Life cycles and drift of Trichoptera from a woodland stream in Minnesota

CHARLES C. KRUEGER
Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN, U.S.A. 55108

and

Department of Natural Resources, New York State College of Agriculture and Life Sciences, Cornell University, Ithaca, NY, U.S.A. 14853

AND

EDWIN F. COOK
Department of Entomology, University of Minnesota, St. Paul, MN, U.S.A. 55108

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Life cycles of Trichoptera from a stream riffle were determined from analyses of monthly size−frequency distributions of larvae, pupal densities, and observations of adult emergence. Two types of univoltine life cycles were observed (H. B. N. Hynes’ classification): slow seasonal for Brachyceromorpha americana, Brachycentrus occidentalis, and Microzona klaene, and fast seasonal for Lepidostoma bryanti. The life cycle for Glossosoma intermedium was primarily bivoltine with summer and winter generations; however, some larvae of the summer generation were suspected to overwinter as pupae or terminal instar larvae and emerge in the spring. Larval B. americana and L. bryanti showed peak drift prior to pupation and emergence which thus appeared seasonally associated with life cycle. Stream drift of M. klaene and G. intermedium was low and exhibited no clear association with life cycle or season. Drift of B. americana, M. klaene, L. bryanti, and G. intermedium was not correlated to standing stocks (p < 0.05).


L’analyse de la distribution de fréquence des tagiles, de la densité des nymphes et des observations sur l’émergence des adultes ont permis d’établir les cycles biologiques des diverses espèces de trichoptères dans la zone rapide d’un ruisseau. Il y a deux types de cycles biologiques univoltins (selon la classification de H. B. N. Hynes): un cycle saisonnier lent (Brachyceromorpha americana, Brachycentrus occidentalis et Microzona klaene), et un cycle saisonnier rapide (Lepidostoma bryanti). Le cycle biologique de Glossosoma intermedium est généralement bivoltin et il y a une génération d’été et une génération d’hiver; cependant, il semble que certaines larves de la génération d’été aient passé l’hiver sous forme de nymphes ou de larves de dernier stade et aient émergé au printemps. Chez B. americana et L. bryanti, la nymphose et l’émergence sont précédées d’une importante dérive qui semble associée de façon saisonnière au cycle biologique. La dérive de M. klaene et de G. intermedium est faible et ne semble pas reliée de façon particulière au cycle biologique ou à la saison. La dérive de B. americana, de M. klaene, de L. bryanti et de G. intermedium n’est pas reliée à la biomasse (p < 0.05).

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Introduction

Life cycle studies are often an important adjunct to investigations of benthic invertebrate communities. Knowledge of life cycles can be useful in the development of efficient sampling programs for species of interest (Cummins 1975; Resh 1979). Such programs may utilize irregular sampling intervals and changing mesh sizes in capture nets in order to reduce sample sorting time. Studies of ecological energetics also require life cycle information to make secondary production estimates. For example, the size−frequency method of production estimation uses the duration of larval life (cohort production interval) as part of the calculation (Benke 1979). Knowledge of the length of larval stages therefore is a prerequisite in research that uses this production estimation method (Waters 1979). Observations on the life cycles of invertebrates in unperturbed ecosystems should also prove useful for comparison with populations from altered environments (e.g., thermally). Several studies have intensively investigated the life cycles of Trichoptera fauna from lotic waters (e.g., Décamps 1967; Ulfstrand 1968); however, few have related the seasonal patterns of stream drift to life cycles (Anderson 1967; Elliott 1964; Cloud and Stewart 1974).

The present study reports the life cycles and drift patterns for some of the Trichoptera genera that occur in a small, spring-fed stream. This study was part of a larger investigation on the secondary production of invertebrates in Minnesota streams (Krueger and Cook 1981; Krueger and Waters 1983).

Methods

Invertebrate collections were taken from North Branch Creek (43°38′ N, 92°14′ W), a first-order stream located in the unglaciated southeast corner of Minnesota. The stream lies in an area of karst topography and originates from a limestone cave. The stream had an average width of 6 m at base flow and an average discharge of 0.166 m³·s⁻¹. Further information on the site location has been reported by Krueger and Waters (1983).

Ten benthic samples were taken once per month from March 1977 to February 1978 from a riffle in North Branch Creek. Collections were made with a modified Surber sampler (0.1 m²) fitted with 471 μm mesh netting (Krueger and Cook 1981). Sample locations were determined through a stratified random process to ensure that collections were taken throughout the length of the riffle.

Duplicate invertebrate drift samples (24 h) were collected at the downstream end of each study riffle immediately prior to bottom sampling each month. Stream discharge was at base flow on each of the dates sampled. The drift nets were constructed of 471 μm mesh and measured 15 × 30 × 180 cm. Discharge through the nets was measured at the end of the 24-h period. Daily drift rates by month were

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1Address for correspondence.
calculated in the manner described by Waters (1972). These drift rates estimate the total number or weight of individuals that would pass over the riffle if the stream discharged 1 m$^{-1} \cdot$ s$^{-1}$ for 24 h. Bottom and drift invertebrate samples were preserved in 10% Formalin in the field.

Caddisfly larvae abundant in the bottom samples were separated by taxon into size classes based on body lengths or pronotum widths. Specimens that were in good condition when measured were removed from cases and set aside by size class for later weighing. Mean individual wet weight was measured to the nearest 0.1 mg for each size class after centrifugation to remove excess water. Pupae in the bottom samples were separated by taxon and counted. Species identifications were based on adults collected streamside by hand net, captured by drift net, or reared from larvae. Further information about sampling procedures has been reported elsewhere (Krueger and Cook 1981; Krueger and Waters 1983).

Results

Brachycentrus americanus (Banks): Brachycentridae

Size–frequency distributions of larvae by month for B. americanus indicated a univoltine life cycle with larvae occurring for approximately eleven months from August to June (Fig. 1). Larvae grew rapidly in the spring (March through the end of May) and were pupating by late May and June. Adult emergence and egg incubation apparently occurred in July since no larvae were collected and pupal densities had declined sharply. Small larvae of the new cohort were first collected in August and grew rapidly through November. Little or no growth occurred during the winter months.

Univoltine life cycles for B. americanus have been previously reported from other locations in North America. In Oregon, data from stream drift suggested that B. americanus was univoltine with generations starting in late summer (Anderson 1967). Univoltinism was also indicated for this species in Colorado; however, pupation did not occur until late summer, which caused the population to overwinter as eggs (Mecom 1972). Gallepp (1974a) reported B. americanus in Wisconsin as univoltine and that it grew slowly in autumn and winter but more rapidly in the spring.

Daily drift during the year exhibited two maxima, in the spring (March–April) and in the autumn (October–November) (Fig. 1). Little or no drift occurred at other times of year. Stream drift was not correlated with larval standing stocks ($r = 0.04$, Fig. 1). The high drift rate in the spring may have been related to movements associated with pupation while the autumn drift occurred in a period of rapid larval growth. Gallepp (1974b) reported that movements of B. occidentalis increased immediately preceding pupation and were associated with a wandering behavior possibly in search of pupation sites. Anderson (1967) reported that B. americanus exhibited high drift in the fall and winter when larvae were small.

Brachycentrus occidentalis (Banks): Brachycentridae

Analysis of seasonal size distributions of larvae indicated a univoltine cycle with larvae present for approximately 11 months from May through April (Fig. 2). Larvae collected on March 1 occupied a broad size range, although most (68%) were larger than 7.0 mm in length. This size distribution remained through the end of March. In late April, larval numbers were low and nearly all animals were pupating (Fig. 2). Adult emergence was observed at the end of April and in May. Small larvae of the new generation were first collected in May. A marked decrease in abundance of larvae observed in the June samples may have been caused by a flood that occurred earlier in the month. Larval growth of the new cohort appeared rapid in the summer months of July and August; however, so few larvae were collected in the autumn and winter months that growth patterns were uninterpretable for the remaining period. The life cycle of occidentalis differed from americanus in that adult emergence occurred in the spring rather than in the summer and larvae were generally larger during most months (Figs. 1 and 2).
A similar univoltine life cycle for *B. occidentalis* has been described from Lawrence and Parfrey’s Glen Creeks, Wisconsin (Gallepp 1974b; Karl and Hilsonhoff 1979). Univoltine life cycles have also been reported for other species of this genus, *B. spinæ* (Ross and Wallace 1981) and *B. americanus* (Anderson 1967; Mecom 1972; Gallepp 1974a; present study).

Stream drift rates of *B. occidentalis* in North Branch Creek only occurred in the spring prior to the June population decline (Fig. 2). Although large numbers of small larvae were present in May, little drift occurred. Daily drift was correlated with larval standing stocks (*r* = 0.78; *p* < 0.01); however, this association should be interpreted cautiously because of the
possible population instability during the summer months.

*Micrasema kluane* Ross and Morse: Brachychirintidae

Size–frequency histograms of larvae clearly indicated a univoltine life cycle with larvae occurring for approximately ten months from July to April (Fig. 3). Growth for these larvae appeared to be slow in March, but accelerated in April. Maximum densities of pupae occurred in April and May. In May, larval numbers were greatly reduced and adults were first observed. Young larvae of the new cohort appeared in July and grew rapidly through November. Growth was slow through the winter months and would probably have resumed in spring.

Previous accounts of the life cycle of *M. kluane* were not found in the literature. Univoltine life cycles for other species of *Micrasema* have been reported from Pyrenean streams, France, for *vestitum, longulum, moestum, difficile, and minimum* (Décamps 1967; Décamps and Lafont 1974). *Micrasema morosum* deviated from this pattern and took 1 to 3 years to complete its life cycle depending on the altitude of the stream (Décamps and Lafont 1974).

Stream drift of *M. kluane* larvae was low throughout the life cycle and was not correlated to the standing stocks ($r = 0.12$; Fig. 3). Descriptions of stream drift for *Micrasema* were not found in the literature.

*Lepidostoma bryanti* (Banks): Lepidostomatidae

Monthly size–frequency distributions clearly indicated a univoltine life cycle with larvae occurring for approximately eight months from September to April (Fig. 4). The narrow size ranges of larvae within months suggest that pupation, emergence, and egg hatching occurred within relatively short time intervals. During March and April larvae grew rapidly into the largest size classes. In May, only pupae (Fig. 4) and adults were observed and egg laying presumably followed shortly thereafter. Egg incubation and diapause may have occurred from May to August since no larvae were collected during this period. Larvae of the new cohort were first collected in September and grew rapidly through November. Larval growth was slow in the winter months from December through February.

A similar univoltine life cycle has been reported for *L. bryanti* from Parfrey’s Glen Creek (Karl and Hilsenhoff 1979). The major difference in the life cycle descriptions between the two studies is the presence in Parfrey’s Glen Creek and absence in North Branch Creek of small larvae in the summer. Karl and Hilsenhoff (1979) reported that this species preferred pools over riffle areas as habitat. In the present study, small larvae (<1 mm) may have been present during the summer in habitats other than riffle areas. Univoltinism has been reported for the species of *Lepidostoma* that follow: *unicolor* (Anderson 1967; Winterbourn 1971; Grafius and Anderson 1980), *quercina* (Grafius and Anderson 1979), *costalis* (Karl and Hilsenhoff 1979), *griseum* (Karl and Hilsenhoff 1979), *cascadense* (Grafius and Anderson 1980), and three unidentified species (Mackay 1969).

Stream drift of larval *L. bryanti* increased in the spring to a peak in April just prior to pupation (Fig. 4). Daily drift occurred at low levels during the rest of the year. Drift rates appeared significantly correlated to larval standing stocks (Fig. 4; $r = 0.71$, $p < 0.01$). This statistical association was largely dependent on the April collections and was nonsignificant when these data were omitted ($r = 0.04$). Peak spring drift rates have also been reported for *L. unicolor* from Oregon (Anderson 1967).

*Lossosoma intermedium* (Klapálek): Glossosomatidae

Larval size distributions and adult emergence patterns revealed a bivoltine life cycle for *G. intermedium* (Fig. 5). Large larvae of the winter generation, probably in their terminal instar, occurred in early spring (March–April) but had disappeared by May. Adults were observed in April and May.
Fig. 5. Pronotum width frequency, adult daily drift, pupal densities, larval daily drift, and standing stock estimates for *Glossosoma intermedium* from North Branch Creek, 1977 March to 1978 February. The number below each histogram is the number of individuals collected. Vertical lines represent 1 SE on one side of the estimates.

(Fig. 5) and egg laying presumably followed their emergence. Small larvae of the summer generation first occurred in May and grew steadily into larger size classes until autumn when another adult emergence was observed. Larvae of the new winter generation were collected in the October bottom samples. These larvae grew rapidly during the winter so that by February most of the larvae (78%) were in the two largest size classes. Since large larvae were present throughout the autumn and early winter, we suspect that some larvae of the summer generation do not emerge in the autumn but delayed pupation and emergence until the following spring. This interpretation is further supported by the presence of pupae throughout the year (Fig. 5). The minimum length of larval life was 6 months from October to April for the winter generation and 5 months from May to November for the summer generation. The maximum length was 11 months from May to April.

The present study is the first report of bivoltinism for *G. intermedium*. Ulfstrand (1968) reported that this species was univoltine in Swedish streams with larvae found from August to November. These populations overwintered as pupae and emerged as adults from June to August. Karl and Hilsenhoff (1979) reported that this species was univoltine with overlapping generations. This population showed two emergence periods with pupae present from April to July. Bivoltinism as reported in the present study, however, is apparently not uncommon among species of *Glossosoma*. Life cycles similar to that described for *intermedium* in the present study have been reported for *penitus* from an Oregon stream (Anderson and Wold 1972; Anderson and Bourne 1974) and for *nigrior* from a Michigan stream (Kovalak 1978).

Stream drift of larvae was low, highly variable, and exhibited no clear association with standing stocks (*r* = 0.08), adult emergence, or season (Fig. 5). Waters (1962) reported that stream drift of *G. intermedium* in Valley Creek, Minnesota, exhibited a peak in August.

**Discussion**

Among the Trichoptera species described in the present study, two types of univoltine life cycles were observed (Hynes 1961 classification): slow seasonal for *B. americanus*, *B. occidentalis*, and *M. kluane*, and provisionally, fast seasonal for *L. bryanti*. The life cycle for *G. intermedium* was classified as fast seasonal when bivoltine and slow seasonal for univoltine generations. With the exception of *B. americanus*, the life cycles of each of these caddisflies were similar in having a winged phase in the spring. Asynchrony of life cycles may be important in preventing competition between the congeneric *B. americanus* and *B. occidentalis*. Gallepp (1977) has suggested that spatial segregation may also exist between these two species, with *B. americanus* more abundant in upstream areas and *B. occidentalis* abundant in downstream areas.

Although the Trichoptera in the present study constituted 12% of the total macrobenthic standing stock by weight, they represented only 3% of the mean daily drift of benthos averaged over the year (Krueger 1979). These comparisons were in agreement with the observation that Trichoptera larvae in general exhibit low drift rates (Müller 1974). Notable exceptions of high drift rates have been observed particularly in the family Limnephilidae (e.g., Waters 1968), none of which were substantially represented in the study riffle in North Branch Creek. The caddisflies included in this report comprised 39% of the Trichoptera annual mean standing stock by weight in the study.
area (Krueger 1979). The balance of the standing stock mainly consisted of Hydropsychidae.

Seasonal patterns in drift may be related to several factors such as current velocity, water temperature, growth, and life cycle (Waters 1972; Müller 1974). In the present study, the drift of B. americanus and L. bryanti showed peak drift prior to proposed periods of pupation and emergence and thus appeared seasonally associated with life cycle. The observation that drift of these caddisflies was not correlated to standing stocks is not unusual (Waters 1972). High stream drift rates of Trichoptera larvae prior to pupation have been reported for Potamophylax cingulatus (Otto 1971), Oligophlebes sigma (Pearson and Kramer 1972), B. occidentalis (Gallepp 1974b), and Cheumatopsyche (Cloud and Stewart 1974) and is apparently not uncommon among Trichoptera species. Movements prior to pupation may be related to feeding activity due to changing nutritional requirements or the search for suitable pupation sites (Otto 1971; Gallepp 1974b; Cloud and Stewart 1974). The influence of life cycle stage on drift suggests that comparisons of drift—production relationships (Waters 1972) should be made among species with similar seasonal patterns of drift.

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