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1835

POPULATION DYNAMICS AND ROLE OF TWO SPECIES OF *LEPIDOSTOMA* (TRICHOPTERA: LEPIDOSTOMATIDAE) IN AN OREGON CONIFEROUS FOREST STREAM[1]

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Abstract. The aim of this study was to gather quantitative field and laboratory data on the role of *Lepidostoma cascadense* (Milne) and *Lepidostoma unicolor* (Banks) in the processing of conifer needles in a stream ecosystem.

Samples were collected monthly in a riffle-pool section of Mack Creek, Lane County, Oregon, USA. For *L. cascadense*, maximum larval density was 812/m² and instantaneous growth rate was 1.5%/d. The larvae grew slowly throughout the winter and pupation occurred in May and June. In contrast, *L. unicolor* increased very little in size during the winter and grew very rapidly during June and early July, reaching a maximum larval density of 320/m² and with an instantaneous growth rate (March through July) of 2.7%/d. Production of *L. cascadense* was estimated as 0.31 $g \cdot m^{-2} \cdot yr^{-1}$ and that of *L. unicolor* was 0.23 $g \cdot m^{-2} \cdot yr^{-1}$. In addition to temporal separation in periods of maximum growth, the two species occurred in different microhabitats. *L. cascadense* larvae were found within the sediments and debris while *L. unicolor* occurred on the surface of the debris.

Laboratory studies were conducted with *L. unicolor* larvae. Consumption and fecal production rates (measured gravimetrically) increased with higher temperature, greater food density, or longer conditioning time of the food, and decreased with increased size of the larvae.

Production and biomass of *L. cascadense* and *L. unicolor* in Mack Creek are minor in relation to other insects in the system. However, because of high consumption rates and low assimilation efficiency, the processing of large particulate organic matter by these two species contributed significantly to the food available to collectors in the study area.

Key words: aquatic; growth; Lepidostoma; *life histories; Oregon; population dynamics; respiration; shredders.*

INTRODUCTION

Small streams with riparian vegetation canopies tend to receive most of their energy in the form of terrestrial litter fall rather than as autochthonous primary production (Hynes 1963, Cummins 1973, Gosz et al. 1978). Litter fall may be dominated by deciduous leaves, as is common in Eastern U.S. streams, or by the more refractory conifer needles and wood, as is the case in many streams in the Cascade Range in Oregon.

The work reported here was part of our studies on the role of caddis larvae in the processing of allochthonous organic material (Anderson and Grafius 1975, Anderson 1976, Anderson et al. 1978). In a previous study (Grafius and Anderson 1979), *Lepidostoma quercina* Ross was examined as representative of species feeding on deciduous leaves. *L. quercina* is a fall-growing species, with its major growth period timed to allow maximum exploitation of deciduous leaf input to the stream. It occurs primarily in streams in the coastal range and Willamette Valley in Oregon (Anderson 1976). It was of considerable interest to find that members of the same genus are also instrumental in the processing of more refractory conifer needles (Sedell et al. 1975). Examination of larvae collected by Sedell et al. plus extensive emergence collections and larval rearing from Mack Creek revealed that the dominant species involved were *Lepidostoma cascadense* (Milne) and *Lepidostoma unicolor* (Banks).

Data were collected on population dynamics and life histories of these two species in Mack Creek. Laboratory studies of feeding and respiration were conducted with *L. unicolor*. Of particular interest were: (1) the impact of *L. cascadense* and *L. unicolor* on the stream ecosystem in terms of food consumption, fine particulate organic matter production, and production; (2) mechanisms reducing competition for food between the two species; and (3) possible adaptive significance of factors such as life history and bioenergetic responses to temperature, food quality, or food density.

METHODS AND MATERIALS

Field population studies

Mack Creek is a third-order stream, located in the H. J. Andrews Experimental Forest in the Cascade Range approximately 85 km east of Eugene, Oregon. The sampling site is at an elevation of 775 m, stream width is about 6 m, mean discharge 0.60 m³/s, and gradient 20%. Water temperatures range from 2° to 12°C but remain below 5° much of the year (November

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through May or June). The surrounding vegetation is old-growth Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and western red cedar (*Thuja plicata* D. Don.), with some vine maple (*Acer circinatum* Pursh.). Annual precipitation is generally 250–300 cm.

Mack Creek, typical of many small streams on the western slopes of the Cascade Range, experiences large fluctuations in stream flow due to the seasonal nature of the precipitation. Peak winter flows are 1000 to 2000 times summer flows and the stream varies widely in depth, width, and amount of debris present.

The site chosen for intensive study was a pool formed above a large natural log jam, and the riffle, above and to one side of the pool. 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 1–2 m wide and 10–12 m long.

Samples were collected monthly (19 October 1974 to 31 July 1975) with a 0.1-m^2 Surber sampler (mesh 250 μm). A stratified sampling scheme was used, with three or four samples each from riffle and pool strata. Because there was little current flow in the pool, the sampler was used to delineate the area to be sampled and the substrate and associated insects were scooped by hand into the collection net. Larvae were kept on ice and sorted under a binocular microscope while they were still alive. Sorting of fresh samples had two advantages over sorting preserved samples: (1) larvae were much easier to find among the debris when they were still alive and moving, and (2) dry masses could be determined from fresh rather than preserved specimens. Random samples of each available instar were oven-dried (60°), cooled in a desiccator, and weighed to the nearest 1 or 10 μg on a Cahn 4100 Electrobalance. Data were analyzed as stratified samples, grouped according to instar. Instantaneous growth rate was estimated as the slope of a regression of natural logarithm of mean mass vs. time. Instantaneous mortality rate was estimated as the slope of natural logarithm of mean number per square metre vs. time.

Laboratory studies of feeding and growth of L. unicolor

Food consumption and fecal production were measured gravimetrically. Douglas-fir needles were collected by shaking a tree to dislodge those that were near abscission. The needles were conditioned in aerated containers of dechlorinated tap water in the laboratory at 13°–15° for 4–5 mo. Pieces of wood or leaves from the field were added occasionally to aid in fungal colonization of the needles. Although the needles were not examined rigorously to determine taxa of fungi involved, general appearance of the needles at 50× magnification was very similar to field-collected needles. Fungi colonizing detritus in Oregon streams tend to be of terrestrial rather than aquatic (e.g., hyphomycete) origin (F. Triska, *personal communication*) and decomposition in the laboratory followed the pattern of color and gross structural changes described by Hayes (1965) for conifer needle decomposition on the forest floor. Well-decomposed needles collected from Mack Creek, chosen for their dark color, were used in some experiments. The latter were presumed to have been in the stream for at least 9 mo, from the previous autumn when most of the litter entered the stream.

Larvae were kept individually in 3 × 4 cm plastic ice cube compartments. Consumption was measured by initially determining the wet masses of small groups of needles (≈three times the expected consumption), feeding them to the larvae, and determining the dry mass of the remainder. A small number of uneaten fragments were sometimes produced and these were sorted by hand and included with the uneaten food. The wet masses of other groups of needles were determined at the same time, oven-dried and the dry masses determined to obtain conversion values from wet to dry mass. Using these conversion values, the initial wet masses of the "fed" needles could be compared with dry masses of the same needles after feeding. Wet masses were taken by blotting the needles on paper towel and allowing them to air dry for 1 min before weighing. Needles could not be dried prior to feeding since microbial components have been shown to be important stimuli to feeding (Kaushik and Hynes 1971, Kostalos 1972, Grafius 1974). Larvae were killed and the dry masses determined at the end of the respective experiments.

In the growth experiments, case measurements (length and width of the anterior opening) were used to estimate initial mass of individual larvae. Samples of larvae representing a range of case sizes were killed and the dry masses determined at the beginning of the experiment. Dry masses of these larvae were compared with an index of their respective case volumes (length × width^2). A regression equation computing dry mass from case volume was calculated. This equation was used to estimate initial masses for larvae used in the experiment.

Instantaneous growth rates were calculated as: (natural logarithm final mass − natural logarith initial mass) × time^{-1}.

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 four larvae per flask, depending on larval size. Pieces of conifer needles were included in the flasks to serve as food and substrate. Flasks were not shaken, in order to simulate more closely the pool habitat of *L. unicolor*. The long duration of the experiments (24–72 h) compensated for any loss in efficiency of gas ex-

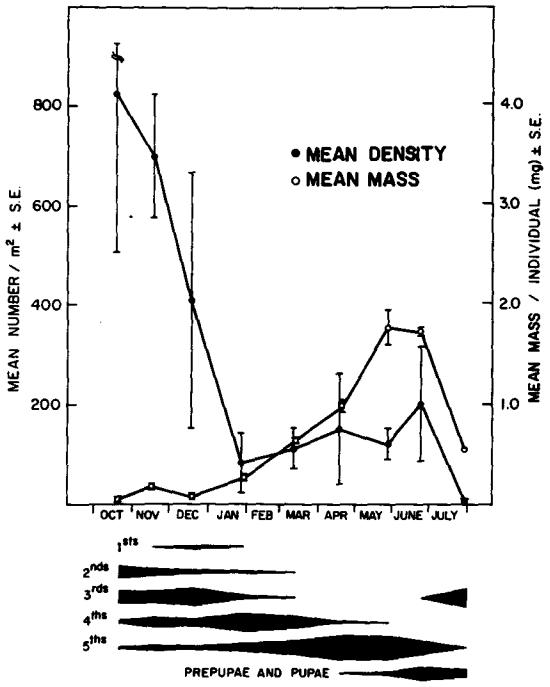

FIG. 1. Densities, mean masses, and instar distributions (relative proportion of individuals in each instar) for *Lepidostoma cascadense* larvae and pupae from Mack Creek, Lane County, Oregon.

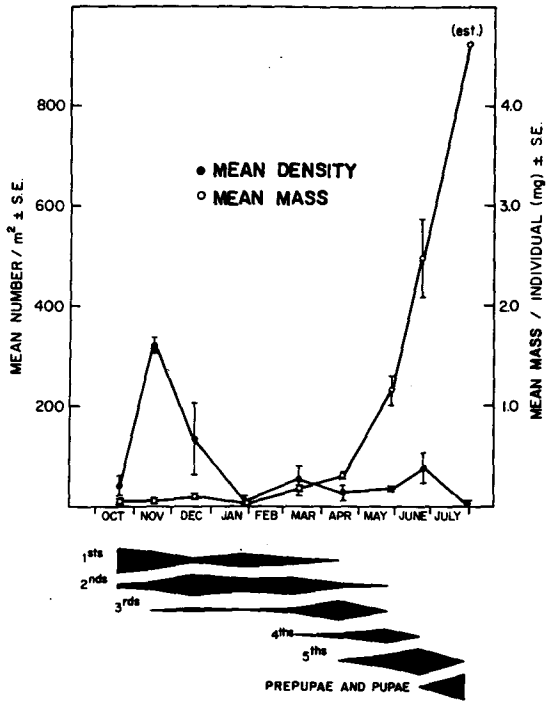

FIG. 2. Densities, mean masses, and instar distributions (relative proportion of individuals in each instar) for *Lepidostoma unicolor* larvae and pupae from Mack Creek, Lane County, Oregon.

change caused by the lack of agitation. There were no significant changes in respiration rate during the course of the experiments. At the end of each experiment, the larvae were removed to determine masses and the needles and insect cases were returned to the flask. Respiration was again measured and these values were subtracted from the respiration of insect + case + needles, to give an estimate of insect repiration.

Respiratory Q_{10} (the factor of increase over a 10° temperature change) was calculated from the slope of the natural logarithm of respiration rate vs. temperature. These values served as generalized indices of the effects of temperature. Q_{10}'s of 2.0–3.0 are considered normal for most poikilotherms (Warren 1971).

RESULTS AND DISCUSSION

Field population studies

Maximum density of *L. cascadense* was 812 larvae/m² in October. Density decreased during the autumn and early winter and then remained at about 100–200/m² during the late winter and early spring (Fig. 1). Larval densities were higher in the pool than in the riffle area (22:1). First or second instars made up a high proportion of the larvae collected in the riffle (44%), compared with 15% overall, suggesting that larvae hatch from eggs in the riffle regions and migrate to the pools.

Mean mass per individual increased from 0.06 mg in October to 1.77 mg in late May (Fig. 1). Although not dominant in any sample period, first instars had masses of approximately 5 μg per individual. Mean mass decreased slightly from November to December due to an influx of first instars. These newly hatched individuals may have come from egg masses wetted or re-wetted by changing water levels. As is characteristic of many species of caddis, the final (=fifth) instar was the longest larval stage, predominating from March through June, and accounting for most of the larval growth. Final instars increased in mean mass from 0.353 mg in December to 1.815 mg in June.

Mean biomass of *L. cascadense* showed an early peak (127 mg/m²) in November (before water levels began to rise), decreased slightly with higher water levels and correspondingly larger habitat area in December and January, and then increased gradually to a maximum of 348 mg/m² in June.

Larval densities of *L. unicolor* (Fig. 2) were much lower than those of *L. cascadense*. Densities of *L. unicolor* increased from October to November, due to the appearance of first instars, but then decreased in December, even though first instars were still appearing, since water levels were rising and therefore the area inhabited by larvae was increasing. Larval densities dropped to a low of 10/m² in January and fluctuated between 23 and 77/m² until July when emer-

TABLE 1. Instantaneous growth and mortality rates for field populations of *Lepidostoma cascadense* and *L. unicolor*.

	Interval	Growth rate* (%/day)	r^2	Mortality rate* (%/day)	r^2
L. cascadense	Oct–May	1.5	0.90	0.4	0.40
L. unicolor	Nov–July	1.9	0.85	1.0	0.42
	Mar–July†	2.7	0.99	1.7	0.50

* Estimated from regressions of ln mean mass or ln mean density vs. time.
† Period of active growth.

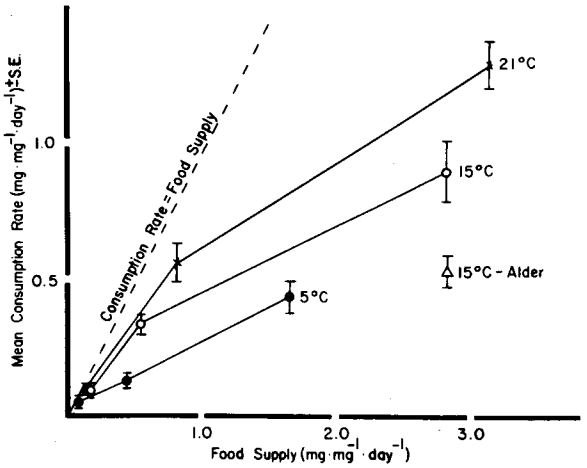

FIG. 3. Consumption rates for early- to mid-final instar *Lepidostoma unicolor* fed different densities of laboratory-conditioned Douglas-fir needles at three temperatures, or alder leaves at one density and temperature.

gence began. The June peak was partially due to the effects of dropping water levels concentrating larvae in a smaller area of stream. As was true for *L. cascadense*, *L. unicolor* larvae were more concentrated in the pool than in the riffle (25:1) and first and second instars made up a much greater proportion of the larvae collected in the riffle (100%) than the overall proportion (65%).

Mean mass per individual increased from 0.021 mg in October to 2.472 mg in June (Fig. 2). In contrast to *L. cascadense*, the duration of the final instar of *L. unicolor* was short, with final instars predominating only in the June samples. Larvae had completed their growth and pupation had occurred by the July sample date, so no masses were obtained for mature *L. unicolor* in 1975. Mean masses of mature larvae were 4.71 mg ($s_{\bar{x}}$ = 0.26) on 28 June 1974 and 4.56 mg ($s_{\bar{x}}$ = 0.34) on 10 July 1976. Maximum mean mass in 1975 was therefore estimated as 4.65 mg. In spite of the short duration of the final instar of *L. unicolor*, most of the larval growth occurred in this stage. Within 6 wk final-instar larvae increased in mean mass from 1.61 mg to about 4.65 mg, more than double the mature mass of *L. cascadense*.

Mean biomass of *L. unicolor* showed a slight peak in November, when water levels were still low (15 mg/m²), and reached a maximum of 190 mg/m² in June. Further increase in biomass probably occurred with growth of the final instars in early July.

Instantaneous growth rates for *L. cascadense* and *L. unicolor* reflect the slow growth of *L. cascadense* in contrast to the rapid growth of *L. unicolor* during the spring and early summer (Table 1). Mortality rates for the two species were not significantly different ($P > .05$).

Numbers of both *L. unicolor* and *L. cascadense* in the samples were observed to correspond closely to the amount of conifer needles present in the study section from month to month. *L. unicolor* is particularly vulnerable to displacement by freshets, as the larvae occur almost exclusively on the surface of the deposited conifer needles. This displacement is not necessarily disadvantageous, as the larvae will settle out further downstream along with their detrital food supply.

Production, estimated following Ricker's (1946) method, was 0.31 $g \cdot m^{-2} \cdot yr^{-1}$ for *L. cascadense* and 0.23 $g \cdot m^{-2} \cdot yr^{-1}$ for *L. unicolor* (assuming 4.65 mg/individual, 30/m² on 15 July). Annual turnover ratios (*P/B*) were estimated as 9.6 for *L. unicolor* (0.23 g/m² production: 0.024 g/m² mean annual biomass) and 3.7 for *L. cascadense* (0.31 g/m² production: 0.084 g/m² mean annual biomass). The latter value is low in comparison with other univoltine species (Waters 1966). The low turnover ratio for *L. cascadense* may be due to the lower food quality of the less completely conditioned conifer needles available in the winter and early spring as compared to those utilized by *L. unicolor* in May and June. The low turnover ratio may also reflect the effects of low temperature during *L. cascadense*'s major growth period.

Laboratory studies of feeding and growth of L. unicolor

In previous work (Anderson and Grafius 1975, Sedell et al. 1975) it was shown that conifer needles were consumed by *L. unicolor* only after several months of conditioning and, even then, growth rates were very low. Gravimetric methods of comparing ingestion and egestion to measure assimilation efficiency were unsuitable for this species because case-pillaging frequently resulted in fecal production that was higher than the measured losses of the proffered food.

The objective of the present experiments was to measure consumption and growth of *L. unicolor* larvae as affected by food density of conifer needles and temperature for comparison with similar studies of *L. quercina* fed alder leaves (Grafius and Anderson 1979). Early to mid-final instars of *L. unicolor* were fed

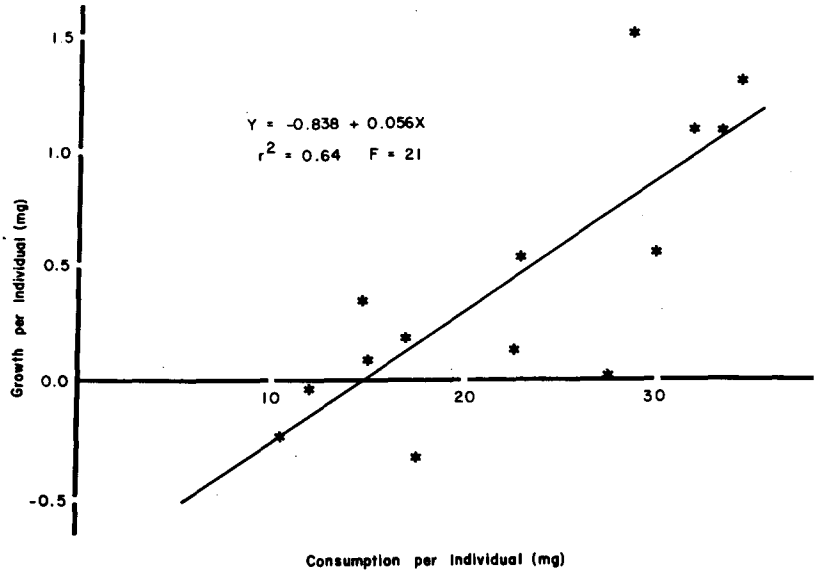

FIG. 4. Growth of mid-final instar *Lepidostoma unicolor* fed field-collected conifer needles for 13 d at 15°C compared with total food consumption. The F value is significant ($P < .01$).

Douglas-fir needles that had been conditioned in the laboratory for 5 mo. Larvae were acclimated at the experimental temperature for 3 d. There were nine temperature/food density treatments with Douglas-fir needles, plus one treatment with alder leaves at 15°C as a high-quality food source. There were 15 to 20 larvae (=replications) in each treatment. Food was changed and consumption measured every 4 d during the 12-d experiment. An initial sample of 24 larvae was measured for case size and the dry mass determined to obtain a predictive equation for mass based on size.

Consumption rates increased with temperature and food density far beyond the level where food supply exceeds consumption ($P < .01$) (Fig. 3) and decreased with increasing size of the larvae ($P < .01$). At 15° and high food density, the consumption of Douglas-fir needles was significantly higher than that of alder leaves ($P < .05$). Alder contains about 4% nitrogen, compared with 1.4% in conifer needles (Iversen 1974) and *L. unicolor* was apparently responding to the lower food quality of conifer needles by increasing consumption, a strategy shown for other shredders (Anderson and Cummins 1979). Slansky and Feeny (1977) and Iversen (1974) have reported increased consumption in response to low nitrogen content in the food.

Consumption rate continued to increase with increased food supply at least up to the point where the latter was more than three or four times the amount consumed (Fig. 3). Also, larvae tended to feed primarily on one or two needles, even though five to ten or more were available. This contrasts with the behavior of *L. quercina* which reached maximum consumption when the supply of alder leaves only slightly exceeded the amount consumed (Grafius and Anderson 1979). The response of *L. unicolor* to increased food supply indicates that larvae discriminate among food items and that needles probably differ in quality even among laboratory-conditioned needles of the same "age." This behavior may particularly benefit conifer-feeding larvae because the needles require long periods of microbial conditioning and those available in the field may have had weeks to months, or even years, of conditioning. At the other extreme, *L. quercina* discriminates little among food items, probably because alder leaves are palatable and nutritious shortly after they enter the stream (Grafius and Anderson 1979).

No significant growth occurred in any of the above temperature/food density treatments, except with alder leaves as food (4.6% per day, $s_{\bar{x}} = 0.8$). The greatest loss of mass (4.5% per day, $s_{\bar{x}} = 1.18$) was at 21° with high food density (where the highest feeding rate also occurred). Mortality was 15% or less in all treatments, except at 21° with medium food density (35%) and 21° with low food density (47%). Thus the 5 mo of laboratory conditioning was inadequate for conifer needles to become suitable food for *L. unicolor*. Significant growth rates of 1.0%/d ($s_{\bar{x}} = 0.4$, $n = 14$) were obtained for final instars fed well-conditioned, field-collected conifer needles for 13 d at 13°. The consumption rates were similar to estimates with the laboratory-conditioned needles (1.12 $mg \cdot mg^{-1} \cdot d^{-1}$, $s_{\bar{x}} = 0.10$). Therefore growth of *L. unicolor* is dependent on the availability of a well-conditioned food source. The growth rates were much lower than for larvae fed alder leaves in the previous experiment. The differences in quality of laboratory- and field-conditioned needles are probably related to conditioning time or differences in temperature or microbial inocula.

Comparing growth on field-collected needles and to-

TABLE 2. Mean respiration rate of *Lepidostoma unicolor* larvae at three different temperatures.

Temperature	*n*	Mean mass ± SE (mg)	Mean respiration rate ± SE (μL $O_2 \cdot mg^{-1} \cdot h^{-1}$)
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

TABLE 3. Regression analyses of natural logarithm of respiration rate vs. temperature (5°, 10°, or 15°C) for selected size classes of *Lepidostoma unicolor* larvae.

Instar	Weight range (mg)	*n*	r^2	Slope ± SE	Q_{10}
4th–early 5th	0.8–2.5	13	0.45	0.057 ± 0.019	1.8
mid 5th	2.6–4.0	21	0.50	0.078 ± 0.018	2.2
late 5th	4.1–7.2	15	0.49	0.087 ± 0.025	2.4

tal consumption per individual gives an estimate for growth efficiency of 5.6% (Fig. 4). Assuming an assimilation efficiency of 10% on Douglas-fir needles (probably an overestimate), net growth efficiency for *L. unicolor* would be approximately 56%, compared with 27.1% for *L. quercina* (Grafius and Anderson 1979). This may explain the rapid growth of *L. unicolor* on alder leaves (4.6% per day). *L. unicolor* is apparently much more efficient in utilizing assimilated food than is *L. quercina*, perhaps an adaptation allowing exploitation of poorly assimilable food resources such as conifer needles.

Respiration measurements

Mean respiration rate for *L. unicolor* larvae increased significantly with increased temperature (Table 2). Respiratory Q_{10} was estimated at 1.99 over the range of 5–15°, indicating little or no ability to regulate respiration in response to changes in temperature. Larval masses ranged from 0.78 to 7.21 mg and respiration decreased significantly with increased size of the larvae ($P < .01$). At a given temperature, the relationship between respiration rate and larval mass was almost linear. Size-specific respiration rates were calculated (from regressions of respiration rate vs. larval mass at each temperature) in order to examine the interactions between temperature and larval size more closely. Although the results were variable, there was little indication that any particular size class exhibited an ability to regulate respiration with respect to temperature (Fig. 5), in contrast to the results for *L. quercina* (Grafius and Anderson 1979) or *Clistoronia magnifica* Banks (Limnephilidae) (Grafius 1977). A grouping of respiration rates according to size also showed no significant respiratory regulation with respect to temperature (Table 3). These results are not surprising, since *L. unicolor* from Mack Creek rarely experience temperatures greater than 10°.

Timing of *L. unicolor*'s life cycle may be particularly critical for maintaining respiratory homeostasis. Respiration rates estimated for larvae in Mack Creek at ambient field temperatures during the period of active growth were nearly constant (Fig. 6). This is the result of offsetting effects of increasing temperature (and therefore increased respiration rate) at the same time that larval mass is increasing (and respiration rate is therefore decreasing). This passive mechanism for maintaining respiratory homeostasis, proposed by

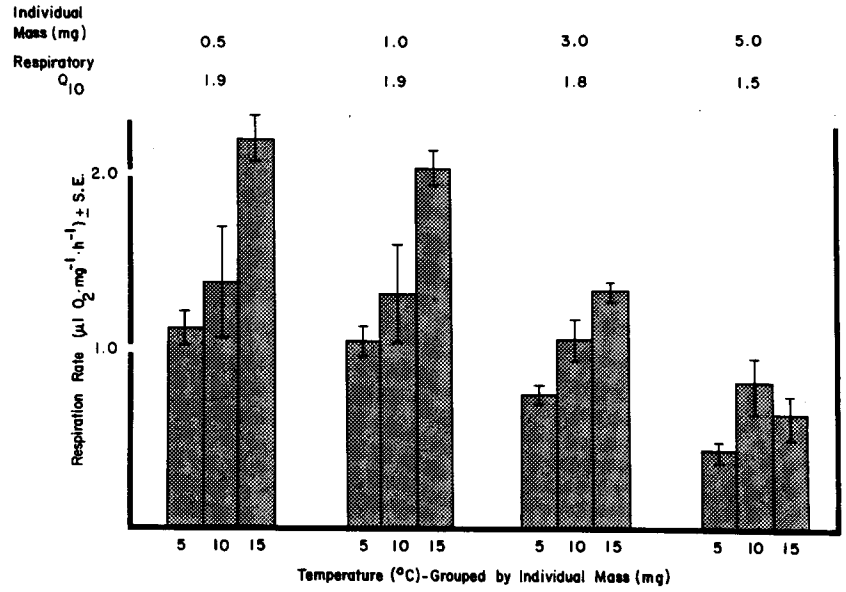

FIG. 5. Respiration rates estimated for specific sizes of *Lepidostoma unicolor* larvae at three temperatures.

Vannote (1978), probably occurs in a variety of spring-growing species. In warmer streams such as in southern California or in the Coast Range of Oregon, *L. unicolor* larvae might be expected to grow most rapidly earlier in the season, or to have a warmer temperature range for optimal growth. In contrast, in the Metolius River (Jefferson County, Oregon), a constant-temperature spring-fed stream, *L. unicolor* apparently lacks a stimulus for synchronization of its life cycle. There, mature larvae are found during most of the year and adult emergence occurs from April through October (Anderson 1976), whereas emergence from Mack Creek occurs primarily in late July and August.

Species differences

Temporal segregation between *L. cascadense* and *L. unicolor* is shown in the periods of active growth exhibited by larvae of the two species (Figs. 1 and 2). *L. cascadense* larvae grow steadily and slowly from November through April or May while larvae of *L. unicolor* grow very little until water begins to warm in late May and grow most rapidly in June and July. Instantaneous growth rates for *L. cascadense* and *L. unicolor* are similar (1.5%/d vs. 1.9%/d, respectively). However, when the instantaneous growth rate for *L. unicolor* is calculated over its period of active growth (March through July), its growth rate in the field (2.7%/d) is similar to that reported for *L. quercina* which feeds on alder leaves, a much more nutritious food source (Grafius and Anderson 1979).

The differences in major growth period and mature larval masses between *L. cascadense* and *L. unicolor* larvae may reflect trade-offs between combinations of temperature and food conditioning (Table 4). Food quality of conifer needles is low and the interactions between temperature, food conditioning, and availability may be crucial to larval growth and survival. It is suggested on the basis of the species' distribution (cold rapid streams in the Rockies and Cascades; Ross 1946, Anderson 1976), that *L. cascadense* is adapted to cold temperatures. Adapted to function and grow at cold temperatures, *L. cascadense* may be better able to utilize poor quality food. At warmer temperatures, where maintenance costs are higher, higher quality food (=better conditioned) may be required. Mature size of *L. cascadense* may be limited by the increased maintenance costs associated with larger size or by the time available for growth at cold temperatures. In the latter case, mature larvae should be larger in years when water temperatures warm up more slowly. In contrast to *L. cascadense*, *L. unicolor* feeds and grows most rapidly when food is more completely conditioned but water temperatures (and therefore maintenance costs) are higher.

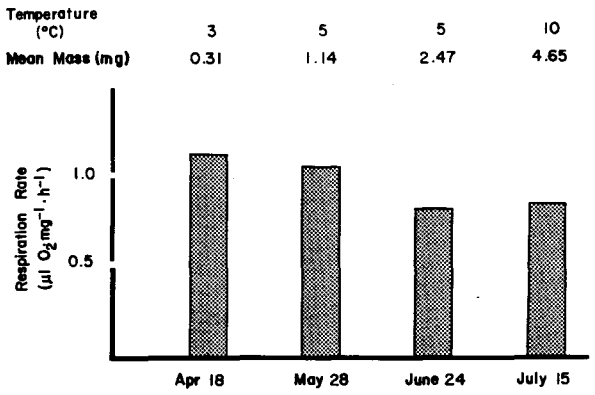

FIG. 6. Estimated respiration rates for *Lepidostoma unicolor* larvae in Mack Creek. Water temperatures and mean larval masses are also indicated.

Unlike the two Mack Creek species, *L. quercina* utilizes alder leaves that enter the system primarily in late summer and fall and are rapidly processed by microbial and invertebrate activity, allowing little flexibility in the time of utilization (Grafius and Anderson 1979).

Spatial segregation between *L. cascadense* and *L. unicolor* populations is maintained on a microhabitat level. Larvae of *L. unicolor* are rarely found beneath the surface of the debris (except just prior to pupation), while larvae of *L. cascadense* are often found at depths of 10–20 cm or more in the substrate. This difference in behavior is reflected by the case types and mature larval sizes of the two species. *L. unicolor*'s case is a log-cabin type composed of irregularly placed bits of twig and needles, providing camouflage on the surface of the debris but perhaps hindering movement within the substrate. *L. cascadense*, in contrast, has a smooth, tapered case of sand grains, and mature larval size is much smaller than *L. unicolor*, facilitating its burrowing into the debris.

TABLE 4. A comparison of environmental variables with growth rate and mature larval mass for two species of *Lepidostoma*.

Species	Growth period	Water temperature (°C)	Conditioning time of food* (mo)	Instantaneous growth rate (%/day)	Mean mature larval mass (mg)
L. cascadense	Nov–May	3°–5°	1–7	1.5	1.9
L. unicolor	Mar–July	3°–10°	5–9	2.7	4.6

* Assuming most conifer needles enter the stream in the fall when water levels rise and lateral movement of debris into the stream occurs.

Conclusions

Larval populations of *L. cascadense* and *L. unicolor* exhibit both spatial and temporal separation, even though adults, eggs, and larvae of both are found at approximately the same time and larvae of both species occur in the same regions of the stream.

L. unicolor larvae in the laboratory showed no ability to maintain constant respiration rates in response to changes in temperature. However, respiration rates estimated for larvae in the field were nearly constant, supporting Vannote's (1978) model for spring-growing species. This passive mechanism is in contrast to the apparent direct control of respiration exhibited by the fall-growing caddises, *L. quercina* and *C. magnifica*.

In terms of biomass, the significance of *L. cascadense* and *L. unicolor* in Mack Creek is small. Mean annual standing crop of both species together was 0.11 g/m^2, less than 2% of the total mean insect biomass estimated for Mack Creek (6.3 g/m^2, Grafius 1974).

Production of *L. cascadense* and *L. unicolor* is also probably of minor importance in comparison with other species in Mack Creek. Assuming a turnover ratio (production: mean biomass) of ten (Waters 1969), total insect production in Mack Creek might be as high as 63 $g \cdot m^{-2} \cdot yr^{-1}$. Since nearly half of the biomass in Mack Creek comprises species requiring 2 yr or more to complete a life cycle (Pteronarcidae, Perlidae, Elmidae, and Megaloptera), the actual turnover ratio would be lower and annual production is probably 10–20 $g \cdot m^{-2} \cdot yr^{-1}$. Even on this basis, *L. cascadense* and *L. unicolor* would comprise less than 5% of the insect production.

The processing of large particulate organic materials and the production of fine particles are probably the most significant impacts on Mack Creek by the two lepidostomatids. Mean consumption rate of *L. unicolor* on field-collected conifer needles at 15°C was 1.44 $mg \cdot mg^{-1} \cdot d^{-1}$ (Fig. 3). Assuming that consumption rates at 5° are approximately half of comparable rates at 15° (see Fig. 3), consumption of well-conditioned needles by the two populations of lepidostomatids would be 0.08 $g \cdot m^{-2} \cdot d^{-1}$ or about 29 $g \cdot m^{-2} \cdot yr^{-1}$. Fecal production (≈90% of consumption) would be nearly 50× the production of the two species and would probably support collector production equal to 5× the *Lepidostoma* production (assuming 10% efficiency of conversion).

Although only rough approximations, these values indicate the importance of *L. unicolor* and *L. cascadense* in the processing of large particulate organic materials in Mack Creek. The above comparison also emphasizes the importance of using rates (i.e., processing or production) rather than measurements of standing crop, for comparisons of the relative importance of species or populations in a given system.

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Literature Cited

Anderson, N. H. 1976. The distribution and biology of Oregon Trichoptera. Technical Bulletin 134, Oregon Agricultural Experiment Station, Corvallis, Oregon, USA.

Anderson, N. H., and K. W. Cummins. 1979. The influences of diet on the life histories of aquatic insects. Journal of the Fisheries Research Board of Canada **36**:335–342.

Anderson, N. H., and E. Grafius. 1975. Utilization and processing of allochthonous material by stream Trichoptera. Internationale Vereinigung für Theroetische und Angewandte Limnologie, Verhandlungen **19**:3038–3088.

Anderson, N. H., J. R. Sedell, L. M. Roberts, and F. J. Triska. 1979. The role of aquatic invertebrates in processing wood debris in coniferous forest streams. American Midland Naturalist **100**:64–82.

Cummins, K. W. 1973. Trophic relations of aquatic insects. Annual Review of Entomology **18**:183–206.

Gosz, J. R., R. T. Holmes, G. E. Likens, and F. H. Bormann. 1978. The flow of energy in a forest ecosystem. Scientific American **238**:93–102.

Grafius, E. 1974. The conversion of allochthonous material by stream detritivores. Thesis. Oregon State University, Corvallis, Oregon, USA.

———. 1977. Bioenergetics and strategies of some Trichoptera in processing and utilizing allochthonous materials. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Grafius, E., and N. H. Anderson. 1979. Population dynamics, bioenergetics, and role of *Lepidostoma quercina* Ross (Trichoptera: Lepidostomatidae) in an Oregon woodland stream. Ecology **60**:433–441.

Hayes, A. J. 1965. Studies on the decomposition of coniferous leaf litter. II. Changes in external features and succession of microfungi. Journal of Soil Science **16**:243–257.

Hynes, H. B. N. 1963. Imported organic matter and secondary productivity in streams. Proceedings of the XVI International Congress of Zoology **3**:324–329.

Iversen, T. M. 1974. Ingestion and growth in *Sericostoma personatum* in relation to the nitrogen content of ingested leaves. Oikos **25**:278–282.

Kaushik, N. K., and H. B. N. Hynes. 1971. The fate of dead leaves that fall into streams. Archiv für Hydrobiologie **68**:466–515.

Kostalos, M. S. 1972. A study of the detritus pathway: the role of detritus and the associated microflora in the nutrition of *Gammarus minus* Say (Amphipoda: Gammaridae). Dissertation. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

Ricker, W. E. 1946. Production and utilization of fish populations. Ecological Monographs **16**:373–391.

Ross, H. H. 1946. A review of the nearctic Lepidostoma-

tidae. Annals of the Entomological Society of America 39:265–291.
Sedell, J. R., F. J. Triska, and N. M. Triska. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: I. Weight loss and associated invertebrates. International Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 19:1617–1627.
Slansky, F., Jr., and P. Feeny. 1977. Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. Ecological Monographs 47:209–228.
Vannote, R. L. 1978. A geometric model describing a quasi-equilibrium of energy flow in populations of stream insects. Proceedings of the National Academy of Science of the USA 75:381–384.
Warren, C. E. 1971. Biology and water pollution control. W. B. Saunders, Philadelphia, Pennsylvania, USA.
Waters, T. F. 1966. Production rate, population density, and drift of a stream invertebrate. Ecology 47:595–604.