


AN ABSTRACT OF THE THESIS OF

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Title PHYSIOLOGICAL ECOLOGY AND STRUCTURE OF BENTHIC
COMMUNITIES IN A WOODLAND STREAM

Abstract approved


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This thesis reports a portion of a general ecological study of a stream under conditions of controlled flow and low levels of organic enrichment. It is concerned with the effects of experimental variations of light intensity and concentration of soluble organic enrichment imposed on seasonal variations of temperature and total light energy received upon the periphyton and benthic plants. Suitable enrichment was predicated on establishment and maintenance of an abundant growth of Sphaerotilus and involved the isolation and study of this organism in pure cultures, in laboratory streams as well as in the experimental stream.

Abundant growth of Sphaerotilus was obtained in cultures at temperatures of 5, 10, 15, 20, 25, and 30°C while in the laboratory streams and the experimental stream, the organism produced abundant growths at a range of temperatures from 2 to 12°C. A variety of carbon and nitrogen sources was investigated for maintenance of

growth of Sphaerotilus. Abundant growth was produced when the enrichment included a specific nitrogen source combined with a specific carbon source. A carbon-nitrogen ratio of 8 to 1 proved satisfactory for maintaining Sphaerotilus in the stream.

An investigation of the cropping effect of stream snails indicated that the presence of large numbers of snails decreased the standing crop of Sphaerotilus both in the laboratory streams and the experimental stream.

A method was devised for determining the daily mean percentages of full sunlight reaching the four experimental sections of Berry Creek. Approximately 4 percent reached the shaded sections and 50 percent reached the light sections during the summer months. The range of mean saturating light intensities on the four experimental sections was from 250 to 950 footcandles.

Methods designed to sample the plant communities in the experimental sections of the stream included: artificial substrates (microscope slides) used to observe the density and diversity of micro-algae; a system of grids used to record distribution of the plant biomass; and the removal of a portion of the stream substrate for the detailed examination of the benthic community. Both microscopic and macroscopic observations indicated that twice as many species and greater numbers of autotrophic organisms were present in the unenriched than in the enriched sections.

Sub-samples of the harvested and homogenized materials scoured from the stream substrate, were used to determine biomass, organic matter, caloric content and pigment content. The biomasses from the enriched sections were greater than those from the unenriched sections, but contained large amounts of silt and were lower in organic matter and caloric content. The mean percentages of organic matter for the sections were: shaded, unenriched-33; light, unenriched-42; shaded, enriched-19 and light, enriched-19.

The range of chlorophyll a from the four experimental sections was 0.03 to 0.28 g/m². The concentration of chlorophyll, when representing spatial and seasonal variations, is an acceptable measure of the productive ability of communities in shallow, rapidly flowing streams.

A photosynthesis-respiration chamber was used to determine primary production and community respiration for each of the experimental sections. The range of rates of gross primary production expressed as mean O₂,g/m²/day for the unenriched sections was 0.62-2.47 and 0.53-0.59 for the enriched sections. Annual rates of gross primary production in glucose equivalents ranged from 0.07 kg/m² for the enriched sections to 0.30 for the unenriched.

The stream communities were characterized as heterotrophic communities with production-respiration ratios ranging from 0.47-0.85 for the unenriched and 0.16-0.20 for the enriched sections.

The efficiency of the fixation of light energy as organic matter was 1.90-2.23 for the unenriched and 0.37-2.70 for the enriched sections. The photosynthetic efficiencies of the communities on the experimental sections of Berry Creek were much lower than those reported for most laboratory communities, but were comparable to other natural aquatic communities.

PHYSIOLOGICAL ECOLOGY AND STRUCTURE OF BENTHIC
COMMUNITIES IN A WOODLAND STREAM

by

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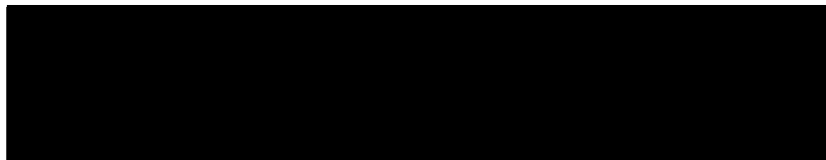


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PHYSIOLOGICAL ECOLOGY AND STRUCTURE OF BENTHIC COMMUNITIES IN A WOODLAND STREAM

INTRODUCTION

As they flow toward the sea, streams and rivers become increasingly enriched. The accrual of this enrichment causes changes in the various communities of a stream system. An adequate evaluation of the significance of such changes demands a better understanding of the energy relationships of streams.

Some earlier studies concerned with the need for a closer surveillance of stream pollution were published by Purdy (72), Naumann (58), and Reese (76). Numerous other contributions have been made toward a better understanding of the biology of polluted waters (42, 5, 67, 21, 35, 9, 99, 31 and 32). Many studies of the impact of artificial enrichment (pollution) of streams have been limited to subjective evaluations of qualitative changes occurring in the higher trophic levels of the biota. In the main, they have emphasized factors other than primary productivity of streams.

Introduction of the concept of trophic dynamics (45) and the emphasis placed on the efficiency of energy transfer within the ecosystem (33), have encouraged a better understanding of the energy relationships of entire aquatic systems. To this end, several approaches have been taken to the study of primary production in flowing waters.

Numerous investigators have successfully used submerged glass micro-slides for sampling the periphyton community (22, 76, 6, 68, 10, 15, 24, 82 and 81). However, this method is inadequate to estimate production of a stream community as it does not provide representative samples of all forms contributing to total primary production. Odum (61), Teal (89, 90) and Hoskins (29) developed methods for estimating productivity in some flowing waters, but McConnell and Sigler (52) showed these methods are unsuitable in shallow, rapidly flowing streams and rivers.

Ecosystems may be defined as combinations of interrelated communities of organisms and as such are difficult to study in nature. Because of these difficulties, some researchers have used laboratory methods to investigate the metabolism of parts of a system. Odum and Hoskins (62) and McConnell (51) studied the metabolism of enclosed microcosms. McIntire et al (54) and McIntire and Phinney (55) reported studies conducted in laboratory streams housed in a building equipped to control light and other factors influencing plant growth. While each of these studies made contributions toward the understanding of ecosystems, their artificial nature has still remained.

Several investigations have emphasized the relationship of plant pigments and the capacity for photosynthesis as reported earlier by Emerson, Green and Webb (19). Reviews of the experimental

evidence for this relationship have indicated variations in the production per unit of chlorophyll a (63, 86). However, Edmondson (17) and Ryther (80) have reported some optimism in correlating chlorophyll with productivity. Various adaptations of this method for estimating production in streams have been made (26, 95 and 36).

In attempts to correlate chlorophyll and photosynthesis on a quantitative basis, McConnell and Sigler (52) and Kobayasi (37) made use of the light and dark bottle method to estimate gross production. McConnell and Sigler (52) acknowledged the tendency for suppression of metabolism inherent in this method as discussed by Odum (61) and Strickland (86). In addition, some investigators have shown stimulating effects of current on nutrient uptake and growth of algae (1, 22, 4, 96, 97 and 53).

The apparent objections to previously discussed methods of estimating production in shallow streams might be partially alleviated by use of the technique reported by McIntire et al (54). This involved the enclosure of a part of the natural stream community within a specially designed photosynthesis-respiration (P-R) chamber. The chamber was fitted with tubes allowing adequate circulation and exchange of stream water. A lucite plate, which permits the desired illumination, is sealed in place as the top of the chamber.

A preliminary study by Dever (13) demonstrated the suitability of the P-R chamber for estimation of net production and community

respiration in a turbulent stream. This technique has been modified by Lane (43) to allow investigations, in situ, in shallow, rapidly flowing streams.

The present investigation was designed to contribute to a better understanding of energy relationships in natural aquatic systems. The problem involved a study of the influence of organic enrichment, illumination intensity and season on the structure and metabolism of benthic communities in a small woodland stream. Many of the techniques reported herein have been modified from those used in similar investigations, while others originated with this project.

DESCRIPTION OF EXPERIMENTAL STREAM AND RESEARCH AREA

The Berry Creek experimental stream facilities are located in the northeastern part of Benton County, Oregon approximately ten air-line miles from Corvallis. Berry Creek is a tributary of Soap Creek, which flows into the Luckiamute River, and on to the Willamette River. The drainage basin of Berry Creek is underlaid by rocks of the Siletz River volcanic series. The water in Berry Creek is derived from the volcanic substrate, which fact probably accounts for the perennial flow.

A 1500-foot portion of Berry Creek, with a gradient of one foot in 75 feet and consisting of a series of alternating riffles and pools located in a mixed woodland, was under flow control. Except for record maximum flows, the typical winter and spring flow for Berry Creek was approximately ten to twenty cubic feet per second with late summer and early fall low flows of 0.1 cubic foot per second. From late fall to early summer the stream flow in the experimental section was controlled at approximately 0.5 cubic foot per second. This was accomplished by means of a concrete diversion dam and the excess flow was diverted into a bypass canal. The areas of each experimental section of the stream are shown in Table 1.

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

The four experimental sections within the controlled flow portion of the creek (Figure 1) were separated from each other by boxes containing two thirty-two mesh per inch saran screens. The screen boxes were designed to minimize the movement of small aquatic forms, as well as larger animals, from one section to another. This allowed comparison of animals contained within the various sections of the stream.

Enriching solutions were introduced into the stream at the head of experimental section three where the entire stream flow entered a baffled mixing chamber. Enrichments were introduced into the mixing chamber through plastic tubing from a gas controlled, continuous flow, metering apparatus housed near the stream.

The dense canopy covering the stream was removed from sections II and IV. The undisturbed canopy in sections I and III was

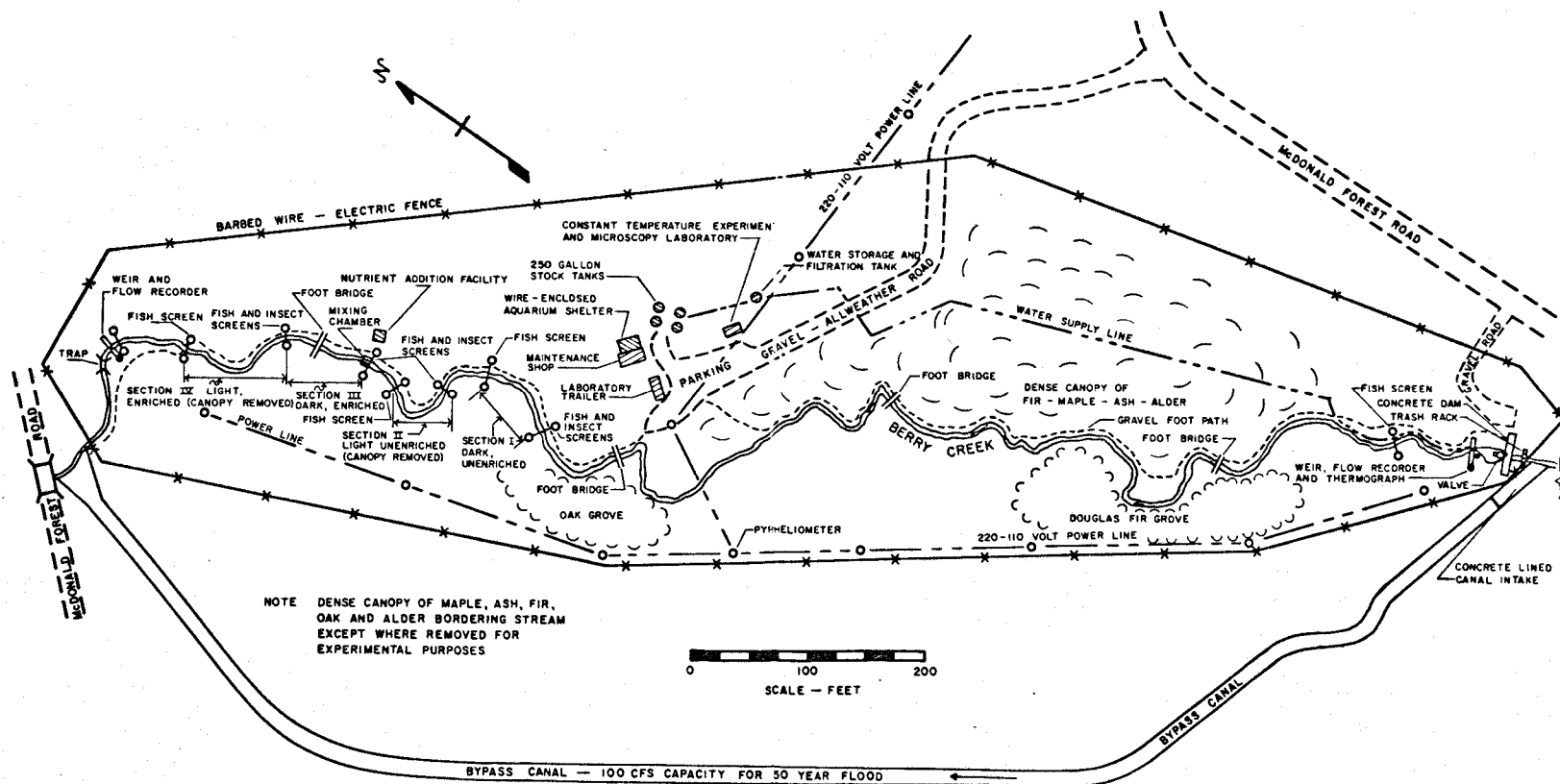


Figure 1. Diagram of Berry Creek Experimental Stream showing research facilities

mainly composed of red alder (Alnus rubra) and big leaf maple (Acer macrophyllum) with a few representatives of Oregon white ash (Fraxinus latifolia), Douglas fir (Pseudotsuga menziesii), Oregon white oak (Quercus garyana), black cottonwood (Populus trichocarpa) and willow (Salix mackenziana).

The chief consumers of plant material in the stream probably were the extremely abundant stream snail (Oxytrema silicula) and the freshwater limpet (Lanx newberryi). Other larger aquatic forms inhabiting the stream were: crayfish (Pacifastacus leniusculus trowbridgii), cut-throat trout (Salmo clarki clarki), reticulate sculpin (Cottus perplexus), brook lamprey (Lampetra planeri), Pacific giant salamander (Dicamptodon ensatus), rough-skinned newt (Taricha granulosa granulosa) and red-legged frog (Rana aurora).

Field laboratory facilities located within the experimental area were serviced by an all-weather road and both 110 and 220 volt electrical power. Water for the laboratory facilities was provided by a two-inch polyethylene pipe that conducted the water from the flow control dam to a filtration system from which distribution was completed through smaller plastic pipes to the various facilities.

EXPERIMENTAL PROCEDURES AND RESULTS

In field studies, much effort is expended in selection of suitable equipment and techniques. Many must be originally designed, as in this investigation. Here, an attempt was made to relate research using laboratory cultures and laboratory streams with that in the natural stream system. Correlation of these studies required continuing surveillance of a number of factors influencing stream ecology.

Experimental Stream Apparatus

The stream flow was continuously monitored by two model F. Stevens Recorders, one at each end of the experimental stream area. These instruments recorded changes in rate of flow, influent and effluent, of the controlled flow portion of the stream (Figure 2). The low flow rates during summer months are correlated with minimum numbers of periphyton genera and individuals in the unenriched sections I and II of Berry Creek. Likewise, a similar minimum occurred in the winter months. The phenomenon of spring and autumn peaks of abundance characteristic of unenriched sections I and II did not occur in the enriched sections III and IV. In these latter sections, a relatively constant minimum was maintained throughout the year except for two peaks of abundance induced by altering concentrations of nitrogen enrichment (Figure 3).

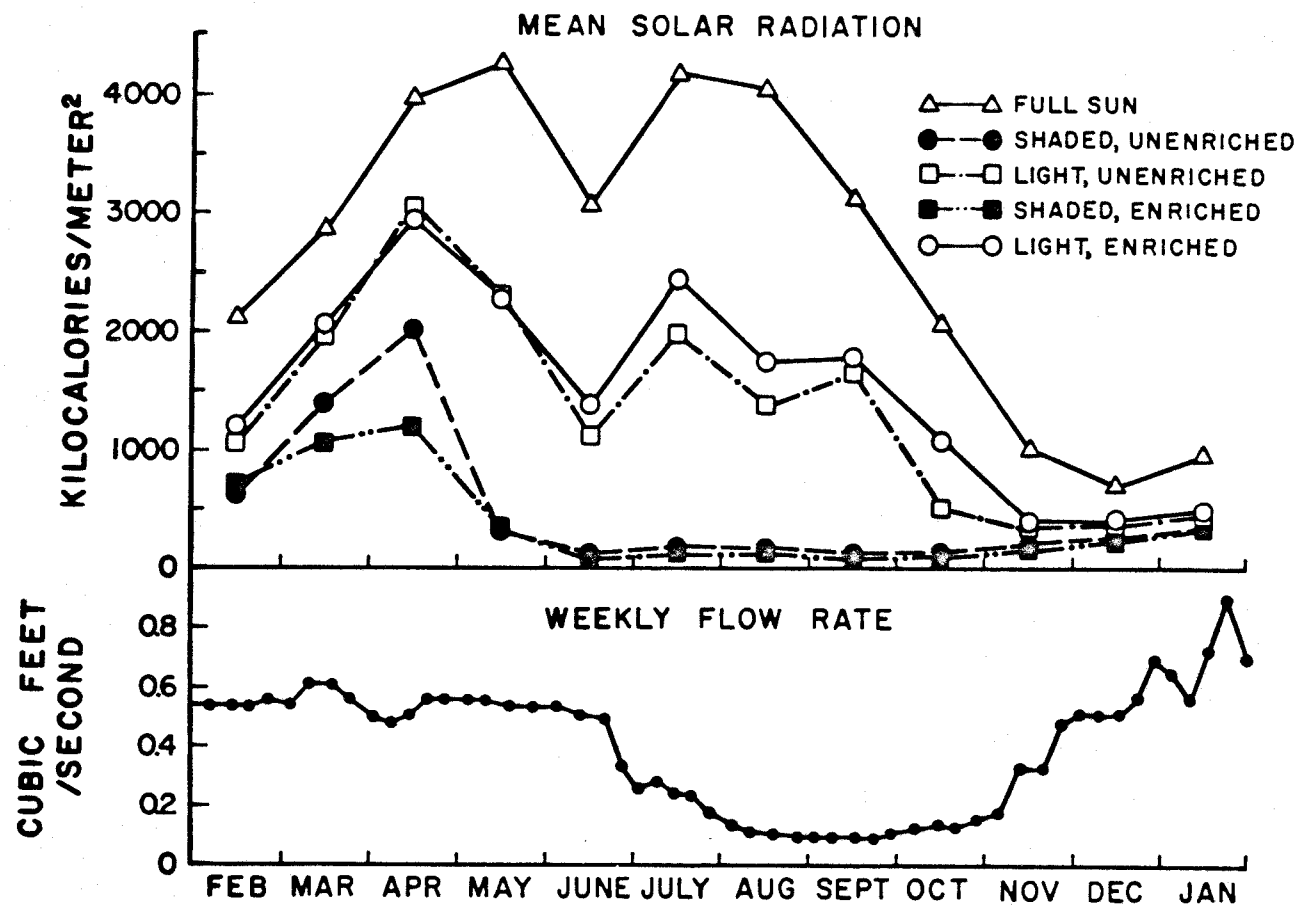


Figure 2. Mean daily estimates of solar radiation for four experimental sections and the open sky and weekly rates of flow, effluent from the experimental sections, Feb., 1964 through Jan., 1965

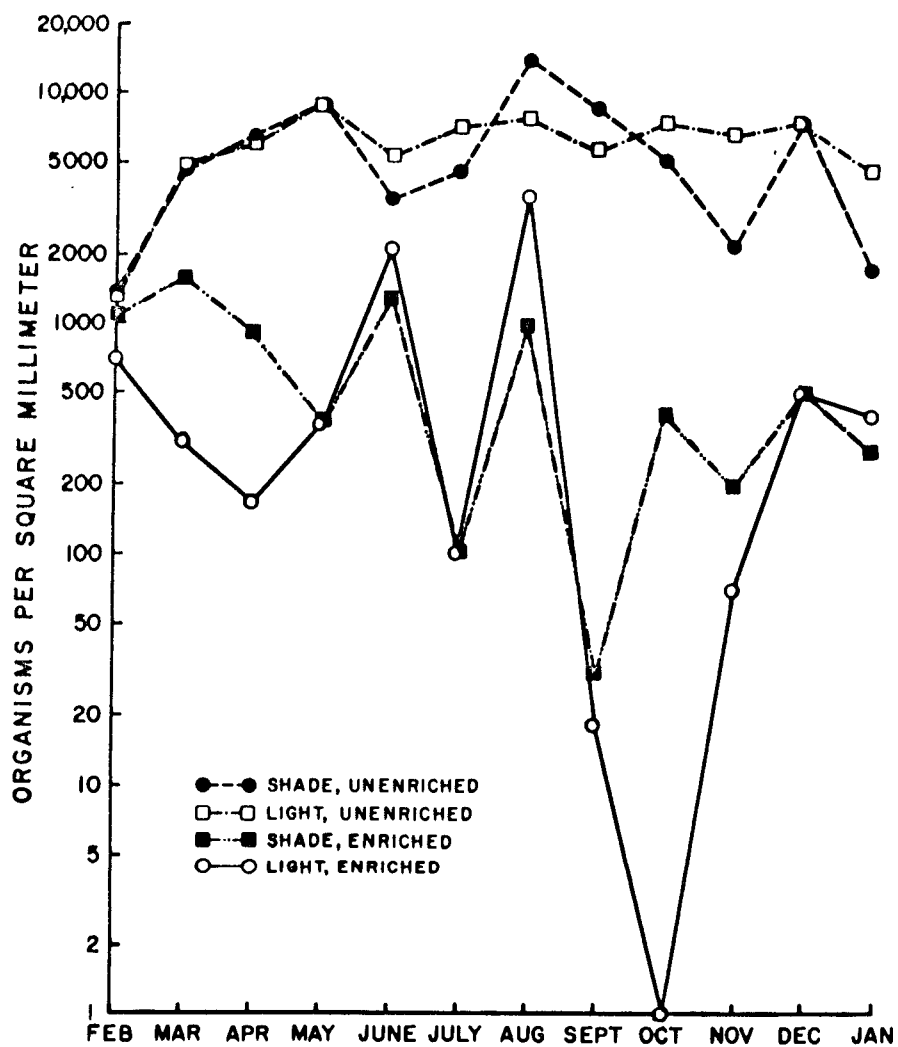


Figure 3. Numbers of individual autotrophic periphyton organisms per square millimeter on artificial substrates from the four experimental sections of Berry Creek, Feb., 1964 through Jan., 1965

The chemical characteristics of the stream water are summarized in Table 2. These data are grouped into four different seasons for convenience and provide water quality information for years 1959-1963. Since only minor differences were evident during the five year period, analysis was discontinued. These determinations were made of water from the unenriched sections of the stream and manipulation of stream nutrients (Table 8) was not monitored.

The temperature of the stream water was continuously recorded by Auto-Lite, model 1000, Recording Thermographs. Similar instruments were also used for recording the temperature of the water in the laboratory streams. There was considerable decrease in temperature of the creek water during May, November and December with lows of 2.8°C , -2.2°C , -1.2°C respectively. The variations between maximum and minimum weekly temperatures (Figure 4) were greatest during April, May, November and December reflecting unstable weather conditions for those months.

Solar energy received by the experimental area was recorded by a Belfort, model Five Recording Pyrheliograph which was continuously exposed to the open sky. This instrument recorded the daily rate of insolation from which the gram calories of light energy per square centimeter per day, could be calculated. A large part of the canopy was removed from experimental sections II and IV while the canopy of the other two experimental sections remained intact.

Table 2. Summary of water quality for Berry Creek, 1959-1963*

Characteristic of constituent	Fall				Winter		
	11/1/59	11/5/60	11/23/61	10/30/62	2/25/60	2/22/62	1/8/63
Specific conductance (micromhos at 25 °C)	136	135	93	132	83	84	91
pH	7.4	7.6	7.3	7.5	7.4	7.1	7.5
Color	5	5	30	10	10	25	10
Dissolved solids mg/l	94	98	80	92	62	63	71
Hardness mg/l as CaCO ₃	55	54	35	54	31	33	36
Silica (SiO ₂) mg/l	24	23	21	26	22	21	22
Iron (fe) mg/l	0.07	0.14	0.19	0.08	0.18	0.12	0.13
Calcium (Ca) mg/l	13	13	8.0	14	8.0	8.0	9.0
Magnesium (Mg) mg/l	5.5	5.4	3.7	4.5	2.7	3.2	3.4
Sodium (Na) mg/l	6.3	6.2	4.9	6.6	3.7	4.1	4.4
Potassium (K) mg/l	0.8	0.1	0.6	0.5	0.4	0.3	0.1
Bicarbonate (HCO ₃) mg/l	74	74	44	74	42	44	50
Carbonate (CO ₃) mg/l	0	0	0	0	0	0	0
Sulfate (SO ₄) mg/l	1.6	0.4	2.0	1.2	1.0	1.6	1.6
Chloride (Cl) mg/l	5.5	6.8	5.8	5.0	3.5	4.5	3.5
Fluoride (F) mg/l	0.1	0.0	0.1	0.0	0.1	0.1	0.1
Nitrate (NO ₃) mg/l	0.1	0.2	0.4	0.0	0.2	0.1	0.1
Phosphate (PO ₄) mg/l	0.01	0.4	0.05	0.06	0.00	0.03	0.03

* These analyses were made under the supervision of L. B. Laird, District Chemist, U.S. Geological Survey, Portland, Oregon.

Table 2. Continued*

Characteristic of constituent	Spring					Summer		
	5/7/60	6/15/60	5/23/61	5/17/62	4/30/63	8/30/60	8/7/61	8/13/62
Specific conductance (micromhos at 25° C)	89	103	90	92	84	136	124	137
pH	7.4	7.4	7.5	7.6	7.3	7.5	7.8	7.8
Color	10	5	10	5	15	5	5	5
Dissolved solids mg/l	67	76	70	68	71	96	86	93
Hardness mg/l as CaCO ₃	34	42	36	36	34	55	53	56
Silica (SiO ₂) as mg/l	22	23	22	24	20	24	24	26
Iron (fe) mg/l	0.16	0.18	0.13	0.19	--	0.29	0.21	0.23
Calcium (Ca) mg/l	8.5	10	9.0	8.0	8.5	13	12	14
Magnesium (Mg) mg/l	3.1	4.1	3.4	4.0	3.3	5.4	5.5	5.1
Sodium (Na) mg/l	4.2	4.8	4.6	4.4	4.2	6.6	6.0	6.9
Potassium (K) mg/l	0.2	0.2	0.0	0.3	0.2	0.2	0.4	0.6
Bicarbonate (HCO ₃) mg/l	48	58	52	50	47	78	72	78
Carbonate (CO ₃) mg/l	0	0	0	0	0	0	0	0
Sulfate (SO ₄) mg/l	0.4	1.2	0.0	1.0	1.4	1.4	0.4	1.2
Chloride (Cl) mg/l	3.0	3.5	3.5	3.5	3.5	4.8	4.0	4.5
Fluoride (F) mg/l	0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.1
Nitrate (NO ₃) mg/l	0.1	0.1	0.2	0.0	0.1	0.1	0.3	0.2
Phosphate (PO ₄) mg/l	0.04	0.05	0.03	0.04	0.3	0.03	0.04	0.04

* These analyses were made under the supervision of L. B. Larid, District Chemist, U. S. Geological Survey, Portland, Oregon.

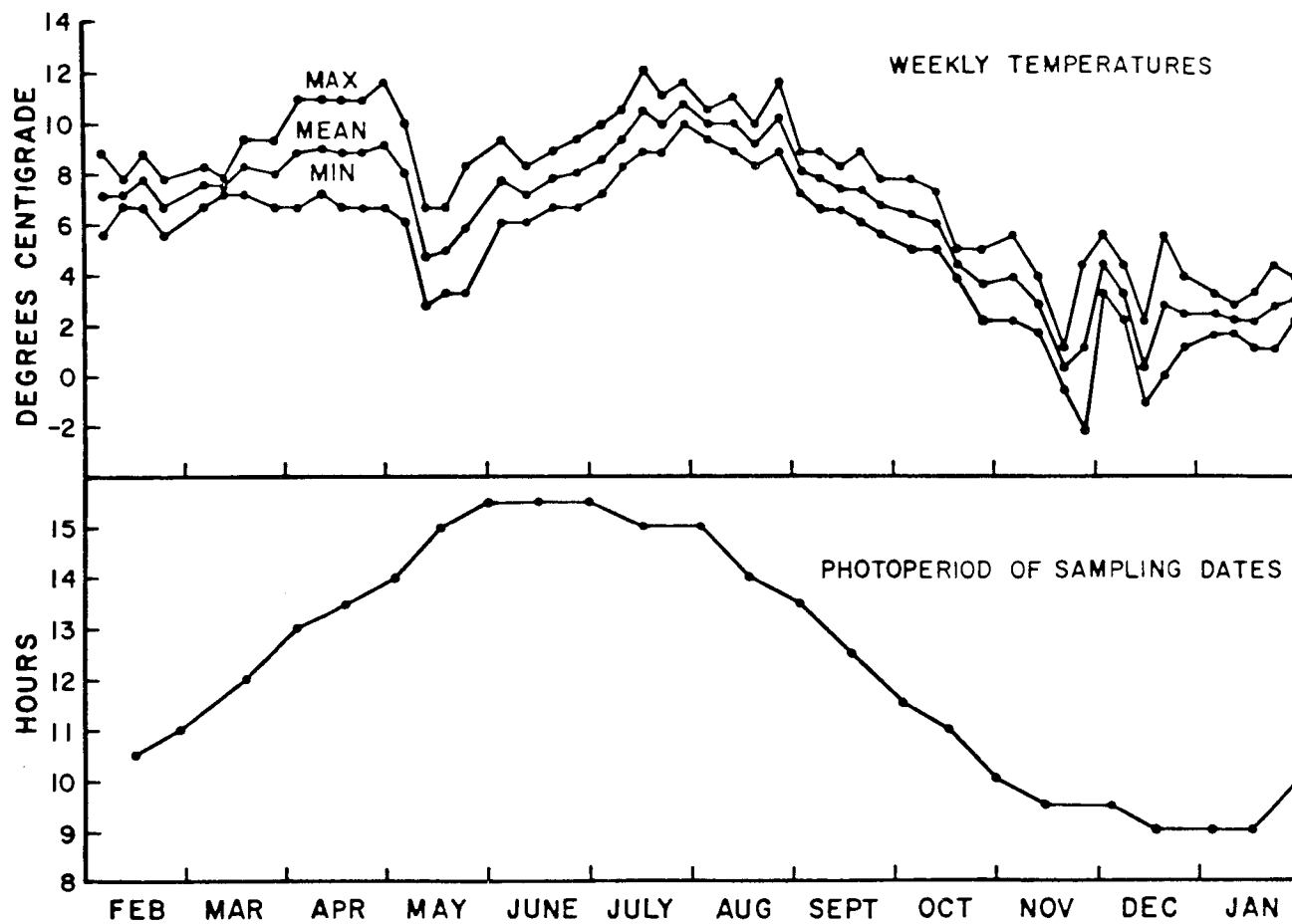


Figure 4. Weekly fluctuations in water temperatures of the experimental stream and lengths of light periods on dates when primary production was measured, Feb., 1964, through Jan., 1965

This provided varied light intensities for the experimental sections.

In order to calculate relative efficiency of primary production in stream communities, the light energy reaching the stream must be determined with reasonable accuracy. Instruments used for such determinations must be portable and easily maneuverable in order to permit the taking of large numbers of light readings for adequate surveillance of the vastly contrasting areas involved. Light integrating systems have been designed for such purposes; however, the cost of such systems is prohibitive for extensive use (40, 47 and 79).

Satisfactory results were achieved at Berry Creek with a Weston Sunlight Illumination Meter, model 756. This instrument allowed the taking of sufficient numbers of incident light readings to determine the daily mean percentages of full sunlight reaching the different experimental sections of the stream. The above percentages were determined at two-week intervals during this investigation. Modifications of this procedure have been used to determine the amount of incident light reaching a given area at a given instant (56, 64, 65 and 92).

The visible light energy reaching the sections with undisturbed canopy during two different periods is summarized in Table 3. In the period November to May, the percentages of available energy reaching these two sections were 36 and 32 respectively while from May to November the percentages of full radiant energy (visible light)

were five and three respectively. Sections II and IV, from which the canopy had been removed, were exposed to an approximately fixed rate of isolation with mean percentages of 48 and 55 respectively. These data are in reasonable accord with percentages of 1-7 and 30-60 listed by Ovington and Madgwick (64) and 10 and 50 given by Vezina and Grandtner (93). Figure 2 and Figure 4 show the seasonal distribution of radiation and length of daily photoperiod and indicated that the early summer period was rainy and cool, with considerable decrease in incident light.

Energy values were estimated for the light that reached the experimental sections of the stream by applying the above percentages to data recorded by the Pyrheliograph. Approximately 40 percent of the incident light reaching the riffles was assumed to be photosynthetically active radiation (74).

Nutrition and Growth of *Sphaerotilus natans*

The initial stages of this investigation were concerned with establishing and maintaining conditions in Berry Creek similar to those in polluted rivers. This investigation is the first known attempt at maintaining a controlled flow stream in a relatively polluted condition in order that the entire stream ecology might be studied. This approach presented many unique problems. Preliminary studies emphasized the need for reconciling these problems prior to attempting any elaborate experiments.

Table 3. Percentage of solar radiation reaching the four experimental sections.
February 1964 to January 1965

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Shaded, unenriched	29	49	50	7	4	4	4	4	7	20	34	35
Light, unenriched	49	69	77	53	36	47	34	53	25	37	52	45
Shaded, enriched	33	41	30	7	3	3	4	3	6	18	35	35
Light, enriched	57	72	74	53	45	58	43	57	50	40	56	50

Mean Percentage of Solar Radiation

Shaded, unenriched - 21

Shaded, enriched - 18

Light, unenriched - 48

Light, enriched - 55

Sphaerotilus natans is one of the dominant organisms of many polluted rivers (41, 71, 14 and 75) and would serve as an index for the establishment of a heterotrophic community. Failure of several attempts to maintain Sphaerotilus in the stream indicated a need for further information concerning its biology. A three fold plan was undertaken that included isolation and pure culture studies of the organism, studies of growth of the organism in semi-isolated conditions in laboratory streams, and finally studies of growth in the woodland stream.

Culture studies of Sphaerotilus natans

Cultures of a strain of Sphaerotilus natans grown from inoculum isolated from Berry Creek were used to study the effects of temperature and supplemental nitrogen on uptake of radioactive carbon. Several investigators reported no growth for Sphaerotilus at 5 °C (8, 28, 44, 57, 85 and 100). During the winter months Sphaerotilus grows in Berry Creek at temperatures of 2-3 °C and persists in the stream even though the temperature may be below zero for weeks at a time (Figure 4). These observations dispelled the idea that low temperatures might prevent the growth of the organism. However, accurate and quantitative information was needed to determine the range of temperatures at which the Berry Creek strain of Sphaerotilus natans would grow. Six temperatures ranging from 5-30 °C and three levels

of nitrogen as 0.05, 0.10 and 0.20 percent urea were selected for culture experiments with three replications each. Since the primary aim of these experiments was to provide understanding of Berry Creek, the basic medium was a 0.5 percent solution of sucrose in creek water. To this was added the desired nitrogen treatment and radioactive carbon source (universal label) to provide an activity of 0.01 μC per milliliter. Inoculum was added to forty milliliter aliquots of the medium and incubated at the predetermined temperatures for specific periods. Each culture was then filtered onto a weighed HA Millipore filter, and dried overnight at 2°C in a desiccator. The filters were re-weighed to determine biomass and counting rates were recorded by an automated Nuclear Chicago Beta Counter, model C-110-B. Specific activity was determined from the counting rates and recorded as activity per hour of culture time. Sphaerotilus produced considerable growth at all six temperatures (Table 4). Using mean dry weight as a criterion, the cultures grown at 5°C produced as much as those grown at 10°C and 20°C . The maximum production was at 30°C but the specific activity per gram weight at this temperature was considerably less than at most other temperatures.

An optimum range of $25\text{-}30^{\circ}\text{C}$ was revealed when dry weight was used as the criterion of production, but when specific activity was used as the criterion, a range of $10\text{-}20^{\circ}\text{C}$ was observed. This discrepancy may offer some explanation for the wide variation in

Table 4. Dry weight produced and specific activity accumulated per hour at various temperatures by Sphaerotilus natans, in culture

Enrichment Group*		Temperature in degrees Centigrade					
		5	10	15	20	25	30
A	dry wt, mg/hr	0.010	0.008	0.013	0.010	0.013	0.013
B		0.015	0.013	0.013	0.014	0.014	0.016
C		0.014	0.013	0.016	0.014	0.017	0.021
	mean dry wt, mg/hr	0.013	0.011	0.014	0.013	0.015	0.017
	Specific activity/ mg dry wt/hr	546	945	785	861	613	559

* A = 0.05% urea, B = 0.10% urea and C = 0.20% urea. (The basic medium was 0.5% solution of sucrose in creek water.)

temperature ranges for optimum growth reported by other workers: Linde (44), 30-35°C; Zikes (100), 25-29°C; Stokes (85), 30°C; Höhn (28), 10-15°C. The possibility cannot be overlooked that strains of Sphaerotilus similar to those from Berry Creek have adapted to a variety of temperatures. With few exceptions, cultures at all temperatures showed increase in dry weight with increase in nitrogen. Maximum production occurred at the highest nitrogen concentration and, within this group of cultures, a temperature range of 25-30°C. An inexpensive shaking apparatus designed specifically for these culturing experiments is shown in Appendix VIII.

Growth of Sphaerotilus in laboratory streams

Requirements for growth of Sphaerotilus natans in semi-isolated cultures in laboratory streams were also studied. A series of six laboratory streams were constructed of 3/4-inch plywood and sealed with several coats of non-toxic white paint. Each stream was about 12.5 cm deep with a surface area of 0.5 square meter and a capacity of 45 liters. Water from Berry Creek was passed through a 500-gallon filter packed with granular pumice to remove larger organisms and debris. The exchange rate in each stream was 200 milliliters per minute and the desired current velocity was maintained by adjustable speed paddle wheels. Water temperatures were recorded by an Auto-Lite Recording Thermograph, model 1000. Black polyethylene

sheeting was secured over the top of the streams to exclude light and insects. Nutrients were added to the stream by means of a continuous metering apparatus, and were combined with the influent creek water in separate mixing chambers before entering each stream. The effluent from each stream was filtered and the collected material dried and weighed to determine rates of export.

Initial experiments in the laboratory streams were designed to determine the suitability of a variety of carbon and nitrogen sources. Evaluation of these sources were based on the production of an excellent, good, fair or poor growth of Sphaerotilus (Table 5).

Of the three carbon sources investigated, corn syrup resulted in the least production and in one case gave a negative response. With two exceptions, sucrose and dextrose produced comparable results as sources of carbon for culturing Sphaerotilus. Of the four nitrogen sources investigated, peptone resulted in the greatest production followed by urea, powdered milk and whey. Powdered milk and whey were the bulkier sources of nitrogen and presented the most difficulty in dispensing and peptone was the most expensive source used.

The carbon sources, sucrose and dextrose, and nitrogen sources, urea and peptone, which initially produced the maximum biomass were included in additional experiments to determine their suitability in enriching Berry Creek. The summary in Table 6 shows glucose

alone to be approximately 30 percent more productive than sucrose alone for growing Sphaerotilus. In combination with peptone as a nitrogen source, glucose produced about 36 percent more than sucrose. However, if urea was the source of nitrogen, sucrose produced approximately 13 percent in excess of glucose.

Table 5. Effects of various sources of carbon and nitrogen on growth of Sphaerotilus natans

Carbon Source	Nitrogen Source	Evaluation of Growth
corn syrup	powdered milk	/
	powdered whey	/
	peptone	/
	urea	/
sucrose	powdered milk	//
	powdered whey	//
	peptone	///
	urea	////
dextrose	powdered milk	//
	powdered whey	//
	peptone	///
	urea	//
//// excellent, /// good, // fair, / poor		

Comparisons of the July 5 to July 25 experiment with that of July 25 to August 15 showed notable differences in production when enriching rates were doubled (Table 6). The above experiments showed an increase in biomass of 2 percent when sucrose was doubled

Table 6. Effect of continuous enrichment on the accumulation of Sphaerotilus natans in laboratory streams. Data expressed as dry weight of biomass in g/m²

Period	Enrichment		Biomass	Mean Temp.
	Carbon Source	Nitrogen Source		
July 5 -	sucrose-2ppm	none	3.51	8.8
July 25	sucrose-2ppm	peptone-0.1ppm N	4.94	
	sucrose-2ppm	urea-0.1ppm N	5.57	
	glucose-2ppm	none	4.23	
	glucose-2ppm	peptone-0.1ppm N	6.80	
	glucose-2ppm	urea-0.0.1ppm N	4.71	
July 25 -	sucrose-4ppm	none	3.57	8.9
Aug. 15	sucrose-4ppm	peptone-0.2ppm N	7.29	
	sucrose-4ppm	urea-0.2ppm N	9.66	
	glucose-4ppm	none	5.57	
	glucose-4ppm	peptone-0.2ppm N	10.00	
	glucose-4ppm	urea-0.2ppm N	8.09	
Aug. 15 -	sucrose-2ppm	none	3.14	11.9
Sept. 13	sucrose-2ppm	peptone-0.1ppm N	4.19	
	sucrose-2ppm	urea-0.1ppm N	6.06	
	glucose-2ppm	none	4.94	
	glucose-2ppm	peptone-0.1ppm N	8.71	
	glucose-2ppm	urea-0.1ppm N	5.79	

Summary: (mean of three experiments)

sucrose	none	3.41
sucrose	peptone	5.47
sucrose	urea	7.10
glucose	none	4.92
glucose	peptone	8.50
glucose	urea	6.19

and 31 percent when dextrose was doubled. An increase in biomass of 47 percent occurred when peptone was doubled and 70 percent when urea was doubled.

Addition of plastic screen partitions modified each laboratory stream to allow various stocking rates of the stream snail Oxytrema silicula. Large numbers of these small gastropods were recorded by Earnest (16), in experimental sections III and IV of Berry Creek and quantitative information was needed regarding their influence on the standing crop and export of Sphaerotilus in the stream.

The results of laboratory stream experiments (Table 7) indicate some correlation between snail populations and standing crop of Sphaerotilus. The accumulated biomass and export determined for the control stream were combined to compose the accountable (reconciled) biomass. Differences occurring between this amount and similar combinations from the other laboratory streams were listed as decreases in biomass and not accounted for. These data show a progressive decrease in standing crop of Sphaerotilus with increases in snail populations. As snail numbers were increased, the reconcilable biomass also progressively decreased. This decrease which could not be accounted for, in either export or standing crop, was considered to have been ingested by the snails.

Table 7. Accumulation of Sphearotilus biomass in laboratory streams stocked with the aquatic snails Oxytrema silicula *

Stocking rate; (numbers/m ²)	0	20	40	100	200	300	320	400	500	560
Stocking rate: (weight in grams/m ²)	0	14	28	64	126	190	202	252	310	358
Accumulated biomass (g/m ²)	8.57	8.04	7.77	7.35	5.37	4.72	4.24	3.84	2.48	1.52
Export (g/m ²)	3.46	3.44	3.63	3.87	4.41	3.47	3.49	2.18	1.71	1.33
Biomass accounted for.	12.03	11.48	11.40	11.22	9.78	8.19	7.73	6.02	4.19	2.85
Biomass unaccounted for.	0	0.55	0.63	0.81	2.25	2.84	4.30	6.01	7.84	9.18

* Growth period of 21 days.

Experimental Enrichment of Berry Creek

The experiments in the laboratory streams served as a basis for similar studies in Berry Creek itself. Many of the combinations and concentrations of carbon and nitrogen enrichment rated equally well in the laboratory streams and Berry Creek. The factors of availability and desirable dispensing characteristics were used as final criteria for the selection of sucrose and urea as nutrients to be used in the creek. The nutrients were added to the stream by means of a permanently situated, gas controlled, continuous metering apparatus. The concentration of enrichments was adjusted periodically to compensate for variations in stream flow rate (Figure 2). On two occasions, these concentrations were also adjusted experimentally to observe their influence on the autotrophic periphyton community (Figure 3).

In May, 1964, after several months of continuous addition, the nitrogen enrichment was discontinued (Table 8). This decreased the population of heterotrophs and a peak biomass of autotrophic periphyton occurred in both enriched sections in June. At that time, the nitrogen enrichment was again initiated and one month later the relative population densities of autotrophs and heterotrophs had reversed. The nitrogen enrichment was then discontinued for a second time and a repeated peak abundance of autotrophic forms occurred in August.

Table 8. Influence of mean rates of enrichment on percentages of organic matter in the biomass in Berry Creek

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Nitrogen enrichment in ppm.	0.5	0.5	0.5	--	0.5	--	0.5	0.5	0.5	0.5	0.5	0.5
Carbon enrichment in ppm.	1.0	2.0	4.0	6.0	10.0	4.0	10.0	4.0	4.0	4.0	4.0	4.0
Mean percentage organic matter in unenriched sections.	31	45	45	45	43	55	50	48	45	40	20	25
Mean percentage organic matter in enriched sections.	35	27	27	27	27	15	17	30	27	32	15	17

Following that, the nitrogen enrichment was reinstated and continued throughout the remainder of the study. In this investigation, a carbon-nitrogen enrichment ratio of eight to one was the most desirable combination for maintaining the Sphaerotilus biomass at a density comparable to that in polluted rivers.

Sampling Plant Communities in the Experimental Stream

Some effects of increasing the organic constituents of a stream are more obvious than others. A technique that has proven beneficial in studying some of the less obvious effects is the observation of the density and diversity of the benthos and periphyton.

Determination of Abundance of Periphyton by Counting

Determination of the abundance of periphyton was accomplished by using spring clips to suspend micro-slides in Berry Creek with their surfaces parallel to the stream flow, a method which has been used in modified form since 1884 (82). During this study each glass slide remained in the stream for a period of three weeks. The slides then were removed and placed in a screw-top coplin jar which had been completely submerged and removed to a portable field laboratory situated within the experimental stream area, Figure 1.

Identification, in situ, was based in part on keys by Hustedt (30)

and Smith (83). Patrick, Hohn, and Wallace (68) have shown no significant difference between counts made of diatoms attached to glass slides and those that had been removed. Numerous techniques for determining periphyton density have been used (18, 12, 48, 46, 15, 38 and 98). In this study, the micro-algae were counted microscopically, using the Whipple Ocular Micrometer, and counts were recorded of kinds and number of individuals per square millimeter (Appendices I - IV). A comparison of these data show lower percentages of autotrophic organisms in the enriched sections (Figure 5) and a mean number of three genera occurring in the enriched sections compared to a mean of six genera occurring in the unenriched sections. Bacillariophyceae, Cyanophyta and autotrophic bacteria, to various extents, dominated the autotrophic periphyton of each experimental section (Figure 6).

The dominant Bacillariophycean community in the shaded, unenriched section was smaller in the shaded, enriched section where constituents of Cyanophyta and Chlorophyta occurred in larger numbers. Fewer autotrophic bacteria associated with more Cyanophyta appeared in the light, enriched section in comparison to its unenriched counterpart. For most of the time, both enriched sections were covered generally, by heavy growths of Sphaerotilus natans.

Following microscopic examination, permanent mounts of the

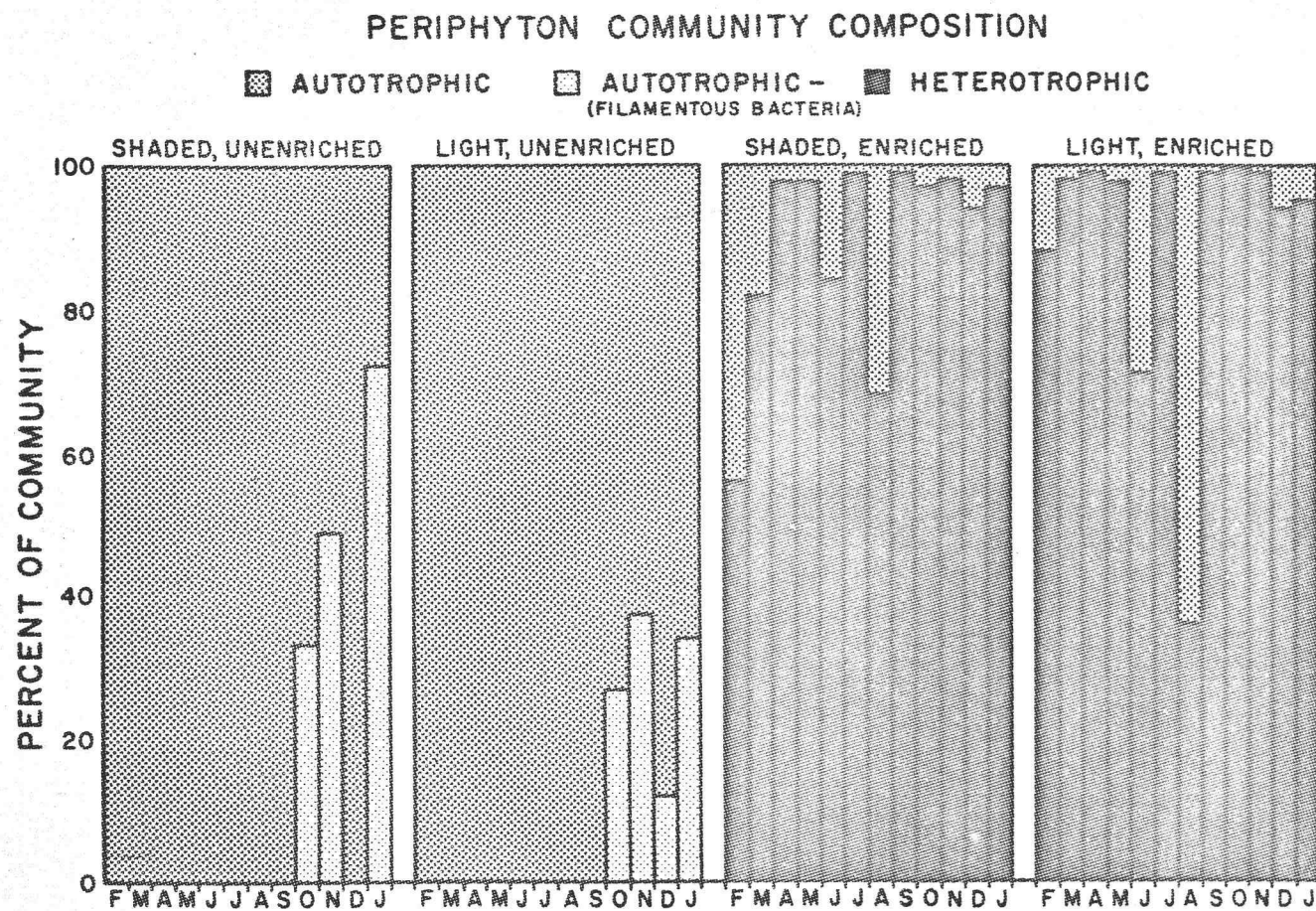


Figure 5. Composition of the periphyton communities of the four experimental sections of Berry Creek, Feb., 1964 through Jan., 1965

AUTOTROPHIC PERIPHYTON COMMUNITY COMPOSITION

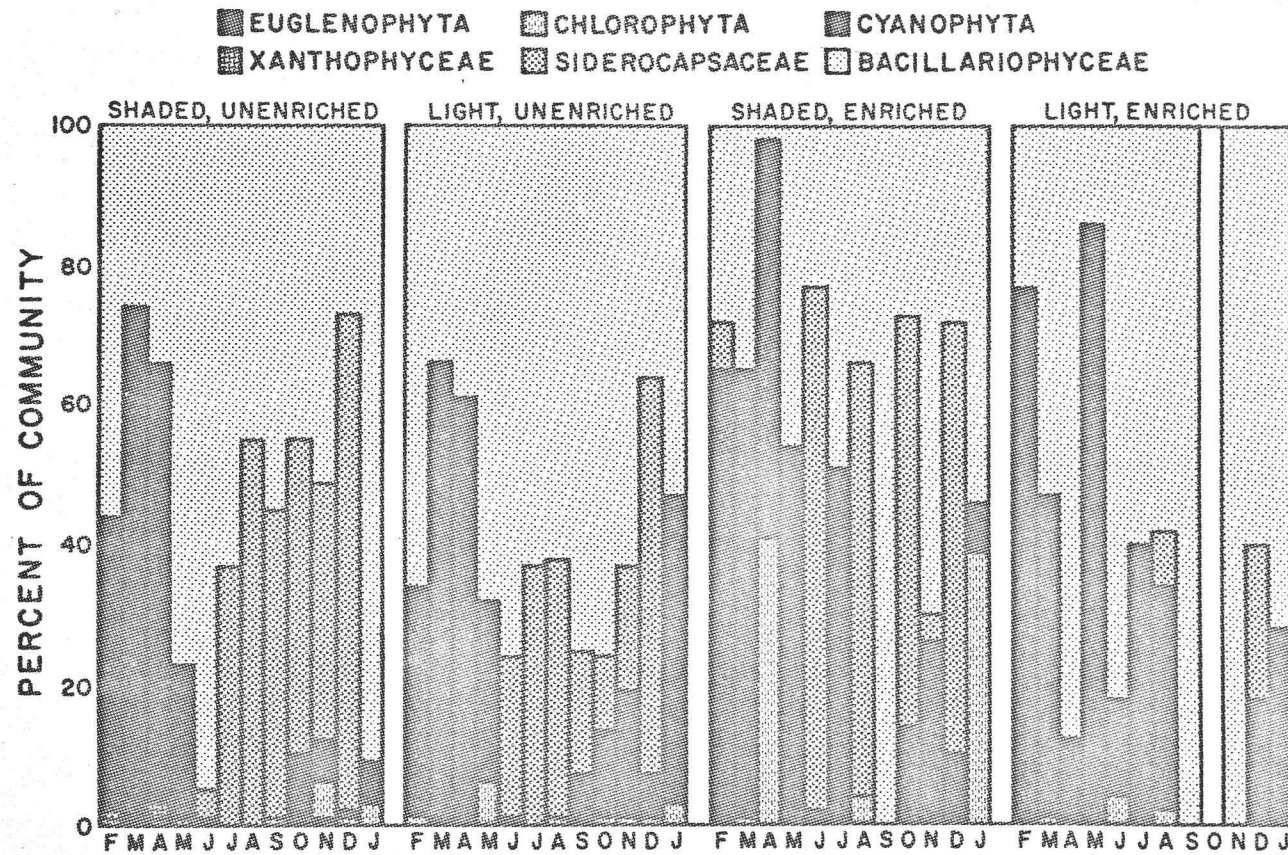


Figure 6. Composition of the autotrophic periphyton communities of the four experimental sections of Berry Creek, Feb., 1964 through Jan., 1965

algae were prepared by the technique referred to below. The purpose for which a permanent slide mount is intended dictates, in part, the techniques followed in its preparation. Incineration of micro-algal materials, by any means, destroys all constituents except the siliceous frustules of diatoms. Use of this procedure was obviated by the desire to preserve all micro-algae in a recognizable state and original distribution on the slide. The large number of micro-slides examined and the time required in handling them, demanded a schedule with simplicity, flexibility and minimum time required for preparation. With these criteria in mind, the schedule below is offered as a method of preparing permanent slide mounts of micro-algae. This schedule, which is adaptable to change, includes the following steps:

1. Place slide in 50 percent alcohol for 1-2 minutes.
2. Transfer slide to 70 percent alcohol for 1-2 minutes.
(This step may be omitted if plasmolysis is not objectionable.)
3. Transfer slide to absolute alcohol for 2-5 minutes.
(Note: More complete dehydration reduces emulsions in next step.) A small amount of fast green stain may also be used in this step if desired.
4. Transfer slide quickly to xylol for 2-12 hours.
(Time may be shortened if complete clearing of cells is not critical.)
5. Remove slide from xylol (do not allow to dry), apply one drop of balsam or Hyrax to area to be preserved and quickly affix cover slip.

Exemplary of the adaptability of this schedule is the ease of incorporating an extraction procedure for pigment analysis.

Determination of the Relative Abundance of *Sphaerotilus*

A method used for estimating relative abundance of the benthic community in the experimental stream consisted of recording distribution of the plant biomass on maps that divided each riffle into a grid of rectangles each including two square meters. This system, modified from one used by Blum (3) and Dever (13), was used only in the enriched sections of Berry Creek where fluctuations in the density of *Sphaerotilus natans* were especially noted. The rectangles were rated weekly in one of four categories: negligible (0-2X), light (3X-10X), medium (11X-20X) and heavy (above 20X). The X represented a one-inch tuft of *Sphaerotilus* consisting of from one to three plumes. Observations were recorded weekly as percentages of the riffle credited to each of the four categories. Summaries of these observations appear in Appendices VI and VII.

Sphaerotilus densities were correlated directly with the amount of carbon and nitrogen enrichment. Comparisons of Table 8 and Appendices VI and VII show absence of *Sphaerotilus* during the month of February coincided with a low rate of carbon enrichment even though the nitrogen enrichment was known to be adequate. The two-fold increase in sucrose during March had no visible effect but when the

sucrose was increased again in April, Sphaerotilus became visible in both enriched sections.

To test the response of Sphaerotilus to nitrogen enrichment, the urea was discontinued in May. At this time, even with an increase in sucrose, the densities of Sphaerotilus decreased. In June, both carbon and nitrogen concentrations were increased and a corresponding increase in biomass occurred in the latter part of June and in July. Since response to changing environmental conditions does not occur as suddenly in nature as in laboratory cultures, it was desirable to discontinue the nitrogen enrichment a second time. During July the urea was omitted and a considerable decrease in Sphaerotilus was observed during the month of August. The nitrogen enrichment was initiated again in August but the increase in Sphaerotilus biomass did not occur until September. This emphasizes again the delayed response observed in natural systems. Both nitrogen and carbon enrichments were constantly maintained after August, 1964 as Sphaerotilus densities in both enriched sections strongly indicate (Appendices VI and VII).

Determination of the Relative Abundance of Benthic Plants

Because of the shallow water on the riffles, both benthos and periphyton have been combined in the study of Berry Creek. However, the real benthos did not attach to glass slides and a simplified

index was included to indicate the presence of these benthic plants occurring in the stream (Appendix V). These data indicate a peak of abundance of these benthic plants during the months of March, April and May.

Determination of Abundance by Detailed Examination of Stream Substrate

A method used for sampling the benthic and periphyton communities of the stream was the removal of a portion of the stream substrate for detailed examination. This was done by carefully excavating 0.2m^2 areas of the stream substrate, fitting porcelain enameled steel trays of that size into the cavities, and recomposing the substrate on the trays. The pattern of substrate on the trays resembled the original arrangement in the surrounding stream bed as closely as possible. Three trays were fitted into each of four experimental sections in this manner. Each tray remained in the stream for three months prior to removal, and was returned to the stream near the end of the day that it was removed. Once a month, a tray from each section was carefully removed from the stream and sealed in the photosynthesis-respiration chamber (Figure 7) described by McIntire et al (54). Following estimation of primary production and community respiration, the substrate on the tray was scoured relatively free of organisms and removed from the chamber. The suspension of

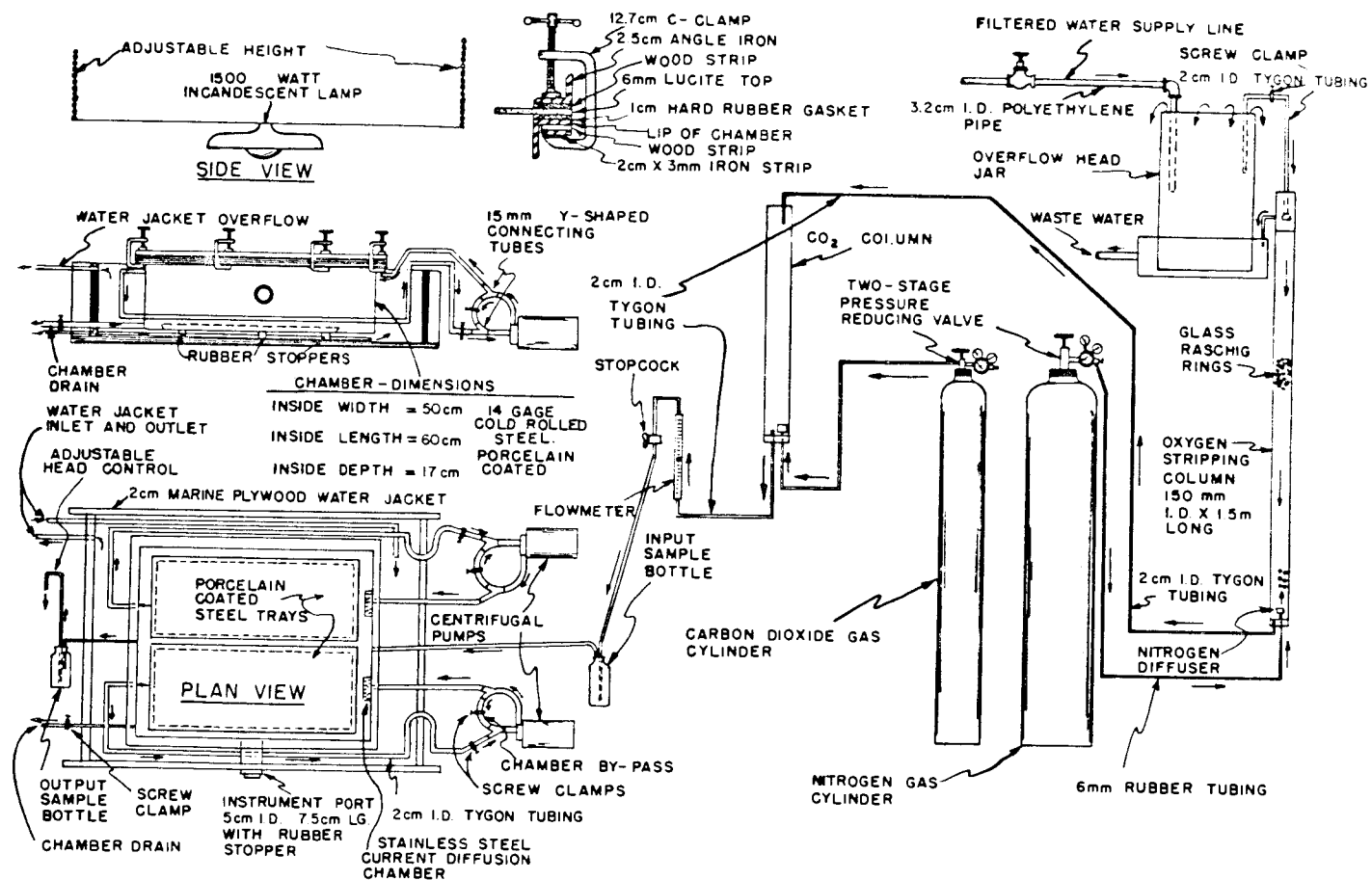


Figure 7. Diagram of the photosynthesis-respiration chamber

harvested materials was removed from the chamber and homogenized. Samples of the suspension were removed for determination of biomass, organic matter, caloric content, pigment analysis, and species composition.

Biomass. A 400 milliliter sample of the homogenate was dried to determine the biomass recorded as dry weight of the harvested material (Table 9). Material harvested from the light, unenriched riffle was more abundant than that from the shaded, unenriched riffle but considerably less abundant than harvested from either of the enriched sections. In the shaded, unenriched section, the biomass was larger during the early summer months. Biomasses from both enriched sections were somewhat erratic but were greater during the fall and winter months.

Organic matter. The content of organic matter was determined by ignition of the dried materials (Table 10). Analyses of the biomasses showed larger amounts of organic matter in the shaded, unenriched section, in February and August while the light, unenriched section contained most during May and June. In the shaded, enriched section, organic matter was highest in December, January and March and in the light, enriched section peak amounts occurred in November, December and January. These data are summarized in Table 7 which indicates the mean organic matter content of the unenriched

Table 9. Estimates of biomass, expressed as grams of dry weight of the harvested material/m²

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Shaded, unenriched	67	25	30	13	11	11	43	13	13	9	57	73
Light, unenriched	81	113	103	275	169	105	95	70	105	118	78	120
Shaded, enriched	144	221	125	49	204	158	220	275	116	120	707	601
Light, enriched	95	86	168	63	35	127	68	17	15	339	639	866
Mean dry weight harvested material, g/m ²												
Shaded, unenriched - 30						Shaded, enriched - 245						
Light, unenriched - 119						Light, enriched - 210						

Table 10. Estimates of biomass, expressed as grams of organic matter/m²

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Shaded, unenriched	23	9	13	10	4	7	22	7	7	3	8	11
Light, unenriched	23	59	47	122	85	52	47	31	36	38	21	38
Shaded, enriched	50	75	42	14	36	18	27	40	24	42	86	118
Light, enriched	34	18	37	17	13	20	16	8	5	102	96	116
Mean organic matter, g/m ²												
Shaded, unenriched	- 10						Shaded, enriched	- 48				
Light, unenriched	- 50						Light, enriched	- 40				

sections is much greater than for the enriched sections.

Caloric values. Caloric values (Table 11) were determined using a Parr semi-micro Oxygen bomb Calorimeter, model 1411, following techniques described by the Parr Instrument Company (66). There was a reasonable correlation between caloric values and organic matter determined for the unenriched sections (Table 10 and Table 11). A general increase in organic matter and caloric values was observed for the shaded, unenriched section during early spring with a considerable decrease during May and June. This was followed by a similar increase and decline during the autumn months.

A correlation between organic matter content and caloric value was observed in the light, unenriched section which showed a continual increase during the spring and summer months and a gradual decline in the months that followed. Determinations for the enriched sections were very erratic throughout the year. Caloric values in the light, unenriched section were consistently higher and those of the shaded, unenriched consistently lower than were values for the other sections. The harvested materials from both enriched sections contained great amounts of silt which caused biomasses from these sections to weigh more than from the unenriched sections. However, the mean results of the combustion of these materials indicated that both enriched sections contained less organic matter and caloric

Table 11. Estimates of biomass, expressed as kilocalories/m²

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Shaded, unenriched	87	38	57	5	15	16	99	30	28	11	3	4
Light, unenriched	89	286	207	484	367	73	199	121	135	133	77	165
Shaded, enriched	216	183	169	81	483	9	87	9	65	139	29	168
Light, enriched	75	123	123	71	52	12	62	31	20	37	40	39
Mean kilocalories/m ²												
Shaded, unenriched	- 34			Shaded, enriched - 136								
Light, unenriched	- 195			Light, enriched - 57								

content per square meter than the light unenriched section.

Chlorophylls and carotenoids. Pigment concentrations were determined by the techniques described by Richards with Thompson (77). Table 12 records the seasonal variations in chlorophyll a for the four experimental sections and the mean concentrations. In order of decreasing concentration the means were: 276 mg/m² for the light, unenriched section, 32 for the shaded, unenriched, 29 for the shaded, enriched and 25 for the light, enriched section. The mean ratios of total carotenoids to chlorophyll a were higher in the enriched sections than the unenriched sections (Table 13). A summary of these data shows the comparison of the total amounts of five pigments from 12 monthly determinations (Figure 8).

The light, unenriched section produced the largest amounts of chlorophylls a, b, and c and nonastacin carotenoid and the least amounts of astacin carotenoid. Differences between the remaining three sections were not great, except that the shaded, unenriched section showed the largest amounts of nonastacin carotenoid.

Ratios of chlorophyll a to organic matter and chlorophyll a to total carotenoids show various seasonal fluctuations (Figure 9). A summary comparing mean amounts of chlorophyll a and gross production from the enriched and unenriched sections shows lower values in the enriched sections than the unenriched for each of the above ratios (Figure 10).

Table 12. Estimates of chlorophyll a expressed as mg/m²

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Shaded, unenriched	33	68	31	30	49	39	23	10	5	12	37	61
Light, unenriched	37	78	110	839	832	270	203	276	182	332	71	84
Shaded, enriched	23	47	19	18	15	29	24	25	16	34	78	32
Light, enriched	24	27	73	22	16	12	8	7	4	21	57	34
Mean chlorophyll <u>a</u> , mg/m ²												
Shaded, unenriched	- 32					Shaded, enriched	- 29					
Light, unenriched	- 276					Light, enriched	- 25					

Table 13. Ratio of total carotenoids expressed as MSPU/mg chlorophyll a

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Shaded, unenriched	.284	.206	.505	.232	.384	.336	.387	.919	.137	.547	.463	.304
Light, unenriched	.413	.279	.359	.346	.262	.267	.089	.270	.283	.265	.317	.193
Shaded, enriched	.261	.406	.616	.506	.503	.944	.932	.506	.414	.714	.343	.565
Light, enriched	.494	.557	.382	.263	.695	.647	1.090	.779	.526	.773	.356	.277
Mean Ratio												
Shaded, unenriched - .407 Shaded, enriched - .559												
Light, unenriched - .279 Light, enriched - .570												

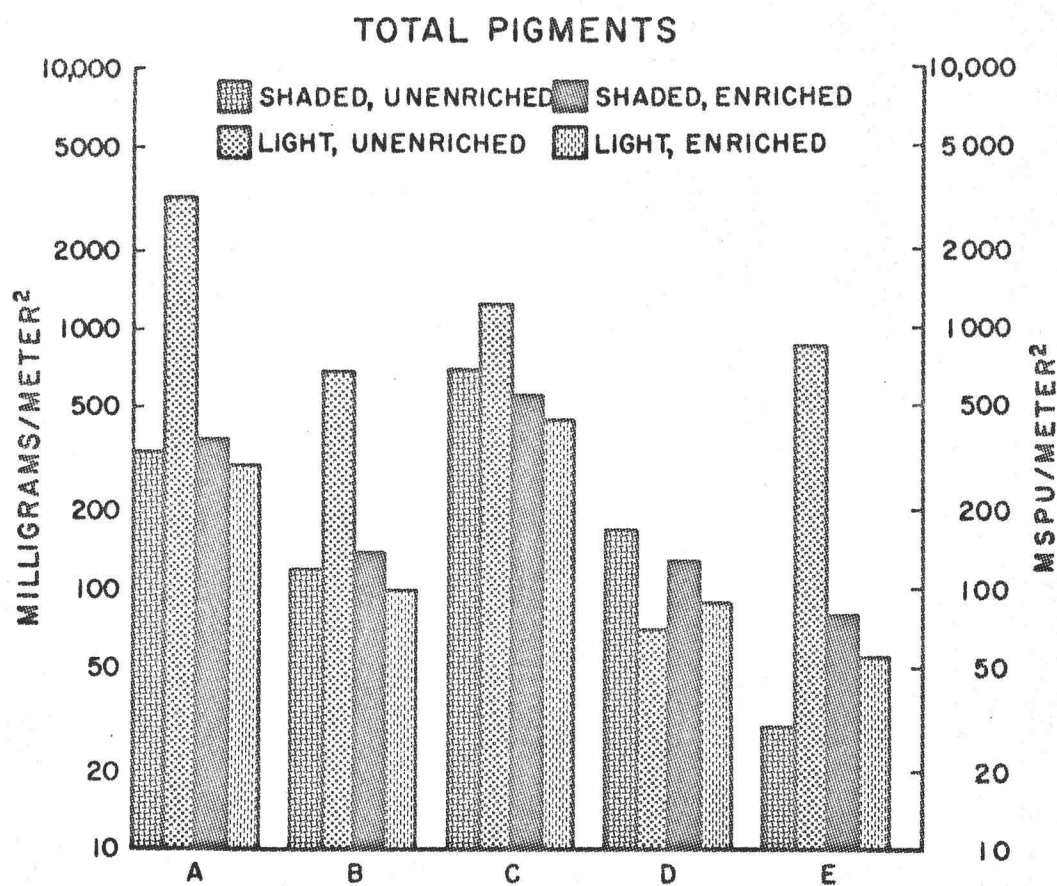


Figure 8. Comparison of relative concentrations of pigments from the four experimental sections of Berry Creek; A = chlorophyll a, B = chlorophyll b, C = chlorophyll c in mg/m^2 and D = astacin carotenoids, E = nonastacin carotenoids in MSPU/m^2 , Feb., 1964 through Jan., 1965

Lane (43) found that considerable amounts of chlorophyll a remained on the substrate from which harvested materials had been removed. The present study and many similar studies have not included pigment extraction of the scoured substrate. However, a trial made during the final stages of this investigation showed that complete removal by scouring organic materials from the substrate was not successful. In order to estimate the magnitude of error involved, a portion of scoured substrate was submerged overnight in a solution of 90 percent acetone and pigment concentrations were determined. Results of these determinations indicated that 50 percent or more of the chlorophyll a content may be retained on the scoured substrate from the enriched sections and lesser amounts from the unenriched sections.

Species composition of the harvested materials were identical with those determined from the microscope slides and grid record and no additional forms were listed. In conjunction with this phase of the study, an experiment was designed to investigate the possibilities of using artificial substrates. Concrete blocks, nonglazed clay tile slabs and new rocks not indigenous to the stream were composed on additional trays in the stream. Observations were recorded as to the time required for colonization of the artificial substrate by plant communities similar to those on the surrounding native stream bed. No quantitative tests were performed with the various types of substrate but all the different types underwent a period of colonization

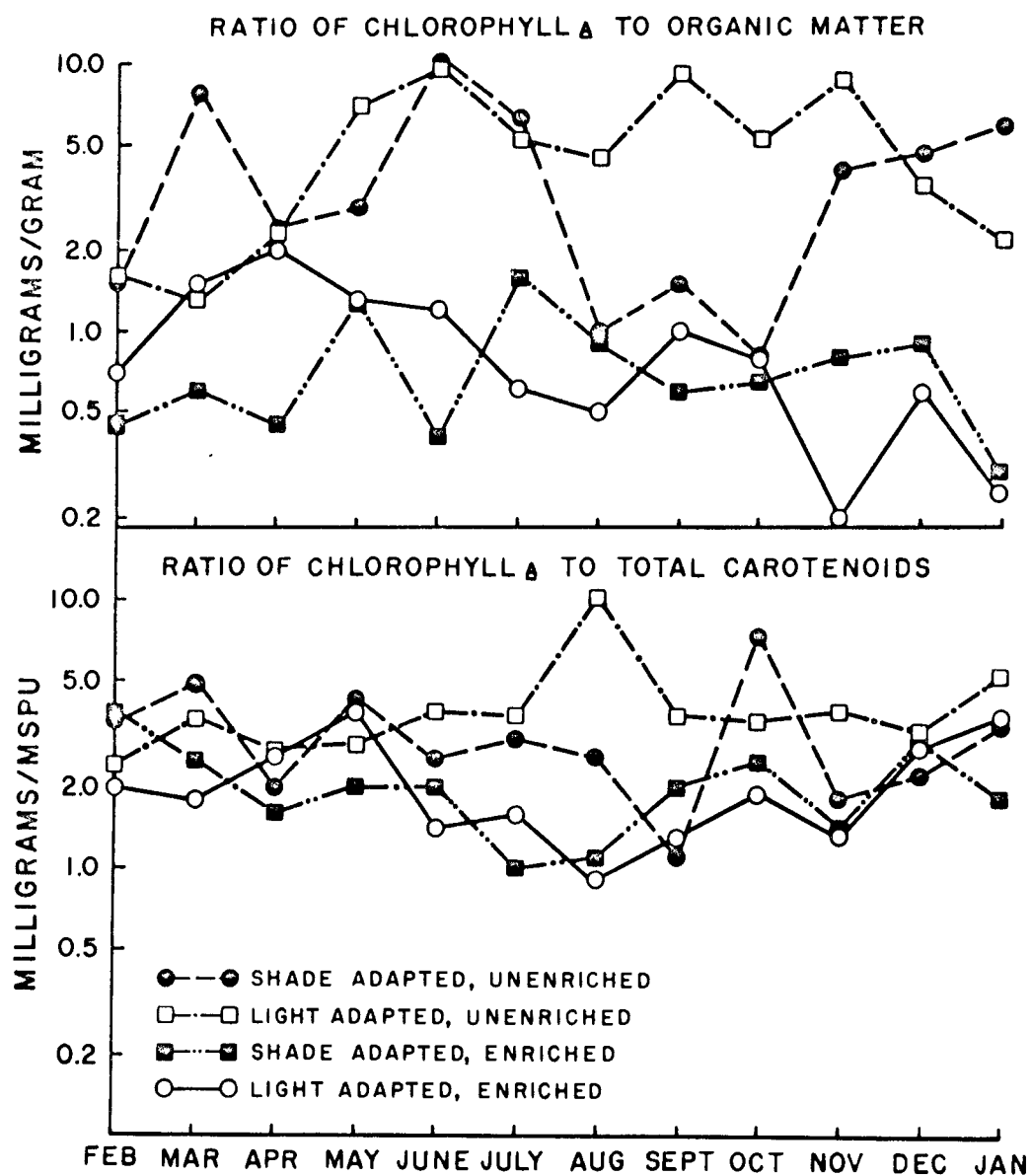


Figure 9. Ratios of chlorophyll a to organic matter and chlorophyll a to total carotenoids for the four experimental sections of Berry Creek, Feb., 1964 through Jan., 1965

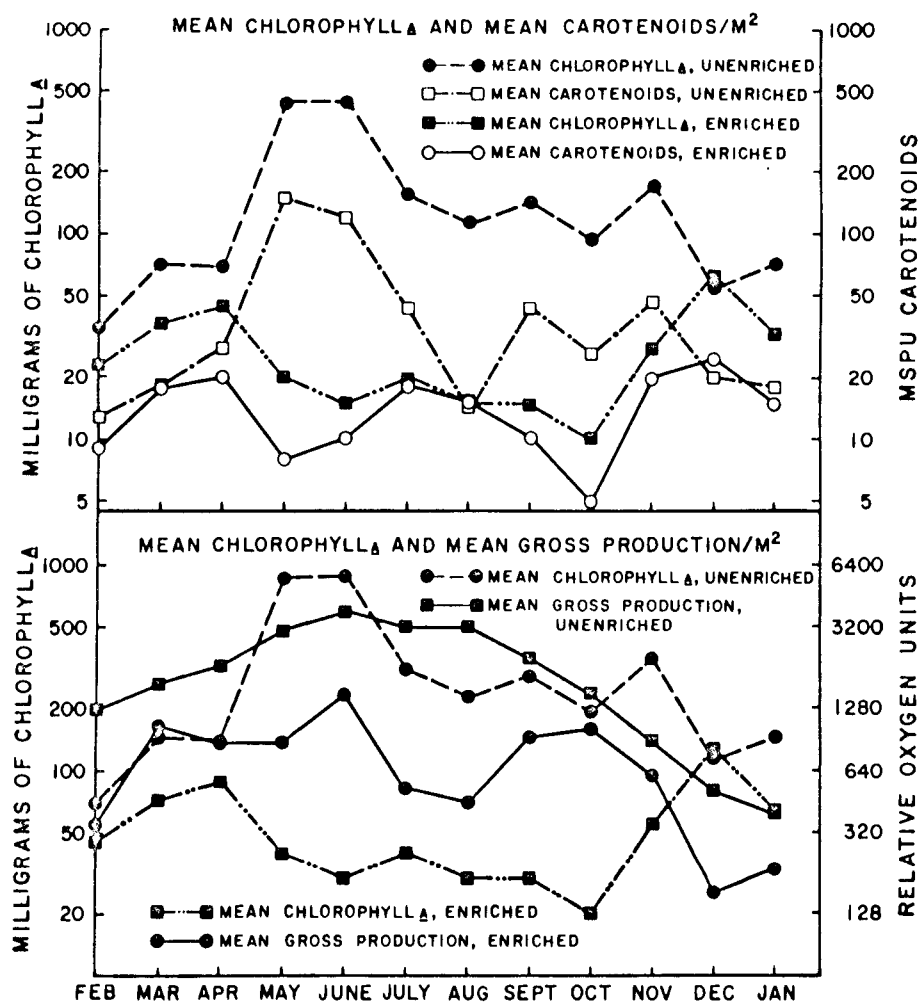


Figure 10. Comparisons of the means of chlorophyll_a and total carotenoids and means of chlorophyll_a and gross production for the unenriched and enriched sections of Berry Creek, Feb., 1964 through Jan., 1965

of approximately three months by which time the density was equal to that of the surrounding stream bed community. This is compared with a requirement of 5-8 weeks reported by Waters (95) and one year by Blum (3). More extensive studies of this nature have been made by Cook (10) and others reviewed by Sládečková (82).

Measurement of Primary Production and Community Respiration

The substrate on the trays remained intact in the stream for three months. This period was required to adequately colonize the substrate to an extent comparable with the surrounding stream bed. Following colonization, one tray (0.2m^2) from each experimental section was removed from the stream each month and sealed in a photosynthesis-respiration (P-R) chamber. The volume of the P-R chamber was 50 liters and exchange rates approximating 200 milliliters per minute were maintained during the periods of photosynthesis and respiration. The procedure followed was modified from that described by McIntire et al (54). Estimates of primary production (Table 14) and community respiration (Table 15) were made by measuring the changes in concentration of dissolved oxygen by the Alsterberg Modification of the Winkler Method (2). In the P-R chamber, the community was allowed to reach an equilibrium in the dark for a period of 10-12 hours corresponding to the normal dark period of the

Table 14. Estimates of oxygen produced, expressed as $\text{mg/m}^2/\text{day}$

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Shaded, unenriched	833	1092	918	1029	841	731	518	784	412	151	87	75
Light, unenriched	1138	1537	2335	3760	5160	4185	4388	2612	1942	1251	718	563
Shaded, enriched	244	703	527	632	902	505	479	626	652	792	105	211
Light, enriched	313	925	856	775	1443	317	210	829	971	189	136	117
Mean O_2 , mg/m^2												
Shaded, unenriched	- 623						Shaded, enriched	- 532				
Light, unenriched	- 2467						Light, enriched	- 590				

Table 15. Estimates of oxygen consumed, expressed as $\text{mg/m}^2/\text{day}$

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Shaded, unenriched	1440	1500	1800	1800	3000	1080	600	1272	1584	720	408	480
Light, unenriched	1272	2664	2400	4920	3312	3720	3432	2832	2400	3240	3000	1320
Shaded, enriched	1992	2544	2400	3000	5520	3840	2352	4104	4320	3480	3552	4152
Light, enriched	2040	1680	2280	2640	6240	3840	2376	4248	3888	3912	2424	3720
Mean O_2 , mg/m^2												
Shaded, unenriched	- 1307						Shaded, enriched	- 3438				
Light, unenriched	- 2876						Light, enriched	- 3274				

photoperiodic cycle under which the community developed. Following the dark period, the community was exposed to different illumination intensities in each of a series of five light periods, with a duration of one hour apiece. The different intensities of light were: 72, 130, 440, 820 and 2000 foot candles for communities from the shaded rifles and 120, 340, 670, 1400 and 2350 foot candles for the sun adapted communities. The range of adjustment available in the research apparatus governed the selection of the levels of light intensity. The intensity of each successive light period was increased in an attempt to estimate the productive capacity of shade and sun adapted communities under varying light conditions and to determine saturating light intensities (Table 16). At the beginning and end of each period of different light intensity, the concentrations of dissolved oxygen in the influent and effluent water was determined. The net rate of oxygen change during the periods of photosynthesis was calculated according to an equation suggested by McIntire et al (54).

$$\text{Net Oxygen change} = Ft \left[\frac{E_o + E_1}{2} - \frac{I_o + I_1}{2} \right] + V(E_1 - E_o)$$

where

F = rate of exchange in liters per hour.

t = time interval in hours.

E_o = dissolved oxygen concentration in mg/liter of the effluent water at the beginning of the time interval.

E_1 = dissolved oxygen concentration in mg/liter of effluent water at the end of the time interval.

I_0 = dissolved oxygen concentration in mg/liter of influent water at the beginning of the time interval.

I_1 = dissolved oxygen concentration in mg/liter of the influent water at the end of the time interval.

V = volume of water in P-R chamber.

The P-R chamber was darkened at the end of the last period of light exposure and covered with several thicknesses of black polyethylene sheeting. After approximately one hour, allowed for the community to come to equilibrium in the dark, the concentrations of dissolved oxygen in the influent and effluent were determined at one hour intervals for a period of three hours. Estimates of community respiration (Table 15) show that greater amounts of oxygen are consumed during the summer months on each of the riffles, at temperatures of 12°C compared with spring temperatures of 4 to 6°C.

The influence of temperature on respiration and gross primary production by periphyton communities in laboratory streams has been studied by Phinney and McIntire (70). They showed that considerable increases in respiration and production occurred when temperatures were increased within the range of 6 to 20°C. It is reasonable to assume that the range of spring to summer temperatures listed above for Berry Creek produces a similar influence on the stream

Table 16. Saturating light intensities in foot candles determined for samples from the four experimental sections

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Shaded, unenriched	400	800	900	1500	700	400	500	200	650	600	350	150
Light, unenriched	1800	300	700	1000	750	1000	800	800	1700	300	1100	1000
Shaded, enriched	150	300	300	200	400	300	150	200	450	200	200	150
Light, enriched	500	350	1000	900	900	150	150	300	400	250	350	250
Mean Saturating Intensities												
Shaded, unenriched - 600							Shaded, enriched - 250					
Light, unenriched - 950							Light, enriched - 450					

community. Estimates of mean respiration for the experimental sections were: shaded, unenriched = $1307 \text{ mgO}_2/\text{m}^2/\text{day}$; light, unenriched = 2876; shaded, enriched = 3438 and light, enriched = 3274 (Table 15). These data emphasized the greater respiration rates in the enriched sections than in the unenriched sections.

The rate of gross photosynthesis was estimated by adding the net oxygen evolution during the periods of photosynthesis to the mean rate of oxygen consumption during the dark period of respiration. With these data, a curve of the monthly rate of production was constructed for each experimental section by plotting the rate of gross photosynthesis at the different light intensities in the P-R chamber. It was assumed that the production rate determined once each month represented a mean of the productive ability of the community for that month.

Mean estimates of oxygen production (Table 14) for the four experimental sections in $\text{mgO}_2/\text{m}^2/\text{day}$ were: light, unenriched = 2467; shaded, unenriched = 623; light, enriched = 590; and shaded, enriched = 532. The light, unenriched riffle generally showed an increase in production during the spring and summer months, followed by a gradual decline for the remainder of the year. Spring and autumn peaks of production were observed on each of the remaining riffles and mean production estimates were very similar in all three cases as shown above.

Ratios of community respiration to organic matter content (Figure 12) shows two very distinct peaks of oxygen consumption and gross production for three of the experimental sections. These peaks occur in the months of May-June and September-October. The one exception is the light, unenriched riffle which showed a much longer period of production from May to November with a maximum occurring in August.

In order to estimate the total production for the month, light intensity values were measured on each experimental riffle at two-hour intervals over an entire day. The measurements were taken at two-week intervals and a mean for each month was determined. These mean values were applied to the appropriate rate of production curve to estimate the production per square meter per day in each of the experimental sections of the stream (Figure 11).

Assuming a photosynthetic quotient of 1.25 (80), the production estimates for each month were combined to calculate the total production per year expressed as glucose units in $\text{Kg/m}^2/\text{year}$. These data for the four experimental sections are compared with a variety of river communities and two laboratory streams (Table 17).

These light data were also used to estimate the total energy received by each experimental section and to calculate ecological efficiencies which were listed as gross production/kilocalorie/ m^2 (Table 18 and Figure 13). Mean efficiencies for the four experimental

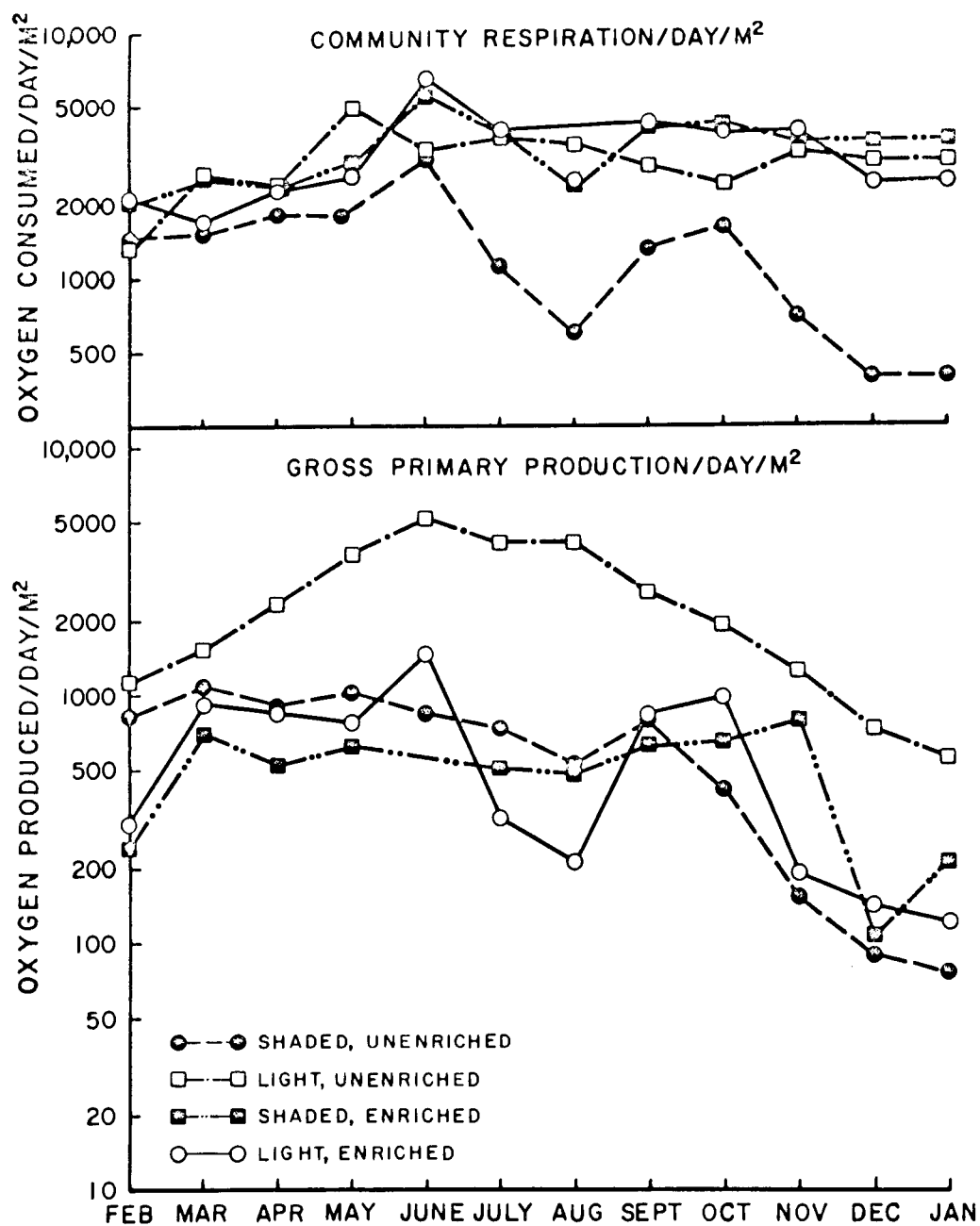


Figure 11. Rates of community respiration and gross production determined for the four experimental sections of Berry Creek, Feb., 1964 through Jan., 1965

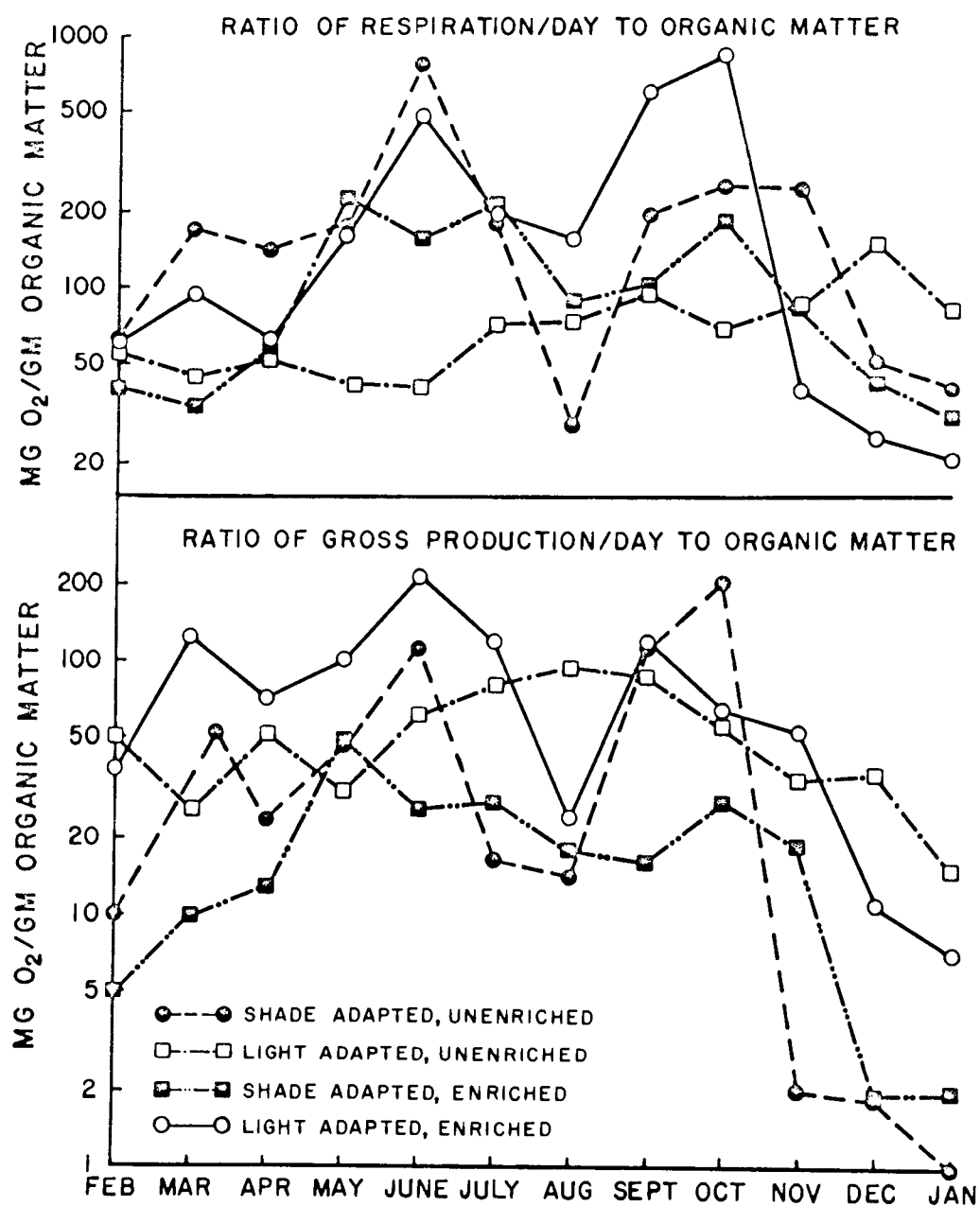


Figure 12. Ratios of the daily rate of community respiration to organic matter and of gross primary production to organic matter determined for four experimental sections of Berry Creek, Feb., 1964 through Jan., 1965

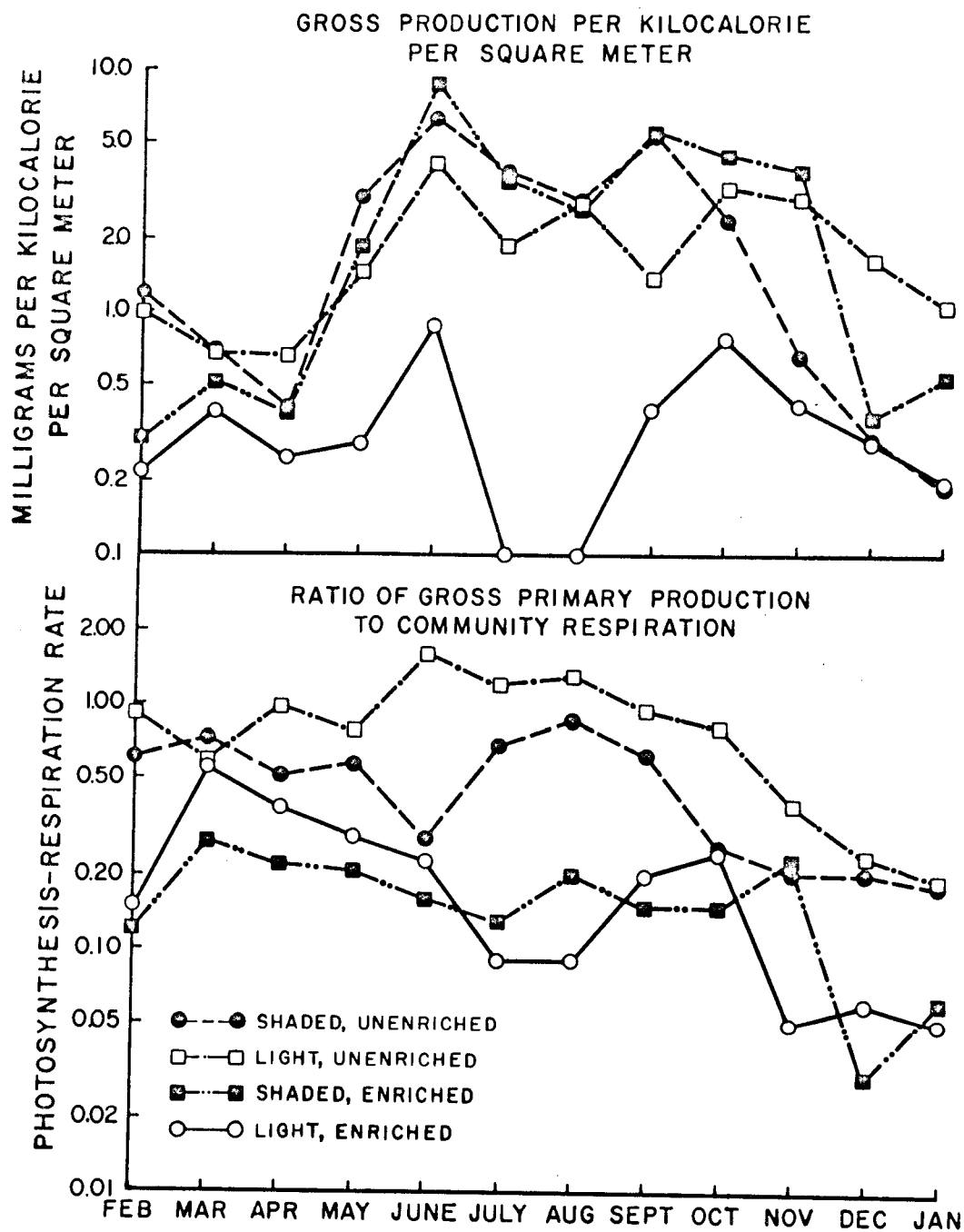


Figure 13. Gross primary production per kilocalorie per square meter and ratios of gross primary production to community respiration (P/R ratios) calculated for the four experimental sections, Feb., 1964 through Jan., 1965

Table 17. Comparative annual rates of gross primary production

Water	Glucose produced kg/m ² /year
(1) Logan River:	
Canyon section	1.2
Third impoundment	4.6
Canyon Road below first impoundment	5.0
Mendon Bridge, last riffle before valley base level	3.1
(2) Laboratory Stream 1, light adapted (343 days)	1.3
Laboratory Stream 6, shade adapted (343 days)	0.9
(3) Arakawa River:	
Canyon section	0.10-0.44
Lower section	0.15-0.91
Berry Creek:	
Shaded, unenriched riffle	0.07
Light, unenriched riffle	0.30
Shaded, enriched riffle	0.06
Light, enriched riffle	0.07

(1) McConnell and Sigler, 52;

(2) McIntire et al, 54;

(3) Kobayasi, 37.

Table 18. Ecological efficiencies expressed as gross production/kilocalorie/m²

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Shaded, unenriched	1.19	0.68	0.40	3.00	6.14	3.76	2.82	5.26	2.40	0.66	0.31	0.19
Light, unenriched	0.96	0.68	0.66	1.44	4.06	1.84	2.78	1.36	3.26	2.95	1.65	1.11
Shaded, enriched	0.30	0.52	0.38	1.84	8.77	3.40	2.62	5.47	4.38	3.84	0.37	0.54
Light, enriched	0.22	0.39	0.25	0.29	0.90	0.11	0.10	0.40	0.78	0.41	0.30	0.20
Mean Efficiencies												
Shaded, unenriched	- 2.23						Shaded, enriched	- 2.70				
Light, unenriched	- 1.90						Light, enriched	- 0.37				

sections were: shaded, unenriched - 2.23, light, unenriched - 1.90, shaded, enriched - 2.70, and light, enriched - 0.37.

These mean efficiencies are compared with efficiencies estimated for a variety of natural communities, algal cultures and laboratory streams (Table 19). This comparison emphasizes the low efficiency of light adapted, enriched communities; however, the efficiencies for each of the experimental sections were within reasonable agreement with those of most other natural communities.

Data for this phase of the study were also used to determine the photosynthesis-respiration (P/R) ratios for each of the experimental sections (Table 20). Comparisons of the ecological efficiencies (Table 18) with P/R ratios (Table 20) indicated comparable estimates for the unenriched sections, but those for the enriched sections were more difficult to reconcile.

Table 19. Efficiencies of fixation of usable light energy by various communities as compared to those of Berry Creek expressed as gross production/usable light

Community	Percentage	Source
Laboratory microcosm	3	Odum and Hoskin (62)
Silver Springs	5.3	Odum (61)
Georgia salt marsh	6.1	Teal (90)
Root Spring	0.2	Teal (89)
Marine phytoplankton, visible sunlight below saturation intensity	17.5	Ryther (80)
Chlorella, small cultures (5000-8000 lux)	12 - 15	Wassink, Kok, and van Oorschot (94)
Chlorella, small cultures (1500-3000 lux)	20 - 24	Wassink, Kok, and van Oorschot (94)
Laboratory Stream 1 (<u>ca.</u> 6000 lux)	12.8	McIntire (55)
Laboratory Stream 6 (<u>ca.</u> 2000 lux)	22.7	McIntire (55)
Berry Creek:		
Shaded, unenriched riffle	2.23	
Light, unenriched riffle	1.90	
Shaded, enriched riffle	2.70	
Light, enriched riffle	0.37	

Table 20. Ratio of gross primary production to community respiration

	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Shaded, unenriched	0.60	0.73	0.51	0.57	0.28	0.68	0.86	0.62	0.26	0.21	0.21	0.16
Light, unenriched	0.90	0.58	0.97	0.77	1.60	1.20	1.32	0.93	0.81	0.39	0.24	0.43
Shaded, enriched	0.12	0.28	0.22	0.21	0.16	0.13	0.20	0.15	0.15	0.23	0.03	0.05
Light, enriched	0.15	0.55	0.38	0.29	0.23	0.09	0.09	0.20	0.25	0.05	0.06	0.03
Mean Ratio												
Shaded, unenriched	- 0.47						Shaded, enriched	- 0.16				
Light, unenriched	- 0.85						Light, enriched	- 0.20				

DISCUSSION

The riffles of Berry Creek are covered by rapidly flowing water to a depth of approximately six inches. Because the stream is shallow, the benthic community in this study included both real benthos and periphyton.

The spring and autumn peaks of numbers of periphytic organisms in the unenriched sections of Berry Creek parallel reports by Butcher (6) of similar peaks for oligotrophic waters with corresponding winter and summer lows. Transeau (91) attempted to explain this phenomenon by classifying algae into six seasonal types. Kofoed (39), Allen (1), and Pearsall (69) did not agree that this was a temperature (seasonal) response, but rather a response to availability of nutrients because diatoms were most abundant in fresh-water rich in nitrate and silica and possessing a low basic ratio. These investigators have referred to peaks of abundance following periods of flooding which replenish depleted nutrients in oligotrophic waters.

The data presented for Berry Creek (Figure 3) also indicated that this phenomenon occurred in response to available nutrients (enrichment). A low flow rate of oligotrophic waters occurring in summer months provided an opportunity to test this hypothesis. These conditions should, and did, cause a decrease in the periphyton in the unenriched sections (Figure 3). However, solar radiation and

temperature also decreased during part of this period of growth and the decreased occurrence of periphyton could not be explained by oligotrophy alone.

If the nutrient level in the enriched sections was decreased, during the same period of time as above, to a range less tolerable for the abundant heterotrophic community, yet providing sufficient nutrients for autotrophic growth, the autotrophic community should show a definite increase. Such an increase did occur during both experimental periods as described earlier and as shown in Figure 3.

These data support the notion that a deficiency (oligotrophy), as well as an over abundance (pollution), of nutrients may periodically induce minimums of occurrence in the kinds and number of organisms.

Table 2 also shows the degree of oligotrophy which existed in Berry Creek coincidental to the periods of low periphyton occurrence. Analyses for the winter season, as well as for May and June, show a considerable decrease in: biocarbonate, nitrate, silica, magnesium, potassium, chloride, sodium, calcium, dissolved solids and specific conductance.

In May, low temperatures occurred during a period of increasing production and increasing kinds and numbers of autotrophic periphyton. During June the reverse was true. This observation provided further evidence that the summer minimum occurred in response to

some factor other than temperature. The winter minimum of numbers of periphytic organisms in the unenriched sections of Berry Creek, on the other hand, was coincident with low nutrient levels, low temperatures, shorter photoperiods and decreased solar radiation. Since limiting factors become more critical toward the extremes (60), it is possible that minimum as well as maximum numbers of organisms occur in response to an indistinguishable complex of limiting factors.

Radiation intercepted by tree cover plays a major role in the energy balance of forested communities. At Berry Creek, a relationship was noted between the amount of full available energy and that received on the stream in each section. However, this was not so pronounced in the shaded sections (Figure 2). As available radiation increased there was an increase in total quantity of light, but a decrease in the percentage reaching the stream. These data are in accord with similar investigations (64, 11, 25, and 93).

Readings of incident light were taken at two-hour intervals during an entire day while in comparable investigations readings were taken only on completely unobscured days and within two hours of zenith (64, 56). Vezina (93) separated light observations into clear, partially cloudy, and overcast days. In the majority of cases, values have been limited to extrapolations from a few measurements taken during a seasonal period (64, 11, 56, 37, and 78).

In the twelve months surveillance of insolation at Berry Creek, a pyrliograph was recording continuously. Appendix (IX) records thirty days taken at random during the light study. It is noteworthy that only one of the thirty was without clouds and approximately 75 percent of the sampling days received less than 65 percent of the light received on the cloudless day. This provided adequate reasons for measuring insolation during the entire day and on all types of days regardless of the overcasting conditions.

Considerable emphasis has been placed on the importance of the effect of different wave lengths of light on plant growth. The principal plant photochemical reactions may generally be considered as: photosynthesis (435 and 675 $m\mu$); chlorophyll synthesis (445 and 650 $m\mu$); phototropism (370, 445 and 475 $m\mu$); photomorphogenic induction (660 $m\mu$) and photomorphogenic reversal near 730 $m\mu$. Gates (23) has given a brief review of some of the work committed to the study of spectral distribution of solar radiation at the earth's surface. However, work has been limited in spectral analysis of light under forest canopies.

The major portion of light that penetrates the forest canopy is within the green band near 560 $m\mu$ and the processes listed above are relatively unaffected in this range (78). In contrast, Ovington and Madgwick (64) have indicated that sun flecks resulting from holes in the canopy may be capable of admitting, for brief intervals,

sufficient amounts of light to allow the primary photo-chemical reactions to continue in the periphyton community. In addition, Sverdrup et al. (87) showed that, in nature, diatoms have their greatest growth where red components of light are much reduced and blue and green light prevails. Likewise, Strickland (86) has shown systrophism (plastid aggregation) in some Bacillariophyceae due to high light intensity.

It would be desirable to investigate the various wave lengths of light which penetrate the canopy of a mixed woodland, but its continuous monitoring for any length of time appears to be most impracticable. Robertson and Holmes (78) have shown that meaningful comparisons in different wave bands of solar radiation are made impossible by scattered clouds, broken sky cover, and clouds passing across or in the vicinity of the sun. It is assumed that comparable discrepancies would be noted by reorientation of leaves within the canopy by wind and other agents and by the effects of the natural gross changes in a stand of mixed woodland.

Results obtained from the light, enriched section were not extremely different from those received from the two shaded sections. No correlation between variations in mean solar radiation and production was shown in any of the experimental sections (Figures 2 and 11). It was assumed that the light reaching the stream in each section was of saturating intensity. Support for this assumption is shown

by the mean saturating light intensities determined for the communities of the four experimental sections (Table 16).

Several studies have been made of the importance of the effect of day length on algal production (27, 84, 50, 88, and 20). Figures 2, 4 and 11 appear to show a definite relationship between day length and production of benthic communities in shallow, rapidly flowing streams. This correlation is probably related both to day length and rate of insolation of the stream. When comparisons are made of Figures 2 and 11, however, the rate of insolation does not appear to be the major factor involved. The production estimates for the shaded riffles do not closely correspond to the peak of insolation during the spring months or to the increased insolation during fall months when production is decreasing.

The primary producers in the light, enriched section were mostly the periphyton and comparisons made of the Figures 2 and 11 show an alternation of peaks of insolation with peaks of production in this section. This may be indicative of the suppressive influence of high intensity illumination on the periphyton production in shallow streams.

The culture experiments have shown that the Berry Creek strain of Sphaerotilus natans produced good growth at a wide range of temperatures and was capable of adapting to quite low temperatures. These data agree with estimates of growth of Sphaerotilus in

Berry Creek, determined during periods of very low temperature (Figures 4 and 5). Both sets of experiments indicated a direct response to available nitrogen (Table 4 and Appendices VI and VII). These data also emphasize the importance of the availability of nutrients in oligotrophic waters, more pronounced in Berry Creek during the summer months (Table 2).

The low rate of production by corn syrup in the laboratory streams was not explained beyond the fact that it contained an unknown preservative. In some cases the syrup actually appeared to inhibit growth while excellent growth was produced by other carbon sources when combined with a specific nitrogen enrichment. Sucrose produced maximum growth in combination with urea as the nitrogen source and dextrose showed highest production with peptone.

An explanation for the specificity of carbon and nitrogen combinations was not attempted. An increase in rates of nitrogen enrichment was equally pronounced with sucrose and dextrose as carbon sources. However, when no nitrogen enrichment was available, increases in the dextrose produced greater increases in production than did a comparable increase in sucrose.

In experiments designed to study the influence of stream snails on the standing crop and export of Sphaerotilus, it was assumed that with similar rates of enrichment, production of Sphaerotilus was comparable in each laboratory stream. It was further assumed that

the rate of growth of Sphaerotilus, in relation to cropping, was equivalent in each of the streams. The added effect of competitive cropping was recognized but no adequate method was available for its estimation.

Regardless of the specific explanation, the fact remained that increasing numbers of snails paralleled disappearance of Sphaerotilus biomass which was assumed to have been ingested by them.

It was obvious from various studies in culture and laboratory streams that the availability of nutrients was an important factor limiting the growth of Sphaerotilus in Berry Creek. It also follows that the presence of grazers in the stream intensified the difficulty of maintaining desirable growths of Sphaerotilus.

Table 8 shows lower percentages of organic matter contained in the biomass of the enriched sections. This could have been caused by the dense mat of Sphaerotilus filtering silt from the creek water. This has been studied at length by Naumann (58) and Jaag (34) who described the purifying, as well as the polluting effects of Sphaerotilus. Wurtz (99), in his work with pollution at outfalls from milk processing plants and sugar refineries, concluded that the presence of Sphaerotilus natans is an index of organic pollution. He recommended using Endoplastoderma and Torula in the treatment of waste waters which are rich in sugars in order to reduce pollution and produce a useful food by-product, tourteaux. To date, however, his

recommendations of biological recovery from pollution have, in the main, gone unheeded.

A review of investigations similar to that of Berry Creek shows definite, and 'suspected universal, correlation between the density and diversity of micro-algae. In a simplified diversity index of the river Severn, Reese (76) shows a dominant community of: Cocconeis, Gomphonema, Nitzschia, Synedra, Achnanthes and Navicula with seasonal periodicities expressed as abundant, frequent, rare and very rare.

Likewise, in studies of calcareous streams, Butcher (4) described Cocconeis as one of the dominant organisms of a climax algal community variously persistent throughout the year. He projected a climax association of algae for most rivers and his list of Bacillariophyceae was remarkably similar to that for Berry Creek. Margalef (49) indicated that flowing waters favor the benthic organisms and that an indigenous community can develop only if it is capable of competing in a particular environment. The importance of the periphyton has been emphasized by Hynes (31) who indicated that the periphyton in aquatic systems may be considered, in many respects, more important than macrophytes as oxygenators.

In his work with biological indicators of pollution, Campbell (7) stressed the individual requirements of each species and showed the need for knowing these requirements in order to predict the nature of

any particular environment. Conversely by knowing the physical, chemical and biological characteristics of an environment, a prediction could be made of the occurrence of organisms.

Campbell (7) showed age and color characteristics for Sphaerotilus natans which progressed from white to olive green, blue, gray and rusty brown. His study also included descriptions of zones of pollution and self-purification with accompanying dominant species as follows: recently polluted zone (Sphaerotilus natans and blue-green periphyton), zone of active decomposition (Leptomitius), recovery zone (blue-green and some green periphyton) and zone of clean water (blue-green and green periphyton and larger green algae). The similarities of Campbell's observations to those of Sphaerotilus and pollution zones in Berry Creek are considered significant.

In a study by Butcher (6), a wide difference occurred between densities of algae in oligotrophic and eutrophic waters. He emphasized a seasonal change in abundance for all rivers with minimum occurrence in winter and maximum in spring and fall. The occurrence of different dominant species in spring and fall was suggested as the reason for the two peaks of abundance, and the climax community was listed as: Cocconeis, Chamaesiphon and Ulvella. Results of these investigations are mostly in agreement with those for Berry Creek.

In a most significant study of the algae of enriched waters,

Butcher (5) emphasized the need for a knowledge of the biological conditions of a river at various stages of breakdown. He used submerged slides to sample periphyton and indicated that any stream environment supporting a periphyton count of more than 10,000/sq. mm. was in an unstable state. His description of succession from Sphaerotilus to Nitzschia to Chamaesiphon to Cocconeis is similar to observations made in Berry Creek. His suggestion of this succession as a general rule for any river, polluted with organic materials, appears to be acceptable.

The grid system used to record distribution and density of benthos in Berry Creek involved the staking of a permanent observation grid along the entire riffle area of each section. In an earlier study by Blum (3), lengths of rope were used to estimate distances on occasion and no permanent grid was maintained. Observations made of the enriched sections of Berry Creek indicated a greater biomass of Sphaerotilus in section IV (light, enriched) than in section III (shaded, enriched).

The enrichments were introduced into Berry Creek at the beginning of section III and were carried by the turbulent waters to the pool at the end of the section. Here the enrichments were contained briefly in a natural reservoir of slower flowing waters which may have allowed additional decomposition of the enrichments to a more usable form in section IV. This natural pool may have served as a

gigantic culture vessel that provided seed inoculum to section IV. The abundant growth of Sphaerotilus in section III is not to be overlooked, but when changes were made in the amount of enrichments, the time required for recovery was always greater in section III.

Of significance here is the concurrence of these data with those of the study of micro-algae. These include two separate evaluations of the influence of organic enrichment on the aquatic environment. The maximal and minimal occurrence of micro-algae alternated with maxima and minima of Sphaerotilus. These analyses have proven to be satisfactory for evaluating the extent of organic pollution in streams.

A comparison of the dry weight of the harvested materials with the estimates of organic matter indicated that a closer relationship existed in the unenriched sections than in the enriched. Sections I and II showed mean organic matter percentages of 33 and 42 respectively and the mean percentages for section III and section IV were 19.6 and 19.1 respectively. These data indicate a greater percentage of silt and debris in the harvested materials from both enriched sections and emphasize the filtering characteristics of Sphaerotilus.

The accumulation of leaf material in Berry Creek during the months of November, December and January may be compared to the accrual of allochthonous materials in the Oconee River (Nelson and Scott, 59). Estimates of organic matter were higher in the enriched

sections than in the unenriched during these months and could have been due to leaf materials entangled in the Sphaerotilus community.

In general, caloric determinations of the harvested materials showed fluctuations as did those for organic matter. However, the high content of silt and debris mixed with materials harvested from the enriched sections during November, December and January tended to reduce the caloric value even though organic matter/m² increased during this time. It follows that caloric values, harvested biomass and organic matter determinations for the light, unenriched riffle were more closely related than were those for any other section.

Odum (60) indicated that chlorophyll a in natural communities tends to adjust to 1.0 g/m² regardless of the thickness of the photosynthetic zone. A range of 0.1 to 3.0 g/m² has been compiled by Odum, McConnell and Abbott (62) for chlorophyll a concentrations in a variety of natural communities and algal cultures. In laboratory stream studies (McIntire and Phinney, 55) chlorophyll a ranges of 0.14 to 1.30 and 0.48 to 2.01 g/m² were observed.

In Berry Creek, a chlorophyll a range of 0.03 to 0.28 g/m² was observed. These concentrations are slightly less than those given above but are well within the ranges observed in other shallow streams as follows: Logan River, Utah, 0.30 g/m² (McConnell and Sigler, 52), Arakawa River, Japan, 0.04 g/m² (Kobayasi, 37) and

two small streams in Oregon, 0.05 to 0.08 g/m² (Lane, 43).

Rabinowitch (73) compared chlorophyll a to organic matter ratios and compiled a range of 0.16 to 4.9 percent of dry weight for the green algae. In comparison with these, McIntire and Phinney (55) observed a chlorophyll a range of 0.4 to 2.0 percent of organic matter for laboratory streams. From Tables 10 and 12, the mean percentages of organic matter as chlorophyll a have been determined for the Berry Creek experimental section as follows: shaded, unenriched = 0.32; light, unenriched = 0.55; shaded, enriched = 0.06; and light, enriched = 0.06.

A comparison of chlorophyll a and total carotenoids (Table 13 and Figure 9) shows large amounts of total carotenoids in both enriched sections and reduced amounts of chlorophyll a in these same sections. A summary (Figure 10) shows a definite influence of organic pollution on concentrations of chlorophyll a and total carotenoids in streams and rivers. In this figure the pigment concentrations determined for the enriched sections are less than those for the unenriched sections.

Observations made of artificial substrate placed in Berry Creek agree generally with those made by other investigators. It was noted that clay tile slabs that had remained in the stream for three to six months, prior to quantitative analyses, upon return to the stream were colonized more readily than were new slabs. This may be indicative of a conditioning period required for all artificial substrates

and merits further investigation. In comparison to this, Blum (3) indicated that one year was required for complete succession to a climax algal community on artificial substrate. In observations made at Berry Creek, time required for colonization was more extended in winter months. More time was also required for colonization of substrate on lighted riffles than shaded ones and considerably less time was required in the enriched section in comparison to the unenriched.

In an earlier study, Lane (43) indicated an error in chlorophyll a concentrations determined for materials harvested from the substrate of small streams. Near the end of the present study the same error was detected. These original data were not altered, but a correction of the mean chlorophyll a for each of the four experimental sections was determined in order to obtain a more realistic value for the range of production.

These corrected mean production values for each of the sections are: shaded, unenriched = $0.63 \text{ mgO}_2/\text{hr}/\text{mg}$ of chlorophyll a; light, unenriched = 0.69; shaded, enriched = 0.59; and light, enriched = 0.60. These values are in reasonable agreement with a similar range of values of 0.5 to $0.7 \text{ mgO}_2/\text{hr}/\text{mg}$ chlorophyll a for the Logan River (McConnell and Sigler, 52). These investigators also assumed the lowest production rate for the winter season in the Logan River to be 10 percent of that for the summer (July). The data for

the Berry Creek study show the lowest production rate for the winter months as 11 percent of that for the month of highest production and 13 percent of the mean production for months of May, June, July and August. Strickland (86) listed a production range of 1 to 10 mgC/hr which is in the range of 2.5 to 25 mg/O₂/hr/chlorophyll a and McIntire and Phinney (55) showed production ranges of 0.2 to 1.4 and 0.4 to 0.7 mg O₂/hr/chlorophyll a for experimental stream studies. In a study of the Arakawa River, Kobayasi (37) determined that production ranged from 2.1 to 4.9 mg O₂/hr/mg chlorophyll a. However, these values are somewhat higher than others for streams listed above.

Annual mean rates of gross primary production for Berry Creek are in good agreement with those determined for a variety of other communities shown in Table 17. A remarkable pattern of comparability is expressed by these comparisons which include distantly removed natural communities and two laboratory streams. Emphasis is placed here on the fact that the Berry Creek study is the only one which shows separate estimates for shaded, light, unenriched and enriched sections of a stream.

Monthly and mean values for ecological efficiency of the four experimental sections appear in Table 18. Estimates for the shaded sections of the stream show greater differences between the summer maxima and the winter minima than do the light sections. It may

appear that enrichment increases efficiency of production on shaded riffles, but the plant biomasses on the shaded riffles are similar in efficiency and chlorophyll a content.

It was assumed that natural variations in two different stream sections, and experimental errors, would account for some of the differences in the two shaded riffles shown above. In view of these considerations, it can only be stated that low level organic enrichment does not appear to reduce the ecological efficiency (gross production/usable light) of shaded stream communities. However, the reverse of this situation exists when the effects of enrichment on light adapted, stream communities are considered. Light adapted communities of streams would appear more drastically affected by organic pollution than are shade adapted communities.

The ecological efficiency in the light, enriched section is only about 20 percent of that in the light, unenriched section (Table 18). The estimates of ecological efficiencies for the four experimental sections of Berry Creek are compared with other natural and laboratory communities (Table 19). These estimates are in good agreement with estimates of comparable natural communities.

A summary showing a definite influence of enrichment on stream communities is given in Figure 10 where mean chlorophyll a content and mean gross production estimated for the enriched sections are compared with those for the unenriched sections. With one

exception, the chlorophyll a content and production in the enriched sections are considerably less than in the unenriched sections. Estimates of chlorophyll a content for the enriched sections which were greater during the months of October to December than for the other months was probably due to tree leaves entangled in the mat of Sphaerotilus when determinations were made.

The influence of enrichment is further indicated by ratios of respiration and gross production to organic matter (Figure 12). In both comparisons, the enrichment appears to modify the light, enriched section for it is very similar to the shaded, unenriched section. These similarities also include approximately corresponding periods of high and low production and consumption of oxygen.

Since this study involved the enrichment of a stream community with a supplemental carbohydrate, it was important to know what effect this might have on community respiration. Data from two separate experiments show the following results: mean respiration without enrichment was 31.0 mg oxygen and mean respiration with enrichment was 31.75 mg oxygen consumed. It was assumed from these data that supplemental carbohydrate enrichment provided little or no stimulation to community respiration. These assumptions agree with Odum and Hoskins (62) who found that neither photosynthesis nor respiration was stimulated by a supplemental carbohydrate source.

Comparisons of the production-respiration ratios (Table 20) show that the community metabolism of each of the four experimental sections of Berry Creek is heterotrophic in nature. Autotrophic organisms in the enriched sections contribute approximately 20 percent of the energy required for community respiration while the unenriched sections receive approximately 50 percent or more of the energy required for respiration from autotrophic organisms. P/R ratios greater than 1.0 developed on the light, unenriched riffle for only three summer months. The total amount of energy fixed by autotrophic organisms in Berry Creek is inadequate to maintain community metabolism without additional natural energy substrates in the form of leaves and other allochthonous materials.

SUMMARY AND CONCLUSIONS

A method was devised for determining the daily mean percentages of full sunlight reaching the four experimental sections of Berry Creek. Energy values were estimated from the percentage of light reaching the stream. It was determined that repeated instantaneous measurements of incident light representative of spatial, daily and seasonal variations provide a satisfactory method for estimating average values for light energy in a given area.

This is the first known investigation of a controlled flow stream in a condition of low level enrichment during a study of the general ecology of the stream. The polluted condition was contingent upon the establishment and maintenance of an abundant growth of Sphaerotilus. This required knowledge of the biology of Sphaerotilus and involved a three-fold plan of investigation which included: isolation and studies of the organism in pure culture; studies of growth of the organism in semi-isolated conditions in laboratory streams; and growth studies in the experimental stream.

A culture of a strain of Sphaerotilus natans, isolated from Berry Creek was used to study some of the effects of temperature and supplemental nitrogen on the uptake of radioactive carbon. This revealed that the greatest specific activity was incorporated into cultures grown at 10-20°C and that available nitrogen had a direct effect on growth.

Growth requirements for Sphaerotilus natans were also studied in semi-isolated cultures in laboratory streams. These experiments were designed to determine suitable carbon and nitrogen sources for growing Sphaerotilus. Glucose and peptone or sucrose and urea in a carbon-to-nitrogen ratio of eight to one were determined to provide adequate enrichment for abundant growths of Sphaerotilus.

In the enriched sections of Berry Creek, a common stream snail is present in populations of several thousand per square meter. Evaluation of the influence of great numbers of these on the standing crop and export of Sphaerotilus was also studied in laboratory streams. The standing crop of Sphaerotilus decreased directly with increasing numbers of snails and this decrease was not accounted for in the export. It was assumed that an amount of Sphaerotilus equivalent to the amount of the decrease in standing crop was ingested by the snails.

The experiments in cultures and laboratory streams served as a basis for similar studies in Berry Creek. Concentrations of 4-6 ppm of sucrose and 0.5 ppm of nitrogen equivalent as urea maintained desirable levels of growths of Sphaerotilus in the stream. It was also discovered that autotrophic organisms and Sphaerotilus biomasses were directly affected by changes in the rate of enrichment.

Methods designed to sample the plant communities in the four experimental sections of the stream included: a micro-slide technique

used to observe the density and diversity of micro-algae; a grid system of recording distribution of the plant biomass for estimating relative abundance of the plant community; and the removal of a portion of the stream substrate for the detailed examination of the benthic community.

Microscope slides were submerged in the experimental sections of the stream. The organisms were identified and recorded as kinds and numbers per square millimeter. The results show twice as many kinds and greater numbers of autotrophic organisms in the unenriched than the enriched sections.

The enriched riffles were divided into a grid of rectangles, each with an area of two square meters. Each week the percentage of cover in the grids was recorded. The biomasses of Sphaerotilus responded directly to variations in rates of enrichment.

Removal of 0.2 m^2 areas of the stream substrate allowed the detailed examination of the biomass of each experimental section. The substrate was scoured relatively free of organisms and returned to the stream. Sub-samples of the homogenized, harvested materials were used to determine biomass, organic matter, caloric content and pigment analysis.

In general, organic matter content and caloric values of the biomasses were greater and in reasonable accord for the unenriched sections but the enriched sections were more difficult to reconcile.

When representing spatial and seasonal variations, the concentration of chlorophyll is an acceptable measure of the productive ability of communities in shallow, rapidly flowing streams. Oxygen production per unit of chlorophyll a appeared to be more uniform when production measurements were determined at light intensities similar to those for which the community had been adapted.

The use of an acceptable artificial substrate in shallow, rapidly flowing streams could possibly expedite research techniques. In Berry Creek, non-glazed clay tile slabs were very satisfactory and required three to four months for colonization.

A photosynthesis-respiration chamber was used to estimate the primary production and community respiration for each of the four experimental sections of Berry Creek. Saturating light intensities were considerably lower in the enriched sections.

Shade adapted communities showed short term maxima of production in the spring and fall months while light adapted communities were productive throughout the summer months. Peak production in the shade adapted communities was generally thought to be due to increased abundance of two different seasonal species groups and to available nutrients. The production by the light adapted communities was directly related to photoperiod and rate of insolation.

Annual rates of gross production were estimated for each of the experimental sections and compared with a variety of natural

communities and two laboratory streams. It was found that estimates of 0.07 to 0.30 kg/m²/year in glucose equivalents for Berry Creek were well within the range of production estimates for comparable natural communities.

Values for ecological efficiency were estimated for each of the experimental sections. Enrichment (organic pollution) has a more definite and drastic effect on light than on shaded communities. It was shown that organic pollution could reduce the efficiency of a light adapted community by 90 percent. The values estimated for Berry Creek are in good agreement with estimates of comparable communities.

Comparisons of the production-respiration ratios distinguished each of the experimental sections as being heterotrophic in nature. Of the energy required for community respiration, the autotrophic organisms contribute approximately 20 percent in the enriched and 50 percent in the unenriched sections. Energy fixed by autotrophic organisms in Berry Creek was inadequate to maintain community metabolism without additional energy supplements.

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APPENDICES

Appendix I. The generic composition of the periphyton on a shaded, unenriched riffle after three-week's growth (organisms/mm²).

	Feb.				Mar.			
	1	2	3	4	1	2	3	4
BACILLARIOPHYCEAE								
Achnanthes	10	100	20	620	--	--	--	--
Cocconeis	10	170	70	210	20	20	30	110
Diatoma	--	20	--	--	--	--	--	20
Fragilaria	--	180	--	--	--	--	--	--
Frustulia	--	--	--	20	--	--	--	--
Gomphonema	10	--	--	70	70	--	--	560
Pleurosigma	--	20	--	--	--	--	--	--
Melosira	--	40	--	--	60	--	20	93
Meridion	50	134	--	190	1800	700	40	422
Navicula	10	70	90	100	1100	250	40	50
Nitzschia	--	--	--	--	--	--	10	--
Rhoicosphenia	10	80	20	--	370	--	--	--
Stauroneis	--	--	--	--	--	--	10	--
Surirella	--	--	--	--	110	--	--	--
Synedra	30	620	--	--	--	--	--	--
Tabellaria	10	23	100	30	20	--	--	40
CHLOROPHYTA								
Tetraspora	--	20	--	--	--	--	--	--
CYANOPHYTA								
Chroococcus	--	--	110	2310	4230	3810	4400	3690
AUTOTROPHIC BACTERIA								
Siderocapsa	--	--	30	--	--	--	--	--

Appendix I. Continued

	Apr.				May			
	1	2	3	4	1	2	3	4
BACILLARIOPHYCEAE								
Achnanthes	--	--	--	--	340	60	--	--
Amphiprora	--	--	--	--	30	--	--	--
Cocconeis	1350	220	110	450	5360	5470	2910	1230
Diatoma	--	--	960	--	--	--	20	--
Fragilaria	--	--	--	--	--	--	1010	30
Melosira	200	--	1900	--	--	--	70	--
Meridion	140	80	--	1490	10	--	4120	20
Navicula	260	100	1450	--	3260	2830	1040	110
Nitzschia	70	--	--	--	--	--	80	--
Pinnularia	20	--	--	--	--	--	--	--
Rhoicosphenia	40	--	--	--	--	--	--	--
Synedra	--	--	10	240	--	--	210	--
Tabellaria	180	20	100	--	370	80	580	--
CHLOROPHYTA								
Chlamydomonas	--	--	30	--	--	--	--	--
CYANOPHYTA								
Anabaena	--	70	--	--	--	--	20	60
Chroococcus	160	1220	6800	9260	1220	1420	5650	--
Oscillatoria	--	--	--	--	--	--	--	10
XANTHOPYCEAE								
Tribonema	--	--	600	--	--	--	--	--
AUTOTROPHIC BACTERIA								
Siderocapsa	--	--	--	--	--	--	--	140

Appendix I. Continued

	June					July			
	1	2	3	4	5	1	2	3	4
BACILLARIOPHYCEAE									
Achnanthes	--	--	--	--	10	--	--	--	--
Amphiprora	30	--	--	--	--	--	--	--	--
Cocconeis	1130	2920	5910	1080	880	460	190	5620	5440
Cymbella	30	--	--	--	--	--	--	--	--
Fragilaria	570	--	--	380	400	--	--	--	--
Melosira	--	--	260	20	--	--	--	--	--
Meridion	180	--	--	120	--	--	--	--	--
Navicula	290	100	370	20	--	40	--	--	--
Nitzschia	20	--	--	--	--	--	--	--	--
Rhoicosphenia	--	--	--	40	30	--	--	--	--
Tabellaria	220	--	--	--	--	--	--	--	140
CYANOPHYTA									
Anabaena	10	--	--	--	--	--	--	--	--
Chroococcus	33	--	--	--	--	--	--	--	--
AUTOTROPHIC BACTERIA									
Siderocapsa	160	40	60	--	470	120	140	2810	3760

Appendix I. Continued

	Aug.					Sept.			
	1	2	3	4	5	1	2	3	4
BACILLARIOPHYCEAE									
Cocconeis	4060	4510	5710	4650	4840	4560	3670	5860	3090
Eunotia	--	--	--	--	--	30	--	--	--
Fragilaria	--	--	--	--	--	--	--	--	10
Melosira	--	--	--	--	--	--	30	--	--
Meridion	--	--	--	--	--	--	--	220	140
Navicula	--	--	--	190	1050	840	--	--	300
Tabellaria	220	380	--	--	120	580	40	250	250
CHLOROPHYTA									
Stigeoclonium	--	--	--	--	--	30	--	--	--
AUTOTROPHIC BACTERIA									
Siderocapsa	3500	1550	21040	3280	1950	3000	4370	4200	4100

Appendix I. Continued

	Oct.					Nov.			
	1	2	3	4	5	1	2	3	4
BACILLARIOPHYCEAE									
Achnanthes	--	--	--	70	--	--	--	--	--
Caloneis	--	--	--	30	--	--	--	20	--
Cocconeis	420	2990	2960	--	800	550	180	2130	210
Diatoma	--	--	--	--	--	--	40	--	--
Fragilaria	10	--	--	--	--	20	--	80	--
Melosira	--	--	--	270	--	--	--	70	--
Meridion	60	--	--	--	--	--	100	70	--
Navicula	--	360	740	270	--	140	350	100	150
Rhoicosphenia	--	20	20	--	40	--	210	--	220
Stauroneis	--	--	--	10	--	--	--	--	--
Tabellaria	390	970	1200	--	--	40	--	260	--
CHLOROPHYTA									
Chlamydomonas	--	--	--	--	--	--	90	--	330
Stigeoclonium	--	--	--	--	--	--	--	10	--
CYANOPHYTA									
Chroococcus	120	990	970	520	--	--	240	--	590
EUGLENOPHYTA									
Euglena	--	--	--	--	--	--	10	--	40
AUTOTROPHIC BACTERIA									
Spirillum	--	--	--	6150	6440	6330	1500	640	840
Siderocapsa	3920	3560	3780	590	--	610	910	1040	920

Appendix I. Continued

	Dec.				Jan.				
	1	2	3	4	1	2	3	4	5
BACILLARIOPHYCEAE									
Achnanthes	--	--	--	--	--	--	150	450	250
Cocconeis	1430	740	840	770	360	3040	720	390	180
Diatoma	--	--	40	20	--	--	--	--	--
Fragilaria	150	180	60	40	--	--	--	110	270
Gomphonema	--	--	--	10	40	170	--	--	--
Melosira	--	--	--	--	--	--	190	--	--
Meridion	--	--	40	20	--	--	--	440	730
Navicula	1000	550	460	1070	900	160	200	170	200
Pinnularia	--	--	--	--	--	--	--	70	--
Rhoicosphenia	--	--	70	100	40	50	40	--	100
Surirella	--	--	40	20	--	--	--	--	--
Synedra	--	--	--	--	--	--	--	60	--
Tabellaria	530	590	210	200	100	220	100	--	120
CHLOROPHYTA									
Chlamydomonas	--	--	40	80	--	80	40	--	--
Stichococcus	--	--	10	--	--	--	--	--	--
Stigeoclonium	40	40	20	60	70	100	--	--	--
CYANOPHYTA									
Chroococcus	--	--	480	--	--	--	--	260	260
AUTOTROPHIC BACTERIA									
Spirillum	--	--	--	--	7040	7750	7900	--	--
Siderocapsa	9030	8140	4290	1510	--	--	510	--	--

Appendix II. The generic composition of the periphyton on a light, unenriched riffle after three week's growth (organisms/mm²).

	Feb.				Mar.			
	1	2	3	4	1	2	3	4
BACILLARIOPHYCEAE								
Achnanthes	--	--	--	--	430	--	--	300
Cocconeis	50	140	20	260	380	20	50	120
Gomphonema	50	--	10	890	--	--	--	10
Melosira	--	--	--	370	200	--	--	--
Meridion	20	160	20	280	300	--	--	--
Navicula	--	200	20	250	60	--	--	--
Nitzschia	--	--	--	--	110	--	--	--
Rhoicosphenia	20	360	--	--	--	--	--	--
Synedra	20	20	--	--	--	--	--	--
Tabellaria	20	60	20	260	340	--	--	--
CHLOROPHYTA								
Chlamydomonas	--	20	--	--	--	--	--	--
CYANOPHYTA								
Chroococcus	--	--	350	1420	1540	2760	490	8280

Appendix II. Continued

	Apr.				May			
	1	2	3	4	1	2	3	4
BACILLARIOPHYCEAE								
Achnanthes	--	--	--	--	1580	190	--	--
Cocconeis	1450	220	250	160	2980	4130	1230	1780
Diatoma	--	--	--	--	460	230	--	--
Fragilaria	--	--	--	--	--	--	330	50
Gomphonema	30	--	--	--	--	--	--	--
Melosira	2120	--	--	--	--	--	610	--
Meridion	110	10	3440	670	3790	2350	270	--
Navicula	280	170	130	--	--	--	430	70
Nitzschia	370	--	--	--	1210	310	--	90
Rhoicosphenia	20	--	--	--	--	--	--	--
Syndera	--	--	--	90	--	--	90	--
Tabellaria	--	--	--	--	1840	1000	--	--
CHLOROPHYTA								
Chlamydomonas	--	--	--	--	1880	470	--	--
CYANOPHYTA								
Anabaena	--	80	--	--	--	--	60	100
Chroococcus	1340	4040	5760	3600	5460	2490	960	580

Appendix II. Continued

	June					July			
	1	2	3	4	5	1	2	3	4
BACILLARIOPHYCEAE									
Achnanthes	10	--	--	--	20	--	--	--	--
Amphiprora	50	--	--	--	--	--	--	--	--
Cocconeis	2340	2390	6090	6150	4800	6360	6760	4280	3560
Fragilaria	30	--	--	--	--	--	--	--	--
Melosira	80	--	--	--	--	--	--	--	--
Meridion	--	--	110	--	50	--	--	--	--
Navicula	--	40	300	--	290	--	--	--	--
Nitzschia	10	--	--	--	--	--	--	--	--
Synedra	20	--	--	--	--	--	--	--	--
Tabellaria	20	--	--	--	30	--	--	--	--
CYANOPHYTA									
Anabaena	100	--	--	--	--	--	--	--	--
Chroococcus	200	--	--	--	--	--	--	--	--
AUTOTROPHIC BACTERIA									
Siderocapsa	400	100	370	3800	1640	1040	530	2260	3750

Appendix II. Continued

	Aug.					Sept.			
	1	2	3	4	5	1	2	3	4
BACILLARIOPHYCEAE									
Amphiprora	--	--	--	--	--	40	40	20	--
Cocconeis	420	2950	6780	7220	7270	6940	3650	3340	2530
Fragilaria	--	--	--	--	--	--	--	120	940
Melosira	--	--	--	--	--	--	--	--	340
Meridion	--	--	--	--	--	--	--	120	120
Navicula	100	220	--	170	--	--	--	3270	1300
Nitzschia	--	--	--	--	--	--	170	--	--
Pinnularia	--	--	--	--	--	--	--	--	30
Rhoicosphenia	--	--	--	--	--	--	--	--	70
Synedra	--	--	--	--	--	--	--	40	--
Tabellaria	--	--	--	--	--	20	--	--	--
CHLOROPHYTA									
Chlamydomonas	40	--	--	--	--	--	--	--	--
CYANOPHYTA									
Anabaena	--	--	--	--	--	--	--	--	80
Chroococcus	--	--	--	--	--	--	--	--	160
AUTOTROPHIC BACTERIA									
Siderocapsa	2480	1880	3620	5880	840	1750	680	900	860

Appendix II. Continued

	Oct.					Nov.			
	1	2	3	4	5	1	2	3	4
BACILLARIOPHYCEAE									
Achnanthes	--	--	--	--	--	--	--	--	340
Cocconeis	1350	2610	4000	310	4340	760	3100	3880	510
Diatoma	--	--	--	--	--	90	--	--	--
Fragilaria	1020	--	--	190	--	--	--	--	--
Gomphonema	--	250	160	--	90	60	90	--	--
Melosira	1200	--	--	70	--	80	--	--	--
Meridion	160	200	710	--	--	--	280	160	--
Navicula	520	850	--	390	670	50	410	230	160
Nitzschia	--	--	--	--	150	--	100	--	--
Pinnularia	60	--	--	30	--	70	--	--	--
Rhoicosphenia	60	60	100	--	--	50	--	--	--
Stauroneis	--	--	--	20	--	--	--	--	--
Synedra	--	--	--	40	--	30	--	--	--
Tabellaria	--	380	1560	--	80	60	150	190	110
CHLOROPHYTA									
Stigeoclonium	--	50	270	--	40	--	--	80	--
CYANOPHYTA									
Anabaena	100	--	--	200	--	--	--	--	--
Chroococcus	1160	440	220	280	1000	--	2530	--	400
AUTOTROPHIC BACTERIA									
Siderocapsa	380	740	820	470	590	700	920	970	490
Spirillum	--	--	--	5450	4950	3470	2650	2360	1400

Appendix II. Continued

	Dec.				Jan.				
	1	2	3	4	1	2	3	4	5
BACILLARIOPHYCEAE									
Achnanthes	--	--	--	--	--	--	--	600	--
Cocconeis	820	1690	270	1330	1970	950	170	290	350
Fragilaria	--	--	70	760	--	--	110	140	--
Gomphonema	--	--	--	200	240	210	--	--	--
Meridion	150	600	770	800	--	--	300	1280	190
Navicula	380	890	470	1560	510	220	140	--	270
Nitzschia	--	--	--	--	--	--	100	--	--
Rhoicosphenia	160	130	--	--	--	--	--	--	110
Synedra	--	--	40	110	--	--	--	--	--
Tabellaria	240	520	--	--	--	--	--	--	--
CHLOROPHYTA									
Chlamydomonas	--	--	200	540	180	--	90	--	--
Stigeoclonium	30	70	70	130	90	30	--	--	--
CYANOPHYTA									
Chroococcus	480	1460	--	--	--	--	320	2100	4260
AUTOTROPHIC BACTERIA									
Siderocapsa	4350	6040	3920	--	--	--	--	--	--
Spirillum	--	--	--	3960	3690	4230	--	--	--

Appendix III. The generic composition of the periphyton on a shaded, enriched riffle after three week's growth (organisms/mm²).

	Feb.				Mar.			
	1	2	3	4	1	2	3	4
BACILLARIOPHYCEAE								
Achnanthes	--	20	200	--	990	--	--	--
Cocconeis	--	120	50	20	470	50	20	--
Gomphonema	--	--	60	--	--	--	--	--
Melosira	--	200	--	--	--	--	--	--
Meridion	--	30	--	30	50	--	--	240
Navicula	--	--	--	--	70	--	--	--
Pinnularia	--	20	--	--	--	--	--	--
Rhoicosphenia	--	270	--	--	20	--	--	--
Stauroneis	--	--	--	--	--	--	--	20
Synedra	--	20	--	--	--	--	--	--
Tabellaria	--	160	70	--	130	--	--	240
CHLOROPHYTA								
Stigeoclonium	--	--	--	--	40	--	--	--
CYANOPHYTA								
Chroococcus	100	200	140	2450	470	780	1100	1730
AUTOTROPHIC BACTERIA								
Siderocapsa	210	--	100	--	--	--	--	--
HETEROTROPHIC BACTERIA								
Sphaerotilus	--	--	1820	3800	1860	5750	10150	10600

Appendix III. Continued

	Apr.				May			
	1	2	3	4	1	2	3	4
BACILLARIOPHYCEAE								
Cocconeis	--	50	--	--	170	30	--	270
Fragilaria	--	--	--	--	--	--	--	20
Meridion	--	--	--	--	90	30	--	--
Navicula	--	60	--	--	--	--	--	30
Nitzschia	--	--	--	--	--	--	--	10
Pinnularia	--	--	--	--	--	--	--	20
Tabellaria	--	--	--	--	--	--	--	10
CHLOROPHYTA								
Chlamydomonas	--	1500	--	--	--	--	--	--
CYANOPHYTA								
Chroococcus	--	120	480	1560	580	120	--	--
Oscillatoria	--	--	--	--	100	--	--	--
HETEROTROPHIC BACTERIA								
Sphaerotilus	12000	15600	100000	100000	20000	14700	20000	12500

Appendix III. Continued

	June					July			
	1	2	3	4	5	1	2	3	4
BACILLARIOPHYCEAE									
Amphiprora	--	--	20	--	--	--	--	--	--
Caloneis	--	--	20	--	--	--	--	--	--
Cocconeis	210	90	240	460	70	70	90	--	--
Fragilaria	20	--	10	30	--	--	--	--	--
Gomphonema	--	--	10	--	--	--	--	--	--
Melosira	--	50	100	20	--	--	--	--	--
Meridion	--	--	20	20	--	--	--	--	--
Navicula	--	30	40	--	--	20	--	--	--
Pinnularia	--	--	10	--	--	--	--	--	--
Rhoicosphenia	--	20	50	--	--	--	--	--	--
Synedra	--	--	--	--	--	--	--	10	--
Tabellaria	--	--	10	--	--	--	--	--	--
CYANOPHYTA									
Chroococcus	--	--	--	100	--	120	80	--	--
AUTOTROPHIC BACTERIA									
Siderocapsa	--	40	230	4600	--	--	--	--	--
HETEROTROPHIC BACTERIA									
Sphaerotilus	9900	4800	3700	5650	9850	9600	9300	4900	4850

Appendix III. Continued

	Aug.					Sept.			
	1	2	3	4	5	1	2	3	4
BACILLARIOPHYCEAE									
Cocconeis	70	80	250	240	860	120	--	--	--
Navicula	--	--	--	--	150	--	--	--	--
Rhoicosphenia	--	--	--	--	50	--	--	--	--
CHLOROPHYTA									
Chlamydomonas	60	90	20	--	--	--	--	--	--
AUTOTROPHIC BACTERIA									
Siderocapsa	840	410	760	--	1070	--	--	--	--
HETEROTROPHIC BACTERIA									
Sphaerotilus	3000	2920	1180	--	--	6000	10200	10550	10700

Appendix III. Continued

	Oct.					Nov.			
	1	2	3	4	5	1	2	3	4
BACILLARIOPHYCEAE									
Cocconeis	--	90	140	30	50	90	100	190	110
Navicula	--	--	--	80	50	--	50	--	--
Tabellaria	--	--	110	--	--	--	--	--	--
CYANOPHYTA									
Chroococcus	--	--	110	--	--	--	--	--	--
AUTOTROPHIC BACTERIA									
Siderocapsa	--	540	580	60	--	30	--	--	--
HETEROTROPHIC BACTERIA									
Sphaerotilus	14100	--	14150	14650	15950	16350	8500	6800	7800

Appendix III. Continued

	Dec.				Jan.				
	1	2	3	4	1	2	3	4	5
BACILLARIOPHYCEAE									
Cocconeis	190	--	170	--	60	70	--	--	--
Fragilaria	--	--	--	--	--	--	--	--	90
Meridion	--	--	--	--	--	--	60	--	70
Navicula	--	40	--	100	--	60	50	--	40
Tabellaria	--	60	50	--	50	40	--	--	--
CHLOROPHYTA									
Chlamydomonas	--	--	--	--	--	--	100	300	--
Stigeoclonium	--	--	--	--	30	--	--	--	--
CYANOPHYTA									
Chroococcus	--	--	100	120	--	--	--	--	80
AUTOTROPHIC BACTERIA									
Siderocapsa	170	710	360	120	--	--	--	--	--
HETEROTROPHIC BACTERIA									
Sphaerotilus	8500	10700	9700	6100	4600	7600	9050	8650	8300

Appendix IV. The generic composition of the periphyton on a light, enriched riffle after three week's growth (organisms/mm²)

	Feb.				Mar.			
	1	2	3	4	1	2	3	4
BACILLARIOPHYCEAE								
Achnanthes	--	--	210	--	90	--	--	130
Cocconeis	30	100	40	40	30	40	40	80
Gomphonema	--	--	10	10	--	--	--	--
Meridion	--	--	20	--	30	120	--	--
Navicula	20	70	20	20	--	--	--	--
Rhoicosphenia	--	--	--	--	20	20	--	--
Surirella	--	--	--	--	20	--	--	--
Synedra	--	--	--	20	--	--	--	--
Tabellaria	--	30	20	--	40	--	--	--
CHLOROPHYTA								
Stigeoclonium	--	--	--	--	10	--	--	--
CYANOPHYTA								
Anabaena	--	--	--	--	60	--	--	--
Chroococcus	--	--	40	2140	200	40	80	200
HETEROTROPHIC BACTERIA								
Sphaerotilus	4350	4600	5600	6150	10250	12950	15300	13750

Appendix IV. Continued

	Apr.				May			
	1	2	3	4	1	2	3	4
BACILLARIOPHYCEAE								
Cocconeis	330	40	--	--	40	20	30	60
Melosira	30	--	--	--	--	--	--	--
Meridion	30	90	--	--	20	20	--	--
Navicula	10	20	--	--	--	--	--	--
Nitzschia	10	--	--	--	--	--	--	--
Rhoicosphenia	--	--	--	--	10	--	--	--
Tabellaria	--	20	--	--	--	--	--	--
CYANOPHYTA								
Chroococcus	--	--	--	--	360	460	80	360
Oscillatoria	80	--	--	--	--	--	--	--
HETEROTROPHIC BACTERIA								
Sphaerotilus	15600	13700	100000	100000	10250	12900	20000	14200

Appendix IV. Continued

	June					July			
	1	2	3	4	5	1	2	3	4
BACILLARIOPHYCEAE									
Achnanthes	--	--	--	--	20	--	--	--	--
Amphora	--	--	20	--	--	--	--	--	--
Amphiprora	--	--	30	--	--	--	--	--	--
Cocconeis	100	1620	4760	480	220	100	100	--	--
Fragilaria	--	--	50	160	--	--	--	--	--
Gomphonema	--	--	40	--	--	--	--	--	--
Melosira	--	--	60	--	--	--	--	--	--
Meridion	--	--	50	--	20	--	--	--	--
Navicula	--	100	130	90	--	50	20	--	--
Nitzschia	--	10	50	10	--	--	--	--	--
Pinnularia	--	--	10	--	--	--	--	--	--
Rhoicosphenia	--	10	70	--	--	--	--	--	--
Stauroneis	--	--	20	--	--	--	--	--	--
Synedra	--	--	40	--	--	--	--	--	--
Tabellaria	--	--	30	--	20	--	--	--	--

CHLOROPHYTA

(Continued on
next page)

Appendix IV. Continued

	June					July			
	1	2	3	4	5	1	2	3	4
CHLOROPHYTA (continued)									
Chlamydomonas	310	--	--	--	--	--	--	--	--
Cosmarium	--	--	10	--	--	--	--	--	--
Stigeoclonium	--	30	60	20	--	--	--	--	--
CYANOPHYTA									
Anabaena	--	--	--	80	--	--	--	--	--
Chroococcus	60	160	580	360	220	60	120	--	--
Oscillatoria	--	--	100	--	--	--	--	--	--
AUTOTROPHIC BACTERIA									
Siderocapsa	--	90	530	210	--	--	--	--	--
HETEROTROPHIC BACTERIA									
Sphaerotilus	7500	4100	4850	7600	3000	10500	11250	8650	4250

Appendix IV. Continued

	Aug.					Sept.			
	1	2	3	4	5	1	2	3	4
BACILLARIOPHYCEAE									
Cocconeis	310	2880	390	360	730	70	--	--	--
Fragilaria	190	2650	--	--	--	--	--	--	--
Meridion	--	290	--	--	--	--	--	--	--
Navicula	590	320	230	70	190	--	--	--	--
Nitzschia	--	--	70	--	--	--	--	--	--
Synedra	140	--	--	--	--	--	--	--	--
CHLOROPHYTA									
Chlamydomonas	--	100	--	--	--	--	--	--	--
Stigeoclonium	--	180	--	--	--	--	--	--	--
CYANOPHYTA									
Chroococcus	--	2160	3420	240	--	--	--	--	--
Oscillatoria	80	--	--	--	--	--	--	--	--
AUTOTROPHIC BACTERIA									
Siderocapsa	620	1390	7200	3580	740	--	--	--	--
HETEROTROPHIC BACTERIA									
Sphaerotilus	2500	1900	3090	2910	--	20000	100000	100000	100000

Appendix IV. Continued

	Oct.					Nov.			
	1	2	3	4	5	1	2	3	4
BACILLARIOPHYCEAE									
Achnanthes	--	--	--	--	--	--	--	--	120
Cocconeis	--	--	--	--	--	--	--	--	140
HETEROTROPHIC BACTERIA									
Sphaerotilus	100000	100000	100000	100000	100000	50000	20000	10000	9050

Appendix IV. Continued

	Dec.				Jan.				
	1	2	3	4	1	2	3	4	5
BACILLARIOPHYCEAE									
Cocconeis	170	110	110	250	130	270	90	90	160
Gomphonema	--	--	--	--	50	--	--	--	--
Meridion	--	--	110	--	--	--	120	160	--
Navicula	--	80	--	350	160	70	--	--	130
Tabellaria	60	--	--	--	--	60	--	--	--
CYANOPHYTA									
Chroococcus	--	160	60	80	--	--	80	220	280
AUTOTROPHIC BACTERIA									
Siderocapsa	--	220	320	--	--	--	--	--	--
HETEROTROPHIC BACTERIA									
Sphaerotilus	9800	8600	7750	4900	4050	6400	8700	9750	9700

Appendix V. Seasonal occurrence of Benthic plants not attached to slides*

	Feb.				Mar.			
	I	II	III	IV	I	II	III	IV
Batrachospermum				/	/ / /	/	/ / /	/
Chiloscyphus		/		/	/	/ / /	/	/
Funaria		/		/	/	/ / /	/	/
Gleochloris								
Melosira					/ / /	/	/	/
Nostoc				/				/ / /
Phormidium								
Prasiola								
Vaucheria						/		/

Observations for the months of June- Jan. were summarized as follows:

Section II - Chiloscyphus and Funaria / / to / / /

Section IV - Nostoc and Funaria / to / /

*occasional = /, frequent = / /, abundant = / / /.

Appendix V. Continued *

	Apr.				May			
	I	II	III	IV	I	II	III	IV
Batrachospermum	/ /	/	/ /	/	/	/	/	/
Chiloscyphus		/ / /				/ / /		
Funaria		/ / /		/		/ / /		/
Gleochloris	/ /	/	/ /	/	/		/	
Melosira	/		/					
Nostoc				/ /				/ / /
Phormidium	/		/					
Prasiola	/	/	/	/				
Vaucheria		/		/		/		/ /

* occasional = /, frequent = / /, abundant = / / /.

Appendix VI. Percentage of relative abundance of Sphaerotilus natans in the shaded, enriched section (determined by the grid system).

Observation densities*	Feb.				Mar.				Apr.				May			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Negligible	--	--	--	--	--	--	--	--	--	80	55	70	75	80	85	80
Light	--	--	--	--	--	--	--	--	--	15	20	15	25	15	10	20
Medium	--	--	--	--	--	--	--	--	--	5	25	15	--	5	5	--
Heavy	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--

* Negligible = 0 - 2X, Light = 3 - 10X, Medium = 11 - 20X and Heavy = more than 20X.
X = one inch tuft (of 1-3 plumes) of Sphaerotilus.

Appendix VI. Continued

Observation densities	June					July					Aug.				
	1	2	3	4	5	1	2	3	4		1	2	3	4	5
Negligible	75	70	65	35	35	25	20	15	15		--	10	50	80	90
Light	25	15	15	30	25	10	5	10	5		55	55	45	20	10
Medium	--	15	20	35	25	15	20	15	15		20	35	5	--	--
Heavy	--	--	-	--	15	50	55	60	65		25	--	--	--	--
Observation densities	Sept.					Oct.					Nov.				
	1	2	3	4		1	2	3	4	5	1	2	3	4	
Negligible	70	55	50	40		35	25	15	15	15	--	--	--	--	
Light	25	30	25	30		20	15	20	15	15	5	--	--	--	
Medium	5	15	25	30		15	20	20	25	20	30	20	15	5	
Heavy	--	--	--	--		30	40	45	45	50	65	80	85	95	

Appendix VI. Continued

Observation densities	Dec.				Jan.				
	1	2	3	4	1	2	3	4	5
Negligible	--	--	--	--	--	--	--	--	--
Light	--	--	--	--	--	--	--	--	--
Medium	5	5	5	5	10	5	5	5	5
Heavy	95	95	95	95	90	95	95	95	95

Appendix VII. Percentages of relative abundance of Sphaerotilus natans in the light, enriched section (determined by grid system)

Observation densities *	Feb.				Mar.				Apr.				May			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Negligible	--	--	--	--	--	--	--	--	--	25	25	10	10	10	35	20
Light	--	--	--	--	--	--	--	--	--	30	10	60	50	50	25	30
Medium	--	--	--	--	--	--	--	--	--	45	65	30	40	40	40	30
Heavy	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	20

* Negligible = 0 - 2X, Light = 3 - 10X, Medium = 11 - 20X and Heavy = more than 20X.
X = one inch tuft (of 1-3 plumes) of Sphaerotilus.

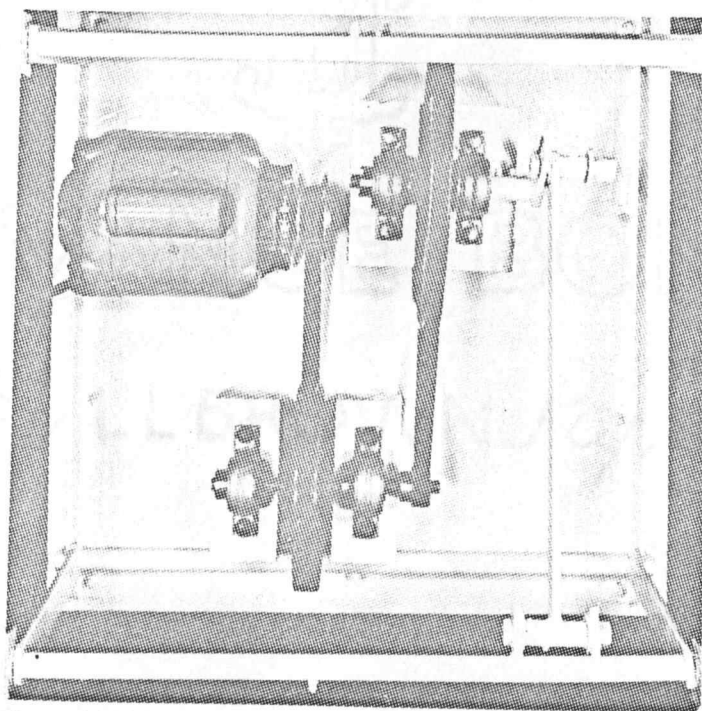
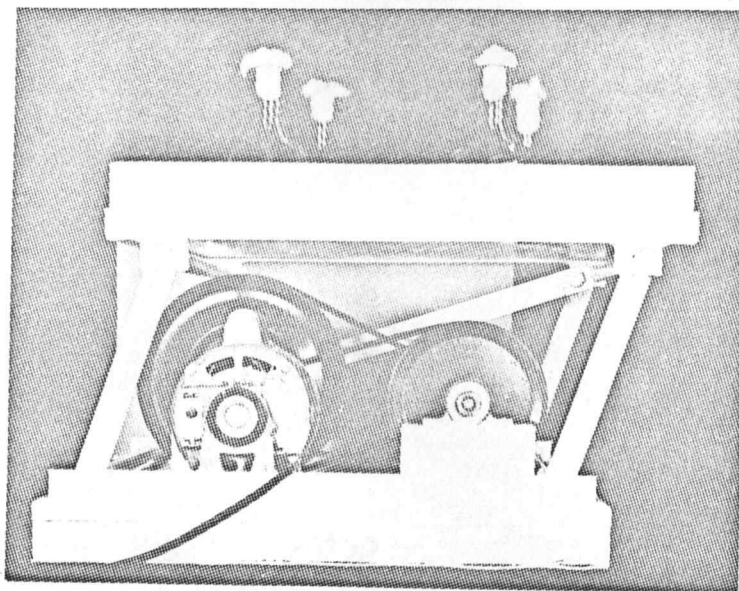
Appendix VII. Continued

Observation densities	June					July				Aug.				
	1	2	3	4	5	1	2	3	4	1	2	3	4	5
Negligible	20	15	15	--	--	--	--	--	--	10	10	10	25	55
Light	30	40	20	--	--	--	--	--	--	60	70	75	65	45
Medium	30	25	45	10	--	--	--	--	--	25	15	15	10	--
Heavy	20	20	20	90	100	100	100	100	100	5	5	--	--	--
Observation densities	Sept.				Oct.					Nov.				
	1	2	3	4	1	2	3	4	5	1	2	3	4	
Negligible	55	35	--	--	--	--	--	--	--	--	--	--	--	
Light	35	45	55	35	--	--	--	--	--	--	--	--	--	
Medium	10	20	45	55	25	--	--	--	--	--	--	--	--	
Heavy	--	--	--	10	75	100	100	100	100	100	100	100	100	

Appendix VII. Continued

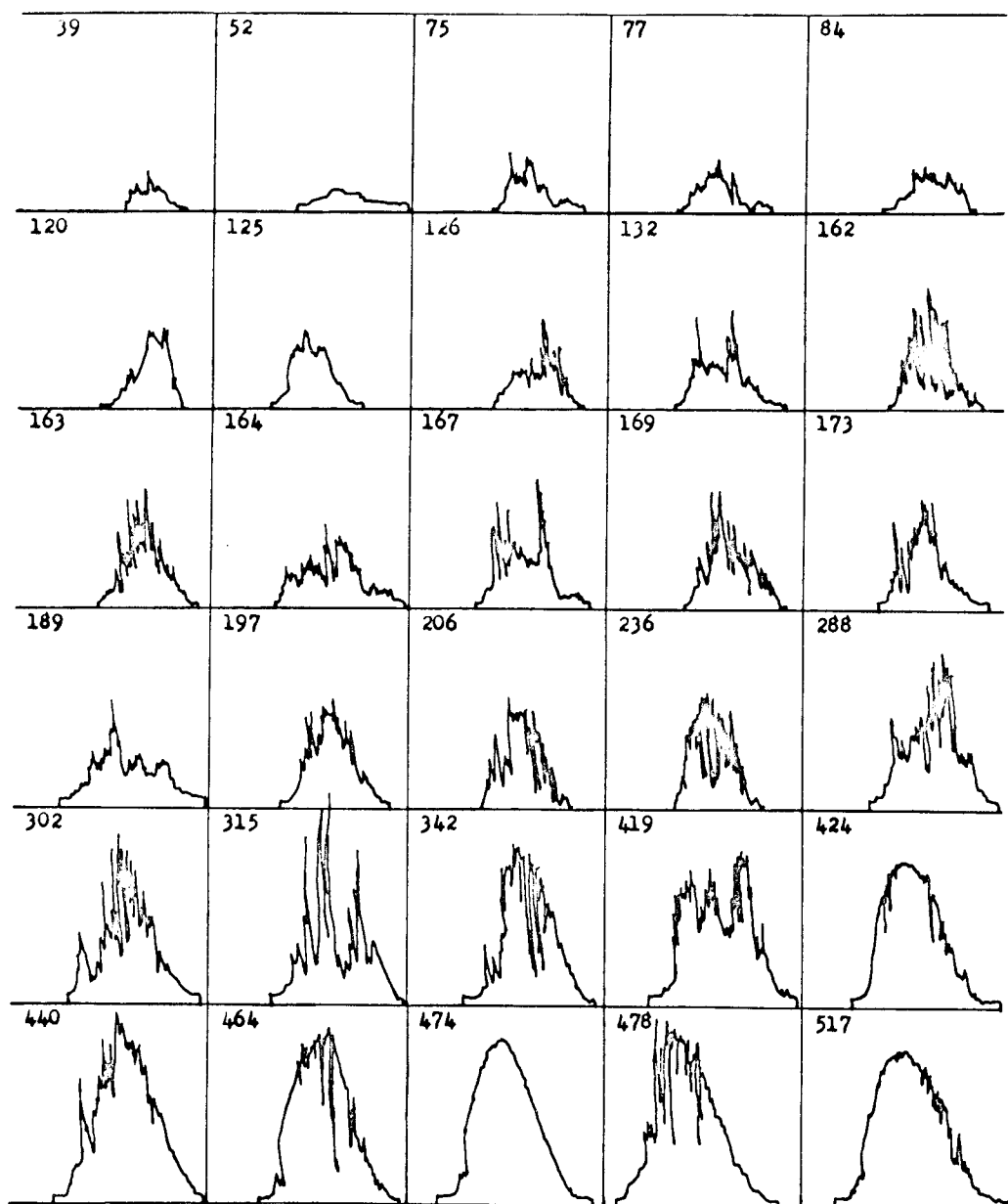
Observation densities	Dec.				Jan.				
	1	2	3	4	1	2	3	4	5
Negligible	--	--	--	--	--	--	--	--	--
Light	--	--	--	--	--	--	--	--	--
Medium	--	--	--	--	--	--	--	--	--
Heavy	100	100	100	100	100	100	100	100	100

Appendix VIII.



A convenient shaking apparatus for growing micro-organisms

Appendix IX.



Pyrheliograph recordings of total available radiant energy for thirty sampling days and expressed as gram calories per square centimeter, Feb., 1964 through Jan., 1965