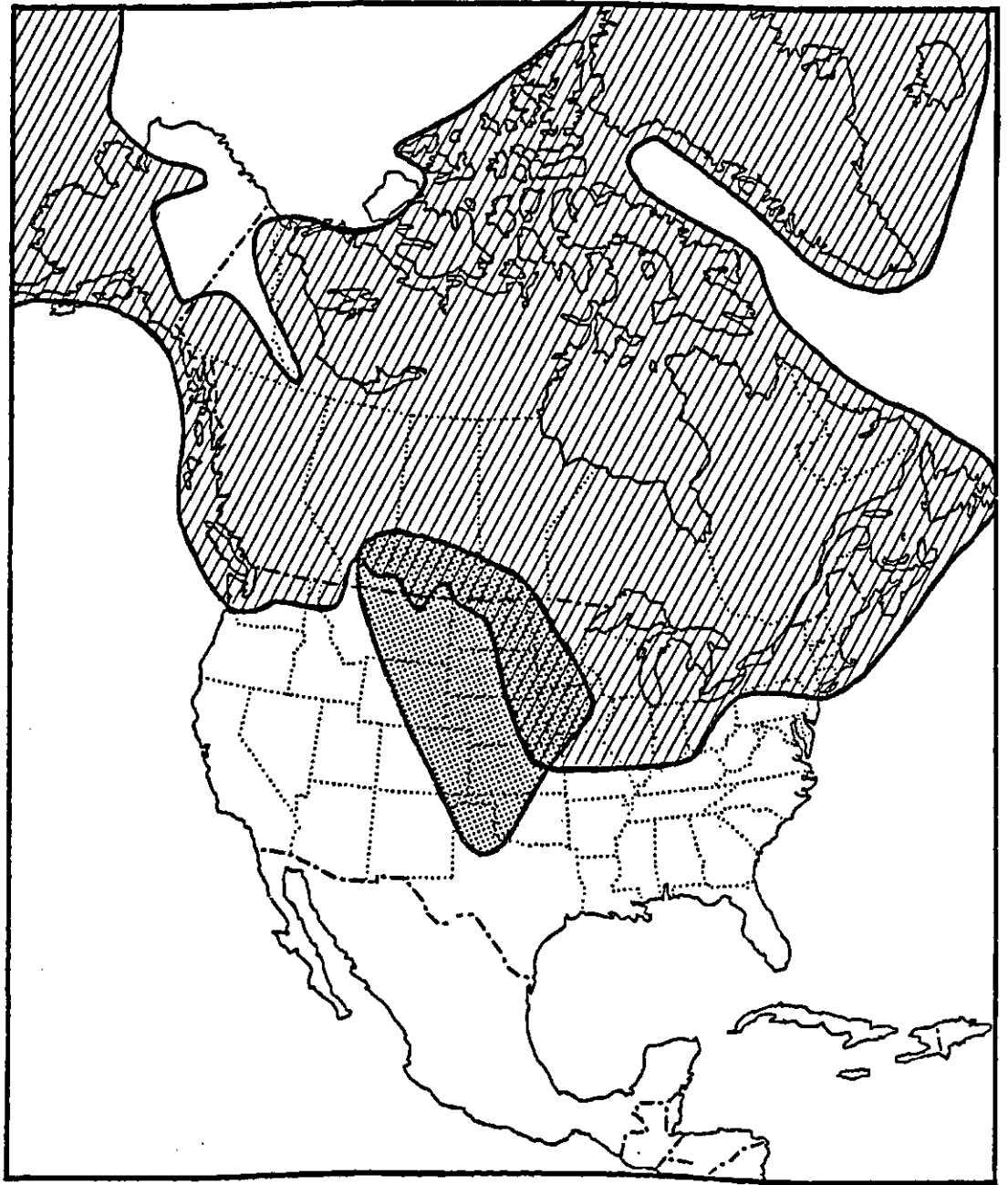
western - Sonoran: restricted to the Colorado River system in the southwestern United States (and Saskatchewan).

(M) - also found in the Mackenzie River system, N.W.T.

Wisconsin (and probably also during previous Pleistocene glaciations), which led to speciation. Overlap in the present-day ranges of eastern and western heptageniid species occurs only in the parklands and boreal forest of central Canada (Manitoba, Saskatchewan and eastern Alberta). Other species of small animals, such as other insects and birds, have similar patterns of distribution (Howden 1969, Lehmkuhl 1980).

Eastern and western heptageniids are separated today by the prairies. No heptageniids are known from the prairies in southern Saskatchewan or the United States, probably because of the heat, aridity and low stream current velocities. At its maximum extent, the Wisconsin Ice Sheet extended south into what is now the northern prairies. Although the eastern part of the modern prairie region was apparently covered by boreal forest during the Wisconsin (Matthews 1979), grasslands were present farther west. Furthermore, Wisconsinan boreal forests in central North America were probably more open and more arid than contemporary boreal forests (Gruger 1972), and may not have provided suitable habitats for heptageniids. Thus, the combination of the Ice Sheet and the prairies (and the desert and semi-desert south of the prairies) could have formed a complete barrier between eastern and western heptageniid populations (Figure 92).

Brunnschweiler (1962), Whitehead (1973) and Ross (1979) suggest that there was a continuous band of tundra and boreal forest along the southern edge of the Wisconsin Ice Sheet. This could have provided a connection between eastern and



- ▨ - Maximum Extent of the Wisconsin Ice Sheet  
▤ - Present Extent of the Prairie

Figure 92. Maximum extent of the Wisconsin Ice Sheet (17,000 years B.P.; from Mason and Lehmkuhl 1985), and present-day extent of the prairies (from Lehmkuhl 1980) in North America.



western heptageniid populations. However, recent palynological evidence suggests that eastern boreal and western cordilleran forests were completely, or nearly completely, separated for the entire Wisconsin period (Gruger 1972). Thus, eastern and western heptageniid populations may have been separated for much or all of the Wisconsinan glaciation.

#### 4.10.2 Post-glacial colonization of Saskatchewan

During the early retreat of the Wisconsin Ice Sheet, both the Saskatchewan River system (Elson 1967) and Glacial Lake Agassiz (into which most of northern Saskatchewan drained) (Matsch 1983) drained into the Mississippi/Missouri River system. These connections would have provided potential colonization routes for heptageniids from the southeastern United States (Lehmkuhl 1972a). Later in the Wisconsin deglaciation, the Saskatchewan River drained into Lake Agassiz, which in turn drained into the Great Lakes (Elson 1967). This connection would have provided an opportunity for heptageniids from the Appalachian region to colonize both the Saskatchewan Rivers and boreal forest streams.

The Saskatchewan Rivers originate in the Rocky Mountains of Alberta. Thus, western, montane heptageniids have also had an opportunity to colonize the Saskatchewan Rivers.

Several Sonoran mayfly species have also been collected in the Saskatchewan Rivers (Lehmkuhl 1976b, 1980). These species apparently have invaded from the Colorado River system. Although the Saskatchewan and Colorado River systems

probably have never been connected, the headwaters of the Colorado and Missouri Rivers are only 80 km. apart. Adult heptageniids could conceivably have crossed this distance (Lehmkuhl 1976b). The headwaters of the Missouri and Saskatchewan Rivers are also relatively close to one another, and the Saskatchewan River flowed into the Missouri during the early stages of the Wisconsin deglaciation. Thus, Sonoran mayflies may have colonized the Saskatchewan River via the Missouri River. Although no Sonoran mayflies are known from the Missouri River, they may have been present before the destruction of most mainstream habitats by dams and impoundments (Lehmkuhl 1976b). Furthermore, one Sonoran mayfly (Anaetris exima) has been collected in the Milk River, a tributary of the Missouri, in southern Alberta (D. Soluk pers. comm.).

#### 4.10.3 Effects of post-Wisconsin dispersal on present-day heptageniid distribution patterns

The initial colonization of Saskatchewan, following the retreat of the Wisconsin Ice Sheet, would probably have been through connections to southern drainage systems in unglaciated areas. The Saskatchewan Rivers have been connected to both southeastern and southwestern refugia and thus could possess faunal elements from both areas. However, boreal streams and rivers have always drained to the east and would probably have been initially colonized from southeastern refugia only. Is this difference in the sources of potential post-Wisconsinan colonizers responsible for the

observed faunal differences between the Saskatchewan River and boreal faunal zones? Are faunal differences between these zones due to the presence of western heptageniids in the Saskatchewan River system, but not in the boreal forest?

Six of the seven characteristic boreal species (as identified by DCA) are eastern; only one, Nixe simplicoides, is western (Table 27). The characteristic Saskatchewan River fauna consists of three western, six eastern and one transcontinental species, and three species that are known only from Saskatchewan, or Saskatchewan and Alberta. Thus, there are more western heptageniid species in the Saskatchewan Rivers than in the boreal forest. However, the difference is small. Furthermore, three of the eastern Saskatchewan River species, Heptagenia flavescens, Raptoheptagenia cruentata and Stenonema terminatum, are not found in boreal Saskatchewan; two of these species are among the five that are most characteristic of the Saskatchewan River zone and are more or less restricted to the South Saskatchewan River upstream from Lake Diefenbaker.

There are no obvious physical barriers to dispersal that might prevent faunal exchange between the Saskatchewan Rivers and boreal streams. Several boreal streams (with typical boreal faunas) are tributaries of the Saskatchewan River, providing a direct connection between the two faunal zones. Furthermore, most or all Saskatchewan heptageniids both have the ability and have had the opportunity to colonize suitable stream habitats throughout the province. Several common boreal species (including Heptagenia pulla, Stenacron

interpunctatum and Stenonema vicarium) are found as far west as northern Alberta, and the Mackenzie River, Northwest Territories, and another (Leucrocuta hebe) is found in the Cypress Hills; one common western, Saskatchewan River species (Heptagenia elegantula) is common in southern Manitoba.

Therefore, post-Wisconsin dispersal routes do not provide an adequate explanation of present-day heptageniid distribution patterns in Saskatchewan. Environmental regulation provides a better explanation of observed distribution patterns.

#### 4.11 Habitat Separation Among Congeneric Species

Three genera of heptageniids are represented by more than one species in Saskatchewan: 1) Heptagenia - five species, 2) Nixe - four species, and 3) Stenonema - three species.

##### 4.11.1 Habitat separation among Stenonema species

The three Saskatchewan Stenonema species are not closely related. S. terminatum and S. vicarium belong to two (of three) different phyletic lines within the subgenus Maccaffertyum; S. femoratum belongs to a different subgenus, Stenonema (Bednarik 1978).

The three species have very different distributions in Saskatchewan. S. femoratum is the only Saskatchewan heptageniid living predominantly in lentic habitats. S. terminatum and S. vicarium inhabit different major faunal zones; S. terminatum is almost completely restricted to the Saskatchewan River zone, and S. vicarium has been collected only in the boreal zone. S. femoratum and S. terminatum were never collected at the same site; S. vicarium was only rarely collected at the same site as either of the other two species. Wherever two Stenonema species were collected at the same site, one species was uncommon or rare. Thus, these three Stenonema species are widely separated, ecologically and biogeographically, in Saskatchewan.

#### 4.11.2 Habitat separation among Nixe species

The four Saskatchewan Nixe species are found in the boreal forest, and all except N. simplicoides (which is also found in the South Saskatchewan River upstream from Lake Diefenbaker and in the Cypress Hills) are restricted to the southeastern boreal forest. In multivariate analyses of intensive study data, these four species are separated into two groups: 1) N. rusticalis and N. simplicoides, which are characteristic of high gradient streams; and 2) N. inconspicua and N. lucidipennis, which are characteristic of other boreal streams. However, in the extensive study, N. lucidipennis is also associated with high gradient streams and N. inconspicua is not clearly associated with either boreal subzone. Thus, the four Nixe species do not show clear habitat separation among observed heptageniid faunal zones or subzones.

The three species belonging to the subgenus Nixe, N. inconspicua, N. lucidipennis and N. rusticalis have mutually exclusive distributions. Only rarely were any two of them collected at the same site. These three species appear to be quite well separated along two environmental gradients: stream gradient (drop in altitude per unit longitudinal distance) and water temperature (Figure 93). N. rusticalis is found mainly in cold, high gradient streams; N. lucidipennis is found mainly in cold, low gradient streams; and N. inconspicua is found mainly in warm, low gradient streams. Thus, the three Saskatchewan N. (Nixe) species demonstrate within-subzone habitat separation.

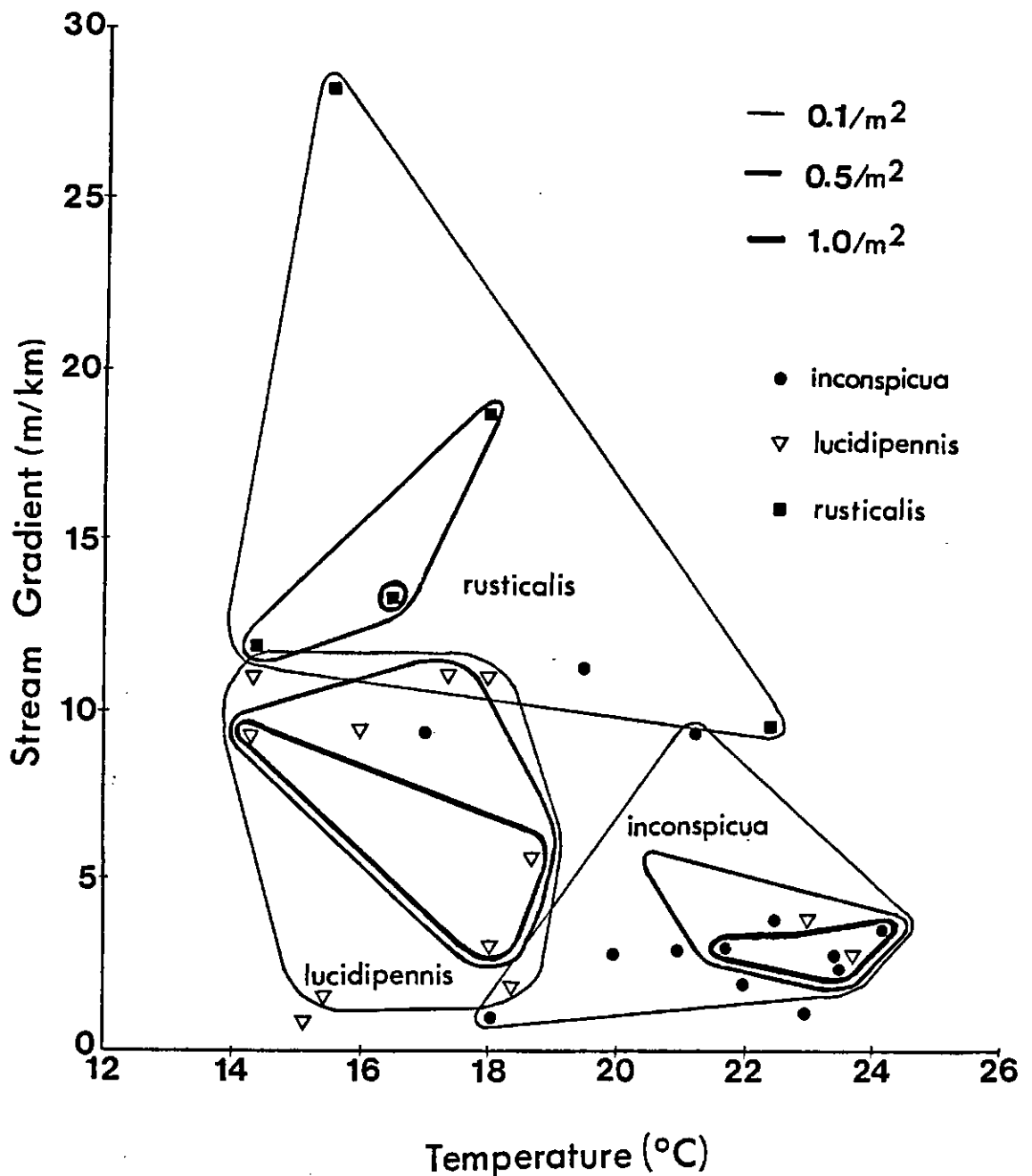


Figure 93. Habitats of *Nixe inconspicua*, *N. lucidipennis* and *N. rusticalis*, as defined by stream gradient and water temperature. Dots represent sites at which *Nixe* species have been collected. The position of each site is determined by its gradient and water temperature. Lines of increasing thickness represent contours of increasing abundance of each species (numbers per square meter in sweep net samples). Note that habitat overlap among species decreases as abundance increases.

The fourth Saskatchewan Nixe species, N. simplicoides belongs to a different subgenus, Akkarion (Flowers 1980). N. simplicoides was frequently collected at the same site as the three N. (Nixe) species, and its habitat (as defined by stream gradient and water temperature) overlaps widely with that of all three (Figure 94). The habitat of N. simplicoides does not differ from that of the other three species in any other measured environmental parameter, and all four species have similar life cycles. Thus, N. simplicoides appears to coexist with N. (Nixe) species. Coexistence may be related to the taxonomic distance between the two subgenera, or to historical differences in distribution. N. simplicoides is western and probably spent the Wisconsin glaciation in the western refugium; all N. (Nixe) species are eastern. Therefore, Nixe simplicoides was probably separated from the other three species during the Wisconsin glaciation, and has only come into contact with them, in Saskatchewan, since the retreat of the Wisconsin Ice Sheet. It is possible that these species have not been in contact long enough for mechanisms to reduce competition between N. simplicoides and the other three species to develop. Alternatively, N. simplicoides and N. (Nixe) species may show microhabitat separation.

Stream gradient is directly related to current velocity. The apparent importance of stream gradient in defining the habitats of Nixe species is probably due to this relationship. Thus, habitat separation among Nixe species is apparently regulated by current velocity and water temperature.



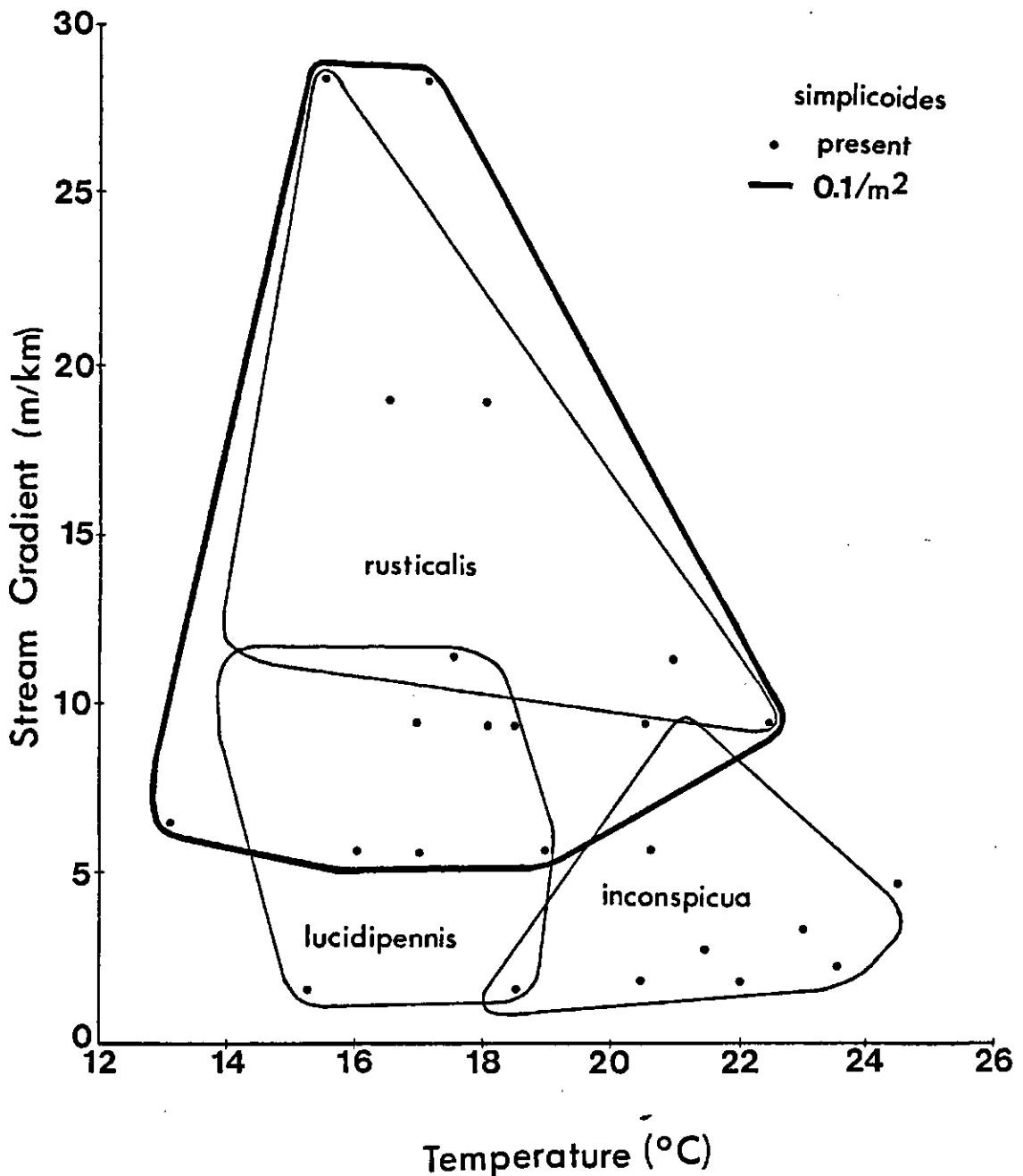


Figure 94. Habitats of *Nixe inconspicua*, *N. lucidipennis*, *N. rusticalis* and *N. simplicoides*, as defined by stream gradient and water temperature. Dots represent all sites at which *N. simplicoides* has been collected; the thick line surrounds all sites at which its density (in sweep net samples) exceeds 0.1 per square meter. The narrow lines surround sites at which the densities of *N. inconspicua*, *N. lucidipennis* and *N. rusticalis* exceed 0.1 per square meter.

The third and fourth extensive study DCA axes appear to be partly related to within-subzone habitat separation among Nixe (Nixe) species. Nixe species and the high gradient and nearby low gradient streams in which they occur both have wide ranges of ordination scores on these two axes (Figure 95). Furthermore, current velocity and water temperature, which appear to define habitat separation among Nixe species, are the most important environmental parameters on the third and fourth axes (Figure 96).

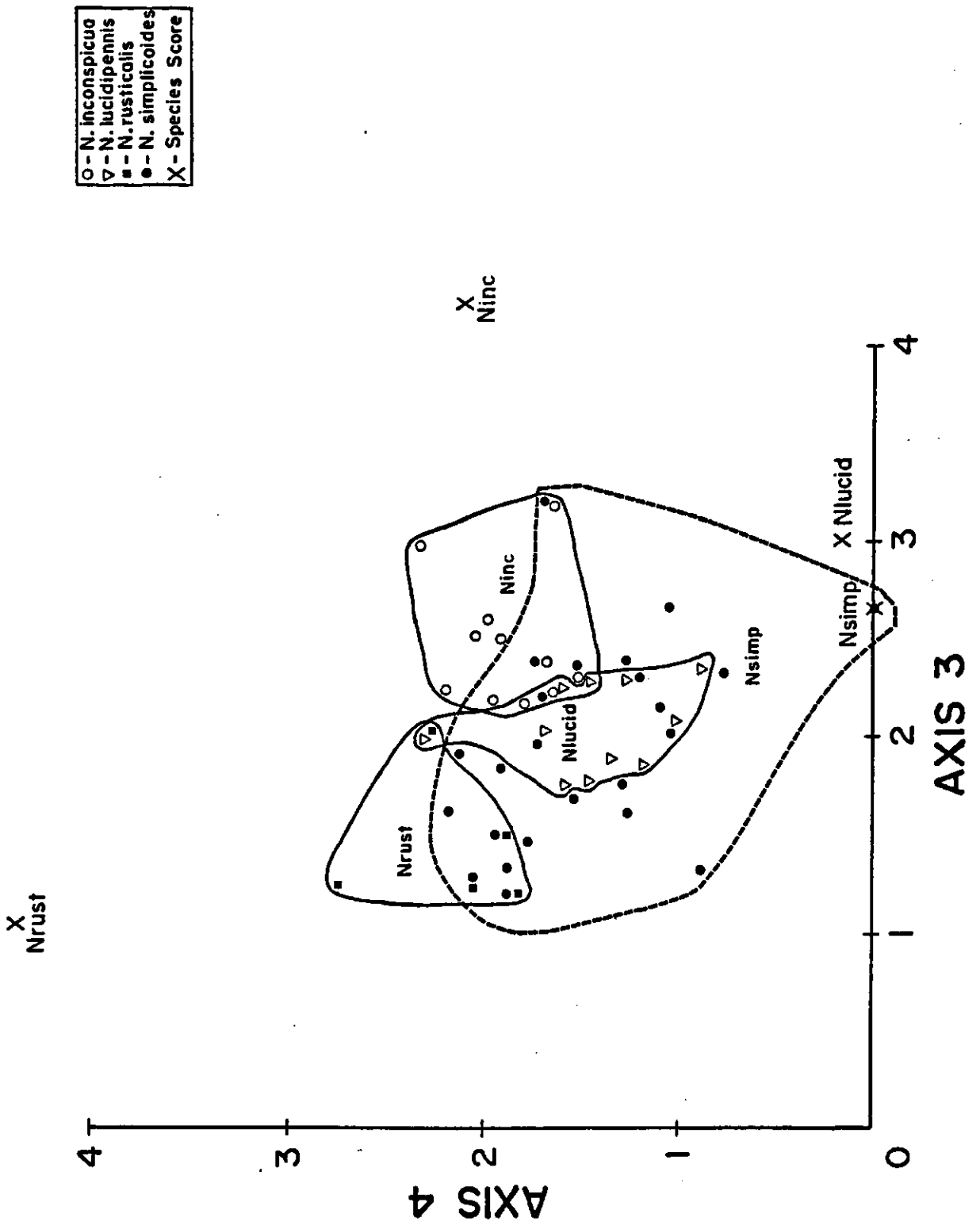
#### 4.11.3 Habitat separation among Heptagenia species

Three of the five Saskatchewan Heptagenia species, H. adequata, H. diabasia and H. elegantula, are closely related and belong to the same phyletic group. The other two species, H. flavescens and H. pulla, are not very closely related to each other or to the first three species and belong to two different phyletic groups (E. Whiting, unpublished data).

The distributions of Heptagenia species do not overlap in the boreal forest. H. diabasia is the only Heptagenia species in most eastern parkland streams and rivers; H. pulla is the only Heptagenia species at most other boreal sites.

However, all five Heptagenia species occur in the Saskatchewan River zone; and all five are common at some sites, such as sites 1, 3 and 4 on the South Saskatchewan River upstream from Lake Diefenbaker. Thus, no habitat separation is evident among Heptagenia species within the Saskatchewan River zone. Temporal or microhabitat separation may be present, but has not yet been investigated.

Figure 95. DCA ordination of extensive study data; third and fourth axis scores of Nixe species and sites at which Nixe species have been collected. Solid lines surround all sites at which each N. (Nixe) species has been collected; the broken line surrounds sites at which N. simplicoides has been collected.



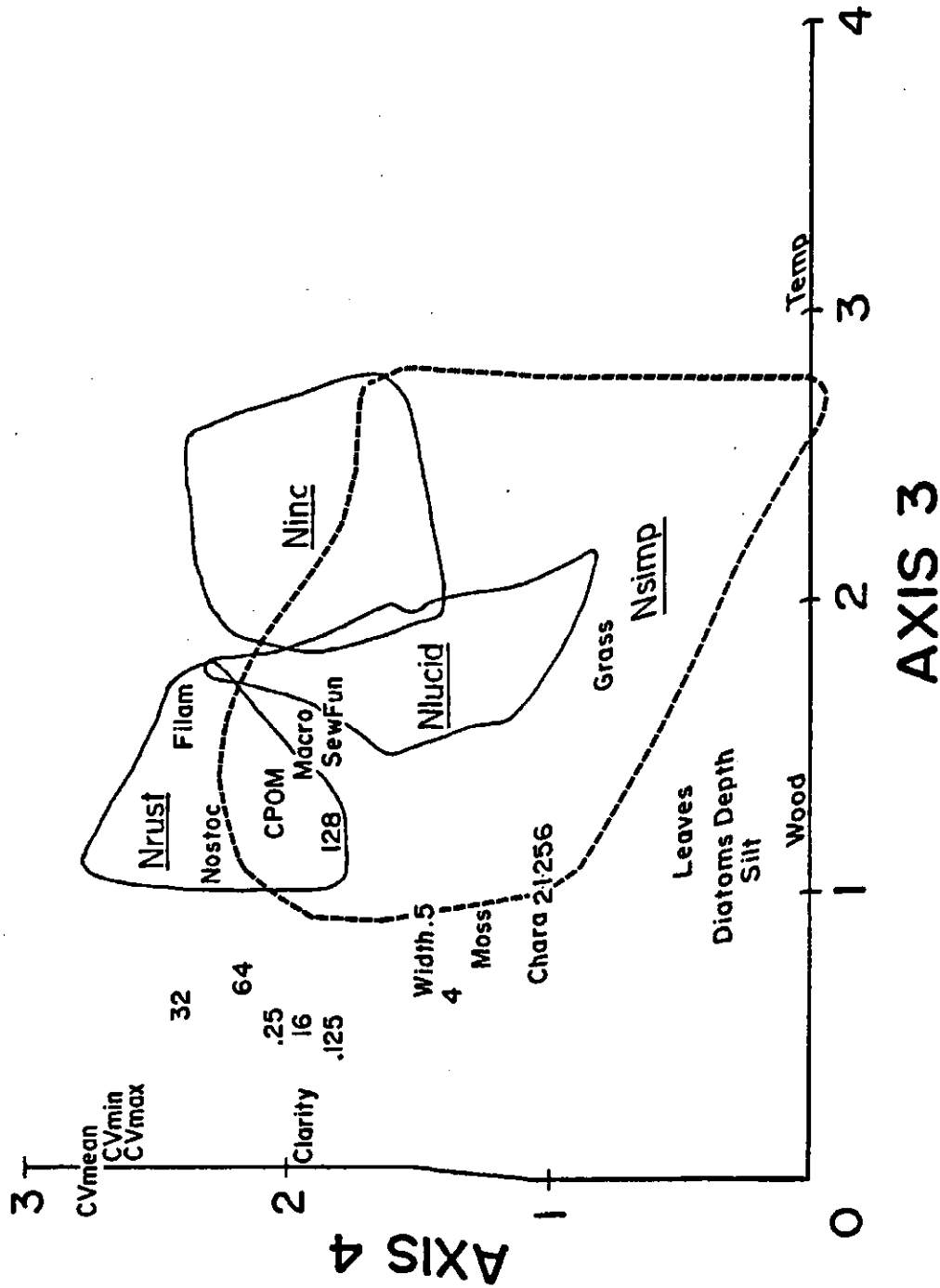


Figure 96. Ordination of extensive study data: third and fourth axis hybrid ordination environmental scores. Abbreviated environmental names are explained in Figure 75. Solid lines surround all sites at which each Nix (Nix) species has been collected; the broken line surrounds sites at which N. simplicoides has been collected.

## 5 SUMMARY AND CONCLUSIONS

### 5.1 Stream Faunal Distribution Patterns in Saskatchewan

Two heptageniid faunal zones, the Saskatchewan River and boreal zones, are present in Saskatchewan. These zones are evident in classifications and ordinations of quantitative data from the intensive study, and of qualitative data from the extensive study. The similarities in zonal patterns among analyses using different types of data, different study areas, and different analysis techniques indicate the validity and importance of these two faunal zones.

Non-heptageniid mayflies (Lehmkuhl 1976a), stoneflies (Dosdall and Lehmkuhl 1979) and caddisflies (Smith 1975, 1984) show similar zonation, with distinct Saskatchewan River and boreal faunas. A third faunal zone, the Cypress Hills, is evident in the distributions of non-heptageniid mayflies and stoneflies (Lehmkuhl 1976a, Dosdall and Lehmkuhl 1979). Although this zone is not evident in heptageniid distributions, because of the paucity of its heptageniid fauna, it probably constitutes a valid stream insect faunal zone. Regardless, the Cypress Hills zone is of limited importance in Saskatchewan because of its small size.

Intrazonal distribution patterns differ more among data types, analysis methods, and taxonomic groups. The heptageniid fauna of high gradient streams is distinct in all analyses, indicating that high gradient boreal streams constitute a valid heptageniid faunal subzone. High gradient streams may even constitute a separate major zone. Two

additional boreal subzones, low gradient southern boreal and parkland streams, and Shield streams and rivers, are evident in the extensive study. However, these areas were inadequately sampled and hence not apparent in the intensive study. Thus, their validity cannot be substantiated.

Boreal subzones have not been observed in studies of other stream insects in Saskatchewan (other mayflies, stoneflies and caddisflies), except for differences between Shield and southern boreal caddisfly faunas (Smith 1984). This suggests that subzonal distribution patterns differ among taxonomic groups, or that subzonal patterns can only be resolved with the use of quantitative analysis techniques (which have not been applied in other studies of stream insects in Saskatchewan).

Distribution patterns within the Saskatchewan River zone are related primarily to the positions of dams and impoundments. The richness of heptageniid, other mayfly (Lehmkuhl 1976a), stonefly (Dosdall and Lehmkuhl 1979) and caddisfly (Smith 1975) faunas is higher upstream and lower immediately downstream from Gardiner Dam than elsewhere in the Saskatchewan Rivers. Some large parkland and southern boreal streams are faunally similar to the Saskatchewan Rivers. However, this similarity has not been observed in stream insects other than heptageniids.

## 5.2 Environmental Explanation of Distribution Patterns

Consistent, environmental differences between the two

major faunal zones, and among faunal subzones, are apparent in weighted averages hybrid ordinations. The Saskatchewan River and boreal faunal zones differ in stream size, water temperature, siltation and allochthonous grass, which are generally greater in the Saskatchewan River zone, and in water clarity, diatom growth, sandiness and allochthonous leaves and wood, which are greater in the boreal zone.

Within the Saskatchewan River zone, sites downstream from Gardiner Dam are generally more similar to boreal streams and have lower current velocities than sites upstream from Lake Diefenbaker. Large southern boreal streams that have heptageniid faunas similar to that of the Saskatchewan Rivers are warmer and have lower current velocities than the Saskatchewan Rivers.

High gradient boreal streams are generally smaller and faster-flowing, and contain more allochthonous material than other boreal streams, while low gradient southern boreal and parkland streams generally have the lowest current velocities and greatest sewage fungus growth. Shield streams and rivers tend to be colder and faster-flowing than southern boreal streams.

Most of the observed environmental differences among heptageniid faunal regions can be related to differences in stream size, and associated longitudinal gradation of physical parameters (especially water temperature, silt load and current velocity) and organic matter characteristics. The three major faunal regions in the intensive study area, the Saskatchewan River faunal zone, and the high gradient and



other boreal subzones, correspond in size (stream order) to the three longitudinal organic matter zones in the river continuum concept (Vannote et al 1980). High gradient streams correspond to small headwater streams (first to third order), with low water temperatures, little suspended or benthic silt, high current velocities, and large amounts of large particle allochthonous organic matter. Other boreal streams correspond to medium-sized streams (fourth to sixth order), which are warmer and more open, and in which autochthonous production provides an important source of organic matter. The Saskatchewan Rivers correspond to large rivers (seventh and higher order), which are very warm and silty, and in which most of the available organic matter is partially processed, fine particulate material from upstream.

Longitudinal differences in organic matter characteristics may be more important in regulating heptageniid distribution patterns than differences in physical parameters. Faunal differences among the three regions represent two separate community gradients, suggesting a response to two separate environmental gradients. Longitudinal zonation in organic matter characteristics involves two separate environmental gradients (one from coarse particulate allochthonous organic matter to autochthonous production, and another from autochthonous production to fine particulate, partially processed organic matter). Longitudinal changes in physical parameters, on the other hand, form a single, more or less continuous gradient (Leopold, Wolfman and Miller 1964). However, evidence for the

regulation of heptageniid distribution patterns by organic matter type is not conclusive.

Streamside terrestrial vegetation may also affect heptageniid distribution patterns by modifying the effects of stream size. Forests provide large amounts of large-particle organic matter and reduce autochthonous production and water temperature through shading. The effect of terrestrial vegetation on heptageniid distribution patterns in Saskatchewan is suggested by: 1) the similarity between high gradient, headwater streams and other, medium-sized boreal streams, both of which are located in the boreal forest, 2) the faunal similarity between some large parkland rivers, which are only fifth or sixth order but contain grassland or agricultural land in their watersheds, and the larger Saskatchewan Rivers, and 3) the slight faunal similarity between Saskatchewan River sites located in the boreal forest and boreal streams.

Observed distribution patterns can also be associated with differences in climate and topography. However, coincident differences in stream size and terrestrial vegetation appear to provide a better explanation of most observed distribution patterns. High gradient, headwater stream faunas are generally associated with steep hillsides, although this may be due to an association between headwater streams and steep hillsides, rather than a direct effect of topography on heptageniid distributions. Differences between Shield and southern boreal faunas, and between Saskatchewan River and Saskatchewan River-like faunas may be due to

differences in temperature and topography, although there are coincident differences in streamside vegetation.

Faunal differences among Saskatchewan River sites appear to be due primarily to the effects of dams and impoundments. Sections of the South Saskatchewan and Saskatchewan Rivers affected by dams are environmentally similar to boreal streams because of reduced water temperatures and increased water clarity and plant growth. However, the heptageniid fauna in these areas is a restricted subset of the South Saskatchewan River fauna upstream from Gardiner Dam, rather than a boreal fauna. This suggests that Gardiner Dam has not been in existence long enough to allow colonization by boreal heptageniids.

### 5.3 Other Explanations of Heptageniid Distribution Patterns

Observed heptageniid distribution patterns, unlike those of molluscs and fish, do not appear to be related to drainage basins or historical biogeographical factors. Thus, mayflies appear to be able to disperse between watersheds relatively easily, probably in the adult stage. The apparent lack of importance of historical factors may also be due to the central position of Saskatchewan in North America. Heptageniids from both southeastern and southwestern refugia have been able to colonize Saskatchewan. This is not true of other areas of North America where historical factors associated with Wisconsin glaciation may still affect distribution patterns.

#### 5.4 Quality of Environmental Data

The environmental data collected in this study are less reliable than the biological data. Because of time and resource limitations, some measurements of environmental parameters were necessarily crude. The sampling interval was probably too long for assessing some environmental parameters such as water temperature, which may vary substantially over a two or three week period. However, reducing the sampling interval to a duration suitable for measuring water temperature would have greatly reduced the number of sites that could have been sampled, without substantially increasing the quality of the biological data. Other environmental parameters such as diatom growth and organic matter quality should have been assessed quantitatively instead of subjectively. Diurnal variation in water temperature should have been measured at more sites. Hybrid ordinations and bivariate correlation analyses both indicate that variation in water temperature might be important in regulating heptageniid distribution patterns; however, reliable conclusions cannot be drawn from the small number of measurements taken.

Chemical parameters were not measured, but water chemistry is probably not important in regulating stream insect distributions except in cases of severe pollution (Hynes 1970, Lehmkuhl 1979a). Two recent multivariate studies (Culp and Davies 1982, Wright et al. 1984) have found associations between stream insect distribution patterns and some chemical parameters (phosphorus, nitrogen and

alkalinity). However, in both of these studies, associations between distribution patterns and chemical parameters appeared to be related to eutrophication, due either to artificial nutrient enrichment or to differences in watershed vegetation. Thus, these chemical parameters probably affect stream insect distributions through their effects on algal growth and organic matter type rather than directly. Any such chemical differences that might affect heptageniid distributions in Saskatchewan should be detected by directly monitoring algal growth.

#### 5.5 Evaluation of the Use of Multivariate Techniques in Describing and Explaining Heptageniid Distribution Patterns

Multivariate statistical techniques are very useful in locating and quantitatively describing the distribution patterns of heptageniid mayflies. Distribution patterns indicated by multivariate analysis are very similar to those determined subjectively for heptageniids and other stream insects, but are more detailed. Additional patterns that could not be located subjectively (in this study or others), are present in the results of multivariate analyses. Furthermore, the quantitative description of distribution patterns by multivariate methods greatly facilitates the environmental interpretation of distribution patterns.

Other studies of stream invertebrate macrodistribution patterns (Bruns et al. 1982, Culp and Davies 1982, Bronmark et al. 1984, Wright et al. 1984) have also used multivariate

techniques successfully. Multivariate analysis of microdistribution patterns (Sheldon and Haick 1981) has been less successful.

Classification is most useful in the recognition and definition of faunal zones. Faunal zones can also be recognized in two-dimensional ordination plots but are neither as obvious nor as well defined as in classifications. Ordinations are more useful for describing relationships among faunal zones and relating faunal zones to individual species distributions. Ordinations are also superior to classifications in dealing with low diversity sites and in robustness (i.e. ordinations vary less among data sets than do classifications).

The superiority of ordinations over classifications in this study may be partly due to the ordination technique used, DCA. DCA is superior to other ordination techniques because: 1) it corrects for non-linearly related, spurious higher level axes (the arch problem) and compression of species and sample scores near the ends of ordination axes; 2) it is based on Gaussian species distribution curves; and 3) it is able to deal effectively with large data sets that contain many zero values. The success of ordinations in describing distribution patterns may also be due to ease with which the multidimensional nature of ordinations can be displayed and interpreted.

Only Wright et al. (1984) have previously used DCA to analyze macroinvertebrate distribution patterns. Culp and Davies (1982) used reciprocal averaging which is identical to

DCA except that it does not correct the arch and end compression problems.

Superior classifications might be produced by two-way indicator species analysis (TWINSpan). TWINSpan is theoretically superior to most other classification techniques because it is divisive (Gauch 1982). Divisive classification techniques begin with the entire population of objects to be classified, and divide the population into progressively smaller classes. Divisive techniques are more likely to produce globally optimum classifications than agglomerative ones (such as Ward's method, which was used in this study). However, TWINSpan cannot be used to locate homogenous, distinct clusters, which is the primary purpose of classification in this study.

Multivariate analyses of heptageniid distribution patterns using qualitative (species presence/absence) data are almost as good as those using quantitative data. All important distribution patterns can be elucidated using qualitative data. However, some sites are apparently misclassified (in both classifications and ordinations), and distances between some clusters are exaggerated. Both of these problems are due to the weight given rare species in qualitative data analysis. Objective removal or downweighting of rare species might improve multivariate analyses of qualitative data. Given the greater cost of collecting quantitative data, qualitative data are probably adequate for most multivariate biogeographical studies.

Weighted averages hybrid ordination is useful for

describing associations between observed heptageniid distribution patterns and environmental parameters and thus for suggesting possible environmental explanations of observed distribution patterns. Canonical correlation analysis would probably provide better environmental explanations. Canonical analysis also provides estimates of how well distribution patterns can be explained environmentally. However, suitable programs for canonical analysis were not available at the time of this study. Hybrid ordination has not been used previously in studies of stream insect distribution patterns; canonical analysis has never been correctly used in studies of stream organisms.

#### 5.6 Directions for Future Study

This study investigates the macrodistribution patterns of heptageniid mayflies in Saskatchewan. Similar studies should be conducted on other stream organisms and whole stream communities, and over broader geographical areas, to assess the generality of observed distribution patterns. For some groups of aquatic insects, such as mayflies, stoneflies and caddisflies, existing collection records may be adequate for multivariate analyses (using qualitative data) of distribution patterns in Saskatchewan, and perhaps in much of North America. However, for many other organisms, neither collection records nor basic taxonomic information is adequate for a rigorous analysis of distribution patterns. It is not presently possible to study the distribution patterns of entire stream communities in North America, as has



recently been done in Britain by Wright et al. (1984).

A potential environmental explanation of observed heptageniid distribution patterns has been suggested based on associations between distribution patterns and measured environmental parameters. The type of stream organic matter appears to be the most important factor in regulating heptageniid distribution patterns. However, several climatic and physical factors vary coincidentally with organic matter type. The importance of these different environmental factors should be tested in experimental studies, using either artificial laboratory streams or environmental manipulation of natural streams. Laboratory studies of the food preferences of heptageniid larvae would be especially useful in assessing the the importance of organic matter type in regulating distribution patterns. The Pasquia Hills would be a good location for environmental manipulation experiments, because of the diversity of stream habitats present, the small size (and hence manageability) of many of the streams present, and the lack of other human interference in the area.

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## Appendix 1. Weighted averages hybrid ordination programs.

## Program 1:

```

GET FILE          ENVIRON
DO REPEAT         VAR1=ENVPAR1 TO ENVPAR33/
                  VAR2=X1 TO X33
COMPUTE           VAR2=VAR1*AXIS1
END REPEAT
ASSIGN MISSING X1 to X33(999)
COMPUTE           DUMMY=1
RAW OUTPUT UNITWTAVE.DAT
AGGREGATE          GROUPVARS=DUMMY/VARIABLES=ENVPAR1 TO ENVPAR33,
                  X1 TO X33/AGGSTATS=SUM/RMISS=999
FINISH

```

## Program 2:

```

FILE NAME         WTAVE.SPS
VARIABLE LIST     V1,V2,ENVPAR1 TO ENVPAR33,X1 TO X33
N OF CASES        1
INPUT MEDIUM     WTAVE.DAT
INPUT FORMAT      BINARY
MISSING VALUES   ENVPAR1 TO X33(999)
DO REPEAT         VAR1=ENVPAR1 TO ENVPAR33/
                  VAR2=X1 TO X33
COMPUTE           VAR2=VAR2/VAR1
END REPEAT
RAW OUTPUT UNITWTAVE.OUT
WRITE CASES       (F8.2,/)X1 TO X33
FINISH

```

Two separate programs, here designated Program 1 and Program 2 are required. The two programs are run sequentially. ENVIRON is a pre-existing SPSS data file containing standardized values for 33 environmental parameters as variables ENVPAR1 to ENVPAR33, and site ordination scores (from a previous DCA ordination of species x sites data) as variable AXIS1. The vector of hybrid ordination environmental parameter scores is output in a system file called WTAVE.OUT. With the format specified, scores are output on separate lines in the order that the

environmental parameters were originally specified in ENVIRON. Vectors for a higher level axis may be generated by changing the ordination scores variable (AXIS1) in line 5 of Program 1 to a variable specifying the site scores for that level, and running the programs again.

Appendix 2. Description of Acanthomola pubescens,  
n. gen., n. sp.

During the past several years, larvae of an undescribed heptageniid species (Figure 97) have been collected from the South Saskatchewan River in Saskatchewan and from the Athabasca River in Alberta. These larvae superficially resemble those of Epeorus and the oriental genus Bleptus in general body shape, and in the absence of a median caudal filament. However, they differ from Epeorus in the very small gill lamellae on the first abdominal segment and from both Epeorus and Bleptus in the single basal denticle on the tarsal claw, the ventral insertions of the first two abdominal gills, and numerous details of the mouthparts. The mandibles and maxillae are especially distinctive and are unlike those of any described heptageniid. The molar area of the mandible is less than half as long as in heptageniine mayflies, and the armature of the molar area is reduced to a few stout spines. The crown of the maxillary galea-lacinia is rounded and bare. The maxillary palpus is long, very slender, and bare. Because of the peculiar mouthparts, and the unique combination of other characters, I propose a new genus, Acanthomola for these larvae.

Adults of Acanthomola are unknown.



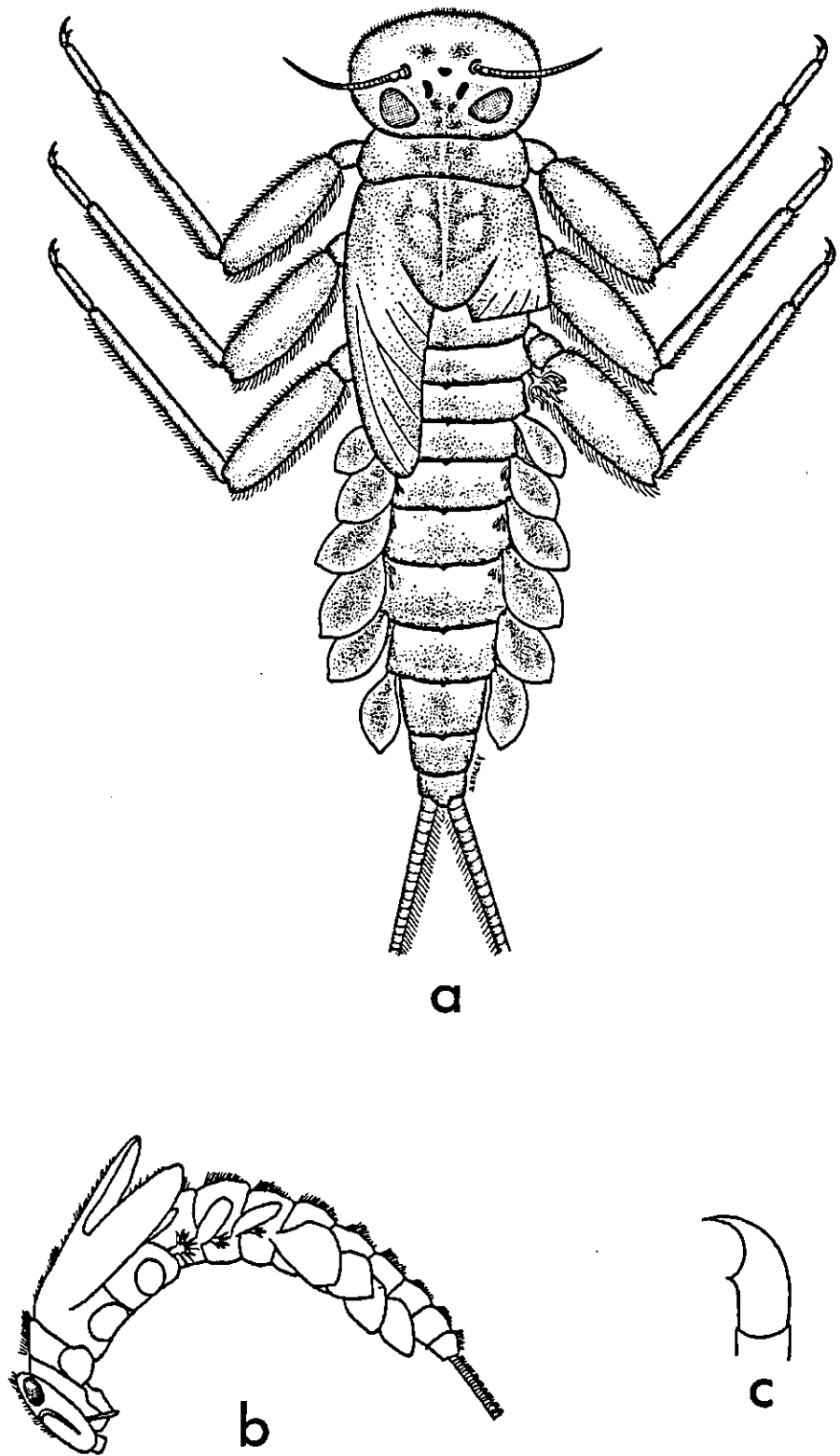


Figure 97. Acanthomola pubescens larva. a) dorsal view with wing pads on right side removed to expose abdominal gills, b) lateral view showing dorsal hair setae, c) tarsal claw.

Acanthomola, n. gen.

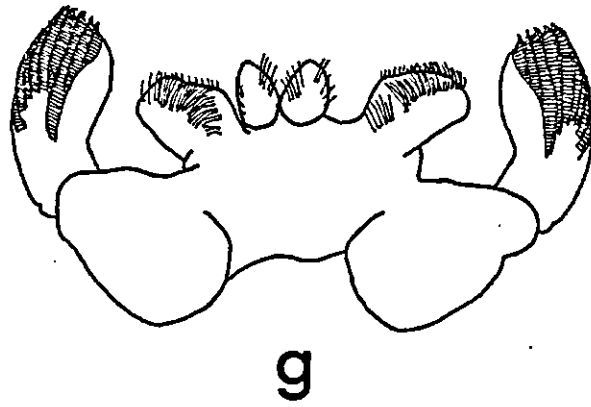
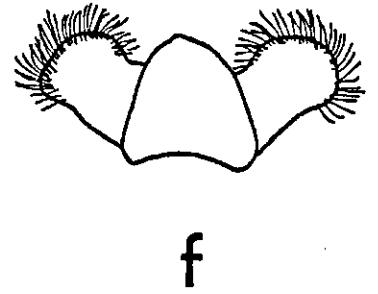
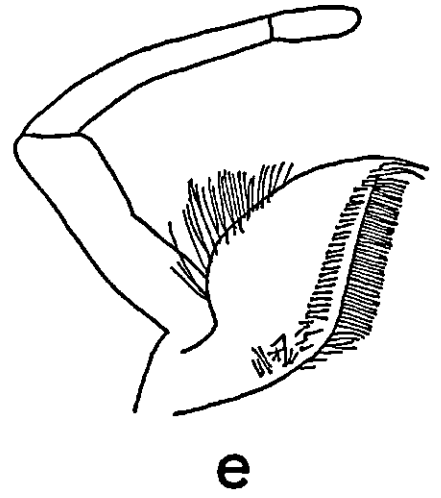
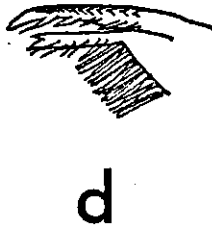
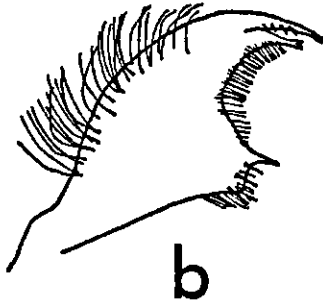
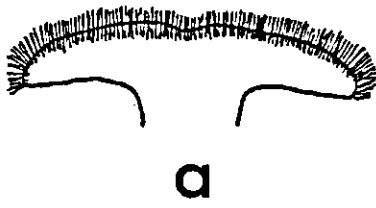
## Diagnosis

Acanthomola can be distinguished from all other heptageniids by its peculiar mandibles and maxillae (Figure 98). The molar area of the mandible is only 0.3-0.5 times as large as in other Heptageniinae, but is much larger than in predaceous genera (Raptoheptagenia, Pseudiron and Spinadis). The armature of the molar area is reduced to a few stout spines, again unlike any other Heptageniinae. The crown of the maxillary galea-lacinia is rounded and bare. In all other heptageniids, except Epeorus, Raptoheptagenia, Pseudiron and Spinadis, the crown of the galea-lacinia is angular and bears setae and/or spines in the apical half. The maxillary palpus is completely bare, unlike any other heptageniid except Pseudiron.

Acanthomola larvae superficially resemble Bleptus larvae in the general body shape, shapes of the abdominal gills and absence of a median caudal filament. Acanthomola larvae differ from Bleptus larvae in the following characters: apex of the galea-lacinia with 2 or 3 stout spines, instead of bare; labrum laterally expanded and 0.5-0.7, instead of 0.2, times as wide as the head capsule; tarsal claw with a single basal denticle, instead of 2-3 subapical denticles; posterior margin of the femur and tibia with a dense fringe of hairs, instead of a row of small spines; gills on abdominal segments 1 and 2 inserted ventrally, instead of laterally; gill 7 with a filamentous tuft; and caudal filaments with dense mesal fringes of setae, instead of sparse intersegmental setae.

98. Mouthparts of Acanthomola pubescens larva.

- a) labrum (x 40) b) right mandible (x 75),  
c) and d) details of incisor and molar area of left  
mandible (x 150), e) right maxilla (x 75),  
f) hypopharynx (x 40), g) labium (x 40).



Acanthomola larvae resemble Epeorus larvae in the general body shape and absence of a median caudal filament, but differ from Epeorus larvae in the small lamellae and ventral, instead of lateral, insertions of abdominal gills 1 and 2; absence of a dense fringe of setae on the anterior margin of the head capsule; lateral expansion of the labrum; and single basal denticle, instead of 2-5 subapical denticles, on the tarsal claw.

Acanthomola larvae resemble Raptoheptagenia larvae in general body shape, dorsal covering of setae, and shapes and insertions of the first abdominal gills, but differ from Raptoheptagenia larvae in the large lamellae on gills 2-7; lateral, instead of ventral, insertions of gills 3-7; and absence of a median caudal filament.

Acanthomola larvae key to couplet 21 (Anepeorus (= Raptoheptagenia) or Spinadis) in Edmunds, Jensen and Berner's (1976) key to North American mayflies, but cannot be keyed further because of conflicting characters. The gills of Acanthomola vary in shape and position, as in Spinadis, but dorsal abdominal spines are absent, as in Raptoheptagenia. If the ventral insertions of abdominal gills 1 and 2 are ignored, Acanthomola keys to Epeorus in Edmunds, Jensen and Berner's key.

#### Description

Mature larva (Figure 97). Lengths: Body 9 mm; caudal filaments (broken) approximately 8-8.5 mm.

Head capsule: 1.3-1.6 times as wide as long,

approximately trapezoidal in shape and widest just anterior to antennal bases; anterior and lateral margins convex, posterior margin straight to slightly concave; anterior margin with a fringe of very short, fine setae. Compound eyes not extending to postero-lateral margins of head capsule in either sex. Dorsal surface of head capsule between compound eyes from just anterior to antennal bases to posterior margin with dense, fine setae; rest of dorsal surface of head capsule with very short, fine setae. Labrum (Figure 98a) 0.5-0.7 times as wide as head capsule, with a dense fringe of setae along its anterior margin. Left and right mandibles (Figure 98b) similar; incisors (Figure 98c) well-developed; outer incisor blunt apically, with 4 or 5 long spines on its inner surface, and a row of short denticles on its outer surface; inner incisor bifid or trifid with a row of stout setae; molar area (Figure 98d) reduced to a small raised area with a sharp apical and a blunt basal spine, several spine-like setae between these spines, and a number of longer, hair-like setae in the region of the basal spine; a row of long setae extends from the base of the inner incisor to the base of the molar area; outer surface of mandible with a fringe of long hair-like setae. Galea-lacinia of maxilla (Figure 98e) with 2 or 3 elongate apicomesal spines, a dense row of long inner setae, a row of shorter lateral setae, and a fringe of long hair-like setae on the outer margin; crown of galea-lacinia bare; maxillary palpus long and slender, 2-segmented, 2nd segment 1.5-2 times as long as basal segment, with a distinct subapical constriction separating an

apparently moveable but unarticulated apical subsegment; palpus bare. Hypopharynx (Figure 98f) with ligula conical and superligula slightly expanded. Labium (Figure 98g) with glossae twice as long as wide; paraglossae broader, only slightly longer than wide; labial palpi large, basal segment quadrate, apical segment twice as long as wide and twice as long as paraglossae, apex of apical segment with several dense rows of apically curved setae; glossae with sparse setae, paraglossae with 2 dense apical fringes of stout setae.

Thorax: Pronotum widest at or near middle; posterior margin broadly and shallowly emarginate. Pro-, meso-, and metanotum covered with dense, fine setae; setae longest mid-dorsally, becoming shorter laterally and absent on lateral margins; wing pads covered with shorter, fine setae. Legs of typical heptageniid shape; femur quite broad, approximately 0.3 times as wide as long, with a short, blunt, apical, thumb-like projection; tibia 1.3 times as long as femora, tarsus 0.3 times as long as femur; tarsal claw (Figure 97c) with a slender, basal denticle; posterior margins of coxa, femur and tibia, and anterior margin of femur all with dense fringes of long setae; anterior margins of femur, tibia and tarsus each with a row of small peg-like setae.

Abdomen: Posterior margins of tergites 1-9 with a small median tubercle; lateral margins of tergites 1-7 expanded laterally, especially in the posterior 1/2; a short, sharp posterolateral spine present on tergites 3-7; abdominal

tergites densely covered with fine setae; setae longest mid-dorsally, becoming shorter laterally and absent on lateral margins. Gill (Figure 99) on segment 1 inserted ventro-laterally, lamella greatly reduced and shorter than fibrilliiform tuft; gill on segment 2 inserted ventrally, lamella larger and broader, longer than fibrilliiform tuft; gill on segment 3 inserted ventrolaterally, lamella larger than but similarly shaped as on segment 2; gills on segments 4-6 inserted laterally, lamellae broader than on segment 3; gill on segment 7 inserted laterally, lamella somewhat narrower than on segments 4-6; fibrilliiform tufts becoming progressively smaller anteriorly to posteriorly, from 0.6-0.8 times as long as lamella on segment 2, to 0.3 times or less as long as lamella on segment 7; no visible tracheae on gill lamellae except a faint branch near the anterior margin. Two caudal filaments, each with setae along the inner margin and outer margin bare; terminal filament absent.

Etymology: Acantho, Gr., spiny; mola, L., a mill; referring to the spiny molar area of the mandible.

Type-species: Acanthomola pubescens, n. sp.

Acanthomola pubescens, n. sp.

Mature larva. Lengths: body 9 mm; caudal filaments (broken) approximately 8-8.5 mm. General color dirty white to very pale greyish brown with darker brown markings.

Head capsule: Mostly pale, with a brown median area between the compound eyes extending from the lateral ocelli to the posterior margin, and a diffuse brown spot anterior to



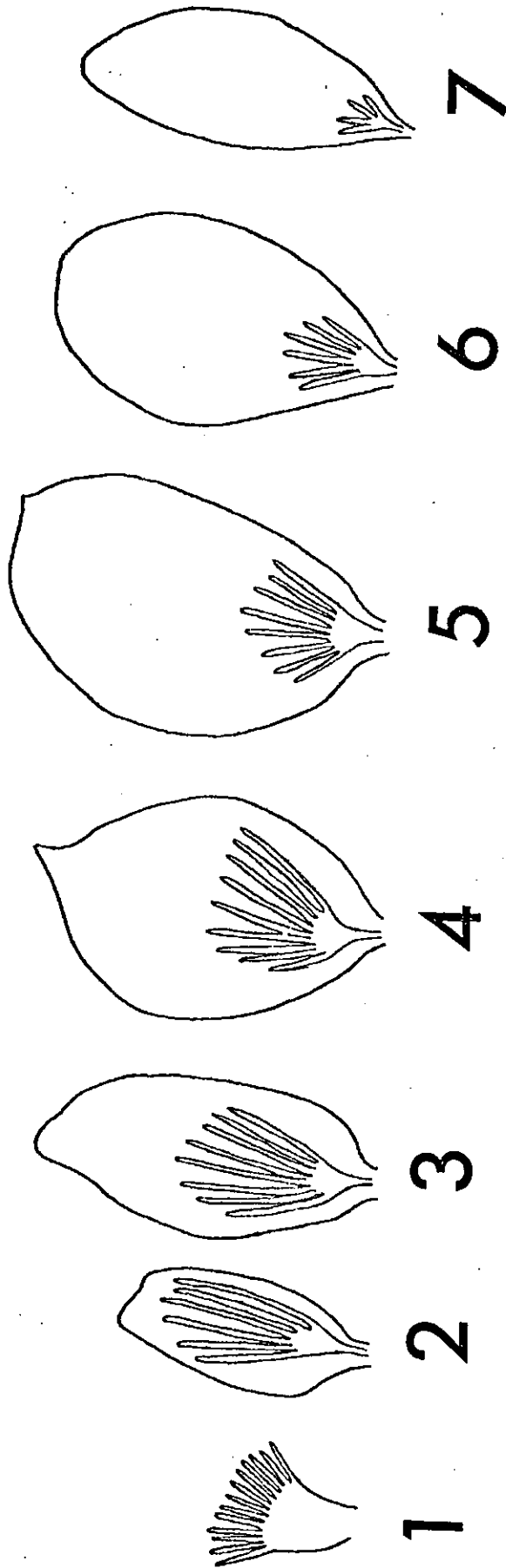


Figure 99. a) to g) gills on abdominal segments 1 to 7 of Acanthomola pubescens larva.

each antennal base. Antenna entirely pale. Mouthparts pale except for setae on the maxilla, labium and labial palp, which are golden brown.

Thorax: Pronotum mostly pale with a wide brown median stripe, a narrow brown submedian streak, and a brown posterior margin. Mesonotum pale with a brown median stripe, a brown lateral spot anterior to each wing pad base, and a brown area in the posterior  $1/3-1/2$  between the wing pad bases; mesothoracic wing pads mostly pale with brown veins and brown mesal and lateral margins. Metanotum pale with a brown posteromesal spot. Venter of thorax entirely pale. Legs pale; femur tinged with brown in posterior  $1/4-1/2$ , posterior edge dark brown; tibia and tarsus entirely pale; tarsal claw tipped with dark brown; setae on posterior margin of femur golden brown; other setae pale to faintly tinged with brown.

Abdomen: Tergites 1-9 brown mesally with a pale submedian mark, fading to pale brown laterally; tergites 1-4 with pale marks approximately round, restricted to the anterior  $1/2$  of the tergite, and extending to or nearly to the anterior margin; tergites 5-9 with pale marks narrower, elongate and centered on or near the middle of each tergite; submedian streaks on tergites 8 and 9 sometimes faint; tergite 10 mostly pale with a brown median stripe and a brown posterior margin. Venter of abdomen entirely pale. Gill lamellae and fibrilliform tufts translucent and colorless to white or very pale brown. Caudal filaments pale brown with darker brown joinings basally, fading to uniformly white or pale smokey apically.

Holotype: Nearly mature male larva, in alcohol.

Saskatchewan: South Saskatchewan River at Lemsford Ferry (south of Kindersley). 12 July 1970, D.M. Lehmkuhl.

Paratypes: Three immature larvae in alcohol and 1 immature larva on slide, same collection data as holotype; 1 nearly mature larva, body in alcohol, head and mouthparts on slide, Alberta: Athabasca River 200 km downstream from Athabasca, 22 June 1981, Alberta Environment; 1 immature larva in alcohol, same locality, 18 June 1981, Alberta Environment; 2 immature larvae in alcohol, Alberta: Athabasca River 120 km downstream from Athabasca, 18 June 1981, Alberta Environment; 3 immature larvae in alcohol and 1 immature larva on slide, same locality, 22 June 1981, Alberta Environment. I also have approximately 50 earlier instar larvae.

Etymology: Latin, named for the dense hair setae on the dorsum of the body and on the legs.

#### Systematic Remarks

I can find no differences between the South Saskatchewan River and Athabasca River specimens. The 2 (or 3) populations apparently belong to the same species.

Acanthomola appears to be a very primitive heptageniid. The larvae possess several character states that, according to Jensen (1972), are plesiomorphic for the family Heptageniidae including: the shape of the head capsule; anterior margin of the head capsule with sparse setae only; incisors slender and subequal; galea-lacinia with a submedian

row of setae, but without apical pectinate spines; glossae rounded; hypopharynx with a conical ligula and only slightly expanded superligula; abdominal gills with thickened lamellae and well-developed fibrilliform tufts; and caudal filaments setaceous. The very small gill lamellae on abdominal segment 1, shared by Acanthomola, Cinygma and Bleptus, may also be plesiomorphic.

Acanthomola appears to belong to Jensen's (1972) Phyletic Line 1 which includes Epeorus, Ironodes and Bleptus and is a sister group to the rest of the Heptageniinae. Acanthomola possesses two character states that are plesiomorphic for Phyletic Line 1 but apomorphic for the family Heptageniidae: a reduced number of setae on the crown of the galea-lacinia and the absence of a median caudal filament. Faint to indistinct tracheae on the abdominal gills, present in Acanthomola, Epeorus, Ironodes and Bleptus, may also be plesiomorphic for this lineage.

Acanthomola does not appear to be closely related to Epeorus, Ironodes or Bleptus. It is most similar to Bleptus, but this similarity appears to be due to symplesiomorphy.

Acanthomola shares several apomorphic characters with the three predaceous heptageniid genera, including: abdominal gills 1 and 2 inserted ventrally (in Acanthomola, Raptoheptagenia and Spinadis); lamellae on gills 2-5 with pointed apices; tarsal claw with a single basal denticle; maxillary palpus with a long, slender apical segment, but lacking setae or possessing only sparse setae; apex of the galea-lacinia without hair setae; molar area of the

mandible reduced in size, and bearing only a few spines. Acanthomola is also similar to Spinadis in the shapes of the abdominal gills and presence of dorsal abdominal tubercles.

The size of the molar area and rounded crown of the galea-lacinia of Acanthomola appear to be intermediate between typical heptageniine mouthparts and those of the predaceous genera. This suggests that Acanthomola may be a descendant of a lineage that gave rise to one or more of the predaceous genera. Similarities in several other characters, including the shapes and insertions of the abdominal gills and presence of dorsal abdominal tubercles, also suggest an evolutionary relationship between Acanthomola and Spinadis.

Possible phylogenetic relationships of Acanthomola to other heptageniids are shown in Figure 100. The association of Raptoheptagenia with other Heptageniinae is based on similarities in internal anatomy (Jensen 1972).

Similarities among Acanthomola and the predaceous genera might be due to convergence to predaceous habits. Although Acanthomola does not appear to be predaceous, the shapes of its mandibles and maxillae suggest that one of its recent ancestors was. Further comparisons of Acanthomola with Raptoheptagenia, Pseudiron and Spinadis are required to establish evolutionary relationships among these genera. Examination of adult Acanthomola would also be useful. However it appears unlikely that adult Acanthomola will be obtained in the near future.

Because of its many primitive character states, its resemblance to genera in Jensen's Phyletic Line 1, and the

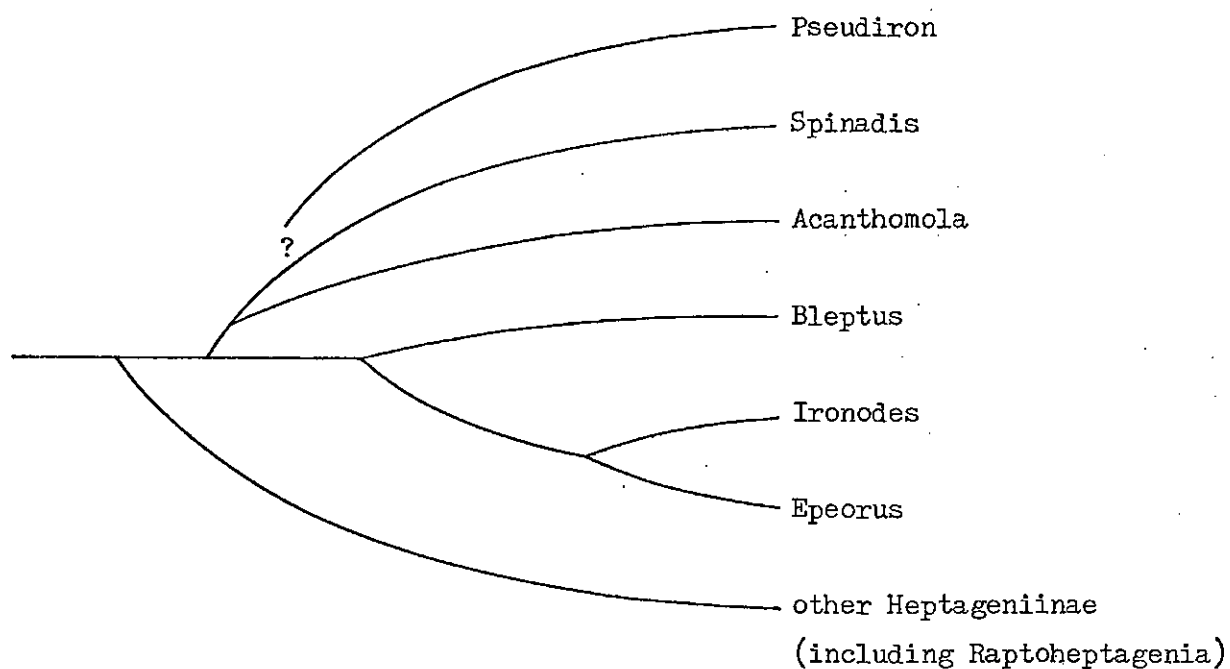


Figure 100. Possible phylogenetic relationships of Acanthomola to other Heptageniidae.

speculative nature of its relationship to predaceous genera, I tentatively assign Acanthomola to the subfamily Heptageniinae.

I have not seen specimens of Bleptus or Spinadis. Descriptions of these genera are from Jensen (1972) (Bleptus), and Edmunds and Jensen (1974) and Flowers and Hilsenhoff (1975) (Spinadis).

### Biology

The biology of Acanthomola is poorly known. All specimens have been collected from large rivers, and the Saskatchewan specimens were collected from an area of fast current and high silt load. Detailed collection data are not available for the Athabasca River specimens. Acanthomola is very rare in the South Saskatchewan River. It has been collected at only one site and on only two occasions in spite of intensive collecting in the area for 15 years. Acanthomola may be slightly more common in the Athabasca River.

The guts of two dissected larvae (including one nearly mature specimen) contained only detritus and a few diatom cells. No recognizable animal fragments were present. However, the mandibles appear to be modified for predation. The apparent detritivory of Acanthomola larvae is thus puzzling and merits further study.

Acanthomola appears to have a summer life cycle. The occurrence of only early instar larvae in collections from mid to late May suggests that most of the year is passed in the egg stage, and that eggs hatch in late spring. Adult emergence probably occurs in late June and early July.

Appendix 3. Raptoheptagenia cruentata, n. gen., new  
association of the larva previously associated  
with Anepeorus and the adult of Heptagenia  
cruentata Walsh

Burks (1953) tentatively associated a rare larva from Illinois with adults of Anepeorus apparently because of similarities in distribution. This association has been widely accepted; Edmunds, Jensen and Berner (1976) state that it is almost certain, although the larvae have never been reared. These supposed "Anepeorus" larvae have been collected in Illinois (Burks 1953; 3 specimens), Indiana (Mancini, Gammon and Carlson 1976; 4 specimens), Ohio (Beckett 1977; 4 specimens), and Saskatchewan. They are extremely rare except in Saskatchewan.

I have recently reared larvae of the type Burks associated with Anepeorus (collected from the South Saskatchewan River at Lemsford Ferry, 40 km south of Kindersley, Saskatchewan, on June 17, 1983 and July 01, 1984) and obtained one adult male and four females. I also have three males and five females which are probably but not positively associated with the larvae. Reared adult males key to Heptagenia cruentata Walsh in Traver (1935) and fit the descriptions of H. cruentata in Traver (1935) and Burks (1953). They are indistinguishable from the types of H. reversalis McDunnough 1924 (= H. cruentata; McDunnough 1929). I therefore conclude that the larvae previously associated with Anepeorus are the immature stage of H. cruentata which



was previously unknown. H. cruentata adults have been previously collected in Illinois (Walsh 1863, Burks 1953), Nebraska (Traver 1935), Tennessee (Berner 1977) and Manitoba (McDunnough 1929).

Because the larvae are very different from those of other Heptagenia species, I propose a new genus, Raptoheptagenia, for this species.

Raptoheptagenia, n. gen.

Description and Diagnosis: Adult males of Raptoheptagenia are very similar to those of Heptagenia and key to Heptagenia in all recent keys. Adult males of Raptoheptagenia differ from those of Heptagenia in the anastomosis of the crossveins in the stigmatic area of the forewing, and in the length of the foretarsus relative to that of the tibia. Two or more stigmatic crossveins are anastomosed in Raptoheptagenia; stigmatic crossveins are usually not anastomosed in Heptagenia. In Raptoheptagenia, the foretarsus and tibia are subequal in length; in Heptagenia, the foretarsus is 1.25 times as long as the tibia. Species-level descriptions of R. cruentata adults, which may be useful in distinguishing R. cruentata from Heptagenia species, are given in Walsh (1863), Traver (1935), and Burks (1953).

Nymphs of Raptoheptagenia (as Anepeorus) have been described by Burks (1953), Jensen (1972), and Edmunds, Jensen and Berner (1976). Figures of the mouthparts are given in Jensen (1972). The larvae can be distinguished from those of

all other heptageniid genera by the predaceous mouthparts (especially the long, slender incisors and reduced molar area of the mandibles), the slender lamellae and ventral insertions of the abdominal gills, and the dense setation on the dorsum of the abdomen (Edmunds, Jensen and Berner 1976).

Nymphal Habits: Nymphal habits are described by Edmunds, Jensen and Berner (1976). Nymphs are active carnivores and inhabit deep water with fast currents and gravel or rubble substrates.

Type Species: Raptoheptagenia cruentata (Walsh) 1863

Etymology: Raptoheptagenia, rapto - to seize or plunder (Latin), referring to the predaceous habits of the larva; and heptagenia - indicating the resemblance of the adults to those of Heptagenia.

Distribution: Illinois, Indiana, Nebraska, Ohio, Tennessee, Manitoba and Saskatchewan. In Saskatchewan, R. cruentata has been collected from several locations on the North and South Saskatchewan Rivers and from the Battle River, a tributary of the North Saskatchewan River.

#### Discussion:

Jensen (1972) derives the genus Anepeorus from the lineage which gave rise to Heptagenia, Stenonema, Stenacron, and several Palearctic genera, based on similarities in the internal anatomy of the larvae (particularly the ventral nerve cord and Malpighian tubules). The association of these larvae with a Heptagenia-like adult supports Jensen's phylogenetic conclusions. Relative to other genera in this

lineage, Raptoheptagenia larvae are very derived but the adults are quite primitive. Because Heptagenia is considered to be the most primitive genus in this lineage (Jensen 1972), it is not possible to say whether Raptoheptagenia is more closely related to Heptagenia than to other genera in the lineage or whether it is simply an early derivative of the lineage.

Because Raptoheptagenia apparently belongs to a relatively derived lineage of heptageniids (within the Heptageniinae) and because of the great similarity between Raptoheptagenia and Heptagenia adults, I believe that Raptoheptagenia should be placed within the subfamily Heptageniinae. Although the larvae are very derived and were previously placed in a separate subfamily, the adults are clearly heptageniine.

The true larva of Anepeorus remains unknown. Larvae of Acanthomola pubescens Whiting and Lehmkuhl 1985, for which adults are unknown, may be the immature stage of Anepeorus rusticus. The two species are both known from the South Saskatchewan River in Saskatchewan and are both extremely rare. However, it is premature to make such an association without rearing. Unfortunately, because of the extreme rarity of A. pubescens larvae and environmental threats to its habitat, it is doubtful they will ever be reared.

Appendix 4. Mean annual abundances of heptageniids in sweep net samples at each intensive study site (ln (number per square meter of stream substrate)). Species names given are abbreviations incorporating the first letter of the genus name (upper case) and the first three or four letters of the species name (lower case).

Site No.	Species								
	Hade	Hdiab	Hele	Hflav	Hpul	Lhebe	Mnip	Ninc	Nluc
1	3.95	0.13	2.32	0	2.34	0	0	0	0
2	1.28	0	1.10	0	0	0	0	0	0
3	3.66	0	3.86	0	1.09	0	0.45	0	0
4	4.16	0	3.65	2.42	1.34	0	0.64	0	0
5	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0
7	0	0	0.33	0	0	0	0	0	0
8	0	0	2.41	0	0.22	0	0	0	0
9	0	0	2.10	0	1.05	0	0	0	0
10	0	0	0.85	0	2.53	0	0	0	0
11	0	0	0.92	0	0.89	0	0	0	0
12	0	0	3.67	1.10	1.60	0	0.93	0	0
13	0	0	2.36	0	1.08	0	0	0	0
14	0	0	1.73	0.23	2.24	0	0	0	0
15	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0
17	0	0	0	0	1.61	2.28	0	0	1.05
18	0	0	0	0	2.90	0.57	0	0	0.54
19	0	0	0	0	2.58	1.43	0	0	0
20	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0.39	0	0	0	0
22	0	0	0	0	2.08	1.60	0	0	0
23	0	0	0	0	0.37	0	0	0	0
24	0	0	0	0	1.63	0.30	0	0	1.02
25	0	0.67	0	0	0	1.66	0	0.37	0
26	0	0	0	0	0	0	0	0	0
27	0	0	0.49	0	2.52	0	0	0	0
28	0	0	0	0	1.81	0	0	0	0
29	0	0	0	0	0.24	0	0	0	0
30	0	0	0	0	3.50	0	0	0	0
31	0	0	0	0	4.00	0.10	0	0	0
32	0	0	0	0	0.82	2.65	0	0.16	0.53
33	0	0	0	0	0.33	1.25	0	0.86	0
34	-	-	-	-	-	-	-	-	-
35	0	0	0	0	0	0.66	0	0	0

## Appendix 4. Continued.

<u>Site No.</u>	<u>Species</u>								
	<u>Nrust</u>	<u>Nsimp</u>	<u>Rcru</u>	<u>Rund</u>	<u>Sint</u>	<u>Sfem</u>	<u>Sterm</u>	<u>Svic</u>	<u>Pcent</u>
1	0	0.64	0.29	0.07	0	0	4.68	0	0
2	0	0	0.81	0	0	0	1.61	0	0
3	0	0	0.62	0	0	0	3.21	0	0
4	0	0	1.02	0.45	0	0	3.91	0	0.45
5	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0.28	0	0.92
8	0	0	0	0	0	0	2.75	0	2.35
9	0	0	0	0	0	0	2.71	0	0
10	0	0	0	0	0.56	0	3.10	0	0
11	0	0	0	0	1.15	0	0.43	0	0
12	0	0	0.60	0	0.25	0	3.01	0	0
13	0	0	0	0	1.77	0	1.49	0	0
14	0	0	0	0	1.76	0	1.46	0	0
15	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0.23	0	0
17	0	0	0	0	3.93	0	0.16	2.74	0
18	0	0	0	0	0	0	0	2.96	0
19	0	0	0	0	0	0	0	3.13	0
20	0	0	0	0	1.22	0	0	0	0
21	0	0	0	0	0	0	0	2.03	0
22	0	0	0	0	0	0	0.69	1.14	0
23	2.39	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	2.10	0
25	0	0	0	0	2.41	0	4.02	0	0
26	0	0	0	0	1.08	0	1.08	0	0
27	0	1.71	0	0	0	0	0	0	0
28	0.45	1.24	0	0	0	0	0	0	0
29	0	1.02	0	0	0	0	0	0	0
30	1.94	2.15	0	0	0	0	0	0	0
31	1.15	2.34	0	0	0	0	0	0.71	0
32	0	0.16	0	0	1.99	0	0	4.56	0
33	0	0	0	0	0.69	0	0	2.75	0
34	-	-	-	-	-	-	-	-	-
35	0	0	0	0	2.57	0	0	0.58	0

Appendix 5. Mean annual abundances of heptageniids in stone samples at each intensive study site (ln (number per square meter of stone)). Species names given are abbreviations incorporating the first letter of the genus name (upper case) and the first three or four letters of the species name (lower case).

Species									
<u>Site No.</u>	<u>Hade</u>	<u>Hdiab</u>	<u>Hele</u>	<u>Hflav</u>	<u>Hpul</u>	<u>Lhebe</u>	<u>Mnip</u>	<u>Ninc</u>	<u>Nluc</u>
1	3.48	0.19	2.67	0	1.70	0	0	0	0
2	3.73	0	3.61	0	0.28	0	0	0	0
3	2.67	0.20	3.40	0.99	1.10	0	0	0	0
4	2.75	0	3.18	0.56	0.30	0	0	0	0
5	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0
7	0	0	2.94	0	0	0	0	0	0
8	0	0	4.13	0	0	0	0	0	0
9	0	0.74	5.00	0	4.32	0	0	0	0
10	0	0	3.21	0	5.64	0	0	0	0
11	0	0.30	4.14	0	4.79	0	0	0	0
12	0.30	0	4.01	0.55	3.11	0	0	0	0
13	0	0	3.67	0.47	3.12	0.23	0	0	0
14	0	0	3.12	0.83	4.31	0	0	0	0
15	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0
17	0	0	0	0	2.84	2.31	0	0	0.25
18	0	0	0	0	4.01	0.82	0	0	0
19	0	0	0	0	3.35	1.41	0	0	0
20	0	0	0	0	2.67	1.03	0	0	0
21	0	0	0	0	1.53	0	0	0	0
22	0	0	0	0	4.10	2.81	0	0	0
23	0	0	0	0	0.77	0.12	0	0	0
24	0	0	0	0	2.76	0.41	0	0	0.34
25	0	1.12	0	0	0.27	2.95	0	0	0
26	-	-	-	-	-	-	-	-	-
27	0	0.40	1.20	0	3.31	0	0	0	0
28	0	0	0	0	2.41	0	0	0	0
29	0	0	0	0	0.82	0	0	0	0
30	0	0	0	0	4.40	0	0	0	0
31	0	0	0	0	4.16	0	0	0	0
32	0	0	0	0	0.67	2.12	0	0	0
33	0	0	0	0	0.29	2.52	0	0	0.70
34	0	0	0	0	0	4.36	0	1.00	0.79
35	0	0	0	0	0.17	2.60	0	0	0

## Appendix 5. Continued.

<u>Site No.</u>	<u>Species</u>								
	<u>Nrust</u>	<u>Nsimp</u>	<u>Rcru</u>	<u>Rund</u>	<u>Sint</u>	<u>Sfem</u>	<u>Sterm</u>	<u>Svic</u>	<u>Pcent</u>
1	0	0	0.17	0	0	0	2.76	0	0
2	0	0	0	0	0	0	1.09	0	0
3	0	0	0	0	0	0	2.56	0	0
4	0	0	0	0	0	0	1.64	0	0
5	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0.60	0	0
7	0	0	0	0	0	0	3.09	0	0
8	0	0	0	0	0.23	0	3.45	0	0
9	0	0	0	0	0.29	0	5.09	0	0
10	0	0	0	0	3.29	0	5.41	0	0
11	0	0	0	0	5.14	0	3.92	0	0
12	0	0	0	0	0.49	0	3.25	0	0
13	0	0	0	0	3.98	0	2.15	0	0
14	0	0	0	0	3.67	0	2.72	0	0
15	0	0	0	0	0	0	0.35	0	0
16	0	0	0	0	0	0	1.21	0	0
17	0	0	0	0	3.70	0	0	2.55	0
18	0	0	0	0	0	0	0	3.36	0
19	0	0	0	0	0.31	0	0	2.35	0
20	0	0	0	0	4.63	0.59	0	3.38	0
21	0	0	0	0	0.15	0	0	4.93	0
22	0	0	0	0	0.49	0	2.10	3.66	0
23	1.69	0	0	0	0	0	0	0	0
24	0	0	0	0	0.13	0	0	3.04	0
25	0	0	0	0	5.66	0	4.50	0	0
26	-	-	-	-	-	-	-	-	-
27	0	1.17	0	0	0	0	0	0	0
28	0.77	0.90	0	0	0	0	0	0	0
29	0	0.27	0	0	0	0	0	0	0
30	1.68	1.40	0	0	0	0	0	0.14	0
31	0.31	0.88	0	0	0	0	0	0.27	0
32	0	0	0	0	2.92	0	0	3.14	0
33	0	0.24	0	0	2.76	0	0	3.15	0
34	0	0.79	0	0	1.12	0	0	2.95	0
35	0	0	0	0	4.57	0	0.22	3.20	0

Appendix 6. Mean annual abundances of heptageniids in log samples at each intensive study site (ln (number per square meter of log)). Species names given are abbreviations incorporating the first letter of the genus name (upper case) and the first three or four letters of the species name (lower case).

[illegible]



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[illegible]

Appendix 7. Mean abundances of heptageniids in sweep net samples at each sampling time (ln (number per square meter of stream substrate)). Sampling times are: 1-early June, 2-late June, 3-July, 4-August, 5-September, 6-October. Species names given are abbreviations incorporating the first letter of the genus name (upper case) and the first three or four letters of the species name (lower case).

<u>Time</u>	<u>Species</u>								
	<u>Hade</u>	<u>Hdiab</u>	<u>Hele</u>	<u>Hflav</u>	<u>Hpul</u>	<u>Lhebe</u>	<u>Mnip</u>	<u>Ninc</u>	<u>Nluc</u>
1	0.63	0.09	0.90	0.10	1.33	0.51	0.20	0.05	0.38
2	0	0	0.89	0.04	1.42	1.01	0.15	0.18	0.30
3	0.26	0.02	1.14	0.06	1.25	0.80	0	0.05	0
4	0.33	0	0.61	0.09	1.30	0.07	0	0	0
5	0.39	0	0.40	0.15	1.08	0.02	0	0	0
6	0.26	0	0.29	0.08	1.03	0.04	0	0	0

<u>Site No.</u>	<u>Species</u>								
	<u>Nrust</u>	<u>Nsimp</u>	<u>Rcru</u>	<u>Rund</u>	<u>Sint</u>	<u>Sfem</u>	<u>Sterm</u>	<u>Svic</u>	<u>Pcent</u>
1	0.24	0.70	0.31	0.05	0.40	0	1.52	0.61	0.16
2	0.53	0.81	0.12	0	0.41	0	0.42	0.61	0.10
3	0.36	0.31	0.02	0.01	0.44	0	0.51	0.35	0.01
4	0.10	0	0	0	0.77	0	0.53	0.97	0
5	0.05	0.04	0	0	0.59	0	1.27	0.95	0
6	0	0	0	0	0.86	0	1.09	1.08	0

Appendix 8. Mean abundances of heptageniids in stone samples at each sampling time (ln (number per square meter of stone)). Sampling times are: 1-early June, 2-late June, 3-July, 4-August, 5-September, 6-October. Species names given are abbreviations incorporating the first letter of the genus name (upper case) and the first three or four letters of the species name (lower case).

<u>Time</u>	<u>Species</u>								
	<u>Hade</u>	<u>Hdiab</u>	<u>Hele</u>	<u>Hflav</u>	<u>Hpul</u>	<u>Lhebe</u>	<u>Mnip</u>	<u>Ninc</u>	<u>Nluc</u>
1	0.20	0.11	1.35	0.05	2.18	1.18	0	0.10	0.22
2	0	0.30	1.06	0	2.77	1.92	0	0.05	0.14
3	0.38	0	1.58	0.05	1.86	1.41	0	0	0.05
4	0.35	0.16	1.49	0.07	2.39	0.33	0	0	0
5	0.53	0.04	1.17	0.19	2.24	0	0	0	0
6	0.32	0	0.84	0.11	1.58	0	0	0	0

<u>Site No.</u>	<u>Species</u>								
	<u>Nrust</u>	<u>Nsimp</u>	<u>Rcru</u>	<u>Rund</u>	<u>Sint</u>	<u>Sfem</u>	<u>Sterm</u>	<u>Svic</u>	<u>Pcent</u>
1	0.06	0.36	0.03	0	1.69	0	1.54	1.23	0
2	0.51	0.83	0	0	1.90	0	0.81	1.40	0
3	0.36	0.07	0	0	0.78	0	0.71	0.82	0
4	0.07	0	0	0	1.76	0.03	1.64	1.43	0
5	0	0	0	0	1.48	0.03	1.92	1.16	0
6	0	0	0	0	0.94	0.04	1.33	1.01	0

Appendix 9. Mean annual values of environmental parameters at each intensive study site. Abbreviated environmental parameter names are explained in Figure 75.

Site No.	Width (m)	Depth (cm)	Temp (°C)	Tmax (°C)	Tmin (°C)	DDays	TempVar (°C)
1	450	200	17.8	22.0	8.5	3920	-
2	300	200	16.2	21.0	7.0	3180	-
3	250	200	17.1	22.0	7.0	2520	-
4	200	200	18.0	20.5	13.0	3180	4.0
5	200	200	9.8	15.0	5.0	2000	-
6	550	200	14.7	19.0	8.0	2890	-
7	450	200	16.4	21.0	4.0	3170	-
8	400	200	16.9	21.0	10.5	3210	-
9	250	200	16.1	19.0	11.5	3130	-
10	200	169	17.4	20.5	13.0	3340	-
11	200	141	17.6	19.5	13.0	3210	7.0
12	200	200	15.7	20.5	10.5	3060	-
13	250	200	18.9	23.0	12.0	2560	-
14	250	200	17.9	24.5	7.5	3510	-
15	250	154	15.1	18.5	9.0	2570	-
16	550	163	13.9	19.0	1.5	2680	-
17	13	112	15.5	18.5	9.0	2910	2.0
18	14	57	14.8	18.0	8.0	2770	-
19	50	194	16.3	20.5	8.0	3030	-
20	50	200	15.8	20.0	9.0	2990	5.0
21	5	30	15.7	19.5	10.0	3000	-
22	13	90	16.4	21.0	9.0	3070	-
23	7	54	13.2	18.0	7.5	2490	-
24	7	57	14.9	18.0	9.0	2710	-
25	11	116	17.3	23.0	9.5	3180	-
26	9	154	15.7	23.0	7.0	2860	-
27	5	47	14.5	21.0	7.0	2660	-
28	9	70	11.5	18.0	4.0	2130	6.0
29	4	36	13.1	17.5	5.0	2450	9.0
30	8	36	11.6	18.0	2.0	2140	-
31	11	54	13.8	22.5	4.0	2470	-
32	10	54	15.8	22.0	5.5	3160	-
33	17	54	14.7	23.5	7.0	2590	13.0
34	17	23	10.2	16.5	6.5	1870	-
35	75	147	17.4	23.5	9.0	3150	8.0

## Appendix 9. Continued.

Site No.	CVmean (cm/sec)	CVmax (cm/sec)	CVmin (cm/sec)	Silt (mm)	Clarity (cm)	CPOM (mg/m <sup>2</sup> )	FPOM (mg/m <sup>2</sup> )
1	70	110	26	4.9	46	290	63
2	17	42	0	44.5	15	96	182
3	41	83	0	13.6	16	649	81
4	68	129	0	12.3	15	146	47
5	16	33	0	2.3	142	68	-
6	12	30	0	4.5	109	229	65
7	50	90	21	4.4	81	642	65
8	31	50	4	4.8	53	658	83
9	75	200	23	2.7	68	869	36
10	54	117	15	2.9	85	935	46
11	52	86	14	3.4	107	633	41
12	45	125	22	7.6	19	555	59
13	23	75	0	3.8	20	469	118
14	27	67	0	3.6	27	419	61
15	51	100	0	0.8	95	708	21
16	29	63	0	2.8	110	905	67
17	15	21	6	5.1	167	968	291
18	55	133	13	2.1	1279	128	168
19	63	100	35	2.7	85	240	62
20	20	45	0	5.3	62	148	76
21	38	86	16	1.9	200	978	94
22	60	100	34	5.9	134	202	86
23	42	133	11	1.8	200	987	77
24	59	133	17	2.3	200	3064	260
25	43	88	8	3.5	14	2487	85
26	21	58	0	9.1	18	2180	132
27	68	200	0	1.8	74	658	70
28	66	200	13	2.9	130	618	15
29	68	167	14	3.4	127	578	48
30	48	108	13	2.7	158	577	97
31	57	117	18	2.9	96	836	58
32	64	125	3	3.2	179	2897	101
33	53	100	11	3.8	108	427	160
34	15	24	11	4.2	116	1029	360
35	35	94	0	3.8	59	1390	221

## Appendix 9. Continued.

Site No.	Substrate Particle Size Classes *										
	(lower limit in mm)										
	256	128	64	32	16	4	2	1	0.5	0.25	0.125
1	0.0	0.0	23.7	19.4	33.4	21.5	0.8	0.3	0.3	0.3	0.3
2	92.3	6.1	0.0	0.2	0.4	0.4	0.1	0.0	0.0	0.3	0.1
3	0.0	47.6	37.1	8.7	2.5	1.8	0.3	0.2	0.3	1.1	0.3
4	0.0	0.0	13.1	29.9	25.6	3.3	14.3	7.6	0.3	0.2	0.1
5	0.0	0.0	0	26.7	29.1	18.2	4.9	7.3	9.1	3.9	0.8
6	0.0	0.0	44.4	34.4	2.4	1.7	0.4	0.4	9.2	5.7	1.4
7	0.0	28.7	59.3	7.5	4.4	0.1	0.0	0.0	0.0	0.0	0.0
8	0.0	33.4	55.4	6.7	2.7	1.4	0.2	0.1	0.0	0.1	0.0
9	0.0	32.8	33.3	22.3	3.1	5.6	0.9	0.4	0.7	0.7	0.2
10	0.0	49.9	25.0	12.5	2.0	4.1	1.4	1.1	1.7	1.7	0.7
11	0.0	62.0	23.8	4.0	1.1	2.4	1.1	0.7	2.4	2.0	0.5
12	0.0	0.0	40.8	31.8	6.7	8.3	1.0	0.4	1.3	6.9	2.8
13	26.1	41.9	21.0	7.2	1.1	0.8	0.3	0.3	0.2	0.5	0.7
14	0.0	75.7	11.6	4.9	1.5	2.4	0.9	0.6	0.6	0.9	0.9
15	0.0	68.0	15.3	7.3	2.3	2.6	0.8	2.1	1.3	0.3	0.0
16	0.0	69.9	13.1	6.7	2.0	4.8	0.8	0.8	0.8	0.7	0.3
17	0.0	52.1	12.3	20.4	4.5	7.2	1.2	0.7	0.4	0.7	0.5
18	0.0	87.8	1.7	3.0	1.2	2.5	0.9	1.0	1.0	0.6	0.2
19	26.5	54.9	3.9	8.4	1.5	3.4	0.6	0.4	0.3	0.2	0.0
20	0.0	78.3	16.8	3.5	0.4	0.3	0.1	0.1	0.3	0.2	0.1
21	22.8	40.2	21.9	4.8	4.0	3.0	1.5	0.5	0.5	0.4	0.3
22	13.0	74.7	8.1	1.3	0.2	0.4	0.2	0.2	0.1	1.1	0.7
23	52.5	12.4	17.2	5.6	1.2	4.3	2.0	1.8	1.6	1.0	0.3
24	7.9	55.7	13.8	8.7	3.5	4.7	2.5	1.6	1.2	0.4	0.1
25	34.8	40.3	6.4	10.5	2.7	2.7	0.5	0.8	0.2	0.6	0.2
26	-	-	-	-	-	-	-	-	-	-	-
27	0.0	0.0	23.8	29.1	9.5	17.6	6.7	4.2	5.0	2.6	1.5
28	29.4	52.8	7.8	5.6	1.1	1.6	0.5	0.4	0.6	0.2	0.0
29	0.0	62.2	23.3	5.7	1.9	3.2	1.2	1.1	0.9	0.4	0.1
30	0.0	77.1	10.9	3.1	2.5	1.9	1.1	1.1	1.3	0.8	0.2
31	0.0	65.0	7.2	10.3	6.0	7.5	1.5	1.0	0.8	0.6	0.1
32	0.0	9.5	19.8	12.6	7.2	21.3	13.2	9.2	4.0	1.6	1.6
33	0.0	31.5	23.2	20.6	7.8	8.8	2.5	1.8	1.7	1.2	1.0
34	0.0	31.5	23.2	20.6	7.8	8.8	2.5	1.8	1.7	1.2	1.0
35	74.5	8.1	8.2	3.8	1.3	1.9	0.6	0.5	0.6	0.1	0.3

\* - Values given are the percentages (by volume) of particles in each size class.

## Appendix 9. Continued.

Site No.	Plant Growth *						
	<u>SewFun</u>	<u>Filam</u>	<u>Nostoc</u>	<u>Diatoms</u>	<u>Moss</u>	<u>Chara</u>	<u>Macro</u>
1	0.5	2.8	1.0	0	0	0	1.8
2	0	1.0	0	0	0	0	0
3	0.7	0.6	0	0	0	0	0
4	0	0.2	0	0	0	0	0
5	3.1	1.7	0	0	0	0	0
6	3.6	2.3	0	0	0	3.9	1.6
7	3.4	2.7	0	0	0	2.0	2.1
8	1.6	2.5	0	0	0	4.3	0
9	0.1	5.1	1.1	0	0	0.6	4.1
10	1.8	6.0	3.5	0	0	1.0	2.1
11	1.7	1.3	3.1	0	0	0	0.9
12	0.4	0.4	0	0	0	0	0
13	1.6	1.3	1.7	0	0	0	0.1
14	1.3	0.9	0.4	0	0	0	0
15	0.9	3.0	0	0	0	0	0
16	3.6	2.5	0	0	0	0	0.1
17	0.5	1.0	3.1	3.5	0	1.6	2.6
18	1.5	1.5	2.3	3.3	0	0	0.4
19	1.3	1.3	1.3	2.4	0	0	0.4
20	2.8	1.3	0.9	1.5	0	0	0.9
21	0.4	2.8	0.3	3.6	0.4	0	0.1
22	0.6	1.8	1.8	3.3	0.6	0	0
23	0.3	0.3	1.8	0.5	0	0	0.1
24	0.4	1.9	4.3	2.3	3.7	0	0.4
25	1.1	2.1	0.9	0	0	0	0.1
26	0.9	0.1	0	0	0	0	0
27	0.6	0.8	1.6	0	0.5	0	0
28	0.1	0	0.6	0	0	0	0
29	0.1	0	0	0	0	0	0
30	1.6	1.0	1.0	1.0	0	0.1	0.1
31	0.5	0.1	1.0	0.6	0.1	0	0
32	0	2.5	1.5	0.8	4.1	0	4.3
33	6.0	2.1	0.5	3.1	0	0	0.1
34	6.1	1.1	0.4	2.6	0	0	0
35	3.4	0.5	3.1	2.1	0.1	0	0

\* - subjectively assigned abundance values between 0 and 7

## Appendix 9. Continued.

Site No.	Allochthonous Organic Matter *		
	<u>Grass</u>	<u>Leaves</u>	<u>Wood</u>
1	1.7	0	1.5
2	0.7	0	0.7
3	2.4	1.6	2.3
4	2.0	0.5	1.0
5	0	0.1	0.1
6	0.9	0.7	0.7
7	1.7	0.6	0.7
8	0.8	0.5	0.9
9	0.1	0	0
10	0.4	0	0
11	0.4	0.1	0
12	1.6	2.8	3.1
13	2.9	0.9	1.1
14	1.3	0	1.3
15	0.1	0	0
16	2.1	1.6	0.3
17	0	2.9	3.5
18	0	3.8	4.1
19	0	0.1	0.4
20	0	0	0.6
21	0	1.3	2.0
22	0	0.6	2.4
23	0	2.3	4.8
24	0	2.3	3.7
25	0.8	1.5	4.8
26	0.8	1.8	5.4
27	0	2.8	3.3
28	0	2.1	1.8
29	0	2.1	3.5
30	0	3.9	2.6
31	0	4.4	4.0
32	0	2.1	1.9
33	0.1	1.8	0.8
34	0.3	1.7	0.9
35	1.0	0.5	0.3

\* - subjectively assigned abundance values between 0 and 7



Appendix 10. Site compositions of subzones in the classification of extensive study data (Figure 66). All sites are in Saskatchewan, unless otherwise indicated.

<u>Subzone</u>	<u>Sites included</u>
Ia	South Saskatchewan River at Red Deer River Forks, bridge north of Leader, grid road north of Prelate, and Lemsford Ferry; North Saskatchewan River at Cecil Ferry.
Ib	South Saskatchewan River at Round Prairie, Saskatoon, Clarkboro Ferry, Hague Ferry, bridge east of Rosthern, St. Laurent Ferry, Fenton Ferry and Birch Hills Hills Ferry; North Saskatchewan River at Lloydminster Ferry, bridge east of Paradise Hill, bridge north of Maidstone, Paynton Ferry, Battlefords Bridge, bridge south of Maymont, Borden Bridge, Petrofka Bridge, Fort Carleton, Wingard Ferry, and south of Crutwell; Saskatchewan River at Gronlid Ferry and 6 km south of Nipawin; Battle River south of Lashburn.
Ic	Saskatchewan River 17 km downstream from Squaw Rapids Power Station and at The Pas, Manitoba; Qu'Appelle River north of Sintaluta, north of Wolseley and at Hwy. 8 north of Moosomin; Assiniboine River at Hwy. 41, Man.; Shell River at Hwy 83, Man.; Carrot River at grid road southwest of Nipawin, Hwy. 163 and near Hwy. 9; Red Earth Creek and McVey Creek at Hwy. 163; Red Deer River and Bowsman River at Hwy. 10, Man.; Swan River north of Benito, Man.; Beaver River at Hwy. 26.
IIa	Battle Creek 25 and 40 km southwest of Fort Walsh Park, Sask., and at Battle Creek and Reesor Lake campsites, Alta.; tributaries of Battle Creek 5 and 10 km. east of Saskatchewan Border; Frenchman River at Hwy. 37 north of Climax and at grid road near Ravenscrag; Bone River south of Tompkins; Swift Current Creek 10 km southwest of Swift Current and at grid road east of Stewart Valley; South Saskatchewan River at Gardiner Dam and Outlook Bridge; Saskatchewan River at Squaw Rapids Power Station; Carrot River at Hwy. 283, Man.; Man River at Hwy. 163; streams 12 and 18 km east of the Saskatchewan border on Hwy. 277, Man.; Beaver River at Hwy. 55 and Hwy. 4; Mistohay Creek at Hwy. 224; Low Creek at Hwy. 104; stream at Cole Bay on Canoe Lake; MacLennan River at Hwy. 2; Bow River at Hwy. 165; Bedard Creek, stream at mile 55, stream 1 km north of Bear River and stream at mile 100, all at Hwy. 106; Sturgeon-Wier River at Hwy. 167; Clearwater River, stream at mile 107, Sandy Lake and Carswell Lake, all at Hwy. 155; Johnson River at Hwy. 105.

## Appendix 10. Continued.

<u>Subzone</u>	<u>Sites included</u>
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| IIb  | Battle Creek at bridge near Fort Walsh Park; Rice River at Hwy. 163; Bainbridge River, Waskwei River, Niska Creek and Pasquia River, all at Hwy. 9; Armit River at Hwy. 3; Kinakin Creek, stream 8 km south of Hwy. 3 and Woody River (south crossing), all at Woody River Road; Swan River at McBride Lake Road; stream at km 8, Hwy. 277, Man.; Steeprock River and Birch River at Hwy. 10, Man.; Roaring River at Provincial Road 488, Man.; West Favel River at Provincial Road 485, Man.; stream at mile 91, Hwy. 106; Ballantyne River at Hwy. 106; stream at mile 10, Hwy. 165; stream at mile 155, Hwy. 155, south of La Loche.   |
| IIc  | Souris River south of Oxbow and at Roche Percee campsite; Pipestone River at Hwy. 8; Qu'Appelle River at Hwy. 6; Assiniboine River at Hwys. 8, 9 and 47; Lilian River at Hwy. 9; Carrot River at Hwy. 23; Red Deer River at Hwy. 23 and grid road north of Somme; Pepaw River at Hwy. 9 and McBride Lake Road; Smoking Tent Creek at Hwy. 3; Woody River, Swan River, West Favel River and Overflowing River, all at Hwy. 10, Man.; Shell River at Provincial Road 367, Man.; Roaring River at Provincial Road 366, Man.; stream near Westray at Provincial Road 282, Man.; Makwa River, Meadow River and Cowan River, all at Hwy. 55; Otter Creek at Hwy. 104; Giekie River at Hwy. 105 and at rapids 15 km upstream from Hwy. 105; Umperville River at Hwy. 105; Torch River at Hwy. 106; Pelican Lake at Pelican Narrows; Wakawasasik Lake south of Sandy Bay. |
| IIId | Steeprock River at Steeprock Lake, Man.; Fir River at Hudson Bay Regional Park; Red Deer River and Overflowing River at Hwy. 9; Woody River at Woody River Road (north crossing); Puskwakau River and Sturgeon-Weir River at Hwy. 106; Nemei River at Hwy. 135; McDougal Creek at Hwy. 120; Nipekamew River at Hwy. 165; Waskesui River, Crean River, Weyakwin River and Montreal River (at La Ronge and 60 km. south of La Ronge), all at Hwy. 2; Waterhen River at Hwy. 155; Keeley River at Hwy. 101.  |

## Appendix 10. Continued.

<u>Subzone</u>	<u>Sites included</u>
Ile	White Gull Creek, Caribou Creek, Cub Creek and Bear River, all at Hwy. 106; Meridian Creek at Hwy. 167; Waterhen River at Hwy. 224; Broad Creek at Hwy. 104; stream just east of Beauval; stream at mile 140, Hwy. 155, north of LaLoche; Douglas River at Hwy. 155, just south of Cluff Lake and 15 km south of Cluff Lake; Mackay Creek, Churchill River, streams at miles 130 and 135, and Waddy River, all at Hwy. 102; streams at km 55, 105, 135, 155, 188, 195 and 215, Hwy. 105.