

Life History and Secondary Production of *Caenis latipennis* (Ephemeroptera: Caenidae) in Honey Creek, Oklahoma

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ABSTRACT The life history and production of *Caenis latipennis* Banks (Ephemeroptera: Caenidae) is described from Honey Creek, Oklahoma. Emergence behavior, fecundity, voltinism, and secondary production were analyzed. *C. latipennis* had an extended emergence with five peaks. Females emerged, molted, mated, and oviposited in an estimated 37 min. Mean fecundity was 888.4 ± 291.9 eggs per individual (range, 239–1,576). Adult female head capsule widths in spring were significantly larger than in summer and fall. Compared with the other seasons, fecundity was significantly higher in early summer when densities were lowest. *C. latipennis* exhibited a multivoltine life cycle with five overlapping generations. Estimated annual secondary production for *C. latipennis* in Honey Creek was 4,404.28 mg/m²/yr, mean standing stock biomass was 274.64 mg/m²/yr, cohort production:biomass ratio was 5.79, and the annual production/biomass rate was 16.04/yr/yr. Standing stock biomass ranged from 7.6 to 705.4 mg/m² during the year. Standing stock biomass did not vary significantly among seasons.

KEY WORDS Ephemeroptera, Caenidae, life history, secondary production

Mayflies (Ephemeroptera) are an important link in the food chain between primary producers and secondary consumers in aquatic ecosystems, especially in second and third order streams in temperate regions where the greatest diversity is found (Brittain 1982, Edmunds and Waltz 1996). Many species are potential indicators of pollution. Despite their importance, the life histories of mayflies are known for <8% of North American fauna (Wallace and Anderson 1996). This lack of life history information for Ephemeroptera hinders progress in explaining community processes and in monitoring and assessing impacts on aquatic ecosystems (Brittain 1982).

Life history information is fundamental to virtually all aquatic studies (Butler 1984) and should be considered in development and interpretation of studies of taxonomy (Oliver 1979, Rosenberg 1979), production (Resh 1979, Rosenberg 1979, Waters 1979b), toxicology (Buikema and Benfield 1979, Rosenberg 1979), environmental impact assessment (Lehmkuhl 1979, Rosenberg 1979), and water resource management (Rosenberg 1979). Benke et al. (1979) and Waters (1979a,b) emphasized that knowledge of basic life histories is mandatory for reasonable estimates of production. Production is defined as the amount of biomass produced by an animal population per unit area per unit of time (Benke 1984, Rigler and Downing

1984). Secondary production is a useful measure associated with life histories because it combines individual growth with population survivorship into a single number and provides useful information quantifying the role of individual species in ecosystem processes (Benke 1984). This information combined with life histories, systematics, and bioenergetics is an important link toward understanding the basic structure and function of aquatic communities (Wallace and Anderson 1996).

Caenis latipennis Banks (Ephemeroptera: Caenidae) is widespread and occurs in almost every state and province in North America (Provonsha 1990, Kondratieff 2005). Provonsha (1990) provided some notations on the habitat, fecundity, and life cycle of *C. latipennis*. Baumgardner (1995) reported an extended emergence (April–September) for *C. latipennis* in southeastern Oklahoma, suggesting an asynchronous life cycle. A study by Nichols and Sites (1999) suggested a univoltine life cycle for the species in Missouri. Life cycles have been reported for other North American species in the genus (Lyman 1955, Clifford et al. 1973, Corkum 1985, Provonsha 1990, Christman and Vorshell 1992, Rodgers 1982), yet, despite widespread distribution, no detailed study describing the life history, including voltinism, emergence behavior, and fecundity has been completed for southern populations of caenids. This may be in part to the difficulty of interpreting an undoubtedly asynchronous life cycle.

This study describes the life history and secondary production of *C. latipennis* in Honey Creek in south central Oklahoma. Specific objectives were to deter-

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mine the number of generations, adult emergence behavior, fecundity, abundance, and secondary production for this mayfly.

Materials and Methods

Study Site and Sampling. Honey Creek flows 25 km northeast through Murray Co., Oklahoma, into the Washita River (Reisen 1976). *C. delicata* (later synonymized with *C. latipennis*; Provonsha 1990) was first reported and described from Murray Co. in 1931 (Traver 1935). The upper 12 km of Honey Creek are intermittent, whereas the lower 13 km are consistently fed by two springs draining the Arbuckle limestone aquifer (Reisen 1975). Herbaceous rangeland (55%) and deciduous forest (40%) dominate land use within the Honey Creek watershed. Honey Creek is a system of travertine falls, bedrock runs, and gravel bottomed pools. Pools support large beds of variable leaf milfoil, *Myriophyllum heterophyllum* Michx.

Samples of nymphs and adults were collected approximately every 2 wk for 13 mo (August 1999–September 2000) from a medium-sized pool ($\approx 126 \text{ m}^2$) directly below a travertine fall. The study pool area ($34^\circ 25.407' \text{ N}$, $97^\circ 04.210' \text{ W}$) was located 300 m upstream from recreational activity within Turner Falls Park operated by the city of Davis, OK. Air and water temperature were recorded continuously throughout the study period at hourly intervals by using Stowaway Dataloggers (Onset Computer Corp., Bourne, MA). Velocity, dissolved oxygen, and pH were measured at all sampling points. Velocity was measured to the nearest 0.01 m/s with a portable electronic meter (model 2000, Marsh-McBirney Inc., Frederick, MD). Dissolved oxygen and pH were measured using portable electronic meters (model 50b, Yellow Springs Instruments, Yellow Springs, OH) and (model 250a, Orion Research Inc., Beverly, MA).

Adult Emergence. Adults were collected quantitatively using 8-W portable UV lights placed over white enamel pans (22.5 by 35.0 cm) filled with 10% formaldehyde. A single light trap was located ≈ 1 m from the stream margin at three locations within the collection site equally spaced ≈ 10 m from each other. A fourth light trap was run without preservative to make adult observations and collect ovipositing females. This light trap also was used to determine when emergence terminated. Three replicate drift nets (300 by 460 mm, 500- μm mesh) placed in steady stream flow were used to collect additional adult emergence information on 27 March and 26 July 2000. Drift nets were collected and sample material was removed every 15 min for 2 h before and after sunset and sunrise. Emergence peaks and oviposition behavior were timed based on number of exuviae and adult females in drift samples. Mating behavior and oviposition observations were made using light sources shined across the stream surface and along margins. Strips of black plastic (4 by 0.5 m) coated with Tangle-Trap Insect Trap Coating (Tanglefoot Co., Grand Rapids, MI) were hung from tree branches directly over the

stream, along its margins, and ≈ 5 m back from the stream to locate adult male swarms.

A Pearson's product moment test (SAS Institute 1998) was used to assess the relationship between adult emergence and sunset time. Sunset/sunrise data were obtained from the U.S. Naval Observatory Astronomical Applications Department Web site (<http://aa.usno.navy.mil/AA/data/>). For computational purposes, sunrise and sunset are defined to occur when the center of the Sun is geometrically 50 arcminutes below a horizontal plane (Seidelmann 1992). Head capsule measurements of adult females from each emergence peak were made with an Olympus Series Cue-2 image analyzer coupled to a dissecting microscope (model SZH, Olympus Optical Co. Ltd., Tokyo, Japan). Measurements were taken across the widest portion of the head capsule. Differences in head capsule width of females among emergence peaks were tested with a Kruskal-Wallis one-way multisample test. Fecundity, egg width, and length were compared among emergence peaks using one-way analysis of variance (ANOVA) (SAS Institute 1998).

Nymphs. Preliminary sampling from a variety of habitats indicated that *C. latipennis* nymphs were most abundant in pools with gravel or cobble mixed with gravel substrate. A stratified random sampling design based on a square meter grid was used. The site was mapped, and all square meters containing suitable substrate ($n = 53$) were identified and assigned a unique identification number. A random list of sample sites was developed and on each collecting trip the location of three replicate samples was determined and marked off the list. No sites were resampled until all sites on the list had been sampled. This ensured at least a 17-wk recovery time between sampling events within a particular square meter.

A Hess sampler (Wildlife Supply Co., Buffalo, NY) equipped with a 363- μm mesh net and 100- μm mesh dolphin bucket was used to take quantitative samples within nymphal habitat. The Hess sampler was modified to enable sampling of substrate without loss of specimens at depths exceeding the height of the sampler (>0.4 m) by adding a mesh covering to the top of the sampler. An opening in the cover permitted the researcher's hand to slide through to disturb substrate. All samples were preserved in 10% formaldehyde. In the laboratory, a decanting method was used to separate organisms and detritus from substrate. This method has shown to be 99% effective in removing *C. latipennis* nymphs from substrate (J.M.T., unpublished data). Nymphs were then picked from detritus and preserved in 70% ethanol.

Evaluation of the degree of development and differentiating stages followed the criterion of Cianciari (1980) based on size of the mesothoracic wing pads in relation to segments of the thorax and abdomen combined with markings including veination and darkening during final stages (Clifford 1970). Development classes I through V were determined as follows: I, no wing pads present; II, clear wing pads present in thoracic region; III, wing-pads with veins present in

thoracic region; IV, wing-pads with veins present in abdominal region or with veins and mottling present in thoracic region; V, wing pads enlarged, with veins and dark mottling reaching abdominal region. Nymphs of the final development class were sexed based on caudal filament morphology. Male caudal filaments lacked distinct bands proximal to abdomen and were enlarged at bases, whereas female caudal filaments displayed distinct banding the entire length of filaments and were not enlarged basally. This was confirmed by the presence of ova in nymphs displaying the second set of characteristics. Voucher specimens of all development classes have been deposited in the University of North Texas Entomology Collection, Denton, TX. Head capsule measurements were measured for use in secondary production estimates with an Olympus Series Cue-2 image analyzer coupled to a dissecting microscope (model SZH, Olympus Optical Co. LTD., Tokyo, Japan). Measurements were taken across the widest portion of the head capsule.

Many samples had high densities of nymphs and required subsampling before development classification and measurement. Subsampling was conducted by dividing a sample into eight equal sections in a 100-mm petri dish and randomly selecting three sections. All three sections were fully picked. If the total number of nymphs did not exceed 100 specimens, additional sections were fully picked until at least 100 specimens had been picked. Efficiency of the subsampling procedure was tested with a chi-square test (Elliott 1977). In conjunction with development class frequency analysis, laboratory derived degree-day (DD) estimates (Taylor and Kennedy 2003) were applied to field temperatures to provide additional information for predicting cohorts.

Secondary Production. Dry mass of preserved *C. latipennis* nymphs was estimated using a simple linear regression (SAS Institute 1998) of natural log (ln)-transformed head capsule width on ln-transformed dry mass. Head capsule widths and dry weights were measured for 132 unpreserved nymphs representing 13 size classes (100- μ m head capsule width increments). Live specimens for size class three through 13 were collected in the field and brought back to the laboratory for measurement. Nymphs of size classes 1 and 2 were reared from eggs oviposited by females from Honey Creek. After measurement, nymphs were placed on clean, preweighed aluminum foil boats. Individuals from size classes 1 and 2 were individually dried in porcelain dishes. Specimens were dried for 24 h at 105°C. After drying, specimens were placed in a vacuum-sealed desiccator for 12 h. Boats with dried nymphs were weighed (+0.0001 mg) on a microbalance (model C-31, Cahn Instruments, Madison, WI).

Estimates of *C. latipennis* standing stock biomass, annual secondary production, cohort production/biomass ratio, and annual production/biomass ratio were made from head capsule width measurements of field-preserved specimens from all sampling dates. Annual secondary production was estimated using the

size frequency method described by Hynes (1961) and Hynes and Coleman (1968), as modified by Hamilton (1969) and Benke (1979). The cohort production interval (CPI), required to calculate annual secondary production for asynchronous species, was estimated from development class frequency distributions of field-collected specimens combined with laboratory rearing data. CPI is the amount of time spent in the aquatic stage relative to 1 yr (Benke 1979). Seasonal differences in standing stock biomass and density were tested with one-way ANOVA (SAS Institute 1998).

Results

Stream Conditions. Honey Creek water temperatures ranged from 3.56°C in January to 29.03°C in August. Air temperature was lowest (-4.69°C) in late January/early February and exceeded 38°C, the maximum recording limit of the thermistor, in mid-July and on several occasions in August and September 2000. Dissolved oxygen was always near 100% saturation and ranged from 6.7 mg/liter in August to 15.6 mg/liter in December. Values for pH averaged 7.6 within a range of 6.9–8.3. Average water flow in the collection quadrants was 0.021 ± 0.004 (mean \pm 1 SE) m/s.

Emergence and Flight Periodicity. *C. latipennis* had an extended emergence period from late March to early December with five peaks (Fig. 1). A fall emergence peak was observed in late September 1999. Initial spring emergence occurred on 27 March 2000 (air temperature, 13°C) and continued throughout the spring, summer, and fall with peaks occurring on 19 April, 18 May, 29 June, and 28 August. Mean female head capsule width was significantly different among the emergence peaks (Kruskal-Wallis one-way multivariate test; $P < 0.0001$). Females were larger during spring emergence and smaller during summer emergence (Student-Newman-Keuls [SNK] nonparametric multiple comparison test; $P < 0.05$; Table 1).

Emergence was observed within a water temperature range of 14 to 27°C, an air temperature range of 9 to 30°C and a daylength range of 10 to 14.4 h. No emergence was observed from 17 December 1999 through 21 March 2000. No nymphs representing the final development class V were observed from 17 December 1999 through 9 February 2000. Development class V nymphs were present in late February and early March (Fig. 1). However, no emergence was observed during this period, even though postsunset temperatures were frequently sufficient for emergence.

Subimago arrival at light traps correlated positively with sunset (Pearson's product moment; $r = 0.89$; $P < 0.0001$). Emergence was nocturnal with subimagos and coming to light traps \approx 85 min after sunset. On the dates just before and after the suspension of emergence, subimagos arrived at light traps in <60 min. The efficiency of UV light traps in correlating emergence with sunset is debatable because some individuals may emerge before sunset and not be attracted to

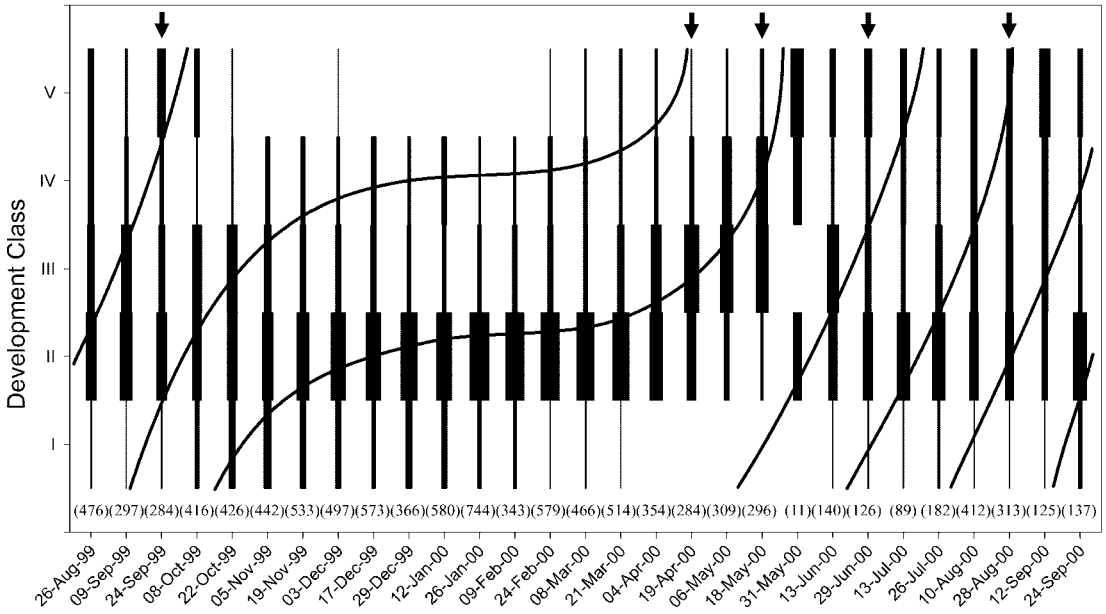


Fig. 1. Relative abundance of *C. latipennis* nymphs in five developmental classes from Honey Creek, OK, August 1999–September 2000. Arrows correspond with emergence peaks. Bar thickness represents the relative proportion of measured individuals in each development class. Sample size is indicated in parenthesis for each date. Bold lines indicate proposed cohorts and represent estimated development rates derived from a combination of developmental class frequency, emergence, and DD estimates for continuous field water temperatures.

light traps. However, drift net samples taken concurrently with light traps on 27 March 2000 indicated that 98% of individuals ($n = 400$) emerged after sunset with a difference of 11 min between peak emergence and arrival of subimagoes in light traps. Molting subimagoes were observed in light traps 5–17 min after arriving at light traps ($n = 6$). Attempts to locate, observe, or sample swarms were unsuccessful. No subimagoes or imagoes were collected on hanging tangle trap sheets, and no swarms were observed with light sources.

Oviposition and Fecundity. Oviposition was observed by imagoes in light traps 14–45 min after subimagoes arrived in light traps ($n = 8$). Field observations of oviposition indicated that females strike water forcibly then rest on the surface before rising and striking water again. Females readily oviposited in light traps, extruding the entire egg mass in a single

ball. Oviposition seems to be traumatic, with post-oviposited female abdomens shrunken and split across the vulvae. Spent female imagoes were observed on water surface 26–35 min after first arrival of subimagoes in light traps ($n = 4$). Gravid females collected in the field readily released egg masses when their abdomens were placed in water. These eggs separated and settled in a single layer on the bottom of vials. Eggs adhered to substrate 30–60 min after oviposition via attachment threads.

Fecundity for 25 field-collected females from the five major emergence peaks ranged from 239 to 1,576 and contained 888 ± 58 (mean ± 1 SE) eggs per individual. One-way parametric ANOVA detected a significant difference in fecundity among the peak emergence periods ($F = 7.61$; $df = 4, 24$; $P = 0.0007$). Fecundity for 29 June 2000 was statistically higher than all other peak emergence periods during the

Table 1. Temporal trends (mean ± 1 SE) for head capsule width, fecundity, egg width, egg length, and nymphal density for *C. latipennis* in Honey Creek

Emergence date	Head capsule width (24)	Fecundity (4)	Egg width (9)	Egg length (9)	Nymphal density (2)
24 Sept. 1999	917.509 \pm 18.18a	664 \pm 142b	95.362 \pm 1.543ab	161.402 \pm 1.773b	1,325.581 \pm 598.922
19 April 2000	1,149.28 \pm 14.88b	996 \pm 58b	98.285 \pm 1.258a	160.473 \pm 1.441b	2,275.194 \pm 1,073.559
18 May 2000	1,100.10 \pm 9.817c	803 \pm 62b	99.399 \pm 1.021a	169.931 \pm 2.047b	1,147.287 \pm 204.326
29 June 2000	1,001.02 \pm 11.73d	1,269 \pm 97a	91.666 \pm 1.937ab	151.385 \pm 2.516c	488.372 \pm 107.414
28 Aug. 2000	967.234 \pm 9.844d	707 \pm 59b	89.589 \pm 0.939b	148.120 \pm 1.116c	1,213.178 \pm 319.456

Degrees of freedom are given in parentheses with each variable. Lowercase letters represent significant differences determined by an SNK nonparametric multiple comparison test ($\alpha \leq 0.05$; head capsule width) or an SNK test (fecundity, egg width, and egg length).

Table 2. Estimated developmental times and associated DD for five cohorts of *C. latipennis* from Honey Creek, OK, during 1999–2000

Cohort	CPI	DD
1	225 ^a	3,183
2	217 ^a	3,048
3	77	1,719
4	70	1,730
5	74	1,711
Mean	132	2,278

^a CPI extended past DD estimates to account for slowed development and lack of suitable emergence conditions during the winter.

study (SNK test; $P < 0.05$). One-way parametric ANOVA detected a significant difference in egg width ($F = 9.15$; $df = 4, 49$; $P < 0.0001$) and egg length ($F = 22.16$; $df = 4, 49$; $P < 0.0001$) among the peak emergence periods. Egg length from June and August peaks was statistically shorter than in all other emergence peaks (SNK test; $P < 0.05$; Table 1).

Seasonal Development and Voltinism. Development class I was not present on five collection dates in the spring and was never very abundant in samples (Fig. 1). Some early instars may have passed through the collection net but when body length, additional width added by the legs, and all the associated debris in samples are considered, it is doubtful that many escaped. A more plausible explanation is that early instar nymphs developed rapidly and passed to the second development class quickly (Newell and Minshall 1978). Developmental class frequency patterns of field-collected nymphs, adult emergence peaks, and developmental lines derived from laboratory DD estimates for egg and nymphal development applied to field temperature data substantiate a multivoltine life cycle with five overlapping generations (Fig. 1). Cohort I was recruited in mid-September, likely as the result of a mid- to late-August emergence. This cohort developed quickly, progressing to development class III and IV, which were well represented throughout winter. As temperatures increased, cohort I continued development in February and March and began emerging in late March, peaking in mid-April. A second winter cohort began development in

mid-October as the result of late September emergence. Eggs oviposited by the fall emergence hatched throughout the fall and winter. As temperature decreased throughout the emergence period, egg development slowed resulting in an extended recruitment of nymphs. This was apparent by a growing abundance of development class II throughout the winter followed by a rise in abundance of higher development classes. The second winter cohort continued to develop and synchronized around an emergence in May. An early summer cohort was recruited in May as a result of oviposition from cohort I and completed development in late June and early July corresponding to a late June peak in emergence. The May emergence of cohort II provided recruitment of second summer cohort in late June, which developed until emergence in August. A final summer cohort was recruited in late July and developed throughout August to emerge in late September. Oviposition from cohorts IV and V are assumed to provide recruitment for the two overwintering cohorts of the following year.

Based on laboratory rearing, *C. latipennis* eggs and nymphs require 132 and 1,709 DD, respectively, for development (Taylor and Kennedy 2003). Egg and nymphal development rates based on DD estimates from continuous field water temperature data were used in conjunction with development frequency data to estimate cohort lines. Approximate developmental times and associated DD for each cohort are represented in Table 2. Development times were substantially longer for the two overwintering generations as a result of slowed development and lack of suitable emergence conditions during the winter. Thus, winter cohorts accumulated almost twice the number of DD necessary for development of *C. latipennis* nymphs.

Biomass and Secondary Production. Mean head capsule width and dry mass values for the 13 size classes of *C. latipennis* from all sampling dates are given in Table 3. A simple linear regression of ln head capsule width and ln dry weight showed a significant relationship ($n = 132$; $F = 4624.7$; $R^2 = 0.97$; $P < 0.0001$). The linear relationship of head capsule width and mass can be explained by the following equation: $\ln \text{dry weight} = -23.09548 - 3.19737 (\ln \text{head capsule width})$. The standard errors for the y-intercept and the slope were 0.298 and 0.04702, respectively.

Annual production of *C. latipennis* in Honey Creek was 4404.28 mg/m²/yr. Standing stock biomass was 274.64 mg/m²/yr. The cohort production:biomass ratio was 5.79/yr and the annual production:biomass ratio was 16.04/yr (Table 4). The cohort production interval was estimated to be 132 d when cohorts I and II were extended beyond laboratory derived DD estimates to account for lack of emergence conditions during the winter (Table 2).

Standing stock biomass did not significantly differ between seasons. A significant difference was observed in mean density between the four seasons (one-way parametric ANOVA; $F = 3.99$; $df = 5, 22$; $P = 0.0207$). Only winter and summer densities were significantly different (SNK test; $P < 0.05$) with the highest abundances occurring in January and March

Table 3. Observed arithmetic means of head capsule width (HCW) and dry mass of the 13 size classes of *C. latipennis* from Honey Creek, OK, Aug. 1999–Sept. 2000

Size class	<i>n</i>	Mean HCW \pm 1 SE, μm	Dry mass, mg
1	79	184.329 \pm 1.759	0.0016
2	1,771	260.590 \pm 0.602	0.0049
3	2,105	346.947 \pm 0.631	0.0124
4	1,432	447.570 \pm 0.771	0.0279
5	1,185	548.633 \pm 0.856	0.0535
6	1,062	650.971 \pm 0.911	0.0924
7	1,050	748.998 \pm 0.889	0.1447
8	828	847.051 \pm 0.999	0.2145
9	484	942.723 \pm 1.287	0.3020
10	219	1,043.807 \pm 1.846	0.4182
11	69	1,133.409 \pm 3.275	0.5442
12	26	1,247.428 \pm 6.231	0.7394
13	2	1,366.150 \pm 29.460	0.9888

Table 4. Secondary production calculations for *C. latipennis* from Honey Creek, OK, Sept. 1999–Aug. 2000

Size class	<i>n</i> , no./m ^{2a}	DM, mg ^b	B, mg/m ^{2c}	Δ in <i>n</i> ^d	DM at loss ^e	DM loss ^f	× 13, mg/m ^{2g}
1	28	0.0016	0.040	-466	0.003	-1.514	-19.688*
2	494	0.0049	2.420	-42	0.008	-0.363	-4.722*
3	536	0.0124	6.646	185	0.020	3.727	48.460
4	351	0.0279	9.792	49	0.040	1.994	25.925
5	302	0.0535	16.157	44	0.040	3.209	41.727
6	258	0.0924	23.839	14	0.118	1.659	21.576
7	244	0.1447	35.306	64	0.179	11.494	149.427
8	180	0.2145	38.610	76	0.258	19.627	255.151
9	104	0.3020	31.408	26	0.360	9.362	121.713
10	78	0.4182	32.619	42	0.481	20.210	262.735
11	36	0.5442	19.591	-28	0.641	-17.970	-230.269*
12	64	0.7394	47.321	53	0.864	45.797	595.364
13	11	0.9888	10.876	11	0.494	5.438	70.699
Total			274.634				1,592.781
Total production = 1,592.781 mg/m ² (365/132) = 4,404.28 mg/m ² /yr							
Biomass = 274.634 Cohort P/B = 5.79 Annual P/B = 16.04							

* Negative numbers set to zero.

^a Number present per square meter of each size class.

^b Mean dry mass (in milligrams) of individuals of each size class.

^c Total mean annual biomass of each size class.

^d Change in number of individuals present between size classes.

^e Mean dry mass of individuals of each size class when lost from the population (calculated as DM^g + DM^h + 1/2).

^f Total dry mass (milligrams) lost with each size class.

^g Dry mass loss × the number of size classes gives mean annual production for each size class.

(6,326 and 6,527 individuals/m², respectively), whereas mean individuals/m² was 42 in May. Average nymphal density for the 13-mo study was 2,398 individuals/m². Variation in abundance of nymphs was observed between years. Average density for September 1999 was 1238 individuals/m² and 508 individuals/m² for September 2000.

Discussion

Multivoltine life cycles are common in Ephemeroptera, especially in warm temperate and tropical waters (Clifford 1982, Brittain 1990). The Honey Creek *C. latipennis* population represents the first documented multivoltine life cycle for a North American *Caenis* species. Multivoltine life cycles have been reported for *Caenis luctrosa* Bürmeister from Spain (Perán et al. 1999) and suggested for *Caenis diminuta* Walker (Berner and Pescador 1988) and *Caenis hilaris* Say (Jacobi and Benke 1991) based on extended emergence.

In contrast to our findings, Nichols and Sites (1999) reported *C. latipennis* as univoltine in streams in the Ozark Mountains. With a distribution covering most of North America, voltinism for *C. latipennis* probably varies along latitudinal and environmental gradients. However, both sites are part of the Interior Highlands and given the proximity of the study sites, the difference in voltinism was surprising. We feel the differences in voltinism may be due to different study designs. Although the field methods used by Nichols and Sites (1999) were adequate for discerning instars and voltinism of *Stenonema mediopunctatum* (McDunough), their study focus, the procedures may not have been sufficient for analyzing voltinism of *C. latipennis*. Nichols and Sites (1999) sampled riffle habitats monthly using a Surber sampler (1100-μm mesh).

Our study indicated that *C. latipennis* nymphs were most abundant in pools with gravel or cobble mixed with a gravel substrate. Sampling suboptimal habitat and the use of a relatively coarse mesh size in the Ozark study may explain the low overall nymphal densities (6–50 per month) and unrepresented size classes (100–300 μm) reported for *C. latipennis*. Additionally, monthly sampling intervals may have been too long to clearly identify overlapping cohorts, especially during summer.

Cohort spreading and overlap complicated interpretation of the *C. latipennis* life cycle, and delineating cohorts was not totally unambiguous. Our analysis of cohorts is still left open to interpretation with as few as two highly asynchronous cohorts plausible. However, we feel the use of development class frequencies combined with egg and larval developmental rates based on laboratory derived DD estimates increased our precision in interpreting cohorts. Using developmental classes decreased variation associated with changes in size due to seasonal changes in environmental constraints such as temperature, flow, and food quality. Ephemeroptera exhibit heterogeneous growth and morphological development, and indeterminate number of instars within or among populations along environmental gradients (Brittain 1990), which can make simple size frequency analysis or its variations misleading or inaccurate in determining voltinism (Clifford 1970; Fink 1982, 1984; Benton and Pritchard 1988). Laboratory-derived data assisted in interpreting areas of cohort overlap in the development frequency histograms. Developmental rates predicted by DD estimates for cohorts I and II were extended due to suppressed emergence and increased DD well beyond the laboratory-derived estimates (Table 2). The three overlapping summer cohorts were defined by development class frequency analysis

Table 5. Fecundity of six *Caenis* spp

Species	Fecundity	Citation
<i>C. amica</i>	95–1787 ^a	Sweeney and Vannote (1978)
<i>C. anceps</i>	448–1,787	Rodgers (1982)
<i>C. hilaris</i>	414–806	Provonsha (1990)
<i>C. horaria</i>	508–607	Clifford (1974)
<i>C. latipennis</i>	812–2,163	Provonsha (1990)
<i>C. moesta</i>	765–1,103	Clifford (1974)

^a Values represent range.

and the addition of DD estimates and adult emergence information. Other studies have successfully described multivoltine life cycles by combining field and laboratory data for Ephemeroptera (Perry 2005) and Diptera (Balci and Kennedy 2002a,b, 2003).

Cohort overlap and asynchronous development provide a selective advantage for *C. latipennis* populations. Weather conditions during the spring emergence period are characterized by highly variable air temperatures. Staggered maturation of the two asynchronous overlapping winter cohorts provide continuous emergence during early spring, ensuring that some individuals will emerge under favorable conditions and successfully reproduce though many are lost to poor weather conditions. Spates and drying events are common disturbances of streams in the region. Miller and Golladay (1996) found that *Caenis* and other mayflies were resistant to spates and intermittent conditions in south-central Oklahoma streams due to their ability to persist in intermittent pools and find refugia during spates. Maintaining individuals in all development classes throughout the majority of the year ensures that at least some individuals with suitable character traits will survive during periods of disturbance or other unfavorable conditions.

Brief adult life spans are typical of Ephemeroptera species and range from 1 to 2 h to 14 d in some oviporous species (Brittain 1982). As a result of its small size and compact, nocturnal swarms, few observations of *Caenis* adult behavior have been recorded (Needham et al. 1935). Despite repeated attempts we were not able to observe swarming activity in the species. However, coordinated aquatic drift and light trap collections indicated that female *C. latipennis* have an adult life span as short as 37 min. This is the shortest adult life span reported for a mayfly species.

Fecundity measurements for *C. latipennis* from Honey Creek occur within estimates of Provonsha (1990) (812–2,163 eggs/individual). Fecundity reports for five other *Caenis* species are presented in Table 5. *C. latipennis* fecundity tends to be among the highest reported for the genus.

In general, species with extended emergence show a gradual decrease in size throughout extended emergence periods (Clifford 1974). *C. latipennis* growth patterns were similar to those reported for other mayflies (McClure and Stewart 1976; McCafferty and Huff 1978; Grant and Stewart 1980; Kondratieff and Voshell 1980, 1984; Soderstrom 1988; Perry 2005). Winter cohorts of *C. latipennis* exhibited increased nymphal growth periods in which greater numbers of DD were accumulated before emergence. This supports the findings of Sweeney (1984) that larger adult size correlates with longer growth period experienced by overwintering generations.

Many studies have reported that fecundity correlates with body size in Ephemeroptera and decreases over periods of extended emergence in multivoltine species (Clifford 1974; McClure and Stewart 1976; Sweeney and Vannote 1978; Grant and Stewart 1980; Kondratieff and Voshell 1980, 1984; Brittain 1982; Soderstrom 1988; Perry 2005). In contrast to these studies, the Honey Creek population of *C. latipennis* showed a significant increase in fecundity during the early summer coupled with decreased adult size. This improbable phenomenon was possible because egg width and length decreased during the summer. Rosillon (1988) reported that *Ephemerella ignita* (Poda) females reared individually always had higher fecundity than females reared in groups. Although no statistical differences were detected among emergence dates for population densities of *C. latipennis*, nymphal densities were lowest during this period of increased fecundity, indicating that population densities may be an important factor influencing fecundity for *C. latipennis* (Table 1). Reduced competition for space and food resources may enable *C. latipennis* females to increase egg production at lower densities. Increased food quality has been reported to increase fecundity in *E. ignita* (Rosillon 1988), *Leptophlebia intermedia* (Traver) (Sweeney et al. 1986), and *Parameletus che-lifer* Bengtsson and *Parameletus minor* (Bengtsson) (Soderstrom 1988) and also may be a factor in Honey Creek during the summer when food webs may be

Table 6. Production estimates for *Caenis* spp. (modified from Perán et. al. 1999)

Species	P (mg/m ² /yr)	P/B	Habitat (location)	Citation
<i>C. luctrosa</i>	6,349.81	15.98	Semiarid stream (Spain)	Perán et al. (1999)
<i>C. latipennis</i>	4,404.28	16.04	Travertine stream (Oklahoma, U.S.A.)	This study
<i>C. simulans</i>	4,200.00	4.20	Cold/mesic plains stream (Minnesota, U.S.A.)	MacFarlane and Waters (1982)
<i>C. amica</i>	676.00	12.72	Experimental stream (Alabama, U.S.A.)	Rodgers (1982)
<i>C. amica</i>	445.05	13.00	Experimental ponds (Virginia, U.S.A.)	Christman and Vorshell (1992)
<i>Caenis</i> spp. ^a	82.10	59.10	Humid/mesic plains stream (Georgia, U.S.A.)	Benke and Jacobi (1994)
<i>C. latipennis</i>	31.00	8.00	Prairie stream (Kansas, U.S.A.)	Stagliano and Whiles (2002)

^a Benke and Jacobi's study included combined production of *C. diminuta*, *C. hilaris*, and *C. maccafferti* and therefore was not used in comparisons.

come more algal versus detrital based. One of these factors, or more likely both, may influence fecundity of *C. latipennis* during the summer. These questions warrant further investigation.

Secondary productivity of *C. latipennis* in Honey Creek is high relative to reports for other *Caenis* species, which range from 31.00 mg/m²/yr to 6349.81 mg/m²/yr (Table 6). Although production estimates for *C. latipennis* were lower than *C. luctrosa*, the two species had similar annual production/biomass (P/B) ratios. *C. luctrosa* exhibits a similar multivoltine life cycle with four overlapping generations and is found in an intermittent stream subject to spates and dewatering (Perán et al. 1999). Disturbance regimes and warm temperatures select for taxa with short developmental times, rapid growth rates, and small terminal size. Populations in warm-temperate streams subject to disturbance tend to be highly productive with rapid growth rates rather than biomass driving productivity (Huryn and Wallace 2000). Comparing secondary productivity for *C. latipennis* with published estimates for *Caenis amica* Hagen (reported as *C. simulans* Lyman; MacFarlane and Waters 1982) illustrates this observation; both species exhibited similar production estimates, yet P/B ratios were 4 times greater for *C. latipennis* (Table 6). Secondary production for *C. amica* in a cool-temperate stream was dependent on accrual of biomass rather than rapid growth rates.

No significant differences existed between seasons in standing stock biomass of *C. latipennis*, although winter and summer densities were significantly different. Biomass was not affected by high winter densities because the majority of the two cohorts were in small size classes. Winter and early spring peaks in seasonal abundance of *C. latipennis* are likely the result of continued recruitment from eggs oviposited in the fall and suppressed emergence during the winter. Low densities in May are likely the result of reduced chances for successful emergence and ovipositing due to varying weather conditions often encountered during early spring. Higher winter abundances have been reported for populations of *C. amica* in experimental ponds (Christman and Vorshell 1992). Abundance patterns opposite to our findings have been observed for *C. luctrosa* with higher densities in summer (Perán et al. 1999).

Basic autecology studies, including describing life histories of aquatic insects are fundamental to the understanding of stream ecology. Our study represents the first documented multivoltine life cycle and the highest secondary production estimate for a *Caenis* sp. in North America. Our results suggest that *C. latipennis* plays a major role in energy transfer within stream ecosystems of the Southwest. This study also demonstrates the flexibility in life history strategies within a single population as well as variation in life cycles among North American *Caenis* species. These findings emphasize the need for more quantitative accounts of population dynamics (life cycle patterns, fecundity, development rates, production, and P/B) of aquatic insect species in streams across environmental gradients.

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