

THE LIFE CYCLE OF *HYDROPERLA CROSBYI* (PLECOPTERA: PERLODIDAE)¹

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ABSTRACT.—*Hydroperla crosbyi* in Texas exhibited a univoltine, fast life cycle over the three-year study period. Adults emerged in February-March when mean daily stream temperature reached ca. 15 C. Reared females in the lab deposited up to three egg masses. Mean fecundity of dissected females was 787 eggs/female. Oviposition in the field was observed and described.

Eggs were triangular in cross section, brown, and measured 400 μm X 535 μm . They underwent an ca. seven-month diapause until mean daily stream temperature decreased to 18 C. Eyespots appeared, and hatching followed in two to three weeks. First instar nymphs were measured and described. Male and female nymphs underwent 12 and 14 instars, respectively, and could be sexed by the sixth. Fast growth occurred in the coldest season and Simuliidae and Chironomidae larvae were preferred food throughout development.

Eggs contained a mean of 6.21 cal/mg. Ash-free mean caloric value of last instar nymphs was 6.0 cal/mg. Adult males and females lost 33.8 percent and 57.6 percent, respectively, of their caloric pool through their ca. 12 days of life.

The life cycles and ecology of North American Plecoptera are relatively unknown. The classic works of Needham and Claassen (1925), Claassen (1931), Frison (1929, 1935, 1942), and Ricker (1952) were primarily taxonomic, with a few largely descriptive notes on morphology, life cycle events, and ecology. Detailed early studies were made by Wu (1923) for *Soyedina vallicularia* (Wu) and Holdsworth (1941a, b) for *Allonarcys proteus* (Newman). Recent papers by Minshall and Minshall (1966), Harper and Pilon (1970), Schwarz (1970), Tarter and Krumholz (1971), Radford and Hartland-Rowe (1971a, b), Harper and Hynes (1970, 1972), Harper (1973a, b), Vaught and Stewart (1974), Stanford (1975), Cather and Gauvin (1975), Hynes and Hynes (1975), and Hynes (1976) are indicative of a resurgent interest in Plecoptera life cycles as supportive knowledge for structural and functional studies at the population and community level.

The only detailed autecological study of a southwestern Nearctic stonefly was reported by Vaught and Stewart (1974) for *Neoperla clymene* (Newman), a widespread species

occurring only in large, permanent rivers. Life cycles of southwestern species should differ markedly from those of boreal species (Harper and Hynes 1972, Harper 1973a, b), due to post-Pleistocene adaptation to drier, warmer climates, and the effects of stream permanence and physicochemical conditions.

Hydroperla crosbyi (Needham and Claassen) is a large perlodid stonefly that is widely distributed throughout the Mississippi Valley from Indiana and Illinois to Arkansas and Oklahoma (Ricker 1952). Stewart et al. (1974) first reported the species from Texas. It is common in streams across the Blackland Prairie into the Edwards Plateau and Eastern and Western Cross Timbers in Texas, and it appears to be a dominant species in the macrobenthic community of Clear Creek in Denton County, Texas, where this study was made. Presence of small nymphs in December, and larger nymphs and adults in March and April, had indicated a fast cycle (Hynes 1970). No previous life cycle studies have been published for any *Hydroperla* species. Stewart and Stark (1977) described the reproductive mor-

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phology and mating behavior of *H. crosbyi*, and Frison (1935) reported nymphal micro-distribution and food habits. The purpose of this research was to make a thorough autecological investigation of *H. crosbyi*, with emphasis on its life cycle.

STUDY STREAM

All sampling and observations were done at several sites along Clear Creek in Denton County, Texas, from Highway 455, ca. 0.5 km west of Bolivar, Texas, to the bridge on Highway 428, ca. 4 km northeast of Denton. Clear Creek originates in Montague County, Texas, and flows through Cooke and Denton counties, merging with Elm Fork of the Trinity River ca. 5 km above Lake Lewisville. Stream discharge is highly variable, depending upon season and rainfall, with the highest levels usually occurring in spring and lowest levels occurring during the summer. In dry years, the stream becomes intermittent during July-September. The substrate consists mainly of sand, with gravel and rock rubble riffles. Packs of leaves and other debris collect on large rocks and fallen tree limbs in riffle areas. The streamside forest is dominated by cottonwood (*Populus deltoides*), sycamore (*Platanus occidentalis*), black willow (*Salix nigra*), and several species of elm (*Ulmus* spp.). As leaves become conditioned by microbes, a successive invasion by macrobenthos, including shredders, collectors, scrapers, and predators, ensues (Cummins 1974). The role of *H. crosbyi* in this sequence was suspected to be that of a dominant macropredator.

MATERIALS AND METHODS

Seasonal growth, instar analysis, food habits, sex ratios, and numbers/m² were determined from quantitative and qualitative samples taken from January 1974 through March 1976. Biweekly qualitative samples were taken from October through March in each year except in October and November 1974, when heavy fall rains prevented access to the stream. A fine (363 μ m) mesh net was used when earlier life stages were

present, and a larger (1 mm) mesh kick net was used for later instars. Specimens were either preserved in 70 percent isopropyl alcohol or transported live to the laboratory for rearing studies. Six quantitative samples were taken each month from November 1975 to March 1976 by kicking up an area of 25 cm² in front of a fine (363 μ m) mesh net; care was taken to sample all typically available habitat types, including leaf debris and rocky substrate. These were preserved in 70 percent isopropyl alcohol and taken to the laboratory for sorting and identification of all organisms. Last instar exuviae were collected in March 1976, to aid in a more precise estimate of the adult sex ratio since adults were difficult to obtain in the field. In an attempt to find eggs or smaller instars, 5 liters of damp substrate from areas with no surface flow and from pools were collected monthly during the period of March through September 1974, preserved in 99 percent isopropyl alcohol, and brought to the laboratory for elutriation (Stewart 1975).

Aspects of adult emergence, mating, and oviposition were determined from field and laboratory observations. The longevity of laboratory-reared adults was determined by holding them in 8-dram, cotton-stoppered, glass shell vials at room temperature, ca. 24 C.

Caloric values of last instar male and female nymphs and their exuviae, newly emerged virgin males, spent (postmated) males, newly emerged virgin females with ova and after ova removal by dissection, spent females (after oviposition), and deposited egg masses were determined and compared. Energy allocated to reproduction (Pr) was equated to the caloric contents of the total amount of eggs deposited by a female. An instantaneous measure of reproductive effort (IRE) was expressed as a percentage of energy going to production of eggs (Pr) and to growth (Pg). After obtaining live weights, individuals were dried in a vacuum oven at 80 C (-15 psi) for 24 hours, weighed, ground with a mortar and pestle, and pressed into pellets of known weights (10-20 mg). The pellets were combusted in a Gentry-Weigert modification of a Phillipson

microbomb calorimeter (Phillipson 1964). The dry weight of material not combusted was considered to be ash weight; therefore, caloric data were expressed as calories/mg ash-free dry weight. Organisms were not bombed individually, but pooled to produce the pellets.

Groups of eggs deposited in March by reared, mated females were incubated in 1974 and 1976. They were held in loosely covered 8-dram vials at 22 ± 2 C until October (1974) and September (1976), then transferred into a Percival E-50 environmental chamber, lowered 1 C per day down to 18 C.

Eggs "in uteri" and deposited eggs were counted, photographed, measured, and described, with special attention given to any gelatinous layers and/or other attachment structures and chorionic sculpturing (Stewart et al. 1969). Scanning electron micrographs were made using an ISI Mini-SEM.

First instar nymphs, hatched from eggs obtained in March 1974, were preserved in 70 percent isopropyl alcohol for drawings and descriptions. The interocular distance of these and field-collected nymphs was measured using a calibrated ocular micrometer, and sex was determined when possible. Live nymphs were placed in styrofoam cups with creek water and kept in the environmental chamber at simulated creek temperature and photoperiod to determine size changes and to rear them to adults. After one sampling date in February 1976, 40 last instar nymphs were divided into three groups and kept at three constant temperatures, 7 C, 15 C, and 25 C, respectively, to determine the effect of temperature on the time required for development and emergence.

Size-frequency histograms, constructed from interocular distances of field-collected nymphs, and the methods of Cassie (1954) and Janetschek (1967) were used to interpret growth and instar development. To supplement these analyses and aid in interpretation, field-collected nymphs of different sizes were reared to successive instars.

Food habits were determined by foregut analysis (Richardson and Gaufin 1971). Forage ratio (FR) (Hess and Swartz 1941) and

electivity (E) (Ivlev 1961) were calculated for determination of food preferences.

Stream temperature was taken on each sampling date with a total immersion thermometer. A seven-day continuous recording thermograph (Tempscribe remote bulb recorder) was placed in the stream in June 1975 and left for the remainder of the study. Stream flow was taken on each sampling date from August 1975 to March 1976, using a Kahl Pygmy Flow Meter calibrated at 0.4714 meters per revolution. Seasonal water samples were taken and analyzed for pH, conductivity, and alkalinity according to standard methods (American Public Health Association 1971).

RESULTS AND DISCUSSION

During the study, pH varied from 7.6 (summer 1975) to 8.1 (winter 1976), conductivity 530 μ mhos (fall 1975) to 1,180 μ mhos (summer 1975), and total alkalinity 212 ppm (fall 1975) to 408 ppm (winter 1976). Stream flow was highly variable, with the highest level observed in October-November 1974 and no flow in June-August 1974. From August 1975 to March 1976, stream flow remained relatively constant at ca. 1.4 m/sec. Temperature ranged from 30 C in June 1974 to 2 C in February 1976. Such highly variable and intermittent conditions of Clear Creek are typical of moderate-sized streams on the western edge of the temperate deciduous forest. Life cycle adjustments of stoneflies such as *H. crosbyi* and *Perlesta placida* (Hagen) through natural selection, which have enabled success in such harsh environments, were of prime interest in this study.

Other dominant insects associated with *H. crosbyi* in Clear Creek included *Isonychia sicca manca* (Eaton), *Choroterpes* (*Neochoroterpes*) *mexicanus* (Allen), *P. placida*, *Corydalus cornutus* (Linnaeus), *Hydropsyche simulans* (Ross), *Cheumatopsyche campyla* (Ross) and *C. lasia* (Ross).

ADULT.—*H. crosbyi* displayed a relatively spontaneous emergence, with adults occurring from mid-February through March during the three-year study period. A similar recurrent emergence pattern has been re-

ported for several stonefly species (Nebeker 1971b, Müller 1973, Kerst and Anderson 1974). Average daily stream temperatures at the onset of emergence were ca. 15 C with 19 C maxima and 13 C minima. Emergence was essentially over and nymphs gone when average daily stream temperatures reached 22 C. As emergence progressed, there was a corresponding decline in nymphal populations. These observations and results of laboratory holding of mature nymphs in environmental chambers suggest that the mean daily stream temperature cue for emergence in *H. crosbyi* is ca. 15 C. Field-collected, mature nymphs held at 7, 19, and 25 C showed a highly significant difference ($P < 0.01$) in the mean number of days to emergence, with most time ($\bar{X} = 44.8$ days) at 7 C, shortest successful emergence ($\bar{X} = 25.6$ days) at 19 C, and 100 percent mortality at 25 C.

The emergence of some stonefly species is apparently dependent on the number of degree days or temperature accumulation during nymphal development (Cummins 1974, Stanford 1975). Several investigators have indicated that events such as emergence and hatching result when a certain temperature cue is attained during periods of increasing or decreasing temperatures (Sheldon and Jewett 1967, Heiman and Knight 1970, Harper and Pilon 1970, Nebeker 1971a, b, Radford and Hartland-Rowe 1971, Sheldon 1972, Harper 1973a, b). The emergence response range (tolerance) to such cues is narrow in nymphs such as *H. crosbyi* and others, effectively synchronizing emergence into a short time period (Macan 1958, Nebeker and Gaufin 1967, Nebeker 1971c, Hynes and Hynes 1975). Since accurate temperature data were not available over successive seasons, and a major egg-incubation experiment was lost due to environmental chamber malfunction, it could not be determined whether temperature accumulation (Baskerville and Emin 1969) influenced the development and emergence of *H. crosbyi*.

Collections of cast exuviae indicated that mature nymphs crawled out of the water onto rocks or debris above the surface of the water or along the bank for transforma-

tion. Similar emergence has been reported for *Paragnetina media* (Walker) (Tarter and Krumholz 1971) and *Isoperla transmarina* (Newman) (Harper 1973a). Adults then either fly or walk to streamside vegetation or debris near the water. Preemergent nymphal sex ratios were ca. 1:1, but collections of exuviae in the middle of the emergence period in March 1976 favored females, 1.0 ♂ : 1.5 ♀, indicating at least a slightly protandrous emergence. Schwarz (1970), Heiman and Knight (1970), Sheldon (1972), and Harper (1973a, b) have reported similar findings for other species.

A seasonal size variation was exhibited in adult *H. crosbyi*. The interocular distance decreased as emergence continued from a mean of 2.0 mm to 1.6 mm for females, and from 1.7 mm to 1.4 mm for males. Khoo (1968a), Schwarz (1970), Sheldon (1972), and Cather and Gaufin (1975) have shown similar variation, indicating that the emergence cue hurries smaller specimens so that full size is not attained (Khoo 1968a).

Adults did not feed; but they were observed to drink water; Hynes (1976) suggested this is probably true of all adult Systellognatha. Dissection indicated that the digestive tract was much reduced.

A period of two to five days is required for maturation of eggs in adult females. *Isoperla clio* (Newman) (Harper 1973a), *Isoperla goertzi* Illies, and *Diura bicaudata* (Linnaeus) (Schwarz 1970) require a similar egg maturation period. Males find females by a tactile or possibly by a pheromone response, and mating takes place on streamside vegetation or debris. Reproductive morphology, mating, and sperm transfer have been described by Stewart and Stark (1977). Sperm transfer in this species is external, and the aedeagus does not function as an intromittent organ. The species exhibits polygamous mating habits. Mated females flew to tree branches from 5 to 10 m above the stream on ca. the fifth day after emergence. An egg mass was extruded from the genital opening located at the rear of the abdominal sternum 8. Between ca. one to one-half hour before sunset, the female began her oviposition flight, approaching the site from upstream. She glided down

and rested briefly on smooth water from 2 to 10 m from the head of a riffle. Contact with water and a slight movement of the abdomen resulted in separation of the mass, which then sank. The female was carried by the current ca. 1 m during this process, then rose off the water, flying back into adjacent trees. Laboratory-held females extruded up to two more egg masses over the next three to five days. Mean life span of mated adult males and females held in the laboratory at simulated light and temperature conditions was 11.4 and 11.6 days, respectively.

Mean numbers of eggs in successive masses for reared females were 330, 235, and 172, respectively. Fecundity of dissected, gravid females was from 442 to 1,418 eggs/♀, with a mean of 787/♀. Smaller females generally contained fewer eggs.

Deposited eggs had the highest caloric value (6.21 cal/mg) of any stage in the life cycle (Table 1). Mean caloric value of ca. 6.0 cal/mg ash-free for late instar *H. crosbyi* nymphs generally agree with those of Cummins and Wuycheck (1971) for immatures of various aquatic insects, McDifft (1970) for *Pteronarcys scotti*, Lawton (1970, 1971) for *Pyrhosoma nymphula* and its prey, Hofsvang (1973) for *Tipula excisa*, and Brown (1974) for *Corydalis cornutus*. Mean ash-free cal/mg of males were signifi-

cantly different from females in all stages (Student's t; $P<0.05$). Few calories (16.34) appear to be lost in transformation, through loss of the exuvium (mostly epicuticle). Males lose 33.8 percent (27.13) of their caloric pool as metabolic heat through their ca. 12 days of life (Table 1).

A mean of 58.99 calories (deposited egg masses) constituted the energy allocated to reproduction (Pr) by females. However, a difference of 110.45 calories between newly emerged virgin females with ova and newly emerged virgin females with ova removed by dissection indicated that 51.46 calories might be resorbed by the female from undeposited eggs to be used for maintenance and metabolic costs involved in mating and oviposition. Energy allocated to growth (Pg) was estimated as the mean biocontent of a newly emerged virgin female with ova removed (106.95 calories), since the first instar was very small and its calories negligible. An instantaneous reproductive effort (IRE) was thus calculated as: $Pr (58.99) / [Pr (58.99) + Pg (106.95)] = 35.5$ percent. Another measure of IRE is the ratio of Pr to female carcass calories. Expressed this way, IRE of *H. crosbyi* was: $Pr (58.99) / \text{female carcass calories } (106.95) = 55.1$ percent. These values compare favorably with RE's determined by Brown (1974) for *C. corn-*

TABLE 1. Caloric values of major stages in the life cycle of *H. Crosbyi*.

Material	$\bar{X}$ dry wt. (mg)	$\bar{X}$ cal/mg Ash-free	N°	$\bar{X}$ Biocontent (cal)
Male, last instar	19.4	6.01	10	116.59
Female, last instar	36.0	5.95	10	214.20
Last instar exuviae	3.0	5.43	10	16.34
Male, newly emerged (virgin)	14.2	5.66	10	80.37
Female, newly emerged (virgin with ova)	36.6	5.94	11	217.40
Female, newly emerged (virgin—ova removed)	18.6	5.75	7	106.95
Male, spent (postmated)	10.2	5.22	8	53.24
Female, spent (after oviposition)	18.7	4.93	8	92.19
Egg masses (total deposited/female)	9.5	6.21	2	58.99

*N = number of determinations

utus. A later discussion of food habits of *H. crosbyi* will show that its general food resources are similar to those of *C. cornutus*. Females lose 57.6 percent (125.21) of their caloric pool as metabolic heat and Pr during their adult life.

EGG.—Eggs are oval shaped, triangular in cross section, brown in color, and an average 400 μm wide by 535 μm long (Fig. 1). They are similar to descriptions of other perlodid eggs such as *Hydroperla fugitans* (Frison 1935), *Isogenoides frontalis* and *Isogenoides zionensis* (Knight et al. 1965), *Perlodes microcephala* and *Diura bicaudata* (Schwarz 1970), and *Pictetiella expansa* and *Isogenoides zionensis* (Baumann 1973). The chorion surface generally lacks the sculpturing so evident in perlids (Stark and Gaufin 1976a, b), the Isoperlinae, and other stoneflies. The crown ridge is reduced and from two to four micropyles occur near the middle on each of the three sides of the egg.

Each egg was enclosed by a gelatinous envelope, whose possible functions include: (1) prevention of desiccation after extrusion and prior to deposition, (2) action as a cementing substance to retain eggs in masses, and (3) attachment of individual eggs to substrate near the site of oviposition (Brinck

1949, Hynes 1970). A gelatinous mushroom-shaped attachment structure, emerging from the crown area of the egg, was prominent for at least the first 48 hours after deposition. Its "carapace" portion appeared as a shriveled mass in older eggs in water and those preserved in alcohol (Fig. 1). Both the envelope and the attachment mushroom were very effective in gluing eggs to glass or other substrate.

Eggs of *H. crosbyi* underwent a long, ca. seven-month diapause from February-March, when deposited, to October-November, when fall rains occurred and mean daily water temperature declined to ca. 18 C. Elutriation (Stewart 1975) of sand substrate from an area where there was no surface flow in July 1974 yielded one *H. crosbyi* egg and several *Perlesta placida* eggs that appeared turgid and alive. The diapause and development of eggs were similar to those of *Diura bicaudata* and *Brachyptera risi* (Khoo 1968b, c) and *Amphinemura delosa*, *A. linda*, *A. nigritta*, and *Prostoia completa* (Harper 1973b), in that eyespots appeared only two to three weeks before hatching.

One group of March 1974 eggs held at 25 ± 2 C until September, when the temperature was reduced 1 C every three to five days, hatched spontaneously at 19 C. This and early November appearance of first instar nymphs in Clear Creek suggest that rejuvenation of streams by fall rains and declining temperatures cue the termination of diapause. Another group of 2,000 March 1976 eggs, held in the laboratory at a constant 23 ± 1 C, hatched over an extended time period of five to eight months.

The diapause is a great advantage since it allows survival through hot summer, when water temperatures might be lethal to young nymphs and many of the intermittent streams inhabited by this species become dry. Several species such as *Zealeuctra arnoldi*, *Z. claasseni*, and *Z. hitei* and *Perlesta placida* that are endemic to, or extend their ranges into, the ecotone between the temperate deciduous forest and grassland are apparently capable of similar fast cycles. This adaptation is similar to several species reported by Hynes and Hynes (1976) in

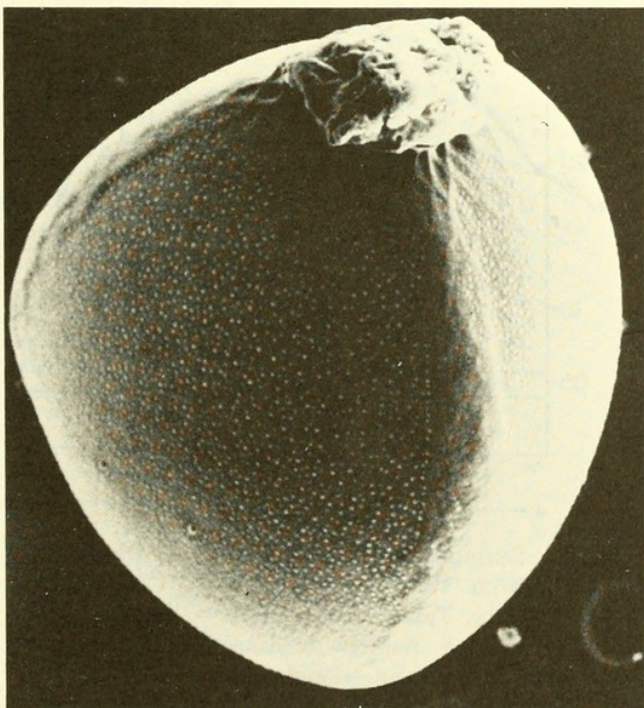


Fig. 1. *Hydroperla crosbyi* egg; SEM, 400x.

semiarid regions of Australia. Further work on their life cycles should provide some interesting comparisons with fauna of similar regions of the two continents. Many stoneflies undergo an egg or nymphal diapause to avoid adverse effects of extended cold or hot temperatures (Hartland-Rowe 1964, Khoo 1968a, b, c, Harper and Hynes 1970, 1972, Harper 1973a).

Eclosion (Fig. 2) follows the same general pattern reported by Heiman and Knight (1970) and Vaught and Stewart (1974); the chorion is torn, and the nymph pushes the hinged cap away and crawls out. Hatching in the field is apparently synchronous, since first instar nymphs in November 1975 were found only over a four-week period. Macan (1958) postulated that synchronous hatching is a disadvantage since competition for food and space would be very intense. This would only apply, however, in situations where numbers approach or exceed the carrying capacity. This theoretical asymptote (K) has not been defined for stream systems, where it would be expected to vary geographically and from year to year. Also, drift might play a large role in dispersing synchronously hatched nymphs.

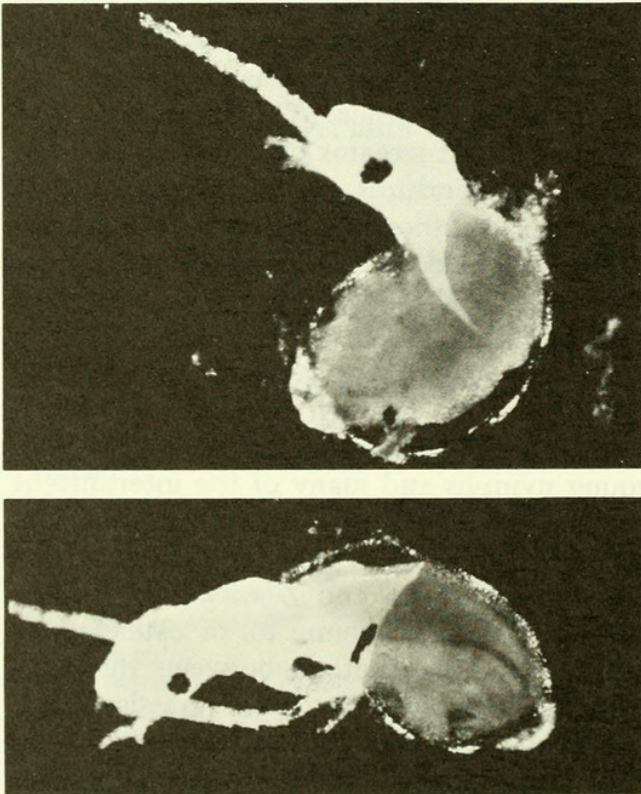


Fig. 2. Eclosion sequence; *Hydroperla crosbyi*.

Although both *H. crosbyi* and *Perlesta placida* occupy similar habitats, have similar diets, undergo an over-summer diapause, and have a relatively synchronous egg hatch (October-November), differential growth rates appear to separate them temporally. Nymphs of *H. crosbyi* grow faster through winter, leading to an emergence in February-March at the time when early instars of *P. placida* are just beginning their growth spurt, leading to an April-May emergence. A thorough comparison can be made in southwestern streams such as Clear Creek, when another current study of the life cycle of *P. placida* is completed (Rosalyn Snellen, personal correspondence).

NYMPHS.—After hatching in October, nymphs grow rapidly through the winter until just prior to February-March emer-

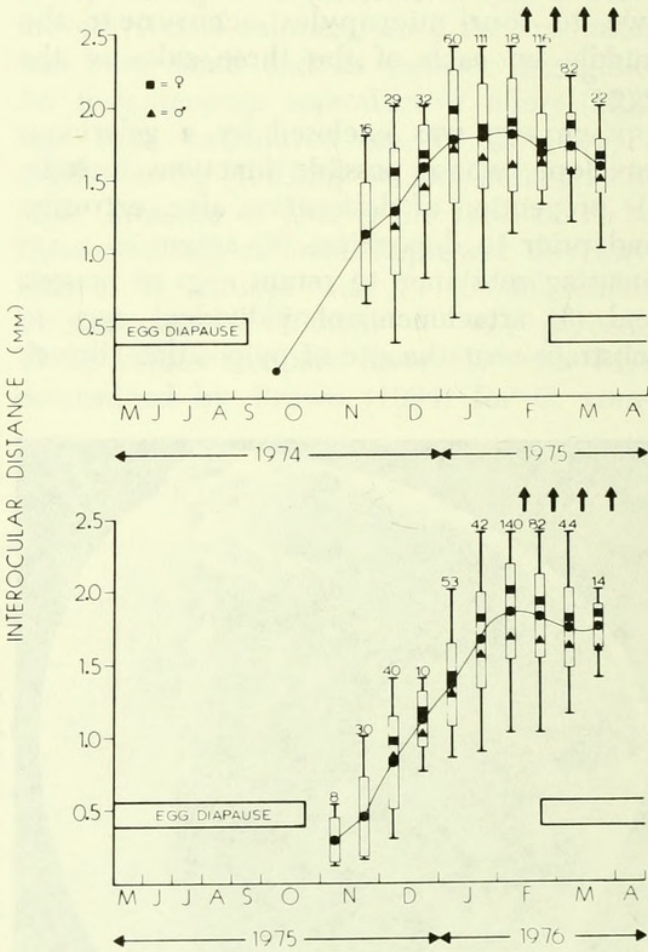


Fig. 3. Seasonal cycle and growth of *Hydroperla crosbyi*, March 1974 to March 1976, Clear Creek, Denton County, Texas: Vertical line = range, number at top of line = number measured, solid circle = mean, solid square and triangle within bars = mean female and male interocular distance, respectively, vertical bar = + & - 1SD, arrow = emergence.

gence (Fig. 3), when water temperatures are coldest (Fig. 4). The species thus fits Hyne's (1961) classification as an F_1 (fast) univoltine cycle. Similar cycles have been reported for *Isoperla clio* and *Isogenus decusus* (Minshall and Minshall 1966); *Amphinemura delosa*, *Prostoia completa*, and *Shipsa rotunda* (Harper 1973b); and *Capnia confusa*, *Utacapnia trava*, *U. columbiana*, *Doddsia occidentalis*, and *Taenionema pacifica* (Stanford 1975). This emphasizes the wide range of adaptation in Plecoptera nymphal growth characteristics since many species such as *Zapada columbiana*, (Hartland-Rowe 1964), *Taeniopteryx nebulosa*, *Nemura meyeri*, *A. borealis*, *N. cinerea*, *Leuctra hippopus*, *Capnia atra*, *Diura nanseni*, *Isoperla difformis*, *I. grammatica* (Svensson 1966), *Isoperla goertzi*, *Diura bicaudata* (Schwarz 1970), *Paragnetina media* (Heiman and Knight 1970), *Pteronarcys dorsata*, *Isoperla frontalis* (Nebeker 1971b), *Brachyptera risi*, *Protonemoura meyeri*, *Amphinemura sulci- collis*, *A. borealis*, *A. standfussi*, *Capnia atra*, *Siphonoperla burmeisteri* (Benedetto 1973), *Neoperla clymene* (Vaught and Stewart 1974), *Megarcys signata* (Cather and Gaufin 1975), and *Pteronarcella badia*, *Skwala parallela*, *Diura knowltoni*, *Isoperla*

fulva, *I. patricia*, *Sweltsa coloradensis*, *Suwallia pallidula*, and *Zapada columbiana* (Stanford 1975) exhibit slow cycles, with most growth occurring at moderate to warmest seasonal water temperatures. Temperature compensation (Cummins 1974) is thus manifested in this species through rapid winter growth, early spring emergence, and diapause for protection against drying or lethal temperatures in summer. This growth pattern is a selective advantage in allowing avoidance of competition for food and space with such species as *Corydalus cornutus* (Brown 1974) and *Perlesta placida*.

First instar nymphs were obtained from egg-hatching experiments and Clear Creek. They were unpigmented, had 9 antennal and 4 cercal segments, and the mean interocular distance was 0.18 mm (Fig. 5). Hynes (1976) indicated that many first-instar Plecoptera exhibit these characters.

Distinctive color patterns became evident through the middle and later instars, and numbers of cercal and antennal segments increased to 30 and 50, respectively. Mouthparts of first-instar nymphs are shown in Fig. 6. Life cycle studies of stoneflies should give attention to good descriptions of first instars to facilitate accurate identifications

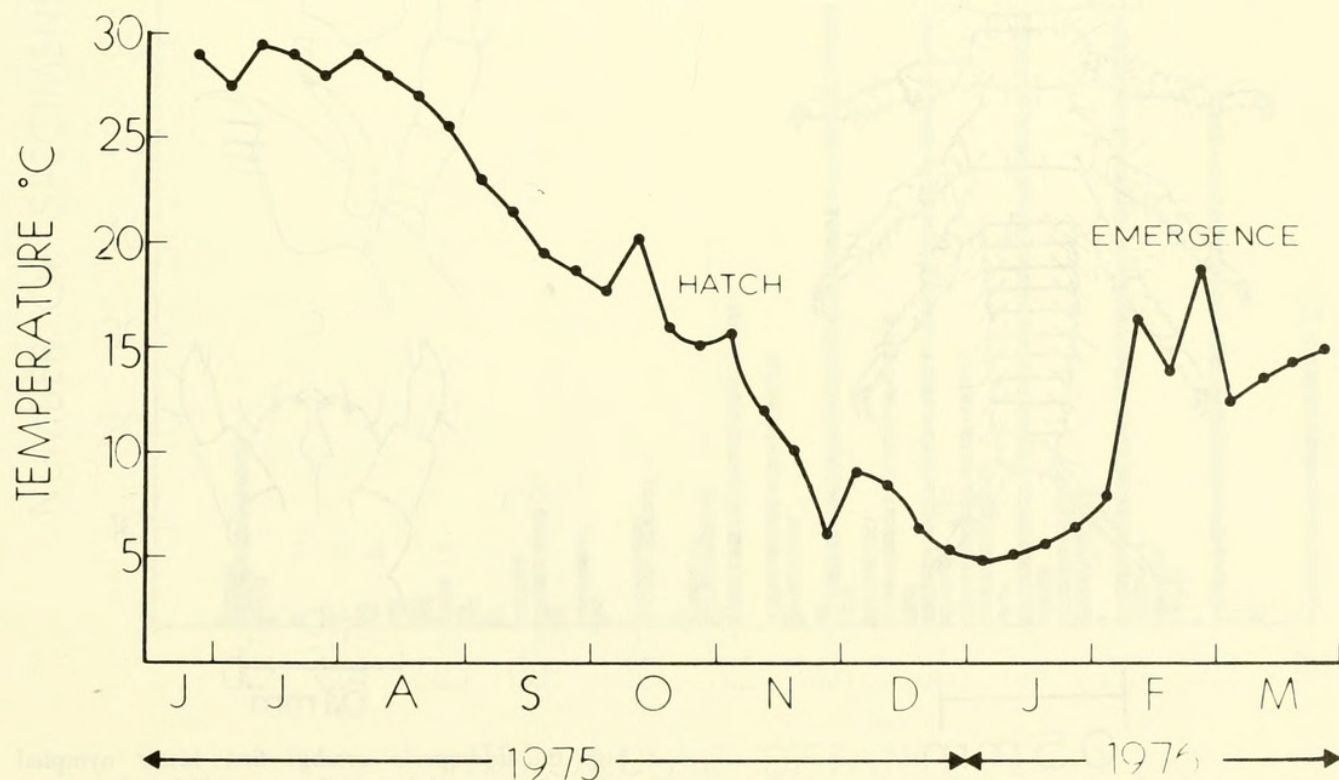


Fig. 4. Mean weekly stream temperature, June 1975 to March 1976.

for future ecological studies. Comparison of Figs. 6 and 7 show the major changes that take place in presence and pattern of setal arrangement and shape of mouthparts between first and last instars; number of palpal segments remain unchanged.

Nymphs can first be sexed at the sixth instar, by differences in the posterior setal arrangement of the eighth abdominal sternum. The fringe is interrupted in females and continuous in males. Dimorphism in setal arrangement, nymphal size, and even eventual presence of the male epiproct, becomes more distinct in postsixth instars. The sex ratio of 870 postfifth instar nymphs sexed throughout the study was 1.0 ♂ :1.1 ♀ . The larger size of female nymphs appears typical of all stoneflies and has been reported by Holdsworth (1941a, b), Heiman and Knight (1970), Tarter and Krumholz (1971),

Brittain (1973), and Vaught and Stewart (1974).

Estimation of nymphal instar number was determined from 971 field-collected nymphs by using a size-frequency histogram (Fig. 8) and the methods of Cassie (1954) and Janetschek (1967) (Figs. 9 and 10, respectively). An expanded discussion of application of these methods is given by Harper (1973b) and McClure and Stewart (1976). These methods indicated 12 and up to 14 instars for males and females, respectively. Similar dimorphism in instar number has been reported by Holdsworth (1941b), McDiffett (1970), and Vaught and Stewart (1974). The size change between most instars was confirmed and these estimates substantiated by rearing field-collected nymphs of various sizes through at least one molt. Of course,

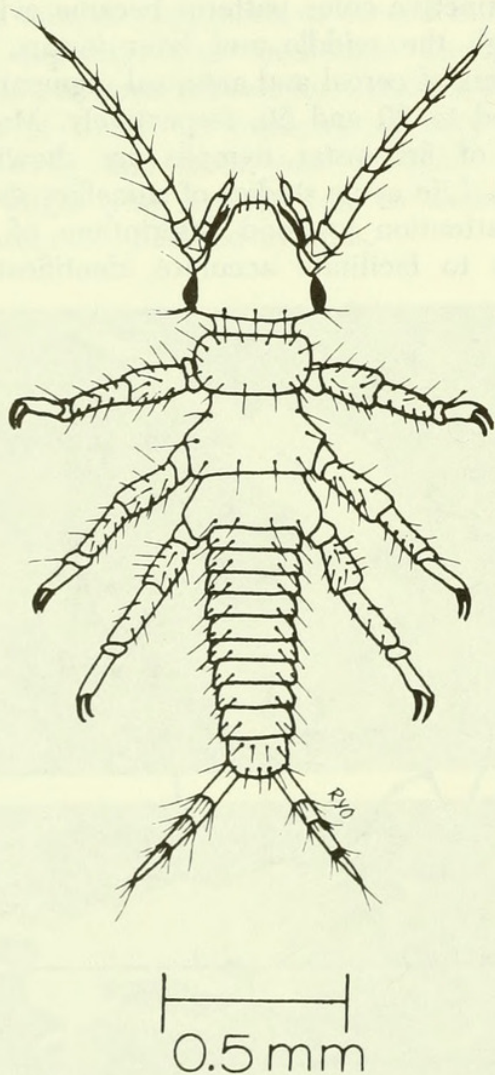


Fig. 5. *Hydroperla crosbyi* first instar nymph.

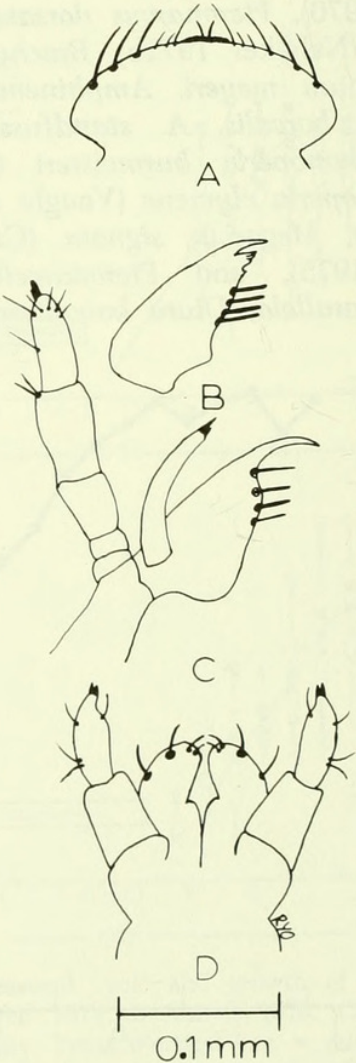


Fig. 6. *Hydroperla crosbyi* first instar nymphal mouthparts: A = labrum, B = mandible, C = maxilla, D = labium.

absolute determination of instars can only be made through rearing individuals from egg to adult, under various physical conditions (Harper 1973b). Stanford (1975) suggested that temperature may influence the number of instars in hemimetabolous insects.

Seasonal food habits of nymphs are shown in Table 2. All calculations are based on numbers of dietary items in the foregut and environment. Gut contents were examined using methods of Richardson and Gaufin (1971), and food availability was calculated from quantitative samples. Larvae of Simuliidae and Chironomidae always made up over 85 percent of the diet (Table 2), and electivity (Ivlev 1961) and forage ratio (Hess and Swartz 1941) consistently indicated that these organisms were preferred or more available. Nymphs of *Isonychia sicca manca* were the third most common dietary item, but preference for them was always negative (or they were less available

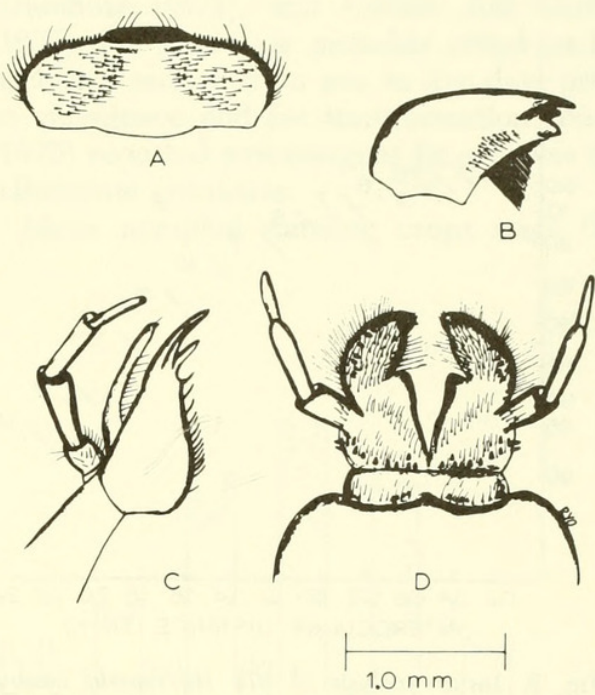


Fig. 7. *Hydroperla crosbyi* last instar female nymphal mouthparts: A = labrum, B = mandible, C = maxilla, D = labium.

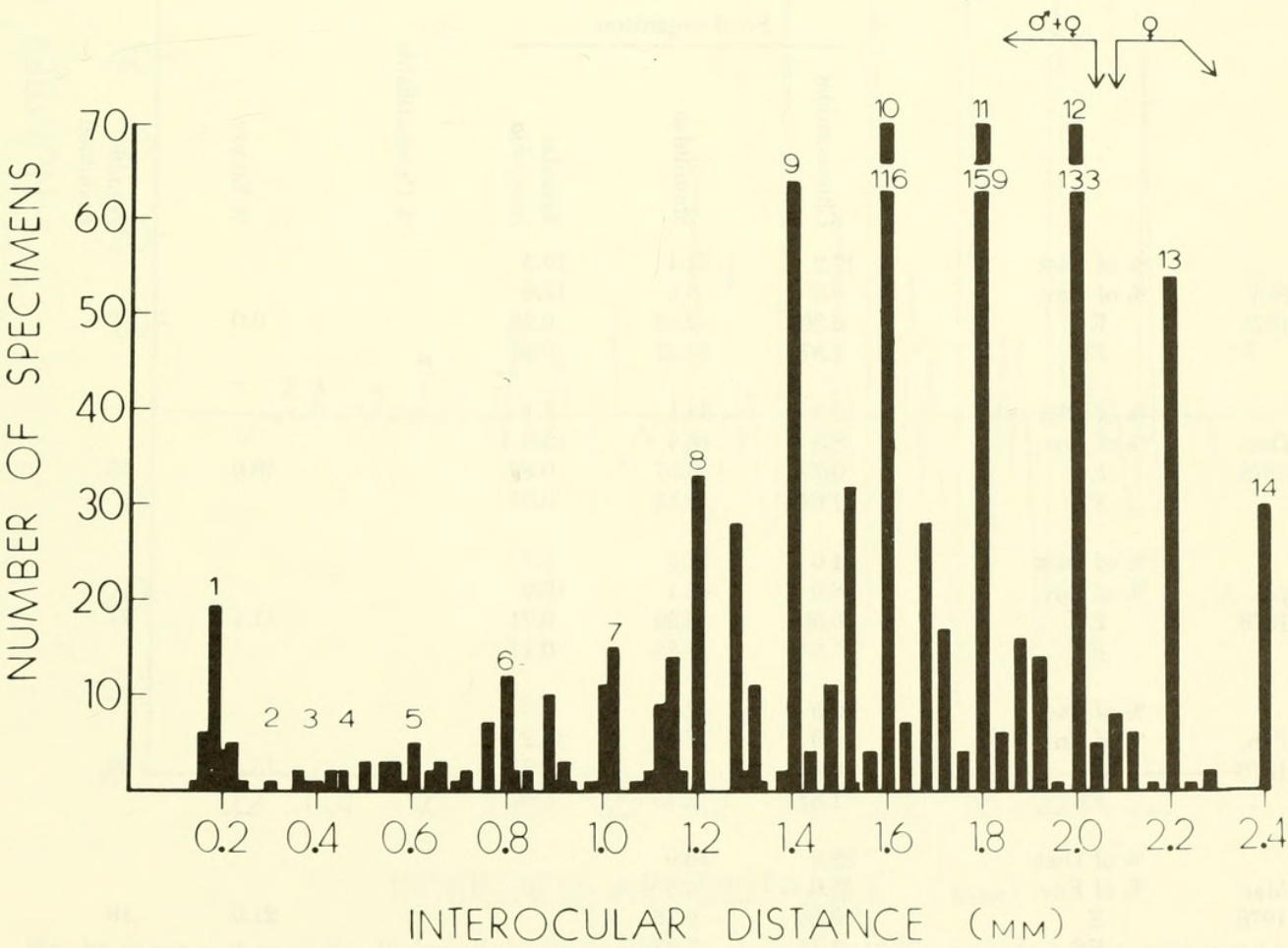


Fig. 8. Interocular distance—frequency of 971 *Hydroperla crosbyi* nymphs, illustrating instars.

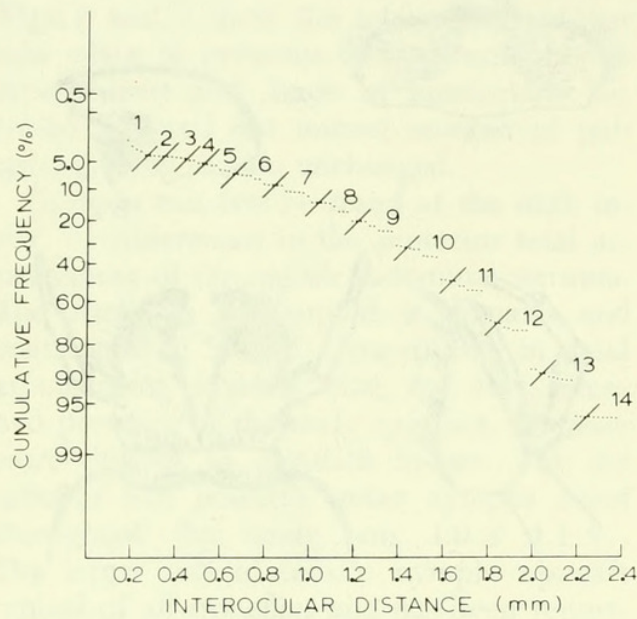


Fig. 9. Instar analysis of 971 *Hydroperla crosbyi* nymphs by Cassie (1954) method.

for feeding). *Drusinus* (Limnephilidae), *Chimarra* (Philopotamidae), *Perlesta* (Perlidae), and unidentified aquatic Lepidoptera occasionally appeared in stomachs but were considered of little importance. Frison (1935) reported large numbers of chironomids in the diet of *H. crosbyi* nymphs. Similar preferences for dipteran larvae have been reported for carnivorous insects (Minshall and Minshall 1966, Tarter and Krumholz 1971, Sheldon 1972, Stewart et al. 1973, Vaught and Stewart 1974, and Cather and Gaufin 1975). Simuliids were predominant to chironomids in the diet from November-January, with electivity or preference greater until January (Table 2). A shift in dietary occurrence became evident in February, with the two components occurring in equal proportions, then simuliids again predominated in March; electivity for sim-

TABLE 2. Seasonal food habits of 110 *Hydroperla crosbyi* nymphs November 1975 to March 1976, Clear Creek, Denton County, Texas.

		Food organisms			% Unidentifiable	% Empty	Number examined
		Chironomidae	Simuliidae	Baetidae <i>Isonychia</i>			
Nov. 1975	% of Diet	17.2	72.4	10.3	0.0		9
	% of Env.	9.2	6.6	17.6			
	E	0.30	0.83	0.26			
	FR	1.87	10.97	0.58			
Dec. 1975	% of Diet	13.6	84.1	1.1	16.0		25
	% of Env.	8.3	16.4	15.0			
	E	0.24	0.67	0.86			
	FR	1.64	5.13	0.07			
Jan. 1976	% of Diet	21.0	77.2	1.7	11.1		27
	% of Env.	6.9	42.1	10.0			
	E	0.50	0.29	0.71			
	FR	3.04	1.83	0.17			
Feb. 1976	% of Diet	42.8	42.8	8.3	3.7	13.3	30
	% of Env.	22.9	17.2	13.2			
	E	0.30	0.43	-0.23			
	FR	1.87	2.49	0.63			
Mar. 1976	% of Diet	28.2	70.0		21.0		19
	% of Env.	25.0	9.5				
	E	0.06	0.76				
	FR	1.13	7.37				

uliids was greater in both these months even though in February their numbers were decreasing because of emergence. Proportion of empty stomachs was highest just prior to emergence (Table 2). Molting nymphs always had empty stomachs. Similar findings were reported by Hanson (1960), Tarter and

Krumholz (1971), and Cather and Gaufin (1975). Fat stores are probably relied on for necessary energy from one to five days prior to emergence and for transformation. Finni (1975) reported preemergent fat reserves for *Allocapnia granulata*. Mean nymphal standing crops were 8.0,

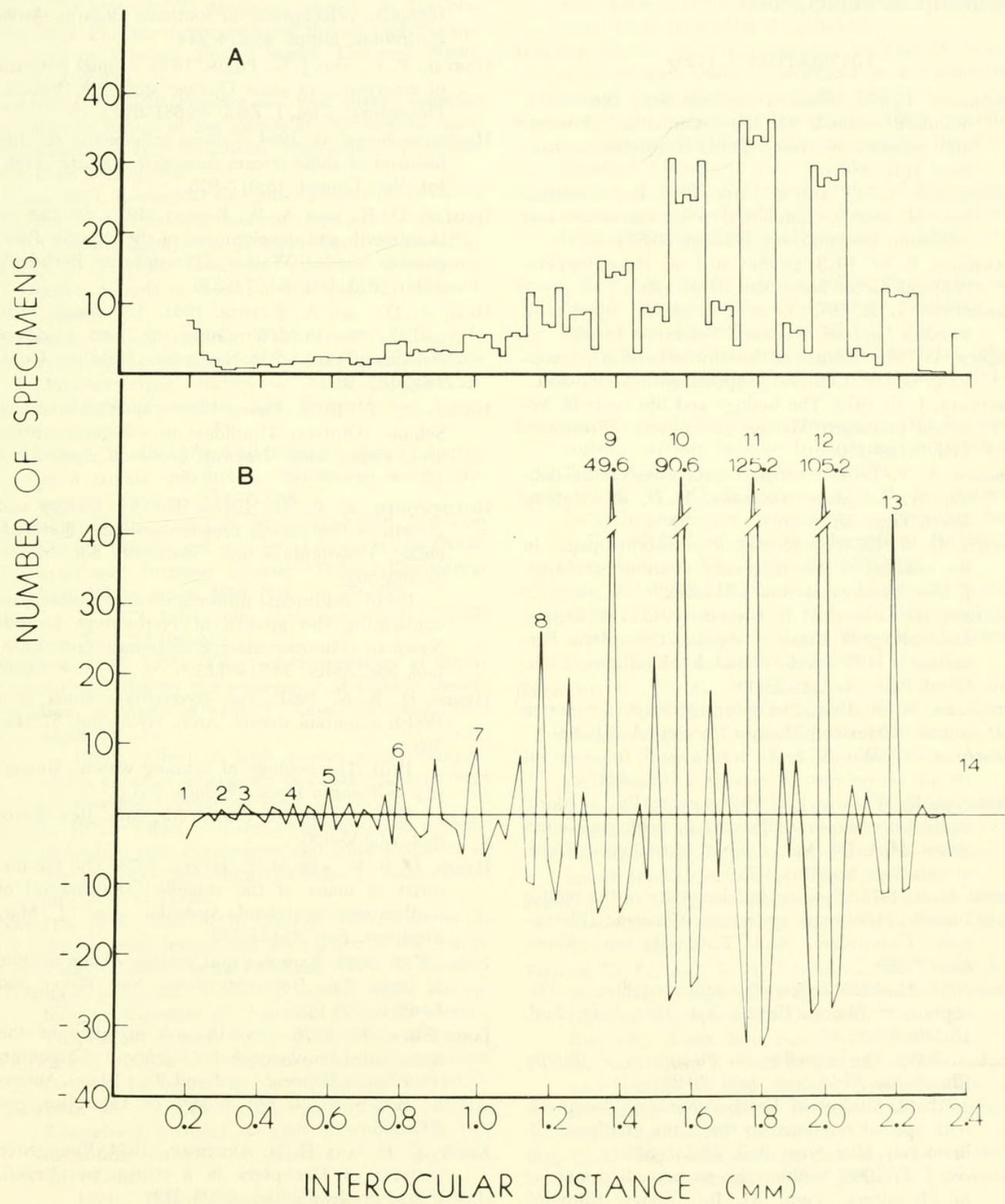


Fig. 10. Instar analysis of 971 *Hydropsyche crosbyi* nymphs by Janetschek (1967) method: A = running mean of five of the frequencies, B = modal periodicity of instars (difference between Fig. 8 histogram and A).

25.6, 40.0, and 21.3/m² each month from December 1975 to March 1976. The lower number in December was probably due to sampling error, peculiarities in micro-distribution, or difficulty in detection of tiny first-instar nymphs. Decreases from February-March were likely an indication of survivorship and emergence.

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