NATURAL HISTORY AND ECOLOGY OF PYCNOPSYCHE LEPIDA, P. GUTTIFER AND P. SCABRIPENNIS (TRICHOPTERA: LIMNEPHILIDAE) IN A WOODLAND STREAM

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Frederick Osborn Howard

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ABSTRACT

NATURAL HISTORY AND ECOLOGY OF *PYCNOPSYCHE LEPIDA*, *P. GUTTIFER* AND *P. SCABRIPENNIS* (TRICHOPTERA: LIMNEPHILIDAE) IN A WOODLAND STREAM

By

Frederick Osborn Howard

Augusta Creek, a brown trout stream in southwestern Michigan, supports an estimated 10 species of large particle-feeding insect detritivores (Shredders). An ecological study of the congeneric group; *Pycnopsyche guttifer*, *P. lepida* and *P. scabripennis*, was conducted using field and laboratory techniques to elucidate the role played by these species. Adults mated, oviposited and produced actively growing larvae in the laboratory. By utilizing groups of larvae from individual egg clutches, laboratory experiments yielded growth, feeding and respiration data. Age specific population measurements and physiological data together with a generalized stream model have been used to estimate the fraction of the overall stream budget under direct or indirect influence of these limnephilids. Natural history information concerning partitioning of the stream bed, food and case materials, emergence, flight period and oviposition, is included along with a proposed energy budget representative of the genus.

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By

Frederick Osborn Howard

A DISSERTATION

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This thesis is dedicated to the memory of my mother, Rosanna, without whose boundless optimism and faith it would never have been possible.

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INTRODUCTION

A striking correlation between the distribution of the limnephilid caddisfly genus Pycnopsyche, and the North American Eastern Deciduous Forest biome and adjacent ecotones, has been demonstrated by Ross (1963). Most clean headwater streams are considered heterotrophic by many investigators (see reviews by Cummins, 1966, 1974; Hynes, 1970a, b; and Fisher and Likens, 1972). More explicitly, these running water communities are characterized by the autotrophically elaborated organic matter imported from terrestrial communities (Nelson and Scott, 1962; Hynes, 1963; Egglishaw, 1964; Minshall, 1967; Triska, 1970; Fisher, 1971; Hall, 1971; Fisher and Likens, 1972; Sedell et al., 1973). The investigations of Percival and Whitehead (1929), Hynes (1961), Minckley (1963), Coffman et al. (1970, 1971), Leathers (1922), Muttkowski (1929), Slack (1936), Jones (1950), Chapman and Demory (1963), Cummins (1964), Warren et al. (1966, 1971), have led to intensive studies of dominant species occupying a particular trophic position, for example, large particle detritivores (Vannote, 1970; McDiffett, 1970; Wallace et al., 1970; Mackay, 1972a, b; and Mackay and Kalff, 1973).

In an attempt to bring together the geological relationship of the deciduous forest biome and the important detritivores in the Augusta Creek system, the natural history of the two components has been the subject of this study. Degradation of forest litter in streams has been investigated by terrestrial and soil ecologists (see review in Petersen and Cummins, 1974). Recently the relationship between terrestrial (soil) and stream communities has been reinforced (Triska, 1970; Kaushik and Hynes, 1968, 1971; Petersen and Cummins, 1974). Microbial components degrade leaf litter in the two environments. Distribution of the benthic insects has been correlated with the distribution of plant detritus by Egglishaw (1964). The importance of autumn-shed leaves as a protein source has been demonstrated by numerous terrestrial ecologists (Phillipson, J. edit., 1971). The importance of microflora to the benthic insects must be stressed since cellulolytic enzymes produced in the guts of aquatic insects have yet to be demonstrated. The rapid leaching of soluble organic materials from leaves reduces the nutrient value to the benthic insects, leaving mostly structural carbohydrates such as cellulose. These leaf surfaces, twigs, bark, and other litter from trees and shrubs serves ideal substrates for microbial colonization. Nitrogen lost to the water column through leaching and introduced through runoff and the intrusion of ground water is available to the microbes which

incorporate it into their own tissues - the cellulose of the accumulated litter serving as a carbon pool. Thus, only the colonized detrital elements become highly nutritional food sources for the benthic detritivores. Recent studies (Kostalos, 1969; Triska, 1970; MacKay, 1972, 1973; Barlocher and Kendrick, 1974a, b), and including those at the Kellogg Biological Station (Suberkrop, unpublished data), indicate that Pycnopsyche spp. preferentially choose and feed on leaves colonized by fungi.

A complex of congeneric species of Pycnopsyche Banks (Trichoptera: Limnephilidae) inhabits Augusta Creek. The density of Pycnopsyche and their occurrence throughout the eastern deciduous biome has made this group an ideal subject for stream detritivore investigations.

The purpose of this study was to elucidate the natural history of Pycnopsyche spp. in Augusta Creek, the ecological role of these species in the degradation of allochthonous detritus and to establish their relationships with the local deciduous forest association.

DESCRIPTION OF STUDY AREA

Augusta Creek, a spring fed, hardwater, brown and brook trout stream (third order water shed, Leopold, et al., 1964) rises as a primary stream approximately 250 meters above sea level in Barry County, Michigan. It follows a southerly course through Kalamazoo County draining a large marsh and joining several other tributary streams, entering the Kalamazoo River as a third order stream at Augusta. The 15 kilometer course of the stream is one of numerous bends, riffles and pools, shaded for most of its length by dense riparian shrubs or a canopy of mixed deciduous trees. Primary production is restricted to small pulses in early spring and late fall corresponding to periods of maximum insolation reaching the stream when shrubs and trees have no leaves or to reaches from which the stream side vegetation has been removed. Principal input to the stream is allochthonous detritus in the form of litter fall from riparian shrubs and deciduous trees. This litter fall peaks at autumn leaf abscission but there is also substantial input distributed throughout the year as twigs, bark, bud scales, floral parts, fruits and seeds (Ovington and Olson, 1963).

With the initiation of the study of leaf processing in Augusta Creek, an attempt was made to describe that portion of the 67.63 square kilometer watershed which made direct inputs of organic matter to the stream. The basin of Augusta Creek is composed of moist to wet muck or shallow

peat soils with marshes, small depressions with slow drainage, and agricultural development (row crops, grains and pasture) on drier sites. Given the latitude and soil type, c climax growth of Black Ash, American Elm and Red Maple is supported, a forest association first described by the American Society of Foresters (J of F, 1932) and then modified by Grimm (1961) to Black Ash, American Elm, Red Maple (Grimm Forest Association, Type 19; GFA-19) specific to Pennsylvania. I further modified "GFA type 19" so it applies to local conditions along Augusta Creek in southwestern Michigan. Because man has caused great changes in forest patterns throughout the world, since variations exist in local soils and climatic conditions, and because of possible intergrading between communities, it is the purpose of this discussion to define the present forest association serving as the principal detrital input source to Augusta Creek. The community, as outlined in Table 1, includes the dominant tree species, associated tree species and shrubs.

METHODS

Field Methods

To obtain reliable growth estimates and behavior patterns for the Pycnopsyche species throughout the study reaches of Augusta Creek, field data from all stages of the life history were collected. Population studies of lotic benthic invertebrates have generated numerous sampling methods (Cummins, 1962; Hynes, 1970). The water currents, substrate type and microhabitat preferences of larval Pycnopsyche spp. warranted the use of a modified Hess (1941) cylindrical, mesh sampler. The cylindrical, mesh design has undergone several revisions (Waters and Knapp, 1961) including the one used in this study (Fig. 1). Larval feeding preferences were assessed by analysis of natural and laboratory-prepared accumulations of leaf material, termed packs (Cummins, et al., 1971), colonized in Augusta Creek. Standing crop estimates of detritus were measured using the techniques of Cummins, et al. (1972). Pupal exuviae were collected for estimates of population size (Corbet, 1957; Lawton, 1970). Adult flight activities were monitored with a variety of light traps, including several new types of UV light traps developed during this study. Oviposition and developmental data were gathered within a specific section of the stream and has been included in the discussion of the natural history. Measured physical parameters of meteorological and geological characteristics have been included in the discussion of Augusta Creek.

Quantitative Samples

Benthic invertebrate sampling as reviewed by Macan (1958b), Cummins (1962, 1975) and Hynes (1970) indicates the importance of careful selection of sampling technique, dictated by the organism to be sampled and the question to be addressed. Also, as detailed by Elliott (1971), techniques must be selected with quantitative analysis in mind.

Larval Pycnopsyche inhabit the bottoms of springs, streams and small rivers. Their microhabitat, as shown by Cummins (1964); Cummins and Lauff (1969); Mackay (1972a,b); and Mackay and Kalff (1973), largely depends upon substrate and current.

The sampler used (Fig. 1) was constructed of a cylindrical metal frame formed of 6.25 mm (¼ in) round steel stock with a band of heavy gauge galvanized sheet metal brazed around the bottom. This frame was covered with a replaceable nitex fabric net of either 0.25 or 1.0 mm mesh with zipper-fitted collecting bags. The net was fastened to the bottom of the frame with a large radiator hose clamp and to the top with Buttoneer (Dennison Manufacturing Company, Framingham, Massachusetts) shank fasteners. Samples were taken by forcing the sampler into the substrate with a twisting motion. An area 0.049 square meters was sampled when the surface of the substrate was disturbed and washed. If the sediments were removed the volume sampled was determined by the depth of sampling.

The collecting bag trailed downstream from the sampler, similar to the Surber (1937) square foot sampler, and all fine material and organisms dislodged from the substrate washed down into the zipper bag.

Samples were taken along randomly selected transects across the stream, with cylindrical cores being taken the entire width of the stream. Three transects were sampled at the Kelfor site on July 28-29, 1971 and December 14, 1971. Numbers of animals were recorded per sample and population estimates were reported as number of Pycnopsyche larvae per square meter of stream bottom. Larval population estimates were calculated as the number of animals collected during the sampling period multiplied by the area sampled.

Adult Light Trapping

Immediately preceding and throughout the period of expected emergence and flight, a large, four-vaned funnel, multicyanide jar, 110 volt, 15 watt flourescent UV. light trap (modified Pennsylvanian trap, Southwood, 1963) served as a monitoring device delineating the Pycnopsyche calendar flight period for Augusta Creek at the Kellogg Forest (Kelfor) site. The trap was emptied on a daily schedule, Pycnopsyche species adults removed, sorted to sex and species and enumerated to determine emergence and flight period. These data were used to support parallel information from emerging specimens reared in laboratory streams.

Several modified Pennsylvanian traps were designed and constructed to monitor other stream sites where twelve volt storage batteries were the only power source. The trap modifications involved a reduction in size and weight to facilitate portability. One eight watt flourescent UV. tube with a small power inverter served as the light source and the vanes were constructed of 2.54 cm x 0.32 cm (1 in. x 1/8 in.) aluminum strap stock with 0.32 cm (1/8 in.) galvanized hardware cloth mesh pop-rivetted to them. These were attached at right angles to a 5.08 cm (2 in.) length of 3.81 cm (1½ in.) PVC plastic pipe at the top and bottom. The flourescent tube fixtures were mounted inside the two sections of PVC pipe with the exposed tube extending between them. Using this design the light source was visible from three hundred and sixty degrees. The outside lower corners of the vane assembly were pop-rivetted to the top of a funnel constructed of 50.8 cm (20 in.) aluminum roll flashing. The small end of the funnel was attached to a lid from a 4.4 liter (1 gallon), wide-mouthed plastic jar. By using plastic jars the weight was minimized and multiple jars would allow easy transport of trap contents to the laboratory and replacement of the killing jar. To collect living adults for mating or marking experiments, several jars were attached in tandem by cutting a hole in the bottom of the first jar the size of the neck of the second and simply screwing them together. Several holes were cut in

the sides and covered with nytex mesh to allow air to circulate. When used as a live trap, sticks, bark, leaves and tissue paper were placed in the jars to serve as substrates for the insects to light on, reducing mortality due to the adults beating against the container attempting to escape. This technique was so successful that copulating pairs of adult Pycnopsyche were observed in the trap.

A third trap design was developed for even greater portability that proved to be quite successful. A flat, two-vane, frame was constructed of 2.54 cm x 0.32 cm (1 in. x 1/8 in.) aluminum strap stock and 0.32 cm (1/8 in.) galvanized hardware cloth. An eight watt, camper wall lamp fitted with a flourescent UV. tube, was mounted centrally on the vane assembly and a funnel with a flat back was constructed with a diameter the same as the vane width. The light and a small 12 volt, motorcycle battery were fitted for coupling, through a length of low resistance wire, with male and female electrical phonograph jacks. The trap was hung from a tree, with a large "S" hook, at streamside with the direction of flow parallel to the vanes.

Daily Exuviae Collections

The aquatic phase of most Trichoptera is terminated by the pupa swimming or crawling to the surface of the water and onto some projecting object to emerge from the pupal exuvia. The pupal skin ruptures along the

medio-dorsal ecdysial line and the imago wriggles out and soon flies or scurries to the cover of nearby vegetation or an overhanging bank. The fragile exuvia remains on the substrate and either dries and blows away, is washed away by rain or high water or is colonized and decomposed by fungi and bacteria. Daily exuviae collections have been utilized in investigations of Odonata (Corbet, 1957; Lawton, 1970) but to date there appears to be no published study on Trichoptera employing this technique. Since the cast pupal skins of Pycnopsyche can be identified to sex and species, with careful collection they can be used to evaluate the emergence patterns. Mackay (Royal Ontario Museum, Toronto, pers. comm.) indicated that differences in caudal projections and palpal segment numbers could be used to identify species and separate sexes in laboratory-reared pupal skins. Genital capsules, spur-sheath number, together with palpal segment numbers, were found to be better characters for separating the Augusta Creek species complex.

Commencing the day following the first adult capture in the Kellogg Forest light trap, a 610 square meter section of Augusta Creek was marked off as an experimental site. All emergence sites (projecting objects, i.e., logs, rocks and stream bank) were carefully collected and the exuviae were preserved in Kahle's solution (Borror and DeLong, 1955) and returned to the laboratory where sorting to sex and species was completed. The following days the

procedure was repeated until no more animals were collected in the light trap. The use of cast pupal skins as indicators of emergence eliminates the variance due to behavioral influences of light patterns, activeness or meteorological effects.

Egg Mass Monitoring

The understood exuviae collection sites, were also censused for oviposition during the first several weeks of the flight period. Beginning August 25, 1971 newly deposited egg masses were marked with color-coded, numbered flower pot stakes. Each day newly deposited egg masses were marked as above and old masses were observed. By August 31, 1971 the banks of the experimental site contained 62 P. lepida egg masses. During this same period seven P. lepida egg masses were oviposited in rearing chambers in a laboratory stream. Observations of larval development were made daily with particular attention paid to the state of the gelatinous matrix surrounding the eggs.

Substrate Particle Size

Approximately ten centimeter deep sediment cores removed during the July, 1971 quantitative sampling were wet-sieved on site and six particle size fractions of sediments retained in the samples were determined volumetrically. Large cobbles which fell only partially within the sample area were marked to show the portion

actually within the sampler. The volume was measured and corrected accordingly. Sediments were divided into six fractions as retained by standard soil testing sieves (0.5-1 mm, 1-2 mm, 2-4 mm, 4-8 mm, 8-16 mm and 16 mm). Each fraction was measured volumetrically, with a lithic strata volume analyser, standardized to within five milliliters. The volume analyser was constructed from a 45 cm (18 in.) length of 16.5 cm (6.5 in.) diameter plexiglass tube cemented to a 34.5 cm x 16.5 cm (13.5 in. x 10.5 in.) base with a one milliliter pipette attached with an elbow, as a micrometer. The water level was adjusted prior to the addition of each sample and displacement was read from the meniscus on the graduations of the pipette. Preliminary standardization was accomplished by measuring displacements of objects of known volume. A second unit was similarly constructed from a 1000 ml Nalgene graduated cylinder and a one ml pipette, to obtain more accurate measurements of small samples. All fractions were hand sorted, enumerated, the substrate was returned to the stream and the animals taken to the laboratory for measurement. Those animals near pupation were placed in experimental chambers in laboratory streams and utilized in mating experiments. Relative sediment volumes per size fraction were compared to numbers of animals collected per sample in order to associate substrate preferences with the Pycnopsyche species present.

Leaf Packs

The fate of single species of terrestrially-produced leaves was investigated as part of the overall processing of allochthonous leaf litter by large particle detrital feeders, or shredders, of the stream community. The diversity of deciduous species occupying riparian environments within the Augusta Creek watershed (Table 1) exerts significant impact on the lotic community structure. Throughout the period designated as autumn abscission, quantities of leaf litter enter the stream complex amounting annually to approximately one to five grams per square meter per day (Petersen and Cummins, 1974). Naturally occurring leaf litter enters the stream through fall-in, blow-in and wash-in. Large quantities accumulate upstream from brush-piles, log jams, rocks or in eddies and alcoves with reduced current velocities. The leaves and accompanying organic litter absorb water and sink. In addition to carrying away large quantities of organic leachate, the currents transport and relocate the debris along the stream bottom. This relocation is extremely critical, with fluctuations due to seasonal spates and droughts. Small- to medium-sized accumulations or packs of assorted leaf species become lodged on the upstream faces of benthic obstructions. These naturally occurring packs of leaf litter were simulated using a technique described by Cummins (1972) and Petersen and Cummins (1974). Leaves near abscission were removed from trees, air dried,

weighed into 10 gm ± 0.1 gm quantities. Initial weights, from subsamples, and all final weights were determined after 48 hrs. oven drying at 50°C. The bundles were dampened to reduce breakage and loosely fastened together with long-shank fasteners with a "Buttoneer", then loosely tethered with nylon monofilament to the narrow face of a standard construction-grade brick (Fig. 2). Bricks containing leaf packs were placed on the stream bottom, narrow face and leaf pack upstream. Direct flow of the water against the laboratory-prepared leaf packs was similar to that on naturally formed packs (See Cummins, et al., 1973).

Kellogg Forest Leaf Pack Transects

An additional experiment was conducted in Augusta Creek from late October, 1971 through early December of that year to evaluate detritus processing by the shredders (Pycnopsyche). Three transects containing a total of 630 g and 840 g respectively of laboratory-prepared 10 g packs of hickory (leaves processed at a medium rate) and oak (a "slow" leaf species) were placed randomly across Augusta Creek at the Kellogg Forest site. This simulation of naturally built-up leaf litter within the stream was to allow near-natural colonization by resident benthic invertebrates. Simultaneous removal and evaluation of the leaf packs was intended to give an estimate of the standing crop of active shredders, leaf-feeding preference and leaf weight loss due to physical and biological

(microbial and detritivore) degradation. P. lepida and P. guttifer were separated and enumerated from leaf species and the leaves were oven-dried (50°C) and reweighed to determine changes in weight per pack of each leaf species. The initiation of the experiment corresponded closely to normal abscission of the leaf species and thus normal processing by natural microflora and macrofauna occurred in the stream. Colonization of leaf packs according to their position along the transects was noted to allow comparison with microdistributions defined during quantitative sampling of Pycnopsyche larvae.

Laboratory Methods

A series of laboratory studies was conducted to quantify the life history events of the detrital feeding Pycnopsyche species. Life history data indicating processing rates of detritus as well as growth, respiration, and assimilation rate and behavior were investigated. Cummins (1971, 1974) proposed a model of energy flow through small streams based, in part, on studies in an experimental lotic system. The major energy source was proposed to be microbially-colonized coarse particulate organic matter (CPOM) in the form of allochthonous leaves, flowers and fruits, branches and bark. A significant portion of this litter is processed through a natural comminuter taking the form of a multiple-species complex of benthic invertebrate: shredders. The physico-chemical

processing of the CPOM by the Pycnosyche spp. (Cummins, et al., 1973; Mackay and Kalff, 1973; Petersen and Cummins, 1974) has been substantiated in part by these experiments.

As discussed by Petersen and Cummins (1974) leaves of different species have different rates of degradation, although no significant differences occurred between seasons or sites (P 0.10) within the stream. Feeding experiments designed to assess effective processing of "slow" and "medium" leaves by shredders were conducted in individual chambers and in combination with other shredders and collectors. Additional shredder processing of "medium" and "slow" leaves was tested in large artificial streams (Cummins, 1972). The use of stream-collected larvae as experimental specimens was accompanied by the use of larvae from laboratory-produced egg masses in an attempt to reduce variability. Gut loading and assimilation were determined utilizing ^{14}C labelled food and respiration rates were measured using both field-collected and laboratory-reared larvae (see Appendix).

Laboratory Oviposition Chamber Experiment

Live-trapped adults of each species of Pycnopsyche were placed in chambers designed to stimulate oviposition on substrates simulating those along Augusta Creek. Oviposition chambers were constructed using a 20.3 cm (8 in.) square cake pan as a base and attaching a 30.5 cm x 20.3 cm x 20.3 cm (12 in. x 8 in. x 8 in.) box of 0.32 cm

(1/8 in.) hardware cloth. The pan was filled with gravel corresponding in size to that yielding the greatest number of burrowed Pycnopsyche spp. pupae. A length of water-logged bark was placed diagonally from one upper corner to mid bottom of the gravel-filled pan and the entire apparatus was placed in a laboratory stream, submerged to a depth of several centimeters above the gravel. The laboratory stream water was maintained at average Augusta temperatures and received natural light from windows. In chambers containing adult Pycnopsyche, egg masses were produced by all four species (a lake-dwelling species, P. subfasciata was also tested in the chambers) within several days of enclosure in the chambers. Oviposition in all cases was on the exposed bark in the same general position as the egg masses found along the stream bank.

Pupae placed in the chambers emerged in general synchrony with the wild population and produced egg masses within several days of emergence. No premature emergence was evident and egg masses were indistinguishable from wild type masses. Egg masses were collected from laboratory oviposition chambers containing laboratory-mated P. guttifer, P. lepida, P. scabripennis and P. subfasciata and placed in growth chambers constructed from plastic Blow-mold bottles containing natural mineral substrates and Augusta Creek water. The chambers were placed in laboratory streams maintained at normal average Augusta Creek temperature. A supply of washed, field-collected

leaf litter was added to each chamber and aeration applied. Water within the chambers was changed weekly and a supply of laboratory-conditioned leaves (Cummins, et al., 1973) was added concurrently. Developing embryos were observed as described above (Egg Mass Monitoring). High hatching rates were recorded with upwards of 200 larvae being produced from many individual egg masses. New larvae wriggled free of the gelatinous matrix and began to feed and build cases immediately.

Feeding and Growth Experiments

Laboratory-produced larvae were used for growth and feeding experiments to reduce variability resulting from age differences in stream-collected animals as well as variability produced by taxonomic confounding in early instars. What little data are available in the literature concerning trichopteran larval ingestion and growth involve predominantly terminal and penultimate instars. However, due to large numbers and rapid growth rates early instars have a significant impact on the benthic community.

Feeding experiments were designed to evaluate the importance of Pycnopsyche larvae to the community and to provide data for future studies of the energetics of other detrital processing species. Small culture dishes (10 cm diam.) were filled with filtered stream water and placed in a laboratory stream maintained at average natural stream temperatures. The laboratory stream was exposed to

near-natural photoperiod from windows and periodic illumination from flourescent lights. All dishes were aerated and water levels maintained by the addition of filtered stream water when necessary. Experimental duration was limited to seven days in most cases, 14 days maximum for one series of later instars, based on earlier observations of the rapid growth of early instars. All experiments followed the same design, with three replicate dishes each containing ten larvae and a fourth dish serving as a leaf control. All dishes were supplied with weighed 9 mm diameter discs of Maple (Acer rubrum), basswood (Tilia americana) or both, chosen to simulate feeding conditions of natural populations at that time. The 9 mm diameter discs, cut with a cork borer from freshly collected and washed Augusta Creek leaf litter, were colonized with the natural microbial flora of the stream at that time. Uniformity in the leaf discs was indicated by low variance in the initial weights. Larvae for any given experiment were taken from the same clutch or cohort; thus all animals were similar genetically and physiologically. Three to five leaf disc subsamples were pre-weighed and oven-dried at 50°C for 24-48 hrs. and reweighed to determine initial weights. A subsample of ten additional larvae from the same cohort was taken, head capsule widths measured, fresh weighed, oven-dried and reweighed. These measurements served as initial head sizes and weights for the experimental animals. At the

end of the experiments all animals were removed, head capsules measured and fresh and oven-dried weights determined. In chamber experiments the water was filtered through 75 μm mesh nitex to remove large particles and through pre-boiled 0.45 μm membrane millipore filters which were then oven-dried and weighed. Relative growth rates (RGR), Consumption Indices (CI), and Efficiency of conversion of food to growth (ECI) (Waldbauer, 1968) were calculated. Growth experiments included Instars I, II and IV, P. lepida; Instars II, III and V, P. scabripennis; and Instars II, III, IV and V, P. guttifer. Considerable moulting occurred during the experiments due to the rapid growth rate displayed by P. lepida and P. guttifer Instar I and II animals. This result in weight losses due to pre- and post-moulting fasting, the shedding of exuviae (Lawton, 1971; Appendices 2-5) and continued respiration without feeding.

Field-collected larvae. These were used in a modification of the above experimental design. Penultimate and, terminal instar P. guttifer were utilized to evaluate their growth and feeding. Animals in these instars are substantially larger and density has been shown to affect growth of later instars of P. guttifer (Cummins, et al., 1973). Three animals per chamber, totalling 45 larvae, were used in this experiment and relative growth rate (Waldbauer, 1968) was calculated. Previous feeding experiments with early instars of most Trichoptera have

been impractical due to problems of collection of significant numbers and their identification as well as the evaluation of the nutrient substrate. Results of the experimental procedure described above indicate broad application for future studies in energetics as well as systematics. The technique of collecting live adults described above (Adult Light Trapping) yielded egg masses from eight species of Trichoptera, and many more could be obtained easily. By rearing larvae from eggs oviposited by predetermined adults, complete life cycle and natural history data could be reported for species under one title and make the taxonomic literature more useful to investigators of stream biology.

Greenhouse Growth Chamber Experiment

Fisher (1971) and Fisher and Likens (1972) showed that in a small woodland stream in New Hampshire, leaf litter was largely processed within the stream, while a large portion of the dissolved matter was exported downstream. Large particle detritivores feeding predominantly on leaf litter, have been investigated by Vannote 1970 (Tipula abdominalis), Wallace, et al. 1970 (Peltoperla maria), McDiffett (Pteronarcys scotti), Triska 1970 (Pycnopsyche scabripennis) and Mackay 1972a, b; Mackay and Kalff 1973 (P. gentilis, P. luculenta, P. scabripennis). All previously reported species show feeding preferences for particular leaf types. The significance of microbial colonization on leaf substrates has

received much attention in recent studies (see review by Cummins, 1974). Coarse and fine particulate matter resulting from detritivory forms an excellent substrate for microbe populations, in turn making rich substrates for collector and/or scraper populations. Other than noting that direct and indirect responses to leaf conditioning are displayed by these shredders, the microbial effect was not specifically approached in this study. An experiment was conducted concerning growth, feeding and survivorship as influenced by density dependent and intra- and inter-specific interactions. The methods involved measurement of organic content, animal growth and mortality in the experimental chambers. Leaves, hand-picked just prior to abscission from a Pignut Hickory (Carya glabra) tree, were dried, weighed and placed in the replicate experimental chambers with 1.5 liters of water from a large experimental stream (Cummins, 1972). After an initial leaching and conditioning period, 25 ml organic foam concentrate, containing aquatic Hyphomycete spores, collected from Augusta Creek was added to the chambers. Leaf weight loss due to leaching was determined independently. Chambers were placed in a 5°C water bath and aerated. Fluctuations in temperature exceeded those occurring in the natural stream for the same period (Chambers 0.1-20°C, Augusta Creek 0.1-12°C). One set of chambers was maintained at 17°C under a 12 hour on - 12 hour off light regime. A seven-day incubation period

for microbial development was allowed before stream-collected animals were introduced. Caddisfly larvae, P. scabripennis, P. lepida, Instar V; P. guttifer Instars IV and V; in varying densities, replications and combinations (Table 2) were placed in the chambers with other shredders- cranefly larvae: T. abdominalis (Say) and T. caloptera (Loew); and collectors - mayfly nymphs: Stenonema fuscum (Clemens), S. tripunctatum (Banks), S. interpunctatum (Walker), and S. canadense (Walker). Animals were categorized according to size class and feeding behavior (i.e. shredders or collectors). Individuals were blotted and weighed to the nearest mg. before and after the experiment. At the termination of the experiment dry weights (50°C.) were measured to the nearest 0.1 mg and percent water was calculated. Since instantaneous growth rate calculations were not significantly different ($P < 0.01$) from relative growth rate calculated after Waldbauer (1968), the latter have been reported throughout.

Instantaneous growth rates were calculated;

$$G_i = \frac{\ln \bar{x} \text{ final individual dry wt.} - \ln \text{initial individual dry wt.}}{\text{time interval}}$$

Relative growth rates were calculated;

$$RGR = \frac{\dfrac{\bar{x} \text{ final individual dry wt.} - \bar{x} \text{ initial individual dry wt.}}{\text{time interval}}}{\text{median individual dry weight over time interval}}$$

An estimate of ingestion was made using leaf weight losses

over the experimental period corrected using control chambers for non-animal feeding and leaching of soluble materials. Consumption indices (CI) and efficiency of conversion of food to growth (ECI) were calculated after Waldbauer (1968) as follows:

$$CI = \frac{\text{mg dry wt food ingested over period}}{\text{median dry wt of animals over period X days}} =$$

$$= \text{mg ingested/mg animal/day}$$

$$ECI = \frac{RGR}{CI}$$

Larval Dissections

Ten P. lepida and P. guttifer terminal instar larvae, collected in Augusta Creek adjacent to the Kellogg Forest site, were dissected to determine sexual differences. Gonadal development could not be observed in any of the specimens. Individuals of P. lepida and P. guttifer had yellowish-colored abdomens but the differences in color of the adipose body in Pycnopsyche did not allow separation of the sexes as was reported in Limnephilus rhombicus (Novak and Sehnal, 1962).

Female Dissection and Egg Enumeration

With autumnal oviposition common among limnephilids, adult female specimens of three species of Pycnopsyche were dissected to ascertain the reproductive condition of individuals during the flight period.

Egg Masses from P. lepida and P. guttifer were collected from the stream bank or laboratory oviposition

chambers. Ova were teased from the gelatine and counted under a Wild M5 dissecting microscope.

During the adult life, Pycnopsyche spp. produce a distinctly odorous exudate which is released from the anus when the animals are handled, excited or distressed. Species could be separated by the odor and I could discern a slight difference between the sexes within a species. An odorous exudate was also reported by Mackay (1972a). Betten (1934) calls attention to a distinct odor produced by Stenophylax (= Pycnopsyche) adults and other limnephilids and implies possible pheromona involvement in mating behavior. Pheromone production in Lepidoptera is well known (e.g. Edwards, 1962) as a reproductive asset. Schneider (1962) reports the non-specific pheromone in saturiids, which seems in conflict with observations of differences between species discernible by this author.

Numbers of eggs within gravid females yielded data similar to those in oviposited egg masses. None of the dissected, spent females contained large numbers of maturing ovarioles. Deposition of one egg mass per female appeared to be the normal pattern among these species.

RESULTS AND DISCUSSION

Population Estimates (Statement)

Each species possesses its own set of dynamic characteristics of natality, mortality, rate of growth and life span. These sets are defined by physiological characteristics in response to environmental parameters and each population responds to the parameters in measurable ways. Pycnopsyche spp. in Augusta Creek exhibit a survivorship curve similar to that of most invertebrates whose success is dependent upon the production of large numbers of eggs and young larvae (Fig. 6). The flight and oviposition period of this limnephilid is closely synchronized with the abscission of deciduous riparian trees and shrubs. Also, abscission of deciduous trees is characteristic at a time when frequent seasonal rains occur. The autumn rains serve to concentrate leaf fall of certain tree species, relocate accumulations of leaves and debris along stream courses through spates, and regulate, by inundating the eggs, the population densities of some related detritivore species. Pycnopsyche spp. emerge in close accord with these autumn activities and their reproductive characteristics are directly affected by the autumn rains. Crichton (1960) contends that frequent autumn rains stimulate mating and oviposition in limnephilids and similar observations were made by Mackay (1972) in West Creek (Quebec). Emergence and oviposition of Pycnopsyche is stimulated

by autumn rains in that low numbers emerge on rainy nights and higher numbers emerge on nights following rain. The lag time allows terrestrial placement of eggs in moist environments without the adverse effects of the rain (Fig. 3, 4). Oviposition sites are proximal to stream margins where heavy rains and depth fluctuations cause significant mortality to undeveloped eggs. High egg mortality occurs when showers are in rhythmic patterns with heavy rains at the end of the period.

Recruitment

Measurement of population densities of early instar larvae was impractical due to the specialized habitat and the highly clumped distribution resulting from their behavioral responses at oviposition and the post hatching period. Environmental factors affecting the recruitment potential had been determined and served as a substantial constraint on the population. The two coexisting species of Pycnopsyche at the Kelfor site have been shown to partition the stream environment during their terminal development through lateral displacement along a current-substrate particle size regime. The adults have partly partitioned the emergence period with some overlap in the latter segment and show extensive overlap during the seven week long flight period (Fig. 4). Emergence period was delineated by field measurement and additional field measurements of egg mass deposition, numbers,

hatching rates and incubation times supplied the ingredients from which to estimate recruitment for P. lepida. Overlap of flight period and oviposition times, placed the two species in potential competition for oviposition sites, larval food and microhabitats. The preponderance of leaf material entering the stream at that time undoubtedly diluted competition for food or case construction materials. Competition for space between larvae was minimized, primarily because of precipitation which caused catastrophic mortality through premature saturation of egg masses and through direct adult competition for optimum oviposition sites.

Although P. guttifer females first appeared on 31 August, significant numbers did not emerge until 8 September (Fig. 4). Therefore, marked egg masses of P. lepida could not be separated from those of P. guttifer and calculations were made using those numbers. A heavy rain (46.3 mm-1.8 in.) occurred on 6 September removing 85 percent of the P. lepida egg masses. Assuming the 21 day incubation time, all eggs deposited after 15 August would have been vulnerable because of their inability to withstand premature submersion. Since P. lepida eggs were first observed on 25 August, all subsequently oviposited masses were subject to losses. Based on observations made in the laboratory, it was assumed that most females did not oviposit until the second or third day after emergence. Two thirds of the

P. lepida females within the study site had emerged by the storm date and produced a calculated potential of 164.6 larvae per m^2. One third of the females remained and could thus produce a calculated 82.3 larvae per m^2. The loss of 85 percent of the potential 164.6 larvae per m^2 left a residual population of 24.7 larvae per m^2. The 82.3 larvae per m^2 added to the residual 24.7 larvae per m^2 would yield an estimated mean population within the experimental site of 107 Instar I P. lepida larvae per m^2. An island present in the experimental site supplied an estimated 30 percent more oviposition area which increased the calculated population to 139.1 Instar I larvae per m^2. The above calculations are derived from field-measured data as shown in Fig. 5.

Population Estimate (Substrate Evaluation)

Density and distributional changes in the numbers of Pycnopsyche species larvae resulting from the quantitative sampling of an area adjacent to the Kelfor site on Augusta Creek (July, 1971) are shown in Fig. 7. Each sample was evaluated for numbers of each Pycnopsyche species, substrate particle size composition and position within the stream. P. guttifer and P. lepida microhabitats were described by Cummins (1964) wherein the partitioning of the stream bottom was delineated by the current regime and substrate particle size. Coarser substrates accompany more rapid currents and finer substrates accompany slower currents. Cummins (1964) has shown that the terminal

instar larvae of these co-occurring limnephilid species partition the substrate with P. lepida occupying faster channel areas with coarse sediments (2, 4 + 8 mm > 35% of total). P. guttifer occupied the margins of the stream in fine sediments (2,4 and 8 mm < 30% of total) with reduced current velocities. This behavioral characteristic of the genus requires investigators to excercise caution in choosing sampling techniques that would not bias the results. Forty-seven terminal instar burrowing P. lepida were collected from the transects across the stream. Placement of the specimens on the schematic drawing delineating the clumped distribution of the two species within the proper current regimes is shown in Fig. 7. Sediment particle size analysis of the core samples within the regions of clumped animals indicated a trend in which P. lepida was usually found when the sum of the volume of 2, 4, and 8 mm particles equalled 35 percent or more of the total volume of the sample. P. guttifer was seldom found in samples unless this fraction fell below 30 percent. Of the 47 P. lepida collected 89 percent of the animals were found within the channel areas having a mean current velocity of 51.3 cm/sec. Of the thirty-nine P. guttifer larvae collected, only 23 percent were located within the same channel areas as P. lepida. The remaining 77 percent of the P. guttifer were situated in current regimes of less than 51.3 cm/sec. All larvae either burrowed (P. lepida) or were fastened down (P. guttifer)

indicating their inactivity and improbably relocation.

Quantitative Samples. A sample was taken on 14 December 1971 to quantify the larval densities of Pycnopsyche in the Kelfor experimental site in Augusta Creek. Three transects totalling 91 cores (0.049 m^2) were evaluated for the age distribution and numbers of the two species. The 31 larvae of P. lepida were all Instar V; 13 of the P. guttifer were Instar IV with one Instar V animal collected. The microdistribution of these animals (Fig. 8) agrees well with the data of Cummins (1964) from Fleming Creek, Michigan. Dry weights of P. lepida placed them near the size at which a feeding shift occurs prior to the burrowing stage and the weights for P. guttifer indicated they were near moulting to Instar V. Final instar feeding of P. guttifer continued into spring with the majority of the animals in areas of reduced current velocities. During this instar, P. guttifer increased in weight approximately 350% over that near the end of Instar IV. Microhabitat separation had already begun with all of the P. guttifer larvae in the marginal areas and 61.3% of P. lepida within the predicted increased current regime. Partitioning observed one week prior to this sampling date had placed 69% of P. guttifer still within the channel with 52% of those animals within 50 cm of the approximate line of reduced current velocity. The ratio of P. lepida to P. guttifer of 2.2:1 is similar to the ratio (2.7:1) measured one

week earlier (7 December 1971) based on larvae collected from three leaf pack transects. Animals in the leaf pack transects were also in the same size classes but had lower mean dry weights, as would be expected if they were still feeding and growing.

Larval Density and Detritivore Effect. Past experiments indicated a shift of invertebrate shredders from leaf species with higher decay coefficients to those species with lower decay coefficients at some point near 50% degradation. Hickory leaves in these transects were approaching this limit (30.06%) at the final sampling. Oak leaves had lost approximately 22% (21.9%) of their mass and shredder species were present in substantial numbers. Not only were both Pycnopsyche species present on both species of leaves, but their relative numbers were nearly identical on the Oak and Hickory (Fig. 9). The majority of the P. lepida (79.4%) and P. guttifer (78.3%) were found on the Oak. Assuming an exponential decay model for the leaf litter (Fisher, 1971; Petersen and Cummins, 1974) and using decay coefficients developed by Petersen and Cummins (1974), the "medium" Hickory and "slow" Oak would achieve their biological half-life within 46-138 days and > 138 days respectively. The percent loss of these leaves during the experiment (35-37 days) is in agreement with the above estimate and the colonization by shredders also conforms to their proposed activity. The predominance of animals

on the Oak leaf packs indicates that the shift to the slower leaf species had already begun, and is also in agreement with previous findings (Petersen and Cummins, 1974). Of the 23 P. guttifer larvae present, 79% were in Instar IV still actively feeding and growing while all P. lepida had reached Instar V, approaching the burrowing stage of their larval life. Remaining leaf material of each species equalled 13.1 gm - Oak/P. lepida larvae and 36.5 gm - Oak/P. guttifer larvae. Hickory leaf material remaining equalled 8.7 gm - Hickory/P. lepida larvae and 87.0 gm - Hickory/P. guttifer larvae. Remaining material of each leaf species could support this population of shredders present with the subsequent food shift displayed by the terminal larvae of both species and the 21-22% of the larvae remaining on hickory could easily process those leaves to their predicted half life.

Subsamples of leaf packs aerated in laboratory chambers were microscopically examined and qualitatively evaluated. Hickory leaves in general had lower numbers and less diversity of Hyphomycete spores along with less hyphae. Bacteria, diatoms and protozoa were present in higher numbers on Hickory leaves. Initially, it was planned to evaluate the larval densities utilizing the leaf pack transects as samplers, but biased sampling may have resulted from leaf packs attracting larvae to specific areas. However, there was close agreement between the ratios of P. lepida to P. guttifer in the leaf transects

(Table 3) and the quantitative samples taken a week later (Table 4). The similarity in the total numbers of each species determined by both methods indicates that the procedures are useful for estimating population size. Similarity also exists between the sampling methods since larvae were found on leaf packs located in predictable current and substrate particle size regimes. Characteristics of the stream, within the leaf transect site appeared to be very similar to that section of the stream within the Kelfor quantitative sampling site.

Pupal Exuviae Enumeration. Pycnopsyche spp. lend themselves to quantitative exuviae sampling because of their size and mode of emergence. The pupa exits from the case, swims or crawls to the interface of the stream and projecting substrate and casts the pupal exuvium about 10 cm from the water surface. The exuvium is readily observable and allows accurate counting of species and sex. If rain falls collections must be made promptly to insure against loss due to "wash-in". Collecting from the downstream end of the experimental site being careful not to create an advancing wave avoids losses of exuviae.

During the fall of 1971, daily collection of cast pupal exuviae within the 610 m^2 Kelfor experimental site were made of the emerging population of Pycnopsyche spp. Emergence of P. lepida began 24 August and the last significant number of cast skins was collected on the

morning of 10 September. P. guttifer did not appear until 1 September with a final significant emergence on 12 September (Fig. 3). Daily inspections continued until 22 October, with a maximum of one to three skins found on any day, up to 19 September; no skins were found thereafter. Four hundred forty (of which 201 were female) of the total 660 P. lepida emerged prior to 1 September when the first P. guttifer emergence took place. The remaining 220 (of which 143 were female) P. lepida occurred during the emergence period of P. guttifer. Emergence for both species lasted approximately two weeks with P. lepida emergence beginning approximately one week ahead of P. guttifer. Final ratios of males to females in P. lepida equalled 356-304 (53.9%-46.1%) respectively and in P. guttifer, 215-163 (57%-43%) respectively. The male:female ratio on a nightly basis shifted from male dominated to female dominated near the midpoint of each species' emergence period. Meteorological effect on emergence was primarily through precipitation with little observable effect of air or water temperature fluctuations. A 24 hour lag effect was demonstrated by both species following each measurable rainfall (Figs. 3, 4), with elevated pulses of emergence the night following rain.

The exuviae collected during the study totalled 1,038, with 660 P. lepida or $1.082/m^2$ and 378 P. guttifer equalling $0.57/m^2$ within the sampling area. Since these

numbers are 89% lower than the population estimates based on quantitative benthic sampling of terminal diapausing larvae (Fig. 3; Table 5), prepupal and pupal mortality is indicated. Eclosion of the imago has long been known as a major point of mortality in insect populations. Three types of mortality during emergence were observed. The first was predation on the pupae as they approached the water surface or once they reached the terrestrial environment prior to ecdysis. Pycnopsyche pupae were observed in the guts of Rana clamitans (green frog) collected during exuviae samplings. The second was incomplete expansion of the wings, resulting in the inability of the imago to fly. The third was incomplete ecdysis in which the adult died partially within the pupal skin and partially emerged. Adults of Pycnopsyche were observed in laboratory chambers in the latter two conditions. In his extensive study of Anax imperator, Corbet (1957) stated that mortality during emergence accounted for ten percent of his study population annually. Corbet also noted that amphibian and avian predators (Turdus m. marula L.) were observed feeding on newly emerged imagos. Mackay (1973) reported Common Grackles (Quiscalus quiscula) feeding voraciously on concentrations of Pycnopsyche larvae during periods of decreased discharge in West Creek (Quebec). I have also observed Common Grackles feeding on Pycnopsyche larvae in a small stream in Pennsylvania. The Green Frog was

the only predator directly associated with Pycnopsyche species during this study but others, including fishes and parasitic nematodes, undoubtedly contribute to mortality.

Adult Flight Period. Data from light traps have been shown to reflect behavioral differences between species and between sexes of a given species (Crichton, 1961, 1965; Nimmo, 1966; Ulfstrand, 1970). It was observed that those caddisflies which normally fly during daylight hours do not appear in any great numbers in light trapped collections. In those caddisfly species which do fly at night the males are collected in proportionately higher numbers than females. Data collected during this study distinctly support the nocturnal activity of the Pycnopsyche species and the greater attraction of males to the UV. light source (H. H. Ross, Univ. Georgia, pers. comm.). Pycnopsyche female adults in one instance were once observed flying near a light trap; however they would alight on shrubs and branches near-by and were not collected by the trap at the same time that males were collected in fairly high numbers. Thus, the females showed a trap shyness and demonstrated that such data can be misleading if they are used as a direct measure of what is flying (Fig. 4).

Males of Trichoptera, including Pycnopsyche species, have been observed by this author to emerge and fly earlier in the calendar flight period than females of the

same species. Mackay (1972) showed that the males of a three species complex of Pycnopsyche in Quebec, partition the daily flight period with P. scabripennis occupying the first time segment, P. gentilis and P. luculenta following in respective segments. Her results also support the present observation that Pycnopsyche species fly almost entirely between sunset and midnight with most animals flying during the first two hours.

Feeding and Growth

High egg densities and hatching rates predicted massive populations of hatching caddisflies. Growth between larval instar I and II involved a two-fold increase in weight and required only 7-9 days. Ready access to numbers of newly hatched, predetermined larvae along with laboratory-observed behavior indicated Pycnopsyche to be an ideal study organism.

Experiments using P. lepida Instar V animals resulted in negative growth in all instances (Table 6). The behavioral response in terminal instars of this species terminates growth after the burrowing phase has been reached, even when the animals pass large quantities of detritus through their guts. When extrapolated, measurements on growth of stream-collected P. lepida larvae in early and mid-December indicated termination of growth by 30 December. Animals nearing 25-30 mg. dry weight by mid-December, will complete their growth and begin burrowing early in January. Laboratory

experiments involving early instars showed high Relative Growth Rates (GR; Waldbauer, 1968), but small size and the variability within an instar tended to obscure the difference. The staggered hatching discussed above has presented difficulties when separating growing larvae within a cohort as well as in an instar. The moulting of individuals within a chamber made the measurement of growth difficult or even indicated negative growth when coupled with mortality. Animals nearing a moult stopped feeding, moulted and increased their size substantially through about a 5% increase in water. This increase in water and size resulted in a larger measurement of the head capsule and fresh weight but little increase in dry weight biomass. Thus if a number of experimental animals near moulting were placed in a chamber with those not near moulting the growth per individual, when expressed as means, was obscured. Larvae of Pycnopsyche fed and gained weight until some crucial point, (by possibly a percent dilution of the hemolymph changing the hormonal balance) and then the larval skin was moulted and rapid expansion of the newly exposed exoskeleton took place (Tables 6, 7, 8). Sclerotized parts hardened and feeding began shortly afterwards. Melanization within the cuticle occurred concomitant with the deposition of sclerotin. Ingestion rates of > 300% body weight per day can occur with measured growth rates sometimes equalling 20-25% per day. Stream-measured Instar IV P. guttifer

showed nearly 7% growth per day over a seven day period (Table 7). During that same period, Instar V P. lepida were growing at about 4.5% body weight per day. P. guttifer were still actively growing with an approximate 1100 percent increase in body weight to be laid down in the remaining five month growing phase. P. lepida were nearing completion of their larval growth requiring about 30-35% increase in the remaining several weeks of this phase of Instar V.

Leaf Feeding

As less resistant ("fast") species of leaves approach 50 percent degradation, the animals begin to shift feeding activities to more resistant ("slow") leaf species that have become conditioned in the interim. The effect here is probably a response to an improved quality of food in the form of richer microbial flora. Nutrients within the "slower" leaves would have become more available to the microbes and the subsequent shift in animal feeding would have lagged slightly behind the increased microbial growth.

P. guttifer utilizes organic detritus throughout its larval development. Early larval instars feed on small particles scraped from detrital surfaces or picked up directly from the substrate. As the larvae grow, more leaf tissue and accompanying microflora are ingested with resultant skeletonization of leaves. Penultimate and terminal instar larvae eat leaf material, including small veins, and rasp the surfaces of coarse wood detritus. The

microhabitat of the larvae closely parallels that of the detritus upon which they feed. Current regimes dictate the accumulations of various detrital materials proportional to their density and specific gravity.

Historical Note

The durability of the silk material in trichopteran cases was demonstrated in an impressive form. A necklace made of the mineral cases of what were distinctly limnephilid-type and appeared to be P. lepida, strung on a rawhide thong (later replaced with string) was brought to my attention. The necklace was reputed to be over 100 years old and thought to have been among the artifacts uncovered in an Indian grave on Hill Island in the Susquehanna River adjacent to Harrisburg, Pennsylvania. The island is a diabase dike which cuts across the river in Londonderry Township, Dauphin County, Pennsylvania. Because of its geomorphic structure this island extended as a high point within the river and served as a meeting place for the Six Nations. Extensive Indian activity is known from published history of this area with the river and its tributaries serving as arteries of transportation during the 18th century. Numerous trading posts and Indian villages are known and artifacts of this culture are being studies intensively by archeologists and museum specialists from the William Penn Museum in Harrisburg. According to curators from the

museum, items used as jewelry included crinoid stems, other fossils, teeth and similar items. The exact history of the necklace is not yet verified other than the ownership by a great great grandmother who lived on a farm on the island and that she had gotten it as a girl and had passed it on to her family as an heirloom. Disregarding the ethnic background of the human manufacturer of the necklace, the age of the cases is in fact remarkable.

Egg Masses

Reproductive potential of Pycnopsyche spp. is displayed by the quantities of eggs deposited along the stream sides during periods of peak emergences. Oviposition was observed within five days of the first pupal skin and almost daily throughout the flight period. Separation of species by eggs was not possible except in conjunction with emergence partitioning. P. guttifer adults were not observed prior to August 31, 1971 and pupal exuviae were not collected until September 1, 1971. From September 1, egg masses in the field could not be separated by species except the previously marked egg masses of P. lepida. All species deposited 5 mm diameter, globular to ovoid, amber-gelatinous masses, which assumed the configuration of the substrate at the point of attachment, and contained 195-250 translucent to cream-colored eggs arranged in tightly aligned rows. The rows

probably resulted from their placement and maturation within the ovary. The gelatin appeared to be uniform throughout with no specific "skin" or thickened coating.

Larval development did not become apparent until the sixth to eight day. The matrix had lost resiliency and embryonic forms appeared folded within the egg chorions. By the tenth to thirteenth day the head capsules and eye spots were discernible and the outline of the larvae assumed the classic "fetal position" with the head facing outward. (See photos: Wiggins, 1973). After 15-18 days the visible chitinous structures were pigmented and certain setae were well developed. After 18-21 days most larvae had left the egg chorions and were actively crawling throughout the amorphous gelatinous matrix. Hatching occurred with those closest to the surface eclosing several days prior to those nearest the substrate. Those larvae that had hatched early were crawling onto the surface of the mass (see photos: Wiggins, 1973). While hatching progressed, the gelatin continued to absorb water from the surrounding environment and began to stream toward the water surface. Once the mass entered the water the remaining gelatin dissipated rapidly and the larvae began feeding and case-building in fine particulate detritus. Egg masses which were not deposited in sites having proper humidity or substrate or those which never reached the stream margin, dried up and perished. In those instances where egg masses were

immersed previous to nearly complete hatchling development, all further development ceased and the mass disintegrated. When egg masses were swelling and a period of dessication occurred, the mass shrivelled and all eggs or hatchlings perished. Dehydrated masses, when returned to a moist environment, disintegrated without further development. During the period of 9 P.M., September 5, 1971 to 4 P.M., September 6, 1971, 4.7 cm (1.8 inches) of rain fell causing a saturation of the exposed portion of the stream bank and a subsequent rise in stream depth. Approximately 85% of the Pycnopsyche egg masses present were washed away or prematurely submerged during this period. Egg masses surviving the excessive rainfall were those deposited under objects and were dependent upon humidity and condensation of dew for their moisture. It is apparent that selection of oviposition site is an important feature of survivorship. The numbers of egg masses (24 were counted in a two meter length of stream bank) deposited during the extended flight period were subjected to spates occurring during August, September and October. This normally serves as a significant source of mortality in the life cycle of Pycnopsyche spp. Macan (1961) reports similar mortality due to misplaced oviposition by several species of mayflies.

Larval Taxonomy

Not withstanding Mackay's (1972 a, b) studies on Pycnopsyche (Banks) larvae, most early larval descriptions of Trichoptera have been extremely brief. Her conclusion regarding early larvae coincide with the present approach in that measurements, weights, case type and behavior must be related to a knowledge of the species complexes present in the stream under study. Head widths, chaetotaxy and weights vary within species and between species. Pigmented spots, "freckles" and blotches were variable within age classes of the same species, even on specimens from the same mass. Head markings varied from finely freckled to nearly fully pigmented with blotches of dark chocolate brown to black in P. lepida. The gular regions appeared finely freckled (resembling newsprint). P. guttifer head capsules were highly variable, generally darker with blotches being nearly contiguous and gular freckling forming doughnut-shaped patterns. Pigmented mesosternal plates present in all three species were found to have diagnostic value when one knew the species complex present at a particular site. The small chitinized plates formed a single dotted line which extended one third the distance from the mesothoracic axillae to the midline. The apostrophe-shaped plates in P. guttifer, formed a small circle in the axillae and single dotted line toward the midline. P. scabripennis had a single dotted line extending from each mesothoracic axillae

toward the midline. The plates on P. lepida were apostrophe-shaped, smaller than those of P. guttifer and formed a single line lacking the axillary circle. Diagnostic chaetotaxy (Flint, 1960) was only accurate when near terminal instar larvae were observed. Later third instars could be separated but only when the species complex was known. Larval cases and case building have been described for P. lepida and P. guttifer (Flint, 1960; Cummins, 1964) and P. scabripennis and P. gentilis (Flint, 1960; Mackay, 1972). Hydatophylax argus (Wallengren) larvae, present at the same site, constructed dorsoventrally flattened leaf disc cases intermediate to the terminal cases which were constructed of chunks of bark and wood, reminiscent of oversized P. scabripennis terminal and pupal cases. Pupation of these two limnephilids was temporally separated but there was an overlap with burrowing terminal P. scabripennis larvae thus placing similar case types in proximity to each other. H. argus in Augusta Creek pupates during late April and emerges in late May or early June and P. scabripennis begins burrowing in the coarse gravel early in May and remains until it emerges in late July or August. The pupal cases could be readily separated by the attachment of H. argus with silken mesh while P. scabripennis only closed the anterior end and fastened the case to several small pieces of gravel. P. guttifer constructed leaf-fragment cases during the early instars

and later added small shell fragments, sand grains and sticks. During the fourth and fifth instars the case type became the typical bulky tube with seeds, thorns, coarse gravel and wood fragments with several long sticks attached lengthwise irregularly along the silk-lined tube. The long sticks usually project beyond both ends of the case. Many of the sticks are cut specifically to length with the strong chewing mandibles rather than being chosen in pre-sized lengths from the environment. The pointed ends following cutting resembled the tree-cutting activities of a beaver. The interior sides of the sticks which rest against the abdomen and thorax of the larvae are tailored to fit the contour. This is in contrast to the critical sorting of sand particles displayed by P. lepida. Early instars of this species also construct leaf-fragment, silk-lined cases with several long sticks projecting posteriorly, resembling those of P. guttifer. Later instars added sand grains of 1-2 mm size to the anterior end of the case until it became quite compact and composed largely of mineral matter. Upon careful examination of the terminal cases of P. lepida it became evident that particle size was more significant than mineral composition. Forty-seven cases examined as a test sample showed that 33.7% of the case materials were actually bark and wood or shell fragments of the same size range as the sand grains. Frequently the terminal case had retained the now fragile projecting

sticks which promptly were eroded away when the larvae burrowed into the gravel. The mean case length of the terminal instar, prepupae and pupae of P. lepida was 18.5 mm.

Pupal Taxonomy

Utilization of pupal characteristics to associate immatures with adults has been described by Vorhies (1909), Milne (1938) and Ross (1944). Taxonomic features; such as the shape and size of dorsal plates with their associated hooks, abdominal gills and antennal segments form the dominant generic key characters. Adult structures formed within the pupal skin are visible either through the skin or after dissection of the adult from the pupal skin. Tibial spurs used in adult taxonomy (P. guttifer and P. lepida, 1-3-3 and P. scabripennis, 1-3-4) develop sheaths on the pupal skins. Genitalia of developing adults are also encased in the pupal skin and thus a definitive genital capsule surrounding the structures is formed. Mackay (1972) reported that caudal appendages and papal segment numbers were satisfactory characteristics to determine species and sex within a three species complex. Palpal segment number, along with tibial spur number and genital capsule, allowed Augusta Creek Pycnopsyche species and sexes to be separated quickly and accurately. Caudal projections may have worked in some complexes (Mackay 1972a) but in Augusta Creek System the above described characteristics were more reliable.

Adult Taxonomy

Adults of the genus Pycnopsyche were first described by Banks (1905). Until 1950, when the genus was reviewed and redefined by Betten, numerous synonymies existed in the literature. Descriptions of the adults of both sexes of Pycnopsyche have been included in Betten (1950). A partial key to adults, pupae and larvae is found in Ross (1944). Others (Flint, 1966; Nimmo, 1971) have included descriptions of particular species in specific locations. Within the study area, adults of Pycnopsyche species were easily separated by sexes using genitalia as described by Betten (1950). Marked differences in wing patterns between P. guttifer, P. lepida and P. scabripennis allowed species to be readily separated. P. guttifer fore wings (approx. 17 mm) were translucent amber-colored with a dark distal margin and a central dark blotch resembling a closed fist with one finger extended proximally. P. lepida possessed similar, slightly smaller (16 mm) amber fore wings with one or two small inconspicuous central dark dots. P. scabripennis had fore wings slightly larger (18 mm) than P. guttifer with the translucent amber base color speckled heavily with tiny dark dots. These characteristics in the study area were sufficient to separate quickly the adults to species. As stated above, individuals could easily be sexed by genitalia. One characteristic I noticed was the distinct odor produced by this genus. Species could be separated readily by odor and subtle differences between sexes could be discerned.

Natural History

Immatures

Of the two species complex which is typical of streams inhabited by Pycnopsyche, the first species, P. lepida, constructs a relatively compact case of mineral matter or small blocks of wood, bark or seeds, similar in appearance to a sand grain or mineral case. The second, P. guttifer, constructs a bulky terminal instar larval case composed mainly of organic materials. Data collected in the present study indicated earlier emergence, slightly higher densities, burrowed diapause, faster growth and a shorter terminal growth phase in P. lepida. This group of characteristics may well be typical of the analog of P. lepida in all two-species Pycnopsyche complexes. The faster growth rate of P. lepida may be attributed to the abundance of early-shed autumn leaves, especially of fast degrading species such as Fraxinus sp. (processing coefficient = K=0.10, Petersen and Cummins, 1974), Ostrya sp. and Caroinus sp. (Mackay, 1973) and medium degrading species Carya sp. and Salix sp. (K = 0.005-0.010, Petersen and Cummins, 1974). The initial growth period occurs in early fall and winter with the terminal larval stage being reached by mid-December. P. guttifer usually emerged two weeks later and overlapped the remainder of the flight period of P. lepida (Fig. 10).

Except the first two weeks, the oviposition period of P. lepida and P. guttifer and competition for optimal sites

apparently occurred with egg masses sometimes being exposed in unsuitable spots or in contact with previously deposited masses.

Little obvious change within the matrix occurred during the first several days except in those situations where water came into direct contact with the gelatin. Usually eggs were laid 5 to 25 cm above the water surface, attached either to the mineral substrate, exposed rootlets, or the bark of a log or heavy root. In a few instances eggs were deposited in exposed sites within the splash zone. These egg masses rapidly absorbed water, disassociated and did not develop. The premature disintegration of gelatinous egg masses observed in the limnephilid Frenesia sp. (Flint, 1956) has not been reported for Pycnopsyche species. Heavy waterlogged bark was used as an oviposition site in laboratory chambers (described previously) and was found to be quite acceptable to four species of Pycnopsyche females as well as those of Phryganea sayi and Ptilostomis ocellifera (Trichoptera: Phryganeidae). Hatching occurred in three weeks given optimum conditions. The hygroscopic gelatinous matrix in which the eggs were laid was observed to be an irreversible colloid; once absorption of water began, development within the egg proceeded and the process of water uptake could not be reversed. Premature immersion of egg masses resulted in disintegration and the death of the developing embryos. Newly hatched larvae (Instar I) fed and built cases immediately upon emerging from the

gelatin into the fine particulate debris along the stream edge. Organic detritus, particularly decaying leaf material, was ingested and growth was rapid; moulting to Instar II occurred in eight or nine days. Instar II animals continued to feed actively and grow rapidly, adding leaf fragments to their cases frequently. Moulting to Instar III occurred in 19-22 days. Instars III and IV required about 30-45 days per instar followed by a two-phase terminal instar period. Leaf material and coarse woody detritus was added to the case as growth proceeded. In both Augusta Creek species the later instars added small, thin, laterocaudally-projecting sticks along the sides of the silken tube. Phase one of the terminal instar P. lepida development showed a shift to the compact type of case which measured approximately 5 mm x 20 mm, while P. guttifer retained its bulky organic case which was approximately 7 mm x 22 mm with caudally projecting twigs. P. lepida displayed an intense growth period of about 12 weeks with a mean dry weight increase from 3.8 mg to 72.9 mg. A similar increase in weight in P. guttifer was extended to about 28 weeks into early summer. Phase two was an extended dormancy lasting 24 weeks for P. lepida, which burrowed into the gravel substrate with the posterior end of the case flush with the stream bottom. P. guttifer fastened its case to some stationary submerged object. The inactive dormancy assumed by species of Pycnopsyche is unusual in that they possess the ability to reestablish

their positions once they are physically disturbed.

Prepupal activity in all species involves the closure of the anterior end of the tube with a fine silk mesh. Relocation of the case and attachment of pepples follows in some of the burrowing species. Simple attachment to relatively stationary objects occurs in the non-burrowing species. Pupation of P. lepida and P. guttifer in Augusta Creek lasted three to five weeks. Pupae remained active within the case, undulating the abdomen and causing currents of oxygenated water to flow through the tube. If pupae were removed from their cases they would swim actively and undulate when lying on the substrate. Upon completion of the pupation period, the pupae which have well-developed mandibles (e.g. Wiggins, 1966), cut through the silk mesh closure, swim to the surface and crawl onto a projecting rock, log or the stream bank. The pupal skin splits along a mediodorsal ecdysial line, the adult emerges, the wings expand and harden, and the adult flies or scurries to protective vegetation or under an overhanging bank.

Habitat selection and case building behavior displayed by the Pycnopsyche species in this study was apparently genetically controlled. Feeding preference seemed to be controlled by physical parameters rather than biological ones. Newly hatched larvae entered the margins of the streams in regions of low current velocities having concentrations of fine detritus and microbially-conditioned

autumn leaf litter. Feeding and case building were strongly influenced by the oviposition site of the female. Ethological parallels between this limnephilid trichopteran and many lepidopterans were noticeable throughout the life cycle. The choice of oviposition sites with "preferred" larval food supplies as well as larval silk production are known in most lepidopteran species. The feeding, growth and case construction in the Pycnopsyche complex led to emergence, oviposition and hatching times closely tied to autumn abscission and aquatic degradation and disappearance of leaf litter in the stream system. During late winter and early spring P. guttifer larvae utilize detrital materials in case construction which have densities and particle sizes similar to the surrounding concentrations of detritus. Leaf materials have degraded and fragmented by this time, leaving mostly the more resistant coarse particulates, coated with microbes, as the main food supply. P. guttifer has shifted its feeding activities mainly to rasping the woody detritus and eating isolated leaf material. During this time period, when leaf detritus was sparse and P. guttifer were not yet fastened down, the larvae appeared in great numbers (densities as high as 330-365/m^2) in pockets containing accumulations of coarse wood and twigs. Close inspection of the coarse detritus revealed numerous twigs which had been gnawed by Pycnopsyche larvae. Thus the cases of these terminal instar P. guttifer were constructed

of the same materials that made up the pockets of detritus and contained similarly gnawed twigs. When handfuls of detritus were reintroduced several meters upstream the major portion of the material, including Pycnopsyche larvae, settled in the same pocket within one to three minutes. Microdistribution of this species during the last instar appears to be a function of physical displacement by water currents due to similarity between the density of the case and the detrital component in which the animal lives. This agrees with the findings of Mackay (1972a) and Mackay and Kalff (1973) in which they found larval P. gentilis and P. luculenta in their leaf cases drifting with, and proportional to transported leaf litter.

Additional consideration was given in this study to the distribution of P. lepida where case construction and feeding activity changed along with migration during the final larval growth phase. The movement of P. lepida larvae into the faster current regime dictates their predominant placement in areas such that the case density and size are comparable to the substrate particles. Feeding during this migration includes some leaf material, a minor amount of wood raspings and grazing on periphytic algae (Cummins, 1964); the relative abundance of these materials being dictated by light and current regimes. This shift in diet of the two Pycnopsyche species occurs at the time when the amount and location of allochthonous

detritus is limited and an increase in benthic primary production occurs - primarily in the form of an attached diatom bloom. The partitioning of the stream bottom by these coexisting species at the time of decreased allochthonous detritus and increased periphyton growth appears to be the evolutionary trend to reduce competition. High densities of species with leaf cases sometimes result in larvae feeding on the cases of other larvae. It has been suggested by Mackay (1972) that the shift in case type in some species of Pycnopsyche is to eliminate case "predation" due to depletion of leaf litter in the stream.

The two-species complex of Pycnopsyche in Augusta Creek combines the bulky, relatively camouflaged case in P. guttifer and an unpalatable-camouflaged case, plus burrowing behavior, in P. lepida. Ivlev (1961) demonstrated the protective significance of Trichoptera cases and burrowing in the Chironomidae. In a phryganeid caddis larva, predation by three species of fish, increased from a mean of 4%, to 21.3%, to 74.7% for those with cases, half cases and no cases respectively. The results of this experiment support the selective advantage against predation, of building a bulky, unpalatable larval case. Predation by fishes on chironomid larvae burrowed to different depths into the substrate was observed. Rates of predation dropped from a mean of 59%, to 28%, 10.7%, 2.7%, and 0% at 0 cm, 2 cm, 4 cm, and 10 cm depths respectively. If application of Ivlev's experiments can

be related to Pycnopsyche case type (bulky, unpalatable and camouflaged) and burrowing behavior, one would assume relatively low rates of fish predation on terminal instar larvae.

Adults

The strong active flight of Pycnopsyche is generally restricted to the early evening hours with most flights occurring within a four hour period beginning at one hour past sunset. Mackay (1972a, b) has shown even further partitioning of the daily flight period by males of three species of Pycnopsyche in West Creek (Mont St. Hilaire, Quebec). The mean adult life of this genus is about one month, with males flying more actively than females. Males were attracted in greater numbers to the light trap than females as has been reported for other Trichoptera (Ross, 1944; Mackay, 1972a, b; Crichton, 1960; Gower, 1967). Along Augusta Creek, mating occurs on various substrates although it is believed that most mating occurs on riparian vegetation.

CONCLUSION

Pycnopsyche species in Augusta Creek, were found to partition the physical environment according to current velocity and substrate particle size, as well as by their emergence, flight and oviposition periods, reducing competition between the congeneric species. Feeding and growth rates closely coincided with input, colonization and deterioration of detritus in the stream. Life history data including the emergence, flight period and oviposition potentials, can adequately describe the population characteristics of these limnephilids in the study stream system. The processing capability of these species, along with that of the other aquatic large particle detritivores, supports the predictions of other investigators.

Investigations utilizing aquatic invertebrates as study organisms require considerable knowledge of their biology. Often, insufficient fundamental life history, taxonomy and ecology data are the cause of incomplete conclusions concerning broader questions at the population or system level. The data reported herein should add substantially to the growing knowledge of the ecological relations in stream communities. Energy flow and nutrient cycling make a clearer picture when processing potentials,

population densities and behavioral characteristics can be overlaid. The relationship between these biological characteristics and the physical parameters clarifies one significant aspect of stream organic particle processing. The balance between biology and environment has been indicated in this study with regard to the possible triggering mechanisms of emergence and oviposition. The same mechanisms can also regulate the success or failure of these phenomena through premature inundation of eggs or larvae. Microhabitat selection and shifts in food habits also indicate a distinct relationship to physical parameters such as current regimes. There is a physical placement of P. guttifer larvae according to case construction materials within areas having abundant sources of food substances having densities (specific gravities) similar to those of the cases. It is difficult to separate what leads to preferences for food and case materials, internally initiated movement or the physical proximity of these items. Given preferences within the physical microhabitat, the larvae will choose microbially conditioned substrate over non-colonized food materials. However, the colonization itself tends to be affected by the same physical parameters regulating the placement of the food and trichopteran consumer. Given the coupling of the physical factors affecting both Pycnopsyche species in the stream community - the rapid growth of early instars, the storage of food reserves and

extended diapause, the behavioral qualities of the larvae, papae and adults, and the organic particle processing of these insects - the evolutionary relationships of Pycnopsyche spp. within the Eastern Deciduous Biome is striking.

Table 1 Watershed Forest Type- Augusta Creek, Michigan. Black Ash- American Elm- Red Maple Association modified to comply with dominant vegetation in the study site.

1. Most trees of this species have died from Dutch Elm Disease.
2. In some of the first order (headwater) streams these species may be dominant species.

Dominant Tree species	
Black Ash	(*Fraxinus nigra*) Marsh.
American Elm[1]	(*Ulmus americana*) L.
Red Maple	(*Acer rubrum*) L.
Associate Tree Species	
American Hornbeam	(*Caroinus caroliniana*) Walt.
Basswood	(*Tilia americana*) L.
Bur Oak	(*Quercus macrocarpa*) Michx.
White Oak	(*Quercus alba*) L.
Red Oak	(*Quercus rubra*) L.
Yellow Birch	(*Betula lutea*) Michx.
Silver Maple	(*Acer saccharinum*) L.
Tamarack[2]	(*Larix laricina*)(Du Roi)K.Koch
Green Ash	(*Fraxinus pennsylvanica* var. *lanceolata*)(Vahl) Fern.
Shrubs	
Silky Dogwood	(*Cornus amomum*) Mill.
Red Osier Dogwood	(*Cornus stolonifera*) Michx.
Swamp Rose (Marsh)	(*Rosa oalustris*) L.
Buckthorn	(*Rhamnus cathartica*) L.
Nannyberry	(*Viburnum lentago*) L.
High Bush Cranberry	(*Viburnum trilobum*) Marsh.
Willow	(*Salix c. lucida*) Muhl.
Whorled loosestrife	(*Decodon verticillatus*)(L.)Ell.
Thicket Serviceberry	(*Amelanchier canadensis*)(L.) Medic.
Spicebush	(*Lindera benzoin*)(L.) Blume.
Ninebark	(*Physocarous opulifolius*) (L.) Maxim.

Table 2 Replication, densities and combinations of animals used in growth experiments.

# of chambers	Total # individuals/ chamber	Duration of experiment	Number of individuals / chamber				
			P.lepida	P.guttifer	P.scabripennis	Stenonema	Tipula
3	20	95	10	0	0	0	0
2	40	75	0	30	0	0	10
3	30	86	10	0	0	10	10
3^1	30	61	10	0	0	10	10

Table 3 Leaf pack transects. Distribution and density of *Pycnopsyche* spp. populations on leaf packs. Transects (T_3, T_2, T_1) made up of 25 bricks containing oak (Q) or hickory (C) leaf packs. Kelfor site December 7, 1971.

#/species	# & %/sp/Q	# & %/sp/C	%/sp in predicted microhabitat	Microhabitat
63 *P.lepida*	50(79%)	13(21%)	89%	channel
23 *P.guttifer*	18(78%)	5(22%)	31%	margin

Table 4 Quantitative sample. Distribution and density of Pycnopsyche spp. populations. Three full stream width transects (T_3, T_2, T_1) made up of 25 cm cores, Kelfor site December 14, 1971.

#/instar species	Total sample area	#/m^2/sp.	%/sp. in predicted microhabitat	Microhabitat
31 P.lepida V	4.47m^2	6.94/m^2	(N-19) 61.3%	channel
14 P.guttifer IV		3.13/m^2	(N-14) 100%	margin

Table 5 Quantitative sample. Distribution and density of *Pycnopsyche* spp. populations. Three full stream width transects (T_3, T_2, T_1) made up of 25 cm sample cores. Kelfor site July 28, 1971.

#/species	Total sample area	#/m^2/sp.	%/sp. in predicted Microhabitat	Microhabitat
47 *P.lepida*	4.7627m^2	9.868/m^2	(N-42) 89%	channel
39 *P.guttifer*		8.189/m^2	(N-30) 77%	margins

Table 6 Results of *P. lepida* laboratory feeding and growth experiments.

Species	Larval Instar	Survivors $\bar{x}$ #/chamber ± SD	Relative growth (mg/mg/day) ± SD	Consumption Index (mg/mg/day) ± SD	Efficiency of Consumption (Relative growth) consumption Index	Total % growth change ± SD	% Growth/day	Total growth mg ± SD
P.lepida	I-II	8.33 ± 1.53	0.0698 ±0.014	2.016 ± 0.399	0.0367 ±0.016	27.0	3.9	0.057
P.lepida	I-II	10.0 ± 0.0	0.0569 ±0.014	-4.484 ± 2.33	-0.0161 ±0.0101	31.5	4.5	0.1083
P.lepida	II	9.0 ± 1.0	0.0354 ±0.015	-1.362 ± 1.382	-0.0391 ±0.025	11.1	1.6	0.05900
P.lepida	V		-0.0137 ±0.012			-9.382 ±6.41	-1.34 ± 0.91	-2.996 ± 2.04
P.lepida	V*		0.04456			36.95	5.3	7.896

*Larvae collected over 7 day period in two sampling methods in Augusta Creek.

Table 7 Results of *P. guttifer* laboratory and field feeding and growth experiments.

Species	Larval Instar	Survivors $\bar{x}$ #/chamber±SD	Relative growth (mg/mg/day)±SD	Consumption Index (mg/mg/day) ± SD	Efficiency of Consumption (Relative growth) consumption Index	Total % growth change ± SD	% Growth/day	Total growth mg ± SD
P. guttifer	II-III	7.33± 1.53	0.0095± 0.054	3.93± 0.880	0.00462 ±0.0026	-25.82	-3.7	-0.26
P. guttifer	III	6.0± 3.0	-0.018± 0.038	1.777± 0.664	-0.0144± 0.026			
P. guttifer	III	5.33± 0.58	0.0080± 0.0053	-0.447± 1.26	-0.0286± 0.057			
P. guttifer	III		0.0110					
P. guttifer (^{14}C)	III		0.337	2.256	0.1494			
P. guttifer	IV		0.0364± 0.024					
P. guttifer	IV		0.0484Δ					
P. guttifer	V		0.0266± 0.40	2.253± 0.90	0.0132± 0.022			

Table 7 (continued)

P. guttifer	V		0.0517± 0.039					
P. guttifer	V		0.0809± 0.061			-21.73± 12.35	-3.107± 1.77	-5.527± 2.81

* calculated from $\bar{x}$ 5 animals at 24 hrs. ($\bar{x}$CI at 60 hrs. = 4.103)
means (N=16 & N=11) Leaf Transect and Quantitative Sample respectively
mean (N=3) Greenhouse Chamber Experiment (3 chambers)

Table 8 Results of *P. scabripennis* laboratory feeding and growth experiments.

Species	Larval Instar	Survivors $\bar{x}$ #/chamber±SD	Relative growth (mg/mg/day)±SD	Consumption Index (mg/mg/day) ± SD	Efficiency of Consumption (Relative growth) consumption Index	Total % growth change ± SD	% Growth/day	Total growth mg ± SD
P.scabripennis	II-III	8.33± 1.53	0.0117± 026	2.2459± 0.555	0.0071± 0.012			
P.scabripennis	V	5.122± 0.476	0.0180	.00351	5.12821			
*P.scabripennis**	V		-0.0078± 0.005			-5.233± 3.55	-0.75± 0.51	-1.607± 1.00

* Greenhouse Chamber Experiment $\bar{x}$ (3 chambers)

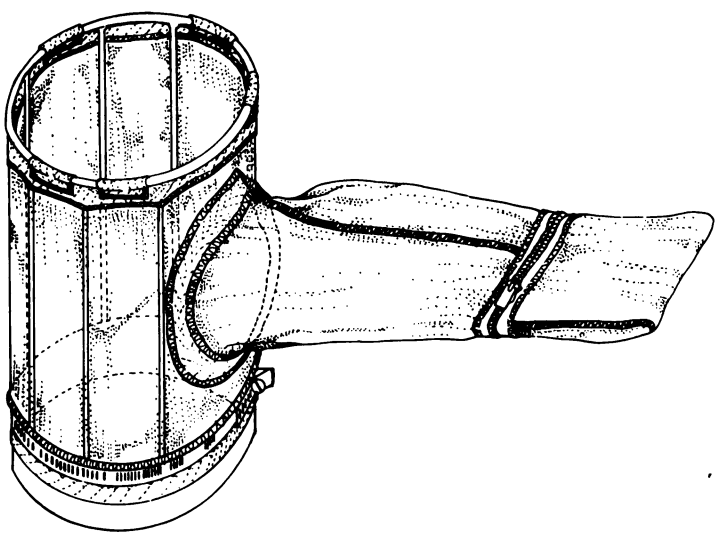


Fig. 1 Modified (Hess, 1941; Waters and Knapp, 1961) benthic sampler. (0.049m^2 sample area).

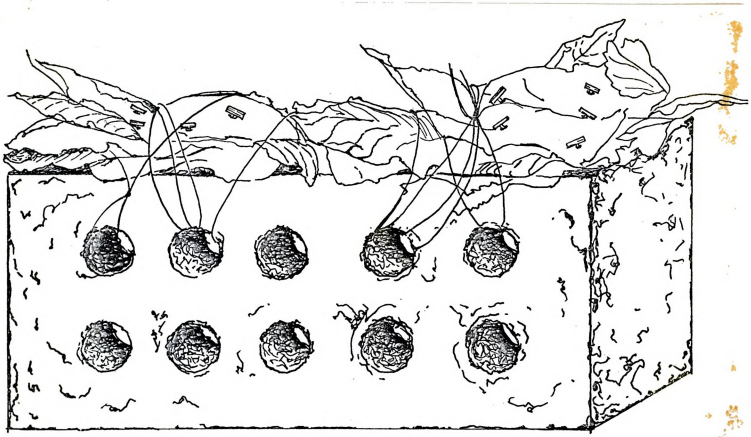


Fig. 2 Laboratory-prepared leaf pack showing two packs fastened with buttoneers and lashed to a standard construction brick with monofilament.

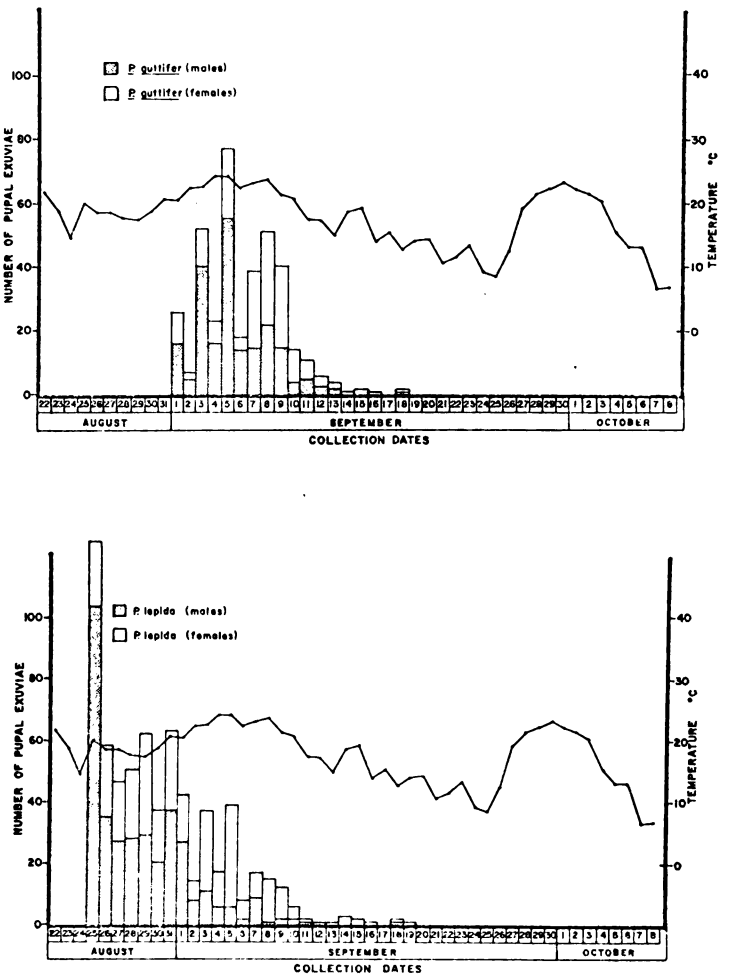


Fig. 3 Emergence period for P. lepida and P. guttifer on Augusta Creek (1971).

Note: Rainfall on 9/2= 0.71 cm (0.28 in.); 9/4 = 0.23 cm (0.09 in.); 9/6= 4.67 cm (1.84 in.).

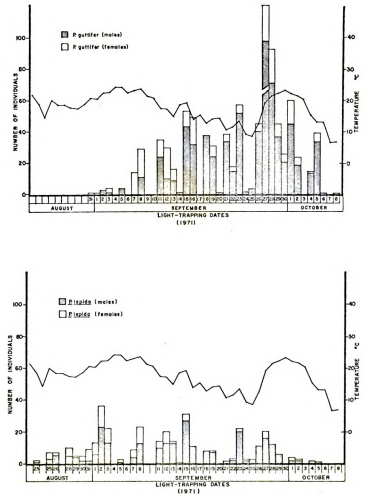


Fig. 4 Flight period results from 1971 for P. guttifer and P. lepida at Kelfor site, Augusta Creek.

Measured from experimental site	Eggs	$\bar{x}$ #♀♀	% hatching /egg mass	Max. #eggmasses/ m. stream bank	$\bar{x}$ #eggmasses/ m. stream bank	total lngth. (m.) str. bnk.	str. area (m^2)	egg mortality
		A	B	C	D	E	F	G

$\bar{x}$ recruitment potential = $Z = \frac{(D)\ (E)\ (A)\ (B)}{(F)} = 164.6/m^2$

$\bar{x}$ number at site corrected for mortality = $Y = (Z) - ((G)\ (Z)) = 24.69/m^2$

2/3 ♀♀ emerged prior to storm and produced $164.6/m^2$
∴ 1/3 ♀♀ could produce ..... $82.3/m^2$
Estimated 30% increase of stream bank due to island within Kelfor experimental site

$\bar{x}$ corrected recruitment potential = (0) + (92.3) = $107/m^2$ + 30% = $139.1/m^2$

Using maximum figures for the egg mass density per meter length of stream bank the calculations are as follows:

$$Z = \frac{(C)\ (E)\ (A)\ (B)}{(F)} = 1128.5/m^2$$

$$Y = (1128.5) - ((0.85)\ (1128.5)) = 169.3/m^2$$

2/3 ♀♀ emerged prior to storm produced $1128.5/m^2$
1/3 ♀♀ could produce $564.3/m^2$
∴ $169.3/m^2$ + $564.3/m^2$ = $733.6/m^2$ + 30% increase = $953.7/m^2$

Fig. 5 Calculation of mean and maximum recruitment potential for Pycnopsyche lepida within Kelfor experimental site, Augusta Creek.

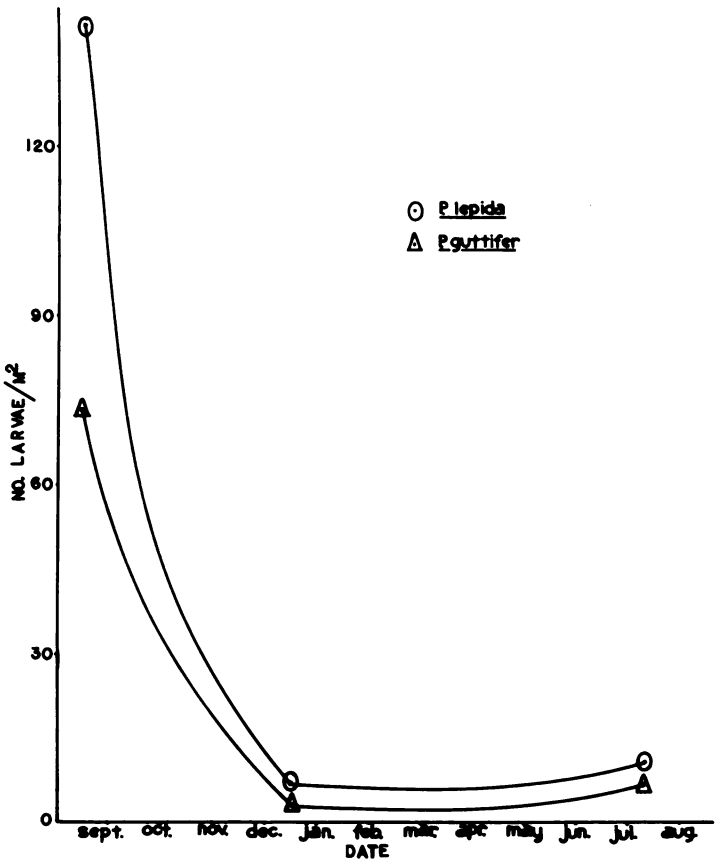
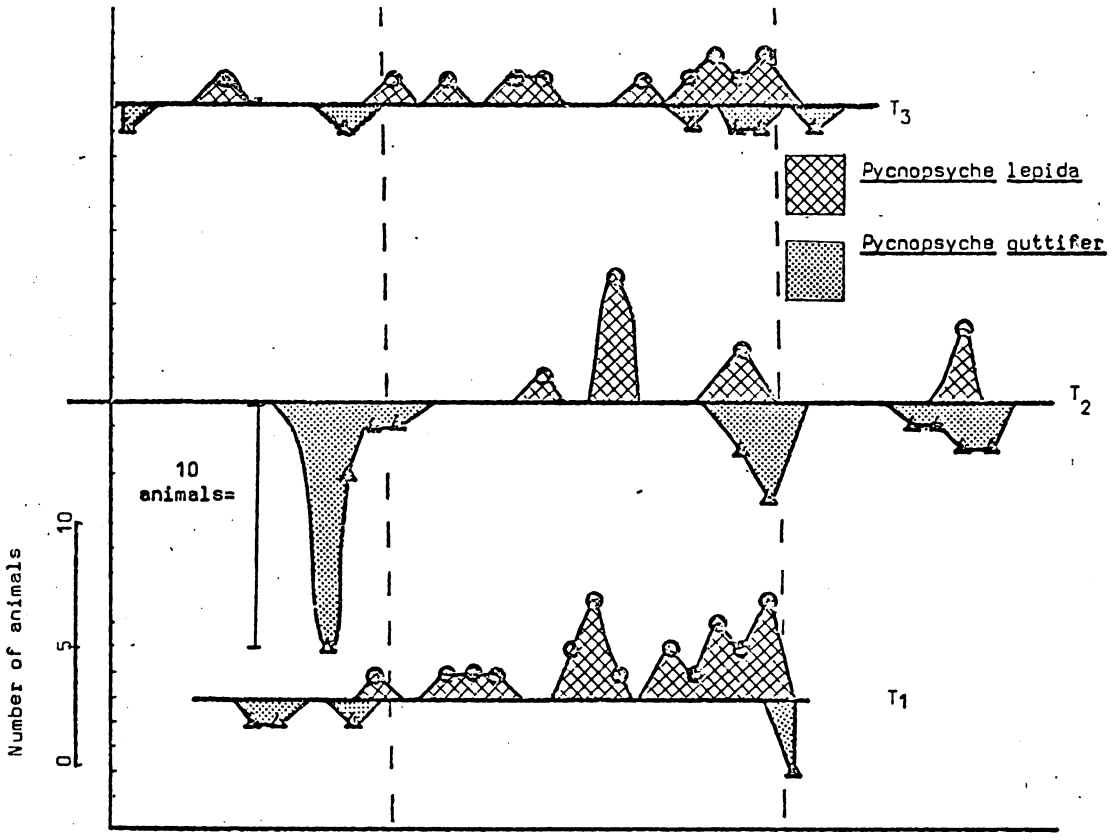
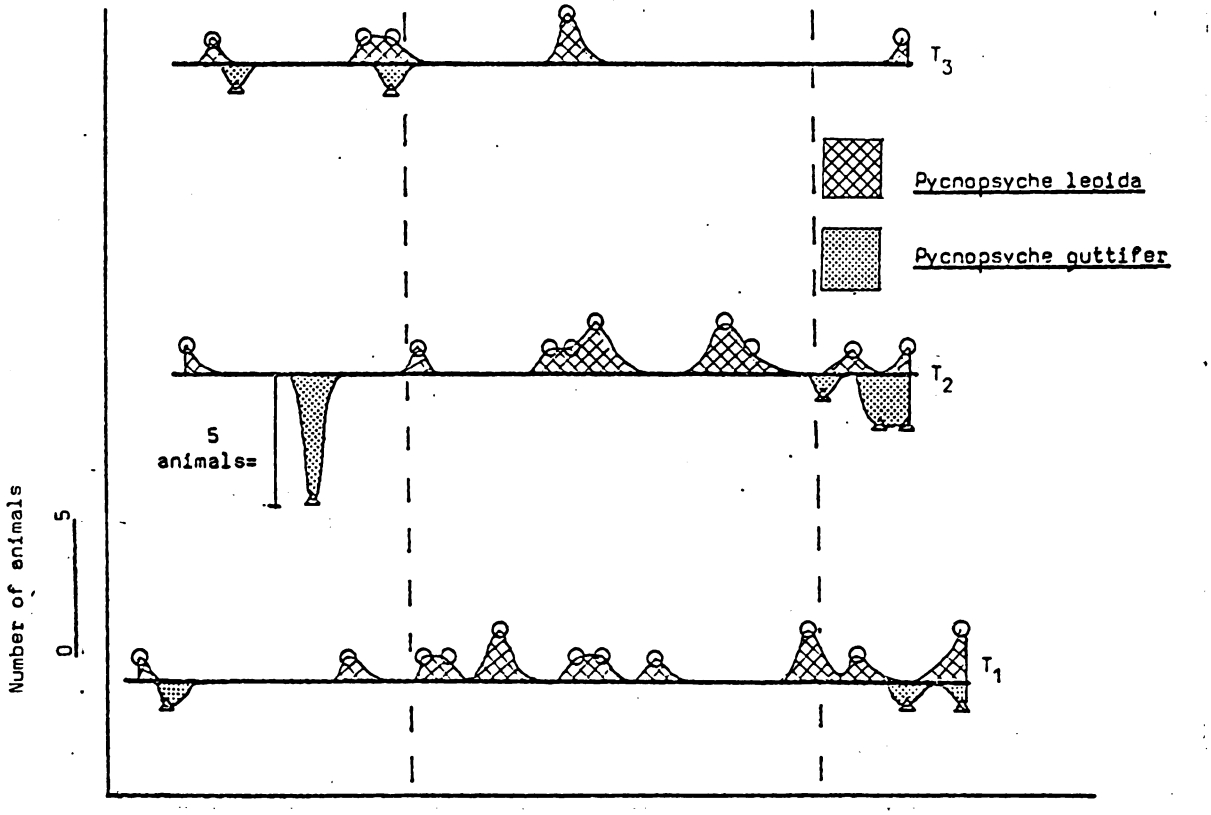


Fig. 6 Estimated population densities of Pycnopsyche spp. larvae in Augusta Creek, 1970-71, based on recruitment (Fig. 7) and quantitative samples (Tables 3 & 4).



5lcm/sec. Current velocity zones 5lcm/sec.

Fig. 7 Quantitative sample. Distribution and density of Pycnopsyche spp. populations. Three full stream width transects (T_3, T_2, T_1) made up of 25 cm diameter sample cores. Kelfor site July 28, 29, 1971.



51cm/sec. Current velocity zones 51cm/sec.

Fig. 8 Quantitative sample. Distribution and density of Pycnopsyche spp. Three full stream width transects (T_3, T_2, T_1) made up of 25 cm diameter sample cores. Kelfor site December 14, 1971.

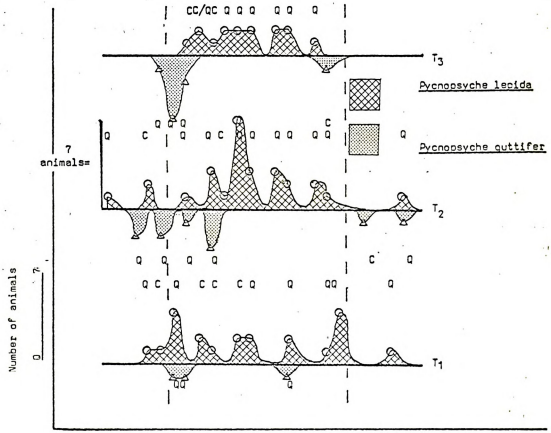


Fig. 9 Leaf pack transects. Distribution and density of Pycnopsyche spp. population on leaf packs. Transects (T_3, T_2, T_1) made up of 25 bricks containing oak (Q) or hickory (C) leaf packs. Kelfor site December 7, 1971.

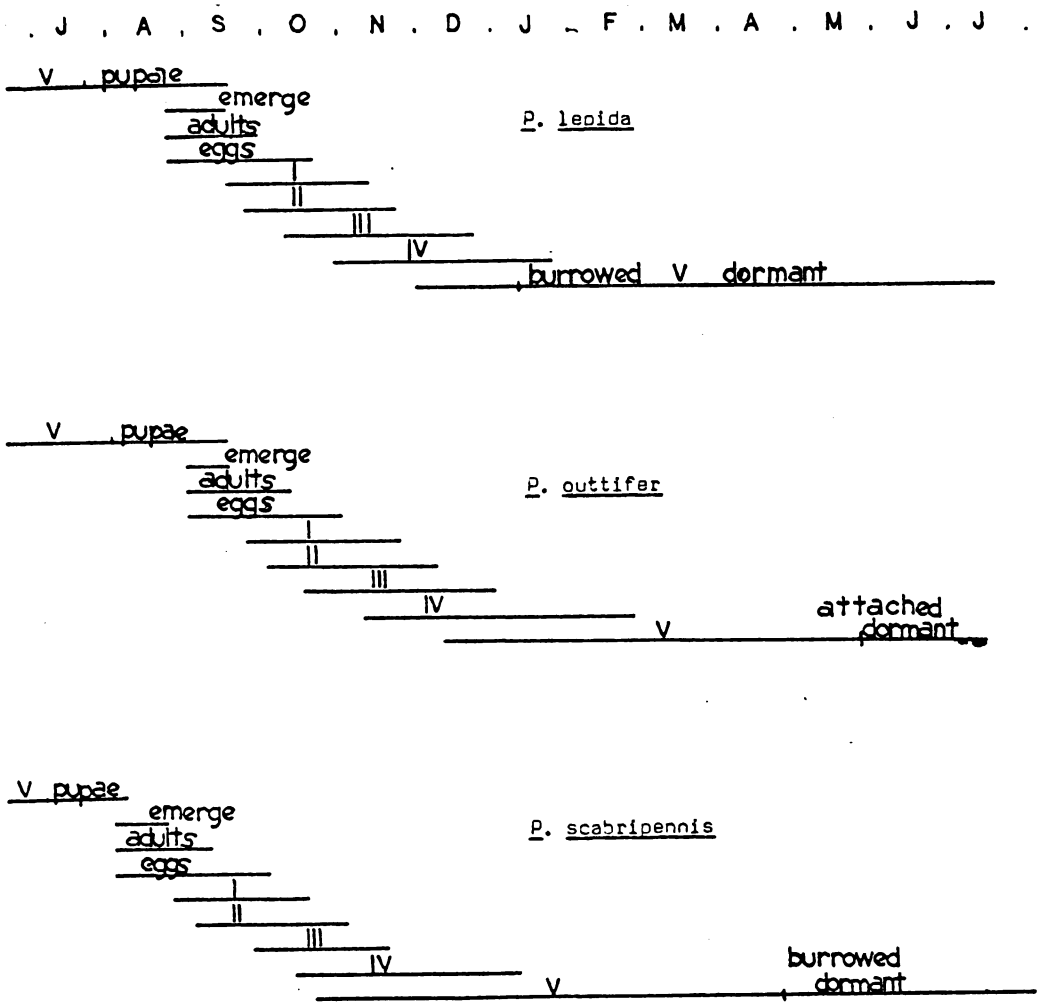


Fig. 10 Life cycles of three species of Pycnopsyche in Augusta Creek (larval instars I-V).

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APPENDIX

APPENDIX

ENERGY BUDGETS FOR *PYCNOPSYCHE*

INTRODUCTION

Energetics studies dealing with streams (Hynes, 1961; Macan, 1963; Minckley, 1963; Egglishaw, 1964; Minshall, 1964; King and Ball, 1967; Ulfstrand, 1968; Tilly, 1968; Coffman *et al.* 1971), as well as the classical studies of Percival and Whitehead (1929) and Allen (1951), have led toward energy budget development and trophic modelling of stream ecosystems (Cummins, 1969, 1972, 1973).

In an attempt to establish the importance of *Pycnopsyche spp.* in the degradation of allochthonous detritus in the Augusta Creek system, an energy budget was constructed. With modification, the budget should allow an investigator to predict the impact of the genus *Pycnopsyche* in a similar stream elsewhere in the deciduous biome.

METHODS

^{14}Carbon Feeding Experiments

Recently, emphasis in aquatic studies have been placed on preferential feeding of detritivores keyed to microbial colonization (Triska, 1970; Mackay, 1972a; Mackay and Kalff, 1973; Barlocher and Kendrick, 1973a, b; Hynes, et al., 1974). Preliminary results showed that P. guttifer larvae feed significantly more on Hickory (Carya glabra) leaf tissue colonized by Hyphomycete fungi than on sterile and/or bacterially colonized leaf tissue (Suberkropp and Howard, unpubl. data).

Numerous feeding studies have been conducted to evaluate assimilation rates of aquatic invertebrates. The techniques and results are variable. Members of the Kellogg Biological Station Stream Group have used radionuclide experiments to assess various members of the macroinvertebrate food web within the stream ecosystem. Studies have been completed using grazers, predators, collectors and shredders feeding on ^{14}C labelled natural and laboratory-prepared food substrates.

Interest in microbial affects on invertebrate diets and leaf degradation, utilizing the microbial component in leaf detritus as a vehicle for isotopically labelling a nutrient substrate, led to an experiment to assess gut loading, consumption index (CI; Waldbauer, 1968) and tissue loading of Instar III P. guttifer. In past studies many organisms have been chosen as experimental

animals with insufficient information on basic ecology. Variables such as temperature, current and photoperiod, along with manipulation of the animals and individual differences within populations have created unaccountable variance in such data. The present study design attempted to minimize the affects of most of the above variables. P. guttifer larvae actively feed and grow on leaf detritus in streams and their residence within leaf litter has been investigated and microhabitat studies have been conducted on P. lepida (Cummins, 1964) as well as P. gentilis, P. luculenta and P. scabripennis (Mackay, 1972a, b). Percent degradation of leaf substrates has been measured (Petersen and Cummins, 1974; Cummins, et al., 1973) along with growth of several stream insects, edibility of leaf tissue being assumed to be primarily a function of texture and microbial colonization. Since P. guttifer larvae tend to occur in slow water areas where their detrital food accumulates, they lend themselves to experimental feeding methods using chambers with reduced currents or agitation by aeration. Observations of larvae during different times of the day and night indicated no specific diel feeding or activity rhythm. The individual variability present in all stream-collected animals due to genetic differences within the population is the factor which has been hardest to define (Elliott, 1968). Field-collections always contain larvae of different ages and lineages. Field-collections of newly hatched larvae or laboratory-produced larvae from the same

cohort would greatly reduce this variability. Therefore, third instar P. guttifer larvae laboratory-reared from egg masses were chosen for this study (Fig.A-1).

Silver maple (Acer saccharinum) leaves colonized by natural microflora were collected from Augusta Creek, washed and cut into 9 mm diameter discs with a No. 6 cork borer (Fig. A-1). The discs were labelled through the microflora by placing them in a plexiglass (30.5 cm diam.) cylindrical chamber with one liter of water which was circulated and aerated and containing 0.4 Microcuries/ml of glucose ^{14}C. Water and leaf discs were sampled every four hours for 24 hours to monitor the uptake of ^{14}C by the microbes. At that point the leaves were washed in distilled water and returned to a cleaned chamber with a new aeration device and covered with fresh filtered stream water. Both the leaf tagging and the feeding experiment were conducted with the chamber in a laboratory stream held at 12°C, corresponding to normal stream temperature, and positioned near a window to approximate normal photoperiod. AKOH trap was included in the chamber to capture $^{14}CO_2$. Ninety-five P. guttifer Instar III larvae from one egg mass were placed in the chamber with the labelled leaves. Five larvae, three leaf discs and one ml sample of water were removed at time zero (0700 hrs.). Similar samples were taken at 4, 6, 8, 10, 12, 16, 24, 36 and 48 hours with additional animal samples being taken at 1, 2, 3, 5 and 60 hours. Some animals were retained in teflon tubes

covered at each end by 1 mm mesh fiberglass screen as adsorption controls. These animals were sampled as three replicates at 4, 6, 12, 24 and 60 hours respectively. Animals and leaf discs were freeze-killed on dry ice and placed in a drying oven at 51°C for 24-48 hours, dry-weighed, pelletized and combusted in a Packard tricarb combustion unit. Using Toluene-TLA (Beckman Co.) coctail, $^{14}CO_2$ was trapped and radioactivity was determined using an ambient temperature Beckman LS 150 liquid scintillation counter with RCA bialkali photomultipliers. Water samples were acidified with H_3PO_4 to drive off $^{14}CO_2$, combined with Triton X (Packard Inst.) and TLA and counted directly in the Beckman Scintillation counter. Correction for ^{14}C adsorption on the animals was made by subtracting the radioactivity of the control animals. Control animal activity was low and relatively constant resulting in little affect on the experimental animal counts. Values for microbial-leaf tissue ingestion were determined by counting the activity of the fed animals and relating the counts per minute (CPM) to those of the labelled leaves. The relationship of the food ingested by the larvae was determined as:

$$\frac{\text{CPM } ^{14}\text{C per larva}}{\text{CPM } ^{14}\text{C per mg substrate}} = \text{mg substrate per mg larva}$$

Respiration

Measurement of respiration has been utilized extensively

by ecologists to evaluate the energetics of populations and communities (Odum, 1957b; Teal, 1957; Till, 1968; Johnson and Brinkhurst, 1971; Petersen, 1974). Effects of temperature, size (age) of the individual, acclimatization, current velocities and substrate particle size have been reported by Rao and Bullock (1954), Keister and Buck (1964), Ericksen (1966), Feldmeth (1970a, b) and Stockner (1971). Sophisticated mathematical manipulations have been applied to laboratory respiration measurements yielding an applicable constant K (respiration consumption in mg AFDW/mg AFDW/day at a respiration rate of 1.0 μl O_2/mg AFDW hour; Southwood, 1966; Petersen, 1974), allowing direct translation of respiratory rate to respiratory tissue consumption. Larvae of Pycnopsyche spp. and stream water were collected from Augusta Creek the morning of each respirometric experiment (Fig. A-2). Larvae were sized roughly by eye to maintain uniformity within the vessels and held in a constant temperature cabinet in petri dishes containing filtered stream water. Gilson Differential Respirometers (models GRP 14 and GRP 20) were prepared according to the technique of Gilson (1963). Filter paper was saturated with ten percent KOH and placed in the vessel sidearms to trap evolving CO_2. Previously collected gravel substrate was boiled and placed in the bottoms of the vessels which were filled with Millipore (0.45 μm) filtered stream water. After the vessels were allowed to equillibrate in the water bath, the animals were added to the vessels and allowed

to acclimate for one hour. At the end of the acclimation period the vessels were closed and readings were taken every fifteen minutes for three hours. Each machine contained correction vessels serving as microbial activity and substrate controls. Data collected were calculated and reported as μl O_2/mg/hr (Cummins *et al.*, 1972), (Table A-1).

RESULTS AND DISCUSSION

^{14}Carbon Feeding Experiment

Data generated by the radiotracer feeding experiment with P. guttifer larvae are shown in Figs. A-3, 4, and 5. As indicated, the data conform to the classic pattern for ingestion and assimilation with the first phase (ingestion) steeply rising until gut loading has been attained (ingestion of tracers = egestion of tracer) and the second phase having a lesser slope as the gut contents are being assimilated and respired away. The transfer of the animals to an unlabelled food source after gut loading and some assimilation were complete would have allowed for the direct determination of egestion and respiration but insufficient animals were available to complete the second phase. The volume of labelled substrate ingested by the larvae during the experiment confirmed the estimated gut loading time for early instars to be 12 hours. The observation that their activity did not assume rhythmic oscillations was also demonstrated.

Rspiration

Respiration of dormant Instar V Pycnopsyche was measured during the period when the larvae of both species in the experimental site were fastened down or burrowed. The extended dormancy of these species is seven months for P. lepida and three months for P. guttifer. Reduced metabolism and thus reduced respiration results in a small weight loss over the time period. Respirometric

measurements of animals collected the first week of July from Augusta Creek were made at 15°C and 17°C. P. lepida larvae had a mean dry weight of 38.51 mg and P. guttifer 38.16 mg; both species were nearing pupation. Mean weights of both species had been determined throughout the year in order to obtain growth estimates. Since burrowed P. lepida averaged 41.36 mg in March, this amounted to a 2.8 mg respiratory loss over the four month period. P. guttifer mean dry weight in March was 24.19 mg with less than three months remaining in its growing phase. From larval measurements, both species attain a mean dry weight near 41 mg. Dormany of P. lepida was approximately six to seven months, during four of which, mean water temperature was 0 to 5.0°C. Beginning in April water temperature rose sharply with mean monthly temperatures increasing from 3.5°C to 21.5°C until time of pupation. P. guttifer did not begin dormancy until the mean monthly water temperature reached 18°C and inactivity extended for two months during which metabolism was reduced to maintenance level.

Results of respirometric determinations for Pycnopsyche spp. are given in Table A-1. In July, burrowed P. lepida larvae averaging 38.51 mg dry weight, measured at ambient stream temperatures of 15°C, consumed only 0.220 ± 0.072 µl O_2/mg/hr (mean ± standard deviation). It might be expected that animals undergoing similar periods of inactivity during primarily warmer intervals would utilize larger

volumes of oxygen even at maintenance level (Fig. A-6). P. guttifer on the other hand had a two to three month dormancy during warmer periods ($\bar{x}$ water temperature 18-21°C) and siplayed an increased oxygen consumption at maintenance level of 0.462 µl O_2/mg/hr. During this two to three month period, P. guttifer respired away biomass equivalent to that utilized by P. lepida in six to seven months.

Respiration rates of Instars III, IV and V of P. lepida collected at the same site and time were simultaneously measured at 10°C. Smaller specimens (III, IV) comprised of larvae from later ovipositions were chosen to make comparisons between the three larval stages (Fig. A-5). Higher oxygen consumption was recorded for small, actively growing Instar III and IV larvae than for the larger Instar V. As stated previously, the growth of terminal instar larvae is confined to the period prior to mid-January. Observations made during larval dissections indicated increased deposition of lipid materials in terminal instar larvae and thus the possibility that growth as increased larval protein may occur primarily during the earlier portion of Instar V with lipid deposition probably occupying the later growth phase prior to dormancy. Oxygen consumption in Instar IV P. lepida (3.093 µl $\pm$ 0.563 O_2/mg/hr) indicating a similarity of metabolic rate of life stages given similar environmental conditions. Higher oxygen consumption by Instar III P. lepida supports this as does the rapid growth observed in

early larval P. lepida, P. guttifer and P. scabripennis. Mackay (1972a) reported similar growth data for P. gentilis, P. luculenta as well as P. scabripennis.

Energetics

Independent measurements of ingestion, assimilation, growth (production) and respiration indicated a low efficiency of conversion of detrital biomass to larval biomass within the genus Pycnopsyche. Measurements of the above components at 10°C, utilizing P. guttifer larvae, allowed the development of an energy budget and the prediction of processing capability of an individual or population of this detritivore in Augusta Creek. As indicated by Petersen and Cummins (1974) large quantities of allochthonous detritus enter streams annually. Because of its high cellulose and lignin and relatively low nitrogen content (after leaching), the material is a poor detrital food source until colonized by microorganisms. Reported budgets of this organic input estimate a mean of 3.0g/m^2/day entering wooded headwater streams (Fisher, 1971; Fisher and Likens, 1972; Liston, 1972; Cummins, 1974). The utilization of this allochthonous material, is directly affected by the rate of microbial, particularly fungal, colonization. Hyphomycete fungi rapidly colonize the litter and thus make available the organic molecules required by the animal consumer component of the benthic community. Morphological and physiological characteristics partition the community into various processing factions,

many of which are dependent upon the capabilities of the shredders to "shower" the remaining detritivores (collectors) with finely separated palatable organic substrates. As indicated by Cummins (1974) shredder organisms, Pycnopsyche included, exist as small numbers of species, capable of feeding on coarse particulate organic matter and most have life cycles that are keyed to the abscission of deciduous leaves. The genus Pycnopsyche is one of this small group of large particle detritivores comminuting leaves and woody detritus to fine particles while supporting its own production. P. lepida and P. guttifer coexist during periods of maximum volumes of leaf fall at autumn abscission and process equivalent quantities of the detrital component. Measured and calculated energy budget components are summarized for a generation of P. guttifer in Fig. A-8 (Ingestion = 2.342 mg/mg/da, Assimilation = 0.115 mg/mg/da, Egestion = 2.227 mg/mg/da, Growth = 0.0376 mg/mg/da and Respiration = 0.0770 mg/mg/da). Primarily measurements and calculations for Instar III larvae have been included in the table, but summation of measurements for multiple instars of the three congeneric species provided similar data.

Summation of ingestion measurements of the larval instars throughout the feeding period allowed for the estimation of the impact of Pycnopsyche populations on standing crop biomass of allochthonous detritus. Estimated

daily ingestion for the P. guttifer population in Augusta Creek spread over the period of active feeding and growth equals 41g/m^2/yr. Assuming similar consumption by P. lepida (Cummins, 1975), totalling 82g/m^2/yr for Pycnopsyche species when compared to an estimated annual input of 1095g/m^2/yr of coarse particulate organic matter (CPOM; Cummins, 1975) equals a processing capability of seven percent of the CPOM by these large particle detritivores. Other detritivores such as Tipula spp. and Pteronarcys sp. undoubtedly account for at least an equivalent amount of processing. This would yield a total shredder processing of near the 20% proposed by Petersen and Cummins (1974).

Table A-1 Larval respiration of Pycnopsyche spp. adjusted by removal of all values greater than 2SD. All measurements made in a Gilson differential respirometer (Gilson, 1963).

Species	Larval Instar	Date	Temp °C.	N	$\bar{X}$ O_2 µl/ mg/hr.	S.D.	S.E.	$\frac{S.D.}{\bar{X}} .100$	$\bar{X}$ dry wt. mg.
P. guttifer	V	7/8/71	17°	6	0.462	0.103	0.042	22.4	38.16
P. lepida	V	7/7/71	15°	6	0.220	0.072	0.029	32.7	38.51
P. guttifer	IV	1/6/71	11°	6	3.486	0.563	0.230	16.2	3.02
P. lepida	IV	12/3/70	10°	3	3.093	0.863	0.499	27.9	2.65
P. lepida	V	12/2/70	11°	5	1.143	0.074	0.033	6.5	28.06
P. lepida	V	12/2-3/70	10°	29	0.873	0.418	0.078	47.9	23.64
P. lepida	III	12/2-3/70	10°	3	4.047	1.405	0.811	34.72	1.11
P. lepida	I	9/30 - 10/1/70	10°	8*	29.125	26.74	7.719	91.8	0.170 / 15 = 0.013
P. guttifer	IV	1/5-6/71	1°	11	0.783	0.316	0.095	40.40	2.79

* N = 1 animal/vessel except Instar I N = 15/vessel.

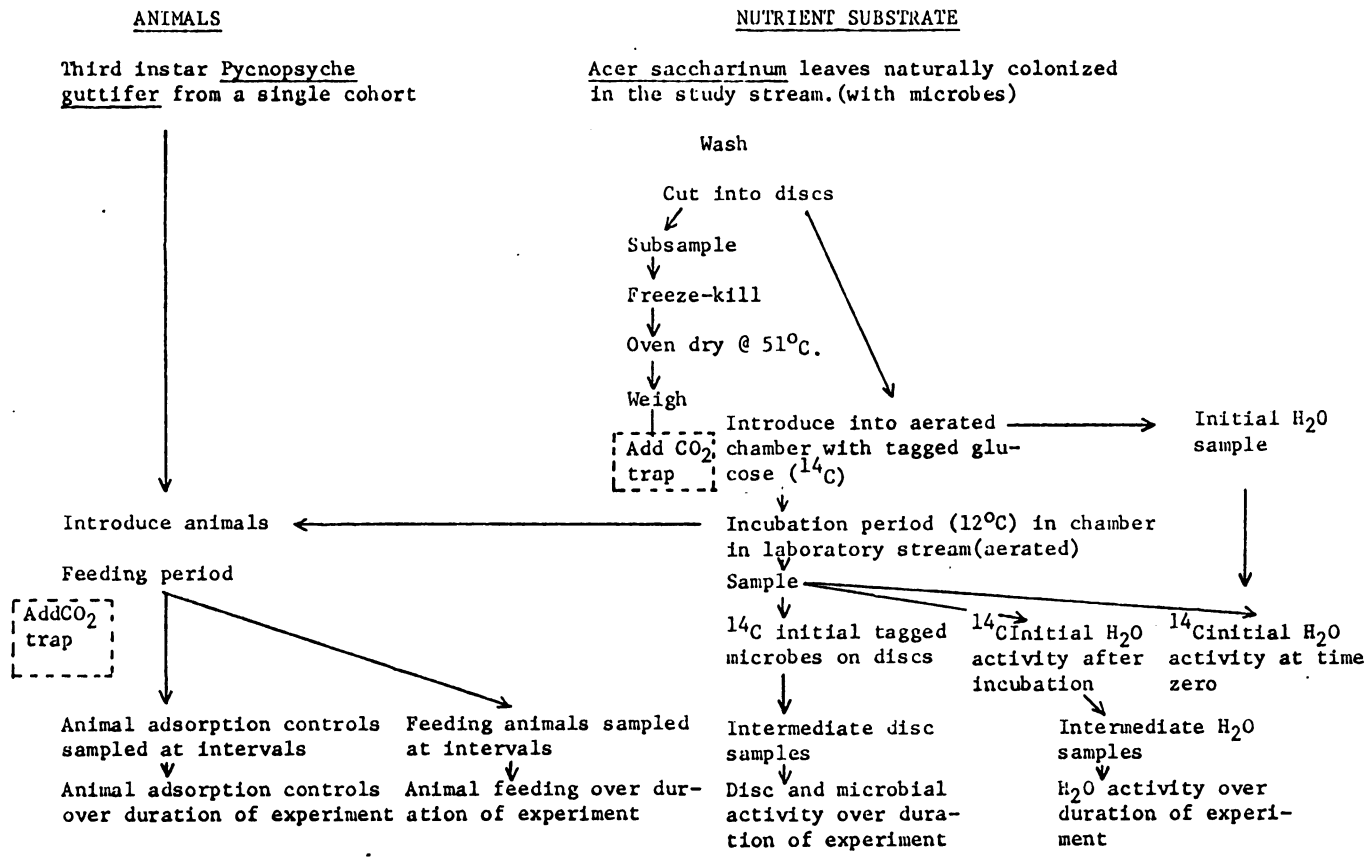

Fig. A-1 Flow diagram of procedure to obtain ingestion rate, gut loading time, tissue loading and CI utilizing ^{14}C glucose-labelled leaf tissue and associated microflora as nutrient substrate, (after Cummins, 1972).

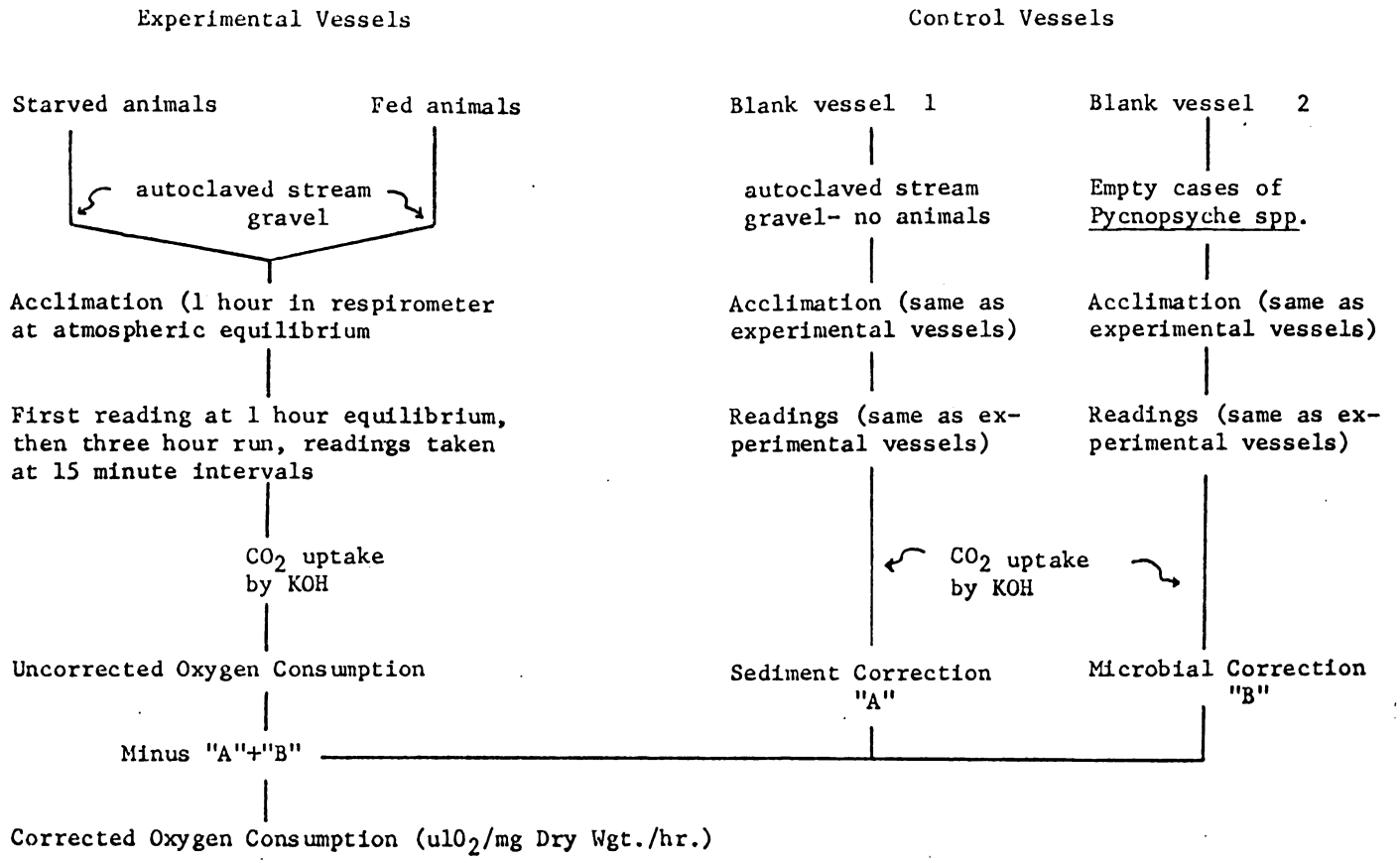

Fig. A-2 Flow diagram of procedure for obtaining respiration measurements for Pycnopsyche spp. (Gilson Differential Respiration). All data calculated by FORTRAN IV program. (TD-D00-2002-17; Cummins, et al., 1972).

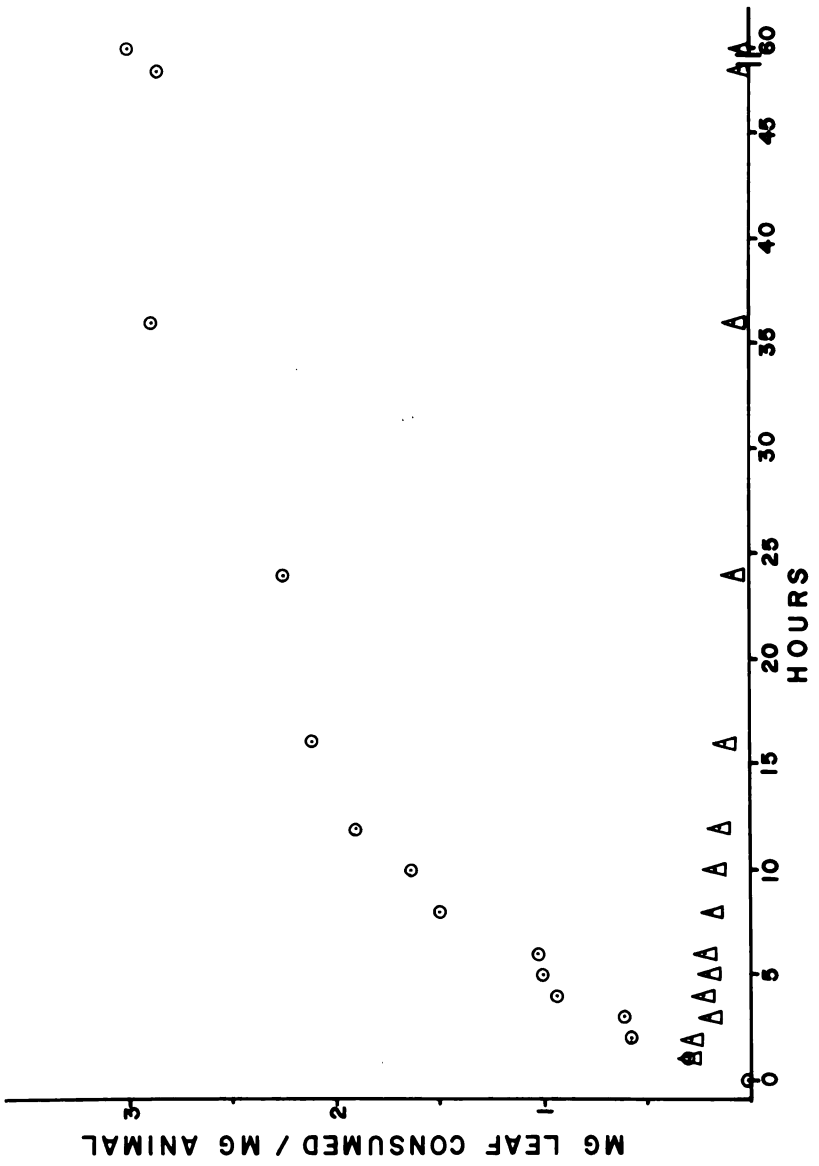

Fig. A-3 ^{14}Carbon uptake by Instar III *P. guttifer* from labelled leaf discs. Mg leaf consumed/mg animal for each sampling time (accumulative) ⊙; adsorption controls Δ.

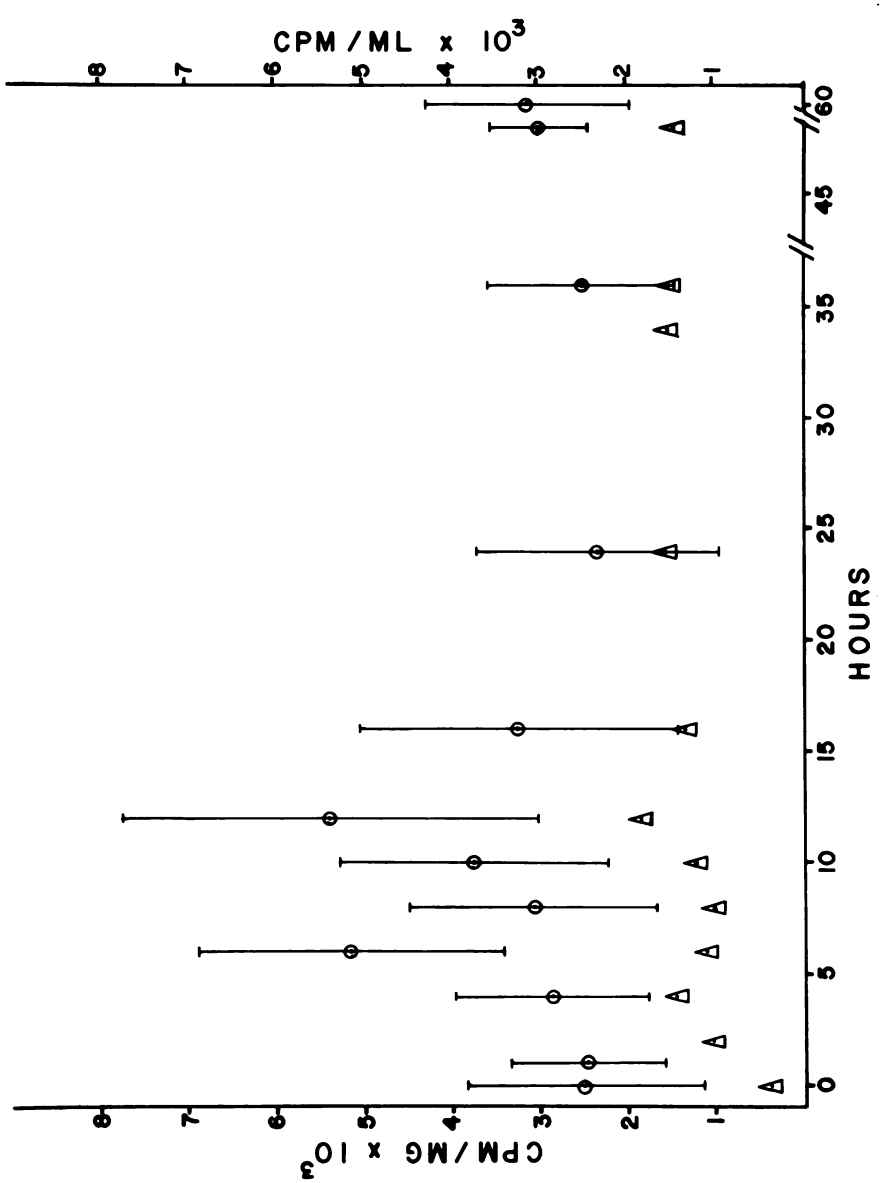

Fig. A-4 ^{14}Carbon uptake in leaf discs used as labelled substrate in Instar III *P. guttifer* feeding experiment. ⊖ Leaf discs ± 2SE; Δ Water (leachate).

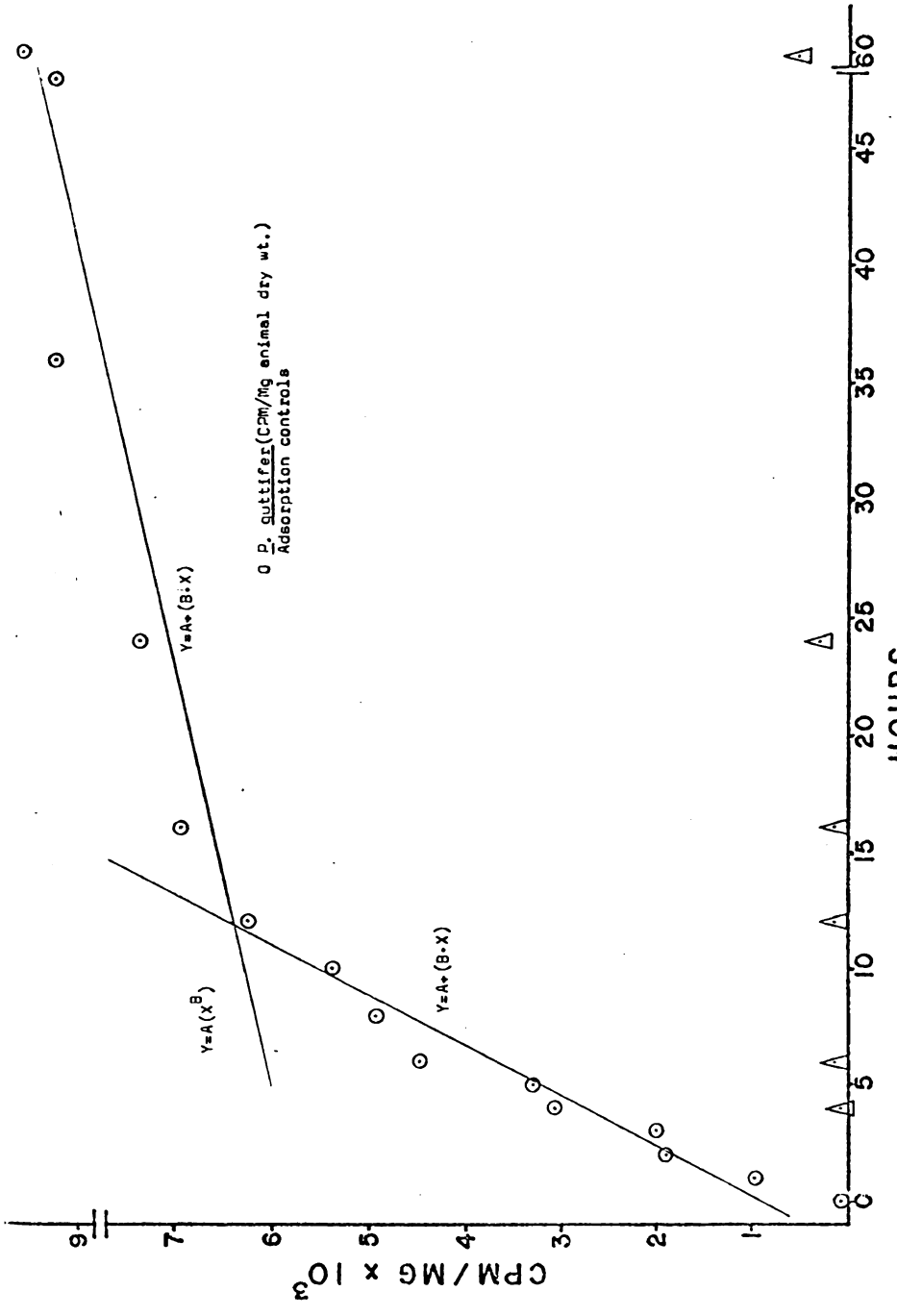

Fig. A-5 ^{14}Carbon uptake in Instar III P. guttifer from labelled leaf discs.

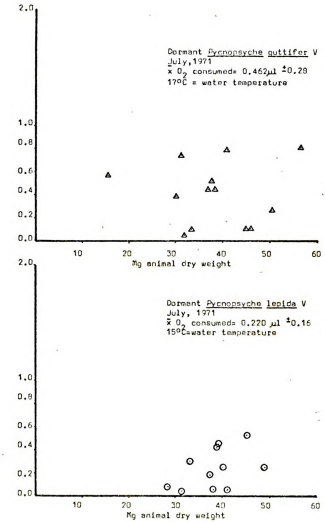

Fig. A-6 Respiration of two species of Pycnopsyche during dormancy.

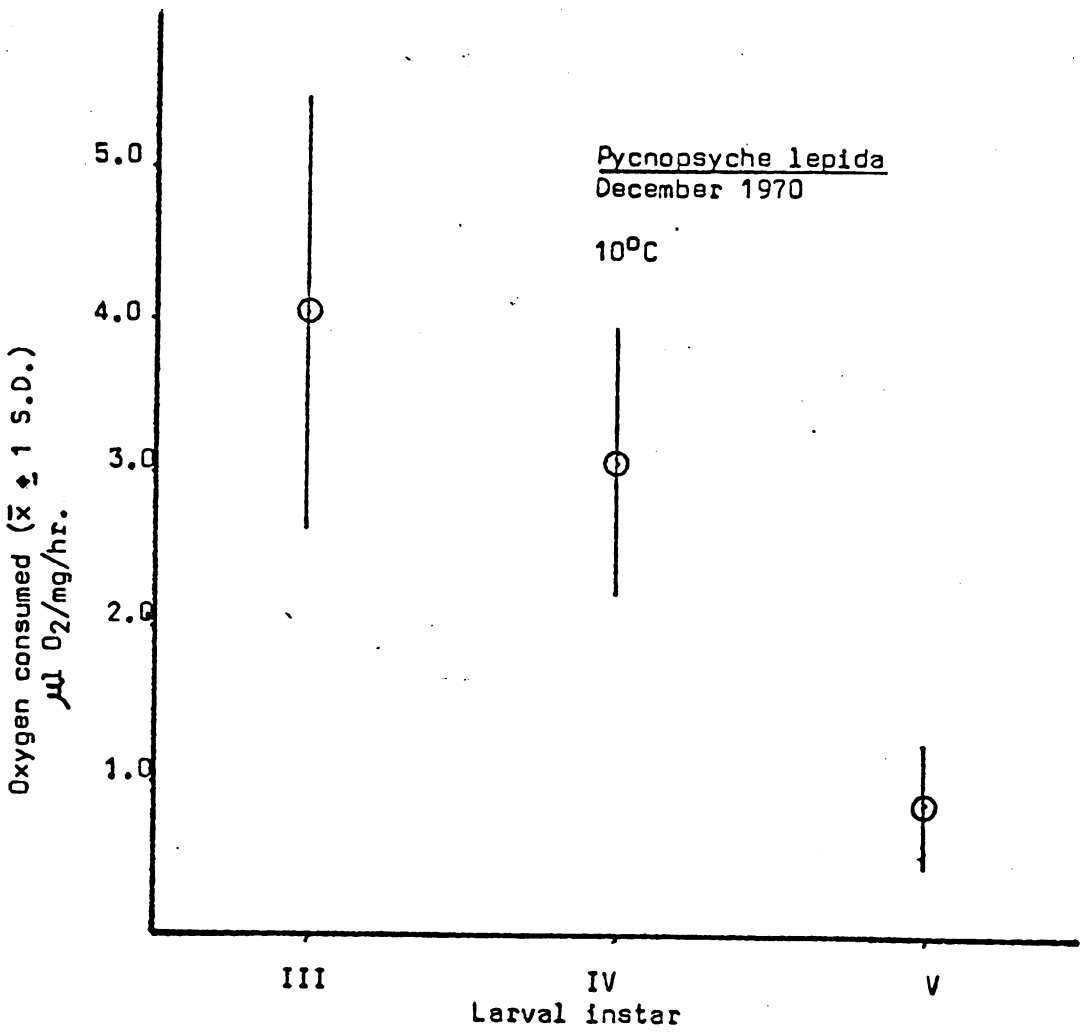

Fig. A-7 Oxygen consumption of Pycnopsyche lepida larvae of 3 overlapping instars at ambient stream temperature.

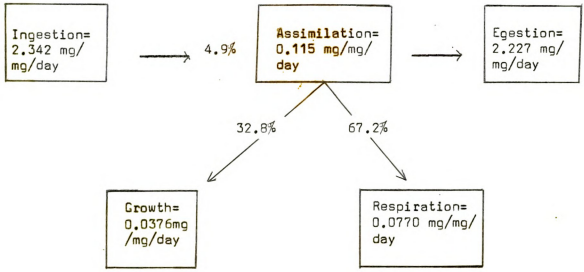

Fig. A-8 Calculated energy budget for P. guttifer in Augusta Creek, Michigan.

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