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POPULATION DYNAMICS, BIOENERGETICS, AND ROLE OF *LEPIDOSTOMA QUERCINA* ROSS (TRICHOPTERA: LEPIDOSTOMATIDAE) IN AN OREGON WOODLAND STREAM[1, 2]

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Abstract. The aim of this study was to gather quantitative field and laboratory data on the utilization of deciduous leaves as food by *Lepidostoma quercina* Ross (Trichoptera: Lepidostomatidae) and estimate the effect of this food processing on the stream ecosystem.

Samples were taken monthly in a riffle-pool section of Berry Creek, Benton County, Oregon. Maximum larval density was 382 per m^2, instantaneous growth rate was 2.7% per day, instantaneous mortality rate was 1.4% per day, and production was 0.19 $g \cdot m^{-2} \cdot yr^{-1}$. The life cycle of *L. quercina* and its period of maximum larval growth corresponded closely with the period of maximum availability of its preferred food (alder leaves) in the stream.

Consumption and fecal production rates were measured gravimetrically. Rates ($mg \cdot mg^{-1} \cdot day^{-1}$) increased with temperature, food quantity, and conditioning time of the leaves, and decreased with increased size of the larvae.

Mean respiration rates of larvae were higher at 10°C than at 5°, but there was no significant difference in mean rates at 10, 15, or 20°C. Respiration rate decreased with increased size of the larvae. Size-specific respiration rates showed regulation of respiration with respect to temperature for small individuals (present in the field in September and October when temperatures are variable) and little or no regulation by large individuals (present in December and January).

Simulation modeling of larval growth based on laboratory data demonstrated that growth and production of *L. quercina* in the field may be limited by a lack of high-quality food (alder leaves) in late summer and early fall. Consumption of leaves by the simulated population was estimated as 3.1 $g \cdot m^{-2} \cdot yr^{-1}$.

Lepidostoma quercina comprised only a small part of the secondary production in Berry Creek (0.19 $g \cdot m^{-2} \cdot yr^{-1}$, vs. 2.2 $g \cdot m^{-2}$ for simuliids) and processed only a small portion of the allochthonous input to the stream. However, significant quantities of fecal material were produced and it was estimated that these fine particles would be sufficient to support ¼ to ½ of the production of simuliids, the dominant riffle species in Berry Creek.

Key words: bioenergetics; caddisflies; consumption; deciduous leaves; growth; Insecta; Lepidostoma; *Oregon; population dynamics; respiration; stream.*

INTRODUCTION

Terrestrial litterfall forms the energy base for most small streams, due to typically heavy shading from surrounding vegetation (Cummins 1974, Hynes 1975). Most of the litterfall enters the stream system as large particles which are degraded by microbial activity and feeding by invertebrates known as shredders (Cummins 1973). Limnephilidae constitute the dominant shredders in many streams in eastern North America (Cummins 1964, 1973; Mackay and Kalff 1973) and are the most abundant caddisflies in Oregon (Anderson 1976). However, in some Oregon streams, members of the family Lepidostomatidae appear to be the major shredders of allochthonous inputs (Sedell et al. 1975).

Lepidostoma quercina Ross is the dominant lepidostomatid in Berry Creek, Benton County, Oregon, and is one of the dominant shredder species in the system. *Lepidostoma unicolor* (Banks) and *Lepidostoma roafi* (Milne) also occur in Berry Creek, but larvae of *L. quercina* are easily distinguished on the basis of case type and seasonal occurrence. This provided the opportunity for detailed field and laboratory studies of a single species, to obtain information on population dynamics, bioenergetics, and impact of this species on the stream system. *Lepidostoma quercina* was of particular interest because its life cycle is geared to allow exploitation of the autumnal pulse of deciduous leaf input. Eggs hatch in summer and larvae grow most rapidly in late fall and early winter when water temperatures are low.

Data were obtained on population dynamics and life history of *L. quercina* and rates of food processing, respiration, and growth were estimated, particularly as these rates are affected by condition of the leaves, temperature, and larval size or age. Independent measurements were made of each of the parameters of the energy budget:

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$$\text{Consumption} = \text{feces} + \text{respiration} + \text{nitrogen excretion} + \text{growth}. \quad (1)$$

The objectives of this study were (1) to estimate the impact of *L. quercina* larvae on the stream system in terms of insect production and quantities of coarse particulate organic material ingested and fine particulate organic material egested, and (2) to assess the possible adaptive significance of life history and bioenergetic response to environmental changes for the larvae in their natural habitat.

Materials and Methods

Field population studies.—The study area was a riffle-pool section of Berry Creek, located 15 km north of Corvallis, Oregon, at an elevation of 75 m. Width of Berry Creek is ≈2 m, mean discharge 0.01 $m^3 \cdot s^{-1}$, gradient 1.7%, and water temperatures range from 2 to 15°C. Surrounding vegetation is a mixed deciduous–conifer forest with dominant species of red 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 semicontrolled flow, due to a dam and a bypass channel that are remnants 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.

Samples were collected monthly (6 August 1974 to 26 February 1975) with a 0.1-m^2 Surber sampler (mesh 250 mμ). A stratified sampling scheme was used, with 3 or 4 samples each from riffle, pool, and "pool-end" strata. The pool-end stratum was a short section of stream at the downstream end of the pool. Most of the leaves accumulated in the pool-end region, because the shallowness of the riffle prevented further downstream movement except during periods of high water. In the pool areas, the Surber sampler was used to delineate the area to be sampled and the substrate and associated insects were scooped by hand into the collection net.

Immediately after returning to the laboratory, all large pieces (>2 mm) of leaves or other organic material were removed and the samples were placed in shallow pans of water at 13°C. A few alder leaves were placed on top of the substrates as a feeding attractant. The leaves and sides of the pans were inspected for larvae periodically for 3 or 4 days. Tests with stream substrate and a known number of larvae demonstrated that this trapping technique was >85% efficient, even for small larvae, which would be very time-consuming to sort by hand. Mature larvae, prepupae, and pupae were sorted by hand because they were large and easy to see and were no longer actively feeding. On each sampling date, random samples of the available instars were dry-weighed and weights were analyzed as stratified samples, grouped according to instar. Larvae were oven-dried at 60°C for 24–48 h and cooled in a desiccator, prior to weighing with a Cahn 4100 or Mettler H16 balance.

Standing crop of particulate litter and debris >≈2 mm diameter was estimated on 4 occasions (29 August 1975 to 30 January 1976). Samples were collected from 3 strata, as before. Material collected was separated into categories of alder leaves, miscellaneous leaves (mainly bigleaf maple) and other (e.g., twigs, bark, and needles). After sorting, samples were oven-dried, cooled in the open air, and weighed.

Laboratory studies of feeding and growth.—Alder leaves were emphasized as a food source because they are preferred over other foods by *Lepidostoma quercina* and form a major portion of the input to Berry Creek and other Willamette Valley and Coast Range streams. Previous feeding studies indicated that alder leaves were preferred over maple leaves or Douglas fir needles by >3:1 (Grafius 1977). Alder leaves are higher in protein and N than other species (Goldman 1961, Triska et al. 1975) and have a longer period of leaf fall (July–December) than the other riparian deciduous trees.

Consumption and fecal production were measured gravimetrically. Leaves were conditioned in a laboratory drippery system (Anderson 1973) for 2–3 wk prior to feeding. Initial amounts of food were estimated using a paired leaf-disk technique. Disks were cut from the leaves with a 8.5 mm cork borer and paired according to position on the leaf and amount of leaf vein included. One disk from each pair was used in the feeding trial and the other was set aside in water. At the end of the trial, the leaf disks were dry-weighed and consumption was estimated as the difference in weight between "fed" and "unfed" groups of disks. Leaves were not dry-weighed prior to feeding because this would destroy microbial components known to be important stimuli to feeding (Kaushik and Hynes 1971, Kostalos 1972, Grafius 1974). During the experiments, larvae were kept in aerated 8.9 cm diameter glass culture dishes with Nytex® screen as a substrate. Four to 12 larvae were kept in each dish (= replication) and an abundance of food was provided (1 or 2 leaf disks per larva ≈2–3 × consumption). Food was changed and feces collected every 2 to 3 days during an experiment. Feces were collected by filtration on preweighed 1.2-μm Millipore® filters. Small particles of uningested food were separated from the feces prior to filtration and included with the uneaten food. This hand sorting was minimal, because larvae left very few food fragments. Therefore, consumption and ingestion will be considered as equivalent, although the former is sometimes defined to include chewed but uningested food fragments. Because the food had been thoroughly preleached, it was assumed that leaching from feces would be similar to leaching from the unfed leaf disks. Larvae were killed and dry-weighed at the end of each

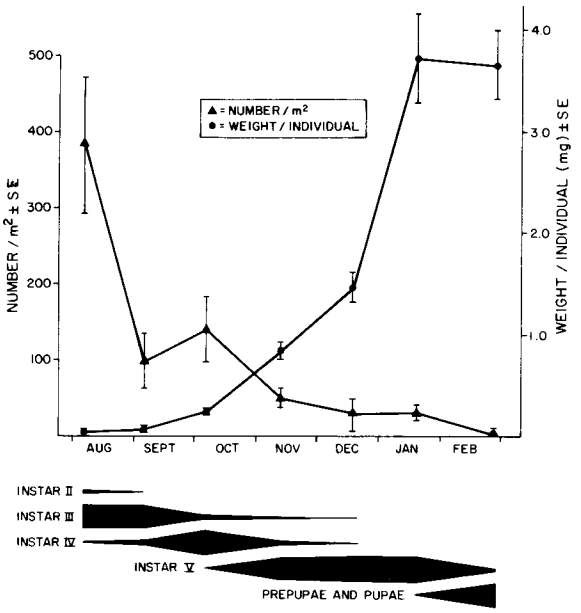

FIG. 1. Population density, mean weight per individual, and instar distribution (%) for *Lepidostoma quercina* larvae in Berry Creek, Oregon.

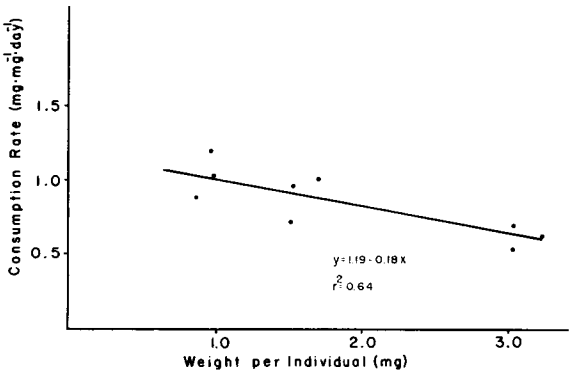

FIG. 2. Consumption rate for mid-final instar *Lepidostoma quercina* larvae fed on alder leaves compared with mean larval weight.

experiment to allow expression of data as rates (e.g., mg consumption·mg body weight^{-1}·day^{-1}). Assimilation efficiencies were calculated as:

$$\text{Assimilation efficiency (\%)} = \frac{\text{consumption} - \text{fecal production}}{\text{consumption}} \times 100. \quad (2)$$

Further descriptions of specific methods will be included in the Results for the respective experiments.

Respiration measurements.—Respiration rates were measured using a Gilson Differential Respirometer. Insects were acclimated for at least 2 wk at the appropriate temperature prior to testing and were tested individually or in groups of up to 5 larvae per flask. Experiments lasted from 24 to 72 h, depending on temperature and size of the larvae. Flasks were not shaken, to more closely simulate the pool habitat of *Lepidostoma quercina*. Pieces of conditioned alder leaf were included in the flasks to serve as food and substrate. At the end of each experiment, the larvae were removed for weighing and the insect cases were returned to the flask along with the remaining food and feces. Respiration was again measured and these values were subtracted from the respiration of leaf + insect + case, to give an estimate of insect respiration. There was no significant change in respiration rate during the course of the experiments ($P < .01$), indicating that there was probably no significant increase in microbial activity or colonization on food or feces. Although measured under artificial conditions, it was assumed that these estimates approximated respiration rates in the field at the respective temperatures.

Respiratory Q_{10} values (the factor of increase over a 10°C temperature change) were calculated from the slope of natural logarithm of respiration rate vs. temperature. Q_{10} values, although often oversimplifications, serve as general indices of response to temperature change. For example, a Q_{10} of 1.0 indicates no change with changes in temperature. A Q_{10} value of 2.0–3.0 (doubling or tripling with every 10°C temperature increase) is normal for most poikilotherms (Warren 1971).

For use in the energy budgets and simulation model, respiration (μl O_2) was converted to equivalent amounts of tissue, assuming 4.9 cal [20.5 J] per ml O_2 (McDiffett 1970) and 5200 cal [21 756.8 J] per g of insect (Cummins and Wuycheck 1971).

RESULTS AND DISCUSSION

Population Dynamics.—Mean population densities decreased from 382 larvae per m² in August to 0.5 per m² in February (Fig. 1). Mean larval weight increased from 0.043 mg to 3.657 mg during this time. As is true for most species of caddisflies, the majority of this growth occurred during the final instar. Mean weights of final-instar larvae increased from 0.442 mg per larva in October to 3.719 mg per larva in January.

Instantaneous growth rate was estimated as 2.7% per day ($r^2 = .96$) and instantaneous mortality rate as 1.4% per day ($r^2 = .85$). Production was estimated as 0.19 g·m^{-2}·yr^{-1} (using the method of Ricker 1946). Turnover ratio (production: annual mean biomass) was 8.6, comparable to other values in the literature (Hynes 1970).

Larvae were more concentrated in pool and pool-end areas than in the riffle area (3:1 during August and September, 11:1 from November through January). Although leaves were concentrated in the pool-end region (pool-end:pool:riffle for leaves = 34:6:1), there was little difference between densities of larvae in the pool or pool-end areas. In completely natural streams where freshets were unrestricted, leaves might be

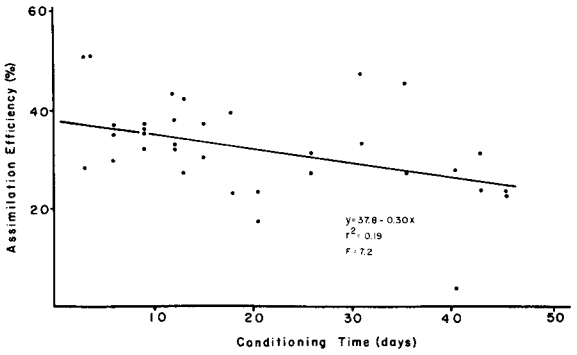

FIG. 3. Assimilation efficiency for *Lepidostoma quercina* larvae fed on alder leaves compared with conditioning time of the leaves.

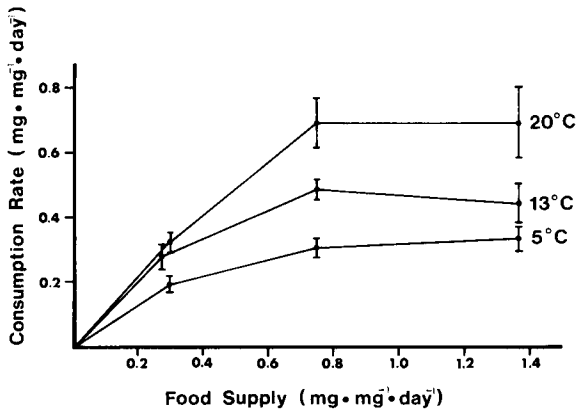

FIG. 4. Consumption rates for final instar *Lepidostoma quercina* larvae at 3 temperatures and 3 food densities. Vertical lines = 90% confidence intervals (reprinted from Anderson and Grafius 1975).

moved more rapidly from pool-end to pool regions of the stream and leaf distribution might correspond more closely to the distribution of *L. quercina* larvae. Quantities of alder and other deciduous leaves throughout Berry Creek were low during the summer and early fall ($\approx$2 g·m^{-2} of alder and 6 g·m^{-2} other leaves). Leaf weight increased by a factor of 8–26 immediately after the first heavy rains in early November (16 g·m^{-2} of alder and 160 g·m^{-2} of other leaves in November and January).

Feeding vs. larval size.—Because of the importance of the final instar and because within-instar changes in consumption rates may be large (Anderson and Grafius 1975), it was important to have accurate measurements of the effects of size within this stage on consumption and fecal production rates. In order to reduce the variability caused by differences in food quality, all food used in this experiment came from 1 alder leaf. Larvae were separated visually into 3 size classes with 3 replications per size class and 4 larvae per replication and were kept at 13°C during the 2-day experiment. Consumption rate (mg·mg^{-1}·day^{-1}) decreased significantly with increased larval weight (Fig. 2). There was no significant correlation between assimilation efficiency and larval weight ($\bar{x}$ = 21.3%, $s_{\bar{x}}$ = 2.0). Experiments with 2nd-, 3rd-, and 4th-instar larvae showed similar decrease in feeding rate with increased size.

Effects of food quality on feeding.—Anderson and Grafius (1975) demonstrated that consumption rate of alder leaves by *L. quercina* increased rapidly after $\approx$3 wk of conditioning of leaves in the field. The relatively high consumption even of newly fallen leaves (0.60 mg·mg^{-1}·day^{-1}) is indicative of the palatability of alder leaves and correlates with their high nitrogen content.

Assimilation efficiencies, calculated using data from the experiment of Anderson and Grafius (1975), decreased significantly ($P < .05$) with conditioning time of the food (Fig. 3). Conditioning time explained 19% of the variability. Other possible sources of variation include: (1) experimental error in collection of feces and measurement of consumption, (2) differences in gut-retention time or digestive efficiency between larvae, and (3) differences in digestability of individual leaves (disks from 3–4 leaves were used in each treatment). This decrease in assimilation efficiency may be an artifact of the methods, because the large amounts of feces produced by larvae feeding on well-conditioned leaves were perhaps more efficiently collected than smaller amounts, when leaves were less palatable. However, a similar result was found by Dale McCullough (Department of Fisheries and Wildlife, Oregon State University, *personal communication*) with the snail *Juga plicifera* (Lea) fed on alder leaves, using Conover's (1966) ash method of estimating assimilation efficiency. The decrease is perhaps a result of higher consumption rates and decreased gut-retention times on well-conditioned leaves.

Consumption and growth as affected by temperatures and food density.—Mid-final instar larvae ($\overline{wt}$ = 2.0 mg), acclimated at the respective temperatures, were fed different densities of alder leaf disks at 5, 13, or 21°C. There were 4 replications with 12 larvae each (=48 larvae) in each temperature/food-density treatment. Food was changed and consumption and fecal production were measured every 3 days during the 12-day experiment. Consumption rate at medium and high food densities increased with temperature, as expected (Fig. 4). There was no significant difference in consumption rate between medium and high food densities, although food was only slightly in excess at medium densities. This indicated that the larvae spent little time searching among the food items or else the leaf disks were of uniform quality.

Assimilation efficiencies in this experiment, corrected for slight losses of case material (mostly due to consumption of case material) during the experiment (primarily at 21°C or low food density), tended to de-

TABLE 1. Mean assimilation efficiency[a] (%) for mid-final instar *Lepidostoma quercina* larvae fed different densities of alder leaves at 5, 13, or 21°C

Food supply	Temperature (°C)		
	5	13	21
low	24.5	15.2	17.1
medium	17.4	19.5	21.2
high	32.5	22.8	22.3

[a] Corrected for slight losses of case material. Measurements were not replicated because case loss could only be measured at the end of the experiment.

crease with increased temperature and increase with higher food density (Table 1). Because the leaves were all conditioned at 13°C and were only at the experimental temperature for a maximum of 3 days, the decrease in assimilation efficiency with increased temperature is unlikely to be due to temperature-induced changes in food quality. It is more likely that it reflects an adaptation by *L. quercina* to cool temperatures. This could be mediated through increased efficiency of digestive enzymes or more efficient nutrient uptake at lower temperatures. A wide variety of biochemical mechanisms increasing enzyme efficiency at lower temperatures are described in Hochachka and Somero (1973). The increase in assimilation efficiency with higher food density was expected, because larvae consume fewer leaf veins and midribs (high in lignin and cellulose).

Growth at 5, 10, or 15°C was measured by estimating initial weight of individual final-instar larvae from a regression of case length × width² vs. larval dry weight. Larvae were kept in separate containers (3 × 4 cm plastic ice cube compartments) in the laboratory with alder leaves as food for 32 days at the respective temperatures (20 larvae per treatment, range of estimated initial weight = 0.22 – 3.26 mg). Significant growth occurred at 5 and 10°C, but not at 15°C ($P < .05$) (Table 2). Although there were no significant differences between growth rates at 5, 10, or 15°C ($P < .05$), the general increase with cooler temperatures may have reflected adaptations to low temperatures. In addition to an inverse relation to growth rate, temperature had a pronounced effect on maturation.

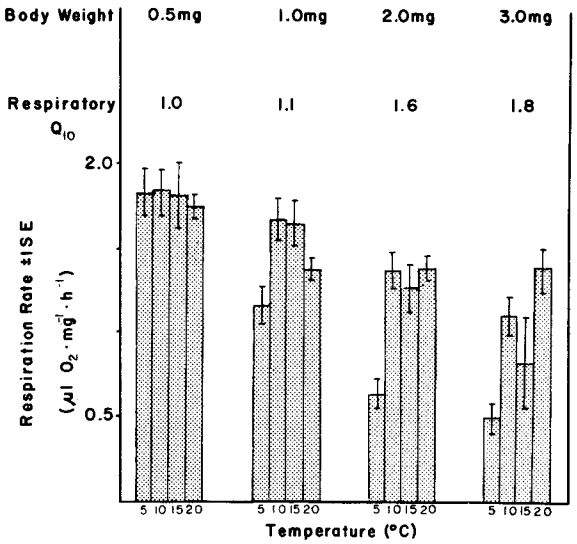

FIG. 5. Respiration rates for specific sizes of *Lepidostoma quercina* larvae at different temperatures.

None of the larvae at 5 or 10° sealed off their cases for pupation, while 40% (8 of 20) of the larvae at 15° began pupating, although they were much below normal mature weights. Premature pupation is apparently a response to high temperature, perhaps because high maintenance costs prevent further growth.

Growth efficiencies.—Feeding, fecal production, and growth were measured at 13°C for mid-final instar larvae by using large numbers of insects and sacrificing a group of 40 to 50 larvae every 3 to 4 days during the 16-day experiment. In this manner, it was hoped that accurate measurements of growth, consumption, and assimilation could be combined to estimate gross and net growth efficiencies.

Mean consumption rate was 0.50 $mg \cdot mg^{-1} \cdot day^{-1}$ ($s_{\bar{x}} = 0.03$) and mean fecal production was 0.44 $mg \cdot mg^{-1}$ ($s_{\bar{x}} = 0.01$). Instantaneous growth rate was 1.9% per day ($s_b = 0.6$, $r^2 = .73$). Gross growth efficiency, the slope of growth vs. amount consumed per larva, was estimated as 3.1% ($r^2 = .75$). Net growth efficiency, the slope of growth vs. assimilation per larva, was estimated as 12.9% ($r^2 = .59$). Other values reported for caddis larvae fed on alder leaves are

TABLE 2. Growth, mortality, and percent pupation for final instar *Lepidostoma quercina* larvae fed alder leaves at 5, 10, or 15°C for 32 days

Temperature (°C)	Growth per individual[a] ± $s_{\bar{x}}$ (mg)	Instantaneous growth Rate[a] ± $s_{\bar{x}}$ (%/day)	Mortality (%)	Pupation (%)
5	0.48 ± 0.13	2.56 ± 0.66	5	0
10	0.48 ± 0.20	1.79 ± 0.84	0	0
15	0.01 ± 0.30	0.65 ± 1.90	10	40

[a] Excluding dead or pupating individuals.

TABLE 3. Mean respiration rates for 3rd through 5th-instar *Lepidostoma quercina* larvae at 4 different temperatures

Temperature (°C)	*N*	Mean weight ± $s_{\bar{x}}$ (mg)	Weight range (mg)	Mean respiration rate ± $s_{\bar{x}}$ (μl $O_2 \cdot mg^{-1} \cdot h^{-1}$)
5	19	2.34 ± 0.33	0.66–4.50	0.77 ± 0.11
10	20	2.04 ± 0.36	0.31–6.43	1.39 ± 0.14
15	28	1.43 ± 0.13	0.07–2.54	1.48 ± 0.12
20	11	1.36 ± 0.23	0.35–2.56	1.63 ± 0.20

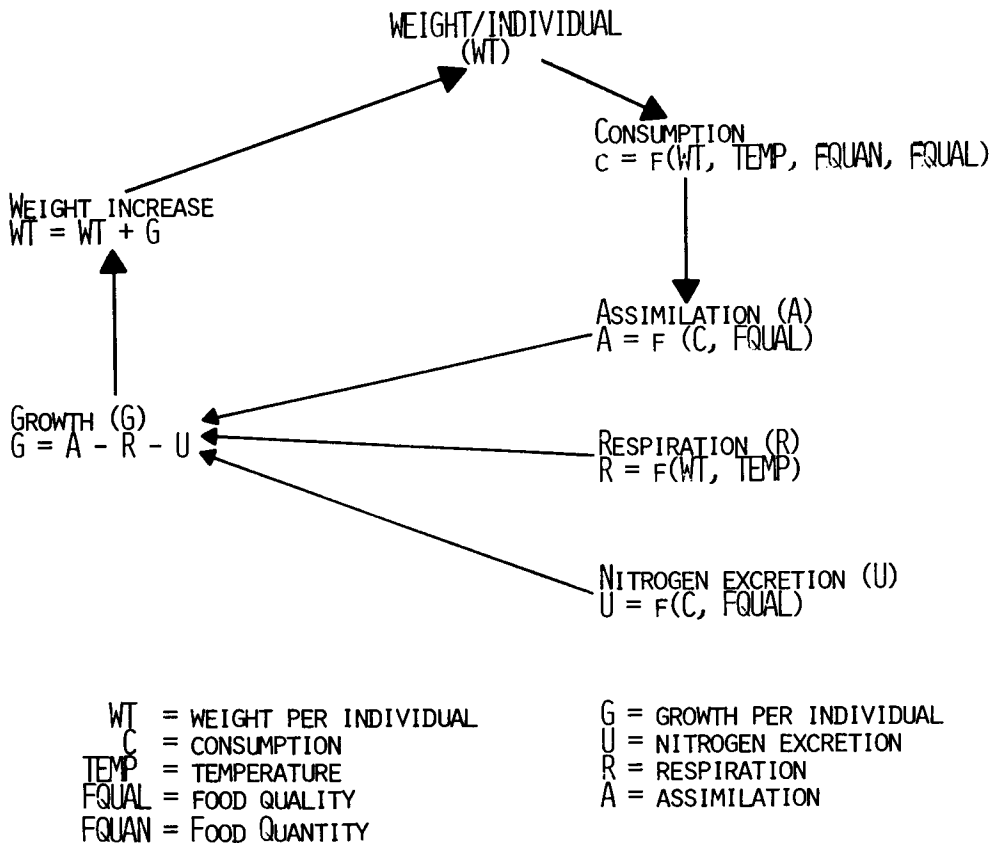

FIG. 6. Flow chart of a simulation model of *Lepidostoma quercina* growth predicted from laboratory data. The notation $C = F(WT)$ signifies that the parameter C is a function of WT.

somewhat higher. For example, gross growth efficiency was 6.0% for *Lepidostoma unicolor* (15°C) and 2–16%, depending on temperature and larval size, for the limnephilid *Clistoronia magnifica* (Banks) (Grafius 1977); and 2–20%, depending on temperature and larval size, for the limnephilid *Potamophylax cingulatus* (Steph.) (Otto 1974). Net growth efficiencies for these species were estimated as 60% for *L. unicolor*, 3–33% for *C. magnifica*, and 12–71% for *P. cingulatus*.

Respiration.—Mean respiration rates of *L. quercina* larvae increased from 5 to 10°C, but showed no significant change between 10, 15, and 20°C (Table 3). Larval weight ranged from 0.07 to 6.43 mg and respiration rate decreased significantly with increased weight ($P < .01$).

To examine the effects of larval size on respiration rate, curvilinear regression analyses (respiration rate = $b_1 + b_2 \exp b_3 \cdot$ mean weight) were performed with the data from each temperature (r^2 values = .19 – .63, significant at $P < .05$). Respiration rates for specific sizes of larvae were estimated from these regression equations and are shown in Fig. 5. The respiration rates of small *L. quercina* larvae, which occur in the field in September and October when temperatures may fluctuate, were much less affected by changes in temperature than were respiration rates of the large larvae, found in the field from December through January. For example, respiration of 4th and early 5th (= final) instar larvae (0.3–1.0 mg dry weight) was not affected by temperature, while respiration of mid- to late-5th instar larvae (2.0–3.0 mg) was significantly affected by temperature (Table 4). Slopes of the regression lines (and Q_{10} values) for the small and large size classes were significantly different (t-test, $P < .05$). This demonstrated that the ability to maintain a constant respiration rate in the face of changing temperature is primarily restricted to the larval stages most apt to encounter temperature variation.

Energy budgets.—A balance of food intake with energy expenditures, as in Eq. 1, was used to estimate potential growth for larvae in the laboratory. An approximation of 3.7 $\mu g \cdot mg^{-1} \cdot day^{-1}$ ammonia nitrogen excretion, equivalent to $\approx 0.7\%$ of consumption, was obtained by confining larvae to a tightly stoppered vial of dechlorinated water and drawing off samples for analysis every 2.5 to 3.5 h (Grafius 1977). The amount of energy theoretically available for growth (Table 5) is much > the actual observed growth (Table 2). This is similar to the results of Otto (1974) with the caddisfly *P. cingulatus* and Nilsson (1974) with the Amphi-

TABLE 4. Regression analyses of natural logarithm of respiration rate vs. temperature for selected size classes of *Lepidostoma quercina* larvae. * = $P < .05$, ** = $P < .01$.

Instar	Weight range (mg)	n	r^2	slope ± SE	Q_{10}
4th to early 5th	0.3–1.0	23	.02 ns	0.013 ± 0.018	1.14
Early to mid 5th	1.1–1.9	28	.16*	0.040 ± 0.018	1.49
Mid to late 5th	2.0–3.0	15	.42**	0.072 ± 0.023	2.06

pod *Gammarus pulex* L. The only large unmeasured losses apparently occurred in the form of dissolved organic materials. Significant excretion of dissolved organics has been shown for several aquatic invertebrates (Johannes and Satomi 1967, Hargrave 1971, D. McCullough, *personal communication*). However, it is difficult to imagine large quantities of dissolved materials going unnoticed in a confined system such as was used in the present study. An overestimate of assimilation (underestimate of fecal production) may also have contributed to the error. The largest error is probably in the estimation of growth rates in the laboratory (Table 2). The accurate estimation of initial weight and growth of *Lepidostoma* larvae is particularly difficult and time-consuming, because larvae cannot be removed from their cases without seriously disturbing them.

Simulation modeling.—A simple discrete-time simulation model was designed to estimate the impact of *L. quercina* on the stream system in terms of food consumed and fine particles produced. The simulation was also used to compare predicted growth (based on laboratory data on feeding and respiration) with field growth rates of *L. quercina* larvae.

The model was based on the relationship shown in Eq. 1. A flow chart is shown in Fig. 6. Initial inputs to the model were: (1) insect weight on day 0; and (2) food supply rate, unlimited for the initial simulation run. Conditioning time was not considered as a factor affecting consumption rate because alder leaves entering Berry Creek are rapidly consumed by *L. quercina* and other invertebrates (e.g., the snail, *Juga plicifera*) and rarely reach the "age" of ≈3 wk when conditioning becomes critical (Anderson and Grafius 1975). The function relating feeding rate to food supply was an estimate for field conditions, based on laboratory data. All other functional relations were least-squares fits of laboratory data. For example, the relationship between consumption rate and temperature was derived from the data in Fig. 4. A temperature regime, similar to temperatures in Berry Creek, was represented by a cosine function. Temperatures in the simulation ranged from 13°C in early August to 5°C in late January, similar to field conditions during 1974–1975. Addition of initial larval density and a mortality curve from the field data allowed estimation of the following population parameters: (1) insect production, (2) total consumption, (3) total fecal production, and (4) gross and net production efficiencies (analogous to gross and net growth efficiencies of individuals).

In the initial run, where food supply was unlimited, growth predicted from the simulation model was more

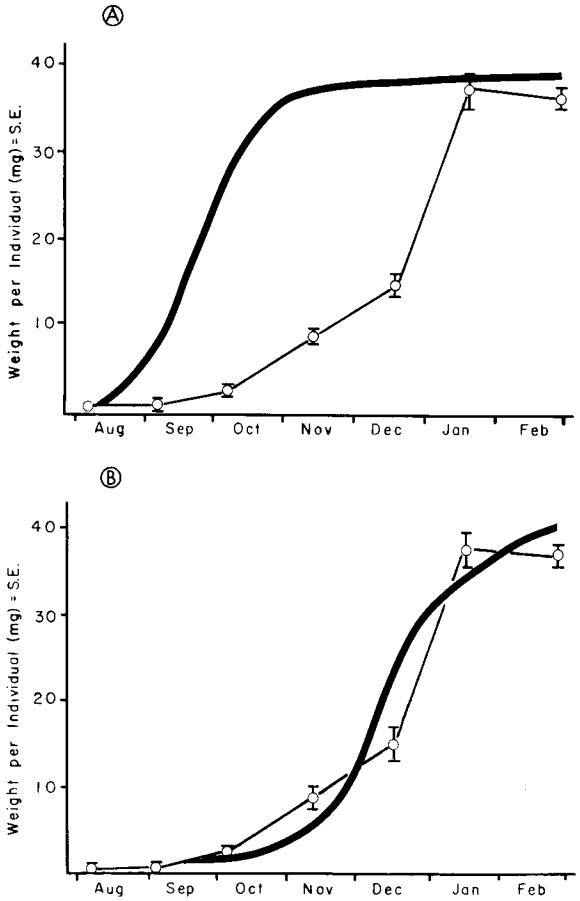

FIG. 7. Comparisons of field mean weights (open circles) with results of simulation modeling of *Lepidostoma quercina* growth (a) when food was unlimited and (b) when alder leaves were limited for the first 80 days of simulation.

TABLE 5. Growth of *Lepidostoma quercina* larvae estimated from laboratory measurements of assimilation and respiration

Temperature (°C)	Consumption rate[a] ($mg \cdot mg^{-1} \cdot day^{-1}$)	Assimilation rate[b] ($mg \cdot mg^{-1} \cdot day^{-1}$)	Respiration rate ($mg \cdot mg^{-1} \cdot day^{-1}$)	Potential growth rate ($mg \cdot mg^{-1} \cdot day^{-1}$)
5	0.32	0.104	0.017	0.085
10	0.40	0.108	0.031	0.074
15	0.48	0.108	0.034	0.071

[a] Estimated from Fig. 2.
[b] Assimilation efficiencies estimated from Table 1.

rapid than growth observed in the field (Fig. 7a). However, growth rates for larvae 1.5 mg or larger and maximum larval weights were similar in both cases. This indicated that the model was generally acceptable but that perhaps assumptions pertaining to growth of small larvae needed closer examination.

The field data on 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, limiting the amount of alder leaves available during the first 80 days (August through October), corresponding to the period of low food availability in the field. When alder was limited, consumption of an alternate food (e.g., maple) was allowed, but at a reduced rate. If the supply of alder leaves was limited to 4 $mg \cdot m^{-2} \cdot day^{-1}$, predicted larval growth could be made to closely approximate field growth (Fig. 7b). The rate of food supply was arbitrarily determined and would vary, depending on factors such as the palatability of alternate foods, searching efficiency of the larvae, and inter- or intraspecific competition. However, the results indicate that a lack of high quality food could be limiting to *L. quercina* growth and production.

Because the model used field data for mortality and population density and food supply was manipulated so that growth corresponded to field conditions, production of *L. quercina* biomass in the food limited simulation was the same as estimated from the field sampling (0.19 $g \cdot m^{-2} \cdot yr^{-1}$). Consumption of alder and maple leaves by the simulated population was 3.1 $g \cdot m^{-2} \cdot yr^{-1}$ and fecal production was 2.4 $g \cdot m^{-2} \cdot yr^{-1}$. Gross production efficiency was 6.1% and net production efficiency was 27.1%. These values for gross and net efficiencies correspond more closely with values in the literature than did the laboratory estimates, perhaps due to the difference in temperature regimes. At the higher temperature of the laboratory experiment (13° vs. a range of 5 to 13°C in the simulation), respiration might be expected to comprise a larger proportion of the energy budget, resulting in reduced growth efficiency. Also, smaller individuals, included in the simulation, might be expected to have lower maintenance costs and correspondingly higher growth efficiencies. Using the laboratory value of 3.1% gross growth efficiency, 0.19 $g \cdot m^{-2} \cdot yr^{-1}$ of production would require consumption of 6.1 $g \cdot m^{-2} \cdot yr^{-1}$ of alder leaves, compared with the estimate of 3.1 $g \cdot m^{-2} \cdot yr^{-1}$, from the simulation model where gross efficiency was 6.1%.

The major role of *L. quercina* in the stream ecosystem is not as a direct source of insect biomass, because production of *L. quercina* was much < the production of Simuliidae (dominant riffle species) in Berry Creek and similar streams (2.2 $g \cdot m^{-2} \cdot yr^{-1}$, Speir 1976). However, the feces produced by *L. quercina* are a highly significant contribution to the food chains of simuliids and other collector species. No data are available on the utilization of insect feces by simuliids. However, because fecal material can theoretically be recycled through the collectors a number of times until all of it has been assimilated, net growth efficiency (assimilation/growth) may be used to directly estimate production from a known amount of fecal material. Using a net growth efficiency of 0.20 (low compared with most estimates, Welch 1963), ≈22% of the simuliid production in Berry Creek could be supported by 2.4 $g \cdot m^{-2} \cdot yr^{-1}$ fecal material. Using a value of 0.50 (simuliids fed on diatoms, McCullough 1975), the above estimate is increased to 54% of simuliid production. Fecal production by *L. quercina* is highest in December, according to the simulation model, and remains at a high level until pupation occurs in February. Therefore, maximum amounts of fecal particles have probably accumulated in the stream in February, corresponding to the time of peak simuliid production.

Conclusions

Lepidostoma quercina is a shredder adapted to West Coast conditions. Its distribution in Oregon, the Willamette Valley and Coast Range, corresponds to areas where red alder is an important riparian species and its life history and major growth period correspond to the time of maximum availability of deciduous leaves as a food source. Larvae show some ability to regulate respiration with respect to temperature. This ability is most pronounced in the early stages that occur in late summer and early fall (Q_{10} = 1.1) when water temperatures are variable. Larger individuals occur in December and January when water temperatures are more stable and cold (≈5°C) and exhibit much less respiratory regulation with respect to temperature (Q_{10} = 2.1). Laboratory growth rates and assimilation efficiencies for mid-final instar larvae were highest at the low temperatures (5–10°C) that this instar normally experiences. Larvae apparently spend little time searching among food items. This behavior might be expected for a species utilizing food that enters the system in a pulse of large particles and requires little microbial conditioning to become palatable and nutritious.

Larvae of *L. quercina* contribute to the decomposition of deciduous leaves in Berry Creek and produce significant amounts of fine particulate material. Quantities of fecal material egested were sufficient to comprise a major portion of the food of collector species. Time of peak production of simuliids (the major riffle species in Berry Creek) corresponds to the time of maximum fine particle accumulation from *L. quercina*. Although abundant food is always available, results of the simulation modeling suggest that growth and production of *L. quercina* may be limited by a lack of high quality food (i.e., alder leaves).

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