LIFE HISTORY, SURVIVAL, GROWTH, AND PRODUCTION OF HYDROPSYCHE SLOSSONAE IN MILL CREEK, VIRGINIA

A Dissertation submitted to the graduate faculty of Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biology.

by

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ABSTRACT

Life history and annual production of *Hydropsyche slossonae* were determined in Mill Creek, Virginia, emphasizing aspects of its early life history. Mill Creek is a first–order stream in the Central Appalachian Ridges and Valleys ecoregion. EAch adult female laid approximately 230 eggs in May and June which hatched in 13 days. Five larval instars were recorded with most individuals overwintering in III and IV instars. Pupation and emergence occurred primarily over a six week period in May and June. No mortality in the egg stage (0%) was detected, while high mortality in I instar (92.9%) was due in part to sibling cannibalism. Second through fifth instars showed constant, low mortality, with high mortality again in the pupal stage; an estimated 0.5% of the original eggs survived to adulthood. Growth analysis revealed two distinct growth phases; one from hatching through IV instar (0.008 mg/day) and a much faster growing V instar in May (0.085 mg/day).

Annual production estimates ranged from 3 to 5 g/m^2 and were highly variable. It may be more precise to estimate production by predicting biomass from survivorship and growth functions than directly from sample data. On a per day basis, production was not constant but varied during the year. Yield per day peaked slightly later than peaks in production. High daily production occurred immediately after hatching due to growth of many small individuals. At the end of the generation, there was another period of high daily production due to fast growth by fewer larger individuals. Most production occurred from March through June. At other times, daily production was relatively low.

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INTRODUCTION

Hydropsychid caddisflies are often dominant aquatic insects in eastern United States streams. They prefer fast flowing water from which they can filter suspended particles using silken nets and are often abundant below impoundments where they filter seston exiting reservoirs (Mackay 1979, 1984a). They have been associated with mild organic enrichment (Hellawell 1986) and seem to flourish in moderately impacted stream segments where they are one of the most common stream insects (Mackay 1979). In order to understand the systems in which these organisms live, it is imperative to know of the organisms themselves. While there have been several studies of hydropsychid life histories, none have detailed all parts of the life cycle or examined survival and growth through the entire life cycle.

The description of a population's life history is an account of the events that occur through the life time of the individuals and link one generation to the next at a variety of levels (Butler 1984). These levels include individuals, populations and ecosystems. The life history can be described by component parts to include: life cycle aspects, reproduction, survival, growth and production. The life cycle is the product of long term evolutionary changes influenced by a species' evolutionary past and is the framework within which the variable components of the species life history works. Survival and reproduction are measures of an individual's success and affect the population's numerical stability. Knowledge of an organism's mortality schedule and reproductive rate aids in understanding how the life history has evolved and what factors were involved in its evolution (Butler 1984). Although

those data are important in understanding how populations are controlled and evolve, few studies have attempted to describe the survivorship of aquatic insect populations (Elliott 1981, 1982a).

At the ecosystem level, the importance of a population is measured by production or energy flow to other trophic levels. Production is influenced by life history in terms of survival and growth. The timing of production and its fate are related to mortality schedule and growth rate. Production is related to the population's interaction with the environment and combines many components of the life history in one number (Benke 1984).

The goal of this project was to describe the life history of *Hydropsyche slossonae* in Mill Creek, Virginia. The specific objectives were to 1) describe the life cycle and its phenology; 2) develop an actual survivorship curve from the number of organisms that enter each stage. This was done by constructing a life table budget; 3) define the shape of the growth curve; and 4) calculate and assess the importance of the various life history parameters in the timing and magnitude of production and yield.

LITERATURE REVIEW

Description and Identification

The order Trichoptera is one of the largest groups of aquatic insects with over 1200 species in North America (Wiggins 1977). The larval stages of all but a few species are aquatic and occur in a variety of freshwater habitats. The group is generally categorized by their case–making behavior which is closely related to their ecological role.

The Hydropsychidae is the most diverse family of net spinning caddisflies (Unzicker et al. 1982). The larvae typically build a fixed funnel–shaped retreat of silk with a feeding net in the downstream end. Although plant material, detritus, and small stones are used in the construction of their retreats, they are not considered case builders except during pupation. *Hydropsyche* spp. often feed as grazers and predators in addition to filter–feeding. Experimental studies have shown that hydropsychid growth rates are much faster when fed animal material or diatoms than when fed fecal or leaf detritus (Fuller and Mackay 1981). Net mesh size is a species–specific trait. In areas where two or more species occur, larvae have been observed to segregate space by flow velocity (Wallace 1975, Malas & Wallace 1977, Edington et al. 1984).

Approximately 70 species of the genus *Hydropsyche* have been described in North America (Schuster and Etnier 1978). Of relevance to the *Hydropsyche* of the eastern United States was the elevation of the *H. morosa* (previously *H. bifida*) species group to the genus *Symphitopsyche*. This separation received mixed acceptance among *Hydropsyche* taxonomists (Schuster 1984). Later Nielsen (1981) elevated the subgenus *Ceratopsyche* to generic status. This included the *morosa*

species group and isolated *Symphitopsyche* in Africa. Although Schuster (1984) supported this grouping, it was also not accepted by many. Recently Scheter et al. (1986) reassigned *Ceratopsyche* to subgenus status. *Hydropsyche slossonae* belongs to the *Ceratopsyche* subgenus.

The subgenus *Ceratopsyche* shows ecological differences from the other *Hydropsyche* (Table 1) . The subgenus *H.* (*Hydropsyche*) tends to inhabit larger rivers than the *H.* (*Ceratopsyche*) (Gordon and Wallace 1975, Schuster and Etnier 1978, Mackay 1979). *Hydropsyche slossonae* is widely distributed over northeastern United States and Canada. The larvae are typically found in cool spring–fed headwater streams.

Larvae of the subgenus *Ceratopsyche* are separated from the other *Hydropsyche* by the presence of club hairs and absence of scale hairs on the abdomen. Diagnosis of the species of *Hydropsyche* larvae has been based on head capsule patterns of fifth instars (Schuster and Etnier 1978). It has been recently shown that fifth instar *H. slossonae* exhibit variable head color patterns (Schefter and Wiggins 1986). Most fifth instar *Hydropsyche* in Mill Creek, Virginia lack the median spots which were the primary characteristic of *H. slossonae* in the old key (Schuster and Etnier 1978). Schefter and Wiggins (1986) suggested using setal characteristics for identification. Identification of earlier instars can be done by characteristics outlined by Mackay (1978). Adult classification is based on the shape of the male genitalia and wing veination. At the specific level, the shape of the male genitalia is of primary importance in identifying adults.

Table 1. Habitat types for species of *Hydropsyche* (*Hydropsyche*) and *Hydropsyche* (*Ceratopsyche*) (from Gordon & Wallace 1975, Schuster & Etnier 1978).

Hydropsyche (*Hydropsyche*)

Small Stream Headwaters	Medium River Mid–Reaches	Large River Tailwaters	Coastal Plain Blackwater
frisoni	*hoffmani*	*orris*	*elissoma*
scalaris	*patera*	*bidens*	*decalda*
betteni	*carolina*	*phalerata*	
depravata	*leonardi*	*valanis*	
demora	*mississippiensis*	*aerata*	
arinale	*venularis*	*potamacensis*	
		cuanis	
		hageni	
		simulans	
		incommoda	
		rossi	
		dicantha	

Hydropsyche (*Ceratopsyche*)

Small Stream Headwaters	Medium River Mid–Reaches	Large River Tailwaters	Coastal Plain Blackwater
sparna	*fattigi*		
morosa	*alvata*		
slossonae	*sparna*		
macleodi	*bifida*		
bronta	*catawba*		
riola	*cheilonis*		
ventura	*recurvata*		
etnieri	*walkeri*		
	alhedra		

Life Cycle

Caddisflies are holometabolous, and the aquatic larvae take from a few months to two years to mature. Length of larval development is species–specific and is influenced by environmental factors such as temperature and food quality. The larvae of most species go through five larval instars (Figure 1). Length of pupation is variable, lasting from a few days to several months. Adults typically live for one to two weeks.

Voltinism

Voltinism refers to the frequency with which life cycles are completed. *Hydropsyche* are generally univoltine, bivoltine or trivoltine (Table 2). Mackay (1984a) found *H. bronta* to be trivoltine (three generations per year) in Ontario, while Ross and Wallace (1983) reported the same species to be univoltine in North Carolina. In general, most species appear to be capable of producing more than one generation per year under optimum environmental conditions. Parker and Voshell (1982) concluded that differences in voltinism are due to interactions between food quality and temperature regime. Food and temperature have been shown to affect growth interactively in other aquatic insects (Sweeney and Vannote 1984, Sweeney et al. 1986a, Sweeney et al. 1986b). Mackay (1979) suggested that because *Hydropsyche* spp. cease growth during the winter, populations (or individuals) that can overwinter in the final larval instar can mature earlier and therefore produce more generations during the growing season, increasing the probability of being multivoltine.

Hydropsyche slossonae is usually univoltine but can be bivoltine at some locations. Ross and Wallace (1983) found *H. slossonae* to be univoltine in North

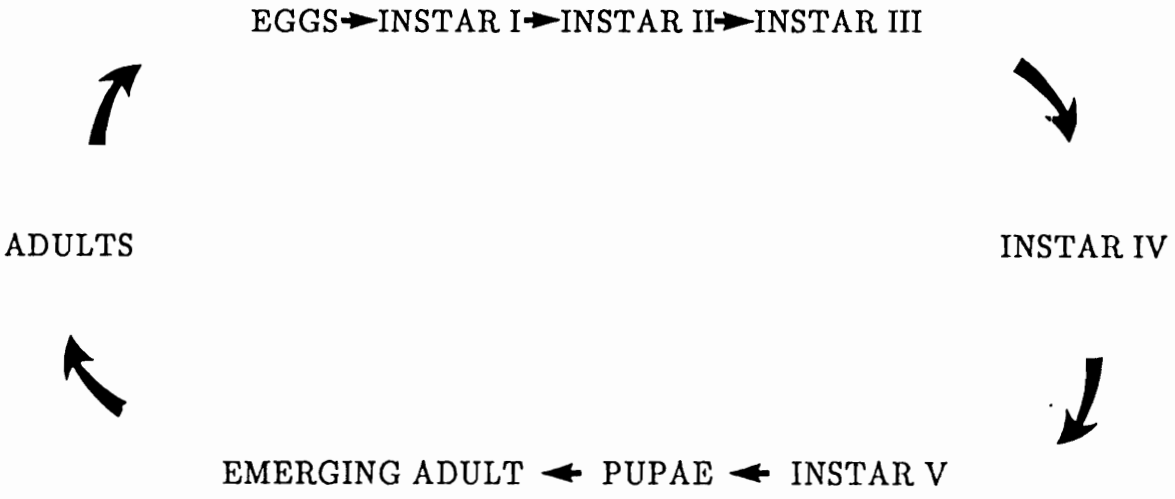

Figure 1. Generalized trichopteran life cycle

Table 2. Summary of life history and production data from the literature for selected species of Hydropsyche.

Species	Voltinism*	Over—Winter	Pupation	Max P/Year	P/B	Location	Reference
H.(C.) riola	uni—bi	5	April			Minnesota	Mackay 1986
H.(C.) slossonae	uni	3+4	May			Minnesota	Mackay 1986
H.(C.) slossonae	bi—uni	5—bi,3—4—uni	May—June uni			Ontario	Mackay 1979
H.(H.) betteni	bi—uni	5—bi,3—4—uni	April—May bi				
H.(H.) dicantha	uni—bi	5—bi,3—4—uni	July—August				
H.(C.) sparna	uni—bi	5—bi,3—4—uni					
H.(H.) scalaris	uni	5—bi,3—4—uni					
H.(C.) bronta	bi—tri or offset cohorts	5	May—June—August			Ontario	Mackay 1984
H.(C.) morosa	bi	5					
H.(H.) incommoda	tri	5	Mar—Apr,June—July,August	1461.8 kgDW/ha	4.2	Virginia	Parker & Voshell 1982
H.(C.) sparna	tri	5		16.2	5.2		Parker & Voshell 1982
H.(H.) venularis	tri	5		776.6	4.0		
H.(C.) slossonae	uni			64 AFDW/m^2	4.9	North Carolina	Ross & Wallace 1983
H.(C.) sparna	uni			174	7.2		
H.(C.) bronta	uni			36	5.1		
H.(C.) betteni	uni		28	5.5			
H.(H.) betteni	bi	3—4—5	Apr—May & Aug—Sept	10g AFDW/m^2	13.74.9	Georgia	Freeman & Wallace 1984
H.(H.) incommoda	uni—bi			19 mgDW/m^2	6.4	Georgia	Benke et al. 1984
H.(H.) elissoma	bi			10.83	7.4		
H.(C.) sparna	uni—bi	3—5	June—Oct	86.3	4.25	Georgia	Benke & Wallace 1980
H.(C.) macleodi	bi	5	April	26.7AFDW mg/m^2	5.44		
H.(H.) incommoda	bi	3	April—Sept	10789.88 AFDW/m	7.67	Georgia	Cudney & Wallace 1980

* — uni = univoltine
bi = bivoltine
tri = trivoltine

Carolina. Mackay (1979) described a population where some individuals were bivoltine and others were univoltine below small impoundments in Ontario, but below a similar impoundment in Minnesota, the population was univoltine (Mackay 1986).

Life Cycle Description

Observations of the oviposition habits of *Hydropsyche* indicate that most egg laying occurs from 30 to 90 minutes after sunset (Deutsch 1984). In *Hydropsyche phalerata*, egg masses contained an average of 367 eggs, and these eggs were largest and most dense in mid–June. Adults oviposited all summer with a peak in June (Deutsch 1984). In general, eggs are laid underwater in clumps of a few to several hundred in a gelatinous mass cemented to submerged stones or detritus. The masses are usually one egg deep and are thought to take 1–2 weeks to hatch (Balduf 1934, Glasgow 1936, Fremling 1960).

In six univoltine populations of *Hydropsyche slossonae* in Minnesota, first and second instars predominated during summer, and the populations tended to overwinter as third instars (Mackay 1986). Pupation in these univoltine populations began in late May and early June, with recruitment of first instar larvae lasting from July to September and November. Head widths increased according to Dyar's law (Mackay 1979), that is, a geometric increase in head width of instars (Table 3). Mackay estimated instar durations from other life history data. Larvae overwintered in III instar.

Adults of *Nectopsyche albida* (Leptoceridae) in Indiana exhibited bimodal seasonal flight patterns with peaks in early spring and late summer (Tozer et al. 1981). This bimodal flight pattern suggests bivoltinism. Hydropsychids probably

Table 3. *Hydropsyche slossonae* instar head widths and durations in months (from Mackay 1978, 1979, Mackay and Waters 1986).

Instar	# Measured	Range (mm)	Mean (mm)	Duration (months)
V	842	1.01–1.30	1.16	2.5
IV	487	0.70–0.93	0.80	2.5
III	428	0.47–0.59	0.53	4.75
II	143	0.34–0.36	0.35	1.0
I	59	0.23–0.25	0.24	0.25

exhibit a similar bimodal flight periodicity when they are bivoltine. Adult *Hydropsyche* spp. are thought to live 2 to 15 days (Glasgow 1936, Badcock 1953, Fremling 1960). Much less is known about adult *Hydropsyche* than thesis immature stages.

Microdistribution

In general, *Hydropsyche* spp. prefer fast flowing water (i.e., riffle areas) (Unzicker et al. 1982). Cellot et al. (1984) found the first two larval instars of *Hydropsyche modesta* and *Hydropsyche contuberalis* near the banks and older instars in the main channel. Early instars may have a positive phototaxis which is thought to be a dispersal mechanism away from shorelines (Coutant 1982). Rutherford and Mackay (1985) found larvae of *Hydropsyche* (*Ceratopsyche*) *morosa*, *H.* (*C.*) *bronta*, *H.* (*C.*) *sparna*, and *H.* (*C.*) *slossonae* to be most numerous in the top layer of substrate. They also found no difference in the distributions of the various instars of these species. Pupae were found at variable depths in the substrate. Pupation usually lasts from 6 to 9 days (Fremling 1960, Rhame and Stewart 1976, Mackay 1979).

Survival

Biotic causes of trichopteran mortality include parasitism and predation. Chironomidae have been documented to cause 66% mortality during the *Hydropsyche* pupal stage in Canada (Rutherford 1986). In Oregon, eggs of the limnephilid caddisflies *Ecclisocosmoecus scylla* and *Hydatophylax hesperus* were preyed upon by a phorid fly *Megaselia alsea* resulting in 38% mortality (Robinson and Wisseman 1983, Wisseman and Anderson 1984). Larvae are regularly eaten by

other caddisflies (Martin and Mackay 1983), and in Mill Creek, I have observed *H. slossonae* in sculpins. Parasites of larval Trichoptera include ichneumonid wasps (Elliott 1982b), Empididae and Chironomidae (Knutson & Flint 1971, 1979, Parker & Voshell 1979, Vinokour & Anderson 1981).

Butler (1984) stated that by knowing the schedule of mortality through the life cycle, we may better understand how life histories are shaped. However, few studies have considered the timing of mortality in caddisflies. *Philopotamus montanus* (Philopotamidae) had a 10% survivorship from egg to II instar. No estimates were given for survival through I instar (Elliott 1981). Only 2 percent of individuals in the English Lake district completed the life cycle and only 0.4 percent of the females survived to lay eggs. Similar survivorship was observed in another English caddisfly, *Odontocerus albicarne* (Odontoceridae) (Elliott 1982a). In this species, losses equaled 99 percent in the eggs and first two instars. Of larvae that reached III instar, only 30 percent pupated and 25 percent of those died. In a south Swedish stream, *Potamophylax cingulatus* was estimated to have a survivorship of 1–2% from egg to imago (Otto 1975).

Production studies that use the size–frequency method are in effect summing losses of the size classes. However, rarely do these papers include raw data and those that do seldom have estimates of I or II instars. For these reasons, most production papers cannot be used to determine survivorship throughout the life cycle.

Cohort methods of production assume perfect synchrony of population growth within cohorts (Benke 1984). This assumption is always violated because no population grows in complete synchrony. Therefore, these methods always give apparent rather than actual survivorship (Benke 1984). Figures 2 and 3 illustrate

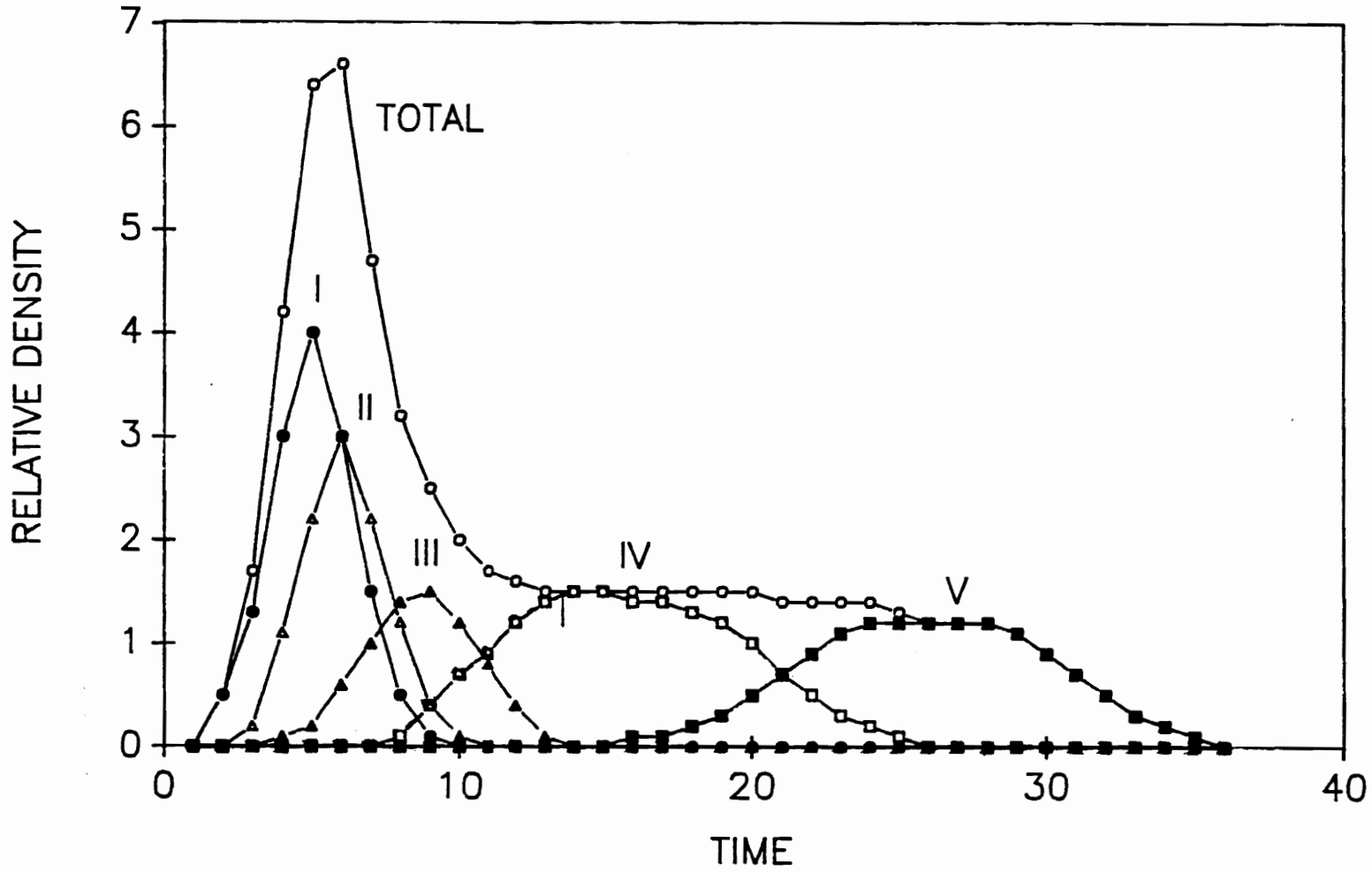

Figure 2. Hypothetical simulation of an apparent survivorship curve from a population with five larval instars. Hatching occurs over a five day period. The apparent survivorship is the total number present on a given day. This simulation was adapted from Benke 1984.

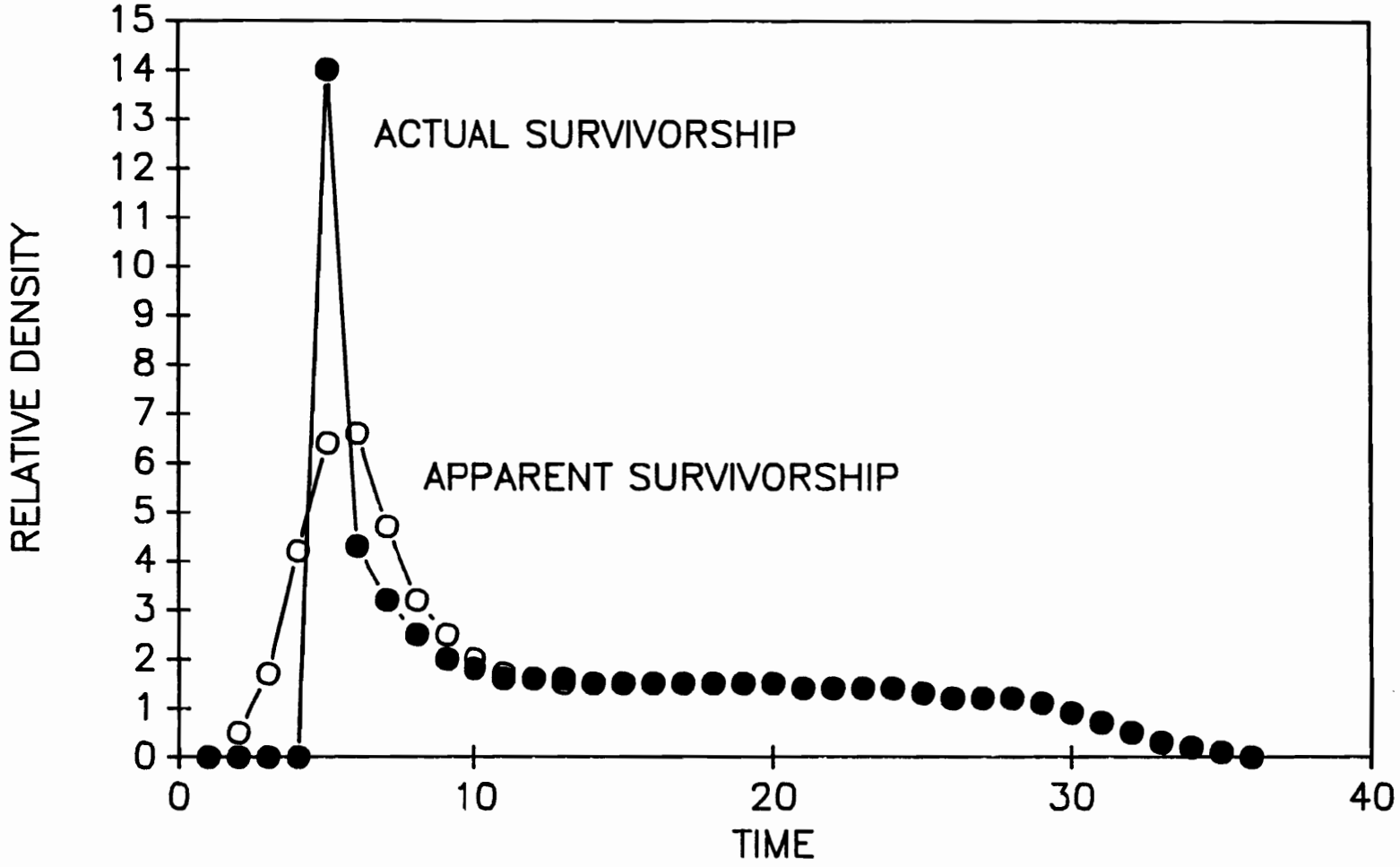

Figure 3. The apparent survivorship curve from Figure 2 and the actual survivorship curve produced b y synchronizing all individuals to hatch the same day.

the difference between apparent and actual survivorship. The apparent survivorship is the density curve plotted over time. Because recruitment of early instars lasts longer than the average life span of an individual, all I instar individuals are not alive at any time. It is therefore possible that maximum density of I instar present on a given date is less than that of older instars or as illustrated in Figure 2, the maximum number of I instars is not an accurate estimate of the number of individuals starting the generation. The actual survivorship curve synchronizes all individuals to start the generation at the same time (Figure 3). Comparison of the two curves (Figure 3) indicates that the number present early in the generation is not an accurate description of how many enter the generation.

Mass and Growth

Mackay (1984b) found that average individual mass of *Hydropsyche* spp. varied least in winter. However, during the summer when the IV instars started emerging, average individual mass was highly variable. In the same study, masses of male and female *Hydropsyche betteni* indicated differential growth.

Production

Production estimates for *Hydropsyche* spp. range from 10 mg/m^2 to 146 g/m^2 dry mass (Table 2). In Virginia, Parker and Voshell (1983) attributed greatly increased production by hydropsychids below a dam to high food quality of seston at this site. Animal material in the form of zooplankton from the lake outlet made up 57% of the production. Benke and Wallace (1980) investigated the trophic basis of production in caddisflies and found 80% of the production was attributable to animal food, while detritus and algae contributed 13% and 8% respectively. Ross

and Wallace (1983) attributed low production of hydropsychids in a headwater stream to low nutrients. Estimated production ranged from 23 to 64 mg AFDM/m^2/year with a diet of 16 to 49% animal material and 38 to 83% fine detritus. Because of the better assimilation efficency, 72% percent of the annual hydropsychid production originated from animal material. In a blackwater river snag habitat Benke et al. (1984) reported that net spinning caddisflies (primarily *H. incommoda*) contributed more than half of the primary consumer annual production. Cudney & Wallace (1980) found greatest production at intermediate flow velocities. They also found winter cohorts to have a higher production than summer cohorts due to greater terminal instar body weights. This was also found to be true in *Hydropsyche morosa* and *Hydropsyche betteni* in the South River, Virginia (Willis et al. 1986).

Mackay and Waters (1986) reported production of *H. slossonae* in Minnesota to be higher (2 to 5x) downstream of small reservoirs than upstream. Annual production estimates at this site ranged from 0.9 to 40 g/m^2 dry mass. The higher production was attributed to higher quality food below the impoundment. It is apparent that hydropsychid production is highly dependent on quantity and quality of food. When animal material is available, production can be increased.

STUDY SITE

Mill Creek is a first–order tributary of the North Fork of the Roanoke River located in Montgomery County, Virginia (lat. 37°15′51′′, long. 80°20′27′′). The stream is approximately 1.25 km long with a gradient of 20 m/km (2% slope) and drains an area of 6.5 km^2. The valley is narrow and has steep walls. There are several springs and caves in the area, and the stream maintains a steady flow even during extended dry periods. A trout pond is located upstream of the study area; however, because of the many springs, it is though to have little effect on the study site.

The stream flows through a narrow valley and is a year–round water supply for livestock. There is a limited riparian canopy, but the steep wooded valley sides shade the channel and provide allochthonous inputs to the stream. The valley floor is as narrow as 10 m in some places. The stream flows over a bedrock channel for approximately 0.5 km and then passes through a culvert after which the channel becomes alluvial to the mouth. The study area was a 22 m reach in the alluvial section with these habitat types: pool, slow riffle and fast riffle (Table 4).

In the North Fork of the Roanoke River, the dominant hydropsychid was *Hydropsyche bronta*, while in Mill Creek *Hydropsyche slossonae* was dominant. Because *Hydropsyche slossonae* was rare in the North Fork and because of the steep sides of the Mill Creek Valley, it was assumed that only limited immigration of adults occurred.

Seasonal water chemistry data presented in Table 5 show little seasonal variability. Dissolved oxygen was near saturation, and the pH was slightly

Table 4. Selected physical variables for the study site habitats in Mill Creek, Virginia. Measurements were made once at base flow.

Parameter	Fast riffle	Slow riffle	Pool
Mean depth (cm)	14.5	15	28
Mean velocity (cm/sec)[a]	51	36	BD
Substrate size	Gravel–Cobble–Boulder	Gravel–Cobble–Boulder	Silt–Mud
Dimensions width × length (m)	2×8	2×6	3×8

BD – Below detection
a – General Oceanics digital flowmeter.

Table 5. Water chemistry data from a single grab sample for Mill Creek, Virginia.

Date	Dissolved[1] Oxygen mg/l	pH[2]	Total[3] Alkalinity mg/l	Hardness[4] mg/l	NO_3[5] Nitrogen mg/l	NO_2[5] Nitrogen mg/l	Total[6] Phosphates mg/l	Ortho[7] Phosphates mg/l
Jan 87	9.0	7.8	239.4	342.0	0.73	BD*	0.01	0.01
May 87	8.0	7.8	222.3	273.6	0.78	BD	0.02	BD
Aug 87	8.0	8.0	239.4	307.8	0.83	BD	0.01	0.01
Nov 87	9.0	8.0	222.3	290.7	0.73	BD	0.01	BD

* BD – level is below detection

1. Winkler Method Std. Methods
2. pH meter (Beckman Model 21)
3. Titration Method (Std. Methods 1986)
4. EDTA Titrimetic Method (Std. Methods 1986)
5. Spectrophometric Method (EPA Methods 353.3)
6. Persulphate Digestion Method (Std. Methods 1986)
7. Ascorbic Acid Method (Std. Methods 1986)

alkaline. Alkalinity and hardness ranged from 222 to 239 mg $CaCO_3$ and 274 to 342 mg $CaCO_3$, respectively, which is 3–4 times the regional average (Virginia Water Control Board). Nitrate nitrogen ranged from 0.73 to 0.83 mg which was within one standard deviation of the regional average (NO_3 0.42 ± 1.15 SD). Both ortho and total phosphate were near the detection limit of 0.01 mg.

METHODS AND MATERIALS

Physical–Chemical Parameters

Temperature records were obtained with a Taylor maximum–minimum thermometer. The thermometer was placed in the fast riffle under a rock and read approximately weekly from June 1987 to June 1988. Accumulated degree days were calculated as the average weekly temperature multiplied by the number of days since the last reading summed over the cohort production interval (CPI).

Stream velocity was measured with a General Oceanics Model 2030, digital flowmeter suspended in a D–frame kicknet frame. In deeper water flow was taken at 60% of the depth from the surface. Discharge was measured in the same place monthly from February 1987 to June 1988, with 5 equally spaced measurements of flow and depth across the width of the stream. Discharge was the product of mean width, depth and velocity (Platts et al. 1983).

Density and Survivorship

Density estimates of eggs, larvae, and pupae were made from random samples taken with a modified Hess Sampler (0.1 m^2) equipped with a 100 μm mesh net. Twenty–nine samples were taken between February 6, 1987 and June 8, 1988. Samples were collected on an irregular basis with intense sampling during pupation, egg laying and during I instar. During other periods when little or no development or growth were occurring, sampling frequency was greatly reduced. The exact sample dates are reported in the results (see Table 8).

Three Hess samples from each of the habitat types (pool, slow riffle and fast riffle) were taken, except during the intensive sampling time (June 10, 1987 through

July 16, 1987) when two samples were taken from each habitat. This reduction in the number of samples taken per sample date was due to concerns over the effect of intensive sampling on the habitat and the population. By taking six 0.1 m^2 samples, 1.3 percent of the study area was sampled on each sampling date. The rest of the year, 9 samples per sample date and approximately 2 percent of the habitat was sampled on each sampling date. Care was taken to disturb as little of the stream bottom as possible. Differences in density of eggs, larval and pupae between the fast riffle area and the slow riffle area, over all time periods, were tested with a paired t–test.

Hess samples were preserved in the field in 10% formalin and transported to the laboratory. *Hydropsyche slossonae* were removed by sorting the entire sample under a dissecting microscope. Head capsules were measured using an ocular micrometer, and individuals were sorted to instar and counted.

Life Histories and Instar Determinations

Number of larval instars was determined by size–frequency distributions of head capsules and Dyars law plots (Dyar 1890). Larvae were then assigned to size classes corresponding to instars (designated I, II, III, IV, V) according to head capsule width. Density estimates of each stage were computed for each habitat type and for the entire study area. Timing of life history events was determined by the presence of the various stages (i.e., eggs, larval instars, pupae, and adults) collected in Hess samples. Cohort production intervals (CPI) were computed from the time the average egg hatched to the time the average larvae pupated (Benke 1984).

In order to determine the mean life span of early instars, 10 egg masses were reared through II instar. These egg masses came from natural and artificial

substrates which were checked daily so the ages of the masses were known. The egg masses were incubated in the field in artificial stream channels. The artificial stream consisted of six, side by side channels each measuring 1.5 m × 0.2 m with a variable depth. Eggs were placed in flow–through chambers (mesh size = 150 μm) with natural photoperiod and temperature regimes. Eggs were initially counted and checked daily to determine hatching time and survival. After hatching the percent in each stage was determined daily until all I instars molted and weekly thereafter. Each container was sampled by removing 25–50 percent of the larvae, sorted to instar and percent of sample comprised by each instar was calculated. All larvae were then returned to the chamber. The mean number of days for 50% of the individuals to complete an instar in the containers was computed.

Pupae and Adult Sampling

An emergence trap, constructed of fiberglass screen mesh with an area of 2.9 m^2, was placed in the fast riffle and suspended so it would not impede flow. Flaps of the screen mesh sealed the trap at the water surface. The emergence trap was in place from 26 May to 14 June, 1988 and emptied approximately daily. The timing of emergence was established in 1987 by light trapping at or near dusk for 15 minutes approximately weekly from April to November and occasionally on warm winter nights. Adults were frozen and later sexed and individually weighed.

Viable pupal density was assessed by examination of the pupae in Hess samples. Nonviable pupae were separated from viable ones by examination of the pupal tissues which appear soft and deteriorated when dead. I also examined the pupae for chironomid parasitism.

Egg Sampling

Numbers of eggs laid were estimated by counting and measuring the area of each egg mass in Hess samples. Egg masses were measured (rectangular length × width) to determine the area of the egg masses which was multiplied by the number of eggs per unit area. Mean number of eggs per unit area of egg mass was determined by directly counting eggs in 25 egg masses. Eggs were left on the stones and returned to the riffle after measurement. In order to determine hatching time, five number–coded artificial substrates (solid bricks) were put in each of the three habitats as ovipositioning sites. The bricks were examined daily during egg–laying periods for new eggs and hatching of old masses. When a new egg mass was encountered, it was circled and numbered with a wax pencil and examined daily until it hatched.

Fecundity was determined by counting eggs in individual females. Adult females were collected by light traps and emergence traps, and frozen. Later the thawed abdomen was opened and the eggs were counted.

Life Tables and Actual Survivorship

In developing life tables for insects, it is preferable to use size or developmental stage (i.e., instar) rather than age (Kirkpatrick 1984). This can be done in the form of a stage–specific (horizontal) life table. However, accurate estimates of the number of individuals entering each instar are necessary. Southwood (1978) presented several methods for doing this and stated that the degree of synchronization is an important consideration in choosing a method. Each stage was treated separately, generating individual presence curves for each instar as in Figure 2. These curves were combined by summing the total number of larvae

present on a date to form an apparent survivorship curve (Benke 1984). A different method of estimating numbers of the smaller instars was necessary due to special problems associated with the lack of synchronization of the earlier life stages. For older instars (III–V), the total number entering an instar should best be approximated by the largest number of a particular instar found at any sampling time plus those in older instars (Southwood 1978). This is because a relatively long period is spent as older instars and mortality is not high (Southwood 1978). This method assumes the life span of the first individuals entering an instar is long enough to allow all individuals to enter it before mortality begins. However, early instars grow faster, and the above assumption is violated. First instars were estimated by assuming 100% survival of eggs, and, therefore, the number of eggs equaled the number entering first instar. One hundred percent survival of eggs was observed. By plotting the number of individuals of I instar through time, calculating the area under this curve, and dividing by the average life span (graphical method of Southwood 1978), the number of individuals that completed I instar was estimated. This became the number entering II instar (Southwood 1978). Early instar life spans were determined in the rearing experiments. The area under the presence curves was estimated by counting squares on graph paper (Southwood 1978). The graphical method assumes that mortality occurred either at the end of the stage or evenly throughout the stage and tended to overestimate the number leaving an instar. These data were then incorporated into a life table and survivorship curves using both stage and age. In order to convert from stage, a discreet variable, to age, a continuous variable, the data were plotted by the day the average individual of each instar entered the stage. From this curve, a standard

age–specific life table was constructed. The life table was constructed using equations and nomenclature of Krebs (1989).

Mass and Growth

Preserved larvae collected by Hess sampling were used to estimate the mass of each instar for each sample date. Formalin preservation has been reported to have little effect on the mass of larval *Hydropsyche* spp. (Cudney & Wallace 1980, Ross & Wallace 1983). For I through IV instars, groups of two or more preserved individuals of each instar from each sampling period were weighed. Fifth instars were weighed individually. Larvae used in mass determinations were dried at 55° C for 24 hours and were then placed in a desiccator for an additional 24 hours. The dried larvae were then weighed on a Kahn 28 electrobalance to the nearest one mg.

Eggs were dissected from females, counted, dried and weighed. Bodies of these females were also dried and weighed to determine percent of adult weight comprised by eggs.

Growth rates for the generation were determined by following average individual mass through time. Several growth equations were used and compared for strength of linear relationships by comparing r^2 values.

Production

The instantaneous growth rate (G) was used to calculate cohort production by the instantaneous growth rate method (Ricker 1946, Allen 1949, 1950, Benke 1984) which is summarized by the equation: $P = G\overline{B}$, where P = production, G = instantaneous growth rate, and $\overline{B}$ = mean biomass between sampling intervals.

Production also was determined using the increment summation, removal summation, and Allen Curve methods. These four methods are very similar and are essentially different ways of estimating the area under the Allen curve (Gillespie and Benke 1979). Calculations used for the increment–summation and removal summation methods are presented in Table 11. Bootstrap confidence limits (Efron 1982, Krebs 1989) were generated for instantaneous growth, increment summation and Allen Curve production estimates with a computer program written by Antoin Morin (Morin et al. 1987). The bootstrap procedure calculates production respectively using density estimates from randomly chosen replicates. From these production estimates, a distribution of possibilities is estimated from which confidence intervals can be calculated. One thousand iterations were used for each run.

The instantaneous growth, increment–summation, and removal–summation methods are termed cohort methods, meaning a distinct cohort must be recognized. Instantaneous growth assumes exponential increase in individual biomass. The removal–summation and increment summation methods are a modification of the Allen curve method, in which numbers are plotted on a mean individual biomass and the area under the curve equals production.

In order to correct for nonsynchronous cohorts and errors associated with negative values, production was calculated on the "corrected" data set. These corrected data estimates are based on numbers from observed survivorship and growth curves. The corrected data are presented in Table 11. This method is similar to that of Waters (1987).

RESULTS

Physical–Chemical Parameters

Stream discharge varied from month to month (Figure 4). In 1987 discharge was high in February, March and April, while in 1988, only March had high discharge. Low discharges were recorded in July and August of 1987.

The temperature in Mill Creek ranged from 23° C in August to 6° C in January (Figure 5). Temperature peaked in August and began declining in September. The minimum temperature occurred between January 9 and 16, 1988, and water temperature started increasing in February . Degree days accumulated nearly linearly, but accumulation was slightly slower during the winter (Figure 6).

Life History

Head–width measurements indicated five larval instars which conformed to Dyar's Rule with a factor of increase of 1.67 (Table 7). *Hydropsyche slossonae* was primarily univoltine in Mill Creek and had a CPI of 345 days (Figure 6).

The earliest day eggs were found in the Hess samples was May 23, 1988, however, I did observe one egg mass on May 18, 1987. The last date *H. slossonae* eggs were observed was June 15, 1987. Mean density of eggs per egg mass was 235.6 ± 21.66 (95% C.I., n = 25). By following marked egg masses in the field and in artificial stream channels, the mean time for an egg mass to hatch was 13 ± 1 (95% C.I., n = 20) days. Trichopteran egg masses similar to those of *H. slossonae* were found after June 15 but were not laid by *H. slossonae*.

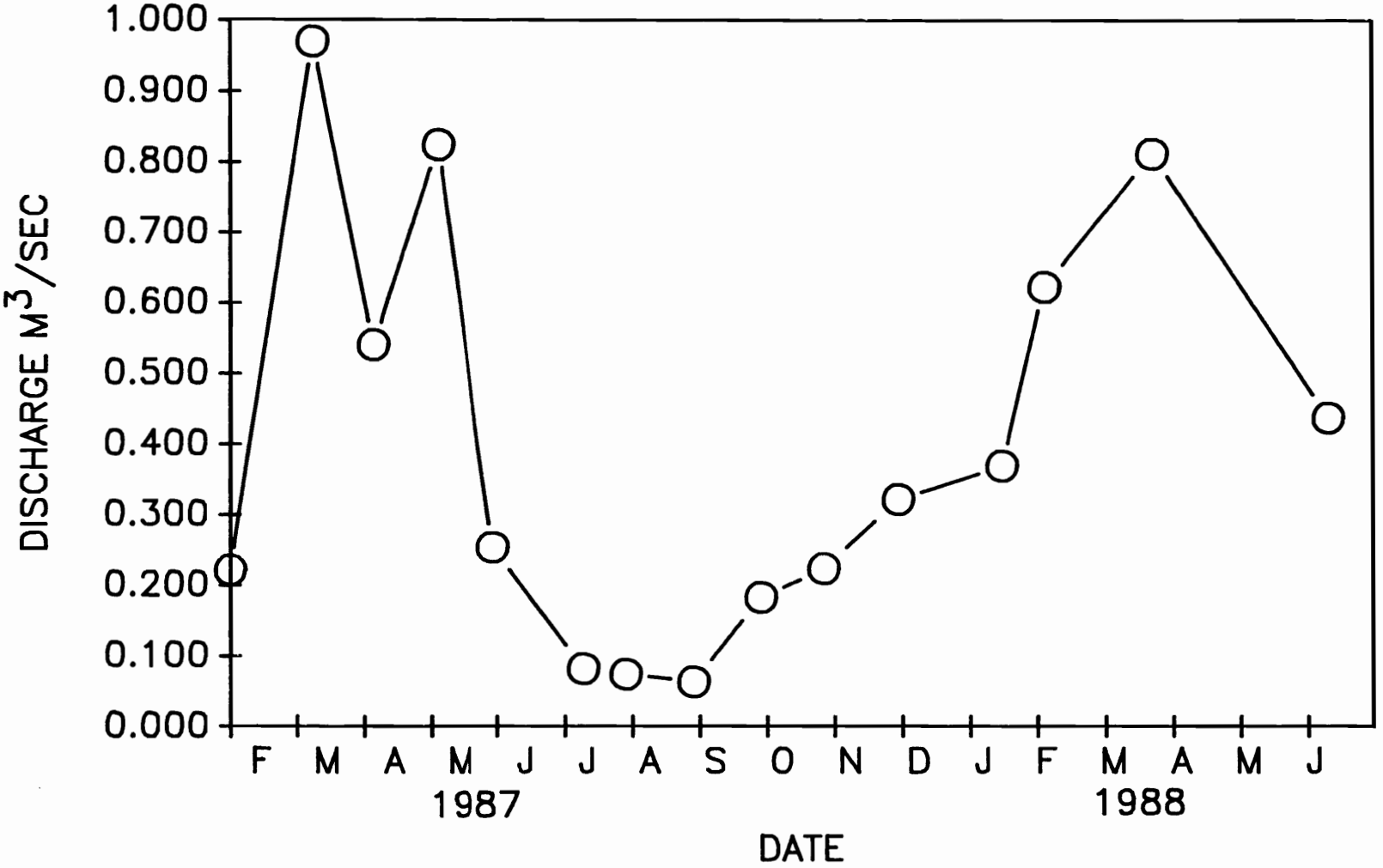

Figure 4. Discharge of Mill Creek, Virginia.

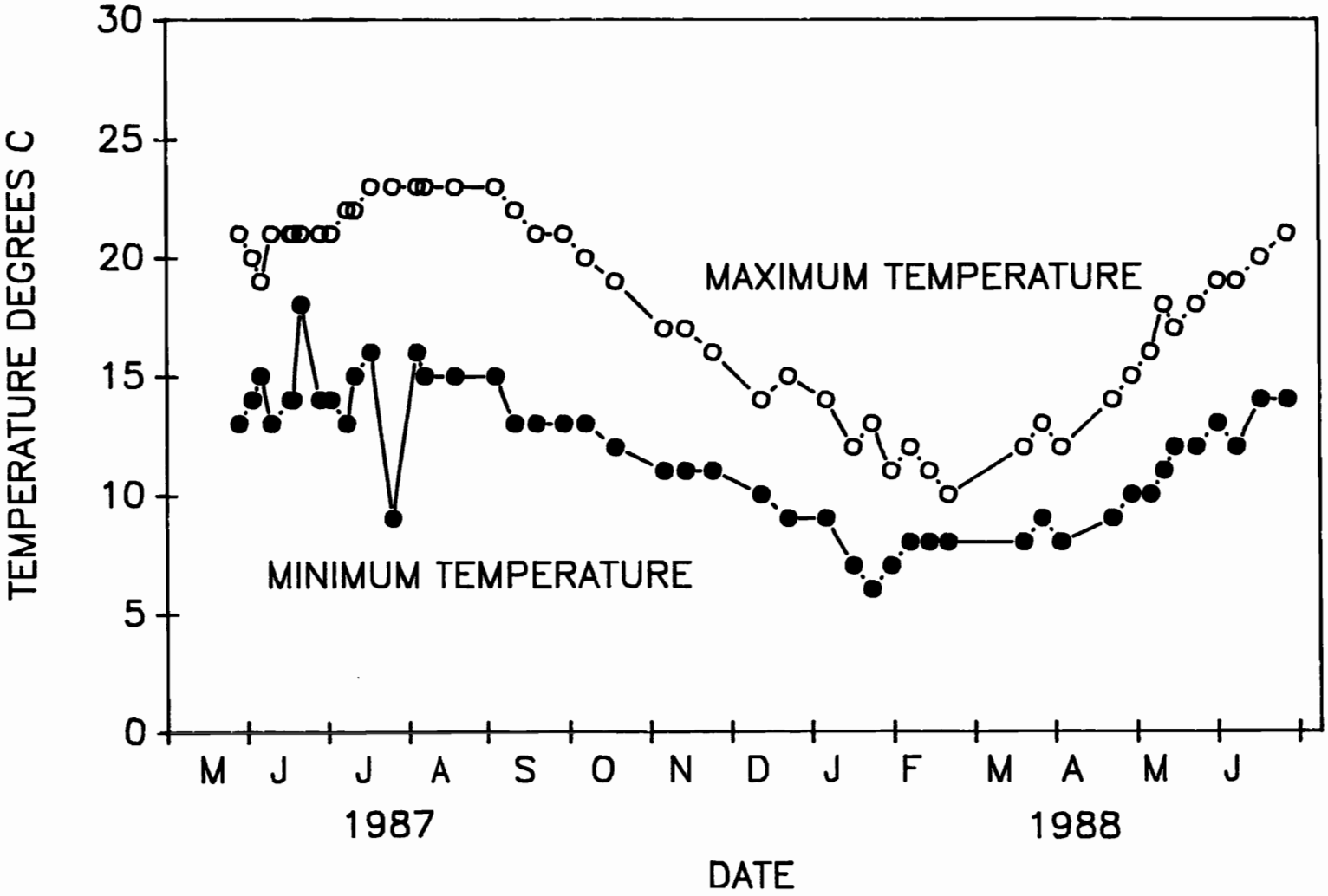

Figure 5. Maximum and minimum weekly temperatures in Mill Creek, Virginia.

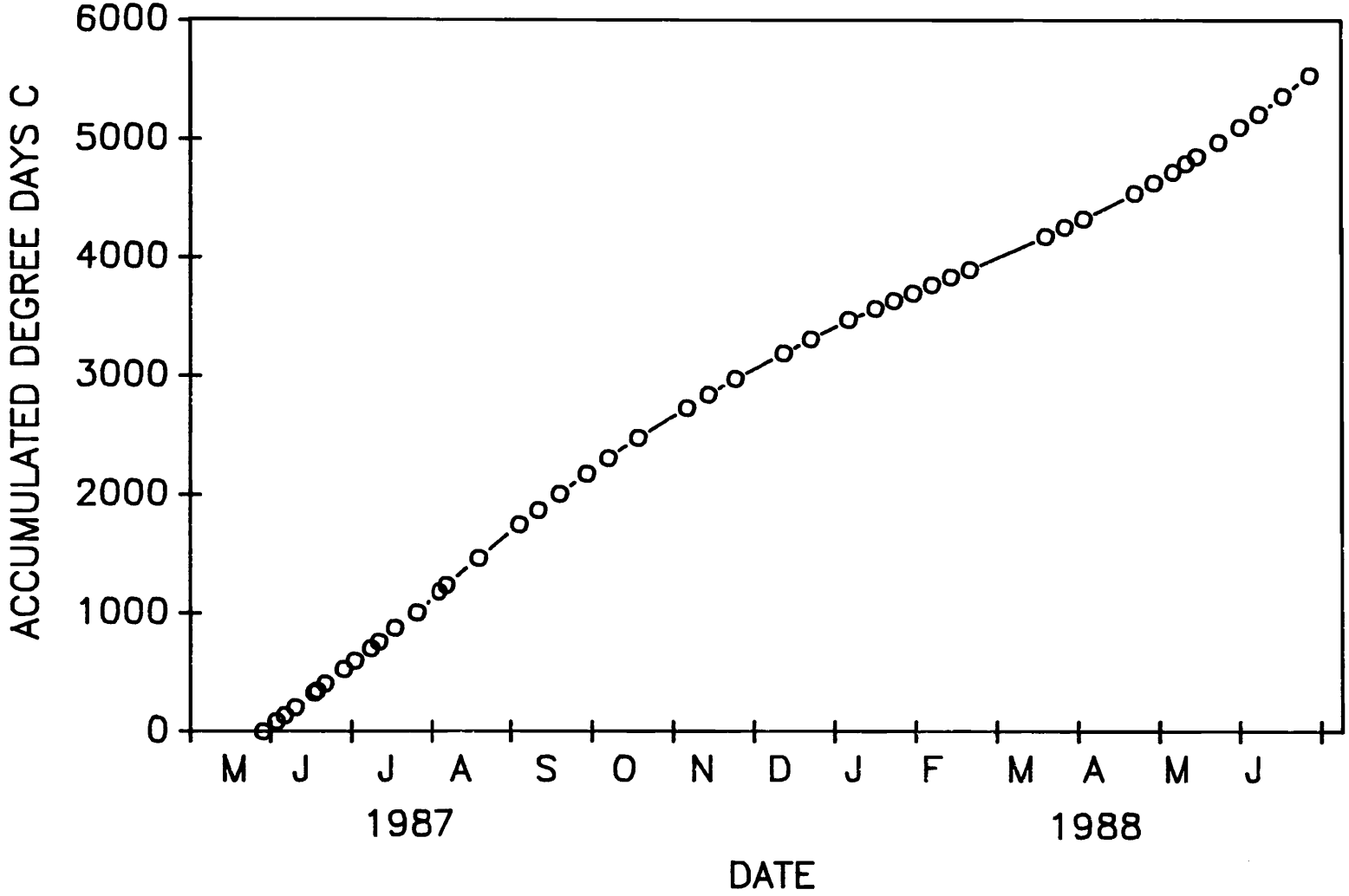

Figure 6. Cummulative Celsius degree–days for Mill Creek, starting at the time of *H. slossonae* egg laying, May 1987.

Table 6. Head capsule widths, mean duration and periodicity of each life cycle stage for *Hydropsyche slossonae* in Mill Creek, Va. Duration of stages Egg through II instar is based on rearing of 10 egg masses in artificial streams. Numbers in parentheses are ranges.

STAGE	Headcapsule width ± 95 % CI (mm)	Number measured	Estimated duration of stage (days)	Month present
EGGS	——	——	13[a]	May 87–June 87
I	.2	5	7–8[a]	June 87
II	.3	13	25[a] (5–246)	June 87–Oct 87
III	0.51 ± 0.02	20	125 (20–347)	June 87–Mar 88
IV	0.79 ± 0.02	20	150 (7–300)	July 87–June 88
V	1.19 ± 0.03	20	30	May 88
Pupae	NM	——	6–9[b]	May 88–June 88
Adults	NM	——	7–9[c]	May 88–June 88

a – From artificial stream experiments
b – From literature (Badcock 1953 and Fremling 1960, Glasgow 1936)
c – From literature (Fremling 1960, Mackay 1979, Rhame & Steward 1976)

NM Not Measured

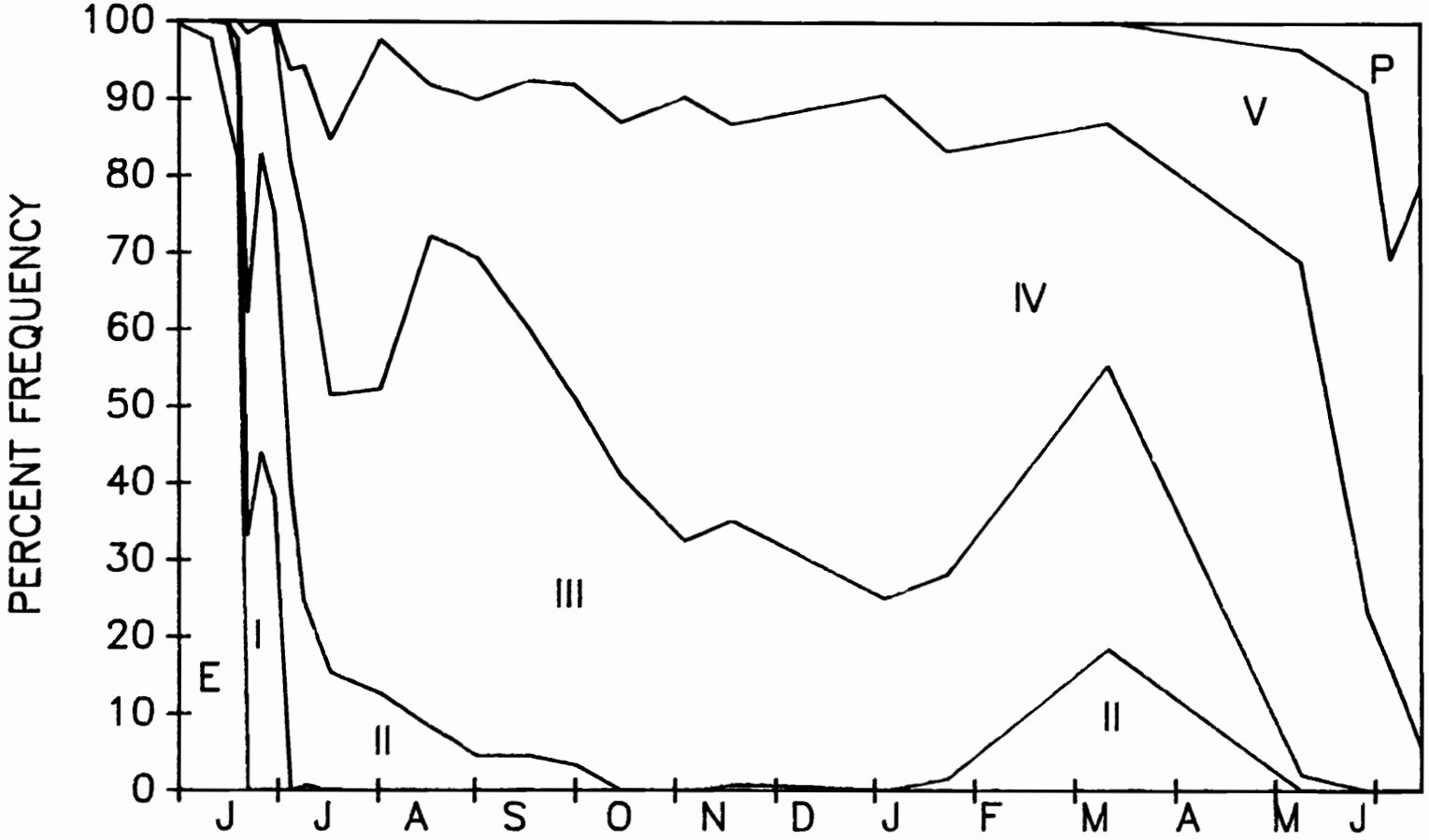

Figure 7. Relative density of aquatic life cycle stages of *Hydropsyche slossonae* in Mill Creek as proportion of each stage relative to the total of that generation. E = eggs, P = pupae, I – IV = first through fifth larval instars.

On two occasions I witnessed egg masses hatching. Both times were in late afternoon. These egg masses were removed from the water and observed under a microscope. In each egg mass all eggs hatched within one hour. Of particular interest was the observation of newly hatched larvae cannibalizing hatching larvae. In both egg masses individuals were observed feeding on adjacent siblings struggling to hatch. I estimated 10–20% of the individuals cannibalized siblings.

First instars appeared in the samples on June 10, 1987, and were present until July 8, 1987. First instars required 7 ± 0.3 days, ($n = 10$) to complete the stage in artificial stream channels. In all of the artificial stream replicates, at least 50% of the individuals were II instar by the 18th of June (25 days). Second instars required from 5 to 246 days to complete the stage, however, most individuals did not spend more than 60 days as II instar (Figure 7).

In early July, some individuals had developed into IV and V instars, but the majority were split between II and III instars. Third instars made up most of the population from mid–August to mid–October, when most developed into IV instars. The majority of individuals overwintered in IV instar. The average individual in the population spent approximately 80% of its time as III and IV instars. Light trapping indicated peak occurrence of adults in May and June, with a few individuals present as early as April (Figure 8). Pupation began in late April to early June and peaked towards the end of the period (Figure 9). Emergence began in early May and also peaked in early June (Figure 9). Well developed ova were present at emergence, and mating was observed within 24 hours after emergence in the emergence trap. The null hypothesis of equal number of eggs in females and laid egg masses was not rejected ($t = 2.46$, $n = 35$, $P < 0.01$). Egg masses were present for 20 days in April and May.

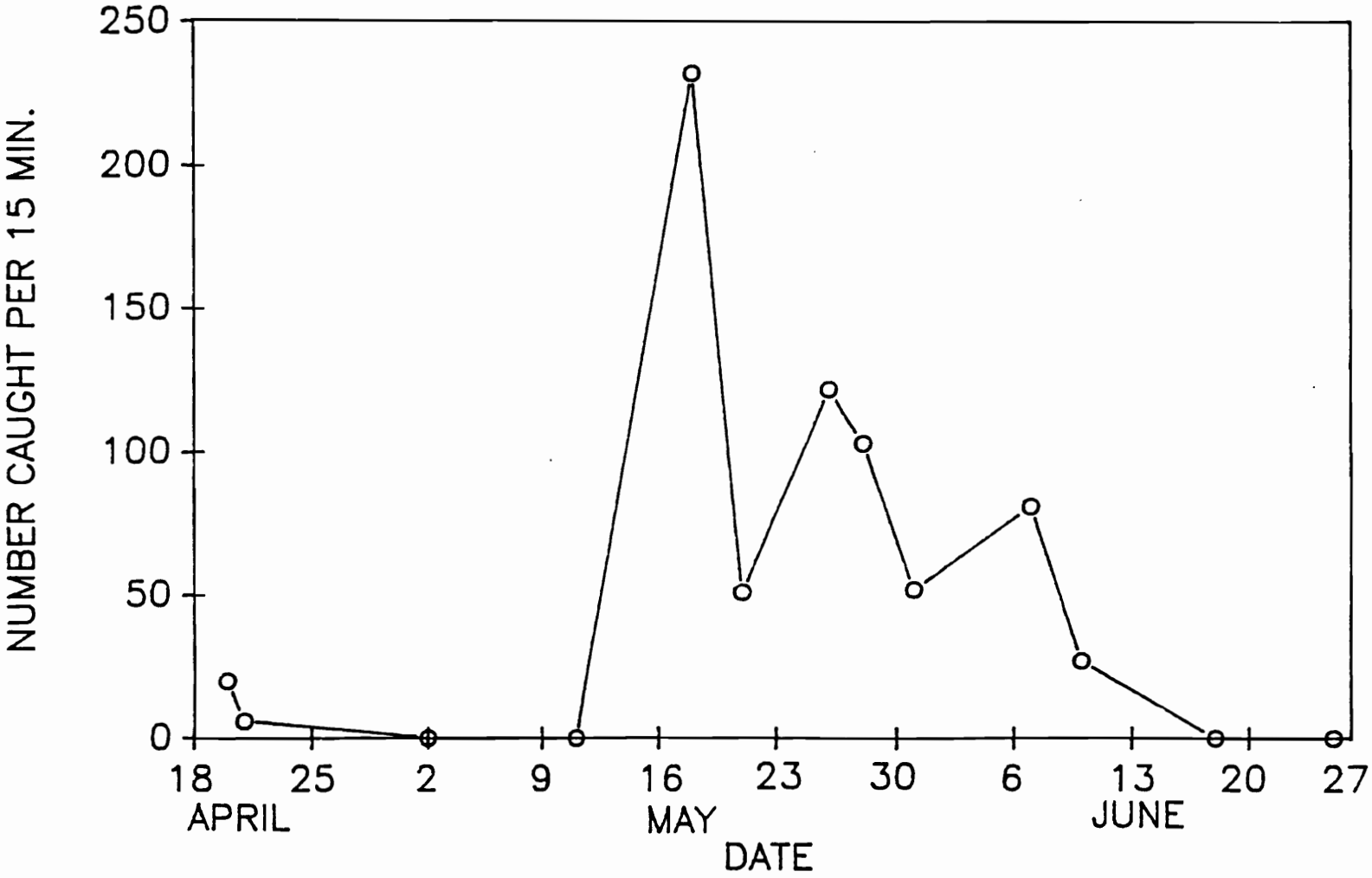

Figure 8. Number of adult *Hydropsyche slossonae* caught in a light trap per 15 minute time intervals in 1987. All collections were made withing 30 minutes of dusk.

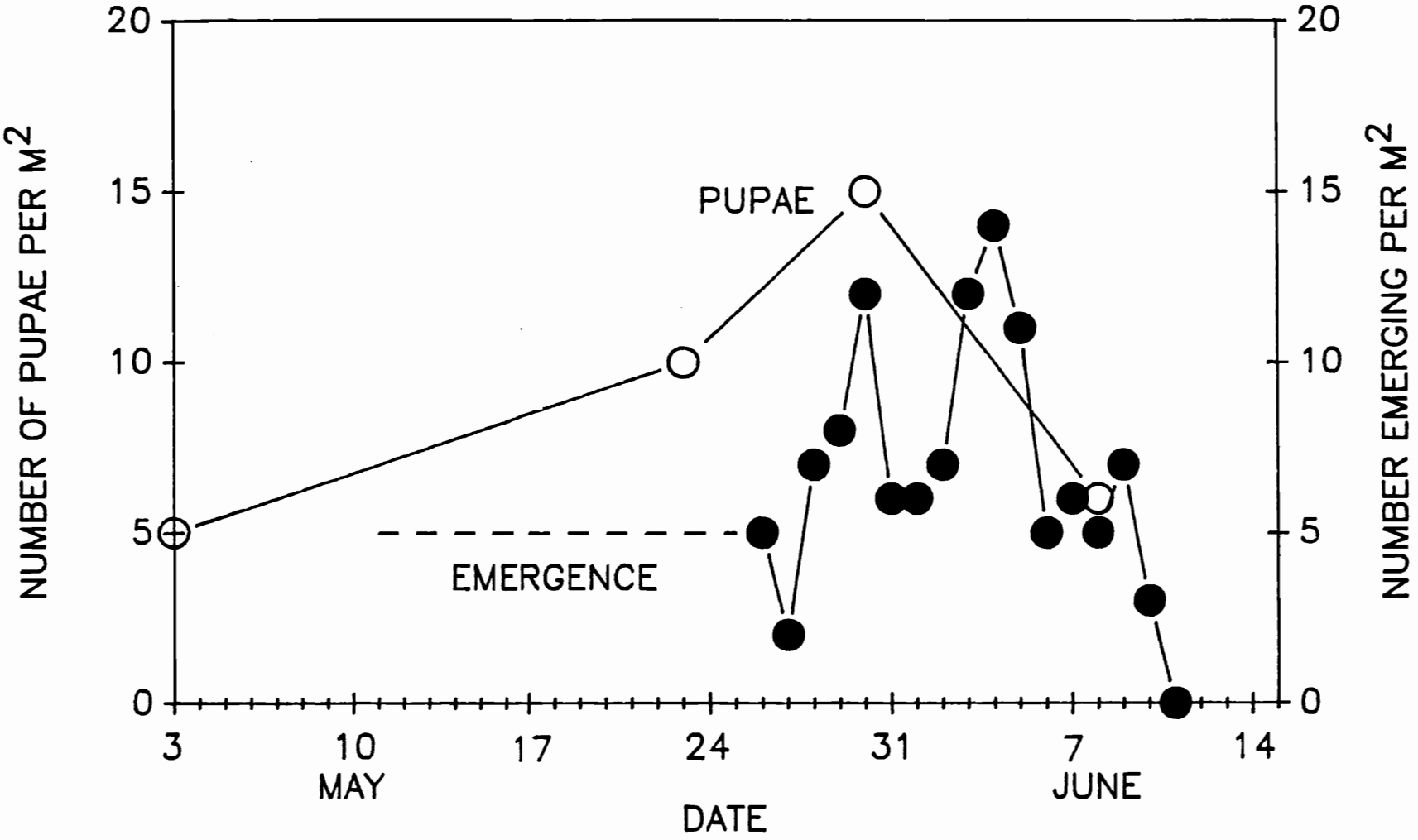

Figure 9. Density of pupating and/or emerging *Hydropsyche slossonae* in Mill Creek, Virginia in 1988. Dashed line estimates timing of early emergence.

Density and Survivorship

Density estimates in each of the three habitat types revealed that no life cycle stages regularly occurred in the pool area. However, at low flow regimes, large areas of the pool resembled a deep slow riffle and *H. slossonae* larvae were then collected (Table 7). Because *H. slossonae* larvae were not present most of the time in the pool, this area was not included in subsequent analyses. The mean monthly densities for the fast riffle, slow riffle and pool habitats were 585.9 ± 49.7 (SE, n = 29), 179.0 ± 15.2 (SE, n = 29), and 6.0 ± 1.02 (SE, n = 29), respectively. Over the period sampled, significantly more larvae were found in the fast riffle area than the slow riffle ($t = 6.271$, $n = 28$, $p < 0.0005$).

More egg masses were laid in the fast riffle area than the slow riffle area ($t = 2.2$, $n = 7$, $p < 0.05$). On the peak day of egg occurrence (June 10, 1987) the fast riffle had 14,387 ± 10,657 (SE, n=2) eggs per square meter. In the slow riffle there were 2572.9 ± 571(SE, n=2) eggs per square meter. Pupal densities were also greater in the fast riffle than the slow riffle ($t = 6.231$, $n=4$, $p < 0.005$). Pupal densities varied from 0 to 2 per m^2 in the fast riffle. In addition, nonviable pupae comprised 55% of the total number of pupae found. Of the nonviable pupae, 20% had a chironomid associated with them.

The number of eggs laid was estimated by plotting the density of eggs in the study area over time (Figure 10) and dividing the area under this curve by the average time spent in the egg stage. Because all of the egg masses examined hatched 100% of the individual eggs (estimate by observation of egg masses), this estimate was also the estimate of the number entering I instar. Highest mortality occurred in I instar (Table 8). Because mortality occurred mostly at the beginning of I instar, the area under the I instar density curve (Figure 11) divided by the

Table 7. Mean density (No./m^2 ± 1 SE) of larval *Hydropsyche slossonae* from each of the three habitat types sampled in Mill Creek, Virginia.

DATE	FAST RIFFLE		SLOW RIFFLE		POOL	
	Mean	SE	Mean	SE	Mean	SE
26 Feb 87	229.4	177.0	103.6	27.9	44.4	19.2
25 Mar 87	37.0	32.0	48.1	23.1	7.4	12.8
23 Apr 87	99.9	109.3	59.2	23.1	14.8	6.4
18 May 87	127.7	70.6	27.8	7.8	33.3	6.4
28 May 87	373.7	503.8	51.8	23.1	3.3	6.4
10 Jun 87	549.5	196.2	33.3	15.7	0.0	0.0
15 Jun 87	233.1	31.4	66.6	47.1	5.5	7.9
18 Jun 87	577.2	78.5	144.3	32.2	5.5	7.9
21 Jun 87	577.2	298.3	155.4	109.9	0.0	0.0.
25 Jun 87	793.7	314.0	949.1	321.8	22.2	15.7
29 Jun 87	643.8	31.8	33.0	125.6	38.9	39.2
04 Jul 87	516.2	204.1	360.8	266.9	0.0	0.0
08 Jul 87	477.3	157.0	294.2	86.3	0.0	0.0
16 Jul 87	321.9	141.3	77.7	78.5	0.0	0.0
31 Jul 87	660.5	180.5	50.0	39.2	0.0	0.0
15 Aug 87	843.6	188.4	33.3	23.5	0.0	0.0
30 Aug 87	1259.9	1561.9	5.6	7.8	0.0	0.0
14 Sep 87	1017.5	464.9	55.5	11.1	0.0	0.0
28 Sep 87	895.4	308.5	111.0	23.1	0.0	0.0
12 Oct 87	543.9	157.4	177.6	22.2	0.0	0.0
31 Oct 87	621.6	29.4	299.7	67.5	0.0	0.0
14 Nov 87	518.0	52.5	321.9	88.8	0.0	0.0
30 Dec 87	876.9	255.3	188.7	22.2	0.0	0.0
18 Jan 88	1091.5	266.5	562.4	133.4	0.0	0.0
06 Mar 88	1372.7	1068.2	NO SAMPLE		0.0	0.0
03 May 88	547.6	501.9	214.6	228.1	0.0	0.0
23 May 88	814.0	39.0	262.7	245.8	0.0	0.0
30 May 88	259.0	113.4	66.6	61.8	0.0	0.0
08 Jun 88	111.0	94.4	136.9	163.5	0.0	0.0
Column Means	585.9	263.0	179.0	80.2	6.0	5.4

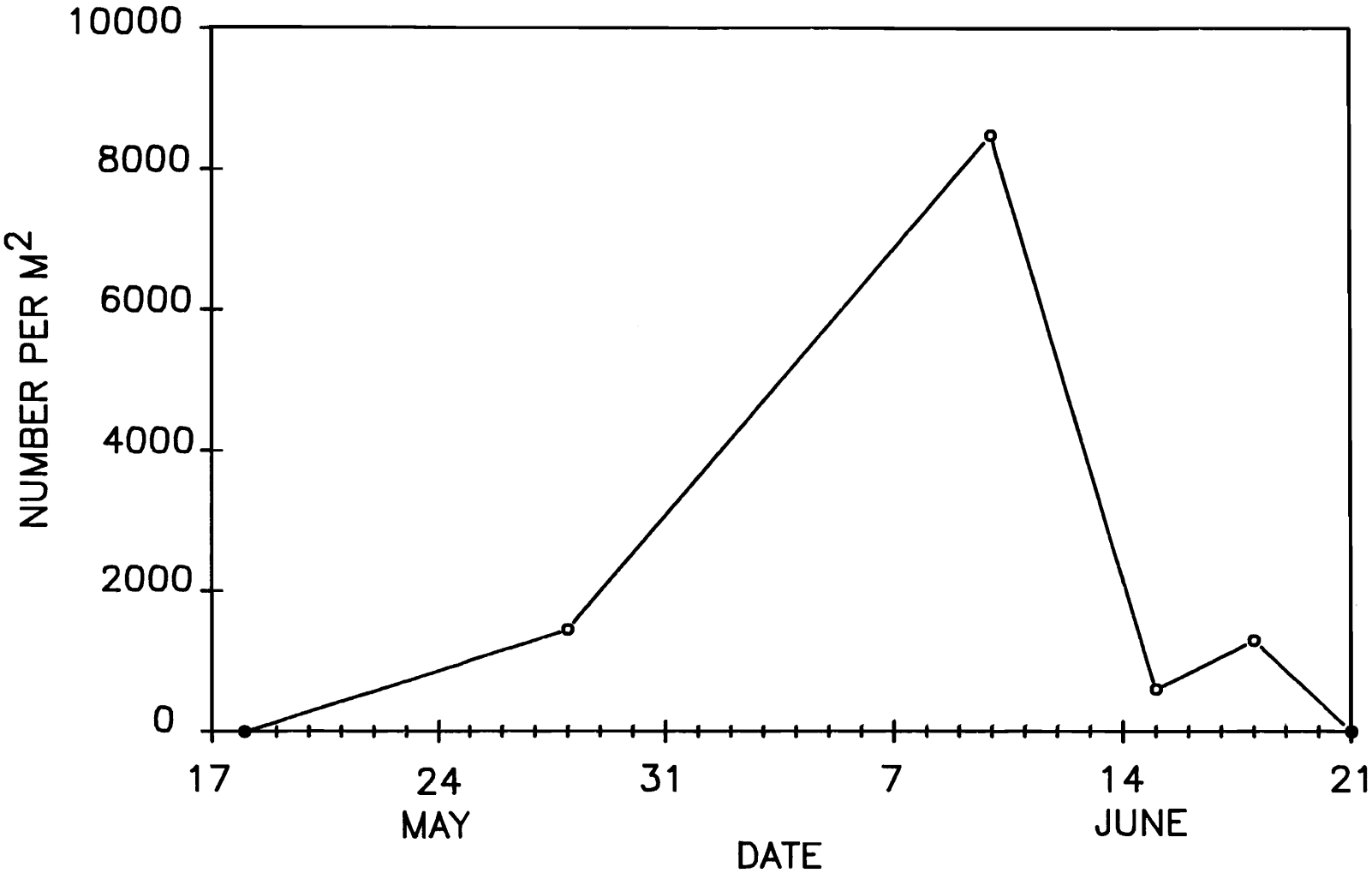

Figure 10. Density of *Hydropsyche slossonae* eggs in Mill Creek, Virginia in 1987.

Table 8. Life Table for 1987–88 generation of *Hydropsyche slossonae* in Mill Creek, Va.

X Stage	Age Days	n_x	d_x	l_x	q_x	L_x	T_x	e_x
EGGS	0	10,300	0	100.0	0	10,000	17,800	1.73
I	14	10,300	9,590	100.0	92.9	5,530	7,530	0.73
II	22	733	233	7.10	31.9	616	2,000	2.73
III	64	500	45	4.8	9.0	477	1,380	2.76
IV	264	455	55	4.4	12.1	427	903	1.99
V	343	400	178	3.9	44.5	311	476	1.19
P	361	222	168	2.2	75.7	131	165	0.74
A	368	54	54	0.5	100	27	27	0.50

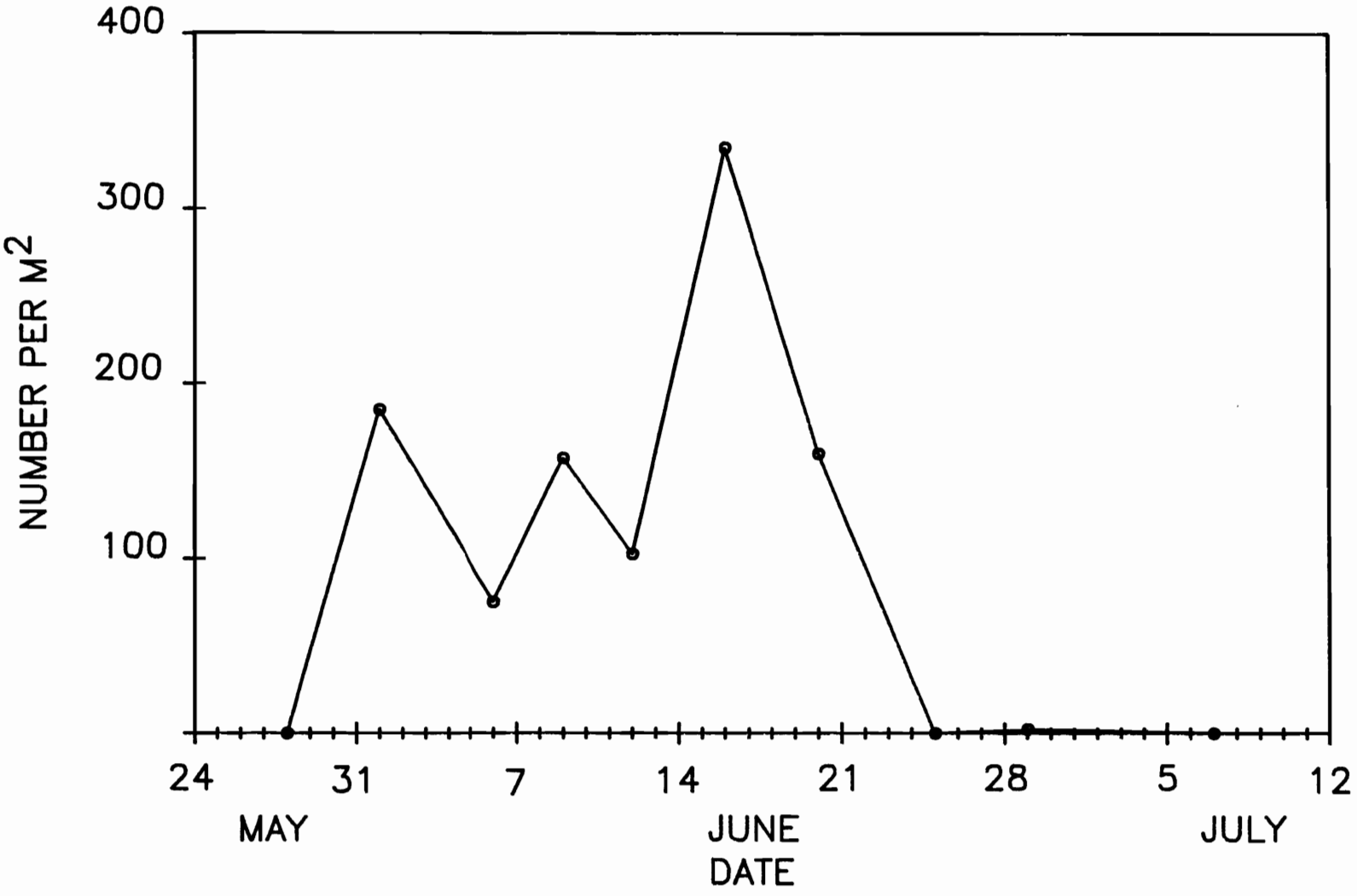

Figure 11. Density of *Hydropsyche slossonae* I instars in Mill Creek, Virginia in 1987.

length of time it took to develop to II instar was used to estimate the numbers entering the II instar. The numbers entering III, IV, and V instars were estimated as the peak number in each instar plus the numbers in successive instars on that date. Those data were used to construct the life table (Table 8).

The actual survivorship curve (Figure 12) is taken from the n_x column of the life table (Table 8). The actual survivorship showed a drastic decline immediately after hatching, while the apparent curve (Figure 12) showed a relatively constant number of individuals. The initial decline in the actual survivorship was followed by a leveling off in numbers through the rest of the year until pupation.

Mortality was low during the other larval stages (Table 8). This allowed the use of the maximum number of organisms found in the instar to be used as the number that entered the stage. Pupae had the second highest mortality rate (life table estimate of 76%). Pupal densities in the life table included only viable pupae and were also estimated by the graphical method (Southwood 1978). Adult densities indicated another time of high mortality associated with emergence. The number entering the adult stage was estimated from the emergence trap.

Mass and Growth

Mean dry mass of eggs remained constant throughout the time they were present (Figure 13). First instars weighed less than eggs early in the stage but increased in mass approximately five fold during the stage. Second instars showed a seven fold increase in mass during this stage. Mass of III instars tripled during the stage and was the lowest proportionate mass increase during any stage. Fourth instars increased five fold and instars V increased from five to 18 fold (Figure 13). Mean individual mass was plotted over time to obtain a growth curve (Figure 14).

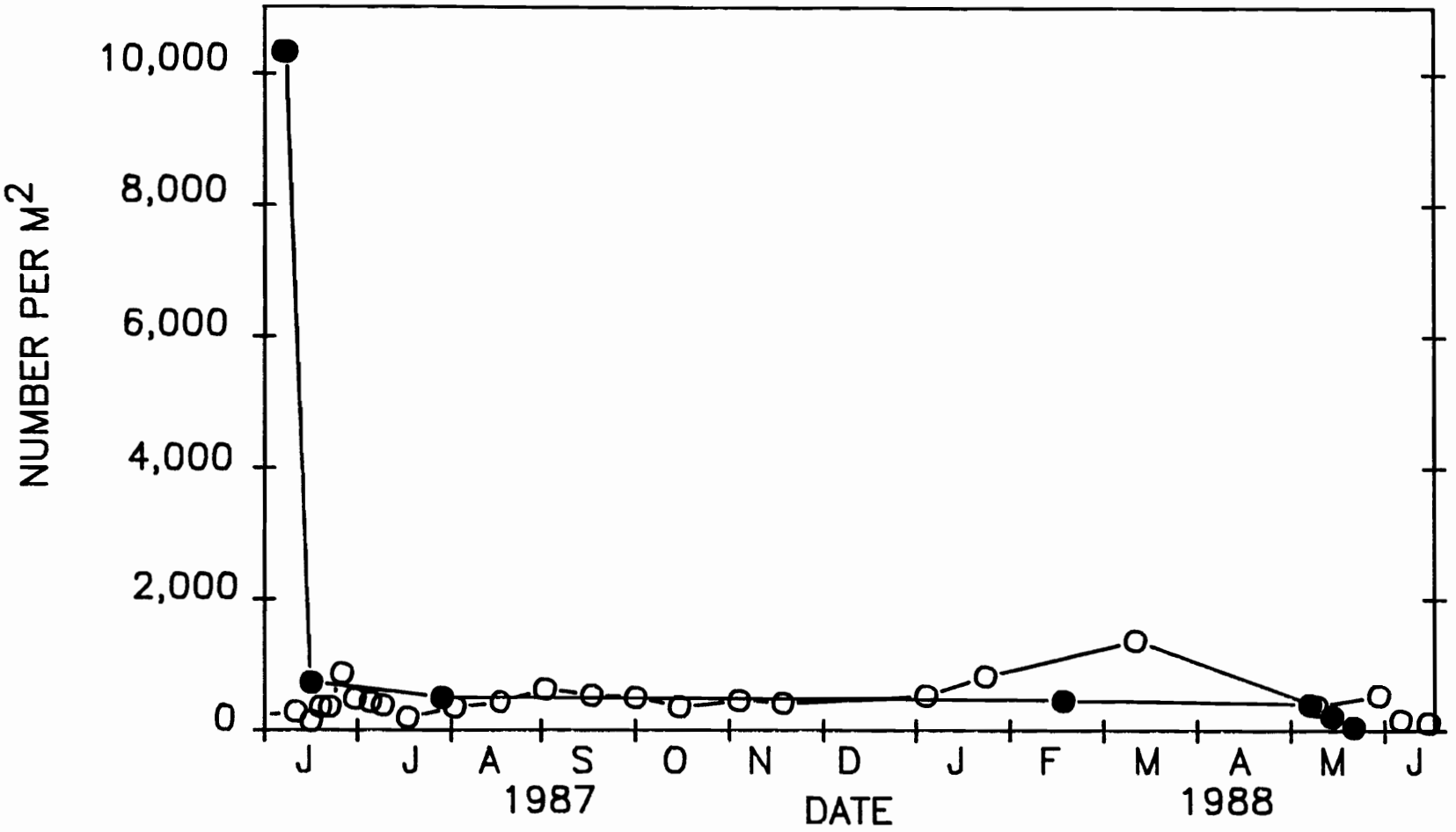

Figure 12. Apparent and actual survivorship curves. The apparent survivorship (open circles) is the density found on each sample date. The actual survivorship (solid circles) is the predicted density if all individuals were synchronized to hatch the same day.

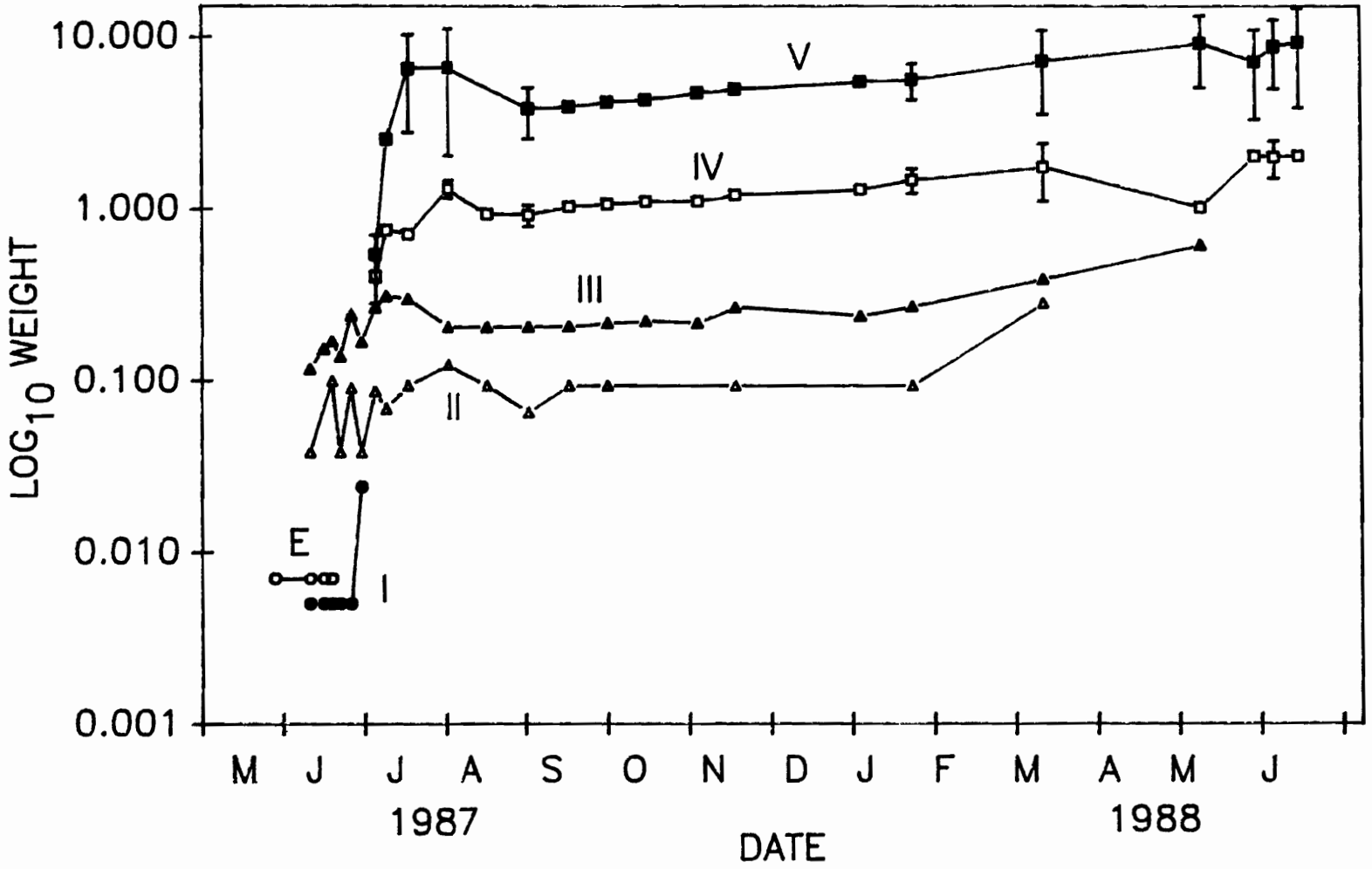

Figure 13. Mean dry mass of the five larval instars per sample date. Vertical lines are 95% confidence limits.

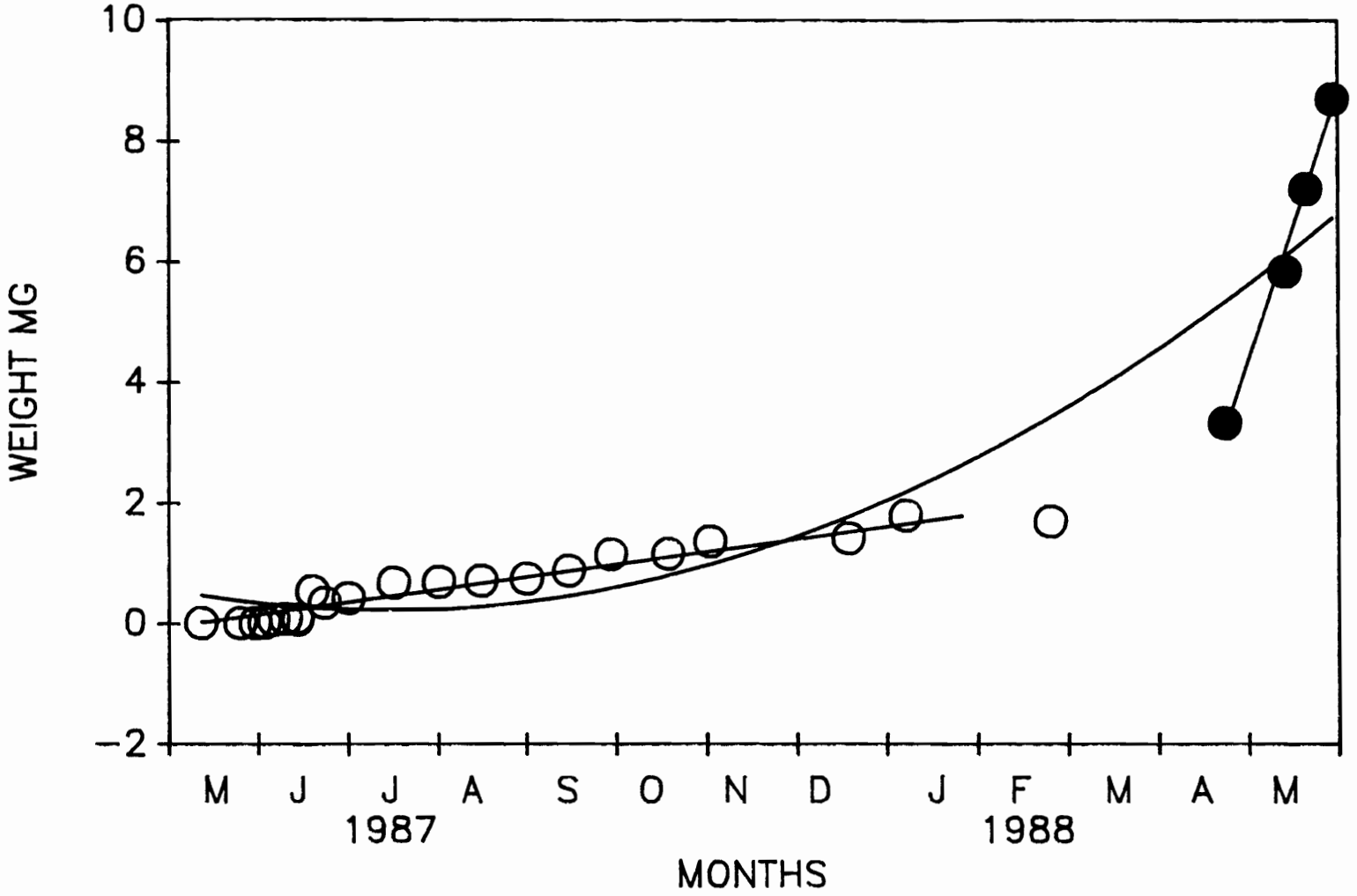

Figure 14. Individual growth curves as mass of the mean individual in the population. The quadratic is fit to the whole data set. The linear equations describe the time periods indicated.

Several equations were tested for goodness of fit to the growth curve (Table 9). All of the slopes were significantly greater from zero (n = 25, p = 0.0005). A quadratic equation showed the best fit (r^2 = 0.94), however, it is hard to evaluate the coefficients in this type of equation because they are difficult to interpret biologically. Fitting the data to two linear equations, one from May 28, 1987 (egg stage) to March 6, 1988 (IV instar) and the second from May 3, 1988 (V instar) to June 8, 1988, (the end of the larval stage), allowed biological interpretations. The growth rates were 0.007 ± 0.0004 (SE, n = 21) mg/day from June 10 through March 6 and 1.48 ± 0.01 (SE, n = 4) mg/day from May 5 to June 8.

Pupal mass was similar to that of V instar. The mean mass of viable pupae over all dates was 5.737 mg ± 0.986 (95% CI, n = 17). Adult mass did not differ significantly by sex. Female adults did show different mass in May compared to June (t = 8.0110, n=20, P = 0.0005). May females weighed 2.4 mg ± 0.388 (95% CI, n = 10) while in June females weighed 6.295 mg ± 0.754 (95% CI, n = 10). In June (the only month examined), eggs made up 44.25% ± 6.289 (95% CI, n = 6) of the body mass (Table 10). Mean fecundity, measured by counting eggs in adults, was 223.0 ± 18.13 (95% C.I., n = 20).

Production

In order to obtain bootstrap confidence limits on the Allen curve, it was necessary to transform the data to a straight line. The best straight line fit to the Allen curve was obtained by log transforming the density estimate and not transforming biomass (r^2 = 0.043) (Table 11). The cohort Allen curve production was 3081.3 mg/m^2. The 95% CIs of the increment summation (4.015.3 mg/m^2) and instantaneous growth (4.139.0 mg/m^2) cohort production estimates overlap that of

Table 9. Growth equations tested for goodness of fit using r^2.

Model	Equations	a ± SE	b ± SE	r^2	n
Exponential	$\ln m = a + bt$	–278 ± 1.23	0.014 ± 0.002	0.68	25
Logistic	$\text{Ln}\frac{(M - m)}{m} = a + bt$, M=9	–5.22 ± 1.27	–0.018 ± 0.002	0.77	25
von Bertalanfy	$\text{Ln}(M - m) = a + bt$, M=45	3.82 ± 0.03	–0.0004 ± 0.00005	0.75	25
Linear I–IV	$m = a + bt$	0.008 ± 0.150	0.007 ± 0.0004	0.94	21
Linear V	$m = a + bt$	–47.530 ± 0.275	0.148 ± 0.010	0.99	4
Quadratic	$m = c + bt + at^2$	a=0.00006, b=0.008, c=.464		0.94	25

m = mass
M = asymptotic mass
t = time (days)

Table 10. Mean fecundity and number of eggs per egg mass of *H. slossonae* in Mill Creek, Va.

		Mean	± 95 C.I.	n
Number of eggs per female		223.00	18.13	20
Number of eggs per egg mass		235.60	21.66	25
Mass of female adults	May	2.30	0.79	10
	June	6.29	0.58	10
Eggs as percent female mass in June		44.25%	6.29	6

the Allen curve method (Table 11). Cohort $P/\bar{B}$ ratios varied from 4.35 to 6.75. This was within the expected range of 4–8. Annual $P/\bar{B}$ ratios were only slightly different than cohort $P/\bar{B}$s. Production was also figured by using the actual survivorship curve (Figure 12) which starts all of the individuals at the same time or synchronizes the cohorts to a common starting point. In this computation, masses were predicted by the linear regressions of growth (Figure 14). This is called a corrected production estimate and removes error associated with non–synchronous cohorts (Table 12). Removal–summation and increment–summation production estimates were made on these corrected data. Corrected estimates were lower but were not beyond the confidence limits of the non–corrected data method. The between sample date production columns (Columns I and J of Table 12) were divided by the number of days between sample dates to get production and yield per day (Figure 15). Production is the rate of tissue elaboration while yield has been defined as the rate of transfer from one trophic level to others (Waters 1977). This was done on both the increment–summation and removal–summation data. The increment–summation method is mean number multiplied by change in mass between sample dates and the removal–summation method is mean mass multiplied by change in numbers. The increment–summation calculation is production and the removal–summation calculation is yield when taken between sample dates. Both production and yield showed peaks early in the generation and late in the generation. In between these two period of high production, a periods of constant low production and yield occurred.

Table 11. Production estimates with 95% C.I. for *Hydropscyhe slossonae* in Mill Creek. Production estimates with confidence intervals were computed with the Morin program. All other estimates were computed by hand according to Benke (1984). Corrected data used biomass estimated from survivorship and growth functions.

METHOD	Cohort Production $mg/m^2/year$	95% Confidence Interval Lower	Upper	Cohort $P/\bar{B}$	Annual $P/\bar{B}$
Raw Data					
Increment Summation	4015.28	2536.28	5485.89	5.67	5.42
Instantaneous Growth	4159.04	2442.49	5712.99	5.87	5.61
Allen Curve	3081.29	2435.36	4008.08	4.35	4.16
Corrected Data					
Increment Summation	3399.626	NA	NA	6.75	6.45
Removal Summation	3471.887	NA	NA	6.5	6.23

NA – Not Available

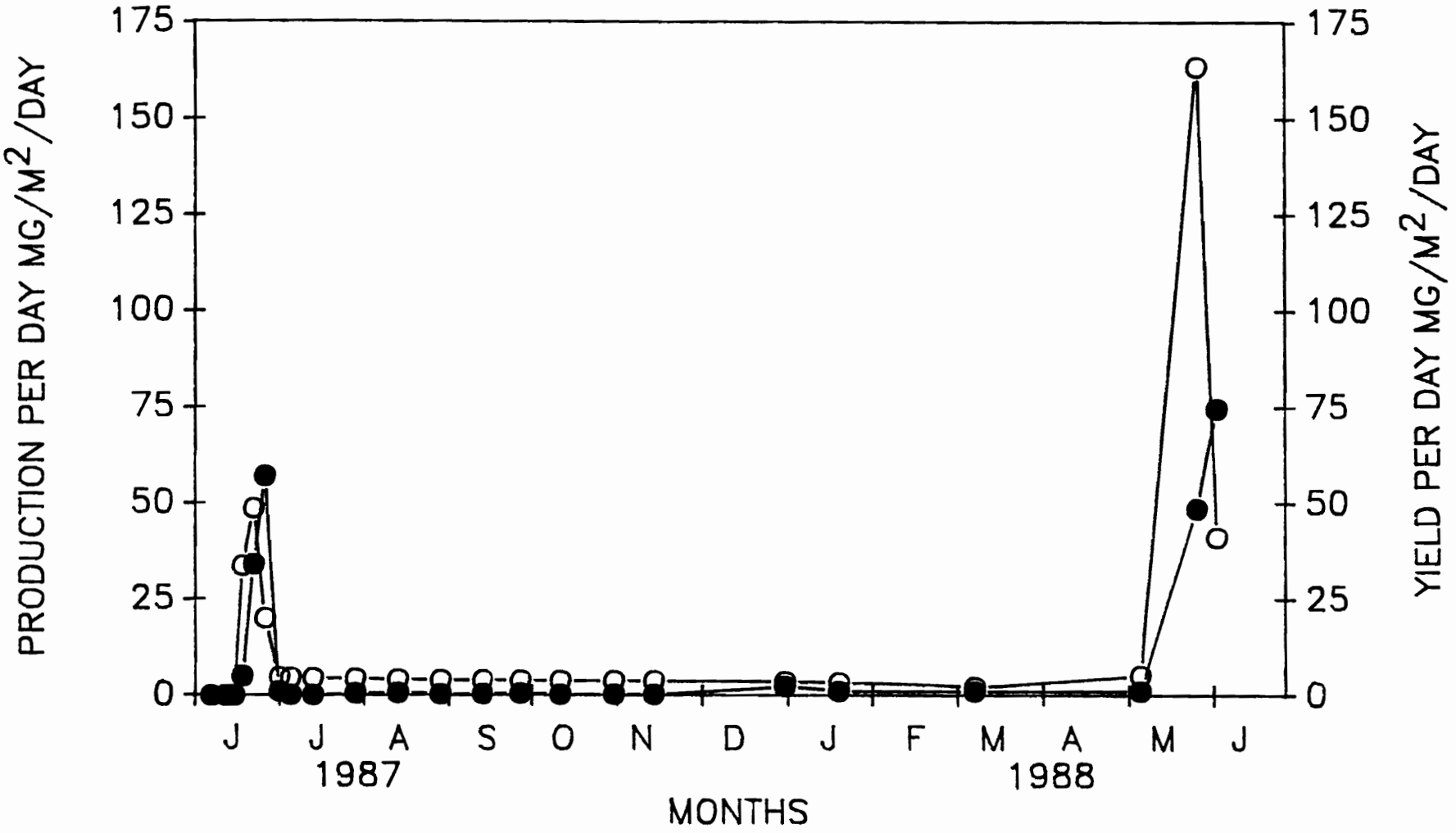

Figure 15. Production and yield on a per day basis.

Table 12. Corrected production calculations for *Hydropsyche slossonae* in Mill Creek, Va. The summation of the I column is the Removal Summation Production. Each entry in this column is yield during the time period. The summation of the J column is the Increment Summation Production estimate. Each entry of the J column is production during the period. The difference between the ISP and RSP estimates is the initial biomass in column H.

A DAYS SINCE EGG LAYING	B NUMBER PER SQUARE METER	C CHANGE IN NUMBER Bi–Bj	D MEAN NUMBER (Bi+Bj)/2	E MEAN INDIVIUDAL WEIGHT	F CHANGE IN WEIGHT Ej–Ei	G WEIGHT AT LOSS (Ei+Ej)/2	H BIOMASS B*E	I REMOVAL SUMMAATION PRODUCTION G*C	J INCREMENT SUMMATION PRODUCTION D*F	K BIOMASS GAIN Hj–Hi
1	10323	0	10323	0.007	0	0.007	72.261	0	0	0
6	10323	0	10323	0.007	0	0.007	72.261	0	0	0
9	10323	0	10323	0.007	0	0.007	72.261	0	0	0
12	10323	1443	9601	0.007	0.014	0.014	72.261	20.202	134.421	114.219
16	8880	3885	6937	0.021	0.028	0.035	186.480	135.975	194.250	58.275
20	4995	4284	2854	0.049	0.035	0.066	244.755	284.919	99.846	–185.073
25	711	44	688	0.084	0.028	0.098	59.682	4.361	19.361	14.910
29	666	11	660	0.112	0.056	0.140	74.592	1.554	36.985	35.431
37	655	11	649	0.168	0.105	0.220	110.023	2.447	68.181	65.734
52	644	28	629	0.273	0.105	0.325	175.757	9.374	66.087	56.713
67	615	27	601	0.378	0.105	0.430	232.470	11.623	63.162	55.272
82	588	11	582	0.483	0.105	0.535	284.004	5.890	61.162	55.272
97	577	11	571	0.588	0.098	0.637	339.276	7.007	56.007	49.000
111	566	11	560	0.686	0.098	0.735	388.276	8.085	54.929	46.844
125	555	6	552	0.784	0.133	0.850	435.120	5.103	73.416	68.313
144	549	5	546	0.917	0.098	0.966	503.433	4.830	53.557	48.727
158	544	11	538	1.015	0.322	1.176	522.160	12.936	173.397	160.461
204	533	33	516	1.337	0.133	1.403	712.621	46.315	68.694	22.379
223	500	34	483	1.470	0.336	1.638	735.000	55.692	162.288	105.596
271	466	34	449	1.806	0.294	1.953	841.596	66.402	132.006	65.604
329	432	11	426	2.100	0.246	2.223	907.200	24.453	104.919	80.466
349	421	88	377	2.346	3.036	3.864	987.666	340.032	1144.572	804.540
356	333	111	277	5.382	1.332	6.048	1792.206	671.328	369.630	–301.698
365	222	222	111	6.714	2.368	7.898	1490.508	1753.356	262.848	–1490.500
380	0		0	9.082			0			–72.261
								3471.887	3399.626	

DISCUSSION

Physical–Chemical Data

Flow patterns have been proposed as a primary factor in determining microdistribution of aquatic insects (Statzner et al. 1988). Discharge Variability probably changed the suitability of the three habitats for *H. slossonae* (Figure 4). At high discharge, the pool area had fast velocities which allowed the occasional appearance of *H. slossonae.* Normal to low flow conditions resulted in reduced flow in the pool area. At high discharge rates there was little difference in flow between the two riffle habitats, and larvae were distributed more evenly in riffle areas. At lower flows the slow riffle habitat became very shallow with many exposed rocks, and larvae were clumped in the fast riffle habitat.

The temperature curve of Mill Creek indicated the stream was influenced by ground water (Figure 5). The large number of springs and seeps along the stream moderated temperature variation diurnally and seasonally. The small amount of seasonal variation resulted in similar degree day accumulation rates among seasons. Accumulated degree days regressed on date gave a nearly straight line (Figure 6) ($R^2 = 0.99$). In this case, date was a good predictor of degree days. Adding temperature to a growth equation did not explain any more of the variation than regressing on date.

Life History

Dyar's law (Dyar 1890) describes the geometric increase in head capsule widths of insects (Table 6). Mackay (1978) used this to associate conspecific instars

in order to validate larval identifications. Dyar's law predicts the reciprocal of the slope (log head width vs. instar) to be in the range of 0.58–0.79 (Dyar 1890). For *Hydropsyche slossonae* in Mill Creek this number was 0.59, and was within the reported range for species with 5 larval instars. This factor of increase predicted a sixth larval instar head width of 2.02 mm, but no larva this large was found.

The univoltine population of *H. slossonae* in Mill Creek (Figure 7) corresponded well to the known life history data for the species (Mackay 1979, 1986). Partially bivoltine populations of *H. slossonae* have been observed in an Ontario lake outlet (Mackay 1979). However, bivoltinism is not as common in *H. slossonae* as in other members of the genus. This may be because *H. slossonae* is usually limited to low order spring runs and smaller streams which have low quantity and quality of food. The population at Mill Creek had a similar life cycle to a *Hydropsyche slossonae* population in a Minnesota stream. This Minnesota stream and Mill Creek, Virginia, appear to have similar temperature regimes (see Mackay 1986).

The egg incubation time of 13 days for *H. slossonae* in Mill Creek was longer than those reported for *H. orris* (Fremling 1960) and *H. colonica* (Glasgow 1936) (8–10 days). Both of these species are in the subgenus *H.* (*Hydropsyche*) and live in larger rivers which are probably warmer than Mill Creek and may account for their shorter egg incubation times.

No variation in egg development was observed within individual females . Emergent females had well developed ova, and mating was observed within 24 hours of emergence (in the emergence trap). Because the number of eggs in adult females did not differ statistically from the number of eggs counted in laid egg masses (Table 10), females are assumed to lay most, if not all, of their eggs at one time and

in one mass. Thus, the number of eggs per egg mass was a good measure of fecundity. Egg masses of *H. slossonae* were not present as long as that reported for a bivoltine population of *H. phalerata*, 20 versus 120 days, respectively (Deutsch 1984).

From observations of 37 marked egg masses and hundreds of hatched egg masses, hatching success of eggs was estimated to be 100%. This is consistent with findings of Cummins and Wilzbach (1989) for *Pycnopsyche guttifer* (Limnephilidae). However, the limniphilid *Ecclisocosmoecus scylla* showed 38% mortality of the egg stage when parasitized by a phorid fly (Wisseman and Anderson 1984). While attempting to rear *Hydropsyche slossonae* egg masses in the laboratory, chironomids were observed associated with egg masses. I suspect the chironomids were feeding on the fungi growing on the eggs. In the laboratory, fungi did cause mortality of some egg masses.

The egg stage had high survival until hatching when sibling cannibalism occurred. Sibling cannibalism has been reviewed by Polis (1981) and Fox (1975) and the following discussion of the potential implications for *H. slossonae* comes primarily from ideas reviewed there. Sibling cannibalism can be considered a way of transferring a large amount of maternal tissue to the next generation. Eggs and early instars are nutrient rich and provide a good food source. Newly hatched coccenillid beetles more than double their survival probabilities by cannibalizing siblings. Eating 2–3 siblings supplied enough energy to molt to II instar (Kaddou 1960). The cannibal not only gained a meal but also eliminated a potential competitor (Fox 1975) and became less vulnerable to attack by other cannibals and predators.

Sibling cannibalism in *Hydropsyche* was most intense at hatching. If using excess egg production as a "food cache" for the next generation is a fitness strategy, the advantage obviously goes to the first hatchlings. Individuals hatching later were vulnerable for two reasons: 1. they may be eaten before freeing themselves from the eggs cases; and 2. they did not have a ready supply of food. In order for a food cache strategy to work, the individuals must hatch nearly synchronously.

The advantage of sibling cannibalism may be in allowing cannibals to reach II instar earlier. This would give cannibals a competitive advantage over non–cannibals. The estimate of 10–20% of all hatchlings that fed on sibling hatchlings is near the 10% survival rates through I instar.

The major larval life history events of *H. slossonae* appeared to coincide well with those reported for univoltine *Hydropsyche* (Mackay 1986). The primary differences were in the timing of various events. Mackay (1979) reported pupation occurred in early June in Ontario and a Minnesota population (Mackay 1979) pupated in May and June. Pupation in Mill Creek occurred earlier in May and a larger proportion overwinter in IV instar than in Minnesota. The Mill Creek population laid eggs earlier, developed to a slightly larger mean instar to overwinter, and started developing again earlier in the spring.

Literature values for length of time spent in pupation for other *Hydropsyche* spp. (Badcock 1953, Fremling 1960, Glasgow 1936) corresponded well to approximate times for *H. slossonae* in Mill Creek (6–9 days). Emergence is estimated from combined emergence trapping, light trapping, and from egg laying data to occur over a 30 day period. Ovipositing is estimated to occur during a 20 day period. Light trapping in 1987 indicated a relatively short flight periodicity corresponding to the time of emergence. A few *Hydropsyche slossonae* were caught

around April 20, 1987. Benthic sampling on April 23, 1987 yielded no egg masses, either because these adults were unsuccessful at reproducing, or so few eggs were laid the sampling missed them. Extensive searching by turning stones in downstream riffles revealed no eggs masses were laid at this time. Also, no pupae were found in either of these samples. Additional light trapping on two warm nights between April 20, 1987 and May 18, 1987 yielded zero *H. slossonae* adults. These adults may have originated from areas other than those sampled and were probably the fastest developing individuals in the stream population. Adult life spans of the genus have been reported as 10–13 days for *H. orris*, and death occurs soon after ovipositing (Badcock 1953, Fremling 1960). There have been no reports of extended ovipositing (multiple egg layings) in hydropsychids (Mackay 1979). Because I found no adult females without eggs, I assumed they died soon after egg laying.

The peak in adult occurrence was in May which corresponds to the primary time of egg laying. Deutsch (1984) reported *H. phalerata* oviposited from 22 May through 22 September in the Susquehanna River, with peak egg laying on June 8. This ovipositing season (123 days) is much longer than for *H. slossonae* in Mill Creek but *H. phalerata* is probably bivoltine, having two generations during this time.

Density and Survivorship

Mean larvae density of *H. slossonae* in Mill Creek was within the range reported by Mackay and Waters (1986) in Minnesota. They found mean densities of $101/m^2$ upstream of an impoundment and $4828/m^2$ in the lake outlet. The mean

density of larvae over all dates in Mill Creek was 406/m^2 (SE = 273). *H. slossonae* preferred the fast riffle area (Table 7).

Recruitment is the addition of new individuals to a population by reproduction or immigration (Ricklefs 1979). Changes from aquatic to terrestrial stages are vulnerable transitions in the life cycle and can be adversely affected by fluctuating water levels (Patterson and Vannote 1979), or unfavorable terrestrial conditions (Kajak 1964, Jonasson 1972). In terms of reproduction, the best estimate of recruitment was from egg density data. As described elsewhere, 100% hatching of eggs was assumed. Therefore, the estimate of egg density was also the estimate of recruitment of first instar larvae. By plotting the densities of eggs over time (Figure 10) and dividing by the amount of time spent as eggs, it was estimated that 10,300 I instars per m^2 entered the population of the combined riffle areas (Figure 10).

Estimates of immigration and emigration are based on changing numbers in the study area during times when reproductive recruitment was absent. A midsummer net movement out of the slow riffle area into the fast riffle reduced the slow riffle density to near zero on August 30, 1987 (Table 7). Apparently the movement was associated with the low flow regime of that time of year (Figure 4). Low discharge resulted in slower velocities in the wide, slow riffle while the fast riffle was a run with higher velocities. Periods of low discharge correspond to movements of *H. slossonae* into the fast riffle area. Although larval density of the slow riffle was near zero on August 30, 1987, the mean density of the entire riffle area (combined slow and fast riffles) was still high. The number of *H. slossonae* inhabiting each riffle area was estimated by multiplying the number per m^2 by the area of each habitat. If all of the individuals in the slow riffle habitat moved to the

fast riffle, it would not account for the increase in fast riffle density. Therefore the congregation in the fast riffle includes individuals from another source area. When discharge increased, the new population dispersed and organisms again inhabited the slow riffle at similar densities.

Just prior to pupation, there was again evidence of movement into the fast riffle. This movement was not related to discharge. During this brief period of faster growth it may be advantageous to be in the fast riffle. Under faster flow more water would be filtered per unit time which would potentially provide more food particles for the larvae. During the winter when filter–feeding nets are absent, *Hydropsyche* switch to different feeding strategies (i.e., grazing or collecting) (Snyder 1988). When *Hydropsyche* switch to grazing or collecting, the faster flow does not aid feeding efficiency. Also, if one assumes that grazing or collecting requires more area to sustain an individual, then expanding the usable feeding area would be advantageous. In the spring, when they again constructed filter–feeding nets, a greater density is possible in the fast riffle.

The mean density of *H. slossonae* per time is the equivalent of the apparent survivorship curve in Figure 12. This type of survivorship curve is often used in production studies (Benke 1984). However, apparent survivorship does not accurately reflect how many organisms pass from one stage to another. On the other hand, the actual survivorship was based on how many organisms enter each stage (the n_x column of the Table 8) (Figure 12). The difference in the two curves was less obvious when egg densities were added to the apparent survivorship curve because the maximum egg density was close to the actual density estimated by the graphical method. Without taking eggs into account, the apparent survivorship curve is an order of magnitude lower in the initial number starting the generation.

These data indicated egg density estimates were necessary to get an accurate description of survivorship.

The l_x column of the life table (Table 8) shows the percent of organisms that started the generation and entered each successive stage. Only 7.1% of the initial number enter the second instar, 2.2% enter pupation and only 0.5% become adults. The e_x column of the life table is expectation of further life. As was predicted for organisms with a type IV survivorship curve, this varies with each stage (Southwood 1978). These data are in close agreement with the findings of Elliott (1981, 1982a) where in *Philopotamus montanus* (Philopotamidae) survival to reproduction was 0.4% and in *Potamophylax eigulatus* survival from egg to imago was 1–2%.

Another way of expressing density survivorship data is in terms of mortality (d_x and q_x of Table 8). The q_x column of the table is mortality expressed as a percentage of organisms alive at the beginning of each stage (successive percentage mortality). Approximately 93% of the individuals that hatched from eggs died quickly, probably due to cannibalism and predation. Mortality was much lower for III and IV instars which were the over–wintering stages. Although more time was spent in these stages than all others, the high survivorship may be partially due to lower activity by larval *Hydropsyche* and predators on *Hydropsyche*. Other than the egg stage, mortality was lowest during V instar in which the average individual spent 30 days. Pupation was another period of high mortality due to chironomid parasitism of the pupae and other calamities. Approximately 55% of the pupae found in Mill Creek were nonviable and approximately 20% of these had chironomids associated with them. The 55% mortality estimate of pupae was in good agreement to life table estimates which predicted high mortality in the pupal

stage. Rutherford (1986) reported chironomid parasites caused 66% mortality of *Hydropsyche* spp. pupae in 2 streams in Ontario, Canada.

Multiplying the number of adults that emerged by average fecundity produced an estimate of the total number of eggs laid ($6021/m^2$). This accounted for only 58% of the eggs laid in the next generation. In order to account for the eggs laid, a female density of $46/m^2$ was needed as opposed to the $27/m^2$ estimated to be produced in the area. If we rule out multiple egg laying, this would seem to indicate that adults were attracted to the study area from adjacent areas in Mill Creek to lay eggs. This may be the case as much of the upstream habitat was bedrock covered with moss which was inappropriate for ovipositing by *Hydropsyche slossonae.* This habitat is selected by larvae of some species (Hildrew 1977). The study area may have acted as a nursery for a larger population, providing good habitat for ovipositing. Another possibility was that sampling in the study area caused enough disturbance to enhance the area for ovipositing. Preferred oviposition sites may have been created by loosening the substrate and cleaning the rocks. If this is true much of the initial decline in numbers may not be mortality but rather emigration to the bedrock areas.

Mass

Mean mass of an individual egg (0.007 mg) was a little more than that of early I instar (0.005 mg). This difference was probably due to the mass of the egg case which was shed.

Each instar showed a distinct increase in individual mass toward the end of each stage, indicating faster growth late in the stage (Figure 13). As the majority of these individuals molted to the next instar, a decrease in that instar's mean mass

was observed. This decrease was due to lighter individuals entering the instar and lowering the mean mass. The fluctuation during the early part of II instar (Figure 13) may have been due to the various groups entering the stage at various times. When I instars enter the stage the mean mass of the II instar drops. After ecdysis, growth was slowed again until the end of the II instar.

These fluctuations in mass are different than generalized growth patterns in insects (Sehnal 1985). *Notonecta glauca*, an aquatic heteropteran, was reported to grow in distinct steps at the end of each stage (Teissier 1931 cited in Sehnal 1985). Sehnal (1985) explained this as water gained for stretching the carapace. This was not the case in *Hydropsyche*, because the pattern was based on dry mass. The dry mass increased seems to be associated with molting. Another possible reason for *Hydropsyche* instar growth patterns being different is the reduced amount of hard exoskeleton in Trichoptera larvae. Hard–bodied organisms have limited stretching abilities and would be expected to add mass fastest while filling out the new exoskeleton (Sehnal 1985). Soft bodied organisms can stretch the integument a great deal. Molting is triggered in part by stretching so it would be expected that a large gain in mass would occur just prior to ecdysis (Sehnal 1985).

In other insects, pulsed growth has been associated with fluctuations in feeding rates (Sehnal 1985). Insects are known to change intake and excretory patterns in response to the molting cycle. The assimilation efficiency is not thought to change because oxygen consumption is reduced during the periods of lower food consumption (Sehnal 1985).

Few aquatic insect studies have tried to fit growth data to various growth curves to find the best fit. Most workers assume either linear or exponential growth. Mass data regressed by date resulted in two linear regressions ($r^2 = 0.99$

and 0.97) (Table 9). One was fitted from hatching through IV instar and the other was for the V instar to pupation. From the variety of growth curves utilized (Table 9), the two straight lines seemed to be the most biologically explainable. The two distinct phases for growth for *H. slossonae* indicated a change in assimilation efficiency, feeding rate, or food quality.

Mass regressed on accumulated degree days, resulted in linear regressions with similar r^2s values (0.99 and 0.97) as did the two linear regressions of mass by date. This was probably due to the small amount of seasonal change in temperature. Both accumulated degree days and calendar days were equally good predictors of weight. Little of the variation in growth was accounted for by temperature. Another interesting point was that although growth continued through winter (Figure 14), development did not (Figure 7). Low temperature apparently inhibited development while growth continued.

Many aquatic insects have faster growth rates at the end of their larval development. Univoltine chironomids can gain 99% of their individual biomass in two distinct growth spurts in the last three months of development (Ward & Cummins 1978). Benke and Jacobi (1986) reported that most individual biomass accumulation in a variety of mayflies occurs at the end of the nymphal life. Food consumption was not reported in either of these studies. Fuller and Mackay (1980) reported that *Hydropsyche slossonae* III to V instars fed primarily on detritus and diatoms in fall and winter. In spring and summer, their food habits changed to 10–20% animal material. This higher quality food corresponded to the beginning of net spinning in spring. The Mill Creek population also switched to net spinning in spring. There could be a relationship between a change in food habits and the reported change in growth rates.

Adult male mass did not differ significantly from female mass. Reported data on *Hydropsyche betteni* seems to be contradictory as to differences between sexes. Mackay (1984b) found no mass differences between sexes, while Ross (1944) did find differences. Mackay (1984b) found sexual differences in mass for other species. Because of large variation in adult mass and relatively small differences between the sexes, differences that may exist would require large sample sizes to detect.

Production

Morin et al. (1987) emphasized the importance of knowing the assumptions of the various production methods. Cohort production estimates (Removal–summation, increment–summation, Allen Curve, and instantaneous growth) assume perfect synchrony in populations. In other words, they assume all individuals begin the generation on the same day and grow synchronously. This assumption is rarely met and it is often impossible to pick out cohorts within a generation.

The removal–summation and increment–summation methods of calculating production are ways of estimating the area under the Allen curve. In the removal–summation method, the mean weight is multiplied by the change in number ($\bar{w} \times \Delta N$). The increment–summation method multiplies the mean number by the change in weight ($\bar{N} \times \Delta w$). The final estimates differ by the initial standing stock which should be added to the increment–summation estimate.

In calculating production by the increment–summation and removal–summation methods, the final columns (I and J in Table 12) are summed to get the production estimates. The numbers in the increment–summation column

are production (tissue elaboration) between time intervals while the removal–summation numbers are yield (loss to other trophic levels). The difference between the two columns is biomass gained between the sample dates.

The instantaneous growth method of calculating production ($P = G\bar{B}$) multiplies the instantaneous growth rate (G) by the mean biomass over time($\bar{B}$). The growth rate term is a function of individual mass and can be figured for the whole time period by dividing the maximum larval mass by the initial mass. The mean biomass over the period is a function of survival and growth. It is in this biomass term that the assumptions of exponential mortality and growth are concerned. Actually, the assumption of the method is that biomass lost by mortality equals mass gained by growth.

Uncorrected cohort production in this study ranged from 3.1 to 4.2 g/m^2/year depending on calculation method (Table 12). Production of hydropsychids can be extremely variable with literature values ranging from 0.9 to 325.0 g/m^2year. The upper extreme is from a lake outlet in central Virginia and at that time was higher than any other aquatic community level production estimate (Parker & Voshell 1983). The high production was from a group of several *Hydropsyche* (*Hydropsyche*) species and did not contain any of the *Hydropsyche* (*Ceratopsyche*). The lower estimate was from a population of *H. slossonae* in Minnesota (Mackay & Waters 1986). In the same Minnesota study at a site below a lake outlet, *H. slossonae* produced 40.0 g/m^2/year. The area below a lake outlet should be considered unusually good habitat for *Hydropsyche.*

Production estimates were also calculated on corrected data. This is similar to the analysis of Waters (1987) for *Hydropsyche slossonae.* The corrected data were mass and densities predicted by the growth curve and survivorship curve. This

in effect synchronized the cohorts and removed the error associated with negative production due to a decrease in numbers or mass (and sampling error). These production estimates were slightly lower than with the raw data estimates. Confidence limits could not be calculated because the regressions were made on the whole data set with no replicates. Production estimates on the corrected data fell within the 95% C.I. of the raw data. The advantage of using the corrected data method was a reduction in variability resulting in a smooth Allen curve. The disadvantage was the loss of confidence intervals.

The cohort $P/\bar{B}$ ratios for the raw data were less than for the corrected data because of the higher production estimate of the corrected data. The corrected data also lessened the degree of truncation and increased the $P/\bar{B}$ (Waters 1987). Annual $P/\bar{B}$ ratios were very similar to cohort $P/\bar{B}$ because the mean cohort production interval was 349 days (near one year). Population $P/\bar{B}$ ratios were near 5 as was predicted (Waters 1969).

Production and yield were plotted on a per day basis (production between sample dates/number of days between sample dates) to get an understanding of how production and yield varied through the year (Figure 15). The daily increment–summation method results in daily production because it takes into account the biomass added to the population by growth. High daily production was seen early in the generation due to fast growth. During most of the year, the daily production was low due to slow growth. High daily production began again in mid–March corresponding to the time when most individuals were molting to V instar. The faster growth associated with this stage resulted in higher production starting on sample day 223 (March 6) due to a positive change in biomass. Yield (daily removal–summation method) showed a much narrower peak late in the

generation. Increased yield began on day 333 (May 23) and was associated with the loss of relatively few large individuals. This increase reflected a negative change in biomass. As would be predicted, yield lagged production.

The two periods of intense production indicated those times when the population was most important to community energy flow. Actually, during the year two generations overlap to form one period of high production. This period started around mid March or April and went through early June. During this period, production averaged 60–70 $mg/m^2/day$. During the rest of the year, production was about 5–10 $mg/m^2/day$.

These results indicate that it is erroneous to consider production as a constant rate as is usually reported such as production per year. Rather, population production is variable with relatively short periods of fast growth resulting in high production. This supports sampling more intensively at times when most of the production occurs as has been suggested by some researchers (Morin et al. 1987).

An assumption of all production methods is the absence of immigration and emigration, or rather the assumption that the two are equal and balance each other. Almost all production studies make this assumption (Benke 1984). However, movement is always occurring even in these relatively sessile retreat building hydropsychids. I have not made estimates of migration into and out of the study area, however, observations made during the study do deserve discussion.

One large scale migration was apparently flow related. Movement was primarily out of the slow riffle habitat during low flow periods and vice versa when discharge increased (Table 7). Over the course of the year, immigration is believed to equal emmigration. The other detected movement was from the slow riffle habitat to the fast riffle. Because production was based on combined data from the

two areas, the effect was minimal. I am assuming, in this case, no net loss or gain due to migrations.

Another observed movement was of adults to the study area to lay eggs. Eggs produced outside the study area are technically attributable to the these other areas. The error in production is only the initial biomass of the eggs. These eggs may be the source of another error in the production estimates. The loss of many individuals from the study area immediately upon hatching has been treated as mortality but there is a possibility some of the loss could be due to emigration. In either case it was probably not correct to count this as production of the study area. However, I have not attempted to correct the production estimates for these possibilities.

Spreading Risk

Variation in the life cycle timing within populations is an important part of the population's ability to withstand environmental variability. Variation in life history timing should not be viewed as noise or random variation but rather as an important characteristic of the population which spreads the risk of environmental calamities over time (den Boer 1968, Andrewartha and Birch 1984, Grossberg 1988). Aquatic insects have several distinct life cycle stages with different mortality factors. In *Hydropsyche*, the terrestrial adult is effected by sudden changes in weather and predation, the aquatic eggs are vulnerable to drops in water levels resulting in desiccation and the larvae may be most vulnerable to predation and variable food supplies. Each of these changes from terrestrial to aquatic habitats

represents a particularly vulnerable period (Kajak 1964, Jonasson 1972, Patterson and Vannote 1979).

Different stages of the life cycle have very different survival probabilities. Variability in the timing of the life cycle prevents all individuals from entering a particularly vulnerable stage at the same time and being exposed to the same calamity. This may be particularly important in pupal metamorphosis to adults because pupae metamorphose without regard to terrestrial weather conditions. Emergence during a late spring frost could result in high mortality among adults. By spreading out the emergence (by variable development) there is less likelihood that all individuals would be affected adversely.

It is reasonable to conclude that individuals entering a particular stage at different times would experience different risks and environmental conditions which would result in differing mortality and growth rates. Because the variation in a life history is the result of many evolutionary factors, better accuracy in describing the variation within a life history will aid our understanding of how life histories evolve.

LITERATURE CITED

Allen, K. R. 1949. Some aspects of the production and cropping of freshwaters. Report, Sixth Science Congress. 1947. Trans. Royal Society New Zealand. 77(5):222–228.

Allen, K. R. 1950. The computation of production in fish populations. New Zealand Science Review. 8:99.

Andrewartha, H. G., and L. C. Birch. 1984. The Ecological Web: more on the distribution and abundance of Animals. The University of Chicago Press. Chicago, 506.

Badcock, R. M. 1953. Observation of oviposition under water of the aerial insect *Hydropsyche augustipennis* Curtis (Trichoptera). Hydrobiologia. 5:222–225.

Balduf, W. V. 1934. The Bionomics of Entomophagous Insects Part II. J. Swift Co., Inc. Surrey, England. Reprinted by E. W. Classey Ltd., 1974.

Benke, A. C. 1984. Secondary production of aquatic insects in V. H. Resh and D. M. Rosenberg, Ed. The Ecology of Aquatic Insects. 289–322. Prueger, New York.

Benke, A. C., and D. I. Jacobi. 1986. Growth rates of mayflies in a subtropical river and their implications for secondary production. J. of the North American Benthological Society, 5:107–114.

Benke, A. C., and J. B. Wallace. 1980. Trophic basis of production among net–spinning caddisflies in a southern Appalachian stream. Ecology 61(1):108–118.

Benke, A. C., T. C. Van Arsdall, D. M. Gillespie, and F. K. Parrish. 1984. Invertebrate productivity in a subtropical blackwater river: The importance of habitat and life history. Ecol. Mono. 54(1):25–63.

Butler, M. G. 1984. Life histories of aquatic insects in V. H. Resh and D. M. Rosenburg, Ed., The Ecology of Aquatic Insects, Praeger, New York.

Cellot, B., M. Bournaud and H. Tachet. 1984. The movements of the larvae of *Hydropsyche* (Trichoptera) in a large river. Proc. of the 4th International Symposium on Trichoptera J. C. Morse (ed.) Series Entomologica 30. Dr. W. Junk, The Hague.

Coutant, C. C. 1982. Positive phototaxis in first instar *Hydropsyche* cockerelli Banks (Trichoptera). Aquatic Insects. 4(1):55–59.

Cudney, M. D. and J. B. Wallace. 1980. Life cycles, microdistribution, and production dynamics of six species of net–spinning caddisflies in a large southeastern (USA) river. Holartic Ecology. 3:169–182.

Cummins, K. W. and M. A. Wilzbach. 1989. Experimental studies of growth and mortality of a stream caddisfly. Paper presented at the 1989 meeting of the North American Benthological Society, Guelph, Ontario.

den Boer, P. J. 1968. Spreading the risk and stabilization of animal numbers. Acta Biotheretica. 18:165–194.

Deutsch, W. G. 1984. Oviposition of Hydropsychidae (Trichoptera) in a large river. Can. J. Zoology. 62(10):1988–1994.

Dyer, H. G. 1890. The number of molts of lepidopterous larvae. Psyche. 5:420–422.

Edington, J. M., M. A. Edington, and J. A. Dorman. 1984. Habitat partitioning amongst hydrpsychid larvae of a Malaysian stream. Proc. 4th International Symposium on Trichoptera J. C. Morse (ed.) Series Entomologica 30. Dr. W. Junk The Hague.

Elliott, J. M. 1981. A quantitative study of the life cycle of the net–spinning caddisfly, *Philopotamus moutanus* (Trichoptera: Philopotamidae) in a lake district stream. J. Animal Ecology. 50:867–883.

Elliott, J. M. 1982a. A quantitative study of the life cycle of the case building caddis *Odonotocerum albicarne* (Trichoptera: Odontoceridae) in a lake district stream. Freshwater Biology. 12:241–255.

Elliott, J. M. 1982b. The life cycle and spatial distribution of the aquatic parisitoid *Agriotypus armatus* (Hymenoptera: Agriotypidae) and its caddisfly host *Silo pallipes* (Trichoptera: Goeridae). J. Animal Ecology. 51:923–941.

Efron, B. 1982. The Jack–knife, the Bootstrap, and other resampling plans. Society of Industrial and Applied Mathematics, Philadelphia.

Fox, L. R. 1975. Cannibalism in Natural Populations. Ann. Rev. Ecol. Syst. 6:87–106.

Freeman, M. C., and J. B. Wallace. 1984. Production of net spinning caddisflies (Hydropsychidae) and black flies (Simulidae) on rock outcrop substrates in a small southeastern piedmont stream. Hydrobiologica. 112:3–15.

Fremling, C. R. 1960. Biology and possible control of nusiance caddisflies of the upper Mississippi River. Res. Bull. Iowa Agr. Home Econ. Expt. Stat. 483:356–379. 95

Fuller R. L., and R. J. Mackay, 1980. Feeding Ecology of three species of *Hydropsyche* (Tricoptera: Hydropsychidae) in Southern Ontario. Can. J. Zoology. 58:2239–2251.

Fuller, R. L., and Mackay, R. S. 1981. Effects of Food Quality on the grwoth of three *Hydropsyche* species (Tricoptera: Hydropsychidae). Can. J. Zoology. 59(6):1133–1140.

Gillespie, D. M. and A. C. Benke, 1979. Methods of calculating cohort production from field data – some relationships. Limnology and Oceanography. 24(1):171–176.

Glasgow, J. P. 1936. The bionomics of Hydropsyche coloniea McLack and *Hydropsyche philpotti* Till. Proc. Royal Entomological Society. London Ser. A. 11:122–128.

Gordon, A. E., and J. B. Wallace. 1975. Distribution of the family Hydrpsychidae (Trichoptera) in the Savannah River basin of North Carolina, South Carolina and Georgia, USA. Hydrobiologia. 46:405–424.

Grosberg, R. K. 1988. Life–history variation within a population of the Colonial Ascidian *Botryllus schoolooser*. I. The Genetic and Environmental Control of seasonal variation. Evolution. 42(5): 900–920.

Hellawell, J. M. 1986. Biological indicators of freshwater pollution and environmental management. Elsevier Applied Science Publications. London. 509.

Hildrew, A. G. 1977. Ecological aspects of life history in some net–spinning Trichoptera. Proc. of the 2nd Int. Symposium on Trichoptera. Junk. The Hague. 269–281.

Jonasson, 1972. Ecology and production of the profundal benthos in relation to phytoplankton in Lake Esrom. Oikos supplementam, 14:1–148.

Kaddou, I. K. 1960. The feeding behavior of *Hippodamia quinquesignata* (Kirby) larvae. Univ. California Publ. Entomology. 16:181–232.

Kajak, Z. 1964. Remarks on conditions influencing the appearance of new generations tendipredidae larve. Ekologia Polska Seria A, 49:111–119.

Kirkpatrick, M. 1984. Demographic models based on size, not age, for organisms with indeterminate growth. Ecology. 65(1):1874–1884.

Knutson, L. V., and O. S. Flint. 1971. Pupae of empididae in pupal cocoons of Rhyacaphilidae and Glossosomatidae. Proc. Ent. Soc. Washington. 73(3):314–318.

Knutson, L. V., and O. S. Flint. 1979. Do dance flies feed on caddisflies? Further evidence (Diptera: Erapididae; Trichoptera). Proc. Ent. Soc. Washington. 81(1):32–33.

Krebs, C. J. 1989. Ecological Methodology, Harper & Row Publishers, New York, 654.

Mackay, R. J. 1978. Larval identification and instar association in some species of *Hydropsyche* and *Chematopsyche* (Trichoptera: Hydropsychidae). Ann. Entom. Soc. America. 71(4):499–509.

Mackay, R. J. 1979. Life history patterns of some species of *Hydropsyche* (Tricoptera: Hydropsychidae) in Southern Ontario. Can. J. of Zoology. 57:963–975.

Mackay, R. J. 1984a. Life History Patterns of *Hydropsyche bronta* and *H. morosa* (Tricoptera: Hydropsychidae) in summer–warm rivers in Southern Ontario. Can. J. Zoology. 62: 271–275.

Mackay, R. J. 1984b. Some causes of variation in estimates of mean weights for *Hydropsyche* larvae (Trichoptera: Hydropsychiae). Can. J. Fisheries and Aquatic Sciences. 41:1634–1642.

Mackay, R. 1986. Life cycles of *Hydropsyche riola*, *Hydropsyche slossonae* and *Chematopsyche pottiti* (Trichoptera: Hydropsychidae) in a spring fed stream in Minnesota. Am. Mid. Nat. 115(1):19–24.

Mackay, R., and T. F. Waters. 1986. Effects of small impoundments on Hydropsychid caddisfly production in Valley Creek, Minnesota. Ecology 67(6):1680–1686.

Malas, D., and J. B. Wallace. 1977. Strategies for coexistence in three species of net–spinning caddisflies (Trichoptera) in second–order southern Appalachian streams. Can. J. Zoology. 55:1829–1840.

Martin, I. D., and R. J. Mackay. 1983. Growth rates and prey selection of two congeneric predatory caddisflies (Trichoptera: Rhacophilidae). Can J. Zoology. 61:895–900.

Morin, A., T. A. Mousseau and D. A. Roff. 1987. Accuracy and Precision of secondary production estimates. Limnology and Oceanography. 32(6):1342–1352.

Nielsen, A. 1981. On the evolution of the phallus and other male terminalia in the Hydropsychidae with a proposal for a new generic name. Proc. of the 3rd Int. Symp on Trichoptera. ed by G. P. Maretti Series Entomolica, 20:273–278.

Otto, C. 1975. Energetic relationships of the larval population of *Potamophylax cingulatis* (Trichoptera) in a south Swedish stream. Oikos 26:159–169.

Parker, C. R., and J. R. Voshell, Jr. 1979. *Cardiocladius* (Diptera: Chironimidae) larae ectoparasitic on pupae of Hydropsychidae (Trichoptera). Environmental Entomology. 8:808–809.

Parker, C. R., and J. R. Voshell, Jr. 1982. Life histories of some filter–feeding Trichoptera in Virginia. Can. J. Zoology. 60:1732–1742.

Parker, C. R., and J. R. Voshell. 1983. Production of filter feeding Trichoptera in an impounded and a free–flowing river. Can. J. Zoology. 61:70–87.

Patterson, J. W., and R. L. Vannote 1979. Life history and population dynamics of *Heteroplectron americannus*. Environmental Entomology, 8:665–669.

Platts, W. S., W. F. Megahan, G. W. Minshall. 1983. Methods for evaluating stream, riparian and biotic conditions. United States Department of Agriculture General Technical Report. INT–138. 70.

Polis, G. A. 1981. The Evolution and Dynamics of intraspecific Predation. Ann. Rev. Ecol. Syst. 12: 225–251.

Resh, V. H., and D. M. Rosenberg, Eds. 1984. The ecology of aquatic insects. Praeger, New York. 625.

Rhame, R. E., and K. W. Stewart. 1976. Life cycles and food habits of three Hydropsychidae (Trichoptera) species in the Brazos River, Texas. Trans. Am. Entomol. Soc. 102:65–99.

Ricker, W. E. 1946. Production and Utilization of Fish populations. Ecol. Mono. 16:373–391.

Ricklefs, R. E. 1979. Ecology. 2nd Edition. Chiron Proess, Incorporated. New York. 966.

Robinson, W. B., and R. W. Wisseman. 1983. A new species of Megaselia in group VII (Diptera: Phoridae). Proc. Ent. Soc. Wasington. 85(2):282–285.

Ross, H. H. 1944. The caddis flies, Trichoptera of Illinois. Bull. Nat. Hist. Surv. Illinois. 23:326.

Ross, D. H., and J. B. Wallace. 1983. Longitudinal patterns of production, food consumption, and seston utilization by net spinning caddisflies (Trichoptera) in a southern Appalachian stream (USA). Holartic Ecology. 6:270–284.

Rutherford, J. E. 1986. Mortality in reared hydropsychid pupae (Trichoptera: Hydropsychidae). Hydrobiologia. 132:97–111.

Rutherford, J. E., and R. J. Mackay. 1985. The vertical distribution of hydropsychid larvae and pupae (Trichoptera: Hydropsychidae) in stream substrates. Can. J. Zoology. 63:1306–1315.

Rutherford, J. E., and R. J. Mackay. 1986. Patterns of pupal mortality in field populations of *Hydropsyche* and *Chematopsyche* (Tricoptera: Hydropsyche). Freshwater Biology, 16: 337–350.

Schefter, P.W., and G. B. Wiggins. 1986. A systematic study of the nearactic larvae of the *Hydropsyche morosa* Group (Trichoptera: Hydropsychidae). A Life Sciences Miscellaneous publication of the Royal Ontario Museum. Toronto. 94.

Schefter, P.W., G. B. Wiggins, and J. D. Unzicker. 1986. A proposal for assignment of Certopsyche as a subgenus of Hydropsyche with new synonyms and a new species (Trichoptera: Hydropsychidae). J. North American Benthological Society. 5(1): 67–84.

Schuster, G. A. 1984. *Hydropsyche? – Symphitopsyche? – Ceratopsyche?*: A Taxonomic enigma. Proc. of the 4th Interational Symposium on Trichoptera. J. C. Morse (ed.) Series Entomologica 30. Dr. W. Junk. The Hague.

Schuster, G. A., and D. A. Etnier. 1978. A manual for the identification of the caddisfly genera *Hydropsyche* Pictet and *Symphitopsyche* Ulmer in eastern and central North America (Trichoptera: Hydropsychiae). EPA Research and Development Manual. 129 pp.

Sehnal, F. 1985. Growth and Life Cycles. In. Kerkut, G. A. and L. I. Gilbert (Eds.), Comprehensive Insect Physiology, Biochemistry and Pharmacology. Vol. 1. Pergamon Press, NY and London.

Snyder, C. D. 1988. The impact of seasonally changing feeding habits on the secondary production and accumulation of mercury in a filter–feeding caddisfly. Masters Thesis – VPI & SU, Blacksburg. 51.

Southwood, T. R. E. 1978. Ecological Methods. Chopman and Hall. London. 524p.

Standard Methods: For the examination of water and waste water, 16th Edition. 1986. American Public Health Association. New York.

Statzner, B., J. A. Gore, and V. H. Resh. 1988. Hydraulic stream ecology: observed patterns and potential applications. J. North American Benthological Society. 7(4):307–360.

Sweeney, B. W., and R. L. Vannote. 1984. Influence of food quality and temperature on life history characterstics of the parthenogenetic mayfly, *Cleon triangulifer*. Freshwater Biology. 14:621–630.

Sweeney, B. W., R. L. Vannote, and P. J. Dodds. 1986a. The relative importance of temperature and diet to larval development and adult size of the winter stonefly, *Soyedina carolinesis* (Plechoptera: Nemouridae). Freshwater Biology. 16:39–48.

Sweeney, B. W., R. L. Vannote and P. J. Dodds. 1986b. Effects of temperature and food quality on growth and developement of a mayfly, *Leptophlebia intermedia*. Can. J. Fisheries Aquatic Sciences. 43:12–18.

Teissier, G. 1931. Reserches morphologique et Physiologique sur la Croissance des Insectes. Trav. Stat. Biol. Roscoff, 9: 29–238.

Tozer, W. E., V. H. Resh, and J. O. Solem. 1981. Bionomics and adult behavior of a lentic caddisfly, *Nectopsyche albida* (Walker). Am. Midl. Nat. 106(1):133–144.

U.S. Environmental Protection Agency. 1983. Methods for chemical analysis of water and wastes. Cincinnati. EPA–600/4–79–020. 521.

Unzicker, J. D., V. H. Resh, J. C. Morse. 1982. Trichoptera. ch. 9 In: A. R. Brighma, W. U. Brigham and A. Gnilka editors. Aquatic Insects and Oligochaetes of North and South Carolina. 13.9. Midwest Aquatic Enterprises, Mahomet, IL.

Vinikour, W. S., and R. D. Anderson. 1981. Diptera larvae (Empididae and Chironomidae) in Trichoptera pupal cases (Glossosomatidae and Linmnephilidae). Entomological News. 92(2):69–74.

Wallace, J. B. 1975. Food partitioning in net–spinning Trichoptera larvae: *Hydropsyche venularis, Chematopsyche etrona,* and *Macronema zebratan* (Hydropsychidae). Ann. Ent. Soc. America. 68:463–472.

Ward, G. M., and K. W. Cummins. 1975. Effects of food quality on growth of a stream detritivore, *Paratendipea albimanus* (Meigen) (Dipter: Chironomidae). Ecology 60:57–64.

Waters, T.F. 1969. The turnover ratio in production ecology of freshwater invertebrates. The American Naturalist. 103: 173–185.

Waters, T. F. 1977. Secondary production in inland waters. Advances in Ecological Research. 10:91–164.

Waters, T. F. 1987. The effect of growth and survival patterns upon the cohort ratio. J. of North American Benthological Society 6(4): 223–229.

Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press, Toronto.

Willis, L.D., C. D. Snyder, and A. C. Hendricks. 1986. Life history and production of two speciesx of *Hydropsyche* (Tricoptera: Hydropsychidae) in the South River. Paper presented at the 1986 meeting of the North American Benthological Soiety, Lawrence, Kansas.

Wisseman, R. W., and N. H. Anderson. 1984. Mortality factors affecting Trichoptera eggs and pupae in an Oregon Coast Range Watershed. Proc. of the 4th International Symposium on Trichoptera. J. C. Morse (Ed.). Series Entomologica 30. Dr. W. Junk. The Hague.

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EDUCATION

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M.S. Zoology, 1984. University of Arkansas, Fayetteville, AR. Thesis Title: Distribution and Habitat Requirements of the Ozark Cavefish, Amblyopsis rosae.

B.S. Biology, 1979. Southwestern Oklahoma State University, Weatherford, OK.

COMPETENCIES

Stream Ecology	Bioassays	Biomonitoring
Environmental Assessment	Geohydrology	Ichthyology
Population Biology	Limnology	Chemistry
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EXPERIENCE

Regional Biologist. Virginia Water Control Board. Roanoke, VA. September, 1988 - present.

* Assess water quality via biological monitoring
* Design, coordinate and review special studies
* Assist in emergency pollution response program
* Review monitoring programs and supervise data collection

Graduate Research Assistant. Biology Dept. VPI&SU, Blacksburg, VA June, 1984 - 1988

* Designed and coordinated a study of benthic insect production to determine the chronic effects of Hg
* Designed and coordinated a detailed study on the life history of a hydropsychid caddisfly
* Coordinated contracted biomonitoring projects
* Coordinated fish collection and analysis for Hg effects
* Supervised collection of data for modeling Hg dynamics
* Managed day to day laboratory operations
* Trained, supervised and evaluated laboratory technicians
* Performed bioassays for a superfund site
* Identified and processed samples of aquatic invertebrates
* Taught General Biology Laboratories

Graduate Research Assistant. Zoology Dept. University of Arkansas, Fayetteville, AR. September, 1981 - May, 1984
* Designed and coordinated a study of the effects of sewage pollution on leaf decomposition
* Coordinated a distributional study of the Ozark cavefish
* Coordinated sampling for a two year drift study
* Coordinated a community production study
* Aided in research dealing with longitudinal zonation and the River Continuum Concept
* Shared responsibilities in the daily operation of the laboratory
* Taught freshman Biology Laboratories and Environmental Biology

MEMBERSHIPS AND ACTIVITIES
* North American Benthological Society
* Society of Environmental Toxicologists and Chemists
* American Association for the Advancement of Science
* Sigma Xi, The Scientific Research Society
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GRANTS AND AWARDS

Mary Miller Wildlife Conservation Award and Stipend. 1978.

Distribution and Abundance of the Ozark Cavefish, Amblyopsis rosae. Cave Research Foundation Grant. 1982.

Distribution and Abundance of the Ozark Cavefish, Amblyopsis rosae. Arkansas Natural Heritage Commission Grant. 1983.

Recovery Plan for the Ozark Cavefish, Amblyopsis rosae. U.S. Fish and Wildlife Service Endangered Species Program Contract. 1985.

PRESENTATIONS AT SCIENTIFIC MEETINGS

1. L. D. Willis, and A. V. Brown. Distribution of the Ozark Cavefish (Amblyopsis rosae) - Great Plains Limnological Conference. 1982.

2. L. D. Willis, P. P. Brussock, and A. V. Brown. Leaf Detritus in a cave and its associated spring - Great Plains Limnological Conference. 1983.

3. A. V. Brown, L. D. Willis, and P. P. Brussock. Effects of sewage pollution on the White River, Arkansas - Arkansas Academy of Science. 1983.

4. L. D. Willis. Cave Ecology - Boston Mountain Grotto (An Arkansas Caving Group). 1983.

5. L. D. Willis. Cave Ecology - Eco. Evening - A University wide Ecology Group at Fayetteville, Arkansas. 1983.

6. A. V. Brown, P. P. Brussock, and L. D. Willis. Flow reduction may explain sporadic occurance of Craspedacusta sowerbyi (Trachylina) Medusae - Arkansas Academy of Science. 1984.

7. L. D. Willis, P. P. Brussock, and A. V. Brown. Leaf litter processing in an Ozark cave stream - North American Benthological Society. 1985.

8. C. D. Snyder, L. D. Willis, and A. C. Hendricks. Life History and Production of Isonychia bicolor (Walker) (Ephemeroptera: Siphlonuridae) from the South River, Virginia- North American Benthological Society. 1986.

9. L. D. Willis, C. D. Snyder, and A. C. Hendricks. Life History and Production of two species of Hydropsyche (Hydropsychidae) in the South River, Virginia - North American Benthological Society. 1986.

10. L. D. Willis, A. C. Hendricks, and P. F. Nicoletto. Mercury levels in water, total suspended solids and fish from the South and South Fork of the Shenandoah Rivers in Virginia. Poster session Ecological Society of America. 1986

11. P. F. Nicoletto, A. C. Hendricks, and L. D. Willis. Sexually dimorphic accumulation of Mercury in four species of Centrachid fishes: a cost of reproduction? Poster session Ecological Society of America. 1986.

12. L. D. Willis, A. C. Hendricks, and P. F. Nicoletto. Relationships between Mercury levels in fish, water and total suspended solids from the South and South Fork Shenandoah Rivers. Society of Environmental Toxicology and Chemistry. 1986.

13. L. D. Willis and C. D. Snyder. Effects of sudden increase in discharge on the drift of aquatic insects and larval fish. North American Benthological society. 1987.

14. C. D. Snyder, A. C. Hendricks and L. D. Willis. Life history and production of Ephoron leukon (Williamson) (Ephemeroptera: Polymitarcidae) from the South River, Virginia. North American Benthological Society. 1987.

15. C. D. Snyder, L. D. Willis, and A. C. Hendricks. The impact of a seasonal shift of feeding habits on the accumulation of

mercury in a filter feeding caddisfly. North American Benthological Society. 1988.

16. L. D. Willis and A. C. Hendricks. Life History, Survival and Growth of Hydropsyche slossonae in Mill Creek, VA. North American Benthological Society. 1989.

17. A. C. Hendricks, C. D. Snyder and L. D. Willis. The Production of a Hydropsychid Caddisfly in a Fourth Order Moutain Stream Contaminated with Mercury. Symposium International Limnology. 1989.

18. L. D. Willis and A. C. Hendricks. Survival, Growth and Production of a Population of Hydropsyche slossonae. North American Benthological Society. 1990.

19. A. C. Hendricks, L. D. Willis and C. D. Snyder. Effects of a 100 year flood on the benthos of a fourth order stream. North American Benthological Society. 1990

PUBLICATIONS

1. Brown, A. V., L. D. Willis, and P. P. Brussock. 1983. Effects of sewage pollution in the White River, Arkansas, on benthos and leaf detritus decomposition. Final Report to Arkansas Water Resources Research Center, Fayetteville, Arkansas. 28.

2. Brown, A. V., L. D. Willis, and P. P. Brussock. 1983. Effects of sewage pollution in the White River, Arkansas. Arkansas Academy of Science Proceedings. 37:13-18.

3. Brussock, P. P., L. D. Willis, and A. V. Brown. 1984. Flow reduction may explain sporadic occurance of Craspedacusta sowerbyi (Trachylina) Medusae. Arkansas Academy of Science. Note 1.

4. Brown, A. V. and L. D. Willis. 1984. Cavefish (Amblyopsis rosae) in Arkansas: Populations, Incidence, Habitat Requirements and Mortality Factors. Final Report to the Arkansas Game and Fish Commission. 61.

5. Willis, L. D. and A. V. Brown. 1985. Distribution and habitat requirements of the Ozark cavefish, Amblyopsis rosae. American Midland Naturalist. 114(2):311-317.

6. Willis, L. D. 1986. Recovery Plan for the Ozark Cavefish Amblyopsis rosae. Prepared for the U.S. Fish and Wildlife Service Endangered Species Program. 42.

7. Brussock, P. P., L. D. Willis, and A. V. Brown. 1988. Leaf

Detritus Processing in an Ozark Stream. Journal of Freshwater Ecology 4(3): 263 - 269.

8. Snyder, C. D., L. D. Willis and A. C. Hendricks. 1991. Life history and production of Ephoron leukon from the South River, Virginia. J. North American Benthological Society 10(1):57 -67.

9. Hendricks, A. C., C. D. Snyder and L. D. Willis. 1990. Life history and production of a hydropsychid caddisfly in a mercury contaminated river. Verh. Int. Ver. Limnol. In Press.

10. Willis, L. D. and A. C. Hendricks. Growth, survivorship and production of Hydropsyche slossonae in Mill Creek, Virginia. In Prep.

11. Hendricks, A. C., L. D. Willis and C. D. Snyder. Effects of a 100 year flood on the benthos of a fourth order stream. In Prep.

12. Willis, L. D. and A. C. Hendricks. Cohort strategies for spreading the risk in Hydropsyche slossonae. In Prep.

14. Willis, L. D., A. V. Brown and P. P. Brussock. Production of Mayflies in a fifth order Ozark Stream. In Prep.