THE RELATIONSHIP BETWEEN SOME PHYSICAL FACTORS AND MAYFLIES EMERGING FROM SOUTH DUCK RIVER AND COWAN CREEK, MANITOBA

J.F. Flannagan, D.G. Cobb and M.K. Friesen

Freshwater Institute, Central and Arctic Region, Department of Fisheries and Oceans, 501 University Crescent, Winnipeg, Manitoba, Canada, R3T 2N6

ABSTRACT

A total of 25 species of mayflies were collected in the open water season from emergence traps located along two streams in the Duck Mountain area of Manitoba. Each stream produced 24 species. Cowan Creek produced 368 individuals m^{-2} and South Duck River 630 individuals m^{-2}. Considering the difference in reaches sampled these densities are not considered significantly different. The densities of mayflies collected during this study were similar to densities collected in other Canadian studies, despite differences in chemistry and biological factors such as species composition. Multiple regression analyses of the density and species distribution of the mayflies against temperature (day-degrees and mean annual temperature) and hydrologic factors including indices of instability indicated that: number of species present was related to total degree-day accumulation and stability of the substrate (R^2 = 0.727, P = 0.001); density of mayflies was found to be related to the median reach substrate size and the mean annual temperature (R^2 = 0.411, P = 0.042). In addition, the density of 4 species was found to relate positively to substrate stability, while the density of 3 species related negatively to substrate stability. Five species had temperature as a determinant in their density distribution and 12 species either did not occur in sufficiently large numbers, at sufficient stations or did not show any relationship between their distribution and physical factors.

INTRODUCTION

Poor spawning success of the walleye, *Stizostedion vitreum* (Mitchell) in Dauphin Lake, Manitoba and other large lakes of the Canadian Prairies, has been attributed to substrate instability and sedimentation problems in their spawning streams (Gaboury 1985). Both of these problems have been intensified by clearing of the land for agriculture and straightening of the streams to "improve" spring melt-water run-off. Among other impacts, straightening of the streams has increased their slope, and thus their erosive power, while clearing of the land has increased the load of fine sediments being added to the streams.

Recent studies (e.g. Statzner and Higler 1986, 1985, Newbury 1984, Winterbourn *et al.* 1981, and others) have suggested that hydrological conditions play a very large role in controlling the distribution of aquatic insects in streams. This suggests that aquatic insects could be indicators of substrate instability and/or sedimentation in the walleye spawning streams.

In 1980 we studied the emergence of aquatic insects from two streams (South Duck River and Cowan Creek) in the Duck Mountains Provincial Park and Forest Reserve, Manitoba (Fig. 1). These streams are pristine in their upper reaches. The lower reaches, although flowing through agricultural land, are protected by a broad band of

I.C. Campbell (ed.) Mayflies and Stoneflies, 233–242.

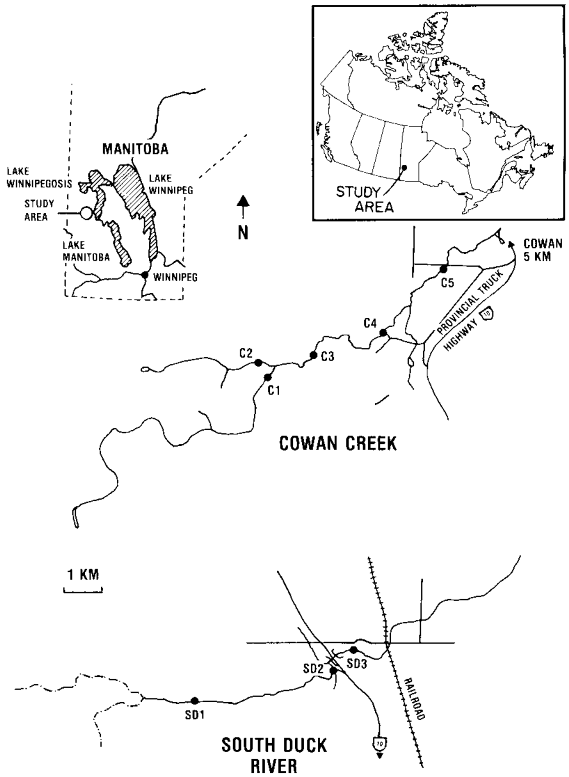

Fig. 1. Location of the South Duck River, Cowan Creek and the sampling sites on the streams.

natural riparian vegetation. The streams serve as a control for studies of the Dauphin Lake walleye spawning streams further south.

This paper describes an investigation of the species composition, emergence periods, spatial distribution and abundance of the adult Ephemeroptera from these two streams and attempts to relate the distribution and abundance to hydrological conditions.

STUDY AREA

The South Duck River (SD) and Cowan Creek (C) originate on the Manitoba Escarpment, a 400 M high step in the Canadian Prairies composed of Cretaceous shale with a glacial till overburden. The streams have a groundwater base flow, are cool and permanent in summer and, in spite of air temperatures reaching $-40\,^{\circ}C$ or lower, remain flowing in some reaches throughout the winter. Stations SD1, C1, C2 and C3 are upstream of any agricultural activity. Stations SD2, SD3, C4 and C5 are located in areas of light agricultural activity but, as previously mentioned, are well protected from this activity. Stations SD2 and C4 are located in areas of previous beaver activity, and thus have low slopes and fine substrates. Where possible we located 1 trap in a riffle and 1 in a pool at each station. Cobb *et al.* (1984) provide a more detailed description of the stations and area.

METHODS

Insect emergence was collected from 12 May to 20 September 1980 using two 1 m^3 box emergence traps (Flannagan 1978) at each station except C4 where only 1 trap was used. Traps were emptied every second day and various physical and chemical parameters were measured each sampling day (see Cobb *et al.* 1984, Friesen *et al.* 1984 for details).

Each sampling station and trap site was characterized hydrologically using the methods described by Newbury (1984).

Since we were particularly interested in examining the relationship between mayfly distribution and stability of the substrate, two instability indices were included in the hydrological data: tau/median trap substrate size and tau/median reach substrate size. Tau, the shear stress imposed in the substrate is, according to Newbury (1984), approximately equal to the size in centimetres of rounded substrate in incipient motion at bank full conditions. Thus the indices give a relative measure of the instability of the substrate inside and in the general area of the traps. A negative relationship with these indices therefore indicates a preference for a stable substrate and vice versa.

A stepwise forward selection multiple regression analysis procedure was used to correlate dependent variables with possible independent variables (Draper and Smith 1966). Conservative criteria were used for entry of the variables; only

Table 2. Temperature and hydrological data for the various stations on South River and Cowan Creek

	S-D 1-1	S-D 1-2	S-D 2-1	S-D 2-2	S-D 3-1	S-D 3-2	C 1-1	C 1-2	C 2-1	C 2-2	C 3-1	C 3-2	C 4	C 5-1	C 5-2
Slope	0.01	0.01	0.009	0.003	0.031	0.031	0.013	0.013	0.033	0.033	0.036	0.036	0.006	0.009	0.003
Shear stress ($kg \cdot m^{-2}$)	2.90	2.90	2.90*	0.99	11.78	11.78	2.73	7.26	7.26	7.20	7.20	7.20	3.40*	2.52	1.74
B.F. depth (cm)	29	29	16	33	38	38	21	21	22	22	20	20	28	28	28
Trap Substrate (cm)	13.7	13.7	7.7	0.01	40.0	46.3	14.3	10.1	30.0	20.0	29.0	29.0	2.0	17.0	17.0
Reach Substrate (cm)	13.7	13.7	7.7	7.7	46.3	46.3	14.3	14.3	24.3	24.3	29.0	29.0	2.0	17.0	17.0
$\frac{\text{Shear stress}}{\text{Trap substrate}}$	0.21	0.21	0.36	9.90	0.25	0.25	0.19	0.27	0.24	0.36	0.25	0.25	1.70	0.15	0.10
$\frac{\text{Shear stress}}{\text{Reach substrate}}$	0.21	0.21	0.36	0.13	0.30	0.25	0.19	0.19	0.30	0.30	0.25	0.25	1.70	0.15	0.10
Total degree Days	1624	1624	1924	1924	1822	1822	1383	1383	1582	1582	1582	1582	2095	2305	2305
Mean annual temperature (°C)	4.5	4.5	5.3	5.3	5.0	5.0	3.8	3.8	4.3	4.3	4.3	4.3	5.7	6.3	6.3

* corrected for shale (see Newbury 1984).

Table 1. Mean density and species composition of mayflies at the various stations sampled on South Duck River and Cowan Creek

	S-D 1	S-D 2	S-D 3	C 1	C 2	C 3	C 4	C 5	Ratio of ♀ : ♂	# Traps present
Ameletus sp	0	1	0	0	0	1	0	0	both ♀♀	2
Baetis brunneicolor McD.	30	30	58	29	14	56	1	12	1.2	15
B. flavistriga McD.	38	45	187	12	15	113	9	35	3.0	15
B. hageni Eaton	0	1	1	1	0	3	0	1	0.3	7
B. harti McD.	3	3	63	0	1	1	1	11	3.2	11
B. intercalaris McD.	9	20	115	1	6	3	3	11	0.6	13
B. pluto McD.	54	18	65	7	11	24	13	4	0.6	15
B. pygmaeus (Hagen)	7	32	36	6	2	2	2	78	1.0	13
B. quilleri Dodds	10	1	13	1	0	27	4	2	1.5	9
B. tricaudatus Dodds	170	103	187	35	89	233	6	23	1.1	15
Brachycercus sp.	0	1	0	0	1	1	0	36	1.1	5
Centroptilum sp.	18	38	0	0	2	0	0	7	2.4	5
C. convexum McD.	0	3	0	1	1	2	2	93	1.3	8
C. conturbatum McD.	1	27	0	2	11	7	2	67	1.0	11
C. infrequens McD.	1	6	1	2	102	36	0	22	1.3	10
C. rufostrigatum McD.	6	52	1	0	5	2	3	24	1.0	12
C. nr *walshi* McD.	1	77	1	0	0	1	0	1	1.0	6
Cloeon rubropictum McD.	0	0	0	0	0	0	0	1	–	1
Epeorus albertae (McD.)	0	3	1	1	0	0	0	9	2.0	6
Ephemerella sp.	1	12	13	0	0	1	0	9	1.9	8
Heptagenia pulla (Clemens)	0	2	1	0	0	0	0	1	0.6	4
Paraleptophlebia debilis (Walk.)	181	54	27	8	42	109	16	136	19.8	15
Pseudocloeon turbidum McD.	10	31	29	1	1	2	1	50	2.0	12
Siphlonuris alternatus (Say)	0	2	1	0	0	0	0	0	0.3	2
Stenonema vicarium (Walk.)	0	2	1	0	0	1	0	18	1.8	6
# Species present	16	24	19	14	15	20	12	23		

variables which increased the R^2 values by more than 0.1 and which had a partial probability of not more than 0.04 were included in the equation. It is obvious from Table 1 that the possible independent variables are intercorrelated, so several different equations might have had the same predictive capacity. Thus the regression relationships are meant to demonstrate that several physical parameters affected the response, and are not meant to be predictive nor to show the relative importance of the different variables.

RESULTS

Temperature and hydrological data characterizing the sites of each emergence trap are presented in Table 1.

A total of 25 species of Ephemeroptera emerged into the traps on the two streams combined. Each stream produced 24 species. *Cloeon rubropictum* was not collected from the South Duck River and *Siphlonurus alternatus* was not collected from Cowan Creek (Table 2). 3310 (368. m^{-2}) mayflies were collected from 9m^2 of traps in Cowan Creek while 3,781 (630. m^{-2}) were collected from 6 m^2 of traps in the South Duck River. Densities of mayflies in individual traps varied from 67. m^{-2} at C4 to 1118. m^{-2} at SD3.1, while numbers of species per trap varied from 9 at C1.1 to 22 at C5.2 (Table 2). *Paraleptophlebia debilis* and 4 *Baetis* species were collected from every trap and, at the other extreme, *Cloeon rubropictum* was collected from only 1 trap.

Most species commenced their emergence in

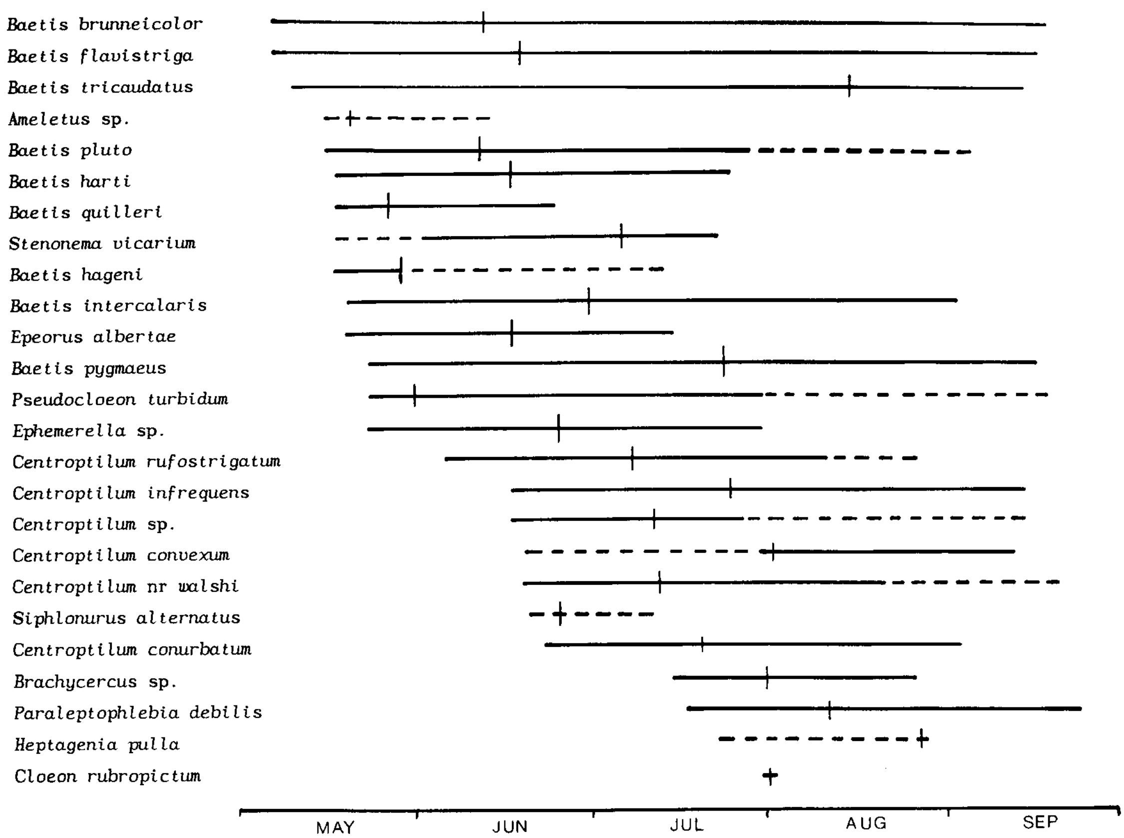

Fig. 2. Emergence times of the various species of mayflies – both streams and all sites combined. The time of 50% hatch is indicated.

May or June, although a few (*Brachycercus* sp., *Heptagenia pulla* and *Paraleptophlebia debilis)* did not start until July and one species, *Cloeon rubropictum,* was not collected until August (Fig. 3). Length of emergence period was variable, some species completed their main emergence in less than two weeks, e.g. *Baetis hageni,* while others emerged continuously over the whole open-water season, e.g. *Baetis intercalaris* (Fig. 3). It should be remembered that Fig. 3 lists emergence from all stations combined and that at individual stations emergence periods were often much shorter.

The multilinear regression analyses (Table 3) suggested that when all traps from both streams were taken together the total density of mayflies was related to the size of the substrate in the reach in which the traps were set and the mean annual temperature. This correlation was significant at $P = 0.42$ and these two factors together explained 41% of the variation in the samples. The number of species present in any trap was a function of the degree days minus the instability index for the reach (tau/reach median substrate). This correlation was significant at $P < .001$ and explained 72.7% of the variation in the data. Table 3 also lists the analyses of the individual species density distributions and the factors affecting them. The various models presented in the table account for up to 97.3% (*C.* nr *walshi)* of the variation in the data. Only species in which significant correlations were found are listed.

DISCUSSION

Cowan Creek appears to be a typical headwater stream. The mean annual water temperature in-

Table 3. Results of multiple regression analyses (number of observations in each case is 15)

Dependent variable	Independent variable	R^2 after entry	Final probability of partial F value
Density of Ephemeroptera	median reach substrate	0.22	0.032
	mean annual T°	0.41	0.072
Number of species present	Degree days	0.533	0.001
	$\frac{\text{shear stress}}{\text{median reach substrate}}$	0.727	0.013
Density of *B. harti*	median trap substrate	0.339	0.102
	median reach substrate	0.476	0.033
Density of *B. flavistriga*	median reach substrate	0.417	0.009
Density of *B. intercalaris*	shear stress	0.402	0.005
	slope	0.696	0.001
Density of *B. pygmaeus*	mean annual T°	0.382	0.001
	Bank full depth	0.516	0.013
	$\frac{\text{shear stress}}{\text{median reach substrate}}$	0.704	0.023
Density of *Brachycercus* sp	mean annual t°	0.497	0.001
	$\frac{\text{shear stress}}{\text{median reach substrate}}$	0.643	0.122
	$\frac{\text{shear stress}}{\text{trap substrate}}$	0.716	0.034
Density of *Centroptilum* sp.	$\frac{\text{shear stress}}{\text{median trap substrate}}$	0.777	0.001
Density of *C. conturbatum*	Bank full depth	0.513	0.001
	shear stress	0.691	0.001
	slope	0.836	0.010
Density of *C. rufostrigatum*	$\frac{\text{shear stress}}{\text{median trap substrate}}$	0.782	0.002
	bank full depth	0.901	0.001
Density of *C. convexum*	Bank full depth	0.518	0.003
	Shear stress	0.644	0.015
	Median trap substrate	0.749	0.050
Density of *C. walshi*	$\frac{\text{shear stress}}{\text{median trap substrate}}$	0.973	0.001
Density of *Epeorus albertae*	Bankfull depth	0.610	0.001
	Shear stress	0.740	0.021
Density of *Ephemerella* sp.	Mean annual T°	0.285	0.012
	Median reach substrate	0.412	0.024
	Median trap substrate	0.596	0.047
Density of *Stenonema vicarium*	Degree-days	0.584	0.001
	$\frac{\text{shear stress}}{\text{median reach substrate}}$	0.761	0.006
Density of *Pseudocloeon turbidum*	Mean annual T°	0.261	0.002
	Bankfull depth	0.465	0.013
	$\frac{\text{shear stress}}{\text{median reach substrate}}$	0.615	0.063

creases progressively from the source downstream and the slopes are gentle towards the source, steeper in the middle reaches and gentle again in the lower reaches (Table 1). Mayfly densities and species diversity follow the same progressively increasing pattern as the temperature except at station C4 which was low in both density and diversity of mayflies (Table 2). This station had a soft, very uniform substrate of small, mostly shale, particles embedded in sand. Sprules (1947) and others (see review by Brittain 1982) have shown that species diversity and density in streams is related to the variety of habitats available, uniform substrates tending to produce low species diversity and density of mayflies. Station C4 demonstrates this well.

South Duck River, on the other hand, had its lowest slopes and warmest water at our middle station (SD2). Species richness was highest at this station while mayfly densities were highest at the site furthest downstream, SD3 (Table 2). This latter site had a large median substrate size and a very steep slope. This suggests that high mayfly diversity may be related to high water temperature and/or low slopes, while density may be related to steep slopes and/or large substrates.

The regression analyses of all the data together (Table 3) suggest that mayfly densities are positively influenced by both annual temperature and reach median substrate size. Since the range of annual temperatures available in this study was small and was only 0.3 °C different between SD2 and SD3, the major determinant in the model is reach substrate size, which was largest at SD3. Similarly, the number of species present was found to be set by degree-days and modified slightly by the stability of the substrate (Table 3). Degree-days in South Duck River reached a maximum at SD2. Thus although South Duck River does not follow the classical temperature, slope and substrate profile, it is not anomalous in terms of the distribution and abundance of its mayfly fauna.

The South Duck River produced 630 mayflies m^{-2} and Cowan Creek produced 368 mayflies m^{-2}. Densities of stoneflies (Friesen *et al.* 1984) and brook trout (Franzin and Harbicht 1985) in South Duck River are also about double those in Cowan Creek, but Cobb *et al.* (1984) found similar densities of caddisflies in the two streams. Temperature data (Table 1) shows that Cowan Creek stations C1, C2 and C3 were all colder than the furthest upstream station in South Duck River, suggesting that the reaches of stream sampled by these three stations were closer to the stream source than any station sampled in South Duck River.

Headwater streams, or headwater areas of streams, have generally been found to have fewer species and lower densities of mayflies than middle reaches (Harper and Harper 1982, Brittain 1982), thus the difference in mean densities recorded for these two streams is likely not real but is rather a function of the reaches sampled.

Comparisons with other mayfly emergence studies in Canada is made difficult by a number of factors including the variations in chemistry, zoogeographic restrictions in the ranges of mayfly species and "order" of streams sampled. Harper and Harper (1982) collected 88-704 mayflies m^{-2} belonging to 22 species in soft or acid water tributary streams in Quebec. Only 4 or 5 species of mayflies are common to our study and theirs, but the densities and total number of species collected are remarkably similar. Sprules (1947) and Ide (1940) studied emergence of aquatic insects from streams, including tributary streams, in Algonquin Park, Ontario. Five of the six species Sprules found at his furthest upstream station and about half of the species from his three upper stations are in common with the species recorded here. Densities of Ephemeroptera in Sprules' study were in the same ranges as ours. Ide's (1940) densities were somewhat higher (399–6,527 m^{-2}). Boerger and Clifford (1975) studied emergence of mayflies from a brown-water stream in Alberta and collected 348 mayflies m^{-2}, representing 15 species. Only 3 or 4 species are in common with our study. Harper and Harper (1984) studied streams in Ontario that are similar in chemistry to the Duck Mtn streams. They collected 4–18 species and 38–4992 individuals m^{-2}. About half of these species are in common with the Duck Mtn. species and the densities are in the same range. Clifford (1980) reports 375 nymphs m^{-2} as an average of all published Holarctic mayfly studies.

Thus, in spite of the differences in location, chemistry and species composition, Cowan Creek and South Duck River have about, or slightly above, the expected density and diversity of mayflies. However, what is apparently unique about these streams is that one family, the Baetidae, dominates – providing over 80% of the specimens and almost three quarters of the species in the traps. These streams probably partly or totally dry up in periods of extreme drought as evidenced by the lack of cold water species (Table 2), in spite of presumed historical opportunity (Flannagan and Flannagan 1984). In other isolated mountain areas or oceanic islands, baetids are perhaps the most opportunistic family (Edmunds 1972). Thus their dominance here is perhaps not unexpected.

In view of apparent similarities in mayfly density and diversity despite wide variation in biological and chemical conditions, it seems probable that physical parameters such as hydrologics and temperature control mayfly abundance in streams. Overall species richness and density have been discussed earlier. In the cases for individual species, species not listed in the multilinear regression analyses (Table 3) fall into two groups:

a) Species that did not emerge in sufficient numbers and/or were not recorded from sufficient stations to provide a reliable model. These were *Cloeon rubropictum, Siphlonurus alternatus, Ameletus* sp., *Baetis hageni* and *Heptagenia pulla*.

b) Species which did not show any significant relationship between occurrence and physical factors. These were: *Baetis brunneicolor, B. pluto, B. quilleri, B. tricaudatus, Centroptilum infrequens* and *Paraleptophlebia debilis*.

These species may show a significant relationship with physical factors if a wider range of habitats is examined or, their density distributions may indeed be independent of the physical factors.

The 14 remaining species show significant relationships between their density distribution in the two streams and the physical factors (Table 3). Since the relationship between abundance and the substrate instability factor (tau/median substrate size (cm)) is of particular importance in our study these 14 species have been arranged into 3 groups:

Group 1 relationship with substrate instability factor is negative, i.e. increase in stability results in increase in density or vice versa.

Group 2 relationship with substrate instability factor is positive, i.e. decrease in stability causes increase in density or vice versa.

Group 3 no relationship with stability but significant relationship with another hydrological factor.

In addition a further group (4) can be established, that in which temperature is a controlling or important factor in determining the density of mayflies.

The species fitting into the various groups are:

Group 1 *Brachycercus* sp., *Stenonema vicarium, Baetis pygmaeus, Pseudocloeon turbidum*.

Group 2 *Centroptilum rufostrigatum, Centroptilum* sp., *C.* nr *walshi.*

Group 3 *Centroptilum conturbatum* (depth, shear stress, slope); *C. convexum* (depth, shear stress, median substrate size); *Baetis flavistriga* (median substrate size); *B. harti* (median substrate size); *B. intercalaris* (slope, shear stress); *Epeorus albertae* (depth, shear stress); *Ephemerella* sp. (median substrate size).

Group 4 *Brachycercus* sp., *Stenonema vicarium, Baetis pygmaeus, Pseudocloeon turbidum, Ephemerella* sp.

Thus besides the overall increase in species with increase in substrate stability, 4 species will increase, and 3 will decrease their numbers, in response to an increase in stability. Temperature although largely controlling the overall density of mayflies seems to have a significant direct effect only on five species. The remaining species respond to a variety of other factors of which median substrate size appears to be the most important single factor followed by shear stress (Table 3).

CONCLUSIONS

The mayfly faunas of Cowan Creek and South Duck River are similar to each other allowing for the difference in reaches sampled. In addition they are not different in density or number of species from streams of very different chemical and biological make up. The density of total mayflies in the streams was found to be related to the substrate in the reach sampled and the annual temperature of the water. The number of species present was related to the number of degree-days and the stability of the reach. Approximately half of the species collected were either not present in sufficient numbers and/or at sufficient stations to allow reliable analyses of factors controlling their density or showed no significant relationships with physical factors. The remaining species could be divided into four groups depending on whether temperature, stable substrates, unstable substrates or other hydrological factors affected their density distribution.

ACKNOWLEDGEMENTS

We would like to thank T. Keast, M. Haworth, L. Bernier, V. de Jong and P. Yao, for technical assistance, B. deMarch for assistance with the multiple regression analyses, J. Craig for reviewing the manuscript and P. Flannagan for reviewing and typing the manuscript.

REFERENCES

Boerger, H. and Clifford, H.F. (1975). Emergence of mayflies (Ephemeroptera) from a northern brown-water stream of Alberta, Canada. *Verh. Internat. Verein. Limnol.* 19: 3022–3028.

Brittain, J.E. (1982). Biology of mayflies. *Ann. Rev. Entomol.* 27: 119–147.

Clifford, H.F. (1980). Numerical abundance values of mayfly nymphs from the Holarctic region. *In* Flannagan, J.F. and Marshall, K.E. (eds) *Advances in Ephemeroptera Biology*. Plenum Press, N.Y.

Cobb, D.G., Flannagan, J.F. and Friesen, M.K. (1984). Emergence of Trichoptera from two streams of the Duck Mountains in West-Central Manitoba. *In* Morse, J.C. (ed.) *Proc. 4th Internat. Symp. Trichop. Ser. Entomol.* 30: 75–87. Dr. W. Junk Publ. The Hague.

Draper, N.R. and Smith, H. (1966) *Applied Regression Analysis*. John Wiley and Sons, New York.

Edmunds, G.F. Jr. (1972). Biogeography and evolution of Ephemeroptera. *Ann. Rev. Entomol.* 17: 21–42.

Flannagan, J.F. (1978). Emergence of caddisflies from the Roseau River, Manitoba. *In* Crichton, M.I. (ed.) *Proc. 2nd Internat. Symp. Trichoptera*. Dr.W. Junk Publ., The Hague.

Flannagan, P.M. and Flannagan, J.F. (1984). The post-glacial origin and present distribution of the mayflies (Ephemeroptera) of Manitoba, Canada. *In* Landa, V. *et al.* (eds) *Proc. 4th Internat. Conf. Ephemeroptera*. CSAV.

Franzin, W.G.and Harbicht, S.M. (1985). An evaluation of the relative success of naturalized brook charr, *Salvelinus fontinalis* (Mitchell), populations in South Duck River and Cowan Creek, Duck Mountain Region, Manitoba. *Can. Tech. Rep. Fish Aquat. Sci.* 1370: iv + 21 p.

Friesen, M.K., Flannagan, J.F. and Cobb, D.G. (1984). Emergence of stoneflies (Plecoptera) from South Duck River and Cowan Creek in the Duck Mountain region, Manitoba. *Am. Midl. Nat.* 111: 69–80.

Gaboury, M.N. (1985). A fisheries survey of the Valley River, Manitoba with particular reference to walleye (*Stizostedion vitrium)* reproductive success. *Man. Dept. Nat. Resources Fish. Ms. Rep.* 85–02, 149 pp

Harper, F. and Harper, P.P. (1984). Phenology and distribution of mayflies in a Southern Ontario lowland stream. *In* Landa, V. *et al.* (eds) *Proc. 4th Internat Conf. Ephemeroptera*. CSAV.

Harper, P.P. and Harper, F. (1982). Mayfly communities in a Laurentian watershed. *Can. J. Zool.* 60: 2828–2840.

Ide, F.P. (1940). Quantitative determination of the insect fauna of rapid water. *Univ. Toronto Stud. Biol. Serv.* 47: 7–20.

Newbury, R.W. (1984). Hydrologic determinants of aquatic insect habitats. *In* Resh, V.H. and Rosenberg, D.M. (eds) *The Ecology of Aquatic Insects*. Praeger N.Y.

Sprules, W.M. (1947). An ecological investigation of stream insects in Algonquin Park, Ontario. *Univ. Toronto Stud. Biol. Ser.* 56: 1–81.

Statzner, B. and Higler, B. (1985). Questions and comments on the river continuum concept. *Can. J. Fish. Aquat. Sci.* 42: 1038–1044.

Statzner, B. and Higler, B. (1986). Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwat. Biol.* 16: 127–139.

Winterbourn, M.J., Rounick, J.S. and Cowie, B. (1981). Are New Zealand stream ecosystems really different? *N. Z. J. Mar. Freshwat. Res.* 15: 321–328.