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A study was performed of the influence of enrichment on the production and food relations of the stream snail, Oxytrema silicula, in the Berry Creek experimental stream from October, 1963 through February, 1965. Four experimental stream sections that were separated from each other by screens were used in the study. Two upstream sections (I and II) were not enriched; receiving energy only from sunlight and natural allochthonous materials. Two downstream sections (III and IV) were continuously enriched with sucrose and urea. As a result, growths of the bacterium Sphaerotilus natans developed on the riffles of these sections. The removal of trees from alongside Sections II and IV resulted in smaller quantities of leaves and more sunlight reaching these sections than reached Sections I and III.

Snails were removed monthly from a 0.26 m^2 area of riffle of each section and were separated into different size-groups. The

groups were considered to represent the 1959, 1960, 1961, 1962, 1963, and 1964 year-classes. Production for each age-class was calculated from measurements of growth rate and average biomass.

Aquarium experiments with snails of sizes similar to those of the 1961 year-class, which were the most abundant in the stream, established relationships between rates of growth and food consumption during two seasonal periods. Estimates of annual total food consumption in each section were based upon these relationships and upon knowledge of the growth rates of 1961 year-class snails and of the total snail biomass of all age-classes.

Laboratory stream experiments were performed which established that snails were able to utilize Sphaerotilus for growth. Results of studies in which snails, along with different types of leaves, were suspended in packets in an unenriched and in an enriched section of the stream showed that the most abundant leaves, alder and maple, were utilized by snails but that oak leaves were not. Comparison of rates of decomposition of leaves suspended alone in packets in the stream indicated that decomposition was greater in enriched than in unenriched sections.

Snail production was found to be approximately seven-fold greater in enriched than in unenriched sections. Most of the production in enriched sections was by the 1960 year-class of snails. Production was greatest in unenriched sections by younger

age-groups than in enriched sections. Food consumption, like production, was estimated to be approximately seven-fold greater in enriched than in unenriched sections .

Some relationships between snail production and the energy resources of the different sections are discussed.

Production of the Snail Oxytrema silicula (Gould)
in an Experimental Stream

by

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Production of the Snail Oxytrema silicula (Gould)
in an Experimental Stream

INTRODUCTION

Studies of the ways in which the energy from sunlight and allochthonous materials enters into the production of aquatic organisms have been underway at the Berry Creek experimental stream since 1959. An important part of these studies has been the investigation of the changes in the energy resources and production of cutthroat trout and other organisms that result from low-level enrichment of the stream with sucrose or with sucrose and urea. Enrichment, which began in 1960, has resulted in growths of the filamentous bacterium, Sphaerotilus natans, on the riffles of sections of the stream receiving these materials. These growths were erratic until the Spring, 1964, when nitrogen in the form of urea was added to the stream resulting in more uniform growths throughout the year. An increase in the production of trout occurred in the enriched sections which was related to an increase in the abundance of aquatic insects (Warren et al., 1964). Another effect of enrichment was an apparent large increase in the biomass of snails over that of the unenriched sections. In order to quantify this difference and to better understand the energy relationships involved, a study was undertaken of the production and food relations of snails in enriched and unenriched sections of the experimental stream. The study described

herein was carried on between October, 1963 and March, 1965.

Since gastropods are frequently only a minor portion of the fauna they have been largely neglected in earlier productivity or ecological studies. The few workers studying terrestrial snail population dynamics have for the most part estimated only snail biomass (Foster, 1937; Strandine, 1941). Macan (1950) measured the numerical densities of the pond snail, Hydrobia. Odum (1957) collected Oxytrema catenaria from the bottom of Silver Springs and measured its contribution to the energy budget of the river. In his study of a small spring, Teal (1957) measured the energy contribution of the aquatic snail, Physa. More recent attempts to determine standing crops of aquatic snails include those of Hairston (1961) and Najarian (1961). Growth rate studies on aquatic snails are limited to the work of Pesigan (1958) who worked with the economically important snail, Oncomelania.

Oxytrema silicula is a common inhabitant of freshwater streams of the Pacific Northwest. Its distribution has been established from the Shasta River of California to Southwest Washington, and from the Cascade Mountains to the Pacific Ocean. This species is placed in the sub-class Prosobranchia and the order Mesogastropoda. A conical, elongate shell, spiral operculum, and sessile eyes results in this snail being placed in the family Pleuroceridae. Ching (1957) gives a more complete description of this species and

presents information on its feeding and digestive systems. The presence of a crystalline style and gastric shield is evidence of its ability to utilize carbohydrate in its diet.

The snail is most abundant on the riffles of streams. In Berry Creek only small numbers of large-size snails are found in the pools. The eggs of Oxytrema are deposited on the undersides of rocks in the riffles and are contained in blue-green gelatinous masses. Eggs may be found in Berry Creek from April through September, but the greatest numbers are present during late spring.

In this study measurements of snail production were based upon biomass and growth rate information obtained from samples of snails removed monthly from the riffles of four sections of Berry Creek. Snails from each monthly sample were grouped according to size frequency. The biomass of each size-group was determined directly by weighing all individuals. Estimates of growth rate were based upon the changes in mean weight of individuals of a given size-group from one monthly sample to another.

The food relationships of the snails were also studied. Aquaria were used to study the relationships between snail growth rate and food consumption rate. Laboratory streams in which cultures of Sphaerotilus were maintained were used to establish some relationships between snail growth and snail biomass. The utilization of leaves by snails was investigated by placing snails in packets

containing different species of leaves and suspending them in the stream for varying periods of time.

METHODS AND MATERIALS

Experimental Facilities

Berry Creek, which has been described in detail by Warren et al. (1964), is a typical, small woodland stream with an even gradient and rubble bottom with regularly interspersed riffles and pools. A 1500 foot section of the stream has been brought under complete flow control by means of a diversion dam and a bypass channel. The lower portion of the controlled section of the stream has been divided into four experimental sections, each consisting of a riffle and a pool (Figure 1). Screen panels (32 meshes per inch) inserted into special screen boxes prevented the movement of all but the very small stream organisms and most of the particulate organic matter from one section to another. The experimental sections were numbered consecutively I, II, III, and IV, proceeding downstream. The sections differed in total area, but the riffle-pool relationship remained reasonably constant (Table 1). Part of the 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. For this reason, Sections II and IV received more sunlight and less leaf fall than did the other sections. The most important differences between the sections, however,

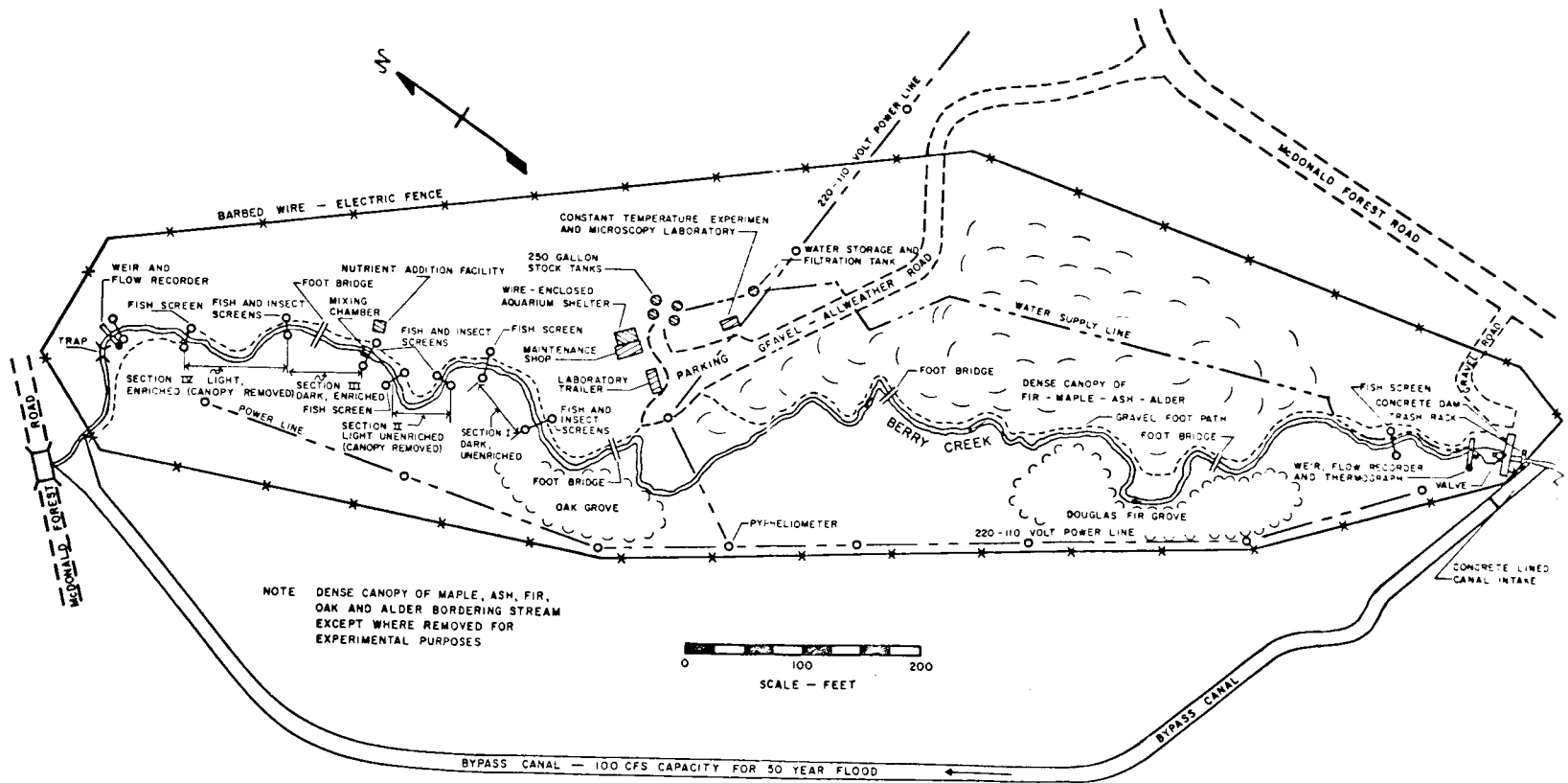


Figure 1. Diagram of Berry Creek Experimental Stream showing research facilities

were those associated with the presence of large amounts of Sphaerotilus resulting from the organic enrichment. The enriching solutions were introduced at the upstream end of Section III. Sucrose alone was added from 1960 to 1963. Nitrogen was introduced in 1963 as urea in an attempt to maintain more uniform growths of Sphaerotilus. Concentrations of sucrose and urea were maintained in the stream at 4.0 and 0.4 mg/l, respectively.

Table 1. Areas of the experimental sections of Berry Creek in square meters.

Stream type	Experimental section number			
	I	II	III	IV
Riffle	21.5	19.1	42.2	41.8
Pool	21.5	13.0	16.5	10.4
Total	43.0	32.1	58.7	52.2

Leaf fall from trees along the stream was an important source of allochthonous material entering the stream. The leaves were mainly from red alder (Alnus rubra), big leaf maple (Acer macrophyllum), Oregon white oak (Quercus garryana), black cottonwood (Populus trichocarpa), and Oregon ash (Fraxinus latifolia).

Stream flow through the controlled section was maintained at $0.5 \text{ ft}^3/\text{sec}$ except during periods of low summer flow when the entire discharge of Berry Creek was utilized (Figure 2). A recording thermometer was used to obtain records of water temperature

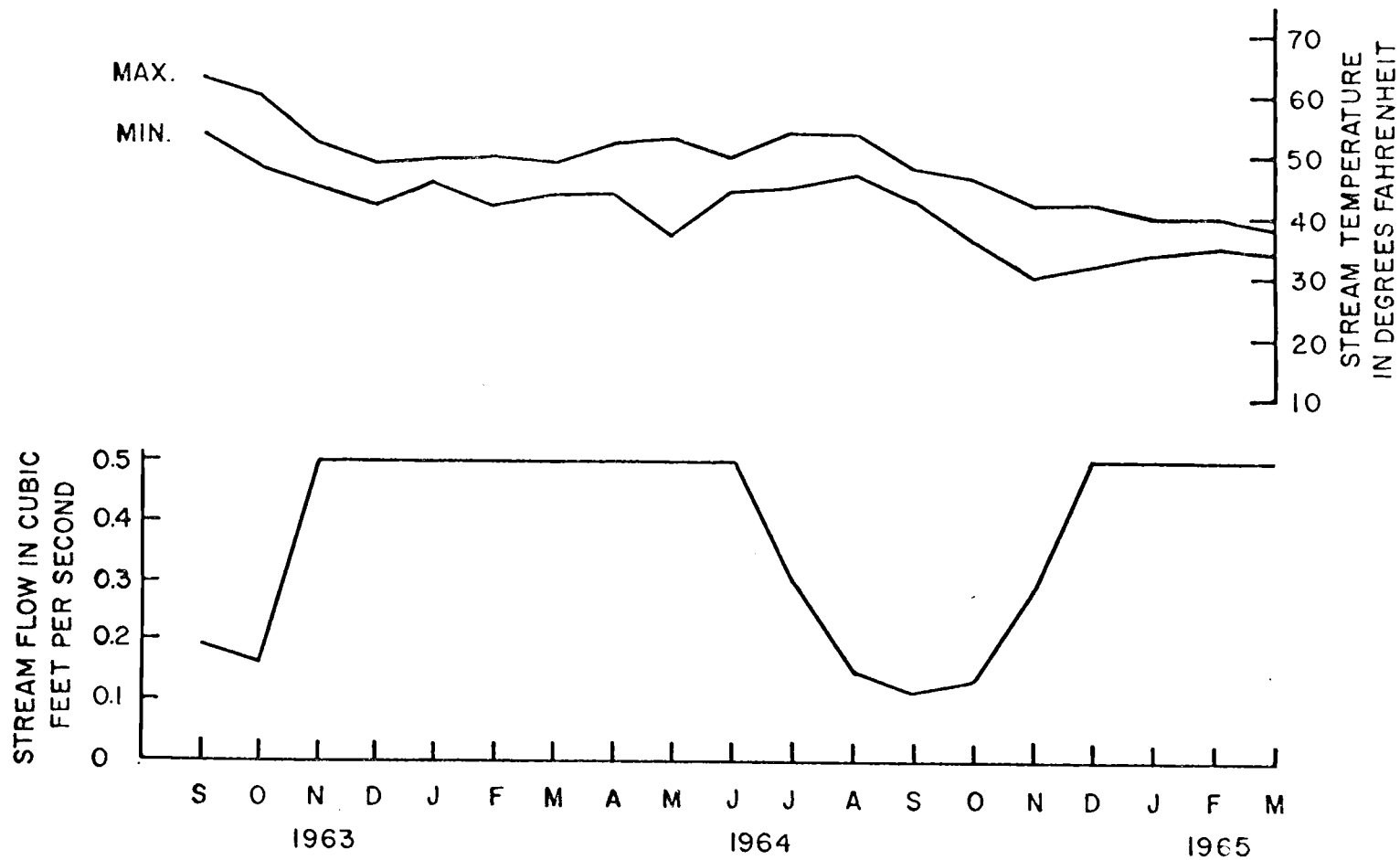


Figure 2. Stream flow and maximum and minimum stream temperature in the controlled section of Berry Creek.

during the course of study (Figure 2). Periodic analyses of chemical constituents of the stream water were made by the U. S. Geological Survey and these are summarized in Table 2 for different seasonal periods during 1963 and 1964.

Sampling Procedures

A device was used for collecting samples of snails that enclosed a 0.26 m^2 area of riffle bottom. The rectangular frame of the sampler was fitted tightly to the stream bottom by means of an attached foam-rubber gasket. The sides and upstream end of the sampler were covered with plastic screen and the downstream end opened into a nylon screen bag. The device made it possible to sample the entire benthic fauna. Removal of the snails was essentially complete. Most of the snails were picked from the rubble which was removed for scrubbing. The remaining snails were taken from the gravel and sand which was removed from the stream bottom and placed in white porcelain pans. Although some of the snails of sizes less than a few millimeters were undoubtedly left on the stream bottom, their biomass relative to the total biomass of snails removed was probably very small. The snails from each sample were held in containers with circulating water for five hours. This period was sufficient to insure that the snails opened their opercula and released any sand or other debris which could cause error in determining

Table 2. Water quality summary for the Berry Creek experimental stream during the Summer and Fall of 1962 and Winter and Spring, 1963.

Characteristic or constituent	Summer	Fall	Winter	Spring
Specific conductance (micromhos at 25 ° C)	137	132	91	84
pH	7.8	7.5	7.5	7.3
Color	5	10	10	15
Dissolved solids ppm	93	92	71	71
Hardness ppm as CaCO ₃	56	54	36	34
Silica (SiO ₂) ppm	26	26	22	20
Iron (Fe) ppm	0.23	0.08	0.13	--
Calcium (Ca) ppm	14	14	9.0	8.5
Magnesium (Mg) ppm	5.1	4.5	3.4	3.3
Sodium (Na) ppm	6.9	6.6	4.4	4.2
Potassium (K) ppm	0.6	0.5	0.1	0.2
Bicarbonate (HCO ₃) ppm	78	74	50	47
Carbonate (CO ₃) ppm	0	0	0	0
Sulfate (SO ₄) ppm	1.2	1.2	1.6	1.4
Chloride (Cl) ppm	4.5	5.0	3.5	3.5
Fluoride (F) ppm	0.1	0.0	0.1	0.1
Nitrate (NO ₃) ppm	0.2	0.0	0.1	0.1
Phosphate (PO ₄) ppm	0.04	0.06	0.03	0.3

their weight. Dead snails, which could be distinguished by their red-colored shell and chalky-white nacre, were removed from the samples.

Size Grouping and Measurement of Snails

Preliminary sampling indicated that the snails in the experimental sections could conveniently be separated into five different size-groups. The size range of individuals in the largest size-group was greater than in the smaller size-groups, but because of the paucity of numbers of large snails further size grouping was not considered feasible. The diameter of the shell at the first whorl dictated into which of the five size-groups a snail was placed. Shell-length measurements are used in studies of some terrestrial snails (Strandine, 1950); however, they could not be used in this study because of spire erosion that is common among these snails.

With the exception of the snails recruited during the summer of 1964, all other groups of snails moved from one size-group to the next larger size-group during the course of the study. It was, therefore, convenient to identify the size-groups according to the year in which the young were hatched. The size-groups in descending order of size were considered to be the 1959, 1960, 1961, 1962, 1963 and 1964 year-classes. Only five size-groups were recognizable during the study since the largest and next largest size-groups tended to

merge into one group at the time the youngest snails began to appear in the samples. Grouping according to year-class remained subjective since it was not possible to age the snails. An unknown number of year-classes may have been included in the group identified as the 1959 year-class.

Each group of snails was dried in an oven at 70° C. Constant dry weights were obtained within 72 hours. Weights of the groups of snails were obtained using an Ohaus or Mettler balance, both sensitive to 0.01 grams. In weighing individual snails a Mettler model P balance sensitive to 0.001 grams was employed.

Estimation of Biomass, Growth Rate, and Production

Snail samples were usually taken during the first week of each month. There were often differences, however, in the numbers of days between sampling dates. In order to express snail biomass on a monthly basis the total dry weight of snails in each year-class was plotted on calendar paper against the date of sampling. Curves were then fitted to these points. The biomass values at the beginning and end of each month were then taken from the curves and used in computing an arithmetic mean biomass value for snails during that monthly period. The mean snail weights were obtained by dividing the total monthly biomass of snails of a given year-class by the number of snails within that year-class. These were also plotted

on calendar paper for each sample date. Values taken from curves fitted to these data were used to represent the mean weights of the snails on the first and last day of each month.

Monthly growth rates for the different year-classes were computed using the values determined graphically from the curves described above. The mean weight of the snails at the beginning of the month was subtracted from the mean weight at the end of the month and this value was divided by the average of the two mean weights. Growth rates could then be expressed as milligrams of growth per gram of snail per month.

Snail production was estimated by multiplying values of snail growth rate by the mean biomass values for each year-class in each experimental section during each sampling interval. Production in this sense is consistent with the definition of production given by Ricker (1958) as "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."

For purposes of determining if important differences resulted from the subjective grouping of snails, all of the snails collected from Section III during August and November, 1964, were weighed separately. Numbers of snails were plotted against snail weight at one milligram intervals. The distribution of numbers versus weight indicated that rather definite modes existed that were most clearly

defined for the smaller snails. Although the relationship was undoubtedly biased somewhat by differential spire erosion, the modes were believed to be reasonably representative of the different year-classes of snails. Median weights were computed for the different weight-frequency distributions for comparison with the graphically obtained mean weights of the different year-classes in the August and November samples. The results of the comparison of the two methods are treated in the subsequent section (Results and Interpretation).

Estimation of Food Consumption

Estimates of the food consumed by all the snails in the experimental sections were based on a comparison of the growth rate of the 1961 year-class with the growth rate of like-sized snails kept in aquaria and given different rations of food. Studies of the relationship between food and growth were performed during May and December, 1964.

During the May, 1964, experiment the snails were given a specially prepared food consisting of 20 parts milled alder leaves, 1 part powdered whole milk, 2 parts powdered wheat germ, and 2 parts sodium alginate. The ingredients were blended, then spread into thin sheets and fixed with a solution of calcium chloride. The calcium alginate bound the food making it easier to handle and

minimized food losses through the exchanged water. Freshly deciduated maple leaves were fed during the Fall, 1964 experiment in an effort to more closely approximate the kind of food being consumed by the snails in Berry Creek during this period.

Snails were kept in separate groups of 30 each and fed rations which ranged from below those required for maintenance to all the snails would consume. Food was replaced at five-day intervals. Any uneaten food was removed, dried in an oven at 70° C and weighed so that total food consumed could be estimated.

Growth rates of the snails kept in aquaria were computed by dividing values of change in weight for each group during the course of the study by the average weight values at the beginning and end of the experiment and then dividing that quotient by the number of days in the experiment. Rates of food consumption were computed in a like manner by dividing the quantities of food consumed by each group of snails by its average biomass value and by the number of days in the period. Rates of growth and rates of food consumption could then be related graphically on coordinate paper, with the growth rate values situated on the ordinate and the food consumption rates on the abscissa.

The total food consumed by the snails in the stream sections was estimated by multiplying the graphically-obtained daily consumption rate values corresponding to the daily growth rate values of the

snails of the 1961 year-class by the number of days in the monthly sampling interval and in turn by the total biomass of all year-classes present in that section during the sampling interval.

Utilization of Sphaerotilus by Snails

Studies were performed during August and October, 1964, on the ability of snails to utilize Sphaerotilus for growth. Different biomasses of snails of sizes similar to that of the 1961 year-class were stocked in laboratory streams in which growths of Sphaerotilus were maintained. The biomasses of snails added to different streams during the summer and fall experiments ranged from 14 to 334 and 51 to 474 g/m² (wet weight), respectively. The area of each stream was approximately 0.5 m². The snails were confined by screens to an area of approximately 0.2 m².

Enrichment of the laboratory streams with sucrose and urea in concentrations similar to those used in Berry Creek resulted in good growths of Sphaerotilus. Water velocities of approximately 0.5 fps were maintained by electrically-driven paddlewheels.

Snails were removed and weighed after 21 days and production values for each group were determined directly from measurements of changes of snail biomass since there was no mortality during the experimental period.

Utilization of Leaves by Snails

Plastic-screen packets, each containing 30 medium-sized snails along with measured quantities of either alder, maple or oak leaves, were suspended during July and August, 1964 in the pools of unenriched Section I and enriched Section III for the purpose of determining which of these major leaf types entering Berry Creek were most readily utilized by the snails. Packets containing only leaves were also suspended in the stream so that the utilization of leaves by organisms other than snails could be evaluated. The packets were removed after periods ranging from 7 to 24 days. The leaves were dried at 70° C and weighed. Comparisons were then made between the dry weights of leaf material remaining and calculated dry weights of fresh leaves added to the packets at the beginning of the experiment.

Caloric Conversion

Dry weight values of the snails and the estimated values of food consumed by the snails were converted into caloric equivalents using caloric values of the different materials obtained through oxygen bomb calorimetry. A Parr semi-micro calorimeter No. 1411 was used for all determinations. The average caloric value of snails was much lower than the average caloric values of other

materials on a dry weight basis (Table 3). The snail values are low because the shells comprise approximately 86 percent of the dry weight of the snail.

Table 3. Average caloric values per gram dry weight of experimental materials.

Material	Kilocalories per gram dry weight
Snails	0.910
Alginate preparation	4.352
Maple leaves	4.585
<u>Sphaerotilus natans</u>	4.268

Converting the weights into caloric equivalents permitted biomass and production values to be expressed in kilocalories per square meter of riffle area (kcal/m^2) and rates of growth of snails in the stream to be expressed in calories per kilocalorie of snail biomass per month (cal/kcal/month). Results of aquarium studies on rates of growth and food consumption are expressed in calories per kilocalorie of biomass per day (cal/kcal/day).

RESULTS AND INTERPRETATION

Growth Rates

Values used in estimating the growth rates of the different year-classes of snails were obtained graphically from the growth curves for each year-class sampled between 1963 and 1965 (Figure 3). The curves were fitted to the points by eye giving more weight to the values represented by larger numbers of snails. It may be noted that the curves for the 1960 year-class were fitted to values which, during a part of the study, were indistinguishable from values for the 1959 year-class. It can be seen, also, that the 1964 year-class was recruited somewhat earlier in Sections II and IV than in Sections I and III. The reason for this is not understood, but it can be hypothesized that earlier spawning in the sections from which the leaf canopy had been removed may have been related to differences in the photoperiod or in the intensities of light reaching these sections. Teal (1957) has cited the results of Jenner (1951) which indicated that the pulmonate snail, Physa, spawned only after the daily photoperiod was greater than 13 hours.

Weight-frequency plots for the samples obtained from Section III during August and November (Figures 4 and 5) indicated that rather different modes existed and that these could reasonably be

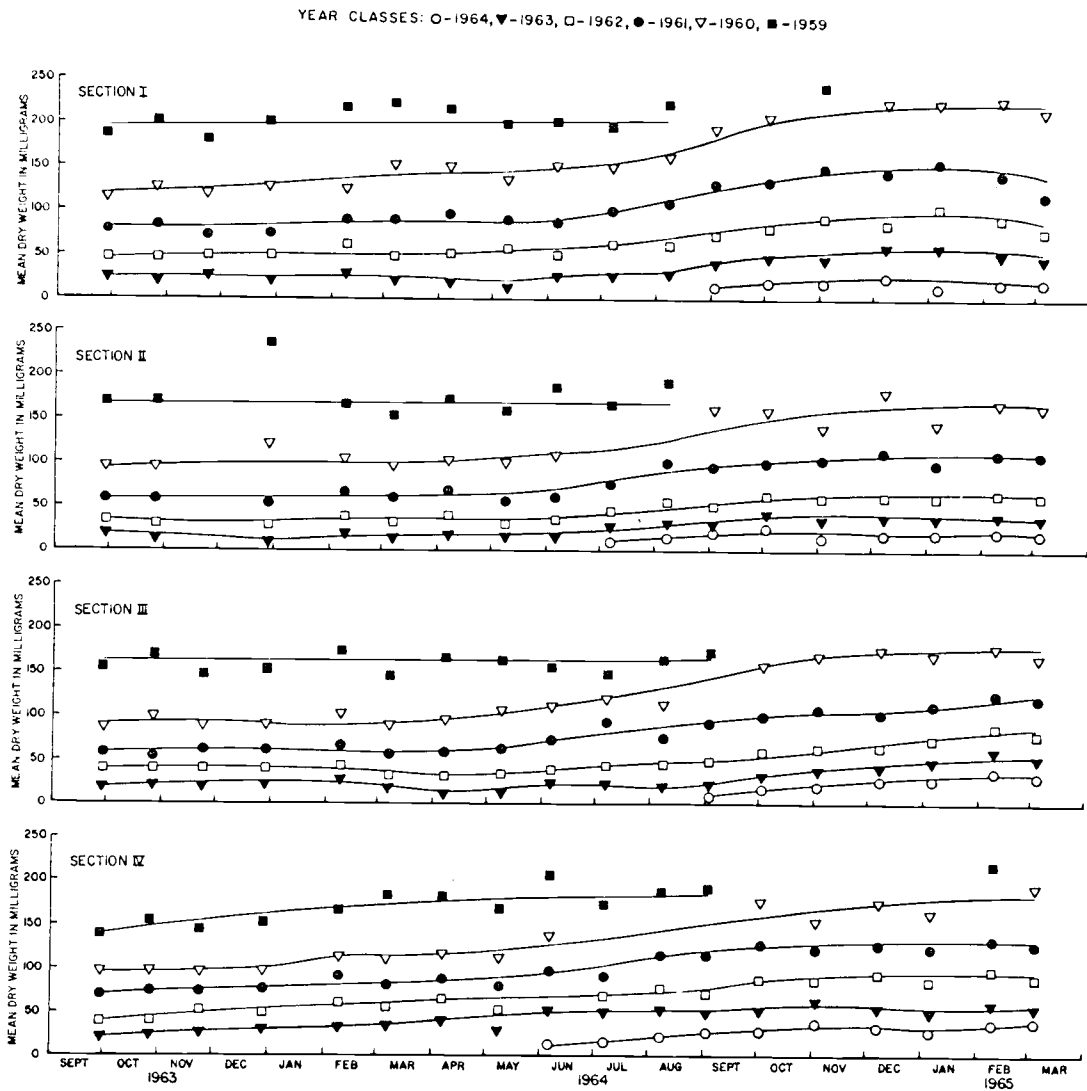


Figure 3. Curves relating values of mean snail weight, in milligrams, to sampling dates. Values taken from the curves were used to compute monthly growth rates for each year class of snails in each experimental section.

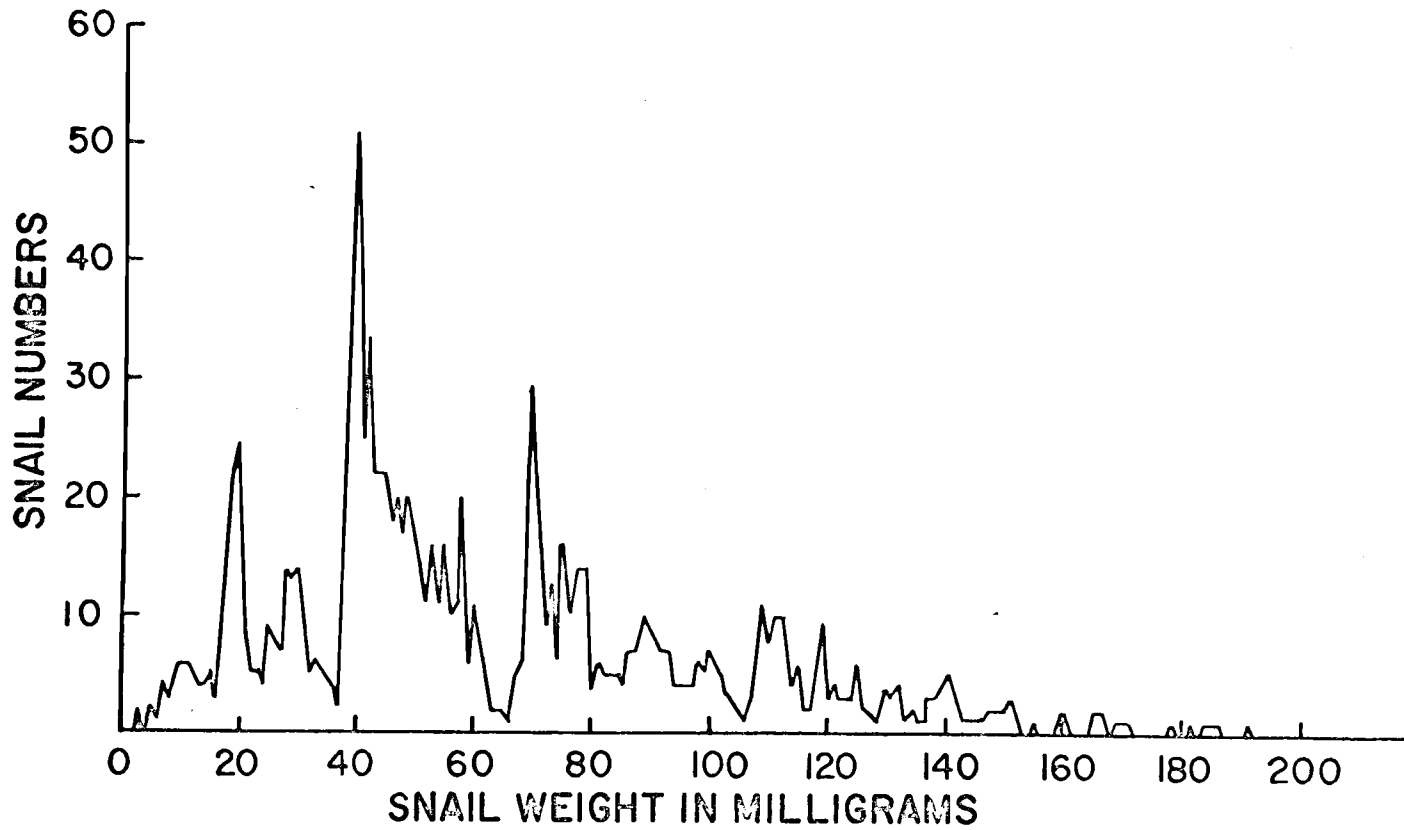


Figure 4. Weight-frequency of all snails in biomass sample taken from section III, during August, 1964.

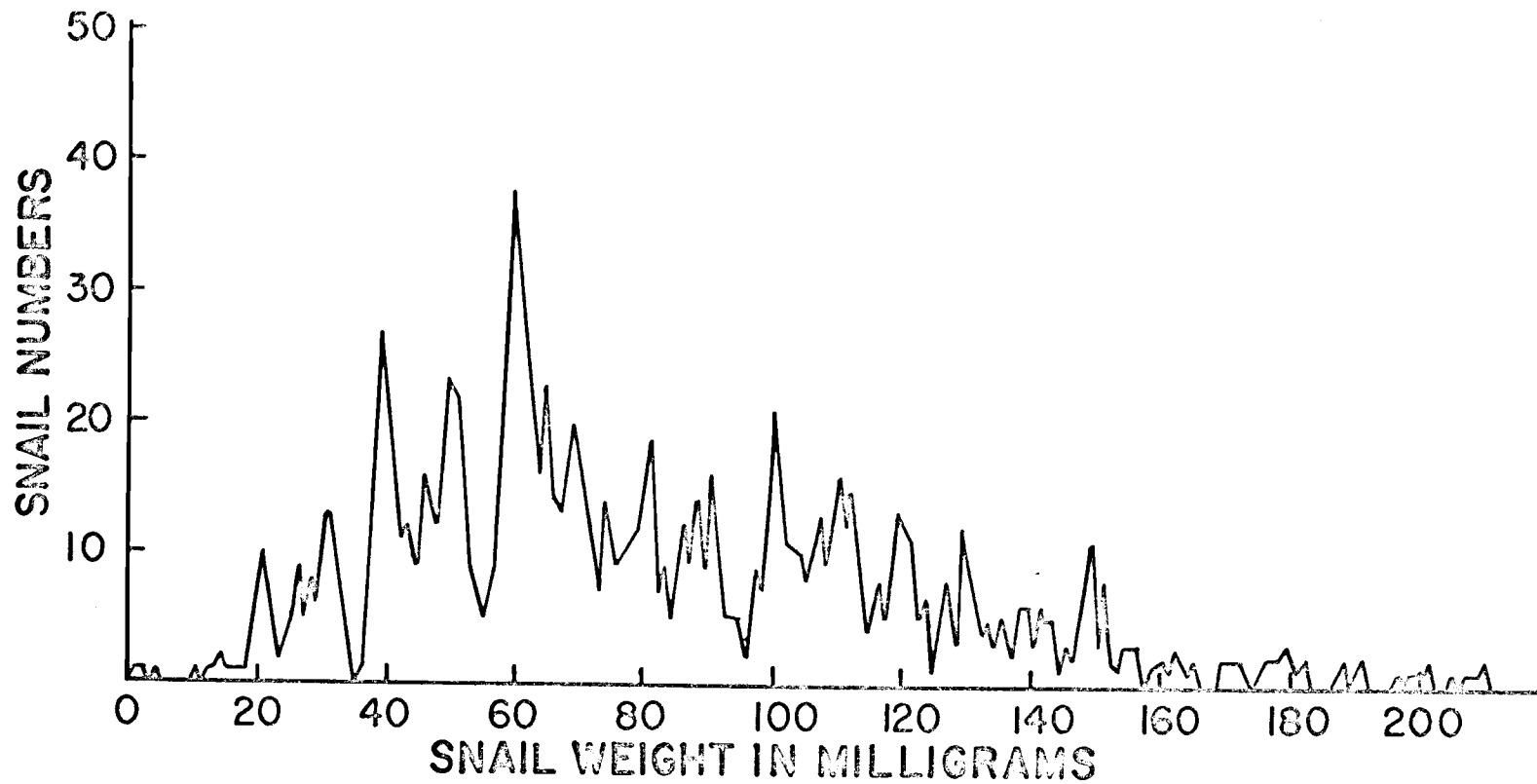


Figure 5. Weight-frequency of all snails in biomass sample taken from section III, during November, 1964.

related to the different year-classes. For the August, 1964 sample the sizes of individually weighed snails that were considered to represent the 1964, 1963, 1962, 1961, 1960, and 1959 year-classes ranged approximately from 0-15, 16-37, 38-65, 66-105, and 106-190 milligrams, respectively. The respective ranges of sizes for the same year-classes represented in the November sample were approximately from 0-35, 36-55, 56-95, 96-145, and 146-210 milligrams.

A comparison of the mean weights of snails of the 1963, 1962, 1961, and 1960 year-classes obtained by subjective sorting with median weight values obtained for the different weight-frequency distributions is presented in Table 4. The 1964 and 1959 year-classes could not be compared since the 1964 year-class had not yet appeared in the August sample and the 1959 year-class had merged with the 1960 year-class by the time the November sample was taken. Assuming that gross errors did not occur in relating the weight-frequency distributions to the different year-classes, any differences in the values obtained by the two methods could reasonably be attributed to error resulting from the comparison of mean and median values and to experimental error. Since the values obtained using the two methods were quite similar it was concluded that for the purposes intended in the study the subjective size grouping by shell diameter was adequate.

Table 4. Comparison of mean snail weights taken from growth curves with median weights obtained for the weight-frequency distributions of snails collected from Section III on August and November, 1964. Values are in milligrams dry weight.

Year-class	Growth-curve August-November		Weight-frequency August-November	
1963	22	40	22	45
1962	43	65	47	71
1961	76	108	82	113
1960	132	169	125	164

Mean monthly growth rate values were computed for each year-class for each experimental section (Tables 5 to 10). The growth rate values for any given year-class varied considerably from month to month, but in general they were highest during the summer months for all year-classes. It can also be observed from these tables that the growth rates of the various year-classes were not strikingly different between sections.

Biomass

The quantities of snails collected from a given section varied between monthly sampling intervals, suggesting that the snails were not always evenly distributed throughout the riffle areas. The fitting of curves to the sample biomass values to permit the expression of biomass on a monthly basis resulted in a general smoothing of

Table 5. Monthly growth rate, biomass, and production of snails of the 1964 year-class.

Months	Section I			Section II			Section III			Section IV		
	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)
Jun 1964										400	2.28	0.91
Jul				400	3.22	1.29				286	6.65	1.90
Aug				181	7.98	1.44				181	22.24	4.02
Sep	375	3.01	1.13	200	6.83	1.37	467	2.35	1.10	222	25.56	5.67
Oct	190	3.47	1.79	22	10.68	0.24	273	4.27	1.17	258	15.41	3.98
Nov	83	2.70	0.22	-117	12.26	-1.43	148	14.01	2.07	31	10.33	0.32
Dec	0	1.89	0.00	0	5.15	0.00	161	16.00	2.58	-63	6.02	-0.38
Jan 1965	0	1.02	0.00	95	3.85	0.37	57	12.50	0.71	47	6.30	0.30
Feb	-139	0.47	-0.20	-47	6.41	-0.30	27	21.43	0.58	130	5.88	0.76
Totals			2.94			2.98			8.21			17.48
Means		2.08			7.04			11.75			11.17	

Table 6. Monthly growth rate, biomass, and production of snails of the 1963 year-class. Annual production and annual mean biomass values are for the period March, 1964 through February, 1965. Total production and total mean biomass are for the 17 month period October, 1963 through February, 1965.

Months	Section I			Section II			Section III			Section IV		
	Growth Rate (cal/kcal/mo.)	Mean Biomass (kcal/m ²)	Production (kcal/m ²)	Growth Rate (cal/kcal/mo.)	Mean Biomass (kcal/m ²)	Production (kcal/m ²)	Growth Rate (cal/kcal/mo.)	Mean Biomass (kcal/m ²)	Production (kcal/m ²)	Growth Rate (cal/kcal/mo.)	Mean Biomass (kcal/m ²)	Production (kcal/m ²)
Oct 1963	43	1.47	0.06	-54	5.60	-0.30	167	24.65	4.12	174	4.10	0.71
Nov	0	1.23	0.00	-250	3.85	-0.96	38	26.79	1.02	113	2.87	0.32
Dec	0	0.88	0.00	-154	3.01	-0.46	0	40.44	0.00	69	4.73	0.33
Jan 1964	41	0.70	0.03	154	2.31	0.36	-38	34.84	-1.32	81	9.45	0.77
Feb	0	0.88	0.00	194	1.40	0.27	-213	17.16	-3.65	45	10.15	0.46
Mar	-83	1.75	-0.15	0	1.58	0.00	211	4.90	1.03	137	18.56	2.54
Apr	-140	3.68	-0.51	154	3.50	0.54	0	1.75	0.00	120	24.69	2.96
May	140	3.33	0.47	54	3.96	0.21	256	5.08	1.30	87	31.16	2.71
Jun	264	2.98	0.79	146	3.78	0.55	44	11.21	0.49	41	38.87	1.59
Jul	154	3.85	0.59	204	13.13	2.68	-44	14.78	-0.65	0	26.79	0.00
Aug	182	9.10	1.29	230	23.99	5.52	167	20.20	3.37	20	19.26	0.39
Sep	112	13.13	1.47	111	18.91	2.10	295	33.79	9.97	75	29.76	2.23
Oct	101	12.26	1.24	51	19.08	0.97	182	38.52	7.01	53	26.79	1.42
Nov	56	11.03	0.62	25	18.21	0.46	133	43.59	5.80	-35	16.98	-0.59
Dec	38	7.00	0.27	0	6.48	0.00	91	36.77	3.35	-55	21.92	-1.21
Jan 1965	0	3.33	0.00	-24	5.25	-0.13	90	28.19	2.54	19	20.34	0.39
Feb	-54	3.33	-0.18	-51	9.45	-0.48	34	38.34	1.30	54	21.53	1.16
Totals												
Annual			5.90			12.42			35.51			13.59
17 mos.			5.99			11.33			35.68			16.18
Means												
Annual		6.22			10.60			23.08			24.71	
17 mos.		4.69			8.43			24.76			19.28	

Table 7. Monthly growth rate, biomass, and production of snails of the 1962 year-class. Annual production and annual mean biomass values are for the period March, 1964 through February, 1965. Total production and total mean biomass are for the 17 month period October, 1963 through February, 1965.

Months	Section I			Section II			Section III			Section IV		
	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)
Oct 1963	- 20	5.25	-0.11	- 61	8.05	-0.49	25	53.22	1.33	118	14.01	1.74
Nov	- 21	3.15	-0.07	- 32	1.40	-0.04	24	45.52	1.09	105	13.83	1.45
Dec	0	1.93	0.00	32	1.23	0.04	- 49	38.52	- 1.89	58	12.78	0.74
Jan 1964	41	2.63	0.11	61	2.80	0.17	- 25	14.88	- 0.37	73	18.91	1.38
Feb	39	4.73	0.18	29	3.68	0.11	- 26	19.78	- 0.51	51	21.01	1.07
Mar	19	12.78	0.24	0	2.63	0.00	-141	33.79	- 4.76	49	25.39	1.24
Apr	0	16.46	0.00	- 29	5.43	-0.16	29	51.47	1.49	31	28.54	0.88
May	55	10.33	0.57	57	5.95	0.34	82	54.10	4.44	15	99.44	1.49
Jun	69	11.38	0.79	105	4.38	0.46	169	57.60	9.73	22	154.94	3.41
Jul	125	11.38	1.42	140	16.28	2.28	65	70.21	4.56	36	130.78	4.71
Aug	111	17.16	1.90	122	26.96	3.29	41	145.31	5.96	69	100.14	6.91
Sep	88	21.88	1.93	108	23.29	2.51	95	167.72	15.93	101	98.92	9.99
Oct	81	17.68	1.43	67	21.88	1.47	134	117.30	15.72	58	88.41	5.13
Nov	54	15.58	0.84	16	17.16	0.27	105	132.71	13.93	44	52.52	2.31
Dec	21	8.75	0.18	31	7.53	0.23	95	103.65	9.85	11	53.22	0.59
Jan 1965	0	4.38	0.00	0	11.38	0.00	75	61.98	4.65	0	53.57	0.00
Feb	- 75	5.60	-0.42	- 16	16.11	-0.26	58	80.01	4.64	11	64.60	0.71
Totals												
Annual			8.88			10.43			86.14			37.37
17 mos.			8.99			10.22			85.79			43.75
Means												
Annual		12.77			13.24			89.64			79.22	
17 mos.		10.06			10.35			73.39			60.66	

Table 8. Monthly growth rate, biomass, and production of snails of the 1961 year-class. Annual production and annual mean biomass values are for the period March, 1964 through February, 1965. Total production and total mean biomass are for the 17 month period October, 1963 through February, 1965.

Months	Section I			Section II			Section III			Section IV		
	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)
	Oct 1963	- 13	9.28	-0.12	16	11.04	0.17	17	41.32	0.70	42	83.34
Nov	13	5.43	0.07	- 16	7.88	-0.13	17	54.27	0.92	40	42.19	1.69
Dec	25	2.63	0.07	- 16	16.11	-0.26	- 17	45.52	- 0.77	20	19.08	0.38
Jan 1964	12	4.38	0.05	0	18.56	0.00	0	38.69	0.00	32	62.85	2.01
Feb	24	8.58	0.21	16	12.08	0.19	- 34	65.30	- 2.22	25	109.42	2.74
Mar	12	16.46	0.20	16	5.25	0.08	34	81.94	2.79	24	127.80	3.07
Apr	- 12	19.78	-0.24	16	5.25	0.08	49	99.09	4.86	35	132.15	4.63
May	35	13.31	0.47	62	5.08	0.31	147	99.62	14.64	56	80.54	4.51
Jun	109	11.73	1.28	86	5.95	0.51	104	87.36	9.09	83	71.78	5.96
Jul	117	11.20	1.31	96	14.88	1.43	83	75.11	6.23	95	208.31	19.79
Aug	129	22.06	2.85	109	19.08	2.08	22	197.66	4.35	66	273.12	18.03
Sep	78	27.84	2.17	60	18.73	1.12	115	255.61	29.40	46	214.64	9.87
Oct	58	20.48	1.19	38	16.98	0.65	39	197.84	7.72	24	226.88	5.45
Nov	35	34.84	1.22	9	9.98	0.09	28	196.61	5.51	12	200.28	2.40
Dec	27	31.51	0.85	18	4.03	0.07	27	123.08	3.32	19	140.76	2.67
Jan 1965	- 6	8.75	-0.05	9	7.18	0.06	53	73.53	3.90	8	119.05	0.95
Feb	- 48	7.35	-0.35	- 9	12.96	-0.12	66	106.80	7.05	- 8	201.34	-1.61
Totals												
Annual			10.90			6.36			98.86			75.72
17 mos.			11.18			6.33			97.49			86.04
Means												
Annual		18.77			10.44			132.84			166.38	
17 mos.		15.03			11.23			108.19			136.08	

Table 9. Monthly growth rate, biomass, and production of snails of the 1960 year-class. Annual production and annual mean biomass values are for the period March, 1964 through February, 1965. Total production and total mean biomass are for the 17 month period October, 1963 through February, 1965.

Months	Section I			Section II			Section III			Section IV		
	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)
Oct 1963	16	18.56	0.30	31	22.06	0.68	10	80.54	0.81	10	126.40	1.26
Nov	8	7.88	0.06	10	1.40	0.01	10	63.03	0.63	10	127.63	1.28
Dec	15	4.55	0.07	20	1.75	0.04	-43	63.03	-2.71	30	84.38	2.53
Jan 1964	22	4.73	0.10	-10	12.61	-0.13	-11	65.65	-0.72	72	72.13	5.19
Feb	15	8.40	0.13	-10	16.63	-0.17	11	85.78	0.94	45	99.27	4.47
Mar	14	16.28	0.23	20	7.00	0.14	54	108.55	5.86	22	134.81	2.97
Apr	14	16.98	0.24	39	5.25	0.20	71	127.80	9.07	43	117.30	5.04
May	28	11.73	0.33	38	5.25	0.20	75	87.89	6.59	41	70.03	2.87
Jun	33	12.61	0.42	36	5.78	0.21	86	115.55	9.94	47	71.78	3.37
Jul	75	15.06	1.13	76	15.41	1.17	80	143.39	11.47	52	169.82	8.83
Aug	98	26.26	2.57	93	19.26	1.79	94	187.50	17.63	70	232.85	16.30
Sep	94	28.36	2.67	85	18.73	1.59	92	222.35	20.46	59	212.72	12.55
Oct	57	20.31	1.16	59	16.63	0.98	73	196.96	14.38	44	226.20	9.95
Nov	23	25.91	0.60	32	10.15	0.32	23	198.01	4.55	36	199.93	7.20
Dec	18	21.01	0.38	25	4.90	0.12	17	123.60	2.10	29	140.76	4.08
Jan 1965	9	7.53	0.07	12	7.53	0.09	5	73.53	0.37	28	118.53	3.32
Feb	0	8.23	0.00	0	12.08	0.00	11	106.27	1.17	6	176.48	1.06
Totals												
Annual			9.80			6.81			103.59			77.54
17 mos.			10.46			7.24			102.54			92.27
Means												
Annual		17.52			10.66			140.95			155.93	
17 mos.		14.96			10.72			120.55			140.05	

Table 10. Monthly growth rate, biomass, and production of snails of the 1959 year-class.

Months	Section I			Section II			Section III			Section IV		
	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)	Growth Rate (cal/ kcal/ mo.)	Mean Biomass (kcal/ m ²)	Production (kcal/ m ²)
	Oct 1963	5	29.76	0.15	0.00	14.18	0.00	0	9.98	0.00	56	16.28
Nov	0	10.85	0.00	0.00	0.53	0.00	0	11.73	0.00	47	10.50	0.49
Dec	5	3.85	0.02	0.00	1.05	0.00	0	16.11	0.00	45	15.76	0.71
Jan 1964	5	6.65	0.03	0.00	16.46	0.00	0	16.63	0.00	31	23.46	0.73
Feb	0	11.91	0.00	0.00	22.06	0.00	0	17.16	0.00	30	28.89	0.87
Mar	5	15.58	0.13	0.00	8.05	0.00	0	16.98	0.00	17	36.24	0.62
Apr	5	17.33	0.09	0.00	4.90	0.00	6	36.77	0.22	17	36.07	0.61
May	0	14.88	0.00	0.00	7.70	0.00	6	27.29	0.22	17	21.36	0.36
Jun	5	9.63	0.06	0.00	13.13	0.00	6	26.26	0.16	0	16.98	0.00
Jul	5	8.05	0.04	0.00	12.08	0.00	12	24.51	0.29	6	21.88	0.13
Aug							12	19.26	0.23	0	20.48	0.00
Totals			0.52			0.00			1.12			5.43
Means		12.84			10.01			20.23			22.53	

values taken from the curves. Biomass values for a given year-class (Tables 5 to 10) were generally higher during the summer and fall months. Growth was undoubtedly the most important factor governing biomass increase, but in addition there were probably increases in biomass per unit area; resulting from a return to the riffles of snails that had burrowed into leaves and other debris along the edge of the riffles during the colder winter months and as a result of decreases in riffle area with reductions of stream discharge during the summer months. The most striking differences in snail biomass were those associated with enrichment. The mean biomasses in the enriched sections were many-fold greater than those of the unenriched sections.

Production

Monthly snail production values were estimated for each year-class for each experimental section and are presented in Tables 5 to 10 along with the monthly values of growth rate and mean biomass used in the computation. Production values for the period March, 1963 through February, 1964 have been summarized in Table 11 to show the contribution to total annual production by the different year-classes in each experimental section. The values obtained during the last 12 months of the study were used because the experience gained in sampling and size grouping the snails made these values

more reliable.

Table 11. Production by each year-class and total production for unenriched Sections I and II and for enriched Sections III and IV during the period March, 1964 through February, 1965. Values are in kilocalories per square meter.

Year-class	Section			
	I	II	III	IV
1964	2.94	2.98	8.21	17.48
1963	5.90	12.42	35.51	13.59
1962	8.88	10.43	86.14	37.37
1961	10.90	6.36	98.86	75.72
1960	9.80	6.81	103.59	77.54
1959	0.52	0.00	1.12	5.43
Total	38.94	39.00	333.43	227.13

Annual production values in unenriched Sections I and II were very similar. Most of the production in Section I was distributed among the older age-groups, whereas in Section II most of the production was by the younger snails. The reason for this difference is not known. Liverworts, mosses and algae were more abundant in sunlit Section II than in Section I and these may have created a more favorable habitat for the younger snails. Annual production in the enriched sections was approximately seven-fold greater than that in the unenriched sections. The greater production in Section III than in Section IV can probably be attributed to the greater abundance of food. Larger quantities of leaves entered Section III which provided

an energy source additional to that made available by the Sphaerotilus. In both enriched sections the greatest production was from the 1960 year-class. These snails were recruited during the summer of the year in which enrichment was first introduced into the experimental stream.

Snail production was higher during the period from October, 1964 through February, 1965 than during the same period in 1963 and 1964 for all year-classes of snails for which the comparison could be made. For purposes of comparing production during these periods, production values taken from Tables 6 to 9 were summarized and expressed as means for the unenriched and for the enriched section (Table 12). The proportional increases in production were different between the four year-classes during the latter five-month period. In general, however, production in the unenriched sections increased approximately three-fold, whereas in the enriched sections the increase was approximately five-fold. Some of the factors which may have influenced these results will be considered in the Discussion.

Table 12. Comparison of mean snail production values for the unenriched sections and for the enriched sections between the periods October, 1963 through February, 1964, and October, 1964 through February, 1965. Values are in kilocalories per square meter.

Experimental treatment and period	Year-class			
	1960	1961	1962	1963
Unenriched				
Oct. 1963- Mar. 1964	0.54	0.13	-0.50	-0.50
Oct. 1964- Mar. 1965	1.86	1.80	1.87	1.32
Enriched				
Oct. 1963- Mar. 1964	6.84	4.47	3.01	1.38
Oct. 1964- Mar. 1965	24.09	18.68	28.76	10.62

Food Consumption

The growth rates relating to the rates of food consumption for the snails held in aquaria were significantly different for experiments performed in the spring and fall (Figure 6). The efficiency with which the snails converted their food into body tissue during the spring experiment was much greater than during the fall experiment. Differences in the shapes of the two curves can probably be attributed to seasonal or temperature effects, although differences in the kinds of foods given the snails may have influenced the relationships. A

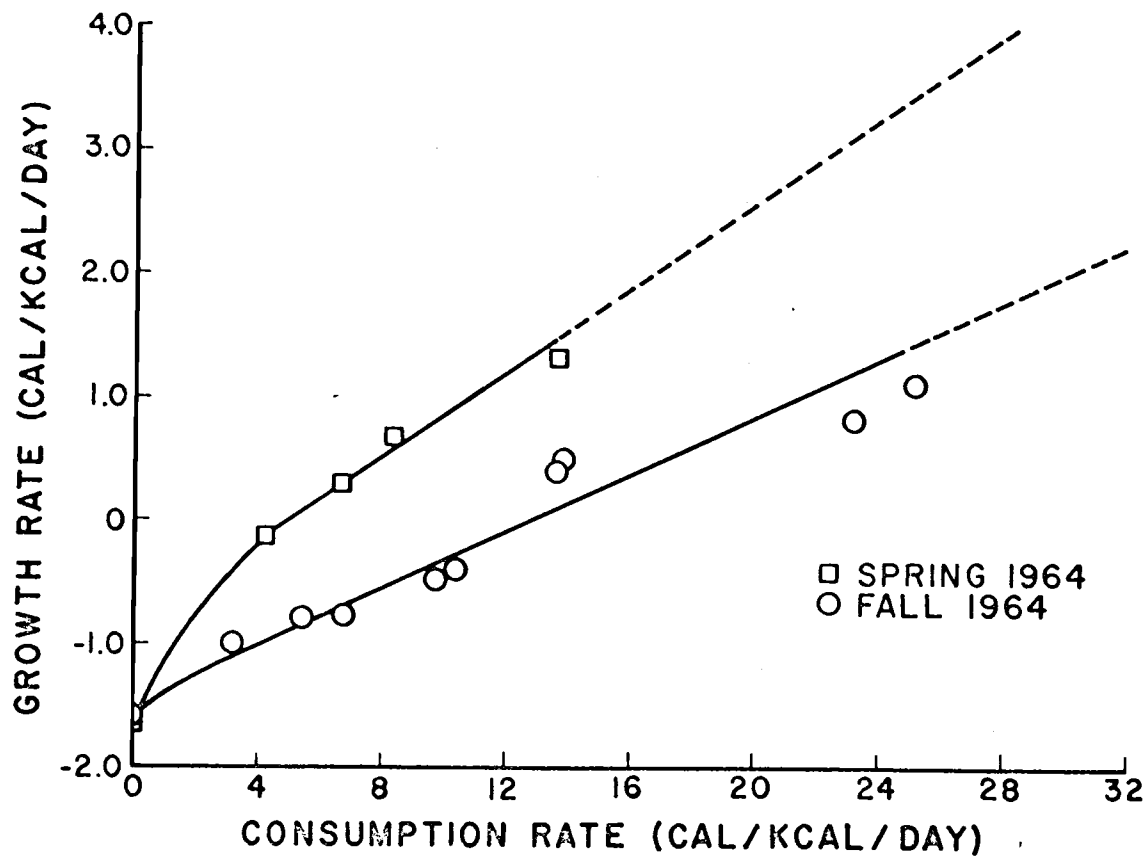


Figure 6. Relationship between rates of food consumption and growth of snails held in aquaria and fed different rations of known caloric value. The spring and fall experiments were carried on for 60 and 42 days, respectively.

comparison between the two experiments of the maintenance requirements of the snails as indicated by consumption rate values which correspond to points of zero growth on the curves shows that more than twice as much energy was required during the fall than during the spring.

Some of the growth rate values computed for the snails of the 1961 year-class in Berry Creek were higher than those obtained for snails of similar sizes for which growth rate-consumption rate relationships were established and it was necessary to extrapolate both curves (Figure 6) in order to obtain estimates of consumption rate for the faster growing stream snails. The greatest amount of extrapolation was required for the spring experiment. The curve established for the spring experiment was used in estimating food consumption for snails during the months of April through August, whereas the curve established during the fall was used for the months of October through March.

Estimates of food consumed by all year-classes of snails in the experimental sections were based upon the rates of consumption by the 1961 year-class. Food consumption rates for large size-groups of animals of a given species are generally considered to be smaller than for the smaller size-groups. If this is true for snails, then lower food consumption rates for snails older than the 1961 year-class would, to some extent, be compensated for by higher

food consumption rates for snails younger than the 1961 year-class. Considering that the curves were not well defined for each year-class during each seasonal period, the estimates of food consumption must be considered approximate. These estimates, however, are sufficient to show the major differences in food consumption between the different sections (Table 13). The values of total food consumption show that food consumption, like production, was approximately seven-fold greater in the enriched sections than in the unenriched sections. However, there was a smaller difference in consumption between enriched Sections III and IV than was noted for production in these sections (Table 11). Factors that may have been related to this difference are considered in the Discussion.

Table 13. Estimated monthly food consumption in kilocalories per square meter by all year-classes of snails in each experimental section for March, 1964 through February, 1965.

Month	Section			
	I	II	III	IV
March	31	13	168	212
April	7	6	143	122
May	36	15	246	150
June	38	22	209	225
July	42	54	214	402
August	67	78	159	352
September	45	44	552	244
October	67	61	396	362
November	59	32	369	230
December	43	16	250	202
January	9	17	217	148
February	0	10	316	145
Total	444	368	3,239	2,794

Utilization of *Sphaerotilus* by Snails

The greater abundance of snails in the enriched sections of Berry Creek provided circumstantial evidence that snails benefited greatly from the presence of *Sphaerotilus*. Basic to the study was the determination of whether snails could, in fact, utilize the bacterium for growth. The results of the two laboratory stream studies (Figure 7) indicated that snail production in the laboratory streams was not greatly different from the production recorded for snails in the enriched sections of Berry Creek during comparable seasons and periods of time. The production of snails in both experiments increased with increases of snail biomass over the entire range of biomasses stocked in the laboratory streams. Somewhat greater production occurred during the fall experiment than during the summer experiment. The reason for this difference is not understood since the growth rates of snails in the enriched sections were even slightly higher during the August experiment than during the October experiment (Table 8).

Utilization of Leaves by Snails

The quantities of leaves consumed by snails were determined from changes in the weights of the leaves while they were suspended in packets with groups of snails in an enriched and an unenriched

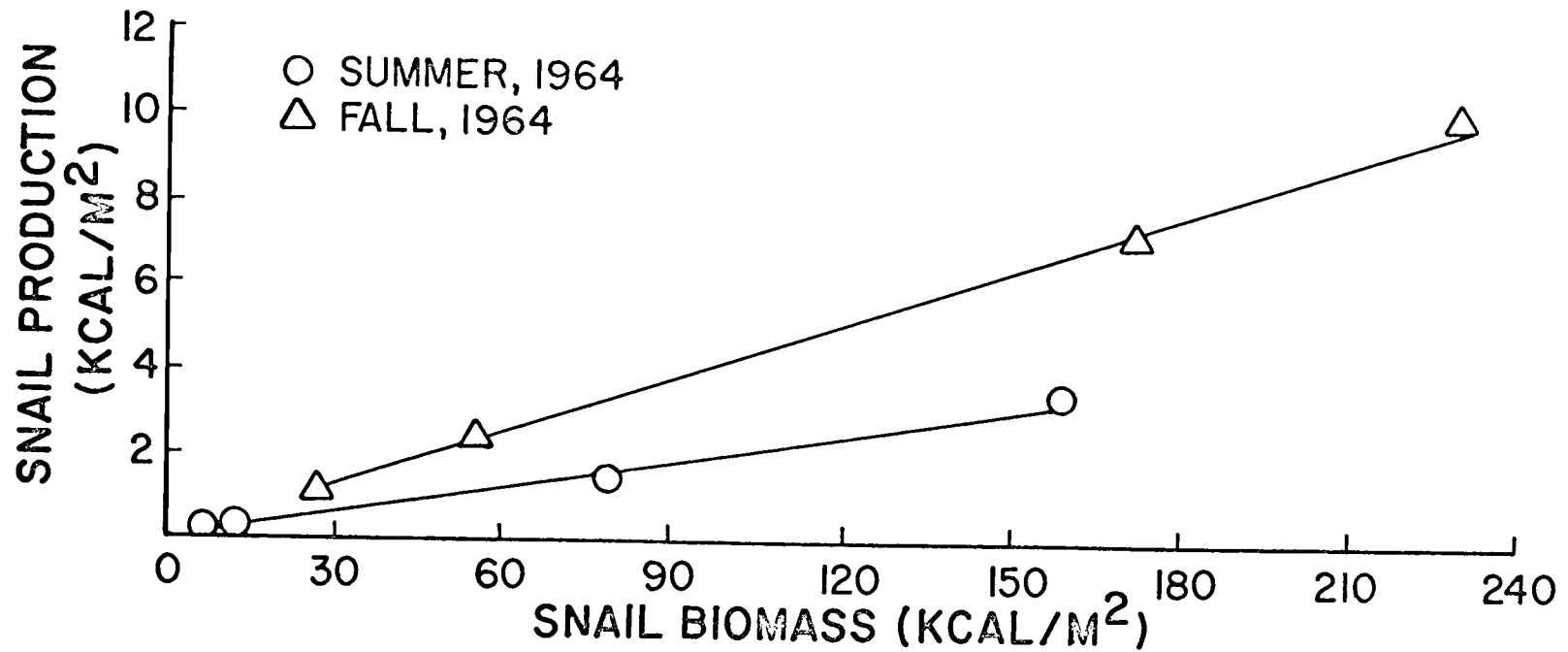


Figure 7. Relationship between snail production and snail biomass in laboratory streams. Enrichment of the streams with sucrose and urea produced heavy growths of Sphaerotilus natans.

section. Consumption values relative to mean snail biomass and to the number of days in the study are presented for the different leaf species (Table 14). Corrections were made for leaf weight losses from causes other than snail consumption by applying weight changes in snail-free packets.

The results of the first experiment indicated that oak leaves were not utilized appreciably by the snails. There were some differences during this experiment between the rates of consumption of alder and maple, but considering the results of the second experiment in which the consumption rates of both species were very similar the differences may be referable to experimental error.

Table 14. Consumption rates of snails on alder, maple, and oak leaves (Experiment I. July, 1964) and alder and maple leaves (Experiment II. August, 1964) suspended in packets in an unenriched section and in an enriched section of Berry Creek. Values are in milligrams dry weight of leaf per gram dry weight of snail per day.

Days suspended	Exp. I			Exp. II				
	10	17	24	7	10	13	15	17
Unenriched								
Alder	2.7	2.3	1.7	2.5	2.3	2.2	2.2	2.2
Maple	3.6	3.6	2.8	2.3	2.3	2.4	2.3	2.3
Oak	0.3	0.0	0.1	-	-	-	-	-
Enriched								
Alder	0.7	1.9	3.2	2.3	2.2	2.3	2.3	2.2
Maple	1.6	4.5	2.4	2.2	2.3	2.2	2.3	2.3
Oak	0.3	0.0	0.0	-	-	-	-	-

A comparison of the rates of utilization of leaves by organisms other than snails between the enriched and the unenriched section indicated that leaves were decomposed more rapidly in the enriched section. This suggests that enrichment may have enhanced decomposition by microorganisms.

The leaf packet studies were of short duration, therefore the results can not be applied to different seasons, but the results do suggest that consideration should be given to species differences when evaluating the contribution of leaf fall to the energy resources of the snails.

DISCUSSION

Results have been presented which show that snail production in enriched sections of Berry Creek was increased approximately seven-fold over that of unenriched sections during the period from March, 1964 through February, 1965. These differences can best be ascribed to the differences in the energy resources of the sections. Growths of Sphaerotilus resulting from enrichment of the stream have provided a source of energy not afforded the snails in the unenriched sections. Methods have not yet been perfected for measuring the production of Sphaerotilus, therefore, the quantitative relationship between snail production and this food source has not been established. Laboratory stream studies (Figure 7) have demonstrated that snails utilize Sphaerotilus for growth and that the substantial increases in snail production in the enriched sections over that of the unenriched sections are attributed to the presence of the bacterium.

Growth rate measurements of snails did not indicate striking differences between enriched and unenriched sections. Large differences, however, have developed between the biomasses of snails in enriched and unenriched sections since enrichment was begun in 1960. This suggests that the increased production in enriched sections may in part be attributed to decreased rates of mortality, about

which little is known. The presence of Sphaerotilus may have resulted in better survival of the very young snails. A great portion of the annual snail production during this study was from the 1960 and 1961 year-classes which probably benefitted greatly during the early years of enrichment.

Annual snail production in Section III was approximately 47 percent greater than in Section IV. It has been suggested that this difference may have resulted from consumption of leaves which were more abundant in Section III than in Section IV. Quantitative estimates of the leaves that fell during the Fall, 1963, and remained on the riffles of Sections I, II, III, and IV amounted to 1652, 756, 1611, and 537 kcal/m², respectively (Davis, 1963). No measurements of leaf fall were made during the Fall, 1964. It is assumed that the relative quantities of leaves entering the different sections during the Fall, 1964, were relatively similar to those quantities estimated for the Fall, 1963. The values for leaf fall during 1963 may be compared with the estimated values of food consumption (Table 13). It may be noted that leaf fall could account for approximately one-half of consumption in Section III and approximately 20 percent of the consumption in Section IV had the leaves been consumed only by snails. If it can be assumed that Sphaerotilus production values were similar between the two enriched sections then it might be inferred that the greater snail production in Section III was in some

way related to the increased quantities of leaves deposited in this section.

The benefit derived by snails from the consumption of decomposer organisms is not known. The bacteria and fungi that decompose leaves may be important direct sources of food for snails or they may act to change the composition of leaves and other organic materials so that they are more easily utilized by the snails. There was a higher rate of decomposition of leaves in the enriched section as indicated from the leaf packet studies which suggests that enrichment may have resulted in greater numbers of decomposer organisms.

It was shown that leaf fall in Section I was more than twice as great as in Section II yet snail production was similar between the two sections. The estimated values of food consumption were similar in both sections (Table 13). These results would suggest either that leaves were utilized proportionately less in Section I than in Section II or that snails in Section II, which received more insolation, derived a larger part of their energy requirements from algal production. Reese (1966), in a study of the physiological ecology and structure of benthic communities in Berry Creek during 1964 and 1965, has shown that, except for Section II during April, June, July, August, and September, the ratios of gross photosynthesis to community respiration were always less than one. A photosynthesis-respiration chamber described by McIntire et al. (1964) was used in

making these determinations. Because of the difficulties of separating plant respiration from community respiration no values are available for net plant production in Berry Creek. Reese estimated the algal production in glucose equivalents for the different sections based upon the assumption that the photosynthetic quotient was equal to 1.25. The caloric equivalents of the values he obtained for Sections I, II, III and IV were approximately 262, 1025, 225, and 262 kcal/m², respectively. His results suggest that primary production could have been an important source of energy for the snails in Section II in addition to that of leaves. The low value of primary production in Section IV which received more insolation than Section III suggests that enrichment may have had the effect of reducing primary production in this section.

The differences in snail production between the 1963-1964 and 1964-1965 experiments for the period October through February (Table 11) probably cannot be ascribed to experimental error. The introduction of urea into the stream during the Spring, 1964, resulted in more uniform growths of Sphaerotilus than during the previous year. Increases in snail production in the enriched sections could have resulted from this increased food supply. There were substantial increases in the biomass of snails in the enriched sections except for the 1963 year-class in Section III during the spring and summer of 1964. Since production is the product of average biomass and growth

rate, reasonably high values of production during the Fall, 1964 and Winter, 1965 might be expected even though snail growth rates were generally lower during this period. Differences in production between the unenriched sections during the two periods being compared cannot satisfactorily be explained. One possible reason is that water temperatures were more moderate during the Summer and Fall, 1964, than during a similar period of the previous year (Figure 2) and this may have resulted in better snail growth. This is speculative, however, since snail growth rate information for the Summer and Fall, 1963, are not available for comparison and the relationship between snail growth and temperature has not been established.

The annual mean biomass and production of mixed-sizes of cutthroat trout during 1963 and 1964 (McIntyre, 1967) and the biomass and production of snails in enriched and unenriched sections of Berry Creek may be used to compare the effects of enrichment of the stream on these different forms. The respective values of mean biomass and production for trout in unenriched sections were 2.89 and 0.17 kcal/m², whereas values for snail biomass and production were 11.01 and 38.85 kcal/m². In enriched sections, the trout biomass and production values were 3.42 and 4.25 kcal/m², respectively. Snail biomass and production in these sections were 72.36 and 278.40 kcal/m², respectively.

No snail production values are available from the literature for comparison with those obtained for Berry Creek. Measurements have been made by other workers of the biomass of several species of aquatic and terrestrial snails. The comparative values shown in Table 15 are based upon body weight (less shell weight) in pounds per acre. Values given by Odum have been adjusted by factors obtained for Oxytrema silicula.

Macan (1950) has reported numerical densities of the aquatic snail Hydrobia to be 10,000 per square meter but weights of these snails were not given.

Table 15. Biomass in pounds per acre (flesh weight only) of snails in Berry Creek compared with values determined by other workers.

Animal	Section	Pounds per acre	Source
<u>Oxytrema</u>	I	405.0	Berry Creek
<u>Oxytrema</u>	II	354.0	Berry Creek
<u>Oxytrema</u>	III	2263.0	Berry Creek
<u>Oxytrema</u>	IV	2434.0	Berry Creek
<u>Polygyra</u>		141.0	Foster
<u>Oxytrema</u>		17.0	Odum
<u>Succinea</u>		7.8	Strandine

Lindeman (1942) proposed that energy relationships in ecological systems could be studied by assigning organisms to particular "trophic levels." Autotrophic plants constitute the first trophic level; herbivores, the second; carnivores consuming primarily herbivores, the third; and animals consuming primarily carnivores, the fourth. Comparisons between production values of successive trophic levels can be made yielding estimates of "trophic level production efficiency" (Odum, 1954). Warren et al. (1964) have questioned the usefulness of these efficiency values. The results of the study of snail production in Berry Creek can be used as an example of the difficulties inherent in trophic level analysis. Snail production in Berry Creek is essentially terminal in that it is not utilized to any great extent by aquatic carnivores. The largest portion of the energy of snail production ultimately passes directly from the ecosystem as heat from decomposer respiration. McIntyre (1967) found that annual trout production and food consumption in Section III during 1964 and 1965 was 4.62 and 32.28 kcal/m², respectively. Using trout food consumption as an approximation of herbivorous food organism production, trout production efficiency would be 14 percent. If annual snail production in this section (333.43 kcal/m²) were included in the herbivore trophic level, trout production would be 1.3 percent. These results tend to confirm those of Davis and Warren (1965) which showed that the inclusion of both snails and

herbivorous food organisms in the herbivore trophic level results in misleading carnivore production efficiency values.

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