THE LIFE HISTORY AND ECOLOGY OF
THE STONEFLY NEOPERLA CLYMENE (NEWMAN) (PLECOPTERA:PERLIDAE)

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The objective of this investigation was to provide new and more detailed information on the life history and ecology of Neoperla clymene, through an intensive study of the species in the Brazos River, Texas. Nymphal development was determined from 737 specimens from monthly quantitative samples, and bi-monthly qualitative samples taken from November 1970 to October 1971. A total of 443 nymphs were collected during the months of March, April, May, and July to determine the kinds and numbers of food organisms consumed by N. clymene, and to investigate periodicity and electivity of feeding. Light trap samples were taken from March to September 1971 for determination of emergence cycle and adult sex ratios. Mating, fecundity, incubation and egg descriptions were determined through field and supplemental laboratory observations. The conclusions of this investigation were:

- 1) Emergence, mating and oviposition of adults was nocturnal, reaching a peak during the months of June and July.

2) Mean fecundity of dissected virgin females was 646 eggs, up to 3 egg masses were obtained from females held in laboratory aquaria and they averaged 98 eggs/egg mass. The number of eggs per egg mass from field-collected females ranged from 59-324, with a mean of 173.

3) Adults did not feed.

4) Eggs measured 0.240 mm mean diameter and 0.400 mm mean length. They were spindle shaped, brown in color, with longitudinal striations, and enclosed in a gelatinous envelope which dissolved soon after oviposition. The anterior end of the egg bore a stalk and gelatinous crown.

5) Eggs required about 25 days for incubation under simulated environmental conditions. The eclosion process took about 3 hours.

6) First instar nymphs were hairy, less sclerotized and exhibited 3 segmented cerci; the mean head capsule width and wing-pad lengths were 0.17 mm and 0.11 mm, respectively.

7) Nymphs required one year of development from the egg stage to adult; water temperature was the main factor influencing seasonal growth.

8) Nymphs underwent up to 23 instars (males from 18 to 20, and females from 20 to 23 instars).

9) Growth consisted of three phases. An initial rapid increase was exhibited between instar 1 and 2. Growth remained relatively constant among nymphs from instar 3 to 11. The third phase (instar 12 to 23) was thought to be a result of sexual dimorphism of nymphs coming into effect in the 11th or 12th instar.

10) Food consisted primarily of animal matter. Major food items included Trichoptera eggs, Cheumatosyche larvae, N. clymene eggs, Chironomid larvae, Thraulodes nymphs, Simulium larvae and Nematodes.

11) N. clymene nymphs exhibited diurnal periodicity in feeding, with a predominance of nocturnal feeding.

12) Significant overlap of diets was exhibited in March and April 1971 by N. clymene and Corydallus cornutus, but no significant overlap was exhibited in May.

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CLYMENE (NEWMAN) (PLECOPTERA:PERLIDAE)

THESIS

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TABLE OF CONTENTS

	Page
LIST OF TABLES	iv
LIST OF ILLUSTRATIONS	v
Chapter	
I. INTRODUCTION	1
Description of Study Area	
II. METHODS AND MATERIALS	7
Field Methods	
Laboratory Methods	
III. RESULTS AND DISCUSSION	10
Adult	
Egg	
Nymph	
Growth	
Development	
Standing Crops	
Food	
Summary	
BIBLIOGRAPHY	52

LIST OF TABLES

Table	Page
1. Sample Date Temperatures and Dissolved Oxygen.	26
2. Stomach Contents of 443 <u>N. clymene</u> Nymphs	39
3. Electivity of Specific Food Organisms by <u>N. clymene</u>	43
4. Coefficient of Dietary Overlap Between <u>N. clymene</u> and <u>C. cornutus</u>	47

LIST OF ILLUSTRATIONS

Figure	Page
1. Egg of <u>Neoperla clymene</u>	14
2. Egg of <u>Neoperla clymene</u> After Approximately 20 Days of Incubation	16
3. First Instar Nymph of <u>Neoperla clymene</u>	18
4. Latter Instar of Nymph of <u>Neoperla clymene</u>	20
5. Seasonal Wing-pad Growth of 737 <u>N. clymene</u> nymphs .	22
6. Seasonal Head Capsule Growth of 737 <u>N. clymene</u> Nymphs	24
7. Wing-pad Length-Frequency of 737 <u>N. clymene</u> Nymphs, Illustrating Instars	28
8. Head Capsule Width-Frequency of 737 <u>N. clymene</u> Nymphs, Illustrating Instars	30
9. Wing-pad Progression With Successive <u>N. clymene</u> Instars	33
10. Head Capsule Progression With Successive <u>N.</u> <u>clymene</u> Instars	35

CHAPTER I

INTRODUCTION

Neoperla clymene, first described as Chloroperla clymene by Newman (1839), is widely distributed over the eastern and southern United States and Canada (Illies, 1966). It is apparently the only eastern Nearctic stonefly with sufficient vagility to establish populations as far southwestward as Arizona and New Mexico during and since Pleistocene glaciation (Stewart et al., unpublished). Except for the early descriptions and illustrations of adults (Newman 1839, Klápálek 1923a, Needham and Claassen 1925, Frison 1935 and Hynes 1952) and those of nymphs (Claassen 1931, Frison 1935, and Hilsenhoff 1970) and eggs (Needham and Claassen 1925 and Knight et al. 1965) little information on the biology of this species is available.

Claassen (1931) mentioned that nymphs are carnivorous, and "feed apparently largely upon insect larvae." Frison (1935) gave brief notes on seasonal distribution, succession and habits of nymphs and adults; he reported that the alimentary tract of a dissected nymph was full of insect remains,

particularly the head capsules of chironomid larvae.

Good comprehensive studies of the autecology of other stoneflies include Mackereth (1957), Minshall et al. (1966), Heiman and Knight (1970), Coleman and Hynes (1970), Langford (1971) and Radford and Hartland-Rowe (1971). Mackereth (1957) studied the seasonal distribution and feeding habits of sixteen species of Plecoptera from a single stream and its tributaries. Minshall et al. (1966) described the life history and ecology of Isoperla clio (Newman) and Isogenus decisus Walker, including feeding habits. Heiman and Knight (1970) studied the growth and development of the stonefly Paragnetina media Walker and found that growth rate varied directly with temperature. Langford (1971) investigated the distribution, abundance and life histories of stoneflies and mayflies in a British river, warmed by cooling-water from a power station. Radford and Hartland-Rowe (1971) described the life cycles of some stoneflies and mayflies in Alberta, and concluded that there seems to be a strong correlation between life cycles and food availability.

Most other studies have dealt with more specific aspects of Plecoptera life cycles and ecology. Holdsworth (1941 a & b) elucidated the total number of instars of Pteronarcys proteus Newman through measurements of head capsule width and

observations of wing-pad development. Hartland-Rowe (1964) investigated factors influencing the life histories of some stream insects in Alberta, including Plecoptera, and concluded that life histories are influenced greatly by water temperature. Relations between dissolved oxygen, temperature, and flow on the mechanical activity and survival of Pteronarcys californica Newport were reported by Knight and Gaufin (1964). Stewart et al. (1969) reported the reproductive morphology and mating behavior of Perlesta placida (Hagen). Minshall (1969) and Nebeker (1971) indicated the effect of altitude on the life histories of several species of Plecoptera. Nebeker (1971) investigated the effect of water temperature on nymphal feeding rate, emergence, and adult longevity of the stonefly Pteronarcys dorsata (Say), and found a strong correlation between water temperature and feeding. Radford and Hartland-Rowe (1971) observed the emergence patterns of Plecoptera in two mountain streams in Alberta. Food studies (Frison 1929 & 1935 ; Hynes 1941; Richardson and Gaufin 1971) have included many British Plecoptera and several species of the Northern and Western United States. Other workers (Jones 1950; Chapman and Demoray 1963) have included foods of Plecoptera in their ecological investigations of streams.

Recent excellent life history studies of other aquatic insects include those of Maxwell and Benson (1963), Lutz (1968), Benke (1969), Thut (1969), Trottier (1966 & 1971) and Murvosh (1971). Maxwell and Benson (1963) observed the wing-pad and tergite growth of mayfly nymphs of two species. Lutz (1968) used head capsule width to determine the life history of the odanate Lestes eurinus Say. Benke (1969) proposed a method of comparing individual growth rates of aquatic insects, based on head capsule width and wing-pad length. Thut (1969) studied the feeding habits of several species of the Trichoptera genus Rhyacophila. The emergence, sex ratio, and effect of temperature on the life cycle of the odanate Axax junius Drury was reported by Trottier (1961 & 1971). Murvosh (1971) presented a very comprehensive study on the ecology of the water penny beetle Psephenus herricki DeKay.

The objective of this research was to provide new and more detailed information on the life history and ecology of Neoperla clymene, through an intensive study of the species in the Brazos River, Texas. Such information, in most instances lacking for members of riffle macrobenthos communities, is desirable for structural and functional community analysis, and productivity studies.

DESCRIPTION OF STUDY AREA

The study was conducted on a large riffle just below the conjunction of the Brazos River and Dark Valley Creek above the Texas State Highway 4 Bridge, approximately 20 miles below Possum Kingdom Dam, Texas. At this site, the highly modified river flows eastward through a deep limestone canyon.

A 10 to 15 cfs leakage of cold, clear water from the Possum Kingdom Reservoir hypolimnion, through the spillway gates and turbines, maintains a minimal flow in the river, except under extreme drought conditions. Periodic discharges due to high rainfall on the upper Brazos watershed, or to hydroelectric power demand, lend very erratic flow characteristics to the river. Average discharge past the U. S. Geological Survey Highway 4 gauging station over the past 46 years has been 1,103 cfs; maximum discharge of 95,600 cfs occurred June 16, 1930. The Possum Kingdom Dam was completed in 1941, and the Reservoir largely regulates river characteristics for at least 35 miles downstream.

The substrate is deep, with gravel-rubble at the surface, intermingled with sand beginning at 5-10 cm. Except during peak discharge periods, the study riffle ranged in depth from 6 to 30 cm, and was principally confined to a narrow

channel approximately 11 meters wide, against the south canyon wall. In August 1971, in anticipation of high flows into the river from heavy rains, releases of 2750 cfs through the turbines, and flood releases through the spillway gates were initiated. These resulted in a total discharge of over 82,895 acre-feet of water through September 5, creating a flooding of the study area from 1 to 3 meter depths. For this reason, August samples were not feasible on the study riffle.

Dominant streamside vegetation at the study site consisted of Salix sp. and Ulmus sp., shading approximately one-half of the riffle during the day.

N. clymene is the only stonefly present in the modified river, although Perlesta placida occurs in the nearby Dark Valley Creek, and is occasionally picked up in light trap samples. Approximately 30 species of riffle insects are associated with N. clymene at the Brazos study site. These are discussed later in conjunction with food availability. The surface standing crops of these organisms reached maximum levels of 38,516 organisms/m² during the months of June and July.

CHAPTER II

METHODS AND MATERIALS

Three quantitative samples, for determination of standing crops and food availability, were taken with a modified Hess square-foot sampler at monthly intervals except August, throughout the period of November 1970 to October 1971. Samples were preserved, sorted, counted and weighed according to methods suggested by Hynes (1971).

Nymphal development was determined from specimens taken in the quantitative samples, and from bi-monthly qualitative samples taken in the riffle with an aquatic net and preserved in 70% alcohol. Head capsule width and wing-pad length were measured with an ocular micrometer.

Diurnal qualitative samples were taken at 6-8 am, 2-4 pm and 9-11 pm during the months of March, April, May, and July, 1971 for determination of food habits and feeding periodicity. Preparation and examination of nymphal "stomachs" followed procedures of Richardson and Gaufin (1971), except in some cases complete dissection was performed. Reference slides of associated riffle organisms and their specific sclerotized

structures were prepared for comparisons. Data were analyzed using the Electivity Index of Ivlev (1961). Spring food of N. clymene was also compared with that of Corydalis cornutus L., an associated riffle insectivore (Friday 1971, unpublished thesis) from the same sampling times, utilizing the Coefficient of Dietary Similarity of Zaret and Rand (1971).

Light trap samples were taken bi-monthly from March to September 1971 using a device described by Stewart et al. (1970), for determination of emergence cycle and adult sex ratios. Mating, fecundity, incubation and egg descriptions were determined through field and supplemental laboratory observations. The latter involved laboratory mating as described by Stewart et al. (1969), dissections of gravid females, and incubation of eggs at simulated stream temperatures and prevailing light duration, in a Percival E-50 environmental chamber.

Depth, flow and temperature were recorded for each sampling date. Depth was taken with a meter stick, and flow was measured with a Kahl Pygmy Flow meter, calibrated at 0.4714 meters per revolution; daily flow volume was also available from an adjacent U. S. Geological Survey gauging station. Temperature was taken with a total immersion °C

thermometer. Water samples were taken once during the study in June 1971, and analyzed according to Standard Methods (1965) for total hardness, chlorides, and alkalinity. D. O. (Winkler Method) and pH (portable Hach pH Kit) were taken monthly.

CHAPTER III

RESULTS AND DISCUSSION

Adult

Emergence cycles of stoneflies have perhaps been given more attention than other aspects of the life cycle (Frison 1935, Ricker 1943, Jewett 1959, Gaufin et al. 1966, Sheldon and Jewett 1967, Radford and Hartland-Rowe 1971). Harper and Pilon (1970) indicated that time of emergence of each species is similar from year to year, despite climatic variations.

Frison (1935) gave early June through August as the seasonal distribution of adult N. clymene in Illinois with the greatest abundance in July. Data from light trap samples, and supplemental data from earlier and concurrent studies on the Brazos River (two years) indicate an earlier initial emergence in Texas, beginning in May, and continuing into September. Peak emergence occurs for a two-month period in June and July. The species definitely falls into the summer-emerging category of Hynes (1970).

Emergence is nocturnal, with the greatest activity occurring approximately one hour after dusk. During peak emergence in June, great numbers of pre-emergent naiads and exuviae were observed on rocks along the waters edge.

Transformation was observed in several instances; approximately twenty minutes elapsed from the time nymphs crawled out of water onto rocks, until the light-colored adults took flight. Adults are secretive by day, and hide in shaded areas under rocks or in dense vegetation at stream-side.

The adult sex ratio of randomly samples individuals from the light box during peak emergence in late June was 1 male to 5 females (37 individuals). Since earlier and later emerging individuals were not sexed, no explanation for this unexpected ratio can be given. In a closely related species, Paragnetina media, Heiman and Knight (1970) reported only males present during the week following first emergence. It is assumed that, as in other stoneflies, N. clymene exhibits a more favorable male/female sex ratio during early phases of the emergence cycle helping to insure higher mating frequency at the onset of female emergence.

Mating was observed in many instances on the walls of the light box. These and laboratory pairings indicated mating

behavior to be quite similar to that reported for Perlesta placida by Stewart et al. (1969).

Mean fecundity of 10 dissected virgin females was 646 eggs. One to three egg masses were obtained from females held in laboratory aquaria, and they averaged 98 eggs per egg mass. The number of eggs per extruded egg mass from field-collected females ranged from 59-324, with a mean of 173. Heiman and Knight (1970) reported an estimate of 200-500 eggs per extruded mass in Paragnetina media, but made no mention of fecundity.

Exact means of oviposition was not successfully observed; however, egg masses were extruded by females held in laboratory aquaria only during the night. This, and numerous observations of egg-carrying females on the light box at night suggest nocturnal oviposition. Fruitless attempts to find females at the waters edge around rocks or vegetation, simultaneously with the night-time flights and light box observations, suggests that egg masses are dropped or washed into the water during flight. Brink (1949) and Minshall (1966) indicated this to be the typical means of oviposition in smaller species of Setipalpia.

The digestive tract of dissected field-collected adults were reduced and empty. Frison (1935) made note that most

true nocturnal forms such as Neoperla are nonfeeders, however, laboratory-held adults ingested water from saturated cotton, when offered.

Egg

Needham and Claassen (1935), and Knight et al. (1965) gave diagrammatic drawings of N. clymene eggs, but did not illustrate or discuss the gelatinous envelope or stalk. Egg measurements made during the study agree closely with those given in those two papers.

Eggs from field-collected adults averaged 0.240 mm in diameter and 0.400 mm in length. They were spindle-shaped and brown in color, with longitudinal striations (Fig. 1). At oviposition, each egg was enclosed by a gelatinous envelope, which dissolved within 24 hours. Prevention of dessication after extrusion and prior to deposition, and adherence to substrate materials at the site of oviposition (Brink 1949, Hynes 1970) are postulated functions of this envelope. Hynes (1970) discussed the advantage of such structures found on the eggs of lotic insects; retention of eggs in the area where greatest abundance of food and optimum physical conditions would prevail for hatching nymphs, should enhance survival.

Fig. 1. Egg of Neoperla clymene

The anterior end of the egg bears a stalk and gelatinous crown (Fig. 1). These apparently supplement the adhering function of the envelope. Similar gelatinous structures have been illustrated and discussed for several stonefly species (Hynes 1941, Brink 1949, Stewart et al. 1969).

Viable eggs from laboratory- and field-mated females were incubated in glass vessels, containing 500 ml of Brazos River water, at the prevailing stream temperature of 24°C. and photoperiod of 15 hours light/9 hours dark. Water was constantly aerated, and eggs were examined daily.

At approximately 20 days, eyespots of the developing nymph became evident at the posterior end of the egg (Fig. 2). Hatching began at 25 days and continued through 33 days. Impending eclosion was evidenced by a circular tearing about 0.057 mm from the posterior end of the egg, just above the nymphal pronotum. After 5 minutes, the cap, thus separated, was pushed open, with an intact "hinge" on one side, and the nymph began emergence from the egg.

The eclosion required an average of 3 hours; successful nymphs became active in the bottom of the incubation vessel. In several instances, nymphs were observed to be unable to free themselves from the egg and soon died. Attempts to rear nymphs were unsuccessful.

Fig. 2. Egg of Neoperla clymene after approximately 20 days of incubation.

Nymph

Growth.—Except for the description of habitat by Frison (1935), little information regarding N. clymene nymphal biology is available. Studies concerning seasonal growth and development, food habits and population characteristics have not been reported.

The rather standardized method of utilizing head capsule width and/or wing-pad length for characterizing development in hemimetabolous aquatic insects has been used by several workers (Wu 1923, Holdsworth 1941 a & b, Maxwell and Benson 1963, Lutz 1968, Benke 1969, and Heiman and Knight 1970). Total length has also been used (Samal 1923, Hartland-Rowe 1964, Minshall 1966, and Radford and Hartland-Rowe 1971), however, this measurement is considered somewhat unreliable due to variation in the extent of telescoping of abdominal segments.

First instar nymphs (Fig. 3), obtained from egg incubation experiments, were hairy, less sclerotized and exhibited three-segmented cerci; the mean head capsule width and wing-pad lengths were 0.17 mm and 0.11 mm, respectively. Later instar nymphs are darker tan or yellowish, bear very few

Fig. 3. First instar nymph of Neoperla clymene.

hairs, except between cercal segments, and exhibit increasing numbers of cercal segments (Fig. 4).

Seasonal growth of N. clymene nymphs is shown in Fig. 5 and 6. Most early instar nymphs begin appearing late in the summer, from the June-July adult peak emergence and oviposition. A short spurt of fall growth is experienced before a period of slow size-increase sets in through the winter. This pattern generally fits the "slow" classification of Hynes (1961). The wide size ranges or "overlap" through the winter is probably due to the prolonged emergence period of adults of the previous season. Hynes (1961) pointed out the selective advantage for carnivores in exhibiting a wide size distribution at any given time, in order that they might exploit the full range of available food.

Growth is resumed in March and continues until emergence (Figs. 5 and 6). Appearance of nymphs from early oviposition, and full-grown nymphs account for the widening size range beginning in July. Also, the absence of very early instars (expressed as low size ranges) throughout the cycle in Figs. 5 and 6 is probably due to coarseness of the sampling nets.

The lack of individuals with pre-emergent wing-pad lengths (1.77 to 2.44 mm) and head capsule widths (2.10 to

Fig. 4. Latter instar of nymph of Neoperla clymene.

2.66 mm) after September (Figs. 5 and 6), through the winter and until May, suggests that the life cycle of N. clymene is univoltine. However, the large overlap in sizes exhibited throughout the year and possible egg or nymphal diapause, unobserved throughout the study period, do not completely exclude the possibility of a 2-year cycle.

Figs. 5 and 6 show that the rate of growth of N. clymene nymphs is affected by stream temperatures. The influence of water temperature on growth of stream insects has been recently reported by several researchers (Hartland-Rowe 1964, Heiman and Knight 1970, Langford 1971, Radford and Hartland-Rowe 1971, Trottier 1971).

Temperature-DO measurements of sampling dates are given in Table 1. Dissolved oxygen never varied more than 2 ppm from O₂ saturation at recorded temperatures. Although these monthly measurements do not reflect daily fluctuations, they do indicate seasonal trends when flow is constant. It is considered that these DO characteristics of the Brazos River have little effect on survival or rate of growth of N. clymene nymphs. Knight and Gaufin (1964) studied the influence of temperature and water flow on survival of Pteronarcys californicus nymphs, which were subjected to varied exposure per-

Fig. 5. Seasonal wing-pad growth of 737 N. clymene nymphs;
vertical line=range, horizontal line=mean,
vertical bar=standard deviation.

Fig. 6. Seasonal head capsule growth of 737 N. clymene nymphs; vertical line=range, horizontal line=mean, vertical bar=standard deviation.

TABLE 1. Sample Date Temperatures and Dissolved Oxygen

Months	Recorded Temp. (°C)	Recorded DO	O ₂ Satur- ation (ppm)	Difference Between Recorded & Saturation
Nov	16	9.2	10.0	.80
Dec	11	10.4	11.1	.70
Jan	9	9.6	11.6	2.00
Feb	18	11.0	9.5	1.50
Mar	15.5	8.9	10.1	1.20
Apr	20.5	8.2	9.1	.90
May	27.5	7.0	8.0	1.00
Jun	28.0	6.1	7.9	1.80
Jul	25.0	7.1	8.4	1.30
Aug	23.0	8.8	8.7	.10
Sep	21.0	7.2	9.0	1.59
Oct	23.5	8.2	8.6	.40

1. Standard Methods (1965)

iods of reduced DO in the laboratory. They concluded that the species was able to survive intermittent and even extended periods of reduced DO without mortality.

Flow characteristics of the Brazos River are very erratic, due to factors previously mentioned. Flow through the riffle area varied from 5.8 cfs February 16, 17 to 14,300 cfs at 3 am August 31 (U. S. Geological Survey Data; Highway 4 gauging station). Apparently N. clymene nymphs are very tolerant of rivers with large flow fluctuations.

Chemical conditions in the Brazos River at the peak of development of nymphs (July) included: total hardness 512 ppm, Calcium hardness 372 ppm, Chlorides 517 ppm and alkalinity 108 ppm. Ph, taken monthly, varied from 8.0 to 8.5.

Development.-Size frequency histograms, based on wing-pad lengths and head capsule widths, are shown in Figs. 7 and 8. These indicate that N. clymene nymphs undergo up to 23 instars. Reductions in numbers of individuals with increase in development probably reflects increasing mortality; i.e. survivorship.

Variation within instars was noted (indicated by base of vertical bars) through the 17th instar. The source of this variation was not determined, but could have been a reflection

Fig. 7. Wing-pad length-frequency of 737 N. clymene
nymphs, illustrating instars.

Fig. 8. Head capsule width-frequency of 737 N. clymene
nymphs, illustrating instars.

of sexual differences. Rearing experiments and determination of pre-emergent condition, indicated that the maximum wing-pad lengths and head capsule widths of males were 1.77 to 1.99 mm and 2.10 to 2.33 mm, respectively. Therefore males underwent 18 to 20 instars. Females were also represented in these size ranges, but continued growth from 1.99 to 2.44 mm wing-pad length and 2.33 to 2.66 mm head capsule widths, indicating that they underwent 20 to 23 instars. Schoenemund (1912) found that male Perla cephalotes Dinocras cephalotes (Curtis) , passed through fewer than the 32 instars exhibited by the female.

Holdsworth (1941) sampled natural populations of Pteronarcys proteus, which requires 3 to 4 years to complete its life cycle, and found that they underwent 13 instars. This is one of the few papers that report the effect of sexual dimorphism on stonefly development during later instars. Claassen (1931) indicated a range of 22 or more instars for stoneflies reared from eggs based on the findings of Schoenemund (1912), Samal (1923) and Wu (1923). Actual determinations of instars from sampling natural populations are rare in the literature.

Logarithms of mean wing-pad lengths and head capsule widths, plotted against instar numbers (Figs. 9 and 10).

Fig. 9. Wing-pad progression with successive N. clymene
instars.

Fig. 10. Head capsule progression with successive N.
clymene instars.

INSTAR NUMBER

indicated a phasic growth of N. clymene nymphs. A geometric progression is obtained, as suggested by Dyar (1890); however, three phases are indicated. Although these figures indicate a 2.00 progression factor for wing-pad length and 2.35 for head capsule width from instar 1 through 2, an actual measurement difference of only 0.11 mm and 0.17 mm for wing-pad length and head capsule width, respectively, indicates that essentially all the early instars were detected between reared, and field-collected nymphs. A 1.19 mm (wing-pad length) and 1.15 mm (head capsule width) mean progression factor was exhibited from instars 3 through 11, and a mean progression factor of 1.08 mm (wing-pad length) and 1.31 mm (head capsule width) was exhibited in the third phase. Perhaps this was due to the influence of sexual dimorphism as early as the 11th or 12th instar. As would be expected, the overall growth progression factor decreases with increasing instar number. Holdsworth (1941) reported a similar effect in the later instars of Pteronarcys proteus nymphs. In that study, growth ratios remained somewhat constant among nymphs to the 10th instar, then decreased progressively more in females than in males; females underwent two additional instars.

Since growth is logarithmic, plots such as those in Figs. 9 and 10 should result in a straight line if all instars are

represented. However, this does not preclude a phasic growth characteristic as exemplified in N. clymene. Dyar (1890) suggested that exceptions to a constant progression ratio might occur. Most of the literature dealing with Dyar's Law has concerned insects with fewer instars than those exhibited by stoneflies.

True growth progression in the later growth phase should be expressed separately for male and female nymphs. Not until late in the study was a method for sexing N. clymene nymphs determined. A small cleft becomes evident on the 8th abdominal sternite of females, beginning as early as the 11th or 12th instar.

Standing Crops.—Based on quantitative samples taken during the study, and supplemental data from an associated community study on the riffle, standing crops of Neoperla nymphs during the study period ranged from 21.52 individuals/m² in July to 225/m² in May. Gravimetric analysis showed a maximum of 1.40 gm/m² blotted wet weight during May.

Food.—Results of stomach analyses are presented in Table 2. Of the 443 stomachs examined, 275 (62.08%) contained food items. Food consisted primarily of animal matter. Although volumetric analysis was not made, the unidentifiable plant

TABLE 2. Stomach Contents of 443 N. clymene nymphs.

	MARCH				APRIL				MAY				JULY				% OF TOTAL INGESTED ORGANISMS
	6am- 8am	2pm- 4pm	9pm- 11pm	6am- 8am	2pm- 4pm	9pm- 11pm	6am- 8am	2pm- 4pm	9pm- 11pm	6am- 8am	2pm- 4pm	9pm- 11pm	6am- 10am	2pm- 4pm	9pm- 11pm		
NUMBER OF ORGANISMS ²																	
Cladocera	1			5	2	6										.63	
Copopoda																2.74	
Diptera																	
Chironomidae																	
Larvae	1		7	3	2	4	1	3	6	3	2	2				7.17	
Pupae					4		2	1				7				2.95	
Simuliidae																	
Simulium	12	3		3		8	1		1							5.90	
Ephemeroptera																	
Baetidae																	
Isonychia										1						.21	
Heptageniidae																	
Heptagenia															1	.21	
Leptophlebiidae																	
Thraulodes	2	2	4	4	1	4	2	4	5	6						6.32	
Lepidoptera																	
Pyralidae																	
Elophila					2			1					1			.84	
Nematoda			1		1		1				6		12	2		4.85	
Plecoptera																	
N. clymene									2		1	1				1.47	
N. clymene egg										3	1	33				7.80	

TABLE 2. Continued

TABLE 2. Continued

	MARCH			APRIL			MAY			JULY			% OF TOTAL INGESTED ORGANISMS
	6am- 8am	2pm- 4pm	9pm- 11pm	6am- 8am	2pm- 4pm	9pm- 11pm	6am- 8am	2pm- 4pm	9pm- 11pm	6am- 10am	2pm- 4pm	9pm- 11pm	
NUMBER OF ORGANISMS ²													
Trichoptera													
Hydropsychidae				4	2	3	3	1	4	20	5	12	10.94
<u>Cheumatosynche</u>													
Philopotamidae									1	3	1		1.05
<u>Chimarra</u>				1						77	31	115	46.94
Trichoptera eggs													
Monthly Total	29	59	41								346		
Empty Stomachs													
(%)	34.8	60.0	53.8	40.5	57.6	25.9	37.9	54.3	30.1	31.7	42.5	20.0	
Total Stomachs	23	20	26	27	32	37	40	25	51	82	40	40	
NUMBER OF STOMACHS ³													
Unidentifiable													
Animal Matter	5	4	8	5	6	8	2	7	10	20	11	14	
Detritus		1	2	5	2	2	5	2	3	10	10	7	
Mineral	1	2	1	3	1	3		2	1	11	2		
TEMPERATURE (C)													
	14	16.5	15	18	20	19	25	27	26	24	25	27	

1. One of two samples in July was taken at 10 am.

2. Represents numbers of specific items found in the gut during each time period.

3. Represents number of stomachs in which items occurred, rather than number of organisms.

and organic material, classified as detritus, and mineral matter, were noted to make up a minor portion of stomach contents. Ingestion of these components was considered incidental in aquisition of prey, or possibly present in prey guts.

Major food items consisted of Trichoptera eggs, Cheumatopsyche larvae, N. clymene eggs, Chironomid larvae, Thraulodes nymphs, Simulium larvae and Nematodes. They represented 46.94, 10.94, 7.80, 7.18, 6.32, 5.90 and 4.85 percent of 475 ingested food items, respectively (Table 2). Trichoptera eggs and N. clymene eggs made up a large percentage of the total ration but were only ingested during the month of July, correlating with increased availability, through peak emergence and oviposition of adults.

The consistently larger percentages of empty stomachs during the 2-4 pm samples, suggest that N. clymene nymphs exhibit a diurnal periodicity in feeding. The 6-8 am and 9-11 pm samples, which would reflect night-time feeding, yielded the largest percentage of full stomachs, suggesting a predominance of nocturnal feeding.

Overall percentage of empty stomachs decreased progressively from March through July with increasing temperature.

The highest feeding rate occurred in July (Table 2). Nebeker (1971) found this relationship between temperature and feeding rate in Pteronarcys dorsata in the laboratory, and concluded that highest feeding rates occurred near temperatures which were also optimum for development and adult emergence.

An attempt to determine if N. clymene exhibits preferences in feeding on other riffle organisms was examined utilizing the Electivity Index of Ivlev (1961) (Table 3):

$$E = (r_i - p_i) / (r_i + p_i)$$

where:

r_i = relative content of any ingredient in the ration (as a percentage of the whole ration, or simply as a ratio of the particular part of the ration to the whole).

p_i = relative value of the same ingredient in the food complex of the environment.

Negative electivity is indicated by values from -1 to 0, random feeding (absence of electivity) by values of 0, and positive electivity (or feeding preference) by values from 0 to 1. Ivlev (1961) suggested that this index should be applicable to organisms other than fishes.

TABLE 3. Electivity¹ of Specific Food Organisms by N. clymene.

ORGANISMS EATEN	MARCH			APRIL			MAY			JULY		
	r _i	P _i	E	r _i	P _i	E	r _i	P _i	E	r _i	P _i	E
<u>Chironomidae</u>												
Larvae	27.58	1.22	.91	15.25	.80	.90	24.39	2.83	.79	2.03	.27	.77
Pupae				6.77	.09	.97	7.31	.03	.99	2.03	.00	1.00
<u>Simulium</u>	51.72	5.83	.79	18.64	30.24	-.24	4.87	.02	.99			
<u>Heptagenia</u>										.29	.86	-.50
<u>Isonychia</u>										.29	.07	.61
<u>Thraulodes</u>	13.79	.82	.89	15.25	10.02	.21	26.82	12.93	.35	1.74	5.23	-.87
<u>Elophila</u>				3.38	.09	.94	2.43	.08	.94	.29	.26	.05
<u>N. clymene</u>							4.87	3.06	.23	.58	.09	.73
<u>Cheumatosyche</u>				15.25	28.39	-.30	19.51	41.42	-.36	10.75	52.73	-.66
<u>Chimarra</u>				1.69	1.34	.12	2.43	.65	.58	1.16	.55	.36

$$1. E = \frac{r_i - P_i}{r_i + P_i} \quad (\text{Ivlev 1961})$$

Table 3 shows electivity indices for all organisms ingested by N. clymene nymphs, for which food availability was determined (i.e. Copepoda, Cladocera, Nematodes, N. clymene eggs and Trichoptera eggs, shown in Table 2, were not sampled).

Apparently, Chironomid larvae are available throughout the spring and N. clymene nymphs show a positive electivity or preference for them. A very strong electivity is expressed for Chironomid pupae as they become available beginning in April.

March and May electivity for Simulium larvae are high; the negative electivity expressed in April (even though approximately the same number of total larvae were consumed in March and April; Table 2) may be an expression of functional response; i.e. as Simulium larvae increase beyond a certain level, necessary for forming a critical percentage of N. clymene food, proportionately fewer are taken. Simulium were unavailable on the study riffle, during July sampling.

The mayflies Heptagenia and Isonychia, although available on the riffle during March-May, were not ingested by N. clymene presumably because they were in late instars and were above prey threshold size; hatchlings from spring emergence, became available beginning in July. Positive election was

exhibited for Isonychia and negative election for Heptagenia.

Even though the Pyralid Lepidopteran Elophila occurred in sparse density, positive electivity is shown for it by N. clymene in April and May, and its utilization approaches randomness in July (Table 3).

N. clymene exhibited cannibalism in May and June. Electivity increased from May to July, when larger numbers of late instar nymphs were present.

Although the caddisfly Cheumatopsyche made up a significant portion of the ration of N. clymene, negative electivity was expressed, perhaps a functional response as discussed previously for Simulium. Cheumatopsyche is by far the most dominant organism in the study riffle macrobenthos, throughout the year. A consistent positive electivity was shown for Chimarra.

These data are consistent with previous studies indicating the predominance (and preference?) of Chironomids, Simuliids and mayflies as dietary components of carnivorous stonefly nymphs (Jones 1950, Mackereth 1957, Minshall et al. 1966, and Richardson and Gaufin 1971).

In an attempt to compare feeding of N. clymene with the associated carnivore Corydalus cornutus, the extent of dietary

overlap (Zaret and Rand 1971) was calculated (Table 4) by the following equation:

$$\hat{C} = \frac{2 \sum_{i=1}^S X_i Y_i}{\sum_{i=1}^S X_i^2 + \sum_{i=1}^S Y_i^2}$$

where: C = overlap coefficient

S = total number of food categories

X_i = that proportion of total diet of species

X taken from a given category of food i.

C varies from 0, when the samples are completely distinct (containing no food categories in common), to 1 when the samples are identical with respect to proportional food category composition. Values greater than 0.60 indicate significant overlap. Stomach data for C. cornutus, for the same time period, were utilized from Friday (1971).

Both predators utilized Chironomid larvae and pupae, Simulium, the mayfly Thraulodes, Elophila, N. clymene and Cheumatopsyche, at some time through the 3-month period.

Monthly coefficients of dietary overlap (Table 4) indicated that significant dietary overlap occurred between these two predators during March and April. Significant overlap was

TABLE 4. Coefficient of Dietary Overlap Between
N. clymene and C. cornutus.

	MARCH		APRIL		MAY	
	C = .73		C = .72		C = .54	
	X_i^1	Y_i^2	X_i	Y_i	X_i	Y_i
<u>Stenelmis</u>				1.63		.53
Chironomidae						
Larvae	27.58	2.08	15.25	1.63	24.39	11.22
Pupae			6.77		7.31	.53
<u>Simulium</u>	51.72	39.58	18.64	37.70	4.87	9.09
Pupae		2.08		6.55		4.27
<u>Tabanus</u>		2.08				
<u>Isonychia</u>		4.16		1.63		.53
Caenidae				1.63		3.74
<u>Heptagenia</u>				1.63		
<u>Thraulodes</u>	13.79		15.25	6.55	26.82	1.60
<u>Elophila</u>		2.08	3.38		2.43	1.60
<u>N. clymene</u>		2.08			4.87	3.20
<u>Cheumatopsyche</u>		14.58	15.25	21.31	19.51	32.08
<u>Hydropsyche</u>		14.58		9.83		25.13
Hydroptilidae						
Case		6.25				2.67
Pupae				1.63		
Leptoceridae				1.63		
Limnephilidae						.53
<u>Chimarra</u>			1.69		2.43	
Misc. Adults		2.08				
Misc. Pupae		6.25		1.63		2.67

1. X_i - % of total ration each food item represents in N. clymene stomachs.

2. Y_i - % of total ration each food item represents in C. cornutus stomachs.

not exhibited in May, perhaps due to the 38.4% representation of Simulium pupae (4.27%), Caneid mayflies (3.74%), Hydropsyche (25.13%), Hydroptilids (2.67%) and miscellaneous pupae (2.67%) in the diets of Corydalis; these organisms were never eaten by N. clymene, and the larger percentage of Hydropsyche in the May Corydalis stomachs represented a shift in overall diet.

Organisms present on the riffle, that were not ingested by N. clymene through the March-July sampling period included Turbellaria, Sphaeromidae, Talitridae, Baetis, Caenis, Centroptilum, Hexagenia, Tricorythodes, Didymops, Erpetogomphus, Gomphus, Argia, Hydropsyche, Leptoceridae, Limnephilidae, Rhyacophilidae, Psychomyiidae, Hydroptilidae, Elmidae, Dryopidae, Tabanidae, Planorbidae, Ancyliidae, and Sphaeridae.

Summary

1. The life history of Neoperla clymene (Newman) was studied over a 12-month period from November, 1970 to October, 1971.

2. Emergence and oviposition of adults was nocturnal reaching a peak during the months of June and July.

3. Mean fecundity of virgin females was determined to

be 646 eggs. Up to 3 egg masses were obtained from females held in laboratory aquaria, and they averaged 98 eggs per egg mass. The number of eggs per egg mass from field-collected females ranged from 59-324, with a mean of 173.

4. The digestive tract of dissected field-collected adults were reduced and empty, however, laboratory-held adults ingested water from saturated cotton, when offered.

5. Eggs from field-collected adults measured 0.240 mm mean diameter and 0.400 mm mean length. They were spindle shaped, brown in color, with longitudinal striations, and enclosed in a gelatinous envelope which dissolved soon after oviposition. The anterior end of the egg bore a stalk and gelatinous crown.

6. Viable eggs from laboratory and field-mated females required 25 days for incubation under simulated environmental conditions. The eclosion took an average of 3 hours.

7. First instar nymphs, obtained from egg incubation experiments, were hairy, less sclerotized, and exhibited 3 segmented cerci; the mean head capsule width and wing-pad lengths were 0.17 mm and 0.11 mm, respectively.

8. A plot of monthly head capsule widths and wing-pad lengths indicated that nymphs require one year of development

from the egg stage to adult. Water temperature was suggested as the main factor influencing seasonal growth.

9. Size-frequency histograms of head capsule width and wing-pad lengths indicated a total of 23 instars, with males undergoing 18 to 20 instars and females 20 to 23 instars, due to sexual dimorphism exhibited by pre-emergent nymphs.

10. A plot of the log of mean head capsule widths and wing-pad lengths against instar number indicated that growth consisted of three phases. An initial rapid increase was exhibited between instar 1 and 2. Growth remained relatively constant among nymphs from instar 3 to 11. The third phase (instar 12 to 23) was thought to be a result of sexual dimorphism of nymphs coming into effect in the 11th or 12th instar.

11. Based on quantitative samples taken during the study, and supplemental data from an associated community study on the riffle, standing crops of N. clymene nymphs ranged from 21.52 individuals/m² in July to 225/m² in May. Gravimetric analysis showed a maximum of 1.40 gm/m² blotted wet weight during May.

12. Of the 443 stomachs examined during the months of March, April, May, and July 1971, 275 (62.08%) contained food items. Food consisted primarily of animal matter. Major

food items included Trichoptera eggs, Cheumatosyche larvae, Thraulodes nymphs, N. clymene eggs, Chironomid larvae, Simulium larvae and Nematodes.

13. N. clymene nymphs exhibited diurnal periodicity in feeding with a predominance of nocturnal feeding.

14. Food preference of N. clymene nymphs was examined utilizing the Electivity Index of Ivlev (1961). Chironomid larvae and pupae, the Pyralid Lepidopteran Elophila, and the Trichopteran larvae Chimarra were positively elected for whenever available. The Dipteran Simulium, the Ephemeropterans Heptagenia and Isonychia, and the Trichopteran larvae Cheumatosyche exhibited either a shift of electivity or negative electivity entirely which was thought to be a functional response. N. clymene nymphs also exhibited cannibalism in May and June.

15. In an attempt to compare feeding of N. clymene with the associated carnivore Corydalis cornutus, the extent of dietary overlap (Zaret and Rand, 1971) was calculated. Monthly coefficients of dietary overlap indicated that significant overlap occurred between these two predators during March and April. Significant overlap was not exhibited in May.

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