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Title: THE ECOLOGY AND PRODUCTION DYNAMICS OF FOUR BLACK FLY SPECIES (DIPTERA: SIMULIIDAE) IN WESTERN OREGON STREAMS

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Ecological and production studies of *Prosimulium caudatum* Shewell, *P. dicum* Dyar and Shannon, *Simulium arcticum* Malloch and *S. canadense* Hearle (Diptera: Simuliidae) were made in 1971 and 1972 in three streams near Corvallis, Oregon. The purpose of the study was to characterize the biology and population dynamics of larvae, and to compare the production of the four species under various spatial and temporal conditions.

A total of 54 annual production estimates was derived utilizing 37 stations. In addition, 17 annual drift and 22 emergence (as pupae) determinations were made. Data on the physical and chemical characteristics of the streams, and on larval associates, parasites, predators and food types were obtained at all stations. Laboratory experiments provided data on feeding rates and predator impact.

The two *Prosimulium* species always coexisted, and occurred in

all streams. Simulium arcticum and S. canadense were studied in two streams only. All species were univoltine and had egg stage durations exceeding 40 weeks. Prosimulium spp. larvae appeared in mid-February and were on riffles for an average of 10.3 weeks. Simulium arcticum hatching began about six weeks later. Larvae of this species developed in an average of 8.8 weeks. Development of S. canadense began about nine weeks later than for Prosimulium spp. but lasted nearly as long. All four black flies had six larval instars.

All larvae were filter feeders, and fed primarily on the suspended materials in the streams. Detritus made up from 65-90% of the diet, with the rest being filamentous algae. Alimentary tract clearing of larvae was usually accomplished in less than one hour.

Black fly immatures were associated with about 75 other benthic insect species. Of these, nine were likely important simuliid natural enemies. Fish were minor black fly predators. Gastromermis nematodes occurred in about 3% of all mature simuliid larvae.

Annual losses due to drift averaged about 6%. Simuliid drift appeared to be a function of standing crop density. Growth-related crowding may also have been a factor. Effects of diel light conditions, temperature and discharge were minimal.

A diel emergence pattern existed for Simulium spp. adults only. The time between emergence and oviposition was likely about 0.5 week for all species. Emergence at most stations was single peaked, and averaged 3.6 weeks in duration.

The sampling universe at each station could be effectively partitioned to exclude areas where larvae did not exist. Thus, the weekly stratified random sampling program provided population estimates with error terms of usually 15% or less. All quantitative data were expressed on a per m^2 of overall riffle basis (and not on a per m^2 of habitat basis) to make the study more comparable to other benthic research.

Density, biomass and production differences between stations, streams and years were minimal for each species, and therefore were treated as replicates. Initial densities ranged from over 11000 to about 16000 larvae/m^2. Mortality for aggregates of all species was similar, with about 70% of all losses occurring during the first half of larval life. Growth for all species was generally logistic and averaged over 0.090 g/g per day annually.

Production, averaged for 1971 and 1972, in g/m^2, was: P. caudatum, 2.644; P. dicum, 2.908; S. canadense, 3.141; and S. arcticum, 3.950. This species ranking also held for initial density, mean density and mean biomass. Biomass and production were almost always closely correlated. Mortality variations had a greater influence on production than did growth rate.

Averaged for all species, the mean total mortality due to drift and parasites was 6.2% and 0.5% respectively. An average of 10.7% of colonizing larvae survived to emerge. Predator-caused losses

were estimated to provide the 82.6% needed to balance the loss budget.

Black fly larvae were the dominant processor of suspended materials in the three streams. On the average, they outnumbered all other primary consumers combined on riffles by a factor of 27. Simuliid larvae functioned as the primary prey reservoir for as many as 20 species of insect carnivores from February through June of both years.

The Ecology and Production Dynamics of Four Black Fly Species (Diptera: Simuliidae) in Western Oregon Streams

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THE ECOLOGY AND PRODUCTION DYNAMICS OF FOUR BLACK FLY SPECIES (DIPTERA: SIMULIIDAE) IN WESTERN OREGON STREAMS

INTRODUCTION

The development and success of human civilization has classically been greatly influenced by waterway utilization. Yet for thousands of years, both still and flowing inland waters have been taken for granted. These sometimes fragile entities often are allowed to become unproductive or unusable due to human activities associated with the development of technology.

It has been only within the last few decades that we in society have started to think in an ecologically oriented manner. Finally, streams and rivers are being viewed as resources which reflect either the beneficial or detrimental aspects of human existence. With this new insight has come an acceptance and funding of investigations into the crucial interrelationships which make these systems function.

In order to characterize how streams "work," preliminary research must be accomplished on the physical and biological entities that are present. In many areas of the world, this has been done. It now appears time that more quantitative investigations are initiated to keep up with the accomplished descriptive work.

The research presented in this dissertation has been designed to fill an information gap about a stream-inhabiting insect. Adults of simuliids are economically important pests of man and domestic animals. Perhaps more meaningful though, the larvae have been characterized by a number of studies as being a crucial link in lotic-based trophic relationships (Hynes, 1972). Black flies may be good models of primary consumers in the rhithron fauna, since they generally occur in substantial numbers and have simple life cycles.

By investigating both biological and ecological aspects of four western Oregon Simuliidae species, this research should lay the groundwork for a more complete understanding of this group. Specifically, the objectives of this study have been: (1) to describe the biology of the species, (2) to characterize in a quantitative manner the population dynamics of natural aggregates of larvae and pupae and (3) to integrate this information in order to describe and compare the production of the four species under various spatial and temporal conditions.

LITERATURE REVIEW

Aspects of Stream Research

Although investigations on streams have been accomplished for a great many years, it has been only recently that research directed specifically at lotic situations has come into its own. Logically, most early stream workers were limnologists primarily concerned with the physical or biological characteristics of lakes. Many of these early investigators were influenced and prepared by the classic concepts of biological interrelationships in waters (Forbes, 1887), physical limnology (Birge, 1907; Birge and Juday, 1911), and ecosystems (Thienemann, 1926). Important initial stream studies were accomplished on plankton (Kofoid, 1908), the biology of aquatic organisms (Forbes and Richardson, 1913), and pollution effects on lotic animals (Shelford, 1917). These workers were largely responsible for making the separate and necessary scientific discipline that stream biology is today.

Investigations of the physical and chemical nature of running waters have been well treated in Hutchinson (1957), section A of Ruttner (1965), and the first three chapters of Hynes (1972). Generally, it can be summarized that streams are highly dynamic entities, closely tied to geologic characteristics of associated channels and prevailing climatic conditions. Furthermore, both the chemical

and physical nature of water, along with characteristics of the outside environment, have been shown to be highly influential on the type and character of the organisms present (Cummins *et al.*, 1966).

Biological research has not only shown how diverse in character the aquatic fauna can be, but has also clearly demonstrated the high degree of interaction between organisms living in the lotic situation. These facts have been especially well shown by the excellent community-level studies in England by Hynes (1961) and in Lapland by Ulfstrand (1968).

To date, a fair number of energy-flow investigations have been accomplished on aquatic invertebrates. Most of these have used the systems-based viewpoints expressed by Odum (1957) and Teal (1957). Trophic relationships have been studied by Cummins (1964), Mecom and Cummins (1964) and Chapman (1966), but only recently characterized in a workable sense (Cummins *et al.*, 1966; Coffman, 1967; Coffman *et al.*, 1971).

A detailed energy flow investigation has been completed in New Hampshire by Fisher and Likens (1973). This study is especially applicable to researchers of small streams, due to the dominance of allochthonous materials as the energy input that drives the ecosystem.

Nelson and Scott (1962) have demonstrated how detritus can be central in importance to a stream community. Other investigations on the role of allochthonous detritus to lotic inhabitants were made by

Hynes (1963), Minshall (1967, 1968) and Kaushik and Hynes (1968). The effect of detritus on the distribution of benthic animals was discussed by Egglishaw (1964). Additional distributional studies have been made by Ulfstrand (1967) and Cummins and Lauff (1969).

Investigations concerning the food habits of aquatic insects have shown that much diversity and overlapping exists, and food-specific classifications are many times difficult or impossible to make (Jones, 1949, 1950; Chapman and Demory, 1963; Koslucher and Minshall, 1973). Cummins (1973) summarizes the current research by classifying insect trophic categories and elaborating each as to food type and feeding mechanism. This author emphasizes the importance of quantifying nutrient utilization (assimilation) in future studies. The comprehensive paper of Mann (1969) serves to clarify much current thought, especially as to methodology, about the dynamics of aquatic ecosystems.

Effective sampling of benthic organisms has been recognized as usually being difficult and time consuming. Random, stratified random and systematic programs appear to have the greatest possibilities, especially the latter two. Some or all of these techniques have been used and reviewed by Hansen _et al_. (1953), Macan (1958, 1961) and Cummins (1962). Cochran (1963), Edmondson and Winberg (1971) and Elliott (1971a) have elaborated on the statistics associated with these methods of sampling. Current techniques of estimating

drift have been reviewed by Elliott (1970). Sampling problems associated with using nets of different mesh sizes were treated by Mundie (1971) and Zelt and Clifford (1972).

Production

Perhaps the best parameter available for studying the ecology and true dynamic nature of a species or population is production. It involves not only tissue, its elaboration and, perhaps loss, but closely reflects the physical and biological characteristics of the system and its interactions with the aggregate under investigation. Production is defined by Warren (1971) as

> . . . the total tissue elaboration of a population per unit of area per unit of time regardless of the fate of that tissue, whether or not it survives to the end of a period, with one exception. Tissue that is elaborated by a population but is subsequently metabolically utilized for its own maintenance, during the time period over which production is being measured, cannot correctly be included as a part of the production of a population.

The classic paper of Lindeman (1942) expressed the initial concepts of trophic relationships within biological systems. This holistic approach has become questionable in its usefulness, but was of enormous importance to the beginning of a whole new line of ecological investigation. Ivlev (1945) did not treat the system initially as a whole, but used the species of greatest interest as the working basis of his approach. This concept has developed into a most workable one

for most investigators, due especially to its logical viewpoint in looking at both simple and complex biological systems.

Most early production studies on animals were strongly influenced by Ivlev. They were generally economic in nature, and accomplished on fish. These investigations not only produced a clearer understanding of fish population dynamics, but provided important new mathematical formulae and models (Clark et al., 1946; Ricker, 1946; Ricker and Foerster, 1948). Generally, these authors stated that production can be expressed, over a set interval of time, as the product of instantaneous growth rate and mean biomass parameters. Exponential growth, as described by its instantaneous coefficient, usually cannot occur over any long period of time. As Chapman (1968) pointed out, this estimator will serve as a good approximation, especially if short time intervals of measurement are used. In situations where brief measurement intervals are possible, both relative (Kimerle and Anderson, 1971) and instantaneous growth rates will be about the same.

Perhaps the most important of all early production studies was the classic work of Allen (1951). This investigation included stream invertebrates as well as fish, and evolved an efficient graphical method of production estimation. Neess and Dugdale (1959) not only used a modified form of the "Allen curve" for chironomid production calculations, but investigated the mathematical basis of the technique.

Negative production may result when there is a decrease in average weight of an individual over a period of time. This controversial concept has been reviewed and utilized by Warren *et al.* (1964).

Waters (1962a) proposed a method of calculating production, based on relationships between biomass, drift and emergence of *Baetis vagans* McDunnough. This technique was shown to have distinct possibilities, but also some potentially serious limitations (Waters, 1966).

Indirect methods of production investigation have been designed or modified on an estimated cohort biomass basis by Hynes and Coleman (1968), Fager (1969) and Hamilton (1969), and a respiration basis by McNeill and Lawton (1970). These types of production calculation appear to be most applicable to community-level studies.

Using various techniques, reliable production estimates have recently been calculated for a number of aquatic invertebrates. These include *Microtendipes chloris* (Meigen) (Kajak and Rybak, 1966), *Glyptotendipes barbipes* (Staeger) (Kimerle and Anderson, 1971), *Baetis bicaudatus* Dodds and *Oligophlebodes sigma* Milne (Pearson and Kramer, 1972), *Hexagenia* spp. (Hudson and Swanson, 1972), and *Ephemerella subvaria* McDunnough (Waters and Crawford, 1973). The latter authors compared the Hynes-Coleman, Allen, Ricker instantaneous growth, and "removal summation" (Anderson and Hooper, 1956) techniques, and found all but the first gave very consistent results.

"Turnover ratio" may be defined as the proportional relationship between annual cohort production and mean annual population biomass of that cohort. These ratios have been investigated since Lindeman (1941) looked experimentally at the relationship between generation numbers and annual population means in his production calculations. Allen (1951) pointed out the inherent underestimating qualities of the Lindeman concept.

Waters (1966) suggested that closely related species in ecologically similar situations would have turnover ratios very much alike. He proposed that, if substantiated, this concept would greatly simplify some energy flow studies since production could be estimated relatively easily by multiplying mean annual population biomass by an appropriate turnover ratio figure. Using data obtained from other investigators, Waters (1969b) showed that turnover ratios for aquatic insects can be very constant.

The Biology of Simuliidae

A great portion of the research presented in the following sections has complex ecological implications. Due to the variable nature of many of these interactions, the biological basis upon which most are regulated have sometimes been obscured. To facilitate an ease in presentation and understanding, a summary of the general

biology of simuliids is given below. More detailed discussions of some of the references are given in subsequent chapters.

Black fly eggs are roughly trianguiar in shape and range in length from 0.2 to 0.4 mm (Peterson, 1959b). Females usually deposit between 200 and 500 eggs per individual, but may produce as many as 800 in a single gonotrophic cycle (Davies and Peterson, 1956). Oviposition may vary from the scattering of eggs while females fly over water (Fredeen et al., 1951) to the complete submergence of the fly for egg deposition on a substrate (Peterson, 1956). Incubation time may range from a few days for species without an egg diapause (Davies, 1949) to many months for simuliids which overwinter in that stage (Sommerman et al., 1955).

Black fly larvae are tube shaped, have a single thoracic proleg, and are about seven times longer than wide. Larval instar length may range from 0.5 to over 12 mm. Larvae are attached to substrates by an anal circlet of hooks which may be imbedded into a mat of silk secreted from paired labial glands (Chance, 1970). A pair of large head fans are present on the great majority of larvae and are used to filter food from the water column. Although simuliid larvae have retractable "gills" located near the anus, these structures are probably osmoregulatory in function (Krogh, 1939). Gas exchange is generally thought to be cuticular (Wigglesworth, 1949).

Immediately after hatching, larvae usually drift downstream freely or on silk threads until a substrate of suitable character is encountered. The settling, attachment and orientation of larvae is influenced not only by current (Maitland and Penney, 1967), but also plant growth, silt accumulations, food availability, illumination, rheotactic behavior and substrate type, texture and color (Nielsen, 1950; Zahar, 1951; Chutter, 1968). Current velocities and temperatures under which larval simuliids exist often vary greatly, and some species may have characteristic ranges or tolerances (Davies and Syme, 1958). The idea of an innate current requirement (Wu, 1930) appears to be valid since, although some species can tolerate low oxygen levels, no black fly larva can survive long in still water, even if it is saturated with oxygen (Hynes, 1972).

Flowing water is also important in its role of bringing suspended food materials to the animals. The few fanless black flies (*Gymnopais*, *Twinnia*, some first-instar *Prosimulium*) scrape food materials from the substrate on which they live (Davies *et al.*, 1962). All other simuliid larvae filter nutrients from water, though they can scrape the substrate for food when suspended sources are low (Davies, 1949). Although foods may vary, the most important components of the diet of black fly larvae are leaf detritus and both unicellular and filamentous algae (Peterson, 1956; Anderson and Dicke, 1960). It has been suggested that bacteria may be an important source of nutrition

(Fredeen, 1960, 1964), but the true role of these microorganisms has not been clearly established. Some simuliids may be carnivores, since Stone and Snoddy (1969) recorded larvae feeding upon isopods.

Black flies normally have six larval instars, although some may have as few as four or as many as seven (Davies et al., 1962). Larval development times range from about one month for species which develop quickly after hatching, to over seven months for those which overwinter or aestivate in the larval stage (Peterson, 1970b). Chemical characteristics of water such as pH, dissolved oxygen and solids, and carbonates, most likely affect black fly larvae only when levels are extreme (Chutter, 1968).

The drifting of simuliid larvae has been noted by many investigators (Carlsson, 1962; Elliott, 1971; Waters, 1972), and appears to occur with all species. Waters (1962b) showed that simuliid drift is little affected by diel conditions and freshets, but is increased by mechanical means such as people disturbing the habitat. By contrast, Anderson and Lehmkuhl (1968) demonstrated that an increase in water volume can result in higher drift rates, and Elliott and Minshall (1968) indicate that a definite difference in black fly drift can occur between day and night conditions. Pesticides may cause simuliid drift for over 100 km in large rivers (Fredeen, 1974). Normal distances are probably less than 50 m per day (Waters, 1972). Upstream movements of larvae have been recorded by Elliott (1971b).

The natural enemies of black fly larvae, although fairly well known, still have an almost unknown impact on natural populations. Microsporidian protozoans (Davies, 1957) and mermithid nematodes (Welch and Rubzov, 1965) have been found to be common larval parasites. A long list of black fly predators are recorded. These include mayflies and dragonflies (Cameron, 1922), stoneflies (Jones, 1950), caddisflies and ants (Peterson and Davies, 1960), beetles and true flies (Peterson, 1960), crayfish (Speir, 1969), fish (Wolfe and Peterson, 1959) and birds (Snoddy, 1967).

Final instar larvae construct a silken cocoon for anchoring and protection of the pupae. Simuliid pupae have specialized tubular or filamentous breathing structures which are sufficiently diverse in morphology to be of taxonomic use. Pupal development times are short, from a few days to over two weeks, and are most affected by water temperature (Stone, 1964). Although little is known about natural enemies of pupae, fast growing algal mats, mites, fish, crayfish and birds may all be important (Sommerman _et al._, 1955; Peterson, 1960).

Adult black flies usually emerge from their cocoon in a gas bubble and float to the stream surface; after a few seconds of cuticular hardening, they are able to fly (Davies _et al._, 1962). Females of a few species have fully-developed eggs at emergence, but the majority require a blood meal from a homoiothermous animal to complete a

gonotrophic cycle (Davies, 1961). In some cases where the female emerges with immature eggs and has sufficient nutrients, ovarian development may take from two to five days. This time may be increased by a week for females that require a blood meal (Ussova, 1961). Adult male black flies do not feed on blood, and the adults of both sexes may obtain nutrients from the nectar of flowers (Davies and Peterson, 1956).

The majority of black flies appear to mate during flight, probably while in a swarm (Hocking and Pickering, 1954). Adults may travel up to 50 miles from breeding areas (Rempel and Arnason, 1947), though common distances are eight miles or less (Baldwin *et al.*, 1975). Parthenogenetic forms or species are known to occur, especially in the arctic and sub-arctic zones of Europe and North America (Downes, 1962). The life span of adults if fairly short, two months probably being the extreme (Nicholson and Mickel, 1950).

Depending on the species involved, the area, and the physical conditions encountered, simuliids may have from one to over seven generations per year (Stone and Snoddy, 1969). Characteristic patterns of seasonal species succession have been noted by Obeng (1967).

The biting and blood-sucking nature of many black fly females has made the group economically important in three ways: (1) simuliid females are sometimes a severe nuisance to humans: (2) blood losses and gadding by many domestic animals result in reduced fitness,

decreased milk and meat production and, occasionally, death (Nicholson and Mickel, 1950); and (3) at least three important diseases are transmitted, human and bovine onchocerciasis (Blacklock, 1926; Steward, 1937) and bird malaria (*Leucocytozoon* spp.) (Bennet and Fallis, 1960).

MATERIALS AND METHODS

Study Species

In order to complete a critical population dynamics study of black flies in natural habitats, certain characteristics were deemed necessary in the selection of species to be investigated. These were: (1) species that could be identified in the larval and pupal stages, (2) a simple life cycle, (3) inherent behavioral characteristics to insure sampling ease and success, and (4) adequate numbers in locations convenient for study.

Black fly larvae and pupae primarily inhabit the upper surface of rocks in stream riffles. These concentrations of animals are natural populations, even though a great deal of drift-related emigration is possible. In this dissertation, biological populations of simuliids will be referred to as aggregates. This will minimize the confusion possible when references are made to sampling and statistical populations or populations of other organisms.

Of the 11 simuliid species screened for this study, representatives of two genera were selected. These four black flies, *Prosimulium caudatum* Shewell, *P. dicum* Dyar and Shannon, *Simulium arcticum* Malloch and *S. canadense* Hearle, not only occur throughout the study area, but were found to be ideal for this type of investigation.

As with all Prosimulium species (Peterson, 1970a, b), P. caudatum and P. dicum have one generation per year and a generally well synchronized hatching time and cohort development. The larvae and pupae of both were always found together in the three streams investigated.

Prosimulium caudatum is a fairly common western Oregon black fly. This species may be restricted to coastal areas west of the Cascade Mountains in British Columbia, Washington and Oregon, since it has never been collected from interior locations (Peterson, 1970b). The female was, in part, first described by Dyar and Shannon (1927) as P. dicum. Shewell (1959) characterized the species by not only describing the female, male, larva and pupa, but ascertaining some aspects of its biology.

Prosimulium dicum occurs in both coastal and inland areas of British Columbia, Washington, Oregon and northern California. Dyar and Shannon (1927) described the female, and the remaining stages were characterized by Shewell (1959).

Peterson (1970a, b) provided a morphological basis for separating all stages of P. caudatum and P. dicum. Identification and separation of the stages of all Oregon Prosimulium species present was initially difficult, but with experience and technical advice (Peterson, personal communication, 1971: Entomology Research Institute, Canada Department of Agriculture, Ottawa), it was found to be relatively easy, though time consuming.

Simulium arcticum and S. canadense also were univoltine in the study streams, although Speir (1969) found both occasionally had two generations per year in the Marys River, Benton County, Oregon. The abundant immature stages of the two were distinctive enough to be easily separated. Neither Simulium species was generally found on the same riffle or ever included in the same station with the other.

Simulium arcticum is widely distributed throughout the western United States and Canada. Malloch (1914) described the female and Cameron (1922) characterized the remaining stages, as S. simile. The taxonomic keys of Stone (1956) are most useful for the identification and separation of S. arcticum from related species. In some areas this species is a serious pest, attacking man and domestic animals. Considerable attention has been paid to its economic importance (Hearle, 1932) and control (Rempel and Arnason, 1947; Fredeen, 1962, 1969).

Simulium canadense is primarily distributed throughout the coastal states and British Columbia, but it has been found as far east as South Dakota. The crude original description of the male and female, as S. virgatum canadensis, by Hearle (1932), has been improved by Twinn (1938) and Stone (1963). Initial descriptions of the larva and pupa have not been found. The keys of Stone (1956) were used for identifying pupae and adults. Speir (1969) studied the larvae,

and Stone (personal communication, 1969: U.S. National Museum, Washington, D.C.) confirmed the identification.

Experiments conducted in 1970 and 1971 showed that fairly substantial mechanical disturbances were needed to dislodge the larvae of all species studied, and the general behavior when shadowed or slightly disturbed was to tightly curl until the stimulus was removed or a certain period of time had passed. This knowledge alleviated any fears of loss of animals due to sampling activity on nearby substrates. Observations on other prospective black fly species showed that the larvae of at least two, S. pugetense Dyar and Shannon and S. vittatum Zetterstedt, often released their hold on the substrate upon minor mechanical disturbance or even, occasionally, shadowing.

A voucher series of specimens has been deposited in the Entomology Department Museum, Oregon State University, Corvallis. This set represents larvae, pupae and adults of all four black fly species. Eggs of P. caudatum and P. dicum are also included.

Study Streams

This investigation was carried out during 1971 and 1972 at a number of locations on three permanent streams near Corvallis, Benton County, Oregon (Figure 1). The streams (Berry Creek, Oak Creek and Soap Creek) were chosen for a number of reasons. The most important of these were: (1) similar and contrasting physical

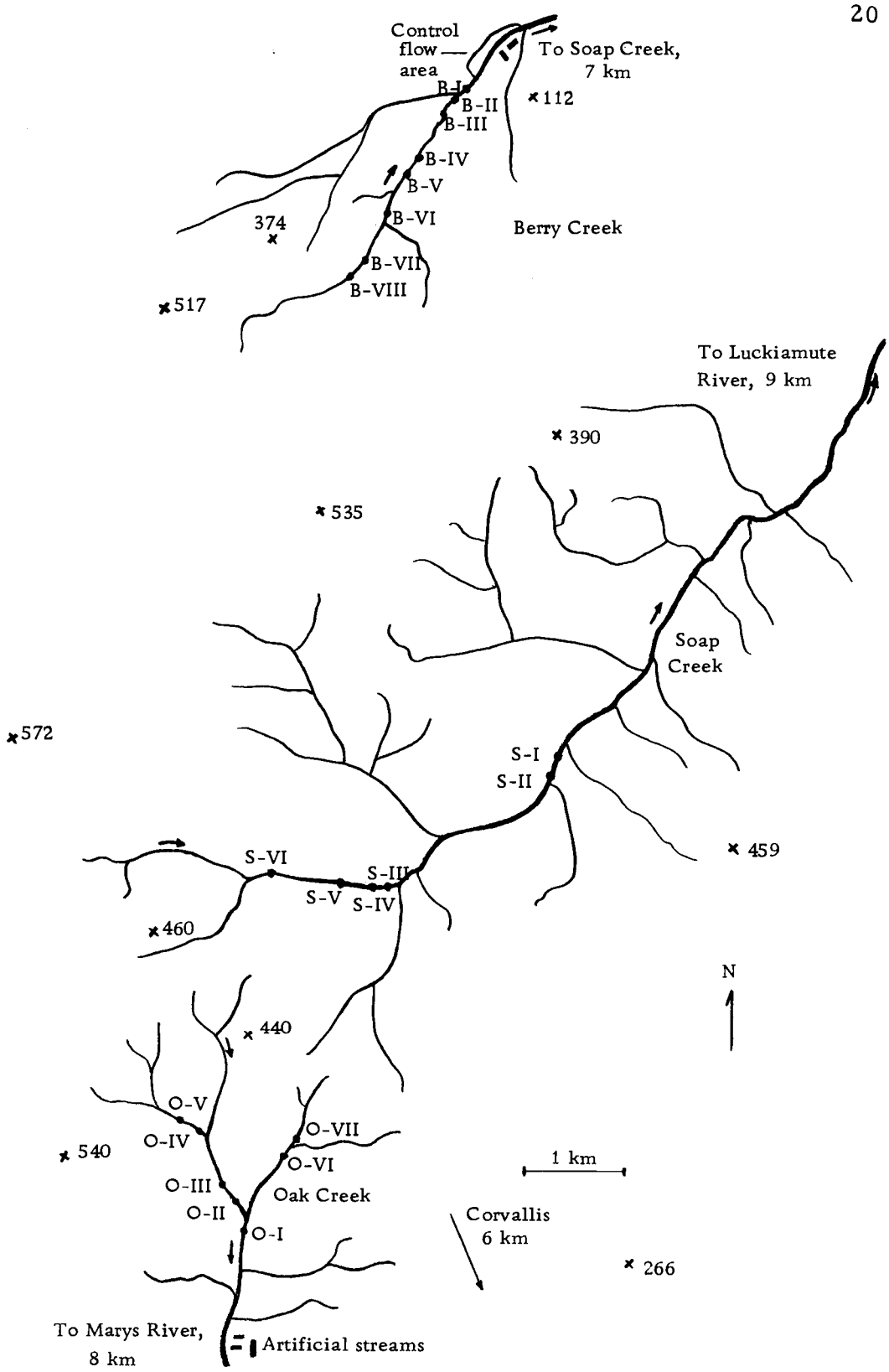


Figure 1. Map showing all sampling stations on Berry, Oak and Soap Creeks, 1971 and 1972. Elevations are in meters.

conditions, (2) black fly species present, and (3) the close proximity of the research areas to laboratory facilities.

The period during which research occurred was limited by life cycles of the black flies. This duration ranged in overall extent from approximately early January to late June of both years. Consequently, all physical, chemical and biological parameters treated in the study are based on either this time period or the duration that certain species existed on riffles.

In addition to population sampling, water temperature and current velocity readings were usually taken at each station every week. Daily maximum-minimum water temperatures were recorded at some sites with the few Taylor No. 5458 instruments available. Current velocity was measured with pitot tubes constructed of tubular plastic (Figure 5). These devices were calibrated initially and at intervals in culverts where flow-rate could be calculated. At a convenient area near the lower station of all three streams, total cross-section dimensions were determined so, along with velocity data, discharge figures during each sampling period would be available.

Total water hardness and pH readings were made on all three streams using a Hach AL-36-WR portable testing kit. Dissolved oxygen measurements were taken in 1971 but then discontinued because all streams were supersaturated during the sampling period.

Data on locational and physical characteristics for each stream are summarized in Table 1. Station data are given in Tables 2 and 3. Parameters listed in Table 1 vary slightly from those in Tables 2 and 3 because measurements were taken both at stations and other accessible sites along the streams.

Table 1. Characteristics of the research streams, January through June. Data are averaged for 1971 and 1972.

	Berry Creek	Oak Creek	Soap Creek
Distance (km) and direction from Corvallis	16, N	6, NW	15, N
Length (km) and direction of flow	10, NE	13, S	21, NE
Elevation range (m)	61-335	69-427	58-457
Width range (m)	0.9-3.7	0.5-2.9	1.1-6.3
Temperature range (^{o}C)	<1.1-21.2	<1.0-21.6	2.0-19.8
Temperature mean (^{o}C)	8.5	10.5	10.8
Velocity range (cm/sec)	< 3.0-64.0	<3.0-67.1	<3.0-67.1
Discharge range (m^3/sec)	< 0.1-2.1	<0.1-1.8	0.5-5.2
Discharge mean (m^3/sec)	0.7	0.5	2.0

As Figures 2, 3 and 4 illustrate, water temperature patterns were similar for all three streams between years. Discharge was monitored occasionally at convenient low-elevation stations so representative figures would be derived for the entire stream. Since

Column explanations for Tables 2 and 3.

1 = station number

2 = black fly species present; 1 = *P. caudatum*, 2 = *P. dicum*, 3 = *S. arcticum*, 4 = *S. canadense*

3 = distance from base station (km)

4 = station elevation (m)

5 = mean stream width (m)

6 = mean riffle area (m^2)

7 = mean riffle depth; water level to top surface of rocks composing riffle (cm)

8 = usable substrate area (cm^2)

9 = temperature range and mean (^oC)

10 = velocity range and mean (cm/sec)

11 = discharge range and mean (m^3/sec)

12 = pH range

13 = total hardness range (mg/l as $CaCO_3$)

Table 2. Biological, physical and chemical characteristics of the sampling stations on Soap (S), Berry (B) and Oak (O) Creeks, January through June, 1971.

1	2	3	4	5	6	7	8	9	10	11	12	13
S-III	3	-	149	4.6	7.1	4.9	4220	3.4-18.8	6.1-42.7 (24.6)	0.7-5.2	6.6-7.2	<17.1-17.1
S-IV	3	0.2	150	4.1	5.5	4.5	5213	(11.3)	3.0-27.0 (21.0)	(2.0)		
S-V	3	0.5	154	3.9	6.5	10.8	4941		3.0-51.8 (34.1)			
S-VI	1,2	1.3	224	1.3	6.7	6.2	5547		12.2-67.1 (37.9)		6.4-6.9	<17.1-17.1
B-I	3	-	150	1.9	5.8	10.0	4605		<3.0-36.6 (19.3)	<0.1-2.1		
B-II	3	0.2	157	1.6	4.9	5.4	4951		3.0-42.7 (26.8)	(0.7)		
B-III	3	0.3	158	2.0	5.1	9.3	5430		3.0-61.1 (30.5)			
B-VI	1,2	1.6	240	1.4	6.4	5.8	3732	2.3-15.2	9.1-54.9 (35.4)		6.6-6.7	17.1-85.5
B-VII	4	2.1	289	1.4	5.0	7.9	5990	(8.6)	3.0-33.5 (22.9)			
B-VIII	4	2.2	293	1.2	5.8	5.2	4892		6.1-42.7 (26.1)			
O-I	1,2	-	154	2.1	6.9	5.8	4721	1.5-20.9	9.1-64.0 (40.3)	<0.1-1.8	6.5-6.8	<17.1-34.2
O-II	1,2	0.3	155	1.8	6.6	6.5	4272	(12.0)	6.1-57.9 (32.8)	(0.5)		
O-III	1,2	0.3	156	1.8	5.9	7.0	3853		6.1-51.8 (28.5)			
O-IV	1,2	1.3	223	1.5	6.2	8.2	5670	1.8-18.3	12.2-67.1 (37.0)		6.5-7.0	<17.1-17.1
O-V	1,2	1.4	228	1.2	5.1	3.1	5256	(10.2)	6.1-54.9 (31.6)			
O-VI	1,2	0.9	193	0.9	5.1	6.8	4584		<3.0-64.0 (27.2)			

Table 3. Biological, physical and chemical characteristics of the sampling stations on Soap (S), Berry (B) and Oak (O) Creeks, January through June, 1972.

1	2	3	4	5	6	7	8	9	10	11	12	13
S-I	4	-	118	5.4	6.1	4.8	5579		3.0-45.7 (21.2)		6.7[a]	
S-II	4	0.2	119	5.1	5.5	6.3	4146		6.1-39.6 (32.0)			
S-III	3	2.3	148	5.0	6.7	5.5	4291	2.5-19.1	6.1-42.7 (37.5)	0.5-4.8	6.8-7.1	<17.1-17.1
S-IV	3	2.4	149	4.7	6.0	6.0	5447	(10.2)	<3.0-61.1 (28.4)	(1.7)		
S-V	3	2.7	153	3.7	5.4	3.1	4973		6.1-45.7 (25.0)			
S-VI	1,2	3.5	224	1.8	7.4	7.1	4411	2.0-16.4 (10.8)	9.1-54.9 (40.3)		6.0-6.7	<17.1-17.1
B-I	3	-	156	2.3	6.3	3.9	4871		6.1-51.8 (36.1)	<0.1-1.8		
B-II	3	0.2	157	2.6	5.1	8.5	4541		3.0-33.5 (26.6)	(0.6)	7.0[a]	
B-III	3	0.3	159	1.8	5.4	7.3	5843		<3.0-33.5 (21.9)			
B-IV	4	1.0	192	2.1	6.0	7.8	5305	1.7-20.6	<3.0-42.7 (33.0)		6.3-6.8	34.2-68.4
B-V	4	1.1	193	1.7	5.2	4.2	5959	(8.6)	3.0-27.0 (14.3)			
B-VI	1,2	1.6	239	1.2	6.1	5.6	4509		6.1-64.0 (38.5)			
B-VII	4	2.1	288	1.2	5.0	6.1	5105		<3.0-39.6 (30.4)			
B-VIII	4	2.2	292	0.9	4.9	10.1	4397		3.0-30.5 (24.3)		6.7-6.9	17.1-34.2
O-I	1,2	-	154	2.1	6.5	10.3	5075	1.0-19.2	<3.0-45.7 (38.2)	<0.1-1.5	6.7-7.2	<17.1-17.1
O-II	1,2	0.3	155	2.4	5.2	4.0	3821	(10.5)	9.1-57.9 (44.7)	(0.5)		
O-III	1,2	0.4	159	1.9	6.5	8.2	6074		6.1-42.7 (38.5)			
O-IV	1,2	1.4	223	2.2	5.9	5.7	5789		6.1-33.5 (28.2)			
O-V	1,2	1.4	224	1.3	6.1	5.1	5570	1.3-17.3	9.1-51.8 (46.3)		6.6-6.9	<17.1-17.1
O-VI	1,2	0.9	193	0.9	5.4	6.4	3097	(9.3)	3.0-42.7 (40.0)			
O-VII	1,2	0.9	195	1.0	4.7	9.4	4005		6.1-54.9 (49.8)		6.9[a]	

[a]Single observation

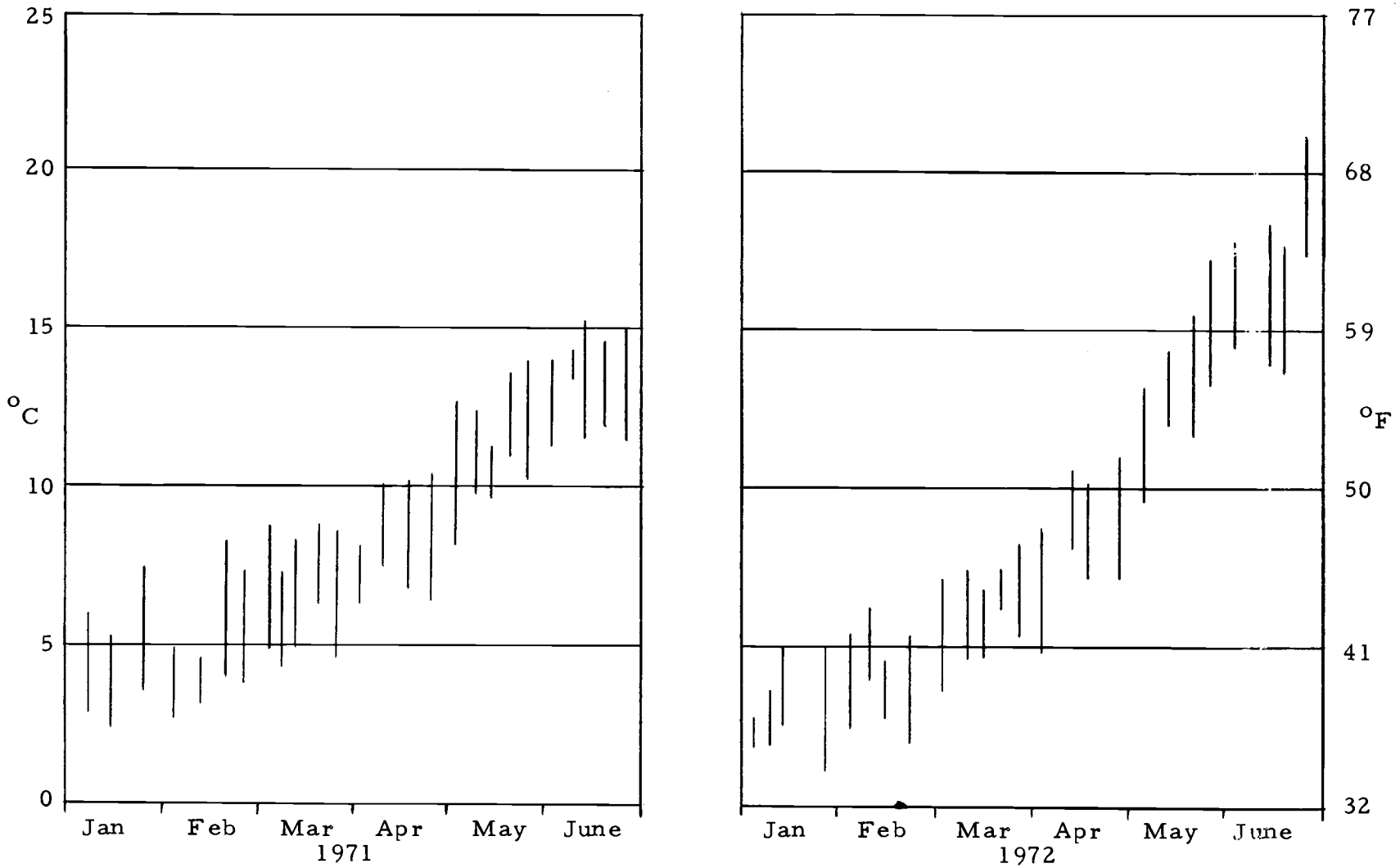


Figure 2. Weekly range of water temperature at Berry Creek stations B-VI (1971) and B-IV (1972), January through June.

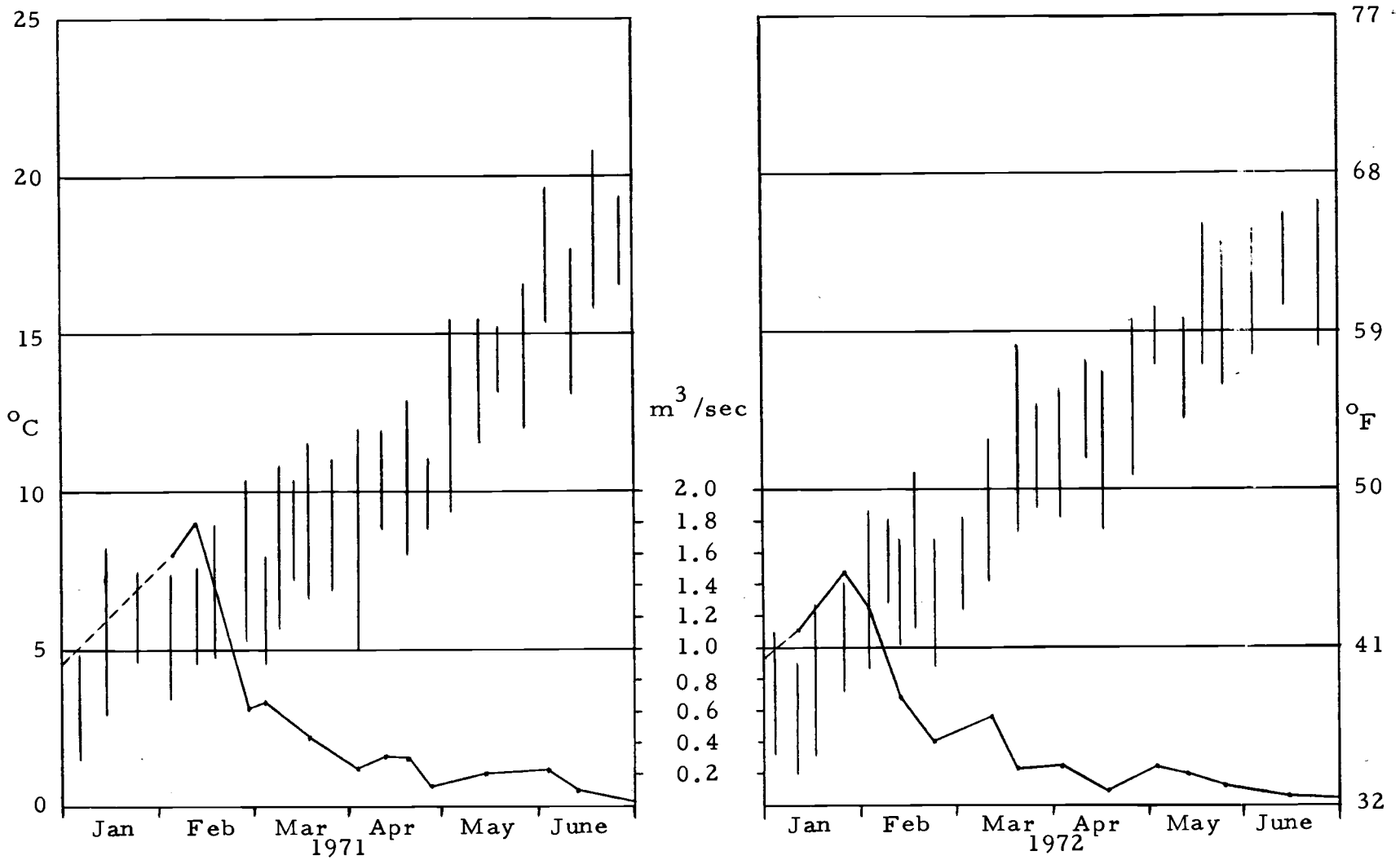


Figure 3. Discharge and weekly range of water temperature at Oak Creek station O-I, January through June, 1971 and 1972.

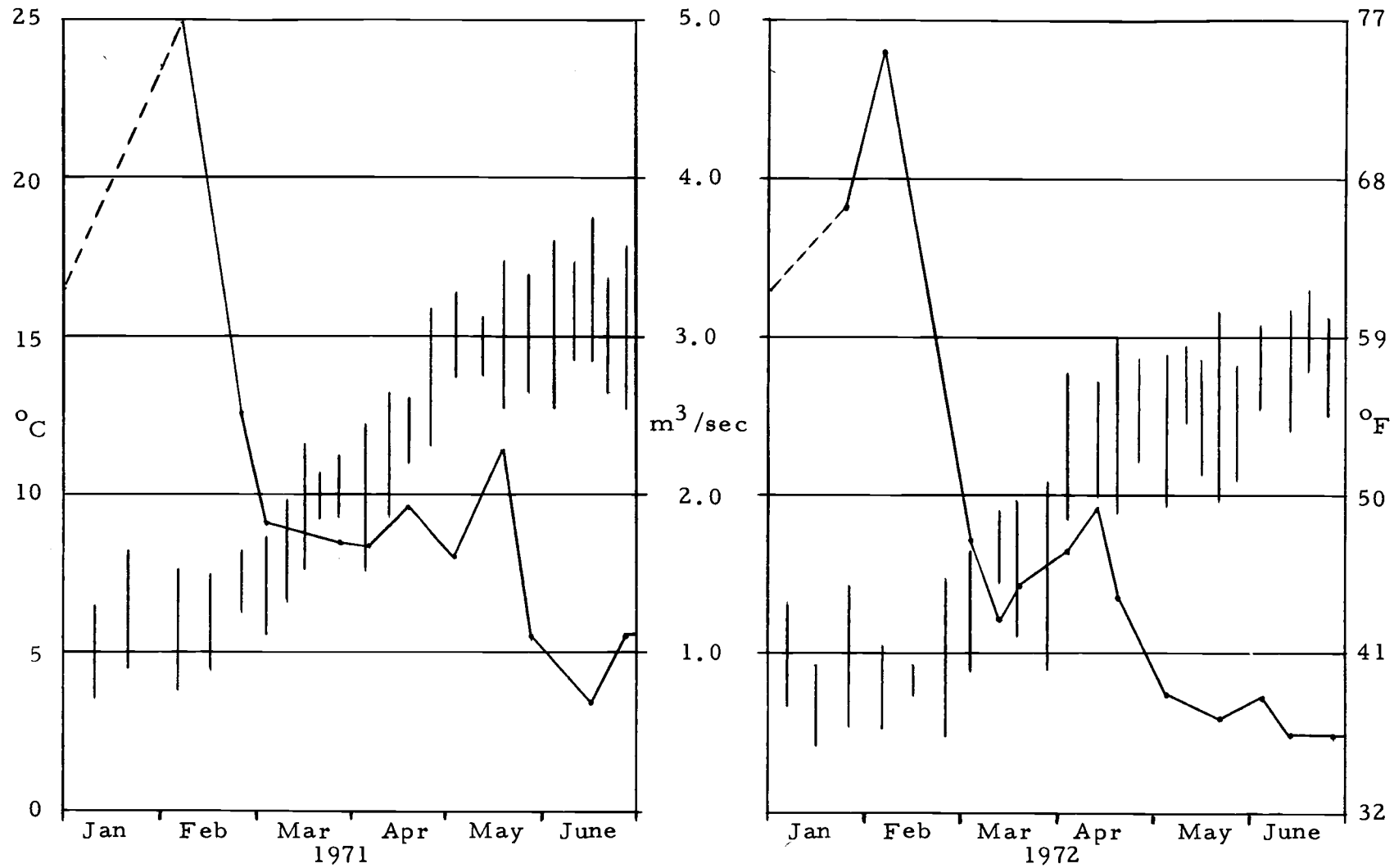


Figure 4. Discharge and weekly range of water temperature at Soap Creek Station S-III, January through June, 1971 and 1972.

temperature and discharge were not measured at the same station on Berry Creek, discharge is not shown in Figure 2. Flow regimes of Berry and Oak Creeks were very similar.

The major portion of each stream studied could be categorized as a rhithron habitat as defined by Hynes (1972) on the basis of temperature, flow and oxygen characteristics. Invertebrate inhabitants may not all have been ideal cold stenothermic forms, but most certainly were characteristic of the lotic situation. An extremely diverse insect fauna has been found to occur in Berry and Oak Creeks (Kraft, 1963; Anderson and Lehmkuhl, 1968; Kerst, 1970; Anderson and Wold, 1972; Wold, 1974). Though little data exists for Soap Creek, it appears to be comparable in most faunal characteristics to the other two.

Plant forms within the streams are also diverse, though dominated by diatoms and a relatively few species of filamentous algae (McIntire, personal communication, 1972: Department of Botany, Oregon State University, Corvallis).

Though some interstream differences occurred between invertebrate and plant forms, all three had a similar fish fauna. The coastal cutthroat trout (*Salmo clarki clarki* Richardson) was by far the most abundant fish, and inhabited pools throughout the research area. Sculpins (*Cottus* spp.) occasionally occurred on riffles. Coho and chinook salmon, and steelhead trout also have been found in all three

streams. None was seen by the author, most likely because population levels remained low.

The underlying substrate for all streams is essentially the same, being a non-permeable rock of volcanic origin (Baldwin, 1959). Riffles are also primarily composed of igneous rubble. Stones vary from coarse-grained gabbro-basalt and agglomerate types to fine-grained forms closely resembling felsite. Rock sizes commonly range from 15 to 75 cm in diameter. Soils associated with the streams are almost all related types of silty clay loam varying in thickness from 68 to 127 cm (Moore, personal communication, 1972: Department of Soils, Oregon State University, Corvallis).

The vegetation surrounding all three streams is very similar, being dominated by second-growth Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), with western red cedar (Thuja plicata Don.), red alder (Alnus rubra Bong.), big-leaf maple (Acer macrophyllum Pursh.), Oregon ash (Fraxinus latifolia Benth.), Oregon oak (Quercus garryana Dougl.), willow (Salix sitchensis Sans.), black cottonwood (Populus trichocarpa Torr. and Gray), and occasional pine, fir, hemlock and dogwood. Principal shrubs along the study areas were currant (Ribes sanguineum Pursh.), service berry (Amelanchier florida Lindl.), salmonberry (Rubus spectabilis Pursh.), thimbleberry (Rubus parviflorus Nutt.) and kinnikinnic (Arcostaphylos uva-ursi Spreng.). Ground cover near the stream banks was

dominated by horsetail (Equisetum arvense L.), fern (Polystichum spp. and Polypodium spp.), and Solomon's seal (Smilacina sessilifolia Nutt.).

Due to shading by the dense overstory, especially in the upper portion of all streams, comparatively little periphyton occurred on benthic substrates. Warren et al. (1964) estimated that from 75 to 90% of all energy introduced into Berry Creek comes in the form of allochthonous leaf material. This is probably a realistic range, and likely holds true for Oak and Soap Creeks. Overstory associated with the lower study portions of all creeks was less than upstream, especially for Soap Creek. Algal growths on rock were heaviest in these downstream areas.

Though allochthonous input was partly in the form of conifer needles, the overwhelming portion appeared to come from deciduous trees. Whereas needle introduction was fairly constant throughout the year (a small peak occurred in August of both years), broad-leaf inputs were primarily restricted to August through November. Initial breakdown was fairly slow, with leaves remaining as introduced for about a month. Processing then proceeded at a fast rate. By the time initial simuliid aggregates appeared, allochthonous material from the previous year was thoroughly distributed in the streams.

Site Selection and Stations

Preliminary stations for initial monitoring were set up late in 1970, and the study sites were selected in early 1971 when black fly aggregates became apparent. The author's experience with life histories and habitat specificities of the simuliids of the region (Speir, 1969, and unpublished data) proved to be extremely helpful in predicting appropriate sites. A concerted effort was made, and was largely successful, to choose sampling locations well away from areas disturbed by fellow biologists or children.

When large numbers of early-instar larvae of one or more study species were detected in a stream area, associated riffles were judged as to overall suitability for sampling. Larvae of most simuliids are not able to tolerate deep-water situations, even if in high-velocity streams (Zahar, 1951). Thus, riffles were used only if in fairly wide, flat beds so that any increases in water discharge would be dissipated laterally and not affect substrate suitability to any great extent.

To be convenient for sampling, the selected riffles were comparatively small, ranging from about 4 to 7 m^2 (Tables 2 and 3). Since a great many different areas of larval activity were initially present, it was possible to choose riffles that were fairly homogeneous as to rock distribution, depth and surface type. The great majority of

study riffles were composed of smooth, fine-grained, ovoid-flat igneous rocks approximately 15 to 45 cm in circumference.

An attempt was made to select relatively isolated riffles with well defined pools at both ends. This was done to simplify the collection and analysis of drift data for individual areas.

Sixteen sampling stations were established in 1971, and 21 the following year (Figure 1; Tables 2 and 3). Study riffles, although at the same general location for both years, were never identical, since it was not known how much impact 1971 sampling would have on the same riffle in 1972. The distance between first and second year riffles was usually about 5 to 15 m. Since larval concentrations were first detected at different times at various locations, subsequent sampling days from place to place were occasionally different, even though the stations may have been close in proximity.

Benthos Sampling and Statistics

The microhabitat to be sampled was the upper surface of fine-grained stones on riffles. At a given site, the maximum surface area (designated as usable substrate) occupied by simuliid aggregates remained relatively constant throughout the larval duration. Even during intervals of rapid growth, when larvae were subjected to crowding, or when high mortality reduced the density, the boundaries of usable substrate remained constant. Estimates of usable substrate

are listed for all stations in Tables 2 and 3 (column 8). Because larval black fly habitat requirements were so obviously limited, areas which would tend to increase population estimator variance if used, such as spaces between rocks, areas too deep or shallow, and substrates of very light color, grainy texture, and/or with very heavy algal growth, were not sampled. As is discussed later, these non-occupied areas are included in area calculations when the data are expressed on a square meter basis.

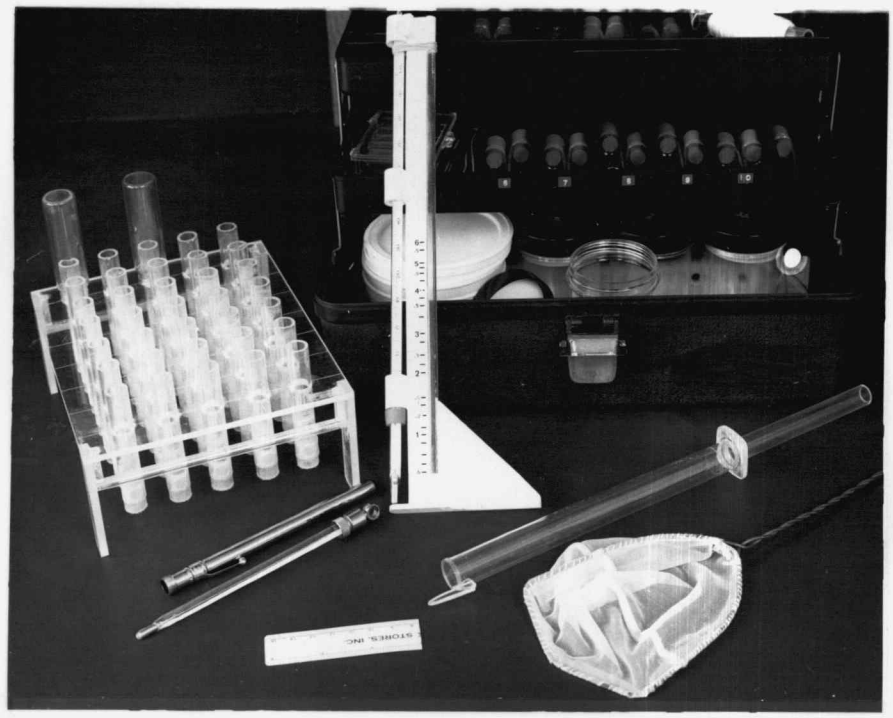
A stratified random sampling program was used to obtain estimates of absolute density of black fly larvae and associated data on mortality and emergence. The wood-framed sampling grid had an area of 6912 cm^2 and was divided into 12 equal-sized strata of 24 x 24 cm (576 cm^2) with twine (Figures 7 through 9). Each stratum was divided into quarters, and each of these further subdivided into 36 units of 4 cm^2 using a movable, plastic-framed sub-sampler. The entire grid contained 1728 of these basic 2 x 2 cm units, which were selected for sampling using a table of random numbers.

The number of samples required for a population estimate error of 15% was determined experimentally. Two 4 cm^2 samples from each stratum (24 samples, 96 cm^2 total) provided the required precision.

Larvae were removed from the substrate within the 4 cm^2 sample units by dislodging them with a special probe into a fine-meshed

Figure 5. Devices used in laboratory experiments and field sampling. From left to right: rearing cylinders with two emergence tubes, thermometer, ruler, pitot tube with thermometer, sampling tube and sampling net.

Figure 6. Artificial stream trough at the Oak Creek Entomology Facility. Water circulation between channels is possible since the longitudinal center-board has large openings at either end. Dark substance coating stream sides and paddlewheel is algae. In the left channel section is a rearing chamber.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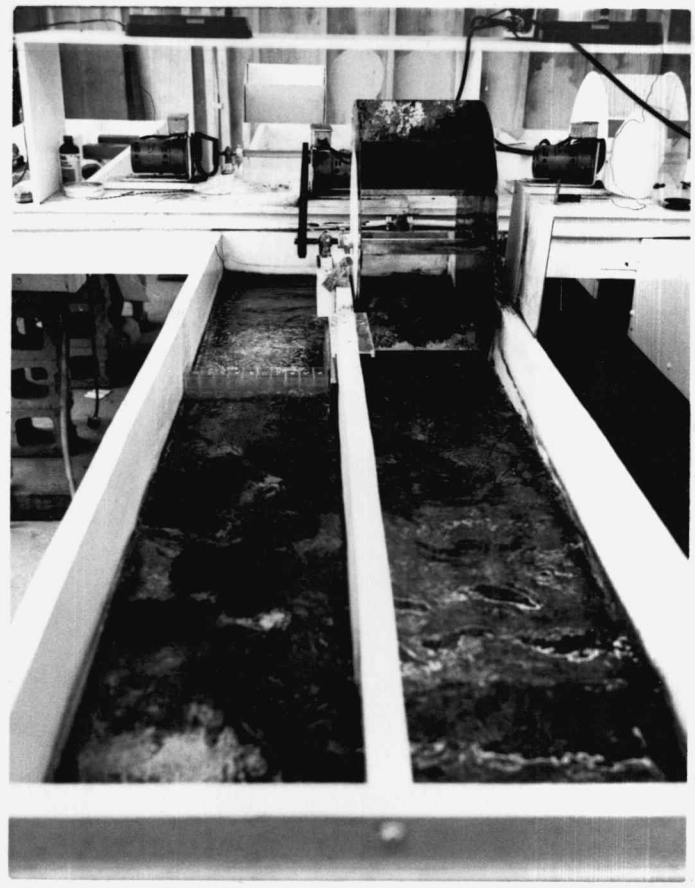


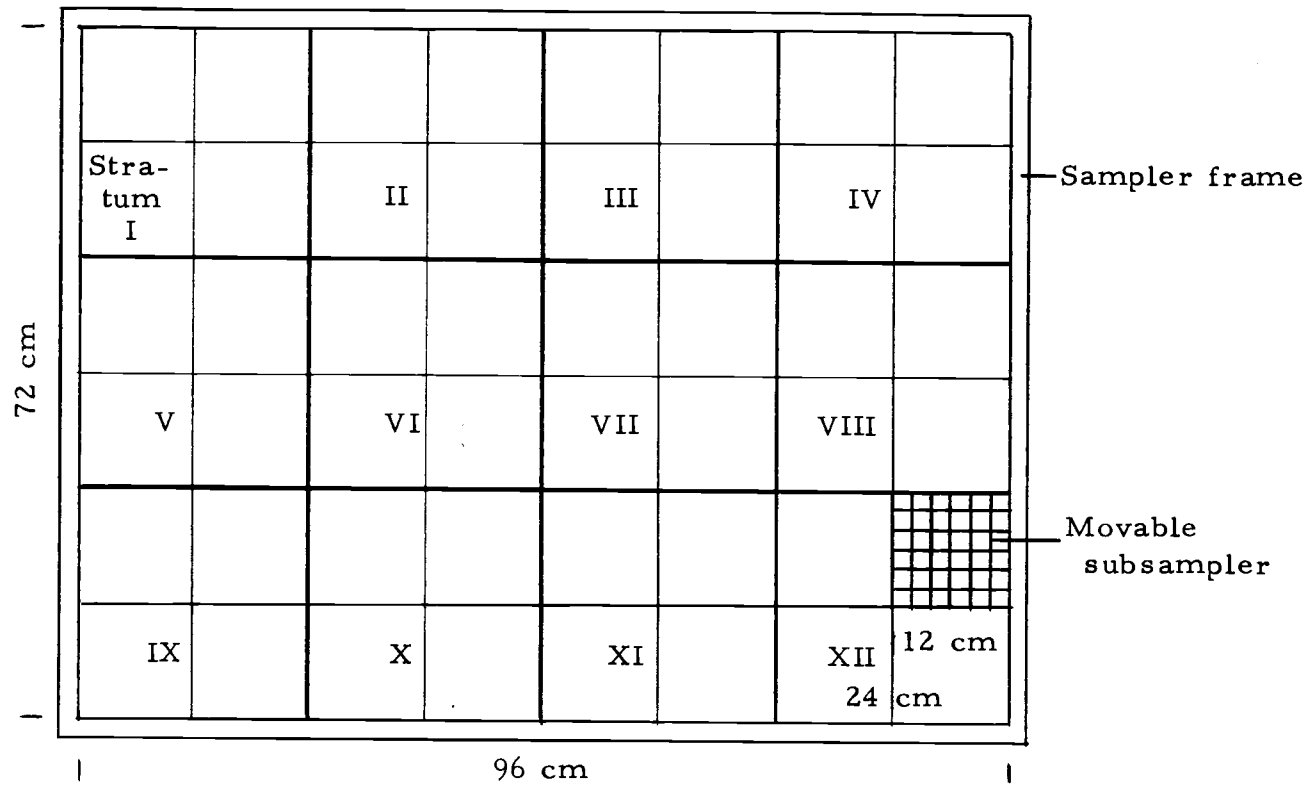


Figure 7. Diagram of stratified random sampling device.

Figure 8. The technique used in sampling black fly larvae during the study. The author is looking through and dislodging larvae with the sampling tube. An immersed net is in position to catch drifting individuals.

Figure 9. The sampling grid in position over a riffle. This is an early sampling model, and does not conform exactly in dimension to the text description. In the water on the right can be seen the downstream drift net.

aquarium net that was either hand-held or fastened immediately downstream from the sample area. The probe was fixed to the sealed transparent end of a hollow plastic tube (Figure 5) so that, in operation, the author could look down the device and dislodge larvae from the substrate within the delineated area (Figure 8). A wire grid placed about 4 cm below the sub-sampler assured that the tube remained vertical and fairly steady even in high velocity currents.

The sampling procedure was initially quite difficult, but with practice, it proved to be both rapid and efficient. Sampling grid location over each study riffle was kept constant with semi-permanent stakes, markings on the suspension ropes and marks aligning the sampler corners to substrate locations.

Data in this dissertation have mostly been presented on a m^2 of overall riffle basis (overall area under the sampling grid). This was accomplished by treating each usable substrate estimate with the appropriate conversion factor characteristic of that station. Only one factor was necessary at a site, since the area inhabited by larvae remained relatively constant. Conversions were produced by dividing usable substrate by the sampling universe area (6912 cm^2) and then expanding the data to a square meter.

Conversions to overall riffle parameters were made in order to present the data in a comparable form to that of other population dynamics and production studies. This was necessary because most

benthic investigations have been made on organisms with less obvious habitat specificity than black flies. Minimal possibilities therefore exist for microhabitat sampling, and data must be expressed per unit of benthos area such as a square meter.

For further comparative purposes, density, biomass and production data are presented in two additional ways: (1) m^2 of usable substrate (area only where the larvae could inhabit) and (2) m^2 of total riffle (total area under the sampler plus the remainder of the riffle).

Notation and formulae (Freese, 1962; Cochran, 1963; Edmondson and Winberg, 1971) for the statistical analysis of the population sampling program used were:

y_{hi} = observed value

N = number of 4 cm^2 unit samples/universe

N_h = number of 4 cm^2 unit samples/stratum

n_h = number of 4 cm^2 samples/stratum ($n_h = 2$)

$\bar{y}_h$ (stratum sample mean) = $\Sigma y_{hi}/n_h$

$\bar{Y}_h$ (stratum true mean) = $\Sigma y_{hi}/N_h$

$S^2_{h'}$ (stratum sample variance) = $\Sigma y^2_{hi} - \frac{(\Sigma y_{hi})^2}{n_h} / n_h - 1$

S^2_h (stratum true variance) = $\Sigma (y_{hi} - \bar{Y}_h)^2 / N_h - 1$

$\bar{y}_{st}$ (population mean) = $\Sigma N_h \bar{y}_h / N$

$$S\bar{y}_{st} \text{ (standard error of } \bar{y}_{st}) = \sqrt{\Sigma(\frac{N_h}{N})^2 \frac{S^2_{h'}}{n_h}}$$

$$T_{st} \text{ (total population)} = \Sigma N_h \bar{y}_h$$

$$ST_{st} \text{ (standard error of } T_{st}) = \sqrt{\Sigma N_h^2 S^2_{h'} / n_h}$$

$$\text{CI (95\% confidence limits)} = \pm 2 \text{ SE}$$

Many of the statistical operations needed in the study were accomplished by the use of teletype-based, interactive and conversational programming modes in the OS-3 computer. Examples of error term calculations using actual station data appear in Appendix I.

Drift and Emergence Sampling

Larval black fly drift off the study riffles was estimated at five stations in 1971 and seven stations in 1972. The drift samplers utilized were wood-framed, and had a bag of about 0.5 m of trailing 333 micron Nitex netting material attached. The rectangular opening of the devices varied; the instantaneous area sampled ranging from 890 to 2154 cm^2. Samplers were placed both above and below each study riffle (Figure 9). Twenty-four hour drift collections were made weekly, generally just before benthos samples were taken.

The total amount of drift sampled per net was determined in conjunction with experiments accomplished in the controlled-flow area of Berry Creek (Figure 1). This location was ideal since fish screens

fitted with fine netting were available for use in early 1971. Drift net catches were mathematically expanded and compared with total numbers of simuliid larvae captured in adjacent downstream screens using Student's t-test. Statistically reliable field estimates usually were derived when drift nets removed 65% to 95% (mean of 88%) of the drift coming from riffles. Conversion factors for estimating total daily drift were thus relatively small, ranging from 1.05 to 1.54 (mean of 1.18). The total number of simuliid larvae entering and leaving each site per week was thereby determined by adjusting the 24 hour catch figures with the calculated percent of drift sampled by each up and downstream net and multiplying by seven. Since drifting larvae came almost completely from the usable substrate area of riffles, calculations converting drift to a per m^2 of overall riffle basis were easily accomplished. Estimates of drift occurring at sites before sampling began were made in the same general way as is subsequently described for production.

Laboratory trials accomplished in 1972 tested the efficiency of drift sampling devices by utilizing frames fitted with the 333 micron netting normally used, and a 102 micron material. The finer nitex bag was oriented downstream on the device. Collections made 12 and 24 hours after Prosimulium spp. egg hatching occurred showed no significant difference in the sampling potential of the two nets. This was, in part, due to the tendency of first-instar larvae to attach to the

333 material, even though they appeared able to pass through. Second-instar simuliids also showed this attachment behavior, but were probably not small enough to clear the net mesh anyway. Losses of larger sized larvae never occurred from the 333 material in laboratory streams.

Upstream movement of simuliid larvae that settled in pools after drifting was investigated using a technique similar to the one described by Elliott (1971b). Sampling nets used were approximately 40 cm long and had openings ranging from 25 to 80 cm^2. The wood-framed entrances were placed facing downstream in both rock and sand-gravel situations. The distal end of each net (mesh of 333 microns) extended upstream, and was attached to the bottom so it could not drift with the current. Each device was allowed to remain at least 12 hours in a location before sampled organisms were removed.

Emergence of black fly adults was estimated by removing and counting pupae rather than from an adult trapping program. The counts were made at 22 sites (8 in 1971 and 14 in 1972) as part of the weekly larval sampling program. Double the area (192 cm^2) was sampled for pupae as was accomplished for larvae in order to minimize errors associated with low densities. The duration of the pupal stage was less than the sampling interval (Prosimulium spp., 0.8 week; Simulium spp., 0.5 week). To compensate for emergence that

would be missed between sampling periods, larvae with black, mature histoblasts were counted as pupae. These individuals were within one or two days of pupation, or about one week from emergence. Pupal and emergence mortality was determined in laboratory stream experiments. These losses were relatively low, ranging from 0.7% to 1.2% (mean of 1.0%). Adult emergence, based on pupal counts and converted to numbers per m^2 of overall riffle, were corrected for pupal and emergence mortality.

Biomass estimates were based on weights of adults that emerged in laboratory streams. The weight loss between mature larvae and adults was calculated for each species under these conditions. Mean larval weights varied between stations. The conversion factor for mature larval weight:adult weight was therefore applied to station-specific larval weights to obtain the appropriate adult biomass at each location.

Caloric determinations made on adults gave the following results, in kcal/g, for 1971 and 1972 respectively: *P. caudatum*, 4.766 and 4.927; *P. dicum*, 4.965 and 4.803; *S. arcticum*, 5.152 and 4.849; and *S. canadense*, 4.870 and 5.316. Conversions to emergence in kcal/m^2 were made using these data.

Biomass and Growth

Field samples were generally sorted within a maximum of five

hours after collection. The larvae were checked for identification and parasites, counted, dried at 55° to 62°C for 24 hours and then weighed. A 24-hour desiccation period always followed drying. Dry weights to 0.01 mg were made using a Mettler Type H-16 balance. Initial counts and corresponding weights were converted to a m^2 of overall riffle basis using the conversion factor of suitable substrate/sampled area calculated for each location.

Dry weight biomass was converted to kilocalories based on determinations obtained with a Parr No. 1411 semi-microbomb calorimeter (methodology similar to Edmondson and Winberg, 1971). Mean values, in kcal/g, for species during 1971 and 1972 respectively were: P. caudatum, 5.286 and 5.013; P. dicum, 5.360 and 4.951; S. arcticum, 4.825 and 4.898; and S. canadense, 5.422 and 5.274. Only one conversion figure was used per species for each year since mean kilocalorie determinations made at various times during the sampling program were almost all within one single error term.

Data in this dissertation primarily have been presented on a weight (g/m^2) basis. Conversions to energy coefficients were accomplished for two reasons: (1) to derive absolute estimates of the amount of energy contained in larvae and adults of all species and (2) to make elaborated standing crop and production data as comparable to other studies as possible. Estimates of drift, emergence, biomass

and production on a kcal/m^2 basis are presented in Appendices IV, V and VIII for all simuliids.

Mean weekly biomass, as grams or kilocalories per m^2 of overall riffle, was calculated as:

$$\overline{B} = \frac{B_1 + B_2}{2}$$

where: B_1 = biomass at time 1

B_2 = biomass at time 2

Variance of the mean weekly biomass term was calculated by using the formula of Chapman (1967):

$$V(\overline{B}) = 1/4\,[V(B_1) + V(B_2) + 2\,\mathrm{cov}\,(B_1\ B_2)]$$

Samples used for B_1 and B_2 estimation were taken independently, so the covariance term was always zero.

Larval growth rates were investigated and determined both in the field and laboratory. Weekly biomass data for each station were used to estimate field growth rate. The mean daily instantaneous growth rate was calculated using the Ricker (1958, 1968) formula:

$$G = \frac{\log_e \overline{w}_2 - \log_e \overline{w}_1}{\Delta t}$$

where: $\log_e \overline{w}_2$ = natural log of the mean weight per larva at time 2

$\log_e \overline{w}_1$ = natural log of the mean weight per larva at time 1

Δt = sampling interval ($\Delta t = 7$)

Laboratory studies on growth were conducted in artificial streams at the Oak Creek Entomology Facility (Figure 6), where the light regime and air and water temperatures were similar to the field situation. The stream water contained adequate food for normal growth, but had a higher level of green algae and diatoms, and less detritus than would occur naturally. Concise descriptions of the indoor channels appear in Warren and Davis (1971).

All four study species were used in experiments at the Oak Creek laboratory. In addition, comparative tests were accomplished on the larvae of *P. exigens* Dyar and Shannon, *S. decorum* Walker, *S. piperi* Dyar and Shannon, *S. vittatum* Zetterstedt, and the large stream forms of *S. arcticum* and *S. canadense*. Laboratory growth rates were calculated in the same way as described earlier.

Production

Estimates of production were derived by using the formula of Ricker (1946, 1968):

$$P = G\overline{B}$$

where: P = production in $g/m^2/week$ ($kcal/m^2/week$)

G = weekly instantaneous growth rate

$\overline{B}$ = mean biomass in g/m^2 ($kcal/m^2$)

The formula of Chapman (1967) was used to provide variance terms of weekly production estimates. This expression was:

$$V(P) = G^2 V(\overline{B}) + \overline{B}^2 V(G) + 2G\overline{B} \text{ cov } (G\overline{B})$$

where: $\text{cov } (G\overline{B}) = r\sqrt{V(G)\ V(\overline{B})}$

and: $r = 0$ if G and $\overline{B}$ are negatively correlated

$r = 1$ if G and $\overline{B}$ are positively correlated

Confidence limits for each production estimate were calculated according to the formula:

$$CI = 2\sqrt{V(P)}$$

where: CI = approximate 95% confidence limits

Weekly production figures for each species on a study riffle were summed, producing estimates for the entire growth period at each station. Production was determined from mid-February to late June in 1971 and from early February to early July the following year.

Related investigations showed that weekly samples accurately estimated the biomass of each successive instar. There was little possibility of consistent larval exuviae loss, so compensatory conversion factors were not necessary.

Since larval concentrations usually were not detected at locations immediately after settling, a method was devised to back calculate production during the time between riffle colonization and initial sampling. Larval growth rates (weight gain in mg/day) were determined in artificial streams for *P. caudatum* and *P. dicum*, and also *P. exigens*, *S. piperi* and *S. vittatum*. The use of non-study species

was necessary to estimate S. arcticum and S. canadense rates, because newly-emerged larvae of these species could not be found. Daily values for the five were averaged since similar. These data were put in a table of weight gain per day for the first seven days of larval development (Appendix II-A). Field sampling always occurred within a week of initial colonization, so the time elapsed between settling and sampling was determined by comparing the mean weight of field-sampled larvae with the growth rate table. This estimate also gave a close approximate time of hatching, since laboratory experiments indicated the drifting period between egg eclosion and settling was extremely short.

Numbers of larvae present on the riffle at initial colonization were found by extrapolating from a smoothed survivorship curve back from the ordinate axis (sampling day number I), to a point described as sampling day number one minus the calculated estimate of first settling (day I-1) (Appendix II-B). This point was determined from Appendix Table II-A. The reliability of this method was tested by back calculating the week one (I) standing crop from the week two (II) data and comparing this result with the known value. Most estimates extrapolated from the curve were within 5% of the actual determination (range of 0.2% to 13.5%). Comparisons between linear regression calculated and sample calculated colonization densities

also were accomplished. These determinations averaged 4.2% in difference (range of 0.3% to 9.1%).

Biomass for the estimated sample was found by multiplying the calculated initial settling number (I-1) by 0.002 mg, the weight of a two-hour old black fly larva. Mean biomass, growth rate and production were calculated by the same methods as previously described. Appendix II provides a complete sample calculation of the pre-sampling technique.

Turnover ratio determinations were made for each species at all stations, and calculated by the formula:

$$TR = P/\overline{B}$$

where: P = annual production in g/m^2 ($kcal/m^2$)

$\overline{B}$ = mean annual standing crop in g/m^2 ($kcal/m^2$)

Food Types and Feeding Experiments

Determinations were made during both years on the types and relative importance of natural foods for all four species. Larvae, sampled monthly from non-study riffles, were identified and dissected, generally while fresh. Gut contents were placed on a microscope slide, thoroughly mixed, and observed using a Zeiss GFL 658 phase-contrast microscope. Algae (keys of Thompson, 1959; McIntire, personal communication, 1971: Department of Botany, Oregon State

University, Corvallis), organic detritus and miscellaneous gut materials were identified where possible. The relative importance of each food type was calculated by expanding counts based on samples delineated by the use of an ocular grid in the microscope.

Experiments were conducted in 1972 to determine the gut clearing rate of all four study black flies in artificial streams at the Oak Creek laboratory and in a small tank in the Entomology Department on campus. This latter system was 0.9 m long, 0.3 m wide and 15 cm deep. Water was maintained at a depth of 6 to 8 cm and recirculated down a 0.4 m long incline situated in the tank using a Gorman-Rupp Type 210 non-submersible pump. The water velocity over the incline was maintained, as a thin sheet of about 4 cm, at about 35 cm/second. The dominant algae in the Oak Creek streams were; Melosira varians Agardh., Oedogonium spp., and Synedra spp., and at the O. S. U. campus; Schizothrix calcicola (Agardh.) Gomont.

Larvae taken from riffles adjacent to sampling stations were allowed to clear all natural food substances from guts, and feed and acclimate for 24 hours in the artificial streams. A large amount of the unicellular green algae, Chlamydomonas spp., was then added to the stream. This provided a marker in the guts of all simuliids present. Larvae were then sampled at about 10 minute intervals and dissected. Gut length and degree of mark advance was measured in 20 to 40 larvae taken at each sampling time. Data were compiled as the

average percent of mark advance/gut length/unit time, and eventually as the mean gut clearing time for the larvae of each species.

Natural Enemies

To determine the density of simuliid predators, two types of examinations were made on riffles of all streams in 1972. In one, organisms inhabiting the upper surface of rocks in 10 to 15 riffles per stream were collected at about one-third and two-thirds through the larval duration of associated simuliids. The other was a more intensive collection of organisms from two riffles per stream to a depth of 15 cm into the bottom. These latter samplings were accomplished at about the mid-point of larval durations. Collections taken by both methods from Berry, Oak and Soap Creeks were from *S. canadense*, *Prosimulium* spp. and *S. arcticum* riffles, respectively. The potential predators were counted, identified, measured and often dissected. Density data were expressed as numbers per m^2 of overall riffle.

Predator impact studies were conducted in laboratory streams in 1972 using all four black fly species as prey. The potential predators used were: *Acroneuria californica* (Banks), *Alloperla fraterna* Frison, *Alloperla* spp., *Calopsectra* spp., *Ephemerella doddsi* Needham, *Hydropsyche* spp., *Isogenus* sp., *Isoperla* spp., *Parapsyche elsis* Milne, *Rhyacophila* spp. and *Sialis californica* Banks. In these experiments, known densities of black fly larvae on field-collected

rocks were placed in laboratory streams and allowed to acclimate. Nitex cages enclosed the substrates, so flows comparable to the natural situation could occur with no loss of larvae. Cage dimensions averaged about 30 cm by 25 cm by 18 cm. When the prey appeared normal in behavior, the predators were placed in non-inhabited parts of the enclosures. Quantitative observations as to predation on the black flies were made at least every six hours for one week. Similar predation experiments were undertaken using simuliid pupae as prey.

Most density, drift and emergence samples were screened to determine the number and type of any parasites encountered. Suspect protozoans and other internal microorganisms of simuliids were identified by the late Ivan Pratt (1972: Department of Zoology, Oregon State University, Corvallis). Nematodes were treated by Nickle (1972: U.S.D.A., Beltsville, Maryland).

RESULTS AND DISCUSSION

Species Composition and Habitat Segregation

Areas of moderate to heavy *Prosimulium* spp. density were fairly well distributed throughout the length of Oak Creek. In Berry and Soap Creeks, concentrations of the two species occurred only in the upstream portions, approximately above stations B-V and S-V respectively (Figure 1). Both *Simulium* species were spottily distributed along the latter two streams. Overlapping occurred only once, this being in the vicinity of station S-II. In this case, the riffle was dominated by *S. canadense* larvae, but a few *S. arcticum* immatures were well interspersed. Small concentrations of the latter species occurred in Oak Creek, but were not investigated.

The locations where immatures of the two genera existed differed substantially. *Prosimulium* spp. larvae were found on elongate riffles, approximately 2 to 5 m in length and separated by pools of comparable or larger dimensions (Figure 10). Original riffle measurements data are given in Tables 2 and 3. The mean dimensions of a typical *Prosimulium* spp. riffle were 4.1 m long and 1.6 m wide.

Riffles where *Simulium* spp. occurred were approximately 1 to 2 m long and separated by even smaller-sized pools (Figure 10). These riffle-pool-riffle areas were from 10 to 15 m long and generally

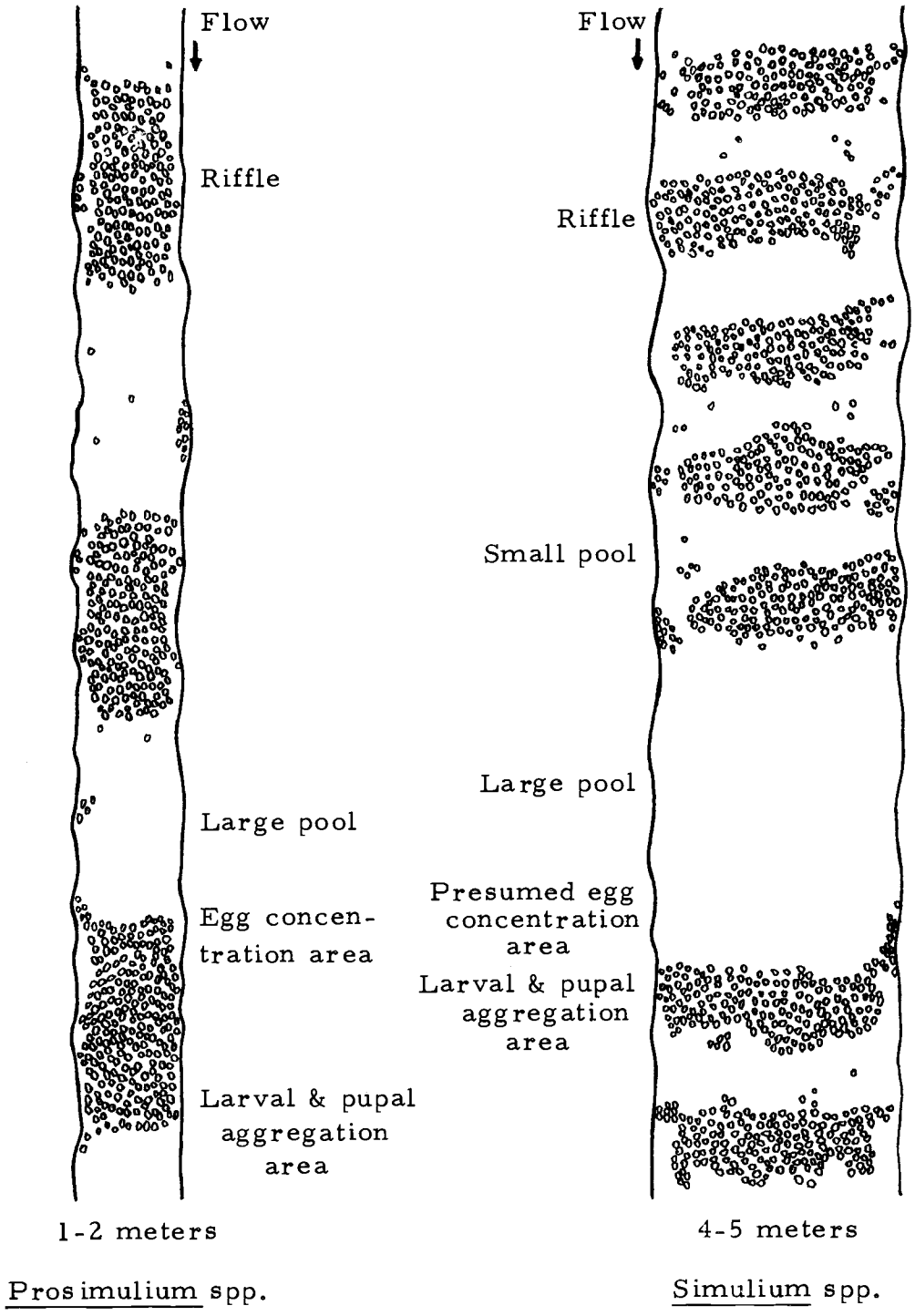


Figure 10. Diagram showing typical Prosimulium spp. and Simulium spp. inhabited riffle situations.

terminated at both ends by deep, elongate pools. The average number of riffles in one of these systems was five. A representative Soap Creek riffle inhabited by S. arcticum or S. canadense would be 1.3 m long and 3.9 m wide. Berry Creek sites averaged about the same in length, but were only 1.8 m wide.

Riffles illustrated in Figure 10 are diagrammatic, though as representative as possible. Prosimulium spp. sites in all streams were as shown. The Berry Creek Simulium spp. situation was generally as illustrated for the other stream, only with riffle widths reduced by about half.

There is some evidence that the species composition of black flies is not static in western Oregon. Oak Creek was one of the streams surveyed in 1967-1968 (Speir, 1969). At that time, only three species of simuliids were collected, P. exigens, P. fulvum and S. vittatum. Later season investigations that may have detected S. arcticum were not made in detail. The two common Prosimulium species in the present study were not detected, which suggests that earlier they were either absent or occurred in very low numbers. The stream has not undergone any obvious physical or biological alterations in the last five or so years which could influence faunal variations.

At the species level, some black flies may be transitory in occurrence, perhaps having a succession of forms dominating in

certain areas over given periods of time (Obeng, 1967). As both Prosimulium species appear to have been in the watershed for well over 20 years (Smith, 1963; Speir, unpublished data), a sudden successional related appearance would be unlikely. Data from many workers on simuliid disease epidemiology in Africa and North and South America indicate the flies are usually stable as to species composition over time (Garnham and McMahon, 1947; Fredeen, 1969).

As apparent for the great majority of animals, cyclic density variations are not only common, but often characteristic (Southwood, 1966). Due either to innate or external influences, the black fly aggregates in question may have fluctuated greatly over time. To date, no supportive evidence has been located in the literature to demonstrate that simuliids undergo cyclic fluctuations. Indeed, it is hard to comprehend of factors which when applied or removed could alter larval densities from being extremely low to overwhelmingly dominant in the span of three or four years.

General monitoring along all three streams indicates that, in the two years since all main aspects of the current investigation have ceased, larval densities within most aggregates have consistently diminished. These reductions have all been minor, probably never exceeding 10% fewer animals per year than the previous season. The consistency of these observations indicates that density fluctuations do

exist, but not to the sudden degree that seems to have occurred between 1968 and 1971.

Life History

Life cycle and density data have been diagrammatically presented for *Prosimulium* spp., *S. arcticum* and *S. canadense* in Figure 11. This information will serve to characterize differences in seasonal duration of the various life stages so that subsequent ecological discussions might have a basis for reference. *Prosimulium caudatum* and *P. dicum* data are combined since both species always coexisted. Egg and initial larval densities are assumed to be equal for all species, since no mortality data were elaborated on ova.

Egg Stage, Overwintering and Oviposition

Prosimulium spp. ova were rarely seen, though all three streams contained abundant concentrations of larvae. A total of 17 *P. caudatum* and six *P. dicum* egg masses were found in the vicinity of station O-IV in early February, 1972. In January, 1973, two additional *Prosimulium* spp. egg groupings were discovered 5 km downstream from station O-I.

All egg masses were white, flattened aggregations, generally round in outline and measuring from 2 to 7 mm in diameter. The

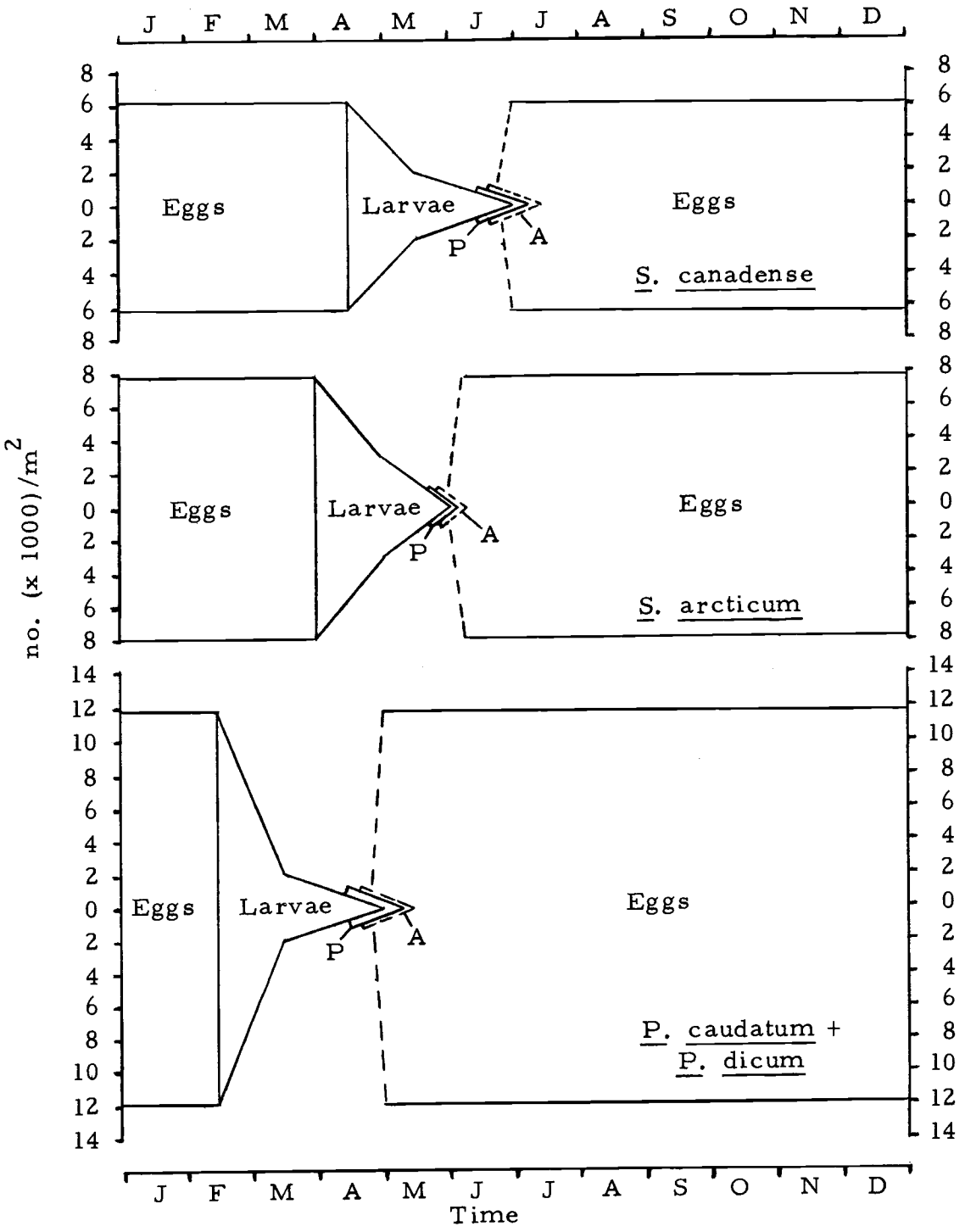


Figure 11. Diagrammatic representation of Prosimulium spp., S. arcticum and S. canadense life cycles and densities. Data have been averaged between all stations and both years. P = pupae; A = adults. Dotted lines signify approximations.

eggs were semi-triangular in shape, and tightly packed in a fairly uniform manner. Both species averaged about 14 ova per mm^2 of mass. Prosimulium spp. egg dimensions are given in Table 4.

Table 4. Black fly egg measurements, in mm.

	No. Examined	Length Range and Mean (mm)	Width Range and Mean (mm)	Depth Range and Mean (mm)
P. caudatum	30	0.33-0.38 0.35	0.15-0.19 0.17	0.09-0.15 0.12
P. dicum	17	0.33-0.41 0.37	0.17-0.21 0.18	0.09-0.16 0.12
S. arcticum	20	0.25-0.33 0.29	0.14-0.22 0.17	0.12-0.17 0.14
S. canadense	20	0.22-0.34 0.26	0.14-0.25 0.16	0.11-0.15 0.12

Egg aggregates were located in the splash zone and madicole region on the downstream side of dark, fine-grained, periphyton-free stones. Prosimulium caudatum masses were constantly found from 5 to 10 cm lower on identical substrates than those of P. dicum. Virtually all egg masses were concentrated on stones located adjacent to the upstream pool of Prosimulium spp. inhabited riffles (Figure 10). These observations suggested that Prosimulium spp. oviposition may have commonly occurred only at comparable substrate locations. Eggs at these sites underwent from 6 to 10 months of desiccation per year, and therefore probably had a diapause.

The great quantities of first-instar larvae that suddenly appeared early in both study years indicated the mass eclosion of overwintering eggs. A total of only 54 P. caudatum and 102 P. dicum larvae were collected in all three streams between July and December, 1971. These third and later instar individuals made up less than 0.001% of the total number of Prosimulium spp. larvae eventually in streams.

The stage or stages in which Prosimulium spp. spends the winter months vary greatly between species and locations (Peterson, 1970b). Speir (1969) determined that P. caudatum overwintered in larger Oregon streams primarily as ova, but that over 1% of the individuals present during the winter months were larvae. The same study indicated that P. dicum overwintering was accomplished only in the egg stage.

Simulium arcticum eggs were never collected, even though locations inhabited by immatures of the species were intensively examined and sampled. Fredeen et al. (1951) found that S. arcticum females commonly deposit ova singly while flying low over stream pools. These workers conclude that, after sinking, eggs become distributed over and within the stream benthos. Measurements in Table 4 are of eggs dissected from females. These ova, though immature, are probably close to the fully developed size.

Since less than 0.0007% of all S. arcticum larvae collected were taken between September, 1971 and February, 1972, overwintering occurred almost entirely in the egg stage in the study streams. Larvae taken during the fall-winter months were third through sixth instar.

It appears that either eggs or larvae, or both, may commonly be the overwintering stage(s) of S. arcticum (Fredeen et al., 1951; Sommerman et al., 1955). In Shotpouch Creek, Lincoln County, Oregon, the species spent the winter fairly equally divided between eggs and early to middle-instar larvae (Speir, 1969).

A total of 36 probable S. canadense ova were taken in a pool dredge sample in late March, 1972, 3 m upstream from station B-V. The eggs were placed in an artificial stream, but failed to hatch. Dissected ova contained larvae which were morphologically identical to S. canadense first instars taken later on riffles. Oviposition behavior may be variable, as Peterson (1959b) observed S. canadense females laying eggs on rocks slightly covered or being sprayed by rapidly moving water. Dimensions of eggs, obtained from the field and laboratory-reared females, are presented in Table 4.

Approximately 0.0001% of all S. canadense larvae were collected in the streams between September, 1971 and February, 1972, indicating overwintering to almost totally occur in the egg stage. Larvae existing during the winter were second to sixth instar. In other locales, winter has been determined to be spent as eggs (Peterson, 1959b) or early to middle-instar larvae (Speir, 1969).

Since both S. arcticum and S. canadense ova were likely located in pools, desiccation was impossible. Though a diapause state almost certainly was reached, low temperature egg development might also have occurred (Fredeen, 1959a).

To date, little can be specifically concluded as to physical and biological factors which influence the oviposition and overwintering of black flies. As more research is accomplished, the situation becomes increasingly complex. Species thought to have one mode of overwintering or oviposition are found to commonly have two or more (Sommerman et al., 1955; Peterson, 1959a, b; Davies et al., 1962).

For both Oregon Prosimulium species studied, substrate plus appropriate associated water conditions appear to have been of major importance in egg laying. Not only were all ova of both found on dark, fine-grained rocks, but estimates showed these areas to be in the water splash zone at the time of oviposition. Conditions necessary for Simulium spp. egg laying may perhaps be much more general than for Prosimulium spp. Riffles associated with presumed oviposition sites of all species were never consistently shaded or open. This indicated that in none were gravid females always positively phototrophic, as was observed by Zahar (1951).

Eclosion Intervals

Larval eclosion generally occurred earliest at the lower

elevation stations where mean water temperature was higher. Station elevations and water temperatures (when taken) have been presented in Tables 2 and 3. Table 5 summarizes hatching date intervals for each black fly by year. Estimates of hatching at each riffle, using the pre-first sampling day technique (I-1), were found to be in error by an average of $\pm$ 1.1 days. Prosimulium spp. eclosion occurred at temperatures ranging from 3.1 to 4.3°C, and Simulium spp. at 4.5 to 9.3°C. Between low and high elevation sites, mean hatching date differences, in days, were: P. caudatum, 13.5; P. dicum, 17.5; S. arcticum, 10.5; and S. canadense, 4.0. Stations of close proximity (200 m or less) had minimal temperature differences. Eclosion date differences at these sites varied by an average of 1.4 days.

Prosimulium dicum hatching followed that of P. caudatum by an average of four days during both years. Simulium arcticum and S. canadense egg eclosion occurred 6 to 7 and 9 to 10 weeks, respectively, later than that of Prosimulium spp.

Delayed egg hatching, as indicated by late arriving first-instar larvae on riffles, was rarely noted. This was true both for ova deposited in masses (Prosimulium spp.) and those possibly buried in stream sediments (Simulium spp.). Only at station B-VI (1971) were any juvenile first-instar larvae (P. caudatum) taken the week after estimated hatching had occurred. In other investigations, simuliid eclosion times have been found to be less synchronized. Speir (1969)

Table 5. Black fly egg hatching dates and durations, and larval stage durations averaged for all stations during 1971 and 1972. Temperature data are only for the time larvae inhabited riffles.

Species	Year	No. Stations	Temp. Range (°C)	Temp. Mean (°C)	Egg Hatching Date (range)	Egg Duration Mean (weeks)	Larval Duration Mean (weeks)
P. caudatum	1971	8	3.1-15.5	8.4	Feb 11-24	40.1	10.6
	1972	9	4.3-15.4	8.4	Feb 2-16	40.4	10.3
P. dicum	1971	8	3.7-15.8	9.0	Feb 15-Mar 6	40.5	10.2
	1972	9	4.3-17.0	8.8	Feb 3-19	40.8	9.9
S. arcticum	1971	6	9.3-18.0	14.5	Mar 27-Apr 9	42.2	9.9
	1972	6	4.5-15.2	12.1	Mar 20-28	42.3	8.7
S. canadense	1971	2	8.0-19.0[a]	10.8[a]	Apr 15	41.1	9.9
	1972	6	7.2-20.6	12.9	Apr 6-13	40.4	10.7

[a]Estimate

Table 6. Laboratory (L) hatching times and durations for *Prosimulium* spp. eggs collected Feb. 2, 1972. Field data (F) are from observations, not collections. Figures utilizing 90% of individuals have been used since hatching occasionally lasted for days.

Mean Water Temp. (°C)	*P. caudatum*			*P. dicum*		
	No. Eggs	Time between Collection & Initial Hatching (days)	90% Hatching Duration (minutes)	No. Eggs	Time between Collection & Initial Hatching (days)	90% Hatching Duration (minutes)
10.5[L]	58	11.2	89	78	16.4	112
9.5[F]		10.4[a]			14.0[a]	
8.2[L]	41	13.1	168	46	15.2	210

[a]± 0.5 day estimate

found newly-hatched larvae of P. caudatum, S. arcticum and S. canadense colonizing riffles for almost two weeks, whereas P. dicum hatching was observed to take less than seven days. As Grenier (1949) has shown for S. nolleri, eggs from a single mass may hatch for as long as 50 days.

Artificial stream experiments using eggs of both Prosimulium species collected at the same time gave comparable results as those of the field (Table 6). Prosimulium caudatum eclosion preceded that of P. dicum by about four days. As these data also indicate, effects of temperature were inconsistent between the two species. While P. caudatum egg development was shortened by higher temperatures (11.2 days: 13.1 days), the opposite was observed for P. dicum (16.4 days: 15.2 days).

Laboratory experiments showed that once hatching had started, it could largely be completed in as little as 90 minutes at temperatures close to those of the field (Table 6). Prosimulium dicum hatching was found to average about 25% longer than for P. caudatum. Water temperature had an apparent effect on eclosion, as duration times at 10.5°C were only about half those at 8.2°C.

Breaking of diapause was probably due to different factors for the two genera. On-site estimates showed that rising waters usually reached desiccated Prosimulium spp. egg masses less than a week before hatching occurred. Prosimulium caudatum ova would hatch

earlier than those of P. dicum, as observed, since they were lower on rocks and came in contact with the rising water first. Simulium spp. egg development initiation was likely more directly related to water temperature changes, since they were always immersed.

Dispersal of Newly Hatched Larvae

Natural colonization was never seen in the field, but observations were accomplished on Prosimulium spp. individuals on a laboratory riffle. First-instar larvae were found to be well distributed over all available substrates and very little clumping was evident 30 minutes after most hatching had been completed. In the text, a distinction will be made between downstream dispersal of newly eclosed larvae ("drift") and downstream movements of individuals in the water column (drift).

Observations made during P. caudatum and P. dicum eclosion and subsequent "drifting" showed that newly hatched larvae do not enter the water column to reach settling sites. All individuals that were able to be followed remained in the 2 to 3 mm thick dead water area that is associated with the flowing water-substrate interface (Ambuhl, 1959). This area not only occurred above the surface of stones, but, in a thickness of up to 6 mm, in between artificial stream substrates. Larvae moved in the dead water area at between 1 and 7 cm/sec (average of approximately 2 cm/sec). The motion was

one of turbulent bouncing. Immatures in the layer appeared to be totally out of control, yet the vast majority were able to attach in apparently "preferred" locations of limited dimension. Many other benthic invertebrates deposit eggs on substrates in a way comparable to simuliids. It would be logical to assume that newly hatched individuals of, for example, Baetis or Agapetus, have similar "drifting" characteristics.

Prosimulium spp. larvae were consistently found concentrated on stones in the extreme lower portions of riffles (Figure 10). Juvenile larvae primarily colonized the same riffles upon which the eggs were deposited. This assumption was strongly supported by the fact that at O-I and O-IV (where ova were found) and at eight other Prosimulium spp. locations, larvae were rarely found on riffles immediately downstream from isolated aggregates. Thus, distances of dispersal were largely limited by the length of riffles on which oviposition occurred. In the study streams, the "drift" distance for the initial colonization was from 3.6 to 5.3 m (mean of 3.9 m). Subsequent drift and reattachment was estimated to take place at very low levels.

"Drift" distances for newly hatched Simulium spp. larvae had to be estimated, since only a few eggs of one (S. canadense) were ever located. Most major pools near Simulium spp. sites were not only large, but had very low water velocities at hatching time. It was

doubtful that juvenile first-instar larvae could traverse up to 10 m of pool bottom in order to reach suitable riffles.

Theoretically, it would have been most advantageous to the successful development of larval aggregates if females consistently oviposited near the downstream end of pools or if eggs drifted comparatively great distances while sinking. In either case, ova would eventually be concentrated near potentially suitable sites. The small aggregate of presumed S. canadense ova was indeed found in the far downstream end of a Berry Creek pool.

In both Berry and Soap Creeks, riffle areas immediately downstream from the largest pools consistently had greatest Simulium spp. larval densities (Figure 10). Assuming that ova were concentrated in downstream pool locations, first instars "drifted" approximately 0.1 to 1.3 m for S. arcticum and 0.1 to 0.8 m for S. canadense before settling. As with Prosimulium spp., little first-instar Simulium spp. "drift" occurred below initial colonization sites.

Prosimulium spp. and Simulium spp. larvae either initially colonized a riffle in a fairly uniform manner, or settled in certain slightly more suitable areas and then quickly moved out laterally over available substrates, or both. With growth, some lateral movements probably took place, otherwise larvae would have been in a more crowded state than was actually observed.

Factors Influencing the Spatial Distribution of Larvae

Larvae of all species were generally well distributed on the upper surfaces of stones in fast-moving water. Principal substrate characteristics have been summarized in Table 7. Though attachment locations varied between species, there were two prerequisites which had to be fulfilled before larvae could colonize and live normally.

1. All stones had to be of very fine grain. Substrates generally exhibited the classical basalt appearance and feel. If matrices were uniform enough, granitic-appearing rock types could be utilized. Only rarely was a small simuliid aggregate found associated with a fine-grained inclusion of a typically coarse-grained rock.
2. All stones had to be dark in color. This characteristic ranged from gray-black to almost jet black. Dark red-orange stones were also utilized. Higher concentrations of *S. arcticum* immatures were found on slightly lighter-hued substrates than were larvae of any other species.

The vast majority of *Prosimulium* spp. and *Simulium* spp. larvae were consistently oriented parallel to the stream flow. This was because most riffles selected for study were generally flat in cross-section and had uniformly even water flows. Grenier (1949) and

Table 7. Habitat characteristics under which black fly larvae existed. Data are averaged for 1971 and 1972. B, O and S = Berry, Oak and Soap Creeks respectively.

	P. caudatum	*P. dicum*	*S. arcticum*	*S. canadense*
Overstory	heavy	heavy	light-moderate[B] light[S]	light[B] light-moderate[S]
Substrate material	rock			
Substrate hue	gray-black			
Substrate texture	fine grain			
Substrate shape	ovoid-flat			
Attached growth	minimal	minimal	periphyton	periphyton
Substrate size range (cm)	2-24	2-24	2-32	6->50
Substrate size mean (cm)	12.5	12.5	12.1[B] 9.5[S]	10.2[B] 13.8[S]
Overall current velocity range (cm/sec)	<3.0-67.1	<3.0-67.1	<3.0-58.5	<3.0-45.7
90% current velocity range (cm/sec)	15.2-45.9	15.2-45.9	13.7-33.2	19.6-38.1
90% current velocity mean (cm/sec)	41.3	40.8	28.3	25.4
Depth range (cm)	<1.0-15.8	<1.0-15.8	2.1-17.6	1.8-14.9
Depth mean (cm)	6.5	6.5	7.1	6.7
Temp. mean during time larvae inhabited riffles (°C)	7.2[B] 8.8[O] 8.4[S]	7.5[B] 9.4[O] 9.0[S]	11.9[B] 13.3[S]	11.4[B] 13.4[S]
Temp. range during time larvae inhabited riffles (°C)	3.1-15.5	3.7-17.0	4.5-18.0	7.2-20.6
6 mo. Temp. range (°C) (Jan-June)	1.0-20.9	1.0-20.9	2.5-19.1	1.7-20.6
Est. temp. mean (°C) at 200 m elevation during late May	14.5	14.5	13.9	15.1

Maitland and Penney (1967) found that a positive relationship exists between laminar water flow and "normal orientation" of simuliid larvae. Occasionally, larval concentrations were found adjacent to small substrate surface cracks, pockets and humps. Though micro-current measurements were impossible, it appeared that velocities were comparatively lower in these areas. Individuals found near substrate "flaws" usually were oriented in a very haphazard manner, perhaps indicating the presence of cross-currents.

For only S. arcticum was a variation noted in where larvae of different sizes were located. Smaller individuals (<4.0 mm) were occasionally found in greater concentrations from 3 to 12 cm upstream on substrates than were the larger-sized larvae. No consistent differences in stream velocity or habitat depth could be detected between the two areas.

Larvae of all species were found to be tolerant of a wide range of water velocity (Table 7). Since pitot tube measurements were least accurate at the upper and lower limits, data excluding the highest and lowest 5% of velocity readings were considered most representative of the natural situation. Simulium spp. larval aggregates were consistently associated with higher stream discharges yet lower water velocities than those of Prosimulium spp. This was primarily due to the physical nature of areas in which immatures were found. Prosimulium spp. larvae were almost always situated on riffles

confined by narrow stream banks. Individuals of Simulium spp. generally inhabited locations of greater width that effectively dissipated velocity. Stream width data for all stations are presented in Tables 2 and 3.

Average depths at which larvae existed varied little between species (Table 7). The pooled mean for all was 6.7 cm. Prosimulium spp. and Simulium spp. individuals usually were found in highest concentrations on the downstream, upper surface portion of stones. This tendency has been reported as being common with larvae of the four species in small and large Oregon streams (Speir, 1969).

Larvae of all simuliid species existed under similar temperature ranges (Table 7). Differences in mean temperatures during periods that individuals inhabited riffles reflects the time of year larvae of each species developed in each stream. It is unlikely that temperature limited the distribution of black flies within and between Berry, Oak and Soap Creeks, because both temperature and altitude ranges (Tables 2 and 3) were so similar for the three streams.

Potential levels of food materials suspended in the water column were never considered to limit the distribution of black flies. All streams had numerous, well distributed riffles (and associated pools) at which suitable water flows and habitat depths occurred during the time of year when colonization would take place. Attachment for larvae of all species was therefore most obviously regulated by the

interaction between available optimum substrate and characteristics of the water. Comparatively few stones of suitable hue and texture were associated with specifically optimum velocity and depth conditions. Colonizing individuals therefore encountered relatively limited areas on which to settle. Nevertheless, sufficient submerged stones were distributed across most riffles where aggregates existed to insure the great majority of colonizing immatures a place to attach. Low first-instar larval "drift" past primary attachment sites corroborated this fact.

The substrate-flow-depth interaction could not account for all areas where larval concentrations did not exist though. Many riffles were found that appeared to have optimum characteristics for black fly inhabitation, yet levels of immature activity remained nil or very low. Obviously, if simuliid oviposition did not occur in these areas, the condition of settling locations was immaterial.

On a generic level, one factor was determined to consistently influence larval distribution. Prosimulium spp. immature stages were never found on substrates with noticeable accumulations of periphyton. Generally, the opposite was true for Simulium spp. A strong positive relationship was found to exist between riffles with attached algal-detritus concentrations and amount of overstory. Suspended algae that commonly collected on rocks throughout all streams could only grow fast enough to keep ahead of grazing

activities in areas with comparatively high illumination. This was apparently also true for any "permanent" periphyton forms characteristic of stream substrates.

Downstream areas of Berry and Soap Creeks where Prosimulium spp. was absent or rare had considerably less overstory than upstream locations. Berry Creek overstory was slightly more dense than at Soap Creek, and consequently more Prosimulium spp. aggregates inhabited riffles in the former stream. Both locations along these streams where Prosimulium spp. larvae commonly occurred had more trees near the banks than did Simulium spp. areas.

In Oak Creek, little relationship could be seen between S. arcticum aggregates and locations of reduced overstory. Since the species was fairly well distributed in small numbers throughout the stream, colonization may have been as complete as possible. Simulium arcticum larvae were probably more tolerant of bare rock substrates than S. canadense, since individuals of the former were often found on less periphyton-covered stones in Soap and Berry Creeks than the latter. The ability of S. arcticum immatures to inhabit areas of comparatively diverse substrate condition (Speir, 1969) may explain why it is so well distributed throughout central and western North America (Stone, 1965).

The few times when Prosimulium spp. occurred on Simulium spp. characteristic sites, immatures of both genera were few in

number and well distributed throughout the riffle-pool-riffle systems (Figure 10). Simulium spp. larvae on Prosimulium spp. riffles were slightly more abundant, and concentrated at the upstream end of the riffles.

Berry, Oak and Soap Creeks all had generally abundant riffles suitable for larvae of both genera, though neither type was ever characteristic of one area of any stream. Pools associated with Prosimulium spp. were of comparable dimension and flow to apparently fulfill Simulium spp. oviposition needs. Potential Prosimulium spp. egg laying sites at Simulium spp. related riffles had similar characteristics to those areas of normal oviposition activity. Many S. arcticum and S. canadense sites had optimum water levels during the times Prosimulium spp. egg laying would have occurred.

The reason why each genus was so closely "tied" to riffles of certain morphology was not determined, but adult behavior may have been involved. Each genus (or species) perhaps had undetected behavioral traits which, along with previously treated physical factors, critically limited potential areas of inhabitation. These might have been especially related to mating or oviposition locations or conditions, since immatures in the water could exist under variable temperature, depth and current influences. If emigration effects from drift and adult activity were minor, as indeed the former was found to be, aggregates of each species probably would remain at or

near the original colonization location as long as physical and biological influences remained tolerable. Assuming flight distances to be minimal, a small "colonization cycle" (Muller, 1954) may have existed for each species at a riffle or a limited section of stream. That is, adults emerged and mated, females flew upstream and oviposited, eggs hatched and resulting larvae "drifted" downstream to settle in areas where pupae eventually would be produced.

Number, Size and Duration of Larval Instars

The mean duration of the larval period, pooled for 1971 and 1972, was (in weeks): *P. caudatum*, 10.4 ± 0.2; *P. dicum*, 10.1 ± 0.2; *S. arcticum*, 8.8 ± 0.3; and *S. canadense*, 10.5 ± 0.4 (Table 5). All four species have six larval instars, at least in the confines of the research area. Figure 12 illustrates the pattern of instar development for *P. caudatum*. Since differences in duration were minimal between instars of both *Prosimulium* species, the figure represents the general pattern for *P. dicum* as well. Head capsule measurements for *P. dicum* averaged, in mm: instar I, 0.09; II, 0.19; III, 0.34; IV, 0.53; V, 0.66; and VI, 0.87. Histograms of head width data are given for *S. arcticum* in Figure 13 and *S. canadense* in Figure 14.

Samples, though rarely synchronized with individual peak instar densities, were taken often enough to provide a generally clear

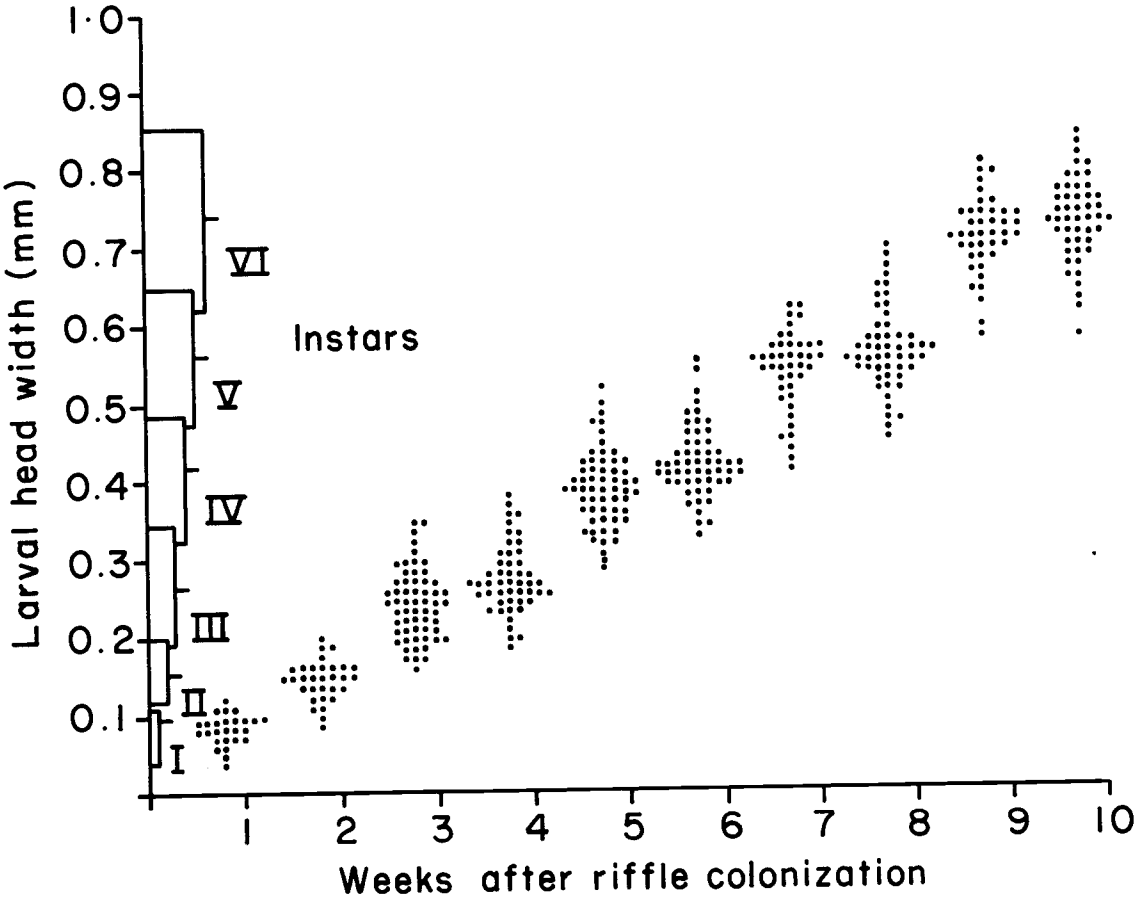


Figure 12. Prosimulium caudatum larval head-capsule width measurements over time. Each point equals two measurements. Range and mean head-capsule data for each instar are given along the ordinate axis.

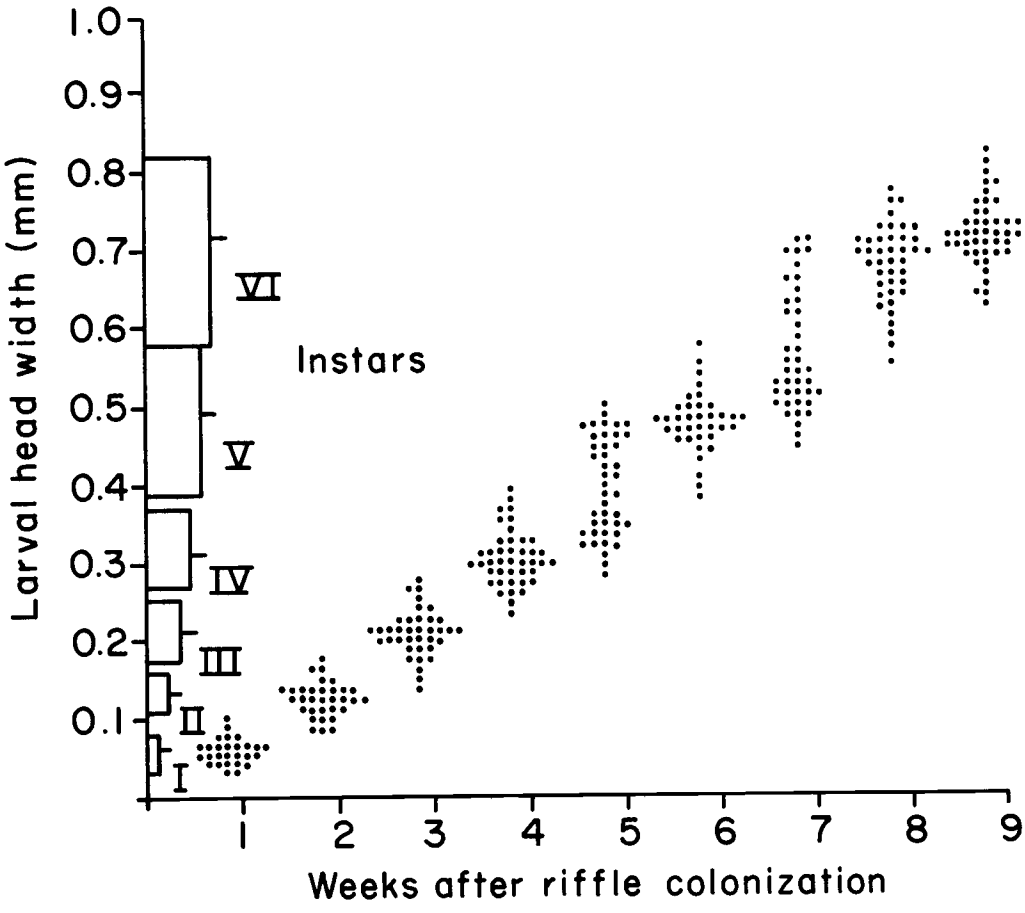


Figure 13. Simulium arcticum larval head-capsule width measurements over time. Each point equals two measurements. Range and mean head-capsule data for each instar are given along the ordinate axis.

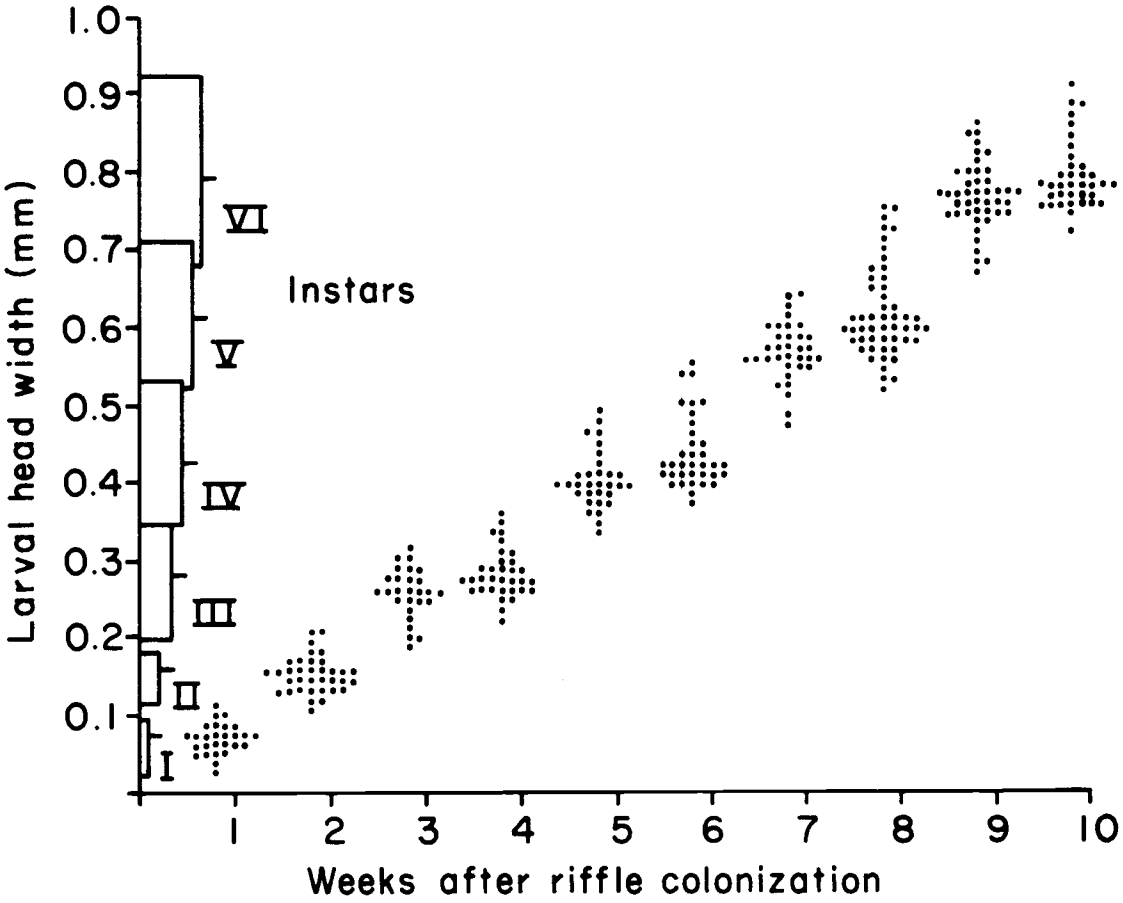


Figure 14. Simulium canadense larval head-capsule width measurements over time. Each point equals two measurements. Range and mean head-capsule data for each instar are given along the ordinate axis.

picture of instar progression. Slight time-related modifications were made on all figures in order to represent, as realistically as possible, characteristic instar development patterns on a weekly basis following colonization.

Length and weight data for instars of all study species are presented in Table 8. Estimates have been averaged between years. First-instar larvae of both Simulium species were consistently smaller and lighter than those of Prosimulium spp. Though shorter in length, final-instar S. canadense individuals exceeded those of P. caudatum by 4.5% in weight.

Both size and weight of the two Simulium species were unexpected, since S. arcticum and S. canadense specimens taken from the Marys River, Benton County, Oregon in 1968 were commonly found to be as much as 20% smaller (Speir, 1969). Prosimulium spp. individuals were of comparable size as ones from other areas of both Oregon and Washington (Speir, unpublished data).

The duration of the final instar of all species was variable in the field. Some individuals pupated about one week after molting, whereas most continued on riffles for at least two weeks. Laboratory observations confirmed that differential durations were not the result of sampling error. Crowding with growth may have commonly occurred in aggregates, but early pupation would not decrease crowding because pupae took up much more space than did mature larvae. Food

Table 8. Larval instar lengths, weights and durations for black flies. All data are averaged for 1971 and 1972.

Instar	Length Mean (mm)	Length Range (mm)	Weight Mean (mg)	Weight Range (mg)	Duration (days)
			P. caudatum		
I	0.9	0.5-1.3	0.006	0.001-0.020	7.4
II	1.7	1.2-2.4	0.028	0.015-0.042	8.1
III	2.8	2.2-3.6	0.092	0.037-0.139	11.8
IV	4.1	3.4-5.3	0.274	0.115-0.324	16.5
V	5.9	5.1-6.9	0.479	0.309-0.537	16.3
VI	7.6	6.5-8.7	0.688	0.503-0.764	15.0
			P. dicum		
I	0.9	0.5-1.2	0.007	0.001-0.022	7.2
II	1.9	1.2-2.4	0.033	0.017-0.056	8.2
III	3.1	2.3-3.7	0.112	0.049-0.168	10.5
IV	4.7	3.4-5.3	0.304	0.150-0.354	14.1
V	6.8	4.9-7.2	0.561	0.337-0.641	16.8
VI	9.1	6.7-10.3	0.851	0.594-0.970	15.0
			S. arcticum		
I	0.7	0.5-1.0	0.004	0.001-0.020	6.8
II	1.3	0.8-1.9	0.025	0.017-0.037	6.5
III	2.4	1.6-3.0	0.084	0.031-0.108	8.2
IV	3.8	2.7-4.5	0.191	0.085-0.219	12.5
V	5.3	4.1-6.4	0.354	0.192-0.423	13.1
VI	7.2	6.0-8.5	0.594	0.391-0.700	14.7
			S. canadense		
I	0.8	0.4-1.1	0.004	0.001-0.019	6.8
II	1.7	0.9-2.3	0.019	0.015-0.044	7.3
III	2.7	2.1-3.5	0.071	0.031-0.123	13.7
IV	4.0	3.3-5.4	0.210	0.117-0.296	13.1
V	5.6	5.0-6.4	0.483	0.264-0.501	15.2
VI	7.4	6.1-8.3	0.719	0.488-0.782	17.5

availability was not considered to be limiting, as potential nutrient levels in streams probably increased throughout larval life periods. Though some black flies have characteristically rapid final instar durations (S. vensutum Say; Davies, 1949), times usually vary little for each species. For the Oregon simuliids, it appeared that development differences were completely random.

Over 84% of all sixth-instar larvae developed at least for one week after molting. Percentages of larvae continuing for the next two weeks were approximately 59 and 41. Though variations did occur, the mean duration times illustrated in Table 8 were considered to be generally representative of the natural situation. When totaled with the durations calculated for the other five instars, the inclusion of the estimated sixth-instar time closely approximated annual riffle inhabitation durations (Table 5).

Initial instar development times were very similar for all species. Averaged instar one and two times, in days, were: P. caudatum, 7.8; P. dicum, 7.7; S. arcticum, 6.7; and S. canadense, 7.1. Maximum durations for Prosimulium spp. were characteristic of fourth or fifth instars, depending on the species. Final instar Simulium spp. were consistently on riffles for longer times than were the earlier instars.

Annual S. arcticum larval durations were about the same as those found for the species in Alaskan streams of similar temperature

(Sommerman *et al.*, 1955). To date, insufficient research has been accomplished on the other three black flies for comparisons to be made.

Larval Feeding

All black fly larvae possessed head fans and were largely filter feeders. The two fans were apparently used in alternation when active feeding was taking place. Time intervals between the opening and closing process varied greatly, ranging from a fraction of a second to over three minutes. A single feeding motion usually was completed in less than one quarter of a second. Laboratory observations indicated that all larvae, especially individuals over 5 mm in length, accomplished the opening-closing process at shorter intervals in slower ($<$ 5 cm/sec) rather than faster ($>$20 cm/sec) current velocities. Feeding actions appeared to be independent of food density or temperature (range of 6.2 to 15.0 ^{o}C).

Using the *Chlamydomonas* marker technique, it was determined that larval gut-filling times were usually less than one hour (Table 9). *Prosimulium* spp. immatures were initially treated separately, but the data indicated the two species were very similar in feeding rates. The mean gut-loading time for *Prosimulium* spp. was 36.5 minutes. Durations averaged 45.9 and 55.9 minutes for *S. arcticum* and *S. canadense* respectively.

Table 9. Alimentary tract clearing rates of black fly larvae, by percentage, in 1972.

Species & Size Range (mm)	No. Experiments	No. Animals	Mean % of Gut Cleared at (minutes)							
			10	20	30	40	50	60	70	80
P. caudatum & *P. dicum* 2.8-9.2	8	225	34.1	65.2	91.2	99.4	100			
S. arcticum 3.6-7.1	4	150	20.8	45.1	73.8	94.7	100			
S. canadense 4.0-7.3	5	155	16.7	38.6	60.6	81.7	91.8	97.5	99.9	100

Table 10. Alimentary tract contents of black fly larvae, by percentage. Data are pooled for all streams and both years.

Species	Size Range (mm)	No. Examined	Mean Detritus (%)	Mean Fil. & Non-diatom Algae (%)	Mean Diatoms (%)	Mean Misc. (%)
P. caudatum *P. dicum*	2.0-9.1	527	89.2	8.4	1.2	1.2
S. arcticum	2.2-7.3	394	66.7	30.6	1.5	1.2
S. canadense	2.0-8.5	283	62.7	34.4	1.5	1.4

These estimates were similar to most of those found in the literature. Ladle et al. (1972), using charcoal as a marker, found Simulium spp. larvae of various sizes commonly exchanged gut contents in from 20 to 30 minutes. Clearing times averaging one hour were determined for Simulium sp. by McCullough (1975). The situation may be far from uniform for all black flies though, as Davies (1949) found that P. hirtipes larvae take as long as a week to empty the gut at 40 to 50 ^{o}F.

Food-passing experiments were accomplished in artificial streams at low, medium and high Chlamydomonas concentrations (as judged by the intensity of the color) and temperature (range of 6.8 to 14.1 ^{o}C). Larvae represented the final four instars of all species and ranged in length from 2.8 to 9.2 mm. A few second-instar individuals were also utilized. Food density, temperature and larval size variations had no consistent effect on feeding rates.

The quantity of particulate material processed by black fly larvae was calculated by integrating the field density estimates with data on gut loading times and gut dimensions. Assuming food to be abundant throughout the larval duration, the suspended algal and detrital material processed by an average-sized aggregate was: P. caudatum, 164 g; P. dicum, 178 g; S. arcticum, 184 g; and S. canadense, 151 g dry weight per cohort life. These figures are about 20% the estimates derived for S. equinum L. and S. ornatum Meigen

by Ladle et al. (1972). During times of maximum inhabitation, densities of the two species in England were as much as 20 times greater than those of Oregon black flies. The difference between processing estimates in the two studies was almost completely nullified when simuliid populations were put on a par.

Results of gut-content analyses are given in Table 10. Black flies tend to be non-selective in their feeding, so gut contents are representative of the proportions of suspended materials that are available. Detritus was always the major food component in the guts, while the proportion of algae tended to increase from January through June. Prosimulium spp. in Soap Creek was an exception in that the amount of algae ingested did not increase. This was apparently because the riffles in upper Soap Creek were heavily shaded, and there was no marked increase in algae late in the season.

The proportion of algae consumed by Simulium spp. was significantly greater than that of Prosimulium spp. (Table 10). In part this may be due to the earlier occurrence of Prosimulium spp. (before the spring bloom of algae), but it is also related to behavior. Simulium spp. larvae were consistently found on substrates that had abundant algae, whereas Prosimulium spp. larvae were not. Peterson (1956) has observed that Simulium spp. larvae may supplement filter feeding by scraping algae from the substrate. This behavior was observed in my artificial streams and may account for

the fact that, compared with Prosimulium spp., the guts of Simulium spp. contain not only a greater quantity of algae, but also a greater variety of typically benthic species (Table 11).

Data in this table are pooled between 1971 and 1972 as no consistent floral differences were detected in larvae between years. Chaetophora spp. or Stigeclonium spp. and Oedogonium sp. were by far the most abundant algal forms in Simulium spp. guts in both Berry and Soap Creeks. Principal Prosimulium spp. alimentary tract contents were Palmella spp. and a complex of approximately six diatom taxa.

These differences in alimentary tract contents indicated an algal-based food particle size preference existed for the two genera. The great majority of algal materials in mature Prosimulium spp. guts averaged in the 5 to 30 micron range, whereas particle sizes ingested by Simulium spp. were approximately 20 to 70 microns. This was an especially interesting observation, considering mature Prosimulium spp. larvae are usually larger and more robust than Simulium spp. immatures (Table 8). The cibarial measurements accomplished on representatives of the four species indicted "mouth" and length parameters were closely related in a positive manner. In spite of average differences, minimum and maximum plant pieces were about 5 microns (diameter) and 200 microns (long) for both genera.

Table 11. Algae contained in the alimentary tracts of black fly larvae in 1971 and 1972. + = uncommon; ++ = common; +++ = abundant; A = all streams; B, O and S = Berry, Oak and Soap Creeks respectively.

	P. caudatum *P. dicum*	*S. arcticum*	*S. canadense*
Bacillariophyta			
Achnanthes spp.	+A	+BS	+BS
Cocconeis sp.	++BS	+B	+B
Fragilaria spp.	++OB	+B	+B
Gomphonema spp.	+A	++BS	++BS
Melosira spp.	+A	+S	
Navicula spp.	++A		
Nitzschia sp. #1	++A		
Nitzschia sp. #2		++BS	++BS
Rhoicosphenia sp.			++B
Surirella sp.	+A	+BS	+BS
Synedra spp.	+A	+BS	+BS
Tabellaria sp.	+S	++BS	++BS
Chlorophyta			
Chaetophora spp. or *Stigeclonium* spp.		+++BS	+++BS
Chlamydomonas spp.	++A	++BS	++BS
Cosmarium sp.	+B	+B	+B
Microspora spp.		++S	+S
Oedogonium sp.	++A	+++BS	+++BS
Palmella spp.	+++OB	+B	+B
Spirogyra sp.		++S	+S
Ulothrix sp.	++A	++BS	++BS
Chrysophyta			
Tribonema sp.	+S	+BS	+S
Cyanophyta			
Oscillatoria spp.		+S	+S
Schizothrix sp.	+A	+S	+B
Rhodophyta			
Batrachospermum sp.		+S	

Most detritus appeared to have originated from the leaves of deciduous trees, although the shredded conditions encountered made determinations difficult. The ratio of broad leaf to evergreen components in alimentary tracts was estimated to average 14:1 by volume for all species. Miscellaneous substances were, in order of decreasing importance, sand and silt grains, wood fragments, remnants of arthropod sclera and appendages, and caddisfly wing scales.

No consistent differences in particle sizes of ingested detritus were noted between Prosimulium spp. and Simulium spp. larvae of comparable size. Most particles in the guts ranged from 10 to 250 microns in diameter, with the average being approximately 45 microns. Ingestion of long pieces of detritus and algal filaments was observed occasionally, especially in larvae over 5 mm in length. These strands were sometimes one-fourth as long as the alimentary tracts in which they were found.

Sand and silt levels in the guts remained generally constant for all species. Larvae examined after stream silt loads were high had particle levels similar to individuals sampled at normal load periods.

Food availability was never considered to be limiting because, throughout the season, all larvae that were dissected had completely full alimentary tracts. Food materials in the foregut were usually packed in a much more concentrated manner than the rest of the alimentary tract. Often, the anterior part of the gut was noticeably

expanded with its contents. Normal dimensions returned when food materials were allowed to leave via a slit in the midgut. Individuals sampled at lower elevation sites had food percentages generally comparable to larvae from highest altitude locations.

Longitudinal breakdown of gut contents was almost non-existent in larvae of all species. Even under high magnification (+950X), the appearance and number of particles in the foregut and hindgut changed little. Kaushik and Hynes (1971) have shown that stream debris, especially leaf detritus, often has abundant bacterial and fungal growths associated with it. Nutritional needs of simuliid larvae were possibly fulfilled by algae and leaf detritus, accompanying microorganisms, or a combination of both. The fact that black fly larvae are able to successfully exist and develop on a diet of bacteria has been demonstrated by Fredeen (1964). This does not mean that the normal nutrient source in the natural environment is bacteria or fungi, though food breakdown data from the current study suggests this to be a strong possibility.

Larval and Pupal Associates

Table 12 lists benthic insects that coexisted with simuliid aggregates. Organisms designated as common were abundant on some or most riffles at one time or another. Uncommon forms occurred in densities of about 5 per m^2. Since the two *Prosimulium*

Table 12. Benthic insects associated with black flies in 1971 and 1972. + = uncommon; ++ = common; A = all streams; B, O and S = Berry, Oak and Soap Creeks respectively.

	P. caudatum P. dicum	S. arcticum	S. canadense
Ephemeroptera			
Baetis bicaudatus Dodds	++A	++BS	++BS
B. tricaudatus Dodds	++OS		+BS
B. sp. #1	++O		
B. sp. #2		+S	
Cinygmula reticulata McDunnough		+BS	+B
C. sp.	+BS		+S
Epeorus spp.	+OS	++S	+S
Ephemerella doddsi Needham	++A	++BS	++BS
E. spp.		+B	
Paraleptophlebia temporalis (McDunnough)	+BO	++B	++B
P. sp. #1	+O		
P. sp. #2		+S	+S
Rhithrogena sp.			+BS
Plecoptera			
Acroneuria californica (Banks)	++A	++BS	++BS
Alloperla coloradensis (Banks)	+BO		+B
A. fraterna Frison	+O	+S	+BS
A. sp. #1	+B	+BS	+BS
A. sp. #2	+S	+S	
Brachyptera sp.			+B
Capnia porrecta Jewett	+O	+S	
C. projecta Frison	+BO	+B	+B
C. sp. #1		+B	
C. sp. #2		+S	+S
Eucapnopsis brevicauda (Claassen)	+O		
Isoperla mormona Banks	+O		+B
I. trictura (Hoppe)		+S	+S
I. sp.	+BO	+B	
Leuctra sara Claassen	+BO		
L. sp.		+S	

(Continued on next page)

Table 12. (Continued)

	P. caudatum P. dicum	S. arcticum	S. canadense
Nemoura californica Claassen		+B ++S	
N. cinctipes Banks	+B		
N. cornuta Claassen		+B	+B
N. sp.	+OS		
Peltoperla brevis Banks	+O		
P. sp.		++S	
Megaloptera			
Protochauliodes sp.		+S	+S
Sialis californica Banks	+A	+BS	+BS
Coleoptera			
Ectopria sp.	+BO	+B	+B
Lara avara Le Conte	+B	+S	
Narpus concolor Le Conte	+BS	+BS	+BS
Psephenus sp.		+S	+S
Trichoptera			
Agapetus bifidus Denning	+B		+B
Glossosoma penitum Banks	+BS	++BS	+BS
Hydropsyche spp.	++A	++BS	++BS
Micrasema dimicki (Milne)		+S	+S
Neophylax rickeri Milne		+S	
N. splendens Denning		+S	
Parapsyche elsis Milne		+B	+BS
Polycentropus sp.		+S	+S
Psychomyia lumina (Ross)		+B	
Rhyacophila spp.	++A	++BS	++BS
Diptera			
Agathon canadensis (Garrett)		+BS	+BS
Bibiocephala grandis Osten Sacken			+B
B. sp.	+OS	+S	
Calopsectra spp.	+S ++BO	++BS	++BS
Chironomidae (unidentified)	+A	+BS	+BS

(Continued on next page)

Table 12. (Continued)

	P. caudatum P. dicum	S. arcticum	S. canadense
Dixa spp.	+A	+S	+BS
Heptagyia sp.	+S	+S	
Maruina lanceolata Kincaid		+BS	+BS
Prosimulium exigens Dyar and Shannon	+O		
P. fulvum (Coquillett)	+S		
Simulium piperi Dyar and Shannon		+B	+B
S. pugetense Dyar and Shannon		+BS	+S
S. vittatum Zetterstedt		+B	+BS

species existed together, associated organisms were the same for both.

At least 2 alderflies, 13 mayflies, 23 stoneflies, 5 beetles, 13 caddisflies and 18 true flies were associated to one degree or another with larvae and pupae of the four simuliid species. Baetis bicaudatus and Rhyacophila spp. were the only organisms always found on riffles inhabited by black flies. Other consistently common forms were Acroneuria californica, Calopsectra spp., Ephemerella doddsi and Hydropsyche spp. (with all four simuliids) and Glossosoma penitum (with S. arcticum). Larvae and pupae of Prosimulium exigens and P. fulvum were occasionally found in small numbers intermingled with individuals of the other two Prosimulium species in Oak and Soap Creeks respectively. Four other black fly species were associated with S. arcticum and S. canadense, but occurred at very low densities.

Black flies were always the dominant organisms on all study riffles, exceeding the most numerous associates like Baetis bicaudatus or Calopsectra spp. by from 15 to over 280 times. Between weeks three and six of larval development, there was about 100 times more simuliids than the most abundant single species and 20 times all associated forms. Black fly biomass usually exceeded that of all other riffle inhabitants by a factor of 2 to 14, with the mean being approximately 7.

Though many taxa often differed between Prosimulium spp., S. arcticum and S. canadense riffles, relative numbers and biomass were generally constant. This was primarily due to the overwhelming dominance of a few species at the majority of research sites. Of the approximately 10 insect species that were found at most study sites in the three streams, nine are considered carnivores in the literature and are treated as such in the subsequent section on predators.

The most numerous non-insect invertebrates on riffles were snails and triclad flatworms. Physa sp. was found in its greatest densities in Soap Creek, whereas Oxytrema spp. occurred in similar concentrations in all three streams. Densities averaged 0.9 snails per square meter. Gut analyses showed that these gastropods feed on periphyton and were of no apparent direct or indirect threat to black fly immatures. Individuals of Phagocata spp. and Polycelis spp. ranged from 2 to 18 mm in length. They were quite uniformly distributed throughout the riffles, averaging about 15 worms per square meter. The latter was about eight times more abundant than the former.

Predator Studies

Cutthroat trout and other pool-inhabiting fish primarily feed on drifting invertebrates. Since discussions in this section are more riffle related, most fish will be treated in the drift portion of this dissertation. Sculpins (Cottus spp.) occasionally frequented riffles in

all three streams. With the use of a flexible plastic tube, the great majority of gut-content material was removed from two of these fish associated with Prosimulium spp. riffles. No simuliid larval or pupal fragments were found.

Flatworms were not treated in detail during this study, even though they are often carnivorous. Since sizes were small (mean length of 8 mm) and densities low (mean of 15/m^2), the impact of these organisms was considered minor. Macan (1963) theorizes that Polycelis spp. may be an important egg predator to stream invertebrates like Prosimulium spp. which have vulnerable masses of ova. This is probably true though only when flatworm densities are exceptionally high in eutrophic situations.

The density of potential invertebrate predators was sampled in all three streams by both rock-surface collections and by deep-substrate riffle collections as described in the Materials and Methods section. The two techniques gave similar estimates of the number of predators on rock surfaces, and were therefore averaged. The more intensive method was required only for Sialis californica, since the larvae occurred buried to several centimeters into the stream bottom.

As demonstrated by gut-content analyses, immatures of Acroneuria californica, Ephemerella doddsi, Hydropsyche spp., Rhyacophila spp. and Sialis californica consumed black fly larvae under natural conditions. Densities of these species are listed for

riffles of P. caudatum and P. dicum (Oak Creek), S. arcticum (Soap Creek) and S. canadense (Berry Creek) in Table 14 ($\overline{D}$ columns). Alloperla fraterna, A. spp., Calopsectra spp., Isogenus sp., Isoperla spp. and Parapsyche elsis were the potential predators which did not feed on simuliid larvae in the field or laboratory.

Under natural conditions, it could never be determined how simuliid fragments came to lodge in alimentary tracts of examined animals. Specific identification of ingested pieces of black fly larvae was found to be impossible since most were badly broken up. This prevented any conclusions as to the extent of multiple feeding. Both laboratory and field data indicated that simuliid larval cannibalism, which Peterson and Davies (1960) have recorded, did not occur.

Food consumption by the predators associated with black fly aggregates was tested in artificial streams. Of the five species that naturally consumed simuliid larvae, only Hydropsyche spp. immatures failed to feed in the laboratory. Currents in experimental enclosures were likely too low to facilitate the normal behavior of these caddisflies. Predation on black fly pupae did not occur.

Feeding experiments are summarized in Table 13, with the taxa ranked in order of increasing predation ($\overline{N}$ column), top to bottom. All four simuliid species have been pooled, since statistically significant differences did not exist between experiments conducted on each at high and low densities.

Table 13. Predator feeding on black fly larvae in artificial streams, 1972.

Predator (Length)	Day 1		Day 2		Day 3		Day 4		Day 5	
	P	C	P	C	P	C	P	C	P	C
E. doddsi (13-15 mm)	224	2	222	0	222	1	221	0	221	2
A. californica (16-19 mm)	272	9	263	9	254	7	247	10	237	10
Rhyacophila spp. (12-14 mm)	350	19	331	16	315	13	302	18	284	14
S. californica (17-29 mm)	446	27	419	24	395	24	370[a]	18	332	20
Control	250	-	250	-	249[a]	-	249	-	248[a]	-

	Day 6		Day 7		Day 8		$\overline{N}$
	P	C	P	C	P	%	
E. doddsi	219	1	218	0	218	2.7	0.1
A. californica	227	7	220	11	209	23.2	1.5
Rhyacophila spp.	270	14	256	15	241	31.1	2.6
S. californica	332	24	308	20	288	35.2	3.7
Control	248	-	248	-	248	-	-

P = no. of black fly larvae (4.0-7.0 mm) present/day
C = no. of black fly larvae consumed/day
a = dead black fly larva
% = percent of initial larvae consumed
$\overline{N}$ = mean no. of black fly larvae consumed/day

A consistent diel feeding habit was noted only for S. californica larvae, which fed at about a 20% higher level at night. This characteristic has been noted for sialids by Evans (1972).

The tendency for black fly larvae to release from the substrate to escape capture was low. Laboratory and field observations on non-predaceous invertebrates moving about over simuliid aggregates showed that, upon the 237 contacts made, an average of 85% of the larvae left the attachment surface. The resulting downstream movement was followed by a return to the same general departure location for about 99% of the individuals, since silk had been employed upon release. Of the thousands of larvae mechanically disturbed into drifting during population sampling, approximately 2% accomplished the procedure without a silk strand. Considering the two forms of evidence, it is assumed that larval black fly losses by predators are due almost wholly to consumption. Carnivore-caused drift mortality may be as high as 2%, but likely is lower.

By integrating field predator densities with laboratory feeding data, daily and monthly predation impact estimates were derived (Table 14). Species have been arranged according to increasing consumption contribution (%T_m, column), top to bottom. The Hydropsyche spp. consumption figure was obtained by noting that each individual contained an average of one simuliid larva and assuming the caddisfly gut was changed once per day. The data of Cummins (1973)

Table 14. Calculated impact of predation on field populations of black fly larvae, 1972.

Predator (Length)	$\overline{N}$	Oak Creek $\overline{D}$	Oak Creek C_m	Soap Creek $\overline{D}$	Soap Creek C_m	Berry Creek $\overline{D}$	Berry Creek C_m	$\%T'_m$
E. doddsi (4-19 mm)	0.1	3.0	9.3	1.8	5.6	3.8	11.8	0.5
A. californica (4-37 mm)	1.5	2.3	107.0	3.1	144.2	3.0	139.5	7.5
S. californica (15-24 mm)	3.7	2.0	229.4	5.0	573.5	3.5	401.5	24.3
Hydropsyche spp. (5-13 mm)	1.0	21.1	654.1	10.8	334.8	13.1	406.1	25.5
Rhyacophila spp. (5-14 mm)	2.6	12.9	1039.7	3.6	290.2	14.0	1128.4	42.2
T_m			2039		1349		2087	
T_D			65.8		43.5		67.3	

$\overline{N}$ = mean no. of black fly larvae consumed/day
$\overline{D}$ = predator density/m^2
C_m = no. of black fly larvae consumed/m^2/month/predator
T_m = total no. of black fly larvae consumed/m^2/month
T_D = mean no. of black fly larvae consumed/m^2/day
$\%T'_m$ = mean percent consumption contribution/predator

and McCullough (1975) indicate this gut-loading time to be a realistic estimate.

Despite variable predator densities, consumption impacts (Table 14; T_m, T_d) between streams were remarkably similar, especially for Berry and Oak Creeks. This was primarily due to the compensatory nature of the carnivores between streams. For example, losses in Berry Creek due to S. californica were generally equalized in Oak Creek by Hydropsyche spp. Low Soap Creek losses due to Rhyacophila spp. were partially compensated for by S. californica larvae, but not enough to make the situation closely comparable with the other two streams. Further discussion on the impact of predators is given in the Dynamics and Mortality of Black Fly Aggregates section.

Parasite Studies

The only parasites found in the body cavity of black fly larvae were nematodes of the genus Gastromermis. It could not be determined whether more than one species was present (Nickel; personal communication, 1972: U.S.D.A., Beltsville, Maryland). Of the over 1000 pupae and adults examined, none ever contained a worm. Although hydrachnellid mites were occasionally found in samples, none could ever be implicated as being parasitic on black flies.

Nematodes were present in simuliid larvae about 4 mm or more in length. Actual minimum sizes affected were: P. caudatum, 4.1 mm; P. dicum, 4.4 mm; S. arcticum, 3.7 mm; and S. canadense, 4.1 mm. Nickel (1972) determined that many aquatic insects acquire parasites through the process of feeding. Smaller simuliid larvae did not ingest worms probably because the feeding fans or mouth was too small. Nematodes of from 0.1 to 3.5 mm in length were certainly available for consumption, as plankton net samples taken from late January, 1971 to mid March, 1972 determined. As black flies grew, capture and ingestion of parasites was likely facilitated, causing the observed infection level increases over time in larval aggregates.

The sudden appearance of sixth-instar black fly head capsules in laboratory and field drift collections resulted from mature worms leaving the body cavity of hosts. Only the sclerotized head occurred in drift samples because, after death, the abdomen remained attached to the substrate and disintegrated in the current. Since the vast majority of drifting head capsules originated from final-instar simuliid larvae, host and parasite life cycles were likely as closely synchronized as has been found for other black flies and mosquitoes (Welch, 1962; Peterson et al., 1968).

Gastromermis infection levels were generally similar in larvae of all four species, ranging from 0.5% to 6.5% (Table 15). Original data are located in Appendix III. Only maximum infection percentages

Table 15. Maximum percentage parasitism of black fly larvae by *Gastromermis* in 1971 and 1972.

Species	Stream	1971	1972
P. caudatum	Berry		3.3
	Oak	4.1	3.4
	Soap		6.5
Mean		4.1[a]	4.4
P. dicum	Berry		3.5
	Oak	4.0	3.3
	Soap		1.8
Mean		4.0[a]	2.9
S. arcticum	Berry	1.4	2.2
	Soap	2.0	1.9
Mean		1.7	2.1
S. canadense	Berry	4.7	1.0
	Soap	5.6	0.5
Mean		5.2	0.8
Prosimulium spp. Mean		4.1	3.6
Simulium spp. Mean		3.4	1.4
Prosimulium spp. + *Simulium* spp. Mean		3.6	2.7
Prosimulium spp. + *Simulium* spp. Mean (1971 + 1972)		3.1	

[a]Single observation

were representative of potential parasite-related losses to black fly aggregates. This was because these levels, which primarily occurred during the latter part of the larval duration, were non-additive in effect since only final-instar individuals succumbed.

Between up and downstream stations, infection percentages of Prosimulium spp. and Simulium spp. aggregates were very similar. The level of parasitism was quite low in this study. Welch (1962) and Welch and Rubzov (1965) commonly found simuliid aggregates with up to 100% of larvae infected. The fact that only one worm was found per simuliid was unexpected, since multiple parasitism appears to be a common occurrence (Welch, 1964).

Potential parasite effects were actually less than perhaps indicated. Maximum (total) infection levels and resulting mortality almost always occurred when very reduced simuliid densities were present on riffles. Therefore, aggregates of final-instar larvae (approximately 1500 individuals/m^2) and not early instars (up to 25,000 individuals/m^2) were affected. Resulting losses, when treated with the four species mean of 3.1%, would be in the neighborhood of 45 instead of over 700 individuals/m^2. Additional parasite considerations appear in the Dynamics and Mortality of Black Fly Aggregates section.

Drift

Figures 29 through 32 in the Production section illustrate the dynamic nature and consistently low levels of drift commonly encountered for larvae of all black fly species. Original weekly drift data are located in Appendix IV. At all riffles, a generally positive relationship existed between standing crop and downstream movements of larvae.

Averaged for both years, the numbers of simuliid larvae in the drift compared to the mean numbers on the benthos trended fairly consistently from a low of 0.4% during week one to a high of 4.6% for the final sampling period (mean of 2.2%). Trends between drift biomass and standing crop were similar, the range and mean being 1.0% to 4.4%, and 2.7% respectively. No species had consistently different drift to standing crop characteristics from one another.

Pooled two year drift to standing crop density correlations for all species ranged from 0.41 to 0.84, with the relationship at 6 of the 17 sites being significant at the 95% level. The mean r value was 0.69. Drift to standing crop biomass correlations produced a mean r of 0.37 (range of -0.21 to 0.67). These comparisons were made only on data from the start of week two to the end of the larval life, since drift during the first week that larvae were on riffles was variable. The consistent nature of the density-based relationship strongly indicated

drift to be a fairly uniform function of standing crop numbers. In streams which had been treated with DDT, Dimond (1967) also determined that a close relationship existed between standing crop density and benthic drift. This pattern of downstream movement may be roughly comparable to the "constant" drift situation found by Waters (1965) for Baetis and Gammarus.

Data for Prosimulium spp. presented as curves in Figure 15 representatively illustrate the generally close relationship that was found to exist between drift and mean standing crop density for all species. Pooled annual figures have not been used since individual species data best show the two early-season drift patterns encountered. Short-term increases in downstream movements during the final weeks of riffle inhabitation occurred at only two stations, perhaps indicating that pre-emergence drift common to other aquatic taxa (Elliott, 1967) was rare.

Low early-season drift in Prosimulium spp. and Simulium spp. aggregates was typical, even though greatest numbers of larvae inhabited riffles during these times. Of the 17 locations monitored, 13 had lower first than second week drift. Larvae below about 2 mm in length were generally harder to completely dislodge than those of larger sizes during population sampling. This appeared related to a behavioral rather than a physical response, since the anal circlet hold of these tiny individuals could be broken comparatively easy.

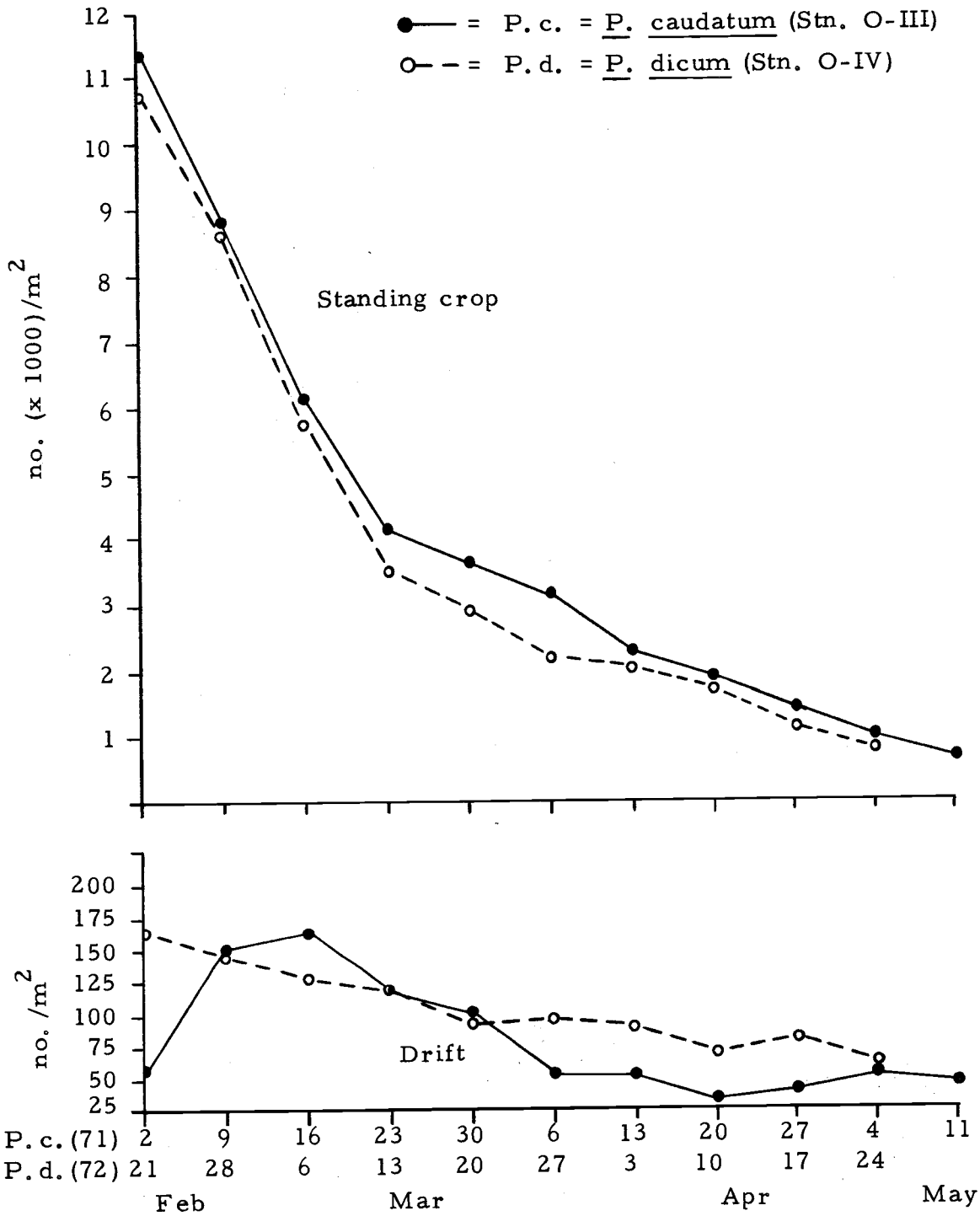


Figure 15. Comparison of mean standing crop density and drift of P. caudatum and P. dicum larvae with time. Dates represent the end point of weekly periods.

Upon breakage of the normal attachment mode, first and perhaps second-instar larvae resisted drifting by rapid movements of the mouth (probably for silk deposition), proleg and anal hooks with the substrate. If similar gyrations occurred when early-instar larvae became disturbed naturally, rates of drift would have been comparatively low. This type of behavior would be ecologically advantageous to the aggregate, since the great majority of larvae perished that drifted.

Physical crowding, as a result of increase in body size with larval growth, was probably an important cause of drift losses. Elliott (1968) also attributed the increased drift of larger Hydropsyche spp. larvae to crowding. The space occupied by an individual black fly larva is determined not only by the area required for attachment with the anal hooks, but also by the distance that the head and body move during filter feeding. Laboratory and field observations indicated that a larva moves through an arc of from 60 to 80 degrees while feeding, and this movement appears to determine the space requirements of the individual. Attachment release and subsequent movements over the substrate occurred occasionally, but these motions were probably unimportant to normal interlarval distances.

Had densities on rocks remained constant, it would have been possible to investigate the precise relationship between standing crop, crowding and drift. But on all riffles, comparatively heavy

concentrations of individuals occurred for no apparent reason on certain substrate sites. Thus, these areas became limited in space earlier than others. Quantifying the extent of immature concentrations was found to be impossible, as crowding sometimes varied to a great extent between riffles.

As discussed in the forthcoming section on aggregate dynamics, invertebrate predator feeding is theorized as being the main cause of larval mortality. Since carnivores thus appeared to regulate standing crop, and a positive relationship existed between standing crop and drift, predators indirectly influenced downstream movements of black flies. Carnivores directly causing drift was unlikely, since, when disturbed, simuliid larvae almost always left the substrate attached to a silk thread.

Variable light, temperature and discharge (as indicated by rainfall) conditions appeared not to affect the drift of third and fourth-instar larvae in any consistent manner (Table 16). Means for each experimental period showed rates to be slightly higher during the daylight hours. Estimates for the two Prosimulium species were initially found to be similar and therefore pooled.

Data taken in early February, 1973 from the Entomology Farm Prosimulium spp. riffle indicated that first-instar larvae may have different drift characteristics than larger sized individuals. During the six days that diel observations were made, 68 of a total of 95 larvae became trapped in nets at night.

Table 16. Precipitation (discharge), temperature and day-night drift of Prosimulium spp. larvae off a large Oak Creek riffle in March, 1972.

Date (March, 1972)	Precipitation (cm/day)	Mean Temperature (°C)	800-2000 Hours Drift (no. /day)	2000-800 Hours Drift (no. /night)
8	0	-	-	-
9	trace	8.4	7	29
10	0.69	8.1	34	6
11	1.55	9.2	16	10
12	1.17	8.7	5	13
13	0.61	9.5	11	2
14	0.28	9.2	18	9
15	trace	10.3	lost	13
16	trace	9.6	11	27
20	0.05	10.8	-	-
21	0.25	9.3	12	19
22	2.36	10.5	7	30
23	0.58	10.9	9	16
24	0.08	11.6	24	7
25	0.36	12.7	27	19
26	0.46	10.3	21	24
27	0.30	11.8	20	9
28	0.20	12.0	38	13
29	trace	12.4	18	24
30	0.05	11.9	7	16
	Mean	(9-16)	14.6	13.6
	Mean	(21-30)	20.3	17.7

During late April, 1973, at a large isolated riffle near station S-III, drift readings were taken for four full days. These observations showed that for medium-sized S. arcticum larvae (mean length of 3.8 mm), drift rates may be higher during the day than night. Resulting data were, as numbers captured per 12 hours: day, 136; night, 89. As with the Entomology Farm Prosimulium spp. observation, daily catches of S. arcticum larvae remained proportionally the same in most cases as for the total.

Simuliid larval drift must be extremely variable, as the results of other researchers indicate. Elliott and Minshall (1968) have found that black flies in England commonly exhibit a strong diel pattern, with nocturnal movements being by far the dominant. Water temperature fluctuations were determined by Pearson and Franklin (1968) to be the most important factor to simuliid drift in Utah and Colorado. These workers also found that downstream movements could be influenced by dissolved oxygen, turbidity, depth, date and water level fluctuations. Comparisons were made using available Oregon determinations of the last four categories to drift. No consistent or even moderately close relationship was found to exist.

Holt and Waters (1967) have found high light intensitites to experimentally have a depressing effect on the nocturnal drift of Baetis and Gammarus. Though only nine observations could be made in the three Oregon research areas, consistent drift variations were never noted between times of high or low illumination.

Non-eclosion related drift distances for larvae of all species were estimated to be generally small, commonly ranging between 1 and 3 m. The limited data indicated that maximum distances were usually attained by larvae under 4 mm in length during times of greatest water flow. McLay (1970) found that chironomid larvae, which resemble simuliid immatures in habitat and size characteristics, may drift up to 8 m in less than an hour. Since my study riffles were isolated and had intervening pools with low water velocities, immatures probably settled out faster and attained shorter mean drift distances than at more representative black fly locations. Velocities immediately downstream from the aggregates may not have been too critical though, since Simulium spp. immatures generally were in faster pool-water situations than Prosimulium spp., yet did not drift any further.

Anderson and Lehmkuhl (1968) have found black fly larvae to be one of the major components of drift during freshets in Oak Creek. In the current study, correlations between drift and both short and long term velocity or discharge fluctuations were all very low or negative (mean r of 0.14). Three possible explanations exist as to why the two Oak Creek studies varied.

1. Species utilized by Anderson and Lehmkuhl were unknown. Since that study was accomplished in the autumn and during the time that changes in black fly species composition may have been

taking place in the stream, it is very possible that P. caudatum and P. dicum were not involved and S. vittatum was.

2. Large concentrations of drifting larvae may be the result of an additive effect involving many riffles. Sites in the current study perhaps had such low velocities, that most larvae attained unusually low drift distances.

3. Logically, freshets had more effect on "catastrophic drift" if variations in water volume were great. Since the earlier research was done during a season of characteristically high precipitation, short term water volumes changed by as much as a factor of five. In the recent study, this difference was usually less than two.

In 1972, two sets of experimental stream trials were accomplished using third through fifth-instar larvae of all species. The first tested the reaction of larvae to a rapid change in current velocity. This was done by damming up the streams for one to two seconds, then releasing the plank held upstream from larval aggregates. As the surge of water struck attached larvae, an average of 16% released hold. Of these, none was ever seen to drift without a silk strand attached to the substrate. A similar occurrence has been seen by Tarshis and Neil (1970) for simuliids in Michigan.

Experiments of a more practical nature were completed using a small non-submersible pump with which current velocity changes much

like those of the field could be approximated. Velocity variations were accomplished in about 30 seconds, and final flows exceeded those of the original by about 20 cm/sec. Of the over 400 larvae used, only 18 released their hold on the substrate. All but two of these returned to about the original place of attachment by the use of silk strands. Though only general, both experiments showed that black fly larvae were affected by variations in water velocity, but that substrate vacation was usually temporary.

Data from nets located upstream from black fly aggregates illustrated how few drifting simuliids were available for colonization. Average potential immigration was 12.1, 5.9 and 8.8 larvae per week for all appropriate Prosimulium spp., S. arcticum and S. canadense stations respectively. These extremely low figures (less than 7% of weekly drift for all species) again may not have been representative due to the isolated nature of most riffles.

Larvae in the water column almost certainly could not be established directly on riffles. Settling in pools had to take place, then subsequent up or downstream crawling to suitable sites. In a pool situation, the natural tendency of larvae probably is to go upstream. All individuals observed moving in the field and laboratory did this.

Upstream movement trends by larvae were very inconsistent, and could never be directly correlated with drift rates. Over 70% of

all apparent migrations were accomplished by larvae over approximately 4 cm in length. Numbers of upstream moving individuals ranged from zero to 12.1% of those drifting. The mean was 0.3%. Elliott (1971b) calculated that upstream movements of Simulium spp. were only 50 cm per 12 hours in laboratory experiments. This was the lowest upstream distance attained by any of the 15 invertebrates he studied.

During normal flow conditions, most drifting larvae eventually settled in pools and rarely returned to riffles from which they originated. For all practical purposes, simuliid downstream movements were terminal. With the many fish and invertebrates that inhabited most pools, the chance that black fly immatures could survive in these slow water situations was miniscule.

As Warren et al. (1964) and McIntyre (1967) have demonstrated in Berry Creek, simuliid larvae are a common, though generally minor component of the cutthroat trout diet. These fish appear to obtain the overwhelming portion of their food from the drift. Percent of black fly contribution to total fish stomach contents, by weight, in the two studies ranged from zero to 11.4. The mean was 2.4%. Fish densities were unknown in the current research, but probably averaged about five per pool in all streams (McIntyre; personal communication, 1972: Department of Fisheries and Wildlife, Oregon State University, Corvallis). Considered together, consumption and density data tend

to corroborate the observation that drift rates of black fly larvae were consistently low. Cutthroat trout thus had little opportunity to become major predators of simuliids.

One positive case of riffle re-colonization was observed. When the March 30, 1971 samples showed that unusual losses had occurred at station O-IV, a visual check was made of the riffle with a diving mask. This observation confirmed that large numbers of larvae had left the area. Five weeks later, P. dicum larval densities increased 46% over the previous sampling period. Prosimulium caudatum numbers decreased normally. Again, underwater observations confirmed that re-colonization had indeed taken place. Larvae that suddenly appeared on the riffle almost certainly came from upstream, since the closest downstream aggregate was over 25 m away. The most proximal site of Prosimulium spp. activity was about 12 m upstream.

Annual drift determinations have been listed in columns one and two of Table 17. Columns three through six present density, biomass and production comparisons to drift by percentage relationship. Averaged two year drift density was higher for P. caudatum than P. dicum by 15.3%. Biomass for the latter species was 20.7% more though, mostly reflecting the relatively larger size of P. dicum individuals. Simulium canadense annual drift was about twice that of each of the other three species.

Table 17. Annual black fly larval drift and percentage comparisons with density, biomass and production in 1971 and 1972.

Station and Year	Drift (no./ m^2)	Drift (g/ m^2)	Initial Density/ Drift (%)	Mean Density/ Drift (%)	Mean Biomass/ Drift (%)	Annual Production/ Drift (%)
			P. caudatum			
O-III (71)	574	0.130	4.6	13.5	16.7	4.5
O-IV	993	0.182	9.1	23.8	30.1	7.5
O-III (72)	846	0.209	7.7	14.9	22.2	7.2
O-IV	694	0.169	7.1	14.2	20.3	6.1
O-VII	554	0.153	8.6	17.2	18.7	6.7
Mean (71+72)	732	0.169	7.4	16.7	21.6	6.4
			P. dicum			
O-III (71)	856	0.331	5.1	14.5	37.7	10.0
O-IV	652	0.132	4.7	14.2	24.2	5.5
O-III (72)	392	0.134	2.4	7.6	15.8	5.0
O-IV	791	0.250	6.8	18.9	30.4	8.4
O-VII	484	0.171	4.4	12.9	27.0	7.7
Mean (71+72)	635	0.204	4.7	13.6	27.0	7.3
			S. arcticum			
B-I (71)	435	0.145	3.9	9.6	18.2	5.1
S-III	721	0.206	8.0	14.4	16.2	5.7
B-I (72)	838	0.210	4.0	10.5	16.5	4.7
S-III	592	0.184	4.7	10.5	17.8	5.0
Mean (71+72)	647	0.186	5.2	11.3	17.2	5.1
			S. canadense			
B-VII (71)	1443	0.428	9.1	23.3	38.8	11.7
B-V (72)	1331	0.374	7.1	18.6	34.1	10.1
S-I	792	0.165	7.0	15.5	18.7	5.6
Mean (71+72)	1189	0.322	7.7	19.1	30.5	9.1

Total standing crop reductions due to downstream larval movements ranged from a mean of 4.7% (P. dicum) to 7.7% (S. canadense). Averaged for all species, annual drift was only 6.9% of production. Data expressing the relationship between drift, mean density and mean biomass have been included for potential comparative purposes, since some investigators only have reliable average standing crop estimates. Annual drift, as a proportion of mean density or mean biomass, ranged from 7.6% to 38.8% (mean of 19.6%). This difference between annual and average estimates illustrates how drift impact can be misjudged using only mean standing crop parameters.

Pupae

Pupae of all species occurred in the same general location on rocks as did individuals of the previous developmental stage. There was a slight tendency, especially in Simulium spp., for pupae to be in areas of lower current velocity than larvae. This behavior has been found to be common with many simuliid species (Maitland and Penney, 1967).

Length, weight and duration ranges and means for pupae of all species are listed in Table 18. Pupae averaged 79.1%, 76.4%, 81.3% and 83.3% of the mature larval weights for P. caudatum, P. dicum, S. arcticum and S. canadense respectively. As with larvae, Simulium spp. pupae were larger by up to 20% than those examined from other

Table 18. Lengths, weights and durations of black fly pupae, averaged for 1971 and 1972. L = laboratory trial.

Species (no. of pupae examined)	Length Mean and Range (mm)	Weight Mean and Range (mg)	Duration (days) Mean	Duration (days) Range	Temp. Mean (°C)
P. caudatum (74)	5.0 3.8-5.9	0.544 0.498-0.572	5.1 6.0	4.8-7.3 5.5-6.5	12.8 L 11.7
P. dicum (61)	5.2 4.1-5.9	0.650 0.612-0.717	4.5 5.6	4.1-6.3 4.8-5.9	12.8 L 11.7
S. arcticum (41)	4.5 3.1-5.6	0.483 0.451-0.510	2.8 3.7	2.4-4.1 3.5-4.3	15.9 L 13.7
S. canadense (46)	4.5 3.5-5.9	0.599 0.560-0.643	3.3 3.6	2.8-4.9 3.0-4.5	16.2 L 15.0

Oregon streams (Speir, unpublished data). Prosimulium spp. individuals were about of equal size in both studies. As has been demonstrated previously (Stone, 1964), development time decreases with increasing water temperature. Water averaging 1°C warmer shortened Prosimulium spp. and S. canadense durations approximately 17% and 8% respectively. For S. arcticum, a 25% reduction in development time was the result of an increase in temperature of about 2°C.

For estimates of the total life cycle (Table 5), a duration of 0.8 and 0.5 week was used for Prosimulium spp. and Simulium spp. respectively. The pupal-stage life of black flies is much shorter than that of larvae or adults. Durations reported in the literature range from 2.5 hours (Tarshis, 1973) to over 15 days (Puri, 1925). For most species, it is about five days.

Pupae were weighed without cocoons, and the great amount of tissue loss between mature larvae and pupae was primarily caused by these protective enclosures. Cocoon weights accounted for about 70% of the reduction in all species. Averaged between years, cocoon weights were: P. caudatum, 0.094 mg; P. dicum, 0.135 mg; S. arcticum, 0.079 mg; and S. canadense, 0.089 mg.

Cocoon construction was observed for P. caudatum and S. arcticum. The process took from 55 to 108 minutes (mean of 80 minutes) for the 12 Prosimulium caudatum individuals maintained in laboratory streams at an average of 12.8°C. Simulium arcticum cocoon formation ranged from 35 to 85 minutes (mean of 50 minutes) at about 14.5°C. Peterson (1956) found that the construction process for S. canadense took from 40 to 60 minutes to complete.

The cocoons of only S. arcticum pupae were consistently lower in apex profile (by as much as 15%) in faster water velocity situations. It was not certain whether larvae constructed the cocoons in this way, or if the current disintegrated the protective enclosures to a greater degree in faster than slower waters.

Emergence and Adults

Over 5000 adult Prosimulium spp. and Simulium spp. were reared from pupae. Mating was never observed, and all eggs laid in the laboratory and placed in artificial streams failed to develop or

hatch. Only rarely was the actual process of emergence seen. The pattern of emergence was determined by recording numbers of newly emerged flies from artificial streams at two to six hour intervals.

Two P. caudatum and six P. dicum adults were seen emerging in laboratory streams averaging 12.5°C. They rose to the surface enveloped in an air bubble and could fly within about five minutes. This pre-flight time was spent drifting on the water surface. Diel patterns of emergence were not present for Prosimulium spp. in the laboratory. In holding cages with vials of sugar water, 71 adults lived from a few hours to 13 days. The mean laboratory life span was about 64 hours for P. caudatum and 29 hours for P. dicum. Neither sex consistently emerged first. As Table 19 illustrates, sex ratios for both species generally favored females.

Females of both Prosimulium species emerged with immature ovaries. A few individuals produced seemingly mature ova in 24 hours or less. Over 85% of all dead females dissected, no matter which species or what age, contained only small numbers of undeveloped eggs. The mean value was 4.6 ova per individual. Mouthparts of Prosimulium spp. females are very well developed. If laboratory observations represent the natural situation, females are anautogeneous upon emergence and require a blood meal before oviposition can occur. Shewell (1959) notes that adults of both species are capable of taking blood, though normal hosts are unknown.

Table 19. Sex ratios of adult and pupal black flies in 1971 and 1972.

Species	Stage	1971		1972	
		♀	♂	♀	♂
P. caudatum	adult	250	228	384	301
		(1.1)	(1.0)	(1.3)	(1.0)
	pupa			172	153
				(1.1)	(1.0)
Total				556	454
				(1.2)	(1.0)
P. dicum	adult	239	164	318	260
		(1.5)	(1.0)	(1.2)	(1.0)
	pupa			67	94
				(1.0)	(1.4)
Total				385	354
				(1.1)	(1.0)
S. arcticum	adult	76[a]	117[a]	738	694
		(1.0)	(1.5)	(1.1)	(1.0)
	pupa			491	566
				(1.0)	(1.2)
Total				1229	1260
				(1.0)	(1.0)
S. canadense	adult	39	54	520	446
		(1.0)	(1.4)	(1.2)	(1.0)
	pupa			209	176
				(1.2)	(1.0)
Total				729	624
				(1.2)	(1.0)

[a]Sex ratio biased as only early-emerging adults were sexed.

The one S. arcticum adult observed emerging from an artificial stream was able to fly almost immediately. Water temperature at emergence of most laboratory reared individuals averaged about 14.5°C. For 48 adults, the life span ranged from two hours to eight days, and averaged 49 hours. In 1971, only the earliest emerging adults were sexed. The following year when analyses were accomplished during the entire emergence period, the sex ratio was 1:1 (Table 19). Data from both years indicate that males begin emergence about three days earlier than females, as was also reported by Abdelnur (1968) in Alberta. In the laboratory, two emergence peaks were observed occurring at about 700 and 1900 hours. It was not determined if field emergence patterns were the same. Peterson (1956) found a similar twin-peaked emergence characteristic in natural aggregates of black flies in Utah.

Dissected laboratory-reared S. arcticum females, no matter what age, generally had mature appearing ovaries (as defined by Davies, 1961). Fully-developed eggs were never present in newly emerged individuals. After emergence, over 48 hours passed before normal appearing ova were observed. Females rarely laid eggs in the laboratory; the maximum number deposited by one individual being 16. Many authors have alluded to the severe biting nature of S. arcticum females (Rempel and Arnason, 1947; Peterson, 1956; Fredeen, 1969). Berry and Soap Creek specimens certainly had well-developed

mouthparts. Considering laboratory findings, it was thought probable that most or all females needed a blood meal before truly mature ova could be produced.

Three S. canadense adults were seen emerging from artificial streams (mean temperature of 15.0 ^{o}C) and none was enclosed in an air bubble. Upon emergence from the stream, all three "scrambled" on to the sides of the channel and remained there about ten seconds, one minute and three minutes, respectively, before flying. As with S. arcticum adults, emergence in the laboratory increased slightly at about 700 and 1900 hours each day. Field emergence patterns are unknown. Sex ratios slightly favored females (Table 19). Neither sex consistently emerged first. The adult life span, using 156 caged individuals, ranged from about one hour to 13 days. The mean was 71 hours.

Fifteen newly-emerged S. canadense females had mature ovaries. Oviposition was common in the laboratory, and occurred on any available solid surface or on the water. Egg masses ranged from 10 to 86 eggs, the average being 38. The mean number of eggs deposited per female was 96 (range of 34 to 212). Females have very weakly developed mouthparts, as has also been reported by Peterson (1959) in Utah. Most simuliids that have more than a single ovarian cycle need one blood meal, perhaps more (Davies et al., 1962).

Simulium canadense females, which could not feed, were autogeneous and likely had only one gonotrophic cycle.

Adult length and weight data are presented in Table 20 for the four species. Prosimulium spp. males averaged 14% and 5% more in length and weight, respectively, than females. The situation was reversed for Simulium spp., as females were 6% longer and 8% heavier than males. Adults averaged 95.0% (range of 94.5% to 95.3%) the weight of pupae, with exuviae accounting for most of the 5% difference. Between adults and mature larvae, the mean weight relationship was 76.0% (range of 72.2% to 79.4%). Weight reductions between larvae and adults were very similar to those of some mosquitoes (Brust, 1967).

As observed with the prior two stages, Simulium spp. adults were consistently larger than those from other Oregon streams (Speir, 1969). Simulium arcticum and S. canadense individuals exceeded in size by 16% and 28% respectively adults from the Marys River. Prosimulium spp. individuals, if anything, were slightly smaller in the current study.

For total life cycle durations (Table 5), the period of time between emergence and oviposition has been estimated at 0.5 week for all species. This is a realistic time, considering the short adult activity periods found in the laboratory, and the data of other workers. Ussova (1964) has determined that mating commonly takes place very

Table 20. Lengths and weights of male and female black flies. Data are averaged between 1971 and 1972.

Species	Sex	Body Length (mm)		Dry Weight (mg)	
		Mean	Range	Mean	Range
P. caudatum (64)	♀	3.2	3.1-3.7	0.496	0.402-0.585
	♂	3.7	3.5-4.0	0.537	0.439-0.704
P. dicum (39)	♀	3.4	3.1-3.8	0.599	0.524-0.672
	♂	4.0	3.3-4.5	0.629	0.500-0.731
S. arcticum (29)	♀	3.3	2.3-4.1	0.488	0.429-0.564
	♂	3.0	2.1-4.1	0.431	0.356-0.498
S. canadense (25)	♀	3.4	2.6-3.9	0.584	0.551-0.636
	♂	3.3	2.3-3.6	0.558	0.519-0.583

Table 21. Comparison of numbers of black flies emerging annually, and rate and duration of the emergence period. Data are averaged between stations and years.

	P. caudatum	*P. dicum*	*S. arcticum*	*S. canadense*
Annual emergence (no. /m^2)	1405	986	1874	1065
% Emerging in:				
Week 1	12	30	13	29
Week 2	39	55	48	53
Week 3	41	13	26	18
Week 4	8	2	13	-
Emergence duration mean (weeks)	3.7	3.4	4.0	3.7

soon after the latter emerging sex becomes available. Though some females needing blood show strong host preferences, most appear able to utilize a wide range of mammalian or avian species (Lewis, 1960). This includes most North American Prosimulium species and S. arcticum (Peterson, 1956, 1959a, b; Abdelnur, 1968). Host location and subsequent feeding procedures are therefore probably accomplished quickly (Ussova, 1964). Though many pre-oviposition egg maturation types are extant, judging from the findings of Pokof'eva (1959), most individuals may have emergence to oviposition times of from one to three days.

Black fly emergence at the 22 field sites was estimated by counting the pupae, as described in the Materials and Methods section. Figures 29 through 32 in the Production section illustrate the relationships that existed between growth, biomass, production, drift and emergence. Appendix V contains original weekly data.

With few exceptions, emergence gradually increased to a single peak approximately half way through the entire period of adult eclosion. Only one twin-peaked pattern was ever observed (S. arcticum; B-I, 1972). At this station, the emergence period was extended, even though numbers of adults produced were comparable to other S. arcticum sites.

Table 21 lists emergence for all species, averaged between years. The span of the emergence period was estimated from

laboratory studies as well as general observations at most study riffles, whether pupae were actually collected or not. Even though comparatively short larval development times existed for all species (Table 5), emergence durations were not considered excessively long. Davies (1950) found that emergence times for populations of P. hirtipes (Fries), a species with a similar life cycle to that of P. caudatum and P. dicum, commonly spanned between 6 and 41 days (mean of 20 days). A univoltine species, S. euryadminiculum Davies, had duration times of from 3 to 22 days (mean of 11 days).

Davies (1950) also found a generally uniform sex to emergence duration relationship existed for many of the species he studied. For example, P. hirtipes female emergence lasted about ten days longer than for males. No consistent sex related emergence duration trends could be found for any of the black flies in the current study.

No correlation could ever be made in the field between emergence and environmental cues such as temperature or day length changes. Though continuous temperature records were kept for artificial stream experiments, never was a change in temperature ever associated with emergence. Laboratory experiments indicated that pupal duration was strongly influenced by water temperature (Table 18). Emergence initiation likely was directly proportional to the time required for pupal maturation to occur at the prevailing water temperature.

Mean annual emergence, pooled for 1971 and 1972, ranged from 986 adults/m^2 and 0.608 g/m^2 for P. dicum to 1874 adults/m^2 and 0.863 g/m^2 for S. arcticum (Table 22). Of all larvae initially on riffles, 10.7% on the average survived to emerge (range of 7.2% for S. canadense to 14.6% for S. arcticum). Averaged for the four species, emergence was 22.1% of production. As with drift, percentages using mean density and biomass data are presented for potential comparative purposes, since some studies are based primarily on these estimates.

Density

Initial larval standing crop numbers varied considerably between species. Once development began though, most simuliid aggregates had very similar patterns of density decline. Figures 16 and 17 show instantaneous density curves for all four species in 1971 and 1972 respectively. By using actual station data, and not mean annual estimates, commonly occurring variations have been illustrated with curves generally representative of the average field situation for each species.

Since the substrate upon which sampling occurred was efficiently partitioned, the reliability of density data was high. Approximately 81% of all total population estimates fell within the 15% error limit used as a desired criterion. Errors above this level mostly occurred

Table 22. Annual black fly emergence and percentage comparisons with density, biomass and production in 1971 and 1972.

Station & Year	Emergence (no. /m^2)	Emergence (g /m^2)	Initial Density / Emergence (%)	Mean Density / Emergence (%)	Mean Biomass / Emergence (%)	Annual Production / Emergence (%)
			P. caudatum			
O-I (71)	1755	0.886	13.0	34.5	96.1	29.3
O-III	1547	0.781	12.4	36.4	100.0	27.3
O-IV	1341	0.687	12.3	32.1	113.9	28.3
O-I (72)	1908	1.017	13.4	30.2	108.7	29.1
O-II	1031	0.550	9.9	20.4	70.9	20.5
O-III	1495	0.797	11.3	26.3	84.6	27.4
O-IV	1237	0.659	12.6	25.3	79.2	23.6
O-VII	927	0.494	14.4	28.7	60.3	21.5
Mean (71+72)	1405	0.734	12.4	29.2	89.2	25.9
			P. dicum			
O-I (71)	722	0.436	8.2	18.2	42.0	11.9
O-III	1289	0.779	7.7	21.8	88.7	23.6
O-IV	1185	0.716	8.5	25.9	131.1	30.1
O-I (72)	1393	0.869	8.0	18.4	70.0	18.0
O-II	774	0.483	7.6	16.9	45.5	14.4
O-III	670	0.419	4.1	13.0	49.4	15.5
O-IV	980	0.612	8.4	23.4	74.4	20.5
O-VII	878	0.547	8.0	23.3	86.4	25.4
Mean (71+72)	986	0.608	7.6	20.1	73.4	19.8

(Continued on next page)

Table 22. (Continued)

Station & Year	Emergence (no. /m^2)	Emergence (g /m^2)	Initial Density / Emergence (%)	Mean Density / Emergence (%)	Mean Biomass / Emergence (%)	Annual Production / Emergence (%)
			S. arcticum			
S-III (71)	1856	0.880	20.7	37.0	69.4	24.3
B-I (72)	2062	0.947	9.8	25.8	74.5	21.2
S-III	1703	0.763	13.4	30.2	74.0	20.6
Mean (71+72)	1874	0.863	14.6	31.0	72.6	22.0
			S. canadense			
B-VII (71)	1134	0.663	7.1	18.3	60.1	18.1
B-V (72)	1082	0.625	5.8	15.1	57.0	17.0
S-I	980	0.540	8.7	19.2	61.1	18.2
Mean (71+72)	1065	0.609	7.2	17.5	59.4	17.8

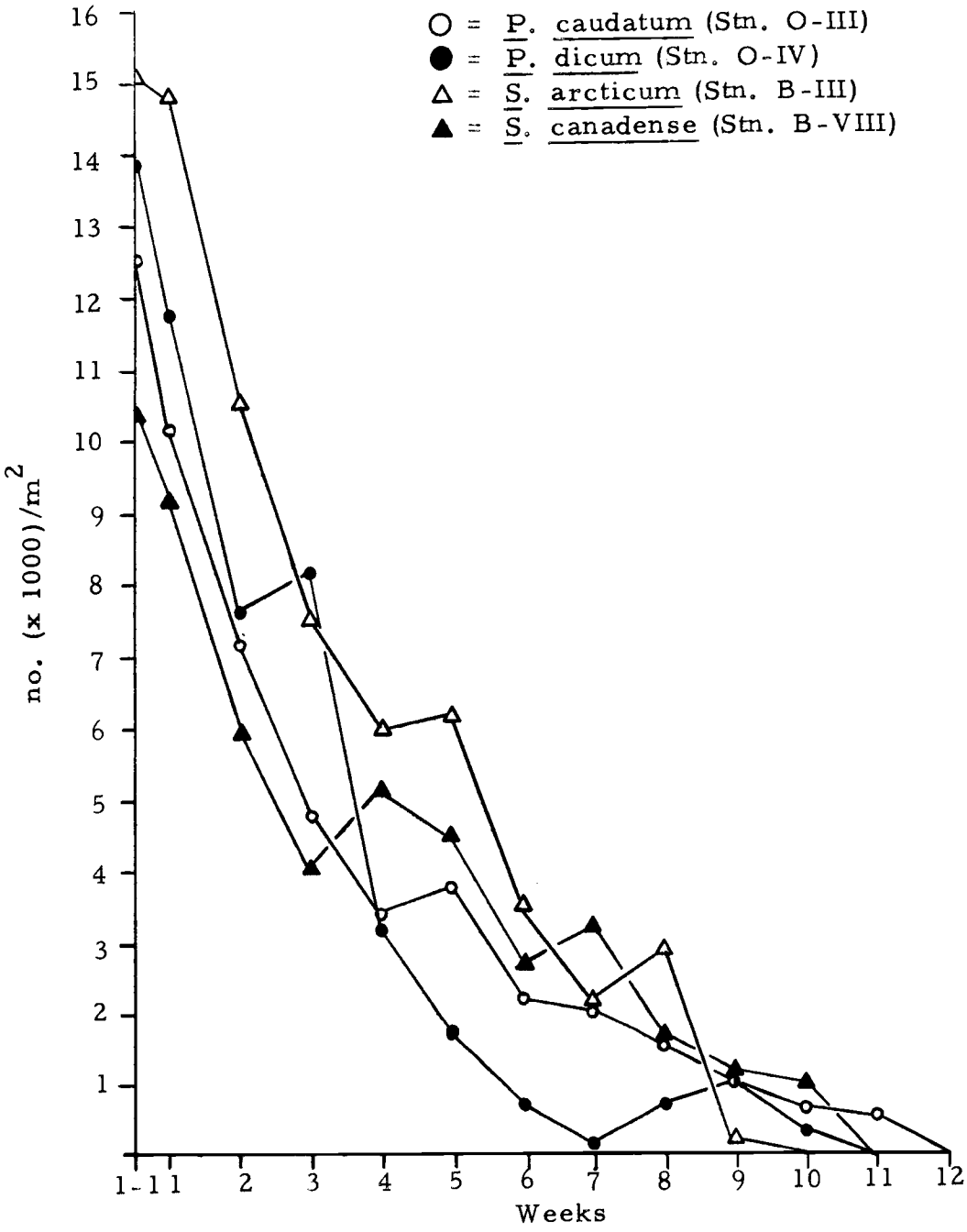


Figure 16. Black fly larval density change over time at four stations in 1971.

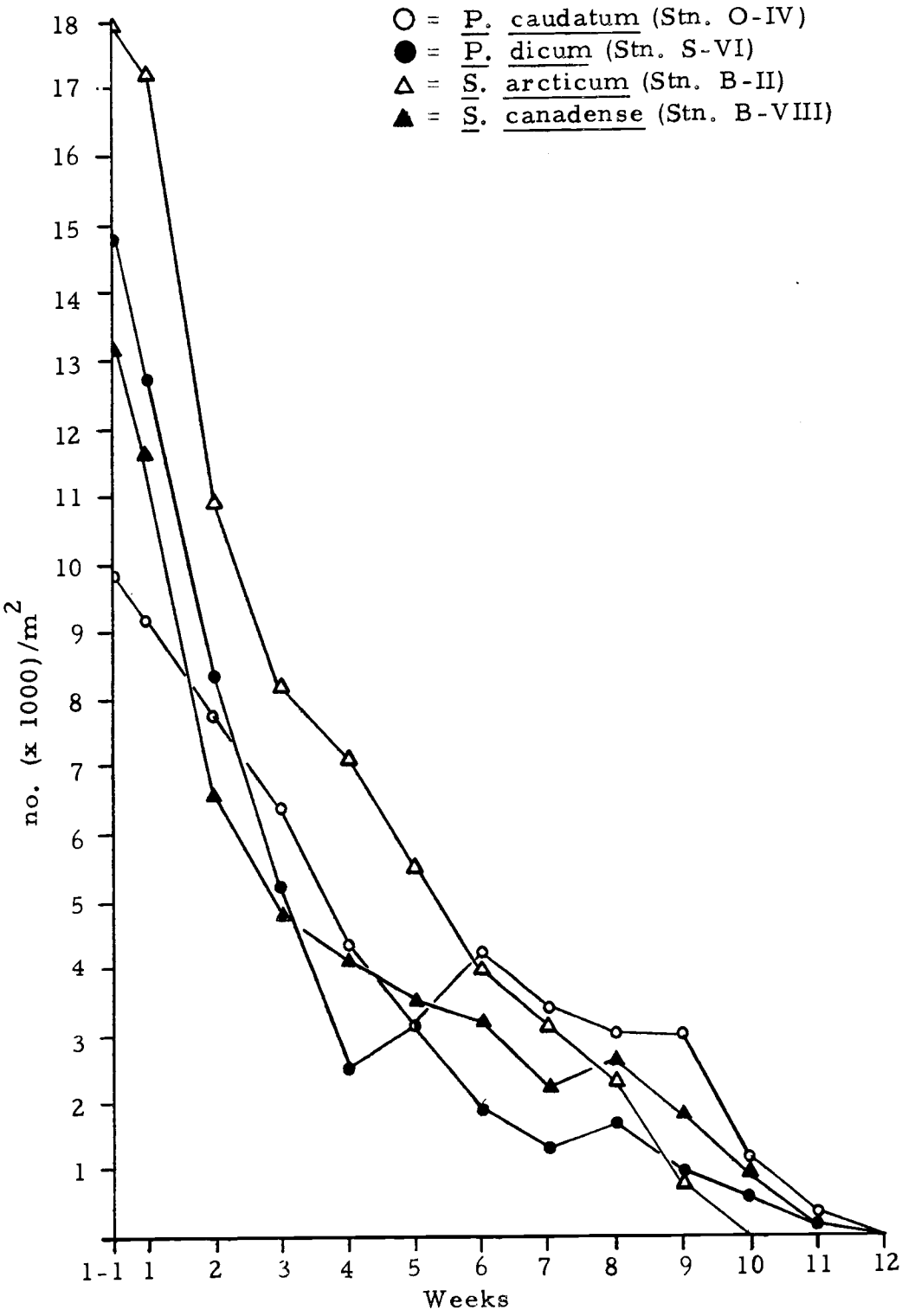


Figure 17. Black fly larval density change over time at four stations in 1972.

late in the season when larval numbers were comparatively low. During the first three-quarters of the larval duration for all species, the mean coefficient of variation (as defined by Simpson et al., 1960) was 6.24 (range of 3.16 to 9.32). For the last quarter, this value was 10.11 (range of 7.92 to 16.18).

At only two riffles were exceptional decreases in standing crop noted. As Figure 16 shows, the drop in P. dicum numbers at station O-IV (1971) was much more dramatic than at the more representative locations illustrated, especially after about week four. Density reductions for P. caudatum at O-IV were almost identical, though not shown. A very similar occurrence was observed slightly later in the larval period of S. canadense at station B-IV (1972). Losses between consecutive weeks at these two stations were 41%, 49% and 34% respectively during times of maximum reduction. Normally, this figure would have been about 18% for the Prosimulium species and 12% for S. canadense. Prosimulium caudatum, P. dicum and S. canadense mean annual density was lowered, from average aggregates of the same species, about 9%, 2% and 10% respectively.

The reason why larval losses were so great in such a short period of time was never determined. No evidence of pollution or unusual stream temperatures, silt loads or discharges were found during the density reductions. The remaining larvae at the two stations appeared evenly distributed over available substrates, and

were "healthy" when examined at later dates. Prosimulium dicum losses occurred at least a week earlier from the O-IV site than for P. caudatum. This indicated that one known cause of drift, direct mechanical disturbance (Waters, 1962b), was probably not involved. If it had been, larvae of both species would have left the riffle together. The variability between the two species is further illustrated by the fact that only P. dicum larvae re-colonized the riffle.

Station and year related annual densities have been illustrated in Figures 18, 19, 20 and 21 for P. caudatum, P. dicum, S. arcticum and S. canadense respectively. Sites are oriented from lowest to highest initial densities, left to right. Correlation coefficients between initial and mean density are listed in Table 23. As these data show, the two characteristics were significantly correlated at the 95% level or better for all species except perhaps S. canadense in 1971. Only two estimates came from that year, but judging from the data in Figure 21, a close relationship existed. Slight variations occurred in the initial to mean density relationship at many locations; for example, between P. caudatum stations O-II and O-V (Figure 18, 1971). These inconsistencies were almost always due to minor differences in mortality between riffles. The interaction of density, mortality and biomass will be discussed with production.

Standing crop summarizations in Table 24 contrast larval densities between years for all species. Original initial and mean

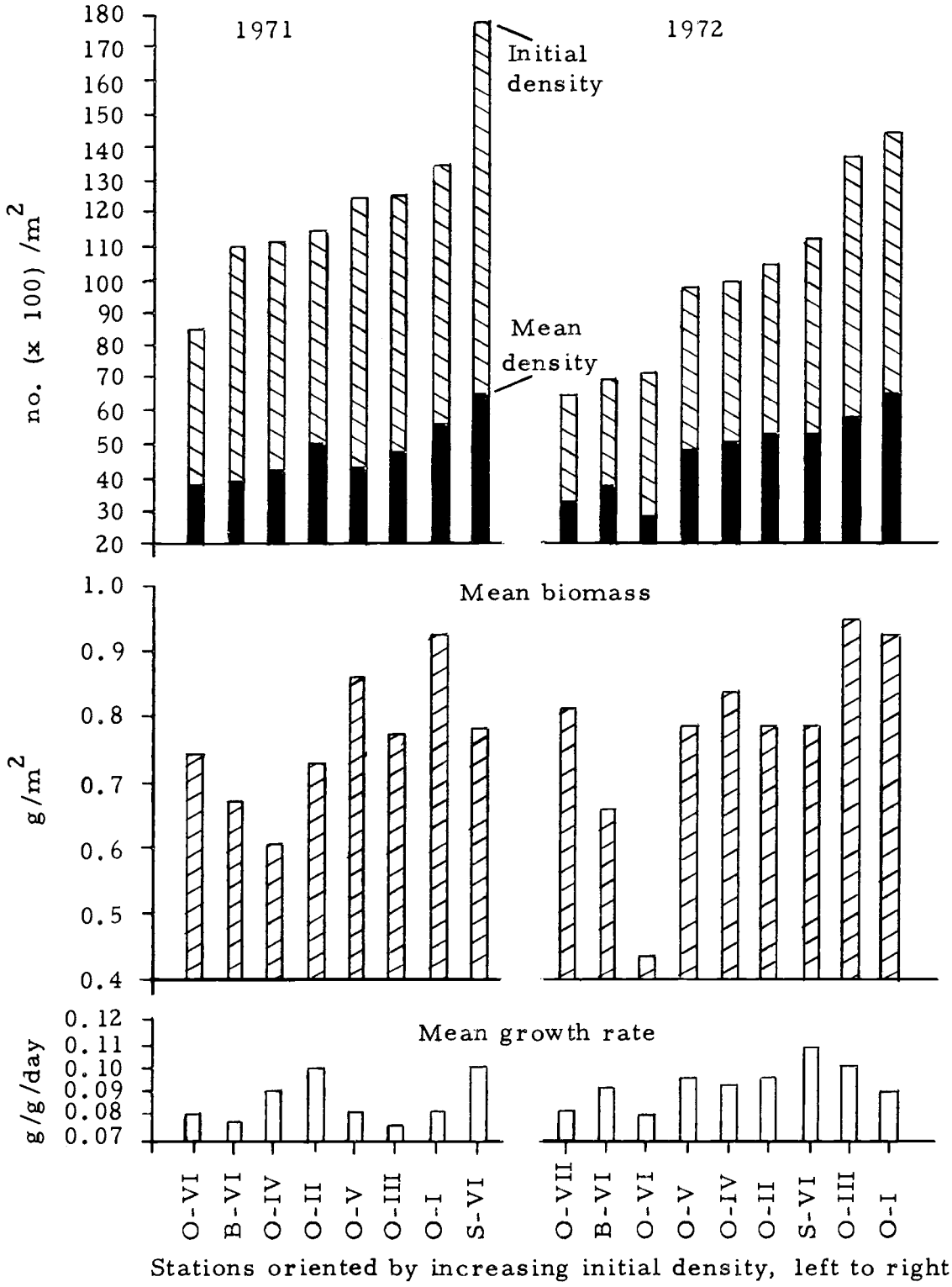


Figure 18. Larval density, biomass and growth rate at all P. caudatum stations in 1971 and 1972.

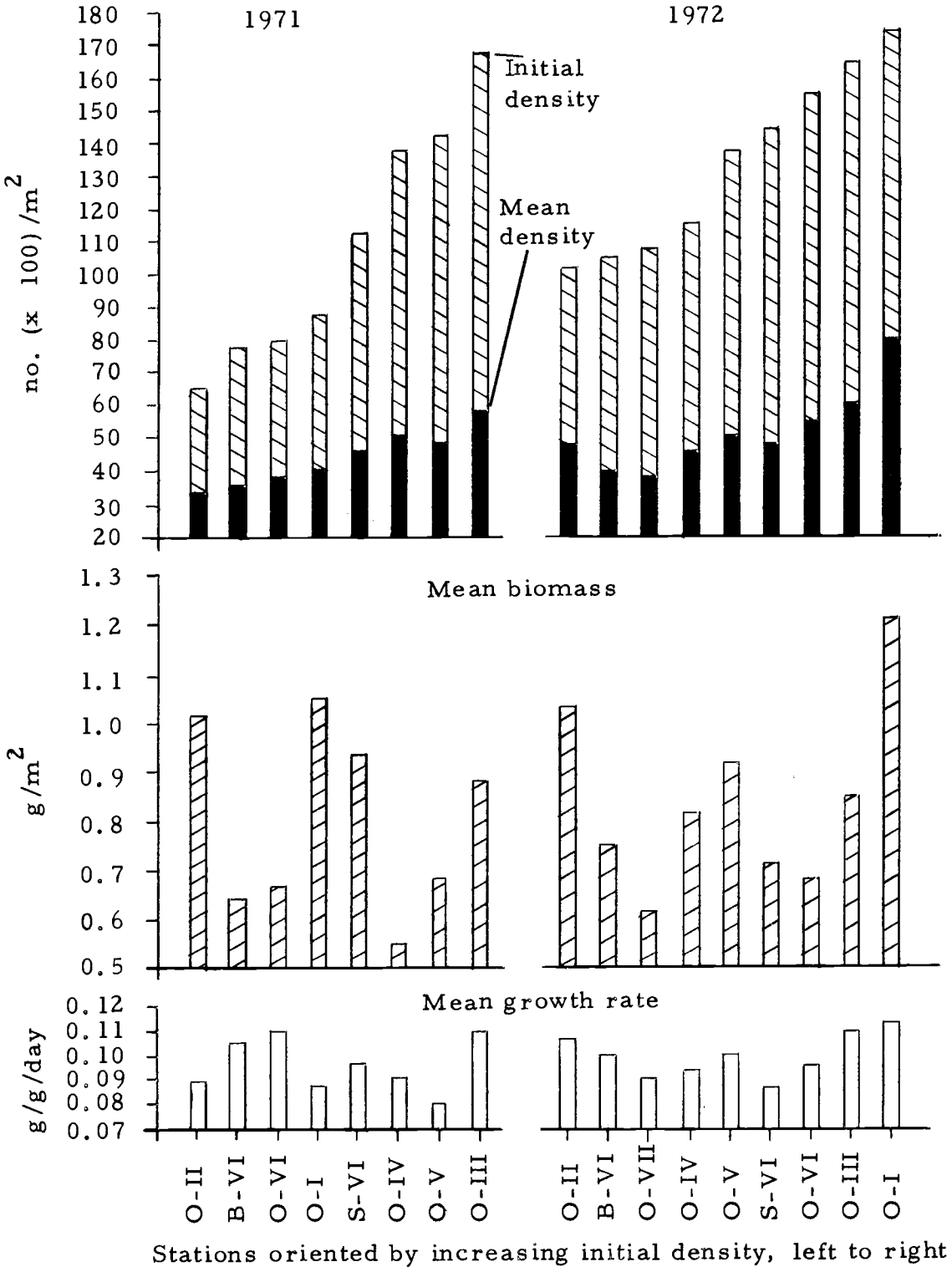


Figure 19. Larval density, biomass and growth rate at all P. dicum stations in 1971 and 1972.

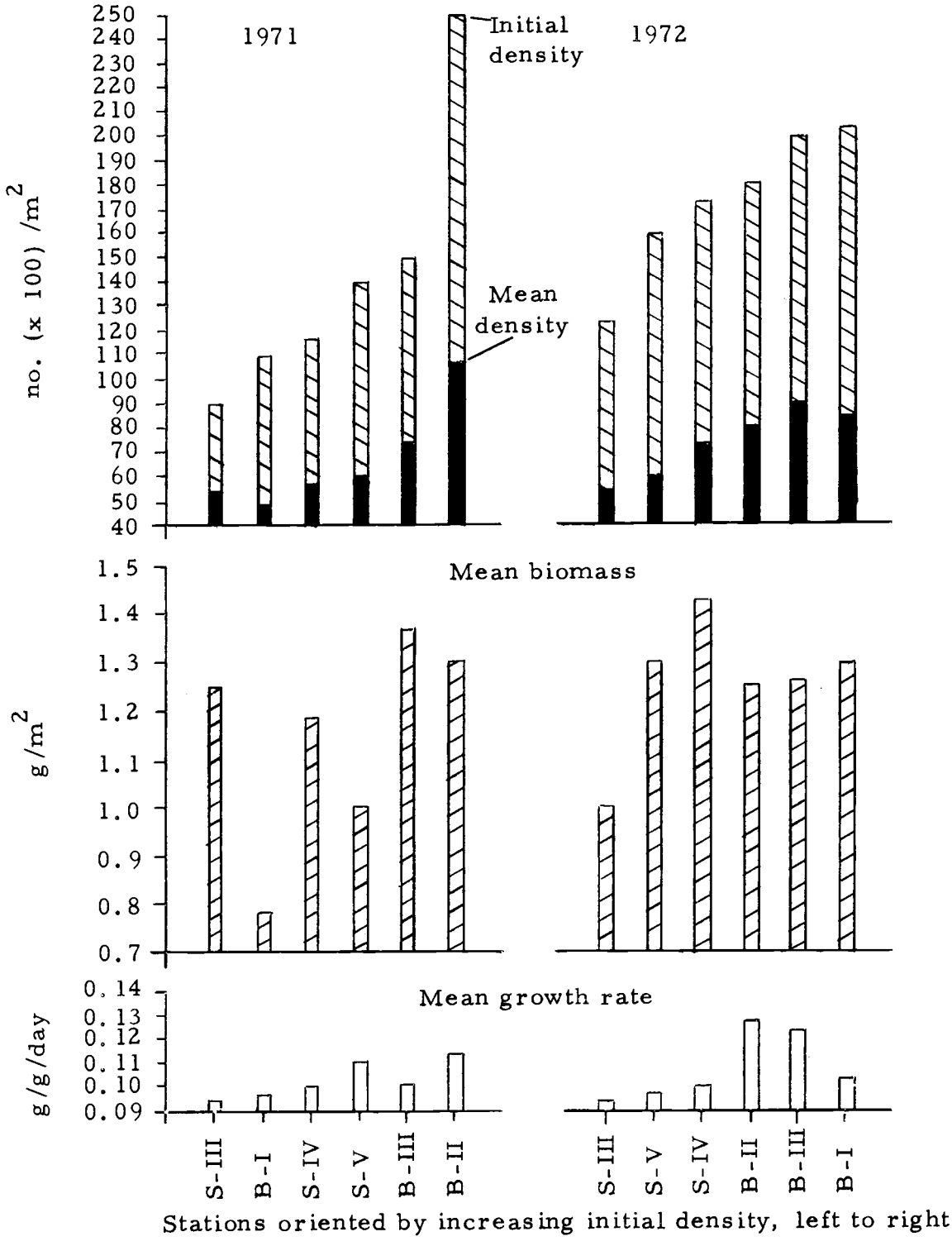


Figure 20. Larval density, biomass and growth rate at all S. arcticum stations in 1971 and 1972.

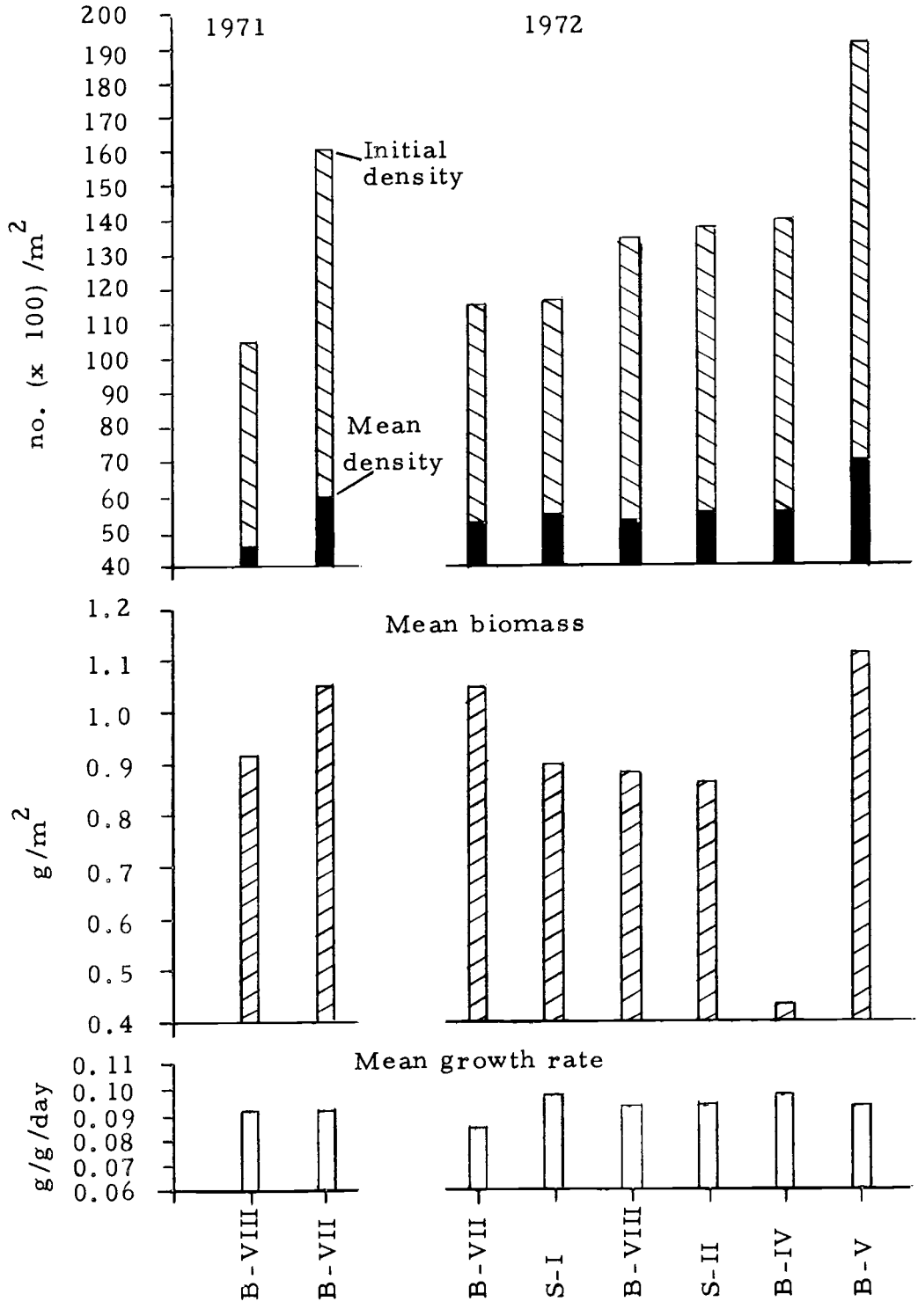


Figure 21. Larval density, biomass and growth rate at all S. canadense stations in 1971 and 1972.

Table 23. Correlation coefficient (r) values for *P. caudatum* (Pc), *P. dicum* (Pd), *S. arcticum* (Sa) and *S. canadense* (Sc) between density, biomass, growth rate and production variables. Data for 1971 and 1972 are situated to the top right and bottom left respectively.

		1971				
		Initial Density	Mean Density	Mean Biomass	Mean Growth Rate	Annual Production
1972						
Initial Density	Pc		0.89**	0.40	0.45	0.83*
	Pd		0.93**	-0.24	0.06	0.11
	Sa		0.97**	0.32	0.91*	0.73
	Sc		-	-	-	-
Mean Density	Pc	0.93**		0.31	0.70	0.71*
	Pd	0.77*		-0.02	0.12	0.31
	Sa	0.88*		0.51	0.92**	0.84*
	Sc	0.89*		-	-	-
Mean Biomass	Pc	0.65	0.80**		-0.21	0.80*
	Pd	0.30	0.76*		-0.32	0.88**
	Sa	0.48	0.33		0.49	0.86*
	Sc	0.20	0.49		-	-
Mean Growth Rate	Pc	0.58	0.72*	0.48		0.08
	Pd	0.23	0.54	0.61		-0.43
	Sa	0.47	0.82*	0.02		0.79
	Sc	0.11	0.07	-0.29		-
Annual Production	Pc	0.81	0.94**	0.90**	0.62	
	Pd	0.44	0.85**	0.93**	0.40	
	Sa	0.70	0.40	0.82*	-0.11	
	Sc	0.72	0.68	0.96**	-0.61	

*$P < 0.05$

**$P < 0.01$

Table 24. Comparison of black fly initial and mean larval density within and between 1971 and 1972.

	1971 Mean (N) S.E.	1972 Mean (N) S.E.	1971 + 1972 Mean (N) S.E.
	P. caudatum		
Initial density (no. /m^2)	12266 (8) 939	10012 (9) 865	11072 (17) 677
Average density (no. /m^2)	4538 333	4579 398	4560 255
% Average/initial density	37.3	45.9	40.9
	P. dicum		
Initial density (no. /m^2)	10912 (8) 1298	13519 (9) 919	12291 (17) 822
Average density (no. /m^2)	4172 293	4867 379	4540 251
% Average/initial density	40.1	36.3	38.5
	S. arcticum		
Initial density (no. /m^2)	14358 (6) 2298	17604 (6) 1228	15981 (12) 1335
Average density (no. /m^2)	6537 941	7497 516	7009 533
% Average/initial density	46.3	42.7	45.0
	S. canadense		
Initial density (no. /m^2)	13178 (2) 2760	13542 (6) 1123	13450 (8) 975
Average density (no. /m^2)	5395 798	5251 390	5287 324
% Average/initial density	40.9	39.1	39.8

density data for all stations appear in Table 28 in the Production section. As briefly discussed below, larval density varied comparatively little for each species between years.

Average initial density of S. arcticum was consistently highest of the four species during 1971 and 1972. Simulium canadense colonization numbers were next, being about 15% less than those of the other Simulium species. Prosimulium dicum density, averaged for both years, was 9% lower than for S. canadense and exceeded that characteristic of P. caudatum by about 10%.

Though 1971 P. caudatum mean initial density exceeded that of 1972 by about 23%, average density was higher in 1972 by only 1%. Second year P. dicum mean initial and average standing crop numbers were greater than those of 1971 by approximately 24% and 17% respectively. Simulium arcticum mean initial and average densities were about 23% and 15% greater respectively during 1972. Considering the magnitude of numbers involved, S. canadense densities were remarkably similar between years.

Although minimum and maximum colonization densities for each species varied by a factor of two, first-instar larval numbers were minimal in difference at the majority of stations. Using two standard errors of the mean as a general indication of variation, pooled annual data were: P. caudatum, 12.2%; P. dicum, 13.4%; S. arcticum, 16.7%; and S. canadense, 14.5%. The average for all species was 14.2%.

Larvae of P. caudatum and P. dicum always existed together on riffles. Mean initial density, pooled for both species in 1971 and 1972, was 23,177 and 23,530 larvae per m^2, respectively. Average standing crop figures were 8,710 and 9,446 larvae per m^2. Respective confidence limits of colonization means averaged 15.4% and 13.9%.

Density differences between streams have not been illustrated, and will be discussed with production. Generally, Prosimulium spp. densites remained constant between Berry, Oak and Soap Creeks. Averaged for 1971 and 1972, S. arcticum and S. canadense larval numbers were about 25% and 13% greater in Berry than in Soap and Oak Creeks, respectively.

Mortality

Larval mortality, expressed as percentage loss per week of the initial colonization density, is given in Figure 22 for all black fly species. By week three, less than half of all larvae were present on riffles, and over 70% mortality occurred by week six. The inflection at week eight for P. caudatum, P. dicum and S. canadense primarily indicates the initiation of pupation (which is considered a "mortality" of larvae). The point at which pupation began for S. arcticum is not apparent in Figure 22, but it started about at week six.

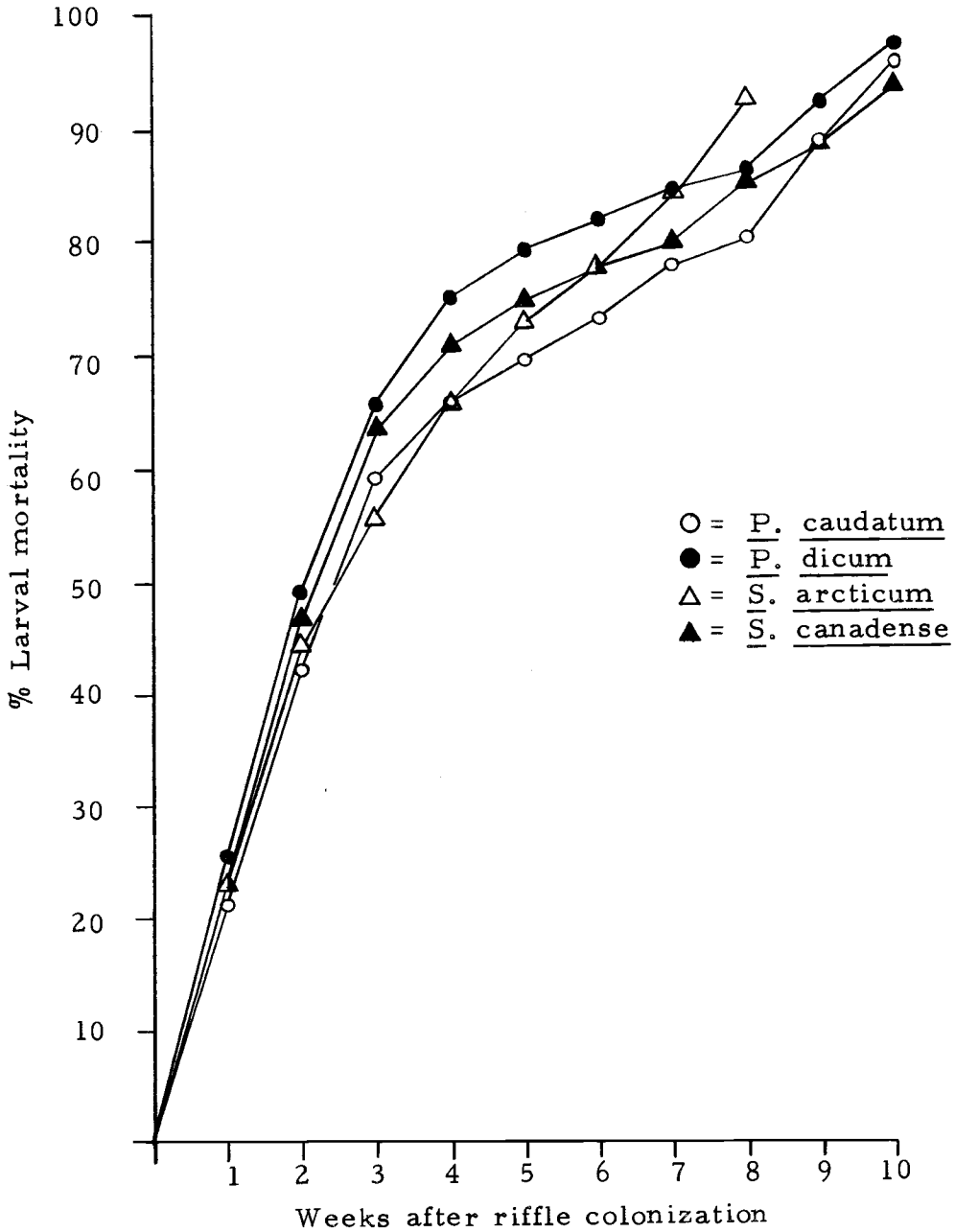


Figure 22. Cumulative larval mortality of black flies, expressed as percentage of initial numbers colonizing riffles. Data are averaged for all stations and both years.

Table 25 illustrates mortality by instar for all species. Percentages reflect average loss of each larval instar from riffle colonization through emergence. Mortality patterns of the four species were fairly similar. The greatest losses generally occurred in the first instar and decreased gradually until instar six, where mortality averaged only 6.4% of initial densities.

Average cohort mortality was: P. caudatum, 87.3%; P. dicum, 92.0%; S. arcticum, 88.3%; and S. canadense, 92.1%. The maximum and minimum mortalities for all species were 95.9% (P. dicum; O-III, 1972) and 79.3% (S. arcticum; S-III, 1971). The variation in losses was minor on a station, stream or year basis. Averaged for all species, two standard errors were 12.6% of the associated annual mortality means.

Daily instantaneous mortality rates, averaged for both years, were: P. caudatum, 0.028; P. dicum, 0.036; S. arcticum, 0.035; and S. canadense, 0.035. The mean for all species was 0.034. These data express total mortality over the entire larval life period, and include effects of predators, parasites and drift. Comparably higher rates associated with the first three weeks of riffle inhabitation were 0.045, 0.061, 0.040 and 0.050 respectively. Simulium arcticum mortality during this period of time was the lowest, illustrating the more uniform loss situation for this species.

Averaged for both years, early season P. dicum instantaneous mortality was about 35% greater than losses for P. caudatum, even though the two species were on identical riffles. This difference was not due to drift, since downstream movements by P. caudatum larvae exceeded those of P. dicum by 4% during this time. Size differences between Prosimulium spp. larvae early in the season were minimal, indicating predator "selectivity" (Wylie, 1967) was not facilitated. Since P. dicum standing crops were usually higher than those of P. caudatum, predators may have encountered and captured more larvae of the former species. Carnivores would have to feed in a density dependent manner in order for larger proportions of P. dicum larvae to be taken. This type of situation has not been found for benthic animals, but occasionally occurs with terrestrials (Chant, 1961).

Table 25. Mortality of black fly larval instars expressed as percent of initial numbers colonizing riffles. Data are averaged for all stations and both years.

Instar	P. caudatum	P. dicum	S. arcticum	S. canadense
I	24.2	25.8	22.8	24.0
II	24.6	22.9	20.1	21.8
III	20.5	20.4	18.4	18.2
IV	13.1	14.0	18.9	15.9
V	10.7	11.5	14.3	12.2
VI	6.9	5.4	5.5	7.9

Biomass

Figures 18 through 21 illustrate the relationships that existed between larval density and biomass at all stations for the four species. The generally low, variable nature of initial and mean density to mean biomass correlations (mean r of 0.38; Table 23) reflect what is apparent in the figures. Though relationships between mean density and mean biomass occasionally were close (P. dicum, 1972), these characteristics usually trended in a very inconsistent manner.

With few exceptions, variations in standing crop between riffles were primarily influenced by the timing of mortality. For example, high mid-season P. dicum larval losses occurred at station O-IV in 1971 (Figure 19). Since comparatively few large individuals were involved, density was not greatly affected but mean biomass dropped sharply. Excessive early-instar mortality (P. dicum; O-V, 1971) reduced the density without greatly influencing the biomass.

Annual larval biomass data for the four black flies are summarized in Table 26. A generally direct relationship was found to exist between the biomass at colonization, and the maximum and average annual biomass for all species. For P. caudatum, P. dicum and S. canadense, maximum standing crop occurred 8.1 weeks after larval eclosion (range of 5.6 to 9.4 weeks). For the faster developing S. arcticum, the average was 6.3 weeks (range of 4.7 to 7.4 weeks).

Table 26. Comparison of black fly larval biomass within and between 1971 and 1972.

	1971 Mean (N)	1972 Mean (N)	1971 + 1972 Mean (N)
	P. caudatum		
Biomass at colonization (g/m^2)	0.022 (8)	0.022 (9)	0.022 (17)
Maximum instantaneous biomass (g/m^2)	1.700	1.907	1.826
Annual average biomass (g/m^2)	0.761 0.036 (SE)	0.772 0.052 (SE)	0.767 0.031 (SE)
	P. dicum		
Biomass at colonization (g/m^2)	0.025 (8)	0.029 (9)	0.027 (17)
Maximum instantaneous biomass (g/m^2)	1.797	1.891	1.842
Annual average biomass (g/m^2)	0.802 0.066 (SE)	0.855 0.064 (SE)	0.830 0.045 (SE)
	S. arcticum		
Biomass at colonization (g/m^2)	0.029 (6)	0.036 (6)	0.032 (12)
Maximum instantaneous biomass (g/m^2)	2.377	2.266	2.305
Annual average biomass (g/m^2)	1.161 0.085 (SE)	1.254 0.055 (SE)	1.208 0.050 (SE)
	S. canadense		
Biomass at colonization (g/m^2)	0.027 (2)	0.027 (6)	0.027 (8)
Maximum instantaneous biomass (g/m^2)	2.367	2.093	2.254
Annual average biomass (g/m^2)	1.012 0.092 (SE)	0.876 0.096 (SE)	0.910 0.076 (SE)

Averaged between years, P. dicum mean annual larval standing crop exceeded that of P. caudatum by 8.2%. In 1972, biomass averaged 4.1% greater for the pooled species than in 1971. Annual Prosimulium spp. biomass averaged 1.559 g/m^2 in 1971 and 1.634 g/m^2 the following year. Prosimulium spp. larval biomass in all three streams was generally comparable. As expected, the 1971 lowest standing crop for both species occurred at O-IV, where there was unusually high mortality midway through the larval duration.

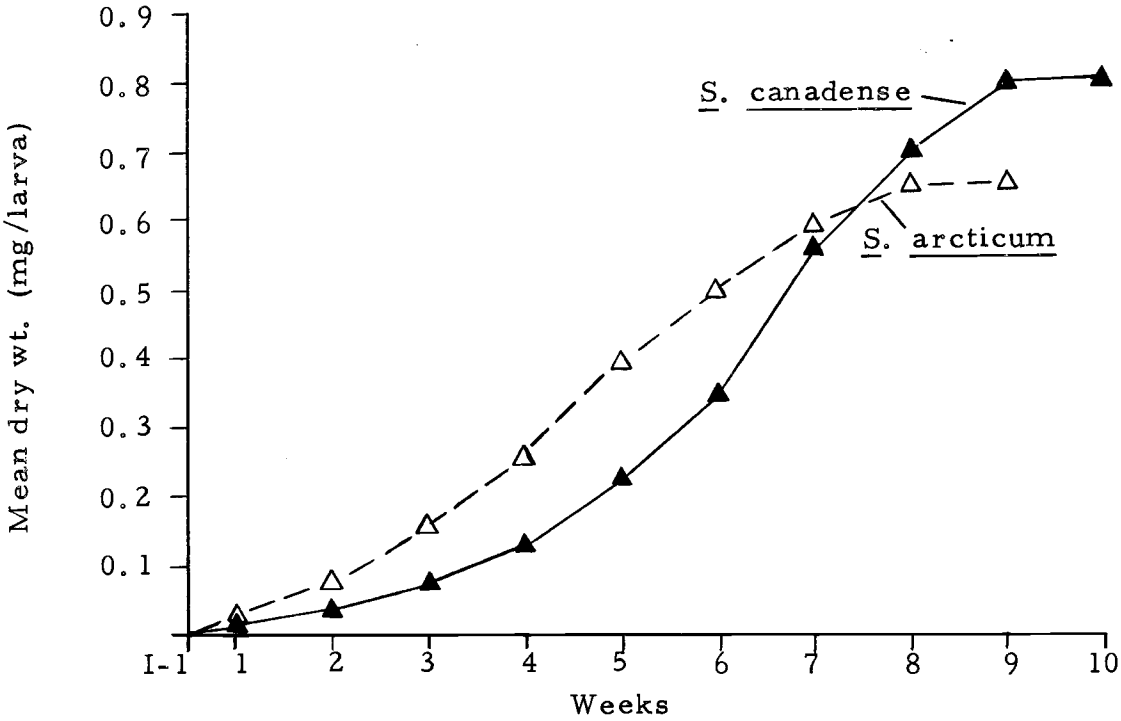
Simulium arcticum mean standing crops averaged 8.0% higher in 1972 than 1971. Annual larval biomass means were very similar between streams, with Soap Creek aggregates exceeding those of Berry Creek by only 2.5%. Second year S. canadense biomass was 13.4% lower than that of 1971 primarily because of the unexpected larval mortalities at station B-IV.

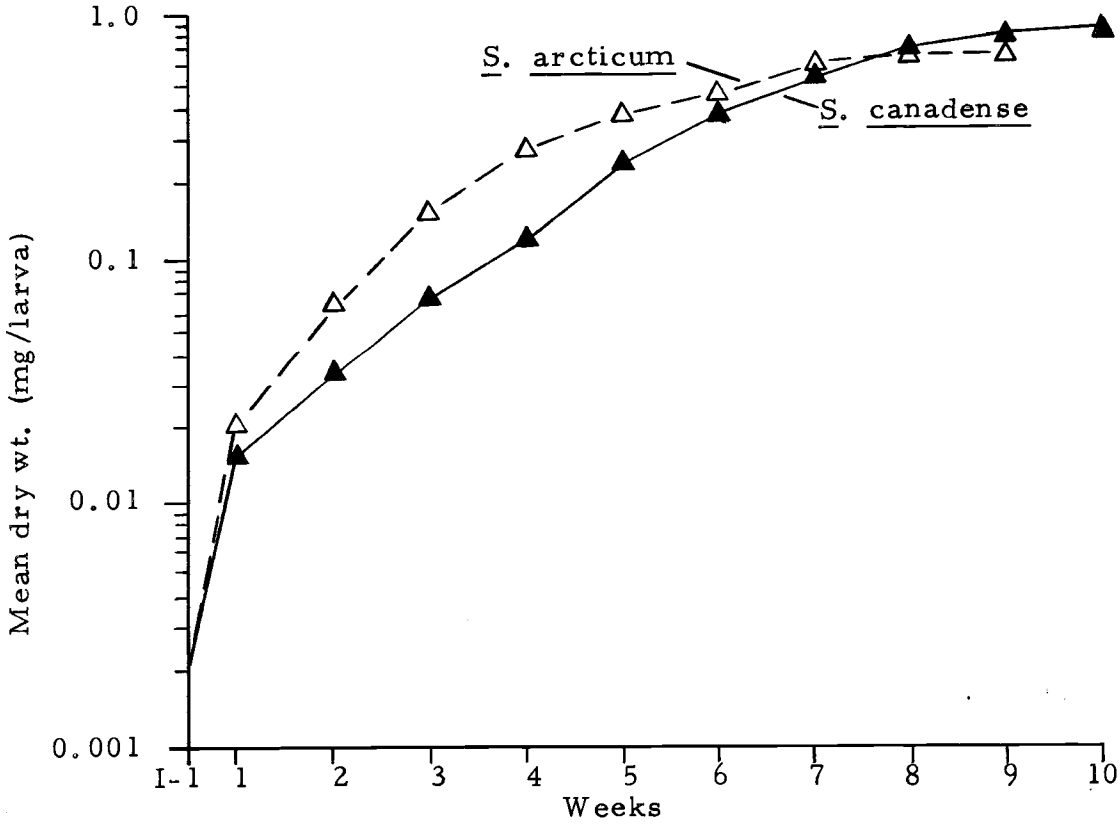
Growth

All four species of black flies exhibited a generally logistic form of larval growth. This has been illustrated for the two Simulium species, on an arithmetic and logarithmic basis, in Figures 23 and 24 respectively. The growth of S. arcticum was more linear than for any other species. The curves for Prosimulium spp. were generally intermediate between the other two species.

Figure 23. Mean weight of S. arcticum and S. canadense larvae at all stations in 1971 and 1972, plotted on an arithmetic scale.

Figure 24. Mean weight of S. arcticum and S. canadense larvae at all stations in 1971 and 1972, plotted on a logarithmic scale.


0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Mean dry wt. (mg/larva)
S. canadense
S. arcticum
I-1
1
2
3
4
5
6
7
8
9
10
Weeks


1.0
0.1
0.01
0.001
Mean dry wt. (mg/larva)
S. arcticum
S. canadense
I-1
1
2
3
4
5
6
7
8
9
10
Weeks

Figures 25 and 26 illustrate the decrease in growth rate with time for P. caudatum and P. dicum respectively. Weekly estimates have been produced by averaging all stations for that particular time period. First and second-instar Prosimulium spp. larvae grew extremely fast, with average daily rates of 0.100 to 0.400 occurring during the first two or three weeks. Growth then gradually decreased through the remaining instars. The point of most obvious inflection generally occurred at the end of the second-instar stadia and start of the third stadia. Prosimulium caudatum mean growth at about weeks 1.5 and 8.5 were 45% and 9% respectively that of week 0.5. For P. dicum, the comparable figures were 46% and 10%. Half-week data are used since growth rates were calculated as the average of samples taken every seven days.

Laboratory growth rates of P. caudatum in 1972 were so similar to the 1971 field data that they essentially occur on the same curve in Figure 25. In artificial streams, the P. dicum estimates were also close to those of the natural situation in early 1971, but subsequently dropped off for the remainder of the season (Figure 26).

Averaged for both years, S. arcticum growth rates at weeks 1.5 and 8.5 were about 52% and 2% respectively those of the initial sampling period (Figure 27). Growth gradually decreased between larval instars, and no inflection point was evident separating high from low rates of weight increase. As newly emerged first-instar

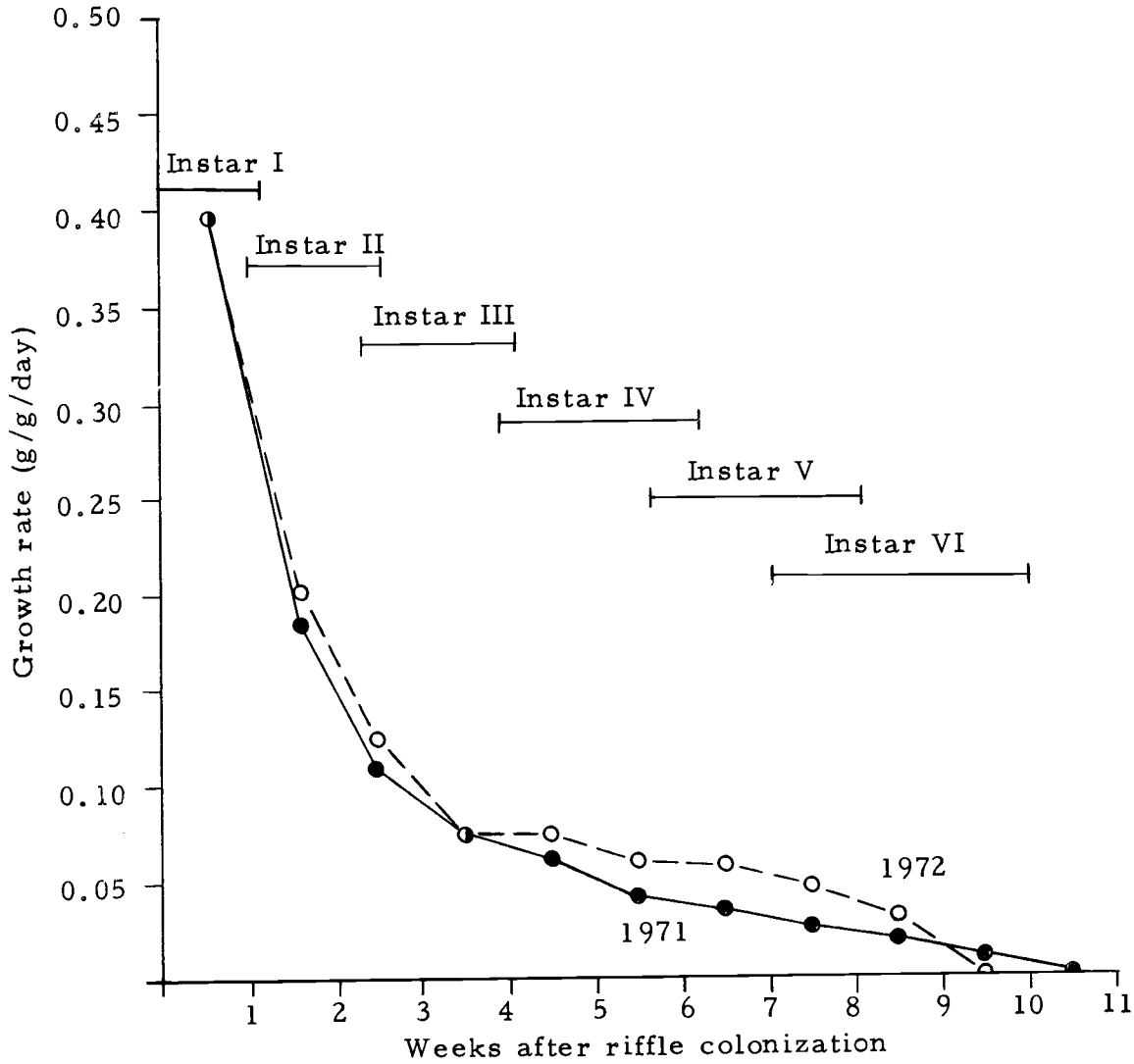


Figure 25. Mean daily instantaneous growth rates for P. caudatum larvae in 1971 and 1972, averaged for all stations. The laboratory growth curve (1972) is essentially the same as for the 1971 field. Horizontal lines indicate the approximate duration of each instar.

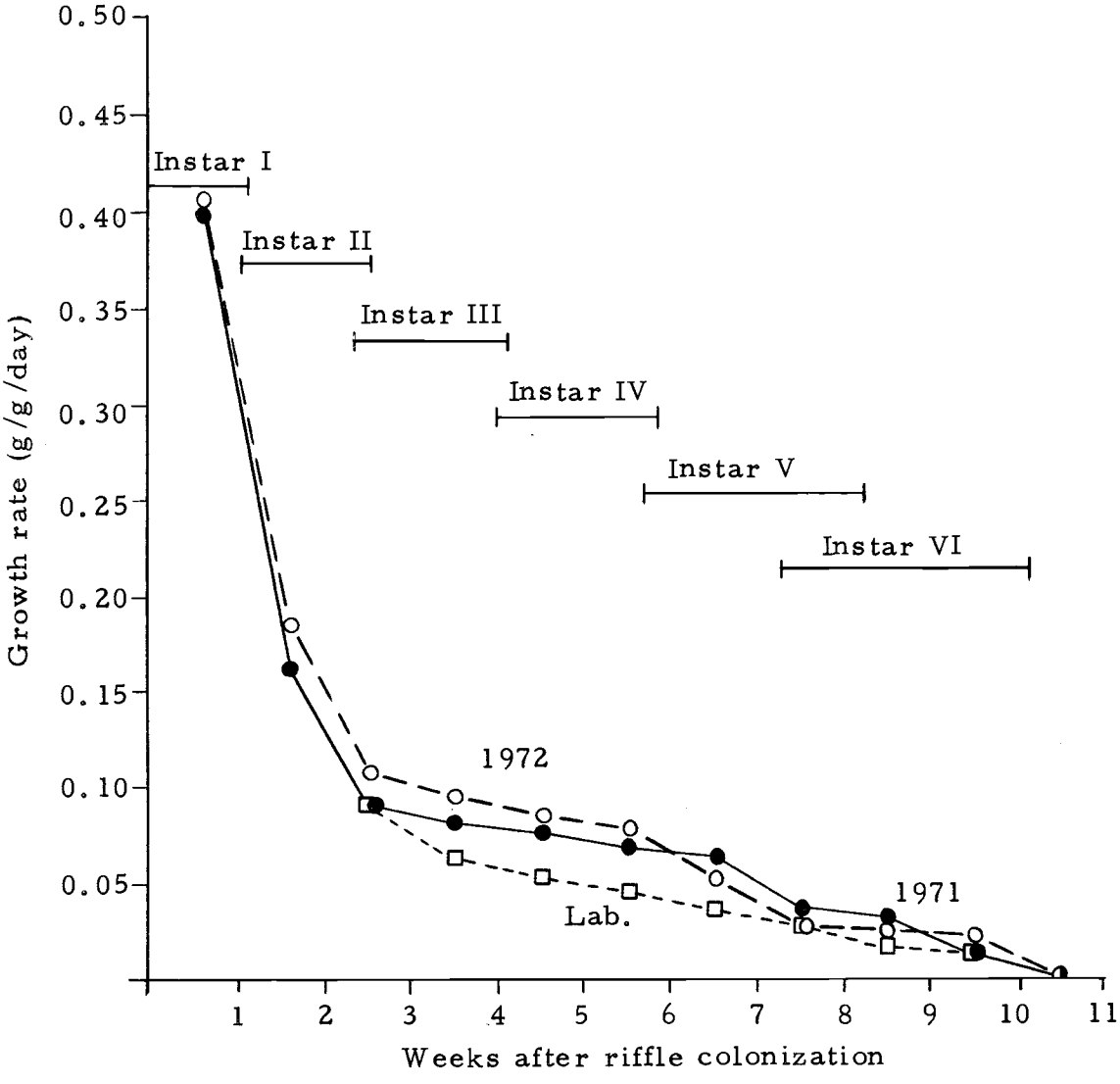


Figure 26. Mean daily instantaneous growth rates for P. dicum larvae in 1971 and 1972, averaged for all stations. Horizontal lines indicate the approximate duration of each instar.

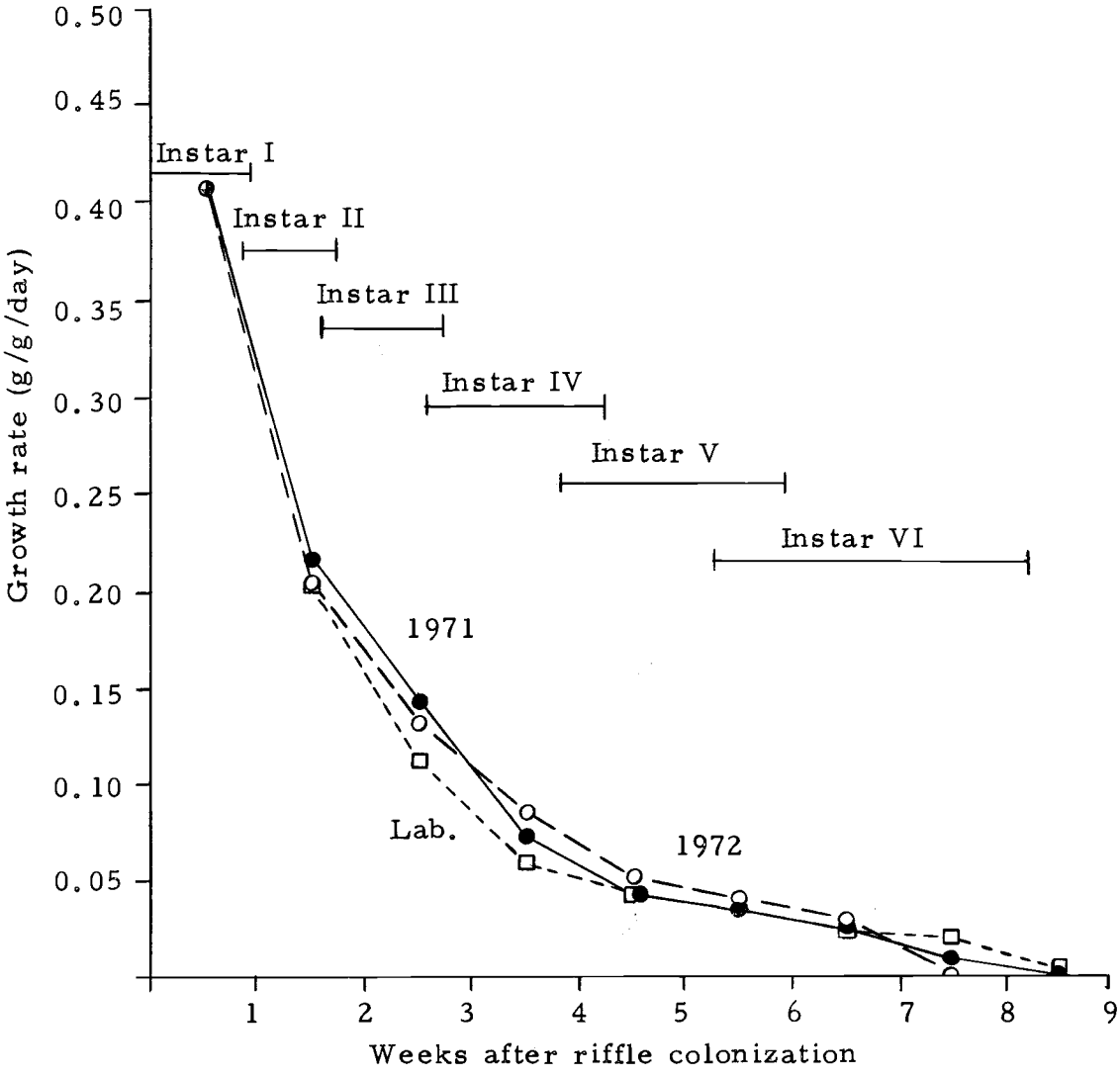


Figure 27. Mean daily instantaneous growth rates for S. arcticum larvae in 1971 and 1972, averaged for all stations. Horizontal lines indicate the approximate duration of each instar.

S. arcticum larvae were not available for laboratory experiments, initial estimates came from 1971 first sampling period data. Artificial stream estimates, elaborated in 1972 only, generally corroborated the more linear growth form of S. arcticum larvae.

Simulium canadense mean growth rates at weeks 1.5 and 8.5 were approximately 26% and 5% respectively those of the earliest sampling period (Figure 28). Only first-instar larvae attained mean daily growth rates consistently above 0.100. The change in growth at week 1.5 was almost certainly related to differences between first and second-instar individuals. Initial S. canadense 1972 laboratory growth estimates were derived from 1971 first sampling period data. Until week four, larvae reared in artificial streams grew at comparable rates as those of the field in 1972. After the fourth week, laboratory growth was consistently higher for the next 24 days. As discussed subsequently, temperature likely caused growth variations in all species.

Mean cohort instantaneous growth rates have been plotted for the four species in Figures 18 through 21. As is evident for all species except S. canadense (Figure 21), some variation occurred in growth between most stations. This was mainly due to the inconsistent nature of first and second-instar larval growth. Early-season growth rate variations were responsible for unusually high or low data at 14 of the 16 stations where noticeable differences occurred. Growth

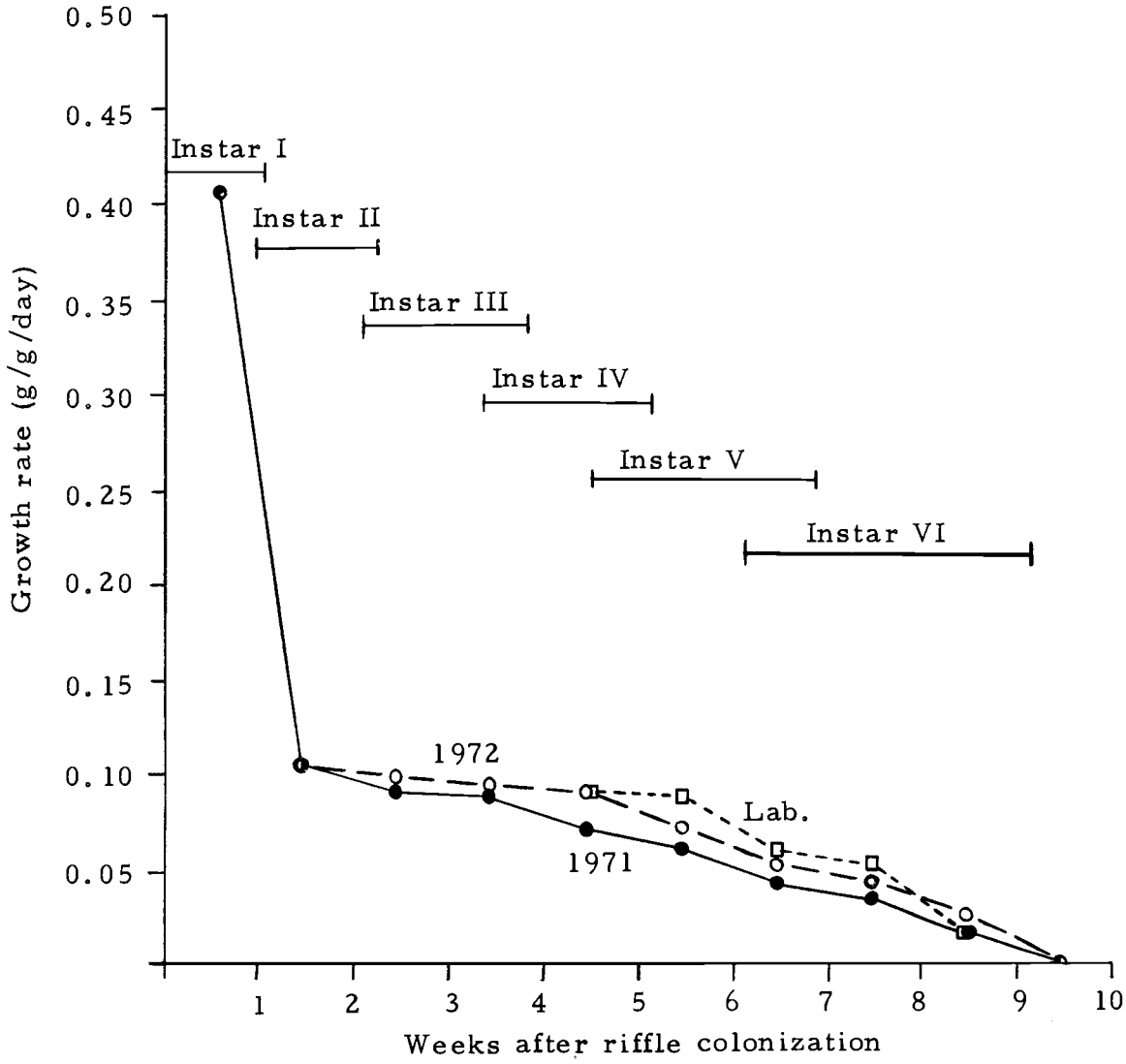


Figure 28. Mean daily instantaneous growth rates for S. canadense larvae in 1971 and 1972, averaged for all stations. Horizontal lines indicate the approximate duration of each instar.

rates had a minimal effect on the density to biomass relationship. This was related to two factors which often acted together.

1. Growth differences were usually temporary, and mainly involved very small individuals. Thus, the potential for biomass change was low.
2. Variations in mortality usually nullified biomass increases which could result from high growth.

Data in Table 27 summarize field and laboratory growth rates for all species. Original weekly estimates appear in Appendix VIII. Confidence intervals (two standard errors) averaged only 4.2% of associated means. This reflected the fact that, although high and low estimates ranged moderately, the pattern of growth rates was very constant for each species between stations, streams and years.

Black fly mean daily cohort growth, averaged for all species, was 0.096. This is an extremely high rate when compared to some common aquatic insects. Baetis bicaudatus and Oligophlebodes sigma (Pearson and Kramer, 1972) rates were found to average approximately 86% less than the mean simuliid figure. For Ephemerella subvaria (Waters and Crawford, 1973) and Hexagenia spp. (Hudson and Swanson, 1972) this difference was 80% and 85% respectively. Cohort growth of Glyptotendipes barbipes in the laboratory was estmated to be comparable to that of the field (Kimerle, 1969), and averaged about 7% higher than for the mean simuliid larval value.

Table 27. Comparison of black fly larval instantaneous daily growth rates within and between 1971 and 1972. Initial = approximately week 1.

	1971 Mean (N)	1972 Mean (N)	1971 + 1972 Mean (N)
	P. caudatum		
Initial laboratory growth		0.405[a]	
Average laboratory growth		0.090[a]	
Initial field growth	0.386 (8)	0.392 (9)	0.389 (17)
Average field growth	0.087	0.095	0.091
	0.003 (SE)	0.003 (SE)	0.002 (SE)
	P. dicum		
Initial laboratory growth		0.400[a]	
Average laboratory growth		0.089[a]	
Initial field growth	0.397 (8)	0.384 (9)	0.391 (17)
Average field growth	0.096	0.098	0.097
	0.003 (SE)	0.022 (SE)	0.002 (SE)
	S. arcticum		
Initial laboratory growth		0.403[a]	
Average laboratory growth		0.094[a]	
Initial field growth	0.403 (6)	0.408 (6)	0.406 (12)
Average field growth	0.102	0.107	0.104
	0.004 (SE)	0.007 (SE)	0.004 (SE)
	S. canadense		
Initial laboratory growth		0.406[a]	
Average laboratory growth		0.101[a]	
Initial field growth	0.406 (2)	0.403 (6)	0.405 (8)
Average field growth	0.092	0.092	0.092
	0.000 (SE)	0.002 (SE)	0.002 (SE)

[a]Single series of growth rate estimates

Negative growth rates were often calculated during the final week or two of larval life for all species. These estimates were always minor, and resulted in reduced annual production of less than 0.2% on the average. Negative rates were almost certainly the result of weight estimation errors between final-instar larvae of comparable size.

Growth and Temperature

Temperature has been demonstrated to have an extremely variable effect on the growth of aquatic invertebrates (Bar-Zeev, 1958; Hilsenoff, 1966; Kierans and Fay, 1968; Pajunen and Sundback, 1973). Judging from the laboratory and field data, the situation is no different with larvae of Oregon simuliids.

Growth rates consistently declined while water temperatures increased in both field and laboratory situations. Weekly correlations between the two characteristics ranged from -0.81 to -0.29, with the mean r value being -0.62. Though the negative relationship was high, this did not implicate temperature as limiting growth. Normal growth curves for a great many animals show the same decreasing slope with age as do those of *Prosimulium* spp. and *Simulium* spp., but are not necessarily directly regulated by temperature.

Water temperatures in all three streams averaged from 0.2 to 1.4°C warmer in 1971 than 1972. *Prosimulium caudatum*, *P. dicum*

and S. arcticum annual growth rates during the second year exceeded those of 1971 by approximately 9%, 2% and 5% respectively (Table 27). Growth was the same between years for S. canadense larvae. Correlations between mean annual growth rate and temperature for all species ranged from -0.43 to 0.45 (mean r of 0.21).

Mean annual artificial stream water temperatures exceeded those of the natural environment by an average of 2.3°C during 1972, but field growth rates for P. caudatum and P. dicum were 5% and 10% higher respectively than in the laboratory. This difference in Prosimulium spp. rates was due to which instars were apparently influenced by temperature. For P. caudatum, growth rate variations primarily involved third through fifth-instar larvae, whereas all P. dicum larval instars had higher field than laboratory growth. Unlike Prosimulium spp., larvae of the Simulium species reacted differently to temperature. First through fifth-instar S. arcticum larvae accounted for the 14% higher field than laboratory growth rates. Artificial stream grown S. canadense larvae had generally higher growth rates than in the field. This involved fourth and fifth-instar individuals for the most part, with the excess being 10%.

Growth rate variations between Prosimulium spp. and Simulium spp. larvae in the field and laboratory probably were never influenced by food shortages, since guts were always full and streams contained so much suspended material. Based on field (1971 to 1972) and

laboratory to field (1972) determinations already mentioned, Prosimulium spp. and S. arcticum growth was lower in warmer than colder water. In both trials, S. canadense rates were either equal or higher at increased temperature. These data were consistent enough to indicate that, although all four species did not respond the same, interspecific differences existed in their reaction to temperature.

The comparisons discussed earlier have been generally based on relationships between mean annual temperature and growth rate, and are perhaps too gross to obtain definitive data. However, in the laboratory streams where continuous recording thermographs were used, no consistent relationship was ever apparent between short term temperature variation and change in growth rate. These experiments included all four species of black flies, and temperature fluctuations as great as 2.8°C in four hours. Normal variations of temperature used in comparisons averaged 1.2°C in from seven to ten hours.

Growth and Mortality

Neess and Dugdale (1959) implied that growth/mortality ratios (instantaneous rate of growth/instantaneous rate of mortality; G/Z) may be constant for ecologically equivalent aquatic species. As expected, since the annual dynamic nature of all four Oregon simuliids was about the same, G/Z relationships were relatively close.

Averaged two-year ratios for P. caudatum, P. dicum, S. arcticum and S. canadense were 3.25, 2.69, 2.97 and 2.63 respectively. The mean was 2.89. These data were very similar to estimates obtained for Chironomus plumosus (L.): 2.00 (Dugdale, 1955) and Hexagenia spp.: 1.61 to 2.42 (Hudson and Swanson, 1972), indicating that ratios may show some consistency between aquatic invertebrates that occupy very different niches.

Chapman (1967) feels that G/Z ratios will remain constant only for short periods of time, at least for fish. This may not be the case with invertebrates. Anderson and Hooper (1956) found that ratios of Tanytarsus jucundus (Walker) varied little from a mean value of 0.93. In the current study, minimum and maximum black fly G/Z ratios taken throughout the cohort life, averaged only 7% of the means.

Production

A total of 54 production estimates were derived during both years of research utilizing 34 Prosimulium spp. and 20 Simulium spp. sites. In the following discussions, production determinations are expressed at two levels: (1) individual stations (riffles) for a given species, and (2) mean of any number of stations (on a species, stream or year basis). Indeed, one of the major advantages of this study was that production replicates were obtained for several species, whereas

in most previous studies, the data are limited to one, or a very few, production determinations.

Production Dynamics

Figures 29, 30, 31 and 32 illustrate biomass, drift, emergence, growth and production relationships for P. caudatum (O-III, 1971), P. dicum (O-III, 1972), S. arcticum (B-I, 1972) and S. canadense (S-I, 1972) respectively. Data presented are as representative of the overall two-year situation for each species as possible while showing some commonly occurring variations. Examinations of most riffles indicated that larval and pupal biomass decreased to zero within a week after sampling had ceased. Data in all four figures express this finding. Summarizations of production, along with initial and mean density, and mean biomass at each station, appear in Table 28. Original weekly growth, biomass and production data are located in Appendix VIII.

Larval standing crop development for all species was similar, though minor variations occurred at almost every station. Initial biomass increase was rapid due to the generally dominant interaction of high density and growth rate over mortality. Development continued until a change in the complex interrelationship between mortality and growth caused a flattening and eventual decline in the characteristic. Examinations of all pertinent Prosimulium spp. and Simulium spp. data revealed that highest weekly production rates rarely occurred at

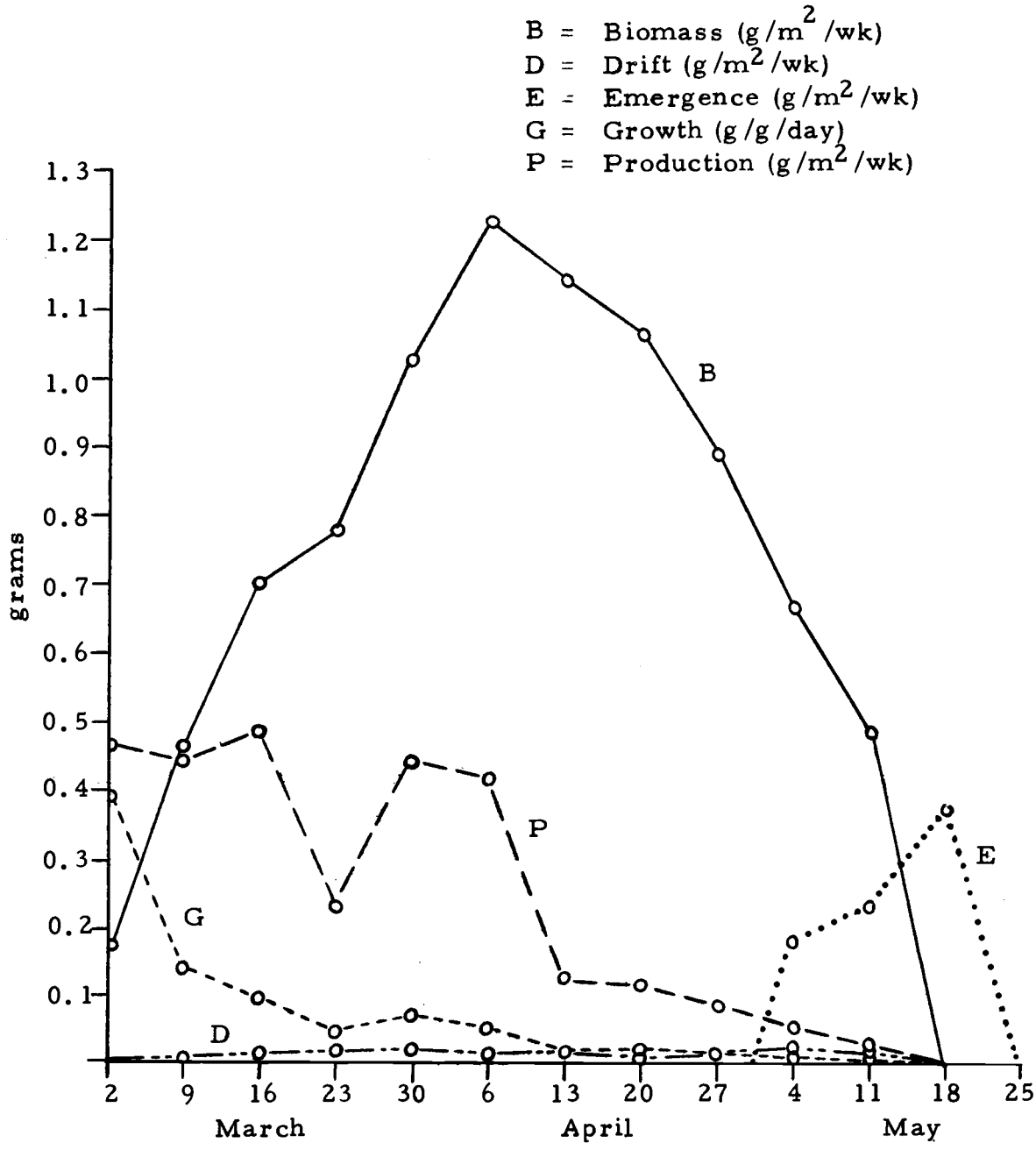


Figure 29. Biomass, drift, emergence, growth and production of P. caudatum at station O-III, 1971. Dates represent the end point of weekly periods.

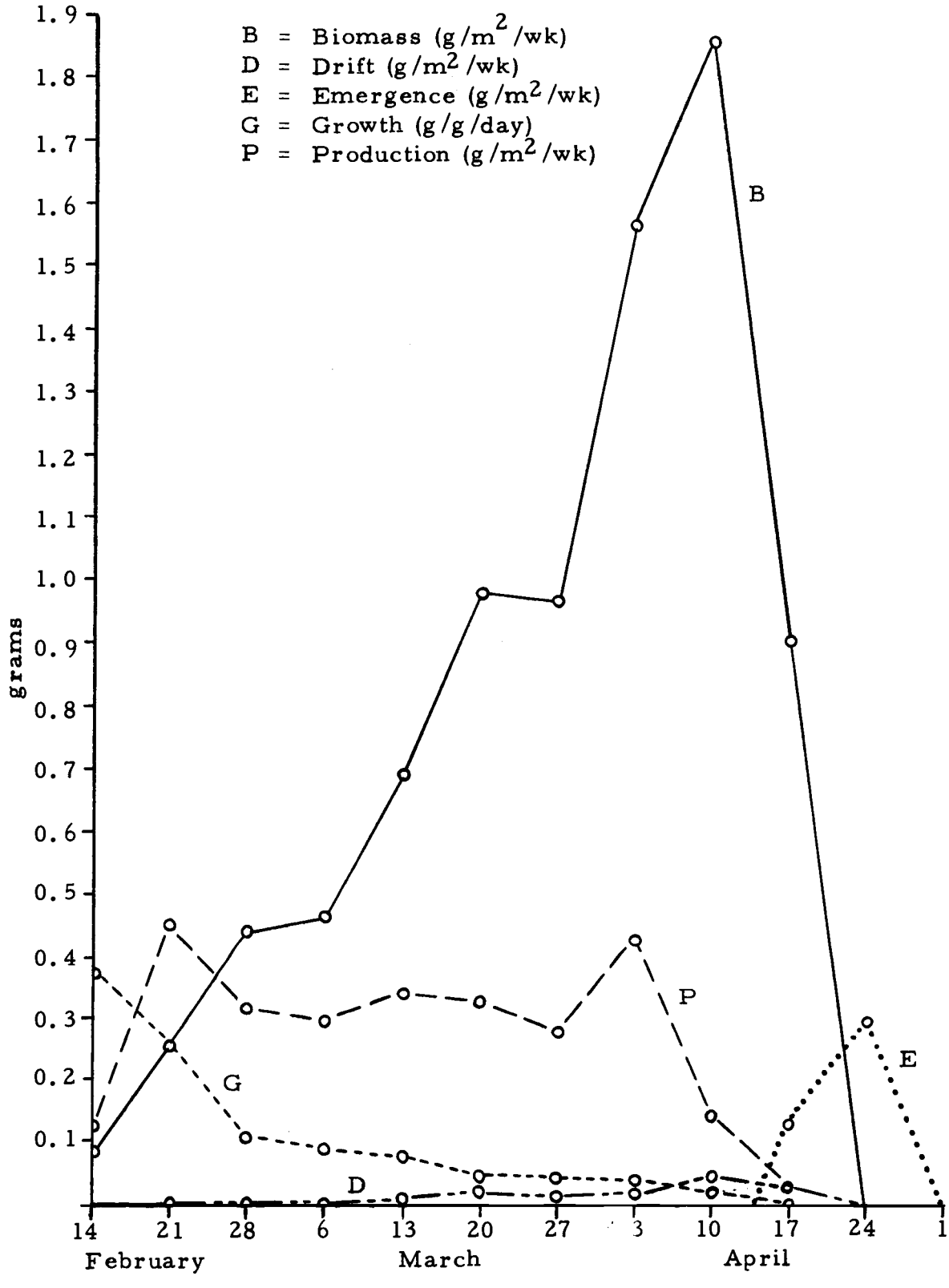
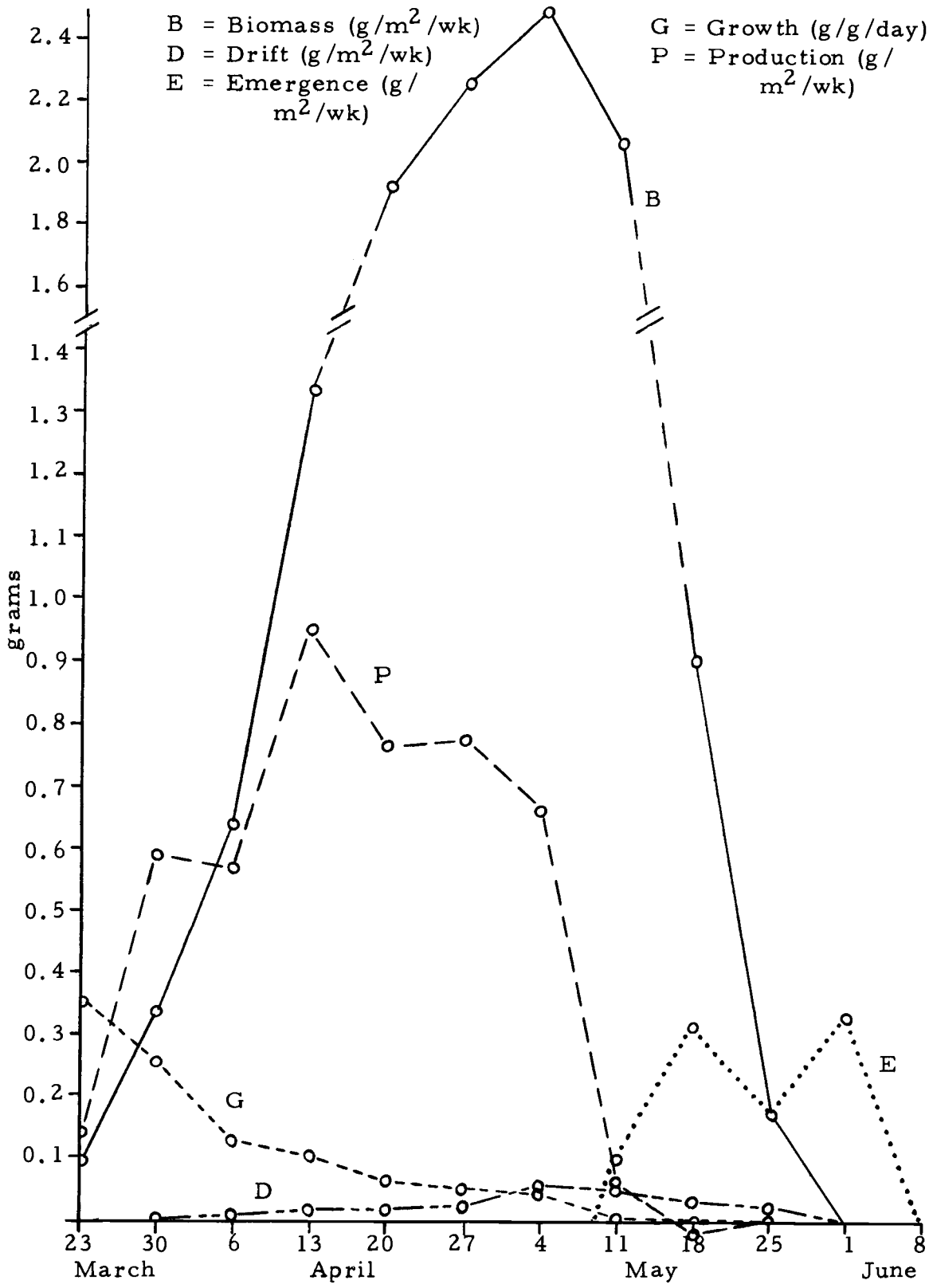


Figure 30. Biomass, drift, emergence, growth and production of P. dicum at station O-III, 1972. Except for the initial sampling duration (4 days), dates represent the end point of weekly periods.

Figure 31. Biomass, drift, emergence, growth and production of *S. arcticum* at station B-I, 1972. Except for the initial sampling duration (4 days), dates represent the end point of weekly periods. Note scale change on ordinate axis.


B = Biomass (g/m2/wk)
D = Drift (g/m2/wk)
E = Emergence (g/m2/wk)
G = Growth (g/g/day)
P = Production (g/m2/wk)
grams
2.4
2.2
2.0
1.8
1.6
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
B
P
G
D
E
23
30
6
13
20
27
4
11
18
25
1
8
March
April
May
June

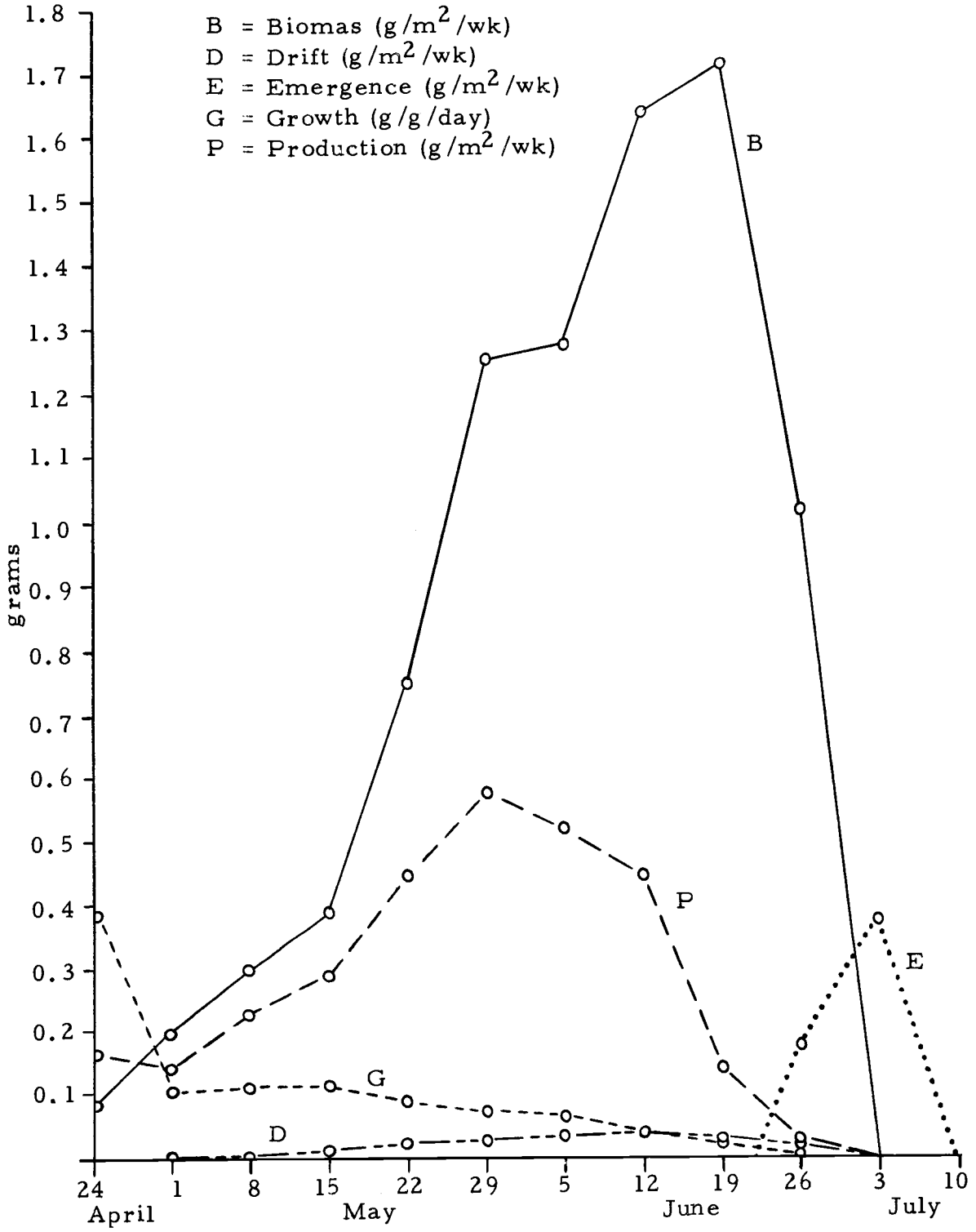


Figure 32. Biomass, drift, emergence, growth and production of S. canadense at station S-I, 1972. Except for the initial sampling duration (5 days), dates represent the end point of weekly periods.

Table 28. Density, biomass, production and turnover ratio data for black flies at all 1971 and 1972 stations.

Station	Initial Density (no./m^2)	Mean Density (no./m^2)	Mean Biomass (g/m^2)	Annual Production (g/m^2)	Turnover Ratio (P/$\bar{B}$)
1971			*P. caudatum*		
B-VI	10938	3677	0.669	2.381	3.6
S-VI	17708	6469	0.778	3.052	3.9
O-I	13542	5084	0.922	3.028	3.3
O-II	11458	4962	0.729	2.561	3.5
O-III	12500	4245	0.780	2.865	3.7
O-IV	11120	4176	0.604	2.431	4.0
O-V	12500	4053	0.861	2.856	3.3
O-VI	8542	3636	0.742	2.426	3.3
			P. dicum		
B-VI	7813	3494	0.641	2.164	3.4
S-VI	11281	4265	0.937	2.857	3.0
O-I	8854	3961	1.037	3.651	3.5
O-II	6563	3294	1.018	3.117	3.1
O-III	16667	5906	0.870	3.300	3.8
O-IV	13958	4578	0.546	2.381	4.4
O-V	14063	4289	0.689	2.695	3.9
O-VI	7917	3586	0.670	2.351	3.5
			S. arcticum		
B-I	11146	4527	0.796	2.819	3.5
B-II	25000	10860	1.277	4.589	3.6
B-III	15104	7205	1.356	4.193	3.1
S-III	8958	5019	1.274	3.625	2.8
S-IV	12188	5713	1.220	3.974	3.3
S-V	13750	5896	1.043	3.523	3.4
			S. canadense		
B-VII	15938	6192	1.103	3.654	3.3
B-VIII	10417	4597	0.920	3.197	3.5

(Continued on next page)

Table 28. (Continued)

Station	Initial Density (no./m^2)	Mean Density (no./m^2)	Mean Biomass (g/m^2)	Annual Production (g/m^2)	Turnover Ratio (P/$\bar{B}$)
1972			*P. caudatum*		
B-VI	7396	3555	0.663	2.324	3.5
S-VI	10938	5061	0.774	2.772	3.6
O-I	14271	6314	0.936	3.495	3.7
O-II	10417	5062	0.776	2.685	3.5
O-III	13229	5680	0.942	2.912	3.1
O-IV	9932	4888	0.832	2.787	3.4
O-V	9792	4769	0.780	2.602	3.3
O-VI	7813	2652	0.428	1.467	3.4
O-VII	6458	3229	0.819	2.297	2.8
			P. dicum		
B-VI	10533	3923	0.751	2.464	3.3
S-VI	14792	4481	0.736	2.924	4.0
O-I	17396	7577	1.242	4.834	3.9
O-II	10208	4569	1.061	3.344	3.2
O-III	16458	5160	0.849	2.701	3.2
O-IV	11667	4195	0.823	2.987	3.6
O-V	14167	4985	0.914	3.004	3.3
O-VI	15625	5144	0.690	2.431	3.5
O-VII	11004	3765	0.633	2.232	3.5
			S. arcticum		
B-I	21146	7989	1.271	4.459	3.5
B-II	18021	8289	1.229	3.957	3.2
B-III	20000	9084	1.225	4.033	3.3
S-III	12708	5636	1.031	3.700	3.6
S-IV	17813	7558	1.440	4.460	3.1
S-V	15938	6427	1.329	4.065	3.1
			S. canadense		
B-IV	13542	4734	0.450	2.261	5.0
B-V	18750	7175	1.097	3.685	3.4
B-VII	11250	4771	1.090	3.360	3.1
B-VIII	13125	4736	0.870	2.907	3.3
S-I	11250	5101	0.884	2.963	3.4
S-II	13333	4986	0.864	3.102	3.6

the same time between locations, or when maximum density or biomass were present. There appeared to be no consistent upper or lower threshhold interactions between growth, standing crop and mortality that determined whether tissue elaboration was to increase, remain the same or decline.

The interrelationship between growth, standing crop and mortality governed both long and short-term variations in rates of biomass and production increase or decrease. Growth and mortality could either act separately, or in conjunction with one another. The former may be partially illustrated by S. arcticum data (Figure 31). Production drops during March 31-April 6 and April 14-20, 1972 were mostly caused by unusually low growth rates. Mortality remained "normal" in these periods, this fact being reflected by the uniformity of biomass. Data in Figure 32 (S. canadense) show how production was altered during a time of comparatively high mortality (May 30-June 5, 1972). Larval growth rates in this period were, if anything, slightly higher than normal. In most instances, growth and mortality functioned together to cause production variations. This can be most obviously observed between March 17-23, 1971 in Figure 29 (P. caudatum). The regulatory influence of the two characteristics usually was more subtle than in the case illustrated.

As pointed out by Cummins (1973), early-instar larvae of insects have classically been neglected due to the ease of

accomplishing research on larger instars or more advanced stages. The author suggests that much more work should be done on early-instar individuals, since they usually are associated with maximum population densities, and high growth and feeding rates. Quantitative sampling of sufficient precision to accurately apportion the contribution of each instar to standing crop, growth or production is rarely possible. This is because of the difficulty in adequately estimating numbers of small individuals. Kimerle and Anderson (1971) found that cohort production errors of up to 20% were possible due to losses in sampling of first and second-instar Glyptotendipes barbipes. In the current study, losses of early-instar black fly larvae were miniscule since the net used for benthos sampling had a mesh of approximately 50 microns. Even if 10% of first and second-instar larvae were missed, annual production for all species would have been reduced by less than 2%.

Cumulative annual production for all species is presented on an instar basis in Figure 33. The density, weight and growth rate data for these calculations were approximated from two year averages of the field and laboratory data. These figures appear in Appendix VI.

Annual production estimates calculated from instar mean growth and biomass data were very similar to those of the normally used instantaneous growth method of Ricker (1968). Instar-related production determinations (in g/m^2) and deviations from the mean field

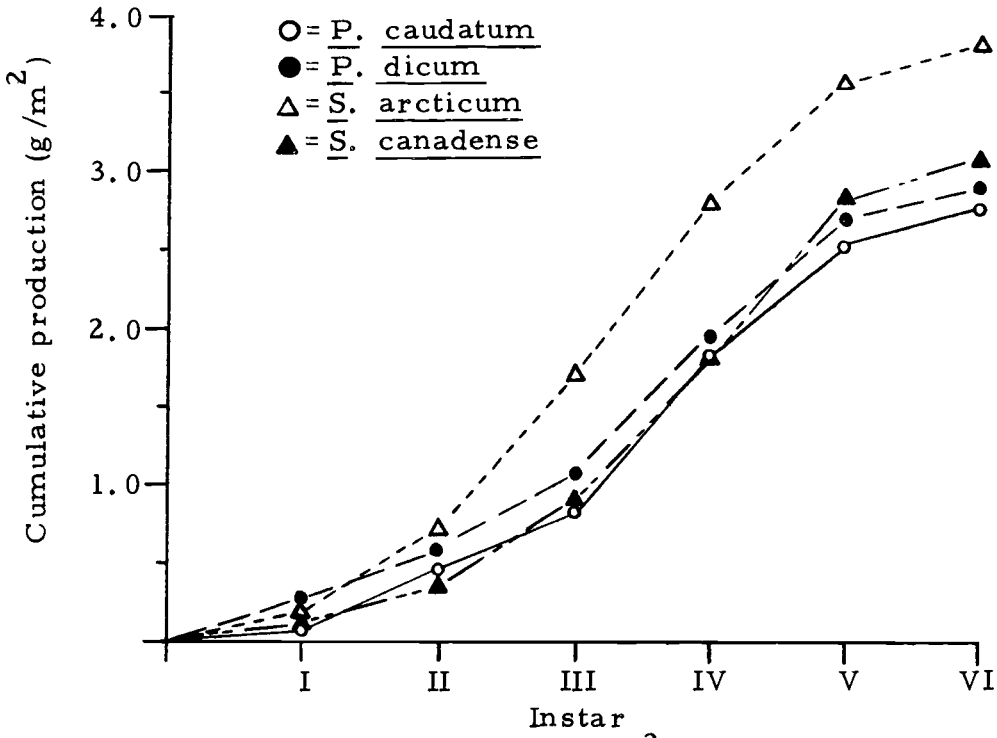


Figure 33. Cumulative production (g/m^2) for black fly larval instars, averaged for all stations and both years.

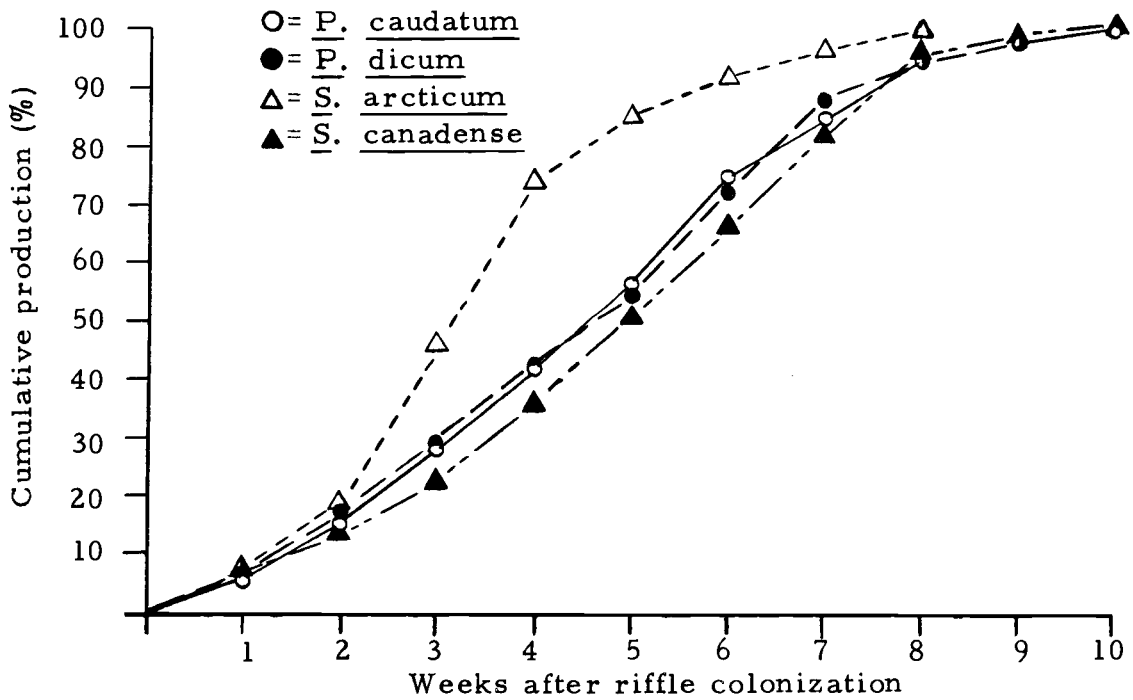


Figure 34. Cumulative production percent over time for black fly larvae, averaged for all stations and both years.

estimates were: P. caudatum, 2.711 (+2.5%); P. dicum, 2.890 (-0.6%); S. arcticum, 3.813 (-3.5%); and S. canadense, 3.097 (-1.4%). The closeness of each estimate to the instantaneous growth calculated determination was slightly artificial, since some latitude was possible (and was taken) in determining instar densities. Experimentally, it was found that instar production changed very little no matter where density was set, as long as larval numbers data were within error terms. Tissue elaboration estimates were most dependent on mean larval size and growth parameters, and since each was representative, final annual determinations came close to those of the field.

The highest production occurred during the fourth instar for P. caudatum, P. dicum and S. arcticum, but rates for instars three and five were only slightly lower (Appendix VI). Greatest S. canadense production occurred in instar five. For the species as just listed, the first three instars accounted for 32.7%, 38.2%, 45.2% and 28.3% of all tissue elaborated. The amount of production contribution by larvae of aquatic insects may be variable. For example, production by the first two and last two larval instars of Glyptotendipes barbipes was estimated by Kimerle and Anderson (1971) to be 14.8% and 85.2% of the total.

Weekly cumulative production percentages, averaged for both years, have been presented in Figure 34 for all species. Original estimates appear in Appendix VII. As these data illustrate, 50% of all

production occurred for P. caudatum, P. dicum and S. canadense by week five. Between weeks six and seven, the 75% level was reached for the three simuliids. The comparatively short duration of S. arcticum larvae caused 50% and 75% production levels to occur just after week three and week four respectively. Production for all species was associated more with the larval instars present during the first half of riffle inhabitation. This conclusion is also apparent from Figure 33 when it is considered that Prosimulium spp. and Simulium spp. instars one through four were on riffles during approximately the first half of larval growth periods. Duration data for instars of all species appear in Table 8 and Appendix VI.

Density, Biomass and Production Relationships

Figures 35 through 38 graphically illustrate the relationship that existed between initial density, mean density, mean biomass and annual production at all stations for the four black flies. Stations are ranked by increasing larval production, left to right. Mean biomass and production estimates were significantly correlated for all species for both years (mean r of 0.88; Table 23). The mean density to production relationship was statistically close in all cases but P. dicum (1971) and S. arcticum and S. canadense (1972). The overwhelming majority of Prosimulium spp. and Simulium spp. density, biomass and production trend inconsistencies were directly related to

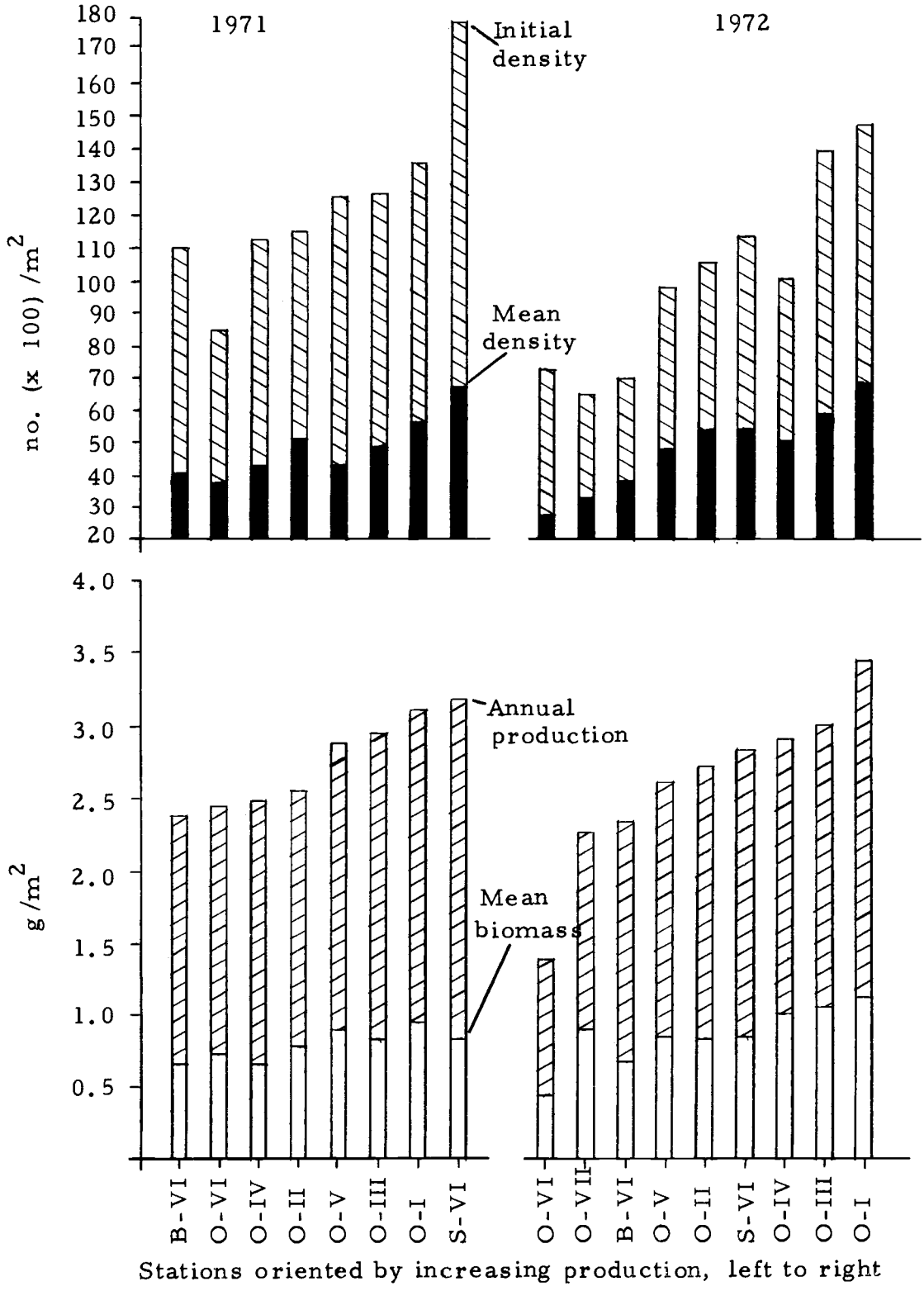


Figure 35. Larval production, density and biomass at all P. caudatum stations in 1971 and 1972.

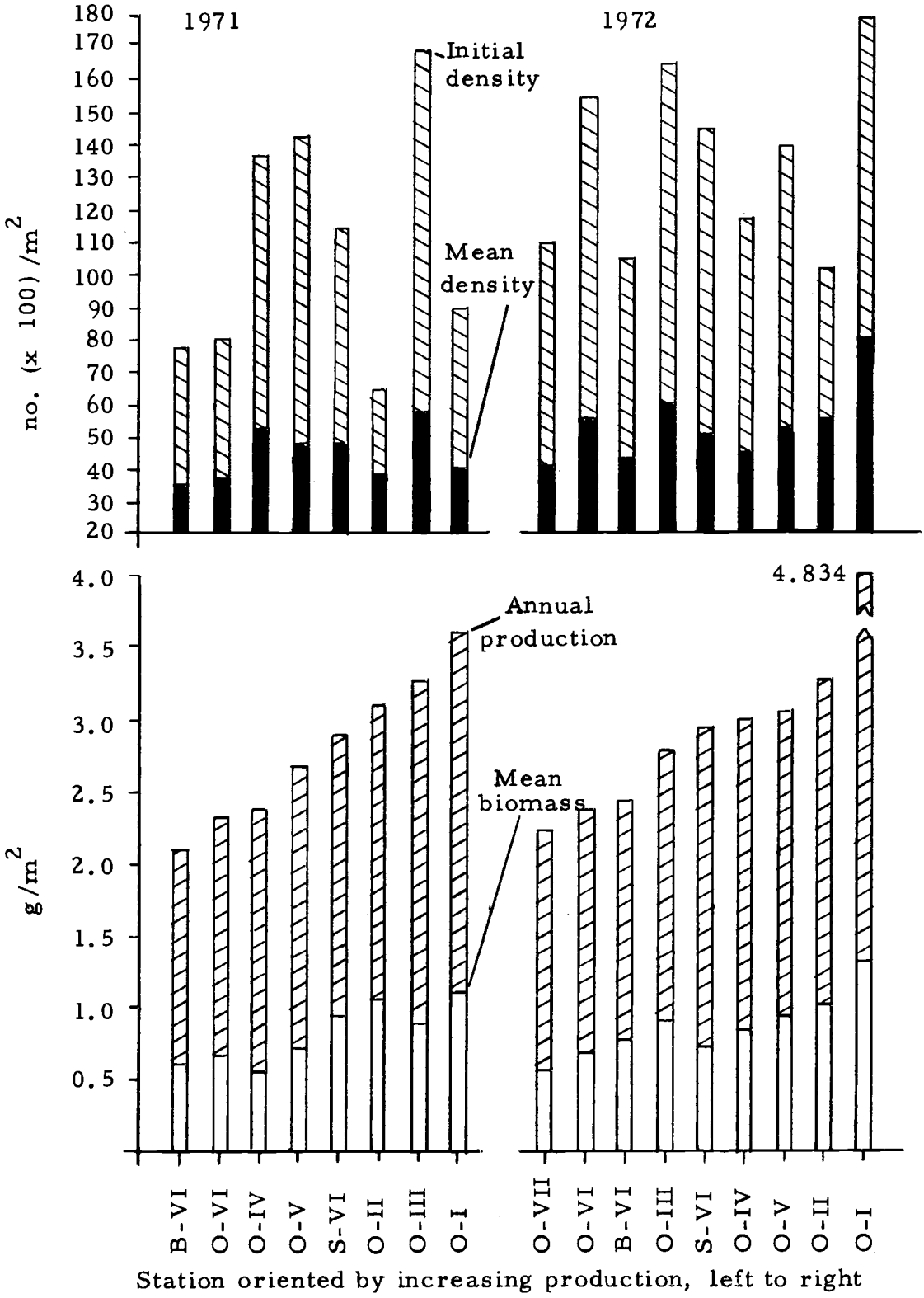


Figure 36. Larval production, density and biomass at all P. dicum stations in 1971 and 1972.

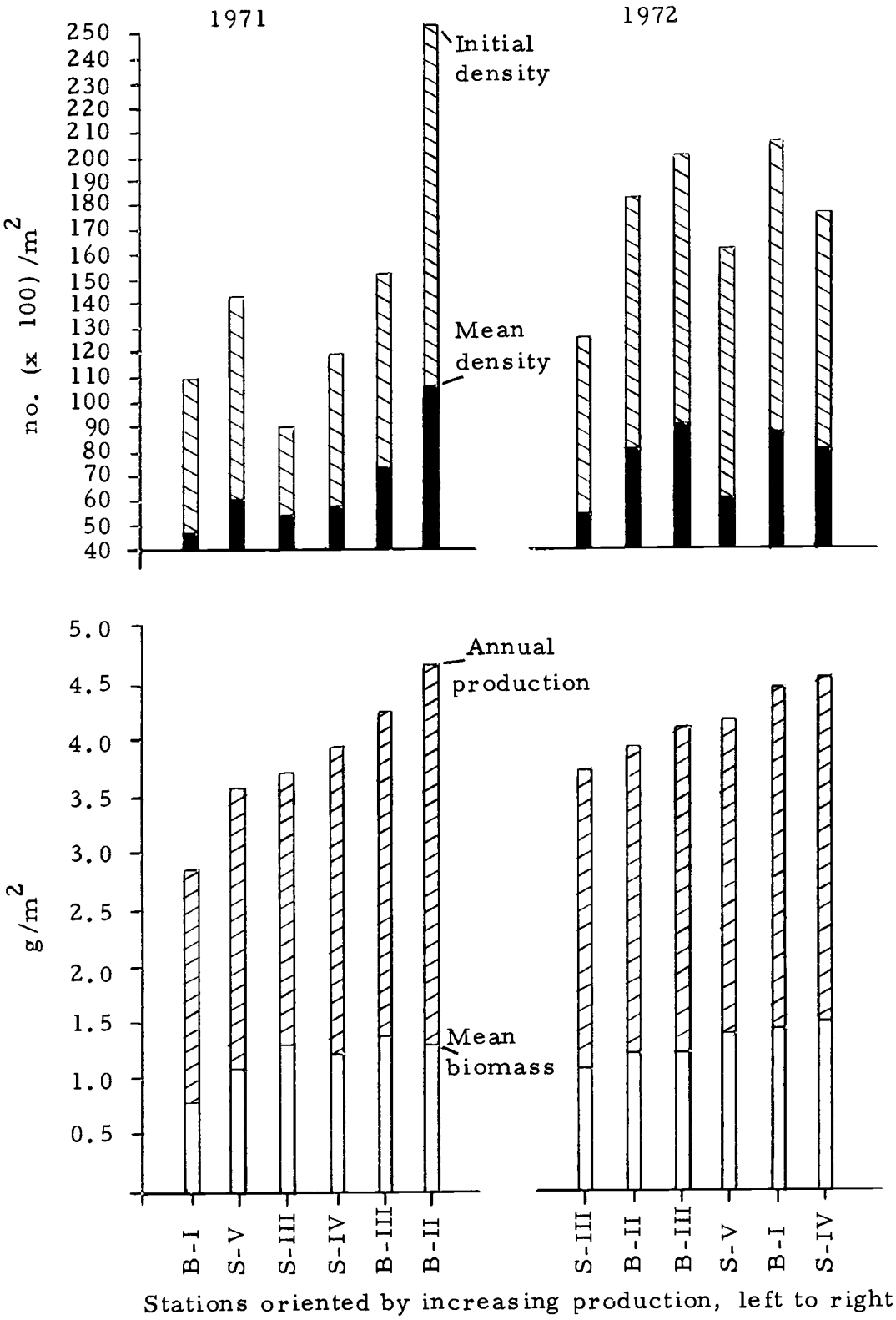


Figure 37. Larval production, density and biomass at all S. arcticum stations in 1971 and 1972.

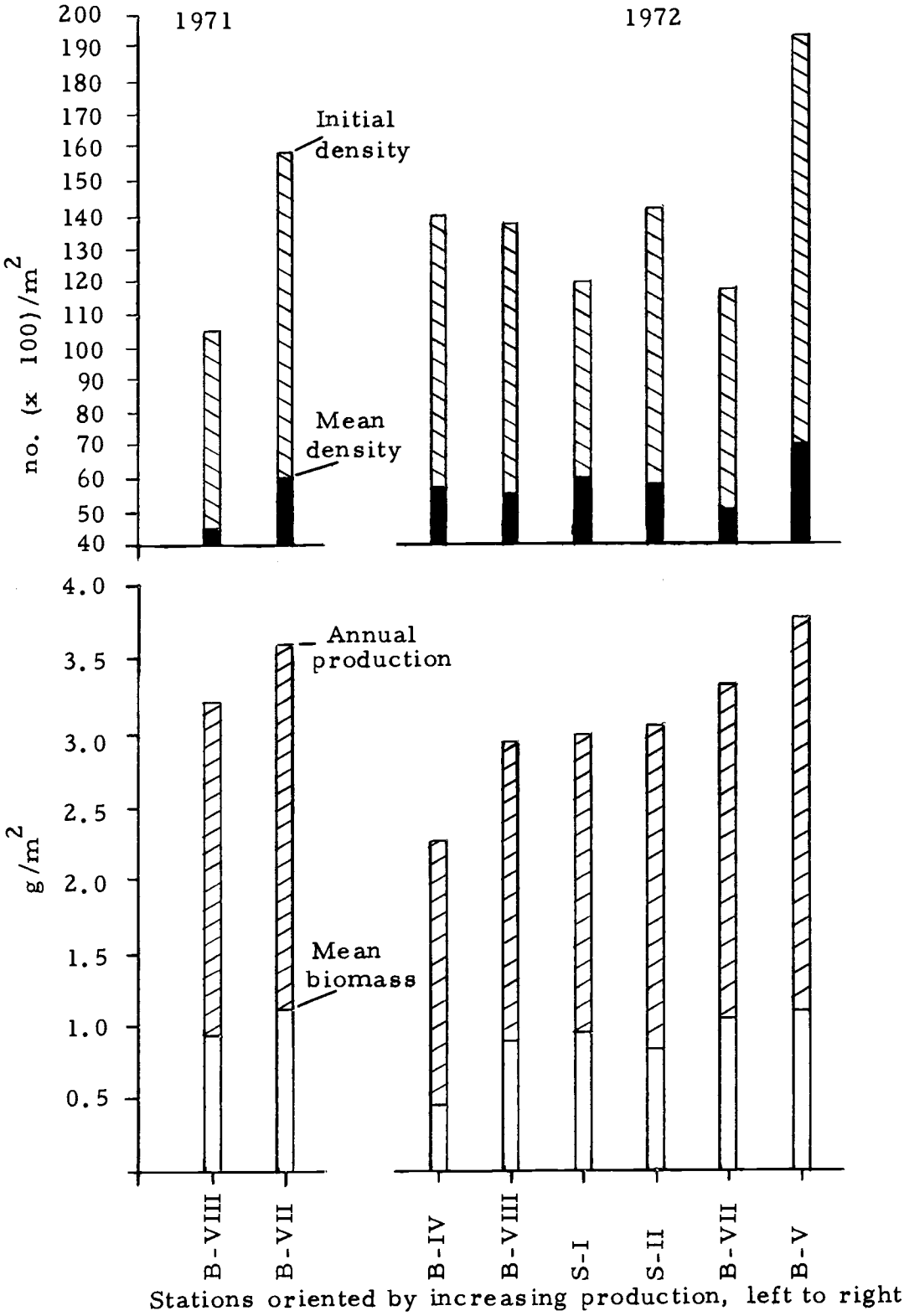


Figure 38. Larval production, density and biomass at all S. canadense stations in 1971 and 1972.

periods of variable mortality. Usually, only high mid-season mortality noticeably decreased production (P. dicum: O-IV, 1971; S. canadense: B-IV, 1972), since early and late-season losses involved low producing small (minimal biomass) or large (slow growing) larvae.

Differences in growth rates between aggregates had much less affect on production than did mortality. The major variations in growth rate were almost entirely associated with the early instars, when little tissue elaboration was taking place. For example, when production from sites with the lowest growth rate during the first two weeks was recalculated using the observed highest growth rate data, annual production was only increased by: P. caudatum, 1.0%; P. dicum, 0.4%; S. arcticum, 0.8%; and S. canadense, 0.7%. Correlations between growth rate and production were generally low for all species (mean r of 0.11; Table 23). Observations certainly suggest that, though production is governed by the interaction between growth and standing crop, growth rate was not singular in importance or effect to dynamic variations.

Production Comparisons between Streams, Species and Years

Data in Table 29 compare annual black fly production in the three streams. During both years, maximum production occurred for

Table 29. Annual black fly larval production (g/m^2), by stream, in 1971 and 1972.

Year & Stream	*P. caudatum*	N	*P. dicum*	N	*S. arcticum*	N	*S. canadense*	N
1971								
Berry Creek	2.381	1	2.164	1	3.867	3	3.426	2
Oak Creek	2.695	6	2.916	6	-		-	
Soap Creek	3.052	1	2.857	1	3.707	3	-	
1972								
Berry Creek	2.324	1	2.464	1	4.150	3	3.053	4
Oak Creek	2.606	7	3.076	7	-		-	
Soap Creek	2.772	1	2.924	1	4.075	3	3.033	2

P. caudatum in Soap Creek, *P. dicum* in Oak Creek and *S. arcticum* in Berry Creek. Only one stream was investigated for *S. canadense* in 1971, but the following year, Berry Creek production was slightly higher than in Soap Creek. *Prosimulium* spp. interstream differences were artificial, since only in Oak Creek were replicates accomplished. Minimum or maximum production rates of larvae in this stream were very similar to the singular determinations from Berry and Soap Creeks. In the three cases where more valid comparisons existed because of multiple trials, *S. arcticum* and *S. canadense* production means between streams were never statistically significant in difference. Since interstream variations appeared minimal, all production estimates for each species have been treated as replicates and combined.

Mean annual production, in order of increasing characteristics by species, was (in g/m^2): P. caudatum, 2.644; P. dicum, 2.908; S. canadense, 3.141; and S. arcticum, 3.950 (Table 30). Averaged for 1971 and 1972, confidence intervals ranged between 6.7% and 10.9% of production means. These data reflect the relatively small differences that existed in production, not only between stations and streams, but years as well.

Prosimulium caudatum average annual production was about 4% higher in 1971, P. dicum was 6% higher in 1972, S. canadense was 12% higher in 1971 and S. arcticum was 9% higher in 1972. With few exceptions, this was also the annual trend for initial and mean density, and mean biomass (Tables 24 and 26).

On a riffle basis, only Prosimulium spp. production was additive since the two species always coexisted. Prosimulium spp. production averaged 5.515 g/m^2 in 1971 and 5.585 g/m^2 the following year. Prosimulium caudatum plus P. dicum initial standing crop and production data have been presented by station in Table 31. Prosimulium dicum was generally the dominant species, though in 7 of the 17 comparisons, P. caudatum had higher production. Averaged for both years, tissue elaboration by the former species exceeded that of the latter by 10.0%.

Had growth and mortality remained constant for larvae of the four species at all stations, annual production would have always been

Table 30. Comparison of black fly larval production within and between 1971 and 1972.

	1971 Mean (N)	1972 Mean (N)	1972 + 1972 Mean (N)
	P. caudatum		
Weekly production (average; g/m^2)	0.255 (8)	0.254 (9)	0.255 (17)
Weekly production (maximum; g/m^2)	0.452	0.497	0.480
Annual production (total; g/m^2)	2.700 0.099 (SE)	2.593 0.183 (SE)	2.644 0.105 (SE)
	P. dicum		
Weekly production (average; g/m^2)	0.277 (8)	0.303 (9)	0.289 (17)
Weekly production (maximum; g/m^2)	0.492	0.512	0.503
Annual production (total; g/m^2)	2.814 0.183 (SE)	2.991 0.258 (SE)	2.908 0.158 (SE)
	S. arcticum		
Weekly production (average; g/m^2)	0.431 (6)	0.475 (6)	0.451 (12)
Weekly production (maximum; g/m^2)	0.957	0.916	0.936
Annual production (total; g/m^2)	3.787 0.250 (SE)	4.112 0.122 (SE)	3.950 0.132 (SE)
	S. canadense		
Weekly production (average; g/m^2)	0.346	0.282	0.319
Weekly production (maximum; g/m^2)	0.562	0.643	0.590
Annual production (total; g/m^2)	3.426 0.229 (SE)	3.046 0.196 (SE)	3.141 0.162 (SE)

Table 31. Initial density (no. /m^2) and annual production (g/m^2) for *Prosimulium* spp. larvae at all 1971 and 1972 stations.

Station	1971		1972	
	Initial Density	Production	Initial Density	Production
B-VI	18751	4.545	17813	4.788
S-VI	29166	5.909	25730	5.696
O-I	22396	6.679	31667	8.329
O-II	18021	5.678	20625	6.029
O-III	29167	6.165	29687	5.613
O-IV	24896	4.812	21459	5.774
O-V	26563	5.551	23959	5.606
O-VI	16459	4.777	23438	3.898
O-VII			17396	4.529
Mean	23177	5.515	23530	5.585
SE	1783	0.265	1633	0.415

Table 32. Comparison of initial density and annual production on a m^2 of usable substrate and a m^2 of overall riffle basis for black flies. Data are averaged for all stations and both years.

	P. caudatum	*P. dicum*	*S. arcticum*	*S. canadense*
	Initial density (no. /m^2)			
m^2 Usable substrate	16460	18544	22270	18067
m^2 Overall riffle	11072	12292	15981	13456
	Production (g/m^2)			
m^2 Usable substrate	3.938	4.383	5.542	4.240
m^2 Overall riffle	2.644	2.908	3.950	3.141

a direct function of colonization density. The numbers of larvae colonizing riffles in all streams was fairly constant at most locations. The confidence intervals for pooled two-year colonization density means averaged 14.2%. Though variations did occur, the relationship between initial larval numbers and production was a generally close one (mean r of 0.62; Table 23). Because generally equal numbers of larvae were settling on substrates of variable dimension (two-year range of 3732 to 6074 cm^2), there was a negative correlation between production and surface area (mean r of -0.64) when the data were expressed on the basis of a m^2 of usable substrate.

With the m^2 of overall riffle situation, which is how data have been presented in this dissertation, the relationship between area and production was low (mean two-year r of 0.24). This was because the mathematically expanded data on a m^2 of overall riffle basis had the effect of masking substrate based relationships. For example, if equal larval numbers colonized two riffles that had 2000 cm^2 and 4000 cm^2 of usable substrate, density of the former (as m^2 of usable substrate) would be twice that of the latter. When the two were expanded to a m^2 of overall riffle basis though, densities would be equal. Thus, differences between numbers of settling larvae (or production) and riffle sizes were compensated for.

Data in Table 32 compare density and production on a m^2 of overall riffle and m^2 of usable substrate basis. As illustrated for the

latter, comparatively great amounts of tissue were elaborated on limited surface areas. On an annual average basis, density, biomass and production per m^2 of usable substrate consistently exceeded those determinations on a m^2 of overall riffle by about 30%. Original m^2 of usable substrate based initial density and production data appear in Appendices IX and X respectively.

Comparisons of production estimates between m^2 of usable substrate and m^2 of overall riffle illustrate how conclusions can vary depending on sampling procedure. This study was initially designed to present data on a m^2 of overall riffle basis, so it would be comparable with the majority of other benthic studies. Sample variance was minimized by concentrating on the microhabitat where black fly immatures lived. Most other workers have had to sample comparatively broad areas since the animals they investigate do not have clearly discernible habitats. Random samples taken at each study site in sufficient quantities could have correctly indicated that a slightly positive relationship existed between production and riffle area. Conclusions would not have been possible as to the true nature of production to usable substrate interactions though. Thus, one aspect of the study would be lost. It is not unlikely that the results of other studies mask actual biological characteristics, especially as to interrelationships between dynamic processes of natural populations and specific ecological habitat requirements. Black fly larvae certainly do not

appear unique in the fact that they require restricted physical characteristics in order to exist in the niche occupied.

In addition to the other two methods of data presentation, production has also been considered on a m^2 of total riffle basis. This presentation not only accounts for areas where black fly larvae occur, but also the remainder of the riffle on which inhabitation is apparently impossible. Pooled two-year production, in g/m^2, was: P. caudatum, 0.438; P. dicum, 0.481; S. canadense, 0.578; and S. arcticum, 0.679. These data, which are an average of about 83% less than estimates on a m^2 of overall riffle basis, are considerably lower than for most other aquatic insects (Table 33). This is because the data in the table generally reflect production over the entire area where the organisms occur, whereas the black fly estimates are expressive of both inhabitable and unsuitable portions of the riffle.

Indirect Methods of Calculating Production

With the interest in quantitatively characterizing energy flow in ecosystems, the development of indirect methods of calculating production is desirable. It would be an overwhelming task to calculate production by Ricker's (1968) growth or Allen's (1951) graphical methods for each species in a stream community. To date, techniques have been developed utilizing estimates of cohort biomass (Hynes and Coleman, 1968), respiration (McNeill and Lawton, 1970), turnover

Table 33. Comparative production (g dry wt/m^2) and turnover ratio (annual production/mean biomass) estimates of aquatic insects.

Species and Source	Annual Production (g/m^2)	Turnover Ratio
Prosimulium caudatum	2.644	3.5
Prosimulium dicum	2.908	3.5
Simulium arcticum	3.950	3.3
Simulium canadense	3.141	3.5
Sialis californica	1.88	1.1
Sialis rotunda (Azam, 1969)	2.63	2.5
Insect macroconsumers in Bear Brook, N.H. (Fisher and Likens, 1973)	4.10	4.5
Hexagenia spp. (Hudson and Swanson, 1972)	1.498	2.6
	1.525	2.4
	1.844	2.6
	2.113	2.7
	2.314	2.6
Simulium equinum	2.34	
Simulium ornatum (Ladle *et al.*, 1972)	3.56	
Baetis bicaudatus	1.28-4.30	1.4-4.6[a]
Oligophlebodes sigma (Pearson and Kramer, 1972)	0.65-2.13	1.6-5.3[a]
Baetis vagans (Waters, 1966)	2.0[a]	3.2
Ephemerella subvaria (Waters and Crawford, 1973)	4.2[a]	4.2

[a]Estimated conversion

ratio and drift (Waters, 1966, 1969b) and emergence (Illies, 1971). In the current study, all methods but the one based on respiration are discussed.

The Hynes-Coleman Technique. Using the Hamilton (1969) modification of the Hynes and Coleman (1968) technique, annual production estimates were derived for *Prosimulium* spp. and *S. arcticum* in 1972. These determinations exceeded those calculated by the Ricker growth method by an average of 33%. Exactly why such differences exist has not yet fully been examined, and communications are still being exchanged between myself and Dr. Hamilton. There is a strong possibility that length-width data used in some critical conversions are wrong. Slight changes in this parameter have experimentally been found to change results drastically.

Turnover Ratios. As discussed by Waters (1969b), turnover ratios (annual production/mean biomass) of freshwater invertebrates are relatively constant, ranging from approximately 2.5 to 5.0 and averaging about 3.5. Mean 1971 plus 1972 turnover ratios were: *P. caudatum*, 3.5; *P. dicum*, 3.5; *S. arcticum*, 3.3; and *S. canadense*, 3.5. The overall range was 2.8 to 5.0 (Table 28), but over 90% of the estimates were between 3.0 and 4.0. Data were so similar that even intergeneric differences were not apparent. These ratios are comparable to estimates derived for other aquatic insects, especially those found in lotic situations (Table 33).

At stations O-IV (P. caudatum and P. dicum, 1971), and B-IV (S. canadense, 1972), turnover ratios were the highest recorded: 4.0, 4.4 and 5.0 respectively. Unusually high Prosimulium spp. larval losses occurred at about the same time midway through riffle inhabitation periods. The higher S. canadense turnover ratio reflects the greater degree to which biomass became retarded due to later larval losses.

The mean turnover ratio for all four black fly species was 3.5. This figure can be used along with biomass data to provide a remarkably good production estimate for the simuliids of this Oregon research. By multiplying the mean biomass data for each species by the 3.5 estimate, annual production differed from the Ricker growth method by only an average of 2.8%. This illustrates how functional the use of a single turnover ratio figure can potentially be, especially in a community situation, where more than one species is involved.

Drift and Production. Waters (1961) first advanced the proposition that drift could be used as an index of production, based on studies of Baetis, Gammarus and other aquatic invertebrates. Pearson (1970) demonstrated a positive correlation between production and drift of Oligophlebodes sigma and Baetis bicaudatus. However, Elliott and Minshall (1968) and Bishop and Hynes (1969) stated that drift was not a reliable index of production of many benthic insects.

In the present study, no one drift rate conversion factor (annual production/annual drift) was found that gave production estimates with acceptable error terms for all species or even one genus. Using gross two-year mean drift factors of 16, 14, 20 and 11 for P. caudatum, P. dicum, S. arcticum and S. canadense, drift calculated: Ricker's growth calculated production estimates differed by 2.2%, 1.8%, 5.8% and 11.3% respectively. As shown by Waters (1972) though, few benthic invertebrates have as uniform a drift as reported in the current study. Production estimates would therefore not be as easily facilitated or precise for most aquatic taxa, even if species-related conversions were utilized.

Emergence and Production. Illies (1971) demonstrated that emergence was a quantifiable portion of production, at least for some benthic insects. Thus, if the relationship between the two parameters was constant, a simple, perhaps efficient method of production calculation could be devised. Conversion factors, if complete enough in coverage of various taxa, would especially facilitate investigations of community production.

Production/emergence (P/E) ratio data are presented for all species in Tables 34 and 35. By utilizing the mean two-year P/E ratio of 4.6, production estimate errors compared to the Ricker growth method were: P. caudatum, 21.7%; P. dicum, 3.8%; S. arcticum, 0.5%; and S. canadense, 10.8%. Except for the

Table 34. Comparison of emergence and production (g/m^2) for black flies in 1971 and 1972.

Species	No. Estimates	Mean Emergence	Mean Production	Production/ Emergence Ratio	
				Mean	Range
		1971			
P. caudatum	3	0.785	2.775	3.4	3.3-4.2
P. dicum	3	0.644	3.112	5.1	3.3-8.4
S. arcticum	1	0.880	3.625	4.1	-
S. canadense	1	0.663	3.654	5.5	-
		1972			
P. caudatum	5	0.704	2.798	4.0	3.4-4.9
P. dicum	5	0.586	3.223	5.5	4.1-6.9
S. arcticum	2	0.855	4.080	4.8	4.7-4.9
S. canadense	2	0.583	3.324	5.5	5.5-5.5

Table 35. Production/emergence ratio means and standard errors for black flies, pooled for years and species.

	Year(s)	No. Estimates	Production/Emergence Ratio	
			Mean	Standard Error
P. caudatum	1971 + 1972	8	3.8	0.2
P. dicum	1971 + 1972	8	5.4	0.5
S. arcticum	1971 + 1972	3	4.6	0.2
S. canadense	1971 + 1972	3	5.5	0.1
All species	1971	8	4.3	0.4
"	1972	14	4.8	0.3
"	1971 + 1972	22	4.6	0.2

P. caudatum estimate, these determinations are well within confidence limits associated with most production studies. Prosimulium caudatum emergence-calculated data were underestimates for both years, perhaps indicating that the species may have a more complex production to emergence relationship. Alternatively, with the minimum number of replicates, variations may have reflected sampling error. For estimating the total production of all pooled species, the 4.6 factor gave a figure only 2.3% different than the one elaborated by the Ricker growth technique.

Similar P/E ratios, at least for P. dicum, S. arcticum and S. canadense, characterized the relative uniformity that was found to exist between simuliid population (aggregate) dynamics. As summarized by Waters (1969b), production/biomass and production/emergence ratios will generally be most similar in populations where a close relationship exists between initial and final numbers of individuals. This situation certainly appeared characteristic of the four simuliid species studied.

Considering the degree to which small changes in P/E ratios experimentally altered production estimates, it should not be expected that one, two or even a few conversions will be enough to adequately investigate community characteristics (Speir and Anderson, 1974). Minor differences exist between data in this dissertation and the work of Speir and Anderson, because the published tables were adjusted for

some anomalous mortality data. Therefore, production estimates at stations O-IV and B-IV were calculated as if unusual standing crop reductions had not taken place. It was felt that by using these, and not the low determinations, researchers would have a slightly more realistic picture of an idealized system.

Comparison of Simuliid Production with Other Aquatic Insects

Annual production for the species listed in Table 33 range from about 1.5 to 4.2 g/m^2. Estimates for Oregon black flies exceed those of most other organisms by 25 to 50%. In general, simuliid production may be expected to be higher than that of the majority of benthic invertebrates, because of the larval aggregate patterns. Black flies rarely exist in moderate numbers during most of the larval period. Either they are absent (or scarce) or they are abundant. Thus, studies specifically oriented to black flies will be biased towards the latter situation and will result in overestimates of production when compared to organisms which do not have such limited habitat characteristics.

Simulium equinum and *S. ornatum* values derived by Ladle *et al.* (1972) are the result of three "summer" generations for the former and three "summer" and one "winter" generation for the latter species. The annual production is similar to that of the current study for univoltine species.

Black fly production determinations from Lapland by Ulfstrand (1968) have not been presented in Table 33 because his day-based data cannot readily be transformed into annual rates. By expressing Oregon estimates on a daily basis, comparisons can be accomplished though. During periods of maximum production, Schonbaueria annulitarsis Zetterstedt exceeded S. arcticum by about 9% and the other three simuliids by an average of 16%. Other Lapland black flies (Cnephia tredecimata Edwards, Gnus forsi Carlssen and Simulium truncatum Lundstrum) had daily production rates ranging from 16% lower to 23% higher than the mean for the four Oregon species.

Dynamics and Mortality of Black Fly Aggregates

Since each contributing factor to simuliid mortality was generally quantified, calculations using all relevant data were made to determine how descriptive the effect would be in estimating the total loss of black fly larvae and pupae. Table 36 lists the average annual impact of predators, parasites and drift for each simuliid species. It can be seen by comparing field-calculated with actual larval mortality percentage figures, that a gross underestimate resulted from the estimations.

Parasite and drift-related losses had minimal potential for error since sample size was large and sample precision was generally high. Mortality estimates associated with predators were, on the average,

Table 36. Calculated annual predator, parasite and drift impacts on the density dynamics of black flies. All density data are in no. /m^2 and have been averaged for all stations and both years.

	P. caudatum	*P. dicum*	*S. arcticum*	*S. canadense*
Initial larval density (ID)	11072	12292	15981	13456
Mortality by predation (PM)	2395	2326	2680	4947
Percent predation (PM/ID)	21.6	18.9	16.8	36.8
Surviving larvae (ID-PM)	8677	9966	13301	8509
Mortality by parasitation (PAM)	59	50	88	57
Percent parasitation (PAM/ID)	0.5	0.4	0.6	0.4
Surviving larvae (PM-PAM)	8618	9916	13213	8452
Mortality by drift (DM)	732	635	647	1189
Percent drift (DM/ID)	6.6	5.2	4.1	8.8
Surviving larvae (PAM-DM)	7886	9281	12566	7263
Field-calculated mortality (%) (PM+PAM+DM/ID)	28.8	24.5	21.4	46.0
Actual mortality (%) (emergence/ID)	87.3	92.0	88.3	92.1
Difference of underestimate	58.5	67.5	66.9	46.1
Additional mortality by predation needed to balance underestimate	6500	8300	10250	6200
Calculated total mortality by predation	8895	10626	12930	11147
Calculated percent predation	80.3	86.5	80.9	82.8

educated generalizations. Even if laboratory feeding rate data were good, the experiments were not elaborate enough to determine differences in predator effectiveness with variable prey size. This relationship may have been most critical, since the majority of losses normally occurred when larvae were small (Figure 39).

In order to obtain total mortality figures as determined from field data, predator impacts would have to be increased by a factor of from 2.3 to 4.8. Increases of these magnitudes may appear excessive, but can be rationalized. Minimum larval sizes of Prosimulium spp., S. arcticum and S. canadense used in laboratory predation studies were 5.2 mm, 5.3 mm and 5.6 mm respectively. Calculated predator impacts have all been based on immatures of these sizes. Predators on the majority of black fly riffles were generally slow-growing forms, and changed little in size during the 8 to 10 weeks that simuliid larvae occurred. Assuming that carnivore nutritional needs also varied only to a small degree during this time, the effects on smaller-sized black fly larvae could have been much higher than estimated.

Using a mean prey size of 5.0 mm, Table 37 illustrates potential numbers of smaller-sized individuals that would be consumed by carnivores to obtain comparable weight (energy) needs. Even if only 10% of the simuliid larvae of each size class in Table 37 actually had been consumed over the theoretical time present on riffles, predator-caused mortality needed to balance the underestimate (Table 36) would have been easily met.

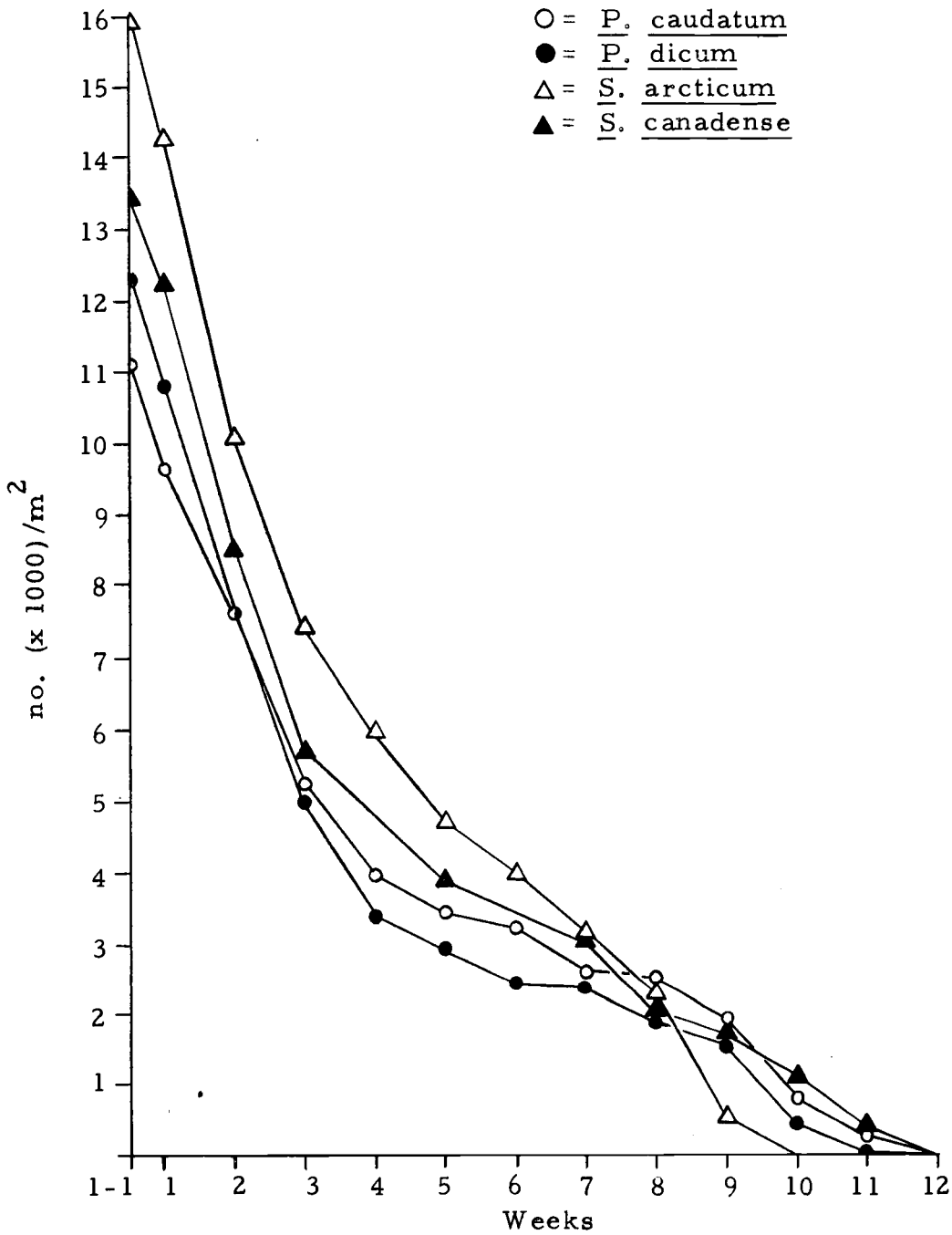


Figure 39. Black fly larval survivorship, averaged for all stations and both years.

Table 37. Calculated data showing numbers of 1-4 mm size class black fly larvae needed to equal the weight of 5 mm individuals. Densities (losses) are in no. /m^2/day. L = laboratory determination.

Larval size (mm)	Mean wt. (mg/larva)	No. larvae required by predators/day		
		P. caudatum & *P. dicum*	*S. arcticum*	*S. canadense*
5[L]	0.209	32.9	43.5	67.3
4	0.098	70	93	145
3	0.039	175	235	365
2	0.013	525	700	1100
1	0.002	3425	4550	7050

The one predator group that was not studied in detail probably had little effect on larval black fly mortality. As mentioned in an earlier section, flatworms were both low in density and small in size on most riffles. Even if they fed on early-instar larvae, little potential existed for substantial simuliid losses.

Using the calculated predator impact figure adjusted for prey size differences, and integrating this estimate with field data on parasites and drift, the total loss from the initial standing crop is 89.3%. Mortality contribution by predators, parasites and drift are 82.6%, 0.5% and 6.2% respectively. These data have been averaged for all species, since differences in parameters were generally minimal. Coupled with the mean emergence percentage of 10.7, these

data summarize the dynamic nature of an average Oregon black fly aggregate in a realistic manner.

The Function of Simuliidae in Oregon Stream Ecosystems

Streams are complex systems in which energy passes through a series of trophic levels. Unlike terrestrial ecosystems though, the cycling of most basic elements is greatly reduced due to displacement by water movements. Because streams are open systems, trophic studies describing interactions between various components of the lotic environment have been both difficult and slow in coming. Due to time limitations, energy input, ingestion, egestion, assimilation and respiration were either superficially treated or not investigated in the current study. Nevertheless, the role of black flies in allochthonous-based streams can be realistically surmized.

Black fly larvae may be classified as filter feeders, collectors, primary consumers, or any number of ways. The fact remains, that larvae of this family convert either living or dead plant biomass (energy) in streams into a more concentrated animal-based state. Once assimilated, this energy is excreted or used for respiration and growth, and eventually for reproduction. Simuliids were by far the dominant primary consumers on the riffles in all three streams. This role appears to be very critical to trophic interrelationships, since it

"breaks" the plant-animal interface. Black flies are especially important in allochthonous-based systems, due to the apparent effectiveness of their filter feeding.

By integrating data on intrastream larval distributions, life cycle durations and tissue elaboration, total production estimates were derived for black flies from three similar streams. Only the study species have been included in estimates. Total production per stream was (in g/year): Oak Creek, 372; Berry Creek, 340; and Soap Creek, 471. Drift estimates for the respective streams averaged (in g/year): 26, 24 and 33. These data are for the length of each stream where black fly aggregates occurred. They are considered conservative estimates because the portions of the stream not conducive to inhabitation (pools, backwaters, unsuitable riffles, etc.) have been excluded from the area calculations.

Nevertheless, the potential supply of energy contributed by simuliids to subsequent consumer levels was comparatively great. This was true not only as prey for carnivores, but also because they conditioned food materials for other organisms in the system. Though data indicated that detrital and algal breakdown was minimal during passage through their guts, at the rates that simuliid larvae egested alimentary canal contents, only slight changes in condition could potentially be important to processing.

There are three main pathways by which black fly tissue is transferred to higher trophic levels.

1. Simuliid eggs, larvae and pupae are consumed on riffles. Mostly, this is an interaction between larvae and invertebrate predators.
2. Simuliid larvae, and perhaps adults, are consumed in the drift by both invertebrate and vertebrate predators. In the current study, drifting larvae were generally unimportant to insect carnivore and fish consumption since so few released substrate hold. The extent to which adults are lost in streams may be high. I have observed many drowned females stuck to their submerged egg masses.
3. Adults, and perhaps the remaining three developmental stages, are consumed by terrestrial animals. The extent to which adults are preyed upon, primarily while flying, is unknown. Peterson (1960) and Snoddy (1967) have observed birds and terrestrial insects feeding on black fly immatures.

On an individual riffle basis, black fly larvae were the primary reservoir organisms for a diverse number of carnivore taxa for approximately two months. When larval biomass was highest, simuliid individuals exceeded all other primary consumers combined on riffles by a factor of 27.

SUMMARY AND CONCLUSIONS

This investigation was the first to quantitatively characterize black fly aggregate dynamics in a fairly complete manner. Though all aspects could not be probed, enough data were certainly accumulated to give realistic indications as to the general ecology of all four species. It is expected that this study will realize its potential when utilized with other related stream investigations.

Species Composition and Life History

Prosimulium caudatum and *P. dicum* occurred in Oak, Soap and Berry Creeks, while *S. arcticum* and *S. canadense* primarily existed in the latter two streams. *Prosimulium* spp. larval densities fluctuated over time to a high degree in Oak Creek. In the span of less than five years, concentrations of these two species went from undetectable to dominant, but were relatively constant during 1971 and 1972. Both *Simulium* species may also demonstrate this variable density characteristic, since numbers of all study simuliids in the three streams have generally declined since 1972.

Life cycles of all four species were very similar (Figure 11). *Prosimulium caudatum* and *P. dicum* always coexisted on riffles, with early-instar larvae usually appearing in mid-February. *Simulium arcticum* and *S. canadense* rarely occurred together, and

development for all stages followed that of Prosimulium spp. by about 6 to 7 and 9 to 10 weeks respectively.

All species primarily overwintered in the egg stage, with the initiation of eclosion likely being a function of temperature. Prosimulium spp. hatching, since eggs desiccated, may have been regulated by water level changes as well. Ova of all four species almost certainly went into diapause, as the duration of the egg stage was over 40 weeks. Eclosion times were very synchronous, ranging between low and high elevation stations by about 11 days. Hatching durations appeared short, the maximum being about three hours.

Prosimulium spp. aggregates were associated only with elongate riffles averaging about 4 m in length and having large pools at both ends. Most oviposition apparently took place in splash zones of substrates adjacent to upstream pools. "Drift" of newly-hatched larvae normally occurred for almost the entire length of the riffle before settling took place. Larval aggregates concentrated primarily in the lower portions of each riffle. Inhabitation sites of larvae were usually on the same riffle where oviposition occurred.

Locations characteristic for aggregates of S. arcticum and S. canadense were riffle systems associated with elongate pools. Each of the approximately five separate riffles within a series averaged about 1.5 m long. Simulium spp. oviposition probably occurred over the surface of pools. Eggs then sank to the bottom,

generally in the downstream area of each pool. Larvae primarily colonized the riffle immediately downstream from oviposition sites. "Drift" distances for colonizing larvae averaged less than 1 m.

Upon hatching, immatures of all species did not enter the water column. Newly-emerged larvae remained in the dead layer between flowing water and the stream bottom until substrates of suitable characteristics were encountered. Drifting after primary settling had occurred was very low.

Prosimulium spp. and Simulium spp. colonization was influenced primarily by substrate color and texture. Only rocks that were dark in hue and fine in grain could be utilized. In addition, stream velocity, temperature and water depth prerequisites had to be met before first-instar settling could occur, but there was considerable latitude in these requirements.

The maximum amount of substrate utilized by an aggregate rarely changed to any measurable degree throughout the year. Larvae appeared able to exist at variable densities, as long as flow, food and substrate characteristics were optimum. With few exceptions, immatures of all species were located on the upper surface of substrates, oriented parallel to the water flow.

Variations in interstream distribution were primarily influenced by generic-related colonization preferences. Prosimulium spp. immatures could only inhabit rocks with minimal algal growths,

whereas Simulium spp. larvae rarely occurred in areas completely free of periphyton. Thus, Prosimulium spp. aggregates were situated in areas of heavy overstory, while Simulium spp. concentrations almost always occurred at sites with comparatively higher illumination.

During the study period, riffle inhabitation by a given Prosimulium spp. or Simulium spp. larval aggregate was relatively permanent. This may have been due to adult behavior, since larvae were able to exist under diverse temperature, velocity and depth conditions. The most logical characteristics which would tend to keep black fly concentrations in a restricted area were related to mating conditions or oviposition locations. It was probable that a small scale "colonization cycle" (Muller, 1954) existed at each simuliid inhabited riffle or at least over a limited section of stream.

All species had six larval instars. Generally, duration periods were shortest for the first two instars, and longest for instars five and six. Simulium canadense had instars with both the shortest and longest mean durations: instar one, 6.8 days; instar six, 17.5 days.

Total larval durations averaged, in weeks: P. caudatum, 10.4; P. dicum, 10.1; S. arcticum, 8.8; and S. canadense, 10.5. Though differences did exist, all three research streams were similar in temperature ranges and means (estimated mean annual temperature at 200 m elevation in late May: Berry Creek, 15.1°C; Oak Creek, 14.5°C; and Soap Creek, 13.9°C). It was likely that the variations

in larval durations were minimal because of the temperature similarities both within and between the streams.

Larvae of all species fed primarily on particles suspended in the water column. Simulium spp. apparently also utilized periphyton. The percentage of detritus in alimentary tracts was 89.2, 66.7 and 62.7 for Prosimulium spp., S. arcticum and S. canadense respectively. Filamentous algae was the other major component of the diet. Alimentary canal contents generally reflected food levels in the streams. Detrital gut contents usually declined in importance and algal components increased as the season progressed. Variations in this pattern appeared related primarily to the effect of upstream overstory and subsequent allochthonous input. On the average, over 90% of the detritus in alimentary tracts originated from deciduous trees. Particle size of ingested detritus was similar for both genera, but differed for algae. Simulium spp. ingested algal fragments averaged about 40% larger than for Prosimulium spp. About 30 species of algae occurred in simuliid larval alimentary canals.

Alimentary tract clearing was accomplished for all black flies in approximately an hour or less. There appeared to be no consistent larval size, food supply, and temperature or velocity influence on passing rates. The amount of suspended algae and detritus processed by an average black fly aggregate was 169 g (dry weight) per cohort life. Judging from the fully-packed nature of most guts and the rapid

experimental clearing times, food was never considered a limiting factor to any simuliids. The slight degree to which alimentary canal contents were processed longitudinally suggested that actual nutrients utilized by all simuliids were the microflora associated with ingested particles.

Approximately 75 benthic insect species were associated either intimately or occasionally with black fly immatures. Of the common forms, all but Baetis spp., Calopsectra spp. and Glossosoma penitum were real or potential simuliid natural enemies. Black fly larvae acted as the primary prey reservoir for as many as 20 species of insect carnivores from February through June of both years. Density and feeding studies showed that the most potentially effective predators (with mean number of simuliid larvae consumed per day) were: Ephemerella doddsi (0.1), Hydropsyche spp. (1.0), Acroneuria californica (1.5), Rhyacophila spp. (2.6) and Sialis californica (3.7). On a stream basis, total predator feeding influence on mid to large-sized simuliid larvae, as mean percent of standing crop consumed per day, averaged: Oak Creek (Prosimulium spp.), 0.7; Soap Creek (S. arcticum), 0.6; and Berry Creek (S. canadense), 0.9. Carnivore related mortality was never observed for black fly pupae.

Sculpins were associated with riffles, but probably did not feed on black flies. Pool-inhabiting cutthroat trout had little impact on simuliids, since so few larvae released substrate hold and drifted.

Had trout fed on the entire drift, they would have been responsible for only about a 6% total annual loss from an average aggregate.

Gastromermis nematodes were the only parasites found in black fly larvae. Infection levels averaged 3.1% of all sixth-instar simuliids examined. Parasites apparently gained entrance into larvae through feeding activities of the hosts. Never was more than one worm found in a simuliid. Infections of pupae and adults did not occur. Life cycles of parasites and hosts were closely linked, with the former emerging only when the latter attained larval maturity. Potential mortality effects of Gastromermis were minor, as comparatively few final-instar black fly larvae ever existed upon which losses could occur.

Drift was consistently low for aggregates of all species. On a weekly basis, average downstream movements for the four simuliids was approximately 2% of mean density and mean biomass. Annual drift reduced initial densities by an average of 6.2%. Rates were comparably low for early-season riffle inhabiting individuals, since first-instar larvae had an innate resistance to release from substrates.

Simuliid larval drift appeared to be a fairly constant function of standing crop density. Growth-related crowding may have affected drift rates, but this could not be determined for certain. Diurnal, temperature and discharge influences to downstream movements appeared low, though inconsistent data concerning the former were

elaborated. Current velocity changes caused larvae to release, but this rarely occurred without a silk strand.

Drift distances were short for both Prosimulium spp. and Simulium spp., the overall mean being about 2 m. Settling probably could not occur directly from the water column to substrate. Thus, settling in a pool and subsequent upstream movements had to occur before suitable locations could be utilized. Since so few larvae were in the water column and upstream migrations averaged but 0.3% of drift, riffle re-colonization was almost certainly minor.

For all species, the pupal stage was the shortest lived developmental stage. Durations averaged: Prosimulium spp., 0.8 week; Simulium spp., 0.5 week. The duration was affected by water temperature, being reduced by as much as 25% by an increase of 2°C.

Adults of both Prosimulium species and S. arcticum almost certainly emerged in the anautogeneous state and required a blood meal to complete egg maturation. Female mouthpart and ovary condition data suggested that S. canadense adults were unable to feed, and required no additional nutrients in order to produce viable ova. Though sex ratio data were variable, an indication of slightly higher female production was extant for Prosimulium spp. and S. canadense. For these species, neither sex consistently emerged first. Simulium arcticum males not only began emergence slightly later than females, but generally outnumbered them.

Emergence initiation did not appear to be directly influenced by day length changes or short term water temperature fluctuations. Data suggested that the time when pupation occurred plus the temperature under which that stage developed determined when adult activity would begin. Prosimulium spp. emergence occurred in a fairly consistent manner once initiated. Though minor in degree, Simulium spp. emergence had two apparently characteristic peaks at about 700 and 1900 hours. The mean duration of emergence for all species ranged from 3.4 weeks (P. dicum) to 4.0 weeks (S. arcticum).

No direct emergence to oviposition duration data were elaborated in the study, but determinations from the literature suggested that this time was realistically estimated at 0.5 week per species. Averaged for the four simuliids, approximately 10% of all colonizing larvae eventually survived to emerge as adults. This comparatively high survival reflects the interaction between minimal drift and low natural enemy effects. Total life cycle mortality certainly was higher, since calculations did not take into account egg or adult losses.

Population and Aggregate Dynamics

Density, growth, mortality, biomass, production, drift and emergence data for all species in 1971, 1972, and the average of both years, have been presented in Table 38. These estimates, especially for 1971+1972, effectively characterize the dynamics of each species.

Table 38. Average annual density, growth, mortality, biomass, production, drift and emergence for black flies in 1971, 1972 and the two pooled years.

	P. caudatum	P. dicum	S. arcticum	S. canadense
	1971			
Initial density (no. /m^2)	12226	10912	14358	13178
Mean density (no. /m^2)	4538	4172	6537	5395
Mean daily inst. growth	0.087	0.096	0.102	0.092
Mean daily inst. mortality	0.027	0.036	0.026	0.036
Mean biomass (g/m^2)	0.761	0.802	1.161	1.017
Production (g/m^2)	2.700	2.815	3.787	3.426
Turnover ratio	3.6	3.6	3.3	3.4
Drift (no. /m^2)	784	754	578	1443
Drift (g/m^2)	0.156	0.232	0.176	0.428
Emergence (no. /m^2)	1548	1065	1856	1134
Emergence (g/m^2)	0.785	0.644	0.880	0.663
	1972			
Initial density (no. /m^2)	10020	13519	17604	13542
Mean density (no. /m^2)	4579	4867	7497	5251
Mean daily inst. growth	0.095	0.098	0.107	0.092
Mean daily inst. mortality	0.030	0.037	0.037	0.035
Mean biomass (g/m^2)	0.772	0.855	1.251	0.876
Production (g/m^2)	2.593	2.991	4.112	3.046
Turnover ratio	3.4	3.5	3.3	3.6
Drift (no. /m^2)	698	556	715	1062
Drift (g/m^2)	0.177	0.185	0.197	0.270
Emergence (no. /m^2)	1320	939	1883	1031
Emergence (g/m^2)	0.703	0.586	0.855	0.583
	1971 and 1972			
Initial density (no. /m^2)	11072	12292	15981	13456
Mean density (no. /m^2)	4560	4540	7012	5286
Mean daily inst. growth	0.091	0.097	0.104	0.092
Mean daily inst. mortality	0.028	0.036	0.035	0.035
Mean biomass (g/m^2)	0.767	0.830	1.208	0.910
Production (g/m^2)	2.644	2.908	3.950	3.141
Turnover ratio	3.5	3.5	3.3	3.5
Drift (no. /m^2)	732	635	647	1189
Drift (g/m^2)	0.169	0.204	0.186	0.322
Emergence (no. /m^2)	1405	986	1874	1065
Emergence (g/m^2)	0.734	0.608	0.863	0.609

Simulium arcticum consistently was the dominant species, but all parameters listed in the table differed between black flies by less than a factor of two. For example, mean 1971+1972 colonization densities ranged from over 11,000 larvae/m^2 for P. caudatum to about 16,000 larvae/m^2 for S. arcticum.

Error terms associated with most population estimates were in the 10-15% range. These data are extremely good when compared to other field research programs where standard errors in excess of 25% are common. This precision was possible because the sampling universe could be effectively partitioned due to the narrow substrate-based habitat specificity of the larvae. The area inhabited by larvae of all species was relatively constant throughout the cohort duration, and is designated as usable substrate. Sampling was accomplished only in this area. To provide estimates as comparable with as many other studies as possible, the data were expanded to a per m^2 of over-all riffle basis. Little precision was lost in conversion, since usable substrate parameters were so constant and could be measured accurately.

Instantaneous mortality rates, averaged for both years, were almost identical for P. dicum, S. arcticum and S. canadense, though somewhat lower for P. caudatum (Table 38). On an instar basis, mortality decreased (in a smoothed curve) from about 25% in instar one to 6% in instar six. Larval density was reduced by over 60%

during the first three weeks of riffle inhabitation. Variations in mortality were primarily a function of early-season larval losses.

Growth for all species was generally logistic, though the S. arcticum situation bordered on the linear. Highest daily instantaneous growth rates were characteristic of first-instar larvae, and consistently averaged over 0.250. Average annual instantaneous growth was above 0.090 per day for all species (Table 38). The greatest variation in growth rate occurred in the first and second instars. Temperature regulation of either short or long term growth could never be demonstrated to consistently occur for all species. Between laboratory and field determinations accomplished in 1972, P. caudatum, P. dicum and S. arcticum growth rates were generally lower in waters of higher temperature. For S. canadense, rates were elevated in warmer water. This was the temperature-based pattern between 1971 and 1972 determinations for the species in the natural environment also. Data from the two sets of observations indicate the differences between Prosimulium spp. and S. arcticum, and S. canadense were real.

Biomass and production increase was rapid for larvae of the four black fly species at all locations since initial density and growth were great enough in magnitude to compensate for mortality. Eventually, there came a critical time in each aggregate when effects of mortality exceeded those of growth. When this extremely variable

point was reached, biomass development was retarded. Though biomass was single peaked at almost all locations, maximum production levels differed temporally. This was due to the compensatory interaction between growth and mortality.

Had changes in growth and mortality been minimal between riffles, biomass and production would have been directly related to initial density (Table 38). Variation in time of mortality had a more important effect on differences in production between locations than did growth. High early-season mortality reduced the standing crop, but since the individuals involved had little biomass, production was not greatly affected. Late-season losses had little effect because only a comparatively few, slow-growing individuals were involved. Occasionally, mid-season losses were exceptionally minimal or high. In these instances, production was indeed altered.

First and sixth-instar larvae of all species had the lowest production. Prosimulium spp. and S. arcticum instar four produced the most, whereas for S. canadense, tissue elaboration was highest for instar five. Production for all simuliids was over 50% completed by the time larval durations were half finished, the maximum for this period being about 75% (S. arcticum).

Variations in annual production between years or streams could not be directly correlated with potential influencing factors like temperature or food supply. These characteristics were likely not of

variable enough nature to cause measurable differences. Annual production in g/m^2, averaged for both years, was: P. caudatum, 2.644; P. dicum, 2.908; S. canadense, 3.141; and S. arcticum, 3.950.

Of the indirect methods of calculating production, a single value for turnover ratio and for production/emergence ratio provided estimates of mean annual production for all species within about 2.5% of that from Ricker's growth technique. The Hynes-Coleman and drift methods were much less reliable, and gave acceptable data only when a ratio for each individual species was used.

Population dynamics for the four black flies was able to be generally characterized, since investigations encompassed all pertinent biological and ecological aspects. The mean total mortality due to drift and parasites was 6.2% and 0.5% respectively. An average of 10.7% of colonizing larvae survived to adulthood. Carnivore density and feeding data, when applied to the natural loss situation, grossly underestimated potential predator effects. By adjusting predator impact data for prey size differences, the 82.6% figure needed to balance the total mortality budget could be derived.

In three western Oregon streams, many biological characteristics of four simuliid species were found to be surprisingly consistent. This was true not only for aspects of timing and duration, but for some ecological interrelationships as well. How representative these data

are for other aquatic insects will be determined as more research is accomplished. Judging from the literature (Hynes, 1972), similarities of this nature will only be characteristic of taxonomically related forms existing in almost identical habitats.

The Oregon black flies studied play a crucial role in the ecology of streams in which they exist. Many of the interactions between these organisms and the associated physical and biological environment have been demonstrated to be most complex. It should be expected that research into the dynamics of lotic ecosystems will elaborate equally complicated results. Hopefully, this present study will provide a foundation upon which more realistically quantitative investigations can be based.

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APPENDICES

APPENDIX I

SAMPLE STATISTICAL ANALYSIS CALCULATION FOR *PROSIMULIUM CAUDATUM* LARVAL POPULATION AT STATION O-II, 1972

Appendix I.

	Strata											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Observed value (y_{hi})												
Sample 1	5	7	19	5	14	0	2	4	28	14	0	5
Sample 2	12	3	5	8	10	4	1	9	17	2	7	9
No. of unit samples/stratum (N_h)	117	82	103	91	108	70	80	84	131	115	91	97
Stratum sample mean ($\bar{y}_h$)	8.50	5.00	12.00	6.50	12.00	2.00	1.50	6.50	22.50	8.00	3.50	7.00
Stratum true mean ($\bar{Y}_h$)	0.15	0.12	0.23	0.14	0.22	0.06	0.04	0.16	0.34	0.14	0.08	0.14
Stratum sample variance ($S^2_{h'}$)	24.50	8.00	98.00	4.50	8.00	8.00	0.50	12.50	60.50	72.00	24.50	8.00
Stratum true variance (S^2_h)	1.42	0.69	3.68	0.95	2.67	0.23	0.06	1.12	8.02	1.70	0.53	1.06
No. samples/universe (N)	1169											

Population mean ($\bar{y}_{st}$) $\Sigma N_h \bar{y}_h / N = 10199/1169 = 8.73$

Standard error of population mean ($S\bar{y}_{st}$) $\sqrt{\Sigma \left(\frac{N_h}{N}\right)^2 \cdot \frac{S^2_{h'}}{n_h}} = \sqrt{1.45} = 1.20$

Total population (T_{st}) $\Sigma N_h \bar{y}_h = 10199$

Standard error of total population (ST_{st}) $\sqrt{\Sigma N_h^2 \cdot S^2_{h'} / n_h} = \sqrt{1979314.0} = 1406$

95% Confidence limits (CI) $\pm 2\ SE = \pm\ 2812$

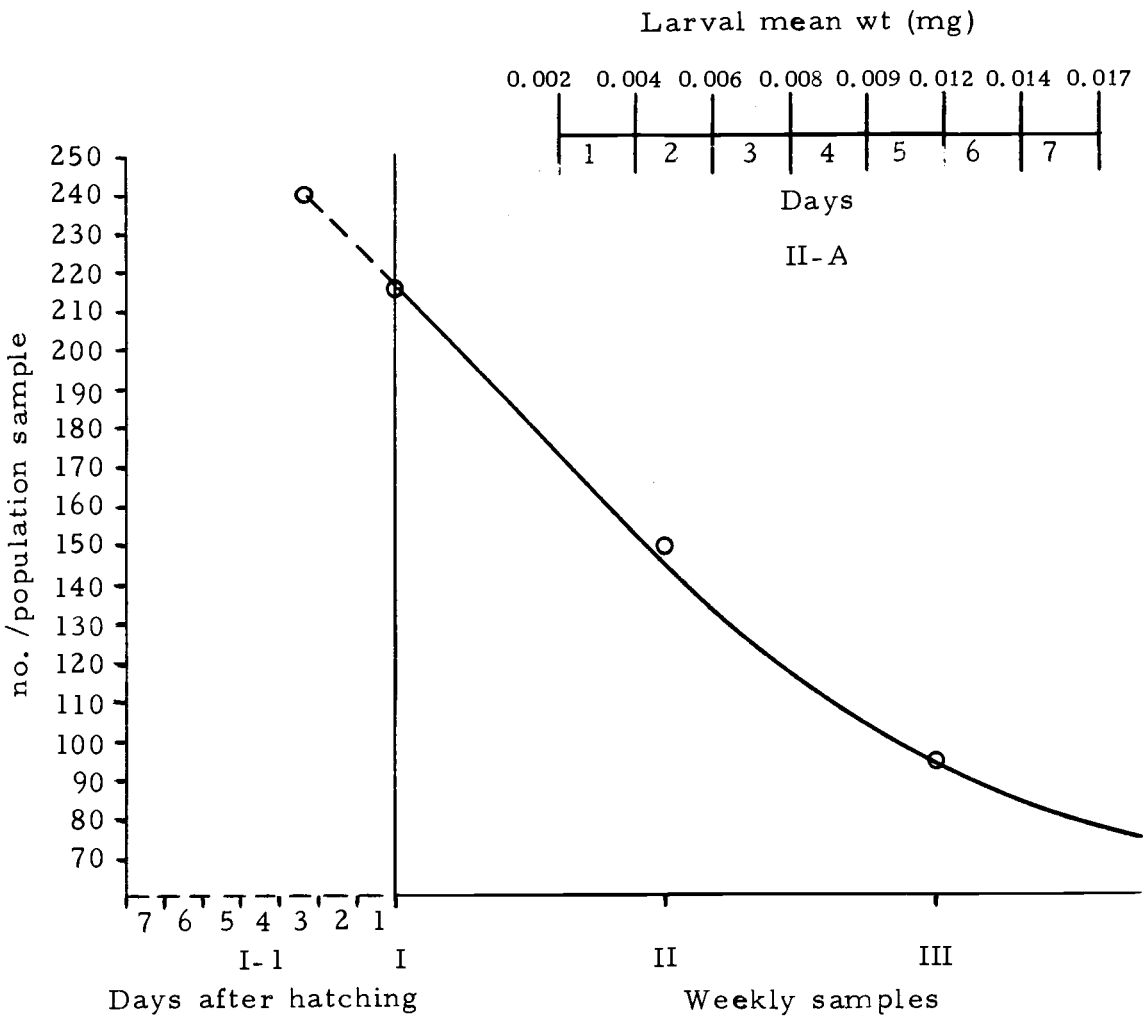
APPENDIX II

SAMPLE CALCULATION OF DENSITY AND BIOMASS AT TIME I-1, AS ILLUSTRATED ON THE FOLLOWING PAGE

II-A. Table showing mean weight gain in mg/day for newly emerged simuliid larvae. Sampling day #I for station B-II, 1971 (S. arcticum) gave a mean weight result of 0.007 mg. Placed on the table, this weight indicates that the larvae present on the riffle had been there for approximately 2 1/2 days.

II-B. Calculation of I-1 estimate by following the smoothed mortality curve to the left of I (sampling day #I). Point at which day 2.5 (from II-A) and curve meet is the approximate number of larvae present at the initial time of colonization.

II-C. Calculation of biomass at I-1 and subsequent operations. Numbers of larvae at I-1 are multiplied by 0.002 mg (see text) to give biomass estimate. Mean biomass ($\overline{B}$), growth rate (G) and production (P) per square meter of riffle are calculated according to the method of Ricker (1968). B = biomass of sampled larvae in mg. $\overline{w}$ = mean weight per larva, carried to three places to reduce possibility of error build-up in logarithms (numbers in parentheses).



II-B

I-1 = 240
B = 0.48
$\overline{w}$ = 0.002 (-6.21461)
I = 216
B = 1.48
$\overline{w}$ = 0.007 (-4.96185)

G = 1.253
$\overline{B}$ = 0.102

P = 0.128

II-C

Appendix II. Components in the I-1 estimation technique. See previous page for explanation.

APPENDIX III

LARVAL AND PUPAL *GASTROMERMIS* INFECTION DENSITIES AND PERCENTAGES

Larval and pupal size classes reflect weekly or bi-monthly samples taken throughout the developmental period.

Appendix III-A. Prosimulium caudatum.

Stream and Year	Larval Length Range (mm)	Larval Mean Length (mm)	No. Examined	No. of Gastromermis	Percent Infection
Oak Creek 1971	2.0-2.7	2.5	64	0	0
	3.2-4.1	3.5	50	0	0
	4.0-5.6	4.8	124	3	2.4
	5.1-7.4	6.3	150	4	2.7
	6.9-7.5	7.2	290	12	4.1
	4.0-5.9p	5.1	80	0	0
Oak Creek 1972	0.9*-2.0*	1.5*	300*	0	0
	1.5-2.7	2.3	830	0	0
	2.7-3.5	2.9	800	0	0
	3.1-4.4	3.6	556	1	0.2
	3.9-4.6	4.3	1000*	17	1.7*
	4.5-5.9	5.1	1000*	9	0.9*
	5.5-7.0	6.5	1670	30	1.8
	6.7-8.1	7.5	1600*	54	3.4*
	4.1-5.8p	4.9	300*	0	0
Berry Creek 1972	3.0-3.6	3.2	60*	0	0
	3.5-4.5	4.1	240	3	1.3
	4.4-5.6	5.2	120	0	0
	5.9-7.2	6.9	150	2	1.3
	6.7-7.9	7.3	150	5	3.3
	4.1-5.8p	5.2	135	0	0
Soap Creek 1972	1.9-2.5	2.2	25	0	0
	2.5-4.0	3.0	117	0	0
	3.8-5.0	4.6	250	2	0.8
	3.9-6.6	5.9	475*	9	1.9*
	6.2-7.5	7.1	400	26	6.5
	3.8-5.7p	5.1	50	0	0

p = pupae

*approximate

Appendix III-B. Prosimulium dicum.

Stream and Year	Larval Length Range (mm)	Larval Mean Length (mm)	No. Examined	No. of Gastromermis	Percent Infection
Oak Creek 1971	3.1-4.3	3.4	50	0	0
	3.8-5.3	4.5	91	1	1.1
	5.407.0	6.6	150	1	0.7
	6.8-8.2	7.4	150	6	4.0
	8.0-9.6	8.9	100	3	3.0
	4.1-5.6p	5.0	100	0	0
Oak Creek 1972	2.2-4.0	2.9	800*	0	0*
	3.6-5.6	3.8	550*	0	0*
	3.9-5.2	4.7	324	2	0.6
	5.0-6.5	5.4	1000*	9	0.9*
	6.3-7.8	7.0	1000*	13	1.3*
	7.5-9.3	8.4	250	4	1.6
	8.4-10.0	9.1	1100*	36	3.3*
	4.4-5.9p	5.2	217	0	0
Berry Creek 1972	3.4-4.2	3.7	225	0	0
	4.7-5.8	5.1	100	0	0
	5.6-7.0	6.5	146	1	0.7
	6.3-8.1	7.8	150	2	1.3
	7.9-9.5	9.0	200	7	3.5
	4.6-5.7p	5.2	150	0	0
Soap Creek 1972	1.9-2.9	2.5	57	0	0
	2.4-4.8	3.9	167	0	0
	4.0-6.0	5.3	150	0	0
	5.5-6.8	6.1	150	1	0.7
	6.2-7.9	7.6	283	1	0.4
	7.8-9.9	9.1	456	8	1.8
	4.2-5.7p	4.9	113	0	0

p = pupae

*approximate

Appendix III-C. *Simulium arcticum*.

Stream and Year	Larval Length Range (mm)	Larval Mean Length (mm)	No. Examined	No. of *Gastromermis*	Percent Infection
Berry Creek 1971	0.9*-2.1*	1.8*	150	0	0
	1.7-3.5	2.8	61	0	0
	3.3-5.2	4.6	100	0	0
	4.7-6.0	5.3	100	0	0
	5.5-7.5	6.9	370	5	1.4
	3.6-5.5p	4.5	150	0	0
Soap Creek 1971	1.3-4.1	3.2	100	0	0
	3.0-5.0	4.6	300*	2	0.7*
	3.9-5.8	5.0	162	0	0
	5.9-7.6	7.3	100	2	2.0
	3.4-5.4p	4.6	100	0	0
Berry Creek 1972	0.8-1.3	1.0	45	0	0
	1.6-4.3	3.5	350	0	0
	4.1-4.9	4.7	550*	1	0.2*
	4.4-6.1	5.4	1200*	11	0.9*
	5.8-7.3	6.2	445	7	1.6
	6.9-7.8	7.1	1112	24	2.2
	3.4-5.6p	4.4	150	0	0
Soap Creek 1972	1.1-3.1	2.0	75*	0	0
	1.9-3.5	3.1	200	0	0
	3.0-5.1	4.3	250	3	1.2
	4.3-5.9	4.9	625	3	0.5
	4.0-6.4	5.7	1000	19	1.9
	6.4-7.6	7.1	750	10	1.3
	3.1-5.6p	4.5	275	0	0

p = pupae

*approximate

Appendix III-D. *Simulium canadense*.

Stream and Year	Larval Length Range (mm)	Larval Mean Length (mm)	No. Examined	No. of *Gastromermis*	Percent Infection
Berry Creek 1971	1.6-2.3	2.1	82	0	0
	2.5-2.9	2.7	20	0	0
	2.9-4.7	3.6	156	0	0
	4.5-6.0	5.1	90*	2	2.2*
	5.8-6.5	6.2	150	7	4.7
	6.1-7.6	7.2	361	12	3.3
	3.8-5.8p	4.5	100	0	0
Soap Creek 1971	2.7-2.9	2.8	34	0	0
	3.2-5.1	4.6	106	0	0
	5.0-6.3	5.6	100*	0	0
	6.1-7.5	7.2	250	14	5.6
	3.5-5.9p	4.7	88	0	0
Berry Creek 1972	1.5*-2.9*	2.3*	117	0	0
	2.5-4.1	3.8	450	0	0
	3.7-5.5	5.0	150	1	0.7
	5.2-7.1	6.4	280	0	0
	6.2-7.9	7.4	820	8	1.0
	3.5-5.5p	4.4	100	0	0
Soap Creek 1972	2.3-4.0	3.5	250	0	0
	3.0-4.8	4.3	250	0	0
	4.3-6.1	5.7	550	1	0.2
	6.0-7.4	7.1	1022	5	0.5
	3.7-5.8p	4.5	80	0	0

p = pupae

*approximate

APPENDIX IV

ORIGINAL WEEKLY AND ANNUAL DRIFT DATA FOR ALL BLACK FLY SPECIES

Prosimulium caudatum estimates are in Tables 1-5, *P. dicum* in Tables 6-10, *S. arcticum* in Tables 11-15 and *S. canadense* in Tables 16-17.

Table IV-1. Prosimulium caudatum drift at station 0-III, 1971.

Date		Drift		
		no. /m^2/wk	g/m^2/wk	kcal/m^2/wk
Feb.	24-2	31	0.000	0.000
March	3-9	124	0.011	0.058
	10-16	131	0.014	0.074
	17-23	87	0.017	0.090
	24-30	75	0.017	0.090
	31-6	26	0.010	0.053
April	7-13	26	0.013	0.069
	14-20	10	0.005	0.026
	21-27	18	0.012	0.063
	28-4	25	0.016	0.085
May	5-11	21	0.015	0.079
Total		574	0.130	0.687

Table IV-2. Prosimulium caudatum drift at station 0-IV, 1971.

Date		Drift		
		no. /m^2/wk	g/m^2/wk	kcal/m^2/wk
Feb.	20-23	86	0.001	0.005
	24-2	217	0.007	0.037
March	3-9	195	0.012	0.063
	10-16	98	0.014	0.074
	17-23	114	0.025	0.132
	24-30	101	0.031	0.164
	31-6	87	0.040	0.211
April	7-13	70	0.036	0.190
	14-20	15	0.009	0.048
	21-27	4	0.003	0.016
May	28-4	6	0.004	0.021
Total		993	0.182	0.961

Table IV-3. Prosimulium caudatum drift at station 0-III, 1972.

Date		Drift		
		no. /m^2 /wk	g /m^2 /wk	kcal /m^2 /wk
Feb.	11-14	106	0.001	0.005
	15-21	140	0.002	0.010
	22-28	124	0.007	0.035
	29-6	82	0.006	0.030
March	7-13	43	0.009	0.045
	14-20	56	0.015	0.075
	21-27	76	0.032	0.160
	28-3	89	0.045	0.226
April	4-10	74	0.051	0.256
	11-17	56	0.041	0.206
Total		846	0.209	1.048

Table IV-4. Prosimulium caudatum drift at station 0-IV, 1972.

Date		Drift		
		no. /m^2 /wk	g /m^2 /wk	kcal /m^2 /wk
Feb.	12-14	50	0.000	0.000
	15-21	101	0.002	0.010
	22-28	89	0.003	0.015
	29-6	51	0.003	0.015
March	7-13	69	0.009	0.045
	14-20	90	0.017	0.085
	21-27	57	0.016	0.080
	28-3	45	0.023	0.115
April	4-10	70	0.045	0.226
	11-17	54	0.030	0.190
	18-24	18	0.013	0.065
Total		694	0.169	0.846

Table IV-5. Prosimulium caudatum drift at station 0-VII, 1972.

Date		Drift		
		no. /m^2 /wk	g /m^2 /wk	kcal /m^2 /wk
Feb.	15-21	73	0.001	0.005
	22-28	70	0.003	0.015
	29-6	62	0.006	0.030
March	7-13	93	0.016	0.080
	14-20	66	0.013	0.065
	21-27	39	0.014	0.070
	28-3	31	0.012	0.060
April	4-10	38	0.028	0.140
	11-17	47	0.034	0.170
	18-24	35	0.026	0.130
Total		554	0.153	0.765

Table IV-6. Prosimulium dicum drift at station 0-III, 1971.

Date		Drift		
		no. /m^2 /wk	g /m^2 /wk	kcal /m^2 /wk
Feb.	27-2	54	0.000	0.000
March	3-9	104	0.003	0.016
	10-16	123	0.009	0.048
	17-23	96	0.014	0.075
	24-30	67	0.017	0.091
	31-6	78	0.032	0.172
April	7-13	87	0.047	0.252
	14-20	89	0.068	0.364
	21-27	96	0.084	0.450
May	28-4	62	0.057	0.306
Total		856	0.331	1.774

Table IV-7. Prosimulium dicum drift at station 0-IV, 1971.

Date		Drift		
		no. /m^2 /wk	g /m^2 /wk	kcal/m^2 /wk
March	4-9	37	0.001	0.005
	10-16	134	0.006	0.032
	17-23	158	0.014	0.075
	24-30	111	0.017	0.091
	31-6	79	0.023	0.123
April	7-13	72	0.029	0.155
	14-20	35	0.019	0.102
	21-27	7	0.005	0.027
	28-4	4	0.004	0.021
May	5-11	15	0.014	0.075
Total		652	0.132	0.706

Table IV-8. Prosiumulium dicum drift at station 0-III, 1972.

Date		Drift		
		no. /m^2 /wk	g /m^2 wk	kcal/m^2 /wk
Feb.	11-14	30	0.000	0.000
	15-21	89	0.003	0.015
	22-28	54	0.003	0.015
	29-6	23	0.005	0.025
March	7-13	35	0.009	0.045
	14-20	39	0.017	0.084
	21-27	27	0.013	0.064
	28-3	19	0.016	0.079
April	4-10	45	0.040	0.198
	11-17	31	0.028	0.139
Total		392	0.134	0.664

Table IV-9. Prosimulium dicum drift at station 0-IV, 1972.

Date		Drift		
		no. /m^2/wk	g/m^2/wk	kcal/m^2/wk
Feb.	16-21	140	0.002	0.010
	22-28	123	0.006	0.030
	29-6	102	0.012	0.059
March	7-13	98	0.019	0.094
	14-20	64	0.020	0.099
	21-27	71	0.035	0.173
	28-3	61	0.036	0.178
April	4-10	42	0.035	0.173
	11-17	51	0.048	0.238
	18-24	39	0.037	0.183
Total		791	0.250	1.237

Table IV-10. Prosimulium dicum drift at station 0-VII, 1972.

Date		Drift		
		no. /m^2/wk	g/m^2/wk	kcal/m^2/wk
Feb.	16-21	17	0.000	0.000
	22-28	70	0.002	0.010
	29-6	62	0.002	0.010
March	7-13	35	0.007	0.035
	14-20	78	0.022	0.109
	21-27	70	0.026	0.129
	28-3	31	0.016	0.079
April	4-10	58	0.045	0.223
	11-17	51	0.040	0.198
	18-24	12	0.011	0.054
Total		484	0.171	0.847

Table IV-11. Simulium arcticum drift at station B-I, 1971.

Date		Drift		
		no. /m^2 /wk	g /m^2 /wk	kcal /m^2 /wk
March	27-31	46	0.001	0.005
	1-7	54	0.004	0.019
April	8-14	46	0.006	0.029
	15-21	66	0.021	0.101
	22-28	79	0.031	0.150
	29-5	50	0.025	0.121
May	6-12	34	0.019	0.092
	13-19	31	0.019	0.092
	20-26	20	0.013	0.063
June	27-2	9	0.006	0.029
Total		435	0.145	0.701

Table IV-12. Simulium arcticum drift at station S-III, 1971.

Date		Drift		
		no. m^2 /wk	g /m^2 /wk	kcal /m^2 /wk
April	8-13	125	0.002	0.010
	14-20	99	0.004	0.019
	21-27	72	0.011	0.053
	28-4	92	0.021	0.101
May	5-11	101	0.037	0.179
	12-18	94	0.046	0.222
	19-25	68	0.041	0.198
	26-1	42	0.026	0.125
June	2-8	28	0.018	0.087
Total		721	0.206	0.994

Table IV-13. Simulium arcticum drift at station B-I, 1972.

Date		Drift		
		no. /m^2 /wk	g /m^2 /wk	kcal/m^2 /wk
March	20-23	128	0.001	0.005
	24-30	158	0.004	0.020
	31-6	107	0.008	0.039
April	7-13	86	0.015	0.073
	14-20	65	0.016	0.078
	21-27	47	0.020	0.098
	28-4	93	0.052	0.255
May	5-11	82	0.049	0.240
	12-18	44	0.027	0.132
	19-25	28	0.018	0.088
Total		838	0.210	1.028

Table IV-14. Simulium arcticum drift at station S-III, 1972.

Date		Drift		
		no. /m^2 /wk	g /m^2 /wk	kcal/m^2 /wk
March	28-3	53	0.001	0.005
April	4-10	84	0.006	0.029
	11-17	79	0.009	0.044
	18-24	75	0.017	0.083
	25-1	67	0.020	0.098
May	2-8	56	0.025	0.122
	9-15	79	0.044	0.216
	16-22	65	0.041	0.201
	23-29	32	0.021	0.103
Total		592	0.184	0.901

Table IV-15. *Simulium canadense* drift at station B-VII, 1971.

Date		Drift		
		no. /m^2 /wk	g /m^2 /wk	kcal /m^2 /wk
April	15-20	220	0.002	0.011
	21-27	198	0.007	0.038
	28-4	124	0.010	0.054
May	5-11	93	0.012	0.065
	12-18	105	0.027	0.146
	19-25	208	0.080	0.434
	26-1	257	0.128	0.694
June	2-8	152	0.094	0.510
	9-15	58	0.044	0.239
	16-22	28	0.024	0.130
Total		1,443	0.428	2.321

Table IV-16. *Simulium canadense* drift at station B-V, 1972.

Date		Drift		
		no. /m^2 /wk	g /m^2 /wk	kcal /m^2 /wk
April	6-9	97	0.000	0.000
	10-16	170	0.002	0.011
	17-23	164	0.008	0.042
	24-30	178	0.014	0.074
May	1-7	116	0.016	0.084
	8-14	75	0.019	0.100
	15-21	124	0.050	0.264
	22-28	145	0.069	0.364
	29-4	73	0.045	0.237
June	5-11	100	0.079	0.417
	12-18	89	0.072	0.380
Total		1,331	0.374	1.973

Table IV-17. *Simulium canadense* drift at station S-I, 1972.

Date		Drift		
		no. /m^2 /wk	g/m^2 /wk	kcal/m^2 /wk
April	20-24	57	0.000	0.000
	25-1	138	0.003	0.016
May	2-8	122	0.005	0.026
	9-15	102	0.011	0.058
	16-22	125	0.022	0.116
	23-29	85	0.024	0.127
	30-5	62	0.029	0.153
June	6-12	53	0.033	0.174
	12-19	27	0.020	0.105
	20-26	21	0.018	0.095
Total		792	0.165	0.870

APPENDIX V

EMERGENCE AT ALL 1971 AND 1972 STATIONS FOR ALL BLACK FLY SPECIES

Appendix V-A. Prosimulium caudatum.

Station & Year	Date		Emergence		
			no. /m^2 /wk	g /m^2 /wk	kcal/m^2 /wk
0-I	April	21-27	49	0.025	0.119
1971		28-4	359	0.181	0.863
	May	5-11	518	0.262	1.249
		12-18	829	0.418	1.992
	Total		1755	0.886	4.223
0-III	April	28-4	361	0.182	0.867
1971	May	5-11	459	0.232	1.106
		12-18	727	0.367	1.749
	Total		1547	0.781	3.722
0-IV	April	21-27	154	0.079	0.377
1971		28-4	370	0.189	0.901
	May	5-11	817	0.419	1.997
	Total		1341	0.687	3.275
0-I	April	11-17	112	0.060	0.296
1972		18-24	607	0.325	1.605
	May	25-1	1189	0.632	3.120
	Total		1908	1.017	5.021
0-II	April	11-17	56	0.030	0.148
1972		18-24	202	0.108	0.533
	May	25-1	773	0.412	2.034
	Total		1031	0.550	2.715
0-III	April	4-10	265	0.141	0.696
1972		11-17	1178	0.628	3.100
		18-24	52	0.028	0.138
	Total		1495	0.797	3.934
0-IV	April	11-17	270	0.144	0.711
1972		18-24	567	0.302	1.491
	May	25-1	400	0.213	1.052
	Total		1237	0.659	3.254
0-VII	April	11-17	100	0.053	0.262
1972		18-24	670	0.357	1.763
	May	25-1	157	0.084	0.415
	Total		927	0.494	2.440

Appendix V-B. Prosimulium dicum.

Station & Year	Date		Emergence		
			no. /m^2 /wk	g/m^2 /wk	kcal/m^2 /wk
0-I	April	28-4	103	0.062	0.308
1971	May	5-11	619	0.374	1.857
	Total		722	0.436	2.165
0-III	April	21-27	149	0.090	0.447
1971	May	28-4	722	0.436	2.165
		5-11	418	0.253	1.256
	Total		1289	0.779	3.868
0-IV	April	21-27	98	0.059	0.293
1971		28-4	366	0.221	1.097
	May	5-11	570	0.344	1.708
		12-18	151	0.092	0.457
	Total		1185	0.716	3.555
0-I	April	11-17	521	0.325	1.561
1972		18-24	872	0.544	2.613
	Total		1393	0.869	4.174
0-II	April	11-17	301	0.188	0.903
1972		18-24	473	0.295	1.417
	Total		774	0.483	2.320
0-III	April	11-17	189	0.119	0.572
1972		18-24	481	0.300	1.441
	Total		670	0.419	2.013
0-IV	April	25-1	980	0.612	2.939
1972					
0-VII	April	18-24	46	0.029	0.139
1972	May	25-1	832	0.518	2.488
	Total		878	0.547	2.627

Appendix V-C. Simulium arcticum.

Station & Year	Date		Emergence		
			no. /m^2 /wk	g /m^2 /wk	kcal/m^2 /wk
S-III 1971	May	26-1	257	0.122	0.629
	June	2-8	1083	0.513	2.643
		9-15	516	0.245	1.262
	Total		1856	0.880	4.534
B-I 1972	May	5-11	195	0.090	0.436
		12-18	683	0.313	1.518
		19-25	460	0.211	1.023
	June	26-1	724	0.333	1.615
	Total		2062	0.947	4.592
S-III 1972	May	16-22	298	0.133	0.645
		23-29	927	0.416	2.017
	June	30-5	478	0.214	1.038
	Total		1703	0.763	3.700

Appendix V-D. Simulium canadense.

Station & Year	Date		Emergence		
			no. /m^2 /wk	g /m^2 /wk	kcal/m^2 /wk
B-VII 1971	June	9-15	464	0.271	1.320
		16-22	464	0.271	1.320
		23-29	206	0.121	0.589
	Total		1134	0.663	3.229
B-V 1972	June	5-11	145	0.084	0.447
		12-18	581	0.335	1.781
		19-25	356	0.206	1.095
	Total		1082	0.625	3.323
S-I 1972	June	20-26	318	0.175	0.930
	July	27-3	662	0.365	1.940
	Total		980	0.540	2.870

APPENDIX VI

LARVAL INSTAR PRODUCTION USING AVERAGED 1971 AND 1972 DENSITY, WEIGHT, GROWTH, DURATION AND BIOMASS DATA

Appendix VI-A. Prosimulium caudatum.

Instar	Mean Assumed Density (no. /m^2)	Mean Weight (mg/larva)	Growth (g/g/day)	Instar Duration (days)	Biomass (g/m^2)	Production (g/instar)	Production (% instar)
I	9400	0.006	0.297	7.4	0.056	0.123	4.5
II	6800	0.028	0.190	8.1	0.190	0.293	10.8
III	4400	0.092	0.101	11.8	0.396	0.471	17.4
IV	3300	0.275	0.066	16.5	0.908	0.994	36.7
V	2500	0.479	0.034	16.3	1.198	0.655	24.2
VI	700	0.688	0.024	15.0	0.482	0.175	6.4
Total						2.711	

Appendix VI-B. Prosimulium dicum.

Instar	Mean Assumed Density (no. /m^2)	Mean Weight (mg/larva)	Growth (g/g/day)	Instar Duration (days)	Biomass (g/m^2)	Production (g/instar)	Production (%/instar)
I	10200	0.007	0.320	7.2	0.071	0.164	5.7
II	7100	0.033	0.189	8.2	0.234	0.363	12.6
III	4200	0.112	0.116	10.5	0.470	0.574	19.9
IV	2700	0.304	0.071	14.1	0.821	0.820	28.4
V	2200	0.561	0.037	16.8	1.234	0.756	26.2
VI	600	0.851	0.028	15.0	0.511	0.213	7.2
Total						2.890	

Appendix VI-C. Simulium arcticum.

Instar	Mean Assumed Density (no. /m^2)	Mean Weight (mg/larva)	Growth (g/g/day)	Instar Duration (days)	Biomass (g/m^2)	Production (g/instar)	Production (%/instar)
I	15100	0.004	0.388	6.8	0.060	0.158	4.
II	12100	0.025	0.282	6.5	0.303	0.555	14.6
III	9900	0.084	0.148	8.2	0.832	1.009	26.5
IV	7100	0.191	0.066	12.5	1.356	1.115	29.[illegible]
V	3200	0.354	0.047	13.1	1.133	0.699	18.3
VI	900	0.594	0.035	14.7	0.535	0.277	7.3
Total						3.813	

Appendix VI-D. Simulium canadense.

Instar	Mean Assumed Density (no./m^2)	Mean Weight (mg/larva)	Growth (g/g/day)	Instar Duration (days)	Biomass (g/m^2)	Production (g/instar)	Production (% instar)
I	12400	0.004	0.388	6.8	0.050	0.132	4.3
II	8400	0.019	0.213	7.3	0.160	0.249	8.0
III	5300	0.071	0.096	13.7	0.376	0.496	16.0
IV	3900	0.220	0.083	13.1	0.858	0.930	30.0
V	2800	0.483	0.052	15.2	1.352	1.063	34.3
VI	800	0.719	0.023	17.5	0.575	0.227	7.4
Total						3.097	

APPENDIX VII

PRODUCTION CONTRIBUTION PERCENTAGE FOR BLACK FLY LARVAE, BY WEEK

Data are averaged for all stations and both years

Week	*P. caudatum*	*P. dicum*	*S. arcticum*	*S. canadense*
1	5.2	5.9	5.9	6.2
2	10.7	11.4	12.6	7.9
3	12.2	11.9	28.6	9.5
4	13.8	12.4	26.1	12.5
5	15.2	16.0	12.4	14.1
6	16.8	15.3	8.2	17.0
7	11.3	12.9	4.9	15.2
8	9.9	8.2	1.3	12.9
9	3.8	4.1		3.8
10	1.1	1.9		0.9
P_H	57.1	57.6	73.2	50.2

P_H = Production completed during first half of larval life.

APPENDIX VIII

ORIGINAL WEEKLY AND ANNUAL GROWTH, BIOMASS AND PRODUCTION FOR ALL BLACK FLY SPECIES

Prosimulium caudatum estimates are in Tables 1-17, *P. dicum* in Tables 18-34, *S. arcticum* in Tables 35-46 and *S. canadense* in Tables 47-54.

Table VIII-1. Prosimulium caudatum production at station B-VI, 1971.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Feb.	11-16	0.414	2.485	0.110	0.582	0.273	1.446
	17-23	0.155	1.085	0.299	1.581	0.324	1.715
	24-2	0.094	0.657	0.421	2.225	0.277	1.462
Mar.	3-9	0.063	0.441	0.731	3.864	0.322	1.704
	10-16	0.058	0.404	0.959	5.096	0.387	2.048
	17-23	0.032	0.224	0.906	4.789	0.203	1.073
	24-30	0.035	0.245	0.722	3.871	0.177	0.935
Apr.	31-6	0.025	0.172	1.149	6.074	0.198	1.045
	7-13	0.023	0.160	1.327	7.015	0.212	1.122
	14-20	0.004	0.026	0.482	2.548	0.013	0.066
	21-27	-0.004	-0.028	0.186	0.983	-0.005	-0.028
Mean	0.082		0.669	3.536			
Total						2.381	12.586
Turnover ratio						3.6	

Table VIII-2. Prosimulium caudatum production at station S-VI, 1971.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Feb.	21-23	0.418	1.253	0.073	0.386	0.091	0.481
	24-2	0.213	1.488	0.230	1.216	0.342	1.808
Mar.	3-9	0.134	0.935	0.474	2.506	0.443	2.342
	10-16	0.093	0.648	0.739	3.906	0.479	2.532
	17-23	0.065	0.455	0.922	4.874	0.420	2.220
	24-30	0.053	0.371	1.201	6.348	0.446	2.358
	31-6	0.033	0.232	1.330	7.030	0.309	1.633
Apr.	7-13	0.032	0.224	1.150	6.079	0.258	1.364
	14-20	0.024	0.116	1.007	5.323	0.167	0.883
	21-27	0.020	0.137	0.698	3.690	0.096	0.507
May	28-4	0.001	0.005	0.269	1.422	0.001	0.005
Mean	0.099		0.778	4.113			
Total						3.052	16.133
Turnover ratio						3.9	

Table VIII-3. Prosimulium caudatum production at station O-I, 1971.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Feb.	20-23	0.347	1.386	0.062	0.328	0.086	0.455
	24-2	0.211	1.476	0.197	1.041	0.291	1.538
Mar.	3-9	0.137	0.956	0.429	2.268	0.410	2.167
	10-16	0.092	0.642	0.776	4.102	0.498	2.632
	17-23	0.060	0.423	1.059	5.598	0.448	2.368
	24-30	0.048	0.338	1.179	6.232	0.399	2.109
	31-6	0.040	0.277	1.048	5.540	0.290	1.533
Apr.	7-13	0.028	0.197	1.391	7.353	0.274	1.448
	14-20	0.014	0.095	1.842	9.737	0.175	0.925
	21-27	0.012	0.085	1.587	8.389	0.135	0.714
	28-4	0.004	0.029	0.894	4.726	0.026	0.137
May	5-11	-0.002	-0.017	0.228	1.205	-0.004	-0.021
Mean		0.083		0.922	4.872		
Total						3.028	16.005
Turnover ratio						3.3	

Table VIII-4. Prosimulium caudatum production at station O-II, 1971.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Feb.	21-23	0.366	1.099	0.043	0.227	0.047	0.248
	24-2	0.215	1.504	0.135	0.714	0.203	1.073
Mar.	3-9	0.144	1.008	0.369	1.951	0.372	1.966
	10-16	0.094	0.659	0.585	3.092	0.386	2.040
	17-23	0.061	0.426	0.571	3.018	0.243	1.284
	24-30	0.054	0.379	0.885	4.678	0.335	1.771
	31-6	0.035	0.245	1.209	6.391	0.296	1.565
Apr.	7-13	0.035	0.246	1.529	8.082	0.376	1.988
	14-20	0.022	0.154	1.367	7.226	0.211	1.115
	21-27	0.020	0.140	0.596	3.150	0.083	0.439
May	28-4	0.004	0.029	0.296	1.565	0.009	0.048
Mean		0.095		0.729	3.855		
Total						2.561	13.537
Turnover ratio						3.5	

Table VIII-5. Prosimulium caudatum production at station O-III, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	24-2	0.392	2.741	0.170	0.899	0.466	2.463
Mar.	3-9	0.139	0.973	0.457	2.416	0.445	2.352
	10-16	0.098	0.687	0.698	3.690	0.480	2.537
	17-23	0.043	0.300	0.769	4.065	0.231	1.221
	24-30	0.062	0.432	1.023	5.408	0.442	2.336
	31-6	0.048	0.337	1.222	6.459	0.412	2.178
Apr.	7-13	0.015	0.106	1.146	6.058	0.121	0.640
	14-20	0.015	0.104	1.066	5.635	0.111	0.587
	21-27	0.013	0.091	0.890	4.705	0.081	0.428
	28-4	0.011	0.078	0.654	3.457	0.051	0.270
May	5-11	0.007	0.051	0.481	2.543	0.025	0.132
Mean		0.077		0.780	4.121		
Total						2.865	15.144
Turnover ratio						3.7	

Table VIII-6. Prosimulium caudatum production at station O-IV, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	20-23	0.347	1.386	0.041	0.217	0.057	0.301
	24-2	0.215	1.504	0.213	1.126	0.320	1.692
Mar.	3-9	0.137	0.960	0.394	2.083	0.378	1.998
	10-16	0.093	0.650	0.539	2.849	0.350	1.850
	17-23	0.061	0.424	0.743	3.927	0.315	1.665
	24-30	0.051	0.354	1.232	6.512	0.436	2.305
	31-6	0.036	0.249	1.444	7.633	0.360	1.903
Apr.	7-13	0.029	0.201	0.692	3.658	0.139	0.735
	14-20	0.011	0.077	0.376	1.988	0.029	0.153
	21-27	0.013	0.092	0.463	2.447	0.043	0.227
May	28-4	0.002	0.016	0.267	1.411	0.004	0.021
Mean		0.090		0.604	3.193		
Total						2.431	12.850
Turnover ratio						4.0	

Table VIII-7. Prosimulium caudatum production at station O-V, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	24-2	0.424	2.970	0.205	1.084	0.609	3.219
Mar.	3-9	0.140	0.981	0.469	2.479	0.460	2.432
	10-16	0.092	0.644	0.544	2.876	0.350	1.850
	17-23	0.051	0.354	0.577	3.050	0.204	1.078
	24-30	0.050	0.347	1.140	6.026	0.396	2.093
	31-6	0.036	0.253	1.285	6.793	0.325	1.718
Apr.	7-13	0.027	0.192	1.395	7.374	0.268	1.417
	14-20	0.015	0.108	1.447	7.649	0.156	0.825
	21-27	0.008	0.057	0.966	5.106	0.055	0.291
May	28-4	0.008	0.056	0.581	3.071	0.033	0.174
Mean		0.085		0.861	4.551		
Total						2.856	15.097
Turnover ratio						3.3	

Table VIII-8. Prosimulium caudatum production at station O-VI, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	24-2	0.377	2.639	0.117	0.618	0.309	1.633
Mar.	3-9	0.139	0.972	0.308	1.628	0.299	1.581
	10-16	0.098	0.686	0.499	2.638	0.347	1.808
	17-23	0.055	0.385	0.592	3.129	0.228	1.205
	24-30	0.057	0.399	0.645	3.409	0.257	1.359
	31-6	0.037	0.259	1.156	6.111	0.299	1.581
Apr.	7-13	0.033	0.232	1.241	6.560	0.288	1.522
	14-20	0.024	0.169	1.314	6.946	0.222	1.173
	21-27	0.020	0.143	1.175	6.211	0.168	0.888
May	28-4	0.005	0.036	0.377	1.993	0.014	0.074
Mean		0.085		0.742	3.924		
Total						2.426	12.824
Turnover ratio						3.2	

Table VIII-9. Prosimulium caudatum production at station B-VI, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	2-7	0.384	2.303	0.076	0.381	0.175	0.877
	8-14	0.128	0.896	0.197	0.988	0.177	0.887
	15-21	0.080	0.563	0.322	1.614	0.181	0.907
	22-28	0.078	0.543	0.471	2.361	0.256	1.283
	29-6	0.071	0.496	0.644	3.228	0.319	1.599
Mar.	7-13	0.067	0.471	1.035	5.188	0.487	2.441
	14-20	0.051	0.354	1.015	5.088	0.359	1.800
	21-27	0.038	0.263	1.247	6.251	0.328	1.644
	28-3	0.004	0.027	1.210	6.066	0.033	0.165
Apr.	4-10	0.004	0.025	0.348	1.745	0.009	0.045
Mean		0.091		0.663	3.324		
Total						2.324	11.648
Turnover ratio						3.5	

Table VIII-10. Prosimulium caudatum production at station S-VI, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	6-7	0.458	0.916	0.038	0.190	0.035	0.175
	8-14	0.205	1.435	0.113	0.566	0.162	0.812
	15-21	0.132	0.926	0.249	1.248	0.231	1.158
	22-28	0.076	0.530	0.327	1.639	0.173	0.867
	29-6	0.088	0.612	0.561	2.812	0.343	1.719
Mar.	7-13	0.069	0.483	0.776	3.890	0.375	1.880
	14-20	0.059	0.409	1.180	5.915	0.483	2.421
	21-27	0.054	0.380	1.480	7.419	0.562	2.817
	28-3	0.033	0.231	1.688	8.462	0.390	1.955
Apr.	4-10	0.003	0.019	1.208	6.056	0.023	0.115
	11-17	-0.002	-0.013	0.354	1.775	-0.005	-0.025
Mean		0.107		0.774	3.881		
Total						2.772	13.894
Turnover ratio						3.6	

Table VIII-11. Prosimulium caudatum production at station O-I, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	12-14	0.366	1.099	0.054	0.271	0.059	0.296
	15-21	0.204	1.427	0.169	0.847	0.241	1.208
	22-28	0.123	0.859	0.334	1.674	0.287	1.439
	29-6	0.072	0.507	0.418	2.095	0.212	1.063
Mar.	7-13	0.060	0.419	0.579	2.903	0.243	1.218
	14-20	0.076	0.533	1.158	5.805	0.617	3.093
	21-27	0.063	0.442	1.657	8.307	0.732	3.670
	28-3	0.052	0.367	1.755	8.798	0.644	3.228
Apr.	4-10	0.040	0.281	1.638	8.211	0.460	2.306
	11-17	0.001	0.005	1.261	6.321	0.006	0.030
	18-24	-0.001	-0.009	0.710	3.559	-0.006	-0.030
Mean		0.093		0.936	4.692		
Total						3.495	17.521
Turnover ratio						3.7	

Table VIII-12. Prosimulium caudatum production at station O-II, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	12-14	0.418	1.253	0.037	0.185	0.046	0.231
	15-21	0.182	1.273	0.163	0.817	0.207	1.038
	22-28	0.120	0.842	0.314	1.574	0.264	1.323
	29-6	0.075	0.525	0.494	2.476	0.259	1.298
Mar.	7-13	0.071	0.496	0.628	3.148	0.311	1.559
	14-20	0.067	0.472	0.767	3.845	0.362	1.815
	21-27	0.053	0.371	0.904	4.532	0.335	1.679
	28-3	0.048	0.337	0.940	4.712	0.317	1.589
Apr.	4-10	0.048	0.333	1.519	7.615	0.506	2.537
	11-17	0.006	0.045	1.626	8.151	0.073	0.366
	18-24	0.001	0.007	0.678	3.399	0.005	0.025
Mean		0.099		0.776	3.890		
Total						2.685	13.460
Turnover ratio						3.5	

Table VIII-13. Prosimulium caudatum production at station O-III, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/day)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	11-14	0.347	1.386	0.061	0.306	0.084	0.426
	15-21	0.194	1.355	0.177	0.887	0.240	1.203
	22-28	0.120	0.843	0.338	1.694	0.285	1.429
	29-6	0.088	0.614	0.404	2.025	0.248	1.243
Mar.	7-13	0.076	0.530	0.782	3.920	0.414	2.075
	14-20	0.054	0.376	1.154	5.785	0.434	2.176
	21-27	0.050	0.352	0.980	4.913	0.345	1.729
	28-3	0.039	0.270	1.564	7.840	0.422	2.115
Apr.	4-10	0.027	0.187	2.228	11.169	0.417	2.090
	11-17	0.002	0.016	1.352	6.778	0.022	0.110
Mean		0.100		0.942	4.721		
Total						2.912	14.596
Turnover ratio						3.1	

Table VIII-14. Prosimulium caudatum production at station O-IV, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	12-14	0.366	1.099	0.037	0.185	0.041	0.206
	15-21	0.192	1.344	0.117	0.587	0.157	0.787
	22-28	0.111	0.777	0.249	1.248	0.193	0.968
	29-6	0.077	0.542	0.352	1.765	0.191	0.957
Mar.	7-13	0.084	0.589	0.426	2.136	0.251	1.258
	14-20	0.068	0.478	0.754	3.780	0.360	1.805
	21-27	0.062	0.434	1.183	5.930	0.513	2.572
	28-3	0.059	0.411	1.543	7.735	0.634	3.178
Apr.	4-10	0.029	0.206	1.959	9.820	0.404	2.025
	11-17	0.004	0.026	1.500	7.520	0.039	0.196
	18-24	0.001	0.008	0.536	2.687	0.004	0.020
Mean		0.096		0.832	4.172		
Total						2.787	13.972
Turnover ratio						3.4	

Table VIII-15. Prosimulium caudatum production at station O-V, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/wk)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	12-14	0.418	1.253	0.043	0.216	0.054	0.271
	15-21	0.187	1.312	0.126	0.632	0.165	0.827
	22-28	0.119	0.836	0.280	1.404	0.234	1.173
	29-6	0.077	0.540	0.467	2.341	0.252	1.263
Mar.	7-13	0.074	0.519	0.558	2.797	0.290	1.454
	14-20	0.059	0.411	0.605	3.033	0.249	1.248
	21-27	0.057	0.399	1.036	5.193	0.413	2.070
	28-3	0.053	0.371	1.326	6.647	0.492	2.466
Apr.	4-10	0.040	0.282	1.552	7.780	0.438	2.196
	11-17	0.001	0.005	1.288	6.457	0.006	0.030
	18-24	0.002	0.011	0.828	4.151	0.009	0.045
Mean		0.099		0.780	3.909		
Total						2.602	13.043
Turnover ratio						3.3	

Table VIII-16. Prosimulium caudatum production at station O-VI, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	16-21	0.392	2.351	0.079	0.396	0.186	0.932
	22-28	0.115	0.806	0.204	1.023	0.164	0.822
	29-6	0.080	0.557	0.209	1.048	0.116	0.582
Mar.	7-13	0.079	0.556	0.158	0.792	0.088	0.441
	14-20	0.069	0.480	0.334	1.674	0.160	0.802
	21-27	0.057	0.401	0.576	2.887	0.231	1.158
	28-3	0.056	0.393	0.563	2.822	0.221	1.108
Apr.	4-10	0.043	0.299	0.777	3.895	0.232	1.163
	11-17	0.007	0.051	0.916	4.592	0.047	0.236
	18-24	0.005	0.037	0.573	2.872	0.021	0.105
May	25-1	0.001	0.004	0.274	1.374	0.001	0.005
Mean		0.082		0.428	2.144		
Total						1.467	7.354
Turnover ratio						3.4	

Table VIII-17. Prosimulium caudatum production at station O-VII, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	15-21	0.382	2.674	0.086	0.431	0.230	1.153
	22-28	0.120	0.837	0.206	1.033	0.172	0.862
	29-6	0.089	0.624	0.412	2.065	0.257	1.288
Mar.	7-13	0.069	0.485	0.592	2.968	0.287	1.439
	14-20	0.052	0.367	0.611	3.063	0.224	1.123
	21-27	0.051	0.355	1.001	5.018	0.355	1.780
	28-3	0.050	0.348	1.128	5.655	0.393	1.970
Apr.	4-10	0.033	0.231	1.480	7.419	0.341	1.709
	11-17	0.003	0.019	1.761	8.828	0.033	0.165
	18-24	0.001	0.005	0.911	4.567	0.005	0.025
Mean		0.085		0.819	4.105		
Total						2.297	11.514
Turnover ratio						2.8	

Table VIII-18. Prosimulium dicum production at station B-VI, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	15-16	0.450	0.916	0.028	0.150	0.026	0.139
	17-23	0.212	1.482	0.088	0.413	0.114	0.611
	24-2	0.146	1.020	0.203	1.088	0.207	1.110
Mar.	3-9	0.112	0.787	0.348	1.865	0.274	1.469
	10-16	0.083	0.579	0.476	2.551	0.276	1.479
	17-23	0.056	0.393	0.569	3.050	0.224	1.201
	24-30	0.050	0.351	0.897	4.808	0.315	1.688
	31-6	0.049	0.342	1.045	5.601	0.357	1.914
Apr.	7-13	0.039	0.275	1.365	7.316	0.375	2.010
	14-20	0.002	0.012	1.118	5.992	0.013	0.070
	21-27	-0.005	-0.036	0.481	2.578	-0.017	-0.091
Mean		0.109		0.641	3.438		
Total						2.164	11.600
Turnover ratio						3.4	

Table VIII-19. Prosimulium dicum production at station S-VI, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	20-23	0.402	1.609	0.065	0.348	0.105	0.563
	24-2	0.227	1.589	0.206	1.104	0.327	1.753
Mar.	3-9	0.117	0.818	0.396	2.123	0.324	1.737
	10-16	0.088	0.618	0.501	2.685	0.310	1.662
	17-23	0.072	0.501	0.842	4.513	0.422	2.262
	24-30	0.050	0.353	1.113	5.966	0.393	2.106
	31-6	0.044	0.309	1.455	7.799	0.450	2.412
Apr.	7-13	0.035	0.246	1.497	8.024	0.368	1.972
	14-20	0.014	0.095	1.584	8.490	0.150	0.804
	21-27	0.001	0.009	1.306	7.000	0.012	0.064
May	28-4	-0.001	-0.004	0.971	5.205	-0.004	-0.021
Mean		0.095		0.937	5.024		
Total						2.857	15.314
Turnover ratio						3.0	

Table VIII-20. Prosimulium dicum production at station O-I, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	24-2	0.400	2.803	0.120	0.643	0.336	1.801
Mar.	3-9	0.155	1.088	0.479	2.567	0.521	2.793
	10-16	0.080	0.563	0.825	4.422	0.464	2.487
	17-23	0.079	0.556	1.161	6.223	0.646	3.463
	24-30	0.056	0.394	1.445	7.745	0.569	3.050
	31-6	0.038	0.263	1.645	8.817	0.433	2.321
Apr.	7-13	0.034	0.240	1.556	8.340	0.373	1.999
	14-20	0.029	0.203	1.310	7.022	0.266	1.426
	21-27	0.005	0.035	1.193	6.394	0.042	0.225
May	28-4	0.000	0.001	0.632	3.388	0.001	0.005
Mean		0.088		1.037	5.556		
Total						3.651	19.570
Turnover ratio						3.5	

Table VIII-21. Prosimulium dicum production at station O-II, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	26-2	0.389	1.946	0.042	0.225	0.082	0.440
Mar.	3-9	0.210	1.472	0.210	1.126	0.309	1.656
	10-16	0.124	0.866	0.484	2.594	0.419	2.246
	17-23	0.067	0.470	0.671	3.597	0.315	1.688
	24-30	0.058	0.403	0.688	3.688	0.277	1.485
	31-6	0.053	0.371	1.268	6.796	0.470	2.519
Apr.	7-13	0.041	0.285	1.954	10.473	0.557	2.986
	14-20	0.034	0.236	2.202	11.803	0.520	2.787
	21-27	0.013	0.088	1.817	9.739	0.160	0.858
	28-4	0.003	0.020	1.069	5.730	0.021	0.113
May	5-11	-0.004	-0.026	0.491	2.632	-0.013	-0.070
Mean		0.090		1.018	5.458		
Total						3.117	16.708
Turnover ratio						3.1	

Table VIII-22. Prosimulium dicum production at station O-III, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Feb.	27-2	0.376	1.504	0.083	0.445	0.125	0.670
Mar.	3-9	0.217	1.516	0.232	1.244	0.352	1.887
	10-16	0.126	0.882	0.480	2.573	0.423	2.267
	17-23	0.095	0.662	0.754	4.041	0.499	2.675
	24-30	0.076	0.530	1.135	6.084	0.602	3.227
	31-6	0.051	0.359	1.304	6.989	0.468	2.508
Apr.	7-13	0.043	0.301	1.199	6.427	0.361	1.935
	14-20	0.042	0.292	1.252	6.711	0.366	1.962
	21-27	0.011	0.077	1.279	6.855	0.098	0.525
May	28-4	0.001	0.008	0.714	3.827	0.006	0.032
Mean		0.104		0.878	4.708		
Total						3.300	17.688
Turnover ratio						3.8	

Table VIII-23. Prosimulium dicum production at station O-IV, 1971.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass ($kcal/m^2$)	Production ($g/m^2/wk$)	Production ($kcal/m^2/wk$)
Mar.	4-9	0.392	2.351	0.136	0.729	0.320	1.715
	10-16	0.166	1.160	0.378	2.026	0.438	2.348
	17-23	0.087	0.607	0.761	4.079	0.462	2.476
	24-30	0.076	0.530	0.843	4.518	0.447	2.396
	31-6	0.070	0.490	0.656	3.516	0.321	1.721
Apr.	7-13	0.051	0.354	0.496	2.659	0.176	0.943
	14-20	0.050	0.350	0.213	1.142	0.075	0.402
	21-27	0.030	0.207	0.345	1.849	0.071	0.381
	28-4	0.015	0.105	0.849	4.551	0.089	0.477
May	5-11	-0.004	-0.025	0.732	3.924	-0.018	-0.096
Mean		0.093		0.546	2.929		
Total						2.381	12.763
Turnover ratio						4.4	

Table VIII-24. Prosimulium dicum production at station O-V, 1971.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass ($kcal/m^2$)	Production ($g/m^2/wk$)	Production ($kcal/m^2/wk$)
Mar.	4-9	0.414	2.485	0.164	0.879	0.408	2.187
	10-16	0.077	0.536	0.296	1.587	0.159	0.852
	17-23	0.123	0.861	0.349	1.871	0.300	1.608
	24-30	0.095	0.667	0.537	2.878	0.358	1.919
	31-6	0.074	0.517	0.681	3.650	0.352	1.887
Apr.	7-13	0.050	0.348	0.674	3.613	0.235	1.260
	14-20	0.047	0.331	1.173	6.287	0.388	2.080
	21-27	0.035	0.248	1.305	6.995	0.324	1.737
	28-4	0.018	0.133	1.126	6.035	0.150	0.804
May	5-11	0.003	0.021	0.910	4.878	0.019	0.102
	12-18	0.001	0.006	0.292	1.565	0.002	0.011
Mean		0.085		0.689	3.692		
Total						2.695	14.447
Turnover ratio						3.9	

Table VIII-25. Prosimulium dicum production at station O-VI, 1971.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Mar.	6-9	0.347	1.386	0.030	0.161	0.042	0.225
	10-16	0.157	1.099	0.109	0.584	0.120	0.643
	17-23	0.142	0.996	0.206	1.104	0.205	1.099
	24-30	0.115	0.802	0.345	1.849	0.277	1.485
	31-6	0.078	0.549	0.461	2.471	0.253	1.356
Apr.	7-13	0.055	0.388	0.736	3.945	0.286	1.533
	14-20	0.051	0.357	0.887	4.754	0.317	1.699
	21-27	0.042	0.297	1.460	7.826	0.434	2.326
	28-4	0.039	0.276	1.564	8.383	0.432	2.316
May	5-11	-0.003	-0.023	0.632	3.388	-0.015	-0.080
Mean		0.102		0.670	3.590		
Total						2.351	12.602
Turnover ratio						3.5	

Table VIII-26. Prosimulium dicum production at station B-VI, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Feb.	3-7	0.416	2.079	0.084	0.416	0.175	0.866
	8-14	0.141	0.989	0.199	0.985	0.197	0.975
	15-21	0.119	0.834	0.290	1.436	0.242	1.198
	22-28	0.098	0.688	0.441	2.183	0.303	1.500
	29-6	0.074	0.519	0.587	2.906	0.305	1.510
Mar.	7-13	0.050	0.351	1.192	5.902	0.418	2.070
	14-20	0.038	0.269	1.234	6.110	0.332	1.644
	21-27	0.041	0.289	1.079	5.342	0.312	1.545
	28-3	0.018	0.124	1.356	6.714	0.168	0.832
Apr.	4-10	0.002	0.015	0.826	4.090	0.012	0.059
Mean		0.100		0.751	3.720		
Total						2.464	12.199
Turnover ratio						3.3	

Table VIII-27. Prosimulium dicum production at station S-VI, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Feb.	9-14	0.392	2.351	0.145	0.718	0.341	1.688
	15-21	0.127	0.887	0.344	1.703	0.305	1.510
	22-28	0.129	0.904	0.541	2.678	0.489	2.421
	29-6	0.103	0.721	0.651	3.223	0.469	2.322
Mar.	7-13	0.060	0.417	0.958	4.743	0.399	1.975
	14-20	0.041	0.288	1.153	5.709	0.332	1.644
	21-27	0.037	0.256	0.941	4.659	0.241	1.193
	28-3	0.035	0.245	1.144	5.664	0.280	1.386
Apr.	4-10	0.008	0.055	1.149	5.689	0.063	0.312
	11-17	-0.001	-0.009	0.665	3.292	-0.006	-0.030
	18-24	0.005	0.032	0.333	1.649	0.011	0.054
Mean		0.085		0.736	3.645		
Total						2.924	14.475
Turnover ratio						4.0	

Table VIII-28. Prosimulium dicum production at station O-I, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Feb.	11-14	0.402	1.609	0.099	0.490	0.159	0.787
	15-21	0.215	1.504	0.377	1.867	0.567	2.807
	22-28	0.118	0.828	0.836	4.139	0.692	3.426
	29-6	0.093	0.648	1.331	6.590	0.862	4.268
Mar.	7-13	0.075	0.528	1.519	7.521	0.802	3.971
	14-20	0.052	0.365	1.607	7.956	0.587	2.906
	21-27	0.047	0.327	1.815	8.986	0.594	2.941
	28-3	0.036	0.253	1.789	8.857	0.453	2.243
Apr.	4-10	0.012	0.084	1.677	8.303	0.141	0.698
	11-17	-0.004	-0.026	0.874	4.327	-0.023	-0.114
Mean		0.105		1.242	6.150		
Total						4.834	23.933
Turnover ratio						3.9	

Table VIII-29. Prosimulium dicum production at station O-II, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Feb.	11-14	0.347	1.386	0.038	0.188	0.053	0.262
	15-21	0.226	1.584	0.200	0.990	0.317	1.569
	22-28	0.126	0.880	0.412	2.040	0.363	1.797
	29-6	0.095	0.666	0.458	2.268	0.305	1.510
Mar.	7-13	0.073	0.511	0.822	4.070	0.420	2.079
	14-20	0.051	0.360	0.945	4.679	0.340	1.683
	21-27	0.048	0.337	1.648	8.159	0.555	2.748
	28-3	0.041	0.286	2.494	12.348	0.713	3.530
Apr.	4-10	0.018	0.129	2.106	10.427	0.272	1.347
	11-17	0.001	0.006	1.064	5.268	0.006	0.030
Mean		0.103		1.061	5.254		
Total						3.344	16.555
Turnover ratio						3.2	

Table VIII-30. Prosimulium dicum production at station O-III, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Feb.	11-14	0.376	1.504	0.080	0.396	0.120	0.594
	15-21	0.256	1.792	0.251	1.243	0.450	2.228
	22-28	0.105	0.738	0.435	2.154	0.321	1.589
	29-6	0.089	0.624	0.456	2.258	0.285	1.411
Mar.	7-13	0.071	0.498	0.679	3.362	0.338	1.673
	14-20	0.047	0.327	0.970	4.802	0.317	1.569
	21-27	0.041	0.284	0.966	4.783	0.274	1.357
	28-3	0.039	0.275	1.560	7.724	0.429	2.124
Apr.	4-10	0.011	0.078	1.852	9.169	0.144	0.713
	11-17	0.004	0.026	0.903	4.471	0.023	0.114
Mean		0.104		0.849	4.204		
Total						2.701	13.372
Turnover ratio						3.2	

Table VIII-31. Prosimulium dicum production at station O-IV, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass ($kcal/m^2$)	Production ($g/m^2/wk$)	Production ($kcal/m^2/wk$)
Feb.	16-21	0.427	2.565	0.139	0.688	0.357	1.768
	22-28	0.146	1.019	0.401	1.985	0.409	2.025
	29-6	0.108	0.754	0.577	2.857	0.435	2.154
Mar.	7-13	0.078	0.546	0.729	3.609	0.398	1.970
	14-20	0.052	0.367	0.922	4.565	0.338	1.673
	21-27	0.046	0.319	0.932	4.614	0.297	1.470
	28-3	0.042	0.291	1.277	6.322	0.372	1.842
Apr.	4-10	0.038	0.269	1.318	6.525	0.355	1.758
	11-17	0.005	0.032	1.069	5.293	0.034	0.168
	18-24	-0.001	-0.010	0.787	3.896	-0.008	-0.040
Mean		0.094		0.823	4.076		
Total						2.987	14.788
Turnover ratio						3.6	

Table VIII-32. Prosimulium dicum production at station O-V, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass ($kcal/m^2$)	Production ($g/m^2/wk$)	Production ($kcal/m^2/wk$)
Feb.	10-14	0.358	1.792	0.093	0.460	0.167	0.827
	15-21	0.215	1.504	0.290	1.436	0.436	2.159
	22-28	0.126	0.879	0.475	2.352	0.418	2.070
	29-6	0.074	0.517	0.594	2.941	0.307	1.520
Mar.	7-13	0.066	0.459	0.724	3.585	0.332	1.644
	14-20	0.052	0.365	0.834	4.129	0.304	1.505
	21-27	0.043	0.300	1.628	8.060	0.488	2.416
	28-3	0.032	0.226	1.845	9.135	0.417	2.065
Apr.	4-10	0.013	0.089	1.471	7.283	0.131	0.649
	11-17	0.001	0.004	0.909	4.500	0.004	0.020
Mean		0.098		0.914	4.524		
Total						3.004	14.875
Turnover ratio						3.3	

Table VIII-33. Prosimulium dicum production at station O-VI, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Feb.	19-21	0.366	1.099	0.058	0.287	0.064	0.317
	22-28	0.204	1.427	0.162	0.802	0.231	1.144
	29-6	0.141	0.986	0.259	1.282	0.255	1.263
Mar.	7-13	0.097	0.678	0.285	1.411	0.193	0.956
	14-20	0.082	0.577	0.609	3.015	0.351	1.738
	21-27	0.061	0.429	0.916	4.535	0.393	1.946
	28-3	0.047	0.328	0.843	4.174	0.277	1.371
Apr.	4-10	0.047	0.330	0.827	4.094	0.273	1.352
	11-17	0.035	0.248	1.365	6.758	0.339	1.678
	18-24	0.005	0.034	1.267	6.273	0.043	0.213
May	25-1	0.003	0.021	0.583	2.886	0.012	0.059
Mean		0.099		0.690	3.415		
Total						2.431	12.037
Turnover ratio						3.5	

Table VIII-34. Prosimulium dicum production at station O-VII, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Feb.	16-21	0.375	2.251	0.110	0.545	0.248	1.228
	22-28	0.106	0.744	0.199	0.985	0.148	0.733
	29-6	0.128	0.896	0.238	1.178	0.213	1.055
Mar.	7-13	0.103	0.723	0.485	2.401	0.351	1.738
	14-20	0.074	0.518	0.700	3.466	0.363	1.797
	21-27	0.050	0.350	0.678	3.357	0.237	1.173
	28-3	0.037	0.259	1.007	4.986	0.261	1.292
Apr.	4-10	0.037	0.256	1.059	5.243	0.271	1.342
	11-17	0.016	0.113	0.988	4.892	0.112	0.555
	18-24	0.005	0.035	0.804	3.981	0.028	0.139
Mean		0.093		0.633	3.135		
Total						2.232	11.052
Turnover ratio						3.5	

Table VIII-35. Simulium arcticum production at station B-I, 1971.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Mar.	27-31	0.358	1.792	0.069	0.333	0.124	0.598
Apr.	1-7	0.225	1.576	0.297	1.433	0.468	2.258
	8-14	0.156	1.093	0.727	3.508	0.795	3.836
	15-21	0.072	0.506	1.040	5.018	0.526	2.538
	22-28	0.041	0.289	0.972	4.690	0.281	1.356
	29-5	0.036	0.250	1.240	5.983	0.310	1.496
May	6-12	0.030	0.207	1.388	6.697	0.287	1.385
	13-19	0.003	0.021	1.050	5.066	0.022	0.106
	20-26	0.003	0.024	0.681	3.286	0.016	0.077
June	27-2	-0.005	-0.037	0.261	1.259	-0.010	-0.048
Mean		0.092		0.796	3.843		
Total						2.819	13.602
Turnover ratio						3.5	

Table VIII-36. Simulium arcticum production at station B-II, 1971.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Mar.	29-31	0.418	1.253	0.102	0.492	0.128	0.618
Apr.	1-7	0.266	1.861	0.482	2.326	0.897	4.328
	8-14	0.111	0.778	0.912	4.400	0.710	3.426
	15-21	0.086	0.602	1.187	5.727	0.715	3.450
	22-28	0.049	0.346	1.443	6.962	0.499	2.408
	29-5	0.051	0.358	1.498	7.228	0.536	2.586
May	6-12	0.039	0.276	1.976	9.534	0.545	2.630
	13-19	0.036	0.249	2.102	10.142	0.523	2.523
	20-26	0.005	0.035	1.026	4.950	0.036	0.174
Mean		0.118		1.277	6.162		
Total						4.589	22.143
Turnover ratio						3.6	

Table VIII-37. Simulium arcticum production at station B-III, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Mar.	28-31	0.402	1.609	0.088	0.425	0.142	0.685
Apr.	1-7	0.238	1.668	0.352	1.698	0.587	2.832
	8-14	0.178	1.245	0.969	4.675	1.206	5.819
	15-21	0.071	0.495	1.585	7.648	0.785	3.788
	22-28	0.046	0.323	2.220	10.712	0.717	3.460
	29-5	0.027	0.189	2.217	10.697	0.419	2.022
May	6-12	0.031	0.215	1.577	7.609	0.339	1.636
	13-19	0.001	0.010	1.636	7.894	0.016	0.077
	20-26	-0.003	-0.018	1.017	4.907	-0.018	-0.087
Mean		0.110		1.356	6.542		
Total						4.193	20.232
Turnover ratio						3.1	

Table VIII-38. Simulium arcticum production at station S-III, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Apr.	8-13	0.421	2.526	0.095	0.458	0.240	1.158
	14-20	0.168	1.176	0.424	2.046	0.499	2.408
	21-27	0.125	0.873	0.924	4.458	0.807	3.894
	28-4	0.066	0.465	1.407	6.789	0.654	3.156
May	5-11	0.045	0.314	1.591	7.677	0.500	2.413
	12-18	0.043	0.302	2.201	10.620	0.665	3.209
	19-25	0.016	0.109	2.394	11.551	0.261	1.259
	26-1	0.001	0.009	1.534	7.402	0.014	0.068
June	2-8	-0.003	-0.019	0.768	3.706	-0.015	-0.072
Mean		0.093		1.274	6.147		
Total						3.625	17.493
Turnover ratio						2.8	

Table VIII-39. Simulium arcticum production at station S-IV, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Apr.	8-13	0.392	2.351	0.132	0.637	0.310	1.496
	14-20	0.203	1.421	0.500	2.413	0.711	3.431
	21-27	0.140	0.981	1.190	5.742	1.167	5.631
	28-4	0.062	0.437	1.633	7.879	0.714	3.445
May	5-11	0.030	0.210	1.698	8.193	0.357	1.723
	12-18	0.029	0.205	2.179	10.514	0.447	2.157
	19-25	0.018	0.123	2.103	10.147	0.259	1.250
	26-1	0.004	0.030	1.098	5.298	0.033	0.159
June	2-8	-0.010	-0.072	0.328	1.583	-0.024	-0.116
Mean		0.096		1.220	5.888		
Total						3.974	19.176
Turnover ratio						3.3	

Table VIII-40. Simulium arcticum production at station S-V, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Apr.	9-13	0.428	2.140	0.119	0.574	0.255	1.230
	14-20	0.192	1.341	0.301	1.452	0.404	1.949
	21-27	0.146	1.019	0.870	4.198	0.887	4.280
	28-4	0.071	0.494	1.689	8.149	0.834	4.024
May	5-11	0.047	0.327	1.930	9.312	0.631	3.045
	12-18	0.027	0.187	1.429	6.895	0.267	1.288
	19-25	0.029	0.200	0.920	4.439	0.184	0.888
	26-1	0.006	0.044	1.030	4.970	0.045	0.217
June	2-8	0.003	0.020	0.790	3.812	0.016	0.077
Mean		0.105		1.043	5.035		
Total						3.523	16.998
Turnover ratio						3.4	

Table VIII-41. Simulium arcticum production at station B-I, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Mar.	20-23	0.347	1.386	0.096	0.470	0.133	0.651
	24-30	0.250	1.749	0.336	1.646	0.588	2.880
	31-6	0.127	0.890	0.634	3.105	0.564	2.762
Apr.	7-13	0.102	0.711	1.333	6.529	0.948	4.643
	14-20	0.057	0.400	1.918	9.394	0.767	3.757
	21-27	0.049	0.343	2.254	11.040	0.773	3.213
	28-4	0.038	0.263	2.496	12.225	0.656	3.213
May	5-11	0.004	0.027	2.067	10.124	0.056	0.274
	12-18	-0.005	-0.032	0.899	4.403	-0.029	-0.142
	19-25	0.003	0.021	0.164	0.803	0.003	0.015
Mean		0.097		1.271	6.223		
Total						4.459	21.839
Turnover ratio						3.5	

Table VIII-42. Simulium arcticum production at station B-II, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Mar.	22-23	0.458	0.916	0.065	0.318	0.060	0.294
	24-30	0.251	1.758	0.204	0.999	0.359	1.758
	31-6	0.180	1.258	0.549	2.689	0.691	3.385
Apr.	7-13	0.114	0.800	1.219	5.971	0.975	4.776
	14-20	0.058	0.404	1.767	8.655	0.714	3.497
	21-27	0.041	0.287	1.836	8.993	0.527	2.581
	28-4	0.041	0.286	1.870	9.159	0.535	2.620
May	5-11	0.007	0.050	1.700	8.327	0.085	0.416
	12-18	0.002	0.011	0.993	4.864	0.011	0.054
Mean		0.128		1.229	6.021		
Total						3.957	19.381
Turnover ratio						3.2	

Table VIII-43. Simulium arcticum production at station B-III, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Mar.	22-23	0.458	0.916	0.066	0.323	0.060	0.294
	24-30	0.270	1.886	0.254	1.244	0.479	2.346
	31-6	0.145	1.014	0.648	3.174	0.657	3.218
Apr.	7-13	0.116	0.812	1.144	5.603	0.929	4.550
	14-20	0.060	0.417	1.497	7.332	0.624	3.056
	21-27	0.052	0.365	1.772	8.679	0.647	3.169
	28-4	0.044	0.307	1.994	9.767	0.612	2.998
May	5-11	0.003	0.021	1.792	8.777	0.038	0.186
	12-18	-0.002	-0.013	1.002	4.908	-0.013	-0.064
Mean		0.127		1.225	6.001		
Total						4.033	19.753
Turnover ratio						3.3	

Table VIII-44. Simulium arcticum production at station S-III, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Mar.	28-3	0.392	2.741	0.151	0.740	0.414	2.028
Apr.	4-10	0.142	0.997	0.589	2.885	0.587	2.875
	11-17	0.108	0.757	1.102	5.398	0.834	4.085
	18-24	0.055	0.385	1.391	6.813	0.536	2.625
	25-1	0.047	0.330	1.463	7.166	0.483	2.366
May	2-8	0.042	0.296	1.569	7.685	0.464	2.273
	9-15	0.032	0.223	1.518	7.435	0.339	1.660
	16-22	0.004	0.029	1.068	5.231	0.031	0.152
	23-29	0.004	0.027	0.430	2.106	0.012	0.059
Mean		0.092		1.031	5.051		
Total						3.700	18.123
Turnover ratio						3.6	

Table VIII-45. Simulium arcticum production at station S-IV, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Mar.	28-3	0.413	2.890	0.286	1.401	0.826	4.046
Apr.	4-10	0.149	1.041	0.763	3.737	0.794	3.889
	11-17	0.097	0.678	1.132	5.545	0.767	3.757
	18-24	0.066	0.462	1.434	7.024	0.663	3.247
	25-1	0.052	0.362	2.083	10.203	0.754	3.693
May	2-8	0.029	0.205	2.107	10.320	0.432	2.116
	9-15	0.015	0.103	1.955	9.576	0.201	0.984
	16-22	0.002	0.013	1.759	8.616	0.023	0.113
Mean		0.103		1.440	7.053		
Total						4.460	21.845
Turnover ratio						3.1	

Table VIII-46. Simulium arcticum production at station S-V, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Mar.	28-3	0.377	2.639	0.201	0.984	0.530	2.596
Apr.	4-10	0.155	1.087	0.585	2.865	0.636	3.115
	11-17	0.129	0.904	1.085	5.314	0.981	4.805
	18-24	0.063	0.445	1.402	6.867	0.624	3.056
	25-1	0.046	0.325	1.501	7.352	0.488	2.390
May	2-8	0.038	0.263	2.163	10.594	0.569	2.787
	9-15	0.010	0.072	2.379	11.652	0.171	0.838
	16-22	0.003	0.019	1.780	8.763	0.034	0.167
	23-29	0.005	0.037	0.857	4.198	0.032	0.157
Mean		0.092		1.329	6.510		
Total						4.065	19.911
Turnover ratio						3.1	

Table VIII-47. Simulium canadense production at station B-VII, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Apr.	15-20	0.427	2.565	0.196	1.063	0.503	2.727
	21-27	0.110	0.767	0.490	2.657	0.376	2.039
	28-4	0.092	0.647	0.710	3.850	0.459	2.489
May	5-11	0.084	0.590	0.692	3.752	0.408	2.212
	12-18	0.063	0.441	0.917	4.972	0.404	2.190
	19-25	0.051	0.358	1.384	7.504	0.495	2.684
	26-1	0.043	0.303	1.516	8.220	0.459	2.489
June	2-8	0.030	0.213	1.394	7.558	0.297	1.610
	9-15	0.021	0.145	1.797	10.730	0.287	1.556
	16-22	-0.003	-0.021	1.639	8.887	-0.034	-0.184
Mean		0.092		1.103	5.979		
Total						3.654	19.812
Turnover ratio						3.3	

Table VIII-48. Simulium canadense production at station B-VIII, 1971.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Apr.	15-20	0.384	2.303	0.101	0.548	0.233	1.263
	21-27	0.103	0.718	0.213	1.155	0.153	0.830
	28-4	0.092	0.643	0.280	1.518	0.180	0.976
May	5-11	0.096	0.674	0.564	3.058	0.380	2.060
	12-18	0.081	0.564	1.036	5.617	0.584	3.166
	19-25	0.072	0.503	1.233	6.685	0.620	3.362
	26-1	0.042	0.292	1.627	8.822	0.475	2.575
June	2-8	0.038	0.263	1.752	9.499	0.461	2.500
	9-15	0.011	0.077	1.293	7.011	0.100	0.542
	16-22	0.002	0.011	1.007	5.460	0.011	0.060
Mean		0.092		0.920	4.987		
Total						3.197	17.334
Turnover ratio						3.5	

Table VIII-49. *Simulium canadense* production at station B-IV, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Apr.	8-9	0.458	0.916	0.045	0.237	0.041	0.216
	10-16	0.175	1.224	0.108	0.570	0.132	0.696
	17-23	0.095	0.663	0.155	0.817	0.103	0.543
	24-30	0.090	0.631	0.169	0.891	0.107	0.564
May	1-7	0.093	0.652	0.333	1.756	0.217	1.144
	8-14	0.093	0.650	0.859	4.530	0.558	2.943
	15-21	0.078	0.547	1.273	6.714	0.696	3.671
	22-28	0.052	0.364	0.745	3.929	0.271	1.429
	29-4	0.039	0.270	0.359	1.893	0.097	0.512
June	5-11	0.011	0.078	0.396	2.089	0.031	0.163
	12-18	0.004	0.028	0.341	1.798	0.010	0.053
	19-25	-0.001	-0.007	0.300	1.582	-0.002	-0.011
Mean		0.099		0.450	2.372		
Total						2.261	11.923
Turnover ratio						5.0	

Table VIII-50. *Simulium canadense* production at station B-V, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Apr.	6-9	0.347	1.386	0.086	0.454	0.119	0.628
	10-16	0.163	1.139	0.217	1.144	0.247	1.303
	17-23	0.107	0.751	0.349	1.841	0.262	1.382
	24-30	0.104	0.730	0.488	2.574	0.356	1.878
May	1-7	0.086	0.603	0.644	3.396	0.388	2.046
	8-14	0.066	0.461	1.299	6.851	0.599	3.159
	15-21	0.045	0.316	1.923	10.142	0.608	3.207
	22-28	0.041	0.290	1.648	8.692	0.478	2.521
	29-4	0.036	0.255	1.768	9.324	0.451	2.379
June	5-11	0.012	0.086	1.869	9.857	0.161	0.849
	12-18	0.002	0.012	1.334	7.036	0.016	0.084
Mean		0.092		1.097	5.784		
Total						3.685	19.436
Turnover ratio						3.3	

Table VIII-51. *Simulium canadense* production at station B-VII, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Apr.	12-17	0.407	2.442	0.123	0.649	0.300	1.582
	18-24	0.083	0.578	0.278	1.466	0.161	0.849
	25-1	0.090	0.630	0.370	1.951	0.233	1.229
May	2-8	0.087	0.612	0.456	2.405	0.279	1.471
	9-15	0.089	0.624	0.666	3.512	0.416	2.194
	16-22	0.064	0.446	1.405	7.410	0.626	3.302
	23-29	0.046	0.325	2.126	11.213	0.691	3.644
	30-5	0.036	0.250	1.747	9.214	0.437	2.308
June	6-12	0.016	0.112	1.685	8.887	0.189	0.997
	13-19	0.002	0.011	1.982	10.453	0.022	0.116
	20-26	0.001	0.006	1.041	5.490	0.006	0.032
Mean		0.084		1.090	5.748		
Total						3.360	17.724
Turnover ratio						3.1	

Table VIII-52. *Simulium canadense* production at station B-VIII, 1972.

Date		Growth (g/g/day)	Growth (g/g/wk)	Biomass (g/m^2)	Biomass (kcal/m^2)	Production (g/m^2/wk)	Production (kcal/m^2/wk)
Apr.	13-17	0.428	2.140	0.110	0.580	0.235	1.239
	18-24	0.115	0.804	0.221	1.166	0.178	0.939
	25-1	0.093	0.653	0.301	1.587	0.197	1.039
May	2-8	0.088	0.614	0.458	2.415	0.281	1.482
	9-15	0.084	0.588	0.711	3.750	0.418	2.205
	16-22	0.070	0.493	1.071	5.648	0.538	2.785
	23-29	0.047	0.331	1.275	6.724	0.422	2.226
	30-5	0.034	0.241	1.626	8.576	0.392	2.067
June	6-12	0.020	0.140	1.752	9.240	0.245	1.292
	13-19	0.002	0.016	1.232	6.498	0.020	0.105
	20-26	-0.002	-0.017	0.556	2.932	-0.009	-0.047
Mean		0.089		0.870	4.590		
Total						2.907	15.332
Turnover ratio						3.3	

Table VIII-53. Simulium canadense production at station S-I, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Apr.	20-24	0.389	1.946	0.081	0.427	0.158	0.833
	25-1	0.104	0.728	0.193	1.018	0.141	0.744
May	2-8	0.106	0.744	0.298	1.572	0.222	1.171
	9-12	0.108	0.757	0.385	2.030	0.291	1.535
	16-22	0.086	0.601	0.741	3.908	0.445	2.347
	23-29	0.066	0.459	1.252	6.603	0.575	3.033
June	30-5	0.058	0.405	1.278	6.740	0.518	2.732
	6-12	0.039	0.272	1.632	8.607	0.444	2.342
	13-19	0.012	0.084	1.704	8.987	0.143	0.754
	20-26	0.004	0.026	1.014	5.348	0.026	0.137
Mean		0.097		0.884	4.664		
Total						2.963	15.628
Turnover ratio						3.4	

Table VIII-54. Simulium canadense production at station S-II, 1972.

Date		Growth		Biomass		Production	
		(g/g/day)	(g/g/wk)	(g/m^2)	(kcal/m^2)	(g/m^2/wk)	(kcal/m^2/wk)
Apr.	20-24	0.389	1.946	0.103	0.543	0.200	1.055
	25-1	0.088	0.619	0.183	0.965	0.113	0.596
May	2-8	0.107	0.749	0.232	1.224	0.174	0.918
	9-15	0.090	0.627	0.358	1.888	0.224	1.181
	16-22	0.108	0.754	0.529	2.790	0.399	2.104
	23-29	0.068	0.477	0.933	4.921	0.445	2.347
	30-5	0.059	0.414	1.236	6.519	0.512	2.700
June	6-12	0.056	0.393	1.931	10.184	0.759	4.003
	13-19	0.018	0.128	2.005	10.574	0.257	1.355
	20-26	0.003	0.022	1.167	6.155	0.026	0.137
July	27-3	-0.002	-0.013	0.568	2.996	-0.007	-0.037
Mean		0.089		0.864	4.557		
Total						3.102	16.359
Turnover ratio						3.6	

APPENDIX IX

INITIAL BLACK FLY LARVAL DENSITY PER SQUARE METER OF USABLE SUBSTRATE AT ALL 1971 AND 1972 STATIONS

Station & Year	P. caudatum	P. dicum	P. caudatum + P. dicum
B-VI (1971)	20258	14470	34728
S-VI	22066	14278	36344
O-I	19826	12963	32789
O-II	18359	10618	29157
O-III	22424	29899	52323
O-IV	13334	17015	30349
O-V	16438	18494	34932
O-VI	12880	11938	24818
		S. arcticum	
B-I (1971)		16730	
B-II		34902	
B-III		19226	
S-III		14672	
S-IV		16160	
S-V		19235	
		S. canadense	
B-VII (1971)		18391	
B-VIII		14718	

	P. caudatum	P. dicum	P. caudatum + P. dicum
B-VI (1972)	11338	15969	27307
S-VI	17140	23179	40319
O-I	19437	23693	43130
O-II	18844	18466	37310
O-III	15054	18739	33783
O-IV	11692	13930	25622
O-V	12151	17580	29731
O-VI	17437	34872	52309
O-VII	11145	18877	30022

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Appendix IX. (Continued)

	S. arcticum
B-I (1972)	30006
B-II	27430
B-III	23659
S-III	20470
S-IV	22603
S-V	22152

	S. canadense
B-IV (1972)	17644
B-V	21749
B-VII	15232
B-VIII	20632
S-I	13938
S-II	22228

APPENDIX X

ANNUAL BLACK FLY LARVAL PRODUCTION IN GRAMS PER SQUARE METER OF USABLE SUBSTRATE AT ALL 1971 AND 1972 STATIONS

Station & Year	P. caudatum	P. dicum	P. caudatum + P. dicum
B-VI (1971)	4.410	4.008	8.418
S-VI	3.803	3.560	7.363
O-I	4.433	5.345	9.778
O-II	4.144	5.043	9.187
O-III	5.140	5.920	11.060
O-IV	2.964	2.903	5.867
O-V	3.756	3.544	7.300
O-VI	3.658	3.545	7.203
		S. arcticum	
B-I (1971)		4.231	
B-II		6.407	
B-III		5.337	
S-III		5.937	
S-IV		5.269	
S-V		4.928	
		S. canadense	
B-VII (1971)		4.216	
B-VIII		4.517	

	P. caudatum	P. dicum	P. caudatum + P. dicum
B-VI (1972)	3.563	3.777	7.340
S-VI	4.344	4.582	8.226
O-I	4.760	6.584	11.344
O-II	4.857	6.049	10.906
O-III	3.314	3.074	6.388
O-IV	3.328	3.566	6.894
O-V	3.229	3.728	6.957
O-VI	3.274	5.426	8.700
O-VII	3.964	3.852	7.816

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Appendix X. (Continued)

	S. arcticum
B-I (1972)	6.327
B-II	6.023
B-III	4.771
S-III	5.960
S-IV	5.660
S-V	5.650
	S. canadense
B-IV (1972)	2.946
B-V	4.274
B-VII	4.549
B-VIII	4.570
S-I	3.671
S-II	5.171