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Rates of Algal Production and *Sphaerotilus* Assimilation in the Logan River, Utah

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RATES OF ALGAL PRODUCTION AND *SPHAEROTILUS* ASSIMILATION IN THE LOGAN RIVER, UTAH

by

Gary D. Beers

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

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in

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Gary D. Beers

Theories are fine as tools to understanding but are not in themselves contributions to truth. Any clever scientist can sit down, marshall the facts at hand, and bounce out of his arm chair with a theory. The scientist who is great is the one who proposes a theory and then attempts to prove or disprove it rather than the one who proposes a theory and then goes off grinning to greener pastures leaving the onerous job of proof or disproof to others.

Vincent C. Dethier (1962, p. 95)

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ABSTRACT

Rates of Algal Production and Sphaerotilus Assimilation

in the Logan River, Utah

by

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Utah State University, 1969

Major Professor: Dr. John M. Neuhold
Department: Wildlife Resources

The rates of algal production and Sphaerotilus assimilation in the lower Logan River benthos were investigated in 1966 and 1967.

The rate of annual gross primary production (3,416 Kcal/m^2/yr) was estimated from the relation of pigments to the photosynthetic rate of benthic communities in a submersible, metabolism chamber. The photosynthetic rate was predicted with high precision when a measure of the accessory pigments (D480/D665 and/or chlorophyll-c) was considered with the chlorophyll-a. The pigment density estimates were obtained from the community present on paraffin-coated, concrete hemispheres after immersion in the river for periods ranging from 11 to 20 weeks.

The daily rate of energy utilization by Sphaerotilus (1.3 cal/m^2/day) was estimated from the observed generation time of this bacterium on glass slides suspended in the river at various locations and metabolic coefficients obtained from other sources. The magnitude of microbial activity in the river water was estimated to be 448 cal/m^2/day. The accumulation rate of Sphaerotilus biomass on glass slides was 0.3 mg (net weight)/m^2/48 hours, and could be predicted from the temperature,

nitrate (plus nitrite) content, and the dissolved organic carbon content of the river water. The generation time of Sphaerotilus (average was 20 hours) could be predicted from temperature, nitrate (plus nitrite) content, and velocity of the water. The daily P/B coefficient for this bacterium was 1.20.

(88 pages)

INTRODUCTION

The energy flow through aquatic communities is dependent upon the rates of primary production and decomposer assimilation. Light energy has to be transformed to chemically-bound energy by photosynthetic processes before it is available for utilization by heterotrophic organisms. In most communities, the main organisms responsible for this transformation are the green plants, but photosynthetic bacteria may participate to a large degree in some instances. In comparison with photosynthetic processes, chemosynthetic processes are of little importance in the formation of chemically-bound energy (Steemann Nielsen, 1963). Decomposer assimilation performs an absolutely vital function in each community, because, if it did not occur, all the nutrients would soon be tied up in dead bodies, and no new life could be produced (Odum and Odum, 1959). This vital function is the mineralization of organic matter. Producers and decomposers are sine qua non conditions for the existence of a functional community (Odum and Odum, 1959).

Odum (1957), Teal (1957, 1962), and Kriss (1963) are among the few who have studied rates of primary production and decomposer assimilation in natural, aquatic communities. Macfadyen (1964) has presented some evidence to support the contention that decomposer activity limits over-all productivity of several communities (grassland, salt marsh, and marine phytoplankton).

This study was an attempt to investigate portions of these two trophic levels in the benthic communities of a large stream in Northern Utah. The main objectives were to estimate the rates of gross primary production and decomposer (Sphaerotilus, a filamentous bacterium) assimilation in the benthos of the Logan River, Utah.

LITERATURE REVIEW

The literature review is presented in three main sections. The first considers the theoretical aspects of algal and bacterial productivity. The second considers Sphaerotilus biology. The third considers the methods utilized in the study.

The literature on the theoretical aspects of primary productivity is abundant; Strickland (1966) presented an excellent, comprehensive, critical review of this subject. The Proceedings of the Tenth Pacific Science Congress (Doty, 1961) and the First Symposium held in the International Biological Program (Goldman, 1965) contain most of the pertinent, recent work.

The literature on the theoretical aspects of bacterial assimilation rates (productivity) in aquatic communities is scarce. Kriss (1963), Zobell (1946), Sorokin (1961), Rittenberg (1963), Zhukova (1963), Zhukova and Fedosov (1963), Ivanov (1955), and Romanova and Zonov (1964) presented some of the better discussions on this topic. They used either amount of substance produced or increase in numbers to indirectly measure productivity. Simple enumeration is a useful tool with which to measure microbial production, since growth of unicellular organisms, such as bacteria, is directly related to numbers of individuals. Senez (1962) discussed some general aspects of the energetics of bacterial growth.

The literature dealing with the biology of the bacterial genus Sphaerotilus is sizeable. The majority of the publications is concerned

with the laboratory rather than with the field biology of this organism. Heukelekian and Crosby (1955, 1956, 1956a) and Harrison and Heukelekian (1958) present excellent reviews of the work concerning Sphaerotilus.

Three of the better papers on the physiology of this bacterium are Stokes (1954), Hohnl (1955), and Rouf and Stokes (1964). Recent papers of interest on this topic are Waitz and Lackey (1961), Gaudy and Wolfe (1961), Dondero, Phillips, and Heukelekian (1961), and Razumov (1962).

The concentration of glucose, the concentration of nitrogen, the biochemical oxygen demand (BOD): nitrogen : phosphorus ratio, and the velocity of flow factors which can influence the growth of Sphaerotilus, were studied in the laboratory under simulated stream conditions by Phillips (1960).

There are few good papers on the field biology of Sphaerotilus. Wuhrmann (1964), Wuhrmann et al. (1967), and Phaup and Gannon (1967) presented some interesting results obtained from studies of slime infestations in outdoor, artificial streams experiencing various pollution levels. In England recent studies (Dept. Sci. Ind. Res., 1963) reported that about 9,200 grams organic carbon/hr/mile were extracted from a stream receiving paper-mill effluent was attributed to the metabolism of Sphaerotilus. Rheinheimer (1959) made the interesting observation that the mass development of this bacterium in the Elbe River, Germany, created a phosphate shortage and delayed nitrification. Southgate (1948) and Cawley (1958) emphasized that temperature was one of the main limiting factors to the growth of this organism. Amberg and Cormack (1960) and Amberg et al. (1962) reported studies on the factors

affecting Sphaerotilus growth in the Columbia River. The problems of growth were discussed by Heukelekian (1959).

Additional publications on Sphaerotilus morphology and ecology in flowing waters are Pawlaczyke (1961), Razumov (1962), and Pipes and Jones (1963). Heukelekian and Crosby (1956) and Wilson et al. (1960) reviewed the use of trawls, nets, boxes, and glass slides as samplers of slime infestation in flowing waters.

Cooke (1956), Lund and Talling (1957), and Sladeckova (1962) presented extensive reviews of the methods used to obtain samples of "attaching" organisms in waters. Butcher et al. (1940) utilized glass slides to collect Sphaerotilus growths in a polluted river. Beers and Neuhold (1968) presented a method of benthic community sampling and subsequent pigment extraction for primary production estimates.

Many attempts have been made to estimate the metabolic activity of benthic communities which were placed inside artificial enclosures. Early methods utilized bell jars (Odum, 1957; Pomeroy, 1959). More recently, methods have involved incorporating water flow into the apparatus along with improved techniques for oxygen determinations (Odum and Hoskin, 1958; McIntire et al., 1964; O'Connell and Thomas, 1965). Wetzel (1965) reviewed aquatic plant research where metabolism was measured by net-oxygen change or the rate of radioactive-carbon uptake.

GENERAL DESCRIPTION OF THE STUDY AREA

The study area was located on the floor of Cache Valley (elevation 1,350 m) approximately 5 kilometers west of Logan, Utah. The portion of the Logan River designated as the study area extended downstream a distance of 12 kilometers from the Mendon Bridge (Figure 1). The slope of the river bed along this distance was less than 3 meters. The stream bottom consisted of finely-divided material and some gravel, and the banks were brushy or undercut.

The river flow was augmented by inflows from a spring-fed tributary, Seven-Mile Creek, and several irrigation returns. The annual discharge pattern of the river, as monitored at the Mendon Bridge by the United States Geological Survey (U.S.G.S.), was typical of small rivers in the West with mountains dominating the watershed. Minimum flow (1.4 to 5.7 m^3/sec) usually occurs in August and maximum flow (28.3 to 36.8 m^3/sec), due to snow melt on the watershed, usually occurs in May. The remainder of the year the flow seldom exceeds 12 m^3/sec. Seven-Mile Creek discharge was relatively constant during the study (1965 to 1967), ranging from 0.3 to 0.6 m^3/sec. Sewer Creek discharge varied from less than 0.1 m^3/sec in the late summer (August) to nearly 1.1 m^3/sec during the winter (December). This variation was caused by the diversion of pond effluent for irrigation purposes during the warmer months (mid-April to November) and by the diversion of effluent to the Logan River during the remaining months. An idea of the comparative magnitudes of flow during the year can be obtained from

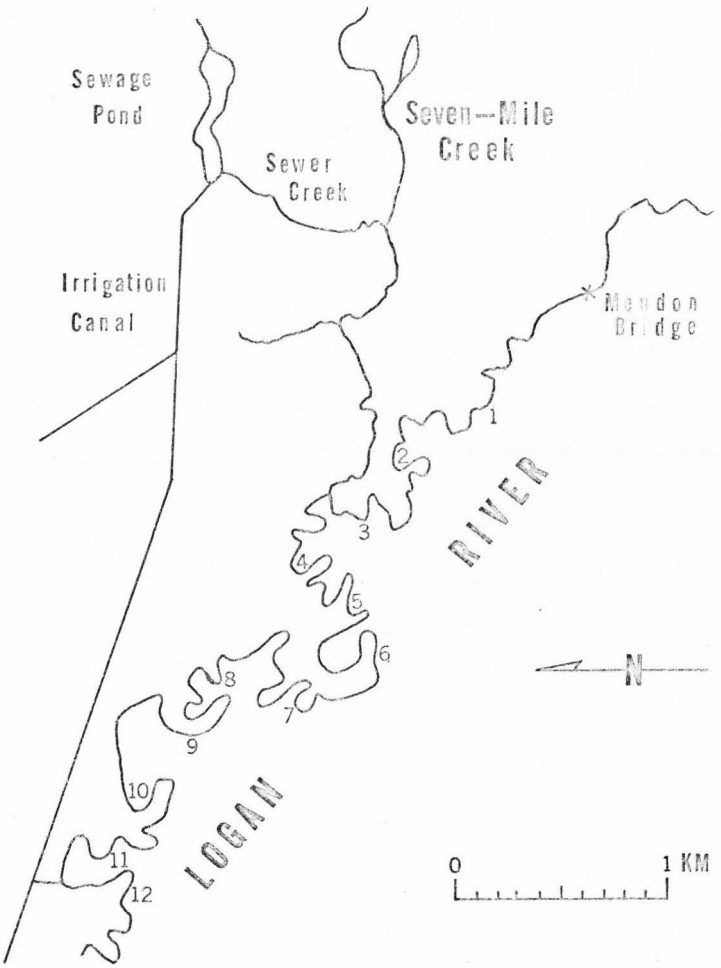

Figure 1. Map of the study area. Numbers indicate distance (km) downstream from the Mendon Bridge. Water flows were traced from U.S.G.S. map (Wellsville quadrangle, Utah-Cache County, 1962).

a consideration of volume ratios. During the warmer months the Sewer Creek:Seven-Mile Creek:Logan River ratio was about 1:4:13, and during the colder months the ratio was about 1:1:6.

Some pertinent physical and chemical data from Logan River and pond waters are available from several sources (Table 1).

Certain aspects of the aquatic communities in the study area have been investigated. McConnell (1958) and Clark (1958) studied the algal components of the river biota. More recently, Matthews and Neuhold (1967) and Erman (1968) investigated the fish and invertebrate populations, respectively.

TABLE 1. Pertinent chemical and physical data of waters in the study area.

Water Station	Measurement	Range	Mean	Source
Mendon Bridge (1956-57)	NO_3 ppm[1]	0.0-4.9	-	McConnell, 1958
	PO_4 ppm	0.0-0.8	-	"
	K ppm	0.1-2.0	-	"
	Cl ppm	6.0-8.0	-	"
	SO_4 ppm	12-15	-	"
	Ca ppm	28-58	-	"
	Mg ppm	24-28	-	"
	Na ppm	5-25	-	"
	HCO_3 ppm	240-264	-	"
	TDS ppm[2]	185-230	-	"
	Turbidity[3]	2-12	-	"
Mendon Bridge (1965)	Ca ppm	34-75	55	U.S.B.R.[4], 1965
	Mg ppm	13-26	20	"
	Na ppm	3-8	5	"
	K ppm	0.8-2.3	1.2	"
	CO_3 ppm	0.4-1.1	0.7	"
	HCO_3 ppm	160-336	240	"
	Cl ppm	3-9	6	"
	SO_4 ppm	10-35	21	"
	TDS ppm[5]	180-336	235	"
	E.C.[6]	292-540	410	"
	pH	7.4-8.5	8.1	"
	Temp. ^oC	3-22	-	"
Sewage Pond Effluent (1952)	NO_3 ppm	0.5-1.4	0.9	Schreeder, 1955
	NO_2 ppm	0.8-1.7	1.2	"
	Cl ppm	6-13	9	"
	D.O. ppm[7]	7-10	8	"
	B.O.D. ppm	3-29	9	"
	Coliform MPN (1,000's)	-	4	"

1 - ppm equals parts per million (mg per liter)
2 - TDS equals total dissolved solids
3 - Data reported in terms of SiO_2 standards (ppm)
4 - United States Bureau of Reclamation, Logan, Utah
5 - Data reported in terms of total settleable solids
6 - Electrical conductivity of the water in micromhos
7 - Dissolved oxygen concentration of the surface water

BENTHIC PRIMARY PRODUCTIVITY STUDY

Methods

Selection of River Stations

The study area was partitioned into two sections based on the entrance of Seven-Mile Creek. Both sections were divided into 30.5 m divisions. Thirteen and 14 divisions, respectively, were selected by lot as station sites. Actual site location within the selected division was determined by accessibility. Survey stakes marked site locations. Stations were labelled as to river distance from the Mendon Bridge; viz., Station 7.35 was located 7.35 km downstream from the bridge. Stations are listed in Appendix A.

Pigment Measurements

Two sizes of paraffin-coated concrete hemispheres were placed on the river bed at each station. The hemispheres had curved surface areas of 1,321 cm^2 (radius = 14.5 cm) and 868 cm^2 (radius = 11.8 cm), and weighed about 13 and 8 kilograms, respectively. Hemispheres designated for the lower section were cast with three, tapered, metal-capped wooden stakes extending (30 cm) from the basal surface. Their purpose was to keep the substrate from sinking into the layer of silt lining most of the river bed in the lower section.

These artificial substrates were used instead of the natural substrates present of the river bed to obtain estimates of algal pigments for several reasons. First, uniform substrates allowed a more

precise comparison of algal communities found in diverse river habitats by removing the effects of substrate type and shape. Second, bed elements in the study area seldom exceeded 15 cm across the largest diameter and in the lower section substrate consisted mainly of gravel, sand, and silt particles. The hemispherical shape was chosen because it resembled the general shape of most well-worn bed elements.

The paraffin method of coating substrates as described by Beers and Neuhold (1968) was used in this study.

The technique of pigment extraction was also included in the above paper. Absorption measurements of the acetone extracts (1-cm light path) were made with a Beckman spectrophotometer at 665, 645, 630, 510, 480, and in some cases 430 mμ. Quantities of chlorophyll -a, -b, -c, and carotenoids were calculated using the modified equations presented by Strickland and Parsons (1965). At 430, 480, and 665 mμ, the extract absorption was used as a pigment parameter (D430, D480, and D665).

From February to April, 1966, a preliminary study was conducted to obtain an estimate of the time required before the chlorophyll -a content of the epilithic community on a substrate ceased to be closely related to immersion time. Twenty concrete cylinders (height = 13.5 cm, radius = 4.8 cm, exposed surface area = 474 cm^2) were placed in the river at Station 0.05. At two week intervals 5, 3, 6, and 6 substrates were removed for pigment measurements. Acetone extractions were carried out in tight-sealing bottles at $0^{o}C$. From this point, chlorophyll -a was determined by the method of Strickland and Parsons

(1965). The results (Figure 2) indicated that chlorophyll -a was not closely related to the length of time the substrates had been in the water after an immersion period of six weeks. Waters (1961) reported a period of 3 to 8 weeks was sufficient for adequate colonization. Keup (1966) utilized about the same time period for colonization of substrates by algae. Ten weeks was decided upon as a minimum immersion period for substrates in this study.

Stream Benthos Metabolism Measurements

The metabolism of benthic, stream communities was estimated from dissolved-oxygen concentration changes in a continuous-flow apparatus. Several rocks from a stream bed were placed in a submerged, closed system of circulating, stream water. The net amount of oxygen released or taken up by the organisms (gross primary production minus community respiration) was obtained from differences in dissolved-oxygen determinations made on water samples from the apparatus and the river. Upon completion of an experiment, the rocks were removed and the plant pigments contained in the epilithic community extracted with acetone. Optical densities of the extract at various wave-lengths (665, 630, 510, 480 and 430 mμ) were measured with a spectrophotometer. The exposed surface area of each substrate was estimated by pressing metal foil over the substrate, trimming away the excess, and weighing the amount needed to cover the surface. An area estimate was obtained by dividing the amount of foil used by the weight of 1 m^2 of foil.

The continuous-flow apparatus (Figure 3) consisted of a hemisphere, submersible pump, plastic connections, and support platform. The hemisphere was constructed of 0.32 cm thick, clear plexiglas with

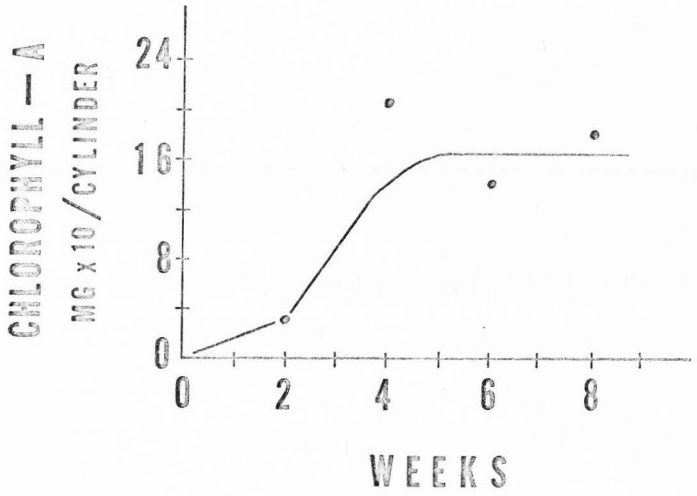

Figure 2. Average amounts of chlorophyll-a on artificial substrates at two-week intervals following placement in the Logan River near Mendon Bridge, Spring of 1966. (Line eye-fit to data.)

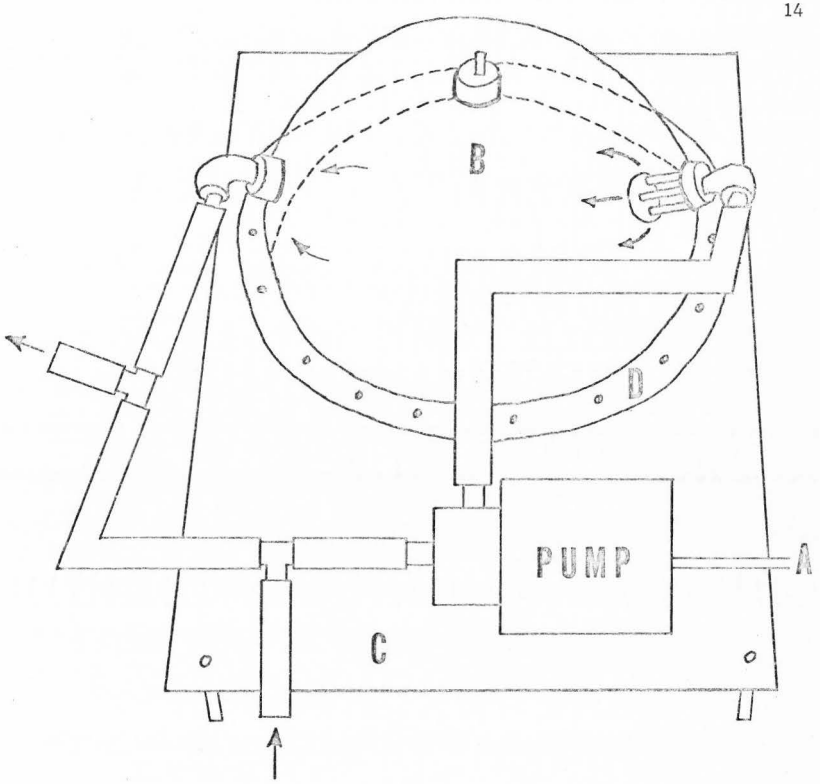

Figure 3. Diagramatic presentation of submersible, metabolism chamber. A= electrical connection to the variable transformer and generator, B= plexiglas hemisphere, C= support platform, and D= flange over cork gasket. Scale is 1:4.

a 20.32 cm radius. A 3.81 cm flange over a circular, cork gasket bolted the chamber to the platform. The resulting seal permitted little water leakage. Two side openings permitted entrance and exit of circulating water, and the top opening, when unplugged, allowed the release of entrapped air. A circular, perforated baffleplate placed at the entrance of water into the chamber dispersed the incoming flow. A waterproof, centrifugal pump (115 V, A.C., 60 cycle, "Little Giant Vaporizer Company") was bolted to the support platform. This platform consisted of a 0.63 x 50.80 x 76.20 cm steel plate with 7.62 cm-long bolts as supports. Plastic tees positioned in the tube carrying water from the chamber to the pump permitted the withdrawal of a water sample from the chamber while it was under water and in operation.

Positioned on the stream bank near the location of the apparatus in the stream were a variable transformer (Varivac, 115 V, A.C., input, 130 divisions, "General Radio Company"). and a portable generator (115 V, A.C., 60 cycle, "Homelite Company"). The speed of the pump was governed by the setting on the transformer.

The conversion factor between pumping rate and transformer setting was determined in the laboratory. Total volume of the apparatus was 11.8 liters. The pumping rate was a linear function of the setting, in the range of 60 to 100 transformer divisions. The equation expressing this function was

$$V = 27.25 (S - 60) + 730 \quad (1)$$

where V equals pumping rate in ml/min, and S equals transformer setting. At a setting of 60, the pump recycled the water once every 16.2 minutes while at a setting 100 the value was 5.2 minutes. A transformer setting

of 75 was used in all field experiments resulting in a recycling time of 9.5 minutes.

To withdraw a sample of water, one end of a rubber tube was attached to the tee nearest the chamber and the other end placed in a plastic bucket held upright at the water surface above the apparatus. Outlets from the tees were unclamped, the stream water was drawn in the tee nearest the pump, and the chamber water was pumped out the first tee. Samples were collected in three BOD bottles positioned in the bucket, and the bottles were allowed to overflow for 30 seconds. Next, three stream water samples were collected beneath the surface with a large, plastic syringe (volume = 250 ml). All samples were fixed and titrated in the field in accordance with the azide modification of the Winkler method (APHA, 1960).

The above operation was completed under daylight conditions for estimates of net community production, and then with a tarp over the apparatus to exclude light for estimates of community respiration. Gross photosynthesis estimates were obtained from the sum of the two above measurements.

Net change in quantity of dissolved oxygen in the apparatus was calculated using the following equation

$$dOXY/dt = DO_2V_2 - DO_1 (V_2-V_1) - DO_3V_1 \qquad (2)$$

where,

dOXY/dt = net change of dissolved oxygen in milligrams per hour.

dOXY = change in quantity of oxygen during the sampling interval,

and dt = sampling interval in hours,

DO_1 = dissolved oxygen concentration (mg/l) of the water sample taken from the apparatus at the start of the sampling interval,

DO_2 = dissolved oxygen concentration (mg/l) of the water sample taken from the apparatus at the end of the sampling interval,

DO_3 = dissolved oxygen concentration (mg/l) of the water sample taken from the stream at the start of the sampling interval,

V_1 = volume (liters) of water pumped out of the apparatus into the bucket and bottles (sum of volume of bottles and overflow),

and,

V_2 = volume (liters) of water contained by the apparatus (11.8 - volume of rocks in liters).

The following example is provided as an aid to a clearer understanding of the use of the above equation.

Given: 1100 - Water samples were withdrawn from apparatus for dissolved oxygen analysis. Volume of the three bottles plus overflow equals 1,100 ml. Average dissolved oxygen content of these samples equals 6.0 mg/l. Average oxygen content of the stream water equals 6.0 mg/l and remains constant for the duration of the experiment. This was not true during the actual experiments.

1200 - The above procedure is repeated. Volume of the bottles plus overflow equals 1,200 ml. Average dissolved oxygen content of these samples equals 7.5 mg/l.

1300 - The above procedure is repeated. Volume of the bottles plus the overflow equals 1,000 ml. Average oxygen content of these samples equals 9.0 mg/l. The volume of the rocks in the chamber is estimated to be 2,800 ml by water displacement.

Calculation:

1100 to 1200

$$dOXY/dt = 7.5\ (11.8-2.8) - 6.0\ (11.8-2.8-1.1) - 6.0\ (1.1)$$

$$= +\ 13.5 \text{ mg oxygen/hour}$$

1200 to 1300

$$dOXY/dt = 9.0\ (11.8-2.8) - 7.5\ (11.8-2.8-1.2) - 6.0\ (1.2)$$

$$= +\ 16.3 \text{ mg oxygen/hour}$$

Notice that DO_2 in the first calculation becomes DO_1 in the second calculation.

Results and Discussion

Pigment Estimates

The substrate coatings were processed for pigment extraction on four occasions from June, 1966 to November, 1967. The effect of substrate size on quantity of chlorophyll -a was tested within each time period and section of the river. Analysis of variance was calculated utilizing a randomized block design (blocks = stations, treatments = substrate sizes) and the resultant "F" values were tested for significance at the 0.90 level. If substrate size had a signficant effect on the quantity of chlorophyll -a, then the data from the smaller substrates were expended by the ratio of the two areas (1.52). This was done for the smaller substrates at upstream stations during sample periods I, II, and III (February to July). Section means and 95 percent confidence intervals within each sample period are available (Table 2).

Only during the sample period II were the pigment data from the upstream section significantly different from those values from the downstream section (Table 2). There was no signficant difference in

TABLE 2. Pigment measure mean and 95 percent confidence limits for each of the river sections within each sampling period. Within the parentheses are the "student's" t values used in testing the hypothesis that the mean of the upstream data equalled the mean of the downstream data. Single asterisked values indicate rejection of the hypothesis at alpha equal to 0.05.

Sample Period	Days in River	Section of River	No. of Stations	Chlorophyll** A	Chlorophyll** B	Chlorophyll** C	Carotenoids**	D480/665	D430/D665
June-Sept. 1966	78	Upper	11	7.8±0.9	4.4±0.7	1.7±0.3	3.9±0.5	1.35+0.11	n.m.
	78	Lower	12	9.9±2.0	4.2±0.8	2.6±0.8	4.6±1.0	1.19±0.02	n.m.
				(0.9)	(0.2)	(1.3)	(0.7)	(0.4)	-
Sept. 1966-Jan. 1967	116	Upper	13	4.5±0.8	2.1±0.4	1.0±0.3	2.5±0.5	1.52±0.02	n.m.
	116	Lower	11	11.6±3.4	5.2±2.3	4.4±1.9	6.6±1.1	1.55±0.25	n.m.
				(5.5*)	(3.5*)	(4.1*)	(6.1*)	(0.1)	-
Feb. - July 1967	152	Upper	6	3.1±2.0	1.5±1.0	0.7±0.4	2.0±1.4	1.82+0.15	n.m.
	152	Lower	6	1.4±1.0	1.1±0.8	1.2±0.5	0.8±0.6	1.61±0.26	n.m.
				(1.7)	(0.6)	(0.8)	(1.5)	(0.3)	-
July-Nov. 1967	118	Upper	10	9.0±2.4	2.2±0.6	6.6±2.3	5.3±1.5	1.54±0.18	3.11±0.48
	118	Lower	7	7.8±3.9	2.3±1.1	7.0±2.8	4.5±2.1	1.59±0.16	3.02±0.81
			76	(0.8)	(0.2)	(0.3)	(0.7)	(0.1)	(0.1)

n.m. = not measured
** = milligrams per 0.12 square meter

the yellow:green pigment ratio (D480/D665) during this period. If the ratio is accepted as an index of the qualitative nature of the algal members of the benthic communities, then the observed difference in sample period II can be said to be of a quantitative nature. The combination of relatively low river volume and high volume of sewage-pond effluent diverted to the river during this period might have been responsible for greater algal growth below the entrance of the tributary. The tributary volume was diluted by a factor of about 8 during this period and factors ranging from 10 to 30 during the other periods. Inorganic nutrients, such as nitrates and phosphates, are common in effluent from sewage, oxidation ponds and can be stimulants for plant growth. Sewer Creek (Figure 1) water was quantitatively analyzed for nitrate, phosphate, and dissolved organic carbon during August 8-12, 1966. The respective concentrations were 1.7, 0.15, and 3.0 mg/l. The stannous chloride method (APHA, 1960) was utilized for the soluble, inorganic phosphate determination. The remaining methods are presented in the Sphaerotilus study methods.

An average and an indication of variability are presented for each of the four pigments and the two pigment ratios (Table 3). The average amount of chlorophyll -a (0.06 gms/m^2) was not as large as the estimate reported for the canyon section of the river (0.30 gms/m^2; McConnell and Sigler, 1959). The earlier study used the equation of Richards and Thompson (1952), while the equation of Strickland and Parsons (1965) was used in the present study to estimate the amount of chlorophyll -a. A comparison of the two equations suggested that the result of the former equation was 30 to 35 percent larger than the result of the latter equation. This comparison was made using

TABLE 3. Mean and 95 percent confidence limits for various pigment variables. Statistics were calculated from a data pool of all four sampling periods, 1966-67.

Pigment Measure	Stations	Mean	Confidence Limits
Chlorophyll -a	76	55 mg/m^2	± 7 mg/m^2
Chlorophyll -b	76	23 "	± 4 "
Chlorophyll -c	76	23 "	± 5 "
Carotenoids	76	30 "	± 4 "
D480/D665	76	1.49 "	± 0.06
D430/D665	17	3.07	± 0.20

representative data from the Logan River. Talling and Driver (1961) suggested that the Richards and Thompson (1952) equation overestimates amount of chlorophyll -a by 25 percent or more. Furthermore, the earlier study employed natural and concrete rocks as sampling devices, and the present study used paraffin-coated, concrete substrates.

As reported by Beers and Neuhold (1968), the estimate of chlorophyll -a density from uncoated, concrete substrates was 1.52 times larger than the value from paraffin-coated substrates. This was attributed to the surface irregularities of concrete which afforded more area and sites for attachment. McConnell and Sigler (1959) reported that chlorophyll -a density estimates from concrete rocks were within the range of those values obtained from natural rocks. If the density values from the earlier study were reduced by 35 percent and the value from this study expanded by 1.52, then a more realistic comparison of the two studies could be made. The canyon estimate would be about 0.20 gms/m^2, and the valley estimate would be about 0.09 gms/m^2 for chlorophyll -a.

Three versions of the yellow:green pigment ratio were computed for the four Utah streams and are presented for comparisons with pigment ratios in other aquatic communities (Table 4). The four streams are identified in the text of the next section. An opportunity to collect pigment data from benthic communities on and around Amchitka, Alaska, was taken during August and September, 1967 and the data were included in this presentation. The absorbance ratios can be directly compared, but the ratios based on pigment amounts are not all directly comparable, because investigators used different equations to estimate

TABLE 4. A tabulation of yellow:green pigment ratios for various aquatic communities.

Pigment Ratios				
Absorbance		Weight carotenoids/	Community	
D480/D665	D430/D665	chlorophyll -a	Description	Source
			FRESHWATER (benthos)	
1.49	3.07	0.54	Logan River	-
1.34	3.06	0.81	Swan Creek	-
1.54	2.69	0.52	Blacksmith Fork River	-
1.23	2.68	0.43	Little Bear River	-
0.97-2.07	-	0.36-0.77	12 streams, Amchitka, Alaska	-
1.51-2.90	-	0.55-1.13	4 lakes, Amchitka, Alaska	-
1.60-2.73	1.60-467	-	*English Lakes	Gorham, 1960
			FRESHWATER (phytoplankton)	
0.83-1.58	-	-	Columbia River (1963-64)	Cushing, unpublished
-	4.32-6.98	-	8 lakes, Spain	Margalef, 1964
			BRACKISH WATER (phytoplankton)	
-	-	2.17	Cochin Bay, frontwater	Qasim and Reddy, 1967
-	-	2.84	Cochin Bay, backwater	Qasim and Reddy, 1967
			MARINE (benthos)	
1.32-1.60	-	0.49-0.58	2 tidal pools, Amchitka, Alaska	-

TABLE 4 (continued)

Pigment Ratios				
Absorbance		Weight carotenoids/ chlorophyll -a	Community Description	Source
D480/D665	D430/D665			
			MARINE (phytoplankton)	
-	2.3-2.8	-	general range	Currie, 1962
-	3.0-3.5	-	predom. diatoms	Margalef, 1960
-	4.0-5.6	-	predom. dinoflagellates	Margalef, 1960
-	3.10	0.26	*Mediterranean Sea	Margalef, 1963
-	-	0.27-0.37	Vineyard Sound	Yentsch and Vaccaro, 1958
-	-	0.19-0.36	Departure Bay	McAllister et al., 1961
-	-	0.11-1.05	*Departure Bay	Anita et al., 1963
2.17	3.03	-	*Woods Hole Waters	Yentsch, 1960
			CULTURES	
-	-	0.31-1.65	mixed	McAllister et al., 1964
-	-	0.29-0.67	diatoms	Yentsch and Vaccaro, 1958
3.35	4.50	-	*Cyclotella (diatom)	Yentsch, 1960
1.80	2.67	-	*Amphidinium (dinoflagellate)	Yentsch, 1960
-	-	0.34-0.71	*Dunaliella (green flagellate)	Yentsch, 1962
-	-	0.11-1.05	*Skeletonema (diatom)	Cassie, 1963
2.94	3.38	-	*Chlamydamonas (green flagellate)	Yentsch, 1960

* Ratios were estimated from data presented in the source paper.

the amount of pigments. There do not appear to be any clear associations between magnitude of ratio and community type.

Metabolism Estimates

In order to develop a general statement, metabolism measurements of benthic communities were conducted at three locations in the Logan River and one location in each of the following rivers: Swan Creek, Little Bear River, and Blacksmith Fork River. Swan Creek was located on the western watershed of Bear Lake, Utah-Idaho, and the remaining three rivers were located on the eastern watershed of Cache Valley near Logan, Utah. The total areas of the substrates used in each experiment were similar and ranged from 0.11 to 0.15 m^2. Additional data on these stream communities are available (Appendix B).

The average rate of gross, primary photosynthesis in the four streams was 0.8 mg O_2/hr/mg chlorophyll -a (Table 5). This rate is in general agreement with the results from metabolism experiments with complete communities in the canyon section of the Logan River (McConnell and Sigler, 1959).

Strictly speaking, oxygen changes in aquatic communities can be interpreted in terms of gross, primary production (P) and community respiration (R) rates. Communities described by a P/R ratio greater than 1 are given an autotrophic status (Odum, 1956). However, for most autotrophic communities, an approximate value for the rate of net, primary production (P_n) can be obtained by subtracting R from P. The main assumption is that most of the respiration rate can be traced to benthic plants. When this is done, as it is in this study, then the P_n value will probably be an underestimate of the true value.

TABLE 5. Chlorophyll -a based rates of benthic, algal photosynthesis. Data are from metabolism chamber experiments in the indicated water flow.

	Logan River[1]	Logan River[2]	Swan Creek	Blacksmith Fork River	Little Bear River	Logan River[3]
Sampling Date (1967)	9-29	10-4	11-1	11-4	11-8	11-22
Hours of Experiment	1200-1600	1315-1715	1105-1505	1115-1400	1030-1430	1100-1230
Water Temperature (^{o}C)	10	9	8	4	8	5
Solar Radiation[4] ($cal/cm^2/min$)	0.58	0.52	0.32	0.39	0.13	0.13
Assimilation Rates ($mg\ O_2/hr/mg$ chloro -a)						
Gross Production	0.96	n.m.	0.68	1.08	0.61	n.m.
Net Production	0.55	0.41	0.57	0.69	0.52	1.46
Dominant Flora	green algae	green algae	moss	brown algae	brown algae	brown algae

n.m. = not measured
1 - below list impoundment, natural rocks
2 - above Twin Bridges, natural rocks
3 - below Mendon Bridge, concrete hemisphere
4 - measured with Weston Illumination Meter (Model 1756) in foot-candles, but converted to energy units with a known relationship (Table 14)

An attempt was made to construct a pigment-based equation to predict the rates of net and gross primary production within a reasonable error utilizing the data from the six metabolism experiments. At present, there are no grounds for postulating that the function should be expressed in other than a linear relationship (Cassie, 1963). Simple correlation values between pigment measures and each of the two rates of primary production (Figure 4) suggests some strong relationships. Chlorophyll -c, chlorophyll -a, and the D480:D665 ratio might occupy prominent positions in the equations predicting net and gross production. Rates of net and gross production were regressed against combinations of these three pigment variables and a few combinations with other pigment variables. Certain measures of the precision of these prediction equations for the two rates are presented (Table 6 and Table 7).

Certain combinations of the pigment variables appear to be better predictors of the two rates than others based on the coefficient of variation, F-test with its level of significance, and square of the correlation coefficient. Chlorophyll -c predicted the rate of net production with high precision (r^2 = 0.9663 and CV% = 10.36), and was improved slightly by the additional consideration of chlorophyll -a (r^2 = 0.9921 and CV% = 4.11).

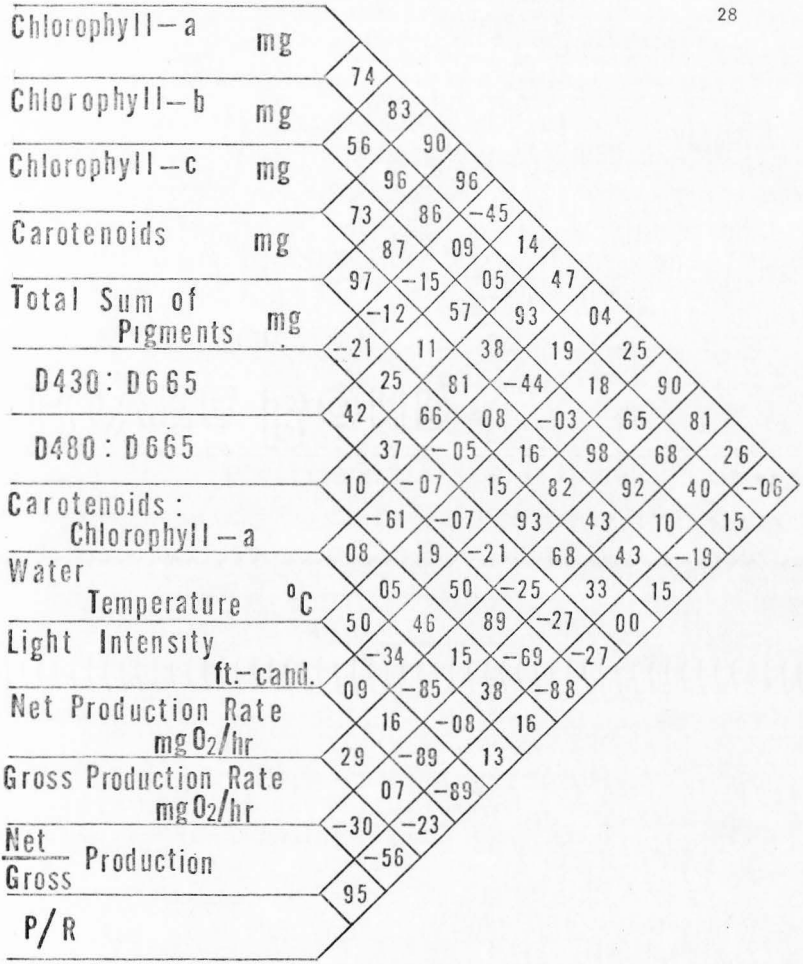

Figure 4. Correlation coefficients (rx100) between pigments, rates of production, water temperature, and solar radiation. Assuming a correlation coefficient equal to zero as a null hypothesis, the correlation coeficients can be tested for significance at the 95 percent level. The hypothesis is rejected if $|r| \geq 0.81$ for the top eleven entries (n=6) and if $|r| \geq 0.95$ for the bottom three entries (n=4).

TABLE 6. Parameters of selected equations regressing net primary production on various pigment measures from benthic, stream communities (n=6).

Pigment Variables	a_R^2 (%)	b_F	c_{CV} (%)
Chlorophyll -a	84.44	17.56(.975)	24.28
Chlorophyll -c	96.63	114.60(.999)	10.36
Carotenoids	66.90	8.08 (.95)	32.45
Sum of Pigments	87.05	26.88 (.995)	20.31
Chlorophyll -a, Chlorophyll -b	81.48	6.60 (.90)	28.01
Chlorophyll -a, Chlorophyll -c	99.21	189.01 (.999)	4.11
Chlorophyll -a, Carotenoids	81.49	66.04 (.995)	28.02
Chlorophyll -a, Sum of Pigments	87.10	10.13 (.95)	23.39
Chlorophyll -a, D430:D665	85.70	8.99 (.90)	24.64
Chlorophyll -a, D480:D665	95.50	31.88 (.99)	13.82

a - square of the correlation coefficient.

b - F-value with the level of significance enclosed with parenthesis

c - coefficient of variation = $\frac{(\text{residual mean square})^{1/2}}{\text{mean of dependent variable}}$

TABLE 7. Parameters of selected equations regressing gross primary production on various pigment measures from benthic, stream communities (n=4).

Pigment Variables	a_R^2 (%)	b_F	c_{CV} (%)
Chlorophyll -a	65.24	3.8(.75)	32.04
Chlorophyll -c	84.37	10.8(.90)	21.30
Carotenoids	18.26	0.5(.25)	48.79
Sum of Pigments	46.76	1.8(.50)	39.34
D430:D665	6.43	0.1(.10)	52.21
D480:D665	79.36	7.7(.75)	24.42
Chlorophyll -a, Chlorophyll -c	87.18	3.4(.50)	27.27
Chlorophyll -a, Carotenoids	85.69	2.9(.50)	28.81
Chlorophyll -a, D430:D665	66.81	1.0(.25)	43.95
Chlorophyll -a, D480:D665	96.45	13.6(.75)	14.36
Chlorophyll -c, D480:D665	99.94	828.9(.975)	1.87
Chlorophyll -a+-c, D480:D665	98.83	42.2(.75)	8.23

a - square of the correlation coefficient

b - F-value with the level of significance enclosed with parenthesis

c - coefficient of variation = $\frac{(\text{residual mean square})^{1/2}}{\text{mean of dependent variable}}$

The quantitative expression for these two relationships are:

$$\hat{Y}_{np} = 11.084 + 0.715 \text{ (chlorophyll -c)}, \quad (3)$$

and

$$\hat{Y}_{np} = 7.037 + 0.544 \text{ (chlorophyll -c)} + 0.173 \text{ (chlorophyll -a)}. \quad (4)$$

Chlorophyll -c, also, predicted the rate of gross production with acceptable precision ($r^2 = 0.8437$ and CV% = 21.30), but this precision could be substantially improved by the inclusion of the D480/D665 ratio ($r^2 = 0.9994$ and CV% = 1.87). The quantitative expression for the improved equation is:

$$\hat{Y}_{gp} = -78.447 + 0.706 \text{ (chlorophyll -c)} + 73.975 \text{ (D480:D665)}. \quad (5)$$

In the above equations the pigment variables, chlorophyll -c and chlorophyll -a, should be expressed as milligrams per 0.13 square meter, and the respective predicted dependent values will be in terms of mg oxygen per hour per 0.13 square meter. The multiplication of the rate value by 7.575 will produce the rate in terms of mg oxygen per hour per square meter.

The rates of oxygen evolution (photosynthesis) by benthic communities in several Northern-Utah streams were better related to chlorophyll -c and chlorophyll -a, or D480/D665, than to chlorophyll -a alone. Interpretative comments of the indicative value of the three pigment variables to the rate of photosynthesis are presented separately.

The prime, and perhaps only photocatalyst in algal photosynthesis is chlorophyll -a (Brody and Brody, 1962). As a consequence, chlorophyll -a should occupy a place in any set of pigment variables used to predict

photosynthetic rates of algal communities.

A credible explanation for the place of chlorophyll -c in the pigment relationship to photosynthesis may be offered on the basis of the "Engelmann Concept" or "Emerson Effect" (Rabinowitch, 1951; Brody and Brody, 1962). Briefly, this concept states that radiant energy absorbed by pigments other than chlorophyll -a is transferred to chlorophyll -a before it can be used in photosynthesis. If such a situation existed in the Utah-stream communities, then accessory pigments would be expected to have some importance along with chlorophyll -a in the regression equations. Apparently this situation did exist, and chlorophyll -c was probably participating as an active sensitizer in photosynthesis.

Strickland (1966) stressed the importance of considering the amounts of accessory pigments in addition to chlorophyll -a when utilizing methods based on pigment content to estimate rates of algal photosynthesis. In addition to the data presented for some Utah streams, there were some marine phytoplankton investigations which presented evidence for this approach. In the North-East Atlantic Ocean, Currie (1957) obtained a better relationship between carbon-14 productivity data and the sum total of all pigments rather than between productivity data and chlorophyll -a values alone. Cassie (1963) investigated the relationship between pigments and gross, primary productivity diatom cultures. He obtained a better estimate of productivity by incorporating into the equation, in addition to chlorophyll -a, one other pigment, either chlorophyll -c or carotenoids. The correlation coefficient for his regression of productivity on chlorophyll -a values alone was 0.36, on chlorophyll -a and chlorophyll -c was 0.97, and on chlorophyll -a and

carotenoids, 0.68. McAllister et al. (1964) reported that at low light intensities the rate of gross photosynthesis was proportional to the sum total of all pigments, irrespective of species or culturing conditions. By contrast, they reported that the rate of maximum photosyntheiss was poorly related to pigment composition, the best correspondence being with chlorophyll -a. Research on natural, diatom populations in the South Atlantic Ocean presented some evidence for the role of chlorophyll -c in the energy-transferring mechanism of phytoplankters that are light-color limited (Mandelli, 1967).

The yellow:green pigment ratio has significant importance in the relationship of pigments to the rates of photosynthesis (Equations 4 and 5). The sensitivity of this ratio to nutrient depletion and supply, taxonomic composition, age of most algae, and succession in algal communities makes it useful in the prediction of the photosynthetic rate. Evidence to support the relationship between the carotenoids; chlorophyll -a ratio and nutrient deficiency (phosphate and nitrate) and algal culture age was found by Yentsch and co-workers (Yentsch, 1962). Castellvi (1964) reported, also, on the relationship between D430:D665 and nutrient depletion and supply. Margalef (1967) presented evidence that D430/D665 reflected community structure, particularly taxonomic composition and succession. He also set primary production (measured by the carbon-14 technique) as a function of the D430/D665 ratio (Margelef, 1963, 1965). Odum and Odum (1959, p. 87) pointed to the potentiality of yellow:green pigment ratio as a useful index to fluctuations in the vigor of the primary trophic level of whole communities.

It is of some interest to note that D480/D665 was more highly correlated with rates of photosynthesis in Utah streams than D430/D665 (Figure 4). Although these two ratios were related ($r = +.42$) they were not identical. Differences are possibly due to the relative participation of pigments in light absorption at 430 and 480 mμ. Carotenoids are responsible for most of the absorption at 480 mμ while the chlorophylls account for a large portion of the absorption at 430 mμ (Rabinowitch, 1951). Therefore, absorption at 480 mμ may be more independent of chlorophyll concentration (especially chlorophyll -a) than absorption at 430 mμ. Extensive research concerning various yellow: green pigment ratios is needed to clarify the significance of various ratios.

In summary, the findings from this study indicated that other pigment measures, in addition to chlorophyll -a, should be considered when making pigment-based estimates of the rate of net, oxygen production by benthic communities. Many factors can be expected to affect the precision of the relationship of chlorophyll -a to photosynthetic rates in aquatic communities. Strickland (1966) suggested that the relationship could be imporved if amounts of other pigments were not ignored, and Margalef (1965) suggested that the inclusion of a measure of "structure" will improve the relationship. Both of these suggestions were used and the resulting relationships (Equations 4 and 5) accounted for essentially all of the variation in the rates of net and gross oxygen production.

It should be pointed out that the experiments were conducted within a short period and under midday light and temperature conditions.

If the experiments had been conducted over a longer period which would have included more variations in light intensity and water temperature, then the relationship probably would have included these two variables in addition to the pigment variables.

Primary Production Estimates

Two environmental factors were considered before primary production in the study area was estimated. The area of the river bed in the 12 km section of the river was 10.4 hectares where the mean width of the river was 8.7 m (3 to 14 meters at the 95 percent confidence level). An approximation of the mean hours of light intensity greater than 0.1 cal/cm^2/min was 10.5 hr/day, or 3800 hr/year (estimated from Figure 5). There is evidence that most algal photosynthesis is light saturated above 0.1 cal/cm^2/min (Strickland, 1966).

The rate of net primary production was estimated to be 100 mg oxygen/hour/square meter utilizing the two-pigment equation (4) and the appropriate pigment values (Table 3). An estimate of the annual net production for the study area was estimated thus:

$$(100 \text{ mg } O_2/m^2/hr)\ (3800 \text{ hr}) = 380 \text{ gm } O_2/m^2/yr$$

$$(380 \text{ gm } O_2/m^2/yr)\ (10.4 \times 10^4 \text{ } m^2) = 39{,}520 \text{ Kg } O_2/yr$$

An estimate of the annual gross production for the study area was calculated in a similar manner utilizing Equation (5) and the appropriate data from Table 3, and equalled 101,504 Kg O_2/yr. This result is contrasted with some available data from other studies of flowing waters (Table 8).

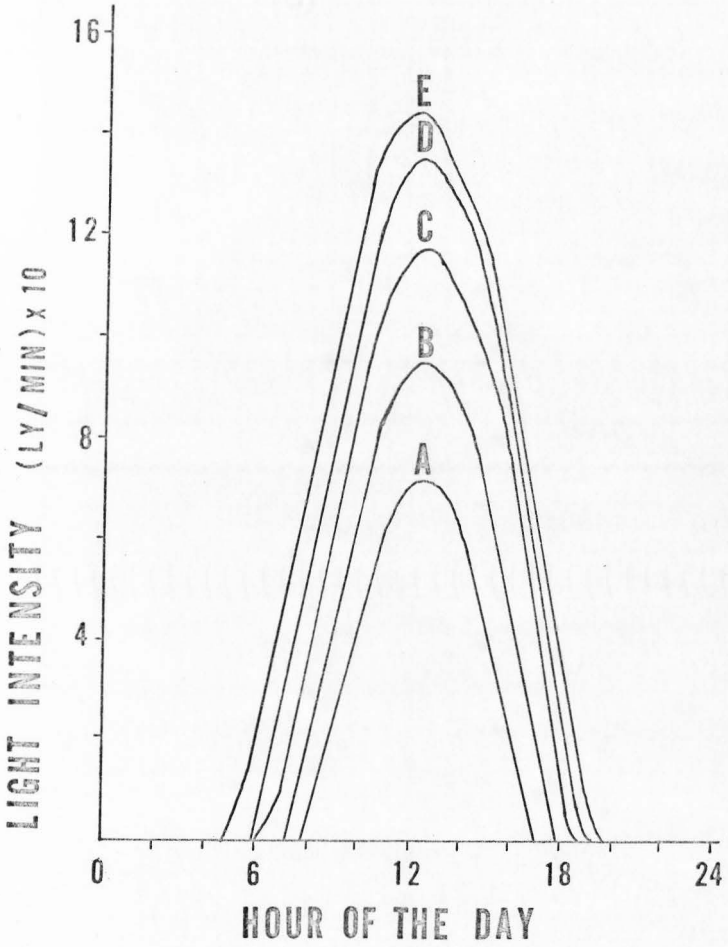

Figure 5. Daily changes in sunlight intensity at Logan, Utah. Data obtained from U.S.U. Meterology Department. A= January 16, B= February 19, C= March 20, D = April 24, and E = June 1,1966.

TABLE 8. Estimate of annual gross primary production rate and P/R ratio for various lotic communities.

Water Flow	Annual Rate[1]	P/R	Method	Source
Logan River (USA)				
Lower Section	3,416	1.5	Pigment	-
Upper Section	4,483	-	Pigment	McConnell & Sigler, 1959
Ararawa River (Japan)				
Lower Section	3,010	1.5	Pigment	Kobayasi, 1961
Upper Section	770	1.9	Pigment	Kobayasi, 1961
Madison River (USA)	34	3.1	pH	Wright & Mills, 1967
Blue River (USA)	13,300	0.9	Oxygen	Duffer & Dorris, 1966
Ivel River (England)	12,250	1.1	Oxygen	Edwards & Owens, 1962
Oconee River (USA)	319	0.3	Oxygen	Nelson & Scott, 1962
Silver Springs (USA)	10,220	2.9	Oxygen	from Odum, 1956
Birs (Switzerland)	64,050	2.8	Oxygen	"
Kljasma (Russia)	3,066	1.3	Oxygen	"
Itchen River (England)				
Summer	12,410	0.8	Oxygen	"
Winter	4,745	0.3	Oxygen	"

[1] Annual gross primary production rate expressed in terms of Kcal/sq. meter/year. Conversion factors used in standardization to this rate are presented in Table 14.

SPHAEROTILUS STUDY

Methods

Exposed-Slide Technique

A pair of glass slides (0.1 x 2.5 x 7.5 cm) was positioned vertically from a wire suspended between a bouy and anchor at each river station. Each slide was held in position parallel to the direction of water flow by taping a small wire with a terminal loop to each slide edge and resting the lower loop on a knot in the suspension wire. One slide was suspended at a depth of 10 to 20 cm while a second was suspended at a depth of 30 to 40 cm. The second slide served as a spare in case the first one was unuseable or damaged.

Each slide was treated to free its surface of organic matter prior to its use. After remaining in alcohol for several hours, the slide was rinsed and stored in distilled water.

The slides, after in the water for a required time, were removed, dried, fixed by heat, and stained with a solution of 1 percent erythrosin in 5 percent phenol solution as suggested by Kriss (1963). Henrici (1936) reported that a 5 percent erythrosin solution was satisfactory for his work with freshwater bacteria on slides.

A preliminary study was conducted (April 21 to 23, 1966) at Station 9.3 employing the suspended-slide technique. The slides were observed after immersion periods of 24, 48, and 72 hours. In counting, the number of filaments of a given cell length per field was recorded,

the area of a field being 0.003526 cm^2. Solitary cells of Sphaerotilus were not counted. Henrici (1936) suggested a count of 50 fields per slide for most studies of freshwater bacteria. This count is laborious and it was an "a priori" assumption that a count of 30 fields would be sufficiently representative of the entire slide. The fields were spaced by means of a graduated mechanical stage over an area 13 x 39mm in the center of the slide. All counts were made with a 40X objective and a 10X focusing ocular.

Changes in Sphaerotilus colonization and reproduction rates were considered in reaching a decision on which of the three exposure periods was adequate. Rate of filament settlement on a slide reached a peak during the 24 to 48 hour interval and receded during the 48 to 72 hour interval (Figure 6a). Thus, it would seem that this bacterium had essentially colonized a slide after 48 hours. The generation time, or reproduction rate, of the filaments on a slide was calculated using equation (6).

$$\text{Generation time (hrs)} = T/(\log_2 C/F) \qquad (6)$$

where T equals immersion time in hours, C equals total number of Sphaerotilus cells counted in thirty fields, and F equals total number of Sphaerotilus filaments counted in 30 fields.

The generation time did not vary greatly with time (Figure 6b). Values based on each exposure time were within 10 percent of the overall mean (22 hours). Thus, each of the three immersion periods predicted approximately the same generation time. A 48 hour exposure period was selected, because this period was equivalent to the other two periods for estimating generation time, and the slide was essentially colonized by this time.

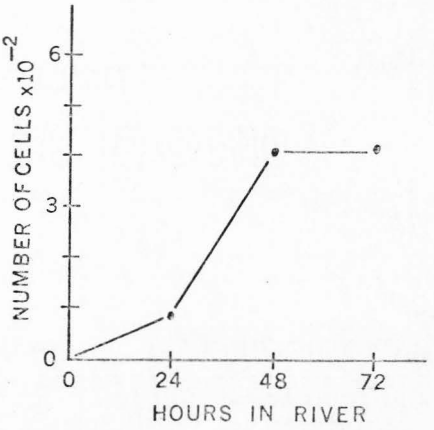

Figure 6a. Estimates of Sphaerotilus standing-crop on glass slides (30 fields) after immersion in the Logan River for 1,2,3, days April 1966.

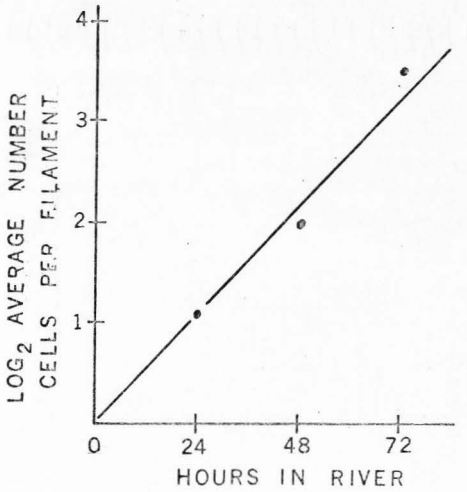

Figure 6b. Estimated generation time of Sphaerotilus filaments present on glass slides (30 fields) after 1,2, and 3 days, April,1966.

The "a priori" assumption that a count of 30 fields per slide would be sufficiently representative for the entire slide was examined with an appraoch based on an information theory function. If every field per slide were counted, then a filament length frequency distribution could be constructed. One measurement of this distribution would be filament diversity and expressed as follows:

$$D = -\Sigma\, n/N \log_2 n/N \qquad (7)$$

where D equals filament diversity, n equals number of filaments of a certain length, and N equals total number of filaments. The n/N value will be referred to as p in Figure 7. This is the Shannon-Wiener information function (Quastler, 1958). As the number of fields counted increases, the D value based on these fields approaches the D value based on the entire slide. The above approach was based on ideas presented by Margalef (1957, Figure 5).

The results of this approach (Figure 7) suggested that the intervals containing the D value based on the entire slide for the immersion periods of 24, 48, and 72 hours would be 0.20 to 0.40, 2.40 to 2.60, and 4.20 to 4.40, respectively. The D values were confined to these intervals after counting at least 20 fields per slide; therefore, it was concluded that a count of 30 fields would be sufficiently representative of the entire slide.

The values of the information function, $F(p) = -p \log_2 p$, for p equals 0.001 to 1.000 can be obtained (Appendix C). Goldman (1953) listed the logarithm to base 2 of the numbers from 1 to 10,000, and Ash (1965) presented abbreviated tables of values for $-\log_2 p$ and $-p \log_2 p$ where p = 0.01 to 1.00.

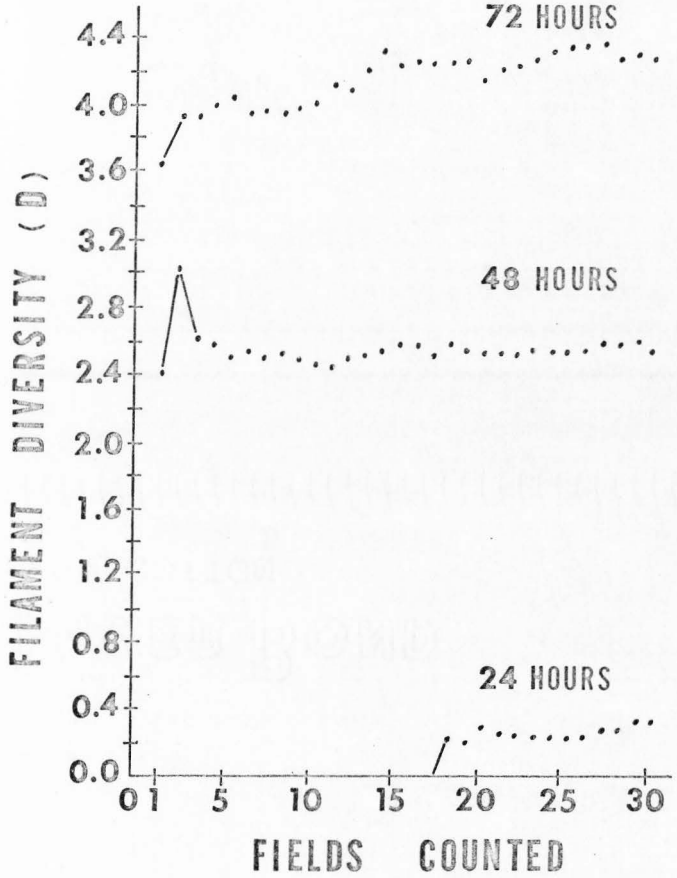

Figure 7. Changes in Sphaerotilus filament diversity (D) with number of fields counted and immersion time in the Logan River, April, 1966.

The general appearance and relative size of the bacterium studied are evident in Figures 8a and 8b.

Measurement of Selected Water Quality Parameters

Temperature was taken 15 centimeters below the water surface with a mercury thermometer graduated in 0.1°C divisions. Water velocity was measured with a pygmy current meter (Price Type AA) for a period of 60 seconds at a depth of 15 centimeters. Paired BOD bottles were used to collect water samples 15 cm below the water surface for dissolved-oxygen analysis. Winkler reagents with the azide modification (APHA, 1960) were added dropwise to the samples. These were later titrated with 0.01N sodium thiosulfate solution in the laboratory.

Analyses were initiated in the laboratory within two hours of field collection and conducted in duplicate. Hydrogen ion concentration was measured with a pH meter (Beckman Zeromatic). Five-day biochemical oxygen demand (BOD) of the collected samples was determined by the standard method (APHA, 1960) except the samples were not diluted and buffer solutions were not added. A volume of water sample was suction filtered through a membrane filter ("Millipore," HA 0.45 μ), and the filtrate was set aside for later inorganic nitrogen and organic carbon analysis. The inorganic nitrogen present as nitrate and nitrite in the filtrates was determined by the phenoldisulfuric acid method with the addition of hydrogen peroxide (APHA, 1960). Optical density of samples was measured with a Beckman spectrophotometer at 410 mμ. Dissolved organic carbon was determined by wet ashing a filtrate aliquot (100 to 200 ml) with a mixture of potassium dichromate and concentrated sulfuric acid,

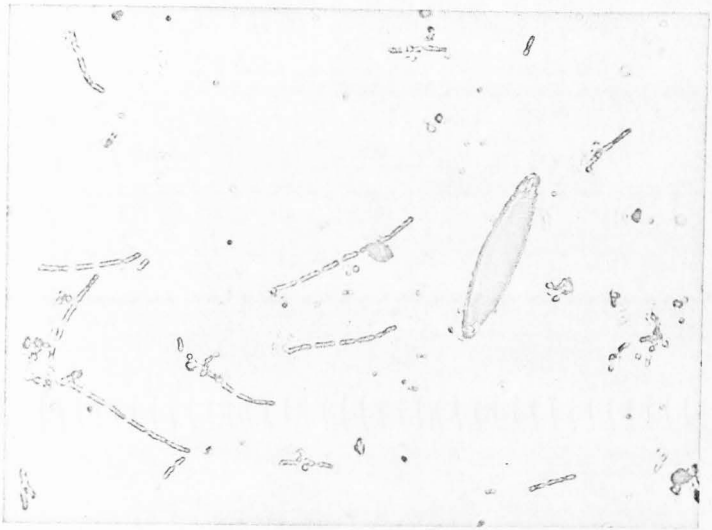

Figure 8a. Microphotograph of glass slide community after 48-hours exposure in the Logan River, October 1967 (Station 9.30). Magnification is near 450X. The prominent organism is a pennate diatom probably Navicula, and the filamentous organisms were designated Sphaerotilus.

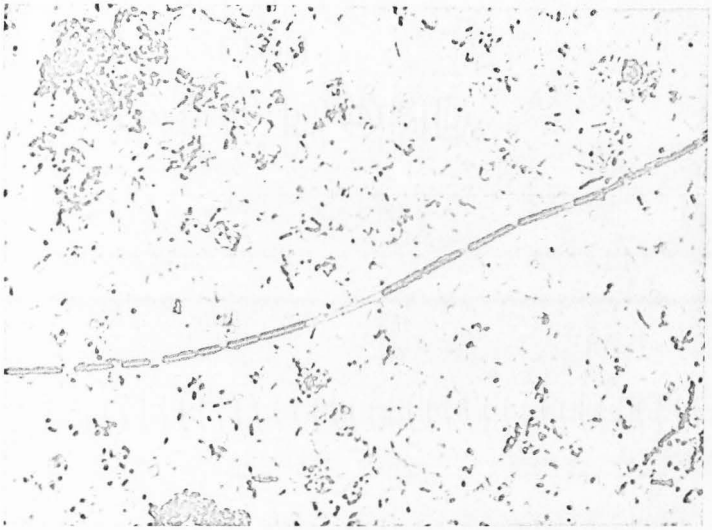

Figure 8b. Microphotograph of glass slide community after 48-hours exposure in the Sewage Pond Effluent, May 1966. Magnification is near 450X. A Sphaerotilus filament transverses a field containing many smaller bacteria. Notice the sheath between cells of the filament in the center of the photograph.

and then measuring in a spectrophotometer the decrease in extinction at 440 mμ of the dichromate solution after it had been reduced by the organic matter (Maciolek, 1962; Strickland and Parson, 1965). Glucose was used as the carbon standard and the results of this method were given in terms of glucose-carbon equivalents. Strickland and Parsons (1965) stated that generally the true carbon content is within 10 to 20 percent of the value given by this procedure. This method probably was a reasonably accurate measure of the dissolved organic matter available to aquatic, heterotrophic microorganisms.

Results

On November 25, 1966, pairs of slides were suspended at Stations 3.45, 4.50, 8.50, 10.50, 11.00, 11.50, and 13.50 for 48 hours. Later microscopic examination of 30 fields per slide did not locate any Sphaerotilus filaments. At all eight stations the water temperature was 4.5°C, dissolved organic carbon ranged from 0.9 to 4.2 mg/l, water velocity ranged from 15 to 72 cm/sec, and nitrate nitrogen ranged from 1.1 to 1.8 mg/l.

Eight sets of Sphaerotilus and water quality data were obtained on four dates from July to October, 1967. Date and stations visited were July, 9.5; August, 9.3 and 11.5; September, 7.5 and 9.3; and October, 7.4, 9.0 and 11.5. A summary of these data is contained in Table 9.

An additional set of measurements was made in July at Station 0.05 which was over 3 km upstream from the tributary entrance, but Sphaerotilus filaments were not found upon examining the exposed slides.

TABLE 9. Summary of *Sphaerotilus* and water quality data from Logan River experiments, July to October 1967.

Measurement	Range	Mean	Station 0.05
Temperature	10.0-21.0°C	13.7	11.2
Velocity	0-16 cm/sec	6	80
pH	7.3-8.7	8.2	7.9
Diss. Org. Cargon	0.8-5.3 mg/l	2.8	8.4
Diss. Oxygen	6.2-8.8 mg/l	7.8	2.3
$NO_3 + NO_2$	0.88-3.10 mg/l	1.88	2.7
B.O.D.	6.6-26.4 mg/l	14.3	7.0
No. Filaments[1]	16-1,507	563	-
No. Cells[1]	58-6,426	2,777	-
$\text{Log}_2 \frac{\text{cells}^1}{\text{filaments}}$	1.8336-3.0000	2.393	-
Biomass[1]	0.006-0.788 mg/m^2	0.340	-
D Values[1]	2.13-4.34	3.05	-

[1]Measurements pertain to *Sphaerotilus* present on glass slides.

Data from this source constitute the last column in Table 9.

The estimates of Sphaerotilus biomass (Table 9) were obtained from the product of number of cells per 30 fields and weight of a single cell. The latter value (1.26×10^{-7} mg) was based on a cylinder-shaped cell (diameter 2μ, length 10μ; Pringhseim, 1949) and on a specific gravity of bacterial protoplasm equal to 1.0. These data were expanded to a square meter basis by a factor (943.3) based on the area of 30 fields.

Filament diversity, D values (Table 9), based on organisms seen per 30 fields was calculated as previously outlined. The consistency of these data with that of the preliminary study of 48 hours (Figure 7) indicated that a count of 30 fields was adequate as predicted.

An attempt was made to determine which of the water quality parameters were correlated with variations in the standing crop (number of cells) and growth rate ($\log_2$ cells/filaments) of Sphaerotilus on glass slides, and, thus, could be employed to predict these two measures of the bacterial population with reasonable error. A matrix of simple correlation coefficients among these variables (Figure 9) suggests that dissolved organic carbon, nitrates and nitrites, stream velocity, and water temperature might be useful in predicting each of the two bacterial measures. The regression equations that have been generated by a step-wise deletion procedure are presented in Table 10. The square of the correlation coefficient, the F-value with its level of significance, and the coefficient of variation were used as criteria for selecting the "best" prediction equation for each measure. On this basis, the "best" prediction for the number of cells could be made from the dissolved organic carbon, nitrate and nitrite, and water temperature

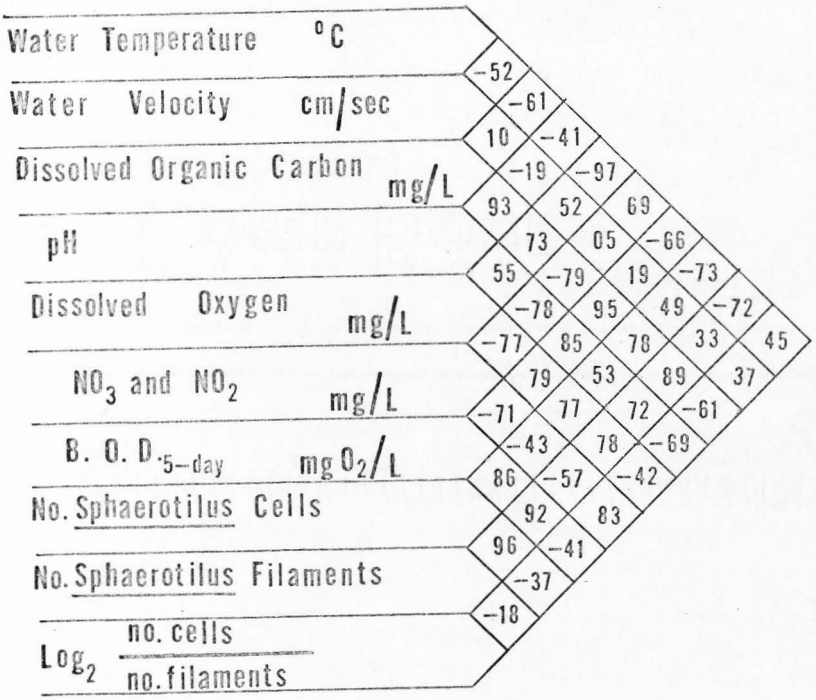

Figure 9. Correlation coefficients (rx100) between measures of stream bacteria and water quality parameters. Data from Logan River, July to October, 1967. Assuming a correlation coefficient equal to zero as the null hypothesis, the coefficients can be tested at the 95 percent level. The hypothesis is rejected if $|r| \geq 0.70$ (n=8).

TABLE 10. Parameters of selected equations regressing two measures of *Sphaerotilus* population dynamics on various water quality variables (n=8).

Y Variable	Water Quality Variable	a_R^2 (%)	b_F	c_{CV} (%)
No. Cells	DOC,	61.57	9.6 (.95)	64.21
No. Cells	DOC, Temp	71.26	6.2 (.95)	60.50
No. Cells	DOC, Temp, NO_3	94.06	21.1 (.99)	30.90
No. Cells	DOC, Temp, NO_3, Velocity	94.10	11.9 (.95)	35.57
Log_2C/F	NO_3	69.24	13.5 (.95)	9.69
Log_2C/F	NO_3, DOC	69.86	5.8 (.90)	10.52
Log_2C/F	NO_3, pH	69.59	5.7 (.90)	10.61
Log_2C/F	NO_3, Velocity	80.38	10.2 (.95)	8.49
Log_2C/F	NO_3, Velocity, temperature	82.22	6.2 (.90)	9.06
Log_2C/F	NO_3, Velocity, temp., DOC	82.22	3.5 (.90)	10.44

a - square of correlation coefficient

b - F-value with level of significance indicated within parenthesis

c - coefficient of variation = $\frac{(\text{residual mean square})^{1/2}}{\text{mean of the dependent variable}}$

variables. The "best" prediction of the average generation time could be made from nitrate (plus nitrite) and water velocity variables.

The results (Table 10) indicate that the variability in either standing crop of growth rate of Sphaerotilus on glass slides after immersion for 48 hours in the Logan River can be stated in a quantitative relationship with dissolved organic carbon, inorganic nitrate and nitrite, water temperature, and water velocity. The two chemical measures and water temperature provide the basis for the "best" equation for predicting the standing crop of Sphaerotilus (Equation 8). On the other hand, inorganic nitrate and nitrite, and water velocity are the basis for the "best" equation for predicting the average generation time of the filaments (Equation 9).

$$\hat{Y}_{cells} = -16.811 - 443.257\ (Temp) + 2488.233\ (NO_3) + 1510.710\ (DOC) \quad (8)$$

$$\hat{Y}_{\log_2 c/f} = 1.631 + 0.345\ (NO_3) + 0.019\ (velocity) \quad (9)$$

Discussion

The sensitivity of Sphaerotilus development to food concentration, water velocity, and water temperature has been established by various investigations (see review by Harrison and Heukelekian, 1958). The most important environmental factors from the standpoint of slime growth in the Columbia River appeared to be velocity, temperature, and phosphate content (Amberg and Cormack, 1960). In outdoor artificial streams, investigators have pointed to strong relationships between these environmental factors and growth of slime but have not made quantitative statements on these associations (Wuhrmann, 1964; Wuhrmann et al.,

1967; Phaup and Gannon, 1967). Phillips (1960) reported some data obtained from simulated stream environments that indicate to some extent the complexity of the relationship of food concentration and water velocity to the slime development on glass substrates. For example, consider the following interpretations of his results (Figure 10). At the higher glucose concentration, growth was more responsive to changes in velocity than at the lower concentration. At the lower concentration growth was similar at all three velocity levels. At the lowest velocity, growth was proportional to velocity during the early stages (3 days) and then proportional to glucose concentration during the later stages (8 days).

Finally, Oginsky and Umbreit (1959) indicated that during the early stages of bacterial population growth the temperature of the environment determines to a large extent the generation time, or growth rate.

The average rate of Sphaerotilus biomass accumulation on glass slides in the Logan River is very small when compared to the rates of slime accumulation reported in other investigations (Table 11). Two possible explanations are offered for the difference. All of the rates cited for comparision were obtained from studies of slime infestations in nutrient-rich waters. The Logan River was relatively nutrient-poor, having less than 72 mg/l dissolved organic carbon or a glucose-equivalent concentration less than 1 mg/l (Table 9). In most instances, the cited data were based on dry weight of slime which consisted mainly, but not entirely, of Sphaerotilus.

The average generation time based on eight slides positioned in the Logan River during 1967 was about 20 hours (2.393 divisions per

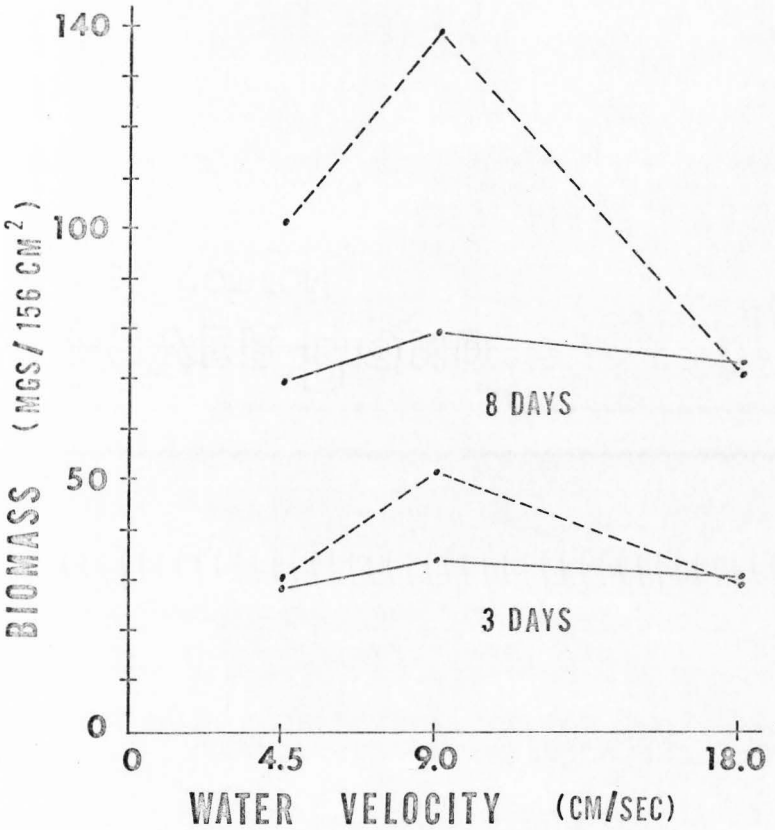

Figure 10. Changes in Sphaerotilus biomass density due to changes in water velocity, length of glass slide immersion period, and food concentration. Points connected by the dotted lines indicate a food concentration of 20 mg glucose/l, and the points connected by a solid line indicate a concentration of 10 mg glucose/l. (From data presented by Phillips, 1960, Table 15.)

TABLE 11. A comparison of slime accumulation rates in various aquatic environments.

Slime Accumulation Rate ($mg\ m^{-2}\ 48\ hr^{-1}$)	Water	Source
0.3	Logan River	-
3,600*	Model River, molasses added	Wuhrmann et at., 1967
4,000-8,580*	River with beet-sugar wastes	Dept. Sci. Ind. Res., 1963
40-310*	Sewage Treatment Plant effluent	Heukelekian & Crosby, 1956
	Laboratory Stream Conditions	Phillips, 1960
1,329-2,215*	20 ppm glucose	
13-77*	10 ppm glucose	
679-2,709*	5-40 ppm glucose	
1,226-1,496*	10 ppm glucose, flow levels	
426-1.118*	various BOD:N:P ratios	
390-678*	10 ppm glucose, 5 ppm NH_3, and 2 ppm PO_4^{-}	

* Units of original data converted to stated rate.

48 hours, Table 9). This value compares favorably with values from eutrophic lakes (Table 12).

It would be interesting to speculate on the rate of energy utilization by Sphaerotilus in the Logan River benthos. A reasonable appraoch was suggested by Kriss's (1963) treatment of marine microbial productivity. Utilizing the formula developed by Ierusalimskii (1954) concerning growth rates of aquatic microorganisms on glass slides, Kriss (1963) made estimates of the rates of organic matter utilization due to microbial metabolism in several marine environments. Ierusalimskii's formula is

$$P = A + B = a\,m\,c\,t + b\,m\,t \qquad (10)$$

where

P = total quantity of organic matter utilized;
A = the quantity of organic matter, the oxidation energy of which is used for increasing the biomass of bacteria;
B = the quantity of organic matter, the oxidation energy of which is utilized for the "basic metabolism" of bacteria (i.e., preservation of living functions without growth);
a = the trophic coefficient, i.e., the expenditure of the material supplying energy (organic substance) necessary to produce a unit of bacterial biomass;
b = coefficient of basic metabolism, i.e., the expenditure of the material supplying energy (organic substance) for the needs of the "basic metabolism" of a unit of bacterial biomass per unit time;
m = biomass of bacteria (dry weight);
c = coefficient of growth (the increase of a unit of microbial biomass during growth and reproduction per unit time);
and t = time (Kriss, 1962, p. 412-413).

He assumed the coefficient a to be equal to 3; and coefficient b per day to be equal to 0.5.

Taking the mean biomass of Sphaerotilus to be 0.30 mg/m^2 wet weight (0.024 mg/m^2 dry weight where 8 percent wet weight equals dry weight; Popp and Bahr, 1952) and the daily mean growth coefficient (P/B)

TABLE 12. A comparison of bacterial generation times in diverse aquatic environments.

Water Body Type	Name	Water Temp. (°C)	Generation Time (hrs.)	P/B*	Source
River	Logan River	14	20	1.20	-
Lakes (eutrophic)	Alfufievsky	31	14	1.35	Kuznetsov, 1958
	Yamat	26	14.5	1.23	"
	Dudanakov	26	35	0.63	"
Lake (mesotrophic)	Glubokoye	7	78	0.31	"
Lake (oligotrophic)	Baikal	8	218	0.15	"
Lake	Rybinsk-Stausee	18	7-120	0.2-3.7	Kuznetsov et al., 1966
Lakes	2 reservoirs	10	3-42	0.6-8.0	Straskrabova-Prokesova, 1966
Sea or Ocean	Black Sea, Bay	-	71**	0.34	Kriss, 1963
	Black Sea, Open	-	185**	0.13	"
	Caspian Sea	-	69**	0.35	"
	Pacific Ocean	-	30**	0.80	"
	Artic Ocean	-	33-200**	0.12-0.72	"

* Percent daily increase of baterial biomass. See Kriss (1963) for discussion of this coefficient.

** Calculated from P/B coefficient where 24 hr/g.t. = P/B.

to be 1.20, the following calculation can be made utilizing Equation 10.

$$P = (3.0 \times 0.024 \times 1.20) + (0.5 \times 0.024) = 0.21 \text{ mg/m}^2\text{/day}$$

If the organic substance is assumed to be glucose, the rate of energy utilization by Sphaerotilus in this study was about 0.21 mg glucose/m^2/day, or 0.8 cal/m^2/day.

Jordan and Jacobs (1944) studied the food requirements of Bacterium coli under various conditions. The estimates of the amount of food used in the maintenance of the full activity of the cell in unit time apart from reproduction were 0.474×10^{-9} and 0.440×10^{-9} mg per cell per 24 hours. The estimates of the amount of food used in the production of a new cell were 1.083×10^{-9} and 1.063×10^{-9} mg. Their estimate of dry weight (organic matter content) of the studied bacterium was 1×10^{-10} mg/cell. From these data, estimates of coefficient a (4.4 mg organic matter/mg cell/24 hr) and of coefficient b (10.73 mg organic matter/mg new cell) were made for utilization in Equation 10. This resulted in a P value of 0.37 mg organic matter/m^2/day, or, where the organic matter had a calorific value of 5 cal/mg, a P value of 1.9 cal/m^2/day.

An average of both P estimates was 1.3 cal/m^2/day or 0.4 mg glucose/m^2/day. Taking this rate and the river bed area from the confluence to the end of the study area to be 68,000 m^2, Sphaerotilus probably would utilize 27.2 gm glucose/day. An estimate of the glucose content of the water above this section was about 2,000 gms. The average glucose-equivalent concentration was 39 mg/m^3 (Table 9) and the average depth assumed to be 0.8 m. Less than 1 percent of the energy present as glucose-equivalent in the river water was apparently utilized by the Sphaerotilus populations.

One estimate of the magnitude of microbial activity can be obtained from a consideration of the oxygen demand of the river water (BOD measurement). The mean, daily rate of oxygen uptake was 2.86 mg O_2/l/day (0.817 cal/l/day) at 20°C (Table 9). The actual rate *in situ* would be less because the mean, river water temperature was colder (13.7°C, Table 9) than 20°C. Assuming that the rate of bacterial population growth doubles for a 10°C increase in temperature (Q_{10} = 2.0, Oginsky and Umbreit, 1959) the *in situ* estimated rate at 13.7°C was 0.56 cal/l/day. This rate on an area basis equals 448 cal/m^2/day. The rate of energy utilization by *Sphaerotilus* (1.3 cal/m^2/day) is a small portion of the microbial activity in the river (448 cal/m^2/day). In summary, *Sphaerotilus* does not appear to occupy a prominent position based on energetic considerations of the decomposer community.

A COMPARISON OF THE RATES OF PRIMARY PRODUCTION AND *SPHAEROTILUS* ASSIMILATION IN THE LOWER LOGAN RIVER

A comparison of the main results of the two studies (Table 13) will be briefly discussed. A direct comparison of the data has little practical meaning, because one estimate was from a dominant portion of the producer trophic level and the other estimate was from a single genus of the decomposer trophic level. One meaningful comparison could be made on the basis of the rate of metabolism per unit of standing crop. In energy units, the rate for algae would be 0.14 cal/cal of biomass/day while the rate for the bacterium would be 2.16 cal/cal of biomass/day. This is in agreement with the well-known inverse relationship between size of organism and metabolism per unit of biomass (Odum and Odum, 1959; Prosser and Brown, 1961). Stanier et al. (1963) listed the normal range of volume for Eubacteria and blue-green algae as 1 to 50 μ^3 and for unicellular algae (eucaryotic) as 5,000 to 15,000 μ^3.

TABLE 13. A comparison of algae and *Sphaerotilus* energetics in the Logan River.

Trophic Level in Benthos	Standing Crop (cal/m^2)	Metabolic Rate ($cal/m^2/day$)
Producers (algae)	64,000	9.359 (gross production)
Decomposers (*Sphaerotilus*)	0.6	1.3 (total assimilation)

TABLE 14. Presentation of conversion factors utilized in the standardization of various expressions.

Conversion Factor	Source
1.55×10^{4} ft-candles = g-cal/cm^{-2}min = Langley/min	Strickland, 1958
72 g organic carbon = 1 g glucose = 0.94 g oxygen	McIntire & Phinney, 1965
1.0 g oxygen = 3.5 Kcal	McIntire & Phinney, 1965

CONCLUSIONS

1. The mean pigment densities in the Logan River benthos were calculated to be 55 mg/m^2 for chlorophyll -a, 23 mg/m^2 for chlorophyll -b, 23 mg/m^2 for chlorophyll -c, and 30 mg/m^2 for carotenoids. The mean yellow/green pigment ratios were calculated to be 1.49 (D480/D665) and 3.07 (D430/D665).
2. The mean assimilation rate as determined in the metabolism chamber was estimated to be 0.8 mg O_2/mg chlorophyll -a/hr.
3. The measures of accessory pigments should be considered, in addition to chlorophyll -a, when utilizing pigment-based methods to estimate rates of primary production. In this study, the important accessory pigment measures were chlorophyll -c and the D480/D665 ratio.
4. The annual rate of gross primary production in the river benthos was estimated to be 3,416 $Kcal/m^2/yr$. The annual rate of benthic community respiration was estimated to be 2,257 $Kcal/m^2/yr$. The P/R ratio was about 1.5.
5. The accumulation rate of Sphaerotilus biomass on suspended glass slides was 0.3 mg (wet weight)/m^2/48 hours, and could be predicted from the dissolved organic carbon content, nitrate (plus nitrite) content, and temperature of the water. The generation time of this bacterium was estimated to be about 20 hours and could be predicted from temperature, nitrate (plus nitrite) content, and velocity of the water. The daily P/B coefficient was estimated to be 1.20 for Sphaerotilus.

6. The rate of organic matter utilization by Sphaerotilus was estimated to be 0.4 mg glucose/m^2/day, or 1.3 cal/m^2/day. The magnitude of microbial activity in the river was estimated to be 448 cal/m^2/day. A comparison of these two rates suggests that Sphaerotilus does not occupy a prominent position in the decomposer community.
7. The rate of metabolism per unit of biomass was greater for Sphaerotilus (2.16 cal/cal of biomass/day) than algae (0.14 cal/cal of biomass/day).

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n.s. = original paper not seen
( ) = title translation of a paper not printed in English

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APPENDICES

APPENDIX A

Location of pairs of artificial substrates in the Logan River, Utah.

Station Number	Station Designation (km downstream from Mendon Bridge)
1	0.07
2	0.25
3	0.48
4	0.63
5	1.49
6	1.75
7	1.97
8	2.35
9	2.75
10	3.09
11	3.14
12	3.19
13	3.28
16	3.75
17	3.95
18	4.10
19	5.33
20	5.38
21	5.63
22	6.10
23	6.63
24	7.35
25	7.48
26	8.10
27	9.30
28	10.69
29	11.55

APPENDIX B

Additional Data on the Stream Communities used in the Metabolism Experiments

Water Flow	Substrate Area (m^2)	Chlorophyll (mgs) A	B	C	Carotenoids (mgs)	D430:D665	D480:D665
Logan River[1]	0.12	37.0	11.0	10.0	17.9	2.93	1.35
Logan River[2]	0.13	44.4	11.5	4.9	22.4	2.46	1.21
Swan Creek	0.13	60.9	34.8	31.2	49.9	3.06	1.34
Blacksmith Fork River	0.15	63.6	15.0	46.6	33.1	2.69	1.54
Little Bear River	0.11	40.1	7.2	17.2	17.6	2.68	1.23
Logan River[3]	0.13	7.0	2.0	2.0	3.4	3.20	1.40

[1] below 1st impoundment, natural rocks

[2] above Twin Bridges, natural rocks

[3] below Mendon Bridge, concrete hemispheres

APPENDIX C

Values for Two Information Functions

A Fortran IV program was written to compute values of the information functions, $F(p) = -\log_2 p$ and $F'(p) = -p \log_2 p$, for $p = 0.001$ to 1.000. The printed output consists of two parallel, vertical columns of values. Figures in the leftmost column are solutions of the former function while the ones in the rightmost column are solutions of the latter function for the values of p. Total time is 93 seconds utilizing the IBM system 360/model 44 computer located at Utah State University.

Program Deck

```
C       Fortran IV program to compute values
C       of - log2p and -p log2p for p
C       = 0.001 to 1.000
        read (5,1) X
    1   format (F6.5)
    2   Y = X/1000.0
        C = -(ALOG(Y)/0.693147)
C       C = -Log2p
        B = (Y*C)
C       B = -p log2p
        write (6,3) C,B
    3   format (1H, 20X, E13.5, 20X, E13.5)
        X = X + 1.0000
        IF (X - 1,000.0) 4, 4, 5
    4   go to 2
    5   continue
        end
```

Data Deck

Single card with the digit 1 punched in column 1.

VITA

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Doctor of Philosophy

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