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## CARNIVORY BY AN AQUATIC DETRITIVORE, *CLISTORONIA MAGNIFICA* (TRICHOPTERA: LIMNEPHILIDAE)<sup>1,2</sup>

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**Abstract.** The limnephilid caddisfly, *Clistoronia magnifica*, was reared through three generations on a detritus-based diet enriched with wheat grains and green grass. Developmental time was reduced and weight of mature larvae and pupae was increased by addition of enchytraeid worms to the above diet. Supplemental feeding on animals is also likely in the field but its importance would be underestimated because, in comparison with detritus, animal tissue would be a small component of the gut contents.

**Key words:** Caddisfly; carnivore; detritivore; feeding habits; growth rate; Oregon; rearing.

### INTRODUCTION

Cummins' (1973) review of trophic relations of aquatic insects indicates that a significant portion of the material cycling and energy flow in freshwater systems involves the processing of organic matter by insects. Studies of ingestion, using visual analysis of gut contents, (e.g., Brown 1961, Thorup and Iversen 1974, Hall and Pritchard 1975) have demonstrated that plant detritus forms the base of most food webs in these systems. Gut analysis is useful in demonstrating the processing accomplished by aquatic insects. However, as Cummins (1973) suggests, nutritional interpretation of the data is difficult because items digested rapidly, and therefore least likely to be observed, may be the most nutritious. Worms and other soft-bodied invertebrates are digested rapidly and their retention time in the gut will be short. Similarly, the microbial flora associated with detritus is difficult to census but it is more nutritious than the more obvious, but highly refractory, lignin and cellulose components.

This study is part of a project on developing methods for continuous culture of aquatic insects. Studies of growth and trophic relations could then be based on the entire larval interval instead of restricted to short-term feeding trials or to gut analysis. In my laboratory I have reared several limnephilid caddisflies, including species of *Hesperophylax*, *Hydropsyche*, *Limnephilus* and *Pseudostenophylax*, through a complete generation on a detritus diet. However, compared with field material the resulting adults were frequently undersized. Also, some had malformed wings and others failed to emerge from the pupal exuviae. It seemed probable that these results were due to the nutritional inadequacy of the food, though rearing conditions, especially temperature

and photoperiod, could also be contributing factors. The experiments reported herein were designed to determine whether the quality or vigor of laboratory cultures of the caddisfly *Clistoronia magnifica* (Banks) could be improved by augmenting a plant-based diet with some animal food.

The only field data for *C. magnifica* are from Winterbourn's (1971a) study from Marion Lake, B.C. He described it as an early-season univoltine species inhabiting submerged marginal vegetation and open sediments throughout the lake. Based on gut content analysis of 35 specimens, he classified *C. magnifica* as a sediment feeder. The gut contained a mixture of plant fragments, algal cells, amorphous detritus and a very few arthropod remains. He could not determine whether the animals were 'actively selected' or ingested along with the sediment. However, he implied that the prey ingestion was of minor importance in *C. magnifica* and in the other detritivores studied because there was rarely more than one to three animal fragments present in guts dominated by detritus.

### METHODS AND MATERIALS

The *C. magnifica* culture was initiated from egg masses collected from Fay Lake, Linn County, Oregon, in the Cascade Mountains. Larvae were reared in aerated pans of tap water with sand substrate at 15.6°C and long days (16 h light : 8 h dark). Pans were washed and the water replaced once or twice a week to remove fecal material and excess decomposing food.

Alder leaves (*Alnus rubra*), conditioned in water for 1-2 wk to allow microbial colonization, were the basic food for the first-generation larvae. Conifer needles, conditioned for several months, were used primarily for case construction but may also have been ingested. Wheat grains and green grass were also provided. These were readily consumed within a few hours, demonstrating that microbial colonization was not a prerequisite for feeding on these foods.

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Care was taken not to have an excess of wheat as the fermentation and/or deoxygenation from decomposition led to high mortality. In the later instars, the use of grass in the diet was discontinued largely because it was not convenient to maintain a supply.

Second-generation larvae were obtained from laboratory-reared adults. The initial experiment was conducted with third-instar larvae (6 wk old) to determine whether they would feed on live invertebrates, and if so, the effects on growth and fecal production. White worms (*Enchytraeidae*) from a laboratory culture were used as prey. Fifteen larvae were placed in a petri dish with sand, conifer needles, and half of a conditioned alder leaf (150 mg dry wt) and 12 white worms ( $\approx 8$  mg dry wt). A control dish with 15 larvae, paired by case length with the worm-fed group, was set up with sand, conifer needles and the other half of the alder leaf. The dishes were examined daily or every 2nd day for 10 days. Each time, the feces were removed from the food and substrate by several rinsings and then collected by filtration on Millipore® membrane filters (5  $\mu$ m pore size). Fecal collections were dried at 60°C for 24 h and weighed. Twelve live worms were added each time the dishes were cleaned. The caddisfly larvae were observed feeding on the worms but no attempt was made to quantify the amount consumed because of the difficulty of recognizing and collecting the fragments of the dead worms.

Five larvae from both the experimental and control series were sacrificed on day 10 for a comparison of weights. These were dried for 24 h at 60°C and then weighed. The remaining 10 larvae in each series were reared until all had moulted to the fourth instar (to day 30) and then dry-weighed individually. An excess of alder leaves, and worm supplement in the experimental dish, was maintained.

Worm-supplement feeding was also conducted with second-generation larvae taken from the stock culture at 12 wk when the larvae were late fourth or early fifth instar. Differences in procedure from the first trial were: (1) the control and experimental diets included wheat grains, as this was standard for the stock cultures; (2) rearing was continued until the larvae sealed off their cases for pupation, that is, after achieving maximum growth; (3) experiments were carried out in a "drippy," a series of trays with a variable rate of water exchange (Anderson 1973), to minimize O<sub>2</sub> deficits due to decomposing wheat or worms.

The cultures were examined at least twice a week and food added if needed. Quantities provided or consumed were not measured, but the approximate proportions available, by weight, were: worms, 1; wheat, 40; alder leaves, 200. Two-day fecal collections were taken twice during wk 4 to obtain an

index of food consumption. Some larvae were dry weighed at this time to compare weights between the treatment and control larvae.

The worm-supplement feeding was repeated with larvae of the third laboratory generation in drippy trays, starting with 30 larvae about 7 wk old (15 late third- and 15 early fourth-instar larvae) in each of the experimental and control groups. These larvae were progeny of adults that had been reared on the standard vegetative-based diet. The larvae were reared to newly-moulted pupae, at which time they could be sexed, and were then dry weighed. In addition to comparing pupal weights between treatments, the rate of larval development was compared without sacrificing the larvae, using instar duration, case size, and type of case constructed as criteria.

## RESULTS

Second-generation *C. magnifica* larvae with the worm-supplement feeding initiated in the third instar moulted about 1 wk earlier than the group fed on alder leaves and were 50% heavier after 30 days (Table 1). Expressed as a growth rate, the worm-supplement group increased 0.14 mg/day compared with .08 mg/day for control larvae. Fecal production rates were consistently higher for the control, suggesting a lower assimilation efficiency of the detritus-based food (Table 1).

The data indicate that development rate of mid-instar larvae was enhanced by the food supplement, but the apparent difference in growth rates could have been overestimated. The experiment was terminated when the control series had all moulted to fourth instar. By this time most of the worm-supplement group had been fourth instars for several days and had completed the rapid spurt of growth that characteristically occurs in the early part of an instar.

Even with the addition of wheat to the diets, the trend for greater growth is also apparent for the worm-supplement group of second-generation larvae reared from late fourth instar to the prepupal stage (Table 2). This interval represents all of the final instar, which is the major feeding and growth period when  $\approx 80\%$  of the total tissue is elaborated. The results are consistent with those obtained for third-instar larvae, with more rapid development and heavier larvae being produced with the worm supplement. There was no difference in case length for the mature larvae of the two groups. The daily growth rate for the final 10–12 wk of larval development was 0.31 mg/day in the worm supplement and 0.24 mg/day in the control, or about 2–3 $\times$  greater than that of third-instar larvae.

All larvae in the second-generation feeding trials were sacrificed for dry weights without being sexed. Thus, to determine whether the enhanced growth

TABLE 1. Effects of addition of enchytraeid worm supplement to an alder-based diet on growth, development, and fecal production of 2nd laboratory generation *Clistoronia magnifica* larvae. Experiment started with larvae 6 wk old (3rd instar)

Parameter measured	Worm supplement		Control	
	N		N	
Fecal production (mg/mg·day)				
Days 1-4	15	0.60	15	0.79
5-8	15	0.27	15	0.48
29	10	0.29	10	0.81
Time to instar IV (days)	10	16.4 ± 4.2	10	23.5 ± 3.1
Mean weight, Day 30 (mg)	10	5.18 ± 0.96	10	3.40 ± 0.65

due to the worm-supplement diet was related to sex, the feeding experiments were repeated in the third generation and the individuals were reared until they could be sexed as pupae. These food supplement studies were initiated with larvae 7 wk old (late third- and early fourth-instar). The rate of instar development was more rapid and time to larval maturity was shorter with the worm supplement as had been demonstrated with the second generation feeding trials.

A behavioral trait that proved useful as an index of larval development was the rebuilding of the larval case (a change from vegetable to mineral material) that occurs towards the end of the final instar. The length of the sand and conifer needle portions of the cases were measured. By wk 12 (5th wk of experiment), when the first sealed cases were found in both series, 56% of the case material was sand in the worm-supplement group, compared with 23% in the control.

Though in both the control and supplement series the mean weight of male pupae was slightly lower than that of female pupae, the differences were not significant ( $p > .05$ ). The means and 95% confidence intervals were (in milligrams): control males:  $35.89 \pm 2.15$ ; females:  $37.53 \pm 1.77$ ; worm supplement: males  $40.35 \pm 3.14$ ; females:  $42.68 \pm 2.44$ .

Both sexes required similar times for development. Significant differences in mean weights between the treatments occurred for pooled males plus females, and for females. The confidence intervals overlapped slightly for males; the lack of demonstrable difference is probably because of small sample size (nine males in worm-supplement group and 11 in the control).

The combined effect of more rapid development and larger size resulting from the supplement diet is demonstrated by plotting the cumulative weight and time of pupation for the two groups (Fig. 1). Development was enhanced by the worm supplement. For example, by day 100 (from hatching), 80% of the worm-supplement group had pupated compared with 36% in the controls and the biomass of pupae was  $2.6\times$  greater in the worm-supplement than in the control. Actually, both groups developed very rapidly, progressing to the pupal stage by 13-16 wk from hatching possibly because temperature in the rearing room was  $1-2^{\circ}\text{C}$  above the setting of  $15.6^{\circ}\text{C}$  for about a month. Also, the larvae used in the experiment were the earliest and most vigorous in the stock culture so neither the duration nor the final weights are necessarily typical for the species. However, this does not negate the comparison between feeding regimes because the larvae were selected for uniformity in the two series.

TABLE 2. Effects of addition of enchytraeid worm supplement to an alder and wheat based diet on growth, development, and fecal production of 2nd laboratory-generation *Clistoronia magnifica* larvae. Experiment started with larvae 12 wk old (late fourth and early fifth instar)

Parameter measured	Worm supplement		Control	
	N		N	
Fecal production (mg/mg·day)				
Days 28-30	20	0.10	18	0.18
34-37	14	0.09	14	0.19
Mean weight (mg)				
Day 35	11	25.70 ± 6.30	11	15.31 ± 3.87
At maturity (prepupae)	9	47.50 ± 3.69	18	39.71 ± 2.65
Time to maturity (days) (from wk 12)	9	73.2 ± 4.3	18	87.7 ± 3.7

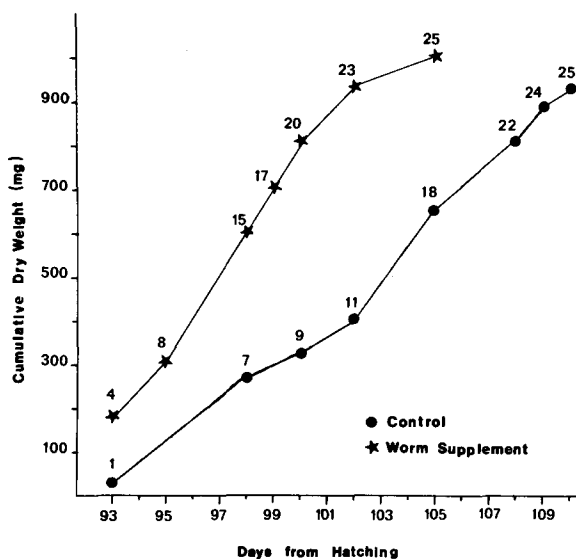


FIG. 1. Comparison of cumulative biomass of 3rd laboratory-generation *Clistoronia magnifica* at pupation when reared on a vegetative-based diet and with a worm supplement. The number that had pupated by each date is also indicated.

#### DISCUSSION

The laboratory rearing has demonstrated that *C. magnifica* has considerable plasticity in its life cycle. Larval duration in the field is about 6–7 mo (Winterbourn 1971a), but under laboratory conditions at 15–17°C, this can be reduced to < 4 mo with a complete generation being produced in < 6 mo. As far as I am aware, this is the first caddisfly to be reared on a continuous basis.

The food habits of the larvae are also extremely catholic. Wheat grains and fresh grass were consumed though neither would occur in the larval habitat. These foods were included as other feeding studies had indicated that laboratory-conditioned leaves, as the entire nutrient source, were inadequate for rearing through the duration of the larval stage. Though Winterbourn (1971a) described *C. magnifica* as a sediment feeder, the behavior in skeletonizing leaves would put them in the shredder category.

Several field studies have implicated food quality in the food preference and growth of caddis larvae. Iversen (1974) correlated the growth of *Sericostoma personatum* with the nitrogen content of various species of leaves, and Otto (1974) showed that *Potamophylax cingulatus* larvae fed on beech leaves were only half the weight of those fed alder. Cummins (1973) reported that larvae of a detrital-feeding population of *Glossosoma nigrum* achieved a final weight only about one third of that characteristic of an algal feeding population. Winterbourn (1971b) stated that with *Banksiola crotchii*, a change from

algal to a carnivorous diet was obligatory in the final instar to obtain the rapid increase in body weight required before pupation.

No comparison can be made between the size of laboratory-reared *C. magnifica* and field populations because weight data are not available for the latter. However, our current studies have demonstrated that it is possible to maintain the weight of *C. magnifica* through successive generations by providing the worm supplement. Based on the experiments with the second- and third-generation larvae reported above, small quantities of white worms were provided in the routine feeding of the fourth-generation stock culture. Mean pupal weight was 41.96 mg ( $n = 46$ ), which is very similar to the 41.84 mg for the third-generation worm-supplement group.

Alder leaves were always the dominant type of food consumed by *C. magnifica* larvae under all feeding conditions. This was apparent from the amount of feeding damage and from examination of the fecal material. Some selection for worms occurred as they were obviously consumed in a higher proportion than they occurred in the substrate. The observed effect of the worm supplement on the increased growth rate of the larvae is attributed to the nutritional quality of the prey, rather than to an indirect effect of the worms increasing the nutritional value of the detritus. The worms occurred in too small a quantity to affect detritus quality by their feeding activities.

The present study has shown that *C. magnifica* larvae are opportunistic feeders and will consume animal food when it is available. Observations of feeding on dead fish by limnephilids (Brusven and Scoggan 1969) and the commonly noted cannibalism, which increases with food stress (e.g., Gallepp 1974), also indicate that typical detritivore-herbivore caddis larvae are facultatively carnivorous.

Animal tissue is a high quality food source, especially for protein (essential amino acids) required for growth. The lipid component from animals also may be an important supplement to a detritus-based diet because much of the weight increase of final-instar larvae is due to fat storage. A deficiency of linolenic acid causes wing abnormalities in several Lepidoptera (Grau and Terriere 1967). The occurrence of similar wing malformations in *C. magnifica* adults, and in other limnephilids (Anderson 1974), when the larvae were reared on detritus, might also be related to fatty acid deficiencies.

The detritus habitat of *C. magnifica* larvae contains an abundance of small invertebrates such as midges, oligochaete worms, and crustaceans that are encountered during the normal feeding activities. It is highly probable that supplemental predation on these forms provides an integral component of the diet of *C. magnifica* larvae in the field.

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