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Title: LIFE HISTORY AND PRODUCTION STUDIES OF SIALIS CALIFORNICA BANKS AND SIALIS ROTUNDA BANKS (MEGALOPTERA:SIALIDAE)

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Norman H. Anderson

Comparative ecological studies of Sialis californica Banks and Sialis rotunda Banks were made in Western Oregon from 1966 to 1968. Field collections for S. rotunda were made in fish holding pond at the Oak Creek laboratories, 5 miles west of Corvallis, Benton County, and for S. californica in enriched sections of Berry Creek experimental stream, 13 miles north of Corvallis.

Life histories were determined in aquaria, in laboratory streams and the natural habitats. S. rotunda, predominantly a pond species, completed its life cycle in one year in all situations. S. californica, commonly a stream species, took one or two years depending on oviposition time and food availability. Both species were reared successfully in the laboratory through all stages of their life cycle. There are ten larval instars. The larvae are carnivorous and feed on insects and other small benthic organisms.

Biweekly or monthly samples were collected from the two locations for density, biomass, growth rate and production studies. Density and biomass of *S. rotunda* in the pond were much higher than for *S. californica* in the stream. Enrichment with sucrose and urea resulted in differences in density and biomass of *S. californica* between the four experimental sections at Berry Creek. The unenriched section usually had a high density but low or similar biomass compared with the enriched sections which had few individuals. The lower density in the enriched sections was associated with unfavorable substrate conditions for early-instar larvae because of dense mats of the filamentous bacterium, *Sphaerotilus natans*. Larger larvae were not hindered by the *S. natans* filaments and had rapid growth because food was abundant.

Production of both species was calculated by two methods: (1) Ricker's (1946) method, the product of growth rate and mean biomass; and (2) Allen's (1951) graphical method, using numbers per m^2 and mean individual weight at each sampling date. The results from both methods were comparable, with the graphical method usually providing a slightly higher estimate of production. Annual production of *S. rotunda* in the pond was 13.18 Kilocalories/ m^2. This was more than double the production of *S. californica* in any of the sections of Berry Creek. In Berry Creek, the population in the unenriched section had low growth rate but the density of larvae resulted in high biomass and a comparable production to that in the enriched sections. The accumulated annual production was: unenriched, 4.94 Kilocalories; enriched, 6.34 Kilocalories.

The relationship between larval growth and food consumption rate was established by experiments in laboratory streams during summer and winter. These data were used to estimate food consumption by field populations. In the pond, *S. rotunda* larvae consumed 137 gms/m^2/year. In Berry Creek, individuals in enriched sections consumed one and half to two times more food than did individuals in the unenriched section.

Life History and Production Studies of
Sialis californica Banks and *Sialis rotunda* Banks
(Megaloptera:Sialidae)

by

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LIFE HISTORY AND PRODUCTION STUDIES OF *SIALIS CALIFORNICA* BANKS AND *SIALIS ROTUNDA* BANKS (MEGALOPTERA:SIALIDAE)

INTRODUCTION

Aquatic insects are of direct economic importance in at least three major respects: beneficial as fish food; harmful as blood-sucking biting flies and potential carriers of diseases of man and animals; and either beneficial or harmful in connection with water pollution and sewage disposal. Aquatic insect larvae are generally the most conspicuous and adaptive animals in the freshwater environment. In general, this is the energy-storing stage, and the stage at which many of the restrictive habitat-partitioning mechanisms are in effect.

To understand the role of insects in aquatic communities it is necessary to recognize the species and to study their biology. Unfortunately, such information is not available for most taxa. It is the purpose of this study to provide such data for *Sialis californica* Banks and *Sialis rotunda* Banks.

Biological studies of *S. californica* were initiated as part of a larger program designed to elucidate the important energy pathways in a woodland stream ecosystem. Warren *et al.* (1964), Reese (1966), McIntyre (1967) and Earnest (1967) have reported on production of various trophic levels in Berry Creek, Corvallis, Oregon.

S. californica was an abundant carnivore in the stream and possibly a competitor for food with the fish. Thus the present study was undertaken to assess the role of S. californica. When S. rotunda was found nearby, it was decided to expand the research to include a comparison of the two species.

The objectives of the study were: (1) to describe major morphological and ecological differences between the larvae of S. rotunda and S. californica; (2) to determine their life histories; (3) to study the food habits of the larvae; (4) to obtain an estimate of the production of the species in two habitats; and (5) to estimate food consumption.

The Megaloptera are a small order of primitive insects called alder flies and dobson flies, distributed throughout the temperate and tropical regions of the world. This order is represented by only two families, Sialidae and Corydalidae, the former with only one genus, Sialis Latreille in the Nearctic region (Ross, 1937). Sialis, the alder flies, are found throughout the United States and Canada with a distinctive eastern and western grouping of species.

Previously no life history or production studies had been made on S. rotunda or S. californica. The information in the literature on the life history of other species of Sialis is meagre and confusing. Most of the literature pertains to systematics and deals with identification of adults.

The first description of a *Sialis* larva, *S. fuliginosa* Pictet, was published over two centuries ago by Rosel in 1749 (Cuyler, 1956). Needham and Betten (1901) and Davis (1903) gave biological data on *Sialis infumata* Newman, while the bionomics of the common European species, *Sialis lutaria* L. was described by Lestage (1918), Syms (1934), and Dubois and Geigy (1935). The latter represents the only thorough investigation with a complete account of development and metamorphosis as well as extensive information on the habitat of the larva. Ross (1937) contributed a monograph of the Nearctic genus *Sialis* and briefly summarized observations made previously by other workers. Townsend (1939) and Flint (1964) have described four new species of *Sialis*. Cuyler (1956) recorded 20 species of Megaloptera in Eastern United States. He listed 13 species of *Sialis* and described two larvae, *S. itasca* and *S. americana*. He gave a very brief description of the habitats where the larvae were collected.

Most of the freshwater production studies have dealt with fish populations. A few studies provided estimates of the relative turn-over in insect populations, eg. Anderson and Hooper (1956), Dugdale (1955), Hayne and Ball (1956), and Waters (1966).

MATERIALS AND METHODS

Oak Creek Fish Pond

Population studies of *S. rotunda* were made in a small fish holding pond near Oak Creek Fisheries Laboratory, five miles west of Corvallis. The pond was dug in 1960 and, until 1964, was fertilized for fish studies. The only fish in the pond during the present study was the Western mosquito fish, *Gambusia affinis* (Baird and Girard).

The pond is almost circular with a surface area of 70 square meters and a maximum depth of 65 cms. Water level was maintained through its supply from a spring-fed stream. Water temperature was recorded on a Taylor Weather-Hawk thermograph. The vegetation around the pond was alder (*Alnus* spp.), willow (*Salix* spp.), rushes (*Scirpus* spp.) and sedge (*Cyperus* spp.).

Samples were taken from May 1967 to May 1968. Four samples were taken with a six-inch Ekman dredge at approximately two week intervals from May to November and at monthly intervals from November to May. Samples were collected on 18 sampling dates during the total study period.

The samples were taken to the laboratory where they were washed through a 60-mesh sieve and the larvae were sorted from the debris. Measurements of length, head-width and weight were made for each individual. The larvae were kept in a refrigerator for two days in bottles with some water, to collect the feces for food habit studies, and then returned to the pond.

Berry Creek Stream

The field work for *S. californica* was initiated at Berry Creek, a small woodland stream that has been described in detail by Warren *et al.* (1964). It is located approximately 13 miles north of Oregon State University campus and flows in a general northerly direction into Soap Creek, which enters the Luckiamute River, a tributary of the Willamette River, draining foot-hills along the western edge of the valley. A 1,500 foot section of the stream has been brought under flow control by means of a diversion dam and a bypass channel. Water enters the experimental stream through a regulating valve. The flow is continuously recorded at two V-notch weirs, one immediately below the dam and the other where the water leaves the experimental section (Figure 1). The lower third of the controlled part of the stream has been divided into four experimental sections, each consisting of a riffle and a pool, numbered I, II, III, and IV proceeding downstream. At the upstream end of each section, Saran screens (32 meshes/$in.^2$) supported by box-like structures have been fixed to prevent the movement of fish, most of the insects and other organisms from one section to another. The pool areas of the sections I, II, III, and IV,

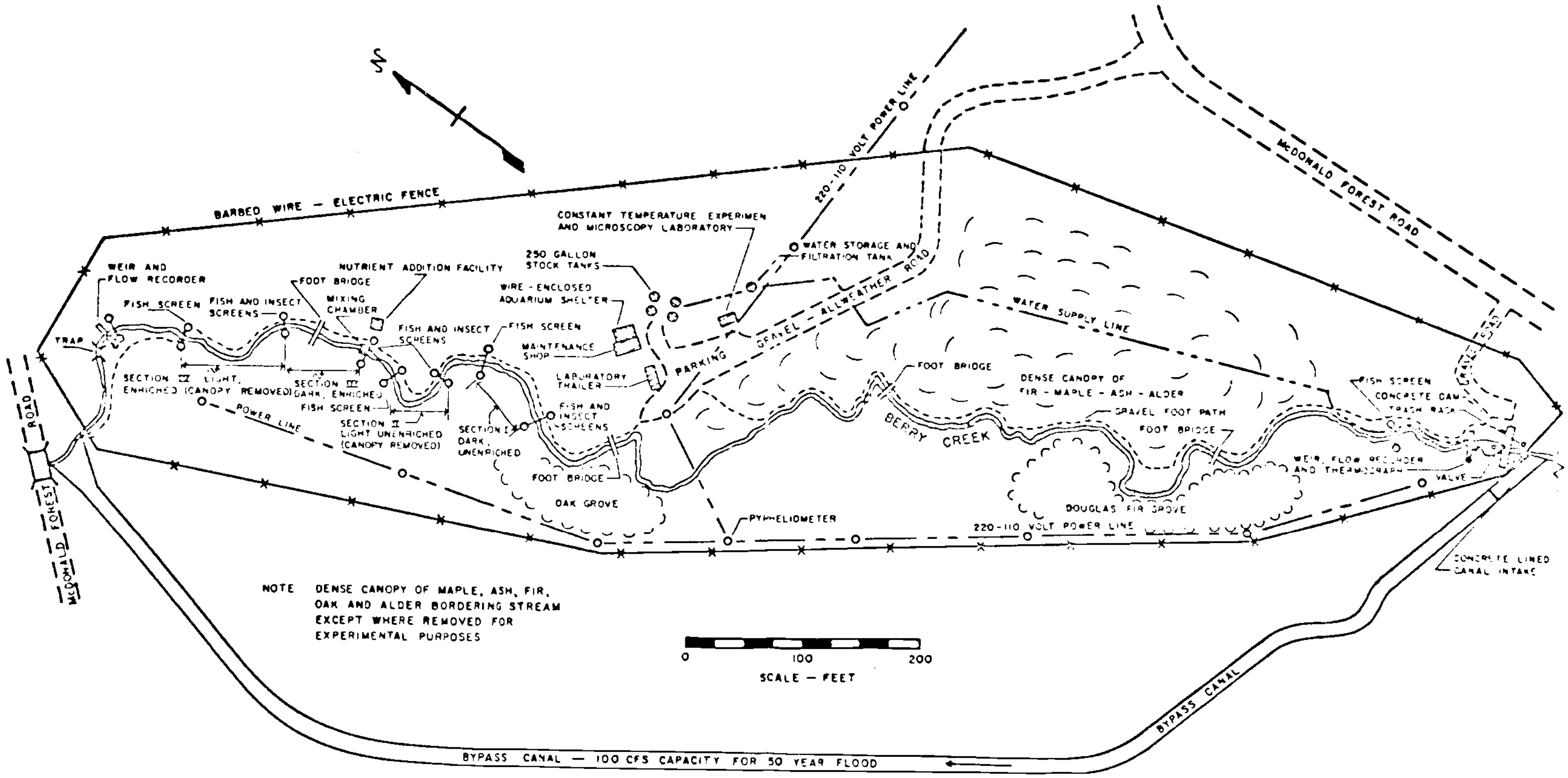


Figure 1. Diagram of Berry Creek Experimental Stream showing research facilities.

where the present studies were made are 24.49, 15.42, 15.85 and 17.76 m^2, respectively.

A major objective of the Berry Creek project is to measure trout production with different amounts of enrichment. Since 1960, sections III and IV had been enriched by introducing solutions of sucrose and of urea at the upstream end of section III at an approximate concentrations of 4.0 and 0.5 mg/liter, respectively. Enrichment resulted in dense growths of the filamentous bacterium, Sphaerotilus natans. This nuisance organism is common in streams polluted with organic wastes. The importance of Sphaerotilus in the food chain at Berry Creek has been extensively discussed by Warren et al. (1964). The point of introduction of solutions was moved to the upstream end of section II in March 1965. Part of forest canopy over sections II and IV had been removed during earlier studies to determine the effect of light intensity and quantity of leaf fall on the stream community. The stream is shaded by red alder (Alnus rubra Nutt.), big leaf maple (Acer macrophyllum Pursh.), Oregon white oak (Quercus garryana Dougl.), black cottonwood (Populus trichocarpa Torr. and Gray), and Oregon ash (Fraxinus latifolia Benth).

Further changes were made during the present studies. When the study began in May 1966, the stream was in the above described condition. In February 1967, it was flushed by blocking the diversion canal and channelling all of the flow through the experimental section.

The freshet removed the accumulated debris from the stream and greatly reduced the population of *Sialis* and also other organisms. Enrichment of all sections was completely stopped after this time. In September 1967, screens between the sections were removed which allowed the free movement of organisms from one section to another.

Stream flow through the controlled sections was maintained at 0.5 cu. ft./sec. except during low flow in the summer months. Water temperature was recorded throughout the period of study by a thermograph. Figure 2 represents the record of water flow and temperature.

Monthly samples of *S. californica* were taken from the pools, I, II, III, and IV from May 1966 to December 1967. Samples taken by Dr. N. H. Anderson from December 1965 to April 1966 have also been included in the results.

At the beginning of the study, samples were collected using a rectangular box enclosing 0.23 m^2 bottom area. The bottom of the sampler had a four-inch layer of foam rubber to give a tight fit on the substrate. The substrate of the enclosed area was removed with an aquatic net. With this method we were not able to collect early-instar larvae. An improved technique that was efficient in collecting all larvae was the pipe sampler (Figure 3). The sampler consisted of a one meter length of aluminum irrigation pipe that enclosed an area of 0.029 m^2. The pipe had five holes evenly spaced throughout

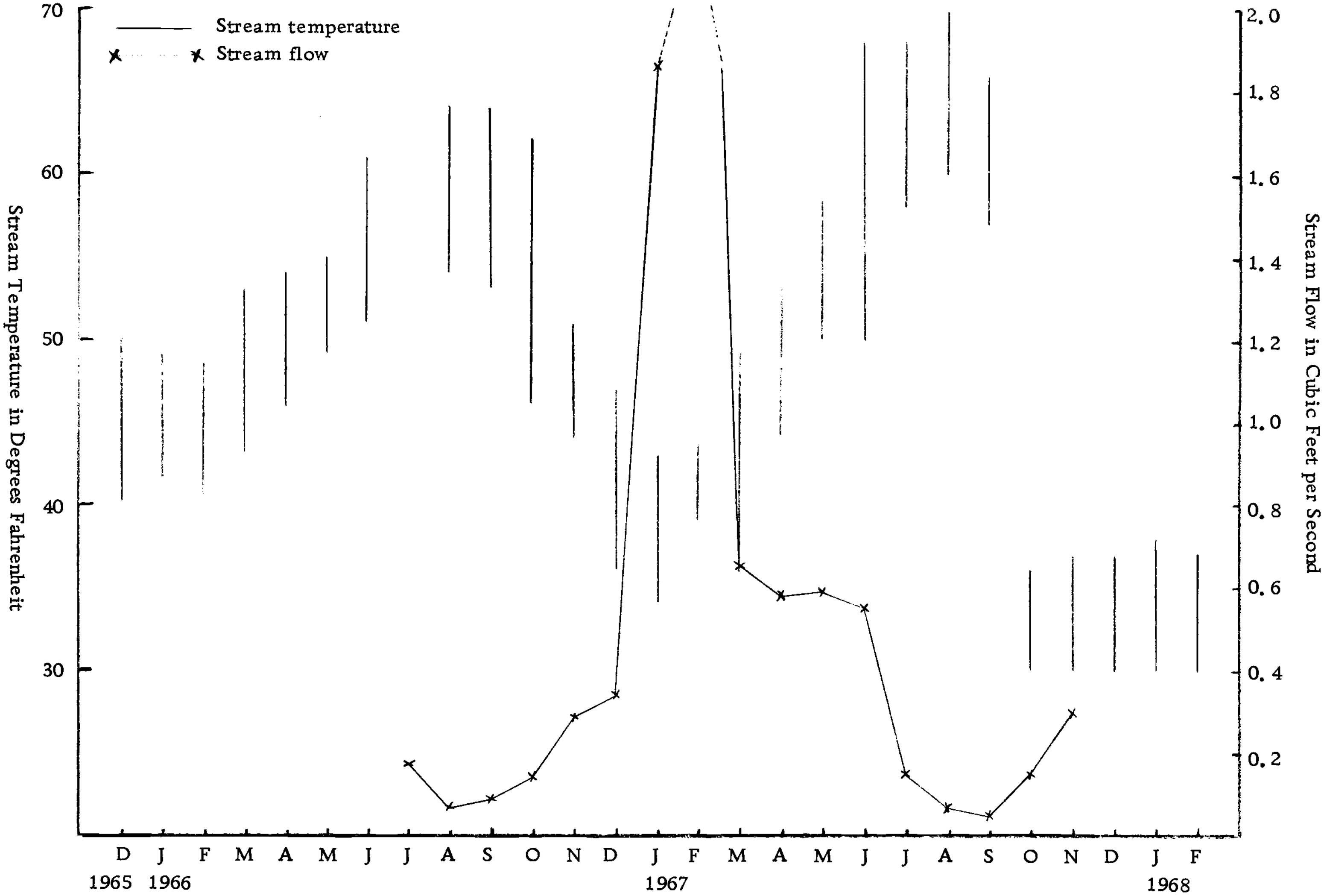


Figure 2. Stream flow and maximum and minimum temperature in Berry Creek.

Figure 3. Gorman-Rupp centrifugal pump sampler.

its length, plugged with rubber stoppers. One end of the pipe was fixed with foam rubber to form a seal on the substrate. When the sampler was in place, a Gorman-Rupp centrifugal pump, fitted with two cm tubing was used to pump out the material from the area enclosed. Timely removal of the rubber stopper immediately below the water level permitted the replacement of water evacuated by the pump. The outlet tubing from the pump was placed in a 50-mesh wire bucket to collect the sample.

On each sampling date, 24 samples were collected: 8 from section I, 5 from section II, 5 from section III, and 6 from section IV. Each sample was placed separately in a bottle and taken to the laboratory where they were washed, sorted, and measured in the same manner as described for S. rotunda. These larvae were also kept in the refrigerator for two days to collect the feces and then returned to their respective stream sections.

Field Experiments

Cages

To determine the length of the larval stage under field conditions, cages of 60 cm × 45 cm × 45 cm were kept in the pond and the stream. The cages were wooden frames covered on the sides and bottom with 0.333 nitex screen. One cage was set up with natural substrate on July 10, 1967, in the pond with 20 larvae of *S. rotunda*, and two cages in the stream on December 22, 1966, with 12 larvae of *S. californica* in each cage. Food was added approximately two to three week intervals and the larvae were measured at the same time. Tubificid worms from a culture maintained at Fisheries Laboratory were put into the cage as food for *S. rotunda*. At Berry Creek, the substrate was collected from the pools, washed through sieves and the organisms obtained in this way were used as food for *S. californica*.

Pit-fall Traps

To collect the larvae leaving the water to pupate, two 3 foot-boards were inserted into the soil in the form of V near the edge of water. A jar with some soil was kept at the junction of two boards where the two arms of the V unite. The larvae leaving the water from the open side migrated and fell into the bottle. The width of the opening at the water's edge was three feet, so each trap collected the larvae migrating from a known length of pond or stream side.

Laboratory Experiments

Laboratory experiments were conducted in an aquarium with a temperature range of 68°-74°F. throughout the year, and in a laboratory stream with great daily and seasonal fluctuations.

The laboratory stream is located at the Aquatic Entomology

Laboratory at Oak Creek. It consists of a divided wooden trough, measuring 234 × 30 × 24 cm through which the water is recirculated (Figure 4). A water current was maintained by a 51-cm paddle wheel driven by an electric motor. Water temperatures were recorded with a thermograph. The rearing jars used in laboratory stream had openings of 5.0 cm × 2.5 cm on each side. The windows and tops were covered with 0.333 nitex screen, which permitted the water to flow through the jars. Two or three small rocks were put in the jars to simulate a more natural habitat.

Life cycle studies of S. rotunda and S. californica were made in the aquarium with constant air bubbling and also in the laboratory stream. Food consumption studies were conducted in the laboratory stream in different seasons.

Larvae were reared through all instars in small jars, submerged in water. They were taken out of the water when ready to pupate and placed individually on damp soil. The adults were enclosed in screen cages of 20 cm × 20 cm × 45 cm for mating and oviposition.

Caloric Conversion

Growth rates, biomass, production and food consumption values were converted into caloric equivalents. A Parr semi-micro bomb calorimeter No. 1411 was used for these determinations.

The mean percent dry weights and mean caloric values

Figure 4. Laboratory stream at Aquatic Entomology Laboratory, Oak Creek.

determined for the materials used in the experiments are given in Table 1.

Table 1. Mean percent dry weight and mean caloric values per gram dry weight of experimental materials.

Materials	Percent dry weight	Kilocalories per gm dry weight Range	Mean
S. rotunda larvae	16.2	5.312-5.352	5.332
S. californica larvae	18.2	5.376-5.419	5.398
Tubificid worms*	16.2	5.336-5.986	5.491

*From Brocksen *et al.* (1968).

LIFE HISTORY OF *SIALIS ROTUNDA* AND *SIALIS CALIFORNICA*

General Morphology

Though the mature larvae of *S. rotunda* and *S. californica* can be readily distinguished by color patterns, the younger larvae cannot be separated in this manner. A comparative study revealed few morphological characters that would separate the two species, other than the shape of the labrum. Distinguishing features are given in Table 2 and the mature larvae are compared in Figures 5 and 6.

The following description of larvae of *S. rotunda* and *S. californica* gives the characters thought to be of generic significance.

Head (Figure 7a)

Prognathous, quadrate, flattened, smooth and shiny; each lateral eye spot with six ocelli; antenna (Figure 7b), four-segmented, basal segment 0.3 mm, shorter and wider than others, second segment 0.6 mm, third segment 0.38 mm and fourth segment 0.38 mm; epicranial suture, distinct, the frontal arms originating approximately 2/3 distance from base of head to epistomal suture; occipital suture incomplete on dorsal side; clypeus narrow, apical margin elevated laterally; labrum (Figure 7c), semicircular, produced apically into a bifid flap, antero-lateral margin crenulated;

Table 2. Distinguishing characteristics of the larvae of *S. rotunda* and *S. californica*.

Characters	*S. rotunda*	*S. californica*
Head	Light to dark brown with slight blackish tinge; uniform on all portions of head.	Light to dark brown, anterior portion from frontal arms darker than posterior portion.
Labrum	Apex bifid (cleft), distal margin with 11-12 crenulations on each side, deeper than *S. californica*.	Apex bifid, 12-13 shallow crenulations on each side.
Thorax	Dark brown with mid-dorsal furrow.	Brown with mid-dorsal furrow.
Abdomen	Black with a prominent median whitish band from first to last abdominal segment. Intersegmental membrane and bases of gills light.	Uniform reddish brown.
Tracheal gills	Whitish.	Slightly pigmented.
Size range (mature larvae)	14-18 mm.	16-22 mm.

Figure 5. Mature larva of Sialis rotunda.

Figure 6. Mature larva of Sialis californica.

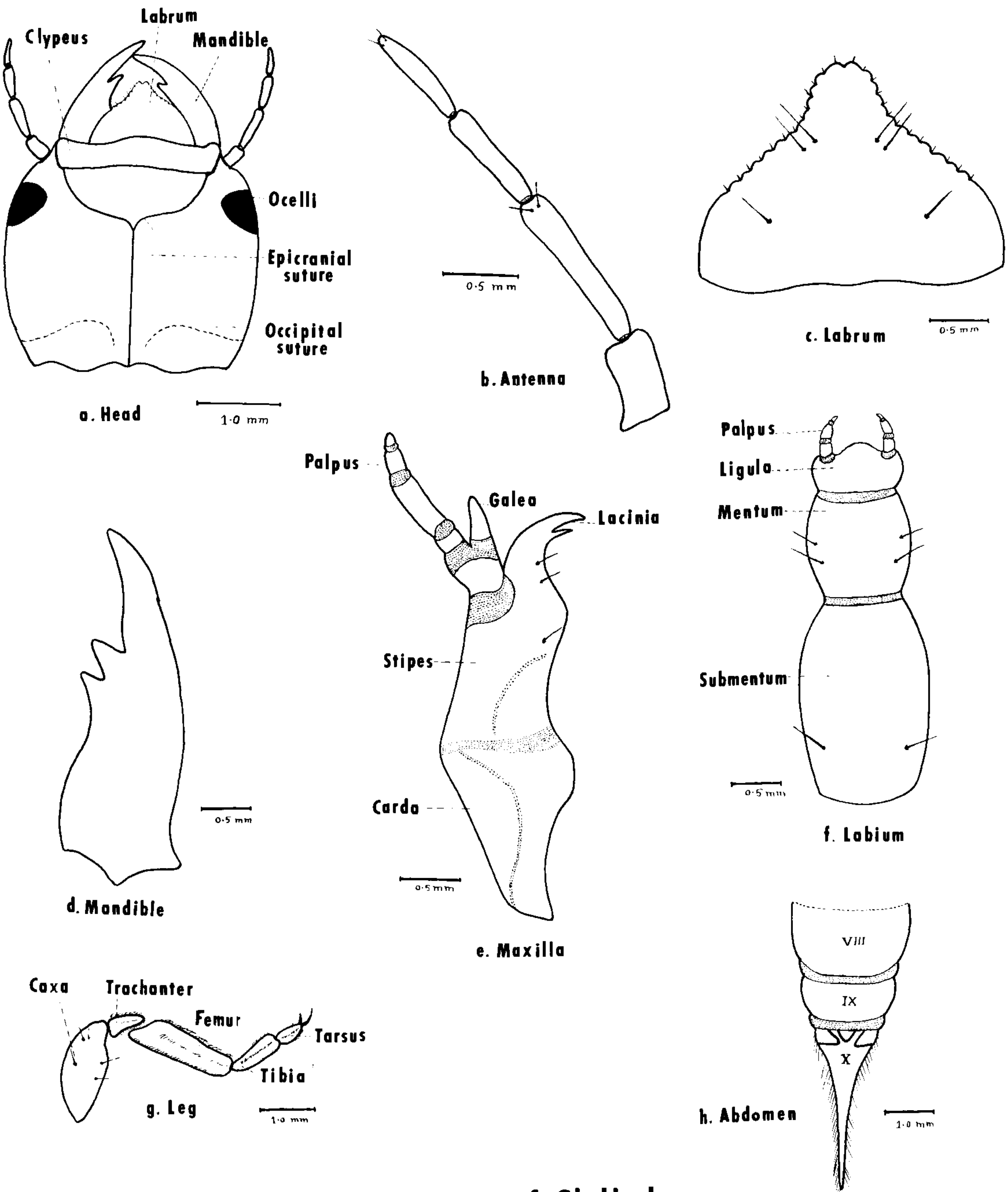


Figure 7. Structures of *Sialis* larva.

mandible (Figure 7d), large, pointed at apex, convex on outer margin, with two large teeth on mesal margin; maxillae (Figure 7e), well developed, each possessing a cardo, stipes, 2-toothed lacinia, cone-shaped galea and a four-segmented palpus; labium (Figure 7f), narrow, consisting of submentum, mentum and ligula; labial palpi 3-segmented.

Thorax

Pro-, meso- and meta notum sclerotized with a mid-dorsal furrow and much broader than long; meso- and metanotum slightly concave anteriorly and convex posteriorly; a pair of minute spiracles in membrane between pro- and meso-thorax. The three pairs of legs are clothed with rows of long and short setae and similar in structure; coxa flattened and long; tarsus with a pair of unequal claws (Figure 7g).

Abdomen

Robust, ten-segmented, broadened anteriorly and tapering posteriorly to a caudal filament. First seven segments with thin walled, segmented gills (or filaments), bearing a few long setae and traversed by trachae; gills four-segmented on segments 1 and 2, and five-segmented on segments 3 to 7. Segment 10 (Figure 7h), broad at base with two furrows originating from base and extending posteriorly for a short distance; segment terminating in a long, flexible median setiferous filament.

The adults of both the species are similar in form and smoky-black in color, but S. rotunda is much smaller than S. californica and slightly lighter in color (Figure 8). Genitalia provide the best characters for separation of species, although other characters are of value. Ross (1937) described the characteristics of adults of Nearctic species.

Males of S. rotunda can easily be separated from S. californica males. In the former, the head is elevated between the eyes, forming a ridge bearing a blunt point surmounted by a conspicuous, thick tuft of black setae. In S. rotunda the clypeus also has a similar tuft of setae, but this is absent in S. californica.

Habitat Preferences

According to published reports, Sialis larvae occupy a wide range of habitats. Davis (1903) and Ross (1937) stated that the larvae of various species of Sialis inhabit a variety of fresh water situations, including small streams, large rivers and lakes, and for the same species it may be equally variable. Dubois and Geigy (1935) found S. lutaria in a Swiss lake where the bottom consisted of chalk with sparse vegetation and Miall (1895) reported the same species from both mud-bottomed ponds and slow streams. Needham and Betten (1901) stated that the larvae of American species occur in weedy and trashy areas. Davis (1903) found larvae of S. infumata in

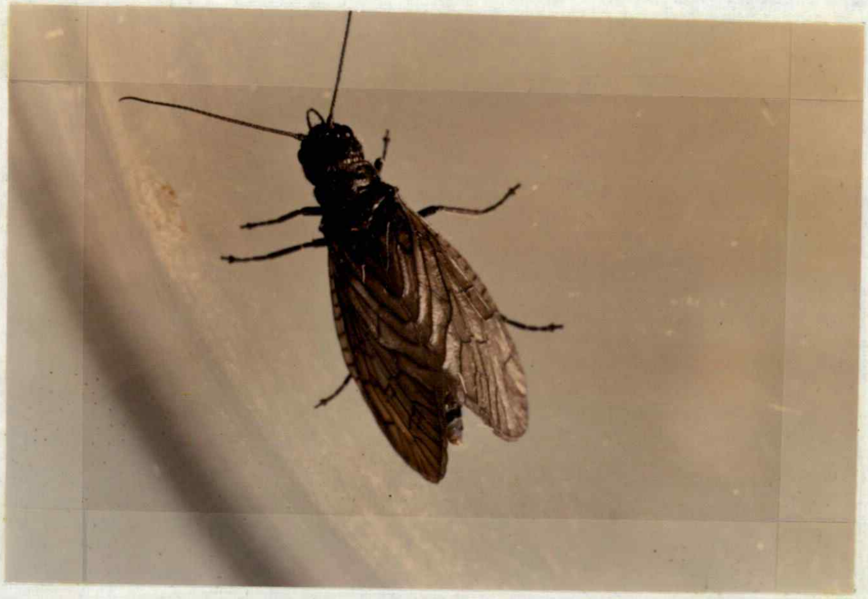


Figure 8. Adult of Sialis rotunda.

sandy-bottomed streams.

In the present study *S. rotunda* and *S. californica* were found to occupy different habitats. *S. rotunda* was collected from ponds and other lentic situations with a muddy substrate, whereas *S. californica* has been collected mostly in pools in streams. Collections from locations other than the study sites have further confirmed this ecological separation of the two species. However, in some sites the larvae do occur together. For example, in a backwater of the Metolius River where the water velocity was slow and organic debris had accumulated both species were obtained.

A record of water depth and substrate was kept of the places where samples were taken in routine collections at Berry Creek and Oak Creek pond. Larvae of both species were obtained from the water depths of 5 cm to 65 cm, but maximum numbers were present at a depth of 15 cm to 25 cm.

Laboratory Life-history Studies

The eggs of both species were collected in the field in June 1966 and rearing of all stages was conducted in aquaria and laboratory streams for determination of the life cycle.

Measurements of different stages and durations of egg stage, different larval instars, pupal and adult stages are summarized in Tables 3 and 4 for *S. rotunda* and *S. californica* respectively.

Table 3. Size, weight, and duration of stages of S. rotunda reared at 68°-74° F.

Stage		No. of specimens	Body length (mm)			Head width (mm)			Weight (mgs)			Duration of stages (days)		
			Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
Egg		12										8	10	8.3
Larval instar	I	14	1.13	1.20	1.16	0.26	0.30	0.29	0.03	0.03	0.03	10	14	12.2
	II	11	1.50	1.90	1.69	0.30	0.38	0.35	0.11	0.11	0.11	12	16	14.6
	III	9	1.75	2.40	2.17	0.38	0.53	0.45	0.20	0.20	0.20	5	7	6.0
	IV	9	2.25	3.20	2.60	0.45	0.60	0.53	0.45	0.45	0.45	5	8	5.5
	V	9	3.50	4.10	3.82	0.53	0.68	0.62	0.56	1.20	0.94	7	9	7.6
	VI	9	4.20	5.10	4.74	0.68	0.83	0.77	1.05	2.45	1.85	6	10	7.3
	VII	9	5.02	6.00	5.31	0.75	0.98	0.91	1.80	3.65	3.45	5	11	8.5
	VIII	9	6.50	8.00	7.22	0.98	1.20	1.08	4.43	7.90	5.80	16	35	28.0
	IX	8	8.00	11.50	10.89	1.28	1.58	1.44	7.90	22.8	15.59	30	53	47.0
	X	8	12.00	16.50	13.85	1.80	2.48	2.07	23.70	55.90	37.90	35	108	88.14
Pupa											21.20	5	7	5.4
Adult	Male										4.94	4	7	5.0
	Female										7.88			

Table 4. Size, weight, and duration of stages of *S. californica* reared at 68°-74° F.

Stage		No. of speci-mens	Body length (mm)			Head width (mm)			Weight (mgs)			Duration of stages (days)		
			Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
Egg		12										8	12	8.4
Larval instar	I	11	1.13	1.20	1.18	0.26	0.30	0.29	0.03	0.03	0.03	10	14	11.6
	II	9	1.58	1.80	1.67	0.30	0.38	0.36	0.11	0.11	0.11	10	17	13.8
	III	9	1.80	2.78	2.30	0.45	0.53	0.47	0.20	0.20	0.20	4	6	5.2
	IV	8	2.25	3.20	2.65	0.53	0.60	0.57	0.65	0.65	0.65	4	9	5.9
	V	8	3.50	4.50	3.90	0.68	0.75	0.70	1.25	1.95	1.70	5	9	5.9
	VI	8	5.00	6.00	5.40	0.83	0.98	0.88	3.20	4.75	4.35	5	8	6.8
	VII	8	6.00	7.50	6.90	1.05	1.28	1.17	4.35	7.40	6.30	7	10	8.5
	VIII	7	9.00	10.50	9.80	1.50	1.65	1.59	8.60	19.75	15.85	21	46	32.0
	IX	7	11.50	13.00	12.30	1.80	2.10	1.95	21.20	39.60	30.20	65	87	76.0
	X	7	15.50	17.00	16.40	2.40	2.93	2.57	48.40	80.50	68.50	81	124	101.0
Pupa											44.60	5	8	6.6
Adult	Male										6.45	4	8	5.0
	Female										12.63			

Egg Stage

Eggs of both species are cylindrical, rounded at the top and with a curved process. The egg masses of the two species can be easily differentiated. *S. rotunda* eggs are laid in an almost vertical position (Figure 9) and the number of eggs in each mass ranges from 300 to 500. Freshly laid eggs are brown, turning to dark brown as they develop. *S. californica* eggs are laid in a slanting position with most of the surface area exposed (Figure 10) and each egg mass contains 400 to 700 eggs. Freshly laid eggs are pale in color and become brown near hatching.

The eggs of both species hatch within 8 to 12 days, depending on the temperature.

In the laboratory, the eggs were kept in petri plates with moist blotting paper. Hatching takes place during the night, very often between 10 and 11 p. m. Practically all of the larvae emerge simultaneously (Figure 11), by tearing a slit in the micropylar end with their head and legs.

Larval Development

There are no published records of *Sialis* spp. being successfully reared for a complete generation, so accurate data were not available on the durations, and the differences in size and structure

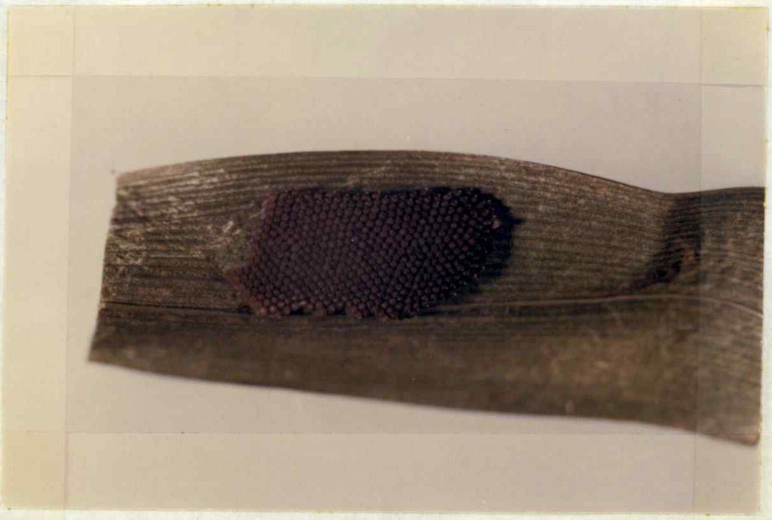


Figure 9. Egg mass of Sialis rotunda.

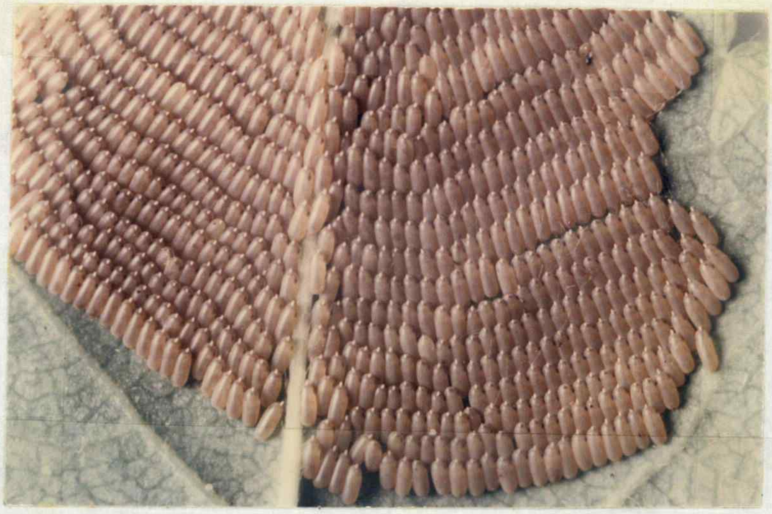


Figure 10. Egg mass of Sialis californica.

Figure 11. Hatching of egg mass of Sialis rotunda.

of the successive instars. Dubois and Geigy (1935) failed to rear S. lutaria through its stages and resorted to comparative measurements of larvae dredged from the lake. Such difficulties in the past led to different conclusions by different workers in regard to the larval period and number of instars. In the present studies, no difficulty was found in rearing Sialis through all stages. The number of instars and the duration of each is given in Tables 3 and 4. Though mortality was high in the first instar, several hundred larvae were reared individually during this study.

The first-instar larvae were quite active from the time of hatching and spent most of the time swimming. Their bodies were almost transparent and tracheal trunks could easily be seen extending along each side. They possess all of the appendages. The gills and antennae were segmented as described earlier for full grown larvae. They were provided with finely chopped tubificids as food. Though they grasped food with the mandibles, food consumption was minimal and most of the development in this instar depends on food reserves from the egg. The alimentary canal can easily be seen through the transparent cuticle and usually it was empty.

The second-instar larvae were similar to the first instar, with a slight increase in length and head-width. The alimentary canal was noticeably distended after feeding on tubificids. There was no development in coloration, so it was still not practicable to separate the larvae of the two species. Though the larvae swim frequently, they were less active than the first-instar larvae. The duration of these two instars was longer in both species compared to next five instars (Tables 3 and 4).

The third-instar larvae developed coloration and the species could be separated by microscopic observation. S. rotunda larvae developed a light black color and S. californica, a slight pinkish tinge. They do not swim as much and mostly stay at bottom of the jar resting or walking. They fed on small tubificids which did not have to be chopped.

The other larval instars had a progressive increase in intensity of coloration. From the fourth instar onward the species could be recognized without using a microscope. The size and amount of food was increased as they grew. On an average they required three or four tubificids (about 0. 6 mg per worm) in the later instars.

Moulting generally took place during the night, but at times occurred during the day. In moulting, the cuticle splits along the dorso-median line of the head, prothorax and mesothorax. The head and the thorax were drawn out first, then the legs and finally the abdomen. The newly moulted larva was very soft and whitish on the head and body, changing to the characteristic color and becoming sclerotized within few hours.

Individual rearing in aquaria showed that there were ten larval instars in both species. Mean duration of the larval stage was 204 days for S. rotunda and 275 days for S. californica when reared at 68°-74°F. However, because these specimens were reared at a high temperature and had an excess of food provided, the rate of development was presumably faster than it would be under field conditions.

Results from rearings in the artificial streams in an unheated building more closely approximate field conditions. This study started on September 20, 1966, with twelve individuals of each species, using window jars described earlier through which the water flows constantly. Food was provided in the same way as for larvae in aquaria. The larvae used at this time were not newly hatched but had completed their early development in the field. Both the species completed their life cycle the following spring so larval development was slower than under aquarium conditions. S. rotunda started pupating in March and all individuals pupated by early May 1967, whereas S. californica pupated by early June. Growth in these conditions is compared with growth in field cages in Figures 15 and 16.

Pupal Stage

Under laboratory conditions, the mature larvae could not leave the water to pupate, so some mortality occurred at this stage. Careful observation revealed a characteristic type of behaviour that enabled me to detect the specimens that were ready to pupate.

The larvae did not feed, became sluggish and curled up on their side. When such changes were observed, the larvae were taken out of water and kept in a jar of soil where they transformed to pupae within two to three days. Pupation usually took place during the night.

Freshly-moulted pupae of both species had almost the same color and body shape as the larvae, except they possessed wing pads and lacked tracheal gills. Figures 12 and 13 show the pupae of _S. rotunda_ and _S. californica_ respectively. The pupae do not form any cocoon and lie with body curled within the pupal cell. Near emergence the pupae became black and adults emerged within five to eight days in both species.

Adult Stage

In the laboratory, adults emerged at different times of the year. The first adult of _S. rotunda_ was obtained in October 1966 and of _S. californica_ in February 1967. After that time, many adults emerged, with maximum emergence in April-May.

The adults reared in the laboratory were confined in screened cages with small twigs of plants and some water, and mating behavior and oviposition were observed.

Copulation has also been studied and described for other _Sialis_ species by Killington (1932) and Dubois and Geigy (1935). In addition,

Figure 12. Pupa of Sialis rotunda.

Figure 13. Pupa of Sialis californica.

Geigy and Dubois (1935) studied the physiology of senses of S. lutaria to determine the factors which direct the males towards females. The antennae and labrum were regarded as the most likely loci of the perceptive organ. He mentioned that when the labrum was amputated, the males pursued the females only when they chanced to encounter them and then only dilatorily, and without affecting copulation. When both the labrum and the antennae were removed, the males lost completely their ability to orient themselves without reference to the female.

The ovaries of the females and the testes of males are mature when they emerge. Several males pursue a female and attempt to force themselves underneath the female as she walks around. After one male is chosen, the pair face each other and vibrate their antennae for a few seconds, after which the female moves a short distance, followed quickly by the male. The male goes head-first under the tip of the female's wings. If his advances are accepted, the female stops, and the male takes his position below her abdomen. The male then elevates the tip of his abdomen between the wings, into the copulatory position (Figure 14). In the laboratory copulation lasted for about five to ten minutes. Dubois and Geigy (1935) reported that a transparent, gelatinous spermatophore is introduced into the vagina and the female draws the sperm packet into her body by gradually inverting the evaginated vagina. Killington (1932) reported

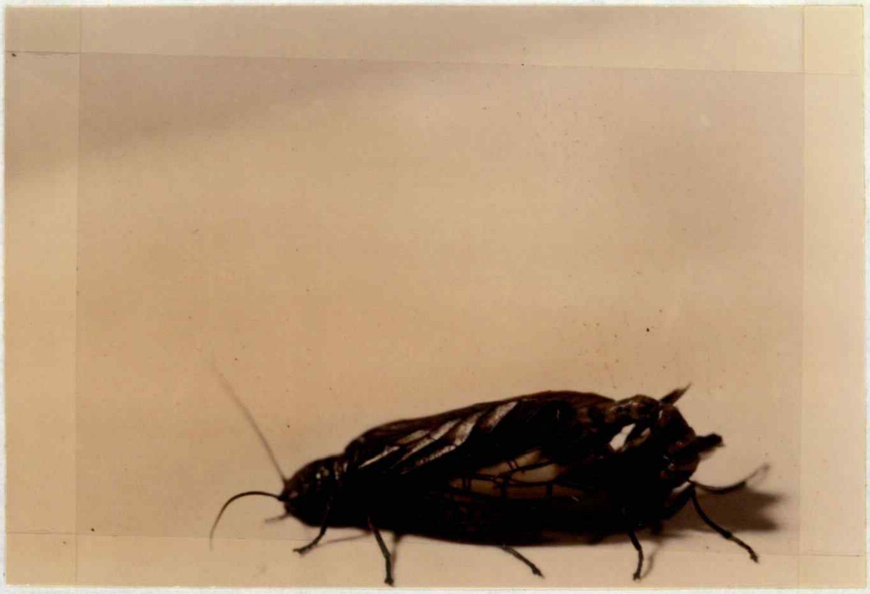


Figure 14. Copulation position in Sialis rotunda.

a different mechanism of sperm transfer. A few minutes after separation, the female bent her abdomen forward between her legs and ate the spermatophore. In the present study this behaviour was never observed.

Although Dubois and Geigy (1935) failed to obtain oviposition of S. lutaria in captivity, no difficulty was experienced in the present study. The mated females laid eggs either the same day or next day on leaves and on the walls of cages. A sticky substance is secreted before oviposition. This material firmly attaches the eggs to the surface. The female bends the tip of her abdomen to touch the substrate and swings the abdomen towards left and right of the mesal line and deposits a row of eggs. After one transverse row is completed she moves forward slightly and completes another row. The number of eggs in each row varies from 4 or 5 to 20 or 25, depending on the shape of the substrate. Egg masses of S. rotunda are narrower than those of S. californica because the smaller female cannot swing her abdomen as far to the sides and also because she bends the abdomen into an almost vertical position to deposit the eggs vertically. S. californica females can swing the abdomen in a wider arc as the eggs are laid in a slanting position. Females can deposit a second mass of eggs.

Field Life-history Studies

Egg Stage

The eggs are laid in the field on vegetation or any other object that projects over the water. *S. rotunda* eggs were observed at Oak Creek pond in May and June of 1966, 1967 and 1968. In all these years many egg masses were present on the vegetation around the pond.

S. californica eggs were present at Berry Creek. It was practically impossible to count the numerous egg masses laid in May-June of 1966 in the experimental area of stream. Egg patches were numerous in sections I, II, and III but not in section IV, due to lack of favorable vegetation or objects over the water in the latter. In section I, certain branches, which projected over the water, were completely covered with egg masses. In 1967 there was a marked decrease in the number of eggs because of flushing the stream in February 1967, which washed away most of the larvae from the stream.

The eggs of both species hatch in eight to twelve days depending on temperature. The eggs were parasitized by a hymenopterous parasite which is discussed later.

Larval Development

Cage studies provided good information about the development and duration under natural conditions, even though the amount of food supplied differed from that available in the field.

In the pond cage, all the larvae of *S. rotunda* completed their life cycle in one year and similar conclusions were drawn from field collected larvae, because after June, no older larvae were found in samples.

Out of 24 larvae of *S. californica* in two cages at Berry Creek, about 15 larvae completed their life cycle in one year and four larvae were carried over to the second year, the others dying at different times. These results support the idea that the life cycle can take one or two years depending upon conditions. In the routine collections from different sections of Berry Creek, the majority of the larvae in enriched sections were developing fast because of abundant food and apparently completed their life cycle in one year. Many larvae in the unenriched section I were apparently taking two years. This difference has now been confirmed by the field rearing.

Pupal Stage

Collections of larvae which leave the water and migrate to shore for pupation were made by fixing pit-fall traps at certain places near pond and stream. S. rotunda larvae begin to pupate as soon as the weather warms up in the spring. Pupation extends from April to June, usually occurring during May. S. californica larvae pupate from May to early July with most of the pupation in June.

During the 1966 pupation period 12 pit-fall traps were fixed at Berry Creek. Twelve larvae were collected in the traps and brought to the laboratory where they pupated and emerged into adults. During 1967, three traps were fixed at the pond and 16 at the Berry Creek. At the pond 134 larvae of S. rotunda were obtained in three traps, with their respective numbers in each trap being 51, 19 and 64 (Appendix I). It was noted that the trap with the maximum number of larvae was located at a place where there was sparse vegetation that did not obstruct the migration of larvae leaving water and also the water depth was less at that end. The trap which collected the fewest larvae was in a grassy area and also the water was deeper at that end. In the field many pupal exuviae were collected on the ground surface near pond.

Only four larvae were obtained from Berry Creek traps in 1967; the decrease from 1966 was because there were not many larvae left in the stream after flushing.

Adult Stage

S. rotunda adults were first seen in mid-April but maximum emergence occurred during May. The first adult of S. californica was observed at Berry Creek as early as May 4, and a few more adults were seen by the end of May but maximum emergence occurred during mid-June.

The adults of both species, especially the males, are active during warmest hours of mid-day, swarming on vegetation along the shore. The adult females do not fly much and mostly walk on the plants. They were observed to fall down into the bushes on slight touch. The abdomen is swollen and heavy. Dissection of a few adults has shown that the ovaries completely fill the abdomen and also extend into the thorax.

Dubois and Geigy (1935) found whitish and yellow pollen scattered over the head and thorax of some adults and this led to the supposition that the adults visit flowers to feed. In the present study, however, adults were found at different parts of the plants and also were found to lick the flowers, but their feeding is doubtful. Dissections also showed that the alimentary canal is not developed.

Studies of sex-ratio have indicated that in order to establish a true ratio for Sialis adults, laboratory reared individuals should be considered. Adults collected from the field and also reared in the laboratory were separated into two sexes by a study of genitalia.

Field collections of adult S. rotunda were made by sweeping with an insect net from April 22, 1967 to May 25, 1967. The sex-ratio of all the collected individuals is given in Table 5.

Table 5. Sex-ratio of S. rotunda from field collections.

Date	Males	Females	Total	Sex-ratio (%) Males	Sex-ratio (%) Females
April 22, 1967	17	2	19	89.5	10.5
April 31, 1967	9	4	13	69.0	31.0
May 5, 1967	21	14	35	60.0	40.0
May 11, 1967	43	18	61	70.5	29.5
May 25, 1967	4	5	9	44.4	55.6
Total	94	43	137	70.2	29.8

In the laboratory rearings, out of 34 adults of the same species, 14 were males and 20 were females (ratio = 41.2:58.8).

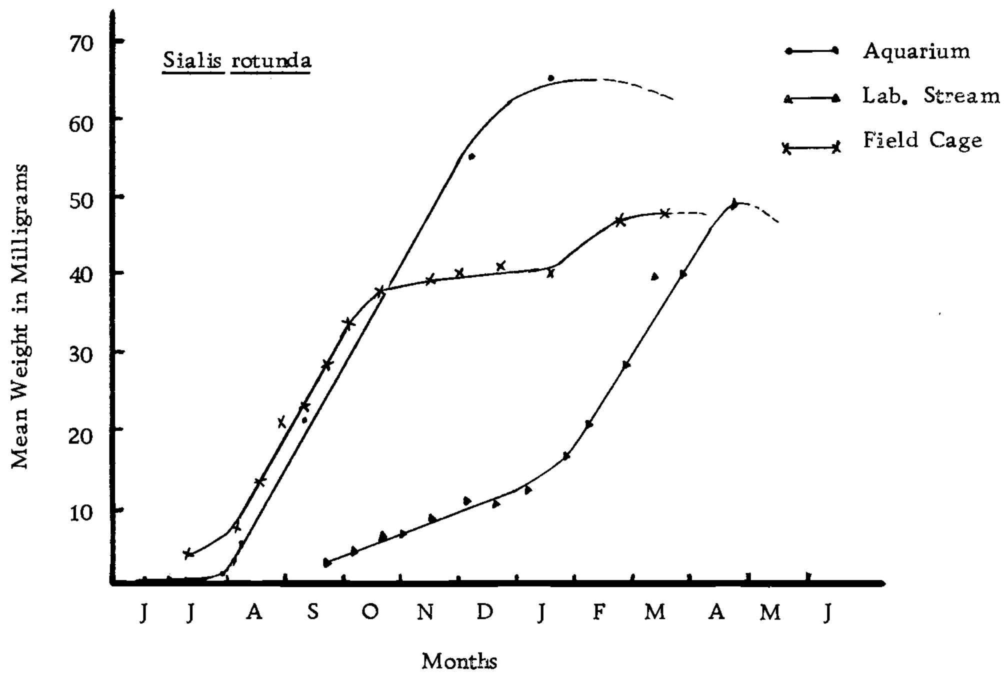
As mentioned earlier, it is difficult to collect the females in the field since at the slightest touch, they fall into the bushes. They do not fly much because of the heavy abdomen.

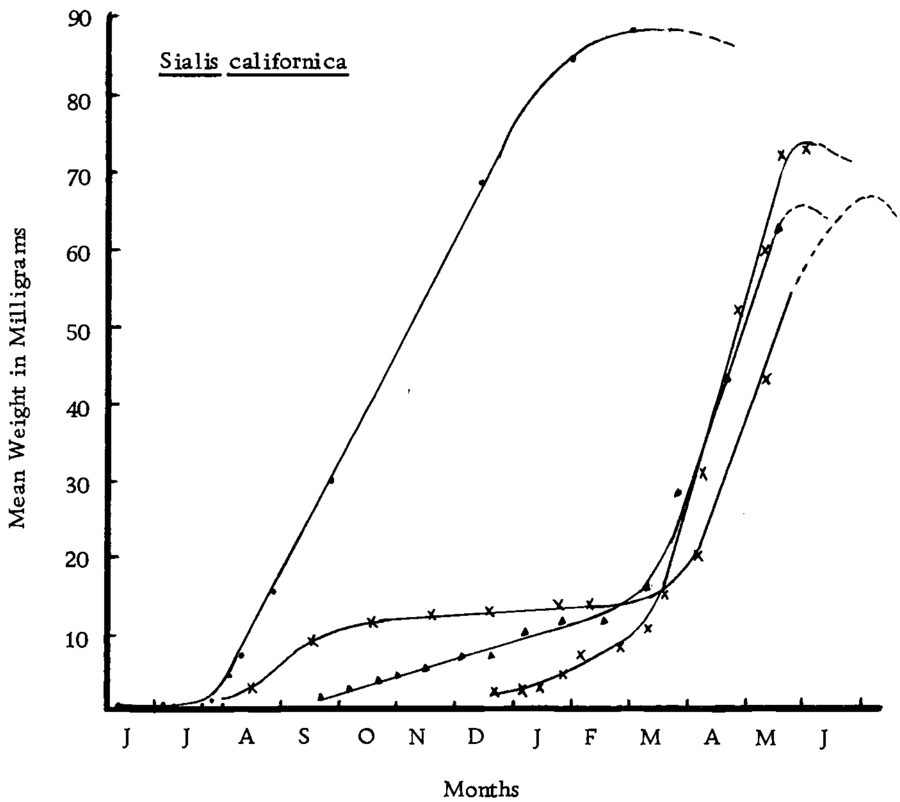
Growth, Length-weight and Length-headwidth Relationships

The life history studies began with the attempt to raise the two Sialis species from egg to adult, primarily to obtain the number of instars, the total duration of life cycle and to find morphological differences between the successive instars. As the studies went on, the idea of recording some data on growth was conceived and carried into effect by measuring their lengths, head widths and weights.

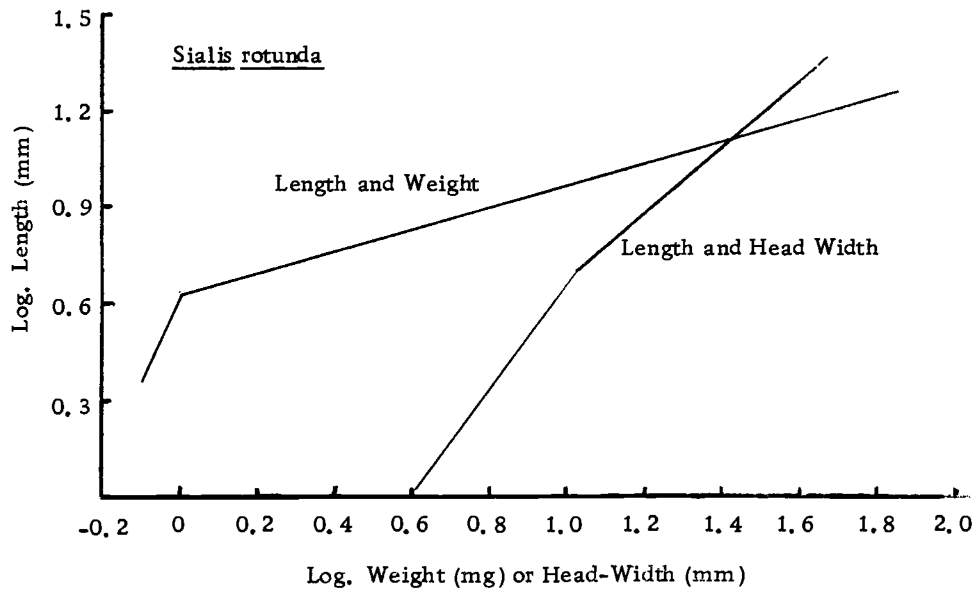
The growth obtained for both species under different situations of aquarium, laboratory stream and field cages are presented in Figures 15 and 16 for *S. rotunda* and *S. californica* respectively. Both species had similar growth curves under aquarium conditions. The curves for the laboratory stream specimens differed from those in aquarium, but again there was no difference between species, as conditions of temperature and food were the same for both species. However, the difference in growth of *S. rotunda* and *S. californica* in field cages is attributed to effects of food. As mentioned earlier, *S. rotunda* larvae were given tubificid worms from a culture at the Fisheries Laboratory, whereas *S. californica* larvae were provided food from substrate of Berry Creek. The curves thus represent the effects of different factors of growth, i.e., aquarium with high temperature and optimum food, laboratory stream with fluctuations of temperature and optimum food, and cages with natural fluctuation of temperature and different amounts of food.

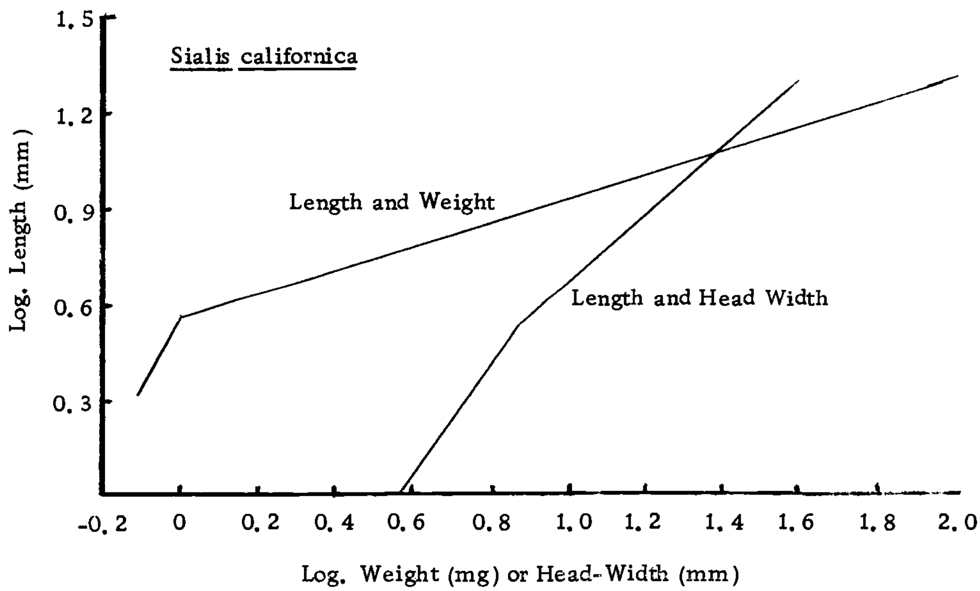
The logarithmic relationships between length and weight, and head-width and weight for both species are presented in Figures 17 and 18. These relationships are based on a large quantity of data obtained during routine field sampling and also from laboratory-reared





Figures 15 and 16. Growths of Sialis rotunda and Sialis californica larvae in Aquarium, Laboratory Stream and Field Cages.





Figures 17 and 18. Length-Weight and Length-Headwidth relationships in Sialis rotunda and Sialis californica larvae.

specimens. These relationships were used in converting the lengths to weights when only lengths were measured.

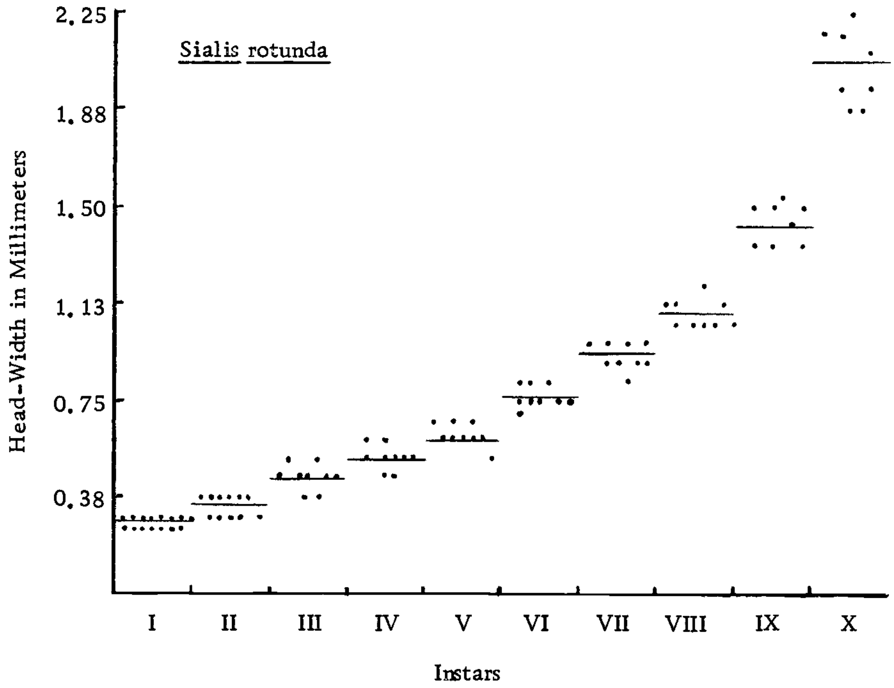
An attempt was made to determine whether head-width measurements could be used to separate the instars. Measurements were made on aquarium-reared larvae at each successive moult. Figures 19 and 20 represent the trend by which head-widths increase from instar to instar for S. rotunda and S. californica, respectively.

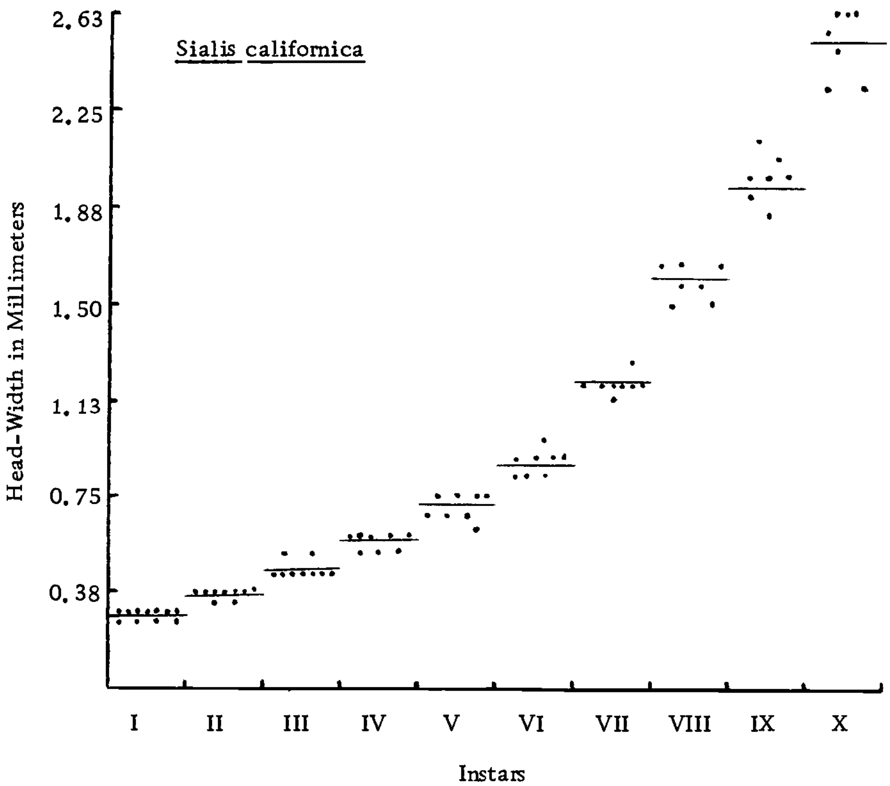
There was a difference in the head-width measurements from one instar to the next, but it is difficult to separate the early instars as there is some overlap. However, larvae from the fifth instar onwards can be separated on the basis of head-width measurements. Even the specimens collected from variable field populations can be separated with accuracy in the later instars.

Analysis of Food and Feeding Habits

The feeding behaviour of the larvae of both species was observed in aquaria by providing different kinds of food organisms collected from the natural habitat. The larvae consume small prey without chewing. If the prey is larger then they capture it with their mandibles, manipulate part into their pharynx, and sever the remainder.

Feeding tests were made in the laboratory, using chironomid larvae, tubificid worms, mayfly nymphs, caddis worms, damselfly





Figures 19 and 20. Head-widths of all instars of reared *Sialis rotunda* and *Sialis californica* larvae.

naiads and water mites. They ate all of these organisms except water mites. Cannibalism was also frequent in aquaria.

Davis (1903) reported that larvae of S. infumata in captivity consumed soft bodied caddis worms, small larvae of Chauliodes (Megaloptera) and individuals of their own species. Dubois and Geigy (1935) performed feeding experiments with larvae of S. lutaria in which they fed oligochaete worms, nymphs of Ephemeroptera, and larvae of Trichoptera and Diptera.

Food Habits in Natural Habitats

An attempt was made to determine the kinds of food organisms that were consumed in the natural habitats. In the beginning many difficulties were experienced. At each collection time certain individuals were preserved in alcohol:formalin (9:1), but when these specimens were dissected, most of them were empty. It was found that this was due to regurgitation of food when the larvae were put in preservative. Later it was observed that if larvae were kept alive in some water for a day or two after the collections, they passed out the undigested parts in the form of small pellets covered with a peritrophic membrane. Analysis of the pellets gave qualitative, but not quantitative, data since the sclerotized parts in the feces could be identified. Moreover, this technique permitted returning the larvae to the field site after the data were obtained.

Large collections of S. californica larvae also made in backwaters at the Metolius River for these studies. Five collections were made from July 1967 to January 1968.

The pellets containing parts of chironomid larvae, mayfly nymphs and crustacean shells could easily be separated. Moreover, the pellets with aquatic worms could also be recognized based on comparisons with pellets from laboratory reared specimens.

In the Metolius River samples, mayfly nymphs were always an important component of the diet (Table 6). Chironomids were usually a major item but they decreased (9%) in November and to zero in the small January sample. The most interesting part of Metolius food habits study was that Crustacea (ostracods), were a common food item in most samples. Worms were also an important source of food. Other items, listed as miscellaneous, include caddisflies and stoneflies as well as unidentified organisms.

In the pond, the most important source of food for S. rotunda was tubificid worms (Table 7). Bottom samples indicated that these w orms were a dominant benthic organisms in pond. Mayfly nymphs and chironomid larvae were not found in all fecal samples. Crustacea were an uncommon food item at this site. The miscellaneous organisms included damselfly naiads, small Sialis larvae and unidentified organisms.

Chironomid larvae and mayfly nymphs were the two important

Table 6. Relative occurrence of identifiable organisms in fecal pellets of S. californica from the Metolius River.

Month	No. of Sialis larvae	Percentage of total number identified				
		Chironomids	Mayflies	Worms	Crustacea	Miscellaneous
July	51	29.4	15.7	17.7	23.5	13.7
August	67	38.8	22.4	22.4	5.9	10.5
September	41	19.5	34.2	2.4	24.4	19.5
November	32	9.4	31.2	18.8	0	40.6
January	11	0	27.3	18.2	9.1	45.4

Table 7. Relative occurrence of identifiable organisms in fecal pellets of S. rotunda from Oak Creek pond.

Season	No. of Sialis larvae	Percentage of total number identified				
		Chironomids	Mayflies	Worms	Crustacea	Miscellaneous
Summer	108	27.8	20.4	42.4	3.6	5.8
Fall	96	16.3	19.4	48.9	6.8	8.6
Winter	67	7.7	16.4	61.0	0	14.8
Spring	78	11.8	17.8	37.7	1.5	31.2

kinds of food for *S. californica* in Berry Creek (Table 8). The contents of many of the pellets could not be identified, in part because of the varied fauna in the stream.

There does not seem to be any major difference in the choice of food during different seasons. In general, the *Sialis* larvae are indiscriminate feeders, and the benthic organisms that are abundant form the major part of their diet.

Parasites, Predators and Diseases

The eggs of both *S. rotunda* and *S. californica* were parasitized by the hymenopterous parasite *Trichogramma semblidis* (Aurivillius).[1] The parasitized eggs turned completely black (Figure 21).

Dr. Burks (*in litt*) stated that this is a Holarctic species restricted to the eggs of aquatic insects in nature, although it can be reared on *Ephestia* eggs in the laboratory. It has two types of males, a winged and wingless form. All the males obtained from the parasitized eggs of *S. rotunda* and *S. californica* were wingless.

There is considerable literature on *T. semblidis* and Salt (1937) discussed in detail the correct naming of the parasite. Lestage (1918) reported parasitism of *Sialis* eggs as *Trichogamma evanescens* W.,

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[1] Determined by Dr. B. D. Burks, Insect Identification and Parasite Introduction Research Branch, U. S. Department of Agriculture.

Table 8. Relative occurrence of identifiable organisms in fecal pellets of S. *californica* from experimental sections of Berry Creek.

Season	Stream section	No. of *Sialis* larvae	Percentage of total number identified			
			Chironomids	Mayflies	Worms	Miscellaneous
Fall 1966	I	64	18.5	20.7	13.1	47.7
	II	31	32.5	25.6	16.0	25.8
	III	21	36.1	25.0	19.4	19.4
	IV	24	41.7	16.6	16.6	25.0
Winter 1966-1967	I	39	34.3	17.4	13.8	34.5
	II	12	25.0	43.7	6.3	25.0
	III	14	35.7	28.6	7.1	28.6
	IV	10	28.6	40.5	0	30.9
Summer 1967	I	7	0	20.0	0	80.0
	II	38	18.4	29.7	15.4	37.1
	III	26	26.9	15.0	15.6	43.1
	IV	24	33.3	11.1	13.4	42.3
Fall 1967	I	4	0	0	0	100.0
	II	12	18.2	27.3	18.2	36.3
	III	4	0	0	0	100.0
	IV	5	40.0	0	0	60.0
Winter 1967	I	3	0	0	0	100.0
	II	18	11.5	35.4	0	53.1
	III	6	0	0	0	100.0
	IV	0	0	0	0	0

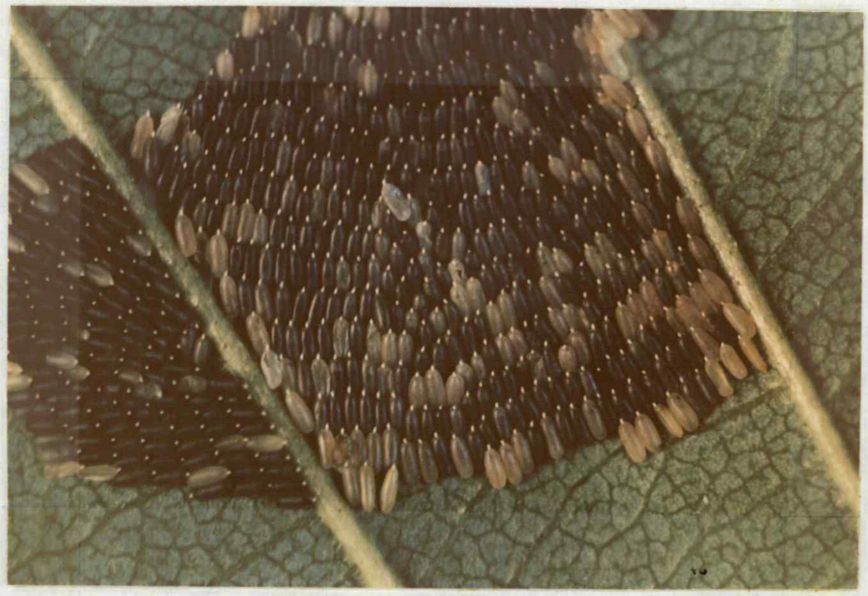

Figure 21. Parasitized egg mass of Sialis californica.

a misidentification of *T. semblidis*. According to Balduf (1939), Silvestri (1908) made a thorough study of this parasite as related to hosts other than *S. lutaria*.

The extent of parasitization was about 14% in *S. rotunda* compared with 37 to 65% in *S. californica* (Appendix II). The difference in the level of parasitization between the species results from the time of egg-laying and probably the egg laying position. The occurrence of *T. semblidis* is synchronized with the oviposition period of *S. californica* (June - July), whereas the peak period for *S. rotunda* eggs is in May, and only the latest egg masses are subject to parasitization. *S. rotunda* eggs are laid in an almost vertical position, thus only exposing the ends of the eggs. The eggs of *S. californica* are laid in slanting position, thereby exposing much of the surface area for the parasite to deposit its eggs into the host eggs. When parasitization occurs most of the eggs of *S. californica* in a mass are attacked whereas parasitization of *S. rotunda* eggs occurs sparsely.

Fish are predators of *Sialis*. Warren *et al*. (1964) and McIntyre (1967) reported *S. californica* larvae in the stomach contents of cutthroat trout from experimental sections of Berry Creek. The older *Sialis* larvae themselves are predators of young larvae, as found in the food habit studies.

The larvae are subject to attack by an unidentified fungus. The fungus first appears at the tip of the tracheal gill, gradually penetrating to entire gill and then to other gills. The larvae turn black and die. The fungus infection in laboratory rearing was only two to three percent.

SUMMARY - COMPARISON OF LIFE CYCLE OF THE TWO *SIALIS* SPECIES

The life-histories of *S. rotunda* and *S. californica* in the field are compared diagrammatically in Figure 22 and are summarized below:

S. rotunda. This species completes its life cycle in one year in Western Oregon. The adults emerge from April to June. Oviposition commences in late-April or early May and larvae first occur about two weeks later. The larval stage lasts about 10 to 11 months and pupation occurs in April and May.

S. californica. The present study indicates that this species takes one or two years to develop, depending on oviposition time and food availability. The adults emerge from May to July. Oviposition commences in mid-May when both males and females are found, and the larvae first occur about late May. Most of the larvae take one year to develop but those hatching from eggs laid in late July may take two years if enough food is not available.

In the aquarium and laboratory stream both species completed their life cycle in one year. In the cages all larvae of *S. rotunda* and about 75% of *S. californica* developed in one year.

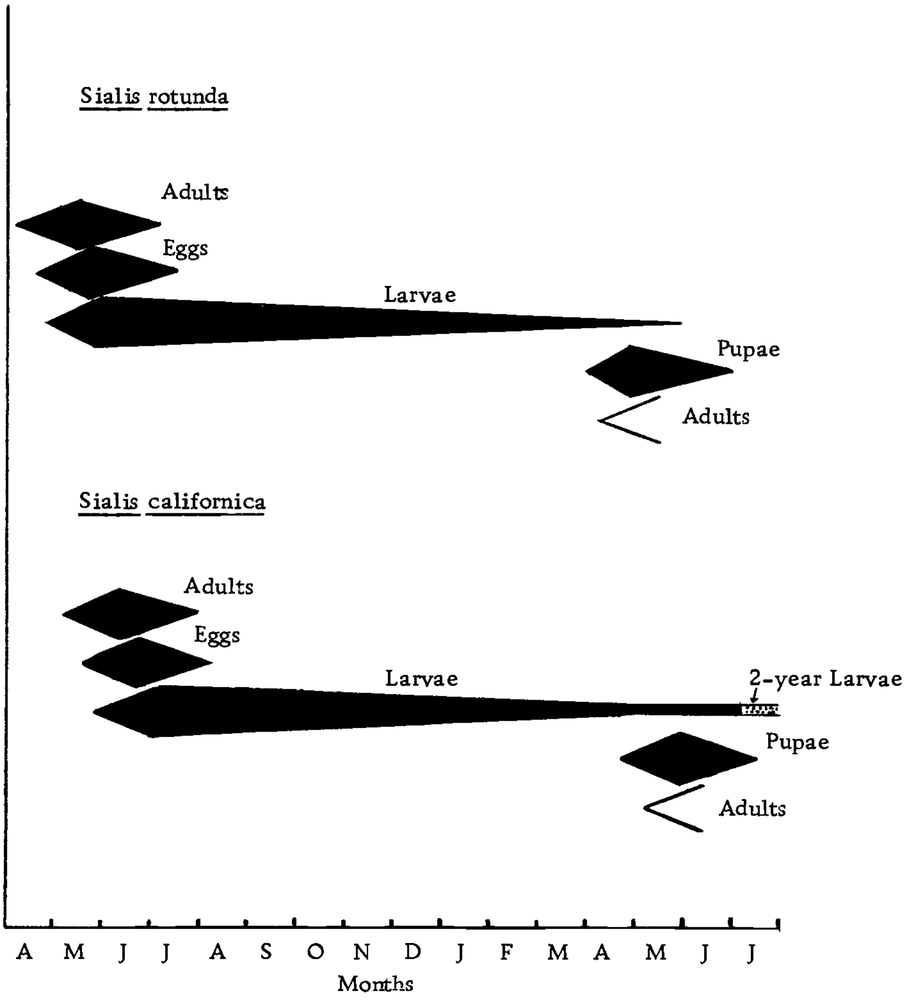

Figure 22. Comparison of life-cycle of Sialis rotunda and Sialis californica in the field.

DENSITY, BIOMASS AND GROWTH RATES OF FIELD POPULATIONS

In the study of insect populations, the numbers and biomass are important. The density and biomass of *S. rotunda* larvae are given in Figures 23 and 24 for the Oak Creek pond from May 1967 to May 1968. In Figures 25 and 26, the data are given for *S. californica* larvae in the four experimental sections of Berry Creek during the entire sampling period from December 1965 to December 1967.

Hatching of *S. rotunda* started in May and the larval population increased to a maximum by mid-July. The numbers decreased at a uniform rate until March, and then markedly more in late April and May when the larvae left the water to pupate. Throughout the summer, growth rate was high so the biomass increased with time (Figure 24) until winter. The decrease in numbers and biomass during February is probably a sampling error whereas the increase in biomass during March is a real effect, because moulting and rapid growth occur at this time when water temperature begins to increase.

It was found that larvae of this species were almost uniformly distributed in the pond and there were no major factors causing fluctuation in numbers except natural mortality. In addition, sampling of the mud bottom with an Ekman dredge was more accurate than the methods used for the stream study.

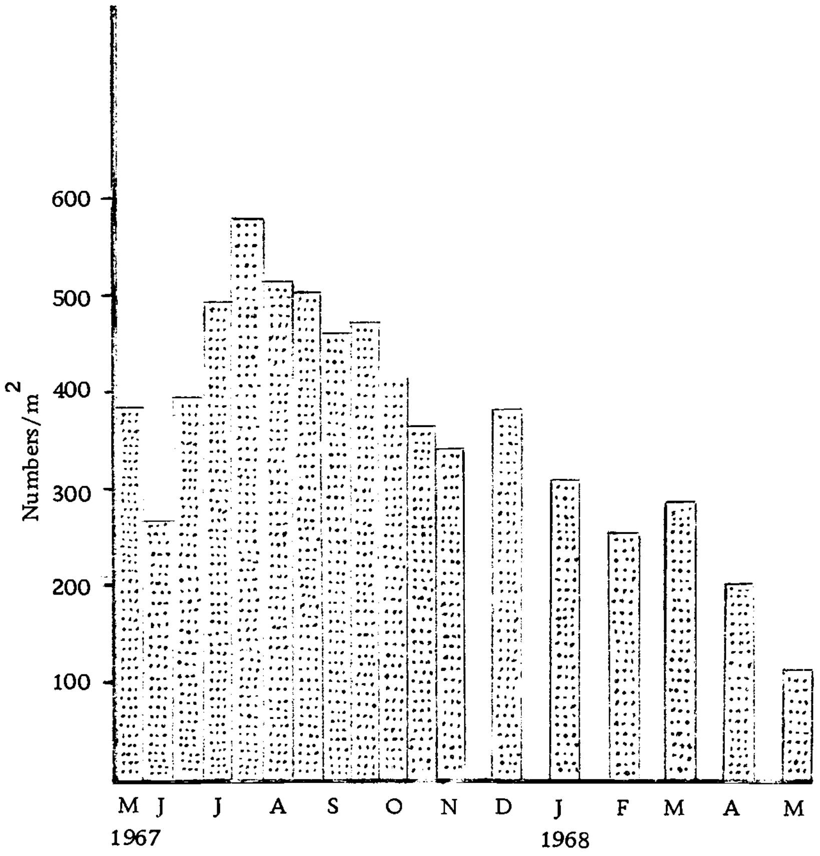

Figure 23. Numbers of Sialis rotunda larvae/m^2 in Pond during May 1967 to May 1968.

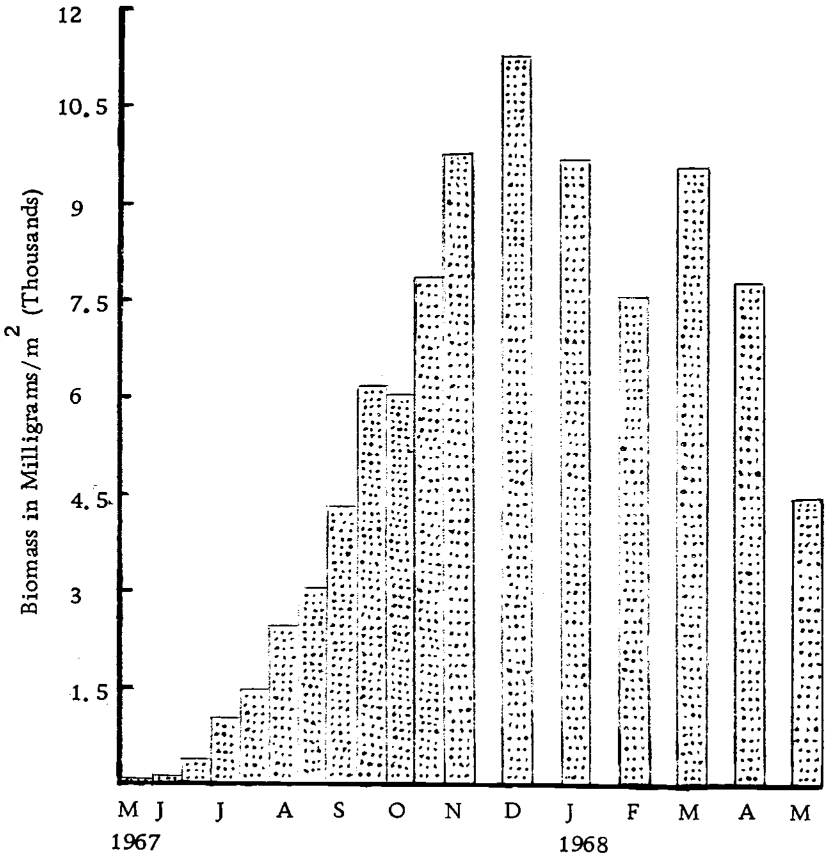

Figure 24. Biomass of Sialis rotunda larvae/m^2 in Pond during May 1967 to May 1968.

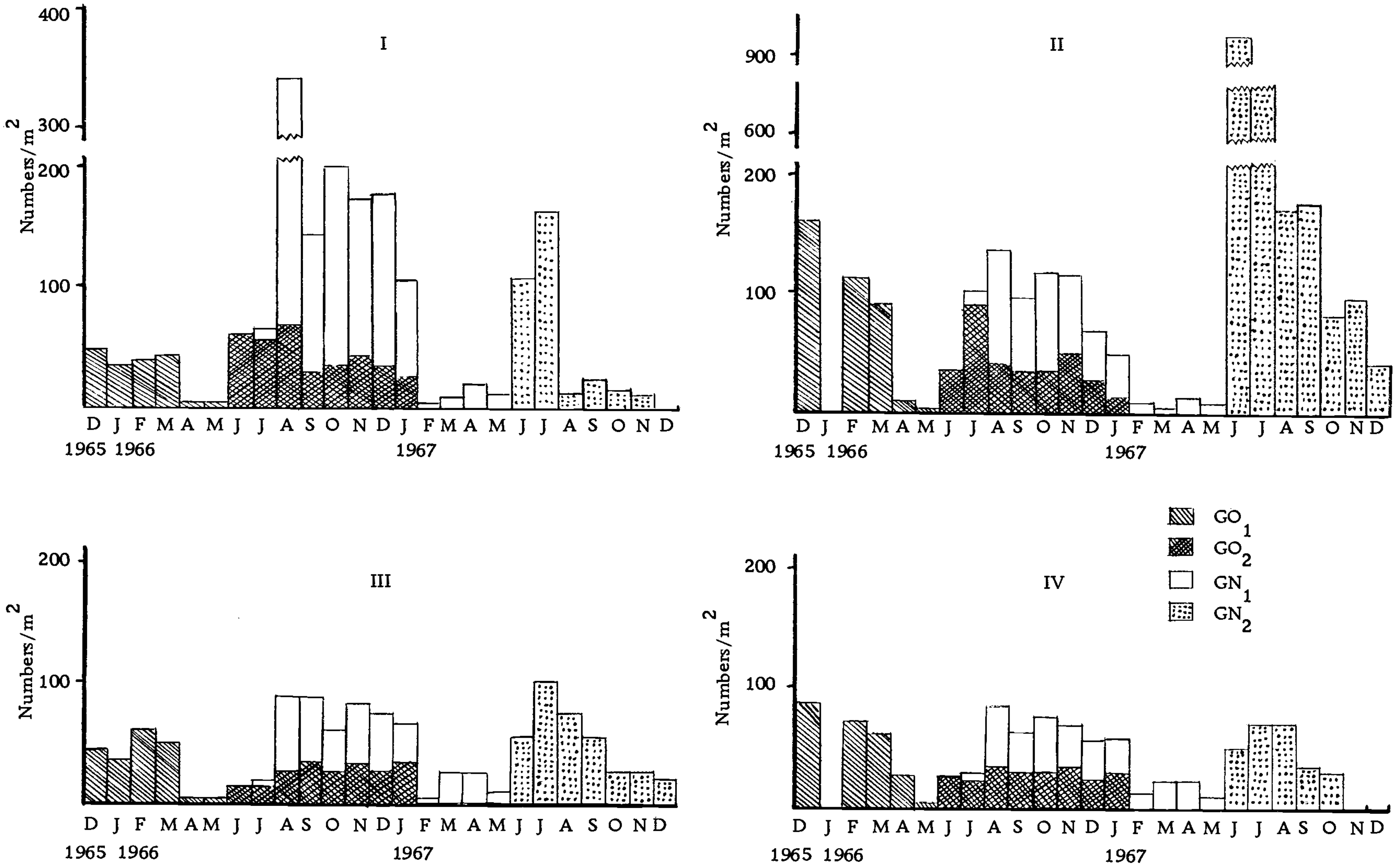

Figure 25. Numbers of different age groups of Sialis californica larvae/m^2 in four sections of Berry Creek from December 1965 to December 1967.

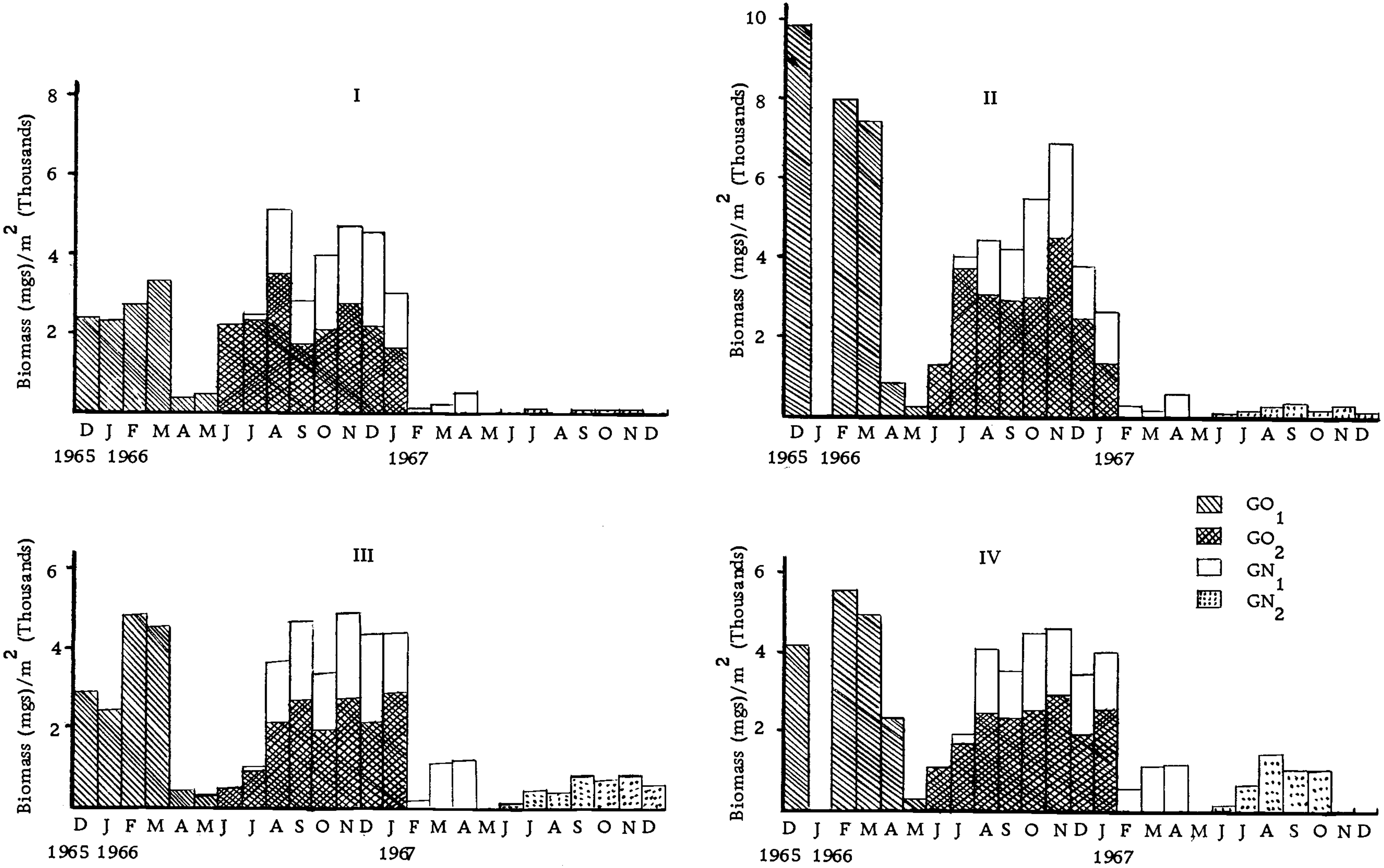

Figure 26. Biomass of different age groups of *Sialis californica* larvae/m^2 in four sections of Berry Creek from December 1965 to December 1967.

The population data for S. californica are more variable and difficult to interpret than for S. rotunda: (1) the pool habitat was variable and difficult to sample, (2) a satisfactory sampling procedure was not developed at the start of the program, (3) the species has a complex life cycle, and (4) the stream was subjected to several experimental procedures and to flushing during the study period. Though the manipulations had an undesirable effect with respect to calculations of annual production, they were useful in elucidating some aspects of the life cycle, and in demonstrating the effects of enrichment on growth and development.

The following abbreviations are used to designate different age groups of S. californica:

GO_1. Collected from December 1965 to May 1966. This group pupated in May and June 1966 and may have represented one and two year old individuals.

GO_2. Collected from June 1966 to January 1967 (Flushing occurred in February 1967). These larvae developed from eggs laid in 1965 but did not pupate in 1966.

GN_1. Collected from July 1966 to January 1967 along with GO_2 larvae. This group consisted of younger larvae from eggs laid in 1966 by GO_1 adults.

GN_2. Collected from June 1967 to December 1967. These developed from eggs laid in May and June, 1967.

From December 1965 to July 1966 (GO_1), the samples were obtained with the box sampler and aquatic dip net. Most small larvae were not collected. This was not a serious error during winter and early spring as most of the larvae were large. However, when eggs began hatching in May or June and no early instars were collected in either June or July, the pipe sampling method was initiated. The larvae collected in June and July were holdovers from the 1965 generation which did not develop fast and were probably from eggs laid very late in the season. The error introduced by not collecting small larvae in June and July 1966 was not too great because of their small biomass.

Section I had the lowest number and biomass of mature larvae (GO_1) and section II had the maximum. The number of larvae dropped to a minimum in all four sections by May 1966 when pupation occurred.

The number of GO_2 larvae was highest in section I in most months. For example, based on the August samples, when pipe sampling started, the number per m^2 of this group of larvae in the four sections was: I, 68; II, 41; III, 27; and IV, 34. However, mean weight (mg) per larva in the sections was: 51.9, 74.3, 76.7 and 77.9, respectively. This indicates the relative quantities of food that had been available in the four sections. Monthly estimates of the benthic pool organisms were not made. However, all insects in the December benthos samples were counted and measured. These collections are considered typical of the relative standing crop in the four sections, and correlate well with the observed differences in biomass of *S. californica*. The number per m^2 of benthic organisms was: section I, 7841; section II, 18,248; section III, 19,070; and section IV, 17,450. Moreover, the food organisms in enriched sections were much larger than in section I. For example, the mean length of 50 chironomid larvae from each section was: 2.5 mm; 4.4 mm; 3.9 mm; and 5.1 mm, in sections I, II, III and IV respectively.

A marked difference occurred in the numbers of GN_1 larvae between the unenriched section I and the enriched sections from August onwards. For example, in August, section I had more larvae than three sections combined, but the biomass was approximately equal in each section. Thus, even though fewer larvae developed in sections II, III and IV, their rapid growth rate under the enriched conditions tended to equalize the biomass in each section. Larvae under 4 mm were rarely collected in the enriched sections, especially in sections III and IV, even though egg masses were numerous on the overhanging vegetation. It is believed that the main cause of mortality was the growth of *Sphaerotilus* in the enriched sections. Laboratory observations showed that small larvae get entangled in the *Sphaerotilus* filaments, their tracheal gills get covered with the sticky material and the larvae eventually die. Thus only a few larvae survived that occurred along the edge of the pools or other suitable situations, where Sphaerotilus was sparce. The larger larvae are not inhibited by the Sphaerotilus, and those that survive the critical early stages develop very fast because of abundant food.

From May 1967 to December 1967, the S. californica population consisted of a single age group, GN_2, because practically all of the larvae that remained after flushing pupated in May (Figure 25). Egg deposition was not as high as in 1966, indicating the apparent catastrophic removal of larvae from the stream during flushing, which influenced the number of adults. Though stream flow was still controlled at 0.5 c.f.s., the creek was in a more natural condition than in previous years, and the data are probably more typical for S. californica populations under Western Oregon conditions than previously. Much of the accumulated detritus was removed by flushing, the enrichment was stopped and the barriers between sections were removed.

The differences in numbers and biomass in the four sections (Figures 25 and 26) are attributed to available food, habitat suitability, and gradient of the stream. For example, in August 1967, the number of larvae per m^2 were 13, 171, 75 and 70 in sections I, II, III and IV respectively and the mean individual weight (mg) was: 1.56, 1.75, 5.22 and 20.08. By autumn the numbers of larvae had declined drastically. This was caused by a lack of food, which resulted in starvation, cannibalism, and/or downstream dispersal. The larvae in section II also were sparce and had poor growth. The pools in sections III and IV were deeper, with silt substrate so they still had abundant food. The habitat for Sialis was probably improved in that the mats of Sphaerotilus were no longer present. With abundant food available, the larvae in these two sections developed very fast.

The growth rate data were obtained by measuring the larvae of both species caught in routine collections. It was apparent in the early work that growth rates varied substantially in different sections of the stream. Consequently it would not be possible to establish a single standard growth curve for production studies for the four sections. Therefore, growth rates were calculated separately for the pond and each age group and each stream section.

The mean biweekly or monthly growth rates were computed according to the following method:

$$\frac{\dfrac{W_2 - W_1}{\dfrac{W_1 + W_2}{2}}}{T} \qquad \begin{array}{l}\text{(Gain or loss in mgs)}\\ \text{(Mean weight in gms)}\\ \text{(Number of days in interval)}\end{array}$$

W_1 = Mean individual weight at time 1.

W_2 = Mean individual weight at time 2.

T = Number of days during time 1 and time 2.

This relative growth rate is expressed as milligrams of growth per gram of biomass per day (mg/gm/day). To estimate production, all the figures were converted to calories and the growth rate is expressed as cal/Kcal/day. The values obtained are given in Table 9 for S. rotunda and in Tables 10 to 12 for S. californica.

The growth rate values varied considerably from month to month. Such variation is expected with animals like insects where moulting is the main factor responsible. It is very difficult to measure actual tissue weight changes of the larvae. The larvae take on water at the time of moult (Wigglesworth, 1965). The percentage of dry weight is low at actual moulting time and increases as the larvae approach the next moult. The number of moults in Sialis is greater than that in many other insects. In addition, sampling error might be responsible for some of the differences in growth rates.

The growth curves were also drawn for S. rotunda (Figure 27) and S. californica (Figure 28) from the mean weight at each sampling time. These curves were fitted by eye. Mean weights read from these curves for each month are given in Appendices III and IV for S. rotunda and S. californica, respectively. These data were used to compute production by Allen's graphical method.

In S. rotunda (Figure 27), development was rapid after hatching and then slowed down because of low water temperature. Development rate increased again in the spring until the time of pupation in

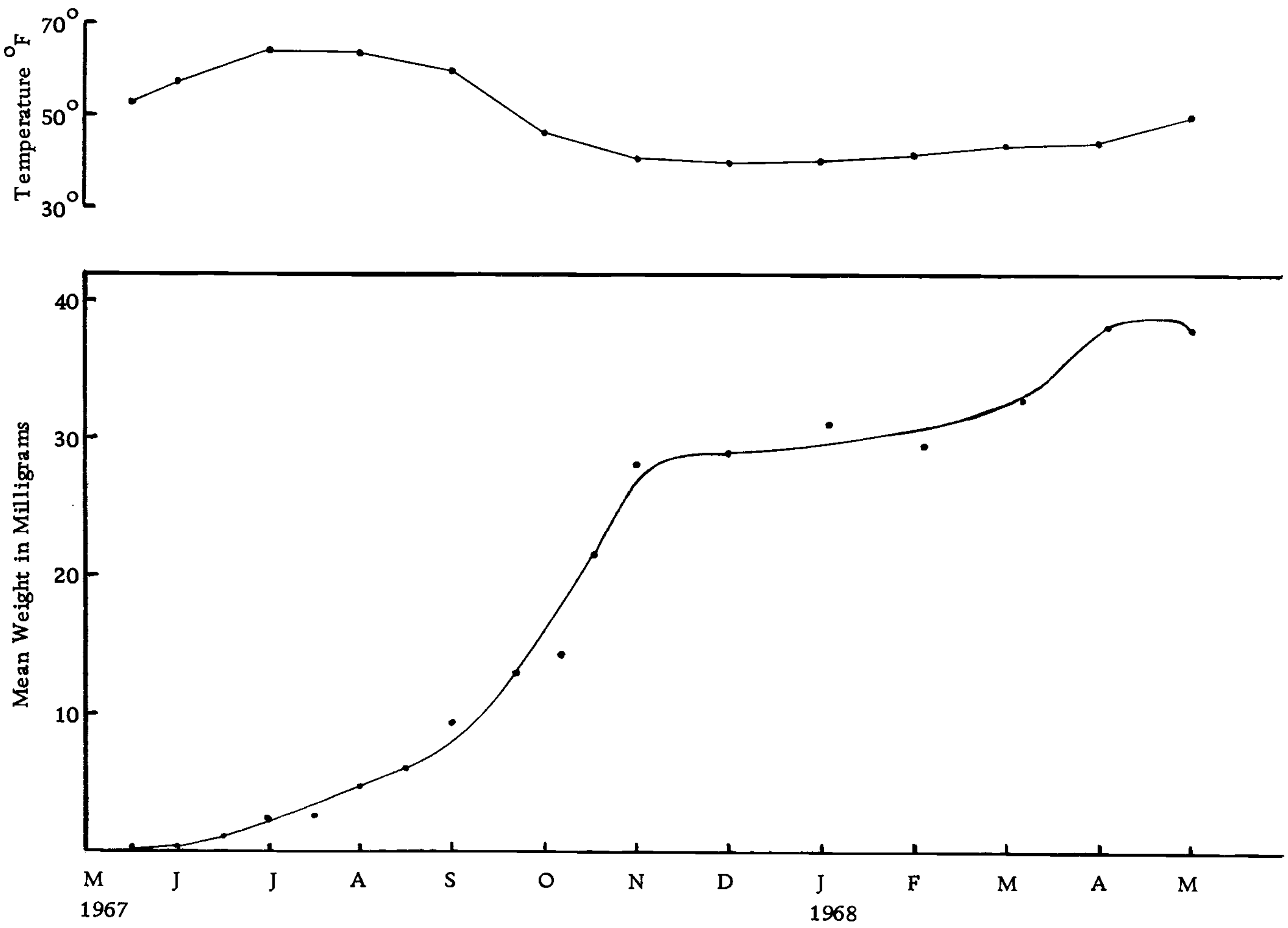

Figure 27. Mean Weight of Sialis rotunda larvae at each sampling interval in Pond from May 1967 to May 1968.

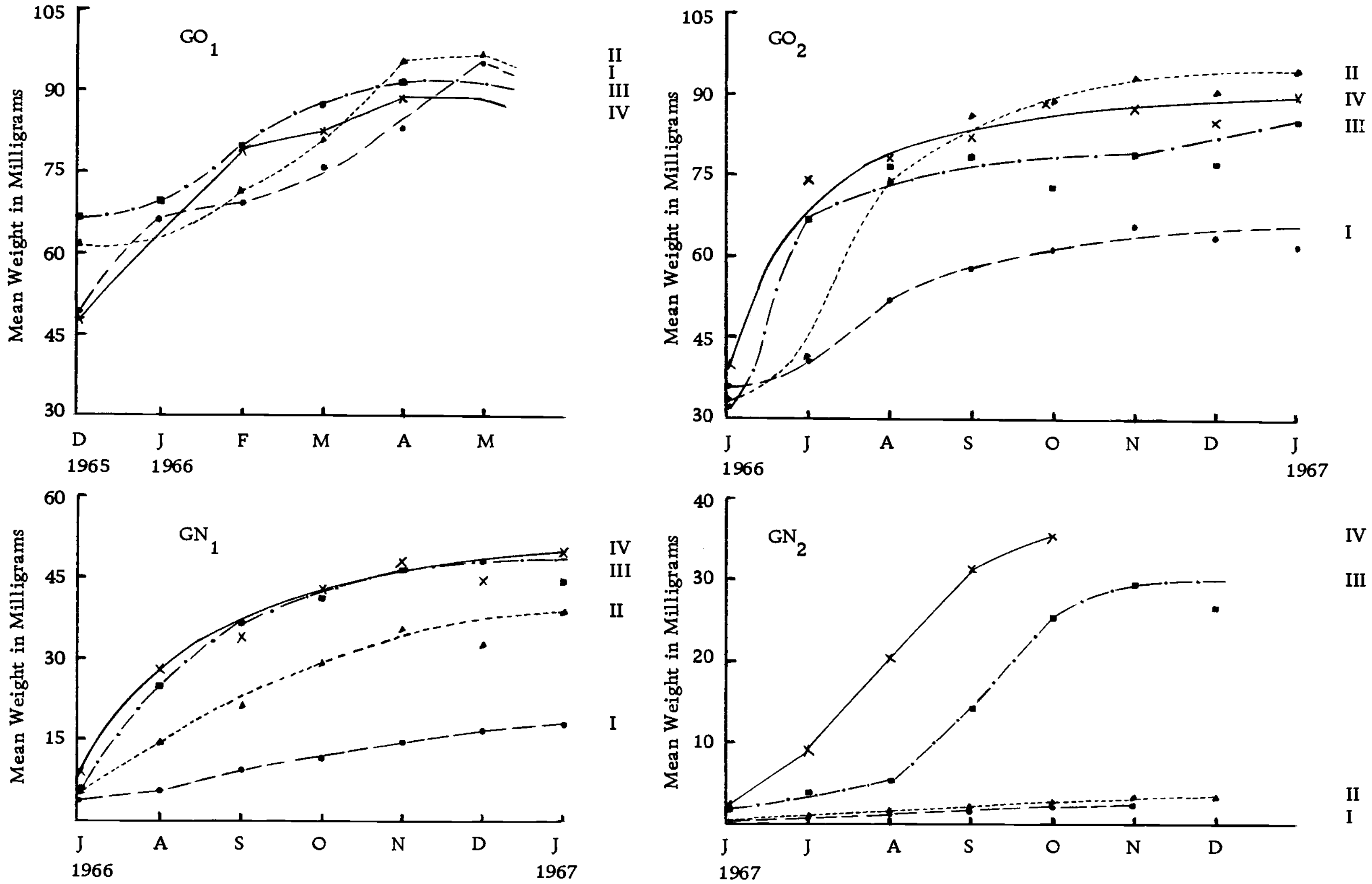

Figure 28. Mean Weight of different age groups of Sialis californica larvae in four sections of Berry Creek.

April - May.

In Berry Creek (Figure 28) the growth curves of all sections for the GO_1 group were similar, because only the mature larvae which emerged during following May and June were obtained in the samples. The GO_2 and GN_1 groups show the effect of enrichment on growth. Unenriched section I had low growth in both cases compared to other three enriched sections. The enrichment effect is even more evident in growth curves of GN_2. Section II had high growth when it was being enriched, but after flushing and stopping the enrichment program, it is just equal to section I. Sections III and IV, although not being enriched, still had high growth in the GN_2 group because of more accumulated organic matter and more midges as food for *S. californica*.

PRODUCTION

Production has been estimated for *S. rotunda* and *S. californica* by two methods: (1) by a mathematical procedure, involving the product of growth rate and mean biomass (Ricker, 1946), and (2) by the graphical method presented by Allen (1951).

Ricker's formula for production is:

$$B = k\bar{P}$$

where: B = Production rate in cal/m^2/day.

k = Relative growth rate in cal/Kcal/day.

$\bar{P}$ = Mean biomass in Kcal/m^2.

The calculation of relative growth rate, k, is described in a previous section. The mean biomass, $\bar{P}$, in a sampling interval is the sum of the biomass at the start and end of the interval, divided by two. This was converted to Kilocalories/m^2. The value of B obtained as production rate in cal/m^2/day was multiplied by the number of days in the sampling interval and divided by 1000 to obtain production in terms of Kilocalories/m^2 for that interval. The values per m^2 for one year for *S. rotunda*, and for four age groups of *S. californica* in their respective periods in each stream section were obtained by summing the positive or negative values of respective intervals.

Monthly and total production values, mean biomass and growth rate values are given in Table 9 for S. rotunda and in Tables 10 to 12 for S. californica. Production in this sense is consistent with the definition given by Ricker (1958): "the total elaboration of new body substance in a stock in a unit of time, irrespective of whether or not it survives to the end of that time." During certain months production values were negative. The importance of considering such values as negative production has been discussed by Warren et al. (1964).

Three graphs are required to compute production by Allen's method: (1) mean weight per individual, plotted against time; (2) numbers per m^2 plotted against time; and (3) the weights plotted against numbers, for each sampling date, obtained from the smoothed curves (1) and (2). The area under the curve, equals production. An example of calculations for this method is given in Figure 29 to estimate the production of S. rotunda in the pond. The numbers and mean wet weights per individual obtained from smoothed curves prior to computation of production are given in Appendices III and IV for S. rotunda and S. californica, respectively.

Table 13 summarizes the total production values of both species. In general the two methods gave comparable results, with the graphical method usually providing a slightly higher estimate.

Production values for S. rotunda (Table 9) are for one generation for one year. There is not much difference in the values obtained

Table 9. Growth rates, mean biomass, and production of S. rotunda in Oak Creek pond during 1967-1968.

Month	Growth Rate (cal/Kcal/day)	Mean Biomass (Kcal/m^2)	Production (Kcal/m^2)
May 1967	51.78	0.07	0.06
June I	60.34	0.21	0.19
June II	50.29	0.62	0.47
July I	13.40	1.09	0.20
July II	33.32	1.69	1.01
August I	16.76	2.36	0.55
August II	27.32	3.17	1.39
September I	18.62	4.54	1.52
September II	5.91	5.28	0.50
October I	36.36	6.02	2.41
October II	21.25	7.63	2.59
November	0.90	9.10	0.25
December	2.22	9.07	0.64
January 1968	-2.25	7.46	-0.50
February	4.15	7.41	0.89
March	4.82	7.51	1.09
April	-0.55	5.29	-0.08
Total			13.18
Mean		5.18	

Table 10. Daily growth rate, mean biomass, and production of S. californica of GO_1 in four sections of Berry Creek.

Month	Section I			Section II			Section III			Section IV		
	Growth Rate (cal/ Kcal/ day)	Mean Biomass (Kcal/ m^2)	Production (Kcal/ m^2)	Growth Rate (cal/ Kcal/ day)	Mean Biomass (Kcal/ m^2)	Production (Kcal/ m^2)	Growth Rate (cal/ Kcal/ day)	Mean Biomass (Kcal/ m^2)	Production (Kcal/ m^2)	Growth Rate (cal/ Kcal/ day)	Mean Biomass (Kcal/ m^2)	Production (Kcal/ m^2)
Jan. 1966	13.87	2.28	0.67				1.78	2.61	0.10			
				2.59	8.81	1.19				9.34	4.76	2.31
Feb.	1.40	2.46	0.11				4.32	3.56	0.48			
Mar.	3.07	2.95	0.26	4.64	7.58	1.02	3.07	4.61	0.41	0.75	5.15	0.11
Apr.	3.29	1.80	0.16	5.83	4.06	0.64	1.62	2.43	0.11	3.34	3.58	0.32
May	3.29	0.38	0.05	-11.88	0.53	-0.26	-10.80	0.32	-0.14	-10.31	1.27	-0.54
Totals			1.25			2.59			0.96			2.20
Means		1.97			4.20			2.71			2.95	

Table 11. Daily growth rate, mean biomass, and production of *S. californica* of GO_2 and GN_1 in four sections of Berry Creek.

Month	Section I			Section II			Section III			Section IV		
	Growth Rate (cal/ Kcal/ day)	Mean Biomass (Kcal/ m^2)	Production (Kcal/ m^2)	Growth Rate (cal/ Kcal/ day)	Mean Biomass (Kcal/ m^2)	Production (Kcal/ m^2)	Growth Rate (cal/ Kcal/ day)	Mean Biomass (Kcal/ m^2)	Production (Kcal/ m^2)	Growth Rate (cal/ Kcal/ day)	Mean Biomass (Kcal/ m^2)	Production (Kcal/ m^2)
GO_2												
Jul. 1966	3.90	2.30	0.25	2.73	2.47	0.19	24.38	0.63	0.43	21.62	1.30	0.79
Aug.	6.83	2.94	0.72	16.23	4.38	2.56	4.15	1.70	0.25	1.28	2.35	0.11
Sept.	3.53	2.60	0.28	5.06	2.96	0.45	0.68	2.35	0.05	1.81	2.47	0.13
Oct.	1.96	1.88	0.11	0.84	2.95	0.07	-2.37	2.30	-0.16	2.47	2.40	0.18
Nov.	2.04	2.41	0.17	1.43	3.69	0.18	2.41	2.31	0.19	-0.39	2.71	-0.04
Dec.	-1.01	2.46	-0.08	-1.02	3.41	-0.10	-0.85	2.37	-0.06	-0.98	2.40	-0.07
Jan. 1967	-1.00	1.84	-0.05	1.80	1.86	0.09	3.23	2.47	0.22	1.78	2.18	0.11
Totals			1.40			3.44			0.92			1.21
Means		2.35			3.10			2.02			2.26	
GN_1												
Aug. 1966	13.08	1.57	0.74	26.32	1.38	1.31	36.37	1.53	1.57	28.02	1.42	1.43
Sept.	15.24	1.31	0.60	12.06	1.33	0.48	12.38	1.75	0.59	6.17	1.28	0.24
Oct.	6.53	1.46	0.29	10.89	1.85	0.60	3.33	1.67	0.17	7.19	1.52	0.33
Nov.	8.25	1.09	0.31	6.06	2.40	0.50	3.87	1.77	0.23	3.92	1.76	0.23
Dec.	3.44	2.14	0.22	-2.76	1.85	-0.15	1.09	2.21	0.07	-2.82	1.56	-0.13
Jan. 1967	2.72	1.88	0.14	5.96	1.31	0.22	-2.70	1.87	-0.14	4.00	1.44	0.16
Totals			2.30			2.96			2.49			2.26
Means		1.58			1.69			1.80			1.50	

Table 12. Daily growth rate, mean biomass, and production of *S. californica* of GN_2 in four sections of Berry Creek.

Month	Section I			Section II			Section III			Section IV		
	Growth Rate (cal/ Kcal/ day)	Mean Biomass (Kcal/ m^2)	Production (Kcal/ m^2)	Growth Rate (cal/ Kcal/ day)	Mean Biomass (Kcal/ m^2)	Production (Kcal/ m^2)	Growth Rate (cal/ Kcal/ day)	Mean Biomass (Kcal/ m^2)	Production (Kcal/ m^2)	Growth Rate (cal/ Kcal/ day)	Mean Biomass (Kcal/ m^2)	Production (Kcal/ m^2)
June 1967	86.73	0.02	0.02	32.84	0.05	0.02	127.18	0.07	0.13	130.10	0.12	0.23
July	22.53	0.03	0.02	44.44	0.11	0.15	33.31	0.24	0.25	43.34	0.38	0.51
Aug.	47.36	0.03	0.04	50.28	0.24	0.35	9.30	0.39	0.11	25.98	1.01	0.76
Sept.	5.13	0.03	0.01	6.53	0.33	0.06	30.75	0.57	0.53	13.90	1.22	0.53
Oct.	7.52	0.04	0.01	4.39	0.29	0.04	18.40	0.73	0.42	4.19	1.03	0.13
Nov.	4.70	0.04	0.01	6.32	0.24	0.05	5.09	0.74	0.11			
Dec.				2.54	0.20	0.02	-3.68	1.33	-0.16			
Totals			0.11			0.69			1.39			2.16
Means		0.02			0.21			0.58			0.75	

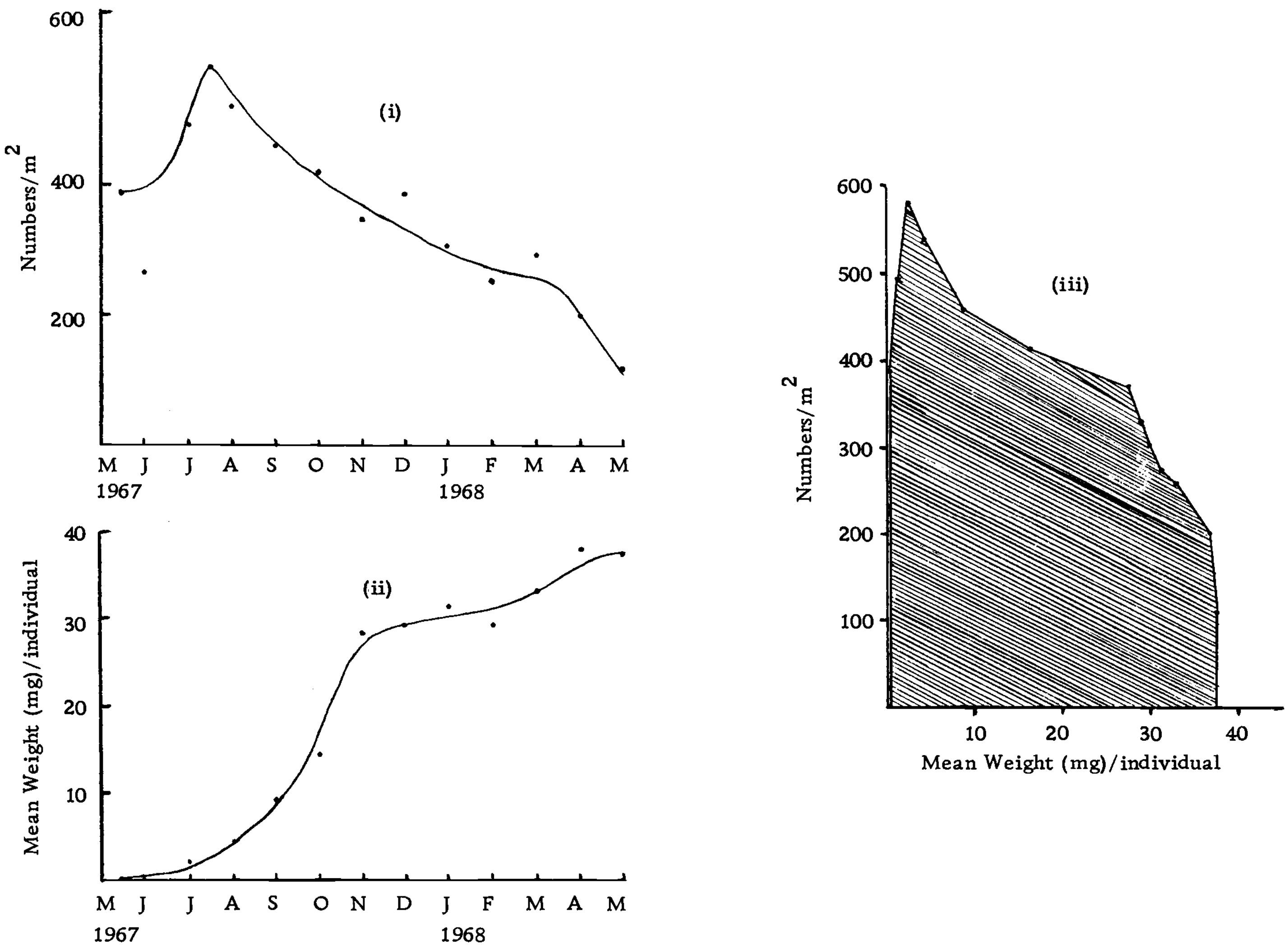

Figure 29. Graphical representation for Computation of Production of <u>Sialis rotunda</u> larvae in Pond by Allen's method: (i) Numbers of larvae/m^2 (ii) Mean Weight (mg) per individual (iii) Production (Mean Weight vs. Numbers).

Table 13. Comparison of production of S. rotunda and S. californica by Ricker's method and Allen's method.

	Production Kcal/m^2	
	Ricker	Allen
S. rotunda (May, 1967-April, 1968)	13.18	12.74

	Section I		Section II		Section III		Section IV	
	Production Kcal/m^2		Production Kcal/m^2		Production Kcal/m^2		Production Kcal/m^2	
S. californica	Ricker	Allen	Ricker	Allen	Ricker	Allen	Ricker	Allen
GO$_1$ (Jan. 1966-May 1966)	1.25	1.31	2.59	2.83	0.96	0.97	2.20	2.90
GO$_2$ (July 1966-Jan. 1967)	1.40	1.62	3.44	3.32	0.92	1.53	1.21	1.70
GN$_1$ (Aug. 1966-Jan. 1967)	2.30	2.60	2.96	2.77	2.49	2.49	2.26	1.89
GN$_2$ (June 1967-Dec. 1967)	0.11	0.16	0.69	0.99	1.39	1.50	2.16	1.90

between Ricker's (13.18 Kcal/m^2) and Allen's (12.74 Kcal/m^2) methods. These values represent the production estimates from a natural habitat without any enrichment or undue disturbances.

For comparing the production values of the different sections of Berry Creek, only the results obtained by Ricker's method are presented, though the difference between the two methods is not great. It is realized that these production estimates are subject to considerable error. Nevertheless, when the data are considered as three experiments (GO_1, $GO_2 + GN_1$, and GN_2), the relative production is a useful method of comparing Sialis in the four sections.

Production for the age group GO_1 (Table 10) was greater in enriched sections II (2.59 Kcal/m^2) and IV (2.20 Kcal/m^2) compared with section I (1.25 Kcal/m^2). Section III, though enriched, had low production (0.96 Kcal/m^2), because the number of surviving individuals was small.

In the GO_2 experiment (Table 11), section II had more than twice the production (3.44 Kcal/m^2) of unenriched section I (1.40 Kcal/m^2). Sections III (0.92 Kcal/m^2) and IV (1.21 Kcal/m^2) had low production because the biomass was low in these sections. The biomass was contributed by very few individuals, whereas in section I, though almost equal in total to sections III and IV, was composed of many small individuals.

In GN_1 group (Table 11), section II as before had the maximum production (2.96 Kcal/m^2) and the other three had almost similar values (I, 2.30; III, 2.49; and IV, 2.26 Kcal/m^2).

Pronounced changes occurred in all four sections after flushing and stopping the enrichment program. Section II which had maximum production during the enrichment period, had low production (0.69 Kcal/m^2) in the GN_2 experiment (Table 12). Section I was also seriously affected (0.11 Kcal/m^2). Section III and IV became somewhat more suitable habitats for young larvae after flushing. Section III in this experiment had 11-fold (1.39 Kcal/m^2) and section IV, 18-fold (2.16 Kcal/m^2) more production than section I. It is significant that this high production in section IV was realized even though no larvae were collected in this section in the last two months of study.

Monthly production, accumulated production, and biomass per m^2 for S. rotunda in the pond and for S. californica in the four experimental sections are presented in Figures 30 and 31, based on data obtained by Ricker's method. The production values of GO_2 are added to that of GN_1, because the two age groups occurred at the same time. The values of negative production are marked dark.

Though the data for Berry Creek are not complete for twelve consecutive months for all age groups, the part of production missed was not great. Most of the annual production occurs during the summer and fall months, and data are available for that period for

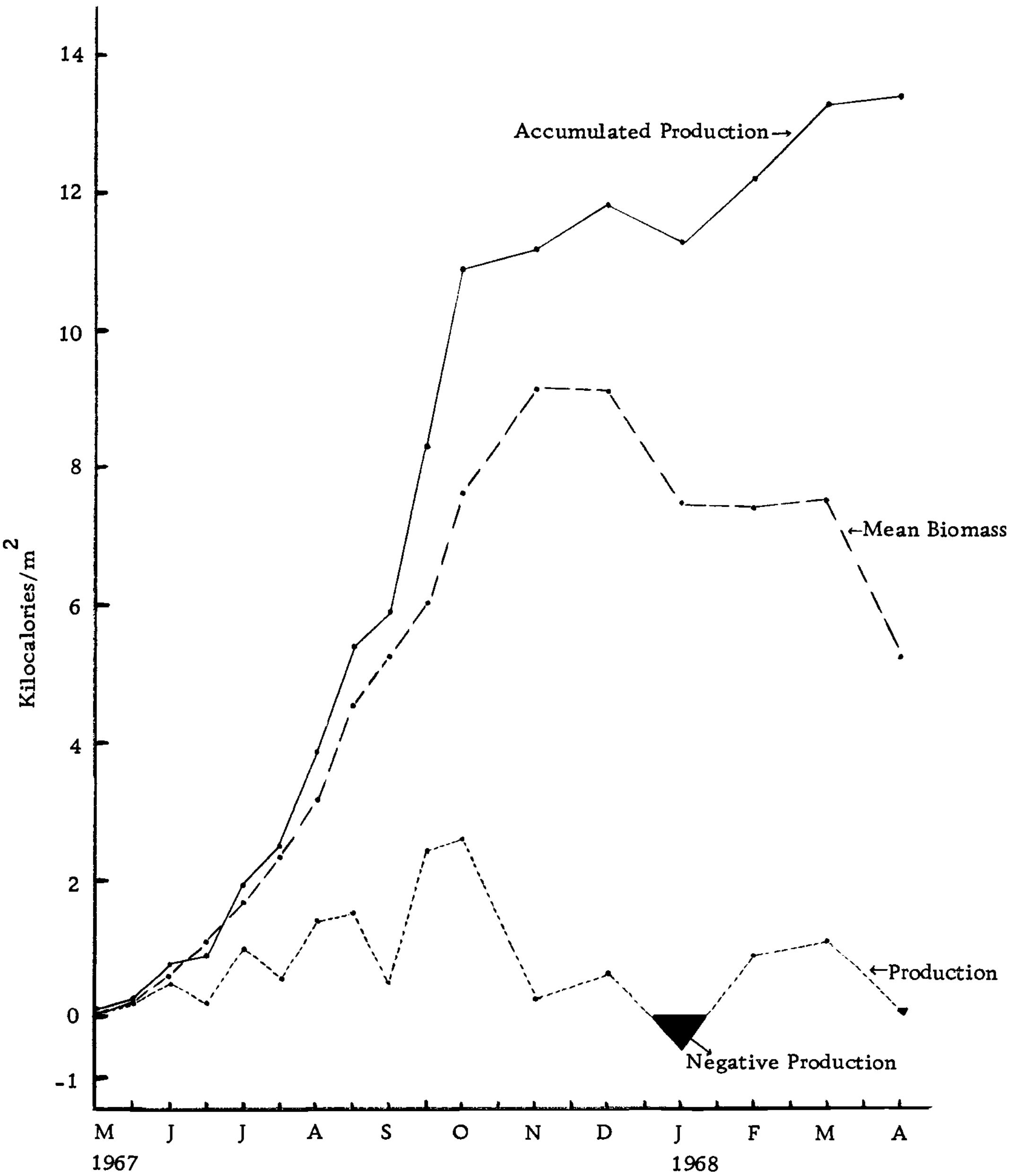

Figure 30. Monthly Mean Biomass, Production and Accumulated Production of Sialis rotunda larvae for twelve months in Oak Creek Pond.

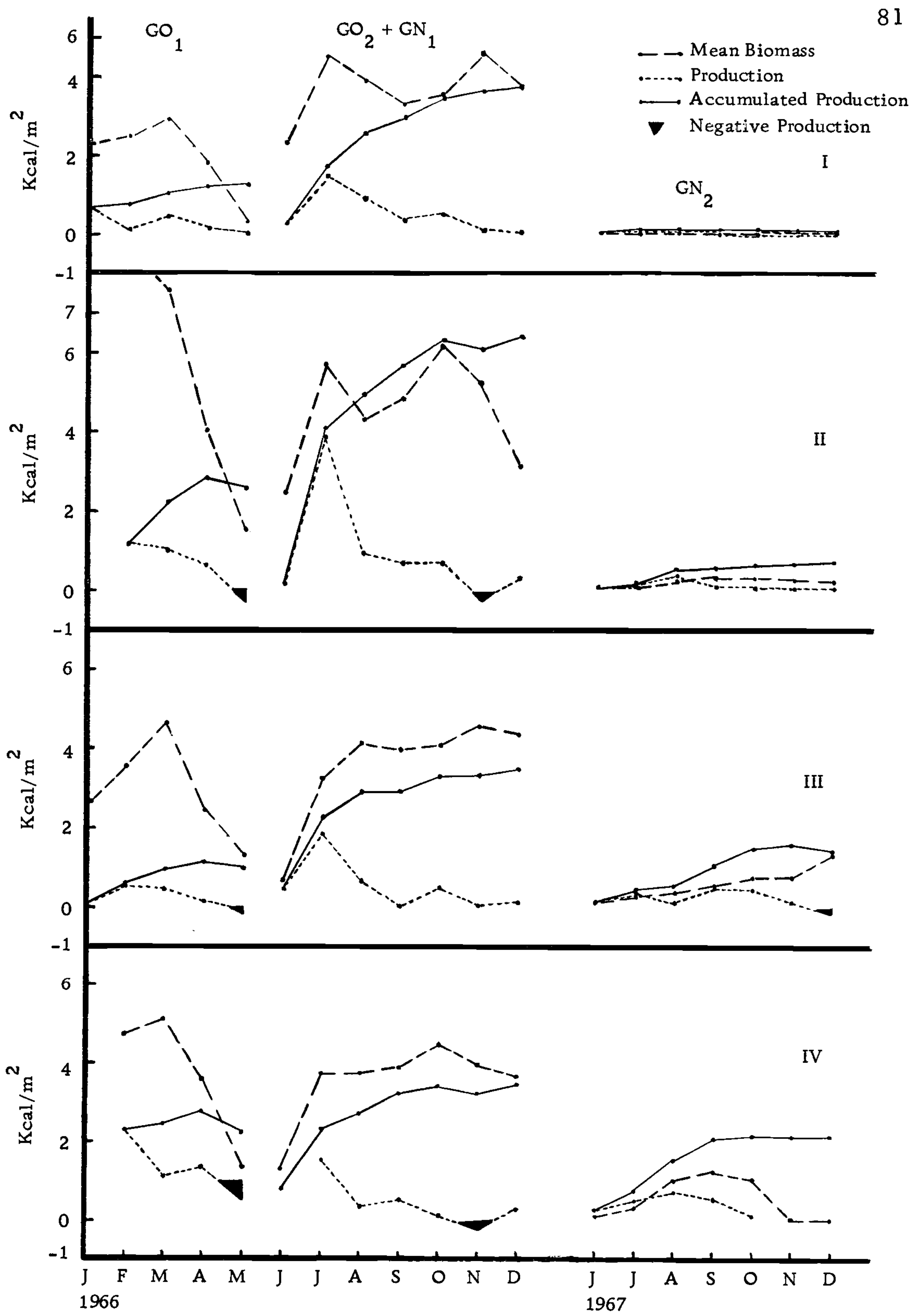

Figure 31. Monthly Mean Biomass, Production and Accumulated Production of different age groups of Sialis californica larvae in four sections of Berry Creek.

GO_2 and GN_1 groups which were present together. In addition, data of GO_1 for five months represent the production of old larvae. The only part missed is the production of young larvae which occurred along with GO_1 larvae but could not be sampled. The summation of production values obtained for GO_1, GO_2 and GN_1 which are for about one year, is 4.95, 8.99, 4.37 and 5.67 Kilocalories/m^2 for sections I, II, III, and IV, respectively.

A comparison between the production values of S. rotunda in the pond and S. californica in the unenriched section I of Berry Creek will show the role of these carnivores in two different ecosystems. Production values in the pond and in the stream section I were 13.18 and 4.95 Kilocalories/m^2, respectively. The pond is a relatively stable and closed system and had a Sialis production about three times greater than the stream section which was subject to many variable changes. Moreover, the experimental stream section was being compared during a period when stream flow was held relatively constant. The estimate of 4.95 Kcal/m^2 for production of Sialis is probably much higher than would be expected in a natural stream. In Berry Creek after the flushing of the stream, production for seven months was only 0.11 Kcal/m^2.

FOOD CONSUMPTION

Laboratory Food Consumption Experiments

Davis and Warren (1968) reviewed various methods of estimating food consumption. They suggested that the most reliable method was to conduct laboratory growth rate studies at various times of the year at several rations of available food. The growth rate of the organisms in nature can then be used to estimate the amount of food consumed. They mention that this method is relatively simple, but its accuracy depends upon the untested assumption that the energy costs of activity in aquaria or jars are similar to the cost in nature.

Growth rates were determined at several food consumption rates for both species of *Sialis* during the summer of 1967 and winter 1967-1968. Specimens were reared individually in jars placed in the laboratory stream.

In the summer experiment, 24 individuals of each species were used. Twenty individuals were fed on different rations of tubificid worms (average weight of 0.6 mg per worm) and the other four larvae were starved. The amount of food was increased for certain individuals mid way through the experiment. The amount of food received by each larva is given in Tables 14 and 15.

The winter feeding experiment was conducted in the same

Table 14. Food received by *S. rotunda* larvae in laboratory growth-rate experiments.

	Individual No.	Number of tubificids received (days) 1-15	16-30	31-45	46-60	Total	Mean/day
Summer Expt.	1 - 5	15	15	15	15	60	1
	6 - 10	30	30	30	30	120	2
	11 - 12	30	30	60	60	180	3
	13 - 17	60	60	60	60	240	4
	18 - 20	60	60	90	90	300	5
	21 - 24	0	0	0	0	0	0
Winter Expt.	1 - 5	7.5	7.5	7.5	7.5	30	0.5
	6 - 12	22.5	22.5	22.5	22.5	90	1.5
	13 - 20	45.0	45.0	45.0	45.0	180	3.0
	21 - 24	0	0	0	0	0	0

Table 15. Food received by S. californica larvae in laboratory growth-rate experiments.

	Individual No.	Number of tubificids received (days) 1-15	16-30	31-45	46-60	Total	Mean/day
Summer Expt.	1 - 5	15	15	15	15	60	1
	6 - 10	30	30	30	30	120	2
	11 - 12	30	60	75	75	240	4
	13 - 15	75	75	75	75	300	5
	16 - 20	75	90	112.5	112.5	390	6.5
	21 - 24	0	0	0	0	0	0
Winter Expt.	1 - 5	7.5	7.5	7.5	7.5	30	0.5
	6 - 10	22.5	22.5	22.5	22.5	90	1.5
	11 - 15	45.0	45.0	45.0	45.0	180	3.0
	16 - 18	0	0	0	0	0	0

manner, using 24 larvae of S. rotunda and 18 larvae of S. californica. The rations were reduced because the larvae were not consuming much at this time of the year (Tables 14 and 15).

The results for mean growth with different rations are given in Figures 32 and 33 for S. rotunda and S. californica, respectively. Each increase in ration resulted in greater growth. The highest rations were considered maximum because some food was not consumed. The number of moults were almost constant for most individuals within each group. During 60 days of the summer experiment, the larvae of both species moulted twice with all rations except the highest one. On the latter they moulted three times. In winter, only the larvae with the highest ration completed an instar.

The growths were significantly different during summer and winter experiments for both species. These differences are attributed to seasonal temperatures, as the kind of food given in both the experiments were same. The field growth in winter months was also similar to laboratory data.

The starved larvae lived for a remarkable length of time, although they lost some weight and none moulted. This indicates the possibility of living in the field at a very low level of food for a long time.

Out of 20 larvae of each species during summer, three larvae of S. rotunda and two of S. californica died during the 60 days

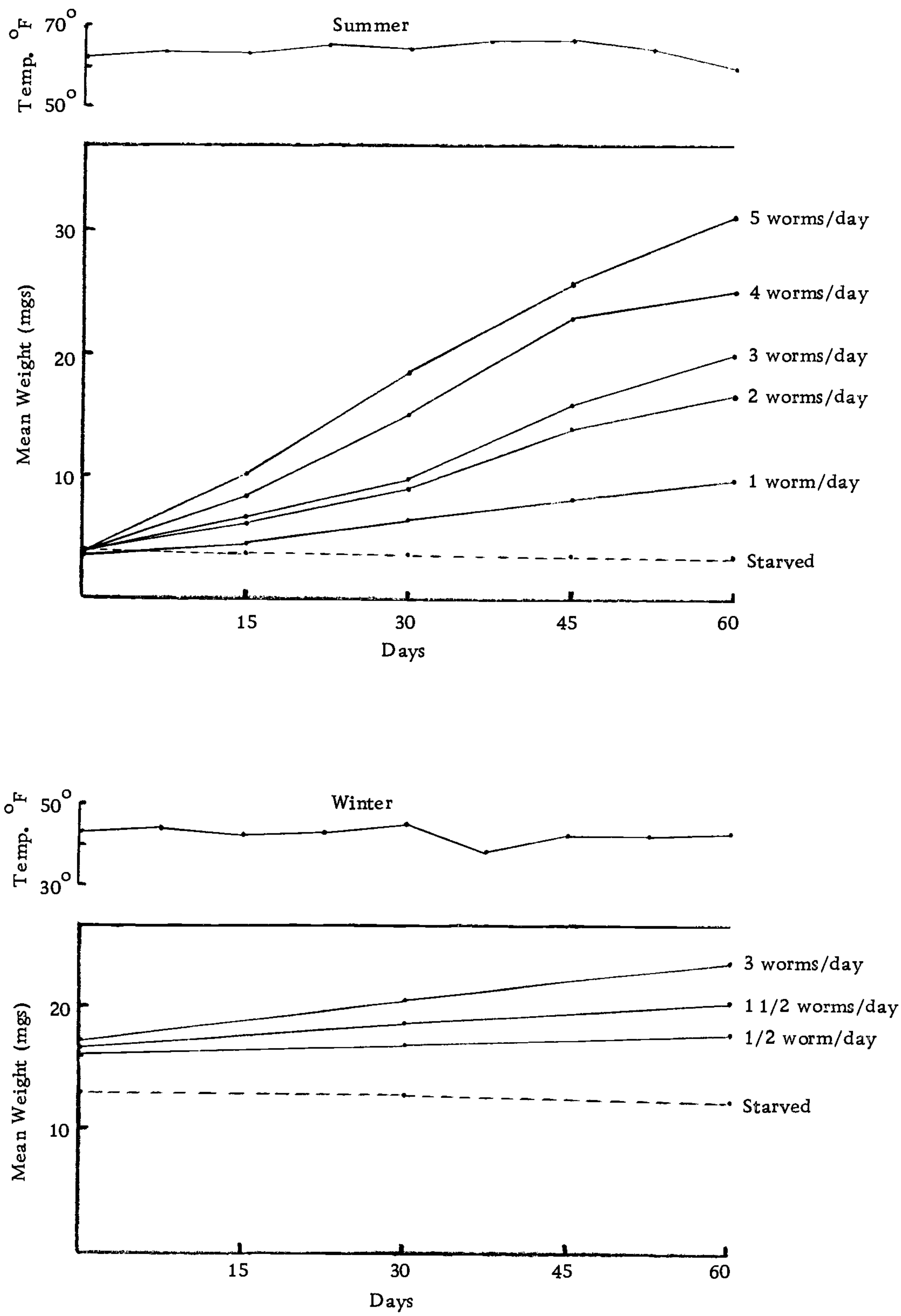

Figure 32. Mean Weights of Sialis rotunda larvae fed different rations of tubificid worms during summer and winter experiments in Laboratory Stream.

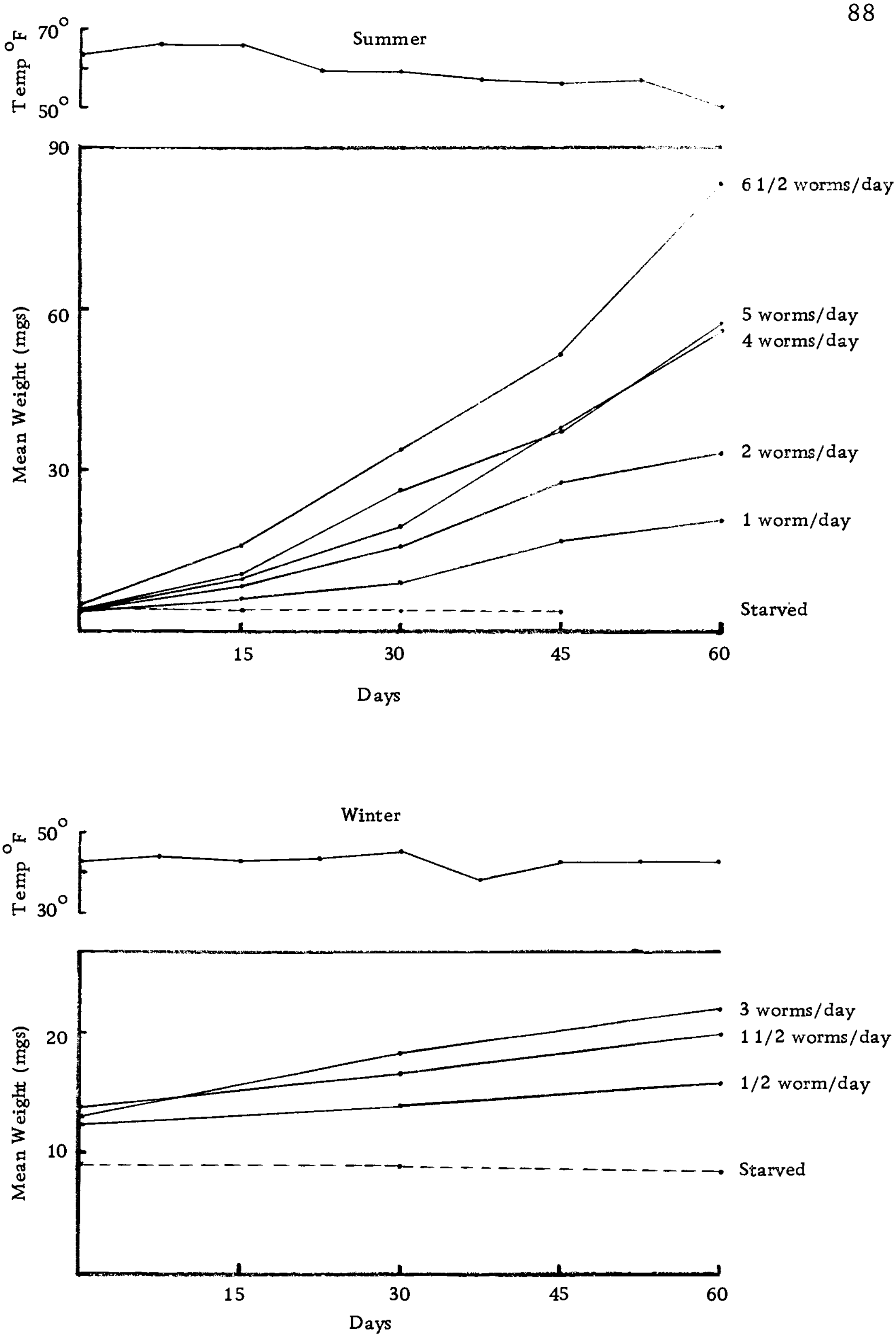

Figure 33. Mean Weights of <u>Sialis californica</u> larvae fed different rations of tubificid worms during summer and winter experiments in Laboratory Stream.

experiment, which is probably due to natural mortality. Of the starved individuals, two *S. rotunda* and one *S. californica* died before the end of the experiment. During the winter experiment, two fed larvae and one starved larva of *S. rotunda* died, whereas there was no mortality in *S. californica*.

Estimate of Food Consumption by Field Populations

Relative daily growth rates and food consumption rates of the experimental larvae were computed for estimating food consumption by field populations. The experimental data of growth rate-food consumption rate were variable, especially in the summer experiments. Much of the variability can be attributed to error in measuring actual tissue weight changes of the larvae during moult cycle. As mentioned earlier the percentage of dry weight is low at actual moulting time and increases as the larvae approach next moult. Such variations have also been reported by Davis and Warren (1965) from their studies with Plecoptera.

Data from the summer and winter experiments with both species were fitted to regression lines (Figures 34 and 35):

$$\beta = \frac{\Sigma XY}{\Sigma X^2}$$

where X = Food consumption rate in calories/Kilocalorie body weight/day.

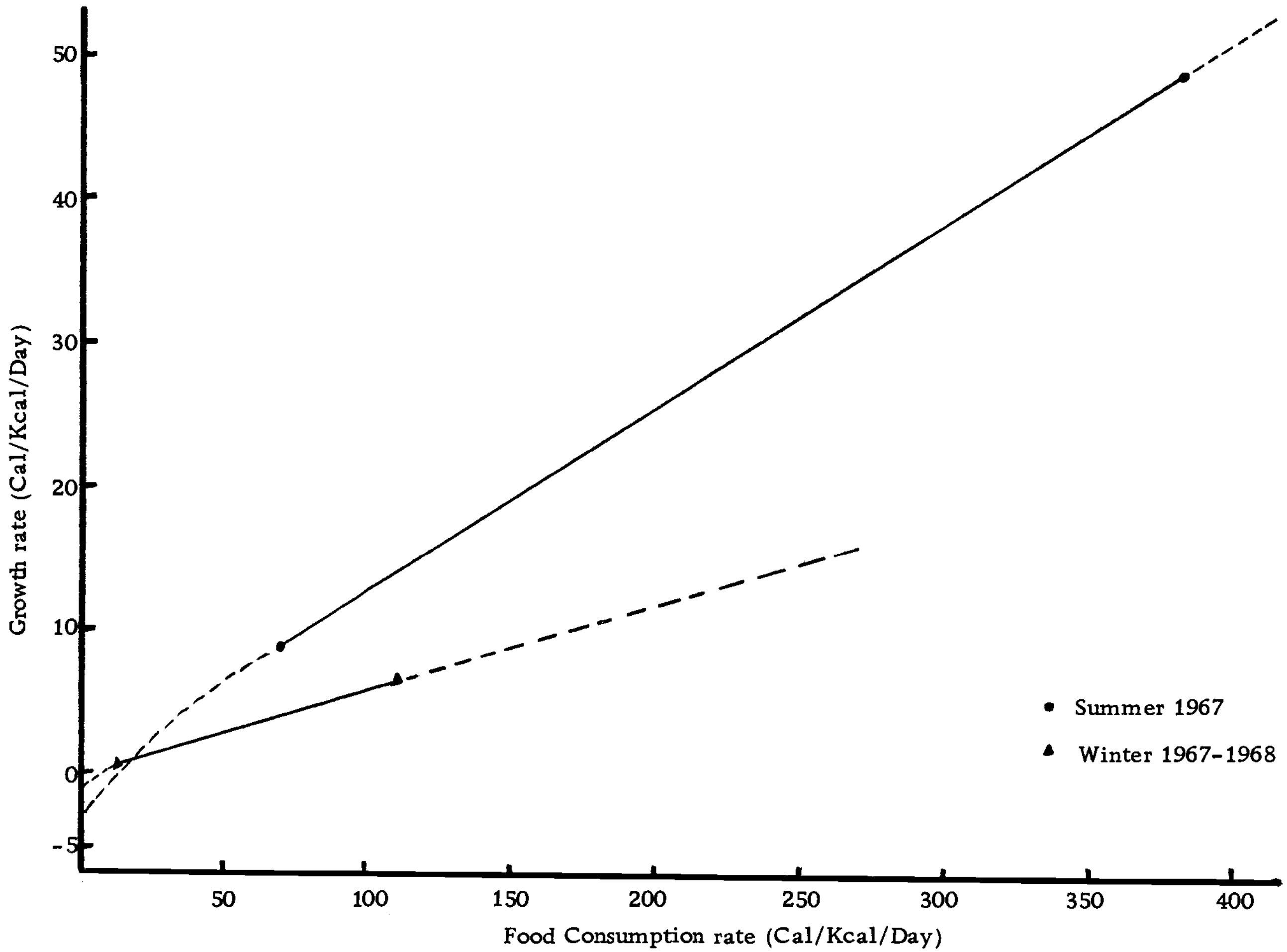

Figure 34. Regression of Food-Consumption rate on Growth-rate of Sialis rotunda larvae held in jars in Laboratory Stream and fed different rations of food.

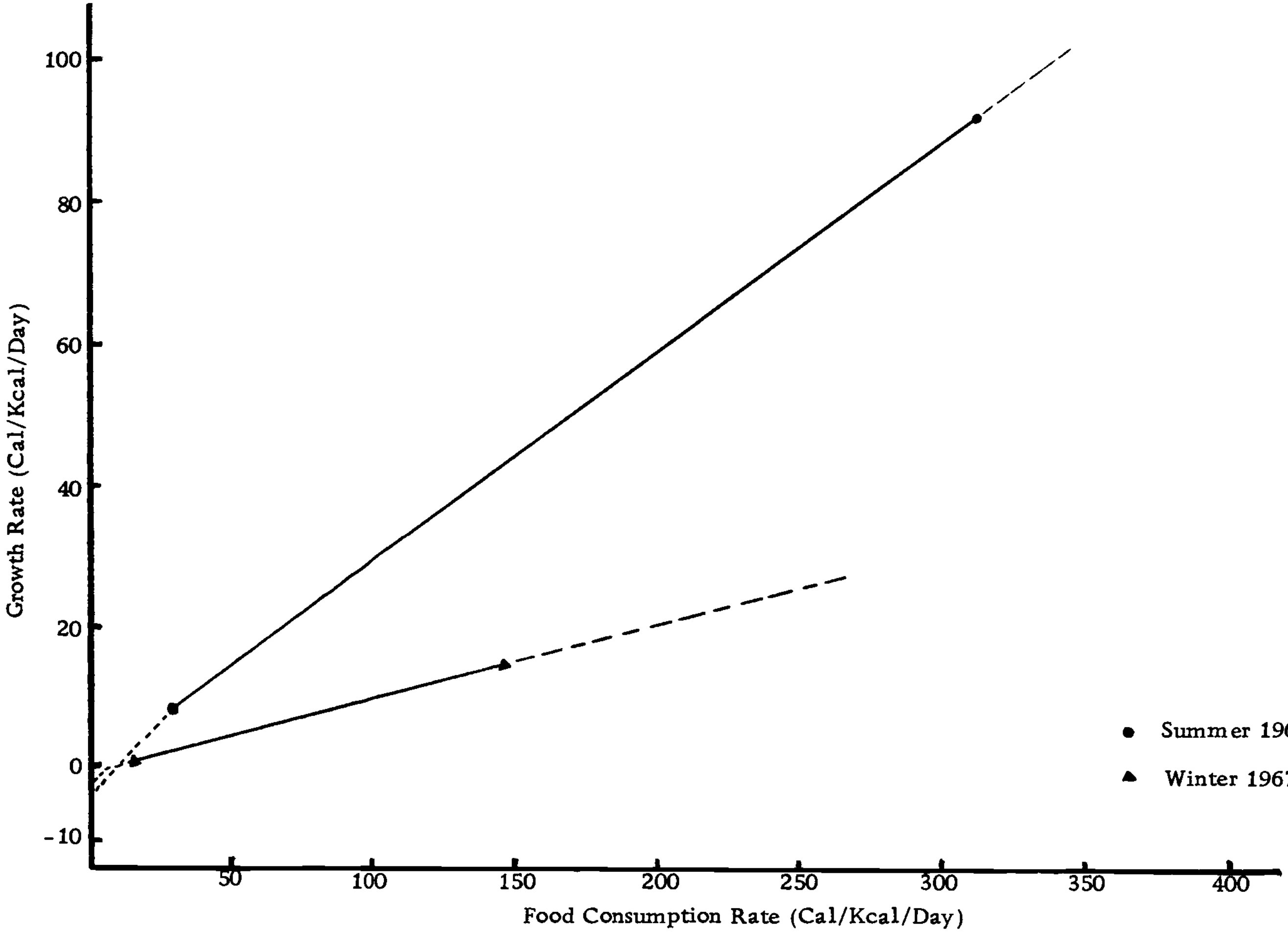

Figure 35. Regression of Food-Consumption rate on Growth-rate of *Sialis californica* larvae held in jars in Laboratory Stream and fed different rations of food.

Y = Growth rate in calories/Kilocalorie body weight/day.

The values of β obtained were:

S. rotunda:	Summer experiment = 0.129
	Winter experiment = 0.059
S. californica:	Summer experiment = 0.295
	Winter experiment = 0.104

The formula used to give a good fit was for a regression line through the origin of X and Y. Growth rates were not determined at very low rations of food consumption, but it is obviously not realistic to have a straight line relationship in this part of the graph. The lines were extrapolated (broken lines) toward a point representing a growth rate of zero at an assumed level of food consumption allowing for a maintenance ration. The lines for summer experiments were also extrapolated at high growth rates to estimate the food consumption rates of very early instar larvae.

The estimates of total amount of food consumed per m^2 during a given interval were obtained by multiplying the daily food consumption rate (read from the regression line) by the mean biomass/m^2, by the number of days in the interval.

The food consumption estimates for _S. rotunda_ in the pond for one year and for all age groups of _S. californica_ in each stream section are given in Table 16. The estimates are expressed as

Table 16. Estimate of food consumption of field populations of *S. rotunda* in Oak Creek pond and *S. californica* in four sections of Berry Creek. (prey = chironomid of mean length 3.5 mm)

	Food consumed Kcal/ m^2	Gms/ m^2	Prey/ m^2	Prey/Pond (70 m^2) Number (Thousands)
S. rotunda	118.74	137.39	354	24,787

S. californica

Age Groups	Section I Food consumed Kcal/ m^2	Gms/ m^2	Prey/ m^2	Prey/ pool (24.49 m^2) No. (1,000)	Section II Food consumed Kcal/ m^2	Gms/ m^2	Prey/ m^2	Prey/ pool (15.42 m^2) No. (1,000)	Section III Food consumed Kcal/ m^2	Gms/ m^2	Prey/ m^2	Prey/ pool (15.85 m^2) No. (1,000)	Section IV Food consumed Kcal/ m^2	Gms/ m^2	Prey/ m^2	Prey/ pool (17.76 m^2) No. (1,000)
GO_1	5.27	5.35	14	338	12.42	12.63	33	502	5.46	5.55	14	237	11.90	12.11	31	554
GO_2	7.37	7.50	19	473	13.57	13.81	36	549	6.23	6.34	16	259	6.92	7.04	18	322
GN_1	10.20	10.38	27	655	11.79	11.99	31	477	10.22	10.40	27	425	8.87	9.03	23	413
GN_2	0.41	0.41	1	26	2.79	2.84	7	113	6.18	6.29	16	257	7.16	7.28	19	333

Kilocalories equivalents of food consumed/m^2 and as grams (wet weight) of food consumed/m^2. These values are also expressed in terms of numbers of chironomid larvae consumed/m^2 and the consumption by the entire *Sialis* population in the pond and pools of each stream section of Berry Creek. Mean weight for an "average" chironomid was taken as 0.388 mg, based on specimens 3.5 mm in length.

Based on these data, one larva of *S. rotunda* consumed an average of 2.6 chironomids/day and about 940 chironomids during the larval period. The entire population was estimated to consume 9617.3 grams in a year.

In Berry Creek a substantial number of chironomids were consumed by *S. californica*, which otherwise was potentially available to trout. The larvae in unenriched section I consumed much less compared to enriched sections II, III, and IV. During the enrichment program one *Sialis* larva in section I consumed 2.08 chironomids/day, whereas in enriched sections II, III, and IV, the consumption was 3.23, 3.00, and 3.55 chironomids/day, respectively.

DISCUSSION AND CONCLUSIONS

Apparently, this is the first detailed study of the life history of American Sialis, covering all the stages and habits during the life cycle. An important ecological finding was different habitat preferences of the two species. This was evident not only in the two study areas, but also from collections made at many other locations in Oregon. The important factors segregating their distribution within the habitats seem to be appropriate substrate and water current; with muddy substrate and still water for S. rotunda and flowing water with organic debris for S. californica.

Both the species are indiscriminate feeders and can have a considerable effect on the density of prey population if the predators occur in significant numbers. Moreover, food consumption experiments at different levels of available food revealed that they are adapted for survival during intervals of low prey density, in that they can live for a considerable length of time without prey.

Though previous workers failed to rear Sialis in the laboratory, it is felt from the present study that it is not too difficult to colonize them in the laboratory. There is high mortality in the early instars, especially first and second, and this is suspected to be the reason which discouraged other workers from continuing further rearings. The high mortality in the early instars also occurs in nature, as has been demonstrated by comparing the number of larvae obtained in samples and the number of eggs laid. Thus once they complete few early instars in about one month, it is easy to rear them for the rest of their life cycle of about eight to nine months. Cannibalism can be minimized by providing suitable substrate and enough food. Provision could be made for the larvae to leave the aquarium or any other colonizing site at the time of pupation. It has been demonstrated that the adults will mate and oviposit in laboratory cages, so these species could be colonized and mass-reared for experimental purposes. This insect has been used in many physiological and anatomical studies (Dethier, 1942; DuBois, 1938; Selman, 1961, 1965; Shaw, 1955; Staddon, 1955), and would be useful for some ecological experiments, such as predator-prey and competition studies.

Differences in density and biomass of the two species are a result of the habitat in which they occur. Even though Berry Creek had low numbers and biomass compared to population in a natural pond, the S. californica population was much higher than would occur in a stream having a natural flow regime. The favorability of the pools at Berry Creek had been enhanced by the accumulation of silt and organic matter in the pools because of controlled flow conditions.

It was more difficult to obtain accurate samples at Berry Creek because of the uneven nature of substrate, whereas the pond had a muddy substrate which was very easy to sample with Ekman dredge.

In addition, several experimental procedures and flushing of the stream affected the density and biomass as compared with the more stable conditions in the pond, so the data for _S. rotunda_ are more accurate than for _S. californica_.

Differences in density and biomass of _S. californica_ between the four experimental sections of Berry Creek resulted primarily from the effects of enrichment with sucrose and urea. This treatment led to development of the bacterium, _Sphaerotilus natans_. Though removal of the forest canopy resulted in differences in number of egg masses deposited, this was not an important factor in determining population size.

The growth of _Sphaerotilus_ caused a heavy mortality of early instar larvae in the enriched sections. McIntyre (1967) reported that growths of _Sphaerotilus_ increase the food base for small trout, but may decrease the suitability of streams as spawning areas. A similar effect is believed to have occurred with _S. californica_; growth of _Sphaerotilus_ was unfavorable for early-instar larvae because they become entangled in the filaments, but larger larvae were not impeded by the bacterium, and developed rapidly because food was abundant.

Growth rate measurements indicated striking differences between enriched and unenriched sections. The increased growth rate in enriched sections was obviously due to abundant food, especially chironomids and mayflies. The effect of enrichment was confirmed by the results after flushing and stopping of enrichment in that growth rate in section II decreased considerably.

A number of methods of estimating production are available. Juday (1940) and Lindamen (1941) have expressed the annual production of plankton and bottom fauna in lakes as the product of average stock and the number of "turnovers"--apparently equivalent to the annual number of life cycles. As pointed out by Allen (1951), "this method actually gives an underestimate of the annual production because it is based on the incorrect assumption that the stock of every generation at any moment of sampling must be equal to the total production of that generation, whereas the stock at any moment must be less than the total production, both by the amount that has been embodied in the individuals which have died prior to sampling, and by the amount which will be added by the further growth of the surviving individuals after the sampling date." In general, two methods available are theoretically satisfactory. Ricker's (1946) mathematical procedure demands laborious calculations but has been considered to yield valuable results. Allen (1951) presented a graphical method and discussed its advantages. It provides a convenient means of smoothing the results prior to computation where the data are subject to irregular error, due to sampling and similar causes, when the data are accurate the graphical method shows the effects of real irregularities and fluctuations due to seasonal and other causes. It was felt in the present study that sampling difficulties would cause many irregularities, especially in Berry Creek, so production was computed by this method and compared with Ricker's method. In general the two methods gave comparable results, with the graphical method usually being a slightly higher estimate.

Production in the pond was greater than in any of the sections of Berry Creek, even if that latter is extrapolated to a period of 12 months by adding some probable value for the period when production was not determined.

The differences in the production of different age groups in four sections of Berry Creek are attributed to differences both in numbers of individuals, biomass contributed and to different growth rates. Though the growth rates in section I were not high compared with the rates of other sections during enrichment program, the numerical superiority in section I led to high biomass resulting in comparable production estimates in other sections. Davis and Warren (1965) found a somewhat similar relationship of production to biomass during their laboratory stream experiments with sculpins (*Cottus perplexus* Gilbert and Evermann). Production rates increased with increase of biomass up to an optimal level and decreased with further increase of biomass. However, in Berry Creek the density or biomass of *S. californica* never seemed to have reached the maximum. Section II had high biomass during enrichment program and the production was also correspondingly highest. The percent mortality of early instars in this section was probably similar to mortality in the other enriched sections, but high population density may have resulted from downstream drift from section I. Section I, because of the highest number of individuals compared with all other sections had equal or slightly more biomass than enriched sections and this resulted in comparable production to other sections.

In the post-flushing period (GN_2), the biomass in sections I and II was considerably less than that in sections III and IV. This resulted in much less production in the former even though relative growth rates are always high in early instars. In section III and IV growth rates were also high and, coupled with a higher biomass than in sections I and II, this resulted in 11-18 fold greater production in III and IV. This example indicates the value of production as an ecological parameter. An estimate is obtained of the amount of energy fixed by a species compared with biomass or numbers which only reflect the standing crop.

The comparative annual production figures from different studies of insects are given in Table 17. *Sialis* species in the present study have high production values and this is particularly striking because most of the results are for the herbivore trophic level.

Table 17. Comparison of production of Sialis spp. with estimates for other insects.

Location	Annual Production gms/m^2	
Oak Creek pond (S. rotunda)	15.26	
Berry Creek (S. californica Unenriched section)	5.03*	
Berry Creek (S. californica Enriched section)	6.45*	
Afon Hirnant Stream (Carnivores)	0.45	Hynes (1961)
Afon Hirnant Stream (Herbivores)	3.47	Hynes (1961)
Valley Creek, Minnesota (Mayfly, Baetis vagans, Ephemeroptera)	9.10	Waters (1966)

*Data for age groups $GO_1 + GO_2 + GN_1$ only.

The analysis of data in terms of food received by single individual per day has shown that the individuals in enriched section consumed one and half to two times more food compared to unenriched section. Though confidence limits of the population food consumption estimates were not established, the estimates will be in the right order of magnitude. No examples were found in the literature to enable a comparison to be made between the food consumed by a population of Sialis and other comparable predators.

In general, food conversion efficiencies were higher in early instars of both species and also during months with high temperature. In comparing the two species, S. californica had a higher conversion efficiency than *S. rotunda*.

In Berry Creek, the cutthroat trout (*Salmo clarki clarki* Richardson) is the principal product of interest to man. Warren *et al.* (1964) have shown increased production of trout in the enriched sections and also an increase in its food organisms. Chironomids were the insect group that increased most strikingly in the diet of trout after enrichment. *Sialis* has been reported in variable amounts in the stomach contents of trout by Warren *et al.* (1964) and McIntyre (1967), but not as an important food item. The production of *Sialis* is not of much importance in view of its minor role as a food for trout. However, its presence as a food resource could be of value at certain times because it may be available to fish during the months when other organisms are not available.

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APPENDICES

Appendix I. Larvae of *S. rotunda* obtained in pit-fall traps on shore at Oak Creek Pond in 1967.

Date	Trap No. 1	Trap No. 2	Trap No. 3
April 5	6	0	0
April 7	0	2	0
April 12	1	0	3
April 17	0	3	4
April 21	1	5	7
April 27	5	0	10
May 2	8	2	11
May 6	4	0	8
May 10	6	2	4
May 15	9	0	2
May 19	0	0	3
May 25	4	3	6
June 2	2	0	1
June 12	3	1	2
June 16	0	0	0
June 30	2	1	3
Total	51	19	64

Appendix II. Record of Parasitization of *S. rotunda* eggs at Oak Creek pond and *S. californica* eggs at four sections of Berry Creek.

S. rotunda

Month and Year	Total egg masses counted	Parasitized egg masses
May 16, 1967	20	0
May 23	31	0
June 2	25	2
June 7	16	3
June 10	21	5
June 14	19	5
June 16	15	6
Total	147	21

S. californica

Month and Year	Section I		Section II		Section III		Section IV	
	Total	Parasitized	Total	Parasitized	Total	Parasitized	Total	Parasitized
June 14, 1966			134	97	55	31	14	3
May 22, 1967	4	0	3	0	8	0	0	0
May 31	11	3	8	2	11	0	0	0
June 8	21	8	12	8	15	2	0	0
June 14	32	11	14	7	19	4	0	0
June 23	34	26	15	11	31	16	0	0
Total (1967)	102	48	52	28	84	22	-	-

Appendix III. Numbers/m^2 and mean weight/individual (mg) of S. rotunda larvae in Oak Creek pond obtained by smoothing of curves to compute production according to Allen's method.

Month	No. /m^2	Mean weight
May 1967	387	0.14
June I	389	0.36
June II	410	0.96
July I	495	1.50
July II	581	2.55
August I	540	4.25
August II	502	6.25
September I	461	8.75
September II	444	12.00
October I	417	16.25
October II	407	21.60
November I	371	27.50
November II	351	28.75
December I	332	29.00
December II	318	29.50
January I, 1968	303	30.00
January II	290	30.50
February I	276	31.25
February II	268	32.00
March I	260	33.00
March II	240	34.25
April I	205	36.75
April II	165	37.50
May I	110	37.50

Appendix IV. Numbers/m^2 and mean weight/individual (mg) of _S. californica_ larvae of different age groups in four sections of Berry Creek obtained by smoothing of curves to compute production according to Allen's method.

	Section I								Section II							
	GO_1		GO_2		GN_1		GN_2		GO_1		GO_2		GN_1		GN_2	
Month	No/ m^2	Mean wt	No/ m^2	Mean wt	No/ m^2	Mean wt	No/ m^2	Mean wt	No/ m^2	Mean wt	No/ m^2	Mean wt	No/ m^2	Mean wt	No/ m^2	Mean wt
Dec. 1965	48	49.0							161	61.5						
Jan. 1966	44	66.0							138	64.3						
Feb.	39	69.0							113	70.8						
Mar.	39	74.5							91	81.0						
Apr.	9	84.0							9	95.5						
May	9	95.5							4	95.5						
June			75	36.3							91	37.7				
July			65	40.6	300	3.6					73	48.5	112	5.2		
Aug.			56	51.9	250	5.8					57	74.3	96	14.6		
Sept.			49	57.7	208	9.2					43	83.0	84	23.0		
Oct.			43	61.2	170	11.2					33	88.7	74	29.3		
Nov.			37	64.0	133	14.8					28	91.5	64	33.5		
Dec.			31	65.0	105	16.4					25	94.0	54	37.5		
Jan. 1967			26	65.0	81	17.7					23	95.0	44	36.6		
June 1967							111	0.14							920	0.05
July							167	0.29							540	0.30
Aug.							33	1.60							330	1.80
Sept.							18	1.80							178	2.10
Oct.							16	2.30							82	2.40
Nov.							13	2.70							60	3.00
Dec.							0	0							41	3.20

Appendix IV. Continued

	Section III								Section IV							
	GO_1		GO_2		GN_1		GN_2		GO_1		GO_2		GN_1		GN_2	
Month	No/ m^2	Mean wt	No/ m^2	Mean wt	No/ m^2	Mean wt	No/ m^2	Mean wt	No/ m^2	Mean wt	No/ m^2	Mean wt	No/ m^2	Mean wt	No/ m^2	Mean wt
Dec. 1965	75	66.2							87	47.9						
Jan. 1966	57	69.2							78	63.5						
Feb.	40	79.4							70	79.4						
Mar.	22	87.1							61	81.3						
Apr.	4	91.2							26	89.1						
May	4	91.2							4	89.1						
June			30	32.8							39	39.8				
July			30	66.8	68	5.2					37	71.0	55	9.3		
Aug.			30	76.7	62	25.2					34	77.8	51	28.2		
Sept.			30	78.2	57	35.0					31	82.3	47	36.0		
Oct.			30	78.2	51	41.5					29	85.0	42	42.2		
Nov.			30	79.1	47	46.2					26	87.4	38	46.0		
Dec.			30	79.1	40	47.7					23	89.0	33	48.0		
Jan. 1967			30	84.8	34	47.7					20	89.3	29	49.5		
June 1967							55	1.2							51	2.4
July							103	4.0							70	9.3
Aug.							75	5.2							65	20.5
Sept.							53	14.2							47	31.3
Oct.							37	25.4							29	35.7
Nov.							25	29.7							0	0
Dec.							21	29.7							0	0