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THE INFLUENCE OF DETRITAL FOOD QUALITY AND TEMPERATURE ON THE LIFE HISTORY AND GROWTH OF *PARATENDIPES ALBIMANUS* (MEIGEN) (DIPTERA: CHIRONOMIDAE) IN A MICHIGAN HEADWATER STREAM

By

Grover Milton Ward

A DISSERTATION

Submitted to
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in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

THE INFLUENCE OF DETRITAL FOOD QUALITY AND TEMPERATURE ON THE LIFE HISTORY AND GROWTH OF PARATENDIPES ALBIMANUS (MEIGEN) (DIPTERA: CHIRONOMIDAE) IN A MICHIGAN HEADWATER STREAM

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Grover Milton Ward

An autecological study of the stream detritivore Paratendipes albimanus (Meigen) in Augusta Creek, Kalamazoo County, Michigan included investigations of the natural history and pattern of growth, as well as a determination of the effects of temperature and detrital food quality on the growth rates of laboratory populations. Measurements of changes in dry weight biomass revealed that the Augusta Creek population was univoltine, with a flight and oviposition period from late June to mid July. P. albimanus had a rather complex pattern of growth, in which development was divided into four distinct periods. Two brief periods of growth during the summer and fall left the overwintering population as a mixture of I and II instars. The two final growth phases occurred in April and June and together represented 99% of the final population biomass accumulation.

Studies in laboratory situations and in large scale experimental streams determined that variations in

temperature, within the range 5-20°C, produced linear changes in larval growth rates, however, rates were constant when corrected for amount of heat accumulation (day-degrees).

Day-degree accumulations proved to be a consistent estimate of developmental velocity and timing of emergence. The Augusta Creek population required 650 day-degree days after winter in order to begin emergence, while laboratory populations required approximately 700 day-degrees.

Laboratory experiments determined that growth rates of larvae responded to food with differing microbial densities. Those substrates with higher microbial activities and biomasses produced the higher growth rates in the order pignut hickory > white oak > insect feces > natural stream detritus. Substrate ATP and respiration rate were determined to be adequate estimates of food quality.

With a combination of field and laboratory data, observed natural growth patterns were explained in terms of growth regulating environmental factors. Food quality inhibited growth in summer and in May, while temperature and a second factor (perhaps photoperiod) prevented growth in winter. Temperature was a general control of growth rates except when overriden by other factors.

DEDICATION

To my mother, Edith, and the memory of my father, Grover--Thank you for allow-me to choose my own way and supporting me at every turn.

ACKNOWLEDGMENTS

During my years as a graduate student, many people have contributed toward the successful completion of this degree. To all who have helped, my thanks. I must thank individually, however, those who have helped me most. Dr. Kenneth W. Cummins, teacher and colleague, has provided continual support and encouragement during this project. Dr. Gerald A. Moshiri, whose guidance and direction during my first years as a graduate student has, in large part, led me in the direction I have chosen.

I would also like to thank my guidance committee, Drs. M. J. Klug, F. W. Stehr, and E. E. Werner for their suggestions and criticisms during this study. Dr. D. R. Oliver has aided greatly by giving of his time and expertise. Also, I would like to express my appreciation to Kathy Erdman whose excellent artistic work produced the drawings in the text.

To my wife Amy I owe special thanks. Her unwaivering patience and support, as well as timely criticisms, will always be appreciated.

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INTRODUCTION

Life History Studies

Based on general survey and ecological studies, the broad outlines of temperate chironomid life cycles have been established. Studies of tropical and polar species have significantly broadened this overview and further research will undoubtedly result in the discovery of still more life history variations. A more complete understanding of the life cycles and growth patterns of major biotic components, such as the midges, must be obtained if the functioning of benthic communities is to be fully understood. The autecological approach to studies of entire life cycles is a kind of intensive research needed, and has been encouraged by Hynes (1970), Oliver (1971), and Danks (1971a), as the best method to study the biology of the Chironomidae.

Although autecological studies of lentic species have been published (e.g., Sadler, 1935; Walshe, 1951; Biever, 1967; Danks, 1971a; Jónasson, 1972), stream dwelling species have not been the subject of this type of research. Lotic Chironomidae are diverse and have long posed major taxonomic and ecological problems. Recent analyses of stream chironomid communities (Saether, 1968; Lehman, 1971;

Lindegaard-Petersen, 1972; Coffman, 1973) have revealed that large numbers of species inhabit many stream systems.

The objective of this study was to describe the life history, particularly the larval growth pattern of the midge, Paratendipes albimanus (Meigen), as a small, but very abundant fine particle feeding detritivore (collector-gatherer, Cummins 1973, 1974) from an extensively studied depositional-lotic habitat. P. albimanus was studied using the autecological approach in Augusta Creek, a small first-order (Strahler, 1964), woodland stream in Michigan.

Taxonomy

Meigen first described the species as Chironomous annularis in 1804, but in 1818 renamed the species albimanus (Townes, 1945). In 1911 Kieffer erected the genus Paratendipes and assigned albimanus as the type species. Seven North American species have now been described, but only the larvae of albimanus is known. Consequently identification of P. albimanus should be made from adult males, those from larvae only being suspect.

Distribution and Ecology

In Thienemann's (1954) review of the Chironomidae, ecological notes on P. albimanus showed its distribution to be holarctic and the habitat to be eurytopic, including pools, ponds, oligotrophic to eutrophic lakes as well as

upland and lowland streams. Collections were reported from northern and central Europe and North America. Distribution in North America is from Ontario and New York, south to North Carolina and Arkansas and west throughout the midwest to Idaho and California (Townes, 1945; Sublette, 1960; D. R. Oliver, Personal Communication). The major ecological documentation for P. albimanus (Table 1), indicates micro-habitats ranging from streams to littoral, sublittoral and profundal zones of lakes having substrates of either sand, mud, or a mixture of the two. In streams, this species has been found in greatest abundance in slack flow regions where significant accumulations of fine particulate organic matter (FPOM) occur, but may also be numerous in erosional areas.

Phenology

Based on phenological data of previous studies, one finds conflicting conclusions regarding the voltinism of this species. Townes (1945) collected this species from May to September and concluded it had several generations per year (only as bivoltine in Lake Chautauqua, N.Y.; Townes, 1938). Other authors have concluded the species is either univoltine or bivoltine in standing waters (Table 1) and univoltine in flowing waters. In general, emergence of the winter generation occurs later in streams (June-July) than in lakes (May-June) and is generally later than other species in the same habitat.

Table 1. Summary of literature data on Paratendipes albimanus (Meigen).

Reference	Habitat	Life Stage[1]	Microhabitat	Flight Period(s)	Comments
Johannsen (1937)	Small streams near Ithaca, New York	L,P,A?	Sewage contaminated brook	Not given	
Townes (1938)	Lake Chautauqua, New York	L,A	Fine sand with more or less muck, esp. in weed beds; 0.5 m to 6.5 m	June and August	Usually 50 to 300 per m^2 but up to 5500/m^2
Nietzke (1938)	Die Kossau, Germany	L,P,A	Mud in moderate and slack flows	Not given	High densities
Brundin (1949)	Oligotrophic lakes, Sweden	A	Lower littoral zone	July	
Thienemann (1950)	Lunzer, Germany	L,P,A	Mud at depth of 0.5 to 1 m	May and August	
Hall (1951)	River Itchen and Ober Water, England	L,P,A	Fine gravel and silt with a covering of mud and debris	Not given	
Curry (1954)	Hunt Creek, Michigan	L,P,A	Backwater areas in sand and mud and also in beaver ponds at depth of 1-8 ft.	Not given	Abundant when found and easily reared
Dittmar (1955)	Aabach, Germany	L,P?,A	Mud in mid-stream	June	
Roback (1957)	Several streams in Pennsylvania	L,P,A	Rock and gravel areas, as well as in mud	Not given	

Riess (1968a)	Lake Constance, Germany	L,P,Pe,A	Sandy sublittoral and profundal zones; up to 30 m	May-June and August	Eurybathic; numerous in sandy sublittoral zone
Riess (1968b)	Several European alpine lakes	A	Not given	Not given	
Iovino and Minor (1970)	Beaver Reservoir, Arkansas	L,A	Not given	May-June	
Lehman (1971)	Fulda River, Germany	L,P,Pe,A	Mud near bank regions	June	Rare
Learner and Potter (1974)	Small ponds, England	A	Not given	June	42/m^2 emerging
Present Study	Augusta Creek, Michigan	L,P,Pe,A	Sand and gravel riffles as well as depositional areas along stream margins	June-July	10,000/m^2 in riffles 30,000/m^2 in Pools
Present Study	Hamilton Lake, Michigan	L,P,A	Fine particulate detritus near mouth of inlet stream; up to 9 m	June	Distribution restricted to delta region

[1]L = larva, P = pupal, Pe = Pupal exuvia, A = adult

Temperature Studies

The increased use of surface waters as a coolant for industrial processes and power generating facilities poses a potential threat to those ecosystems which receive the heated effluents. The eventual changes which ecosystems must surely undergo when long-standing thermal regimes are altered are basically unknown; however, studies describing the effects of thermally altered habitats have become more prevalent, especially after increased energy generation became a national goal.

Lotic systems seem particularly vulnerable in this regard since much of the aquatic biota is stenothermal. Death of organisms may be one response to lethally high temperatures (Walshe, 1948; Biever, 1967), but more subtle longer term effects may be equally disastrous. Temperatures above the upper lethal limit may eliminate an organism quickly, but decreases in competitive abilities or alterations in life history patterns may eventually eliminate a species just as effectively.

Many effects of temperature on the distribution and life histories of stream insects have been summarized by Hynes (1970). A review of temperature effects on growth suggests that some stream insects, such as the Plecoptera, Trichoptera, and Simuliidae, possess very low temperature thresholds for development. Growth of larvae in these

groups could continue at low temperatures, while other species, such as several of the Ephemeroptera, have higher developmental thresholds and cease growth when temperatures fall below 5-6°C (Hynes, 1970).

Theoretically, increased winter temperatures could increase the growth rates of those species which do grow in winter, or perhaps initiate growth in some species which would not normally grow. The ultimate threat is that adults would appear when the terrestrial environment was too hostile, and either be lethal or too harsh to permit normal mating behavior. Nebeker (1971a) has shown early emergence in the laboratory of ten species of aquatic insects whose larvae had been subjected to abnormally high winter temperatures. Considerable variation in the timing of emergence of a species also has been observed where altitudinal changes produced gradients in water temperature (Nebeker, 1971b).

Investigations on the effects of temperature on chironomid larvae have been few compared to those for other groups. Studies by Konstantinov (1958a and 1958b) have shown that chironomid larval growth is under general thermal control and that day-degree accumulations can be used to predict emergence of species with relatively short generation times. Miller (1941), Mundie (1957), and Potter and Learner (1974) have studied the day-degree requirements of natural populations. Biever (1967) and Nebeker (1973) concentrated on

establishing upper thermal limits and optimum growing temperatures for several lentic species and Walshe (1948) has demonstrated that stream species generally have a lower thermal resistance than standing water species.

Although chironomids are one of the most common of aquatic insect families, relatively little is known of growth responses when changes in temperature occur. This study is an effort to supply understanding in this area.

Food Quality Studies

The importance of detritus to the structure and function of ecosystems has been emphasized in recent years (e.g., Reichle, 1975). Detritus constitutes the major energy source of heterotrophic headwater streams. Studies such as those of Nelson and Scott (1962), Minshall (1967), Fisher and Likens (1973), and the review of Cummins (1974) have documented the structure of headwater streams and described the functional relationships between system components.

Fisher and Likens (1973) and Cummins (1974) discussed the sources of detrital inputs to streams and Cummins (1974) and Petersen and Cummins (1974) reviewed potential interactions between particulate organic matter (POM or detritus) and benthic macroinvertebrates. The relationship of the microbial communities on detritus particles to the nutrition of macroinvertebrates has received considerable attention.

A number of studies have implicated microorganisms as important components of animal diets (Newell, 1965; Hargrave, 1970; Brinkhurst et al., 1972; Calow, 1975; Davies, 1975) while Baker and Bradnam (1976) questioned their importance, although lack of attention to native gut flora renders the conclusions questionable.

While the precise role that microorganisms play in the diet of aquatic macroinvertebrates has yet to be determined, it has been presumed that microbiologically related, nutritional differences can produce significant changes in the life cycle of a macroinvertebrate.

The term, food quality, was used by Cummins (1974, 1975) to compare different substrates as potential foods for macroinvertebrates. Substrates with higher microbial densities are of higher quality than those with low microbial densities. Microbial densities are a reflection of inherent chemical differences between substrates when all other factors are equal and may vary between substrates as a function of conditioning time and particle surface area. Differential in situ microbial colonization rates have been observed between "fast" (e.g., ash, hickory) and "slow" (e.g., oak, aspen) leaves (Petersen and Cummins, 1974; Suberkropp and Klug, 1976), and comparatively higher activity has been observed on smaller particles, due to increased surface area (Newell, 1965; Hargrave, 1972).

Food quality can be defined simply as nutritional value per unit of intake. Thus, food quality would be synonymous with food quantity if the microbes attached to detrital particles are the sole source of nutrition and none of the detrital matrix is of value. Traditionally, food intake has been measured as the weight of substrate ingested. However, if the microbial biomass represents the major source of nutrition and microbial densities vary among particle types and sizes, then the weight of particles ingested alone is not an adequate measure of actual nutritional intake.

In studies in which food particle size was not manipulated, quality differences between foods resulted in increased growth rates, decreased generation times (Biever, 1967; Bärlocher and Kendrick, 1973) and increased survivorship (Biever, 1967). Increased autumnal lipid reserves in the caddisfly Potamophylax cingulatus (Otto, 1974) were attributed to a seasonal increase in the food quality of autumn-shed leaves in a Swedish stream. Marzolf (1964), Newell (1965), and Hargrave (1970) have observed higher animal densities and body sizes in areas with rich microfloras.

Most studies on the effect of food quality on stream organisms have focused on shredders using whole leaf substrates. Bärlocher and Kendrick (1973) found food preferences and survivorship differences among leaf species and

leaf-fungus combinations fed to Gammarus, while Iversen (1974) observed faster growth on leaves with higher organic nitrogen content and Cummins (1974) reported differential Tipula growth on "fast" and "slow" leaf litter. Extension of food quality studies to other functional groups, collectors and scrapers, are now needed.

Quality differences in stream fine particulate organic matter (FPOM) detritus (< 1 mm diameter) have not been investigated, and extension of conclusions about quality differences in whole leaves to the fine particles generated from their decomposition presently can only be inferred (Short, 1977). Presumably, differences in animal preference due to physical attributes of conditioning time, such as leaf toughness, would become less important after reduction in particle size during extended residence time in the stream, but inherent differences in chemical properties may still reside in the fine particles.

The object of these experiments was to determine whether foods of widely different qualities (microbial densities) would produce significant differences in detritivore (P. albimanus) growth rates and if laboratory measurement of food quality could be extended to natural stream systems to aid in interpreting field growth patterns.

METHODS

Study Site

Augusta Creek is a third-order, hardwater, brook and brown trout stream arising in Barry and Kalamazoo counties in southwestern Michigan. It has a drainage area of about 70 km^2 and a mean annual discharge of about 1.4 m^3/sec (50 cfs). The system is composed of groundwater charged tributaries and those arising out of lakes and marshes. The stream meanders through wetlands, pastures, farm lands, and mixed deciduous forests before entering the Kalamazoo River near Augusta, Michigan.

Although P. albimanus was found at several locations throughout the watershed, major emphasis was at site B (Figure 1). This first-order tributary drains a tamarack swamp and flows into Hamilton Lake, a small, hardwater, oligotrophic lake. The stream is 1-2 m wide and has a mean annual discharge of 0.08 m^3/sec (3 cfs). The site has a low mean daily temperature, 0-1°C, in January and a high mean daily temperature, 15-16°C, in June-August (Figure 2); the total annual day-degree accumulation (Andrewartha and Birch, 1954) is 3200-3300.

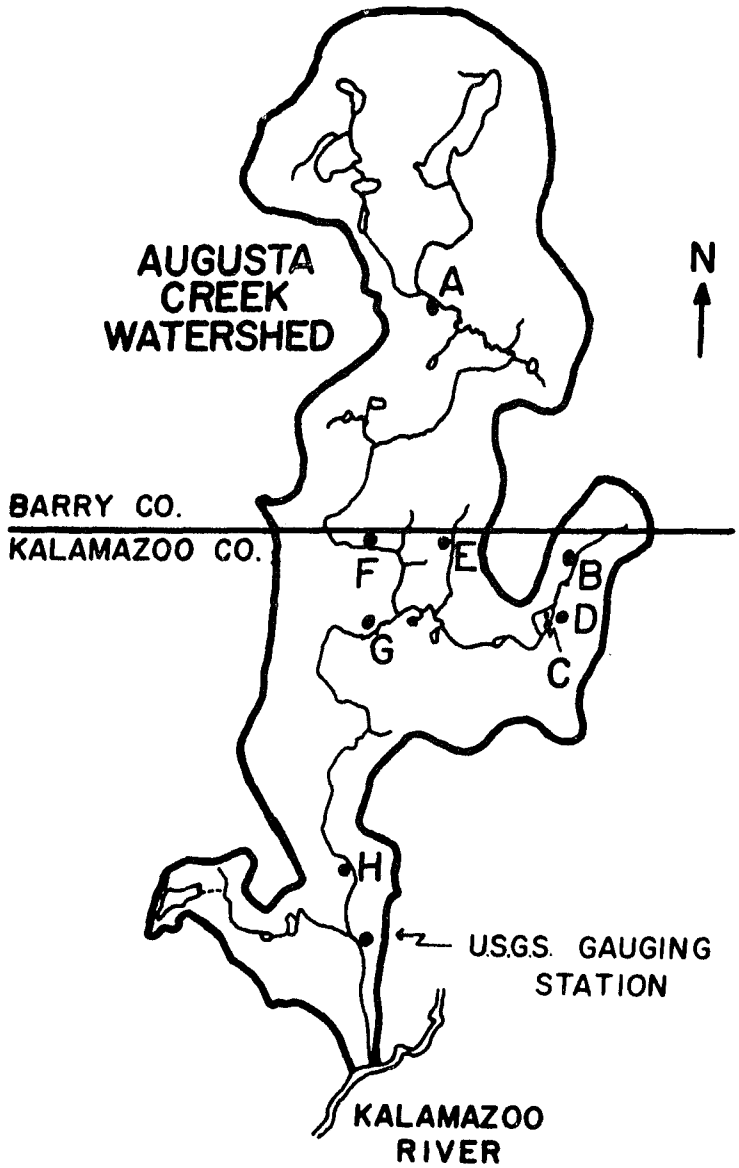

Figure 1. Augusta Creek watershed, Barry and Kalamazoo counties, Michigan. Various sampling sites are indicated by letter codes in Table 2.

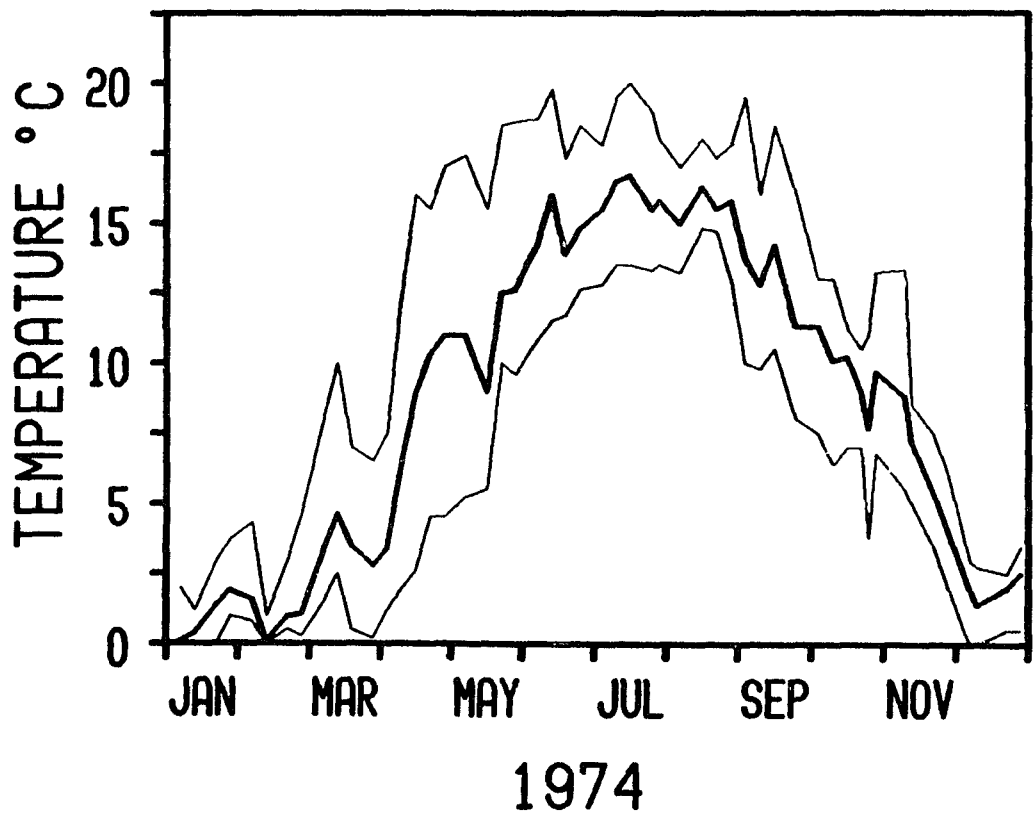

Figure 2. Annual temperature pattern for Augusta Creek, site B, 1974. Given are mean daily and weekly minimum and maximum temperatures.

Hamilton Lake, with an area of 10 ha and maximum depth of 25 m, receives waters from Augusta, creating a littoral and delta area near the mouth of the stream. As is common in many glaciated watersheds, streams flow through a number of small lakes along its course, and the effluent waters from Hamilton Lake constitute a continuation of a main branch of the Augusta Creek drainage network.

Experimental Stream Facilities

Enclosed artificial stream systems (Cummins, 1972) were available for use with large experimental populations. Each of two recirculating, 4000 l concrete bottom streams were temperature and photoperiod controlled. Channels were 11 m long, and 1 m wide and from 0.25 to 0.5 m deep. Both erosional and depositional habitats were present, with a depositional zone of 3 m^2 near the downstream end of the system.

The streams were used to test the effects of increased winter temperatures on the overwintering population and to determine emergence patterns when field collection methods failed to provide adequate numbers of adults and/or pupal exuvia.

Life History Studies

Animal Collections

Egg masses were collected by using 0.5 mm mesh screening on metal framing (30 x 90 cm), placed on the stream bottom during the emergence period. Eggs were harvested daily and the screens replaced. Larvae were sampled quantitatively in riffles with a box sampler (900 cm^2, Coffman et al., 1971). Likewise a small plexiglass cylinder (16.2 cm^2) was used to collect undisturbed sediment in depositional areas. Pupal exuvia were collected from behind either artificial or natural debris barriers. In addition to several natural barriers, styrofoam sheets (183 x 30 x 2.5 cm; Figure 3) were cut and placed at the downstream end of the study reach, a modification of the sampling procedure of Coffman (1973). Openings in the body of the barrier allowed two short posts to act as anchors but permitted it to float freely, rising or falling with stream depth. The barrier stretched across the entire channel and captured floating pupal exuvia, moribund insects, and other material. Trapped particulate drift was removed with a small dip net and preserved. The device worked most efficiently at low discharges and velocities, and proved to be very efficient when used in the artificial stream facility described above.

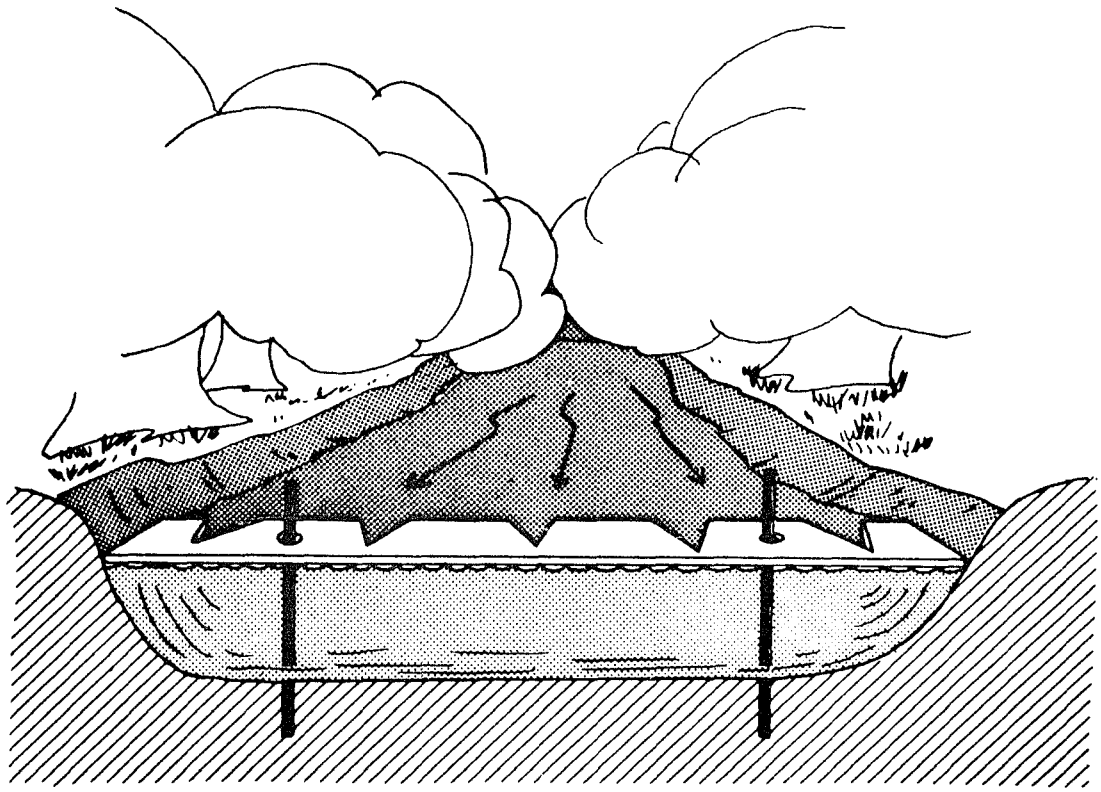

Figure 3. Schematic diagram of device used to collect floating pupal exuvia in Augusta Creek, and in the artificial stream system.

Biomass Measurements

Specimens collected during this study were sorted live from the sediment with the aid of a stereo microscope. After allowing animals to empty their gut tracts, they were placed on aluminum foil pans, and dried at 50°C to a constant weight, and weighed on a Cahn Electrobalance fitted with a digital readout to 1 µg. Since in most cases larval weights were less than 5 µg per individual, groups of individuals were weighed and mean weights calculated.

Species Identification

Reared adults with associated larval and pupal exuvia, as well as field collected adults, were identified by Dr. D. R. Oliver, Biosystematics Research Institute, Agriculture Canada. Specimens from this study were conspecific with European material identified as P. albimanus by Lehman (1971). Voucher specimens were deposited in the Canadian National Insect Collection (Lot numbers 74-269 and 74-703).

Temperature Studies

Design of Laboratory Experiments

Qualitative collections of larvae for each experiment were made in Augusta Creek at site B (Figure 1). Short duration experiments utilized IV instars while longer duration experiments began with II-instars.

Treatment temperatures ranged from 5°C to 20°C, in increments of 5°C. These temperatures covered a range experienced by larvae in this habitat. Each treatment combination contained three replications, and larval weights from each were a mean of two determinations. Initial and intermediate weights were obtained by sacrificing a subsample of 15 larvae in each of two determinations from each treatment replication. Final values were mean weights of all surviving larvae in the treatment replication, usually 10-15 in each determination. These experiments were performed in temperature controlled Frigid Units^{R}, held to $\pm$ 2°C. Larvae were placed in either 500 ml Erlenmeyer flasks for short term experiments or in 3 gallon aquaria for longer term tests. Substrates consisted of natural stream detritus in a particle size distribution similar to that of the natural habitat.

Growth rates for each treatment were calculated from mean weights at the beginning and end of each time period tested by the following:

$$k = \frac{\ln \left(\frac{\text{Final Weight}}{\text{Initial Weight}} \right)}{\text{days}}$$

Growth rates based on day-degrees were obtained by substituting day-degrees for days in the growth equation. Results from this equation approximated those obtained by using the equation of Waldbauer (1968).

Design of Experimental Stream Studies

The artificial streams described above were utilized for studies of overwintering populations. Second-instar larvae were collected from site B in November and held at 8°C in these streams until initial samples were taken in mid December. At that time, temperature in stream 1 was lowered to approximately 5.5°C and raised in stream 2 to about 10.5°C. Changes in population densities and mean weight of the larval population were followed until emergence the next summer.

Both riffle and pool habitats were present in the streams, with cobble the predominant substrate in the riffle and fine particulate detritus from sites B and H in depositional areas. Larvae of P. albimanus were found in both habitats, although 99% inhabited depositional areas.

At intervals of about three weeks, three 16 cm^2 quantitative samples were removed from depositional zones in each stream. Larvae were sorted live, dried, and weighed on a Cahn Electrobalance. Growth rates were calculated as described above.

Temperature regimes in these systems, as well as those in Augusta Creek, were determined through gravimetric integration of recorder tracings from a spring-driven recording thermometer (The Bristol Company). Mean daily values were determined at approximately seven day intervals.

Food Quality Studies

Animal Collections

Fourth instar larvae of P. albimanus were collected at site B during May of 1975 and egg masses were obtained from the stream bottom in July of 1975 and held at 5°C until needed.

This midge larva feeds by gathering fine particulate detritus from the sediments. Early instars are quite small (total length 0.5-2.0 mm, head capsule width 40-50 μm) consuming only very small detrital particles (25-40 μm diameters, depending on the instar). Mature larvae, with head capsule widths up to 210 μm, ingest particles up to 125 μm in size. Nearly 100% of the gut contents of field collected larvae is detrital material. P. albimanus falls into the "collector-gatherer" category in the functional trophic scheme of Cummins (1973, 1974, 1975).

Animals used in feeding studies were starved before being placed in 500 ml aerated flasks containing the treatment substrates. Larvae were at the same developmental stage and approximately equal biomass. Each treatment combination was replicated and 30 animals placed in each flask. Initial mean dry weights were determined by sacrificing 10 randomly selected animals from each flask. After 14 days, mean dry weight, of surviving larvae were determined for each flask. Survivorship was high on all substrates.

Substrates

Four particulate food sources were chosen, designed to cover a range of possible nutritional types. Each substrate was tested at 10, 15, 20°C, chosen to cover the range that occurs during the major growth phase of P. albimanus. Natural stream detritus was collected from the same reach as the animals, dried and sieved to a particle size range < 250 μm < 75 μm. Cultures of the cranefly shredder Tipula abdominalis provided insect feces, which were collected weekly, frozen until needed, and washed, dried and sieved before being used. Feces represented a material thought to be intermediate in quality between fresh leaves and native particulate detritus having a long stream resident time.

Leaves of two deciduous trees common in the watershed, pignut hickory (Carya glabra) and white oak (Quercus alba) were collected during the autumn of 1974 and stored. The two leaf types were labeled "slow" (oak) and "medium" (hickory) by Petersen and Cummins (1974) in comparing decay rates and presumably quality differences among various leaf species in the Augusta Creek watershed. Prior to use, leaves were incubated for six weeks in large aquaria with an inoculum of stream water augmented with mineral salts to stimulate microbial growth, dried, ground and sized by sieving. These leaf-derived particles were intended to

simulate natural substrates produced from decomposition processes in Augusta Creek.

To each flask, 3 ± 0.01 g of substrate plus an inoculum of stream detritus was added and allowed to incubate at a given temperature for 15 days. The inoculum consisted of fresh stream detritus equal to 1% of the wet weight of the test substrate. Measurements of total N, C/N and organic matter content were performed before introduction of animals and at the end of the experiment while estimates of substrate ATP and substrate respiratory rate were made at the time of the final sample. Substrate ATP content was analyzed as described by Suberkropp and Klug (1976) and respiration was measured with a Gilson Differential Respirometer (Gilson, 1963). Total N and C were determined with a Carlo Erba Elemental Analyzer fitted with a CSI^{R} 208 integrator. Organic matter content was measured from percent loss on ignition at 550°C after 24 hours.

Field Methods

Detritus from site B, Augusta Creek, was collected at approximately monthly intervals and respiratory rate measured and replicated in a Gilson Respirometer, ash free dry weight (AFDW) was calculated from percent loss on ignition after 48 hours at 550°C (Cummins et al., 1977).

RESULTS

Distribution and Life History

General Pattern

P. albimanus was collected at several sites within the Augusta Creek watershed. Highest densities occurred mainly in small first-order tributaries but the species was also found in a nearby lake, a small spring and in several second- and third-order reaches downstream (Table 2 and Figure 1). Although found in riffles and pools during a large part of its life cycle, the preferred habitat during the major developmental phase of the life history appeared to be depositional zones, especially along stream banks and in pools where fine detritus (fine particulate organic matter, FPOM, plus associated microbiota) accumulated.

An interesting ecological contrast was provided by the existence of larvae in both the stream and Hamilton Lake. Drifting detritus from the influent waters of Augusta Creek settled in a deltaic fan, creating a littoral zone of soft muck, which contrasted sharply with the marl benches and concretions in the remainder of the lake. A very marked difference in distribution of *P. albimanus* occurred between these two zones; larvae being common up to 9 m depth in the

Table 2. Description of study sites and relative abundance of P. albimanus in the Augusta Creek watershed.

Site[1]	Habitat	Type of Sediment	Temperature Range °C	Relative[2] Density	Stream Order
A	Slack current downstream from an impoundment	Deep accumulations of fine particulate detritus	0-23	***	1
B	Erosional zone in moderate current	Gravel and sand riffle	0-15	**	1
	Depositional zone along stream margin	Moderate accumulations of fine particulate detritus	0-15	****	1
C	Hamilton Lake, in delta region near inlet stream	Fine particulate sediments from Augusta Creek	2-17	**	-
D	small spring with slow current	Sand overlain with accumulations of fine particulate detritus	6-20	*	1
E	Erosional zone	Sand	0-15	*	1
F	Erosional zone	Gravel and sand	0-22	*	2
G	Depositional zone along stream margin	Fine particulate detritus over sand	0-20	*	3
H	Depositional zone along stream margin	Sand and gravel overlain with moderate accumulations of fine particulate detritus	0-20	*	3

[1] See Figure 1 for site locations.

[2] Abundance: * = minimum, ** and *** = intermediate densities, **** = maximum.

delta area, but completely absent from the zone outside the settling detritus. Although it is unknown to what extent drifting animals from Augusta Creek may have colonized this habitat and supplemented a resident population, there were substantial differences in the growth pattern of the two populations (see below).

P. albimanus was a univoltine, summer emerging species in Augusta Creek, with a flight time from late June to mid July. In the field, development began immediately after hatching. A complex pattern of development (Figures 4 and 5) consisted of four distinct periods of growth, with the overwintering period equally dividing the four. This produced an annual growth curve which was stair-step in the early instars and exponential near its completion.

Larvulae appeared within a few days after oviposition and averaged 0.5 mm in length and weighed 0.5 µg (Table 3). Whereas many Chironomini molt and continue growth during the summer, P. albimanus larvae remained in the first-instar and did not gain weight through the rest of the summer and early fall. During this period, stream temperatures were approximately 15°C, the same as had been experienced by the latter stages of the previous generation. Data from several laboratory experiments with first-instar larvae revealed that 15°C was not inhibitory to growth when animals were fed high quality food sources (see Table 14, page 72).

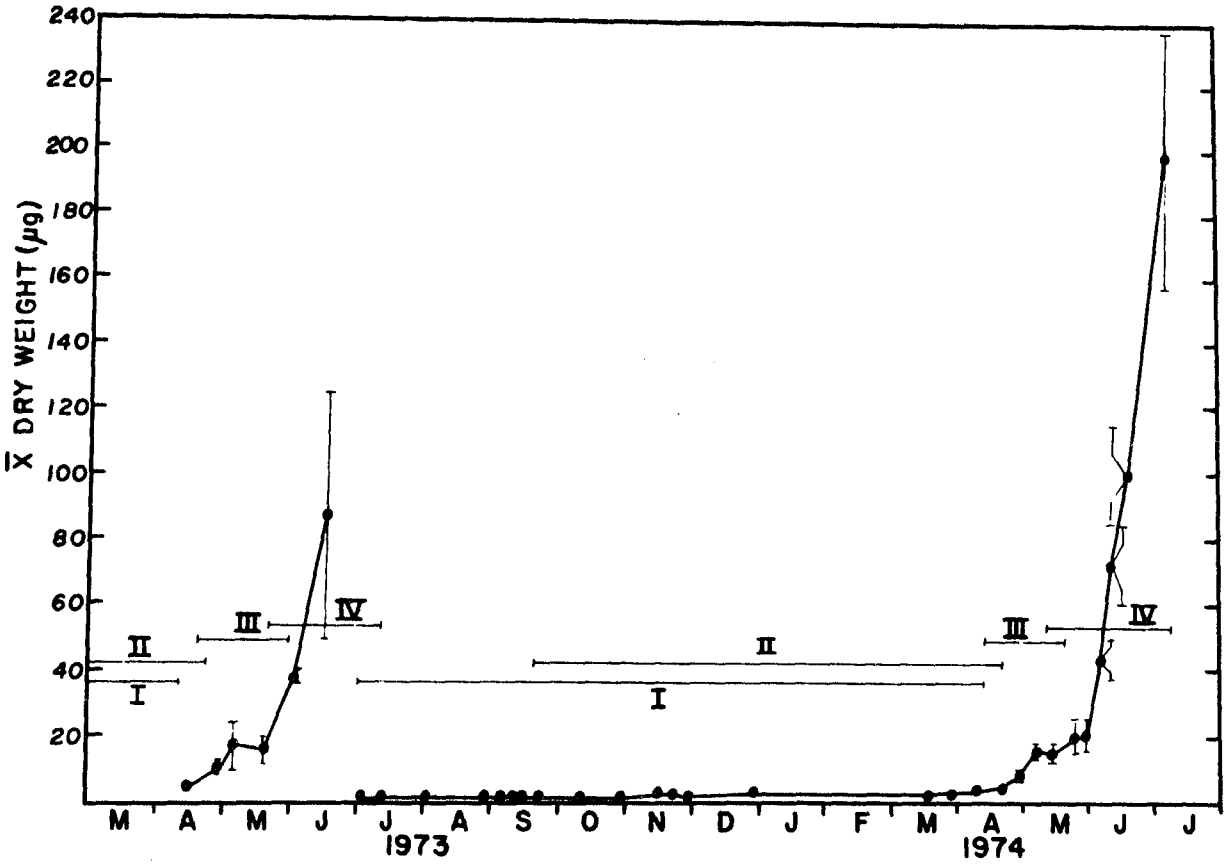

Figure 4. Annual growth pattern of Paratendipes albimanus (Meigen) drawn on linear scale to emphasize rapid growth near the end of the life cycle. Roman numerals indicate temporal distribution of instars.

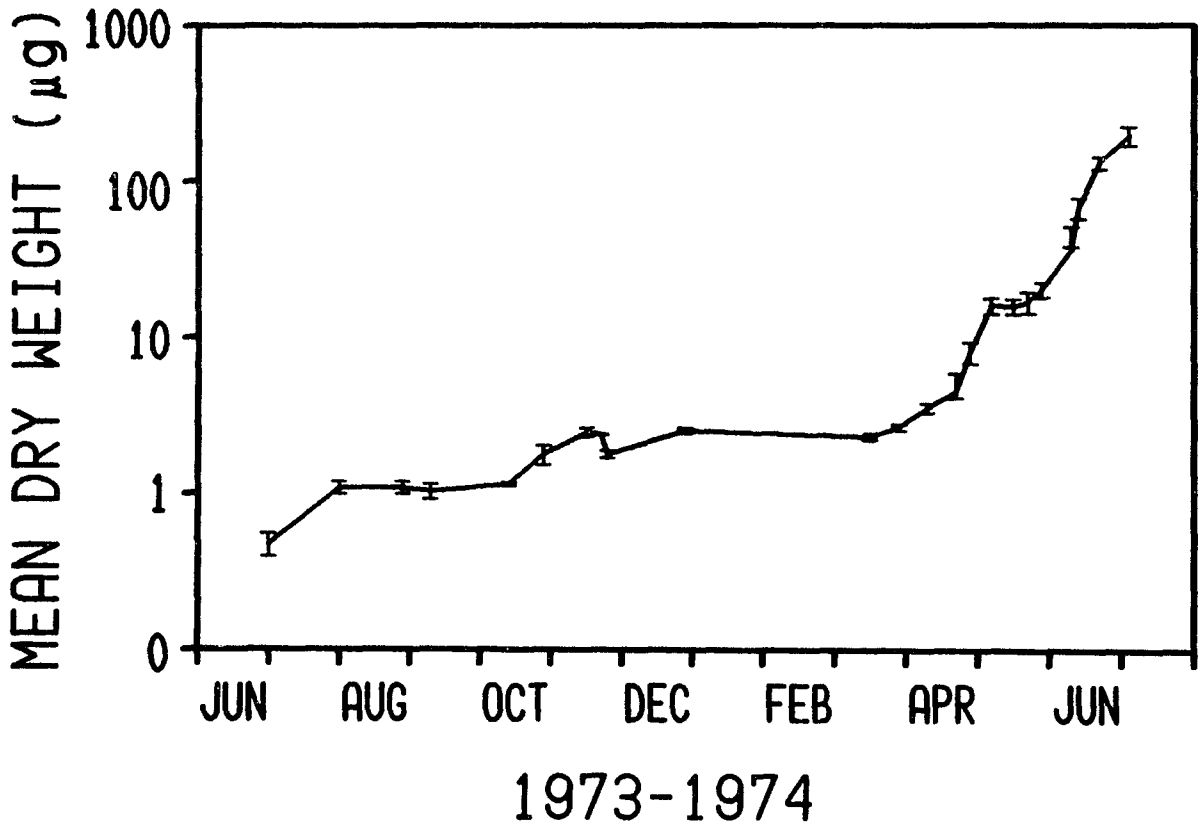

Figure 5. Annual growth pattern of P. albimanus drawn on log scale to emphasize growth in early instars.

Table 3. Changes in weight and length of Augusta Creek (site B) *P. albimanus* population.

Months	Range of Mean Dry Weight (µg)	Range of Total Length (mm)	Life Stage	Percent of Maximum Larval Mean Weight
July	-	0.209	Egg	-
July	0.5-1.0	0.4-1.3	I	< 1
August	1.0	0.4-1.3	I	0
September	1.0	0.4-1.3	I	0
October	1.0-2.5	0.7-1.9	I and II	< 1
November-March	2.5	0.7-1.9	I and II	0
April	2.5-10.0	0.7-3.5	II and III	4
May	10-25	1.5-4.0	III and IV	8
June	25-197	3.0-8.0	IV	87
June-July	77-127	3.13-4.27[1,2]	♂ Pupae	-
June-July	140-241	2.98-4.43[1,2]	♀ Pupae	-
June-July	77-173 45-121[2]	-	♂	-
June-July	125-333 60-190[2]	-	♀	-

[1]Abdominal length.

[2]Collected from experimental streams.

However, larvae in the laboratory ceased growth at the same weight as natural populations when temperature and food regimes were meant to simulate natural conditions.

During the latter part of October and early November, the mean weight per individual of the population increased to 2.5 µg (Figures 4 and 5). A majority of the population molted to second-instar, but those failing to molt at this time apparently remained as first-instar until spring. Most larvae were 1-1.5 mm long, but first-instars were 0.5-1 mm. This fall growth lasted about three weeks and ended as stream temperatures fell below 4°C.

Observations of P. albimanus in other habitats, both natural and experimental suggested that this growth period might be prolonged or more intense when temperature regimes were higher at this time of the year. In Hamilton Lake, overwintering larvae had a mean dry weight of 4-16 µg: the smallest larvae from 9 m and the largest from 2 m. The mean daily temperature in the shallow littoral zone was higher than Augusta Creek over the same period due to increased solar insolation and the reduced effect of ground water. Larvae collected from site B for use in laboratory experiments were kept at 8°C from early November until early December, and were observed at the beginning of the experiment to be somewhat larger than the Augusta Creek population. No dry weight increases or changes in age distribution

occurred in the population during the remaining winter months. This developmental level was rather rigidly held, since larvae kept in culture at 10-15°C from November to March grew only slightly.

Growth was renewed in spring when mean daily temperatures reached 4-5°C and continued at an increasing rate until halted by another growth pause in May (Figures 4 and 5). During this period mean weight fell, then increased slightly during a two to three week period. In both 1973 and 1974 this pause began during the second week in May and terminated during the third or fourth week; larval growth was then rapid until the initiation of emergence in late June.

As larvae reached maturity, the thorax of the prepupal stage became progressively whiter and more swollen, the largest larvae weighed 240 µg and the smallest about 70 µg. Mature larvae first appeared during the second week in June and could be found until the second week in July. The largest mean weight per individual, 197 µg, was measured during a time of mostly female emergence. The mean weight of male pupae was 109 µg and female pupae 192 µg.

As shown in summary of P. albimanus in Table 3, more than 25% of the annual cycle was spent as first-instar (1700-1800 total day-degrees) and over 75% occurred before third-instar larvae began (2300-2400 total day-degrees). During these first nine months, only about 1% of the final

larval dry weight biomass was accumulated, while 87% was accumulated during the last 30 days, almost exclusively by fourth-instar larvae.

Year-to-year differences in the pattern of growth for 1972-1975 generations were quite small. Weights of larvae during the summer and after the fall growth spurt were the same in 1974 and 1975 and the mean weights of overwintering larvae were all within tenths of a µg. Emergence was between the 20-23 of June in all years.

Obtaining emergence data from field populations was difficult because adults were not readily attracted to lights traps, and their resting places were not discovered. Consequently, the experimental stream facility was employed to determine the daily and diel pattern of emergence from a large experimental population. During the fall of 1973 these streams were stocked with first- and second-instar larvae collected from Augusta Creek (site B) and allowed to overwinter at temperatures near those in the field (natural population approximately 1-5°C; experimental 5-6°C). The following June a comprehensive sampling strategy (Corbet, 1964), utilizing the collecting device shown in Figure 3, was employed to collect pupal exuvia from all adults emerging from the system. From an original population of near 72,000 in December, over 2,200 adults emerged (3.0%). Peak emergence from the experimental population occurred on the

ninth day and the maximum numbers of adults appeared each day just after sunset (Figure 6). For unexplained reasons, adults were attracted to the UV light traps inside the enclosed artificial streams while the same traps attracted few individuals in the field. Field collected ♀♀ were more frequently attracted than were ♂♂. It was not unusual for a nightly catch to be a high percentage or even completely ♀♀.

Considerable variation occurred in the coloration of adults captured from the experimental streams. A sharply contrasting black and white foretibia is diagnostic of this species, but all degrees of color development were encountered. A completely pale foretibia was present in newly emerged specimens and complete color development required one or two days.

Egg Masses and Larvulae

The collection of large numbers of egg masses of P. albimanus allowed for observation of egg hatching and the activity of larvulae. At the time of each emergence, the metal collecting screens were placed in both depositional and erosional zones at site B. In 1974 over 450 egg masses were collected, with about equal numbers coming from each zone. Oviposition usually began between the 20th and 24th of June and although eggs could be found as late as the 15th of July, peak oviposition had passed by the 5th or

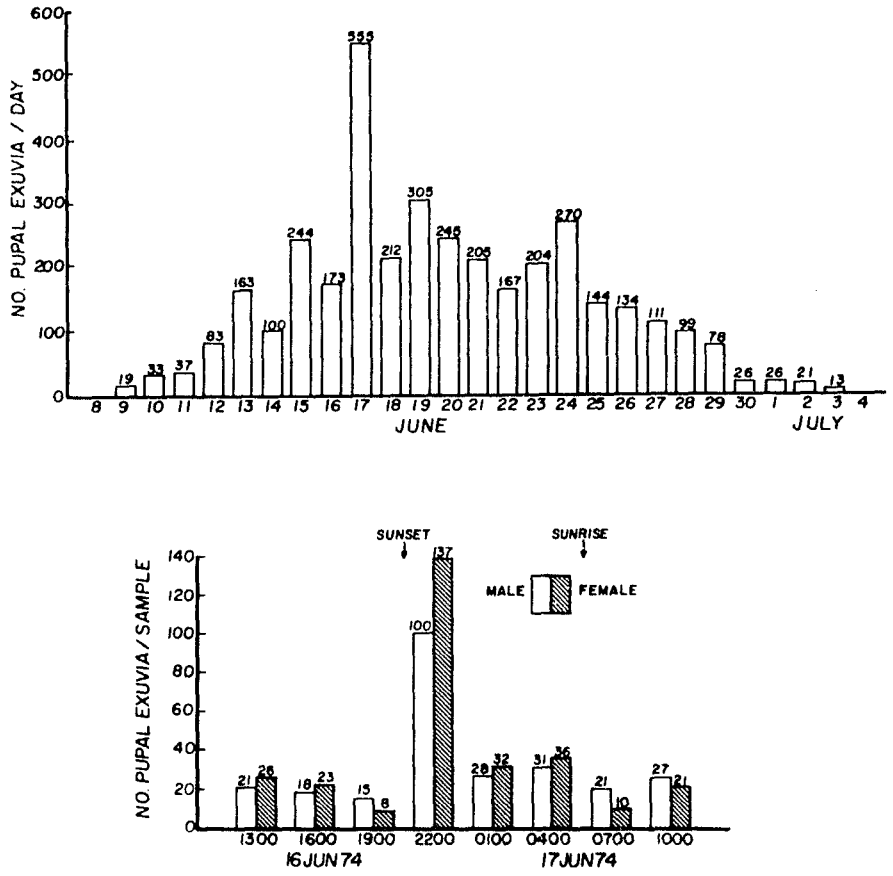

Figure 6. Upper: Emergence pattern for a population of P. albimanus in an experimental stream system. Number above each bar represents the quantity of pupal exuvia captured each day.

Lower: Diel emergence pattern for the same experimental population of P. albimanus. Numbers above each bar represent the quantity of pupal exuvia captured at each three hour interval.

6th of July. Newly laid masses were easily seen as clear, jelly-like hemispheres held fast to the screen, but within hours of deposition sufficient drifting detritus had adhered to partially or entirely obscure them.

Egg masses had a diameter of 3.76 mm, $\pm$ 0.498 sd and contained between 250 and 450 eggs. Individual eggs were kidney shaped, approximately 209 µm ($\pm$ 3.1 sd) long and 74 µm ($\pm$ 0.9 sd) wide (Figure 7). Experiments revealed egg hatching to be temperature dependent, but within the range of 10°C to 25°C not critical to percent success. All masses held at temperature $\geq$ 10°C completed hatching within several days, but no activity was observed in those held at 5°C for 60 days.

Newly hatched larvae were very active and remained within the egg mass for several hours and before reaching the surface appeared to be consuming the gelatinous matrix. Prior to completion of hatching in a particular mass, the gelatinous matrix began to break up into several pieces. Digestive tracts of the larvulae escaping the interior of the matrix soon became filled with the detritus adhering to the outer surface of the egg mass. Seven to ten days after hatching, colorless larvae became a faint pink, which deepened after two or three weeks to the familiar dark red of the more mature larvae. Newly hatched larvae tended to be quite active under direct light, but experiments revealed

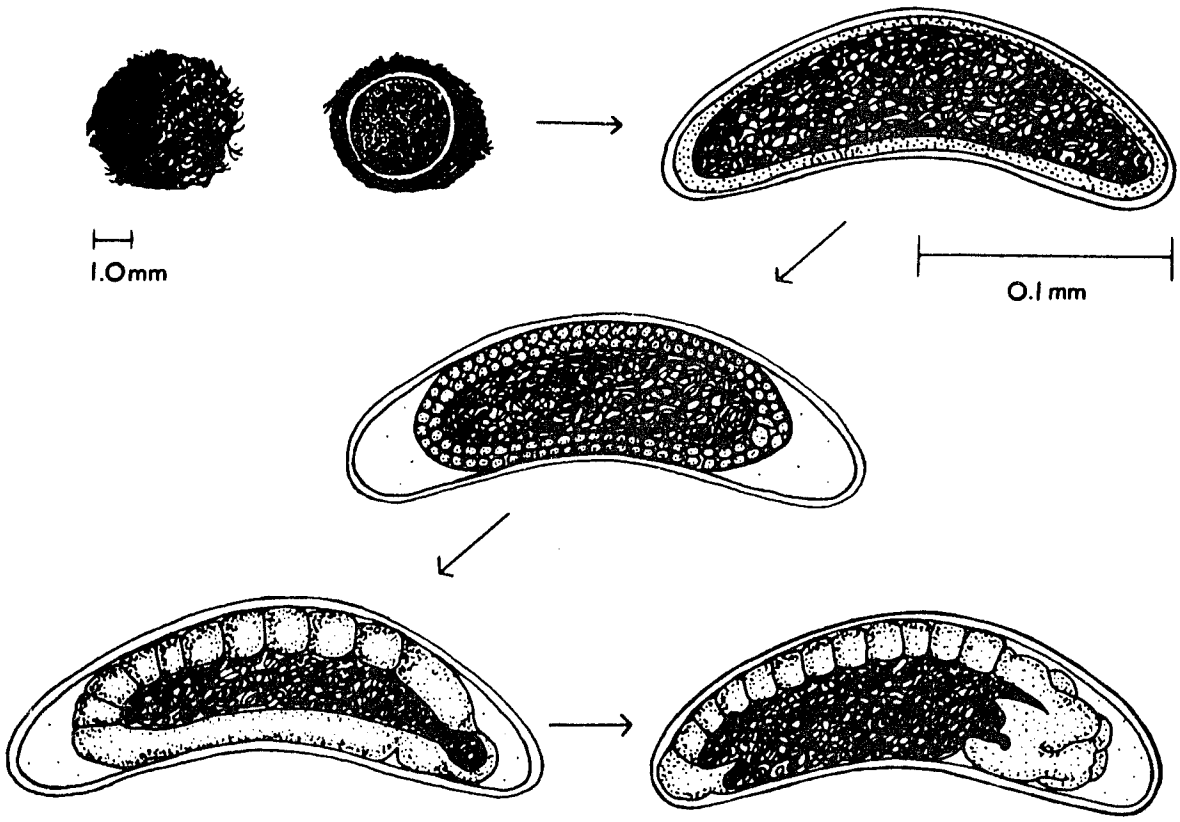

Figure 7. Sequence of egg maturation of P. albimanus, from egg mass until near time of eclosion.

no photoactic response. In comparing stream species with other Chironomidae, Oliver (1971) noted that positive phototaxis in a rheophilic species would be disadvantageous, increasing the probability that the larva would be swept away from its habitat by the current.

Morphometry of Larvae

Previous studies of the Chironomidae have employed a number of measurements to determine the instar category of individual specimens (Sadler, 1935; Berg, 1950; Ford, 1959 and others). In the present study, six measurements were evaluated as to adequacy for estimating instar category (Table 4). Of the six, only total length was inconsistent. Head widths and lengths, measured prior to slide mounting, were consistently more variable than mandible length, width of the basal antennal segment and width of the four median teeth on the mentum (Table 4). The small size of the early instar head capsules required that measurements be made with a compound microscope, a time consuming procedure when large numbers of specimens must be processed. When instar determinations were made from previously mounted specimens, the latter three characters proved to be reliable indicators since these characters do not distort under the moderate cover slip pressure during mounting.

For each larval molt, the size increase ratios of the latter five characters in Table 4 were calculated (Table 5).

Table 4. Summary of morphometric data for larvae of P. albimanus.

	I $\bar{x} \pm$ sd Range	II $\bar{x} \pm$ sd Range	III $\bar{x} \pm$ sd Range	IV $\bar{x} \pm$ sd Range
Total Length (mm)	0.829± 0.363 1.31 - 0.39	1.40 ± 0.279 1.87 - 0.69	2.66 ± 0.541 3.50 - 1.53	4.94 ± 1.129 8.00 - 3.00
Head Length (mm)	0.075± 0.009 0.094- 0.059	0.110± 0.017 0.124- 0.099	0.182± 0.022 0.216- 0.146	0.292± 0.021 0.322- 0.248
Head Width (mm)	0.048± 0.003 0.053- 0.043	0.068± 0.006 0.076- 0.055	0.115± 0.011 0.135- 0.099	0.194± 0.012 0.216- 0.173
Width of Four Median Teeth (µm)	5.42 ± 0.225 5.76 - 5.28	8.27 ± 0.300 9.12 - 7.68	14.69 ± 0.643 15.79 -14.04	26.72 ± 0.798 28.00 -25.70
Mandible Length (µm)	28.53 ± 1.009 29.76 -26.40	39.49 ± 2.469 43.29 -34.72	62.47 ± 4.754 70.20 -53.82	109.49 ± 4.451 120.50 -99.40
Width of Basal Antennal Segment (µm)	5.17 ± 0.336 5.76 - 4.80	7.84 ± 0.743 9.36 - 6.24	11.52 ± 0.683 12.87 - 9.982	17.66 ± 0.563 18.72 -16.30

Table 5. Ratios of size increases for certain anatomical characters in larvae of P. albimanus.

	I-II	II-III	III-IV	$\bar{x}$	$\bar{x}$ of last 2
Head Length	1.466	1.654	1.604	1.575	1.629
Head Width	1.416	1.691	1.687	1.598	1.689
Width of Four Median Teeth	1.526	1.780	1.820	1.708	1.800
Mandible Length	1.484	1.580	1.752	1.572	1.666
Width of Basal Antennal Segment	1.440	1.530	1.530	1.500	1.530

According to Dyar's Rule, the increase in size of a sclerotized structure at each molt should follow a set geometric progression (Chapman, 1969). Ford (1959) reported the lack of adherence to the rule when applied to Chironomus rempleii (Remple, 1936) and to Cricotopus elegans (Berg, 1950), but presented data supporting the rule when applied to Prodiamesa olivacea, Corynoneura scutellata and Anatopynia trifascipennis. With the exception of the very different growth ratio between instars I and II, due to the dramatic morphological changes, the rule would apply to P. albimanus.

Thienemann (1954, pp. 234-240) reviewed the work of Thienemann and Zavrel (1916), Dorier (1933), and Sadler (1935) describing the larvulae of various species of Chironomidae. Kalugina (1959) and Sublette and Sublette (1973) added information on several more species in the

subfamily Chironominae. These authors observed differences among instars in body shape, the proportion of head size to body size, and the size proportions of other body parts. Differences in detail of the head capsule have also been reported (Dorier, 1933; Kalugina, 1959; Sublette and Sublette, 1973). These involved the color and shape of the mentum, shape of the mandible, and ratios of lengths of the antennal flagellomeres. The absence of ventral tubules and various setae on the mandible have been noted by others. The most detailed information has come from studies of Chironominae, but Dorier (1933) observed similar differences in Psectrocladius obvius (Orthocladiinae).

In the present study of P. albimanus, significant differences were seen in the shape and color of the mentum, sculpturing of the ventromental plates, structure of the antenna and setation of the mandible.

Mentum. During the development of this species, the shape and coloring of the mentum underwent considerable change before reaching the pattern described in taxonomic keys (Figures 8a,b,c,d). The four median teeth of instar I were raised above the remaining teeth, but by instar III, the medians had become recessed. The third and fourth lateral teeth of instar III and IV were fused, with the third smaller than the fourth, but in instar I and II these teeth were quite separate and the third was larger.

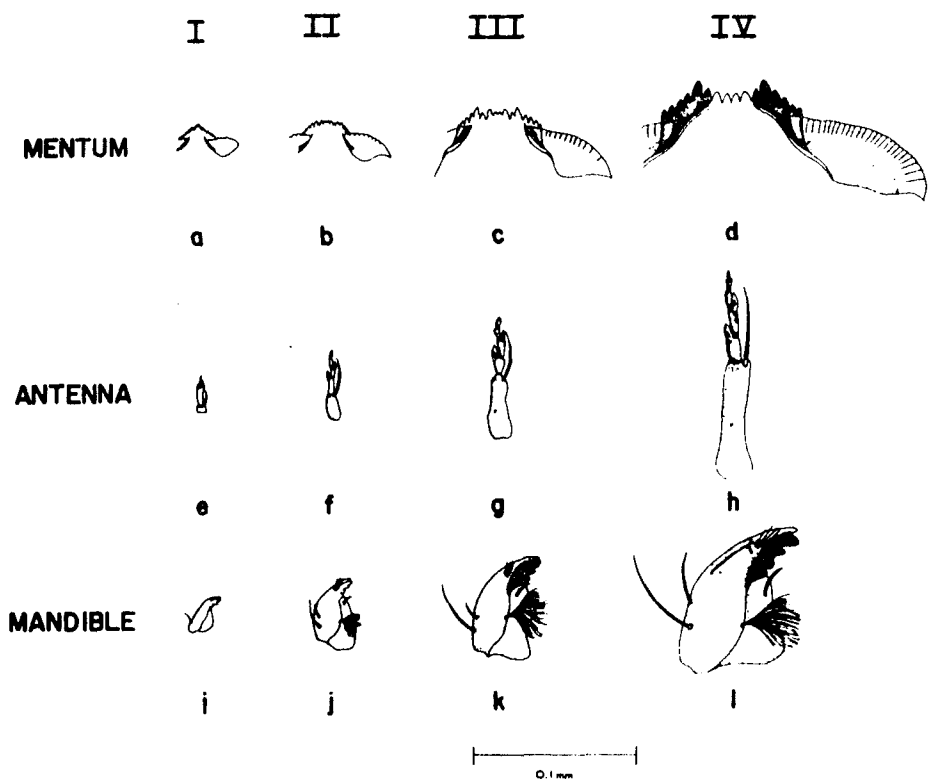

Figure 8. Mentum, antenna and mandible for instars I-IV in P. albimanus. Depicted are overall changes in size and shape of head parts.

Little or no color developed until instar III, and full color was present only in instar IV when the four median teeth were quite pale and the laterals were dark brown.

The ventromental plates also exhibited change during molting. Sculpturing on the anterior edge changed from a pattern which was scalloped on the medial half but without a pattern on the lateral half (Figure 8a) in instar I, to a crenulate one across the entire margin in later instars (Figures 8a,b,c,d). With each molt the number of crenulations increased but not the relative size of each.

Antenna. Significant changes also were observed among instars in the structure of the antenna (Figures 8e,f,g,h). Six antennal segments are characteristic of his genus, but the first-instar P. albimanus had only five. Segment two was unusually long, about twice that of instars II and III. It is possible that this segment is really a combination of the second and third, but so indistinctly separated to be obscured under the light microscope, or it splits at the first molt to become two segments. In either case, segmentation does not become distinct until the second-instar.

Length-width ratio of the basal antennal segment changed at each molt during the larval life from 0.5 in the first-instar to 3.8 in the fourth. The length of antennal flagellomeres are given in Table 6 and revealed that the antennal ratio (length of basal flagellomere:length of remaining

Table 6. Relative lengths of flagellomeres in larvae P. albimanus.

Segment Number	Instar			
	I	II	III	IV
1	3.2	7.0	14.4	17.7
2	5.6	3.0	4.0	5.3
3	2.4	3.0	5.5	4.0
4	1.6	2.0	3.0	3.7
5	1.0	1.0	1.0	1.7
6	-	1.0	1.0	1.0

flagellomeres) also changed with each instar. The basal antennal segment of instars I and II also lacked a ring organ. This structure appeared in instar III in the location described by Johannsen (1937).

Both lauterborn organs were observed on segment two in instar I, however, in later instars they opposed each other on the distal ends of segments two and three (Figures 8f,g,h). Lauterborn organs in instar I also seemed to be incompletely separated, and gave segment two the appearance of having a flared distal end. Lauterborn organs were roughly equal to the length of the segment they opposed except in instar IV, in which the organ on segment two was about 0.6 the length of segment three. Antennal segments were straight for the most part, except three and four in instar II which were curved, with the concave side toward the lauterborn organ.

The Augusta Creek specimens of P. albimanus instar IV agree very closely with the description given by Johannsen (1937). However, in instars III and II the description of instar IV became less and less applicable and there was no agreement with instar I.

Mandible. The general shape of the mandible did not change significantly during molting, and except for the lack of a mandibular brush and preapical comb in instar I, the description matched that of Johannsen (1937) (Figures 8i,j,k,l). Also, one of the two bristles on the convex side of the mandibles appeared at the first molt and again little or no color developed until the fourth instar, in which the apical tooth was pale and the proximal teeth were dark brown.

Population Density

The density of P. albimanus was followed in both riffles and pools at Augusta Creek site B over two cycles from December 1972-July 1974 (Figure 9). Density changes seemed to follow different patterns in the two habitats. Riffle densities were highest in early fall, several months after egg hatching was presumed complete and gradually decreased throughout the remainder of the life cycle, decreasing to zero by early spring at roughly the same time as the pools densities were at their peak. Rather stable densities had occurred throughout the winter months in the pools but

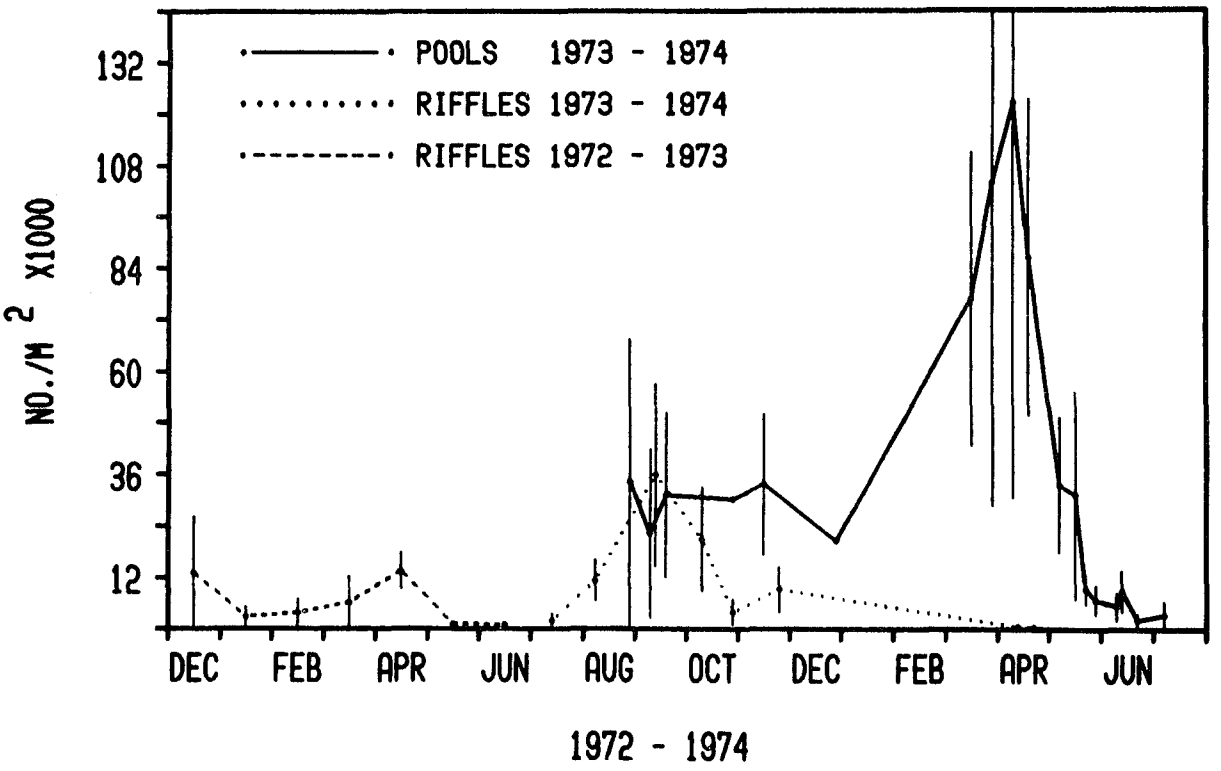

Figure 9. Changes in larval densities of P. albimanus in riffle and pool habitats during the 1973-1974 generation and the latter part of the 1972-1973 generation.

suddenly increased sharply in the spring. Very high densities were recorded in several consecutive weeks (Figure 9), but fell rapidly when larvae began their major developmental period.

Since recruitment from eggs was not considered possible during the winter months, the sudden increase in pool densities most likely resulted from immigration from riffles. Movement of larvae away from unsuitable habitats has been proposed for Chironomidae (Bay et al., 1966; Hilsenhoff, 1968), and the riffle habitats might have become unsuitable for larvae at this time of the year because of poor food supply or some other environmental parameter.

Effects of Temperature on Larval Growth

Growth Rate of P. albimanus in Augusta Creek

Description of the growth pattern of P. albimanus provided data for the calculation of natural population growth rates. Data for the 1973-1974 generation are presented in Table 7, expressed on both a daily and a day-degree basis.

The major feature of the growth pattern was pauses or cessations that were nearly complete. Virtually no growth occurred during 60% of the annual cycle--summer, winter or in early May. The overwintering period accounted for 60% of the non-growth period and 37% of the annual cycle.

Table 7. Growth rates of P. albimanus in Augusta Creek (site B), July 1973-July 1974.

Sample Date	Mean Dry Weight µg	Number Weighed	k_d mg/mg/day	Days	k_{d-d} mg/mg/d-d	Day-degrees	Mean Daily Temperature °C
07-01	0.42	419	-	-	-	-	-
08-02	1.13	80	0.03093	32	0.002506	395	15.0
08-29	1.12	109	-	-	-	-	-
09-08	1.14	221	-	-	-	-	-
10-11	1.13	660	0.00000	70	0.000000	753	14.7
10-30	1.54	131	0.01629	19	0.003904	79	10.2
11-15	2.52	164	0.03078	16	0.01376	36	6.2
11-21	2.42	84	-	-	-	-	-
12-30	2.48	120	-	-	-	-	-
03-17	2.40	373	-	-	-	-	-
03-31	2.69	517	0.00048	136	0.000000	0	2.3
05-07	15.3	164	0.04698	37	0.009246	188	9.1
05-14	14.6	168	-0.00669	7	-0.001338	35	9.0
05-21	19.5	54	0.04134	7	0.004864	60	12.5
05-30	20.0	42	0.002813	9	0.000306	83	13.2
06-20	143.3	48	0.09377	21	0.008752	225	14.7
07-04	197.0	12	0.02273	14	0.002017	158	15.2
Annual Mean 1974			0.01667	368	-	-	-
[1]Corrected Annual Mean			0.04213	146	0.004884	1259	-

[1]Mean corrected to include only days when the mean daily temperature was above 4°C.

Individual daily growth rate estimates varied considerably during the year (Table 7), due in large measure to the three growth cessations. However, significant amounts of variation were a result of seasonal differences in temperature and food quality (discussed below). In addition, rate measurements may have been high or low if made just prior to or just after the summer or fall growth cessations, because exact dates of the beginning and end of these periods were unknown.

Temperature control over growth rates of poikilothermic animals is well documented, but variations in growth rates due to temperature can be eliminated by the day-degree summation technique (Andrewartha and Birch, 1954). Heat accumulation, the basis of this procedure, is calculated by summing the mean temperatures over period involved. In this study, mean daily temperatures, from either Augusta Creek or experiments, were summed for days of observation. Although not used extensively for aquatics, day-degree summations frequently have been used to predict emergence of economically important terrestrial insect populations. The day-degree technique has been refined by the recognition of lower and upper thermal developmental thresholds for insect larvae. Since insects are not able to grow at low (or high) temperatures, the lower thermal limit (in °C) is subtracted from the mean temperature for the time interval

to obtain effective day-degrees. This sums only the heat from days with a positive day-degree value, days when temperatures are below or above the threshold for development not being counted.

If changes in insect growth rate are linearly related to changes in temperature, day-degree evaluations will eliminate the effects of temperature in daily rate estimates. Since laboratory experiments have determined that P. albimanus larvae exhibit such a relationship, the growth rates of natural and experimental populations have been expressed on both a daily and a day-degree basis. However, temperature was not the only environmental variable regulating the growth rate of P. albimanus. Even after elimination of temperature effects, growth rates still varied, probably due primarily to food quality and photoperiod. Poor food quality was considered a major factor in producing the growth cessations in summer and early May. Because the exact relationship between food quality and growth has not been determined, rates were not corrected for this factor. Some index of food quality is needed which can be used similarly to the lower thermal threshold in calculating growth rates. One possibility shown to correlate well with growth in laboratory experiments is a measure of the microbial biomass on particles which are consumed.

Data from several generations of P. albimanus in Augusta Creek have established the details of the growth pattern. The mean weights of larvae in summer, winter and in spring were quite similar from year to year, as was the timing of each of the several growth cessations, establishing the growth pattern as a constant feature of the life cycle in Augusta Creek.

Year to year consistency of growth rates and maximum size reached at maturity should be a feature of insect life cycles, provided that regulating variables repeat at the same relative magnitudes. The longest continual period of P. albimanus growth was in spring; rates for the 1973-1974 generations are compared in Table 8. These data showed that rates for the spring period were quite similar from year to year. From the beginning of spring until just prior to emergence, a period when temperatures varied from a mean daily of 5°C to 15°C, growth occurred at a rate of 5% of body weight day^{-1} and 0.6% of body weight day-degree^{-1}. Except for that part of May when growth was inhibited, rates increased to 9% of body weight day^{-1} and 0.9% of body weight day-degree^{-1} (Table 8).

The annual growth rate of P. albimanus was calculated two ways: one included all days within the calendar year, the other excluded all days and day-degrees during which larvae failed to grow (Table 7, page 47).

Table 8. Comparisons of spring growth rates for three annual cycles of P. albimanus in Augusta Creek (site B). Given are rates from the end of winter until near the beginning of emergence.

Generation	Dry Weight (µg)	Days	Day-degrees	k_d (mg/mg/day)	$k_{d\text{-}d}$ (mg/mg/day-degree)	Mean Temperature (°C)
1972-1973						
18 April	4.36	-	-	-	-	-
14 June	94.14	[1]57	510	0.05390	0.006024	12.0
1973-1974						
31 March	2.69	-	-	-	-	-
20 June	143.3	[1]79	591	0.05032	0.006733	11.3
1974-1975						
25 March	2.23	-	-	-	-	-
21 June	157.1	[1]72	677	0.05909	0.006283	13.4
Three Year Mean				0.05443	0.006346	

[1]Number of days in which the mean daily temperature was above 4°C.

Growth Rates of Experimental Populations

Spring Populations. For an initial test of the effects of temperature on growth rates on P. albimanus, fourth-instar larvae were collected from site B in Augusta Creek in early June, approximately three weeks prior to emergence. Treatment temperatures ranged from 5-20°C in 5°C increments. Temperatures experienced by this species in Augusta Creek ranged from less than 1 to 18-20°C, with mean daily temperatures from less than 1 to 16°C. During the period April to June, the major growth phase of this species, mean daily temperatures ranged from 5 to 15°C. Thus, the highest temperature tested was slightly higher than usually experienced by the natural populations, although Walshe (1948) has shown that P. albimanus larvae survive well up to 33°C.

Data for experiment A (Table 9) show that more than a fifteen fold increase in mean growth rate was observed over the range of temperatures tested.

Temperature quite obviously had an effect on growth rates and the data were subjected to regression analysis to determine whether the effects on growth rate were linear with temperature. The results (Figure 10) revealed that large amounts of the variance around the growth rates were explained by changes in temperature (r^2 =.99). Since the effect of temperature on the growth of P. albimanus can be described with a linear equation, it should be possible to

Table 9. Comparisons of growth rates of laboratory populations of P. albimanus held at constant temperature. Rates are expressed on a daily and day-degree basis. Experiment A utilized IV-instar larvae and experiment B began with II-instar larvae.

Experiment		5°C	Days or (D-D)	10°C	Days or (D-D)	15°C	Days or (D-D)	20°C	Days or (D-D)
A	mg/mg/day	0.005068	10	0.03316	10	0.05620	10	0.07518	10
	mg/mg/day-degree	0.005068	10	0.005526	60	0.005109	110	0.004699	160
B	mg/mg/day	0.007866	146	0.03051	97	0.04508	63	0.10059	19
	mg/mg/day-degree	0.007866	146	0.005086	582	0.004098	693	0.006287	304

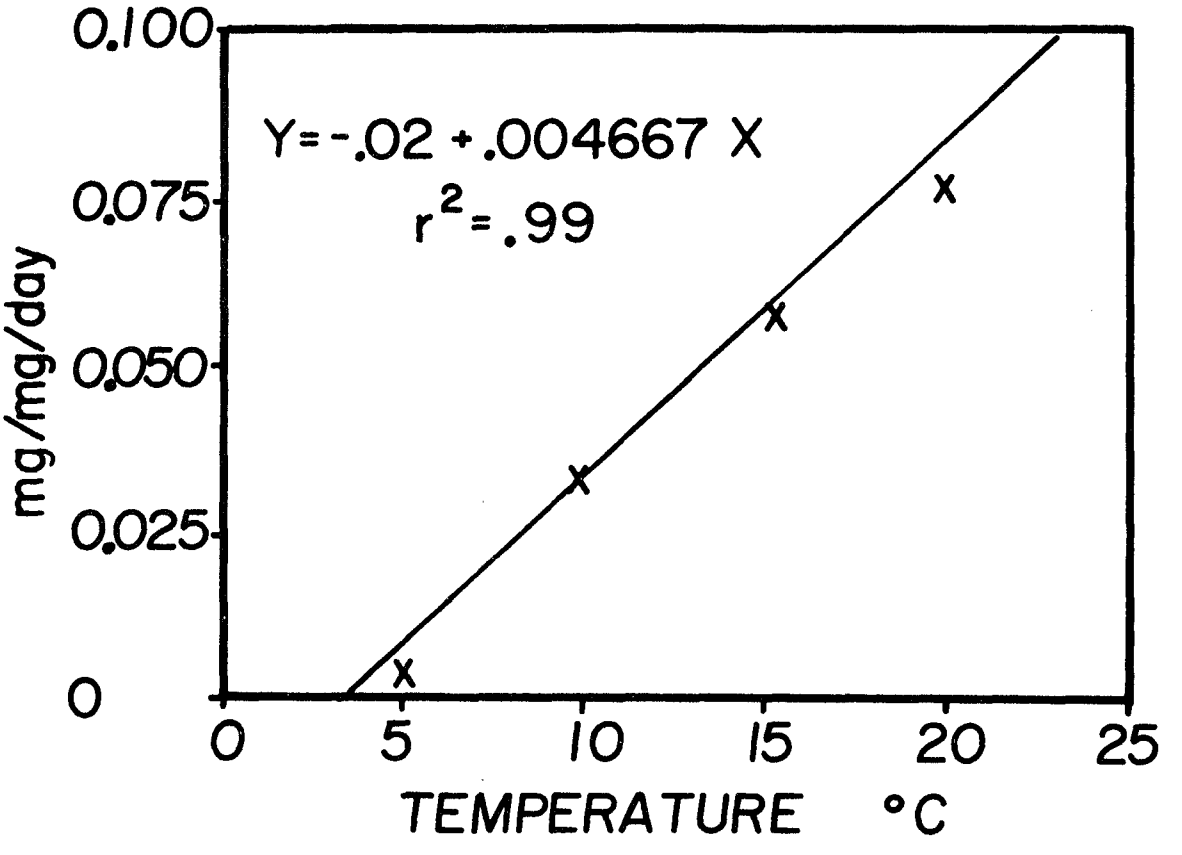

Figure 10. Linear regression of mean daily growth rate vs temperature for a laboratory population of P. albimanus.

eliminate the effects of temperature on the growth rate calculations by use of the day-degree summation technique. In the equation for calculating growth rate (Table 9), a day-degree summation was substituted for time. Expression of growth as mg weight gain·mg body weight^{-1}·day-degree^{-1} removed much of the variance around the daily growth rates (Table 9).

Since experiment A (Table 9) was short-term (10 days) and utilized only IV-instar larvae, a longer duration test was designed to include the entire spring growing period, during which larvae in the natural population attain 99% of their final weight. Second-instar larvae, collected during the first week in April, were placed at 5, 10, 15 and 20°C, and following acclimation, changes in dry weight biomass were followed until emergence.

Although growth tended to be more variable than in the previous experiment, rates expressed on a day-degree basis eliminated much, but not all, of the variance in daily rates. Growth rates at all temperatures except 20°C, were similar when expressed on a day-degree basis (Table 9).

In experiments A and B (Table 9), larvae in the 20°C treatment tended to have a lower although statistically non-significant ($P < 0.05$) day-degree growth rate than the other treatments. Although growth rates at temperatures higher than 20°C were not tested, it is possible that 20°C

approaches the upper developmental threshold for normal growth rates of P. albimanus populations in Augusta Creek.

When day-degree growth rates (experiments A and B) were analyzed by a single variable ANOVA test, calculated F values were not significantly different. Thus the results and statistical analysis of experiments A and B suggest that growth rates of P. albimanus are comparable when the effect of temperature is eliminated as a variable in rate calculations, and the mean day-degree growth rate for the two experiments were extremely close (A = 0.005100 and B = 0.005104; Table 9).

To this point, these studies on the effects of temperature have been limited to times when growth in this species was continuous, however, several growth inhibition periods were known from the natural population. The winter, usually a time when the growth of chironomids is curtailed by low temperatures, also proved to inhibit growth of P. albimanus.

Overwintering Populations. Having described the effects of temperature on small laboratory populations during growth phases, the response of a large experimental population to increased winter temperatures was examined in the artificial stream channels described above. Data from field populations of P. albimanus indicated that growth stopped in November when temperatures fell below 5°C and began again in spring when temperatures increased above 5°C.

Laboratory results revealed that some growth was possible at 5°C, but larvae failed to gain any weight during winter or spring when temperatures were in the range of 2-4°C. Therefore 4°C was considered the lower developmental threshold temperature, although linear regression analysis (Figure 10) suggested 3.4°C as the lowest temperature at which growth could occur. These observations agree with those of Oliver (1971) who suggested a 4°C growth threshold for Chironomini, but are in contrast with data of Konstantinov (1958a) who demonstrated a range of 7-10°C for several species of Chironomini.

The objective of the experiment was to investigate the effects on growth of slightly increased winter temperatures--increases of 2-4°C, or 7-9°C. Water temperatures in the two 4000 l artificial streams were held between 5-6°C and 10-11°C respectively all winter. Each stream was stocked with more than 50,000 II-instar larvae. Up to 99% of these individuals inhabited the 3 m^2 depositional areas. Riffles covered 7 m^2 upstream. Animals, collected in November and held in both streams at 8°C until mid December, when the two temperature regimes were established, were subsampled at approximately monthly intervals for biomass and density changes until emergence began the following summer.

During the overwintering period (November-April), the Augusta Creek population added no biomass, however, the two

experimental populations, under temperature regimes increased by 3 and 8°C, did grow slightly, but at a slower rate than predicted from field observations at similar temperatures (Figure 11). Growth in the 5°C stream did approach rates measured in laboratory cultures, but less than those observed in the field. Growth rates in the 10°C stream were significantly lower than even the slowest laboratory rates.

Growth rates obtained from this experiment have been summarized according to overwintering and actively growing periods for comparisons between the two treatments (Table 10). Daily growth rates at 10°C were approximately twice those at 5°C, but on a degree-day basis they were reversed. Many more day-degrees accrued at 10°C (approximately 5 per day) without any corresponding increase in growth. Daily growth rates at 5°C were similar to those observed in laboratory experiments, although day-degree rates were only about one half of laboratory rates.

Quite obviously, these experimental populations responded differently to temperature than did the larvae tested in the spring, possibly inhibited by poor food quality or some other factor. This conclusion is supported by the observation that in early spring, without any change in temperature regimes, larvae in the 10°C stream increased both their daily and day-degree growth rates by a factor of

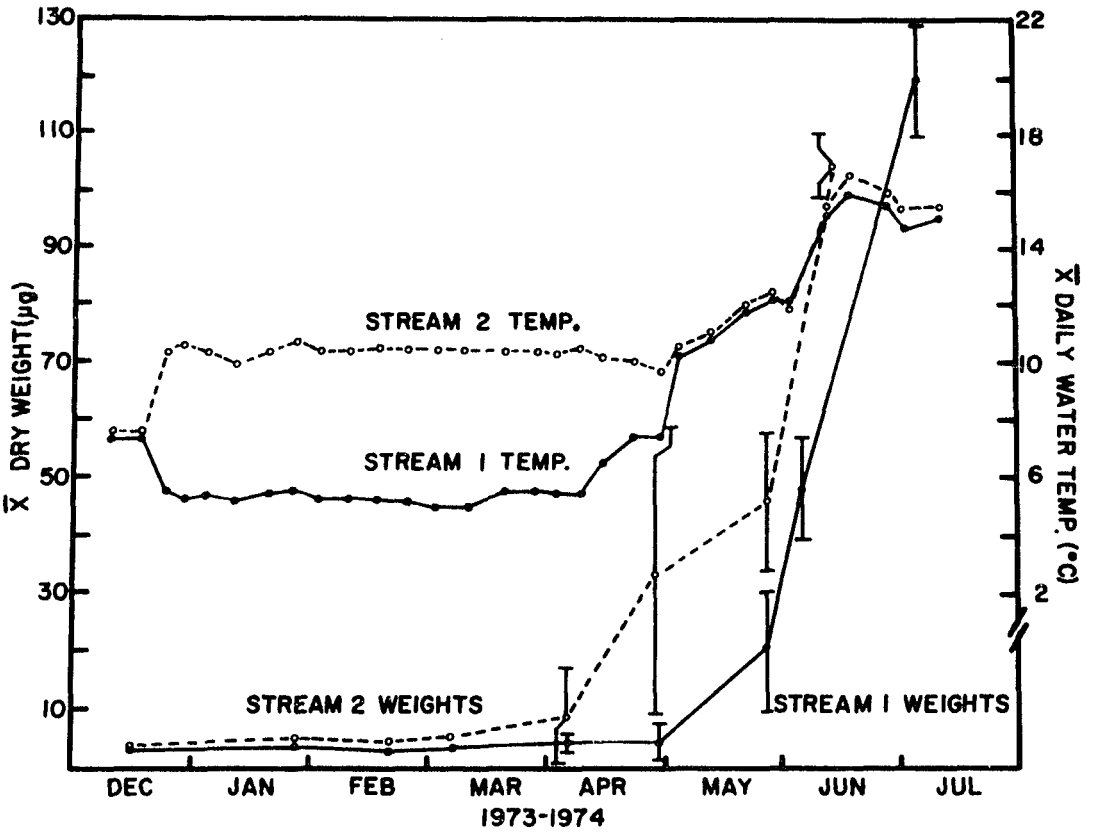

Figure 11. Growth pattern of a population of P. albimanus held in an artificial stream system overwinter.

Table 10. Comparisons of growth rates of P. albimanus from two 4000 l experimental streams. Population in stream 1 was held at 5°C from 14 December 1973 until late April 1974 while the population in stream 2 was held at 10°C from 14 December 1974 through June of 1974.

Sample Date	Mean Dry Weight (µg)	k_d (mg/mg/day)	Days	k_{d-d} (mg/mg/d-d)	Day-degrees	Mean Temperature (°C)
			Stream 1			
14 December 1973	2.66	-	-	-	-	7.4
29 April 1974	4.90	0.00449	136	0.002588	236	5.7
6 June 1974	48.60	0.06038	38	0.008062	285	11.4
			Stream 2			
14 December 1973	3.31	-	-	-	-	7.4
10 April 1974	8.10	0.00765	117	0.001213	738	10.3
4 June 1974	107.4	0.04699	55	0.007062	366	10.6

six, while the other experimental population at 5°C, continued its very slow growth until temperatures were allowed to warm later in the spring. This increase in growth rate, initiated between April 10 and 29, agreed with similar observations of early April growth in field populations. These increased growth rates were high compared with previous laboratory estimates but were similar to field measurements at the same temperature.

As indicated above, the lack of significant growth in winter, even under favorable temperature conditions, and the sudden initiation of rapid growth in early spring implicated environmental factors other than temperature in the regulation of growth of P. albimanus. Presumably food and of course temperature are not likely candidates since these variables were controlled within the experimental design. The regulation and synchronization of growth through photoperiodic responses is common among insects, although not well documented for chironomid species. Paris and Jenner (1959) and Englemann and Shappirio (1965) suggested that short day lengths inhibited the growth of Metriocnemus knabi and Chironomus tentans respectively, but no direct evidence was obtained for suggesting that photoperiod inhibits the growth of P. albimanus.

Summer Populations. A second prolonged non-growth period occurred during the summer, shortly after hatching

of field populations. A brief period of growth occurred shortly after eclosion, but failed to continue beyond a mean weight of approximately 1 µg. This non-growth period lasted about 10 weeks, extending into fall, and covered a period when stream temperatures were at their maximum (15-16°C). These temperatures were not inhibitory to spring populations nor to newly hatched larvulae. Terminal weights of I-instar larvae in certain laboratory experiments were similar to those attained by larvae under field conditions.

Effects of Temperature on Timing of Emergence

Experimental Populations

Experiments which produced data on growth rate also provided emergence information. This allowed testing of the hypothesis that the timing of emergence is a function of the heat accumulation by the population. Developmental rates and emergence periods of terrestrial species have been shown to follow this principle (see review of Andrewartha and Birch, 1954). Aquatic insects should respond in an even more predictable fashion since the added factors of humidity and widely fluctuating daily temperatures are removed.

Konstantinov (1958a), after observing the laboratory growth of several species of Chironomini, concluded that the

day-degree summations can accurately estimate developmental velocity. Information on natural populations of chironomid larvae was provided by Miller (1941), who observed a consistent pattern of heat accumulation necessary for emergence of lake chironomids.

Mundie (1957) and Potter and Learner (1974) observed that day-degree requirements for the second generation in bivoltine reservoir species were substantially less than that required for the overwintering generation. Differences found by Potter and Learner (1974) varied from 300 to 1100 day-degrees, however, differences between the two estimates would have been reduced by correcting day-degree estimates for the lower developmental threshold temperature for each species. Substantial differences in effective day-degree requirements for the two generations still remained after Mundie (1957) applied the correction.

Experimental populations of P. albimanus were used to determine whether emergence occurred at a given heat accumulation under constant laboratory conditions and in the artificial streams under variable conditions. Under constant conditions, larvae held from April until emergence at 10, 15, 20°C, required about 700 day-degrees (Table 11). This was the case at 10, 15 and 20°C, however, after 146 days the 5°C treatment was terminated, since according to estimates based on other treatments, another 550 days would have been necessary to begin emergence.

Table 11. Comparison of day-degree intervals required for emergence of P. albimanus from both field and experimental conditions. Day-degree summations began on the first day in spring when mean daily temperatures rose above 4°C and continued until evidence of first adults.

Treatment	Days	Day-Degrees
	Augusta Creek	
1972-1973	88	685
1973-1974	80	605
1974-1975	72	677
Three Year Mean		656
	Experimental Stream System	
Stream 1	82	523
Stream 2	75	527
	Laboratory Populations	
5°C	146	No Emergence
10°C	115	690
15°C	64	704
20°C	45	720

In a long term experiment, conducted in the artificial streams under variable temperature conditions, adult emergence began in both streams after the same day-degree interval. Spring growth in the 5°C stream was delayed three weeks by low temperatures, while the population in 10°C stream initiated growth immediately after release from the winter inhibition.

Each larval population required more than 500 day-degrees following the overwintering period to mature and begin emergence. These data cannot be compared directly to other day-degree accumulations in Table 11, for larvae were initially larger in this experiment than in the constant temperature laboratory tests. Consequently, they needed fewer day-degrees to reach maturity. Although overwintering larvae in the artificial streams did gain weight during the winter, and therefore utilized some of the heat available, no correction factor was applied to add any effective day-degrees to those summed after the winter.

Natural Population

The growth rates shown in Table 8 led to similar dates (June 20th-24th) of first emergence in 1973-1975. Since the exact dates of emergence were not determined, heat summations for Augusta Creek in the springs of 1973-1975 have been accumulated to June 21 (Table 11). Day-degree accumulations did not begin until temperatures increased above 4°C,

and that was subtracted from each day to arrive at an effective day-degree summation after that date. Consequently, dates when the first day-degree began to accrue were different in each year, yet by June 21 of each year approximately 650 day-degrees had accumulated.

Effects of Food Quality on Larval Growth

Leaf fragments of two deciduous trees common in the watershed, feces of the "shredder" Tipula abdominalis and native stream detritus were compared. These four substrates cover a wide range of food types from one predicted to be very nutritious (ground, conditioned hickory leaves) to one thought to be a poorer food source (natural detritus). The resulting growth rate data, microbial biomass and activity estimates of the foods, were analyzed by a two-way ANOVA with a priori comparisons of means. Treatment comparisons were between leaf fragments and natural stream detritus plus Tipula feces; between insect feces and stream detritus; and between particles of hickory and oak leaves.

Extimates of microbial biomass and respiration rate, total N, C and percent organic matter were used as measures of food quality. Two-way ANOVA was also used to analyze differences in these parameters among the particulate foods tested. In addition, substrate ATP content and respiration rate were regressed on animal growth rates to test for linear relationships.

Microbial Biomass and Respiration of the Substrates

Measurement of microbial biomass and respiratory rate of the four treatment substrates followed similar patterns (Table 12 and Figure 12). Particles of pignut hickory contained more ATP and respired at a higher rate than did particles of white oak, white oak was higher in both categories than *Tipula* feces, which was higher than native detritus. These trends held at all temperatures tested.

Results of the two-way ANOVA (Table 13) suggested that a significant difference in ATP content and respiratory rate existed between hickory and oak particles ($P < 0.05$) and between leaves and the two other substrates ($P < 0.001$), but only respiratory rates differed between *Tipula* feces and natural detritus.

Suberkropp and Klug (1976) measured higher ATP content on whole leaves of hickory compared to oak during a study of leaf decomposition processes in Augusta Creek. These data would support the hypothesis that at least for some period of time after decomposition begins, particles generated from leaf breakdown do maintain differential densities on microbes. Presumably these would be bacteria rather than fungi, since particle sizes were small.

Particles recently generated from leaf decay may be able to maintain a much more dense microbial community than older particles (leaves - vs - *Tipula* feces plus natural

Table 12. Growth rate responses of laboratory populations of P. albimanus to changes in temperature and detrital food quality. Given are mean daily growth rates along with estimates of food quality.

Temp. °C	Substrate	[1]Animal Growth Rate	[2]ATP Content	[3]Respiration Rate	[4]Total N	C/N	[5]Organic Content
10	Pignut Hickory	0.1051	23.56	0.175	3.658	13.97	82.83
	White Oak	0.0691	16.33	0.109	1.487	33.64	85.38
	Insect Feces	0.0300	2.47	0.076	1.424	39.78	82.28
	Native Detritus	0.0250	1.72	0.030	3.016	17.81	57.70
15	Pignut Hickory	0.1318	25.44	0.195	3.682	13.65	87.16
	White Oak	0.1184	18.60	0.126	1.611	31.00	88.76
	Insect Feces	0.0776	3.00	0.090	1.147	44.86	81.90
	Native Detritus	0.0469	0.01	0.049	3.242	18.26	56.13
20	Pignut Hickory	0.1523	29.83	0.252	3.246	14.33	85.33
	White Oak	0.1389	17.60	0.235	1.671	29.83	86.78
	Insect Feces	0.0988	4.12	0.167	1.511	34.65	84.73
	Native Detritus	0.0296	0.83	0.052	3.181	16.89	59.73

[1] k_d = (ln(Final Wt/Initial Wt))/Days

[2] Nanomoles ATP·g AFDW^{-1}

[3] ml O_2 ·g AFDW^{-1}· hr^{-1}

[4] % of AFDW

[5] % loss on ignition after 48 hrs at 550°C

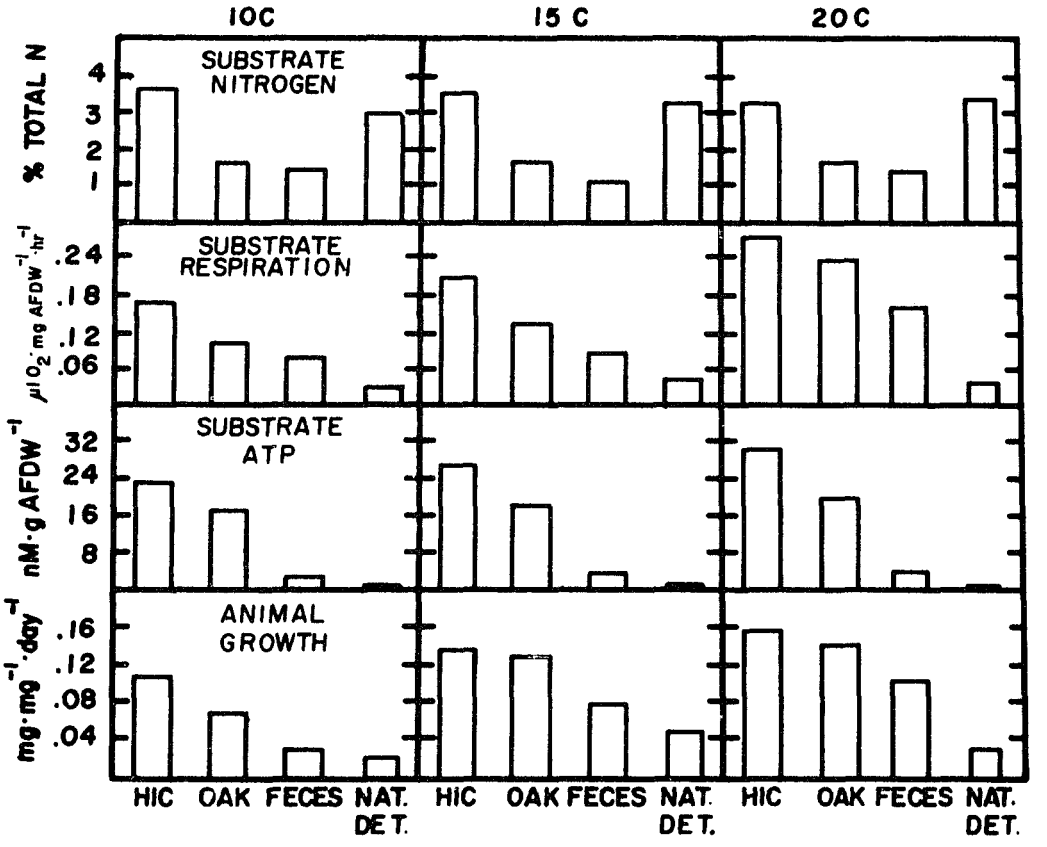

Figure 12. Comparison of mean daily growth rates of P. albimanus vs substrate ATP, respiratory rate and N content.

Table 13. Statistical summary of two-way ANOVA, for mean daily growth rates of P. albimanus and estimates of detrital food quality in Table 12.

Comparisons	Animal Growth	Substrate ATP	Substrate Respiration
Substrates			
Pignut Hickory-vs-White Oak	NS	*	*
Leaves-vs-Native Detritus + Feces	***	***	***
Feces-vs-Native Detritus	*	NS	***
Temperature	**	NS	***
Interaction	NS	NS	NS

*$P \leq 0.05$
**$P \leq 0.01$
***$P \leq 0.001$
NS Not significant

detritus, $P < 0.001$). The loss of ability to sustain high microbial densities may be due to the buildup of refractory N compounds (Suberkropp et al., 1976).

Substrate N, C/N, and Organic Matter Content

In general, analysis of total N, C/N and percent organic matter of the substrates failed to correlate with the differences in ATP content and substrate respiration rate. With the exception of native detritus (57%) organic matter content was quite high (82-87%). Oak was the highest (87%), and hickory and Tipula feces were quite similar (Table 12).

The analysis of total N and C showed somewhat different results. Native detritus and hickory had approximately the same levels of both nitrogen and carbon, while oak and Tipula feces had somewhat lower values for nitrogen. Ratios of C to N are difficult to interpret since substrates which produced both the lowest and the highest larval growth rates had low C/N values. These C/N ratios did not discriminate between forms of N, refractory N in natural stream detritus and any labile N in leaf particles were treated similarly.

Laboratory Growth of P. albimanus

Spring Population. Growth rates of P. albimanus revealed that significant differences existed among the treatments tested (Tables 12 and 13, and Figure 12). Leaf fragments produced a growth rate 1.3 to 3 times higher than other substrates, and feces proved to be a better food than natural stream detritus. Although the growth rates on ground hickory were higher than oak at every temperature, differences were not significant at the 5% level probably due to the high variance associated with the growth rates. A similar trend in growth rates existed at all temperatures; hickory > oak > feces > native detritus. It is interesting that native detritus proved to be the inferior food compared to the others tested and yet this substrate was collected from Augusta Creek during a period when P. albimanus was growing at its maximum rate ($k = 0.0800$ at 15°C).

Growth rates for P. albimanus fed native detritus were about one-half that of natural populations at the same temperatures (10 and 15°C).

Summer Populations. Larvae of P. albimanus did not grow in Augusta Creek between August and mid-October. Investigations of temperature effects (discussed above) suggested that other factors were inhibiting growth at this time. An experiment varying food type revealed that natural detritus failed to allow growth beyond the larval weight observed in the field, but that ground and conditioned particles of hickory leaves were sufficiently nutritious for larvae to complete a full generation. After 60 days at 15°C, larvae fed natural stream detritus remained at I-instar, while the population fed hickory leaf particles were either IV-instar, pupae or adults (Table 14). Hickory leaf partcicles were known to produce a higher larval growth rate (Table 12) and now known to be able to stimulate a population not normally growing.

Regression Analysis of Growth Rates vs Food Quality

Regression analysis of data in Table 12 indicated that a linear relationship existed between growth rate of P. albimanus and estimates of substrate ATP content and the substrate respiration rate (Table 15 and Figure 13). Thus this would suggest that microbial densities on detrital

Table 14. Results of growth study in which larvulae of P. albimanus were fed particles of either pignut hickory leaves or natural stream detritus.

Substrate (<250 µm > 75 µm)	[1]Initial Mean Dry Weight (µg)	N	Final Mean Dry Weight (µg)	N	Developmental Stage after 60 Days at 15°C
Pignut Hickory	0.35	250	111.0	41	IV-instar, Adults
Natural Detritus	0.35	-	0.73	15	I-instar only

[1]Initial weights for both treatments obtained from one random sample of larvulae prior to their addition to treatment substrate.

particles can significantly influence macro-consumer growth rates and that the quality of the food particles, as estimated by the extent of microbial colonization, may be an important variable in growth patterns of field populations.

Effects of Food Quality on Day-Degree Growth Rates

Data in Table 16 demonstrate the impact of food type on laboratory estimates of growth rates when effects of temperature are removed from rate calculations. Two of the substrates, ground hickory and oak leaves, produced a substantially higher growth rate than Tipula feces or natural stream detritus. A two-way ANOVA (Table 17) suggests that day-degree rates do not vary with temperature but rather with food type.

Table 15. Significance levels, equations, and coefficients of determination for linear regression analysis of growth rates of P. albimanus vs substrate ATP content and substrate respiratory rate.

Temp. °C	Substrate ATP -vs- Animal Growth	Substrate Respiration -vs- Animal Growth
	***	***
10	$Y = 0.0182 + 0.0037 X$	$Y = 0.0012 + 0.6055 X$
	$r^2 = 0.94$	$r^2 = 0.77$
	**	**
15	$Y = 0.0579 + 0.0029 X$	$Y = 0.0295 + 0.5615 X$
	$r^2 = 0.87$	$r^2 = 0.79$
	*	***
20	$Y = 0.0613 + 0.0033 X$	$Y = 0.0012 + 0.5892 X$
	$r^2 = 0.68$	$r^2 = 0.91$

*$P \leq 0.05$
**$P \leq 0.01$
***$P \leq 0.001$

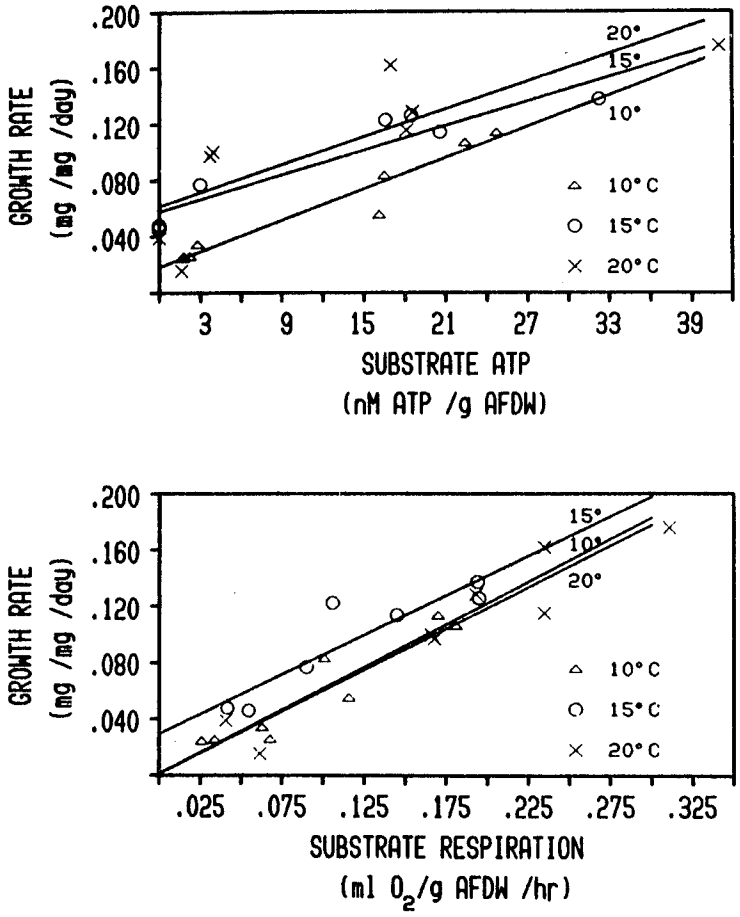

Figure 13. Regression data for mean daily growth rate of P. albimanus vs substrate ATP and respiratory rate of the food particles.

Table 16. Comparisons of day-degree growth rates ($mg \cdot mg^{-1} \cdot day\text{-}degree^{-1}$) for laboratory populations of P. albimanus fed four substrates of widely differing food quality.

Temp. °C	Substrates			
	Hickory	Oak	Tipula Feces	Native Detritus
10	0.01544	0.01477	0.004992	0.004167
15	0.01198	0.01076	-	0.004277
20	0.009519	0.009049	0.006175	-

Table 17. Summary of results of a two-way ANOVA testing the effects of temperature and food quality on day-degree growth rates of P. albimanus.

Source - Comparisons	Significant levels
Substrate	***
Hickory -vs- Oak	ns
Tipula Feces -vs- Native Detritus	ns
Leaves -vs- Tipula Feces + Native Detritus	***
Temperature	ns
Interaction	ns

ns = not significant
* $P \leq 0.05$
** $P \leq 0.01$
*** $P \leq 0.001$

The implication is that, shifts in the quality of detritus, either seasonally or short-term, will alter detritivore growth rates, lowered food quality producing reduced growth rates.

DISCUSSION

Life History of P. albimanus

The growth pattern of P. albimanus included an overwintering population with an age structure unlike that of most Chironomidae. In his review of the overwintering of north temperate Chironomidae, Danks (1971b) reported that many Chironomini overwinter as instars-III or III and IV, often with a predominance of IV, unless conditions are unfavorable and retard growth in the fall. Lindeman (1942) states that early instar larvae of Chironomus plumosus did not overwinter well in Cedar Bog Lake, and Danks (1971b) suggested that there may be a limit to the instars capable of overwintering. Since the Augusta Creek population of P. albimanus was dominated by instar-II during the winter months, and included a small proportion of instar I in late winter, it is evident that at least some species can overwinter as early instar larvae in temperate latitudes.

Recently, Shiozawa and Barnes (1977) have reported that larval Tanypus stellatus Coquillett overwinter in Utah Lake, Utah as a mixture of I, II, and a few III instars. The major developmental period occurred after overwintering and

emergence began in early July. This pattern is, of course, similar to that of P. albimanus.

In the field, larvae maintained their prewinter weight from November to March. Overwintering larvae exposed in the laboratory to elevated temperatures grew very slowly, environmental factors other than temperature alone appear to control the initiation of growth in the spring.

The major period of development of most Chironomini is in summer and fall. Jónasson (1972) and Charles et al. (1972/1973) studied a number of temperate lentic species and showed that a majority of the growth occurred prior to winter, with a final period of growth in spring leading to emergence. P. albimanus showed the opposite pattern. Little development (1%) occurred before winter and 85% occurred during the last 30 days of the annual cycle. Thus, it was one of the last species of the overwintering Augusta Creek community to emerge. Late emergence from both lakes and streams has commonly been observed in this species (Table 1) and thus the winter age structure and type of growth seen in Augusta Creek may extend to other habitats where this species has been found.

The Relationship Between Temperature, Food Quality and Macroconsumer Growth Rates

The connection between food quality and growth rates in macroinvertebrates has been made (e.g., Cummins, 1974;

Otto, 1974); therefore, given the assumption that deposit-feeding species obtain a significant portion of their energy from microbes attached to sediment particles, rate of growth should be a function of microbial biomass.

Estimates based on ATP content and respiration rate of the four particulate categories indicated that large differences in the density of the attached microbial community did occur. Increases in growth rate of P. albimanus larvae fed the four detrital substrates correlated well with the microbial densities. Linear regression analysis revealed that changes in growth rates of P. albimanus were linear with changes in microbial biomass, thus microbial density may be an adequate measure of the quality of a food source. Natural detritus, shown here to support only a low microbial biomass and activity in both field and laboratory situations, might therefore be considered an abundant but rather low quality food source during most of the year.

Sources of fine particulate detritus (FPOM; < 1 mm in diameter) have been discussed by Fisher and Likens (1973) and Cummins (1974). Major inputs come from the decomposition and processing of leaves, wood, and other parts of terrestrial plants, directly from algal cells, molecular aggregation (Lush and Hynes, 1973) and animal frass and runoff from the surrounding watershed. Major inputs of detritus to headwater streams in the temperate zone usually

occur in the fall and spring (Cummins, 1974), and together with the metabolic activities of microbes should produce seasonal changes in the quality of the detritus standing crop. Major inputs of uncolonized detritus might decrease detrital quality temporarily, but within a short time microbial densities (= quality) would increase. Between periods of major detrital inputs, quality probably generally decreases as microbial metabolism utilizes the most labile fractions and that remaining becomes increasingly refractile, and less susceptible to microbial attack. Thus, microbial density and therefore particulate food quality for collectors, would decrease.

Various sources of fine particulate detritus represent potentially different qualities. Detrital particles derived from wood is of low quality (Anderson et al., 1977), but algal cells and plant reproductive parts represent high quality sources. Decomposing leaf material generates particulates of various qualities, depending on the species, rate of conversion to small particles and portion of the leaf. Fragments of "fast" leaf species (Petersen and Cummins, 1974) lowest in structural material (i.e., cellulose and lignin) would be of high quality, particularly if the conversion to FPOM is direct and rapid.

Significant inputs of high quality detritus, such as that derived from algae or reproductive plant parts,

probably results in only short term changes in overall detritus quality. Inputs from leaf material provide longer term increases in quality as FPOM is generated from leaf processing for several months. Such temporary increases in particulate quality undoubtedly affect the growth rates of resident collectors.

Seasonal shifts in food quality have been proposed by Otto (1974), since the energy content of the leaf shredding caddis fly Potamophylax increased after leaf fall and declined following the disappearance of alder, the preferred leaf type. Otto attributed the increase in larval lipid content to ingestion of alder leaves and the decrease to feeding on alternative food sources lower in quality such as beech. Alder was reported by Petersen and Cummins (1974) to be rapidly processed and to have a high nitrogen content by Goldman (1961).

Seasonal responses to food quality can be seen in the pattern of growth in the deposit-feeding collector P. albimanus. As the data from laboratory experiments have indicated, larval growth is very sensitive to differences in food quality. Certain phases of the growth of field populations of P. albimanus appear to be related to differences in food quality rather than changes in temperature. The growth pattern of P. albimanus in Augusta Creek is characterized by discontinuous increases in biomass, with four distinct

periods of growth separated by intervals when no increase in biomass occurred. The cessation of growth over winter can be explained by temperatures below the laboratory demonstrated threshold for growth (4°C), but not the lack of growth during the summer (late July, August and September) or mid-spring (first three weeks in May). Temperatures during summer (mean daily 15°C) were not inhibitory to laboratory populations nor were the 10°C temperatures experienced during May. Explanations for this type of growth are more clear if detrital quality is added to the story.

Particulate detritus standing crop and associated respiratory rate for the size range > 0.45 μm < 75 μm are shown in Figure 14. Some conclusions can be drawn regarding seasonal changes in quality of fine particles. General seasonal control of respiration was apparent as increased rates at warmer temperatures, although there were exceptions. Winter respiratory rates were higher than in May, even though the latter was a period of much higher temperature (1°C vs. 10°C). Also, winter rates were similar to October when mean daily temperature was 15°C. Respiration rates at the same temperature varied considerably during a season. For example, highest summer rates were observed in July with lower rates during the remainder of the warm season even though the temperature averaged 15°C over the entire period. A rather large reservoir of detrital particles was

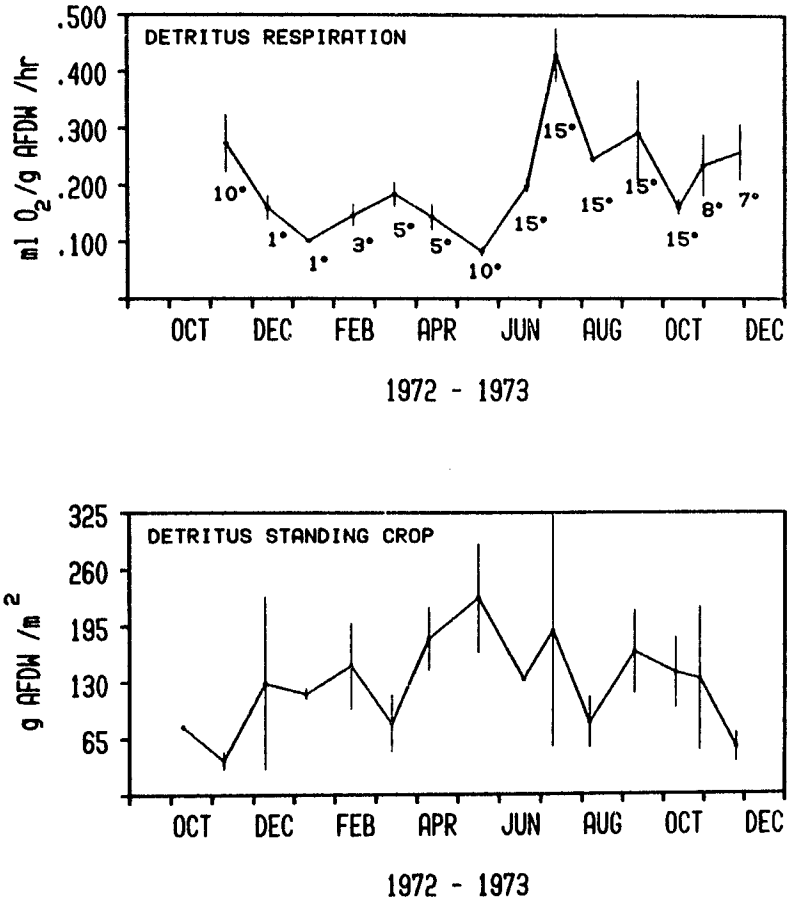

Figure 14. Annual cycle of detritus standing crop and respiratory rates in Augusta Creek, Michigan, site B, 1972-1973. Particle size range < 75 µm > 0.45 µm (modified from Cummins et al., 1977).

maintained throughout the year, with an increase from fall to spring and a decrease throughout the summer (Figure 14).

The data (Figure 14) indicate that the system maintained a relatively high activity during the winter, probably reflecting rapid metabolism of particles generated from decomposition of autumn leaf litter input. A major increase in the standing crop of poorly colonized FPOM in May presumably accounted for the observed initial decrease in respiratory rate followed by a high rate later in the spring after a period of microbial colonization. Metabolism of the labile fraction of the detritus and the increase in refractory compounds probably led to the decreasing quality of the detritus during summer.

A combination of temperature and food quality effects, leads to an explanation of the growth pattern of P. albimanus larvae. Larvulae hatch in July, grow rapidly for a short time on the high energy stores remaining from the egg. However, when they reach about 1 μg individual^{-1}, larvulae cease growing for the remainder of the summer. The quality of the summer detritus is not sufficient to sustain growth in early instars; therefore, larvulae fail to grow.

A second spurt of growth occurs for 3 to 4 weeks in late October and early November, until temperatures fall below 4°C, shortly after the autumnal diatom bloom and leaf input. Inputs of high quality particles derived from algae

and leaf material in October were reflected in the relatively high respiratory rates in November (1972 and 1973), which likely produced the growth.

Animals failed to grow during the winter at temperatures below 4°C, but development was renewed in the spring at favorable temperatures. Growth rate increased during April as temperatures increased, but stopped again in early May, even though temperatures were about 10°C. This was observed in both 1973 and 1974 during the same weeks in May. At this time, detritus standing crop was at an annual high, and respiratory activity at its lowest; therefore, a large detrital input with little microbial biomass in April and May possibly decreased overall particle quality and limited growth. By the end of May growth was rapid and continued until emergence in June and July. This period of rapid growth coincided with the period of most intense detrital microbial respiratory activity.

An alternative possibility for the growth cessation in May suggests that this was a period of synchronous molting by third-instar larvae. Molting would have to have been synchronous, and last one to two weeks, because mean larval weight failed to increase appreciably during this time. Molting by only a fraction of the population would have led to some increase in mean weight.

With the exception of Jónasson (1972), no clear examples of multiple environmental control of collector growth rates have been documented. Jónasson concluded that oxygen tensions, temperature and food controlled growth rates of a profundal midge species in Lake Esrom. In this study, at least temperature and food quality have been shown to affect growth rates and life history patterns of P. albimanus.

Learner and Potter (1974) have shown that Chironomous riparius has seven generations in a pond below a sewage outfall, but only 3 generations in another nearby pond. The rich microflora, sustained by sewage inputs may have been the stimulus for more rapid growth.

In streams P. albimanus has only one generation although in lakes it may be bivoltine (Table 1). Temperatures in Augusta Creek are warm enough for multiple generations, but other environmental conditions are not suitable. Since thermal regimes do not prevent multiple generations here, food quality is a likely limiting factor. Detritus in lakes, derived extensively from algae and aquatic plants rather than terrestrial sources, is probably of generally higher quality. Although peaks of input to the lake benthos undoubtedly occur, continuous sedimentation from the plankton is undoubtedly significant. White (1974) reported that summer sedimentation rates in Lawrence Lake, Michigan were 30-50% of peak values in spring and fall. Such amounts

could certainly provide inputs sufficient to produce a second generation of P. albimanus.

The life history of P. albimanus appears flexible as indicated by the eurytopic nature of its habitats. Temperature controls seasonal growth, preventing development in winter and limiting growth during fall and spring, but detrital food quality appears to be equally important in regulating growth. Growth may be slowed or arrested by poor food quality, or accelerated to produce multiple generations if continuous supplies of high quality food are available.

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