1981

Chemical and physical influences on invertebrate drift in subarctic Alaskan streams

Jacqueline Doyle LaPerriere
Iowa State University

8122534

LAPERRIERE, JACQUELINE DOYLE

CHEMICAL AND PHYSICAL INFLUENCES ON INVERTEBRATE DRIFT IN SUBARCTIC ALASKAN STREAMS

Iowa State University PH.D. 1981

University Microfilms International 300 N. Zeeb Road, Ann Arbor, MI 48106

Chemical and physical influences on invertebrate drift in subarctic Alaskan streams

by

Jacqueline Doyle LaPerriere

A Dissertation Submitted to the

Graduate Faculty in Partial Fulfillment of the

Requirements for the Degree of

DOCTOR OF PHILOSOPHY

Department: Animal Ecology

Major: Water Resources

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

For the Major Department

Signature was redacted for privacy.

For the Graduate College

Iowa State University
Ames, Iowa

1981

TABLE OF CONTENTS

INTRODUCTION

Downstream movement of invertebrates floating in the water column of streams is called invertebrate drift. The phenomenon was first described by Needham (1928) who was netting terrestrial insects floating on the water surface to assess their importance as fish food. His nets, placed so that they sampled throughout the water column, caught many aquatic invertebrates as well.

Several studies show that drift is an important source of fish food particularly to salmonids (Elliott 1967c, 1970, 1973; Griffith 1974). Others (Chaston 1968, Metz 1974) report that drift is unimportant in the diet of trout, but these studies are of caged fish in the former, and restricted to six days one September in the latter, and therefore, may not allow generalization of their findings. Managers who accept that drift is an important source of food to fish need to be able to predict the amount of drift a given stream will produce. My study was undertaken to provide a means of making such predictions for subarctic, Alaskan streams.

The first study of this nature was conducted by Waters (1961) who sampled seven streams in Minnesota that varied widely in alkalinity, but were nearly identical hydrologically. He used alkalinity as an indicator of stream productivity (Needham, 1938; Armitage 1958) and found drift strongly correlated with alkalinity. He concluded that, "This apparent direct relationship of drift rate to level of productive capacity suggests that the drift rate might be employed as an index to the net production rate of stream bottom fauna...."

Despite the fact that the streams were hydrologically similar, events including local storms caused current velocity differences, and such events were associated with changes in the magnitude of drift. However, he felt that these "errors" could be eliminated by obtaining mean annual drift values for streams. Later (Waters 1972), when reviewing the subject of stream drift, he acknowledged that current effects are probably important and had not been studied. Müller (1974) also identified current effects as an unstudied subject in his review.

Standing crop of stream invertebrates is not always related to drift within a stream (Elliott 1967c, Hildebrand 1974, Hynes 1975, Reisen and Prins 1972, and Waters 1961, 1964, and 1966), though it sometimes is (Pearson and Franklin 1968, Pearson and Kramer 1972). Nevertheless, drift is proposed to be a density-dependent mechanism for the removal of excess production of lotic invertebrates as their populations approach carrying capacity (Waters 1966).

Waters (1965) definition of behavioral drift as, "...drift that occurs as a result of some behavior characteristic of the animals that respond to changes in light intensity, which causes a diurnal periodicity in drift..." does not require active entrance into the water column (emigration), or need not be the result of the aggression of another organism, but both are often presumed. The behavior involved may simply be the movement to the substrate-water interface to forage, which has been observed (Chapman and Demory 1963, Elliott 1967c).

This position subjects the organism to current effects which can dislodge them. A more productive stream, therefore, presents more invertebrates to the possibility of drift.

Minshall and Winger (1968) imply that intraspecific encounters result in drift, and are caused by "...crowding and jostling of the animals." Elliott (1967c) concludes that drifting invertebrates have lost their "grip", or "...are jostled by their fellows." If this is true then it might be concluded that stream benthic invertebrates are substrate-limited, and further, that this is a cause of a behavior which produces "behavioral drift" (Waters 1965). However, substrate limitation of benthos is said to be true only for very large rivers such as the Mississippi (Benke et al., 1979).

While there is much published research on the search for environmental factors that may be the "triggers" of behavioral drift, (Bishop and Hynes 1969, Müller 1974, Ulfstrand 1968, and Waters 1972), there is none on certain ethological aspects of the supposed behavior. No one has published a direct observation of a benthic organism actively letting go of the substrate, or swimming up into the water column to initiate drift.

The hypothesis that intraspecific encounters result in one or both of the participants entering the drift was rejected in a recent study (Wiley and Kohler 1980). From 78 hours (real time) of time-lapse microcinematographic observation of the benthic invertebrates of Hunt Creek, Michigan they found that encounters between organisms of the same species usually result in small movements, and only 2% result in emigration.

They also observed that organisms near the projecting edges of rock were the most likely to be swept away. This observation supports the hypothesis (Elliott 1967a,b; Hynes 1975) that drift occurs primarily because of mechanical dislodgement, since organisms near the center of the tops of rocks are likely to be in the boundary layer of low water velocity (Hynes 1970), while those near the edges may be out of this layer and subject to the current. My study addressed the mechanical dislodgement hypothesis by testing the relationship of the hydrologic and morphometric parameters associated with fluid stress on the streambed to the average, per-day amount of invertebrate drift between streams. This stress is thought to be the cause of the entrainment of sediment, and I hypothesized that it is also a primary cause of invertebrate drift.

Previous studies of the effects of current on invertebrate drift in actual streams have been descriptive (Walton et al. 1977). Several have reported a direct relationship between invertebrate drift rate and discharge (Maciolek and Needham 1951, Bournaud and Thibault 1973, Hynes 1975, and Zelinka 1976). On the contrary, in studies of regulated streams, drift rate has been found inversely related to discharge (Minshall and Winger 1968, Hinkley and Kennedy 1973). Townsend and Hildrew (1976) found a direct relationship between drift rate and velocity at low velocities (<11.5 cm/sec). Most of these studies report a lack of any relationship between discharge and drift concentration, and the relationship between average velocity and drift concentration is not mentioned.

Each of these studies, however, is of a single stream, and therefore the potential for variation in discharge and average velocity is smaller than it would be from stream-to-stream, and, probably too small to illustrate the effects of current on drift. In fact, during the first field season (1978) of my study, I collected data on the stream morphometry, hydrology, and invertebrate drift at the head and foot of selected riffles in an effort to attempt to quantify the influence of riffle morphometry on invertebrate drift. It was necessary to select riffles in several different streams to find sufficient variation in selected parameters. Statistical examination of the data showed that invertebrate drift was similar among different sites of the same stream, but significantly different among streams. Therefore, the study was redesigned for the 1979 field season to examine the sources of the among-stream variation.

The objectives of my study became to (1) determine the effects of stream productivity on the amount of invertebrate drift from stream-to-stream within a high-latitude region, and (2) to quantify the effects of stream current variation on invertebrate drift among streams. The specific hypotheses tested were:

(1) that invertebrate drift among streams is directly related to stream alkalinity,

(2) that invertebrate drift among streams is directly related to the biomass of the suspended algae, as measured by chlorophyll _a_ concentration,

(3) that the concentration of invertebrate drift among streams is inversely related to the discharge,

(4) that the concentration of invertebrate drift among streams is directly related to the average velocity, and,

(5) that the rate of invertebrate drift (export) among streams is directly related to average velocity.

STUDY AREA

Site Selection

Thirteen stations (Figure 1) on tributaries of the Tanana River were sampled five times approximately monthly between May 15 and September 12, 1979. The Tanana River is a major feature of the Intermontane Plateau of interior Alaska, which lies between the Brooks Range (Rocky Mountains) to the north, and the Alaska Range (Coast Mountains) to the south. Ultimately the Tanana flows into the Yukon River which flows to the sea.

The stations were selected to represent the morphometric, hydrologic and chemical parameters of the region. Stations were sited near highway bridges for easy access, but were located out of the influence of the structure. Selected descriptive parameters for these stations are presented in Table 1.

Some human disturbance was noted on Goldstream, O'Connor and Banner Creeks. Early in this century gold dredging occurred in the headwaters of Goldstream Creek and along the valley of Banner Creek. Gold mining still occurs in the Banner Creek valley with four placer operations reported active in the summer of 1979. Construction activity, particularly road building, pipeline crossing, and gravel extraction are recent in the upper Goldstream. A gold claim is still maintained in the headwaters of O'Connor Creek, but there is no evidence of recent activity. Prospecting is occurring along Spinach Creek, but gold removal activity has not yet begun.

Figure 1. The study area. Stations marked by numbers

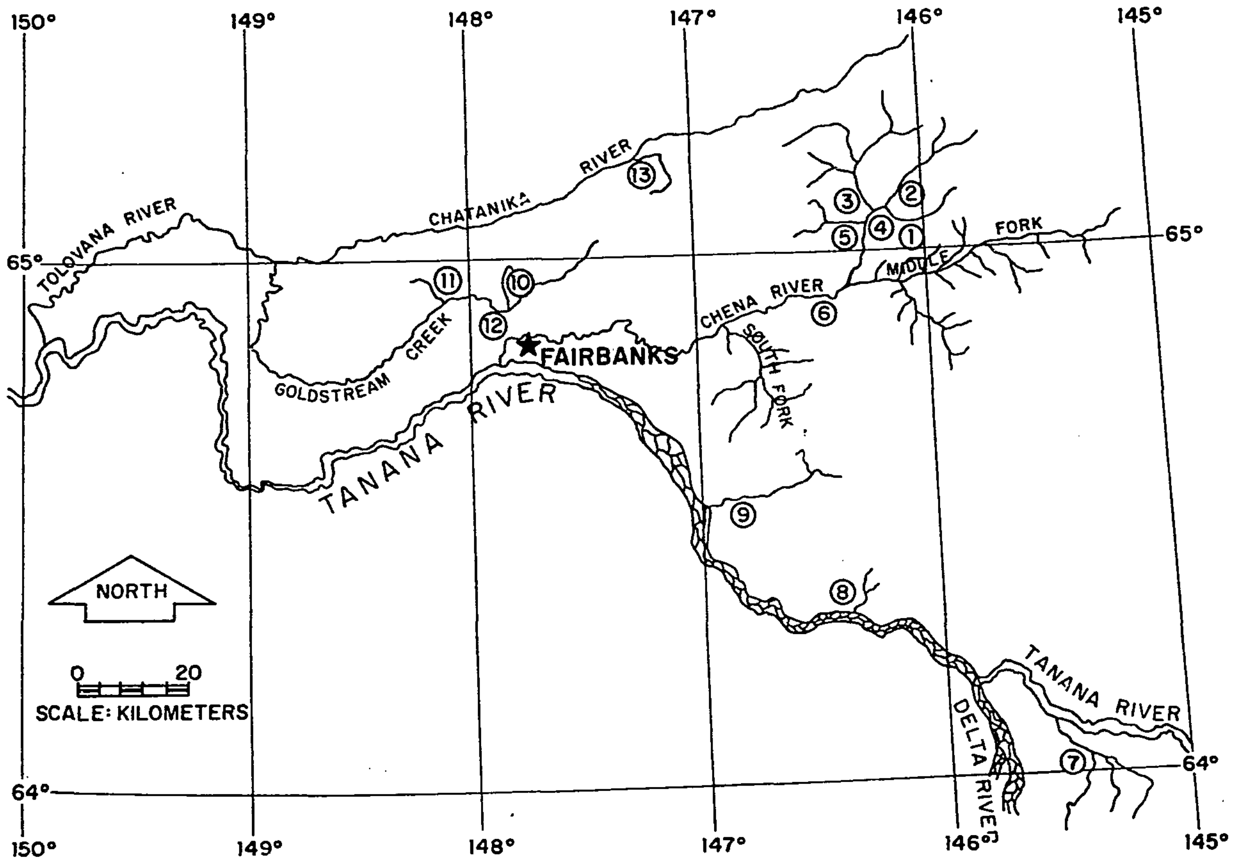

150°
149°
148°
147°
146°
145°
65°
64°
TOLOVANA RIVER
CHATANIKA RIVER
GOLDSTREAM CREEK
FAIRBANKS
CHENA RIVER
SOUTH FORK
MIDDLE FORK
TANANA RIVER
DELTA RIVER
NORTH
0 20
SCALE: KILOMETERS
1
2
3
4
5
6
7
8
9
10
11
12
13

Table 1. Selected Descriptive Parameters of the Study Stations

Station Number	Station Name	Location	Watershed Area Upstream (km^2)	Mean Discharge (m^3/sec)
1	Monument Creek	65°04'N,146°05'W	85	1.48
2	North Fork	65°04'N,146°05'W	229	2.71
3	West Fork	65°04'N,146°10'W	433	4.18
4	Big Bend	65°03'N,146°12'W	779	9.98
5	Angel Creek	65°02'N,146°12'W	99	1.70
6	Gaging Station	65°54'N,146°25'N	2437	30.1
7	Delta Clear-water	64°05'N,145°35'W	911[b]	21.0
8	Banner Creek	64°17'N,146°21'W	52	0.14
9	Little Salcha	64°30'N,146°59'W	173	1.07
10	O'Connor Creek	64°55'N,147°53'W	32	0.07
11	Spinach Creek	64°55'N,148°10'W	26	0.04
12	Goldstream Creek	64°54'N,147°57'W	258	0.75
13	Kokomo Creek	65°10'N,147°18'W	105	0.56

[a]Slope within 305 m of the station.

[b]The tributaries of this stream are influent, but are included in measurement of the watershed area.

[c]Dam located approximately 305 m upstream of station.

[d]Dam located approximately 183 m upstream of station.

Mean Average (m/sec) Velocity	(m) Mean Width	Local Slope[a]	Vegetation	Disturbance Observed
0.86	6.48	0.012	boreal	none
0.83	12.00	0.015	boreal	none
0.81	20.73	0.004	boreal	none
1.06	35.26	0.005	boreal	none
0.94	10.73	0.004	boreal	none
-	39.62	0.003	boreal	none
0.90	48.77	0.002	boreal	none
0.44	4.04	0.009	boreal	placer mining
0.75	8.47	0.001	muskeg	beaver dam[c]
0.60	1.77	0.013	muskeg	none
0.14	3.52	0.006	muskeg	none
0.72	6.30	0.014	muskeg	dredged
0.48	6.16	0.004	muskeg	beaver dam[d]

Climatology

The study area lies in the subarctic and being continental is subject to wide temperature extremes. At Fairbanks the mean maximum July temperature is about 21°C and the mean minimum January temperature is -27°C. The mean annual temperature is currently -4°C (Hartman and Johnson, 1978); therefore, the area is underlain by discontinuous permafrost. Ice-rich stream valleys contain muskeg and ice-free valleys have boreal vegetation.

Precipitation is low (about 51 cm per year) and most occurs in summer, although snowpack runoff is usually the largest flow event. Nevertheless, reduced infiltration, due to the occurrence of wet permafrost, and low evaporation and transpiration in this area, allow stream runoff to be significant throughout the ice-free season. Low flow occurs during winter when only groundwater contributions are made (Hartman and Johnson, 1978).

Geology

The geology of the area consists of recent alluvium through the valleys, with some granitic intrusions. These are common along the upper Chena River where they can be seen as torrs on the ridgetops near Angel Creek, and where quarrying has been conducted near the highway.

Delta Clearwater Creek is fed by a massive aquifer of undelineated size. Geophysical surveys have been conducted which give the depth to bedrock as 450-750 m at the measured locations. Because of the great size of this aquifer the flow of the Clearwater is very steady, varying only 10% in the three years it has been gaged by the

United States Geological Survey (Dorothy Wilcox, Fairbanks, Alaska, 1979, personal communication). Its surface tributaries are intermittent with visible flow only occurring at spring runoff, and during some summer storm events. The remaining study streams have smaller aquifers, and surface runoff during summer storm events causes their flow to be more variable.

METHODS

Drift Sampling

Replicate samples of drift organisms were collected five times, monthly between May and September, 1979, for 24 hours at each station during each sampling run using nets constructed from a design by Waters (1969). Net mouth size was 120 cm^2, the overall length 2 m, and the mesh 1.2 mm. Both mouth and cod end were reinforced with flexible plastic cloth. Nylon cords were attached through grommets at the four corners of the mouth and tied together 85 cm forward. A single 150 cm cord was attached to the knotted net cords and to a 9 cm x 19 cm x 39 cm concrete block. Visual examination determined that turbulence created by the anchor block was dissipated before flow entered the net.

Stations were established during the first sampling run by marking the banks at both ends of a line perpendicular to the streamflow and the mouths of the nets were set on that line each time. At each station this line was set by eye at mid-length of a riffle, where drift is maximum (Brown and Brown, 1979). Two nets were placed near mid-stream at points where the approximate average velocity was judged to be, by eye.

When the nets were retrieved, the cod end was opened over a screened bucket (516 micron mesh) and the net was washed down with buckets of water. The sample was placed in a labeled wide-mouthed polyethylene bottle, and covered with 95% ethanol. Drift organisms from one of the replicate samples were later sorted from the debris in an enamel pan and preserved in 95% ethanol. Counting was conducted in a Syracuse watch glass under a stereo dissecting microscope. These samples were dried at 60°C to steady weight, and weighed to the nearest 0.0001 g on a digital single pan balance. Unattached ecdyses, larval fishes, the shells of gastropods, and the cases of caddisflies were removed before weighing.

Hydrology and Hydraulics

Discharge was measured at each station each time that nets were set. A temporary staff gage was placed in the stream, and the discharge was remeasured if the water level had changed at the end of the 24 hour netting period. Formal gages are maintained by the United States Department of the Interior, Geological Survey, at Stations 6 and 7, with continuous recording at Station 6 and daily readings taken at Station 7. Current velocity was also measured at the center of the mouth of each net with a Gurley or Pygmy meter as it was set and retrieved to allow estimation of the volume of water filtered.

Discharge measurement activities provided the following data: stream width, cross-section area, discharge, average velocity and average depth. Slope was measured once at each station for approximately 305 m (1000 ft), using a method suggested by William W. Mendenhall of the School of Engineering, University of Alaska, Fairbanks. The elevation difference between twenty points 15.25 m apart along the wetted edge of the stream was measured consecutively using a water level of transparent tubing with meter sticks attached at each end. The cumulative rise was plotted versus cumulative distance and the slope was found for the best straight line through the points.

Water Quality Parameters

Field test kits (Hach Chemical Company) were used for the measurement of pH and alkalinity. Water temperature was measured with a mercury-filled glass thermometer. Available carbon was calculated from the alkalinity, pH and temperature data using the table provided in Saunders et al. (1962). Specific conductance was measured with a thermally compensated single probe meter.

Planktonic chlorophyll a was measured following the method published by the International Biological Program (Golterman, 1969). Replicate 1000 ml samples were filtered through fine glass fiber filters using a hand vacuum pump. The filters were stored in the dark over desiccant and were frozen as soon as they reached the laboratory.

Replicate 50 ml water samples were frozen for determination of total phosphorus using the method of Gales et al. (1966). Chlorophyll a and total phosphorus analyses were completed by November 1, 1979.

Data Analysis

Station means were calculated for each parameter measured. If a parameter was measured more than once a day at a station, daily means were used in calculating station means. Table 2 presents a description of the parameters from which the station means were calculated. All data collected and analyzed are contained in the Appendix.

Regression analysis and stepwise multiple regression were performed on the station means of selected parameters using a Honeywell 66/20 computer. Mean values of pH were obtained by converting the individual data to hydrogen ion concentrations, obtaining the mean for

Table 2. Parameters used in Data Analysis

Name	Abbreviation	Units	Sample Size (n) per Station per 1979 Season	Transformation
INVERTEBRATES				
weight	WT	mg	5	
weight concentration	WTC	mg/m^3	5	natural log
number	NUM	No.	5	
number concentration	NUMC	$No./m^3$	5	natural log
weight export	WTCEX	mg/day	5	natural log
number export	NUMCEX	No./day	5	natural log
ALGAE				
chlorophyll - concentration	PCHLOR	mg/m^3	10	
chlorophyll - export	EXCHLR	mg/day	10	natural log

WATER QUALITY				
Alkalinity	ALK	mg/l as $CaCO_3$	15	
available carbon	AVC	mg/l	5	
specific conductance	SPCON	µmhos/cm	5	
pH	PH		10	
total phosphorus	TPHOS	mg/m^3	10	
temperature	TEMP	°C	5	
HYDROLOGIC				
width	WIDTH	m	5	
cross-sectional area	XSECT	m^2	5	natural log
discharge	DISCH	m^3/sec	5	natural log
average velocity	AVEL	m/sec	5	
average depth	AVDEP	m	5	
slope	SLOP		1	
net velocity	NETVEL	m/sec	10	
Manning's roughness	MANN		1	
WATERSHED				
watershed area	WARE	km^2	1	natural log
relief	REL	m	1	

each station, and taking the negative logarithm. Methods P1R for simple and multiple regression and P2R for stepwise regression of the Biomedical Computer Programs (BMDP) software were utilized (Dixon and Brown, 1979). Natural log transformations were performed using Fortran statements on those parameters which were determined to be skewed by examination with a detailed data descriptive program, P2D, of the BMDP program set.

Invertebrate drift data were expressed both as concentrations and as exports. Concentration was the number (or weight) of organisms caught in the net divided by the volume of water that had passed through the net. Export was the number (or weight) of organisms that had passed the sampling point in a 24-hour period, and was calculated by multiplying the concentration by the stream's discharge during the 24-hour period.

RESULTS AND DISCUSSION

Most of the drift samples were numerically dominated by dipterans (true flies). Ephemeroptera (mayflies) usually were next in numbers, and Trichoptera (caddisflies) and Plecoptera (stoneflies) alternated in being third most numerous. Each of these insect orders, however, was numerically dominant in occasional samples. Notable examples were the samples of June 5 and July 3, 1979 at O'Connor Creek (Station 10) that contained 981 (94%) and 1393 (72%) mayflies, respectively. All were of a single genus Ameletus sp. (Siphlonuridae). Aquatic Collembola (springtails), Hemiptera (bugs), Lepidoptera (moths), and Coleoptera (beetles) were also captured occasionally. Non-insectan aquatic invertebrates including Annelida (worms), Eubranchiopoda (clam shrimps), Hydracarina (water mites), Gastropoda (snails), and Pelecypoda (clams) also were occasionally caught. Terrestrial invertebrates represented only a small percentage of the numbers of organisms caught in the larger streams, but as much as 25% in the smaller streams. These were included in the drift in my study.

Table 3 presents the station mean values and their standard errors for selected parameters of drift and stream chemistry, hydrology and morphometry. Regression analysis was conducted on station mean values of the various parameters.

Stream Productivity and Invertebrate Drift

The first hypothesis tested was that invertebrate drift among streams is directly related to stream alkalinity. Using simple linear

Table 3. Means and standard errors of drift parameters and selected physical, chemical and biological parameters of the study streams

Station	Number Concentration (No./100 m^3)	Weight Concentration (dg/m^3)	Number/Export (1000/day)	Weight Export (g/day)
1	10±4	6±2	12±4	6±2
2	14±9	9±4	33±28	20±10
3	7±4	4±2	24±14	8±3
4	6±2	4±3	48±23	37±30
5	12±8	7±5	18±16	10±9
6	4±3	2±2	101±98	47±39
7	22±17	5±1	405±298	73±20
8	49±42	30±32	6±5	2±2
9	6±1	5±5	6±5	3±2
10	307±358	286±299	22±28	6±6
11	73±56	38±23	3±2	0.2±0.2
12	39±48	17±18	23±27	7±6
13	4±3	2±2	2±3	1±1

[a]Data missing.

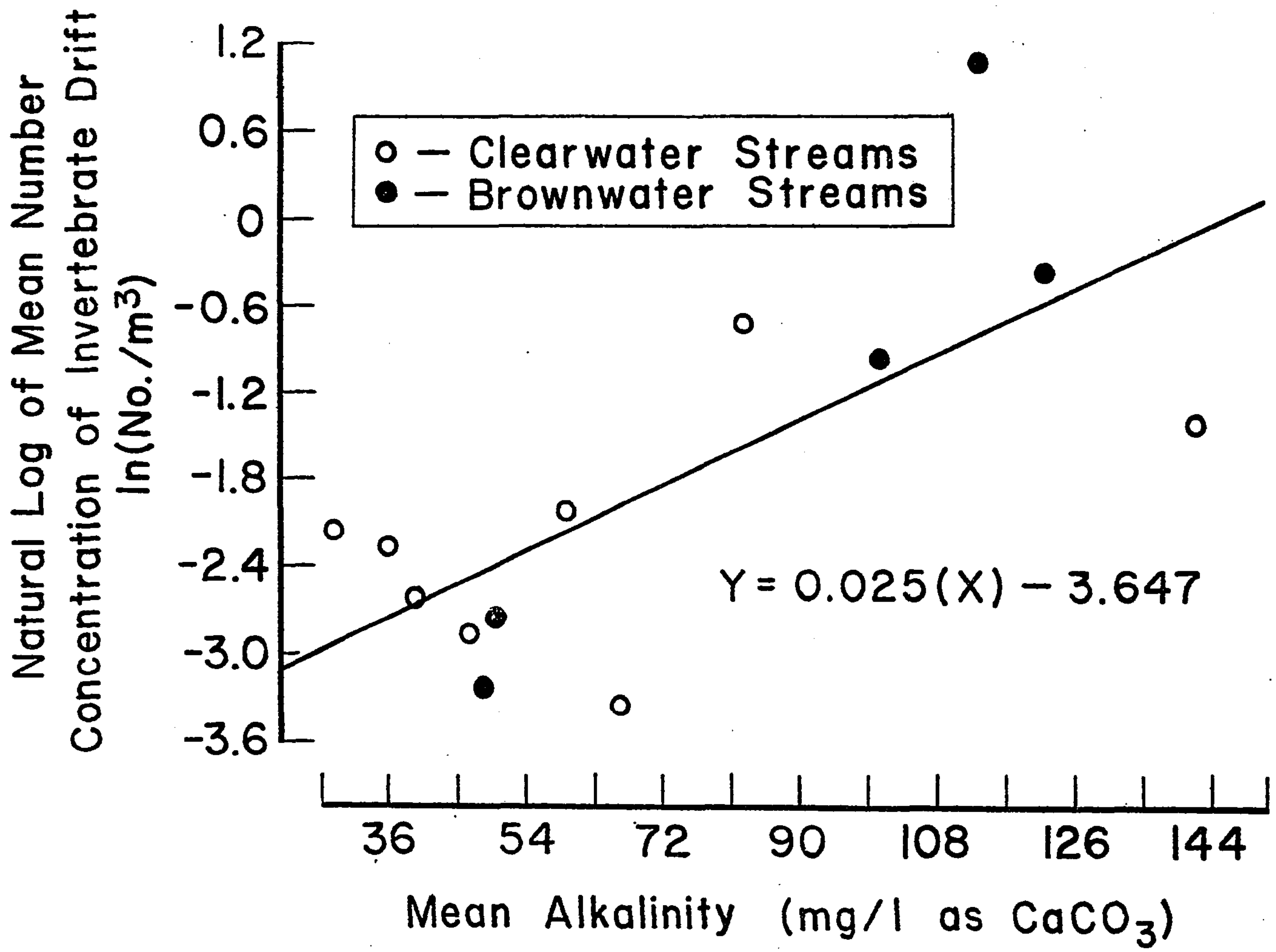
Average Velocity (m/sec)	Discharge (cms)	Alkalinity (mg/l as $CaCO_3$)	Chlorophyll *a* (mg/m^3)	Total Phosphorus (mg/m^3)
0.86±0.17	1.48±0.39	36±5	0.31±0.18	3.6±1.1
0.83±0.14	2.71±0.79	59±7	0.33±0.22	4.0±2.7
0.81±0.13	4.18±0.76	40±5	0.46±0.30	5.0±3.9
1.05±0.09	9.98±1.77	47±9	0.19±0.13	4.8±1.6
0.94±0.08	1.70±0.44	29±4	0.40±0.19	3.2±1.9
--[a]	30.1±4.3	66±9	0.72±0.29	6.6±4.4
0.90±0.03	21.0±2.1	142±7	0.74±0.47	7.2±3.1
0.49±0.09	0.14±0.06	82±15	0.63±0.63	10.0±3.7
0.75±0.16	1.07±0.74	50±8	1.10±0.50	26.0±7.7
0.60±0.15	0.07±0.04	113±19	0.43±0.59	23.2±2.6
0.14±0.01	0.04±0.01	123±16	0.34±0.16	9.0±1.7
0.72±0.12	0.75±0.19	100±4	1.12±0.84	31.8±16.1
0.48±0.12	0.56±0.39	49±14	0.93±0.47	15.8±4.7

regression analysis, a significant relationship was only found for number concentration ($r^2 = 0.503$; $P = 0.01$) (Figure 2). However, using using stepwise linear regression analysis, alkalinity was selected as the second parameter (after average velocity) in the equations for the rate of invertebrate drift (export) both as numbers and as weight per time. These relationships will be shown in the next subsection.

The rationale that alkalinity is related to stream productivity is based on the idea that carbon, derived from bicarbonate and carbonate alkalinity, is an algal macronutrient. In older studies, the algae are assumed to be the food source of the benthic invertebrates, and thus, the productivity of the algal population is assumed to have an influence on the size of the benthic invertebrate population, and alkalinity is used as a productivity index (Needham 1938, Armitage 1958). Recent studies (Cummins 1973, Vannote et al. 1980) have shown the importance of allochthonous materials, particularly tree leaves, as food for some stream benthic invertebrates. It should, however, be noted that allochthonous inputs to the study streams are probably extremely low. Values measured for the Chena River (represented in my study by Stations 1 through 6) were only about 20% of the lowest published values from temperate region studies (M. Oswood, Fairbanks, Alaska, 1980, personal communication). Many interior Alaskan boreal streams are at or above the tree line, and trees are rare and stunted in muskeg.

In this study, the benthic algal populations were assessed by measuring the amount of algae suspended in the water column assuming a

Figure 2. The relationship between alkalinity and invertebrate drift number concentration for thirteen subarctic, Alaskan streams


Natural Log of Mean Number
Concentration of Invertebrate Drift
ln(No./m³)
1.2
0.6
0
-0.6
-1.2
-1.8
-2.4
-3.0
-3.6
○ — Clearwater Streams
● — Brownwater Streams
Y = 0.025(X) − 3.647
36
54
72
90
108
126
144
Mean Alkalinity (mg/l as CaCO3)

direct relationship between the amount of suspended algae in a stream and the size of the benthic algal standing crop (Swanson and Bachmann, 1976). Chlorophyll a content, which is an indicator of biomass, and is relatively easy to measure, was utilized.

The relationship between alkalinity and the chlorophyll a content of the suspended algae was insignificant between the study streams (Figure 3). The study streams can be divided into two types, muskeg (or brownwater) and boreal (or clearwater) on the basis of watershed vegetation type and the associated water color. Muskeg vegetation is underlain by permafrost and decomposes slowly releasing tannins and other organic acids into the water flowing over and through the organic material. These organic acids give characteristic brown colors to standing and flowing waters in muskeg-filled valleys.

When separate analyses were conducted for the two stream types on the relationship between alkalinity and chlorophyll a there was a positive and significant ($r^2 = 0.716$; $P = 0.05$) relationship found for boreal streams (Figure 4). The relationship for muskeg streams was non-significant (Figure 5). The negative trend of this relationship is likely responsible for the lack of significance of the positive relationship for all of the streams.

A significant ($P = 0.005$) relationship was found between total phosphorus and chlorophyll a, as seasonal means, for all of the study streams (Figure 6). The coefficient of determination ($r^2 = 0.594$) indicated that nearly 60% of the variation in the chlorophyll a of suspended algae in selected interior Alaskan streams was explained by the

Figure 3. The relationship between alkalinty and the chlorophyll *a* content of the suspended algae of thirteen subarctic, Alaskan streams

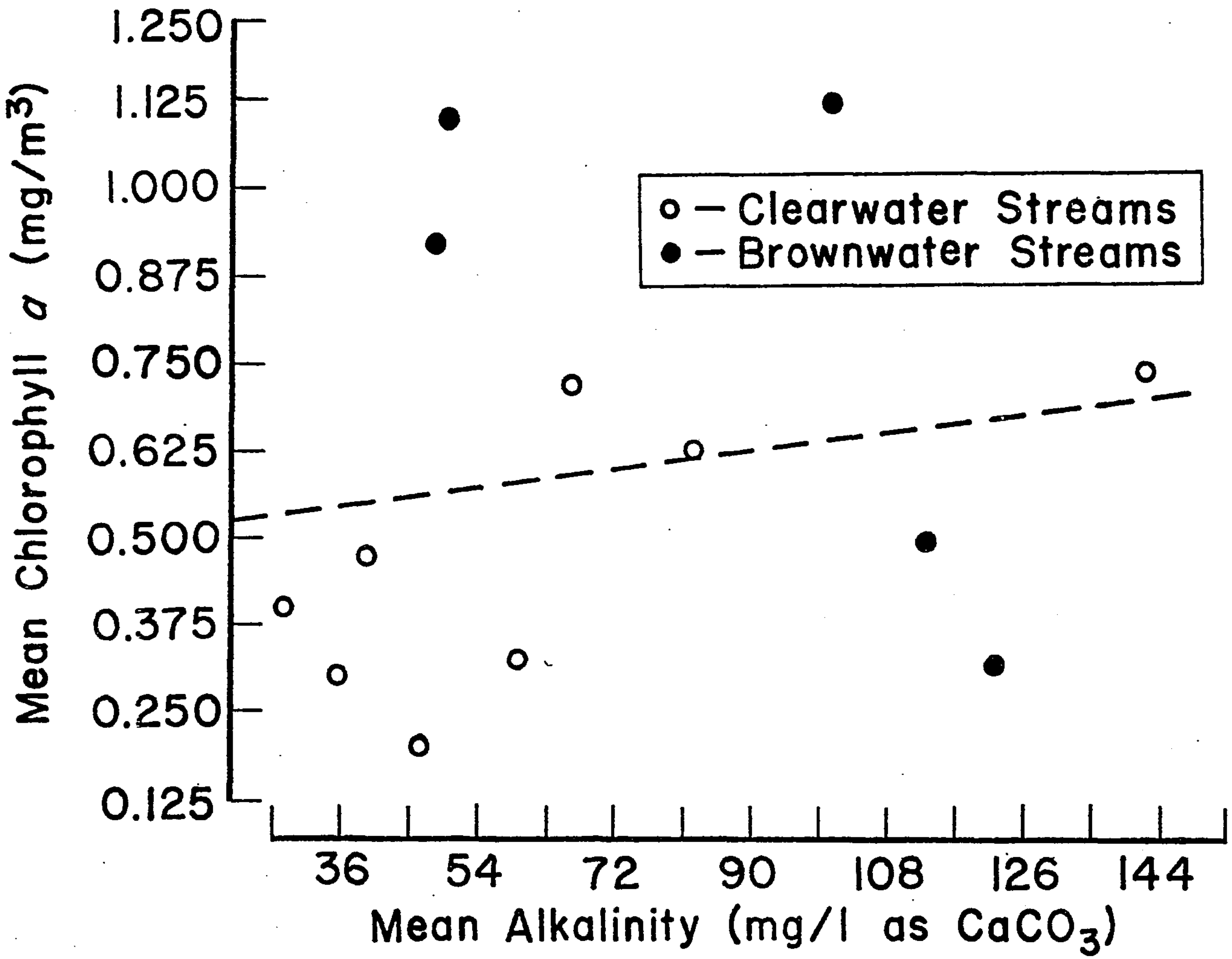

Mean Chlorophyll a (mg/m3)
1.250
1.125
1.000
0.875
0.750
0.625
0.500
0.375
0.250
0.125
36
54
72
90
108
126
144
Mean Alkalinity (mg/l as CaCO3)
o – Clearwater Streams
• – Brownwater Streams

Figure 4. The relationship between alkalinity and the chlorophyll *a* content of the suspended algae of eight subarctic, clearwater streams in Alaska

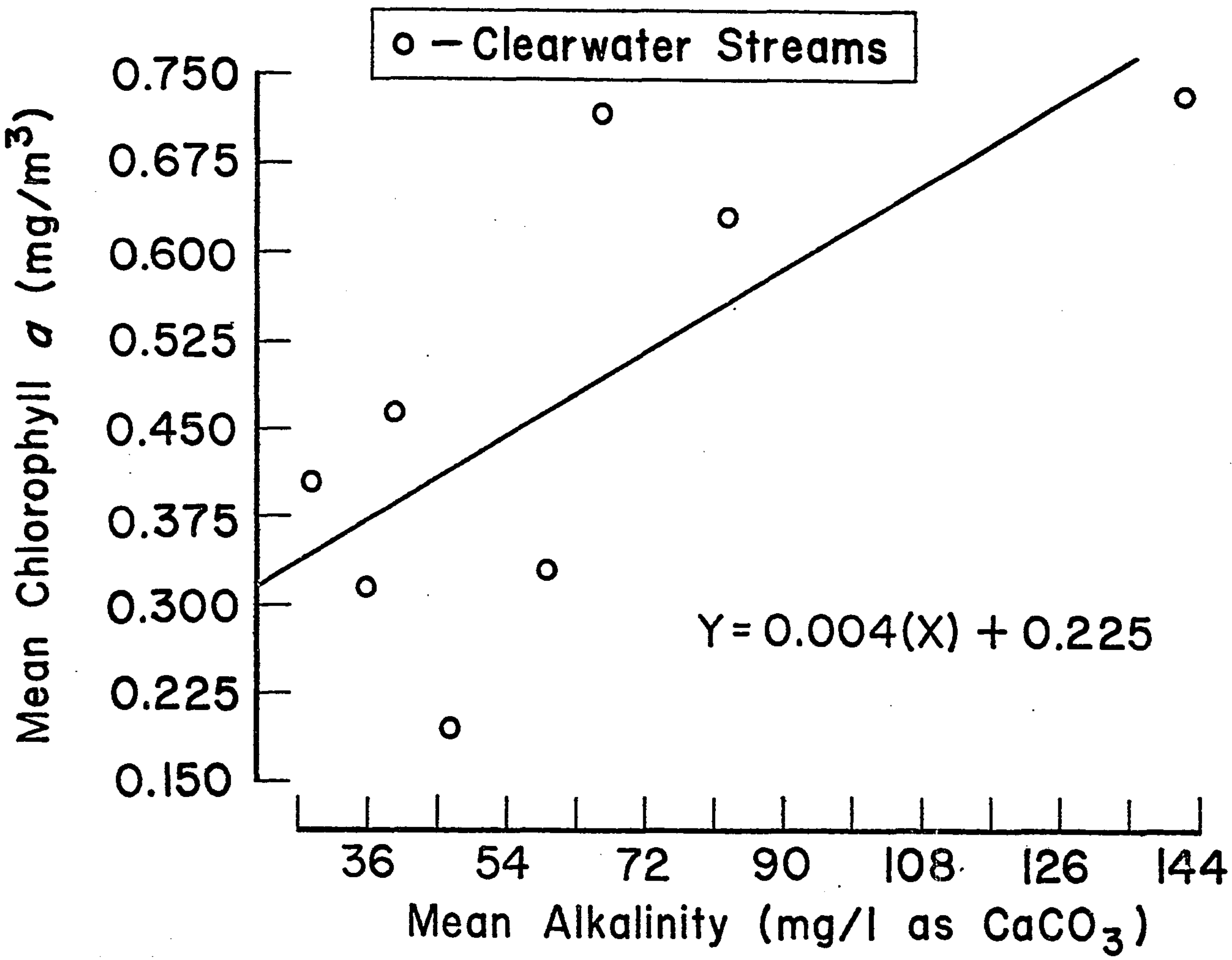

o – Clearwater Streams
0.750
0.675
0.600
0.525
0.450
0.375
0.300
0.225
0.150
Mean Chlorophyll a (mg/m³)
Y = 0.004(X) + 0.225
36
54
72
90
108
126
144
Mean Alkalinity (mg/l as CaCO₃)

Figure 5. The relationship between alkalinity and the chlorophyll *a* content of the suspended algae of five subarctic, brownwater streams in Alaska

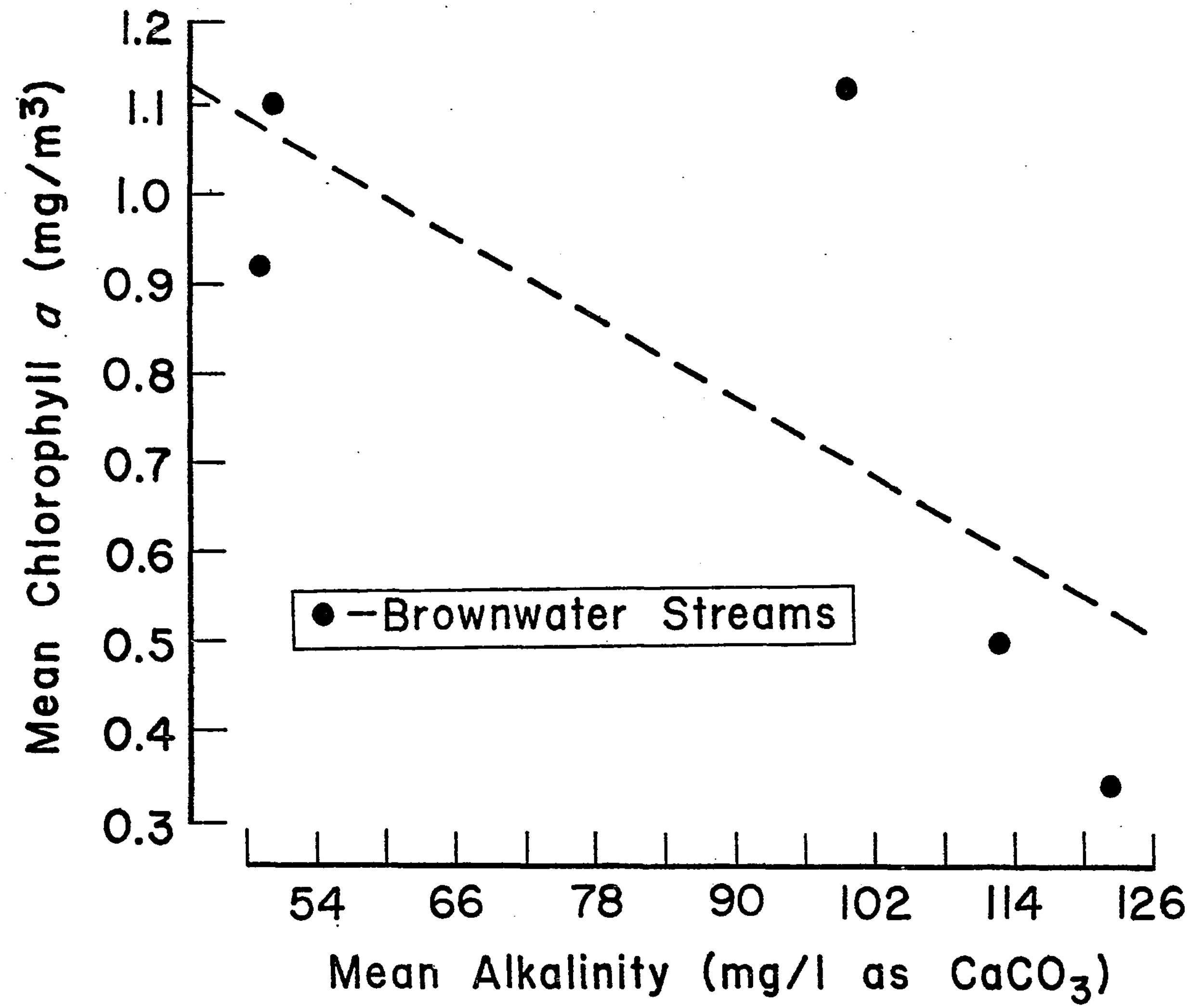
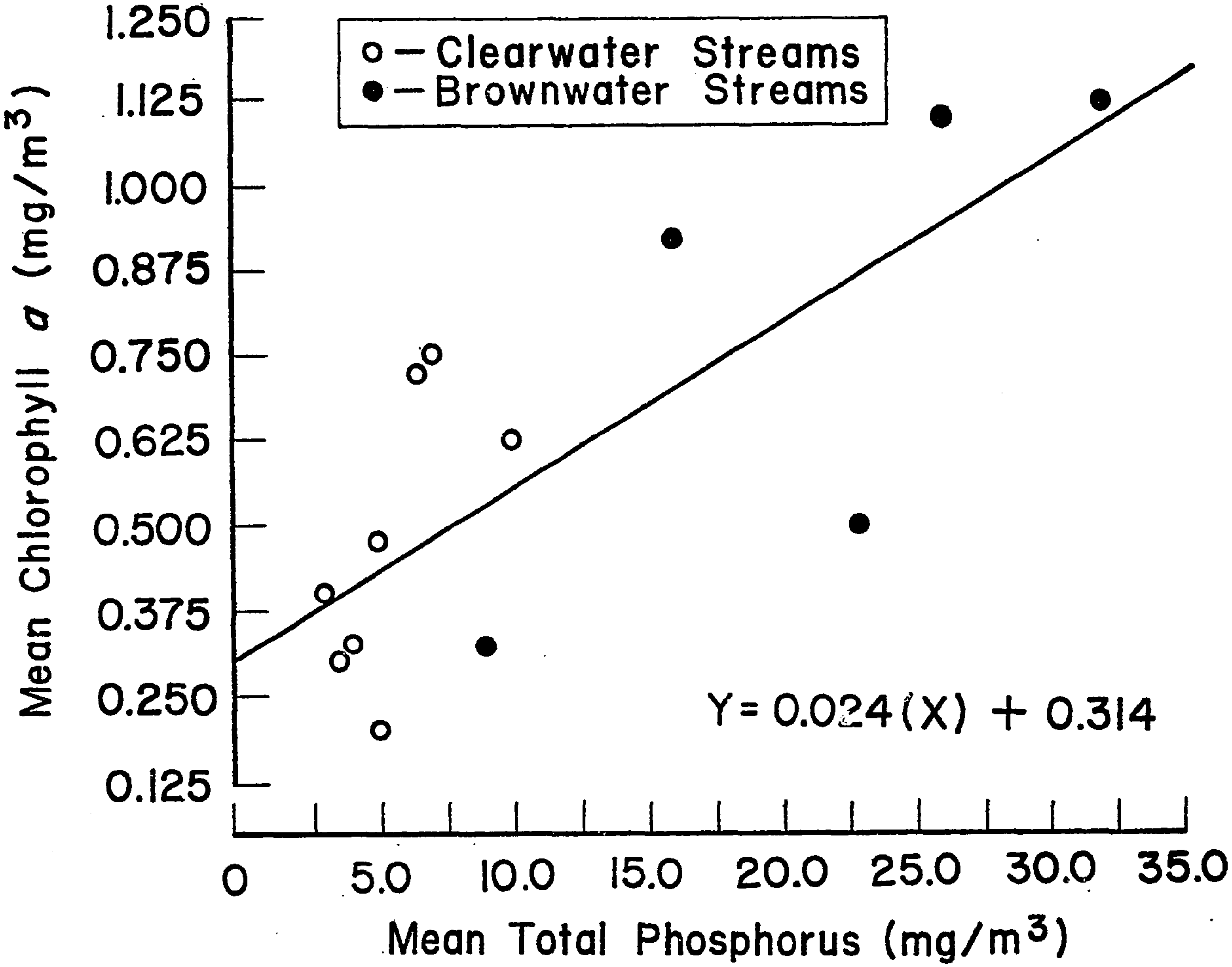

1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
Mean Chlorophyll a (mg/m3)
54
66
78
90
102
114
126
Mean Alkalinity (mg/l as CaCO3)
● —Brownwater Streams

Figure 6. The relationship between total phosphorus and the chlorophyll *a* content of the suspended algae of thirteen subarctic, Alaskan streams



1.250
1.125
1.000
0.875
0.750
0.625
0.500
0.375
0.250
0.125
Mean Chlorophyll a (mg/m3)
o – Clearwater Streams
● – Brownwater Streams
Y = 0.024 (X) + 0.314
0
5.0
10.0
15.0
20.0
25.0
30.0
35.0
Mean Total Phosphorus (mg/m3)

concentration of total phosphorus. Algae in lakes are expected to be limited by phosphorus, the major nutrient that is likely to be found in low concentration (Schindler, 1977). This was a significant new discovery for streams. We were not able to demonstrate this in Iowa streams (Kilkus et al. 1975), where the soils in the watersheds are rich and contain relatively high phosphorus, but a similar relationship has recently been found for Missouri streams with low phosphorus concentrations (J. R. Jones, University of Missouri, Columbia, Missouri, 1980, personal communication).

No significant relationships were found between chlorophyll a concentrations and invertebrate drift concentrations (weight or number) between streams. The relationship seemed to be positive for boreal streams, but negative for muskeg streams and for all streams. Thus, it was not possible to show that the benthic invertebrates were completely dependent on the benthic algae as a food source.

There are two explanations for this finding. It is possible that in streams where benthic invertebrate populations are high, grazing of the benthic algae is intense enough to reduce the standing stock of benthic algae and thereby of the resulting suspended algae. This phenomenon is known to occur at certain seasons in ponds and seas (Brown, 1971). The benthic invertebrates may be independent of the algae if they are relying on a different food source. While they are probably not heavily reliant on leaf litter, for the reasons mentioned above, it is likely that they are utilizing allochthonous materials in subarctic streams.

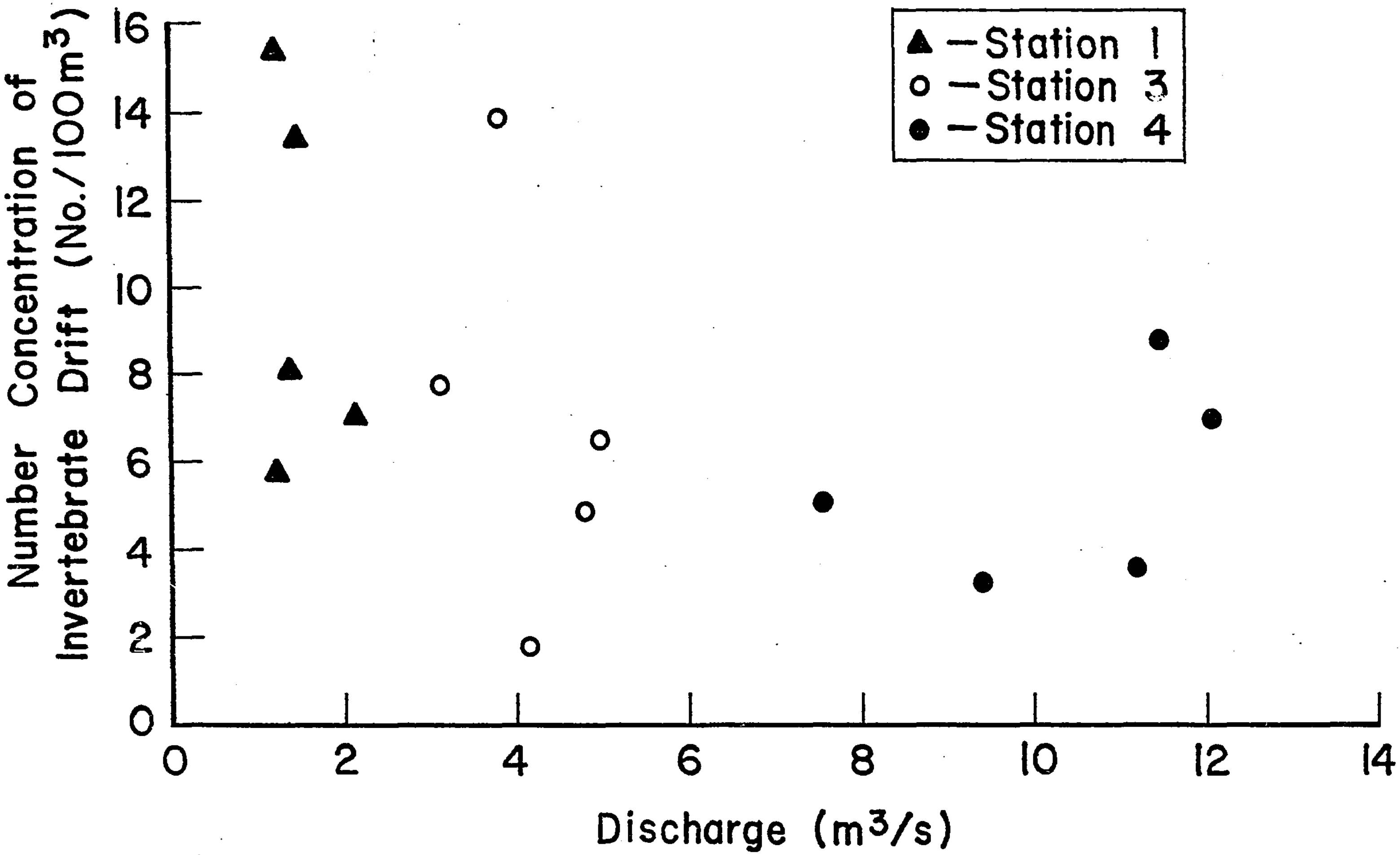
A similar lack of direct relationship between algae and invertebrates in brownwater streams of northern Canada has led to speculation that the invertebrates of these systems may feed on particulate forms of organic acids or on the associated bacterial flora (R. Wallace, 1977, personal communication). Alkalinity measurements can include the negative ions of the salts of weak organic acids such as tannins and lignins. These species are among those called "false alkalinity" because the carbon they contain is not readily available to plants. This may explain why I found that alkalinity was strongly related to invertebrate drift yet was unable to find the expected links between alkalinity and stream algae, and between the algae and the invertebrate drift.

Stream Hydromechanics and Invertebrate Drift

The effects of discharge

The effects of discharge on drift concentration within streams, if any, cannot be shown using the data of my study. The variability of the drift parameters tended to be much higher than that for discharge within streams of the study (e.g. Figure 7). There also may be an artifact caused by the scheduling of the sampling effort. If drift is the result of mechanical dislodgement by the current, then an eccentric storm effect should be expected with more removal occurring on the rising limb of the hydrograph than on the falling, as is known for seston (Bilby and Likens 1979). Quantification of the effect of discharge within streams will require special scheduling of sampling during storm events, to assure that samples are taken before peak discharge occurs, when drift is probably maximum for the event.

Figure 7. The relationship between discharge and invertebrate drift number concentration of three subarctic, Alaskan streams



Number Concentration of
Invertebrate Drift (No./100m3)
16
14
12
10
8
6
4
2
0
0
2
4
6
8
10
12
14
Discharge (m3/s)
▲ —Station 1
○ —Station 3
● —Station 4

Among streams a strong inverse relationship was found between discharge and invertebrate drift concentration. For weight concentration the resulting equation (Figure 8) (r^2 = 0.582; P = 0.005) was:

$$\ln(\overline{WTC}) = -0.507 \ln(\overline{DISCH}) - 2.235.$$

The abbreviations used are explained in Methods. A bar over a parameter name indicates stream mean value. For number concentration the resulting equation (Figure 9) (r^2 = 0.497; P = 0.010) was:

$$\ln(\overline{NUMC}) = -0.451 \ln(\overline{DISCH}) -1.702.$$

In stepwise multiple regression analysis, however, alkalinity was the first variable selected in the equation explaining number concentration, having a larger coefficient of determination (r^2 = 0.503) than discharge. Discharge was selected second and explained an additional 28% of the variation, and the following equation resulted:

$$\ln(\overline{NUMC}) = 0.020 (\overline{ALK}) -0.329 \ln(\overline{DISCH}) -3.156.$$

Therefore, the main effect seen in examining the relationship of discharge and invertebrate drift concentration is a kind of "dilution". This probably results because the relationship between stream wetted perimeter and discharge, both within streams and among streams in geologically similar regions, is a power function (Leopold et al. 1964) similar to the form:

$$w = a\ Q^b$$

Figure 8. The relationship between discharge and invertebrate drift weight concentration for thirteen subarctic, Alaskan streams.

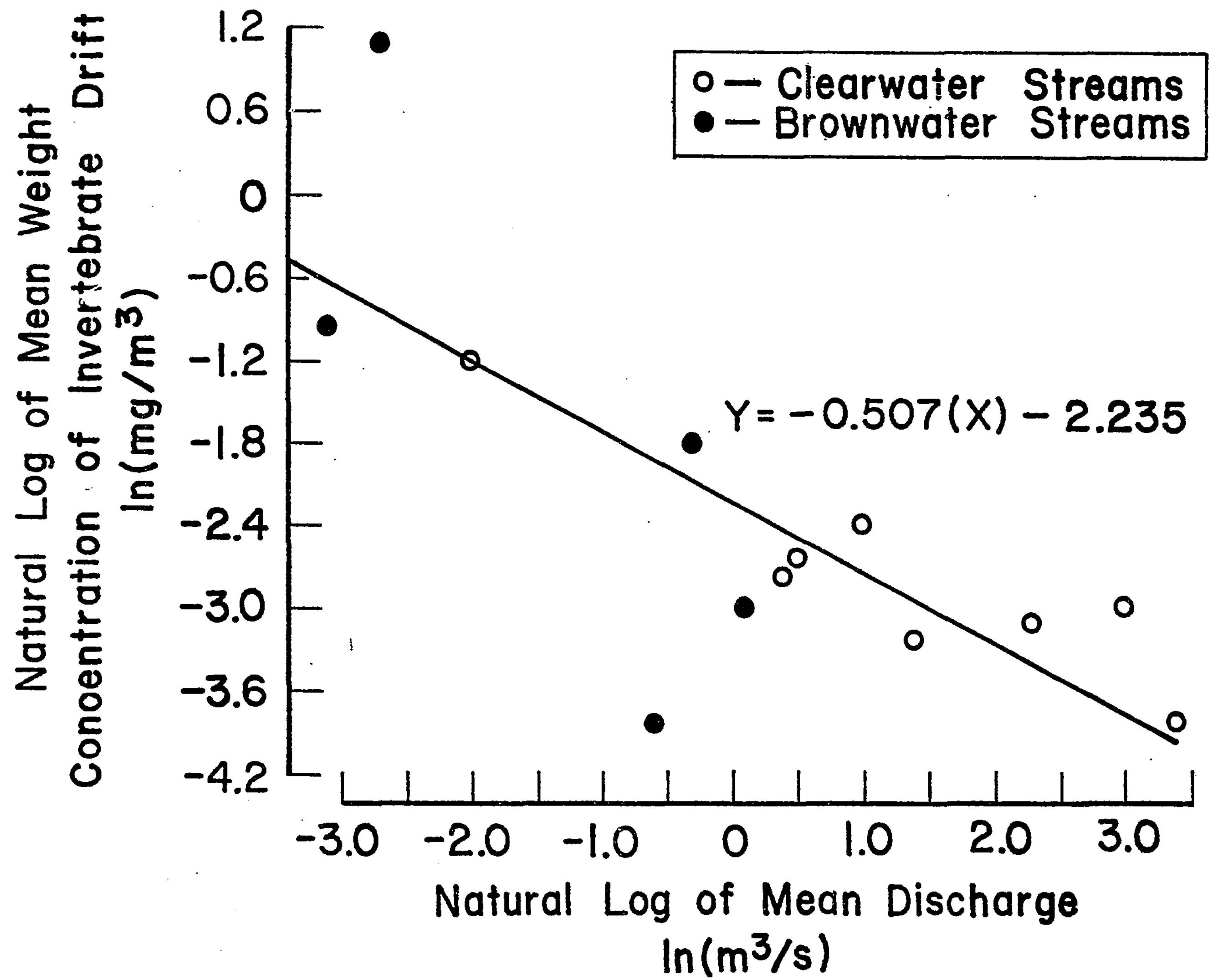
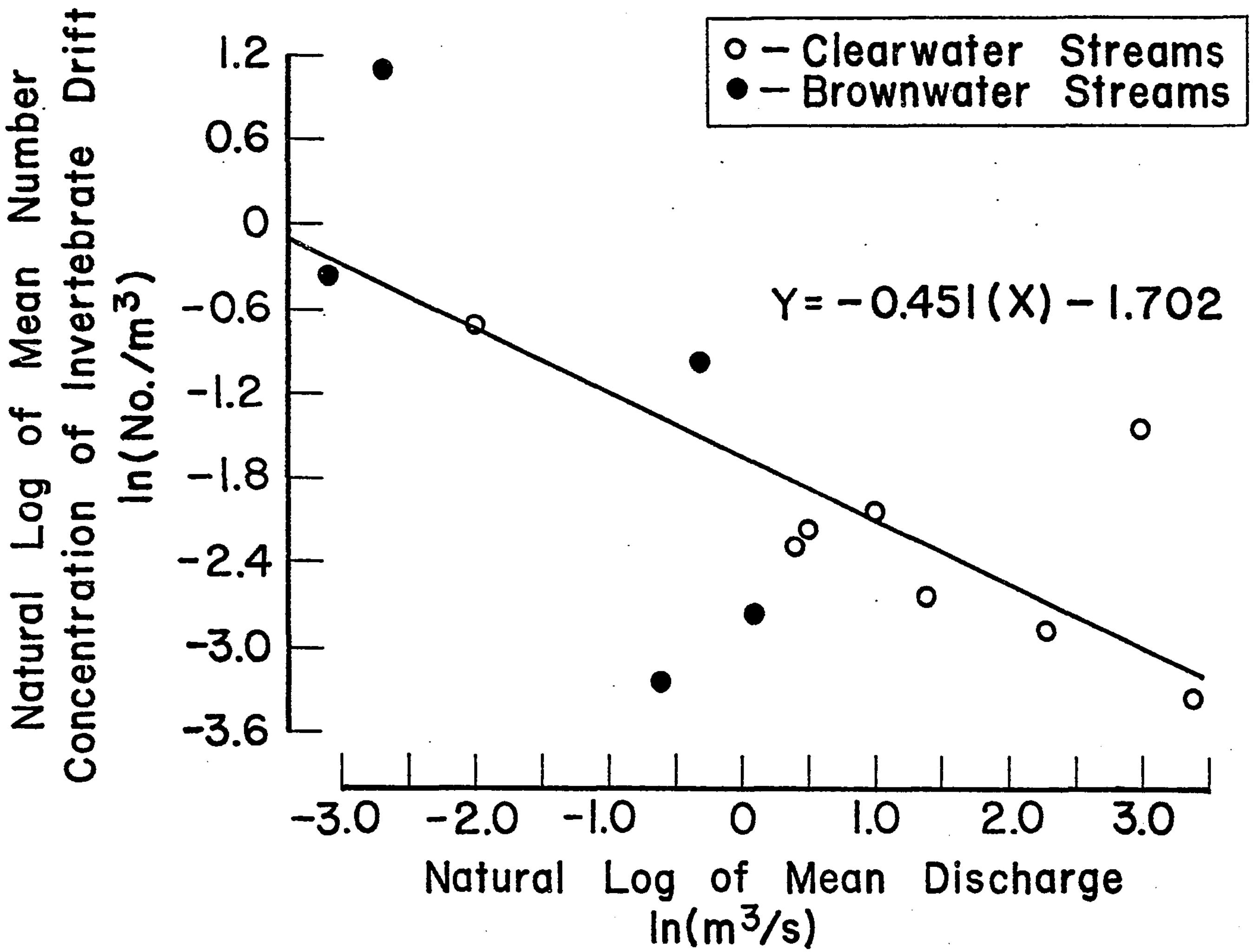

Natural Log of Mean Weight
Concentration of Invertebrate Drift
ln(mg/m3)
1.2
0.6
0
-0.6
-1.2
-1.8
-2.4
-3.0
-3.6
-4.2
o — Clearwater Streams
● — Brownwater Streams
Y= -0.507(X) - 2.235
-3.0
-2.0
-1.0
0
1.0
2.0
3.0
Natural Log of Mean Discharge
ln(m3/s)

Figure 9. The relationship between discharge and invertebrate drift number concentration for thirteen subarctic, Alaskan streams


○ – Clearwater Streams
● – Brownwater Streams
Y= –0.451 (X) – 1.702
Natural Log of Mean Number
Concentration of Invertebrate Drift
ln(No./m3)
1.2
0.6
0
-0.6
-1.2
-1.8
-2.4
-3.0
-3.6
-3.0
-2.0
-1.0
0
1.0
2.0
3.0
Natural Log of Mean Discharge
ln(m3/s)

wherein w symbolizes channel width and Q symbolizes discharge, and a and b are an empirical coefficient and exponent. Values of b vary near 0.5 among streams (Leopold et al. 1964). (Wetted perimeter is equivalent to width for most natural channels.) Therefore, the substrate-water interface is similar in size for widely varying discharges, evidenced by the fractional exponent in the relationship. If the number of benthic invertebrates per unit area of bottom is similar from stream-to-stream (not examined in my study), or is explained by a productivity factor, then an inverse relation between discharge and invertebrate drift concentration is expected.

The effect of discharge on the rate of invertebrate drift was not examined in my study either within or among streams. Since discharge is multiplied by concentration to obtain the rate of drift, there is an obvious positive mathematical relationship between discharge and rate because discharge appears in rate. Therefore, I felt it sufficient only to examine the effect of discharge on drift concentration and not on drift rate.

The effects of average velocity

Because of its relatively small variability, average velocity data from my study yields no relationships with invertebrate drift within streams. Among streams no significant regressions were found between average velocity alone and invertebrate drift concentration. However, stepwide multiple regression selected average velocity as the third parameter to explain number concentration and the resulting equation was:

$$\ln(\overline{NUMC}) = 0.026\,(\overline{ALK}) - 0.790\,\ln(\overline{DISCH}) + 4.337\,(\overline{AVEL}) - 6.666.$$

This equation explained over 90% of the variation in drift number concentration among streams ($r^2 = 0.931$; $P = 0.001$).

Furthermore, average velocity was found significantly, and positively related to the rate of invertebrate drift expressed as weight or as numbers per day. The linear regression between average velocity and drift weight export was:

$$\ln(\overline{WTCEX}) = 3.766\,(\overline{AVEL}) + 6.490,$$

(Figure 10) ($r^2 = 0.587$; $P = 0.005$). The regression between average velocity and drift number export was:

$$\ln(\overline{NUMCEX}) = 3.844\,(\overline{AVEL}) + 6.983,$$

(Figure 11) ($r^2 = 0.491$; $P = 0.025$).

Stepwise multiple regression analysis chose alkalinity as the second parameter to explain the rate of drift though there was not a significant simple regression between alkalinity and the rate of drift. The resulting equation for drift weight export was:

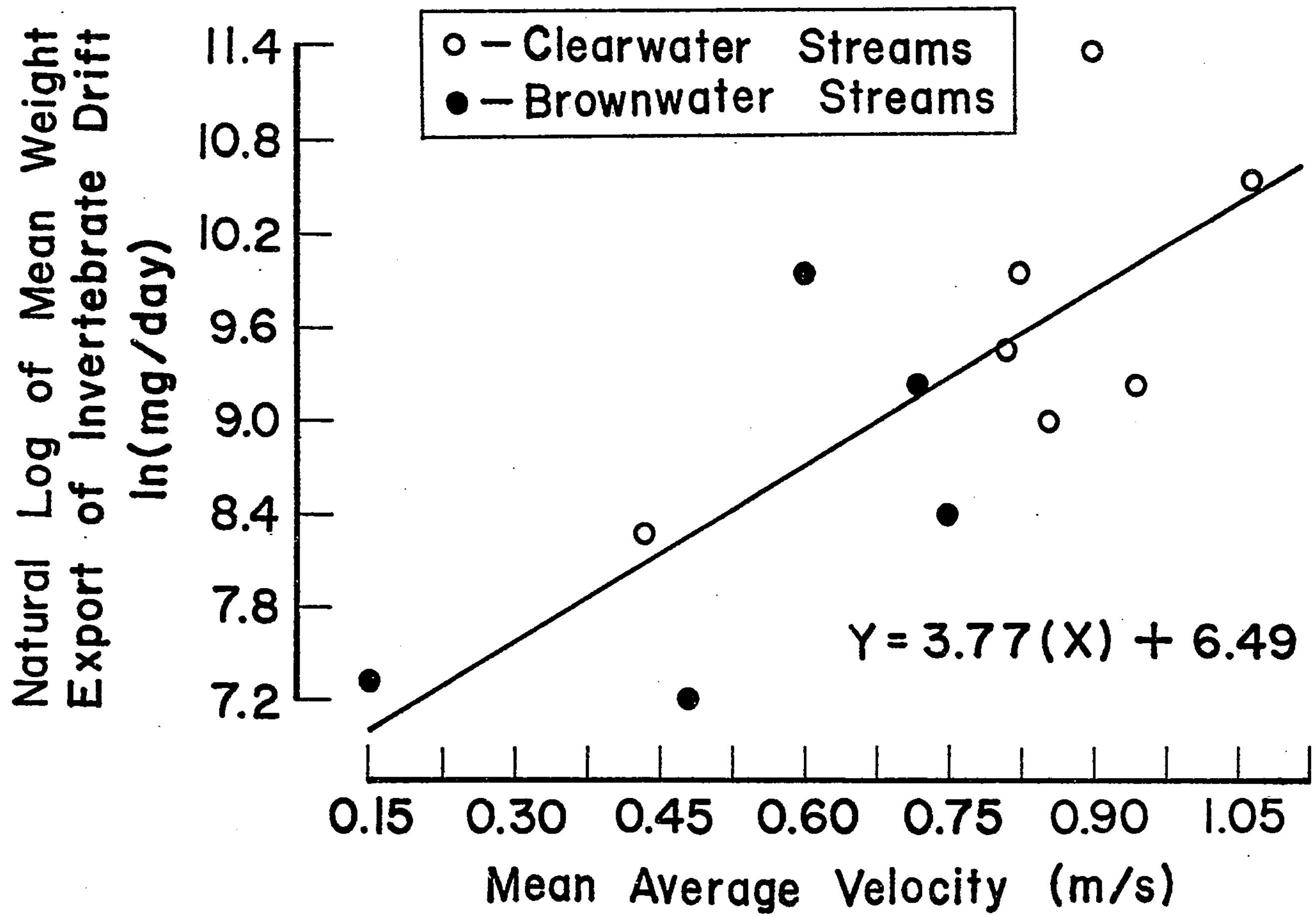
$$\ln(\overline{WTCEX}) = 5.115\,(\overline{AVEL}) + 0.021\,(\overline{ALK}) + 4.025,$$

($r^2 = 0.912$; $P = 0.005$). For drift number export the equation obtained was:

$$\ln(\overline{NUMCEX}) = 5.595\,(\overline{AVEL}) + 0.027\,(\overline{ALK}) + 3.781,$$

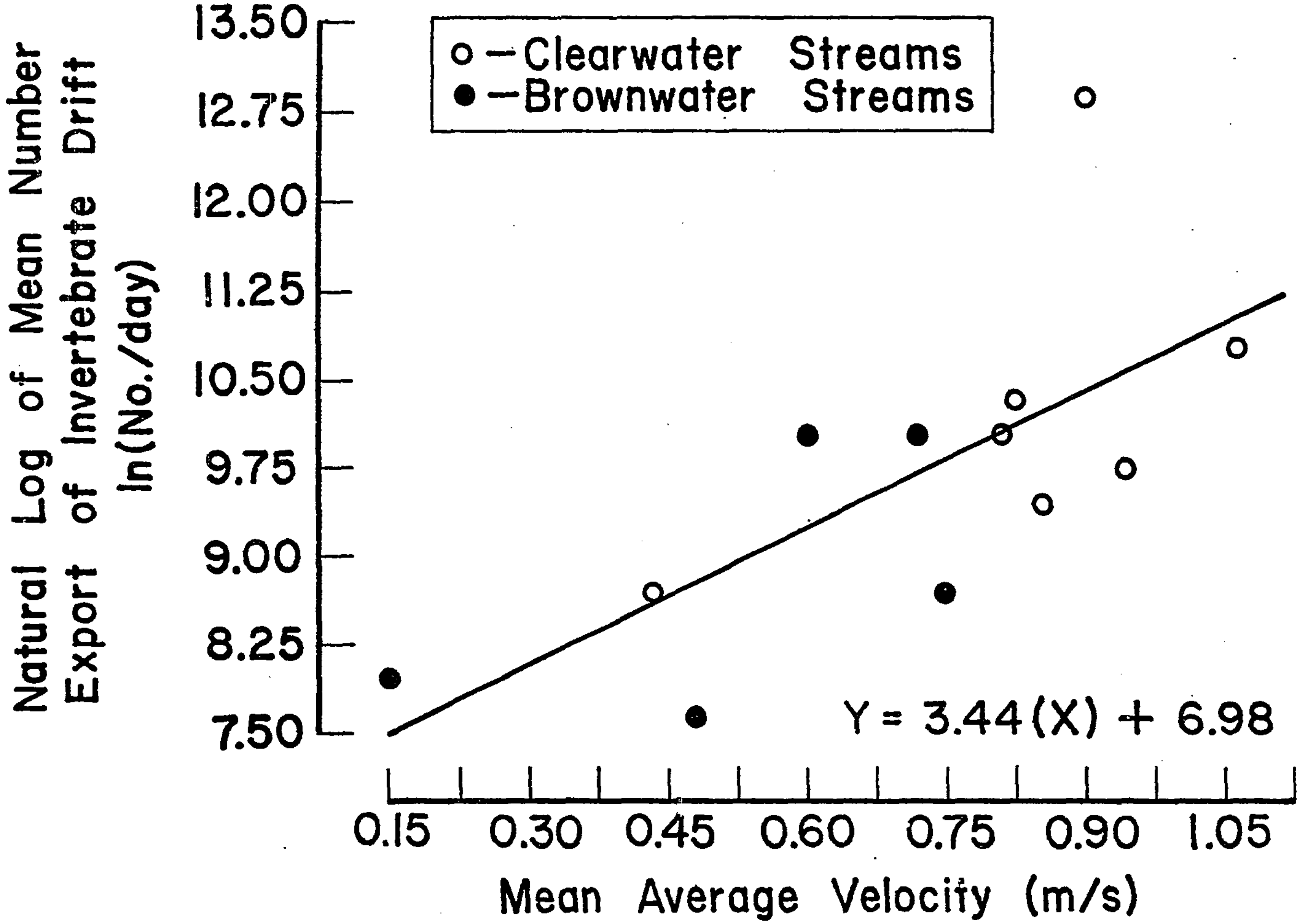
($r^2 = 0.931$; $P = 0.005$).

Figure 10. The relationship between average velocity and invertebrate drift rate, as weight per time (mg/day), for thirteen subarctic Alaskan streams



o – Clearwater Streams
● – Brownwater Streams
Natural Log of Mean Weight
Export of Invertebrate Drift
ln(mg/day)
11.4
10.8
10.2
9.6
9.0
8.4
7.8
7.2
Y = 3.77(X) + 6.49
0.15
0.30
0.45
0.60
0.75
0.90
1.05
Mean Average Velocity (m/s)

Figure 11. The relationship between average velocity and invertebrate drift rate, as numbers per time (No./day), for thirteen subarctic, Alaskan streams


Natural Log of Mean Number Export of Invertebrate Drift
ln(No./day)
13.50
12.75
12.00
11.25
10.50
9.75
9.00
8.25
7.50
o – Clearwater Streams
● – Brownwater Streams
Y = 3.44(X) + 6.98
0.15
0.30
0.45
0.60
0.75
0.90
1.05
Mean Average Velocity (m/s)

The influence of alkalinity and discharge on invertebrate drift among streams has been discussed above. The positive relationship of average velocity with both concentration (expressed as numbers per volume of water) and rate of invertebrate drift among streams begins to quantify the effects of current on the drift phenomenon. If drift occurs because of mechanical dislodgement of invertebrates from the substrate by the current, then there is probably an analogy between sediment transport and invertebrate drift. Entrainment (the initial lifting up) of sediments is a result of down channel stress. This stress in non-accelerating flow is equal to the shear stress of the stream bed on the water, and can therefore be expressed as a function of the product of slope and hydraulic mean depth (hydraulic radius). Fluid stress in this kind of flow is correlated with average velocity, because of the correlations of average velocity with depth and slope (Leopold et al. 1964). No significant relationships were found between slope, mean depth, or their product and invertebrate drift parameters. This may be due to the fact that after invertebrates and sediments are lifted from the stream bed, other forces explain why they remain in the flow or settle out. Many aquatic invertebrates can swim, and this surely complicates the question.

In fact, sediment transport in streams is somewhat poorly understood because the understanding is based on only a few rigorously derived relationships in a matrix of mostly empirical relationships (Leopold et al. 1964). One of the earliest of the empirical relationships was discovered by experiment - that sediment transport rate is highly correlated with velocity (Gilbert, 1914). Since drift transport was also found to be highly correlated with velocity, I have concluded that invertebrate drift is somewhat analogous to sediment transport. This conclusion gives support to the hypothesis that drift is mainly the result of mechanical dislodgement.

SUMMARY AND CONCLUSIONS

The hypotheses tested and the results obtained were:

(1) that invertebrate drift among streams is directly related to stream alkalinity, (accepted),

(2) that invertebrate drift among streams is directly related to the biomass of the suspended algae, as measured by chlorophyll _a_ concentration, (not accepted),

(3) that the concentration of invertebrate drift among streams is inversely related to the discharge, (accepted),

(4) that the concentration of invertebrate drift among streams is directly related to the average velocity (accepted), and,

(5) that the rate of invertebrate drift among streams is directly related to average velocity, (accepted).

In summary, it was found that about 58% of drift weight concentration among streams could be explained by an inverse relationship with discharge. About 93% of drift number concentration among streams could be explained by direct relationships with alkalinity and average velocity, and an inverse relationship with discharge. Over 90% of the variation in the rate of drift among streams, expressed as either weight or numbers exported per time, was explained by direct relationships with average velocity and alkalinity. The positive influence of alkalinity on drift was expected based on the findings of Waters (1961). However, the effects of current had never before been quantified among streams.

The hypothesis that invertebrate drift in streams is a function of the water flow is often stated in the literature (Maciolek and Needham 1951, Bournaud and Thibault 1973, Hynes 1975, and Zelinka 1976). In these studies, discharge is found to be directly related to the export of drift, but unrelated to drift concentration. As noted above, this positive relationship is simply a mathematical result of comparing a variable against another variable in which it is a factor, and is somewhat meaningless. Only Townsend and Hildrew (1976) report a relationship between water velocity and export, restricting their findings to low velocities (<11.5 cm/sec). Each of these published studies was conducted on a single stream over some length of time.

In my study, several different interior Alaskan streams were sampled in an attempt to vary the hydrologic parameters as much as possible, more than they would vary with time in any one stream. The relationships obtained, therefore, should be applicable to subarctic streams from small to quite large (up to 20 cms). Whether or not the obtained relationships are predictive remains to be tested, because seasonal mean data are not available for streams in this region other than those used in obtaining the equations.

My study also found significant relationships between water velocity and invertebrate drift. These relationships, however, were derived among streams for seasonal means of the parameters, and not just within a single stream. The relationship of Townsend and Hildrew (1976) applies to understanding the effects of storms on the invertebrates of a stream. The relationships I found, however, apply to the more general effects of water velocity on drift. I found that a stream with a higher mean average velocity (but not necessarily higher discharge) is likely to have both a higher concentration (in numbers) and higher exports in weight and numbers of invertebrate drift. I hypothesized that invertebrate drift is analogous to sediment transport in streams, in that both correlate with stream average velocity.

ACKNOWLEDGEMENTS

This project was funded in part by funds (A-061-ALAS) provided by the United States Department of the Interior as authorized under the Water Research and Development Act of 1978. Other funds were provided by the Community Employment and Training Assistance Division of the State of Alaska Department of Community and Regional Affairs. Additional funds were provided by the State of Alaska through the University of Alaska.

My thanks to all those who assisted with the field work: Dr. David and Cathy Wartinbee, T. Winston Hobgood, and Huan vinh Luong. Special thanks to those who helped as volunteers: Joyce Beelman, Martha Baldridge, and especially to my son, Arthur J. L. LaPerriere, IV, who worked for over a week as my only assistant.

I would like to thank my committee for its confidence and encouragement. Special thanks to Dr. Roger Bachmann and his current and former students who were a great help in design of the field work.

Finally, I would like to thank those who assisted with data analysis: Pat Fox, Dr. Daniel E. Canfield, Jr. and Dr. John R. Jones. I take full responsibility, of course, for the data presentation, which is not necessarily according to their advice. Thanks to all those who, in addition to the above, discussed the phenomenon of drift with me: Drs. David Zimmer and David Rosenberg, who provided hypotheses, and my daughter Monique, who provided unbiased common sense thoughts.

REFERENCES

Armitage, K. B. 1958. Ecology of the riffle insects of the Firehole River, Wyoming. Ecology 39:571-580.

Benke, A. C., D. M. Gillespie and F. K. Parrish, with T. C. Van Arsdall Jr., R. J. Hunter, and R. L. Henry III. 1979. Biological basis for assessing impacts of channel modification: invertebrate production, drift, and fish feeding in a Southeastern blackwater river. Report ERC 06-79. School of Biology in cooperation with Environmental Resources Center, Georgia Institute of Technology, Atlanta. 187 pp.

Bilby, R. E., and G. E. Likens. 1979. Effect of hydrologic fluctuations on the transport of fine particulate organic carbon in a small stream. Limnol. Oceanogr. 24:69-75.

Bishop, J. E., and H. B. N. Hynes. 1969. Downstream drift of the invertebrate fauna in a stream ecosystem. Arch. Hydrobiol. 66:56-90.

Bournard, M., and M. Thibault. 1973. The drift of organisms in flowing waters (in French, English summary). Ann. Hydrobiol. 4:11-49.

Brown, A. L., 1971. Ecology of fresh water. Harvard University Press, Cambridge, Massachusetts. 129 pp.

Brown, A. V., and K. B. Brown. 1979. Diel drift of aquatic insects and juvenile fish within a riffle of the White River in Arkansas. Unpublished paper presented at the 27th annual meeting of the North American Benthological Society, Erie, Pennsylvania, April 18-20, 1979.

Chapman, L. J., and R. Demory. 1963. Seasonal changes in the food ingested by aquatic insect larvae in two Oregon streams. Ecology 44: 140-146.

Chaston, I. 1968. A study on the exploitation of invertebrate drift by brown trout (Salmo trutta L.) in a Dartmoore stream. J. Appl. Ecol. 5:721-729.

Cummins, K. W. 1973. Trophic relations of aquatic insects. Ann. Rev. Entomol. 18:183-206.

Dixon, W. J., and M. B. Brown, eds. 1979. Biomedical computer programs P-Series. University of California Press, Berkeley. 880 pp.

Elliott, J. M. 1967a. The life histories and drifting of the Plecoptera and Ephemeroptera in a Dartmoor stream. J. Animal Ecol. 36: 343-362.

Elliott, J. M. 1967b. Invertebrate drift in a Dartmoor stream. Arch. Hydrobiol. 63: 202-237.

Elliott, J. M. 1967c. The food of trout (Salmo trutta) in a Dartmoor stream. J. Appl. Ecol. 4:59-71.

Elliott, J. M. 1970. Diel changes in invertebrate drift and the food of trout (Salmo trutta L.). J. Fish. Biol. 2:161-165.

Elliott, J. M. 1973. The food of brown and rainbow trout (Salmo trutta and S. gairdneri) in relation to the abundance of drifting invertebrates in a mountain stream. Oecologia 12:329-347.

Gales, M. C., A. C. Julian, and E. C. Kroner. 1966. A method for the quantitative determination of total phosphorus in filtered and unfiltered water. J. Am. Water Works. Assoc. 58:1363-1368.

Gilbert, G. K. 1914. The transportation of debris by running water. U.S. Geol. Surv. Prof. Paper 86. 363 pp.

Golterman, H. L., ed. 1969. Methods for chemical analysis of fresh-waters. International Biological Program Handbook No. 8 (Revised third printing). Blackwell Scientific Publications Ltd., Oxford England. 166 pp.

Griffith, J. S. 1974. Utilization of invertebrate drift by brook trout (Salvelinus fontinalis) and cutthroat trout (Salmo darki) in small streams in Idaho. Trans. Am. Fish. Soc. 103:440-447.

Hartman, C. W., and P. R. Johnson. 1978. Environmental atlas for Alaska. Institute of Water Resources, University of Alaska, Fairbanks. 95 pp.

Hildebrand, S. G. 1974. The relation of drift to benthos density and food level in an artificial stream. Limnol. Oceanogr. 19: 951-957.

Hinkley, T. M., and H. D. Kennedy. 1973. Fluctuations of aquatic and terrestrial invertebrates in drift samples from Convict Creek, California. Northwest Sci. 46:270-276.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto. 555 pp.

Hynes, J. D. 1975. Downstream drift of invertebrates in a river in southern Ghana. Freshwater Biol. 5:515-532.

Kilkus, S. P., J. D. LaPerriere, and R. W. Bachmann. 1975. Nutrients and algae in some central Iowa streams. J. Water Poll. Control Fed. 47:1870-1879.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. Freeman and Company, San Francisco, Calif. 522 pp.

Maciolek, J. A., and P. R. Needham. 1951. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California. Trans. Am. Fish. Soc. 81:202-217.

Metz, J.-P. 1974. The invertebrate drift on the surface of a prealpine stream and its selective exploitation by rainbow trout (Salmo gairdneri) (in German, English summary). Oecologia 14:247-267.

Minshall, G. W., and P. V. Winger. 1968. The effect of reduction in streamflow on invertebrate drift. Ecology 49:580-582.

Muller, K. 1974. Stream drift as a chronological phenomenon in running water ecosystems. Ann. Rev. Ecol. and Systematics. 5:309-323.

Needham, P. R. 1928. A net for the capture of stream drift organisms. Ecology 9:339-342.

Needham, P. R. 1938. Trout Streams. Comstock Press, Ithaca, N.Y.

Pearson, W. D., and D. R. Franklin. 1968. Some factors affecting drift rates of Baetis and Simuliidae in a large river. Ecology 49:75-81.

Pearson, W. D. and R. H. Kramer. 1972. Drift and production of two aquatic insects in a mountain stream. Ecol. Monogr. 42:365-385.

Reisen, W. K., and R. Prins. 1972. Some ecological relationships of the invertebrate drift in Praters Creek, Pickens County, South Carolina. Ecology 53:876-884.

Saunders, G. W., F. B. Trama, and R. W. Bachmann. 1962. Evaluation of a modified C14 technique for shipboard estimation of photosynthesis in large lakes. Great Lakes Res. Div. Publ. No. 8. University of Michigan, Ann Arbor. 66 pp.

Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes. Science 195:260-262.

Swanson, C. D., and R. W. Bachmann. 1976. A model of algal exports in some Iowa streams. Ecology 57:1076-1080.

Townsend, C. R. and A. G. Hildrew. 1976. Field experiments on drifting colonization and continuous redistribution of stream benthos. J. Anim. Ecol. 45:759-772.

Ulfstrand, S. 1968. Benthic animal communities in Lapland streams. Oikos Suppl. 10:81-92.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sidell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

Walton, O. E., Jr., S. R. Reice, and R. W. Andrews. 1977. The effects of density, sediment particle size and velocity on drift of Acroneuria abnormis (Plecoptera). Oikos 28: 291-298.

Waters, T. F. 1961. Standing crop and drift of stream bottom organisms. Ecology 42:532-537.

Waters, T. 1964. Recolonization of denuded stream bottom areas by drift. Trans. Amer. Fish. Soc. 93:311-315.

Waters, T. 1965. Interpretation of invertebrate drift in streams. Ecology 46:327-334.

Waters, T. F. 1966. Production rate, population density, and drift of a stream invertebrate. Ecology 47:595-604.

Waters, T. F. 1969. Invertebrate drift ecology and significance to stream fishes. Pages 121-134 in T. G. Northcote, ed. Symposium on salmon and trout in stream. H. MacMillan Lectures in fisheries. University of British Columbia, Vancouver.

Waters, T. F. 1972. The drift of stream insects. Ann. Rev. Entomol. 17:253-272.

Wiley, M. J., and S. L. Kohler. 1980. An assessment of biological interactions in an epilithic stream community using time-lapse macrocinematography. Unpublished paper presented at the twenty-eight meeting of the North American Benthological Society. Savannah, Georgia, March 26-28, 1980.

Zelinka, M. 1976. Mayflies (Ephemeroptera) in drift of trout streams in Beskydy Mountains. Acta Entomol. Bohemoslov. 73:94-101.

APPENDIX: RAW AND PROCESSED NUMERICAL DATA

The following abbreviations are used as column headings:

S- station number
DAY- Julian day of year
NUMB- number of invertebrates in sample
NUMC- number concentration - number invertebrates divided by volume of water filtered (no/m^3) by the net
WEIGHT- dry weight of invertebrates (mg)
WTC- weight concentration - weight of invertebrates divided by volume of water filtered (g/m^3) by the net
NMCEX- number exported - rate of invertebrate drift expressed as numbers per day passing the sampling point
WTCEX- weight exported - rate of invertebrate drift expressed as milligrams per day

NETV- net velocity - velocity of water passing through the net (m/sec)

AVEL- average velocity - average velocity of the stream (m/sec)

ADEP- average depth - average depth of the stream (m)

WIDT- stream width (m)

XSCT- stream cross-sectional area (m^2)

DSCH- stream discharge (m^3/sec)

SPC- specific conductance (mhos/cm)

ALK- alkalinity (mg/l as $CaCO_3$)

pH- negative logarithm of the hydrogen ion concentration

TP- total phosphorus (mg/m^3)

TEMP- temperature (°C)

CHLA- chlorophyll a concentration of the suspended algae (mg/m^3)

AVC- available carbon (mg/l)

S	DAY	NUMB	NUMC	WEIGHT	WTC	NMCEX	WTCEX	NETV	AVEL	ADEP	WIDT	XSCT	DSCH	SPC	ALK	pH	TP	TEMP	CHLA	AVC
1	135	52	0.06	76.4	86	6262	9201	0.79	0.74	0.27	6.3	1.7	1.24		34	7.5	4	8.0	0.18	8.8
1	170	75	0.08	40.6	44	9556	5173	0.82	0.70	0.27	7.2	1.9	1.36	65	29	7.1	4	9.0	0.10	8.4
1	198	68	0.07	49.6	52	13202	9627	0.85	1.13	0.28	6.8	1.9	2.15	58	34	7.1	5	10.0	0.32	9.9
1	219	98	0.14	32.7	45	16983	5667	0.64	0.89	0.27	6.2	1.6	1.44	70	41	7.1	3	10.0	0.36	12.0
1	247	82	0.16	52.7	100	16041	10311	0.50	0.83	0.24	5.9	1.4	1.20	65	41	7.1	2	6.0	0.58	12.0
2	138	45	0.04	136.1	124	9898	29933	0.97	0.88	0.28	11.2	3.2	2.79	102	49	7.5	7	4.5	0.00	13.0
2	170	207	0.22	141.0	148	41398	28201	0.85	0.69	0.26	12.1	3.2	2.21	115	58	7.3	7	8.3	0.22	16.0
2	198	217	0.24	64.5	73	78966	23469	0.79	0.96	0.29	13.2	3.9	3.73	120	59	7.3	2	10.0	0.51	16.0
2	219	79	0.09	27.8	31	23441	8250	0.81	0.94	0.28	11.8	3.3	3.12	127	62	7.2	2	10.0	0.40	17.0
2	242	76	0.09	84.4	96	12618	14010	0.78	0.66	0.22	11.8	2.6	1.68	140	68	7.3	2	7.0	0.54	19.0
3	138	13	0.02	14.8	22	6854	7809	0.61	0.70	0.28	21.0	6.0	4.19	77	34	7.5	8		0.00	8.8
3	170	48	0.14	20.7	60	46023	19852	0.30	0.72	0.26	20.2	5.3	3.81	80	41	7.0	10	9.0	0.40	13.0
3	198	27	0.05	12.7	23	19951	9384	0.50	0.91	0.25	21.2	5.3	4.81	85	36	7.0	2	10.0	0.76	11.0
3	219	49	0.07	30.6	41	28088	17540	0.67	0.99	0.24	20.9	5.0	4.99	88	41	7.1	4	10.0	0.44	12.0
3	242	57	0.08	29.2	40	20887	10703	0.65	0.72	0.21	20.4	4.3	3.12	96	48	7.1	1	8.5	0.72	14.0
4	138	30	0.03	18.7	20	26009	16202	0.83	0.97	0.31	30.9	9.7	9.40	85	34	7.5	6	6.0	0.04	8.8
4	172	44	0.04	42.1	35	35832	34288	1.06	1.11	0.29	35.0	10.1	11.3	86	41	7.0	7	9.0	0.14	13.0
4	213	64	0.07	83.9	92	73275	96035	0.81	1.18	0.29	35.9	10.3	12.1	96	55	7.1	3	9.0	0.37	16.0
4	221	81	0.09	39.0	42	72106	34732	0.82	1.07	0.20	45.4	8.9	9.55	95	55	7.1	4	8.5	0.14	16.0
4	247	46	0.05	20.0	22	33635	14616	0.80	0.96	0.27	29.0	7.9	7.58	98	48	7.1	4	7.0	0.26	14.0
5	144	94	0.09	137.3	127	11583	16916	0.96	1.05	0.16	9.1	1.5	1.55	53	27	6.9	6		0.14	9.2
5	172	256	0.26	120.4	120	45423	21360	0.89	0.95	0.19	11.5	2.2	2.05	50	25	6.9	3	7.5	0.29	8.2
5	200	81	0.09	28.3	32	16604	5801	0.80	0.95	0.19	11.7	2.2	2.12	57	27	7.0	4	8.0	0.43	8.4
5	221	70	0.07	32.8	33	10664	4996	0.88	0.94	0.16	11.9	1.9	1.75	54	34	7.0	2	9.0	0.62	11.0
5	247	67	0.08	31.5	38	7196	3384	0.73	0.82	0.13	9.4	1.3	1.03	49	34	7.0	1	6.0	0.54	11.0
6	144	11	0.02	6.9	11	44557	27900	0.54			39.6		28.3	110	62	7.1	9		0.58	19.0
6	172	25	0.03	14.3	16	80394	45960	0.81			39.6		34.0	115	64	7.3	13	10.0	0.29	17.0
6	200	61	0.09	37.3	54	271784	166250	0.61			39.6		35.4	128	55	7.2	4	12.0	1.04	15.0
6	221	34	0.04	16.9	19	87602	43513	0.77			39.6		26.0	135	75	7.3	2	11.0	0.80	20.0
6	247	9	0.01	9.7	11	23483	26807	0.75			39.6		27.0	150	75	7.2	5	7.0	0.87	22.0

S	DAY	NUMB	NUMC	WEIGHT	WTC	NHCEX	WTCEX	NETV	AVEL	ADEP	WIDT	XSCT	DSCH	SPC	ALK	pH	TP	TEMP	CHLA	AVC
7	151	92	0.11	30.9	37	171822	57694	0.74	0.85	0.43	48.8	21.2	18.0	260	137	7.4	7	6.0	0.14	37.0
7	178	360	0.49	41.9	57	839458	97720	0.65	0.89	0.45	48.8	22.2	19.8	230	137	7.5	8	5.0	1.05	36.0
7	207	265	0.30	52.4	58	587727	116197	0.79	0.94	0.52	48.8	24.8	23.0	270	150	7.4	5	7.0	1.34	40.0
7	226	103	0.14	39.2	52	265406	101022	0.66	0.92	0.50	48.8	24.3	22.3	265	150	7.5	12	6.0	0.54	39.0
7	249	67	0.08	35.6	44	160790	85441	0.71	0.91	0.49	48.8	24.2	22.1	260	137	7.5	4	4.5	0.62	35.0
8	151	154	0.22	98.0	40	3347	2130	0.62	0.51	0.08	4.1	0.3	0.18	171	62	7.2	13	11.0	0.10	17.0
8	178	73	0.16	32.5	70	1567	697	0.52	0.38	0.08	3.9	0.3	0.11	194	75	7.2	7		0.14	22.0
8	207	363	0.62	208.5	357	11736	6741	0.52	0.55	0.09	4.3	0.4	0.22	200	82	7.3	15	9.0	0.73	22.0
8	226	76	0.29	27.5	106	1894	685	0.34	0.35	0.05	3.8	0.2	0.08	210	103	7.4	8	12.0	0.51	28.0
8	249	428	1.16	310.2	843	11702	8481	0.37	0.39	0.07	4.0	0.3	0.12	200	89	7.4	7	6.0	1.66	24.0
9	151	50	0.06	37.2	47	2641	1965	0.71	0.65	0.10	7.4	0.7	0.49	83	50	7.2	21	12.0	0.43	14.0
9	178	63	0.07	10.6	12	4687	789	0.78	0.76	0.13	7.6	1.0	0.76	93	48	7.3	16		1.66	13.0
9	211	65	0.08	23.3	27	15423	5528	0.76	0.99	0.24	9.9	2.4	2.35	65	41	7.0	28	10.0	1.52	13.0
9	226	25	0.06	8.0	15	2847	910	0.47	0.57	0.15	8.2	1.2	0.70	83	62	7.3	36	12.0	0.87	17.0
9	249	21	0.04	65.6	142	4199	13118	0.41	0.77	0.15	9.2	1.4	1.07	65	48	7.1	29	6.0	1.01	14.0
10	156	981	3.18	1298.0	4204	32886	43513	0.35	0.71	0.10	1.6	0.2	0.12	210	103	7.3	22	6.0	0.26	29.0
10	183	1951	9.21	1589.9	7506	67390	54918	0.84	0.75	0.06	1.9	0.1	0.08	204	96	7.3	23	11.0	1.48	26.0
10	205	382	1.21	246.9	779	4425	2860	0.36	0.56	0.04	2.0	0.1	0.04	199	103	7.3	24	10.0	0.04	23.0
10	228	181	1.32	178.1	1300	3092	3085	0.22	0.38	0.04	1.7	0.1	0.03	240	144	7.5	27	8.6	0.21	37.0
10	253	199	0.44	233.2	513	2144	2513	0.78	0.60	0.06	1.6	0.1	0.06	210	120	7.5	20	4.0	0.18	31.0
11	156	63	0.53	27.2	228	2610	1127	0.12	0.14	0.11	3.6	0.4	0.06	200	109	7.4	12	4.5	0.29	29.0
11	183	298	1.69	119.0	674	7142	2852	0.32	0.15	0.09	3.6	0.3	0.05	220	116	7.4	8	7.0	0.62	31.0
11	205	40	0.19	35.2	169	502	530	0.21	0.14	0.07	3.4	0.3	0.04	210	109	7.4	8	8.0	0.22	29.0
11	228	84	0.61	32.0	234	1651	629	0.16	0.15	0.06	3.5	0.2	0.03	235	144	7.5	9	6.0	0.29	37.0
11	253	88	0.65	78.0	574	2378	2108	0.15	0.15	0.08	3.5	0.3	0.04	230	137	7.4	8	3.5	0.26	37.0
12	156	240	0.36	148.8	221	22250	13795	0.60	0.74	0.16	6.3	1.0	0.72	200	96	6.8	18	12.0	0.94	34.0
12	183	696	1.23	256.6	453	69492	25610	0.50	0.63	0.18	5.8	1.0	0.65	198	96	6.8	26	14.0	0.30	33.0
12	205	167	0.17	86.1	86	15549	8017	0.89	0.89	0.19	6.5	1.2	1.08	194	103	6.9	38	14.0	0.58	33.0
12	228	89	0.17	31.2	60	8524	2987	0.46	0.59	0.15	6.5	1.0	0.58	198	103	6.8	57	12.0	1.31	34.0
12	253	32	0.04	10.7	14	2634	881	0.68	0.75	0.15	6.4	1.0	0.72	194	103	6.7	20	7.0	2.46	41.0
13	162	50	0.07	36.6	53	6770	4957	0.62	0.60	0.27	6.4	1.8	1.09		34	6.9	23	5.0	0.65	12.0
13	191	17	0.02	10.4	14	1729	1057	0.64	0.58	0.22	6.4	1.4	0.84	70	34	6.9	18	8.0	1.74	11.0
13	213	7	0.02	0.4	1	745	43	0.32	0.47	0.13	6.2	0.8	0.39	115	55	7.0	12	9.0	0.58	17.0
13	232	18	0.06	8.6	30	1309	625	0.32	0.37	0.11	5.8	0.6	0.24	145	62	7.0	12	8.5	0.72	19.0
13	255	5	0.01	2.1	4	202	85	0.42	0.36	0.10	5.9	0.6	0.22	134	62	7.0	14	5.0	0.94	20.0