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The life history of *Dicosmoecus atripes* (Hagen) (Limnephilidae:Trichoptera) in a Rocky Mountain stream of Alberta, Canada, with special reference to aggregation formation.

by

Vytenis Gotceitas

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science

Department of Zoology

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Fall, 1982

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The life history of *Dicosmoecus atripes*(Hagen) (Limnephilidae:Trichoptera) in a Rocky Mountain stream of Alberta, Canada, with special reference to aggregation formation submitted by Vytenis Gotceitas in partial fulfilment of the requirements for the degree of Master of Science.

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Supervisor

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Date..September 28, 1982.....

Abstract

Dicosmoecus atripes (Hagen) has a 2-year life cycle in Dyson Creek, Alberta, a second order foothills stream of the eastern Canadian Rockies. Emergence and oviposition occur from August to mid-October. Low water temperature seems to be the most important factor responsible for the 2-year life cycle. The first winter is spent as first instar larvae, the second as inactive fifth (final) instar larvae in aggregations on the underside of cobbles.

Laboratory experiments were conducted to examine the factors involved in the formation of these overwintering aggregations by fifth instar larvae. Larvae formed aggregations in the absence of environmental variations (e.g. current, substrate, etc.), that could function in bringing larvae together to a 'suitable' site of attachment in the field. When selecting an attachment site, larvae selected substrates with attached conspecifics already present, over substrates without attached conspecifics. *Dicosmoecus atripes* larvae appear capable of tactile/visual recognition of conspecifics, and use their presence on a substrate as cues for selecting a site for attachment.

Annual production was estimated at 91.4 mg/m^2/year, with an annual P/B ratio (turnover ratio) of 4.97.

Larval diet and microhabitat changed between instars. The proportion of diatoms in the diet of early instar larvae was significantly ($P<0.001$) greater than that of third and later instars. Early instar larvae inhabit stream margins,

while larvae of third and later instars were mainly found in mid-stream reaches. Larvae of all instars preferred pool areas to riffles. First and second instar larvae inhabit similar microhabitats. However, the abiotic factors important in microhabitat selection seemed to differ between these instars. Third, fourth and fifth instar larvae showed a similar trend.

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taking me after the "Big ones" even though I wasn't quite finished.

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Chapter 1.

I. Introduction

The terms life history and life cycle have often been used indiscriminately in the literature. The life cycle of an organism has been defined as "a series of stages in form and function through which an organism passes between the recurrence of specified primary stages (e.g. egg to egg)" (Buikema and Benfield, 1979). My definition of life history includes an organism's life cycle, as well as its distribution, diet, production, and response(s) to abiotic and biotic factors in its environment.

Life history studies have received much less attention among freshwater ecologists in recent years. Part of this decrease in emphasis seems to be a direct result of coinciding trends in general ecological research from descriptive to quantitative studies (Resh, 1979). Another and perhaps even more influential reason is the lack of support for such research, often simply because of its basic nature (Waters, 1979). As basic as life history studies may be, their importance in providing background data for more detailed ecological studies cannot be disputed. For example, Resh (1979) emphasized how information from life history work (e.g. intraspecific distributional patterns) could be used to reduce the number of samples and therefore time and effort necessary to minimize sampling variability. Waters (1979) stressed the need for adequate data on benthic invertebrate life histories in quantitative ecological research and outlined several practical applications of such

data in pollution control and fisheries management. For example, accurate life history data are important for benthic production computations and therefore for fisheries management programs based on benthic production.

My study responds to a call for more basic life history data on freshwater benthic invertebrates (Waters, 1979) and deals with the life history of a population of *Digosmoecus atripes* (Hagen) in Dyson Creek, Alberta. Questions about voltinism in *D. atripes* populations (G.B. Wiggins, person. comm.), age specific diet and microdistribution, production, and the formation of larval aggregations during prolonged periods of inactivity were all examined.

The formation of larval aggregations during pupation is a common phenomenon among caddisflies (G.B. Wiggins, pers. comm.). However, few studies have looked at the actual formation or significance of these aggregations. The formation of these aggregations may involve some behavioral interaction between larvae or may simply be the result of individual larvae reacting in a similar manner to some set of environmental factors. I investigated this phenomenon by examining the processes involved in the formation of overwintering aggregations by *D. atripes* larvae.

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II. The life history of *Dicosmoecus atripes*(Hagen) (Limnephilidae:Trichoptera) in a Rocky Mountain stream of Alberta, Canada.

Abstract

Dicosmoecus atripes(Hagen) has a 2-year life cycle in Dyson Creek, Alberta, a second order foothills stream of the eastern Canadian Rockies. Emergence and oviposition occur from August to mid-October. The first winter is spent as first instar larvae, the second as inactive fifth(final) instars in a form of diapause. No growth was observed in overwintering first instar larvae, and a significant ($P<0.05$) weight loss was recorded in overwintering fifth instar larvae. Temperature seems to be the most important factor responsible for the 2-year life cycle.

Annual production was estimated at 91.4 mg/m²/year, with an annual P/B ratio of 4.97.

Larval diet and microhabitat changed between instars. The proportion of diatoms in the diet of early instar larvae was significantly ($P<0.001$) greater than that of third and later instars. Early instar larvae inhabit stream margins, while larvae of third and later instars were mainly found in mid-stream reaches. Larvae of all instars preferred pool

areas to riffles. First and second instar larvae inhabit similar microhabitats. However, the abiotic factors important in microhabitat selection seemed to differ between these instars. Third, fourth and fifth instar larvae showed a similar trend.

Introduction

Members of the genus *Dicosmoecus* are among the largest of caddisflies and are often abundant in lotic habitats of western North America and northeastern Asia (Wiggins and Richardson, 1982). In a recent review of this genus, Wiggins and Richardson (1982) concluded that three of the four North American species are generalized predator-shredders as final instar larvae and have 2-year life cycles. The fourth species, *Dicosmoecus gilvipes*, is a univoltine grazer. *Dicosmoecus gilvipes* and *D. atripes* are the two most common North American species. The biology of *D. gilvipes* is known from studies in California (Lamberti and Resh, 1979; Hart and Resh, 1980) and Montana (Hauer and Stanford, 1982). However, little is known about the wider ranging (Alaska to New Mexico) *Dicosmoecus atripes*.

This study examines the life cycle and biology of a population of *Dicosmoecus atripes* in Dyson Creek, Alberta. Factors influential in accounting for a 2-year life cycle are discussed, and special emphasis is placed on analysis of instar-specific diet and microhabitat selection.

Study Site

This study was conducted on a 2 km stretch of Dyson Creek, Alberta (50° 37'N, 114° 39.2'W), a second order foothills stream of the eastern slopes of the Canadian Rockies (Fig.1). Dyson Creek arises at an elevation of

2133 m and flows for 12 km before entering the Sheep River at an elevation of 1463 meters.

The 2 km study area (elevation 1584-1524 m) has a mean stream width of 5.8 m, depth of 25.9 cm (mean pool depth=32.1 cm, mean riffle depth=18.9 cm, max. depth 1.2 m), and current velocity of 0.26 m/sec (mean pool current vel.=0.12 m/sec , mean riffle current vel.=0.42 m/sec, max. current vel.=1.15 m/sec). The substrate is predominantly cobbles and pebbles, with some areas of bare bedrock and patches of gravel, sand or both (substrate classification after Cummins, 1962). The study area flows through open meadow, ravine and forested reaches primarily of willow, aspen and white spruce.

Water temperature, recorded with a Ryan 30-day thermograph, ranged from 0°C in winter to 14°C in summer (Fig.2). Mean summer temperature (June-September,1980) was 9°C. The stream is typically ice-covered from October to May, with an average winter water temperature of 0.5°C. Degree days were calculated using mean monthly temperatures over 1 year. Since no growth was recorded at temperatures below 0.5°C, this was taken as the minimum temperature in these calculations. The number of degree days for Dyson Creek was 986.5/year.

Methods

Quantitative and qualitative benthic samples were collected weekly during the summer and autumn of 1980 and spring and summer of 1981. Pool and riffle areas were sampled alternately every other week. To avoid previous sampling effects, no pool or riffle was sampled more than once per year.

Quantitative samples were taken with a Surber-type sampler (30x30 cm frame, mesh size=250 um) at 1 m intervals along transects extending across the stream. Thirty samples per week were taken during summer and autumn (May-October) and 5-10 samples per month in the winter. Transects were set so the same area would not be sampled twice. Samples were taken to a substrate depth of 5 cm and were initially sorted in the field by running the sample through a series of sieves (5.08 cm, 2.54 cm, 4.76 mm, 2.49 mm). *Dicosmoecus atripes* larvae retained by the 5.08 and 2.54 cm sieves were preserved in Kahle's fluid in the field. Substrate and animals in the 4.76 and 2.49 mm sieves were preserved in the field and sorted in the laboratory under a dissecting microscope. The larvae were then counted for density and production estimates. To determine larval instars, head widths (dorsally across the eyes) were measured under a dissecting microscope at 40x, using larvae from both quantitative and qualitative samples. Qualitative samples were collected throughout the year with a dip net (mesh size=250 um).

Three rearing cages (1.2x0.6x0.6 m), covered with nylon window screening, were used to rear pupae in the stream. To determine if all members of a cohort had a 2-year life cycle, larvae that achieved the fifth instar during the summer of 1980 were placed in cages (20 larvae per cage) in late August and observed to the end of October 1980.

Qualitative samples of at least 30 larvae in each instar were collected for weighing. Based on a temporal separation (see Results) four stages of fifth(final) instar larvae (V_1,V_{11},V_2,V_{22}) were designated and samples of all four weighed. Larvae were oven-dried (60°C, >72hours), cooled in a desiccator and weighed to the nearest 0.0001 mg on a Cahn 25 Automatic Electrobalance or to 0.0001 gm on a Mettler type H6 balance. From necessity, larvae had to be preserved prior to weighing. Larvae were preserved in Kahle's fluid and weighed within 5 days of the time collected. Weight loss is minimal with this procedure (R.J. Mackay, pers. comm.).

Annual production and annual turnover ratio (P/B) were calculated using the instantaneous growth method (Waters and Crawford, 1973; Waters, 1977). Because *D. atripes* has a 2-year life cycle in Dyson Creek (Fig.3), production estimates for members of all cohorts present (i.e. 1978,1979,1980) between July 1980 and June 1981 were summed to determine overall annual production.

To determine diet of larval *Dicosmoecus atripes*, the foregut of 10 larvae of each instar were prepared as

outlined in Cummins (1973), except animal material was not separated from other gut contents. Relative abundance (percent composition per gut) of diatoms, other algae, detritus and animal material in the gut of larvae of each instar was determined by counting (at 400x) 10 random whipple grids per larva, and then combining the results for the 10 larvae of each instar. The gut contents of 10 first instar larvae and 5 second instar larvae were combined per slide. A total of 30 fifth instar guts were analysed , 10 from animals just after molting to fifths (V_1), 10 from fifths prior to overwintering (V_{1_2}), and 10 from fifths in their second summer(V_2). To test for differences in diet between instars, the data were subjected to an arcsine(x) transformation and analysis of variance.

Water depth, current velocity at 0.6x the water depth (using a F583 Water current meter-- Price Pygmy type), predominant substrate type enclosed by the sampler, and distance from shore were recorded for each of the 470 quantitative samples taken. Each of these designated abiotic factors was divided into a number of categories (e.g. substrate: 1=sand, 2=gravel, 3=pebble, 4=cobble and 5=bedrock) and the relative proportion of each category present in each factor calculated. For example, 27 of 470 samples were from a sandy substrate; therefore 6% of all substrate types sampled was sand. If *D. atripes* larvae are not selective with respect to these abiotic factors, then the relative proportion of larvae collected in association

with each abiotic factor category should approximate the relative proportion of each category sampled. That is, of all *D. atripes* larvae collected in each instar, the percentage collected from a sandy substrate should approximate 6% if larvae are not selective towards substrate types. To check for instar-specific selection, the relative proportion of larvae associated with each category of each abiotic factor was calculated for each instar. For example, 106 of a total of 150 first instar larvae(or 71%) were collected from a sandy substrate. These data were compared graphically and by a Chi-square goodness of fit test to those obtained for current velocity, substrate, position across stream and depth.

The effects of current, substrate type, distance from shore, and depth on the distribution of *D. atripes* larvae were analysed using multiple regression analysis (BMDP computer program P6D). Data were analysed by instar on individual sampling dates (30 samples/date). Only dates for which more than 30% of the samples collected contained larvae of the instar in question were used. The 30% value was chosen to ensure all instars would be included in the analysis, because fifth instar larvae(V_2 and V_{22}) usually appeared in less then 10 samples per any sampling date. A log(x+1) transformation was applied to the data to randomize the residuals. Samples with zero animals were included in the analysis.

Results

Life Cycle

Head capsule measurements of larval *Dicosmoecus atripes* revealed five distinct instars during the life cycle (Table 1). The range of head capsule widths for third, fourth and fifth instar larvae from Dyson Creek were comparable to those reported by Wiggins and Richardson (1982) for *D. atripes* populations over the entire geographic range of the species. Although morphologically identical, fifth instar larvae were divided into four categories on a temporal basis: (V_{1})just after molting (August first year),($V_{1,}$)prior to overwintering (September-October first year),(V_{2})just after overwintering (May-June second year), and ($V_{2,}$) prior to pupation (July-August second year).

The *D. atripes* population in Dyson Creek, Alberta, has a 2-year life cycle (Fig.3). A single egg mass collected in September 1980 and maintained in an in-stream rearing cage produced first instar larvae in October. No first instar larvae were collected in winter samples, but were present in May and June 1981. It appears that first instar *D. atripes* larvae hatch in autumn and either grow very slowly during winter or cease growing and overwinter in some form of resting stage. Development was rapid during the following summer, and final instar larvae (V_{1}) were present by early August. In late September these larvae formed aggregations on the underside of cobbles where they overwintered as fifth instar larvae ($V_{1,}$). Up to 87 larvae per cobble was

recorded; the average number was 15 larvae per cobble. This winter resting stage appears to be ateleo-diapause (low-intensity diapause) as described by Mansingh (1971), because if the cobble is disturbed at any time after the larvae attach, the larvae detach from the cobble, move away, and attach under another cobble. However, larvae do not detach if the cobble is not disturbed. Similar results were obtained from manipulation of live animals kept in a laboratory environmental chamber under simulated winter conditions.

The following spring (April-May), overwintering larvae (V_2) became active again, resumed feeding, dispersed and were ready to pupate (V_{22}) by mid-July. At this stage larvae again formed aggregations, similar to those of overwintering larvae, on the underside of cobbles. After attaching they underwent a 1 to 3 week prepupal diapause. Pupation took another 1 to 3 weeks, after which the pharate adult typically detached the larval case from the cobble and emerged.

None of the fifth instar larvae (V_1) placed in the in-stream rearing cages (August-October, 1980) pupated in their first year. Therefore, a 2-year life cycle appears to hold for the entire *D. atripes* population in Dyson Creek.

Larval Cases

First instar *Dicosmoecus atripes* larvae constructed cases of vegetation. A vegetative case was retained through

the early part of the fifth (V_1) instar, at which time it was replaced by a case entirely of stone. Construction of the stone case involved addition of sand grains to the anterior end of the vegetative case and removal of the vegetative case from the posterior end of the completed stone case. Larvae overwinter and pupate in stone cases. *Dicosmoecus atripes* larval cases are similar in construction to those described for *Dicosmoecus gilvipes* larvae (Hauer and Stanford, 1982).

A shift in microhabitat accompanied the shift in case material. Larvae in vegetative cases were mainly found on the surface of the substrate, whereas stone cased larvae inhabited the underside of cobbles. In response to this shift, a stone case should provide more protection (e.g. against abrasion) than a vegetative case.

Density and Production

Maximum density of *D. atripes* larvae in Dyson Creek was estimated at five larvae per m^2 (Fig. 4, fourth instars). Density estimates from sampling dates approximately 1 year apart were similar (Fig.4, e.g. V_2 and II instars in June 1980/81). The calculated higher densities of late instar larvae as opposed to earlier instar larvae is probably an artifact of the collecting procedure and distributional patterns of the various instars (see Figs. 8-11).

The mean dry weight for larvae of each instar and change in weight between instars are shown in Figure 5. Two

periods of significant weight loss (t-test, $P<0.05$) occurred during the fifth instar: one during pupation and the second, a loss of almost half the body weight, during overwintering.

The annual production of *D. atripes* larvae in Dyson Creek was calculated at 91.4 mg/m²/year (Table 2). This estimate fits into the lower range of values reported for other species of Trichoptera (9.9-2,880 mg/m²/year; Waters, 1977). The annual P/B ratio (turnover ratio) was 4.97; which is in the general range reported for other aquatic invertebrates (Waters, 1969; Waters and Crawford, 1973). My estimates should be taken as minimal, because sampling of early instar larvae could have been improved by incorporating the knowledge obtained in this study on instar specific distribution into the sampling scheme.

Food Habits

The analysis of larval food habits indicated that the diatom component changed significantly between second and third instar larvae (ANOVA, $P<0.001$). This resulted in a switch from predominantly diatoms during first and second instars, to detritus in third, fourth, and fifth instars (Figs. 6&7).

I observed late instar *D. atripes* larvae (III-V) feeding on macroinvertebrates (e.g. larvae of the Trichoptera: *Ecclisomyia* sp.) in the field, but could not determine whether *D. atripes* larvae had actually caught the prey. In the laboratory, *D. atripes* larvae would actively

feed on enchytraeids (Annelida:Oligochaeta), and therefore may eat live animals in the field should the opportunity arise. Other prey items found in gut contents of *D. atripes* were Trichoptera, Ephemeroptera, Chironomidae and Plecoptera larvae. After an exceptionally severe rainstorm in mid-summer 1980, numerous accumulations of green vegetation, especially aspen and willow leaves, were noted in Dyson Creek. *Dicosmoecus atripes* larvae appeared capable of locating such occasional inputs of rare food items, since uncommonly large congregations of *D. atripes* larvae were observed feeding on this material. Similar observations were made by Hart and Resh (1980) for a population of *Dicosmoecus gilvipes* larvae in California.

Microhabitat

Dicosmoecus atripes larvae of all instars preferred pool areas to riffle areas ($P<0.05$). Distribution of larvae of the various instars in relation to current velocity, substrate type, position in stream and depth, is shown in Figures 8-11. The distribution of larvae in each instar with respect to current velocity, substrate type, position across stream and depth was not related to the proportion of eac of these factors sampled (Chi-square, $P<0.05$) except for instar $V_{2,2}$ and current. Larvae of all instars appeared prefer low current velocities. First and second instar larvae selected shallow areas of fine substrate along the stream margin. Third and later instar larvae were found

across the stream channel, selecting deeper areas of coarse substrate. These trends are summarized for larvae of each instar in Table 3.

Results of the multiple regression analysis summarizes the factors most highly correlated with choice of microhabitat during each instar (Table 4). These results are consistent with instar specific trends in microdistribution (Table 3) and demonstrate that factors involved in habitat choice may differ between larvae of different instars even where microhabitat is similar. For example, selection for fine substrate and areas near shore in first instar larvae, and low current and shallow areas in second instar larvae (Table 4), both result in larvae of these instars inhabiting the stream margin (Table 3).

Discussion

Life Cycle

Hartland-Rowe (1964) concluded that temperature, especially low winter temperature, was a very important factor influencing life histories of Plecoptera and Ephemeroptera in Gorge Creek, Alberta (see Fig.1). The 2-year life cycle of *Dicosmoecus atripes* in Dyson Creek, with a zero growth period in first instar larvae and an inactive stage in fifth instar larvae during the winter, seems predominantly related to low water temperatures in winter. Support for this conclusion comes from observations

on a *D. atripes* population in Flynn Creek, Oregon, where the population has a 1-year life cycle, developing from egg to fifth instar larvae in about 4 months (December-March) (B. Wisseman, pers. comm.). The average water temperature of Flynn Creek during this 4 month period was 8.3°C. *Dicosmoecus atripes* larvae in Dyson Creek develop from first to fifth instar in 4 months as well. But this occurs during summer (May-August), when average water temperature in Dyson Creek is comparable (9°C) to the average winter water temperature in Flynn Creek. During winter (October-April), average water temperature in Dyson Creek is 0.5°C, and *D. atripes* larvae do not seem to grow. The number of degree days for Flynn Creek, calculated from temperature data reported by Chapman (1961) and considered typical (B. Wisseman pers. comm.), was 3347 per year compared to 987 per year for Dyson Creek.

Temperature may not be the only factor responsible for the different voltinism of the Alberta and Oregon populations. A difference in food quantity, quality or both may also be important (Anderson and Cummins, 1979). No quantitative data on the quantity or quality of available food resources for *D. atripes* in Dyson Creek were collected; but based on diet analysis, some qualitative information is available.

Since *D. atripes* larvae are shredders (Wiggins and Richardson, 1982), the autumnal imput of allochthonous material should provide a substantial food supply during

autumn and winter for both first and fifth instar larvae in Dyson Creek. The life cycles of many shredders seem keyed to this autumnal pulse of allochthonous material, with a corresponding period of major growth in late autumn and early winter (Anderson and Cummins, 1979). This appears to be the situation for *D. atripes* larvae in Flynn Creek, Oregon (B. Wisseman, pers. comm.). Since detritus makes up over 60% of the gut content in fifth instar *D. atripes* larvae in Dyson Creek (see Figs. 6&7), the presence of an inactive overwintering stage in this instar does not seem related to availability (i.e. quantity) of food. Low water temperature, therefore, seems the most important factor in overwintering of fifth instar larvae.

Although detritus is consumed by first instar *D. atripes* larvae and may be abundant during autumn and winter, the relatively large amount of diatoms (>60%) in their diet (see Figs. 6&7) suggests that diatoms could be important for overwintering in first instar larvae. Although Dyson Creek is ice-covered from mid-October to early May, substantial autochthonous production of diatoms (e.g. *Ceratoneis arcus*, *Rhoicosphenia curvata*, *Diatoma hiemale v.mesodon*, *Meridion circulare* ,etc.) found in first instar gut contents can be expected, and the quantity and quality of this food item should not be significantly limiting over the winter(M. Hickman, pers. comm.). Given this food resource, first instar *D. atripes* larvae have the potential for considerable growth over the winter; the fact that no

growth occurs seems to be the effect of low water temperatures.

Instar-specific Microhabitat

Just as diet of aquatic macroinvertebrates has been shown to change during the life cycle (Fuller and Stewart, 1977, 1979; Fuller and Mackay, 1980), one might expect a similar phenomenon with respect to choice of microhabitat and factors affecting that choice. Numerous studies have illustrated the effects of current velocity (Chutter, 1969; Corkum et al., 1977; Minshall and Minshall, 1977; Rabeni and Minshall, 1977), substrate type (Higler, 1975; Corkum et al., 1977; Resh, 1977; Lamberti and Resh, 1979; Minshall and Minshall, 1977; Rabeni and Minshall, 1977; Reice, 1980), position in stream (Resh, 1977), depth (Chutter, 1969) and other abiotic factors (e.g. Statzner, 1981) on the distribution of various lotic macroinvertebrates. However, few studies have treated these factors, either individually or in combination (Ulfstrand, 1967; Gore and Judy, 1981), as they relate to microdistribution during the life cycle of a single species. Different microdistribution patterns for different larval instars have rarely been reported (Cummins, 1964; Williams and Hynes, 1973; Resh, 1977; Hildrew et al., 1981).

In addition to instar-specific changes in diet, *D. atripes* larvae also showed instar-specific changes in microhabitat selection. First and second instar larvae were

found in similar microhabitats, along the stream margin. Highest concentrations of these larvae were in areas along the stream margin with submerged vegetation. Larvae were observed moving over this vegetation, apparently grazing on associated flora (e.g. diatoms, M. Hickman, pers. comm.) and fauna, and would cling tenaciously to this vegetation if disturbed (e.g. during dip-net sampling). It appears, therefore, that this bank vegetation serves both as a substrate for *D. atripes* larvae and their food. Although bank-side vegetation was not incorporated in the analysis on microdistribution, it could prove an important factor in distribution of early instars.

During the third instar, *D. atripes* larvae move from the banks and eventually occupy the entire channel of the stream; this bank to bank distribution is also exhibited by fourth and fifth instar larvae. Third instar *D. atripes* larvae are quite large (mean head width=1 mm, body length=1 cm), and since they inhabit the upper surface of the substrate, they are conspicuous. Predation by dippers (*Cinclus mexicanus*:Cinclidae) on third and later instar larvae found along the stream margin was frequently observed. Therefore, this lateral movement may in part be in response to avian predation. This selective pressure need not be restricted to Dyson Creek, as the distribution of dippers overlaps that of *Dicosmoecus atripes* over its entire geographic range.

Selection for deeper midstream reaches by fifth instar larvae during the winter would seem advantageous because there would be less chance of the water freezing into the substrate in these midstream areas. This may also ensure submergence during pupation the following summer should water levels recede drastically, as can happen during exceptionally dry years.

The change to a stone case during the early part of the fifth (V_1) instar may, in part, be an adaptation for overwintering and also for pupation. When compared to a case of vegetation, a stone case would appear to offer greater protection to an inactive animal against predation, mechanical injury, or both. A change to a stone case prior to overwintering would also ensure the presence of a case the following spring, as a vegetative case could suffer from decomposition or even attack by shredders during the 7 or 8 months of winter. Attacks on the cases of leaf-cased caddisfly larvae (*Pycnopsyche gentilis*) by other "leaf-feeders" is known to occur (Mackay, 1972; Mackay and Kalff, 1973).

Intraspecific Competition ?

Cushman et al. (1977) suggested that habitat differentiation between various sizes of *Diplectrona modesta* larvae (Trichoptera) may function as a mechanism in reducing competition, if competition is at all present. Although I have no direct evidence that intraspecific competition

occurs among *D. atripes* larvae, it is interesting that diet and microhabitat change significantly during the third instar. These changes effectively move third instar larvae into areas previously utilized by co-occuring fifth ($V_{2,2}$) instar larvae at approximately the time the fifth instar larvae are preparing to pupate. Therefore, could the observed spatial and dietary patterns between larvae of different instars, in part, be a response to a 2-year life cycle and resulting overlapping generations? In Flynn Creek, Oregon, *D. atripes* has a 1-year life cycle and no overlap in generations. In this population no shift in microhabitat between instars has been noted, and diet remains to be analysed (B. Wisseman, pers. comm.). Investigation for age-specific trends in other benthic macroinvertebrates with univoltine and bi- or even trivoltine populations may reveal, and provide possible mechanisms for avoiding, intraspecific competition.

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grants from the Natural Sciences and Engineering Research Council of Canada and the Boreal Institute for Northern Studies.

Table 1. Dicosmoecus atripes larval instars, from head width measurements (mm) measured across the eyes.

Instar	Mean Head Width (Range) mm
I (n=47)	0.513 (0.476-0.547)
II (n=127)	0.729 (0.666-0.809)
III (n=201)	1.109 (0.904-1.217)
IV (n=264)	1.479 (1.309-1.642)
V (n=576)	1.985 (1.761-2.189)

Table 2. Calculation of production of Dicosmoecus atripes larvae in Dyson Creek, Alberta, by the instantaneous growth method. G= instantaneous rate of growth (ln Wt/Wo), B= mean standing crop (Bt+Bo/2), P= production for interval between successive dates. (1b, 2b, 3b & 10b- V & V larvae; 11b & 12b- I, II & III larvae from 1981).

Date	Standing Crop-B (mg/m^2)	Mean weight (mg)	G	B (mg/m^2)	P= GB (mg/m^2)
1:18-25.6.80	0.9	0.6			
			1.361	3.6	4.9
2: 6-16.7.80	6.2	2.34			
			1.446	19.3	27.9
3:20-30.7.80	32.3	9.94			
			1.049	41.9	44.0
4: 6-14.8.80	51.6	28.4			
			0.071	39.8	2.8
5:22-28.8.80	27.9	30.5			
			0.013	29.9	0.4
6: 8-19.9.80	31.9	30.9			
			0.280	30.3	8.4
7: 6-7.10.80	28.6	40.9			
			-0.162	28.2	-4.6
8:14-15.11.80	27.8	34.8			
			-0.347	22.1	-7.7
9: 13.5.81	16.4	24.6			
			0	12.5	12.1
10: 2-8.6.81	8.6	64.8			
1b:18-25.6.80	19.4	64.8			
			0.159	16.7	2.6
2b: 6-16.7.80	13.9	76.0			
			0.000	11.4	0.00
3b:20-30.7.80	8.9	76.0			
10b: 13.5.81	0.1	0.1			
			0.143	0.2	0.02
11b: 2.6.81	0.2	0.1			
			1.215	0.5	0.6
12b: 8.6.81	0.8	0.4			

Total P =91.4

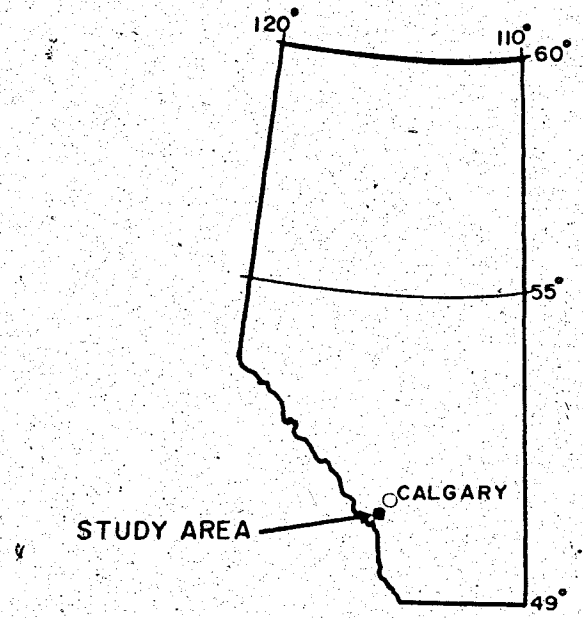
Table 3. Instar-specific trends in the microdistribution of Dicosmoecus atripes larvae in Dyson Creek, Alberta.

Instar	Current	Substrate	Position across stream	Depth	Microhabitat
I	Low	Sand	Margin	Shallow	Stream Margin
II	Low	Sand	Margin	Shallow	Stream Margin
III	Low	Bedrock	Midstream	Deep	Midstream Reaches
IV	Low	Bedrock	Midstream	Deep	Midstream Reaches
V	Low	Cobbles	Midstream	Deep	Midstream Reaches
V	/	Cobbles	Midstream	Deep	Midstream Reaches

Table 4. A summary of the multiple regression analysis on the series of samples of *Dicosmoecus atripes* larvae from Dyson Creek, Alberta.

Instar	Date	Significant Factor(P<0.05)	T Value	P(2-Tail)
V	8.9.80	none		
	6.8.80	current	-3.465	0.002
		depth	3.283	0.003
	22.8.80	position across stream	2.413	0.023
	1.8.80	none		
IV	6.7.80	depth	2.171	0.04
	20.7.80	none		
III	6.7.80	current	-2.267	0.032
		substrate	2.898	0.008
		depth	2.829	0.009
II	28.6.81	current	-2.837	0.009
		depth	-2.221	0.036
I	20.6.81	position across stream	-2.587	0.016
	8.6.81	substrate	-3.790	0.001
V	13.5.81	none		

n=30 for all dates



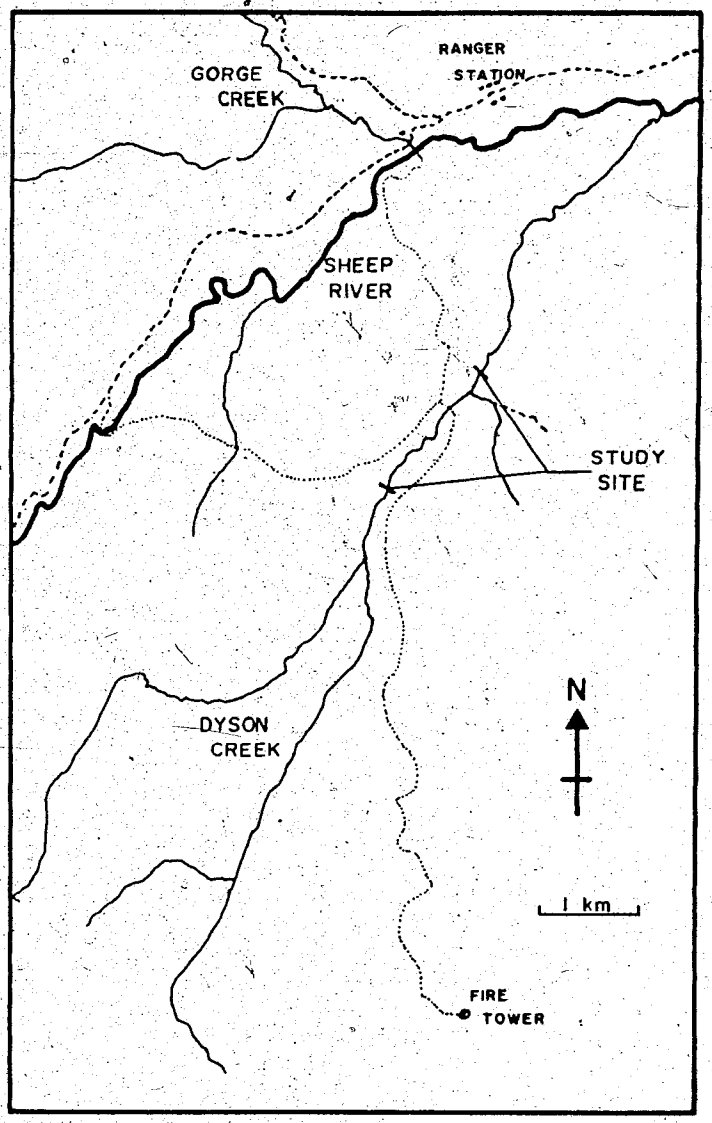


Figure 1. Dyson Creek watershed, Sheep River Wildlife Sanctuary, Alberta. Approximately 85 km S.W. of Calgary, Alberta.

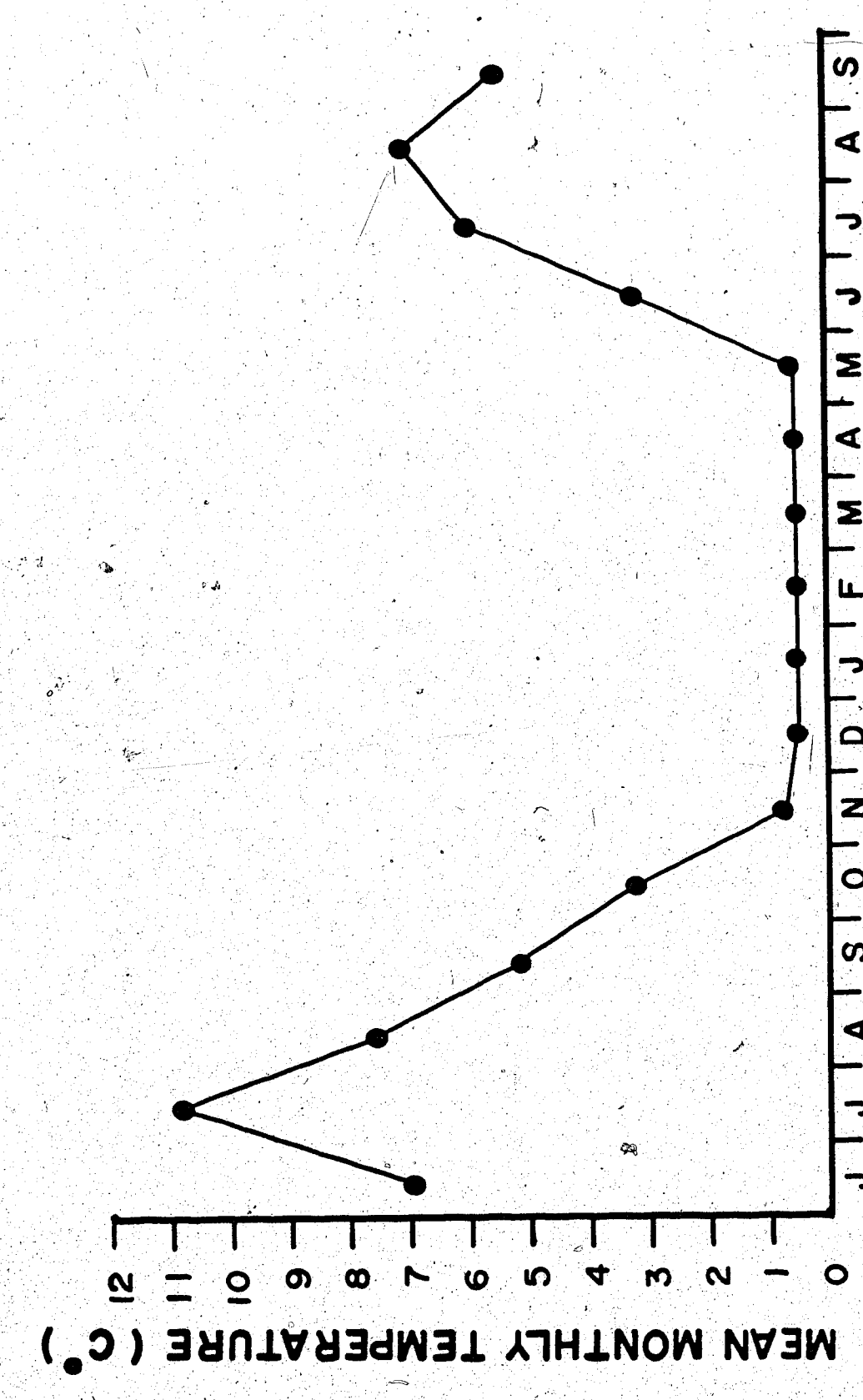


Figure 2. Mean monthly water temperature within study site on Dyson Creek, Alberta. (Range of standard error: 0.03-0.1).

Figure 3. Life cycle of three cohorts (1978, 1979, 1980) of Dicosmoecus atripes in Dyson Creek, Alberta. The presence of eggs(EGG), adults(ADULT), pupae(PUPA), prepupa (P.P.), and monthly distribution of larval instars(I-V) is shown. Samples were collected from June 1980 to July 1981.

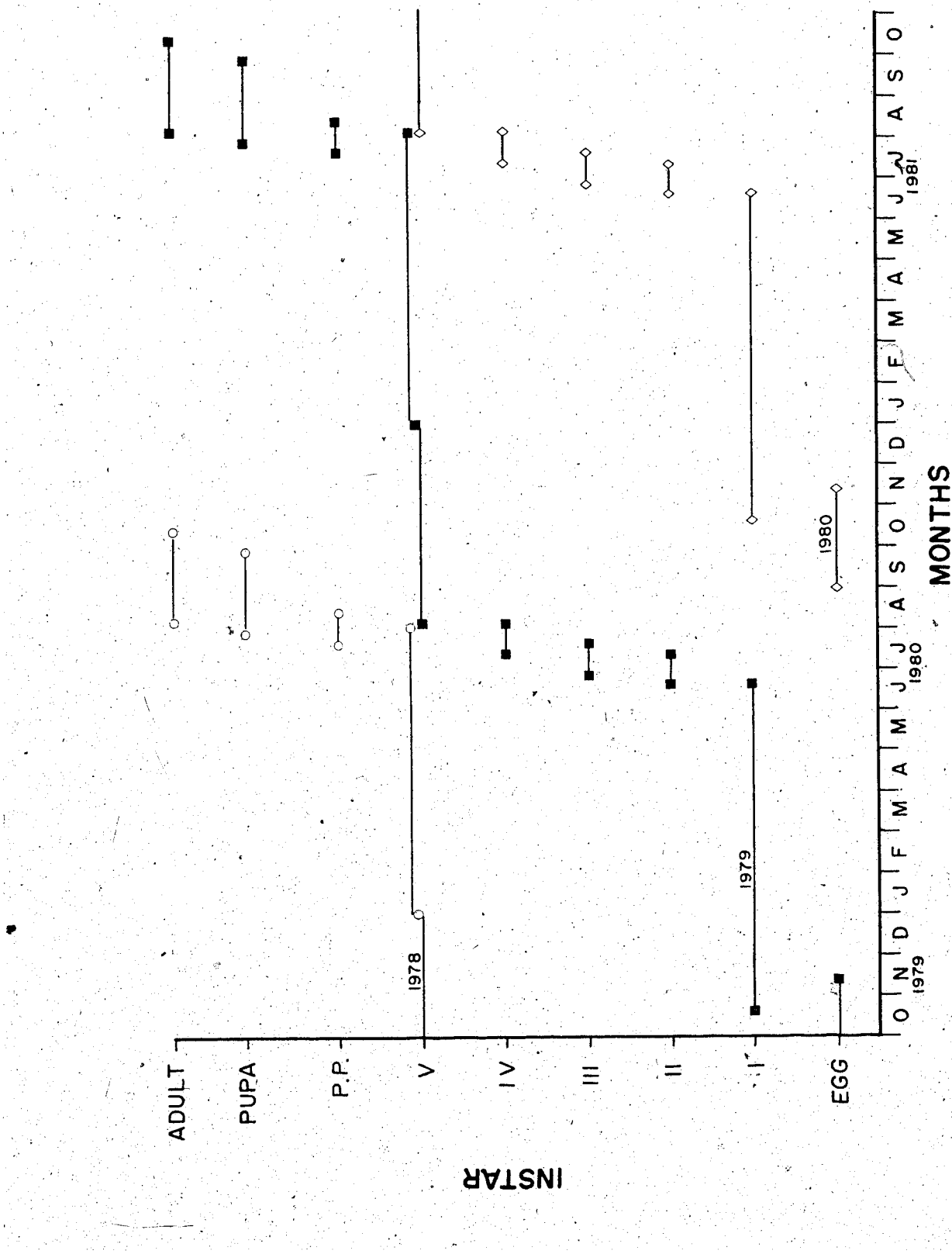

ADULT
PUPA
P.P.
V
IV
III
II
I
EGG
INSTAR
1978
1979
1980
1979
1980
1981
O N D J F M A M J J A S O N D J F M A M J J A S O
MONTHS

Figure 4. Density estimates (number/m^2) of Dicosmoecus atripes larval instars(I-V) in Dyson Creek, Alberta, from June 1980 to July 1981. V_1 represents fifth instar larvae in their first summer (Aug.-Sept.), V_2 fifth instar larvae in their second summer (May-Aug.). (Range of standard error: 0.2-0.6)

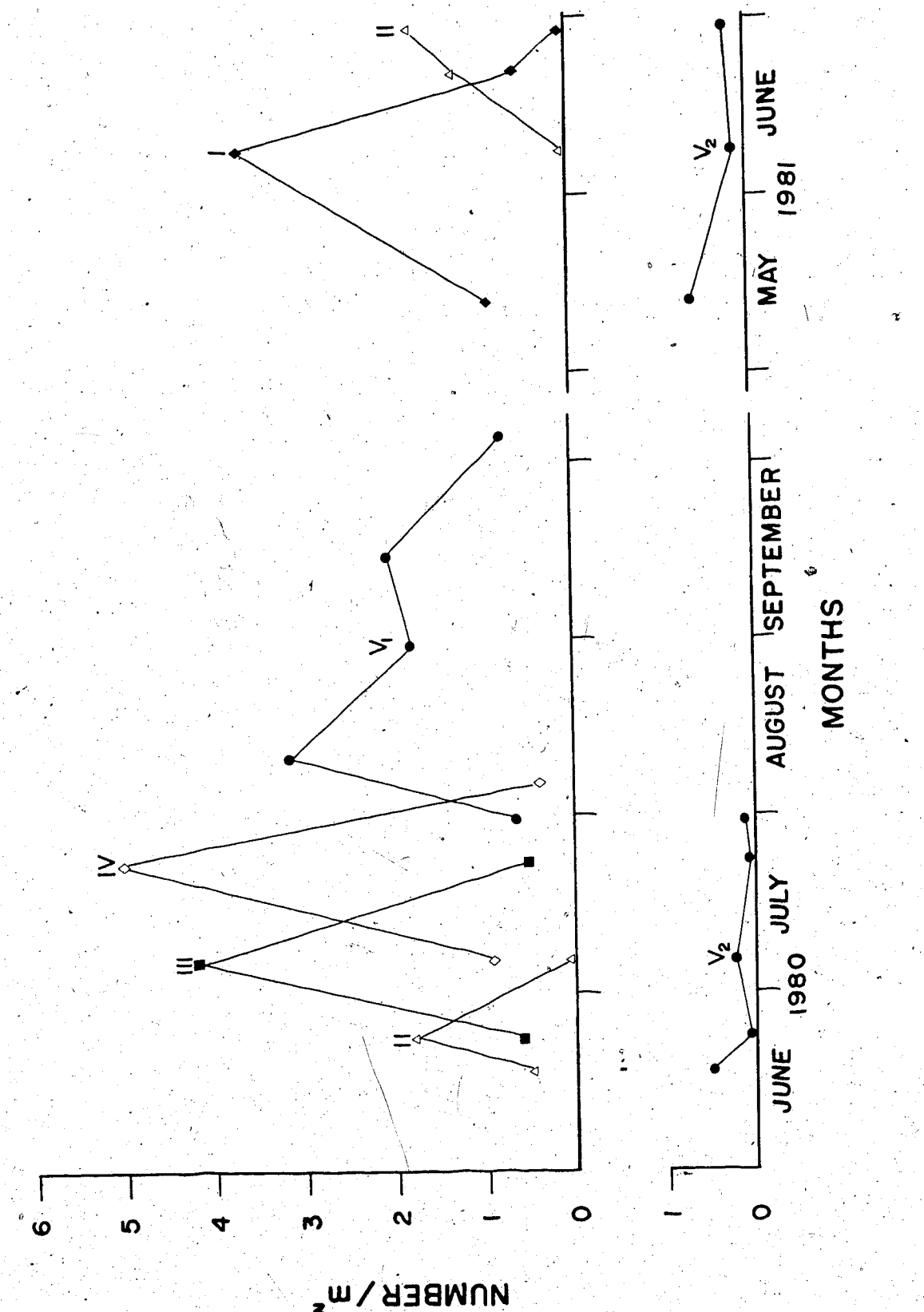

NUMBER / m²
0
1
2
3
4
5
6
II
III
IV
V1
V2
JUNE
1980
JULY
AUGUST
SEPTEMBER
MAY
1981
JUNE
MONTHS

Figure 5. Instar-specific mean dry weight (mg) of Dicosmoecus atripes larvae in Dyson Creek, Alberta. Values between instar mean weights indicate weight increase or decrease(-) in mg between instars. Values below instar numbers indicate number of animals weighed. (Range of standard error of mean dry weight was 0.03-0.10) See text for explanation of V_1-V_{22}.

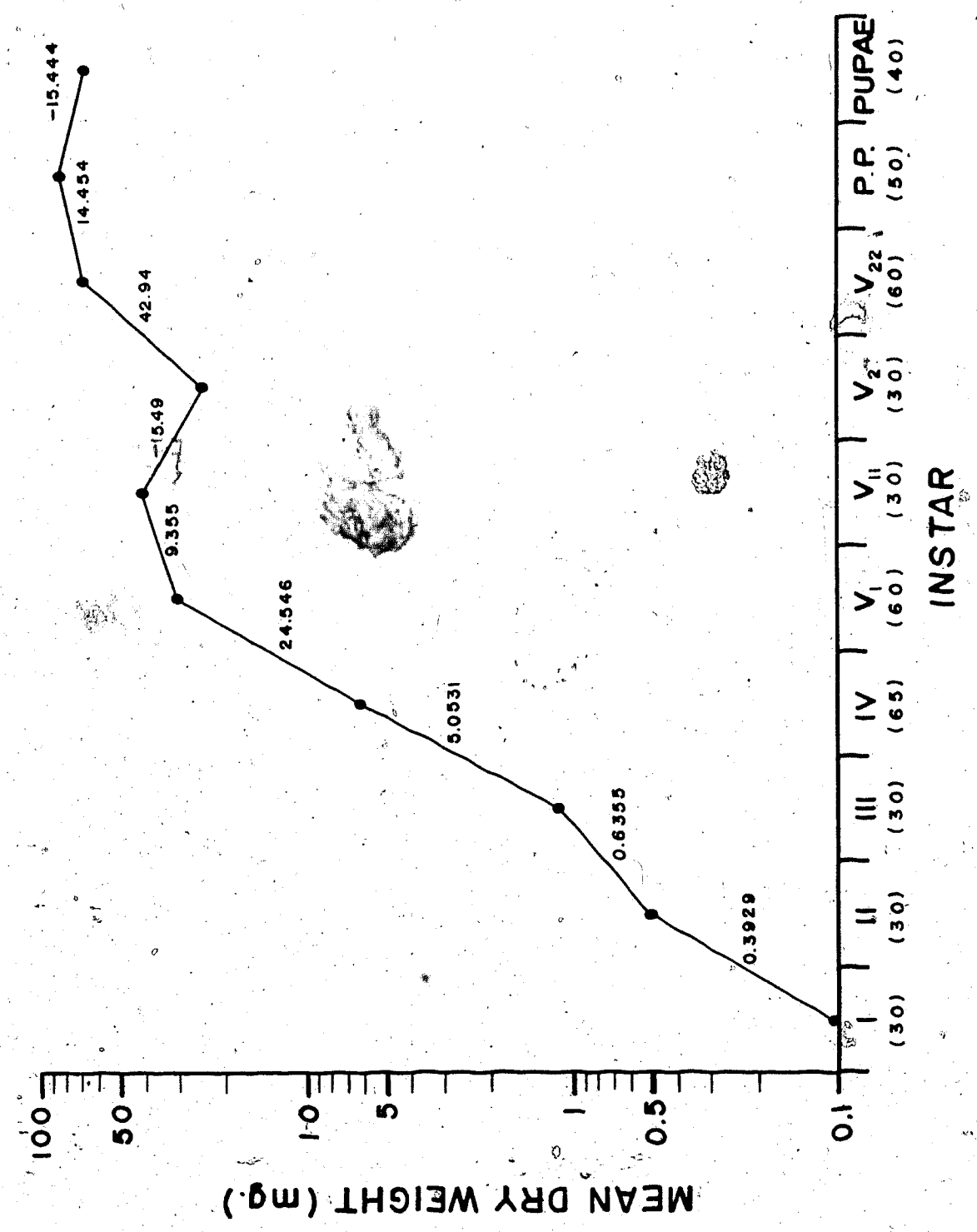
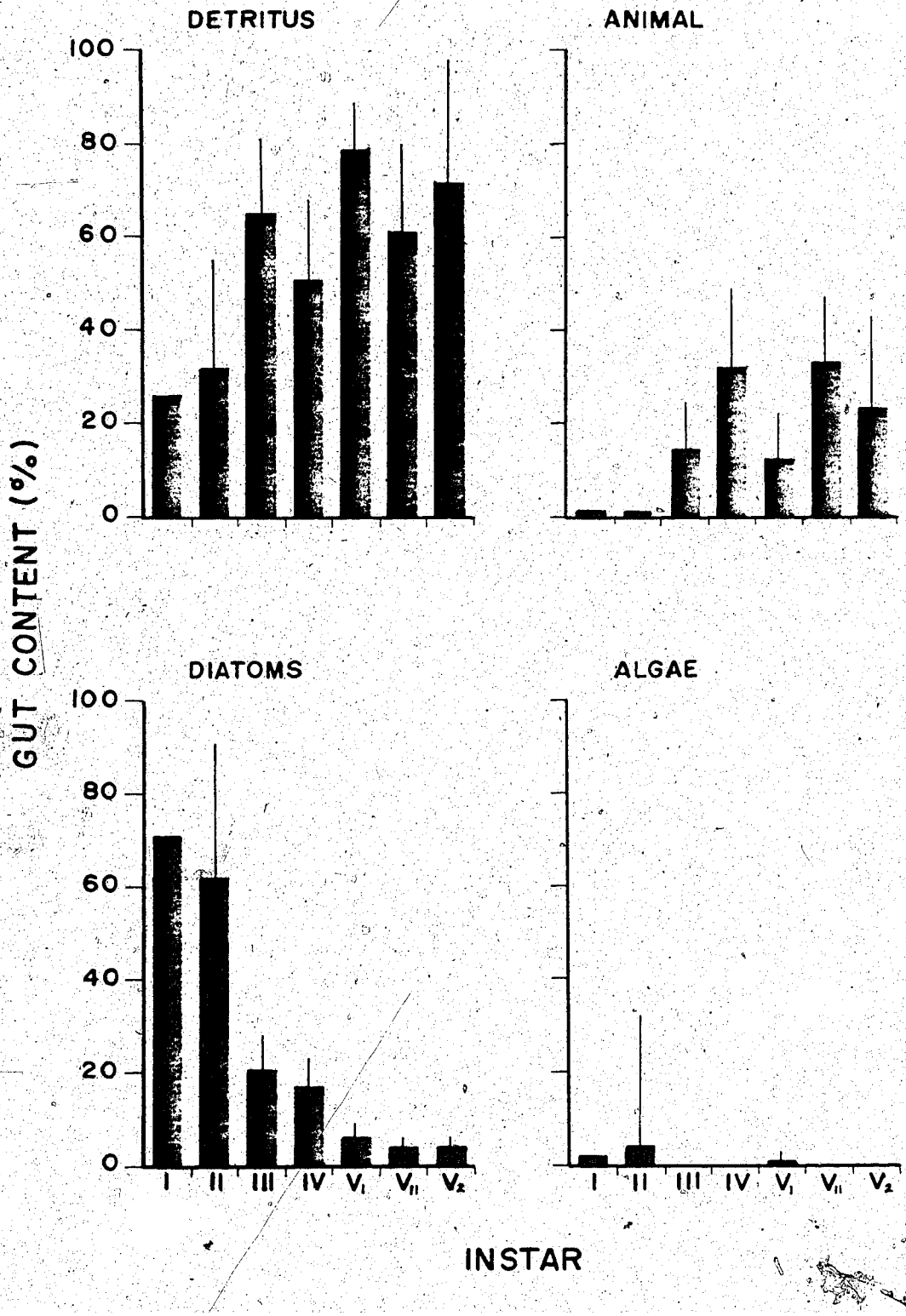

MEAN DRY WEIGHT (mg.)
100
50
10
5
1
0.5
0.1
0.3929
0.6355
5.0531
24.546
9.355
15.49
42.94
14.454
15.444
I (30)
II (30)
III (30)
IV (65)
V_I (60)
V_II (30)
V_2 (30)
V_22 (60)
P.P. (50)
PUPAE (40)
INSTAR

Figure 6. Changes in the percent composition of detritus, animal, diatom, and other algal components in the gut contents of Dicosmoecus atripes larvae of the five instars. Vertical bars are standard error (no standard error could be calculated for instar I).


DETRITUS
ANIMAL
DIATOMS
ALGAE
GUT CONTENT (%)
100
80
60
40
20
0
I
II
III
IV
V I
V II
V 2
INSTAR

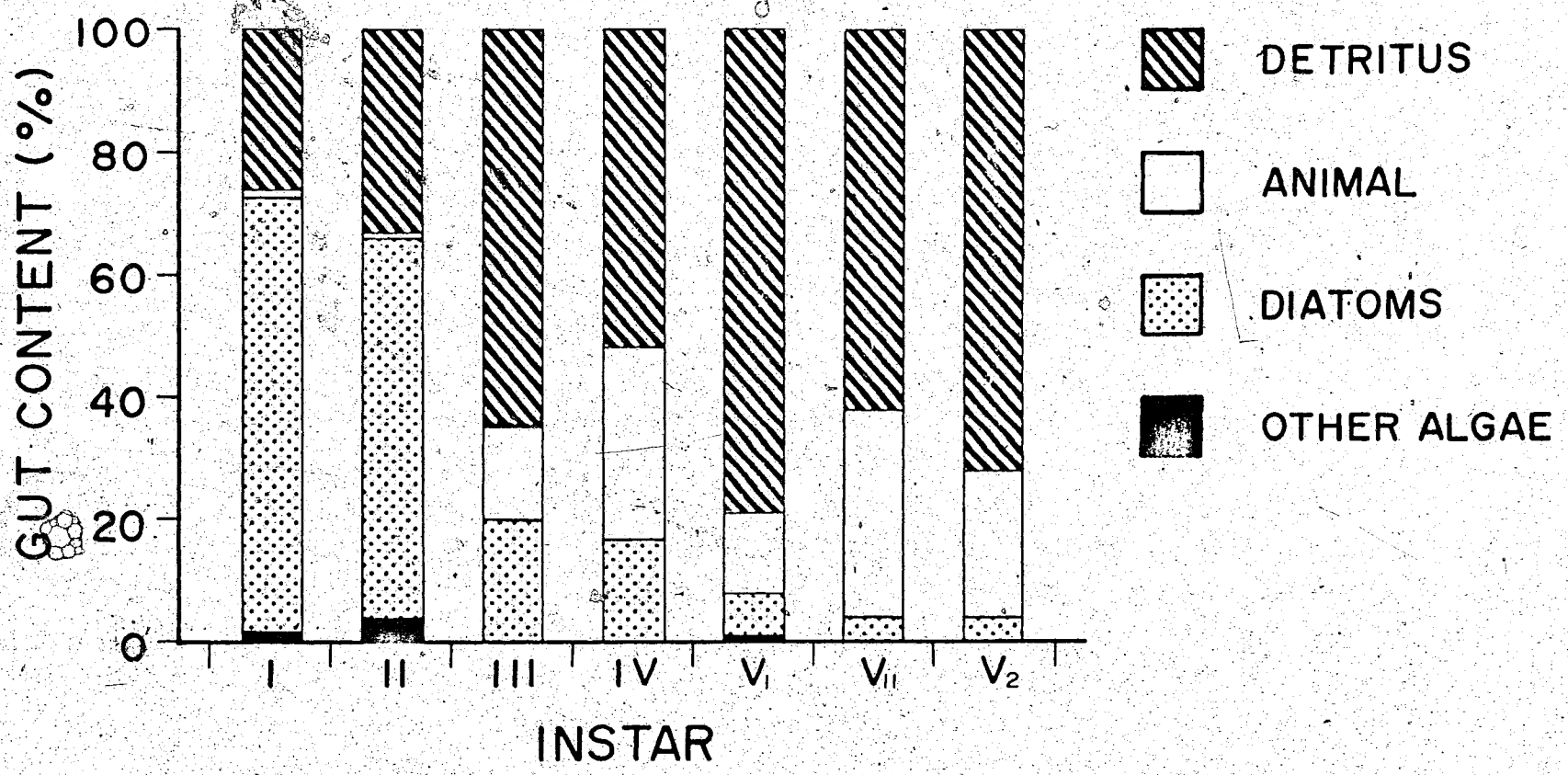
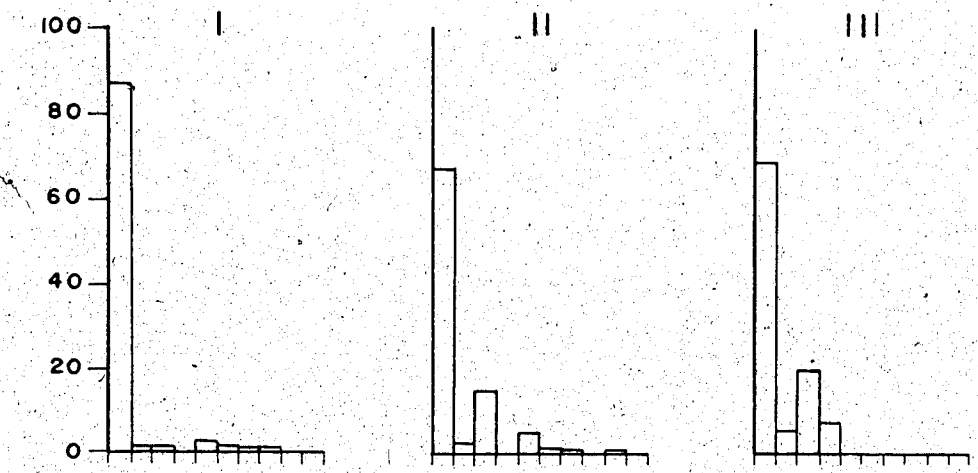
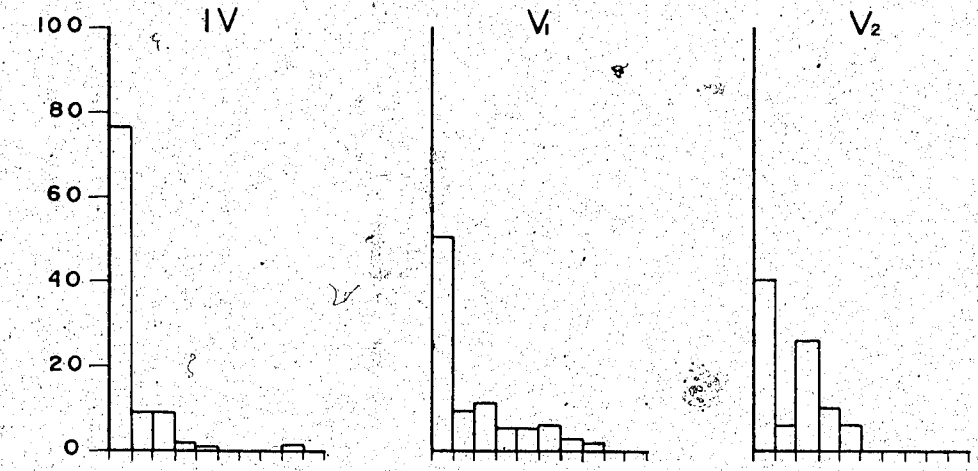


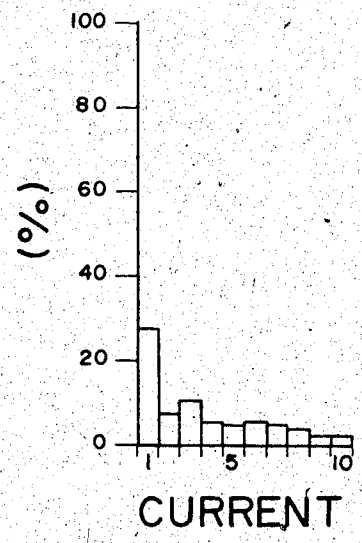
Figure 7. Percent composition of food material in guts of Dicosmoecus atripes larvae by instar (I-V). Each bar represents the combined analysis of 10 guts/instar.

Figure 8. A: The relative proportion each current category (1-10) comprised of the total number of samples taken. B: The distribution of Dicosmoecus atripes larvae (instars I-V) with respect to current velocity. Data are expressed as a relative proportion with respect to each current category of all the larvae collected for each instar. For graphical analysis current velocities were categorized into 0.05 m/sec increments (1=0.00-0.05, 2=0.05-0.10, 3=0.10-0.15, 4=0.15-0.20, ... 10=0.50 and greater m/sec).


100
80
60
40
20
0
I
II
III


100
80
60
40
20
0
IV
V1
V2

B


100
80
60
40
20
0
(%)
1
5
10
CURRENT

A

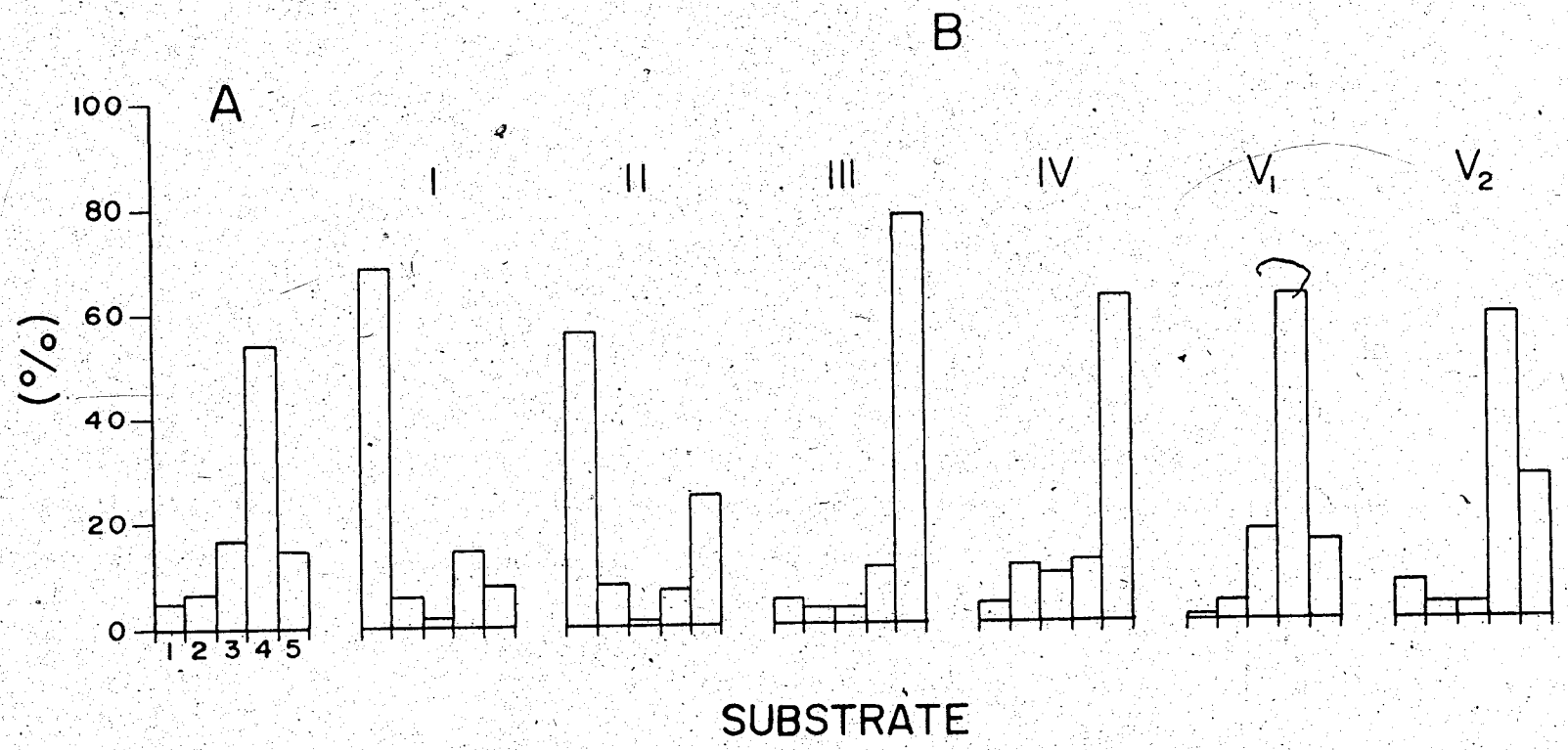


Figure 9. A: The relative proportion each substrate category (1-5) comprised of the total number of samples taken. B: The distribution of Dicosmoecus atripes larvae (instars I-V) with respect to substrate type. Data are expressed as a relative proportion with respect to each substrate category of all the larvae collected for each instar. Substrate was categorized (1-5) by size (after Cummins, 1962); 1=sand, 2=gravel, 3=pebble, 4=cobble, 5=bedrock.

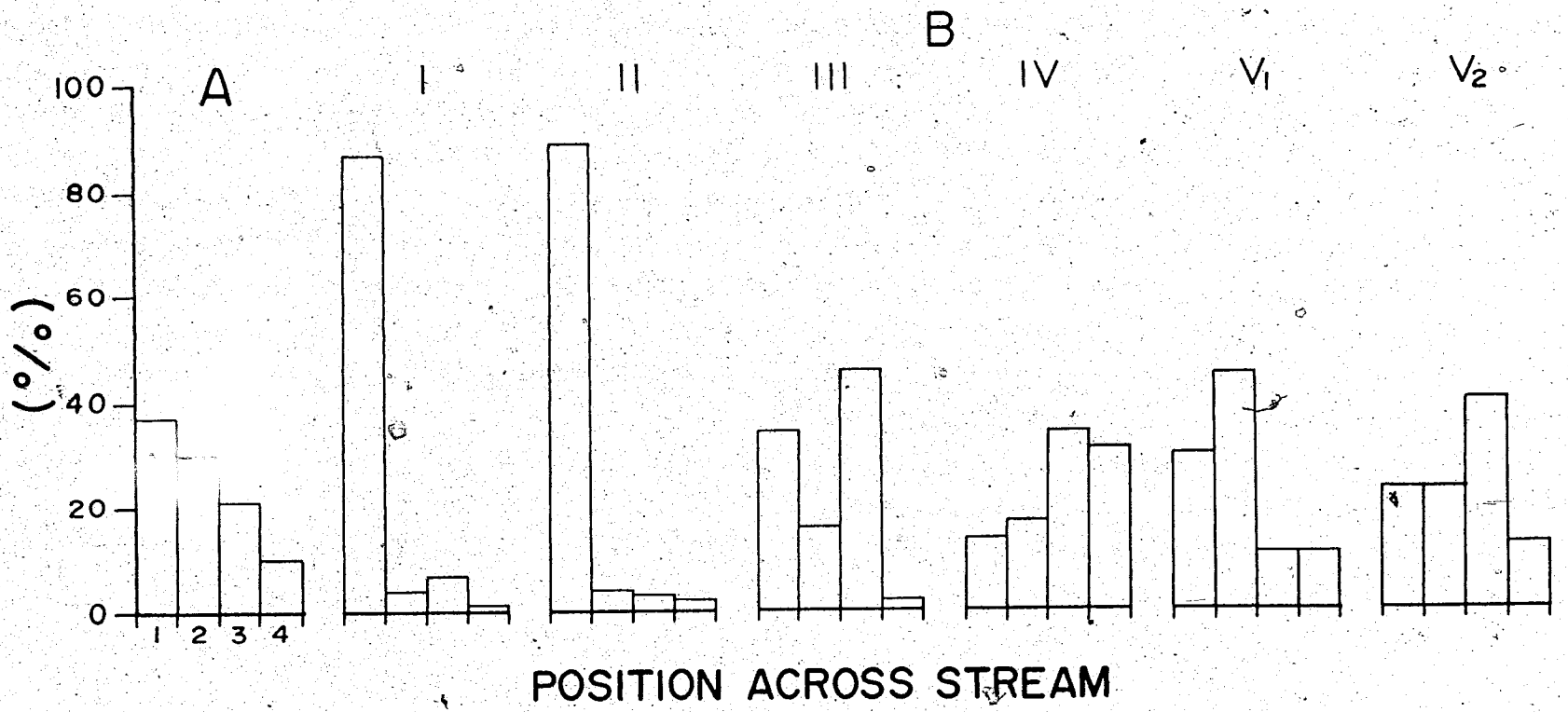
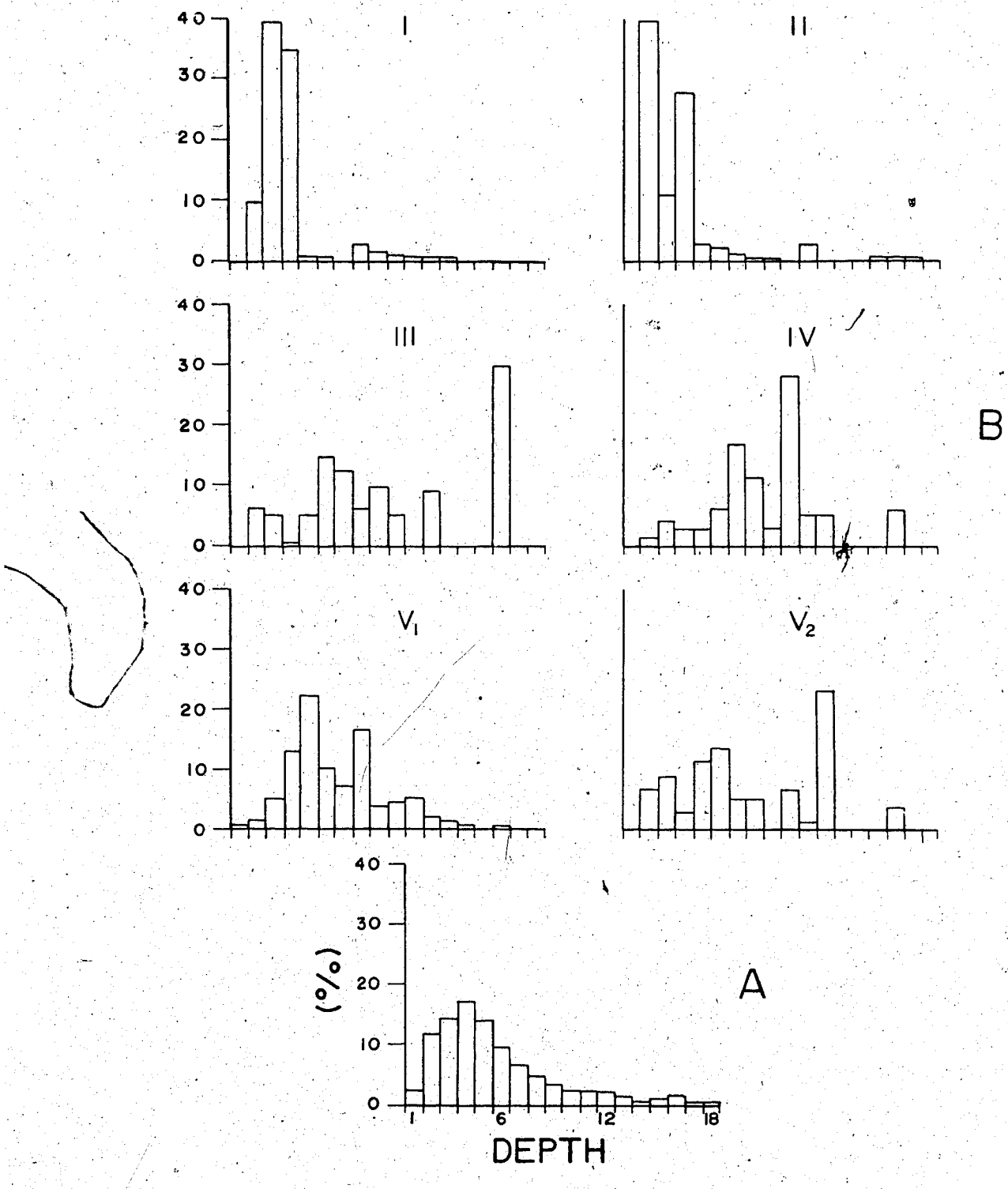


Figure 10. A: The relative proportion each 'position across stream' category (1-4) comprised of the total number of samples taken. B: The distribution of Dicosmoecus atripes larvae (instars I-V) with respect to the position across the stream where they were collected. Data are expressed as a relative proportion with respect to each 'position across stream' category of all the larvae collected for each instar. (1=stream margin, 2=2 m from shore, 3=3 m from shore and 4=midstream (i.e. greater then 3 m from shore)).

Figure 11. A: The relative proportion each water depth category (1-18) comprised of the total number of samples taken. B: The distribution of Dicosmoecus atripes larvae (instars I-V) with respect to water depth. Data are expressed as a relative proportion with respect to each water depth category of all the larvae collected for each instar. For graphical analysis water depth measurments were categorized into 5 cm increments (1=0-5, 2=5-10, 3=10-15, 4=15-20, ... 18=85-90 cm or greater).


I
II
III
IV
V1
V2
B
A
(%)
DEPTH
0
10
20
30
40
1
6
12
18

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III. Formation of aggregations by overwintering fifth instar *Dicosmoecus atripes* larvae (Limnephilidae:Trichoptera): an experimental analysis.

Abstract

Laboratory experiments were conducted to examine the formation of overwintering aggregations by fifth instar *Dicosmoecus atripes* larvae from a population in Dyson Creek, Alberta.

Larvae formed aggregations in the absence of environmental variations (e.g. current, substrate, etc.), that could function in bringing larvae together to a 'suitable' site of attachment in the field. In selecting an attachment site, larvae selected substrates with attached conspecifics already present over substrates without attached conspecifics. Given the choice between an attachment site with empty conspecific larval cases attached or glass shell-vials similarly attached, *D. atripes* larvae chose the site with conspecific larval cases. It appears that *D. atripes* larvae are capable of tactile or visual recognition of conspecifics, and use their presence as cues in attachment site selection.

There was no experimental evidence of chemical cues between larvae in aggregation formation.

Introduction

The formation of pupal aggregations is a common phenomenon among larval caddisflies (G.B. Wiggins, pers. comm.); however, few studies have looked at factors involved in their formation. An aggregation of animals may result from individuals responding to one another in a gregarious manner, or by individuals reacting in a similar fashion to some set of environmental factors thereby inadvertently coming together. The results of several studies (Scott, 1958; Campbell and Meadows, 1972; Otto, 1976; Otto and Svensson, 1981) indicate that aggregation formation in caddisfly larvae is not strictly the result of habitat heterogeneity, which brings animals together at a 'suitable' attachment site, but apparently has a gregarious component as well.

In the field, fifth instar *Dicosmoecus atripes* (Hagen) larvae form aggregations of inactive larvae on the underside of cobbles not only when they pupate but also when they overwinter (Chapter 1). A series of laboratory experiments were designed to determine what factors are involved in the formation of these overwintering aggregations. Aggregation in the absence of environmental heterogeneity and the effect of conspecifics on attachment site selection were examined to determine whether aggregation was in response to abiotic factors or the presence of conspecifics.

Methods

All experiments were conducted in an environmental chamber under simulated winter conditions. Water temperature was maintained at 0.5-1°C, and a light to dark regime of 8:16 hrs was used.

Fifth instar *D. atripes* larvae were collected from overwintering aggregations in Dyson Creek, Alberta (50° 37' N, 114° 39.2' W) (site previously described in Chapter 1). In the laboratory, larvae were kept in the environmental chamber at all times. Larvae, when not being used in an experiment, were held in large coolers with cobbles provided for attachment. No larva was used in more than one experiment. After use, larvae were eventually returned to Dyson Creek.

Experiments were conducted in clear plastic tanks (29x18x13 cm), and a plastic wading pool (1.5 m diam., 31 cm deep). Larvae were always introduced simultaneously into the centre of these containers. In all experiments, ceramic tiles (19.5x9.2x1 cm, -International Brick and Tile Ltd.) were provided as substrates for attachment. A preliminary experiment indicated that *D. atripes* larvae would attach to these tiles. It was assumed that all tiles were identical. Tiles were scrubbed and soaked (24 hrs) between experiments to eliminate any possible conditioning effect produced by attaching larvae.

Methods specific to each experiment are outlined with the experiment in question.

Aggregation in the absence of environmental heterogeneity

When first discovered in the field, I thought that aggregations of overwintering fifth instar *D. atripes* larvae were a result of individual larvae choosing a common site for overwintering based on some set of abiotic factors. If this was the situation, in the absence of any abiotic cues (e.g. current, depth, etc.), and given a number of identical substrates for attachment to choose from, one would expect a random distribution of larvae to result.

Experiment 1 -- Two tiles were placed in each of 10 tanks (Fig. 1). Fifteen larvae were introduced into each tank and allowed to attach. The resulting distribution of attached larvae was tested against a predicted random distribution using the Binomial test ($P=0.5$). The experiment was run twice.

In both runs the distribution of attached larvae was significantly different from the predicted random (50/50) distribution on the two tiles ($P<0.005$) (Table 1). A Wilcoxon matched-pairs signed-ranks test was used to check for any inherent gradient in the environmental chamber, which might have affected the choice of tile and resulted in aggregation. In both runs the results were not significant ($P>0.1$). Therefore, no gradient was apparent and the null-hypothesis of no difference between the tiles presented for attachment was not rejected.

Experiment 2 -- To simulate the field situation more closly (i.e. area and number of available substrates), eight tiles were placed into the pool (Fig. 2). Forty larvae were introduced into the pool and allowed to attach. The resulting distribution of larvae was tested against a predicted uniform distribution using the Chi-square goodness of fit test. The experiment was run twice.

In both runs the distribution of attached larvae was significantly different from the predicted uniform distribution of five larvae per tile ($P<0.005$) (Table 2).

The results of these experiments indicate that in the absence of environmental heterogeneity overwintering fifth instar *D. atripes* larvae still form aggregations. This does not mean that an abiotic component is not important in the field, but the implication is that a biotic component is also influential in the formation of these aggregations.

Effects of conspecifics on aggregation

Since overwintering fifth instar *D. atripes* larvae aggregate even under homogeneous environmental conditions, the role of conspecifics in aggregation formation becomes a pertinent question.

The presence of conspecifics as cues in selecting a habitat has been demonstrated for several groups of animals (Scott, 1958; Otto, 1976; Kiester, 1979; Simser and Coppel, 1980; Simon, Karban and Lloyd, 1981). Therefore, the effect of previously attached larvae on attachment site selection

by conspecific was examined.

Two tiles and five larvae were placed into each of 10 tanks. These larvae were marked, by slipping a ring of rubber tubing over their cases, and allowed access to only one of the tiles in each tank. The position of the accessible tile was altered between tanks (i.e left or right side). Once all five larvae had attached in each tank, both tiles were made available for attachment, and 10 other larvae were introduced into each tank and allowed to attach.

The null-hypothesis that the presence of previously attached *D. atripes* larvae has no effect on choice of attachment site by conspecifics was tested using a Wilcoxon matched-pairs signed-ranks test (Wilcoxon M-P S-R test) by comparing the distribution of attached larvae to a predicted random distribution.

Using a one-tailed test to determine whether the empty tile was preferred, the results (Table 3) were significant ($P<0.02$). Therefore it appears that the previously colonized tile was preferred as a site for attachment. In no tank did the original five larvae detach from the tile they initially attached to.

These results indicate that the presence of conspecifics has a positive effect on the choice of attachment site by other larvae. The implication is that larvae may recognize conspecifics already attached to a substrate, and that this is influential in their choice of an attachment site.

Recognition of conspecifics

In selecting substrates already occupied by conspecifics when attaching, *D. atripes* larvae may be able to recognize the presence of other larvae on these substrates. Two possible means of recognition are tactile/visual, chemical or both.

Tactile/visual recognition of conspecifics

When *D. atripes* larvae have attached to overwinter the only tactile/visual cue indicating their presence on a substrate to other larvae is their case. Since *D. atripes* larvae select substrates with conspecifics already attached, what effect would the presence of empty conspecific larval cases attached to a substrate have on attachment site selection by other *D. atripes* larvae?

Empty fifth instar *D. atripes* larval cases, taken from overwintering larvae in the field, were boiled and oven dried (24 hrs at 60°C) in an attempt to eliminate any possible chemical cues in the case materials themselves. The use of empty larval cases precluded the presence of any chemical cues produced by the larvae themselves. Five cases were attached to each tile (Fig. 3), using Silastic 732RTV adhesive/sealant (Dow Corning). The sealant was allowed 3 days in the air and 2 days of soaking in water to cure before being used in the following experiments.

Experiment 1 -- One bare tile and one tile with empty cases attached(marked tile) were placed into each of 10

tanks. The position of the marked tile was altered between tanks. Ten larvae were introduced into each tank and allowed to attach.

The null-hypothesis that the presence of empty *D. atripes* larval cases has no effect on the choice of attachment site was tested using a Wilcoxon M-P S-R test by comparing the distribution of attached larvae to a predicted random distribution.

Experiment 2 -- Identical to experiment 1, except only one larva was introduced into each tank. The purpose was to check for possible group effects in site selection.

The results of experiments 1 (Table 4) and 2 were significant ($P<0.005$, 1-tailed). In experiment 2, all larvae attached to the marked tile. Therefore, it appears that the marked tile was preferred as a site of attachment.

In these experiments *D. atripes* larvae, in groups and individually, reacted to the presence of empty conspecific larval cases attached to a substrate by selecting that substrate for attachment. Since objects similar to *D. atripes* larval cases are not found attached to or associated with substrates selected for attachment in the field, the implication is one of tactile/visual recognition of conspecific cases when selecting an attachment site. But, is it actually conspecific recognition, or would the presence of similarily attached objects make a substrate preferred for attachment?

Tactile/visual discrimination

Empty glass shell-vials (9x30 mm, 0.25 dram) were attached to tiles, five per tile, in the same manner as the empty cases in the previous experiment.

Experiment 1 -- One bare tile and one with shell-vials attached(marked tile) were placed into each of five tanks. The position of the marked tile was altered between tanks. Ten larvae were introduced into each tank and allowed to attach.

The null-hypothesis that the presence of shell-vials has no effect on the choice of attachment site was tested using a Wilcoxon M-P S-R test by comparing the distribution of attached larvae to a predicted random distribution.

The results (Table 5 A) were not significant ($P>0.05$, 2-tailed). Therefore, the null-hypothesis cannot be rejected and the presence of shell-vials on a tile does not seem to have any effect on attachment site selection by *D. atripes* larvae.

Experiment 2 -- Two tiles, one with shell-vials attached and one with empty *D. atripes* larval cases attached, were placed into each of eight tanks. Sixteen larvae were introduced into each tank and allowed to attach.

The null-hypothesis that tiles with shell-vials attached were preferred for attachment was tested using a Wilcoxon M-P S-R test by comparing the distribution of attached larvae.

Results (Table 5 B) were significant ($P<0.004$, 1-tailed). Therefore, it appears that the tile with empty *D. atripes* larval cases was preferred as a site of attachment over the tile with attached shell-vials.

These experiments indicate that *D. atripes* larvae differentiate between attached glass shell-vials and empty larval cases, and only use the presence of larval cases in attachment site selection. Although not conclusive, these results lend support to the contention that *D. atripes* larvae can recognize conspecifics by tactile/visual cues. Therefore, tactile/visual recognition of conspecifics appears to be involved in selecting a site for attachment, but chemical cues may also be used.

Chemical recognition of conspecifics

The use of chemical communication in terrestrial insects is well known (Borror et al., 1976). Although most commonly reported as a means of mate location (Chapman, 1975), "assembling scents", which also produce aggregations of individuals, have been reported (Simser and Coppel, 1980). Recently chemical messages have been suggested to influence predator/prey interactions among larval lotic insects (Peckarsky, 1980; Peckarsky and Dodson, 1980). Therefore some form of chemical cue might also function in the formation of *D. atripes* larval aggregations. If this were true one would expect this chemical to be released into the water by attaching or attached larvae. Other larvae

would then respond to this chemical and cue in on attaching conspecifics.

A chemical gradient experiment was set-up with a central experimental tube and a tank at both ends (Fig. 4). One tank contained 15 *D. atripes* larvae which had attached to a tile, the other a bare tile. The flow of water from both tanks into the experimental tube was equal. The experiment was run five times. The tube was thoroughly flushed, and the tanks and position of the tank with larvae in it (i.e. left or right end of the tube) changed after each run of the experiment.

Individual *D. atripes* larvae were introduced into the centre of the tube and their position (whether the larva was in the left or right half of the tube) recorded at 5 minute intervals over a 60 minute observation period (i.e. 12 observations per larva). Timing started only after the larva began to move. If a larva was at the left end of the tube or moving left in the left half of the tube it was taken as indicating positive selection for that half of the tube, and a score of 1 was assigned to the left half of the tube. A score of 1/2 was assigned to the left half of the tube if a larva was moving right in the left half of the tube, because this was taken to imply a negative selection for the left half of the tube. Scoring for the right half of the tube differed only with respect to direction of movement. Score values were arbitrarily selected. Scores from all 12 observations were summed for the right and left halves of

the tube for each larva.

The null-hypothesis that equal time was spent in both halves of the tube was tested using a Wilcoxon M-P S-R test by comparing the directional distribution of the five larvae to a predicted random distribution.

The results (Table 6) were not significant ($P>0.05$, 2-tailed). Therefore, the null-hypothesis that equal time was spent in both halves of the tube cannot be rejected.

The implication of the above experiment is that no chemical is released by attaching or attached *D. atripes* larvae that might function as a cue for larvae in recognition of conspecifics and formation of aggregations.

Discussion

My experiments indicate a gregarious component in the formation of overwintering aggregations in fifth instar *D. atripes* larvae. Larvae 'prefer' to attach to substrates where conspecifics have already attached. Larvae also seem capable of tactile/visual recognition of conspecifics when selecting for an attachment site.

The formation of aggregations at pupation by larval *Potamophylax latipennis* (Trichoptera:Limnephilidae) was shown to occur in the absence of abiotic factors considered important in attachment (Campbell and Meadows, 1972). Scott (1958) demonstrated that *Potamophylax (Stenophylax)* spp. larvae chose to attach to substrates where other larvae had

already attached to pupate. Otto (1976) found that *Potamophylax cingulatus* larvae were attracted to the presence of empty larval cases from previous years in selecting a pupation site, and that the presence of several newly settled larvae made that substrate highly attractive to other larvae still seeking a site for pupation. Although not tested, I would predict similar results with fifth instar *D. atripes* larvae when forming pupal aggregations, based on the similarities of my results and those reported above.

Responses to patchiness in suitable habitat (Lamberti and Resh, 1979; Simser and Coppel, 1980), localized food abundance (Hildrew and Townsend, 1980; Sloan and Aldridge, 1981) or anti-predator/parasite behavior (Hamilton, 1971; Clark and Robertson, 1979; Heinrich and Vogt, 1980; Otto and Svensson, 1981) may all result in the formation of aggregations of animals.

Aggregation as a result of localized food abundance can be dismissed as a factor in both pupal and overwintering aggregations in *D. atripes* larvae. Feeding stops during pupation, and fifth instar *D. atripes* larvae do not appear to feed during the winter (person. observ.).

Patchiness in suitable habitat might play a role in selecting a site for pupation, overwintering, or both in the field. But patchiness by itself fails to explain the behavioral aspects of aggregation formation demonstrated in my study. Likewise, if a similar gregarious component exists

in the formation of pupal, overwintering, or both aggregations in other caddisflies, similar responses to environmental heterogeneity by individual animals would not suffice as an explanation for these aggregations.

Pupal aggregation as a means of anti-parasite behavior has been inferred in a population of *Potamophylax cingulatus* larvae (Otto and Svensson, 1981), which also show "gregarious behavior" (Otto, 1976). Predator/parasite pressure might influence the development of gregarious behavior by resulting in the creation of the "selfish herd" (Hamilton, 1971) effect, wherein, animals attempt to reduce their chances of being attacked by a predator or parasite by seeking cover in a group.

During the winter, I found no predators in Dyson Creek large enough to remove attached *D. atripes* larvae. Also, of the 1,100 overwintering fifth instar *D. atripes* larvae collected for my study, none showed any sign of predation or parasitism within their cases. Predator/parasite pressure on pupating *D. atripes* larvae was not thoroughly examined for in the Dyson Creek population. Thirty pupae and 60 prepupae were collected, and none showed any external sign of predation or parasitism within the case. However, if predators capable of detaching pupating larvae were present during the summer, they could potentially serve as pressure selecting gregarious behavior during pupation.

Aggregations of *D. atripes* pupae have been recorded by other workers as well (Wiggins and Richardson, 1982;

B. Wisseman, pers. comm.). If aggregation during an inactive stage (such as pupation) is advantageous, in areas where *D. atripes* populations have a 2-year life cycle and overwinter as inactive larvae, gregarious behavior during this period of inactivity may be behaviorally equivalent to that observed during pupation.

Acknowledgements

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Table 1. The distribution of attached Dicosmoecus atripes larvae given a choice of two identical bare tiles on which to attach (n=15 larvae per tank) under homogeneous environmental conditions. The experiment was run twice.
(Left and right refer to the side of the tank the tile was on)

Tank	Left Tile	Right Tile
1	15	0
2	5	10
3	14	1
4	9	6
5	15	0
6	15	0
7	0	15
8	13	2
9	13	2
10	3	12
1	0	15
2	0	15
3	14	1
4	14	1
5	7	8
6	1	14
7	12	3
8	4	11
9	8	7
10	1	14

Table 2. The distribution of attached Dicosmoecus atripes larvae given a choice of eight identical bare tiles on which to attach (n=40 larvae per run) under homogeneous environmental conditions. The experiment was run twice.
(For identification, tiles were assigned numbers arbitrarily)

	Tile 1	Tile 2	Tile 3	Tile 4	Tile 5	Tile 6	Tile 7	Tile 8
(run 1)	1	19	1	0	2	0	17	0
(run 2)	2	0	0	32	0	4	0	2

Table 3. The distribution of attached Dicosmoecus atripes larvae given a choice of a tile with conspecifics already attached (marked tile) or a bare tile on which to attach (n=10 larvae per tank).

Tank	Marked Tile	Bare Tile
1	9	1
2	9	1
3	4	6
4	9	1
5	10	0
6	10	0
7	2	8
8	7	3
9	5	5
10	10	0

Table 4. The distribution of attached Dasybranchus atripes larvae given a choice of a tile with empty conspecific larval cases attached (marked tile) or a bare tile on which to attach (n=10 larvae per tank).

Tank	Marked Tile	Empty Tile
1	9	1
2	10	0
3	10	0
4	10	0
5	9	1
6	7	3
7	7	3
8	9	1
9	10	0
10	9	1

Table 5. The distribution of attached Dicosmoecus atripes larvae (A) given a choice of a tile with empty glass shell vials attached (marked tile) or a bare tile on which to attach (n=10 larvae per tank).
(B) given a choice of a tile with empty glass shell vials attached (vile tile) or a tile with empty conspecific larval cases attached (case tile) on which to attach (n=16 larvae per tank).

(A)

Tank	Marked Tile	Empty Tile
1	0	10
2	10	0
3	9	1
4	3	7
5	0	10

(B)

Tank	Vile Tile	Case Tile
1	2	14
2	1	15
3	5	11
4	2	14
5	3	13
6	1	15
7	1	15
8	5	11

Table 6. The distribution of time spent in the left or right half of the chemical gradient tube by Dicosmoecus atripes larvae (n=1 larva per run). Results are the summed totals of scores (see text for scoring) for the left and right halves of the tube over 12 observations per run. (*- indicates end of tube with tank with attached D. atripes larvae present).

Run	Left	Right
1	6.5*	5.5
2	5	7 *
3	6 *	5
4	6	6 *
5	6 *	6

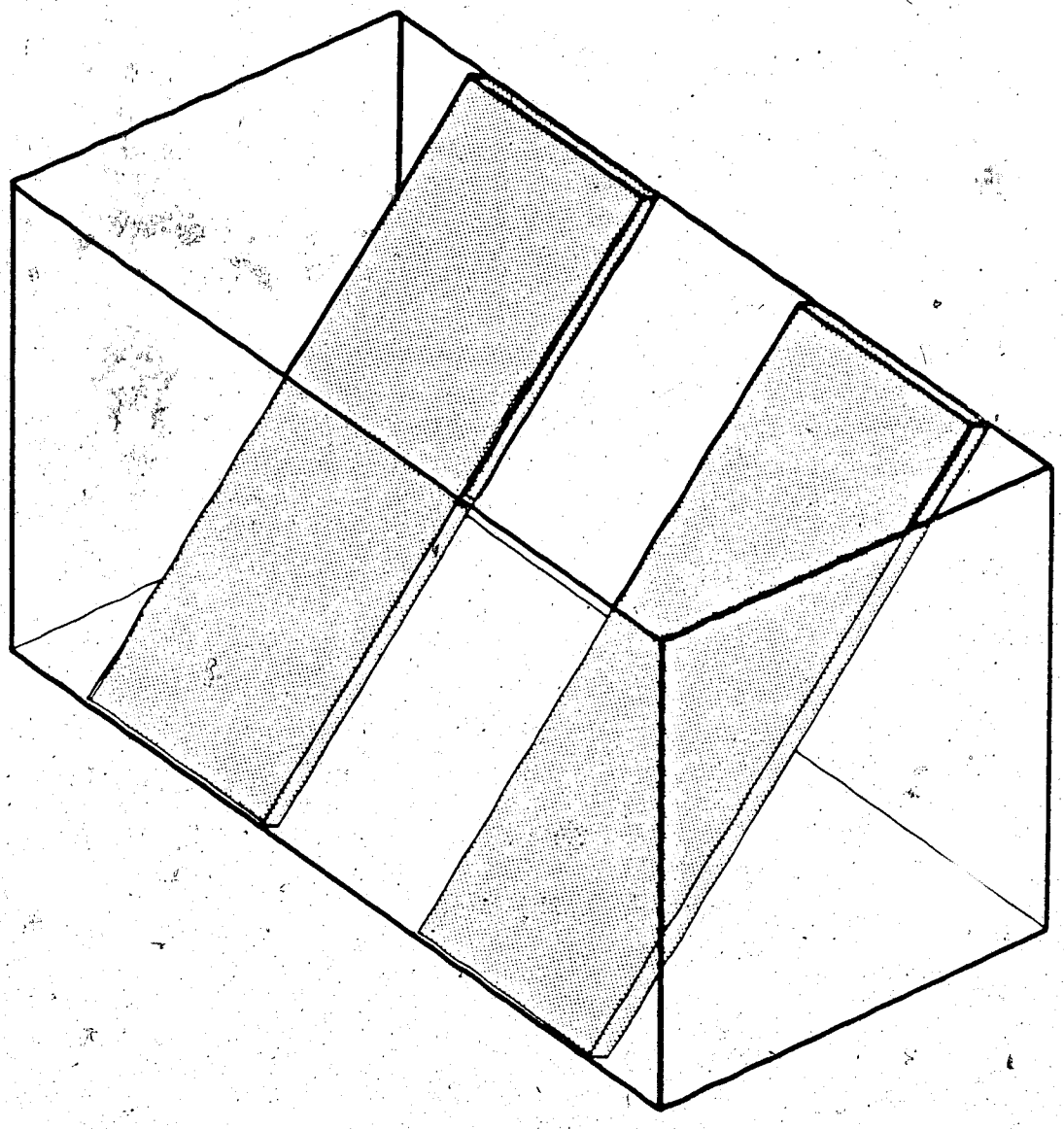


Figure 1. Experimental tank with two ceramic tiles for attachment.

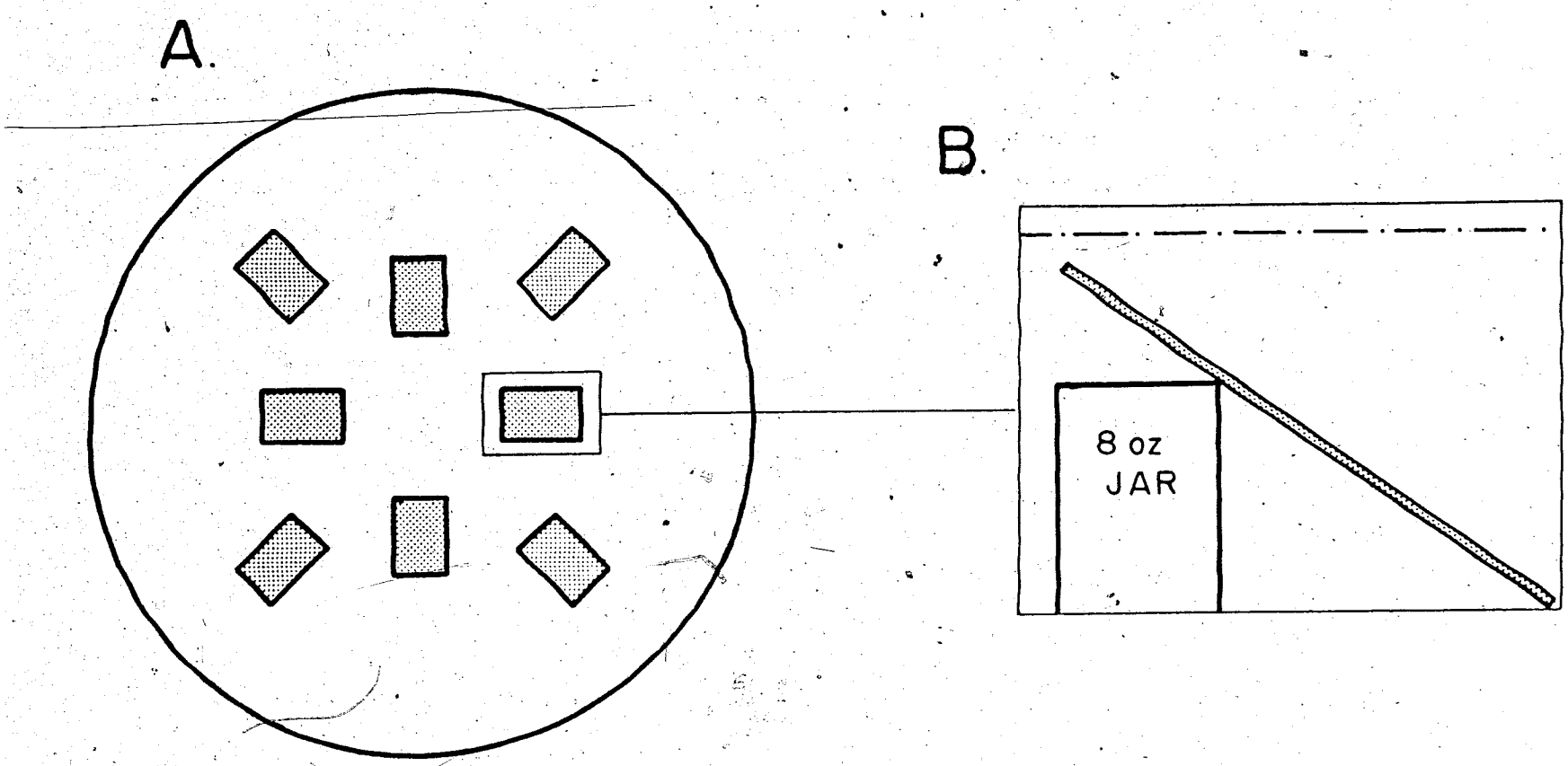
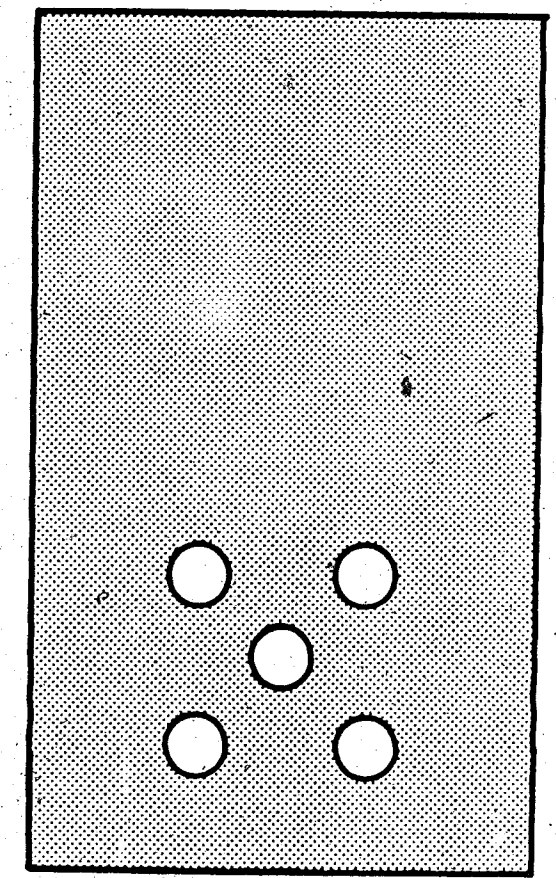
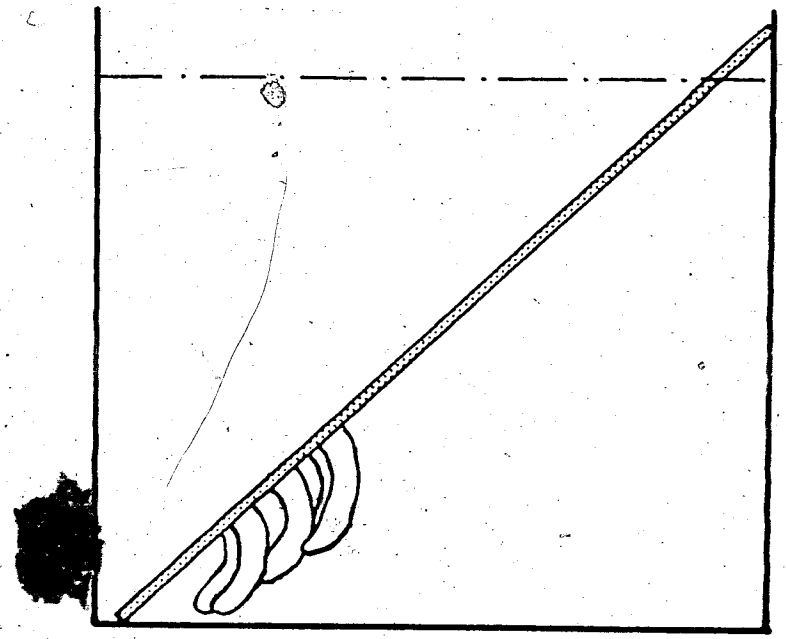


Figure 2. A: Experimental pool with eight ceramic tiles for attachment (top view-looking down into pool). B: Side view of ceramic tile, to demonstrate how tiles were raised off the substrate to provide an attachment site (-·-·-·-=water level).



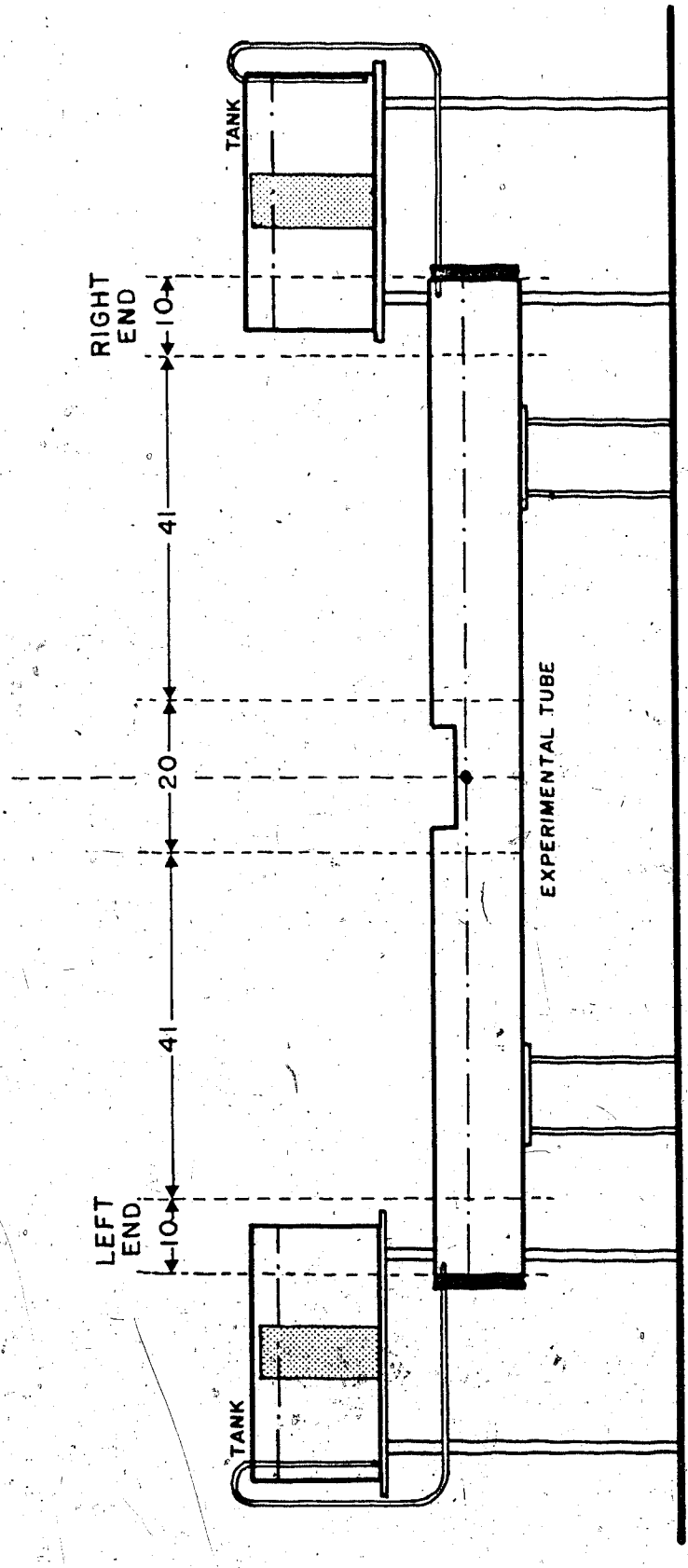
A.



B.

Figure 3. A: Ceramic tile with five empty Dicosmoecus atripes larval cases (O) attached. The pattern of attached larval cases was identical on all tiles. B: Side view into tank showing how tiles with empty D. atripes larval cases attached were positioned (-•-•-•-=water level).

Figure 4. Chemical gradient experimental set-up. Numbers indicate length and position of the tube considered left and right ends (10 cm), left and right halves (41 cm), and the central region (20 cm) (-•-•-•-=water level). Animals were introduced into the square opening in the centre of the tube. To permit flow through the tube, a drain hole for overflow was provided in the central region of the tube. The tanks at the left and right end of the tube each had a ceramic tile and water. For each run of the experiment only one tank had attached *Dicosmoecus atripes* larvae on the tile (n=15).


TANK
RIGHT END
10
41
20
41
LEFT END
10
TANK
EXPERIMENTAL TUBE

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IV. Discussion

Life Cycle

Temperature and food quality and quantity have been shown to be influential in determining voltinism of benthic invertebrates (Anderson and Cummins, 1979). The population of *Dicosmoecus atripes* in Dyson Creek, Alberta, has a 2-year life cycle, which appears primarily related to temperature. There is no growth in *D. atripes* larvae during winter (October-April). The first winter is spent as first instar larvae and the second as inactive fifth (final) instar larvae in aggregations attached to the underside of cobbles.

From the analysis of instar-specific diet, a switch from predominantly diatoms in first and second instar larvae to detritus in third, fourth and fifth instar larvae was noted. Diatoms identified in the gut content of first instar larvae collected in May should be present in similar quantity and quality throughout the winter (M. Hickman, person. comm.). Fifth instar *D. atripes* larvae have been identified as predator-shredders (Wiggins and Richardson, 1982), and, as such, the input of allochthonous material in the autumn should provide a substantial food source. Therefore, food availability would not appear to be the primary factor for overwintering in first and fifth instar larvae.

In Flynn Creek, Oregon, the *D. atripes* population has a 1-year life cycle, developing from egg to fifth instar larvae in 4 months, December to March (B. Wisseman, person.

comm.). The average temperature for Flynn Creek during this period is 8.3°C. *Dicosmoecus atripes* larvae in Dyson Creek develop from first instar to fifth instar in 4 months as well. But this occurs during summer (May-August), when average water temperature in Dyson Creek is comparable(9°C) to the average winter water temperature in Flynn Creek. During winter (October-April), average water temperature in Dyson Creek is 0.5°C, and *D. atripes* larvae do not seem to grow.

The implication is that winter water temperature in Dyson Creek is too low for growth in *D. atripes* larvae, and the relatively low water temperature during the summer does not allow completion of development in 1 year. Temperature therefore seems to be the primary factor in the observed 2-year life cycle in Dyson Creek.

A similar phenomenon exists between populations of *Dicosmoecus gilvipes* in Montana and California. The *D. gilvipes* population in Montana has a 2-year life cycle (Hauer and Stanford, 1982), while in California it is univoltine (Lamberti and Resh, 1979). I would predict that an analysis of these life cycles would show temperature to be the most important factor determining this observed voltinism. I would also predict that both a longitudinal and latitudinal zonation of these two life cycle patterns could be established for *D. atripes* and *D. gilvipes* populations.

Instar-specific Microdistribution

It is well known that the distribution of animals is affected both by biotic and abiotic factors, and that the effects these factors have may vary throughout the life cycle of an animal. However, in most studies on abiotic factors influencing distribution of benthic macro-invertebrates, age-specific patterns of microdistribution have not been examined.

In my study, *Dicosmoecus atripes* larvae exhibited instar-specific microhabitat selection. First and second instar larvae select shallow areas of fine substrate (i.e. sand) along the stream margin. Third instar larvae move out from the stream margins to occupy the entire stream channel, a characteristic retained by fourth and fifth instar larvae. Larvae in these later instars also select for deeper areas and coarse substrate (i.e. cobbles).

The shift in microhabitat during the third instar coincides with a shift in diet, from predominantly diatoms in first and second instar larvae to detritus in third, fourth and fifth instar larvae. This shift in microhabitat and diet by third instar larvae effectively moves these larvae into areas of the stream previously occupied by conspecific fifth instar larvae, as the latter become inactive prior to pupation. The absence of these age specific patterns in a univoltine population of *D. atripes* in Flynn Creek, Oregon (B. Wisseman, pers. comm.) where no overlap of generations occurs, suggests that the observed

patterns in the Dyson Creek population may reduce possible intraspecific competition.

It would be interesting to examine for similar age specific trends in other benthic macroinvertebrates where univoltine and bi- or even trivoltine populations are known to exist in separate localities. These data could reveal, and suggest possible mechanisms for avoiding intraspecific competition.

Aggregation

In Dyson Creek, fifth instar *D. atripes* larvae overwinter in aggregations of inactive larvae attached to the underside of cobbles. Field observations indicated that not all apparently suitable (e.g. size, shape, position and location) cobbles were being utilized as overwintering sites. Often, a number of apparently suitable cobbles would be found next to one another, but only one would have an aggregation of attached *D. atripes* larvae. Therefore, it was felt that these aggregations were a result of individual larvae cueing into a set of abiotic factors that made one particular cobble a preferred site of attachment.

In the laboratory, given a choice between a number of identical substrates in a homogeneous environment, *D. atripes* larvae still formed aggregations. A series of experiments showed that *D. atripes* larvae appear capable of tactile/visual recognition of conspecifics and choose to attach to substrates where conspecifics are already

attached. Based on similarities in results between my study and other studies dealing with pupation aggregation in other caddisfly larvae (Campbell and Meadows, 1972; Otto, 1976), I would predict a gregarious component in the formation of pupal aggregations in *D. atripes* larvae as well.

Fifth instar *D. atripes* larvae do not appear to feed during the winter. Therefore, localized food abundance would not seem an important factor in the formation of overwintering larval aggregations. Aggregation in response to patchiness in suitable habitat might be important in the field. However, this factor alone does not explain the behavioral component in aggregation formation by *D. atripes* larvae noted in my study.

Overwintering aggregation by *D. atripes* larvae as an anti-predator or anti-parasite behavior, while plausible, lacks support, because I was unable to identify any potential predator or parasite pressure during the winter in Dyson Creek. However, if such pressure exists during pupation, and aggregation during this period of inactivity is advantageous, aggregation while overwintering may simply be an extension of this behavioral response to a prolonged period of inactivity.

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