LIFE HISTORY AND SECONDARY PRODUCTION OF *CAENIS LATIPENNIS* BANKS (EPHEMEROPTERA: CAENIDAE) IN HONEY CREEK, OKLAHOMA

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A study of the life history and secondary production of *Caenis latipennis*, a caenid mayfly, was conducted on Honey Creek, OK. from August 1999 through September 2000. The first instar nymph was described. Nymphs were separated into five development classes. Laboratory egg and nymph development rates, emergence, fecundity, voltinism, and secondary production were analyzed. *C. latipennis* eggs and nymphs take 132 and 1709 degree days to develop. *C. latipennis* had an extended emergence with five peaks. Females emerged, molted, mated, and oviposited in an estimated 37 minutes. Mean fecundity was 888.4 ± 291.9 eggs per individual (range 239 –1576). *C. latipennis* exhibited a multivoltine life cycle with four overlapping generations. Secondary production was 6,052.57 mg/m^2/yr.

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CHAPTER 1

INTRODUCTION

Life histories and secondary production

Life history information is fundamental to virtually all aquatic studies (Butler, 1984) and should be considered in development and interpretation of studies in taxonomy (Oliver, 1979; Rosenberg, 1979), production (Resh, 1979; Rosenberg, 1979), toxicology (Buikema and Benfield, 1979; Rosenberg, 1979), assessing environmental impacts (Lehmkuhl, 1979; Rosenberg, 1979), and water resource management (Rosenberg, 1979). Over the past few decades, trends in ecological research began shifting from descriptive autecology toward more quantitative methods such as mathematical modeling and systems analysis (Resh, 1979). This shift continues today as interest and need for a more holistic discipline dedicated to solving broad ecological and increasingly applied environmental problems become more apparent. These trends have led to a decline in studies dedicated to basic life history descriptions. Recent life history studies typically are based on sampling designs developed for different objectives when conversely, sampling design based on life history data could meet objectives more quickly and more accurately (Resh, 1979).

Life cycle is often confused with life history. Butler (1984) defines life cycle as “the sequence of morphological stages (egg, larvae, pupae, adult) and physiological processes (metamorphosis, dormancy, regional dispersal, and reproduction) that link one generation to the next.” Life cycles are species specific. Life history is the quantitative and qualitative details of the variable events that are associated with the life cycle such as fecundity, growth phenology and rate, mortality, and emergence patterns (Butler, 1984). Life histories often exhibit intrapopulation and intraspecific variation (Butler, 1984; Price, 1997).

Secondary production is an important measure for population studies because it combines individual growth and population survivorship into a single number (Benke, 1984). Production is defined as the amount of biomass produced by an animal population over a unit of time (Benke, 1984; Rigler and Downing, 1984). Secondary production can provide useful information quantifying the role of individual species in ecosystem processes (Benke, 1984). This information can further be utilized in determining how life history parameters are influenced by ecosystem processes (Benke, 1996).

Study organism

The insect order Ephemeroptera or mayflies, represent the oldest of winged insects with fossil records dating back to the Carboniferous and Permian periods. Ephemeroptera is a small order with nineteen families, 200 genera, and approximately 2000 species (Brittain, 1982). As of February 2001, there are 680 species recognized in North America (McCafferty, 2001). Representatives of Ephemeroptera can be found in many types of freshwater environments, excluding Antarctica, high arctic regions, and many small oceanic islands. The greatest diversity of mayflies is found in second- and third-order streams in temperate regions (Brittian, 1982; Edmunds and Waltz, 1996). Many species are potential indicators of pollution, and all mayflies are an important link in the food chain between primary producers and secondary consumers in aquatic ecosystems. The lack of life history information for Ephemeroptera hinders progress in explaining community processes and in monitoring and assessing impacts on aquatic ecosystems (Brittain, 1982).

Caenidae represents a widely distributed mayfly family occurring in a broad range of both lentic and lotic habitats. Caenids are among the smallest mayflies but often occur in very large numbers (Provonsha, 1990). Caenidae and Neoephemeridae compose the superfamily Caenoidea, one of two cosmopolitan clades within the pannote mayfly genera (McCafferty and Wang, 2000). Nymphs of Caenidae are sometimes indistinguishable from Neoephemeridae except for the caenids' absence of hind wing pads and the fibrilliform tuft on the gills of abdominal segments 3 - 6 (Edmunds, Jensen and Berner, 1976; Provonsha, 1990). Sometimes confused with Tricorythidae, caenids possess gills on abdominal segment 1 and have subquadrate operculate gills, while tricorythids lack gills on segment 1 and have triangular operculate gills. North American genera of Caenidae include *Caenis* Stephens, *Brachycerus* Curtis, *Amercaenis* Provonsha, and *Cercobrachys* Soldan (Provonsha, 1990). Twenty-four species occur in North America, *Brachycerus* and *Caenis* include all but three (McCafferty, 2001).

The genus *Caenis* was first described from the type species, *Caenis macrura* in London, England by Stephens (1835). The first North American species to be described was *C. hilaris* (Say), 1839. McDunnough (1931) provided the first comprehensive treatment of North American caenid species describing ten *Caenis* species. Four years later Traver (1935) published keys to all North American Ephemeroptera. Traver's work provided the first key to North American *Caenis* and described two new species. Later Burks (1953) described a new *Caenis* species in his inventory of Illinois mayflies. Three more species were described before Provonsha (1990) revised the entire genus. This revision recognized 11 North American species, which are separated into the diminuta and hilaris groups based on shared characteristics of the larvae, adults, and eggs.

Caenis latipennis was originally described by Banks (1907) from Pullman, Washington. Provonsha's (1990) revision of North American *Caenis* relied on continuums in body length and coloration to make the following synonym:
C. latipennis = C. forcipata McDunnough n. syn., *C. jocosa* McDunnough n. syn., *C. delicata* n. syn., *C. gigas* Burks n. syn. *C. latipennis* is widespread and occurs in almost every state and province in North America (Figure 1). It is considered absent only from the Rocky Mountain area and extreme southeastern regions (Provonsha, 1990). Provonsha (1990) describes larvae as preferring little or no current and inhabiting substrates including sand, mixed gravel, emergent plants, detritus, and other debris.

Ephemeroptera are hemimetabolous insects. The majority of ephemeropteran life cycles are spent in the aquatic environment followed by a short terrestrial period concerned with reproduction (Brittian, 1990). The basic mayfly life cycle begins with the egg, which varies in development from ovoviparity to periods up to 10-11 months. Nymphs have an indeterminate number of instars and development periods span from 3-4 weeks to 2 ½ years. Among the aquatic insects, mayflies are unique in having two winged stages, the subimago and imago. Many theories exist as to why Ephemeroptera possess a subimago stage. Aid in breaking water surface tension during emergence, the necessity of two molts to complete sexual development, or the retention of a primitive trait because of lack of selection pressure on short-lived stages have all been suggested (Brittian, 1982). Life cycles of mayflies are typically univoltine with multivoltine species increasing in tropical and temperate regions (Brittian, 1990).

Variation in voltinism is common in Ephemeroptera, especially smaller species (Brittian, 1982; Lauzon and Harper, 1986). Univoltine life cycles are typical for Ephemeroptera species but multivoltine species are common in temperate and tropical regions (Brittian, 1990). Evidence supports variable life cycles among and within *Caenis* species. These life cycles may be misleading if not sampled correctly and completely, especially for temperate and tropical populations. Increased sample size and frequency, emergence peak data, and laboratory rearing need to be considered when interpreting life cycles of latitudinally dynamic species.

Caenis amica Hagen 1861 is the most widely distributed and encountered *Caenis* spp. in North America (Provonsha, 1990); consequently, it is the most widely studied species in North America. Research on northern populations including localities in Illinois (as *C. simulans* [Lyman, 1955]), Pennsylvania and Indiana (Provonsha, 1990), and Alberta, Canada (as *C. simulans* [Clifford et.al., 1973]) report a univoltine life cycle for *C. amica*. Bivoltine populations seem to occur in middle latitudes (Rodgers, 1982; Christman and Vorshell, 1992) with the exception of an Alberta, Canada population (Corkum, 1984). Edmunds et al. (1976) reports *C. amica* as bivoltine with two summer generations for the United States. No reports on voltinism have been made for *C. amica* in the southern parts of its distribution, but emergence data supports the possibility of multivoltine (more than 2 generations) populations. *C. amica* emerges throughout the warm months of April through September in Southeast Oklahoma (Baumgardner, 1995) and March through November in the Southeastern United States (Berner, 1977; Unzicker and Carlson, 1982). Extended emergence and warm temperatures could support multiple generations for *C. amica*.

Caenis diminuta Walker 1853 is the most common species of *Caenis* in the southeastern United States (Provonsha, 1990). Rodgers (1982) reports a bivoltine life cycle in artificial streams from Alabama. Extended emergence has been reported for southeastern populations (Berner, 1977; Jacobi and Benke, 1991) and year round emergence has been reported in Florida (Berner and Pescador, 1988). Berner and Pescador (1988) imply multivoltinism while Jacobi and Benke (1991) suggest multiple generations occurring during the summer months for this species.

Caenis hilaris is a common to the eastern half of the United States. *C. hilaris* was reported as bivoltine from Indiana with peak emergence in July and September (Provonsha, 1990). This concurs with data indicating emergence from June to October for Oklahoma (Baumgardner, 1995) and Georgia (Jacobi and Benke, 1991). Jacobi and Benke (1991) suggest multiple generations which would support year round emergence reported in Florida (Berner and Pescador, 1988).

No life history data was available for *C. latipennis* until Nichols and Sites (1999) published *C. latipennis* as univoltine from Missouri. Data for south central Oklahoma indicate two peaks in late instars for June and August (reported as *C. delicata* [Magdych, 1979]) suggesting multiple generations. Baumgardner (1995) reports an extended emergence (April through September) for *C. latipennis*. Extended emergence and warm temperatures give support to the idea that *C. latipennis* is multivoltine at southern latitudes.

European records classify Caenidae as having Type IV swarming behavior. This classification is characterized by a more complex flight involving more frequent alterations between active and passive flight. In most mayfly species only males swarm, yet sex ratios for *Caenis* species show a substantial number of females present in swarms. Male to female ratios recorded for European *Caenis* species include *C. macrura* (68:18), *Caenis horaria* L. (130:34), and *Caenis undosa* Tiens (50:8). Decreased reliance on visual receptors may become less useful when females occur in swarms, thus explaining why *Caenis* males do not have divided compound eyes (Brodskiy, 1973).

Research objectives

The purpose of this research was to describe the ecology and energetics of *Caenis latipennis* Banks (Caenidae) in Honey Creek. Specific objectives were to determine the number of generations, development rates, adult emergence, fecundity, abundance, and secondary production rates throughout the year. Nymphal development stages are described and male and female adult antennal structure and wing size are compared with inferences to mating behavior.

Study area and site description

A unique geological feature of the Arbuckle Mountains is the Timbered Hills group. This area consists of basal Reagan Sandstone and an overlying Honey Creek Limestone. All streams flowing across limestone beds in the Arbuckle Mountains typically dissolve calcium carbonate and carry it away downstream in solution (Ham, 1969). Honey Creek is a second order limestone stream flowing parallel to the fault trace separating the Cool Creek and McKenzie Hill formations of the Arbuckle Mountians of southern Oklahoma (Reisen, 1976; Ham, 1969). Honey Creek is unique to the region in that calcium carbonate precipitates from the stream waters creating a spongy-textured travertine bed. Photosynthesizing blue-green algae assists in the precipitating of calcium carbonate by raising the pH in the stream. This travertine bed, built up through time, created Turner

Falls, which at one time stood 45 meters. Increased rainfall during the middle Pleistocene caused the stream to cut into the travertine bed it had built, reducing the waterfall to its present height of about 23 meters. Today the travertine bed is maintaining a steady state with precipitation of calcium carbonate from stream-floor deposits occurring at about the same rate as mechanical removal during floods (Ham, 1969).

Honey Creek flows 25 km northeast into the Washita River (Reisen, 1976). The upper 12 km of Honey Creek are intermittent, while the lower 13 km are consistently fed by two springs draining the Arbuckle limestone aquifer (Reisen, 1975) (Figure 2). Herbaceous rangeland (55%) and deciduous forest (40%) dominate landuse, within the Honey Creek watershed (Table 1). Honey creek is a system of slow moving, gravel-bottomed pools broken up by bedrock pools and falls. Pools support large beds of the aquatic macrophyte *Myriophyllum heterophyllum*, or Variable leaf milfoil. This plant is a native plant not to be mistaken with the exotic-invasive Eurasian water milfoil. Magdych (1979) previously studied mayfly microdistribution within *M. heterophyllum* beds in a similar stream in south central Oklahoma.

Previous research on Honey Creek was performed in the 1970's and in recent years. Reisen (1975, 1976a, 1976b, 1976c) investigated numerous aspects of Honey Creek including Simulidae drift and ecology, macroinvertebrate distributions, drift of Stratiomyidae and Ceratopogonidae, distribution of periphyton, and productivity of *M. heterophyllum*. Life histories of *Camelobaetidius mexicanus* (Traver and Edmunds) 1968 and *Mayatrichia ponta* Ross 1944 have recently been completed in Honey Creek. *C. mexicanus* was determined to have a multivoltine life cycle with 3 generations per year (Wagner, 1995). Wang (1997) reported a multivoltine life cycle with 5 generations for

M. ponta. Honey Creek is the type locality for *M. ponta* (Wang, 1997). *C. delicata* was first reported and described, and later made synonymous with *C. latipennis,* from Murray Co., Oklahoma in 1931 (Provonsha,1990; Traver, 1935).

CHAPTER 2

MATERIALS AND METHODS

Collection of nymphs

Nymphs were quantitatively collected every two weeks using a Hess sampler with a 363 μm net from August 1999 to September 2000. The Hess sampler was modified to enable sampling of substrate at depths exceeding the height of the sampler (> 0.4mm) by adding a mesh covering to the top of the sampler. An opening in the cover permitted the researcher's hand to slide through for sampling (Figure 3). Preliminary sampling from a variety of habitats indicated that *C. latipennis* populations were most abundant in pools with gravel or cobble mixed with gravel substrate.

A large pool containing 53 square meters of suitable substrate was selected for sampling. The pool was approximately 300 m upstream from recreational activity at Cedar Ridge pool. The sampling site was mapped out into a square meter grid based on a central transect. All square meters containing suitable substrate were identified and assigned a number. The list of square meters of suitable substrate was randomly ordered. Each collecting trip the three highest square meters on the list were sampled and marked off the list. No sites were resampled until the list had been completed. This insured an adequate 17-week recovery time within sampling sites. All samples were field-preserved in 10% formaldehyde. In the lab, 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. Nymphs were then picked from detritus and preserved in 70% ethanol.

Development analysis

Development was studied by frequency analysis of development classes based on wing pad development and markings. Cianciara (1980) used a similar method to interpret life cycles of mayflies.

Adult collection

Adult emergence peaks were determined from three 8-Watt UV light traps set when temperatures were sufficient for adult emergence to occur (10ºC). Traps were set along stream margins equally spaced throughout a collection site. Mating behavior and oviposition observations were attempted using light sources shined across the stream surface and along margins. Attempts to locate swarms were made using plastic strips coated with Tangle Trap hung over stream, stream margins and riparian zones. An additional 8-Watt UV light trap was used without preservative to make adult observations and collect ovipositing females. Fecundity was measured by counting eggs from preserved females collected on peak emergence dates. Adult emergence times were determined by collection of final instar exuvium with drift nets and observing first occurrence of adults at light traps.

Laboratory rearing

Egg masses were collect from females attracted to light traps and reared from egg to adult in the laboratory. Eggs were reared in open vials submerged in plastic containers filled with stream water. Temperature effects on growth rates were determined by rearing egg batches on a twelve-hour light cycle at 15ºC, 20ºC, and 25ºC. These temperatures were comparable to temperatures for Honey Creek reported by previous investigators (Reisen, 1976; Wagner, 1995; Wang, 1997). Larvae were fed with detritus decanted from substrate in the field.

Secondary production

Dry mass of *C. latipennis* nymphs was estimated using live nymphs. Benthic samples were collected in Honey Creek and brought to the laboratory in stream water. Larvae were broken into 13 size classes based on 100 um increments of HCW. Live nymphs of size classes 3 through 13 were collected from these samples. Nymphs of size classes 1 and 2 were reared from eggs oviposited by adults from Honey Creek. Head capsule widths of 132 nymphs were measured with an Olympus Series Cue-2 image analyzer (Olympus, Tokyo) and Olympus SZH dissecting microscope. Measurements were taken across the widest portion of the head capsule and nymphs were placed on clean, preweighed aluminum foil boats. Specimens were dried for 24 h at 105ºC. Following drying, specimens were placed in a vacuum-sealed desiccator for 12 h. Boats with dried nymphs were weighed (+0.0001mg) on a Cahn C-31 microbalance (Cahn Instruments, Madison, WI). Individuals from size classes 1 and 2 were individually dried in porcelain dishes and added to balance one at a time, tarring balance after each individual had been weighed. Data for head capsule width in millimeters and dry mass in milligrams were transformed using the natural log (ln) transformation. A dry biomass conversion was derived from a simple linear regression of ln head capsule width on ln dry mass (SAS Institute 1996).

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 one year (Benke, 1979).

Physico-chemical measurements

Velocity, pH, and dissolved oxygen were measured each sampling date. These measurements were taken at all sample locations in an attempt to measure within the microhabitat of the organism. Velocity was measured to the nearest 0.01 m/s with a Marsh-McBirney model 2000® portable electronic meter. pH was measured using an Orion model 250a® portable electronic meter. Dissolved oxygen was measured using a YSI model 50b® portable electronic meter. Water and air temperature were measured throughout the study period on an hourly interval using Onset Stowaway Dataloggers®. Rainfall data was acquired from the National Climatic Data Center (http://www.ncdc.noaa.gov/) and sunset/sunrise data was obtained from USNO's Astronomical Applications Department (http://aa.usno.navy.mil/AA/data/).

CHAPTER 3

RESULTS AND DISCUSSION

Physico-chemical parameters

Physico-chemical data for Honey Creek are listed in Table 2. Dissolved oxygen ranged from 6.7 mg/l in August to 15.6 mg/l in December. Values for pH did not differ between sampling dates very much. Values for pH averaged 7.6 and ranged from 6.9 to 8.3. Flow was minimal in most collection quadrants ranging from 0 to 0.15 m/s. Unstable substrate such as gravel is usually associated with low flow. Water temperatures ranged from 3.56º C in January to 29.03º C in August (Figure 7). Air temperature was lowest (–4.69º C) in late January and early February. Air temperature rose above the capacity of the data logger (38º C) in mid July and on several occasions in August and September, 2000 (Figure 8).

Description of first instar and development classes

First instar nymphs are unpigmented, lightly sclerotized, lack gills, and has an overall body length, excluding cerci, of approximately 350 μm (Figure 4). The head has sparse setae on lateral and apical margins. Compound eyes are located on posterio-lateral margins of head. Three ocelli are present (one medial and two lateral) anterior to compound eyes. Head capsule width is approximately 100 μm. Antennae are five segmented with three setae on segment two, one setae on segment three, two setae on segment four, and two setae on segment five. One segmented labial and maxillary palps, and a general lack of setae characterize mouthparts. Thoracic segments lack wingpads.

Legs (Figure 4c) lack distinction between tarsal segment and tibia. However examination of later instar nymphs showed a separation at the base of the second large spine or the 1st tibia spine. Tarsus and tibia each have a stout spine on inner margin and two setae on outer margin. The fibia have two setae present. Tarsal claws are sharply pointed with a cluster of spines in apex of curve of claw. Abdominal segments have 1-2 lateral setae and a row of spinules. Three five segmented cerci are present. A cluster of three or four spines is present on the apical end of segments 1-3. Two lateral setae are present at the apical end of segments 2, 4, and 5.

Development class I is represented by first instar nymphs (Figure 4) with no wingpads present. Development classes II through V are represented in Figure 5 and are as follows: II = clear wingpads present in thoracic region, III = wingpads with veins present in thoracic region, IV = wingpads 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 sexes based on caudal filament morphology. Male caudal filaments lacked distinct bands proximal to abdomen and were enlarged at bases while female caudal filaments displayed distinct banding the entire length of filaments and were not enlarged basally (Figure 6). This was confirmed by the presence of ova in nymphs displaying the second set of characteristics. The male to female sex ratio of 583 nymphs examined was 1.09 : 1.

Laboratory Rearing

Eggs collected in the field and brought back to the laboratory were incubated under three different temperature regimes. Egg broods incubated at 14 – 15ºC first hatched on day 28 (*n*=3). Eclosion for egg broods occurred in 12 to 14 days at 19 – 21ºC (*n*=6). At

25ºC, egg broods hatched in 8–10 days (*n*=7)(Figure 9). The minimum critical threshold for egg development was 9.9ºC determined by the following regression model: Developmental Rate = 0.00763(Temperature) – 0.07596 (r^2 = 0.9515, F test, n = 16, p < 0.0001) (Figure 9). On average, eggs took 132 degree days to develop.

Nymphs were successfully reared at 20ºC. Mean number of days to emergence was 85 days (n = 11) (Figure 10). Nymphs reared at 15ºC did not pass through the 1st instar. No live nymphs were observed after one week in rearing chambers. Nymphs were not successfully reared through complete lifecycle at 25ºC due to incubator malfunction. Average development units from egg to adult was 1709 degree days at 20ºC.

Emergence and flight periodicity

Field data and observations indicate that *C. latipennis* has an extended emergence period from late March to early December with five peaks (Figure 12). Fall emergence in 1999 yielded a large peak in late September. Spring emergence peaked on 19 April 2000 and was followed by a late spring peak on May 18th. Summer emergence had two peaks occurring on 29 June 2000 and 28 August 2000.

Adult emergence was observed within an air temperature range of 9ºC to 30ºC and a day length range of 599 to 866 minutes. Emergence of *C. latipennis* was never observed below a temperature threshold of approximately 9ºC. No emergence was observed on 19 November when air temperature fell to 9ºC, but did occur on December 3rd when air temperature approached 17ºC. The next sampling date (December 17th) coincided with the shortest day length for the study, and temperature during predicted emergence time fell to 7ºC. No emergence was observed on December 17th and the following 7 sampling dates (29 Dec 1999 – 21 Mar 2000). Nymphs were only present in development classes I

– IV from 17 Dec 1999 thru 09 Feb 2000 (Figure 13). Development class V nymphs were present in late February and early March and may have emerged during warm periods, however post sunset temperatures did rise to the emergence temperature range for these sampling dates and no emergence was observed. Initial spring emergence occurred on 27 March 2000 when air temperature was 13ºC and was followed by an emergence at an air temperature of 9ºC on 04 April.

Extended emergence periods are common at southern latitudes for *Caenis* species (Berner, 1977; Baumgardner, 1995;. Jacobi and Benke, 1991; Unzicker and Carlson, 1982). In general, species with extended emergence periods have larger emerging individuals in the spring and gradually decrease in size throughout the emergence period (Clifford, 1974). Mean female head capsule widths were significantly different among the emergence peaks (Kruskal-Wallis one-way multisample test, $p < 0.0001$). SNK nonparametric multiple comparison test ($\alpha = 0.05$) separated the rank sums of the five dates into four statistically different groups:

19 April 2000 18 May 2000 29 June 2000 28 August 2000 24 Sept 1999

Females were larger during spring emergence and smaller during summer emergence (Figure 14). Larger adult size usually correlates with longer growth period experienced by over wintering generations and greater time to assimilate nutrients (Sweeney, 1984). This has been observed in many multivoltine mayflies (Grant and Stewart, 1980; Kondratieff and Voshell, 1980, 1984; McCafferty and Huff, 1978; McClure and Stewart, 1976; Soderstrom, 1988; Wagner, 1995) and caddisflies (Johnson et. al., 1998, Rhame and Stewart, 1976). This increase in body size for over wintering generations may have effected minimum temperature requirements for emergence. 9ºC was the approximate low temperature threshold for emergence, yet initial spring emergence occurred at 9ºC. Increased body size of late developmental stage nymphs during the initial emergence may have increased ability to emerge at lower temperature.

Adult arrival at light traps was positively correlated with sunset time (Pearson's product moment, $r^2 = 0.89$, $p < 0.0001$). Adults were nocturnal, coming to light traps approximately 85 minutes after sunset. This time was less than 60 minutes on dates at the end and beginning of emergence periods. Drift net samples taken concurrently with light traps on 27 March 2000 indicated a difference of eleven minutes between peak emergence and arrival of adults in light traps on this date (Figure 15). Molting subimagos were observed in light trap 5 to 17 minutes after adults first arrived in light traps ($n = 6$). Oviposition was observed in light traps 14 – 45 minutes after first arrival of adults in light traps ($n = 8$). Spent females were observed on water surface 26 – 35 minutes after first arrival of adults in light traps ($n = 4$) (Table 3).

Falling temperatures may have contributed to an abrupt decrease in time between sunset and emergence on dates at the end and beginning of emergence periods, although this change did not occur under similar diel temperature regimes during the study. Brief adult life spans are typical of Ephemeroptera species and range from 1-2 hours to up to 14 days in some oviviporous species (Brittian, 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). Field observations indicate female *C. latipennis* emerge, go through a subimaginal molt, mate, and oviposit in as little as 37 minutes (Figure 16). This is the shortest adult life span reported for a mayfly species.

Synchronization of large numbers of adults around annual and diel peaks and short flight periodicities suggest an *r* selected adaptive strategy of predator avoidance (Price, 1997). Mackey (1978) suggests a similar adaptive strategy for *C. macrura* where mass emergence provides a glut of food which satiates predation, thus increasing frequency of mating, oviposition and enhancing recruitment.

Mating behavior

Attempts to locate, observe, or sample swarms were unsuccessful. No adults were collected on hanging tangle trap sheets and no swarms were observed. Although mating behavior failed to be eludicated, large aggregates of males and females were observed when using a mercury vapor light trap.

Measurements of pedicel length revealed that male pedicel length was significantly longer than female pedicel length (two-sample Man Whitney U test, $z = 5.6145$, $p < 0.0001$)). Along with more complex locomotive and sensory equipment, males of most insects have more elaborate eyes and antennal structure (Thornhill and Alcock, 1983). Brodskiy (1973) has reported similar sexual dimorphism in antennal structure of *Caenis*, especially in the pedicel. *Caenis* males do not have eyes divided into two functional parts like other mayflies. Eyes as receptors become less useful in swarms after dark. Increased male pedicel length may provide area for sensory structures used to detect female wing beat frequencies in low light conditions. Females have larger wings and therefore the difference in wing beats, tone, and sound intensity should differ between sexes (Brodskiy, 1973). This mating system has been demonstrated in Culicidae (Diptera). Roth (1948) found that sound waves emitted from *Aedes aegypti* female wing beats stimulate fibrillae of male mosquitoes and relay a signal along the flagellum to the

Johnston's organ. Roth (1948) performed experiments using tuning forks and audio oscillators and found that *A. aegypti* males were attracted to frequencies similar to female wing beats. This provides a mate finding mechanism for low light conditions where visual receptors are not adequate.

Oviposition and Fecundity

Field observations of oviposition indicate that females slap water forcibly then rest on the surface before rising and slapping water again. Females oviposited readily in light traps, extruding the entire egg mass in a single ball. Oviposition appears to be traumatic, with post-oviposited female abdomens shrunken and split across the vulvae. Gravid females collected in the field released egg masses when placed on water. These eggs separated and settled in a single layer on the bottom of vials. Eggs adhered to substrate 30 to 60 minutes after oviposition via attachment threads. Provonsha (1990) reports that deployment of attachment threads occurs from a few minutes up to 1½ hours. He suggests that variation in time required for deployment of attachment structures have selective value in that individual egg broods are well dispersed by water currents.

Fecundity for twenty-five field-collected females from the five major emergence peaks ranged from 239 to 1576 and contained 888.4 ± 291.9 eggs per individual on average. Provonsha (1990) reports fecundity as 812 – 2163 for *C. latipennis.* Fecundity measurements for *C. latipennis* from Honey Creek were within Provonsha's estimates. Fecundity reports for five additional *Caenis* species are presented in Table 4. *C. latipennis* fecundity tends to be among the highest reported for the genus.

One-way parametric ANOVA detected a significant difference in fecundity among the peak emergence periods (F=7.61, p=0.0007). Fecundity for 29 June 2000 was statistically higher than all other peak emergence periods during the study (Student-Newman-Keuls test, $\alpha = 0.05$; Figure 17). Pearson's product moment correlation analyses showed a significant, but weak, correlation between head capsule width and fecundity (r=0.60729, p=0.0006). In general, fecundity correlates with body size in Ephemeroptera and therefore decreases over periods of extended emergence or between winter and following generations in multivoltine species (Brittian, 1982; Clifford, 1974; Sweeney and Vannote, 1978). This has been observed in many multivoltine mayflies (Grant and Stewart, 1980; Kondratieff and Voshell, 1980, 1984; McClure and Stewart, 1976; Soderstrom, 1988; Wagner, 1995). Data for *C. latipennis* did not conform to these typical observations in mayfly fecundity. Female size did decrease with each peak after the early spring peak (Figure 14). Fecundity followed a similar pattern until early summer emergence. Mean fecundity for the 29 June 2000 emergence peak was significantly higher than all other emergence peaks (Figure 17). Two possible factors may explain this deviation from reports for other species with extended emergence. This high fecundity occurred during very low densities of nymphs (Figure 19). Rosillon (1988) reports that *Ephemerella ignita* (Poda) females reared individually always have higher fecundity then females reared in groups. This suggests that fecundity can be density dependent. Another factor that can affect fecundity is food quality. Increased food quality has increased fecundity in *E. ignita* (Rosillon, 1988), *Leptophlebia intermedia* (Traver) (Sweeney et al., 1986), and *Parameletus chelifer* Bengtsson and *Parameletus minor* (Bengtsson) (Soderstrom, 1988). One of these factors, or more likely both, may have some influence on this high fecundity in early summer.

Seasonal development and voltinism

C. latipennis exhibited a multivoltine life cycle with peak emergences occurring in late September (fall), late April through mid May (spring), late June (early summer) and August (late summer). Interpretation of the *C. latipennis* life cycle was complicated by cohort spreading and overlap. Rearing of eggs to adults under controlled laboratory conditions (Figure 11), patterns of developmental class frequencies of field collected nymphs (Figure 13), and emergence collections (Figure 12) substantiate a multivoltine life cycle with four overlapping generations.

Egg and nymph development rates based on degree day estimates from continuous water temperature data indicated that eggs oviposited by the fall generation (Cohort 1) hatched throughout the fall and winter. Eggs oviposited during the beginning of the fall emergence (water temperature = 16ºC – 25ºC) had a fast development rate and nymphs hatched almost immediately. As temperature decreased throughout the emergence egg development slowed resulting in an extended recruitment of nymphs. This hatching regime resulted in three sub cohorts or three different development strategies derived from the fall emergence (Figure 19). Nymphs recruited early during the fall emergence were able to develop quickly before temperatures dropped and over winter in the 3rd and 4th development classes. These nymphs are referred to as sub cohort 2a. Nymphs in the 5th developmental stage were recorded from this sub cohort by late February. The lack of the 1st developmental stages in April and May indicate that few of the adults from sub cohort 2a successfully mated and oviposited (Figure 13). Eggs oviposited later in the fall developed slower and nymphs recruited from these eggs over wintered in earlier development classes. As water temperatures increased in the spring these nymphs continued to develop emerging in April as sub cohort 2b. Eggs oviposited at the end of the fall emergence period developed slowly with hatching beginning in late winter (February). These nymphs developed with rising temperatures to emerge in mid May (Cohort 2c). These two spring emergence periods provided nymphal recruitment that produced two distinct summer cohorts (Cohort 3 and 4) (Figure 19). Oviposition from summer cohorts provided nymphal recruitment for the fall generation of the following year.

Air temperatures during the spring are highly variable at Honey Creek. The ability of a cohort to spread individuals among development stages provides a selective advantage for *C. latipennis* populations. This bet hedging mechanism insures that some individuals will emerge under favorable conditions and successfully reproduce even though many are lost to premature emergence. This mechanism also provides for resource partitioning during annual peaks in density of *C. latipennis*. Cohort overlap and asynchronous development also increase resistance to disturbance by providing individuals in all development and size classes to cope with disturbance. This insures that at least some individuals with suitable character traits will survive during periods of disturbance. Spates and drying events are common disturbances of streams in south-central Oklahoma and Texas. Miller and Golladay (1996) showed that *Caenis* nymphs showed high resistance to spates and intermittent conditions in south-central Oklahoma. They hypothesized that *Caenis* nymphs had greater ability to seek refugia during spates and were more tolerant to pool conditions during dewatering. This resistance explains relative high abundance of *C. latipennis* in Honey Creek, which has an intermittent upper portion and a perennial lower portion. Both sections are influenced by spates.

Relative abundance of nymphs in each of the five development classes over time showed similar results (Figure 13). The fall generation was defined by an increase in development class V in conjunction with an emergence peak. Continuous recruitment from fall ovipostion was represented by a growing abundance of development class II throughout the winter months followed by a rise in abundance of higher development classes. In addition, development classes III and IV were well represented throughout winter. Individuals recruited in early fall over winter at these higher development classes and emerged in conjunction with the April emergence peak. Individuals recruited later over winter at lower development classes and emerged during the May peak. An early summer cohort was recruited in May and completes development in late June corresponding to a late June peak in emergence. Recruitment of an additional summer cohort occurs in late June and develops until emergence in August.

Proposed cohort lines from development frequency analysis agreed with egg and larval development rates based on degree day estimates (Figure 20). Cohort 1 is well represented by development frequency analysis and degree day estimates. The over wintering generation (Cohort 2) corresponds well with development frequency analysis and the three predicted sub cohorts. The two fast developing summer cohorts are clearly defined by development frequency analysis and degree day estimates.

Multivoltine life cycles are common in Ephemeroptera, especially in warm temperate and tropical waters (Clifford, 1982; Brittian, 1990). The *C. latipennis* population in Honey Creek exhibits a non-seasonal multivoltine life cycle type described by Clifford (1982). Clifford lists 3 records of this life cycle type for *Caenis* but does not site examples or name species. *C. luctrosa* from Spain is the only other documented non-seasonal multivoltine population (Peran et al., 1999). Non-seasonal multivoltine life cycles are typical of tropical areas and are difficult to interpret without the combination of laboratory and field data (Brittian, 1982). For this reason, information on non-seasonal life cycles of mayflies is limited, and it is quite possible many more examples exist within temperate regions. Berner and Pescador (1988) and Jacobi and Benke (1991) suggest multiple generations for *C. diminuta* and *C. hilaris* based on extended emergence in the southeastern United States.

Variation in voltinism is common in Ephemeroptera, especially smaller species (Brittian, 1982; Lauzon and Harper, 1986). Univoltine life cycles are typical for Ephemeroptera species, but multivoltine species are common in temperate and tropical regions (Brittian, 1990). Life cycles vary among and within *Caenis* species. *C. amica* has been reported as univoltine at northern latitudes (as *C. simulans* [Clifford et.al., 1973]; [Lyman, 1955]; Provonsha, 1990). One Canadian population (Corkum, 1984) has been reported as bivoltine. Two populations from experimental systems in the southeastern United States have also been reported as bivoltine (Christman and Vorshell, 1992; Rodgers, 1982). *C. diminuta* (Rodgers, 1983), and *C. hilaris* (Provonsha, 1990) have been reported as bivoltine. Berner and Pescador (1988) and Jacobi and Benke (1991) suggest these species may be multivoltine in the southeast. Nichols and Sites (1999) report *C. latipennis* as univoltine from the Ozark Mountains. This population occurs within the Interior Highlands, which also includes the Arbuckle Mountains. With a distribution covering most of North America, *C. latipennis* voltinism does probably vary along latitudinal and environmental gradients. However, insufficient sample size may have been more influential than latitude and environment on the results of the

Nichols and Sites (1999) study. These life cycles may be misleading if not sampled correctly and completely, especially for temperate and tropical populations. Increased sample size and frequency, emergence data, and laboratory rearing are necessary when interpreting life cycles of latitudinally dynamic species.

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 5. A simple linear regression of ln head capsule width and ln dry weight showed a significant relationship ($n = 132$, $F = 4624.7$, $r^2 = 0.97$, $p < 0.0001$) (Figure 21). The linear relationship of head capsule width and mass can be explained by the following equation: ln dry weight = -23.09548 – 3.19737 (ln head capsule width). The standard errors for the Y-intercept and the slope were 0.298 and 0.04702.

Annual production of *C. latipennis* in Honey Creek was calculated to be 6,052.57 mg / m^2 / yr. Standing stock biomass was 274.64 mg/m^2/yr. The cohort production: biomass ratio was calculated to be 5.79 / yr and the annual production: biomass ratio was 22.03 / yr (Table 6). Field and laboratory data estimated development time to be 60 days for the fall generation, 232 days for the winter generation, and 44 and 49 days for the summer generations. Mean development time for the four generations was 96 days, which served as the cohort production interval.

Secondary productivity of *C. latipennis* in Honey Creek is high relative to reports for other *Caenis* species. Reported production values for other *Caenis* species range from 82.1 mg/m^2/yr to 6349.81 mg/m^2/yr and are presented in Table 7. Production for *C. latipennis* was similar to *C. luctrosa* from a semiarid stream in Spain. Both species had production values over 6,000 mg/m^2/yr. *C. luctrosa* exhibits a similar multivoltine life cycle with 4 overlapping generations and is found in an intermittent stream subject to spates and dewatering (Peran, 1990). Substantially lower production values and production:biomass ratios are reported for bivoltine species *C. amica* (Christman and Vorshell, 1992; Rodgers, 1982) and *C. simulans* (MacFarlane and Waters, 1982). High production values can be attributed to feeding behavior and life history attributes of communities in warm temperate streams. The highest levels of production are found in warm to cool-temperate streams dominated by filter-feeders, which are able to accrue and maintain high levels of biomass. Populations in warm-temperate streams subject to disturbance tend to also be highly productive. Disturbance regimes and warm temperatures select for taxa with short development times, rapid growth rates, and small terminal size. Rapid growth rates rather than biomass tend to drive high productivity in these streams (Huryn and Wallace, 2000). Productivity of *Caenis* species follows this trend and is dependent on rapid growth rates rather than biomass. This is demonstrated by high productivity of *C. latipennis* and *C. luctrosa* which exhibit rapid growth rates in systems exposed to disturbance regimes versus low productivity of *C. amica* which has slower growth rates and is reported from experimental systems (no natural disturbance).

Standing stock biomass and abundance of *C. latipennis* are presented for each season in Table 8. Standing stock biomass did not significantly differ between seasons. A significant difference was observed in mean density of the four seasons (one-way parametric ANOVA, $F = 3.99$, $p = 0.0207$). Student-Newman-Keuls test ($\alpha = 0.05$) determined that only winter and summer densities were significantly different.

Average density for the 13 month study period was 2398 individuals /m^2. Abundance of nymphs throughout the study was highest during January and March with 6326 individuals/m^2 and 6527 individuals/m^2 respectively. Density was lowest, 43 individuals/m^2, during late May. Variation in abundance of nymphs was observed between years. Average density for September 1999 was 1238 individuals/m^2 and 508 individuals/m^2 for September 2000 (Figure 22).

No significant differences existed between seasons in standing stock biomass of *C. latipennis*, though winter and summer densities were significantly different. Biomass was not affected by high winter densities because the majority of the cohort was 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 effects of lack of recruitment in conjunction with emergence in early spring. This pattern in abundance is similar to *C. amica* in experimental ponds (Christman and Vorshell, 1992). This population had higher abundance in the winter. Abundance patterns opposite to our findings have been observed for *C. luctrosa* with higher densities in summer months (Peran et al., 1999). Annual variation in density may have been the result of continued drought conditions and high temperatures in the region or just natural variation between years.

Table 1. Land use for the Honey Creek drainage basin, OK.

Landuse	**Area in km^2**	**% Coverage**
Commercial and Services	58.7	0.119
Cropland and pasture	579.8	1.175
Deciduous Forest	20089.8	40.714
Herbaceous Rangeland	27216.9	55.158
Reservoirs	12.9	0.026
Residential	155.4	0.315
Transportation, Communications, Utilities	781.7	1.584
Transitional Areas	448.2	0.908

Table 2. Physico-chemical data for Honey Creek, OK, August 1999 – September 2000.

Date	Temp. °C	DO	pH	Flow
26 Aug 1999	26.9	10.9	7.28	-
	26.9	10.78	7.28	-
	26.9	10.92	7.26	-
09 Sept 1999	23.74	7.44	7.65	0.03
	23.74	7.53	7.63	0.04
	23.74	7.9	7.68	0.1
24 Sept 1999	18.54	10.71	7.88	0.01
	18.54	10.71	7.87	0
	18.54	10.71	7.85	0.12
08 Oct 1999	19.01	11.01	7.67	-0.02
	19.01	10.99	7.66	-0.01
	19.01	10.93	7.74	-0.02
22 Oct 1999	16.3	9.61	7.44	-0.02
	16.1	9.98	7.53	0
	16.3	10.65	7.62	0
05 Nov 1999	17.6	13.45	7.65	-0.03
	17.6	13.4	7.71	-0.04
	17.6	8.58	7.65	0

DO = dissolved oxygen, milligrams per liter

Table 2 continued. Physico-chemistry data for Honey Creek, OK.

Date	Temp. °C	DO	PH	Flow
19 Nov 1999	16.4	10.81	7.74	-
	16.4	10.7	7.7	-
	16.4	10.8	7.72	-
03 Dec 1999	14.7	11.54	7.76	0
	14.7	11.69	7.8	-0.02
	14.7	11.67	7.82	-0.01
17 Dec 1999	9.8	15.56	6.9	-
	9.2	15.43	7.03	-
	9.3	15.63	7.02	-
29 Dec 1999	8.8	12.3	6.95	-
	8.5	12.5	7.15	-
	8.8	11.6	7.33	-
12 Jan 2000	14.9	12.75	7.87	-0.02
	14.8	12.54	7.8	-0.02
	14.8	12.62	7.81	-0.01
26 Jan 2000	6.92	-	-	-
	6.92	-	-	-
	6.92	-	-	-

DO = dissolved oxygen, milligrams per liter

Table 2 continued. Physico-chemistry data for Honey Creek, OK.

Date	Temp. °C	DO	PH	Flow
09 Feb 2000	14.1	10.08	7.61	-
	13.3	11.15	7.6	-
	13.7	10.85	7.66	-
24 Feb 2000	15.1	10.76	7.56	-
	15.1	10.43	7.53	-
	15.1	10.72	7.59	-
08 Mar 2000	18.4	10.5	7.2	-0.01
	17.5	10.85	7.27	-0.01
	17.5	11.07	7.31	0.03
21 Mar 2000	14.78	10.01	7.33	
	14.78	9.98	7.29	
	14.78	10.34	7.21	
04 April 2000	18.3	9.4	7.49	-0.02
	18.2	9.31	7.42	-0.01
	18.2	9.92	7.37	0.02
19 April 2000	23.2	9.92	7.19	0
	22.2	10.35	7.22	-0.03
	22.6	9.01	7.23	-0.01

DO = dissolved oxygen, milligrams per liter

Table 2 continued. Physico-chemistry data for Honey Creek, OK.

Date	Temp. °C	DO	PH	Flow
06 May 2000	22..9	10.11	7.44	-
	22.3	9.35	7.47	-
	22.2	9.15	7.43	-
18 May 2000	24.3	9.55	7.51	-
	24.2	10.15	7.51	-
	24.2	10.22	7.49	-
31 May 2000	28.4	9.41	7.64	0.01
	28.4	9.36	7.59	0.01
	28.3	9.54	7.61	0.02
13 June 2000	24.1	8.6	7.62	-0.01
	23.6	9.64	7.6	-0.02
	23.6	10.05	7.7	0.15
29 June 2000	20.7	9.27	7.83	0.02
	21.1	9.56	7.86	0.01
	20.8	8.57	7.83	-0.02
13 July 2000	25.6	8.7	7.84	-
	25.5	8.85	7.85	-
	25.4	8.99	7.88	-

DO = dissolved oxygen, milligrams per liter

Table 2 continued. Physico-chemistry data for Honey Creek, OK.

Date	**Temp. °C**	**DO**	**PH**	**Flow**
26 July 2000	26.7	10.02	7.48	-0.02
	26.6	10.2	7.56	0
	26.5	9.38	7.64	0.01
10 Aug 2000	29.2	6.7	7.85	0.01
	29.1	7.44	7.83	-0.01
	29.1	6.88	7.77	0.02
28 Aug 2000	29.4	7.76	7.95	-
	29.1	7.51	7.94	-
	29.2	7.43	7.99	-
12 Sep 2000	28.1	7.35	7.91	-
	28.1	7.23	7.85	-
	28	7.26	7.89	-
26 Sep 2000	19	8.03	8.29	0
	18.9	8.1	8.32	0
	18.9	8.19	8.25	-0.01

DO = dissolved oxygen, milligrams per liter

Table 3. Emergence phenology of adult females from Honey Creek, OK. Subimago molt, oviposition, and spent females are represented as minutes after arrival in light trap.

Date	Sunset	LT arrival	Subimago molt	Oviposition	Spent Females
24 July 1999	1937	98		30-45	
5 Aug 1999	1927	78	11	14	
18 Aug 1999	1913	93		23	35
26 Aug 1999	1903	87	17	37	26
31 Aug 1999	1856	86	13	17-24	27
9 Sep 1999	1844	82	10	14-30	28-34
16 Sep 1999	1834	89		21	
30 Sep 1999	1814	101			
8 Oct 1999	1803	87		17	
15 Oct 1999	1754	88			
22 Oct 1999	1746	89			
29 Oct 1999	1738	92			
5 Nov 1999	1732	59			
3 Dec 1999	1718	54			
27 Mar 1999	1846	55			
4 Apr 2000	1852	87	5		
19 Apr 2000	1904	87	6		
6 May 2000	1917	84			
18 May 2000	1927	93			
31 May 2000	1936	89			
13 Jun 2000	1942	88			
28 Aug 2000	1859	86			
12 Sep 2000	1839	86			
26 Sep 2000	1819	91			

Table 4. Published reports of fecundity for six species of *Caenis*.

Species	**Range of Fecundity**	**Citation**
C. amica	95 – 1787	Sweeney and Vannote, 1978; Rodgers, 1983
C. anceps	448 – 567	Provonsha, 1990
C. hilaris	414 – 806	Provonsha, 1990
C. horaria	508 – 607	Clifford, 1974
C. latipennis	812 – 2163	Provonsha, 1990
C. moesta	765 – 1103	Clifford, 1974

Table 5. Observed arithmetic means of head width and dry mass of the 13 size classes of *C. latipennis* from Honey Creek, OK, August 1999 – September 2000.

Size Class	***n***	**Mean HCW, mm**	**Dry mass, mg**
1	79	184.3 ± 15.6	0.0016
2	1770	260.6 ± 25.3	0.0049
3	2105	346.9 ± 28.9	0.0124
4	1432	447.5 ± 29.4	0.0279
5	1185	548.6 ± 29.4	0.0535
6	1061	650.9 ± 29.6	0.0924
7	1049	748.9 ± 28.8	0.1447
8	826	847.1 ± 28.7	0.2145
9	483	942.7 ± 28.3	0.3020
10	218	1043.8 ± 27.4	0.4182
11	68	1133.4 ± 28.1	0.5442
12	25	1247.4 ± 34.8	0.7394
13	2	1366.1	0.9888

Table 6. Secondary production calculations for *C. latipennis* from Honey Creek, OK, September 1999 – August 2000.

Size Class	*n*, no./m^{2}[a]	DM, mg[b]	B, mg/m^{2}[c]	Δ in *n*[d]	DM at loss[e]	Dm loss[f]	x 13,mg/m^{2}[g]
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				1592.781

Total Production = 1592.781 mg/m^{2} (365/96) = 6,052.57 mg/m^{2}

Biomass = 274.63 Cohort *P*/*B* = 5.79 Annual *P*/*B* = 22.03

[a] Number present per square meter of each instar.
[b] Mean dry mass (in milligrams) of individuals of each instar.
[c] Total mean annual biomass for each instar.
[d] Change in number of individuals present between stadia.
[e] Mean dry mass of individuals of each instar when lost from the population (calculated as $DM^{x} + DM^{x+1} / 2$).
[f] Total dry mass (milligrams) lost with each instar.
[g] Dry mass loss × the number of size classes gives mean annual production for each size class.

*For the purpose of calculation all (-) numbers were set to 0.

Table 7. Reported production estimates for *Caenis* spp. (Modified from Peran et al., 1999).

Species	**P (mg/m2/yr)**	**P/B**	**Habitat (Location)**	**Citation**
C. luctrosa	6349.81	15.98	Mediterranean semiarid stream (Spain)	Peran et al., 1999
C. latipennis	6052.57	22.03	Traveritine stream (Oklahoma, U.S.A.)	This study
C. amica	445.05	13.00	Experimental ponds (Virginia, U.S.A.)	Christman & Voshell, 1992
C. amica	676.00	12.72	Experimental stream (Alabama, U.S.A.)	Rodgers, 1982
C. simulans	4200.00	4.20	Cold/mesic plains stream (Minnesota, U.S.A.)	MacFarlane & Waters, 1982
*Caenis spp.**	82.10	59.1	Humid/mesic plains stream (Georgia, U.S.A.)	Benke and Jacobi, 1994

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

Table 8. Seasonal density and standing stock biomass ranges (means) for *C. latipennis* from Honey Creek, OK, September 1999 – August 2000.

Season	***N***	**Density (no./m2)**	**Standing Stock (mg/m2)**
Autumn	6	1151-3856 (2147)	78.8-215.7 (146.1)
Winter	7	1419-6326 (3908)	58.6-338.4 (302.9)
Spring	7	42-6527 (2847)	7.6-705.4 (302.9)
Summer	6	345-2392 (1003)	66.1-307.3 (126.4)

Figure 1. Geographic distribution of *C. latipennis* across Bailey's (1995) ecotones of North America.

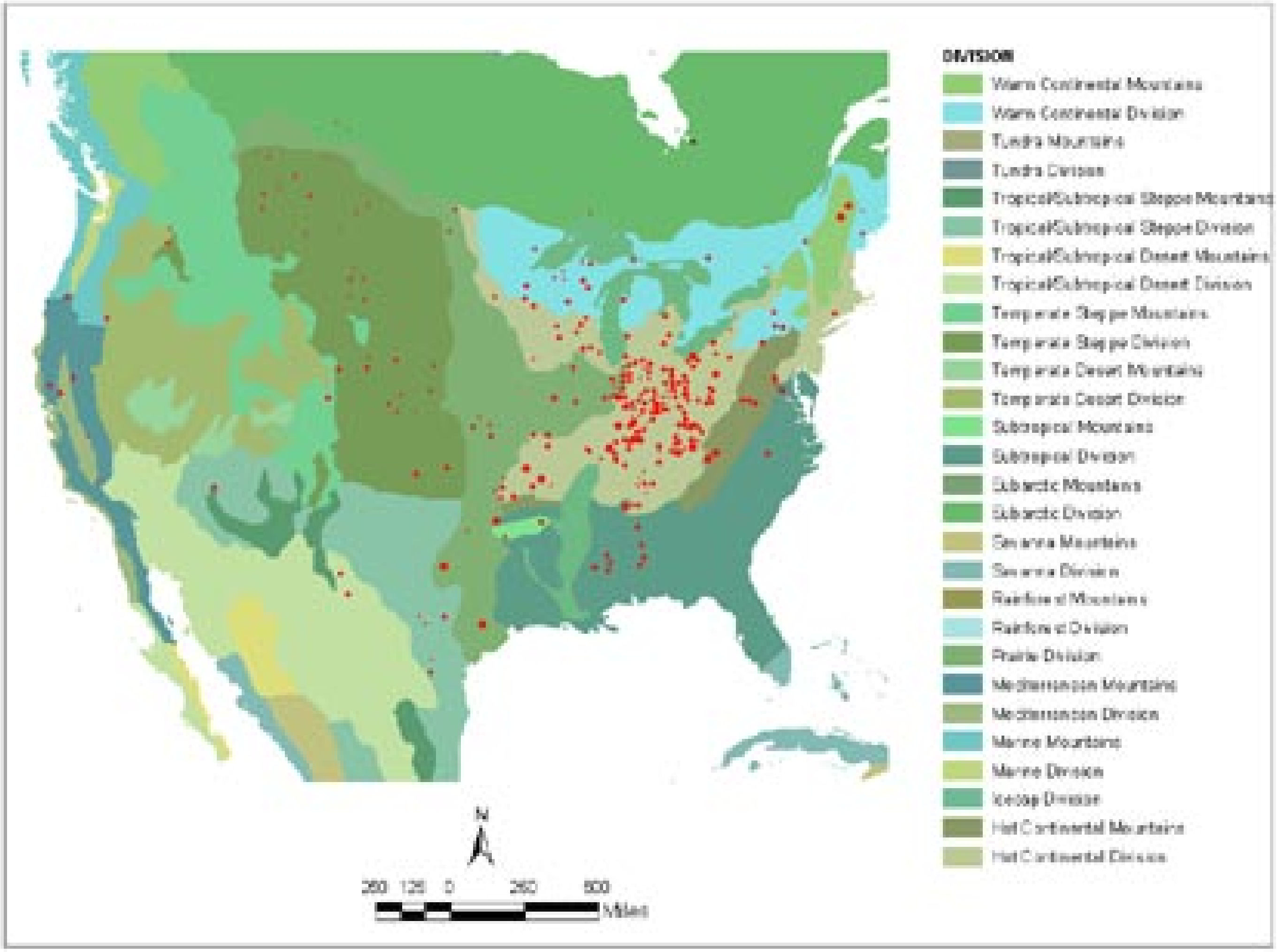

DIVISION
Warm Continental Mountains
Warm Continental Division
Tundra Mountains
Tundra Division
Tropical/Subtropical Steppe Mountains
Tropical/Subtropical Steppe Division
Tropical/Subtropical Desert Mountains
Tropical/Subtropical Desert Division
Temperate Steppe Mountains
Temperate Steppe Division
Temperate Desert Mountains
Temperate Desert Division
Subtropical Mountains
Subtropical Division
Subarctic Mountains
Subarctic Division
Savanna Mountains
Savanna Division
Rainforest Mountains
Rainforest Division
Prairie Division
Mediterranean Mountains
Mediterranean Division
Marine Mountains
Marine Division
Icecap Division
Hot Continental Mountains
Hot Continental Division
N
250 125 0 250 500
Miles

Figure 2. Honey Creek drainage basin in Murray Co., OK.

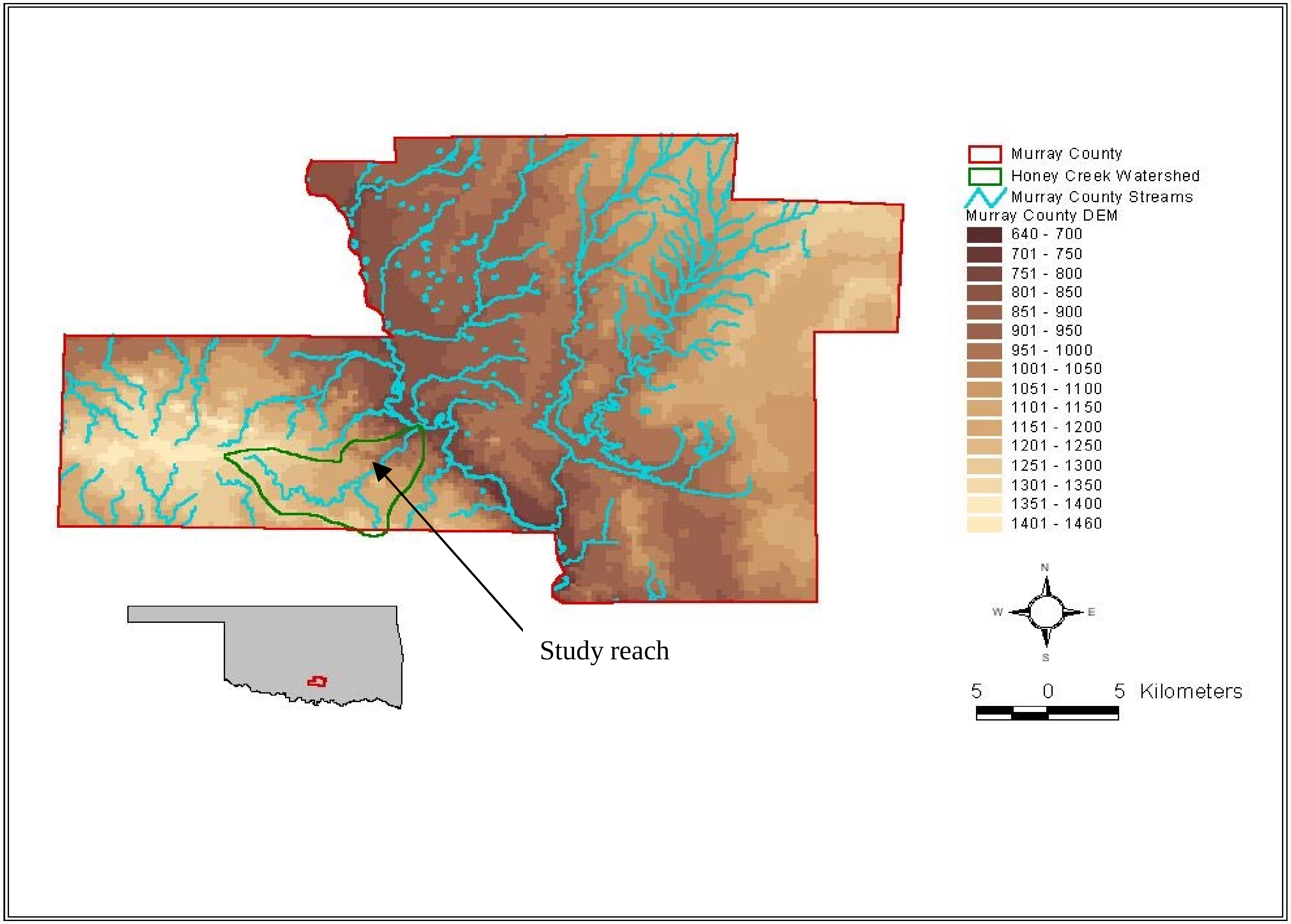

Murray County
Honey Creek Watershed
Murray County Streams
Murray County DEM
640 - 700
701 - 750
751 - 800
801 - 850
851 - 900
901 - 950
951 - 1000
1001 - 1050
1051 - 1100
1101 - 1150
1151 - 1200
1201 - 1250
1251 - 1300
1301 - 1350
1351 - 1400
1401 - 1460
N
W
E
S
5 0 5 Kilometers
Study reach

Figure 3. Modified Hess sampler.

Figure 4. First instar nymph (Development class I).

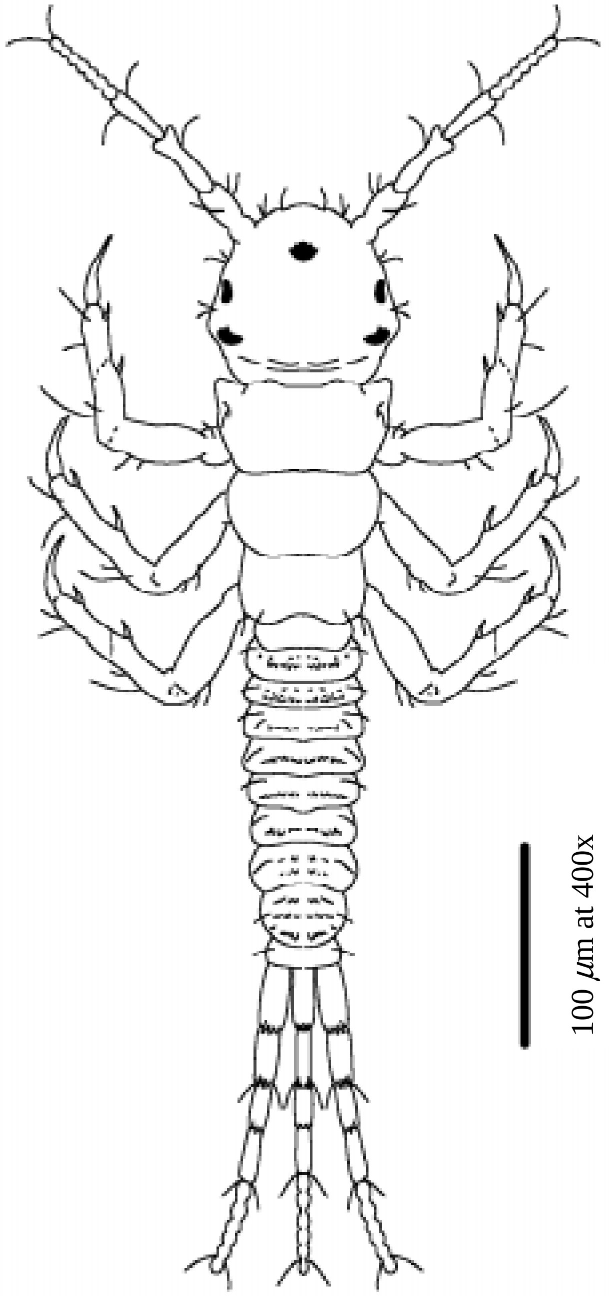
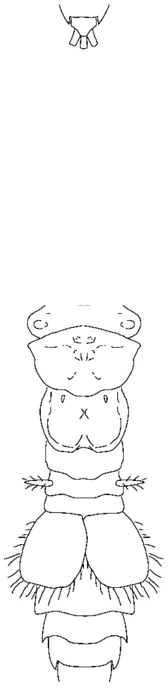
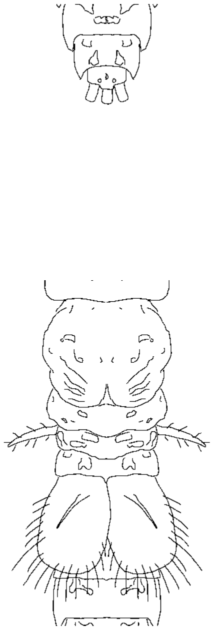

100 μm at 400x

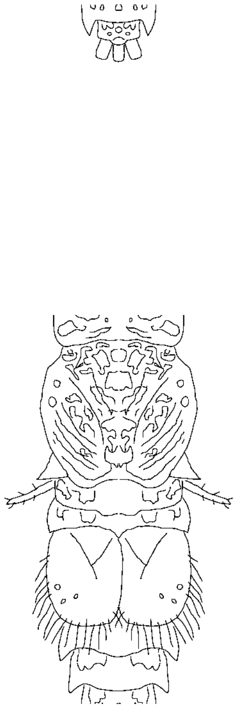
Figure 5. Development class II through IV of *C. latipennis*.



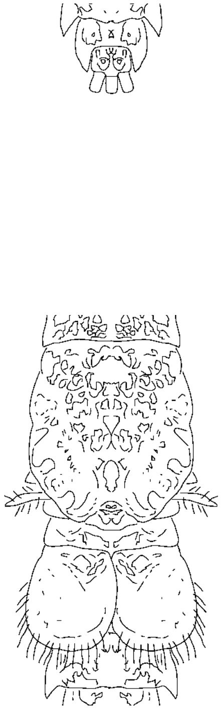
Dev. II



Dev. III

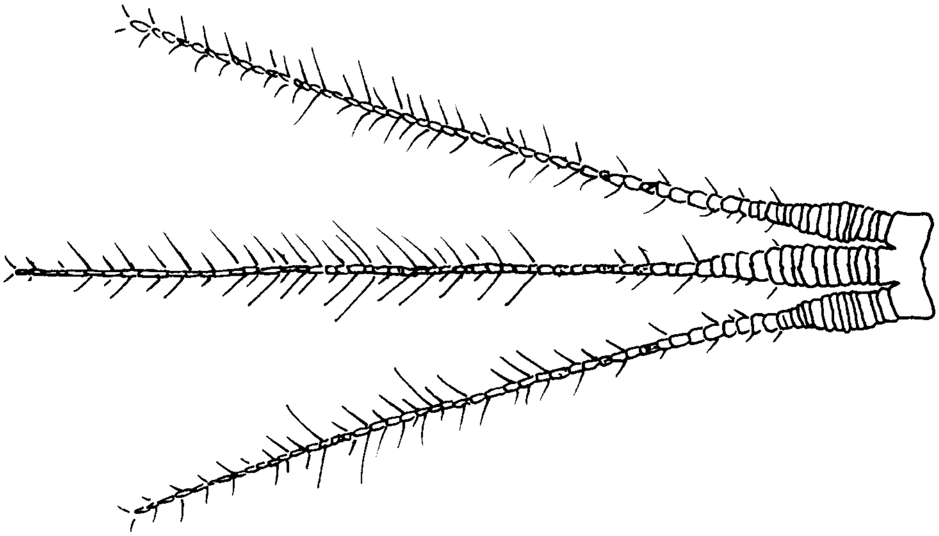


Dev. IV



Dev. V

Figure 6. Sexual dimorphism in caudal filaments of male (M) and female (F) *C. latipennis* development class V nymphs.



1mm / 600x

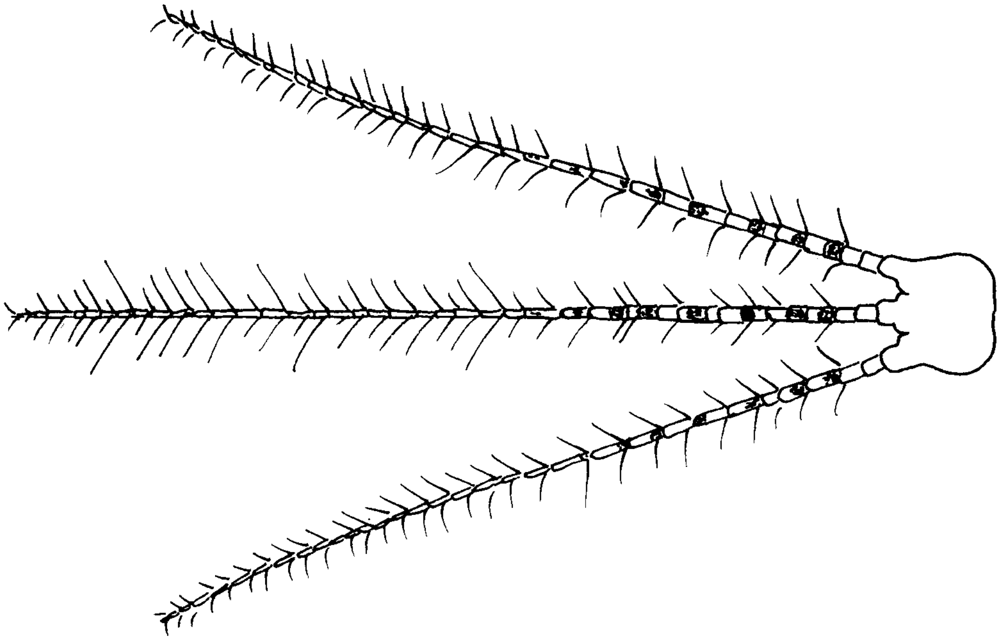


Figure 7. Maximum and minimum water temperatures (°C) for Honey Creek, OK., August 1999 – September 2000.

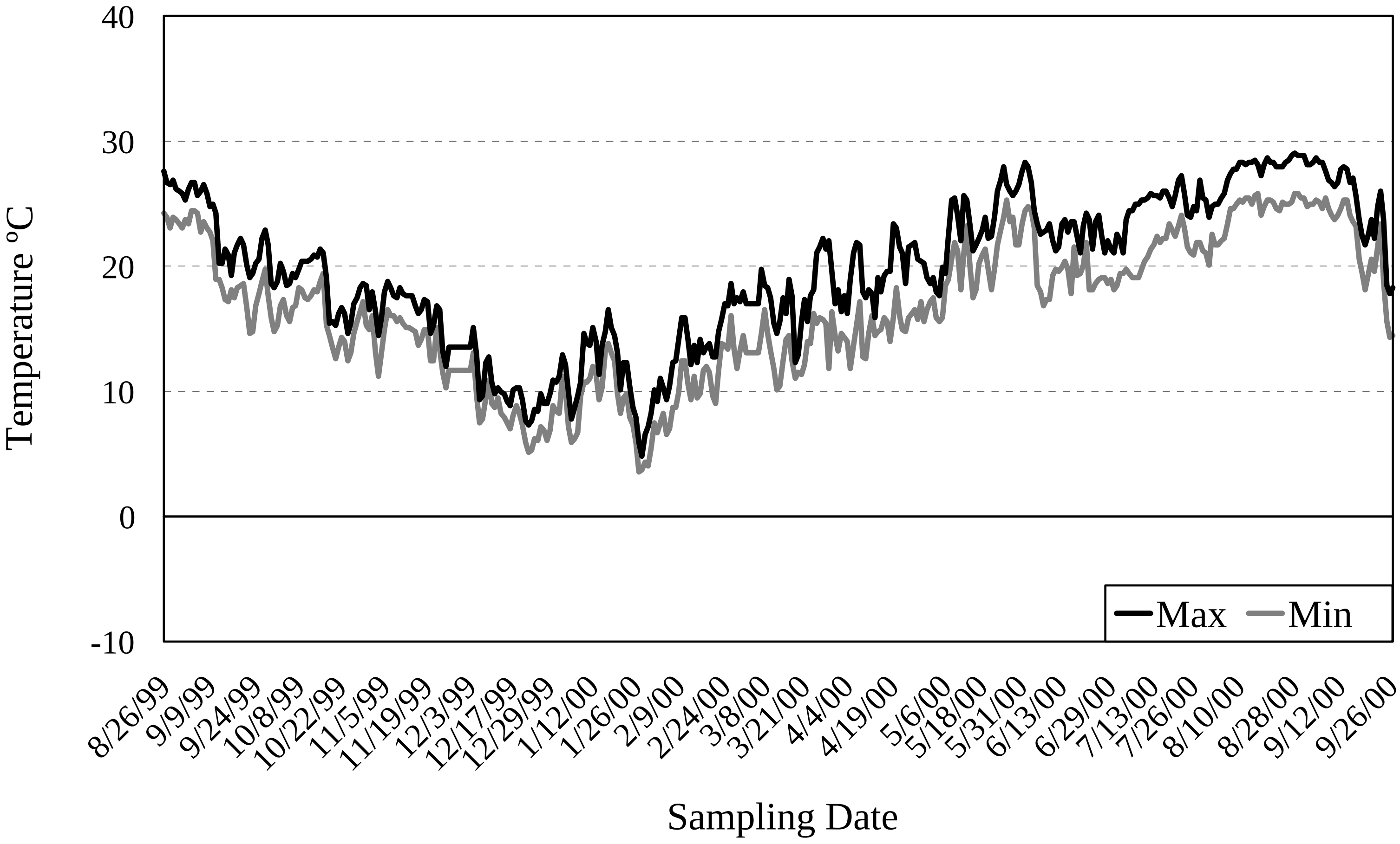
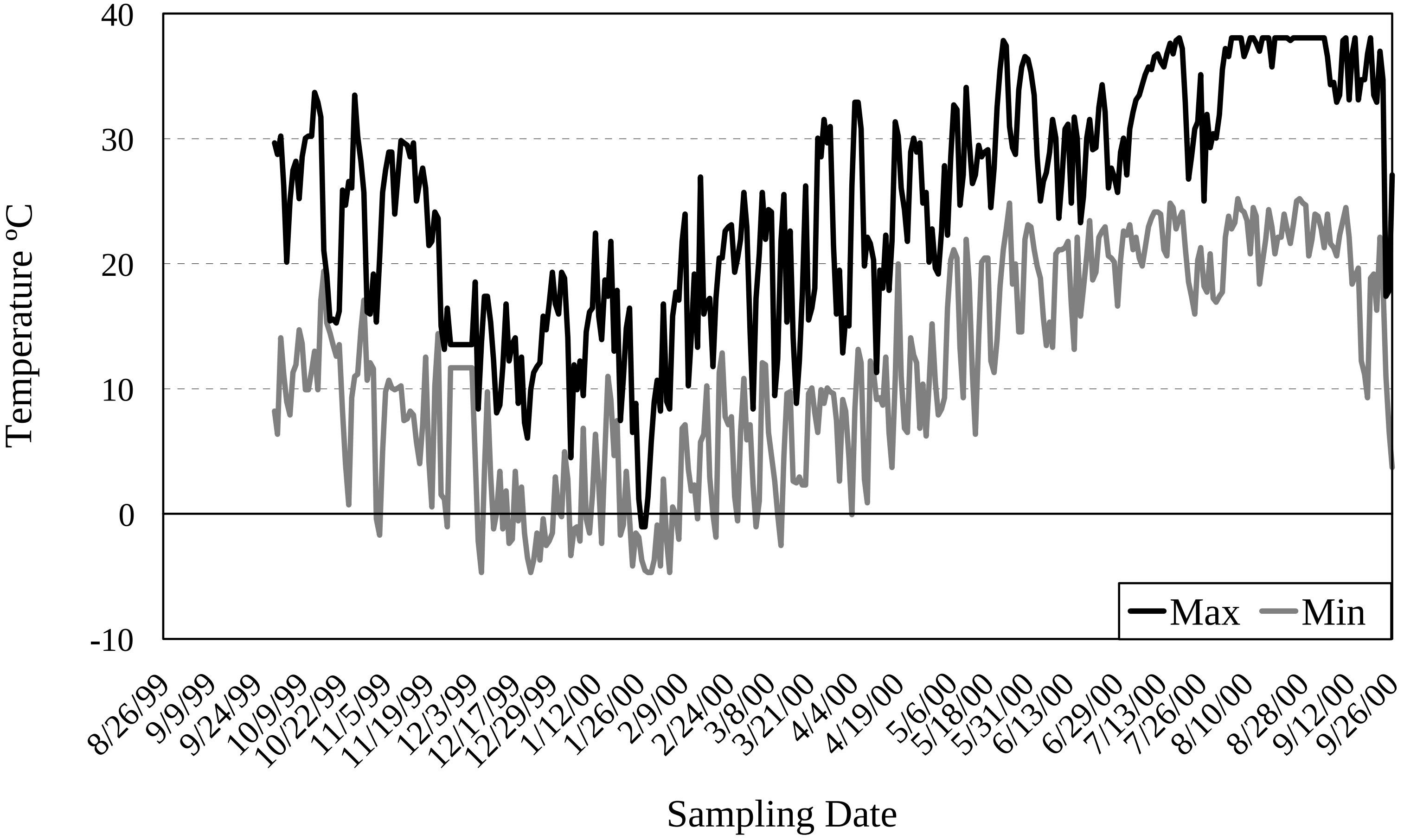

40
30
20
10
0
-10
Temperature °C
Max
Min
8/26/99
9/9/99
9/24/99
10/8/99
10/22/99
11/5/99
11/19/99
12/3/99
12/17/99
12/29/99
1/12/00
1/26/00
2/9/00
2/24/00
3/8/00
3/21/00
4/4/00
4/19/00
5/6/00
5/18/00
5/31/00
6/13/00
6/29/00
7/13/00
7/26/00
8/10/00
8/28/00
9/12/00
9/26/00
Sampling Date

Figure 8. Maximum and minimum air temperatures (°C) for Honey Creek, OK., October 1999 – September 2000.



Temperature °C
40
30
20
10
0
-10
Max
Min
8/26/99
9/9/99
9/24/99
10/9/99
10/22/99
11/5/99
11/19/99
12/3/99
12/17/99
12/29/99
1/12/00
1/26/00
2/9/00
2/24/00
3/8/00
3/21/00
4/4/00
4/19/00
5/6/00
5/18/00
5/31/00
6/13/00
6/29/00
7/13/00
7/26/00
8/10/00
8/28/00
9/12/00
9/26/00
Sampling Date

Figure 9. Mean development times for eggs of *C. latipennis* incubated at three different temperatures.

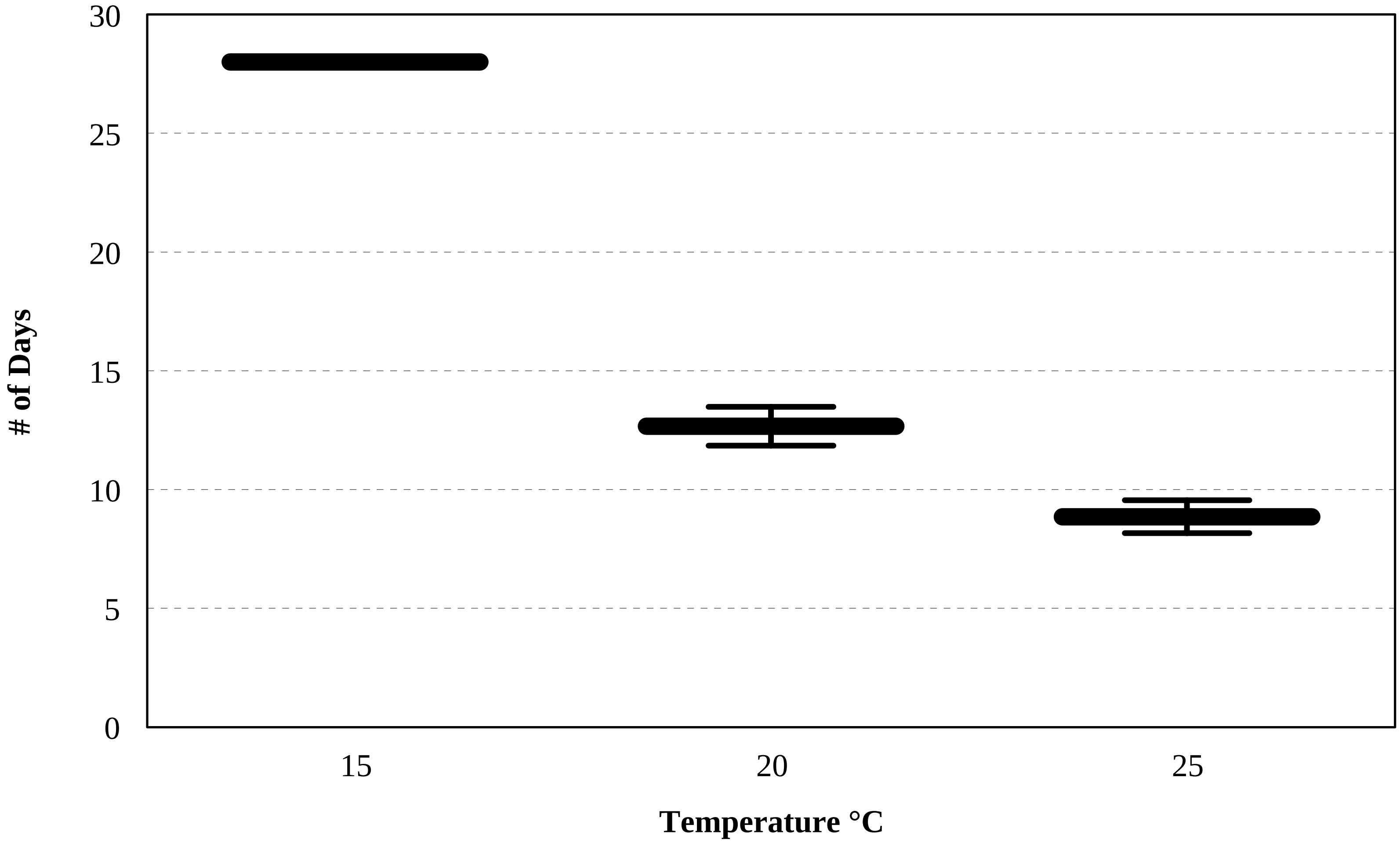

30
25
20
15
10
5
0
# of Days
15
20
25
Temperature °C

Figure 10. Critical thermal minimum for development of *C. latipennis* eggs derived from regression of development rate vs temperature (°C).

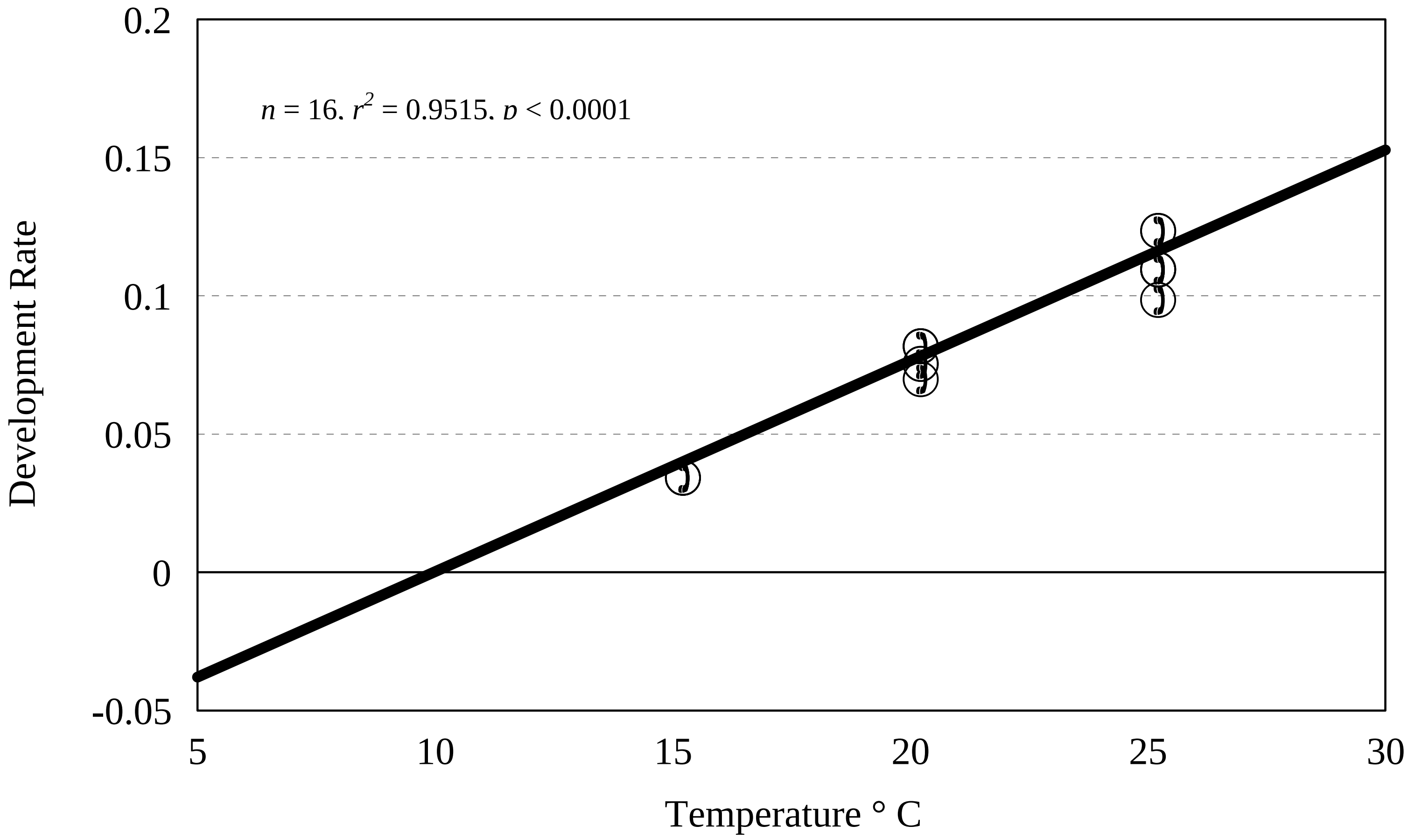

n = 16, r2 = 0.9515, p < 0.0001
Development Rate
0.2
0.15
0.1
0.05
0
-0.05
5
10
15
20
25
30
Temperature ° C

Figure 11. Development of *C. latipennis* nymphs in the laboratory at 20°C. Mean days to emergence, indicated by arrow, equals 85.

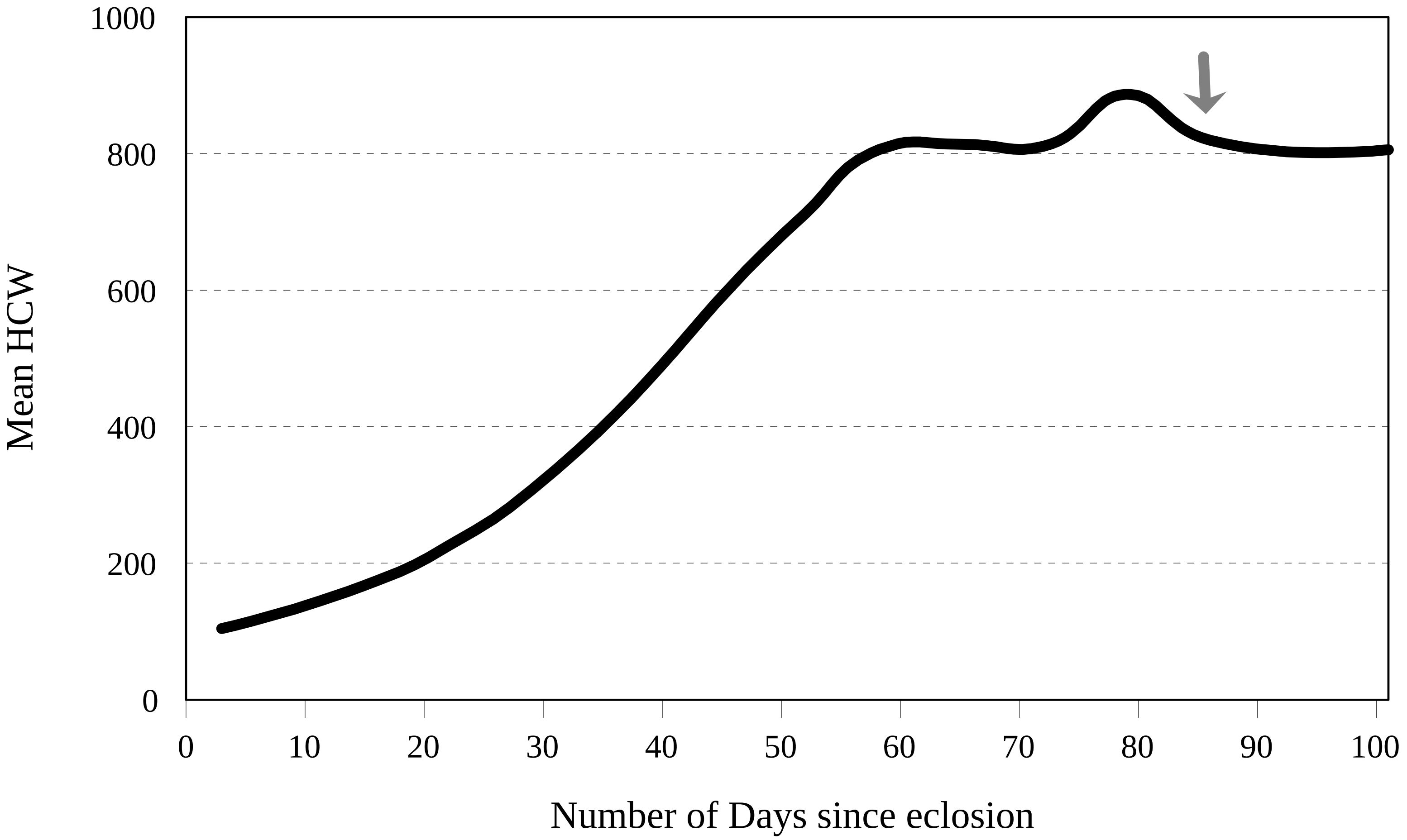

1000
800
600
400
200
0
Mean HCW
0
10
20
30
40
50
60
70
80
90
100
Number of Days since eclosion

Figure 12. Peaks in emergence for *C. latipennis* from Honey Creek, OK., August 1999 – September 2000.

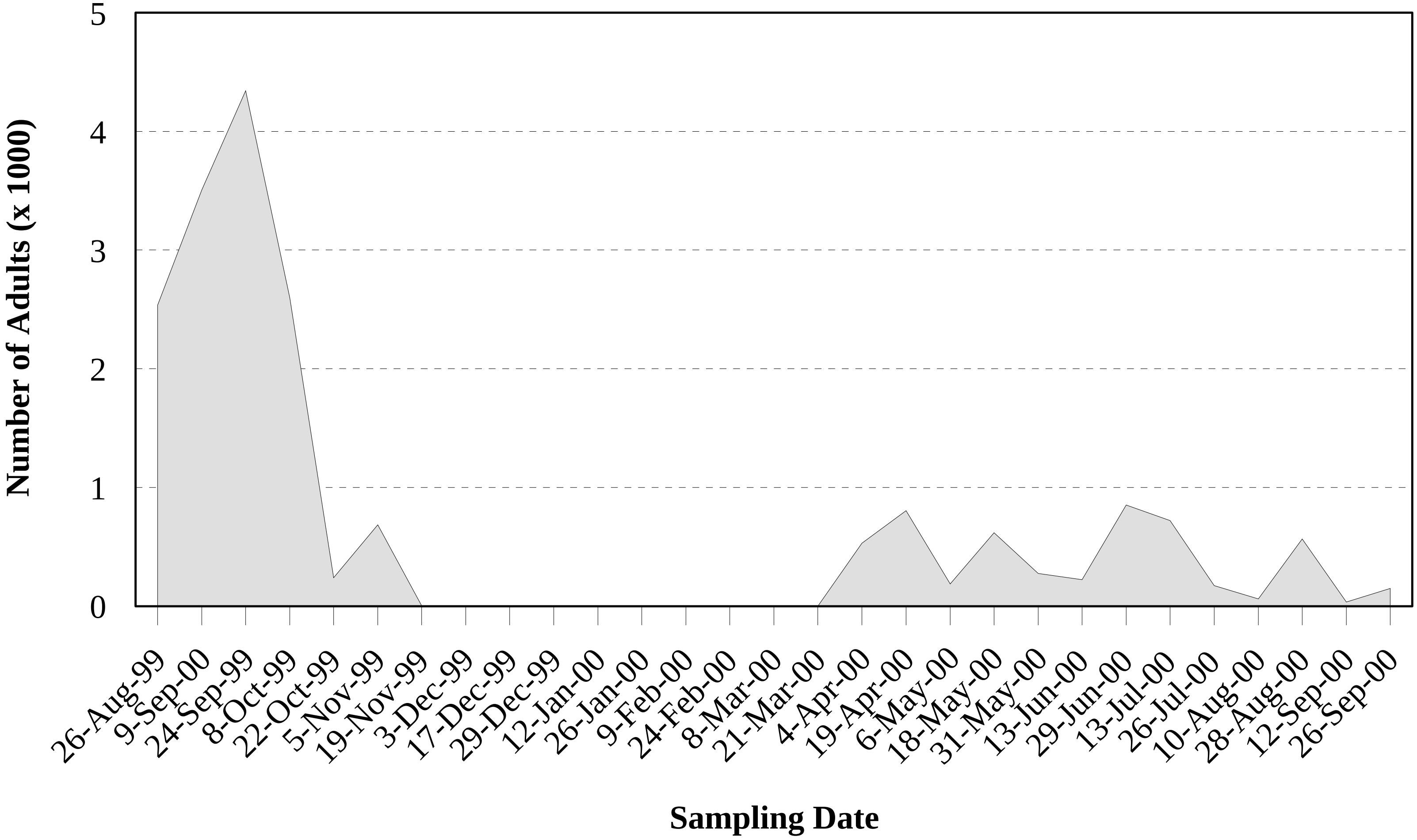

Number of Adults (x 1000)
0
1
2
3
4
5
26-Aug-99
9-Sep-00
24-Sep-99
8-Oct-99
22-Oct-99
5-Nov-99
19-Nov-99
3-Dec-99
17-Dec-99
29-Dec-99
12-Jan-00
26-Jan-00
9-Feb-00
24-Feb-00
8-Mar-00
21-Mar-00
4-Apr-00
19-Apr-00
6-May-00
18-May-00
31-May-00
13-Jun-00
29-Jun-00
13-Jul-00
26-Jul-00
10-Aug-00
28-Aug-00
12-Sep-00
26-Sep-00
Sampling Date

Figure 13. Relative abundance of *C. latipennis* nymphs in development classes from Honey Creek, OK., August 1999 – September 2000. Arrows correspond with emergence peaks and lines represent proposed cohorts.

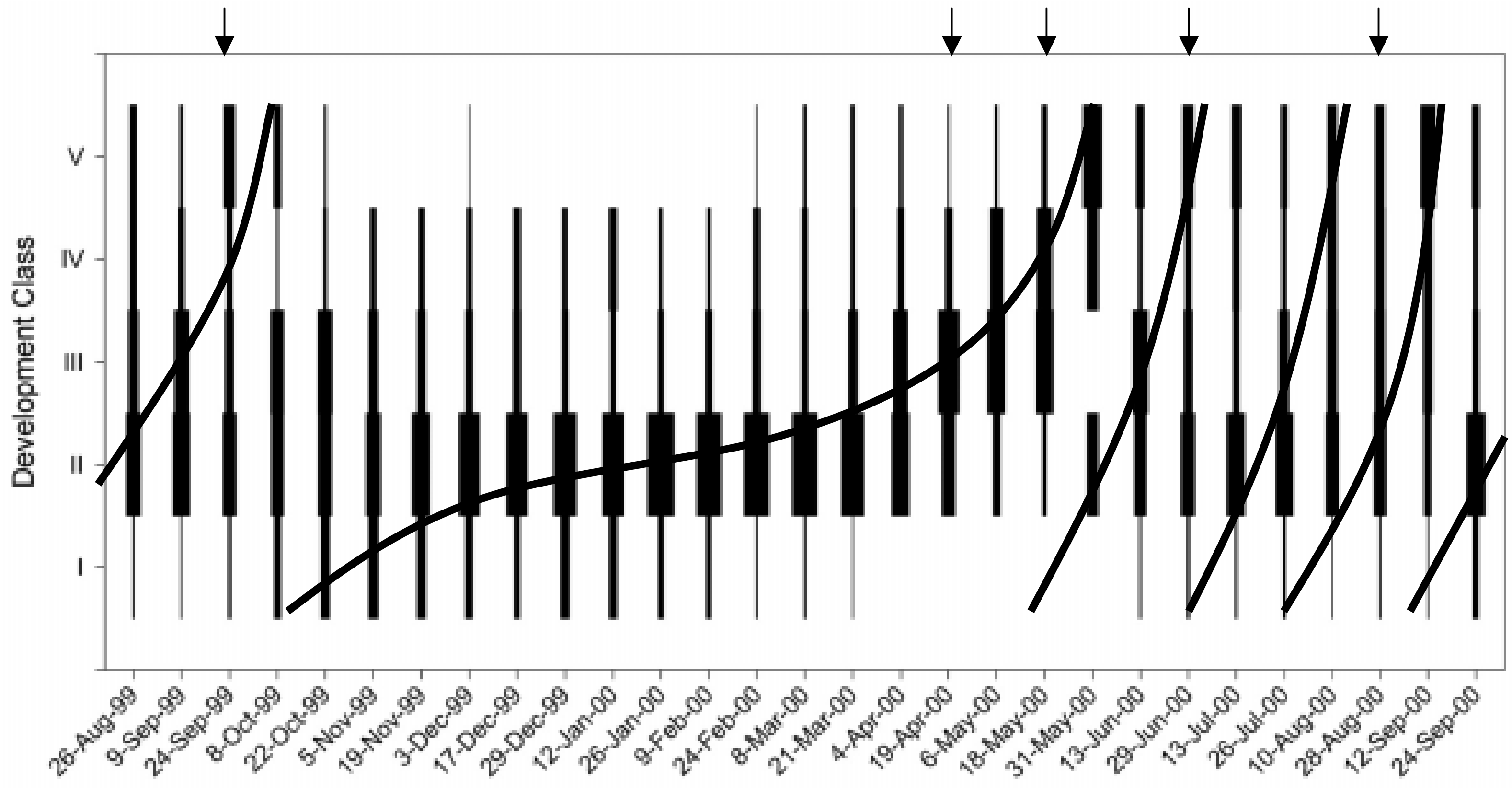
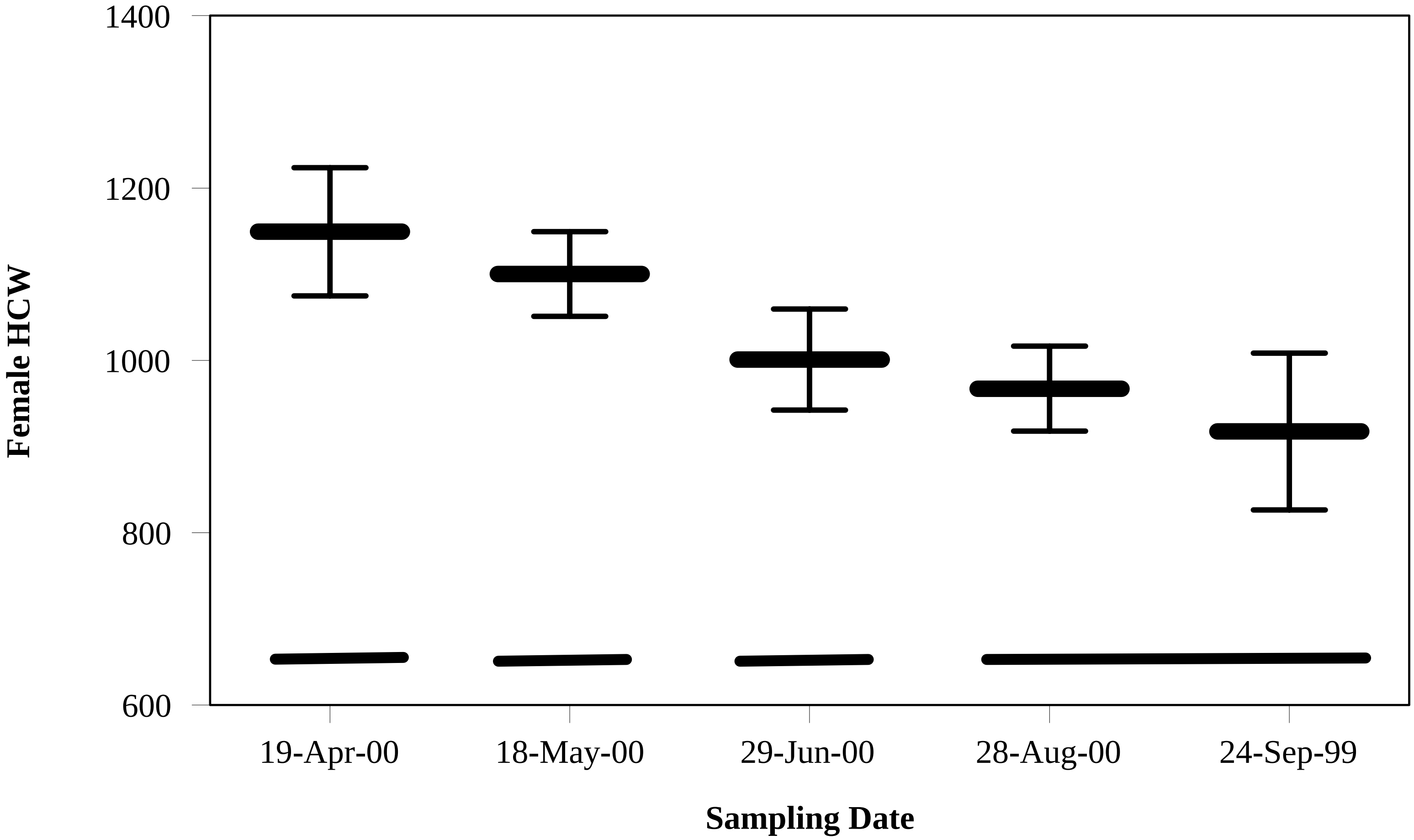

Development Class
V
IV
III
II
I
26-Aug-99
9-Sep-99
24-Sep-99
8-Oct-99
22-Oct-99
5-Nov-99
19-Nov-99
3-Dec-99
17-Dec-99
29-Dec-99
12-Jan-00
26-Jan-00
9-Feb-00
24-Feb-00
8-Mar-00
21-Mar-00
4-Apr-00
19-Apr-00
6-May-00
18-May-00
31-May-00
13-Jun-00
29-Jun-00
13-Jul-00
26-Jul-00
10-Aug-00
28-Aug-00
12-Sep-00
24-Sep-00

Figure 14. Mean female head capsule widths of *C. latipennis* from Honey Creek, OK. for 5 emergence peaks between August 1999 and September 2000. Lines show significant differences between emergence peaks.



Nonparametric SNK on ranked data

Figure 15. Time of emergence of *C. latipennis* in Honey Creek, OK., determined by drift nets. Arrival of adults at light traps is indicated by arrow.

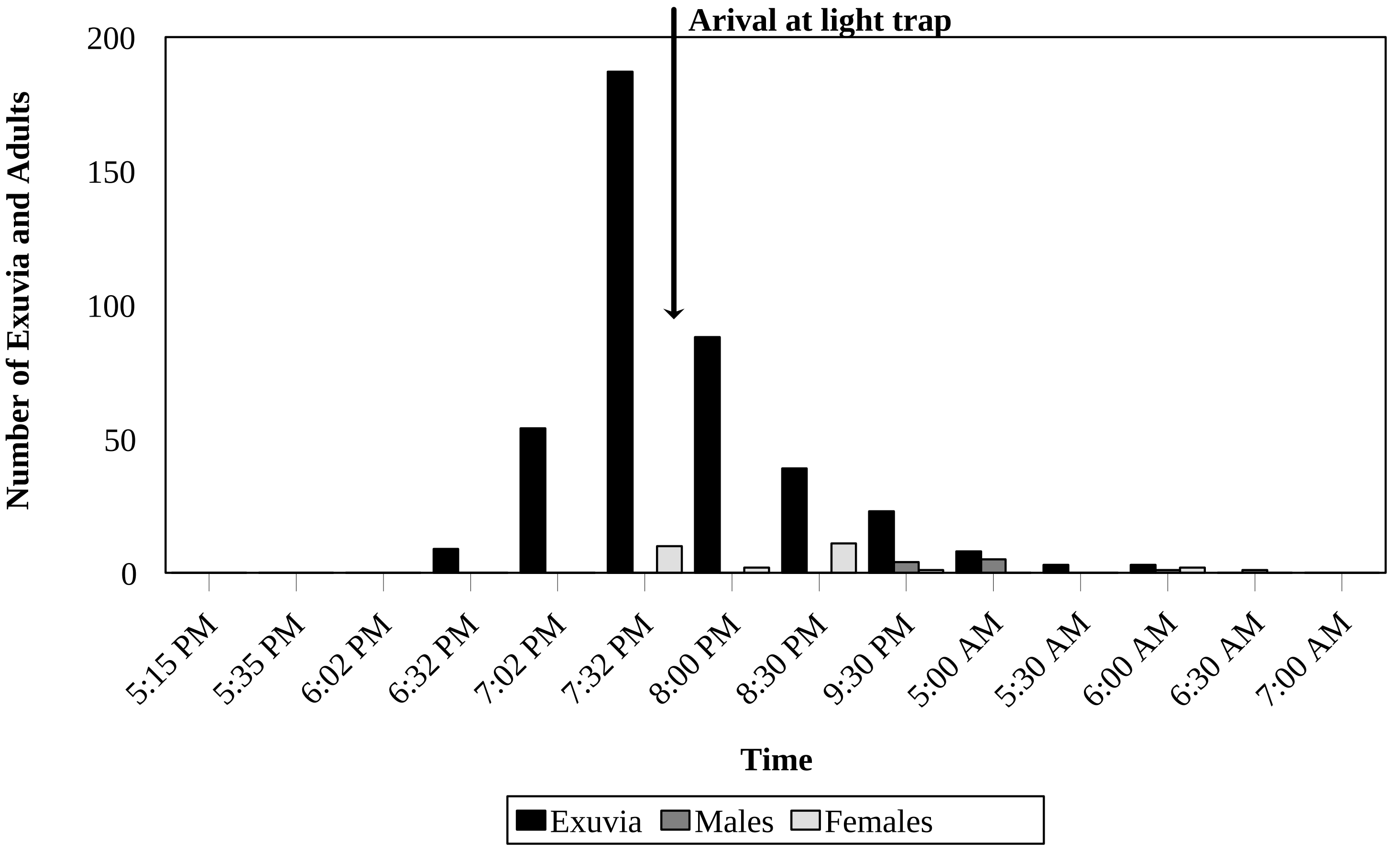

Arival at light trap
Number of Exuvia and Adults
200
150
100
50
0
5:15 PM
5:35 PM
6:02 PM
6:32 PM
7:02 PM
7:32 PM
8:00 PM
8:30 PM
9:30 PM
5:00 AM
5:30 AM
6:00 AM
6:30 AM
7:00 AM
Time
Exuvia
Males
Females

Figure 16. Flow diagram of timing of adult female behavior of *C. latipennis* in Honey Creek, OK.

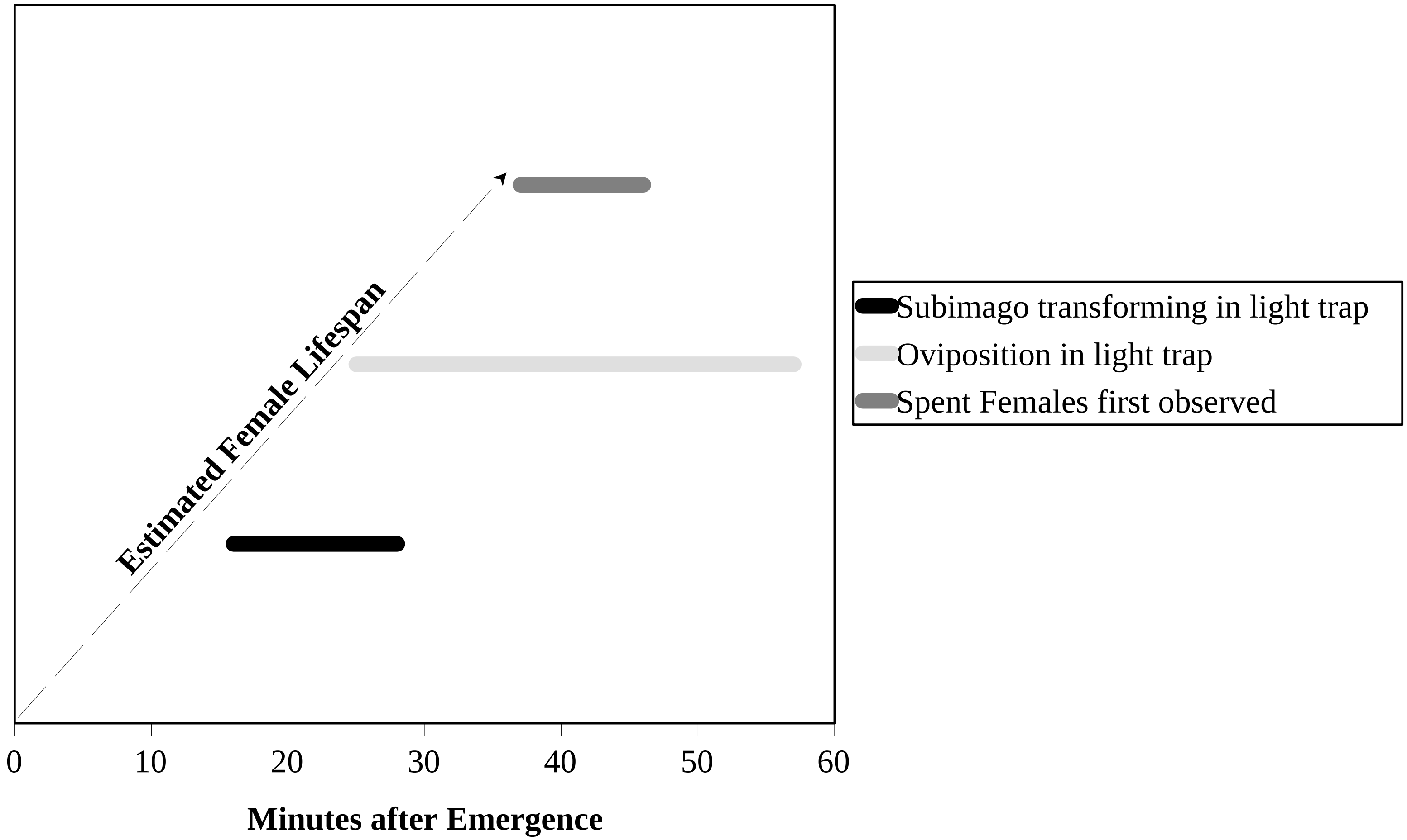

Estimated Female Lifespan
0
10
20
30
40
50
60
Minutes after Emergence
Subimago transforming in light trap
Oviposition in light trap
Spent Females first observed

Figure 17. Mean fecundity of *C. latipennis* from Honey Creek, OK. for 5 emergence peaks between August 1999 and September 2000. Lines show significant differences between emergence peaks.

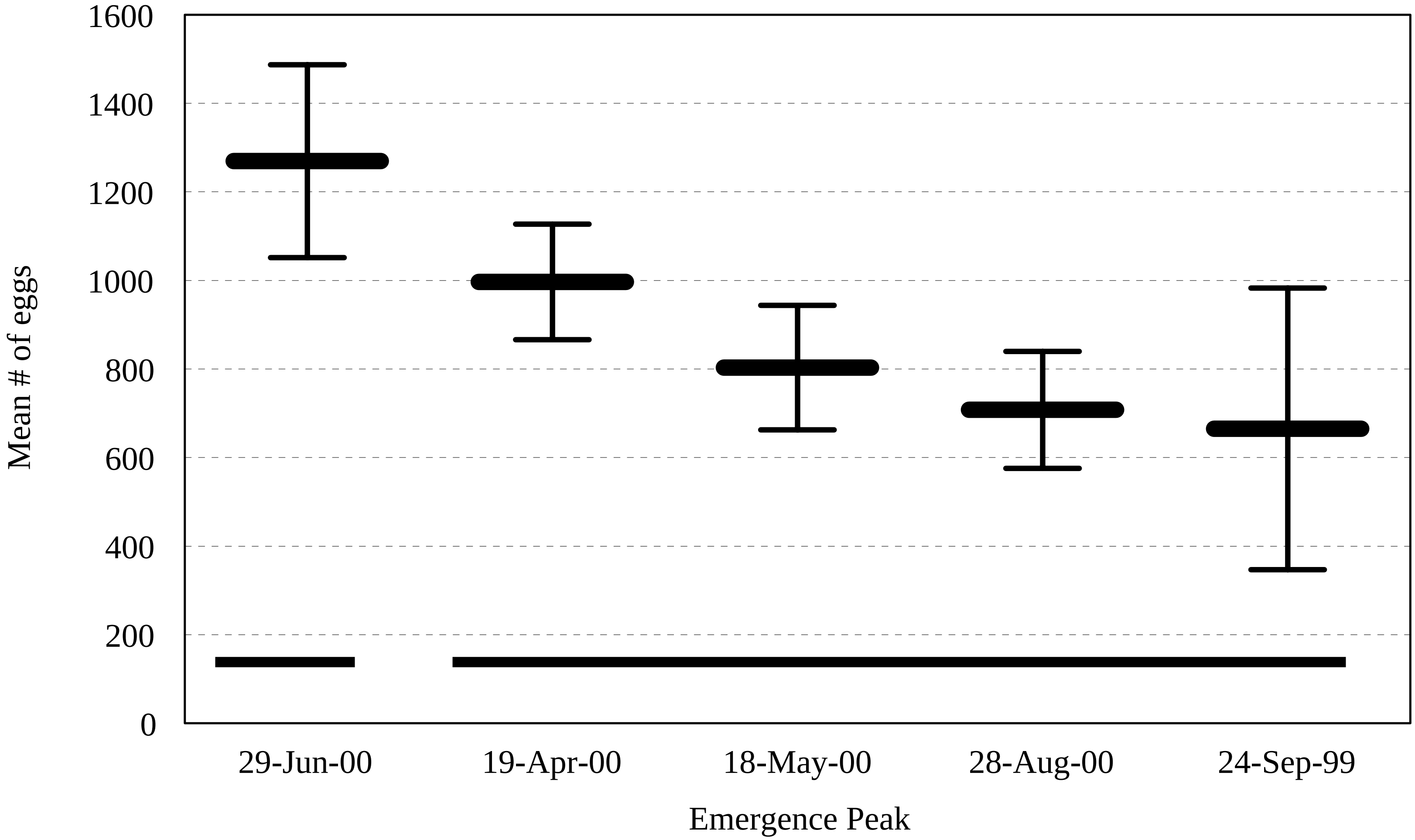
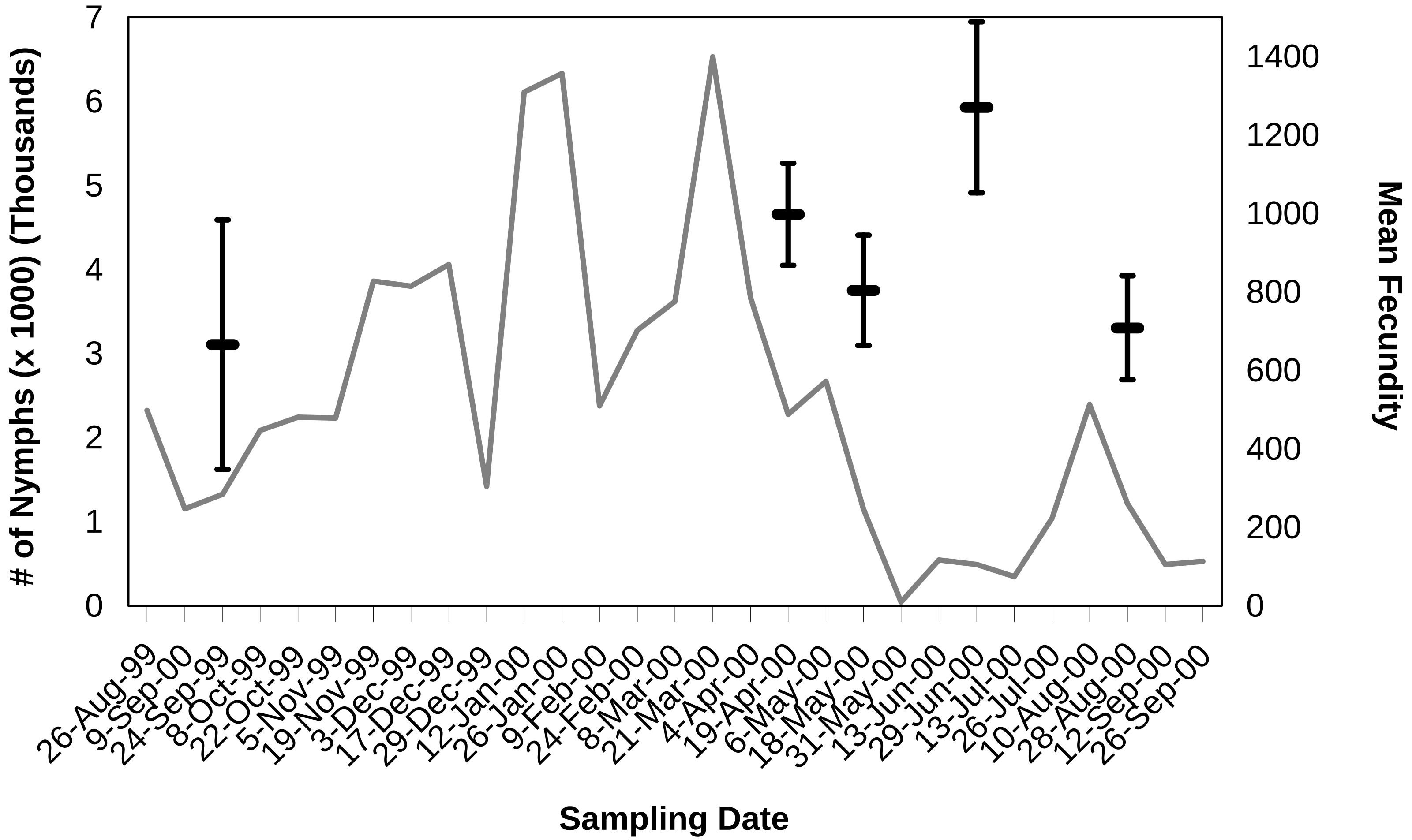

Mean # of eggs
1600
1400
1200
1000
800
600
400
200
0
29-Jun-00
19-Apr-00
18-May-00
28-Aug-00
24-Sep-99
Emergence Peak

Figure 18. Fecundity in relation to density of *C. latipennis* nymphs from Honey Creek, OK., August 1999 – September 2000.



# of Nymphs (x 1000) (Thousands)
0
1
2
3
4
5
6
7
Mean Fecundity
0
200
400
600
800
1000
1200
1400
26-Aug-99
9-Sep-00
24-Sep-99
8-Oct-99
22-Oct-99
5-Nov-99
19-Nov-99
3-Dec-99
17-Dec-99
29-Dec-99
12-Jan-00
26-Jan-00
9-Feb-00
24-Feb-00
8-Mar-00
21-Mar-00
4-Apr-00
19-Apr-00
6-May-00
18-May-00
31-May-00
13-Jun-00
29-Jun-00
13-Jul-00
26-Jul-00
10-Aug-00
28-Aug-00
12-Sep-00
26-Sep-00
Sampling Date

Figure 19. Egg and nymph development rates of *C. latipennis* applied to degree day estimates for continous water temperature in Honey Creek, OK., August 1999 – September 2000. Humps indicate peaks in emergence. Lines represent egg development, and color blocks represent nymphal development periods for cohorts and subcohorts.

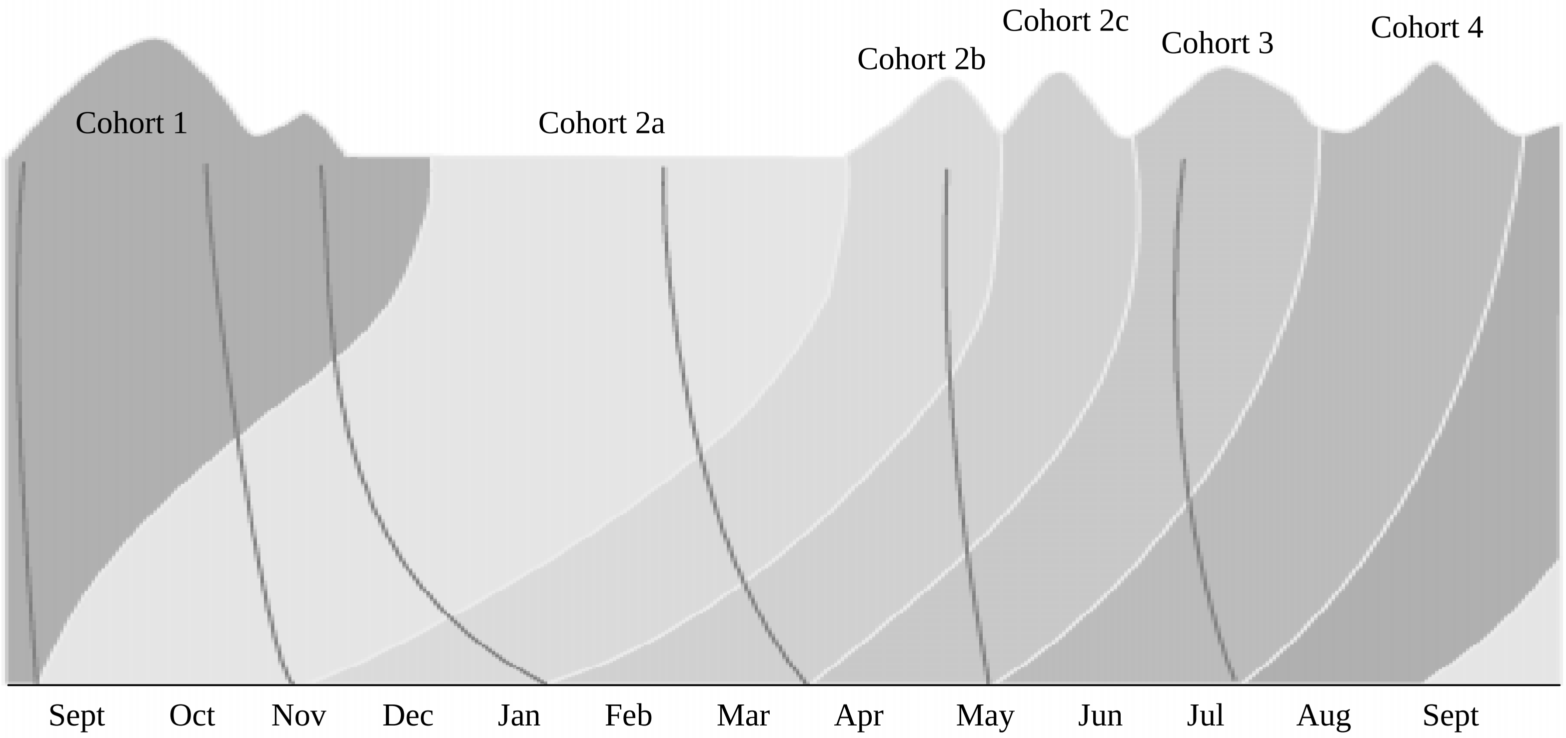

Cohort 1
Cohort 2a
Cohort 2b
Cohort 2c
Cohort 3
Cohort 4
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sept

Figure 20. Proposed cohort lines from development frequency data (Figure 13) in relation to egg and nymph development rates based on degree day estimates from continuous water temperature from Honey Creek, OK.

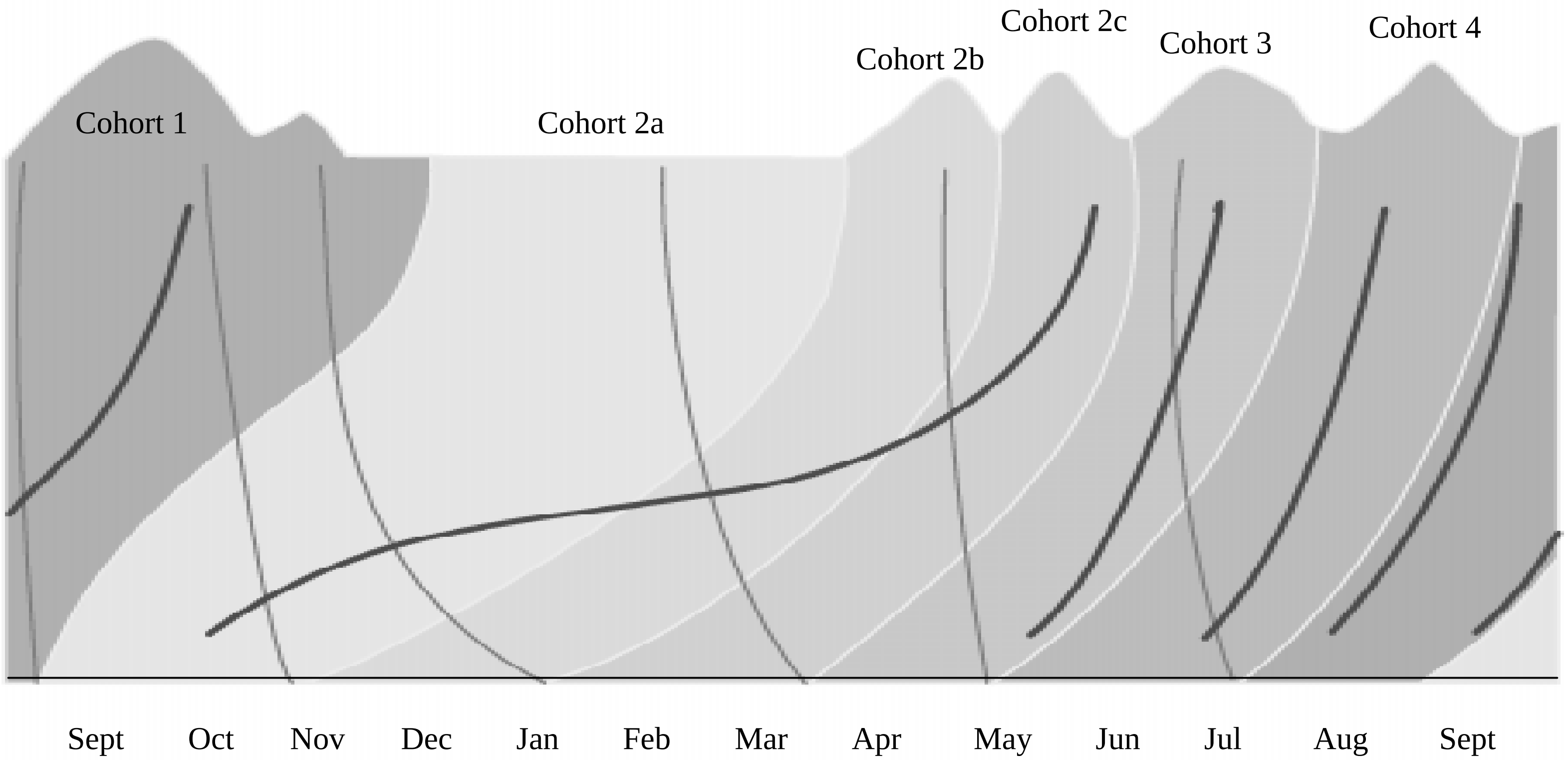

Cohort 1
Cohort 2a
Cohort 2b
Cohort 2c
Cohort 3
Cohort 4
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sept

Figure 21. Linear relationship of ln HCW and ln Dry weight for live *C. latipennis* nymphs from Honey Creek, OK.

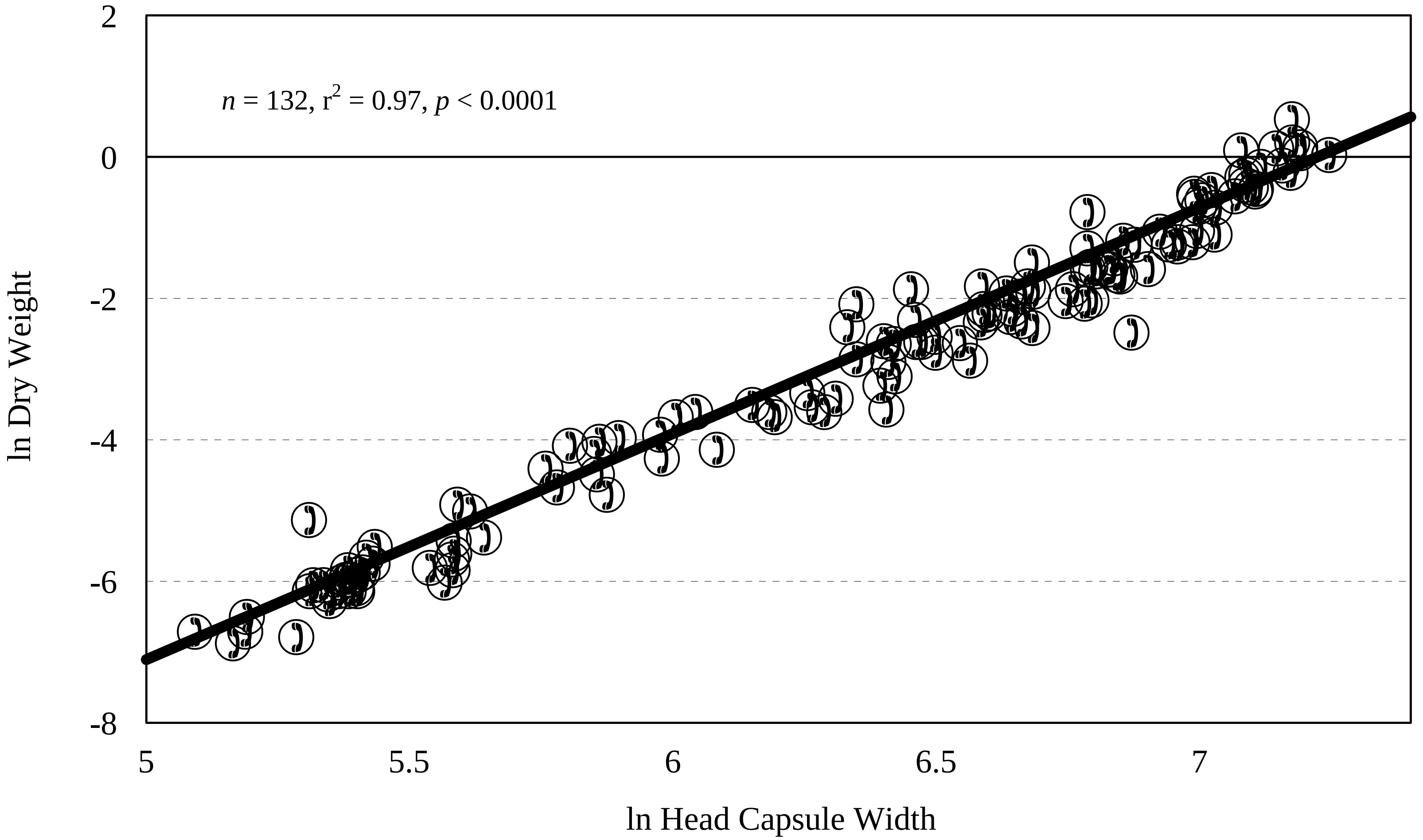
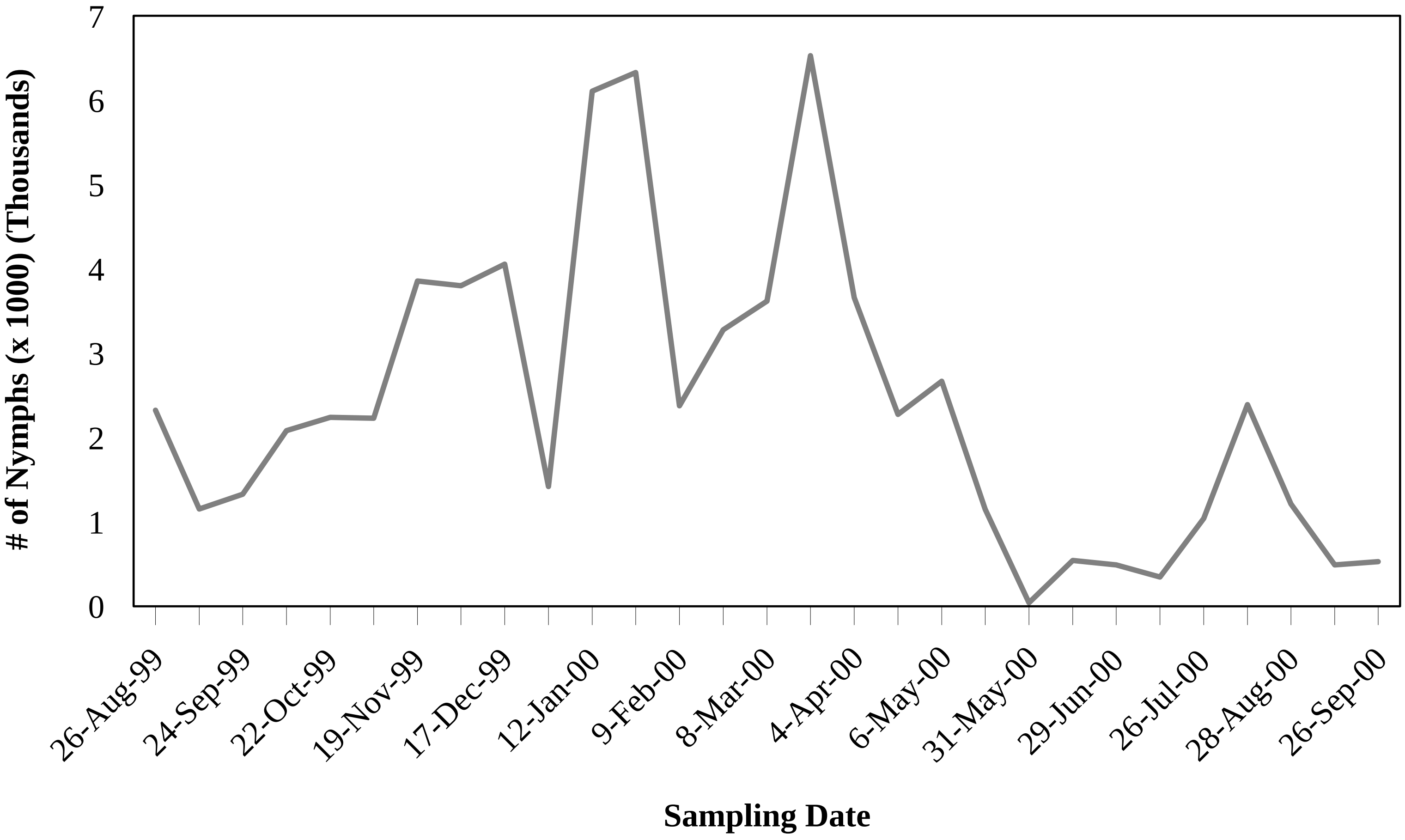

$n = 132$, $r^2 = 0.97$, $p < 0.0001$
2
0
-2
-4
-6
-8
5
5.5
6
6.5
7
ln Dry Weight
ln Head Capsule Width

Figure 22. Relative densities for the *C. latipennis* population from Honey Creek, OK., August 1999 – September 2000. Density is calculated as no./m^2.



# of Nymphs (x 1000) (Thousands)
7
6
5
4
3
2
1
0
26-Aug-99
24-Sep-99
22-Oct-99
19-Nov-99
17-Dec-99
12-Jan-00
9-Feb-00
8-Mar-00
4-Apr-00
6-May-00
31-May-00
29-Jun-00
26-Jul-00
28-Aug-00
26-Sep-00
Sampling Date

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