Verh. Internat. Verein. Limnol.	19	3083–3088	Stuttgart, Dezember 1975

Utilization and processing of allochthonous material by stream Trichoptera

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With 4 figures in the text

The dependence of benthic fauna in small streams on the import of organic material from the surrounding watersheds has been clearly recognized (e.g. Hynes 1963; Egglishaw 1964). The rate of disappearance of leaf packs in streams has been correlated with the abundance of invertebrate shredders (Petersen & Cummins 1974; Sedell et al. 1975). To study the role of aquatic insects in this processing of organic materials, we are using caddisfly larvae as experimental animals. These larvae are a conspicuous element of the fauna of lotic systems and several studies have demonstrated the diversity of feeding behavior within the order. Caddis larvae occupy all of the functional feeding groups (grazers, shredders, collectors, predators) and have even been shown to consume fish carcasses (Brusven & Scoggan 1969). Though most taxa are generally assigned to only one of the above functional groups, most species are, at least in part, omnivorous.

Quantification of the impact of invertebrates on their food resources requires detailed data on both field population dynamics and on their feeding behavior. In this paper we deal only with the latter — qualitative and quantitative studies of feeding, growth and egestion. Instead of a large-scale program of gut-content analysis, we are screening for species that occupy different feeding niches and that can then be used for laboratory studies.

Feeding trials were conducted in small dishes of aerated water, or in a drippery system of pans with a slow rate of water exchange (Anderson 1973). Some species were reared from egg masses, while others were collected as larvae in the field. Gravimetric methods were used for determining ingestion and egestion. Materials were oven-dried at 60 °C for 24—48 hrs.

The variables that we have identified as important factors affecting processing rates by caddis larvae are: temperature; food density and availability; food preference and quality; and weight and within-instar age of the larvae.

Food consumption as influenced by food density and temperature

Larvae of *Lepidostoma quercina* Ross (Lepidostomatidae) were fed on conditioned *Alnus* leaf discs at 3 temperatures and 3 food densities for 12 days (Fig. 1). The larvae were final instars (mean wt. 2 mg), collected in the field in November when water temperatures ranged from 5—10 °C. As was expected, consumption rate increased with both temperature and food density. Between the low and high food densities, mean consumption increased from 19 to 33 % body weight/day at 5 °C, compared with 29 to 44 % at 13 °C, and from 32 to 69 % at 20 °C. As there was no change in consumption rate between the medium and high food densities, it is suggested that, where searching time is minimal, maximum consumption of a highly preferred food can occur at a food concentration of about 75 % of the body weight of the larvae.

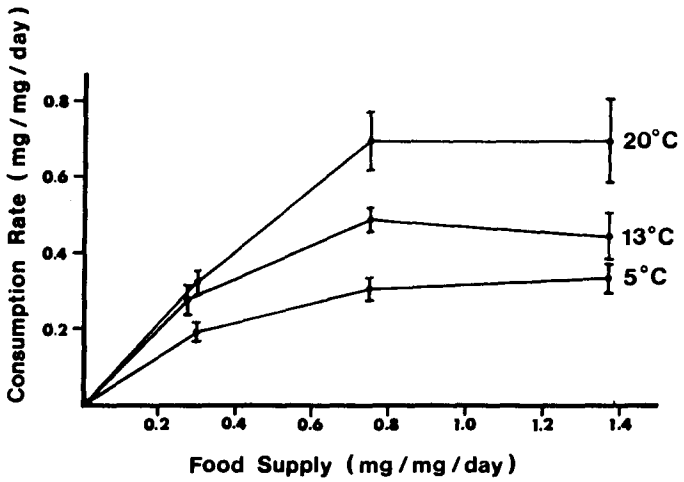

Fig. 1. Consumption rate of final-instar *Lepidostoma quercina* larvae at 3 temperatures and 3 food densities. Vertical lines = 90 % confidence intervals.

Food consumption as a function of conditioning time

L. quercina larvae were fed on *Alnus* leaves that had been incubated in a stream for up to 46 days. Consumption was measured, using a paired leaf-disc technique, at 3-day intervals. As the experiment was conducted over a 2-month interval, larval weights ranged considerably (means of 0.61 to 4.54 mg/indiv.), so consumption rate was standardized for body size to that of an individual at the time of leaf-fall (1.0 mg).

Consumption rates were constant for conditioning times up to 3 weeks (Fig. 2 a); after that time, the regression line indicates an increase of 0.054 mg/mg/day for each day of incubation. The relatively high consumption rate of the unconditioned leaves demonstrates the exceptional palatability or preference for *Alnus*. Newly-fallen *Alnus* leaves are quickly colonized by *L. quercina*, other caddis larvae, and snails *(Oxytrema)* in western Oregon streams. The significant increase in consumption rates after 3 weeks of incubation is correlated with conditioning by microbial flora, as was demonstrated by leaf-pack experiments (SEDELL et al. 1975). The fact that all consumption rates are higher than those in Fig. 1 is due to the inverse relationship between body weight and relative consumption rate (see Fig. 4).

In the leaf-pack experiments, the *Alnus* leaves were skeletonized in 1 to 2 months in the autumn, whereas conifer needle packs *(Pseudotsuga,* Douglas-fir) were largely untouched by invertebrates between October and April. During late spring, these conifer packs were stripped by the feeding and case-building of *Lepidostoma unicolor* (BANKS), so feeding studies of this species were initiated. Preliminary trials indicated maximum consumption rates of over 3 times body weight/day on old, darkened needles collected in the stream.

The effect of conditioning time on consumption of *Pseudotsuga* needles was examined using needles incubated in the laboratory at 13 °C for 12 to 142 days (Fig. 2 b). Feeding rates ranged from 0.20 mg/mg/day for 12-day needles to 0.66 mg/mg/day for 142-day needles, compared with 1.53 mg/mg/day for field-collected needles (estimated to be conditioned for 9 months). The regression of laboratory conditioning time vs. consumption rate gives an increase in consumption rate of 0.0033 mg/mg/day for each day of conditioning. Each point in Fig. 2 b represents a mean of 35 to 40 measurements. The low correlation coefficient is partially due to variation in body weight of the larvae (addition of body weight to the regression model increases the R^2 to

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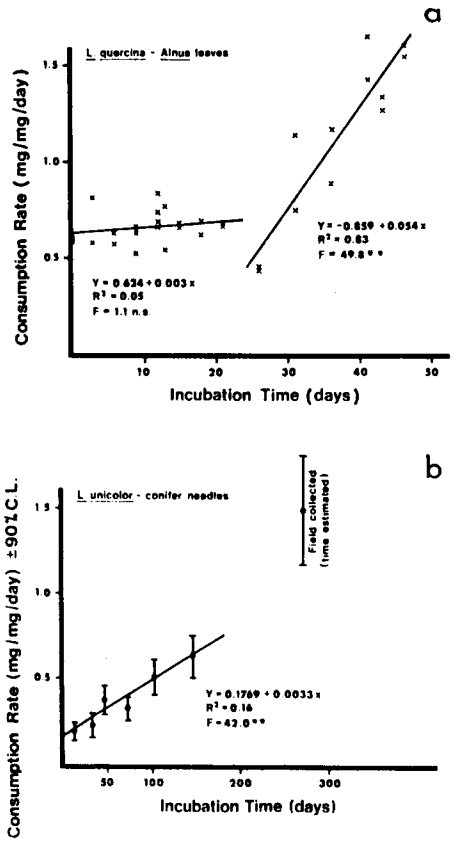

Fig. 2. Consumption rate of final-instar *Lepidostoma* spp. larvae as a function of food conditioning time. (a) *L. quercina* fed *Alnus* leaves at 11 °C. (b) *L. unicolor* fed *Pseudotsuga* needles at 13 °C.

0.39). Conversion of wet weight of needles to estimates of dry weight consumption also increased the variability.

The 3-fold difference in feeding on field-collected material compared with needles conditioned in the laboratory could result from differences in conditioning time. However, it is also possible that inadequate inoculation, or some aspect of the laboratory conditions, delayed the rate of microbial colonization in laboratory cultures.

Growth rate comparisons of *Lepidostoma quercina* and *L. unicolor*

Growth rates were measured over 11 to 12 days in conjunction with the conditioning experiments and by feeding both species on *Alnus* leaves and *Pseudotsuga* needles at 13 °C. These trials were conductet at different times because the 2 species have distinctive seasonal cycles. *L. quercina* makes most of its growth in autumn and winter and emerges in March and April. *L. unicolor* larvae are in the final instar during the spring and summer, and emergence peaks in July and August.

Both species lost weight when fed on laboratory-conditioned needles, and grew rapidly with conditioned *Alnus* leaves as food (Fig. 3). Growth of *L. unicolor* on field-collected needles was 2.6 %/day, which is comparable with *L.*

quercina on *Alnus* (1.9 %/day). The exceptionally high relative growth rate of *L. unicolor* on *Alnus* is interesting. WINTERBOURN (1971) stated that at Marion Lake, B. C., the gut contents of this species were almost exclusively deciduous leaves. However, in our study stream in the Cascade Range, the life cycle of *L. unicolor* largely precludes the use of deciduous leaves during the late instars when most of the growth occurs. From April to June, when mean larval weight increases from 1.0 to 4.8 mg, there are practically no deciduous leaves available in the stream.

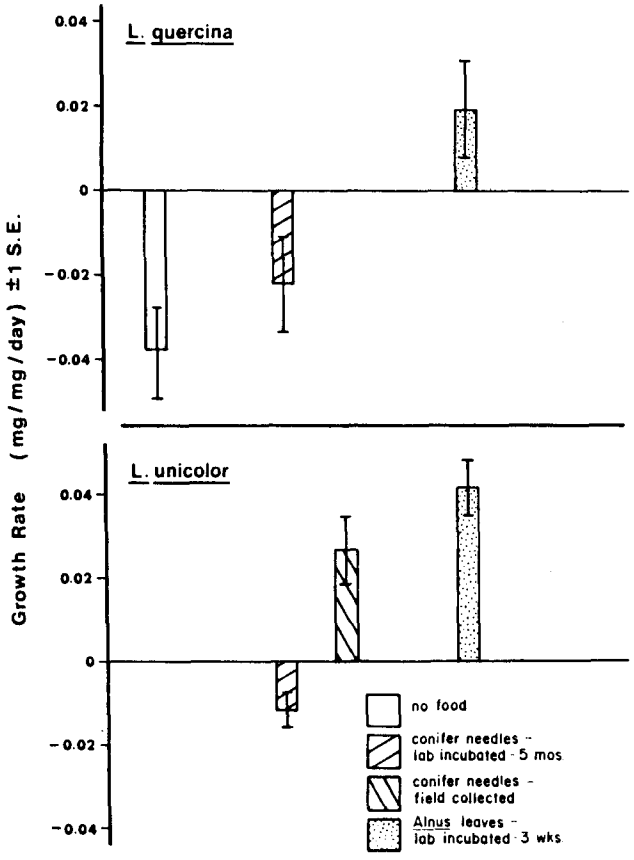

Fig. 3. Growth rates of final-instar *Lepidostoma* spp. larvae with various foods at 13 °C.

Feeding studies of laboratory-reared *Pseudostenophylax edwardsi* larvae

The limnephilid, *P. edwardsi* (BANKS) is being used for long-term feeding and egestion studies because it is amenable to laboratory rearing (ANDERSON 1974). Variability of the data using laboratory-reared material is reduced as the larvae can be of a known feeding history and known within-instar age.

The growth of laboratory-reared *P. edwardsi* larvae fed on conditioned *Alnus* leaves is comparable to that in the field at least up to the early part of the final instar, but reared adults are undersized. This may be due to inadequate nutrition; a higher-energy food may be required for laying down fat reserves in the final instar. However, effects of temperature and photoperiod on final-instar development need to be further investigated before the effects of food quality can be fully assessed.

Dry weights of feces provide a rapid and simple method of measuring the processing of allochthonous material by caddis larvae. As only 10—25 % of leaf material is assimilated, the major portion of the ingested material is passed through the gut as feces.

Relative rates of fecal production for the 5 instars of *P. edwardsi* are compared in Fig. 4. There is a significant decrease in fecal production (expressed as mg/mg/day) with increase in body weight and with the instar. Within an instar, the same decreasing trend is apparent (except for the anomalous point for the third instar). Field-collected larvae acclimated in the laboratory for a few days before testing, show the same trend as do the reared larvae.

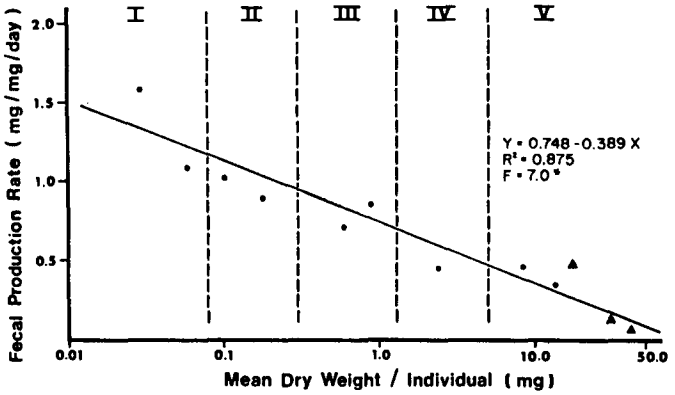

Fig. 4. Relative fecal production rate of *Pseudostenophylax edwardsi* larvae, fed conditioned *Alnus* leaves at 13 °C as a function of age and weight ($\log_{10}$ scale). Circles = laboratory-reared larvae; Triangles = field-collected larvae.

Using the egestion data as an index of consumption, it is apparent that in the early part of each instar there is a period of intensive feeding and growth and then decreased consumption rates in the latter part of the instar. Though relative consumption rates decrease with successive instars it should be noted that the consumption and egestion rates per individual are much greater for final instar larvae than for the earlier instars. Also, because of the much longer duration of the final instar, the impact of this stage on the food supply may be much greater than that of the other instars.

In comparison with the conditioned *Alnus* leaves, the feces are higher in lignin (+ 9 %) and cellulose (+ 5 %). This indicates that the larvae utilize the microbial flora and possibly some of the more readily digestible leaf components while the more refractory portion is egested as finely-ground feces.

Discussion

In adopting a holistic approach in stream ecology it is necessary to classify invertebrates into functional groups, but fine resolution studies of individual species are also desirable to obtain insights into the mechanisms or processes that influence the rates of energy flow or nutrient cycling. For modelling purposes it is difficult to arrive at realistic average values of rates, such as food consumption or growth, until more data are available for several species in each of the functional feeding groups.

Shredding insects, such as caddis larvae, occupy a key role in the energy and nutrient transfer from terrestrial to stream systems. In addition to converting primary production to animal tissue that is consumed by aquatic and terrestrial predators, they increase the rate of degredation of allochthonous material. The copious amounts of feces have a large surface area which increases the rate of microbial decomposition. This fine particulate material is then available for filter- and sediment-feeders leading to another series of energy and nutrient transfers.

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