THE EFFECTS OF SUBSTRATE STABILITY/DISCHARGE RELATIONSHIPS ON THE AQUATIC INSECTS OF WILSON CREEK, MANITOBA

by

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A Thesis

Submitted to the Faculty

of

Graduate Studies

The University of Manitoba

In Partial Fulfilment of the

Requirements for the Degree

of

Master of Science

Department of Entomology

June 1990

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DONALD G. COBB

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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ACKNOWLEDGMENTS

I am indebted to Dr. T.D. Galloway for the opportunity to conduct this study and for acting as my supervisor throughout the duration of my graduate work, and Mr. J.F. Flannagan who inspired me to further my academic career, and provided me support and guidance over the course of this study. I am grateful to Dr. R. Arginal, Mr. T. Madaford, Mr. D. Macdonnel, Mr. D. Chaput, Ms. R. Bernatski, Ms. S. Bernatski, and Ms. S. Wetmore, for their valuable assistance and patience during all phases of the study. A special thanks to the following two committee members. Dr. R.E. Roughley of the Department of Entomology provided valuable guidance and suggestions regarding this thesis. Dr. R. Newbury of the Wilson Creek Watershed Research Station, opened my mind to the nature of streams. His hospitality, guidance, and patience throughout this study is much appreciated. Mr. J. Thomlinson faithfully provided stream flow data. Appreciation is extended to Parks Canada for permission to conduct this study within Riding Mountain National Park. I dedicate this thesis to my wife Kathy, and my two children, Brian and Heather who supported and endured during the many hours I spent away from home while completing this thesis.

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This thesis is presented in the manuscript format. As such, some
duplication of site descriptions and materials and methods is necessary.
A portion of chapter 4 was presented at the conference and accepted for
publication in the proceedings of the VIth International Symposium on
Ephemeroptera, Granada, Spain, July, 1989. Part 5 was presented at the
conference and submitted for publication in the proceedings of the VIth
International Symposium on Trichoptera, Lodz, Poland, September, 1989.
Part 3 will be submitted to the Canadian Journal of Fisheries and Aquatic
Sciences in 1990.

ABSTRACT

The aquatic insects were studied in three reaches of Wilson Creek, a small headwater escarpment stream in West-central Manitoba, to examine the effects of discharge/substrate stability relationships on the abundance, diversity and distribution of the insect community. Substrate stability ranged from a maximum of 80% to a minimum of 20% substrate at incipient motion at bankfull discharge. Immature insects were sampled monthly and following spates from May 1986 to May 1988 using a modified Hess sampler. Adults were collected three times per week from May to September in 1986 using $1m^2$ box emergence traps.

A total of 11 mayfly, 15 caddisfly, and 10 stonefly taxa was collected during the study. Insect density and diversity were negatively correlated to discharge and substrate stability at all stations. A substrate stability model could be used to explain more variation in the data for the whole stream than discharge. When station effect was introduced into the model, the regression was improved for discharge, but not for substrate stability.

The effects of a stable riffle constructed in the most unstable reach had a mitigating effect on the community of insects. Insect density declined up to 94% following spates in the unstable reach, but not at the introduced stable riffle. The stable riffle supported a

larger proportion of filter feeding caddisflies than the unstable reach during low flows.

Life history adaptations were examined for 22 mayfly, stonefly and caddisfly species in the most unstable reach in relation to frequency, intensity and duration of disturbance, as indicated by substrate movement. Forty-one per cent of species examined were univoltine, with winter growth, and emerged prior to spring floods. Another 41% of species had complex life cycles, with multivoltinism or multiple cohorts. One species was semivoltine, but was collected infrequently. Life history adaptations of most species are suited for existence in an unstable, frequently disturbed habitat.

It is concluded that substrate stability is an important determinant of diversity and abundance of aquatic insects in Wilson Creek, and should be considered when characterizing disturbance and its role in controlling aquatic insect communities.

1.INTRODUCTION

Streams are complex ecosystems, and much attention has been devoted to understanding the factors which determine the structure of benthic macroinvertebrate communities of flowing waters. Whether studying life histories, estimating production, or carrying out a general ecological study of a species or assemblages of species, an understanding of factors which determine density, diversity and distribution of aquatic insect communities is essential. To conduct environmental impact studies, factors which lead to variability in aquatic insect communities must be taken into account. Data from these studies is often complex, and not easily interpreted simply as a cause and effect scenario.

It is partly the complexity of these ecosystems, along with the aesthetics associated with working in streams, that has led to a great interest in the field of aquatic entomology. From a personal perspective, I have always been challenged by the intricacies of riverine ecosystems, and by the interesting adaptations of aquatic insects to allow them to inhabit a wide variety of niches. This has been the driving force in my pursuit of an understanding of deterministic factors in stream ecology.

Just as streams are not in a steady state, so the field of aquatic entomology has historically been in a state of constant change. Minshall (1988) reviewed the changing trends of thought regarding

factors which control stream systems. Historically, density dependent (deterministic), biotic factors received most of the attention, ranging from functional feeding groups which make use of available nutrients along the gradient of rivers (Cummins et al. 1983), to nutrient spiralling (Newbold et al. 1981). Other biotic factors proposed included predation and competition (see Peckarsky 1984). The development of these theories culminated in a variety of equilibrium models of insect community structure (Vannote et al. 1980, Newbold et al. 1981).

I thought these were very interesting holistic theories, which forced me to focus my thoughts on global stream ecological concepts. But, when I went into the field, I was troubled by the observable and overpowering effect of high discharge, associated with spring snow melt, and summer spates resulting from rain storms, these periods when the whole stream took on a different appearance. It seemed to me that there must be an overriding determinant which aquatic insects must first overcome after which important factors such as feeding, predation, competition and temperature become important.

It has been suggested in recent critiques of holistic, deterministic theories (Winterbourn et al. 1981, Statzner and Higler 1985) that hydrological factors were important determinants of lotic ecosystems, and that disturbance was not included in many of the deterministic theories. Newbury (1984) introduced benthic ecologists to hydrological methods useful to analyse and characterize lotic habitats. When applied to unstable rivers, regardless of which

hemisphere, much of the variability of insect species abundance, richness and distribution could be explained by measurable hydrological factors (Sagar 1986, Scrimgeour et al. 1988, Flannagan et al. 1990).

The study of hydrological processes as important determinants of stream ecosystems is in its infancy, but as suggested by Resh et al. (1988) these processes are probably the most important determinants of stream ecosystems. However, the problem with many of the hypotheses presently being developed, is that they have yet to be tested on a wide geographical scale. Discharge and flow regime are two hydrological factors currently used to measure disturbance, and have been shown to be important in characterizing aquatic insect habitats. There are, however, other factors which need to be addressed, for example the varying effects of discharge on substrate movement in different sections within a stream and among streams (Minshall 1988). I undertook this study hoping to shed some light on the effect of discharge/substrate stability relationships on the aquatic insects. I realized that probably more questions would result from my study than those which could be answered, but hoped the information resulting from the investigation of one small stream, could be expanded upon and tested over a wider range of streams.

Much of the thrust of the study resulted from work on streams in the Dauphin Lake drainage basin, in which substrate stability problems resulting from stream channel and watershed changes, have affected the aquatic insects (Cobb and Flannagan 1989) and probably the spawning success of walleye. However, as with any study in an anthropogenically

impacted drainage basin, it was difficult to separate factors causing the impact. By studying a small pristine stream within a national park, it was hoped these problems could be overcome.

The purpose of my study was to investigate the effects of substrate stability/discharge relationships on the aquatic insect community of Wilson Creek. Within the scope of the study I proposed to address spatial and temporal effects of changes in discharge and its related substrate movement on abundance, diversity and distribution of aquatic insects. I also proposed to examine life histories of insects as affected by substrate stability, specifically, those insects which were able to survive in the more unstable reaches. Finally, I proposed to put my findings into context of theories currently being used to explain aquatic insect ecology.

2. REVIEW OF PERTINENT LITERATURE

When I undertook this study in 1986, the literature (pre 1984) pertaining to spatial/temporal discharge/substrate stability relationships as an important factor in the ecology of aquatic insects was limited. In fact, there were relatively few examples in the literature in which aquatic insect habitats were characterized using any of the available analytical methods commonly used by hydrologists. I suggest that it was not because biologists were unaware of the importance of flowing water, rather they were unaware of hydrological methodology available to them to measure, analyse and thus characterize aquatic insect habitats. These methods have been used by hydrologists and engineers for decades for flood forecasting in the design of drainage channels, bridges, dams, and highways (Benson 1962).

Subsequent to the start of my study, there has been an exponential increase in the number of papers appearing in the literature in which aquatic insect community structure, and species distribution were examined from a hydrological perspective in general, and more specifically from a stochastic perspective (Fig.1). What caused this increase? A brief historical perspective, in which I trace the trend of benthic researchers' theories of the importance of biotic and abiotic factors in controlling aquatic insects in flowing waters, will in essence act as a review the pertinent literature to my study. At the same time, I hope to give the reader a feel for the direction of future lotic invertebrate research.

FIGURE 2-1. Cumulative growth in number of papers dealing with
hydrological factors and their effect on aquatic insects.
(Data from Resh and Rosenberg 1984, Minshall 1988, Resh et al.
1988).
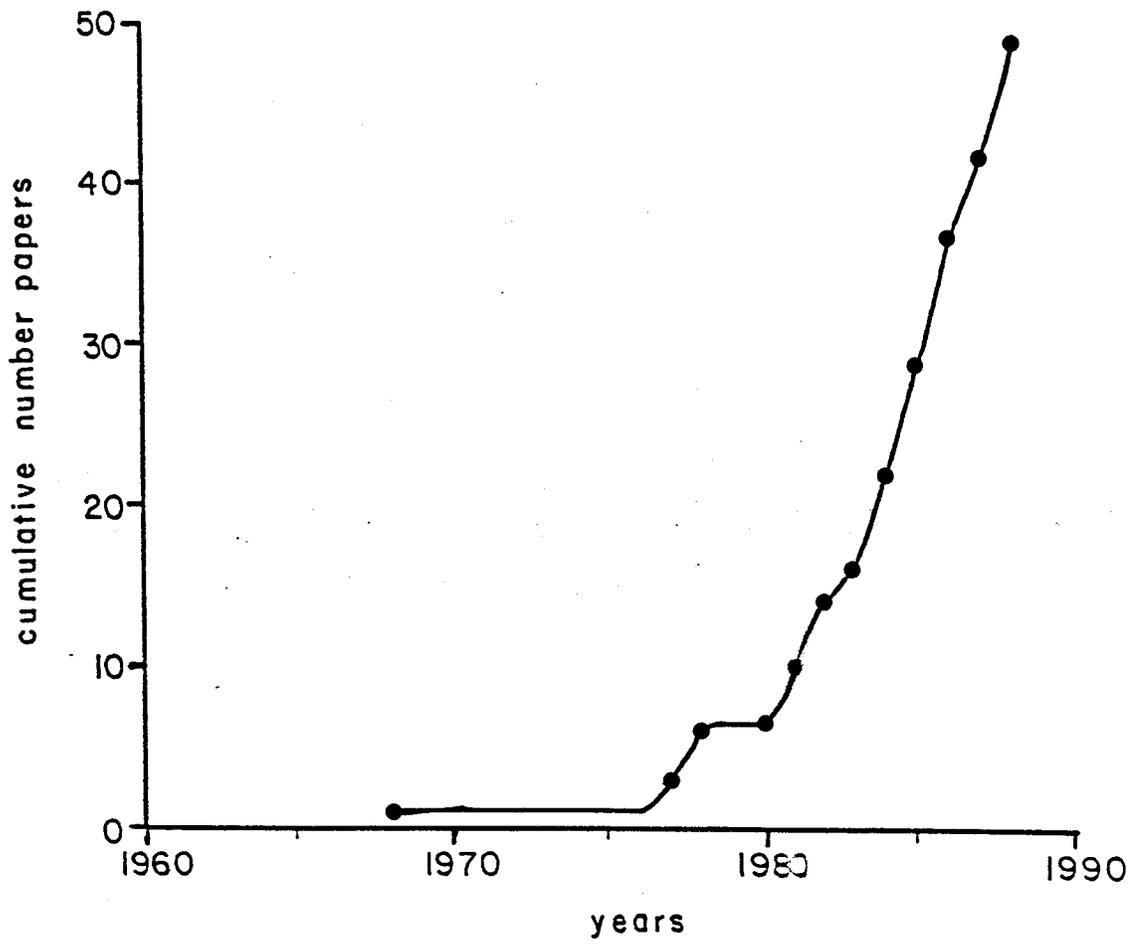
2.1 Traditional concepts of determinants of lotic insect communities

Prior to the mid-1980's, most researchers who studied factors affecting insects of lotic waters examined deterministic (density dependent) factors. In a review of the derivation of stream ecological theory, Minshall (1988) outlined the major shifts in emphasis throughout the decades.

Biotic production and food resources were considered important factors from the mid-1950's to the early 1980's. These processes included energy flow and organic matter processing (e.g. Cummins et al. 1983), and trophic relations (e.g. Wiggins and Mackay 1978, Anderson and Cummins 1979). Beginning in the 1960's, biotic factors such as predation, and competition among insects were heavily studied (Peckarsky 1979, McAuliffe 1984, see Peckarsky 1984, for review). Beginning in the 1970's nutrient dynamics were considered important (Newbold et al. 1981, see Merritt et al. 1984, for review).

In a synthesis of deterministic theories as major determinants of aquatic insect communities, there were various equilibrium models of community structure proposed (Vannote et al. 1980, Newbold et al. 1981). Perhaps the most famous and controversial theory, the River Continuum Concept (RCC)(Vannote et al. 1980), is a holistic concept of dynamic equilibrium in biological communities. Changes in functional feeding groups were based on sources of organic matter along the gradient from headwaters to high order rivers. The basic principles of this theory were developed in the absence of disturbance, and resulted in an ongoing controversy (see Winterbourn et al. 1981, Statzner and Higler 1985). In

spite of its short comings, the RCC, in receiving much criticism, changed the direction of thinking for a few researchers, which led into the early 1980's and a new era of stream ecosystem research.

2.2 An era of change

In the early 1980's, opponents of the RCC suggested that abiotic factors were as important, if not more important tran biotic ones. The main basis for their views was that many of the factors examined in the RCC (e.g. temperature, food resources, predation, competition), did not function on a global scale (Statzner and Higler 1985). There were exceptions to the proposed gradient of insect communities and their changes according to functional feeding groups (see Statzner and Higler 1985, Perry and Schaeffer 1987).

Statzner (1981) suggested that hydrological (abiotic) factors were important determinants of aquatic insect community structure, but was uncertain as to the overall significance of these factors. He related the distribution of various aquatic insects to combinations of depth, slope and velocity. Gore and Judy (1981) measured flow, depth and velocity in conjunction with benthic samples and related the distribution of insects to these parameters. Nowell and Jumars (1984) described the flow environment at the level of benthic insects. These researchers characterized aquatic habitat at the insect, or micro-level.

A different scale of hydrological determinants was examined in the early 1980's, that of the effect of floods on the communities of aquatic insects at the meso- or whole reach scale. Large reductions of aquatic

insects were associated with floods, and subsequent recovery was documented (Gray and Fisher 1981, Fisher et al. 1982). Apart from documenting these events, there was no attempt to analyse them hydrologically with respect to frequency, intensity and duration, and to characterize aquatic insect habitats in this manner. In many respects, these results were similar to those already reported throughout the literature (e.g. Moon 1940, Allen 1959, Anderson and Lehmkuhl 1968), with no attempt to analyse frequency, intensity and duration of floods with respect to potential adaptations required for survival under various flow regimes. There was, however an attempt to characterize the predictability of disturbance and to put disturbance into an ecological perspective with respect to life histories and other ecological aspects of aquatic insects necessary to survive these disturbances. This was an important recognition by researchers.

In spite of the short comings of these studies, it was apparent that flowing water was acting on insects at different scales. Newbury (1984) reviewed hydrological processes which act on different size and time scales according to a ..." framework of structure, process and time." Newbury described ways to measure, analyse and characterize aquatic insect habitats at the micro- (near-insect), meso- (reach), and macro- (drainage basin) levels. He suggested that

"discovering the points of fitness ... between

the patterns of hydraulically determined habitats and

biological systems is an absorbing challenge for all

researchers." (Newbury 1984 p.354).

This review, in my opinion, probably had the greatest impact on the benthic research community since Hynes' (1970) review of the ecology of running waters. This is evident from Fig. 1, where the growth in frequency of papers dealing with hydrological factors affecting insects began shortly after 1984. Benthic researchers now were aware of methods commonly used by hydrologists to measure, analyse and describe aquatic insect habitats, and were aware of several spatial and temporal scales in which hydrological processes could be examined to characterize lotic benthic insect habitats, and that these scales were not mutually exclusive of one another.

3.3 Recent concepts of lotic insect community determinants

As a result of reviews concerning flowing water environments of aquatic insects (Statzner 1981, Nowell and Jumars 1981), an increase in studies concerning local flow conditions at the insect level, i.e. the micro-level (Statzner and Holme 1982, Statzner 1988, Craig and Chance 1982, see Statzner et al. 1988 for review) has occurred. Filter feeding insects select specific combinations of velocity, slope and depth which when combined, form parameters such as froude number, shear stress, and Reynold's number (Osborne and Herricks 1987, Wetmore 1987).

However, as Newbury (1984) suggested, there are several scales of hydrological determinants, and of particular importance to my study is the whole reach or meso-scale. Aquatic habitat on the meso-scale is a combination of hydrological factors and geological conditions. These factors include year to year and seasonal peak flow events, and the

movement of substrate associated with them. These flow events are related to spring snow melt, high precipitation in summer, or winter rains, depending upon the geographical location and its associated climate.

Reductions in standing stock of insects have frequently been related to increased discharge, but until recently the importance of these events to the structure of the insect community has been neglected. Historically, the effect of a flood on aquatic insects was at most the documentation of a reduction of standing stocks of insects, with perhaps an observation that a reach of a stream appeared to suffer greater losses than another reach (Allen 1959). Newbury (1984) suggested that analytical methods used by hydrologists could provide insight into the effects of flood duration, frequency, and intensity upon aquatic insect communities.

Recently, flood events and their affect on aquatic insects have been examined from a historical flow perspective (Stanford and Ward 1983, Irvine 1985, McElvary et al. 1989). Resh et al. (1988) analyzed predictability, contingency, and constancy of flow for drainage basins with a different flow regime using Colwell's (1974) theory of predictability. Although unsure of the implications of their findings on aquatic insect biology, Resh et al. (1988) saw the methodology as having potential to determine frequency, intensity and duration of disturbance, or that discrete event in time which disrupts ecosystem, community, or population structure, through changes in the physical environment, or resource availability. They do conclude that the predictability of

discharge should be an important consideration in studying aquatic insect evolution with respect to life history strategies, and biotic interactions such as predation and competition.

However, not all spates result in loss of aquatic insects. Cowie (1980) found no effect of a flood on densities of invertebrates, but reported that the substrate was large and very stable. Similarly, non-Simuliidae aquatic insect densities in a granite-boulder substrate lake outflow stream did not vary during spring peak discharges (Giberson and Hall 1988). Allen (1959) reported that floods affected insect densities differently depending upon the stability of the substrate. Although it was observed that substrate was stable or unstable in these studies, there was no attempt to analyse the actual bed stability.

For decades hydrologists have analysed substrate stability in the design of channels (Newbury 1984). As depth of flow increases, so does the tractive force (shear stress) acting on the substrate and insects associated with them. The stability of a reach of stream is a function of the bed paving material, the average slope of water and the depth of flow (discharge). Substrate stability as used in the determination of aquatic insect habitats had not been quantitatively analyzed prior to the mid-1980's.

Recently, attention has been focused on rivers with substrate stability problems. Unstable rivers in New Zealand are characterized by frequent spring and summer floods, resulting in low species diversity of aquatic insects, with those species present growing rapidly and having multivoltine life cycles (Sagar 1986, Scrimgeour and Winterbourn 1988).

Substrate instability was in part responsible for a reduction in diversity of Trichoptera emerging from several reaches of the Ochre River, Manitoba (Cobb and Flannagan in press).

Experimental manipulations have been conducted in order to examine the effects of substrate movement on aquatic insects. Periodic disturbance of substrate has been shown to cause measurable reductions in insect density (Clifford 1982, Reice 1985, Doeg et al. 1989). Recovery was very rapid in these experiments, and overall community composition was not altered. These experimental plots were small, relative to a whole reach of stream, and recovery pathways may have been quite different from those which would occur for a whole reach of stream. Malmqvist and Otto (1987) used artificial substrates of different specific density to test the effect of tractive force, and found that species differed in their preference of substrates. Although considerable insight into recovery of individual stones, or patches of substrate was provided in these experiments, they tell us little about spatial and temporal effects of substrate stability/discharge relationships along a whole stream (Minshall 1988).

The role of disturbance in aquatic ecosystems has led to the replacement of equilibrium models (Resh 1988) with new models to explain stream ecosystem community structure. In the intermediate disturbance hypothesis (Connell 1978), equilibrium competitor species are overwhelmed by colonizers in a highly disturbed regime, while during long stable periods, predators dominate. Both these situations lead to low species diversity. When disturbance is intermediate, there is a balance between

predators and colonizers, resulting in the maximum species richness. This theory was applied to streams by Ward and Stanford (1983) Hemphill and Cooper (1983)(but see Reice 1985, Doeg et al. 1985). Disturbance was also included in the dynamic equilibrium model (Huston 1979), where species diversity is determined by the influence of the environment on the net outcome of species interactions, rather than on the relative competitive abilities of the species. It appears that the applicability of the above theories can only be determined when the frequency, intensity and duration of disturbance is calculated for each watershed (see Resh et al. 1988). I feel that it is of prime importance to determine the spatial/temporal effect of the disturbance by examining the effect of substrate stability during these events, and that my study is timely in the context of recent developments in stream community ecology.

3. THE EFFECT OF DISCHARGE/SUBSTRATE STABILITY RELATIONSHIPS ON THE AQUATIC INSECTS OF WILSON CREEK, MANITOBA

3.1 ABSTRACT

The aquatic insects were studied in three reaches of Wilson Creek, Manitoba, a small headwater escarpment stream, from 1986-1988 in order to show the effects of discharge/substrate stability relationships on the abundance, diversity and distribution of the insect community. Substrate stability ranged from a maximum of 80% to a minimum of 20% stable at bankfull discharge.

A total of 11 taxa of mayflies, 15 taxa of caddisflies, and 10 taxa of stoneflies was collected. All but a few taxa were present at all stations. Insect densities were negatively correlated with increasing discharge and substrate movement at all stations. The regression model using substrate stability explained more of the variation in the data than discharge, unless station effect was included. Changes in densities following two summer spates ranged from 94% at the most unstable reach, to no reduction at the most stable reach. Most insect species showed high resiliency, with density and diversity returning to pre-spate levels during periods of low flow.

Temporal and spatial effects of substrate stability/discharge relationships affect aquatic insect densities. I suggest that an examination of substrate movement should be included in any hydrological analysis of the effects of flowing water on aquatic insects.

3.2 INTRODUCTION

Streams are complex ecosystems, and much attention has been devoted to understanding the factors which determine benthic macroinvertebrate community structure. An understanding of factors which regulate and control density and diversity and distribution of aquatic insect communities is essential in life history, production and ecological studies. It is also important to understand these factors in environmental impact studies, as data are not easily interpreted because of the highly variable environment from which samples are taken.

Historically, density dependent (deterministic) biotic factors were thought to drive lotic aquatic insect ecosystems (see review by Minshall 1988). These included food resource partitioning by functional feeding groups (Cummins et al. 1973), predation and competition (Peckarsky 1984, McAuliffe 1984), and culminated in a variety of equilibrium models of insect community structure (Vannote et al. 1980, Newbold et al. 1981). The basic principles of deterministic theories were developed in the absence of disturbance, and the effect of hydrological factors were totally ignored (Statzner and Higler 1985), and as such were much criticized.

The role of physical disturbance, usually in the form of floods, may be the dominant determinant in stream ecology (Resh et al. 1988). The direct biological effect of floods on riverine insect populations has been well demonstrated (see Hynes 1970, Gray and Fisher 1981, Sagar 1986). However, the hydrological events themselves, e.g. intensity, frequency, periodicity of floods, have not been analyzed by biologists to

characterize benthic habitats, and to explain species diversity, distribution and abundance.

The role of substrate stability as a determinant of aquatic insect habitat rarely has been studied. Experimental disturbance in small patches of substrate has been examined (Reice 1985), and artificial substrates of different density and therefore different stability at a given flow have been used (Malmqvist and Otto 1987). The investigators examined changes in community structure following disturbance. Although they gained valuable insight into colonization rates of disturbed substrates, the experimental patches were small in relation to the natural stream. Any effects which may have resulted from actual stability phenomena were masked. There are no investigations within a natural stream ecosystem in which spatial/temporal effects of substrate stability have been studied (Minshall 1988).

The purpose of the present study was to investigate the effects of substrate stability/discharge relationships upon the aquatic insects of a small pristine stream, Wilson Creek, Manitoba. The basic hypothesis of this study was that aquatic insect density and diversity would differ with varying substrate stability. Spatial/temporal variability of substrate stability was studied in three reaches representative of a range of substrate stability at bankfull discharge. In addition an experimental stable riffle was constructed within an unstable reach in order to show the effect of equal discharge upon stable vs. unstable substrates within the same reach of stream.

3.3 MATERIALS AND METHODS

3.3.1 Study Area

Wilson Creek, a fourth order stream (1:50,000 scale) with a drainage area of 22km^2 is located in west-centra Manitoba (50° 43' N, 99° 33' W) (Fig. 1). It is one of many streams rising on the Manitoba escarpment, a 400 meter (m) high bench of Cretaceous shale overlain by glacial till (Newbury 1983). Originating in Riding Mountain National Park at an elevation of 747 meters above sea level (m.a.s.l.), Wilson Creek descends steeply to 340 m.a.s.l. over a distance of 6.4 km. A drainage canal connects the creek to the Turtle River which eventually flows into Dauphin Lake.

This watershed was chosen for several reasons. It was the site of a 25 year study to investigate the feasibility of flood storage dams and sediment control related to flooding problems in the surrounding agricultural district. A continuous gauging station has been operational for over 30 years. As a result of this study there is a long-term historical data base of hydrological and meteorological information. Many of the relationships between hydrological and geological processes have been derived from these data (Newbury 1984). Wilson Creek is part of the Dauphin Lake drainage basin. Many of the rivers in this basin have been heavily altered through channelization (Chapman 1987), resulting in substrate instability, sedimentation and other problems associated with drainage improvement for agricultural practices (Newbury and Gaboury 1988). The Wilson Creek watershed is situated entirely within a protected National Park and is outside the direct effects of

FIGURE 3-1. Map of Wilson Creek, Manitoba with location of sampling
    sites (B1, B2, W1, and W1S) of 1986-1988 Wilson Creek aquatic
    insect study.

Pack

Horse

Creek

Wilson

Creek

W1S

W1

B1

Bald

Hill

Creek

B2

study area

drainage divide

N

0   0.5   1.0
Km
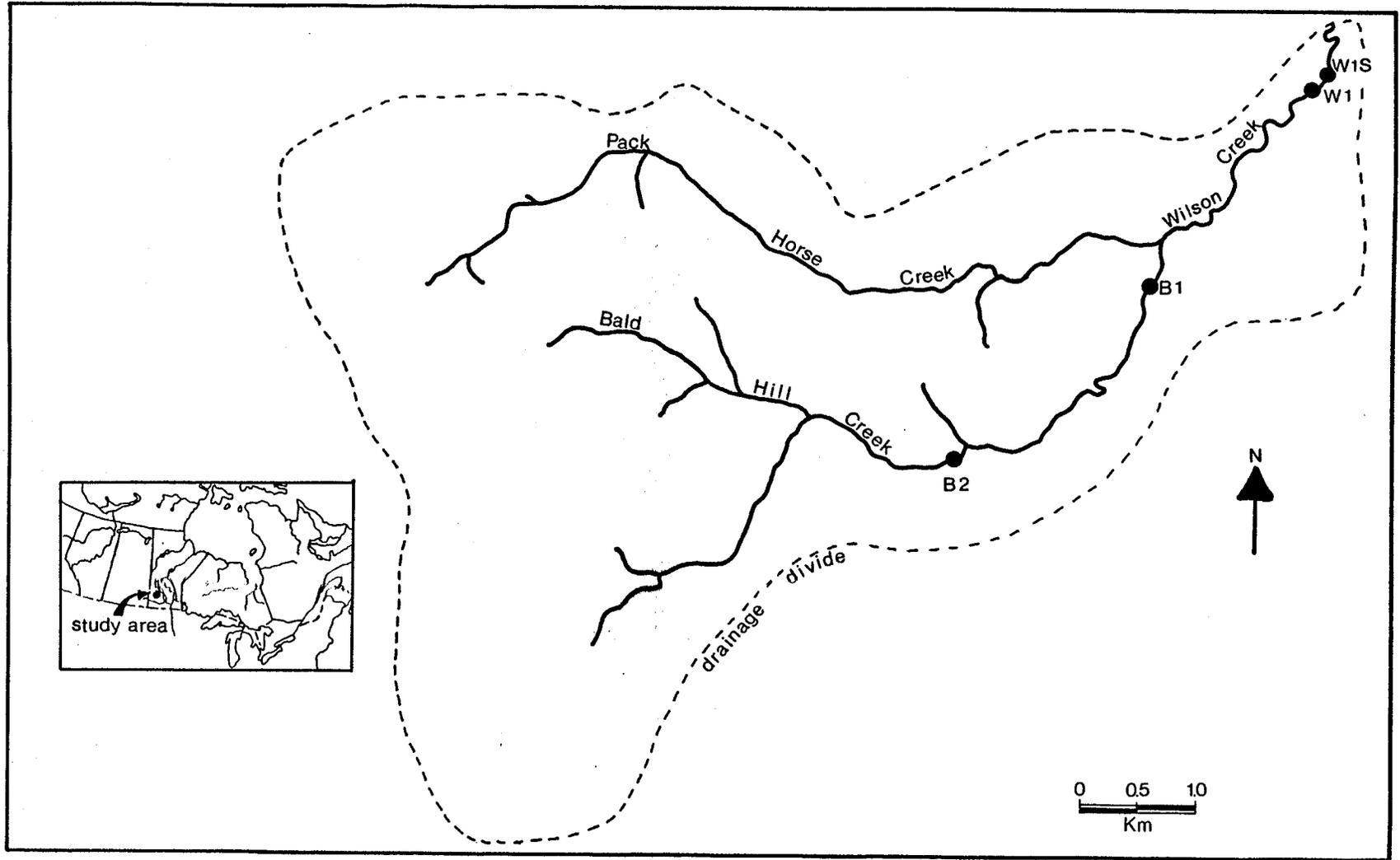
agricultural development. Any effects of substrate instability on aquatic insects will not be confounded by other factors associated with agricultural areas.

Three stations were established in natural reaches of the stream (Fig. 1). Station W1 located near the park boundary, 100 m upstream from the gauging station, was situated in the least stable reach. The bed paving material was composed of shale, deposited from upper eroding reaches. Station B1, was 3 km upstream from station W1, in a reach of higher gradient, and slightly larger substrate, composed of cobble to small boulders overlaying gravel. This is a transport zone, in which shale material is transported during moderate floods, and larger material moves during peak flows. This reach of stream is approximately 50% stable at bankfull discharge. Station B2, was 3 km upstream of station B1, and upstream of the junction of Conway Creek and Bald Hill Creek. This station was in the most stable reach, characterized by a boulder-dominated channel. At peak discharge, substrate at B2 was 80% stable.

Riparian vegetation was present at all stations, consisting primarily of alders. Surrounding vegetation was mixed forest predominantly spruce, aspen, and birch. Ground water input was present throughout the stream, resulting in a uniform thermal and chemical gradient along the length of the study area. Macrophyte growth on the rocks was rare, but there was a dense coating of marl (calcium carbonate) during low discharge periods. During floods, the marl was either scoured off or dissolved.

Within the most unstable reach, a stable riffle (W1S) was constructed to examine the effects of stable riffles on the hydrology and aquatic fauna of this reach. Details of its construction are presented in chapter 5 of this thesis.

3.3.2 Hydrology

Various hydrological parameters were measured in order to choose the sample reaches which would cover a range of substrate stability at bankfull flow conditions. These measurements were also required to derive the relationships between substrate stability (as a % of bed material at incipient motion) and discharge for each reach. A brief description, the methods, and formulae follow, while for a more detailed explanation refer to Chow (1964) and Newbury (1984). The symbols in each of the formulae are explained in Appendix 1.

Discharge

Discharge was monitored continuously at the Wilson Creek weir, station no. 05LJ033 (Water Survey of Canada), and was suitable for the lower reach. However, discharge was required in all reaches in order to calculate tractive force and thus the % of bed material at incipient motion for a given discharge. Discharge was measured for the upper reaches at several sample times, while peak discharge was estimated from the relationship between drainage area and discharge where the ratio of drainage area between two reaches approximates the ratio of bankfull discharge for those reaches (Newbury 1984). This ratio was applied to

most recent peak discharge at the weir prior to the sample period in question.

Mean depth of flow (present)

Mean depth of flow for each reach was determined by measuring a cross-section of the flow using a surveyor's measuring tape stretched across the stream at right angles to the direction of flow (Fig. 2). Depth was measured with a meter stick every 0.5 m. Three transects were run at each reach to get an average depth for the reach. Mean depth of flow for each sample reach was measured over a range of discharges in order to derive a relationship between depth of flow and discharge.

Mean depth of flow (bankfull)

Since bankfull discharge, or that discharge which fills the stream channel, is rarely observed, it was necessary to estimate the depth of flow at bankfull discharge (Fig.2). This was done by close examination of the banks of the stream channel. Texture of the flood plain (above bankfull) are finer than the banks of the channel itself; vegetation often shows signs of scouring at the height of bankfull flow. Once chosen, several transects were run, depths measured, and average bankfull depth of flow across the channel estimated.

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FIGURE 3-2. Cross-sectional view of stream channel with parameters measured in hydrological analyses in 1986-1988 Wilson Creek aquatic insect study.

flood plain | channel | flood plain

bankfull depth

present flow

bankfull width
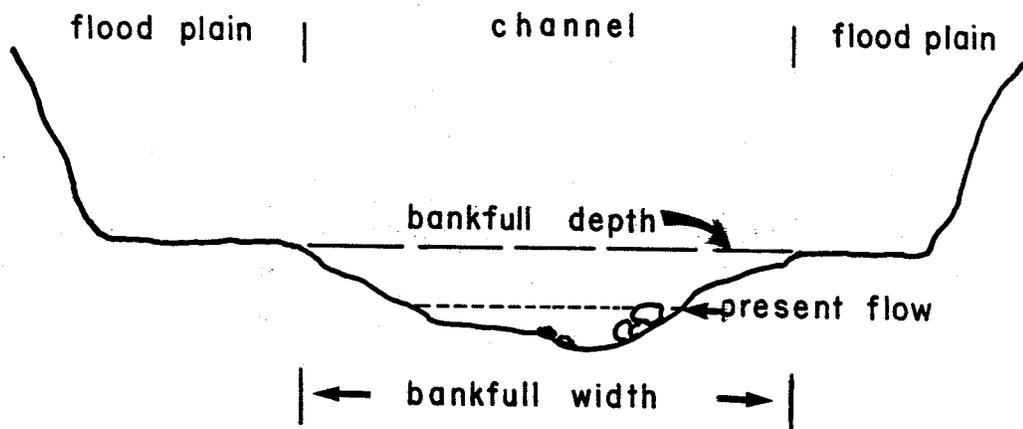
Slope

Average slope of each reach was measured using a surveyor's level and elevation rod. Average slope was calculated as the change in elevation (rise/run) over approximately 60 m of stream reach. Substrate particle size

Stream bed paving materials were characterized for each reach by walking through the reach and at every three steps randomly selecting bed paving material. This was done for 96 stones. Each stone was measured on three axes: length, width, height. Mean particle size ($\emptyset_{50}$) was then calculated ($\emptyset_{50}$ = L(cm)+W(cm)+H(cm)/3). Mean particle size was then ranked and arranged in a cumulative frequency curve for each station (e.g. Fig.3).

Bed paving material at incipient motion

The energy (tractive force) required to move a rounded particle is approximately equal to the median diameter of the particle (Lane 1955). Tractive force (tau) is calculated as:

τ (kg/m^2) = depth * slope of reach * 1000 (specific wt. of water). Approximately one half the tractive force is required to move an equal mean diameter of shale due to the flat shape and density of this material (Magalhaes and Chau 1983). For a given depth of flow, the per cent of substrate at incipient motion can be calculated from the cumulative frequency plot of substrates.

FIGURE 3-3. Cumulative frequency curve of stream bed paving materials in stations of 1986-1988, Wilson Creek. Station W1 ◊ ,W1S △ ,B1 + , B2 ■ .
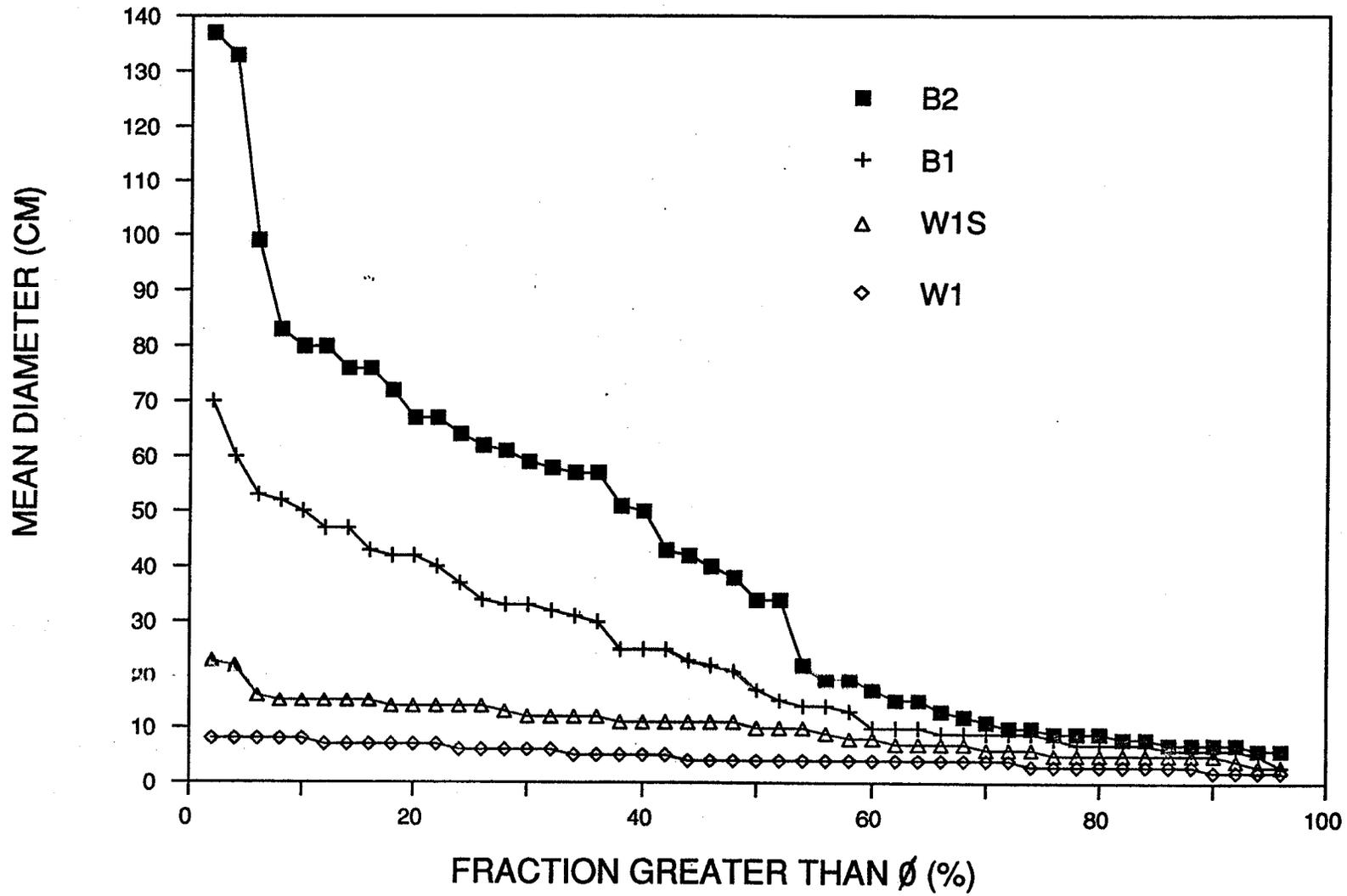
Temperature

Temperature was measured continuously at station W1 from April to
October in 1986 and 1987 using a Ryan submersible thermograph. In order
to compare station W1 with the other stations, temperature was measured
at each of the sample times at all stations, and these were then
comparedwith the thermograph.

Historical stream flow analysis

In order to characterize the hydrological habitat to which aquatic
insects are exposed, several methods were used to analyse the flow
regime. The first method was by direct examination of the hydrograph for
the years of record. By this method the average number of times
(periodicity) and seasonality that a flow occurred annually could be
calculated. A second method was to calculate the number of days or years
(frequency) in which a particular flow was equalled or exceeded (% flow
greater than) using a cumulative per cent frequency graph. Finally, the
predictability, contingency and constancy of flows were calculated for
this stream (Colwell's index of predictability) (Colwell 1974). Each of
the methods and calculations are presented in Appendix 2.

3.3.3. Invertebrate Sampling

Benthic sampling

Aquatic insects were collected using a modified Hess sampler
(Waters and Knapp 1961) with an area of 0.10 m^2, and a mesh size of 400
μm. Five samples were collected at each sample time. Samples were

stratified randomly, such that only riffle areas of each reach were selected, while within the riffle the Hess was placed over substrates which would fit within the area of the sampler. Large stream bed materials were removed, scrubbed and measured for average particle size, while the remaining stream bed material was stirred to a depth of approximately 10 cm. Sample water depth was measured at each sample time, while average velocity near each sample was measured in 1986.

Samples were collected monthly from May to October and following any precipitation-related spates in 1986 and 1987. Samples were also collected in late March (pre spring snow melt) and during or at the end of the spring peak discharge in 1987 and 1988. All samples were preserved in 4% formalin, and later transferred to 70% ethanol. Specimens were identified to order, and mayflies, stoneflies and caddisflies were identified to genus and species where possible.

Adult emergence

Adult insects were collected using a 1 m^3 emergence trap (Flannagan 1978), with a frame constructed of aluminium angle, covered by 400 um mesh on four sides (one with a v-shaped zipper for entrance), and with 3 mm thickness Plexiglass^R on the top to protect emerged insects. Two traps were set at each of stations W1 and B1 in 1986 and were sampled on Tuesday and Friday from mid-May through late September. Samples were collected using an aspirator, and preserved in 70% ethanol.

3.3.4. Statistical Analyses

Data from benthic samples were converted to mean number per square meter (10x). The variances were usually larger than the means, and there was a significant correlation ($r=.9912$, 9 df, $p<.001$) between the mean and variance; therefore to normalize the data and homogenize the variances the data were transformed logarithmically ($\log$ no./$m^2 + 1$) (Elliot 1973). This transformation removed the correlation between the means and variances ($r= .365$, 9 df, $p > 0.05$), and met the requirements of normalized distributions. Discharge data was normalized using the $\log_{10}$ transformation, while the per cent bed material at incipient motion was transformed using arc $\sin \sqrt{\text{prop. bed material}}$.

Relationships among hydrological parameters, substrate movement and trends of aquatic insect densities were examined using regression analysis, and significance tests of differences in trends between stations were performed using ANCOVA (SAS 1985). The hypotheses tested are summarized in Table 1, with the hypothesis rejection performed at the $\alpha = 0.05$ level of probability in all analyses. Hypotheses H1 tested the null hypotheses that increases in discharge had no effect on temporal ($H1_0$) and spatial ($H1_1$) patterns of substrate movement. Hypotheses H2 and H3 tested the effect of changes in discharge and substrate movement on aquatic insect densities, with the null hypothesis that changes in discharge or substrate movement had no effect on the density of aquatic insects. The effect of a 1986 June ($H4_0$) and September ($H4_1$) spate (1-day pre and 2-days post) on the density of benthic insects at each

Table 3-1. Description of hypotheses tested during Wilson Creek aquatic
insect study 1986-1988.

H1: Effect of discharge on substrate motion

    $H1_0$: (Temporal) Changes in discharge had no effect on substrate

        motion within each station.

    $H1_1$: (Spatial) Changes in discharge had equal effects on substrate

        motion between stations.

H2: Effect of discharge on aquatic insect density

    $H2_0$: (Temporal) Changes in discharge had no effect on aquatic

        insect density within each station.

    $H2_1$: (Spatial) Changes in discharge had equal effects on aquatic

        insect density between stations.

H3: Effect of substrate movement on aquatic insect density

    $H3_0$: (Temporal) Changes in substrate movement had no effect on

    aquatic insect density within each station.

    $H3_1$: (Spatial) Changes in substrate movement had equal effect on

    insect density between stations.

H4: Effect of summer spates on "artificial" stable riffle

    $H4_0$: $D_{W1}^1 = D_{W1S} = D_{B1}$ (June 23) $= D_{W1} = D_{W1S} = D_{B1}$ (June 26)

    $H4_1$: $D_{W1} = D_{W1S} = D_{B1}$ (Sept 25) $= DW_1 = D_{W1W} = D_{B1}$ (Sept 26) .

---

[1] D = density of aquatic insects at station indicated.

station was tested using a two-way ANOVA. The model used in this analysis was:

insect density $(no./m^2+1)$ = sample time + stn + time*stn + error,

which compared time effect, station effect and the interaction of station and time. When significant differences were detected, Least Squared Means were compared (SAS 1985). The null hypothesis tested (H4, Table 1), was that at each station there was no change in density of aquatic insects following a spate.

In order to compare spatial and temporal trends of community diversity, Simpson's index as modified by Pielou (1969) was used as an index of diversity:

$$I = 1 - \Sigma [n_i (n_i - 1)/ N (N - 1)],$$

where, I = diversity index,

                     n_i = number individuals of the ith species,

                     N = total number of individuals.

In this index, diversity increases with increasing value of I. Temporal trends of similarity in species lists were compared using Jaccard's coefficient of similarity (Hellawell 1978):

$$J = c / a + b - c,$$

where, J = coefficient of similarity,

                     a = number species in community A,

                     b = number species in community B,

                     c = number species in both communities.

In order to compare the similarity of species, and their relative contribution to the community between stations and at various times, Czekanowski's coefficient of similarity (Hellawell 1978) was calculated:

$$C = 2W / A + B,$$

where, C = similarity coefficient,

W = sum of the lesser measure of abundance of each species common to both communities,

A = sum of measures of abundance in community A,

B = sum of measures of abundance in community B.

A high value in both Jaccard's and Czekanowski's similarity indices is indicative of similar communities. In each analysis, data from before the spring flood (March), during the spring flood (April), before and after the June and September, 1986 spates were used.

3.4 RESULTS

3.4.1. HYDROLOGY AND PHYSICAL

A description and hydrological summary of each of the sample sites is presented in Table 2.

Discharge

There was a large spring snow storm-related peak discharge (7.7 m^3/s) in 1986 (Fig.4), followed by two summer and one fall rainfall-related peaks (25 June, 18 July, and 25 September). In 1987, there was an average spring peak flow (2.2 m^3/s), followed by an unusually dry summer and no rainfall-related spates. The spring discharge of 1988 was slightly lower in magnitude than an average spring peak discharge.

3.4.1.2. Relationships between hydrology and substrate stability

Station B2 had the largest mean average substrate, followed by station B1, W1S and W1 (Table 2). Tractive force at bankfull discharge was similarly ranked. The relationships between discharge and per cent bed paving material for each station were highly correlated (Table 3). When all stations were combined, There was a positive exponential relationship between discharge and per cent bed material at incipient motion when all stations were combined. Using ANCOVA (SAS 1985), station W1 was significantly different from all the other stations (p = 0.0006), while the remaining stations did not differ among themselves (p > 0.5) (Table 3).

Table 3-2. Description of hydrological characteristics of sample stations of Wilson Creek aquatic insect study 1986-1988.

	W1	W1S	B1	B2
Drainage Area (km^2):	22.1	22.1	11.1	8.6
Slope of reach (%):	1.0	2.5	2.7	3.6
Median bed material size (cm):	4.0	10.0	22.0	34.0
Bankfull conditions				
Width (m):	4.3	4.3	3.5	3.8
Depth (m):	0.35	0.30	0.30	0.31
Discharge (m^3/s):	2.7	2.7	1.6	1.6
Tractive force (kg/m^2):	3.5	7.5	8.4	10.8
Bed material at incipient motion (%):	80.0	20.0	50.0	20.0

FIGURE 3-4. Discharge (m^3/s), March to October 1986-1987, at
    Wilson Creek weir during aquatic insect study (Environment Canada
    1987-1989).
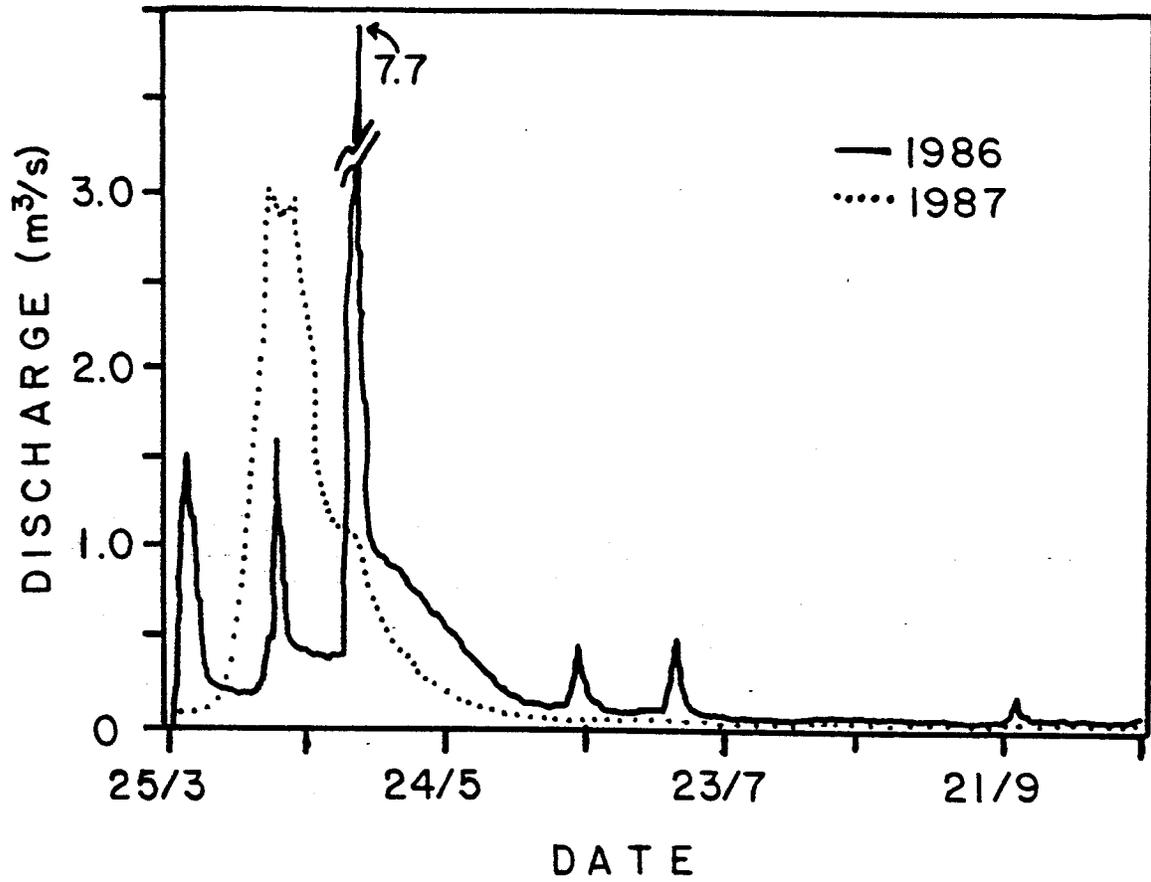
Table 3-3. Summary of regression analysis for hydrological and aquatic insect relationships from Wilson Creek 1986-1988. All analyses of insect orders performed on $\log_{10}$ (no/m^2 + 1) transformed data. Results presented as regression coefficient (r^2); F value (df model,error) which unless specified are the same for all analyses at each station. All relationships significant ($p < 0.05$) unless denoted by ns.

MODEL	REGRESSION COEFFICIENT				
	W1	W1S	B1	B2	ALL
1. $M = QX + Q_2^2X + E$	.9748;328(2,16)	.9488;138(2,14)	.9414;129(2,17)	.9336;70(2,12)	
$M = QX + Q^2X + STNX + QX*STNX + Q^2X*STNX + E$					.9600;182(8,61)
2. $EPHEM = QX + Q_2^2X + E$	.7438;23.22	.6991;16.2	.5440;10.1	.5136;5	.5734;46(2,68)
$EPHEM = QX + Q^2X + STNX + QX*STNX + Q^2X*STNX + E$					.674;11(11,60)
$EPHEM = MX + M_2^2X + E$	.8520;46.0	.7262;18.6	.6753;17.7	.8388;31.2	.7015;79.7(2,68)
$EPHEM = MX + M^2X + STNX + MX*STNX + M^2X*STNX + E$					.8133;23(11,60)
3. $PLEC = QX + Q_2^2X + E$	.8766;56.8	.7543;21.5	.7069;20.5	.7957;23.4	.7387;96(2,68)
$PLEC = QX + Q^2X + STNX + QX*STNX + Q^2X*STNX + E$					.8231;25(11,60)
$PLEC = MX + M_2^2X + E$	.8427;42.27	.5813;9.72	.5934;12.4	.6988;13.9	.6742;69(2,68)
$PLEC = MX + M^2X + STNX + MX*STNX + M^2X*STNX + E$					.7468;16(11,60)
4. $TRICH = QX + Q_2^2X + E$	.8597;49	.5639;9.1	.6116;13.4	.4763;5.5	.4708;30(2,68)
$TRICH = QX + Q^2X + STNX + QX*STNX + Q^2X*STNX + E$					.8120;23(11,59)
$TRICH = MX + M_2^2X + E$	.7718;27	.5954;10.3	.5197;9.2	.5079;6.19	.5485;41(2,68)
$TRICH = MX + M^2X + STNX + MX*SNTX + M^2X*STNX + E$					.7773;18(11,59)
5. $CHIR = QX + Q_2^2X + E$	.6579;15.4	.3451;3.7	.1757;1.8ns	.0039;.024ns	.2750;13(2,68)
$CHIR = QX + Q^2X + STNX + QX*STNX + Q^2X*STNX + E$					.4517;5(11,61)
$CHIR = MX + M_2^2X + E$	.7623;15.7	.5138;7.4	.2559;2.9ns	.2111;1.6ns	.3278;16(2,68)
$CHIR = MX + M^2X + STNX + MX*STNX + M^2X*STNX + E$					.5522;6(11,61)
6. $OTHERS = QX + Q_2^2X + E$	.6317;13.7	.3742;4.2	.3243;4.08	.2318;1.8ns	.3291;17(2,68)
$OTHERS = QX + Q^2X + STNX + QX*STNX + Q^2X*STNX + E$					.5246;6(11,60)
$OTHERS = MX + M_2^2X + E$	.6820;17.2	.4315;5.3	.3125;3.86	.2528;2.03ns	.4353;26(2,68)
$OTHERS = MX + M^2X + STNX + MX*STNX + M^2X*SNTX + E$					.5409;6(11,60)
7. $TOTAL = QX + Q_2^2X + E$	.8338;40.1	.7023;16.5	.7833;30.7	.6604;11.7	.6614;66(2,68)
$TOTAL = QX + Q^2X + STNX + QX*STNX + Q^2X*STNX + E$					.8142;23(11,59)
$TOTAL = MX + M_2^2X + E$	.8896;64.5	.7714;23.6	.7283;30.7	.6515;11.2	.7620;108(2,68)
$TOTAL = MX + M^2X + STNX + MX*STNX + M^2X*STNX + E$					.8393;28(11,59)

$Q = \log_{10}$ discharge (m^3/s)
M = arc sin$\sqrt{}$prop. subst. in motion

Analysis of historical flow data

A summary of the 1986 discharge data and comparison with historical flow data is presented in Table 4. The spring bankfull discharge moved a proportion of the bed paving material, with station W1 having the largest per cent moved (75%), and station B2 the least (20%). This magnitude of discharge was equalled or exceeded in 67% of the years, but only occurred for 0.8% of the days, and only once per season on average. Summer (June) and fall (September) spates of 1986 resulted in a portion of bed paving material at incipient motion at station W1, but not at the other stations. Historically the June spate occurred less frequently and with less duration, as compared to the September spate.

Predictability of flow regime

Using Colwell's index of predictability, Wilson Creek, had a predictability index of 0.42, a constancy index of 0.13, and a contingency index of 0.29. Adopting the criteria of Resh et al.(1988), where a predictability of .31 was considered highly unpredictable, Wilson Creek had a relatively unpredictable flow regime.

3.4.2. BENTHIC INSECTS

3.4.2.1. Species composition and seasonal trends of abundance

A total of 11 taxa of mayflies (Table 5), 10 taxa of stoneflies (Table 6), and 15 taxa of caddisflies (Table 7) was collected during the study. To allow comparisons of stations and season, the per cent composition by species for the May to October period was calculated.

Table 3-4. Comparison of 1986 mean daily discharge with historical flow data (1965-1985) for Wilson Creek, Manitoba. Annual flow > 1986 discharge calculated from annual peak discharge; periodicity is the average number of events per year from visual inspection of hydrograph. Spring is the maximum snow melt related discharge.

| | SPRING | | | | | JUNE | | | | | SEPTEMBER | | |
	W1	W1S	B1	B2		W1	W1S	B1	B2		W1	W1S	B1	B2
1986														
DISCHARGE (M^3/S)	2.7	2.7	1.6	1.6		.3341	.3341	.1671	.1671		.0623	.0623	.031	.031
% BED PAVING MATERIAL AT INCIPIENT MOTION	80	20	50	20		12	0	0	0		8	0	0	0
HISTORICAL														
% > DISCHARGE (ANNUAL)		67					27					80		
% > DISCHARGE (DAILY)		0.8					18					53		
PERIODICITY		1					3.7					5.6		
PREDICTABILITY		HIGH					LOW					MODERATE		

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Table 3-5. Species composition, and per cent of mean density Ephemeroptera (May to October) from monthly samples in 1986 and 1987 from Wilson Creek, Manitoba aquatic insect survey.

Species	W1		W1S		B1		B2	
	1986	1987	1986	1987	1986	1987	1986	1987
Siphlonuridae								
Siphlonurus sp.	0.0	0.0	0.0	0.01	0.0	0.0	0.0	0.0
Ameletus sp.	1.1	5.0	2.5	3.5	0.2	1.95	0.01	0.15
Baetidae								
Baetis flavistriga McDunnough	1.8	3.3	1.1	0.05	1.0	0.5	3.2	12.9
B. tricaudatus Dodds	11.0	3.2	13.5	16.6	58.4	36.5	94.8	54.8
Pseudocloeon turbidum McD.	16.0	51.9	33.8	47.2	26.5	39.5	0.5	7.0
Centroptilum infrequens McD.	0.0	0.03	0.0	0.0	0.0	0.0	0.0	0.0
Heptageniidae								
Nixe (Akkarion) simplicioides (McD.)	10.9	10.3	21.4	11.3	6.35	10.1	0.5	1.31
Leptophlebiidae								
Leptophlebia cupida (Say)	1.8	20.4	1.5	14.5	0.2	0.0	0.0	0.0
Paraleptophlebia debilis (Walker)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Ephemerellidae								
Ephemerella cf. inermis Eaton	60.0	4.4	26.2	6.5	7.4	11.3	0.5	22.4
Tricorythidae								
Brachycercus sp.	0.0	0.0	0.0	0.03	0.0	0.0	0.0	0.0
Mean Density (no./m^2)	317.3	1019.9	515.2	636.6	878.8	985.0	4122.7	2062.0

Table 3-6. Species composition, and per cent of mean density Plecoptera (May to October) from monthly samples in 1986 and 1987 from Wilson Creek, Manitoba aquatic insect survey.

Species	W1 1986	W1 1987	W1S 1986	W1S 1987	B1 1986	B1 1987	B2 1986	B2 1987
Nemouridae								
Malenka californica (Claassen)	0.4	0.7	2.7	1.6	3.2	17.3	4.4	17.2
Zapada cinctipes (Banks)	4.7	21.7	16.9	37.5	36.2	28.0	55.17	65.4
Taeniopterygidae								
Taeniopteryx nivalis (Fitch)	0.0	0.1	0.1	1.0	0.0	0.0	0.0	0.0
Capniidae	81.4	66.0	64.9	52.6	50.0	40.5	32.8	1.5
Capnia coloradensis Claassen			collected as adults only					
C. gracilaria Claassen			collected as adults only					
Utacapnia trava (Nebeker and Gaufin)			collected as adults only					
Pteronarcyidae								
Pteronarcys dorsata (Say)	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0
Perlodidae								
Isoperla bilineata (Say)	6.0	2.7	2.9	1.9	5.2	4.3	6.9	14.7
Skwala parallela (Frison)	1.2	0.9	2.8	1.7	0.5	0.1	0.1	0.0
Chloroperlidae								
Haploperla brevis (Banks)	6.2	7.5	9.6	3.6	4.8	9.8	0.6	1.1
Mean Density (no./m^2)	1191.2	2451.3	1346.0	3532.0	1611.5	2000.0	1133.4	974.0

Table 3-7. Species composition, and per cent of mean density Trichoptera (May to October) from monthly samples in 1986 and 1987 from Wilson Creek, Manitoba aquatic insect survey.

Species	W1 1986	W1 1987	W1S 1986	W1S 1987	B1 1986	B1 1987	B2 1986	B2 1987
Polycentropodidae								
Polycentropus pentus Ross	0.0	2.5	0.1	3.2	0.02	0.5	0.0	0.5
Hydropsychidae								
Cheumatopsyche oxa Ross	3.2	8.5	0.7	19.0	1.2	3.0	3.2	6.8
Hydropsyche alhedra Ross	4.4	1.7	12.0	2.1	4.3	4.1	8.8	12.2
H. slossonae Banks	9.5	24.5	13.0	27.5	4.4	6.8	16.5	42.2
Rhyacophilidae								
Rhyacophila angelita Banks	0.0	0.0	0.4	0.0	0.6	0.5	1.3	0.5
Glossosomatidae								
Glossosoma intermedium (Klapálek)	0.8	6.9	1.6	2.8	40.3	58.8	56.4	17.9
Hydroptilidae (combined)	0.0	1.7	0.0	0.5	0.02	0.12	0.18	0.1
Hydroptila sp.								
Ochrotrichia sp.								
Oxytheira sp.								
Phryganeidae								
Ptilostomis ocillifera (Walker)	0.8	1.7	0.0	0.2	0.08	0.0	0.0	0.0
Brachycentridae								
Brachycentrus occidentalis Banks	11.8	0.4	7.9	8.3	1.98	12.3	2.1	0.01
Limnephilidae								
Hesperophylax incisus Banks	5.5	0.0	6.7	2.1	1.3	0.6	1.9	0.9
Limnephilus sp.	0.0	0.0	0.0	0.1	0.03	0.0	0.11	0.0
Lepidostomatidae								
Lepidostoma pluviale (Milne)	64.0	52.2	58.0	34.0	45.8	13.3	9.4	18.6
Leptoceridae								
Oecetis avara (Banks)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mean Density (no./m^2)	153.0	591.6	347.4	467.8	1044.9	1420.4	679.4	2558.0

Within the Ephemeroptera, station W1 and W1S were numerically dominated by _Pseudocloeon turbidum_ McD.(46 and 40% respectively), followed by _Ephemerella_ cf. _inermis_ Eaton (26 and 20.5% respectively). The dominant mayfly species at station B1 were _Baetis tricaudatus_ Dodds (49%) and _P. turbidum_ (29%) while the dominant species at station B2 was _B. tricaudatus_ (85%). Within the Trichoptera, stations W1 and W1S were numerically dominated by _Lepidostoma pluviale_ Milne (74 and 51% respectively) and _Hydropsyche slossonae_ Banks (15 and 19% respectively), station B1 was dominated by _Glossosoma intermedium_ Klapálek (49.9%) and _L. pluviale_ (31%), and station B2 was dominated by _G. intermedium_ (36%) and _H. slossonae_ (29.4%). The Plecoptera were dominated by species of the family Capniidae (three species combined due to difficulty in distinction among immature stages) at stations W1, W1S and B1, followed by _Zapada cinctipes_ (Banks). At station B2, the reverse order of dominance occurred.

At station W1, all orders of insects had greater densities in 1987 than 1986. Station W1S had generally comparable average densities for both years in the mayflies and caddisflies, while due to a larger abundance of winter stoneflies had larger numbers in 1987 than 1986. Station B1 had similar densities for both years, while station B2 had higher densities of mayflies in 1986 than 1987, and higher densities of caddisflies in 1987 than in 1986 (Tables 5 to 7).

All stations had relatively low densities during spring (May 1986, April 1987, 1988), had higher densities by the following sample periods, and with the exception of station W1 in 1986, had consistently high

FIGURE 3-5. Seasonal trends of abundance of (A) Ephemeroptera, (B) Plecoptera, (C) Trichoptera at stations B2, B1, W1S, and W1 on Wilson Creek, 1986-1988.
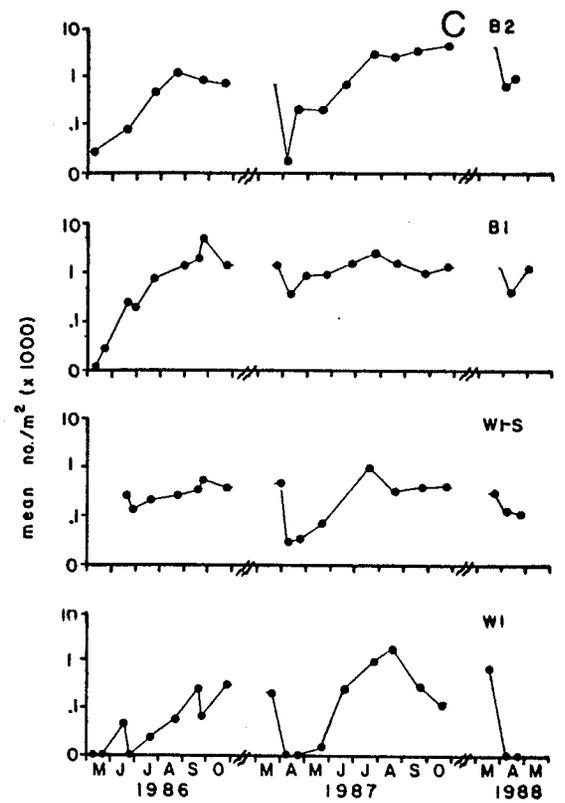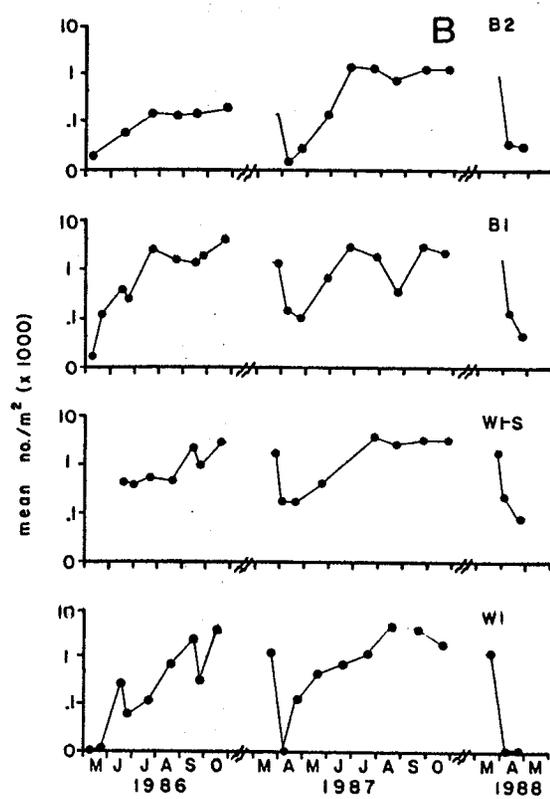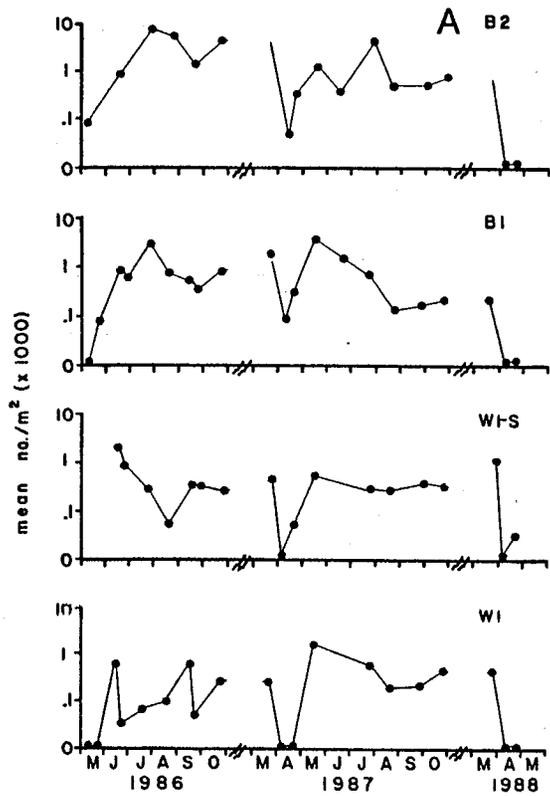
FIGURE 3-6. Seasonal trends of abundance of (A) Chironomidae, (B)
     Others, (C) Total invertebrates at stations B2, B1, W1S, and W1 on
     Wilson Creek, 1986-1988. Black flies separated from others(.....).
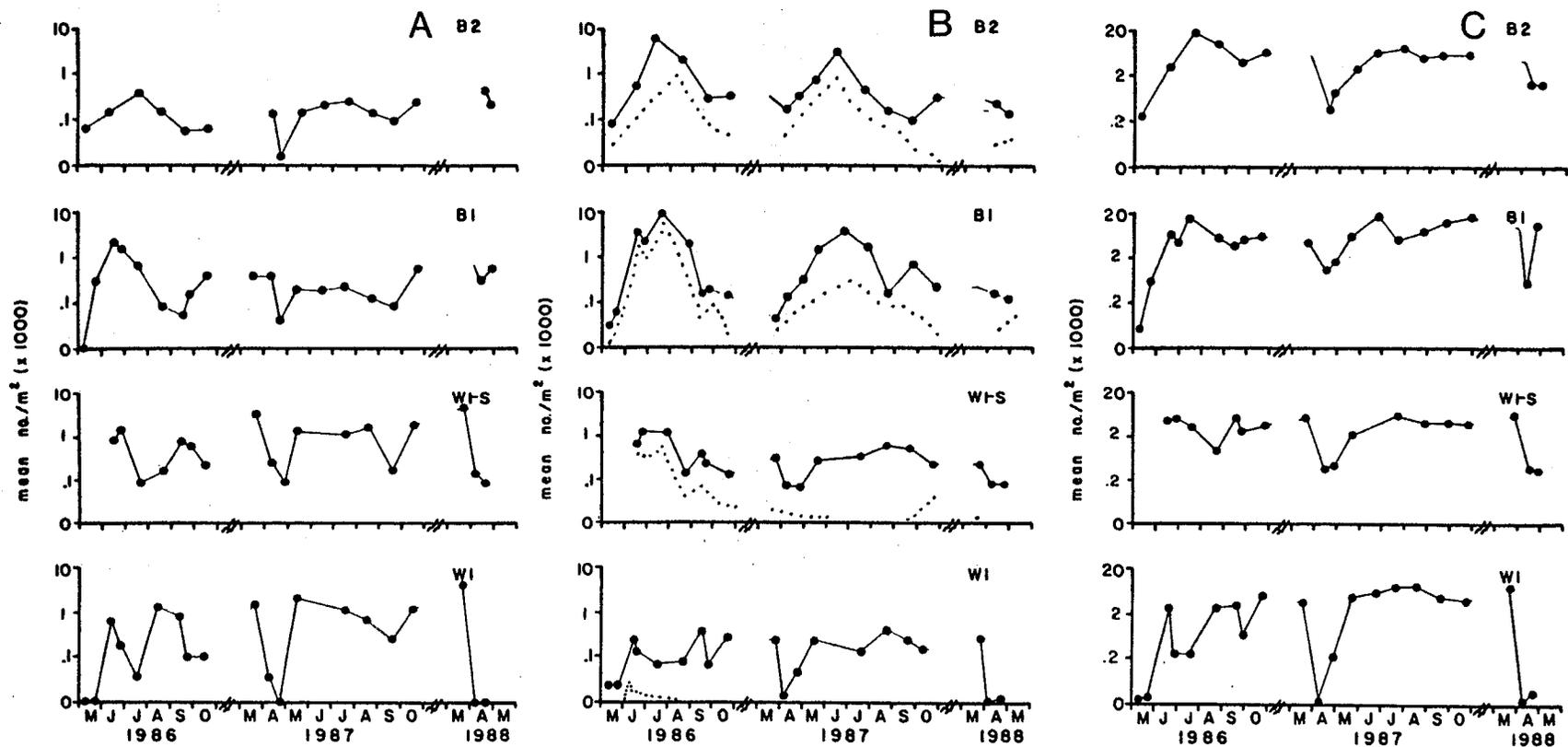
densities throughout the season (Fig. 5 and 6). There were several reductions in benthic densities at station W1 (June, July, and September) during the 1986 sampling period, while this trend was not evident in 1987.

Relationships between hydrological parameters and aquatic insects

Aquatic insect densities at each station, with the exception of chironomids and others (black flies, beetles, flatworms and annelids) at station B1 and B2, were significantly negatively correlated (p < 0.05) with the most recent peak discharge and the per cent of substrate in motion related to that discharge (Table 3). When data for all the stations were combined, the relationship between aquatic insect density and per cent of substrate in motion accounted for as much as 77% (e.g. Ephemeroptera) of the variability, while the relationship between aquatic insect density and most recent peak discharge accounted for only 44% (e.g. Ephemeroptera) of the variability, a significant station effect (Table 3). When station effect was included in the model, the regression coefficient was greatly improved for the relationship between aquatic insect densities and most recent peak discharge, e.g. Ephemeroptera (r^2 = .70) while including station effect into the model only slightly improved the regression for the relationship between aquatic insect densities and the per cent of substrate in motion (r^2 = .81). The only case where combined data for discharge accounted for more of the variability than substrate movement when station effect was ignored was for the Plecoptera.

Table 3-8. Summary of comparisons (ANCOVA) of relationships between discharge and substrate movement vs. aquatic insect densities at sample stations on Wilson Creek, 1986-1988.

		DISCHARGE				SUBSTRATE MOVEMENT			
		W1	W1S	B1	B2	W1	W1S	B1	B2
Ephemeroptera	W1								
	W1S	NS				NS			
	B1	*	NS			NS	NS		
	B2	***	*	NS		***	**	**	
Plecoptera	W1								
	W1S	**				NS			
	B1	NS	NS			NS	NS		
	B2	NS	**	*		NS	*	NS	
Trichoptera	W1								
	W1S	***				**			
	B1	***	**			***	*		
	B2	***	*	NS		**	NS	NS	
Others	W1								
	W1S	**				*			
	B1	***	NS			**	NS		
	B2	***	NS	NS		*	NS	NS	
Chironomidae	W1								
	W1S	*				NS			
	B1	NS	NS			NS	NS		
	B2	NS	*	NS		NS	*	NS	
Total	W1								
	W1S	**				NS			
	B1	***	NS			*	NS		
	B2	***	NS	NS		NS	NS	NS	

NS $p > 0.05$
* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
Others = Black flies, annelids, beetles, flatworms

When the relationships between hydrological parameters and aquatic insect densities were compared among stations, the model describing the relationships between discharge and benthic densities at station W1 differed from the other station most often (Table 8). The only consistently occurring differences between stations with respect to substrate movement and benthic densities occurred in the Trichoptera and Others groups, with station W1 differing significantly from the remaining stations.

Effect of spates on aquatic insect densities

When densities of aquatic insects one day pre and 2 days post spate in June, 1986 were compared, all groups at station W1, the unstable reach, had highly significant reductions in densities ($p < 0.001$), with the exception of the Others group (Table 9). The Ephemeroptera had the largest reduction (94%). Stations W1S and B1 had reductions in densities ranging from 8.4% to as high as 49%, however only reductions in the Ephemeroptera at station B1 were statistically significant. In September, a similar pattern was evident. All groups declined significantly at station W1, while at the other stations only the Ephemeroptera at B1 were reduced significantly (51%).

Community structure analyses

Species diversity at stations W1S and B1 (Fig. 7), as indicated by the Simpson's diversity index, was relatively constant over the periods examined, diversity associated with the spring and fall flood was reduced

Table 3-9. Effects of 23 June and 25 September, 1986 spates on aquatic insect densities in Wilson Creek, Manitoba. Aquatic insect densities (no./m^2 +/- standard error) transformed using $\log_{10}$ (no./m^2 + 1) for two-way ANOVA. When ANOVA were significant, means were compared using least squared means.

Group	Stn	Density 23 June (pre)	Density 25 June (post)	% Change	Density 24 Sept. (pre)	Density 26 Sept. (post)	%Change
Ephemeroptera	W1	816.0 (155.6)	46.0 (10.8)	-94.4 ***	800.0 (195)	74.0 (12.5)	-90.8 ***
	W1S	1244.0 (87.3)	998.0 (159.1)	-19.8 ns	390.0 (88.7)	420.0 (151.3)	+ 7.7 ns
	B1	1054.0 (183.3)	596.0 (78.0)	-43.4 *	532.0 (71.7)	260.0 (54.4)	-51.1 *
Plecoptera	W1	378.0 (79.8)	76.0 (16.9)	-80.0 ***	2390.0 (331.3)	606.0 (92.0)	-74.6 ***
	W1S	548.0 (108.8)	502.0 (128.2)	- 8.4 ns	2690.0 (435.5)	1516.7 (1006)	-43.6 ns
	B1	528.0 (135.3)	310.0 (61.0)	-41.2 ns	1174.0 (202.8)	1700.0 (28.3)	+44.8 ns
Trichoptera	W1	51.9 (9.16)	3.99 (2.45)	-92.5 ***	342.0 (61.5)	70.0 (12.5)	-79.5 ***
	W1S	243.9 (33.5)	209.8 (52.7)	-14.0 ns	384.0 (103)	786.7 (236.8)	+105 *
	B1	105.9 (26.6)	86.0 (14.3)	-18.8 ns	1290.0 (154.3)	2622.0 (800.1)	+103 ns
Chironomidae	W1	932.0 (228.4)	236.0 (74.1)	-74.7 ***	1030.0 (290.6)	110.0 (28.8)	-89.3 ***
	W1S	852.0 (233.8)	1092.0 (220)	+28.2 ns	1060.0 (331.4)	520.0 (120.1)	-49.0 ns
	B1	3050 (326.2)	1542 (227.3)	-49.0 ns	34.0 (6.78)	192.0 (37.6)	+464 ***
Others	W1	236 (51.8)	186 (55)	-21.2 ns	462.0 (110.2)	82.0 (22.7)	-82.5 **
	W1S	862 (176)	1428 (629)	+65.7 ns	568.0 (170)	266.7 (46.7)	-53.0 ns
	B1	5402 (1472)	3252 (1551)	-39.8 ns	154.0 (15.0)	172.0 (28.5)	+11.7 ns
Total	W1	2434 (248)	554 (66.1)	-77.2 ***	5020.0 (698.7)	942.0 (81.1)	-81.2 ***
	W1S	3860 (357)	4362 (630)	+13.0 ns	5092.0 (895.0)	3510.0 (1120)	-31.0 ns
	B1	10178 (1676)	5838 (1848)	-42.0 ns	3184.0 (318.4)	4946.0 (1039)	+55.0 ns

ns = p > 0.05
* = p < 0.05
** = p < 0.01
*** = p < 0.001
Others = Black flies, flatworms, annelids, beetles

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FIGURE 3-7. Seasonal trends of index of diversity (Simpson's), index of
     similarity (Jaccard and Czekanowski) prior to and following spates
     at each station on Wilson Creek in 1986-1987.   Symbols: Simpson's
     index W1●, W1S■, B1○. Symbols for similarity indices: W1-W1S●,
     W1-B1 ■ , W1S-B1 ○ .
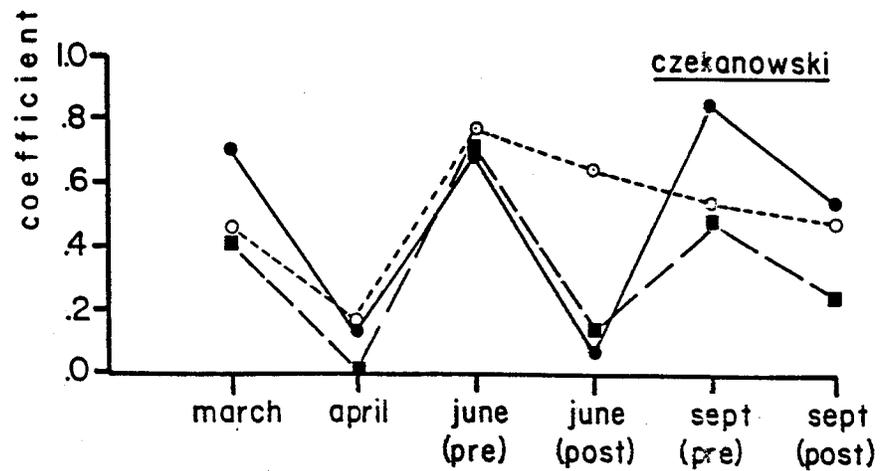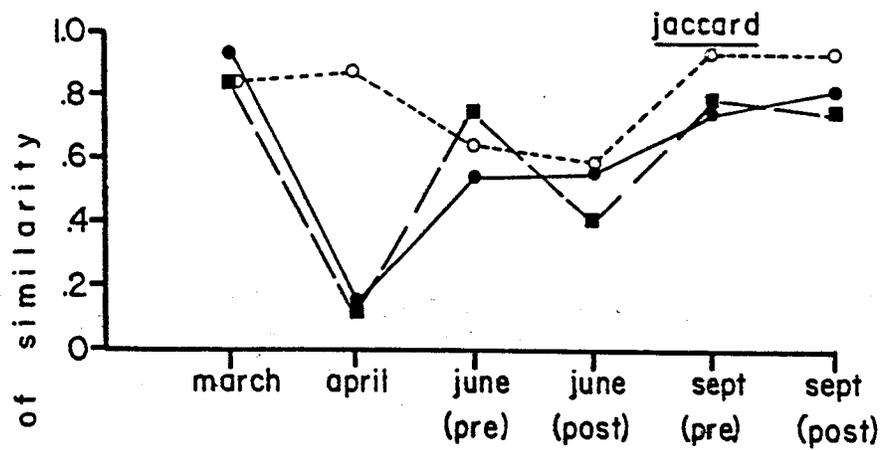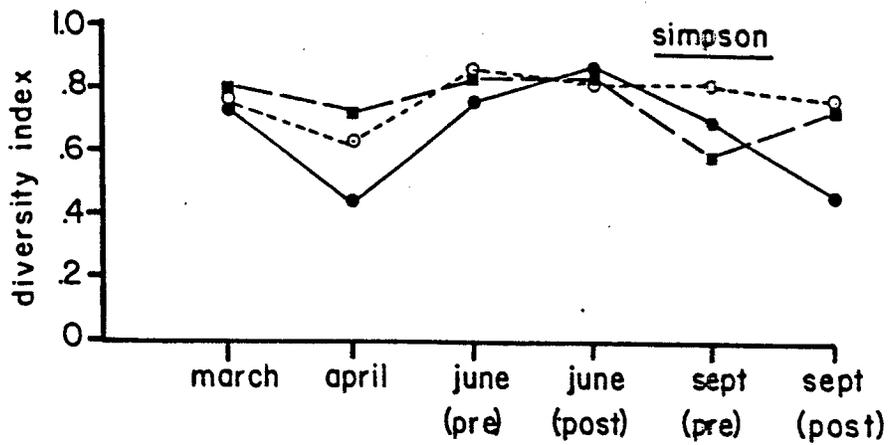
at station W1. Reduced diversity was not the case for the June spate at station W1.

Using Jaccard's coefficient of similarity, in which species associations are examined, stations W1S and B1 were more similar during the spring flood than the other combinations of stations, while the index was insensitive to differences resulting from the June and September spates. The Czekanowski coefficient of similarity, takes into account species similarity as well as relative contribution to the communities. All stations had similar indices prior to spates, whereas during the spring spate there was a high degree of dissimilarity between all stations. During the June spate, only stations W1S and B1 maintained their similarity, while during the September spate there was a high degree of dissimilarity only at station W1 and B1.

3.5. DISCUSSION

In the present study, aquatic insect density could be modelled at each station using both most recent peak in discharge and its related % of substrate at incipient motion for that reach. In addition, insect densities were highly correlated to overall stream substrate stability. Equal discharge had varying effects on aquatic insects associated with substrates of different stability within the same reach, as shown with the pilot study with the artificial riffle, and the effects of two summer spates. The spates had relatively little effect on the insects at station B1 and the artificial stable riffle, as compared to dramatic reductions of insects at the natural unstable reach. These effects (as high as 90% reduction) were somewhat surprising as only 8% (September) and 12% (June) of the bed paving material was at incipient motion. Thus temporal and spatial effects of substrate stability/discharge relationships were demonstrated in this study.

3.5.1. Substrate/discharge relationships

Examining the hypothesis tested during this study (Table 1), in the first hypothesis, that of effect of discharge on substrate motion, both null hypotheses were rejected. It was concluded that there was not enough evidence to accept the hypothesis that changes in discharge had no effect on substrate motion, nor was there enough evidence to accept the hypothesis that these changes were equal among stations. Station W1 was significantly different from the other stations, being most sensitive to changes in discharge. This was, of course related to the shale

substrate, the dominant paving material of this reach, which is moved more readily than rounded particles (Magalhaes and Chau 1983).

3.5.2. Discharge/aquatic insect density relationships

Reductions in aquatic insects are associated with large increases in discharge (see review by Hynes 1970, also Gray and Fisher 1981, Fisher et al. 1982, Sagar 1986). Even minor spates can cause minor reductions in densities of insects in some rivers (Sagar 1986), through increased drift from dislodged immature insects (Anderson and Lehmkuhl 1968), scouring by substrate movement (Sagar 1986), or by saltation (Culp et al. 1985). However, there have been floods in which no effect on density of insects was reported (Cowie 1980, Giberson and Hall 1988), or at best there were spatially varied effects reported with some stream reaches experiencing reductions, while other reaches showed no reductions in densities (Allen 1959).

In the second hypothesis, that of the effects of discharge on aquatic insects, there was a strong station effect, thus a single spate had a spatial effect on aquatic insects within the stream as a whole, as reported by Allen (1959). A relatively small amount of the total variation in the model could be explained by discharge alone, while a much larger portion of variation is explained when the effect of station is included in the model. From these data, it was apparent that some factor(s) was an important determinant of the insect community of Wilson Creek.

3.5.3. Substrate movement and aquatic insect densities

A significant station effect in the relationship between discharge and insect densities is important from a stream ecology view point. Discharge and predictability of flow regimes are used as indicators of disturbance in recent theories on the effects of disturbance on aquatic insects (e.g. Resh et al. 1988). The recognition of the importance of discharge and disturbance is a critical step in the development of this recently emerging topic of lotic insect ecology, but I feel there is an component lacking. Allen (1959) subjectively decided that more stable reaches of a stream were not impacted by a spate, while less stable reaches experienced detectable reductions. Although subjective, these findings were indicative of the importance of spatial effects of substrate stability on aquatic insect density.

In the third hypothesis, station effect was ignored, and little change in the amount of variation could be accounted for by substrate movement when compared to the model which included station effect. By modelling the effects of the movement of substrate as a whole, one could predict the effects upon the insect community within the whole stream.

The only instances where major differences between stations could be consistently found, were in the Trichoptera and others groups. Within the Trichoptera, G.intermedium was dominant at stations B1 and B2, while rare at the other two stations. This species was the most resistant to spring spates at the two stations where it was present. It has a behavioural adaptation which may be advantageous for surviving the spring floods. In late fall, this species aggregates on the lower, and

rear face of substrates (author's observation). The prime purpose of this behaviour is unknown, but may be to avoid spates. During spring floods, individuals of this species which are attached to larger substrates than the tractive force of an average spring peak flood can move (B1-50%, B2-80%) are protected from scouring. Because over 80% of the stream bed paving materials in the unstable reach (W1) are moving during spring floods, this behavioural adaptation would not be suitable for this habitat. It was surprising to find that in the two years of the study, this caddisfly species did not eventually colonize the artificial riffle, with only a few individuals present at any sample time. It is probable that G. intermedium is not a vagrant species, as are some of the other species (e.g. Baetis spp., E. inermis) in this stream. Anderson (1967) and Flannagan (personal communication) reported that G. intermedium made up, at best, only a minor component of drift in streams where this species is a major component of the caddisfly fauna. Further studies into the behaviour of this species should be undertaken to investigate the possible function of aggregation. In a larval transplant experiment, where larvae from the upper reaches would be moved into a stable riffle, the question as to whether this species could survive in a stable riffle in the lower reaches of this watershed could be answered. I feel that aggregation, and low dispersal are two characteristics of G. intermedium which make this species a good indicator of substrate stability.

Within the others group, the Simuliidae, made up 90% of the total at both stations B1 and B2, while making up less than 5% of the others at

stations W1 and W1S (Fig. 6). Larvae and pupae of black flies attach to substrates, and similar to the situation with G. intermedium this behavioral adaptation makes it possible to resist high flows, provided the substrates are stable. Giberson and Hall (1988) found that during spring peak flows, densities of black fly larvae attached to large stable substrates, were not affected. Waters (1962) reported no change in drift of black fly larvae during a small freshet in a stream, but noted an increase when children played in the stream and scoured the substrates. Because of their absence from station W1 and W1S, the regression curves of abundance and substrate movement for these stations differed from stations B1 and B2.

3.5.4. The effects of summer spates on aquatic insect densities

In the least stable reach of Wilson Creek (W1), two spates resulted in significant reductions (77% June and 94% September) ($p < 0.001$) in total number of insects (Table 9). In the stable riffle, subjected to equal discharge, no significant decrease in numbers occurred, while there were reductions ($p < 0.05$) only in the Ephemeroptera at station B1. A change of greater than 50% was required to be statistically detectable as a reduction, due to the small number of samples and large variability among samples. By increasing sampling effort, more subtle changes may be detectable, as it is likely that during minor spates, some free living insects were swept away by the increased shear stress acting upon them.

In experiments designed to test the effect of varying substrate stability on aquatic insect communities, Malmqvist and Otto (1987) found that some species preferred more stable artificial substrates, while others dominated on less stable ones. Robinson and Minshall (1986) reported that bricks which were disturbed more frequently had lower diversity and density of species. Reductions in densities of aquatic insects as high as 90% (Reice 1985) and 84% (Doeg and Lake 1989) occurred on experimentally disturbed patches of substrates.

The importance of substrate movement as opposed to discharge as a measure of disturbance (Resh et al. 1988) to aquatic insects was evident from the summer spates in my study. The construction of larger, and replicated riffles in future studies would allow increased sampling effort without fear of over-sampling the riffle, and thus allow more rigorous statistical tests.

3.5.5. Community structure

Some of the characteristics of stream insect communities controlled by biotic factors include low species turnover and constancy of species richness despite possible perturbation, i.e. resistance. Alternately, communities controlled by stochastic factors have high species turnover, or low resistance to perturbation, and rapid recolonization, to pre-disturbance levels, or high resilience (Lake and Doeg 1985). Aquatic insects in many unstable rivers were characterized as stochastic communities following disturbances sufficient to cause substrate movement (Gray and Fisher 1981, Reice 1985, Sagar 1986, Doeg et al. 1989). In all

studies where substrates were disturbed, whether by experimentation, or in natural streams, both abundance and species richness declined. However, the former was of greater magnitude than the latter. Each stream recovered to pre-disturbance levels from within several to several tens of days presumably from downstream colonization through drift, oviposition by adults, or life history adaptations (Scrimgeour et al. 1988).

In Wilson Creek, all stations, although the magnitude of reduction varied, were characterized by reduced numbers (low resistance) during flows great enough to move at least 8% of the bed paving substrates. The insect community was resilient in that the abundance and diversity rebounded at all stations during extended periods of low flow. Species diversity was unchanged at the more stable reaches, whereas at the unstable reaches, diversity was reduced during spates.

Most of the mayfly, stonefly, and caddisfly fauna of station W1 of Wilson Creek, are considered low in resistance, and high in resiliency. Life history adaptations for the majority of species at station W1 were favourable for survival in an environment where substrates are disturbed in a predictable fashion in spring and fall, while not so predictably during the summer (Chapter 4). For the remaining species, which are univoltine with slow seasonal development, behavioural adaptations may account for their presence in this reach of stream, although further studies would be required to elucidate these adaptations for each species.

At the more stable reaches (B1 and B2), the abundance of several species following spates (e.g. _Glossosoma_ _intermedium_) may indicate that the fauna was resistent. These species were rare at station W1, so it would appear that they had low resistance and resilience, i.e. not able to rapidly recolonize following scouring discharges. This presents an ecological dilemma, for depending upon the stability of substrates, and intensity of flood, a species may or may not be considered resistant. The term of resistance and resiliency should be used carefully, and in the context of substrate stability/discharge relationships.

One of the ongoing debates within the field of aquatic ecology is to what extent species interactions occur both in the presence and absence of disturbance. Most of the deterministic theories were derived from experiments conducted under ideal flow conditions in the field or laboratory. Peckarsky (1983) reported that during stable periods of flow, competition and predation were functioning, but she also reported that during spates, all interactions were disrupted. Similarly, Hemphill and Cooper (1983) reported competitive interactions between two filter feeding insects, a species of _Hydropsyche_ and a species of black fly. During periods of low flow, the caddisfly out-competed the black fly for position in the flow net. However, these interactions were affected by disturbance, such that following floods, black flies recolonized the substrates more quickly, and persisted in the stream. These two taxa were present at stations B1 and B2 of Wilson Creek. In 1986, during a summer of several spates, following a very high spring flood, there were greater densities of black flies during July, August and September than

for the same period of 1987. Conversely, there were higher densities of Hydropsychidae during the same periods in 1987 than during 1986. This trend is supportive of the dynamic equilibrium model (Huston 1979), in which diversity is determined by the influence of the environment on the net outcome of species interactions. One of the theories of the Intermediate Disturbance hypothesis (Connell 1978), where in the absence of disturbance superior competitors would eliminate inferior ones is not supported by the trend found in my study. In Wilson Creek, no species were eliminated during the recovery phase following floods, or during extended periods of quiescence. These species interactions are very complex, and need more research, as it was not the objective of this study to elucidate competition or predation interactions. Other abiotic factors should not be ignored when comparing periods of disturbance and quiescence. With changing discharge (depth of flow), changes in the distribution of flow types (e.g. Froude number) occur, and it is probable that the density of black flies is dependent upon particular combinations of depth of flow, velocity and slope, which may not be readily available, if available at all, when discharge (depth of flow) is low, as was the case in 1987. The importance of depth of flow and its related hydraulic characteristics has been shown by Hauer and Benke (1987) who reported that as discharge increased, production of black flies increased and vice versa.

3.5.6. Disturbance and stream ecosystem dynamics

It appears from the literature and perhaps this study, that both deterministic (density dependent) and stochastic (density independent) processes can function (Power et al. 1988) depending upon the frequency, magnitude and duration of disturbance. This brings us to the most important point with respect to disturbance. What constitutes a disturbance and what characteristics are required to analyse disturbance so an aquatic insect habitat can be described? Resh et al. (1988) used the definition of disturbance from Pickett and White (1985) as "any relatively discrete event in time that disrupts ecosystem, community, or population structure, and that changes resources, availability of substratum, or the physical environment". In Wilson Creek, it has been shown that there was a reduction of insects (i.e. approximately 50%) following any flood capable of moving 8-12 per cent of the substrate. Using this as my criterion of disturbance, it was possible to use historical flow data and construct the average , or general hydrologically determined aquatic insect habitat of Wilson Creek. I have taken from the model describing the relationships between discharge/substrate movement and density of insects, flows required to produce an effect, which I have chosen as 10% of the substrate at incipient motion (the mean of the two summer 1986 values), calculated the per cent of days in each month of such an event, and calculated the predictability, constancy and contingency (Colwell 1974) for each of the natural reaches (Table 10). Since the predictability of discharge (as in Resh et al. 1988) is based on annual variation and constancy, the same

value should be derived for each of the stations, since discharge is proportional to the drainage area above the reach. Substrate stability for a given discharge, is a function of slope, tractive force and substrate composition, and as I have shown, varies from reach to reach. When predictability was calculated within each reach using 10% movement of substrates, station W1 was highly unpredictable (P = .3848), station B1 moderate to highly predictable (P = .6573), and station B2 was highly predictable (P = .7159). So it is evident that the predictability can vary within a stream when using substrate stability values. This is important for stream insect communities, because regionally, reaches within and among unregulated streams will have similar predictability of discharge, simply because they are situated within the same climate, and the climate dictates the timing of discharge above base flow. For example, in temperate climates, there may be relatively large annual spring snow-melt related peak flow, followed by several smaller summer rain storm related spates, and an autumnal increase in flow, related to fall rain storms coupled with reduction in evapotranspiration. However, within the same geographic region, based on geological features, predictability within reaches of streams and between streams, based on movement of substrates related to discharges, can be quite different. This has greater impact on aquatic insect communities than flow regime alone.

Table 3-10. Colwell's predictability of disturbance for 1986-1988 Wilson
Creek aquatic insect study sample stations using flow regime
(discharge) and substrate movement (events moving 10% of
substrate). Calculations of flow regime as in Resh et al.(1988).
Calculations of substrate movement using number days in month in
which >10% substrate at incipient motion.

STATION	FLOW REGIME(DISCHARGE)			SUBSTRATE MOVEMENT		
	P	M	C	P	M	C
W1	.42	.13	.29	.38	.12	.26
B1	.42	.13	.29	.66	.12	.54
B2	.42	.13	.29	.72	.10	.62

P = predictability
M = contingency
C = constancy

3.6. CONCLUSIONS AND FUTURE RESEARCH

The study of the role of disturbance as a determinant of stream insect community structure is in its infancy. However, it is becoming increasingly clear that disturbance is of major importance, and as some researchers believe, is the major organizing factor of stream communities (Resh et al. 1988).

I have demonstrated the overpowering influence of discharge/substrate stability relationships on the aquatic insects in the small study of Wilson Creek. There is evidence to suggest that discharge alone cannot be used to describe aquatic insect habitat, but that one must examine the movement of substrates associated with that discharge.

As unpredictable as Wilson Creek is, especially in the lower reaches, it is evident that the insect species of this creek are very resilient, as they are able to recolonize even the most unstable reach within the same season. Suitable behavioural and life history adaptations of these species are required for survival in this reach in particular and in Wilson Creek as a whole. An examination of life history adaptations of commonly occurring species will be discussed in the next chapter.

I feel that the next step in resolving the effect of abiotic determinants on aquatic insects is to study a range of streams within the same geographical region, model the discharge/substrate stability relationships, analyse the historical flow data, and characterize the hydrological habitat, while concurrently examining the spatial and temporal changes in community structure of aquatic insects. By expanding

the scope of the present study, it would be possible to determine whether

the aquatic insect/hydrological relationships derived for Wilson Creek

are applicable to all rivers and streams.

3.7. ACKNOWLEDGEMENTS

4. LIFE HISTORIES OF EPHEMEROPTERA, PLECOPTERA AND TRICHOPTERA IN WILSON CREEK, MANITOBA, WITH REFERENCE TO SUBSTRATE STABILITY

4.1 ABSTRACT

Mayfly, stonefly and caddisfly life histories were investigated as part of a study into substrate stability/discharge relationships and aquatic insects in Wilson Creek, Manitoba, Canada. Ninety-four per cent reductions in mayfly density occurred in the most unstable, shale-paved reach, following spates. Twenty-two species were abundant during prolonged periods of low flow and were able to complete their life cycle. Life histories of 41% of the species were univoltine with winter growth, and winter-late spring emergence. Another 41% of species were multivoltine, or had multiple cohorts. Only 3 species were univoltine with slow seasonal development.

When historical flow data are examined, the life history adaptations can be seen to be advantageous for survival in a frequently disturbed, unstable environment, such as in the most unstable reach of Wilson Creek. Life history timing of most species avoid predictable spring spates, while unpredictable summer spates are overcome through a combination of fast seasonal development, multivoltinism and behavioural adaptations.

4.2 INTRODUCTION

The role of disturbance in stream ecology has been ignored until recently, and may be the dominant determinant in stream ecology (Resh et al. 1988). For years researchers have been aware of the impact of floods on aquatic insects, but did little to characterize benthic habitats with respect to frequency, intensity, and periodicity of these events, perhaps because they were unaware of applicable hydrological techniques for these analyses. Newbury (1984) described simple techniques to characterize hydrological habitats. He described ways to analyse movement of substrates, and suggested that substrate stability may be an important component of aquatic habitats.

Large reductions in benthic invertebrate densities following floods in rivers with unstable substrates have been reported (Gray and Fisher 1981, Sagar 1986, Scrimgeour and Winterbourn 1989). Reductions in aquatic insect diversity have been attributed in part to substrate stability in the Ochre River, Manitoba, Canada (Cobb and Flannagan, in press).

Adaptations which allow insects to exist in unstable, flood-prone streams include rapid development, multivoltinism, egg diapause, effective recolonization mechanisms and behavioral avoidance (Gray 1981, Fisher et al. 1982, Scrimgeour and Winterbourn 1989). Species with rapid development are able to complete their life cycle between scouring discharges, this period often being only several weeks (Sagar 1986). Multivoltine life cycles ensure that adults are available for repopulation of scoured reaches of streams for several periods during a

season. Effective recolonization mechanisms include high rates of both drifting from upstream stable reaches of stream, and dispersal of adults. Behavioural adaptations can include avoidance of spates by lateral and vertical migrations within the stream channel (Williams 1984).

In 1986 and 1987 the aquatic insect fauna of Wilson Creek, Manitoba was studied to investigate the influence of substrate stability/discharge relationships on the density and diversity of the insect fauna. These relationships were studied for three reaches of varying substrate stability. Life histories for the most commonly occurring mayfly stonefly and caddisfly species of Wilson Creek were examined. The life history strategies are examined in the context of frequency, intensity and predictability of discharge and related substrate movement in Wilson Creek, with emphasis on the most unstable reach.

4.3 MATERIALS AND METHODS

Study Area:

Wilson Creek, a fourth order stream with a 22 km^2 drainage basin, is located in west-central Manitoba (50° 43' N, 99° 33' W) (Fig. 1). It is one of many streams originating on the Manitoba escarpment, a 400 m high bench of Cretaceous shale overlain by glacial till (Newbury 1983). The source is 747 meters above sea level (m.a.s.l.), in Riding Mountain National Park, and Wilson Creek descends steeply to 340 m.a.s.l. over a distance of 6.4km.

Wilson Creek was chosen as a study site for several reasons. It was the site of a 25 year study to investigate the feasibility of flood storage dams and sediment control related to flooding problems in the surrounding agricultural district (Newbury 1983). As part of this study, a continuous gauging station has been maintained, providing a long-term data base of hydrological and meteorological information. Many relationships between hydrological and geological processes have been derived from these data (Newbury 1984).

Four stations were established along the stream for the aquatic insect study (Fig 1). Station W1, situated near the Park boundary, is the most unstable reach and is the focal point of this paper. Reference will be made to stations B1 and B2, each with progressively more stable bed paving material at bankfull discharge. Descriptions of various attributes of the stations are presented in Table 1.

FIGURE 4-1. Map of Wilson Creek, with sample stations (B2, B1, W1, and W1S) of 1986-1988 aquatic insect study.

W1S

W1

Pack

Horse

Creek

Wilson

Creek

B1

Bald

Hill

Creek

B2

study area

drainage   divide

N

0   0.5   1.0

Km
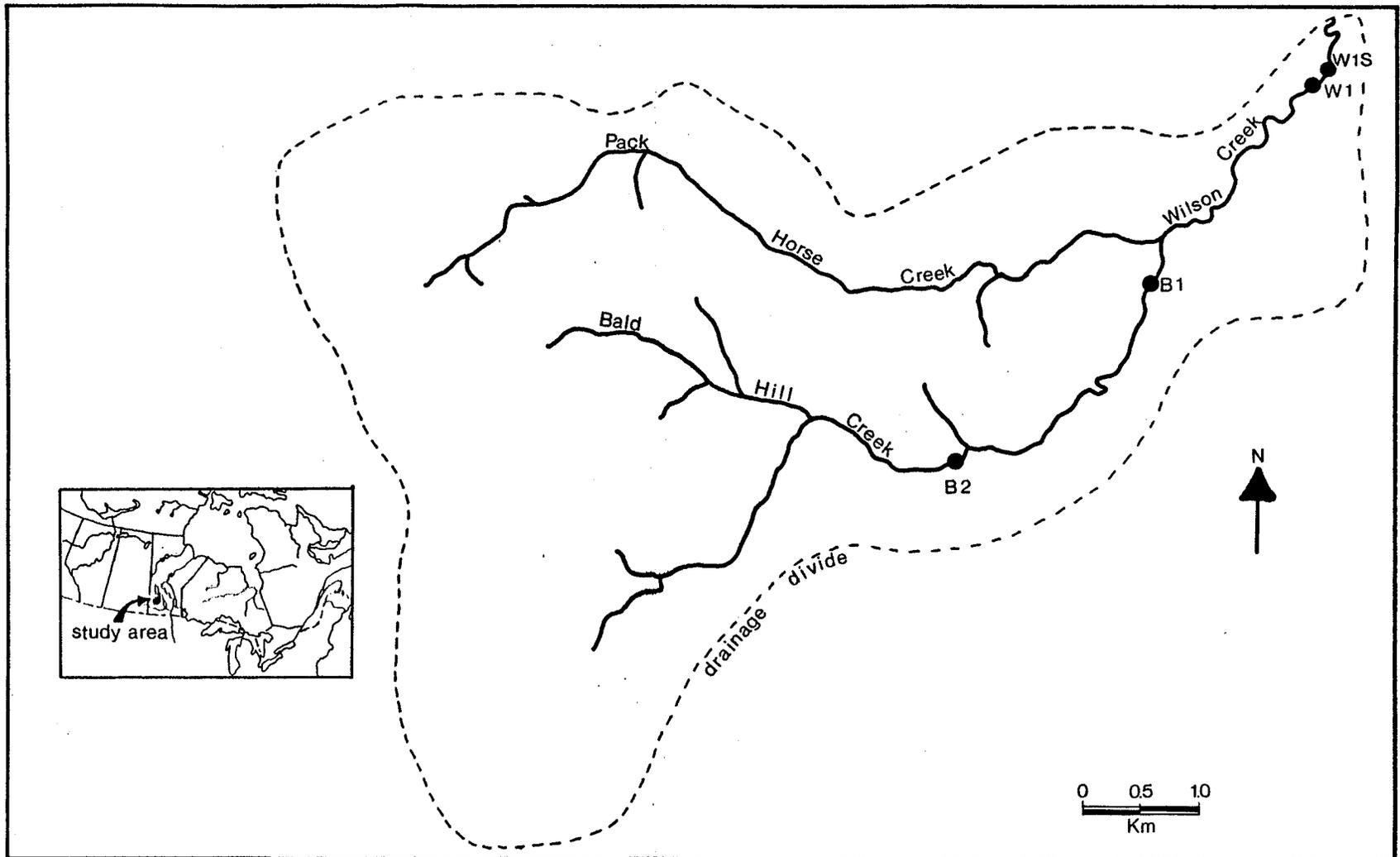
Table 4-1. Description of hydrological characteristics of sample stations of Wilson Creek aquatic insect study 1986-1988.

	W1	W1S	B1	B2
Drainage Area (km^2):	22.1	22.1	11.1	8.6
Slope of reach (%):	1.0	2.5	2.7	3.6
Median bed material size (cm):	4.0	10.0	22.0	34.0
Bankfull conditions				
Width (m):	4.3	4.3	3.5	3.8
Depth (m):	0.35	0.30	0.30	0.31
Discharge (m^3/s):	2.7	2.7	1.6	1.6
Tractive force (kg/m^2):	3.5	7.5	8.4	10.8
Bed material at incipient motion (%):	80.0	20.0	50.0	20.0

Hydrology:

In order to determine the effect of channel bed material movement on aquatic insects, several hydrological relationships were derived using techniques described in detail by Newbury (1984). The average % slope of reaches was measured with a surveyor's level. The mean diameter of bed paving material (mean l x w x h) was measured, ranked and plotted on a cumulative frequency curve. Movement of channel bed paving materials is a result of tractive forces acting upon them, where tractive force (kg/m^2) = mean depth of flow x slope of channel x 1000 (specific weight of water) . Thus for a given discharge, the tractive force can be described if the mean depth of water and slope is known. Average depth of flow was measured over a range of discharge at each station in Wilson Creek to gain this relationship. Tractive force is approximately equal to the median diameter (cm) of rounded, non-compacted particles at incipient motion (Lane 1955), while approximately 1/2 the tractive force is required for an equivalent mean diameter of shale to be at incipient motion (Magalhaes and Chau 1983). From these derived relationships the % of the stream bed paving materials at incipient motion for a given discharge was obtained.

Benthic invertebrate sampling:

Aquatic insects were sampled monthly as well as immediately following spates from May to October 1986, and from March to October, 1987 using a modified Hess (Waters and Knapp 1961) bottom sampler (area 0.1 m^2) with a 400 μm mesh net. Samples were preserved in 4% formalin,

later sorted and identified to genus and species when possible and stored in 70% ethanol.

Using two, 1 m^2 emergence traps (Flannagan 1978), adult insects were sampled Tuesday and Friday from May to September, 1986 to assist in species identification and life history patterns.   Samples were stored in 70% ethanol and identified to lowest possible taxon.

Life cycles of mayfly, stonefly and caddisfly species which occurred in sufficient numbers at station W1 were analyzed.   Total body length (front of head to base of cerci) of mayfly and stonefly nymphs, and ocular head width of caddisfly larvae were measured for of at least 30 specimens.   Where only a few specimens were available for life history analysis, specimens from nearby stations were incorporated.

Life cycles were classified by voltinism, and growth was described as slow or fast for each generation (Clifford 1982).   No attempt was made, within this scheme, to categorize overwintering of nymphal or egg stages.

4.4 RESULTS

Mean water depth was correlated with discharge (Table 2). Since discharge was continuously monitored, it was possible to calculate mean depth of flow for flood peaks prior to each sample time. Tractive force, was then calculated from the mean water depth. The % of stream bed material in motion at each sample period was derived from the cumulative frequency of measured particles, using the relationship between tractive force and mean diameter of shale particles at incipient motion. Total insect density was negatively correlated with % bed material at incipient motion (Table 2).

Station W1 is more likely to have scouring discharges during the summer months than B1, as indicated by the comparison of 1986 flow data with historical flow data (Table 3). Samples collected one day prior and 2 days post spate in both June and September allowed an estimate of the % reduction of insects resulting from these spates. At station W1, the June spate resulted in reductions ranging from 80% (p < 0.001) for stoneflies, to 94% (p < 0.001) for mayflies, while the September spate resulted in reductions ranging from 75% (p < 0.001) for stoneflies to 85% (p < 0.001) for mayflies (Table 3). At station B1, there was no detectable reduction in stonefly or caddisfly densities, and only a 51% reduction (p < 0.05) of mayflies during the two spates.

Ephemeroptera life histories

Seven species (Table 4) of Ephemeroptera were collected in sufficient numbers to construct life history information. Five of the

Table 4-2. Relationship between hydrological factors and Plecoptera, Trichoptera and Ephemeroptera at stations W1, W1S and B1 of Wilson Creek (1986-1988).

Model	Correlation Coefficient (r)[*]			
	W1	W1S	B1	B2
$\log q = a \log d + b$	.9151	.9032	.8953	.9032
$M = Qx + Q^2x + E$	.9748	.9488	.9414	.9336
$Plec = Mx + M^2x + E$	.8427	.5813	.5934	.6988
$Trich = Mx + M^2x + E$	.7718	.5954	.5197	.5079
$Ephem = Mx + M^2x + E$	.8520	.7262	.5540	.5136

q = discharge (m^3/s)
d = mean water depth
M = arc sin prop subst. in motion
E = error term in model
[*] all correlation coefficients significant $(p < 0.05)$

Table 4-3. Comparison of 1986 mean daily discharge with historical flow data (1965-1985) for stations B2, B1, W1 and W1S of Wilson Creek, and reductions of aquatic insects associated with spates in 1986. Historical flow calculated from annual peak discharge, periodicity from visual inspection of hydrograph.

==

| | SPRING | | | | JUNE | | | | SEPTEMBER | | | |
	W1	W1S	B1	B2	W1	W1S	B1	B2	W1	W1S	B1	B2
1986												
DISCHARGE (m^3/s)	2.7	2.7	1.6	1.6	.3341	.3341	.1671	.1671	.0623	.0623	.031	.031
% BED PAVING MATERIAL AT INCIPIENT MOTION	80	20	50	20	12	0	0	0	8	0	0	0
% REDUCTION MAYFLIES		N/A			94***	19ns	43*	N/A	91***	+8ns	51*	N/A
% REDUCTION STONEFLIES		N/A			80***	8ns	41ns	N/A	75***	43ns	+48ns	N/A
% REDUCTION CADDISFLIES		N/A			93***	14ns	19ns	N/A	80***	+105*	+103ns	N/A

HISTORICAL				
% > DISCHARGE (ANNUAL)	67		27		80
% > DISCHARGE (DAILY)	0.8		18		53
PERIODICITY	1		3.7		5.6
PREDICTABILITY	HIGH		LOW		MODERATE

----

ns = p > 0.05
* = p < 0.05
** = p < 0.01
*** = p < 0.001
N/A = pre and post data not available
for comparison

seven species had univoltine life cycles, while the life cycles of the remaining two species appeared to be multivoltine. Pseudocloeon turbidum McD. (Fig. 2), and Nixe (Akkarion) simplicioides (McD.), species with univoltine life cycles, had fast seasonal growth. Both species first appeared in May as small nymphs (<2.0mm) and developed rapidly until first emergence in late June for P. turbidum and mid-July for N.(A). simplicioides. The three remaining species with univoltine life cycles had slow seasonal cycles. An example of this life history strategy, Ephemerella nr. inermis Eaton first appeared in late August as small nymphs (< 2.0mm), and emerged in late June (Fig. 2). The other two univoltine species with slow seasonal development, Ameletus sp. and Leptophlebia sp., first appeared as small nymphs in late July, and were last collected in April. Only one adult specimen of Ameletus sp. was collected from the emergence traps in late May.

Baetis tricaudatus Dodds (Fig. 2) and B. flavistriga McD. had multivoltine life cycles. There were two distinct emergence peaks, one from mid-June to mid-July and a smaller one from early August to early September. An overwintering generation of B. tricaudatus hatched in late September, grew through the winter, matured by late May and emerged in early June. A second generation appeared as tiny nymphs in late July, matured rapidly and emerged by late August and early September.

Plecoptera life histories

Life history diagrams were constructed for nine species of stoneflies (Fig. 3), of which three univoltine patterns of development

FIGURE 4-2. Life history patterns of mayflies at station W1 of Wilson Creek. Upper: adult emergence in 1986, Lower: histogram of nymphal growth. Bars represent % of population at a particular body length at sample time.

Pseudocloeon turbidum

Total Number Emerged

40 30 20 10 0 10 20 30 40

MARCH | APRIL | MAY | JUNE | JULY | AUG | SEPT | OCT

♂♂
♀♀

Body length (mm)

60 50 40 30 20 10 0.0

% of Population

Ephemerella nr inermis

Total Number Emerged

10 5 0 5 10

MARCH | APRIL | MAY | JUNE | JULY | AUG | SEPT | OCT

♂♂
♀♀

Body length (mm)

9.0 8.0 7.0 6.0 5.0 4.0 3.0 2.0 1.0

% of Population

Baetis tricaudatus

Total Number Emerged

10 5 0 5 10

MARCH | APRIL | MAY | JUNE | JULY | AUG | SEPT | OCT

♂♂
♀♀

Body length (mm)

9.0 8.0 7.0 6.0 5.0 4.0 3.0 2.0 1.0 0.0

?

% of Population

78
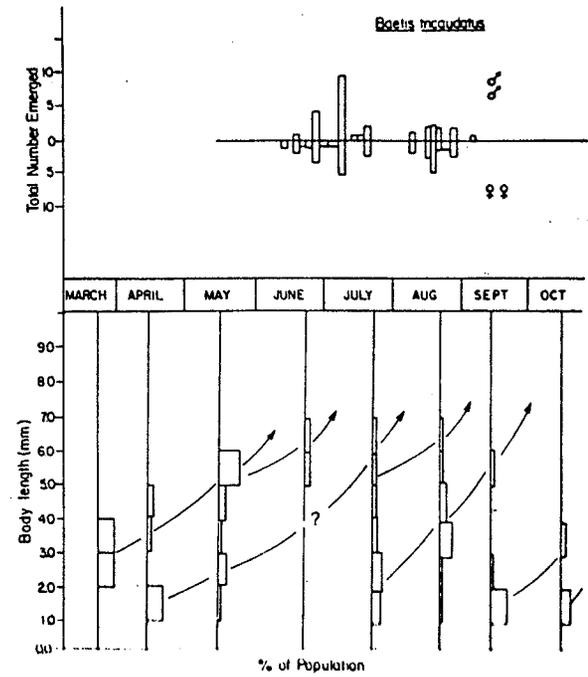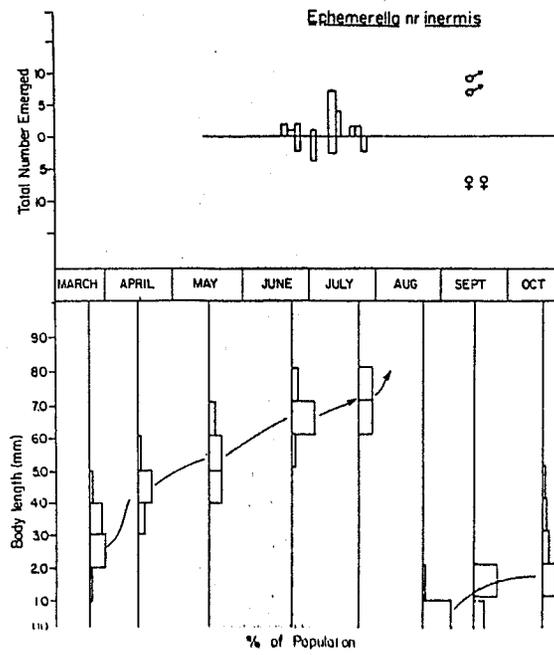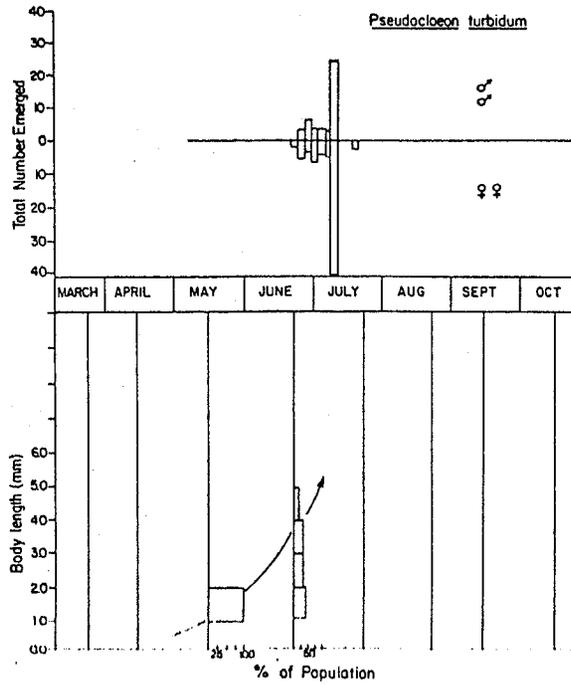
FIGURE 4-3. Life history patterns of stoneflies from station W1 of
       Wilson Creek. Upper: adult emergence in 1986, Lower: histogram of
       nymphal growth. Bars represent % of population at a particular
       body length at sample time.

Zapada cinctipes

Haploperla brevis

Malenka californica
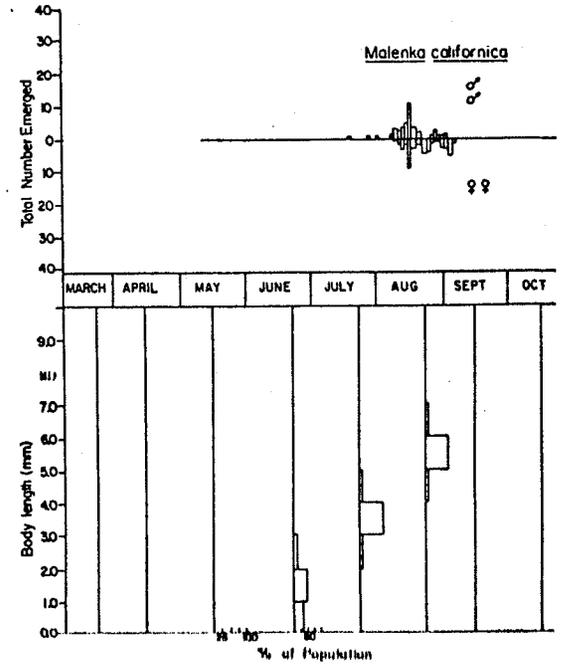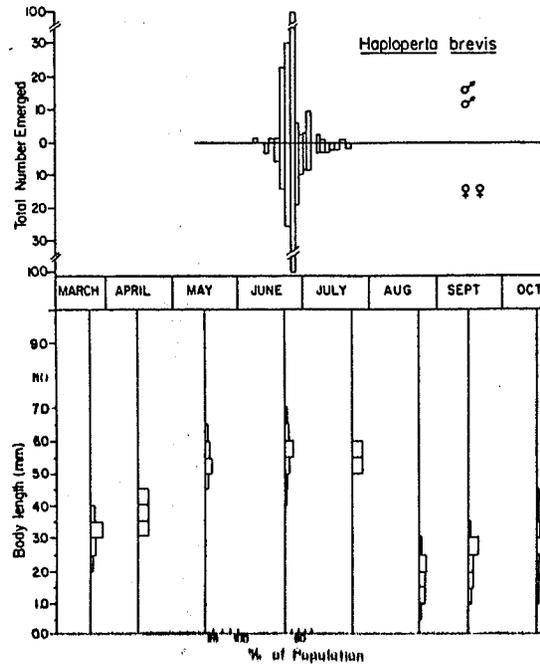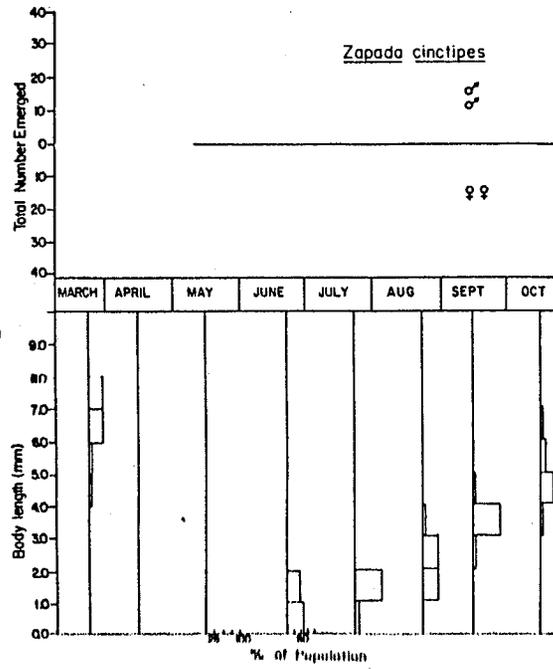
were apparent. <u>Zapada</u> <u>cinctipes</u> (Banks), <u>Taeniopteryx</u> <u>nivalis</u> (Fitch), and the three Capniidae species, are all considered winter stoneflies. This group of species first appeared in the benthic samples in June, grew little until late August, after which they grew rapidly throughout the winter and emerged from March until late April (author's personal collections). The second pattern was that for <u>Haploperla</u> <u>brevis</u> (Banks) and <u>Isoperla</u> <u>bilineata</u> (Say), with slow seasonal growth. <u>Haploperla</u> <u>brevis</u> was first collected in benthic samples in August, and emerged from mid-June to mid-July, while <u>I</u>. <u>bilineata</u> was first collected in late June, and emerged in mid-May to early June. The third stonefly life cycle pattern was a univoltine one, with fast seasonal development. <u>Malenka</u> <u>californica</u> (Claassen), was first collected in late June, grew rapidly, and emerged from late July to early September.

All commonly occurring species of caddisflies were univoltine, but some species had more than one cohort during a season (Fig. 4). The three species of Hydropsychidae, <u>Glossosoma</u> <u>intermedium</u> (Klapálek), and <u>Lepidostoma</u> <u>pluviale</u> (Milne), had two cohorts, with emergence several weeks apart, or had continuous emergence. <u>Brachycentrus</u> <u>occidentalis</u> Banks was univoltine, with short synchronous emergence in early May.

Using the terms of Clifford (1982), there were several life history strategies exhibited by the 22 stonefly, caddisfly and mayfly species (Table 4). Forty-one per cent of the species were univoltine, with slow seasonal development and emergence prior to or surrounding peak spring discharge. Only 13% of the univoltine species with slow seasonal development had summer emergence. Forty-one per cent of the species had

FIGURE 4-4. Life cycle patterns of Trichoptera at station W1 of Wilson
      Creek. Upper: adult emergence in 1986, Lower: historgram of larval
      growth. Bars represent % of population at a particular ocular head
   width at sample time.

Lepidostoma pluviale

Glossosoma intermedium

Brachycentrus occidentalis
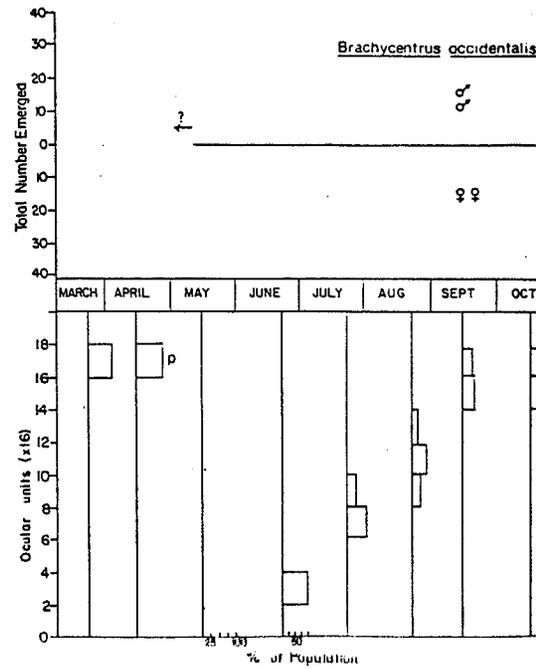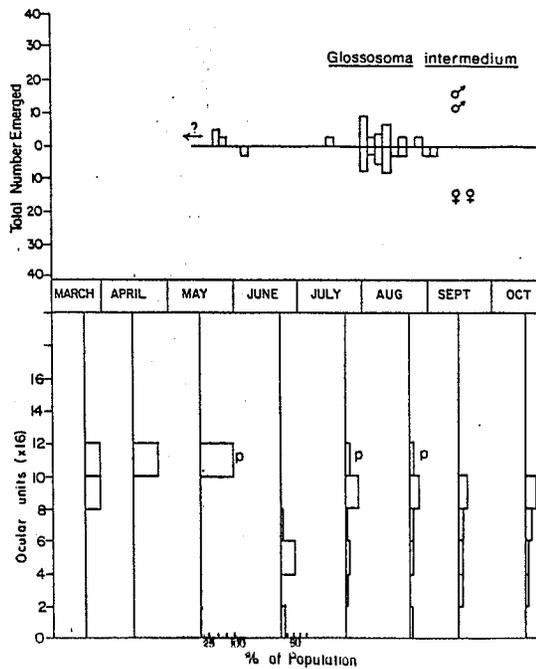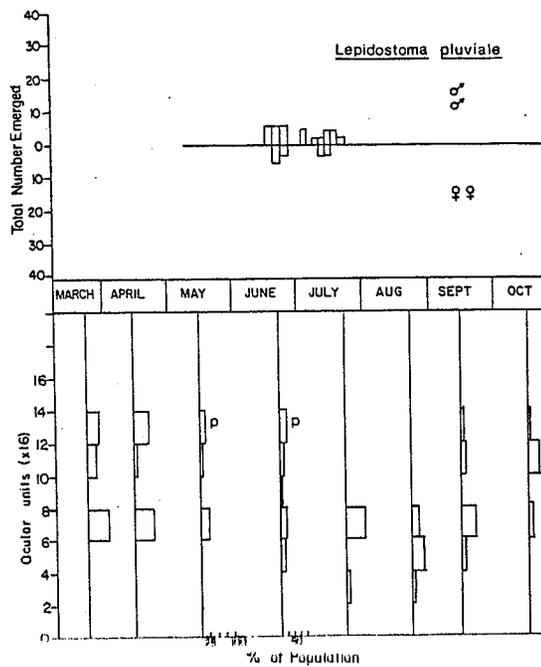
Table 4-4. Life history strategies of aquatic insects in Wilson Creek, and summary of known life history strategies from published sources
Per cent of known North American taxa in parenthesis (bold faced numbers= % by voltinism, regular faced numbers= % by development
type for given voltinism. Plecoptera genera- calculated from Stewart and Stark (1988), Ephemeroptera species- from Clifford (1982),
Trichoptera genera- calculated from Wiggins (1977). Some taxa reported to have several strategies, therefor totals may be > 100%.

	WILSON CREEK TAXA WITH PARTICULAR LIFE CYCLE TYPE		
LIFE CYCLE TYPE	PLECOPTERA	EPHEMEROPTERA	TRICHOPTERA
1. UNIVOLTINE (64)		(73)	(80)
SLOW SEASONAL GROWTH		(65)	
WINTER-SPRING EMERGENCE (30)	Zapada cinctipes Taeniopteryx nivalis Capniidae (3 spp.) Skwalla paralella	Leptophlebia sp. Ameletus sp.	Brachycentrus occidentalis
SUMMER-FALL EMERGENCE (69)	Haploperla brevis Isoperla bilineata	Ephemerella nr. inermis	
FAST SEASONAL GROWTH		(37)	
WINTER-SPRING EMERGENCE			
SUMMER-FALL EMERGENCE (1)	Malenka californica	Pseudocloeon turbidum Nixe simplicioides	
2. MULTIVOLTINE OR MULTIPLE COHORTS (1.5)		(37)	(6)
SLOW SEASONAL GROWTH			
WINTER-SPRING EMERGENCE			Glosossoma intermedium (cohort 1)
SUMMER-FALL EMERGENCE		Baetis tricaudatus (winter generation) Baetis flavistriga (winter generation)	Glosossoma intermedium (cohort 2) Hydropsyche slossonae (cohorts 1 and 2) H. alhedra (cohorts 1 and 2) Cheumatopsyche oxa (cohorts 1 and 2) Lepidostoma pluviale (cohorts 1 and 2)
FAST SEASONAL GROWTH			
WINTER-SPRING EMERGENCE			
SUMMER-FALL EMERGENCE		Baetis tricaudatus (summer generation) Baetis flavistriga (summer generation)	
3. SEMIVOLTINE (35)	Pteronarcys dorsata	(4)	(14)

complex life cycles. Of these, five species were univoltine, but with several cohorts developing concurrently, and 2 species were multivoltine. Thirteen per cent of the species were univoltine with fast seasonal development.

4.5. DISCUSSION

Within North American mayflies, caddisflies and stoneflies, most taxa are univoltine (Table 4). Plecoptera have the largest proportion of semivoltine (35%), and fewest multivoltine (1.5%) genera of the orders. Mayflies have a relatively large proportion of multivoltine taxa (36.7%). Most univoltine species of mayflies have slow seasonal development (65%).

In Wilson Creek, the life cycle of four of the seven mayfly species, P. turbidum and N.(A). simplicioides of the univoltine group, and B. tricaudatus and B. flavistriga of the multivoltine group, all exhibited fast seasonal growth. The latter two species exhibited fast seasonal summer growth (late July-early September), and slow seasonal winter growth (September-June), a life cycle most commonly reported for these species (Clifford 1982, Rader and Ward 1987). Ciborowski and Clifford (1984) reported a third generation which hatched in June and emerged in July for B. tricaudatus. A third generation of this species from Wilson Creek is not ruled out. By sampling monthly, a cohort may have been missed. Also, June and a July spates may have sufficiently disrupted this cohort so as to make it undetectable in the length frequency histograms.

Pseudocloeon spp. are reported as having bivoltine life cycles (Clifford 1982), however P. turbidum in this stream was clearly univoltine. Although other factors such as food type, competition, thermal regime and chemistry undoubtedly contribute to the success of a species, rapid development of a single cohort following spring peak

discharge appeared to be a life history adaptation suitable for existence in the unpredictable environment of the most unstable reach of the stream. Pseudocloeon turbidum constituted nearly 50% of total mayfly density for the two years of the study (Table 3).

The remaining three species have slow seasonal life cycles. Ameletus sp. and Leptophlebia sp. both completed growth before spring peak discharge. Leptophlebia sp. has been reported to commence emergence in mid-May at a slightly higher latitude (Clifford et al. 1979). These two species may have emerged at the onset of or just after the spring peak discharge in Wilson Creek; the latter situation would seem to satisfy life history requirements to extreme flow events. Further research will be required to elucidate the emergence phenology of these two species. Ephemerella nr.inermis, the third species with slow seasonal univoltinism was present at all times of the study period. Although its abundance was reduced by spates, the species recovered rapidly, and subsequently completed its development. This genus is reported as being one of the most abundant mayfly species in stream drift (Ciborowski and Clifford 1983, Armitage 1977), and as such has the potential to recolonize this reach of Wilson Creek rapidly from stable upstream reaches.

The most commonly occurring life history pattern for the Plecoptera was a univoltine one characterized by slow summer growth, followed by fast winter growth and emergence in late winter-early spring (60% of species). This total is higher than for North American stoneflies, in which only 21% of the genera have this life cycle pattern (Table 4). The

winter stoneflies exhibited this pattern. Nymphal diapause in the hyporheic zone is reported for many Capniidae and Taeniopterygidae (Harper and Hynes 1970). The combination of summer diapause in the hyporheic zone and fast winter growth, may be optimal in an unstable reach of stream, winter being a period of base flow where the risk from scouring discharge is minimal. Most emergence would be completed before the predictable peak in spring run-off.

Pteronarcys dorsata (Say) was the only semivoltine species collected in the study, and was rare. No adults were collected, so it is not known if these rare individuals represent a reproducing population, or the result of adults immigrating from other rivers in the area, and nymphs surviving only part of their life cycle. The lack of species exhibiting this life history strategy suggests that semivoltinism is not a suitable strategy for existence in unstable frequently disturbed streams. However, temperature regime, or some other factor may preclude semivoltine species from headwater streams. An experimental manipulation may determine the effect of cool temperatures or scouring discharges on the development of semivoltine species in Wilson Creek. For example one could transplant several hundred nymphs to a stable and unstable reach and monitor their subsequent development.

Three species of stoneflies were univoltine with summer growth and emergence. Of these Malenka californica was abundant at the stable upper reaches of the creek, while only rarely collected in the unstable shale. Haploperla brevis and Isoperla bilineata were common in the unstable reach, survival of these two species may be dependent upon some

behavioural adaptations. Chloroperlidae stoneflies, for example, have very flat bodies, and are highly adapted for crawling within interstitial spaces, and are reported as spending much of their life cycle in the hyporheic zone (Peckarsky 1983, Stanford and Gaufin 1974).

Eighty-three per cent of the caddisflies for which life histories could be determined, had two cohorts developing simultaneously, but staggered by several weeks (Table 4). This appears to be a successful strategy for the survival of species in frequently disturbed reaches of streams, as it allows several opportunities for completion of a life cycle. Several caddisfly species were collected during the study, but were not abundant enough to elucidate their life cycle. For example Hesperophylax incisus and Ryacophila vao were collected, and are probably univoltine. It is probable that a larger proportion of the caddisfly fauna than reported in Table 4 is univoltine.

No attempt was made to characterize egg development time. Brittain (1982) cautioned that absence of small nymphs from samples does not necessarily mean egg diapause, as tiny nymphs may be deep in the substrates. Humpesch (1981) confirmed this possibility with a lab study of life histories of a Heptageniidae species. Mesh size also has been shown to alter the interpretation of life cycles, where small (<2 mm) nymphs can be missed using large mesh samplers (Suter and Bishop 1980).

With these cautions in mind, several species in Wilson Creek appeared to have extended periods before egg hatch. For example, it appeared that P. turbidum spent up to 9 months in the egg stage, because no nymphs were collected during these months in over 50 samples during

two seasons, while small nymphs of other species were adequately sampled. Clifford (1982) reported that about 25 % of all mayfly life cycles have long periods of egg dormancy in winter. He suggested that the adaptive significance of this strategy may be related to harsh winter conditions, allocation of food resources, or avoidance of predation. In station W1 of Wilson Creek, it appears that the adaptive significance of egg diapause favours survival under the prevalent flow regimes.

In order to put the life cycle patterns of insects in Wilson Creek into an ecological context, an examination of the historical flow data for Wilson Creek is necessary. When the historical flow data (Environment Canada 1965-1986) was examined, a spring snow melt-related discharge of 2.7 m^3/s or greater, during which at least 75% of the bed paving material would be in motion at station W1, occurred in 2 out of 3 years (Table 3). The regularity with which this snow melt- related flow or a greater one occurred in late April/early May is considered highly predictable. During a summer spate (June 1986) only 12% of the bed paving material was at incipient motion, but a large reduction in insect density was recorded at W1, while no change in insect density was detected at station B1, where no bed paving material were estimated to be at incipient motion. Historically, an equal or greater rainfall-related discharge at station W1 occurred during the summer months in less than 27% of the years and was much less predictable. This discharge occurred on average 3.7 times over an entire season. Slightly less, but still significantly disruptive, was a September 1986 discharge in which 8% of the stream bed paving material was at incipient motion. On average,

spates of the magnitude in which approximately 8% of the bed paving material is at incipient motion occurs 5.6 times a year. It appears that species with semivoltinism or slow seasonal development and/or lacking suitable behavioural adaptations would rarely complete development in an average year, when about 6 disturbances would occur.

The insect fauna of streams subject to severe and unpredictable disturbance is classified as having low resistance; i.e. large reductions in abundance following spates, and high resilience, with recovery to pre-disturbance densities and diversity within several months (Reice 1985, Doeg et. al. 1989). Insect species with rapid development, multivoltine life cycles, and effective recolonization mechanisms were most prevalent in these streams. However, as discussed in Chapter 3, the resistance of an aquatic insect population appears to depend upon the substrate stability of the reach, and the intensity of discharge examined.

The mayflies, stoneflies and caddisflies of Wilson Creek appear to be typical of fauna influenced by stochastic factors. Life history or behavioural adaptations of most species are suited for existence the unstable, frequently disturbed reach of stream. Substrate stability as determined by frequency, duration, intensity and predictability of discharge should be an important component in life history studies of aquatic insects. When information on insect life histories from other streams is examined with respect to substrate stability/discharge relationships, the importance of these relationships in the evolution of aquatic insect life history adaptations may be realized.

4.6. ACKNOWLEDGEMENTS

5. THE EFFECTS ON THE TRICHOPTERA OF A STABLE RIFFLE CONSTRUCTED IN AN UNSTABLE REACH OF WILSON CREEK, MANITOBA, CANADA

5.1. ABSTRACT

As part of a study into the effects of discharge/substrate stability relationships on the aquatic insects of Wilson Creek, a 5 m long stable riffle was constructed in an otherwise unstable shale reach. The purpose of the pilot project was to investigate the hydrological design and feasibility of such a structure, and also to test the effects of equal discharge on differing substrate stability. Reductions in Trichoptera density ranging from 92% to 81% were observed in the unstable reach following each of two summer spates, while densities within the stable riffle changed little (-14% ($p > 0.05$) and +49% ($p > 0.05$)). Examination of historical flow records indicated the ecological implications of spatial/temporal differences in substrate stability. During periods of quiescence, local flow conditions created by the stable riffle material appeared to benefit filter-feeding caddisflies.

The stable riffle constructed within an unstable reach of Wilson Creek has the potential of providing habitat for aquatic insects during spates, while at the same time providing a wider range of local flow conditions during low flow period.

5.2 INTRODUCTION

Physical disturbance in stream ecology, although neglected until recently, may be the dominant determinant in stream ecology (Resh et al. 1988). The biological effects of floods on populations of lotic insects are well documented (see Hynes 1970, Gray and Fisher 1981, Sagar 1986). However, the hydrological events themselves, e.g. intensity, frequency, periodicity of floods, have not been used by biologists to characterize lotic benthic habitats, perhaps because they were unfamiliar with hydrological techniques for these analysis. Newbury (1984) indicated some simple hydrological techniques useful in characterizing aquatic habitats. He described ways to analyse movement of substrates, and suggested that substrate stability may be an important component of aquatic insect ecology.

There are several recent attempts to analyse substrate stability and its effect on aquatic insects. Reductions in diversity of Trichoptera emergence has been attributed in part to substrate instability in the Ochre River, Manitoba, Canada (Cobb and Flannagan, in press). Floods sufficient to move stream bed materials have been analyzed in an unstable river in New Zealand (Scrimgeour and Winterbourn 1989). Field experiments have been conducted into the effect of substrate disturbance on stream benthic communities through periodic tumbling and disruption of substrates (Reice 1985, Doeg et al. 1989), and on the effect of stability of artificial "stones" with different mass on aquatic insects (Malmqvist and Otto 1987). There are few studies designed to study spatial and

temporal effects of substrate stability in natural streams (Minshall 1988).

In 1986 and 1987 the aquatic insect fauna of Wilson Creek, Manitoba was studied to investigate the influence of substrate stability/discharge relationships on the density and diversity of the insect fauna. These relationships were studied in three reaches of varying substrate stability. At the least stable reach a pilot project was initiated to investigate the feasibility of creating a stable substrate. The main objectives of constructing the stable riffle were to test the effect of equal discharge upon different substrate stability within the same reach of stream, and also to consider whether benthic productivity might be enhanced for fisheries projects in unstable shale reaches of Manitoba escarpment streams. This paper is a summary of the mitigating effects of an introduced stable riffle on the caddisfly fauna. The effects of intensity, frequency and periodicity of spates on the Trichoptera in the unstable reach and the introduced stable riffle are compared.

5.3. MATERIALS AND METHODS

Wilson Creek, a fourth order stream with a $22km^2$ drainage basin, is located in west-central Manitoba (50° 43' N, 99° 33' W) (Fig. 1). It is one of many streams originating on the Manitoba escarpment, a 400 m high bench of Cretaceous shale overlain by glacial till (Newbury 1983). The source is 747 m above sea level (m.a.s.l.), in the Riding Mountain National Park, the Creek descends steeply to 340 m.a.s.l. over a distance of 6.4 km.

Wilson Creek was chosen as a study site for several reasons. It was the site of a 25 year investigation of the feasibility of flood storage and sediment control dams to alleviate flooding problems in the surrounding agricultural district (Newbury 1983). As part of this study, a continuous water flow gauging station and meteorological site has been maintained, providing a long-term data base. Many relationships between hydrological and geological processes have been published from these data (Newbury 1984).

Three reaches along the length of the stream were chosen for the aquatic insect study (Fig 1). Station W1, situated near the Park boundary, was situated in the least stable reach. Within this reach, a stable riffle (W1S) was constructed. Descriptions of various attributes of these stations are presented in Table 1.

Local field stones, large enough so as not to be moved at bankfull discharge, were selected to construct the stable riffle. Mean diameter was 10 cm with a range of 5 to 25 cm. The field stones were placed in the stream without specific design criteria to examine riffle dynamics

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FIGURE 5-1. Map of Wilson Creek, with location of stable (W1S) and
   unstable (W1) sampling stations in 1986-1988.

Pack

Horse

Creek

Wilson

Creek

W1S

W1

B1

Bald

Hill

Creek

B2

study area

drainage divide

N

0   0.5   1.0
Km
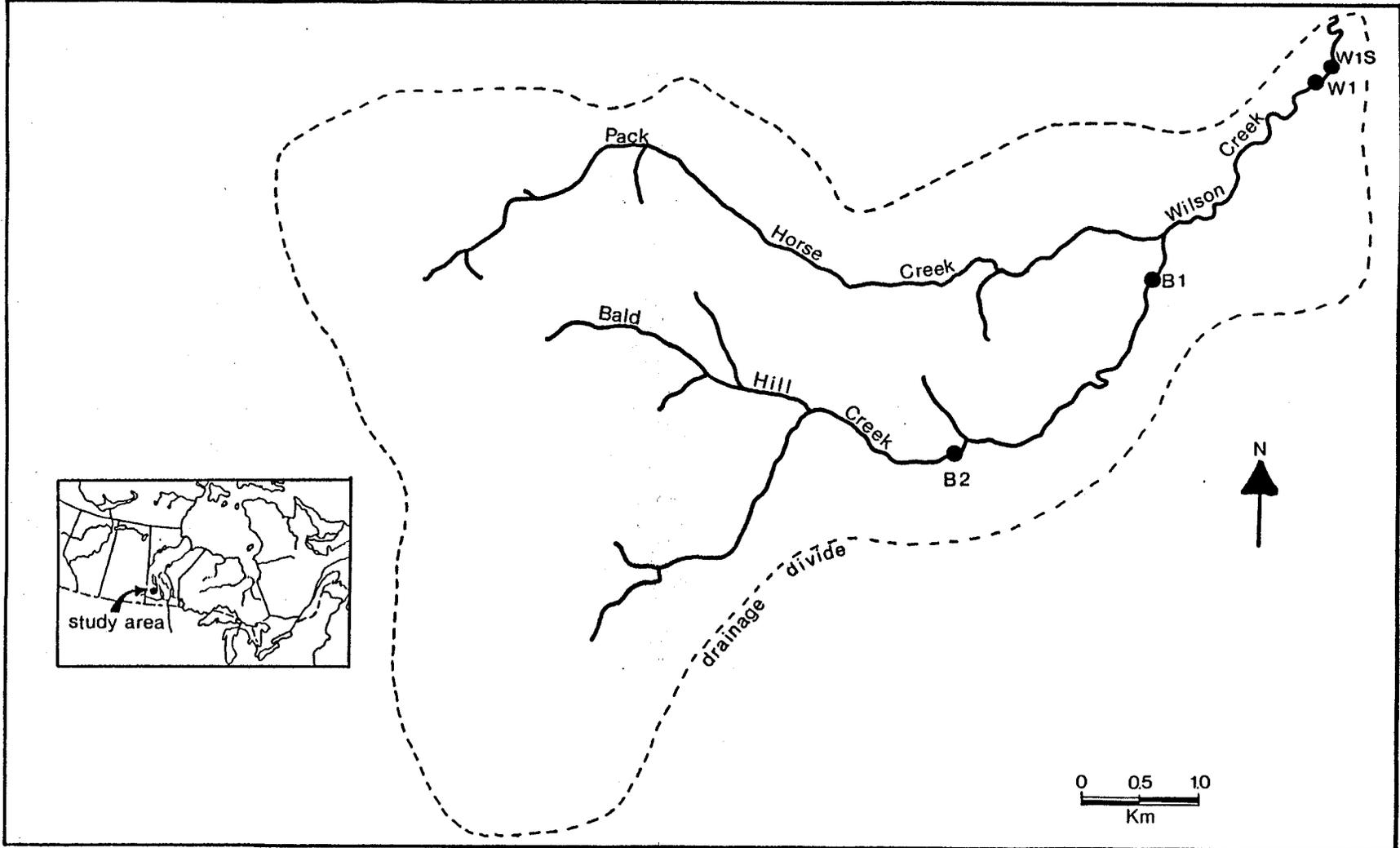
Table 5-1. Physical and hydrological characteristics of stations W1 (unstable) and W1S (stable) of Wilson Creek, Manitoba 1986-87 (adapted in part from Newbury 1984).

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	W1	W1S
DRAINAGE AREA (km^2):	22.1	22.1
SLOPE (%):	1.0	2.5
MEDIAN CHANNEL PAVING MATERIAL (cm):	4.0	10.0
BANKFULL CONDITIONS		
WIDTH (m):	4.3	4.3
DEPTH (m):	0.35	0.30
DISCHARGE (m^3/s):	2.7	2.7
TRACTIVE FORCE (kg/m^2):	3.5	7.5

NEGATIVE EXPONENTIAL HYDROLOGICAL AND TRICHOPTERA RELATIONSHIPS (r^2):

DISCHARGE VS % SUBSTRATE IN MOTION:	.8392	.5334
DISCHARGE VS DENSITY TRICHOPTERA:	.8201	.5898
% SUBSTRATE IN MOTION VS TRICHOPTERA	.7060	.6154

during the summer. The riffle was 5 meters long, with a slope of 2.5%. The riffle was constructed in May 1986, and monitored until May 1987. The centre of this riffle had filled in with shale by the spring of 1987, so a second riffle was constructed in May 1987, using similar field stones. However several large (35 cm median diameter) boulders were positioned to create one head of water at the top of the riffle and another half-way along the length of the riffle to flush shale through during spates. This riffle was 10 m in length with an initial slope of 2.5%.

Several hydrological relationships were derived using techniques described in detail by Newbury (1984). The average % slope of reaches was measured with a surveyor's level. The mean diameter of bed paving materials (mean l x w x h) was estimated, ranked and plotted on a cumulative frequency curve. Movement of channel bed paving materials is a result of the tractive force acting upon them, where tractive force (kg/m^2) = mean depth of flow x slope of channel x 1000 (specific weight of water; kg/m^3). Thus for a given discharge, the tractive force can be described if the mean depth of water and slope are known. Average depth of flow was measured over a range of discharges at each station to provide this relationship. Tractive force is approximately equal to the median diameter (cm) of rounded, non-compacted particles at incipient motion (Lane 1955), while approximately 1/2 the tractive force is required for an equivalent mean diameter of flat shale substrates to be at incipient motion (Magalhaes and Chau 1983). The % of the stream bed

paving materials at incipient, motion for a given discharge was obtained using these relationships.

Aquatic insects were sampled monthly as well as immediately following spates from May to October 1986, and from March to October 1987 using a modified Hess (Waters and Knapp 1961) bottom sampler (area 0.1 m^2) with a 400 μm mesh net. Five samples were taken from each station at each sample time. Samples were preserved in 4% formalin, later sorted and identified to genus and when possible to species and stored in 70% ethanol.

The relationships between hydrological parameters and Trichoptera density were tested using regression analysis (SAS 1985). The effect of two summer spates on caddisfly densities was tested using ANOVA on log transformed data. When significant differences were found, means were compared using SNK multiple means comparison test with alpha = 0.05.

5.4. RESULTS

There was a large spring snow storm-related peak in 1986 followed by three summer rainfall-related peaks (Fig.2). In 1987 there was an average spring peak flow, followed by an unusually dry summer and no rainfall-related spates.

The various hydrological parameters measured for station W1 and W1S were all correlated (Table 1). Per cent of bed material and density of Trichoptera were more highly correlated with discharge at station W1 than W1S. However, the relationship between density of Trichoptera and % of bed material in motion was approximately the same for both stations.

A total of 12 species of Trichoptera was collected during the study (Table 2), with station W1 having 10 species and station W1S having 12. Average total caddisfly density for the period of June to October was lower in 1986 ($153.1/m^2$) than in 1987 ($597.9/m^2$) at station W1, while station W1S had similar densities for the two years. Lepidostoma pluviale (Milne) was the most abundant species at the two stations, comprising greater than 30% of the caddisflies irrespective of year or station. Glossosoma intermedium (Klapálek) which comprised >50% of the Trichoptera in the upper reaches (Cobb unpubl. data.) occurred in low densities at both stations.

Trichoptera densities before and after both the June and September spates differed significantly (p < 0.001, ANOVA). Station W1S in June had greater densities than station W1 prior to and after the flood, while in September station W1 pre-spate, W1S pre- and post-spate densities did not differ (Table 3). Total Trichoptera were reduced at station W1

FIGURE 5-2. Mean daily discharge (m^3/s) for Wilson Creek, Manitoba at station W1 for March to October, 1986 and 1987.
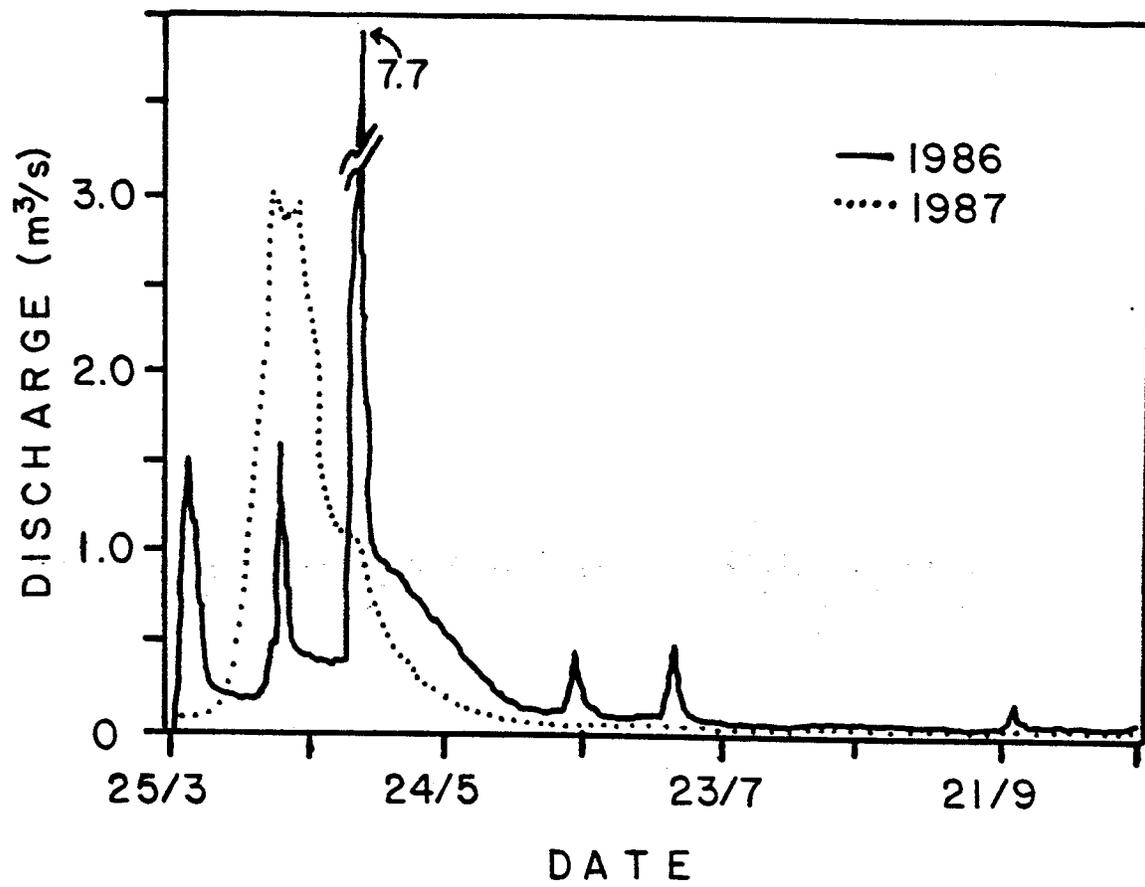
Table 5-2. Trichoptera species composition and mean abundance
(number/m^2) from June to October, 1986 and 1987 for stations
W1 (unstable) and W1S (stable) of Wilson Creek, Manitoba.

SPECIES	1986		1987	
	W1	W1S	W1	W1S
Lepidostoma pluviale (Milne)	97.8	201.1	313.1	159.0
Hydropsyche slossonae Banks	14.6	45.7	146.3	129.0
H. alhedra Ross	6.8	41.7	10.0	10.0
Cheumatopsyche oxa Ross	4.8	2.3	50.0	89.0
Brachycentrus occidentalis Banks	18.1	26.0	10.0	39.0
Glossosoma intermedium (Klapálek)	1.3	5.7	41.0	13.0
Polycentropus pentus Ross	0.0	0.3	15.0	15.0
Hesperophylax incisus Banks	8.4	23.3	0.0	10.0
Ptilostomis ocellifera (Walker)	1.3	0.0	2.5	1.3
Ochrotrichia sp.	0.0	0.0	10.0	2.5
Limnephilus sp.	0.0	0.3	0.0	0.0
Rhyacophila sp.	0.0	1.3	0.0	0.0
Total No./m^2	153.1	347.7	597.9	467.8

Table 5-3. Effects of June and September 1986 spates on the mean (+/- s.e.) density of Trichoptera in stations W1 and W1S of Wilson Creek, Manitoba. Significant differences tested using SNK multiple means comparison test (alpha = 0.05) on log (no./m^2 +1) transformed data.

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STATION	DATE	JUNE 1986		SEPTEMBER 1986	
		DENSITY	% CHANGE	DENSITY	% CHANGE
W1	1 d PRE	52.0 (9.16)b		364.0 (82.3)a	
W1	2 d POST	4.0 (2.45)c	- 92.0	68.0 (13.2)b	- 81.3
W1S	1 d PRE	244.0 (33.6)a		358.0 (98.0)a	
W1S	2 d POST	210.0 (52.8)a	- 13.9	564.0 (26.8)a	+ 49.4

note: within each month densities followed by different letters are significantly different by SNK test (alpha = 0.05).

during the June (92% loss) and September (81% loss) 1986 spates
(P < 0.001, SNK), while no significant change (P > 0.05) in abundance
resulted from these spates at station W1S.

5.5. DISCUSSION

The stable riffle (WlS), had approximately twice as many caddisflies as the unstable station in 1986. This was attributed to the effect of several summer spates on the unstable station. Increases in shear stress during these spates initiated substrate movement resulting in loss of animals. The magnitude of loss of caddisflies was similar to that reported by Reice (1985), who reported up to 90% reductions in insects following experimental disturbance of substrates. Trichoptera responded to relatively minor spates in which only 8% of the bed paving material was at incipient motion, as predicted using the relationships derived by Magalhaes and Chau (1983). Newbury (1984) cautioned that these relationships were developed in laboratory flumes, and that in nature the situation is much more complex, for example the removal of finer substrates can initiate the movement of larger ones. However, reductions of invertebrates during relatively minor spates are reported for other unstable streams (Sagar 1986), so it appears that the movement of a relatively small proportion of bed paving materials results in detectable reductions in aquatic invertebrates.

The varying response of the two stations, both subjected to the same discharge supports the views of Statzner et al. (1988) who suggested that it is not sufficient to examine a single factor such as discharge, but that it is important to examine the combination of hydraulic factors such as shear stress and how these factors combine to determine the aquatic insect habitats. Minshall (1988) stressed the importance of spatial effects of spates on the movement of substrates, but stated that

this subject has been relatively unexplored. The importance of substrate stability to aquatic insects is clearly evident from the results of this small scale pilot study, along with the results of the overall Wilson Creek study.

The stable riffle was not only more resistant to movement during spates, it also created a more varied hydraulic habitat. For example the distribution of the Froude number, a dimensionless combination of velocity (v), depth of water (d) and gravitational acceleration (g), where Fr = V^2/gd, and an indicator of the state of the flow, was different between the stable riffle and the unstable shale reach during the summer of 1987, when discharge was relatively low (Fig.3). The stable riffle had a higher proportion of Froude values above the critical flow value of 1.0 (i.e. when flow changes from quiescent to shooting flow) than the unstable riffle.

Filter feeding caddisflies are reported to exhibit specific preferences for different local flow conditions. Fuller and Mackay (1980) suggested, and Osborne and Herricks (1987) demonstrated, that turbulence was an important determinant in the distribution of Hydropsychidae larvae. The flow net concept of Vallentine (1967) is also important in the distribution of filter feeding Trichoptera, presumably through the more efficient capture of food particles as flow approaches the critical zone (Froude =1.0) (Wetmore 1987). When Trichoptera from the present study are grouped according to functional feeding groups (Merritt and Cummins 1984), filter feeders were more abundant (% of total)in the stable riffle in 1987 (Table 4).

FIGURE 5-3.   Distribution of Froude number at randomly selected sample
      sites within stations W1 and W1S in Wilson Creek, Manitoba.
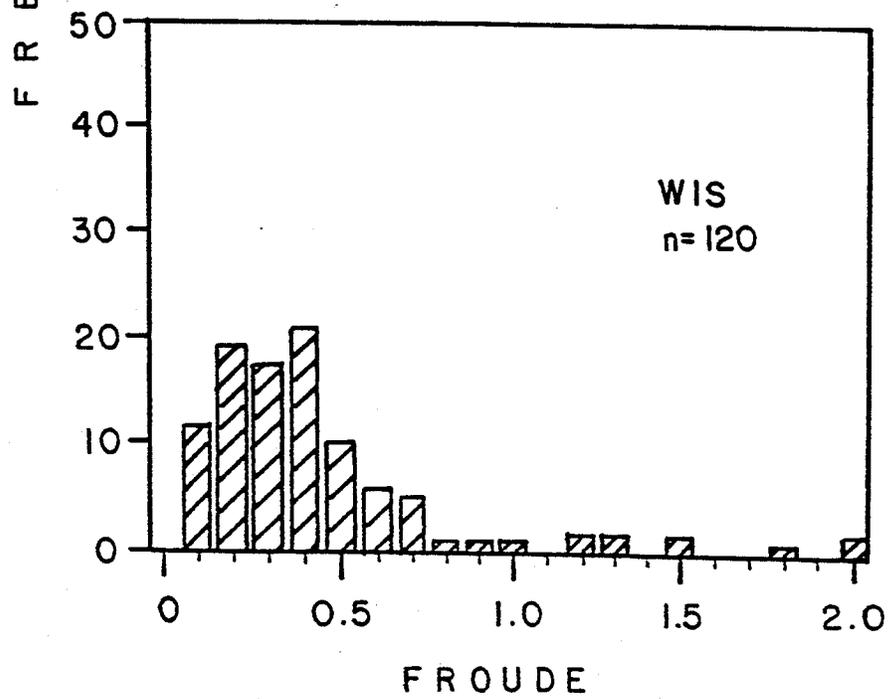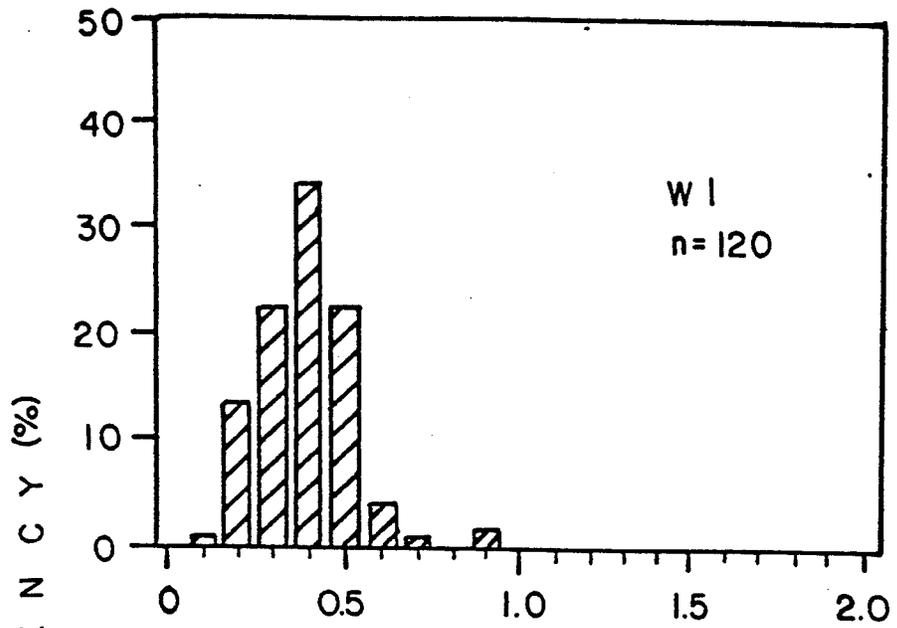
Table 5-4. Comparison of relative abundance (% of total number) of functional feeding groups (Merritt and Cummins 1984) of Trichoptera at stations W1 (unstable) and W1S (stable) of Wilson Creek for 1987.

FUNCTIONAL FEEDING GROUP	W1	W1S
SHREDDERS (GATHERERS)	52.6	36.3
COLLECTORS (FILTERERS)	36.4	57.0
PREDATORS	2.5	3.3
SCRAPERS, PIERCERS	8.5	3.4

Table 5-5. Comparison of 1986 discharge with historical flow data (1965-1985) for stations W1 and W1S of Wilson Creek, Manitoba. Annual flow > 1986 discharge calculated from annual peak discharge, periodicity is the average number events/year from visual inspection of hydrograph.

| | JUNE | | SEPTEMBER | |
	W1	W1S	W1	W1S
1986 DISCHARGE (m^3/s)	.3341		.0623	
% BED PAVING MATERIAL AT INCIPIENT MOTION	12	0	8	0
HISTORICAL % DISCHARGE (DAILY)	18		53	
PERIODICITY	3.7		5.6	

On the average a flow equal to or greater than the June spate occurred 4 times a season, with the September spate having a periodicity of 7 (Table 5). The September spate discharge was equalled or exceeded over 50% of the days historically, thus at least 8% of bed paving material was at incipient motion for over 50% of the days, on the average, at station W1, while major components of the substrates at station W1S would theoretically be 100% stable.

The examination of historical flow records is critical in characterizing the frequency, intensity, and duration of flow events, and related substrate movement, and how these hydrological factors determine aquatic insect habitats. In the present study, station W1, with highly mobile shale substrates, appears to be an unsuitable environment for caddisflies at least 183 days of the year. The flow data for 1986 are probably closer to the norm for this station, while 1987, a dry year with no summer spates was a rare occurrence. McElvary et al. (1989) reported year to year variation in aquatic invertebrates, with reductions related to years with flows sufficient to move substrates.

The introduction of a stable riffle had a mitigating effect on caddisflies during summer spates. This has important implications for fisheries projects. The inclusion of riffles in the design of Manitoba escarpment headwater flood-storage dams (Gaboury pers. comm.) would enhance the standing stocks of natural food sources for fish stocked in reservoirs created by dams constructed in the unstable reaches of streams.

Future studies should include the construction of more riffles to strengthen the statistical significance of the results, and also to test the effects of more frequent spates on the insects of these riffles. An investigation into the lack of anticipated colonization of the stable riffle by <u>Glossosoma</u> <u>intermedium</u> should also be undertaken, as this species, with its aggregation behaviour, appears to be a good indicator of substrate stability.

5.6. ACKNOWLEDGEMENTS

6. GENERAL DISCUSSION

The aquatic insects of Wilson Creek are greatly influenced by hydrological processes. Aquatic insect densities were shown to respond to changes in discharge at each of the stations, however each station was affected to a different degree for given discharges. As a result, a relatively small amount of the variation could be explained by discharge. When station effect was introduced into the model, there was an increase in the regression coefficient. Substrate stability had a greater overall effect on aquatic insect density. Most of the variability in density for the whole stream could be explained by the model including substrate stability, while adding station effect did little to improve the regression coefficient. Discharge alone as a disturbance is important, though not as important as the relationship between substrate stability and discharge.

In a small-scale experiment, where a stable riffle was constructed in the unstable reach, I demonstrated the varying effect of equal discharge on different substrate stability. Standing stocks of insects following spates were unchanged in the stable riffle, while reductions occurred in the unstable reach. Perhaps unstable reaches of channelized (unstable) streams can be rehabilitated with suitably designed stable riffles. The application of substrate stability/discharge relationships could have potential in the management of fisheries through increased production of food organisms of stream dwelling fish species, and through higher spawning success of lake and river species utilizing rehabilitated reaches of channelized streams.

In attempting to analyse disturbance of aquatic insect habitat, flow regimes (discharge) have been analyzed, while the effect of substrate scouring associated with these discharges has often been ignored. Resh et al. (1988), for example were interested in quantification of disturbance in terms of floods, rather than the biological response. They concluded that predictability of hydrologic regimes was important in the evolution of aquatic insects life histories. Certainly, being able to quantify and analyse aquatic insect habitats in this way is a major contribution to the study of insects, and will no doubt lead to great insight into abiotic factors affecting aquatic insects. I believe, however, that the aquatic ecosystem can be better described by an examination of spatial/temporal effects of substrate stability/discharge relationships and their effect on the aquatic insects.

Most species of aquatic insects in Wilson Creek were characterized by life history adaptations which may have resulted from selective pressures other than for survival in an unstable environment, but which none the less are suited for existence in the most unstable reach of Wilson Creek. These adaptations included: univoltine fast seasonal development, multi-voltinism, univoltinism with several simultaneous cohorts, timing of development and emergence coincident with quiescent periods of flow. The life history strategies of insects of Wilson Creek are consistent with species of other frequently disturbed rivers in which unpredictable scouring discharges favour insects with the above mentioned life history adaptations (Sagar 1986, Gray 1981, Scrimgeour et al. 1988).

What remains to be examined is how life history strategies of insects in rivers covering a range of frequency of disturbance differ from one another. Again, the lack of hydrological information prevents a definitive examination of this question on a broad geographical scale. In Manitoba rivers less susceptible to scouring discharges, several stonefly species with semivoltine life histories have been collected (Cobb and Flannagan 1989, Flannagan pers. comm.). These rivers are also larger and warmer, consequently, further research is necessary to elucidate relative importance of factors determining the community structure of aquatic insects and their life history strategies resulting from these factors.

Several species ($\underline{E}$. $\underline{inermis}$, $\underline{I}$. $\underline{bilineata}$, $\underline{H}$. $\underline{brevis}$) had slow seasonal development, and were present as immatures through most of the year. In order to inhabit the most unstable reach, they appear to have behavioural adaptations (burrowing, highly mobile to reach extreme stream edge), or they must be predominant in the drift, to allow recolonization from upper stable reaches . These species deserve future examination of adaptations to elucidate their strategies for survival in unstable environments.

When I started this study, I fully expected to find large differences in species assemblages between the three natural reaches of stream. I expected to find fewer species in the most unstable reach than the stable ones. There were only a few taxa ($\underline{M}$. $\underline{californica}$, $\underline{G}$. $\underline{intermedium}$, Simuliidae) which failed to become established in the unstable reach. This may have been, in part, because of fewer spates

occurring throughout the study period than on average, thus the system was stressed to a lesser extent than during an average year. Many of the rarer species might not have been present had there been six summer spates, as occurs on average at Wilson Creek. Perhaps the similarity of species between reaches is related to the close proximity of stations to each other. The whole watershed is only 6 km in length, and there may be ample opportunity for recolonization of denuded reaches through drift and oviposition from more stable reaches. In a small watershed chemistry and temperature, are more constant among stations, but species differences may have been more dramatic if there were several tens of kms between reaches of differing stability. In addition, the hyporheic zone has been suggested as a pool for colonization following floods (see review by Williams 1984).

I have made some fairly strong statements regarding weaknesses of traditional theories in explaining aquatic insect ecology on a global scale, while claiming that substrate stability is a very important factor to be examined in ecological studies. One way to support my arguments is to attempt to apply the theory to a wider scale. Herein lies the problem. Statzner (1986) lamented the lack of usable hydrological information in the literature. Similarly, I was able to find usable data for only 8 rivers in the world where species lists and necessary hydrological data are available, but these covered a wide geographic range (Table 1). The number of species of mayflies, stoneflies and caddisflies was negatively correlated ($p < 0.001$) with increasing average number of scouring discharges/year (Fig. 1). This is

a preliminary examination, but hopefully with an increased awareness of hydrological measurements required for this type of analysis, researchers will include these data when describing their study sites. Expanding this data set would be an exciting study, which hopefully can be continued.

In describing the habitat template for global flow conditions, Minshall (1988, p.278) used flow predictability and change in flow as his parameters, and characterized K, r, and A strategies, and identified in which quadrat of the diagram they would lie, and presented examples of stream types in each category. I suggest that rather than use flow predictability, he should have used predictability of scouring discharges (Fig. 2). This would allow for the characterization of reaches within streams, and among streams within a geographical range, as well as on a global basis.

I conclude that the community as a whole is determined by stochastic (abiotic) factors, that is the frequency, magnitude and duration of substrate moving discharges. Most of the species exhibited low resistance but high resilience to floods, the result of favourable life history and behavioral adaptations. There is evidence that the dynamic equilibrium theory (Huston 1979) best fits this stream.

Several implications arise from this study. First, aquatic insects can be useful as indicators of substrate stability, and can be useful in testing relationships among various hydrological parameters. Second, hydrological factors are important determinants of aquatic insect habitat. This is important when considering a sample regime in

conjunction with an ecological study, or an environmental impact study. Any cause/effect scenario can easily be confounded by natural variability resulting from differing substrate/discharge relationships both spatially and temporally.

Table 6-1. List of sources of rivers in the world for which authors
   supplied the number of scouring discharges per year, and species
   lists for mayflies, stoneflies and caddisflies.

RIVER	COUNTRY	SOURCE
Sycamore Creek	Arizona (U.S.A.)	Gray 1981
Big Sulphur Creek	California (U.S.A.)	McElvary et al.1989
Harp Lake Outflow	Harp L. Ontario (Can.)	Giberson pers.comm.
Roseau River	Manitoba (Can.)	Flannagan pers.comm.
Cowan Creek and S.Duck River	Manitoba (Can.)	Cobb et al. 1984 Friesen et al. 1984
Ochre River	Manitoba (Can.)	Cobb and Flannagan in press
Wilson Creek	Manitoba (Can.)	this study
Rakaia River	New Zealand	Sagar 1986
Ashley River	New Zealand	Scrimgeour and Winterbourn 1989

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FIGURE 6-1. Relationship between number of scouring discharges per year
and the number of species of mayflies ● , stoneflies ■ , and
caddisflies ▼ . Sources as in Table 1.
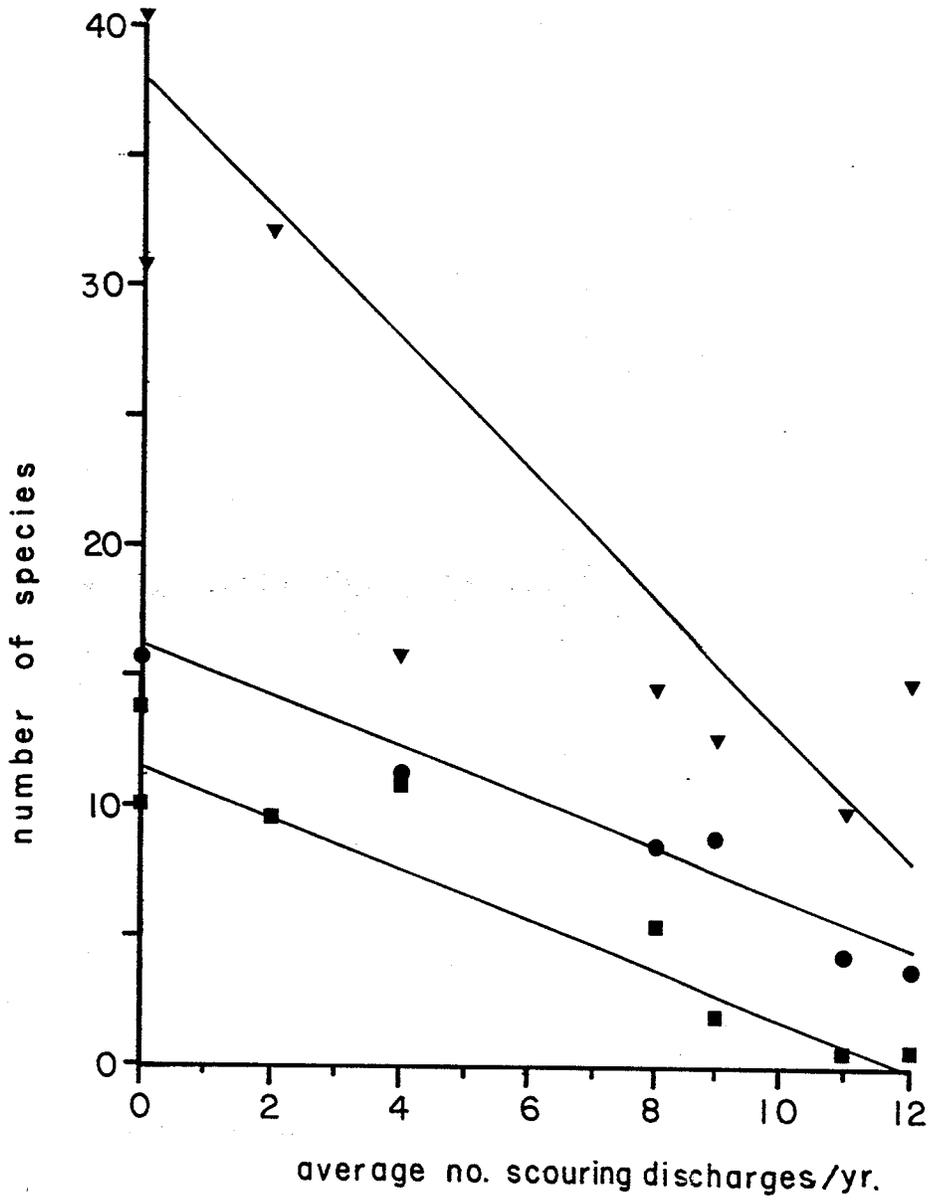
FIGURE 6-2. Modification of Minshall's (1988) perception of effects of flow on aquatic insect life history strategies. K= life cycle adapted to stable environment, and longer than one year, r= life cycle adapted to unstable environment, usually less than or equal to one year. A= life cycle adapted to severe environments.
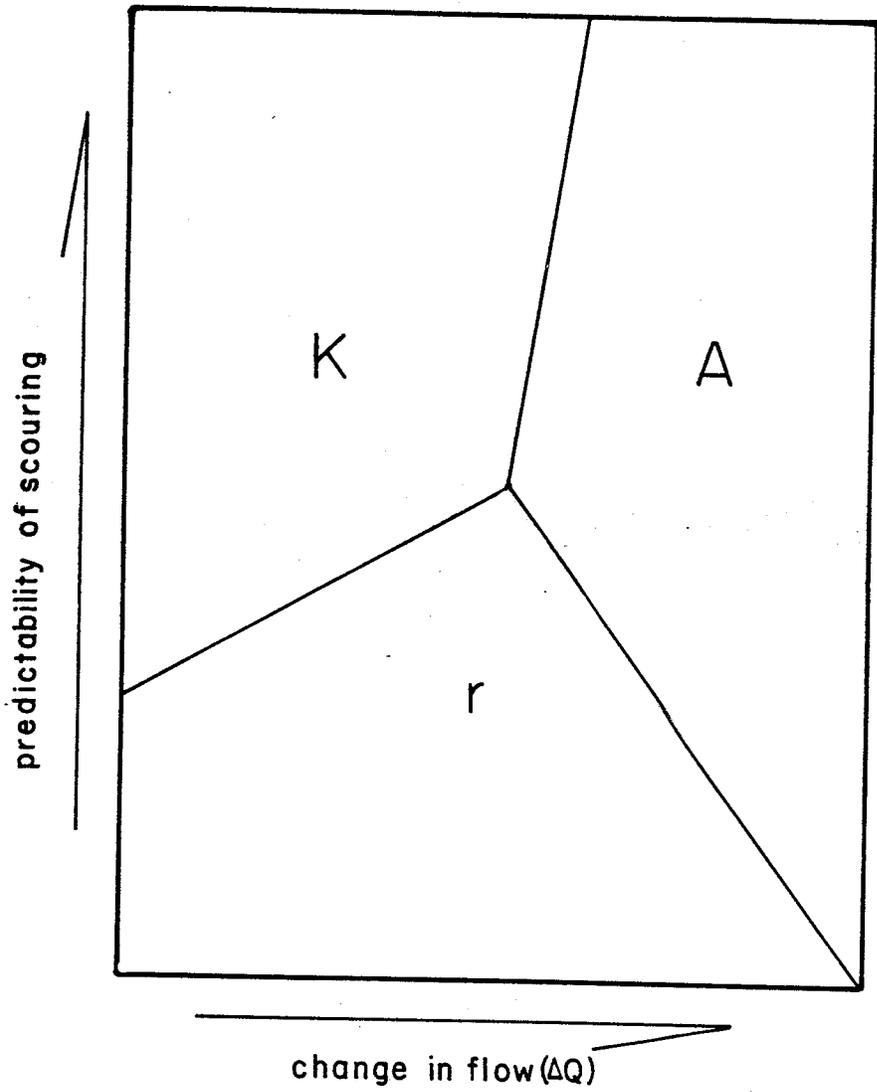
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Appendix 1. Description of formulas and symbols used in hydrological anaylses in Wilson Creek aquatic insect study.

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1. Mean substrate particle size (cm) = l+w+h / 3.

2. Tractive force (kg/m^2) = d*s*1000(specific wt. water; kg/m^3)

3. Slope (%) = (change in height (rise) / distance (run)) x 100

4. Froude number = V^2 / gd

where:
      l = length
      w = width
      h = height
      d = mean depth of water
      s = slope
      v = velocity (m^3/s)
      g = gravitational acceleration (L/T^2)

Appendix 2a. Methods of calculation of Colwell's (1974) index of predictability for flow regime, using Resh et al. (1988), for Wilson Creek using historical flow data (1969-1981).

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1. Construct frequency matrix for maximum flows where classes represent log (base 2) of the range of flows in the class. For example, class 1 represents flows > 1 < 2 L / s; class 2 represents flows > 2 < 4, L / s, etc. Each number in the matrix represents number of years that the maximum monthly flow fell into that class (total=11).

Class	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Y	$\frac{Y_i}{Z}\log\frac{Y_i}{Z}$
0														
1														
2	1	1											2	-.028
3	1	3	1								2	1	8	-.074
4	2	1	1				1			2	2	2	11	-.090
5	4	3	2			1	1	1		2	2	3	19	-.121
6	2	2	5				1	2				5	17	-.115
7	1	1	1				5	4	3	1	1		17	-.115
8		1		1		2	2	1	2	2	3		14	-.103
9				1	4	2		1	3	2			13	-.099
10				1	3	1	1		1				7	-.068
11					3	3				2	1		9	-.08
12					4	2	1	1	1				9	-.08
13					1	2	1						4	-.046
14						1							1	-.016
15									1				1	-.016
													132	-1.051

S = no. of states = 16

2. Calculations using the following formula:

N_{ij} = number of cycles for which phenomenon is in state i at time j, = each individual entry in the matrix.

X_j = column totals = ΣN_{ij}

Y_i = row totals = ΣN_{ij}

Z = grand total = $\Sigma\Sigma N_{ij}$

Uncertainty with respect to time is: $H(x) = -\Sigma\left(\frac{X_j}{Z}\log\frac{X_j}{Z}\right) = 1.079$

Uncertainty with respect to flood intensity is $H(y) = -\Sigma\left(\frac{Y_i}{Z}\log\frac{Y_i}{Z}\right) = 1.051$

Uncertainty with respect to interaction of the two is $H(xy) = -\Sigma\Sigma\left(\frac{N_{ij}}{Z}\log\frac{N_{ij}}{Z}\right) = 1.779$

Predictability (P) $= 1 - \dfrac{H(XY)-H(X)}{\log S} = 0.42$ Contingency (M) $= \dfrac{H(X)+H(Y)-H(XY)}{\log S} = 0.13$ Constancy (C) $= 1 - \dfrac{H(Y)}{\log S} = 0.29$

Appendix 2b. Methods for calculation of index of predictability of scouring discharges in Wilson Creek, using number
    of days in month in which > 10% of substrate at incipient motion (1969-1980).
===
1. Construct similar matrix to above, except use per cent of days in month in which > 10% of substrate at incipient motion
    as class categories. Since no scouring discharges occurred between November and March, only the remaining months are used.

Station W1

Class	Apr	May	June	July	Aug	Sept	Oct	Y	$\frac{Y_i}{Z}\log\frac{Y_i}{Z}$
<1	1	1	1	7	8	5	6	29	-.1597
1-5	0	0	1	1	2	4	2	10	-.1151
6-10	3	2	1	1	0	0	0	7	-.0947
11-20	0	1	0	0	0	0	2	3	-.0549
21-40	0	0	3	1	0	0	0	4	-.0667
41-80	4	1	3	0	1	2	1	12	-.1258
81-100	3	6	2	1	0	0	0	12	-.1258
								77	-.7427

2. Using formula of appendix 2a: P = .3848   M = .2636   C = .1212

Station B1
Class

Class								Y	
<1	3	7	6	10	10	10	10	56	-.1006
1-5	1	0	1	0	0	0	1	3	-.0549
6-10	4	1	3	1	1	0	0	10	-.1151
11-20	3	2	1	0	0	1	0	7	-.0947
21-40	0	0	0	0	0	0	0		
41-80	0	1	0	0	0	0	0	1	-.0245
81-100	0	0	0	0	0	0	0		
								77	-.3898

P = .6573   M = .1106   C = .5388

Station B2
Class

Class								Y	
<1	5	7	8	10	10	10	11	61	-.0801
1-5	4	2	1	1	1	0	0	9	-.1089
6-10	1	0	2	0	0	0	0	3	-.0549
11-20	1	1	0	0	0	1	0	3	-.0549
21-40	0	1	0	0	0	0	0	1	-.0245
								77	-.3234

P = .7159   M = .0986   C = .6173