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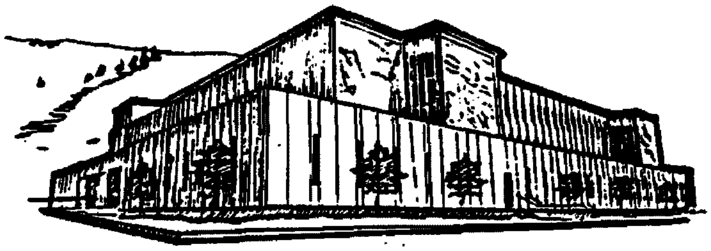

THE PHENOLOGY AND DISTRIBUTION OF PREIMAGINAL BLACK FLIES (DIPTERA:SIMULIIDAE) IN A WESTERN MONTANA LAKE-OUTLET

By

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The Phenology and Distribution of Preimaginal Black flies (Diptera:Simuliidae) in a Western Montana Lake-outlet (108 pp.)

Director: Andrew L. Sheldon A.L.S.

I investigated species composition, phenology, voltinism, and longitudinal and microdistribution of preimaginal black flies (Diptera:Simuliidae) in Owl Creek, the outlet of a mesotrophic lake in Missoula County, Montana, USA. I sampled ten sites from the lake outfall to 4500 meters downstream with weekly or biweekly collections from January 1986 to May 1987. To confirm larval and pupal identifications, these stages were reared to adults, and I measured larval head capsules to elucidate instars and cohorts of the four most abundant species.

At least eight species of the family Simuliidae occurred in Owl Creek. Larvae of *Prosimulium exigens* were present from October until pupation in April and May and were absent during summer. This species was univoltine with an abundant overwintering cohort having nine instars and a spring cohort with eight instars. *Simulium vittatum* and *Simulium arcticum* were multivoltine and larvae were present throughout the year. Both species had synchronized overwintering and spring cohorts and multiple asynchronous summer cohorts. The winter and early summer cohorts of *S. vittatum* had eight instars, and the summer cohorts had seven. Pupation occurred throughout the summer. The winter cohort of *S. arcticum* had eight instars, while the spring and summer cohorts had seven. Pupation occurred mainly in April and May and irregularly through the summer. *Simulium tuberosum* was multivoltine with two synchronized spring cohorts and multiple asynchronous summer cohorts. Each cohort had six instars, pupation occurred from May through October, and larvae were absent during winter. Phenologies of *Simulium verecundum* and *Simulium decorum* were similar to *S. tuberosum*.

Distinct longitudinal patterns of distribution were observed in winter and summer, but were less apparent during spring and fall. In winter, *P. exigens* occurred at all longitudinal sites, while *S. vittatum* and *S. arcticum* were restricted to the first 500m below the outfall. In summer, *S. vittatum* and *S. decorum* were primarily observed in the first 500m, *S. tuberosum* and *S. verecundum* at all longitudinal sites, and *S. arcticum* only at sites below 500m. These patterns may be related to longitudinal decreases in temperature and seston during the winter and summer. The relative lack of longitudinal change in distributions observed during spring and fall may have been related to higher flows during these seasons.

ACKNOWLEDGEMENTS

I would like to thank the members of my committee, Andy Sheldon, Vicki Watson and Kerry Foresman for their support, encouragement and patience throughout the completion of this project. I want to especially thank Andy who introduced me to stream ecology and black flies, which were familiar to me only through their blood-feeding activity.

I would also like to thank the zoology department for the opportunity to teach as a teaching assistant. The positions were challenging, and I learned a great deal from the professors that I worked with, Kerry Foresman, Phil Motta, Del Kilgore, Vince Resh, Ken Stewart, and Andy. Nancy and the rest of the administrative staff were very helpful throughout my time in Missoula and Dewayne Williams provided his assistance with the hand-drafted figures in the thesis.

Confirmation that I was identifying the black flies correctly was provided by Dr. R. V. Peterson of the Systematics Entomology Lab, U.S.D.A., and is gratefully acknowledged. In addition, the Sigma Xi Society provided a Grant-in-Aid of Research of $250.00.

I want to thank my aquatic ecology comrades, Yvonne Vadeboncoeur, Mike Young and Tom Jones for tolerating blood-seeking black flies and an old guy buzzing around the lab. My parents, Jim and Betty Eaton, provided periodic funding for my intellectually rewarding, but monetarily impractical career.

Finally, I would like to thank my wife, Alexine, for her love, support, and threats not to marry me until the thesis was completed.

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INTRODUCTION

Streams which drain standing bodies of water often contain filter-feeding larvae of the family Simuliidae (Diptera: Nematocera). Studies characteristically show diverse, high density and unique assemblages of species, which change rapidly and dramatically with distance downstream (Ulfstrand 1968; Carlsson et al. 1977; Wotton 1979; Back and Harper 1979). These changes occur over very short distances when compared with the gradual longitudinal succession observed in lotic systems which do not drain lentic bodies (Hynes 1970). Species diversity is greater in these systems than in non-outlet systems of comparable order (Ulfstrand 1968; Hynes 1970). Longitudinally, within a lake-outlet system, the overall density of preimaginal simuliids decreases and species composition changes (Carlsson et al. 1977; Sheldon and Oswood 1977; Wotton 1979; Back and Harper 1979). Various species characteristically occur in greatest abundance either near the outfall or in downstream areas less influenced by the lake (Wotton 1979; Back and Harper 1979). In addition, life history parameters, which are the primary focus of this paper, may vary among outlet and non-outlet lotic systems, as well as longitudinally within an outlet (Wotton 1982, 1987).

The diversity and change observed in lake-outlet systems reflects the existence of a complex ecological gradient described by Oswood (1976), "as lake water being acted upon by stream processes". The gradient may be visualized as longitudinal distributions of abiotic and biotic variables, which in combination produce a longitudinal series of ecological niches. This variety of niche space over such a short stretch of lotic channel allows the coexistence of many species. In addition to supporting species unique to the area, the conditions existing between the lake and the "normal" stream may alter the life history parameters of species whose populations range both within and beyond the gradient.

The purpose of this investigation is to examine the distributions and life histories of the simuliid species living along a lake-outlet in western Montana. Previous studies in this outlet have recorded dramatic longitudinal declines in the overall density of simuliids and other filter feeders (Sheldon and Oswood 1977; Oswood 1976, 1979). The specific objectives are: 1) determine the species composition of the simuliid assemblage, 2) describe the phenology and voltinism of the most abundant species, 3) record the longitudinal distribution of the species and 4) record the distribution of the species among microhabitats within a longitudinal site.

Black flies (Diptera:Simuliidae) are an economically and ecologically important family of insects (Kim and Merritt 1987). Adult females are biting pests of humans, cattle and other mammals in the northern prairies and coniferous forests of Canada and Siberia (Fredeen 1969). In addition, they are vectors of human and wildlife diseases, including onchocerciasis or "river blindness", which affects an estimated 20 million people in Africa and unknown numbers in Mexico and Central America (Laird 1981). The larvae of black flies are ubiquitous components of lotic systems, where they function as filtering-collectors (Cummins 1987). They are able to filter very small particles, including bacteria and colloids, from the water column (Colbo and Wotton 1981). Cummins (1987) concludes that their most important role in lotic systems is the conversion of ultra fine organic matter (UPOM), which is abundant and high in energy, to particles of larger size through the production of their feces.

To facilitate a comparison of gradient variables and the distribution of simuliids in lake-outlet streams, I will refer to the terminal regions of the stream gradient as the outfall reach and the downstream reach. The hypothetical outfall reach begins at the lake and extends to a point downstream. This is the area of most rapid change for the variables and faunal distributions associated with the flow of lake water into a stream channel. Beginning at a point beyond the terminus of the outfall reach, the downstream reach begins and continues indefinitely. This reach is characterized by less rapid longitudinal changes in the variables and faunal distributions associated with the lake-outlet stream. The actual lengths of the outfall and downstream reaches and the distance between them will depend on the particular lake-outlet system and the variable or faunal distribution in question. In this paper, I will attempt to delimit these regions with respect to the distribution of simuliids in Owl Creek.

For the purposes of the following discussion, I will compare abiotic and biotic variables between lake-outlet and non-outlet streams and between outfall and downstream reaches. Certain abiotic variables such as latitude, altitude, stream size, slope, etc. will be considered equal.

Some of the variables cited as important to the ecology of preimaginal simuliids in lake-outlet systems are temperature, flow, quantity and quality of food, oviposition behavior and interspecific interactions (Carlsson et al. 1977; Wotton 1987; Harding and Colbo 1981). The behavior of these variables in outlet versus non-outlet systems and outfall versus downstream reaches is outlined below as a basis for interpreting the results of this investigation.

The temperature regime that an aquatic poikilotherm encounters determines to a large extent its rate of development (Sweeney 1978). This in turn affects voltinism, seasonal succession and many other life history parameters. Annual temperature regimes in lake-outlet streams show generally warmer temperatures in summer and winter and a slower response to changes in air temperature than is observed in non-outlet streams (Edington 1966; Ulfstrand 1968; Parker and Voshell 1982). Warmer temperatures in the outflow of a temperate, dimictic lake during summer and winter are due to thermal stratification within the lake (Wetzel 1983). The slower response to changes in air temperature is due to the insulating effect of the relatively large volume of water present in the lake. Diel temperature patterns of non-outlet streams more closely track daily changes in air temperature, while lake-outlets are influenced by the relatively reduced temperature fluctuations occurring in the lake (Edington 1966; Ulfstrand 1968). This is important because development in insects is controlled not only by mean daily temperature, but also by the associated range of daily temperatures (Beck 1983; Sweeney 1978).

Another characteristic of the temperature regime in lake-outlet systems is the reduced occurrence of ice cover. In geographic regions where streams normally freeze over, the outfall areas of lake-outlets often remain open due to the input of relatively warm (>0°C) lake water (Colbo 1979; Harper 1981).

The flow regime of a lotic system, with respect to lake-outlet simuliid ecology, affects the stability of the substrate, larval drift and the dynamics of seston (Carlsson et al. 1977; Wotton 1987; Maciolek and Tunzi 1968). The short-term pattern of flow, in general, is dampened in natural lake-outlet systems versus non-outlet systems. The lake modulates the flow to outlets, preventing the rapid changes in discharge observed in non-outlets (Carlsson et al. 1977). The substrate is therefore less subject to disturbance, and the invertebrates have a longer period of time to adjust to changes in flow. Wotton (1987) suggests that flow related drift of larval simuliids is reduced in lake-outlets.

Most of the hypotheses put forth to explain lake-outlet communities concern the quantity and quality of seston in the system (Cushing 1963; Ulfstrand 1968; Carlsson et al. 1977; Sheldon and Oswood 1977; Wotton 1978; Oswood 1979). Seston, the source of nutrition for larval simuliids and other lotic filter feeders, is suspended particulate matter, made up of living organisms, and organic and inorganic detritus (Wallace and Merritt 1980). Sources of seston for the system may be autochthonous, generated within the stream (e.g. the channel bed) or allochthonous, generated outside the stream (e.g. a lake or terrestrial area). An obvious difference between an outlet and a non-outlet system is the allochthonous source of lake-influenced seston. There is a large body of evidence which shows that a lake in the course of a lotic channel alters the quantity and quality of outlet seston.

Particles settle and collect in standing water, so lake-outlets show lower concentrations of seston than non-outlets (Voshell and Parker 1985). In addition, the annual fluctuation in seston concentration, caused by seasonal inputs from benthic and terrestrial sources, is dampened due to the relatively constant input of lake-produced seston (Maciolek and Tunzi 1968; Voshell and Parker 1985; Vadeboncoeur 1988; Sedell et al. 1978).

The high secondary production observed for filter-feeders in lake-outlets and the relatively low seston concentrations suggest that lake-outlet seston is qualitatively superior to seston from non-outlets (Parker and Voshell 1983; Ulfstrand 1968). However, Voshell and Parker (1985) found that the total caloric content of organic seston was higher in a non-outlet, "freeflowing", river than an outlet "impounded" river. They attributed the higher secondary production of the lake-outlet to the ability of the filter-feeders to selectively remove the living component of the seston, limnetic plankton, which is assimilated more efficiently than detritus (Parker and Voshell 1983).

A longitudinal decline in the seston concentration of a lake-outlet system is often hypothesized to explain a highly productive filter feeder guild and its disappearance downstream. However, results fail to show a consistent pattern. Chandler (1937) and Maciolek and Tunzi (1968) document a longitudinal decline in seston concentration, while Carlsson et al. (1977), Sheldon and Oswood (1977), Oswood (1979), Naiman (1982), Voshell and Parker (1985), Valett and Stanford (1987), and Vadeboncoeur (1988) show either no change, an increase, or temporally variable patterns. These results may be reconciled by recognizing the site specific conditions of a system, namely the relative contribution of each source of seston and the temporal variation in the physical transport of seston (Vadeboncoeur 1988; Maciolek and Tunzi 1968). If the relative contribution of seston from non-lake sources, such as the channel bed and riparian zone, is equal to or greater than the lake contribution, a downstream decline in concentration is not observed, and in some cases an increase is documented (Vadeboncoeur 1988). In addition, changes in flow affect the physical transport of seston in a system. Greater transport of seston occurs during high flow periods, while retention occurs during low flow periods (Maciolek and Tunzi 1968; Voshell and Parker 1985; Vadeboncoeur 1988). Therefore, temporal variation in the longitudinal distribution of seston concentration is source and flow specific.

A longitudinal decline in seston quality has been documented in a number of lake-outlet systems, and appears to be one of the most important factors determining the distribution and abundance of simuliids in lake-outlets (Ross and Merritt 1987). Richardson (1984) and Voshell and

Parker (1985) show a downstream decrease in the ratio of organic to inorganic seston, and Voshell and Parker show further that the usable caloric content of the seston in the outfall is higher than the caloric content downstream. Maciolek and Tunzi (1968) and Voshell and Parker (1985) show a compositional change from the more easily assimilated, living seston of the outfall to the detritus dominated seston downstream. Wotton (1984) suggests that lake-produced, microfine particles (>0.5 μ and <10 μ), available only in the outfall reach, are high in nutritive value and allow dense populations of simuliids to develop.

The oviposition behavior of female black flies is also considered one of the major factors determining the distribution and abundance of simuliids in lake-outlets. Carlsson et al. (1977) argue that black flies prefer to oviposit at lake-outlets because of visual and other sensory cues (e.g. a smooth water surface) and shallow, stable substrates for egg laying. Oviposition behavior, however, is to varying degrees species specific, which adds complexity to the general scheme above. This specific behavior appears partly responsible for the longitudinal succession of species observed in these systems (personal observation).

Interactions among species and individuals within a species are frequent in densely populated areas, such as outfall reaches, and may determine in part the spatial and temporal distribution of lake-outlet simuliids. Territorial behavior of larval simuliids among species and conspecifics has been observed and is presumably a response to limited space and food resources (Hart 1986; Harding and Colbo 1981). Harding and Colbo (1981) and Wotton et al. (1979) present direct and indirect evidence of downstream displacement of one simuliid species by another in a lake outfall area. Wotton et al. (1979) also show evidence that smaller larvae are displaced more often than larger larvae in an outfall area, suggesting intraspecific competition as well. Hemphill and Cooper (1983) and Hershey and Hiltner (1988) document a negative correlation between larval simuliids and larvae of the genera _Hydropsyche_ (Trichoptera: Hydropsychidae) and _Brachycentrus_ (Trichoptera: Brachycentridae), respectively. _Hydropsyche_ and _Brachycentrus_ are filter feeders and therefore potential competitors of larval simuliids, and both on occasion are predators of immature simuliids (Davies 1981). Other important predators associated with lake-outlets are larvae of the trichopteran families Rhyacophilidae and Polycentropodidae, and larvae and adults of the dipteran families Empididae and Muscidae (Peterson 1960; Peterson and Davies 1960; Davies 1981; Steyskal and Knutson 1981; Wotton 1987; personal observations). In addition, certain parasites may be more prevalent among the high density simuliid populations at lake outfalls (pers. obs.).

MATERIALS AND METHODS

Study Area:

The study area, Figure 1, has been described by Oswood (1976), Sheldon and Oswood (1977) and McAuliffe (1982 and 1984). Owl Creek is a lake outlet stream located in Missoula County, Montana, U.S.A. (47°7' N, 113°30' W; elevation 1256 meters). The creek drains Placid Lake, which has an area of 449 hectares and a maximum depth of 27 meters. The lake was formed by the damming action of glacial moraine deposits, which collected in the area of the present outlet. Juday and Keller (1978) classified the lake as mesotrophic, based on summer and winter oxygen depletion rates, summer chlorophyll a levels, and transparency measurements during the years 1974 through 1977. Approximately one kilometer below the natural outlet of the lake, a small dam 1.5 meters in height creates a pond-like channel between the lake and the creek. This slowly flowing channel has an average width of 30 meters, a depth of 4 meters, and based on the abundance of macrophytes, appears relatively productive.

Owl Creek is a fourth order stream with a width that varies from 6 to 15 meters in late winter. It flows for approximately 6 kilometers before emptying into a marshy area that drains through several channels into the Clearwater River. The creek has no major tributaries and the channel morphology is fairly homogeneous for the first 3

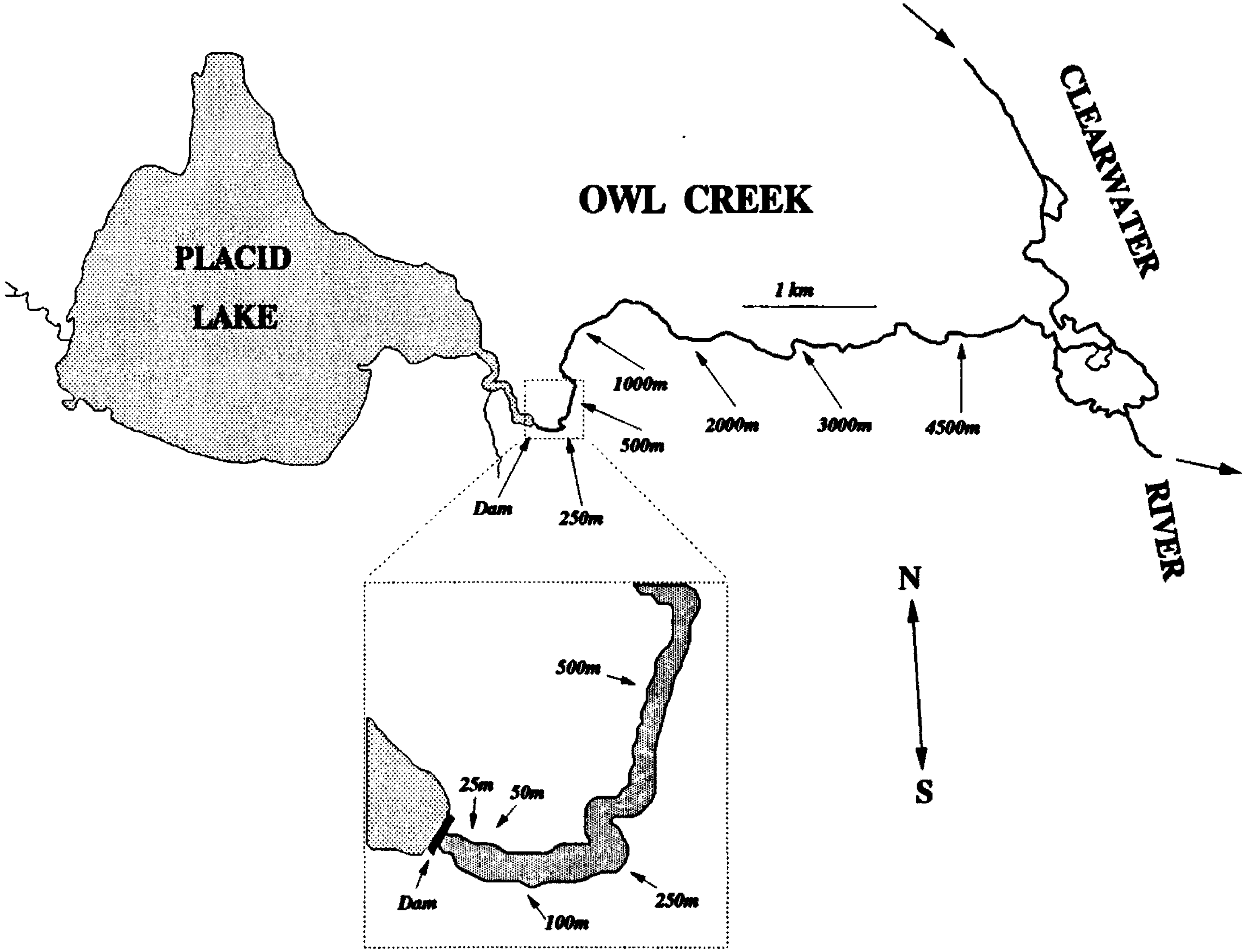


Figure 1. Sampling sites along Owl Creek, Missoula County, Montana, U.S.A..
Inset shows sites from the lake outfall to 500 meters downstream.

kilometers. It contains riffle and pool areas and has an average gradient of 1.5%. The substrate consists primarily of cobbles and boulders, and the riparian zone adjacent to pools supports sedges and cattails. Other riparian and forest vegetation includes willow, alder, dogwood, Englemann spruce, Douglas fir and western larch (McAuliffe 1982).

Flow data for Owl Creek the year previous to this study, 1985, were provided by Vadeboncoeur (1988), and flow data for the Clearwater River in 1985, and for the period of this study, 1986 - 1987, were provided by the U.S. Geological Survey, Helena, Montana (Figure 2). Air temperature and rainfall data 4 kilometers north of the study site were provided by the Seeley Lake Ranger District, U.S. Forest Service, Seeley Lake, Montana (Figures 2 and 3).

Field Methods:

I conducted this study from January 1986 through March 1987. Ten longitudinal sites were established along the creek and spaced progressively closer together as the outfall reach was approached, since this is the area where I expected the most rapid changes in faunal distributions (Figure 1). I collected larvae and pupae of the family Simuliidae from each site weekly from March through November and then biweekly during the remaining winter months. Stones and macrophytes were removed from the stream, and the larvae and pupae were hand picked and preserved in 80% ethanol. The

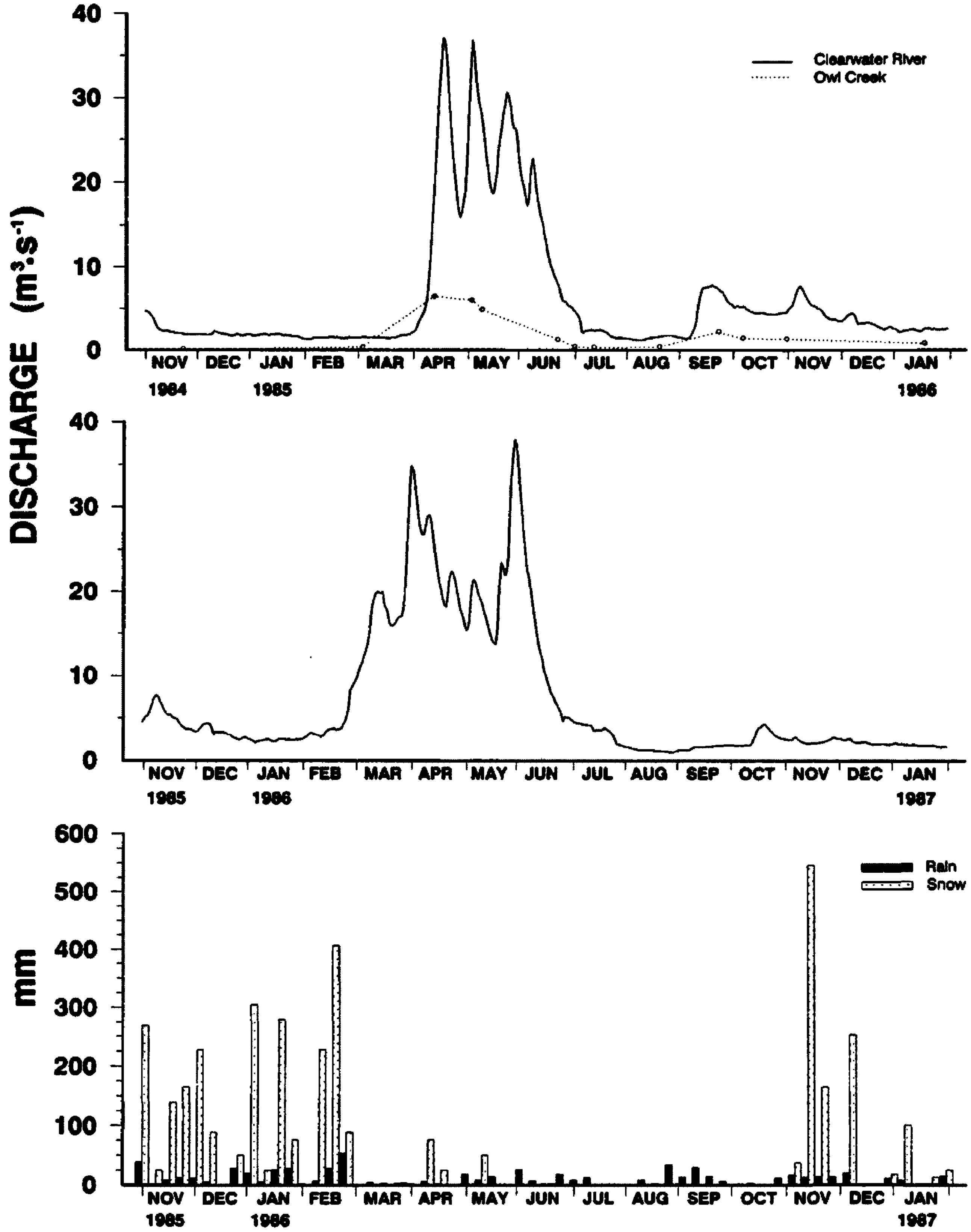


Figure 2. Discharge of the Clearwater River and Owl Creek, 1984-1986.
Discharge of the Clearwater River, 1985-1987.
(Vadeboncoeur 1988 and U.S.G.S. Helena, MT)
Precipitation, 1985-1987, at Seeley Lake Ranger Station, MT.
(U.S.F.S., Seeley Lake, MT)

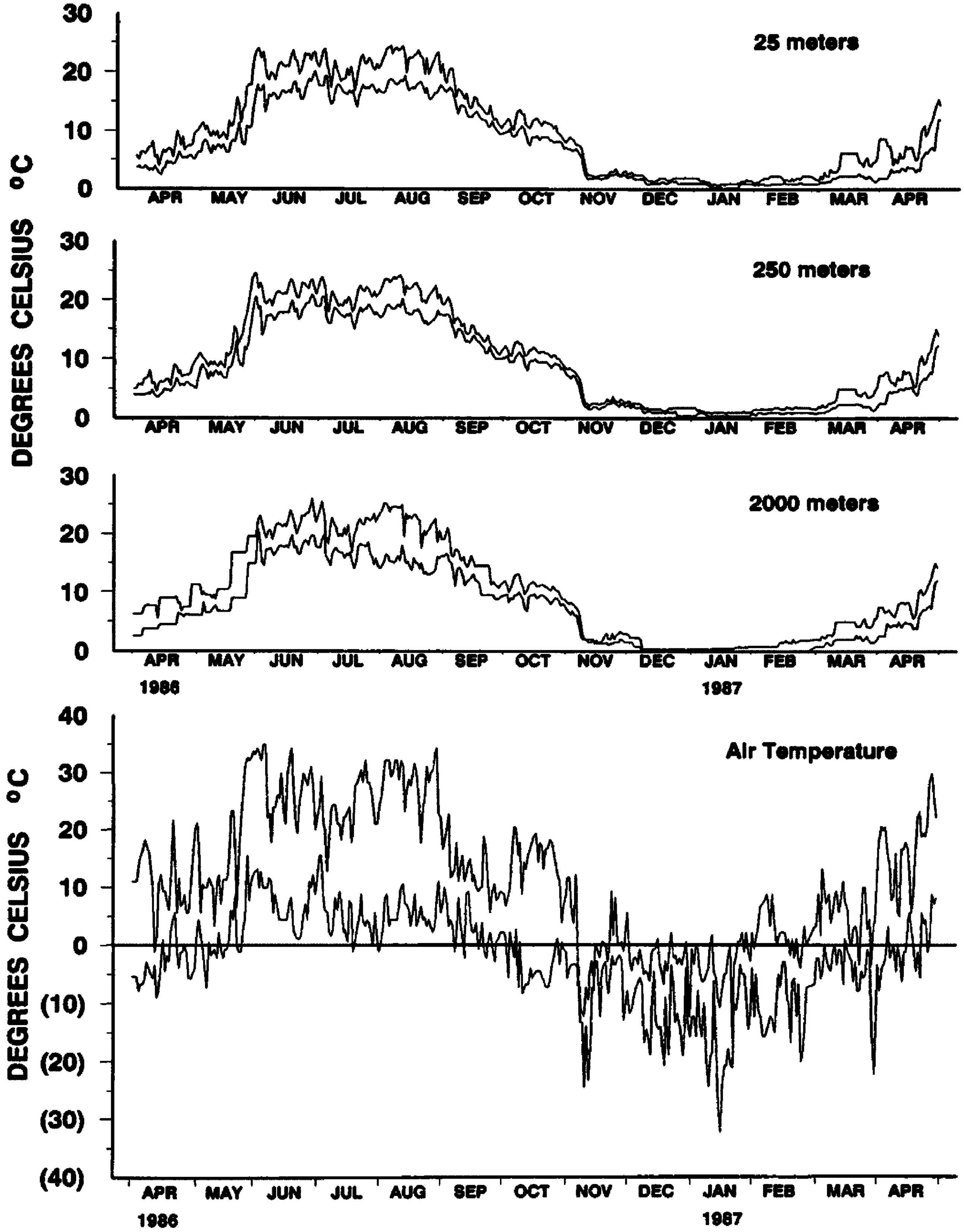


Figure 3. Daily maximum and minimum water temperatures at 25, 250 and 2000 meter sites. Maximum and minimum air temperatures provided by the U.S.F.S., Seeley Lake Ranger District, Seeley Lake, Montana.

specimens were stored separately according to date, longitudinal site and substrate type (stones versus macrophytes). Live larvae and pupae used for rearing were placed in moistened containers and transported to the laboratory in ice coolers.

I noted the activity of adults when present, recording any swarming, mating, oviposition or biting behavior observed. If possible, I collected a sample of the adults being observed with an aerial net and preserved them in 80% ethanol.

I monitored water temperature at three sites, 25, 250 and 2000 meters, using Bristol thermographs; Model IY501-IA, precision ± 0.25 °C (Figure 3). The accuracy of the thermograph record was checked on each sampling date with a mercury thermometer. In addition, I measured spot temperatures at the other sites when sampling. Air temperature was monitored with a calibrated maximum-minimum mercury thermometer at the 2000 meter site.

Laboratory Methods:

For the preserved samples, I first separated the larvae and pupae of the family Simuliidae from debris and other macroinvertebrates and placed the specimens into fresh 80% ethanol. I used a sieve with a mesh size of 120 microns when draining the samples, so that early instars were retained. Larvae and pupae were then sorted to species and counted using a Bausch & Lomb stereo, dissecting scope. For the purpose of distinguishing larval instars and cohorts, I measured the postgena length of the larvae using an ocular micrometer (Fredeen 1976). Larvae were measured to the nearest 0.5 micrometer units (1 unit = 17 μ 'micrometers') at a magnification of 60X.

To aid in species identification, I reared mature larvae and pupae to adults in the lab, using aerated beakers for the larvae and separate containers with moist filter paper for the pupae. This allowed me to associate each of the life cycle stages for a particular species. I shipped some of the reared adults of each species and their associated pupal and larval exuviae, as well as mature larvae and pupae, to Dr. R. V. Peterson of the Systematics Entomology Laboratory, U.S.D.A., Washington, D.C., for verification of my identifications.

Analysis:

Although the effort expended to collect each sample was fairly equitable, the samples can not be considered quantitative. Therefore, to compare the distribution of the species longitudinally and within a site, the counts of each species from a sample are ranked in abundance from greatest to smallest. True replicate samples do not exist, but when the ranked abundances of the species are compared between sites located close to each other on the same date, or consecutive sampling dates at the same site, the patterns of abundance are often similar and therefore support each other. I feel that this method is a valid way of showing rough trends in abundance, but more rigorous quantitative sampling in the future is necessary to confirm this belief.

Determining the number of larval instars for an arthropod species is important for tracking larval development and distinguishing generations or cohorts, which are needed in estimates of production. To determine the number of instars for the simuliids of Owl Creek, I used a combination of morphological and biometrical information. First instars of all larval simuliids have a structure on the dorsal surface of their head capsule called an egg burster, which is lost during ecdysis to the second instar. The last instar can be identified by the presence of dark and well differentiated respiratory histoblasts, visible beneath the thoracic cuticle. These structures function as respiratory organs in the pupae.

The biometrical methods are more subjective and involve the examination of polymodal frequency distributions obtained by measuring a sclerotized structure on a large number of larvae collected throughout the larval development period. The frequency distribution obtained from these measurements will show peak frequencies corresponding with each instar, and the total number of instars should equal the number of peaks.

According to Brooks' Rule (Crosby 1973), a sclerotized structure of a larval arthropod will increase in size geometrically with each instar, and the growth ratio obtained by dividing the size of the structure in a particular instar by the size of the structure in the previous instar is called Brooks' Ratio. For example:

$$\text{B.R.} = (\text{PGL: Instar II}) \div (\text{PGL: Instar I})$$

B.R. = Brooks' Ratio, PGL = length of postgena.

Since the original formulation of this theory, it has been shown that not all sclerotized structures follow the rule exactly. Different structures grow at different rates, and there may be little or no increase in the size of a sclerotized structure between consecutive instars, e.g. Crosby (1974) and Craig (1975). However, Fredeen (1976) and Ross (1979) showed that the length of the postgena in Simulium arcticum and Simulium vittatum, respectively, develops according to Brooks' Rule and is convenient to measure.

I measured the length of the postgena, the lateral sclerite between the mandible and the posterior edge of the head capsule, on larvae of the four most abundant species to determine the number of instars during larval development (Fredeen 1976). To minimize temporal and spatial variation, only larvae from a specific cohort and site were used in the determination (Crosby 1974). The resulting polymodal distribution was divided into separate unimodal (instar) distributions using normal probability graph paper (Cassie 1954).

Figure 4 shows an example of the use of a probability graph paper to separate the larval instars of Prosimulium exigens in one sample. The cumulative percent of the distribution was plotted on a normal probability scale against each size class of the variable measured (length of postgena). Regions along the plot of a polymodal distribution that have a slope approaching zero (inflection points) indicate boundaries between separate unimodal distributions (Cassie 1954). The size-frequency histogram of the measurements is included in Figure 4 for comparison with the probability plot.

The validity of the instar determination was evaluated by plotting the $\log_{10}$ of the mean postgenal length for each unimodal distribution against the number of peaks or instars. If a deviation from the line described by these points was present (see, for example, Figure 9), I suspected that an instar had been missed (Craig 1975). To decide when a deviation was significant, I used Crosby's Growth Rule, which was developed from studies on the instars of the simuliid, Austrosimulium tillyardianum. As stated by Craig (1975), Crosby (1974) "determined criteria to show when and where instars are missing". The Rule states that, "when

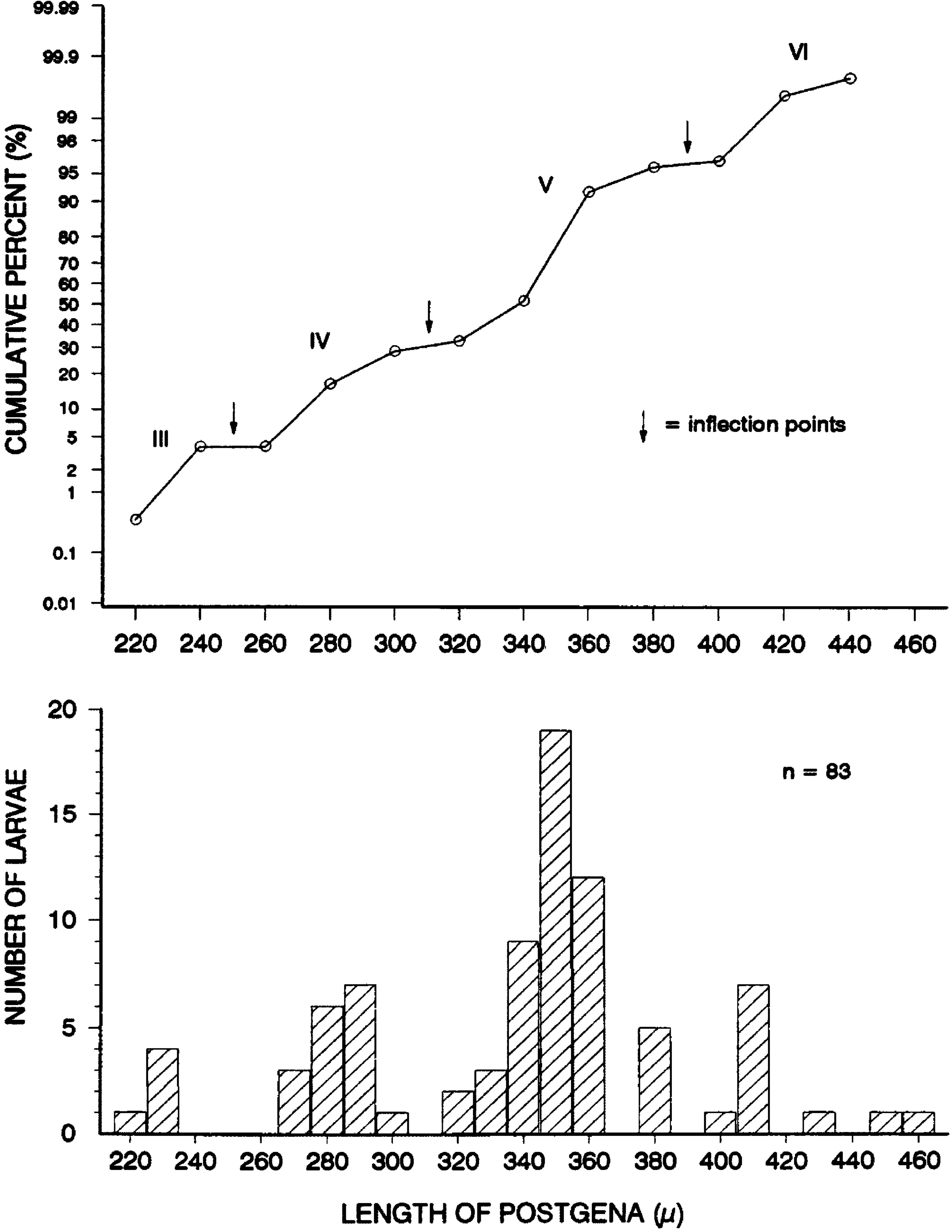


Figure 4. Example 1 of the use of a probability graph for the separation of instars. The figure shows 4 instars within one cohort of P. exigens. Sample: January 19, 1986, 50 meter site. μ = micrometers.

there is a 10% or greater difference between two consecutive Brooks' Ratios, then the deviation around a logarithmic progression is significant and an instar is probably missing or the grouping is somehow incorrect" (Craig 1975). A sample calculation of Crosby's Ratio is shown below.

$$\text{C.R.} = [((\text{B.R.: Instar II to III})-(\text{B.R.: Instar I to II})) \div (\text{B.R.: Instar I to II})] \times 100$$

B.R. = Brooks' Ratio, C.R. = Crosby's Ratio.

I calculated both Brooks' and Crosby's Ratios for the species analyzed. I also compared the size of final instar larvae among different cohorts of a species using Student's t-test for a difference between two means (Sokal and Rohlf 1981).

To distinguish larval cohorts for the four most abundant species, I examined frequency distributions of postgenal lengths from larvae on individual sampling dates. By evaluating these distributions chronologically throughout the larval development period, it was possible to determine the number of cohorts and the voltinism, i.e. the number of annual generations for a species.

I used normal probability graph paper to separate cohorts if the distributions suggested the presence of more than one (Cassie 1954). When more than one cohort is present, the distributions appeared grossly bimodal or

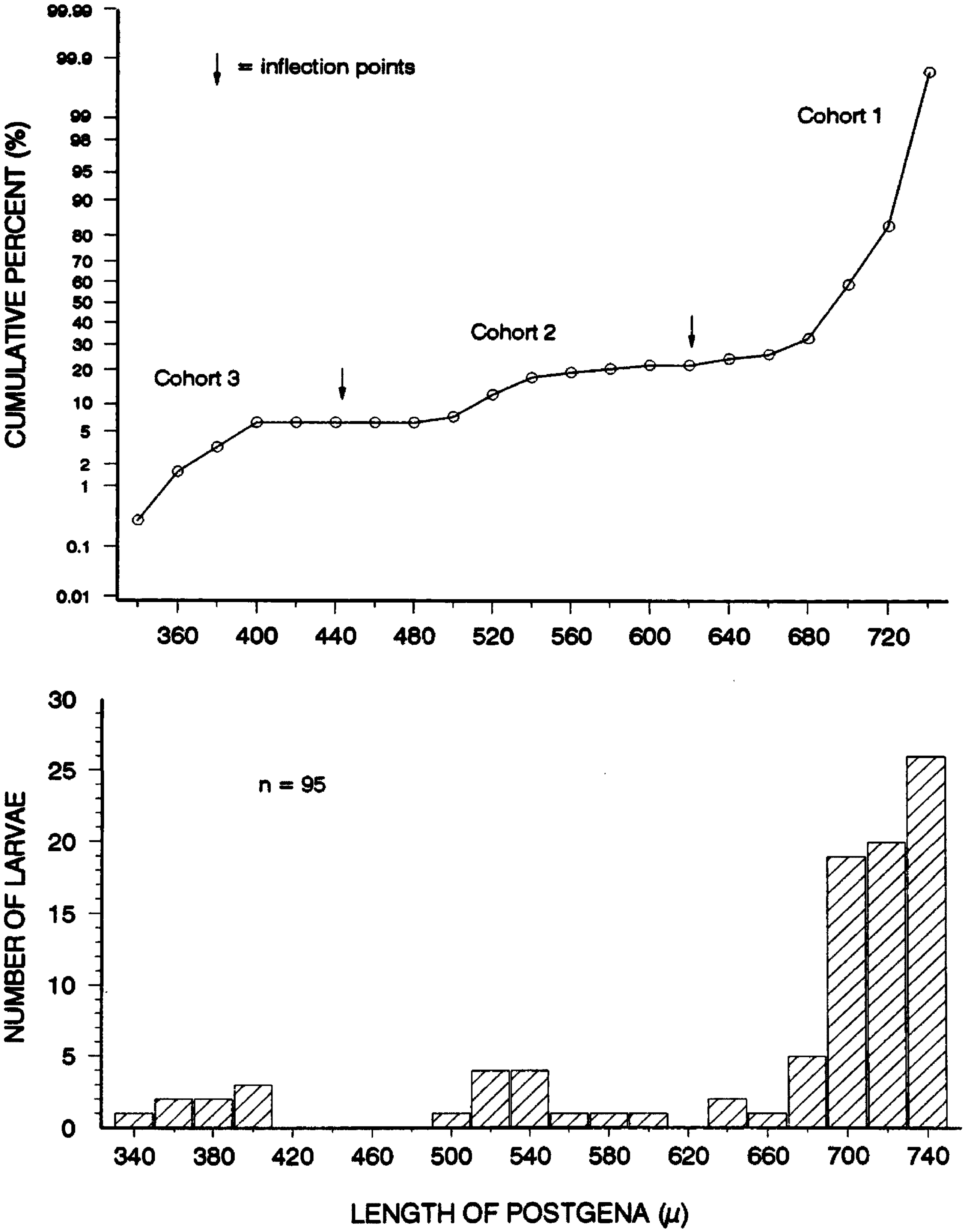


Figure 5. Example 2 of the use of a probability graph for the separation of cohorts. The figure shows 3 cohorts (3 and 2 = spring, 1 = winter) of *P. exigens*. Sample: April 25, 1986, 50 meter site. μ = micrometers.

trimodal. Figure 5 shows an example of cohort separation for larvae of P. exigens from one sample. Regions along the plot with slopes approaching zero (inflexion points) were wider between cohorts than between the instars of one cohort (Figures 4 and 5).

These methods worked well when the cohorts were synchronized as was generally the case during months with relatively low water temperatures, but they were of little use in summer when multiple asynchronous cohorts were present for some species. For the asynchronous periods, I estimated the number of cohorts by dividing the accumulated day-degrees (described below) during the asynchronous period by the number of day-degrees accumulated during one synchronous cohort.

Day-degrees are often used to estimate the physiological time necessary for the development of invertebrate poikilotherms (Taylor 1981). They are a measure of the accumulated heat energy that organisms are exposed to in a particular habitat during a given period of time (Sweeney 1984). Day-degrees are calculated by summing the differences between mean daily temperatures in a habitat and the developmental threshold temperature for an organism over the time period of interest. The threshold temperature is the temperature at which development of the organism being studied is close to zero (Sweeney 1984).

Accumulated day-degrees Celsius (D^oC) were calculated from the thermograph data according to the following formula (Ross and Merritt 1978):

$$\sum_{k=1}^{n} \left[D^{\circ}C = \left(\sum_{i=1}^{24} \frac{T_i}{24} \right) - \mathit{Threshold\ Temperature}(^{\circ}C) \right]$$

D^oC = Day-Degrees Celsius.
n = number of days that day-degrees are accumulated.
T_i = hourly temperature.

The daily mean was calculated using hourly versus daily maximum and minimum temperatures, since continuous records were available. For longitudinal sites, "threshold temperature" was dropped from the formula. For individual cohorts, I summed the day-degrees accumulated from the sampling date when first instars of the cohort were initially observed to the sampling date when pupae were first observed. For the calculations, I used both the standard threshold temperature (0°C) for comparison with other studies, and the coldest field temperature observed when the first instars of a species were present. This second temperature should be a more accurate estimate of the actual physiological threshold temperature for hatching of the eggs and growth of the first instar larvae.

RESULTS

Species Composition:

I was able to identify eight species of the family Simuliidae at Owl Creek. These are listed in Table 1. Dr. R.V. Peterson of the Systematics Entomology Laboratory in Washington D.C. verified my identifications. The verified specimens from the study, including associated larvae, pupae and adults from all eight species were retained for the U.S. National Collection, Lot 87-04215. A subjective judgement regarding the overall abundance of preimaginal simuliids is included in Table 1, and is based on the frequency of observation and relative abundance over all sites and sampling dates.

Table 1. Species of the family Simuliidae: Owl Creek.

Species	Number of Species in Complex	Abundance
Prosimulium exigens		HIGH
Simulium vittatum [1]	2	HIGH
Simulium arcticum [1]	several	HIGH
Simulium tuberosum [1]	6 or 7	MODERATE
Simulium verecundum [1]	2 or 3	MODERATE
Simulium decorum [1]	2 or more	LOW
Simulium canoniculum		RARE
Simulium "aureum" [1, 2]	4 or 5	RARE

1 = Unresolved species complex (R.V. Peterson, personal communication 1987).

2 = True *S. aureum* is not present in North America. The species in Owl Creek is possibly *S. pilosum*, which is a sibling of *S. aureum* (R.V. Peterson, personal communication).

Morphological criteria were used to identify the above species. However, members of the family Simuliidae are known to exist in morphologically indistinguishable, multispecies groups called species complexes. The species in a complex in relation to each other are called sibling species. Some of these complexes have been elucidated using cytotaxonomic techniques (Rothfels 1979) and more recently electrophoretic techniques (Snyder 1982). Of the eight Owl Creek species, six are known from other locations as morphologically unresolved species complexes. These are indicated in Table 1. Some recent studies such as Adler and Kim (1984) and Adler (1986) have investigated the ecology of siblings, and have concluded that the cytological evidence of speciation is supported by field observations showing spatial and temporal segregation of siblings. The resources required to identify and cytotype simuliid larvae from Owl Creek were beyond the scope of this project. Therefore, the results concerning these six species should be interpreted with caution and with the realization that two or more siblings may be present within what appears to be a single species distribution.

Four of the eight species from Owl Creek, Simulium vittatum, Simulium tuberosum, Simulium verecundum and Simulium decorum, have holarctic or nearctic distributions (Crosskey 1987) and have been recorded from outlet streams in eastern North America (Back and Harper 1979; Cupp and

Gordon 1983). *S. decorum*, because of its absence or scarcity in other habitats, is known as a lake-outlet specialist (Wotton 1987). *Prosimulium exigens*, *Simulium arcticum*, *Simulium canonicolum* and *Simulium "aureum"* (*pilosum* ?) are restricted to western North America (Crosskey 1987).

Physical Factors:

The upper hydrograph of Figure 2 shows the flow ($m^3 \cdot s^{-1}$) for Owl Creek and the Clearwater River at Clearwater Junction, Montana during 1985 (Vadeboncoeur 1988; U.S.G.S., Helena, Montana). Although the Clearwater River had a flow approximately four times greater than Owl Creek, the annual periods of low and high flows corresponded with each other. A spring peak in flow following snow melt occurred from March through June. A smaller peak occurred from September through November after fall rains. December through February and July through August were periods of low flow.

The lower hydrograph in Figure 2 shows the flow of the Clearwater River at Clearwater Junction, Montana during the period of my study, 1986 - 1987. The periods of high and low flows were similar to 1985. For the purposes of this study, I will assume that Owl Creek flows followed the pattern of the Clearwater flows, although reduced in volume.

The bottom graph of Figure 2 shows precipitation (mm) of rain and snow during the period of this study (U.S.F.S., Seeley Lake, Montana). Annual precipitation during 1986 totalled 385 mm of rain and 1705 mm as snow.

Figure 3 shows the daily maximum and minimum water temperatures at sites 25, 250 and 2000 meters downstream from the dam; April 1986 through April 1987. Maximum and minimum air temperatures 4 kilometers north of the study site are shown for the same period (U.S. Forest Service, Seeley Lake, Montana).

Table 2. Thermal regime at sites 25, 250 and 2000 meters.

Annual values shown in degrees celsius °C.

SITE		D°C	MEAN ± S.D.	CV	RANGE
25 m	-	3356	9.19 ± 7.30	79	0.5-23.5
250 m	-	3380	9.26 ± 7.50	81	0.5-24.5
2000 m	-	3223	8.83 ± 7.47	85	0.0-26.0

D°C = day-degrees.
S.D. = standard deviation.
CV = coefficient of variation.

Table 2 and Figure 3 contrast the differences in the thermal regime at the three stream sites. Annual day-degrees accumulated from April 1986 through March 1987 and annual mean temperatures were similar at the 25 and 250 meter sites, but were less at the 2000 meter site. The greatest differences in accumulated day-degrees between the two outlet sites and the downstream site were observed during the three coldest months, December, January and February.

The 25 meter site accumulated 119 day-degrees during these months, in contrast to 38 day-degrees at the 2000 meter site. This three month period accounts for 61% of the annual difference in day-degrees between the two sites.

The occurrence of ice also changed longitudinally during the three coldest months. At sites from the dam to 500 meters downstream, the channel was continually open with only a small amount of shelf ice formation occurring in slack-water pools. In contrast, sites from 1000 to 4500 meters downstream were predominantly ice covered by the end of December. This dramatic difference in ice formation corresponded with a longitudinal temperature gradient on the coldest days in January of only 0.5 ^{o}C.

On two dates in December 1986 and three dates in January 1987, I observed anchor ice formations in open riffle areas at downstream sites from 1000 to 4500 meters. I did not observe anchor ice on these same dates in reaches upstream from the 1000 meter site. Anchor ice in streams encases the substrate when it is formed, and then causes scouring as it is warmed and released (Brown et al. 1953; Maciolek and Needham 1952).

Another difference between the two outlet sites and the downstream site was the extent of annual and diel variation in temperature. Table 2 and Figure 3 show that the annual and diel variation increased as distance from the lake increased. The coefficient of variation and the range increase from the 25 to the 2000 meter site (Table 2) and greater diel variation at the 2000 meter site is apparent in Figure 3. Sites near the lake outlet were less influenced by fluctuations in air temperature than those downstream, because of the insulating effect of a large volume of lake water (Edington 1966).

Instar and Cohort Determination:

Prosimulium exigens

Prosimulium exigens appears to have two univoltine cohorts developing in a pattern similar to that of Prosimulium mixtum/fuscum described by Ross and Merritt (1978). First instar larvae of the overwintering cohort hatched in late October and developed gradually through the sixth instar by the end of February. By mid-March the larvae were developing more rapidly and pupation occurred in early May (Figures 6 and 7). This cohort was abundant, well synchronized, and analysis showed nine larval instars (Table 3 and Figures 8 and 9).

Although first instars were present in low numbers throughout the winter months, a pulse of first instars appeared in March creating a low density, asynchronous, spring cohort (Figure 7). Larvae developed over three months and pupation occurred in late May. The appearance of this

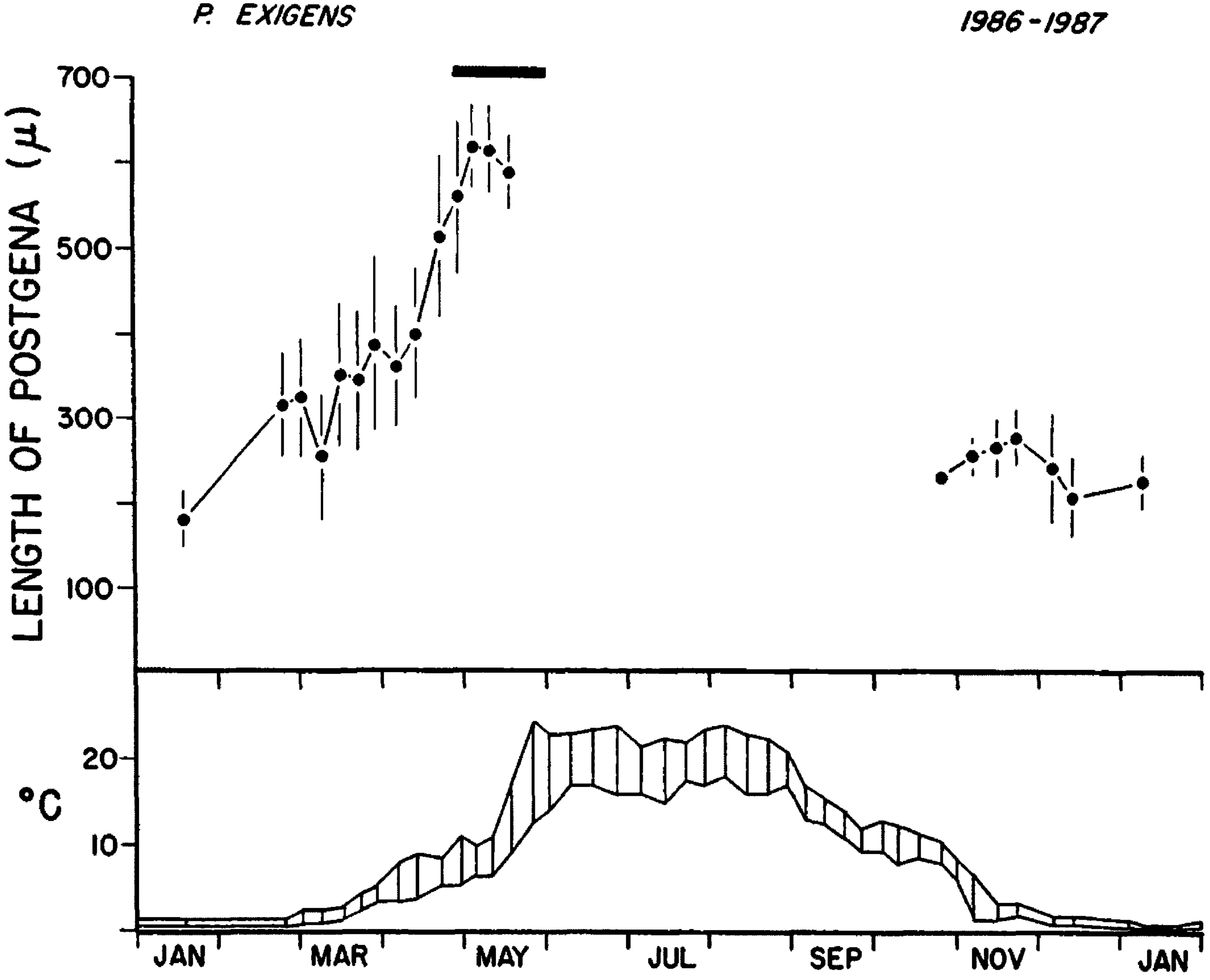


Figure 6. Development of the larval cohorts of P. exigens. The mean ± one standard deviation is shown for the lengths of postgenae (μ) on sampling dates from January 1986 to January 1987 (25 m site). Maximum and minimum water temperatures at the 25 meter site are also shown. Black bars show pupation periods.

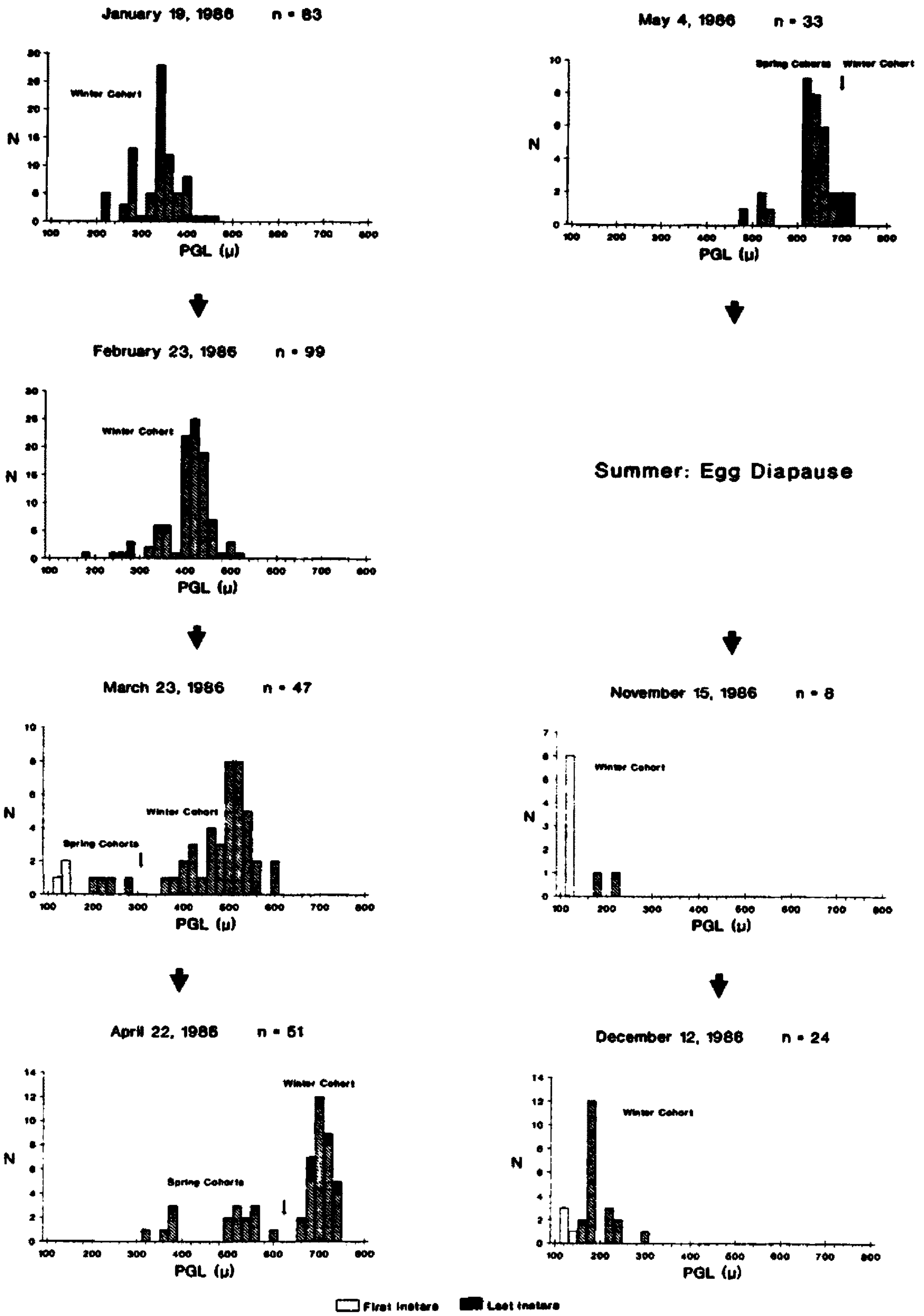


Figure 7. Frequency distributions of the lengths of postgenae for the larvae of Prosimulium exigens on selected dates during 1986 (25 meter site). N = number of larvae, PGL = length of postgena, µ = micrometers.

TABLE 3. *Prosimulium exigens*, lengths of postgenae (µ).

A. Winter Cohort; October - early May.

INSTAR	N	MEAN AND STANDARD DEVIATION	CV^1	Brooks' Ratio	Crosby's Ratio,%	RANGE
I	14	125.07 ± 6.17	5.0			119-136
II	37	172.53 ± 7.46	4.4	1.38	-4.6	162-187
III	37	226.97 ± 10.76	4.8	1.32	-4.9	204-247
IV	41	284.02 ± 16.46	3.8	1.25	-1.6	255-315
V	78	349.70 ± 15.60	4.5	1.23	-1.6	323-383
VI	182	423.75 ± 21.14	5.0	1.21	-0.5	391-468
VII	107	510.71 ± 24.55	4.8	1.21	0.3	476-570
VIII	74	617.63 ± 20.83	3.4	1.21	-5.4	578-655
IX	131	706.41 ± 22.37	3.2	1.14		663-748

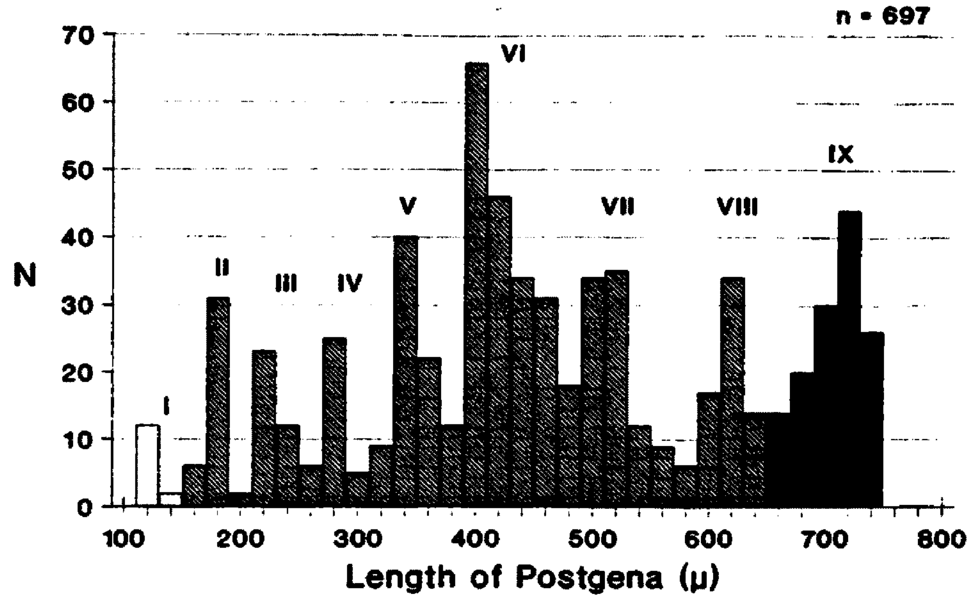
B. Spring Cohorts; March - late May.

INSTAR	N	MEAN AND STANDARD DEVIATION	CV^1	Brooks' Ratio	Crosby's Ratio,%	RANGE
I	3	134.33 ± 9.81	7.9			123-140
II	9	187.22 ± 11.33	6.2	1.39	0.3	174-208
III, IV	12	261.83 ± 20.29	7.9	1.40	0.1	225-293
V	24	366.67 ± 21.97	5.8	1.40	-10.7	327-412
VI	8	458.75 ± 15.07	3.4	1.25	-7.3	446-480
VII	26	532.31 ± 18.57	3.5	1.16	2.6	497-565
VIII	79	633.43 ± 24.34	3.9	1.19		582-684

1 = Coefficient of Variation adjusted for sample size (Sokal and Rohlf 1981).

Prosimulium exigens

Winter Cohort; October - early May



Spring Cohorts; March - late May

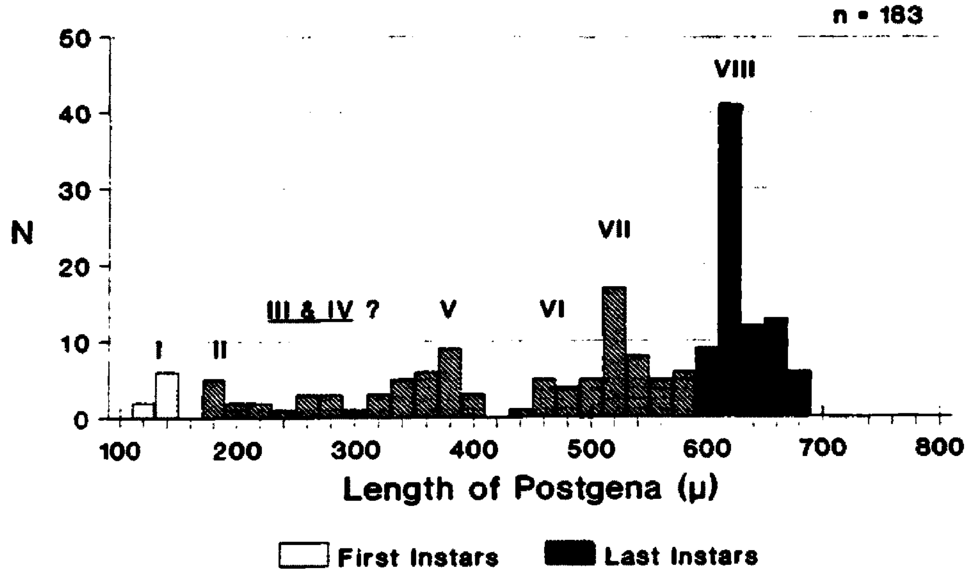


Figure 8. Frequency distributions of the lengths of postgenae for the larvae of Prosimulium exigens. The upper graph shows larvae from the winter cohort and the lower graph shows larvae from the spring cohorts (25 meter site). Roman numerals correspond to larval instars, N = number of larvae, µ = micrometers.

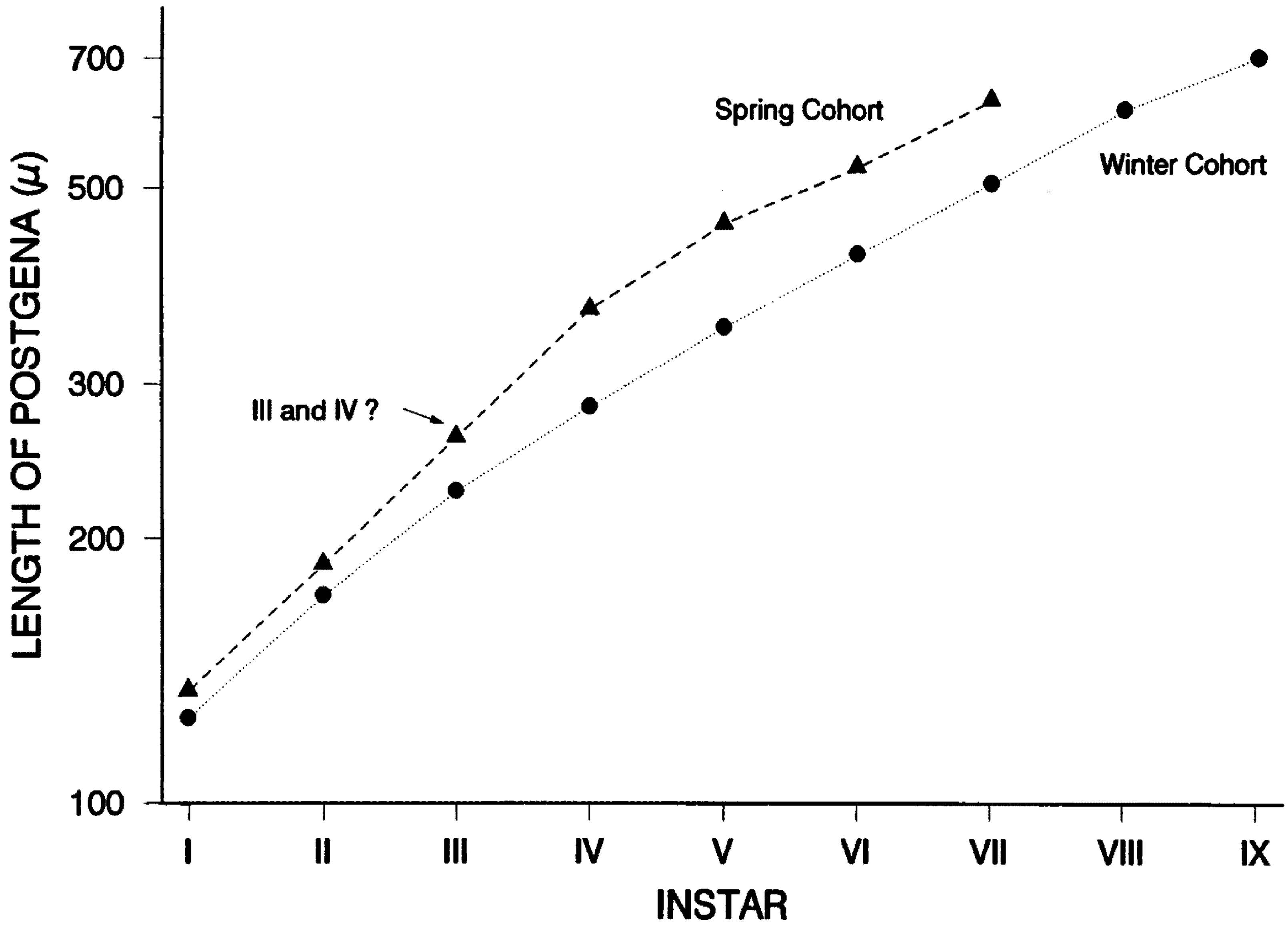


Figure 9. Mean lengths of postgenae ($\log_{10}$scale) for the winter and spring cohorts of P. exigens.

second cohort may have been a result of the increasing temperatures and flows during March (Figures 2 and 3). An increase in flow may have submerged eggs which were previously above the water line, causing a pulse of hatching similar to the one observed by Ross and Merritt (1978). Analysis of this cohort suggested eight instars, but the results are inconclusive because of low numbers of larvae obtained in the intermediate stadia (Table 3 and Figures 8 and 9). I interpreted the greater than 10% drop in the Brooks' Ratio from the fourth to the fifth grouping (or peak) as a missing instar between true instar groupings II and V (Table 3 and Figures 8 and 9). This caused an overestimate of the Brooks' Ratio from instar II to III and the subsequent drop in the ratio from a lumped mean for III and IV to the mean for instar V.

In addition to a difference in instar number for the two cohorts, the last instar larvae of the overwintering cohort were significantly larger than the last instars of the spring cohort ($t = 155.5$, $df = 208$, $P < 0.001$). Ross and Merritt (1978) also reported a difference in instar number and size of terminal instars for the two cohorts of _P. mixtum/fuscum_. The warmer temperatures during the second cohort may explain the shorter development time and the decrease in number of instars.

During development of the winter cohort, 525 $D^{o}C$ accumulated, while 452 $D^{o}C$ accumulated during the spring cohort (0°C = threshold temperature). It is interesting to note that this difference in day-degrees between the two cohorts is approximately one ninth of 525, which is the difference I would expect if each instar developed over approximately equal day-degree periods (i.e. 525 ÷ the number of instars (9) = 58, and 525 - 58 = 467 D°C for eight instars; 467 D°C is close to the 452 D°C of cohort 2). If this estimate of 58 D°C is reasonably close to the actual day-degrees accumulated during the ninth instar of the first cohort, it offers additional evidence of a one instar difference between the two cohorts. However, this is in contrast to the findings of Ross and Merritt (1978), which showed nearly equal day-degree totals for the two cohorts of P. mixtum/fuscum. The difference above could also be explained by a slight difference in the threshold temperature used in the day-degree formula. For example, if the threshold temperature were 0.5 °C, the recalculated day-degrees would be 432 D°C and 416 D°C for cohorts 1 and 2, respectively. Laboratory rearings of eggs would be necessary to determine the exact threshold temperature and the probable explanation for the difference in the observed day-degrees for the two cohorts.

Simulium vittatum

Simulium vittatum was multivoltine in Owl Creek and appeared to have at least four generations (Figures 10 and 11). This is supported by studies conducted in Alberta,

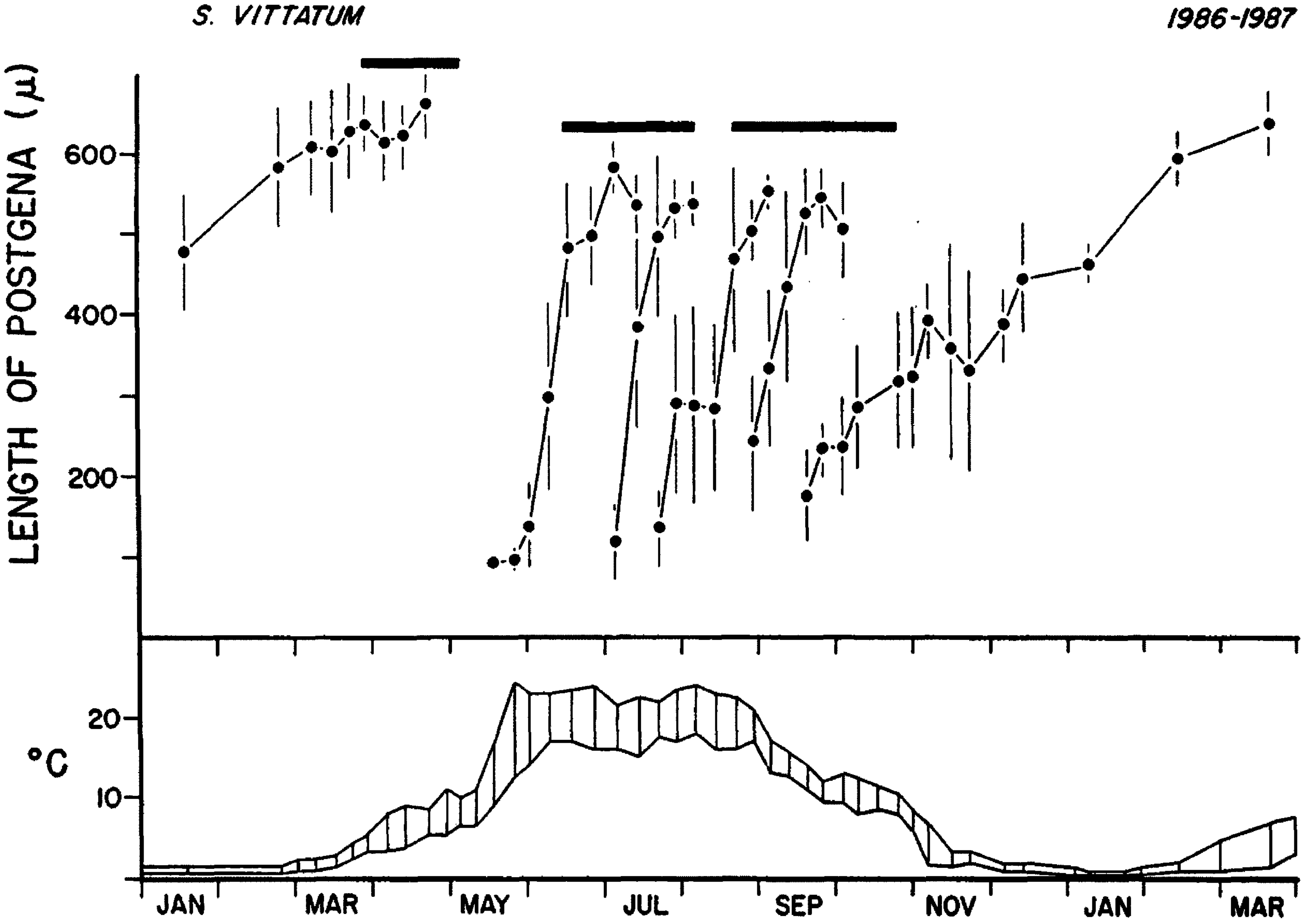


Figure 10. Development of the larval cohorts of *S. vittatum*. The mean ± one standard deviation is shown for the lengths of postgenae (μ) on sampling dates from January 1986 to March 1987 (25 m site). Maximum and minimum water temperatures at the 25 meter site are also shown. Black bars show pupation periods.

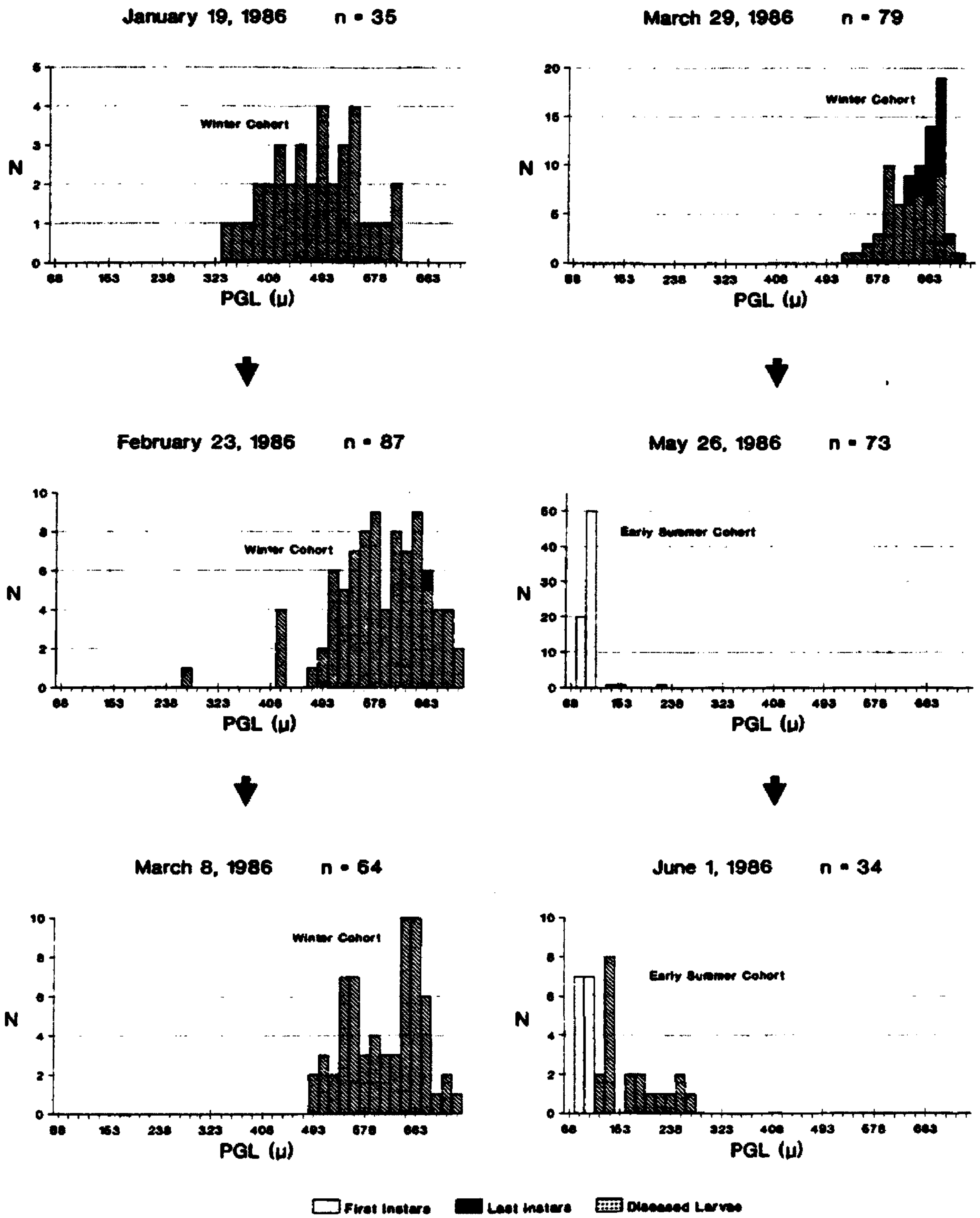


Figure 11a. Frequency distributions of the lengths of postgenae for the larvae of Simulium vittatum on selected dates during 1986 (25 meter site). N = number of larvae, PGL = length of postgena, μ = micrometers.

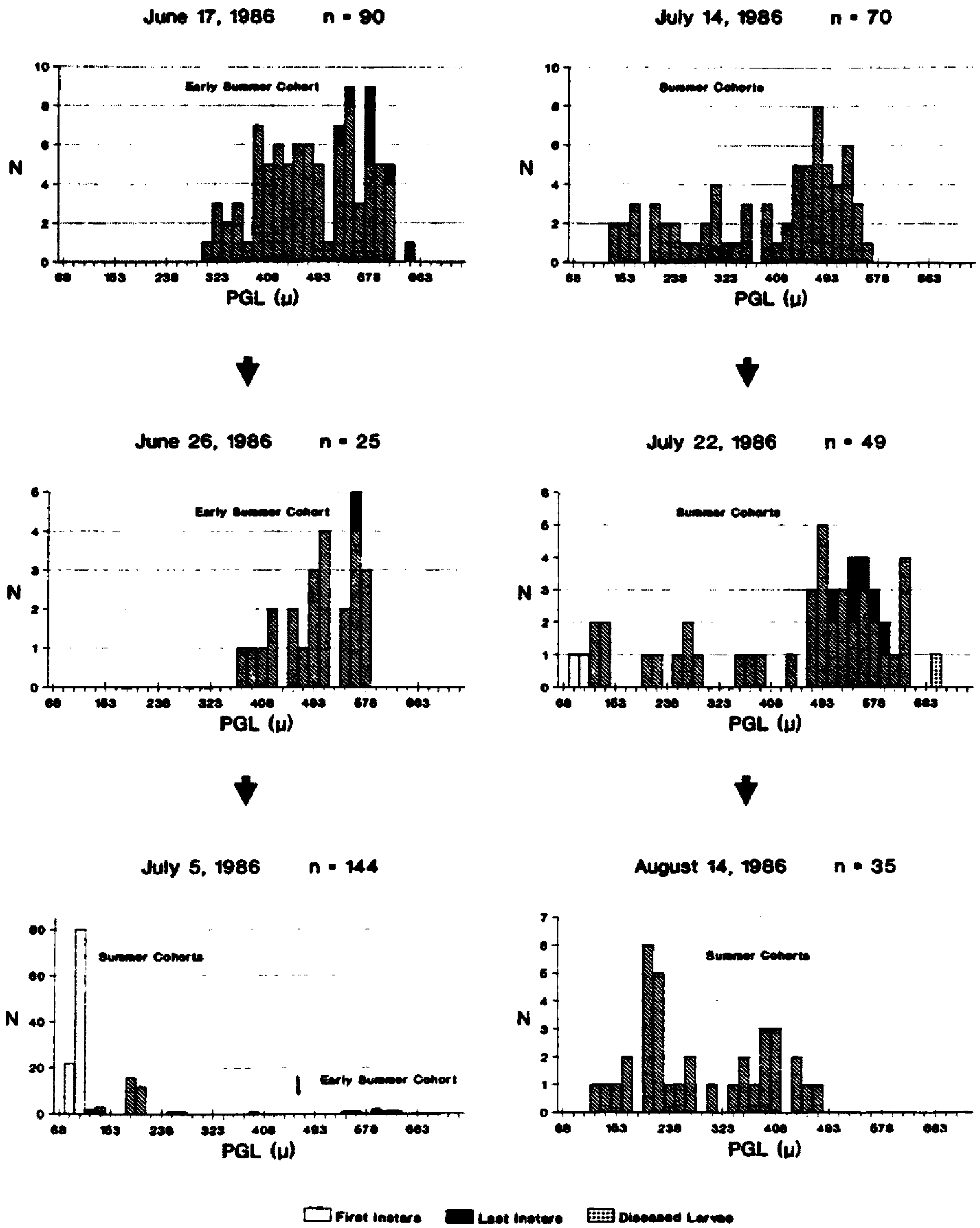


Figure 11b. Frequency distributions of the lengths of postgenae for the larvae of <u>Simulium</u> <u>vittatum</u> on selected dates during 1986 (25 meter site). N = number of larvae, PGL = length of postgena, μ = micrometers.

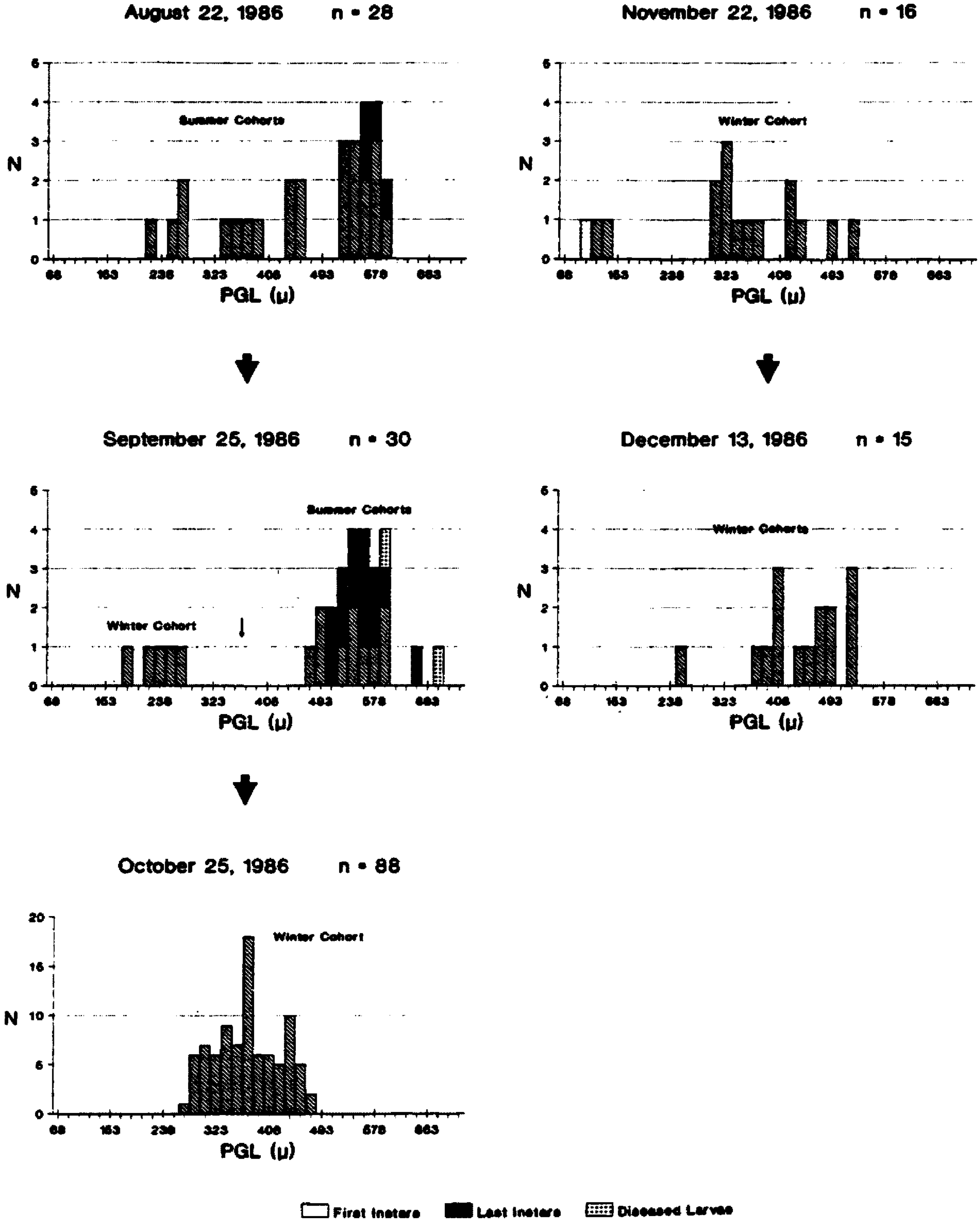


Figure 11c. Frequency distributions of the lengths of postgenae for the larvae of Simulium vittatum on selected dates during 1986 (25 meter site). N = number of larvae, PGL = length of postgena, μ = micrometers.

Saskatchewan, Quebec, Michigan and Pennsylvania (Abdelnur 1968; Fredeen 1985; Back and Harper 1979; Merritt et al. 1978; Adler and Kim 1986). An overwintering cohort with eight instars (Table 4 and Figures 12a and 13) hatched in mid-September and showed a gradual development to the seventh and eighth instars by December (Figures 10 and 11). These late instars passed the winter and pupated from late March to early May, which was the earliest pupation period of the spring emerging species. The cohort was moderately abundant and relatively well synchronized, although recruitment of first instars occurred through November.

After two weeks in mid-May when no larvae were observed, first instars of the second cohort appeared. These were probably the progeny of the overwintering cohort, because I observed the adults of the winter generation ovipositing near the dam during April. This early summer cohort developed rapidly, was well synchronized and abundant. Pupation occurred from mid-June to early July (Figures 10 and 11). The initial groupings of postgenal lengths for this cohort showed seven peaks, but the Brooks' and Crosby's Ratios between groupings V and VII indicated a missing instar (Table 4 and Figures 12a and 13). Therefore, the analysis suggested eight instars. This was equal to the number of instars in the winter cohort, but the terminal instars were significantly smaller in size ($t = 292.8$, $df = 449$, $P < 0.001$). Unlike P. exigens, this decrease in size

TABLE 4. *Simulium vittatum*, lengths of postgenae (μ).

A. Winter Cohort; September - April.

INSTAR	N	MEAN AND STANDARD DEVIATION	CV[1]	Brooks' Ratio	Crosby's Ratio,%	RANGE
I	5	98.60 ± 7.60	8.1	1.40		85-102
II	8	138.13 ± 10.89	8.1	1.38	-1.3	119-153
III	17	191.00 ± 12.79	6.8	1.31	-5.3	170-204
IV	42	250.14 ± 19.61	7.9	1.29	-1.2	221-272
V	88	323.77 ± 22.31	6.9	1.27	-2.2	289-357
VI	142	410.04 ± 28.45	7.0	1.30	2.9	374-459
VII	179	534.41 ± 31.57	5.9	1.22	-6.6	476-578
VIII	274	650.84 ± 31.78				595-731

B. Early Summer Cohort; May - early July.

INSTAR	N	MEAN AND STANDARD DEVIATION	CV[1]	Brooks' Ratio	Crosby's Ratio,%	RANGE
I	199	95.85 ± 8.19	8.6	1.39		85-102
II	12	133.17 ± 6.62	5.1	1.30	-6.6	119-136
III	6	172.83 ± 12.80	7.7	1.30	-0.2	153-187
IV	6	223.83 ± 12.80	6.0	1.28	-1.3	204-238
V	88	286.17 ± 23.23	8.2	1.52	19.2	255-323
VI, VII	142	436.12 ± 44.68	10.3	1.30	-14.7	340-510
VIII	179	567.00 ± 29.77	5.3			527-646

C. Summer Cohorts; July - early October.

INSTAR	N	MEAN AND STANDARD DEVIATION	CV[1]	Brooks' Ratio	Crosby's Ratio,%	RANGE
I	107	97.87 ± 7.33	7.5	1.37		85-102
II	26	134.04 ± 13.88	10.5	1.48	7.9	119-153
III	61	198.15 ± 15.48	7.8	1.36	-7.7	170-221
IV	43	270.42 ± 24.27	9.0	1.36	-0.2	238-306
V	56	368.23 ± 24.96	6.8	1.27	-7.0	323-408
VI	74	466.12 ± 20.87	4.5	1.20	-5.2	425-493
VII	111	559.32 ± 31.34	5.6			510-646

[1] = Coefficient of Variation adjusted for sample size (Sokal and Rohlf 1981).

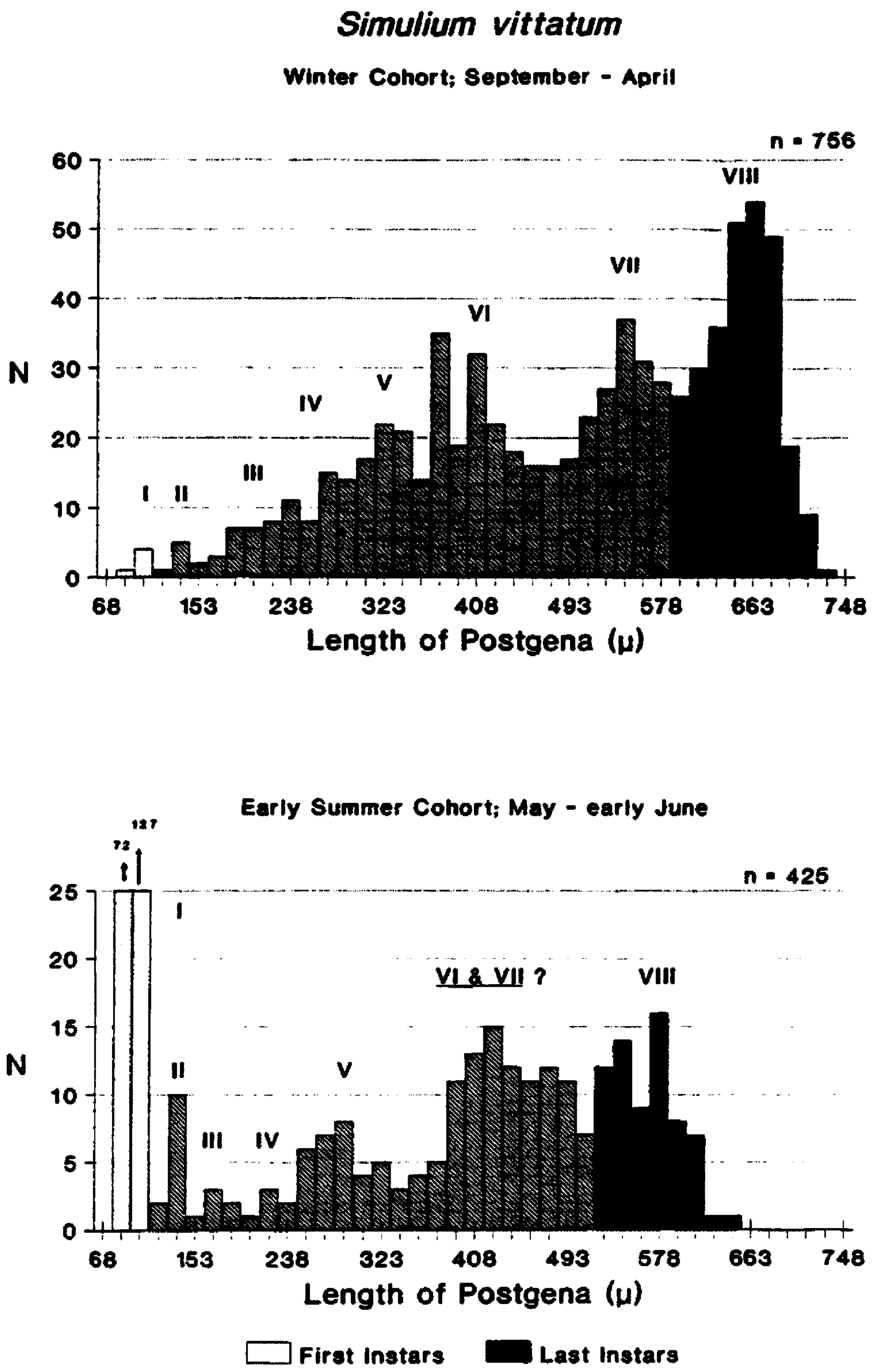


Figure 12a. Frequency distributions of the lengths of postgenae for the larvae of Simulium vittatum. The upper graph shows larvae from the winter cohort and the lower graph shows larvae from the early summer cohort (25 meter site). Roman numerals correspond to larval instars, N = number of larvae, μ = micrometers.

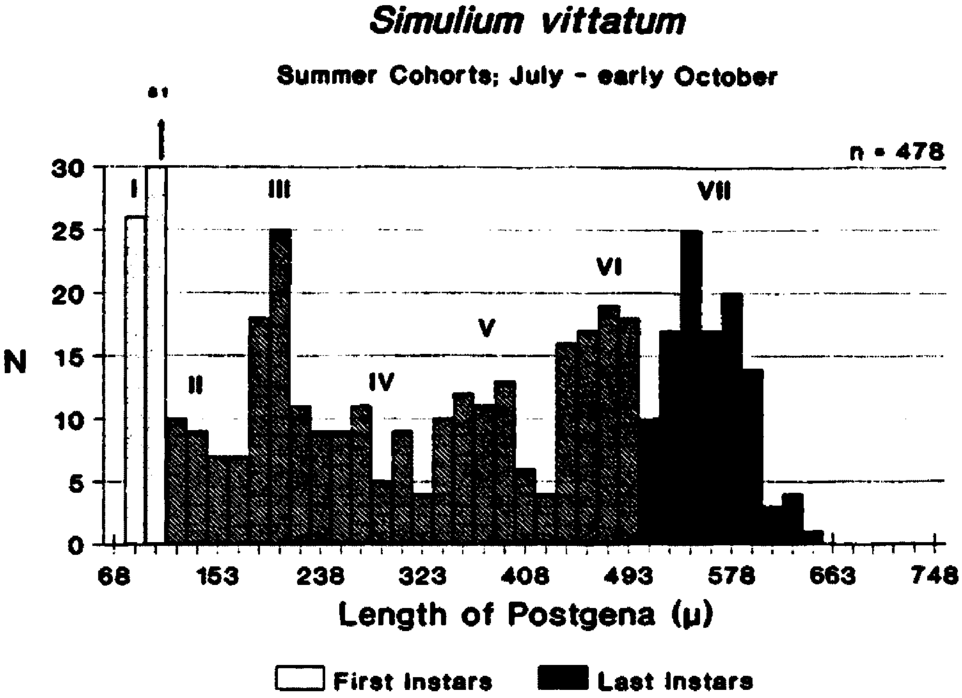


Figure 12b. Frequency distributions of the lengths of postgenae for the larvae of Simulium vittatum. The graph shows larvae from the summer cohorts (25 meter site). Roman numerals correspond to larval instars, N = number of larvae, µ = micrometers.

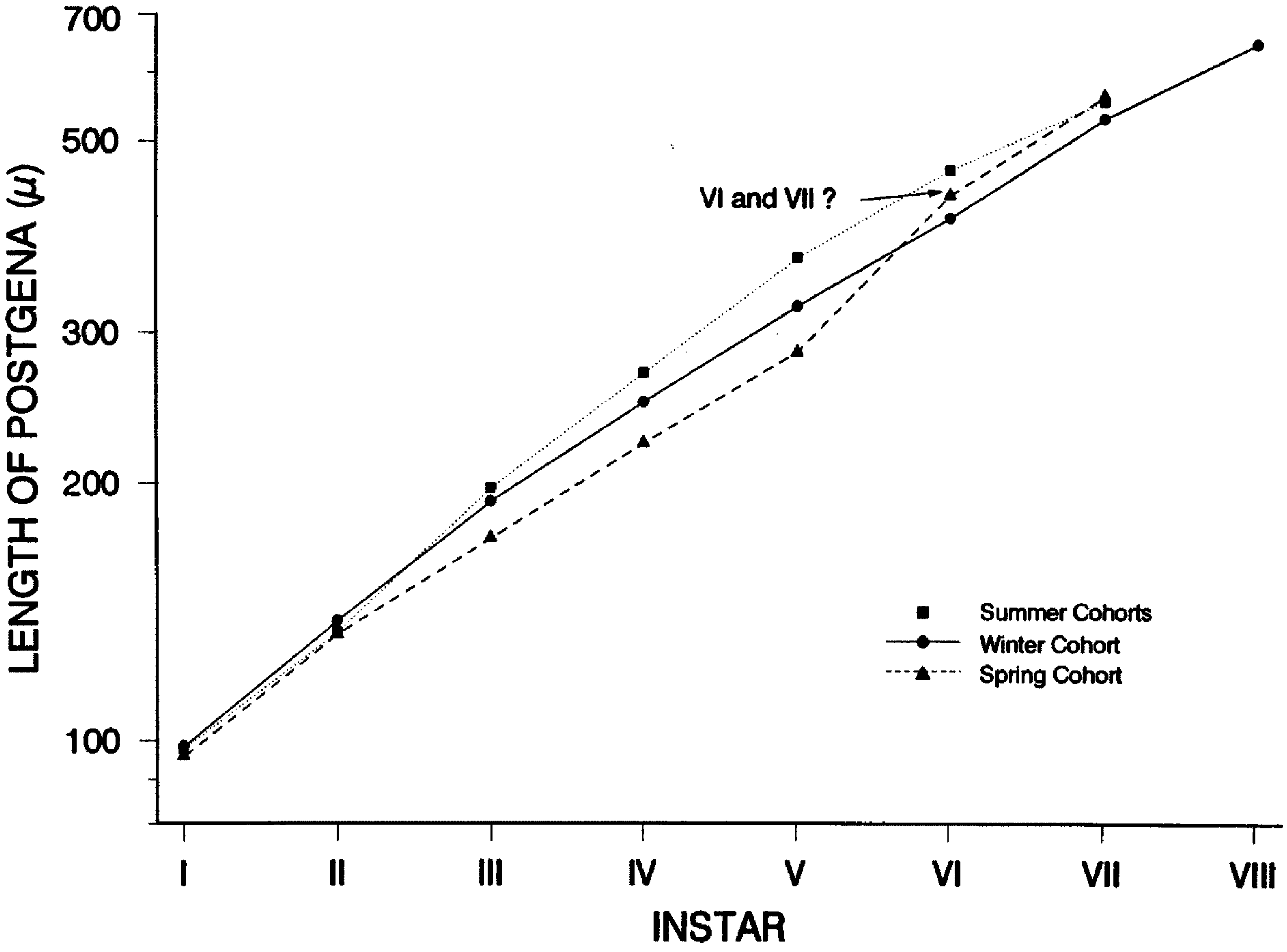


Figure 13: Mean lengths of postgenae ($\log_{10}$ scale) for the winter, spring and summer cohorts of S. vittatum.

did not appear to be accompanied by a decrease in the number of instars.

The summer cohorts were difficult to elucidate. On nearly every sampling date, members of each instar were present (Figure 10 and 11b). I discerned three overlapping groups, but the separation was so subjective that I did not consider them distinct cohorts. In the absence of the temperature constraints which synchronized the development and emergence of the overwintering cohort and the subsequent hatching of the first instar larvae of the second cohort, it is probable that asynchronous cohorts developed. Because development of eggs is rapid and occurs immediately after oviposition at the warmer summer temperatures (Imhof and Smith 1979), slight temporal variation in life history events, such as oviposition or hatching, would create a jumble of cohorts separated only by short time intervals (Crosby 1974). In support of this hypothesis, pupation and oviposition were observed on nearly all sampling dates from early July through late October. Therefore, I feel that multiple asynchronous cohorts were present during this period (Figure 10).

S. vittatum was relatively abundant during the summer, and instar analysis of the lumped summer cohorts clearly indicated seven larval instars (Table 4 and Figures 12b and 13). Terminal instar larvae of these cohorts were significantly smaller in size than those of the winter cohort ($t = 228.4$, df =383, $P < 0.001$), but were significantly larger than those of the second cohort ($t = 17.3$, df = 288, $P < 0.001$). Ross and Merritt (1978) and Ross (1979) distinguished seven larval instars for S. vittatum. Unfortunately, they do not state the season of collection. The difference in instar number between the winter and early summer cohorts and the later summer cohorts may indicate the presence of two sibling species (both cytotypes are known from Alberta; Rothfels and Featherston 1981), or the plasticity of larval development in this species in response to environmental variables, such as temperature and nutrition.

As was true for P. exigens, a few first instar larvae were present during the coldest winter months, so I assumed a threshold temperature of 0°C. Day-degrees accumulated for the winter and early summer cohorts with eight instars were 824 D°C and 874 D°C, respectively. I considered the estimate from the spring cohort to be more accurate, since it was highly synchronized and the beginning and end of the cohort were clearly distinguishable. The total day-degrees for the summer cohort period was 1576 D°C. To estimate the number of possible generations after oviposition by individuals of the early summer cohort, I divided the total day-degrees of the summer period by the day-degrees for the early summer cohort (1576 D°C ÷ 874 D°C = 1.8 cohorts). I also repeated this calculation using an adjusted day-degree value for the early summer cohort if only seven instars had been present, as was observed for the summer cohorts (874 D°C x 7/8 = 765 D°C; 1576 D°C ÷ 765 D°C = 2.1 cohorts). Both give an estimate close to two, so I concluded that, annually, four generations were possible for S. vittatum in Owl Creek. I did not include day-degrees for adult activities and embryonation in the estimate, because these events occur so rapidly during the summer (Imhof and Smith 1979).

Simulium arcticum

Simulium arcticum appeared to be multivoltine in Owl Creek (Figure 14). The studies of Abdelnur (1968) in Alberta and Fredeen (1981) in Saskatchewan assign S. arcticum four and two generations, respectively, although Abdelnur states that successive generations overlap. Currie (1986) concluded that the number of annual generations is uncertain, because four sibling species are known from the Athabasca River alone (Procunier and Shemanchuk 1983), so what may appear as multivoltinism may actually be a temporal succession of sibling species.

Fredeen et al. (1951) and Abdelnur (1968) stated that S. arcticum overwintered in the egg stage in the Saskatchewan and the Athabasca Rivers. However in Owl Creek there was a large overwintering cohort with eight distinct instars (Table 5 and Figures 14, 15a and 16). First instars appeared in late October and developed slowly through the fourth and fifth instars by December. The rate of

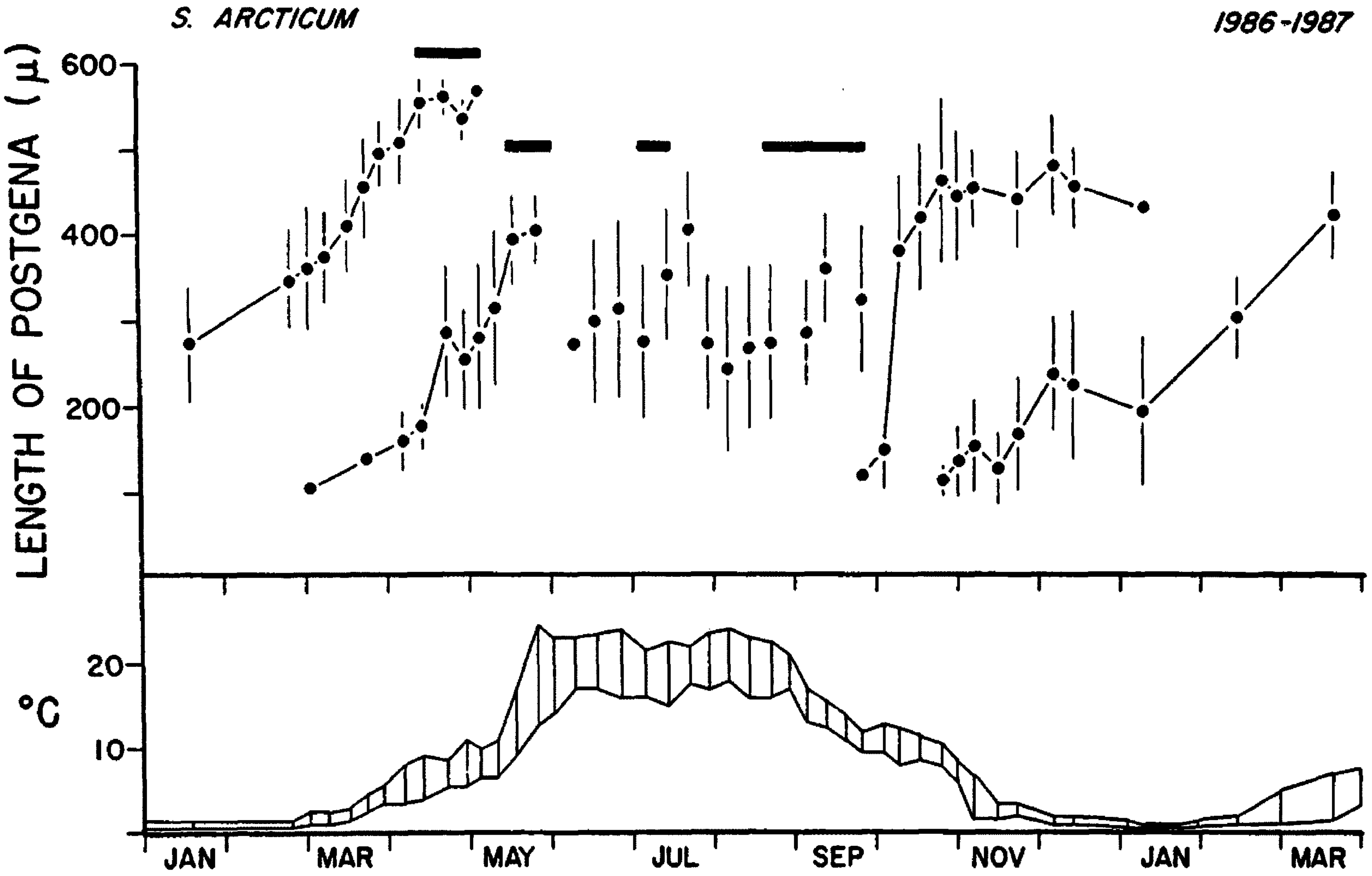


Figure 14. Development of the larval cohorts of *S. arcticum*. The mean ± one standard deviation is shown for the lengths of postgenae (µ) on sampling dates from January 1986 to March 1987 (50 m site for the winter, spring and fall cohorts; 2000 m site for the summer cohorts). Maximum and minimum water temperatures at the 25 meter site are also shown. Black bars show pupation periods.

TABLE 5. *Simulium arcticum*, lengths of postgenae (µ).

A. Winter Cohort; October - April.

INSTAR	N	MEAN AND STANDARD DEVIATION	CV[1]	Brooks' Ratio	Crosby's Ratio,%	RANGE
I	27	104.52 ± 6.15	5.9	1.35		85-102
II	33	140.64 ± 7.69	5.5	1.33	-1.4	136-153
III	41	186.69 ± 14.96	8.1	1.36	2.6	170-204
IV	93	253.90 ± 16.78	6.6	1.24	-8.8	221-272
V	180	315.14 ± 17.23	5.5	1.25	0.7	289-340
VI	305	393.84 ± 19.51	5.0	1.22	-2.0	357-425
VII	189	482.21 ± 20.89	4.3	1.16	-4.9	442-510
VIII	148	561.46 ± 18.17	3.2			527-595

B. Spring Cohort; March - May.

INSTAR	N	MEAN AND STANDARD DEVIATION	CV[1]	Brooks' Ratio	Crosby's Ratio,%	RANGE
I	19	105.58 ± 7.12	6.8	1.32		102-119
II	16	139.19 ± 6.85	5.0	1.35	2.6	136-153
III	42	188.21 ± 10.88	5.8	1.39	2.8	170-204
IV	71	261.70 ± 15.33	5.9	1.33	-4.3	221-289
V	90	348.12 ± 17.10	5.1	1.25	-6.3	306-474
VI	107	433.74 ± 23.51	5.4	1.18	-5.6	391-459
VII	112	510.15 ± 19.43	3.8			476-544

C. Summer Cohorts; June - September.

INSTAR	N	MEAN AND STANDARD DEVIATION	CV[1]	Brooks' Ratio	Crosby's Ratio,%	RANGE
I	0					
II	10	132.60 ± 7.17	5.5	1.40		119-136
III	39	186.13 ± 18.27	9.9	1.35	-3.8	153-204
IV	54	251.22 ± 16.07	6.4	1.26	-7.0	221-272
V	47	315.40 ± 17.30	5.5	1.21	-3.9	289-340
VI	58	380.45 ± 16.49	4.4	1.18	-2.4	357-408
VII	35	447.83 ± 19.75	4.4			425-493

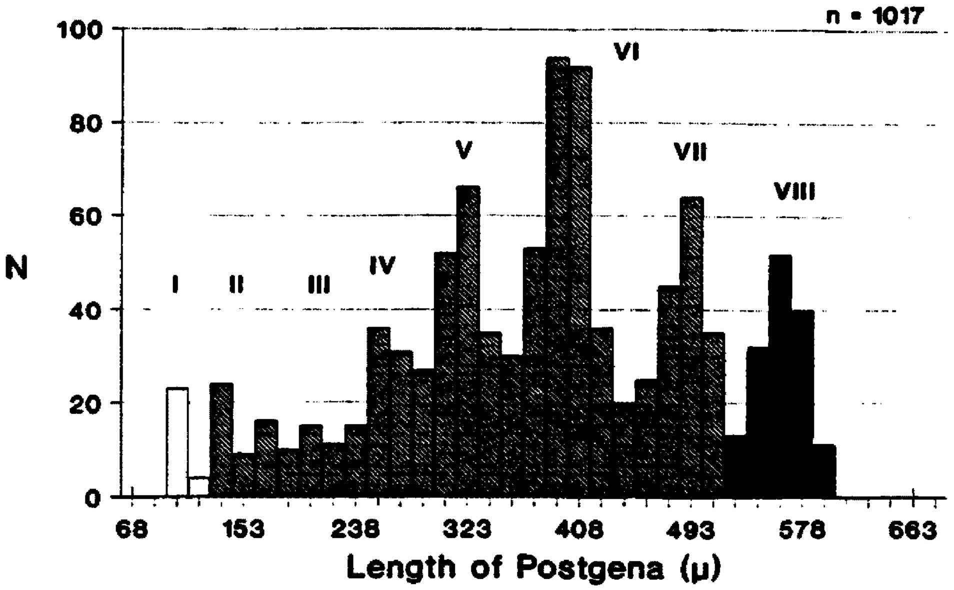
D. Fall "doomed" Cohort; early October - January.

INSTAR	N	MEAN AND STANDARD DEVIATION	CV[1]	Brooks' Ratio	Crosby's Ratio,%	RANGE
I	6	102.00 ± 0.00	0.0	1.21		102-102
II	7	123.86 ± 8.30	6.9	1.34	10.2	119-136
III	8	165.75 ± 7.87	4.9	1.39	3.9	153-170
IV	9	230.44 ± 14.99	6.7	1.36	-2.3	204-255
V	17	313.00 ± 19.99	6.5	1.33	-2.0	272-340
VI	59	416.64 ± 22.85	5.5	1.22	-8.2	357-442
VII	57	509.40 ± 24.03	4.7			459-561

1 = Coefficient of variation adjusted for sample size (Sokal and Rohlf 1981).

Simulium arcticum

Winter Cohort; October - April



Spring Cohort: March - May

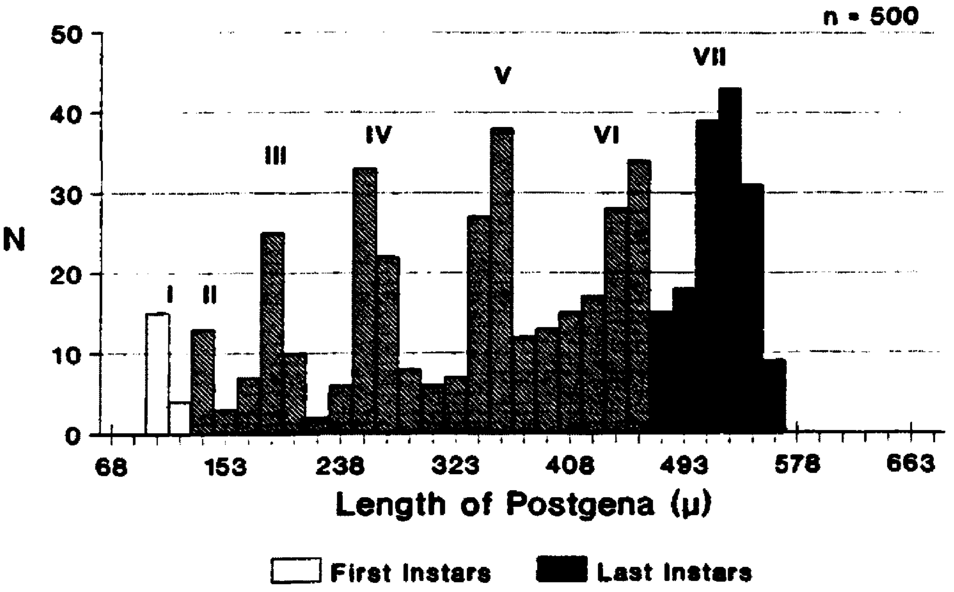


Figure 15a. Frequency distributions of the lengths of postgenae for the larvae of Simulium arcticum. The upper graph shows larvae from the winter cohort and the lower graph shows larvae from the spring cohort (25 meter site). Roman numerals correspond to larval instars, N = number of larvae, μ = micrometers.

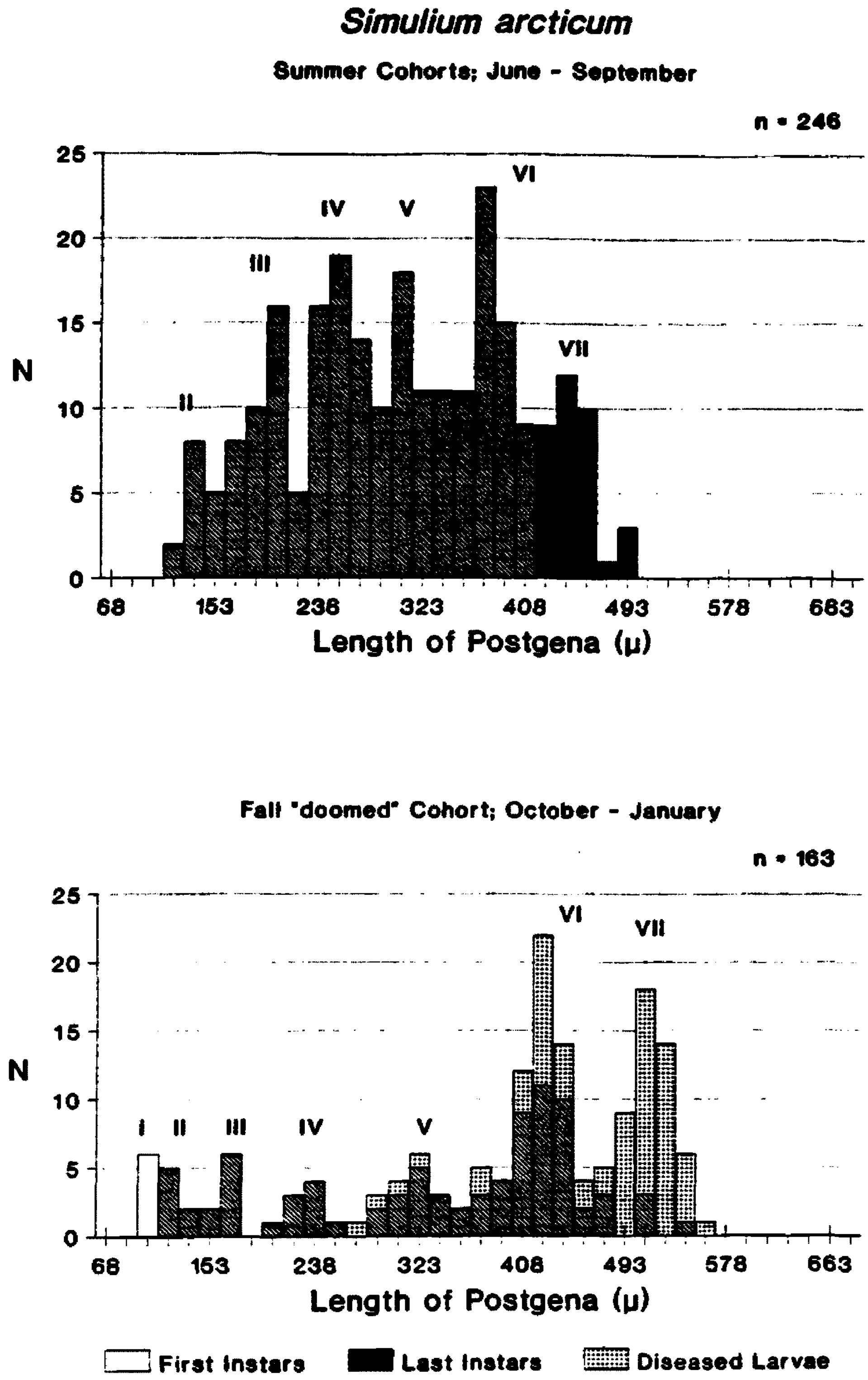


Figure 15b. Frequency distributions of the lengths of postgenae for the larvae of Simulium arcticum. The upper graph shows larvae from the summer cohorts (2000 meter site) and the lower graph shows larvae from the fall cohort (50 meter site). Roman numerals correspond to larval instars, N = number of larvae, µ = micrometers.

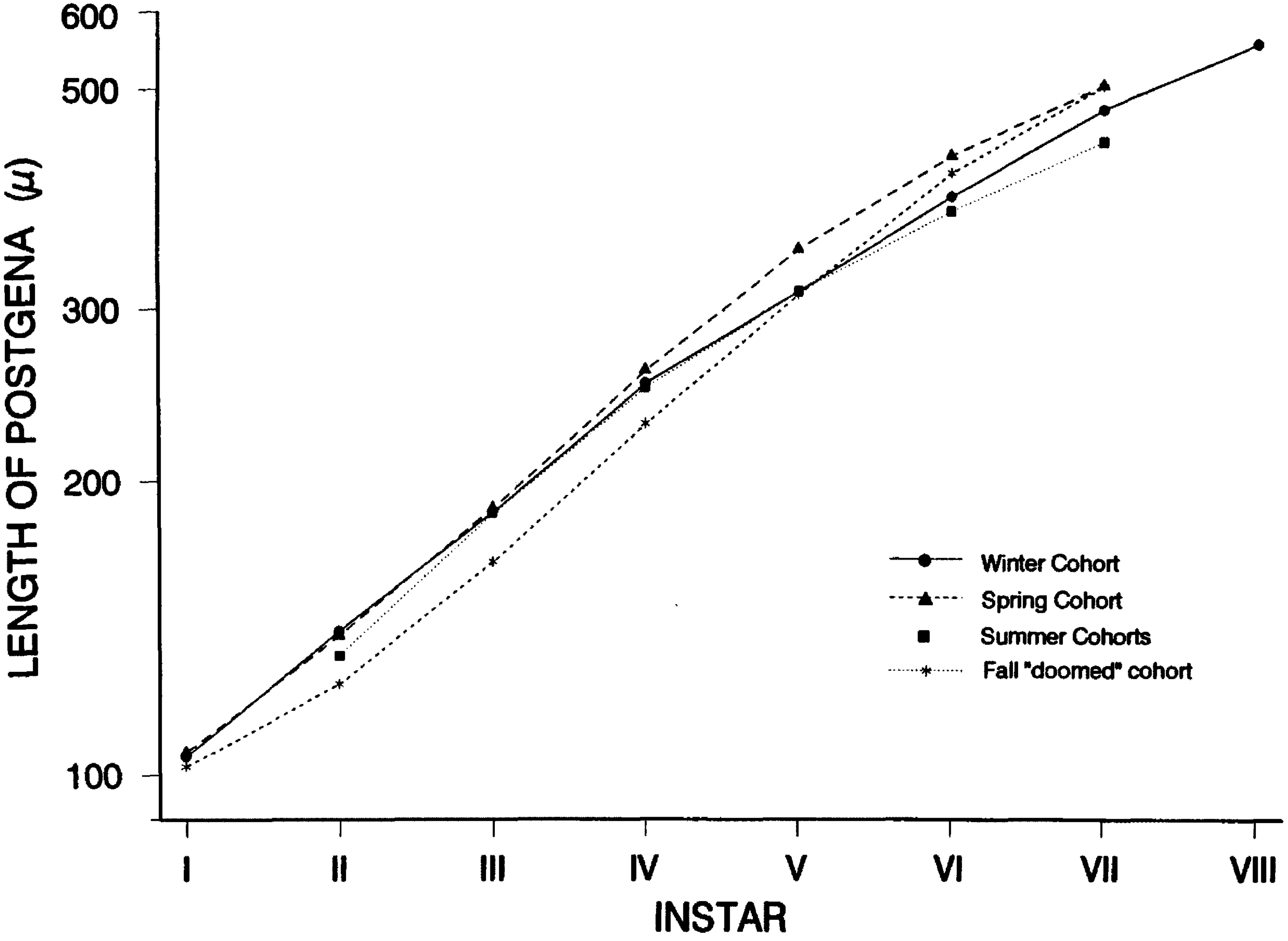


Figure 16. Mean lengths of postgenae ($\log_{10}$ scale) for the winter, spring, summer and fall cohorts of S. arcticum.

development appeared to increase in March and pupation occurred in April and early May. This cohort was well synchronized and appeared to be the most abundant of the overwintering simuliid generations.

Concurrent with the last two months of the winter cohort, a separate spring cohort developed in a pattern similar to the second cohort of P. exigens (Figure 14). Low numbers of first instars were present as early as January, but a distinct cohort did not appear until early March. This cohort developed over three months and pupated from middle to late May. Instar analysis showed seven clearly distinguishable instars, and as expected the terminal instars were significantly smaller than those of the winter cohort ($t = 174.7$, $df = 258$, $P < 0.001$; Table 5 and Figures 15a and 16). This cohort was relatively well synchronized and abundant.

Fredeen (1976) also determined that larvae of S. arcticum, which hatched just after ice-breakup (April) in the Saskatchewan River had seven instars. An overwintering cohort of S. arcticum has not been reported elsewhere. This may be because the majority of investigations have come from more northern latitudes in Canada where temperature or other environmental factors prevent its occurrence. The existence of two concurrent cohorts with differing numbers of instars for S. arcticum has also not been reported . One hypothesis, which may explain the extra instar of the winter cohort in

S. arcticum and P. exigens, is that larvae may require a specific maximum temperature cue for development of pupal and adult histoblasts (Sweeney 1978), and in its absence, larval growth continued and an extra instar developed. For both S. arcticum and P. exigens, the recruitment of first instars for the winter and spring cohorts occurred several months apart, but pupation and emergence are separated by a week or less. This lends support to the hypothesis that larvae at differing stages of development (e.g. seventh versus eighth instars) will begin forming pupal and adult tissues when exposed to the necessary thermal cue. What is not clear for S. arcticum, however, is whether the two cohorts represent two major recruitment periods for the overwintering generation of one species as in P. exigens, or two sibling species with different life histories.

During the summer, S. arcticum was scarce and there was no clear pattern of development (Figure 14). It is likely that multiple, asynchronous cohorts were present as in S. vittatum. The first pupae observed in summer were in mid-July and then not until late August through September. It is therefore possible that these larvae were the progeny of the winter or spring cohorts, although it is just as likely that they are members of a different species. The distribution of postgenal lengths for all larvae from early June to late September showed seven larval instars (Table 5 and Figures 15b and 16). Although this is equal to the number of instars in the spring cohort, the terminal instars are significantly smaller in the summer cohorts ($t = 510.15$, $df = 145$, $P < 0.001$). This, again, could be explained by thermal or nutritional differences during development or by genetic differences among sibling species.

The most unusual cohort I observed at Owl Creek was the fall cohort of S. arcticum. It developed rapidly from late September through late October, and then, in my opinion, because of temperature constraints did not complete its development (Figure 14). As larvae entered the late instars, the frequency of an unidentified disease increased, and no pupae were ever observed. The histoblasts of adult and pupal structures, which usually begin development in the third instar larvae were not present even in the late instars. The entire body and head of the larvae appeared to have small globules similar to those in the photograph of Weiser and Undeen (1981), which show a larva of Simulium ornatum infected with the fungus Coelomycidium simulii. Larvae passed through seven instars comparable in size to the instars of the spring cohort (Table 5 and Figures 15b and 16). Development was synchronous and the cohort was moderately abundant.

It is possible that the disease prevented the cohort from completing its development, but the frequency of the infection in the population and the thermal regime at the time suggested another hypothesis. Weiser and Undeen (1981) state that it is exceptional to find the frequency of a disease in natural populations of simuliids greater than 15%. Therefore, I concluded that the disease, which was present in nearly all late instar larvae, was secondary to a another stress factor. This primary factor, which I feel was a rapid decrease in temperature during October (Figures 3 and 14), caused the entire cohort to be susceptible to the disease. In other words, the day-degrees needed for full development were not available during this time period, and the late instar larvae were physiologically unable to pass the winter. The instars of the overwintering cohort did not develop past the fifth instar until February. I observed this doomed cohort in both 1985 and 1986.

The day-degrees accumulated for the winter cohort with eight instars were 576 D°C and for the spring cohort with seven instars 501 D°C (threshold temperature = 0°C). Adjusting the day-degrees for the winter cohort to a seven instar scenario gave results very close to the spring cohort (576 D°C x 7/8 = 504 D°C). The total day-degrees accumulated for the asynchronous summer cohorts with seven instars were 2004 D°C. This value divided by the day-degrees of the spring cohort, which also had seven instars, indicated that four cohorts were possible during this period (2004 D°C ÷ 501 D°C = 4.0 cohorts). If the winter and spring groups of larvae are considered two cohorts of the same generation, and I assume that S. arcticum is not a species complex at

Owl Creek, then five annual generations were possible during my study. This does not include the fall cohort, which did not complete development.

The day-degrees calculated for the fall cohort were 544 D°C. The end of this cohort was difficult to determine because low numbers of diseased individuals continued to develop into January. The day-degrees accumulated until the disease was first observed in last instar larvae were 246 D°C. In contrast, the day-degrees required for the first larvae to reach maturity in the spring cohort (determined by the presence of dark histoblasts) were 362 D°C. It seems apparent that the day-degrees were sufficient for development of the larvae, but not for development of pupal and adult tissues. The thermal regime of Owl Creek in the autumn appears to miscue an entire cohort of S. arcticum. In a colder or warmer system, development of the cohort would perhaps be delayed until spring or completed in late fall.

Simulium tuberosum

Simulium tuberosum, as in other studies, appeared to be multivoltine (Abdelnur 1968; Fredeen 1985; Adler and Kim 1986). However, Adler (1986) described four siblings of the S. tuberosum complex in Alberta, and Adler and Kim (1986) found some evidence of temporal succession in sibling species of S. tuberosum. In Owl Creek, the first cohort hatched in March, developed rapidly and pupated from middle May through early June (Figure 17). This early spring cohort

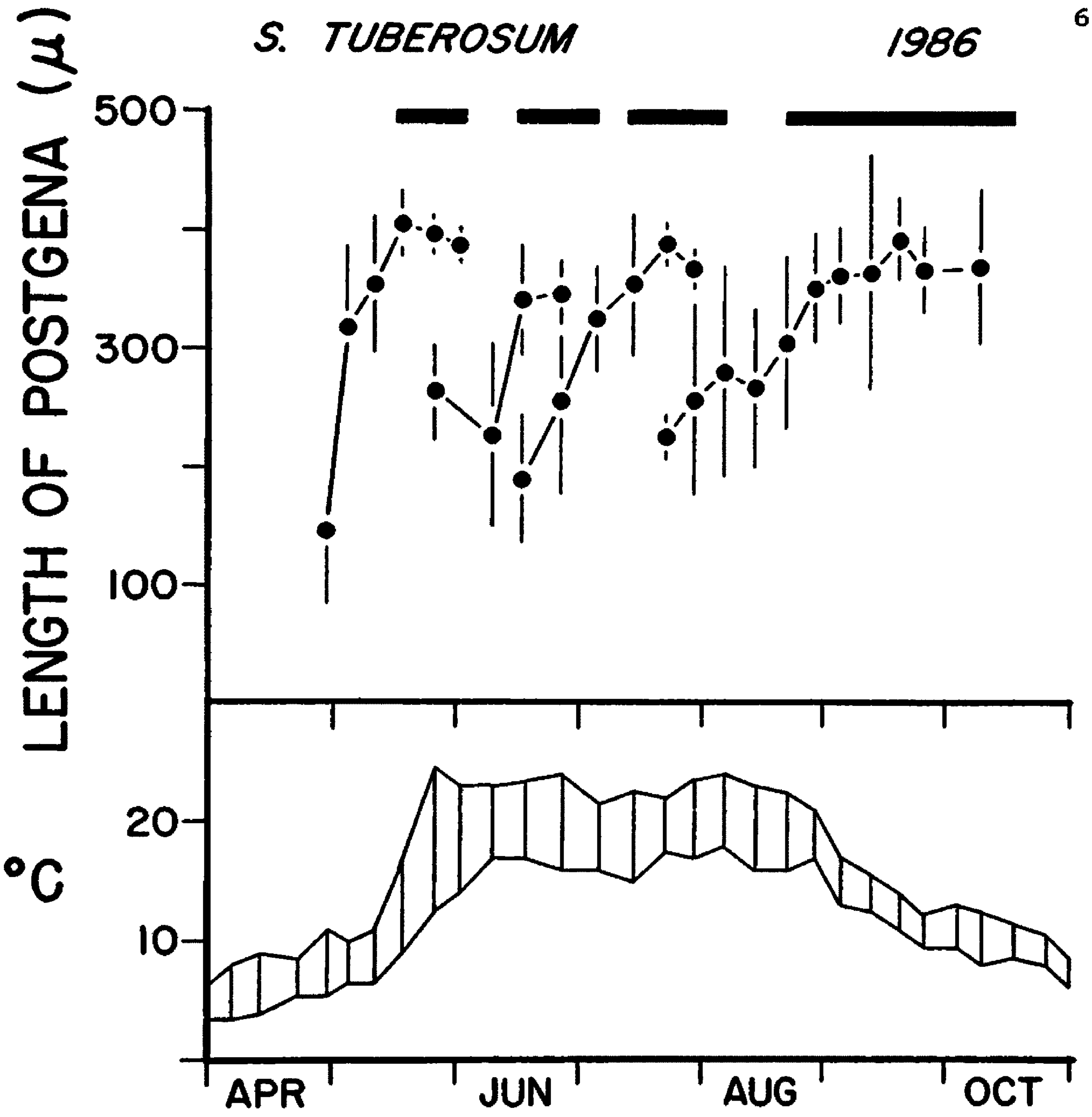


Figure 17. Development of the larval cohorts of S. tuberosum. The mean ± one standard deviation is shown for the lengths of postgenae (μ) on sampling dates from April to October 1986 (25 m site for the early and late spring cohorts; 2000 m site for the summer cohorts). Maximum and minimum water temperatures at the 25 meter site are also shown.

Black bars show pupation periods.

was moderately abundant, synchronized and appeared to have six instars (Table 6 and Figures 18a and 19).

First instars of the second cohort hatched in late May and pupation occurred from middle June to early July (Figure 17). This late spring cohort appeared relatively abundant when compared with other cohorts of S. tuberosum. Analysis showed a synchronized cohort of six instars (Table 6 and Figures 18a and 19). The terminal instars of this cohort were significantly smaller than those of the early spring cohort ($t = 80.5$, $df = 164$, $P < 0.001$), even though the number of instars was the same.

The summer groups were asynchronous, and the larvae from this period were inconclusively separated into six instars (Table 6 and Figure 18b and 19). Larvae from early and intermediate stadia were underrepresented in the collections, possibly because of rapid development of these stages or some bias during sampling. Final instars were significantly smaller than the final instars of the early spring cohort ($t = 56.9$, $df = 199$, $P < 0.001$), but significantly larger than those of the late spring cohort ($t = 30.1$, $df = 177$, $P < 0.001$). The larvae of the summer cohorts were found only downstream from the 250 meter site, and may be a different sibling species than the larvae of the spring cohorts. Figure 17 shows a very subjective grouping of the larvae based on distributions of postgenal lengths and pupation periods. Pupation of these summer

TABLE 6. *Simulium tuberosum*, lengths of postgenae (µ).

A. Early Spring Cohort; March - early June.

INSTAR	N	MEAN AND STANDARD DEVIATION	CV[1]	Brooks' Ratio	Crosby's Ratio,%	RANGE
I	5	85.00 ± 0.00	0.0			85-85
II	15	121.27 ± 5.98	5.0	1.43	6.3	119-136
III	11	183.91 ± 10.25	5.7	1.51	-10.8	170-204
IV	11	248.82 ± 15.72	6.5	1.35	-6.7	221-272
V	34	314.00 ± 18.86	5.9	1.26	-2.7	289-340
VI	94	407.10 ± 19.89	4.3	1.30		357-442

B. Late Spring Cohort; June.

INSTAR	N	MEAN AND STANDARD DEVIATION	CV[1]	Brooks' Ratio	Crosby's Ratio,%	RANGE
I	10	86.70 ± 5.38	6.4			85-102
II	12	121.83 ± 6.62	5.5	1.41	-4.8	119-136
III	29	162.97 ± 10.67	6.6	1.34	4.0	153-187
IV	30	226.67 ± 17.48	7.8	1.39	-5.6	204-255
V	61	297.64 ± 13.03	4.4	1.31	-4.7	272-323
VI	72	372.35 ± 14.02	3.8	1.25		340-408

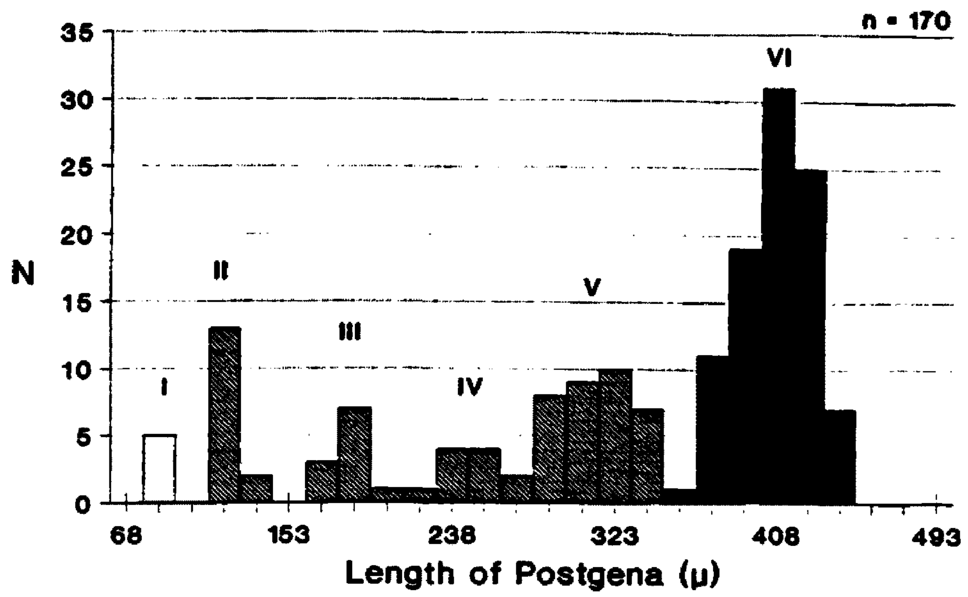
C. Summer Cohorts; mid June - October.

INSTAR	N	MEAN AND STANDARD DEVIATION	CV[1]	Brooks' Ratio	Crosby's Ratio,%	RANGE
I	0					
II	7	121.43 ± 15.30	13.0			102-136
III	25	171.36 ± 15.46	9.1	1.41	-1.7	153-187
IV	69	237.74 ± 21.12	8.9	1.39	-3.1	204-272
V	68	319.50 ± 16.24	5.1	1.34	-10.4	289-340
VI	107	384.64 ± 19.61	5.1	1.20		357-442

[1] = Coefficient of Variation adjusted for sample size (Sokal and Rohlf 1981).

Simulium tuberosum

Early Spring Cohort; March - early June



Late Spring Cohort; late May - June

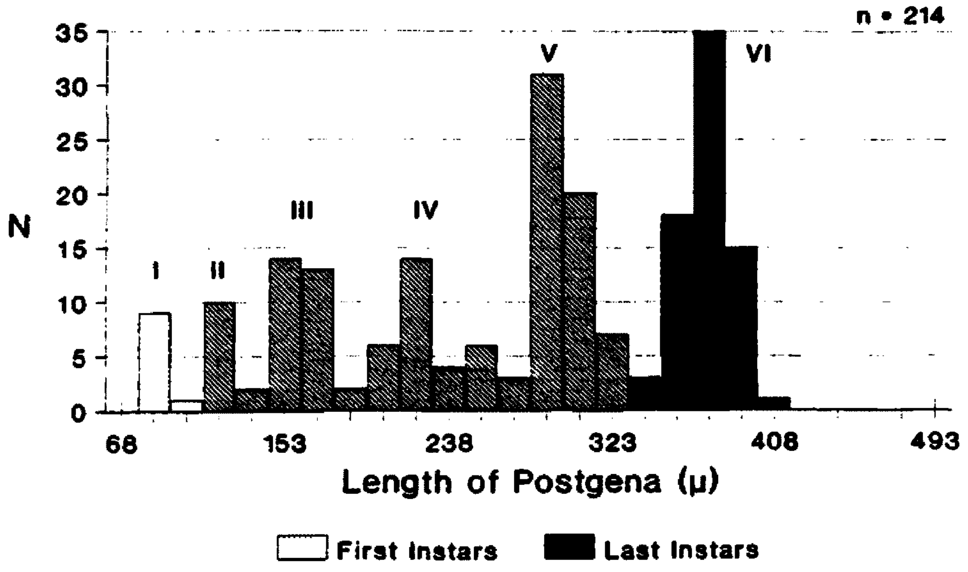


Figure 18a. Frequency distributions of the lengths of postgenae for the larvae of Simulium tuberosum. The upper graph shows larvae from the early spring cohort and the lower graph shows larvae from the late spring cohort (25 meter site). Roman numerals correspond to larval instars, N = number of larvae, μ = micrometers.

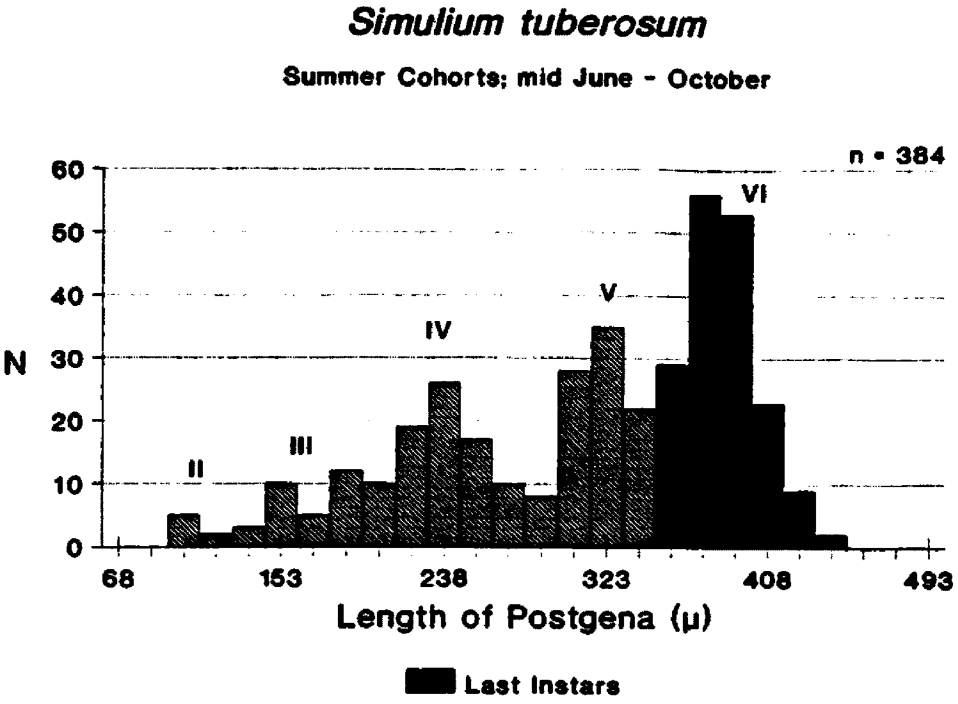


Figure 18b. Frequency distributions of the lengths of postgenae for the larvae of Simulium tuberosum. The graph shows larvae from the summer cohorts (2000 meter site). Roman numerals correspond to larval instars, N = number of larvae, µ = micrometers.

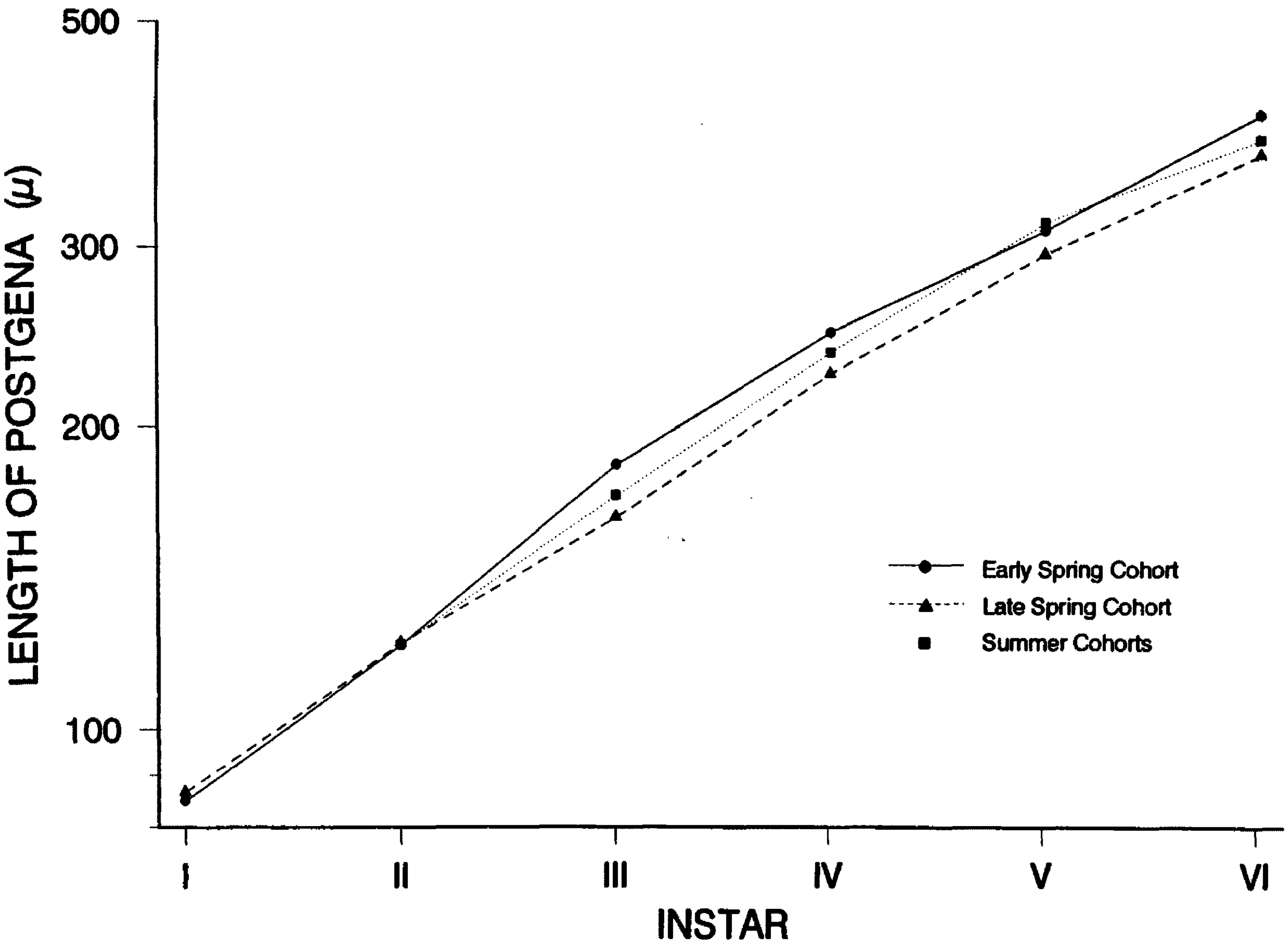


Figure 19. Mean lengths of postgenae ($\log_{10}$ scale) for the early spring, late spring and summer cohorts of S. tuberosum.

larvae occurred from mid-July to mid-August and then September through October.

During the early spring cohort, 571 D°C accumulated, and 402 D°C accumulated during the late spring cohort. First instar larvae of the early spring cohort appeared when the mean temperature was about 3°C. Recalculating the day-degrees using 3°C as the threshold temperature gave much more equitable estimates; 358 D°C for the early spring cohort and 348 D°C for the late spring cohort. This threshold temperature matches the minimum temperature that Adler and Kim (1986) report for the occurrence of the FG sibling of S. tuberosum in Pennsylvania, and Adler (1986) collected this sibling in Alberta. The day-degrees accumulated throughout the summer period were 1228 D°C (3°C = threshold temperature), and a possible three to four cohorts were estimated (1228 D°C ÷ 348 D°C = 3.5 cohorts). According to Currie (1986), the number of annual generations for S. tuberosum ranges from 2 to 4, so my estimate of 5 to 6 may be high. I want to stress that these estimates from the asynchronous summer periods were only an attempt to show the maximum possible number of generations that could have been completed if my assumptions regarding equality of day-degrees between cohorts and the absence of siblings are met. Whether these estimates are valid or useful will require further study of the natural system.

Simulium verecundum and Simulium decorum

Simulium verecundum and Simulium decorum appeared to be multivoltine based on the occurrence of mature larvae and pupae in Owl Creek (Figure 20). Early instars of these species appeared in early April, and pupation occurred intermittently from late May to late October. Abdelnur (1968) estimated three generations per year for S. verecundum and four for S. decorum in Alberta. Back and Harper (1979) found both species to be multivoltine in Quebec. Each species showed synchronized emergence in June, continuous emergence from late June to mid-August, and then sporadic emergence in September.

Simulium canonicolum and Simulium "aureum"

Simulium canonicolum and Simulium "aureum" were rare in Owl Creek. I found larvae of S. canonicolum from early April to late May and pupae on the 11th and 18th of May, 1986. Therefore, it appeared to have one spring generation per year (Figure 20). However, Currie (1986) stated that larvae are found in Alberta from mid-May to mid-November, suggesting that the species is multivoltine. I found one larva of S. "aureum" on the 5th of September, 1986, one pupa on the 19th of September, 1986, and two pupae on the 29th of August, 1986. I could conclude little from this information other than its occurrence in late summer (Figure 20). Abdelnur (1968) reported three generations per year for S. "aureum" in Alberta.

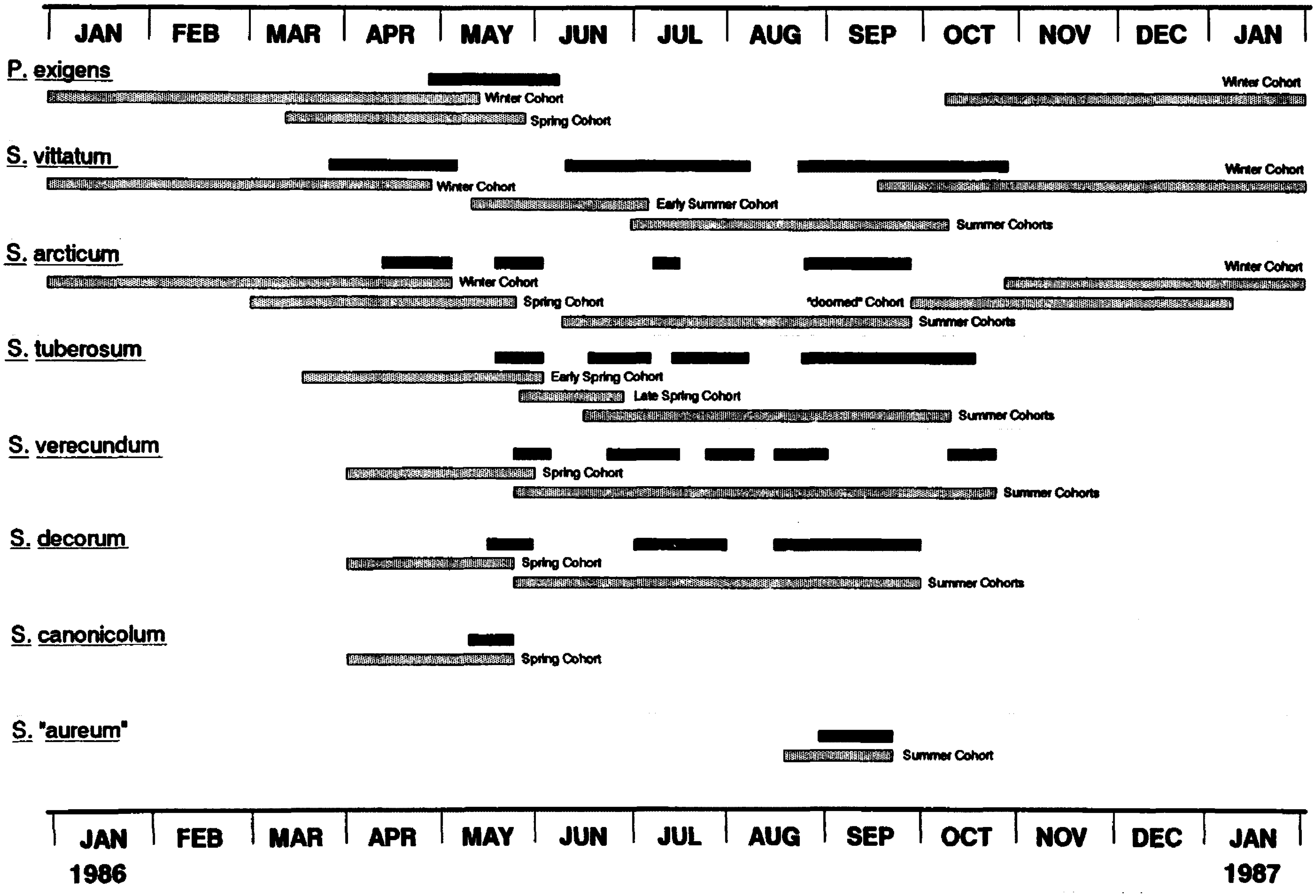


FIGURE 20: The seasonal occurrence of larvae and pupae for species of the family Simuliidae in Owl Creek, Montana.

Pupae ■
Larvae ▨

Phenology and Life History Notes:

Figure 20 summarizes the seasonal succession of larval cohorts and pupae for the simuliid species of Owl Creek. In the following section, I present overall phenologies, as well as observations and inferences about other aspects of their life histories.

Prosimulium exigens

The larvae of Prosimulium exigens occurred from October through May in temperatures ranging from 0 to 18 °C, and pupation occurred in temperatures between 6 and 20 °C. On the 26th of May, 1986 near the 250 meter site, I netted adults of P. exigens from a low-flying, circular swarm in a shady opening beneath some large pine trees. I did not observe coupling, but I suspect it was a mating swarm. Resting adults were collected from the branches of riparian Douglas fir trees on the 8th of May, 1987. I did not observe blood-feeding, although Peterson (1970) described well developed, biting, mouth parts in the adult females. A few adults were collected over the water, flying in an upstream direction on May 26, 1986, but oviposition was not observed. Peterson (1959) observed females ovipositing while in flight at a lake-outlet in Utah. Because of the absence of other life stages after June, I inferred that eggs had been laid in May and June, and then entered a period of diapause until temperatures dropped in October.

Simulium vittatum

Larvae of Simulium vittatum were present throughout the year except for a short period from the 4th to the 18th of May, 1986, when adults were ovipositing and the eggs of the spring cohort were developing. Larvae and pupae were present in temperatures ranging from 0 to 24 °C, and 3 to 24 °C, respectively. I did not observe mating swarms or blood-feeding, although S. vittatum is a well known pest of cattle and other large ungulates (Currie 1986). I did observe oviposition swarms on at least one sampling date per month from April through October, 1986. The swarms varied in density, but usually spanned the width of the creek and extended 1 meter above the waterfall of the dam. Females oviposited in flight by dipping their abdomen on the water, or they landed and cemented their eggs to objects just below the water line. Davies and Peterson (1956) also observed both types of oviposition for S. vittatum in Ontario, but Imhof and Smith (1979) stated that S. vittatum always landed to oviposit. S. vittatum females at Owl Creek also used sedge and cattail leaves and stones near shore as oviposition substrates at sites below the dam, but swarms were not associated with this behavior. Eggs of this species were often recognized, because a spent or dead female was stuck to the egg mass. The layers of eggs on submerged objects near the dam became 5mm thick in places, and rings of dry eggs were left at previous water levels when flows dropped in summer and winter. These egg masses probably contained eggs of S. decorum and S. verecundum as well, since they used the same sites for oviposition. An obvious egg diapause was not observed but is a possibility, because of the status of S. vittatum as a species complex.

S. arcticum

Larvae of Simulium arcticum were present throughout the year in Owl Creek (temperature range = 0 to 24 °C). The temperature range when pupae were present was 3 to 24 °C. Emerging adults, sluggishly climbing from the water to moss covered boulders and riparian grasses, were collected on the 4th and 11th of May, 1986 when the air temperatures were approximately 7 and 5 °C, respectively. Numerous resting adults were also collected from grasses on the 26th of May, 1986, 10 to 20 meters below the dam. Mating and blood-feeding were not observed, although a few females were attracted to the author in September and October, 1986. S. arcticum is known as a major pest of cattle in Alberta and Saskatchewan (Fredeen 1969, 1977). I did not record oviposition until fall. About one hour before dusk on the 3rd, 7th and 25th of October, I observed large swarms of S. arcticum, which extended from 10 to 75 meters below the dam. The swarms reached three meters in height and circulated rapidly more than a meter above the water. Other flies appeared to be dipping their abdomens in the calm water near the shore. It is possible that these were combined mating and oviposition swarms, because the circulation and movement of the upper swarm seemed excessive for oviposition, and males were present. Peterson (1959) described very similar swarms at a lake-outlet in Utah in September 1956 and 1957. He actually observed coupling and viable sperm in the spermathecae of collected females, and concluded that mating in S. arcticum may occur immediately before oviposition.

I was not able to observe a clear link between the adults of one cohort and the larve of a subsequent cohort as I did for S. vittatum, so it is difficult to speculate about the occurrence of a diapause period for the eggs of S. arcticum. Eggs of the winter or spring cohorts may enter a diapause period until hatching of their first instars the following year, or they may hatch immediately and contribute to the summer cohorts (Figure 14). Anderson and Shemanchuk (1987) concluded that the first two cohorts that they observed diapaused until the following year. Their conclusions were based on the occurrence of first instar larvae of the second cohort before the emergence of adults from the first cohort. By the same reasoning, I can conclude that the spring cohort is not the progeny of the winter cohort, but the connections between the other cohorts are not clear. Rearing experiments with eggs and cytotyping larvae would perhaps elucidate this puzzle.

Simulium tuberosum

Eggs of *Simulium tuberosum* were the overwintering stage of this species. Larvae were present from March to October in temperatures ranging from 3 to 24 °C, and pupae occurred in the 7 to 24 °C range. I saw very few adults except a few obtaining a blood meal from the author in late June. They have also been reported as pests of domestic animals. I generally found early instar larvae in samples from trailing riparian vegetation, so it is likely that the adults oviposit in these areas.

Other Species

The phenologies of *Simulium verecundum* and *Simulium decorum* were similar to the phenology of *S. tuberosum*. The overwintering stage was the egg, and larvae occurred from April through October in temperatures ranging from 4 to 24 °C. The pupae were present in the 9 to 24 °C range. *S. verecundum* was captured while ovipositing on sedges and cattails, and a few adults were found among the oviposition swarms of *S. vittatum* near the dam. *S. decorum* was found while ovipositing on the cement pillars and wood flash boards of the dam. Imhof and Smith (1979) recorded similar observations for these species. In addition, a few females of *S. decorum* were collected in October, 1986, while taking a blood meal from humans (Betty Eaton, pers. comm.). *S. decorum* is known as a biter of birds and mammmals, and *S. verecundum* is mammalophilic (Currie 1986).

Simulium canonicolum larvae occurred form April to May within a temperature range of 2 to 11 °C. Presumably, its eggs diapause during the rest of the year. It has been reported to bite humans and domestic fowl (Currie 1986). I found it exclusively on trailing vegetation, so oviposition probably occurs near shore. Simulium "aureum" was too rare at Owl Creek to comment on its life history. Elsewhere, it is reported as ornithophilic and has eggs that diapause during the winter (Currie 1986).

Longitudinal Distribution:

The longitudinal distribution of simuliid larvae in Owl Creek showed marked seasonal changes. I observed five distributional patterns that were relatively constant on successive sampling dates. These periods of stability varied in duration and were separated by shorter transitional periods. Because of variability in the distribution of species within a longitudinal site, I restricted my analysis to samples taken from stones in riffles of the main channel.

Winter

What I call the winter distribution lasted from late November to mid-March. Figure 21 shows a single date during this period, but it is representative of the general distributional pattern. Only the three species with overwintering larvae were present during this period. Prosimulium exigens was present at all longitudinal sites

JANUARY 19, 1986

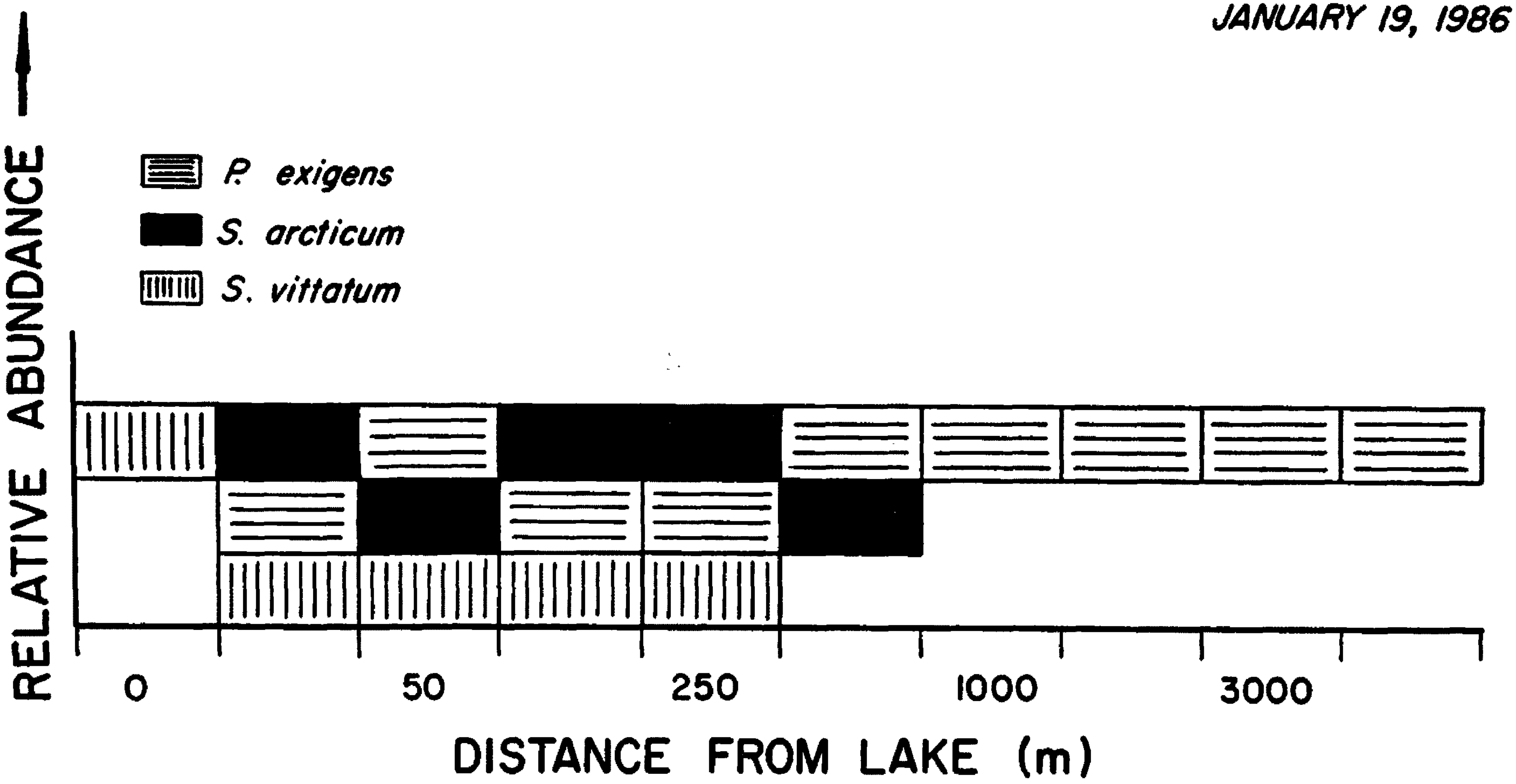


Figure 21. The longitudinal distribution of preimaginal simuliids during winter, 1986. Ranked abundances at ten longitudinal sites are shown (larvae and pupae collected from rocks in riffles).

except the dam. Simulium arcticum was primarily found from 25 to 500 meters below the dam. At sites which they shared, these two species had similar densities and traded ranks from site to site. Simulium vittatum was present from the dam to 250m, although a few individuals were found downstream on some of the sampling dates.

There appeared to be a longitudinal boundary below 500 meters, which separated an outfall reach with three species in the riffles, and a downstream reach with primarily one species. This pattern corresponded well with the occurrence of ice cover and anchor ice, which was minimal or absent above 500 meters. Temperatures at sites below 500 meters averaged close to 0 °C during this period, while those above 500 meters were 0.5 to 1.5 °C (Figure 3).

Spring

There was a transition period from mid-March to mid-April, during which the winter distributions appeared to shift downstream. The overwintering cohorts were reaching maturity during this period, and the spring cohorts of P. exigens and S. arcticum had hatched.

The spring period lasted from mid-April to late May and was similar to the winter distribution, except S. arcticum was found at all longitudinal sites (Figure 22). P. exigens was found at all longitudinal sites and S. vittatum in the first 500 meters. The presence of a definite outfall or downstream area was much less apparent during this period.

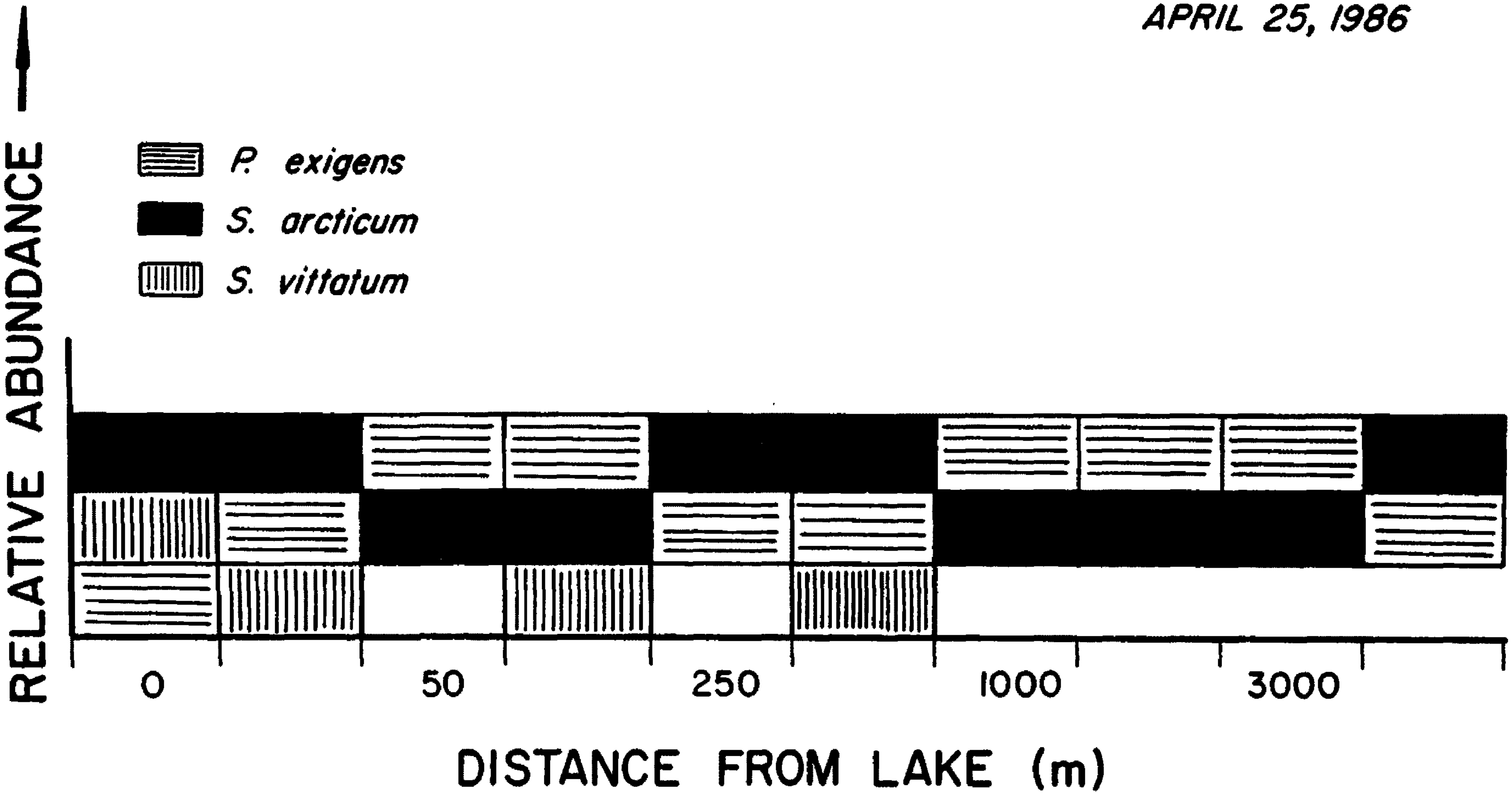


Figure 22. The longitudinal distribution of preimaginal simuliids during spring, 1986. Ranked abundances at ten longitudinal sites are shown (larvae and pupae collected from rocks in riffles).

The larvae of S. arcticum above 500 meters were a mixture from the overwintering and spring cohorts, but larvae below 500 meters were mainly from the spring cohort (Figure 23). This suggested that differential recruitment or migration to downstream areas occurred for the two cohorts . First instar larvae of the spring cohort of S. arcticum were found in early March at sites 25 to 2000 meters, but densities upstream were obviously higher. Flows were high during April, and the stream was free of ice, so conditions for drifting behavior were improved relative to the winter period (Figure 2). Therefore, the predominance of the spring cohort downstream was probably a result of recruitment within the site and drift from upstream sites. In support of the drift hypothesis, Wotton et al. (1979) showed that smaller larvae (e.g. the spring cohort) drifted more often than larger larvae of the same species (e.g. the winter cohort). In addition, Vadeboncoeur (1988) demonstrated that seston levels actually increased downstream during April and May in Owl Creek (see her Figure 3). Therefore, the abundance of food should not have a been a limiting factor in the downstream reach during this period.

The cohorts of P. exigens showed a somewhat different pattern. There was a delay of about two weeks in the development of the winter cohort at the 2000 meter site when compared to the 25 meter site (Figure 24), but first instars of the spring cohort hatched on the same date in early March

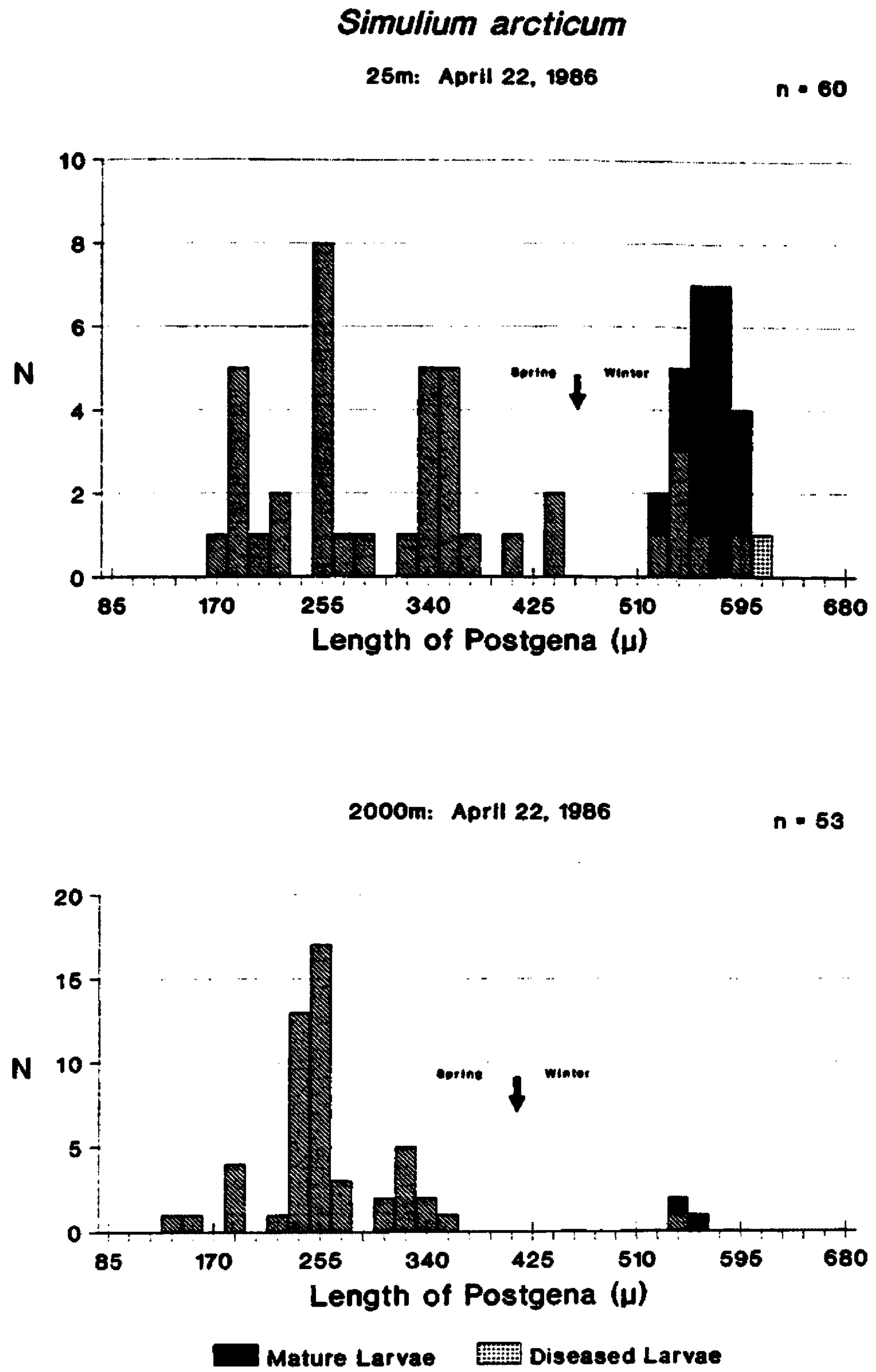


Figure 23. Frequency distributions of the lengths of postgenae for larvae of S. arcticum at the 25 and 2000 meter sites on April 22, 1986. N = number of larvae, μ = micrometers.

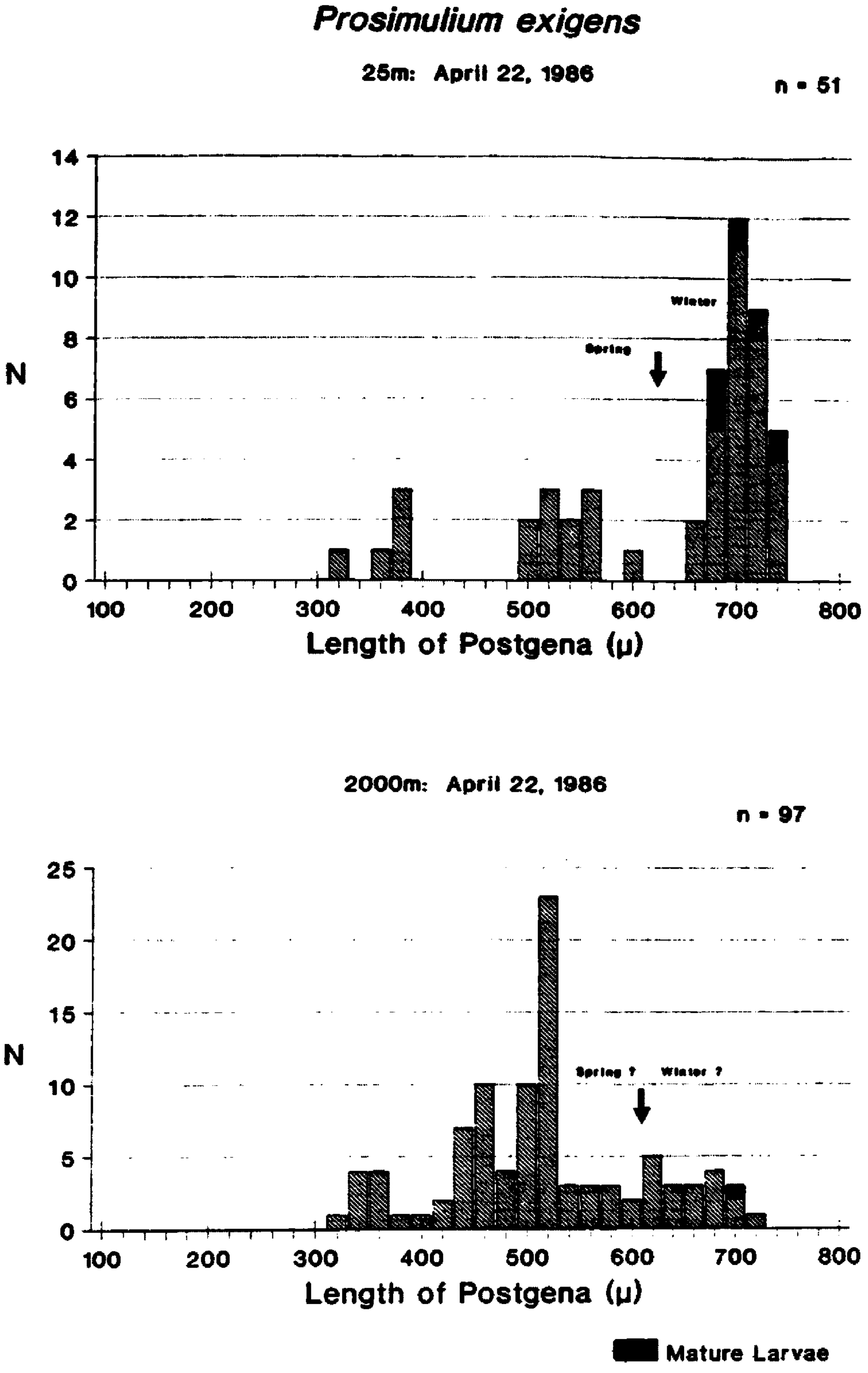


Figure 24. Frequency distributions of the lengths of postgenae for larvae of P. exigens at the 25 and 2000 meter sites on April 22, 1986. N = number of larvae, µ = micrometers.

at all longitudinal sites. Shortly after the hatch, the larvae of the spring cohort at downstream sites became indistinguishable from larvae of the winter cohort, and pupation for the combined cohort occurred concurrently with the outfall spring cohort. It was interesting to note that the combined cohort of the downstream sites had eight definite instars like the spring cohort of the outfall sites, and a small instar grouping that appeared to be the ninth instar (Figure 24). These larvae may have been ninth instar larvae that drifted from outfall sites or a small downstream group that were able to complete nine instars. This provided tentative evidence of a longitudinal as well as temporal decrease in the number of instars for the cohorts of P. exigens in Owl Creek.

Early Summer

The early summer period lasted for only a few weeks in June. It occurred after the disappearance of the abundant winter and spring cohorts of P. exigens and S. arcticum and before the large summer cohorts of S. vittatum. During this period, S. tuberosum was the most abundant species at all longitudinal sites except the dam (Figure 25). The early summer cohort of S. vittatum was the next most abundant species from the dam to 500 meters. S. arcticum was present in small numbers at sites below 500 meters and S. verecundum appeared in low numbers thoughout the creek. S. decorum was present from the dam to 50 meters. Three of these species,

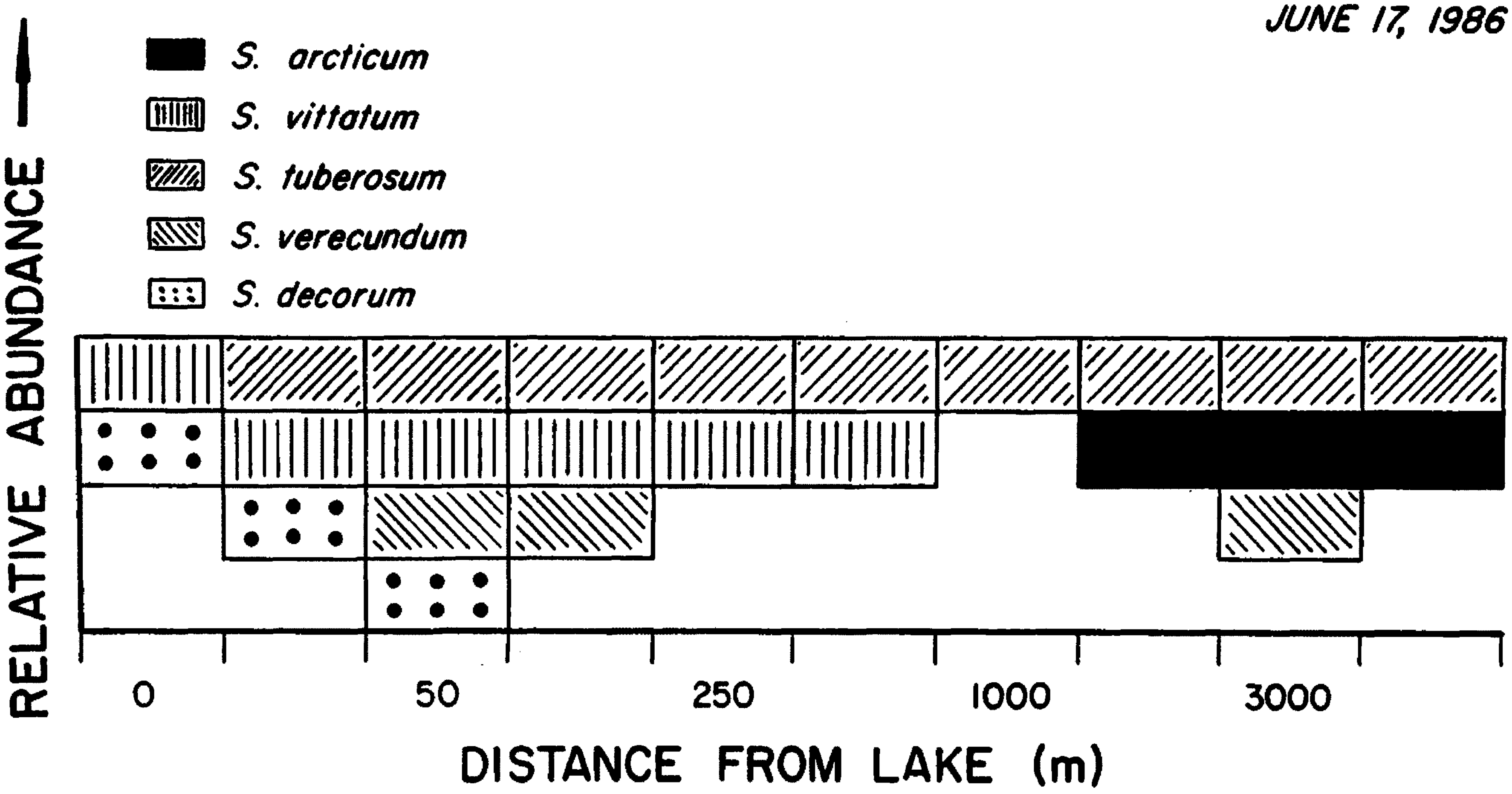


Figure 25. The longitudinal distribution of preimaginal simuliids during early summer, 1986. Ranked abundances at ten longitudinal sites are shown (larvae and pupae collected from rocks in riffles).

S. vittatum, S. decorum and S. arcticum, showed a definite outfall or downstream distribution during this period. Vadeboncoeur (1988) showed a slight longitudinal decrease in seston levels during June.

Summer

The summer period extended from late June to late September and was characterized by marked longitudinal changes in the distributions of all the species (Figure 26). S. vittatum was very abundant at sites above 500 meters and was present in lower numbers below 500 meters. S. tuberosum was the most abundant species at sites below 500 meters, and S. verecundum was most abundant near the dam. S. decorum was most abundant on the dam surfaces, but was also found in low numbers at the 25, 50 and 100 meter sites. Contrary to its winter distribution, S. arcticum was present only at sites below 500 meters. All of these species were developing within multiple asynchronous cohorts during this period.

The boundary or transition zone between an outfall and a downstream reach seemed to occur around 500 meters (Figure 22). This site had the highest number of species, and supported representatives from both the outfall and downstream reach. Species richness was equal between the two areas.

Flows were low during this period (Figure 2) and Vabeboncoeur (1988) showed a longitudinal decline in her counts of bacteria. Fredeen (1964) showed that simuliid

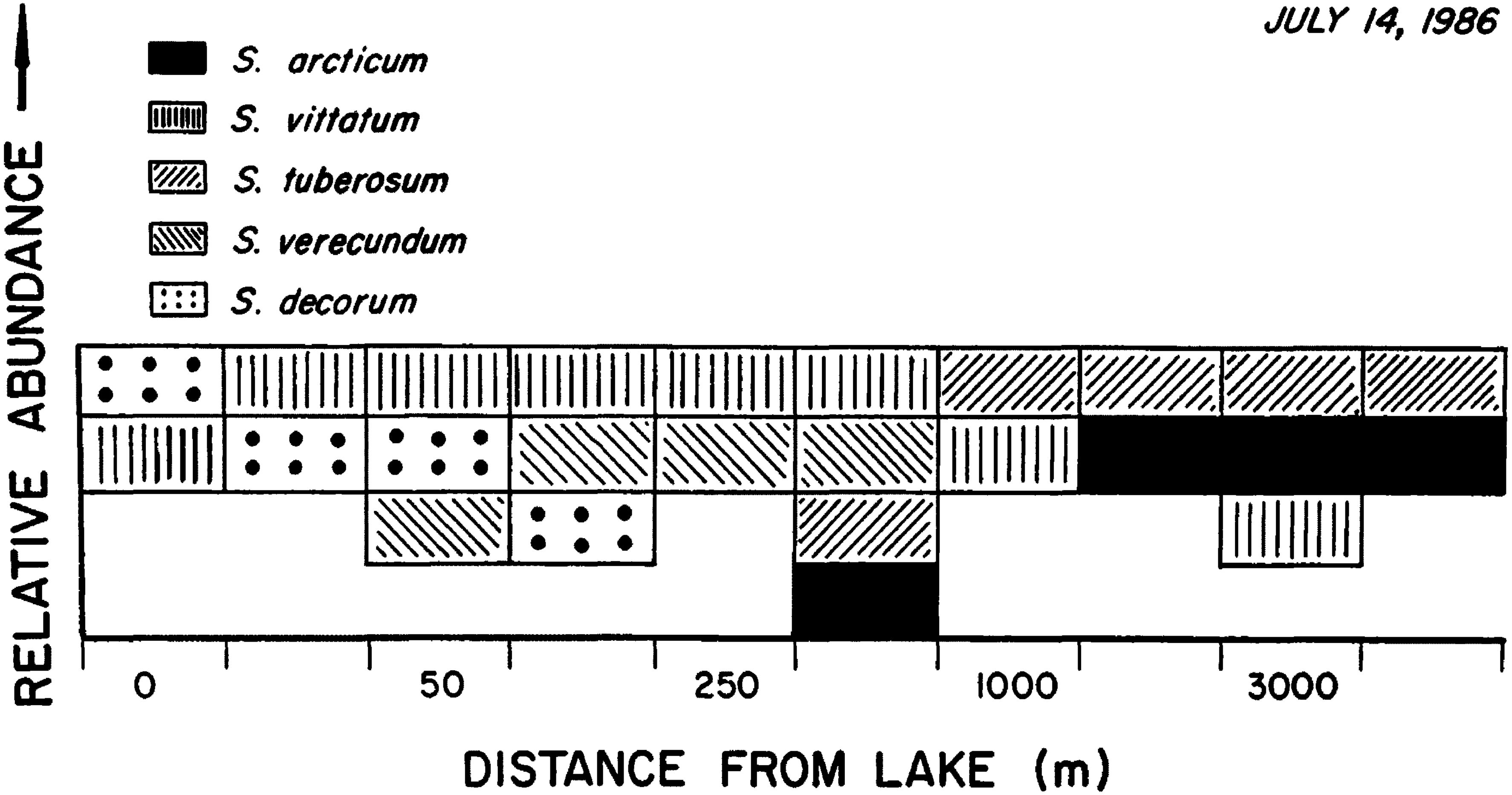

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Figure 26. The longitudinal distribution of preimaginal simuliids during summer, 1986. Ranked abundances at ten longitudinal sites are shown (larvae and pupae collected from rocks in riffles).

larvae can be reared using only bacteria as food, so a longitudinal decline in the quantity of bacteria may be an important factor determining the larval simuliid distributions of summer. There were also large inputs of floating macrophytes from the pond-like channel above the dam during the summer. These provided additional attachment sites for the dense populations of S. vittatum. The occurrence of S. arcticum at sites below 500 meters may have been related to temperature or dissolved oxygen levels. From late July through August, I recorded a 2 to 3 °C drop in the water temperature from the 3000 meter site to the 4500 meter site. The cause may have been an input of ground water as the gradient of the creek leveled near its mouth, and S. arcticum appeared to be more abundant at the colder 4500 meter site.

One variation of the summer pattern was an increase in the occurrence of S. vittatum and S. verecundum at the downstream sites as the summer progressed. The riparian sedges that provided substrates for these two species in early summer were less available as flows dropped below their root beds. Around this same period (late June to mid-August), a bloom of tough, filamentous algae occurred on stones in the main channel from 250 to 3000 meters below the dam. The larvae of S. vittatum and S. verecundum utilized the algae as a substrate, and thus were found more often in the main channel. S. tuberosum, during this period, continued to use the clean areas of stones as attachment sites.

Fall

The fall distributions were similar to those of spring, and lasted from October to mid-November (Figure 27). The last larvae of the summer cohorts had pupated, the overwintering cohorts were hatching, and the fall, "doomed" cohort of S. arcticum was present during this period. S. arcticum was present at all the longitudinal sites, and the first P. exigens were appearing at sites below 250 meters. S. vittatum continued to be present, primarily at sites above 500 meters. As in spring, flows (Figure 2) and probably seston levels were high throughout the creek, which may help to explain the less definite division of an outfall and downstream reach.

Within-Site Distributions:

Figure 28 compares the species composition and ranked abundances of larvae on stones in riffles and on trailing leaves of riparian vegetation. Two sites near the outlet and two downstream are shown during relatively stable periods in winter, spring, summer and fall.

Throughout the year, the number of species on riparian vegetation was generally greater or equal to the number on stones. Some species occurred on the vegetation throughout their preimaginal development, and others utilized these

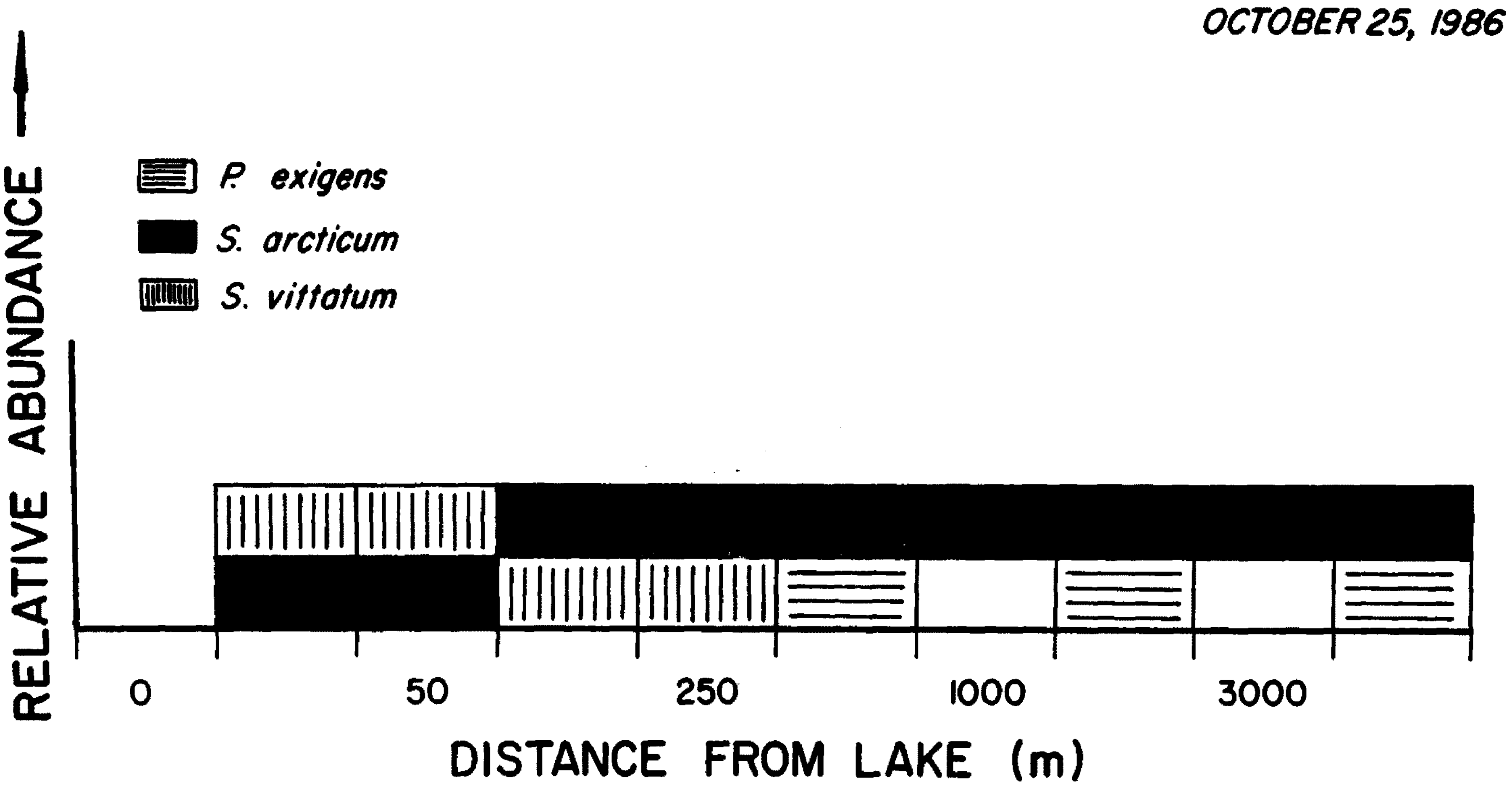

Figure 27. The longitudinal distribution of preimaginal simuliids during fall, 1986. Ranked abundances at ten longitudinal sites are shown (larvae and pupae collected from rocks in riffles).

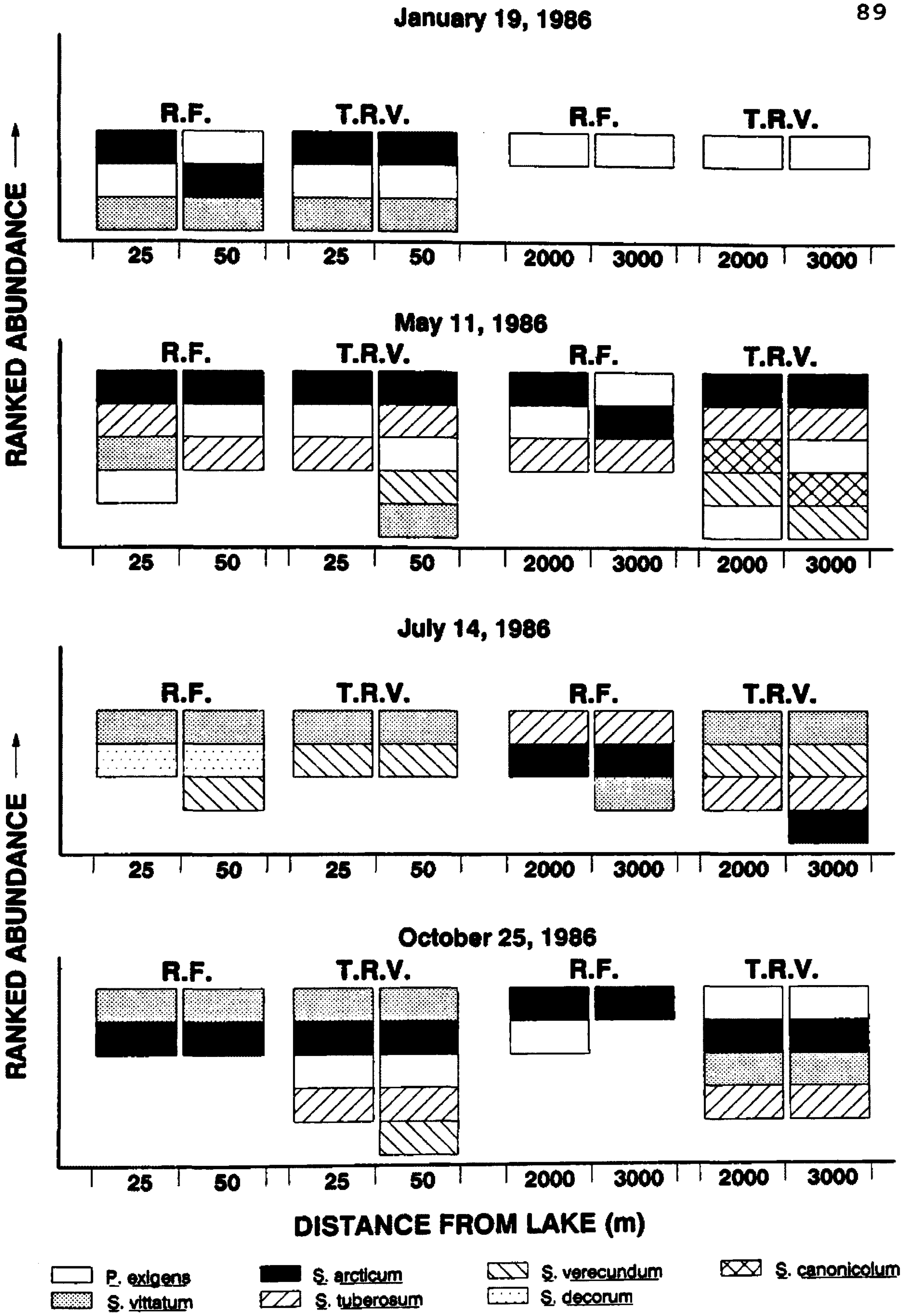

Figure 28. Ranked abundances of preimaginal simuliids collected from rocks in riffles (R.F.) and trailing riparian vegetation (T.R.V.) at two outlet sites and two downstream sites. A representative date is shown for winter, spring, summer and fall.

substrates temporarily as hatcheries or pupation sites. During winter and summer, the outfall sites showed nearly equal compositions and abundances for the two substrate types. Riparian vegetation samples at downstream sites were greater than or equal in species richness to samples from stones, and the abundance ranks were different. In summer, S. vittatum was present on both substrates near the outlet, but was more prevalent on the trailing vegetation at downstream sites. S. verecundum showed a definite preference for trailing vegetation at all longitudinal sites. Its occurrence on vegetation has been well documented (Adler and Kim 1986). In contrast, S. tuberosum, S. arcticum and S. decorum were found more often on stones. Although ranked abundances were the same in winter, there appeared to be a greater percentage of S. vittatum on dead, trailing vegetation near shore than on the densely packed stones.

In spring and fall, the species richness of the riparian vegetation was greater than that for stones. In spring, early instars of S. arcticum and S. tuberosum, which were primarily found on stones at later stages, were present in large numbers on sedges and cattails at nearly all the sites. S. canonicolum, found only during the spring, was found exclusively on trailing sedges. In the fall, mature larvae and pupae of the multivoltine, summer species were found more often on the riparian vegetation. A lateral migration to and from the riparian zone at the beginning and/or end of the larval stage seemed to occur for *S. arcticum* and *S. tuberosum*.

An interesting observation, which has also been recorded by Adler and Kim (1984) and Colbo (1979), is the presence of *S. vittatum* larvae under stones just downstream of a lake-outlet. I only observed this phenomenon during the winter at the 25 meter site. The larvae were dense under unembedded stones in mid-channel, almost to the exclusion of *S. arcticum* and *P. exigens*, which were primarily on the tops of embedded and unembedded stones. The larvae were also observed under stones near shore in currents as low as 10 centimeters per second. I did not expect to find filter-feeding organisms at sites which appeared to be poor for filtering.

The larvae were large and closely packed, so I initially hypothesized that they were undergoing some type of diapause. However, they grew in size during this period (Figures 10 and 11a). Adler and Kim (1984) suggested that larvae of *S. vittatum* were darker in color when attached to stones, because they were scraping periphyton and detritus as well as filtering. In addition, Craig (1977) discovered a Tahitian species that is a scraper. With the accumulation of organic material that occurs at sites near a lake-outlet, it seemed feasible that these larvae were surviving by scraping or collecting detritus. The other advantages of living on the bottoms of stones in the outlet area would be the avoidance of predators and competitors. Benthic feeding fish would have difficulty reaching the larvae, and competition with the dense populations of *S. arcticum* and *P. exigens* could be avoided.

The distributions of pupation sites were also different among the simuliid species of Owl Creek. *P. exigens* pupated on stone surfaces or shrub branches that were situated in areas of rapid current velocity. The pupae were found in masses with several layers of pupae stuck together by interwoven silk cocoons. This was also reported by Peterson (1970) and Currie (1986). *S. arcticum* pupae were also found in areas of rapid current, primarily on stones. Usually a single layer of pupae were present, but during the large emergence period in the spring, alternate layers of *S. arcticum* and *P. exigens* were often observed on a single stone as the winter and then the spring cohorts of these species pupated. *S. vittatum* appeared to pupate most frequently in areas of slower current velocity, such as under stones or on trailing cattail leaves. *S. tuberosum* pupae were found on stones and riparian vegetation. I found pupae of *S. decorum* on the surfaces of the dam and *S. verecundum* primarily on riparian vegetation.

DISCUSSION

Species Composition:

It is likely that I have underestimated the species richness of Owl Creek, because the cytotypes of potential species complexes were not identified. Some of the variation observed among cohorts within a morphological species could be interpreted as flexibility in response to environmental variation or the co-occurrence of ecologically distinct sibling species.

For the cohorts of S. arcticum, there were differences in longitudinal distribution and the number of instars required for development. Anderson and Shemanchuk (1987) showed that the two spring cohorts of S. arcticum were univoltine and separated temporally in the Athabasca River of Alberta, so the presence of sibling species would not be surprising.

S. vittatum also showed different numbers of instars among cohorts in Owl Creek, and the wide range of longitudinal sites and substrate types that it used suggested the possibility of a species complex. Adler and Kim (1984) gathered ecological information on the two North American siblings of S. vittatum in Pennsylvania. Both have been identified in Alberta. The IIIL-1 sibling occurs in lake-outlets and other areas of nutrient enrichment. The IS-7 sibling co-occurred with IIIL-1, but in cooler spring-fed water. If both occurred in Owl Creek, IIIL-1 would most likely predominate in the outfall reach and IS-7 downstream. Adler and Kim (1984) stated that the IIIL-1 sibling was found more often on stones and the IS-7 on trailing grasses. This supports the possibility of the two siblings co-occurring in Owl Creek, because *S. vittatum* is found on both stones and riparian vegetation near the outlet and predominantly on vegetation downstream. As further evidence, they found that the presence of the FG sibling of *S. tuberosum* was a good indicator for the presence of the IS-7 sibling, and *S. decorum* was an indicator for the IIIL-1 sibling. The summer distributions of *S. tuberosum* and *S.decorum* would place the IIIL-1 sibling near the dam and the IS-7 sibling downstream.

Adler (1986) and Pistrang and Burger (1988) found that siblings of the *S. tuberosum* complex exhibited spatial and temporal partitioning of their environment. Adler (1986) also stated that the siblings could be separated by the color of the head capsule and body. I noticed that the earliest cohort of *S. tuberosum* in Owl Creek was dark green to brown, and that summer larvae were primarily yellowish-white, except for a few red individuals. Therefore, it seems likely that two or three siblings of *S. tuberosum* are present at Owl Creek.

Phenology, Voltinism and Preimaginal Development:

As discussed in the results, the phenologies and voltinisms of the simuliid species of Owl Creek were generally comparable to other studies. Their life histories could be grouped as follows. *P. exigens* was the only univoltine species with overwintering larvae, and *S. canonicolum* was univoltine, but larvae did not hatch until spring. *S. arcticum* and *S. vittatum* were multivoltine with overwintering larvae. *S. tuberosum*, *S. verecundum* and *S. decorum* were multivoltine with overwintering eggs.

As in other studies, I observed seasonal changes in the size of larval simuliids (Colbo and Porter 1979; Post 1983). During warmer periods, larvae developed faster and were smaller at maturity. The species of Owl Creek showed two types of developmental flexibility, both of which resulted in size differences between cohorts. The first type was characterized by a change in the number of instars. This was observed between the winter and spring cohorts of *P. exigens* and *S. arcticum*, and the early summer and late summer cohorts of *S. vittatum*. The second type involved a change in the magnitude of growth between instars, without a change in instar number. I observed this pattern among the spring and summer cohorts of *S. arcticum* and *S. tuberosum*, and the winter and early summer cohorts of *S. vittatum*. Ross and Merritt (1978) reported a change in the number of instars between cohorts of *P. mixtum/fuscum*, and Rühm and Sander

(1975) documented a change in the growth of larvae for different cohorts of S. erythrocephalum. Since two of the species in Owl Creek, S. arcticum and S. vittatum, showed both types of developmental flexibility, the type of development may have been dictated by the degree of environmental change between periods when the cohorts developed. Within certain limits of environmental change, only an alteration in the magnitude of growth between instars occurred, but beyond those limits an extra instar was necessary for full development.

Longitudinal and Within-Site Distributions:

The most pronounced changes that I observed in the longitudinal distributions of preimaginal simuliids at Owl Creek occurred during the winter and summer. During both periods, the hypothetical division between an outfall and a downstream reach occurred at approximately 500 meters below the dam. In winter, the number of species dropped from three to one in areas downstream of the transition zone. In summer, species richness was highest within the transition zone and equal for the outfall and downstream areas. The summer distribution seemed to indicate that factors determining the distributional patterns were at intermediate levels at the 500 meter site. Therefore, species characteristic of both the outfall and downstream reaches were present.

During spring and fall, my observations for preimaginal simuliid distributions were similar to those of Vadeboncoeur (1988) for POC and counts of bacteria. Longitudinal changes were much less apparent during these periods, presumably because factors determining distributional patterns were relatively uniform. So, the annual longitudinal distributions showed seasonal expansions and contractions.

Flow, temperature, food and possibly interspecific interactions appeared to play important roles as factors determining longitudinal and within-site distributions. Flows were higher in spring and fall facilitating a more uniform thermal regime and transporting seston not only from the lake, but also from the creek bed (Vadeboncoeur 1988). Therefore, the food available at downstream sites was higher during spring and fall, allowing outfall species to shift their distributions downstream. The higher flows also expanded the wetted perimeter of the creek, so competition for attachment sites should decrease.

In winter and summer, flows were relatively low, and the residence time of creek water was of longer duration. Therefore, fluctuations in the air temperature during these periods had a greater influence on water temperature. In winter, a slight temperature gradient was formed by the input of relatively warm lake water at the outlet. Although slight (1 °C), the effect of the temperature change on the occurrence of ice was dramatic. The outfall sites remained open throughout the winter, while sites below 500 meters became increasingly covered with ice. The open riffle areas at downstream sites experienced periodic episodes of anchor ice, which were observed from December though February. Anchor ice encapsulates the substrate when present, and then scours it as it detaches. It certainly must be considered a major determining factor for the winter distributions, longitudinally and within a site.

In both winter and summer, Vadeboncoeur (1988) reported a longitudinal decline in bacterial counts from the water column and, with the low flows, it is likely that other organic particulates from the lake decline longitudinally. Low levels of dissolved oxygen at the high summer temperatures may be a limiting factor for some species in the nutrient enriched waters of the outfall reach. The most abundant species, which is probably the IIIL-1 sibling of _S. vittatum_, is found below sewage outflows in Pennsylvania. Its ability to tolerate low oxygen levels may give it an advantage in the outfall reach where food is presumably more abundant.

Interspecific and intraspecific competition in the outfall reach is probably highest during the summer and winter when attachment sites are less available and densities are high. It is possible that some of the downstream species are excluded from the outfall reach during these periods. Partitioning of stone surfaces among three relatively abundant species was observed in the winter, and in the summer, only one species, S. vittatum, was highly abundant in the outfall area. The other two species were low in numbers and found only in specialized habitats.

Oviposition behavior also affected the longitudinal and within site distributions. Although I did not observe adults during oviposition, first instars of P. exigens hatched at all longitudinal sites and were initially observed on riparian vegetation. S. arcticum, however, was observed while ovipositing in large swarms near the lake, and the first instars of the overwintering cohort were found much more often at outfall sites on the riparian vegetation. The winter distributions of these species reflected the placement of eggs by females in the fall. S. vittatum was most often observed in swarms just above the dam when ovipositing, but in summer, individual dead females were also collected at downstream sites from egg masses on trailing sedge and cattail leaves. These different behaviors and the two types of oviposition observed at the dam may have been sibling specific. Another interpretation would be that dispersing adults during the summer are more flexible when choosing oviposition sites, but in fall they chose the outfall area to avoid severe winter conditions.

I observed an incredible amount of variation in the life histories of the Owl Creek black flies. Because simuliids are biting pests and disease transmitters, this family of flies is studied extensively. The ultimate purpose of many of these studies is to achieve greater understanding of the family, so that effective control measures may be implemented. The ecological diversity that I have observed is a good argument against generalized control measures. Natural checks on potential pest species may already be present in the natural system. P. exigens, which is not known as a blood-feeder, uses the same areas of the stream and develops during roughly the same time period as the large winter and spring cohorts of S. arcticum. A program, which used a general larvicide to eradicate S. arcticum, would also eliminate its competitor, P. exigens. This could actually compound the pest problem in future years if the pest species was able to recolonize the site, and develop unchecked without its natural competitors.

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