THE LIFE HISTORY AND ECOLOGY OF THE MAYFLY *NEOCHOROTERPES MEXICANUS* ALLEN (EPHEMEROPTERA: LEPTOPHEBIIDAE)

THESIS

Presented to the Graduate Council of the
North Texas State University in Partial
Fulfillment of the Requirements

For the Degree of

MASTER OF SCIENCE

By

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The life history and ecology of *Neochoroterpes mexicanus* was studied from data collected September, 1971, to August, 1972, and January to December, 1973, in the Brazos River, Texas. Nymphal development, instar analysis, voltinism, standing crops, and production estimates were determined from the quantitative samples taken in 1971 and 1972. Aspects of the life history and food habits of 230 specimens were arrived at from qualitative samples and light box captures in 1973. Laboratory investigation in 1973 helped in establishing instar analysis, egg incubation and description, and first instar descriptions.

Neochoroterpes mexicanus appeared to have three generations per year with brood overlap in the summer and fall. It displayed 16 and 19 instars for overwintering and combined summer generations respectively.

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CHAPTER I

INTRODUCTION

The Ephemeroptera are a primitive group of aquatic insects known for their short adult life span and distinctive mating swarms. Benjamin Franklin eulogized their ephemeral existence in a letter to Madam Brillion (Needham et al. 1935), and fly fishermen have long recognized the importance of mayflies in the diets of game fishes.

The order is represented in North America by ten families (Burks 1953); many of which have representatives in the American Southwest. Mayflies are generally considered to be pollution intolerant and are important as pollution indicators (Gaufin and Tarzwell 1952).

Life history studies are needed to help ecologists model communities and assess energy flow. Research into the life history and ecology of mayflies is beginning to accumulate, especially from more northern latitudes. Lehmkuhl has described life cycle events for _Rhithrogena_ _morrisoni_ Banks (1970) and several species of _Paraleptophlebia_ (1971) from Oregon; he has made similar notes on _Baetisca_ (1972) and _Baetis_ _bundyi_ Lehmkuhl (1973) from the western and artic regions of Canada respectively. Clifford (1969, 1970) has worked out detailed life histories for several Ephemeroptera from Canada. Macan (1957 a & b, 1961) and Elliott (1967) have reported the life histories and seasonal growth of several species of mayflies from English streams. Jazdzewska (1971, 1972) indicated feeding habits, life history events, and distributions for several species of mayflies from Poland. Lavandier (1971) described life cycles, emergence and hatching for four species of mayflies from the central Pyrenes. Minshall (1967) reported the life history and ecology of *Epeorus pleuralis* Banks from Kentucky. *Leptophlebia vespertina* (L.) and *L. marginata* (L.) life cycles from a North Wales lake were elucidated by Brittain (1972). Kjellberg (1972) gave a detailed account of the life history of *Leptophlebia vespertina*, with production estimates, from a tarn in Sweden.

Life history and/or ecological studies of mayflies from more southern Neartic latitudes are generally lacking. Berner (1959) and Pescador (1973) have studied mayfly life histories in Florida. Poole (1973) and Cloud and Stewart (1974) reported on drift and vertical stratification respectively of Ephemeroptera and other benthic macrobenthos, including *Neochoroterpes mexicanus* Allen, from the Brazos River, Texas.

Production estimates are becoming an important aspect of ecological studies of aquatic animals (Waters 1973) because they give a quantitative estimate of how much energy a population contributes to the rest of the community. Production estimates for lotic macrobenthos have been arrived at by several different methods. Ricker and Allen (1946, 1949), Allen (1951), Anderson and Hooper (1956), and Hynes and Coleman (1968) have all devised or utilized methodologies for estimating annual production for aquatic animals. All of these methods were utilized by Waters and Crawford (1973) in their paper on *Ephemerella subvaria* McDunnough production. Other excellent reports of stream mayfly production include: Waters (1966) (*Baetis vagans* McDunnough) and Pearson and Kramer (1972) (*Baetis bicudatus* Dodds).

Mayflies occupy a very important trophic position in lotic communities. Although extensive food habits studies are generally lacking, the few definitive papers, including Moon (1938), Jones (1950), Brown (1960), Edmunds (1960), Chapman and Demory (1963), and Gilpin and Brusven (1970), indicate that they are herbivore-detritivores only occasionally ingesting animal matter.

No comprehensive life cycle--ecological studies have been made of any major southwestern United States mayfly species. Recent studies on the Brazos River below Possum Kingdom Dam in Texas have established a recently described leptophlebiid, *Neochoroterpes mexicanus* Allen, as the dominant mayfly. This species makes up ca. 10% of the mean monthly standing crop, is a dietary component of carnivorous insects and fishes (Stewart et al. 1973, Rhame 1973, Vaught and Stewart 1974, and Stewart et al. unpublished data) and is predominant in the drift (Cloud and Stewart 1974). The need, therefore, to thoroughly elucidate the life cycle of this species, with the advantage of collaboration with other members of a team investigating associated riverine insects, established the basis for this research. Major objectives were (1) to elucidate the life cycle with special emphasis on nymphal development, (2) to examine food habits and trophic interrelationships and (3) to determine seasonal abundance and productivity.

Early in the study, reared specimens tentatively identified as *Thraulodes* or *Choroterpes* were sent to R. K. Allen of California State University at Los Angeles. He confirmed all specimens as the new species (in a new subgenus) *Neochoroterpes mexicanus* for which he was preparing a manuscript and description. This was, therefore, an unique opportunity to study an apparently successful endemic Southwestern Neartic species of mayfly immediately subsequent to its discovery.

The study area was a large uniform riffle located approximately 20 miles downstream from Possum Kingdom Reservoir in Palo Pinto County, Texas, immediately above Texas State Highway 4 Bridge. This riffle has been described in detail by Stewart et al. (1973), Rhame (1973), Cloud and Stewart (1974), and Vaught and Stewart (1974).

CHAPTER II

MATERIALS AND METHODS

Standing crops, seasonal growth and voltinism, nymphal sex ratios, instar analysis and production estimates were derived from quantitative samples taken with a modified Hess Square Foot Sampler with a bag mesh size of 158 microns. Three samples were taken semi-monthly from Nov., 1971, to Jl., 1972. Large spates on the river in Sept. and Oct., 1971, and Aug., 1972, resulted in only one sample period during those months.

Standing crop and seasonal growth and voltinism were determined from the above samples preserved in 70% isopropanol. Head capsule length, from the back of the head to the clypeo-labral membrane, and pronotum width (Clifford 1970) were measured with a calibrated ocular micrometer. Generations were determined from the observed seasonal growth cycle and from emergence data obtained with a light box (Stewart et al. 1970 and Rhame 1973) run semi-monthly from Mar.--Sept., 1973, and monthly in Jan., Feb., and Oct.--Dec., 1973.

Size-frequency histograms were constructed for instar analysis, and interpretation was made utilizing the methods of Cassie (1954) and Janetschek (1967). The Cassie method involved plotting cumulative frequences from the size-frequency histogram on probability paper. Modes appeared as sudden increases in per cent frequency, while inflections indicated gradation from one 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 indicate instar modes. Harper (1973) employed this method in studies of stonefly nymphal development. To supplement these data, to help clarify instar separation, and to measure actual size changes between particular instars, field-collected nymphs were reared in styrofoam cups containing 400 ml of river water and were held in the laboratory at temperatures and photoperiods similar to those at the river at the time of capture.

Production was estimated by the Hynes method (Hynes and Coleman 1968) as modified by Hamilton (1969) and utilized by Waters (1973). All nymphs of each predetermined instar were dried in a Grieve Model LO-200C Drying Oven for 12 hr at $67 \pm 1^{\circ}C$, 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 (1 mm mesh size). Nymphs were collected ca. 4 pm and within 1 hr 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 et al. 1954) and examined microscopically at 100x magnification. Five random fields were examined from each gut, and area approximations were expressed in ASU using a calibrated Whipple Disc with a field of view .74 x .74 mm. Taxonomic determination of algae ingested was supplemented 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 environmental conditions for the time of nymphal collection. Diatoms were prepared for identification as outlined by the American Public Health Association (1973).

Subimago sex ratios, size and fecundity were determined from light box samples already described. Egg counts were made seasonally by placing females in Palmer Counting Cells, cutting off the last abdominal segments and teasing out the eggs. Subimagoes 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 successfully obtained from two females collected in the field during the act of oviposition. The eggs were placed in styrofoam cups containing ca. 300 ml of river water, were kept constantly aereated 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 subimagoes preserved in 70% isopropanol. They were dissected out and soaked for 4 days in water and then mounted in CMC-10.

An attempt was made to rear N. mexicanus from small field-collected nymphs in an artificial stream devised and described by Rhame (1973). Field-collected nymphs of N. mexicanus were kept under simulated photoperiod in the laboratory and observed for phototrophism.

CHAPTER III

RESULTS AND DISCUSSION

Subimago

Subimagoes emerged from late afternoon until ca. 1 hr after sunset over the extended period from late Mar. to Nov., 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, utilizing it as a raft.

Individuals which emerged in quiet water along the shore took immediate flight inland. Those which emerged out in the current floated downstream ca. 5 m, took flight in a lateral, upstream direction before alighting on the water, 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. Subimagoes molted and became adults shortly before dawn on the day following emergence; the subimagal life span was therefore ca. 12 hr.

A seasonal size variation was exhibited in the subimagoes. Mean total body length for 98 individuals was greatest in Apr. (male 7.15 mm, female 8.78 mm), least at the end of summer in Sept. (male 5.47 mm, females 5.47 mm) and increased again by Nov. (male 6.10 mm, female 6.58 mm). Seasonal size variations for mayfly nymphs, subimagoes and imagoes have been reported by several authors (Ide 1935, Macan 1957a, 1961, Elliott 1967, and Clifford 1970). Rhame (1973) observed a seasonal size difference in adult Hydrosyche 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 N. mexicanus. Average number of eggs/female for four females was 1,645, 809 and 1,134 in Apr., Sept., and Nov. 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 male: 1.0 female and 1.0 male: 1.2 female in spring and summer--fall for 320 and 229 individuals respectively.

Adults

Adult N. mexicanus began forming large diffuse swarms over land about 0.5 hr 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. Swarms were greatly affected by wind, and males seemed to alight upon rocks, rather than vegetation, during wind gusts or on days when wind was high. Only males 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 behavior continued into mid-afternoon. Adults reared in the laboratory lived less than 12 hr, suggesting that mating and oviposition occur only on the first day after shedding the subimagal exuvium.

Actual mating was similar to that described by Needham et al. (1935) for Paraleptophlebia, Siphlonurus, and Cinygmula, and by

Lehmkuhl and Anderson (1971) for *Paraleptophlebia debilis* Walker. A typical example was an observation of mating in early Oct., 1973, ca.7:30 am. A female flew into a swarm of males ca. 4 m above the ground and was grasped by a male. The two 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. Numerous "collisions" between males and females were observed that were similar to observations reported by Minshall (1967) on the mating of *Epeorus pleuralis*. However, these were only instantaneous contacts and apparently did not result in mating.

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 *Ephemerella rotunda* Morgan (Needham et al. 1935) in that all eggs were deposited at once; however, variations from that species included: (1) *N. mexicanus* did not fly off the water after the oviposition descent, and (2) eggs were not carried in an external mass (as is also the case in many members of the family Caenidae). Spent females were caught floating downstream to the riffle after observed oviposition usually within 1 hr of sunrise. On one occasion, two 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 female indicated she was void of eggs. Eggs were successfully obtained from the second female by placing her in a closed cup of river water.

Egg

Eggs from subimagoes 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 .18 mm x .12 mm diameter.

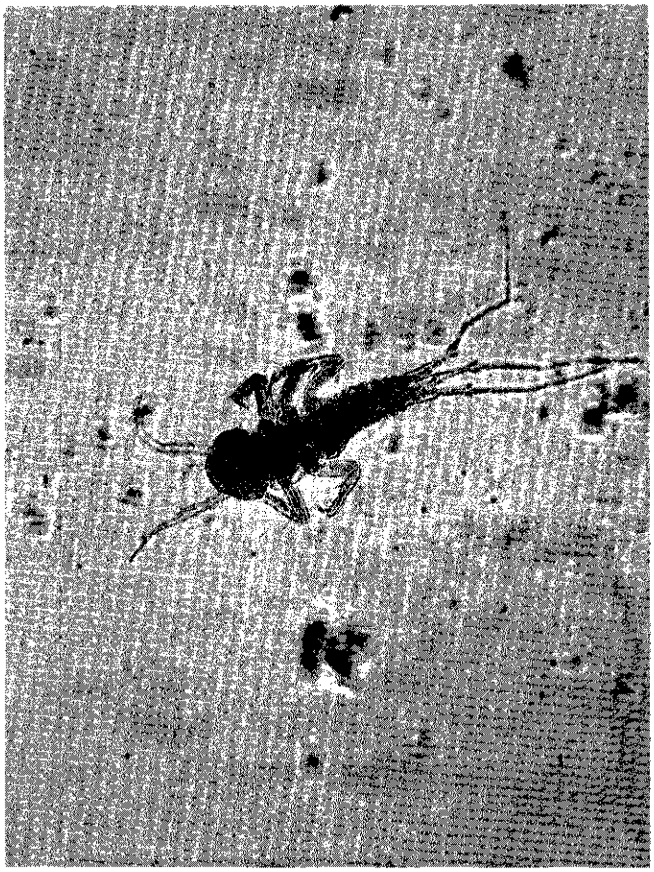
The chorionic sculpturing consisted of many raised sucker-like discs as shown in Fig. 1C (hatched egg); a magnified view of one of these protuberances is shown in Fig. 1D. These may be accessory attachment structures as hypothesized by Koss (1968) for Paraleptophlebis debilis. Peg-like attachment structures, as in Leptophlebia sp. (Koss 1968), were also present and are shown in Fig. 1B. 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. I did not observe any micropylar device; otherwise the eggs fit the family characters of Koss (1968).

Incubation required 13-15 days at 25±1°C and simulated natural photoperiod. Eclosion was not observed although a characteristic longitudinal tear was exhibited by hatched eggs (Fig. 1C).

Nymph

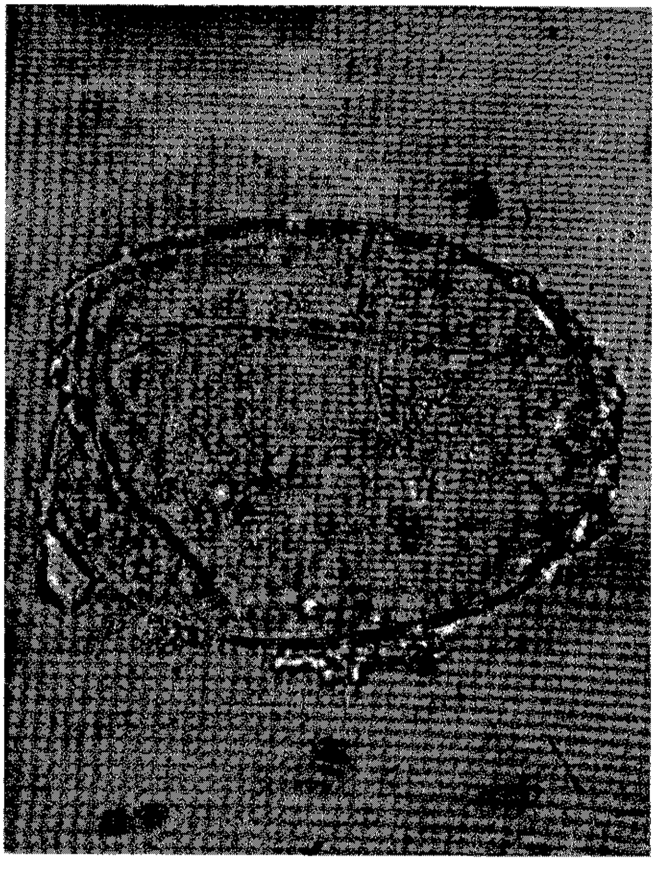
Total body length (excluding cerci) and head length of first instar nymphs were about .45 mm and .09 mm respectively. Early nymphs were transparent, had no gills and exhibited 5-segmented antennae and cerci. Three ocelli were apparent, and the compound eyes were indistinguishable. Rearing of first instars, in aereated styrofoam cups, at simulated temperature and photoperiod was unsuccessful; however they were observed to feed on filaments of blue-green algae. A first instar is shown in Fig. 1A.

Fig. 1. A. First instar of *N. mexicanus* (100x). B. Tangenital view of *N. mexicanus* egg with peg-like attachment structures (AS) (1,000x). C. Hatched egg with chorionic sculpturing and longitudinal tear (450x). D. Chorionic protuberance (P) surrounded by attachment structures (1,000x).

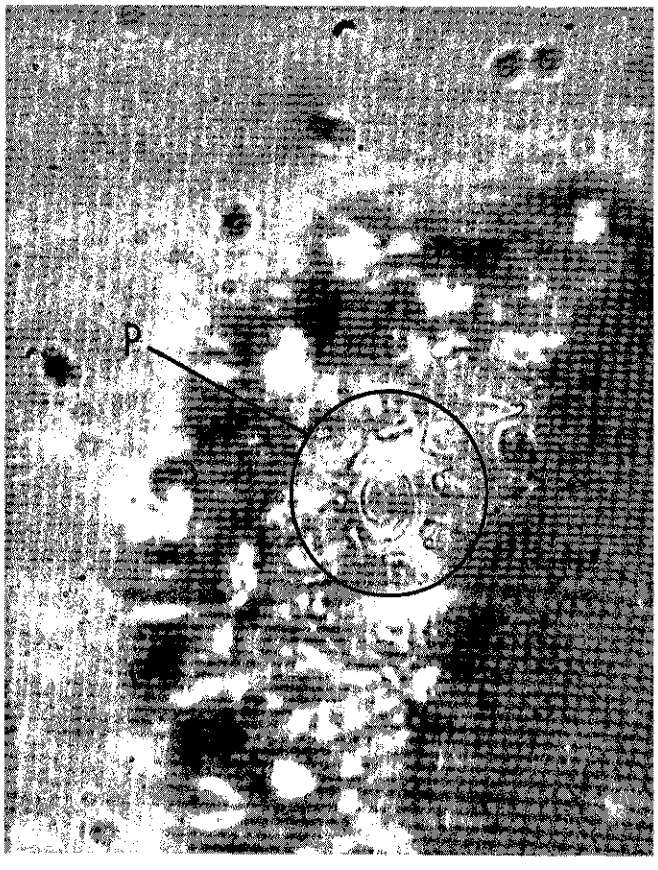


A

B



C



D

Nymphs could be sexed at the seventh and succeeding instars by the presence of 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 1,264 nymphs beyond the sixth instar was 1.0 male: 1.16 female; the ratio of 24 black wing pad individuals was 1:1. These data, and those for sexed subimagoes, indicated that the Brazos population exhibited an approximate 1:1 ratio. Tjonneland (1969, 1972) discussed some factors that might influence sex ratios determined from light trap catches, including a cyclic change through the night in male-female emergence ratio. It would seem desirable to determine ratios from both nymphal and adult populations where possible.

Seasonal Cycle.-Seasonal growth of N. mexicanus is depicted in Figs. 2 and 3. The absence of smaller sizes of nymphs in summer generations might be due to vertical stratification of the species. Poole (1973) showed that large numbers of these smaller sizes were in sub-surface layers during Jl.--Oct., 1972. Absence of these smaller sizes in Aug. was probably due to sampling error, since only 36 N. mexicanus were recovered from 3 ft^2 of riffle area. Spates in Aug. and Sept., 1971, might account for the absence of these small sizes in the Sept. sample. Poole (1973) showed that over 90% of N. mexicanus were 10-20 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. 2 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. 3) showing seasonal distribution of size classes allowed a more discriminating interpretation since gaps between size classes tended to indicate separation of generations.

From Figs. 2 and 3, a three generation seasonal cycle with considerable brood overlap within and between generations was suggested for N. mexicanus during Sept., 1971--Aug., 1972. Additional observations of emergence during the calendar year 1973 corraborated these findings. Drift data of Cloud and Stewart (1974) also indicated three generations for this species, with peaks in emergence occurring in Apr., May, Jl., and Sept.

Adults that emerged in late Mar. and Apr. laid eggs; nymphs from their eggs grew through the spring and early summer to a Jun.-Aug. emergence, peaking in Jl. (Fig. 3). Adults which emerged in May produced nymphs that grew through the summer to emerge Sept.-Nov., with the peak in Oct. The Jun.-Aug. (Jl. peak) adults contributed a brood that grew through late summer and fall with an optional emergence in Dec., dependent on temperature conditions. Data (Figs. 2, 3) from Dec., 1971, indicated an emergence in Dec., but observations and Environmental Science Services Administration air temperature data in Dec., 1973, indicated no emergence. Average monthly temperature for Dec., 1973, was 1.7°C colder than that of Dec., 1971. Daily high temperature in Dec., 1973, did not exceed 0°C for 15 days, whereas in Dec., 1971, this condition prevailed for only 5 days. The fall (Oct.) emerging adults contributed the major overwintering nymphal brood resulting in the spring emergences. With this scheme, one clear overwintering generation with two broods and two summer generations (one reaching a peak in Jl., and the other composed of two broods peaking in Oct. and Dec.)

Fig. 2. Seasonal head capsule growth of 1,817 N. mexicanus nymphs: vertical line=range, horizontal line=mean, vertical bar= standard deviation. Numbers above each date = water temperature (°C).

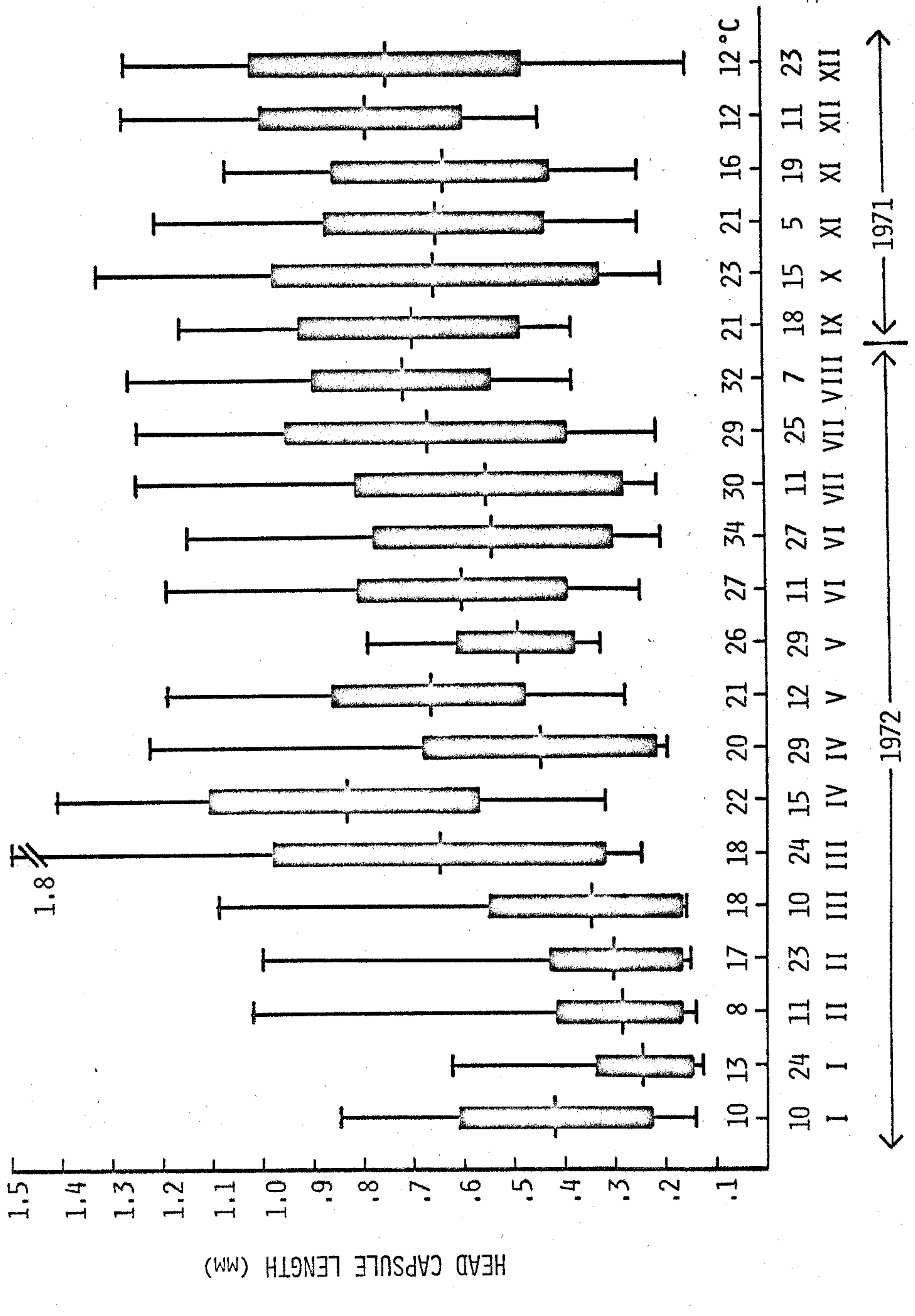
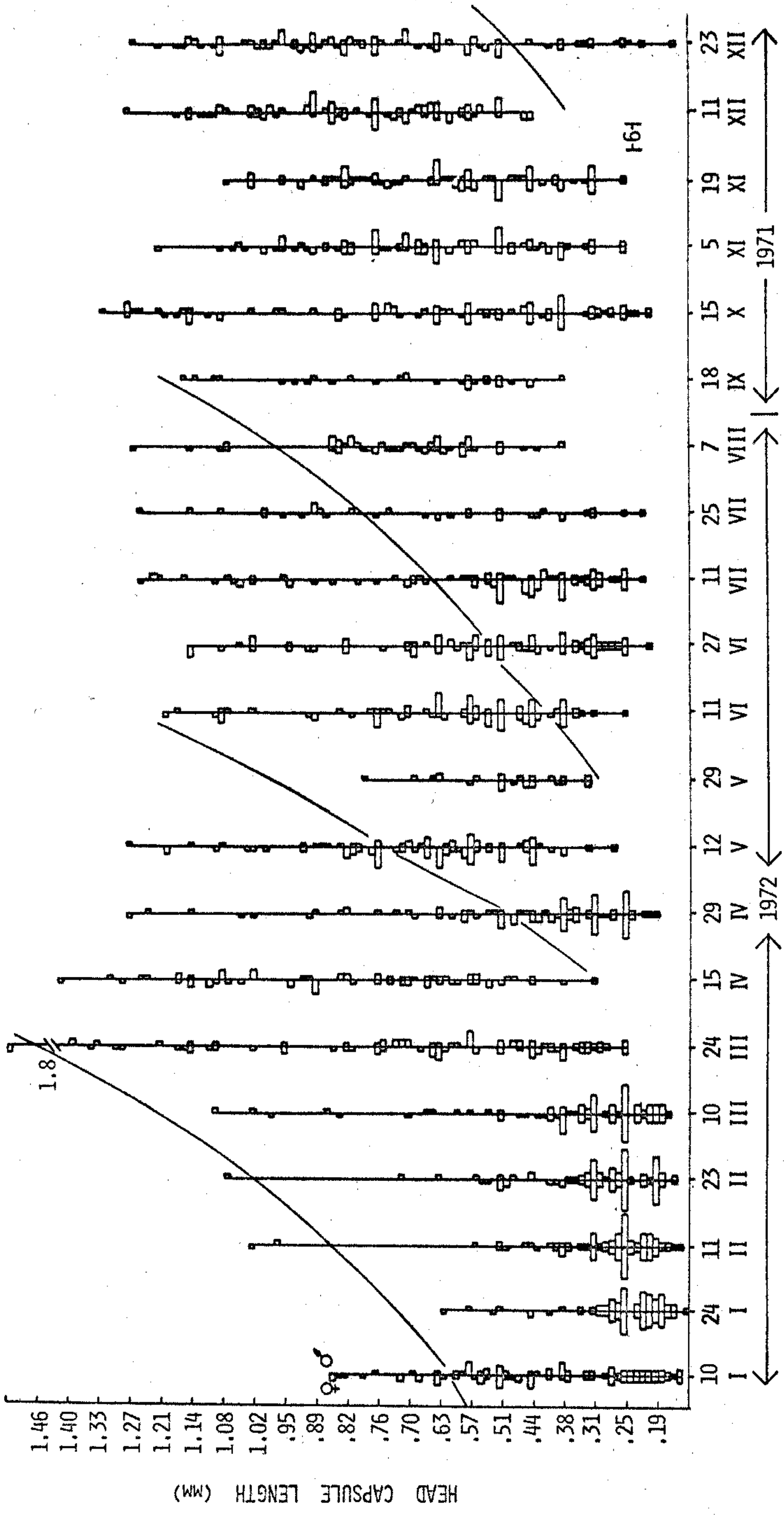

HEAD CAPSULE LENGTH (MM)
1.5
1.4
1.3
1.2
1.1
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
1.8
12°C 23 XII
12 11 XII
16 19 XI
21 5 XI
23 15 X
21 18 IX
32 7 VIII
29 25 VII
30 11 VII
34 27 VI
27 11 VI
26 29 V
21 12 V
20 29 IV
22 15 IV
18 24 III
18 10 III
17 23 II
8 11 II
13 24 I
10 10 I
1971
1972

Fig. 3. Size frequency distribution of the head capsule lengths in each sample. Curved lines delimit generations. N = 1,817.
⊢6⊣ = length of bar = to 6 individuals.


HEAD CAPSULE LENGTH (MM)
1.46
1.40
1.33
1.27
1.21
1.14
1.08
1.02
.95
.89
.82
.76
.70
.63
.57
.51
.44
.38
.31
.25
.19
1.8
♀♂
10 I
24 I
11 II
23 II
10 III
24 III
15 IV
29 IV
12 V
29 V
11 VI
27 VI
11 VII
25 VII
7 VIII
18 IX
15 X
5 XI
19 XI
11 XII
23 XII
1972
1971

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 diffenence was a longer fall emergence for N. mexicanus. Obviously, this complex multivoltine 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 conditions are common among members of the family Baetidae, even from northern latitudes (Needham et al. 1935, Macan 1957a, 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. N. mexicanus seems to fit this theory very nicely, even though its populations are situated in a southern temperate latitude. The temperature moderating effect of the upstream Possum Kingdom Reservoir, with its leakage of hypolimnion water, might help explain the apparent success of this species in this habitat. The temperate photoperiod and colder winter water temperatures (down to 7°C) probably account for the prolongation and synchronization of the more distinct winter generation. Rhame (1973) found a similar multivoltine condition for the Caddisfly Hydropsyche simulans on this same study site.

Development.-Determination of nymphal instars for N. mexicanus by the methods of Cassie (1954) and Janetschek (1967) were given in Figs. 4-7 and

8-11 respectively. Analysis by the Cassie (1954) method indicated that nymphs underwent 16 and 19 instars for winter and combined summer generations respectively (Figs. 4-7) with no observed sex differences. Analysis by the Janetschek (1967) method indicated the same 16 and 19 instars for the winter and combined summer generations (Figs. 8-11) with no sex differences.

Supplemental rearing of field collected nymphs of larger sizes, eg. noting change in head capsule lengths with observed molts, aided interpretation of data from the above two 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. Complete rearing from egg to adult under simulated natural conditions, as attempted unsuccessfully in the laboratory artificial stream, would, of course, have precluded the need to make these extensive analyses. 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 holometabodus larvae such as Diptera by plotting one linear measurement (head capsule length) against another (pronotum width) was attempted, but no clear separation of instars resulted.

Vaught and Stewart (1974) show a sexual dimorphism in instar development in the stonefly _Neoperla_ _clymene_ Newman. Considerable intraspecific variation due to sex, physical and other biological conditions

Fig. 4. Instar analysis of 677 N. mexicanus females of the overwintering generation by the Cassie method.

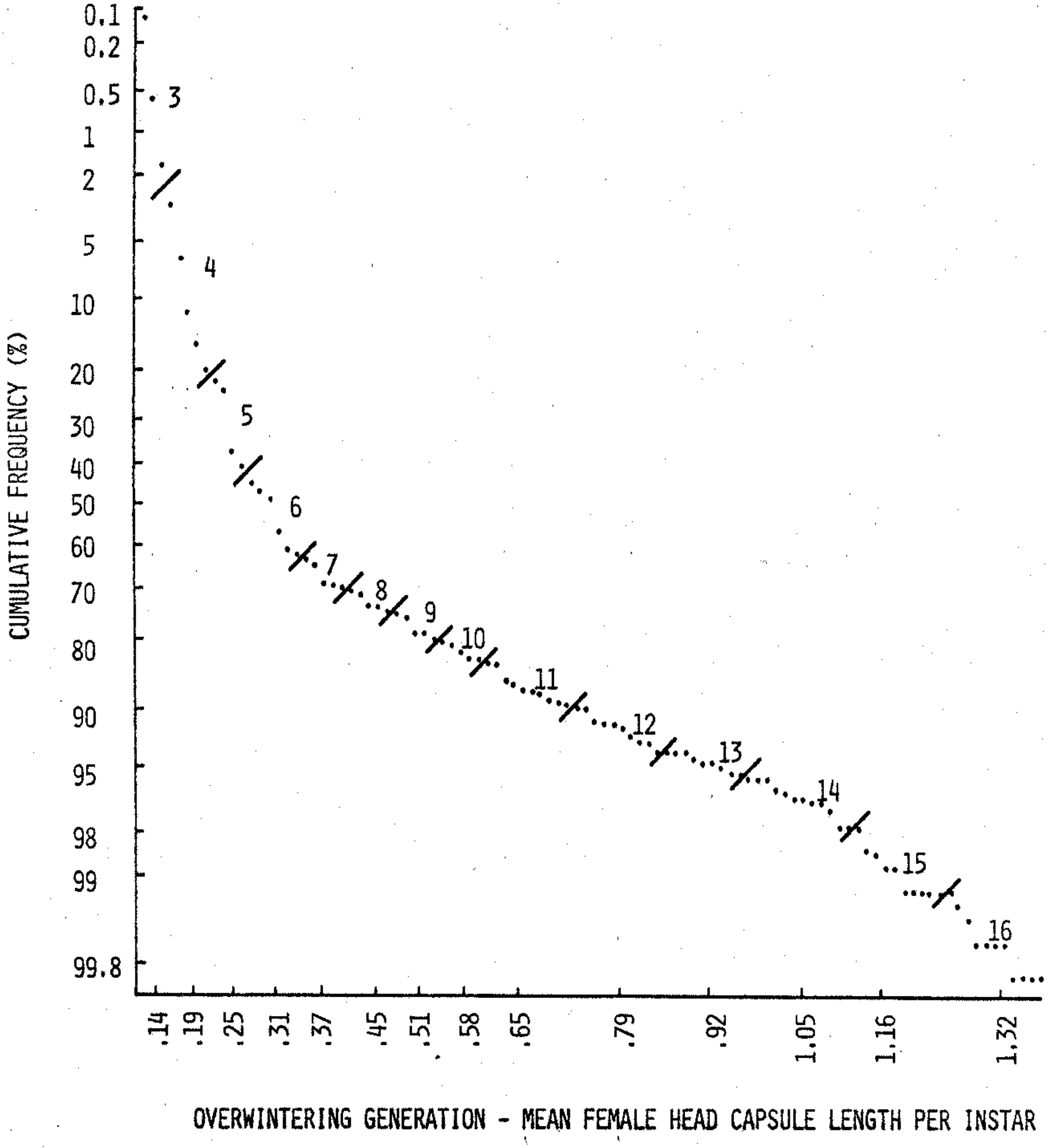
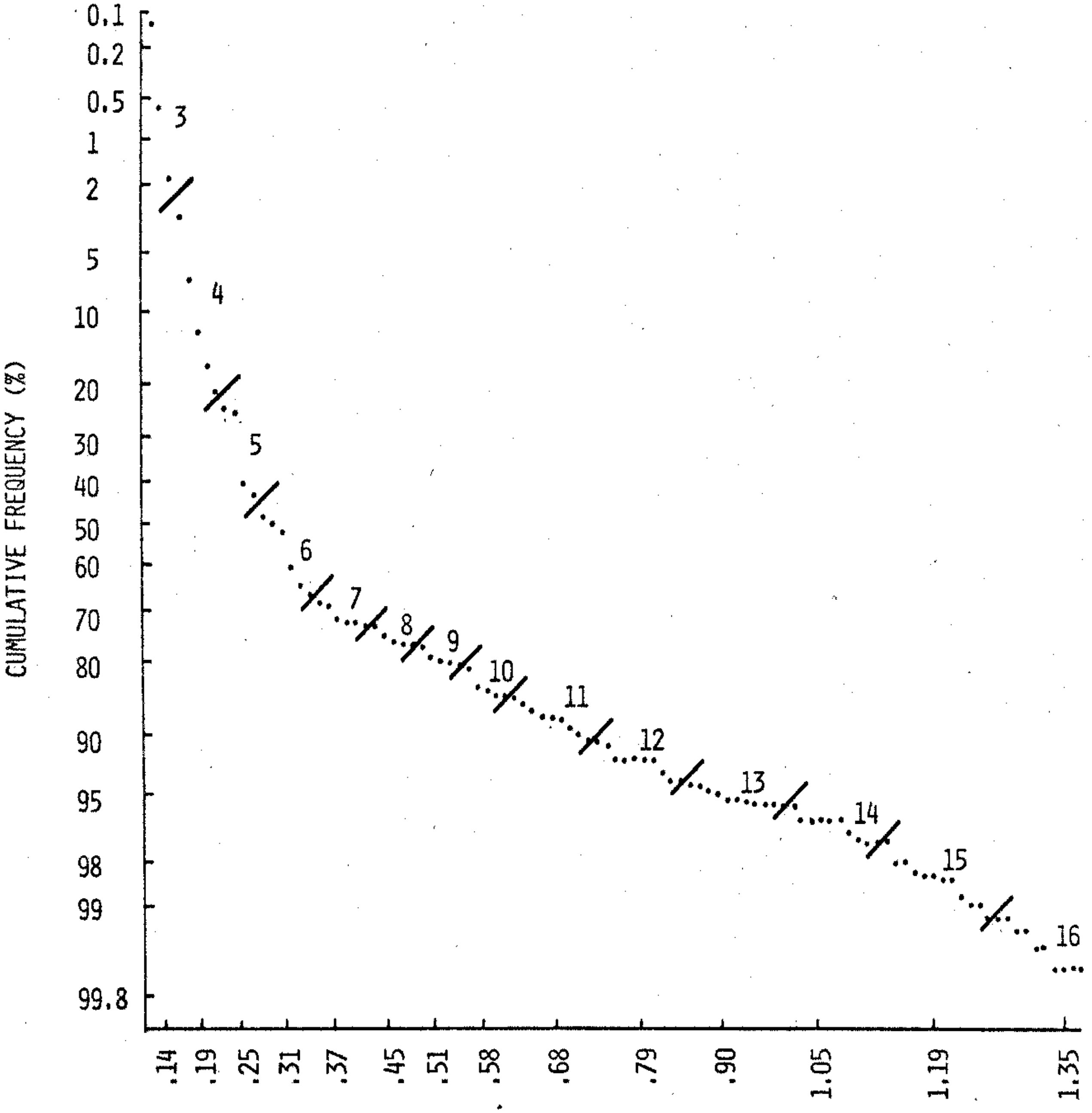

CUMULATIVE FREQUENCY (%)
0.1
0.2
0.5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99.8
3
4
5
6
7
8
9
10
11
12
13
14
15
16
.14
.19
.25
.31
.37
.45
.51
.58
.65
.79
.92
1.05
1.16
1.32
OVERWINTERING GENERATION - MEAN FEMALE HEAD CAPSULE LENGTH PER INSTAR

Fig. 5. Instar analysis of 632 *N. mexicanus* males of the overwintering generation by the Cassie method.



OVERWINTERING GENERATION - MEAN MALE HEAD CAPSULE LENGTH PER INSTAR

Fig. 6. Instar analysis of 548 _N_. _mexicanus_ females from the combined summer generation by the Cassie method.

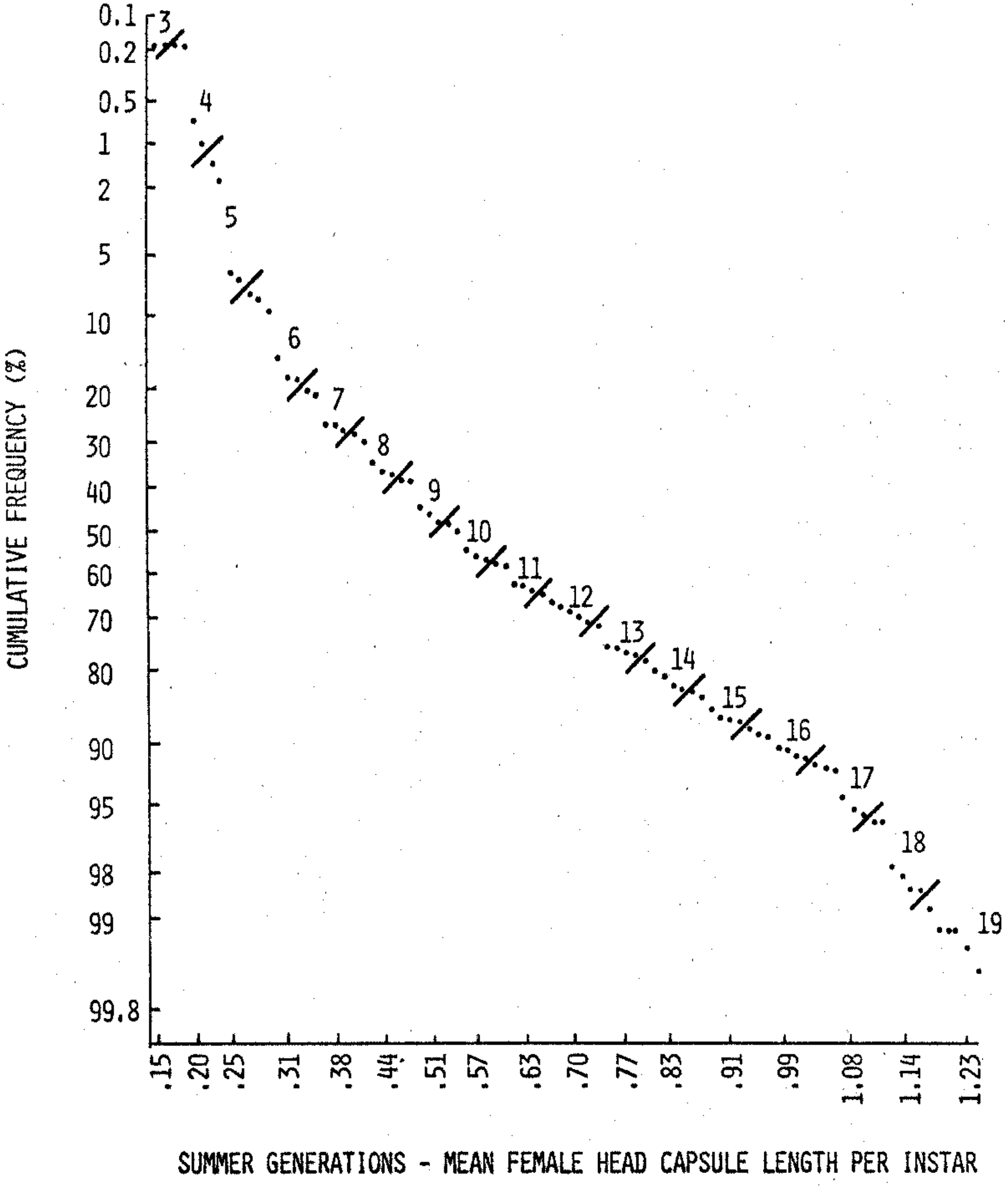

CUMULATIVE FREQUENCY (%)
0.1
0.2
0.5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99.8
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
.15
.20
.25
.31
.38
.44
.51
.57
.63
.70
.77
.83
.91
.99
1.08
1.14
1.23
SUMMER GENERATIONS - MEAN FEMALE HEAD CAPSULE LENGTH PER INSTAR

Fig. 7. Instar analysis of 509 N. mexicanus males from the combined summer generations by the Cassie method.

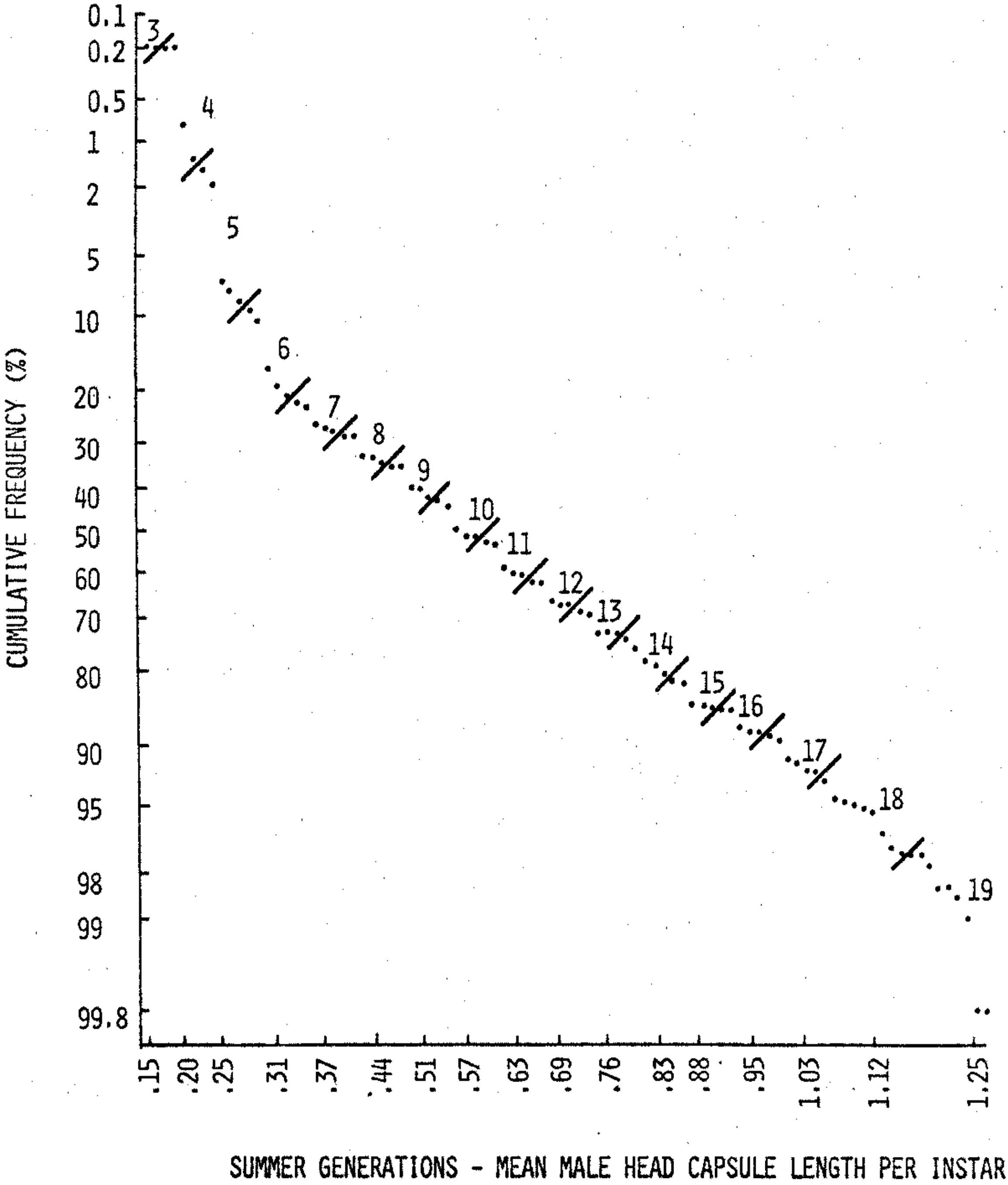

CUMULATIVE FREQUENCY (%)
0.1
0.2
0.5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99.8
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
.15
.20
.25
.31
.37
.44
.51
.57
.63
.69
.76
.83
.88
.95
1.03
1.12
1.25
SUMMER GENERATIONS - MEAN MALE HEAD CAPSULE LENGTH PER INSTAR

Fig. 8. Instar analysis of 677 _N. mexicanus_ females of the overwintering generation by the Janetschek method. A. Size frequency histogram of head capsule lengths. B. Running mean of five of the frequences. C. Modal periodicity of instars.

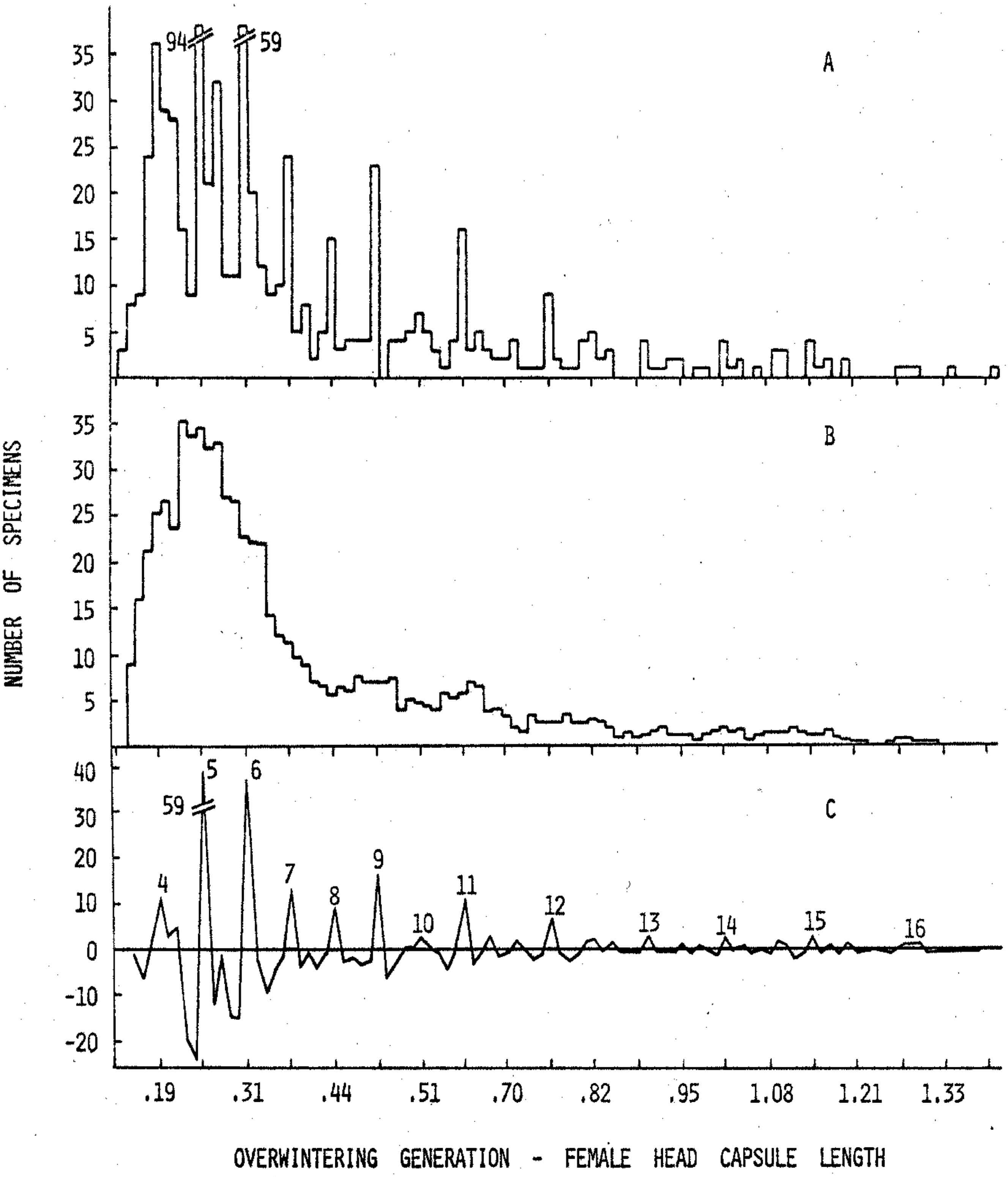

A
B
C
94
59
59
35
30
25
20
15
10
5
40
0
-10
-20
4
5
6
7
8
9
10
11
12
13
14
15
16
NUMBER OF SPECIMENS
.19
.31
.44
.51
.70
.82
.95
1.08
1.21
1.33
OVERWINTERING GENERATION - FEMALE HEAD CAPSULE LENGTH

Fig. 9. Instar analysis of 632 N. mexicanus males of the overwintering generation by the Janetschek method. A. Size frequency histogram of head capsule lengths. B. Running mean of five of the frequences. C. Modal periodicity of instars.

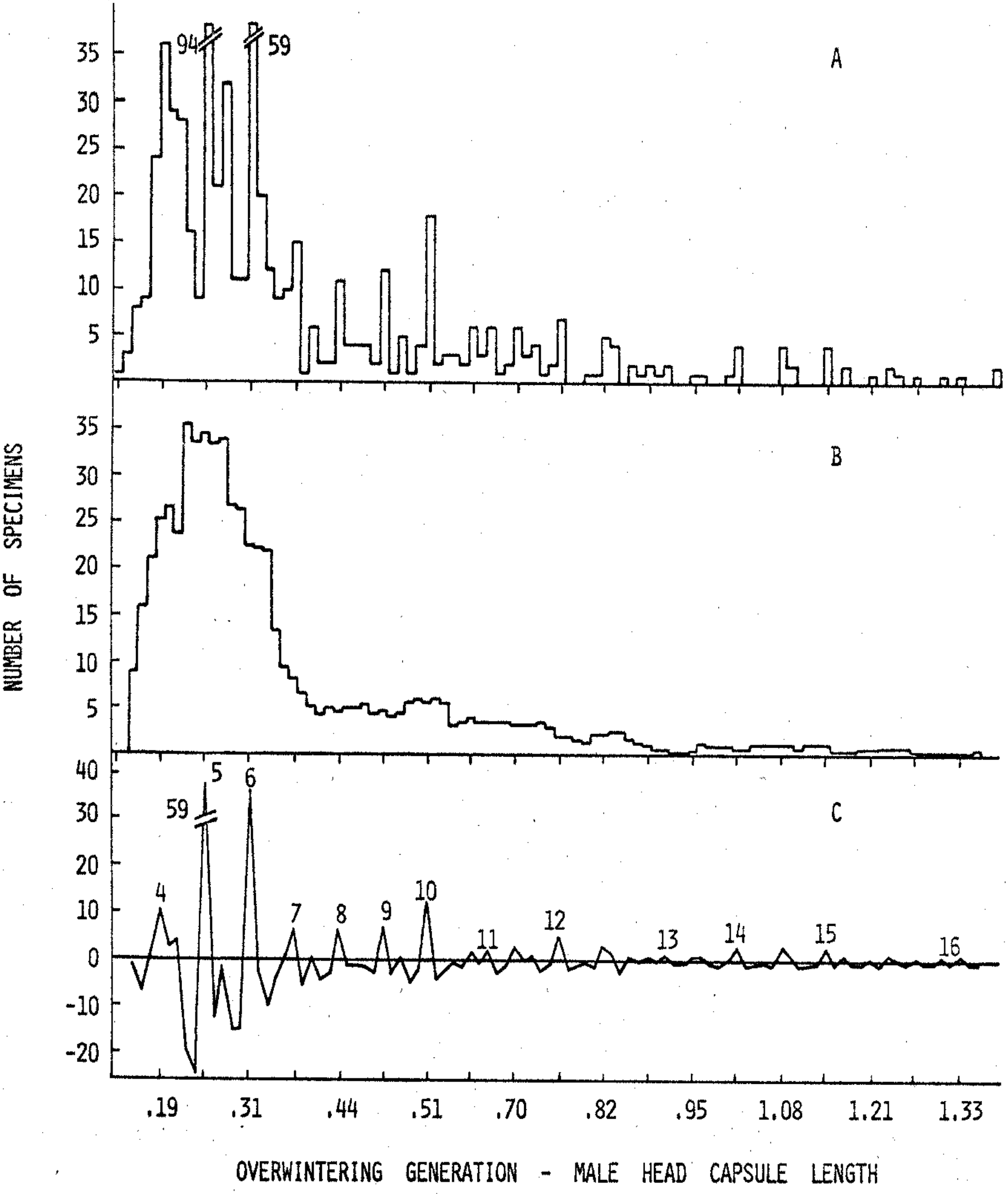

A
B
C
NUMBER OF SPECIMENS
35
30
25
20
15
10
5
94
59
40
0
-10
-20
4
5
6
7
8
9
10
11
12
13
14
15
16
.19
.31
.44
.51
.70
.82
.95
1.08
1.21
1.33
OVERWINTERING GENERATION - MALE HEAD CAPSULE LENGTH

Fig. 10. Instar analysis of 548 N. mexicanus females from the combined summer generations by the Janetschek method. A. Size frequency histogram of head capsule lengths. B. Running mean of five of the frequences. C. Modal periodicity of instars.

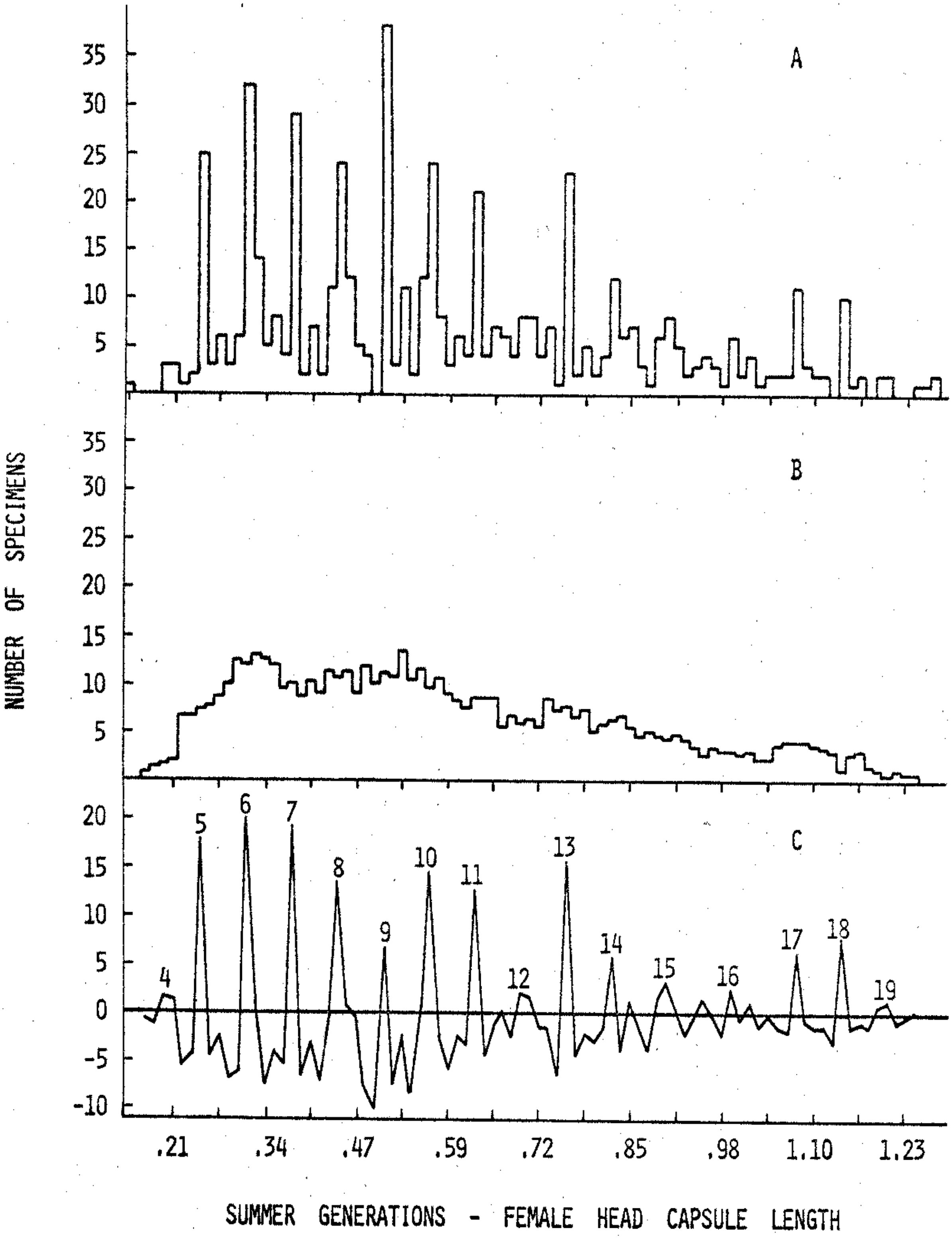
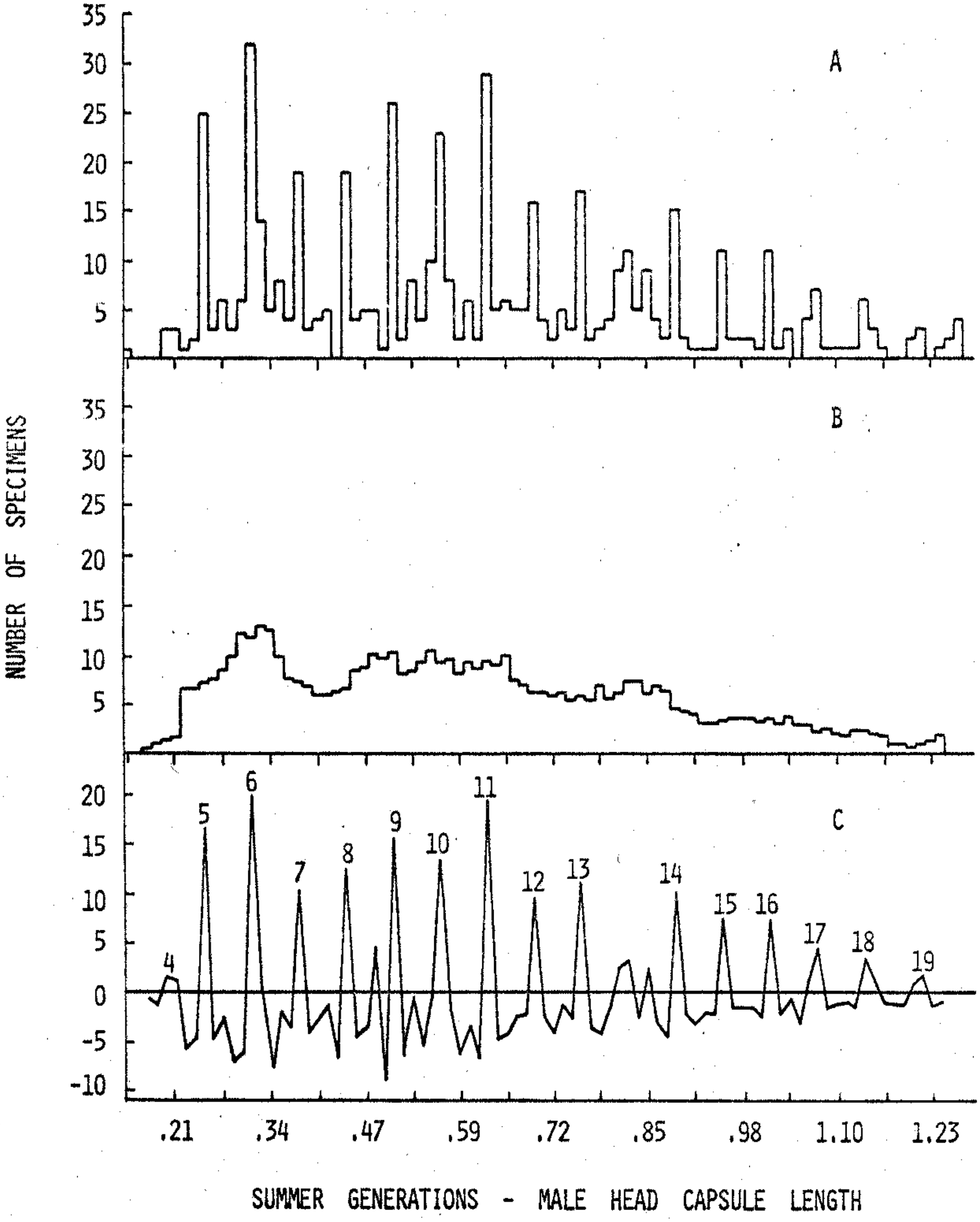

A
B
C
NUMBER OF SPECIMENS
35
30
25
20
15
10
5
35
30
25
20
15
10
5
20
15
10
5
0
-5
-10
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
.21
.34
.47
.59
.72
.85
.98
1.10
1.23
SUMMER GENERATIONS - FEMALE HEAD CAPSULE LENGTH

Fig. 11. Instar analysis of 509 <u>N.</u> <u>mexicanus</u> males from the combined summer generations by the Janetschek method. A. Size frequency histogram of head capsule lengths. B. Running mean of five of the frequences. C. Modal periodicity of instars.


A
B
C
35
30
25
20
15
10
5
0
-5
-10
NUMBER OF SPECIMENS
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
.21
.34
.47
.59
.72
.85
.98
1.10
1.23
SUMMER GENERATIONS - MALE HEAD CAPSULE LENGTH

probably occurs in hemimetabolous insects whose development spans a large number of molts.

The conformance of N. mexicanus to Dyar's (1890) rule was tested by plotting logs of the means of the proposed instars, as determined above, against instar numbers. Figs. 12-15 showed a slightly curved line, indicating Dyar's rule was not strictly adhered to. Harper (1973) found a similar growth characteristic in the hemimetabolous stonefly Nemoura trispinosa Claassen.

Seasonal effect on instar development could be seen in Figs. 12 and 13. 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 Figs. 14 and 15. In all these figures, the head capsules of the reared first instar was included, and the unsampled second instar was estimated, as per Harper (1973). Figs. 4, 5, 8, and 9 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. Growth progression was somewhat reduced in that species subsequent to the eleventh instar, when mean factors were 1.08 (wing pad length) and 1.01 (head capsule width).

Fig. 12. Head capsule length progression with successive *N. mexicanus* instars for females of the overwintering generation.
Open circle represents reared first instars;
X represents unsampled instar.

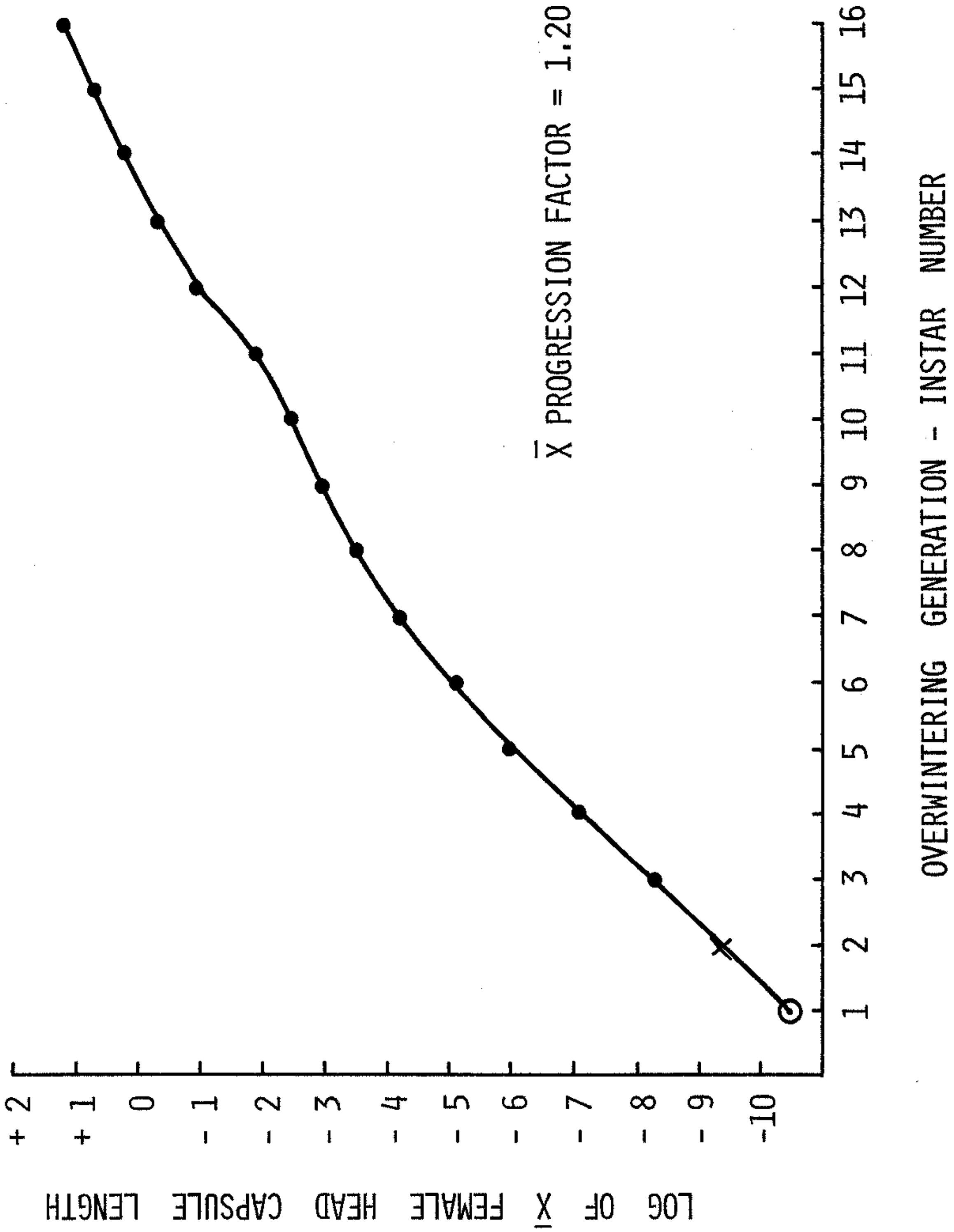

LOG OF $\bar{X}$ FEMALE HEAD CAPSULE LENGTH
+ 2
+ 1
0
- 1
- 2
- 3
- 4
- 5
- 6
- 7
- 8
- 9
-10
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
OVERWINTERING GENERATION - INSTAR NUMBER
$\bar{X}$ PROGRESSION FACTOR = 1.20

Fig. 13. Head capsule length progression with successive N. mexicanus instars for males of the overwintering generation.
Open circle represents reared first instars;
X represents unsampled instar.

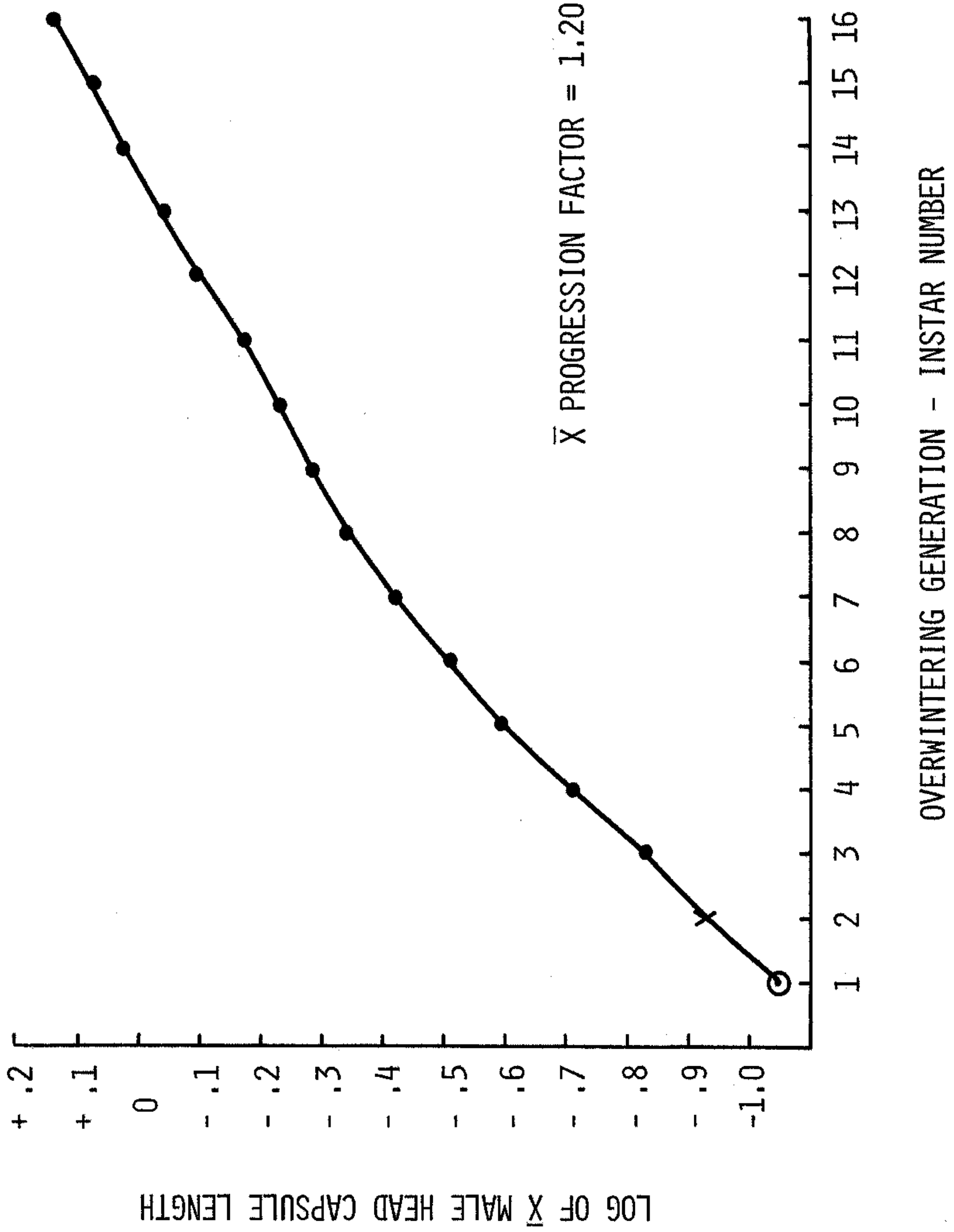

$\overline{X}$ PROGRESSION FACTOR = 1.20
OVERWINTERING GENERATION - INSTAR NUMBER
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
LOG OF $\underline{X}$ MALE HEAD CAPSULE LENGTH
+ .2
+ .1
0
- .1
- .2
- .3
- .4
- .5
- .6
- .7
- .8
- .9
-1.0

Fig. 14. Head capsule length progression with successive _N. mexicanus_ instars for females of the combined summer generations.
Open circle represents reared first instars;
X represents unsampled instar.

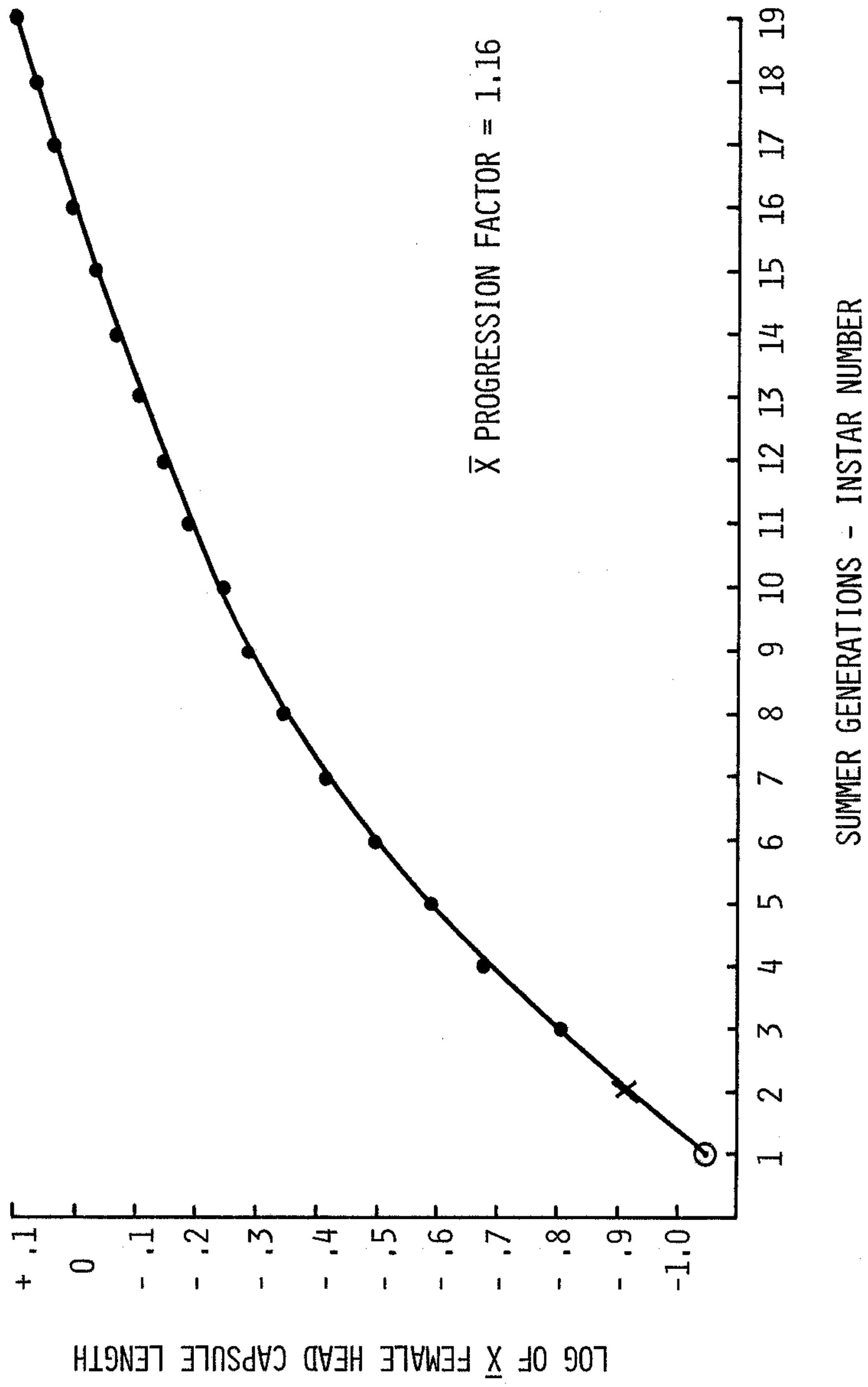
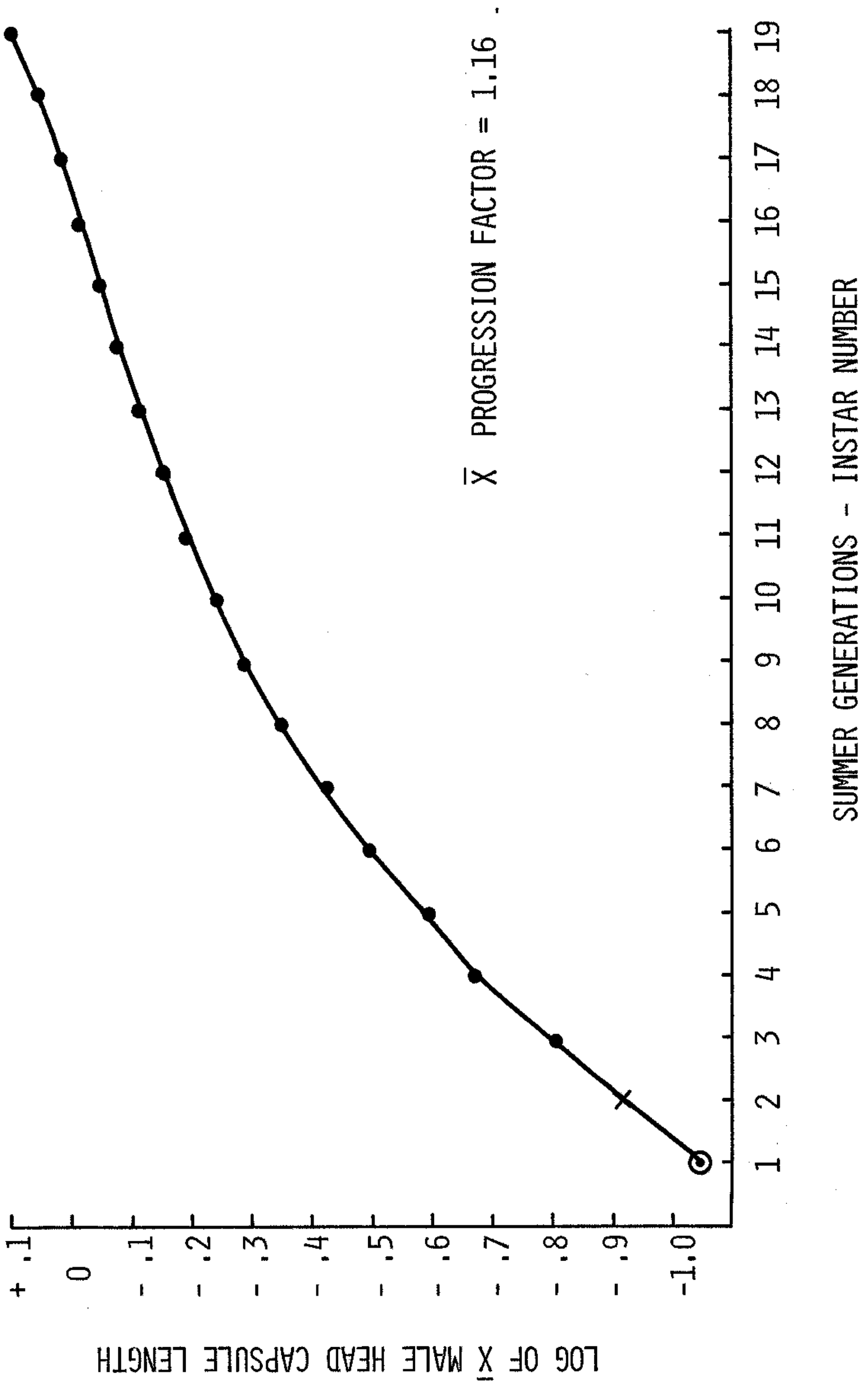

$\bar{X}$ PROGRESSION FACTOR = 1.16
LOG OF $\underline{X}$ FEMALE HEAD CAPSULE LENGTH
+ .1
0
- .1
- .2
- .3
- .4
- .5
- .6
- .7
- .8
- .9
-1.0
SUMMER GENERATIONS - INSTAR NUMBER
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19

Fig. 15. Head capsule length progression with successive *N. mexicanus* instars for males of the combined summer generations. Open circle represents reared first instars; X represents unsampled instar.


LOG OF $\bar{X}$ MALE HEAD CAPSULE LENGTH
+ .1
0
- .1
- .2
- .3
- .4
- .5
- .6
- .7
- .8
- .9
-1.0
SUMMER GENERATIONS - INSTAR NUMBER
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
$\bar{X}$ PROGRESSION FACTOR = 1.16

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 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 four species of Stenonema were fed only detritus.

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

Lowest algal consumption occurred in the fall and late summer (Table 1), which corresponded with the time of greatest detrital abundance (Jones 1950). 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 N. mexicanus nymphs between morning (within 1 hr sunrise) and afternoon (ca. 4 pm) samples (Table 1). Laboratory observations indicated that nymphs were negatively phototropic, so feeding is probably more cryptic during daytime hours, although no pattern of diel shifts in components ingested seemed to be evident. Chapman and Demory

Table 1

Seasonal Food Habits of 230 *Neochoroterpes mexicanus* Naiads
Average Number of ASU/Field[1]

Type of Algae	Sampling Date											
	Jan.		Feb.		Mar.		Apr.		May		Jun.	
	PM	AM	PM	AM[2]	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 Temperature Centigrade	10	7	11	-----	19	13	17	15	25	24	24	21
	Jl.		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	0.57
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 Temperature Centigrade	25	22	33	30	26	26	24	23	20	18	13	8

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[1] Five random fields/individual--10 individuals/sample

[2] No data due to flood conditions

(1963) found a similar diet, periodicity and negative phototropism in *Paraleptophlebia sp*.

Taxa found in the algal dietary food groupings of Table 1 were Greens--*Tetrahedron*, *Cladophora*, *Gloeocystis*, *Ankistrodesmus*, *Scenedesmus*, *Chlorocuccum*, *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-green--*Cyclotella*, *Denticula*, *Frustulia vulgeris*, *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 *N. 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) indicate 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, were observed numerous times to be apparently feeding on morning swarms of *N*. *mexicanus*. Stewart et al. (unpublished data) showed that *N*. *mexicanus* is a dietary constituent of the dusky (*Percina sciera*) and greenthroat (*Etheostoma lepidum*) darters on the study riffle. Associated riffle insects apparently also utilized *N*. *mexicanus* nymphs. Stewart et al. (1973) showed that *N*. *mexicanus* made up 2.2% of the Feb.--May diet of the hellgrammite *Corydalus cornutus*, which ingested a wide range of over 22 different organisms. Vaught and Stewart (1974) reported that *N. mexicanus* nymphs made up over 6% of the diet of the stonefly *Neoperla clymene*, and Rhame (1973) found that even the caddisfly *Hydropsyche simulans* took relatively large numbers of *N. 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, consequently, production are greater than in nearby typically unmodified sluggish and sometimes intermittent rivers. These conditions, and a sandy, silty bottom substrate, prevailed above the Possum Kingdom Reservoir, and based on USGS data, apparently also existed on the study site prior to closing of the Possum Kingdom Dam in 1941. A hypolimnion leakage of 10-15 cfs and erratic flows from the reservoir into the river, described by Stewart et al. (1973), Rhame (1973), Cloud and Stewart (1974), and Vaught and Stewart (1974), have prevailed since this closure. The resultant stability of minimal flow and temperature and the alteration of the substrate appear to have greatly increased available microhabitat and enhanced physical parameters for existence of local insects. A sand-silt substrate was again encountered a few miles below the study site.

Radford and Hartland-Rowe (1971) have concluded that damming of the Kananaskis River in Alberta has reduced the standing crop and species diversity of the river below the Pocaterra Dam because of extremes in flow conditions. Kroger (1973) showed that rapid changes in water level on the regulated Snake River below Jackson Lake Dam left some fish and benthic macroinvertibrates stranded. Fisher and La Voy (1972) showed that fluctuating water levels on the Connecticut River, due to hydroelectric power generation, may have prevented the establishment of normal benthic communities on periodically exposed areas. Lehmkuhl (1972), in a study on the Saskatchewan River below Gardiner Dam, showed that the moderating temperatures by the reservoir had reduced Ephemeropteran standing crops (when compared to an upstream station and a nearby creek) in this section of the river. He further concluded that, "all deep reservoirs in temperate climates (i.e., reservoirs that stratify thermally) that have a hypolimnion drain will cause similar downstream faunal depletion..."

Mean standing crop of N. mexicanus occurring on the bi-weekly (or monthly) sampling dates was 880/m^2; that for N. mexicanus and three species of Hydropsychidae (Rhame 1973) was 5,500/m^2, which was greater than any of the standing crops offered for comparison by Radford and Hartland-Rowe (1971).

Lateral migration of N. mexicanus to take advantage of newly wetted substrate was noted during the first four months of 1973. This was not observed by Kroger (1973) on the Snake River. The high standing crops and number of species found on this riffle would seem to argue against Lehmkuhl's supposition that all temperate thermally stratifying reservoirs with hypolimnion drains would produce depleted benthic fauna downstream from their dams. This disparity was apparently due to geography and climate and to the fact that, generally speaking, the fluctuations on the Brazos, although erratic, were not as great as on the Snake or Kananaskis Rivers. The Brazos endemic species were apparently not as stenothermic in their requirements as were the northern populations described above. The Brazos offered a good example of a modified stream being more productive than if it were unmodified.

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

The Hynes method was utilized because it seemed to lend itself to the utilization of instars rather than arbitrary size classes, and because the Hynes method could be used when cohorts could not be distinguished (Waters 1973). Tables 2, 3, 4, 5, 6, and 7 show the calculation of production for females and males of the overwintering, first summer and second summer generations respectively. Weights were all expressed as dry weight, and individuals younger than the seventh instar were divided equally among males and females. Obvious underestimates resulted from an inability to sample smaller sizes. The Hynes method had been shown by Waters (1973) to give an overestimate when compared to other methods, but it was not known how much the possible overestimate of the Hynes method countered the underestimate of sampling. Waters (1969, 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 to 5. Cohort and annual production and turnover ratios for N. mexicanus are summarized in Table 8. For three cohorts, the average turnover ratios per cohort ranged from 4.49 to 6.19 with an average of 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 average cohort turnover ratio, when summer generations are combined, equaled 5.42, which also agreed fairly well with Waters (1969). Annual turnover ratios were influenced by voltinism, and, as could be seen from Table 8, a greater number of cohorts yielded a larger annual turnover ratio as predicted by Waters (1973). Annual turnover ratios by either method (combined summer generations or not) were in agreement with Waters' data (1969). Waters (1973) had indicated that turnover ratios could be used to compare production estimates (methods), and, since the turnover ratios for N. mexicanus were in agreement with Waters' estimated range, it was assumed that the production estimates must have some validity.

The known geographic distribution in Texas for this newly described species is shown in Fig. 16. Plots were made utilizing the data of Allen (1974) and were supplemented by collections made in May, Jun. and Aug., 1973, to West, Central and East Texas.

Summary

1. A population of Neochoroterpes mexicanus was sampled from Sept., 1971--Aug., 1972 on the Brazos River in Palo Pinto County, Texas. Supplemental observations relating to emergence, mating and oviposition, and nymphal food habits were made in 1973.

Table 2

Calculation of production of _N._ _mexicanus_ females of the overwintering generation by the Hynes method

Instar Number	Mean No./m^2	Mean wt. (mg)	Mean Standing Crop (mg/m^2)	Number Loss/m^2	Wt. at Loss (mg)	Wt. at Loss (mg/m^2)	× 13 Prod. (mg/m^2)
4	21.62	0.0022	0.048				
				-4.44	0.003	-0.012	-0.16
5	26.06	0.0039	0.102				
				3.99	0.006	0.063	0.29
6	22.07	0.0087	0.192				
				9.33	0.009	0.087	1.13
7	12.74	0.0109	0.139				
				4.49	0.013	0.056	0.73
8	8.25	0.0140	0.116				
				-4.13	0.019	-0.078	-1.02
9	12.38	0.0241	0.298				
				6.10	0.030	0.183	2.38
10	6.28	0.0374	0.235				
				-0.54	0.048	-0.026	-0.34
11	6.82	0.0626	0.427				
				-1.79	0.078	-0.140	-1.81
12	8.61	0.103	0.887				
				5.02	0.135	0.678	8.8
13	3.59	0.177	0.635				
				-2.51	0.240	-0.602	-7.83
14	6.10	0.323	1.97				
				3.95	0.500	1.98	25.7
15	2.15	0.747	1.61				
				0	0.890	0	0
16	2.15	0.973	2.09				
				2.15	0.973	2.09	27.2

Mean Female Cohort Standing Crop = 8.75

Total Female Cohort Production = 55.09

Table 3

Calculation of production of *N. mexicanus* males of the overwintering generation by the Hynes method

Instar Number	Mean No./m^2	Mean wt. (mg)	Mean Standing Crop (mg/m^2)	Number Loss/m^2	Wt. at Loss (mg)	Wt. at Loss (mg/m^2)	x 13 Prod. (mg/m^2)
4	21.62	0.0022	0.048				
				-4.44	0.003	-0.012	-0.16
5	26.06	0.0039	0.102				
				3.99	0.006	0.023	0.29
6	22.07	0.0087	0.192				
				12.02	0.009	0.112	1.45
7	10.05	0.0106	0.107				
				5.03	0.012	0.060	0.78
8	5.02	0.0139	0.070				
				-3.05	0.017	-0.052	-0.67
9	8.07	0.0238	0.192				
				-1.44	0.027	-0.039	-0.50
10	9.51	0.0313	0.298				
				0.9	0.041	0.037	0.48
11	8.61	0.0568	0.489				
				1.79	0.072	0.129	1.67
12	6.82	0.0986	0.672				
				3.59	0.105	0.377	4.90
13	3.23	0.138	0.446				
				-0.36	0.180	-0.065	-0.84
14	3.59	0.232	0.833				
				-0.36	0.34	-0.122	-1.59
15	3.95	0.517	2.04				
				3.23	0.55	1.78	23.1
16	.72	0.580	0.417				
				0.72	0.58	0.418	5.43

Mean Male Cohort Standing Crop = 5.91

Total Male Cohort Production = 36.02

Table 4

Calculation of production of *N. mexicanus* females of the first summer generation by the Hynes method

Instar Number	Mean No./m^2	Mean wt. (mg)	Mean Standing Crop (mg/m^2)	Number Loss/m^2	Wt. at Loss (mg)	Wt. at Loss (mg/m^2)	x 15 Prod. (mg/m^2)
5	1.12	0.0029	0.003				
				-7.4	0.005	-0.035	-0.53
6	8.52	0.0068	0.058				
				0.89	0.009	0.008	0.12
7	7.63	0.0130	0.099				
				-3.57	0.017	-0.061	-0.91
8	11.20	0.0212	0.237				
				3.13	0.027	0.086	1.29
9	8.07	0.0328	0.265				
				-2.7	0.037	-0.101	-1.52
10	10.77	0.046	0.495				
				2.7	0.048	0.130	1.94
11	8.07	0.0515	0.416				
				2.24	0.062	0.139	2.08
12	5.83	0.0753	0.439				
				2.69	0.09	0.242	3.63
13	3.14	0.102	0.320				
				0.9	0.12	0.108	1.62
14	2.24	0.131	0.293				
				-2.24	0.15	-0.336	-5.04
15	4.48	0.167	0.748				
				3.13	0.2	0.626	9.39
16	1.35	0.236	0.319				
				-2.24	0.27	-0.605	-9.07
17	3.59	0.326	1.17				
				0.45	0.36	0.162	2.43
18	3.14	0.378	1.19				
				1.79	0.57	1.02	15.3
19	1.35	0.878	1.19				
				1.35	0.878	1.19	17.8

Mean Female Cohort Standing Crop = 7.24

Total Female Cohort Production = 38.53

Table 5

Calculation of production of N. mexicanus males of the first summer generation by the Hynes method

Instar Number	Mean No./m^2	Mean wt. (mg)	Mean Standing Crop (mg/m^2)	Number Loss/m^2	Wt. at Loss (mg)	Wt. at Loss (mg/m^2)	× 15 Prod. (mg/m^2)
5	1.12	0.0029	0.003				
				-7.40	0.005	-0.035	-0.53
6	8.52	0.0068	0.058				
				4.03	0.009	0.036	0.54
7	4.49	0.0118	0.053				
				-4.03	0.014	-0.056	-0.85
8	8.52	0.0179	0.153				
				4.48	0.021	0.094	1.41
9	4.04	0.0265	0.107				
				-4.93	0.031	-0.153	-2.29
10	8.97	0.0392	0.352				
				-0.90	0.044	-0.039	-0.59
11	9.87	0.0502	0.495				
				4.49	0.057	0.256	3.85
12	5.38	0.0659	0.355				
				3.14	0.075	0.236	3.53
13	2.24	0.0916	0.205				
				0.44	0.098	0.043	0.64
14	1.80	0.1170	0.211				
				0.01	0.135	0.001	0.02
15	1.79	0.1580	0.283				
				0.89	0.165	0.147	2.20
16	0.90	0.1650	0.149				
				-3.59	0.195	-0.700	-10.50
17	4.49	0.2160	0.970				
				2.25	0.245	0.551	8.27
18	2.24	0.2580	0.580				
				0.45	0.400	0.180	2.70
19	1.79	0.406	0.727				
				1.79	0.406	0.727	10.90

Mean Male Cohort Standing Crop = 4.70

Total Male Cohort Production = 19.29

Table 6

Calculation of production of _N._ _mexicanus_ females of the second summer generation by the Hynes method

Instar Number	Mean No./m^2	Mean wt. (mg)	Mean Standing Crop (mg/m^2)	Number Loss/m^2	Wt. at Loss (mg)	Wt. at Loss (mg/m^2)	× 15 Prod. (mg/m^2)
5	4.19	0.0029	0.012				
				-4.39	0.005	-0.024	-0.35
6	9.12	0.0068	0.062				
				-3.44	0.009	-0.031	-0.46
7	12.56	0.013	0.163				
				0.6	0.017	0.010	0.15
8	11.96	0.0212	0.254				
				-2.24	0.027	-0.062	-0.92
9	14.2	0.0328	0.466				
				1.79	0.037	0.067	1.01
10	12.41	0.046	0.571				
				-0.9	0.048	-0.043	-0.65
11	13.31	0.0515	0.685				
				2.85	0.062	0.177	2.65
12	10.46	0.0753	0.788				
				1.19	0.09	0.107	1.61
13	9.27	0.102	0.946				
				-1.34	0.12	-0.161	-2.41
14	10.61	0.131	1.39				
				5.83	0.15	0.875	13.1
15	4.78	0.167	0.798				
				-0.45	0.2	-0.09	-1.35
16	5.23	0.236	1.23				
				0.3	0.27	0.081	1.22
17	4.93	0.326	1.61				
				1.04	0.36	0.374	5.62
18	3.89	0.378	1.47				
				2.39	0.57	1.36	20.4
19	1.5	0.879	1.32				
				1.5	0.879	1.32	19.8

Mean Female Cohort Standing Crop = 11.77

Total Female Cohort Production = 59.42

Table 7

Calculation of production of *N. mexicanus* males of the second summer generation by the Hynes method

Instar Number	Mean No./m^2	Mean wt. (mg)	Mean Standing Crop (mg/m^2)	Number Loss/m^2	Wt. at Loss (mg)	Wt. at Loss (mg/m^2)	× 15 Prod. (mg/m^2)
5	4.19	0.0029	0.012				
				-4.93	0.005	-0.024	-0.35
6	9.12	0.0068	0.062				
				2.39	0.009	0.021	0.32
7	6.73	0.0118	0.079				
				-1.64	0.014	-0.023	-0.34
8	8.37	0.0179	0.15				
				-3.83	0.021	-0.080	-1.21
9	12.20	0.0265	0.323				
				2.03	0.031	0.063	0.94
10	10.17	0.0393	0.399				
				-1.34	0.043	-0.058	-0.87
11	11.51	0.0502	0.578				
				3.29	0.057	0.188	2.81
12	8.22	0.0659	0.542				
				-1.2	0.075	-0.09	-1.35
13	9.42	0.0916	0.863				
				-2.09	0.097	-0.204	-3.06
14	11.51	0.117	1.96				
				4.33	0.135	0.585	8.77
15	7.18	0.158	1.13				
				2.25	0.165	0.371	5.57
16	4.93	0.165	0.813				
				1.04	0.195	0.203	3.04
17	3.89	0.216	0.84				
				-0.75	0.245	-0.184	-2.76
18	4.64	0.258	1.20				
				1.8	0.400	0.72	10.8
19	2.84	0.406	1.15				
				2.84	0.406	1.15	17.3

Mean Male Cohort Standing Crop = 10.10

Total Male Cohort Production = 39.60

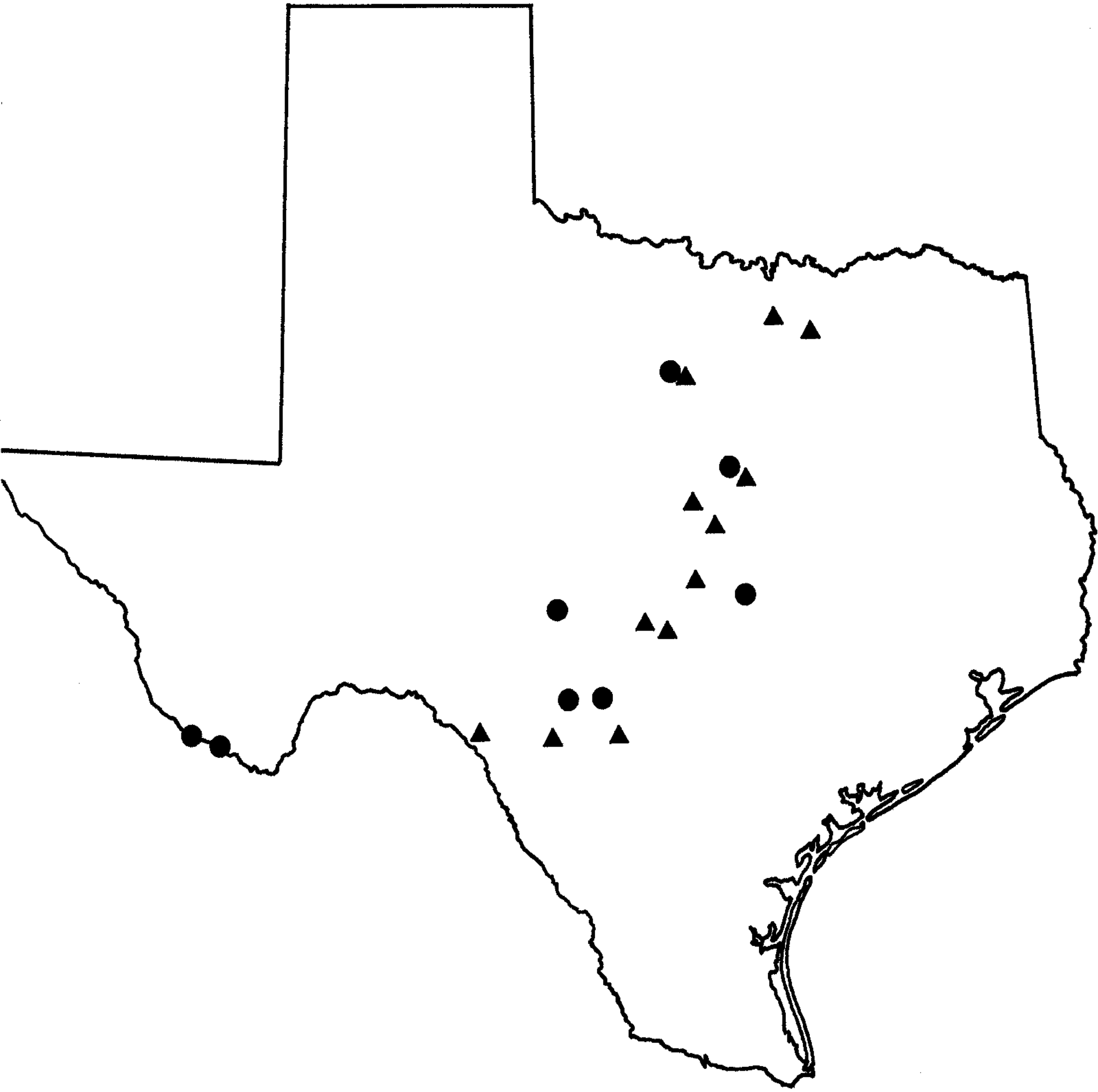
Table 8

Summary of Cohort and Annual Production and Turnover Ratios for *N. mexicanus*

		Summer Generations Separated					
		Overwintering Generation		First Summer Generation		Second Summer Generation	
		M	F	M	F	M	F
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):	Males	94.91					
	Females	153.02					
	Total	247.93					
Annual Turnover Ratio:	Males	14.11					
	Females	16.66					
	Average	15.39					

		Summer Generations Combined			
		Overwintering Generation		Summer Generations	
		M	F	M	F
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):	Males	78.10			
	Females	123.11			
	Total	201.21			
Annual Turnover Ratio:	Males	10.5			
	Females	11.8			
	Average	11.2			

Fig. 16. Geographic distribution of N. mexicanus in Texas. Circles indicate collections made by R. K. Allen.



2. Emergence of *N. mexicanus* occurred late in the afternoon and continued until ca. 1 hr after sunset, during Mar. to Nov. A seasonal variation in total body length of the subimagoes was exhibited. Spring emerging individuals were largest (males 7.15 mm, females 8.78 mm) while late summer individuals were smallest (males 5.47 mm, females 5.47 mm) with fall subimagoes being intermediate (males 6.1 mm, females 6.58 mm).

3. Field and laboratory observations showed that life spans of subimagoes and imagoes of both sexes were less than 24 hr.

4. Mating of *N. mexicanus* occurs in flight with a tandem position being maintained by the two partners. Mating swarms of males are large, diffuse, occur only over land and are usually present only in the morning.

5. Oviposition by *N. mexicanus* females is accomplished by flying upstream, alighting on the surface and apparently extruding all the eggs at once. A seasonal periodicity in fecundity was noted with averages of 1,645, 809, and 1,134 eggs/female for Apr., Sept., and Nov. respectively.

6. The barrel shaped, light colored eggs of *N. mexicanus* measured .18 mm long and .12 mm wide. Eggs displayed chorionic sculpturing with peg-like attachment structures.

7. Incubation time for *N. mexicanus* eggs was 13-15 days at 25±1°C.

8. First instar nymphs were transparent, without gills and had a total body length (excluding cerci) of .45 mm.

9. Sexing of *N. mexicanus* nymphs can be accomplished by the seventh and succeeding instars by observing the divided eye in the males.

10. Sex ratios from 1,264 nymphs and 549 subimagoes indicate a 1:1 relationship.

11. Seasonal head capsule growth of nymphs and emergence data suggested a multivoltine life cycle for N. mexicanus with three relatively distinct generations: an overwintering generation spanning the approximate period Sept.--May, a short summer generation from Apr.--Aug., and a later summer generation from May--Dec. Extended emergence periods produce considerable brood overlap in the nymphal stage.

12. Instar analysis using the methods of Cassie (1954) and Janetschek (1967) and supplemental laboratory rearings indicated 16 instars for both sexes of the overwintering generation and 19 instars for both sexes of the combined summer generations. First and second instars were never sampled.

13. Conformity to Dyar's rule was tested and a slightly curved line was produced with smaller instars showing more rapid growth. Overwintering and combined summer generations mean progression factors were 1.2 and 1.16 respectively.

14. Nymphal stomachs were always over 90% full of detritus, but some algae (primarily diatoms) were ingested on a seasonal basis.

15. Neochoroterpes mexicanus nymphs were found to be constituents in the diets of several vertebrate and invertebrate members of the community.

16. Neochoroterpes mexicanus nymphs were found to be negatively phototrophic.

17. Mean standing crop occurring on the bi-weekly (or monthly) sampling dates was 880 individuals/m^2.

18. Neochoroterpes mexicanus and other members of the riffle community showed high standing crops which reflect an advantageous adjustment to physical conditions created by the damming of the Brazos River.

19. Mean cohort turnover ratio, mean annual turnover ratio and total annual production (dry wt.) were 5.1, 15.3, and 247.9 mg/m^2 respectively for three generations.

20. The geographic distribution of *N. mexicanus* in Texas was elucidated with most populations being in Central Texas.

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