

Life Cycle and Production of the Mayfly *Choroterpes (Neochoroterpes) mexicanus* Allen (Ephemeroptera: Leptophlebiidae)¹

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ABSTRACT

Studies were conducted from 1971-73. Emergence occurred from late afternoon to near sunset March through November. Life span after emergence was less than 24 h, and both subimagos and imagoes exhibited a seasonal variation in total body length. Mating occurs in flight, with ♂ swarms occurring over land during the morning. Females fly upstream, alight on the water and extrude all eggs at once. A seasonal-generation periodicity in fecundity was noted. Eggs are barrel shaped, .18 mm long × .12 mm wide, have elaborate chorionic sculpturing, and peg-like attachment structures. Incubation at 25 ± 1°C required 13-15 days. First instar nymphs measured .45 mm total body length, had 5-segment cerci

and antennae and displayed no gills. The life cycle was multivoltine, with 3 relatively distinct generations. Nymphs underwent 16 and 19 instars in the overwintering and combined summer generations, respectively, and could be sexed beginning in the 7th. Sex ratios of 1264 nymphs and 549 subimagos were 1:1. Nymphs fed on detritus (90%) and algae, with seasonal variation in varieties and percentages. Mean standing crop on bi-weekly (or monthly) sampling dates was 880 individuals/m². Mean cohort turnover ratio, mean annual turnover ratio and total annual production (dry wt) were 5.1, 15.4, and 247.9 mg/m², respectively for the 3 generations.

Choroterpes mexicanus, recently described by Allen (1974), is distributed over much of Texas and Mexico. It is a dominant member of the Brazos River insect community, 2nd only to the caddisfly genus *Cheumatopsyche*. It is an important component in the diets of carnivorous fishes and insects (Stewart et al. 1973, Vaught and Stewart 1974), and exhibits high total drift densities of 1.65 × 10⁴-5.31 × 10⁶ daily, from 1 h before sunset to 1 h after sunrise, throughout the year (Cloud and Stewart 1974).

The ecological importance of *C. mexicanus*, and the fact that no comprehensive life-cycle ecological study has been made on any mayfly endemic to the southwestern United States, led us into this investigation. All sampling was done on that portion of the Brazos River 15-20 mi below Possum Kingdom Dam, TX, described in detail by Stewart et al. (1973).

MATERIALS AND METHODS

Standing crops, seasonal growth and voltinism, nymphal sex ratios, instar analysis and production estimates were derived from 70% isopropanol-preserved nymphs collected in modified Hess (158 μ mesh size) and kick-net samples taken between September 1971 and August 1972. Three Hess and numerous kick-net samples were taken twice-monthly from November 1971 to July 1972; flood releases from Possum Kingdom Reservoir in September and October 1971 and August 1972 allowed only 1 sampling period during those 3 months.

Size-frequency histograms were constructed from head capsule lengths of nymphs, and interpretation was made utilizing the methods of Cassie (1954) and Janetschek (1967). The Cassie method involved plotting cumulative frequencies from the size-frequency histogram on probability paper; modes appeared as sudden increases in percent frequency,

while inflections indicated gradation from 1 instar to another. The Janetschek (1967) method involved subtraction of sliding means from original size-frequency histograms and plotting the resultant positive and negative values; positive peaks indicated instar modes. To supplement these data and to help clarify instar separation, actual size changes between particular instars were determined from field-collected nymphs reared in styrofoam cups containing ca. 400 ml of river water and held in an environmental chamber at temperatures and photoperiods simulating those on the river. A calibrated ocular micrometer was used to measure head length, from the back of the head capsule to the clypeo-labral membrane. Generations were determined from the observed seasonal growth cycle and from emergence data obtained with a light box (Stewart et al. 1970), run semi-monthly March through September 1973, and monthly in January, February, and October to December 1973.

Production was estimated by the Hynes method (Hynes and Coleman 1968) as modified by Hamilton (1969) and utilized by Waters and Crawford (1973). All nymphs of each predetermined instar were dried in a Grieve Model LO-200C Drying Oven for 12 h at 67 ± 1°C, and mean weights/individual were then calculated.

Food habits of nymphs were determined from additional qualitative samples taken monthly throughout 1973 with an aquatic kick net. Nymphs collected at ca. 4 PM, and within 1 h of sunrise on the following day, were stored on ice to retard digestive processes and were dissected in the laboratory. Contents of the fore and midguts were dispersed into a Palmer Counting Cell (Palmer and Maloney 1954) and examined at 100×. Five random fields were examined from each gut, and area approximations were expressed in ASU using a calibrated Whipple Disc with a 0.74 × 0.74 mm field of view. Taxonomic determination of algae ingested was aided by culturing gut samples in a solution of ca. 75% ASM-1 culture medium and 25% sterile soil water extract. These cultures were held in an environmental chamber at simulated natural en-

¹ Study supported in part by the Faculty Research Fund of North Texas State University and U.S. Dept. of Interior Environmental Protection Agency Traineeship #T900115. Received for publication Apr. 7, 1975.

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environmental conditions for the time of nymphal collection. Diatoms were prepared for identification as outlined by the American Public Health Association (1971).

Subimago sex ratios, size and fecundity were determined from light box samples already described. Egg counts were made seasonally by placing ♀ in Palmer Counting Cells, cutting off the last abdominal segments and teasing out the eggs. Subimagos were placed on vegetation in styrofoam cups with clear plastic tops and allowed to molt for determination of life spans. Adults were held in the same manner.

Incubation was determined from eggs from 2 ♀ collected in the field while ovipositing. The eggs were placed in styrofoam cups containing ca. 300 ml of river water, were kept constantly aerated, and were held in a Percival E-50 environmental chamber at simulated seasonal river temperature and photoperiod. A commercial aquarium fungus inhibitor (Jungle Lab. Corp. Fungus Stop) was added to the cups containing the eggs. First instars obtained were mounted in Turtox CMC-10 and photographed.

Eggs used for descriptions and photographs came from subimagos preserved in 70% isopropanol. They were dissected out and soaked for 4 days in water and then mounted in CMC-10. An unsuccessful attempt was made to rear *N. mexicanus* from small field-collected nymphs in an artificial stream devised and described by Rhame and Stewart (1976).

RESULTS AND DISCUSSION

Subimago.—Subimagos emerged from late afternoon until ca. 1 h after sunset over the extended period from late March to November 1973. A similar crepuscular emergence has been noted for *Choroterpes curtus* Kimmins (Tjonneland 1969) and *Iron fragilis* Morgan (Needham et al. 1935). The subimago emerged under water and floated up on the last nymphal exuvium, using it as a raft.

Individuals that emerged in quiet water along the shore took immediate flight inland. Those that emerged out in the current floated downstream ca. 5 m, took flight upstream, dropped to the water surface, then repeated the process at least twice before a final prolonged flight to 25–100 m away from the shore. They alighted on various types of vegetation and immediately assumed a quiet, resting behavior. Subimagos molted and became adults shortly before dawn on the day following emergence; the subimaginal life span was therefore ca. 12 h.

A seasonal size variation was exhibited in the subimagos. Mean total body length for 98 randomly selected individuals was greatest in April (♂ 7.15 mm, ♀ 8.78 mm), least at the end of summer in September (♂ 5.47 mm, ♀ 5.47 mm), and increased again by November (♂ 6.10 mm, ♀ 6.58). Seasonal size variation for mayfly nymphs, subimagos and imagoes have been reported by several authors (Ide 1935, Macan 1957, 1961, Elliott 1967, and Clifford 1970). Rhame and Stewart (1976) observed a seasonal size difference in adult *Hydropsyche simulans* Ross from this same study area. Summer generation adults were

smaller than those emerging from overwintering larvae.

A corresponding seasonal fluctuation in fecundity was exhibited for *C. mexicanus*. Average number of eggs/4 ♀ was 1645, 809, and 1134 in April, September, November, respectively. Larger adults and greater egg production in cooler months probably reflect an advantageous adjustment in the seasonal cycles to optimum stream conditions for incubation and nymphal development. Subimago sex ratios from random light box captures were 1.4 ♂:1.0 ♀ and 1.0 ♂:1.2 ♀ in spring and summer-fall for 320 and 229 individuals, respectively.

Adults.—Adult *C. mexicanus* began forming large diffuse swarms over land about 0.5 h before sunrise. Flight within the swarm consisted of an undulating non-synchronous flight pattern by individual males. Height to the top of the swarms was ca. 4–5 m, and to the bottom ca. 2 m above ground. Only ♂ were found in spider webs on the nearby bridge at a height of ca. 20 m.

In most instances, swarming lasted through the morning hours until around noon; on occasion, swarming continued into mid-afternoon. Adults reared in the laboratory lived less than 12 h, suggesting that mating and oviposition occur only on the 1st day after shedding the subimaginal exuvium.

Actual mating was similar to that described by Needham et al. (1935) for *Paraleptophlebia*, *Siphonurus*, and *Cinygmula*, and by Lehmkühl and Anderson (1971) for *Paraleptophlebia delibis* Walker. A typical example of mating was observed in early October 1973, ca. 7:30 AM. A ♀ flew into a swarm of ♂ ca. 4 m above the ground and was grasped by a male. The 2 then flew in tandem taking the form of the letter "C" beginning at its top. At the bottom of this flight pattern ca. 1 m from the ground, they were captured so that confirmation of sex, maturity and species could be made.

Oviposition was successfully observed late in the study. Females deposited eggs at least 75 m upstream from the head of the riffle in flat flowing water ca. 2 m deep. Behavior was similar to that described for *Ephemera rotunda* Morgan (Needham et al. 1935) in that all eggs were deposited at once; however, variations from that species included: (1) *C. mexicanus* did not fly off the water after the oviposition descent, and (2) eggs were not carried in an external mass. Spent ♀ were caught floating downstream to the riffle after observed oviposition, usually within 1 hr of sunrise. On one occasion, 2 females were caught in flight as they were hovering and appeared ready to oviposit. One was held by its wings, and her abdomen was gently dipped into a cup of river water. Two streams of milky white eggs were spontaneously extruded and were successfully hatched; later dissection of this ♀ indicated she was void of eggs. Eggs were successfully obtained from the 2nd ♀ by placing her in a closed cup of river water.

Egg.—Eggs from subimagos resembled those from adults in both appearance and size. They closely fit the general description of *Choroterpes basalis* Banks

eggs given by Needham et al. (1935), except that they are more rounded in shape and slightly larger, measuring 0.18×0.12 mm diameter.

The chorionic sculpturing consisted of many raised sucker-like discs; these may be accessory attachment structures as hypothesized by Koss (1968) for *Paraleptophlebia debilis*. Peg-like attachment structures, as in *Leptophlebia* sp. (Koss 1968), were also present and are shown in Fig. 1. The eggs adhered to glass or styrofoam, but no continuous adhesive layer was observed. No thread-like attachment structures were observed; however, Traver and Edmunds (1967) pointed out that this may be a characteristic peculiar to the genus *Thraulodes*. The eggs fit the family characters of Koss (1968).

Incubation required 13–15 days at $25 \pm 1^\circ\text{C}$ and simulated natural photoperiod. Eclosion was not observed although a characteristic longitudinal tear was exhibited by hatched eggs.

Nymph.—Total body length (excluding cerci) and head length of 1st instar nymphs (Fig. 2) were about 0.45 mm and 0.09 mm, respectively. Early nymphs were transparent, had no gills and had 5-segmented antennae and cerci. Three ocelli were apparent, and the compound eyes were indistinguishable. First instar nymphs fed on filaments of blue-green algae, but we could not rear them further.

Nymphs could be sexed at the 7th and succeeding instars by the divided eye in males. The upper portion began as a thin line projecting from the inner margin of each eye. This progressively expanded with each molt until the facets became distinguishable. The sex ratio of 1264 post-6th instars was 1.0 ♂ : 1.16 ♀; the ratios of 24 black-wing-pad individuals was 1:1. These data, and those for sexed subimagos, indicated that the Brazos population exhibited an approximate 1:1 sex ratio.

Seasonal Cycle.—Seasonal growth is depicted in Figures 3 and 4. The absence of smaller nymphs in summer generation might be due to vertical stratification of the species. Poole and Stewart (1975) showed that large numbers of earlier instars were in



FIG. 2.—First instar nymphs of *C. mexicanus* (100 \times).

sub-surface layers during July–Oct., 1972. Absence of smaller nymphs in August was probably due to sampling error, since only 36 were recovered from 3 ft² of riffle area. Spates in August and September 1971, might account for the absence of these small sizes in the September sample. Poole and Stewart (1975) showed that over 90% of *C. mexicanus* were 20–30 cm below the surface after similar spates in 1972. Correlation of seasonal head length sizes with observed emergence peaks and periods of growth without recruitment enabled some interpretation of voltinism. The general graphical presentation in Fig. 3 gave a clear indication of seasonal growth progression, the wide overlap of broods in this species made interpretation of voltinism difficult. The more detailed method (Fig. 4) showing seasonal distribution of size classes allowed a more discriminating interpretation since gaps between size classes tended to indicate separation of generations.

From Fig. 3 and 4, a 3-generation seasonal cycle with considerable brood overlap within and between generations was suggested for *C. mexicanus* during September 1971 to August 1972. Additional observations of emergence during the calendar year 1973 corroborated these findings. Drift data of Cloud and Stewart (1974) also indicated three generations of this species, with peaks in emergence occurring in April–May, July and Sept.

Adults that emerged in late March and April laid eggs; nymphs from these eggs grew through the spring and early summer to a June–August emergence, peaking in July (Fig. 4). Adults which emerged in May produced nymphs that grew through the summer to emerge September–November, with the peak in October. The June–August (July peak) adults contributed a brood that grew through late summer and fall with an optional emergence in December, dependent on temperature conditions. Data from December 1971, indicated a possible emergence, but field observations in December 1973, indicated no emergence for that month. Average monthly Environmental Science Services Administration air temp data indicated that December 1971, was considerably

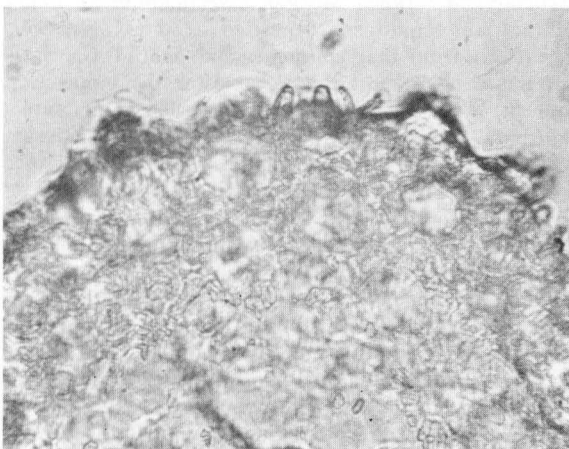


FIG. 1.—Tangential view of *C. mexicanus* egg with peg-like attachment structures (1000 \times).

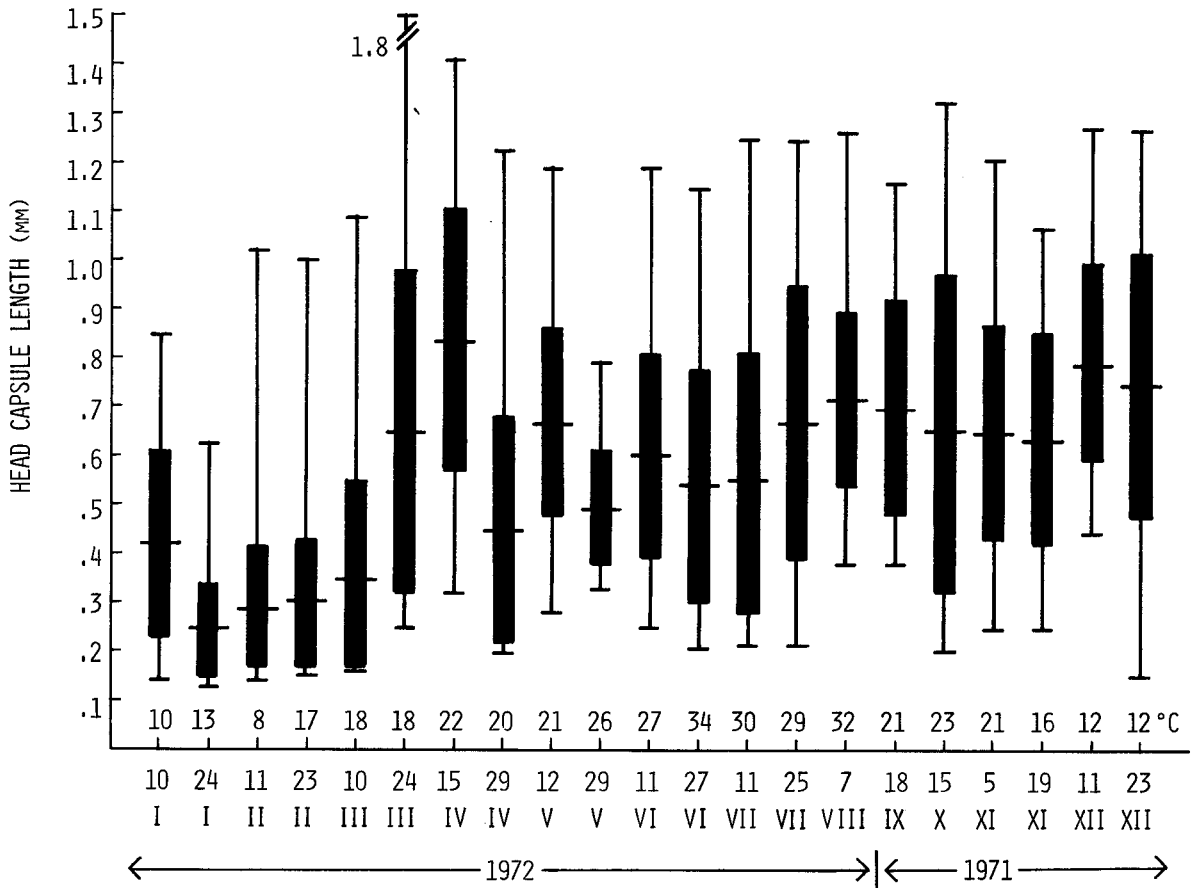


FIG. 3.—Seasonal head capsule growth of 1817 *C. mexicanus* nymphs: vertical line = range, horizontal line = mean, vertical bar = standard deviation.

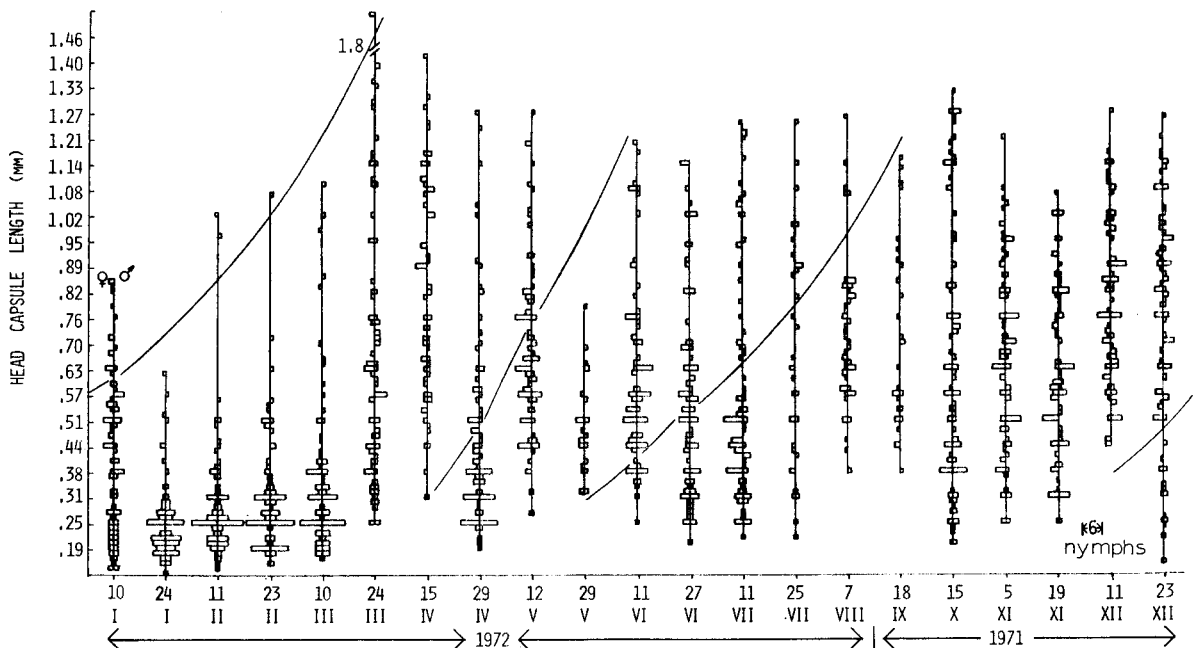


FIG. 4.—Size-frequency distribution of the head capsule lengths of each sample; curved lines delimit proposed generations.

warmer than December 1973. The fall (October) emerging adults contributed the major overwintering nymphal brood resulting in the spring emergences. With this scheme, 1 clear overwintering generation with 2 broods and 2 summer generations (1 reaching a peak in July, and the other composed of 2 broods, peaking in October and December) were suggested. Winter conditions allowed for synchronization of the prolonged summer generations. Waters (1966) found a remarkably similar life cycle for *Baetis vagans* in Minnesota; the only real difference was a longer fall emergence for *C. mexicanus*. Obviously, this complex multi-voltine cycle with much brood overlap was very dynamic, and adjustments of broods and specific emergence times could take place from year to year, taking advantage of physical or biological conditions.

Multivoltine cycles are common among members of the family Baetidae, even from northern latitudes (Needham et al. 1935, Macan 1957, Waters 1966, Elliott 1967, and Pearson and Kramer 1972). The generations are often distinct, especially in bivoltine species, probably because of true seasonal water temperature and photoperiod effects (Clifford et al. 1973). Clifford et al. (1973) have summarized the current understanding of Ephemeroptera life cycles on a latitudinal basis and have concluded that tropical species should display multivoltine cycles with overlapping broods. The life cycle of *C. mexicanus*, whose populations are distributed in southern temperate latitudes, fits this theory very nicely. Its apparent success in this section of the Brazos, that once was intermittent, is probably due to the moderating effect on flow, temperature and turbidity brought about by the leakage of water from the Possum Kingdom Reservoir (since 1940). The temperate photoperiod and cold

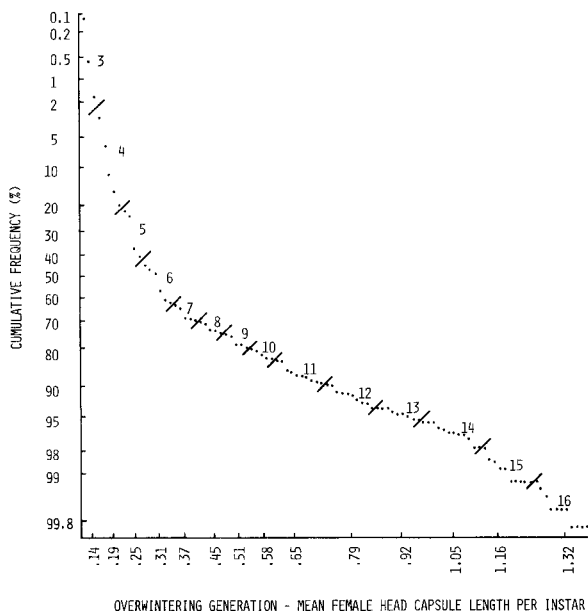


FIG. 5.—Instar analysis of 677 *C. mexicanus* ♀ of the overwintering generation by the Cassie method.

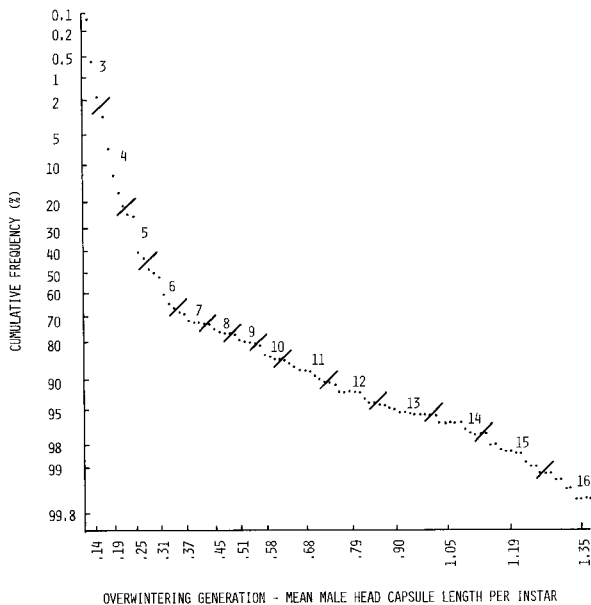


FIG. 6.—Instar analysis of 632 *C. mexicanus* ♂ of the overwintering generation by the Cassie method.

winter water temperatures (down to 7°C) probably account for the prolongation and synchronization of the more distinct winter generations. Rhame and Stewart (1976) found a similar multivoltine condition for the caddisfly *Hydropsyche simulans* on this same study site.

Development.—Determination of nymphal instars for *C. mexicanus* by the methods of Cassie (1954) and Janetschek (1967) are given in Fig. 5–8 and 9–12, respectively. Analysis by each method indicated that nymphs underwent ca. 16 and 19 instars for winter and combined summer generations, respectively (Fig. 5–8) with no observed sex differences.

Supplemental rearing of field collected nymphs of larger sizes, e.g., noting change in head capsule lengths with observed molts, aided interpretation of data from the above 2 methods. These observations were especially helpful in determining real differences in head capsule measurements for the decreasing numbers of larger sizes in the overwintering generation where peaks were unclear (Fig. 5, 6, 9, & 10). Both the Cassie (1954) and Janetschek (1967) methods had the common problems of being somewhat indistinct at either end of the histogram and of presenting graphical data that, without supplementary observations as above, might not be any easier to interpret than the original histogram.

Another method often employed in separating instars of holometabolous larvae consists of plotting one linear measurement (head capsule length) against another (pronotum width); this was attempted, but no clear separation of instars resulted.

Vaught and Stewart (1974) showed a sexual dimorphism in instar development in the stonefly *Neoperla clymene* Newman. Considerable intra-specific

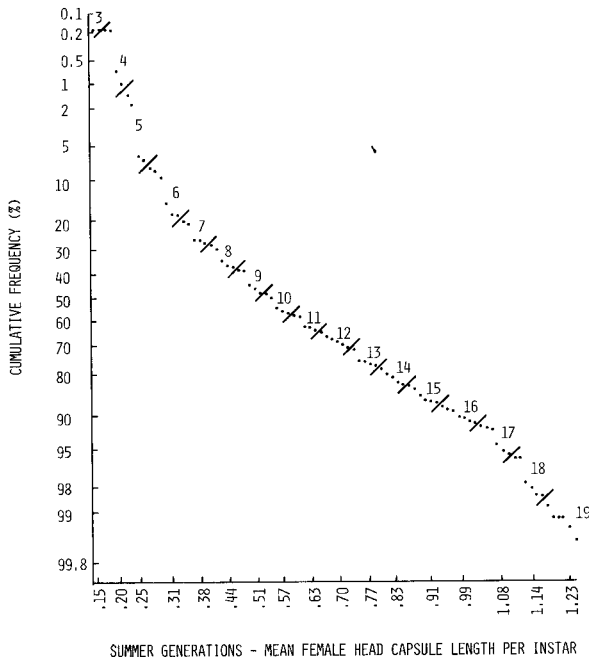


Fig. 7.—Instar analysis of 548 *C. mexicanus* ♀ of the combined summer generations by the Cassie method.

variation due to sex, physical and other biological conditions probably occur in hemimetabolous insects whose development spans a large number of molts.

The conformance of *C. mexicanus* to Dyar's (1890) rule was tested by plotting logs of the means of the

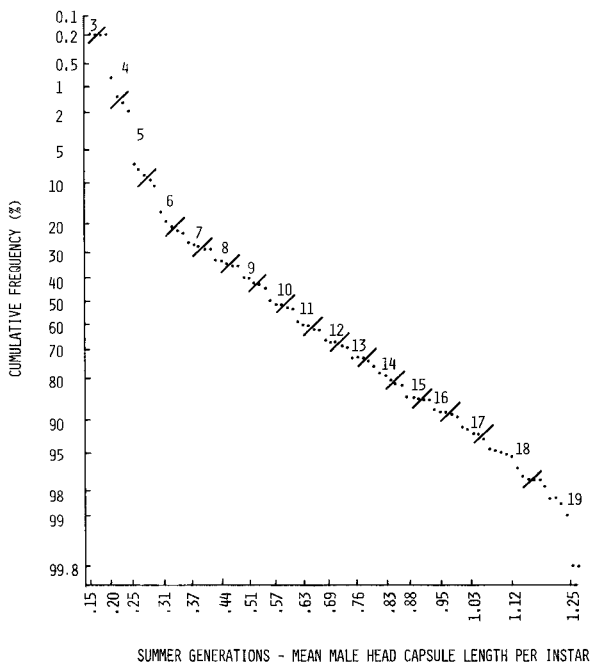


Fig. 8.—Instar analysis of 509 *C. mexicanus* ♂ from the combined summer generations by the Cassie method.

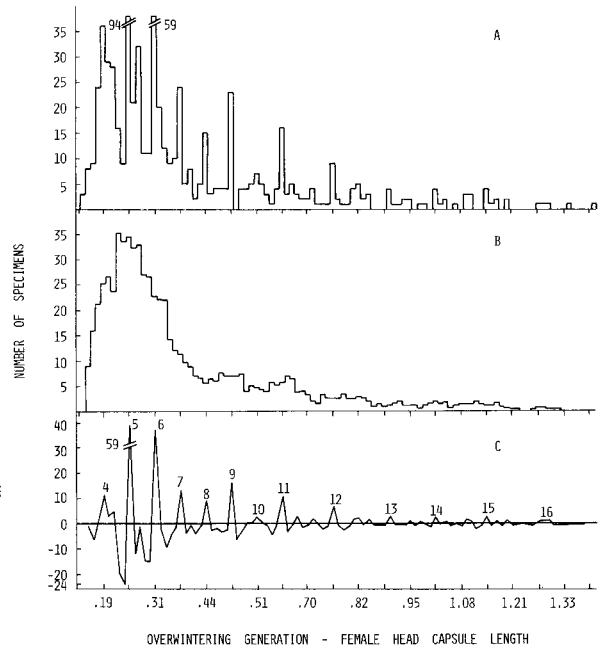


Fig. 9.—Instar analysis of 677 *C. mexicanus* ♀ of the overwintering generation by the Janetschek method: A = size-frequency histogram of head capsule lengths, B = running mean of 5 of the frequencies, C = modal periodicity of instars (represents the difference between histograms A and B).

proposed instars, as determined above, against instar numbers. Fig. 13-16 showed a slightly curved line, indicating Dyar's rule was not strictly adhered to.

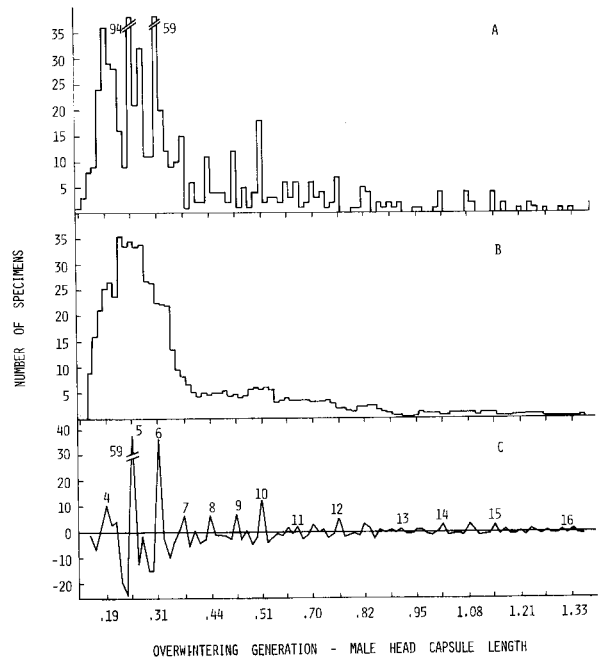


Fig. 10.—Instar analysis of 632 *C. mexicanus* ♂ of the overwintering generation by the Janetschek method. Same legend as Fig. 9.

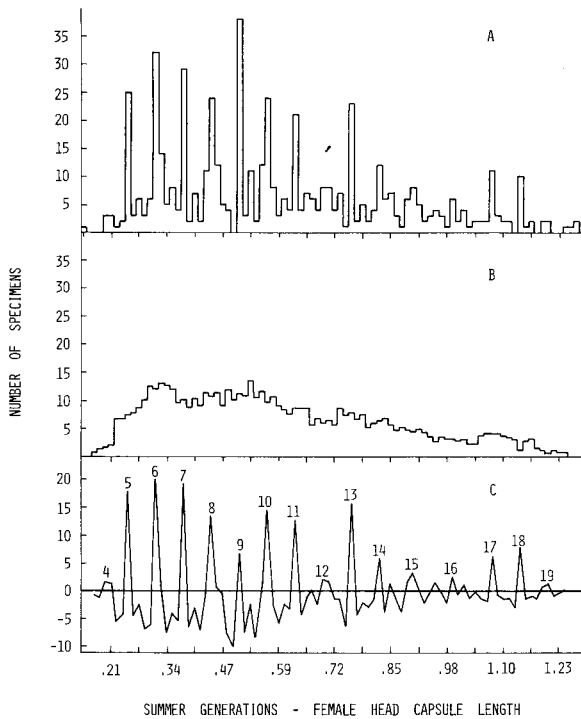


FIG. 11.—Instar analysis of 548 *C. mexicanus* ♀ from the combined summer generations by the Janetschek method. Same legend as Fig. 9.

Harper (1973) found a similar growth characteristic in the hemimetabolous stonefly *Nemoura trispinosa* Claassen.

Seasonal effect on instar development could be seen in Fig. 13 and 14. There was a leveling off of growth during the winter and then a speeding up during the early spring. Growth during the summer was more consistent, as seen in Fig. 15 and 16. In all these figures, the head capsules of the reared 1st instar was included and the unsampled 2nd instar was estimated, as per Harper (1973). Fig. 5 and 6 also show this seasonal effect, which was represented by larger size ranges per instar with more widely separated means. Dyar predicted a geometric progression of around 1.4. The 1.16 for combined summer generations and 1.2 for the winter generation generally agreed with that prediction. Janetschek (1967) found a mean growth progression factor of around 1.19 for several species of Collembolla, and Vaught and Stewart (1974) reported mean growth progression factors of 1.19 (wing pad length) and 1.15 (head capsule width) for instars 3–11 of the stonefly *Neoperla clymene*.

Food and Trophic Position.—Ephemeroptera have generally been considered herbivores (Gilpen and Brusven 1970). Brown (1960) found that *Chloeon dipterum* L. could digest several species of algae. Recent studies, however, have pointed to the importance of detritus in the diets of many species and to the fact that diets of most species were probably adjusted to seasonal abundance of dietary components (Moon

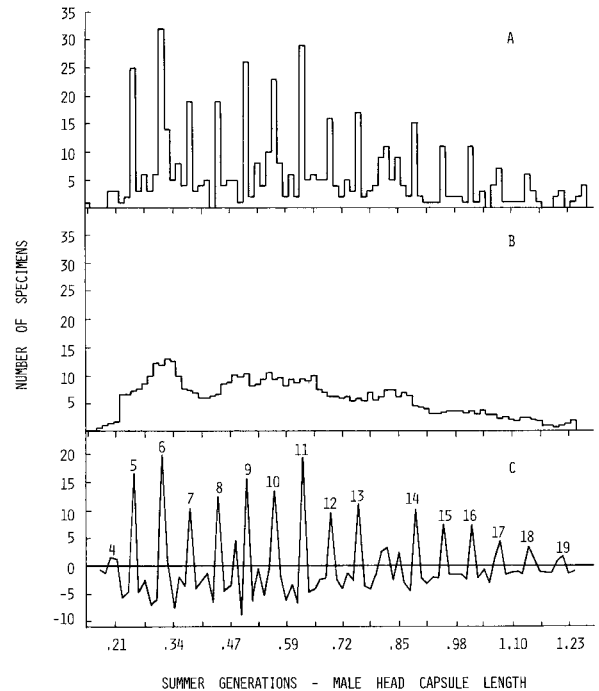


FIG. 12.—Instar analysis of 509 *C. mexicanus* ♂ from the combined summer generations by the Janetschek method. Same legend as Fig. 9.

1938, Jones 1950, Chapman and Demory 1963, Gilpin and Bresven 1970, and Cummins et al. 1973). Cummins et al. (1973) have shown that growth occurred when 4 species of *Stenonema* were fed only detritus.

Choroterpes mexicanus guts contained over 90% detritus, but they exhibited a seasonal variation in the amount and kinds of algae ingested. Table 1 shows that diatoms made up the greatest proportion of algae

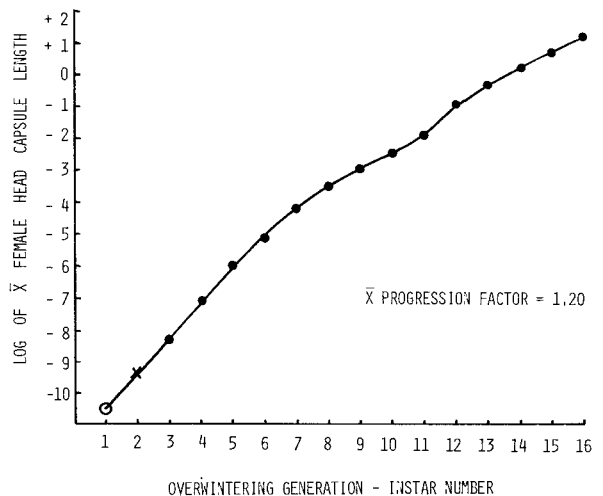


FIG. 13.—Head capsule length progression with successive instars for ♀ of the overwintering generation; open circle = reared 1st instars, X = unsampled instar.

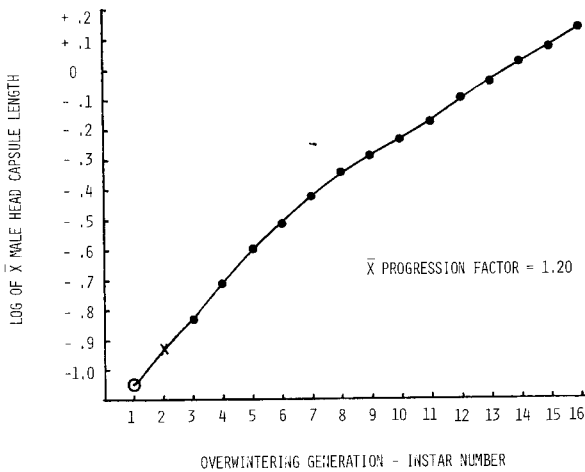


FIG. 14.—Head capsule length progression for ♂ of the overwintering generation.

ingested throughout the year. Highest frequency of algal ingestion occurred in late spring and early summer, when algae was most abundant.

Lowest algal consumption occurred in the fall and late summer (Table 1), which corresponded with the time of greatest detrital abundance. A similar seasonal periodicity was reported in *Paraleptophlebia* sp. by Chapman and Demory (1963) and in several species of mayflies from the St. Marie River in Idaho by Gilpen and Brusven (1970).

Although Jones (1950) observed a diel periodicity in the feeding of *Ephemerella notata* Eaton nymphs, there did not appear to be any major difference in total ingestion by *C. mexicanus* nymphs between morning (within 1 h sunrise) and afternoon (ca. 4 PM) samples (Table 1). Laboratory observations indicated that nymphs were negatively phototrophic, so feeding is probably more cryptic during daytime hours, although no pattern of diel shifts in components ingested seems to be evident. Chapman and Demory (1963) found a similar diet, periodicity and negative phototrophism in *Paraleptophlebia* sp.

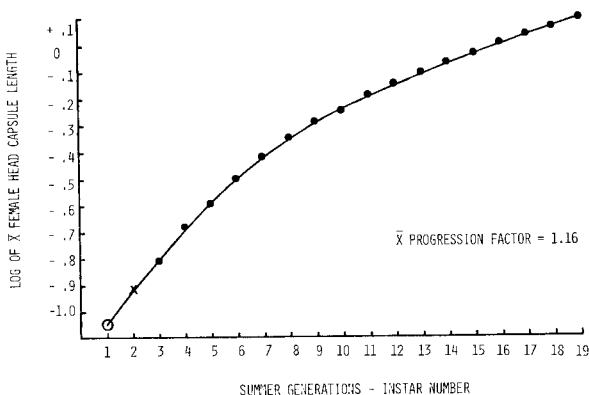


FIG. 15.—Head capsule length progression for ♀ of the combined summer generations.

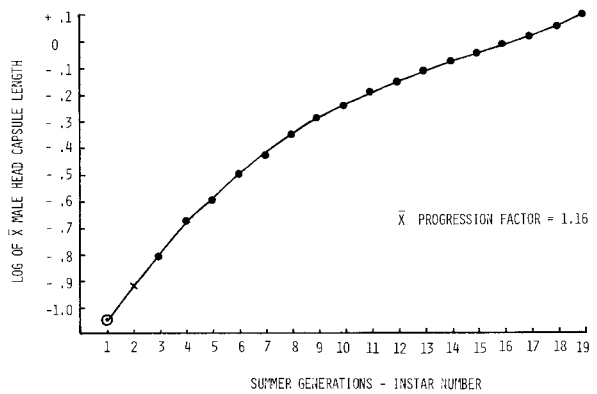


FIG. 16.—Head capsule length progression for ♂ of the combined summer generations.

Taxa found in the algal dietary food groupings of Table 1 were Greens—*Tetrahedron*, *Cladophora*, *Gloeocystis*, *Ankistrodesmus*, *Scenedesmus*, *Chlorococcum*, *Oocystis*, *Rhizoclonium*, *Crucigenia*, *Cosmarium*, *Chlorella*, *Protococcus*, *Ulothrix*, *Kircheriella*, *Haematococcus*, *Eremosphaera*, *Microspora*, *Palmellococcus*, *Mesotaenium*, *Hyalotheca*, *Hormidiopsis*, and *Characium*; Blue-greens—*Merismopedia*, *Eucapsis*, *Chroococcus*, *Gloeocapsa*, and *Melosira*; Yellow-greens—*Cyclotella*, *Denticula*, *Frustulia vulgaris*, *Fragilaria capucina*, *Gomphonema angustatum*, *G. parvulum*, *Gomphoneis herculeana*, *Navicula confervacae*, *N. cryptocephala*, *N. exigua*, and *Rhoicosphenia curvata*.

The trophic function of a herbivore-detritivore, such as *C. mexicanus*, is to convert plant material into animal tissue that can in turn be utilized by other consumers (Gilpin and Brusven 1970). The review of feeding habits of lotic fishes and other vertebrates (Hynes 1970) indicated that large numbers of fishes and some birds feed on mayfly nymphs and winged forms.

A population of swallows, residents of the Highway 4 Bridge adjacent to the study area, appeared to feed on morning swarms of *C. mexicanus*. Stewart et al. (unpubl.) showed that *C. mexicanus* is a dietary component of the dusky darter, *Percina sciera*, and the greenthroat darter, *Etheostoma lepidum* on the study riffle. Associated riffle insects apparently also utilized *C. mexicanus* nymphs. Stewart et al. (1973) showed that *C. mexicanus* made up 2.2% of the February-May diet of the hellgrammite *Corydalus cornutus*, which ingested a wide range of over 22 different organisms. Vaught and Stewart (1974) reported that *C. mexicanus* nymphs made up over 6% of the diet of the stonefly *Neoperla clymene*, and Rhame and Stewart (1976) found that even the caddisfly *Hydropsyche simulans* took relatively large numbers of *C. mexicanus* nymphs in summer months. All these studies were made on the same study site.

Production.—Recent studies on this modified section of the Brazos River generally have indicated that species diversity, standing crops and production are

Table 1.—Seasonal ingestion of algae by 230 *C. mexicanus* nymphs in 1973; avg number of ASU/Field.^a

Type of algae	Sampling date (1973)											
	Jan.		Feb.		March		April		May		June	
	PM	AM	PM	AM ^b	PM	AM	PM	AM	PM	AM	PM	AM
Green	0.30	0.01	0.30	—	0.34	0.17	0.14	2.40	0.45	0.04	0.18	0.17
Blue-green	—	—	0.03	—	—	—	0.08	—	—	—	—	—
Yellow-green	3.01	1.29	3.25	—	3.14	5.38	11.40	12.32	10.28	7.84	6.71	10.60
Other	—	—	0.42	—	0.06	—	0.02	—	—	0.03	0.33	0.32
Total	3.31	1.30	4.00	—	3.54	5.55	11.64	14.72	10.73	7.91	7.22	11.09
Water temp °C	10	7	11	—	19	13	17	15	25	24	24	21
Type of algae	July		Aug.		Sept.		Oct.		Nov.		Dec.	
	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM
	Green	1.59	0.22	0.96	1.85	0.34	0.21	0.42	0.30	0.18	0.19	1.35
Blue-green	—	—	0.11	0.02	0.10	—	—	—	—	—	—	—
Yellow-green	8.50	4.03	0.78	1.23	0.67	0.87	0.86	0.69	0.60	0.70	1.13	1.85
Other	0.13	—	1.68	0.54	—	—	—	0.04	0.02	—	—	0.03
Total	10.72	4.25	3.53	3.64	1.11	1.08	1.28	1.03	0.80	0.89	2.48	2.45
Water temp °C	25	22	33	30	26	26	24	23	20	18	13	8

^a Five random fields/individual—10 individuals/sample.

^b No data due to flood conditions.

greater than in nearby typically unmodified sluggish and sometimes intermittent rivers.

Mean standing crop of *C. mexicanus* occurring on the bi-weekly (or monthly) sampling dates was

880/m². Standing crops for the whole insect community on this riffle have reached over 38,000 organisms/m² during July 1971 (Vaught and Stewart 1974). The high standing crops and number of spe-

Table 2.—Summary of Cohort and annual production and turnover ratios for *C. mexicanus*.

	Summer generations separated							
			Overwintering generation		1st summer generation		2nd summer generation	
			♂	♀	♂	♀	♂	♀
Cohort production (mg/m ²)			36.02	55.09	19.29	38.53	39.60	59.40
Cohort turnover ratios			6.09	6.29	4.1	5.32	3.92	5.05
Average cohort turnover ratio			5.13					
Annual production (mg/m ²):	♂	94.91						
	♀	153.02						
	Total	247.93						
Annual Turnover ratio:	♂	14.11						
	♀	16.11						
	Avg	15.39						
	Summer generations combined							
			Overwintering generation		Summer generations			
			♂	♀	♂	♀	♂	♀
Cohort production (mg/m ²)			36.02	55.09	42.18 68.02			
Cohort turnover ratios			6.09	6.29	4.16 5.13			
Average cohort turnover ratio			5.42					
Annual production (mg/m ²):	♂	78.10						
	♀	123.11						
	Total	201.21						
Annual Turnover ratio:	♂	10.5						
	♀	11.8						
	Avg	11.2						

cies found on this riffle would seem to be an exception to Lehmkuhl's (1972) inference that all temperate thermally stratifying reservoirs with hypolimnion drains would produce depleted benthic faunas downstream from their dams.

Production estimates for multivoltine macrobenthos with distinct generations have been published by Neess and Dugdale (1959) and Pearson and Kramer (1972). Waters (1966) used 2 methods of calculating production for *Baetis vagans* which as already noted, had a growth cycle similar to *C. mexicanus*. He combined the 2 summer generations and did not sex the individuals. Cohort and annual production was calculated for *C. mexicanus* using the Hynes method (Hynes and Coleman 1968) as illustrated by Waters and Crawford (1973). Production was estimated by combining the 2 summer generations, as Waters did for *Baetis vagans*, and by separating the 2 summer generations.

We used the Hynes method because it allowed the use of instars rather than arbitrary size classes, and because it could be used when cohorts could not be clearly distinguished (Waters and Crawford 1973). Weights were all expressed as dry wt, and individuals younger than the 7th instar were divided equally between males and females. Obvious underestimates resulted from an inability to sample smaller sizes. The Hynes method had been shown by Waters and Crawford (1973) to give an overestimate when compared to other methods. Waters (1969) and Waters and Crawford (1973) emphasized cohort turnover ratios (cohort production divided by mean cohort standing crop) as being a constant for freshwater benthic invertebrates with a range of ca. 2.5-5. Cohort and annual production and turnover ratios for *C. mexicanus* are summarized in Table 2. For 3 cohorts, the avg turnover ratios/cohort ranged from 4.49-6.19 with an avg 5.13, which agreed with Waters' (1969, Table 1) data, especially since initial weights were, in all cases, less than 1% of maximum. An overestimate of production might account for the larger cohort and annual turnover ratio. The avg cohort turnover ratio, when summer generations are combined, equaled 5.42, which also generally agreed with Waters (1969). Annual turnover ratios were influenced by voltinism, and, as can be seen from Table 2, a greater number of cohorts yielded a larger annual turnover ratio as predicted by Waters and Crawford (1973). They indicated that turnover ratios could be used to compare production estimates (methods). The turnover ratios for *C. mexicanus* are within their estimated range.

ACKNOWLEDGMENT

We express great appreciation to Dr. R. K. Allen, California State University at Los Angeles for taxonomic determinations of nymphs, subimagos and adults of this recently described mayfly species.

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