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GRADUATE COLLEGE

ECOLOGY OF <u>HELICOPSYCHE</u> BOREALIS (HAGEN) (TRICHOPTERA: HELICOPSYCHIDAE): LIFE HISTORY AND MICRODISTRIBUTION

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PREFACE

This dissertation is prepared as three chapters. Each chapter has been or will be submitted to a refereed journal. The first chapter has been accepted by <u>The American Midland Naturalist</u>. The second . chapter will be submitted to <u>Ecology</u>. The third chapter will be submitted to <u>Aquatic Insects</u>.

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LIFE HISTORY OF <u>HELICOPSYCHE</u> <u>BOREALIS</u> (HAGEN) (TRICHOPTERA: HELICOPSYCHIDAE) IN OKLAHOMA

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ABSTRACT

The life history of <u>Helicopsyche borealis</u> was compared for a 13-month period in two Oklahoma streams that have different thermal regimes. Densities of <u>H</u>. <u>borealis</u> were usually higher in the thermally constant stream. The species was multivoltine with overlapping generations in the thermally constant stream and univoltine in the fluctuating stream.

INTRODUCTION

Larvae of <u>Helicopsyche</u> (Trichoptera; Helicopsychidae) are unusual in that their sand-grain cases superficially resemble snail shells. In fact, the genus was first described as a snail based on the shape of the case alone (Lea 1834). There are five species of <u>Helicopsyche</u> in North America north of Mexico (Wiggins 1977, Denning and Blickle 1979). <u>Helicopsyche borealis</u> (Hagen) is the most common species occurring in clear running water, springs and the littoral zone of lakes and has been found in thermal springs exceeding 34°C (Wiggins 1977). Mackay and Wiggins (1979) reported the occurrence of <u>H. borealis</u> in streams receiving domestic sewage and this species also tolerates petroleum related pollution (Bugbee and Walters 1973).

The life history of <u>H</u>. <u>borealis</u> has only been partially described. Ross (1944) and Williams and Hynes (1974) reported continual emergence of adults from spring to early autumn followed by an egg diapause of five to six months in Illinois and Ontario, respectively. Bane and Lind (1978) studied <u>H</u>. <u>borealis</u> in a tributary of the Rio Grande in Texas. Biomass was highest in the spring and lowest in the winter. Adults were found only in April.

I collected <u>H</u>. <u>borealis</u> from two Oklahoma streams with different thermal regimes for a period of 13 months. I report on life history patterns of <u>H</u>. <u>borealis</u> in these two streams and present new information on egg masses and early case-building behavior.

METHODS

Study Area and Sampling Method

Pennington Creek is a second-order, spring-fed, thermally constant stream in the Arbuckle Mountains of south-central Oklahoma. Caney Creek is a third-order, thermally variable stream in the Ozark Mountain foothills of northeastern Oklahoma (Fig. 1). <u>H</u>. <u>borealis</u> densities were sampled in each of these streams at monthly intervals from May 1981 through May 1982. A modified quadrat sampling technique was used. Stratified random samples of the substratum were collected with a 95 cm² cylinder to a depth of 3 cm. The <u>H</u>. <u>borealis</u> were removed from the substratum, counted and assigned to an age class (see below for technique). Fifty samples per month were collected from each stream from May through August 1981, and 25 thereafter for the remainder of the sampling period. Temperature was measured with an Extech meter (model 651).

Development

The development of 20 egg masses was followed in the laboratory from the time that they were laid through pupation of the resulting larvae. Egg masses were obtained from adults reared from pupae collected from Pennington Creek in July and August 1982. Adults were reared in 76-L artificial streams with screen cage tops. Floating pieces of styrofoam were provided as oviposition surfaces. Observations on hatching and early case making were made in 8 by 2 cm glass fingerbowls under a dissecting microscope. Larvae were reared in 3.8-L glass aquaria. Cases of H. borealis were measured to determine the range of sand particle sizes used in the case. Particles within this range (0.02 - 0.09 mm) were provided for case construction material. Food consisted of periphyton-covered cobble collected from Pennington Creek. Water in all the artificial streams and aquaria was a mixture of one-half Pennington Creek water and one-half distilled water.

I measured 123 egg masses collected from Pennington Creek and a similar, nearby spring-fed stream, Byrd's Mill Spring. For each egg mass I recorded the size of the rock to which the egg mass was attached, the number and location of egg masses on that rock, and the depth of water from which the rock was collected. I measured the maximal and minimal diameter of the egg mass, and the number of individual eggs per mass.

Age determination

The first four instars were readily identifiable by observing molts and measuring head widths of laboratory-reared <u>H</u>. <u>borealis</u>. Midpoints for head width frequency for each instar for the laboratory reared specimens were assigned (I=0.11, II=0.18, III=0.27, IV=0.4 mm) (Fig. 2). The factor of increase between these midpoints is 1.5, which fits Dyar's rule as the typical factor of increase between Trichoptera instars (Mackay 1978). These values are similar to headwidth frequency peaks of field specimens (Fig. 3). Using this factor of increase I calculated the midpoint for the fifth instar to be 0.6 mm. Although both the field and laboratory specimens had peaks at 0.6 mm, there were also peaks at 0.7 mm (Fig. 2, Fig. 3). This may be the result of several factors. There may be sexual dimorphism

in the last instar. There may be a large natural range in the size of the fifth instars due to differential growth. Lastly, larvae may go through six or even seven instars. I have observed larvae with opercula (and thus ready to pupate) with head widths ranging from 0.58 to as large as 0.77 mm. This range is present year round and, thus, is not a seasonal size dimorphism. Resh (1982) reported that larvae in a population of <u>Gumaga nigricula</u> in a California spring would molt as many as 14 times and that larval instars could not be distinguished by head capsule measurement. For the purpose of this study larvae were classified as early instars (head width < 0.5 mm) and late instars (head width > 0.5 mm). Early instars include the first four instars and late instars encompass the fifth and any subsequent instars.

RESULTS AND DISCUSSION

Development

Egg masses of <u>H</u>. <u>borealis</u> were briefly described by Vorhies (1909) and Elkins (1936) as hemispherical yellow masses fastened to an underwater support. In Pennington Creek and Byrd's Mill Spring egg masses occurred on the undersides of partially submerged rocks at the edge of the stream (X depth = 5.5 cm). The rocks with egg masses that were measured averaged 8.1 (S.D. of 2.0) cm maximum by 3.3 ± 1.3 cm minimum diameter. In the laboratory, eggs were laid on the undersides of floating pieces of styrofoam as well as on the sides of the aquaria. Egg masses occurred singly or in clusters of up to 35 in the field (X = 1.5±13.4) but usually occurred singly or in pairs in the laboratory.

Egg masses were a yellow-green gelatinous matrix measuring 5.2±1.0 mm maximum by 4.4±.8 mm minimum diameter (N=143). On the average of 184±40 eggs were evenly spaced within this matrix. This number is lower than the 250 eggs per mass reported by Davis (1965) for <u>H. borealis</u> in an Ohio stream. Differences in fecundity between populations of a species can usually be attributed to local environmental conditions such as food quality and temperature (Sweeney and Vannote 1978, Anderson and Cummins 1979).

At laboratory water temperatures of 19° to 21°C, development proceeded as follows. The body was visible after 10 days and the head distinct after 14 to 15 days. Eggs began to hatch at 16 to 17 days. Hatching took two to three days from the time the first larvae emerged until the last had hatched. Hatching of field-collected eggs has been described in detail by Davis (1965). Upon hatching larvae would crawl over the surface of the egg mass. They began to build cases as soon as they encountered sand particles, whether these were clinging to the egg mass or on the bottom of the finger bowl.

Davis (1965) stated that larvae first built a straight tube case and later began to spiral the case. I found that the case was curved from the beginning and became progressively more helical simply by the larvae adding onto the case tube in a spiral fashion (Fig. 4). Larvae built cases at different rates. Most larvae had built a half circle ranging from 0.56 to 0.77 mm in length by an age of seven days and a complete circle by two weeks. Development time was variable and became more variable with age. Most larvae underwent their first

molt between three and four weeks, their second molt between five and six weeks and their third between six and eight weeks. No fourth molts were observed. Most larvae pupated between 9 and 12 weeks in laboratory rearings.

Population dynamics

Densities of <u>H</u>. <u>borealis</u> were usually higher in thermally constant Pennington Creek than in variable Caney Creek. <u>Helicopsyche borealis</u> was the most abundant macroinvertebrate inhabiting stony substrata in Pennington Creek. In contrast, <u>H</u>. <u>borealis</u> was not dominant in Caney Creek except for a short period in the spring. Populations in both streams were greatly reduced by a heavy flood in October 1981 (Fig. 5). Severe floods in autumn are rare in Oklahoma.

<u>Helicopsyche borealis</u> was multivoltine with overlapping generations in Pennington Creek. Early instars were found 8 months out of 12 but densities were highest in late spring and early summer (Fig. 5). Adults were present year round but were not quantified. Ross (1944) and Williams and Hynes (1974) reported continual spring to autumn emergence of <u>H</u>. <u>borealis</u> in north temperate streams. During the winter egg masses were found in Byrd's Mill Spring but not in Pennington Creek. Early instars were present year round in Byrd's Mill Spring. The temperature of this spring is approximately 17°C all year.

<u>Helicopsyche</u> <u>borealis</u> was univoltine in Caney Creek with densities peaking in April (Fig. 5). Adults were only collected in the summer. Bane and Lind (1978) found that <u>H</u>. <u>borealis</u> biomass peaked in the spring and adults were found only in April in a tributary of the Rio

Grande. They did not report densities. A peak of early instars did occur in January in Caney Creek. Ross (1944) and Williams and Hynes (1974) reported egg diapauses for H. borealis in some north temperate streams. No egg masses were ever observed in Caney Creek. However, it is likely that they occur, as in other localities, on partially submerged rocks in very shallow water. If this is the case, then a succession of warm days, as sometimes occurs in Oklahoma in January, may have caused the eggs to hatch. Densities were much lower in Caney Creek than in Pennington Creek and, thus, it is possible that this January peak may be due to sampling error. The much higher densities of H. borealis in Pennington as opposed to Caney Creek, and differences in voltinism in the two streams may be due to both direct and indirect effects of the constant versus variable thermal regimes. Adult body size and fecundity depend largely on thermal conditions during the larval period (Sweeney and Vannote 1978). Gose (1970) found that the amount of accumulated temperature can influence the number of generations of scrapers and probably affects maximum size attained by an individual cohort. Gray (1981) studied five species of caddisflies, including H. borealis, in a lower Sonoran desert stream. These species reproduced continuously, although total development time was only slightly less than that of univoltine temperate species. The greater number of potential generations was probably related to the warmer stream temperatures.

In thermally constant springs, species which are often univoltine in "natural" streams behave with plasticity to warm water by producing

overlapping summer generations (Hynes 1970). Resh (1982) found that populations of <u>Gumaga nigricula</u> were univoltine in some California streams and multivoltine in nearby thermal springs. Caney Creek actually experiences more annual degree days than Pennington Creek (6,162 to 5,880 for May 1981 through April 1982). However, much of the time Caney Creek experiences extremes while Pennington Creek maintains a mild temperature all year (Fig. 1). Thus, it is probably not annual degree days that are important in this case, but the length of time at an optimum temperature for reproduction. For <u>H</u>. <u>borealis</u> in Oklahoma, this temperature appears to be around 17°C, although early seasonal peaks are probably also related to photoperiod and food changes.

Temperature may also be related to food quality and quantity, which in turn will affect total densities and voltinism. Parker and Voshell (1982) attributed differences in voltinism in <u>Hydropsyche</u> life cycles in two Virginia rivers to an interaction between food quality and temperature regime. Anderson and Cummins (1979) found that temperature and food quality and quantity interact in their effect on voltinism and growth. Low diversity in streams below hypolimnetic release reservoirs has been attributed to seasonal and diurnal thermal constancy which decreases potential niches and thus the number of species (Ward and Stanford 1979, Ward and Dufford 1979). In a constant stream, such as Pennington Creek, food may be available year round while in a fluctuating stream food availability exhibits great temporal variability (Ward and Stanford 1979). A year round optimal temperature for reproduction combined with continuous food

availability would favor the dominance of a species most prolific in this stable habitat. In Pennington Creek, this species appears to be <u>H</u>. <u>borealis</u>. In fact, <u>H</u>. <u>borealis</u> may normally reproduce continuously in Pennington Creek, as it does in nearby thermally constant Byrd's Mill Spring. During the study there was a rare autumn flood which severely depleted the population for several months and could have suppressed reproduction. Fluctuating temperatures and food levels would be more likely to produce a pattern in which species were dominant only for short periods of time. This inconstancy appears to be the situation in Caney Creek.

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FIGURE CAPTIONS

Figure 1. Mean monthly temperatures of Pennington and Caney Creeks.

- Figure 2. Head widths of laboratory-reared <u>Helicopsyche</u> <u>borealis</u>.
- Figure 3. Head widths of field-collected Helicopsyche borealis.
- Figure 4. Comparison of <u>Helicopsyche</u> <u>borealis</u> case size and shape at (a) 4 days, (b) 3 weeks and (c) 7 weeks.
- Figure 5. Mean monthly density of pupae and early and late instar <u>Helicopsyche borealis</u> in Pennington and Caney Creeks. Note that Caney Creek is on a different, expanded scale.









FREQUENCY















MICRODISTRIBUTION OF A CASE-BUILDING CADDISFLY: EFFECTS OF HYDRODYNAMICS, RESOURCE AVAILABILITY, AGE AND CASE ARCHITECTURE

Running head: Microdistribution of a case-building caddisfly.

Key words: benthos, case morphology, current velocity, grazer, <u>Helicopsyche</u>, hydrodynamics, microcurrent, periphyton, stream, substratum, Trichoptera.

10-year index key words: artificial stream, artificial substrate, benthic macroinvertebrate, case morphology, crushing resistance, current velocity, grazing insect, <u>Helicopsyche</u>, hydrodynamics, microcurrent, periphyton, spring-fed stream, substratum, Trichoptera.

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ABSTRACT

The microdistribution of larvae of the caddisfly Helicopsyche borealis was examined in two Oklahoma streams and in the laboratory. The relationship between case architecture and microdistribution was explored with numerical techniques and experimentation. H. borealis exhibited an age-specific preference for depth and current velocity. Age-specific patterns were further documented by laboratory and field experiments in which early instars aggregated on the tops of periphyton-covered substrata in slow water but drifted in fast water. Later instars were more evenly dispersed on the different substratum surfaces and drifted less frequently. Differences between age groups may be related to use of different food and case building materials and the limited ability of early instars to exploit these resources. Heavier cases of later instars apparently act as ballast allowing these larger herbivores access to food patches in fast-flowing microhabitats not available to the early instars. Importance of food was demonstrated by experiments in which all stages preferred food-saturated to food-depleted portions of substrata. In other experiments, drift rates of all stages increased with food deprivation. A field study showed that late instars use larger sand particles in the outer coil of their case under high current velocities. Although these larger particles serve as ballast in fast water, the results of a laboratory experiment indicate that particles are used according to availability. Because larvae use increasingly larger particles

in their cases as they mature, the availability of the appropriatelysized sand grains may be a secondary factor in their age-specific microdistribution. Hydrodynamics and crushing resistance are proposed as compatible selection pressures for the evolution of the helical case. The helical architecture of the case provides ballast and a shape which make the larvae well suited for grazing on exposed surfaces in high-flow environments. The helical shape also provides greater resistance to crushing than other caddisfly cases, allowing <u>H</u>. <u>borealis</u> to exploit the hyporheios in some streams.

INTRODUCTION

Stream-dwelling organisms are usually well-adapted morphologically for life in running water. Anatomical adaptations include streamlining and the flattening of projecting structures as well as the presence of hooks, grapples and frictionpads (Hynes 1970). Stream flow not only directly influences distributions of invertebrates, but indirectly influences microdistributions by alterations in substrate and food availability (Cummins and Lauff 1969, Corkum et al. 1977, Rabeni and Minshall 1977, Minshall and Minshall 1979, Statzner 1981). Specific morphological adaptations thus may allow some groups access to optimal locations for foraging and reproduction. For example, gastropods inhabiting racid water are often thicker shelled, more elongate and/or have a steeper, higher cone than their stillwater relatives. The thicker shell is thought to provide ballast as well as protection from being crushed during spates or by shell-breaking predators (Vermeij and Covich 1978, Bertness and Cunningham 1981, Vermeij 1982a, 1982b). Elongation serves to head the snail into the current. Higher cones are also believed to be more resistant to moving stones (Starmuhlner 1953, Hynes 1970). Concepts about shape and size as adaptations to life in the boundary layer have recently been tested by Statzner and Holm (1982). They suggest that flow around animals is influenced by inconspicuous morphological structures, behavioral patterns or a combination of both. Their results indicate that the velocities around the bodies of benthic invertebrates, and probably the forces

acting on them, are much more complicated than is suggested by the currently accepted boundary layer concept.

The Trichoptera are considered one of the most ecologically diverse orders of aquatic insects. This diversity is seen as an expansion of ecological niches made possible by the secretion of silk threads. By using silk to fashion a variety of shelters, nets and cases, trichopteran larvae have evolved adaptive systems to exploit a wide range of resources. Differences in the design of silken devices coupled with other specialized morphological and physiological adaptations of the larvae augment the number of species that can exploit the resources of a habitat (Wiggins and Mackay 1978, Mackay and Wiggins 1979).

Caddisfly larvae belonging to the superfamily Limnephiloidea construct portable cases using a wide variety of both organic and inorganic materials. Cases of active, lotic limnephilids are usually either streamlined and/or weighted down with "ballast" so that these species are well adapted to feeding on the tops and sides of rocks in swift currents (Wiggins 1977, Wiggins and Mackay 1978, Mackay and Wiggins 1979). Hydrodynamics is believed to be the primary influence in the evolution of these cases (Ross 1964, Jones et al. 1977, Wiggins 1977), although protection from predators, cannibals and parasites may also be important in some instances (Gallepp 1974, Mackay and Wiggins 1979).

Most work on resource partitioning in caddisflies has concentrated on the numerically dominant net-spinners (Wallace and Merritt 1980). Just as different net locations and mesh sizes enable this group to

subdivide available food and habitat (Wallace et al. 1979, Alstad 1982, Thorp 1983), the rich variety in portable case materials and architecture may also represent mechanisms for finer partitioning of spatial and energy resources. The greater overall species richness in the Limnephiloidea suggests that, although gross differences in portable cases are obvious, functional subtleties of these differences are far from understood (Mackay and Wiggins 1979).

Members of <u>Helicopsyche</u> are unusual caddisflies in that their sand-grain cases superficially resemble spiraled snail shells. In fact, the genus was first described as a snail based on the shape of the case alone (Lea 1934). To ascertain the role of the helical case in the microdistribution of <u>Helicopsyche</u> I first determined, through field sampling and experimentation, the microdistribution of one species, <u>H. borealis</u>. This information, coupled with data on case morphology and case-building behavior, was then used to explore the ecological and evolutionary importance of the helical case.

METHODS

Microdistribution: Study Area and Sampling Methods

Pennington Creek is a second-order, spring-fed, thermally constant stream in the Arbuckle Mountains of southcentral Oklahoma. In contrast Caney Creek is a third-order, thermally fluctuating stream in the Ozark mountains in northeastern Oklahoma. Within each of these streams a small stretch containing both pool and riffle areas was selected for study. <u>Helicopsyche borealis</u> densities were assessed in each of these streams at 4-wk intervals from May 1981 through May 1982. A modified quadrat sampling technique was used. Stratified random samples of the substratum were collected with a 95-cm² cylinder to a depth of 3 cm. <u>Helicopsyche borealis</u> were removed from the substratum and counted, and subsamples for organic content and periphyton chlorophyll <u>a</u> were taken.

The following variables were measured: (1) depth; (2) current velocity 10 cm above the substratum (Teledyne-Gurley current meter, model 700); (3) dissolved oxygen (Yellow Spring Instruments meter, model 51B); (4) conductivity (Yellow Springs Instruments meter, model 33); (5) temperature and pH (Extech meter, model 651). Substratum particle size was determined in the laboratory following Carver (1971). Organic content of the substratum was measured by weight loss after ignition at 550°C (Lind 1979). Periphyton was collected by brushing and scraping 490-mm² areas of substratum, placed in distilled water and frozen. Chlorophyll a concentrations were determined

spectrophotometrically following Strickland and Parsons (1972).

Fifty samples per month were collected from each stream from May through August 1981. Precision analyses (Elliot 1973) of these data indicated that 25 samples per month would be sufficient, so I collected that number from each stream for the remainder of the sampling period. Data were analyzed using multiple regression (Neff and Marcus 1980) to determine which measured parameters influenced <u>H</u>. <u>borealis</u> distributions. Larvae were placed in age groups for these analyses. Larvae with head widths < 5 mm were defined as early instars and larvae with head widths > 5 mm were considered final instars (Vaughn 1984).

Microdistribution: Experimental design

Substratum position

General methods

I conducted a series of laboratory and field experiments examining the actual position on the substratum of different instars exposed to high (50 cm/s) and low (5 cm/s) current velocities. Concrete bricks measuring 19.5 X 9.2 X 5.6 cm were left in Pennington Creek for 4 wk and allowed to become colonized with periphyton. Bricks were used because they were easy to manipulate. The size of these surfaces were similar to those exposed on natural rocks in the stream. In addition, bricks have been used by others examining caddisfly microdistribution (Kovalak 1976, 1980). Bricks were taken back to the laboratory and stored in plastic bags under refrigeration before being used in the experiments.

Laboratory trials were conducted in artificial streams similar
to those used by others observing caddisfly behavior (Elliot 1970, Gallepp 1974, 1977). Streams consisted of 5.2-L plexiglass chambers with nylon mesh on the upstream and downstream ends to prevent organisms from escaping but allowing water to pass through. These chambers were placed inside 76-L glass aquaria which were filled with a mixture of 50% distilled water and 50% Pennington Creek water (Fig. 1a). Current velocity in the artificial streams was controlled with Aqualogy Corp. Power Plus filtration pumps. One pump was used for low current velocities producing a Teledyne-Gurley (TG) reading of < 5 cm/s in the water column 10 cm above the substratum. Two pumps were used per stream for high current velocities, producing a TG reading of 50 cm/s. Actual current speeds (Table 1) on the various surfaces of the bricks were measured by salt tablet dissolution rates (McConnell and Sigler 1959).

Pennington Creek exhibits a nearly constant temperature of 17°C throughout the year (Vaughn 1984). Artificial streams were maintained at this temperature and on a 12L:12D photoperiod in growth chambers. Field trials were performed in 32-L rectangular plexiglass boxes (Fig. 1b). During field trials boxes were placed in areas of Pennington Creek where the TG flow closely approximated 5 or 50 cm/s as in the laboratory trials.

Live larvae were aged by measuring their case diameter. Average case diameters were compared to head-width frequency histograms to determine instars (Vaughn 1984). Second, fourth and final instar larvae were used in the experiments. Forty larvae were used per replicate in both laboratory and field trials. Bricks were oriented lengthwise in the streams with the narrow ends perpendicular to the oncoming current. At the beginning of a laboratory trial, larvae were placed at the downstream end of the brick and allowed to disperse for 2 h with the pumps turned off. The pumps were then turned on and the larvae were left for 24 h before observations were made. Hourly observations in three-day preliminary runs demonstrated that larvae moved onto all surfaces of the brick within 2 h and within 8 h selected an area of the brick at which they remained for up to 72 h. Data were converted to density, square-root transformed, and analyzed using two-way analysis of variance (Sokal and Rohlf 1981).

Crevices and indentations

Groupings of three bricks were used to create crevices between bricks. These inter-brick crevices measured 5 mm in width. Indentations approximately 10 mm across and 5 cm deep were scored in bricks with a chisel. The above experiments (laboratory only) were then repeated to determine the effect of substrate heterogeneity on larval position. Data were analyzed with the Mann Whitney \underline{U} test (Sokal and Rohlf 1981) to measure the difference between means of larvae in crevices or indentations under low and high current velocities.

Effects of periphyton

To determine if the preference for certain surfaces is due to periphyton food abundance on those surfaces, I mapped the position of larvae on single bricks which had half of the periphyton removed. Periphyton was removed along the long axis using a wire brush. These

trials were performed in the laboratory only. The Mann Whitney \underline{U} test was used to measure the difference between means of larvae on food-saturated versus food-depleted portions of single bricks.

Periphyton covered surfaces may provide shelter for larvae from currents as well as provide food. To test this hypothesis I examined drift rates of larvae on bricks completely covered with periphyton (food-saturated) versus bricks with no visible periphyton (food-depleted). Drift was measured as the number of larvae positioned off the brick. Data were analyzed using R X C tests of independence of food state versus flow rate (Sokal and Rohlf 1981).

Interstitial position

Williams and Hynes (1974) reported that <u>H</u>. <u>borealis</u> occurred to a depth of 30 cm in the substratum of the Speed River, Ontario. I took core samples in Caney Creek and found few <u>H</u>. <u>borealis</u> in the interstitial habitat. An experiment was designed to determine how far <u>H</u>. <u>borealis</u> travel in the gravel as well as the importance of gravel size and the degree of ground water recharge. Sections of PVC pipe 10.2 cm in diameter and 30 cm in height were filled with gravel 9.5 to 25 mm in diameter (N=4), 2.0 to 5.0 mm in diameter (N=4), and a mixture of these sizes (N=3). Pipe sections were then placed upright in 19-L plastic buckets and covered with a mixture of 50% spring water, 50% distilled water. Half of the replicates were aerated from the bottom with airstones to simulate recharge. The water level was kept even with the top of the gravel in the pipes throughout the experiment. Fifty fourth instar H. borealis were used per replicate.

Larvae were introduced at the top of the gravel in the pipe. Depths of larvae in the gravel were recorded six wk later. Data were analyzed using three-way analysis of variance (Sokal and Rohlf 1981) to measure the effects of depth and aeration among the gravel categories.

Case Architecture: Field study

Sampling and case measurement

Various parameters of <u>H</u>. <u>borealis</u> cases were measured to determine if certain aspects of case structure were associated with particular habitat conditions, such as current speed or particle size availability. I measured 639 cases of larvae and pupae collected in May 1981 for the study of microdistribution described above. The number of characters measured varied from 14 to 22 depending on the amount of coiling in the case. These characters are shown diagrammatically in Figure 2. The A series of measurements described the diameter and average particle size of the total case and of each coil section. The B series described the diameter of the case, the diameter of the edge of the case around the anterior opening, and the average particle size around this opening. Two measurements of height were made, C (total height) and D (anterior opening height). The angle of the coil from the base tube part of the case was determined as angle = $\cos[F^2 + E^2 - D^2 / 2(F)(E)]$. I recorded the dry weight of the case with animal removed.

Data analysis

Data on case morphology were combined with data on microhabitat

from the May 1981 collection sites. This information was analyzed using principal axis factor analysis, rotated to a terminal oblique solution (Mulaik 1972). I used the root-stairing technique (Cattell 1965) to decide how many factors to rotate.

Crushing resistance

The crushing resistance of 24 final instar <u>H</u>. <u>borealis</u> was measured by Roy A. Stein and Libby Marschall of Ohio State University. Crushing resistance was determined manually on a scale of 0 to 0.9 kg.

Case Architecture: Experimental Design

To test the hypothesis that the size of the particle used in the cases is a function of availability, I conducted the following experiment. Larvae were placed in the artificial streams described above except that the bricks were replaced with periphyton covered cobble. Larvae were offered a choice of either: (1) large (0.21-0.59 mm diameter) and small (0.09-0.12 mm) sand particles; or (2) large, medium (0.12-0.21 mm), and small sand particles with which to construct their cases. These choices were offered under both high (50 cm/s) and low (< 5 cm/s) current velocities. Particle size ranges offered were consistent with those found in H. borealis cases (as measured above) and in Pennington and Caney creeks. Three replicates were conducted for each particle size combination and current speed. A total of 200 fourth instar larvae were used per replicate. Larvae were allowed to build cases for 6 to 8 wk. The larvae were then preserved in Kahle's solution. Ten particles in the newly constructed portion of the case were measured per larva. Data were analyzed using two-way

analysis of variance for independence of particle size used and current speed (Sokal and Rohlf 1981).

RESULTS

Microdistribution in Oklahoma Streams

Depth accounted for the largest amount of variation in the distribution of H. borealis in Pennington Creek. This relationship was strongest in the early instars. In Pennington Creek early instars were negatively associated with current velocity, and final instars were usually found in deeper and faster water than were early instars (Fig. 3). An important factor accounting for the abundance of pupae in both streams was the availability of large rocks with a least diameter > 63 mm. Pupae in both of these streams usually occurred in clusters of 20 to 100 individuals on the sides and downstream faces of larger rocks. Food availability, as measured by organic content and chlorophyll a on the substratum, was not found to be associated with distributions in the multiple regressions. The strong relationship between pH and H. borealis density (Fig. 3) was apparently related to a flood in October 1981 that concurrently resulted in a decrease in pH and a severe depletion of the H. borealis populations in both streams (Vaughn 1984). Because the Pennington Creek population was much larger, I used it as the source population for my laboratory and field experiments.

Substrate position

The position of the larvae on the bricks (top, upstream face, downstream face, or sides) in the laboratory was dependent on the current regime, but varied with age/size. Under low current velocities, early instars spent more time on the tops of the bricks than older individuals. Under high current velocities, later instars aggregated on the downstream faces while early instars drifted (Fig. 4). Larvae of all size classes chose significantly different positions on the substratum under the two current regimes (2nd instars, $\underline{F} = 212.31$, P < 0.01; 4th instars, $\underline{F} = 18.25$, P < 0.01; final instars, $\underline{F} = 29.31$, P < 0.01). These same results were obtained in the field trials (Fig. 5).

Effects of shelter

The number of fourth and final instar larvae preferring crevices and indentations to open surfaces of the bricks greatly increased with increased current velocity (Fig. 6; 4th instars, $\underline{U} = 99.5$, P < 0.01; final instars, $\underline{U} = 97.0$. P < 0.01). Second instars did not prefer indentations to open surfaces, probably because they drifted rather than attaching inside indentations ($\underline{U} = 55.5$ ns). Second instars could not be seen in the crevices because of their small size and thus were not tested in crevices.

Effects of periphyton

The combined effect of periphyton covered surfaces may be to lower exposure of larvae to current as well as to provide food. To test this hypothesis I examined drift rates of larvae on bricks completely covered with periphyton (food-saturated) versus bricks with very little algae (food-depleted). Under low current velocities, drift increased greatly with food deprivation. Under high current velocities, drift rates were high regardless of food level (Fig. 7; 2nd instars,

<u>G</u> = 65.28, P < 0.01; 4th instars, <u>G</u> = 51.2, P < 0.01; final instars, <u>G</u> = 21.91, P < 0.01).

To determine if preference for certain brick surfaces is due to periphyton abundance on those surfaces, I mapped the position of larvae on single bricks which had half of the algae removed. Under low current velocities, all size classes of larvae preferred the foodsaturated portions of the brick. As in the previous experiment, under high current velocities differences between food-saturated and fooddepleted surfaces were not statistically significant (Table 2).

Occurrence in gravel

In small and mixed gravel in the laboratory tests larvae were found mainly at depths of less than 3 cm in the substratum regardless of aeration. In large gravel larvae occurred at greater depths, especially in the aerated replicates (Fig. 8). The three-way analysis of variance showed that depths at which <u>H</u>. <u>borealis</u> occurred in the gravel $(\underline{F} = 17.33, \underline{P} < 0.01)$ and the interaction between gravel size and depth ($\underline{F} = 1.72, \underline{P} < 0.05$) differed significantly among the three gravel types.

Natural variation in case structure

I measured various parameters of <u>H</u>. <u>borealis</u> cases to determine if certain aspects of case structure were associated with particular microhabitat conditions. In both streams, the first factor represented an overall larval age/size factor and the second represented a sandy habitat factor. Of the case parameters measured, only particle size was associated with a physical habitat condition, and this was not a strong relationship (loading > 0.5) (Table 3) In Pennington Creek, the size of the particle used in the outer coil of the case (parameter A12), and the width of the outer coil (A11; a variable related to particle size), are weakly correlated with factor 3. Factor 3 is strongly correlated with current velocity and a cobble-type habitat (substrate diameters 25-63 mm and 4-9.5 mm). In Caney Creek the size of the particles used in the outer coil of the case (A6, A12) were negatively correlated with factor 5. This factor was negatively associated with the variable indicating the presence of the largest available substrate sice (diameter > 89 mm). Variables representing particle sizes used in the inner coil of the case (A6, A10) were positively correlated with factor 5 which was positively correlated with a cobblegravel habitat. Cases of final instar H. borealis had a mean crushing resistance of 0.26±0.16 kg.

Particle Size Selection

When fourth instar <u>Helicopsyche</u> <u>borealis</u> were offered a choice of two or three particle sizes in artificial streams under high and low current velocities they were not selective. That is, the results supported the null hypothesis that the size of the particle used in the case is a function of availability (F=0.43 ns).

DISCUSSION

This study has shown that H. borealis prefer specific microhabitats in streams and that these preferences differ with age. Early instars prefer lower current velocities and shallower water than do later instars. Others have reported preferred current speeds and depths of H. borealis, but have not presented information on age. Slobodchikoff and Parrott (1977) examined the distribution of Helicopsyche sp. in Oak Creek, Arizona in a slow area (15-25 cm/s) and a fast area (> 50 cm/s). Densities of Helicopsyche sp. were usually much greater in the fast area. Korboot (1963) found that in a laboratory stream the maximum velocity H. tillyardi could withstand was 54 cm/s. Hopkins (1971) found H. borealis in New Zealand streams at an average depth of 15 to 20 cm and normal flow rate of 17 cm/s in the winter and 6 cm/s in the summer. Williams et al. (1983) examined the distribution of H. borealis in a small Ontario stream (Uxbridge Brook). They reported a distinct lack of correlation between H. borealis density and either depth or current speed. Preferences may have been masked because they took fewer samples and their samples covered larger areas than mine did.

Cummins and Lauff (1969) examined the distribution of <u>H</u>. <u>borealis</u> in trays filled with different sizes of gravel in upstream and downstream portions of a Michigan stream. They found that <u>H</u>. <u>borealis</u> would colonize all of their substrate sizes. Hopkins (1971) also noted a lack of substrate preference in <u>H</u>. <u>borealis</u>. In contrast, Wise

and Molles (1979) concluded that H. borealis was more abundant on small (10-25 mm) than large (> 40 mm) gravel. I found that larval H. borealis did not prefer particular rock or gravel sizes in Canev or Pennington creeks. Pupae, however, tended to aggregate on the downstream faces of larger rocks. A preference of the nonmobile pupae for large rocks would facilitate survival during spates since larger rocks are less likely to be washed away. The preference of pupae for deeper. faster water may merely reflect the fact that larger rocks are more common in fast-water habitats (Hynes 1970). This preference might also serve as a predator-avoidance strategy to escape those predators limited to feeding in slower water. In addition, final instars may select deeper water to avoid desiccation during droughts. Prepupal deep-water seeking behavior has been observed in other mineral case-making caddisflies, notably Glossosoma and Silo (Scott 1958). Pupae almost always occurred in clumps. This behavior has been observed by others studying H. borealis (Comstock 1930, Elkins 1936). Clumping probably facilitates mating since a large number of adults emerge in the same area.

Williams and Hynes (1974) reported the occurrence of <u>H</u>. <u>borealis</u> in the hyporheios from a depth of 30 cm in the Speed River, Ontario. In addition, Williams et al. (1983) found <u>H</u>. <u>borealis</u> at both the surface and interstitial in Uxbridge Brook. Vorhies (1909) reported that this species occurred down to 3 m in the gravel of some Wisconsin lakes (although it is not clear whether these were live larvae or merely buried cases). Gray and Fisher (1981) observed that 70% of

H. mexicana in a Sonoran desert stream occurred on the surface, 26% between 0 and 10 cm, and only 4% as deep as 30 cm. I found few H. borealis in the interstitial in Caney Creek. There was no interstitial habitat to sample in Pennington Creek. In an experiment designed to test the depth to which H. borealis occur in the gravel, I found that most H. borealis stayed near the surface except in large (9.5-25 mm), aerated gravel without smaller particles intermixed. Habitats consisting of this large gravel are uncommon in Oklahoma and Arizona, but may be typical of other regions.

The position of H. borealis larvae on the surface substratum is dependent on the current regime but varies with age and size. All size classes of larvae chose significantly different positions on the substratum under high versus low current velocities. All size classes preferred exposed surfaces under low current velocities. Early instars preferred the tops of bricks under low current velocities and drifted under high current velocities. Later instars also occurred on the top, but were more evenly dispersed over the brick than early instars, and tended to aggregate on downstream faces during high flow. These findings are supported by the work of Williams et al. (1983) in Uxbridge Brook. They looked at the distribution of fifth instar larvae on 10 rocks from a fast water area (75 cm/s) and 10 rocks from a slow water area (<25 cm/s). In fast water, larvae were most numerous on surfaces not exposed to the current. In slower water larvae occurred on the exposed surfaces. Similar behavior has been observed for the "turtle-shaped" mineral case-builder Glossosoma (Scott 1958).

The ecological value of a habitat can be ranked in terms of physical constraints, resource availability and predation intensity (Thorp 1983). The age-dependent preference of <u>H</u>. <u>borealis</u> larvae for specific current velocities, depths and substratum surfaces is largely due to physical constraints and food-resource availability, although predation pressure may also influence their microdistribution. These factors are discussed below.

Physical_constraints

Older, larger <u>H</u>. <u>borealis</u> are generally found in faster water than early instars. Kovalak (1978) studied the relationship between the size of stream insects and current velocity. Because surface to volume ratios are lower in larger insects, he predicted that larger insects should select faster currents to facilitate O_2 uptake. However, this prediction applies primarily to insects which depend on passive diffusion for O_2 uptake. <u>Helicopsyche borealis</u> larvae can actively pump water across their gills (Wiggins 1977). In addition, O_2 uptake in <u>H</u>. <u>borealis</u> does not become dependent on O_2 concentration until the concentration falls below 3.5 ppm (Williams et al. 1983). During my study, oxygen concentrations in Pennington and Caney creeks never fell below 7 ppm. Therefore, oxygen does not appear to be be a limiting factor for any age/size of <u>H</u>. <u>borealis</u> in the streams studied.

<u>Helicopsyche borealis</u> is often found in what are considered thermally stressful environments, such as hot springs (Wiggins 1977). Resh et al. (1984) used field-based thermal bioassays to determine the responses of <u>H. borealis</u> larvae to temperatures ranging from 33° to

45°C. About 50% of the larvae survived a 1-h exposure at 39° and 100% survived a 1-h exposure at 36°C. The migration of late instar H. borealis into faster currents in response to O_2 concentrations is doubtful.

The absence of all ages of <u>H</u>. <u>borealis</u> from pools and backwaters (personal observation) may be due more to absence of, or inaccessibility to, periphyton food, rather than low 0_2 . Scott (1958) found that <u>Glossosoma</u> would not occur in water slower that 20 cm/s because small mineral particles collect among the algae and interfered with grazing. However, I commonly found early instar <u>H</u>. <u>borealis</u> in shallow water with current velocities lower than 20 cm/s, but there was little siltation in these areas. Lamberti and Resh (1983) reported high densities of <u>H</u>. <u>borealis</u> on experimentally enhanced periphyton from a stream with a current velocity of 4 cm/s.

Resource availability

The current and depth preferences of <u>H</u>. <u>borealis</u> as well as their affinity for exposed substratum surfaces may be a result of food availability. <u>Helicopsyche borealis</u> are reported to feed on both detritus and diatoms (Coffman 1967, Coffman et al. 1971, Mecom 1972, Shapas and Hilsenhoff 1976, Williams et al. 1983). In areas where periphyton is abundant, the larvae are proficient grazers. In a series of field experiments Lamberti and Resh (1983) found that <u>H</u>. <u>borealis</u> aggregated on tiles with enhanced periphyton and were responsible for high algal turnover rates. Cummins and Lauff (1969) attributed the lack of substratum preference in H. <u>borealis</u> to a <u>microdistribution</u>

governed by food availability. In my experiments all age groups of \underline{H} . <u>borealis</u> preferred food-saturated to food-depleted portions of bricks. These results suggest that the preference for the tops of rocks may be related to periphyton availability on these surfaces. Periphyton densities are frequently higher on tops of rocks because these surfaces receive more light and are often above the scouring zone near sand and gravel bottoms.

Drift rates increased with food deprivation under low current velocities but were high regardless of food level under high current velocities. This behavior suggests that drift under low current velocity is functional rather than catastrophic (Waters 1972). Larvae may be responding to microspatial patchiness in food abundance by drifting to a new food patch. The preference of <u>H. borealis</u> for shallow water may be due to increased light. While <u>H. borealis</u> are most common in low-velocity, shallow areas, they are notably absent from pools and backwaters. This distribution may be due to the absence or inaccessibility to periphyton because of low light and siltation in these areas (e.g., Scott 1958).

The tendency of later instar <u>H</u>. <u>borealis</u> to move into deeper and faster water and occupy portions of bricks other than the tops may reflect a different or broader feeding niche than earlier instars. Kovalak (1980) reported an increase in the niche breadth of <u>Glossosoma</u> <u>nigrior</u> with size. Similarily, Cummins (1975) found decreased clumping of <u>G</u>. <u>nigrior</u> with increased size. Switches in feeding preferences prior to pupation are features in the life cycles of many aquatic

insects (Anderson and Cummins 1979). Alternatively, this behavior may be a result of case material availability. <u>Helicopsyche borealis</u> use increasingly larger particles in their cases as they mature (Vaughn 1984, Williams et al. 1983). Later instar larvae in Caney and Pennington creeks tended to use larger particles in the outer coil of their cases in fast water as opposed to slower water. Laboratory experiments showed that <u>H. borealis</u>, within an age group, use case particle sizes according to availability. Therefore, late instar <u>H. borealis</u> may move out into deeper, and faster water because the larger particles they require for their case are, because of stream hydrodynamics (Hynes 1970), more available in this area. Allen (1951) found that in New Zealand <u>H. borealis</u> cases were larger in swifter stream reaches. The heavier cases of older instars may act as ballast, allowing them to reach protected locations, such as the backs of rocks, rather than drift in fast water.

Predation

In a preliminary study I performed gut analyses on over 300 fish from Pennington and Caney creeks. None of these fish were feeding on <u>H. borealis</u>. Hopkins (1971) noted that while <u>H. borealis</u> were very abundant in New Zealand trout nursery streams, the larvae were rarely eaten by the trout. Occurrence on exposed surfaces may decrease predation by predators which themselves occur under rocks (Sheldon 1980) or which actively search under rocks (e.g. stonerollers). <u>Mobility</u>

Egg masses of H. borealis in Caney and Pennington creeks occurred

on the undersides of partially submerged rocks at the edge of the streams (Vaughn 1984). Early instars thus, by necessity, start out their life in the slowest, shallowest water. Occurrence of later instars in deeper, faster water may only be a result of post-eclosion dispersal (Kovalak 1980), although if this is true one would expect the larvae to be more randomly distributed. Similarly, although larger instars should be able to move farther and faster than early instars, (Hart and Resh 1980), the larger instars should not restrict their movement towards the center of the stream.

Role of the helical case in H. borealis microdistribution

The microdistribution of <u>H</u>. <u>borealis</u> is governed by a combination of current speed, depth, size of substratum, resource availability and possibly predation intensity. While these factors are important ecologically, I propose that it is the evolution of the helical case which has allowed <u>H</u>. <u>borealis</u> larvae to exploit their particular habitat. There are three alternative hypotheses which I will examine to evaluate the adaptiveness of the helical shape.

Crushing_resistance

Williams et al. (1983) and Williams and Hynes (1974) have proposed that the helical shape of the case is ideal for an hyporheic existence because it so easily fits in the gravel interstices. Williams et al. (1983) examined the crushing resistance (Otto and Svensson 1980) of the cases of fifth instar <u>H</u>. <u>borealis</u> from Uxbridge Brook compared to that of 10 other species of cased caddisflies collected at random from local streams. Despite their comparatively small size, H. borealis

resisted an average pressure of 0.54 kg before collapsing, more than any other species tested. Specimens from Pennington Creek resisted and average pressure of 0.26 kg before collapsing. Williams et al. (1983) proposed that this resistance is made possible by the coiled as opposed to hollow structure of the case and evolved as an adaptation to an interstitial habitat.

The crushing resistance provided by the coiled morphology is not incompatible with a surface existence. A strong case would be important to withstand being crushed during spates. Crushing resistance may also be an antipredator adaptation (see below).

Hydrodynamics

<u>Helicopsyche borealis</u> larvae, because of their case, are hydrodynamically well suited to life in flowing water. Both case shape and ballast contribute to this hydrodynamic adaptiveness. These adaptations allow <u>H. borealis</u> access to areas where other grazers might be excluded because of an inability to maintain themselves on the substratum in the current.

Most stream-dwelling trichopteran larvae build cases with large sand grains. Although this "selection" may be because these are the only materials available, it has the effect of making the larvae heavy and less easily swept away. The heavier cases of older instar <u>H</u>. <u>borealis</u> may serve as ballast and may be one reason these larvae are found in faster water than are early instars. Ballast alone cannot explain why the case is helical as there are many examples of ballast without involving a helical case (see Wiggins 1977). For example, limnephilids

often incorporate large stones which are thought to serve as ballast into the sides of their cases (Nielson 1942, Hynes 1970). The coiled architecture of the helical case may actually allow for more ballast than a simple hemispherical or tube case because more sand grains are packed into the same unit volume.

Recent work suggest that velocities around the bodies of benthic stream invertebrates, and probably the forces acting on them, are more complicated than is proposed by the currently accepted "boundary layer" concept (Ambuhl 1959). The optimal shape for an organism living in a velocity gradient depends on the organism's size and behavior, as well as as the depth of the boundary layer and whether it experiences laminar or turbulent flow (Vogel 1981). The classical examples of animals well adapted to life in flowing water included dorso-ventrally flattened and streamlined organisms. Flatness is actually an adaptation to hide from drag in the low-flow environment of the boundary layer. Streamlining is effective only if the organism always meets the current head on (Vogel 1981). While a streamlined shape may serve the purposes of a filterfeeder, it is probably not the ideal shape for a grazers, such as <u>Glossosoma</u> and <u>Helicopsyche</u>, which may travel randomly over the surface of a rock. At the lower Reynolds numbers which occur near the surfaces of rocks, the increasing friction due to increasing pressure will favor shapes which expose less area per unit volume (Vogel 1981). Rounded edges in a downstream direction and a convex, hemisperical face perpendicular to the flow both work to reduce drag. In addition, a less-flattened shape may work to reduce lift (Vogel

1981). All of the above attributes relate to <u>H</u>. <u>borealis</u> cases. As the larvae move over the surface of a rock grazing, they will always expose a convex, hemisperical face upstream and a rounded edge downstream, no matter what direction they are facing.

Statzner and Holm (1982) have mapped the current velocities around the bodies of freshwater, pattelliform limpets (Ancylus) and mayflies (Ecdyonurus) using laser doppler anemometry. Lifting forces acting on these animals are affected by external morphology (e.g., the gastropod) or behaviorally-controlled apparent morphology (e.g, the mayfly). In A. fluviatilis there was a reduction of velocity in front of the case with the zone of greatest lifting at approximately the highest point of the case. Others have reported that A. fluviatilis living in faster water have shells which are higher and more steeply conical than those in slow water (Starmuhlner 1953, cited by Hynes 1970). This increased height may serve for increased boundary layer control in turbulent water. It may also afford the shell increased crushing resistance (Hynes 1970). The helical, coiled shape of an \underline{H} . <u>borealis</u> case increases the height of the case over a simple hemispherical case such as that of Glossosoma. This increased height may allow H. borealis to increase the height of the boundary layer and, thus, increase the maximum flow rate they can reside in.

Snail mimicry and predation

Berger and Kaster (1979) performed some laboratory predator-prey experiments using snails, <u>Physa</u>, <u>H</u>. <u>borealis</u>, and a straight tubecased caddisfly, <u>Leptocella</u> <u>albida</u>. Trout were used as the predators.

The trout ate the snails but would not feed on either <u>L</u>. <u>albida</u> or <u>H</u>. <u>borealis</u>. Berger and Kaster concluded from these experiments that the unusual shape of <u>Helicopsyche</u> larvae is not due to their being snail mimics, but rather that some kind of common selective factor, such as hydrodynamics, was involved in the evolution of each form. The helical architecture may afford strength to the case which makes them "unprofitable" to predators. The helical case makes the larvae much harder to remove from the case than typical tube case builders (personal observation), and this may discourage predators.

Hydraulic stress and crushing resistance are important and compatible hypotheses for the evolution of the helical case. In fact, the dual adaptability of the case may be responsible for the cosmopolitan distribution of the genus. In areas with deep, gravelly substrata and plentiful groundwater recharge, the helical case shape allows <u>Helicopsyche</u> to survive in the interstitial without being crushed. In open-canopied streams the hydrodynamic aspects of the case allow at least one species, <u>H</u>. <u>borealis</u>, grazing access on surfaces exposed to current. This ability to utilize multiple habitats would give <u>Helicopsyche</u> a competitive advantage over other case builders and may be the reason for their cosmopolitan distribution.

Summary

The microdistribution of <u>H</u>. <u>borealis</u> larvae is age-specific and controlled primarily by current and secondarily by food and case-material availability. The helical architecture of the case provides ballast and a shape which make the larvae well suited for grazing on exposed

surfaces in high-flow environments. Recent models based on the in-stream current velocity preferences of benthic macroinvertebrates successfully predict habitat suitability for benthic organisms within specific streams and are proving to be a useful flow management tool (Gore 1978, Gore and Judy 1981, Bovee 1982). Grazing caddisflies, such as <u>H. borealis</u>, are dependent on the periphyton on exposed rock surfaces. This makes them particularily sensitive to changes in water level and flow rate, because such changes are more dramatic and occur more rapidly on these surfaces than in other stream habitats, such as under rocks or in the gravel. Therefore, knowledge of the adaptive mode with regard to hydrodynamics of these organisms could be incorporated into flow management models in order to improve overall predictability.

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TABLE 1. Current velocities used in the experiments. Teledyne-Gurley current speeds are in the water column 10 cm above the artificial stream bottom. Corresponding salt tablet current speeds were measured on the actual brick surfaces at 17°C.

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Position of salt tablets on brick	Teledyne-Gurley current velocity (cm/s)	Mean salt tablet current speed (cm/s) ± 1 SD (N=10)			
Top	5	15.5 ± 4.1			
	50	37.3 ± 5.9			
Sides	5	16.5 ± 2.4			
	50	37.9 ± 3.5			
Downstream face	5	15.0 ± 1.7			
	50	12.9 ± 1.5			
Upstream face	5	19.7 ± 3.9			
	50	43.0 ± 1.6			

TABLE 2. Mann-Whitney U test for the difference between means of larvae on food saturated versus food depleted portions of single bricks.

Larval age	Current speed (cm/s)	<u>U</u> -value
Second instars	5	3.94 **
	50	0.23 NS
Fourth instars	5	5.84 **
	50	0.17 NS
Final instars	5	5.10 **
	50	0.42 NS

NS = nonsignificant; **, $\underline{P} < 0.01$.

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TABLE 3. Factor loadings	from principal axis factor analysis of combined					
case metric and abiotic habitat data collected from Pennington						
and Caney creeks in May	1981. See Methods for definitions of metric					
characters.						

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	PENNINGTON CREEK			CANEY CREEK					
Character	1	2	3	1	2			4	
Head width	.60	13	.07	-49	.05	11	15	40	
Case iry weight	- 96	11	.19	.38	20	.25	. 39	.03	
A1	. 96	13	.14	-86	19	.10	03	.94	
A2	. 41	.14	.08	.73	32	.30	. 59	.36	
A3	.60	.51	01	-81	07	.23	10	01	
A4	. 56	.08	.05	2	16	.18	.14	16	
A5	.70	09	.11	3	27	17	36	16	
Ae	. ćć	03	*0	.::	23	.38	::		
λ7	. : 5	05	.19	. 20	10	·	.35	.22	
AB	.23	05	.30	.23		.34	.20	شد و	
19		10	.23	2].	:9	.28	.25	
A10	. 27	.32	.22	21	32	:5	.22	-47	
A11	33	03	-11	.21	:0	.18	.02	. 23	
x*2	35		-34	- 37	2	01	10	25	
31	. 97	08	.17	.87	17	-14	.27	CS	
32	. 92	08	.18	5	03	. 90	.05	.03	
33	. 20	11	.01	+54	02	.79	.01	.15	
c	.76	09	-13	2	15	ċ4	.02	06	
0	. :7	05	.25	-67	29	.75	.04	.01	
Angle	29	08	32	:9	.13	35	:0	15	
Current velocity	.13	41	.60	.09	12	07	76	32	
Depth	.04	.10	03	08	.11	.02	.71	.08	
Habitat substrate die	isoter								
> 89 23	13	30	56	02	08	12	26	89	
63 - 89 ==	.06	32	-42	16	03	:2	29	.06	
25 - ć3 ==	.12	26	-60	.14	:9	.22	.01	- 58	
9.5 - 25 ==	.10	13	27	.03	07	05	.37	01	
4 - 9.5 az	. 29	29	- 33	.10	32	-09	.13	.8]	
2 - 4 553	. : •	.83	20	.07	11	.27	.71	. 49	
1 - 2 55	29	.94	13	11	.21	.15	. 24	.21	
.59 - 1 za	:2	.93	13	14	.96	04	.06	13	
.3559 22	09	.39	07	14	.76	04	.05	13	
.2135 ==	07	.92	39	13	.96	03	. 04	13	
.1221 cm	÷.C8	.96	13	02	.04	08	.79	.11	
.3912 ==	10	.88	13	:3	.96	04	.07	12	
< .C9 ==	.06	.38	10	33	÷9.	:5	04	.01	

FIGURE LEGENDS

Fig. 1. Diagram of laboratory and field streams.

Fig. 2. Metric characters used to describe <u>Helicopsyche</u> <u>borealis</u> cases. Redrawn from Wiggins (1977).

Fig. 3. Mean percentage of the variance in the abundance of each age class of <u>Helicopsyche borealis</u> accounted for by abiotic variables in multiple regression. Filled bars are the means of variance accounted for by variables with positive regression coefficients; open bars represent negative coefficients. Percentages less than 1.0 are not shown.

Fig. 4. Mean density of <u>Helicopsyche</u> <u>borealis</u> on different brick surfaces (T=top, U=upstream, D=downstream, S=sides) for low (< 5 cm/s) and high (50 cm/s) current velocities in artificial streams.

Fig. 5. Mean density of <u>Helicopsyche</u> <u>borealis</u> on different brick surfaces (T=top, U=upstream, D=downstream, S=sides) for low (< 5 cm/s) and high (50 cm/s) current velocities in the in-stream boxes.

Fig. 6. Mean frequency of <u>Helicopsyche</u> <u>borealis</u> in crevices and indentations for low (< 5 cm/s) and high (50 cm/s) current velocities.

Fig. 7. Mean frequency of drifting larvae on food-saturated (+) and food-depleted (-) bricks for low (< 5 cm/s) and high (50 cm/s) current velocities.
Fig. 8. Mean densities of <u>Helicopsyche</u> <u>borealis</u> at various depths of aerated and nonaerated large (9.5 - 25 mm), small (2.0 - 5.0 mm), and mixed gravel.

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Mean percentage of the variance in the abundance of each age class of H. berealls accounted for by abiotic variables in multiple regression. Filled bars are the means of variance accounted for by variables with positive regression coefficients, open bars represent negative coefficients. Percentages less than 1.0 are not shown.



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THE ROLE OF PERIPHYTON ABUNDANCE AND QUALITY IN THE MICRODISTRIBUTION OF A STREAM GRAZER, <u>HELICOPSYCHE</u> <u>BOREALIS</u> (TRICHOPTERA: HELICOPSYCHIDAE)

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Running Head: Periphyton and Stream Grazer Microdistribution

ABSTRACT

A series of laboratory and field experiments were performed to determine if the preference of larvae of <u>Helicopsyche borealis</u> (Trichoptera: Helicopsychidae) for exposed rock surfaces in streams was related to patchiness of periphyton food. Larval densities on artificial substrata were highest in areas of high algal chlorophyll <u>a</u>. When offered a choice of three potential foods-- a diatom, a green filamentous or a bluegreen filamentous alga-- larvae showed no preference. Periphyton quality was not as important as abundance in controlling <u>H</u>. <u>borealis</u> microdistribution. Numbers of emerging adults were greatest on green algae and diatoms. By selecting exposed surfaces of rocks, <u>H</u>. <u>borealis</u> larvae place themselves in the microhabitat most likely to contain both abundant and high quality food patches.

INTRODUCTION

While a number of recent papers have examined the consequences of patchiness of food resources to habitat selection (e.g., Fraser and Sise, 1980; Lewis, 1980; Rotenberry and Wiens, 1980; Sih, 1982), this subject has received limited attention with regard to stream invertebrates. Hart and Resh (1980) and Hart (1981) documented the movement patterns and time-activity budget of the caddisfly <u>Dicosmoecus</u> <u>gilvipes</u>. Two thirds of their total activity budget was dedicated to feeding. Animals moved from patch to patch to meet their food requirements.

Larvae of the caddisfly <u>Helicopsyche borealis</u> have been reported as feeding on various combinations of algal, detrital and animal materials (Coffman, 1967; Coffman et al., 1971; Shapas and Hilsenhoff, 1976; Mecom, 1972; Williams et al., 1983). However, they are usually described as grazers and have been found to significantly affect periphyton diversity, density and spatial distribution. Lamberti and Resh (1983) performed experiments in which the effects of periphyton on the density and spatial distribution of <u>H</u>. <u>borealis</u> were assessed by varying the standing crop of periphyton. Larvae aggregated on periphyton patches with high standing crops but became randomly distributed once they reduced periphyton to background levels. Recent papers have documented the life history and microdistribution of <u>H</u>. <u>borealis</u> in Ontario, California and Oklahoma (Williams et al., 1983; Lamberti and Resh, 1983; Resh et al., 1984; Vaughn, 1984a, 1984b).

In a combination field and laboratory study, I found that <u>H. borealis</u>

larvae exhibited age-specific preferences for depth and current velocity (Vaughn, 1984b). These patterns were further documented by laboratory and field experiments during which early instars aggregated on the tops of bricks in slow water and drifted in fast water. Later instars were more evenly dispersed and drifted less. Differences between age groups may have been related to different food resource requirements and the ability to locate food. The importance of food was demonstrated by experiments in which all stages preferred food-saturated to food-depleted portions of bricks and experiments in which drift rates of all stages increased with food deprivation. This paper examines the role of food quantity and quality in the microdistribution of <u>H. borealis</u>, and the effect of these factors on reproductive fitness.

METHODS

Field experiment

A field experiment was designed to determine where <u>H</u>. <u>borealis</u> occurred in the stream in relation to food patches. The experiment was conducted in Pennington Creek, a second-order, spring-fed, thermally constant stream in the Arbuckle Mountains of southcentral Oklahoma. Sections of this stream commonly support large populations of <u>H</u>. <u>borealis</u> (Vaughn, 1984a). Periphyton availability was measured as particulate organic carbon (POC), algal chlorophyll a and type of algae.

Concrete bricks 19.5 by 9.2 by 5.6 cm were placed in Pennington Creek and left for 4 wks. A total of 48 bricks were used: 24 were oriented with the long-narrow side perpendicular to the current and the remainder had the short-narrow side facing the current. Bricks were placed in transects across stream sections in areas of slow (< 10 cm/s), intermediate (10-40 cm/s) and fast (> 40 cm/s) current velocity. Glass slides 2.5 by 7.5 mm were attached to each side of every brick with silicone sealant. The slides provided a surface of known area for quantification of POC and algal chlorophyll a.

Observations were made using a diving mask. I mapped the number of <u>H</u>. <u>borealis</u> in each of four age classes on five sides (top, upstream, downstream, left, right) of every brick. Age classes were early instars (1st through 3rd), fourth instars, final instars and pupae (Vaughn, 1984a). I recorded water depth and current velocity (slow, intermediate or fast) at the site of each brick. I then collected the bricks and removed the <u>H</u>. <u>borealis</u>. Bricks were immediately stored in plastic

bags on ice to prevent drying and/or rapid changes in biomass.

In the laboratory I recorded the presence/absence of diatoms, filamentous green algae (mainly <u>Cladophora</u> sp.) and <u>Chara</u> sp. on each side of the bricks. Glass slides were scraped and sampled for POC and algal chlorophyll <u>a</u>. POC was measured according to Wetzel and Likens (1979). Algal chlorophyll <u>a</u> was determined following Lind (1979). Numbers of <u>H</u>. <u>borealis</u> were converted to density since the different sides of the bricks had different areas.

The resemblance structure of the above habitat-use data was assessed using cluster analysis. Analysis was carried out using NT-SYS software (Rohlf et al., 1979). The data matrix consisted of 184 individual brick sides (columns or OTUs) by 18 habitat variables (rows or characters). Data were standardized to a mean of 0 and a variance of 1.0 so that each data point was expressed in standard deviation units from its row mean. Similarity between habitat variables was calculated as average taxonomic distance (Sneath and Sokal, 1973). These variables were then clustered using an unweighted pair-group with arithmatic averages (UPGMA) type of cluster analysis (Sneath and Sokal, 1973).

Grazing preference

Grazing experiments were conducted to determine if <u>H</u>. <u>borealis</u> larvae preferred one type of algae over another. Periphyton was cultured at 17°C and 12L:12D in growth chambers using stock cultures and growth media (Alga-Gro concentrate, Carolina Biological Supply Co.). Standard glass slides (2.5 by 7.5 cm) were used as a substratum to which the

periphyton could attach. The types of algae used were a diatom, <u>Gomphonema</u> sp., the filamentous green alga <u>Oedogonium</u> sp. and the bluegreen filament <u>Oscillatoria</u> sp.. <u>Gomphonema</u> and <u>Oscillatoria</u> both were abundant in areas of Pennington Creek. <u>Oedogonium</u> occurred in Pennington Creek, usually as an epiphyte on <u>Cladophora</u>, which was the most abundant green filament in the creek. <u>Oedogonium</u> was used in the experiments rather than <u>Cladophora</u> because I had difficulty maintaining cultures of Cladophora.

Preference trials were performed in growth chambers at a constant temperature of 17°C, which was the mean annual temperature of Pennington Creek (Vaughn, 1984a). Trials were conducted in 10 by 14 by 6.5 cm plastic boxes. Boxes were filled to a depth of 5 mm with a combination of 50% Pennington Creek water and 50% distilled water. Slides were arranged side by side in the boxes so that slides with different types of periphyton alternated with each other. I tested each type of algae against the other two types as well as against blank slides as a control (Table 1). Three slides colonized with each algal type and 10 larvae were used per container. Ten replicates were performed for each treatment (Table 1) for second, fourth and final instar H. borealis larvae. Larvae used were from a laboratory colony started from individuals from Pennington Creek. Larvae were deprived of food and acclimated in the growth chambers for 24 h prior to a run. Larvae were then added randomly to the containers and their position was mapped every 10 min for 3 h. This design was based on previous observations using different sizes of containers, numbers of larvae, numbers of slides

and water depths. Replicates were evaluated for homogeneity. Data were then pooled and tested for goodness of fit to a binomial distribution (Sokal and Rohlf, 1981).

Fitness and food type

Reproductive fitness was measured either as fecundity or as the number of emerging adults when no eggs could be obtained. Larvae were reared in plastic containers 20.5 by 27 cm and 26.5 cm deep. The bottoms of the containers were lined with autoclaved gravel and sand. Sand contained the appropriate particle size ranges for the larvae to construct their cases (Vaughn, 1984b). The containers were covered with hardware cloth screen cages 26.5 cm in height. Containers were filled with a combination of 50% Pennington Creek water and 50% distilled water and kept in an environmental chamber at a constant temperature of 17°C and a 12L:12D photoperiod. Floating styrofoam platforms were provided as oviposition sites. Preliminary rearing of <u>H</u>. <u>borealis</u> in the laboratory showed that they would mate and reproduce in these containers and lay eggs on the underside of styrofoam surfaces.

Larvae were fed the same three algal types as in the grazing preference experiment. Containers with bacteria but no algae were used as a control. The experiment was repeated twice: larvae used in trial 1 were collected from Byrd's Mill Spring, Pontotoc Co., Oklahoma (Vaughn 1984a); larvae for trial 2 were collected from Pennington Creek. Second instar larvae were used in both trials. In trial 1 I had four replicates of each algal type and the non-algal control containing 60 larvae each. In trial 2, I used two replicates for

each algal type containing 200 larvae each. In both trials the containers were checked daily for adults and egg masses. Each week the larvae were fed 500 ml of culture fluid containing periphyton in trial 1. The containers were believed to be food-saturated because there was abundant visible periphyton, but actual food levels were not measured. In trial 2, periphyton was cultured on glass slides so that the amount being fed could be quantified. Approximately 40 g dry weight of each algal type was added to each container per week. I measured the amount of algae depleted by the larvae in a week on three occasions. These values averaged: <u>Oedogonium</u>, 2.87 g; <u>Gomphonema</u>, 1.82 g; and <u>Oscillatoria</u>, 0.53 g. I therefore assumed that the system was food saturated. Adults were not removed until they had died. They were then preserved in Kahle's solution and later sexed. Egg masses were removed, the number of eggs per mass tabulated, and then dried and weighed.

RESULTS

Field experiment

The results of the cluster analysis of <u>H</u>. <u>borealis</u> densities and habitat parameters are shown in Figure 1. Second and fourth instar larvae were found most often on the tops of bricks, where algal chlorophyll <u>a</u> levels were high, the current velocity was slow, and <u>Cladophora</u> was present (Cluster A, Fig. 1). Final instar larvae and pupae occurred in fast water on the downstream faces of rocks (Cluster B, Fig. 1). Grazing preference

<u>Helicopsyche borealis</u> larvae in all age classes tested showed no preference for one type of periphyton over another (Table 1). When offered a choice of slides with periphyton or blank slides the larvae always chose the slides with periphyton, no matter what type of periphyton was offered (Table 1).

Reproductive fitness

No egg masses were obtained in trial 1, and only one egg mass was obtained in trial 2. Therefore I used the number of emerging adults as a measure of fitness.

In trial 1, the total number of emerging adults was highest on the filamentous green alga <u>Oedogonium</u>. Adults emerged at approximately the same rate on <u>Oedogonium</u> and the diatom <u>Gomphonema</u> (Fig. 2). In trial 2, very low numbers of adults emerged, and almost all of these were from the <u>Oedogonium</u> replicates (Fig. 3).

DISCUSSION

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Periphyton abundance is an important variable influencing the microdistribution of <u>H</u>. <u>borealis</u> larvae. In this study all but final instar <u>H</u>. <u>borealis</u> preferred the tops of bricks, which was the surface with the greatest quantities of algae (as measured by algal chlorophyll <u>a</u>). Lamberti and Resh (1983) also found that periphyton abundance was important in determining the distribution of <u>H</u>. <u>borealis</u>. In their study larvae aggregated on enhanced periphyton but became randomly distributed once grazing had reduced periphyton to background levels.

Food resources may be patchy with regard to nutritional quality as well as quantity. Growth rates, and ultimately reproductive success, of stream insects increase with increased food quality (Gallepp, 1977; Anderson and Cummins, 1979; Ward and Cummins, 1979; Fuller and MacKay, 1981; Merritt et al., 1982). However, recognition of food patches by stream invertebrates is not necessarily qualitative. Cummins and Klug (1979) found that the ratio of algae to detritus ingested by the grazer <u>Glossosoma</u> was essentially a function of the relative densities of each type of food within a patch of periphyton, although maximal size attained (growth) was positively associated with an algal diet. Gut analyses of <u>H. borealis</u> have shown that, in general, they feed on whatever they encounter, ingesting detritus, diatoms and animal material (Coffman, 1967; Coffman et al., 1971; Mecom, 1972; Shapas and Hilsenhoff, 1976; Williams et al., 1983). In my experiments, I found that <u>H. borealis</u> did not actively select any of the algal

types offered. However, larvae in the fitness experiment consumed more green algae than diatoms, and more diatoms than bluegreen algae. Adult emergence was greater on the green filamentous algae than the other types of periphyton, indicating that this alga or its microbial epifauna may be a higher quality food resource for <u>H</u>. <u>borealis</u> than diatoms or bluegreen algae (but see Anderson and Cummins, 1979). In my field experiment <u>H</u>. <u>borealis</u> larvae were more closely clustered with the green filament <u>Cladophora</u> than with diatoms (Figure 1).

Final instar H. borealis occurred in deeper and faster water than the other instars. This behavior is probably a response to several factors. Final instar larvae may have a different or broader feeding niche. Switches in feeding preferences prior to pupation are features in the life cycles of many aquatic insects (Anderson and Cummins, 1979). Helicopsyche borealis larvae use increasingly larger sand particles in their cases as they mature (Vaughn, 1984a, 1984b; Williams et al., 1983), and larvae select sand particles according to their availability (Vaughn, 1984b). Final instars of H. borealis apparently move out into deeper, faster water where the larger sand particles they use in their cases are, by nature of stream hydrodynamics (Hynes, 1970), more available. Finally, pupae commonly occur in deeper, faster water than larvae, perhaps to avoid both predators and drought (Vaughn, 1984b). Final instar larvae may move into this habitat in preparation for pupation. By preferentially selecting the tops and other exposed surfaces of rocks in streams (Vaughn, 1984b, this study) H. borealis larvae are placing themselves in the microhabitat most likely to contain

both abundant and high quality food patches. The proportion of periphyton to detritus will be higher on exposed surfaces than in crevices because detritus will be swept away by the current and densities of periphyton will be greater because of increased exposure to light and nutrients. . <u>Helicopsyche</u> are unusual catdisflies in that their sand-grain cases superficially resembles a spiraled snail shell. I have proposed (Vaughn, 1984b) that the helical architecture of the case provides ballast and a shape which make larvae well suited for grazing on exposed surfaces in flowing water. That high quality food patches are more available on these exposed surfaces may have been an underlying selection pressure for the evolution of the helical case.

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Treatment	Larval age class	<u>G</u> -statistic
Oedogonium X <u>Gomphonema</u>	2nd instars	0.40 NS
	4th instars	0.11 NS
	Final instars	0.40 NS
<u>Oedogonium</u> X <u>Oscillatoria</u>	2nd instars	0.14 NS
	4th instars	0.12 NS
	Final instars	0.11 NS
<u>Oscillatoria</u> X <u>Gomphonema</u>	2nd instars	0.51 NS
	4th instars	0.51 NS
	Final instars	0.00 NS
<u>Oedogonium</u> X blank slides	2nd instars	3.85 *
	4th instars	7.81 **
	Final instars	6.80 **
<u>Gomphonema</u> X blank slides	2nd instars	5.46 *
	4th instars	7.09 **
	Final instars	6.42 *
<u>Oscillatoria</u> X blank slides	2nd instars	5.78 *
	4th instars	8.07 **
	Final instars	8.53 **

Table 1: Treatments used in and results of the grazing preference experiment.

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FIGURE CAPTIONS

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- Fig. 1: Dendrogram of average taxonomic distances between all measured environmental variables, indicating <u>H. borealis</u> microhabitat preferences. The cophenetic correlation coefficient is 0.78.
- Fig. 2: Frequency of adults emerging on each algal type over time in trial 1.
- Fig. 3: Frequency of adults emerging on each algal type over time in trial 2.



DISTANCE

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NO. OF ADULTS



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