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THE ECOLOGY AND DISTRIBUTION OF IMMATURE BLACK FLIES (DIPTERA: SIMULIIDAE) OF THE ROSE LAKE WILDLIFE RESEARCH AREA, MICHIGAN

By

Douglas H. Ross

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ABSTRACT

THE ECOLOGY AND DISTRIBUTION OF IMMATURE BLACK FLIES (DIPTERA: SIMULIIDAE) OF THE ROSE LAKE WILDLIFE RESEARCH AREA, MICHIGAN

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Sixteen species of Simuliidae were collected from the Rose Lake Wildlife Research Area. *Stegopterna mutata* (Malloch), *Simulium verecundum* Stone and Jamnback and *S. vittatum* Zetterstedt were the most widespread and abundant species. *Cnephia ornithophilia* Davies, Peterson and Wood and *S. vernum* Macquart are new records for the state.

The larval instars of four simuliid species were determined. *Prosimulium fuscum* Syme and Davies, *P. mixtum* Syme and Davies and *S. vittatum* had seven instars, and *St. mutata* had six.

Stream temperature was the most important physical factor regulating larval simuliid population dynamics, determining hatching times and developmental rates. *Prosimulium mixtum/fuscum* required 435°D (degree-days) above 32°F for maturation, while *St. mutata* and *C. dacotensis* Dyar and Shannon needed 450-500 and 860°D, respectively. Stream discharge also influenced the annual dynamics of simuliid populations. Differences in temperature, discharge and chemical properties of different streams could not be related to simuliid species distribution.

ACKNOWLEDGMENTS

I would like to thank Dr. Richard W. Merritt for his enthusiasm, guidance and support in the course of this study. The value of his contributions cannot be adequately described.

I am also indebted to my guidance committee, Drs. K. W. Cummins, F. W. Stehr and J. N. Stuht. Working with them has been a valuable experience.

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My parents deserve a special note of thanks for their patience, support and understanding during these last two years. Without this, my work would have been much more difficult.

And to Penny, for helping me get through it all.

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GENERAL INTRODUCTION

Black flies have a significant impact on man, as well as domestic and wild animals. Certain species of blood-feeding simuliids are known vectors of <u>Onchocerca volvulus</u> (Leuckart), a filarial nematode causing "river blindness" in tropical countries (Crosskey 1973, Jamnback 1973). Arthropod-borne viruses, such as Eastern Equine, Venezuelan and California encephalitides have also been isolated from black flies (Anderson <u>et al</u>. 1961, Sanmartin <u>et al</u>. 1967, Sommerman 1977). Furthermore, simuliid bites are annoying and irritating, causing an array of pathological conditions collectively termed "black fly fever" (Jamnback 1973). Repeated attacks can lead to hypersensitivity reactions requiring hospitalization (Fredeen 1969, Jamnback 1976, Newson 1977). Black fly outbreaks have hindered lumbering, construction and mining during the early spring and summer in fly-infested areas (Fallis 1964, Jamnback 1973, 1976, Watts 1976). Attacks by black flies are also a major deterrent to tourism and related activities (e.g., fishing, hiking, camping, etc.) (Metcalf and Sanderson 1931, Sleeper 1975, Newson 1977, Merritt and Newson 1977).

Both domestic and wild animals also suffer from simuliid attacks. In addition to annoying cattle and reducing meat and milk production (Rempel and Arnason 1947, Fredeen 1956, 1969, Steelman 1976, Hunter and Moorhouse 1976), black flies also cause severe dermatitis and even death in some instances (Burghardt *et al*. 1951, Cameron 1918, Bradley 1935, Fredeen 1956, 1969). Cattle losses resulting from nodules caused by *Onchocerca gutturosa* Neumann and other simuliid-borne nematodes were significant in Australia, Germany, Siberia and South America (Dalmat 1955). In addition, Simuliidae are vectors of *Setaria equina* (Abildgaard), a horse-infesting filarial nematode, and vesicular stomatitis virus (Dalmat 1955, Ferris *et al*. 1955). Sheep, elk and whitetail deer are also attacked by several black fly species (Davies and Peterson 1956, R. Stolz, Department of Entomology, University of Idaho, pers. comm.).

Black flies are known vectors of avian blood parasites. Domestic turkey production in South Carolina during 1969 was decreased significantly by *Leucocytozoon smithi* (Lavern and Lucet) (Sporozoa: Leucocytozoidae) (Noblet and Moore 1975, Noblet *et al*. 1976). Various species of simuliids also transmit *L. bonasae* Clarke to ruffed grouse (Fallis and Bennett 1958), and infections of *L. simondi* Mathis and Leger have caused high mortality (84%) in Canada goose goslings (Tarshis 1972, Herman *et al*. 1975).

Several investigations have been conducted on North American Simuliidae. The black flies of Alabama (Stone and Snoddy 1969), Alaska (Stone 1952, Sommerman 1953, Sommerman *et al*. 1955), Alberta (Abdelnur 1968), eastern Canada (Twinn 1936), Canada and Alaska (genus *Prosimulium* Roubaud) (Peterson 1970), Connecticut (Stone 1964), Minnesota (Nicholson and Mickel 1950), New York (Stone and Jamnback 1955), Ontario (Davies *et al*. 1962, Wood *et al*. 1963), Quebec (Wolfe and Peterson 1959), Utah (Peterson 1960) and Wisconsin (Anderson and Dicke 1960) have been extensively studied. However, very little work has been conducted on Michigan Simuliidae, except for the studies by Wu (1931) and Gill and West (1954) on simuliid ecology and that of Tarshis (unpubl. data, 1963-1973) in the Upper Peninsula. The latter author investigated the role of black flies in leucocytozoonosis of waterfowl.

The objectives of this study were: (1) to determine the species composition, distribution and seasonal abundance of black flies in the Rose Lake Wildlife Research Area; (2) to determine the larval instars and population dynamics of *Prosimulium mixtum* Syme and Davies, *P*. *fuscum* Syme and Davies, *Stegopterna mutata* (Malloch) and *Cnephia dacotensis* Dyar and Shannon; and (3) to determine the effects of different temperatures on the growth and development of *P*. *mixtum* and *P*. *fuscum* larvae in the laboratory. Since immature *P*. *mixtum* and *P*. *fuscum* larvae cannot be separated, they were treated as the *P*. *mixtum/fuscum* complex (Syme and Davies 1958, Davies and Syme 1958) in this study.

PART I

THE LARVAL INSTARS AND POPULATION DYNAMICS OF FIVE SPECIES OF BLACK FLIES (DIPTERA: SIMULIIDAE) AND THEIR RESPONSES TO SELECTED ENVIRONMENTAL FACTORS

INTRODUCTION

The family Simuliidae has been studied extensively due to the medical, economic and veterinary impact of its blood-feeding females (Crosskey 1973, Jamnback 1973, 1976, Steelman 1976). The filter-feeding larvae are important detritivores in lotic habitats (Maciolek and Tunzi 1968, Ladle *et al.* 1972, Cummins 1974, Reisen 1974).

In spite of the significance of this group, the bionomics of many species of black flies remains unknown. Large general studies on the biology, life histories and taxonomy of regional fauna have been conducted, but detailed works on the ecology and population dynamics of individual species are uncommon. Davies (1961) has studied the adult ecology and parity of two *Prosimulium* spp. in Ontario. Field studies by Davies and Smith (1958), Anderson and Dicke (1960), Ladle *et al.* (1972), Ladle and Esmat (1973) and Lewis and Bennett (1974b, 1975) have investigated the life histories of various species, while Reisen (1975, 1977) presented population dynamics and life table data for *Simulium* spp. Laboratory research on the physiology of hibernation of *P. mysticum* Peterson (Mansingh *et al.* 1972, Mansingh and Steele 1973) and larval biology of *S. venustum* Say (Mokry 1976) have also been conducted. Other authors have determined the number of larval instars, with varying values of four (Puri 1925, Smart 1934), six (Cameron 1922, Terterjan 1956, Harrod 1964, Stone and Snoddy 1969, Reisen 1975, Mokry 1976), seven (Johnson and Pengelley 1969, Jedlicka 1972, Mansingh and Steele 1973, Fredeen 1976), eight (Smith 1969) and nine (Crosby 1974, Craig 1975) being found.

This investigation examines the larval instars and population dynamics of four species of Simuliidae (*Prosimulium mixtum* Syme and Davies, *P. fuscum* Syme and Davies, *Stegopterna mutata* (Malloch) and *Cnephia dacotensis* Dyar and Shannon) and their responses to various physical factors. Larval instars of a fifth species, *Simulium vittatum* Zetterstedt, were also determined. Due to the difficulty in separating immature *P. mixtum* and *P. fuscum* larvae, they were grouped together as the *P. mixtum/fuscum* complex (Syme and Davies 1958).

MATERIALS AND METHODS

Study Area

Field work was conducted at the Rose Lake Wildlife Research Area (Clinton and Shiawassee counties), which is owned and operated by the Michigan Department of Natural Resources. The 1350-hectare area contains seven lakes, numerous ponds and nine streams which contain black flies. *Prosimulium mixtum/fuscum* and *St. mutata* were studied in Mud Creek (Site 15) and *C. dacotensis* in the Rose Lake outlet (Site 13). Larvae of *S. vittatum* were collected from Shaw Lake outlet, Byron, Michigan (Shiawassee county) as part of another study.

Field Studies

To obtain estimates of relative abundance of simuliids, artificial substrates were used for sampling (Williams and Obeng 1962, Disney 1972, Ali *et al.* 1974, Lewis and Bennett 1974a). These were made by attaching polythene strips to 30 cm. metal dowels with waterproof pressure-sensitive tape. Strips of different lengths were tested to determine if strip size affected estimates of density. Since no differences were found between 25, 50 and 100 cm. long strips (all 2.5 cm. wide), the smallest was selected to reduce the number of larvae which had to be counted in the laboratory.

Preliminary sampling indicated that larval black flies followed a negative binomial distribution. Analysis of these samples, using the moment estimate of $\underline{k}$ (Elliot 1971), was performed to determine the number of samplers needed. At each site dowels were placed vertically in a 1 m^2 area of substrate at randomly selected coordinates. Samples were collected weekly and larvae were removed from tapes and preserved in 95% ethanol. Attempts were also made to obtain independent estimates of abundance and species composition by measuring macroinvertebrate drift (Waters 1972).

Physical Factors

Stream temperatures were measured with a Weather-measure® three-point recording thermograph (Site 15) and max/min thermometers (Sites 13 and 15). Temperature data were used to calculate degree-days (^{o}D) with the formula: $^{o}D = (Tmax + Tmin) / 2 - 32^{o}F$ (Gage and Haynes 1973). Degree-days accumulated from the initial appearance of first instars to the collection of pupae were used to estimate the physiological time required for larval development of each species. Water velocities were measured using a Gurley Pygmy current meter and used to calculate discharge. Once sufficient data had been collected regression equations (Gill 1978) were calculated to estimate discharge from water depth ($R^2 \geq .9$).

Laboratory Studies

The procedures used for the analysis of field samples are outlined in Figure 1. Subsampling was accomplished with a device modified from Waters (1969), and species identifications were verified by Dr. B. V. Peterson of Agriculture Canada. Post-genal lengths of larval head capsules (Fredeen 1976) were used to construct the length frequency distributions. Analysis of variance by ranks (Kruskal and Wallis 1952, Zar 1974) and distribution-free multiple comparisons (Dunn 1964, Hollander and Wolfe 1973) were applied to the data to determine the number of larval instars. In addition to biometrical techniques, graphical methods (Harding 1949) and morphological characters were also used to separate instars. Each instar series was checked for completeness by plotting the mean post-genal length of each stage against instar number. Any deviation from a straight line indicated that an instar had been missed (Dyar 1890, Wigglesworth 1965).

Rearing Experiments

Containers made from 4-liter plastic pails placed in vermiculite-insulated wastebaskets were used for laboratory rearing. Baskets were kept in a 35°F (1.7°C) walk-in refrigerator and maintained at temperatures of 37, 42, 47, 52 and 57°F with aquarium thermometers. Each pail was equipped with a compressed air source and a thermocouple (connected to a potentiometer to record temperature). Larvae of *P. mixtum/fuscum* (instars 1-3) were collected from

Mud Creek and placed in the rearing tanks. Temperatures were set at 35°F in all tanks when the larvae were introduced (approximating Mud Creek water temperature), and then gradually raised to the desired levels. Natural stream water without a food supplement was used in the containers and changed every five days. Larvae in each pail were sampled every 100°D (varying from 4-20 days), preserved in 95% ethanol and measured to determine mean post-genal lengths.

One-way analysis of variance (with the temperatures as quantitative treatments) and orthogonal contrasts were used to test for differences in the data. Orthogonal polynomial contrasts were applied to the data to determine if any first- to fourth-order equation(s) existed to describe growth patterns (Gill 1978). Preliminary rearing at 42 and 52°F with larvae of S. vittatum was used to estimate variance and calculate proper sample size for the contrasts (Gill 1978).

Late instars of P. mixtum/fuscum were reared in two glass aquaria (after Tarshis 1968) in an environmental chamber (light:dark ratio = 12:12) to investigate the relationship between temperature and pupation. Initial water temperatures were 1°C and were increased 1°C every five days (when water was also changed).

RESULTS AND DISCUSSION

Effects of Discharge on Larval Population Dynamics

The number of black flies colonizing artificial substrates at Site 15 was negatively correlated (r = -.43) with the change in discharge between sampling dates (Fig. 2). Detachment of larval black flies induced by fluctuations in discharge has been observed by other investigators (Zahar 1951, Yakuba 1959, Carlsson 1967, Lewis and Bennett 1975); however, few studies considered the possible influence of discharge on estimates of relative abundance. Clearly, discharge and many other variables (color, depth, exposure time, shape, size and species preference of substrates) must be considered if meaningful estimates of black fly populations are to be obtained (Disney 1972, Pegel and Rühm 1976, Gersabeck 1977). The data reported here on the dynamics of simuliid populations dealt with changes in population age structure through time rather than absolute or relative densities.

Discharge also significantly influenced the annual life cycles of some simuliid species. Exceptionally dry conditions in summer and autumn of 1976 reduced the discharge of Mud Creek approximately 50%, leaving much of the stream bed at Site 15 exposed yet still moist. First instars of

P. mixtum/fuscum and St. mutata appeared in November and January respectively, diminishing in February to less than two percent of the population. However, when melting snow increased discharge in late February, many eggs within the freshly inundated sediments hatched, producing second cohorts of these univoltine species. This was not observed in 1975-1976, when discharge was significantly higher throughout fall and winter.

Although several investigators (Pearson and Franklin 1968, Cowell and Carew 1976, Armitage 1977) have reported that Simuliidae are an important component of stream invertebrate drift, no black fly larvae were collected in drift samples during the present study. This failure may have been caused by low water temperature and discharge, which have been shown to significantly decrease drift during winter (Bishop and Hynes 1969, Waters 1972, Cowell and Carew 1976, Armitage 1977).

Larval Instar Determination

Post-genal length frequency distributions of the first and second cohorts of P. mixtum/fuscum indicated seven and six instars respectively (Fig. 3). Statistical differences between the stages were highly significant ($P < .01$) with the exception of the last two instars of each cohort. However, these were easily separated by the degree of development of the pupal respiratory organ and the graphical method of Harding (1949). Data from the single cohort which occurred in 1975-1976 indicated seven larval instars.

Both cohorts of St. mutata had six instars, and the combined data are shown in Fig. 4. Although statistical analysis indicated five instars ($P < .01$), application of Dyar's (1890) rule revealed a missing instar where the second is shown (Fig. 4). This species also passed through six instars in the previous year.

Analyses were unable to precisely determine the number of instars of C. dacotensis (Fig. 5). Stages 1, 2 and 3 were significantly different from one another and from the remaining group ($P < .01$); however, neither head width, post-genal nor body length would segregate the other instars. Development of the pupal respiratory organ showed three distinct stages within the larger larvae, suggesting six instars; but head and body dimensions overlapped to such an extent that this value can only be regarded as tentative.

Simulium vittatum passed through seven instars which were all significantly different ($P < .01$) (Fig. 6). The length frequency distribution of total body lengths also showed seven distinct groups of larvae.

For all species, except C. dacotensis, the log (base 10) of the mean size of each instar was plotted against the instar number. In each case the data closely approximated a straight line ($R^2 \geq .98$), indicating that no instars had been overlooked (Wigglesworth 1965).

Larval Population Dynamics

Larval development of the two cohorts of P. mixtum/fuscum differed markedly (Figs. 7 and 8). Eggs of the first cohort hatched over a three month period; however, instar development did not proceed much beyond the fourth stage until the end of February, when snow had melted and water temperature increased. Following a period of rapid growth, seventh instars accumulated and pupated synchronously, with few larvae remaining on 9 April, 1977.

Development of the second cohort was more rapid than the first (Fig. 8). Egg hatching lasted only six weeks, and there was no evidence of impeded growth. Last instars were present after six weeks, and pupation was asynchronous, as indicated by the decrease in sixth instars from 20 to 27 April and their subsequent increase again until 11 May (Fig. 8). Both cohorts of P. mixtum/fuscum required approximately 435°D above 32°F for larval development (Fig. 9).

Both genetic and environmental factors may be responsible for the differences in number of instars between genera and congeneric species. The present study showed that the annual population dynamics and number of instars varied in two coexisting cohorts of P. mixtum/fuscum. This was evident in both species of the complex. Differences in the development of these cohorts were largely a result of temperature, or more accurately, heat input. Although both cohorts required essentially the same number of degree-days for larval growth (first cohort, 433°D; second cohort, 437°D) (Fig. 9), larvae of the second cohort matured faster, were smaller in size and had fewer instars than the first cohort (Figs. 3, 7 and 8). Thus, temperature not only influences geographical and local distribution of black flies (Sommerman _et_ _al_. 1955, Macan 1962, Hynes 1970), but also the annual dynamics of single species.

The retarded growth of _P_. _mixtum/fuscum_ observed at low water temperatures agreed with findings of Mansingh _et_ _al_. (1972) and Mansingh and Steele (1973) on a closely related species, _P_. _mysticum_ Peterson. They found that larval growth was very slow below 4°C, and used the term "oligopause" (Mansingh 1971) to describe this state of hibernation intermediate between quiescence and diapause.

The dynamics of the two cohorts of _St_. _mutata_ were similar to those of _P_. _mixtum/fuscum_, and probably also the result of varying degree-day intensities (Fig. 10). Low water temperature prevented significant growth of first cohort larvae beyond the fourth instar until March, when development increased rapidly. Sixth instars accounted for the entire population by 6 April, and synchronous pupation followed shortly thereafter (Fig. 10). Eggs of the second cohort hatched during the first three weeks of March, and larvae grew rapidly, pupating after five weeks. The decrease in sixth instars in late April and their ensuing increase in early May indicated that pupation was asynchronous in the second cohort of _St_. _mutata_ (Fig. 10).

The failure to collect early instars of the first cohort (artificial substrates may have been unsuitable for sampling this species at low discharge) and the difficulty in locating pupae (Davies et al. 1962), made accurate measurement of developmental degree-days difficult. The best estimates obtained ranged from 450-500°D above 32°F.

In contrast to P. mixtum/fuscum, the number of instars of both cohorts of St. mutata in 1977 was constant and the same as the single cohort of the previous year. Data from 1975-1976 also indicated that St. mutata normally pupates later than P. mixtum/fuscum. Thus, the former species may be better adapted to higher stream temperatures, and less likely to undergo the types of temperature-related developmental changes evident in the second cohort of P. mixtum/fuscum.

Eggs of C. dacotensis hatched in less than three weeks, and the first pupae were found 42 days later (Fig. 11). Although the chronological time needed for larval development was short (six weeks), the physiological time required by this species was 860°D above 32°F, much greater than either P. mixtum/fuscum or St. mutata (Figs. 9 and 11). Since females of Cnephia dacotensis do not feed (Krafchick 1942, Nicholson 1945, Stone 1964), it is possible that a longer developmental (physiological) time may be necessary to acquire nutrients for egg maturation. This hypothesis was supported by Davies and Peterson (1956) who found mature eggs in emerging females of C. dacotensis.

Larvae of this species did not hatch until stream temperatures increased in early spring, and a threshold of 32°F used in degree-day calculations for C. dacotensis may be too low, resulting in an overestimate of developmental time. Controlled rearing experiments like those of Mokry (1976) are necessary to establish exact developmental thresholds.

Estimates of degree-days necessary for larval development of P. mixtum/fuscum (435°D) and St. mutata (450-500°D) were similar to that of Davies et al. (1962) for Simulium venustum Say (500°D); however, they differed from those of Davies and Syme (1958) for P. mixtum/fuscum (2000°D) and Mokry (1976) for S. venustum (1000°D). These figures were all based on a threshold of 32°F; however, Davies and Syme (1958) did not present the exact methods used in their calculations. Mokry (pers. comm.) could not account for the large difference between the two estimates; however, since S. venustum cannot complete development below 50°F (Mokry 1976), using 32°F as the developmental threshold could result in an overestimate. If Mokry's calculations were repeated using the higher threshold temperature, the estimate approaches 450-500°D, similar to the values reported here.

Rearing Experiments

Due to excessive mortality at the three highest temperatures, only two samples of P. mixtum/fuscum larvae were collected from each rearing container before the experiment was terminated. Differences in growth between the treatments were insignificant after both 100 and 200°D. Accordingly, no equation of any order was significant in describing the patterns of growth.

These data were similar to results obtained by Mansingh _et al_. (1972) on _P_. _mysticum_ and Davies and Smith (1958), who worked with the closely related Palearctic species _P_. _hirtipes_ Fries. These studies found high larval mortality (97%) within five days at temperatures above 16°C, supporting Rubzov's (1940) hypothesis that such overwintering larvae are cold water stenotherms.

Successful development of the second cohort of _P_. _mixtum_/_fuscum_ in the field was contrary to the above laboratory data. Average stream temperatures during the final month of larval growth exceeded 10°C, with maximums frequently above 20°C. Although these warm conditions may have increased mortality, larvae of the second cohort did mature and pupate (Fig. 8). Carefully conducted rearing experiments, using artificial streams instead of various types of aquaria, are necessary to resolve these discrepancies.

Results from the pupation experiment neither supported nor conclusively refuted the concept of a threshold temperature for pupation (Anderson and Dicke 1960, Davies 1961). No pupae were observed until temperatures were raised to 5°C; however, no synchrony occurred among these larvae. In the two years of this study, pupae of _P_. _mixtum_/_fuscum_ were never encountered until a daily maximum water temperature of 10°C had been recorded in the field. This suggested that a temperature shock (i.e., the occurrence of some maximum temperature for the first time in a year) may trigger the synchronous pupation of these larvae.

Fig. 1. Laboratory procedures used in the analysis of field samples of black fly larvae.

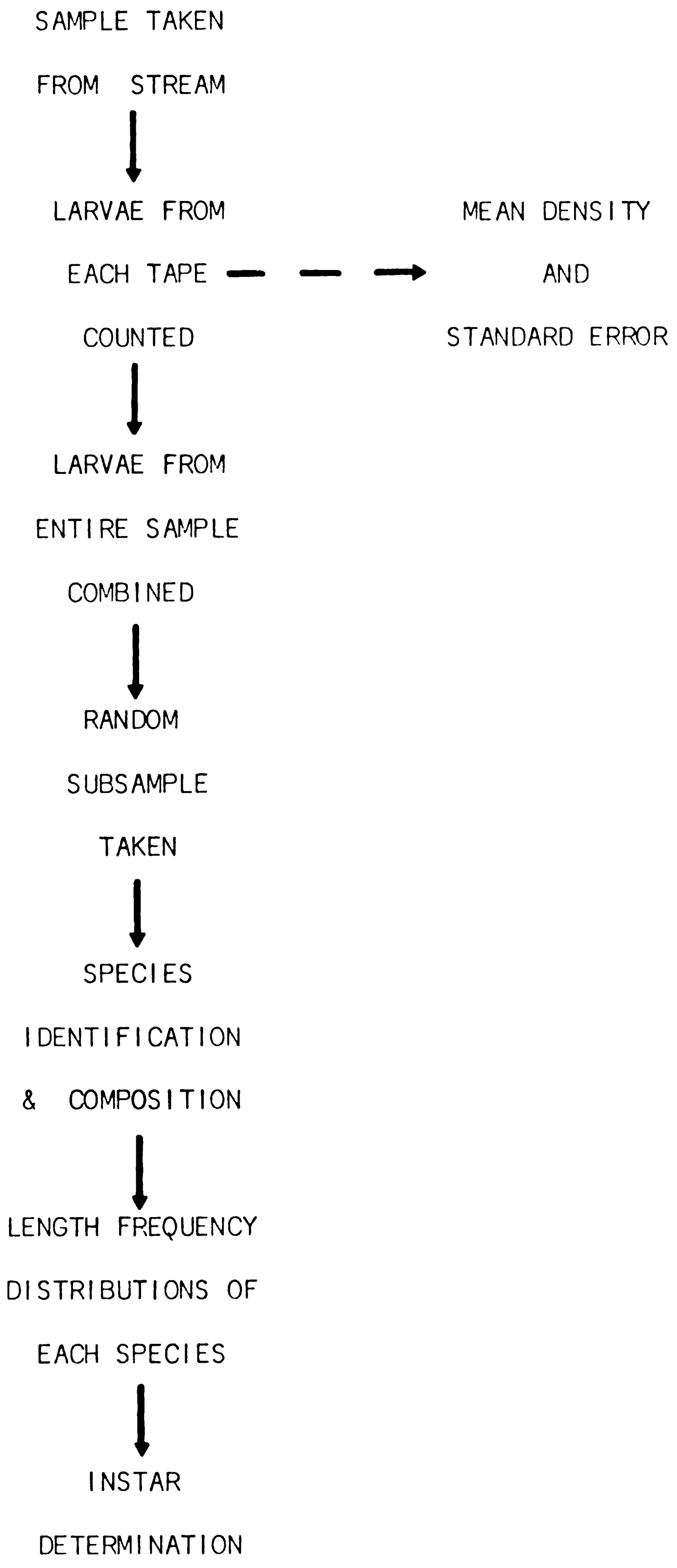

SAMPLE TAKEN FROM STREAM
LARVAE FROM EACH TAPE COUNTED
MEAN DENSITY AND STANDARD ERROR
LARVAE FROM ENTIRE SAMPLE COMBINED
RANDOM SUBSAMPLE TAKEN
SPECIES IDENTIFICATION & COMPOSITION
LENGTH FREQUENCY DISTRIBUTIONS OF EACH SPECIES
INSTAR DETERMINATION

Fig. 2. Correlation between change in stream discharge and change in numbers of black fly larvae on artificial substrates.

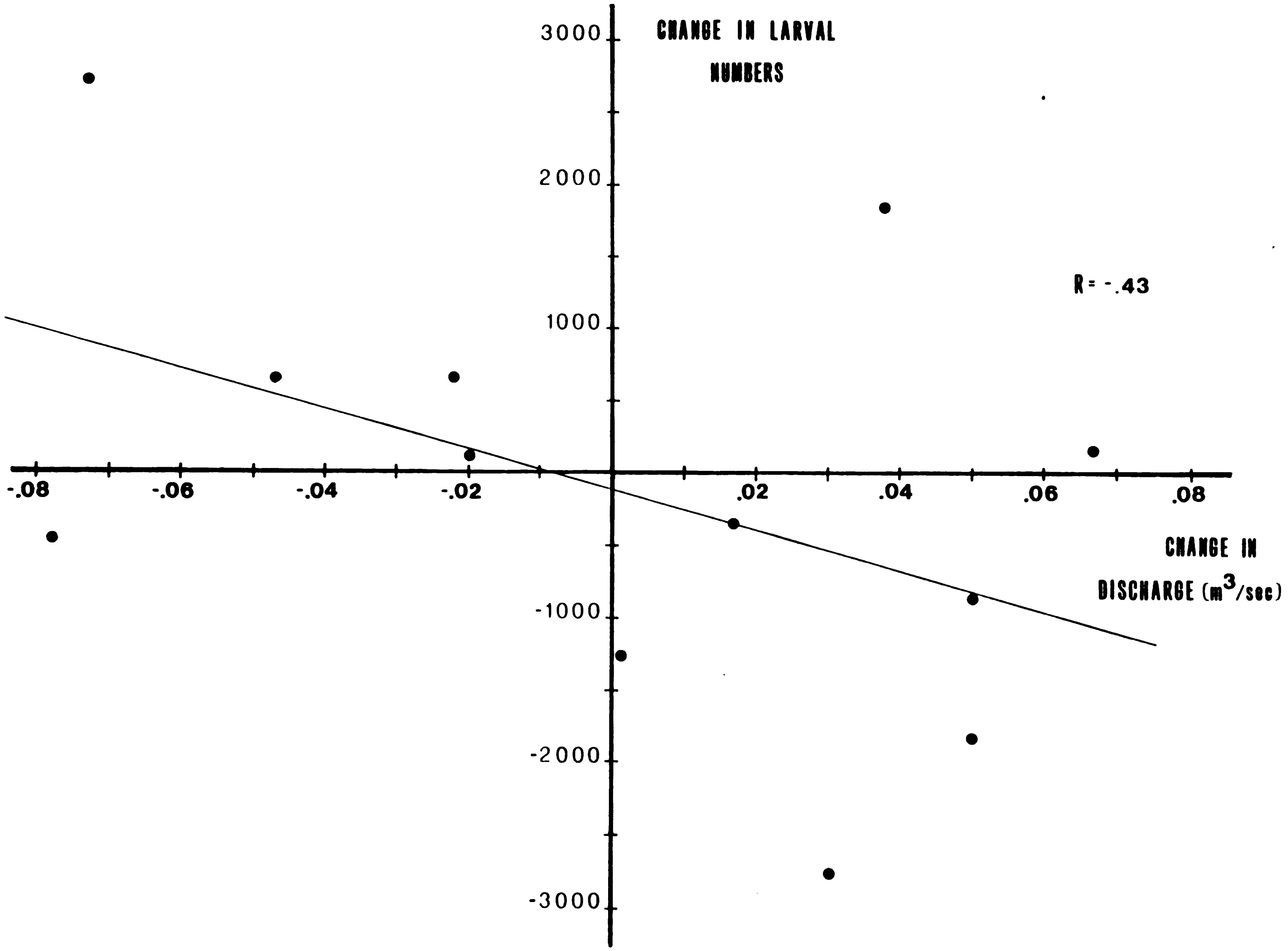

CHANGE IN LARVAL NUMBERS
3000
2000
1000
-1000
-2000
-3000
R = -.43
-.08
-.06
-.04
-.02
.02
.04
.06
.08
CHANGE IN DISCHARGE (m3/sec)

Fig. 3. Post-genal length frequency distributions of the larval instars of two cohorts of *P. mixtum/fuscum*.

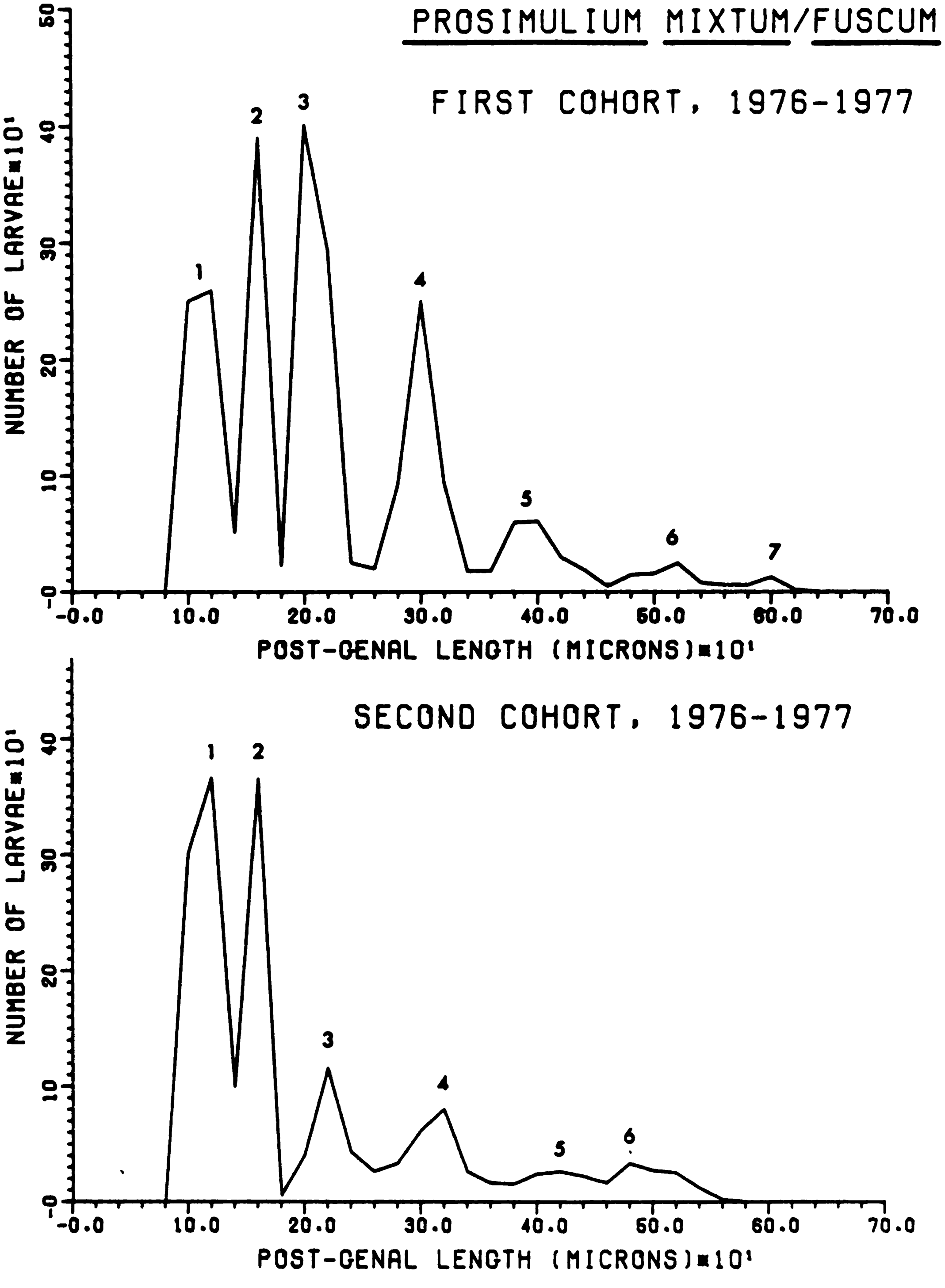

PROSIMULIUM MIXTUM/FUSCUM
FIRST COHORT, 1976-1977
NUMBER OF LARVAE×10¹
0
10
20
30
40
50
1
2
3
4
5
6
7
-0.0
10.0
20.0
30.0
40.0
50.0
60.0
70.0
POST-GENAL LENGTH (MICRONS)×10¹
SECOND COHORT, 1976-1977
NUMBER OF LARVAE×10¹
0
10
20
30
40
1
2
3
4
5
6
-0.0
10.0
20.0
30.0
40.0
50.0
60.0
70.0
POST-GENAL LENGTH (MICRONS)×10¹

Fig. 4. Post-genal length frequency distribution of the larval instars of _St_. _mutata_.

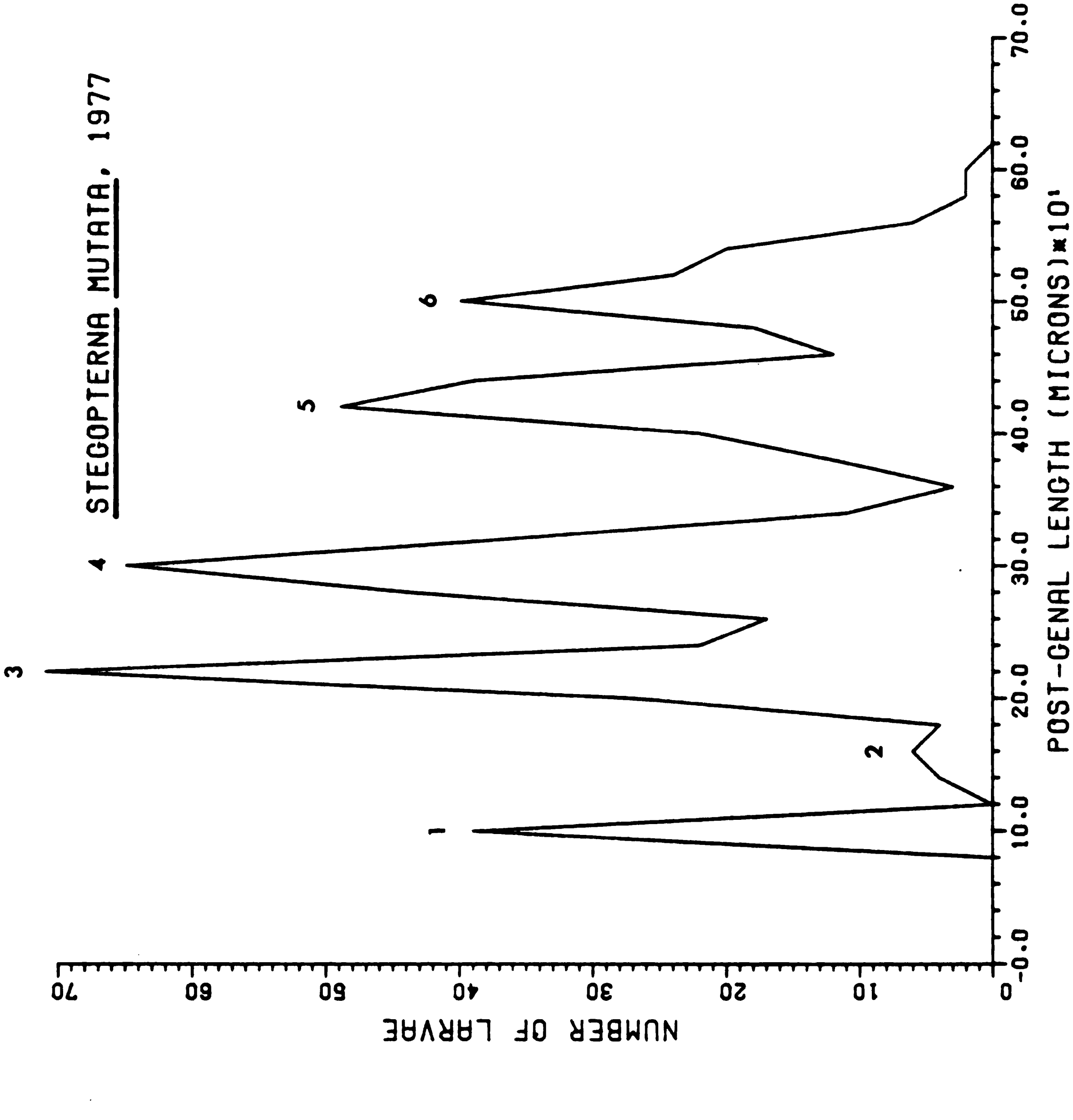

STEGOPTERNA MUTATA, 1977
1
2
3
4
5
6
NUMBER OF LARVAE
0
10
20
30
40
50
60
70
-0.0
10.0
20.0
30.0
40.0
50.0
60.0
70.0
POST-GENAL LENGTH (MICRONS)*10'

Fig. 5. Post-genal length frequency distribution of the larval instars of _C_. _dacotensis_.

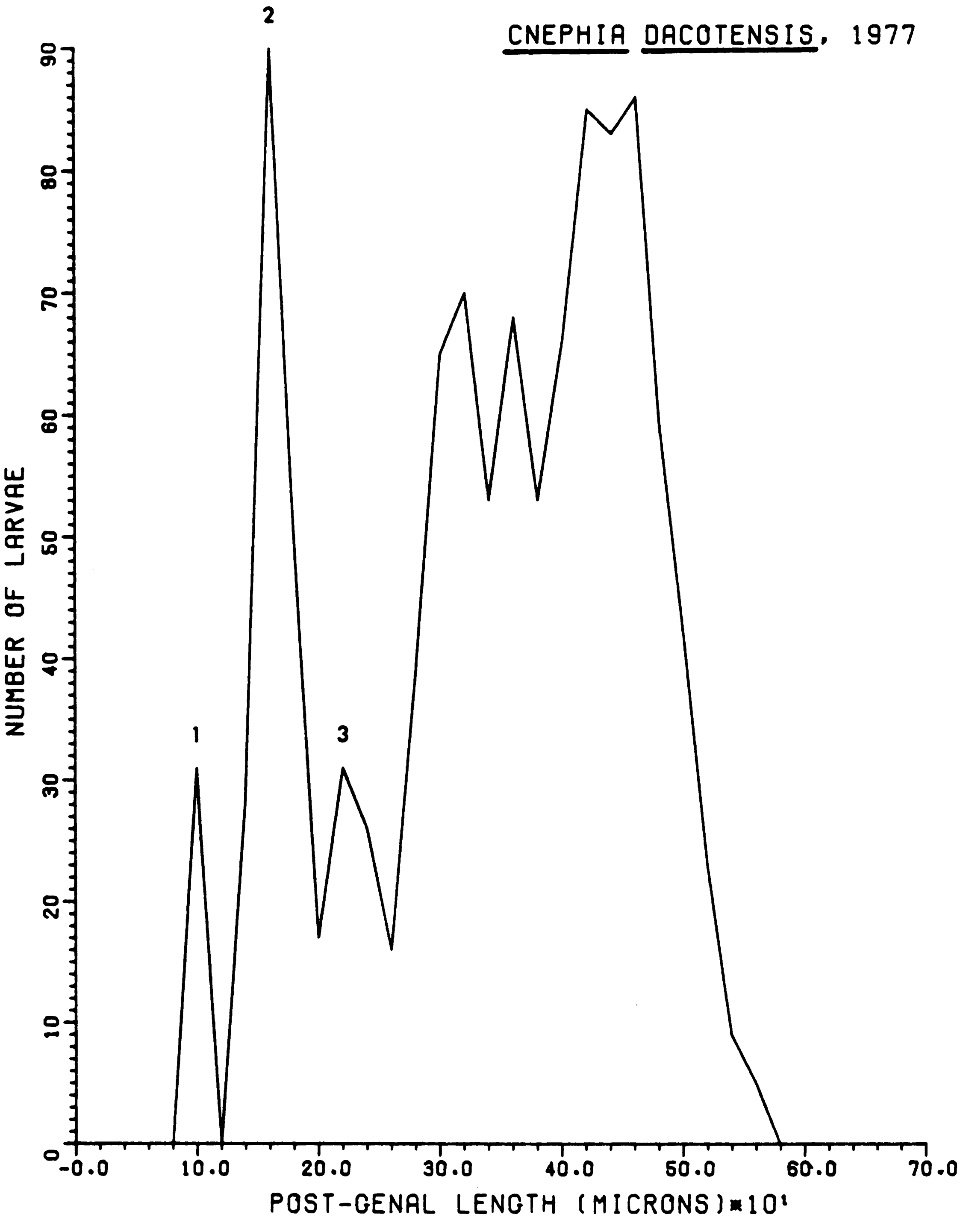

CNEPHIA DACOTENSIS, 1977
NUMBER OF LARVAE
POST-GENAL LENGTH (MICRONS)*10¹
0
10
20
30
40
50
60
70
80
90
-0.0
10.0
20.0
30.0
40.0
50.0
60.0
70.0
1
2
3

Fig. 6. Post-genal length frequency distribution of the larval instars of S. *vittatum*.

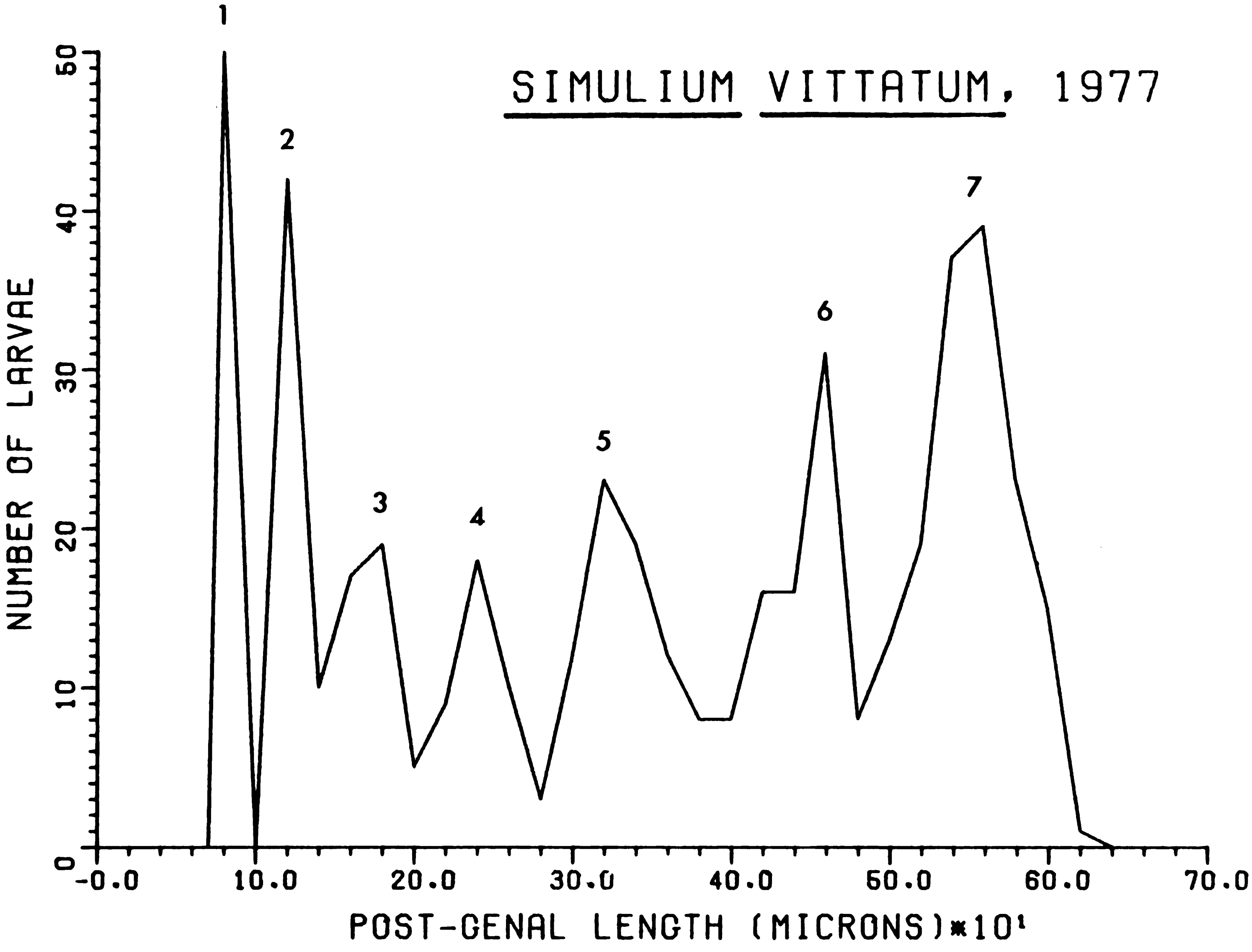
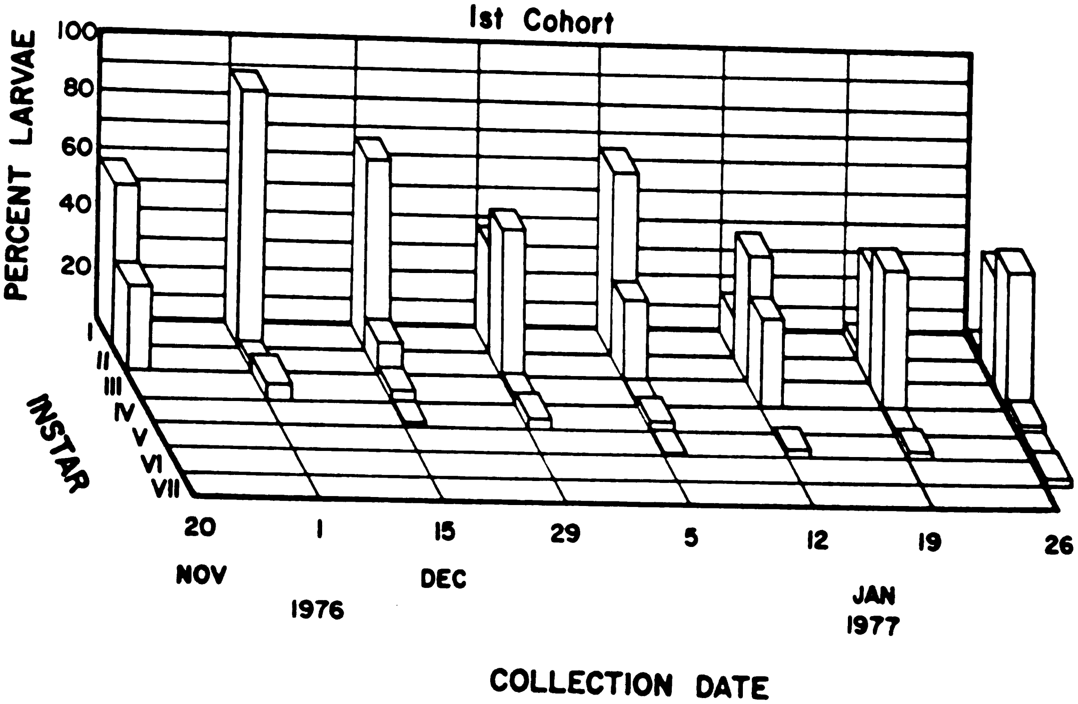

SIMULIUM VITTATUM, 1977
1
2
3
4
5
6
7
NUMBER OF LARVAE
0
10
20
30
40
50
-0.0
10.0
20.0
30.0
40.0
50.0
60.0
70.0
POST-GENAL LENGTH (MICRONS)*10¹

Fig. 7. Larval population structure of the first cohort of *P. mixtum/fuscum* (1976-1977).

Prosimulium mixtum/fuscum



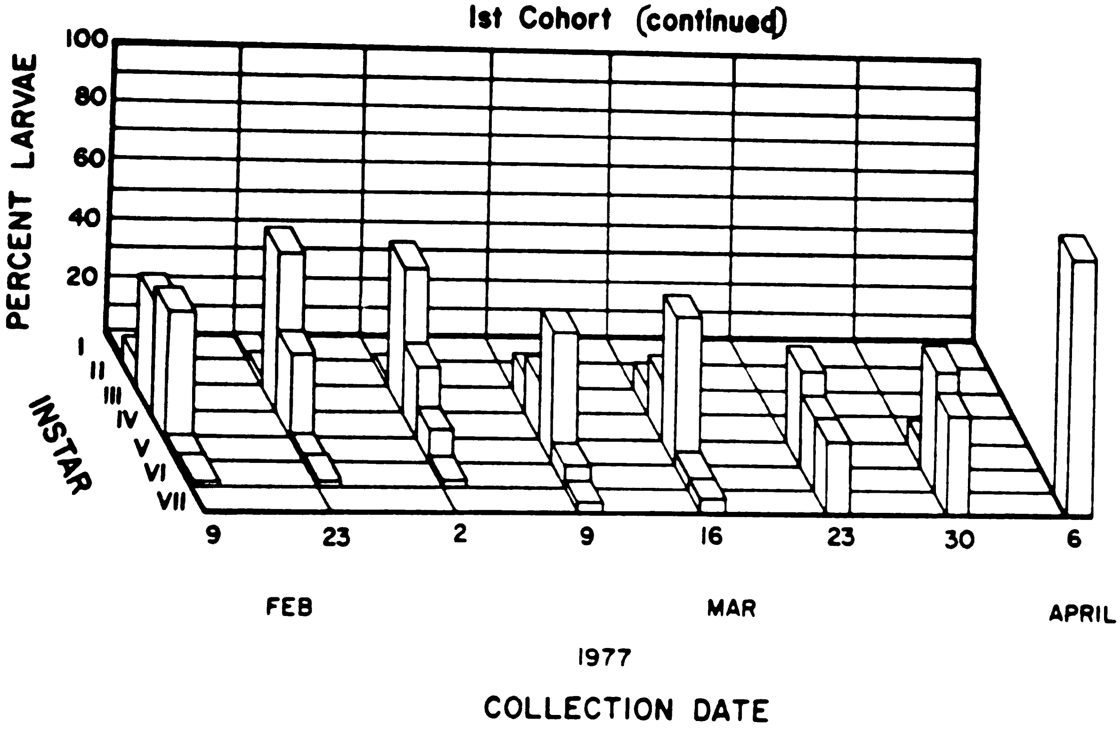


Fig. 8. Larval population structure of the second cohort of P. *mixtum*/*fuscum* (1976-1977).

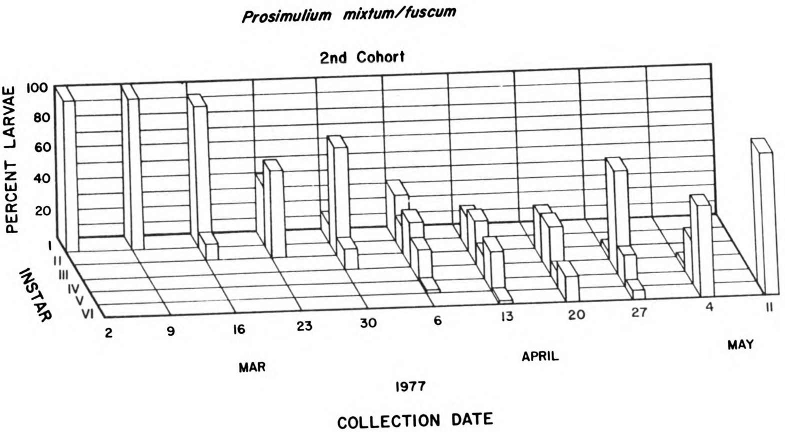

Prosimulium mixtum/fuscum
2nd Cohort
PERCENT LARVAE
100
80
60
40
20
INSTAR
I
II
III
IV
V
VI
2
9
16
23
30
6
13
20
27
4
11
MAR
APRIL
MAY
1977
COLLECTION DATE

Fig. 9. Degree-days required for the larval development of the two cohorts of *P. mixtum/fuscum* (1976-1977).

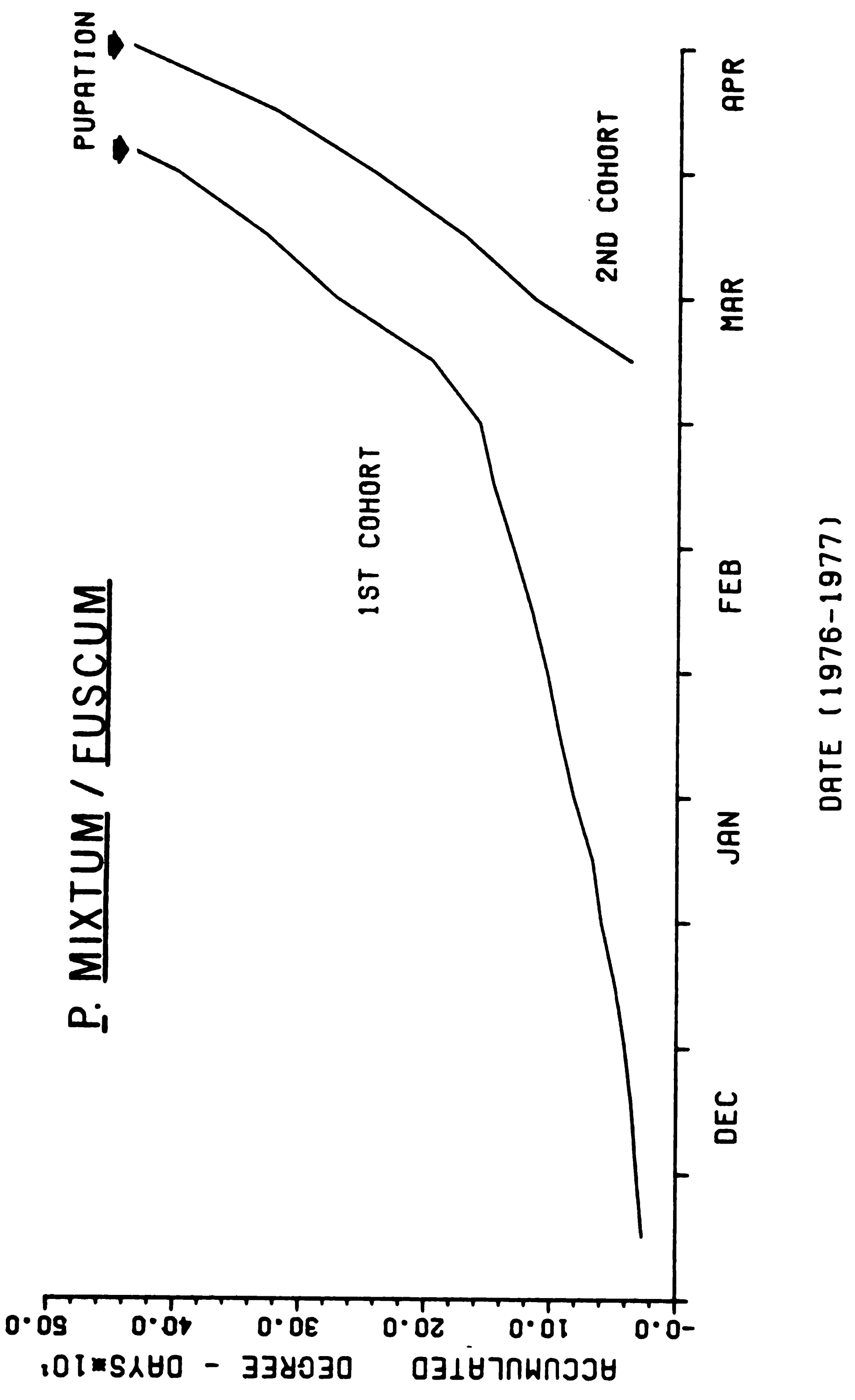
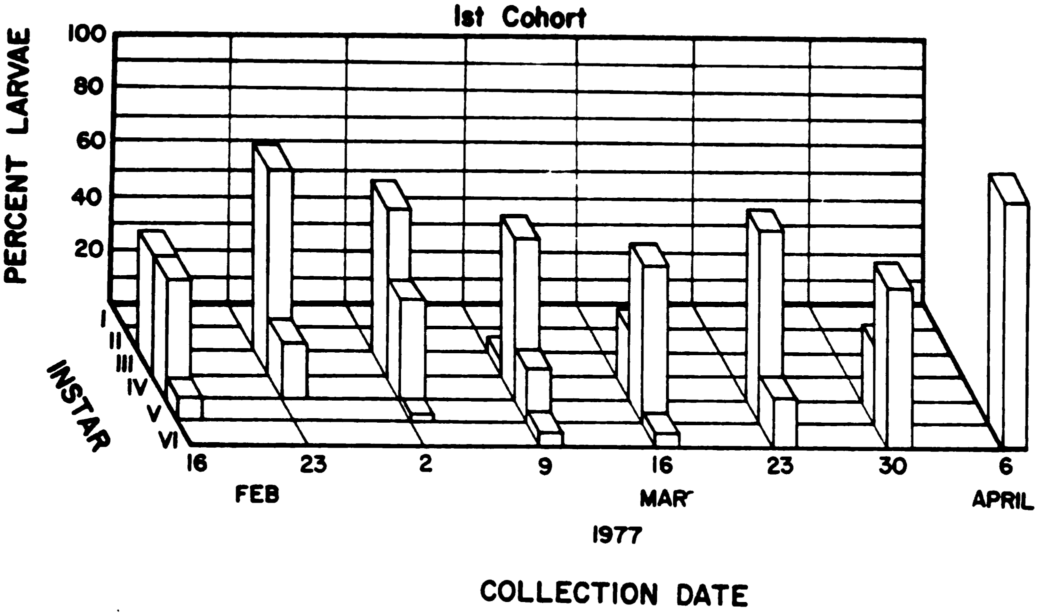

P. MIXTUM / FUSCUM
PUPATION
1ST COHORT
2ND COHORT
ACCUMULATED DEGREE - DAYS*10¹
-0.0
10.0
20.0
30.0
40.0
50.0
DEC
JAN
FEB
MAR
APR
DATE (1976-1977)

Fig. 10. Larval population structure of the two cohorts of St. mutata (1977).

Stegopterna mutata



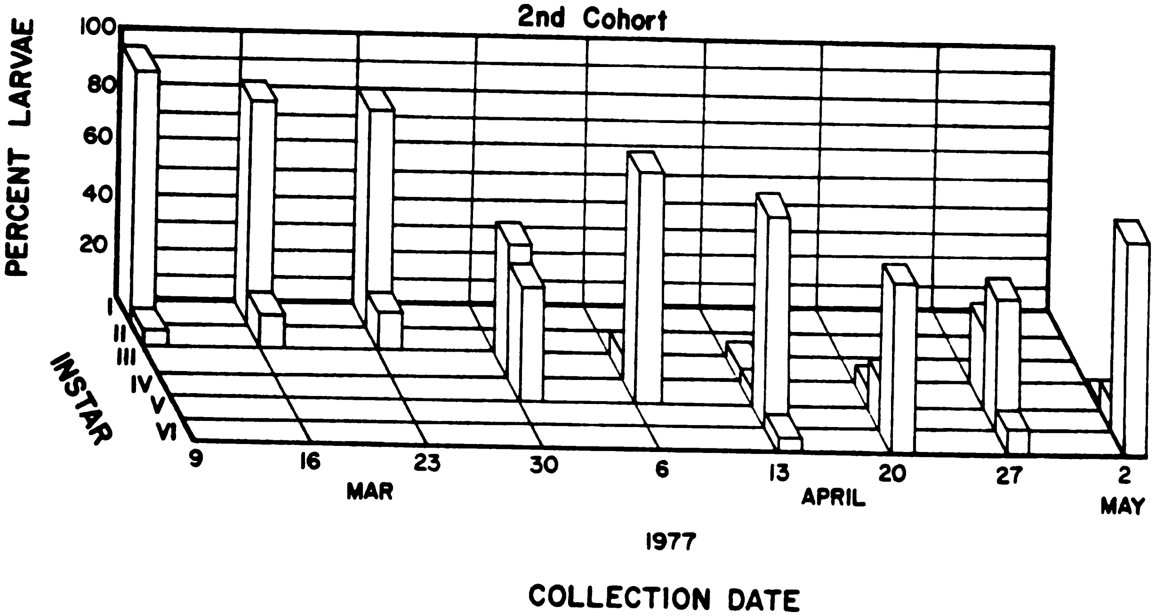
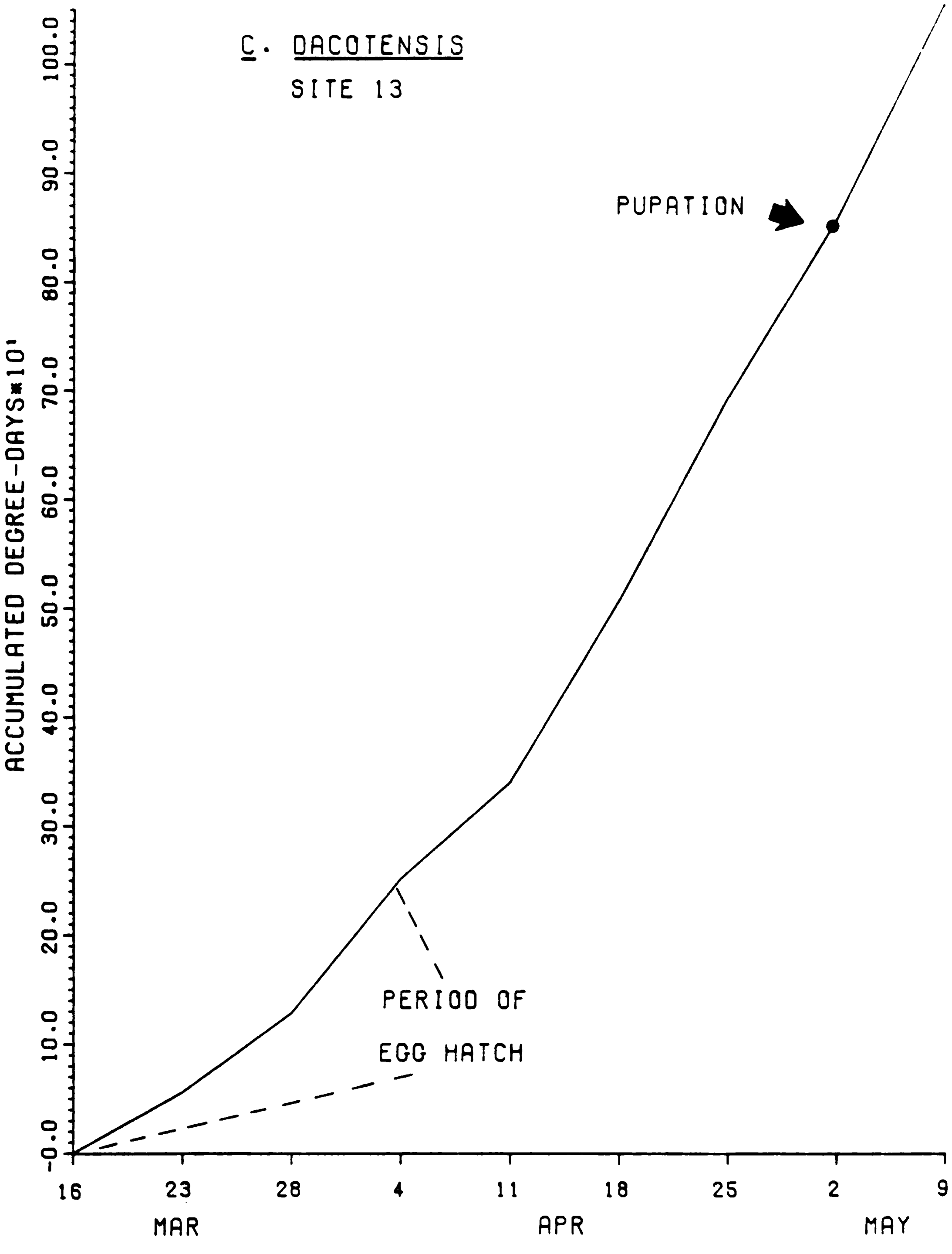


Fig. 11. Degree-days required for the larval development of _C_. _dacotensis_ (1977).


C. DACOTENSIS
SITE 13
PUPATION
PERIOD OF
EGG HATCH
ACCUMULATED DEGREE-DAYS*10'
-0.0
0.0
10.0
20.0
30.0
40.0
50.0
60.0
70.0
80.0
90.0
100.0
16
23
28
4
11
18
25
2
9
MAR
APR
MAY
DATE (1977)

PART II

THE BIONOMICS OF SOME BLACK FLIES (DIPTERA: SIMULIIDAE) FROM THE ROSE LAKE WILDLIFE RESEARCH AREA, MICHIGAN

INTRODUCTION

Prior to the present investigation, little research has been conducted on the Simuliidae in Michigan. Wu (1931) and Gill and West (1954) studied simuliid biology and ecology, and Tarshis (unpubl. data, 1963-1973) studied the role of black flies in waterfowl disease transmission at the Seney National Wildlife Refuge. He recorded 55 species from this area of the Upper Peninsula (I. B. Tarshis, pers. comm.).

This study was initiated to determine the species composition, succession and seasonal abundance of immature simuliids in the Rose Lake Wildlife Research Area in lower Michigan (Fig. 1). Selected physical and chemical characteristics of the streams were also examined in relation to faunal distribution.

MATERIALS AND METHODS

Collection and Identification

Extensive collections of Simuliidae were made at the Rose Lake Wildlife Research Area from March 1975 through May 1977 (Fig. 1). Immature black flies were collected from both natural (stones, vegetation, submersed wood) and artificial (ceramic tiles, plastic tapes) substrates (Williams and Obeng 1962, Lewis and Bennett 1974a). The insects were preserved in the field in 95% ethanol or returned to the laboratory in a plastic container. Larvae were reared in glass aquaria (after Tarshis 1968) using stream water and no food supplement. Field-collected pupae were reared singly on moist filter paper in petri dishes until emergence (Lewis and Bennett 1973). Adult flies were collected from deer and elk in pens at the Rose Lake Wildlife Research Center and from horses on nearby farms. Larval head capsules and adult genitalia were usually mounted to make specific identifications. Material was cleared overnight in 10% KOH, dissected, permanently mounted on glass slides with Euparol® and examined under a compound microscope. Taxonomic publications used in identifications were Stone and Jamnback (1955), Davies _et al._ (1962), Wood _et al._ (1963), Stone (1964) and Peterson (1970). Species determinations were verified by Dr. B. V.

Peterson of Agriculture Canada.

During the winter and spring of 1976, qualitative collections of associated stream insects were made at all study sites. These were preserved in 95% ethanol and later identified to family or genus.

Stream Characteristics

Current velocities of each stream were measured during the spring of 1976 and of 1977 with a Gurley Pygmy current meter and used to calculate discharge. Regression equations (Gill 1978) which estimated discharge from water depth ($R^2 > .9$) were used during the winter of 1977 when ice cover prohibited the use of a current meter. Substrate type and its abundance were noted at each sampling site.

Chemical properties of the streams were investigated at Sites 5, 9, 10, 12, 13, 16 and 17 (Fig. 1) during the winter and spring of 1977. Phenolphthalein and methyl orange alkalinity, total hardness, free carbon dioxide and dissolved oxygen were measured in the field with a Hach® water chemistry kit. Sampling sites were visited bi-weekly and samples were taken at three times during the day: (1) 0730-0930 hours; (2) 1215-1400 hours; and (3) 1635-1825 hours. The longest holding time of a sample (on ice) before analysis was 2.5 hours. Phosphate and nitrate were measured on two dates with a Tecnicon® auto-analyzer.

RESULTS AND DISCUSSION

Bionomics

The 16 species of Simuliidae collected from the study area are listed in Table 1. Stegopterna mutata, Simulium verecundum and S. vittatum were the three most widespread and abundant species, while S. excisum, S. pugetense, S. venustum and S. vernum were uncommon. Cnephia ornithophilia and S. vernum were collected for the first time in Michigan.

The species composition and seasonal occurrence of immature black fly populations in seven creeks are shown in Fig. 2. Life cycle patterns of some species varied in different streams. For example, P. fuscum, P. mixtum and St. mutata overwintered as larvae in Mud and Vermillion Creeks (which flow under the ice), but did not hatch from eggs until late February at Sites 13, 20 and 21 (which freeze solid in winter) (Fig. 2). Similar observations were made for S. verecundum and S. vittatum, whose occurrence and number of summer generations vary with permanence of the stream (Fig. 2; Mud Creek and Sites 13, 20 and 21).

Genus Prosimulium Roubaud.

Five univoltine species of Prosimulium were collected during the study. Low autumn and winter discharge followed by spring flooding from melting snow produced second cohorts of some of these species in 1977 (see Part I). Oviposition by these species occurs in flight when the female taps her abdomen on the water's surface and releases eggs. These eggs settle to the bottom and diapause until autumn or the following spring (Peterson 1970).

Subgenus *Parahelodon* Peterson.

Prosimulium gibsoni (Twinn). - Overwintering eggs of *P. gibsoni* hatch in mid-March, and larvae develop rapidly (Fig. 2). Emergence begins four to five weeks later and lasts about two weeks. Females, whose mouthparts prohibit them from taking a blood meal, contain mature eggs upon emergence (Davies *et al*. 1962).

Subgenus *Prosimulium* Roubaud.

Prosimulium fuscum Syme and Davies and *P. mixtum* S. and D. - These species were widely distributed in the study area and always occurred together (Table 1). Their life cycles varied in different streams, but they usually began hatching in mid-November and developed slowly during the winter months (Fig. 2). Larval growth was rapid following snowmelt and increasing water temperatures in late February, and synchronous pupation occurred in late March. Adults were collected from late March to early May. Both species fed on deer, elk and horses, while *P. mixtum* also engorged on humans. Davies (1961) found *P. fuscum* to be autogenous for the first gonotrophic cycle, with less than ten percent of parous females surviving to become biting pests. In contrast, *P. mixtum* was largely anautogenous and nulliparous females readily fed on man (Davies 1961).

Prosimulium multidentatum (Twinn). - The life cycle of this species varied in different creeks (Fig. 2). Larvae overwintered in streams which continued to flow beneath the ice and pupation occurred in mid-March. In creeks which were frozen until spring, eggs hatched in late February, and these larvae pupated in early April. Adults were collected as late as 20 April. No data on adult feeding were obtained, although females are capable of taking a blood meal (Peterson 1970).

Prosimulium mysticum Peterson. - P. mysticum overwintered in the larval stage in lower Michigan, as in Ontario (Fig. 2) (Mansingh et al. 1972). Mature larvae were collected in mid-March and pupated in late March. Adults were captured feeding on deer in late April.

Genus Cnephia Enderlein.

Subgenus Cnephia Enderlein.

Cnephia dacotensis Dyar and Shannon. - Eggs of this univoltine species hatched from late March to mid-April, depending on water temperature during the spring. Larval development was rapid, and pupation occurred six weeks after eclosion (Fig. 2). Emergence took place in May and was concentrated within a few days. Flies mated on streamside objects (e.g., rocks, vegetation, logs and culverts) soon after emerging, and females oviposited in flight. C. dacotensis females possess weak mouthparts and are incapable of taking a blood meal (Krafchick 1942, Nicholson 1945). Davies *et al.* (1962) reported that this species was highly parasitized by mermithid nematodes, but parasitized larvae were not observed in this study.

Cnephia ornithophilia Davies, Peterson and Wood. - Larvae of *C. ornithophilia* overwintered in large streams such as Vermillion Creek (Fig. 2, Table 2), which flow throughout the winter. Mature larvae were collected from late February through March and pupation occurred during March and early April (Fig. 2). Eggs of this species did not hatch until March in creeks which froze solid during the winter, and pupation occurred in late April (Fig. 2, Sites 13, 20 and 21). Bennett (1960) reported that *C. ornithophilia* (under the name *Cnephia* "U") fed on woodland birds (e.g., crow and ruffed grouse) 1.5-7.5m above the forest floor. This species is capable of transmitting the sporozoan parasite *Leucocytozoon simondi* Mathis and Leger to waterfowl in the laboratory (Tarshis 1972, 1976).

Genus *Stegopterna* Enderlein.

Subgenus *Stegopterna* Enderlein.

Stegopterna mutata (Malloch). - Although diploid and triploid (parthenogenetic) forms of this species occur together in Ontario (Basrur and Rothfels 1959), the present study did not attempt to separate these. Second cohorts of this univoltine species were also produced in 1977 as in *Prosimulium* spp. (see *P. fuscum* and *P. mixtum*). *St. mutata* overwintered as eggs or larvae, depending on the extent of ice in the stream (Fig. 2). Eggs that produced overwintering larvae hatched in January, and larval growth was slow until water temperatures increased in early March. Pupation occurred from late March through mid-April, and adults were collected from mid-April to early May. Overwintering eggs hatched in March and adults emerged in late April (Fig. 2). Larvae of St. mutata were parasitized by Caudospora brevicauda Jamnback (Protozoa: Microsporida) with infection rates as high as 20%. Females of this species were collected feeding on deer and elk.

Genus Simulium Latrielle.

Subgenus Eusimulium Roubaud.

Species of this subgenus are primarily ornithophilic, feeding on birds in a variety of habitats, and are known vectors of avian blood parasites (Fallis and Bennett 1958, Bennett 1960, Anderson and DeFoliart 1961, Stone 1964).

Simulium aureum Fries. - This multivoltine species overwintered in the egg stage and may have two or three generations per year. Eggs hatched in late March and first generation pupae were present in early May (Fig. 2). Eggs, larvae and pupae of other generations occurred throughout the summer until late September (Fig. 2). Engorged females were collected from ruffed grouse exposed 6-7.5m above the forest floor in June (Fig. 1, Site 15; J. N. Stuht, Department of Natural Resources, pers. comm.). These findings agreed with Bennett's (1960) data on feeding habits and occurrence of these flies in late summer. *S. aureum* is a vector of *Leucocytozoon bonasae* Clarke, a blood parasite of ruffed grouse (Fallis and Bennett 1960).

Simulium excisum Davies, Peterson and Wood. - *S. excisum* is a univoltine species which overwintered in the egg stage. Following hatching, larvae developed rapidly in early March and pupation occurred in mid-April (Fig. 2). Bennett (1960) collected females of this species (under the name *S. subexcisum*) engorging on ducks along lake shores, but further studies on its feeding habits are needed (Davies *et al*. 1962).

Simulium pugetense (Dyar and Shannon). - Larvae of this species were collected only once, in early April at Site 26 (Fig. 1). In Ontario, Davies *et al*. (1962) reported that this univoltine species overwintered in the larval stage and emerged in early spring. Females have bifid claws and mouthparts suitable for blood feeding. Oviposition occurs in spring, and eggs diapause until autumn (Davies *et al*. 1962).

Simulium vernum Macquart. - Larvae of this species were also collected only once during the study at Site 27 (Fig. 1). Although *S. vernum* has been previously recorded from North America (Twinn 1936), its biology is not well known. This species is morphologically similar to *S. aureum* and feeds on birds (Peterson 1977).

Subgenus Simulium Latrielle.

Simulium decorum Walker. - Overwintering eggs of this multivoltine species hatched in March and the larvae developed rapidly, pupating in mid-April and emerging at the end of April (Fig. 2). Larvae, pupae and adults of the second generation were collected in mid-July, and a third generation may occur, though it was not observed in this study. Females usually oviposit on streamside objects or vegetation which have water covering or lapping them, but have also been observed ovipositing in flight, similar to Prosimulium spp. (Davies et al. 1962). Although S. decorum females may be autogenous for the first gonotrophic cycle (Davies et al. 1962), they have well-developed mouthparts and have been captured engorging on deer and humans (Davies and Peterson 1956).

Simulium verecundum Stone and Jamnback and S. venustum Say. - These two species are members of a large complex containing many undescribed species with similar life cycles (B. V. Peterson, pers. comm.). S. venustum was collected only once at Site 12, while S. verecundum was widespread and numerous (Table 1). Both multivoltine species overwintered in the egg stage, and S. verecundum eggs hatched in early March. Pupae and adults of the latter species were collected in early to mid-April. Four or five generations may occur, since adults were still on the wing in September and pupae were collected in late November. Females of both species lay their eggs in mats on vegetation at or just below the water's surface. _S_. _venustum_ is a major pest in Canada and the northern United States (Stone and Jamnback 1955, Davies _et_ _al_. 1962), feeding readily on humans, deer, cattle, horses and even birds (Davies and Peterson 1956, Teskey 1960). _S_. _verecundum_ is less annoying to man (Stone 1964).

Subgenus _Psilozia_ Enderlein.

Simulium _vittatum_ Zetterstedt. - This multivoltine species was the most numerous and widespread simuliid in the study area (Table 1). Eggs of the last summer generation hatched in autumn and larvae grew slowly through the winter (Fig. 2). Pupation began in early March and emergence of this first generation occurred in early April. Succeeding generations emerged in mid-June, late July and early September, although some overlap existed (Fig. 2). Oviposition occurs on vegetation and other damp streamside objects, as well as in flight (Davies and Peterson 1956). Engorged females were collected from deer, elk and horses in this study and also feed on sheep (R. Stolz, Department of Entomology, University of Idaho, pers. comm.). _S_. _vittatum_ is not a serious human pest in this region.

Seasonal Succession

Seasonal succession of black fly species is presented in Figs. 3, 4 and 5. Most species occurred at Site 13 during late winter and spring, with eclosion beginning in March following snowmelt (Figs. 2 and 3). _P_. _gibsoni_, _St_.

mutata, *C*. *ornithophilia* and *Simulium* spp. hatched earlier in the month than *C*. *dacotensis*, since later instars of these species were present when *C*. *dacotensis* larvae were first collected. First instars of this latter species were the only ones positively identified because the head capsule sclerotization is weaker than that of the other species (Craig 1974). All eggs of *C*. *dacotensis* had hatched by 4 April, and pupation of this species and *C*. *ornithophilia* occurred four weeks later, with adults emerging in mid-May (Figs. 2 and 3). The life cycles of *P*. *gibsoni* and *St*. *mutata* were also short, requiring approximately six weeks from eclosion to pupation (Figs. 2 and 3). The early peak of *Simulium* spp. was largely *S*. *excisum*, while the later one was 90 to 95% *S*. *verecundum* (Fig. 3). Larval populations declined rapidly in late May following pupation of a large generation of *S*. *verecundum* (Fig. 3). Discharge also declined and the stream ceased to flow by mid-June.

Figures 4 and 5 illustrate the succession of simuliid species in Mud Creek (Site 15) during the 1975-76 and 1976-77 seasons, respectively. Although quantitative sampling did not begin until mid-February (1976), preliminary collections were made in January of that year and in November 1975. Data indicated that *P*. *mixtum*/*fuscum* larvae (immature larvae of these species cannot be separated) hatched in early to mid-November and were the only black flies in the stream until January, when *St*. *mutata* first appeared (Fig. 5). The latter species was less abundant in 1977 than 1976, possibly due to the microsporidian *Caudospora brevicauda*. This parasite infected 20% of the larvae in 1976, preventing pupation and decreasing egg production. Since the parthenogenetic (triploid) form of *St. mutata* is more common than the diploid (sexual) form (Davies and Peterson 1956, Basrur and Rothfels 1959), the 20% reduction in egg-laying females could have resulted in a smaller population the following year.

The time period that *P. mixtum/fuscum* and *St. mutata* populations remained in Mud Creek also varied during the two year study. Larvae of these species were still present in May 1977, while they had all pupated by early April 1976 (Figs. 4 and 5). These differences were due to the second cohorts of each species during 1977 (see Part I). Larvae of the second cohorts did not hatch until early March (1977) and they pupated from mid-April through May (Fig. 5). Data indicated that in lower Michigan, *P. mixtum/fuscum* and *St. mutata* usually pupate in late March and early April, respectively.

The replacement of *Prosimulium* spp. and *St. mutata* by *Cnephia* and *Simulium* spp. was similar at Site 13 (Fig. 3) and in Mud Creek (Figs. 4 and 5). Early instars of *Cnephia* and *Simulium* spp. hatched when larvae of the other two genera neared pupation, thus possibly reducing competition for food and suitable habitat. The successional pattern of *Cnephia* and *Simulium* spp. may also be related to other factors. Following ice-out in spring, temperate-zone lakes experience phytoplankton blooms which result in the production of large quantities of diatoms and other algae (Ruttner 1973). Larval black flies which breed in lake outlets (e.g., Site 13 and Mud Creek) would be exposed to large amounts of food (Carlsson 1967), and they may receive some selective advantage over larvae occurring at other times of the year. *Cnephia dacotensis* has frequently been found in large numbers in lake and pond outlets (Anderson and Dicke 1960, Davies *et al*. 1962, Stone 1964, Gersabeck 1977), and may have evolved a life cycle to exploit these food resources. Some families of net-spinning Trichoptera successfully share habitats and food through temporally asynchronous life cycles (J. B. Wallace, Department of Entomology, University of Georgia, pers. comm.). Further studies are needed on the size, type and quality of particulate materials ingested by different instars and species of Simuliidae to clarify some of these interspecific relationships.

Physical Characteristics of Streams

In this study the most important physical factor regulating larval development in black flies was stream temperature. It played the major role in determining hatching, pupation, emergence, and it was responsible for the timing and duration of the life cycles of each species (see Part I). Temperature has also affected the number of simuliid species in a stream and the life cycles of their parasites and predators (Ezenwa 1974, Lewis and Bennett

1975). Variations in temperature between streams in the study area were negligible and of little use in explaining black fly distribution differences.

Stream discharge also influenced immature Simuliidae. Following prolonged dry conditions, rising water levels flooded unhatched eggs, producing second cohorts of some univoltine species which typically have only one cohort per generation (see Part I). Changes in discharge also affected rates of larval colonization and detachment from artificial substrates, thus influencing estimates of black fly abundance (Disney 1972, Pegel and Rühm 1976, Gersabeck 1977). Yearly variations in discharge determined the number of generations of some multivoltine _Simulium_ spp. during the summer and early autumn. The nature of stream flow also had important implications, with permanent creeks generally having more species of simuliids than temporary streams (Table 2, Fig. 2).

The number of black fly species inhabiting a stream did not appear to be related to the stream's origin (Figs. 1 and 2, Table 2). For example, Mud Creek and Sites 9 and 10 both drain lakes, yet the former stream contained 14 species of simuliids while the latter had only five (Fig. 2). Contrary to studies by Anderson and Dicke (1960) and Davies _et al_. (1962) which found substrate preferences among larvae of different species, gravel, stones, wood and vegetation were utilized by all species collected in the present study. All of these materials were colonized if water velocity was suitable and their surfaces were free from periphyton. Stream depth and width were not related to species distribution, since *P. mixtum*, *P. fuscum*, *St. mutata* and other species occurred in both large and small creeks (Fig. 2, Table 2).

Chemical Characteristics of Streams

Data on the chemical properties of the seven streams showed minor variation between them. All tests for phenolphthalien alkalinity were negative, while methyl orange (bicarbonate) alkalinity was generally high (> 200ppm $CaCO_3$). Water in all streams was hard (150-300ppm $CaCO_3$) (Kevern 1973), and differences between streams were insignificant. Melting snow and rainfall reduced alkalinity and hardness by dilution, as well as nitrate (NO_3) and orthophosphate (PO_4) concentrations. Nitrate and orthophosphate were consistently present at low levels (< 1.1 and $< .02$ppm, respectively), indicating a lack of organic enrichment (Kevern 1973). Dissolved oxygen exceeded 10ppm in all streams except at Sites 9 and 10, where it was less than 6ppm during the winter. This was caused by the formation of pools of stagnating water under the ice cover. The variability of results from the free carbon dioxide tests made estimates unreliable. Other investigators (Carlsson 1962, 1967, Chutter 1968, Ali *et al*. 1974, Ezenwa 1974, Lewis and Bennett 1975) have also measured chemical properties and were unable to correlate differences with simuliid distribution patterns. Grunewald (1972) determined a combination of physical and chemical factors at breeding sites of Boophthora erythrocephala DeGeer which were quite distinct from those of other black fly species; however, such success has not been achieved with other simuliids. Chemicals indicative of organic pollution (e.g., NO_3 and PO_4) are capable of affecting black fly population abundance and distribution by increasing food supplies. Such enriched streams were found to contain significant quantities of microplankton on which large populations of Simulium spp. fed (Chutter 1968, Ali et al. 1974). Habitat preference and oviposition behavior could also influence the distribution of species (Rühm 1971, Lewis and Bennett 1975). More recent studies by Chance (1970, 1977), Kurtak (1973) and Ladle et al. (1977) suggested that the sizes of particulate matter available to filter-feeding black fly larvae in different streams may affect species distribution.

Associated Aquatic Insects

The insects collected in association with immature simuliids from seven streams in the study area are listed in Table 3. With the exception of Sites 13, 20 and 21, the fauna of temporary streams was not as diverse as that of permanent ones (Tables 2 and 3, Fig. 2). Although these collections were not complete, equal effort was expended in each stream, and all samples were taken at the same time of year. Thus, some comparisons can be made between creeks. The number of black fly species occurring in each stream showed a significant positive correlation ($r = .70$) with the number of other insect species in the same stream (Fig. 6). This suggested that factors which influence simuliid distribution may also affect the diversity and abundance of other aquatic insects.

Table 1. List of species and collection sites of immature black flies from the Rose Lake Wildlife Research Area.

SPECIES	SITE NUMBER																				
	1	2	3	4	5	6	9	10	11	12	13	14	15	16	17	18	19	20	21	26	27
Prosimulium fuscum Syme & Davies			X		X					X	X		X	X	X	X	X	X			
P. gibsoni (Twinn)										X	X			X						X	
P. mixtum Syme and Davies			X		X					X	X		X	X	X	X	X	X			
P. multidentatum (Twinn)					X					X	X			X		X	X				
P. mysticum Peterson					X					X			X			X	X				
Cnephia dacotensis Dyar & Shannon					X			X			X	X	X					X	X		
C. ornithophilia Davies, Peterson & Wood					X						X	X	X				X	X			
Stegopterna mutata (Malloch)	X	X	X	X	X					X	X	X	X	X	X	X	X	X		X	
Simulium aureum Fries		X				X	X	X		X	X	X						X	X	X	
S. decorum Walker								X		X						X			X		X
S. excisum Davies, Peterson & Wood											X		X								
S. pugetense (Dyar & Shannon)																				X	
S. venustum Say										X											
S. verecundum Stone & Jamnback	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
S. vernum Macquart																					X
S. vittatum Zetterstedt		X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X		X

Table 2. Characteristics of streams in the Rose Lake Wildlife Research Area.

STREAM	NATURE OF STREAM FLOW	WIDTH	DEPTH	SUBSTRATE(S)[1]	SURROUNDING VEGETATION	ADDITIONAL FEATURES
Vermillion Creek	Permanent	3-10m	.1-1.5m	Stones, submerged wood & trailing vegetation	Lowland brush & woods, & upland woods	Largest stream in study area
Mud Creek	Permanent	1.5-5m	.1-1m	Stones, gravel & submerged wood & vegetation	Marsh, upland & lowland woods	Source at Site 27; low summer discharge
Site 12	Permanent	1-2m	.1-1m	Stones, gravel & trailing grasses	Open meadows	Empties into Vermillion Creek
Sites 1, 2 & 17	Permanent	1-2m	.15-.5m	Submerged wood & vegetation	Lowland brush & upland woods	Drains a spring-fed lake
Sites 13, 20 & 21	Temporary	.75-2m	.1-.75m	Trailing grasses	Marsh & lowland brush	Drains a large lake; ice-bound in winter
Sites 9 & 10	Temporary	1-2m	.1-.5m	Submerged wood & vegetation	Marsh & lowland brush	Drain two small lakes
Site 6	Temporary	.3-.5m	.01-.1m	Gravel & fallen leaves	Gravel pit (no vegetation)	

[1] Substrates from which immature black flies were collected.

Table 3. Aquatic insect fauna associated with immature black flies in the Rose Lake Wildlife Research Area.

TAXON	CREEK						
	Mud Creek	Vermillion Creek	Sites 9 & 10	Site 12	Sites 1, 2 & 17	Sites 13, 20 & 21	Site 6
EPHEMEROPTERA							
Ephemeridae							
Ephemera sp.						X	
Hexagenia sp.		X					
Leptophlebidae							
Leptophlebia sp.	X	X		X	X	X	
Siphlonuridae							
Isonychia sp.		X					
Baetidae		X			X		
Caenidae							
Caenis sp.						X	
Heptageniidae							
Stenonema sp.		X			X		
Stenacron sp.					X		
ODONATA (Anisoptera)							
Aeshnidae							
Boyeria sp.	X	X					

	Mud Creek	Vermillion Creek	Sites 9 & 10	Site 12	Sites 1, 2 & 17	Sites 13, 20 & 21	Site 6
Corduliidae					X		
Gomphidae							
Gomphus sp.		X					
(Zygoptera)							
Calopterygidae							
Calopteryx spp.	X	X		X		X	
Coenagrionidae							
Enallagma sp.		X					
PLECOPTERA							
Perlidae							
Acroneuria spp.		X					
Perlesta sp.	X				X		
Phasganophora sp.		X					
Chloroperlidae							
Isoperla sp.	X			X		X	
HEMIPTERA							
Corixidae	X	X		X	X	X	
Notonectidae							
Notonecta sp.		X					

	Mud Creek	Vermillion Creek	Sites 9 & 10	Site 12	Sites 1, 2 & 17	Sites 13, 20 & 21	Site 6
Belastomatidae							
Belastoma sp.	X	X			X	X	
Lethocerus sp.			X				
Pleidae					X		
Nepidae							
Nepa sp.					X		
Ranatra sp.	X	X				X	
Mesoveliidae							
Microvelia sp.	X						
Gerridae	X	X	X	X	X	X	X
Gerris sp.		X				X	
MEGALOPTERA							
Corydalidae							
Nigronia sp.		X	X				
Sialidae							
Sialis sp.	X			X	X	X	
COLEOPTERA							
Haliplidae							
Peltodytes sp.						X	
Hydrophilidae							
Tropisternus sp.	X						

	Mud Creek	Vermillion Creek	Sites 9 & 10	Site 12	Sites 1, 2 & 17	Sites 13, 20 & 21	Site 6
Dytiscidae							
Agabus sp.		X				X	
Dytiscus sp.		X					
Gyrinidae							
Dineutus sp.		X					
Helodidae			X				
TRICHOPTERA							
Hydropsychidae							
Hydropsyche spp.	X	X		X			
Cheumatopsyche sp.	X				X		
Limnephilidae							
Drusinus sp.	X						
Limnephilus spp.	X	X		X	X	X	
Platycentropus sp.		X			X		
Mollanidae		X			X		
Phryganeidae							
Genus *A* Ross (1959)					X		
Ptilostomis sp.				X	X		
DIPTERA							
Tipulidae	X	X					

	Mud Creek	Vermillion Creek	Sites 9 & 10	Site 12	Sites 1, 2 & 17	Sites 13, 20 & 21	Site 6
Tipulidae (cont.)							
Tipula sp.	X					X	
Limonia sp.	X						
Chironomidae	X	X	X	X	X	X	
Tabanidae	X	X		X		X	
Athericidae							
Atherix sp.		X					
Stratiomyidae	X					X	
Empididae	X						

Fig. 1. The Rose Lake Wildlife Research Area, showing collection sites.

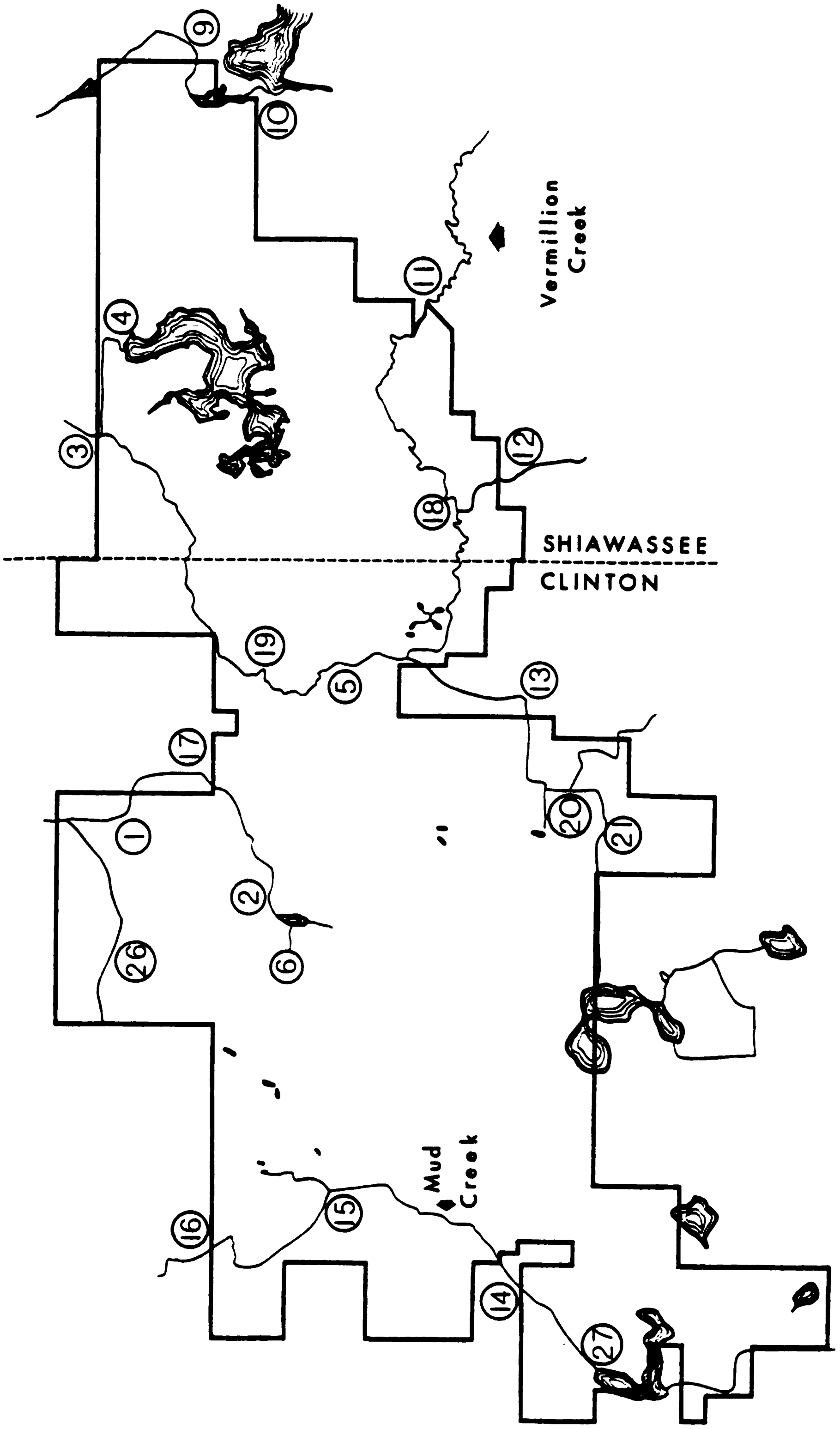
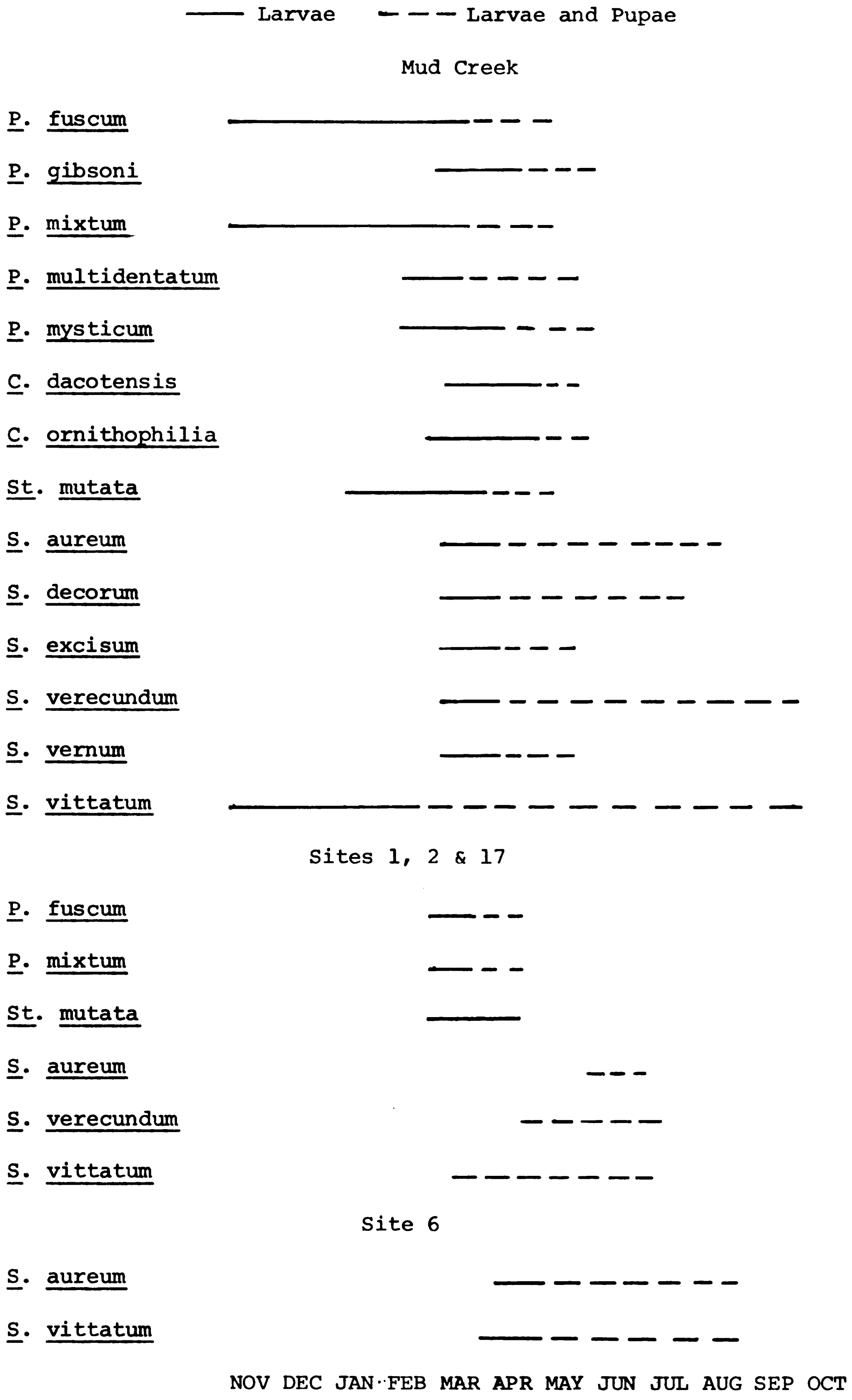
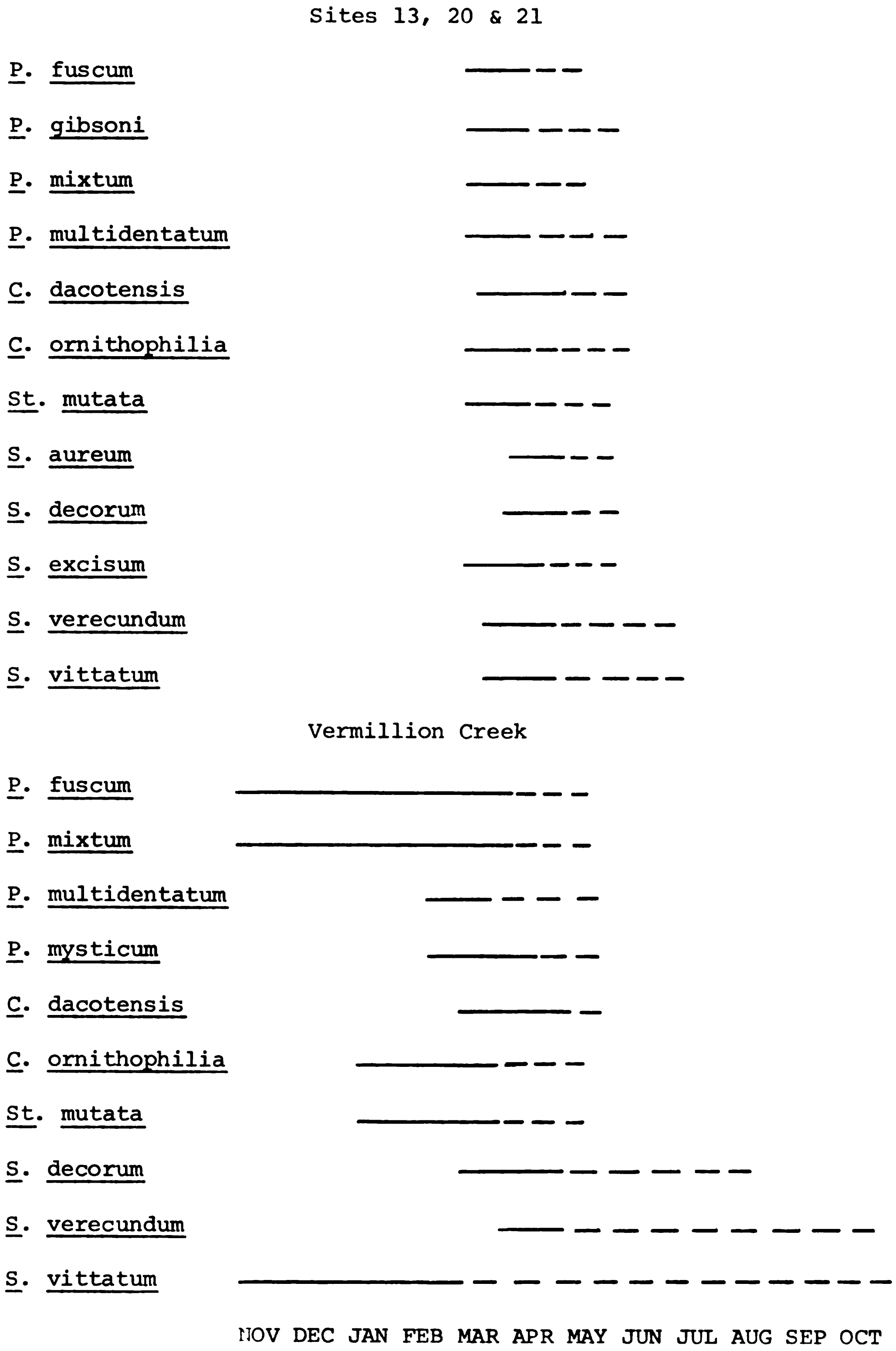

9
10
Vermillion Creek
11
4
3
12
18
SHIAWASSEE
CLINTON
19
5
13
17
1
20
21
2
6
26
Mud Creek
15
16
14
27

Fig. 2. Seasonal occurrence of simuliid larvae and pupae in seven streams of the Rose Lake Wildlife Research Area.


Larvae
Larvae and Pupae
Mud Creek
P. fuscum
P. gibsoni
P. mixtum
P. multidentatum
P. mysticum
C. dacotensis
C. ornithophilia
St. mutata
S. aureum
S. decorum
S. excisum
S. verecundum
S. vernum
S. vittatum
Sites 1, 2 & 17
P. fuscum
P. mixtum
St. mutata
S. aureum
S. verecundum
S. vittatum
Site 6
S. aureum
S. vittatum
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT


Sites 13, 20 & 21
P. fuscum
P. gibsoni
P. mixtum
P. multidentatum
C. dacotensis
C. ornithophilia
St. mutata
S. aureum
S. decorum
S. excisum
S. verecundum
S. vittatum
Vermillion Creek
P. fuscum
P. mixtum
P. multidentatum
P. mysticum
C. dacotensis
C. ornithophilia
St. mutata
S. decorum
S. verecundum
S. vittatum
NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT

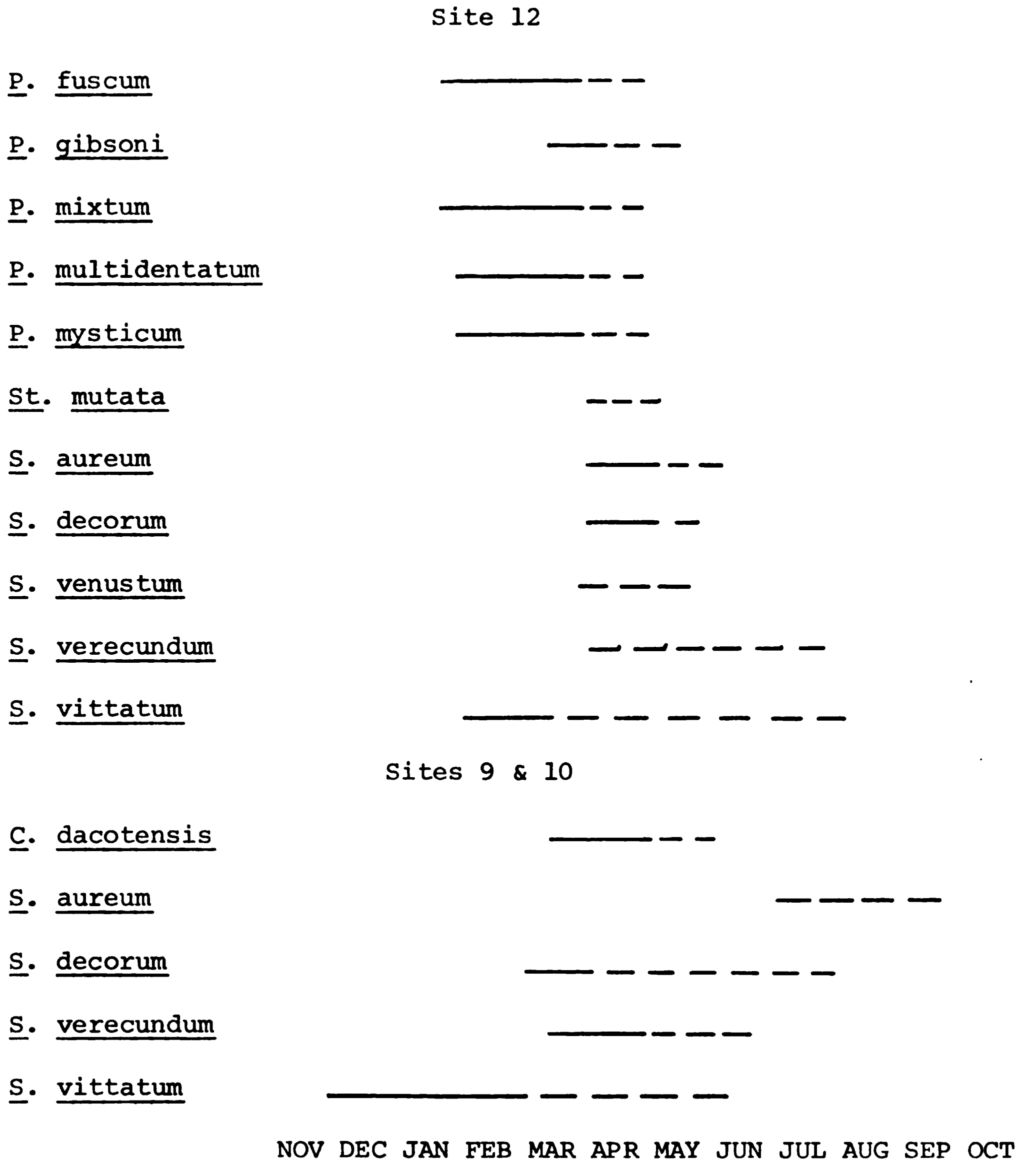

Site 12
P. fuscum
P. gibsoni
P. mixtum
P. multidentatum
P. mysticum
St. mutata
S. aureum
S. decorum
S. venustum
S. verecundum
S. vittatum
Sites 9 & 10
C. dacotensis
S. aureum
S. decorum
S. verecundum
S. vittatum
NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT

Fig. 3. Succession of black fly species at Site 13 (1977).

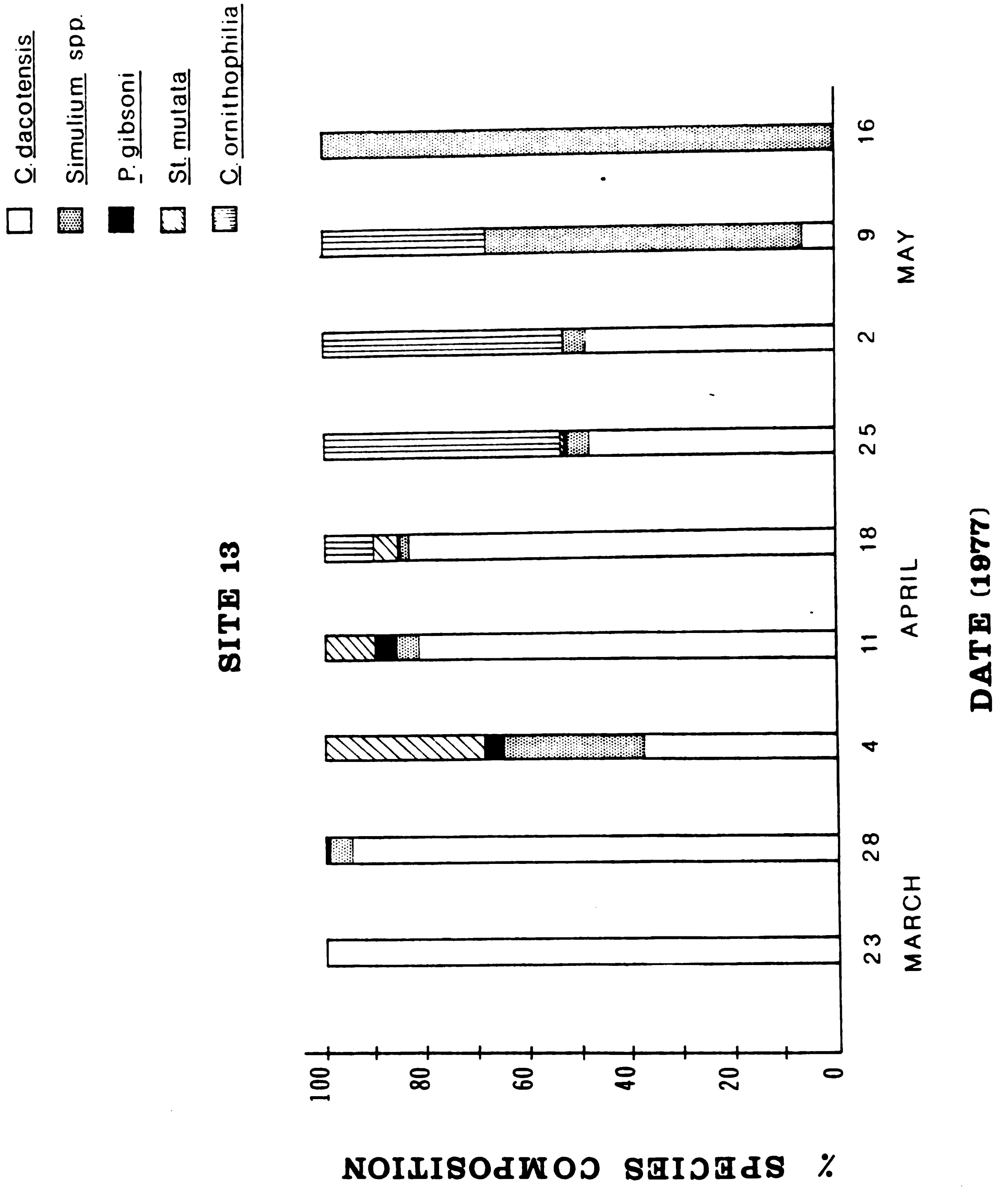

SITE 13
☐ C. dacotensis
▩ Simulium spp.
■ P. gibsoni
▨ St. mutata
▤ C. ornithophilia
% SPECIES COMPOSITION
100
80
60
40
20
0
23
MARCH
28
4
11
APRIL
18
25
2
MAY
9
16
DATE (1977)

Fig. 4. Succession of black fly species at Site 15, Mud Creek (1976).

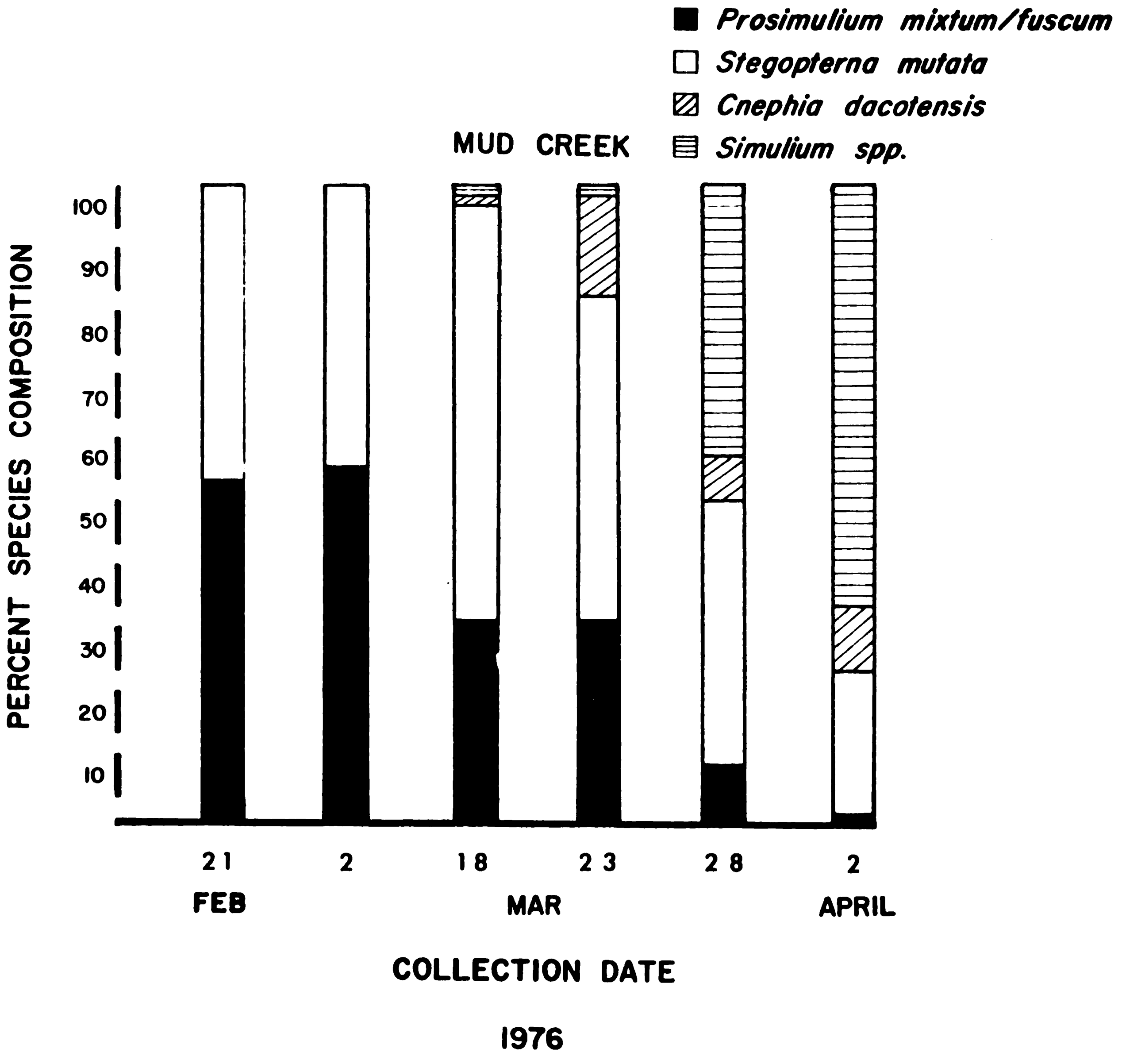

MUD CREEK
■ Prosimulium mixtum/fuscum
□ Stegopterna mutata
▨ Cnephia dacotensis
▤ Simulium spp.
PERCENT SPECIES COMPOSITION
100
90
80
70
60
50
40
30
20
10
21
FEB
2
18
MAR
23
28
2
APRIL
COLLECTION DATE
1976

Fig. 5. Succession of black fly species at Site 15, Mud Creek (1976-1977).

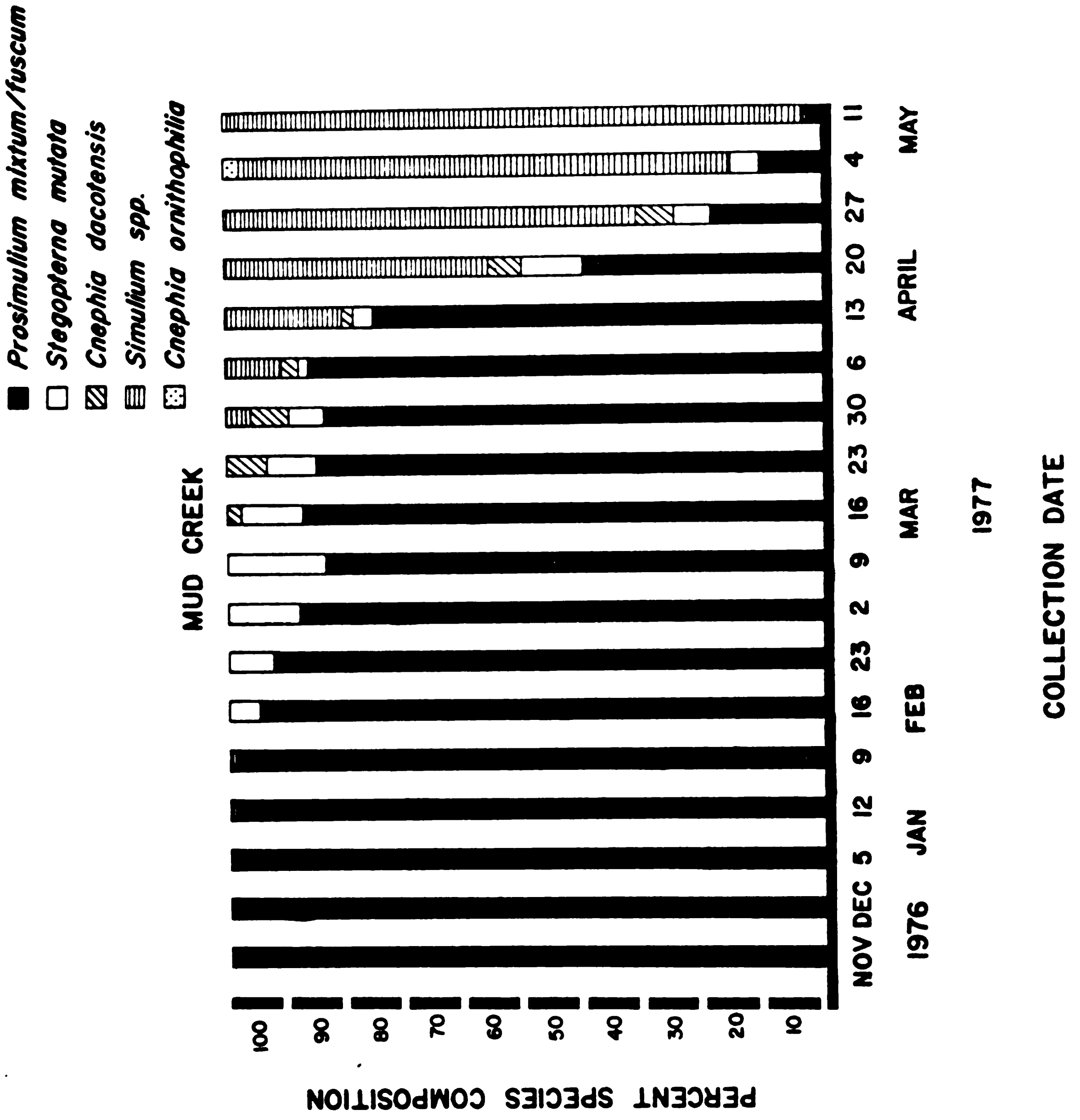
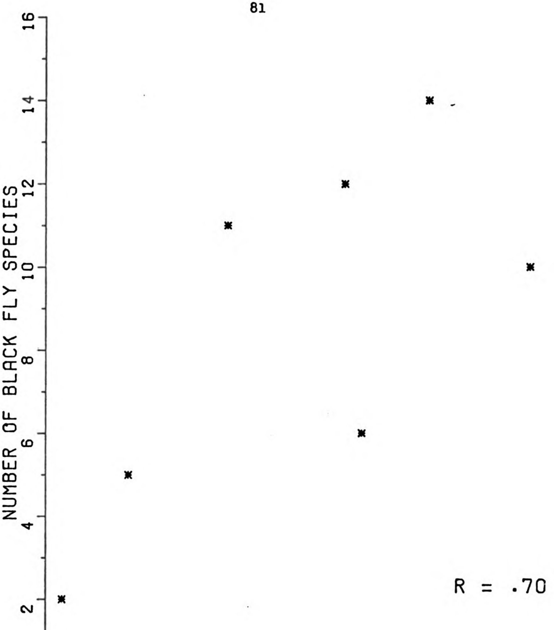

MUD CREEK
Prosimulium mixtum/fuscum
Stegopterna mutata
Cnephia dacotensis
Simulium spp.
Cnephia ornithophilia
PERCENT SPECIES COMPOSITION
100
90
80
70
60
50
40
30
20
10
NOV
DEC
5
12
9
16
23
2
9
16
23
30
6
13
20
27
4
11
JAN
FEB
MAR
APRIL
MAY
1976
1977
COLLECTION DATE

Fig. 6. Correlation between the number of simuliid species and number of other aquatic insect species in seven streams of the Rose Lake Wildlife Research Area.


NUMBER OF BLACK FLY SPECIES
0
2
4
6
8
10
12
14
16
0
5
10
15
20
25
30
NUMBER OF OTHER SPECIES
R = .70

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LITERATURE CITED

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