



Observations of distribution, abundance and production related aspects of aquatic macro-invertebrates in natural thermal gradients
by Richard Allen Oswald

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Zoology
Montana State University
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Abstract:

The aquatic macroinvertebrate communities of the thermal gradients produced by the Ringling-Drumheller, Norris and Potosi hot springs were investigated in 1974 and 1975. The three thermal gradients differed in chemical composition, size and age. Macroinvertebrate samples were collected with Surber and Hester-Dendy samplers and an Ekman grab.

Macroinvertebrate life was excluded by temperatures in excess of 40°C. The communities typical of high thermal regimes appeared to be formed by an exclusion, rather than addition, of genera or species as temperature increased.

Macroinvertebrate numbers, taxa and biomass were found to be negatively correlated with temperature. Despite the observed depression of standing crop at elevated temperatures, higher substrate colonization rates and larger sizes of selected taxa at higher temperatures suggested that production rate may increase with temperature.

Data compiled at the genus-species level indicated that most forms were eurythermal. Cold, hot and intermediate stenothermal forms were also observed. The eurythermal group was further analyzed to yield patterns of cold preference, warm preference, preference for intermediate temperatures or a lack of preference within broader ranges of tolerance.

Abundance at the total, ordinal and genus-species levels was affected by an interaction between temperature and season. Patterns of abundance did not respond the same for all levels of temperature when taken over all seasonal levels.

Data suggest community avoidance of, rather than adaptation to, high temperatures at a relatively small thermal plume. It was speculated that longer adaptation time resulted in a higher thermal tolerance for invertebrate communities at Potosi than at Ringling although this higher tolerance may have been influenced by differences in water chemistry or stability of thermal regime. Data further suggest a higher thermal tolerance for communities of pools or slower flows than for riffle communities.

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Date May 29, 1929

OBSERVATIONS ON DISTRIBUTION, ABUNDANCE AND PRODUCTION
RELATED ASPECTS OF AQUATIC MACROINVERTEBRATES
IN NATURAL THERMAL GRADIENTS

by

RICHARD ALLEN OSWALD

A thesis submitted in partial fulfillment
of the requirements for the degree

of

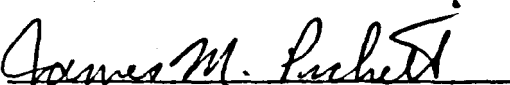
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ABSTRACT

The aquatic macroinvertebrate communities of the thermal gradients produced by the Ringling-Drumheller, Norris and Potosi hot springs were investigated in 1974 and 1975. The three thermal gradients differed in chemical composition, size and age. Macroinvertebrate samples were collected with Surber and Hester-Dendy samplers and an Ekman grab.

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Macroinvertebrate numbers, taxa and biomass were found to be negatively correlated with temperature. Despite the observed depression of standing crop at elevated temperatures, higher substrate colonization rates and larger sizes of selected taxa at higher temperatures suggested that production rate may increase with temperature.

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Abundance at the total, ordinal and genus-species levels was affected by an interaction between temperature and season. Patterns of abundance did not respond the same for all levels of temperature when taken over all seasonal levels.

Data suggest community avoidance of, rather than adaptation to, high temperatures at a relatively small thermal plume. It was speculated that longer adaptation time resulted in a higher thermal tolerance for invertebrate communities at Potosi than at Ringling although this higher tolerance may have been influenced by differences in water chemistry or stability of thermal regime. Data further suggest a higher thermal tolerance for communities of pools or slower flows than for riffle communities.

INTRODUCTION

Environmental temperature has long been considered one of the most important factors affecting life in the aquatic ecosystem. Aquatic communities from similar habitats within similar latitudinal, longitudinal and elevational regions would be expected to be subject to a similar set of thermal regimes. In recent years, biologists have become increasingly concerned with the upward alteration of many of these thermal regimes due to human activities. The primary focus of this concern has been on heated effluents produced by cooling waters discharged from fossil fuel and nuclear-powered electrical generating plants.

Krenkel and Parker (1969) predicted that increased needs for electrical generation would require that approximately one-fifth of the total surface runoff of the contiguous United States would be required for cooling purposes by 1980. This amount could be reduced by the increased use of cooling towers and closed cooling systems; however, these systems could pose an additional threat through their consumptive use of water. The thermal problem could be aggravated by an impending shortage of fossil fuels because nuclear-powered generating plants produce larger amounts of waste heat than fossil fuel plants (Krenkel and Parker 1969).

Concern over possible effects of waste heat on aquatic communities has led to many investigations of effects of increased heat on benthic macroinvertebrates. Laboratory studies have been conducted on

metabolic effects (Newell 1973, Vernberg and Vernberg 1974), lethal limits (Gaufin and Hern 1971, Martin and Gentry 1974, Nebeker and Lemke 1968), growth and development (Lutz 1968, Nebeker 1973, Newell 1975) and emergence (Nebeker 1971a). However, application of laboratory results to field situations should be done with caution (Lehmkuhl 1974, Wurtz and Renn 1965).

Numerous field studies have been conducted on thermal effluents produced by power plants. Thermal effects on drift, development, emergence, distribution and abundance of macroinvertebrates have all been investigated below power plant discharges. Much of this literature has been reviewed on an annual basis (Coutant and Talmage 1975, Coutant and Pfuderer 1974, Coutant and Pfuderer 1973, Coutant and Goodyear 1972). Many of these studies have been complicated, however, by sampling difficulties due to substrate and depth differences (Masengill 1976), variable thermal regimes due to power plant operational requirements (Wurtz and Renn 1965), the presence of other forms of pollutants (Langford 1971, Wurtz 1969) and relatively small elevations in temperature (Wurtz 1969).

Relatively little work has been done on natural thermal effluents produced as a result of hot spring or geyser activity. Hot springs have been defined as those issuing at or above 38°C (Mariner et al. 1976). Some descriptive work has been done on macroinvertebrates inhabiting hot springs (Brues 1924 and 1932, Mason 1939, Provonsha and

McCafferty 1977, Robinson and Turner 1975, Stoner 1923). Work on macroinvertebrate distribution, abundance and production has been done on two rivers, the Firehole and Gibbon in Yellowstone National Park, which receive natural thermal effluents (Armitage 1958 and 1961, Jones 1967, Vincent 1966).

Discharges of hot spring effluents into small spring streams provide unique situations for the study of thermal effects on macroinvertebrates. Advantages lie in the stability of the thermal gradient produced, the ease of sampling due to small size and the long adaptation time involved (Brock 1967). Three such heated springs in southwestern Montana provided an opportunity to compare distribution, abundance, development and production of macroinvertebrates in thermal gradients ranging in temperature from approximately 45°C down to normal ambient temperatures.

DESCRIPTION OF STUDY AREAS

Three southwest Montana hot springs were investigated during the course of the study: the Ringling-Drumheller Well, the Norris Hot Spring and the Potosi Hot Spring. All waters under study were small spring streams, 1 to 4 meters wide. Streams of this size and origin belong to the rheocrene in the classification of Illies (Hynes 1970).

The most intensive study was conducted on the Ringling-Drumheller Well and its resultant thermal plume in the south fork of the Smith River. This well is located in western Meagher County, Montana (SE 1/4, NE 1/4, Sec. 25 T7N R7E) in a semi-arid region with 47 cm of precipitation per year and an average annual temperature of 5.4°C (Groff 1965). The Ringling well had an unusual man-made origin. It was formed in September, 1929 when an attempt to drill for oil produced hot water.

The spring originates at a surface elevation of 167.4 m (5500 ft) with a discharge of approximately $.05 \text{ m}^3 \text{ sec}^{-1}$ (1.8 cfs). A discharge of this magnitude places the Ringling well among the larger hot springs of Yellowstone National Park (Allen and Day 1935). Temperature of the spring at the outflow ranged from 43 to 47°C during the study period. The hot artesian water is believed to acquire its heat from deep circulation in the cave forming zone or a deep fault or fissure and originates in Devonian limestone over dolomite (Groff 1965).

The hot stream flows down a moderate gradient for approximately 500 m where it merges with the upper south fork of the Smith River producing elevated temperatures which are measurable for approximately 2 km downstream. The combined effects of the elevated temperature and the larger volume of the hot spring as compared to the receiving stream (Table 1) acts to produce this relatively large thermal plume.

Table 1. Mean discharges at low (summer and fall) flows of the hot springs and their receiving streams at Ringling and Norris.

	<u>Hot Spring</u>	<u>S. Fk. Smith River</u>
Ringling	.050 m ³ /sec (1.80 cfs)	.027 m ³ /sec (.98 cfs)
	<u>Hot Spring</u>	<u>Hot Spring Creek</u>
Norris	.008 m ³ /sec (.31 cfs)	.200 m ³ /sec (7.12 cfs)

Eight biological sampling stations were selected along this thermal gradient based on temperature differences (Fig. 1). Maximum, minimum and mean observed temperatures are listed in Table 2. Sites 5, 4 and 3 were located within the flow of the hot spring, Site 2 was located above the inflow of the hot spring and Sites 1, 6, 7 and 8 were located in the Smith River below the inflow of the hot spring. Sites 2 and 8 were the upper and lower cold water references, respectively. These two sites became cold enough in winter to be largely ice covered

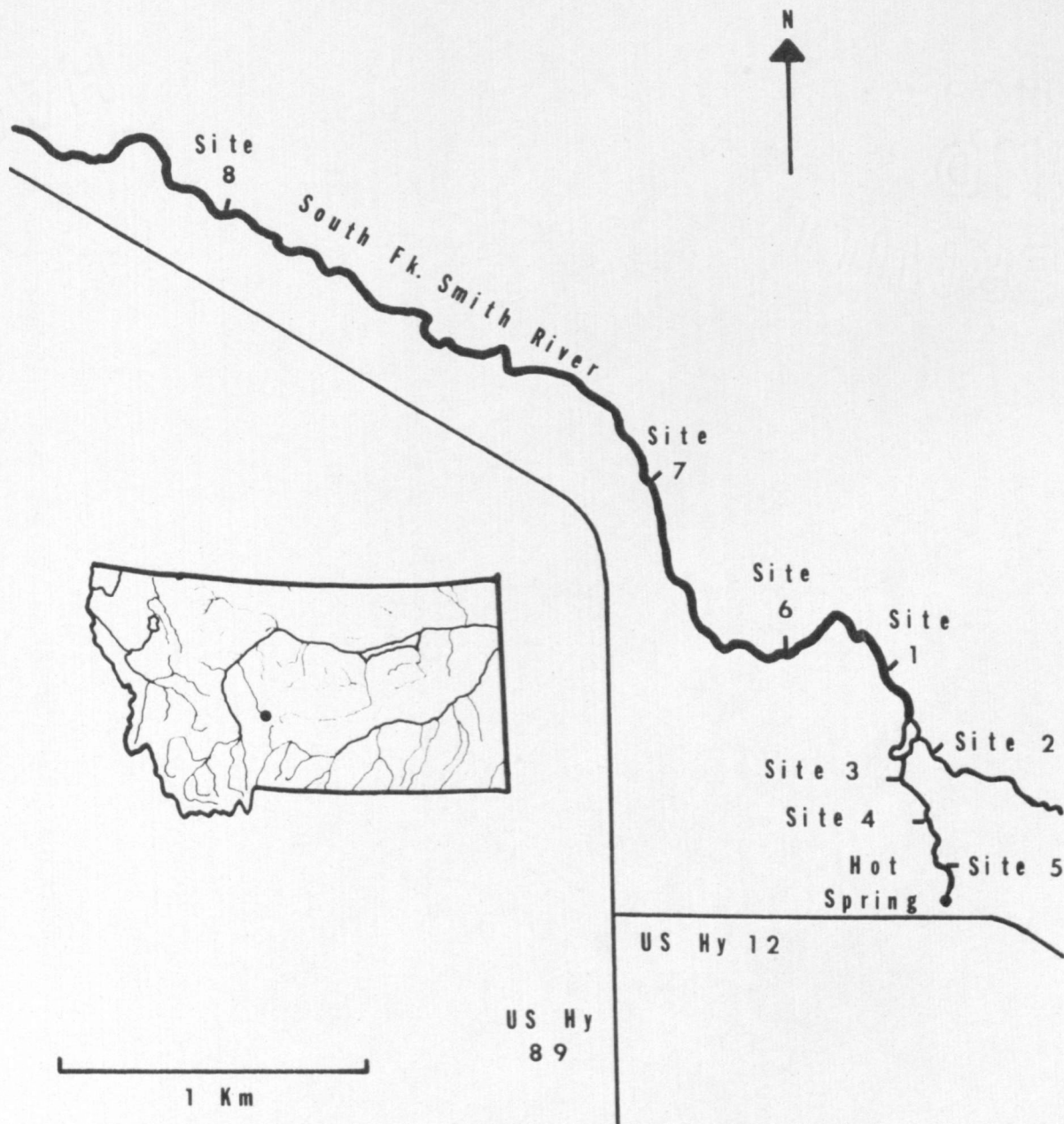


Figure 1. Map of Ringling study area showing macroinvertebrate sample sites.

Table 2. Maximum, minimum and mean observed temperatures (°C) for sample sites at Ringling, Norris and Potosi.

RINGLING	5	4	3	1	6	7	8	2
Maximum	47.0	43.0	41.0	36.0	32.0	28.0	23.0	24.0
Mean Maximum	----	----	35.7	27.0	20.0	15.0	10.0	10.0
Mean Median	45.0	38.0	34.0	24.8	18.6	11.9	8.2	7.9
Mean Minimum	----	----	32.3	23.0	17.0	9.0	7.0	6.0
Minimum	43.0	37.0	29.0	10.0	9.0	2.0	0.0	0.0
NORRIS	5	3	2	1	4			
Maximum	48.0	32.0	16.0	10.0	10.0			
Mean Median	38.8	24.3	10.5	5.3	5.3			
Minimum	29.0	15.0	5.0	0.0	0.0			
POTOSI	2	1	3	4	5			
Maximum	34.0	29.0	24.0	17.0	13.0			
Mean	33.3	27.8	22.5	16.5	12.3			
Minimum	32.0	26.0	21.0	15.0	10.0			

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and frazil or slush ice was observed during the winter of 1974-75 at Site 8. All other sites were considered hot or warmer than ambient. An annual temperature profile for some of these sites is given in Appendix Table 27.

Each sample site was divided into an erosional (riffle) and a depositional (pool) area. The riffles were characterized by fast flows (.30-1.22 m/sec), shallow depths (5-15 cm) and a rubble or cobble substrate bearing filamentous green or, in upper hot spring sites, blue green algae. The pools were characterized by slower flows, deeper water (15-50 cm) and a substrate composed of silt, sand and detritus with some larger algae (*Chara* or *Nitella*) and a few macrophytes.

Chemical data (Table 3) show that the Ringling hot spring is a calcium, magnesium, bicarbonate and sulphate spring. This corresponds to the rarest of the major types of hot spring found in Yellowstone National Park (Allen and Day 1935). The Smith River above the inflow of the hot spring is a calcium, sodium and bicarbonate water. The effect of the Ringling hot spring is to increase the importance of calcium, magnesium and sulphate and decrease the importance of sodium and chloride in the Smith River. The system is characterized by high alkalinities and conductivities throughout. Mean dissolved oxygen levels (Table 4) decrease with increasing temperatures. Chemical and physical parameters measured in the hot spring and the Smith River at Ringling compare favorably with data compiled by Groff (1965) and L.

Table 3. Selected chemical parameters at Ringling, Norris and Potosi.

	Ringling					Norris					Potosi
	5	3	1	7	2	6	5	2	1	4	4
pH	7.42	8.23	8.25	8.38	8.18	8.26	8.27	8.12	8.12	7.98	8.35
K _{s25} (μmho/cm)	1420	1421	1417	1390	1012	879	877	586	340	323	381
Tot. Alk. (me/l)	2.62	2.67	3.22	3.09	3.17	6.30	6.30	4.32	3.05	2.99	.95
Ca ⁺² (mg/l)	302	307	276	156	121	18.4	18.4	37.6	42.4	44.8	10.8
Mg ⁺² (mg/l)	63.7	60.8	45.2	34.0	24.0	3.4	3.4	6.3	8.8	11.2	0.2
Na ⁺ (mg/l)	8.6	8.4	42.0	39.0	59.0	189	187	96.0	27.0	22.0	17.4
K ⁺ (mg/l)	8.0	7.6	5.1	5.0	3.6	14.0	13.8	7.3	5.5	5.2	2.8
SO ₄ ⁻² (mg/l)	958	918	788	408	357	137	114	42.0	26.0	31.0	104
Cl ⁻ (mg/l)	1.8	1.7	2.8	2.8	5.3	22.0	22.0	12.0	9.2	8.7	6.6
F ⁻ (mg/l)	3.1	3.4	2.9	3.2	0.9	8.7	8.7	2.4	1.1	0.8	6.9
SiO ₂ (mg/l)	28.8	28.8	28.0	26.0	28.0	94.0	94.0	50.0	44.0	40.0	49.2

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Table 4. Mean dissolved oxygen levels (mg/l) at Ringling, Norris and Potosi.

Sample Site								
RINGLING	5	4	3	1	6	7	8	2
	3.9	5.4	6.6	7.7	8.6	9.5	9.8	9.0
NORRIS	6	5	3	2	1	4		
	4.9	5.1	6.5	8.6	10.0	10.0		
POTOSI	2	1	3	4	5			
	5.6	6.3	7.1	7.5	7.8			

Bahls (unpublished data, Mont. Dept. Health and Env. Sci., Helena, Mont.).

Norris Hot Spring is located in eastern Madison County, Montana at E 1/2 Sec. 14 T3S R1W. The spring originates at a surface elevation of approximately 1463 m (4800 ft) with a discharge of 530 l min⁻¹ (.31 cfs) and a temperature of 49-52°C. The spring is believed to originate in Precambrian gneiss (Mariner et al. 1976). From its outflow, the spring flows directly into a large plank-lined pool where the water undergoes radiative heat loss, cooling to approximately 38°C when it leaves the pool. The hot stream flows down a gentle gradient for approximately 100 m undergoing little further cooling until it merges with Hot Spring Creek producing a very small thermal plume. The

plume attains a maximum width of about 1.5 m and a length of about 5 m tapering gradually downstream as the cold water forces the warm to shore. In contrast to the situation at Ringling, a relatively small volume of hot water enters the much larger Hot Spring Creek at Norris resulting in a smaller thermal plume (Table 1).

A series of six sampling stations were selected at Norris, again, based on thermal differences (Fig. 2, Table 2). Sites 6 and 5 were located within the hot spring channel, Sites 3 and 2 were located within the thermal plume in Hot Spring Creek and Sites 4 and 1 were the upper and lower cold water references in Hot Spring Creek.

Each site was divided into a riffle and pool format similar to that at Ringling. The substrate at Norris differed from that at Ringling with the riffle areas having rubble interspersed with large amounts of gravel and the pool areas having mainly a sand bottom.

Chemically, Norris differs greatly from Ringling. The spring at Norris is a sodium, potassium, bicarbonate and chloride water (Table 3). This chemical composition corresponds to one of the two most common types of hot spring found in Yellowstone National Park (Allen and Day 1935). Again, in contrast with Ringling, the dilution effect of Hot Spring Creek is evident in that the chemistry of the stream is dominant over the chemistry of the spring. In the stream, calcium replaces sodium as the dominant cation and the sulphate and chloride concentrations are much lower in the stream than in the spring.

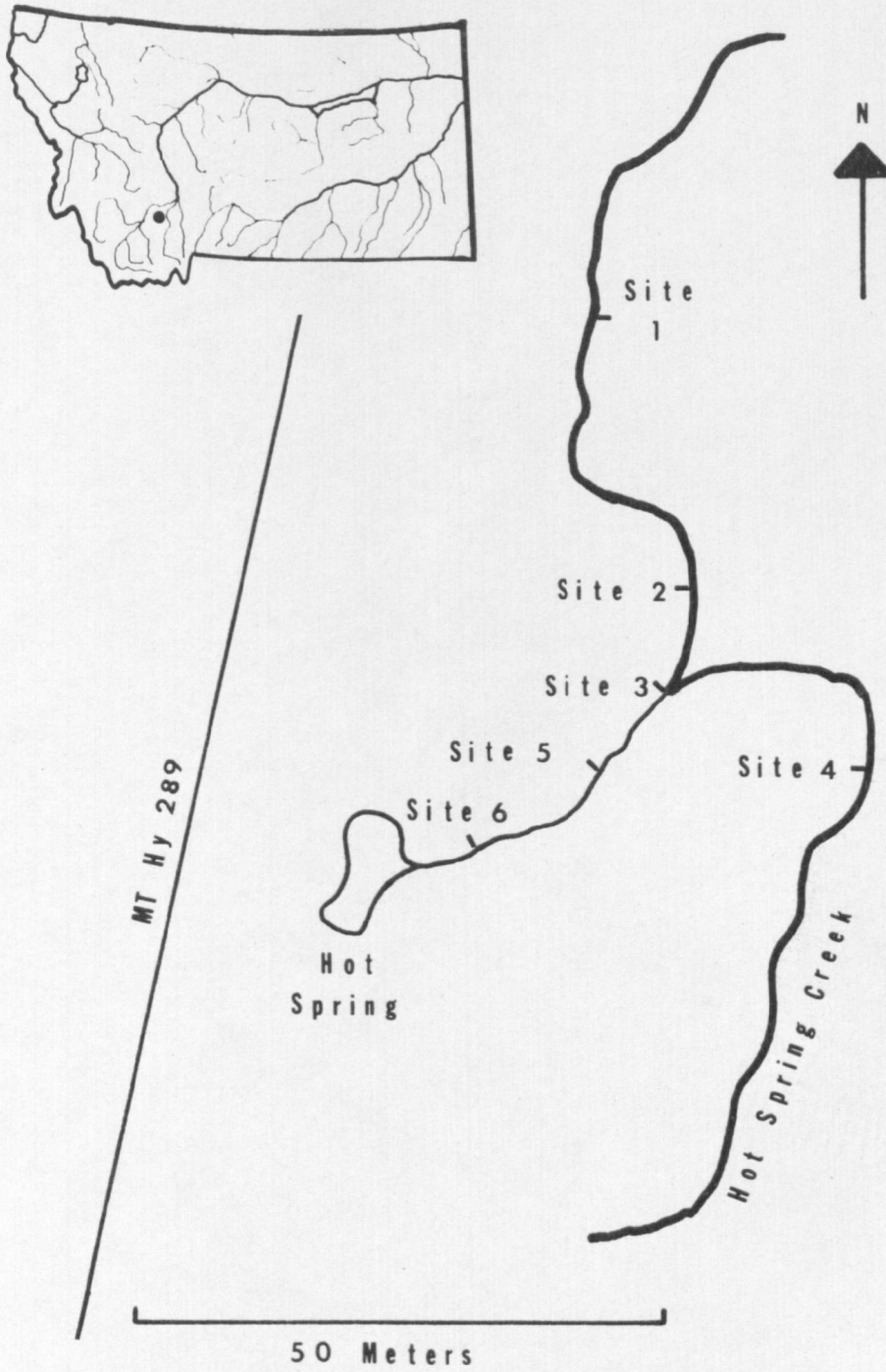


Figure 2. Map of Norris study area showing macroinvertebrate sample sites.

Although thermal effects of the hot effluent are absent six meters below the entry of the hot spring, some chemical effects are evident at Site 1 approximately 50 m below the entry (Table 3). Dissolved oxygen values (Table 4) follow the same trend as those at Ringling. Chemical and physical parameters again compare favorably with those of Mariner et al. (1976) in the hot spring and L. Bahls (unpublished data, Mont. Dept. Health and Env. Sci., Helena, Mont.) in Hot Spring Creek.

Potosi Hot Spring originates on the east slope of the Tobacco Root Mountains in eastern Madison County, Montana. The site is unsurveyed with the spring located at $45^{\circ}36'$ N, $111^{\circ}54'$ W (Mariner et al. 1976). The spring issues from a series of vents at a surface elevation of 1890 m (6200 ft). Mariner et al. (1976) estimated the major source temperature at 50°C and the flow at several hundred liters per minute. They believed that the spring had its origin in granite bedrock and Tertiary volcanic rock.

Potosi Hot Spring is composed of several small channels less than 1 meter wide and 5 to 10 centimeters deep. The substrate is composed of sand and fine gravel. Due to the dendritic nature of the channels, a strong thermal gradient is present within the spring itself and five sampling stations were selected within the gradient (Fig. 3). Thermal data for these sites are found in Table 2. Although these temperatures represent mean values of spot readings taken on sampling dates, very little seasonal variation was observed. Thus the sites at Potosi

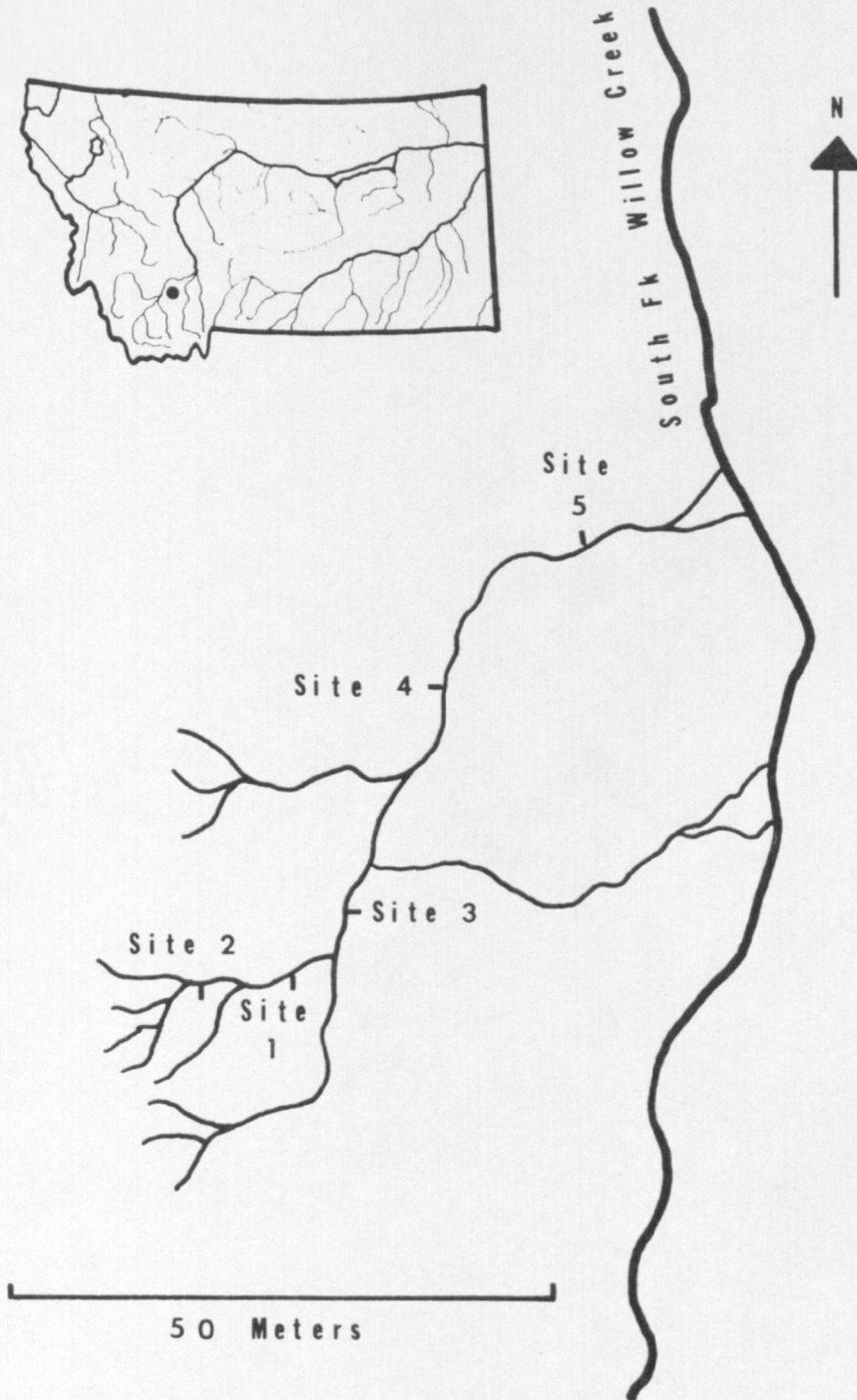


Figure 3. Map of Potosi study area showing macroinvertebrate sample sites.

demonstrated a high degree of thermal stability, probably due to their proximity to the spring source. All sample stations were within 50 m of the spring source. Although the spring produces two thermal effluents into the south fork of Willow Creek, no stations were located in the stream because no appreciable plume is produced by either effluent.

The chemistry of Potosi Hot Spring is given in Table 3. Potosi represents a third type of hot spring with a very low specific conductance and generally much lower ionic concentrations than Ringling or Norris. Dissolved oxygen concentrations decrease with increasing temperature (Table 4). Chemical data compared favorably with that presented by Mariner et al. (1976).

Although chemical and substrate differences are apparent between the study areas, the sample stations are quite comparable thermally due to the similarity of the gradients produced. Differences between the plumes exist in that the plume at Norris is very small in relation to the stream that it enters while the plume at Ringling and the gradient within the spring at Potosi dominate the thermal regimes of the areas under study. A difference between Ringling and Potosi exists in that Ringling had only been producing a thermal effluent for 45 years prior to the present study.

METHODS

A seasonal sampling program was set up at Ringling, Norris and Potosi. Samples from all streams were taken at four-month intervals: in early October of 1974 and mid-February, early June and early October of 1975. An additional sample was taken at Ringling in August, 1975.

Physical

Sample sites at Ringling, Norris and Potosi were selected based on a 5°C decrease in temperature from the hottest sample site down to the ambient temperature of the receiving stream. The selection of sites was made on the temperature gradient present on one day, thus the sites were not necessarily separated by 5°C on a mean annual basis. The 5°C increment was selected as one which would probably be large enough to yield biological differences among sites. An attempt was made to select sites which were similar in substrate, width, depth and current velocity in order to minimize these effects and maximize the effects of temperature.

Flows and discharges were determined with a standard meter stick and a Pygmy Gurley current meter. Discharge was calculated for fall sampling periods at Ringling and Norris using Embody's formula (Welch 1948). The flows presented in Table 1 are reflective of low, stable conditions that should prevail throughout most of the year.

Temperature was measured with a mercury thermometer and a Yellow Springs Instruments Model 54 resistance thermometer on all sample

dates. These spot recordings are the only thermal data that were taken at Potosi. Additional thermal data were collected at Norris for the seven day period immediately following each sample date with Tempscribe seven day constant recording thermographs (Bacharach Instruments). An annual thermal cycle was recorded at Ringling from February 1975 to February 1976 with Tempscribe thermographs and Ryan Model D15 fifteen day constant recording thermographs (Ryan Instruments). Data were collected at Sites 3, 1, 6, 7, 8 and 2. Thermal data for Sites 5 and 4 consisted of spot readings because temperatures at these sites frequently exceeded the upper limits of the aforementioned instruments.

Chemical

Water samples were taken at Ringling (Sites 5, 3, 1, 7 and 2), Norris (Sites 6, 5, 2, 1 and 4) and Potosi (Site 4) for chemical analysis. These samples were analyzed for major cations and anions, silica, pH, conductivity and total alkalinity using standard methods of analyses as described by the APHA (1971). Calcium, magnesium, sodium and potassium were determined spectrophotometrically with a model 151 AA/AE Spectrophotometer (Instrumentation Laboratories). Alkalinity and chloride were determined titrimetrically, sulphate was determined turbidometrically, fluoride by the SPADNS method and silica, colorometrically. Conductivity was measured with a Yellow Springs Instruments Model 31 AC Conductivity Bridge. Determination of pH and

total alkalinity titrations were made with a Beckman Expandomatic pH Meter. Dissolved oxygen was measured at all sites on all dates, in situ, with a Yellow Springs Instruments Model 54 oximeter. The oximeter reading was compared with a Winkler dissolved oxygen determination on each sample date.

Biological

Bottom samples were taken at all sites at Ringling, Norris and Potosi for the collection of macroinvertebrates. Collections were made at Ringling on October 5, 1974 and February 15, June 11, August 11 and October 14 in 1975. Collections were made in both riffle and pool areas. A riffle sample consisted of two collections with a Surber square foot sampler which was modified to sample an area of $.1 \text{ m}^2$. A pool sample consisted of two collections made with a $.023 \text{ m}^2$ Ekman grab. Bottom samples were taken at Norris in a manner similar to that at Ringling with two Surber and two Ekman collections made at each sample site on each sample date. Samples were collected on October 7, 1974 and February 12, June 10 and October 7 in 1975. Bottom samples at Potosi consisted of two collections by Ekman grab at each site on each date. Small channel size and low current velocity prevented the effective use of the Surber sampler at Potosi. Samples were collected on October 11, 1974 and February 16, June 10 and October 7 in 1975.

In addition to the bottom samples, a series of collections was made at Ringling using $.2 \text{ m}^2$ multiple plate artificial substrate samplers (Hester and Dendy 1962). Two Hester-Dendy samplers were placed in each riffle area at Sites 3, 1, 6, 7, 8 and 2 from August 25 through December 4, 1975 and collected at approximately 14 day intervals. No Hester-Dendy samplers were used at Norris or Potosi.

Samples were concentrated in a U.S. Series No. 30 seive, transferred to glass or plastic containers and preserved in 10% formalin. Invertebrates were separated from the sample in the laboratory and placed in 70% ethanol for storage. Through the use of appropriate keys and techniques, all invertebrates were identified to the lowest practical taxon, usually genus or species, and enumerated.

With the exception of the microdrile oligochaetes which were put into Amman's lactophenol for clearing, all invertebrates from the Ringling bottom samples were weighed by genus or species. Total weight of invertebrates collected on each Hester-Dendy sampler was also recorded. Invertebrates were removed from the ethanol, blotted until no moisture appeared on the paper and weighed (Coutant 1962) on a Mettler H 16 electronic balance capable of weighing to the nearest $\text{g} \times 1.0^{-5}$.

Linear measurements such as head length and width were made on four selected genera from Ringling. These measurements were made by

to the nearest .001 mm with an ocular micrometer disc (VWR Scientific Instruments) fitted into a microscope.

Statistical

Macroinvertebrate genus-species distributions were analyzed, in part, through the calculation of an index of similarity (S) developed by Czekanowski (Clifford and Stephenson 1975). The index is described by:

$$S = \frac{2C}{A+B} = 1.0 \text{ maximum similarity}$$

where A = number of taxa occurring at Site A

B = number of taxa occurring at Site B

C = number of taxa common to both Sites A and B

The index is a nearest neighbor comparison of one sample site against all other sample sites. Calculated S values were compiled and used to compare sites at Ringling, Norris and Potosi.

Distributional data were further analyzed to yield patterns of response of individual taxa to temperature. Taxa were placed in one of four categories (i.e., eurythermal, cold stenothermal, hot stenothermal or intermediate stenothermal) based on distributional response to temperature. This method yields information as to which taxa are limited to cold or hot environments and which are adapted to a broad range of temperatures. The method applies quite well to the stenothermal forms since their presence is restricted to a small number of sites. The eurythermal forms, however, present a drawback to this

method in that presence is weighted equally over a wide range of sites without consideration as to whether this presence occurred infrequently at one site and very frequently at another or at an equal frequency throughout.

Patterns of distribution were further analyzed through the use of frequency of occurrence data. This method was used in an attempt to minimize all differences (e.g., chemical, physical, temporal etc.) among study areas and sites and maximize the effects of temperature. It also has the advantage of increasing the sample size for a single variable, temperature. This was done by pooling all samples from Ringling, Norris and Potosi that exhibited similar thermal regimes; e.g., Sites 2 and 8 at Ringling, Sites 1 and 4 at Norris and Site 5 at Potosi were pooled as the coldest group of sites from a total of 104 Surber, Ekman and Hester-Dendy samples at this thermal level. An obvious criticism of this method is that it ignores all differences among the three study areas. Frequency of occurrence was calculated as the number of samples in which an individual genus or species occurred divided by the total number of samples in which it could have occurred at a given thermal level (pooled set of sample sites). Thus, if a genus occurred at Ringling or Potosi but not at Norris, the Norris samples were not included in the frequency calculation.

Frequency of occurrence values were also used to delineate thermal distributional trends. The cold, hot and intermediate stenotherms were

partitioned out on the basis of presence or absence at a thermal level. The eurythermal forms, however, were further subdivided on the basis of temperature associated trends in frequency value (e.g., increased frequency of occurrence as temperature increased).

Data were compiled on the total number of invertebrates per sample for sample sites for the three study areas. Similar data were compiled on numbers per sample at the ordinal and genus-species levels, total weight of invertebrates per sample for the Ringling samples and colonization rates for the Hester-Dendy samples.

In order to determine whether differences observed among treatment (thermal site) means were significant or merely due to sampling error, all treatment means were subjected to a multifactor analysis of variance. This test was selected as one which would best fit the seasonal sampling program that was used. In a one-way analysis of variance, variation due to one treatment, e.g., temperature is compared with variation due to error in an F test. A multifactor analysis of variance divides treatment variation into two factors and considers the interaction between these factors. In this study, temperature was investigated as the primary factor in the determination of numerical differences among sites; however, temperature is influenced by season. The abundance of most aquatic invertebrates also fluctuates on a seasonal basis due to factors such as changes in life stage and mortality within the population. Because the sampling schedule

employed in this study was not continuous, the second factor partitioned out of the treatment variation was variation due to sample date or season. The multifactor analysis of variance also tests the variation due to the interaction between temperature (sample site) and season (sample date). A significant interaction is interpreted to mean that patterns of numerical response to levels of one factor (temperature) is not the same when taken over all levels of the other factor (season). In the calculation of F values, a fixed model was assumed thus implying experimental repeatability and denying randomness of sample.

A Neuman-Keuls Test was also employed to determine which sample sites were significantly different from all other sample sites. This test uses Q values to compare one sample site to all others.

Quantitative data were analyzed for a linearity of response to temperature by means of linear regression and correlation. Numbers and weights from each sample site were regressed against and correlated with temperature. Temperature values assigned to sample sites for each sample date were mean values compiled from mean daily temperatures 8 days prior to and 8 days following a sample date at Ringling and 7 days following a sample date at Norris. Thermal data for Potosi consisted of spot temperature readings taken on the sample date. In the Ringling analysis, Sites 5 and 4 were eliminated due to the virtual lack of a macroinvertebrate community. Site 2 was eliminated because of extreme

deviations from linear numerical thermal patterns. All sites from Norris and Potosi were included in regression-correlation analysis.

All regression equations ($y = ax + b$) were tested with an F test and all correlation coefficients (r) were tested with a T test for statistical significance. Calculation of the coefficient of determination (r^2) provided a means of assessing the percent of variation in the dependent variable (e.g., number of invertebrates per sample) that can be attributed to variation in the independent variable (e.g., temperature).

RESULTS

Qualitative

Checklists and distributions of taxa collected at Ringling, Norris and Potosi are presented in Tables 5, 6 and 7. The distributional data represent a pooling of all sampling methods used at a specific study area (e.g., Surber, Ekman and Hester-Dendy samples at Ringling). An attempt was made to note taxa which appeared infrequently enough as to cast some doubt as to whether they should be considered part of the invertebrate community or a rare product of drift at a particular sample site. These taxa are noted with an asterisk (*) in Tables 5, 6 and 7.

Appendix Table 28 contains a list of taxa collected at sites which always had temperatures in excess of 30°C (4 and 3 at Ringling, 6 and 5 at Norris and 2 at Potosi). This hot spring fauna was composed of 24 taxa representing eight orders. Diptera was the dominant order in the hot springs accounting for 12 of the 24 taxa collected. Of the Diptera collected, the Chironomidae accounted for over half of the taxa present. Taxa found only at these hot sites comprised 8 of the 24 taxa collected while taxa found at cooler sites in addition to the hot sites totalled 16.

Eighty-three taxa were collected at Ringling. No invertebrates were collected at Site 5 (43-47°C). Only one genus, the chironomid *Paraphaenocladus*, was collected at Site 4 (37-43°C). All other sites contained a relatively abundant and diverse fauna with species richness

Table 5. Checklist and distributions of taxa collected at Ringling.

	Sample Site						
	4	3	1	6	7	8	2
Ephemeroptera							
Baetidae							
<i>Baetis</i> sp. A			*	X	X	X	X
<i>Baetis</i> sp. B				X	X	*	
<i>Callibaetis</i> sp.						X	X
Leptophlebiidae							
<i>Choroterpes albiannulata</i> McDunnough	X	X	X	X	X	X	X
Ephemerellidae							
<i>Ephemerella infrequens</i> McD.					X		X
Tricorythidae							
<i>Tricorythodes minutus</i> Traver	X	X	X	X	X	X	X
Caenidae							
<i>Caenis simulans</i> McD.	X	X	X	X	X	X	X
Odonata							
Gomphidae							
<i>Ophiogomphus</i> sp.	X	X	X	X	X	X	X
Aeschnidae							
<i>Aeschna umbrosa</i> Walker					X		X
Coenagrionidae							
<i>Ischnura</i> sp.	X	X	X	X	X	X	X
Hemiptera							
Corixidae							
<i>Hesperocorixa laevigata</i> (Uhler)							*
Trichoptera							
Helicopsychidae							
<i>Helicopsyche borealis</i> (Hagen)	X				X	X	X
Polycentropidae							
<i>Polycentropus</i> sp.	*	*	X	X	X	X	X
Hydropsychidae							
<i>Cheumatopsyche</i> spp.	X	X	X	X	X	X	X
<i>Hydropsyche</i> sp. A				X	X	X	X
<i>Hydropsyche</i> sp. B			*	X	X	X	
<i>Hydropsyche</i> sp. C				X			
Hydroptilidae							
<i>Hydroptila</i> sp.	X	X	X	X	X	X	X

Table 5 (continued).

	Sample Site						
	4	3	1	6	7	8	2
Leptoceridae							
<i>Oecetis</i> sp.						X	
Limnephilidae							
<i>Hesperophylax</i> sp.							X
Coleoptera							
Dytiscidae							
<i>Agabus</i> sp.		X					
<i>Deronectes</i> sp.						X	X
<i>Hydroporus</i> sp.							X
Hydrophilidae							
<i>Helophorus</i> sp.					X		X
Elmidae							
<i>Dubiraphia minima</i> Hilsenhoff			X	X	X	X	X
<i>Microcylloepus pusillus</i> (LeConte)			X	X	X	X	
<i>Optioservus quadrimaculatus</i> (Horn)			X	X	X	X	X
<i>Zaetzovia parvula</i> (Horn)					*		*
Haliplidae							
<i>Halipilus</i> sp.			X		X	X	X
Diptera							
Tipulidae							
<i>Dicranota</i> sp.						X	X
<i>Tipula</i> sp. A						X	
<i>Tipula</i> sp. B							X
Culicidae							
<i>Aedes</i> sp.				X			
Simuliidae							
<i>Simulium</i> spp.			X	X	X	X	X
Chironomidae							
<i>Conchapelopia</i> sp.	X		X	X	X	X	X
<i>Procladius</i> sp.			X	X	X		X
<i>Diamesa</i> spp.					X	X	X
<i>Chironomus</i> sp.							X
<i>Cladopelma</i> sp.					X		
<i>Cladotanytarsus</i> spp.			X	X		X	
<i>Cryptochironomus</i> spp.			X	X	X	X	X
<i>Dicrotendipes</i> sp.			X	X	X	X	X
<i>Endochironomus</i> sp.						X	X

Table 5 (continued).

	Sample Site						
	4	3	1	6	7	8	2
<i>Micropsectra</i> spp.			X	X	X	X	X
<i>Paratendipes</i> sp.			X	X	X	X	X
<i>Phaenopsectra</i> sp.							*
<i>Polypedilum</i> spp.				X	X		
<i>Rheotanytarsus</i> spp.			X	X	X	X	X
<i>Stictochironomus</i> sp.						X	
<i>Tanytarsus</i> spp.			*				
<i>Aericotopus</i> sp.			X	X			
<i>Cricotopus</i> spp.			X	X	X	X	X
<i>Eukiefferiella</i> spp.		X	X	X	X	X	X
<i>Paraphaenocladus</i> sp.	*						
<i>Pseudosmittia</i> sp.		X					
<i>Orthocladus</i> spp.			X	X	X	X	X
Ceratopogonidae							
Tr. <i>Stilobezziini</i>			X	X	X	X	X
Stratiomyidae							
<i>Alluaudomyia</i> sp.					*		
<i>Stratiomyia</i> sp.		X					
Tabanidae							
<i>Chrysops</i> spp.			X	X	X	X	X
<i>Tabanus</i> sp.					*		
Dolichopodidae							
<i>Hydrophorus</i> sp.							*
Empididae					X		
Muscidae		X					
Anthomyiidae							
<i>Limnophora aequifrons</i> Stein						X	
<i>Limnophora torreyae</i> Johannsen				*			
Ephydriidae							
<i>Notiphila</i> sp.					*		
Hydracarina							
Sperchonidae							
<i>Sperchon</i> sp.						X	
Haplotaxida							
Lumbricidae							
<i>Eiseniella tetraedra</i> (Savigny)				*	X	X	

Table 5 (continued).

	Sample Site						
	4	3	1	6	7	8	2
Tubificidae							
<i>Limnodrilus claparedianus</i> Ratzel						X	X
<i>Limnodrilus hoffmeisteri</i> Claparede	X	X	X	X	X	X	X
<i>Limnodrilus udekemianus</i> Claparede			*				
<i>Peloscolex ferox</i> (Eisen)	X	X	X	X	X	X	X
Naididae							
<i>Ophidonais serpentina</i> (Muller)			*	*	X		X
Hirudinea							
Glossiphonidae							
<i>Helobdella stagnalis</i> (Linnaeus)					X		
Erpobdellidae							
<i>Dina anoculata</i> Moore			X				*
Pulmonata							
Physidae							
<i>Physa</i> spp.	X	X	X	X	X	X	X
Lymnaeidae							
<i>Lymnaea</i> spp.	X	X		X			X
Planorbidae							
<i>Gyraulus</i> sp.					X		
Heterodonta							
Sphaeriidae							
<i>Pisidium</i> sp.					X		X
Ostracoda							
<i>Cypris</i> sp.		X					
Amphipoda							
Talitridae							
<i>Hyalella azteca</i> (Saussure)			X	X	X	X	X
Gammaridae							
<i>Gammarus lacustris</i> Sars						X	

X denotes presence

* denotes very rare presence

Table 6. Checklist and distributions of taxa collected at Norris.

	Sample Site					
	6	5	3	2	1	4
Collembola						
<i>Isotomurus</i> sp.	*					
Ephemeroptera						
Siphonuridae						
<i>Ameletus cooki</i> McDunnough						X
Baetidae						
<i>Baetis</i> sp. A			*	X	X	X
Leptophlebiidae						
<i>Paraleptophlebia heteronea</i> McD.			*	X	X	X
Ephemerellidae						
<i>Ephemerella grandis</i> Eaton					X	
<i>Ephemerella inermis</i> Eaton			X	X	X	X
Tricorythidae						
<i>Tricorythodes minutus</i> Traver					X	X
Odonata						
Gomphidae						
<i>Ophiogomphus</i> sp.					X	X
Plecoptera						
Pteronarcidae						
<i>Pteronarcella badia</i> (Hagen)			*	X	X	X
Perlodidae						
<i>Arcynopteryx</i> sp.			*		X	X
<i>Diura knowltoni</i> Frison				X	X	X
<i>Isoperla fulva</i> Claassen				X	X	X
Trichoptera						
Helicopsychoidea						
<i>Helicopsyche borealis</i> (Hagen)					X	X
Hydropsychidae						
<i>Hydropsyche</i> sp. D			X	X	X	X
Brachycentridae						
<i>Brachycentrus</i> sp.			X	X	X	X
<i>Micrasema</i> sp.			*	X	X	X

Table 6 (continued).

	Sample Site					
	6	5	3	2	1	4
Coleoptera						
Curculionidae	X		X			
Elmidae						
<i>Optioservus quadrimaculatus</i> (Horn)				X	X	X
Diptera						
Tipulidae						
<i>Dicranota</i> sp.			X	X		
<i>Hexatoma</i> sp.			X	X	X	X
<i>Tipula</i> spp.			*	X	X	X
Simuliidae						
<i>Simulium</i> spp.				X	X	X
Chironomidae						
<i>Conchapelopia</i> sp.	X		X			X
<i>Procladius</i> sp.						X
<i>Diamesa</i> spp.			X	X	X	X
<i>Odontomesa</i> sp.			X	X	X	X
<i>Chironomus</i> spp.				*		
<i>Cladotanytarsus</i> spp.				X		
<i>Cryptochironomus</i> spp.			X			
<i>Endochironomus</i> sp.						X
<i>Micropsectra</i> spp.					X	X
<i>Microtendipes</i> sp.			X	X	X	X
<i>Phaenopsectra</i> sp.				X		X
<i>Polypedilum</i> spp.			X	X		
<i>Rheotanytarsus</i> spp.			X			
<i>Acricotopus</i> sp.		X	X			X
<i>Cricotopus</i> spp.			*	X		
<i>Eukiefferiella</i> spp.			X	X		
<i>Lymnophyes</i> sp.		*				
<i>Orthocladius</i> spp.			X	X	X	X
<i>Pseudosmittia</i> sp.	X	X				
Ceratopogonidae						
Tr. <i>Stilobezziini</i>						X
Stratiomyiidae						
<i>Eulalia</i> sp.			X			
Tabanidae						
<i>Chrysops</i> spp.						X

Table 6 (continued).

	Sample Site					
	6	5	3	2	1	4
Empididae				*	X	X
Anthomyiidae						
<i>Limnophora aequifrons</i> Stein				*	X	
Haplotaxida						
Lumbricidae						
<i>Eiseniella tetraedra</i> (Savigny)			*	*		X
Tubificidae						
<i>Limnodrilus hoffmeisteri</i> Claparede			X	X	X	X
<i>Limnodrilus udekemianus</i> Claparede					X	*
<i>Peloscolex ferox</i> (Eisen)			X	X	X	X
Naididae						
<i>Ophidonais serpentina</i> (Muller)						X
Hirudinea						
Glossiphoniidae						
<i>Helobdella stagnalis</i> (Linnaeus)						X
Pulmonata						
Physidae						
<i>Physa</i> spp.			X	X	X	X
Heterodonta						
Sphaeriidae						
<i>Pisidium</i> sp.			*	X	X	X
Amphipoda						
Talitridae						
<i>Hyalella azteca</i> (Saussure)					X	X

X denotes presence

* denotes very rare presence

Table 7. Checklist and distributions of taxa collected at Potosi.

	Sample Site				
	2	1	3	4	5
Ephemeroptera					
Baetidae					
<i>Baetis</i> sp. A		X		X	
Tricorythidae					
<i>Tricorythodes minutus</i> Traver		*			
Odonata					
Gomphidae					
<i>Ophiogomphus</i> sp.		X	X	X	X
Libellulidae					
<i>Erythemis</i> sp.		X		X	
Coenagrionidae					
<i>Argia</i> sp.		*		X	
Plecoptera					
Nemouridae					
<i>Nemoura</i> sp.					*
Hemiptera					
Naucoridae					
<i>Ambrysus heidemanni</i> Montandon		X	X		X
Corixidae					
<i>Sigara omani</i> (Hungerford)					*
Trichoptera					
Helicopsychidae					
<i>Helicopsyche borealis</i> (Hagen)				X	X
Hydropsychidae					
<i>Cheumatopsyche</i> sp.		*			
Hydroptilidae					
<i>Oxyethira</i> sp.		*		*	
Philopotamidae					
<i>Chimarra</i> sp.					*
Coleoptera					
Hydrophilidae					
<i>Tropisternus</i> sp.		*			
Elmidae					
<i>Microcylloepus pusillus</i> (LeConte)		X	X	X	X

Table 7 (continued).

	Sample Site				
	2	1	3	4	5
Diptera					
Psychodidae					
<i>Telmatoctopus</i> sp.				X	
Simuliidae					
<i>Simulium</i> spp.				X	
Chironomidae					
<i>Conchapelopia</i> sp.	X	X	X	X	X
<i>Diamesa</i> spp.					X
<i>Cladotanytarsus</i> spp.			X	X	
<i>Micropsectra</i> spp.					X
<i>Polypedilum</i> spp.			X	X	X
<i>Rheotanytarsus</i> spp.	X	X	X	X	X
<i>Tanytarsus</i> spp.				X	X
<i>Cricotopus</i> spp.		*			X
<i>Eukiefferiella</i> spp.				X	
<i>Hydrobaenus</i> sp.				X	
Ceratopogonidae					
<i>Atrichopogon</i> sp.	X				
<i>Tr. Stilobezziini</i>	X		X	X	X
Stratiomyiidae					
<i>Stratiomyia</i> sp.	X				
Haplotaenidia					
Tubificidae					
<i>Limnodrilus claparedianus</i> Ratzel					X
<i>Limnodrilus spiralis</i> (Eisen)					X
<i>Limnodrilus udekemianus</i> Claparede	X	X	X	X	X
<i>Pelosclex ferox</i> (Eisen)		X	X		X
Naididae					
<i>Ophidonais serpentina</i> (Muller)					X
Pulmonata					
Physidae					
<i>Physa</i> spp.	X	X	X	X	
Heterodonta					
Sphaeriidae					
<i>Pisidium</i> sp.			*		

Table 7 (continued).

	Sample Site				
	2	1	3	4	5
Ostracoda					
<i>Iliocypris</i> sp.				X	X
Amphipoda					
Talitridae					
<i>Hyaella azteca</i> (Saussure)	X	X	X	X	X

X denotes presence

* denotes very rare presence

increasing with decreasing temperature. Of the 83 taxa identified, 1% occurred at Site 4, 13% at Site 3, 39% at Site 1, 41% at Site 6, 55% at Site 8 and 57% at Site 2. Diptera was the most well represented order with 39 taxa (47%), 23 of which were genera of the family Chironomidae. Diptera was followed in importance by Coleoptera with nine taxa (11%), Trichoptera with eight (10%), Ephemeroptera with seven (8%) and Haplotaenida with six (7%). Other groups represented were Odonata, Hemiptera, Hirudinea, Pulmonata, Amphipoda, Heterodonta, Ostracoda and Acari. No Plecoptera were collected during the study although a large series of kick samples above Site 2 and below Site 8 yielded several individuals of *Isoperla fulva*. This series of samples also revealed several individuals of the mayfly *Ephemerella grandis* which was not collected during the regular sampling schedule.

Fifty-five taxa were collected at Norris. In the hot spring, Sites 5 and 6, four chironomid genera (i.e., *Conchapelopia*, *Acricotopus*, *Limnophyes* and *Pseudosmittia*), several individuals of the family Curculionidae and a single collembolan, *Isotomurus*, were collected. All individuals of these taxa were collected in the fall samples of 1974. No invertebrates were found in succeeding samples taken at these sites. Of the 55 taxa identified, 5% occurred at Site 6, 4% at Site 5, 36% at Site 3, 51% at Site 2, 56% at Site 1 and 71% at Site 4 reflecting the same trend as the Ringling samples. Diptera was the dominant order with 28 taxa (51%) represented, 18 of which were chironomids.

Diptera were followed in importance by Ephemeroptera with six taxa (11%), Haplotaaxida with five taxa (9%) and Plecoptera and Trichoptera with four each (7%). Other groups represented were Odonata, Coleoptera, Collembola, Hirudinea, Pulmonata, Amphipoda and Heterodonta.

Thirty-eight taxa were collected at Potosi. In contrast to Ringling and Norris, no site at Potosi reached temperatures high enough to exclude macroinvertebrate life. Of the 38 taxa present, 26% occurred at Site 2, 29% at Site 1, 32% at Site 3, 53% at Site 4 and 45% at Site 5. Diptera was the most important order with 15 taxa (39%), 10 of which were chironomids. Haplotaaxida with five species (13%) and Trichoptera with four genera (11%) were the next most important orders. Plecoptera, Ephemeroptera, Odonata, Hemiptera, Coleoptera, Pulmonata, Amphipoda, Heterodonta and Ostracoda were also represented at Potosi.

Presence-absence data were used to calculate indices of similarity (S) as a means of comparing one sample site against all other sites within each study area. Calculated S values for Ringling, Norris and Potosi are given in Table 8. Ringling sites (2, 8, 7, 6 and 1) were characterized by a high degree of similarity (.675-.870) despite the temperature differences. Site 3, located in the hot spring, exhibited a low degree of similarity to any other site. The highest degree of similarity was observed between Sites 1 and 6, the two warmest sites in the plume, with the next highest value observed between Sites 2 and 8,

Table 8. Czekanowski indices of similarity (S) between sample sites at Ringling, Norris and Potosi.

	Site	2	8	7	6	1
<u>Ringling</u>	8	.779				
	7	.695	.702			
	6	.675	.732	.756		
	1	.732	.779	.716	.870	
	3	.203	.172	.207	.217	.267

	Site	1	4	2	3	5
<u>Norris</u>	4	.800				
	2	.724	.667			
	3	.431	.441	.596		
	5	.000	.000	.000	.000	
	6	.000	.047	.000	.167	.500

	Site	2	1	3	4
<u>Potosi</u>	1	.667			
	3	.667	.583		
	4	.552	.625	.688	
	5	.385	.345	.483	.486

the upper and lower cold sites. Site 3 was most similar to Site 1 although the S value was very low.

The highest degree of similarity at Norris was between Sites 4 and 1, the upper and lower cold stations. Site 2 was more similar to Sites 1 and 4 than Site 3 although both Site 2 and Site 3 were within the thermal plume. Sites 5 and 6 had a low degree of similarity with any of the sites in Hot Spring Creek.

Similarity values for Sites 2, 1, 3 and 4 at Potosi were lower than at Ringling (.552-.688), however, these stations did demonstrate a moderately high degree of similarity. In contrast with Ringling and Norris, the hottest station (Site 2) at Potosi had a fairly high degree of similarity to Sites 1, 3 and 4 while the coldest site (Site 5) had a low degree of similarity to all other sites.

Distributional data (Tables 5, 6 and 7) were further analyzed to yield patterns of response of individual taxa to temperature. These data are found in Tables 9, 10 and 11 for Ringling, Norris and Potosi and is based on presence or absence of taxa at a particular sample site.

Data presented in Table 9 place individual taxa from Ringling into eurythermal and stenothermal categories of response. The largest category at Ringling was the eurythermal group (47%) followed by the cold stenothermal group (11%) and the intermediate stenothermal group (10%). In a subdivision of the cold stenotherms, only 14 taxa (19%)

Table 9. Distributional patterns of response to temperature based on the presence or absence of taxa at the specified series of sample sites at Ringling.

PATTERNS OF RESPONSE*			
COLD STENOTHERMAL	INTERMEDIATE STENOTHERMAL	HOT STENOTHERMAL	EURYTHERMAL
Ephemeroptera <i>Callibaetis</i> sp. <i>Ephemerella infrequens</i>	Trichoptera <i>Hydropsyche</i> sp. C	Coleoptera <i>Agabus</i> sp.	Ephemeroptera <i>Baetis</i> sp. A <i>Baetis</i> sp. B <i>Choroterpes albiannulata</i> <i>Tricoorythodes minutus</i> <i>Caenis stimulans</i>
Odonata <i>Aeschna umbrosa</i>	Diptera <i>Cladopelma</i> sp. <i>Polypedilum</i> spp. Empididae	Diptera <i>Acricotopus</i> sp. <i>Paraphaenocladus</i> sp. <i>Pseudosmittia</i> sp. <i>Stratiomyia</i> sp. Muscidae	Odonata <i>Ophiogomphus</i> sp. <i>Ischnura</i> sp.
Trichoptera <i>Polycentropus</i> sp. <i>Oecetis</i> sp. <i>Hesperophylax</i> sp.	Hirudinea <i>Helobdella stagnalis</i>	Hirudinea <i>Dina anoculata</i>	<i>Helichopsyche borealis</i> <i>Cheumatopsyche</i> spp. <i>Hydropsyche</i> sp. A <i>Hydropsyche</i> sp. B <i>Hydroptila</i> sp.
Coleoptera <i>Deronectes</i> sp. <i>Hydroporus</i> sp. <i>Helophorus</i> sp.	Pulmonata <i>Gyraulus</i> sp.	Ostracoda <i>Cypris</i> sp.	Coleoptera <i>Dubiraphia minima</i> <i>Microcylloepus pusillus</i> <i>Optioservus quadrimaculatus</i> <i>Haliphus</i> sp.
Diptera <i>Dicranota</i> sp. <i>Tipula</i> sp. A <i>Tipula</i> sp. B <i>Dicamesa</i> spp. <i>Chironomus</i> sp. <i>Endochironomus</i> sp. <i>Stictochironomus</i> sp. <i>Limnophora aequifrons</i>			Diptera <i>Simulium</i> spp. <i>Conchapelopia</i> sp. <i>Procladius</i> sp. <i>Cladotanytarsus</i> spp. <i>Dicrotendipes</i> sp. <i>Micropeetra</i> spp. <i>Paratendipes</i> sp. <i>Rheotanytarsus</i> spp. <i>Cricotopus</i> spp. <i>Eukiefferiella</i> spp. <i>Orthocladus</i> spp. Tr. <i>Stilobessini</i> <i>Chrysops</i> spp.
Haplotaxida <i>Eiseniella tetradra</i> L. <i>Udekemianus</i> <i>Ophidonais serpentina</i>			Haplotaxida <i>Limnodrilus hoffmeisteri</i> <i>Peloscoides ferox</i>
Heterodonta <i>Pisidium</i> sp.			Pulmonata <i>Physa</i> spp. <i>Lymnaea</i> spp.
Amphipoda <i>Gammarus lacustris</i>			Amphipoda <i>Hyalella azteca</i>
Hydracarina <i>Sperchon</i> sp.			

* Cold stenothermal = presence Sites 2 and/or 8 or range of Sites 7 through 8 and/or 2
 Intermediate stenothermal = presence Sites 6 and/or 7
 Hot stenothermal = presence Sites 3 and/or 1 or range of Sites 3 and/or 1 through 6
 Eurythermal = presence in range of Sites 3, 1 or 6 through 8 and/or 2

Table 10. Distributional patterns of response to temperature based on the presence or absence of taxa at the specified series of sample sites at Norris.

PATTERNS OF RESPONSE*			
COLD STENOTHERMAL	INTERMEDIATE STENOTHERMAL	HOT STENOTHERMAL	EURYTHERMAL
Ephemeroptera <i>Ameletus cooki</i> <i>Baetis</i> sp. A <i>Paraleptophlebia heteronea</i> <i>Ephemerella grandis</i> <i>Tricoorythodes minutus</i>	Diptera <i>Dicranota</i> sp. <i>Cladotanytarsus</i> spp. <i>Polypedilum</i> spp. <i>Cricotopus</i> spp. <i>Eukiefferiella</i> spp.	Collembola <i>Isotomurus</i> sp.	Ephemeroptera <i>Ephemerella inermis</i>
Odonata <i>Ophiogomphus</i> sp.		Coleoptera <i>Curculionidae</i>	Trichoptera <i>Hydropsyche</i> sp. C <i>Brachycentrus</i> sp.
Plecoptera <i>Pteronarcella badia</i> <i>Arcynopteryx</i> <i>Diura knowltoni</i> <i>Isoperla fulva</i>		Diptera <i>Cryptochironomus</i> spp. <i>Rheotanytarsus</i> spp. <i>Pseudosmittia</i> sp. <i>Eulalia</i> sp.	Diptera <i>Hexatoma</i> sp. <i>Conchapelopia</i> sp. <i>Diamesa</i> spp. <i>Odontomesa</i> sp. <i>Microtendipes</i> sp. <i>Acricoctopus</i> sp. <i>Orthocladus</i> spp.
Trichoptera <i>Helicopsyche borealis</i> <i>Micrasema</i> sp.			Haplotaaxida <i>Limnodrilus hoffmeisteri</i> <i>Feloscolex ferox</i>
Coleoptera <i>Optioeservus quadrimaculatus</i>			Pulmonata <i>Physa</i>
Diptera <i>Tipula</i> spp. <i>Simulium</i> spp. <i>Procladius</i> sp. <i>Endochironomus</i> sp. <i>Micropectra</i> spp. <i>Phaenopsectra</i> sp. <i>Tr. Stilobessiini</i> <i>Chrysops</i> sp. <i>Empididae</i> <i>Limnophora asquifrons</i>			
Haplotaaxida <i>Eiseniella tetraedra</i> <i>Limnodrilus udekemianus</i> <i>Ophidonais serpentina</i>			
Hirudinea <i>Helobdella stagnalis</i>			
Heterodonta <i>Pisidium</i> sp.			
Amphipoda <i>Hyalella asteca</i>			

* Cold stenothermal = presence at Sites 1 and/or 4 or range of Sites 2 through 1 and/or 4
Intermediate stenothermal = presence at Sites 3 and/or 2
Hot stenothermal = presence at Sites 6, 5 and/or 3
Eurythermal = presence in range of Sites 6, 5 or 3 through 1 and/or 4

Table 11. Distributional patterns of response to temperature based on the presence or absence of taxa at the specified series of sample sites at Potosi.

PATTERNS OF RESPONSE*			
COLD STENOTHERMAL	INTERMEDIATE STENOTHERMAL	HOT STENOTHERMAL	EURYTHERMAL
Diptera <i>Diamea</i> spp. <i>Micropeetra</i> spp. <i>Tanytarsus</i> spp.	Ephemeroptera <i>Baetis</i> sp. A	Diptera <i>Stratiomyia</i> sp.	Odonata <i>Argia</i> sp.
Haplotaxida <i>Limnodrilus</i> <i>claparedianus</i> <i>L. spiralis</i> <i>Ophidonais serpentina</i>	Hemiptera <i>Sigara omari</i>		Hemiptera <i>Ambrysus heidemanni</i>
Ostracoda <i>Iliocypris</i> sp.	Trichoptera <i>Helichopsyche borealis</i>		Coleoptera <i>Microcyllopus pusillus</i>
	Diptera <i>Telmatoctopus</i> sp. <i>Simulium</i> spp. <i>Cladotanytarsus</i> spp. <i>Eukiefferiella</i> spp. <i>Hydrobaenus</i> sp.		Diptera <i>Conchapelopia</i> sp. <i>Polypedilum</i> sp. <i>Rheotanytarsus</i> spp. <i>Cricotopus</i> spp. <i>Tr. Stilobezziini</i>
			Haplotaxida <i>Limnodrilus udekemianus</i> <i>Pelocolex ferox</i>
			Pulmonata <i>Physa</i> spp.
			Amphipoda <i>Hyalella azteca</i>

* Cold stenothermal = presence at Site 5 or range of Sites 5 and 4
 Intermediate stenothermal = presence at Sites 3 and/or 4
 Hot stenothermal = presence at Sites 2 and/or 1 or range of Sites 2 and/or 1 through 3
 Eurythermal = presence in range of Sites 2, 1 or 3 through 5

were limited in their distributions to the upper and lower cold sites. Most of the major orders (e.g., Ephemeroptera, Odonata, Trichoptera, Coleoptera, Diptera and Pulmonata) had their highest representation in the eurythermal group with Haplotaxida showing its highest representation in the cold stenothermal group. Diptera was the largest contributor to the eurythermal group (41%) followed by the Ephemeroptera (15%) and the Trichoptera and Coleoptera (12%). Diptera was also the dominant order in the hot, cold and intermediate stenothermal groups.

Taxa collected at Norris are listed in Table 10. In contrast with Ringling, the largest group of taxa (55%) were categorized as cold stenotherms. The eurythermal group accounted for 25% of the taxa followed by the hot stenothermal (11%) and intermediate stenothermal (9%) groups. Cold stenotherms that were limited to the upper and lower cold sites totaled 18 taxa (34%). The major orders (e.g., Ephemeroptera, Plecoptera, Diptera and Haplotaxida) had greatest representation in the cold stenothermal group. Diptera was the dominant order in each of the four categories.

Table 11 contains the categorization of taxa from Potosi. The eurythermal and cold stenothermal groups were nearly equal (12 and 11 taxa) and were the two largest groups accounting for 44 and 41% of the total taxa. Again, Diptera dominated all categories.

Distributional data were analyzed to yield a series of frequency of occurrence values for taxa in pooled samples at thermal levels

(Appendix Table 29). Analysis of frequency values yielded a thermal classification of the fauna into eurythermal and hot, cold and intermediate stenothermal responses (Table 12). Under this system, the eurythermal group was further subdivided on the basis of temperature-associated trends in frequency of occurrence. Trends exhibited are; an increase in frequency of occurrence with a decrease in temperature, increase in frequency with increasing temperature, maximum frequency at intermediate temperatures with lower frequency at low and high temperature, and no change in frequency value with change in temperature. In addition to the aforementioned trends, some eurythermal organisms exhibited no linear trend in frequency value and are also listed in Table 12.

Of the 115 taxa categorized in Table 12, 57 (50%) can be classified as eurythermal, 39 (34%) as cold stenothermal, 12 (10%) as hot stenothermal and seven (6%) as intermediate stenothermal. Of the 57 eurythermal taxa, 19 (33%) demonstrated an increased frequency of occurrence at intermediate temperatures, 17 (30%) showed an increase in frequency at low temperatures, six (11%) showed an increase in frequency at high temperatures and six (11%) showed an equal frequency at all temperatures. Nine (19%) of the eurythermal taxa had no linear trend.

A comparison between the presence-absence categorization of taxa and the pooled frequency of occurrence categorization reveals that the thermal distribution of some taxa at a single study area may not be the

Table 12. Distributional patterns of response to temperature based on the frequency of occurrence of taxa in combined samples from Ringling, Norris and Potosi.

Stenoathermal		Eurythermal	
COLD			
Ephemeroptera <i>Anisetus oooki</i> <i>Callibaetis</i> sp. <i>Ephemarellia grandis</i>	Diptera <i>Lymnophyes</i> sp. <i>Paraphasmodolus</i> sp. <i>Pseudomittis</i> sp. <i>Atrichopogon</i> sp. <i>Eulalia</i> sp. <i>Stratiomyia</i> sp. <i>Musoides</i>	Ephemeroptera <i>Baetis</i> sp. B <i>Paraleptophlebia heteronea</i> <i>Ephemarellia inermis</i>	<i>Polypedilum</i> spp. <i>Rheotanytarsus</i> spp. <i>Eukiefferiella</i> spp.
Odonata <i>Aeschna umbrosa</i>	<i>Collembola</i> <i>Isonurus</i> sp.	Trichoptera <i>Polycentropus</i> sp. <i>Hydropsyche</i> sp. B <i>Brachycentrus</i> sp. <i>Micrasema</i> sp.	Haplotaenidae <i>Eisenella tetradra</i> <i>Limnophilus hoffmeisteri</i> <i>Ophidonia serpentina</i>
Flecoptera <i>Nemoura</i> sp. <i>Pteronarcissa badia</i> <i>Arctynopteryx</i> sp. <i>Diura knowltoni</i> <i>Isoperla fulva</i>	Ostracoda <i>Cypris</i> sp.	Diptera <i>Hexatoma</i> sp. <i>Tipula</i> sp. C <i>Stimulium</i> spp. <i>Dixa</i> spp. <i>Dicentropus</i> sp. <i>Microcentropus</i> sp. <i>Tr. Stilobesantini</i>	Amphipoda <i>Hyalina aestiva</i>
Hemiptera <i>Hesperoecia laevigata</i> <i>Stygia ovum</i>	INTERMEDIATE	Haplotaenidae <i>Limnophilus udakianus</i> <i>Limnophilus</i> spp. (immatures)	Trichoptera <i>Cheumatopsyche</i> spp. <i>Hydroptila</i> sp.
Trichoptera <i>Chimarra</i> sp. <i>Oaetia</i> sp. <i>Hesperophylax</i> sp.	Odonata <i>Argia</i> sp. <i>Erythemis</i> sp.	Heterodonta <i>Pisidium</i> spp.	Diptera <i>Tanytarsus</i> spp. <i>Cricotopus</i> spp. <i>Orthocentrus</i> spp.
Coleoptera <i>Deroceras</i> sp. <i>Hydrophilus</i> sp. <i>Helophorus</i> sp. <i>Nastasia parvula</i>	Trichoptera <i>Hydropsyche</i> sp. C <i>Oaethira</i> sp.		Haplotaenidae <i>Pelocoxes ferox</i>
Diptera <i>Tipula</i> sp. A <i>Tipula</i> sp. B <i>Chironomus</i> spp. <i>Eudochironomus</i> sp. <i>Stictochironomus</i> sp. <i>Hydrobaenus</i> sp. <i>Telmatoecopus</i> sp. <i>Alluaudomyia</i> sp. <i>Tabanus</i> sp. <i>Hydrophorus</i> sp. <i>Empididae</i> <i>Limnophora aequifrons</i> <i>Notiphila</i> sp.	Diptera <i>Aedes</i> sp. <i>Cladopsela</i> sp. <i>Limnophora burrowsi</i>		NON-LINEAR
Hydracarina <i>Sperchon</i> sp.	Pulmonata <i>Gyrinus</i> sp.	Coleoptera <i>Dubiraphia minima</i>	Odonata <i>Isonura</i> sp.
Haplotaenidae <i>Limnophilus olaparedianus</i> <i>L. spiralis</i>		Diptera <i>Odonotessa</i> sp. <i>Cladotanytarsus</i> spp. <i>Cryptochironomus</i> spp. <i>Acrisotopus</i> sp.	Hemiptera <i>Ambrysus heidemanni</i>
Ostracoda <i>Illicypris</i> sp.		Pulmonata <i>Physa</i> spp.	Trichoptera <i>Hydropsyche</i> sp. B
Amphipoda <i>Gammarus lacustris</i>			Coleoptera <i>Optocerus quadrimaculatus</i> <i>Malpiga</i> sp.
HOT			Diptera <i>Dironota</i> sp. <i>Micropeetra</i> spp. <i>Chrysopa</i> spp.
Coleoptera <i>Agabus</i> sp. <i>Tropisternus</i> sp. <i>Curculionidae</i>		Ephemeroptera <i>Baetis</i> sp. A <i>Choroterpes albivittatus</i> <i>Ephemarellia infrequens</i> <i>Tricorythodes minutus</i> <i>Ceratis similans</i>	Pulmonata <i>Lymnaea</i> spp.
		Odonata <i>Optiolepis</i> sp.	
		Trichoptera <i>Belichopsyche borealis</i> <i>Hydropsyche</i> sp. A	
		Coleoptera <i>Microsillopsus pusillus</i>	
		Diptera <i>Conchopselopia</i> spp.	

* Cold stenothermal = Thermal Levels 1 or 1 and 2
 Hot stenothermal = Thermal Levels 5, 5 and/or 4
 Intermediate stenothermal = Thermal Levels 3 and/or 2
 Eurythermal = Thermal Levels 4, 5 or 4 through 2 or 1 or 3 through 1
 = increased frequency of occurrence at low temperatures
 = increased frequency of occurrence at intermediate temperatures
 = increased frequency of occurrence at high temperatures
 = equal frequency of occurrence at all temperatures
 Non-Linear = no linear pattern in frequency of occurrence

same when taken over all three study areas. This is exemplified by the tubificid *Limnodrilus udekemianus* which appears as a cold stenotherm at both Ringling and Norris but due to its eurythermal distribution at Potosi, is categorized as eurythermal negative (↘) in overall frequency of occurrence. Other taxa exhibiting different thermal responses at different study areas are *Tricorythodes minutus*, *Baetis* sp. A, *Ophiogomphus*, *Helicopsyche borealis*, *Optioservus quadrimaculatus*, *Dicranota*, *Chrysops*, *Simulium*, *Diamesa*, *Procladius*, *Cryptochironomus*, *Micropsectra* and *Rheotanytarsus*.

Most of the major orders were dominated by eurythermal forms. Eight species of Ephemeroptera (73%) were categorized as eurythermal. Five of these species (e.g., *T. minutus*, *C. albiannulata* and *C. simulans*) had their greatest frequency of occurrence at intermediate temperatures while three (e.g., *E. inermis*) had their highest frequency values at lower temperatures. *Ephemerella grandis*, *A. cooki* and *Callibaetis* sp. were the only mayflies categorized as cold stenotherms. All Plecoptera that were collected were classified as cold stenotherms.

Nine representatives of Trichoptera (64%) were categorized as eurythermal. Four genera (e.g., *Brachycentrus* and *Micrasema*) had their highest frequency values at low temperatures while *Hydropsyche* sp. A and *H. borealis* showed highest frequency values at intermediate temperatures and *Cheumatopsyche* and *Hydroptila* exhibited no change in

frequency with temperature change. Three genera (i.e., *Chimarra*, *Oecetis* and *Hesperophylax*) were categorized as cold stenotherms.

The oligochaetes were dominated by eurythermal forms (71%) such as *L. hoffmeisteri* and *P. ferox*. *Limnodrilus claparedianus* and *L. spiralis* were classified as cold stenotherms.

Coleoptera showed no dominance by eurythermal forms (36%) with both cold (36%) and hot stenotherms (27%) contributing to the fauna. The Coleoptera, along with Diptera, were the only major orders represented in the hot stenothermal group.

Diptera were comprised of eurythermal forms (48%), hot stenotherms (15%) and cold stenotherms (33%). The eurythermal group contained 23 genera, 17 of which were chironomids while six belonged to the families Tipulidae, Tabanidae, Simuliidae and Ceratopogonidae. The cold stenothermal group contained 16 genera, six of which were chironomids while 10 belonged to eight other dipteran families. The hot stenothermal forms were dominated by the Diptera.

All other major groups were represented by low numbers of taxa. Pulmonata contained two eurythermal forms, *Physa* and *Lymnaea*, and one intermediate stenotherm, *Gyraulus*. Two species of Amphipoda were collected, the eurythermal *H. azteca* and the cold stenothermal *G. lacustris*. Collembola, Hemiptera, Acari, Hirudinea, Ostracoda and Heterodonta were also represented in this pooled classification.

Quantitative

Data were compiled on the total number of invertebrates collected in each bottom sample from Ringling, Norris and Potosi. Data were expressed as mean numbers of invertebrates per sample and are presented in Table 13. This table also contains a statistical analysis of the site means in the form of a multifactor analysis of variance.

The mean number of invertebrates present in the riffle (Surber) samples from Ringling demonstrated a marked increase as temperature decreased at Sites 3 through 8. An approximate twofold increase in the number of invertebrates occurred between Sites 3 and 1, 1 and 6 and 6 and 7 with Site 8 being about 30% higher than Site 7. Site 2, the upper cold site, contained about one-fourth as many invertebrates as Site 8, the lower cold site. Variation due to sample date, sample site and the interaction between the two were found to be highly significant. A Newman-Keuls Test indicated that Site 1 was not different from Site 3 and Site 2 did not differ from Sites 1 and 6. All other combinations of sites were found to be significantly different ($P < .05$).

The Ringling pool (Ekman) samples exhibited the same trend as the riffle samples although numerical differences were not as marked. Site 7, rather than Site 8, had the highest number of invertebrates in the pools. In contrast to the riffle areas, Site 2 was approximately equal to Site 8 in number. Analysis of variance showed variation due to date, site and interaction to be highly significant. Newman-Keuls analysis

Table 13. Mean number of invertebrates per sample collected in bottom samples at Ringling, Norris and Potosi with a multifactor analysis of variance.

	Sample Sites						Analysis of Variance *		
	3	1	6	7	8	2	Date	Site	Date x Site
Ringling, Surber	103.2	222.1	486.7	1157.0	1511.0	367.4	HS	HS	HS
Ringling, Ekman	22.6	43.8	54.9	80.8	66.8	69.7	HS	HS	HS
	Sample Sites								
	6	5	3	2	1	4			
Norris, Surber	0.4	1.0	26.3	34.8	367.5	437.1	S	HS	NS
Norris, Ekman	0.3	0.1	64.3	43.0	44.3	38.3	HS	HS	S
	Sample Sites								
	2	1	3	4	5				
Potosi, Ekman	39.5	22.3	20.5	36.5	30.8		HS	HS	HS

* HS = highly significant difference ($P < .01$)

S = significant difference ($P < .05$)

NS = differences non-significant

showed that the only significant difference among sites was found between Site 3 and Sites 7, 8 and 2.

The Norris Surber samples exhibited a marked increase in invertebrate numbers with decreasing temperatures. A large increase occurred between Sites 6 and 5 and Sites 3 and 2 with another large increase found between Sites 3 and 2 and Sites 1 and 4. Site 4, the cold station above the hot spring entry, yielded the highest number of invertebrates per sample. Variation due to sample date and sample site were significant and highly significant; however, the interaction was nonsignificant. Newman-Keuls analysis indicated no significant difference between Sites 1 and 4 or among Sites 6, 5, 3 and 2; however, Sites 1 and 4 were significantly different from Sites 6, 5, 3 and 2.

The Norris Ekman samples exhibited a different trend in that the numbers of invertebrates did not necessarily increase as temperature decreased. The highest number of organisms occurred at Site 3 while Site 2 was approximately equal to Sites 1 and 4. Analysis of variance showed variation due to sample date, site and their interaction to be significant. Newman-Keuls analysis showed no significant difference between Sites 6 and 5 or among Sites 3, 2, 1 and 4; however, Sites 6 and 5 were found to differ significantly from Sites 3, 2, 1 and 4.

The Potosi samples showed no increase in numbers as temperature decreased. The hottest site, Site 2, had the most organisms per sample. Analysis of variance showed that variation due to sample date, site and

their interaction were highly significant. Newman-Keuls analysis showed that Sites 1 and 3 were significantly different from Sites 2 and 4. No other combinations of sites differed significantly.

Total numbers of invertebrates per sample were tested for linearity of response to temperature by linear regression-correlation analysis. Table 14 contains the correlation coefficients (r) and coefficients of determination (r^2) for data from the bottom samples from Ringling, Norris and Potosi. Correlation coefficients for the total of the year's samples indicate that invertebrate numbers were weakly to moderately correlated with temperature in a negative manner. The Norris Ekman samples provided an exception to this trend with a weakly positive (+.335) correlation. Only two of the annual r values, those for the Ringling and Norris Surber samples, proved to be significant. Annual r^2 values ranged from a low of 0% for the Potosi samples to a high of 29% for the Ringling Surber samples.

Seasonal r and r^2 values generally increased over the annual values. Ringling Surber samples from the fall of 1974 and 1975, winter and summer showed a highly significant, strongly negative correlation between invertebrate numbers and temperature. Coefficients of determination for these sample periods indicated that from 79 to 90% of the variation in numbers of invertebrates could be attributed to variation in temperature. Seasonal r and r^2 values for the Ringling Ekman samples demonstrated a weakly negative correlation with the exception of

Table 14. Annual and seasonal correlation coefficients and coefficients of determination^a for the mean number of invertebrates per sample collected in bottom samples: Ringling, Norris and Potosi, as correlated with temperature.

	Time of Sample					
	Annual	Fall '74	Winter	Spring	Summer	Fall '75
Ringling, Surber	-.541** (.29)	-.949** (.90)	-.891** (.79)	+.192 (.04)	-.906** (.82)	-.904** (.82)
Ringling, Ekman	-.255 (.07)	-.369 (.14)	-.037 (<.01)	-.057 (<.01)	-.203 (.04)	-.883* (.78)
Norris, Surber	-.359* (.13)	-.653 (.43)	-.654 (.43)	-.751* (.57)		-.617 (.38)
Norris, Ekman	+.335 (.11)	+.420 (.18)	+.944** (.89)	+.755* (.57)		-.364 (.13)
Potosi, Ekman	-.013 (.00)	0.244 (.06)	-.186 (.04)	+.598 (.36)		-.361 (.13)

^a in parentheses

* significant ($P < .05$)

**highly significant ($P < .01$)

the fall 1975 samples which provided a strongly negative correlation.

The Norris Surber samples showed a moderately to strongly negative correlation (-.617 to -.751) with 38 to 57% of the variation in numbers attributable to thermal variation. Seasonal r and r^2 values confirmed the positive correlation between numbers and temperature in the Norris Ekman samples with significant r values of +.944 and +.755 for the winter and spring samples. Seasonal r^2 values indicated that from 13 to 89% of the numerical variation could be attributed to temperature.

Seasonal r and r^2 values for Potosi samples were generally weakly negative and non-significant. The spring samples provided the strongest correlation which was positive (+.569).

Significant linear regression lines for the total number of invertebrates per sample as regressed against temperature are presented in Figure 4. Numerical-thermal variation for the Ringling Surber samples is described by the equation $y = -44x + 1596$, for the Norris Surber samples by $y = -14.3x + 377.8$ and for the Ringling Ekman samples by $y = -1.5x + 84$.

Data were compiled on the total number of taxa collected in each bottom sample. The mean number of taxa present in each sample for each sampling method is given in Table 15. The general trend at Ringling, Norris and Potosi indicates an increase in total taxa

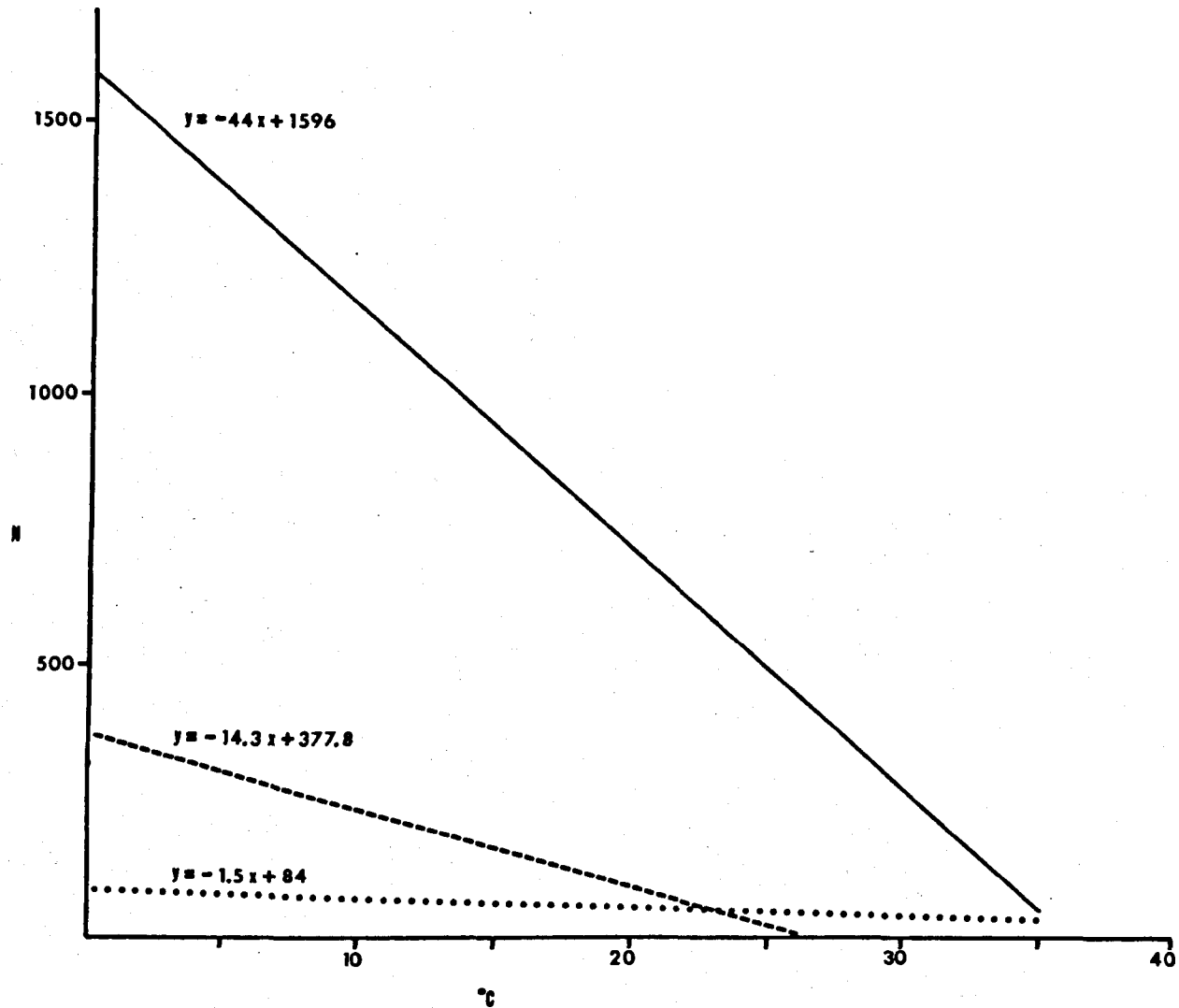


Figure 4. Significant linear regressions of total numbers of invertebrates collected per Ringling Surber (solid line), Ringling Ekman (dotted line) and Norris Surber (dashed line) samples vs. temperature (°C).

Table 15. Mean number of taxa per sample collected in bottom samples at Ringling, Norris and Potosi, with a multifactor analysis of variance.

	Sample Sites						Analysis of Variance *			
	3	1	6	7	8	2	Date	Site	Date x Site	
Ringling, Surber	1.4	11.7	17.0	21.7	16.7	16.4	HS	HS	HS	
Ringling, Ekman	2.2	5.3	6.9	9.2	8.5	8.4	HS	HS	HS	
	Sample Sites									
	3	2	1	4						
Norris, Surber	4.6	7.9	12.9	13.1			S	HS	HS	
Norris, Ekman	7.3	5.5	5.5	7.5			NS	S	HS	
	Sample Sites									
	2	1	3	4	5					
Potosi, Ekman	3.1	4.6	4.6	8.4	5.8			S	HS	HS

* HS = highly significant difference ($P < .01$)

S = significant difference ($P < .05$)

NS = differences non-significant

collected with a decrease in temperature. The Norris Ekman samples provided an exception to this trend with Site 3, at the head of the plume, approximately equal to Site 4, the upper cold reference. Site 7 at Ringling and Site 4 at Potosi had the highest numbers of taxa at their respective study areas. These sites represent the first level of temperature increase over the coldest sites available at the study areas. The highest numbers of taxa present in the Norris Surber samples occurred at Sites 1 and 4. Analysis of variance revealed that variation in numbers of taxa with sample site was highly significant at all three study areas as was the interaction between sample site and sample date.

Newman-Keuls analysis for the numbers of taxa from the Ringling Surber samples indicated that Sites 2 and 8 were not significantly different and that Site 6 was not significantly different from Sites 2 and 8. All other sites were significantly different. For the Ringling Ekman samples, Sites 3 and 1 showed no significant differences from each other but both were different from Sites 6, 7, 8 and 2 which did not differ among themselves. The test of the Norris Surber samples indicated that Sites 1 and 4 did not significantly differ while all other combinations were significantly different. The Norris Ekman samples demonstrated no significant differences among sites. Testing of the Potosi data showed that Site 4 differed from all other sites, Site 2 differed from Sites 4 and 5 and that all other combinations

of sites were not significantly different.

Linear analysis of the total taxa data is given in Table 16. Total taxa were moderately correlated with temperature (-.454 to -.604) for the Ringling Surber and Ekman, Norris Surber and Potosi samples on an annual basis. Annual r^2 values ascribed between 21 and 37% of the variation in numbers of taxa to thermal differences. The Norris Ekman samples, again, provided an exception with a weakly positive total r value (+.054) that was not significant. On a seasonal basis, the r values generally demonstrated a marked increase in the strength of the negative correlation and r^2 values attributed high percentages of variation in the number of taxa to thermal variation. A large number of the seasonal r values proved to be significant.

Linear regressions for the total numbers of taxa collected are described by the equations $y = -.5x + 24.1$ for the Ringling Surber samples; $y = -.2x + 10.9$ for the Ringling Ekman samples; $y = -.4x + 14.0$ for the Norris Surber samples and $y = -.2x + 9.2$ for the Potosi samples. The data for these equations were found to be highly significant. The regression for the Norris Ekman samples was not found to be significant. The significant regressions are graphed in Figure 5.

Numerical data were compiled at the ordinal level for the Ringling, Norris and Potosi study areas. Mean ordinal numbers per sample were calculated and tested for significance of variation (Table 17). The mean percent contribution of each major order to the total number

Table 16. Annual and seasonal correlation coefficients and coefficients of determination^a for the mean number of taxa at the genus-species level per bottom sample at Ringling, Norris and Potosi, as correlated with temperature.

	Time of Sample					
	Annual	Fall '74	Winter	Spring	Summer	Fall '75
Ringling, Surber	-.604** (.37)	-.967** (.94)	-.616 (.38)	-.821** (.67)	-.766** (.59)	-.847** (.72)
Ringling, Ekman	-.515** (.27)	-.731* (.53)	-.955** (.91)	-.188 (.04)	-.527 (.28)	-.529* (.35)
Norris, Surber	-.567** (.33)	-.751* (.56)	-.731* (.54)	-.207 (.04)		-.848** (.72)
Norris, Ekman	+.054 (.01)	-.171 (.03)	+.264 (.07)	+.298 (.09)		-.033 (.01)
Potosi, Ekman	-.454** (.21)	+.235 (.06)	-.943** (.89)	-.701* (.49)		-.417 (.17)

^a in parentheses

* significant ($P < .05$)

**highly significant ($P < .01$)

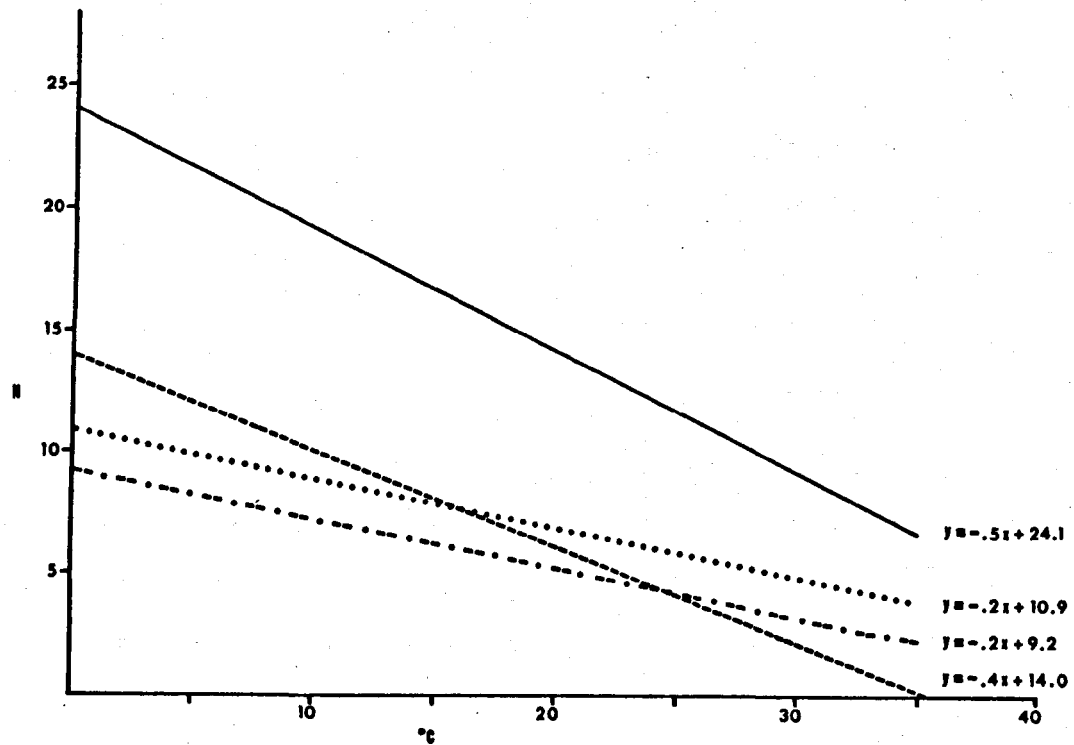


Figure 5. Significant linear regressions of numbers of invertebrate taxa collected per Ringling Surber (solid line), Ringling Ekman (dotted line), Norris Surber (dashed line) and Potosi Ekman (dotted and dashed line) samples vs. temperature (°C).

Table 17. Mean ordinal number and mean percent contribution^a per bottom sample at Ringling, Norris and Potosi, with a multifactor analysis of variance.

	Sample Sites						Analysis of Variance *		
	3	1	6	7	8	2	Date	Site	Date x Site
Ringling, Surber									
Ephemeroptera	0.0 (0.0)	3.1 (1.5)	133.0 (26.0)	317.0 (26.1)	226.5 (11.1)	23.9 (6.0)	NS	NS	NS
Odonata	0.0 (0.0)	1.8 (0.9)	1.7 (0.5)	1.1 (0.07)	0.8 (0.03)	2.5 (0.6)	NS	NS	NS
Trichoptera	0.0 (0.0)	116.9 (33.1)	188.8 (30.5)	554.6 (38.8)	617.9 (30.5)	208.9 (69.4)	NS	NS	NS
Coleoptera	0.0 (0.0)	21.3 (15.6)	52.7 (10.3)	159.0 (16.5)	28.2 (1.3)	39.8 (13.7)	NS	NS	NS
Diptera	1.2 (10.3)	56.3 (36.7)	105.3 (31.4)	105.0 (14.5)	495.3 (38.0)	56.4 (19.6)	NS	NS	NS
Haplontaxida	9.8 (30.8)	8.3 (6.9)	2.6 (2.4)	10.7 (2.8)	0.9 (0.1)	14.2 (5.1)	NS	NS	NS
Pulmonata	79.7 (16.1)	8.0 (2.2)	6.2 (1.3)	7.1 (0.6)	2.4 (0.1)	18.7 (4.1)	NS	NS	NS
Amphipoda	0.0 (0.0)	4.5 (4.7)	0.5 (0.7)	0.4 (0.6)	1.1 (1.2)	2.6 (2.6)	NS	NS	NS
Ringling, Ekman									
Ephemeroptera	0.0 (0.0)	0.1 (0.1)	1.9 (5.9)	5.1 (4.5)	2.6 (3.7)	0.5 (0.8)	NS	S	NS
Odonata	0.0 (0.0)	1.9 (1.3)	0.3 (0.7)	2.5 (1.5)	0.2 (0.3)	0.2 (2.0)	NS	NS	NS
Trichoptera	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.0 (1.3)	0.6 (0.7)	0.1 (0.04)	NS	NS	NS
Coleoptera	0.2 (0.5)	16.8 (27.7)	5.4 (16.5)	7.2 (9.7)	4.0 (5.0)	8.0 (11.7)	NS	NS	S
Diptera	1.8 (34.7)	9.6 (39.6)	41.1 (64.8)	39.7 (56.9)	36.2 (64.9)	21.6 (31.8)	NS	NS	NS
Haplontaxida	15.9 (32.9)	2.8 (21.0)	6.2 (12.1)	2.1 (8.9)	17.9 (17.2)	22.5 (34.5)	NS	NS	NS
Pulmonata	3.6 (19.2)	11.2 (9.1)	0.0 (0.0)	0.2 (1.5)	0.1 (0.1)	0.6 (9.3)	NS	NS	S
Amphipoda	0.0 (0.0)	1.3 (0.8)	0.0 (0.0)	23.2 (16.8)	5.2 (6.4)	0.1 (0.1)	NS	NS	NS
Norris, Surber									
Flecoptera	0.1 (0.7)	2.0 (5.2)	13.0 (5.0)	26.1 (7.1)			NS	NS	NS
Ephemeroptera	1.6 (9.8)	6.8 (15.8)	60.0 (19.9)	51.0 (15.1)			NS	NS	NS
Odonata	0.0 (0.0)	0.0 (0.0)	1.3 (0.5)	2.0 (0.4)			NS	NS	NS
Trichoptera	0.2 (0.7)	4.0 (6.6)	110.6 (23.3)	188.4 (31.1)			S	NS	NS
Coleoptera	0.0 (0.0)	4.8 (7.9)	23.9 (5.6)	33.5 (5.9)			NS	NS	NS
Diptera	7.8 (23.6)	14.1 (36.9)	154.6 (35.0)	117.5 (31.5)			S	NS	NS
Haplontaxida	14.6 (59.9)	2.8 (27.3)	7.9 (3.8)	11.0 (7.1)			NS	NS	NS
Pulmonata	2.0 (5.7)	0.4 (0.6)	1.6 (1.1)	6.0 (1.1)			NS	S	NS
Amphipoda	0.0 (0.0)	0.0 (0.0)	0.3 (0.1)	0.4 (0.4)			S	S	NS

Table 17 (continued).

Norris, Ekman	Sample Sites				Analysis of Variance *			
	3	2	1	4	Date	Site	Date x Site	
Ephemeroptera	1.3 (2.3)	0.3 (0.6)	0.9 (9.2)	0.9 (4.6)	NS NS	NS NS	NS NS	
Diptera	10.5 (18.4)	7.8 (21.9)	12.5 (52.3)	6.4 (25.3)	NS NS	S S	S NS	
Haplotaxida	45.6 (66.5)	34.0 (73.1)	28.9 (25.1)	27.0 (49.1)	HS HS	NS HS	NS NS	
Heterodonta	0.3 (0.7)	0.8 (0.6)	1.4 (2.0)	2.3 (11.8)	NS NS	NS HS	NS NS	
	Sample Sites							
Potosi, Ekman	2	1	3	4	5			
Coleoptera	29.3 (55.3)	8.5 (38.8)	10.0 (51.6)	6.9 (21.4)	1.0 (2.7)	HS HS	HS HS	HS HS
Diptera	5.3 (28.1)	6.9 (17.1)	6.8 (32.2)	12.8 (33.9)	13.5 (42.8)	S HS	NS S	HS HS
Haplotaxida	0.5 (2.6)	0.6 (6.3)	0.3 (0.7)	1.8 (4.5)	10.5 (31.7)	NS HS	HS HS	S HS
Pulmonata	3.9 (10.8)	1.5 (8.1)	0.4 (1.1)	0.4 (1.1)	0.0 (0.0)	HS HS	HS HS	HS HS
Amphipoda	0.5 (2.5)	2.4 (10.8)	2.5 (11.2)	11.9 (31.9)	3.3 (13.1)	S HS	HS HS	S NS

^a in parentheses

HS = highly significant difference (P<.01)

S = significant difference (P<.05)

NS = difference non-significant

of invertebrates per sample was also calculated and included in this table.

Patterns of response of ordinal numbers to temperature can be detected from Table 17. Plecoptera, Ephemeroptera, Trichoptera and Diptera all increased in number as temperature decreased. Pulmonata increased in number as temperature increased at Ringling and Potosi but demonstrated a negative response in the Norris Surber samples. Coleoptera attained its greatest numbers at high or medium temperatures at Ringling and Potosi but also showed a negative trend at Norris. Haplotaxida demonstrated a variability of response to temperature in that they attained their highest numbers at both high and low temperatures.

In terms of ordinal percent of sample, Plecoptera, Coleoptera, Pulmonata and Amphipoda followed trends similar to those of their numerical values. Ephemeroptera attained its greatest percent contribution at intermediate temperatures at Ringling and at Site 2 at Norris. Diptera generally showed no appreciable change in contribution to the community with change in temperature. Haplotaxida demonstrated a higher percent contribution at higher temperatures.

Analysis of variance yielded a high degree of significance for number and percent at the ordinal level. The interaction between temperature and season was found to be significant for 26 of 32 (81%) sets of values tested from Ringling, 10 of 26 (38%) from Norris and 9 of 10

(90%) from Potosi.

Ordinal data were analyzed for linearity of response to temperature through the calculation of r and r^2 values (Table 18). Only those orders which responded significantly to the analysis of variance were tested for linearity of thermal response. Values of r and r^2 were calculated on an annual and seasonal basis. Total r values were weaker and r^2 values lower than those calculated on a seasonal basis. The negative response of numbers of Plecoptera, Ephemeroptera, Trichoptera, Diptera and Amphipoda were confirmed by total and seasonal r values. Coleoptera and Pulmonata exhibited a seasonal variability in the sign of the correlation coefficient; however, all significant r values were positive. Haplotaxida showed a strongly negative trend at Potosi while the only significant r values from Ringling were positive.

A mean r^2 value was compiled from all of the seasonal coefficients of determination for each order. The number of Plecoptera was most strongly influenced by temperature with 50% of the variation in number attributable to thermal variation. Plecoptera was followed by Diptera (35%), Ephemeroptera (34%), Haplotaxida (30%). Trichoptera and Amphipoda (28%) and Pulmonata and Coleoptera (20%).

Numerical data were compiled at the generic or species level for bottom samples from Ringling, Norris and Potosi. Mean number per sample and mean percent contribution were computed and tested with

Table 18. Annual and seasonal correlation coefficients and coefficients of determination^a for the mean number of taxa at the ordinal level per bottom sample at Ringling, Norris and Potosi, as correlated with temperature.

Ringling, Surber	Time of Sample					
	Annual	Fall '74	Winter	Spring	Summer	Fall '75
Ephemeroptera	-.386* (.15)	-.934** (.87)	-.420 (.18)	-.523 (.27)	-.877** (.77)	-.409 (.17)
Trichoptera	-.171 (.03)	-.834* (.70)	-.331 (.11)	-.706* (.50)	-.526 (.28)	-.696 (.48)
Coleoptera	-.157 (.03)	-.271 (.07)	-.144 (.02)	-.233 (.05)	-.463 (.22)	+ .075 (.01)
Diptera	-.409** (.25)	-.708* (.50)	-.750* (.56)	-.494 (.24)	-.782* (.61)	-.759* (.58)
Pulmonata	+ .251 (.06)	-.115 (.01)	-.012 (.00)	+ .860** (.74)	-.240 (.06)	-.462 (.21)
Amphipoda	-.101 (.01)	-.709* (.50)	-.320 (.10)	+ .060 (.01)	+ .786* (.62)	-.296 (.09)
Ringling, Ekman						
Ephemeroptera	-.153 (.02)	-.544 (.30)	-.090 (.01)	-.426 (.18)	-.505 (.26)	+ .086 (.01)
Diptera	-.361** (.13)	-.493 (.24)	-.727 (.53)	-.405 (.16)	-.238 (.06)	-.759 (.58)
Haplotaxida	-.011 (.00)	-.208 (.04)	+ .645* (.42)	+ .697* (.49)	+ .233 (.05)	-.593 (.35)
Amphipoda	-.146 (.02)	-.582 (.34)	-----	-.426 (.18)	-----	0.386 (.15)
Norris, Surber						
Time of Sample						
	Annual	Fall '74	Winter	Spring	Fall '75	
Plecoptera	-.462** (.21)	-.557 (.31)	-.775* (.60)	-.629 (.40)	-.831* (.69)	
Ephemeroptera	-.397* (.16)	-.636 (.40)	-.799* (.64)	-.482 (.23)	-.639 (.41)	
Trichoptera	-.295 (.09)	-.427 (.18)	-.728* (.53)	-.621 (.39)	-.659 (.43)	
Diptera	-.373* (.14)	-.527 (.28)	-.814** (.66)	-.469 (.22)	-.592 (.35)	
Pulmonata	-.074 (.01)	-.425 (.18)	-.404 (.16)	-----	+ .891** (.79)	
Amphipoda	-.206 (.04)	-.609 (.37)	-----	-----	-----	
Norris, Ekman						
Diptera	-.286 (.08)	-.448 (.20)	+ .075 (.01)	-.447 (.20)	-.482 (.23)	
Potosi, Ekman						
Odonata	-.115 (.01)	+ .139 (.02)	-.364 (.13)	-.737* (.54)	-.176 (.03)	
Trichoptera	-.041 (.01)	-.193 (.04)	-.248 (.06)	-----	-.014 (.00)	
Coleoptera	+ .450** (.20)	-.153 (.02)	+ .791** (.63)	+ .863** (.75)	+ .215 (.05)	
Haplotaxida	-.487** (.24)	-.559 (.31)	-.692* (.48)	-.715* (.51)	-.302 (.09)	
Pulmonata	+ .345* (.12)	-----	+ .841** (.71)	+ .496 (.25)	-.075 (.01)	
Amphipoda	-.347* (.12)	-.312 (.10)	-.804** (.65)	-.678* (.46)	-.373 (.14)	

^a in parentheses

* significant (P<.05)

**highly significant (P<.01)




the analysis of variance. These data are shown in Appendix Table 30 for Ringling, Norris and Potosi. Response of genus-species numbers to temperature can be detected from this table. Taxa were categorized on the basis of whether the highest numbers of a genus or species occurred at low, intermediate or high temperatures or occurred at the same level at all temperatures (Table 19). Those taxa exhibiting no linear trend in numerical change with temperature change are also indicated. This system was only applied to taxa that responded significantly to analysis of variance.

Twenty-seven taxa were found to have significant numerical-thermal distributions at Ringling. Of these, nine (33%) were found to occur at higher numbers as temperature decreased, 10 (37%) attained their highest numbers at intermediate temperatures, five (19%) occurred at higher numbers as temperature increased and three (11%) showed no linear response. Ten taxa from Norris had significant numerical distributions. Of these, seven (70%) exhibited a negative response to temperature, one (10%) exhibited a positive thermal response and two (20%) showed no linear response. Of seven taxa categorized from Potosi, one (14%) demonstrated a negative response to temperature, two (29%) attained their highest numbers at intermediate temperatures, three (43%) exhibited a positive thermal response and one (14%) showed no linear response. None of the taxa from the three study areas occurred at the same numerical levels at all thermal


Table 19. Patterns of numerical response to temperature for selected^a genera and species from bottom sample at Ringling, Norris and Potosi.


		Response ^b			
		/	△	\	NT
R i n g l i n g	Ephemeroptera <i>Baetis</i> sp. A	Ephemeroptera <i>Baetis</i> sp. B	Coleoptera <i>Dubiraphia</i> <i>minima</i>	Coleoptera <i>Optioservus</i> <i>quadrinaculatus</i>	
	Trichoptera <i>Hydropsyche</i> sp. A <i>Hydropsyche</i> sp. B	<i>Caenis simulans</i> <i>Choroterpes</i> <i>albiannulata</i> <i>Tricorythodes</i> <i>minutus</i>	Diptera <i>Cladotanytarsus</i> spp. <i>Procladius</i> sp.	Diptera <i>Cricotopus</i> spp.	
	Diptera <i>Simulium</i> spp. <i>Diamesa</i> spp. <i>Micropsectra</i> spp. <i>Rheotanytarsus</i> spp. <i>Orthocladius</i> spp.	Trichoptera <i>Cheumatopsyche</i> spp.	Oligochaeta <i>Limnodrilus</i> <i>hoffmeisteri</i>	Amphipoda <i>Hyaella azteca</i>	
	Oligochaeta <i>Limnodrilus</i> (immatures)	Coleoptera <i>Microcylloepus</i> <i>pusillus</i>	Pulmonata <i>Physa</i> spp.		
		Diptera <i>Conchapelopia</i> spp. <i>Dicrotendipes</i> sp. <i>Paratendipes</i> sp.			
		<i>Pelosclex ferox</i>			
N o r r i s	Plecoptera <i>Isoperla fulva</i> <i>Pteronarcella</i> <i>badia</i>		Oligochaeta <i>Limnodrilus</i> <i>hoffmeisteri</i>	Diptera <i>Orthocladius</i> spp. Pulmonata <i>Physa</i> spp.	


Table 19 (continued).

		Response ^b			
					<u>NT</u>
N o r r i s	Ephemeroptera				
	<i>Ephemerella</i>				
	<i>inermis</i>				
	<i>Paraleptophlebia</i>				
	<i>heteronea</i>				
	Trichoptera				
	<i>Brachycentrus</i> sp.				
	<i>Hydropsyche</i> sp. D				
	Diptera				
	<i>Microtendipes</i> sp.				
P o t o s i	Diptera		Diptera	Coleoptera	Oligochaeta
	<i>Polypedilum</i> spp.		<i>Conchapelopia</i> spp.	<i>Microcylloepus</i>	<i>Limnodrilus</i>
			Amphipoda	<i>pusillus</i>	<i>udekemianus</i>
			<i>Hyalella azteca</i>	Diptera	
			<i>Rheotanytarsus</i>		
			spp.		
			Pulmonata		
			<i>Physa</i> spp.		

^a with significant numerical variation

^b  numbers increase as temperature decreases

 numbers increase at intermediate temperatures

 numbers increase as temperature increases

NT no numerical-thermal trend

levels. Different thermal responses were observed for populations of a genus or species at different study areas. The midge *Rheotanytarsus* responded negatively to temperature at Ringling and positively at Potosi, while *M. pusillus* attained its highest numbers at intermediate temperatures at Ringling but responded positively to temperature at Potosi.

The percent contribution of most of the taxa from Ringling followed the same pattern as the number per sample. Several of the taxa, however, showed a high percent contribution to the community at high temperatures despite their low numbers. *Cheumatopsyche* and *Rheotanytarsus* both had high enough percent contributions at higher temperatures to cause their relative importance in the community to become approximately the same at all thermal levels. *Cricotopus* had a high enough percent contribution at elevated temperatures to become positive in its response while *Dicrotendipes* did the opposite becoming most important to the community at low temperatures. Several taxa (e.g., *C. simulans*, *D. minima*, *Conchapelopia*, *Cryptochironomus* and *Micropsectra*) exhibited a non-significant numerical variation but the variation in percent contribution was significant. Percent contributions of most of the taxa from Norris and Potosi followed the same trends as their numbers.

Analysis of variance yielded a high degree of statistical significance for the variation in both numerical and percent contribution

values from the Ringling and Potosi data. A lesser degree of statistical significance was achieved in the Norris samples. The interaction was significant or highly significant 67 of 88 times (88%) for the Ringling samples, 24 of 54 times (44%) for the Norris samples and 10 of 11 times (91%) for the Potosi samples.

Values of r and r^2 for major genus-species numerical response to temperature are shown in Table 20 and coefficients for genus-species percent contribution are shown in Appendix Table 31 for bottom samples from Ringling, Norris and Potosi. Values were calculated for the entire year's samples as well as individual sample dates.

Total r values for genus-species number per sample from the Ringling Surber samples indicated that most of the taxa (14 of 18) responded in a weakly negative manner (-.052 to -.487) to temperature while four taxa were weakly positive (+.174 to +.391) in response. Only six of the 18 taxa had significant total r values. Total r^2 values ascribed from 0.3 to 24% of the numerical variation to thermal variation. Seasonal r values generally ascribed a higher degree of correlation between genus-species numbers and temperatures than total r values; however, the sign of the coefficient remained the same with few exceptions. *Optioservus quadrimaculatus* had a positive total r value while the summer sample yielded a highly significant -.821. *Simulium*, with a negative total r value, had a positive response in the spring (+.929) while *H. azteca* and *Rheotanytarsus*, both correlated

Table 20. Annual and seasonal correlation coefficients and coefficients of determination^a for mean genus-species number per bottom sample at Ringling, Norris and Potosi, as correlated with temperature.

Ringling, Surber	Time of Sample					
	Annual	Fall '74	Winter	Spring	Summer	Fall '75
EPHEMEROPTERA						
<i>Baetis</i> sp. A	-.134 (.02)	-.226 (.05)	-.613 (.38)	-.535 (.29)	-.831* (.69)	-.953** (.91)
<i>Baetis</i> sp. B	-.052 ($<.01$)	-.437 (.19)	-.317 (.10)	.000 (.00)	-.265 (.07)	-.111 (.01)
<i>Choroterpes albivittulata</i>	-.212 (.05)	-.440 (.19)	-.297 (.09)	-.311 (.10)	-.322 (.10)	-.376 (.14)
<i>Tricoorythodes minutus</i>	-.326* (.11)	-.814* (.66)	-.287 (.08)	-.426 (.18)	-.541 (.29)	-.406 (.17)
TRICHOPTERA						
<i>Chumatopsyche</i> spp.	-.107 (.01)	-.792* (.63)	-.312 (.10)	-.452 (.20)	-.471 (.22)	-.669 (.45)
<i>Hydropsyche</i> sp. A	-.226 (.05)	-.873** (.76)	-.588 (.35)	-.641 (.41)	-.928** (.86)	-.670 (.45)
<i>Hydropsyche</i> sp. B	-.245 (.06)	-.625 (.39)	-.415 (.17)	.000 (.00)	-.765* (.58)	-.507 (.26)
COLEOPTERA						
<i>Dubiraphia minima</i>	+.285 (.08)	-.155 (.02)	+.609 (.37)	+.051 ($<.01$)	+.633 (.40)	+.713* (.51)
<i>Microcyllopus pusillus</i>	-.185 (.03)	-.260 (.07)	-.210 (.04)	-.231 (.05)	-.302 (.09)	-.398 (.16)
<i>Optioserrus quadrinaculatus</i>	+.174 (.03)	-.504 (.25)	+.760* (.58)	-.608 (.37)	-.821** (.67)	+.466 (.22)
DIPTERA						
<i>Stimulium</i> spp.	-.353* (.13)	-.741* (.55)	-.516 (.27)	+.929** (.86)	-.770* (.59)	-.653 (.43)
<i>Cybaotopus</i> spp.	+.391* (.15)	-.446 (.20)	-.362 (.20)	.000 (.00)	+.072 (.01)	-.184 (.03)
<i>Diansoa</i> spp.	-.372* (.14)	.000 (.00)	-.826** (.68)	-.040 ($<.01$)	.000 (.00)	-.649 (.42)
<i>Orthocladius</i> spp.	-.487** (.24)	-.129 (.02)	-.607 (.37)	+.168 (.03)	-.840** (.71)	-.660 (.44)
<i>Rhectanytarsus</i> spp.	-.194 (.04)	-.765* (.59)	-.348 (.12)	.000 (.00)	+.486 (.24)	-.367 (.13)
OLIGOCHAETA						
<i>Limnodrilus</i> (immatures)	-.427** (.18)	-.790** (.62)	-.530 (.28)	.000 (.00)	-.386 (.15)	-.299 (.09)
PULMONATA						
<i>Physa</i> spp.	+.252 (.06)	-.100 (.01)	-.012 (.00)	+.861** (.74)	-.222 (.05)	-.462 (.21)
AMPHIPODA						
<i>Hyalella asteca</i>	-.093 (.01)	-.709* (.50)	-.329 (.11)	+.060 ($<.01$)	+.791* (.63)	.000 (.00)
Ringling, Ekman						
EPHEMEROPTERA						
<i>Caenis simulans</i>	-.161 (.03)	-.648 (.42)	-.000 (.00)	-.426 (.18)	.000 (.00)	+.086 (.01)
COLEOPTERA						
<i>Microcyllopus pusillus</i>	-.145 (.02)	-.185 (.03)	-.000 (.00)	-.226 (.05)	.000 (.00)	-.332 (.11)
DIPTERA						
<i>Cladotanytarsus</i> spp.	+.421** (.18)	.000 (.00)	+.569 (.32)	+.075 (.01)	+.237 (.06)	+.753 (.57)
<i>Conohaplecia</i> sp.	-.037 ($<.01$)	-.068 (.01)	-.108 (.01)	.000 (.00)	.000 (.00)	-.347 (.12)
<i>Dicranotendipes</i> sp.	-.160 (.03)	-.147 (.02)	-.646 (.42)	.000 (.00)	+.059 ($<.01$)	-.548 (.30)
<i>Micropeaetra</i> spp.	-.352* (.12)	-.712* (.51)	-.591 (.35)	+.268 (.07)	-.046 ($<.01$)	-.891** (.79)
<i>Pezotendipes</i> sp.	-.041 ($<.01$)	.000 (.00)	-.507 (.26)	-.103 (.01)	+.067 ($<.01$)	+.219 (.05)

Table 20 (continued).

Kingling, Ekman	Time of Sample					
	Annual	Fall '74	Winter	Spring	Summer	Fall '75
<i>Procladius</i> sp.	+ .490** (.24)	+ .754* (.57)	-.237 (.06)	.000 (.00)	+ .341 (.12)	+ .995** (.99)
<i>Rhectanytarsus</i> spp.	-.349* (.12)	-.133 (.02)	-.804* (.65)	.000 (.00)	.000 (.00)	-.491 (.24)
OLIGOCHAETA						
<i>Limnodrilus hoffmeisteri</i>	+ .279* (.08)	.000 (.00)	+ .730* (.53)	+ .712* (.51)	+ .324 (.11)	+ .204 (.04)
<i>Limnodrilus</i> (immatures)	-.205 (.04)	.000 (.00)	-.584 (.34)	-.426 (.18)	.000 (.00)	-.618 (.38)
<i>Paloscolex ferox</i>	-.047 ($<.01$)	-.208 (.04)	-.392 (.15)	+ .432 (.19)	+ .075 (.01)	.000 (.00)
AMPHIPODA						
<i>Hyalella astwoa</i>	-.146 (.02)	-.582 (.34)	.000 (.00)	-.462 (.18)	.000 (.00)	-.386 (.15)
Morris, Surber						
PLECOPTERA						
<i>Isoperla fulva</i>	-.421* (.18)	-.552 (.31)	-.798* (.64)	-.155 (.02)		-.679 (.46)
<i>Pteronarcissa badia</i>	-.381* (.15)	-.471 (.22)	-.466 (.22)	-.270 (.07)		-.866** (.75)
EPHEMEROPTERA						
<i>Ephemera illa inermis</i>	-.408* (.17)	-.598 (.36)	-.801* (.64)	-.382 (.15)		-.612 (.38)
<i>Paraleptophlebia heteronea</i>	-.227 (.05)	-.590 (.35)	.000 (.00)	.000 (.00)		-.741* (.55)
TRICHOPTERA						
<i>Brachycentrus</i> sp.	-.351* (.12)	-.412 (.14)	-.685 (.47)	-.583 (.34)		-.730* (.53)
<i>Hydropsyche</i> sp. D	-.279 (.08)	-.507 (.26)	-.774* (.60)	-.110 (.01)		-.634 (.40)
DIPTERA						
<i>Microtendipes</i> sp.	-.252 (.06)	-.444 (.20)	-.454 (.21)	-.270 (.07)		-.654 (.43)
OLIGOCHAETA						
<i>Limnodrilus hoffmeisteri</i>	+ .320 (.10)	-.039 ($<.01$)	+ .947** (.90)	-.420 (.18)		.000 (.00)
PULMONATA						
<i>Physa</i> spp.	-.074 (.01)	-.425 (.18)	-.404 (.16)	.000 (.00)		+ .891** (.79)
Morris, Ekman						
DIPTERA						
<i>Orthocladus</i> spp.	+ .238 (.06)	-.440 (.19)	+ .952** (.91)	+ .313 (.10)		-.420 (.18)
OLIGOCHAETA						
<i>Limnodrilus hoffmeisteri</i>	+ .522** (.27)	+ .722* (.52)	+ .718* (.52)	+ .626 (.39)		+ .337 (.11)
Potosi, Ekman						
COLEOPTERA						
<i>Microcyllopus pusillus</i>	+ .449** (.20)	-.174 (.03)	+ .791** (.63)	+ .863** (.75)		+ .215 (.05)
DIPTERA						
<i>Conchapelopta</i> sp.	-.371* (.14)	-.069 (.01)	-.852** (.73)	-.232 (.05)		-.185 (.03)
<i>Polypedilum</i> spp.	-.360* (.13)	.000 (.00)	-.539 (.29)	-.656* (.43)		-.275 (.08)
PULMONATA						
<i>Physa</i> spp.	+ .345* (.12)	.000 (.00)	+ .841** (.71)	+ .496 (.25)		-.075 (.01)

* in parentheses

* significant ($P < .05$)** highly significant ($P < .01$)

negatively with temperature on an annual basis, responded positively in the summer samples (+.791 and +.486). Coefficients of determination were generally much higher on a seasonal rather than an annual basis as exemplified by *Hydropsyche* sp. A which had a total r^2 of .05 and seasonal values ranging from .35 to .86.

Total r and r^2 values for genus-species percent contribution to the Ringling Surber samples indicated that 11 of 20 taxa had a positive response to temperature (+.053 to +.609) while nine responded negatively (-.043 to -.408). Seasonal r values indicated that most of the taxa demonstrated shifts in their response to temperature on a seasonal basis. This is exemplified by *O. quadrimaculatus* and *M. pusillus* which responded positively in winter (+.741 and +.743) and negatively in summer (-.608 and -.249); by *Simulium* which was negative at all seasons except spring (+.839) and by *C. simulans*, *Rheotanytarsus* and *H. azteca* which demonstrated negative trends except in the summer samples in which they became most important at high temperatures (+.779, +.925 and +.754). Some taxa (e.g., *C. albiannulata* and *Baetis* sp. A) maintained a negative correlation at all seasons while others (e.g. *D. minima*, *L. hofmeisteri* and *Conchapelopia*) demonstrated fully positive trends.

Correlation coefficients for genus-species numbers vs. temperature for the Ringling Ekman samples followed the same pattern as the Surber samples. Most of the taxa demonstrated a weakly negative

correlation (-.037 to -.352) while three responded positively (+.279 to +.490). Seasonal values generally followed the trend established by the sign of the annual r value with the exception of *P. ferox* which had positive values in the spring and summer samples.

Total r and r^2 values for genus-species percent contribution to the Ringling Ekman samples showed an increase in positive correlations (6 of 14) while most (8 of 14) remained negative. Most of the taxa showed a seasonal variation in the sign of the correlation.

Total r values for genus-species numbers for the Norris Surber samples showed most of the taxa to be correlated with temperature in a weakly negative manner (-.074 to -.421) with *L. hoffmeisteri* showing the only positive response (+.320). Total r^2 values ascribed from one to 18% of the numerical variation to thermal variation. On a seasonal basis, r and r^2 values increased in strength. Patterns of response, as detected from the signs of the total r values, generally remained the same for the individual sample dates.

Total r values for the percent contribution of individual taxa to the Norris Surber samples were generally higher than those calculated for numerical values with six of 10 taxa responding negatively to temperature (-.040 to -.568) and four responding positively (+.307 to +.535). On a seasonal basis, most taxa followed the trends established by the yearly coefficient with *Orthocladus* and immature *Limnodrilus* exhibiting seasonal variations.

Only two taxa were investigated from the Norris Ekman samples for number per sample. Both *Orthocladius* and *L. hoffmeisteri* responded in a positive manner to temperature (+.238 and +.522). *Limnodrilus hoffmeisteri* maintained its positive thermal response on a seasonal basis while *Orthocladius* showed a seasonal variability. Percent contribution data showed that *L. hoffmeisteri* continued to exhibit a positive thermal response while *Hexatoma*, *P. ferox* and *Pisidium* followed negative trends.

Taxa investigated from Potosi for numbers per sample exhibited positive responses in the cases of *M. pusillus* and *Physa* and negative responses for *Conchapelopia* and *Polypedilum*. Seasonal patterns followed trends established by the sign of the total *r* value for all four taxa. In terms of percent contribution to the sample, *Conchapelopia*, *Polypedilum* and *L. udekemianus* were negative in response while *Rheotanytarsus* was positive.

Production Related Aspects

Mean biomass per sample (wet weight) was calculated for the Ringling Surber and Ekman samples (Table 21). The Ringling Surber samples exhibited a marked increase in biomass as temperature decreased. Site 8, the lower cold site, had the highest biomass while Site 3 in the hot spring had the lowest. Site 2, the upper cold station, had a mean biomass nearly equal to that of Site 6. Analysis of variance

Table 21. Mean biomass (g) of invertebrates per Surber (.1 m²) and Ekman (.023 m²) sample from Ringling with multifactor analysis of variance.

	Sample Site						Analysis of Variance*		
	3	1	6	7	8	2	Date	Site	Date x Site
Surber	.56	.80	1.22	2.61	4.09	1.21	HS	HS	HS
Ekman	.07	.19	.02	.07	.04	.11	NS	NS	NS

* HS = highly significant difference (P<.01)

S = significant difference (P<.05)

NS = differences non-significant

showed that biomass varied in a highly significant manner with season, temperature and the interaction between the two.

Analysis of the Ringling Ekman samples failed to indicate any trend in variation of biomass with temperature. Analysis of variance confirmed this observation, attributing no significance to the variation of biomass on a thermal or seasonal basis.

On a seasonal basis, the highest mean standing crops were attained in the fall samples (Table 22) with the lowest appearing in the spring samples. This trend was followed at each sample site except Site 3 which attained its highest standing crop in the spring sample and its lowest in the summer and fall.

Because standing crop is influenced by the size and number of the contributing organisms and because sample numbers and weights varied significantly with season and thermal site, the mean weight per

Table 22. Mean biomass (g) and numbers of organisms collected in Ringling Surber samples on each sample date.

	Fall '74	Winter	Spring	Summer	Fall '75
Biomass	2.4920	.9289	.6532	1.1850	3.4890
Number	1167.0	476.7	258.3	562.3	741.9

individual organism was calculated on a seasonal and thermal site basis for the Ringling Surber samples (Table 23). This was accomplished by

Table 23. Mean weight (mg) per individual organism, by sample site and season, from the Ringling Surber samples.

Sample Site	<u>3</u>	<u>1</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>2</u>
Weight by Site	5.43	3.60	2.51	2.26	2.71	3.29
Sample Season	<u>Fall '74</u>	<u>Winter</u>	<u>Spring</u>	<u>Summer</u>	<u>Fall '75</u>	
Weight by Season	2.13	1.94	2.53	2.11	4.70	

dividing the mean weight of invertebrates per sample by the mean number per sample for thermal sites and sampling dates. Data contained in Table 23 reflect a general decrease in the size of the individual organism with decreasing temperatures. Site 2 was found to deviate from the general trend in that it appears to most closely resemble Site 1 in value. Seasonal comparisons show similarities in mean weight of individuals between the fall 1974 and winter samples with an increase in weight in the spring samples.

Differences in mean biomass per sample were tested with a Newman-Keuls test. No significant difference was found among Sites 3, 1, 6 and 2 in any combination. Sites 7 and 8 differed significantly from each other and all other sites.

Mean biomass per sample was correlated with temperature for sites at Ringling. Correlation coefficients and coefficients of determination were calculated on an annual and seasonal basis and are found in Table 24. On an annual basis, biomass was weakly correlated with

Table 24. Correlation coefficients and coefficients of determination^a for mean biomass per sample^b; Ringling Surber samples.

<u>Annual</u>	<u>Fall '74</u>	<u>Winter</u>	<u>Spring</u>	<u>Summer</u>	<u>Fall '75</u>
-.336*	-.890**	-.949**	+.753*	-.619*	-.747*
(.11)	(.79)	(.90)	(.57)	(.38)	(.56)

^a in parentheses

^b .1 m²

* significant ($P < .05$)

**highly significant ($P < .01$)

temperature with 11% of the variation in biomass attributed to variation in temperature. Seasonal r values generally showed a strongly negative correlation between biomass and temperature (-.619 to -.949) with 38 to 90% of the variation due to thermal variation. The spring sample provided an exception to this trend with biomass strongly correlated with temperature in a positive manner (+.753). All correlations for mean biomass with temperature were significant or highly significant.

The linear regression for mean sample biomass as dependent on temperature is described by $y = .1x + 3.8$. The regression was found to be significant and is graphed in Figure 6. The rate of change of .1 g per °C applied to the annual, winter, spring and summer samples but the fall samples displayed a higher rate.

Colonization rates of Hester-Dendy artificial substrate samplers were computed for sample sites at Ringling. The samplers were harvested at approximately 14 day intervals with a maximum sample period of 21 days. This is less than the four to eight weeks recommended to achieve colony equilibrium by many authors (Anderson and Mason 1968, Fullner 1971, Hilsenhoff 1969, Nilsen and Larimore 1973). On each sample date, samplers were scraped bare thus presenting a denuded substrate for each sample period. Mean colonization rates were calculated in number of organisms per square meter per day and milligrams per square meter per day for Sites 3, 1, 6, 7 and 8 at Ringling (Table 25). Site 2 was eliminated due to the presence of extremely large populations of *Simulium* which occurred irregularly in some of the samples. Numerical colonization rate was lowest at Site 3. Site 1 exhibited a dramatic increase in rate over Site 3 and Site 6 had the maximum rate with a mean value of 201.3 organisms per square meter per day. The rate was lowest at the lower cool sites, Sites 7 and 8. A similar pattern can be observed in the weight related rates with a marked increase between Site 3 and Sites 1 and 6, the maximum being achieved

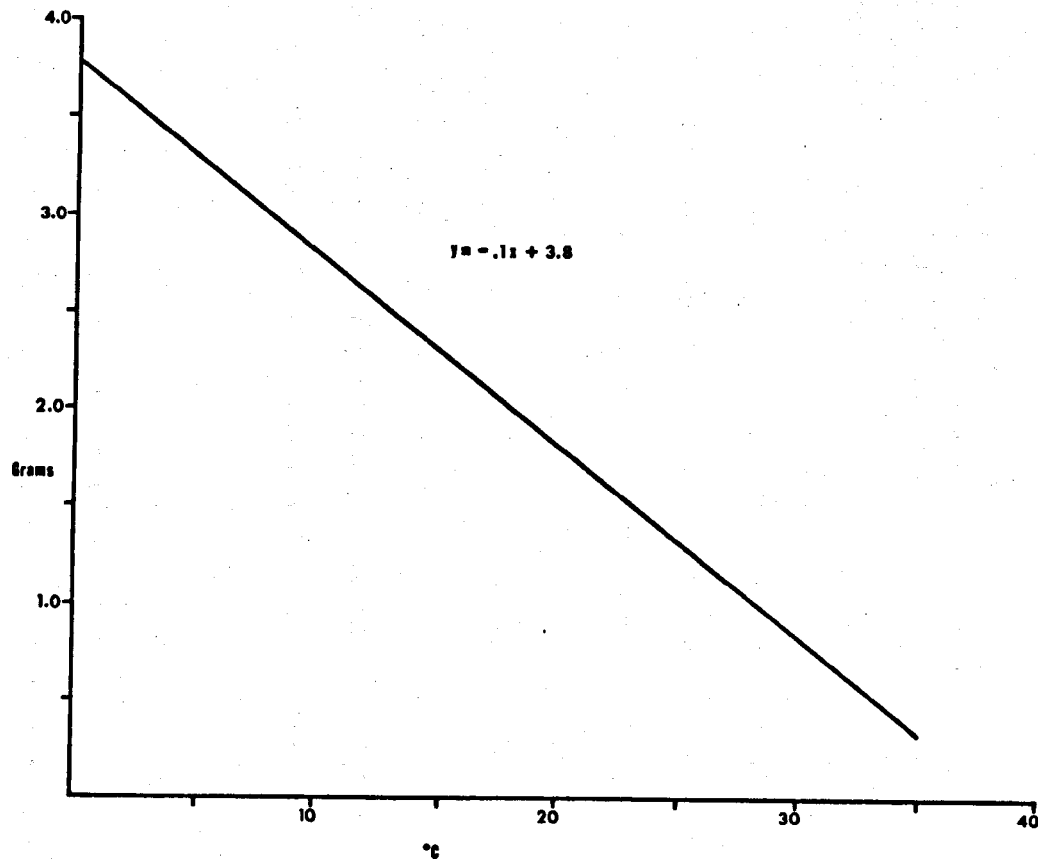


Figure 6. Linear regression of macroinvertebrate biomass and temperature from Surber samples collected at Ringling.

Table 25. Colonization rates of macroinvertebrates on Hester-Dendy samplers with multifactor analysis of variance, Ringling.

	<u>Sample Site</u>					<u>Analysis of Variance</u>		
	<u>3</u>	<u>1</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>Date</u>	<u>Site</u>	<u>Date x Site</u>
No./m ² /day	1.0	102.4	201.3	59.0	73.4	HS	HS	S
mg/m ² /day	69.1	238.8	205.3	95.0	76.1	HS	HS	NS

HS = highly significant difference (P<.01)

S = significant difference (P<.05)

NS = differences non-significant

at Site 1, and a marked drop in rate between Sites 1 and 6 and Sites 7 and 8 as temperatures cooled further. Analysis of variance showed that variation in mean rates of colonization was highly significant.

A Newman-Keuls Test was performed on the colonization rates. The only significant difference that could be detected for the numerical rates was found between the extremes, Sites 3 and 6. The weight related rates showed a significant difference between Sites 1 and 6 and Sites 3, 7 and 8. No difference was found between Sites 1 and 6 or among Sites 3, 7 and 8.

Regression-correlation analysis was performed on the numerical and weight related colonization rates. Both numerical (+.064) and weight related (+.156) colonization rates were very weakly correlated with temperature. The numerical rate of colonization as dependent on temperature was described by the linear regression $y = 1.2x + 62.6$ while

colonization rate by weight was described by $y = 2.1x + 92.1$. Neither the correlations nor the regressions were found to be significant.

Another production related parameter, genus-species mean weight, was compared among the Ringling sample sites. Mean weight was calculated as the total wet weight of each genus or species divided by the total number of individuals weighed. Data from the fall and winter samples were selected for comparison to minimize complications due to emergence, egg stage, spates etc. Mean weights for 25 taxa are presented in Appendix Table 32. All of the taxa exhibited different mean weights at different sample sites with the most marked differences found between the warmer sites, Sites 1 and/or 6, and the cooler sites, Sites 7 and/or 8. Thirteen of the 25 taxa exhibited increased mean weight with increased temperature and an additional four taxa had higher mean weights at higher temperatures without linearity of response. Eight taxa showed a reverse of this trend with increased mean weights as temperature decreased.

Ten taxa common to both Sites 6 and 7 exhibited an increase in weight between the fall 1974 and the winter samples. The difference in mean weight between these samples for each taxon was calculated as the growth increment for that period and divided by 10 to yield a mean increment of growth for Site 6 and Site 7. The mean growth increment for the 10 taxa was 3.09 mg per organism at Site 6 and .28 mg per organism at Site 7.

Comparison of intersite growth rates was further investigated through the use of length frequency analysis. Four taxa; the mayflies *T. minutus* and *C. albiannulata*, the caddisfly *Cheumatopsyche* and the amphipod *H. azteca* were selected because of their common occurrence at a range of thermal sites and an external morphology that lent itself to linear measurement. Head capsule length or width were selected for measurement because of their acceptability for the differentiation of instars by frequency analysis (McCauley 1974, Newell 1976, Terch 1972). No attempt was made to define individual instars due to a lack of sufficient accompanying data (Newell 1976).

In the case of the mayflies, the observation was made that many sizes of individuals were present, ranging from very small early instars to very large individuals whose well developed wing pads, adult eyes and color indicated that they were near emergence. Because of this, a master histogram was constructed for both *T. minutus* and *C. albiannulata* with the result that eight arbitrary instar groups were selected for the former and 10 instar groups were selected for the latter (Figure 7). Head widths for *T. minutus* and head lengths for *C. albiannulata* from the fall sample 1974 were categorized and their frequencies plotted for Sites 6, 7 and 8 for *T. minutus* (Figure 8) and Sites 1, 6, 7 and 8 for *C. albiannulata* (Figure 9). *T. minutus* occurred in all eight instar groups at Site 6 while only the first five groups occurred at Sites 7 and 8. The highest mode was achieved at instar

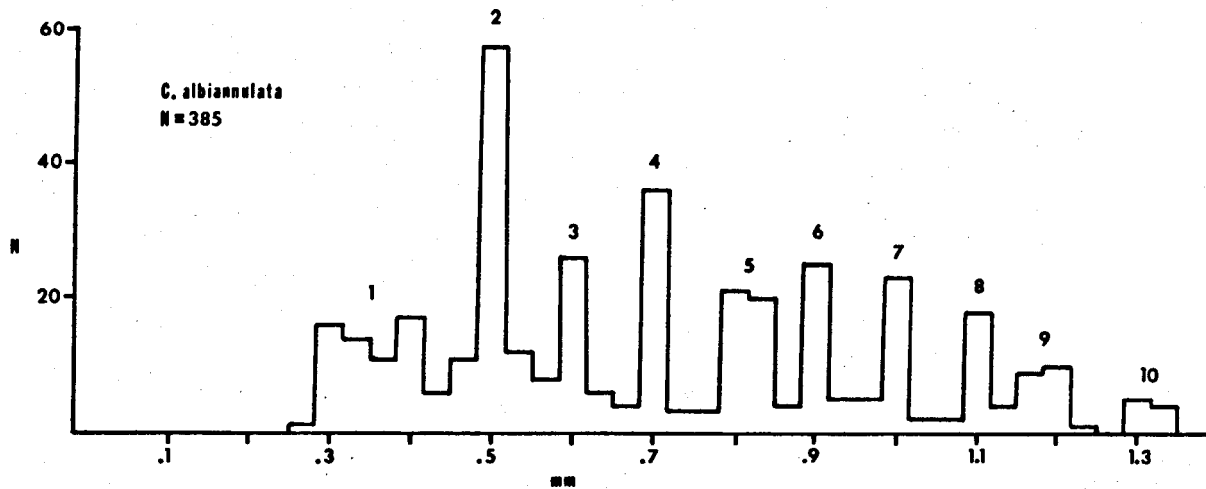
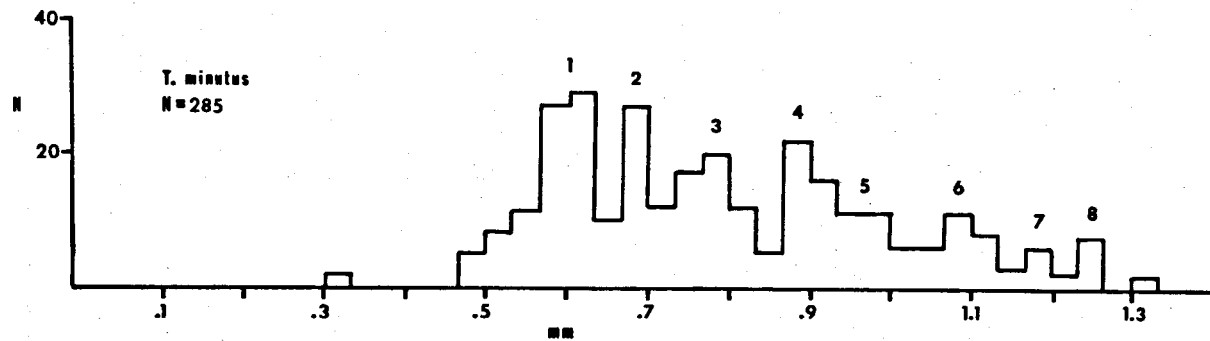


Figure 7. Head width (*Trichorythodes minutus*) and head length (*Choroterpes albiannulata*) frequency histograms used to estimate instar groups (numbers above modes) from samples collected Oct. 5, 1974 at Ringling.

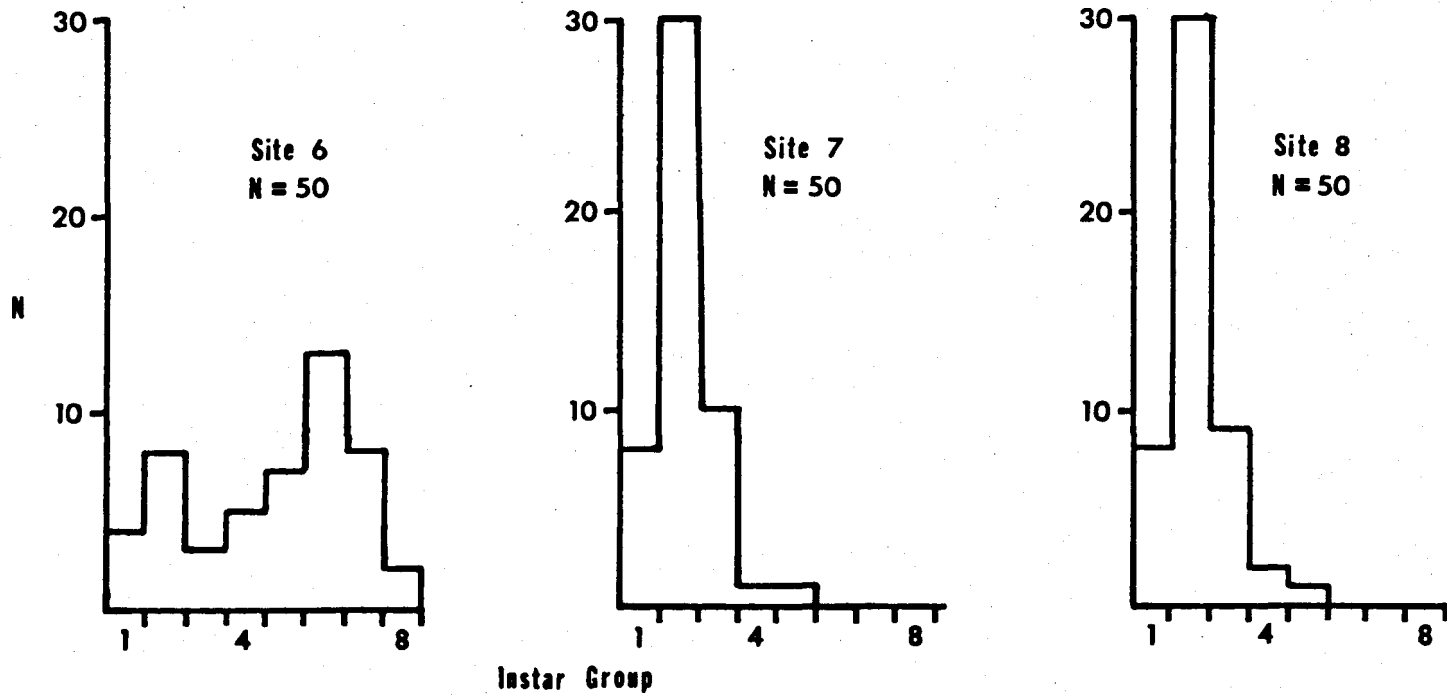


Figure 8. Instar group frequency based on head width measurements of *Trichorythodes minutus* collected Oct. 5, 1974 at Ringling.

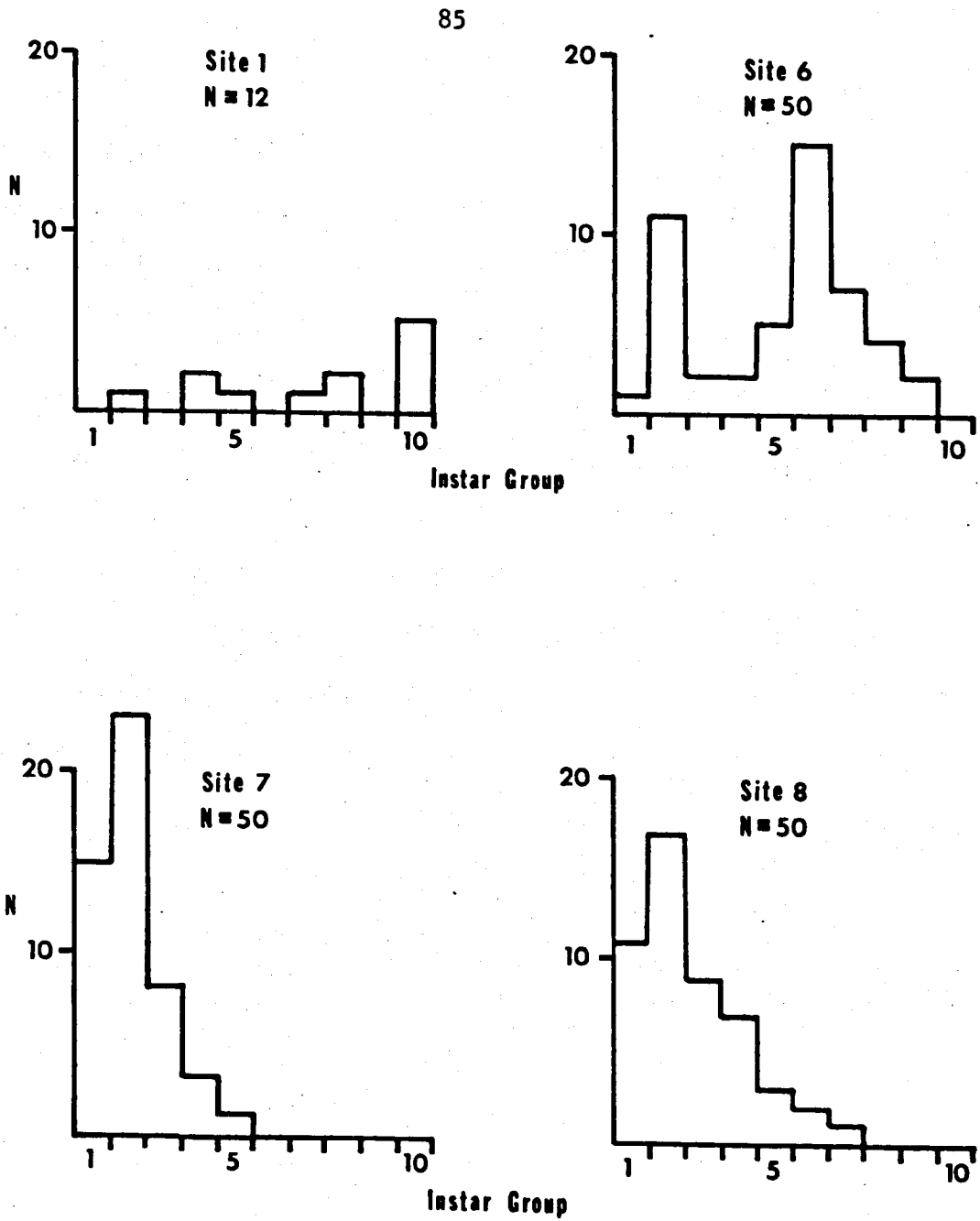


Figure 9. Instar group frequency, based on head length measurements, of *Choroterpes albiannulata* collected Oct. 5, 1974 at Ringling.

group six for Site 6 while the maximum frequency was observed at instar group two at Sites 7 and 8. A similar situation was observed for *C. albiannulata* with nearly a full range of instar groups occurring at Sites 1 and 6 and a lower range of groups represented at Sites 7 and 8. Maximum frequencies of occurrence for *C. albiannulata* occurred at instar group six for Site 6 and instar group two for Sites 7 and 8.

The large range in developmental stage within a single sample was not observed in *H. azteca* or *Cheumatopsyche* thus no instar groups were calculated and only length frequency data were plotted (Figures 10 and 11). *H. azteca* did not show the marked shift toward larger instars at high temperatures that the mayflies did; however, a lack of the smaller instars was noticed at the warmer sites, Sites 1 and 6. The larger instars were found at both warmer and cooler sites. Length frequency data for *Cheumatopsyche* exhibited three modes at each site which did shift appreciably with temperature.

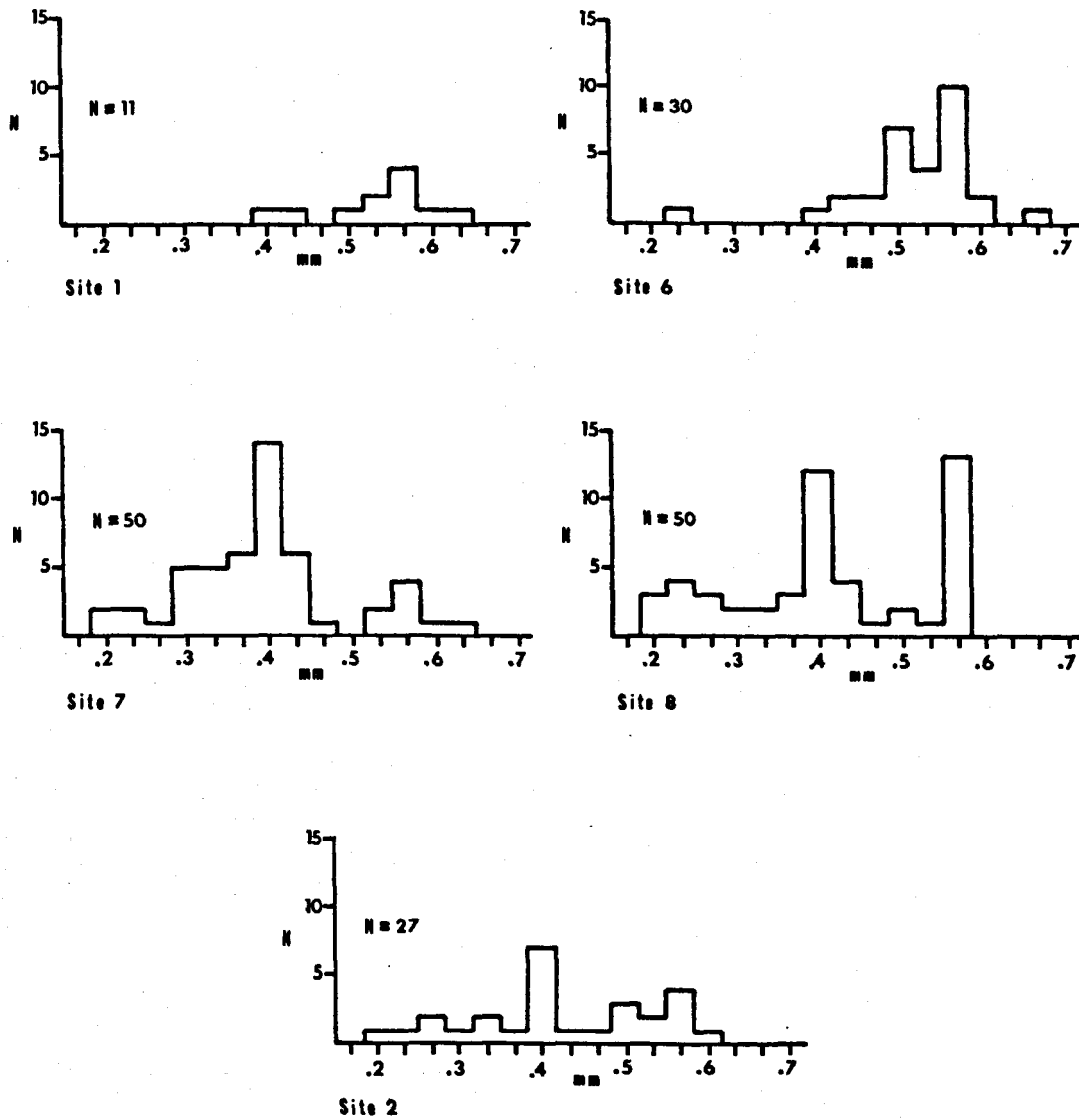


Figure 10. Head length frequency of *Hyalella azteca* collected Oct. 5, 1974 at Ringling.

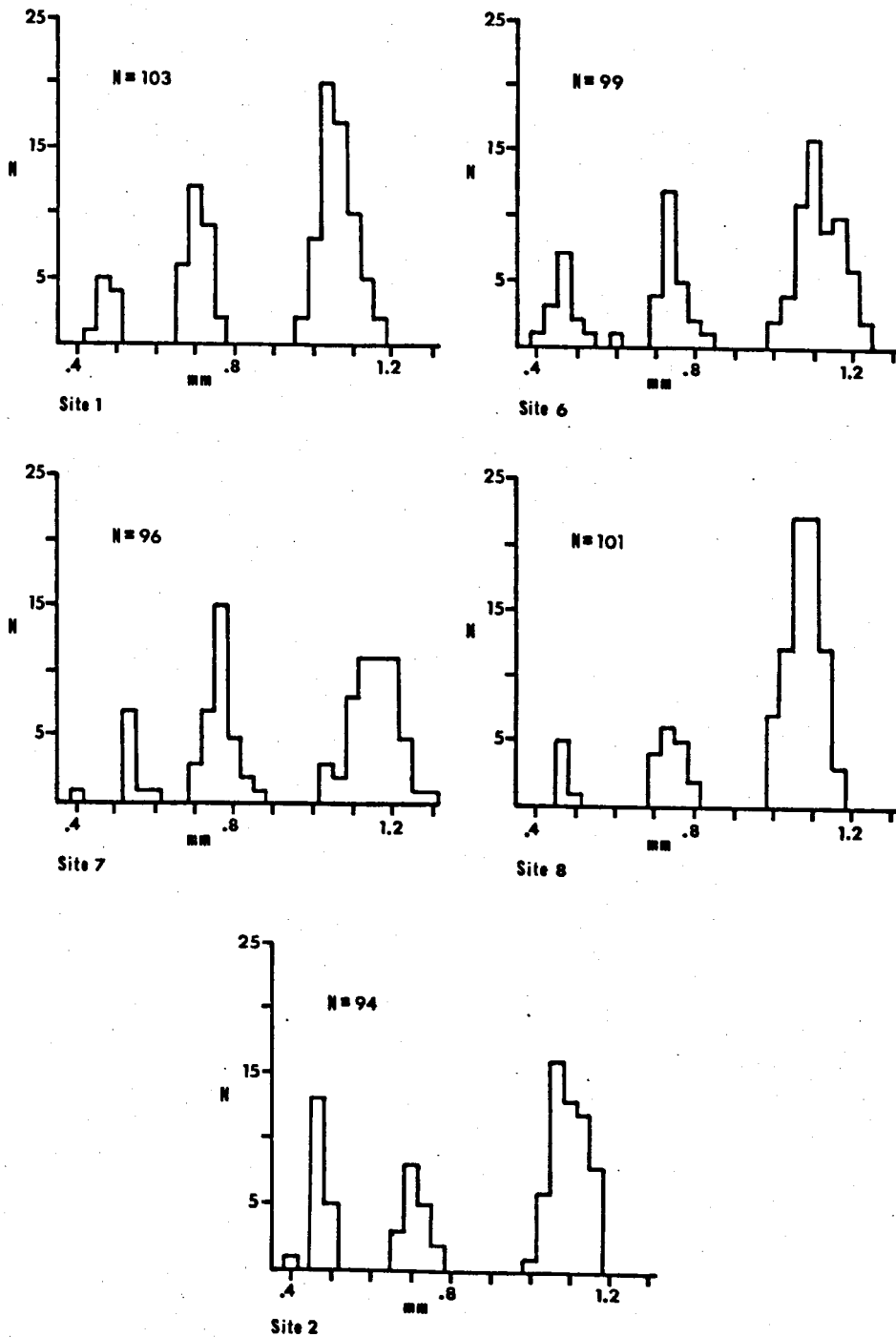


Figure 11. Head length frequency of *Cheumatopsyche* spp. collected Oct. 5, 1974 at Ringling.

DISCUSSION

The thermal regime of a body of water is a function of latitude, altitude and season and fluctuates on a daily and seasonal basis. Dodds and Hisaw (1925) considered average annual temperature, winter minimum, summer maximum, summer average, duration of summer season and duration of ice cover to be the most critical components of water temperature for the aquatic invertebrate community. When the normal thermal regime is disrupted due to the addition of heated water, either from geothermal or man-caused sources, the result is a quantitative and qualitative shift in the macroinvertebrate fauna. These shifts may occur as a result of direct lethality from high temperatures and/or indirect effects on some stage of the life cycle of a species which may result in a reduction in population number or in its ultimate removal from the community (Tarzwell 1970). Although it may be theorized that addition of new species may accompany a thermal shift, this was not observed in the present study.

Direct lethality due to high temperature may not act on the organism as an individual or as a species. The effects of direct lethality on community composition are difficult to distinguish from indirect effects in a field situation and may play a minor role when compared to the latter. Wurtz (1969) questioned the use of maximum temperature on an annual, mean daily or mean annual basis in the determination of thermal effects on invertebrate communities because most north

temperate species are eurythermal. He emphasized the importance of the rate of temperate change.

Attempts have been made to measure upper lethal limits in the laboratory. Gaufin and Hern (1971) measured 96 hr T_{Lm} values from a low of 14.5°C for *Gammarus limmaeus* to highs of 30.5°C for *Hydropsyche* and 32.4°C for *Atherix variegata*. Mean values were 18.8°C for Ephemeroptera, 26.5°C for Trichoptera and 28.7°C for Diptera. Nebecker and Lemke (1968) tested 12 species that were acclimated at 10°C for one week and found a range of 21 to 33°C for 96 hr T_{Lm} values.

Indirect effects of high temperature pertain to phenomena that occur at temperatures below the lethal level. An organism may be able to survive at such temperatures but be unable to successfully reproduce, thus eliminating such a species from the aquatic community at that thermal regime (Nebecker 1971a). In many aquatic insects, a timed sequence of thermal stimuli is often necessary for egg hatching, nymphal development and emergence (Lehmkuhl 1974). If these criteria are met, a species can often tolerate a wide range of temperatures. If the proper temperature is missing for one stage of development, however, the species may be eliminated from the community or its numbers drastically reduced. Low summer temperatures, for example, have been found to remove species from the macroinvertebrate community due to the disruption of this thermal synchrony (Elgmork and Saether 1970, Lehmkuhl 1972, Pearson et al. 1968).

The structure of a macroinvertebrate community may also be influenced by the interactions between temperature and various other factors that determine macroinvertebrate distribution and abundance (Vernberg and Vernberg 1974). One such factor is the amount of dissolved oxygen that is present in the water. The interaction between temperature and dissolved oxygen was demonstrated by Krenkal and Parker (1969) who showed that at 25°C the deoxygenation curve crosses the reaeration curve and sweeps rapidly upward causing oxygen depletion.

Whichever of the aforementioned processes or combination of processes is involved, temperature does exert a strong influence on the determination of the macroinvertebrate communities of a body of water. At high temperatures, this effect seems to be manifested as a process of elimination, rather than addition, of species as temperature increases to the point at which macroinvertebrate life is excluded.

Macroinvertebrate Thermal Maxima

Perhaps the most obvious effect of direct lethality due to high temperature is the exclusion of macroinvertebrate life from the aquatic ecosystem. The data suggest that macroinvertebrates were unable to inhabit sites where temperatures often exceeded 40°C at Ringling and Norris. Similar results were obtained by Durrett and Pearson (1975) who found no invertebrates inhabiting a power plant effluent channel when temperatures exceeded 41°C. Jones (1967) determined that macroinvertebrate life was excluded by temperatures in excess of 43.5°C in

the Firehole River. Brock (1967) found macroinvertebrates inhabiting temperatures up to 43°C in hot springs in Yellowstone National Park.

It is difficult to determine whether invertebrate life is excluded by temperatures in excess of 40°C or by temperatures acting in combination with other factors. Langford (1971) and Wurtz (1969) mentioned the problem of separating thermal effects from the effects of other pollutants in power plant effluents. Brues (1924, 1932) considered low dissolved oxygen levels, high salinities and variable pH values as compounding the problem of high temperatures in hot springs. Gaufin (1962) found that for most stonefly larvae oxygen demands increased very rapidly above 16.5°C. It has been postulated that temperature can interact with other factors, biotic or abiotic, to exert a more profound effect on living organisms than any one factor by itself (Vernberg and Vernberg 1974). This interaction may be additive or synergistic.

The Hot Spring Fauna

The majority of the taxa collected within the flows of the hot springs were not restricted to these heated environments and were also collected at cooler stations. This appears to be consistent with the findings of Robinson and Turner (1975) in some Virginia hot springs and Mason (1939) in an Algerian hot spring. The ability of certain species to inhabit a broad thermal range may be due to an ability to synthesize multiple forms (isozymes) of regular enzymes (Newell 1973). The elimination of most species from the temperature regime of the hot

spring and the restriction of some others to this environment may be due to their inability to synthesize the appropriate isozymes.

Of the taxa that were restricted to the hot springs, some doubt exists as to whether *Isotomurus*, the Curculionidae, the muscid pupae and the midges *Paraphaenocladus* and *Limmophyes* are truly members of the aquatic community. The remaining taxa; *Pseudosmittia*, *Atrichopogon* and *Cypria* may be restricted to elevated temperatures.

Although there does not appear to be a unique thermal fauna created through the addition of species, one has evolved via the elimination of most forms found at the cooler sites. Most genera that are capable of inhabiting hot springs demonstrate a common North American and even a world-wide distribution in these springs (Robinson and Turner 1975). Hynes (1970) stated that a very select fauna is found as temperatures approach 40°C consisting mainly of dytiscid and hydrophilid beetles, stratiomyids, chironomids, oligochaetes and ostracods. Results of the present study indicate that Pulmonata, represented by *Physa* and *Lymnaea*, should be added to this group.

Members of the dipteran family Ephydriidae and the dragonfly *Libellula* have been previously reported as common inhabitants of hot springs (Brues 1924 and 1932, Mason 1939, Provonsha and McCafferty 1977); however, no representatives of these taxa were collected in the present study. Their absence may be due to some thermal-chemical

interaction or other habitat requirements that are limiting in the hot springs under study.

Fauna Of The Thermal Gradients

Faunal distributions within the thermal gradients revealed that many of the taxa were limited to the colder sites. All of the Plecoptera collected during the study were rigidly restricted to the cooler sites. Gaufin (1962) stated that thermal optima for most Plecoptera occur in the range of 10 to 15°C. Armitage (1961) observed that no Plecoptera showed a preference for warmer sites in the Firehole River. Several of the mayfly species were limited to the cooler sites. One of these, *E. grandis*, also showed thermal avoidance in the Firehole River (Armitage 1961). Few chironomids exhibited a thermal avoidance although *Diamesa*, a common inhabitant of cold mountain brooks (Elgmork and Saether 1970), *Endochironomus*, *Phaenopsectra*, *Stictochironomus* and *Chironomus* appeared to be limited to the colder sites. Although *Chironomus* and *Endochironomus* were only collected at cool sites, species of these genera have been found to be tolerant of high temperatures. This cold stenothermal fauna was limited to sites representing observed thermal extremes of 0 to 26°C at Ringling, 0 to 16°C at Norris and 10 to 17°C at Potosi. A further subdivision of this group revealed that the majority of the cold stenotherms were restricted to the coldest sites at each study area. This further restricts the temperature ranges inhabited by most of the cold stenotherms to observed extremes

of 0 to 22.5°C at Ringling, 0 to 10°C at Norris and 10 to 13°C at Potosi.

Another group of taxa appeared to be restricted to intermediate thermal sites. At Ringling and Potosi, the majority of these taxa were found at the first level of temperature increase over the coldest sites present. This slight elevation in temperature may provide a niche for a unique thermal community. Two species of caddis, *Hydropsyche* sp. C and *Heliopsyche borealis*, were limited to intermediate temperatures. *Hydropsyche* has been known to thrive at elevated temperatures (Roback 1962) while *H. borealis* has been collected in hot spring effluents (Brues 1924) and at temperatures as high as 35°C (Roback 1962). The chironomid *Polypedilum* occurred only at Sites 6 and 7 at Ringling, Sites 3 and 2 at Norris and Sites 3, 4 and 5 at Potosi. This genus has been known to be intolerant of temperatures below 4.4°C (Curry 1962) and may require the elevated temperatures of these sites.

No taxa were found to be unique to Site 1 at Ringling or Potosi or Site 3 at Norris. These sites represent the first mixing and cooling points of the three hot springs but do not appear to provide a unique ecological niche for the benthic fauna.

Most of the taxa collected during the study were considered to be eurythermal. Some of these taxa exhibited an ability to inhabit thermal extremes of 0 to 40°C. These extremely tolerant forms included the chironomids *Conchapelopia* and *Eukiefferiella*; the tubificids *L.*

hoffmeisteri and *P. ferox*; and the snails *Physa* and *Lymnaea*. All of these forms have been known to tolerate a wide range of temperatures as well as other environmental conditions. The majority of the eurythermal forms were more restricted to thermal extremes of 0 to a 30-36°C range. Although most north temperate mayflies are considered to be cool or cold water forms; *T. minutus*, *C. albiannulata*, *C. simulans* and *E. inermis* were included in this broadly tolerant group. Brues (1932) collected two other mayfly genera, *Baetis* and *Leptophlebia*, at temperatures of 32.8 and 33.0°C. Several caddis genera (e.g., *Hydropsyche*, *Cheumatopsyche* and *Brachycentrus*) were included in this tolerant grouping. Roback (1962) found most species of *Hydropsyche* and *Cheumatopsyche* to be tolerant of temperatures to 35°C while *Brachycentrus* was not found above 28°C. The majority of the chironomid genera exhibited a broad range of thermal tolerance. Most chironomids have been found to exhibit a range of tolerance of 0 to 32°C while some of the genera collected in the present study (e.g., *Procladius*, *Cryptochironomus*, *Paratendipes* and *Cricotopus*) have been known to tolerate temperatures as high as 34 to 40°C (Curry 1962).

The selection of sites at approximately 5°C increments within the thermal gradients did not reveal communities unique to each sample site. The data suggest, however, that at least four major communities were found in the thermal gradients. The two largest communities, the eurythermal and cold stenothermal faunas, could probably be further

subdivided on the basis of temperature range. The hot and intermediate stenothermal groups may be true examples of uniquely thermal communities. Armitage (1961) investigated the thermal responses of 32 taxa from the Firehole River and concluded that three basic communities were present. The taxa were categorized as exhibiting a cold preference, a warm preference or no preference within the thermal gradient. In a comparison of a heated and cold riffle in the Gibbon River, Vincent (1966) found 41 of 54 taxa common to both riffles while nine were found only in the cold riffle and four were unique to the heated riffle.

Analysis of frequency of occurrence data was most useful in determining patterns of thermal preference for eurythermal taxa. Results revealed four patterns of response within the eurythermal forms. A method of faunal classification that used relative average weights, rather than frequencies of occurrence, was employed by Armitage (1961) on the Firehole River. This method revealed similar groupings with the exception that the largest group in the present study, forms that occurred with the highest frequency at intermediate temperatures, was not observed by Armitage.

Comparison Of Sites Within The Thermal Gradients

A comparison of thermal sites utilizing an index of similarity indicated that strong faunal zonation did not occur at the approximate 5°C increment. This was reflective of the dominance of eurythermal

forms at Ringling and Potosi. A subtle zonation was evidenced through the various alliances of sites closest in temperature, e.g., Sites 1 and 6 at Ringling. The strongest points of differentiation occurred between the hottest sites capable of supporting macroinvertebrate communities and all other sites. Jones (1967) used a coefficient of similarity (C) to compare stations in the Firehole River and found that all stations except those above 43°C exhibited a high degree of similarity. Langford and Aston (1972) found no change in diversity up to 28°C in a series of stations within a power plant effluent. Other researchers have determined that normal invertebrate communities can exist at temperatures up to 32°C in north temperate streams (Bush et al. 1974, Coutant 1962).

Another point of differentiation occurred at Norris between Site 3 and all other sites. The lack of similarity between this site and the cooler sites is attributable to the dominance of cold stenothermal forms at Norris.

Potosi resembled Ringling in that most of the sites were found to bear a close similarity to each other; however, in contrast with Ringling, it was the coolest, rather than the hottest, site that was differentiated from the others. This may be due to the near constant temperatures present at Potosi or the adaptation of a more thermally acclimated fauna.

Both Sites 2 and 8 at Ringling were more similar to Site 1 than Sites 6 and 7. This apparent contradiction may be due to drift into Site 1 from cooler areas upstream. Invertebrate drift has been shown to interact with or be influenced by temperature. Some studies have shown a positive correlation between temperature and drift (Bisson and Davis 1976, Waters 1968) while others have found a negative correlation (Pearson and Franklin 1968). Durrett and Pearson (1975) indicated that drift may have a method of thermal avoidance in a power plant effluent channel. In contrast with the above information, several studies have found that temperature had little or no effect on invertebrate drift (Bishop and Hynes 1969, Cloud and Stewart 1974, Reisen and Prins 1972, Wojtalik and Waters 1970).

Comparison Of The Thermal Gradients

Some physical and temporal differences existed between the three study areas that may help to explain some of the faunal differences that were observed. The spring at Norris produced a small easily avoided plume into Hot Spring Creek whereas the heated gradients produced at Ringling and Potosi were quite large relative to the study areas. Another point of difference concerns the observed stability of temperatures at Potosi while sites at Ringling and Norris were subject to a seasonal range in thermal regime that increased with the distance of the site from the hot spring source. Finally, the man-made spring at Ringling had been producing a thermal gradient for 45 years whereas

the Norris and Potosi gradients had been produced for long periods of time.

Ringling and Potosi were dominated by eurythermal forms while Norris was dominated by the cold stenothermal fauna. This was supported by the high degree of similarity found between most stations at Ringling and Potosi while the cold stations at Norris bore little similarity to Site 3 at the head of the thermal plume. This suggests a strategy of thermal avoidance, rather than adaptation, on a community level. This suggestion is supported, in part, by the responses of several taxa common to two or all three study areas. Nine of the taxa that were classified as cold stenotherms at Norris were found to be eurythermal at Ringling or Potosi. Some of these different responses could be due to species differences when the generic level was treated in the comparison.

A major difference between Ringling and Potosi was observed in the similarity of Site 2 at Potosi to most other sites and the lack of similarity of Site 3 at Ringling to all other sites. These two sites had similar mean temperatures. Conversely, the coolest site at Potosi was sharply differentiated from others within the plume while the upper and lower cold sites at Ringling were quite similar to other sites in the plume. This may be a function of the time required for a community to fully adapt to high temperatures. It is possible that 45 years is not enough time for the adaptation of a large community at Site 3 at

Ringling. It is also possible, however, that these differences are due to the thermal stability or the different water chemistry of the sites at Potosi.

Several taxa common to Ringling and Potosi showed different thermal responses that support these assumptions. *Microcylloepus pusillus*, *Rheotanytarsus*, *Hyalella azteca* and *Limnodrilus udekemianus* were all capable of inhabiting Site 2 at Potosi but were absent from Site 3 at Ringling. Nebecker and Lemke (1968) suggested that longer adaptation time at high temperatures would raise the 96 hr TLM values for many species. Martin and Gentry (1974) found that *Libellula* nymphs collected from a thermal effluent exhibited a significantly higher Critical Thermal Maximum (CTM) and Lethal Temperature (LT) than nymphs of the same genus from a control stream.

Total Numbers Of Invertebrates

Numbers of invertebrates in the Ringling and Norris riffle samples were strongly depressed as temperature increased. Similar numerical depressions at high temperatures were observed by Coutant (1962) and Masengill (1976) in power plant effluents. Contrasting data was presented by Benda and Proffitt (1974), Dahlberg and Conyers (1974), Howell and Gentry (1974) and Vincent (1966) who found numerical increases at higher temperatures.

Samples from pools at Ringling and Norris and the samples from Potosi did not reveal as strong a numerical reduction with temperature

increase as was revealed in the riffle samples. This may be reflective of the apparent higher thermal tolerance of inhabitants of slower flowing waters (Wurtz 1969).

Despite faunal similarities between the upper and lower cold sites at Ringling, large numerical differences existed between the two. The mean number of organisms per sample from Site 2 places it mid-way between Sites 1 and 6 rather than equal to Site 8 as might be expected. This is possibly due to chemical enrichment from the hot spring and/or physical differences such as stream size and flow.

Population estimates of the invertebrate communities of Ringling, Norris and Potosi were made by putting the mean number of invertebrates per sample on a per square meter basis (Table 26). Riffle populations

Table 26. Mean numbers* of invertebrates per m² at Ringling, Norris and Potosi.

Sample Site	<u>3</u>	<u>1</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>2</u>
Ringling Surber	1032	2221	4867	11570	15110	3674
Ringling Ekman	972	1883	2361	3474	2872	2997
Sample Site	<u>6</u>	<u>5</u>	<u>3</u>	<u>2</u>	<u>1</u>	<u>4</u>
Norris Surber	4	10	263	348	3675	4371
Norris Ekman	13	4	2765	1849	1905	1647
Sample Site	<u>2</u>	<u>1</u>	<u>3</u>	<u>4</u>	<u>5</u>	
Potosi Edman	1699	959	882	1570	1324	

* rounded to the nearest whole number

of 11,570 and 15,110 invertebrates per square meter at Sites 7 and 8 at Ringling can be compared with Baril's (1977) estimate of 6,007 per m² on Rosebud Creek which was believed to be rich in invertebrate numbers when compared with other Montana streams.

Numbers Of Taxa Present

The mean numbers of taxa per sample were generally depressed as temperature increased. A similar negative correlation between numbers of taxa and temperature was observed by Coutant (1962) in a series of samples taken at 5°F (2.8°C) increments in the Delaware River. Howell and Gentry (1974) observed an increase in species diversity as temperature decreased. Hopwood (1974), however, found no difference in numbers of taxa between cold stations and stations within a thermal plume in the Mississippi River.

Abundance At The Ordinal Level

Most of the major orders demonstrated a negative numerical response to temperature. Exceptions were shown by the Coleoptera, Pulmonata and Haplotaxida which increased in number with temperature. Howell and Gentry (1974) found that numbers of Ephemeroptera, Plecoptera and Trichoptera decreased while numbers of Diptera increased with temperature in a thermal plume. Hopwood (1974) found that Ephemeroptera and Diptera responded negatively to temperature while Trichoptera numbers increased as temperature increased. Vincent (1966) found numbers of Ephemeroptera and Coleoptera to be highest in

a cold riffle while numbers of Diptera increased in a heated riffle and Plecoptera numbers remained about the same in both riffles in the Gibbon River. Masengill (1976) found that oligochaetes increased in number as temperature increased in a thermal plume in the Connecticut River. This variability of response at the ordinal level may be indicative of the varying thermal regimes of the various areas that were studied or may indicate that the ordinal level is not fine enough to detect thermal effects because of the variable thermal tolerances of the genera and species within an order.

Abundance At The Genus-Species Level

Most of the taxa that showed significantly different mean numbers at Ringling and Potosi reached maximum abundance at intermediate or high temperatures while the majority at Norris were most abundant at low temperatures. This would suggest a better thermal adaptation at Ringling and Potosi and thermal avoidance at Norris.

With few exceptions, patterns of abundance followed patterns previously established by frequency of occurrence analysis.

Cheumatopsyche, *Baetis* sp. B, *Dicrotendipes* and *Pelosclex ferox* deviated from this trend and achieved their maximum abundance at intermediate temperatures. This is probably indicative of a range of thermal optimum within a broader range of thermal tolerance.

Correlation coefficients confirmed patterns of abundance established by the site means for those taxa that achieved maximum

abundance at low or high temperatures. All of the taxa that achieved their maximum numbers at intermediate temperatures were found to be correlated in a weakly negative manner with temperature. This is indicative of a greater abundance at the lower rather than the higher extremes and can probably be viewed as a more rapid numerical decline at supra-optimal rather than sub-optimal temperatures.

Several taxa reached maximum abundance at high temperatures suggesting a high thermal optimum. *Procladius* and *Cladotanytarsus* have been known to exhibit a high thermal tolerance (Curry 1962). *Limnodrilus hoffmeisteri* has been observed to be the most numerous organism in the hottest sites in power plant effluents (Langford and Aston 1972, Masengill 1976). *Physa* was observed to increase with temperature in the Firehole River (Jones 1976) and was found to be one of the most important trout foods in a heated section of the same stream by Kaeding (1976).

Three species of *Hydropsyche* reached maximum numbers at lower temperatures. This genus has been known to be tolerant of high temperatures (Roback 1962) and was one of the numerically dominant organisms collected in a thermal plume in the Mississippi River (Hopwood 1974). This apparent contradiction is probably due to species differences within the genus.

Maximum abundance at intermediate temperatures was observed for several species of mayflies. Baril (1977) found three of these species;

Choroaterpes albiannulata, *Tricorythodes minutus* and *Caenis simulans*, to be capable of withstanding extreme conditions of slow flows, high turbidity and high summer temperatures in Rosebud Creek. *Cheumatopsyche* also reached maximum abundance at intermediate temperatures. This genus has been found to be tolerant of high temperatures as well as a wide range of other physical and chemical conditions (Roback 1962).

Seasonal Variations

Both water temperature and macroinvertebrate abundance fluctuate on a seasonal basis. The multifactor analysis of variance that was utilized partitioned variation due to season, temperature and the interaction between the two. The effect of the interaction on macroinvertebrate abundance is difficult to interpret since no interaction means can be calculated. An example of an interaction is presented (Figure 12) and shows that mean numbers of taxa do not respond the same to levels of one factor (temperature) when taken over all levels of the other factor (season). The mean number of taxa increased between the fall and winter samples for Sites 6 and 7 at Ringling while the number of taxa at Site 8 underwent a drastic reduction in the same period. A significant interaction in the present study could be interpreted as a disruption in the normal patterns of seasonal abundance by temperature. The interaction between temperature and season was found to significantly effect total numbers of invertebrates, numbers of taxa present, and abundance at the ordinal and genus-species levels.

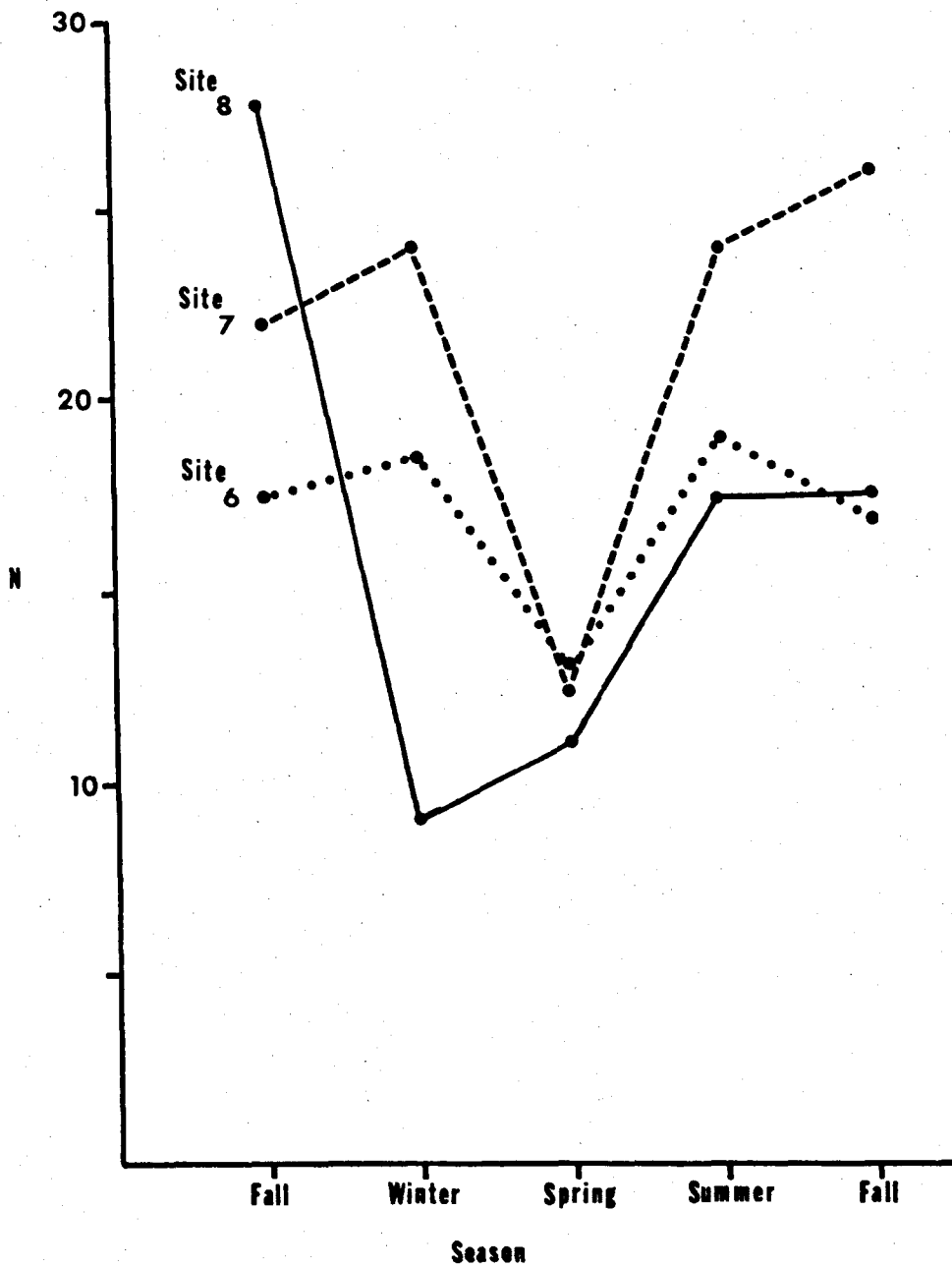


Figure 12. Interaction between temperature and season as it affects number of taxa per sample (N) collected from selected sites at Ringling.

Seasonal variation has been observed in the qualitative and quantitative recovery of invertebrate populations during the winter in thermal plumes. Coutant (1962), Masengill (1976) and Trembley (1962) noted such recoveries in power plant effluents. Winter correlation coefficients, with the exception of the Norris Ekman samples, do not indicate such recovery for the total number of invertebrates or the number of taxa present. This may be a function of the distance between cold and heated sites at Ringling, extreme thermal differences between cold stations upstream and stations in the plumes at Ringling and Norris or the thermal stability of the Potosi sites.

The previously mentioned winter reduction in taxa at Site 8 at Ringling was accompanied by a reduction in total number of invertebrates. These reductions were observed only in the riffle samples and not in those from the pool. These changes were believed to be the result of frazil or slush ice which was observed moving through the riffle on several occasions during the winter of 1974-1975. A similar reduction of a riffle population by frazil and anchor ice was observed by Reimers (1957) and Vincent (1966). Benson (1955) observed entrapment and movement of invertebrates in anchor ice but did not think that numbers were large enough to significantly alter a riffle population.

Standing Crop (Biomass)

The relative productive capacities of stations within the thermal gradient at Ringling were estimated, in part, through the calculation of standing crop as mean biomass per sample. Biomass was found to be substantially increased as temperature decreased. The spring samples provided an exception to this trend with a positive correlation. This was due to an abnormally high biomass present at Site 3 as a result of a large population of gastropods. Similar negative correlations of biomass with temperature were observed by Bisson and Davis (1976) and Coutant (1962). Contrasting data was presented, however, by Armitage (1958) and Vincent (1966) who found that biomass increased with temperature. Although Armitage did find a positive correlation between biomass and temperature (+.386), the correlation was not significant. He did, however, find a highly significant correlation (+.839) between biomass and alkalinity.

Differences in standing crops over an interval of time have been used as indices of animal production (Cummins 1972). Armitage (1958) believed that the difference between minimum and maximum standing crop was indicative of the minimum production over that period of time. It is believed, however, that animal standing crop is relatively constant over a long period of time and that rates of assimilation and exchange between trophic levels and turnover times of various components are the critical factors in stream production (Cummins 1972). Thus, the

smaller standing crops at higher temperatures are not necessarily an indication that production is higher at the cooler sites.

Colonization Rates

Macroinvertebrate numbers and biomass were related to the rate of deposition or colonization on denuded Hester-Dendy artificial substrates. Investigations have related the colonization of artificial substrates with time, thus putting standing crop on a rate related basis. Sheldon (1977) found rate of colonization to fit a power function and found it to be correlated more often with time than with other factors. Nilsen and Larimore (1973) found that colonization rates for both number and weight followed a sigmoidal curve which began with a lag phase of about two weeks, a rapid exponential growth period of about two weeks and a leveling off at about four to six weeks after the carrying capacity or an equilibrium condition was reached. If the assumption is made that the mechanisms of colonization such as direct transport or drift (Waters 1968) are in operation at an equal level throughout the colonization period, then the lag and subsequent rapid growth phases should be related to the acceptability of the sampler as a colonizable substrate. A further assumption could be made that the criteria for the acceptability of a bare substrate for macroinvertebrate colonization would be related to the growth of bacteria, periphyton and filamentous algae and the subsequent entrapment of microorganisms and detritus as a source of shelter and food. Williams

et al. (1977) found that recolonization of a substrate was accomplished, first, by detritivores, followed by periphyton grazers and predators and concluded that colonization was related to the accumulation of various types and sizes of food particles. In this manner, the colonization of bare artificial substrates was related to the productive capacity of a station at which it was placed provided it was harvested prior to equilibrium.

Despite negative correlations existing between standing crop and temperature, colonization rates of the plates were found to increase, up to a point, with temperature. Low colonization rates at Site 3 probably do not reflect the acceptability of the plates for colonization due to the low numbers of invertebrates present and the absence of taxa that showed a preference for the multiplate samplers. The high colonization rates at Sites 1 and 6 are probably indicative of a shorter time period required for the establishment of a suitable food supply for the invertebrates, and hence, a greater productive potential at the higher temperatures. Hopwood (1974) found that colonization rates of artificial substrates were changed enough by temperature to shift generic composition but statistical analysis showed no differences in the numerical rate of colonization between cold and heated sites.

Growth

Increased temperatures have been found to increase the growth rate of many larval insects. This relationship is based on a temperature summation theory in which a certain number of degree days above a temperature of zero growth are required for a larval insect to complete its development (Newell 1975). The temperature-growth relationship may be limited on the upper end by a temperature that is supra-optimal for growth due to the high caloric cost of maintenance (Nebecker 1971c, 1973). Increased larval growth rates may result in early emergence (Nebecker 1971a, Newell 1975) although some species have been found to have other methods for the synchronization of emergence (Lutz 1968, Nebecker 1971b). When early emergence accompanies increased larval growth rates, the result may be a bivoltine or multivoltine population of a species that is univoltine under normal conditions (Newell 1976). This shortened generation time can increase the productivity of a body of water (Nebecker 1971a).

Differences in growth were observed through an estimate of the mean weights of selected genera from the Ringling samples. This comparative method was based on the assumption that different mean weights between sites were indicative of a different timing in the sequence of generations or of different growth rates and thus related to different rates of secondary production. All of the investigated taxa exhibited different mean weights at different thermal sites with

most attaining maximum mean weights at the hotter sites; this suggests that differences in production rate existed at the various temperatures. The growth increment for the 10 taxa common to Sites 6 and 7 was found to be 11 times greater at Site 6 than at Site 7 between the fall 1974 and winter samples. This indicates a higher rate of assimilation, and hence, a higher rate of production at the warmer winter temperatures of Site 6. Hopwood (1974) found higher mean weights in a heated effluent than at cold stations, for selected invertebrate groups in three of seven 35 day periods.

Thermal effects on growth were further investigated through length frequency analysis. The presence of a full range of sizes, including individuals that appeared near to emergence, of *Tricorythodes minutus* and *Choroterpes albiannulata* at the warmer sites indicated that rapid development was accompanied by a shortened generation time. Newell (1976) found that *T. minutus* was bivoltine at colder study sites while a population in a constant temperature spring was multivoltine. *Hyaella azteca* exhibited a shift toward larger instars at higher temperatures while *Cheumatopsyche* showed no shift in size at any thermal site. This may indicate a strong thermal tolerance that was previously demonstrated by its frequency of occurrence and percent contribution responses. The three modes may be indicative of three cohorts of a single species or three different species of the genus.

Results suggest that secondary production rates may be increased at higher temperatures at Ringling. Brock (1967) investigated primary production in a hot spring gradient that ranged from 30 to 70°C. He found that while standing crop was greatest at intermediate temperatures in the range under study, photosynthetic efficiency continued to increase as the temperature increased to 70°C. An increase in primary and secondary production at elevated temperatures may result in increased production at higher trophic levels. Kaeding (1976) theorized that large populations of molluscs, emerging insects and a general good food availability may have been responsible for better trout growth in a heated section than in cold water in the Firehole River.

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APPENDIX

Table 27. Mean daily maximum, minimum and median temperatures (°C) per month and monthly maxima and minima measured from February 1975 through January 1976 at Ringling.

SITE 3	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan
Maximum	35.0	36.0	34.0	37.0	37.0	41.0	40.0	43.0	35.0	34.0	34.0	35.0
Mean Maximum	34.0	34.1	33.7	33.0	34.7	38.7	40.2	39.2	34.4	33.5	33.5	34.1
Mean Median	32.4	32.5	32.0	32.1	33.4	37.2	37.1	37.6	33.4	32.0	32.0	32.2
Mean Minimum	30.7	30.9	30.3	31.2	32.0	35.7	35.0	36.0	32.4	30.4	30.4	30.2
Minimum	29.0	29.0	30.0	30.0	31.0	33.0	33.0	35.0	32.0	30.0	30.0	29.0
SITE 1												
Maximum	29.0	29.0	30.0	29.0	27.0	36.0	36.0	36.0	34.0	26.0	23.0	28.0
Mean Maximum	26.6	28.4	27.0	20.6	21.4	33.5	33.6	33.4	28.1	23.4	21.3	23.0
Mean Median	24.8	25.1	24.8	19.4	19.5	31.0	31.5	31.6	27.2	22.4	20.2	20.9
Mean Minimum	23.0	21.7	22.6	18.2	17.5	28.4	29.3	29.8	26.2	21.4	19.1	18.8
Minimum	21.0	19.0	20.0	17.0	10.0	26.0	26.0	27.0	23.0	15.0	17.0	14.0
SITE 6												
Maximum	19.0	22.0	23.0	24.0	23.0	32.0	32.0	32.0	26.0	20.0	18.0	21.0
Mean Maximum	16.4	19.3	20.4	15.7	16.5	28.3	29.4	27.7	22.1	18.2	15.5	15.8
Mean Median	13.9	17.0	18.0	13.9	14.4	26.2	27.2	24.7	21.0	16.9	14.2	13.8
Mean Minimum	11.3	14.7	15.6	12.0	12.2	24.1	25.0	21.7	19.8	15.6	12.9	11.7
Minimum	9.0	12.0	14.0	10.0	6.0	20.0	22.0	20.0	16.0	11.0	10.0	9.0
SITE 7												
Maximum	14.0	15.0	17.0	20.0	21.0	27.0	28.0	28.0	19.0	14.0	14.0	12.0
Mean Maximum	11.3	12.6	14.0	12.8	13.0	23.9	23.7	20.1	13.8	10.0	8.4	8.7
Mean Median	8.6	9.7	12.2	10.6	12.0	21.3	21.0	17.0	12.7	8.6	6.9	6.7
Mean Minimum	5.9	6.8	10.4	8.4	11.0	18.7	18.3	13.8	11.5	7.1	5.4	4.7
Minimum	4.0	5.0	9.0	7.0	5.0	15.0	17.0	14.0	8.0	5.0	2.0	3.0
SITE 8												
Maximum	7.0	10.0	12.0	17.0	18.0	21.0	22.0	23.0	14.0	10.0	9.0	7.0
Mean Maximum	4.3	7.0	9.0	11.4	11.1	18.6	18.0	16.2	8.9	4.3	4.0	3.9
Mean Median	3.2	5.3	7.3	9.5	9.6	16.4	16.6	14.7	7.7	3.4	3.2	2.8
Mean Minimum	2.1	3.6	5.5	7.6	8.0	14.2	15.2	13.1	6.4	2.5	2.4	1.6
Minimum	0.0	2.0	4.0	6.0	5.0	12.0	14.0	7.0	3.0	0.0	0.0	0.0
SITE 2												
Maximum	7.0	9.0	11.0	16.0	18.0	20.0	24.0	24.0	13.0	12.0	8.0	7.0
Mean Maximum	4.7	6.7	8.8	11.0	11.7	18.5	19.0	15.9	8.7	4.8	4.1	3.6
Mean Median	3.6	4.9	7.0	9.3	10.0	16.4	17.4	14.0	7.4	3.9	3.5	2.7
Mean Minimum	2.4	3.1	5.2	7.6	8.3	14.3	15.8	12.0	6.1	2.9	2.8	1.7
Minimum	1.0	2.0	4.0	6.0	6.0	12.0	12.0	7.0	3.0	1.0	0.0	1.0

Table 28. Taxa collected within the undiluted flows of the hot springs at temperatures above 30°C at Ringling, Norris and Potosi.

Collembola	Stratiomyiidae
<i>Isotomurus</i> sp.*	<i>Eulalia</i> sp. ^a
	<i>Stratiomyia</i> sp. ^a
Hemiptera	Muscidae*
Naucoridae	
<i>Ambrysus heidemanni</i> Montandon* ^a	Haplotaxida
	Tubificidae
Coleoptera	<i>Limnodrilus hoffmeisteri</i> Claparede
Dytiscidae	<i>L. udekemianus</i> Claparede
<i>Agabus</i> sp.* ^a	<i>Peloscolex ferox</i> (Eisen)
Curculionidae*	
Elmidae	Pulmonata
<i>Microcylloepus pusillus</i> (LeConte) ^a	Physidae
	<i>Physa</i> ^a
Diptera	Lymnaeidae
Chironomidae	<i>Lymnaea</i> ^a
<i>Conchapelopia</i>	
<i>Rheotanytarsus</i>	Ostracoda
<i>Acricotopus</i>	Cypris sp.* ^a
<i>Eukiefferiella</i>	
<i>Lymnophyes</i> *	Amphipoda
<i>Paraphaenocladus</i> *	Talitridae
<i>Pseudosmittia</i> *	<i>Hyaella azteca</i> (Saussure) ^a
Ceratopogonidae	
<i>Atrichopogon</i> *	
<i>Tr. Stilobezziini</i>	

* collected only at temperatures above 30°C

^a also collected in hot springs by other researchers

Table 29. Genus-species frequency of occurrence (X 100) in pooled samples collected by all sampling methods at thermal levels composed of sample sites at Ringling, Norris and Potosi with similar temperature regimes.

	Thermal Levels*					
	1	2	3	4	5	6
Collembola						
<i>Isotomurus</i> sp.	0.0	0.0	-	0.0	1.4	0.0
Ephemeroptera						
<i>Ameletus cooki</i>	3.1	0.0	-	0.0	0.0	-
<i>Baetis</i> sp. A	28.1	41.1	35.0	7.1	0.0	0.0
<i>Baetis</i> sp. B	1.6	31.3	25.0	0.0	0.0	0.0
<i>Callibaetis</i> sp.	1.6	3.1	0.0	0.0	0.0	0.0
<i>Choroterpes albiannulata</i>	29.7	32.8	34.4	18.8	0.0	0.0
<i>Paraleptophlebia heteronea</i>	25.0	25.0	-	12.5	0.0	-
<i>Ephemerella grandis</i>	3.1	0.0	-	0.0	0.0	-
<i>E. inermis</i>	56.3	37.5	-	31.3	0.0	-
<i>E. infrequens</i>	1.6	9.4	0.0	0.0	0.0	0.0
<i>Tricorythodes minutus</i>	19.2	26.8	27.5	5.3	0.0	0.0
<i>Caenis simulans</i>	31.3	40.6	40.6	25.0	0.0	0.0
Odonata						
<i>Erythemis</i> sp.	0.0	37.5	0.0	12.5	0.0	-
<i>Ophiogomphus</i> spp.	17.3	14.3	27.5	17.5	0.0	0.0
<i>Aeschna umbrosa</i>	3.1	6.3	0.0	0.0	0.0	0.0
<i>Argia</i> sp.	0.0	25.0	0.0	12.5	0.0	-
<i>Ischnura</i> spp.	12.5	21.9	6.3	18.8	0.0	0.0
Plecoptera						
<i>Nemoura</i> sp.	12.5	0.0	0.0	0.0	0.0	-
<i>Pteronarcella badia</i>	62.5	0.0	-	6.3	0.0	-
<i>Arcynopteryx</i> sp.	25.0	0.0	-	0.0	0.0	-
<i>Diura knowltoni</i>	37.5	12.5	-	0.0	0.0	-
<i>Isoperla fulva</i>	81.3	31.3	-	0.0	0.0	-
Hemiptera						
<i>Hesperocorixa laevigata</i>	1.0	0.0	0.0	0.0	0.0	0.0
<i>Sigara omani</i>	0.0	6.3	-	0.0	0.0	-
<i>Ambrysus heidemanni</i>	0.0	12.5	0.0	12.5	12.5	0.0

Table 29 (continued).

	Thermal Levels*					
	1	2	3	4	5	6
Trichoptera						
<i>Helicopsyche borealis</i>	7.7	17.9	2.5	5.4	0.0	0.0
<i>Polycentropus</i> sp.	12.5	15.6	9.4	6.3	0.0	0.0
<i>Cheumatopsyche</i> spp.	58.3	60.0	50.0	55.0	0.0	0.0
<i>Hydropsyche</i> sp. A	32.5	40.0	35.0	0.0	0.0	0.0
<i>Hydropsyche</i> sp. B	17.5	10.0	20.0	5.0	0.0	0.0
<i>Hydropsyche</i> sp. C	2.5	0.0	25.0	0.0	0.0	0.0
<i>Hydropsyche</i> sp. D	21.9	12.5	-	12.5	0.0	-
<i>Hydroptila</i> spp.	10.9	6.3	9.4	6.3	0.0	0.0
<i>Oxyethira</i> sp.	0.0	12.5	0.0	12.5	0.0	0.0
<i>Chimarra</i> sp.	3.1	0.0	0.0	0.0	0.0	-
<i>Oecetis</i> sp.	3.1	0.0	0.0	0.0	0.0	0.0
<i>Brachycentrus</i> sp.	53.1	25.0	-	12.5	0.0	-
<i>Micrasema</i> sp.	15.6	12.5	-	6.3	0.0	-
<i>Hesperophylax</i> sp.	4.7	0.0	0.0	0.0	0.0	0.0
Coleoptera						
<i>Agabus</i> sp.	0.0	0.0	0.0	0.0	3.1	0.0
<i>Deronectes</i> sp.	6.3	0.0	0.0	0.0	0.0	0.0
<i>Hydroporus</i> sp.	1.6	0.0	0.0	0.0	0.0	0.0
<i>Helophorus</i> sp.	1.6	3.1	0.0	0.0	0.0	0.0
<i>Tropisternus</i> sp.	0.0	0.0	0.0	12.5	0.0	0.0
<i>Curculionidae</i>	0.0	0.0	0.0	6.3	3.1	0.0
<i>Dubiraphia minima</i>	43.8	50.0	46.9	59.4	0.0	0.0
<i>Microcylloepus pusillus</i>	13.9	65.0	52.5	17.5	15.0	0.0
<i>Optioservus quadrimaculata</i>	35.4	14.6	21.9	16.7	0.0	0.0
<i>Zaetzenia parvula</i>	1.6	6.3	0.0	0.0	0.0	0.0
<i>Halplus</i> sp.	9.4	3.1	0.0	12.5	0.0	0.0
Diptera						
<i>Dicranota</i> spp.	3.1	4.2	0.0	2.1	0.0	0.0
<i>Hexatoma</i> spp.	43.8	18.8	12.5	0.0	0.0	0.0
<i>Tipula</i> sp. A	1.6	0.0	0.0	0.0	0.0	0.0
<i>Tipula</i> sp. B	3.1	0.0	0.0	0.0	0.0	0.0
<i>Tipula</i> sp. C	21.9	12.5	6.3	0.0	0.0	-
<i>Telmatoscopus</i> sp.	0.0	12.5	6.3	0.0	0.0	-
<i>Aedes</i> sp.	0.0	0.0	3.1	0.0	0.0	0.0
<i>Simulium</i> spp.	38.5	33.9	27.5	12.5	0.0	0.0
<i>Conchapelopia</i> spp.	29.8	37.5	60.0	33.9	6.9	0.0
<i>Procladius</i> spp.	8.3	10.4	12.5	8.3	0.0	0.0

