The Effect of Temperature on Growth and Development of the Mayfly Tricorythodes minutus Traver

by

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To the Graduate Faculty:

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ABSTRACT

The life history of the mayfly, Tricorythodes minutus Traver was investigated at two stations in Deep Creek, Curlew Valley, Idaho-Utah, and one station in Spring Creek, Bingham Co., Idaho. Station 2 on Deep Creek has a spring source and a constant temperature of 18°C while station 4 has a normal seasonal fluctuation in water temperature. Spring Creek also has a spring source with a temperature regime intermediate between the other stations. T. minutus has a multivoltine life cycle at station 2 in Deep Creek and is bivoltine at the two other stations. Nymphs are detritivores and are distributed widely throughout Idaho and other western states. Adults are very short lived and females can carry up to 1500 eggs. Ecclosion and survival are directly dependent upon temperature. Allometric and absolute growth also were examined in the field and laboratory at several temperatures. Growth of various size classes is approximately sigmoidal reaching a peak of growth at about 4.0 mm in length. Growth is also sigmoid as temperature increases reaching an asymptote at 23°C. Growth rate was converted to mm/degree hours by means of the temperature summation technique. Most rates were similiar following conversion and agreed well with population growth rate measurements and duration of development. The best fit curve of all growth curves was determined by polynomial regression analysis as $Y = -0.125 + 0.178X + 0.023X^2$ where X= total length and Y= growth rate. This insect requires about 25,000°h to complete one life cycle.

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INTRODUCTION

Scientists constantly strive to predict the outcome of particular biological events given the values of certain environmental variables and the knowledge gained from past experience and research. Aquatic biologists have examined life-histories of many aquatic invertebrates and can with limited accuracy predict the growth rate and emergence of some of them. Their predictive ability is limited generally to insect species that have been observed emerging in past years and to a single stream or a few neighboring streams. At present there is no method available to predict the growth and emergence of an insect over its entire geographical range. The ability to predict growth rates and emergence would be of enormous value in productivity studies, especially when large numbers of species would make individual studies impossible. In addition, knowledge of emergence could be invaluable in studies of certain pollutional factors which might be influencing emergence and growth.

Southern Idaho contains an abundance of springs, many of which form streams (rheocrenes) whose temperature is constant or nearly so. This author has observed continuous emergence patterns in many species of aquatic insects inhabiting these spring streams. The observation of extended emergence in constant temperature streams, most of which are from 10-20^{o}C led the author to hypothesize, as others have, that for some aquatic insects duration of the life cycle and timing of emergence are directly related to water temperature. Knowledge of the hourly water temperature may permit prediction of growth and emergence of

those species. If these relationships could be expressed in general equations, such as those relating growth to temperature or time, one could considerably reduce the number of necessary measurement in studies of specific populations.

Life history studies are important as they may aid in the understanding of complex aquatic ecosystems. Multivoltine life cycles have been infrequently reported and studies of this rare phenomenon are infrequent, possibly because the overlapping nature of generations can be determined only by careful laboratory and field studies.

Tricorythodes minutus Traver was selected for investigation for several reasons: (1) it is widely distributed throughout southern Idaho; (2) although generally univoltine, it can have a multivoltine life cycle under some conditions, with all stages of the life cycle present during all months of the year; (3) the nymphs are easily maintained in the laboratory; and (4) its life cycle and ecology have not been investigated.

The objectives of this research were: (1) to determine the life history of T. minutus in a natural stream under relatively constant warm temperatures as well as normal, seasonally fluctuating conditions; (2) to examine all aspects of the life history of T. minutus with emphasis on growth, both allometric and absolute, as a function of temperature; and (3) to formulate a mathematical expression to predict growth rate and emergence under natural environmental conditions and to test the expression by comparing laboratory experiments to field results.

LITERATURE REVIEW

The literature on Ephemeroptera life history studies, growth, and thermal effects is extensive and diverse. The literature will be reviewed to illustrate the author"s research, which was designed to fill gaps that exist.

The genus Tricorythodes is one of six genera in the subfamily Leptohyphinae of the family Tricorythidae. Of these six genera only two, Tricorythodes and Leptohyphes are known from North America, the other genera being found in Africa and Central and South America (Traver 1958, Allen 1967). Spieth (1933) considered Tricorythodes to be an aberrant member of the Ephemerella. Edmunds (1972) suggested that the Tricorythidae were derived from the Ephemerellidae and probably evolved in Africa, since many subfamilies of the Tricorythidae are endemic to the Ethiopian realm. Until 1945, the Tricorythidae and Caenidae were classified as a single family but most workers now believe the Tricorythidae evolved from the Ephemerellidae and are not allied to the Caenidae, even though they have several common morphological characteristics (Edmunds 1972).

McDunnough (1931) changed the generic designation from Tricorythus to Tricorythodes and listed five species in the U.S. and Canada. Needham et al. (1935) listed eight species of Tricorythodes, while Edmunds and Allen (1957) and Berner (1959) each listed ten species from North America. Jensen (1966) claimed that Tricorythodes minutus was the only species of that genus found in the western United States. Since then, Allen (1967) has described T. condylus from Arizona and T. edmundsi from Utah.

Tricorythodes minutus is known to occur in Colorado (Argyle and Edmunds 1962), Utah (Needham and Christenson 1927, Pearson et al. 1968, Winger et al. 1972), Montana (Newell 1971), Washington (Allen, personal communication), and Oregon and Idaho (Jensen 1966). The author has collected this species in many streams of southeastern Idaho.

Recorded ecological studies have not been found for any species of this genus. However, personal observations and published comments indicate Tricorythodes nymphs prefer backwater areas of large rivers and silty areas of smaller streams (Needham et al. 1935, Argyle and Edmunds 1962, Pearson et al. 1968). Some information on the emergence and general morphology of this genus is available in popular literature (e.g.,Swisher and Richards 1971), since this genus is popular among fly fishermen. Some north temperate species of Tricorythodes emerge in July and August (Clemens 1912, McDunnough 1931, Burks 1953, Jensen 1966), while Mexican species emerge in December and January (Traver 1959). Some South American species emerge in January and November (Traver 1959).

All of the species are small (3-7 mm), with three cerci and with gills on abdominal segments two through six. The anterior gill forms a protective shield or operculum. The species is very pubescent, with many small hair-like setae covering all parts of the body. The nymphs are tan to brown in color, while the adults are generally black.

As previously stated, no ecological life history studies have been done on Tricorythodes. The ecological life history outline used by Brinck (1949) and Hynes (1970) was followed for this study. This type of approach has been used by many authors including Ellis (1961), Minshall (1967), and Tarter and Krumholz (1971).

Many life history studies have been done on aquatic insects, but ecological life history studies are much less frequent. The emphasis of many past studies has been determining the duration of the life cycle and the course of events from egg to adult. Investigators usually have been content to approximate the life history of insect species from periodic samples. The method commonly used is based upon increases in body length as a growth criterion. Either mean length is plotted against time, (e.g.,Corbett 1957, Kormondy and Gower 1965) or age structure and growth are represented by a series of length (or instar) frequency histograms (e.g. Hanna 1957, Lutz 1968). Neither of these methods will work for a multivoltine species because of the presence of two or more generations at one time. Unfortunately, for critical work where accurate assessment of growth rate is desired, body measurements are not precise because of differences in contraction and extension of the abdomen during preservation. Clifford (1970a) believes that no single linear dimension is least variable for both males and females. For mayfly life history phenomena, head length (or width) and pronotum width seem to be the most desirable linear measurements, and mesonotum length appears to be least desirable. Males and females should be measured separately.

Previous life history studies have used instars, age classes, or life stages to describe the major features of development. Clifford (1970a) and Lemkuhl (1970) were unable to distinguish instars and so arbitrarily adopted life stages based on the amount of development of the wing pads. Ide (1935b) utilized an "X" factor which represented the ratio of mesothoracic wing-pad length to length of the seventh tergite.

The results were clumped enough to distinguish instars. For many species of insects the number of instars can be determined by measuring head length or width, plotting these data against frequency of occurrence and noting the most common widths. This procedure does not work well for mayflies, possibly because the nymphs may have a variable number of molts, making it impossible to estimate the instar number from head capsule measurements (Clifford 1970b). Another method of determining the number of instars is to rear the animals individually in the laboratory and count the number of cast skins (Clark and Hersh 1939, Rawlinson 1939, Ellis 1961). Ide (1935a) found the instar number corresponds to the number of antennal segments for young mayflies. Rawlinson (1939) showed that morphological changes between one instar and the next sometimes are slight. Changes which appear together in some nymphs occur in widely separate instars of others, making it impossible to define an instar on morphological characters. Rawlinson's (1939) investigations of Ecdyonurus venosus (Fab.) probably is the most thorough life history and morphological investigation of any mayfly done to date. A relatively new method of instar analysis is that of Janetschek (1967), used by Harper (1973) with limited success on Plecoptera.

Individual growth rates seldom have been accurately determined from field sampling, and laboratory studies are even less frequent. According to Benke (1970) this can be attributed to several factors: (1) the taxonomy of closely related species, especially for younger instars, is difficult in many groups; (2) often there is a problem in determining the age of the animals; (3) unbiased random samples often are difficult to obtain; and (4) the growth rates of some species cannot

be determined readily from field sampling owing to their asynchronous development.

There are three important quantitative aspects of growth (Simpson et al. 1963). The first deals with change in shape and will not be considered here. The second concerns the change in some dimension of an animal over time (velocity of growth). As an animal ages, the weight, surface area, and length of its various parts change in a fairly regular manner. This change comprises "growth" in its strictest sense. The third aspect is that of the relative sizes of two dimensions of a single animal (allometric growth). If there is some functional relationship between the magnitude of each of two dimensions and time, there will also be some function relating the two dimensions with each other, with time held constant. Although there have been several studies of growth rates of natural populations of aquatic insects (Ide 1935a, Moon 1939, Harker 1952, Maxwell and Benson 1963, Thorup 1963, Svensson 1966, Larsen 1968, Andersson 1969, Clifford 1970b, Lehmkuhl 1970 and, Harper 1973), none of these dealt with specific individuals. There have been a few laboratory investigations of growth rates (Ide 1935a, Clark and Hersh 1939, Rawlinson 1939, and Ellis 1961), but no comparisons were made between field and laboratory growth rates. Allometric growth studies are much less frequent. Clark and Hersh (1939) studied a hemipteran and Clifford (1970a) investigated allometric growth in a mayfly. Apparently no one has examined both aspects of growth in the laboratory and in the field simultaneously.

Temperature

Effects on communities: Most of the research on the effects of temperature on aquatic communities has been conducted on fish and marine invertebrates (Kennedy and Mihursky 1967) but there are exceptions (e.g. Minshall 1967). Coutant and Goodyear (1972) have produced an excellent review of temperature effects on aquatic organisms. Much of the information available on freshwater macroinvertebrates is scattered through the literature and in need of synthesis. Coutant (1962) found a reduction from upstream values in the number, diversity, and biomass of macroinvertebrates in the Delaware River. Ide (1935a) and Kamler (1965) have also reported similiar faunal reductions due to increased temperatures.

Thermal tolerance: Thermal tolerance is a necessary consideration in an ecological life history study. It is important to know at what temperature growth slows and finally ceases and the range of temperatures the species can tolerate. Thermal resistance varies greatly between species and appears dependent upon thermal history and phylogeny. In the laboratory Whitney (1939) studied the thermal resistance of six species of mayflies and found their upper median temperature limit varied from 20-30°C. Nebeker et al. (1968) found the 96 h median tolerance limits for two species of mayflies were 21.5°C and 25.5°C, respectively. Gaufin and Hern (1971) found the median tolerance for one species of mayfly to be as low as 11.7°C.

Effects on growth and development: Poikilothermic organisms complete their development more rapidly in warm water than in cold. The speed of development at different constant temperatures has been measured for many insects, mostly terrestrial forms. Terrestrial insects do not always respond to temperature rises positively because of additional weather factors, e.g. humidity. Aquatic insects are affected by fewer weather parameters and, in the temperate zone, are subjected to a rather definite yearly temperature regime (Macan 1958, Edington 1966, Hynes 1970). The temperature in winter is near or at zero for several months, rising to summer maxima usually between 20°C and 30°C. Aquatic insects react differently to seasonal temperature fluctuations. For some species metabolism seemingly is unaffected by the cold winter temperatures and the major growth period occurs during this time (Gledhill 1959, Maxwell and Benson 1963, Thorup 1963, Minshall 1967, and Larsen 1968). Other species show delayed egg hatching or no growth during the winter (Moon 1939, Ellis 1961, Svensson 1966, Larsen 1968, Andersson 1969, Clifford 1969, Lehmkuhl 1970, and Elliott 1972).

Brinck (1949) found that Plecoptera eggs can take as long as 152 days to hatch in cold water. Elliott (1972) discovered that Baetis rhodani Pictet eggs that hatched in 10 days at 20°C took 20 days to develop at 10°C and 135 days at 3°C. Thus, low temperatures seem to greatly extend the life cycle of some insects by delaying the hatching of eggs.

Radford and Hartland-Rowe (1971) compared emergence times of several stoneflies in mountain streams of Alberta, southern British Columbia and the northern U.S. They found that earlier emergence of a

species seemed to correlate with warmer water. Nebeker (1971a,b) analyzed the effects of temperatures on stoneflies at different altitudes in a Utah stream. For some species emergence began in January at lower altitudes but was delayed 4-6 months by the colder water at higher altitudes. Laboratory rearing of aquatic insects in elevated winter water temperatures were confirmed by field onservations. There was up to a 5-month premature emergence at the highest of the constant temperatures survived. Gaufin and Hern (1971) found that the stonefly Pteronarcys californica Newport emerged 6 months earlier than usual when maintained at a constant temperature of 18°C.

In the River Thames, Mann (1965) found that a heated outfall caused early reproduction in the mussel Anodonta sp. and the isopod Asellus sp. and reported that the lethal temperature for many benthic organisms is 32-35°C. Lyman (1944) found that cold temperatures increased the length of the subimaginal stage of mayflies. In the amphipod Hyalella azteca (Saussure) time to reach maturity, embryonic development, and growth are all shortened by increasing temperatures (Bovee 1950). Coutant (1967), Andersson (1969), Harvey (1971), and Nebeker (1971a) all reported that increasing water temperature increases the rate of development of freshwater macroinvertebrates. Some disagreement exists, however, for Langford (1971) did not find an increase in development below a heated outfall in England. Lehmkuhl (1972) notes that some mayflies require a period of cold temperatures to stimulate egg development. Thorup (1963) and Larsen (1968) have investigated a developmental response to seasonal temperature fluctuations in the form of mayfly

bivoltine life cycles. One generation has a slow winter growth period and emerges in the spring, and the second generation has a rapid summer growth emerging in late summer. Harker (1952) examined a trivoltine species but was uncertain of the biology of the species. One might expect a species inhabiting a warm or constant temperature stream to be multivoltine but reports of such an occurrence are infrequent. Smith (1968) reported a multivoltine aquatic insect from a spring stream, as did Nebeker (1971b). The life cycle of few multivoltine species has been examined in detail. Andrewartha and Birch (1954) have examined much of the literature on temperature influences on growth and development of terrestrial and aquatic invertebrates. Many of their conclusions will be presented below.

A useful method to represent the speed of development at different temperatures is to plot temperature on the abscissa and either the duration of the life stage under study or the reciprocal of this measurement on the ordinate. The reciprocal is a specialized concept of speed of development and has a number of peculiar properties: e.g., the slope of the curve is a function of the duration of the particular stage under consideration. Developmental-temperature curves for invertebrates consistently show a sigmoid curve that fits the logistic equation. A sigmoid relationship can also be mathematically expressed as a second or third order polynomial when per cent development is unknown.

In nature, animals live in environments where temperature fluctuates and it is desireable to learn the relationship between growth at constant temperatures and growth at fluctuating temperatures. Andrewartha and Birch (1954) state that field experiments indicate fluctuating

temperatures within the favorable range are closely equivalent to the corresponding constant temperature. Therefore, a precise estimate of speed of development can be made by a modified temperature-summation method which takes into account the curvature of the graph. The conclusion is that, provided the diapause-effect is not influencing the results, short-term (e.g., daily) fluctuations in temperature within the favorable range may safely be considered to be equivalent to constant temperature in this range. This is not to say that the average speed of development is the same as that at a constant temperature equal to the mean of the fluctuating temperature. This would imply that the relationship between temperature and speed of development is linear, which it is not. When the fluctuations include extremes outside the favorable range, it is necessary to consider other possibilities.

The rate of development in relation to temperatures has been of interest to biologists. The method has been used to predict the date of emergence of the spring brood of an insect pest to the duration of a generation. Simpson (1903) was one of the first to develop the concept of the "thermal constant" expressed in units of "day-degrees." The thermal constant is the time required to complete development in units of day-degrees. The formula to calculate the thermal constant is that of a parabola $K=y(x-a)$, where K is the thermal constant, y is time required to complete development (if y is in hours, K is expressed in degree-hours, if y is in days K is in degree-days), and (since a is the point of "zero development") x-a is the "effective temperature." As a rough approximation, a day may be taken as the unit for y, and the mean of the daily maximal and minimal temperatures may be substituted

for x. This is the basis for temperature summation. Several researchers have used temperature-summation as day-degrees in aquatic investigations (Miller 1941, Britt 1962, Andersson 1969, and Langford 1971). Others have refined the concept of summation of temperature by using hours instead of days (e.g. Macan 1958, Gose 1970). Winberg (1971) calls this accumulation of thermal input, "the rule of sum of degree-hours," and suggests that the product of time and effective temperatur (above the point of zero growth) is a constant, characteristic for each species. The larger the constant, the longer is the duration of development for a given effective temperature. Temperature summation gives the investigator a basis for comparing life cycles from year to year and growth rates on a weekly or monthly basis. One of the first and most effective uses of degree-days and its relationship to emergence was that of Miller (1941) on lake dwelling midges. In his study of a deep water species, Miller plotted the accumulation of degree-days against time. The number of degree-days to which a larva had been exposed over any period of time at any station could be determined from these curves. One year he noted that half the population had emerged May 28. From the curve the thermal accumulation from spring to this date was 280 degree-days. The next year it was June 2 before 280 degree-days was reached and on that date he found this species was again in the middle of its emergence. Miller also believed that the number of degree-days to which an insect is subjected will limit its northern distribution and may permit more than one generation per year in more southerly locations. He compared four species of Chironomus from Ontario with the same four in Illinois and found that the Ontario species had

one generation per year while the Illinois forms had two generations. Judd (1953) was the next to use temperature summation and calculated the number of degree-days necessary for 35 species of marsh-dwelling aquatic insects to complete their life cycles. Britt (1962) examined emergence patterns of two species of burrowing mayflies in Lake Erie and found a close correlation between growth of nymphs and the number of degree-days. His investigation covered a 5-year period but he concluded that the controlling factor in emergence does not appear to be the total degree-days to which the eggs and nymphs are exposed. Instead, it appears that about 600-700 degree-days are required in the spring. Andersson (1969) used and refined the relationship of growth versus degree-days for the isopod Asellus aquaticus (L.). He decided that since no growth occurred before 3°C only the number of degree-days above 3°C should be used. He found that above 3°C body length plotted against degree-days was linear. Gose (1970) found a good correlation between life cycle duration and degree-days for a caddisfly. He noted that temperature summation is important only above the point of zero growth.

Temperature may control the speed of development but light appears to be important in diel emergence (Morgan 1958, Neuman and Honegger 1969). However, for arctic chironomids an increase in water temperature induced emergence and a decrease inhibited it, whereas light intensity had no effect on diel emergence (Danks and Oliver 1972). Humpesch (1971) found for a mayfly that under constant temperature conditions emergence was normal but was disturbed in permanent light and supressed in total darkness.

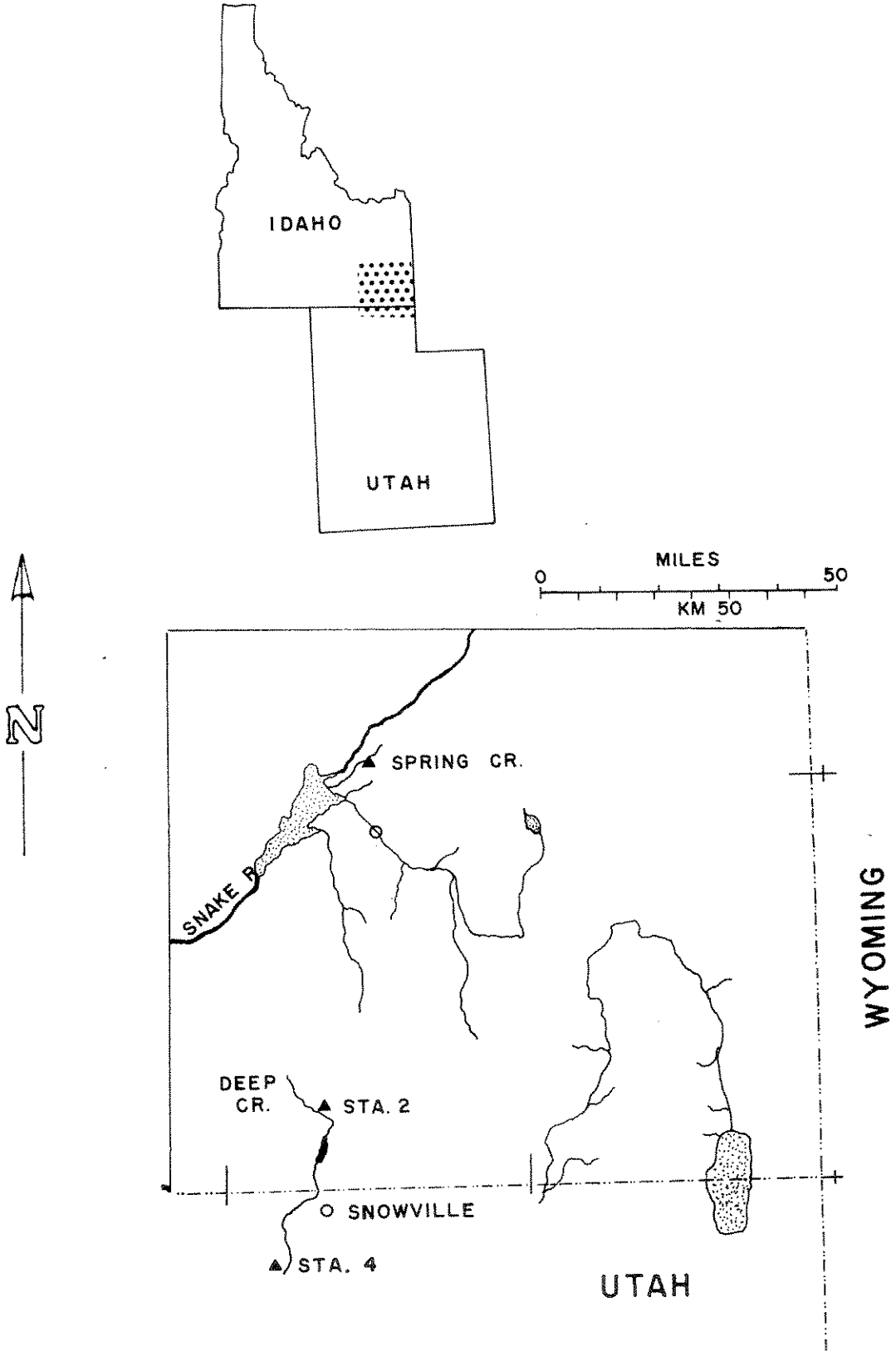
DESCRIPTION OF THE STUDY AREAS

Although two streams were involved in this study, Deep Creek received the most intensive scrutiny because it is here that the multivoltine nature of T. minutus is apparent. Deep Creek lies in Curlew Valley a 3460 km^2 drainage basin on the Idaho-Utah border (Latitude $41^{o}40'$ to $42^{o}30'$ North, longitude $112^{o}30'$ to $113^{o}20'$ West). The east, north, and west sides of the valley are bordered by mountains that rise to 3020 m above sea level. The climate is arid and a wide yearly temperature range exists. Precipitation occurs as rains in the late fall and spring and as snow in the winter. Total annual precipitation is roughly a function of topography, ranging from 31-36 cm at the northern end of the valley to 15-20 cm at the southern end (Anon.1970).

Two stations were utilized on Deep Creek. Deep Creek I.B.P. Station 2 was selected because the multivoltine nature of Tricorythodes minutus was clearly evident there and because a tremendous amount of background information was available due to the I.B.P. research at this station. Deep Creek I.B.P. Station 4 also was selected because of background data and because T. minutus appeared to be univoltine there. Thus station 4 seemed to offer a good comparison with station 2.

Deep Creek rises near Roy summit in the northwest corner of Oneida County, Idaho, flows south for approximately 13 km, and becomes intermittent. Approximately 5 km southwest of Holbrook, Idaho the stream reappears as several springs. From these springs about 1 m^3 sec^{-1} of water flows at a constant temperature of $18^{o}C$. From Curlew Reservoir, Deep Creek flows south for another 20 km as it crosses the Idaho-Utah border and sinks into the desert about 9 km north of the shore of the

Figure 1. Map showing general location of the three study areas in Idaho and Utah.


IDAHO
UTAH
N
MILES
0
50
KM 50
SPRING CR.
SNAKE R.
DEEP CR.
STA. 2
SNOWVILLE
STA. 4
UTAH
WYOMING

Great Salt Lake (Fig. 1). The 3-km section of stream from the springs to Curlew Reservoir was the main study area (I.B.P.Station 2). Some 100 m below the springs a diversion dam is used to divert much of the stream flow into an irrigation ditch, reducing stream flow during the summer months. The morphometry of the stream shows an alternating riffle-pool condition. The substratum is gravel, sand, and some clay. The outer edge of stream meanders usually is composed of clay banks as high as 2 m, while the inner edge of the meanders contain no banks. Some algae and submergent vegetation grow in the riffles and in summer mats of the filamentous alga Cladophora accumulate. The water is clear except on occasion in the spring when the dry channel above the springs contains snow-melt runoff.

The second study area on Deep Creek (I.B.P. Station 4) is about 4 km upstream from where the stream sinks into the desert. In that area the stream flows through a shallow valley. The stream has been dredged in the past and has a relatively straight channel, the riffle-pool morphometry has disappeared and the substratum is mud. The stream banks are heavily overgrown with willows; further away, sagebrush and rabbitbrush predominate. Very little vegetation occurs in the stream and the water usually is turbid.

In order to better understand the life history of Tricorythodes minutus, which is univoltine here, and to test the validity of any prediction, collections of nymphs were also made on Spring Creek, Bingham County, about 12 km west of Fort Hall, Idaho (Latitude 43°2'30" N, longitude 112°33' W, section 25, R 33 E/ T 4 S). Spring Creek is of moderate size, with a discharge of 8 m^3 sec^{-1}. Water chemistry conditions are available in Table 1. It rises as a large spring near Ferry

Butte and meanders southward through bottomland for 15 km before emptying into American Falls Reservoir (Fig. 1). Temperature, like discharge, shows some variation ranging from 6 to 18°C yearly.

The physical and chemical conditions of Deep Creek and Spring Creek are found in Table 1. Spring Creek has a greater volume than Deep Creek, showing a constant mean flow of 8.0 m^3 sec^{-1}. The chemical composition at the three study areas varies widely with Spring Creek having the fewest dissolved solids and station 4 having the greatest. Temperature extremes are the smallest at Spring Creek.

Mean weekly temperatures have been converted to degree-hours and are presented in Table 2. Mean weekly temperatures were used to calculate degree-hours and this method proved as satisfactory as using continuous recorders. Over a 6 month period degree-hours taken from mean weekly temperature varied by less than 1 per cent from data taken from continuous recorders. The yearly totals for station 4 and Spring Creek are very similiar, 92,549 and 95,796°h respectively and station 2 had about twice the total of either station (153,715°h). The 5°C temperature is the point of zero growth for T. minutus and if the thermal values below 5°C are subtracted the available heat becomes, 109,200°h sta.2, 53,088°h sta.4, and 51,996°h Spring Creek.

Table 1. Physical and chemical conditions as discharge (m^3/sec), temperature (^oC), and chemistry (mg/l) for Deep Creek sta. 2 and 4[a] for Sept. 1970-Aug. 1972, and Spring Creek, Dec. 1971-Dec. 1972.

Station	Discharge	Temperature extremes
Station 2 N=27		
max.	1.700	31.5
min.	0.015	-0.8
mean	1.044	
Station 4 N=27	0.461	30.0
max.	0.028	-3.5
min.	0.211	
mean		
Spring Creek N=12		
max.	9.06	17.0
min.	8.78	5.5
mean	8.92	

Station	pH	Calcium	Magnesium	Bicarb.($CaCO_3$)	Chloride	TDS
Station 2						
max.	8.5	140	30	274	163	644
min.	7.6	30	6	165	95	403
mean		62	14	221	123	481
Station 4						
max.	8.6	440	60	324	575	1663
min.	7.8	40	16	175	285	785
mean		130	31	258	365	1165
Spring Cr.						
max.	7.9	60	16	250	18	320
min.	7.9	50	16	210	18	265
mean		55	16	230	18	293

a- from Koslucher (1971), continuous recorders and stage recorders.

Table 2. Degree hours present at Deep Creek[1] and Spring Creek[2].

Date	Sta.2	Sta.4	Date	Spring Cr.
June 1971	14,328	13,248	Dec.1971	7200
July "	14,880	14,880	Jan.1972	6120
Aug. "	14,508	14,880	Feb. "	5376
Sept. "	13,536	13,320	Mar. "	7920
Oct. "	11,830	8,854	Apr. "	8640
Nov. "	12,744	3,600	May "	9000
Dec. "	11,606	2,232	June "	9300
Jan. 1972	12,127	1,637	July "	9300
Feb. "	12,298	2,890	Aug. "	8640
Mar. "	10,788	3,422	Sept."	8556
April "	11,232	5,328	Oct. "	8184
May "	13,838	8,258	Nov. "	7560
TOTALS.....	153,715	92,549		95,796
# above 5°C available for growth.....	109,200	53,088		51,996

1- taken from continuous recorders
2- " " maximum-minimum thermometers.

METHODS AND MATERIALS

Habitat: The habitat of T. minutus was investigated by several means. The description of T. minutus in terms of range was extracted from published records in the United States and abroad and from collection records by the author. Distribution in terms of habitat was examined only at I.B.P. Station 2. Quantitative bottom samples in riffle and reach areas revealed information on monthly densities in both habitats. This information gave some insight into habitat preference. Four benthos samples of 1/16 m^{-2} were taken each month from station 2 with a modified Hess sampler by the I.B.P. Desert Biome research team from Idaho State University. Two additional samples were collected monthly from station 4. Specimens of T. minutus were removed from the samples, counted, and data converted to organisms per m^2. Sex was determined whenever possible and head width, pronotum width, and total length were measured. All measurements were made to the nearest 0.1 mm with an ocular micrometer on a dissecting microscope and length frequency histograms were constructed. Sampling began in June 1970 and continued for 27 months.

Monthly samples were taken from Spring Creek from December 1971 to December 1972. A net (mesh size 390 um, as from Deep Creek) was placed in the stream to catch animals dislodged upstream by disturbing the bottom by kicking. All specimens of T. minutus were preserved and handled like the Deep Creek samples. Water temperature was recorded on continuous recorders in Deep Creep and by maximum-minimum thermometers in Spring Creek.Data on the chemical environment was taken from Koslucher (1971).

Reproduction: Mating habits and oviposition of T. minutus were observed whenever the stream was visited. In addition 18 day-long observation periods were conducted to gather more extensive data on reproduction. Eggs were collected from adults and mature nymphs, the morphology was examined and photographs were taken. Egg counts were made on eggs dissected from nymphs and adults. Egg clusters were collected from ovipositing females and the relationship between cluster diameter and egg counts of the clusters was established, as was the relationship between the number of eggs per cluster and the total egg count. All egg counts were made with a dissecting binocular microscope. The weight of individual eggs was found by weighing a known number of eggs on a Cahn electro-balance, and hatching success was determined by counting hatched and unhatched eggs in laboratory hatching chambers.

Nymphs: Photographs and detailed scale drawings of the nymphs were used to illustrate the morphology of the species. Characteristics peculiar to this species and sexually dimorphic characters were noted. Growth of the nymphs was studied in small growth chambers in the field (Fig. 2) and laboratory. The food habits of T. minutus have been investigated in Deep Creek by Koslucher and Minshall (1973) and their methods were used to gain further insight into food type and maximum particle size ingested. Examination of gut contents was made at 1000X using oil immersion to insure that the smallest diatoms were seen. An ocular micrometer calibrated to 0.001 mm was used to find the largest particles ingested by five nymphs in several 1-mm size classes.

Feeding behavior was observed in live nymphs held in aerated growth chambers and observed under a dissecting microscope.

A concerted attempt was made to learn the number of molts that occur during the life history of T. minutus. In the laboratory cast skins were removed daily from growth chambers. In the field, observations have revealed that many cast skins are carried in the drift and many were collected with drift nets and by picking individual skins from surface of water. In all cases total length of the skins was determined and plotted against frequency of occurrence. Individual skins were weighed on a Cahn electro-balance. Approximately 300 nymphs were weighed individually in the wet, dry, and after ignition condition after head, pronotum, and total lengths were taken. A last method is that of Janetschek (1967) where a histogram is constructed showing the size-frequency of the population. A second histogram is then drawn up giving the running-means of the measurements to show the trend of the samples; for example, a running average of five of the X^{th} size class ($\bar{Y}_x$) is equal to $1/5(Y_{x-2} + Y_{x-1} + Y_x + Y_{x+1} + Y_{x+2})$. When the second histogram is subtracted from the first, the resulting diagram indicates the periodic maxima and minima and thus is a rough method of determining the modes of a multimodal distribution. It can be expected that a determination of the number of modes in the size-frequency distribution of the nymphs will indicate the number of instars; and if Dyar's (1890) rule of a constant relative growth increment between successive instars is followed, the peaks should be at equal distances along a logarithmic scale.

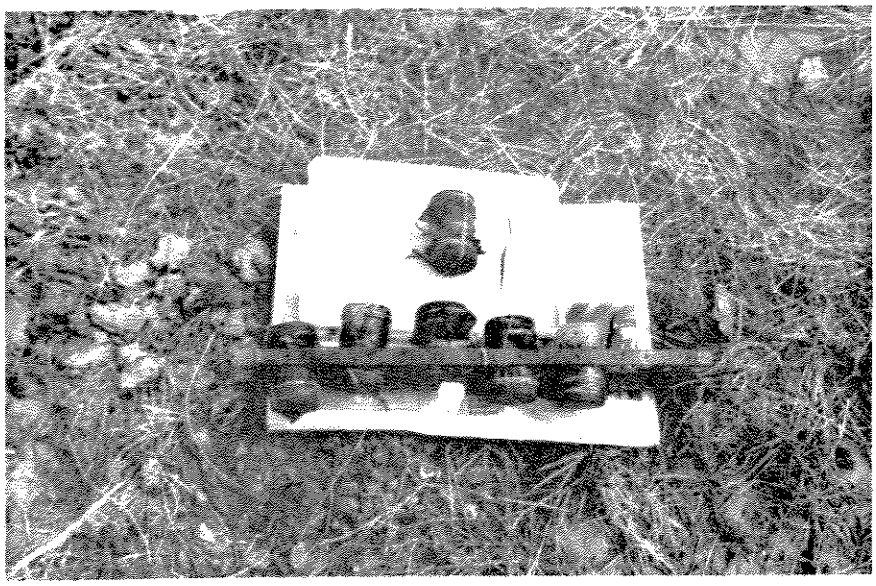
Nymphal mortality is difficult to assess but an estimate of non-predatory mortality was gained from mortality rates in field and laboratory growth chambers.

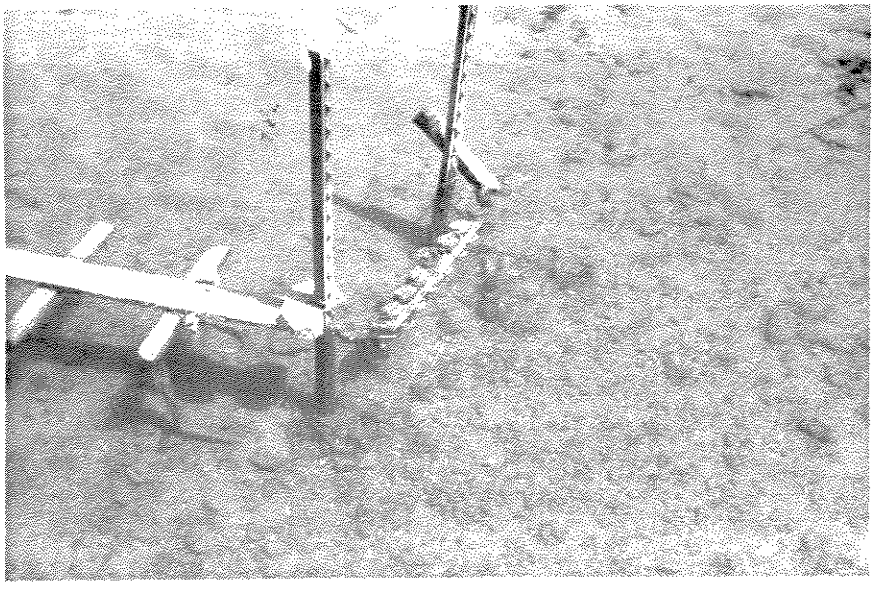
Thermal tolerance: Thermal tolerance tests were run on a mixed size group of nymphs acclimated at three temperatures, 9°C, 15°C, and 21°C. The thermal tests were run for 96 h (8400 min.) and the test chambers were examined every 8 h. Death was assessed as that point at which the nymphs failed to respond to stimuli and did not revive upon placement in room temperature water (ca. 18°C). The median tolerance was that point at which 50% of the organisms died. All thermal tests consisted of ten test organisms and three replicates were run. Environmental chambers were used for precise temperature control (± 1.0°C), excess food was present and photoperiod was 12 hours. The experiment to test the effects of temperature on different size classes was conducted with insects in 1 mm classes (i.e. 1-2 mm, 2-3 mm etc.) acclimated to the mean Deep Creek temperature of 18°C. All tests were run as stated previously.

Growth and development: Growth rates of nymphs were determined in the field and laboratory. Field growth rates were calculated at Deep Creek station 2 and Spring Creek. Field growth chambers consisted of six plastic cylinders separated into two chambers by Nitex screen with removable ends of fine-mesh nylon held in place with rubber bands (Fig. 2). The six chambers fit into hemispherical slots cut into a 47 cm long piece of fiberglass and held firmly in place parallel to

Figure 2. Individual field growth chambers.

Figure 3. Field growth chambers in position in Deep Creek Station 2.





each other (Fig. 3). The fiberglass and chambers were wired between two metal fence posts in the stream bottom and the chambers were positioned about 20 cm off the bottom with the openings of the cylinders placed parallel to stream flow. Some detritus and algae were placed in the chamber with each nymph and additional food materials entered via water currents. The chambers were visited weekly for 6 months and the following measurements taken from the nymphs: total length; head width; pronotum width; head length; meso-metanotum width and length, along with sex determination. In the laboratory, growth chambers modified from Bjarnov and Thorup (1970) were used. The chambers were plastic petri dishes approximately 12 cm in diameter and 20 cm deep, separated into halves by a Nytex screen so as to accommodate two nymphs. A large-gauge hypodermic needle was heated and passed through the plastic, glued into position and attached to an air supply. Tests were conducted at near $4^{\circ}C$ to determine the point of zero growth and at 5° intervals from $4\text{-}29^{\circ}C$. Temperature was controlled by placing the growth chambers in environmental chambers. Photoperiod was held at 14 h light and 10 h dark and some nymphs were reared in complete darkness. The effects of varying temperature was scrutinized by rearing nymphs at $18\pm3^{\circ}C$ (11.0 h at 15° and at $21^{\circ}C$ and a 1 h transition time). The same measurements used in field tests were made on laboratory organisms. Examinations and measurements were made weekly, at which time the water and materials in the chambers were removed and fresh Deep Creek water and food were added. The effects of accumulated waste products was examined by rearing nymphs in

chambers in which the water and wastes were not removed. In growth tests 30 organisms total were studied at each temperature. Test organisms were generally 1-2 mm in length when their growth tests began. Eggs also were reared at all of the experimental temperatures and the onset of hatching, duration of hatching, and success of hatching was noted.

Allometric growth: Both allometry of size and allometry of growth were calculated (Simpson et al. 1960). A total of 284 nymphs were randomly selected for allometric analysis. For the allometry of size studies each body measurement was plotted against every other body measurement (the same measurements as taken in growth studies). From these data a least squares regression was carried out for each pair of measurements for X on Y and for Y on X. In addition, a single "best fit line" was calculated for each pair of measurements. Allometry of growth and resulting constant of allometry was analyzed by using weekly laboratory growth at 19°C by means of the method of Simpson et al. (1960) and Clifford (1970a).

Adults: Adult morphology was examined by using photographs and precise measurements of the adult body, (i.e., wing, body, and cerci dimensions). Live and dead weights were obtained by means of a Cahn electrobalance. Subimaginal skins were collected in the laboratory from molted adults and weighed as above. For females, the percent body weight represented by eggs was found by weighing gravid and spent females. Frequent visits to the study stations and resultant observations gave emergence data such as timing, weather effects, and sites

of emergence. Sex ratios were determined by examining adults captured in aerial nets and by picking adults from vegetation and the surface of the water. Duration of adult stages was calculated by examination of adults in the field as were flight patterns and mating behavior.

RESULTS

The results of this research are concerned with aspects of the growth, development, and life cycle of the mayfly Tricorythodes minutus Traver. Field research was carried out in each of three localities, Spring Creek, Deep Creek station 2, and Deep Creek station 4. Observations on life history phenomena were also made at these field sites and research on growth in relation to temperature was conducted in the laboratory.

Individual growth rates are commonly determined by examining mean total length of the insect population every month and this was done at all three field stations. In addition, one of the first known field studies on growth of single, identifiable individuals was conducted at Deep Creek station 2 and in Spring Creek. Growth also was studied in the laboratory at several temperature regimes. Many aspects of the life history of this mayfly were examined from determination of egg number and weight to nymphal instar analysis. The major emphasis of this work was to determine the effect of temperature on growth rate and to see if the temperature summation technique could be utilized to predict growth rate and development.

Nymphs

General biology: Nymphs of Tricorythodes minutus are 0.4 mm long at hatching (Fig. 4) and lack gills and opercula. The smallest nymph captured in the stream was 0.8 mm in length. By the time the nymph reaches 1.0 mm in length both gills and opercula are present. Male

Figure 4. Early instar nymph of T. minutus, total length about 0.5 mm.

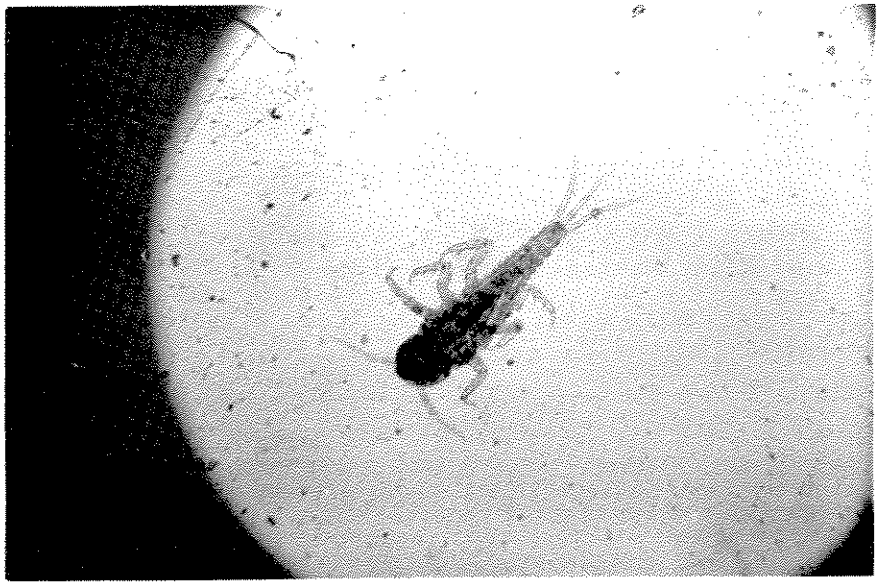
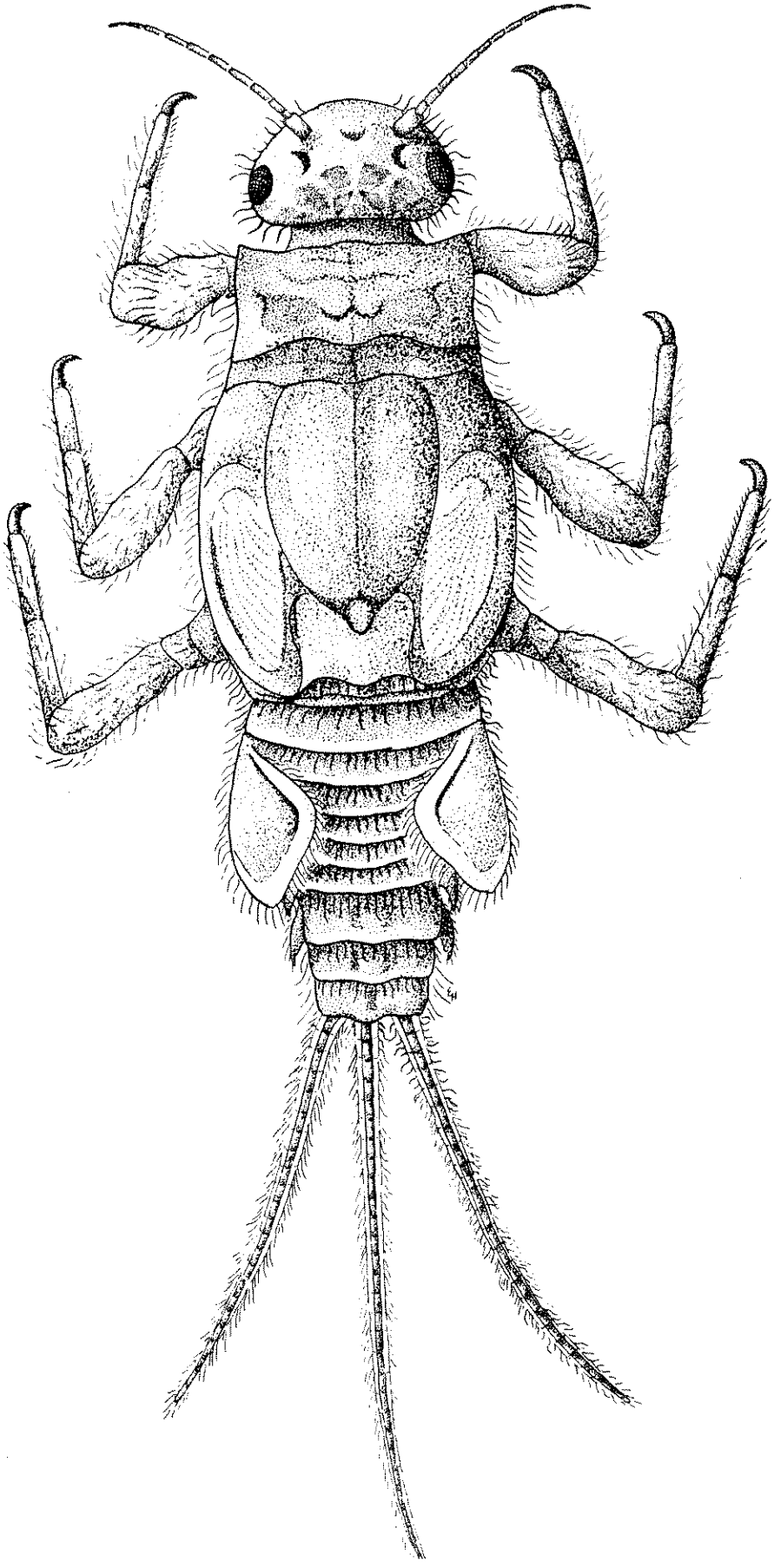


Figure 5. Mature female nymph of T. minutus about 5.5 mm in length and about 25 times actual size.



and female nymphs (Fig. 5) are indistinguishable until they are about 3.0 mm in length. Females and males can then be separated by the presence of a "notch" or cleft on the last sternite of the males, the females retain a rounded sternite. This cleft becomes more pronounced as maturity approaches, with the penes forming along the sides of the cleft. Females attain a larger size than males (Figs. 6-8). Mature males rarely exceed 5.5 mm in length, a 5.9 mm nymph being the largest captured. Females usually attain lengths of 5.5-6.0 mm before emerging; the largest female observed was 7.1 mm long (Figs. 6-8).

Total length has been ignored in the past as a definitive characteristic of insect nymphs because of the variability caused by telescoping of the abdomen. In five comparisons made between total length and the other measurements (Figs. 6-10), the correlation coefficient ranged from 0.93 to 0.97, illustrating that for T. minutus total length is an accurate and consistent measurement. The relationship between total length and each of the two head measurements (Figs.6-7) becomes slightly curvilinear as maturity is approached; this indicates a decreasing rate of head growth relative to change in total length. Plots of total length versus each of the remaining measurements are all linear through the juvenile stages but become slightly curvilinear in later stages of growth. Total length versus meso-metanotum length (Fig. 10) exhibits a brief span in which no data points are present, which illustrates the extremely rapid growth of wing pads from 1.3-1.7 mm. The relation of head width to pronotum width shows the least deviation from the regression line (r=0.99). Table 3 lists statistics not available from the graphs. The coefficient of variation is given for

Figure 6. Head width versus total length for T. minutus nymphs.

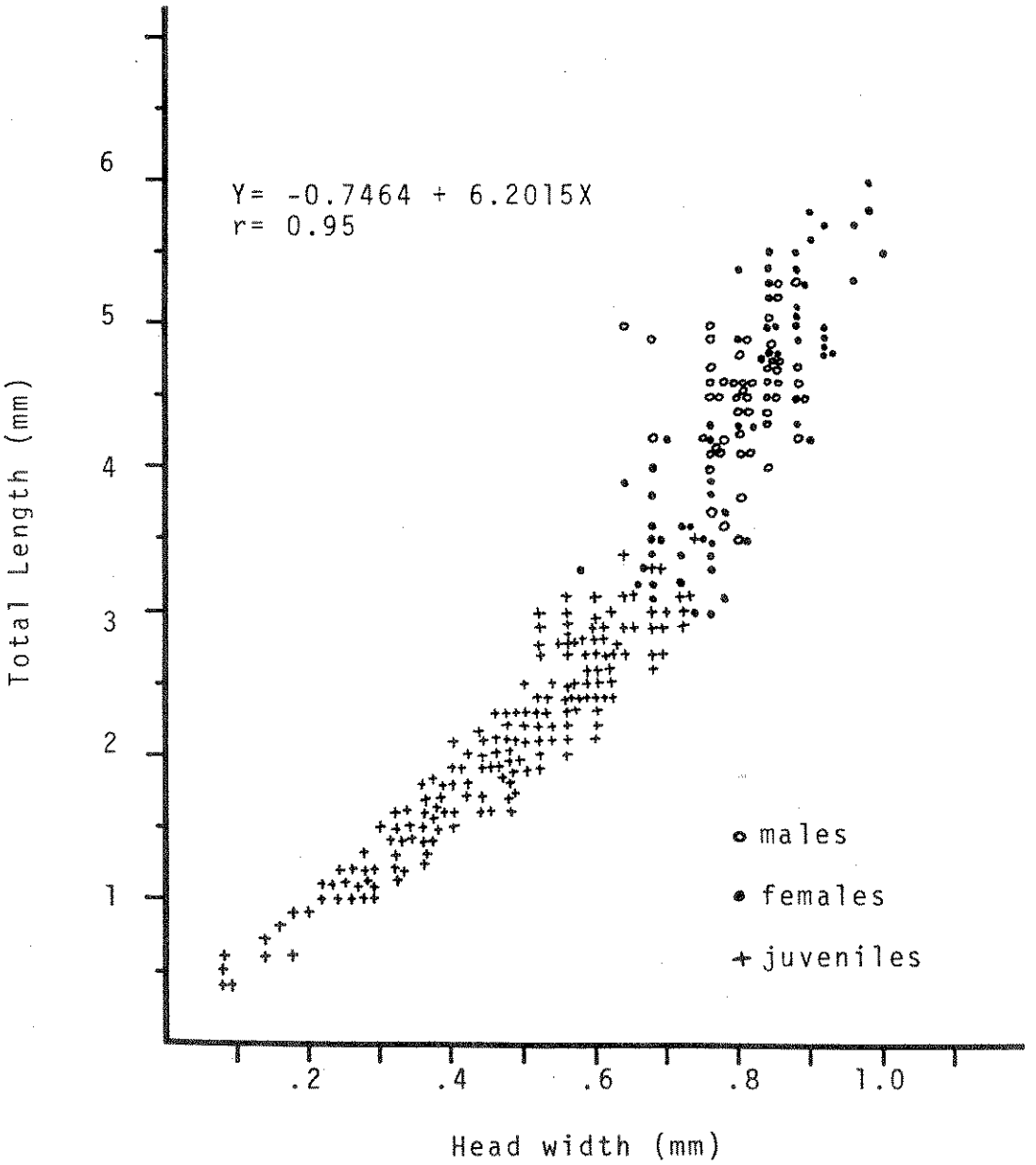

Y= -0.7464 + 6.2015X
r= 0.95
Total Length (mm)
Head width (mm)
1
2
3
4
5
6
.2
.4
.6
.8
1.0
males
females
juveniles

Figure 7. Head length versus total length for T. minutus nymphs.

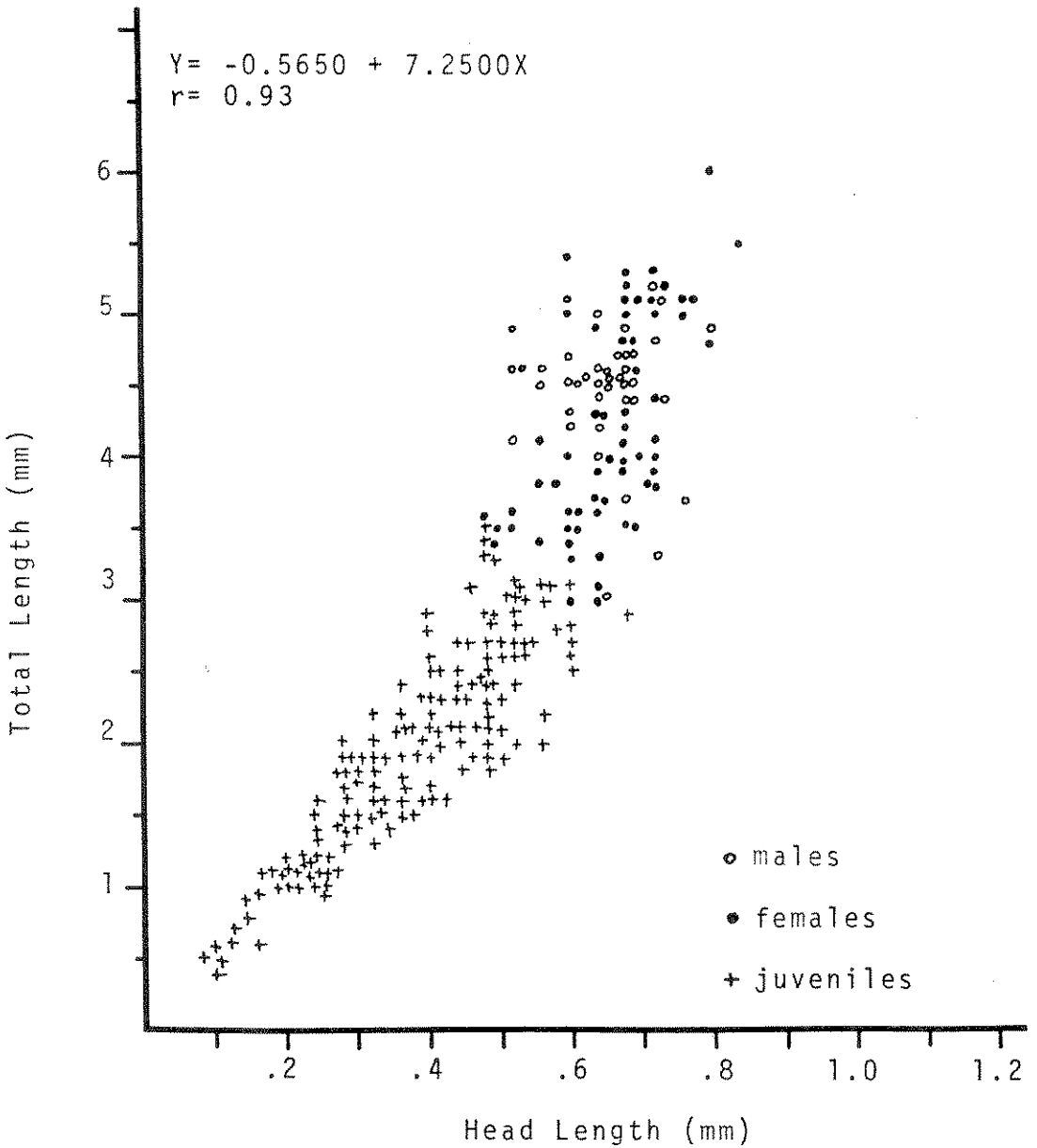

Y= -0.5650 + 7.2500X
r= 0.93
Total Length (mm)
1
2
3
4
5
6
.2
.4
.6
.8
1.0
1.2
Head Length (mm)
o males
• females
+ juveniles

Figure 8. Pronotum width versus total length for T. minutus nymphs.

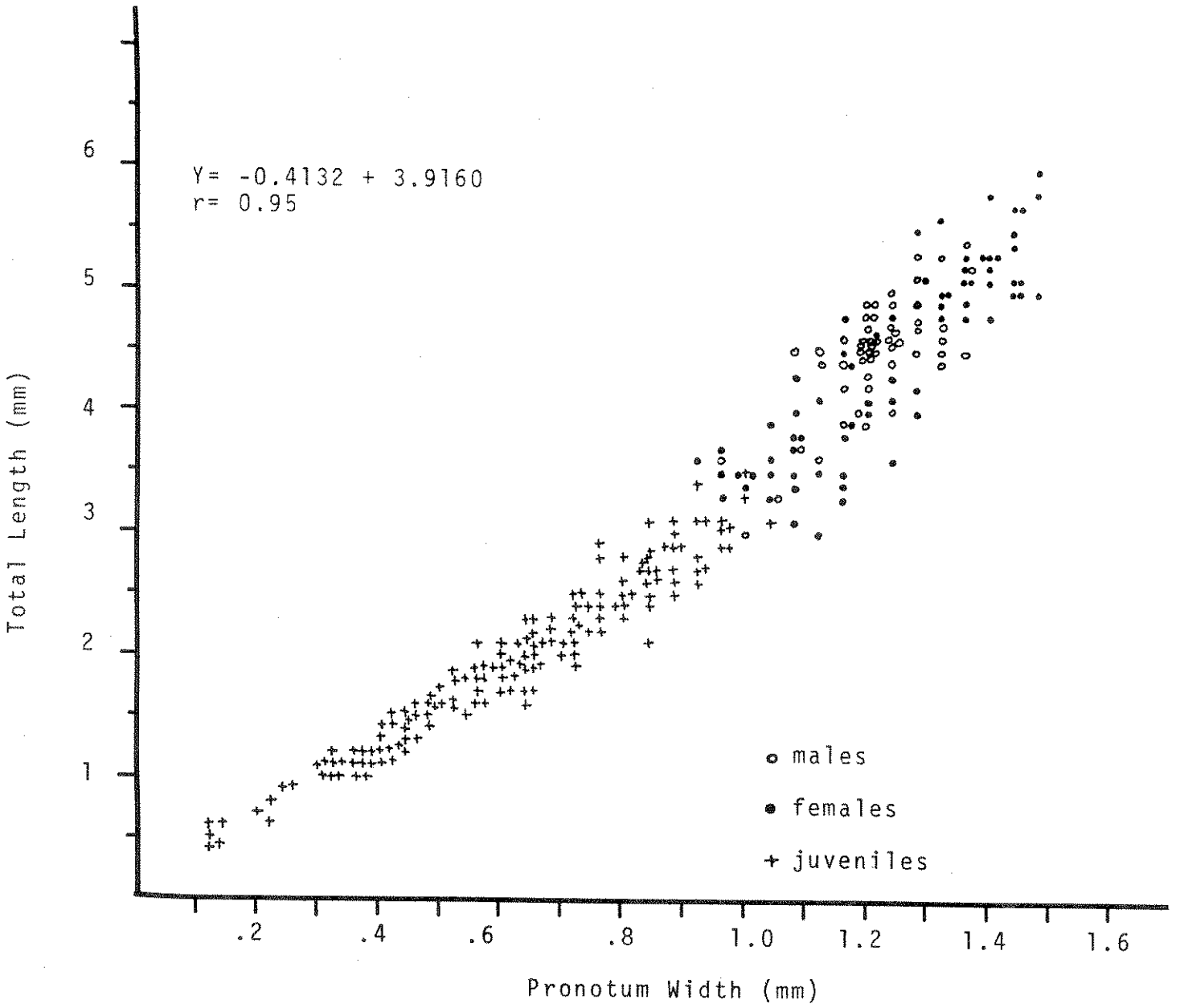

Y= -0.4132 + 3.9160
r= 0.95
Total Length (mm)
1
2
3
4
5
6
.2
.4
.6
.8
1.0
1.2
1.4
1.6
Pronotum Width (mm)
males
females
juveniles

Figure 9. Meso-metanotum width versus total length for T. minutus nymphs.

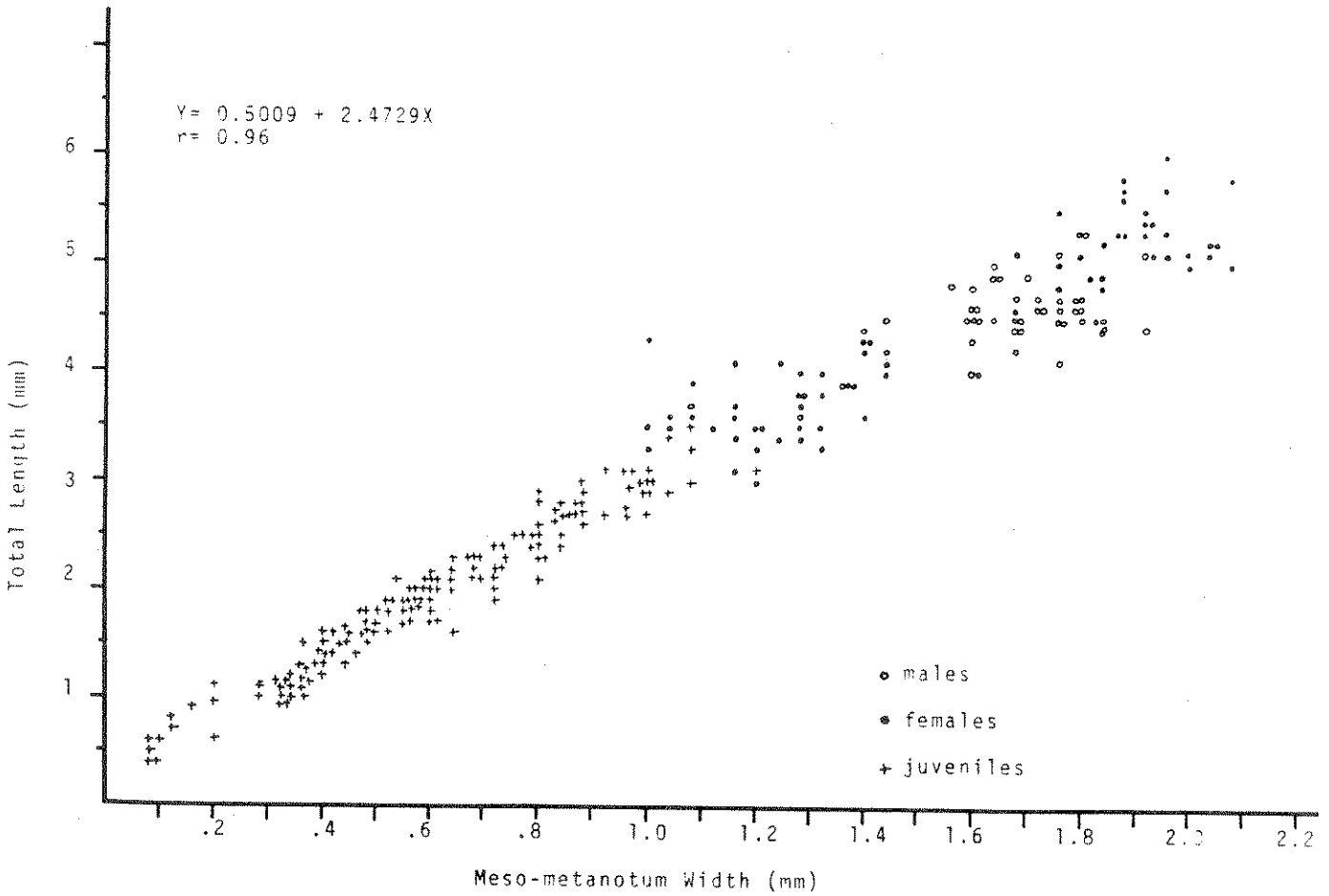

Y= 0.5009 + 2.4729X
r= 0.96
Total Length (mm)
Meso-metanotum Width (mm)
males
females
juveniles
1
2
3
4
5
6
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.2

Figure 10. Meso-metanotum length versus total length for T. minutus nymphs.

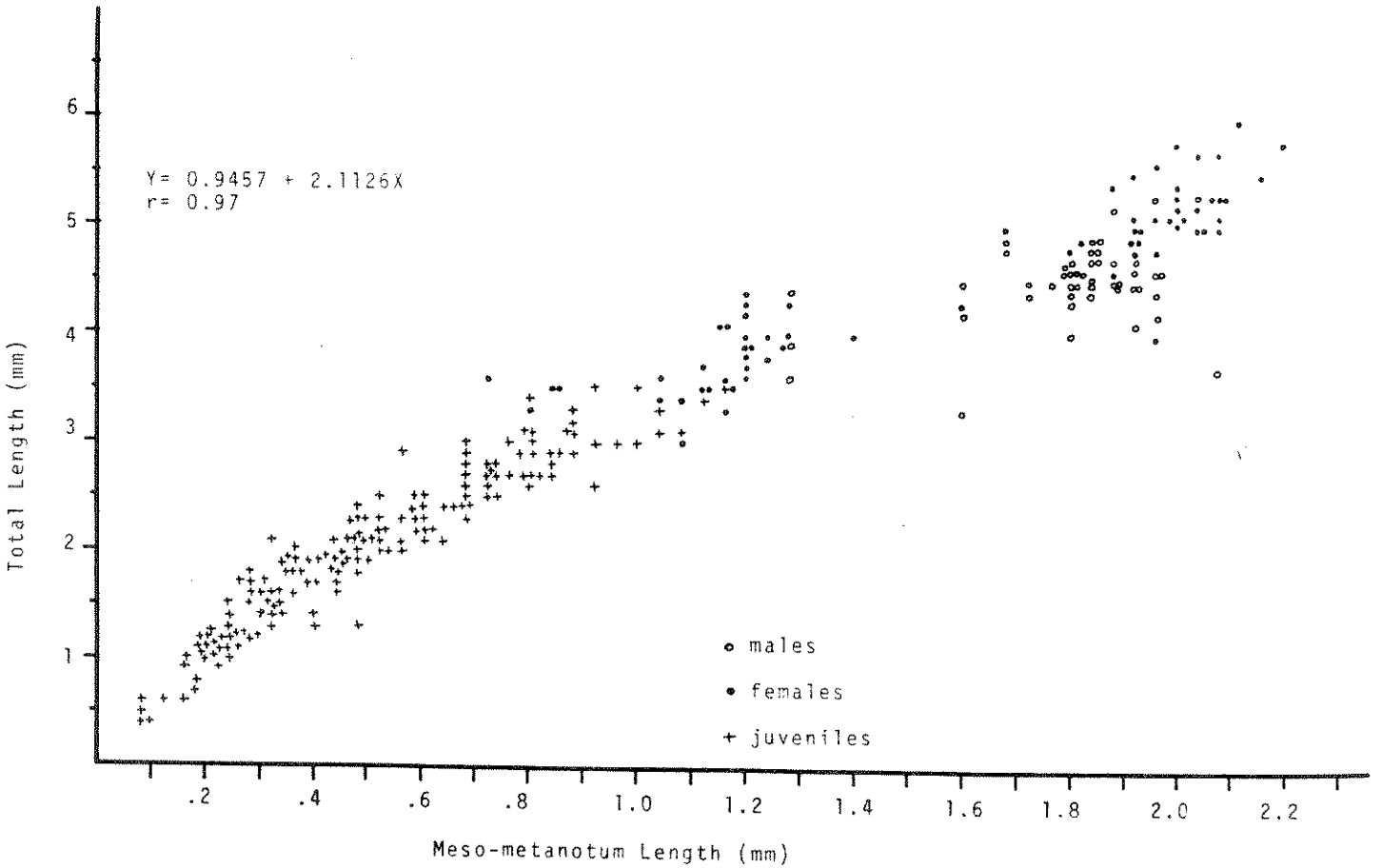

Y= 0.9457 + 2.1126X
r= 0.97
Total Length (mm)
Meso-metanotum Length (mm)
1
2
3
4
5
6
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
o males
• females
+ juveniles

Figure 11. Head width versus pronotum width for T. minutus nymphs.

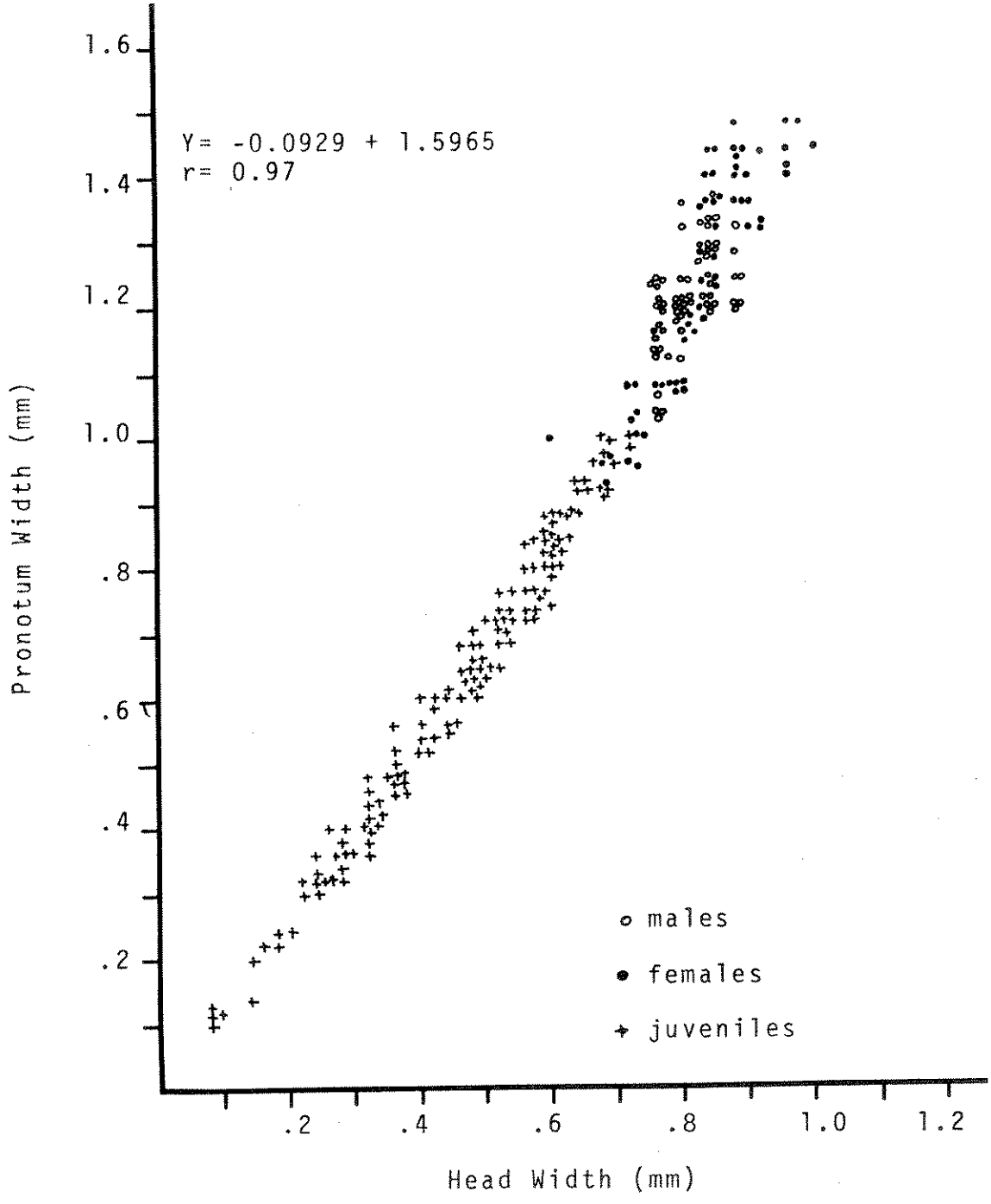

Y= -0.0929 + 1.5965
r= 0.97
Pronotum Width (mm)
1.6
1.4
1.2
1.0
.8
.6
.4
.2
.2
.4
.6
.8
1.0
1.2
Head Width (mm)
males
females
juveniles

Table 3. Statistics of some allometric measurements made on nymphs, not found on graphs. Measurements are in mm, and N=284.

Measurement	Mean	Standard Deviation	Coefficient of Variation
Total length	3.041	1.419	46.7
Head width	0.611	0.218	35.8
Head length	0.497	0.182	36.6
Pronotum width	0.882	0.353	40.1
Meso-meta. width	1.027	0.562	54.8
Meso-meta. length	0.992	0.650	65.6

the six body measurements. This coefficient is a good measure of relative dispersion but not a good measure of variability. High values (CV>10) usually indicate that the sample included animals of decidedly different ages which is the cause of high values in this study.

Length-weight relationships: The relationship of certain body measurements to weight are linear while others are curvilinear. The regression equations presented permit conversion of total length or head width to any of the several wet weight relationships. Table 4 presents a further partitioning of data for males, females and juveniles.

The relationship of dry weight to wet weight (Fig. 14) shows a linear plot on log-log scale (Fig. 15) as does total length vs dry weight. Several nymphs were ignited to determine amounts of organic matter and the results were: males, $\bar{X}$=82.7%; females, $\bar{X}$=85.6%; juveniles, $\bar{X}$=82.9%. Dry weight values can be converted to ash free dry weight based on the amounts of organic matter. These values for per cent organic matter were converted to Kcal/g (Table 5), by using the formula of Y=0.0559X, where X= % organic matter (Winberg 1971). The values obtained by means of this formula were very similiar to the calorific values of T. minutus found by Brass (1971), ($\bar{X}$= 4.721 and 4.767 Kcal/g respectively). The weights of nymphal skins roughly follow a linear form, with the majority of skins weighing between 0.155 and 0.280 mg (Fig. 16).

Growth-allometric: Values of the slope and Y-intercept in the allometric equation for Bartlett's best fit method (Simpson et al. 1960) are given in Table 6. Bartlett's method uses a single line for describing

Figure 12. Head width versus head length for T. minutus nymphs.

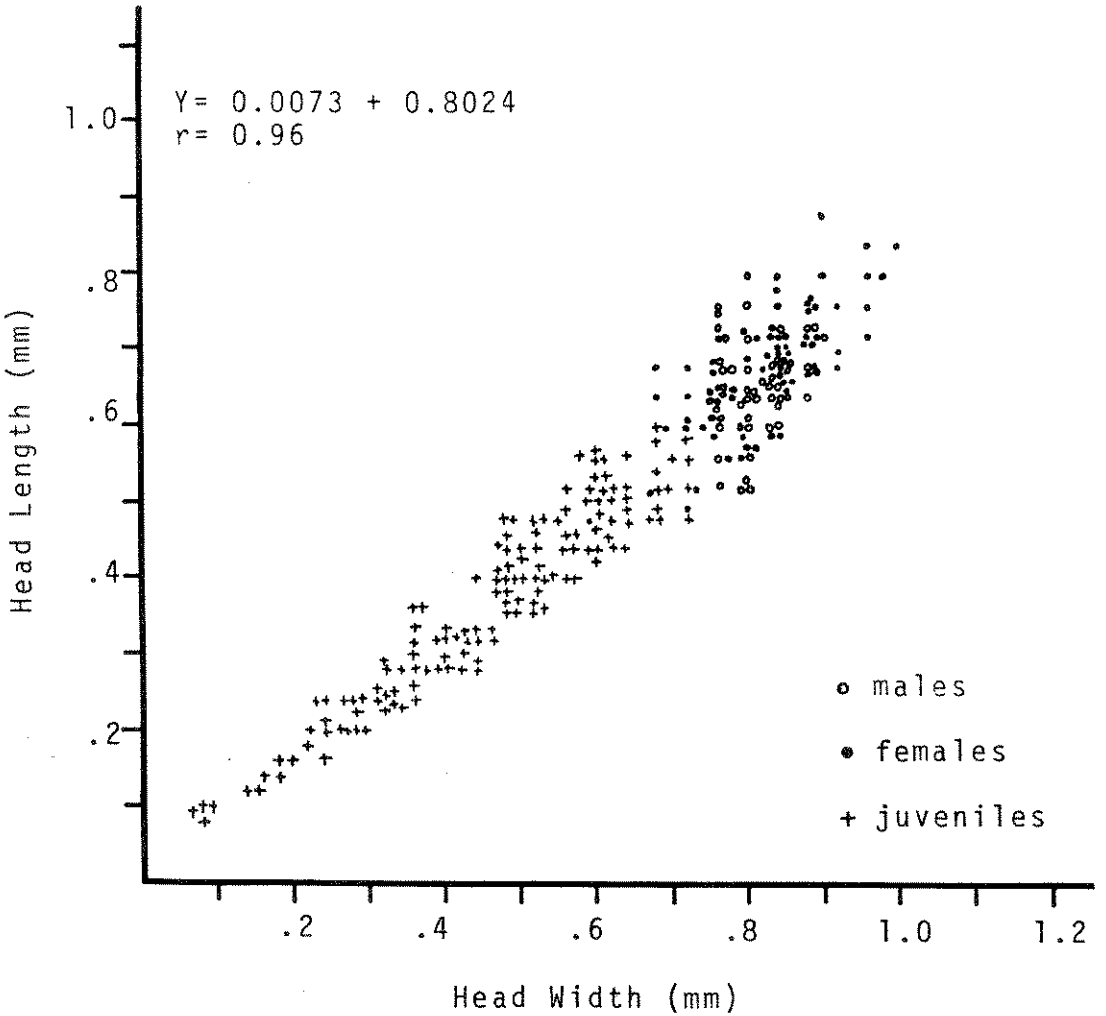

Y= 0.0073 + 0.8024
r= 0.96
1.0
.8
.6
.4
.2
Head Length (mm)
o males
• females
+ juveniles
.2
.4
.6
.8
1.0
1.2
Head Width (mm)

Figure 13. Head width versus meso-metanotum width for T. minutus nymphs.

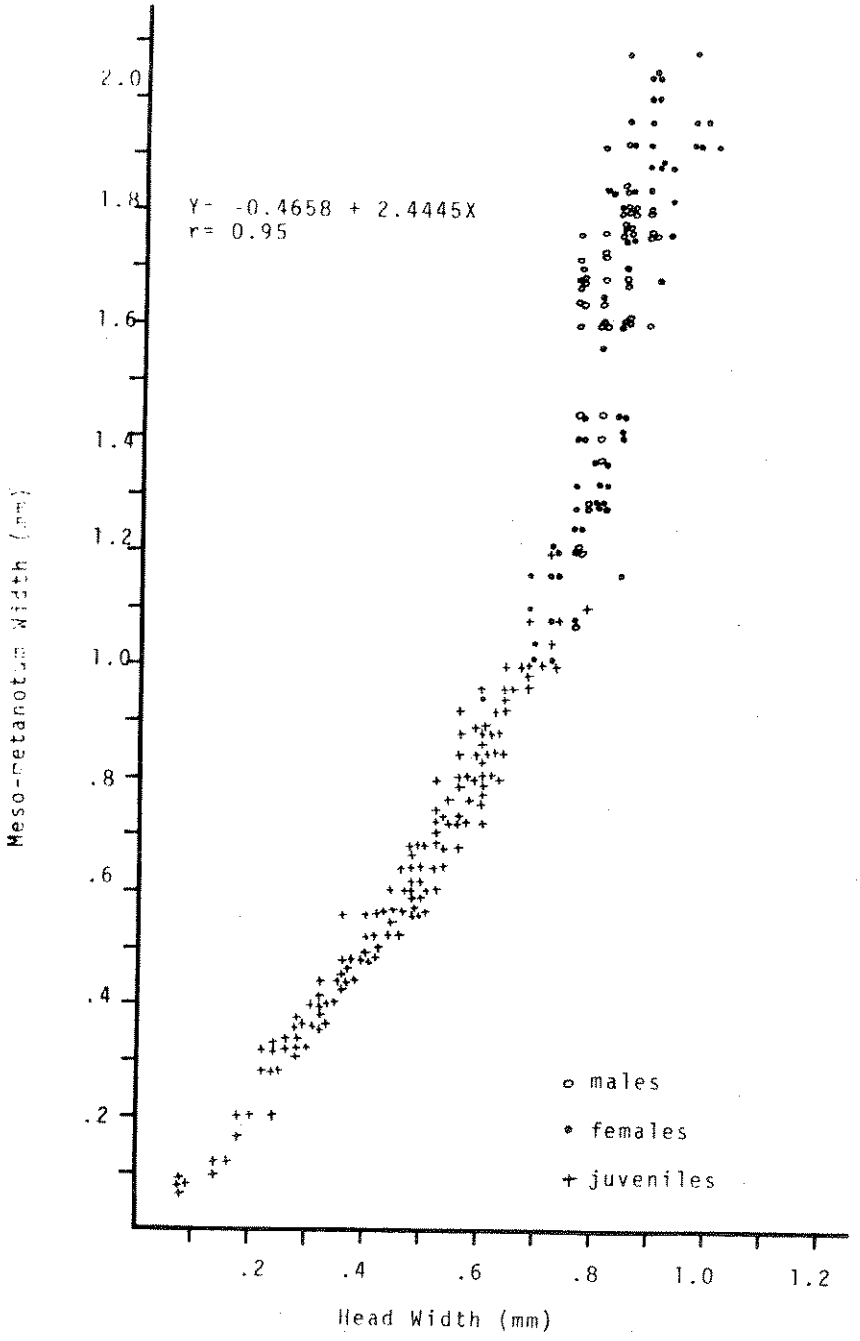

Y= -0.4658 + 2.4445X
r= 0.95
Meso-metanotum Width (mm)
Head Width (mm)
2.0
1.8
1.6
1.4
1.2
1.0
.8
.6
.4
.2
.2
.4
.6
.8
1.0
1.2
o males
• females
+ juveniles

Figure 14. Dry weight versus wet weight for T. minutus nymphs.

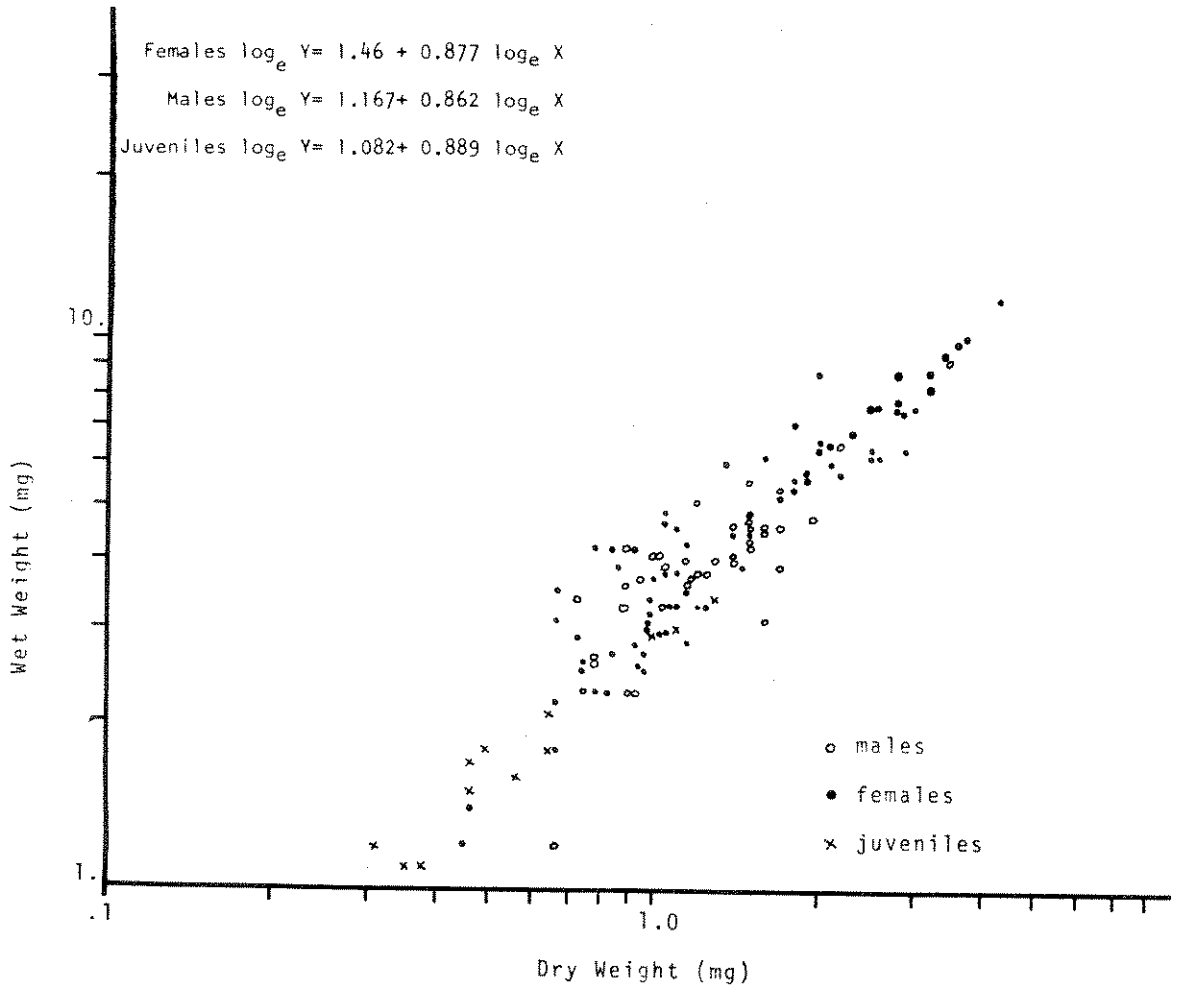

Females $\log_e$ Y= 1.46 + 0.877 $\log_e$ X
Males $\log_e$ Y= 1.167+ 0.862 $\log_e$ X
Juveniles $\log_e$ Y= 1.082+ 0.889 $\log_e$ X
10.
1.
.1
1.0
Wet Weight (mg)
Dry Weight (mg)
males
females
juveniles

Figure 15. Total length versus dry weight for T. minutus nymphs.

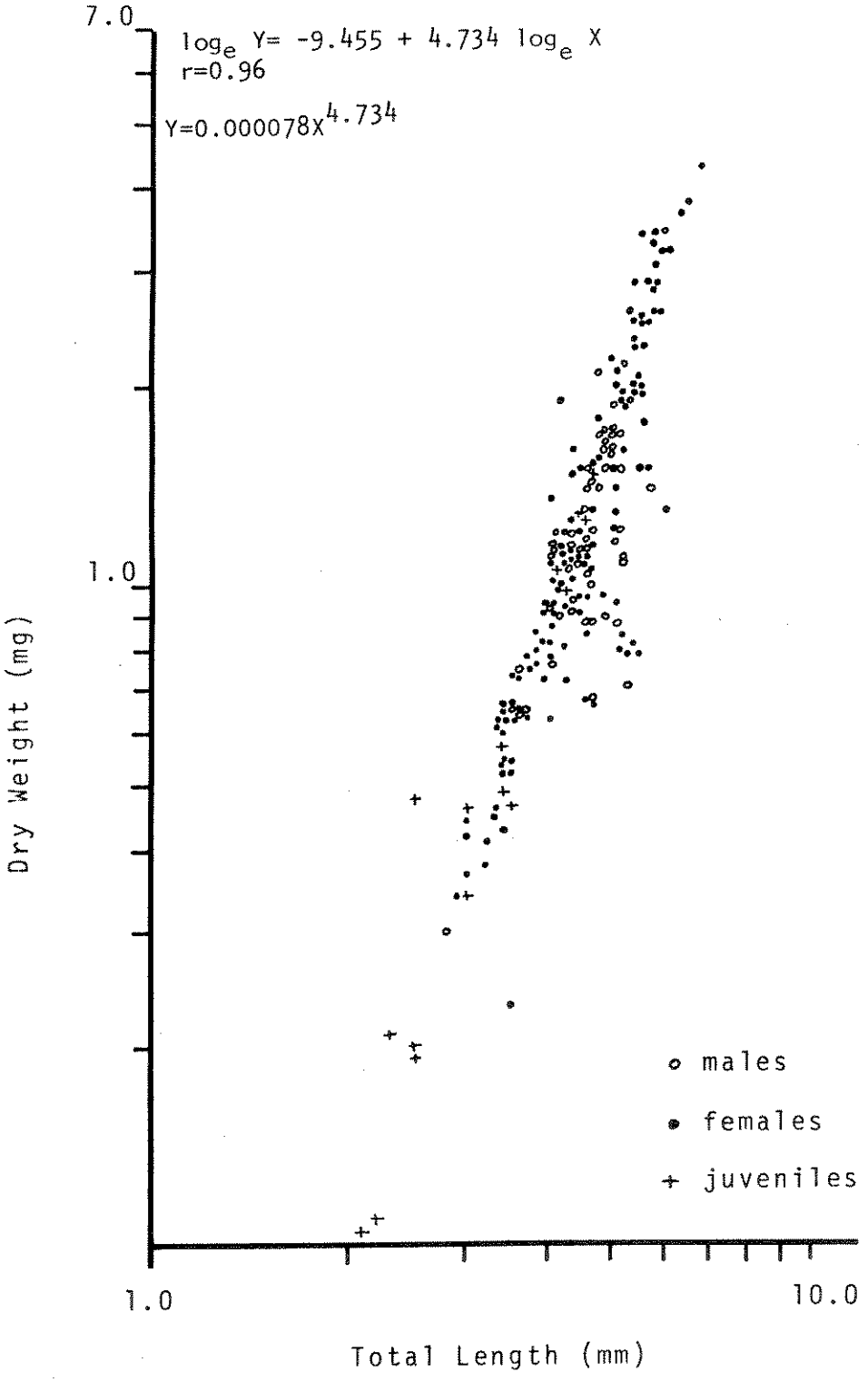

7.0
$\log_e Y = -9.455 + 4.734 \log_e X$
r=0.96
$Y=0.000078X^{4.734}$
1.0
Dry Weight (mg)
males
females
juveniles
1.0
10.0
Total Length (mm)

Figure 16. Total length versus dry weight for cast skins of T. minutus.

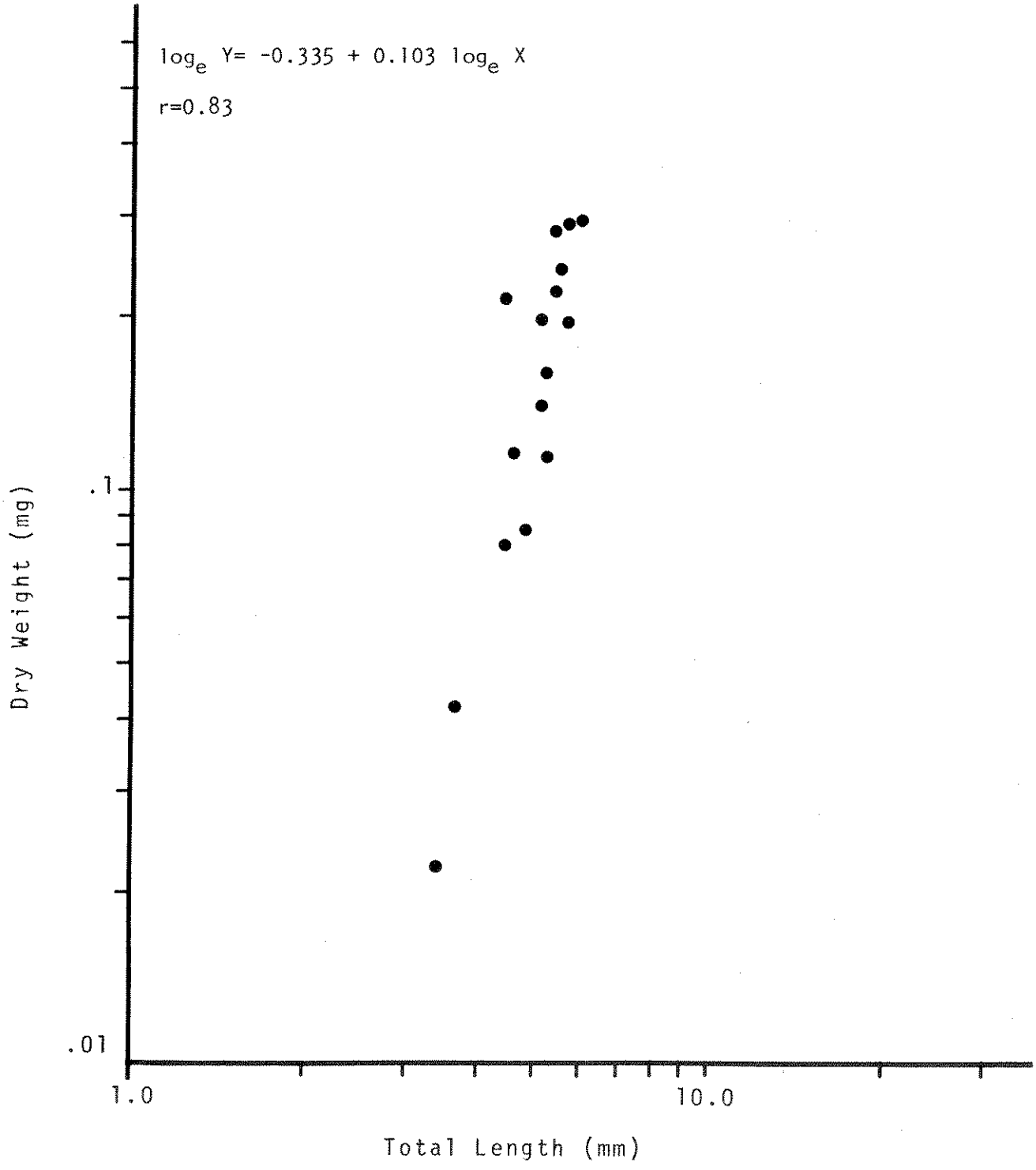

$\log_e Y = -0.335 + 0.103 \log_e X$
r=0.83
Dry Weight (mg)
.1
.01
1.0
10.0
Total Length (mm)

Table 4. Least squares regression analysis for several length-weight relationships of nymphs of T. minutus, where a=Y intercept, b= slope, r= correlation coefficient.

Sex	X	Y	a	b	r	N
Both	head w.	wet wt.	-9.1324	15.0534	0.53	140
Females	" "	" "	-9.5807	15.5161	0.56	100
Males	" "	" "	-7.5799	13.2541	0.48	51
Both	Total l.	wet wt.	-5.2213	2.0421	0.59	140
Females	" "	" "	-5.4014	2.0849	0.61	100
Males	" "	" "	-4.2606	1.8150	0.65	51

Table 5. Calorific values of T. minutus nymphs in (Kcal/g dry wt.) derived by Y=0.0559X, where X=% organic matter.

Sex	N	Y	S.E.	95% conf. limits
Females	40	4.783	0.049	4.649-4.916
Males	14	4.623	0.108	4.390-4.856
Juveniles	13	4.639	0.059	4.510-4.768
Totals	67	4.721	0.039	4.643-4.800
Brass (1971) Mixed population		4.767	1.000	3.767-5.767

the relationship between two measurements, whereas the least squares method defines two regression lines (Table 7). The slope statistic, in a log-log plot of two measurements, can be considered as the ratio of the two parts to each other. Clifford (1970b) used this function in a study of allometry in Leptophlebia cupida (Ephemeroptera). The slope of this power function is also referred to as the "constant of allometry" or alpha (a). When alpha equals 1, the two parts exhibit isometric growth; this condition does not often occur. Clifford (1970a) found isometric growth occurred for only a short time for two body measurements. Alpha was calculated by finding the ratio between total length and each of the five body measurements listed in Table 8. Alpha was calculated every week for the 16 week period required to complete development in the laboratory at 19°C. Since total length and all of the other measurements were changing continually throughout the study, the values of alpha changed concurrently. For example, in the value of alpha for total length, head width gradually increased from 0.298 from week one to week two reaching 0.912 between week 15 and 16 except for the anomalie between weeks 4 and 5. Alpha for many of the measurements was very erratic in the early weeks changing to a pattern of gradual increase (head and pronotum measurements) or gradual decrease (meso-metanotum measurements). Sexes were not differentiated and this may have influenced some of the values.

For T. minutus alpha approached a value of one only during the last weeks of growth (Table 8), indicating an allometric relationship

for most of the life cycle. Head measurements and pronotum width exhibited negative allometry ($a<1$) while meso-metanotum measurements showed positive allometry ($a>1$). Laboratory growth results from the 19°C tests were used because this temperature most closely approaches the mean water temperature at Deep Creek station 2. The decrease in all measurements during the last weeks of development is probably a consequence of a halt in feeding and atrophy of digestive organs just prior to emergence.

Plots of the values of alpha derived from the 19°C laboratory tests are presented in Figure 17. Several total lengths representing most of the instars of T. minutus were used to calculate alpha for the other five body measurements. These calculated values of alpha were then plotted against the same total lengths. The lines joining these values of alpha illustrate growth trends. Each line exhibits a slightly curvilinear relationship, each trending toward a slope of 1 in the final measurements. The ratio of total length to meso-metanotum width most closely approaches a slope of 1 throughout. Some further statistics derived from the allometric study are presented in Table 3.

Development of Nymphs

Life history: The development of T. minutus nymphs in Deep Creek station 2 appears to be multivoltine (Fig. 18). Most length classes (e.g. 1.6-2.5 mm etc.), were present during every month of the 24 month study period. The 1- and 2-mm size classes were predominant in almost every period and this suggests continued recruitment. Nymphs in the 1-mm class (0.6-1.5 mm) were not captured in as large numbers as

Table 6. Slope (b) and Y-intercept (a) of single regression lines using Bartlett's best fit on allometric data.

X	Y	b	a
Total length	head width	0.1432	0.1753
Total length	head length	0.1171	0.1413
Total length	pronotum width	0.2403	0.1513
Total length	meso-metanotum w.	0.3876	-0.1515
Total length	meso-metanotum l.	0.4557	-0.3939
Head width	head length	0.8174	0.0018
Head width	pronotum width	1.6775	-0.1424
Head width	meso-metanotum w.	2.7090	-0.6272
Head width	meso-metanotum l.	3.1808	-0.9508
Head length	pronotum width	2.1521	-0.1385
Head length	meso-metanotum w.	3.3139	-0.6209
Head length	meso-metanotum l.	3.8909	-0.9432
Pronotum width	meso-metanotum w.	1.6148	-0.3971
Pronotum width	meso-metanotum l.	1.8960	-0.6805
Meso-metanotum w.	meso-metanotum l.	1.1741	-0.2142

Table 7. Least squares regression analysis of allometric measurements, where the first set of data is regression X on Y and the following set concerns the same data but Y on X.

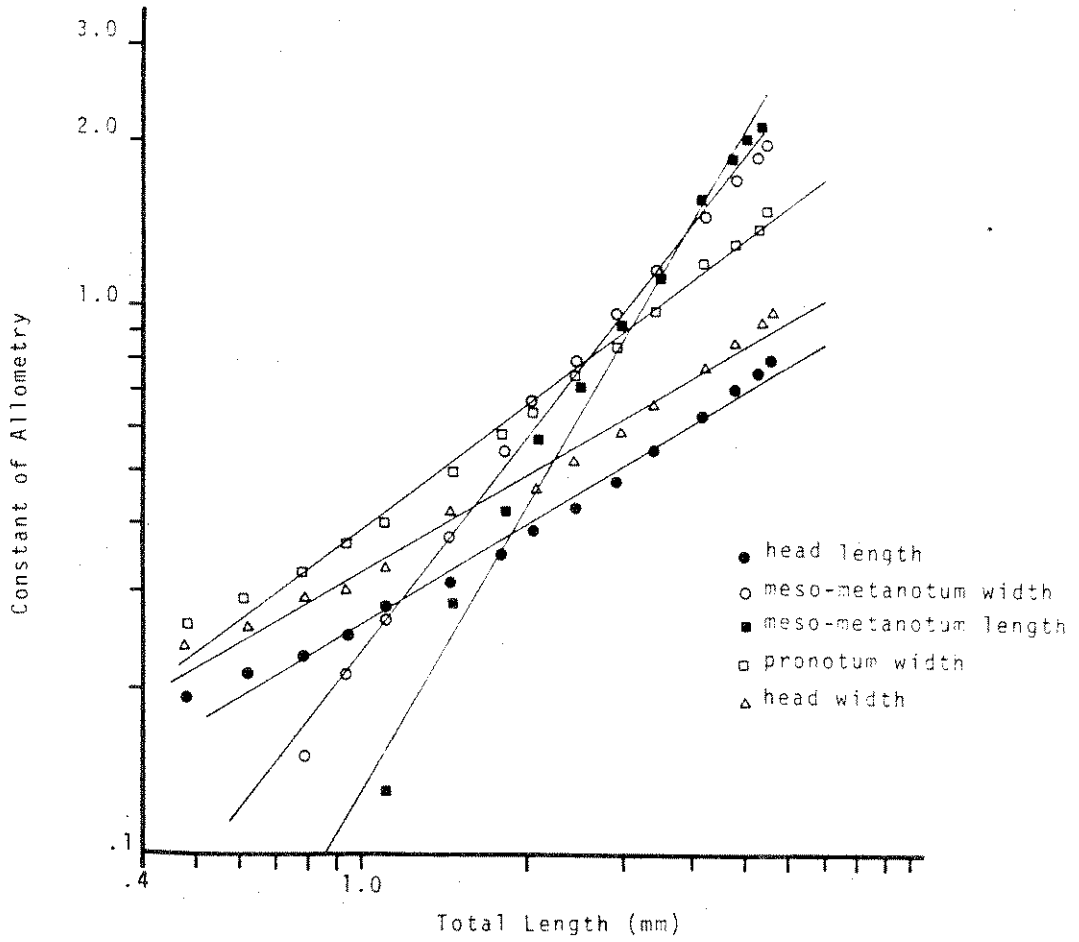
X	Y	Stand. Dev. r	b	95% C.L.±	a	95% C.L.±
Total l.	head W.	.0659	.1466	.0023	.1648	.0104
	r=0.95	.4283	6.2015	.0763	-.7464	.0688
Total l.	head l.	.0672	.1192	.0023	.1347	.0106
	r=0.93	.5237	7.2500	.0011	-.5648	.0838
Total l.	pro. w.	.0784	.2428	.0027	.1436	.0124
	r=0.98	.3150	3.9160	.0383	-.4132	.0503
Total l.	meso. W.	.1118	.3885	.0038	-.1542	.0176
	r=0.98	.2820	2.4729	.0278	.5009	.0437
Total l.	meso. l.	.1654	.4428	.0057	-.3548	.0260
	r=0.97	.3612	2.1126	.0352	.9457	.0547
Head w.	head l.	.0497	.8024	.0088	.0073	.0079
	r=0.96	.0596	1.1536	.0130	.0370	.0095
Head w.	pro. w.	.0595	1.5965	.0106	-.0929	.0095
	r=0.99	.0367	.6087	.0045	.0738	.0058
Head w.	meso. w.	.1789	2.4445	.0319	-.4658	.286
	r=0.95	.0694	.3679	.0068	.2328	.0107
Head w.	meso. l.	.2691	2.7115	.0479	-.6641	.0432
	r=0.91	.0904	.3059	.0088	.3074	.0137
Head l.	pro. w.	.1068	1.8534	.0233	-.0395	.0170
	r=0.91	.0549	.4905	.0067	.0648	.0087
Head l.	meso. w.	.2284	2.8281	.0500	-.3783	.0364
	r=0.84	.0738	.2956	.0073	.1938	.0114
Head l.	meso. l.	.3065	3.1642	.0670	-.5826	.0489
	r=0.78	.0855	.2465	.0083	.2536	.0130
Pro. w.	meso. w.	.1245	1.5520	.0152	-.3411	.0198
	r=0.95	.0784	.6127	.0077	.2527	.0121
Pro. w.	meso. l.	.2219	1.7338	.0270	-.5386	.0352
	r=0.88	.1201	.5117	.0117	.3746	.0183
Meso. w.	meso. l.	.1432	1.1302	.0141	-.1710	.0223
	r=0.95	.1236	.8423	.0121	.1938	.0187

Pro.= pronotum, Mes.= meso-metanotum, w= width, l= length.
N= 284.

Table 8. Allometric constant (a) from laboratory growth at 19°C for total length against the following measurements (all positive).

Week	HEAD Width	HEAD Length	PRONOTUM Width	MESO-METANOTUM Width	MESO-METANOTUM Length
1	0.298	0.331	0.480	3.907	----
2	0.385	0.378	0.540	2.333	----
3	0.428	0.433	0.598	1.849	----
4	1.588	1.593	2.144	5.428	----
5	0.527	0.531	0.681	1.465	2.814
6	0.596	0.582	0.542	1.328	2.006
7	0.634	0.630	0.770	1.268	1.719
8	0.665	0.672	0.793	1.213	1.550
9	0.701	0.692	0.814	1.167	1.426
10	0.735	0.743	0.840	1.144	1.334
11	0.769	0.763	0.861	1.116	1.274
12	0.799	0.803	0.885	1.098	1.222
13	0.825	0.821	0.843	1.086	1.190
14	0.821	0.803	0.945	1.058	1.158
15	0.912	0.840	0.899	1.016	1.116
16					

Figure 17. Logarithmic plot of the constant of allometry and total length for the five body measurements analyzed at 19°C.

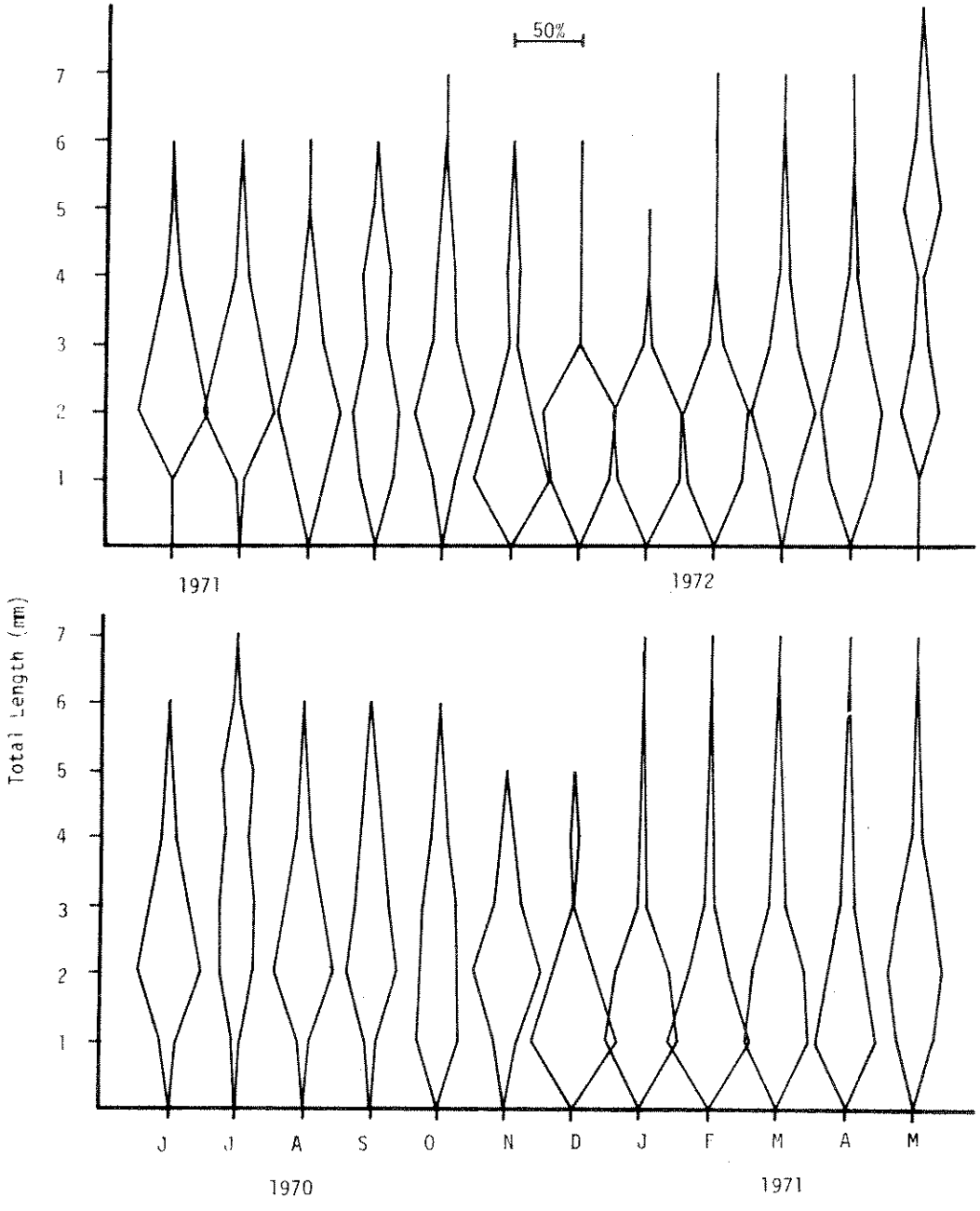

3.0
2.0
1.0
.1
.4
1.0
Constant of Allometry
Total Length (mm)
head length
meso-metanotum width
meso-metanotum length
pronotum width
head width

some of the other classes because of loss through the collecting net (mesh opening 390 um). Nymphs larger than 4.5 mm were usually present and their impending emergence would result in adults being present throughout the year.

The life cycle at Deep Creek station 4 (Fig. 19) deviated considerably from that at station 2. Only small size classes (<4.0 mm) were present from November to April, after which time larger nymphs began appearing. Although the small number of nymphs collected makes interpretation difficult, it seems that T. minutus is bivoltine at this station. Emergence of the mature nymphs present in the June through November period would initiate the second generation as evidenced by very small nymphs in June. These nymphs could complete their development in the June-August period. An August-September emergence of this cohort would start the next generation whose growth is slowed by the cold fall water temperatures. About 25,000°h were available for growth during both the June-August and September-May periods (Table 2).

The life cycle in Spring Creek was also bivoltine (Fig. 20). Mature nymphs were present in almost every month's sample. One cycle begins with egg hatching in August-September and adults emerge from March-June. Assuming that these adults mate successfully and lay eggs, the second generation would begin in May and June. The majority of nymphs captured in June were in the 1.6-2.5 mm size group, a size they could have attained in one month's growth. This group of nymphs grew rapidly throughout the summer emerging in August-September with some isolated individuals emerging in later months. The assumption here is that mature nymphs (>4.5 mm long) will emerge soon, mate and deposit eggs

Figure 18. Percent of all size classes of T. minutus nymphs collected from bottom samples from 1970-72, at Deep Creek station 2.


50%
7
6
5
4
3
2
1
1971
1972
Total Length (mm)
7
6
5
4
3
2
1
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

in the stream. About 25,000°h are available for both generations (Table 2). The life cycle of T. minutus in Spring Creek is not as clear as it is in Deep Creek. The presence of small nymphs (< 2.5 mm) and mature nymphs (>4.5 mm) during most of the year suggests a multivoltine cycle here.

Instar analysis was done by means of head width, total length, and cast skin length according to the method of Janetschek (1962). Although this method has not been used previously on Ephemeroptera, it may apply in the determination of number of instars in an insect group that has continually resisted accurate instar determination. Only six instars could be differentiated on the basis of head measurements alone, which appears to be too low a number for this species. Harker (1973) made head measurements on Plecoptera to the nearest 0.001 mm. The low instar number may be due to the fact that head measurements in the present study were made only to the nearest 0.01 mm.

Cast skins were obtained for almost every body length thus illustrating the variability in the measurements or the wide range of lengths when molting can occur. It was difficult to precisely measure cast skins because of their limp nature. Several modes appeared, however, in the frequency histogram (Fig. 21). Figure 21-B is the sum of the frequency of each 0.1 mm measurement and the two measurements on either side of that measurement. Figure 21-C represents the algebraic sum of Fig. 21-A and Fig. 21-B for each 0.1 mm. If Dyar's rule of constant relative growth increment between successive instars is followed, the peaks should be at equal distances along a logarithmic scale (Fig.22).

Figure 19. Percent of all size classes of T. minutus nymphs collected from bottom samples from 1970-72, at Deep Creek station 4.

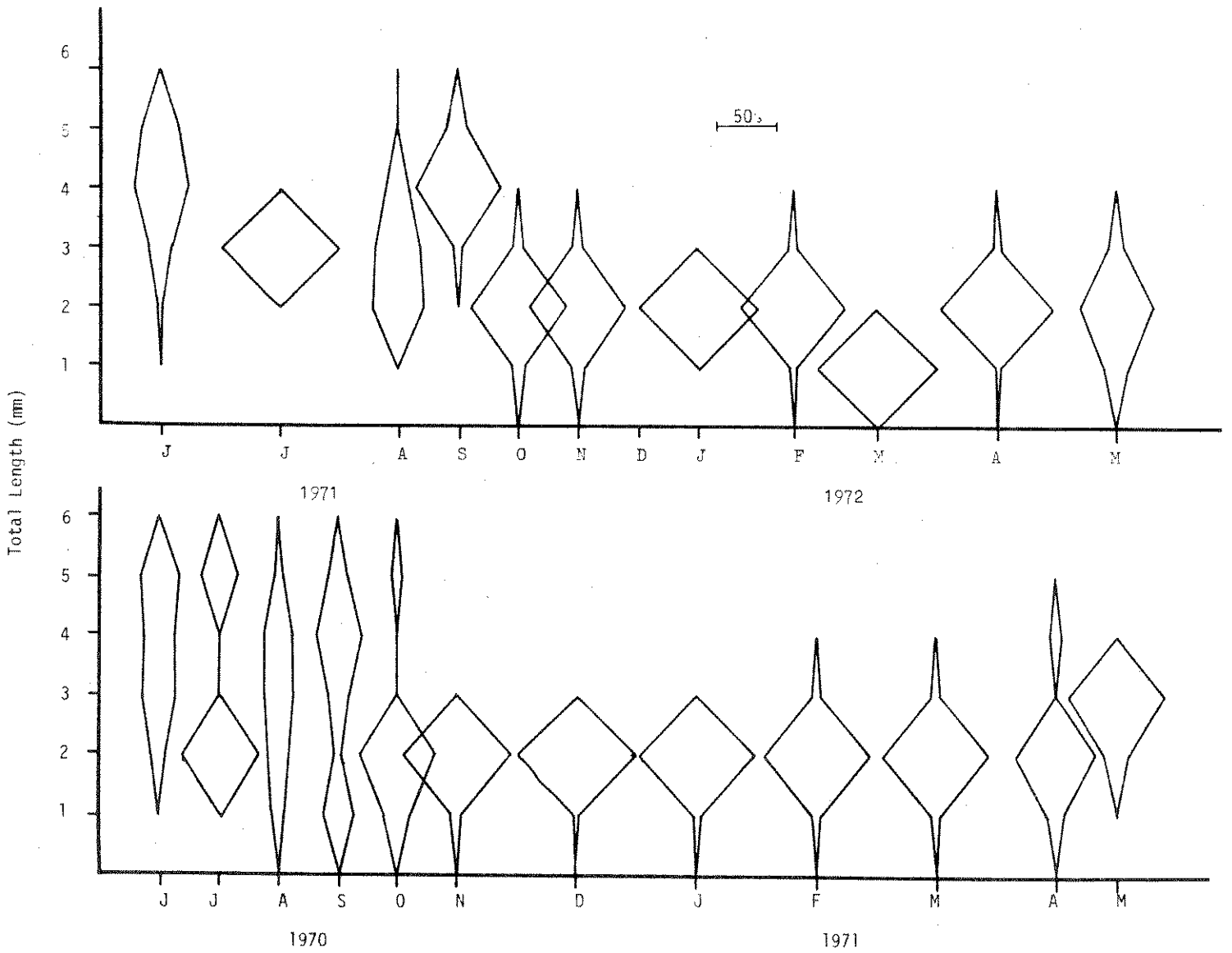
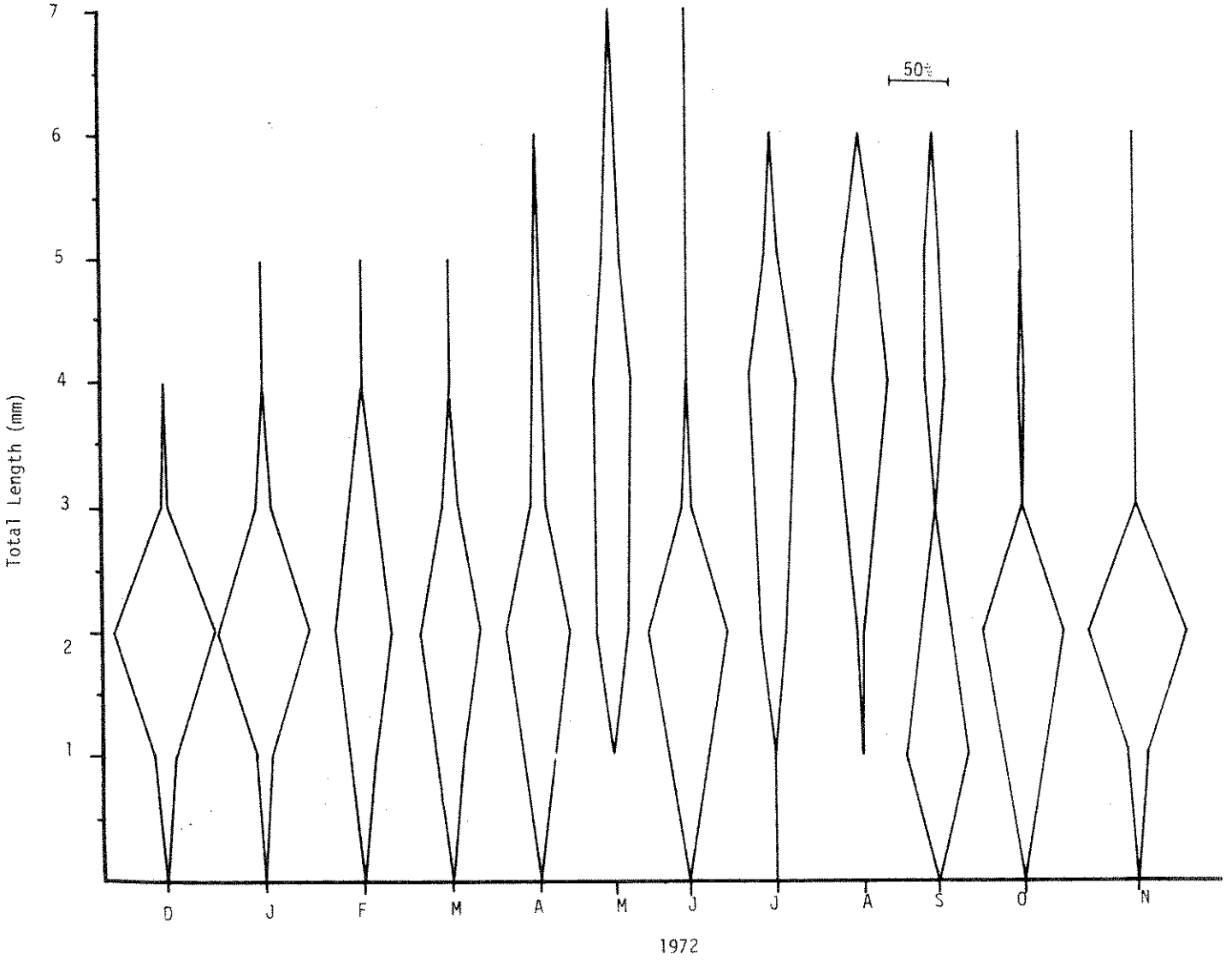

Total Length (mm)
6
5
4
3
2
1
50%
J
J
A
S
O
N
D
J
F
M
A
M
1971
1972
6
5
4
3
2
1
J
J
A
S
O
N
D
J
F
M
A
M
1970
1971

Figure 20. Percent of all size classes of T. minutus nymphs collected from kick samples during 1972 at Spring Creek.


7
6
5
4
3
2
1
Total Length (mm)
50%
D
J
F
M
A
M
J
J
A
S
O
N
1972

but a line connecting the points is slightly curved which illustrates that Dyar's rule is not followed exactly. A gap between points one and two suggests the presence of at least one and probably three additional points, making a maximum of 23 instars. The same technique was used with total lengths (Fig. 23). These values were handled just like the cast skin values (Fig. 21) and resulted in the formation of 16 points. A gap is again found; if three additional instars are added to fill this gap, a total of 19 instars appears. The interesting aspect here is the closeness of instar estimates for the two applications. In fact for 11 instars the two methods agree exactly (Fig. 22). The four extra points obtained at the upper end of the curve probably are for females only, since males seldom grow larger than 5.5 mm in length. If this logic is followed, males would have a maximum of 19 instars and females 23 instars. Although there seems to be some variation in the total length at molting, enough molts occur at predetermined lengths that instar analysis is possible. The total number of molts possible during the insect's life cycle does not seem fixed as emergence can occur anytime the insect reaches about 4.5 mm in length. This variability complicates any attempts to estimate production or to predict emergence.

Mortality rates: Mortality rates were found for nymphs held in culture chambers in the laboratory by recording the number that died and that disappeared from the chambers. Mortality rate varied between 9.1% and 25% (Table 9); the small sample size and unnatural conditions for the nymphs undoubtedly contributed to some of the high values. A breakdown

Figure 21. Instar analysis using total length of cast skins. A is a frequency histogram of total lengths of cast skins from all sources, growth chambers, stream drift, etc., B is the algebraic sum of each measurement and the two values on either side, and C is a plot of the algebraic sum of histograms A and B. The positive peaks represent instars.

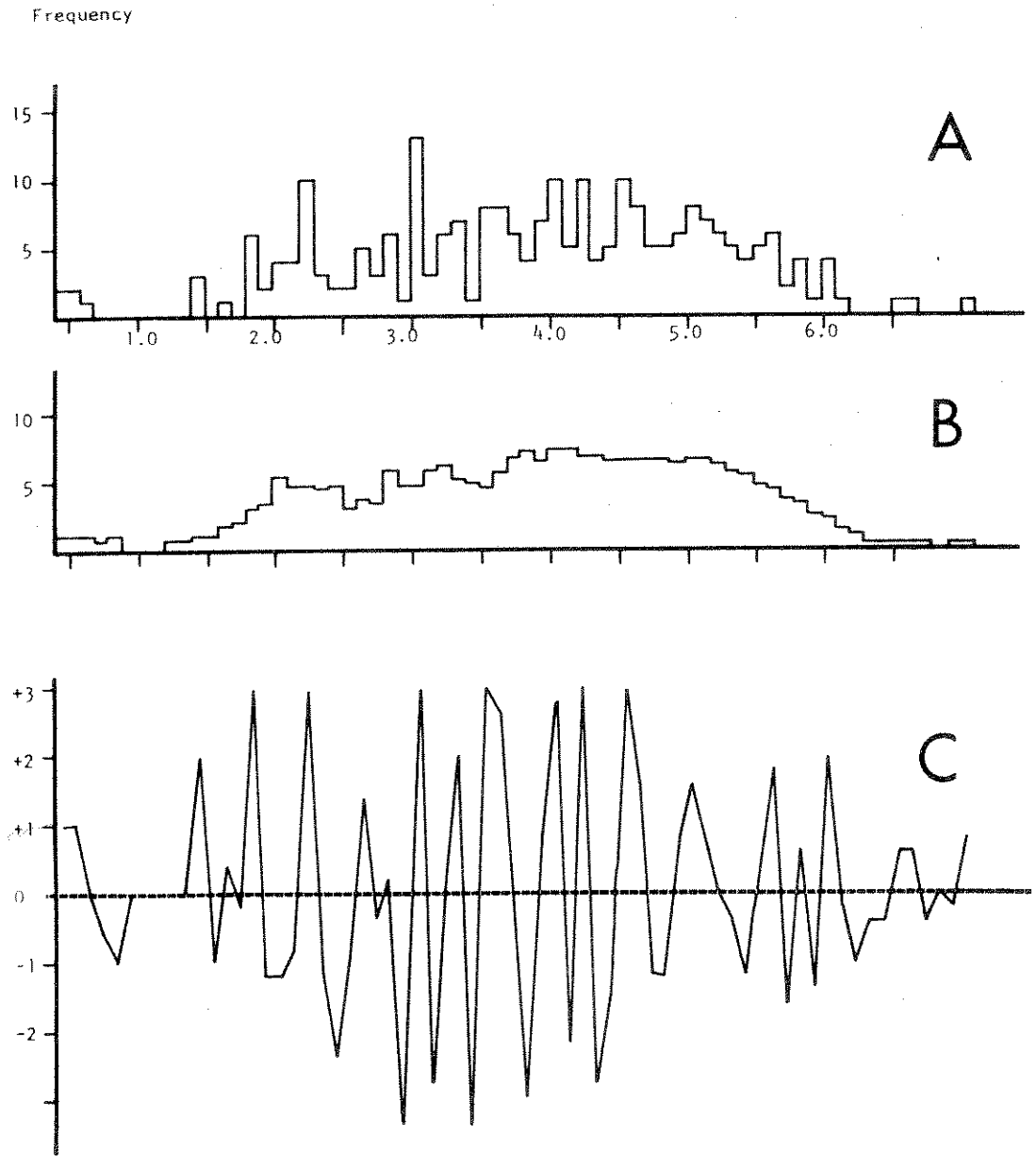

Frequency
15
10
5
1.0
2.0
3.0
4.0
5.0
6.0
A
10
5
B
+3
+2
+1
0
-1
-2
C

Figure 22. Results of instar analysis where instars calculated from total length of nymphs and cast skins are plotted using the Janetscheck method.

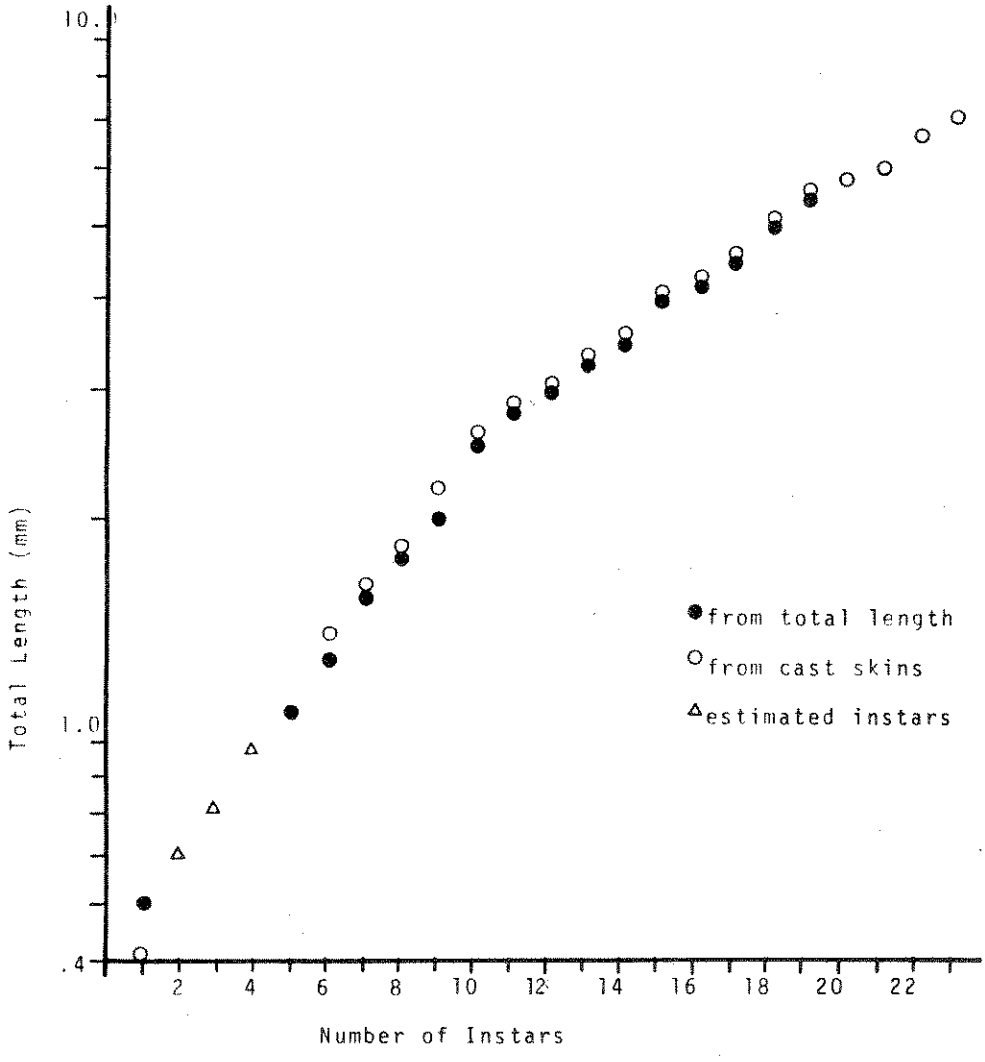
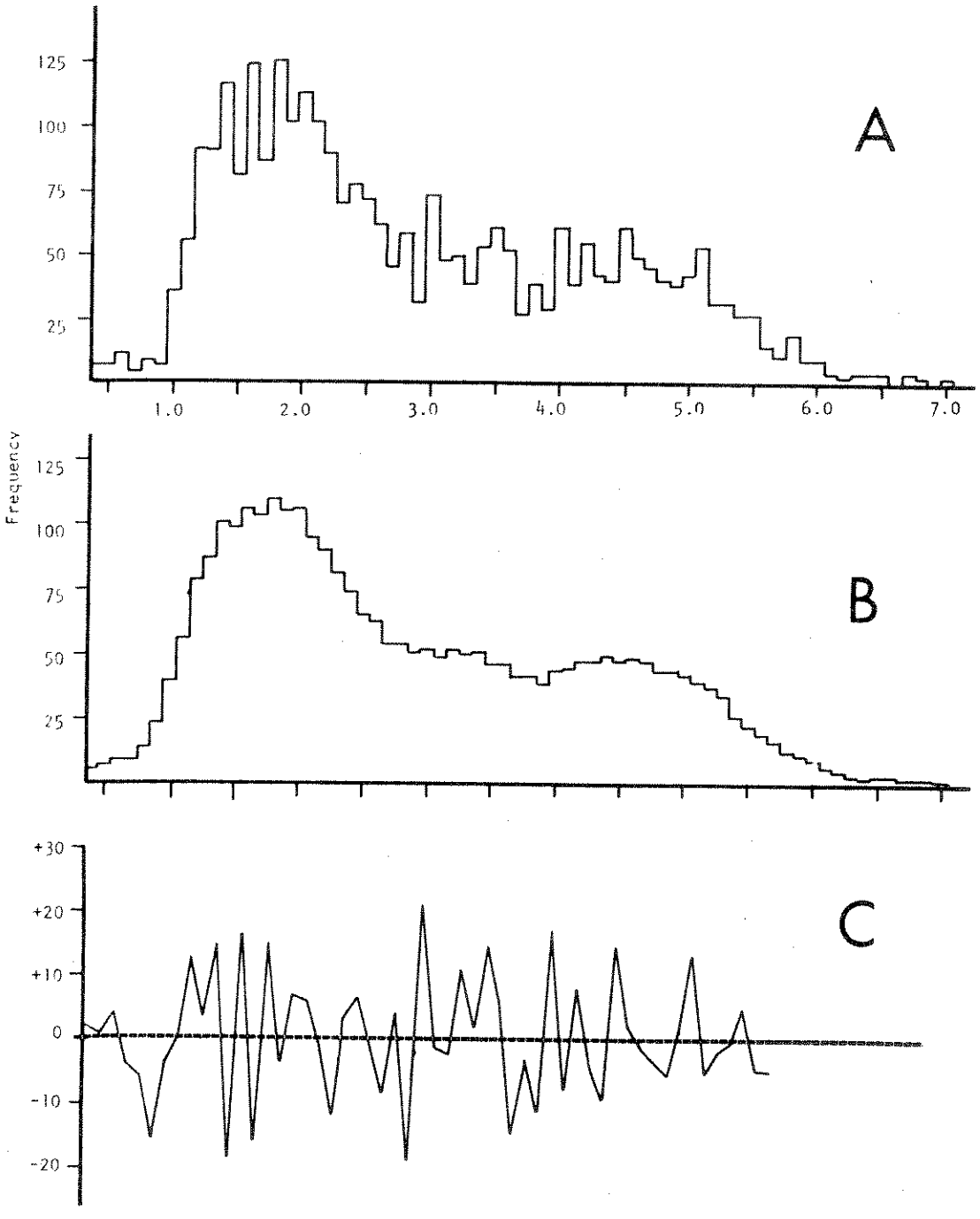

10.
1.0
.4
Total Length (mm)
2
4
6
8
10
12
14
16
18
20
22
Number of Instars
from total length
from cast skins
estimated instars

Figure 23. Instar analysis using total length of nymphs. A is a frequency histogram of total lengths of nymphs from Deep Creek station 2 throughout one year, B is the algebraic sum of each measurement and the two values on either side and C is a plot of the algebraic sum of histograms A and B. The positive peaks represent instars.


125
100
75
50
25
A
1.0
2.0
3.0
4.0
5.0
6.0
7.0
Frequency
125
100
75
50
25
B
+30
+20
+10
0
-10
-20
C

of these rates showed that the highest mortality rates occurred in the smallest size classes: 78% in the 2-mm class; 17% in the 2-3-mm class, and; only 5% in the 3-mm class. In the field growth chambers the rate was 9.1% in Deep Creek and no mortality was evident in the Spring Creek growth chambers.

Table 9. Mortality rates of T. minutus nymphs from field and laboratory growth chambers.

Test	N	Mortality rate
9°	49	14.3%
14	44	25%
18	41	22%
18±3	56	21.4%
19	43	11.6%
23	47	17%
Deep Cr. (field)	55	9.1%
Spring Cr. (field)	6	0

Distribution and Abundance

In Deep Creek station 2, T. minutus often was very abundant, reaching densities as great as 11,250/m^2 (Fig. 24). Only the elmid beetle Optioservus spp. and the amphipod Hyalella azteca exceeded this mayfly in abundance (Minshall et al. 1973). During the first year of the study benthic densities of T. minutus at station 2 averaged 3600/m^2 and decreased to 2200/m^2 during the second year and a mean density of 2700/m^2 was observed over the 27 months of the study (Table 10). Densities of nymphs at station 2 were low during summer months, and high during the winter. The seasonal trend was more

evident in samples from riffle areas (Fig. 24) than from reach areas (Fig. 25). Duplicate monthly samples taken from riffle areas were less variable than those from pools. Stream flow varied drastically due to artificial manipulation and benthic regions often were left exposed probably accounting for low summer densities. Total dry weight biomass of T. minutus was very high (2350-2125 mg) during initial stages of the study but then showed a definite but erratic decline (Fig. 26).

At station 4 benthic densities of T. minutus were consistently lower than at station 2, averaging 290/m^2 over the study period (Table 10). The greatest number collected (1400/m^2) occurred during the winter. No definite seasonal trend was evident (Fig. 28). In many samples there was a wide variation in numbers collected from the monthly duplicate samples. Dry weight biomass estimates at station 4 showed seasonal trends of high values during June and August with low values during the remaining months. Yearly biomass totals and means were about five times less than at station 2. No quantitative sampling was done at Spring Creek.

Food

Laboratory observations on feeding behavior show that T. minutus is a grazer; it moves across the substratum ingesting a variety of items. Table 11 lists the maximum particle sizes that eight different size classes of nymphs ingested. The gut contents constitute about 11 per cent of the total weight of a nymph (range 5.1-18.2%). This is included in the body weights given elsewhere. In feeding, any particle

Table 10. Benthos densities and dry weight biomass estimates of Tricorythodes minutus nymphs from Deep Creek, stations 2 and 4.

Station	Time period	Total number (per m^2)	$\bar{X}$	Total weight (mg)	$\bar{X}$
Station 2	June 1970-June 71	43,318	3610	9.22	0.77
	" 1971- " 72	25,923	2160	4.02	0.34
	" 1972-Aug. 72	4,620	1540	0.99	0.33
Station 4	June 1970-June 71	3,604	300	1.30	0.11
	" 1971- " 72	2,808	234	0.92	0.08
	" 1972-Aug. 72	1,424	475	1.01	0.34

Figure 24. Quantitative bottom sample results of T. minutus nymphs from riffle areas of Deep Creek, station 2. The stippled portion represents the variation between duplicate monthly Hess samples.

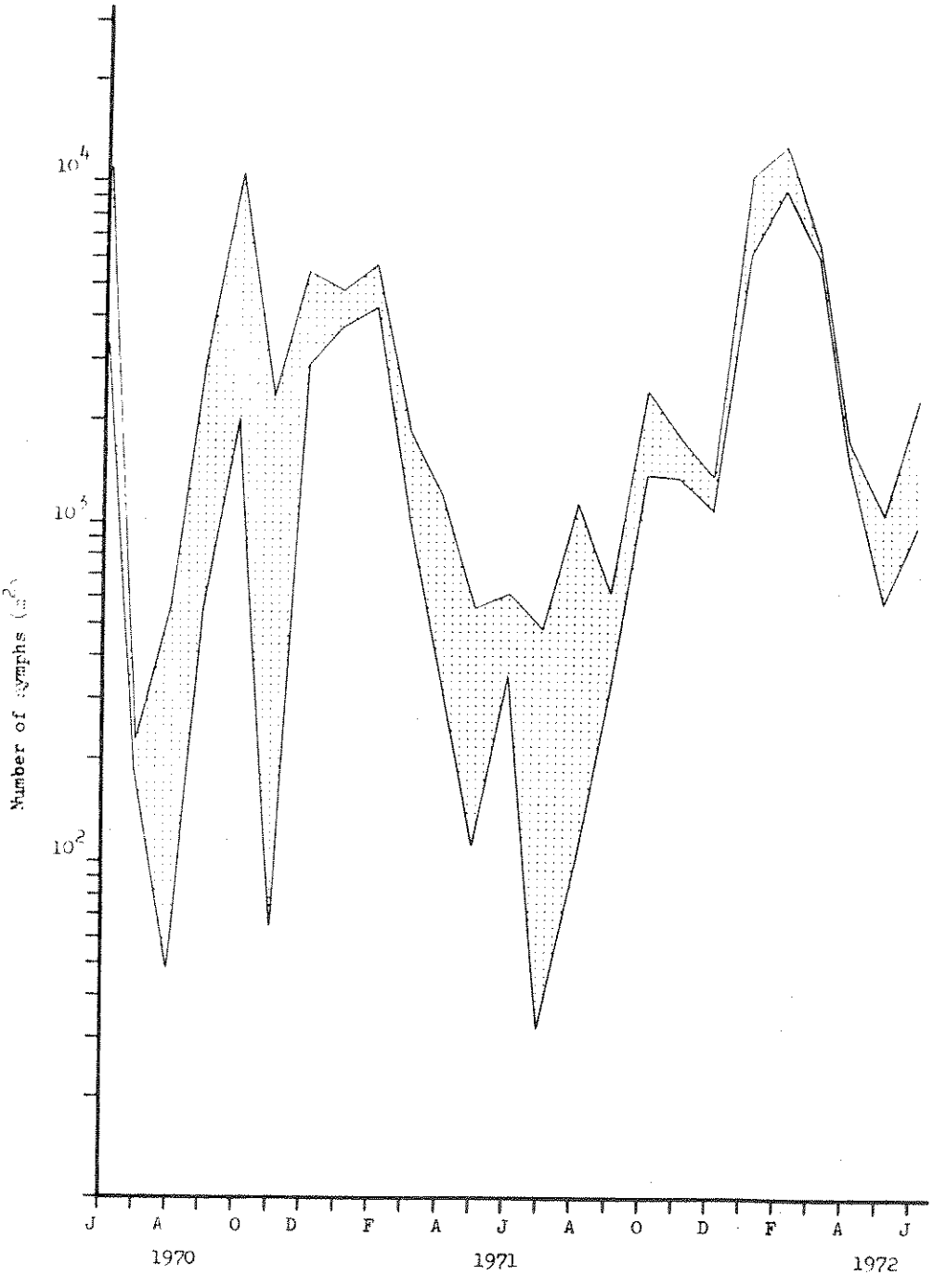

10^4
10^3
10^2
Number of nymphs (m^2)
J
A
O
D
F
A
J
A
O
D
F
A
J
1970
1971
1972

Figure 25. Quantitative bottom sample results of T. minutus from reach areas of Deep Creek, station 2. The stippled portion represents the variation between duplicate monthly Hess samples.

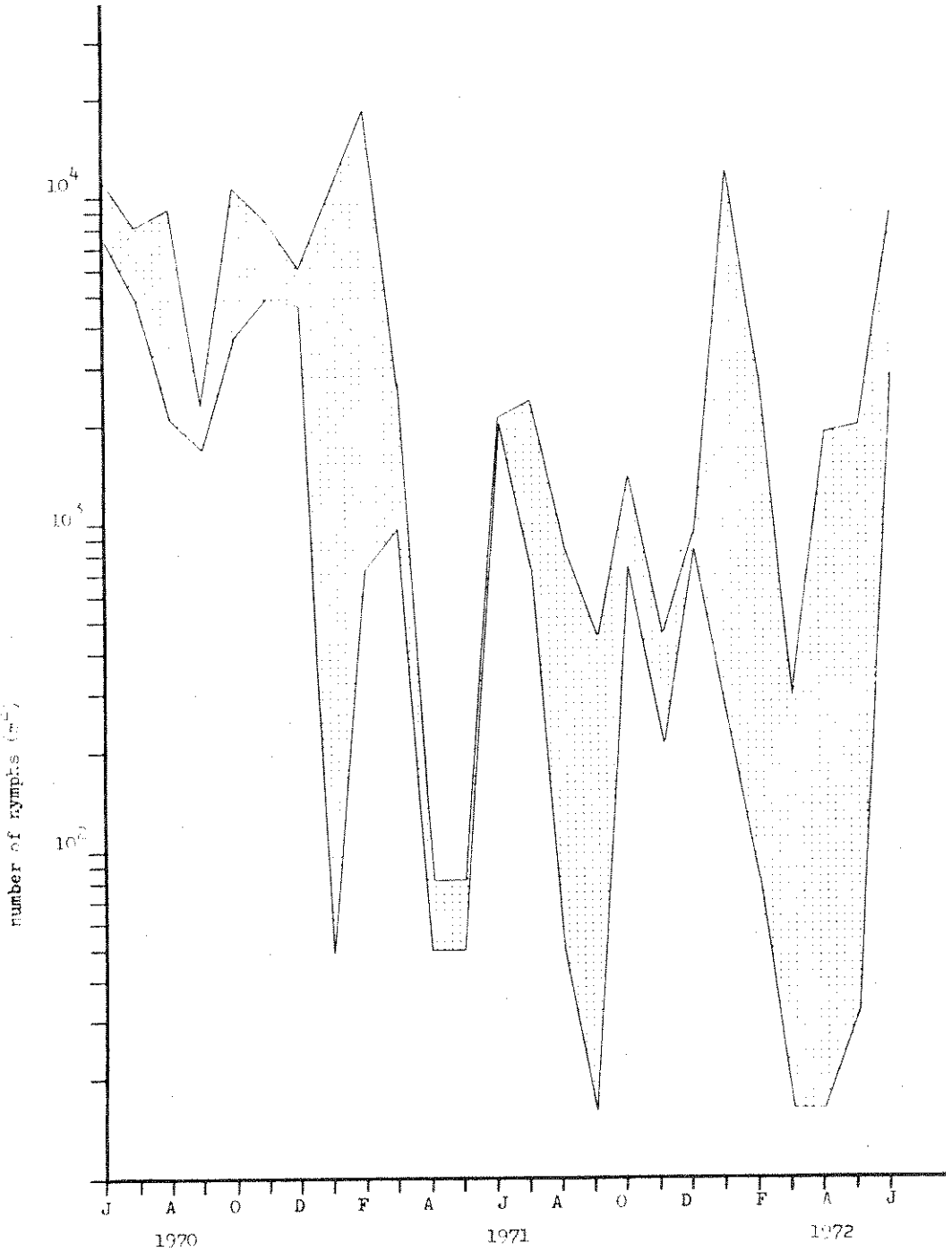

10^4
10^5
number of nymphs (m^{-2})
J
A
O
D
F
A
J
A
O
D
F
A
J
1970
1971
1972

Figure 26. Dry weight biomass estimates of T. minutus nymphs from Deep Creek station 2.

Figure 27. Dry weight biomass estimates of T. minutus nymphs from Deep Creek station 4.

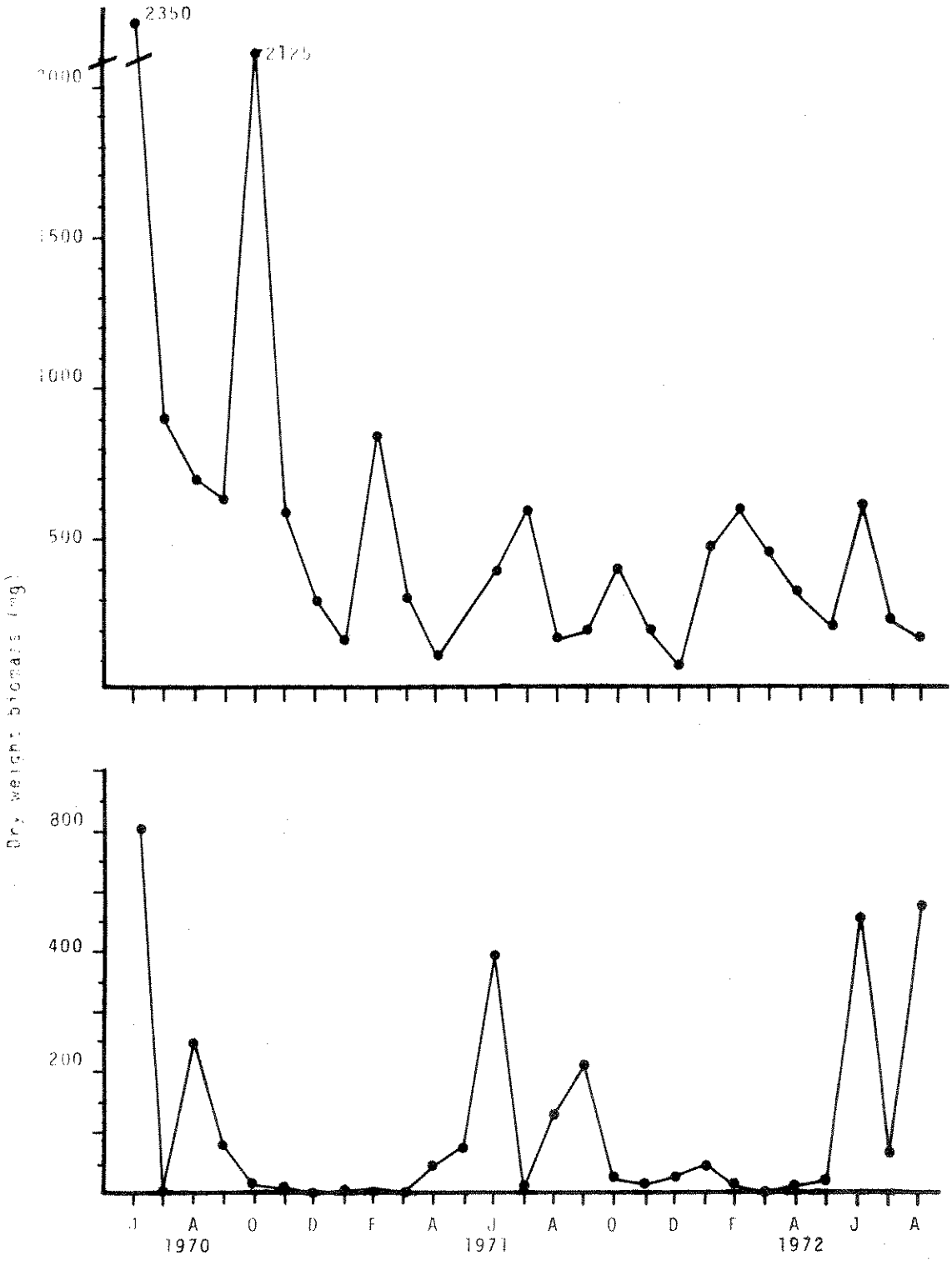
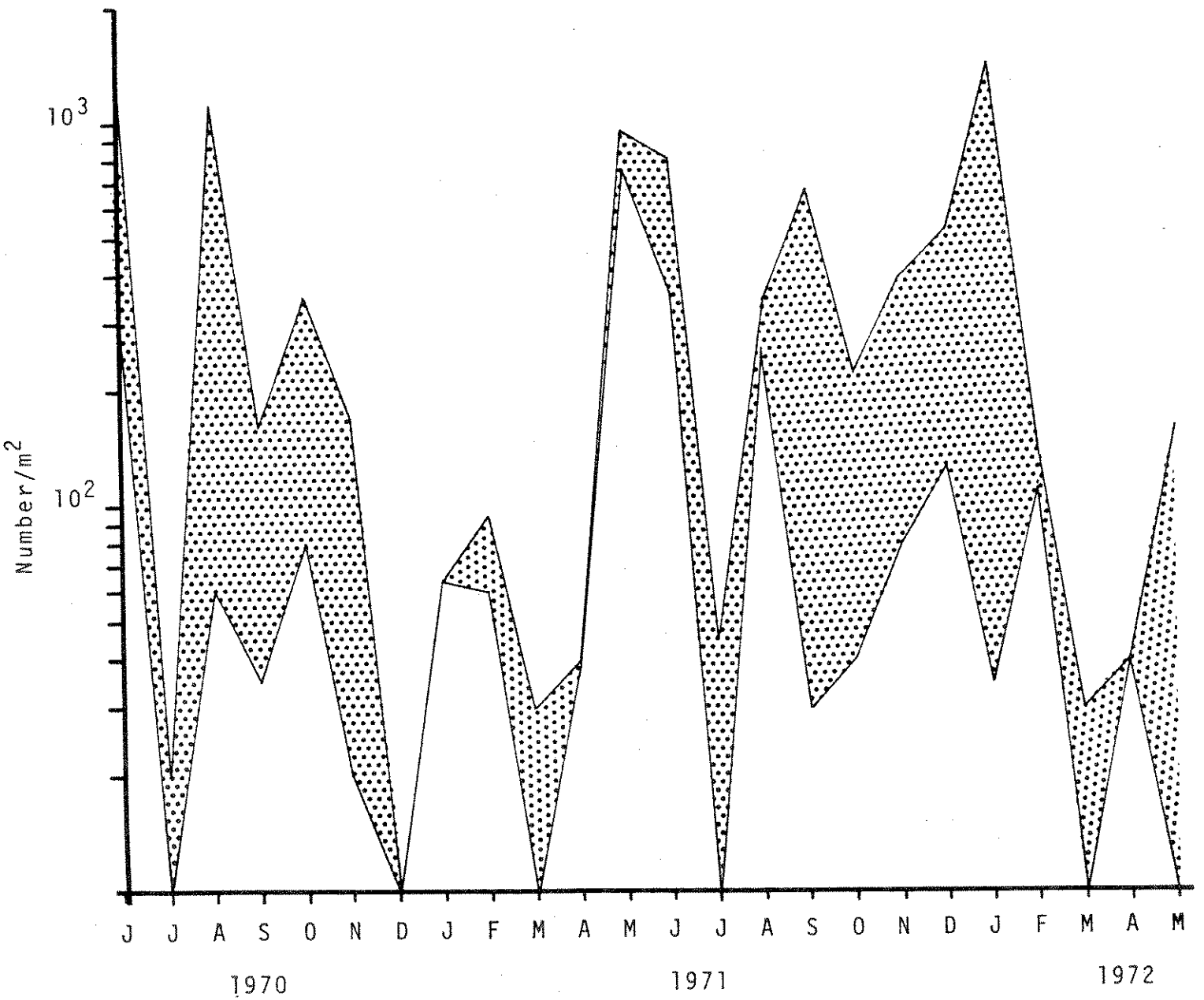

2350
2125
2000
1500
1000
500
800
400
200
Dry weight biomass (mg)
J A O D F A J A O D F A J A
1970
1971
1972

Figure 28. Quantitative bottom samples results of T. minutus from Deep Creek station 4. The stippled area is the variation between duplicate monthly Hess samples.


10^3
10^2
Number/m^2
J J A S O N D J F M A M J J A S O N D J F M A M
1970
1971
1972

small enough to be ingested is taken in and this includes sand, dead organic matter, algae, and other micro-organisms. In the gut, however, only three categories were distinguishable: sand, amorphous organic matter, and diatoms. Koslucher and Minshall (1973) investigated the food habits of T. minutus in Deep Creek but did not distinguish between mineral and organic detritus. In the present study, the two categories were considered separately in order to learn if much of the detritus is mineral and of no metabolic significance. In addition, many of the smallest diatoms shown in the present study to be ingested by the nymphs probably were missed by Koslucher because many of his counts were made at 150X magnification. Figures 29-30 show the three major gut items by percentage for different size classes at different magnifications. Gut contents of Deep Creek nymphs were compared with those of nymphs from Spring Creek. In Deep Creek, mineral detritus comprised the majority of gut items and the Spring Creek gut analysis data showed a similiar trend. Magnification did have an effect in Deep Creek, the percentage of diatoms generally increased with magnification but this trend was less evident in the Spring Creek samples. Most guts were near half-full and this suggests that micro-organisms adhering to the particles may be important as food for Tricorythodes.

In Deep Creek, gut contents for the smallest class nymphs were about 65 per cent sand, 30 per cent organic matter, and 5 per cent diatoms. The percentage of diatoms increased and sand decreased with increasing total length. Gut contents of nymphs larger than 3.4 mm in length contained about equal portions of the three food items.

Table 11. Maximum particle size found in guts of *T. minutus* nymphs. Five guts were examined from each class from nymphs captured during the summer months.

Size class (mm)	Largest particle (mm)
1.6-2.0	0.0056 X 0.0070
2.1-2.3	0.0098 X 0.0098
2.6-3.0	0.0098 X 0.0112
2.7-3.1	0.0098 X 0.0126
3.6-4.1	0.0112 X 0.0140
3.4-4.2	0.0140 X 0.0168
4.4-4.9	0.0168 X 0.0238
4.8-5.3	0.0238 X 0.0238

Figure 29. Gut contents of T. minutus nymphs taken during the summer months from Deep Creek station 2.

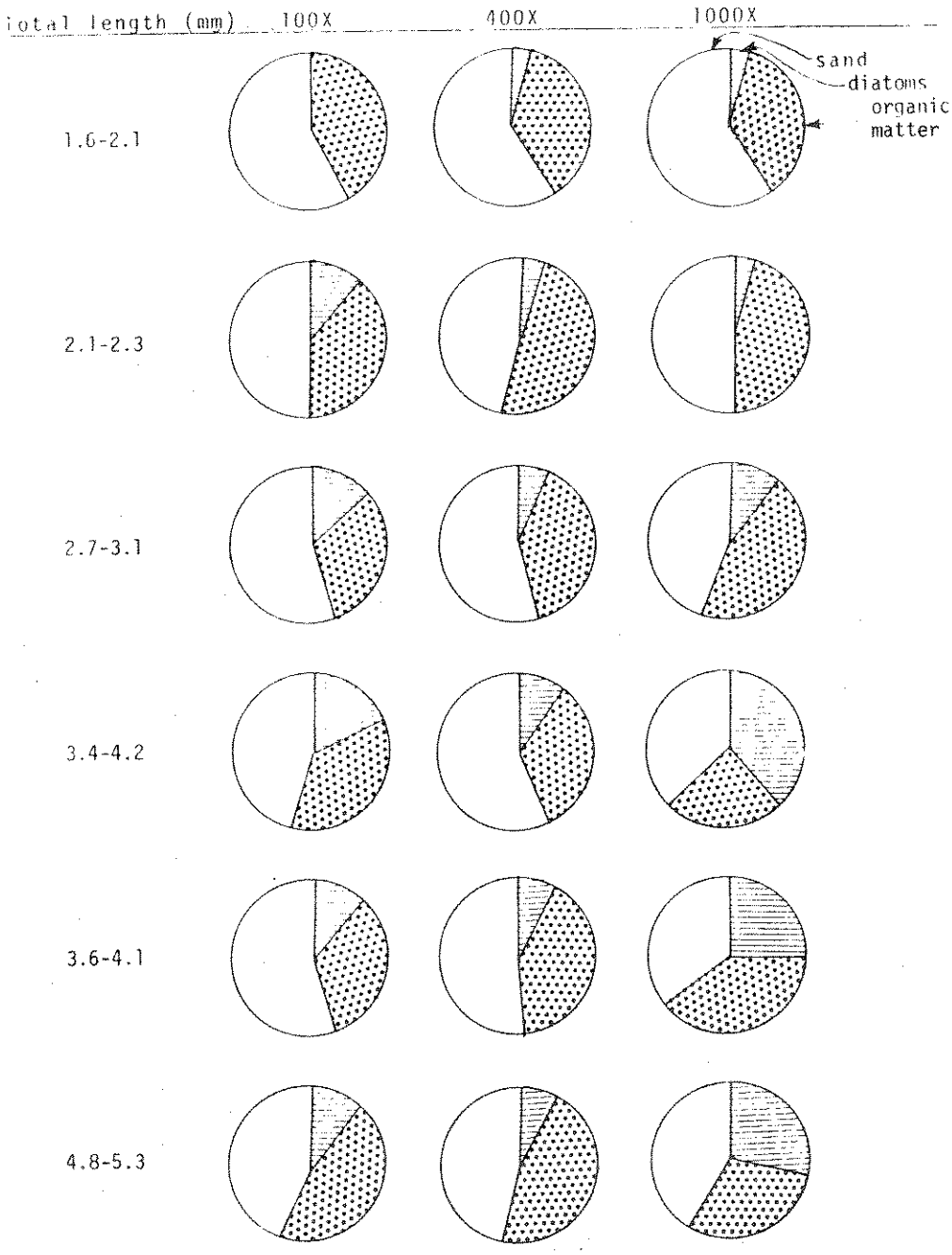
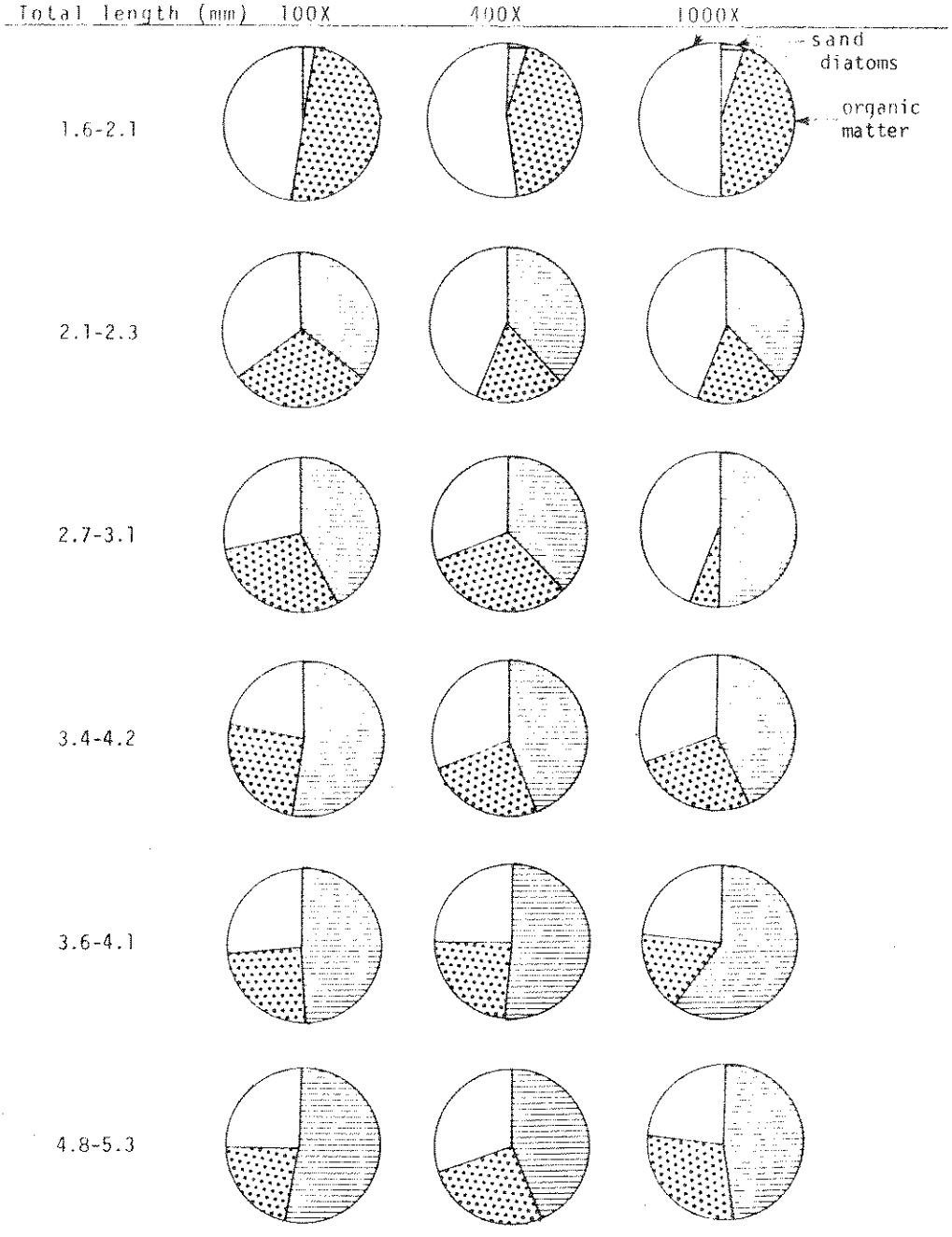

Total length (mm)
100X
400X
1000X
sand
diatoms
organic matter
1.6-2.1
2.1-2.3
2.7-3.1
3.4-4.2
3.6-4.1
4.8-5.3

Figure 30. Gut contents of T. minutus nymphs taken during the summer months from Spring Creek


Total length (mm)
100X
400X
1000X
sand diatoms
organic matter
1.6-2.1
2.1-2.3
2.7-3.1
3.4-4.2
3.6-4.1
4.8-5.3

The trend evident in the Deep Creek samples was also present in the Spring Creek nymphs. Diatoms were a minor component of the guts of the smallest class examined (1.6-2.1 mm) but rapidly became the dominant food item in all of the other size classes.

Subimagoes

Successful emergence from the final nymphal instar always occurs at the water-air interface. The nymph floats to the surface, the nymphal skin splits, and the subimago emerges on the surface of the water. Length at emergence is highly variable in both sexes and emergence of subimagoes as small as 4.5 mm was observed. About one week prior to emergence growth ceases and total length usually decreases by as much as 0.3 mm before emergence occurs.

Field observations revealed that the subimago stage is of short duration, usually lasting less than 30 minutes. Often the subimago will emerge among the aquatic vegetation along the stream edge, crawl up the vegatation, inflate its wings, and undergo its final molt. A variation of this procedure is apparent in the laboratory. Here the subimago emerges on top of the water, inflates its wings, and flies to the nearest window where the final molt occurs. The subimago differs from the adult in that the subimago has opaque wings, cerci as long as the abdomen, and is 0.1 to 0.2 mm longer than the imago.

When the subimago molts, the entire body covering is shed exclusive of the wings. Presumably the wing covering is shed later. Swisher and Richards (1972) report that Tricorythodes shed wing skins while in flight but this was not witnessed in this study. Several subimago skins were weighed and results are reported in Table 12.

Table 12. Weights of subimago skins of T. minutus (ug).

$\bar{X}$	N	S.D.	S.E.	95% c.l.
470	18	4.89	1.15	2.40

Several of the individual cast skins were weighed before and after ignition on a microbalance and no ash was found; thus, the skins are nearly 100% organic matter

Adults

Morphology: The major morphological characteristics of adult T. minutus are listed in Table 13. Males are smaller than females and can be recognized at some distance by the extremely long cerci (up to 16.5 mm and over five times the total body length).

Mating habits: Mating usually occurs in large airborne swarms from 1 to 8 m over the stream. Copulation and coupling happen very rapidly. At Deep Creek station 2, where T. minutus is multivoltine, mating possibly may occur when the adults are not airborne as evidenced by continued reproduction throughout the winter. Another possibility is the occurrence of mating flights during the occasional warm days throughout the winter in the warm air immediately above the stream. The earliest mating flight observed was on February 25. At station 2, mating flights

seem to occur during midday in the spring and fall and about two hours after sunrise and 2-3 hours before sunset during the summer. At Deep Creek station 4 and Spring Creek, mating flights occur during the late afternoon from June to October. Subimagoes have been collected from Spring Creek in August and September as late as one hour after dark. Adults of T. minutus are weak fliers and a breeze of 6 km/h or greater forces them to cease flight.

Oviposition: Egg deposition occurs mainly over riffle areas and typically proceeds as follows: egg deposition takes place within 2 hours of mating, and the adults die soon afterward with many of the adults being trapped in the surface film of the stream. A swarm collects about 1 m over a riffle area and as the swarm moves downstream, females drop out of the swarm, touch the water briefly and immediately return to the group. Now about 2 m above the water, this part of the swarm moves to the upstream portion of the riffle where it drops to the lower strata of adults and again moves downstream. Thus the swarm adopts a parabola shaped pattern above a riffle, suggesting that females may make several trips to the water's surface. The spherical egg clusters sink as the female touches her abdomen to the water and the cluster breaks up in about 1 minute, with the individual eggs acquiring an adhesive nature. Adults live less than 6 hours as evidenced by field and laboratory observations.

Table 13. Adult morphological characteristics (mm).

Character	N	$\bar{X}$	S.E.	95% conf. limits
FEMALES				
total length	49	4.34	0.09	4.12-4.52
head width	49	0.78	0.01	0.76-0.80
pronotum width	49	1.19	0.02	1.15-1.24
wing length	7	5.81	0.26	5.17-6.45
wing width	7	2.57	0.13	2.25-2.89
cerci-medial	3	8.60	0.67	5.70-11.50
cerci-lateral	3	5.10	0.67	2.20-8.00
MALES				
total length	17	3.78	0.05	3.67-3.89
head width	17	0.63	0.01	0.61-0.64
pronotum width	13	0.85	0.02	0.81-0.89
wing length	12	4.26	0.19	3.85-4.67
wing width	12	2.15	0.18	1.76-2.54
cerci-medial	6	15.17	0.53	13.82-16.52
cerci-lateral	6	10.53	0.25	9.89-11.17

Eggs

Morphology: The eggs (Fig. 31) of T. minutus are ovoid in shape, have dimensions of 0.125±0.003 X 0.146±0.004 mm, and have an adhesive disc on one end. The eggs are green but lose this color in water. Fertilized aggs are brown to black and unfertilized eggs appear opaque white. The eggs are covered with small, raised reticulations.

Fecundity: As maturity approaches and the eggs begin to develop, the females become more robust and just prior to emergence their abdomens appear greenish due to the eggs. Female nymphs as small as 3.9 mm can contain as many as 325 eggs and the number increases until emergence (Fig. 32). The greatest number of eggs removed from an adult female was 1504. The larger the total length of a female the greater the number of eggs present (Fig. 32). The mean dry weight for a single egg was 0.870 ug, with a mean ash free dry weight of 0.110 ug, yielding a mean per cent organic matter of 87.51 (Table 14). For a 5.4 mm female weighing about 2.30 mg (Fig. 15) and carrying 1504 eggs weighing 1.308 mg, the eggs would constitute over 56 per cent of the total dry weight of the female. Just prior to oviposition, the eggs are extruded as a spherical mass and held on the subgenital plate until release. Several egg clusters (39) were removed from swarming females and had a mean diameter of 1.085 mm (Table 14). Egg cluster diameter is directly proportional to egg number; the larger cluster (1.62) contained 815 eggs and the smallest (0.93) had 280 eggs (Fig. 33).

Table 14. Measurements and characteristic of the eggs of *T. minutus*.

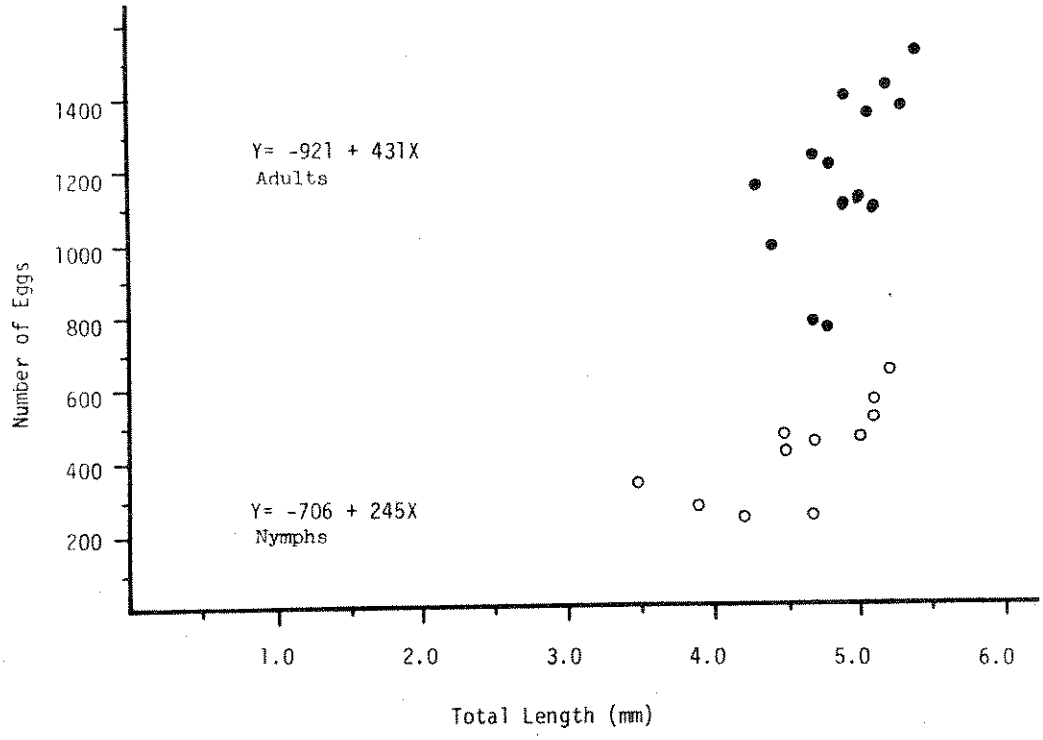
Character	N	$\bar{X}$	S.E.	95% conf. limits
Indiv. egg dry wt. (ug)	8	0.870	0.029	0.801-0.939
Ash free dry wt. (ug)	8	0.110	0.014	0.077-0.143
Per cent organic matter		87.51%		
Egg cluster diameter (mm)	39	1.085	0.026	1.033-1.137

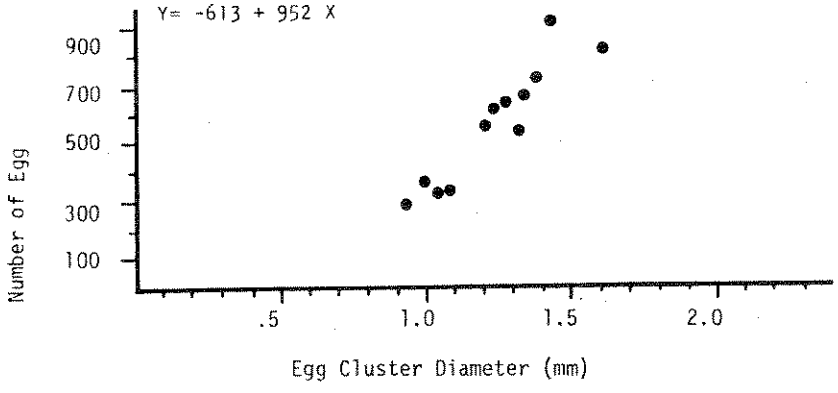
Figure 31. Photomicrograph of hatched (light) and unhatched (dark) eggs of T. minutus.

0.1 mm

Figure 32. Relationship between total number of eggs and total length of nymphs (open circles), and adults (filled circles) of T. minutus .

Figure 33 . Relationship between egg cluster diameter and egg count.


Y= -921 + 431X
Adults
Y= -706 + 245X
Nymphs
Number of Eggs
1400
1200
1000
800
600
400
200
1.0
2.0
3.0
4.0
5.0
6.0
Total Length (mm)


Y= -613 + 952 X
Number of Egg
900
700
500
300
100
.5
1.0
1.5
2.0
Egg Cluster Diameter (mm)

Growth-Absolute

Table 15 lists results obtained on the growth rate of T. minutus at temperatures of 9, 14 (both normal light and total dark), 18, 18±3, 19, and 23°C. Two calculations are given in each block: absolute growth in mm/day, and absolute growth in mm/1000°h (= converted growth rate). Two trends are evident: (1) in general growth rate increased as temperature increased and (2) rate at any given temperature is slow in the small size classes, increases to a peak when the nymphs are 4-5 mm in length, and decreases as maturity is reached. By expressing growth in terms of increase per 1000°h one can compare rates on a common scale and if the rule of temperature summation is followed and other variables (e.g., food quality) are not interfering, the converted rates should be similiar (Fig. 34). After conversion, mean growth rate at 23°C showed the highest rate (0.233 mm/1000°h) while the smallest rate was at 14°C (0.114 mm/1000°h). The 14°C test conducted in darkness resulted in a growth similiar to the normal 14°C test and so the results of the two tests were combined. To test the significance of the differences between the mean converted rates a one-way analysis of variance was calculated (Table 16). An F value of 9.15 resulted in rejection of the null hypothesis of no significant difference in the means and so a multiple range test was conducted. This test revealed that the converted mean growth rates at 9, 14, 18±3, and 19°C were significantly different from the remaining two mean rates ($p < .05$). In order to use this multiple range test, a balanced design was necessary and therefore the growth rates of nymphs of 1.5 to 5.5 mm in length only were utilized.

Table 15

Synopsis of absolute growth of *I. minutus* nymphs in the laboratory. Values are in mm/day except values in parentheses are in mm/1000°h.

Size class(mm)	9°C	14°C	14°C*	18°C	18±3°C	19°C	23°C
<0.5						.0200 (.0438)	
0.5-1.0						.0225 (.0492)	
1.0-1.5		.0096 (.0286)				.0403 (.0882)	
1.5-2.0	.0118 (.0546)	.0423 (.1260)		.1000 (.2110)	.0230 (.0532)	.0450 (.0985)	.0893 (.1616)
2.0-2.5	.0305 (.1412)	.0402 (.1196)	.0210 (.0626)	.0813 (.1882)	.0329 (.0760)	.0470 (.1029)	.0964 (.1744)
2.5-3.0	.0280 (.1296)	.0377 (.1122)	.0318 (.0948)	.1125 (.2604)	.0736 (.1701)	.0656 (.1436)	.1152 (.2085)
3.0-3.5	.0422 (.1954)	.0376 (.1119)	.0283 (.0843)	.1010 (.2340)	.0577 (.1333)	.0752 (.1646)	.1279 (.2314)
3.5-4.0	.0421 (.1953)	.0453 (.1348)	.0267 (.0796)	.1095 (.2529)	.0468 (.1082)	.1928 (.2023)	.1391 (.2517)
4.0-4.5	.0341 (.1579)	.0396 (.1179)	.0288 (.0858)	.1033 (.2387)	.0935 (.2161)	.0902 (.1975)	.1285 (.2325)
4.5-5.0	.0431 (.1995)	.0336 (.1001)	.0289 (.0861)	.1134 (.2619)	.1009 (.2331)	.1746 (.1633)	.1489 (.2695)
5.0-5.5	.0301 (.1394)	.0340 (.1012)	.0056 (.0167)	.1076 (.2486)	.0921 (.2126)	.0612 (.1340)	.1593 (.2883)
5.5-6.0	.0111 (.0514)	.0190 (.0565)		.0943 (.2178)			.1245 (.2253)
6.0-6.5							.0400 (.0724)
mean rates	.0371 (.1718)	.0383 (.1140)	.0274 (.0811)	.1054 (.1981)	.0663 (.1246)	.0722 (.1581)	.1285 (.2325)

* = zero light conditions.

Figure 34. Growth rate of various size classes of nymphs expressed as growth in mm/1000°h.

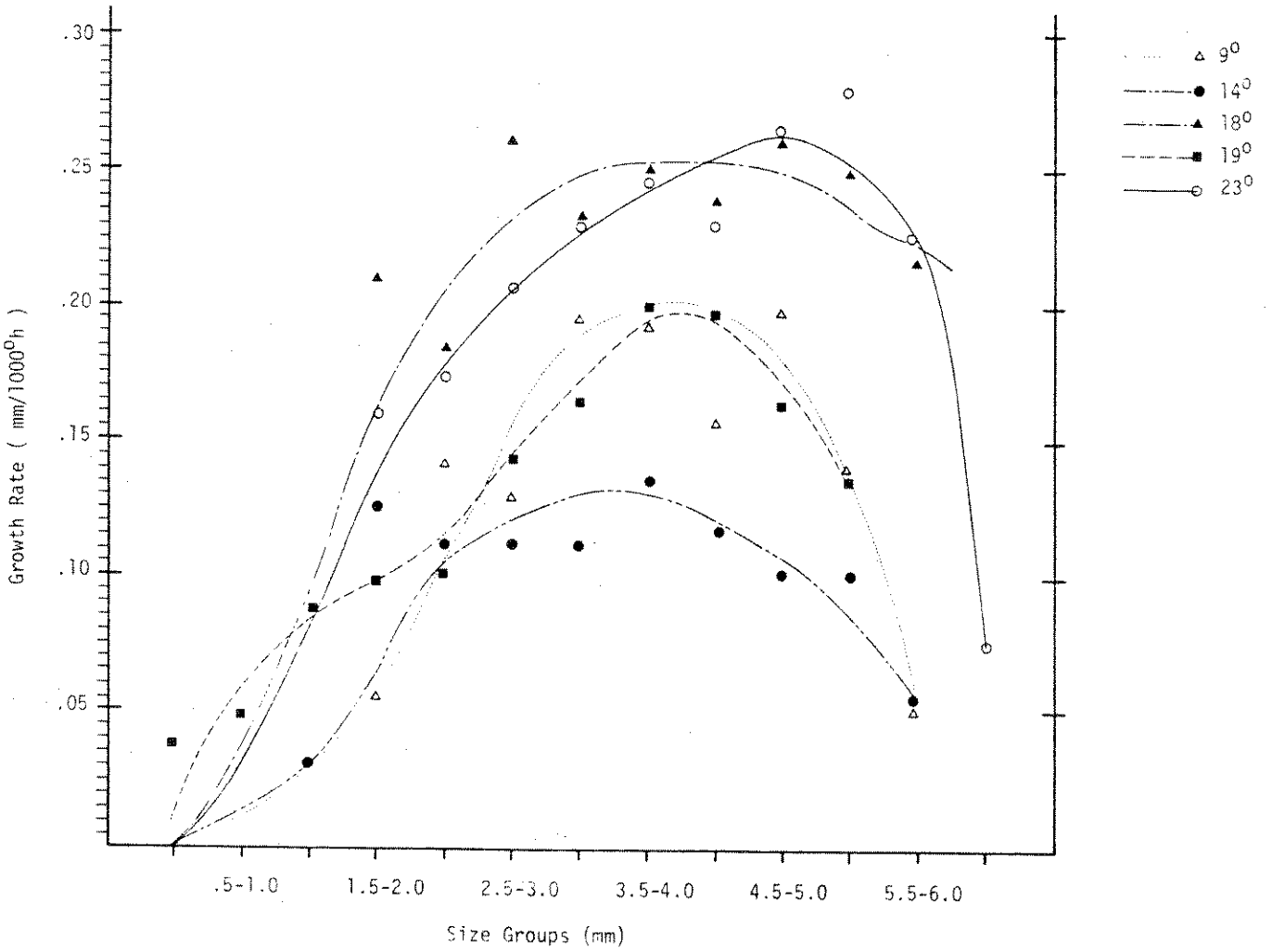

.30
.25
.20
.15
.10
.05
Growth Rate (mm/1000^{0}h)
.5-1.0
1.5-2.0
2.5-3.0
3.5-4.0
4.5-5.0
5.5-6.0
Size Groups (mm)
9^{0}
14^{0}
18^{0}
19^{0}
23^{0}

Table 16

Results of a one-way ANOVA on converted laboratory growth rates at 9, 14, 18, 18±3, 19, and 23°C using a balanced design.

Source of variation	SS	d.f.	mean square
Between means	0.0914	5	0.0183
Within means	0.0829	42	0.0020
	0.1743		

$F = 9.15$ with alpha= 0.05, reject H_0: of no difference.

Student-Newman-Keuls multiple range test,

S.E. = 0.0158

Significant means = $\underline{9^o\ 14^o\ 18\pm3^o\ 19^o}$ $\underline{18^o\ 23^o}$

Table 17

Calculations on laboratory growth of T. minutus using Winberg's (1973) equations for temperature summation;plus logistic calculations.

Temp.(^{o}C)	D (days)	t_0(^{o}h)	t	(t-t_0)	S	Growth rate mm/day	Growth rate mm/1000^{o}h	100/Y	1/D x 1000
9	133.2	120	216	96	12,783	.0371	.1718	0.80	7.5
14	137.5	120	336	216	29,692	.0383	.1140	0.70	7.3
18	48.4	120	432	312	15,101	.1054	.1981	2.10	20.66
18±3	76.9	120	432	312	23,993	.0663	.1246	1.30	13.00
19	70.1	120	456	336	23,554	.0722	.1581	1.40	14.27
23	39.7	120	552	432	21,914	.1285	.2325	2.50	25.19

$\overline{X}$= 21,173^{o}h
s= 6229
SE= 2542
95% conf.limits= ± 6533

t_0= point of zero growth in ^{o}h.
S^{0}= D(t-t_0) in ^{o}h.
D = duration of development from 0.4-5.5 mm.
100/Y = average percent development in one day.

Inherent in the present method of growth determination is the theory that if the growth rates have been determined properly and are an accurate representation of the growth rate response to temperature then when these absolute growth rates are converted to a common base (1000°h) they should be comparable. The result of this conversion is that the rates fell into groups, containing four and two temperatures respectively.

The more commonly used method for this type of experiment is to determine the duration of development (S) in degree-hours by the formula $S = D(t-t_o)$ (Winberg 1971), where D = duration of development in days (or hours), t_o= temperature below which growth ceases (5°C for T. minutus), and t= test temperature. These calculations showed that duration of development (D) is shortest at 23°C (39.7 days) and longest at 9°C (133.2 days) and 14°C (137.5 days). The rates of S are widely divergent for the 9°C and 14°C tests (12,780 and 29,690°h respectively) whereas the results for S for the four other temperatures were similar, ranging from 15,000 to 24,000°h. Thus the latter values give support to the temperature summation method. The mean for the six test temperatures was 21,173°h (± 6533). This agrees with the results obtained from the previous multiple range test, with the values of S for 9°, 14°, 18±3°, and 19°C falling within the confidence limits for the mean. The mean value for S has further significance when field growth is examined later. In addition, values for 100/Y and 1/D X 1000 were calculated (Table 17) to see if the laboratory rates might fit the logistic equation rather than the rule of summation but the values did not fit this treatment.

Growth of nymphs at a constant 18°C and a fluctuating (±3°C) 18°C are somewhat similar (Fig. 35). Nymphs held at the constant temperature had higher rates in the smaller size classes than those at the fluctuating temperature. Growth rates were comparable in the larger size classes. A semi-logarithmic plot of unconverted growth rates (Fig. 36) illustrates more rapid growth with increasing temperature. There is slightly more variation between growth rates at the test temperature in this plot than with the converted rates (Fig. 34).

Table 18 presents a synopsis of field growth rates of individual nymphs measured in Deep and Spring Creeks. The absolute growth increment is greater at station 2 (0.154 mm/day) and about half as much at Spring Creek (0.088 mm/day). After conversion, these rates became comparable, with nymphs from Deep Creek (both sexes combined) growing at a rate of 0.359 mm/1000°h (Fig. 37) and Spring Creek nymphs at 0.299 mm/1000°h; both of these values are greater than laboratory rates. The calculated $\underline{S}$ values from the field (13,100 to 14,700°h; (Table 19), are much lower than most of the laboratory values, even though field values are for growth from 0.4 to 6.0 mm whereas the laboratory values (Table 17) are for growth from 0.4 to 5.5 mm, since laboratory growth terminated at a shorter total length than the field studies. Reduced food quality, reduced competition, buildup of toxic substances, the confining nature of the growth chambers, or perhaps the normal diurnal temperature variation may have influenced growth under laboratory conditions.

Figure 35. Laboratory growth of T. minutus nymphs at a constant and variable 18°C.

Figure 36. Laboratory growth of T. minutus nymphs at four constant temperatures.

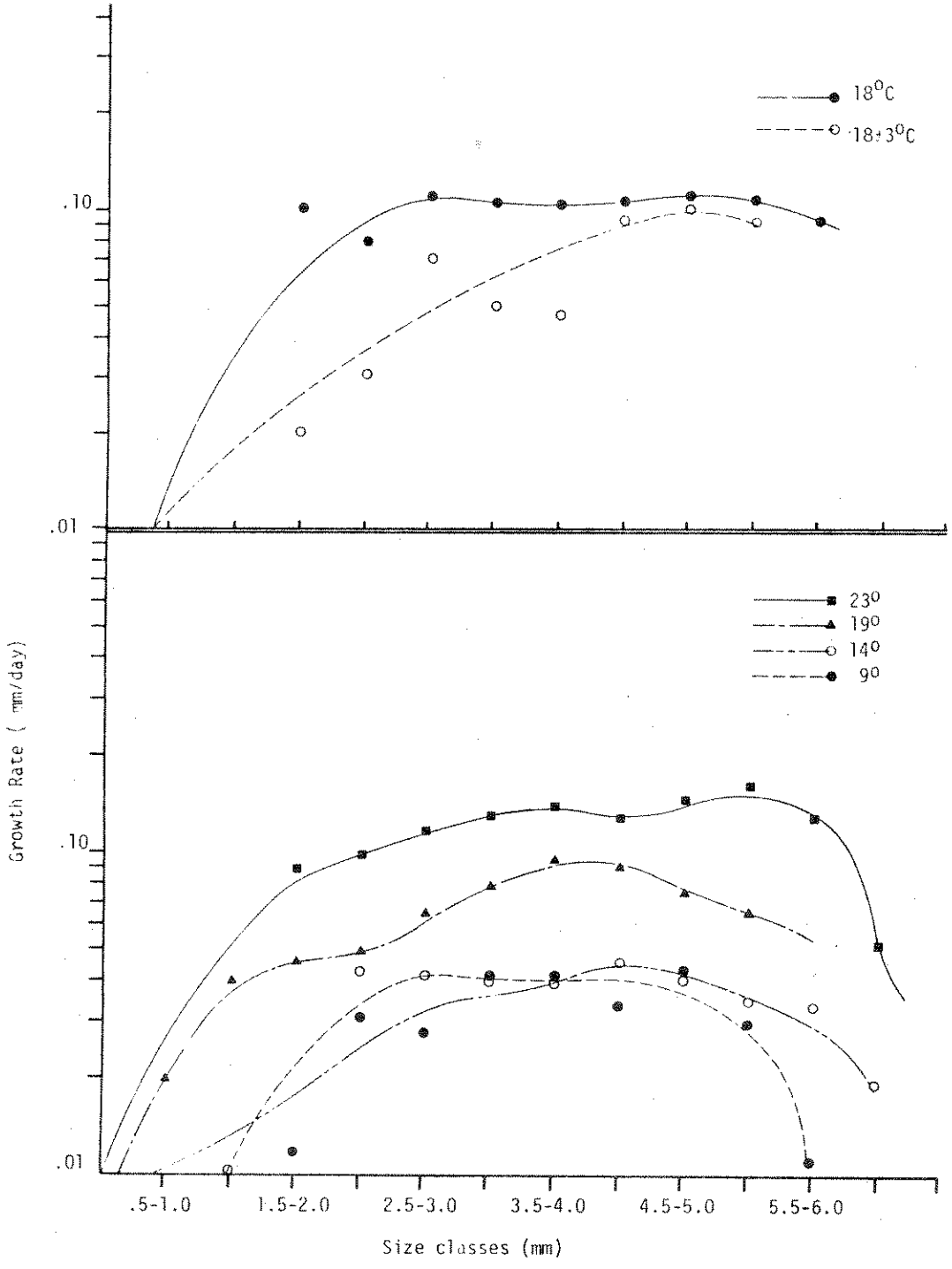

18°C
18±3°C
.10
.01
23°
19°
14°
9°
.10
.01
Growth Rate (mm/day)
.5-1.0
1.5-2.0
2.5-3.0
3.5-4.0
4.5-5.0
5.5-6.0
Size classes (mm)

Table 18

Synopsis of absolute growth of *T. minutus* nymphs held in individual growth chambers in Deep Creek sta.2 and Spring Creek. Values are mm/day, vales in parentheses are mm/1000°h.

Size class(mm)	Deep Creek Sta.2 Females	Males	All sexes	Spring Creek
1.0-1.5		.1210 (.2834)	.1210 (.2834)	
1.6-2.0	.1502 (.3515)	.1714 (.4011)	.1357 (.3175)	
2.1-2.5	.1546 (.3618)	.1714 (.4011)	.1483 (.3470)	.0557 (.1901)
2.6-3.0	.1531 (.3583)	.1511 (.3536)	.1447 (.3386)	.0788 (.2689)
3.1-3.5	.1605 (.3756)	.1664 (.3894)	.1560 (.3650)	.0911 (.3109)
3.6-4.0	.1770 (.4142)	.1835 (.4294)	.1716 (.4015)	.0977 (.3334)
4.1-4.5	.1936 (.4530)	.1725 (.4037)	.1778 (.4161)	.0995 (.3396)
4.6-5.0	.1901 (.4448)	.1548 (.3622)	.1711 (.4004)	.0842 (.2874)
5.1-5.5	.1820 (.4259)	.1240 (.2902)	.1545 (.3615)	.0798 (.2724)
5.6-6.0	.1794 (.4198)	.1456 (.3407)	.1587 (.3714)	.0884 (.3017)
6.1-6.5	.1498 (.3505)		.1498 (.3505)	.0894 (.3051)

Table 19

Calculations on laboratory growth of T. minutus using Winberg's (1973) equations for temperature summation; plus logistic calculations.

Temp.(^{o}C)	D(days)	t_o	t	$(t-t_o)$	S	rate mm/day	100/Y
DEEP CREEK-19^{o}C							
females	43.7	120	456	336	14,700	0.15	2.3%
males	43.1	"	"	"	13,370	0.16	2.4
both sexes + juveniles	43.7	"	"	"	14,700	0.15	2.3
SPRING CREEK-12^{o}C							
both sexes + juveniles	75.7	"	293	173	13,100	0.09	1.3

Figure 37. Field growth rates of T. minutus nymphs, maintained in individual growth chambers, Deep Creek station 2.

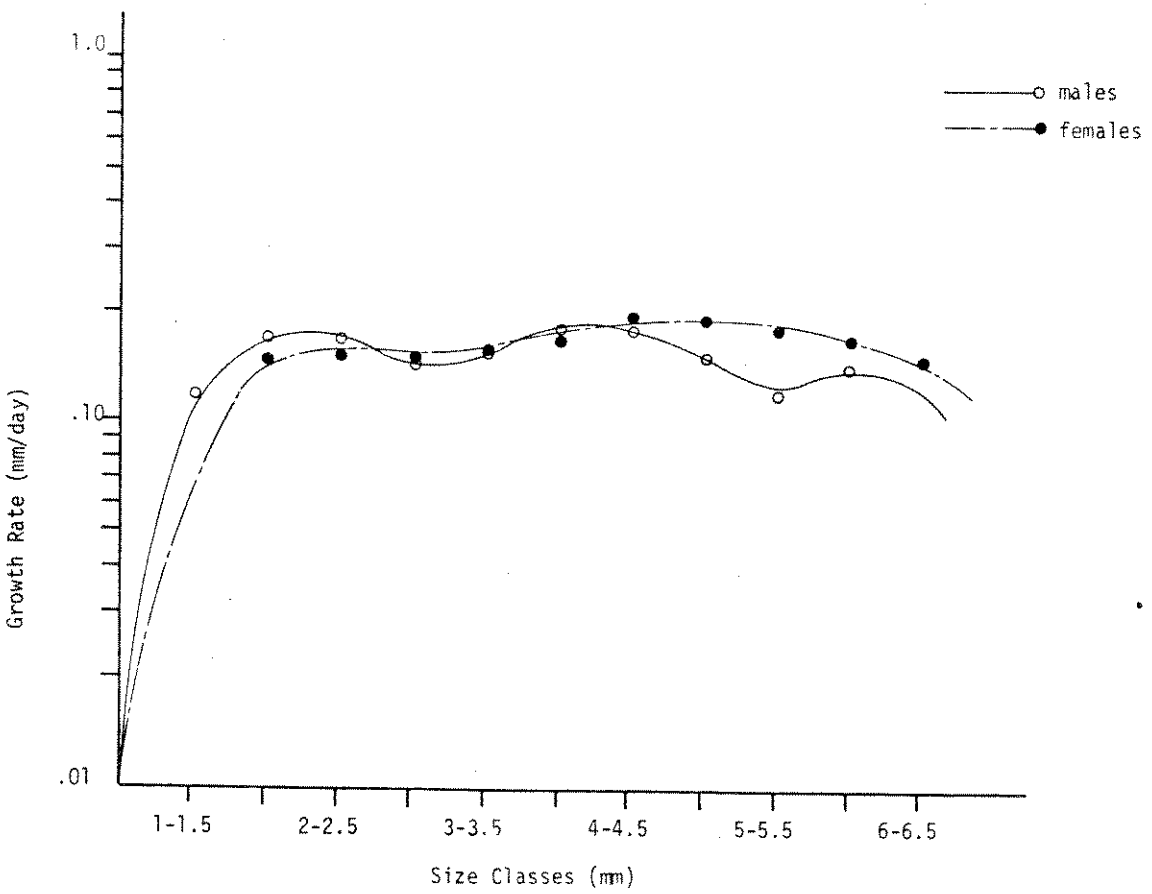

1.0
.10
.01
Growth Rate (mm/day)
males
females
1-1.5
2-2.5
3-3.5
4-4.5
5-5.5
6-6.5
Size Classes (mm)

Figure 38. Mean length and range for T. minutus nymphs collected each month at Deep Creek station 4 and Spring Creek.

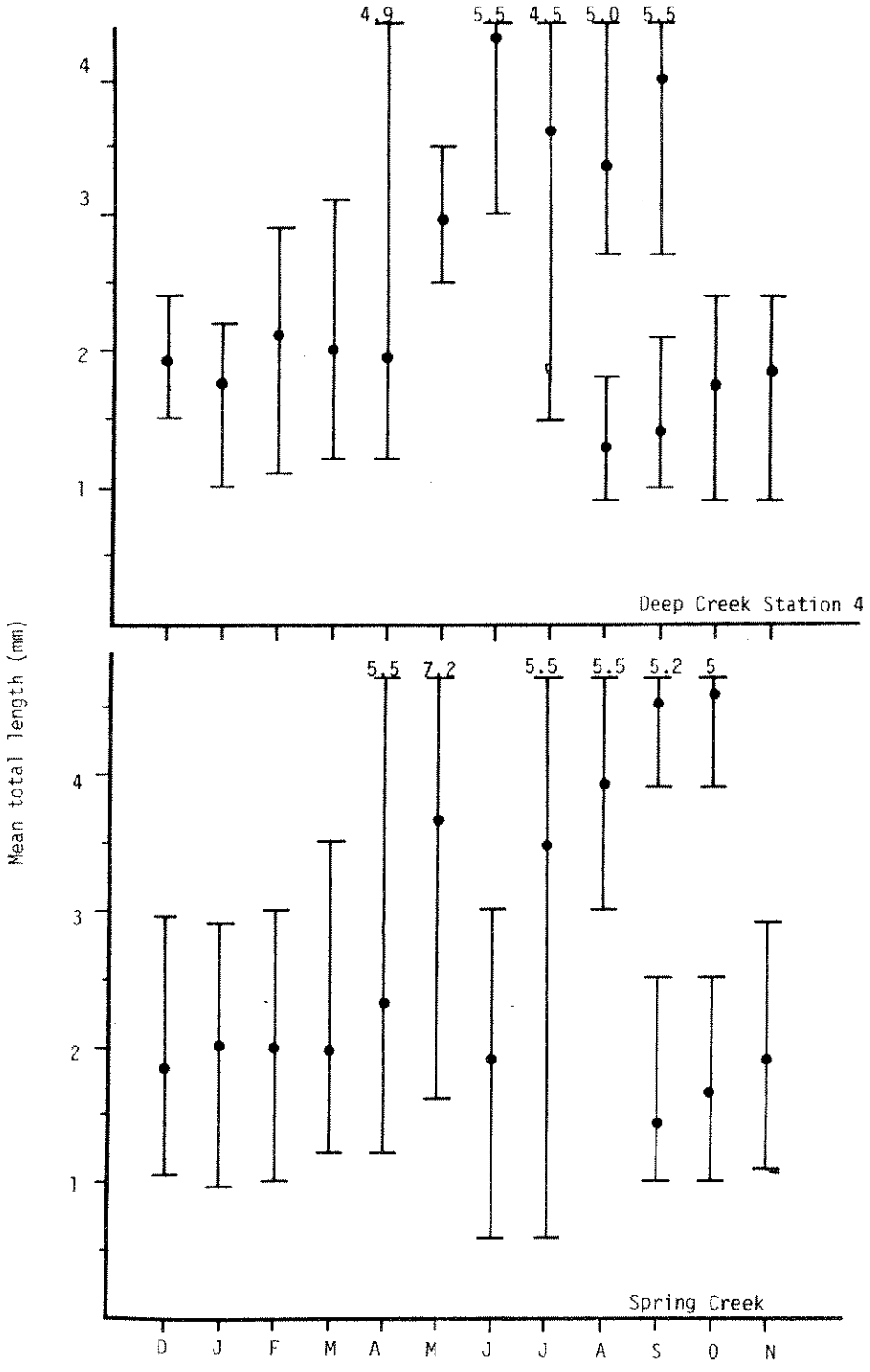

4.9
5.5
4.5
5.0
5.5
Deep Creek Station 4
5.5
7.2
5.5
5.5
5.2
5
Spring Creek
Mean total length (mm)
1
2
3
4
D
J
F
M
A
M
J
J
A
S
O
N

Table 20. Field growth in Deep Creek station 4 as mean length and head width expressed in mm.

Date	N	Total length	Head width	
August 1971	36	2.89	0.593	all nymphs
		3.39	0.677	nymphs>1.8 mm
		1.33	0.333	" <1.8 mm
September "	44	3.29		all nymphs
		4.02	0.714	nymphs>2.3 mm
		1.39	0.322	" <2.3 mm
October "	18	1.75	0.416	
November "	29	1.85	0.416	
December "	41	1.93	0.450	
January 1972	75	1.78	0.433	
February "	16	2.10	0.450	
March "	1	2.00	0.450	
April "	6	1.96	0.464	
May "	10	3.03	0.566	
June "	65	4.33	0.773	
July "	22	3.61	0.692	

It is noteworthy that the increase in mean total length of the field population agreed very well with laboratory growth rates for individual nymphs. Figure 38 shows mean total length for a year at station 4 and Spring Creek and gives a close agreement between the two in that both appear bivoltine. The data upon which these graphs are based are presented in Tables 20-21. If the S (21,173°h) derived from laboratory studies for all tests and 24,788°h for the four significant tests is accepted and applied to the mean total length of the population expressed in Fig. 38, and time of egg hatching is about 1000°h (Fig. 40), then a bivoltine cycle is accepted. A bivoltine cycle at station 4 and Spring Creek should take approximately 24,788 + 1000 x 2 for a total of 51,576°h to complete two cycles per year. Table 2 shows that about 53,090 and 52,000°h were available for growth in station 4 and Spring Creek, respectively; thus two cycles per year would be possible.

Thermal Tolerance

Upper lethal-temperature experiments were conducted at acclimation temperatures of 9, 15, and 21°C with mixed size classes of nymphs. All test organisms were obtained from Deep Creek station 2 at various times of the year. No attempt was made to compare individual time-percent curves, since the differences in tolerance are clear. Tests were terminated at 96 h (8400 min.). The LT_{50} refers to that point where 50 per cent of the organisms have died. The lowest temperature to result in 50 per cent mortality was 24.5°C. In that case nymphs had been acclimated at 9°C; the LT_{50} occurred at 96 h. The shortest LT_{50} was achieved at 35°C after 60 min. with nymphs acclimated at 21°C (Fig. 39). There was some variation in tolerances between classes (Table 22).

Table 21. Field growth in Spring Creek as mean increase in length and head width expressed in mm.

Date	N	total length $\bar{X}$	head width $\bar{X}$	
December 23, 1971	132	1.849	0.467	
January 16, 1972	169	2.042	0.475	
February 21, "	72	1.980	0.490	
March 25, "	42	1.950	0.494	
April 22, "	51	2.304	0.516	
May 29, "	55	3.685	0.723	
June 17, "	429	1.948	0.489	
July 30, "	194	3.472	0.692	
August 20, "	199	3.944	0.755	
September 24, "	200	2.439	0.503	all nymphs
	59	4.485	0.809	nymphs >3.5 mm
	141	1.455	0.374	" <3.5 "
October 22, "	164	1.857	0.445	all nymphs
	10	4.520	0.836	nymphs >3.5 mm
	154	1.680	0.419	" <3.5 "
November 26, "	191	1.904	0.417	all nymphs
	1	4.900	0.840	nymphs >3.5 mm
	190	1.920	0.419	" <3.5 "

Figure 39. Thermal tolerance of T. minutus nymphs expressed as time of survival of 50% of the test organisms at various test and acclimation temperatures.

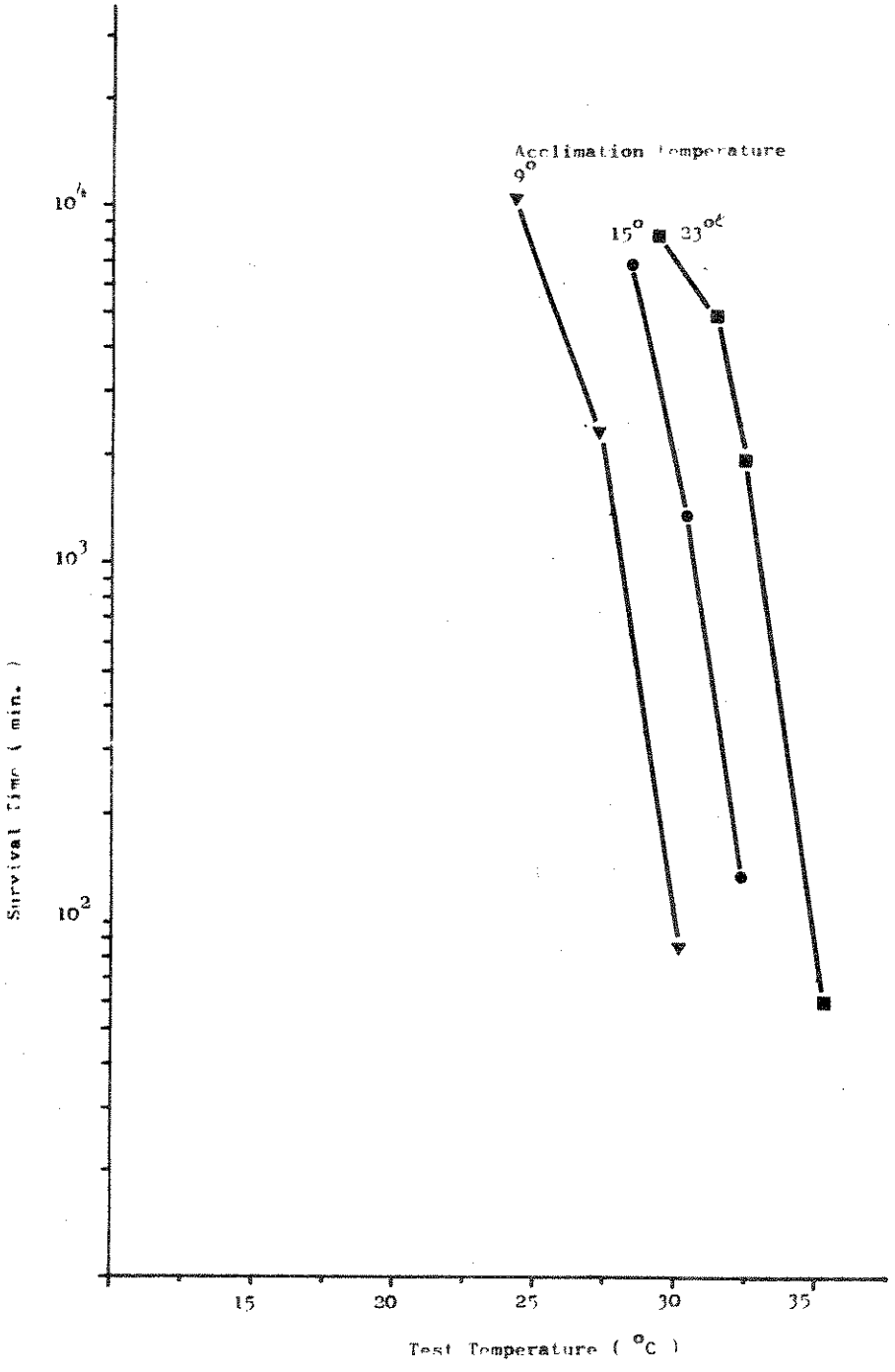

Acclimation Temperature
9°
15°
33°
10^4
10^3
10^2
Survival Time (min.)
15
20
25
30
35
Test Temperature (°C)

Table 22. Thermal tolerance of T. minutus nymphs of mixed size classes.

Acclimation temperature (°C)	Test temperature (°C)	LT_{50} hours--(min.)	
21	35	1.4	(85)
"	33	35.0	(2101)
"	31	83.0	(4999)
"	29	133.0	(7960)
"	27		(8400)
15	32	3.3	(199)
"	30	22.0	(1320)
"	28	113.0	(6760)
"	26		(8400)
9	30	14.0	(840)
"	27	37.0	(2240)
"	25	160.0	(9600)
"	23		(8400)

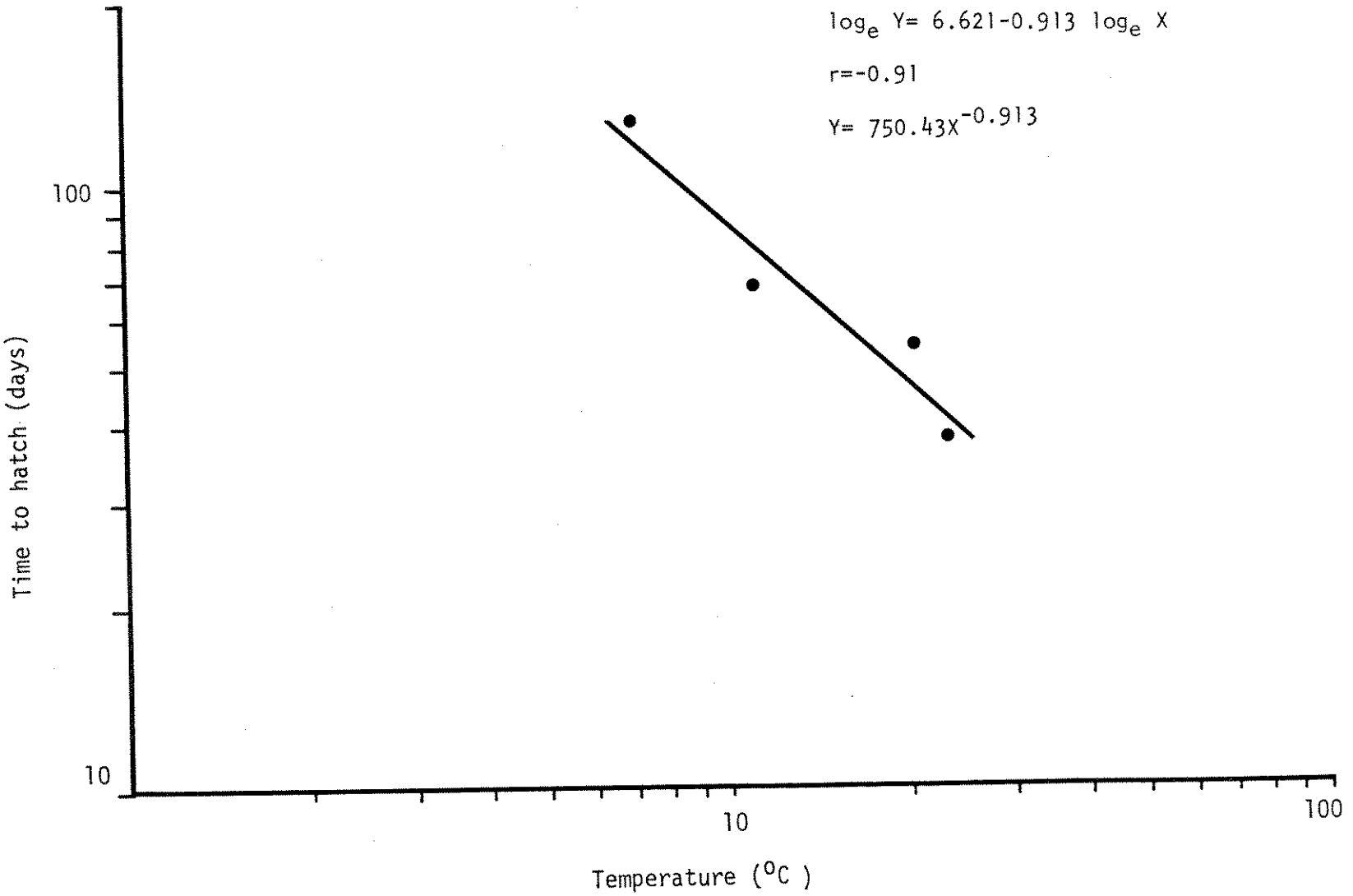
		Nymph size class (mm) - LT_{50} (hours)		
		1-3	3.1-5.0	5.1+
17	30	24.3	26.0	17.3
17	28	103.7	94.7	86.7

Hatching: Length of time for the eggs to hatch was determined in the laboratory at five temperatures (Table 23). The time required to hatch was directly related to temperature. At 7.5°C half of the eggs hatched within 140 days and the hatch lasted 30 days. During this test, 40 eggs were removed after 72 days and placed in a 23°C chamber to determine viability of the eggs. These eggs began hatching in 6 days and a 50 per cent hatch was achieved 2 days later. The highest egg mortality (40 percent) occurred at the lowest test temperature. Most rapid egg maturation occurred at 23°C, at which temperature 50 per cent of the eggs hatched within 36 days and achieved the lowest mortality (6 percent). Egg mortality was a function of temperature. The relationship between time of hatching at various temperatures is logarithmic and predictable (Fig. 40). Elliott (1972) found a similar linear relationship on a log-log plot of egg hatching time vs temperature for Baetis rhodani (Pictet) and listed 12 equations, one for each test temperature.

Table 23. Time required for the eggs of T. minutus to hatch at various temperatures and mortality rates, (days).

Temperature	First occlusion	50% occlusion (days)	(°hours)	Duration	Mortality
7.5°C	125	140	10,500	30	40%
12.5	54	69	8,625	53	23
21.0	40	56	1,176	26	8
23.0	21	39	828	36	6
28.0	-	-	-	-	100

Figure 40. Time required for 50% of the eggs of T. minutus to hatch in the laboratory.


$\log_e Y = 6.621 - 0.913 \log_e X$
r=-0.91
$Y = 750.43X^{-0.913}$
100
10
Time to hatch (days)
10
100
Temperature (^oC)

DISCUSSION

Temperature is a prime regulator of natural processes within the aquatic environment. It governs many physiological functions in organisms with some resulting in complex interactions. Depending on the extent of environmental temperature change, organisms can be activated, depressed, restricted, or killed.

In some cases temperature determines those aquatic species that may be present, controls timing of egg laying and hatching of young, and development. Temperature can attract and kill when the water becomes heated or chilled too suddenly. Cold water generally suppresses development whereas warmer water generally accelerates activity.

Because of its capacity to influence metabolic rate, temperature may be the most important single environmental entity to life and life processes.

Although temperature was found to have a profound effect upon Tricorythodes minutus, the initial stages of this study were concerned with growth exclusive of the effects of temperature. An allometry-of-size analysis gives an indication of change in one body part given a second dimension. Most of these relationships for T. minutus resulted in high correlation coefficients. The highest correlation was between head width and pronotum width ($r=0.97$). One benefit from this analysis was the discovery that total length and any of the other measurements had a high correlation ($r=0.93$ to 0.97) showing that total length is a reliable body measurement. It can, therefore, be used in life history studies as well as the more commonly used head width which also had high correlation values.

Only one published study of allometric growth in mayflies is available for comparison, that by Clifford (1970a) on Leptophlebia cupida (Say). Clifford used the symbol "K" for the constant of allometry, which is usually referred to as "a" or alpha. If two body dimensions have the same geometric growth rates, there will be a constant ratio between them no matter what their size and alpha will equal unity. Two dimensions which maintain a constant ratio of sizes are said to grow "isometrically". In contrast to this simple situation, which is seldom if ever observed, dimensions whose ratio is constantly changing are said to grow "allometrically". In allometric growth the ratio of dimensions, X/Y, is constantly changing while the ratio of rates K_{gx}/K_{gy}= a is constant. If the constant (a) is less than unity, the relationship is described as negative allometry; if greater than unity, positive allometry. There is no biological difference between the two kinds of allometry. There are two kinds of deviation from simple allometry: first, (a) may change continually during growth or second, there may be a sharp change in the constant of allometry at a critical stage in the life cycle. The former is the kind of deviation observed in T. minutus nymphs. Head width, length and pronotum width all exhibit negative allometry whereas meso-metanotum width and length show positive allometry with meso-metanotum width most closely approaching isometric growth. The constant of allometry gradually increases in head width, length, and pronotum width and steadily decreases in meso-metanotum width and length. Clifford (1970a) calculated a single (a) for the means of each of his measurements. Allometric studies are valuable in aquatic investigations. Once growth patterns are established length and

weights of nymphs can be predicted at various stages of the life cycle thus simplifying production studies.

The change in length of T. minutus nymphs through time (absolute growth rate) was examined in the laboratory and in the field and was expressed as increase in length per unit time (mm/day) and mm/1000°h (=converted growth rate). The units, degree hours (°h) or degree days (°d) are used in the "temperature summation" concept. This concept has often been cited as a simple means of comparing growth rates on a common scale and for illustrating the influence of temperature on organismal growth. Nymphal growth rates at six temperatures in the laboratory were compared by analysis of variance. The result was a separation of the mean converted growth rates into two significant groups; one group contained growth rates obtained at 9°, 14°, 18±3°, and 19°C whereas the second group had rates obtained at 18° and 23°C. There are explanations for the separation of the data into two groups. Some presently unknown factor i.e. food quality, waste product buildup, etc. could have been operating during the two tests. Results from the 18° and 23°C tests revealed growth rates much greater than for the other four tests. Unconverted growth rates revealed an acceleration in growth with increasing temperature as the slowest rates were at 14° (no light) and 9°C (0.027 and 0.037 mm/day respectively). The greatest growth rate observed was 0.129 mm/day at 23°C. Growth rate probably decreases at higher temperatures.

Winberg's (1971) formula and laboratory derived growth rates provided S, the number of degree hours necessary to complete development. Values of S varied from a low of 12,783°h (9°C) to a high of 29,692°h at 14°C ($\bar{X}$ = 21,173 ± 6533). When only four significant

temperature results are used (9°, 14°, 18±3°, and 19°C), the resulting mean is S=24,788°h and is utilized later in the derivation of an equation to predict emergence. From this value it is calculated that the nymphs would require 137.5 and 133.2 days at 14° and 9°C respectively to complete development and 39.7 days at 23°C. Although 39.7 days appears to be an extremely rapid development rate, Fremling (1967) reared Hexagenia bilineata nymphs to maturity (over 20 mm in length) in only 79 days at laboratory temperatures of 24-27°C.

The duration of the life cycle and calculations of S has interested investigators. Several values found in the literature are given in Table 24. The value of S showed no pattern between the insect orders and varied from 27,000 to 82,000°h. Such a large variation would suggest that S is species specific. Insects presumably would be limited in their geographical distribution to streams whose yearly thermal history is greater than S and by their thermal tolerance. Presumably a species S requirement would be somewhat flexible to allow for normal annual water temperature variations. Gose (1970) was one of the first to calculate S for an aquatic insect, the caddisfly Stenopsyche griseipennis, in streams of differing thermal histories. He found this species requires 52,800°h for development, and had a univoltine cycle in streams with an S near 52,800°h and was bivoltine in the southern part of its range where S was about 100,000°h. Thus, this insect showed a direct and predictable response to higher water temperatures. All of the examples given in Table 24 are from field studies; no laboratory data were available for comparison.

Studies on duration of development in insects has not been confined to aquatic insects. Glenn (1922) and Shelford (1927) used the

temperature summation concept to predict the emergence of the codling moth and to plan control measures.

Considering the evidence presented here and from past studies, it is interesting that the temperature summation technique has not received greater acceptance. However, it is evident that the concept is not universal throughout the aquatic insect orders and this means that each species must be tested to determine if it conforms to the summation concept. Another deterent to the use of the summation concept is that few investigations examine water temperature continuously on a yearly basis. Many past investigators have also neglected to determine the zero development point (Britt 1962) for a species and this also inhibits further use of the concept.

The laboratory derived growth data at the four significant temperatures was analyzed by n^{th} order regression analysis in an attempt to derive a single best fit line for the four growth curves. The result of that analysis is presented in Figure 41 and is expressed mathematically by the equation:

$$Y = -0.125 + 0.178X - 0.023\ X^2 \qquad (1)$$

where Y = growth rate in mm/1000°h
X = total length in mm.

This second order polynomial describes an almost perfect hyperbola, (Fig. 41). Growth is slow in the smallest nymphs, gradually increasing to a maximum rate in the 3.5-4.5 mm size class after which growth rate decreases rapidly. Growth rate not only decreases but total length of nymphs decreases up to 7 per cent of total length. This relatively unexplored phenomena creates the possibility of a small negative error in all past studies utilizing mean population length as a growth criterion.

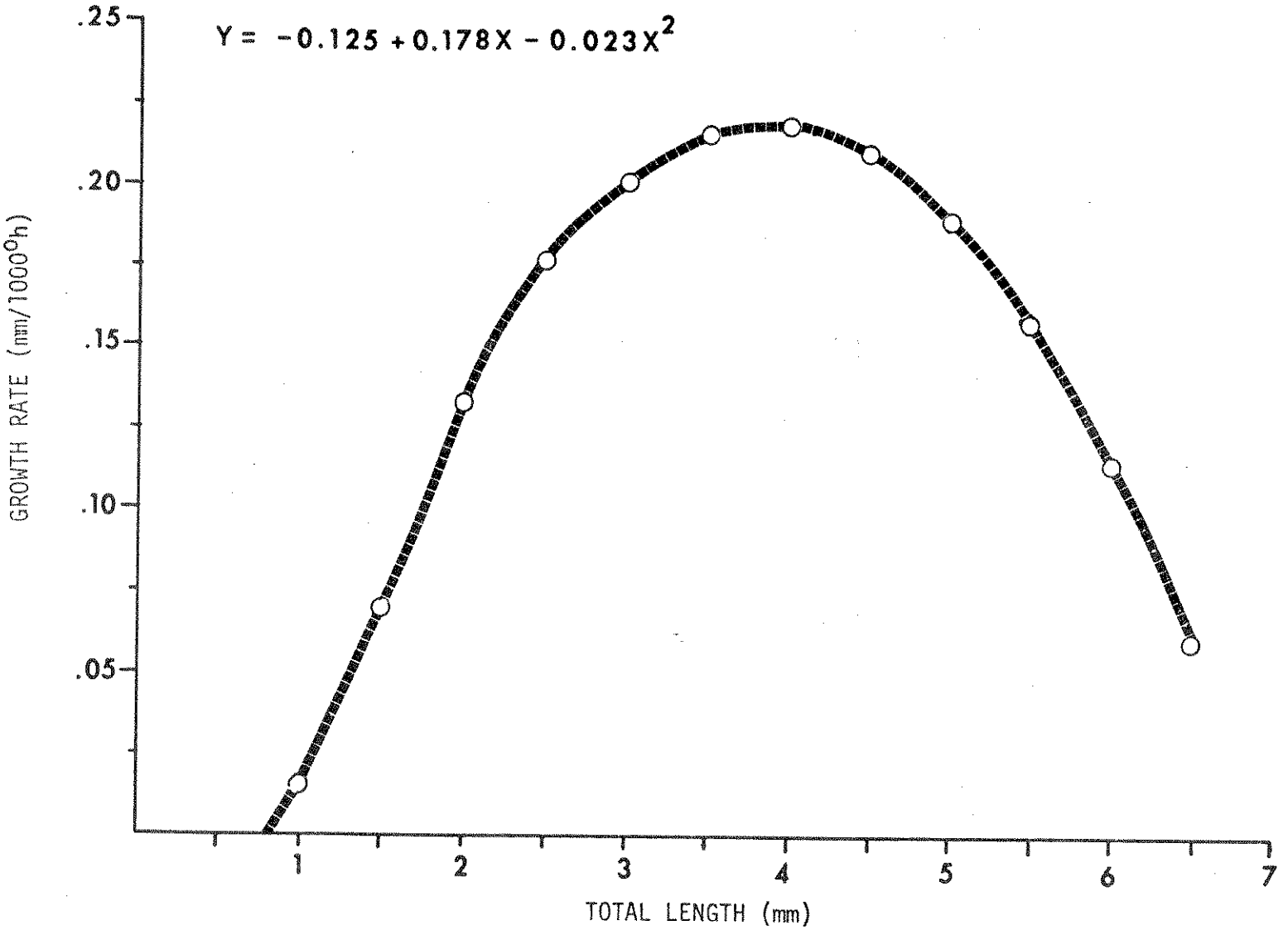
Table 24. Duration of development (S) for some species of aquatic insects taken from published sources and compared with that found for T. minutus.

ORDER	SPECIES	S (h)	REFERENCE
Ephemeroptera	Tricorythodes minutus	24,788[a]	Newell 1975
	Caenis simulans McD.	44,208*	Judd 1953
	Baetis tricaudatus D.	55,920#	Clifford 1969
	Paraleptophlebia debilis (Walker)	31,512#	" "
	Leptophlebia cupida (Say)	27,264#	" "
Odonata	Lestes rectangularis (Say)	31,368*	Judd 1953
	Anax junius (Drury)	62,976*	" "
Trichoptera	Stenopsyche griseipennis	52,800#	Gose 1970
	Agraylea multipunctata C.	54,072*	Judd 1953
	Leptocerus americanus (Bks.)	29,880#	" "
	Banksiola crotchi (Bks.)	70,352#	Winterbourn 1971
	Iecetis inconspicua W.	82,800#	" "
	Lepidostoma unicolor (Bks.)	62,256#	" "
Plecoptera	Nemoura cinctipes (Bks.)	45,120#	Clifford 1969

*= from egg to adult; #= exclusive of eggs.

[a]= temps. of 9°, 14°, 18±3°, and 19°C.

Figure 41. Plot of an n^{th} order regression analysis of the laboratory growth curves showing the single best fit line and resulting equation.


Y = -0.125 + 0.178X - 0.023X²
.25
.20
.15
.10
.05
GROWTH RATE (mm/1000°h)
1
2
3
4
5
6
7
TOTAL LENGTH (mm)

Growth is an important parameter in studies of secondary production and energy flow through aquatic ecosystems. It also permits a thorough examination of life cycle duration and life history. The lack of emergence synchronization is illustrated by emergence that occurs anytime after a nymph reaches 4.5 mm in length.

One may be more concerned with the ultimate consequence of growth (which is duration of nymphal life cycle and subsequent emergence of adults) because of difficulty in accurately measuring daily water temperature, daily nymphal growth, and the subsequent hyperbolic growth curve. Life cycle duration was calculated by applying laboratory derived growth rates to Winberg's (1973) formula and/or by differentiating the second order polynomial presented above. In the field it required observation on emergence periods and accurate recording of the thermal history of the stream above the point of zero development ($+5^{\circ}C$ for T. minutus). Winberg (1973) remarked that most temperature summation studies are confined to the linear portion of the common "S" shaped growth curve (temperature vs development rate) because the curvilinear portion makes calculations complicated.

The typical "S" shaped development curve was not plotted in this study. In this type of graphic representation the ordinate is per cent development and this is impossible to determine for T. minutus because emergence is not fixed but can occur any time after 4.5 mm in length is achieved. Because of an inability to establish the normal "S" shaped growth curve the logistic equation was not applicable in this study. Thus, an alternative was the analysis of growth or total length vs degree hours resulting in the parabola presented in Fig. 41.

This is a unique approach in growth studies in aquatic poikilotherms and has not been used before.

A major emphasis of this research was to formulate an expression to predict duration of the life cycle of T. minutus and validate that expression with field studies. The expression is as follows:

PREDICTION: 24,788°h are necessary above +5°C after occlosion, for T. minutus to complete one life cycle (95% conf. limits = ± 11,229°h). About 1000°h are required to hatch eggs.

VALIDATION:

station	yearly available temp. +5°C (°h)	observed life cycle	predicted life cycle
Deep Cr. sta. 2	109,200	multivoltine	4 cycles/yr.
Deep Cr. sta. 4	53,088	bivoltine	2 cycles/yr.
Spring Creek	51,996	bivoltine	2 cycles/yr.

The high values of the 95% confidence limits occurred because of variations in S from laboratory growth studies that ranged from 29,692 to 23,554°h except for one low value of 12,783°h at 9°C. It is impossible to determine the number of life cycles possible per year at station 2 in the normal manner of plotting per cent composition of size classes per month because of overlapping cycles. An alternative method was attempted by examing growth rates of individuals held in growth chambers in the stream. Rates obtained in this manner and projected

gave a value of S = 14,700°h, about half of the laboratory derived rate and permitting about 7 cycles per year. No adequate explanation was found for this aberration, although one partial source of error may have been the estimation of growth rate of the smaller nymphs (< 1.5 mm) that could not be held in the field growth chambers. The laboratory derived value of S = 15,101°h at 18°C is very close to the field rate of 14,700°h, and both values fall within the 95 per cent confidence interval given in the mathematical expression.

Analysis of the population at Deep Creek station 4 shows T. minutus to have a bivoltine cycle with two emergence peaks and thus agrees with the prediction. The life cycle in Spring Creek also appears to be bivoltine with two emergence peaks. The single year of investigation is probably insufficient to accurately determine life cycle duration. The data suggest an alternative view to the bivoltine cycle. An argument for a univoltine cycle could be made if the June sample is assumed to be inaccurate. The presence of mature nymphs and very small nymphs in the spring months and again in the summer makes a univoltine cycle seem very doubtful.

The life cycle of T. minutus is unquestionably influenced by water temperature. This mayfly has a multivoltine cycle in one portion of a stream, and is yet bivoltine in another section of the same stream and appears univoltine in other areas. This makes it unique among the species that have been studied.

Ephemeroptera life cycles are many and varied as illustrated by the following classification system proposed by Landa (1968):

A. One generation per year.

A1. (Winter species): nymphs hatch in summer and autumn, continue to grow throughout the winter, and emerge the following spring or summer.

A2. (Summer species): nymphs hatch, grow and emerge during a short period of summer, the eggs being in a supposedly diapause state for most of the year.

A3. (Winter species): nymphs hatch and grow in summer and autumn but not in winter, growth resuming in the following spring.

B. Two or more generations in a year.

C. One generation in two or more years.

D. Others.

In Deep Creek the life cycle of T. minutus would be placed in some category of group B. In Alberta, Clifford (1973) found T. minutus to belong in group A2 with adult emergence in August. There may be other exceptions to such classification schemes. The exception illustrates a point discussed by Macan (1970) that life cycles of any one species will vary depending upon its geographical range and resultant change in environmental influence. Characteristics of local populations including life cycle and morphology reflect adaptions to different environmental conditions.

Other insects show varying responses to fluctuating water temperatures. Illies (1952) suggested that a major difference between the mayflies and stoneflies is that growth of mayflies is usually stopped by cold water, but the growth of stoneflies is not. Some species of mayflies, Simuliidae, and caddisflies do show growth during winter months (Hynes 1970). Emergence dates of stream insects may be only partially determined by the rates of development of young stages and also may be controlled by the temperature at emergence (Macan and Maudsley 1968). However, in Deep Creek station 2 this does not seem to hold for Tricorythodes.

Clifford (1973) has summarized many generalities of Ephemeroptera life cycles. In the rainy tropical regions, where temperatures are constant and photoperiod uniform, multivoltine cycles with overlapping generations are common. Few species with temporary cycles are known from the tropics. When emergence is cyclic, it is due to factors other than seasonally varying temperatures and photoperiods, e.g. the lunar rhythms of Povilla adusta Navas (Hartland-Rowe 1958). In Florida, Berner (1950) found few seasonal species.

In the moderate temperate regions (e.g. in North America to about latitude 42°) seasonally varying temperatures and photoperiods are present. Mayflies in this region usually have one generation per year, with some growth in winter. Summer species are found in fewer numbers than winter species. Above 42° latitude in North America there is a tendency for the winter species without winter growth to predominate. There are fewer species with multivoltine life cycles, but species with summer cycles become increasingly more numerous.

In Deep Creek station 2, T. minutus would behave like a tropical insect and except for changing photoperiods, this station is somewhat similar to a tropical stream. Temperature and photoperiod affect aquatic insects in a variety of ways. A species will react to one or both of these factors. T. minutus seems to be little influenced by photoperiod although some response to diel photoperiod was noted for emerging adults. By contrast, the Odonata, of Deep Creek station 2 seem to be influenced more by photoperiod than by temperature. This is evidenced by their ability to maintain normal summer emergence whereas T. minutus and Baetis intermedius, and the caddisfly Hydropsyche occidentalis and Tinodes provo have all become multivoltine under these

constant temperature conditions.

Some insect species illustrate flexible life cycles in response to different climates. Many species of Simuliidae respond to different latitudes or altitudes by alterations in the number of generations passed through during the year (Zahar 1951). Some mayflies of the genus Baetis e.g. B. subalpinus and B. vernus, can respond to warm water by producing more than one summer generation and B. rhodani can dispense with its summer generation in high cool streams (Pleskot 1958). Flexibility in the life cycle of T. minutus may account for its wide distribution in a variety of aquatic habitats in the western United States.

Much more research on insect life histories is needed before one can generalize about factors such as flexibility and adaptability in different thermal regimes. Lehmkuhl (1974) illustrated this with two species of mayflies; Paraleptophlebia debilis (Walker) from Alberta differed in the duration of egg and nymphal stages from the same species in Oregon. Ephoron album (Say) is much less flexible however, as the eggs will not develop until they have been exposed to freezing, egg hatching occurs at 10°C and nymphal maturity is delayed until temperatures of 18 to 20°C are maintained. Lehmukuhl (1974) found that Ephoron album disappeared from a portion of the Saskatchewan River that received hypolimnion drain from a newly constructed dam. This species did not have the genetic flexibility to adjust to the new temperature regime. Ward (1974) witnessed extended mayfly emergence in a stream below a hypolimnion drain reservoir that had a constant cool temperature pattern.

The constant warm waters of Deep Creek station 2 are unique and as a result few similar aquatic habitats have been examined. Nielsen (1951), however, studied the fauna of constant temperature springs in North Jutland. One caddisfly, Apatidea muliebris emerged in late spring, grew during the summer and remained in a diapause state all winter. In another spring area two other species of this same genus were found flying from early spring to late fall, with all stages occurring together at the same time. Such exceptions make generalization of life cycles difficult. Other multivoltine insects may be found as other springs are examined.

In Deep Creek station 2, T. minutus has apparently lost some of the accurate controls that a mayfly population normally require to continue existing (e.g. timing of emergence). Because of the short life span of adult mayflies, timing of emergence is critical for successful mating. Premature or delayed emergence results in selection against those individuals and the result is a finely timed emergence of thousands of adults. This selection pressure has been removed at Deep Creek station 2 since emergence during most days of the year will result in a high probability of successful mating. The problem of synchronization of emergence is overcome by the great densities of nymphs on the substratum, thus increasing the chance of at least a few nymphs emerging simultaneously. Synchrony of diurnal emergence and selection of definite swarm sites would increase the chance of male-female encounters. This need for extremely large populations of nymphs is achieved at station 2 (up to 11,000/m^2). At this density a section of stream 6 m wide by 10 m long would have an estimated population of about 660,000 nymphs and if an equal number emerged daily, the result

would be 1808 adults/day emerging along this small section assuming no mortality, or 900 each at dawn and dusk. When this population estimate is expanded to include the 3 km (18,000 m^2) area of station 2 the number of adults emerging should be enormous, over 32 million/day and would be over 32,000/day if only 1% survival was realized. The high densities necessary for completion of the life cycle at station 2 should permit a simpler community structure. Perhaps this is why only two mayflies predominate here, T. minutus and Baetis intermedius and the entire community has a very low richness.

Fremling (1973) found how nymphs of Hexagenia bilineata synchronize their emergence along most of the Mississippi River. The nymphs were able to grow slowly at winter temperatures, but were unable to complete the last nymphal instar at temperatures less than 19°C. Thus, there was an accumulation of last instar nymphs in early summer. The first emergence of the summer is thus coordinated by winter temperatures. Insects following this type of synchronization would lose their synchrony in isothermal situations.

Much of the life history data gathered in this study reinforces facts known about other species of mayflies, e.g. oviposition, reproduction, subimago and egg morphology. Other life history aspects examined, e.g. thermal tolerance, egg occlusion, nymphal and adult morphology are species specific therefore preventing extensive interpretation.

The food habit study was a small extension of the work of Koslucher and Minshall (1973). Gut contents of nymphs revealed a detritivore habit, including most items small enough to ingest. Closer scrutiny revealed that most of the detritus in the gut was of mineral composition

and of no food value. Microorganisms associated with the mineral and organic detritus may be the major food items. The high densities of T. minutus (up to 11,000 m^2) would suggest this food to be abundant and nutritious. In laboratory growth chambers, nymphs at times subsisted on almost pure green and blue green algal growths. This flexibility in trophic relations may be one reason for the abundance and widespread distribution of this species in the western United States.

Because T. minutus is a detritivore, depositional areas would seem to be the most likely places to find large concentrations of nymphs. This is not the case, however. Other members of this genus do prefer slow, silty areas of rivers or backwater areas (Needham et al. 1935, Pearson et al. 1968). In Deep Creek station 2 equal numbers of nymphs were found in riffle and reach areas. Seasonal distribution in reach areas was erratic and no patterns were evident. A distinct distributional pattern was evident in riffle regions with lowest populations present in July and August and modes evident in early winter. The distribution data from station 2 is somewhat misleading because summer water withdrawls remove most of the flow resulting in much variation between summer and non-summer habitats. T. minutus shows little physiological need for fast currents and is morphologically and behaviorally adapted to very low current flows. In this kind of habitat T. minutus can utilize a food source that is abundant in these areas; small particulate organic matter (POM) that settles in pools, stream margins and backwater areas. Dissolved oxygen levels are probably low in these deposition zones, so T. minutus must live somewhere between stagnant low oxygen regions and moderate current areas. Another popular habitat for nymphs is on the limbs and brush that is deposited in

the stream. Pieces of wood like these often harbor large populations of nymphs.

Sample variations were apparent in reach areas more than in riffle samples. The two monthly samples taken in both habitats were usually no more than 2 m apart yet samples varied by as much as 11,000 m^{-2} (reach area Jan. 1972). The wide variation in some samples illustrates clumping. The low variability in riffles is probably due to the more uniform conditions in that habitat.

Instar analysis of Ephemeroptera has always been a difficult problem. Ide (1935b) used "X" factor and antennal segments to determine instars while Clifford (1970) measured head capsules and others counted nymphal skins cast in the laboratory (Rawlinson 1939, Ellis 1961). None of these methods has proven satisfactory. The new method of instar analysis (Janetscheck 1967) may solve this old problem. In the present study the Janetscheck method was used with two measurements, total length of nymphs and of cast skins. The results were comparable with graphed instars identical for both measurements. An attempt was made to count nymphal skins in laboratory chambers, but this was only partially successful. Microbes rapidly consumed the skins and in one case a nymph was seen consuming its own skin. Nymphal skins often were covered with dozens of individuals of the Protozoan Vorticella and thus skins with attached protozoans could be an excellent quality food. The instar analysis presented above shows fewer instars for males (19) than females (23), a fact not previously reported in published literature. A female living at 23°C completing a life cycle in 40 days would molt about every other day. This would be a tremendous energy expenditure and a time of increased mortality.

Calorific values have been recorded for many species of aquatic organisms (Cummins and Wuycheck 1971). The only calorific values available for T. minutus are those of Brass (1971) who used a bomb calorimeter to gather his results. In this present study per cent organic matter of nymphs was determined by combustion and the formula, $Y = 0.0559X$ where X = per cent organic matter was utilized (Winberg 1971). Brass (1971) found a mean calorific value of 4.767 Kcal/g dry weight and the formula method gave a mean value of 4.721 Kcal/g dry weight. These results would lend support to the formula method and perhaps it should receive further use because of its advantages. An investigator only needs an oven and an accurate balance as opposed to an expensive calorimeter to accurately and rapidly determine calorific values for aquatic insects.

At any body length the shed nymphal skin constitutes about 10 per cent of total nymphal weight. At 23°C a nymph would, therefore, be shedding 10 per cent of its weight every other day. This species must have a remarkable metabolism and a very nutritious food source to make up these losses and still increase in weight. As maturity approaches and the digestive system slowly degenerates and is replaced by reproductive cells, the insect begins to lose this metabolic battle and growth decelerates after about 4 mm is attained. The nymphs soon loses total length and body weight after the last few instars.

The sheer bulk of cast skins of T. minutus in the stream must be tremendous. With a benthic density of 10,000 nymphs per m and assuming a molt every other day (23°C) the number of skins present on the bottom would be huge. Perhaps these skins provide food for aquatic invertebrates or at least a substrate for decomposer organisms that

are in turn consumed by Tricorythodes.

Cast skins are a significant energy loss. A nymph 5.0 mm in total length weighing 1.6 mg would have a calorific content of 7.62 cal and would lose 0.89 cal or 12 per cent of its energy content with each molt.

The study of the eggs of T. minutus revealed some previously unknown facts. Egg counts from mature nymphs were always lower than counts from adults. In life table studies mayfly egg counts should only be made on adult females. The smallest females carried the smallest number of eggs.

Egg occlusion is inversely related to water temperature. There was a 50 per cent occlusion in 39 days at 23°C and this increased to 140 days at 7.5°C. Duration of occlusion and mortality varied inversely with temperature. Cold water, therefore, has more effect than merely a slow down in development time.

Although production estimates were not a prime goal of this research, the data permits production estimates using turnover rates of Waters (1969). Waters discovered that most insect populations have a turnover ratio (production/biomass) of about 3.5. During the June 1970 to June 1972 period, the annual production was 23.18 g m^{-2} at station 2 and only 4.89 g m^{-2} at station 4 for T. minutus. The tendency would be to credit the constant thermal pattern at station 2 with the larger production values. This may or may not be true and caution should be exercised here because Water's turnover value may not be applicable for multivoltine populations.

Undoubtedly, temperature controls every aspect of the life history of T. minutus from length of occlusion to geographic distribution. This study resulted in the acquisition of many new aspects of mayfly life history phenomena. The data gathered in this study lends support to the temperature summation concept, but illustrates that caution shoud be exercised in its application.

It is hoped that studies such as this can help in the formulation of guidelines and standards for thermal discharges into the aquatic environment. It is evident from this study that moderate and constant thermal inputs can result in increased growth and production of some aquatic insects. Other studies stress that some species can not tolerate thermal regimes that deviate from the norm and so much more research is necessary before meaningful thermal standards can be adopted.

ADDENDUM

On page 4 of this dissertation I noted that, "... no life history studies have been done on any species of the genus Tricorythodes." This statement is no longer true with the completion of research on Tricorythodes atratus McD. by Hall (1975) and Hall et al. (1975) on the Mississippi River. Some of Hall's finding on life history, drift, and production are interesting and noteworthy.

T. atratus is similiar to T. minutus in that both emerge at low light intensities and have bivoltine life cycles. In many other cases the two species are dissimiliar. Examples of this dissimiliarity are as follows; T. atratus emerges under water, overwinters in the egg stage, and has a herbivore trophic nature. Growth was not examined during this study.

Hall, R.I. 1975. Life history, drift, and production rate of the stream mayfly Tricorythodes atratus McDunnough in the headwaters of the Mississippi River. Unpubl. Ph.D. Dissertation, Dept. Ent. Univ. Minnesota, St. Paul.

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