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Title: BIOENERGETICS AND STRATEGIES OF SOME TRICHOPTERA IN PROCESSING AND UTILIZING ALLOCHTHONOUS MATERIALS

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N.H. Anderson

The purpose of this study was to provide quantitative information on the utilization and processing of leaves and needles by several species of caddisfly larvae.

Field and laboratory studies were conducted on three species of Lepidostoma Rambur (Lepidostomatidae), from Willamette Valley and Cascade Mountain streams, and on Clistoronia magnifica (Banks) (Limnephilidae) from a Cascade lake. These species were selected to represent a wide range of habitats, food sources, and developmental patterns.

Consumption, fecal production, growth, and assimilation efficiency were measured gravimetrically in the laboratory as influenced by food quality (food type and conditioning time), food quantity, larval size, and temperature. Respiration was measured with a Gilson respirometer as influenced by temperature and larval size.

Consumption rates generally increased with temperature and conditioning of the food, and decreased with increased larval size. Mean assimilation efficiencies were 20 to 30% for L. quercina Ross and C. magnifica fed on alder leaves, 10% for L. cascadense (Milne) fed on Douglas fir needles, and 57% for C. magnifica fed on wheat grains. Assimilation efficiency of alder leaves by L. quercina decreased with conditioning of the leaves, perhaps due to the loss of proteins and carbohydrates from the leaves. Assimilation efficiency of alder leaves by L. quercina decreased with higher temperatures, while assimilation efficiency of alder by C. magnifica increased with temperature. This may reflect physiological adaptations to the species' respective temperature regimes. Maximum consumption rates by L. quercina were reached when food (alder) was only slightly in excess, in contrast to consumption rates by L. unicolor (Banks) which did not reach maximum until food (Douglas fir) was greatly in excess. Net growth efficiency of L. unicolor fed on Douglas fir needles (60%) was higher than for L. quercina fed on alder leaves (13%) or C. magnifica fed on alder plus wheat (33%). Increased food selectivity and higher net growth efficiency are apparently adaptations by L. unicolor for utilizing poorly digestible food.

Respiration rates were highest for smaller larvae. Temperature effects on respiration rates were largest for those species found in habitats with little temperature variation (e.g. Q_{10} for L. unicolor was 1.99). C. magnifica larvae, normally experiencing a temperature range

from 4 to 25°C, showed a respiratory Q_{10} of 1.12, indicating almost complete compensation for changes in temperature. The ability to compensate for changes in temperature appeared to be most pronounced in the larval sizes most often exposed to temperature fluctuations (e.g. first- through fourth-instar L. quercina or late-final instar L. unicolor).

In the field, L. cascadense and L. unicolor appeared to minimize competition for food, occurring in different microhabitats and growing most rapidly at different times of the year. Estimated annual production for the three species of Lepidostoma was nearly identical (0.23 to 0.26 $g \cdot m^{-2}$), requiring approximately 3 $g \cdot m^{-2}$ of deciduous leaves for L. quercina and 9 to 10 $g \cdot m^{-2}$ of conifer needles each for L. cascadense and L. unicolor. Production of fine particulate material was thought to be the species' most important impact on the stream system and could support collector production of up to 5 $g \cdot m^{-2}$. Simulation modeling of L. quercina growth, based on laboratory data on feeding and respiration, suggested that food quality may be the limiting factor for growth in the field.

It was concluded that the species studied exhibited a wide variety of adaptive strategies for using allochthonous foods in their respective habitats and that these strategies result in maximum utilization of food when it is most available and usable. Identification and characterization of different strategy-types could be valuable in understanding stream systems and predicting their behavior.

Bioenergetics and Strategies of Some Trichoptera in Processing and Utilizing Allochthonous Materials

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Edward John Grafius

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Redacted for Privacy

Professor of Entomology
in charge of major

Redacted for Privacy

Acting Chairman of Dept. of Entomology

Redacted for Privacy

Dean of Graduate School

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Typed by Mary Jo Stratton for Edward J. Grafius

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BIOENERGETICS AND STRATEGIES OF SOME TRICHOPTERA IN PROCESSING AND UTILIZING ALLOCHTHONOUS MATERIALS

I. INTRODUCTION

Limnology has traditionally emphasized the study of lentic systems and it is only in recent years that a similar effort has been directed towards streams and rivers. In contrast to lakes and ponds, where much of the energy enters the system directly as sunlight, streams tend to receive most of their energy in the form of allochthonous inputs from the surrounding watershed (Nelson and Scott 1962, Hynes 1963, Chapman 1966, Cummins 1974, Hynes 1975).

Two of the most striking ecological features of stream systems are: 1) the ability to process and utilize incoming allochthonous inputs in the fall and winter months when temperatures are often low (Cummins 1974), and 2) the high efficiency of this utilization even in rapidly-flowing systems. For example, in two small streams that have been studied in detail in this respect (Bear Brook, N.H. and WS 10, Ore.) most of the incoming particulate material was processed and respired and less than one-third was exported in particulate form (Fisher and Likens 1973, Sedell et al. 1973, respectively). The present study was designed to examine aspects of the role of aquatic insects in processing and utilizing allochthonous material.

Until recently few studies have been directed toward examining general biological processes such as primary production, predation, or microbial decomposition. Unless we have an understanding of how these basic processes are influenced by other biological and physical factors, we are severely limited in our understanding of aquatic systems in general. Without this understanding we are also severely limited in the development of accurate explanative and predictive models. As suggested by Odum (1971), models based on the study of processes, such as Holling's (1963) experimental components analysis, tend to be more biologically meaningful and to give more accurate responses to manipulation than models based on a more traditional compartmental approach.

A useful method of classifying and ordering stream processes is the concept of functional feeding groups (Cummins 1973). The first step in the utilization of large particulate organic matter is microbial colonization. This "conditioning" results in increased nutritional value of the litter through accumulation of nitrogen and proteins, and breakdown of structural components such as cellulose and lignins. The next step in the sequence is consumption of the conditioned leaves by members of the shredder functional group. These shredders assimilate a small portion of the material for respiration and growth while the remainder is egested as finely-ground feces. This fine particulate

material is suitable for rapid microbial colonization and subsequent consumption by fine-particle feeders (collectors).

In order to use the functional group concept accurately, it is necessary to have detailed information on the life histories, population dynamics, behavior, and bioenergetics for a variety of species from each functional group. The purpose of this study was to examine processing of allochthonous foods by several species of shredders, from a range of habitats with a variety of natural diets and life histories. In addition to providing quantitative information on the processing of different foods by various species as affected by environmental variation, a bioenergetic approach might allow the assessment of some advantages and disadvantages inherent in different adaptive strategies. Strategies of adaptation have been shown to involve life history and behavior (Mackay 1972, Mackay and Kalff 1973). In the present study it was hypothesized that different bioenergetic responses to environmental change also would be apparent.

Environmental factors known to affect metabolic rates of aquatic invertebrates are: temperature (Lawton 1971, Nilsson 1974, Otto 1974, Sweeney and Schnack in press), current velocity (Feldmeth 1970), oxygen concentration (Knight and Gaufin 1963, Nagell 1973), food quality and quantity (Wallace et al. 1970, Grafius 1974, van der Steen et al. 1973, Bärlocher and Kendrick 1975), photoperiod (Chapman 1969), competition (Eisenberg 1970), and size or physiological age (Edwards 1958, Lawton 1971, Otto 1974).

In this study, temperature effects were of particular interest, especially in relation to the efficient processing of allochthonous material at low temperatures.

Food quality is important since most of the food entering the system is not easily decomposed or digested in comparison to fresh plant material or animal tissue (Hargrave 1970). Also, the presence of large quantities of allochthonous food suggests that food quantity is not directly limiting to aquatic invertebrate growth and production, but food quality may be low enough to be a limiting factor. Food preferences, food consumption, and assimilation of different foods were examined. Behavioral aspects of searching for food items were not extensively studied although they may also be important.

Size or physiological age was studied as another possible factor influencing metabolic rates. Differences in metabolic rates due to size may be large (Anderson and Grafius 1975) and may obscure other differences.

Trichoptera were chosen for study since they form a major order of aquatic insects, including the majority of shredder species in many streams. Species are comparatively well-known taxonomically and larvae can often be identified, at least to genus, on the basis of case type.

The species of Trichoptera studied were chosen to represent a wide range of food resources and habitat types. They are:

Lepidostoma quercina Ross (Lepidostomatidae) from Berry Creek, a Willamette Valley stream where deciduous leaves are the primary food source; Lepidostoma unicolor (Banks) from Mack Creek, a Cascade Mountain stream where conifer needles are one of the major energy inputs; Lepidostoma cascadense (Milne) also from Mack Creek; and Clistoronia magnifica (Banks) (Limnephilidae), a species common in lakes in the Cascade Mountains.

All three species of Lepidostoma were known to be major processors of allochthonous inputs in the locations studied and were easily identifiable in these locations on the basis of case type. Although they comprise only a small portion of the invertebrates present in the streams, it was hypothesized that they would contribute significantly to the system by processing large quantities of organic material and producing large amounts of fine particle material.

The objectives of this study were to examine several species of Trichoptera from a variety of habitats in order to:

1. Quantitatively estimate food processing, respiration, and growth for these species.
2. Measure the effects of temperature, food quality, food quantity, and size or age on processing rates, respiration, and growth.
3. Assess the possible adaptive significance of life history, behavior, and particularly bioenergetic responses to environmental change for the insects in their native habitats.

4. Estimate the impact of these species on the system in terms of insect production and quantities of fine particulate organic material produced.

II. SPECIES STUDIED

The order Trichoptera (caddisflies) is one of the largest orders of aquatic insects and includes about 7000 species. Larvae occur in a variety of habitats, from streams and lakes to marine habitats and hot springs, but most species are found in cool lotic environments where the order is thought to have originated (Wiggins in press). Caddisflies generally have a one-year life cycle, with five larval instars. However, some may have several generations per year or a two-year or three-year life cycle and others are known to have six or seven larval instars (Iversen 1973, Anderson 1976b).

The order can be divided into the superfamilies Rhyacophiloidea (generally free-living forms or saddle-case makers), Hydropsychoidea (net spinners) and Limnephiloidea (tube-case makers). Although many caddis are at least somewhat omnivorous (Winterbourn 1971), the larvae of the Rhyacophiloidea tend to be grazers or predators, larvae in the Hydropsychoidea are usually collectors or predators, and members of the Limnephiloidea are most often shredders or grazers. Species of the Limnephiloidea comprise a major portion of the shredder species in most aquatic habitats and all of the species examined in this study belong to this group.

Larvae of the Limnephiloidea construct a case of sand, plant material, or silk secretions soon after hatching and continue to add to this case or modify it during the larval stage. Advantages of having a

case may include protection from predators and parasites, resistance to desiccation, and resistance to drifting (particularly for species with heavy sand cases). Cased larvae also have an increased ability to absorb oxygen from the water, particularly in lentic habitats (Wiggins in press). This may allow them to utilize food sources such as leaves or needles in areas of low current (e.g. ponds or pool and backwater areas of streams). Case structure may be useful as an aid to larval identification, particularly if the number of species within a genus is known to be low in the study area (Wiggins in press).

The family Lepidostomatidae contains only two genera, Lepidostoma Rambur and Theliopsyche Banks. Only Lepidostoma is known from the western U.S. and 18 species have been reported from Oregon (Anderson 1976b). Lepidostoma larvae are found in lakes, ponds, and streams (mainly in backwaters and pools) and feed primarily on detritus (Chapman and Demory 1963, Winterbourn 1971). Larval cases may be of three types (Fig. 1): chimney-type, square in cross-section, made of quadrate pieces of bark or leaf; log-cabin type, round in cross-section, made of small twigs and needles perpendicular to the length of the case; or sand-grain type, smooth and tubular, tapering toward the rear, made of uniformly-sized sand grains. Most species construct sand-grain cases in the first instar and change to the characteristic type by the late-second or early-third instar.

Figure 1. Lepidostoma spp. larvae and case types: L. unicolor, log-cabin; L. cascadense, sand-grain; and L. quercina, chimney case (reprinted from Anderson 1976b).

Figure 2. Larvae of C. magnifica, first to fifth instar, and pupa, illustrating the wide range in size of larvae (reprinted from Anderson 1976b).

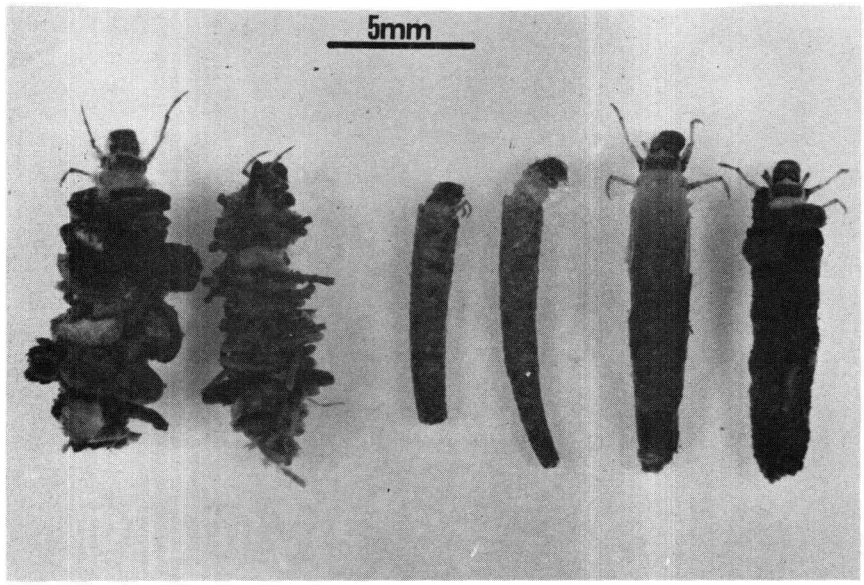


Figure 1.

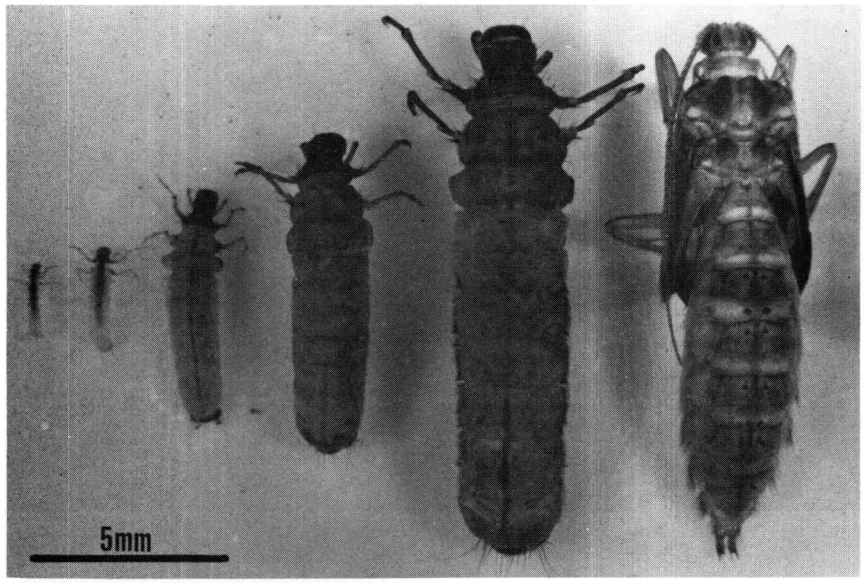


Figure 2.

The family Limnephilidae contains more than 300 species in North America. Members of this family exhibit a wide range of preferred habitats, food sources, life histories, behaviors, and case types. The genus Clistoronia Banks belongs to the subfamily Limnephilinae, the largest and most diverse subfamily, containing more than half of the species in the family. Many of the species in the subfamily (e.g. Pycnopsyche spp., Halesochila taylori (Banks), and Clistoronia magnifica) are known to be shredders (Mackay 1972, Grafius 1974, Anderson 1976a, respectively).

Lepidostoma quercina is a common species in Willamette Valley and Coast Range streams in Oregon and occurs in Oregon, Washington, and Idaho. Early-instar larvae occur in riffle areas in late summer. Larvae construct a chimney-type case as they mature and congregate in pool areas of the stream. By November, most of the larvae are concentrated in the pools and have reached the fifth (=final) instar. The most rapid growth occurs during November and December in the early and middle part of the fifth instar (see Fig. 25, p. 108). Mature larvae weigh an average of 3.5 to 4.0 mg dry weight. Mature larvae and prepupae are often found attached to logs or large sticks near the edges of the stream. Pupation occurs in February and adults are present from March through May.

Lepidostoma unicolor is widely distributed (southern California to British Columbia) and occurs in Willamette Valley, Coast Range,

and Cascade Mountain streams in Oregon. In Mack Creek, eggs were collected from riffle and pool areas in late July and early August. First- and second-instar larvae were collected throughout the winter and early spring and were predominant through March. Early-instar larvae make a typical sand-grain case but begin construction of a log-cabin case by the third instar. As was observed for L. quercina, L. unicolor larvae migrate or are washed into the pool areas of the stream. Winterbourn (1971) found fifth- (=final) instar L. unicolor larvae in all months but September, but in Mack Creek, final-instars were not collected until May (see Fig. 27, p. 116). Mature larvae weigh an average of 4.0 to 5.0 mg dry weight. Pupation occurred in early July and adults emerged from July through early September.

Lepidostoma cascadense is distributed from southern California to the Yukon Territories and is a common species in Cascade streams. Unlike L. unicolor, L. cascadense seems to be primarily restricted to mountainous regions. L. cascadense and L. unicolor are both major processors of conifer needles in Mack Creek (Sedell et al. 1975), but L. cascadense grows and matures more rapidly than L. unicolor. Eggs of L. cascadense are found in July and August and early-instar larvae are most common in late summer and early fall. Larvae retain their sand-grain cases throughout their development. Fifth- (=final) instar larvae, apparently of L. cascadense, were collected on all sampling dates except July 31, and predominated from

March through May when pupation begins (see Fig. 26, p. 113). Mature larvae weigh an average of 1.5 to 2.0 mg; considerably less than either of the other two species. Adults emerge from late July through early September. In addition to the differences in case types, L. cascadense larvae are easily distinguished from L. unicolor on the basis of coloration. Sclerites, legs, and head capsules of L. cascadense are a light yellow, in contrast to those of L. unicolor, which are brown.

Other species of Lepidostoma occurring in Mack Creek are L. hoodi Ross, L. mira Denning, L. roafi (Milne), and L. strophis Ross. These species are all much less abundant than L. unicolor or L. cascadense and form chimney-type cases (Anderson 1976b). L. rayneri Ross has been collected from the MacKenzie River, approximately 35 km downstream from Mack Creek and it forms a sand-grain case, like L. cascadense. Larvae of the two species might be confused, but no specimens of L. rayneri have been identified from extensive larval rearing or emergence collections from Mack Creek and it is probably rare or absent there.

Species of Lepidostoma in addition to L. quercina that may occur in Berry Creek are: L. hoodi, L. roafi, L. strophis (chimney-case makers), L. rayneri, and L. unicolor. However, it is unlikely that any of these would be confused with L. quercina since all are late-spring and summer emergers and only L. roafi and L. unicolor have

been reported from Berry Creek in spite of extensive collections (Anderson 1976b).

Clistoronia magnifica is a common species in lakes in the Cascade Mountains in Oregon, Washington, and British Columbia. Eggs are laid in August and September and larvae grow rapidly during the late summer and early fall, when temperatures may be as high as 25 to 30°C. Larvae reach the fifth (=final) instar in about ten weeks and over-winter in this stage. Pupation occurs in the spring, just after ice-out, when water temperatures begin to rise. Larvae make a tubular case of plant material and change to sand grains during the latter part of the final instar. Mature larvae weigh an average of 30 to 50 mg dry weight, an order of magnitude larger than the Lepidostoma. Even late-third instar larvae weigh more than most of the Lepidostoma (5 mg) and late-fourth instar larvae weigh approximately 10 mg. This wide range of sizes (Fig. 2) allowed detailed examination of the effects of size on metabolic rates. Gut analyses of larvae from Marion Lake, B.C. showed mostly detritus, but also some animal fragments (Winterbourn 1971) and Anderson (1976a) suggests that some animal material may be an important dietary component for these larvae.

III. SITE DESCRIPTIONS

Berry Creek is located in the Willamette Valley, approximately 15 km north of Corvallis, Oregon, at an elevation of 75 m. Width is about 2 m, mean discharge 0.01 $m^3 \cdot sec^{-1}$, gradient 1.7%, and temperatures range from 2 to 15°C. The surrounding vegetation is a mixed deciduous-conifer forest with dominant species of alder (Alnus rubra Bong.), bigleaf maple (Acer macrophyllum Pursh.), and Douglas fir (Pseudotsuga menziesii (Mirb.) Franco).

Berry Creek is a typical heavily-shaded Willamette Valley woodland stream except for semi-controlled flow, a remnant of earlier studies (Warren et al. 1964). This controlled flow significantly reduces the scouring and flushing action of winter freshets and has resulted in the accumulation of fine sediments, particularly in the deeper pool regions. Reduced scouring and flushing may also be responsible for the unusually high populations of L. quercina found in Berry Creek.

The site chosen for quantitative study was a pool 4 m long by 3 m wide and up to 1 m deep, and the riffle immediately downstream (1 to 2 m wide by 15 m long) (Fig. 3).

Mack Creek is located in the H.J. Andrews Experimental Forest in the Cascade Mountains approximately 85 km east of Eugene, Oregon, at an elevation of 775 m. Width is about 6 m, mean discharge 0.60 $m^3 \cdot sec^{-1}$, and gradient 20%. Temperatures range from 2 to 12°C but

Figure 3. Berry Creek sample site in late February: riffle in the foreground and pool in the background.

Figure 4. Mack Creek site chosen for intensive studies of L. cascadense and L. unicolor population dynamics.

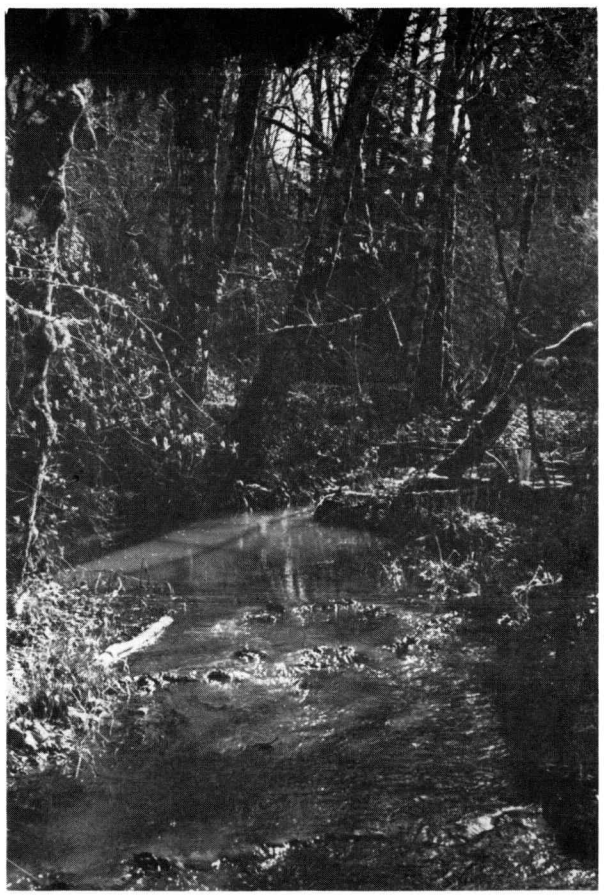


Figure 3.

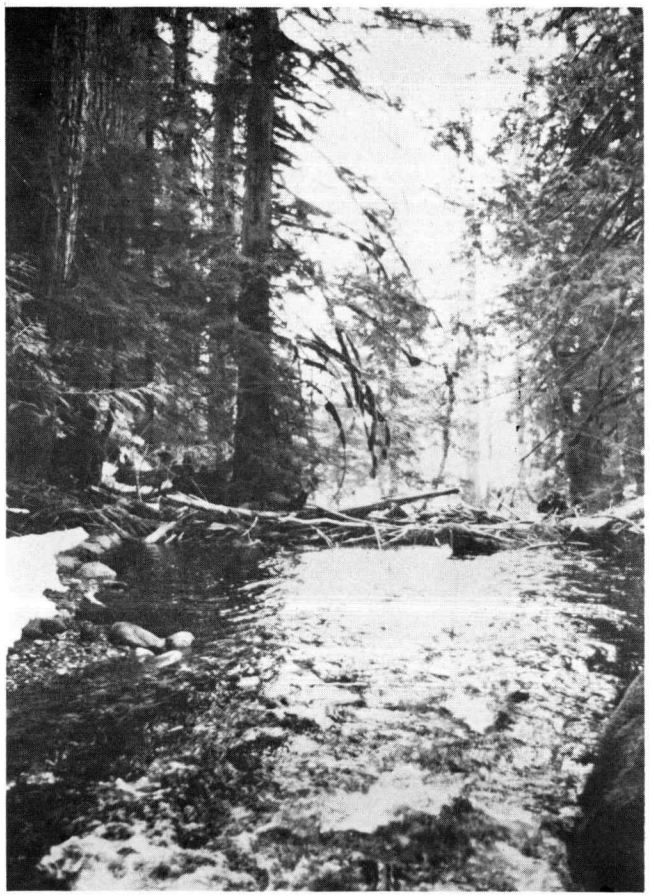


Figure 4.

remain below 5° for much of the year (November through May or June). The surrounding vegetation is old-growth Douglas fir, western hemlock (Tsuga heterophylla (Raf.) Sarg.), and western red cedar (Thuja plicata D. Don.), with some vine maple (Acer circinatum Pursh.). A slightly lower section of stream runs through a small clear-cut. Vegetation is primarily vine maple with some young Douglas fir, cedar, and hemlock.

Mack Creek experiences large fluctuations in stream flow due to the seasonal nature of the precipitation. Peak flows are 1000 to 2000 times low flows. Due to these large fluctuations, the stream varies widely in depth, width, and amount of debris present.

Preliminary studies of L. unicolor were done on randomly selected 50 m stretches of stream in both clear-cut and old-growth sections. The site chosen for the most intensive study was a pool formed above a large natural log jam in the old-growth section, and the riffle adjacent to the pool (Fig. 4). The pool was approximately 4 m wide by 5 m long and up to 1 m deep, with organic debris often deposited to a depth of 10 cm or more. The riffle was 1 to 2 m wide and 10 to 12 m long.

IV. METHODS AND MATERIALS

Laboratory Studies

Ingestion, Egestion, and Growth

Experiments were conducted on replications of individual insects in ice cube trays (3 x 4 cm compartments), or groups of insects in 7.6 cm diameter glass culture dishes or plastic cottage cheese containers (8 cm diameter). Two or three trials of two to four days each were usually conducted in each experiment, using the same groups of insects. Food and water (dechlorinated tap water) were changed and fecal material was collected at the end of each trial. The insects were killed at the end of the experiment and dry-weighed.

All larval weights are weights of freshly-killed specimens. Weights were determined after specimens had been dried at 60°C for 48 hours and cooled in a desiccator. Measurements were made with either a Mettler H16 balance or a Cahn 4100 Electrobalance.

Larvae were removed from their cases before drying by gently squeezing the back of the case or by prodding the rear of the larva with a blunt probe. Wet weighing was not used since dry weighing is more accurate and larvae removed from their cases for wet weighing are generally too disturbed to return to an experiment.

Fecal material was pooled from similar replications and collected by filtration through preweighed 1.2 μm Millipore filters.

Filters and fecal material were dried and reweighed and the amount of fecal material was calculated by subtraction. Food fragments, bits of case material, and pieces of sand were removed from the fecal material before filtration. It was not possible to determine what proportion of filtered material was actually finely-ground uneaten leaf fragments; however, it was thought to be minimal. Larger fragments were never significant compared with the amount of fecal material, and were weighed with the unfragmented portions of the food.

Consumption of Deciduous Leaves. Alder and bigleaf maple leaves were collected shortly after leaf fall, air dried and stored in the laboratory. Before feeding, the leaves were conditioned in a laboratory drippery system (Anderson 1973) at 13 to 15°C for ten days to two weeks. For the experiment measuring the effects of conditioning time on feeding rates by L. quercina, the leaves were conditioned in 1 mm mesh bags in the field for up to 46 days (Anderson and Grafius 1975).

Disks were cut from the leaves with a 8.5 mm diameter cork borer to provide a measured amount of food. The disks from each leaf were paired according to position on the leaf and the amount of leaf vein included. One of each pair was fed to the insects and the other was set aside in water to provide an estimate of the initial amount of food present. At the end of the trial, the leaf disks were rinsed and dry-weighed and the difference between fed and unfed groups

of disks was used as the amount of food consumed. The Cahn balance was particularly useful for this since it has two weighing pans and the differences could be measured directly, if desired.

In order to provide a uniform selection of food items, an attempt was made to supply each group of insects with disks from several leaves and to distribute disks from each leaf between as many replications as possible. However, it is still probable that there was variation between leaves used in different experiments at different times.

Consumption of Douglas fir Needles. Douglas fir needles were collected by shaking a tree to dislodge those that were near abscission. The needles were conditioned in aerated containers in the laboratory at 13 to 15°C for four or five months. Well-decomposed needles collected from Mack Creek, chosen for their dark color and visible fungal colonization, were also used in some of the experiments. These needles were presumed to have been in the stream for at least nine months, from the previous fall when most of the litter enters the system.

Consumption was measured by initially wet-weighing small groups of needles, feeding them to the larvae, and dry-weighing the remainder. Other groups of needles were wet-weighed at the same time and immediately dried and weighed to obtain conversion values from wet to dry weights. Using these conversion values, the initial

wet weight of the fed needles could be compared with the dry weights of the same needles after feeding.

Wet weights were taken by blotting the needles on paper towel and allowing them to air dry for one minute before weighing. Wet to dry weight conversions differed slightly from day to day, depending on factors such as temperature and humidity, but the standard error of the conversion value on a given day was always less than 5 or 10% of the mean. Needles, like the deciduous leaves, were not dried prior to feeding since microbial components have been shown to be important stimuli to feeding (Kostalos 1972, Grafius 1974) and would be destroyed by drying.

Consumption of Wheat Grains. Consumption of wheat grains by C. magnifica was measured by dry-weighing the wheat before and after feeding. Initial weights were corrected for weight loss due to leaching (generally 1 or 2%) using weight loss of grains soaked in water but not fed to insects during the experiment. The wheat grains could be dried and weighed before the experiment since microbial colonization is not a prerequisite to feeding (Anderson 1976a).

Growth. Growth was measured in initial experiments by killing and dry-weighing a sample of randomly-selected larvae and comparing these weights with weights of the remaining larvae after the experiment. This method required large numbers of insects and was not

very precise since weights of individuals were highly variable and the duration of the experiments was generally short.

A more precise method for measuring growth used initial case measurements (length and width) to estimate individual case volume. A sample of the individually measured insects representing a range of case sizes was killed and dry-weighed at the beginning of the experiment. Dry weights of these larvae were compared with their case volumes using regression analysis and an equation computing dry weight from case volume was calculated. This equation was used to estimate initial weights for the larvae used in the experiment. These insects were kept in individual compartments so that growth for each individual could be estimated.

Calculation of Consumption and Fecal Production Rates. Consumption rates (C.R.) and fecal production rates (F.P.R.) were measured gravimetrically as described above and calculated as:

$$\text{C.R. } (\text{mg} \cdot \text{mg}^{-1} \cdot \text{day}^{-1}) = \frac{\text{Initial food (mg) - Food remaining (mg)}}{\text{Time (days) x Final weight of larvae (mg)}}$$

$$\text{F.P.R. } (\text{mg} \cdot \text{mg}^{-1} \cdot \text{day}^{-1}) = \frac{\text{Total feces collected}}{\text{Time (days) x Final weight of larvae (mg)}}$$

Since estimates of initial weight were generally imprecise, final weights were used in calculations. Rates would be underestimated if larvae were growing rapidly since final weight would be an overestimate of the average weight of the larvae. However, feeding

experiments were usually of short duration and growth was minimal, so these errors were thought to be negligible. Feeding trials were generally conducted for a minimum of two days to eliminate errors due to diel fluctuations in feeding rates and to minimize any effects of handling on activity and feeding.

When an individual died or began pupating during a feeding trial, it was considered not to have fed during that trial and its weight was not considered in calculating ingestion or egestion rates. Calculations for previous trials would include the dead or pupated individual's weight. This procedure might result in some overestimation of rates, since feeding or defecation by individuals that died or pupated during a trial would be attributed to other larvae. However, the number of larvae pupating or dying during an experiment was generally low. Also, individuals usually exhibit very low feeding and defecation rates just prior to pupation, reducing the size of the error.

Statistical comparisons used are standard "t" or "F" tests for testing significance (Steel and Torrie 1960), unless otherwise indicated. Levels of significance are denoted by "*" ($P \leq 0.05$) or "**" ($P \leq 0.01$).

Calculation of Assimilation Efficiency. Assimilation efficiency (A.E.) was estimated from the results of the feeding experiments as:

$$\text{A.E.}(\%) = \frac{\text{Amount consumed(mg) - Feces produced(mg)}}{\text{Amount consumed (mg)}} \times 100$$

Errors in the estimation of assimilation efficiency would result from errors in the estimates of feeding or fecal production. Incomplete collection of feces causes an overestimate of assimilation efficiency while an underestimate of consumption causes underestimation of assimilation efficiency. The latter type of error would be especially common when food was of poor quality or limited in quantity. Under these conditions, larvae were observed to feed on their cases. In some experiments, initial estimates of case weight were used to correct for case consumption during the experiment.

Errors in estimation might also occur if fecal production did not correspond to consumption. For example, if the insects were starved before an experiment but retained a full gut at the end or if larvae offered poor food consumed little, but continued to empty their guts, the relation between consumption and fecal production would not reflect assimilation. This might be a source of considerable error since gut contents may make up 30% or more of the insect's weight (S. Cobey, Oregon State Univ. Ent. Dept., unpubl.). In order to minimize this error, larvae were usually acclimated for one to two weeks on the experimental food.

For estimates of assimilation, fecal material was usually pooled from several replications of the same treatment. Assimilation efficiencies were generally not calculated for each individual replication and trial of an experiment since replications with excess fecal

production can easily result in large negative assimilation efficiencies, particularly when consumption is low. For example, if consumption is 0.2 mg and fecal production is 0.6 mg, assimilation efficiency is -300%, compared with a maximum positive value of 100%. This procedure would result in biasing the estimate of assimilation efficiency toward replications where consumption is very low and the error involved is high. Replications with very low consumption rates are also most likely to be abnormal, perhaps due to sick or dying insects.

Calculation of Growth Rates and Efficiencies. Growth rates were expressed as instantaneous rates or as growth per individual. Instantaneous rate was calculated as: 1) the difference in natural logarithm of weight divided by time (when "before" and "after" weights were estimated), or 2) the slope of the regression of natural logarithm of weight versus time (e.g. field studies where weight was estimated at several different times). Instantaneous rates were thought to be most useful since they are corrected for different sizes of larvae, while growth per individual tends to be larger for larger individuals.

Growth efficiencies were calculated as either the ratio of growth to consumption (gross growth efficiency) or the ratio of growth to assimilation (net growth efficiency). The latter reflects how much of the assimilated food is utilized for growth compared with losses to

respiration (e.g. maintenance and activity) or losses such as exuviae, silk secretions, or digestive enzymes.

Growth efficiency can be estimated by using a simulation model (see Results) or by directly measuring consumption or assimilation and growth. Data for consumption rate by C. magnifica versus weight per individual (see Figs. 19 a-f) were used in combination with growth rate data to estimate total consumption per individual over a given time interval.

$$\text{C.R. } (\text{mg} \cdot \text{mg}^{-1} \cdot \text{day}^{-1}) = a + b \cdot e^{-cx}$$

where a, b, and c are constants and x is weight·individual^{-1} (mg) then: Consumption·individual^{-1}·day^{-1} $= ax + bxe^{-cx}$.

If x is a function of time (z)

$$\text{Amt. consumed} \cdot \text{individual}^{-1} = \int_{z_1}^{z_2} (az + bze^{-cz})\, dz$$

$$= a\int_{z_1}^{z_2} z\, dz + b\int_{z_1}^{z_2} ze^{-cz}\, dz$$

If growth is linear with respect to time and k is the growth rate per individual

$$z = kt$$

Then,

$$\text{Amt. consumed} \cdot \text{individual}^{-1} = ak\int_{t_1}^{t_2} t\, dt + bk\int_{t_1}^{t_2} te^{-ckt}\, dt$$

$$= \left[\frac{akt^2}{2} - \frac{b}{c} \cdot e^{-ckt}\left(t + \frac{1}{ck}\right)\right]\Bigg|_{t_2}^{t_1}$$

If growth is a non-linear function of time (e.g. exponential), substitutions can be similarly made. For more complex problems, such as sigmoid growth, a computer program based on a discrete-time approach might be simpler, but for the purpose of estimating efficiencies when growth is nearly linear with time, the above approach is adequate.

When consumption rate is constant regardless of size, and growth is linear with respect to time, consumption per individual can be calculated as:

$$\text{Amt. consumed} \cdot \text{individual}^{-1} = \text{C.R.} \times \text{Wt} \cdot \text{individual}^{-1} \times \text{Time}$$

Respiration Measurements

Respiration rates were measured using a Gilson Differential Respirometer. Temperatures were selected to give a range of temperatures from 5°, the lowest practical limit of the respirometer, to 20°C, above normal environmental temperature for all of the larvae except early-instar C. magnifica. Several different experiments were conducted on each species over an interval of weeks so that different sizes of larvae could be tested. Insects were acclimated at the appropriate temperature for at least two weeks prior to measurement and were tested singly or in groups of up to five per flask, depending on size. Pieces of alder leaf or Douglas fir needles were included in the respirometry flasks to serve as food and substrate.

At the end of each experiment, the insects were removed for weighing and the leaf or needles and insect case(s) were returned to the flask. Respiration was again measured and these values were subtracted from the initial measurements to give an estimate of respiration by the insect(s). Duration of the experiments ranged from about 48 to 140 hours, depending on the size of the larvae and the temperature.

Errors due to multiplication of microorganisms on the food or fecal material or in the water during an experiment were thought to be minimal since experiments were of short duration and there was no apparent increase in respiration rate during the course of an experiment.

Respiratory Q_{10} values, the factor by which respiration rates increase with a 10°C increase in temperature, were calculated from the slope of natural logarithm of respiration rate versus temperature.

$$Q_{10} = e^{10b}, \text{ where } b = \text{slope}.$$

Values were similarly calculated for consumption rates and temperature where data were available.

Nitrogen Excretion Measurement

Ammonia nitrogen excretion was estimated in a single experiment using L. quercina larvae at 13°C. Ten larvae were acclimated at 13° on alder leaves for two weeks and then placed in a

tightly-stoppered 35 ml vial of dechlorinated tap water. All air bubbles were removed from the vial. Four trials were run for 2-1/2 to 3-1/2 hours. At the end of each trial, 30 ml of water were drawn off with a syringe and immediately acidified with 3.4 ml of 1% H_2SO_4. Samples were analyzed for ammonia nitrogen by the Central Analytical Laboratory, Forestry Sciences Laboratory, Oregon State University. Control treatments of water or water and insect cases were similarly analyzed.

It was hypothesized that excreted nitrogen might be a particularly significant source of nitrogen for aquatic microorganisms since the ammonia excretion would be in a readily usable form and would be concentrated in areas of active decomposition. It was also thought that the rate of ammonia excretion might serve as an indicator of whether nitrogen is limiting to growth, as follows:

Usable N in food x Consumption rate - N Excretion rate
= N Available for growth

However, since there is little information available on how much of the nitrogen present in the food is actually available to the insect (see Discussion) or on the metabolic pathways of food utilization by aquatic detritivores, the amount of usable nitrogen in the food is unknown.

Field Population Studies

Field population sampling is concerned with three basic objectives: efficiency, precision, and accuracy.

Efficiency must be maximized since large numbers of samples are generally required for accurate and precise estimates (Needham and Usinger 1956), while time and money for sampling and sample processing are limited. In this study, efficiency was maximized by using stratified sampling based on previous knowledge of life cycles, behavior, and habitat preferences. Sample sorting for caddis larvae can be especially time-consuming since the larval cases are often well camouflaged. Efficiency of sample processing was increased by subsampling where needed, and using a trapping technique for extracting the larvae or sorting samples while larvae were still alive and active.

Precision may be defined as the repeatability of a measurement or the amount of variability associated with the measurement, as in the case of a mean of a series of samples. Precise estimation of density or biomass for a particular species is particularly difficult in lotic systems due to the heterogeneity of the system and generally low numbers of any given species. Precision may be increased by using a stratified sampling scheme, reducing variability as much as possible within any one stratum. In this study, 6 to 11 samples were taken on each sampling date and sampling effort was concentrated in the areas where larval densities were highest and variability was greatest. Even though a relatively large number of samples was taken, and care was used in defining strata, there was still a high amount of variance

associated with larval densities, apparently due to the heterogeneity of the habitat.

Accuracy (or lack of bias) of an estimate is the degree to which that estimate reflects the actual value (bias equals $\bar{x} - \mu$, Cochran 1963). Since actual values are rarely known, accuracy is very difficult to assess. Precision is often used as an index of accuracy, but there is not necessarily any correlation between the two. Any consistent error in sampling, such as not sampling a particular habitat (e.g. the hyporheic zone) or underestimating a particular stage (first instars are rarely sampled accurately) may introduce errors not reflected in the precision of the estimate.

Although biases in sampling, such as those described above, are not included in estimates of precision, some indication of accuracy can be obtained by comparing the results of different sampling techniques (e.g. Surber sampler with frozen core or emergence samples) or by comparing samples of different life stages (e.g. numbers of adults should not exceed numbers of mature larvae and numbers of second-instar larvae should be greater than numbers of thirds).

Accuracy, as well as precision and efficiency, can be increased by careful design of the sampling scheme and choice of techniques to fit the organism being studied. In addition, a significant portion of the study area (about 3%) was sampled on each sampling date, although sampling was not thought to have been extensive enough to affect the populations in the study sections.

Berry Creek. Field samples were taken monthly for L. quercina larvae in Berry Creek with a 0.1 m^2 Surber sampler (mesh 250 μm) from August 6, 1974 to February 26, 1975. Temperature was measured at the time of sampling. A stratified sampling scheme was used (Cochran 1963) with three or four samples each from riffle, pool, and "pool-end" strata. The pool-end stratum was a short section of stream at the upstream end of the riffle, where most of the leaves accumulated.

A trapping technique was used to extract larvae from the samples. Immediately after collection, all large pieces of leaf or other organic material were removed and the samples were placed in shallow pans and kept at 13°C. A few alder leaves were added to each pan and the leaves and sides of the pans were inspected for larvae periodically for three or four days. Tests with stream substrate and a known initial number of larvae demonstrated that this technique was more than 85% efficient, even for small third-instar larvae that would be very time-consuming to sort manually. Nearly mature larvae, prepupae, and pupae were sorted by hand since they were large and easy to see and were no longer actively feeding.

Random samples of each instar were dry-weighed and means and variances for each instar and for the entire population were calculated as stratified samples.

A simple computer program was designed for calculating stratified means and variances for population estimates (App. Table 1). The same program was used to calculate mean larval weights, stratified on the basis of instar.

Standing crop of particulate litter and debris (> 5 mm) in Berry Creek was estimated at the same location, from August 29, 1975 to January 30, 1976. Samples were collected from the three strata, as before. Material collected was separated into categories of alder leaves, miscellaneous leaves (mainly maple) and other (e.g. twigs, bark, or needles). After sorting, samples were oven-dried, cooled in the open air, and weighed.

Mack Creek. Preliminary sampling of L. unicolor was done in 50 m sections of old-growth and clear-cut areas of Mack Creek every two to three weeks from April 26 to August 1, 1974. Habitat was classified as either "unsuitable" (no visible organic debris) or "suitable" (visible amounts of needles, twigs, etc.). Areas of suitable habitat were measured and larvae were counted with a glass-bottomed viewing scope. Areas without organic debris (unsuitable) were checked randomly but larvae were not found in these areas. Numbers of larvae in large pool areas were estimated by counting larvae along several transects or in different parts of the pool. Samples of larvae were collected from clear-cut and old-growth locations for weighings.

This method was only suitable for the larger sizes of L. unicolor since they occur on the surface of the sediment. An accurate survey can be made only at times of relatively low water (late spring, summer, or early fall). Although limited in application and perhaps biased toward larger individuals, this method allowed the frequent surveying of a large area of stream and perhaps gives a better indication of overall larval biomass in the stream than other methods.

From October 19, 1974 to July 31, 1975, Surber samples were taken monthly and sorted for L. unicolor and L. cascadense. Temperature was measured at the time of sampling. A stratified sampling scheme was used, as before, but only riffle and pool strata were defined. Larvae were kept on ice and sorted under a binocular scope while they were alive. Sorting of fresh samples had two advantages to sorting preserved samples: 1) larvae were much easier to find among the debris when they were still alive and moving, and 2) dry weights could be taken on fresh rather than preserved specimens. Random samples of larvae from each available instar were weighed, as before.

Some of the larger samples were subdivided prior to sorting. On a few of the largest samples (>4 liter volume), as little as 1/8 of the original sample was sorted. Subsampling error was thought to be negligible since larvae were generally numerous in the samples that required subsampling.

Adult emergence of L. unicolor and L. cascadense was sampled in several pool areas of the old-growth section of Mack Creek from July 17 to September 6, 1974 and from June 24 to August 23, 1975. Pyramid-shaped traps, 0.2 m^2 in area, were constructed of wood 2 x 2's and aluminum window screen (1 mm mesh) with an inverted wide-mouthed mason jar at the top. A cone of screen inverted inside the mouth of the jar prevented insects from falling back into the water after entering the jar. Samples were collected only infrequently (every one to three weeks) but the insects were prevented from falling from the trap if they died and most were in good condition when collected.

V. RESULTS

Laboratory Studies

Feeding and Growth of L. quercina

Effects of Size on Feeding. Emphasis in this study has been placed on the final (=fifth) instar since it includes most of the larval life cycle, and approximately 90% of the mature final weight is gained during this stage. However, it was necessary to have some data on consumption and fecal production rates for earlier instars. Thus, brief experiments were conducted on consumption and fecal production by second-, third-, and fourth-instar larvae. Length of the experiments was short due to the short duration of the early instars.

In experiment 1, second- and third-instar larvae were separated into 20 replications of five insects each, after a 1-week acclimation. Two 3-day trials were conducted at 13°C. Mean consumption rate of alder for the four replications of second-instar larvae ($\overline{wt}$ = 0.014 mg) was 0.70 $mg \cdot mg^{-1} \cdot day^{-1}$ ($s_{\overline{x}}$ = 0.26) and the mean consumption rate for the third-instar larvae ($\overline{wt}$ = 0.053 mg) was 0.40 $mg \cdot mg^{-1} \cdot day^{-1}$ ($s_{\overline{x}}$ = 0.04) (App. Table 2). The high variability in consumption rates for the second-instar larvae probably resulted from: 1) rapid within-instar changes in feeding rates when instar duration is short (Anderson and Grafius 1975), 2) the difficulty of accurately measuring consumption by very small larvae, 3) the mortality during the experiment,

and 4) the possibility that small L. quercina larvae feed efficiently only on soft, well-conditioned leaves.

Freshly-collected third- and fourth-instar larvae were tested in experiment 2 at 13°C for 24 hours. Consumption rate again was higher for the smaller individuals; 0.93 $mg \cdot mg^{-1} \cdot day^{-1}$ for a mixture of third- and fourth-instar larvae weighing an average of 0.39 mg each and 0.71 $mg \cdot mg^{-1} \cdot day^{-1}$ for large fourth-instar larvae weighing an average of 0.59 mg (App. Table 3). Assimilation efficiencies were 14 and 17%, respectively. These are low in comparison with subsequent experiments, perhaps due to the short duration of the experiment or the lack of acclimation. Consumption rates were somewhat higher than in experiment 1 probably due to the short duration of the experiment or differences in food quality.

Because of the importance of the final instar and since within-instar changes in feeding rates may be considerable (Anderson and Grafius 1975), it was important to have accurate measurements of the effects of size within the final instar on feeding and fecal production rates. Experiment 3 was designed to estimate the effects of size for a range of weights of final-instar larvae. To reduce variation caused by differences in food qualities, all food used in this experiment came from one alder leaf. Insects were separated visually into nine replications of four insects each on the basis of size and were kept at 13°C for the 2-day experiment.

As in experiments 1 and 2, consumption decreased with increased weight of the larvae (Table 1). There was no significant change in assimilation efficiency with larval weight ($P \leq 0.05$). Consumption rates were slightly higher than in experiments 1 and 2 or subsequent experiments, probably since a particularly palatable leaf was chosen for the food. Although the results of experiment 3 are perhaps not indicative of processing rates in the field, they were thought to give the best estimate of the effects of larval size on feeding and fecal production rates.

Effects of Food Quality on Feeding. Food quality was thought to be one of the most important factors affecting processing rates in the field, since an abundance of organic material is present. Thus, consumption and fecal production rates were measured for alder leaves conditioned for various lengths of time and for bigleaf maple leaves and Douglas fir needles, two other common types of litter.

In experiment 4, consumption and fecal production were measured for final-instar larvae fed at 10°C on field-conditioned alder leaves. Two replications of 12 to 15 insects each were used for each treatment (different conditioning times). One 3-day trial was conducted and feces were collected and water changed daily. Leaf disks were rinsed at the time of each fecal collection. The containers were not aerated and some fecal material remained attached to the insects' cases even after careful rinsing. Assimilation efficiencies were

Table 1. Consumption and fecal production by different sizes of final-instar L. quercina larvae fed portions of a single alder leaf.

	Final $\overline{wt}$ (mg)	Consumption Rate ($mg \cdot mg^{-1} \cdot day^{-1}$)	Fecal Production Rate ($mg \cdot mg^{-1} \cdot day^{-1}$)	Assimilation Efficiency (%)
	0.88	0.86	0.72	16.4
	0.96	1.20	0.83	30.8
	0.97	1.03	0.78	23.9
	1.52	0.74	0.52[a]	29.2[a]
	1.52	0.97	0.80	18.0
	1.69	1.03	0.80	22.2
	3.03	0.57	0.43	18.8
	2.96	0.72	0.63	12.5
	3.21	0.63	0.51	20.0
$\overline{x}$	1.86	0.86	0.67	21.3
$s_{\overline{x}}$	0.32	0.07	0.05	2.0

Linear Regression Analyses

	r^2	F
Consumption Rate = $1.192 - 0.178(\overline{wt})$	0.64	13**
$= 1.021 - 0.318(\ln \overline{wt})$	0.61	11*
Fecal Production Rate = $0.887 - 0.117(\overline{wt})$	0.55	9*
$= 0.774 - 0.209(\ln \overline{wt})$	0.52	8*
Assimilation Efficiency (%) = $27.01 - 3.065(\overline{wt})$	0.24	2 n.s.

[a] Some fecal material lost during collection.

probably slightly overestimated as a result. Because of logistics problems, a portion of the experiment was conducted from October 22 to November 1, 1973 and the remainder from December 7 to 10, 1973. This difference in timing is reflected in the larger size of insects used during the later tests and correspondingly lower consumption and fecal production rates (App. Table 4). Consumption rates were corrected to correspond to consumption by a 1.0 mg individual, using the slope of weight versus consumption rate derived in experiment 3.

There was no significant change in corrected consumption rates for insects fed on leaves conditioned up to three or four weeks, but consumption rates increased rapidly after this time (Fig. 5). Fecal production rates showed the same type of relationships to conditioning time and weight as were found for consumption rates (App. Table 4).

There was a slight decrease in assimilation efficiency with conditioning (Fig. 6). This is perhaps the result of a decrease in soluble, easily-digestible compounds in the leaves or the result of shorter gut-retention times with higher feeding rates. However, the result may be an artifact of the technique. Less efficient collection of small amounts of fecal material (produced when food was less conditioned) would cause an overestimate of assimilation efficiency. This should be further investigated since D. McCullough (O.S.U. Dept. of Fisheries and Wildlife, unpubl.) found a similar decrease for the snail Oxytrema

Figure 5. Consumption rates for final-instar L. quercina larvae fed alder leaves at 10°C compared with conditioning time of the leaves.

Figure 6. Assimilation efficiency for final-instar L. quercina larvae fed alder leaves at 10°C compared with conditioning time of the leaves.

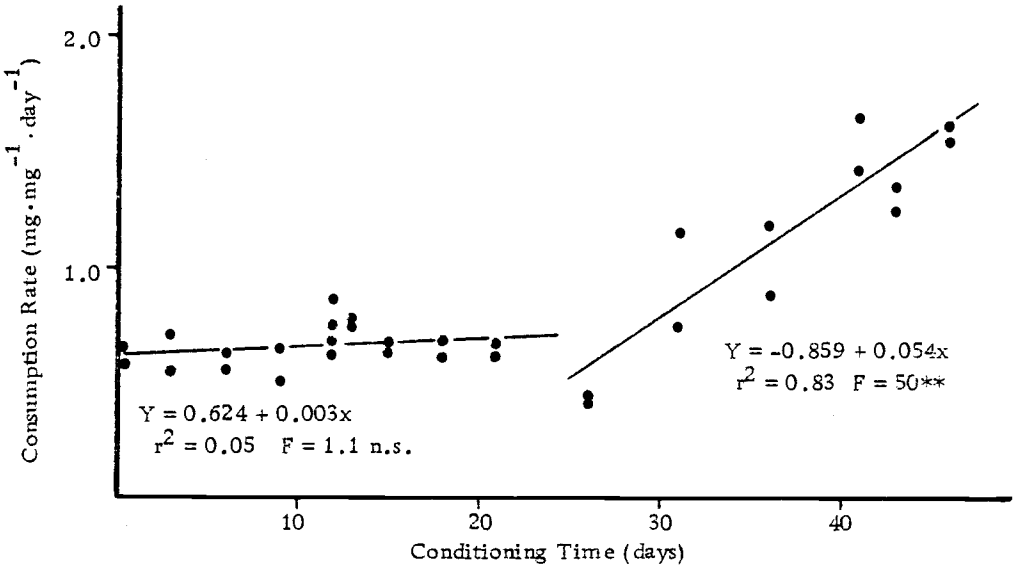


Figure 5.

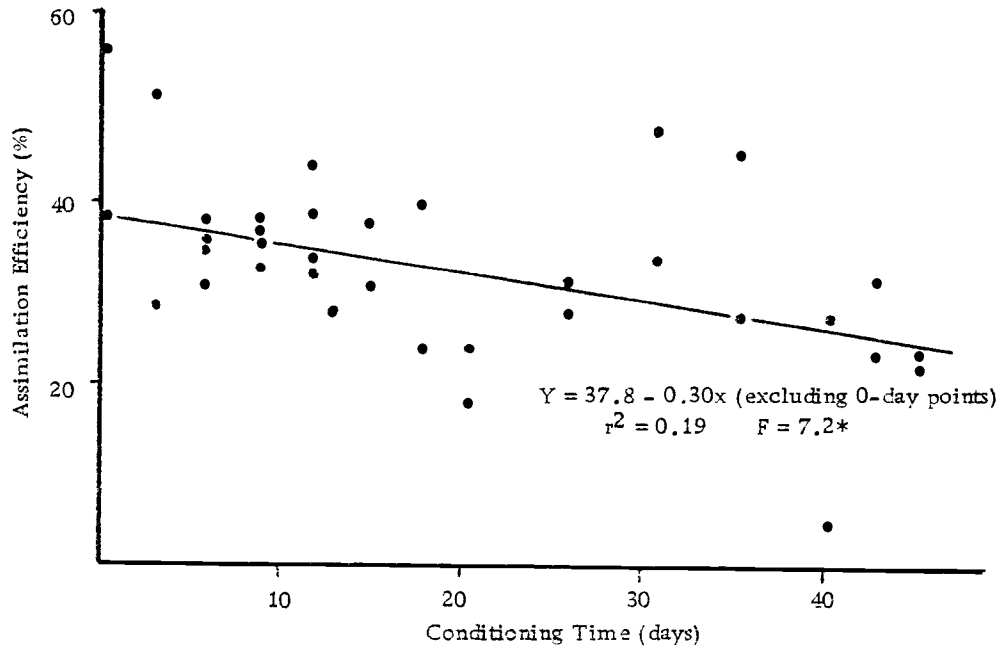


Figure 6.

silicula (Gould) using Conover's (1966) method of estimating efficiency from ash content of food and feces.

In experiments 5 and 6, larvae were acclimated on alder leaves for one week and then moved to the appropriate food for an additional 24 hours before the experiments. As in experiment 4, the dishes were not aerated. Insects were tested during one 2-day trial at 13°C (experiment 5) or two 3-day trials at 15°C (experiment 6).

Consumption rates were highest on alder and alder + maple (Table 2), followed by Douglas fir and alder + Douglas fir (Table 3). Consumption and egestion rates were lowest on maple and maple + Douglas fir. Alder was preferred as food to maple or Douglas fir and Douglas fir was preferred to maple. This preference for Douglas fir over maple might have been reversed if the maple leaves had been well-conditioned (e.g. two months instead of two weeks). The presence of maple leaves seemed to inhibit feeding on Douglas fir, since consumption of Douglas fir was much greater when maple was not present (Table 3). Perhaps maple leaves are poor food but preferred as substrate. Alternatively, the presence of leachate from the maple leaves might reduce the searching efficiency of the larvae or inhibit their feeding.

There was no significant difference in assimilation efficiencies of alder or bigleaf maple, due to the high variability of the estimate for the maple leaves (Table 2), but the results suggest that bigleaf

Table 2. Consumption and fecal production by mid-final instar L. quercina larvae fed alder or bigleaf maple leaves.

Food	Insects		Consumption Rates ($mg \cdot mg^{-1} \cdot day^{-1}$)		Fecal Production	Assimilation Efficiency
	n	$\overline{wt}$ (mg)	alder	maple	($mg \cdot mg^{-1} \cdot day^{-1}$)	(%)
Alder	8	1.34	0.74	-	0.40	46
	8	1.22	0.59	-	0.36	41
	8	1.39	0.64	-	0.36	45
	8	1.52	0.51	-	0.33	41
	8	1.30	0.53	-	0.37	37
	7	1.37	0.50	-	0.34	39
$\overline{x} \pm s_{\overline{x}}$			0.59 ± 0.04		0.36 ± 0.01	42 ± 1.4
Maple	8	1.24	-	0.10	0.09	16
	8	0.58	-	0.44	0.29	36
	8	1.04	-	0.15	0.14	15
	8	1.38	-	0.21	0.11	54
	8	1.32	-	0.17	0.11	40
	8	1.64	-	0.07	0.09	0
$\overline{x} \pm s_{\overline{x}}$				0.19 ± 0.05	0.14 ± 0.03	27 ± 8.1

(Continued on next page)

Table 2. (Continued)

Food	Insects		Consumption Rates ($mg \cdot mg^{-1} \cdot day^{-1}$)		Fecal Production ($mg \cdot mg^{-1} \cdot day^{-1}$)	Assimilation Efficiency (%)
	n	wt (mg)	alder	maple		
Alder + Maple	8	1.55	0.32	-0.01	0.21	31
	8	1.15	0.60	0.06	0.27	58
	8	1.32	0.72	-0.01	0.20	58
	8	1.19	0.40	0.02	0.27	35
	8	1.14	0.41	0.08	0.18	72
	8	1.63	0.34	0.01	0.29	14
$\bar{x} \pm s_{\bar{x}}$			0.47 ± 0.07	0.03 ± 0.02	0.25 ± 0.02	45 ± 8.8

Table 3. Consumption by mid-final instar L. quercina larvae fed Douglas fir, alder, or bigleaf maple leaves.

		Final $\overline{wt}$ mg n	Consumption Rate ($mg \cdot mg^{-1} \cdot day^{-1}$) Douglas fir	alder or maple
1	Douglas fir	1.634 (4)	0.24	-
			0.11	-
2	Douglas fir	2.603 (4)	0.48	-
			0.34	-
3	Douglas fir	2.623 (3)[a]	0.33	-
			0.29	-
	$\overline{x} \pm s_{\overline{x}}$		0.30 ± 0.05	
4	Alder + Douglas fir	2.876 (5)	0.03	0.29
			0.07	0.26
	$\overline{x}$		0.33	
5	Maple + Douglas fir	2.775 (4)	0.12	0.03
			0.12	0.04
	$\overline{x}$		0.16	

[a]One insect died during the first trial.

maple may be less digestible than alder leaves (mean efficiencies of 27.8% and 42.5%, respectively). A longer acclimation period on the maple leaves may have made these data more accurate, since defecation rates may not change immediately with changes in consumption after a shift to a different food.

Effects of Temperature and Food Quantity on Feeding and Growth. Since most of the food processing and growth in the field occurs at low temperatures, feeding and growth were measured over a range of temperatures from 5°C, as low as was practical, to 21°C, slightly higher than normal maximum temperatures. Different food densities were used in the laboratory as an index of larval searching efficiency.

In experiment 7, four replications each with 12 mid-final instar larvae were used in each temperature-food density treatment. Four 3-day trials were conducted. Larvae were acclimated at 13°C for 2-1/2 weeks and then moved to their respective temperatures for three additional days of acclimation. Levels of food supply were chosen so that most of the food in the low food density treatments was consumed in the first day or two of each 3-day trial. At the high food density, food was present in amounts two or three times greater than was consumed. Feces were collected every three days and pooled from all four replications of each treatment.

Four additional replications were kept at 13° and fed conifer needles that had been conditioned in the laboratory for four months

after collection from a stream. For these insects, feeding and feces were measured only once for the 12-day experiment.

Another 48 insects were separated into individual containers, to minimize case destruction, and kept at 13°C without food. Feces from these individuals were collected at the end of the experiment.

In order to measure growth and case consumption during the experiment, 68 insects and their cases were dry-weighed in six groups prior to the experiment to estimate initial weight per insect (2.06 mg, $s_{\bar{x}} = 0.07$) and initial case weight (2.61 mg, $s_{\bar{x}} = 0.05$). Some case destruction apparently occurred in all treatments, perhaps due to crowding or a lack of ideal case material. Estimated case loss was added to consumption to more accurately calculate assimilation efficiency. This correction had only a slight effect on the results, especially at the lower temperatures and/or higher food densities.

Mean consumption rates, fecal production rates, and case-corrected assimilation efficiencies are given in Table 4. Significant increases in consumption rates occurred with higher food density (Fig. 7) or increased temperature (Fig. 8) ($P \leq 0.01$). Food supply only slightly in excess was sufficient to allow maximum consumption (Fig. 7). There was no significant effect of size on consumption rate ($P \leq 0.05$), since larvae were randomly assigned to replications and only a narrow range of mean sizes was represented.

Table 4. Consumption and fecal production by mid-final instar L. quercina larvae fed different densities of food at 5, 13, or 21°C.

Temp.	Food		Consumption		Estimated Total Case Loss	Total Feces Produced	Assimilation Efficiency[a]	Final $\overline{wt} \pm s_{\bar{x}}$
			Total	Rate $\pm s_{\bar{x}}$				
(°C)	Type	Density	(mg)	($mg \cdot mg^{-1} \cdot day^{-1}$)	(mg)	(mg)	(%)	(mg)
5	Alder	Low	238.7	0.19 ± 0.01	19.6	195.0	24.5	2.22 ± 0.20
		Med.	374.0	0.30 ± 0.02	16.0	321.8	17.4	2.17 ± 0.19
		High	359.3	0.33 ± 0.02	23.6	258.5	32.5	2.07 ± 0.13
13	Alder	Low	271.7	0.29 ± 0.02	49.8	272.6	15.2	1.80 ± 0.31
		Med.	614.0	0.47 ± 0.02	44.0	529.9	19.5	2.30 ± 0.12
		High	642.1	0.44 ± 0.04	27.6	514.6	22.8	2.51 ± 0.25
	Conifer	High	99.6	0.12(0.10-0.14)[b]	37.6	114.8	22.5	1.53 ± 0.17
	-	None	-	-	42.3	32.6	22.9	1.25 ± 0.11
21	Alder	Low	241.7	0.32 ± 0.02	58.6	248.8	17.1	1.79 ± 0.13
		Med.	614.4	0.68 ± 0.05	48.5	522.5	21.2	1.74 ± 0.13
		High	799.5	0.69 ± 0.06	41.5	653.6	22.3	2.33 ± 0.21

[a] Corrected for case loss.

[b] Range of four replications.

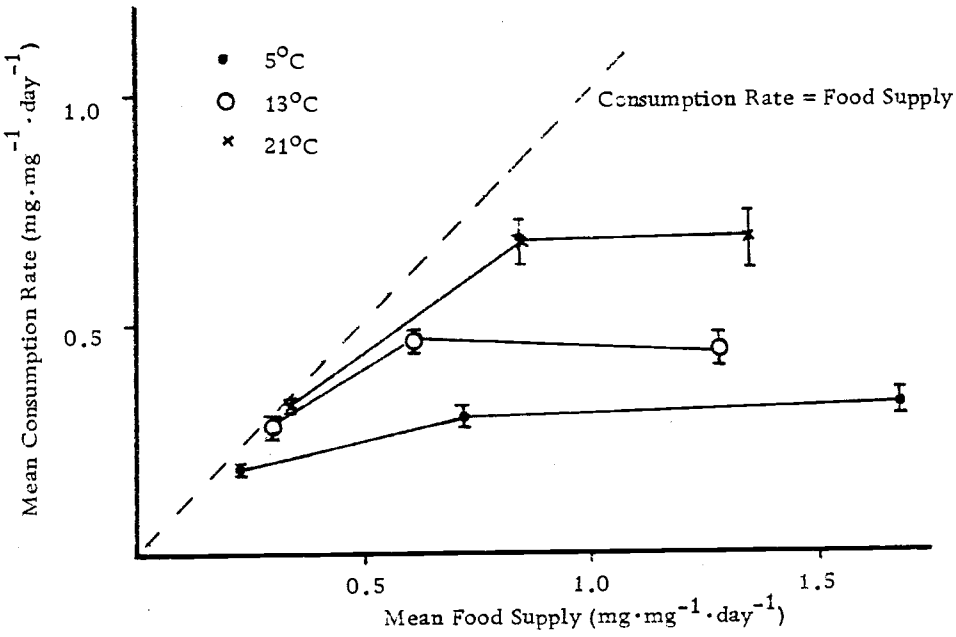


Figure 7. Consumption rates for mid-final instar L. quercina larvae fed alder leaves in comparison to amount of food supplied and temperature.

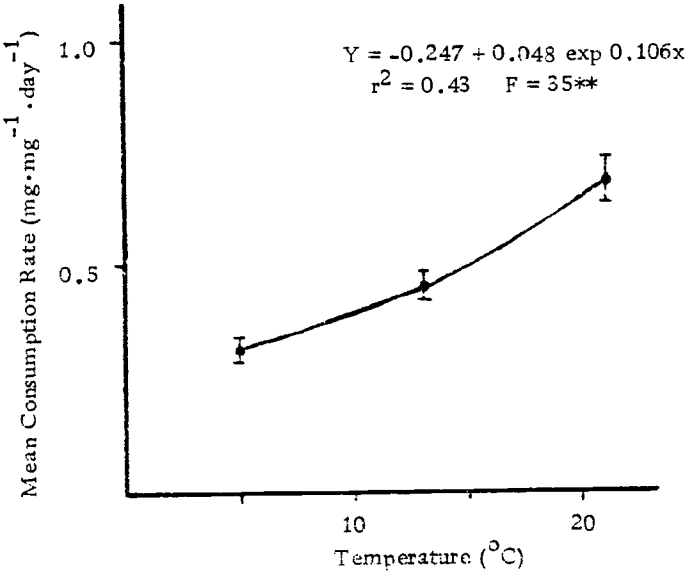


Figure 8. Mean consumption rates for mid-final instar L. quercina larvae fed on medium and high densities of alder leaves at 5, 13, and 21°C.

Analysis of variance of assimilation efficiencies at medium and high food densities (Table 5) showed a significant difference in efficiency with changes in food density ($P \leq 0.01$). There was also a significant effect of temperature-food interaction ($P \leq 0.05$). Duncan's new multiple range test (Steel and Torrie 1960) indicated that the mean assimilation efficiency at 5° - high food (28.3%) was higher than the other means ($P \leq 0.01$).

Case-corrected assimilation efficiencies also showed a general increase with lower temperatures and higher food density (Fig. 9). The increase with higher food densities indicates that gut-retention time is probably not a factor in the decreased efficiency at higher temperatures. Also, it is unlikely that there was any difference in foods at the three temperatures, since the leaves were conditioned at $13^{\circ}C$ for two weeks prior to the experiment and were at the experimental temperatures for a maximum of three days. This increase in efficiency with lower temperatures may reflect a physiological adaptation to low temperatures (e.g. increased digestive enzyme efficiency or increased efficiency of nutrient absorption from the gut).

There were no significant increases in mean size during the experiment (Table 4), but starved larvae or those fed on conifer needles showed significant weight losses ($P \leq 0.05$). Part of this weight loss may have been due to gut-emptying. However, even in the starvation

Table 5. Assimilation efficiencies for mid-final instar L. quercina larvae fed different densities of alder leaves at 5, 13, or 21°C.

Days	Assimilation Efficiency (%)								
	5°			13°			21°		
	low	med.	high	low	med.	high	low	med.	high
1-3	42.1	3.1	22.9	-[a]	15.9	22.4	-[a]	14.1	21.8
4-6	16.4	14.8	28.7	-[a]	8.6	20.1	-[a]	12.8	19.0
7-9	12.3	21.8	28.8	9.6	17.3	17.4	-[a]	17.5	13.9
10-12	5.6	16.5	32.8	-[a]	12.5	18.5	-[a]	17.0	14.4
$\bar{x}$	19.2	14.1	28.3	-	13.6	19.6	-	15.4	17.3
$s_{\bar{x}}$	8.0	3.9	2.0	-	1.9	1.1	-	1.1	1.9

Analysis of variance for medium and high food densities

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F
Total	23	959.705		
Temperature	2	119.372	59.686	3 n.s.
Density	1	328.560	328.560	17**
Temperature x Density	2	157.577	78.789	4*
Error	18	354.204	19.678	

[a] Fecal production exceeded consumption (due to case consumption).

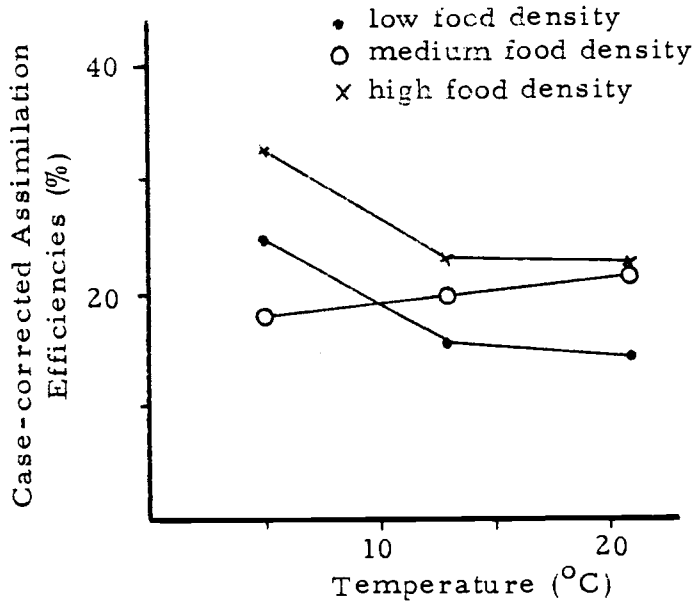


Figure 9. Assimilation efficiencies of mid-final instar L. quercina larvae fed different densities of alder leaves at 5, 13, or 21°C.

treatment, little net gut-emptying apparently occurred since estimated case consumption exceeded the amount of feces collected.

Experiment 8 was similar to experiment 7, except that there were fewer replications and five to ten mature-final instar larvae per replication. Initial weight was estimated as 3.22 mg per insect ($n = 19$, $s_{\bar{x}} = 0.17$). Cases were not weighed.

Due to low feeding rates at this stage, food was rarely limiting even at the low food densities and there was very little difference in results between different densities. Results were therefore averaged for all density levels. Consumption rates were higher at the higher temperatures (Table 6), as in experiment 7, but all rates were much

Table 6. Consumption rate, percent pupation, and final weights for late-final instar *L. quercina* larvae kept at 5, 13, or 21°C for 12 days.

Temp. (°C)	% Pupae or Prepupae	Final $\overline{wt} \pm s_{\bar{x}}$ (mg)	No. of Insects	Instantaneous Growth Rate (%/day)	Mean Consumption Rate $\pm s_{\bar{x}}$ ($mg \cdot mg^{-1} \cdot day^{-1}$)
5	34	3.32 ± 0.16	36	0.26	0.06 ± 0.01
5 (starved)	50	3.12 ± 0.27	14	-0.26	-
13	74	3.67 ± 0.10	60	1.09	0.11 ± 0.02
13 (starved)	86	2.53 ± 0.29	14	-2.01	-
21	80	3.22 ± 0.31	15	0.00	0.27 ± 0.05

lower than those previously measured at the same temperatures (e.g. at 13°C, mean consumption rates were 0.44 $mg \cdot mg^{-1} \cdot day^{-1}$ in experiment 7 and 0.11 $mg \cdot mg^{-1} \cdot day^{-1}$ in experiment 8). These differences in consumption rates were expected from the results of experiments 1 to 3, measuring consumption versus larval size.

As in experiment 7, there were no significant increases in weight. Insects starved at 13°C showed a significant weight loss ($P \leq 0.05$), as before. However, insects starved at 5° showed no significant loss in weight ($P \leq 0.05$), apparently due to lower metabolic costs at that temperature.

Estimation of Growth Rates and Efficiencies. Feeding, fecal production, and growth were measured in experiment 9 for mid-final instar larvae. By using large numbers of insects and sacrificing individual replications at 3- to 4-day intervals, it was hoped that more accurate estimates of growth could be obtained to compare with corresponding estimates of consumption and fecal production.

Larvae were acclimated for three days and kept in unaerated plastic containers with alder leaves as food and substrate. New food was added and feces collected every three or four days. Consumption was measured for the entire length of the experiment. Consumption rates and fecal production rates were consistent throughout the experiment (Table 7), except for the consumption rate estimated for the first three days of the experiment, which was apparently an

Table 7. Consumption, fecal production, and growth of mid-final instar L. quercina larvae at 13°C.

Replication	Day Sacrificed	Insects		Consumption Rate	Fecal Production Rate	Assimilation Efficiency (%)
		n	$\overline{wt}^a \pm s_{\bar{x}}$	($mg \cdot mg^{-1} \cdot day^{-1}$)	($mg \cdot mg^{-1} \cdot day^{-1}$)	
1	0	60	1.40 ± 0.07	-	-	-
2	3	55	1.76 ± 0.08	0.39	0.46	0
3	7	51	1.79 ± 0.06	0.50	0.42	15.1
4	10	41	2.02 ± 0.13	0.54	0.45	17.4
5	13	43	1.96 ± 0.07	0.56	0.45	18.9
6	16	54	1.97 ± 0.07	0.49	0.40	19.4
$\bar{x} \pm s_{\bar{x}}$				0.50 ± 0.03	0.44 ± 0.01	14.2 ± 3.6

Linear regression analyses

	r^2	F	s_b
$\ln(\overline{wt}) = 0.433 + 0.019(\text{Time})$	0.73	11*	0.006
$\overline{wt} = 1.564 + 0.031(\text{Consumption/insect})$	0.75	12*	0.009
$\overline{wt} = 1.644 + 0.126(\text{Assimilation/insect})$	0.59	6***	0.053

[a] Weighed in groups of 6-10 individuals

* Significant at $P \leq 0.05$

*** Significant at $P \leq 0.10$

underestimate. Size of the larvae increased rapidly for the first ten days and leveled off near the end of the experiment. Instantaneous growth rate, estimated from the regression analysis of natural logarithm of weight versus time was 1.9% per day (Table 7). Since consistent consumption, fecal production, and growth rates were obtained, gross and net growth efficiencies could be calculated. Gross growth efficiency, the slope of consumption versus weight, was 3.1% and net efficiency, the slope of assimilation versus weight, was 12.6% (Table 7). Both of these values are probably underestimates since the regression equations in Table 7 predict growth even when consumption is zero. This may be the result of the erroneous value for consumption during the first three days. Also, growth is not linear with respect to consumption, but decreases as larvae get larger and spend more of their energy on maintenance.

Growth at various temperatures was measured in experiment 10 by the method of estimating initial larval weights from case measurements. Larvae were acclimated at 15°C for ten days and at the appropriate temperature for an additional four days. An initial sample of 40 larvae (10 from 5°, 10 from 10°, and 20 from 15°) was measured for case length and width (front and back) and dry-weighed to obtain an equation estimating dry weight from case volume. There were no significant differences ($P \leq 0.05$) in regression coefficients between analyses for the respective temperatures and so all 40

individuals were used to obtain a predictive equation. This equation was used to estimate initial dry weights for the remaining larvae (20 at each temperature). These larvae were kept at the respective temperatures and fed alder leaves for 32 days before drying and weighing.

Significant growth occurred at 5 and 10°C, but at 15° growth was not significant ($P \leq 0.05$) (Table 8). Although mean growth rate decreased with temperature, the differences were not statistically significant ($P \leq 0.05$) and mean final weights for larvae at the three temperatures were almost identical. In spite of the lack of significant differences between growth rates at the different temperatures, this experiment provided much more precise estimates of the effects of temperature on growth than were obtained in experiment 7 (Table 4).

Mortality was low at all temperatures, but 40% of the larvae kept at 15°C began pupating during the experiment although there was no pupation at either 5 or 10°C. The estimated initial weights of the pupating individuals (2.41 mg, $s_{\bar{x}} = 0.34$) was not significantly higher than weights of the remaining larvae ($P \leq 0.01$), and all were smaller than the normal mature size (3.5 to 4.0 mg). This suggests that early pupation is a response to high temperature, perhaps since high maintenance costs prevent further growth.

Figure 10 summarizes the results of experiments 1 to 10 for consumption by L. quercina larvae at 13 to 15°C. Consumption rates decreased with increasing size and were highest on alder leaves.

Table 8. Growth and percent pupation for final-instar L. quercina larvae fed alder leaves at 5, 10, or 15°C for 32 days.

Temp. (°C)	Estimated Initial $\overline{wt} \pm s_{\overline{x}}$ (mg)	Final $\overline{wt} \pm s_{\overline{x}}$ (mg)	Growth per Individual (mg)	Instantaneous Growth Rate (%/day)	% Mortality	% Pupation
5	1.73 ± 0.21	2.21 ± 0.26	0.48 ± 0.13	2.56 ± 0.66	5	0
10	1.70 ± 0.14	2.18 ± 0.24	0.48 ± 0.20	1.79 ± 0.84	0	0
15	2.20 ± 0.25	2.21 ± 0.27	0.01 ± 0.30	0.65 ± 1.90	10	40

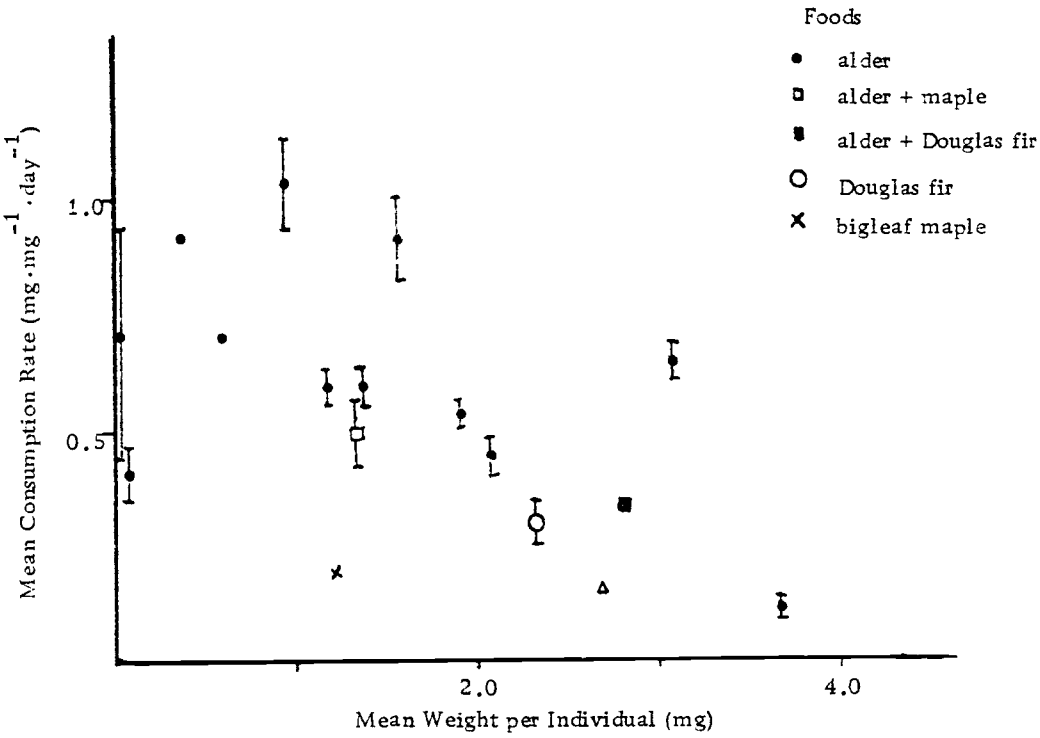


Figure 10. Summary of mean consumption rates by L. quercina larvae on various foods at 13 to 15°C compared to larval size.

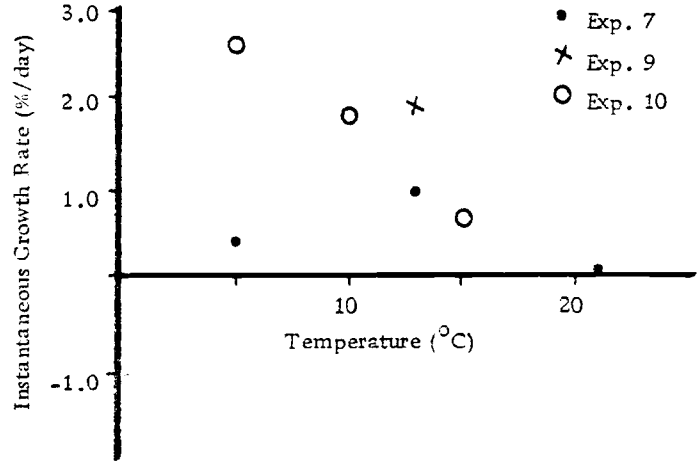


Figure 11. Summary of mean growth rates for L. quercina larvae in the laboratory fed alder leaves at different temperatures.

However, as mentioned, the results of different experiments may not be directly comparable due to factors such as the quality of the particular leaves used for food or the acclimation history of the larvae.

Although variance around individual estimates was high, mean growth rates of larvae in the laboratory generally decreased at higher temperatures (Fig. 11), suggesting that larvae are adapted to grow at cold temperatures. The anomalous point at 5°C is from experiment 7, where variances were particularly high. The increase in growth at lower temperatures correlates with L. quercina's life cycle and food source, since deciduous leaves are most available when water temperatures are low and the most rapid growth occurs in the field in November and December.

Feeding and Growth of L. unicolor

L. unicolor is of particular interest since it feeds actively on highly refractory Douglas fir needles and has been shown to be one of the major processors of conifer needles in Mack Creek (Sedell et al. 1975). A preliminary experiment (experiment 11) measured consumption rates of laboratory-conditioned Douglas fir needles by early- and mid-final instar larvae in order to give initial estimates of feeding rates and to assess the precision of the techniques. Mean consumption rate was 0.84 $mg \cdot mg^{-1} \cdot day^{-1}$ and the standard error was approximately 10% of the mean (App. Table 5). There was no significant

correlation between consumption rate and insect weight ($P \leq 0.05$). Mean consumption rates for larvae in aerated and unaerated containers were not significantly different ($P \leq 0.05$).

Effects of Food Conditioning and Size of Larvae. Consumption and fecal production rates for larvae fed on Douglas fir needles conditioned in the laboratory for different lengths of time were estimated in experiment 12. Laboratory-conditioned needles ranged in appearance from brown or tan, with no visible decomposition or breakage; to black, soft, and frequently fragmented, with visible external fungal growth. Changes in appearance generally followed the changes described by Hayes (1965b). Field-collected needles selected for feeding were dark and had abundant external fungal growth.

There were significant increases in consumption and fecal production rates with increased conditioning time (App. Table 6, Fig. 12). Consumption increased by 0.005 $mg \cdot mg^{-1} \cdot day^{-1}$ for every additional day of conditioning. This contrasts with an increase of 0.054 $mg \cdot mg^{-1} \cdot day^{-1}$ for each additional day of conditioning of alder leaves for L. quercina (see Fig. 5), indicating much more rapid conditioning of the alder leaves. Insect weight also had a significant effect ($P \leq 0.01$) on consumption and fecal production rates, in contrast to the results of experiment 11. The consumption and fecal production rate versus weight slopes of -0.155 and -0.192 are very similar to the slope for L. quercina larvae of -0.178 from experiment 3.

Mean consumption rates were lower than the corresponding fecal production rates for most of the treatments (Fig. 12). Gravimetric methods of comparing ingestion and egestion are obviously not adequate for measuring assimilation efficiency under these conditions. Assimilation efficiency for larvae feeding on conifer needles is very low and is easily obscured by any errors in measurement. Also, consumption of case material or any differences between the rates of gut-filling and gut-emptying will introduce errors into the calculations. Although fecal production cannot be used to calculate assimilation efficiency, it is a measure of the amount of processing.

Effects of Temperature, Food Density, and Larval Size. Consumption and growth of mid-final instar larvae fed on laboratory-conditioned needles were measured in experiment 13, as affected by food density and temperature (similar to experiments 7 and 8 with L. quercina). Larvae were acclimated for three days. Three 4-day trials were conducted. There were nine food density-temperature treatments and one additional treatment at 15° with alder leaves for food. An initial sample of 24 insects was measured for case size and dry-weighed to obtain a predictive equation for weight based on case size. This equation and case measurements were used to estimate initial weight for the remaining larvae as in experiment 10.

As was found for L. quercina, consumption rates increased with temperature and food density (App. Table 7, Figs. 13 and 14) and

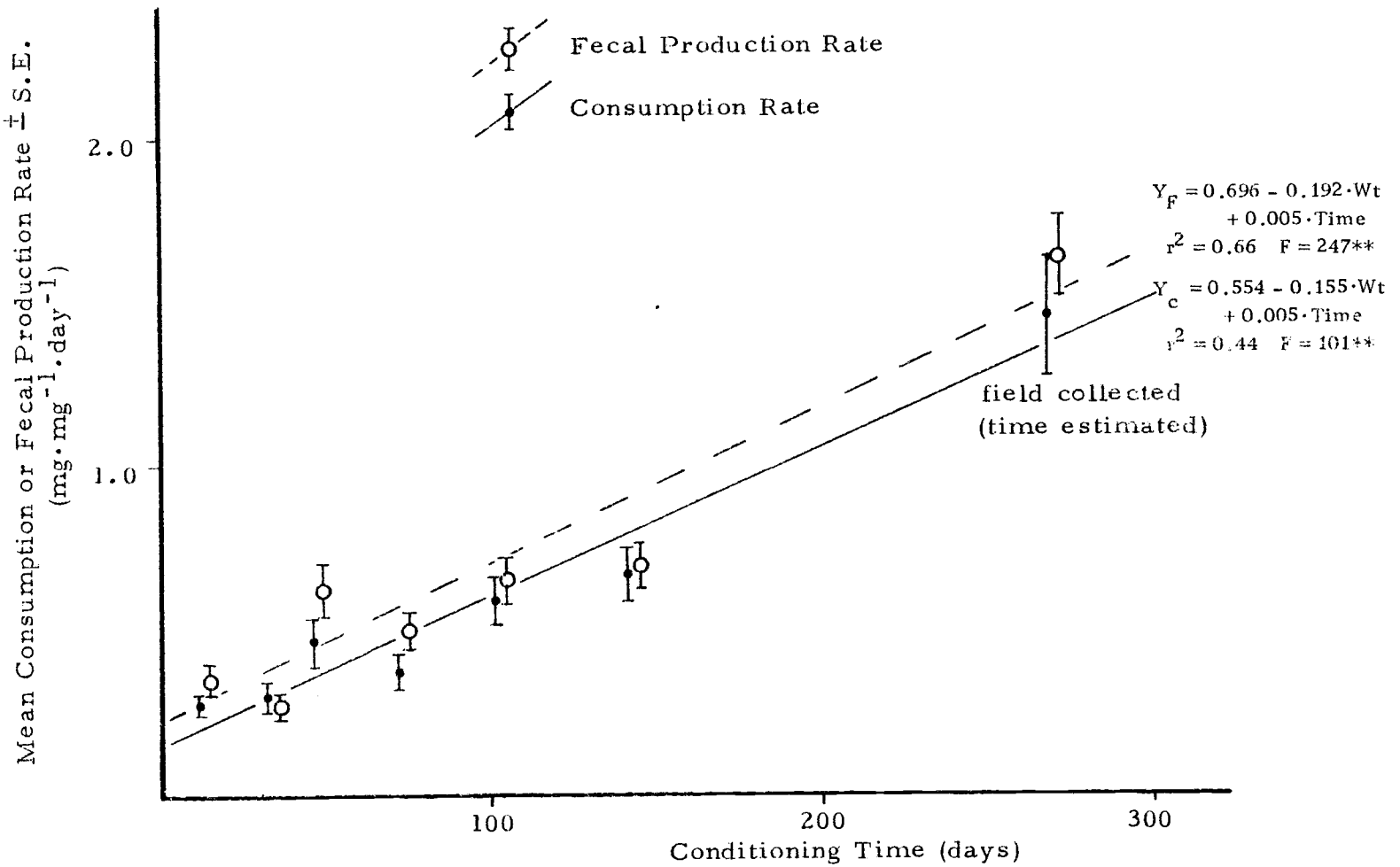


Figure 12. Mean consumption and fecal production rates for early- to mid-final instar L. unicolor at 15°C compared with conditioning time of the food.

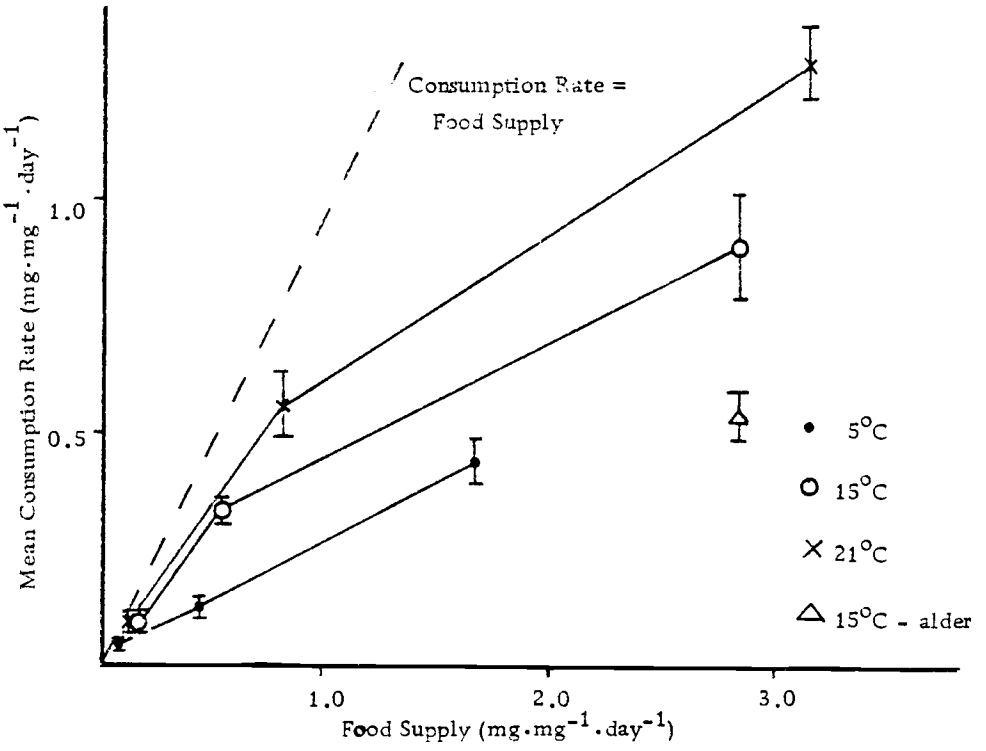


Figure 13. Consumption rates of early- to mid-final instar L. unicolor larvae fed different densities of laboratory-conditioned Douglas fir needles at different temperatures.

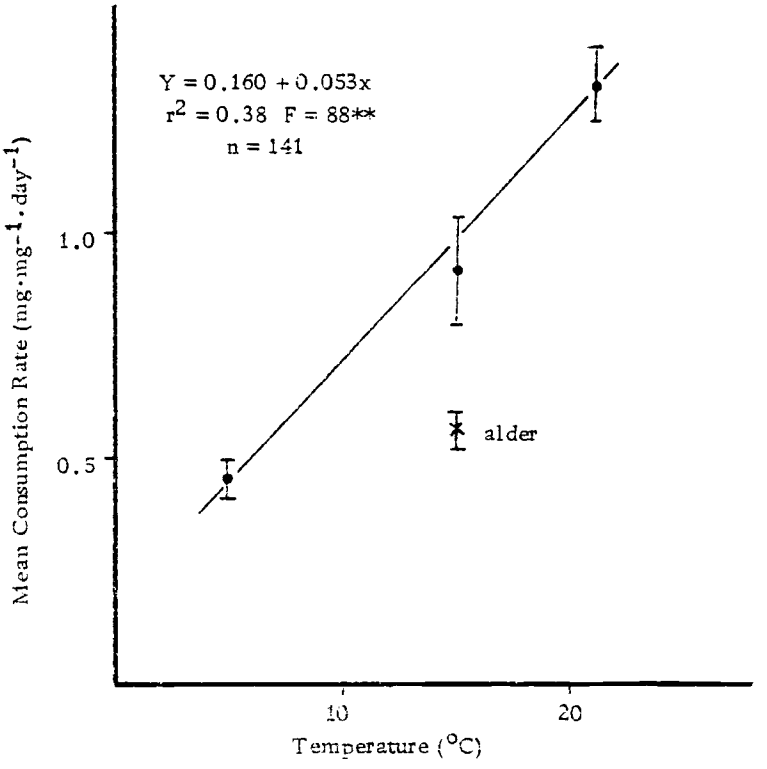


Figure 14. Mean consumption rates by mid-final instar L. unicolor larvae fed on high densities of laboratory-conditioned Douglas fir needles or alder leaves at 5, 15, or 21°C.

decreased with increasing weight of the larvae (App. Table 8). Consumption rate of alder leaves was lower than that of Douglas fir needles at 15°C, in contrast to results for L. quercina, where consumption rate was the same or higher on alder leaves (see Tables 3 and 4). Consumption rates by L. unicolor at the high food density are consistently higher than consumption rates of alder leaves by L. quercina (see Fig. 8). This suggests that L. unicolor may respond to the low quality of Douglas fir needles by increasing consumption, an option not used by L. quercina.

In contrast to the results of experiment 7 with L. quercina, L. unicolor larvae do not exhibit maximum consumption until food is greatly in excess (more than three or four times the amount required). Larvae also tended to feed primarily on one or two needles, even though five to ten or more were available. This is probably due to large variations in quality of individual needles, limiting larvae in their choice of quality food items even though food supply appeared to be ample. A similar limitation by food quality was shown for the pond snail (van der Steen et al. 1973). Alternatively, L. unicolor larvae may feed more rapidly when there is an abundance of substrate. Searching efficiency was thought not to be a factor in these experiments since larvae were kept in 3 x 4 cm compartments.

The only significant growth ($P \leq 0.05$) by larvae in experiment 13 occurred where larvae were fed alder leaves (4.6% per day

instantaneous rate). L. unicolor larvae kept at 5°C and fed medium or high densities of the laboratory-conditioned needles showed some increases in individual weight, but growth was not significantly different from zero ($P \leq 0.05$) and the mean instantaneous growth rates were negative. Largest weight losses and negative growth rates and highest mortality occurred at 21°C. Weight loss at this temperature was high, even at the high food density, in contrast to experiment 7 where L. quercina larvae lost weight at 21° only when food was limited. This difference may be due to insufficient amounts of Douglas fir needles for L. unicolor, even though food density was high. However, it may also reflect either the generally poor nutritive value of the needles in comparison to alder leaves or perhaps the failure of L. unicolor to acclimate to warmer temperatures.

Growth of Larvae Fed Field-collected Needles. Experiment 14 measured growth of mid-final instar L. unicolor fed well-conditioned conifer needles collected from Mack Creek. Larvae were kept at 15°C during the 1-week acclimation and the 13-day experiment. During the acclimation, larvae were fed on laboratory-conditioned Douglas fir needles (five months). Case measurements were used to estimate initial weights as before. Consumption and fecal production were measured over the entire 13 days. Because of the abundant fungal growth on the needles, separation of food from feces was difficult and fungal hyphae may have been weighed with the feces.

Consumption and fecal production rates were similar to estimates from experiments 12 and 13 and fecal production again slightly exceeded consumption (Table 9). Significant increases in weight per individual occurred ($P \leq 0.01$) and instantaneous growth rates were positive, although lower than for larvae fed alder leaves in experiment 13.

Differences in growth rates between larvae fed laboratory-conditioned Douglas fir needles (experiment 13) and larvae fed field-collected needles (experiment 14) are presumably due to differences in conditioning of the two foods. In the laboratory, needles were conditioned for five months while the field-collected needles were assumed to have been in the stream since the previous fall (ca. nine months), or perhaps even longer. Differences in rate of conditioning between field and laboratory may also have occurred due to temperature or microbial inocula. Laboratory temperatures were warmer than field temperatures (13-15°C versus 2-10°). Laboratory-treated needles were not examined microscopically to determine if the microflora were similar to field-collected needles. However, the appearance of the laboratory needles under a dissecting scope (30x) was similar to field-collected ones and decomposition in the laboratory followed the pattern of color and gross structural changes described by Hayes (1965b) for conifer needle decomposition on the forest floor.

Comparing growth per individual with total consumption per individual gives an estimate for gross growth efficiency of 6.0%.

Table 9. Growth of final-instar L. unicolor larvae fed well-conditioned field-collected conifer needles for 13 days at 13°C.

Weight (mg)		Growth		Consumption	Fecal Production
estimated initial	final	mg/indiv.	%/day	($mg \cdot mg^{-1} \cdot day^{-1}$)	
1.192	0.945	-0.247	-1.9	0.86	1.18
1.022	2.087	1.065	2.6	1.30	1.33
1.364	2.847	1.483	2.0	0.79	1.00
1.760	3.032	1.272	1.4	0.88	0.87
1.704	2.764	1.060	1.3	0.92	1.06
0.776	1.114	0.338	2.5	1.03	1.29
0.632	0.810	0.178	3.0	1.63	2.00
1.156	0.820	-0.336	-2.3	1.65	1.92
1.156	1.235	0.079	0.4	0.95	1.09
1.156	1.695	0.539	1.7	1.37	1.29
1.467	1.425	-0.042	-0.2	0.67	0.61
1.704	2.226	0.522	0.9	0.81	0.99
0.895	1.019	0.124	2.5	1.77	2.04
2.029	2.039	0.010	0.2	1.04	1.10
$\bar{x}$ 1.058[a]	1.820	0.432	1.0	1.12	1.27
$s_{\bar{x}}$ 0.175[a]	0.165	0.154	0.4	0.10	0.12

[a]Calculated for the initial sample of larvae used for case size versus weight regression.

(Fig. 15). This compares with a gross growth efficiency of 3.1% for L. quercina larvae fed on alder leaves (Table 7), although the latter was thought to be an underestimate. Assuming an assimilation efficiency of 10% on Douglas fir needles, net growth efficiency for L. unicolor would be approximately 60%, compared with 12.6% for L. quercina. This may explain why L. unicolor grew more rapidly on alder leaves (4.6% per day) than L. quercina. L. unicolor is apparently much more efficient in utilizing assimilated food than is L. quercina, perhaps an adaptation to allow L. unicolor to utilize poorly assimilable foods such as conifer needles.

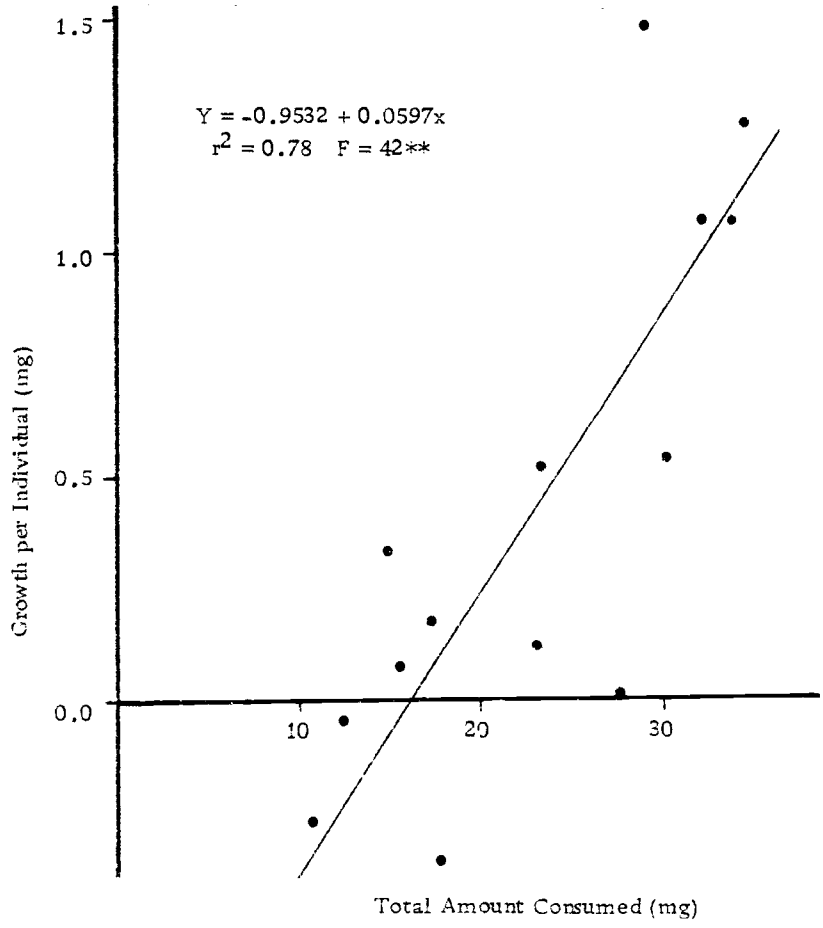


Figure 15. Growth of mid-final instar L. unicolor larvae kept at 15°C and fed field-collected conifer needles for 13 days in comparison with the total amount of needles consumed.

Feeding by L. cascadense

Although extensive experiments were not conducted on L. cascadense because of a lack of time and its small size, it was necessary to have some information on its feeding and fecal production rates since it is also an important species in the decomposition of Douglas fir needles in Mack Creek. It occurs in the same areas of the stream at the same times of the year as L. unicolor and aspects of possible competition between the two species were also of interest.

Consumption and fecal production by final instar of L. cascadense larvae were measured in experiment 15. Treatments were combinations of three temperatures (3, 10, and 21°C) and three food types (alder, bigleaf maple, or Douglas fir). The needles had been conditioned in the laboratory for one year. Larvae were separated into one replication of early- and one of late-final instar larvae (three to six per replication) for each treatment. Insects were acclimated for two weeks and kept in aerated glass culture dishes during the experiment (two 3-day trials and one 4-day trial). Although case consumption was not a problem since L. cascadense's case is made of sand, case fragments were difficult to completely separate from the feces and some sand may have been included in the fecal weights.

Consumption and fecal production were generally higher for the smaller larvae (App. Table 9) and mean rates increased with temperature (Table 10), as expected from the results for L. quercina and

Table 10. Consumption and fecal production by mid-final instar L. cascadense larvae fed Douglas fir, bigleaf maple, or alder leaves at 3, 10, or 21°C.

Temp. (°C)	Food Type	Mean Final Wt. (mg)	No. of Trials[a]	Mean Consumption Rate $\pm s_{\bar{x}}$ ($mg \cdot mg^{-1} \cdot day^{-1}$)	Mean Fecal Production Rate $\pm s_{\bar{x}}$ ($mg \cdot mg^{-1} \cdot day^{-1}$)
3	Alder	1.506	6	0.087 ± 0.014	0.097 ± 0.008
	Maple	0.931	6	0.060 ± 0.013	0.090 ± 0.020
	Douglas fir	1.034	6	0.172 ± 0.040	0.115 ± 0.018
10	Alder	1.111	6	0.338 ± 0.047	0.300 ± 0.029
	Maple	0.891	6	0.122 ± 0.024	0.162 ± 0.038
	Douglas fir	1.136	6	0.120 ± 0.060	0.207 ± 0.032
21	Alder	1.125	6	0.510 ± 0.116	0.450 ± 0.099
	Maple	0.646	3	0.183 ± 0.123	0.403 ± 0.101
	Douglas fir	0.437	3	2.023 ± 1.290	0.230 ± 0.082

Food	Total Consumption (mg)	Total Fecal Production (mg)	Assimilation Efficiency (%)
Alder	83.68	76.37	8.9
Bigleaf maple	18.75	26.46	-
Douglas fir	30.09	27.07	10.0

[a]Trials where fecal material was lost or mortality occurred were excluded.

L. unicolor. Mortality occurred only in the 21°C-maple and 21°C-Douglas fir treatments and mean final weights of larvae in these treatments were considerably lower than at other temperatures or in the 21°C-alder treatment (App. Table 9). This is probably indicative of the combined effects of high temperature and low food quality, similar to effects shown for L. unicolor.

Assimilation efficiencies were again inconsistent, fecal production exceeding consumption in some of the treatments (Table 10), possibly due to sand grains being weighed with the feces. Total amounts consumed and egested indicate that alder leaves and Douglas Douglas fir needles were about equally digestible (assimilation efficiencies of 8.9% and 10.0%, respectively). The assimilation efficiency for alder is questionable since it is much lower than efficiencies on alder reported here or in other studies (Nilsson 1974, Otto 1974). However, assuming that the assimilation efficiencies are correct and that there is no difference in nutritive value of the assimilated foods, Douglas fir needles would be a better food source for L. cascadense since consumption rates on Douglas fir are higher than on alder leaves. Consumption rates on bigleaf maple leaves were lower than on either of the other foods and total fecal production exceeded consumption, suggesting that maple leaves (conditioned for two weeks) were the poorest food source and indicating that some net gut-unloading may have occurred.

Feeding and Development of C. magnifica

Experiment 16 was a series of experiments conducted over a period of several weeks, measuring growth and development, consumption, and fecal production as affected by temperature, food type, and larval size.

Laboratory cultures of C. magnifica larvae were started with 19 first-instar and 41 second-instar larvae in each temperature-food type treatment. Temperatures used were 10, 15, and 20°C. Foods were alder leaves or alder leaves plus wheat grains. Photoperiod was the same as for other experiments (16 light:8 dark). Too few individuals were used to take samples for weight determinations, but instar counts were made weekly on each culture and prepupae were dry-weighed as they occurred.

Growth curves were estimated from final weights and instar distributions (early-fourth instar larvae weigh approximately 5 mg and early-fifth instar larvae weigh about 10 mg dry weight). Times for the earliest individual to reach fourth or fifth (=final) instar, or prepupae and the growth curves (Fig. 16) show that growth was most rapid when larvae were fed alder + wheat. Small larvae grew most rapidly at 20°C, but prepupae occurred first at 15° and were larger at this temperature than at 20°. The only larvae to reach maturity when fed alder leaves alone were those kept at 15°C. Larvae fed alder + wheat at 10°C grew much more slowly than at the other temperatures, but

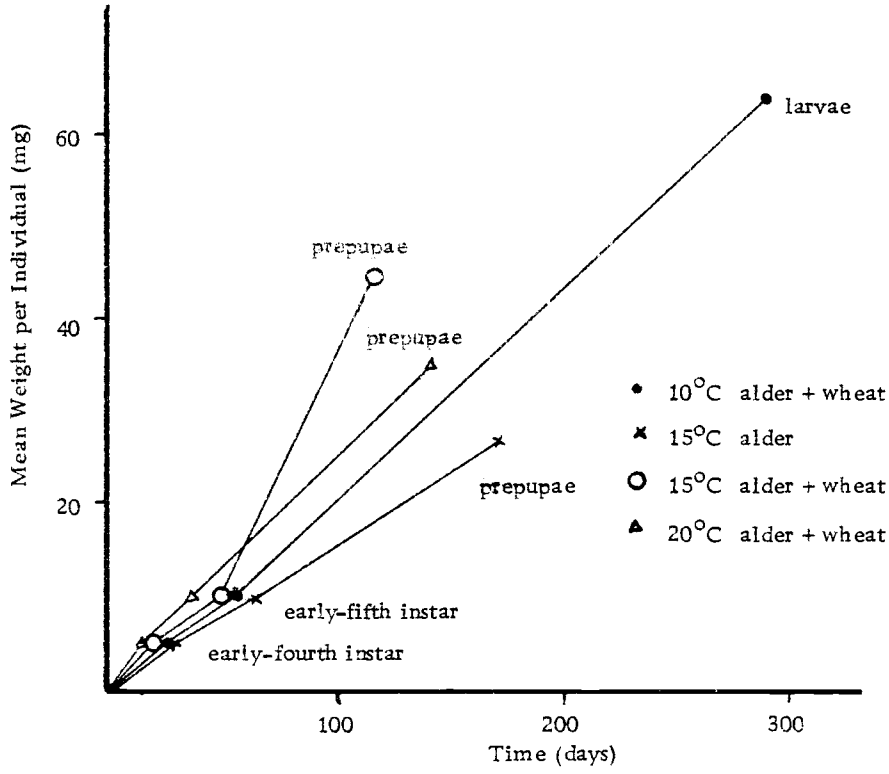


Figure 16. Growth and development of C. magnifica larvae at different temperatures and foods.

showed very low mortality and reached large sizes, although only a few had begun pupation by 290 days. Mature larvae reared at 10°C in other experiments often began pupating soon after being moved to 15°. It is suggested that in the field, larvae continue to grow during the winter until warming water or changing photoperiod stimulates pupation.

Mean degree-days to prepupae ranged from 1740 to 3200, depending on temperature and food type, indicating that this parameter is not adequate to predict development of C. magnifica.

Consumption and fecal production rates were measured periodically on larvae taken at random from the cultures. Two 2-day

feeding trials were conducted on each insect, with food always in excess. Fecal material was collected and pooled for groups of five to ten larvae of similar size. Larvae fed alder leaves at 10° and 20°C failed to grow beyond the early-final instar. Therefore, it was necessary to measure consumption and fecal production for late-final instar larvae under these conditions on individuals acclimated for two weeks after being reared at 15°C on alder + wheat.

Wheat was preferred to alder (3:1), but there was no significant difference ($P \leq 0.05$) in mean consumption rates between alder and alder + wheat treatments at 15 or 20°C (Table 11, Fig. 17). At 10°C mean consumption rate was more than twice as high if wheat was available. Temperature had no significant effect on mean consumption rate of alder + wheat ($P \leq 0.05$), but consumption rate of alder increased with temperature (App. Table 10). Even though mature C. magnifica larvae are much larger than any of the Lepidostoma species, mean consumption rates ($mg \cdot mg^{-1} \cdot day^{-1}$) were very similar (Fig. 18).

To examine the effects of size of C. magnifica larvae on consumption, consumption rates at each temperature and food were compared with the respective larval weights using curvilinear least squares regression analysis (Figs. 19 a-f). At 10°C there was no change in consumption rate with weight, for either of the food treatments (Figs. 19 a and b). Comparing the regression coefficients for the 15 and 20° treatments indicates no significant difference ($P \leq 0.05$) in b_1 values

Table 11. Mean weights, consumption rates, and assimilation efficiencies for C. magnifica larvae fed on alder leaves or alder leaves and wheat grains in four-day feeding experiments.

Temp. (°C)	Food Source	Insects		Consumption Rate ($mg \cdot mg^{-1} \cdot day^{-1}$) $\pm s_{\bar{x}}$			Assimilation Efficiency (%) $\pm s_{\bar{x}}$
		n	$\bar{wt} \pm s_{\bar{x}}$ (mg)	Alder	Wheat	Total	
10	Alder + Wheat	30	14.43 ± 1.99	0.03 ± 0.01	0.38 ± 0.03	0.41 ± 0.03	46.0 ± 6.5
	Alder	25	8.91 ± 1.68	0.16 ± 0.03	-	0.16 ± 0.03	20.2 ± 4.4
15	Alder + Wheat	48	19.13 ± 2.84	0.14 ± 0.02	0.36 ± 0.05	0.50 ± 0.06	52.9 ± 3.0
	Alder	30	6.53 ± 1.24	0.48 ± 0.05	-	0.48 ± 0.05	27.3 ± 2.5
20	Alder + Wheat	21	9.64 ± 1.74	0.20 ± 0.03	0.41 ± 0.08	0.61 ± 0.10	53.5 ± 6.5
	Alder	29	5.13 ± 0.72	0.62 ± 0.06	-	0.62 ± 0.06	36.4 ± 3.6

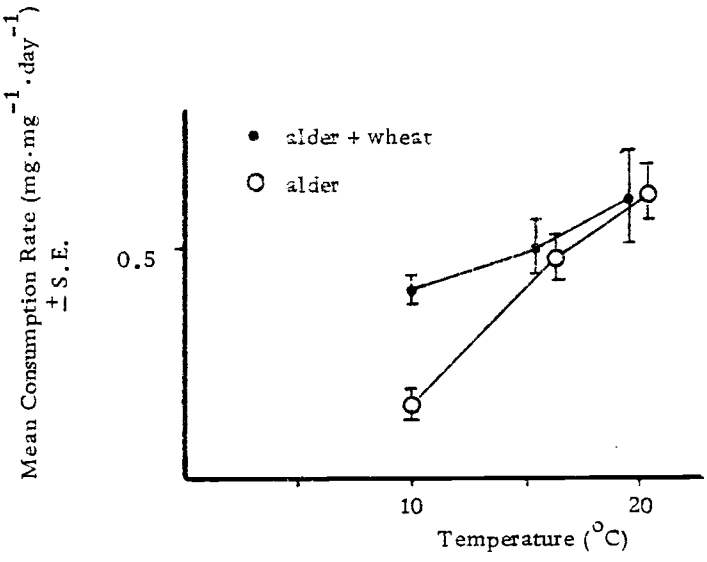


Figure 17. Consumption rate for C. magnifica larvae fed on two diets at 10, 15, and 20°C.

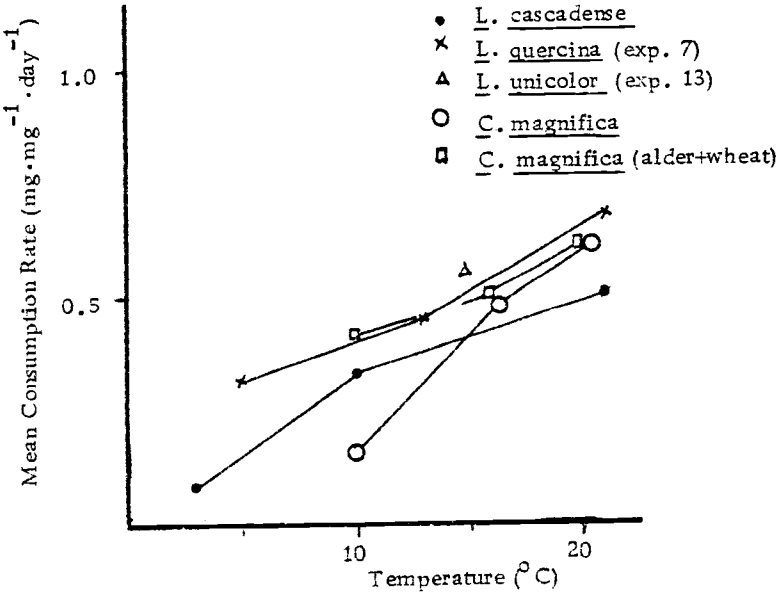


Figure 18. Comparison of mean consumption rates at different temperatures for four species of caddis fed alder leaves.

Figure 19. Consumption rates of alder leaves or alder and wheat grains by third-, fourth-, and fifth-instar C. magnifica at 10, 15, or 20°C.

a. Alder leaves at 10°C.

b. Alder + wheat at 10°C.

c. Alder leaves at 15°C.

d. Alder + wheat at 15°C.

e. Alder leaves at 20°C.

f. Alder + wheat at 20°C.

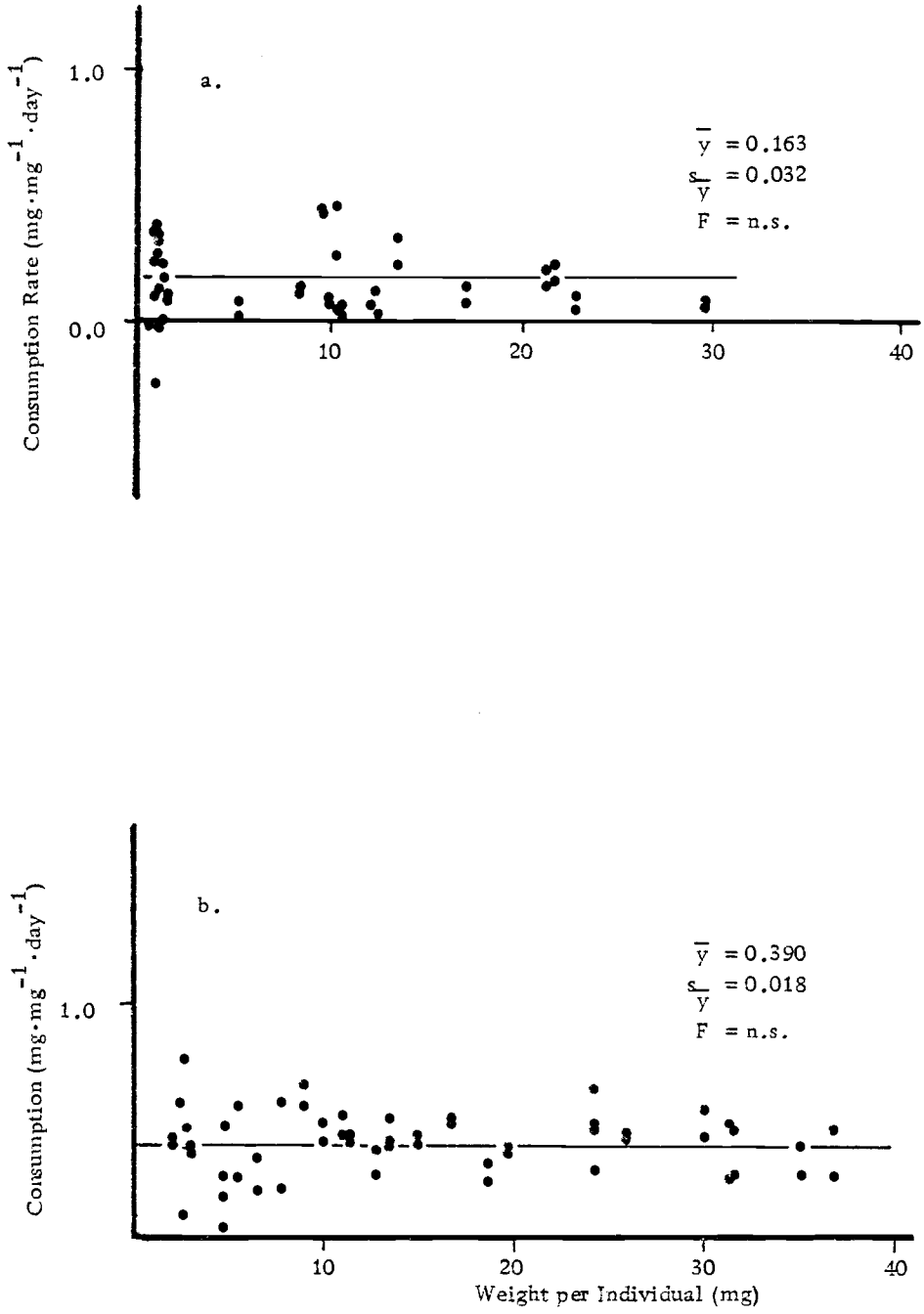

a.
$\bar{y}$ = 0.163
$s_{\bar{y}}$ = 0.032
F = n.s.
Consumption Rate (mg·mg^{-1}·day^{-1})
1.0
0.0
10
20
30
40
b.
$\bar{y}$ = 0.390
$s_{\bar{y}}$ = 0.018
F = n.s.
Consumption (mg·mg^{-1}·day^{-1})
1.0
10
20
30
40
Weight per Individual (mg)

Figure 19.

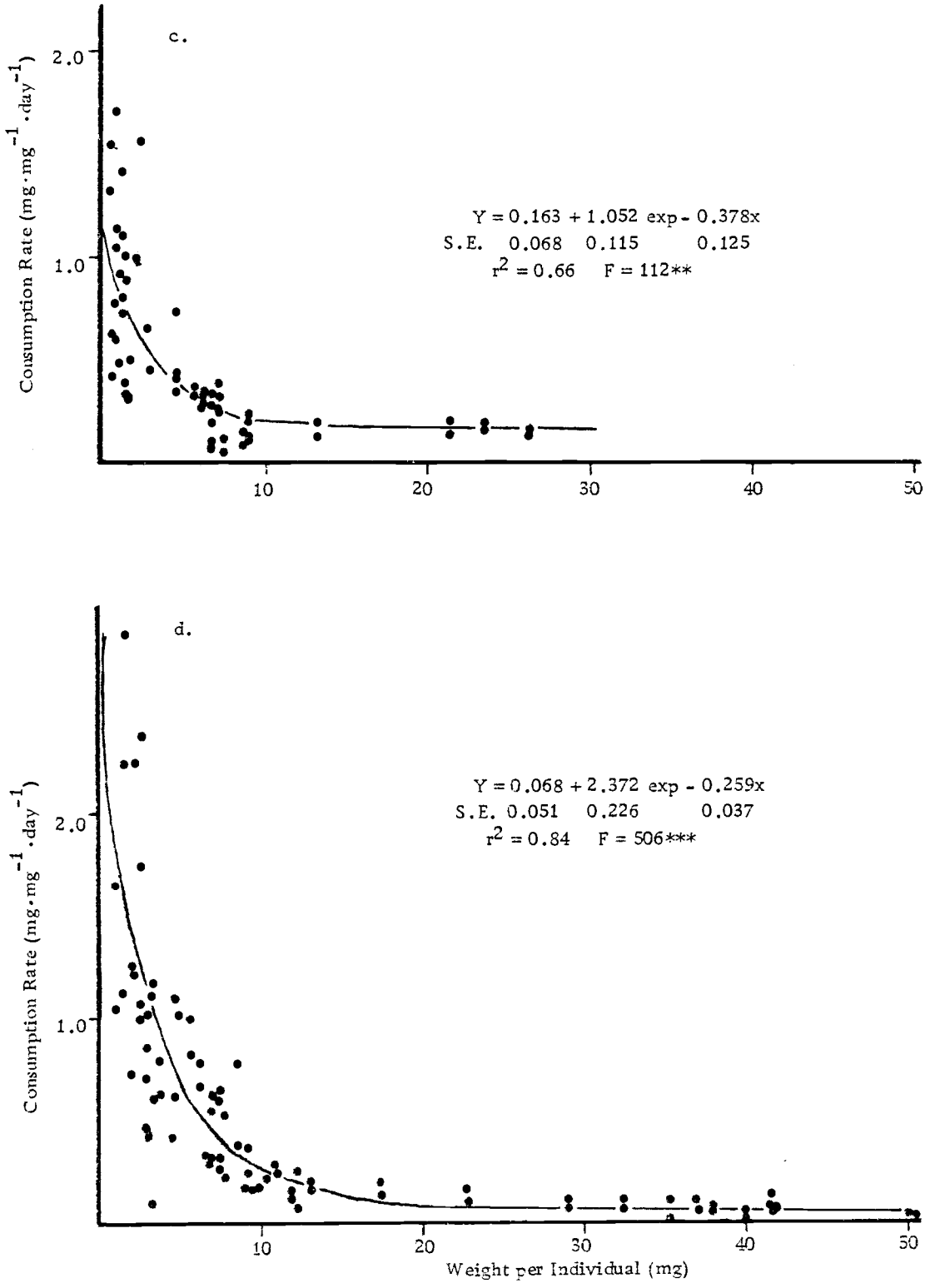

c.
Consumption Rate (mg·mg^{-1}·day^{-1})
2.0
1.0
Y = 0.163 + 1.052 exp - 0.378x
S.E. 0.068 0.115 0.125
r^2 = 0.66 F = 112**
10
20
30
40
50
d.
Consumption Rate (mg·mg^{-1}·day^{-1})
2.0
1.0
Y = 0.068 + 2.372 exp - 0.259x
S.E. 0.051 0.226 0.037
r^2 = 0.84 F = 506***
10
20
30
40
50
Weight per Individual (mg)

Figure 19.

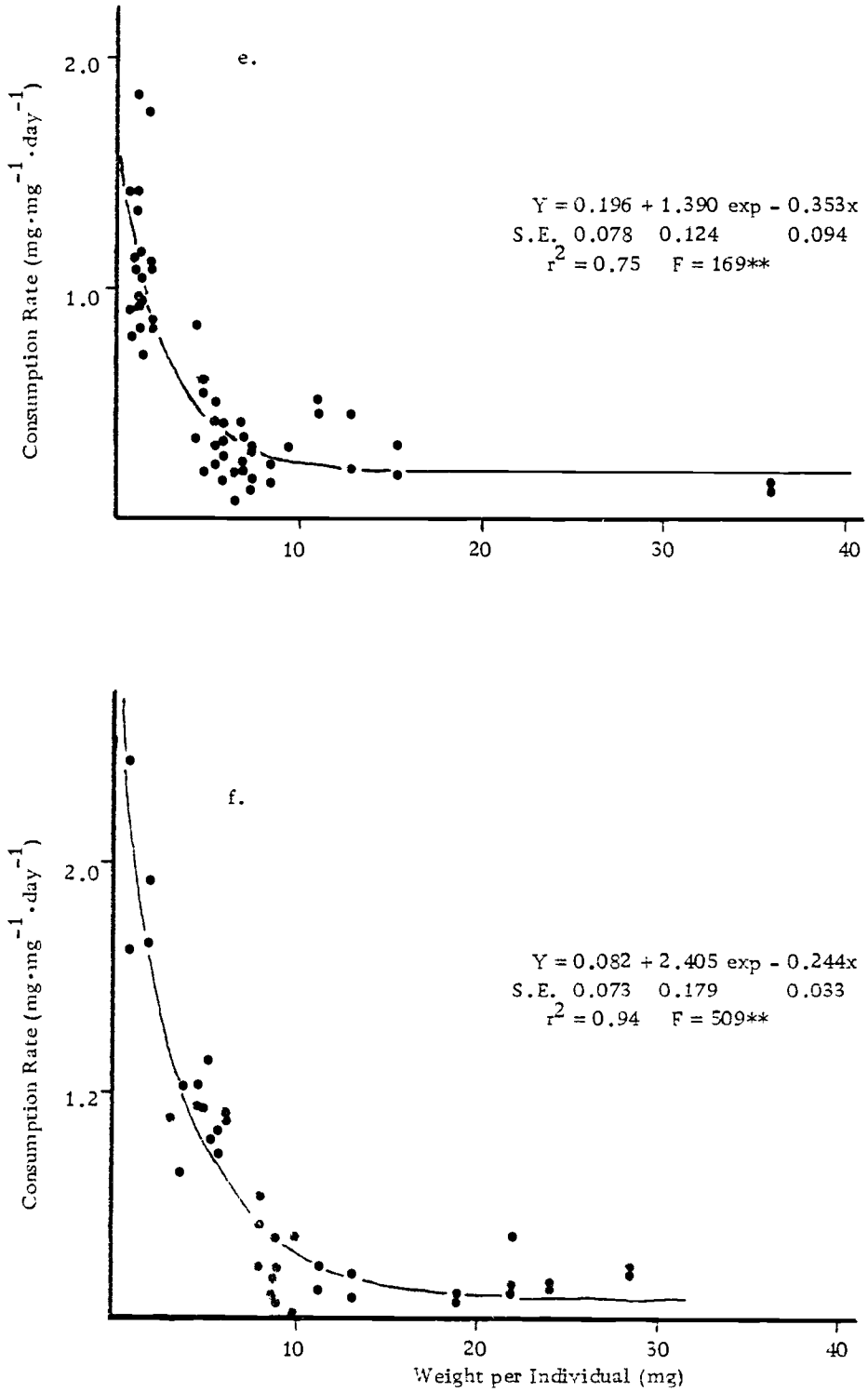

e.
Y = 0.196 + 1.390 exp - 0.353x
S.E. 0.078 0.124 0.094
r² = 0.75 F = 169**
Consumption Rate (mg·mg⁻¹·day⁻¹)
2.0
1.0
10
20
30
40
f.
Y = 0.082 + 2.405 exp - 0.244x
S.E. 0.073 0.179 0.033
r² = 0.94 F = 509**
Consumption Rate (mg·mg⁻¹·day⁻¹)
2.0
1.2
10
20
30
40
Weight per Individual (mg)

Figure 19.

(Y at X = infinity) or b_3 values (amount of inflection in the curves) between temperatures or foods. However, estimates for b_2 ($b_1 + b_2$ = Y-intercept) were significantly higher ($P \leq 0.05$) for the alder + wheat treatments than for treatments fed only alder at either 15 or 20°C. This indicates a higher consumption by small larvae when wheat was present. Estimates of b_2 were almost identical between temperatures for a particular food.

Estimates of consumption rates for specific sizes of larvae at the respective temperatures and foods were made from Figures 19 a-f. This approach allows the examination of temperature effects for specific sizes of larvae. As indicated in Figures 20 a and b, there was a large effect of temperature on consumption rate for small larvae and a much smaller effect for larger larvae. Figures 20 a and b further suggest that high temperatures might be beneficial to small larvae and detrimental to large larvae, at least with respect to consumption rates. This corresponds well with C. magnifica's life history since small larvae (first- through third-instar) are present when water temperatures are highest.

Analysis of the proportion of wheat consumed in the alder + wheat treatments at different temperatures (Fig. 21) shows a significant ($P \leq 0.01$) decrease in proportion of wheat consumed at higher temperatures. This correlates with the higher consumption of alder leaves at higher temperatures when alder was offered alone.

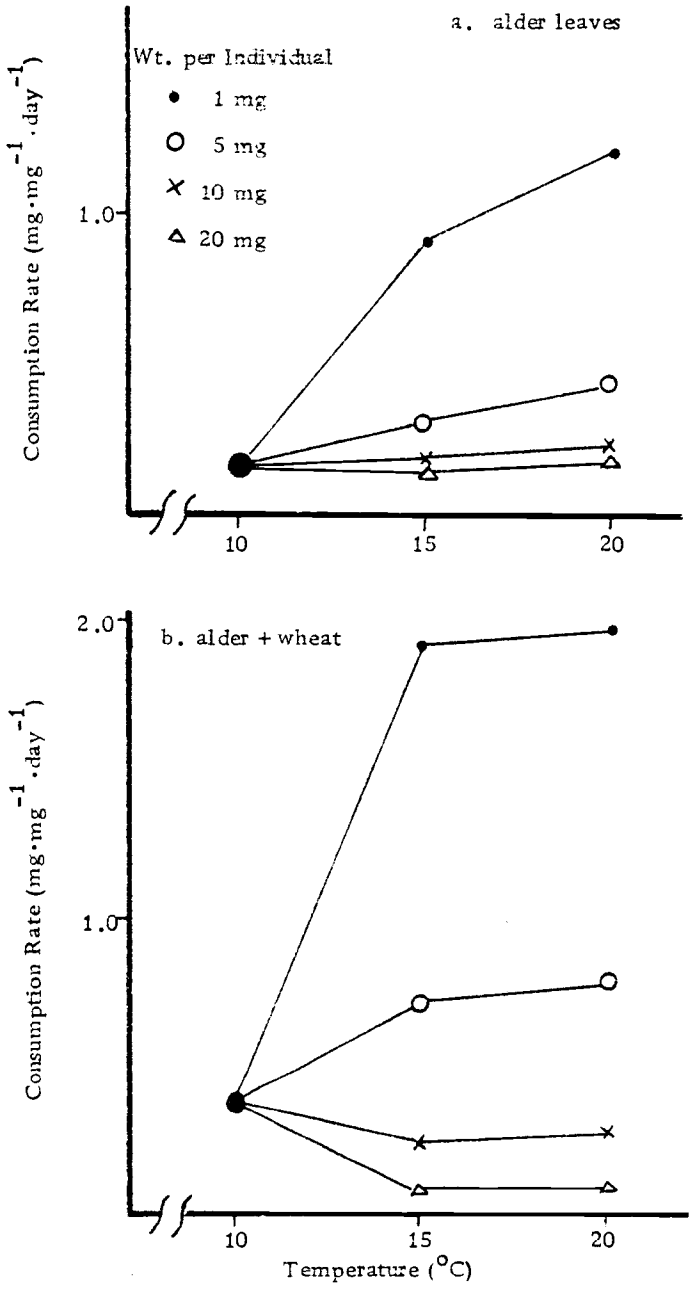


Figure 20. Consumption rates estimated from Figs. 19 a-f for different sizes of C. magnifica larvae fed alder leaves (a) or alder + wheat (b) at 10, 15, or 20°C.

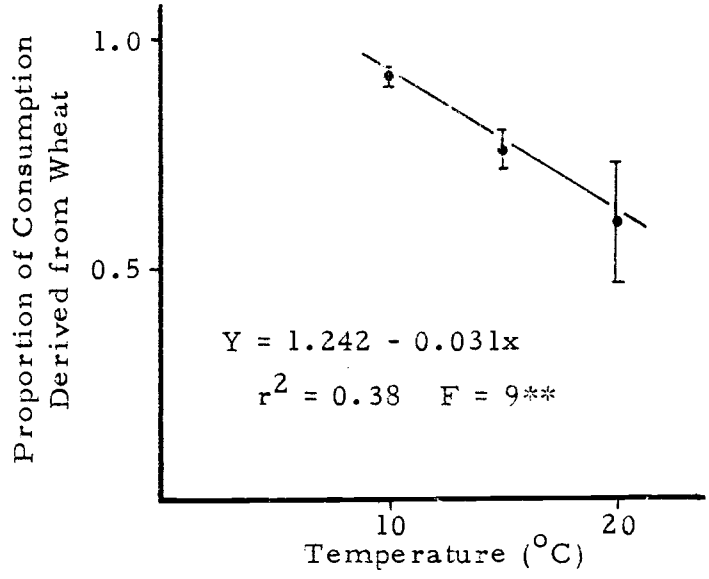


Figure 21. Proportion of consumption derived from wheat for C. magnifica larvae offered alder leaves and wheat grains at 10, 15, or 20°C.

Apparently alder leaves are somewhat more palatable at the higher temperatures. There was no significant effect ($P \leq 0.05$) of larval weight on the proportion of wheat consumed.

Mean assimilation efficiency was higher on alder + wheat than on alder alone (50.6% versus 29.3%). There was no significant effect ($P \leq 0.05$) of larval weight on assimilation efficiency. Wheat comprised an average of 78% of consumption in the alder + wheat treatment. Assuming that the alder in this treatment was assimilated with 29.3% efficiency ($A.E._a$), the assimilation efficiency of wheat ($A.E._w$) by C. magnifica can be calculated as:

$$A.E._a\ (0.22) + A.E._w\ (0.78) = 50.6\%$$

$$\text{then,} \quad A.E._w = \frac{50.6 - (29.3)(0.22)}{0.78}$$

$$= 56.6\%$$

This estimated assimilation efficiency for wheat is high for plant material, but is much lower than values reported for insects feeding on animal tissue. For example, Lawton (1971) measured assimilation efficiencies as high as 95% for the damselfly Pyrrhosoma nymphula (Sulz.).

In contrast to the decrease in efficiency for L. quercina, mean assimilation efficiencies of alder leaves by C. magnifica increased with temperature (Fig. 22). This increase is apparently related to the increased palatability of the alder leaves at higher temperatures. Assimilation efficiency of alder + wheat by C. magnifica did not increase, since the proportion of less-assimilable alder leaves in the diet was increasing.

Since food was conditioned for two weeks at 13-15°C and was at the experimental temperature for only a short length of time, it was concluded that differences in food quality were not responsible for the changes in assimilation efficiencies with temperature for either species. As was suggested for L. quercina, these changes in assimilation efficiency may reflect physiological adaptations to temperature. However, unlike L. quercina, C. magnifica larvae seem to be better adapted to warm temperatures.

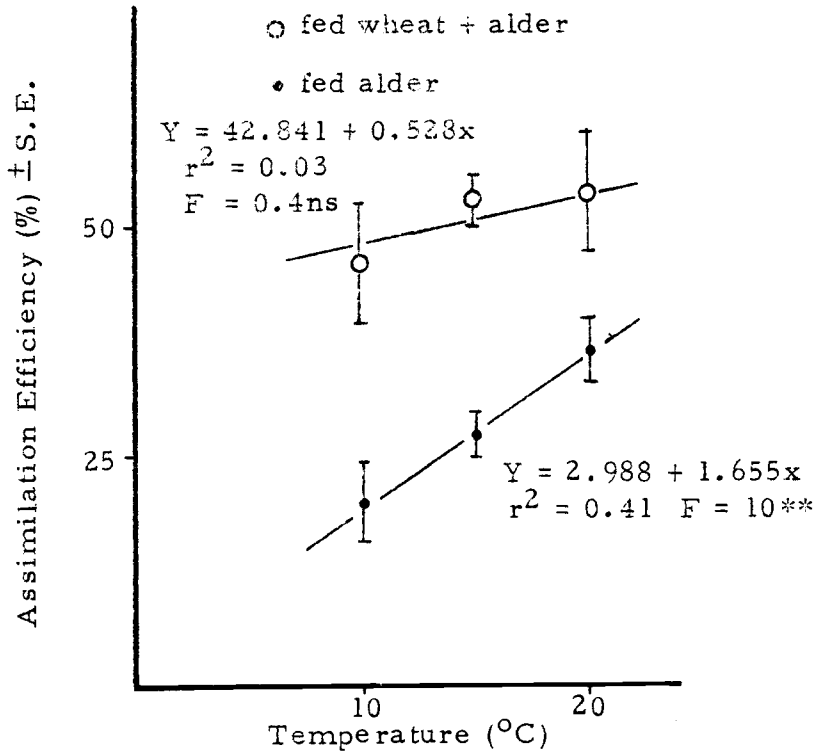


Figure 22. Assimilation efficiency of alder leaves or alder leaves plus wheat grains for third- through fifth-instar C. magnifica larvae at 10, 15, or 20°C.

Gross and net growth efficiencies, estimated from consumption versus weight relationships assuming linear growth (see Methods), indicate that the most efficient growth occurs at 15°C on alder + wheat (Table 12). This is perhaps expected since less energy will generally be spent on maintenance when growth is rapid and the life cycle is short. Gross growth efficiency at 15° on alder (6.3%) is similar to values for L. quercina and L. unicolor (3.1% and 6.0%, respectively). Net growth efficiency (21.3%) is intermediate between those of L. quercina and L. unicolor (12.6% and 60%). Values reported by Otto (1974) for the caddis Potamophylax cingulatus (Steph.) (Limnephilidae) were generally similar to these values (gross growth efficiency = 9.4%,

Table 12. Gross and net growth efficiencies for C. magnifica reared in the laboratory under different conditions.

Temperature (°C)	Food	Total Consumption per Individual (mg)	Length of Larval Stage (days)	Gross Growth Efficiency (%)	Net Growth Efficiency (%)
10	Alder + Wheat	3816.9	290+	1.7	3.3
15	Alder	407.1	171	6.3	21.3
15	Alder + Wheat	268.1	116	16.7	33.0
20	Alder + Wheat	362.5	160	9.7	19.1

net growth efficiency = 42.8%). Net growth efficiencies reported in the literature for other aquatic consumers range from 10 to 90% and tend to be inversely related to assimilation efficiency (Welch 1961). As was suggested for L. unicolor, larvae utilizing very poorly assimilable food sources may be required to be more efficient in the utilization of assimilated material.

Nitrogen Excretion by L. quercina

Ammonia-nitrogen excretion by mid-final instar L. quercina larvae fed on alder leaves was estimated as 3.7 $\mu g \cdot mg^{-1} \cdot day^{-1}$ (Table 13). Assuming that consumption rate is 0.50 $mg \cdot mg^{-1} \cdot day^{-1}$, nitrogen excretion is approximately 0.7% of consumption.

Alder leaves are high in nitrogen in comparison with other species (Goldman 1961, Kaushik and Hynes 1971, Triska and Sedell 1976). Even assuming that one-half of the initial nitrogen is lost by leaching in the first few days (Triska and Sedell 1976), more than enough is potentially available to permit excretion of 0.7% of consumption and 3% per day growth. However, the amount of nitrogen that is present in usable form is not known (see Discussion). Since nitrogen excretion was a minor portion of the material transferred, it was assumed to be proportional to consumption and to vary with food type and no further experiments were conducted on L. quercina or other species. However, if nitrogen is limiting to growth, it will be the

Table 13. Nitrogen excretion by mid-final instar *L. quercina* larvae.

Treatment	Total Weight of Insects or Cases (mg)	Time (hrs)	Final Ammonia-Nitrogen Concentration ($\mu g \cdot ml^{-1}$ = ppt)	Ammonia-N Production ($\mu g \cdot mg^{-1} \cdot day^{-1}$)
10 Insects	17.52	2.5	0.39	4.17
		2.5	0.39	4.17
		3.0	0.39	3.48
		3.5	0.39	2.98
Cases only	22.19	22.0	0.16	-
		23.0	0.08	-
Water	-	0.0	0.16	-
	-	0.0	0.08	-
$\bar{x} \pm s_{\bar{x}}$				3.70 ±0.29

critical material to measure in order to assess food quality and potential for growth.

Respiration Measurements

Mean respiration rates for larvae of L. quercina, L. unicolor, and C. magnifica were very similar, in spite of the large differences in size of the larvae (Table 14). Multiple regression analyses of respiration rate versus larval weight and temperature showed significant effects of both on respiration rates of L. quercina and L. unicolor (App. Table 11). Larval weight also significantly affected respiration rates of C. magnifica larvae. However, the effect of temperature on respiration rates of C. magnifica was not significant. Respiration rates for C. magnifica increased between 5 and 10°C and then decreased slightly between 10 and 20°. Few measurements were made with L. quercina larvae at 20°C and none was made with L. unicolor larvae at 20° because of poor survival during the acclimation period.

In order to more closely examine the effects of size on respiration rates for the respective species and temperatures, regression analyses of respiration rate versus weight were performed with the data for each species and temperature (Figs. 23 a-k). Respiration rates decreased significantly with increased weight for all species and temperatures.

Table 14. Mean respiration rates for three species of caddis larvae at different temperatures.

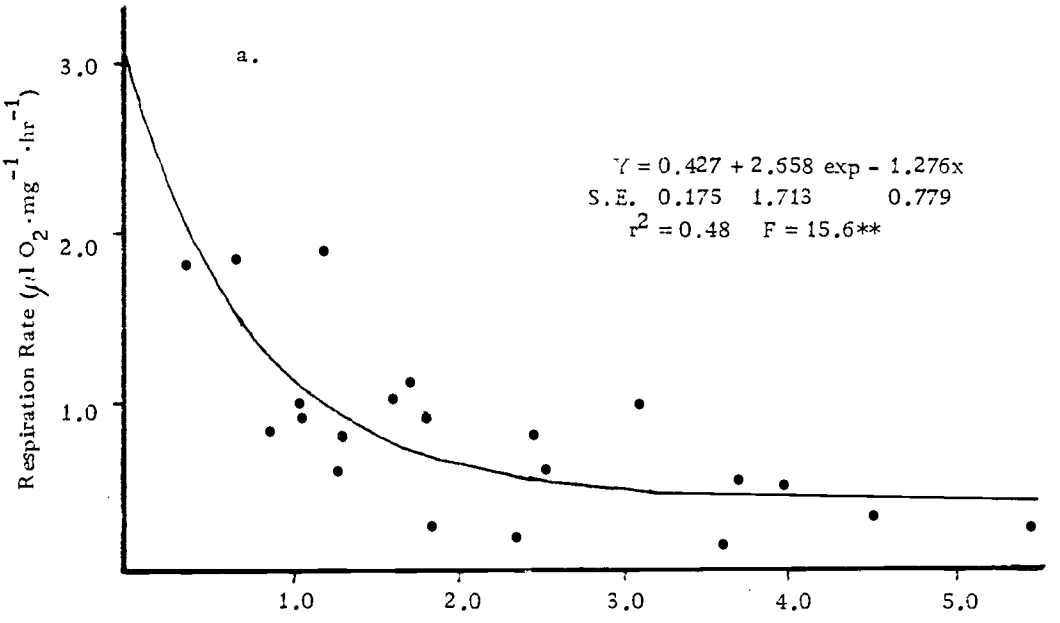
Species	Temp. (°C)	n	Mean Weight $\pm s_{\bar{x}}$ (mg)	Mean Respiration Rate $\pm s_{\bar{x}}$ ($\mu l\ O_2 \cdot mg^{-1} \cdot hr^{-1}$)
L. quercina	5	20	2.34 ± 0.33	0.77 ± 0.11
	10	19	2.04 ± 0.36	1.39 ± 0.14
	15	28	1.43 ± 0.13	1.48 ± 0.12
	20	11	1.36 ± 0.23	1.63 ± 0.20
L. unicolor	5	18	3.64 ± 0.38	0.63 ± 0.07
	10	17	3.68 ± 0.24	0.96 ± 0.10
	15	14	2.78 ± 0.31	1.40 ± 0.12
C. magnifica	5	16	17.36 ± 4.02	0.59 ± 0.06
	10	28	20.77 ± 3.33	1.12 ± 0.12
	15	35	20.44 ± 3.58	0.98 ± 0.13
	20	29	23.33 ± 2.90	0.82 ± 0.09

Figure 23. Respiration rates at different temperatures for three species of caddis larvae compared with individual size.

L. quercina larvae: (a) 5°C; (b) 10°C; (c) 15°C; (d) 20°C.

L. unicolor larvae: (e) 5°C; (f) 10°C; (g) 15°C.

C. magnifica larvae: (h) 5°C; (i) 10°C; (j) 15°C; (k) 20°C.


a.
Y = 0.427 + 2.558 exp - 1.276x
S.E. 0.175 1.713 0.779
r2 = 0.48 F = 15.6**
Respiration Rate (µl O2·mg-1·hr-1)
3.0
2.0
1.0
1.0
2.0
3.0
4.0
5.0

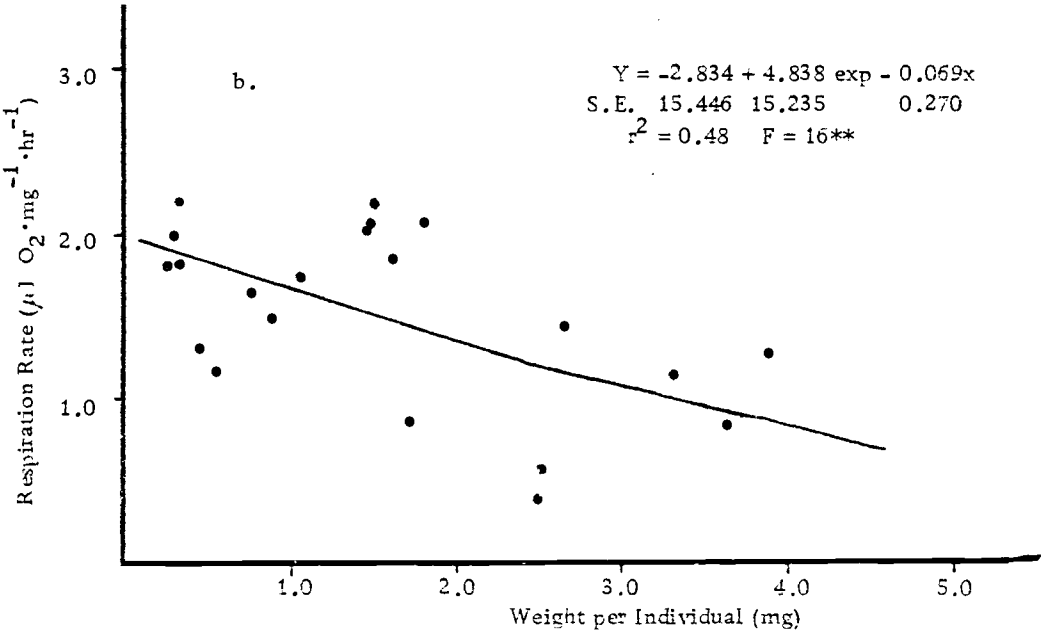

b.
Y = -2.834 + 4.838 exp - 0.069x
S.E. 15.446 15.235 0.270
r2 = 0.48 F = 16**
Respiration Rate (µl O2·mg-1·hr-1)
3.0
2.0
1.0
1.0
2.0
3.0
4.0
5.0
Weight per Individual (mg)

Figure 23.

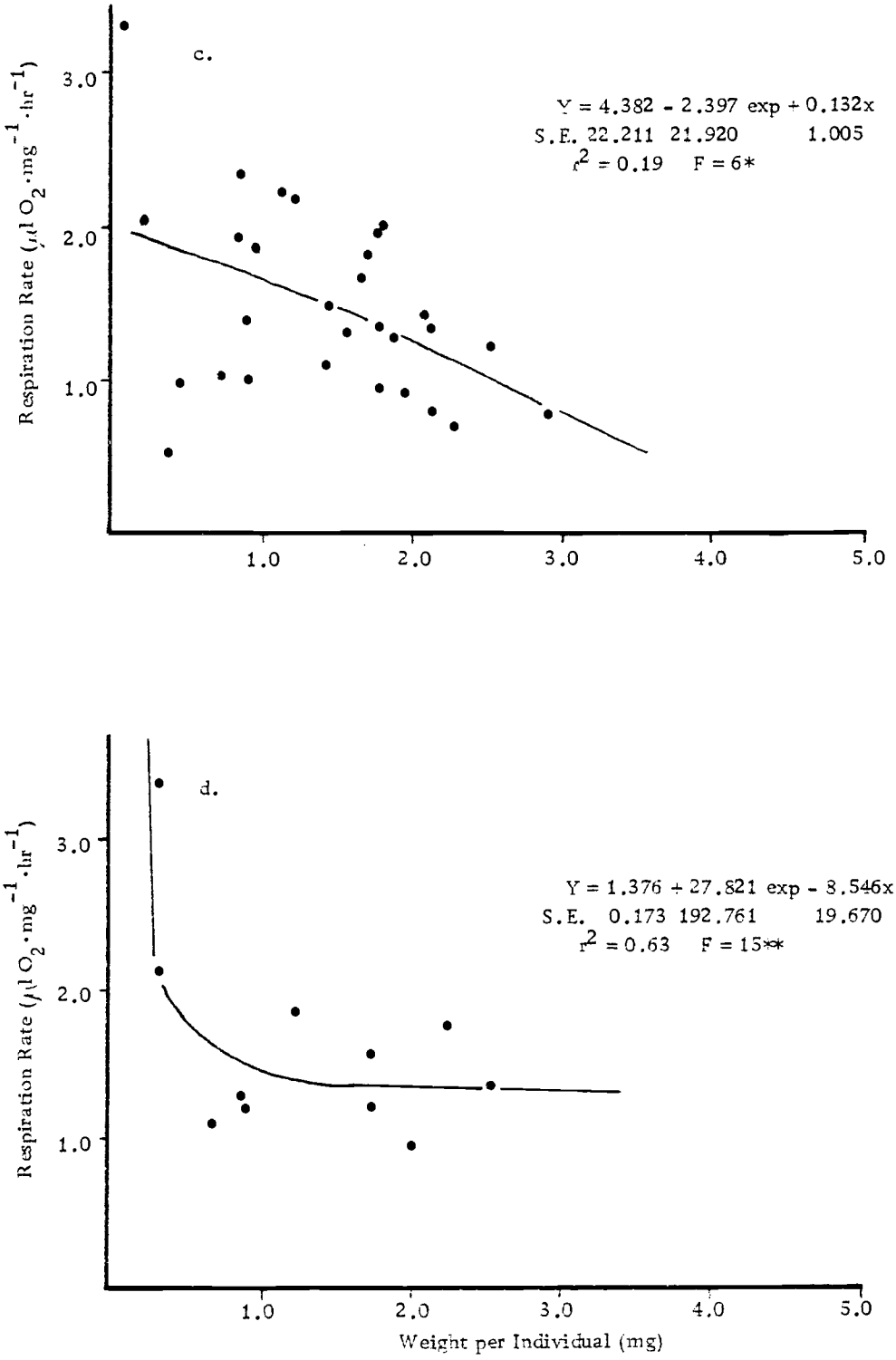

c.
Y = 4.382 - 2.397 exp + 0.132x
S.E. 22.211 21.920 1.005
r^2 = 0.19 F = 6*
Respiration Rate (μl O_2 · mg^{-1} · hr^{-1})
3.0
2.0
1.0
1.0
2.0
3.0
4.0
5.0
d.
Y = 1.376 + 27.821 exp - 8.546x
S.E. 0.173 192.761 19.670
r^2 = 0.63 F = 15**
Respiration Rate (μl O_2 · mg^{-1} · hr^{-1})
3.0
2.0
1.0
1.0
2.0
3.0
4.0
5.0
Weight per Individual (mg)

Figure 23.

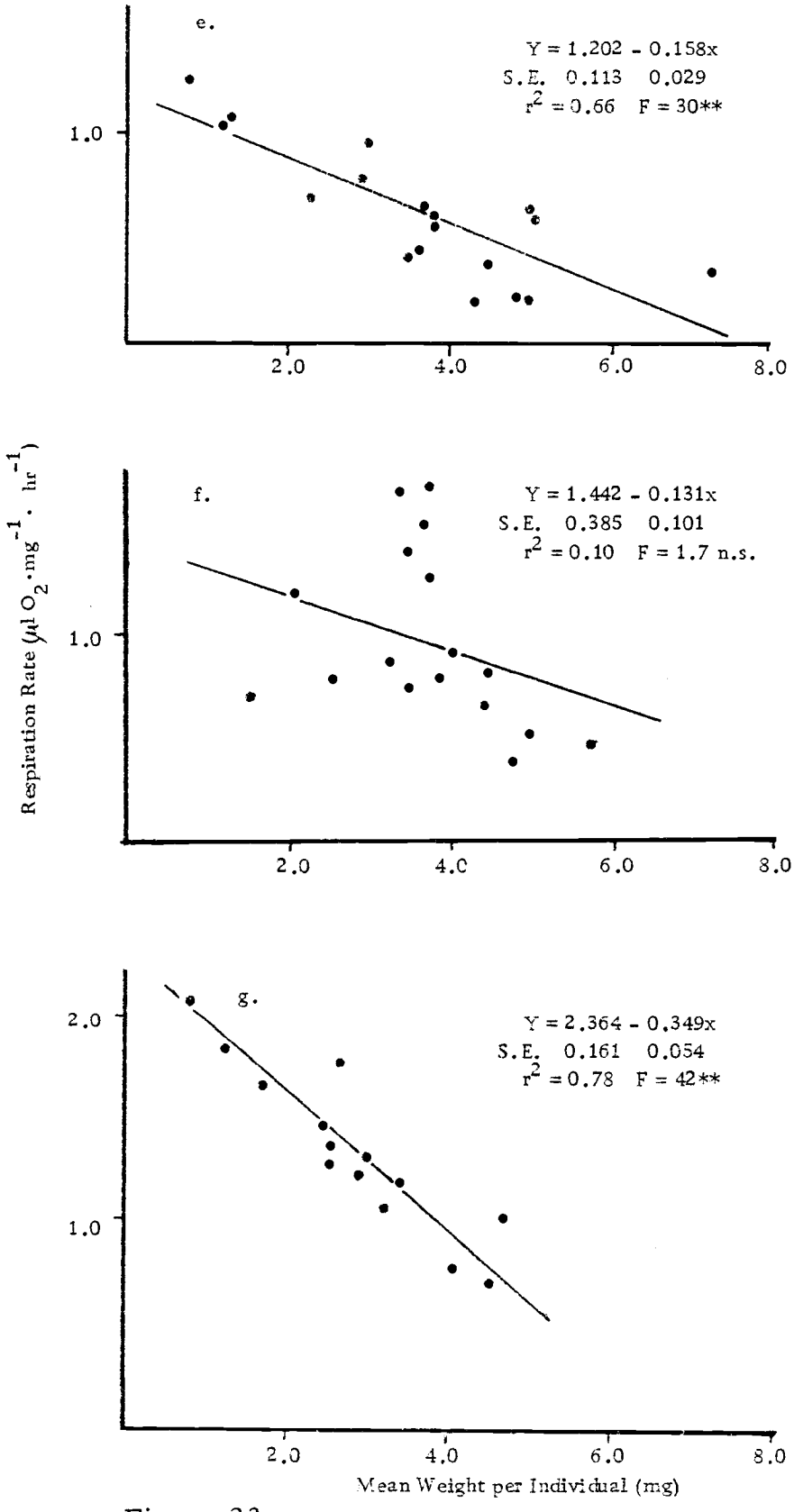
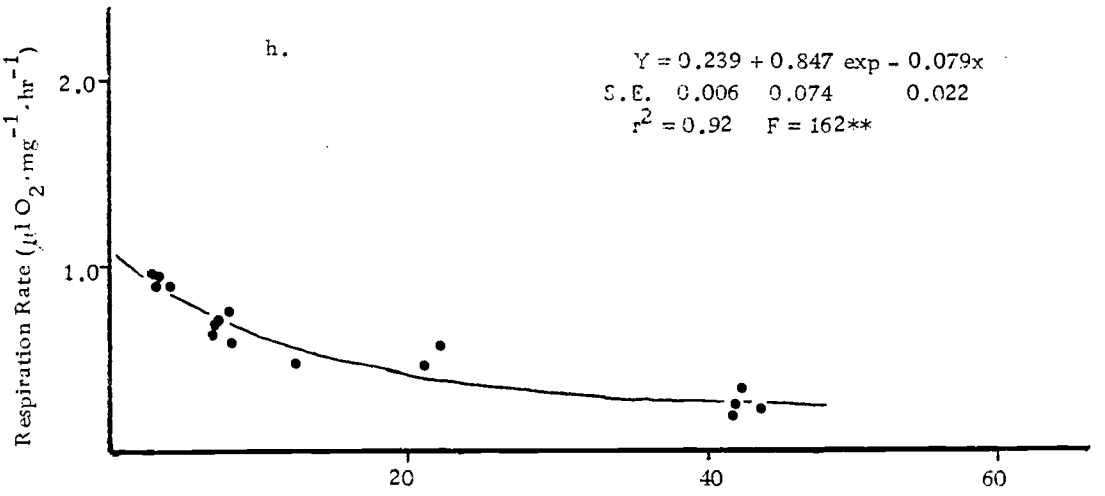

e.
Y = 1.202 - 0.158x
S.E. 0.113 0.029
r^2 = 0.66 F = 30**
f.
Y = 1.442 - 0.131x
S.E. 0.385 0.101
r^2 = 0.10 F = 1.7 n.s.
g.
Y = 2.364 - 0.349x
S.E. 0.161 0.054
r^2 = 0.78 F = 42**
Respiration Rate ($\mu l\ O_2 \cdot mg^{-1} \cdot hr^{-1}$)
Mean Weight per Individual (mg)
1.0
2.0
2.0
4.0
6.0
8.0

Figure 23.


h.
Y = 0.239 + 0.847 exp - 0.079x
S.E. 0.006 0.074 0.022
r2 = 0.92 F = 162**
Respiration Rate (µl O2 · mg-1 · hr-1)
2.0
1.0
20
40
60

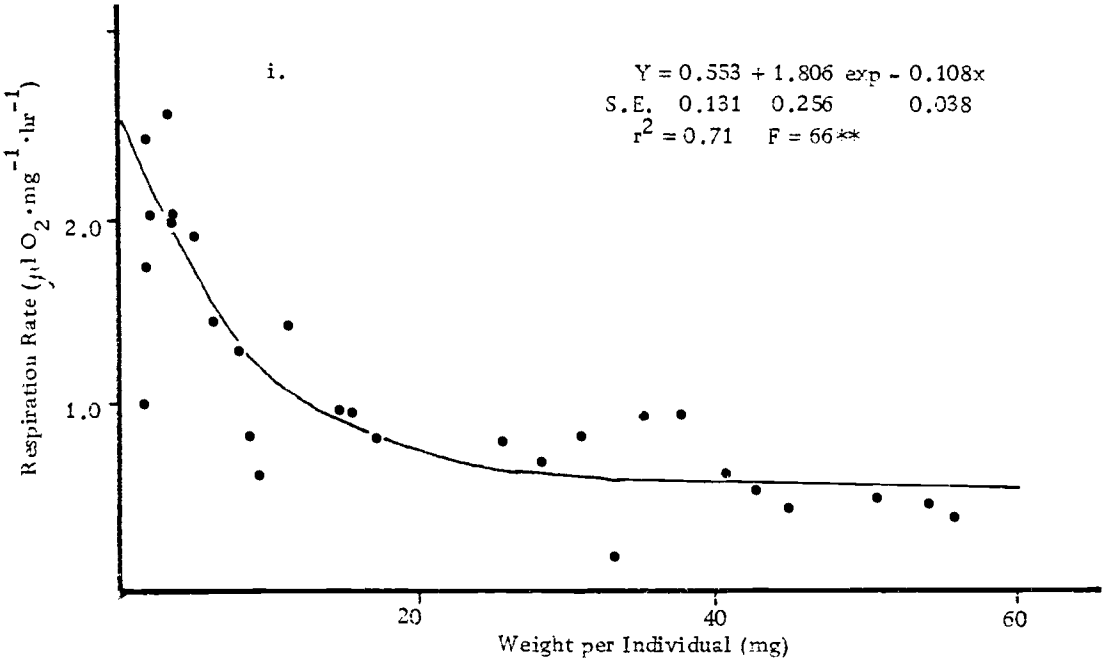

i.
Y = 0.553 + 1.806 exp - 0.108x
S.E. 0.131 0.256 0.038
r2 = 0.71 F = 66**
Respiration Rate (µl O2 · mg-1 · hr-1)
2.0
1.0
20
40
60
Weight per Individual (mg)

Figure 23.

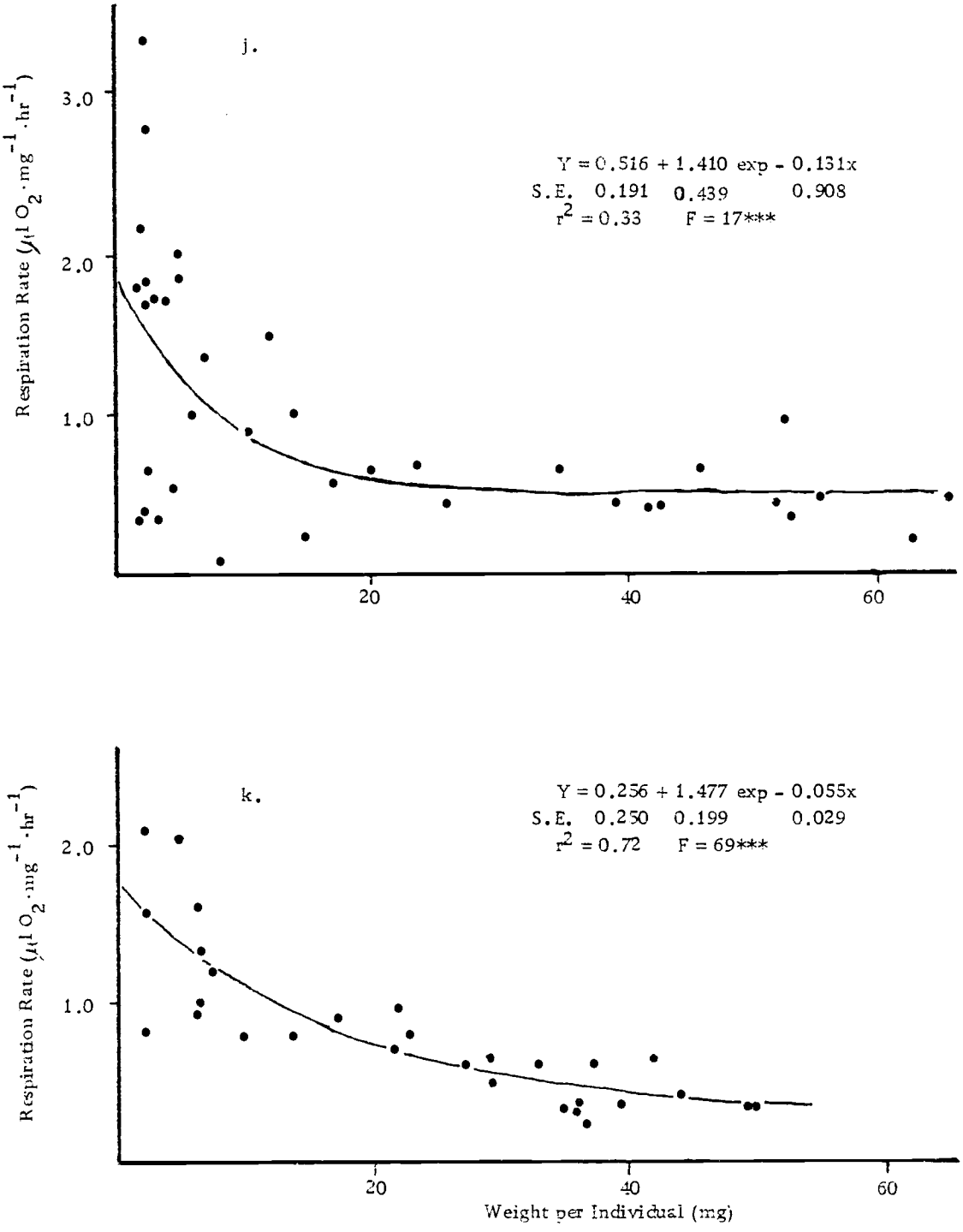

j.
Y = 0.516 + 1.410 exp - 0.131x
S.E. 0.191 0.439 0.908
r2 = 0.33 F = 17***
Respiration Rate (µl O2 · mg-1 · hr-1)
3.0
2.0
1.0
20
40
60
k.
Y = 0.256 + 1.477 exp - 0.055x
S.E. 0.250 0.199 0.029
r2 = 0.72 F = 69***
Respiration Rate (µl O2 · mg-1 · hr-1)
2.0
1.0
20
40
60
Weight per Individual (mg)

Figure 23.

Respiration rates for specific weights of larvae were estimated from Figures 23 a-k and are shown in Figures 24 a-c. The respiration rates of 0.5 mg L. quercina larvae (Fig. 24a), found in the field in September and October when temperatures may fluctuate, were affected by temperature much less than were respiration rates of the 3.0 mg larvae (found in the field from December through February). For L. unicolor (Fig. 24b), respiration rates of all but the largest larvae show sharp increases with increases in temperature. The small larvae are exposed to only slight changes in temperature throughout the winter and spring and late-final instar larvae occur in June and July when water temperatures are increasing. Respiration rates for C. magnifica (Fig. 24c) show only slight changes with changes in temperature from 10 to 20°C, except for the 1.0 mg larvae (ca. second instar), where respiration decreases with temperature. These small larvae are found in the field in late summer and early fall and may experience large diel and seasonal temperature changes.

It appears that a regulatory response to temperature (i.e. no change in respiration with changes in temperature) occurs for species or stages that normally encounter temperature fluctuations over the particular temperature range. Increases in respiration rate with temperature may indicate species or stages unaccustomed to temperature changes (e.g. L. unicolor) or species or stages leaving or entering a normal temperature range (e.g. L. quercina between 5 and

Figure 24. Respiration rates for specific sizes of L. quercina (a), L. unicolor (b), or C. magnifica (c) larvae, estimated from Figures 23 a-k.

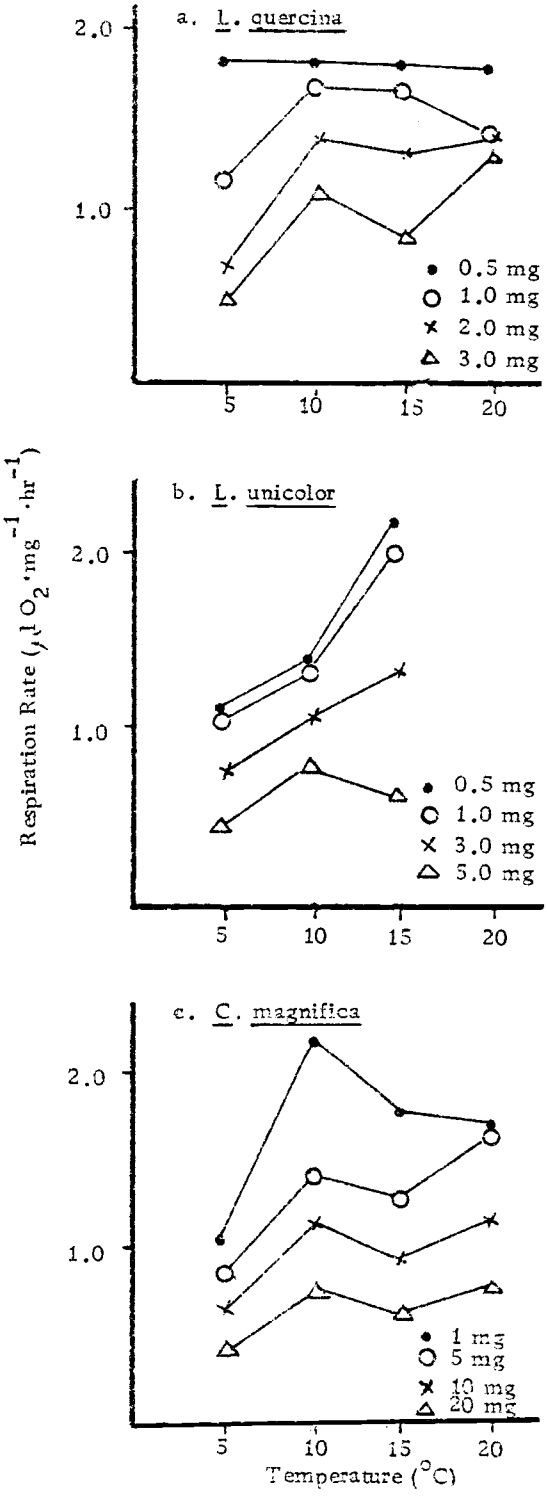

a. L. quercina
2.0
1.0
0.5 mg
1.0 mg
2.0 mg
3.0 mg
5
10
15
20
b. L. unicolor
2.0
1.0
0.5 mg
1.0 mg
3.0 mg
5.0 mg
5
10
15
20
Respiration Rate (μl O2 ·mg-1 ·hr-1)
c. C. magnifica
2.0
1.0
1 mg
5 mg
10 mg
20 mg
5
10
15
20
Temperature (°C)

Figure 24.

10°C). However, it is necessary to compare respiration rates and consumption rates to determine the ultimate effects on growth. For example, an increase in respiration rate may be using energy that otherwise could be used for growth or may be coupled with an increase in consumption rate and be indicative of a general increase in activity. The latter apparently occurs for the species studied with changes in temperature from 5 to 10°C.

The estimates of respiratory and consumption Q_{10} values (Table 15) are lowest for C. magnifica, the species experiencing the largest temperature fluctuations and were highest for L. unicolor, which experiences very little fluctuations in temperature. Respiratory and consumption Q_{10}'s for C. magnifica indicate almost complete compensation for the effects of changes in temperature, while Q_{10}'s for L. quercina suggest a partial ability to maintain constant respiration and consumption rates. Consumption and respiration rates of L. unicolor are most affected by changes in temperature.

Comparisons of Assimilation and Respiration

In order to assess the effects of temperature and food on the species studied, the amount of material potentially available for growth was estimated as assimilation minus respiration and nitrogen excretion (Table 16). The resulting "scope for growth" (similar to Warren 1971, except based on mass balance), increased with

Table 15. Estimated respiratory and consumption Q_{10} values for larvae of three species of caddis.

Species	Respiratory Q_{10}	Consumption Q_{10}	Usual Temperature Range Experienced (^{o}C)
Lepidostoma unicolor	1.99 (5-15^{o}C)	1.75 (5-21^{o}C, Douglas fir)	2-10
Lepidostoma quercina	1.49 (5-20^{o}C)	1.58 (5-21^{o}C, alder)	2-15
Clistoronia magnifica	1.12 (5-20^{o}C)	1.05 (10-20^{o}C, wheat + alder)	4-25+
		1.64[a] (10-20^{o}C, alder)	

[a] Influenced by increased palatability and digestability of alder leaves at higher temperatures.

Table 16. Relationships between consumption, assimilation, and respiration rates for three species of caddis larvae at different temperatures and foods.

Species (Food)	Temp. (°C)	Mean Consumption Rate ($mg \cdot mg^{-1} \cdot day^{-1}$)	($\overline{wt}$)	Assimilation Rate[a] ($mg \cdot mg^{-1} \cdot day^{-1}$)	Mean Respiration Rate[b] ($mg \cdot mg^{-1} \cdot day^{-1}$)	($\overline{wt}$)	Scope for Growth (Assimilation - Respiration) ($mg \cdot mg^{-1} \cdot day^{-1}$)
L. quercina (alder)	5	0.33	2.07	0.079	0.017	2.34	0.062
	13-15	0.44	2.51	0.106	0.033	1.43	0.073
	20-21	0.69	2.33	0.166	0.037	1.36	0.129
L. unicolor (Douglas fir)	5	0.44	2.78	0.029	0.014	3.64	0.015
	15	0.90	1.75	0.059	0.032	2.78	0.027
C. magnifica (alder)	10	0.16	8.91	0.038[c]	0.025	20.77	0.001[c]
	15	0.48	6.53	0.115[c]	0.022	20.44	0.027[c]
	20	0.62	5.13	0.149[c]	0.019	23.33	0.091[c]
C. magnifica (alder+wheat)	10	0.41	14.43	0.203[c]	0.025	20.77	0.173[c]
	15	0.50	19.13	0.248[c]	0.022	20.44	0.221[c]
	20	0.61	9.64	0.303[c]	0.019	23.33	0.278[c]

[a] Assuming assimilation efficiencies of 7.5% on Douglas fir, 25% on alder, and 50.6% on alder+wheat and subtracting 1% of consumption lost to nitrogen excretion.

[b] Assuming 4.9 cal/ml O_2 (McDiffett 1970) and 5200 cal/g of tissue (Cummins and Wuycheck 1971).

[c] Assimilation and respiration rates corrected to correspond to a 10 mg individual, assuming a linear relationship between rate and size (App. Table 10).

temperature for all three species and was higher for C. magnifica larvae fed wheat than for those fed only alder. The values suggested higher growth rates than actually occur, especially at high temperatures. For example, scope for growth for L. quercina is 6 to 12% per day, compared with a maximum observed growth rate of less than 3% per day. Scope for growth for L. quercina was highest at 21°C, while actual growth measured at 21° was near zero.

Predicted growth rates for Gammarus pulex L. (Nilsson 1974) and P. cingulatus (Otto 1974), other species studied in depth in this respect, were also much higher than observed growth rates. Otto (1974) measured exuviae and silk secretions and found them to be relatively minor in relation to growth. Nitrogen excretion, measured in this study, can also be only a minor loss. Assuming that parameters in the above studies were measured and interpreted correctly, the only quantity that might account for the differences between calculated and observed growth is dissolved organic losses (e.g. losses due to digestive secretions, salivary secretions, or incomplete absorption of digested food). Significant excretion of dissolved organics has been shown for a variety of aquatic invertebrates (Johannes and Satomi 1967, Hargrave 1971, McCullough O.S.U. Dept. of Fisheries and Wildlife unpubl.) and has been estimated to be as much as 36% of assimilation (Hargrave 1971).

Dissolved organic losses might be particularly important at high temperatures where consumption rates are highest and gut retention time may be too short to allow complete absorption of the digested nutrients. An increase in excretion or loss of dissolved organics might also be expected at higher temperatures if there was a lack of coordination among the various metabolic pathways, allowing the build-up of intermediate metabolic products; or if enzyme-substrate affinities (and therefore enzymatic efficiencies) were very low.

Field Population Studies

L. quercina Populations in Berry Creek

Population density estimates for *L. quercina* in a riffle-pool section of Berry Creek indicate a decrease in mean density from 382 per m^2 in August to 0.5 per m^2 in February (Fig. 25). Mean weights per individual increased from 0.043 mg to 3.657 mg. As is true for most species of caddis, the majority of *L. quercina*'s growth occurred during the final instar (Fig. 25) and mean weights of final-instar larvae increased from 0.442 mg per individual in October to 3.719 mg per individual in January (App. Table 12).

Minimum biomass was 6.7 mg per m^2 in September and maximum was 119.8 mg per m^2 in January (App. Table 13). Larvae were more concentrated in pool and pool-end areas than in the riffle area (2.8:1 for August through September, 11.0:1 for November through

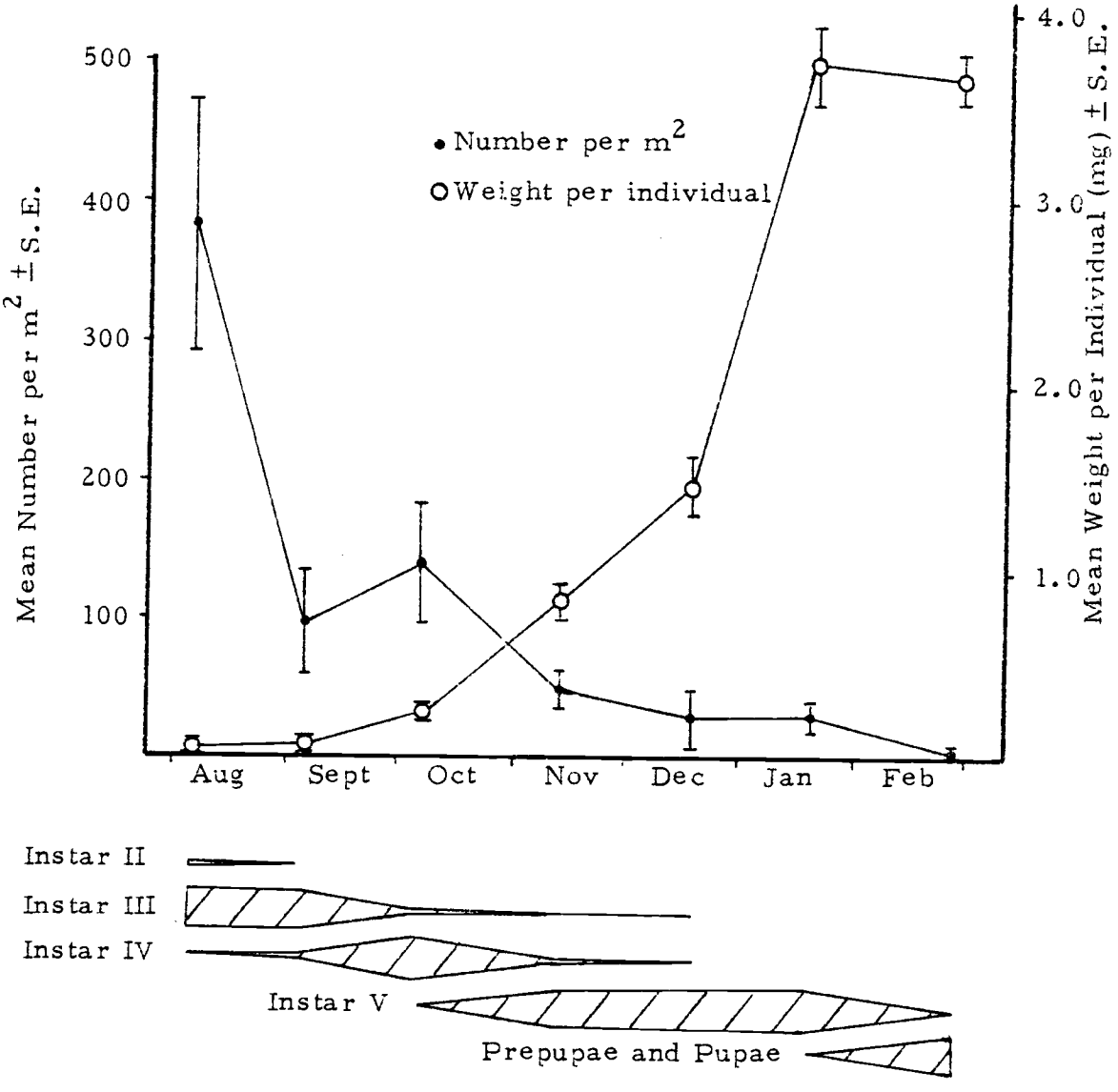


Figure 25. Densities, mean weights, and instar distributions for L. quercina from Berry Creek.

January). There was little difference between mean densities of larvae in pool or pool-end areas.

Weight of alder and other deciduous leaves in Berry Creek was low throughout the summer and early fall and increased by factors of five to ten after the first heavy rains in early November (App. Table 14). In contrast to larval distributions, alder and other leaves were more concentrated in the pool-end area than in the pool area, and were least abundant in the riffle area (33.8:5.5:1, respectively).

Although absolute quantities of alder leaves increased, the ratio of alder to other leaves was much higher in August and October (0.3:1 and 0.4:1, respectively) than in November (0.1:1) or January (0.1:1). This reflects the fact that alder leaves begin falling earlier than other species. In this respect, alder may be a better food source since leaves are available in the late summer when water temperatures are warmer and conditions may be better for insect growth. Alder leaf fall is also more extended than leaf fall for most species and alder is consequently available as food from July through January.

L. unicolor Populations Estimated for Clear-cut and Old-growth Sections of Mack Creek

Total numbers of fourth- and fifth-instar L. unicolor per 50 m section were much higher in the old-growth section of stream than in the clear-cut section (Table 17), although total areas in each section

were nearly equal (300 and 350 m^2, respectively). Maximum densities were 5.3 per m^2 in the old-growth section and 0.5 per m^2 in the clear-cut section. This difference was due, in part, to a larger area of suitable habitat in the old-growth section. Also, larval densities per m^2 of suitable habitat were consistently higher in the old-growth section (Table 17), suggesting different levels of "suitability."

The area of suitable habitat in the old-growth section was drastically reduced in early July when the largest pool in the study section dried up. Although larvae were no longer visible on the surface of the debris in this pool, many of the larvae may have burrowed into the damp substrate to complete their development, since pupae were found in core samples taken from this area.

Mean weights of larvae from the clear-cut section were generally higher than those of larvae from the old-growth section (App. Table 15), suggesting slightly more rapid development in the clear-cut. However, a paired t-test (Steel and Torrie 1960) showed no significant difference ($P \leq 0.05$) between mean weights from the two locations. Instar distributions for larvae from the two locations also suggested that larvae from the clear-cut location were slightly more advanced in development during April and May (App. Table 15), perhaps as the result of slightly higher temperatures in the clear-cut.

Table 17. Population densities of L. unicolor in 50 m lengths of clear-cut and old-growth sections of Mack Creek.

Date	Population Density					
	Clear-cut			Old-growth		
	m^2 of suitable habitat	total no.	no. /m^2 of suitable habitat	m^2 of suitable habitat	total no.	no. /m^2 of suitable habitat
4-26-74	0.3	33	110	(not sampled)		
5-10-74	4.2	119	28	9.2	437	48
6- 5-74	2.6	86	33	9.8	455	46
6-28-74	3.9	163	42	13.1	1584	121
7-10-74	3.4	86	25	3.6	267	74
7-17-74	1.8	0	0	0.7	41	59
8- 1-74	1.5	0	0	0.8	7	9

L. cascadense and L. unicolor Populations in a Riffle-Pool Area of Mack Creek (Old-growth Section)

L. cascadense. Larval densities of L. cascadense were the highest of any of the three Lepidostoma species studied. Maximum density was 812 per m^2 (App. Table 16), compared with a maximum of 382 L. quercina per m^2 in Berry Creek. Larval densities of L. cascadense decreased during the fall and early winter and remained fairly constant at 100 to 200 per m^2 during the late winter and early spring (Fig. 26). Larvae, especially in the fourth- and fifth-instars, were more abundant in the pool than in the riffle area (17.6:1). Total numbers estimated in the study section were perhaps a better index of population dynamics since water levels and total area in the study section fluctuated widely, in contrast to conditions in Berry Creek. Total numbers of L. cascadense were more constant than numbers per m^2 during the early winter and in the spring, times when water levels were changing. Total numbers decreased sharply from December to January, as later-instar larvae became predominant.

Mean weight per individual increased from 0.060 mg in October to 1.773 mg in late May (Fig. 26). Mean weight decreased slightly from November to December due to an influx of first-instar larvae. These newly-hatched individuals may have come from egg masses wetted by the rising water levels. As was found for L. quercina, the

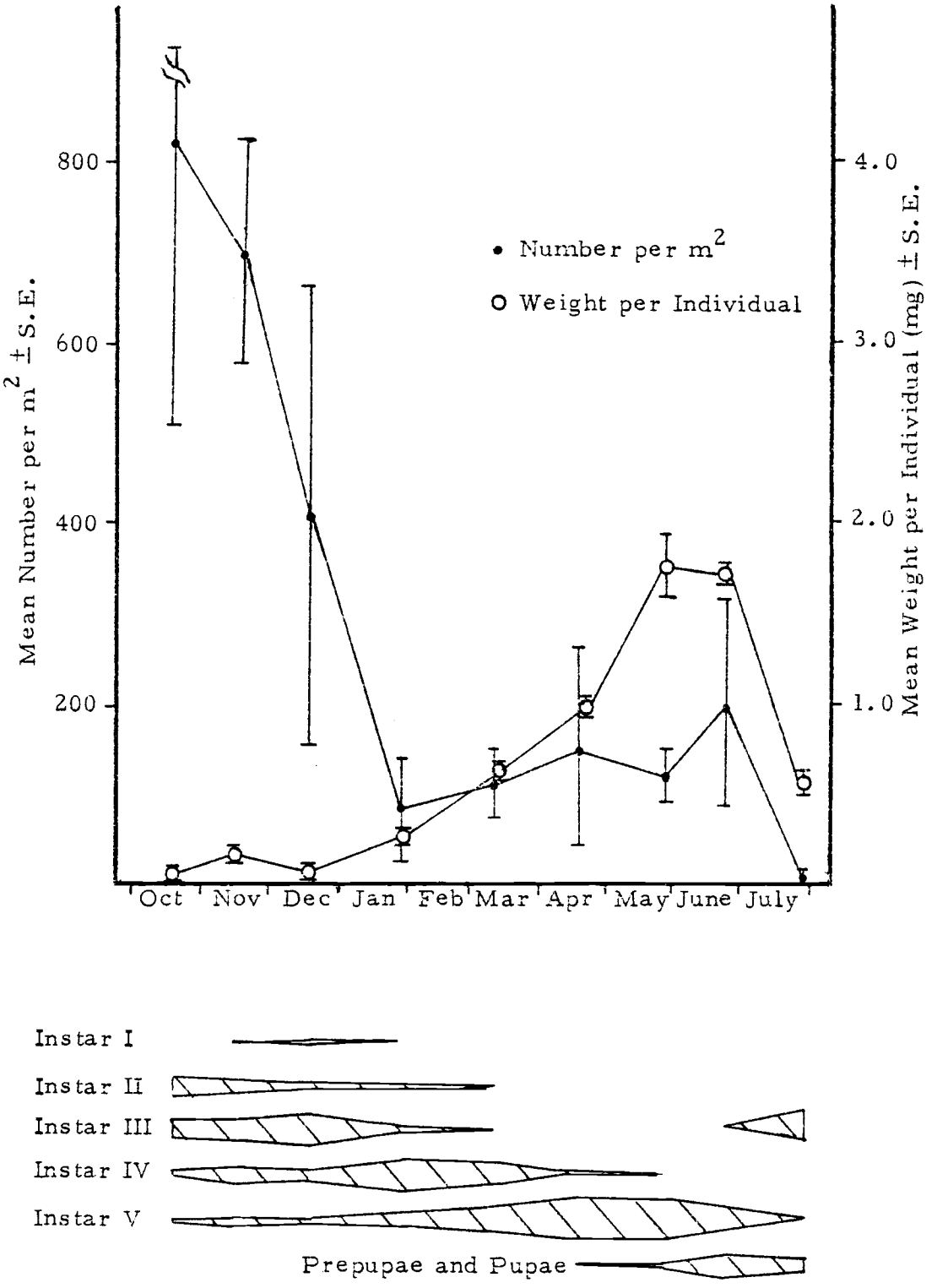


Figure 26. Densities, mean weights, and instar distributions for L. cascadense from Mack Creek.

final instar was the longest larval stage, predominating from March through June, and accounting for most of the larval growth. Final-instar larvae increased in mean weight from 0.353 mg in December to 1.815 mg in June (App. Table 17).

Biomass per m^2 showed an early peak in November, before water levels began to rise, decreased slightly with higher water levels in December and January and then increased gradually to a maximum of 348.1 mg per m^2 in June (App. Table 16). This was nearly three times the maximum for L. quercina in Berry Creek of 119.8 mg per m^2. Total biomass in the study section followed a pattern similar to biomass per m^2, except that maximum total biomass occurred in May, since biomass in the whole section was not biased by falling stream levels. Total biomass in the study section showed a slight peak in November, similar to biomass per m^2. This suggests that the decrease in biomass from November to December was not just the result of "dilution" of larvae over a wider area when water levels rose, but was the result of the decrease in mean larval size due to the influx of first-instar larvae.

L. unicolor. Larval densities of L. unicolor were about the same as densities of L. quercina in Berry Creek (maxima of 320 and 382 per m^2, respectively). Densities of L. unicolor increased from October to November (App. Table 18), due to the appearance of new first-instar larvae. Densities decreased from November to

December, even though first-instar larvae were still appearing, since water levels were rising and the area of the study section was increasing. Larval densities dropped to a low of 10.3 per m^2 in January and fluctuated between 22.8 and 76.7 per m^2 until July when emergence began (Fig. 27). The high of 76.7 per m^2 in June was partially due to dropping water levels, concentrating larvae in a smaller area of stream. As was true for population estimates of L. cascadense, standard errors were often 50% of the mean density and little can be positively determined from month-to-month fluctuations.

Total numbers of L. unicolor in the study section increased from October through December, due to the incoming first-instar larvae. Total numbers were lowest in January and fluctuated between 330 and 1940 larvae from February through June, similar to density, perhaps due to the action of freshets and changes in the amounts of debris in the pool area. Of the three species studied, L. unicolor is perhaps most subject to displacement by freshets since larvae occur almost exclusively on the surface of the debris and have a large, organic matter case. This mobility may be advantageous to the larvae since they tend to be transported with their food supply. Numbers of larvae in the samples were observed to correspond closely to the amount of debris present in the study section from month to month.

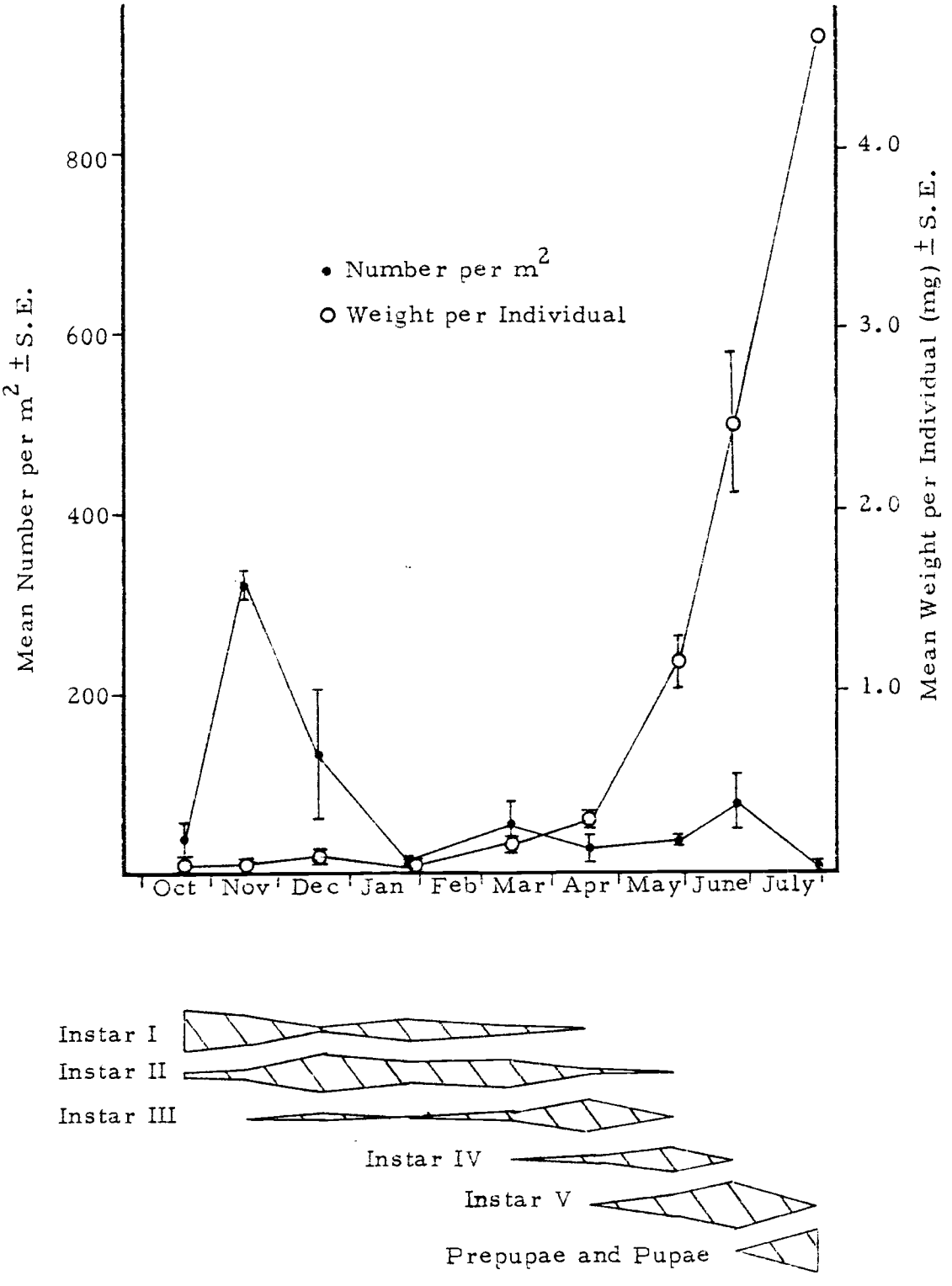


Figure 27. Densities, mean weights, and instar distributions for L. unicolor from Mack Creek.

Mean weight per individual increased from 0.021 mg in October to 2.472 mg in June. In contrast to instar distributions for the other two species, the duration of the final instar of L. unicolor was very short and final instars predominated only in the June samples. By the time of the July sample, larvae had completed their growth and pupation had occurred, so no weights were obtained for mature L. unicolor larvae in 1975. Maximum mean weights per individual for samples collected in the old-growth section of stream were 4.71 mg on June 28, 1974 (App. Table 15) and 4.56 mg on July 10, 1976 ($n = 18$, $s_{\bar{x}} = 0.34$). Maximum mean weight for L. unicolor in 1975 was therefore estimated as 4.65 mg (Fig. 27). In spite of the short duration of the final instar of L. unicolor, most of the larval growth still occurred in this stage. Final-instar larvae increased in mean weight from 1.606 mg in late May (App. Table 19) to a maximum of approximately 4.65 mg in mid-July.

Biomass per m^2 showed an early peak in November when water levels were still low and reached a maximum of 189.6 mg per m^2 in June. Further increases in biomass probably occurred with growth of the final-instar larvae. Maximum biomass per m^2 was somewhat higher than for L. quercina in Berry Creek and was only about half of the maximum biomass of L. cascadense. Total biomass in the study section was fairly constant from November through April, except for a low value in January. This low value is the result of combining low

estimates for mean weight per individual and numbers of individuals in the study section. A similar low value was reported for numbers of L. cascadense in January. These low numbers are perhaps due to errors in sampling, since densities of L. unicolor or L. cascadense in January are not significantly different from corresponding estimates made in December or February (App. Tables 16 and 18).

Emergence Collections of L. cascadense and L. unicolor

Emergence of both species in 1974 and 1975 occurred from June through September (Table 18). L. cascadense adults seemed to be most actively emerging early or late in the summer and L. unicolor emergence showed a maximum in early August. The few fourth- and fifth-instar L. cascadense collected in October (Fig. 26) may have been the progeny of early-emerging adults. Also, the possibility of another species cannot be ruled out (see Species Studied).

Density of emerging adult L. cascadense was estimated for 1974 and 1975 as 207 per m^2 per season (sex ratio 0.99♂: 1♀). Density of L. unicolor adults was estimated as 112 per m^2 per season (sex ratio 0.96♂: 1♀).

Pool area was 5 to 10 m^2 during the summer, compared with a maximum of 39 m^2 in the winter. Differences of this magnitude make it difficult to compare emergence with larval densities. However,

Table 18. Emergence of L. cascadense and L. unicolor from Mack Creek.

Date	No. of Traps	L. cascadense (mean no. /m^2)	L. unicolor (mean no. /m^2)
		1974	
7-17 to 8-1	2	131.5	10.0
8-1 to 8-18	3	10.0	22.0
8-18 to 8-27	3	58.3	10.0
8-27 to 9-6	3	68.3	5.0
		1975	
6-24 to 7-30	2	70.0	20.0
7-30 to 8-17	3	45.0	111.7
8-17 to 8-23	3	30.0	45.0

the total emergence from the study area in 1974-1975 was estimated as 1500 L. cascadense adults per season and 800 L. unicolor adults, compared with larval numbers of 4545 in May for L. cascadense and 1457 in June for L. unicolor. This suggests that the time between final instar and adult may be a period of high mortality. However, estimated numbers of L. cascadense adults, in particular, might have been higher if emergence sampling had been started earlier or extended later into the fall.

Differences in emergence between the two seasons might be the result of different larval population levels or different concentrations of pupae with falling water levels. For example, early drops in water level would cause larvae to migrate to deeper water or burrow into the substrate while late drops in water level might leave pupae

stranded by falling water levels. Also, only a maximum of 0.6 m^2 was sampled for emergence from a 5 to 10 m^2 area and sampling error was large. For instance, numbers of L. cascadense adults collected in three traps on September 6, 1974 were 7, 14, and 20; numbers collected in two traps on July 30, 1975 were 2 and 16. This kind of variability may result from differences in microhabitats; differences perhaps no longer present at the time of emergence.

Instantaneous Growth and Mortality Rates for L. quercina, L. cascadense, and L. unicolor

As indicated in Figure 28, L. quercina larvae grow and reach maturity most rapidly. L. cascadense larvae grow more slowly throughout the winter and L. unicolor grows very little until early spring. Instantaneous growth rates were 2.7% per day for L. quercina, 1.5% per day for L. cascadense, and 1.8% per day for L. unicolor (Table 19). However, when growth rate of L. unicolor larvae was calculated for the actively-growing phase, March through July, instantaneous growth rate was as high as the growth rate of L. quercina. Since temperatures in Mack Creek are still very low in the early spring (see App. Table 18), it is suggested that this very rapid growth by L. unicolor results, at least in part, from a change in food quality, reflecting the conditioning of the food source.

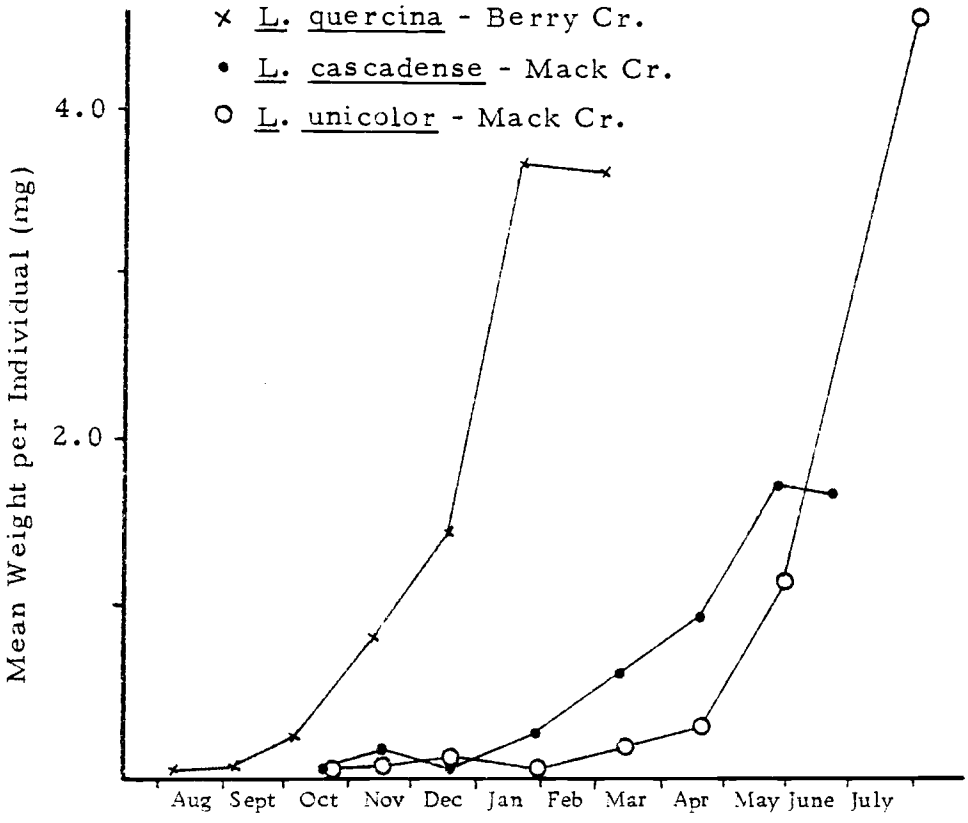


Figure 28. Growth and maximum size of three species of Lepidostoma.

Table 19. Instantaneous growth rates and mean mature weights for L. quercina, L. cascadense, and L. unicolor in the field.

Species	Instantaneous Growth Rates			Time Interval	Mean Mature Weight (mg)
	(%/day)	S.E.	r^2		
L. quercina	2.7	0.3	0.96	Aug. 6-Jan. 19	3.7
L. cascadense	1.5	0.2	0.90	Oct. 19-May 28	1.8
L. unicolor	1.9	0.3	0.85	Nov. 16-July 15	4.7
	2.7	0.3	0.99	Mar. 12-July 15	4.7

Mortality rates do not differ significantly ($P \leq 0.05$) between species, but are somewhat lower for the Mack Creek species (Table 20), in spite of frequent freshets and fluctuations in pool size and amount of debris. However, calculations of mortality rate in this manner assume equal immigration and emigration, probably not a valid assumption in a dynamic system such as Mack Creek.

Table 20. Instantaneous mortality rates for L. quercina, L. cascadense, and L. unicolor in the field.

Species	Instantaneous Mortality Rate			
	(%/day)	S.E.	r^2	time interval
L. quercina[1]	1.4	0.3	0.85	Aug. 6-Jan. 19
L. cascadense[2]	0.4	0.2	0.40	Oct. 19-May 28
L. unicolor[2]	1.0	0.5	0.42	Nov. 16-July 30
	1.7	0.5	0.50	Mar. 12-July 30

[1]Mortality estimate based on numbers per m^2.

[2]Mortality estimate based on total numbers in the study section.

Production and Food Processing by *L. quercina*, *L. cascadense*, and *L. unicolor*

Insect production, estimated as described by Allen (1951), Ricker (1946), or Speir and Anderson (1974) ranged from 0.16 to 0.31 $g \cdot m^{-2} \cdot yr^{-1}$ for the three species (Table 21). Means of the estimates for the respective species were almost identical (0.24 $g \cdot m^{-2} \cdot yr^{-1}$ for *L. quercina*, 0.26 $g \cdot m^{-2} \cdot yr^{-1}$ for *L. cascadense*, and 0.23 $g \cdot m^{-2} \cdot yr^{-1}$ for *L. unicolor*), even though mature size, growth rate, length of larval stage, and population density varied widely between species.

Food processed and fine particle material produced were estimated as 3.07 and 2.36 $g \cdot m^{-2} \cdot yr^{-1}$, respectively for *L. quercina*. For *L. unicolor* and *L. cascadense* combined, the processing and fecal production were 19.2 and 17.8 $g \cdot m^{-2} \cdot yr^{-1}$ (Table 21). These consumption and fecal productions are an order of magnitude larger than the productions for the respective species, indicating the importance of their roles as food processors.

Computer Simulation Modeling of Growth of *L. quercina*

Computer simulation modeling was used to: test my understanding of the system by formulating and testing the model; assess the accuracy of laboratory data on consumption, assimilation,

Table 21. Estimates of production and food processing by L. quercina, L. cascadense, and L. unicolor.

Species	Production ($g \cdot m^{-2} \cdot yr^{-1}$)			Food Processed[a] ($g \cdot m^{-2} \cdot yr^{-1}$)	
	P_a[b]	P_r[c]	P_s[d]	Consumption	Fecal Production
L. quercina	0.29	0.19	-	3.07	2.36
L. cascadense	0.29	0.31	0.19	10.33	9.55
L. unicolor	0.23	0.16	0.29	8.88	8.22

[a] Based on the mean of P_a, P_r, and P_s, assuming net growth efficiency of 0.34 and assimilation efficiencies of 0.23 for L. quercina, and 0.075 for L. cascadense and L. unicolor.

[b] Estimated as described by Allen (1951) using a curve of number per m^2 versus mean weight.

[c] Estimated as described by Ricker (1946) as the product of mean biomass and instantaneous growth rate.

[d] Estimated as described by Speir and Anderson (1974) using mean emergence per m^2 for 1974 and 1975, corrected to an average winter area of approximately three times the summer area and assuming a production:emergence ratio of 4.50.

respiration, and nitrogen excretion by comparing predicted growth against field growth rates; and provide estimates of the impact of the population on the system, in terms of insect production, total food consumed (leaves processed), and total feces produced. Although they comprise only a small proportion of the invertebrates in Berry Creek, it was hypothesized that L. quercina larvae would contribute significantly to the system by processing large amounts of allochthonous material and producing large quantities of fecal material.

The simulation model was based on the following relationship (Warren 1971):

Growth = Assimilation - Respiration - Nitrogen excretion

The assumptions and inputs to the model are given in Table 22. The first assumption is perhaps the most critical, since exuviae and silk secretions are certainly lost and significant excretion of dissolved organics probably occurs. Relationships between consumption rate and food density may also be in error since no data are available on the rate of leaf input to Berry Creek, the searching efficiency of L. quercina larvae in the field, or the effects of competition with other species (particularly the snail, O. silicula) on feeding by L. quercina.

A flow chart of the model is shown in Figure 29 and the Fortran program is given in Appendix Table 20. Initial inputs to the model were: 1) insect weight on day zero (August 6); 2) food supply rate,

Table 22. Assumptions and inputs to the simulation model of *L. quercina* growth.

1. Losses occurring in forms such as dissolved organic compounds, exuviae, or silk secretions, are minimal.

2. Consumption rate is a linear function of insect weight (from experiment 3) and a linear function of temperature (from experiment 7).

3. Consumption rate of the preferred food (alder leaves) is 95% of maximum when food density is three times the maximum consumption rate (estimated from experiment 7).

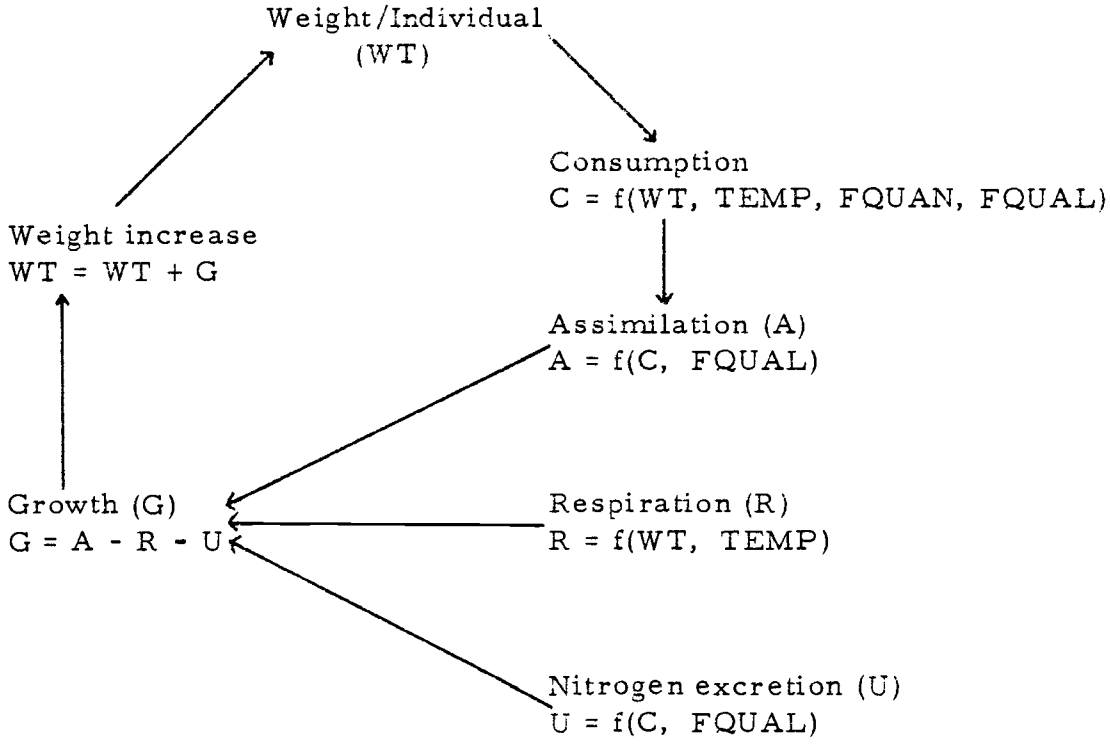
4. Consumption of the alternate food (bigleaf maple leaves) makes up 38% of the difference between maximum consumption rate of alder leaves and actual consumption of alder leaves (estimated from experiment 5).

5. Assimilation efficiency is 23% (experiment 7) and is equal for alder leaves or maple leaves (experiment 5).

6. Conditioning time does not affect consumption rates in the field, since observations indicate that most of the alder leaves in Berry Creek are consumed within a few weeks after entering the stream.

7. Nitrogen excretion is 1% of consumption of alder leaves and 0.5% of consumption of bigleaf maple leaves.

8. Respiration rate is an exponential function of temperature and insect weight. Measurements were converted from μl of O_2 per mg per hr, assuming 4.9 cal per ml of oxygen (McDiffett 1970) and 5200 cal per g of insect (Cummins and Wuycheck 1971).



WT	= weight per individual	G	= growth per individual
C	= consumption	U	= nitrogen excretion
TEMP	= temperature	R	= respiration
FQUAN	= food quantity	A	= assimilation
FQUAL	= food quality		

Figure 29. Flow chart of a simulation model of L. quercina growth predicted from laboratory data.

unlimited for the initial simulation: and 3) number of discrete-time loops per day and number of days to be simulated. A temperature regime, similar to temperatures in Berry Creek, was represented by a cosine function. Temperature in the simulation ranged from 13°C in early August to 5° in late January.

Outputs at the beginning of each simulated day were instantaneous growth rate, insect weight, consumption rate, and fecal production rate. With additional inputs of initial number of larvae per m^2 and mortality (from the field data), the simulation model calculated number per m^2 and biomass per m^2 at the beginning of each day, amount consumed per day by the population, total food consumed, and total feces produced during the simulation.

Predicted growth rates from the initial simulation when alder leaves were not limited, were higher than growth rates in the field, although growth rates for larvae of 1.5 mg or larger and maximum insect weights were similar in both cases (Fig. 30a).

In the model, size is limited by decreasing consumption rates with increased size. When assimilation rate minus nitrogen excretion and respiration is equal to zero, no growth occurs. It is suggested that a similar relationship exists in nature. C. magnifica larvae kept at 10°C, where consumption rate did not decrease with increased size, showed higher final weights than at other temperatures. Also, L. quercina larvae were observed in the laboratory to pupate at smaller weights when temperatures were higher.

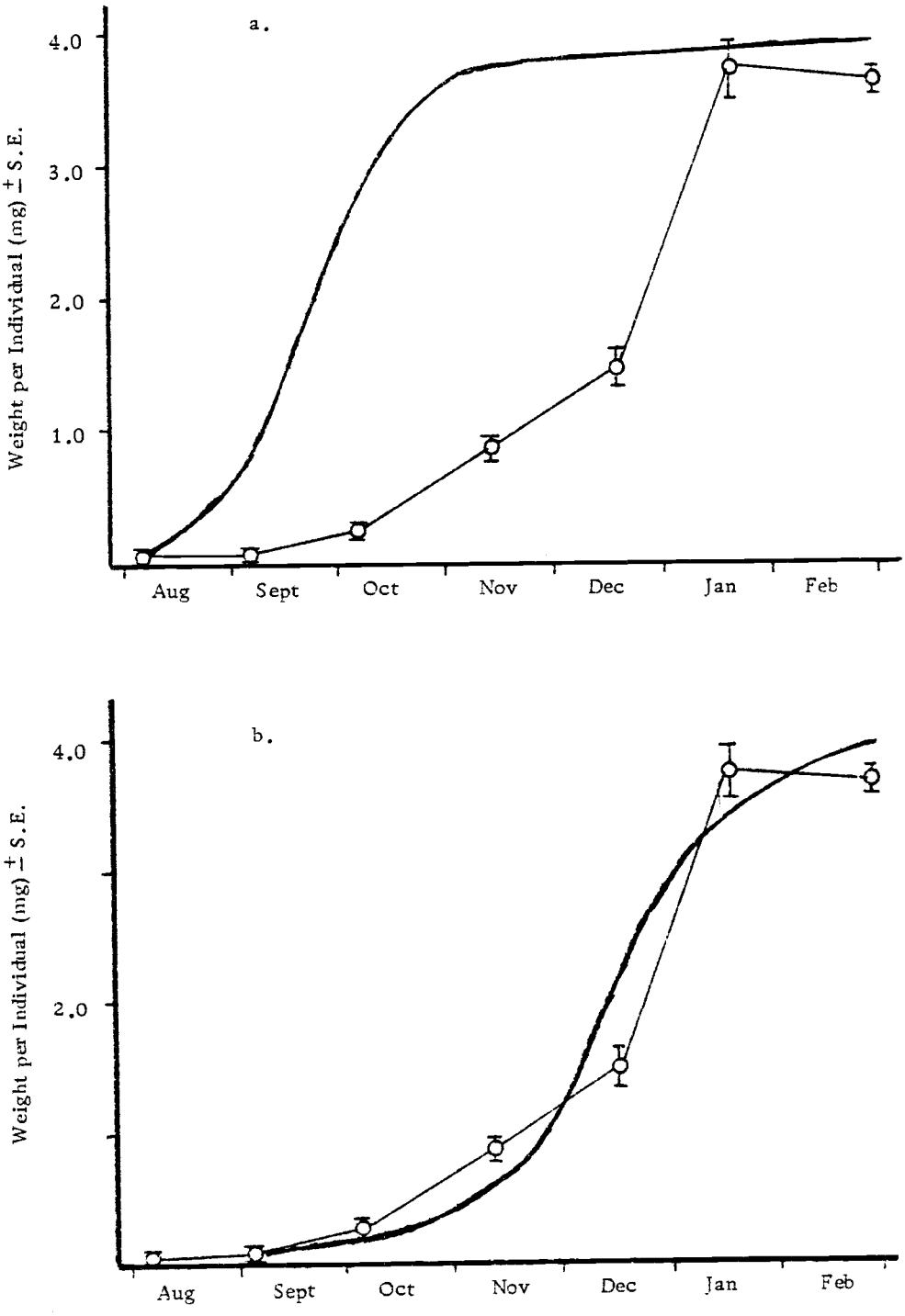


Figure 30. Comparison of field mean weights ($\bar{Q}$) with results of simulation modeling of L. quercina growth when food was unlimited (a) or alder leaves were limited for the first 80 days of simulation (b).

Field data on the standing crop of leaves present in Berry Creek suggested that the supply of alder leaves might be limited during the early part of L. quercina's life cycle, accounting for the difference between predicted and actual growth rates at this time. Further simulations were conducted, with limited amounts of alder leaves available during the first 80 days (August 6 through October 25), similar to the period of low food availability in the field. If the amount of alder leaves was limited to a particular level, individual growth rates predicted for L. quercina could be made to closely approximate field growth rates (Fig. 30b). The rate of food supply used was arbitrarily determined and would vary, depending on factors such as the palatability of alternate foods, searching efficiency of L. quercina, and inter- or intraspecific competition. However, the results suggest that a lack of high quality food may limit L. quercina growth and production.

Total consumption of alder and maple leaves predicted for the population when alder was limited for the first 80 days was 3.1 g per m^2, compared with an estimate of 2.82 g per m^2 in Table 21. Total fecal production was 2.4 g per m^2, and production was estimated as 0.19 g per m^2 per year, compared with estimates of 0.19 and 0.29 g per m^2 from Table 21. Production efficiencies were: 6.2% (gross) and 27.0% (net), compared with estimated growth efficiencies

(thought to be underestimates) of 3.1 and 12.6%, respectively (Table 7).

This consumption was a relatively small proportion of the mean detrital standing crop and production was much less than estimated by Speir (1975) for Simuliidae in Berry Creek and other similar streams (2.2 g per m^2 per year). However, it is suggested that the fine particles produced by L. quercina larvae are a highly significant contribution to the food chains of other species. Also, the reduction in particle size significantly increases microbial growth and colonization rates. Assuming a net growth efficiency of 50% and an assimilation efficiency of 57% (McCullough 1975), approximately 30% of the simuliid production could be supported by fine particles produced by L. quercina, even if these particles were used only once. Fecal production by L. quercina, is highest in December, according to the simulation model, and decreases gradually until pupation occurs in February. Simuliidae are the most abundant riffle species in Berry Creek and the major simuliid production occurs in February and March (Speir 1975) at a time when fine particulate material from L. quercina might be expected to be most abundant.

VI. DISCUSSION

Digestion and Assimilation

Allochthonous food available in streams is highly refractory and generally of low nutritive quality. Lignin plus cellulose content prior to decomposition may range from 18.5% for alder leaves to 38.7% for conifer needles (Triska et al. 1975). The lignin and cellulose forms a complexed matrix with the other components of the leaf; primarily hemicelluloses (xylan-based polymers), pectins, soluble proteins and carbohydrates, and compounds such as organic acids and polyphenols (White et al. 1968, Gray and Williams 1971). After being in the stream for a few days, food quality decreases considerably, since most of the soluble (and therefore easily digestible) compounds are rapidly leached from the leaf tissue (Kaushik and Hynes 1971, Cummins 1974, Triska et al. 1975).

Assimilation efficiencies for aquatic detritivores are generally very low, reflecting the poor nutritive value of the food. For example, Pteronarcys scotti Ricker assimilated only 10.6% of a diet of mixed deciduous leaves (McDiffett 1970) and L. cascadense larvae in this study assimilated only 10.0% of the Douglas fir needles fed to them. The assimilation efficiencies of 20-40% reported here for L. quercina and C. magnifica feeding on alder leaves are much higher than most values in the literature for detritivores, but correspond

closely with efficiencies shown for G. pulex (Nilsson 1974) and P. cingulatus (Otto 1974) fed on alder leaves.

The present study, and McCullough (unpubl.) showed decreases in assimilation efficiency of alder leaves with conditioning. As mentioned in Results, it is doubtful that this is entirely an artifact of the methods used. The nutritional value of the food is apparently decreasing, while other changes (perhaps in texture) result in increased palatability and an increase in assimilation rate (amount assimilated per mg per day). For a food such as alder leaves, microbial colonization is apparently much less important than for less nutritive foods such as Douglas fir needles. This is supported by the high consumption rates and assimilation efficiencies of L. quercina fed newly-fallen alder leaves. Also, Nilsson (1974) showed an increase in assimilation efficiency of beech leaves by G. pulex with conditioning, but no increase in assimilation efficiency of alder leaves. Protein and nitrogen content of alder leaves remains unchanged with conditioning, but increases for other species of leaves such as beech or Douglas fir (Kaushik and Hynes 1971, Iversen 1972, Triska et al. 1975).

Since food quality is low, particularly for species such as L. unicolor or L. cascadense that feed on conifer needles, it might be expected that these species would have evolved the capacity to degrade cellulose or lignins. There are numerous examples in the

literature of insects that produce cellulolytic enzymes or use intestinal symbionts to aid in cellulose digestion (Parkin 1940, Lasker and Giese 1956, Evans and Payne 1964, Wigglesworth 1965, Chapman 1969). However, there is little evidence of cellulose digestion in aquatic invertebrates. Hargrave (1970) found no evidence of ^{14}C-labeled cellulose digestion by the amphipod Hyalella azteca (Saussure) and Bjarnov (1972) found only slight cellulase activity in one species of caddis and G. pulex after examining intestinal enzymatic activity of 10 species of caddis larvae, two species of chironomid midge larvae, and G. pulex. Cummins (Kellogg Biol. Sta., Mich. State Univ., unpubl.) reports symbionts capable of cellulose digestion in hindguts of a number of species of shredders. However, it is not known how beneficial these symbionts are to their hosts since most nutrient absorption in insects occurs in the mid-gut.

Even though cellulose was not generally digestible, Nielsen (1962) and Bjarnov (1972) found numerous instances of digestion of carboxymethyl cellulose and cellobiose (degradation products of cellulose) and xylans. Xylanase, in particular, was found by Bjarnov (1972) in all species of caddis known to be shredders and was absent in the other species examined. Species with enzymes such as xylanase or cellobiase are probably capable of utilizing microbial waste products and perhaps can compete with the microorganisms for partial degradation products of cellulose resulting from exoenzyme activity.

The apparent lack of cellulolytic capability among aquatic detritivores is not surprising if one assumes that some component other than carbon or energy is limiting. In that case, there would be no selective advantage to cellulose digestion since large quantities of food must be processed in order to obtain adequate nutrition.

Nitrogen or phosphorus may be limiting (Hynes 1975) and have been shown to be present in Mack Creek water in concentrations low enough to limit decomposition (Triska et al. 1975). The nitrogen present may also be bound chemically with compounds such as tannins, forming an indigestible complex (Feeny 1970). Other components such as calcium, potassium, niacin, cholesterol, or linoleic acid may also limit nutrition or decomposition rates (Trager 1947, Grau and Terrierre 1967, Egglishaw 1968, Eisenberg 1970). Parkin (1940) suggests that fungi may be an important source of vitamins for wood-boring insects. In the aquatic environment, soluble proteins and nutrients are rapidly leached from the leaf and fungi may be important as sources of proteins and nutrients since they have been shown to actively collect and concentrate nutrients from the surrounding environment (Kaushik and Hynes 1971, Cromack et al. 1974, Ausmus et al. 1976).

Most species of aquatic detritivores apparently rely on fungi and bacteria to provide nutrition (Cummins et al. 1973), in contrast to L. quercina fed on alder leaves. It has been shown that

palatability and consumption rates increase with conditioning of the food (Iversen 1972, Nilsson 1974, Anderson and Grafius 1975, McCullough unpubl.). Changes that occur with conditioning as the result of leaching and microbial activity include: changes in texture and color; loss of soluble proteins, carbohydrates, organic acids, and polyphenols; increased microbial biomass and activity; and increased concentrations and amounts of nitrogen and proteins (Heath and King 1964, Hayes 1965a, b, Hynes and Kaushik 1968, Mathews and Kowalczewski 1969, Iversen 1972, Willoughby 1974, Triska et al. 1975). Of these, changes in texture, reduced polyphenols, increased microbial biomass and activity, and increased nitrogen and protein content seem to be the major factors influencing palatability and consumption rates (Williams 1954, Tanton 1962, Boyd and Goodyear 1971, Kaushik and Hynes 1971, Kostalos 1972, Grafius 1974, Iversen 1974, Bärlocher and Kendrick 1975). Reduced polyphenols may be one of the most important factors, since polyphenolic compounds are known to complex with enzymes, inhibiting digestion by microorganisms or invertebrates (Goldstein and Swain 1965, Benoit and Starkey 1968, Feeny 1970). Perhaps for this reason, species of leaves such as oak or Douglas fir are not consumed immediately after entering the stream, even though protein and nitrogen contents may be high enough to support growth and

invertebrates have shown the ability to evolve mechanisms for cellulose digestion.

Temperature Adaptations by Aquatic Invertebrates

Metabolic rates of "cold-blooded" animals are generally considered to increase with environmental temperature (Bullock 1955, Chapman 1969, Vernberg and Vernberg 1970). However, there are numerous examples of behavioral mechanisms for maintaining constant body temperature and many insects have been shown to produce and retain enough heat to elevate body temperatures (Bullock 1955, Wigglesworth 1965, Cloudsley-Thompson 1970, Heinrich 1974, Casey 1976). Because of the high heat conductance of water, the only aquatic poikilotherms known to be capable of maintaining elevated body temperatures are large, highly active animals such as tuna and sharks (Gordon 1968, Fry and Hochachka 1970).

Aquatic invertebrates have evolved a variety of mechanisms to deal with problems of cold or changing temperatures. In many cases, life cycles or periods of activity correspond to times of suitable temperatures (Hynes 1970b). However, most shredders (e.g. L. quercina and L. cascadense) and many other stream insects grow most rapidly during the fall and winter when temperatures are lowest (Kamler 1973, Cummins 1974, Hynes 1976). Possible mechanisms for maintaining metabolic activity at cold temperatures include

increased enzyme synthesis or the production of more active or cold-adapted enzymes (Applebaum et al. 1964, Mutchmor 1967, Fry and Hochachka 1970). In addition, enzyme-catalyzed reaction rates at low (and perhaps more normal) substrate concentrations may increase with decreased temperature, due to changes in enzyme-substrate affinity (Hochachka and Somero 1973).

Evidence for cold-adaptation by final-instar L. quercina larvae includes: increased growth rate and higher assimilation efficiency at low temperatures and premature pupation at high temperatures. Final-instar L. quercina are probably not adapted to fluctuating temperatures since respiration rate increases with temperature. This is in contrast to the early-instar larvae which maintain constant respiration rate from 5 to 20°C. Therefore, it is concluded that final-instar L. quercina are cold-adapted while earlier stages are adapted to a changing temperature regime, as occurs in late summer and early fall. This flexibility is not maintained in the final instar, perhaps since it is no longer necessary and the energy required to maintain flexibility is needed for the rapid growth that occurs at this time. Also, cold-adapted organisms should function more efficiently at cold temperatures than organisms adapted to a changing temperature regime.

Vannote (1976) proposes a strategy allowing spring-growing species to maintain constant metabolic rates. As the season

progresses, metabolic rates are theoretically kept at an optimal equilibrium by increases due to rising temperatures and decreases due to the larger size of the organisms. Vannote describes this system as a fragile balance between growth and temperature change. Any lag in growth or unusual increase in temperature will result in increased metabolic rates, reducing growth, and finally resulting in stunted adults or failure to mature.

Vannote's model may be a naturally buffered system, assuming that growth decreases on either side of the equilibrium metabolic rate and that species are growing as rapidly as permitted by the rate of temperature increase. If growth exceeds this rate, or if temperature drops, metabolic rates and growth rates will decrease until temperature allows them to return to equilibrium.

Respiration rates for L. unicolor (the only spring-growing species studied) increase with temperature and decrease with size, as required by the model (Figs. 23 e-g). Comparisons of estimated respiration rates at field temperatures with larval size (Fig. 31) show that L. unicolor does maintain almost constant respiration rates during its time of active growth and conforms to Vannote's model.

For species such as C. magnifica that encounter a wide range of temperatures and exhibit temperature compensation in respiration (Q_{10} = 1.12) and consumption (Q_{10} = 1.05 on alder + wheat and 1.64

on alder), potential mechanisms may be production of different isozymes at different temperatures or the inhibition or activation of particular enzymes depending on temperature (Prosser 1964, White et al. 1968, Hochachka and Somero 1983). Also, changes in enzyme conformation at different temperatures may cause compensatory changes in enzyme activity (Prosser 1967, Hochachka and Somero 1973). For example, a particular enzyme at low temperature may have a very low degree of tertiary structure, making it more active, while at high temperatures tertiary structure increases, reducing activity.

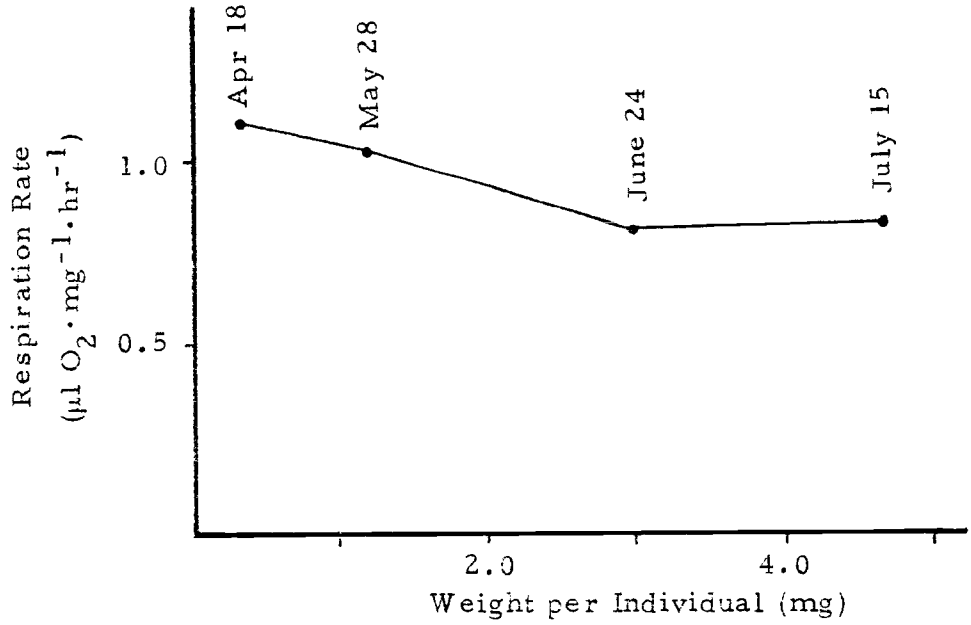


Figure 31. Estimated respiration rates at field temperatures compared with size of L. unicolor larvae.

In view of the numerous examples of regulation of metabolic functions by poikilotherms with respect to temperature and the variety of possible regulatory mechanisms, adaptations by poikilotherms to environmental temperature regimes should be expected in most environments.

Life Styles and Adaptive Strategies

This section discusses facets of behavior, life cycle, and bioenergetics that are thought to be of adaptive value or to add to the fitness of these species in their respective habitats. Comparisons of behavior, life cycle, and energetics for a single species from a variety of habitats would be necessary to determine whether a particular trait is truly adaptive or merely coincidental. In this respect, L. unicolor would be a particularly interesting species to investigate further because of its wide distribution among a variety of habitats.

Since consumption rates by L. quercina larvae were maximal when food was only slightly in excess and larvae in the field were found on a variety of foods, it was concluded that L. quercina does not actively search among food items or else food items were relatively uniform in quality. "Fine-grained" utilization such as this occurs when the time and energy cost of searching is greater than the benefits derived from specialization (MacArthur and Levins 1964). Although consumption rates and assimilation efficiencies were higher

on alder leaves than on bigleaf maple, survival in the laboratory is good on either food and apparently the nutritional benefits are not sufficient to make extensive searching for alder leaves profitable. In addition to nutritional considerations, the food particles utilized by L. quercina tend to form dense leaf packs which increases the cost of searching.

Respiration rates of L. quercina are not greatly affected by temperature (Q_{10} = 1.49), reflecting some ability to compensate for changes in temperature. This homeostasis is strongest in the stages that encounter the largest temperature changes (early-instar larvae). Final-instar larvae exposed to unusually warm temperatures pupated early and before reaching normal mature size. Presumably this reflects a failure to acclimate to the warm temperature and prevents weight loss caused by high metabolic costs at this temperature.

In contrast to L. quercina, L. unicolor was found to feed in the laboratory at maximum rates only when food (Douglas fir needles) was greatly in excess and larvae often consumed only a few needles from a group of 10 or 20. "Coarse-grained" utilization, such as this, suggests that food items in nature are abundant but of unequal nutritional value (MacArthur and Levins 1964). Food particles must be abundant enough so that a large number can be encountered with minimal effort and the differences in nutritional value must more than compensate for the energy cost of searching. Since conifer

needles in Mack Creek are found in all stages of decomposition, while larvae in the laboratory grow only on the most well-conditioned needles or on alder leaves, the benefits of searching are apparent. In response to especially poor food in the laboratory (e.g. fresh needles), larvae would crawl to the surface, take a bubble of air into their case, and float. Larvae kept in window screen cages in the laboratory have even been observed to scrape and ingest particles of aluminum from the screen when caged with only fresh needles as food.

Temperatures in Mack Creek are relatively stable throughout L. unicolor's larval stage (2-10°C) and larval respiration rates respond directly to changes in temperature, exhibiting no ability to compensate (Q_{10} = 1.99). Larvae grow rapidly in the spring when temperatures are apparently optimal. When exposed to above-normal temperatures, final-instar larvae did not pupate during the two-week experiment, in contrast to L. quercina, and significant weight loss and mortality occurred.

C. magnifica is also coarse-grained with respect to food utilization. Larvae in the laboratory efficiently search out wheat grains or enchytraeid worms as food and grow and mature much more rapidly when the diet of alder leaves is supplemented with these other foods (Anderson 1976a). In the field, they are known to ingest small

amounts of animal material (Winterbourn 1971), although this may be only fortuitous.

With respect to temperature, C. magnifica larvae exhibit nearly constant respiratory and consumption rates from 5 to 20°C. High Cascade lakes, as mentioned, undergo large changes in temperature and it is essential that C. magnifica larvae be able to adapt to these large seasonal and diel fluctuations.

Ecosystem Interactions

Eggs and early-instar larvae of all three Lepidostoma species occur in similar areas of the stream in late summer and early fall. However, each species utilizes a different food resource or portion of the food resource, and has a different period of maximum growth. These differences illustrate the close interactions of food resource and temperature as they relate to the life cycles of the respective species.

L. quercina larvae feed on deciduous leaves and grow rapidly in the fall and early winter when this food is most available. L. cascadense feeds primarily on conifer needles beneath the surface of the debris and grows slowly throughout the winter. L. unicolor larvae occur primarily at the surface of the debris, in the same areas of Mack Creek as L. cascadense, and are apparently restricted to the debris surface by their large bulky case. The rapid burst of

growth by L. unicolor larvae in the spring may be the result of more optimal temperatures or more completely conditioned food (or both). Since most of the needles enter the system in the fall, conditioning may not be complete until this time. L. cascadense, feeding beneath the surface, may encounter older, more decomposed needles. It is also possible that decomposition proceeds more rapidly beneath the surface of the debris where current is reduced and excreted nitrogen and other nutrients are more easily "recycled."

L. quercina appears to be well-adapted to a changing temperature regime in the early instars, with temperature decreasing as growth progresses. L. cascadense is probably a truly cold-adapted species, requiring cold temperatures for growth and development. It is perhaps more efficient under these conditions than either L. unicolor or L. quercina. L. unicolor grows most rapidly when temperatures are increasing and follows Vannote's model for spring-growing species.

Distributions of these species reflect food and temperature adaptations. L. quercina is found in Willamette Valley and Coast Range streams where deciduous leaves are common and temperatures tend to be moderately warm (ca. 15°C) in the late summer and decrease as the season progresses. L. unicolor is the most widely distributed of the three species, occurring in Willamette Valley, Coast Range, and Cascade streams. All of these streams exhibit

warming temperatures in the spring. Growth of L. unicolor larvae might be expected to occur earlier in habitats that begin warming earlier in the year. L. cascadense is found in cold habitats at relatively high elevations.

As noted in Results, production for these three species is minor in comparison with other species. However, the fine particulate material produced by these species is a very significant input to the trophic base for collector species in the stream. As mentioned, fine particle material produced by L. quercina might support simuliid production of 0.7 g per m^2 per year, if recycled only once. The fine particle material produced by L. cascadense and L. unicolor in Mack Creek might support production of over 5 g of collectors per m^2 per year, using the same conversion values. In addition, fecal material may be recycled very rapidly through the collectors and is quickly recolonized by microorganisms (Hargrave 1976). Thus, the fine particle material produced by shredders may be reutilized many times and provide a long-term food source for stream invertebrates.

VII. SUMMARY AND CONCLUSIONS

Laboratory studies of ingestion, egestion, growth, and respiration of four species of caddis as affected by temperature, food quality and quantity, and body size showed a wide variety of responses depending on species and size.

Ingestion rates of L. quercina and L. unicolor generally increased with temperature and decreased with body size. Conditioning of alder leaves resulted in increased consumption and fecal production rates for L. quercina after the first three or four weeks of conditioning. Ingestion and egestion rates for L. unicolor increased only one-tenth as rapidly with conditioning of Douglas fir needles.

Consumption rate of Douglas fir needles by L. unicolor did not appear to reach maximum rates even when food density was two or three times consumption. This was in contrast to consumption and fecal production rates for L. quercina on alder leaves which approached maximum rates when food was only slightly in excess. L. unicolor larvae are apparently more selective of food items than L. quercina larvae and/or Douglas fir needles are less uniform in quality than alder leaves.

Assimilation efficiency of alder leaves by L. quercina decreased with conditioning time, apparently due to declining nutritional value of the food. Efficiency decreased with temperature increases, probably due to physiological adaptations to cold temperatures.

Mean consumption rates of alder by C. magnifica larvae were shown to increase significantly between 10 and 15°C, but mean consumption rate of alder between 15 and 20°C and consumption rate of alder + wheat between 10 and 20°C showed no significant changes with temperature. Consumption rate decreased with increased size at 15 or 20°C, but showed no significant change with size at 10°C on either diet. Temperature effects on consumption were different for different sizes of larvae. Consumption rates by small larvae tended to increase with temperature, while consumption rates of larger individuals remained constant when fed alder or decreased slightly when fed alder + wheat.

Assimilation efficiencies of alder leaves and palatability of alder leaves for C. magnifica increased with temperature. It was suggested that the changes in assimilation efficiency with temperature were the result of changes in efficiency of digestive enzymes. The decreased efficiency with higher temperatures for L. quercina might result from cold-adapted enzymes and the increased efficiency for C. magnifica, from warm-adapted or more generalized enzymes.

Respiration rates showed three different types of respiration/temperature relationships. All three species examined showed substantial increases in respiration rate from 5 to 10°C. From 10 to 20°C, however, C. magnifica showed a slight decrease in respiration rate (complete compensation or perhaps over-compensation) and

L. quercina showed a slight increase in respiration (partial compensation). L. unicolor exhibited a substantial increase in respiration rate from 10 to 15°C (no compensation) and very high mortality at 20°C.

In general, respiration Q_{10} values were lowest for species normally encountering the largest variations in environmental temperature. Adaptation or acclimation to various temperatures seem to occur in relation to the environmental temperature and the amounts of temperature variation normally encountered. Potential for acclimation differs with stage of development within a species as well as between species.

Nitrogen excretion by L. quercina larvae was less than 1% of consumption. No further tests were conducted since nitrogen excretion must be a relatively small portion of the materials transferred and was thought to be unimportant unless nitrogen is limiting to the nutrition of the insects.

Sampling in Berry Creek for L. quercina and in Mack Creek for L. cascadense and L. unicolor gave maximum biomasses of 0.12 $g \cdot m^{-2}$ for L. quercina, 0.19 $g \cdot m^{-2}$ for L. unicolor and 0.35 $g \cdot m^{-2}$ for L. cascadense. Production was estimated as 0.24 $g \cdot m^{-2} \cdot yr^{-1}$ for L. quercina, 0.26 $g \cdot m^{-2} \cdot yr^{-1}$ for L. cascadense and 0.23 $g \cdot m^{-2} \cdot yr^{-1}$ for L. unicolor. Instantaneous growth rates were highest for L. quercina (2.7%/day), followed by L. unicolor (1.9%/day),

and L. cascadense (1.5%/day). Time of maximum growth was fall and early winter for L. quercina feeding on deciduous leaves, late fall and winter for L. cascadense feeding on conifer needles, and spring and early summer for L. unicolor feeding on conifer needles. Timing of growth and microhabitat selection resulted in partitioning of the food resources for L. unicolor and L. cascadense, minimizing competition between the two species.

Fine particle production by L. quercina in Berry Creek was estimated as ten times the production of L. quercina and was sufficient to support collector production of at least three times the production of L. quercina. Fine particulates produced by L. cascadense and L. unicolor were approximately 30 times the production of L. cascadense and L. unicolor and were estimated to support collector production of ten times the Lepidostoma production.

The data reported in this and other studies show a variety of adaptive strategies for using leaves and needles in the stream and indicate that these strategies maximize the utilization of these food sources when they are most available and usable (e.g. immediately after falling in the case of alder leaves, and months after entering the system in the case of conifer needles). Food availability is probably the major factor affecting life cycles for these species. Mechanisms have been developed to deal with the effects of cold or fluctuating temperatures that normally occur when food is most

available. Also, L. unicolor showed much more selectivity of food items than did L. quercina, apparently a mechanism allowing L. unicolor to subsist on a variable and generally low quality food source, such as conifer needles.

In view of the large differences in bioenergetic responses to temperature exhibited by L. quercina, L. unicolor and C. magnifica, much more data on other species and other habitats are needed. From the information presented here, it would seem that each species responds in a unique way. However, with more data available, some strategy-types should become evident. For example, strategy-types might be: spring-growing temperature-conformers (L. unicolor), winter-growing cold-adapted (L. cascadense), or fall- and winter-growing regulators or partial regulators with respect to temperature (C. magnifica and L. quercina, respectively).

Identification and characterization of these strategy-types should prove to be very useful in understanding stream systems and predicting their behavior. One major advantage of a system of strategy-types is that it would allow prediction of changes in species composition resulting from perturbations of the system. Also, it might be possible to predict some aspects of life history or bioenergetics of colonizing species. Potentials such as these would greatly strengthen our understanding of aquatic systems and would improve our systems models, since there would be a greater

potential for extrapolation to new systems or different environmental conditions.

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Appendix Table 1. Computer program for analysis of stratified samples.

```
      OS3 FORTRAN  VERSION 3.13          08/03/76  1122

0+001          PROGRAM STRSAMP
0+002    C     A PROGRAM FOR CALCULATING MEAN WEIGHT AND VARIANCE FOR INSECTS
0+003    C     STRATIFIED ON THE BASIS OF INSTAR.
0+004    C     DATA CARD 1 =  NUMBER OF DATA SETS TO BE ANALYSED  ,FORMAT I2
0+005    C     DATA CARD 2 = COLLECTION DATE, NUMBER OF INSTARS AND SPECIES
0+006    C     NAME FOR FIRST DATA SET. FORMAT I6,I2,3A8.
0+007    C     DATA CARD 3 = NUMBER SAMPLED AND TOTAL NUMBER IN ≠FIRST≠ INSTAR,
0+008    C     FIRST DATA SET. FORMAT I3,F3.0.
0+009    C     DATA CARD 4+= INSTAR AND WEIGHT FOR EACH INSECT SAMPLED. FORMAT
0+010    C     I2,F7.4.
0+011    C     REPEAT CARDS 3 AND 4+ FOR EACH INSTAR IN FIRST DATA SET.
0+012    C     REPEAT CARDS 2,3,AND 4+ FOR EACH DATA SET.
0+013          REAL INSMEAN,NTOTAL,INSVAR
0+014    C     READ NUMB. OF DATA SETS,≠≠NRUNS≠≠ AND LOOP AROUND RUNS
0+015          READ(60,1)NRUNS
0+016        1 FORMAT (I2)
0+017          DO 2 K=1,NRUNS
0+018    C     READ NUMBER OF INSTARS,≠NINSTAR≠,SAMPLE DATE,≠SAMDATE≠, AND
0+019    C     SPECIES NAME. LOOP AROUND INSTARS. PRINTOUT SAMPLE DATE AND
0+020    C     SPECIES.
0+021          READ(60,3)SAMDATE,NINSTAR,SP1,SP2,SP3,SP4,SP5
0+022        3 FORMAT(I6,I2,5A8)
0+023          WRITE(61,4)SAMDATE,SP1,SP2,SP3,SP4,SP5
0+024        4 FORMAT(≠-COLLECTION DATE IS    ≠,I6,≠          SPECIES IS    ≠,5A8)
0+025          WTSUM = 0.0
0+026          VAR = 0.0
0+027          TOTAL = 0.0
0+028          TSAM = 0.0
0+029          DO 5 L=1,NINSTAR
0+030    C     READ NUMBER SAMPLED, ≠≠NSAM≠≠, AND TOTAL NUMB. IN INSTAR
0+031          READ(60,6) NSAM,NTOTAL
0+032        6 FORMAT (I3,F3.0)
0+033    C     READ INSTAR, ≠≠INSTAR≠≠ AND WEIGHT,≠≠WT≠≠ FOR EACH INSECT SAMPLED
0+034    C     CALCULATE SUM AND SUM OF SQUARES.
0+035          SUM = 0.0
```

Appendix Table 1. (Continued)

```
0+036            SUMSQ = 0.0
0+037            DO 7 M=1,NSAM
0+038            READ(60,8) INSTAR,WT
0+039          8 FORMAT(I2,F7.4)
0+040            SUM =SUM + WT
0+041            SUMSQ = SUMSQ + WT**2
0+042          7 CONTINUE
0+043  C         CALCULATE SAMPLING FRACTION,##PSAM##,INSTAR MEAN WEIGHT,##INSMEAN##
0+044  C         AND INSTAR VARIANCE,##INSVAR##.
0+045            PSAM = FLOAT(NSAM)/NTOTAL
0+046            INSMEAN = SUM/FLOAT(NSAM)
0+047            INSVAR = (SUMSQ-((SUM**2)/FLOAT(NSAM)))/(FLOAT(NSAM)-0.999999999)
0+048            WRITE(61,9)
0+049          9 FORMAT(# INSTAR  PORTION SAMPLED   MEAN WEIGHT   INSTAR VARIANCE#)
0+050            WRITE(61,10) INSTAR,PSAM, INSMEAN, INSVAR
0+051         10 FORMAT(I4,4X,F9.4,9X,F10.5,4X,F10.5)
0+052  C         CALCULATE WEIGHTED SUM,#WTSUM#,VARIANCE,#VAR#,TOTAL NUMBER,#TOTAL
0+053  C         AND TOTAL NUMBER SAMPLED ,#TSAM#, FOR ALL INSTARS.
0+054            WTSUM = WTSUM +INSMEAN*NTOTAL
0+055             VAR=VAR+NTOTAL*(NTOTAL-FLOAT(NSAM))*INSVAR/FLOAT(NSAM)
0+056            TOTAL = TOTAL + NTOTAL
0+057            TSAM = TSAM  + FLOAT(NSAM)
0+058          5 CONTINUE
0+059            VAR=VAR/TOTAL**2
0+060  C         CALCULATE WEIGHTED MEAN AND PROPORTION SAMPLED
0+061            WMEAN = WTSUM/TOTAL
0+062            PSAM = (TSAM/TOTAL)
0+063            STDERR = VAR**0.5
0+064  C         WRITE MEAN AND VARIANCE AND STANDARD ERROR
0+065            WRITE(61,11)
0+066         11 FORMAT(#0PORTION SAMPLED  MEAN WEIGHT  VARIANCE  STANDARD ERROR#)
0+067            WRITE(61,12) PSAM,WMEAN,VAR,STDERR
0+068         12 FORMAT(F9.2,8X,F10.5,3X,F7.5,3X,F10.5)
0+069          2 CONTINUE
0+070            CALL EXIT
0+071            END

 NO ERRORS FOR STRSAMP
LENGTH OF SUBPROGRAM      00517
RUN
```

Appendix Table 2. Mean consumption rates for second- and third-instar L. quercina larvae fed alder leaves for six days at 13°C.

Instar	Insects		% Mortality	Consumption Rate $\pm s_{\bar{x}}$
	n	$\overline{wt}$ (mg)		($mg \cdot mg^{-1} \cdot day^{-1}$)
2	20	0.014	30.0	0.70 ± 0.26
3	80	0.053	17.5	0.40 ± 0.04

Appendix Table 3. Consumption, fecal production and assimilation efficiencies for third- and fourth-instar L. quercina larvae at 13°C.

Replication	n	Mean Wt. (mg)	Instar	Consumption ($mg \cdot mg^{-1} \cdot day^{-1}$)	Fecal Production ($mg \cdot mg^{-1} \cdot day^{-1}$)	Assimilation Efficiency (%)
1	15	0.59	4	0.71	0.61	14
2	30	0.39	3 (9) 4 (21)	0.93	0.77	17

Appendix Table 4. Consumption and fecal production by freshly-collected final-instar L. quercina larvae fed alder leaves conditioned for up to 46 days.

Date	Conditioning Time (days)	$\overline{wt}$/Individual (mg)	n	Consumption Rate ($mg \cdot mg^{-1} \cdot day^{-1}$)	Fecal Production Rate ($mg \cdot mg^{-1} \cdot day^{-1}$)	Assimilation Efficiency (%)
Oct. 22	13	0.76	15	0.58	0.43	27
		0.75	15	0.81	0.47	42
	43	0.86	13	1.38	0.96	31
		0.61	15	1.35	1.03	23
Oct. 30	12	0.77	12	0.81	0.56	32
		0.88	12	0.75	0.47	38
	26	0.78	12	0.47	0.34	27
		0.90	12	0.47	0.33	31
	31	0.64	12	1.21	0.81	33
		0.77	12	0.79	0.42	47
	36	0.82	12	0.92	0.67	27
		0.81	12	1.21	0.67	45
	41	0.72	12	1.72	1.26	27
		0.71	12	1.49	1.43	4
	46	0.80	12	1.66	1.29	22
		0.93	12	1.57	1.22	22
Dec. 7	0	1.93	12	0.41	0.18	56
		2.17	12	0.39	0.14	65
	3	3.10	12	0.18	0.13	28
		4.54	12	0.17	0.08	51
	6	3.35	12	0.21	0.15	30
		3.14	12	0.18	0.12	35

(Continued on next page)

Appendix Table 4. (Continued)

Date	Conditioning Time (days)	$\overline{wt}$/Individual (mg)	n	Consumption Rate ($mg \cdot mg^{-1} \cdot day^{-1}$)	Fecal Production Rate ($mg \cdot mg^{-1} \cdot day^{-1}$)	Assimilation Efficiency (%)
	9	3.12	12	0.25	0.16	37
		2.57	12	0.24	0.15	35
	9	3.30	12	0.25	0.17	32
		3.71	12	0.16	0.11	36
	12	3.84	12	0.18	0.12	33
		3.47	12	0.22	0.13	43
	15	3.76	12	0.18	0.12	30
		3.77	12	0.16	0.10	37
	18	3.03	12	0.26	0.16	39
		3.84	12	0.18	0.14	23
	21	3.78	12	0.18	0.15	17
		3.66	12	0.18	0.14	23

Appendix Table 5. Consumption of Douglas fir needles by final-instar L. unicolor larvae at 13°C.

Final Weight (mg)	Consumption Rate ($mg \cdot mg^{-1} \cdot day^{-1}$)
1.95	1.08
0.50	0.63
0.76	0.86
1.90	1.07
0.91	0.78
0.68	0.34
2.69	0.66
0.97	0.92
0.43	-0.54
2.06	1.15
0.77	0.92
0.36	0.56
0.79	0.96
1.14	1.23
1.06[a]	0.76
1.06[a]	0.98
0.67[a]	1.70
1.48[a]	1.33
1.33[a]	1.22
0.43[a]	1.21
0.66[a]	0.19
0.82[a]	0.92
$\bar{x}$ 1.05	0.84
$s_{\bar{x}}$ 0.11	0.09

Linear regression analysis of weight versus CR

$r^2 = 0.02$ $F = 0.03$ n.s.

[a]Not aerated

Appendix Table 6. Consumption and fecal production by mid-final instar L. unicolor larvae fed field- or laboratory-conditioned Douglas fir needles.

Conditioning Time (days)	Final wt/Individual $\pm s_{\bar{x}}$ (mg)	Mean Consumption Rate $\pm s_{\bar{x}}$ ($mg \cdot mg^{-1} \cdot day^{-1}$)	Mean Fecal Production Rate $\pm s_{\bar{x}}$ ($mg \cdot mg^{-1} \cdot day^{-1}$)
12	2.522 ± 0.308 (n=18)	0.284 ± 0.033 (n=36)	0.353 ± 0.037 (n=36)
33	2.413 ± 0.305 (n=18)	0.299 ± 0.051 (n=36)	0.270 ± 0.036 (n=36)
47	2.186 ± 0.289 (n=19)	0.474 ± 0.065 (n=38)	0.619 ± 0.076 (n=38)
73	2.806 ± 0.340 (n=18)	0.381 ± 0.042 (n=35)	0.491 ± 0.052 (n=35)
102	3.313 ± 0.508 (n=20)	0.593 ± 0.071 (n=40)	0.644 ± 0.066 (n=40)
143	2.637 ± 0.314 (n=20)	0.671 ± 0.082 (n=39)	0.694 ± 0.073 (n=39)
Field Collected (270 est.)	2.618 ± 0.308 (n=19)	1.444 ± 0.179 (n=38)	1.622 ± 0.115 (n=38)

Appendix Table 7. Consumption and growth by mid-final instar L. unicolor larvae fed different densities of laboratory-conditioned Douglas fir needles at 5, 15, or 21°C.

Temp. (°C)	Food	Amt.	Survival	Final $\overline{wt} \pm s_{\bar{x}}$ (mg)	Mean Consumption Rate $\pm s_{\bar{x}}$ ($mg \cdot mg^{-1} \cdot day^{-1}$)	Mean Food Supply Rate $\pm s_{\bar{x}}$ ($mg \cdot mg^{-1} \cdot day^{-1}$)	Mean Growth $\pm s_{\bar{x}}$ (mg/individual)	Mean Growth $\pm s_{\bar{x}}$ (%/day)
5	Douglas fir	(high)	18/20	2.775 ± 0.375	0.441 ± 0.037	1.646 ± 0.159	0.094 ± 0.256	-0.9 ± 0.2
		(med.)	17/20	2.658 ± 0.452	0.123 ± 0.018	0.427 ± 0.050	0.183 ± 0.306	-1.1 ± 1.1
		(low)	19/20	2.177 ± 0.359	0.045 ± 0.007	0.090 ± 0.011	-0.096 ± 0.213	-1.3 ± 0.8
15	Alder	(high)	16/16	3.239 ± 0.300	0.551 ± 0.038	-	1.190 ± 0.167	4.6 ± 0.8
	Douglas fir	(high)	17/20	1.754 ± 0.246	0.902 ± 0.116	2.818 ± 0.232	-0.247 ± 0.167	-1.1 ± 0.7
		(med.)	20/20	2.280 ± 0.199	0.325 ± 0.020	0.448 ± 0.024	-0.407 ± 0.120	-1.7 ± 0.4
		(low)	19/20	2.593 ± 0.355	0.092 ± 0.013	0.121 ± 0.014	-0.081 ± 0.293	-1.3 ± 1.1
21	Douglas fir	(high)	14/16	1.803 ± 0.243	1.312 ± 0.077	3.114 ± 0.246	-0.530 ± 0.266	-2.8 ± 1.1
		(med.)	11/17	2.038 ± 0.426	0.568 ± 0.066	0.796 ± 0.082	-0.303 ± 0.362	-2.1 ± 1.1
		(low)	8/15	1.578 ± 0.233	0.092 ± 0.010	0.126 ± 0.012	-1.004 ± 0.122	-4.5 ± 0.8

Appendix Table 8. Results of multiple regression analyses of consumption rate versus size and temperature for mid-final instar L. unicolor larvae fed high densities of laboratory-conditioned Douglas fir needles.

CR	= 1.363	- 0.246(Wt)		r^2 = 0.31	F = 62**	n = 96
S.E.	0.076	0.031				
CR	= 0.157	+ 0.053(Temp)		r^2 = 0.38	F = 88**	
S.E.	0.083	0.006				
CR	= 0.662	- 0.170(Wt)	+ 0.042(Temp)	r^2 = 0.51	F = 73**	
S.E.	0.111	0.028	0.005			
lnCR	= -0.520	- 0.301(Wt)	+ 0.056(Temp)	r^2 = 0.64	F = 124**	
S.E.	0.131	0.033	0.006			

**Significant at $P \leq 0.01$

Appendix Table 9. Consumption and fecal production versus food type, temperature, and size for mid-final instar L. cascadense larvae.

Temp. (°C)	Food Type	Replication	Final Mean Wt. and Number		Consumption Rate		Fecal Production Rate
			$\overline{wt}$	n	($mg \cdot mg^{-1} \cdot day^{-1}$)	$\overline{x}$	($mg \cdot mg^{-1} \cdot day^{-1}$)
3	Alder	1	1.689	5	0.13		0.10
					0.07	0.10	0.07
					0.10		0.09
		2	1.322	5	0.03		0.09
					0.09	0.07	0.10
					0.10		0.13
	Maple	1	1.256	5	0.06		0.04
					0.04	0.04	0.09
					0.01		0.03
		2	0.606	5	0.09		0.16
					0.07	0.08	0.12
					0.09		0.10
	Douglas fir	1	1.211	5	0.16		0.08
					0.16	0.13	0.08
					0.07		0.07
		2	0.812	4	0.14		0.17
					0.14	0.21	0.16
					0.36		0.13

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Appendix Table 9. (Continued)

Temp. (°C)	Food Type	Replication	Final Mean Wt. and Number		Consumption Rate		Fecal Production Rate
			$\overline{wt}$ (mg)	n	(mg·mg^{-1}·day^{-1})	$\bar{x}$	(mg·mg^{-1}·day^{-1})
10	Alder	1	1.494	5	0.33		0.31
					0.27	0.32	0.22
					0.35		0.26
		2	0.727	5	0.56		0.43
					0.25	0.36	0.30
					0.27		0.28
	Maple	1	1.198	6	0.07		0.11
					0.06	0.07	0.06
					0.08		0.07
		2	0.522	5	0.16		0.22
					0.20	0.17	0.27
					0.16		0.24
	Douglas fir	1	1.586	4	0.09		0.16
					0.05	0.05	0.12
					0.01		0.14
		2	0.685	4	0.40		0.27
					0.15	0.19	0.24
					0.02		0.31

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Appendix Table 9. (Continued)

Temp. (°C)	Food Type	Replication	Final Mean Wt. and Number		Consumption Rate		Fecal Production Rate
			$\overline{wt}$ (mg)	n	(mg·mg^{-1}·day^{-1})	$\overline{x}$	(mg·mg^{-1}·day^{-1})
21	Alder	1	1.360	5	0.46		0.45
					0.23	0.30	0.24
					0.20		0.10
		2	0.734	3	0.93		0.56
					0.73	0.72	0.75
					0.51		0.60
	Maple	1	0.790	3	0.19		-[a]
					0.43	0.23	0.58
					0.06		0.23
		2	0.332	3	0.60		-[a]
				1 (2 died)	0.45	0.37	1.15
					0.06		0.40
	Douglas fir	1	0.437	3	0.96		0.34
				2 (1 died)	-0.05	0.48	0.14
					0.52		0.07
		2	0.176	3	4.38		3.42
				2 (1 died)	0.28	3.08	0.47
				1 (1 died)	4.59		0.28

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Appendix Table 9. (Continued)

Multiple regression analyses of Douglas fir needle consumption rate versus temperature and size

C.R.	=	1.991	- 1.590(Wt)		$r^2 = 0.30$	F = 7*	n = 18
S.E.		0.573	0.607				
CR	=	-0.384	+ 0.095(Temp)		$r^2 = 0.27$	F = 6*	
S.E.		0.533	0.039				
CR	=	0.996	- 1.063(Wt)	+ 0.050(Temp)	$r^2 = 0.34$	F = 4 n.s.	
S.E.		1.185	0.820	0.052			
$\ln(CR+0.1)^b$	=	-0.212	- 1.266(Wt)	+ 0.015(Temp)	$r^2 = 0.35$	F = 4 n.s.	
S.E.		0.988	0.683	0.043			

[a]Sample lost

[b]0.1 added to CR to avoid natural logarithm of negative values.

Appendix Table 10. Results of multiple regression analyses of consumption rate versus size and temperature for third- through fifth-instar C. magnifica larvae fed alder leaves or alder leaves and wheat grains.

			Alder + Wheat			
CR	=	0.773 - 0.017(Wt)		r^2 = 0.29	F = 75**	n = 188
S.E.		0.045 0.002				
CR	=	0.212 + 0.020(Temp)		r^2 = 0.02	F = 3 n.s.	
S.E.		0.159 0.011				
CR	=	0.569 - 0.017(Wt) +	0.014(Temp)	r^2 = 0.30	F = 39**	
S.E.		0.142 0.002	0.009			
ln(CR+0.1)[a]	=	-0.047 - 0.036(Wt) -	0.014(Temp)	r^2 = 0.51	F = 95**	
S.E.		0.185 0.003	0.012			
			Alder			
CR	=	0.630 - 0.029(Wt)		r^2 = 0.22	F = 46**	n = 162
S.E.		0.041 0.004				
CR	=	-0.045 + 0.030(Temp)		r^2 = 0.10	F = 17**	
S.E.		0.119 0.007				
CR	=	0.185 - 0.028(Wt) +	0.028(Temp)	r^2 = 0.30	F = 35**	
S.E.		0.110 0.004	0.006			
ln(CR+0.3)[a]	=	-0.950 - 0.032(Wt) +	0.045(Temp)	r^2 = 0.28	F = 32**	
S.E.		0.150 0.006	0.009			

[a] 0.1 or 0.3 added to consumption rate to avoid natural logarithm of negative values.

** Significant at $P < 0.01$

Appendix Table 11. Results of multiple regression analyses of respiration rate versus temperature and size for three species of caddis larvae.

		L. quercina		
Respiration Rate	=	1.870 -	0.316(Wt)	
S.E.		0.110	0.050	
$r^2 = 0.34$			F = 39**	
Respiration Rate	=	0.626 +	0.056(Temp)	
S.E.		0.179	0.014	
$r^2 = 0.18$			F = 17**	
Respiration Rate	=	1.362 -	0.271(Wt)	+0.036(Temp)
S.E.		0.206	0.051	0.012
$r^2 = 0.41$			F = 26**	
		L. unicolor		
Respiration Rate	=	1.778 -	0.239(Wt)	
S.E.		0.153	0.042	
$r^2 = 0.41$			F = 33**	
Respiration Rate	=	0.228 +	0.077(Temp)	
S.E.		0.144	0.014	
$r^2 = 0.39$			F = 31**	
Respiration Rate	=	1.035 -	0.192(Wt)	+0.061(Temp)
S.E.		0.181	0.034	0.011
$r^2 = 0.64$			F = 41**	
		C. magnifica		
Respiration Rate	=	1.358 -	0.021(Wt)	
S.E.		0.075	0.003	
$r^2 = 0.36$			F = 60**	
Respiration Rate	=	0.873 -	0.003(Temp)	
S.E.		0.174	0.012	
$r^2 = 0.00$			F = 0.3 n.s.	
Respiration Rate	=	1.223 -	0.021(Wt)	-0.010(Temp)
S.E.		0.147	0.003	0.010
$r^2 = 0.37$			F = 31**	

Appendix Table 12. Mean weights per individual and head capsule widths for different stages of L. quercina collected from Berry Creek.

	Mean Weight per Individual (mg) ($s_{\bar{x}}$, n)					
	second	third	fourth	fifth	Prepupae	Pupae
h.c. (mm):	0.20-0.23	0.30-0.33	0.43-0.47	0.63-0.80		
8-6 -74	0.012 (0.001, 5)	0.044 (0.003, 61)	0.171[a] (- , 0)			
9-5 -74	0.012[a] (- , 0)	0.064 (0.003, 54)	0.171 (0.055, 3)			
10-6 -74		0.080 (0.008, 8)	0.251 (0.013, 83)	0.442 (0.053, 9)		
11-12-74		0.080[a] (- , 0)	0.253 (0.022, 7)	0.940 (0.122, 42)		
12-18-74				1.468 (0.152, 32)		
1-19-75				3.719 (0.186, 31)		
2-26-75				5.511 (- , 1)	4.486 (0.249, 3)	3.038 (0.452, 7)

[a]None weighed. Means and standard errors taken from nearest sample.

Appendix Table 13. Mean population densities, weights per individual, and biomass for *L. quercina* collected from Berry Creek.

Date	Temp. (°C)	Mean No. /m^2 $\pm s_{\bar{y}st}$	$\overline{wt}$/Individual $\pm s_{\bar{y}st}$ (mg)	Wt. /m^2 (mg)	Total in Pool and Riffle No.	Total in Pool and Riffle Wt. (mg)
8- 6-74	13.0	382.3 ± 90.5	0.043 ± 0.023	16.4	10706	459
9- 5-74	11.0	98.3 ± 35.8	0.067 ± 0.029	6.7	2752	188
10- 6-74	10.0	139.9 ± 43.3	0.243 ± 0.010	34.0	5652	1374
11-12-74	9.0	50.0 ± 17.4	0.842 ± 0.093	42.1	2020	1701
12-18-74	9.0	28.6 ± 21.4	1.468 ± 0.152	42.0	1143	1696
1-19-75	7.5	32.2 ± 10.3	3.719 ± 0.186	119.8	1301	4838
2-26-75	8.0	0.5 ± 0.3	3.657[a] ± 0.095	1.8	20	74

[a] Estimate includes insects collected in addition to those found in samples.

Appendix Table 14. Standing crop of particulate organic material (> 5 mm) in a riffle-pool section of Berry Creek.

Date	Weight of Detritus (g/m^2) $\pm s_{\bar{y}st}$		
	Alder Leaves	Other Leaves	Twigs, Bark, etc.
Aug. 29, 1975	1.25 ± 0.96	2.86 ± 1.76	405.38 ± 248.82
Oct. 17, 1975	2.77 ± 3.01	10.31 ± 7.01	47.55 ± 26.26
Nov. 14, 1975	16.85 ± 7.46	113.13 ± 37.66	50.48 ± 33.76
Jan. 30, 1976	15.94 ± 8.61	212.05 ± 86.22	104.92 ± 18.62
$\bar{x}$	9.20	84.59	152.08

Appendix Table 15. Mean weights and instar distributions of L. unicolor from clear-cut and old-growth sections of Mack Creek.

	$\overline{wt} \pm s_{\bar{x}}$ (mg)	n	% Fourth	% Fifth	% Prepupae	% Pupae	$\overline{wt} \pm s_{\bar{x}}$ (mg)	n	% Fourth	% Fifth	% Prepupae	% Pupae
4-26-74	1.442 ± 0.188	40	10	90	-	-	1.109 ± 0.232	28	18	82	-	-
5-10-74	2.740 ± 0.718	12	25	75	-	-	1.567 ± 0.351	30	37	63	-	-
6- 5-74	2.657 ± 0.281	20	5	95	-	-	2.863 ± 0.229	37	3	97	-	-
6-28-74	4.877 ± 0.276	43	-	100	-	-	4.713 ± 0.259	41	-	100	-	-
7-10-74	4.660 ± 0.224	35	-	91	3	6	3.548 ± 0.216	39	-	97	3	-
7-17-74	-						4.010 ± 0.310	17	-	65	6	29
8- 1-74	-						3.120 ± 0.110	18	-	-	6	94

Appendix Table 16. Population densities, mean weights per individual, and mean biomass of L. cascadense in a riffle-pool section of Mack Creek.

Date	Water Temp. (°C)	Total Area (m^2)	% Riffle	$\overline{wt} \pm s_{\overline{y}st}$ (mg)	Mean No. /m^2 $\pm s_{\overline{y}st}$	Biomass /m^2 (mg)	Total in Section No.	Total in Section Wt. (mg)
10-19-74	8.5	12.0	42	0.060 ± 0.009	811.7 ± 359.2	48.6	9741	584
11-16-74	6.0	15.0	40	0.179 ± 0.014	707.0 ± 106.0	126.6	10605	1899
12-19-74	4.5	25.5	59	0.076 ± 0.004	407.9 ± 246.8	31.0	10403	791
1-29-75	2.5	32.0	63	0.257 ± 0.024	80.0 ± 58.5	20.5	2560	657
3-12-75	3.0	39.0	64	0.621 ± 0.045	111.0 ± 39.8	69.0	4330	2690
4-18-75	3.0	35.5	62	0.967 ± 0.054	153.3 ± 113.1	148.3	5443	5263
5-28-75	5.0	38.0	63	1.773 ± 0.135	119.6 ± 31.1	212.0	4545	8057
6-24-75	5.0	19.0	42	1.720 ± 0.034	202.4 ± 113.8	348.1	3846	6614
7-30-75	10.0	15.0	71	0.540 ± 0.02(est)	5.5 ± 0.5	2.6	82	39

Appendix Table 17. Mean weights per individual and head capsule widths for different stages of L. cascadense collected from Mack Creek.

	Mean Weight per Individual (mg) ($s_{\bar{x}}$, n)						
	First	Second	Third	Fourth	Fifth	Prepupae	Pupae
h.c. (mm):	0.13-0.17	0.23-0.27	0.33-0.40	0.53-0.63	0.83-0.93		
10-19-74		0.012 (0.002, 28)	0.046 (0.005, 29)	0.279 (0.011, 5)			
11-16-74		0.018 (0.002, 8)	0.042 (0.004, 30)	0.246 (0.031, 16)	0.434 (0.029, 5)		
12-19-74	0.005 (- , 1)	0.017 (0.003, 3)	0.052 (0.003, 25)	0.149 (0.014, 29)	0.353 (0.074, 2)		
1-29-75		0.017 (- , 1)	0.055 (0.011, 4)	0.208 (0.025, 22)	0.630 (0.149, 4)		
3-12-75				0.227 (0.020, 7)	0.973 (0.105, 13)		
4-18-75				0.326 (- , 1)	0.971 (0.110, 30)		
5-28-75					1.768 (0.150, 22)	2.355 (- , 1)	
6-24-75			0.114 (- , 1)		1.815 (0.052, 14)	1.616 (0.050, 10)	1.670 (0.143, 4)
7-30-75			0.300 (- , 1)				1.290 (- , 1)

Appendix Table 18. Population densities, mean weights per individual, and mean biomass of L. unicolor in a riffle-pool section of Mack Creek.

Date	Water Temp. (°C)	Total Area (m^2)	% Riffle	$\overline{wt} \pm s_{\overline{y}st}$ (mg)	Mean No./m^2 $\pm s_{\overline{y}st}$	Biomass/m^2 (mg)	Total in Section No.	Total in Section Wt. (mg)
10-19-74	8.5	12.0	42	0.021 ± 0.001	42.2 ± 20.6	0.9	506	11
11-16-74	6.0	15.0	40	0.047 ± 0.013	320.0 ± 15.7	15.0	1800	226
12-19-74	4.5	25.5	59	0.078 ± 0.007	132.9 ± 71.0	10.4	3389	264
1-29-75	2.5	32.0	63	0.029 ± 0.006	10.3 ± 9.0	0.3	330	10
3-12-75	3.0	39.0	64	0.176 ± 0.012	49.7 ± 27.0	8.8	1940	341
4-18-75	3.0	35.5	62	0.314 ± 0.018	22.8 ± 11.3	7.2	809	254
5-28-75	5.0	38.0	63	1.144 ± 0.135	33.2 ± 6.2	38.0	1262	1443
6-24-75	5.0	19.0	42	2.472 ± 0.403	76.7 ± 31.7	189.6	1457	3606
7-30-75	10.0	15.0	71	2.785 ± 0.268	4.8 ± 0.4	13.4	72	200

Appendix Table 19. Mean weights per individual and head capsule widths for different stages of L. unicolor collected from Mack Creek.

	Mean Weight per Individual (mg) ($s_{\bar{x}}$, n)						
	First	Second	Third	Fourth	Fifth	Prepupae	Pupae
h.c. (mm):	0.17-0.20	0.30-0.40	0.60-0.67	0.83-0.96	1.10-1.20		
10-19-74	0.010 (0.060, 2)						
11-16-74	0.023 (0.060, 5)	0.113 (- , 1)					
12-19-74	0.031 (0.004, 9)	0.081 (0.010, 16)	0.178 (0.023, 3)				
1-29-75	0.009 (0.003, 3)	0.054 (0.021, 3)					
3-12-75	0.025 (0.003, 3)	0.148 (0.013, 12)	0.653 (0.186, 4)				
4-18-75		0.069 (0.020, 2)	0.202 (0.035, 13)	0.805 (0.191, 2)			
5-28-75				0.567 (0.040, 11)	1.606 (0.301, 7)		
6-24-75					2.472 (0.106, 12)		
7-30-75							2.785 (0.268, 4)

Appendix Table 20. Computer program of simulation model of L. quercina growth.

```
      OS3 FORTRAN  VERSION 3.13            02/23/77  1442

0+001          PROGRAM LOTWO
0+002          REAL LTIME,MORT,NITREXR
0+003          READ(60,3)N,NDAYS,WT,POPI,MORT,FOOD1
0+004        3 FORMAT(I6,I9,2F9.3,F10.4,F6.2)
0+005          WRITE(61,1)
0+006        1 FORMAT(*  NLOOPS     NDAYS    WT.     POP. NO.    MORT.  FOOD*)
0+007          WRITE(61,13)N,NDAYS,WT,POPI,MORT,FOOD1
0+008       13 FORMAT (I6,I9,2F9.3,F10.4,F6.1)
0+009   C      WRITE OUTPUT HEADINGS
0+010          WRITE(61,4)
0+011        4 FORMAT(*0                                BIO          CONSUMPTION        *
0+012       1*FECAL      GROWTH     PRODUCTION  TEMP*)
0+013          WRITE(61,5)
0+014        5 FORMAT(*   DAY     WT.   NO.     MASS    RATE1 RATE2      AMT.    RATE*
0+015         1*       RATE          RATE*)
0+016   C      SET INITIAL ZEROS
0+017          CT=0.
0+018          FPT=0.
0+019          P=0.
0+020          TFOOD1 = 0.
0+021   C      LOOP OVER TIME
0+022          LTIME = 1./FLOAT(N)
0+023          DO 2 J=1,NDAYS
0+024          TIME = FLOAT(J) + FLOAT(I)/FLOAT(N)- 1.
0+025          DO 6 I=1,N
0+026          IF(TIME.LE.80.) FOOD1 = 0.2
0+027          IF(TIME.GT.80.) FOOD1 = 10.0
0+028   C      FIND POPULATION SIZE
0+029          POP = POPI*(EXP((-MORT)*(TIME)))
0+030          TEMP =  9.5 + 4.5*COS((TIME +40)*0.01428)
0+031   C      CALCULATE BIOMASS STANDING CROP
0+032          B=WT*POP
0+033          TFOOD1 = TFOOD1 + FOOD1
0+034   C      CONSUMPTION RATE (MG/MG/DAY)
0+035          CR = (1.356 - 0.178*WT)*(0.2469 + 0.0481*EXP(0.1057*TEMP))
0+036          CR1 = CR*(1. - EXP(-TFOOD1/(CR*9*LTIME)))
0+037          CR2=0.38*EXP(- TFOOD1/(CR*B*LTIME))*CR+ .00001
```

Appendix Table 20. (Continued)

```
0+038  C      ASSIMILATION RATE (MG/MG/DAY)
0+039         AFR = 0.23*(CR1 + CR2)
0+040         FPR = (CR1 + CR2) - AFR
0+041  C      RESPIRATION AND EXCRETION RATES (MG/MG/DAY)
0+042         RESPR = -0.00720 + 0.000789*TEMP + 0.04910*EXP(0.00647*WT)
0+043         NITREXR = CR1*0.01  + CR2*0.005
0+044  C      GROWTH RATE (MG/MG/DAY)
0+045         GR=AFR-RESPR-NITREXR
0+046  C      UPDATE TOTALS
0+047         G=GR*B*LTIME
0+048         C = (CR1 + CR2)*B*LTIME
0+049         CT = CT + (CR1 + CR2)*B*LTIME
0+050         FPT=FPT+FPR*B*LTIME
0+051         P=P+G
0+052         WT=WT+GR*LTIME*WT
0+053         TFOOD1 = TFOOD1 - CR1*B*LTIME
0+054         IF (TFOOD1.LE.0.) TFOOD1 = 0.
0+055       6 CONTINUE
0+056         WRITE(61,7)TIME,WT,POP,B,CR1,CR2,C,FPR,GR,G,TEMP
0+057       7 FORMAT(* *,F5.1,F6.3,F6.1,F8.2,F7.3,2F8.3,F8.3,F9.4,F11.3,F7.1)
0+058       2 CONTINUE
0+059         WRITE(61,8)
0+060       8 FORMAT(*0TOTAL CONSUMPTION   TOTAL FECAL PRODUCTION   TOTAL*
0+061        1* PRODUCTION* )
0+062         WRITE (61,9)CT,FPT,P
0+063       9 FORMAT(F14.2,6X,F18.3,11X,F11.2)
0+064         CALL EXIT
0+065         END

 NO ERRORS FOR LOTWO
LENGTH OF SUBPROGRAM      00742
RUN
```