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PRIMARY PRODUCTIVITY AND ENERGY RELATIONSHIPS IN ARTIFICIAL STREAMS¹

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ABSTRACT

The productivity of algal communities was investigated in two recirculating artificial streams. Emphasis was placed on a study of the effects of various factors on energy flow and on the characterization of artificial streams as a research tool. Productivity was measured by pH and carbon dioxide changes, upstream-downstream oxygen changes, and the biomass of algae collected on artificial substrata.

A temperature increase caused a small, but insignificant, increase in net productivity, while increased light intensity caused an increase in net productivity. A higher current velocity caused an increase in net productivity, significant as shown by riffle vs. pool communities, but not significant between a fast and a slow stream. A shorter, but more frequent photoperiod did not change the rate of production significantly. High chelate concentration caused a reduction in net productivity.

Estimates of net productivity by the carbon dioxide and oxygen methods were in agreement for two out of five studies, while estimates by the biomass of algae on substrata were consistently lower than estimates by the gas methods. Net production varied from 2,815 to 5,565 cal m⁻² day⁻¹, resulting in efficiencies from 3.8 to 9.8%. Efficiencies of gross productivity varied from 6.4 to 16.1%.

INTRODUCTION

Laboratory experiments have contributed significantly to the understanding of primary production in standing waters. Comparable studies relating to production in lotic systems, such as the study of a stream microcosm by Odum and Hoskin (1957), have been few. Considerable potential then remains for the use of artificial streams in the investigation of primary productivity in flowing waters. In the laboratory, it is possible to simplify the community and to isolate or control many environmental factors to determine their influence on productivity. The objectives of this study were to determine the effects of temperature, light, current velocity, and chelates on productivity, to compare methods of measuring primary productivity in flowing waters,

and to characterize the artificial stream as a research tool.

Two artificial streams were established in July 1959 and were allowed to operate until May 1960 before investigations, other than pilot studies, were initiated. Stream variables were controlled and investigated individually by creating differences between the two streams. Thus, the effect of a factor was isolated and its influence on productivity could be measured. The results of the studies were expressed in terms of energy flow and efficiencies, and these, in addition to observations of nutrient concentrations, were used to characterize the artificial streams.

METHODS AND MATERIALS

Each artificial stream (Fig. 1) was established with 246 liters of distilled water and inorganic nutrients (Table 1). Nutrients were recycled by decomposition of algae in the filters and reservoirs; however, to avoid a system entirely dependent on recycling, nutrients were added periodically throughout the study, with major additions as shown in Table 1 and lesser additions as shown in Figs. 2 and 3. Stock solutions were used to replace nutrients removed with water and algal samples.

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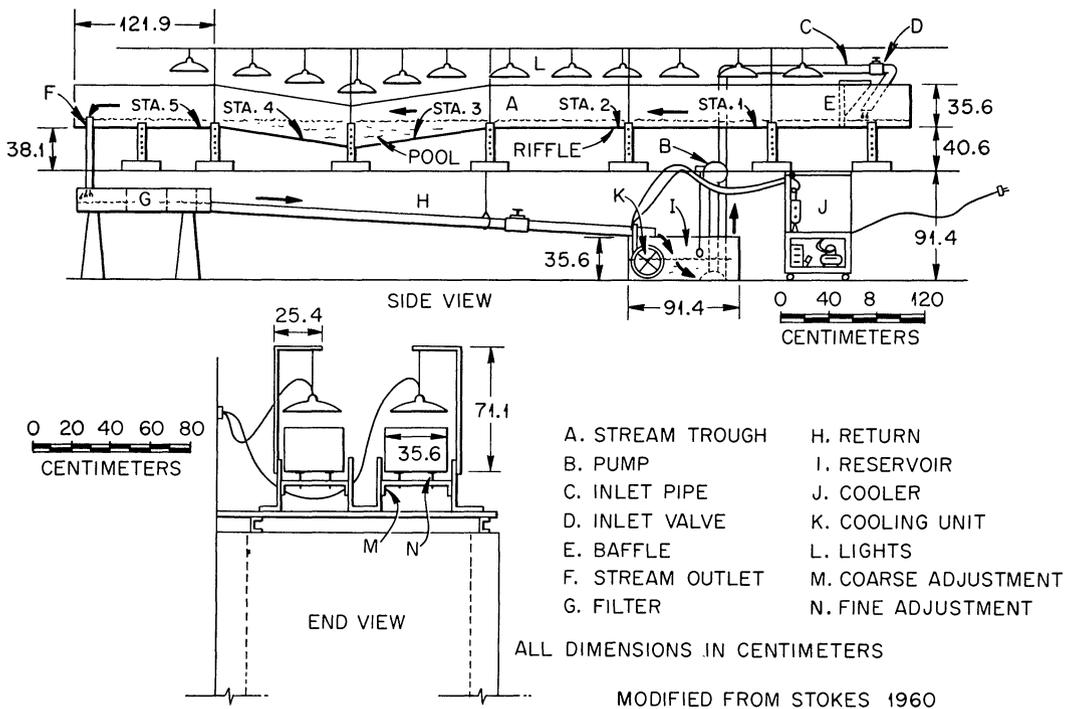


FIG. 1. Diagram of artificial streams.

Radiant energy was supplied by incandescent bulbs equipped with shade reflectors and suspended approximately 40.0 cm above the contour of each stream bottom. The photoperiod was controlled automatically by electric timers. Illumination was measured with a Weston Foot-Candle Meter, Model 614. Measurements were converted to energy units using the factor $1 \text{ lux} = 5.0 \text{ erg cm}^{-2} \text{ sec}^{-1}$ (Rabinowitch 1951) for the photosynthetically available portion of the incandescent spectrum. Energy values under water, at the surface of the periphyton mat, were estimated using the incident readings and approximate extinction coefficients for the red wavelengths (6,000–7,000 Å) as measured with a Beckman Model B spectrophotometer.

The temperature of each stream was regulated within $\pm 1.0\text{C}$ by a thermostatically controlled refrigeration unit with the cooling coil located in the reservoir. Water temperatures were recorded by thermometer and were also measured with a ther-

mometer each time a sample was taken for oxygen analysis.

The rate of discharge and speed of water flow were controlled by adjusting the inlet valves and the gradient of the streams. The flow rate was calculated from discharge measurements and the stream dimensions.

TABLE 1. The concentration of nutrients in milligrams per liter added to each stream

Salt	July 1959	May 1960	July 1960	Oct 1960
KNO ₃	114	58	2.7	2.7
K ₂ HPO ₄	8	6	0.3	0.3
MgSO ₄ ·7H ₂ O	40	18	7.4	7.4
CaCO ₃	40	20	1.0	1.0
FeCl ₃	4	—	—	—
Na ₂ SiO ₃ ·9H ₂ O	19	20	1.0	1.0
EDTA	41	—	—	—
Microelements*	1 ml/liter	—	0.5 ml/liter	0.5 ml/liter

* Stock solution of micronutrients (g/liter):

H ₃ BO ₃ —2.86	(NH ₄) ₆ Mo ₇ O ₂₄ ·4H ₂ O—0.18
MnCl ₂ ·4H ₂ O—1.81	CuSO ₄ —0.05
ZnSO ₄ ·7H ₂ O—0.22	Co(NO ₃) ₂ ·6H ₂ O—0.49

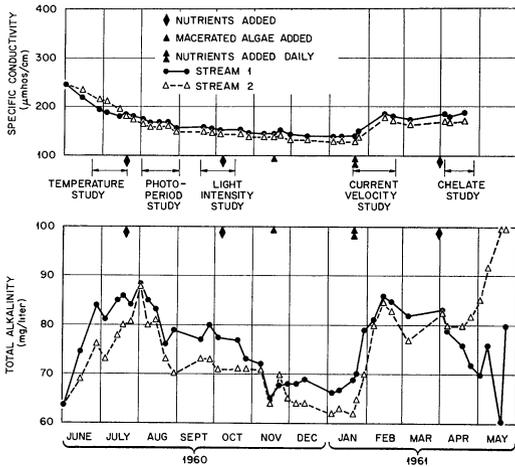


FIG. 2. Specific conductivity and total alkalinity throughout the study period.

The product of stream width and depth divided into the discharge gave the average rate of flow at the point where the dimensions were measured. Water depth in the streams ranged from 2 cm in the riffle area to 20 cm in the pool area.

Specific conductivity was calculated from the measured electrical resistance, corrected to 18C and expressed as $\mu\text{mho}/\text{cm}$. Total solids were measured as total residue (American Public Health Association 1955). Alkalinity was determined by the method described by Welch (1948). The $p\text{H}$ was measured with a Beckman Model H-2 $p\text{H}$ meter, and the concentration of free carbon dioxide was determined by nomogram using measurements of $p\text{H}$, alkalinity, total solids, and water temperature (American Public Health Association 1955).

Concentrations of total and dissolved phosphorus in water samples were determined colorimetrically (Ellis, Westfall, and Ellis 1948). The concentration of cellular phosphorus was determined using the procedure for total phosphorus after ashing the algal samples at 550C. Available nitrogen in water samples was measured by the reduction method, while the organic nitrogen of algal samples was determined by the micro-Kjeldahl procedure (American Public Health Association 1955). Algal samples

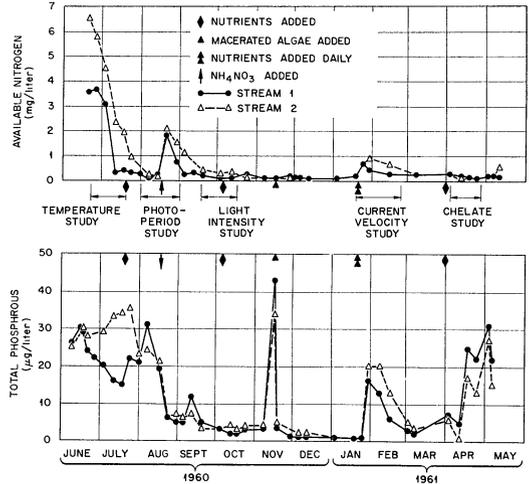


FIG. 3. Available nitrogen and total phosphorus throughout the study period.

were oven-dried at 55C and weighed prior to organic nitrogen analysis.

The caloric value of duplicate samples of algae was measured with a Parr Oxygen Bomb Calorimeter, plain type, series 1300. Samples were oven-dried at 55C, powdered, pelleted, and weighed for caloric analysis.

Gravimetric measurements of algae were recorded after two successive weighings within ± 0.5 mg. Dry weight was determined after oven drying at 55C. Ash-free dry weight, assumed to be organic weight, was measured after ignition of samples at 550C.

The amount of oxygen evolved during photosynthesis was estimated using the upstream-downstream method described by Odum (1956). Water samples were collected at the upstream station, located just before the first incandescent bulb, and at the downstream station, located under the last bulb. The flow of water between stations was timed so the two samples were taken from approximately the same water mass. The difference between the oxygen concentrations of the upstream and downstream stations, after correction for diffusion, was a measure of net production for the area of water under the lights, respiration being automatically subtracted. Efforts to calculate the gas transfer coefficient, K , for dif-

TABLE 2. Rate of production of oxygen in Stream 2 as calculated from measurements taken on 28 June 1960 during the temperature study

Time	(A) Oxygen change (g m ⁻³ hr ⁻¹)	(B)* Diffusion (g m ⁻³ hr ⁻¹)	(C = A + B) Oxygen corrected for diffusion (g m ⁻³ hr ⁻¹)	(D = C + R)† Oxygen corrected for respiration (g m ⁻³ hr ⁻¹)	Gross production (g m ⁻³ day ⁻¹)
7 AM	-0.08	-0.21	-0.29	0.14	
9	0.60	-0.15	0.45	0.88	
11	0.80	-0.13	0.67	1.10	$\bar{D} = 1.081,$
1 PM	0.96	-0.13	0.83	1.26	1.081×12
3	0.92	-0.13	0.79	1.22	hr = 12.98
5	0.72	-0.18	0.54	0.97	
9	-0.08	-0.20	0.28	0.15	

* Diffusion is based on a gas transfer coefficient, K , of 1.75 g m⁻³ hr⁻¹ at 0% saturation, e.g., the saturation deficit at 7 AM = 12% and (B) = 1.75 × 12 = -0.21.

† R is respiration and is based on measurements taken at night and corrected for diffusion. R for this estimate equals 0.43 g m⁻³ hr⁻¹. Net production = gross production - R = 12.98 - (0.43 × 12 hr) = 7.84 g m⁻³ day⁻¹.

fusion corrections produced inconsistent results, so values for K were estimated from tables given by Odum (1956) for comparable water conditions, that is, temperature, depth, and water velocity. The estimated values for K were 0.04/hr for the slow stream, 0.12/hr for the fast stream, 0.06/hr for the stream at 20.0C, and 0.07/hr for the stream at 25.6C and for the streams under standard conditions (*see* Table 3).

Respiration was estimated from oxygen concentrations measured during the dark period and was assumed to be the same during the light period. Estimations of productivity and respiration were calculated in volume dimensions, g O₂ m⁻³ hr⁻¹, and were converted to area dimensions, g O₂ m⁻² hr⁻¹, by dividing the total oxygen produced between stations for a time period by the mean water depth (0.04 m) between stations. A sample calculation of productivity is given in Table 2. Oxygen concentrations were determined by the Alsterberg modification of the Winkler method (American Public Health Association 1955). Oxygen saturation values for use in diffusion corrections were corrected for temperature, atmospheric pressure, and vapor pressure.

The uptake of carbon dioxide by algae was measured indirectly by recording pH changes and converting the changes to carbon dioxide concentrations using the method described by Verduin (1951, 1956). Conversion graphs were made stepwise, by

bubbling respired air through water samples and back-titrating each successive sample with 0.02-N NaOH (Verduin 1960). Three curves were made for each stream, with the curve of the closest date and water conditions being used for a particular productivity estimate.

Diffusion of carbon dioxide into or out of the water was considered to be negligible. The pH, alkalinity, temperature, and total solids in the artificial streams were such that the range of free carbon dioxide in the water was from 0.1 to 1.5 mg/liter. At the lowest pH value (7.8), a small amount of carbon dioxide may have left the system, while at the highest pH value (9.0), a small amount may have entered the water. Thus, carbon dioxide diffusion at the lower pH values would, in part, compensate for diffusion at the higher pH values. Since the greater portion of the diffusion was into the water at the higher pH values, the net effect would be a tendency for the method to underestimate production.

The pH increased throughout the day and decreased throughout the night. The maximum change, recorded by measurements made at the beginning and end of the daily photoperiod, was converted to μ mole CO₂. Carbon dioxide estimates were made, on the same days as the oxygen measurements, from samples taken at the lower end of each stream. Evolution of carbon dioxide by heterotrophic growth in the filters and reservoirs was thus included

TABLE 3. *Standard and study conditions in the artificial streams*

Variable	Study condition		Standard condition*
	Stream 1	Stream 2	
Temperature (C)	20.1	25.6	23.9
Stream velocity (cm/sec)			
Pool	0.6	0.1	0.5
Riffle	4.2	0.6	2.5
Radiant energy (cal m ⁻² day ⁻¹)			
At water surface	66,700	153,200	73,300
At algae surface	52,700	111,000	56,600
Photoperiod (hr)	4 on—4 off	12 on—12 off	12 on—12 off
Chelate (mg/liter)	30	10	Trace

* The standard condition of a variable was in effect at all times except when that variable was being studied, e.g., the streams were always at 23.9C except during the temperature investigation, when the study temperatures were in effect. Standard conditions were the same for both streams.

in measurements by the carbon dioxide method. Respiratory carbon dioxide from the dark areas of the systems reduced the estimates of carbon dioxide evolved by photosynthesis; therefore, carbon dioxide measurements were corrected for respiration in the filters and reservoirs and were thus placed on the same basis as the oxygen estimates.

The third method used to measure net productivity was from the mass of periphyton growing on artificial substrata. Plexiglas rectangles, with an exposed area of 1.5 dm², were placed on each stream bottom at five stations (Fig. 1). Periphyton colonized the Plexiglas and was allowed to grow for a period ranging from 12 to 28 days, the longer periods corresponding to slower growth. A pair of substrata from each station was used for each estimate of productivity for each stream, with the accumulated growths being combined to produce a more representative sample for each measurement. Calculations based on data collected by Stokes (1960) revealed growth from 63 paired substrata to have a mean coefficient of variation of 16.3% with a range of 0–140%.

The periphyton was removed from the substrata, and the ash-free dry weight was divided by the number of days that the substrata were in the stream, less a 3- to 6-day colonization period when growth was too low to be measurable, to give net productivity in g m⁻² day⁻¹. The rate of pro-

duction as estimated by substrata is based on the 24-hr day and is not directly comparable to estimates by the gas methods, which were calculated per 12-hr day (the period of light).

Comparison of productivity estimates by the gas methods was made by converting gas measurements to units of organic weight. The organic products of photosynthesis were assumed to have a mean molecular weight of 180. Photosynthetic quotients (PQ) of 1.1, 1.2, and 1.3 were used in the conversions and were inferred from measurements of the caloric values and the nitrogen content of the algae. Since blue-green algae have a low lipid content, high caloric values and high organic nitrogen values were assumed to indicate a high PQ (1.3). An estimated algal composition of 76% carbohydrate, 21% protein, and 3% lipid was consistent with the mean caloric value of 4,520 cal/g of organic weight of algae.

STANDARD CONDITIONS AND STUDY PROCEDURES

The physical and chemical properties of the artificial streams controlled or altered for the various studies are given in Table 3. The standard conditions of a variable were in effect in both streams except when that variable was being studied. Other relevant properties, not specifically studied, are shown in Figs. 2 and 3. The variable altered for study was maintained in most

cases for at least one month, and productivity measurements were usually made for each stream at the end of the second and fourth weeks. After each study period, the streams were maintained under standard conditions for at least two weeks to allow them to equilibrate.

The velocity of flow (Table 3) appears to be low when compared to natural streams. The highest velocity recorded was 4.2 cm/sec in the riffle area of Stream 1. Odum and Hoskin (1957), in a study of a laboratory stream microcosm, referred to velocities of 8–20 cm/sec as high and those of 2 cm/sec as low velocities, explaining that these were the velocities occurring very near (2.5 mm) the algae and corresponding to much higher velocities in a natural system.

The time from July 1959 until May 1960 served as a period for colonization, algal succession, and equalization of the two streams. The streams were seeded by introducing periphyton-covered stones from a local warm-water stream. Colonization required a few weeks, and the first periphyton was a mixture of green and blue-green algae and diatoms. The first alga to become dominant was *Palmellococcus* sp. Chodat, a green alga, which, after a few months, gave way to a blue-green alga, *Plectonema Boryanum* Gomont, identified by Dr. G. W. Prescott. This small, filamentous alga was the climax species. The genus *Plectonema* is described by Prescott (1951) as becoming yellow or brown with age. The mat of algae in the artificial streams turned to a drab yellow-brown color after *P. Boryanum* became dominant. Nitrogen was low at that time. New growth of this alga was dark green and was apparent in numerous tufts about the periphyton mat and on the artificial substrata. The magnitude of gas exchange during the studies indicated that photosynthesis by *P. Boryanum* in the yellow-brown stage did not cease entirely.

Nutrient effects were not investigated as a part of the study, but inorganic and organic nitrogen and phosphorus were monitored to keep the factors influencing

TABLE 4. *Phosphorus regeneration from decomposition of algae placed in 100 ml of water and stored in the dark at 25C*

Water type	Algae (g wet wt)	Incubation (days)	P released (μ g)	Rate of P released*
Distilled	13.433	5.9	44	0.55
Distilled	14.401	7.0	400	4.00
Stream	16.310	2.0	260	8.00
Stream	13.517	11.7	1,400	8.85

* Rate of micrograms P per gram of algae per day.

productivity limited to the characteristics under study. Water samples were collected weekly for phosphorus and nitrogen analyses, and the data for the overall study were compared by streams. Nutrient concentrations (Fig. 3) indicate a general similarity between the two streams, thus giving support to conclusions made from the studies of controlled variables.

The nitrogen and phosphorus content of the periphyton collected on substrata was used to calculate the percentage composition of the organic matter. Phosphorus calculations were based on the analysis of 113 samples. The mean percentage and standard deviation for organic phosphorus was 0.21 ± 0.11 . The nitrogen content of the periphyton was estimated from the analysis of 62 samples, giving a mean percentage and standard deviation of 3.29 ± 1.63 . The ratio of the nitrogen content to the phosphorus content was calculated at 15.9 for the overall study.

Since the supply of nutrients needed for continued growth depended in part upon decomposition of organic matter in the reservoirs and filter boxes, a brief study was undertaken to determine the rate of phosphorus regeneration. Masses of senescent algae were drained, placed in flasks of distilled water or stream water, and stored in the dark for a number of days. The orthophosphate concentration of the water was determined on removal of the flasks from dark storage. The results (Table 4) indicate that the blue-green algae decomposed easily. The higher rate of phosphorus regeneration occurring in the flasks with stream water may indicate that decomposi-

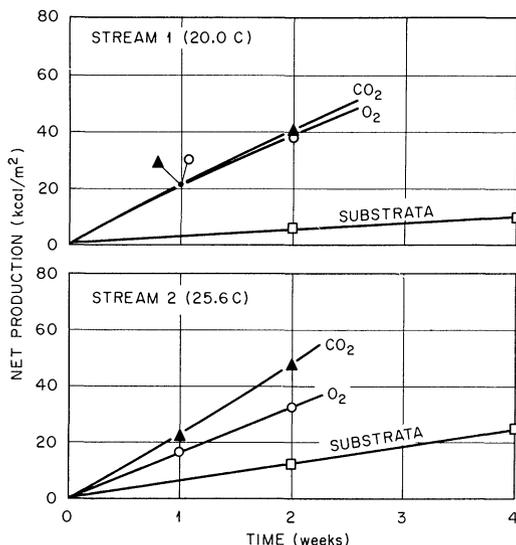


FIG. 4. The effect of temperature on net production in artificial streams as measured by carbon dioxide, oxygen, and substrata.

tion was largely by bacteria rather than by autolysis. The rate of phosphorus regeneration occurring in the flask of distilled water incubated for 7.0 days was higher than in the flask of distilled water incubated for 5.9 days and may be explained by allowing a time period for a bacterial population to build up, since some bacteria were probably present in the stream water initially adhering to the algae. Regardless of the mode, it can be assumed that phosphorus regeneration occurred in the dark areas of the streams at a daily rate of about 8 $\mu\text{g P/g}$ algae.

RESULTS AND DISCUSSION

Effects of study conditions

Temperature—The effect of temperature on the rate of production was determined by creating a difference of 5.6C between the two artificial streams, holding other variables equal, and comparing the net productivity of the two streams.

Measurements of production by the carbon dioxide and substrate methods revealed net production to be highest in the warmer water of Stream 2, while oxygen

measurements showed the opposite (Fig. 4). Statistical analysis of the values in Fig. 4, with a one-tailed student's "t" test for matched pairs with 5 degrees of freedom, indicated no significant difference between production at the higher temperature and production at the lower temperature at the 5% level ($P = 0.2$).

The Q_{10} value (van't Hoff's quotient) generally accepted for photosynthesis is about 2.0, while the range for respiration is about 2.0–2.5. Paauw (1934) studied several green algae and reported, at 15–25C, a Q_{10} range of 1.7–2.1 for carbon dioxide assimilation and a range of 1.7–2.4 for respiration. The mean estimates, by the gas methods, of net productivity in $\text{cal m}^{-2} \text{day}^{-1}$ for the two temperatures were used to calculate the Q_{10} value. A logarithmic relationship was assumed, and the following formula was used:

$$Q_{10} = \left(\frac{P_1}{P_2} \right)^{\frac{10}{t_1 - t_2}}$$

where $P_1 = 2,846$, the net productivity at temperature t_1 (25.6C), and $P_2 = 2,815$, the net productivity at temperature t_2 (20.0C). Thus, $Q_{10} = 1.014^{1.801} = 1.03$. A value of 1.03 for net productivity indicates that respiration increased as much as or more than photosynthesis.

The average net productivity, by the gas methods, for the two streams was 2,815 $\text{cal m}^{-2} \text{day}^{-1}$ for Stream 1 and 2,846 $\text{cal m}^{-2} \text{day}^{-1}$ for Stream 2. Gross productivity for Stream 1 was 4,681 $\text{cal m}^{-2} \text{day}^{-1}$ and for Stream 2 was 5,125 $\text{cal m}^{-2} \text{day}^{-1}$. Net productivity was not significantly higher in the warmer stream, because respiration consumed most of the increase in photosynthesis.

Photoperiod—The effects of photoperiod on productivity were investigated by maintaining the lights of Stream 1 on a "four hours on—four hours off" basis, while the lights of Stream 2 were on continuously for 12 hr and off for 12 hr. Thus, both streams received the same amount of radiant energy daily, but at different intervals. Black crepe paper was draped over the streams to isolate the photoperiod conditions.

It is known that energy fixation by photosynthesis is more efficient under conditions of flashing light than during continuous light owing to the occurrence of certain dark reactions. It is doubtful that dark reactions, which enhance production under flashing light, would be important enough to influence the production rate under the conditions of this study. However, Steemann Nielsen (1960) has shown with C^{14} studies that 1–3% of light saturation fixation occurs in the dark if the period is about 4 hr.

The results of the photoperiod study are given in Fig. 5. Measurements by all three methods show production to be slightly higher under the divided photoperiod of Stream 1. The data of Fig. 5 were subjected to a one-tailed matched pairs test. The analysis showed no significant difference at the 5% level between the productivity of Stream 1 and that of Stream 2 ($P = 0.15$). The statistical analysis suggests that little effect can be attributed to the photoperiods used here as long as the daily quantity of light received is equal for both streams. The mean rate of net energy transfer, by the gas methods, for Stream 1 was $3,626 \text{ cal m}^{-2} \text{ day}^{-1}$, and for Stream 2 the same rate was $3,430 \text{ cal m}^{-2} \text{ day}^{-1}$. The gross energy transfer for Streams 1 and 2 was $6,327$ and $5,796 \text{ cal m}^{-2} \text{ day}^{-1}$, respectively.

Light intensity—The light intensity provided for the two streams was changed from the standard conditions so a difference of over twofold existed between the streams. Stream 1 received the lower incident intensity of $66,700 \text{ cal m}^{-2} \text{ day}^{-1}$ (120 ft-c) provided by 100-w bulbs suspended about 17 inches (43 cm) above the stream bottom. Stream 2 received $153,200 \text{ cal m}^{-2} \text{ day}^{-1}$ (276 ft-c) from 150-w bulbs suspended about 12.5 inches (32 cm) above the stream bottom. The incident energy was slightly greater in the pool areas of both streams, because the lights were lowered to compensate for water depth.

The radiant energy received by Stream 2 was about 1% of the average daylight value ($1.92 \text{ cal cm}^{-2} \text{ min}^{-1}$) and about 15% of the optimum photosynthetic value of $720,000$ –

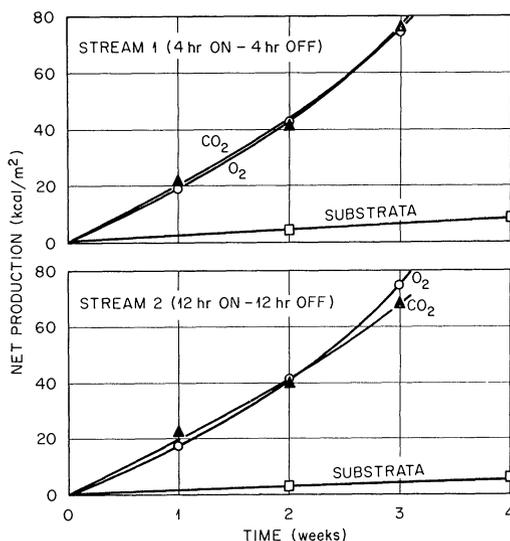


FIG. 5. The effect of photoperiod on net production in artificial streams as measured by carbon dioxide, oxygen, and substrata.

$1,080,000 \text{ cal m}^{-2} \text{ day}^{-1}$ given by Strickland (1960). Kratz and Meyer (1955) reported growth rates to increase rapidly when light was increased from 100 to 180 ft-c (1,076–1,940 lux) and to increase more slowly when light was further increased to 260 ft-c (2,800 lux). A report on *Chlorella* cultures by Myers (1946) gave 35 ft-c (378 lux) as the intensity for the greatest photosynthetic capacity, probably referring to efficiencies, and 100 ft-c (1,076 lux) as the intensity for the greatest growth rate.

The difference in production attributed to light intensity is given in Fig. 6. Measurements by carbon dioxide and oxygen show production to be higher under the higher light intensity of Stream 2. Data from substrata show little difference between the two streams. The production of Stream 2 was significantly greater than that of Stream 1 at the 2.5% level, as demonstrated by a one-tailed matched pairs test ($t = 2.919 > t_{0.975} = 2.571$, $df = 5$). Based on the gas methods, net productivity of Stream 1 was $4,151 \text{ cal m}^{-2} \text{ day}^{-1}$, and that of Stream 2 was $5,548 \text{ cal m}^{-2} \text{ day}^{-1}$. Gross productivity of Stream 1 was $7,172 \text{ cal m}^{-2} \text{ day}^{-1}$, compared with $9,504 \text{ cal m}^{-2} \text{ day}^{-1}$ for Stream 2. Respiration was $3,021$

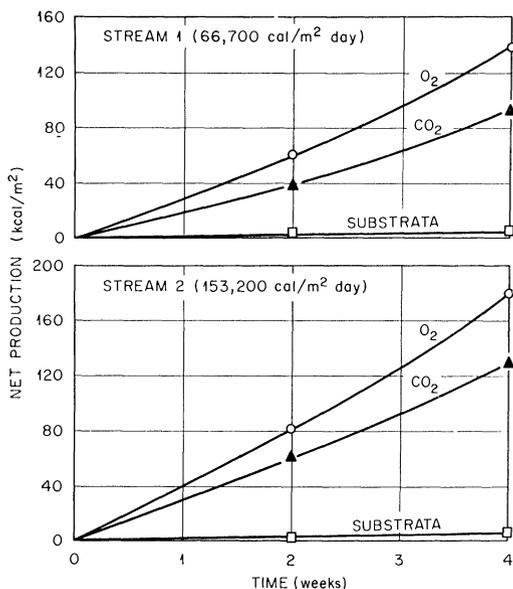


FIG. 6. The effect of light intensity on net production in artificial streams as measured by carbon dioxide, oxygen, and substrata.

cal m^{-2} day $^{-1}$ in Stream 1 and 3,956 cal m^{-2} day $^{-1}$ in Stream 2, the difference corresponding largely to the greater biomass produced in Stream 2.

Current velocity—The effect of flowing water on productivity and on other biological phenomena is one of the major differences between streams and lakes. The belief that water movement influences productivity, directly or indirectly, is one of the main objections against using the light-and-dark-bottle method to measure the production of flowing waters. Gessner and Pannier (1958) studied the respiration of *Anabaena* in Warburg flasks and learned that maximum respiration was reached at a much lower oxygen tension when the flasks were agitated than when the flasks were still. Some recent studies have been directed specifically at determining the current effect. Whitford (1960) theorized that an increase in current produced a steeper diffusion gradient, thus facilitating a better exchange of materials between the cells and the environment. Whitford and Schumacher (1961) reported that CO₂ evolu-

tion by algae was 70% greater in a current than in still water.

Evidence of the effect of flow on productivity was acquired in two ways. Both streams had a riffle and a pool area where the velocity of flow differed. Under standard conditions, the velocity of the pools was 0.5 cm/sec, and the velocity over the substrata in the riffle area was approximately 3.4 cm/sec. Comparison of the growth on artificial substrata at the different stations was used to indicate any effect of the current.

Substrata were located at all five stations (Fig. 1) in both streams, and data from all studies were included in the results. Stations 1 and 2 represent the riffle areas, and Stations 3 and 4 are from the pools. Station 5 is not representative of either area, because light intensity at Station 5 was less than at the other stations. The dry weights from the five stations were subjected to a one-way analysis of variance, and the results show the production of the stations to be significantly different at the 5% level: F ratio for Stream 1 = 10.05 > $F_{0.95}(4,159) = 2.43$, and for Stream 2, the F ratio = 9.47 > $F_{0.95}(4,159) = 2.43$. The station means, in mg dry wt/substrate, in order from Stations 1 to 5 for Stream 1 were 49.2, 56.2, 24.0, 20.1, 8.9, and for Stream 2, 60.9, 50.1, 24.9, 21.4, and 9.1. Kramer's (1956) modification of Tukey's multiple range test revealed the production of Stations 1 and 2 to be significantly different, at the 5% level, from the remaining stations in both streams. Stations 1 and 2 were not significantly different from each other, and Stations 3, 4, and 5 were not significantly different from one another.

Before the higher production of the riffle areas could be attributed entirely to current effect, it was necessary to rule out the effects of nutrients and light intensity. Light measurements and calculations showed that the light intensity at the substrate surfaces, although not constant for all studies, was slightly greater in the pool than in the riffle areas. It is assumed that the slight difference in light quality reaching the substrata as a result of the different water depths did

not influence production enough to alter the conclusions.

Water samples for phosphorus analysis were taken from riffle and pool sites to determine if upstream periphyton were receiving the benefit of greater phosphorus concentrations. The results of eight paired samples from each stream for total phosphorus were analyzed by a two-tailed matched pairs test. Results indicated no significant difference at the 5% level between the phosphorus concentrations of riffle and pool sites in either stream (Stream 1: $P = 0.10$, Stream 2: $P = 0.30$). Thus, it is assumed that phosphorus concentrations did not influence production in the riffle sites more than in the pool sites. Since the phosphorus concentration was as low as any other major nutrient, it is probable that the concentrations of other nutrients did not decrease enough downstream to limit production in the pool. The higher production of the upstream riffle areas is thus attributed to greater current velocity.

Other data on the effect of water velocity on production were collected as in the first studies. The gradient was changed so that Stream 1 had a velocity higher than the standard conditions, Stream 2, a lower one (Table 3). Production, as measured by oxygen, was considerably higher in the faster stream. Carbon dioxide and substrata showed the faster stream to have only a slightly greater production (Fig. 7). A one-tailed matched pairs test indicated that net productivity was not significantly different at the 5% level (productivity in Stream 1 was greater than in Stream 2 at the 10% level, $t = 1.707 > t_{0.90} = 1.476$, $df = 5$).

The mean net and gross productivity, based on the gas methods, in $\text{cal m}^{-2} \text{day}^{-1}$ for Stream 1 were 5,565 and 9,095, respectively, while the same productivity values for Stream 2 were 4,658 and 8,197. Respiration was 3,530 $\text{cal m}^{-2} \text{day}^{-1}$ in Stream 1 and 3,539 in Stream 2, showing that respiration was not higher in the faster stream. A higher net productivity with no increase in respiration indicates a more efficient transfer of radiant energy in the faster

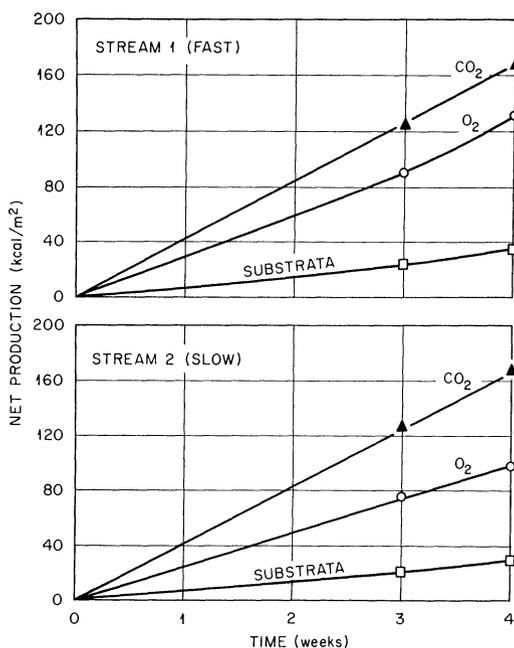


FIG. 7. The effect of current velocity on net production in artificial streams as measured by carbon dioxide, oxygen, and substrata.

stream, possibly resulting from a more efficient nutrient uptake by the algae because of a steeper diffusion gradient.

Chelate—Ethylenediaminetetraacetic acid (EDTA) was used to determine the effects of organic chelation on primary productivity. If certain insoluble nutrients were complexed and brought into solution, while others tied to the insoluble forms were indirectly released into solution, productivity might be increased. Schelske (1962) has shown that ferric iron precipitated in bottom muds can be brought into solution by complexing with chelate. In this study, although phosphorus availability was emphasized, an increase in productivity might be attributed to an increase in some other ion, or production might decrease if a chelated form were less available to the producers.

The effect of chelate additions on the phosphorus concentrations was investigated when the streams were being colonized and established. EDTA was added to each stream at a concentration of 40 mg/liter.

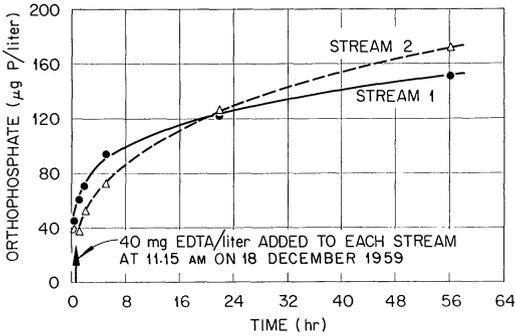


FIG. 8. Action of a chelate on orthophosphate concentration in artificial streams.

Soluble phosphorus concentrations rose rapidly, by 25.83 mg in Stream 1 and 32.47 mg in Stream 2, after 56 hr (Fig. 8). The released phosphorus was assumed to have come from previously precipitated compounds of iron and calcium.

The effect of EDTA on productivity was studied approximately 16 months later. Stream 2 received a concentration of 10 mg EDTA/liter and Stream 1, 30 mg/liter. In view of the previous experiment, it was expected that Stream 1 would show a higher productivity than Stream 2, but the reverse occurred (Fig. 9). A matched pairs analysis using a one-tailed test indicated that net productivity in Stream 2 was greater than in Stream 1 at the 1% level of significance ($t = 3.17 > t_{0.99} = 2.998$, $df = 7$). The mean net and gross productivity in $\text{cal m}^{-2} \text{day}^{-1}$ for Stream 1 were 3,021 and 5,014, respectively, and for Stream 2, 4,011 and 5,890, respectively.

The alkalinity in Stream 2 increased, while that of Stream 1 decreased (Fig. 2). The phosphorus concentration increased slightly more in Stream 1 than in Stream 2 (Fig. 3). Thus, the higher productivity in Stream 2 cannot be accounted for by phosphate release. Possibly, the gross productivity of Stream 1 was inhibited by one of the minor elements, for example, manganese, being unavailable to the algae in the chelated form. Walker (1954) reported that manganese is less available to *Chlorella* when chelated with EDTA than when not.

Productivity, energy transfer, and efficiencies

In an effort to evaluate the effects of various factors on production, three methods were used to measure primary productivity (Table 5). Two-way analysis of variance tests were used to test if results by the oxygen and carbon dioxide methods were different. Substrate values were not included, since they are based on a 24-hr day, while the values by the gas methods are based on the 12-hr light period. If the substrate values are doubled, to exclude night respiration, they are rough approximations for the 12-hr day. The statistical analyses indicated that results by the oxygen and carbon dioxide methods were significantly different in the temperature study, the light intensity study, and the current study (temperature study, $F = 14.224 > F_{0.95} [1,4] = 7.71$; light intensity study, $F = 12.10 > F_{0.95} [1,4] = 7.71$; current study, $F = 19.481 > F_{0.95} [1,4] = 7.71$). The results during the photoperiod study and during the chelate study were not significantly different (photoperiod study, $F = 0.068 < F_{0.95} [1,8] =$

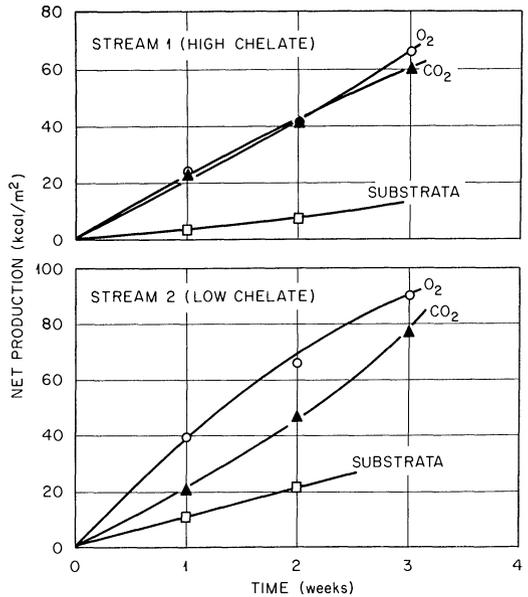


FIG. 9. The effect of chelates on net production in artificial streams as measured by carbon dioxide, oxygen, and substrata.

TABLE 5. Comparison of net production in $g\ m^{-2}\ day^{-1}$ organic weight as measured by the oxygen, carbon dioxide, and substrate methods

Study	PQ	Stream no.	Oxygen method		Carbon dioxide method		Substrate method*
			O ₂	Organic weight	CO ₂	Organic weight	Organic weight
Temperature	1.3	1	0.830	0.598	0.877	0.598	0.088
		2	0.674	0.485	0.942	0.642	0.189
		1	0.724	0.521	0.836	0.570	0.044
Photoperiod	1.3	2	0.620	0.446	1.084	0.739	0.180
		1	0.749	0.540	0.948	0.646	0.070
		2	0.718	0.518	0.972	0.663	0.037
		1	0.969	0.698	0.833	0.568	
		2	0.931	0.670	0.766	0.522	
Light intensity	1.2	1	1.333	0.960	1.477	1.007	0.053
		2	1.405	1.012	1.166	0.795	0.046
		1	1.155	0.903	0.813	0.554	0.042
		2	1.550	1.212	1.296	0.884	0.039
		1	1.418	1.109	1.183	0.807	0.052
Current	1.1	2	1.806	1.412	1.466	1.000	0.043
		1	1.175	1.001	2.034	1.387	0.294
		2	1.040	0.813	1.983	1.352	0.241
		1	1.568	1.336	2.096	1.429	0.317
Chelate	1.2	2	0.888	0.694	1.881	1.283	0.231
		1	1.020	0.798	1.142	0.779	0.098
		2	1.649	1.290	0.965	0.658	0.373
		1	0.734	0.574	0.873	0.595	0.090
		2	1.122	0.877	1.256	0.856	0.326
		1	1.045	0.817	0.902	0.615	
		2	0.988	0.773	1.490	1.016	

* Values for the substrate method are per 24-hr day.

5.32; chelate study, $F = 0.917 < F_{0.95} [1,8] = 5.32$).

Theoretically, the oxygen method and the carbon dioxide method should produce the same estimates. It is worth noting that the two methods did not agree during two studies involving factors (temperature and current velocity) that affect the diffusion rate of gases. Although approximate corrections were made for oxygen diffusion, this appears to remain as a major source of error in the oxygen method, especially in shallow streams.

Estimation of the efficiency of energy transfer by algae requires measurement of the initial radiant energy impinging on the plants and of the energy contained in the final organic products. The initial radiant energy was represented by two values, 1) the incident light at the surface of the water, L_i , and 2) the available light at the surface of the periphyton mat, L_a (Table 6). The mean and standard deviation for

all measurements ($n = 31$) of the caloric content of the algae were calculated as $4,520 \pm 260$ cal. Caloric measurements were made on duplicate samples, and the mean and standard deviation for the most variable and least variable pair of measurements were $4,560 \pm 85$ and $4,945 \pm 7$ cal, respectively. The calories per gram of organic weight used for each study were as follows: 4,923 cal for the temperature study, photoperiod study, and light intensity study; 4,320 cal for Stream 1 and 4,498 cal for Stream 2 during the current study; and 4,338 cal for the streams during the chelate study. These caloric values are the means of calorimetric measurements of algae produced during each particular study.

The energy transfer per m^2 per 12-hr day was calculated for Streams 1 and 2 for each study period (Table 6). The calculations were made by multiplying the mean organic weight estimated by the carbon dioxide and oxygen methods (Table 5) by the calories

TABLE 6. *Energy transfer and efficiencies for periphyton in Streams 1 and 2*

Study	Stream no.	Energy (cal m ⁻² day ⁻¹)				Efficiencies (%)			
		<i>L_i</i>	<i>L_a</i>	<i>P_g</i>	<i>P_n</i>	$\frac{P_g}{L_i}$	$\frac{P_g}{L_a}$	$\frac{P_n}{L_i}$	$\frac{P_n}{L_a}$
Temperature	1	73,300	56,600	4,681	2,815	6.4	8.3	3.8	5.0
	2	73,300	56,600	5,125	2,846	7.0	9.0	3.9	5.0
Photoperiod	1	73,300	56,600	6,327	3,626	8.6	11.2	4.9	6.4
	2	73,300	56,600	5,796	3,430	7.9	10.2	4.7	6.1
Light intensity	1	66,700	52,700	7,172	4,151	10.8	13.6	6.2	7.9
	2	153,200	111,000	9,504	5,548	6.2	8.6	3.6	5.0
Current	1	73,300	56,600	9,095	5,565	12.4	16.1	7.6	9.8
	2	73,300	56,600	8,197	4,658	11.2	14.5	6.4	8.2
Chelate	1	73,300	56,600	5,014	3,021	6.8	8.8	4.1	5.3
	2	73,300	56,600	5,890	4,011	8.0	10.4	5.5	7.1
\bar{X}	1	71,980	55,820	6,458	3,836	9.0	11.6	5.3	6.9
	2	89,280	67,480	6,902	4,099	7.7	10.2	4.6	6.1
Grand mean		80,630	61,650	6,680	3,967	8.3	10.8	4.9	6.4

L_i = incident light energy; *L_a* = available light energy.

P_g = gross energy transfer; *P_n* = net energy transfer.

$\frac{P_g}{L_i} =$ } Trophic level energy intake efficiency or Lindeman's (1942) efficiency or photosynthetic efficiency.

$\frac{P_n}{L_i} =$ } Production efficiency.

per gram of organic material listed for the particular study. The amount of energy transferred by the periphyton was quite similar for most of the studies. Exceptions are the light intensity study and the current velocity study.

When production rates are compared, the artificial streams are lower than most natural ecosystems. This is because the radiant energy for the artificial streams was only about 1% of the average daylight intensity. Comparison of efficiencies indicates the artificial streams to be higher than natural ecosystems. If the "crop yield" or 24-hr net production was estimated for the streams, the efficiencies would be more comparable to those of natural communities. Efficiencies reported for algal cultures are similar to those of the artificial streams. Kok (1952) reported a mean efficiency, presumed to be P_g/L_a , of 20% when all conditions were optimum and algal cultures were dense enough to use all of the available light.

An explanation of the high efficiencies obtained for the artificial streams is based on the general increase in efficiencies when light intensities are decreased (Oorschot 1955) and the light quality of the ecosys-

tem. The predominant wavelengths of incandescent lights are in the red range where the energy per quantum of light is relatively low, thus contributing to higher efficiencies.

CONCLUSIONS

Changes in environmental variables caused significant responses in production rates in some cases and insignificant responses in other cases. It should be noted that the differences in any one variable studied, for example, 20.0–25.6C temperature difference, was the maximum difference that could be maintained by the physical properties of the artificial streams. It is probable, judging from the responses that did occur, that the results would have been significant in more of the studies if the differences in the variables had been greater, for example, a 10C temperature difference rather than a 5.6C difference. It should also be noted that responses to the variables would be indicated more correctly by gross productivity, thus eliminating responses in respiration that tend to mask responses in net production as in the temperature study. Net productivity was used because it is the direct result of the

methods and did not involve corrections for respiration and the included assumptions.

The general agreement of results of the studies with theoretical expectations and with similar studies in natural and other laboratory systems indicates several things. The methods used to measure productivity in flowing water (that is, pH-carbon dioxide changes, oxygen changes, and periphyton collected on artificial substrata) are sufficiently sensitive to reflect the effects of factors influencing the rate of production. The magnitudes of the productivities and efficiencies estimated for the artificial streams are in general agreement with those of natural systems, indicating that the carbon dioxide and oxygen methods are reasonably accurate as well as sensitive.

In the use of artificial streams, it is important to avoid the unnatural system that is entirely dependent on recycling of nutrients and is thus self-limiting, that is, production:respiration ratio of 1. In these studies, adding nutrients before or during each study (Fig. 3) supplied elements in addition to those from decomposition and thus allowed the system to have P:R ratios greater than 1. Artificial streams, then, with adequate areas for decomposition and recycling of nutrients and with sufficient time allowed for the systems to become established, are reasonable replicas of natural systems allowing extension and application of the results to streams in general.

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