Utah State University

DigitalCommons@USU

All Graduate Theses and Dissertations

Graduate Studies

5-1958

Chlorophyll and Productivity in a Mountain River

William J. McConnell
Utah State University

Follow this and additional works at: <https://digitalcommons.usu.edu/etd>

Part of the [Ecology and Evolutionary Biology Commons](#)

Recommended Citation

McConnell, William J., "Chlorophyll and Productivity in a Mountain River" (1958). *All Graduate Theses and Dissertations*. 5060.

<https://digitalcommons.usu.edu/etd/5060>

This Dissertation is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.

CHLOROPHYLL AND PRODUCTIVITY IN A
MOUNTAIN RIVER

by

William J. McConnell

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

of

DOCTOR OF PHILOSOPHY

in

Fishery Ecology

UTAH STATE UNIVERSITY
Logan, Utah

1958

378.242

M7134

c.2

TABLE OF CONTENTS

	Page
Introduction	1
Materials and methods	4
Chlorophyll extractions, natural substrata.	4
Sampling procedures and devices	12
Artificial substrata	17
Relative diffusion methods	18
Duration of insolation methods.	22
Productivity methods	26
Chemical, temperatures, and light methods	30
Physical and chemical description of Logan River (middle section and supplementary stations of lower river) . . .	32
Bottom materials	32
Runoff and turbidities	32
Dimensions of middle section	34
Current velocities.	34
Relative diffusion rates.	37
Insolation and light intensity.	37
Chemistry.	41
Animal community	43
Fish	43
Invertebrates	43
Benthic plant community of the middle section of Logan River and supplementary stations	44
Blue-green algae	44
Chlorophyta.	45
Chrysophyta	46
Rhodophyta	48
Algae at lower supplementary stations	48
Algal distribution	50
Linear distribution	50
Order of colonization.	51
Results and discussion	54
Amount and distribution of chlorophyll	54

	Page
Chlorophyll based productivity.	61
Net productivity and standing crop	69
Summary and conclusions.	73
Literature cited	76

LIST OF TABLES

Table		Page
1.	Comparative rates of gross primary production.	28
2.	Chlorophyll based rates of photosynthesis.	29
3.	Chlorophyll "a" content of several algae from Logan River and vicinity.	72

LIST OF FIGURES

Figure		
1.	Relationship between duration of extraction and degree of extraction.	7
2.	Relationship between optical density and chlorophyll "a".	11
3.	Absorption spectra of typical acetone extractions	13
4.	Relationship between dissolution of sodium chloride and velocity of water.	21
5.	Overlay used in duration of insolation determination . . .	23
6.	Tracings of typical shade photographs	24
7.	Profile of Logan River	33
8.	Ten-year averages of monthly volumes of flow	35
9.	Distribution of average velocities near botton	36
10.	Ranked individual velocities.	36
11.	Ranked relative diffusion rates.	38
12.	Water temperatures.	40
13.	Downstream changes in dissolved solids, turbidity, and chlorophyll on artificial "rocks".	42
14.	Relationship between duration of insolation and standing crop of chlorophyll	57

	Page
15. Relationship between relative diffusion rate and standing crop of chlorophyll	58
16. Curves of photosynthetic response of diverse, aquatic communities.	64

ACKNOWLEDGMENT

A great debt to Dr. William F. Sigler is acknowledged here. He arranged for project support beyond the basic grant and gave much valuable guidance that never impinged on freedom of action. Assistance by the Utah Cooperative Wildlife Research Unit under the direction of Dr. Jessop P. Low is also appreciated.

Provision of the basic grant by the National Institute of Health of the United States Public Health Service made the research possible. My co-worker under this grant, William J. Clark, cooperated closely in the collection of most of the physical and chemical data.

Dr. Francis Drouet identified reference collections of algae which were the basis for identifications in routine algal collections. I also thank the many other people, at Utah State University and on other campuses, who provided valuable suggestions and criticisms.

William J. McConnell

INTRODUCTION

Investigation of primary production in streams and rivers has lagged behind similar investigations in marine and lacustrine environments. Recently, however, Odum (1956) has demonstrated methods that allow the estimation of productivity of most moving waters. For reasons discussed later in this paper, Odum's method is not satisfactory for shallow, very rapid rivers as typified by Logan River. The present investigation then was primarily an exploration of a method possibly applicable to measurement of productivity in shallow rapid rivers.

Investigation of phases of the ecology and distribution of the main contributors to primary production, the benthic algae, was a necessary corollary to intelligent measurement of primary production in Logan River. A recent review of the knowledge of ecology of river algae (Blum, 1956) summarizes this topic.

Most quantitative investigations of river algae have been directly or indirectly concerned with indices of pollution rather than productivity (Jones, 1951) (Reese, 1937) (Patrick, 1949) (Butcher, 1932, 1940, 1945, and 1947). The growth of algae on slides has been a frequently used method of quantitative study, but it is difficult to relate values attained in this fashion to total productivity or standing crop. Statements concerning algal succession and seasonal variation based on counts of algae growing on glass slides in very rapid water appear questionable.

The concepts of productivity measurement basic to methods used in this investigation are little different than those pertaining to marine

and lacustrine environments. The distribution and quantity of chlorophyll in the plankton of lakes was intensively studied by Kosminski (1938) who also foresaw the relation between chlorophyll and lake productivity. Further development of this concept occurred during work by Manning, Juday, and Wolf (1938) and Manning and Juday (1941). Much knowledge of the relation between chlorophyll and productivity has accumulated since these investigations. Ryther (1956) concludes that with knowledge of chlorophyll based rates of photosynthesis, distribution and quantity of chlorophyll and available light one may estimate the primary production of an entire body of water. Edmondson (1955) gives evidence of the usefulness of chlorophyll measurements in making plankton productivity estimates regardless of the taxonomic groups of chlorophyll bearers represented. The relationship of light to aquatic photosynthesis as well as the quantity and quality of light available is summarized by Edmondson (1956). A concise review of the current knowledge of algal photosynthesis is given by Krauss (1956).

The importance of short-term algal photosynthesis in rapid rivers is more obvious than it is in other aquatic habitats. Recycling of fixed energy by the reuse of algal decomposition products in the growth of other algae or aquatic plants is at a minimum in Logan River. Brief psuedo-plankton measurements suggest that a large percentage of the net product of photosynthesis is lost downstream. Nowhere on the bed of Logan River is there evidence of important conservation of organic matter in the form of muck or plant detritus. Although quantities of leaves fall into the river, contributions from terrestrial plants are actually unimportant. Little of the foreign plant material reaching

Logan River is accumulated until it arrives at the impoundments.

The food habits of the dominant fish indicate a complete dependence on aquatic insect larvae (Fleener, 1951) (Zarbock, 1951) (Sigler, 1951). Although the food of North American stream insects has not been intensively investigated, work on the food habits of closely allied insects from British streams shows that algae are the most important food (Badcock, 1949) (Jones and Erichsen, 1949, 1950).

The importance of the benthic algae in Logan River may then be summarized: for practical purposes the entire diet of the terminal consumers (trout, whitefish, sculpins) consists of aquatic insect larvae (diptera, ephemeroptera, trichoptera, and plecoptera) which depend almost entirely for their sustenance on the living, standing crop of benthic algae or freshly fragmented portions of it in the stream drift. The energy transfers implicit in this statement involve solar energy that was probably fixed in carbon compounds by algae within the previous few months only.

MATERIALS AND METHODS

Chlorophyll extractions, natural substrata

Because of the lack of guiding precedent, some of the first chlorophyll extractions were done using a different procedure than that employed at the end of the investigation. The greater efficiency of the final method justified the delay in standardization.

Extractions of the first of 2 series (fall series) of algae growing on natural substrata from the river bed were accomplished by using a technique somewhat like the one Odum and Odum (1955) used to remove chlorophyll from algae growing in coral. The method as used on algae from Logan River involved the removal of all crustose and streaming algae from rocks and then scrubbing any remaining chlorophyll off the rock while rinsing with acetone, the entire process being accomplished in a large enameled tray. Scrapings from several randomly chosen rocks at a transect were then placed in a closely covered enameled bucket and covered with acetone in which they were allowed to soak for 2 or 3 hours. The entire process up to this point was done outdoors during fall afternoons and evenings; consequently, the temperature of the extraction was usually below 10 degrees centigrade. Information gained on the rate of bleaching of chlorophyll at these temperatures and for the duration of these extractions indicated that a negligible loss of optical density occurred.

At the end of the soaking period, the acetone was removed and the entire collection of scrapings was ground with a mortar and pestle. This was a relatively inefficient process because of pebbles incorporated in the algal crusts. Use of power grinders or blenders was not

considered wise because of the incorporated pebbles and the potential fire hazard incurred when acetone fumes were allowed to accumulate close to an electrically operated device. The ground scrapings from a series of rocks were then mixed with fresh acetone and filtered with a venturi type force filter. This procedure was repeated until the resulting filtered extract was a pale yellow color. A colorless extract was not obtainable within a reasonable number of extractions. All of the extractions from 1 transect were then combined and the volume and optical density were measured.

The amount of chlorophyll remaining in rock scrapings after routine extraction was estimated by soaking aliquot portions of representative scrapings in 2 changes of acetone at temperatures below 0 degrees centigrade for about 24 hours per soaking. The long period of soaking was more effective in removing small remaining amounts of chlorophyll than several changes of acetone in a short time. An amount of chlorophyll equal to about 25 per cent of the routine extract was found to be residual. The fall estimate of chlorophyll in the middle section of Logan River was corrected by that amount.

The latter of 2 series of extractions (late winter series) was done by soaking entire rocks supporting algae in acetone rather than removing the chlorophyll containing material. Usually 4 rocks from a transect were placed in a large, enameled, cold pack canner and the interstices filled with glass marbles to reduce the amount of acetone necessary to cover the rocks. A closely-fitted lid was used to exclude light and to restrict air exchange over the extraction. If the rocks were carefully placed and all interstices filled with marbles, the amount of acetone for an extraction was reduced from about 8 liters

to 4 liters.

Two extractions were necessary to remove between 84 and 96 per cent of the chlorophyll at the 95 per cent confidence level. The length of time the algae were allowed to extract varied from 6 to 16 hours for each of the 2 extractions. Usually the total duration of 2 extractions was between 18 and 24 hours. Duration of extraction was not critical as algae of middle Logan River gave up most of their chlorophyll in the first 6 hours of extractions lasting 24 hours and longer (figure 1).

As in the first series, all soaking was done outdoors. The temperature during the late winter extractions ranged from 0 to 6 degrees centigrade. Chlorophyll lost due to bleaching during an average soaking period at the upper part of this temperature range was 15 per cent of the total extraction when the extraction was made as described. When the average amount of chlorophyll not extracted in 2 soakings with acetone (10 per cent) was added to the amount lost because of bleaching, a total loss which was equal to that of the fall series was estimated (25 per cent). The average amount of chlorophyll per unit area of river bottom was corrected by this amount.

Although an equal chlorophyll loss was incurred while using either method of extraction, the way in which the late winter series of extractions was made was more convenient. The scrubbing and rinsing with acetone that had to be done during the fall series of transects exposed the scrubber's fingers to frostbite. Even when wearing lined rubber gloves, the rapidly evaporating acetone caused a serious heat loss in freezing weather. The operation could not be moved indoors because the accumulated fumes constituted a fire and health hazard. The method wherein the

Figure 1. Relationship between duration of extraction and degree of extraction. Each line is based on data from the common extraction of 4 rocks supporting typical encrusting communities of algae.

available. The valley stations are characterized in general by higher phytoplankton densities than the canyon stations and by definite yearly cycles in density. The majority of the pulse forming species at the valley stations were not abundant at the canyon stations.

algae were removed from the rocks required less acetone, however, and could possibly be improved.

The difference in amount of chlorophyll extracted by 2 successive acetone extractions and the total amount present was determined in the following way. Typical communities of algae on small rocks were extracted with 2 soakings in acetone and then placed in water after rinsing off any extracted but clinging chlorophyll with acetone. After a 30-minute water soaking, the rock was placed back in acetone and extracted for at least 6 hours at temperatures below 0 degrees centigrade. This procedure was repeated 3 or 4 times until the latest extraction produced less than 3 per cent of the chlorophyll extracted to that time. The amount of chlorophyll obtained in the original 2 extractions was then compared with the increment obtained by later extractions.

The effectiveness of water soaking between acetone extractions apparently depends on osmotic "flushing." Algal growths that appeared to be completely extracted would give up an unexpected amount of chlorophyll during an additional extraction preceded by water soaking.

Although most extractions contained water in amounts up to 20 per cent by volume, it was determined that the optical density was not altered from what it would have been if the solvent were pure acetone. Portions of an extract diluted by 25 per cent with either acetone or distilled water underwent an identical change in optical density. Water, however, made the extracts capable of holding more materials in suspension and thereby increased the turbidity of the extracts. Gravity filtering through a retentive filter paper removed all interfering turbidity. Volumes were always checked before and after filtering to ascertain evaporation losses.

The blue-green algae in the middle section, as well as most other prevalent forms (Vaucheria, diatoms, Palmella Myosurus), all gave up their chlorophyll very readily without crushing during acetone extraction. In regard to the middle section extractions, the water soaking technique was necessary only to ascertain the average quantity of chlorophyll not extracted in test extractions of small, representative portions of the community which were done to determine the amount of chlorophyll residual in the routine series.

Prasiola mexicana and Chlorella used in productivity comparisons were impossible to extract by merely soaking in acetone and had to be ground with sand and acetone to effect removal of chlorophyll. Some of the plants that were preponderant in the lower river (Cladophora glomerata, bryophytes) gave up less than 50 per cent of their chlorophyll in 2 acetone extractions between which a water soaking was not intercalated. For this reason all the extractions of algae growing on concrete "rocks" as well as the extractions of the natural growths of algae in the spring measurements on the lower river consisted of 2 acetone soakings intercalated with a water soaking. The amount of chlorophyll remaining in lower river growths after this treatment is not known but appeared to be less than 30 per cent of the amount extracted based on the faint green color remaining in the thalli. No corrections were made to account for this residual chlorophyll.

All small volume extractions were carried out in a refrigerator maintained at temperatures below 0 degrees centigrade in sealed or closely covered containers. Under these conditions both diluted and concentrated solutions of chlorophyll were tested for rate of bleaching.

Little or no loss of optical density occurred during 2 weeks of undisturbed storage. If the solutions were removed from the refrigerator, uncovered, and allowed to become warm, and then replaced, a loss of about 3 per cent of the optical density occurred.

Extractions made in the summer were done in a walk-in freezer when they were too extensive to fit in a refrigerator.

Optical density of chlorophyll extractions was measured at 664 millimicrons with a Bausch and Lomb spectrophotometer ("Spectronic 20"). Densities measured at 664 millimicrons were usually the same as those at 665; but by using this wave length, one may take advantage of the small, spectral plateau of which 664 is about the center. Slight errors in wave length above 665 millimicrons can cause significant decreases in optical density. Extractions were diluted until the resulting optical density was within the linear range of the machine's response to concentration of chlorophyll. Optical densities were converted to milligrams of chlorophyll "a" from a ratio based on nomographs constructed by Duxbury and Yentch (1956). Ryther (1956) considers the relationship between rate of photosynthesis and chlorophyll "a" to be more reliable than the relationship involving total chlorophyll. It has been demonstrated that only chlorophyll "a" participates directly in photosynthesis (Gaffron, 1954).

The ratio between optical density of total chlorophyll at 664 millimicrons and the amount of chlorophyll "a" computed by subtracting chlorophylls "b" and "c" was very constant (figure 2). The small, constant proportion of chlorophyll other than "a" is probably related to the predominance of algae having no chlorophyll "b." Palmella Myosurus,

Figure 2. Relationship between optical density and chlorophyll "a."
Light path is 22 millimeters. Algae extracted are:
encrusting blue-greens with Palmella, tailed circles;
Palmella, open circles; Vaucheria, cross; Oscillatoria,
filled circles.

blue-green algae, diatoms, and Vaucheria are considered to be devoid of chlorophyll "b" (Rabinowitch, 1945) (Strain, 1951).

In actual practice the relationship between total optical density and values for chlorophyll "a" only was used to obtain the concentration of chlorophyll "a" in extractions. For an optical path of 22 millimeters and optical density at 664 millimicrons, the following formula was used: (optical density) (extract volume in liters) (6.17) = total milligrams of chlorophyll "a."

Although varying in apparent color from the brown extracts of blue-green algae to bluish-green extracts of Cladophora, the absorption spectra of the acetone extracts of all communities encountered were very similar (figure 3).

Sampling procedures and devices

The 18-mile length of the middle section was divided into 2-mile divisions. Order of sampling of the 9 divisions in fall and spring was determined by lot. A second drawing was made to choose the 0.2 mile zone, within a division, that would contain the transect. Distances were measured by automobile speedometer along a road that followed the course of the river closely. The exact location of the transect which was to be sampled was usually determined by some device such as walking a compass course or heading for a particular tree on the bank without previous knowledge of the stream condition at that point. When a very atypical choice was made, as in the case of an ice-narrowed channel, the transect was moved a random distance upstream within the 0.2 mile area.

Once the transect location was established, the bottom materials were classified by size by dropping a rod every 15 centimeters along a

Figure 3. Absorption spectra of acetone extracts of algae or groups of algae dominating in Logan River.

graduated transect line and counting the number of times the rod touched each of the following categories of bottom material: material less than 2.5 centimeters in minimum dimension, rocks larger than 2.5 centimeters in minimum dimension but less than 12 centimeters, those rocks larger than 12 centimeters minimum dimension, and emerged parts of boulders. The number of times the rod touched a given bottom type, divided by the total number of points sampled, was considered an estimate of the per cent of bottom area covered by that type.

To select rocks for chlorophyll extraction, 6 and 4 points on the transect line were randomized in the fall and late winter series respectively. In the fall series the movable rocks larger than 12 centimeters minimum dimension and nearest to verticals dropped from randomized points on the transect line were chosen for algae removal. The method of rock selection was the same during the late winter series with the exception that the upper size of rocks was limited to a dimension that would allow 4 to fit in the extraction container. This limitation usually restricted the largest dimension to about 25 centimeters. There was no correlation between rock size and amount of chlorophyll per unit area among movable rocks having a minimum dimension exceeding 12 centimeters in the fall sample, so it is doubtful if the restriction of the upper size of rocks in the late winter series affected the accuracy of the estimate of mean amount of chlorophyll per unit area.

The bottom materials having a minimum dimension less than 2.5 centimeters were practically devoid of chlorophyll as were the exposed, dry portions of boulders. In the fall series the rocks between 2.5 centimeters minimum dimension and 12 centimeters minimum dimension were

sampled by pooling a series of these from each of several transects in 1 sample. In the late winter series, 6 or 7 rocks in this category were randomly selected at each of the transects where they were present. The rocks in this size category were then extracted separately from the larger ones.

The stream bed area occupied by any series of rocks obtained at a transect was considered to be the sum of the areas of horizontal projections of each rock. The amount of chlorophyll "a" per unit area was the total weight of chlorophyll "a" obtained in an extraction divided by the river bed area producing that chlorophyll. The weighting of variances and means of strata within the rock size data and in the chlorophyll "a" per unit area data followed methods outlined in Snedecor's section 17.7 (1946). The same section served as a guide for estimation of the variance of the product: (stream bed area occupied by chlorophyll-bearing rocks) (amount of chlorophyll per unit area).

The schedule of chlorophyll sampling at transects, as originally planned, included 3 series of transects. An additional complete series of transects was to have been completed during July following the last series in late winter. The peak of the runoff, however, occurred about 3 weeks later than usual; therefore, another series of transects was not feasible because of unusually high water.

The net effect of short-term changes in algal abundance during unsampled periods on the estimate of the average standing crop of chlorophyll was not determined precisely. Evidence from several sources, however, gives no reason to suspect that such knowledge would cause an important change in the estimate. The amounts of chlorophyll on 5

concrete "rocks" (in mid-July) that had been on the river bed during the spring runoff were within the range of comparable values of chlorophyll from identical artificial substrata removed about the same time the late winter chlorophyll measurements of the natural substrata were made.

The fall series of chlorophyll transects were made over a period of 60 days, that of the late winter series was 30 days. No trend of increasing or decreasing quantity of chlorophyll per unit area was recorded during either period. The difference in mean amount of chlorophyll per square meter of river bed occupied by large rocks (the dominant chlorophyll bearing substrata) between that measured in the fall and that of the late winter series of transects was not significant at confidence levels as low as 50 per cent.

Continuous observation of the algal community of the middle section gave no indication of a large bias in the estimate of the chlorophyll "a" contained in the community. Peaks and low points in the standing crop, though occurring, were not of long duration and seemed to balance out. The upsurge of algae during the decline of the runoff was followed by a general reduction in standing crops in August and September. A cursory measurement of chlorophyll "a" was made during the August depression by common extraction of 2 typical rocks (in the size range of those of the late winter transects) from 4 representative stations. The quantity of chlorophyll "a" per unit area of bottom occupied by these rocks was about 40 per cent of the average values for comparable rocks in the fall and late winter measurements; that is, 0.14 grams of chlorophyll "a" per square meter. Standing crop of chlorophyll is probably at a minimum in August. A peak standing crop occurred in early winter.

Although not measured, it does not appear possible that the contained chlorophyll could have exceeded the average estimate reported by 50 per cent. The opinion is based on judgment developed while sampling standing crops of chlorophyll in the river below impoundments and in canals where the average value estimated for the middle section was exceeded by a factor of 2 or 3. The winter maximum was followed by an observable reduction due to anchor ice and snow cover.

An equilibrium of production and attrition based on a direct dependence of the latter on the former in Logan River is suspected here as the deterrent to compounding of the standing crop as in a plankton bloom. Apparently the risk of an individual thallus being dislodged or broken by the current is in proportion to its length. Blum (1956) suggests that this may be true for at least 1 species. After a period of accelerated attrition, as in the rise of the spring runoff, regrowth of the standing crop is rapid until the thalli again become overextended.

Artificial substrata

To remove the effect of substratum type and shape on experiments concerning the relation between chlorophyll distribution and insolation, relative rate of diffusion, and downstream habitat changes, artificial concrete "rocks" were used. Each "rock" was actually a cylinder of concrete 6 inches high and 9 inches in diameter with a wire loop embedded at the top. Ice cream containers of 2.5 gallon capacity were used as forms. Precautions were taken in choice of concrete and in casting to insure a uniform, smooth surface.

The concrete used was dyed red in the mass to allow greater visibility in turbulent areas of the stream. The red color was a mixed

advantage as it also caused curious fishermen to remove the artificial "rocks" from the stream for closer inspection. This loss of "rocks" was compensated for by placing several more than were needed on the stream bed at each station. Choice of which of those remaining were to be used in the experiment was made by lot.

Although weighing about 16 kilograms each, most concrete "rocks" left in the river during the spring high water period were washed away. They did maintain position during temporary freshets at other times of the year.

Extraction of the chlorophyll contained in algae growing on the concrete "rocks" was accomplished by soaking them in a closely fitting enameled pail with enough acetone to just cover the "rock." About 1.8 liters of acetone were necessary for each of the 2 extractions on each "rock."

Shade formed by bridges was used to provide locations having minimum duration of insolation.

Relative diffusion methods

The most tenable explanation for enhanced plant growth in moving waters is the increase in rate of renewal or removal of gases and dissolved solids in the water bathing the plants (Ruttner, 1926) as quoted by Ruttner (1953). For this reason it is necessary to measure the total water movement occurring close to algae when assessing such diffusion effects. Total water movement determinations infer a measurement of turbulent micro-currents and alternating surges as well as orderly streamlined flow. All mechanical velocity or current meters in use today are incapable of measuring the micro-currents in intimate

contact with algae. The majority are too bulky to be placed in the environment with which we are concerned and in addition they only integrate micro-currents of a relatively large cross section of stream flow. Pitot tubes, besides being difficult to read in rapid, turbulent water, do not record alternating surges or turbulence as water movement. The ideal device to determine the rate of exchange of water molecules over a submerged surface would be one dependent on this very phenomenon. As an approach to this ideal, the rate of dissolution of sodium chloride tablets was used as an index of relative diffusion in this investigation.

The relative rate of diffusion over the surface of cylindrical concrete "rocks" was measured as the total loss by dissolution, of 6, 2.25 gram sodium chloride (salt) tablets during a 1-minute immersion when placed at 6 standard positions over the surface of the "rock." The entire salt tablet was held within 8 millimeters of the substratum by adjustable music wire tongs. The tablet was streamlined in relation to the main current.

The original tablet weights as manufactured are standardized within very close tolerances so that any loss in weight may be considered due to dissolution. Series of tablets placed in individual, identical containers of still water sustained almost identical weight losses during an immersion of several minutes. This last measurement rules out possible different rates of dissolution due to differences in compaction of the tablet.

To further investigate the precision of the method, 2 series of replicated tests were conducted under the conditions of actual use. In a lined canal having smooth, non-turbulent flow, mean weight of salt loss

for 6 replications of 4 tablets each had a coefficient of variation of 3 per cent. The velocity here was 0.6 meter per second. At another situation on Logan River itself, immediately downstream of a cascade where velocities exceeded a meter per second and the flow was very turbulent, 11 replications of 4 tablets each yielded a coefficient of variation of 6 per cent. The 4 tablets in the above tests were placed at the 4 side positions (0, 90, 180, and 270 degrees) of the cylindrical concrete "rock" used for the measurements. Use of 2 top positions also, as in the actual measurements made using salt tablets, would probably have further reduced the variability of the mean loss.

As would be expected, salt loss by dissolution bears an erratic relationship to velocity meter readings in turbulent parts of the river. In smooth flow, as in a lined canal, the relationship is close enough to allow the use of salt dissolution as a measure of velocity. At velocities from 0.3 to 0.9 meters per second, prediction intervals at 95 per cent confidence (Ostle, 1954) were all within 0.08 meters per second (figure 4). Corresponding values of salt loss for 2 tablets and velocity of water in which they were immersed were obtained by mounting the tablets ahead of an Atlas current meter in such a fashion that the normal flow through the meter was not impeded. Because each of several improvements in the calibration technique gave a worthwhile improvement of precision, it is felt that much of the present variability in the velocity-salt loss relationship could be removed by additional improvement in calibration technique.

Vertical gangs of salt tablets mounted on staffs at 2-inch intervals proved useful in exploring velocity distribution with depth.

Figure 4. Relationship between centigrams of sodium chloride dissolved and velocity of water in which 2, 225 centigram tablets were immersed for 1 minute. The least squares regression line is bracketed by lines enclosing the prediction interval at 95 per cent confidence.

Duration of insolation methods

With the exception of changes due to solar altitude and cloud conditions, the chief cause of differences in amount of light reaching plants on the bottom of Logan River is shade formed by mountains and trees. Light intensities incident to the river surface generally reach the bottom undiminished.

The measurement of duration of insolation, the complement of shade, was accomplished by photographing 140 degrees of the celestial hemisphere at each point where a measurement was desired. From one vertical photograph, objects that would intercept insolation at some time of the year could readily be seen when an overlay of sun courses was oriented on the photograph. The overlay consisted of courses the sun would follow on dates coincident with 5-degree intervals of noontime elevation of the sun as observed from a latitude of 42 degrees (figure 5). Data for the construction of the overlay was obtained from a sun azimuth chart published by the United States Hydrographic Office, Washington, D. C., and from Rusts Line of Position Chart (Weems, 1941). Duration of insolation between any 2 dates on the overlay was computed by counting the hours along the 2 courses when the background for the course line consisted of open sky on the photograph. Figure 6 is an interpreted tracing of 2 typical photographs showing the open and occluded areas of the sky that are the basis for calculation. The open sky periods for both dates were then averaged and multiplied by the number of days represented by the interval between sun courses. Total insolation for any desired period consisted of the sum of hours of insolation in each of the 5-degree intervals in the period.

Figure 5. Details of transparent overlay placed over photograph of sky and shade forming objects to determine the duration of insolation. Dashed lines are sun courses at 5-degree intervals of noontime elevation (local civil time). Angular altitudes on the celestial hemisphere are given on the N-S line. Dates around lower half of the 20-degree altitude circle are those on which the sun follows the course adjacent indicated by a dashed line. Each sun course is followed 2 times a year.

Figure 6. Interpreted tracing of 2 heavy shade situations as recorded on vertical wide angle photographs. Dotted areas represent brush, hatched areas represent mountains and a bridge over the point for which a potential shade measurement was desired.

The actual photograph was taken as a negative on 5 x 7 contact printing paper. A simple, handmade, wide angle, pinhole camera, built about a 5 x 7 cut film holder, was used to take the photographs. A focal length of about 20 millimeters gave at least 140 degree coverage of the celestial hemisphere. A minus 4 diopter lens was placed over the 0.5 millimeter pinhole to reduce distortion. When light rays forming a point image are parallel, as in a pinhole camera, negative lenses have a "focusing" effect on oblique rays of light reaching the pinhole which causes them to be focused closer to the center than they would normally be focused. The effect decreases as the rays approach the perpendicular. The useful angular coverage of the camera can be further improved by using an even stronger negative lens (-10 diopters) over the pinhole.

To take a picture the camera was placed on an improvised heavy, iron plane table set up over the rock on the river bottom for which an insolation measurement was desired. After leveling the camera, and orienting it to include the greatest area of sky where the sun appears during some part of the year, the exposure was made by removing the dark slide and rapidly moving out of the angle of coverage. Because of the slow moving shadows of close-by streamside vegetation, the angular difference of position between the camera and the river bed could have caused a small, positive error in the estimates of duration of insolation made at low solar altitudes. This error seldom exceeded 20 minutes in mid-winter when it was at a maximum.

Orientation points necessary to properly place the overlay on the photograph were the sky zenith and true north. The zenith was obtained

as a photograph of a light bulb precisely over the pinhole taken while the camera and filmplane were perfectly level. The position of the zenith was then transferred to other photographs by lining up the border (actually a pencil tracing of the outlines of the film rabbets when the paper was in place) of the zenith standard with the photograph.

True north in mountainous country was easily located by taking a compass bearing on a distant, sharp mountain peak that would appear in the photograph. In flatter country true north was located by including the sun in the picture. By recording the local civil time at which the photograph was taken, an azimuth table could be entered. With knowledge of the sun's azimuth it was then a simple matter to compute true north.

Circles of equal celestial altitude were constructed on the overlay by photographing marks of known angular altitude on a wall while the pinhole camera was level and then measuring the equivalent distances from the zenith on the photograph.

Productivity methods

Efforts were made to apply Odum's (1956) method of estimating productivity by the diurnal oxygen pulse of a stream. The data obtained from the middle section were very erratic and not subject to interpretation. Oxygen values were never more than 0.4 parts per million away from saturation while the range in duplicate samples often approached one-half of this figure. Each condition of shade or turbulence rapidly altered the oxygen concentration of the river water by a small increment as it progressed downstream.

In the deep, slowly flowing stream, produced by the third impoundment on Logan River, diurnal changes exceeding 5 parts per million were

measured and duplicate samples agreed closely. A measurement of the productivity of that part of the river was made on a day in July (table 1). The yearly average was estimated by assuming the lowest winter rate to be about 10 per cent of the July rate.

To gain an idea of the order of magnitude of photosynthesis as related to chlorophyll in Logan River, several series of light and dark bottle type experiments were conducted. The experiments were made with full realization of the probability that running water communities do not photosynthesize at a normal rate when sealed in containers of still water. Attempts to agitate the first series of experiments in the winter were stymied by mechanical difficulties. Any attempts to improve the agitation system would have infringed on the time necessary to complete the primary objectives of the investigation, so agitation was abandoned. It is significant, however, that in the experiment where agitation was partially successful (February 6), a rate of photosynthesis almost double that in any other experiment with the complete community was obtained (table 2).

The winter series of light and dark bottle experiments were conducted in gallon jars fitted with paraffin exclusion plugs. Each plug was provided with a stoppered, half-inch hole through which the water could be siphoned. Rocks supporting typical growths of algae were placed in the jars and sealed. The dark jars were placed in a covered box while the light jars were placed on an improvised bench at the stream side. Temperatures were held close to those of the river by banking the shade side of the jars with snow. Light values were the same as those on the river bottom. The summer series of experiments were done in quart mason

Table 1. Comparative rates of gross primary production

Glucose produced (kilograms per meter squared per year)	Water	Reference	Remarks
0.6	Middle section of Logan River	--	Average rate based on average of fall and late winter chlorophyll per meter squared
4.6	Third impoundment Logan River	--	Average rate by diurnal oxygen curve following method outlined by Odum (1956)
3.0	Canyon Road (below first impoundment Logan River)	--	Average rate based on chlorophyll per meter squared as determined from 2 fall and 2 spring transects
3.1	Mendon Bridge, last riffle before valley base level	--	Average rate based on chlorophyll per meter squared as determined from 1 spring transect
8.8	Eniwetok Atoll	(Odum & Odum, 1955)	Diurnal oxygen curve determination
0.6	Weber Lake	(Manning & Juday, 1941)	Maximum summer photosynthesis of most productive of several Wisconsin lakes
0.2-21.5	Florida Springs (11)	(Odum, 1957b)	Diurnal oxygen curve determina- tions

Table 2. Chlorophyll based rates of photosynthesis of algae in light and dark jar experiments

Date	Gross productivity in milligrams oxygen per hour per milligram chlorophyll "a"	Water temperature in degrees centigrade	Hours of experiment	Light conditions	Dominant algae
February 6	1.1	4.5	13:00-16:00	Thin overcast	Encrusting blue-green and <u>Palmella</u>
February 9	0.6	10.0	13:30-15:30	Sun	Encrusting blue-green, <u>Vaucheria</u> and <u>Palmella</u>
February 12	0.5	10.5	15:30-17:00	Sun	Encrusting blue-green
June 29	0.7	11.5	14:00-16:00	Sun	Encrusting blue-green
June 30	2.1	11.5	13:30-17:30	Sun	<u>Oscillatoria</u> 1/
June 30	0.7	11.5	13:30-17:30	Sun	<u>Vaucheria</u>
June 30	2.7	11.5	13:30-17:30	Sun	<u>Prasiola</u> , detached from rock
July 2	0.3	11.5	15:00-19:00	Overcast	Encrusting blue-green
July 4	0.7	12.0	10:00-16:00	Sun	Encrusting blue-green
July 9	1.0	12.0	14:30-16:30	Sun	<u>Chlorella</u> 2/
July 22	0.07	12.5	17:00-19:30	Shade	Encrusting blue-green
July 22	-0.14	12.5	17:00-19:30	Shade	<u>Oscillatoria</u> 1/

1. From artesian standpipe.
2. Dense culture from aquarium.

jars sealed under the water surface. Jars were tethered to a plank bridge over a canal and allowed to rest on the concrete bottom. The light, temperature, and water chemistry of the canal were identical with the Logan River itself.

Light experiments ran from 2 to 3 hours, dark experiments from 3 to 16 hours. The longer dark experiments led to respiration rates much lower than the short ones; therefore, results from short experiments only were used. The decreased respiration rate of long experiments was associated with the observed death or distress of hundreds of small insect larvae that had crawled from the algae. All respiration rates were chlorophyll based; for obvious reasons such rates can only be approximations. In addition to the light and dark jars, blanks of canal water only were exposed to the same handling and environmental conditions that the other jars were exposed to. Oxygen concentrations of these jars were the basis for determining differences in concentration in the others. No measurable changes in oxygen concentration occurred in blanks.

Rates from each experiment consisted of the pooled data from 3 to 6 jars. No attempt was made to determine the productivity rate from jar to jar because of the difficulty of placing similar quantities of material in each jar and of having the same proportion of chlorophyll in the shadow of the rock on which it was growing.

Chemical, temperatures, and light methods

Determinations of dissolved solids were made by Utah State University Soils Laboratory. Appropriate standard methods were used. Oxygen values were determined by the unmodified Winkler method. Turbidities

were measured with a Hellige turbidometer. Water velocities were determined with an Atlas current meter. Temperatures were taken by placing maximum-minimum thermometers in channels on the underside of disguised, irregular concrete lumps which were allowed to remain on the river bottom continuously during periods of the study.

Intensities of light were measured with a Weston photographic exposure meter. As long as light of one spectral distribution is being measured, comparisons of photocell readings are valid, however, skylight intensities must be adjusted to properly compare them to sunlight intensities (Evans, 1956). Evans' work indicates that with a spectral sensitivity close to that of the meter used in the present studies, skylight measurements must be increased about 10 per cent to be comparable to sunlight measurements.

As recommended by the manufacturer, Weston photometer scale readings of light from a horizontal white surface were multiplied by 4 to obtain foot candles. Values of light reflected from a horizontal, white surface below the surface of the water measured with a submerged photometer were consistently about 55 per cent of those measured in a similar fashion above the water. Such a loss in less than a meter of very clear water departed greatly from precisely measured losses (Davis, 1941), (Whitney, 1938), (James and Birge, 1938). For this reason the problem was further investigated. Measurement of light reflected from a dry, horizontal, white surface when a column of river water 20 centimeters in depth was placed between it and a nonsubmerged light meter showed that the actual loss due to the water was insignificant. The 55 per cent loss originally measured was probably an anomaly due to refraction.

PHYSICAL AND CHEMICAL DESCRIPTION OF LOGAN RIVER (MIDDLE
SECTION AND SUPPLEMENTARY STATIONS OF LOWER RIVER)

Bottom materials

The middle section of Logan River flows for the most part over indurate, calcareous rock strata. A detailed description of the geology of the Logan Quadrangle is available (Williams, 1948). Though having a steep gradient (figure 7), the river bed is relatively stable. The materials composing the river bed are chiefly rubble and small boulders. Random point samples of the horizontal area occupied by each of several classes of bottom materials were, within 95 per cent confidence limits, as follows: rocks having a minimum dimension greater than 12 centimeters, 50-70 per cent; rocks whose minimum dimension was between 2.5 and 12 centimeters, 6-22 per cent; materials having a minimum dimension less than 2.5 centimeters, 15-23 per cent. The finest bottom materials were seldom small enough to be classified as sand. Emerged parts of boulders occupied a horizontal area less than 10 per cent of the bottom area. These did, however, appear more important to a casual observer.

Rocks on the bottom of that part of the middle section above the dugway (figure 7) were equally divided between gray, blocky, calcareous types and tan to brown, rounded boulders of indurate sandstone bordering on a quartzite. The rocks below the dugway were chiefly gray, blocky to flat, calcareous types with fewer sandstone types than were present above the dugway.

Runoff and turbidities

The watershed of Logan River is a section of the Bear River Range

Figure 7. Profile of Logan River showing gradients, stations, and sections referred to in the text.

of the Middle Rocky Mountains in northeastern Utah. The yearly runoff, though peaked in late spring (figure 8), is apportioned throughout the year in such a fashion that a very permanent aquatic habitat exists over most of the river, the exception being the stretch between the second and third impoundments. Turbidities reached a silicon dioxide equivalent of 40 parts per million for brief periods during the early part of the runoff. Over most of the months of study (September 1955 to September 1957), turbidities remained below 5 parts per million.

Dimensions of middle section

The average width of the 29.2 kilometers (18 miles) of Logan River referred to as the middle section is, at the 95 per cent confidence level, between 9.5 and 12.5 meters. There are few pools in this part of Logan River that produce a back eddy. The entire middle section may be described as a series of flat rapids during most of the year. The average depth is between 24 and 40 centimeters, at the 95 per cent confidence level, from August to March.

Current velocities

Surface velocities from August to March ranged from 0.6 to 1.2 meters per second. During the peak of the runoff surface, velocities ranged from 1.2 to 2.7 meters per second. Ranked average velocities 3 inches above the bottom as measured at transects are given in figure 9. Perhaps more descriptive than range or average of velocities is the array of individual velocities. To provide data for such an array, velocities were measured 3 inches above the bottom at random points at 3 stations during the lowest river stage. These data are presented in ranked form in figure 10.

Figure 8. Ten-year (1948-1957) averages of monthly volumes of flow at the mouth of Logan Canyon. Data are from U. S. Geological Survey records.

Figure 9. Ranked, average velocities determined from randomized measurements, 3 inches above bottom on the middle section. Each bar represents the average of several measurements at a transect.

Figure 10. Ranked, individual velocities measured 3 inches above the bottom at random locations on the middle section. Each bar represents an individual measurement.

Relative diffusion rates

Relative diffusion rates, as measured by dissolution of salt tablets held close to substrata supporting algae, were consistently lower in the late winter low water period than they were in the fall when flows were greater (figure 11). That relative diffusion rates over uniformly shaped substrata would be raised in approximate proportion to an increase in flow or lowered proportionately with a decrease seems reasonable. Relative diffusion rates occurring during higher water, however, bore little relation to corresponding low water relative diffusion rates at 1 station (Red Banks). This was because boulders that earlier formed cascades by causing water to flow over their tops simply divided the current during lower water and created areas of very low velocity. Thus, locations having diffusion measurements that were among the highest during high water often had rates among the lowest during low water.

Fall measurements of diffusion rates at Mendon station were made during a period of rapidly fluctuating rates of flow near the end of the irrigation season and are not presented. The spring rates of diffusion (figure 9) reflect the very even flow and smooth bottom type at this station as compared to the other 3 stations used in the study.

Insolation and light intensity

The chief cause of differences in duration of insolation incident to the river bottom, other than those caused by differences in solar altitude or clouds, is shading by stream side vegetation and mountains. Water depth is not great enough to cause an important change in the quality or quantity of light reaching the river bottom. Measurements of light reflected from a level white surface on the river bottom varied

Figure 11. Ranked relative diffusion rates measured over surfaces of cylindrical concrete "rocks" having identical size and shape, during late winter (hatched) and corresponding fall measurements (hatched plus clear area). Fall diffusion rates were not measured at Mendon Bridge. Each bar represents an average of 6 diffusion rates at standard positions over the "rock" surface as determined from the rate of dissolution of sodium chloride tablets.

little over the range of water depths present at a given light intensity. Turbidities were rarely important in screening light. Very turbulent surface conditions occasionally lowered the incident insolation by about one-half over limited areas at the foot of cascades. The average duration of insolation incident to the river during periods when solar altitudes were higher than 20 degrees (instrument limitation) was 1,900 hours per year on the middle section. At the Mendon station where no shading occurred at solar altitudes above 20 degrees, the comparable figure was 2,800 hours. Additional insolation from the sun at altitudes below 20 degrees would have added little to the insolation period of any place on the middle section of Logan River but would have increased the duration of insolation at a completely shade-free location to about 4,400 hours a year. Stream side brush only 9 feet above the bottom of a river 36 feet wide would intercept most of the insolation at solar altitudes of 20 degrees.

The most critical period relative to insolation for photosynthesis occurred during the late fall and early winter. Many portions of the river between Temple Fork and the third impoundment received no insolation for several weeks during this time of the year.

Representative light intensities measured with a photoelectric cell were as follows: open shade, late or early in the day, 100 foot candles; open shade, midday, in summer, 700 foot candles; insolation at solar altitudes of 13 degrees, 2,400 foot candles; insolation at solar altitudes of 68 degrees, 12,000 foot candles.

Maximum and minimum water temperatures occurring during intervals of varying length are presented in figure 12.

Figure 12. Water temperatures at 4 stations on Logan River. Center line is smoothed curve of temperatures taken at random times during the day at intervals of 10 to 20 days. Lines above and below center line are smoothed curves of maximum and minimum temperatures recorded for 10 to 20-day periods. Measurements were started in November 1955 and ended in July 1957.

Chemistry

Determinations were made for dissolved solids known to be plant nutrients and those other materials in solution that were preponderant. The results of 3 series of analysis (fall, winter, and spring) at 4 stations are presented in figure 13. No attempt was made to determine probable important trace elements.

Figure 13. Downstream changes in dissolved solids, turbidity and chlorophyll. Ranges in dissolved solid concentration are based on 3 series of determinations made in September, January, and April 1956-1957. Turbidities are based on measurements made at 10-day to 2-week intervals from August to March 1956-1957. Chlorophyll values are 95 per cent confidence belts for average amount extracted from concrete rocks immersed at stations indicated from August 1956 to March 1957 inclusive.

ANIMAL COMMUNITY

Fish

Fish present are: mountain whitefish Coregonus williamsoni Girard, brown trout Salmo trutta Linnaeus, rainbow trout Salmo gairdneri Gibbons, cutthroat trout Salmo clarki Richardson, Utah sculpin Cottus bairdi semiscaber Cope, and rarely the small fin redbside shiner Richardsonius Balteatus hydroflox Cope (Fleener, 1951) (Sigler, 1951). The summer standing crop of unstocked fish species determined by electrofishing was 21 kilograms per hectare or 19 pounds per acre in 1954 (unpublished data, Utah State Fish and Game Department).

Invertebrates

Insect larvae are the preponderant invertebrates living in Logan River. Data of Hales (1955) can be used to calculate the average density of the most important orders of insects. Based on square foot bottom samples from 3 representative stations sampled at several times of the year, the combined weight of diptera, ephemeroptera, trichoptera, and plecoptera was about 6 grams per square meter. The order of abundance of the 4 dominant orders of insects is open to question.

Other invertebrates do not approach the numbers and mass of insect larvae in Logan River. Free living nematodes and rotifers are common, but all others not discussed here are not present or only occasional.

BENTHIC PLANT COMMUNITY OF THE MIDDLE SECTION OF
LOGAN RIVER AND SUPPLEMENTARY STATIONS

Blue-green algae

There are no true plankters in Logan River, the algae in the drift being derived from the benthic forms. Occasional bryophytes are found, but higher vascular plants are never present in Logan River proper. The middle section is essentially uniform with respect to the climax algal community. Encrusting blue-green algae are dominant over most of the river bottom although not as conspicuous as some other algae. The greatest area of river bottom is colonized during most of the year by Shizothrix fasciculata (Nag.) Gom. A secondary colonizer which greatly augments the bulk of the crusts is Phormidium incrustatum (Nag.) Gom. This last mentioned blue-green species, though probably not covering as extensive an area of the bottom as Shizothrix fasciculata, is at least as important with regard to bulk of crust formed. Shizothrix fasciculata grows best in sunlit situations and is grossly distinguishable as a thin brownish-red to tan, flexible crust. Early stages of Shizothrix fasciculata consist of isolated hemispheroids about 2 millimeters in diameter. As growth progresses in early fall, these individual colonies coalesce into the typical expanded sheets or crusts. Shizothrix fasciculata is generally the earliest permanent growth on experimental substrata placed on the stream bed. Phormidium incrustatum reaches the acme of its development in shaded situations under bridges and close to banks. Very friable crusts that often exceed 30 millimeters in thickness and are bluish-green in color are the chief macroscopic

manifestations of this species. Generally, the encrusting community of Logan River closely resembles that described by Fritch (1929, 1950) in British streams.

In the section of Logan River above the Dugway, Entophysalis rivularis (Kutz) Dr. and Daily is conspicuous as thin black coatings on quartz boulders that apparently are resistant to colonization by other algae.

Ubiquitous but not contributing as much bulk to the standing crop as the encrusting blue-green algae are nostoc species. Of these, Nostoc sphaericum (L.) Vauch. and Nostoc parmelioides Kutz. probably are most frequent. Late winter is the period of greatest abundance of Nostoc.

Other occasionally appearing blue-green species are Phormidium uncinatum (Ag.) Gom., Amphithrix janthina (Mont.) Born. and Flah. and Phormidium subfuscum Kutz.

Chlorophyta

Chlorophyta are not as continually abundant as the blue-green species; however, during short periods chlorophyta may temporarily approach the position of the blue-green species as important producers. During the period when the river is returning to normal levels after the spring runoff peak had been passed and when turbidities are again low (early June to mid-July), Prasiola mexicana J. Ag. becomes abundant. The tops of most shallowly submerged boulders, particularly those close to shore, support dense growths of this algae during the period delimited. By August, however, most of the rocks that support Prasiola mexicana are exposed by falling water levels and the greater part of the crop of this species is dried. During the remainder of the year

occasional plants of this species are found, but it cannot be classed as common. Prasiola mexicana occurs over the entire river above the Crocket Avenue diversion during the peak of its abundance but is most often found below the Dugway during the rest of the year.

Ulothrix zonata (Web. and Mohr) is conspicuous in the late winter as a bright green growth at the water line of emerged boulders. It occurs in slow water near shore most often but is also found in swift parts of the river. Ulothrix zonata does not contribute a significant bulk to the standing crop of algae during its period of greatest abundance.

Cladophora glomerata (L.) Kutz. is never important in the middle section though present in late winter and spring.

Closterium ehrenbergii Menegh. is common in rock scrapings examined with a microscope but never is present in measureable bulk.

Chlorotylum cataractarum Kutz. is common in the lower part of the middle section as another member of the crustose community of algae dominated by the blue-greens. It imparts a bright green color to the otherwise brown or bluish-green crusts. Chlorotylum cataractarum is not widespread and is observable only in early spring. For these reasons it does not contribute an important increment to the yearly algal production.

Chrysophyta

Of the Chrysophyta, Palmella Myosurus (Ducluz.) Lyngb. is the most important representative. This form is also referred to as Hydrurus foetidus (Vill.) Trev. but the first mentioned name has precedence. During the winter months the entire bottom of the river in sunny aspects

is often colored olive-brown by this algae. It is possible that the preponderant contributor to the standing crop of algae in early winter is Palmella Myosurus. Although gradually becoming senescent (gnarled and rubbery with loss of chlorophyll) and disappearing by spring, a secondary upsurge of vigorous young plants occurs during the spring run-off. Palmella Myosurus is often the sole colonizer of cleaned, dried rocks replaced on the river bed during the late fall and winter. This tendency to thrive on clean, new surfaces is extended to recently inundated boulders that have been exposed by previously low waters. There is also a tendency for Palmella Myosurus to flourish in sunlit situations. This alga was difficult to find in Logan River during late summer and early fall but continued to exist during those seasons in cold tributary springs.

Though never as abundant as the blue-green algae or Palmella Myosurus, Vaucheria species are common as sparse growths on the crusts of the blue-green algae in the middle section.

Diatoms are present as epiphytes and on bare rocks at all times. They exist in great numbers but rarely form macroscopic growths. It is difficult to evaluate their role as contributors to the standing crop. It does appear, though, that the position of diatoms on a relative quantity scale (dry weight minus the frustule weight) must be a minor one. As a food item for invertebrates it is suspected that they are relatively more important than their contribution to plant biomass would indicate. Because research on the numbers and kinds of diatoms in drift from Logan River was being conducted concurrently with this study (Clark, 1957), this information will not be duplicated here. It

will suffice to name the dominant, benthic genera: Diatoma, Cocconeis and Navicula. Comparisons of diatoms present in drift with those of the benthos revealed some differences in species composition; however, this matter is also considered by Clark.

Rhodophyta

The Rhodophyta are represented by a species of Batrachospermum (Chantransia stage) that is occasionally associated with crustose blue-green algae from shaded situations.

Algae at lower supplementary stations

The Canyon Road station and the Mendon Bridge station are not part of the middle section. At Canyon Road all the algae described from the middle section are present but the order of relative abundance is different. The total bulk of algae below the first impoundment, where this station is located, greatly exceeds that of the middle section. The chief contributors to the increased biomass are Vaucheria and bryophytes. The Vaucheria species present is probably the same as the one upstream, but identification could not be made because of the absence of sexual parts at all times of the year.

Cladophora glomerata (L.) Kutz. is an important part of the Canyon Road station community in spring. Palmella Myosurus is common during the winter but never assumes the relative position of abundance held by this species in the upper river. The thick carpet of Vaucheria and bryophytes apparently inhibit the growth of Palmella Myosurus because new, clean surfaces placed in the river here support dense growths of this alga.

Encrusting blue-green algae are important as precursors of the

climax community dominated by Vaucheria and bryophytes but are apparently covered by these plants in winter and do not become obvious again until the end of the runoff.

Prasiola mexicana is about as abundant at Canyon Road as in the middle section. With the greatly increased plant bulk the epiphytic diatoms show a corresponding increase.

The station at Mendon Bridge is ecologically different than any upstream portion of the river investigated. Domestic sewage and silt from irrigation return water are pollutants here. In addition to pollution the environment differs in not having large rubble or boulders on the stream bed and in having reduced gradient. The summer algal community is limnetic in character and is not comparable to that of the winter. The water at this time is much warmer than in the remainder of the river (figure 12) and almost without movement because of extensive irrigation diversions. With the end of the irrigation season, the community again becomes one of rapidly moving water. The early spring community is composed of Cladophora glomerata, Chlorotyllium cataractarum, diatoms, Entophysalis rivularis, Entophysalis lemaniae (Ag.) Dr. and Daily, Phormidium incrustatum, Shizothrix fasciculata, and Oedogonium species. Palmella Myosurus is present in midwinter collections. Because of the complexity of the community at Mendon Bridge, it is difficult to determine any order of relative quantity of individual species. Cladophora glomerata, however, appears to dominate the early spring community while diatoms appear most important in early winter collections.

ALGAL DISTRIBUTION

Linear distribution

The differences in flora of the middle section and lower river presented in the previous discussion give an idea of the distribution in space or linear succession of the algae in Logan River. It might be added here that the situation is not without exception and factors other than mere distance from the headwaters or linear distribution are operating in parts of Logan River other than those described. A case in point occurs in the upper Logan River starting immediately above the middle section and continuing upstream for some distance. Vaucheria and Prasiola mexicana dominate the community in late winter in contrast to the community of the middle section in which these 2 algae are not often found at that time. While the encrusting blue-green algae are greatly reduced in quantity, Entophysalis rivularis greatly increases its rock coverage. The side of the middle section receiving water from the upper river (out of Franklin Basin) briefly supports the plant community described for the upper river in contrast to the side which receives water from Beaver Creek which fits the general description of the middle section.

There is little reason to suspect gross water chemistry, water temperatures, or water velocity as being causes of the differing plant communities described in the preceding paragraph. The uniformly smoother and more rounded quartzite rocks and boulders of the upper river as well as reduced quantity of molar agents appear to be the habitat elements most likely to be responsible for differences in algal quality.

and quantity at this location.

Order of colonization

Knowledge of the sequence in which algae colonize new rocks or experimental surfaces in Logan River is a prerequisite to intelligent sampling of the productivity and standing crop of algae. Some algae appear and disappear periodically without any dependence on preceding forms and contributing little to the environment that would aid colonization by other species of algae following them. Chief among these are Prasiola mexicana and Palmella Myosurus. Both of these algae appear to flourish on rock surfaces that were previously exposed during lower water levels; and, therefore, they usually do not succeed other algal communities. As Prasiola mexicana appears in abundance only during the recession of high spring water, observation of its growth on experimental surfaces is not feasible. Palmella Myosurus, however, is the first alga to colonize microslides and cleaned rocks placed on the stream bed during fall and winter.

Early attempts to learn about the succession and species composition of Logan River algae by the glass slide method (Butcher, 1931) were thwarted by overwhelming growths of Palmella Myosurus which were obviously not representative of the algae seeding on seasoned natural substrata.

A series of natural rocks from a dried section of river channel were scoured and placed on the river bed at Red Banks, Logan Cave, and Canyon Road. Set out in November, these rocks supported very dense growths of Palmella Myosurus by December which remained all winter in contrast to a lesser growth on natural rocks close by.

By the end of the spring flood, 8 months after placement, the cleaned rocks no longer supported Palmella Myosurus; but isolated patches of Shizothrix fasciculata appeared on all to varying degrees. No further algal growth was noticed then until the first cool nights of late September drove water temperatures down again. At this time Shizothrix fasciculata and Phormidium incrustatum made noticeable growth and continued to grow until December after which time the visible accumulation of crusts slowed down. During the winter months, 13 to 16 months after placement, the cleaned rocks at Canyon Road supported only isolated patches of Palmella Myosurus in contrast to the heavy growth of the previous winter. This algae was abundant at this time on new surfaces in the river. At this same time at Canyon Road, Vaucheria made its first appearance and produced a moderately heavy growth by April. The cleaned rocks at Canyon Road, however, were still conspicuous by virtue of their below-normal algal coverage when compared to the natural rocks on the stream bed. Bryophytes, although an important element of the plant community on old rocks at Canyon Road, were not present on the cleaned rocks 21 months after placement.

The cleaned rocks at Logan Cave and Red Banks supported a good growth of Palmella Myosurus during the second winter though less than that of the first winter. This alga had almost disappeared, however, before the beginning of spring high water at the upper 2 locations.

At the end of 21 months (August) on the river bed, the dominant algae on all cleaned rocks were encrusting blue-greens. Although the species composition was the same, the crusts at Canyon Road were more massive than those at either of the upper river stations. The heavy

growths of Vaucheria present before and after the runoff at Canyon Road were not present in August, but the crusts on the cleaned rocks were covered with short pieces of Vaucheria which were firmly embedded. Presumably this is the basis for the heavy regrowth of Vaucheria during winter at Canyon Road.

The late summer disappearance of much of the Vaucheria seems to be correlated with increased water temperatures. The situation with regard to quality and quantity of algae at Canyon Road was typical of that below other dams and power races on Logan River. It appears that the main effect of impoundments is that of removing molar agents and thereby allowing a longer succession of algae to occur. This hypothesis is supported by the observation that much of the crust deposited by blue-green algae in the middle river was worn away each year during the spring runoff in contrast to accumulations of several years at Canyon Road. The exceptions to this statement in the middle section occur on some large immovable boulders which maintain crusts deposited in previous years and in slower water near shore where very thick crusts often are confluent and join several rocks together.

RESULTS AND DISCUSSION

Amount and distribution of chlorophyll

The average amount of chlorophyll "a" present on a square meter of the bed of the middle section of Logan River was 0.30 grams (0.25 - 0.35 at 95 per cent confidence). Most of this was contained in algae supported by larger substratum units: rocks having a minimum dimension of 12 centimeters or greater. The 95 per cent confidence band for chlorophyll "a" per square meter of river bed occupied by this size category of rocks extended from 0.30 to 0.40 grams. Those rocks having a minimum dimension between 2.5 and 12 centimeters supported between 0.15 and 0.25 grams per square meter at the 95 per cent confidence level. Less than 6 per cent of all chlorophyll was supported by bottom materials having a minimum dimension smaller than 2.5 centimeters. No trend in average chlorophyll concentration was observable with distance from the river source within the middle section. Seasonal differences are discussed under methods.

Two stations on the lower Logan River supported a much higher standing crop of algae and consequently of chlorophyll "a" than did the middle section. This is probably due to reduction of the bed load by the 3 impoundments in the portion of the lower river with a steep gradient and to the lack of movement of potential molar material after the river reaches the valley. Two measurements, fall and spring, a short distance below the first impoundment (Canyon Road) yielded values of 0.75 and 1.42 grams per square meter respectively. The higher spring value here reflects heavy winter algal growth in lower portions of the river

in which anchor ice does not develop.

A canal diverted from the first impoundment supported 1.03 grams of chlorophyll "a" per square meter during mid-winter.

The benthic algae at Mendon Bridge contained .62 grams of chlorophyll "a" per square meter in one early spring measurement, the time of apparent maximum standing crop.

The preceding values may be compared to benthic determinations of .49 grams per square meter on a coral reef (Odum and Odum, 1955) and 2.95 grams at Silver Springs, Florida (Odum, 1957a).

The range of values of total plankton chlorophyll per square meter of surface in 5 Wisconsin lakes was 15 to 65 milligrams (lake areas: Kosminski, 1938) (chlorophyll content: Manning and Juday, 1941). The average chlorophyll content of these lakes was 32 milligrams per square meter of surface.

Chlorophyll crops on concrete "rocks" were measured to determine the effect of shading and diffusion on the standing crop produced from the end of one runoff period to the beginning of the next one. As all estimates of dry algal biomass would necessarily be derived from chlorophyll measurements, chlorophyll measurements alone are used as the criterion for comparison in the following discussion. From the standing crops of chlorophyll, productivity is also inferred, however, it must be admitted that increased rate of current attrition associated with a high past productivity would tend to decrease the range of standing crop values that might result if algal biomass had not been removed. It is conceivable that under some conditions equal standing crops could be produced in the same period by communities having wide differences in

productivity.

The effect of varying periods of insolation during the 7-month immersion of the artificial "rocks" is suggested in figure 14. Any regression of chlorophyll on light apparently occurs between 600 and 1,000 hours of insolation. More insolation does not appear to produce a proportionately greater crop of chlorophyll while less than 600 hours reduces the chlorophyll to a value that changes little from 600 hours to no insolation. At any single station the range of chlorophyll values at approximately equal durations of insolation varied so widely that a relationship was not clear. It is noteworthy, however, that artificially shaded concrete "rocks" supported only 25 to 50 per cent as much chlorophyll as normally insolated "rocks" at the same station did.

Although locations on the river bed were chosen randomly, the durations of insolation to which "rocks" at a station were subjected were surprisingly uniform when the "rocks" were not placed in artificial shade.

Analysis of the duration of insolation received during the 3 months immediately preceding the removal of the concrete "rocks" from the stream yielded a relationship essentially the same as that in figure 14 which is based on the full immersion period of 7 months.

The relative diffusion rates over the surfaces of the "rocks" were not convincingly relateable to the amounts of chlorophyll produced (figure 15). This was true among "rocks" at a station and between station averages of chlorophyll standing crop. Presumably the minimum rates of diffusion present were sufficient to entirely overcome local

Figure 15. Relationship between average relative diffusion rates over concrete "rocks" and standing crop of chlorophyll produced in 7 months. No values from rocks having chlorophyll crops limited by artificial shade are included in the analysis. Station codes are: Chokecherry, filled circles; Red Banks, crosses; Canyon Road, tailed open circles; Mendon Bridge, tailed filled circles.

depletion of nutrients. Butcher (1946) observed a more abundant growth of algae on glass slides that had been placed in the more rapid sections of the stream than those from slower water and discussed this phenomenon as a generality. The largest standing crops of chlorophyll, on artificial "rocks" and inferentially the highest productivities, in Logan River occurred in the slowest section of the river through chlorophyll at one of the more rapid sections almost equaled this growth. The productivity, based on oxygen production, of the third impoundment of Logan River is far greater than that of an equal area of the river above it or below it, though vascular plants are more important than algae here. In this habitat, velocities are very low. Back eddies and dead waters behind boulders of the middle river are observably less productive than rapid waters close by but this seems to be caused by cyclical deposition and scouring of fine bottom materials in these locations. Small, isolated, slow water areas in rapid streams suffer from heavy deposition of the coarse materials which rapid streams are capable of carrying. More permanent silted areas that occur where the level of the third impoundment causes the river to lose velocity are colonized effectively by Ranunculus. As pointed out by Blum (1956) river algae do not prosper on other than stony bottoms and generally seem more abundant in rapid water, but this observation cannot be extended to mean that rapid rivers are more productive than slow rivers. It is possible that apparently heavier growths of some algae in rapid water may be a reflection of their inability to compete in a mixed community where vascular plants might be highly productive. The lithophilic habit seems to be an example of arrested succession caused by the rigors of

rapid currents. This is the best explanation for the tendency of Palmella Myosurus in the middle Logan River to grow on flat boulders and bed rocks that are scoured by molar action during high water.

With the exception of the concrete "rocks" from Chokecherry, there was an increase in standing crop of chlorophyll with distance downstream. The Chokecherry situation was one of heavy shading; chlorophyll measurements of natural rocks in adjacent, more insolated situations indicate that concrete "rocks" placed in these areas might be expected to support a standing crop of chlorophyll at least as great as that of the station farthest upstream (Red Banks). The tendency for productivity to increase with distance from the source is difficult to attribute to any single factor measured.

Total dissolved solids and individual ions that were measured do not appear closely related to the average quantity of chlorophyll "a" on concrete "rocks" at a station (figure 13). The only ions that increased downstream at about the same rate that standing crop of chlorophyll did were sulfate and chloride. There is no logical reason to expect that these ions could have a beneficial effect on algae; however, dissolved substances in trace amounts, coming from the same source as sulfate and chloride, may have increased algal growth.

Turbidity was highest and lowest at the 2 stations having the highest standing crops of chlorophyll on concrete "rocks" as well as on natural rocks (figure 13). The effect of turbidity is not to be confused with that of the coarser bed load carried by the middle section above the impoundments. These molar materials are dropped out in the impoundments above Canyon Road and are not present at Mendon

Bridge because of reduced velocity.

Temperatures at the 4 stations at which the artificial "rocks" were located did not afford an explanation for the apparent higher productivity of the "rocks" at the lower stations. From October to the end of the experiment in March there were no notable temperature differences between stations (figure 12). Anchor ice was never present at the lower 2 stations, and this may have been partially responsible for the superior standing crops of chlorophyll here.

The evidence given here concerning the effects of the 2 principal variables at any river or stream station, current and shade, indicates that stratification of chlorophyll sampling based on these variables is generally not worthwhile. Differences between stations, however, were indicated. The 95 per cent confidence limits to the mean amount of chlorophyll at each of the 4 stations did not overlap indicating that differences in means were significant at this level. The fact that the means may definitely be considered as coming from different populations of chlorophyll bearing artificial "rocks" demonstrate their utility in evaluating the relative productive biomasses of habitats within a shallow river.

Chlorophyll based productivity

It appears that the maximum amount of chlorophyll in aquatic habitats occurs in benthic communities of moving water systems where the water itself or materials in suspension do not seriously decrease the radiation reaching the plant community.

While in the planktonic community of lakes, the placement of chlorophyll with respect to light is dependent on the caprice of

of currents; in streams it appears that the permanent location of chlorophyll of an adjusted benthic community is, to a much greater extent, a response to selection based on efficient use of radiation income. The term "adjusted" is used here to describe the situation wherein coverage and development in depth of an aquatic benthic community is such that little light reaches the substratum. Teleologically speaking, the liberal use of plant pigments to insure the maximum degree of absorption of light consistent with optimum efficiency is in line with the "development for maximum power output" theory of Odum and Pinkerton (1955). The members of a well-insolated benthic plant community which develop beneath those on the periphery are truly shade plants. Odum (1957a) has demonstrated that the highest chlorophyll content of rooted vascular plants in Silver Springs occurred an appreciable distance below the community open water interface. It is a reasonable assumption that the distribution of chlorophyll in this community and others is determined by the most efficient adjustment to remaining radiation at various depths within the plant mass. The typical communities of Logan River were not amenable to studies of chlorophyll distribution with thickness, but it was observable that a large proportion of the contained chlorophyll was present in the interior of Vaucheria mats and in crusts of the current season formed by blue-green algae.

Data of Kosminski (1938) concerning plankton chlorophyll distribution with water depth in several Wisconsin lakes may be interpreted to indicate that a transitory adjustment to efficient light use may occur but settling out and random redistribution by currents do not

allow such adjustment to become permanent or well developed.

An important conclusion from the foregoing discussion is the need to consider the community photosynthetic response rather than that of isolated benthic plants in bottle experiments. In experiments by Manning, Juday, and Wolf (1938) the general photosynthetic response of each of 5 benthic, aquatic plants (Sagittaria, Spirogyra, Potamogeton, Vallisneria, Cladophora) to increasing light intensities above 2,000 foot candles was different. If, however, we imagine a synthetic community composed of equal portions of each of these plants wherein each plant responded to increasing light intensities as it did in light bottles, the varying rates of photosynthesis would blend into a more predictable response curve which would approach saturation at about 2,000 foot candles and climb only slightly from that intensity to the highest intensities experienced. The photosynthetic rate of entire, natural Florida spring communities, in contrast, closely followed the curve of incident light intensity over the entire range (Odum, 1957b). Community photosynthetic response to light intensity in the third impoundment of Logan River resembled that in the springs (figure 16), the response curve of Silver Springs being similar to those of the other springs in shape if not magnitude. The response of individual members of these last mentioned communities, if subjected to the conditions of the experiment of Manning, Juday, and Wolf (light and dark bottles), might very well be similar to responses obtained in their experiment; but, in the community of which they were a part, conditions not duplicated in light and dark bottle experiments prevailed. Shading by other members of the community and orientation of the chlorophyll

Figure 16. Curves of photosynthetic response of divers, total aquatic communities to changes in solar altitude and consequent changes in incident energy. Curve A is the relative photosynthesis calculated for Atlantic plankton during 2 summer days (Ryther, 1956a); curve B, Weber Lake plankton (Manning and Juday, 1941); curve C, Silver Springs benthos (Odum, 1956); curve D, benthos of third impoundment of Logan River; and curve E, benthos of canal diverted from the first impoundment of Logan River. A symmetry of benthic curves is probably due to unequal morning and afternoon shading.

with respect to the incident light are seldom duplicated in such experiments with benthic plants. Observation of the third impoundment community in Logan River revealed that plants in the interior of Anacharis mats did not receive direct insolation until the sun was high in the sky. At this time it is conceivable that plants on the periphery of the mat were photosynthesizing at a reduced rate but the net effect was a community rate of photosynthesis higher than that at lower solar altitudes. Further evidence for a close relationship between community photosynthesis and all intensities of insolation may be found in plankton data. Chlorophyll based rates of photosynthesis at several depths during 1-hour increments of the insolated day were determined by Manning and Juday (1941) for the Weber Lake plankton community. From these it was possible to calculate the average chlorophyll based rate of photosynthesis in a column of water from surface to bottom at each hour of the insolated day. When these values are plotted against the corresponding time of day, a rate-of-production curve shaped like the one for the third impoundment of the Logan River is obtained (figure 16). When data of Ryther (1956a) for marine plankton are considered similarly (relative photosynthesis weighted by relative volume of water) the resulting curve also reflects the tendency for total community photosynthesis to increase with increasing solar altitude or incident light intensity (figure 16) despite a very pronounced depression of surface photosynthesis during midday. Edmondson (1956), in discussing light use by plankton communities, considers the noontime suppression of plankton photosynthesis in shallow, clear lakes but does not mention the probability that the benthic community would be

well developed in shallow, clear lakes.

The encrusting community of the middle section of Logan River appears similarly subject to rates of photosynthesis different than those of isolated member plants or species closely related to member plants (table 2). That the low chlorophyll based rates of photosynthesis of the encrusting community were not entirely artifacts of the confinement in still water of a moving water community is indicated by the higher rates of photosynthesis of individual algae removed from the natural substratum and suspended in still water. In contrast to detached plants, the rock-supported encrusting communities placed in the experimental jars in their entirety did not maintain their contained chlorophyll in the full intensity of the incident light. The rock supporting the algae shaded a portion of the community and the algae themselves produced a gradient of light within their mass. The effect of development in depth is probably one of reduced chlorophyll based photosynthesis rate but enhanced efficiency in use of incident radiation. Outdoor experiments with Chlorella indicate that algae not exposed to maximum incident light intensity used light more efficiently than algae that were, despite a lowered rate of photosynthesis (Wassink, 1954).

The low rates of photosynthesis determined for the encrusting community of Logan River are probably partially due to the reduced diffusion rate of still water being imposed on algae made compact in growth habit by adaptation to swift currents. These rates probably represent minimum values and will be referred to as such in this paper. Gessner (1937) increased photosynthesis by increments of up to 33 per cent when he agitated bottles containing vascular aquatic plants.

Community chlorophyll based rates of photosynthesis may be calculated from published data by considering all the chlorophyll in the community and the entire insolated period. By using the stated average dry weight of algae biomass and applying the chlorophyll equivalent given, a weight of chlorophyll of 0.49 grams per square meter can be arrived at for Eniwetok Atoll (Odum and Odum, 1955). If the glucose production of 24 grams per square meter per day is then corrected to an oxygen production of 26 grams per day for the same area, an estimate of 4.4 grams of oxygen per gram of chlorophyll per hour of the insolated day will be had. An estimate of 0.5 grams of oxygen per gram of chlorophyll per hour can be calculated for Silver Springs (Odum, 1957a). Data of Manning and Juday (1941) for Weber Lake can be used to arrive at an estimate of 3.5 grams of oxygen per gram of chlorophyll per sunlight hour. These are all values for a midsummer day and presumably are maximal. Because partial agitation of 1 light and dark bottle experiment with a portion of the encrusting community from Logan River increased photosynthesis by about 40 per cent (table 1, February 6) and in light of a similar experience by Gessner (1937), it is inferred that the real rate of photosynthesis in Logan River was about 30 to 50 per cent higher than the average value of 0.7 grams of oxygen per gram of chlorophyll per insolated hour obtained. A value of 0.1 appears reasonable in making productivity estimates.

The estimated total amount of chlorophyll "a" on the 31.7 hectares of river bottom sampled (79 acres) was 95 kilograms $\pm$ 19 kilograms at the 95 per cent confidence interval.

Average duration of insolation on the upper river (based on

measurements at 6 random situations on the river bed at each of 2 typical locations) was about 1,900 hours per year. In addition to this there were about 500 hours of bright shade during which photosynthesis probably proceeded at one-half the rate in sunlight. This increment was incorporated in the estimate by adding one-half of 500 hours to 1,900 hours.

The actual estimate of yearly gross primary production for the middle section of Logan River may then be computed thusly: (1.0 kilograms of oxygen per kilogram of chlorophyll "a" per hour of insolation) (95 kilograms of chlorophyll "a") (2,150 hours of insolation) = 204,250 kilograms of oxygen per year.

Cloudiness was not considered in the estimate of duration of insolation. The winter of 1956-1957 and the spring of 1957 had an above-average number of cloudy days. Actually about 30 per cent of the days from December to June had cloud cover that intercepted a significant part of the incident radiation. Concentration of oxygen in excess of the saturation value, in a canal diverted from Logan River, on a cloudless winter day was about twice the comparable value measured on an average cloudy day. The rate of photosynthesis in 1 light and dark bottle experiment (table 2) on an average cloudy day in summer was also about half the rate on cloudless days.

From the foregoing discussion it might be inferred that photosynthesis on about 16 per cent of the days of the year of productivity measurement was proceeding at 50 per cent of the rate achieved on cloudless days. Since the probable discrepancy was only 8 per cent of the total productivity estimate, the effect of cloudiness was dismissed.

By converting the upper Logan River gross primary production estimate to a rate of production, a comparison can be made with 3 other sections of Logan River and 3 other published values or range of values (table 1). The estimate for the third impoundment is not corrected for diffusion loss. Although low in gross, primary productivity when compared to other moving water habitats the value for Logan River is of the same order of magnitude as a relatively productive lake. This seems anomalous to one who has observed the apparently much greater profusion of life in eutrophic lakes than that present in mountain rivers. Perhaps the explanation lies in the conservation of organic production in lakes by its incorporation in the substratum.

The high figure for the third impoundment of Logan River is in accord with the reputation that all 3 Logan River impoundments have for production of brown trout. Rooted vascular aquatics, Ceratophyllum and Anacharis, are the preponderant producers in this sluggish river type of environment.

Net productivity and standing crop

If we accept Verduin's estimate (1956) of the percentage of gross primary productivity available for growth (20 per cent), the carbon used for growth in the middle Logan River is about 16,000 kilograms. Ryther (1956) summarizes evidence indicating that carbon comprises close to 50 per cent of the ash-free dry weight of algae. A yearly net production of 32,000 kilograms of dry plant material minus ash may therefore be calculated for the middle section of Logan River.

If it is desired to compare this value with the average standing crop, it is necessary to consider the methods available for estimating

the standing crop in Logan River. Direct weighing of the algae was not possible because of the presence of large quantities of calcium carbonate in the community. Ash-free dry weight could not be determined because the heat necessary to ash the organic matter would also change some calcium carbonate to the oxide and thereby add inorganic carbon to the ash-free dry weight. The chlorophyll-dry weight ratio, therefore, seemed most useful for extensive sampling.

The use of chlorophyll content to estimate plant biomass is subject to errors caused by variation in the chlorophyll-dry weight ratio. Rabinowitch's tabulation (1945) of proportions of chlorophyll "a" determined by several investigators to be in green and blue-green algae indicates a range of 0.09 per cent to 2.00 per cent of the dry weight. If laboratory cultures (*Chlorella*) are excluded, the range is reduced. During the course of the present investigations the range of the proportion of chlorophyll "a" in some algae of Logan River and vicinity was from 0.14 per cent to 2.4 per cent (table 3).

Because the species composition and condition of senescence of algal communities were observable in communities sampled from Logan River, it was possible to use the applicable chlorophyll-dry weight ratio correlated with species composition and condition or an approximate weighted average of applicable values in estimating the dry plant biomass. In the middle section of Logan River, a weighted average (1.15 per cent) of the values for Vaucheria, Oscillatoria (a substitute for encrusted blue-green algae) and young Palmella Myosurus was used.

The estimated, average, dry plant biomass of the middle section was 8,000 kilograms. No correction was made for ash in the dry weight

Table 3. Chlorophyll "a" content of several algae from Logan River and vicinity

Algae	Remarks	Per cent chlorophyll "a" based on dry weight
<u>Cladophora glomerata</u>	February	0.55
	March	0.66
	March	0.71
	March	0.71
<u>Palmella Myosurus</u>	February - vigorous	0.98
	March - senescent	0.14
	March - senescent	0.17
	March - senescent	0.15
<u>Vaucheria</u>	February	0.70
	March	1.08
	March	1.06
	March	1.01
<u>Lyngbia & Chlorotylum</u>	From aquarium	2.40
<u>Oscillatoria</u>	From artesian standpipe	1.50
<u>Oscillatoria</u>	From artesian standpipe	1.30

of algae used to determine the chlorophyll-dry weight relationship. If an arbitrary correction of 10 per cent ash is used, the average standing crop is equal to 22 per cent of the ash-free dry weight of yearly net production. The relatively low turnover rate of the standing crop, $4\frac{1}{2}$ times per year, is probably an artifact of underestimation of the productivity of chlorophyll in the community. In addition, low temperatures may have caused net productivity to comprise a larger share of gross productivity than was estimated.

It is interesting to compare the relative proportions of dry weight of producers, herbivores and carnivores in Logan River to those of Eniwetok Atoll as measured by Odum and Odum (1955). By assuming that the dry weights of insects and fish in Logan River are equal to 20 per cent of the fresh weight, we may proceed with the comparison. The dry weight of herbivores in Logan River (insects) amounted to 5 per cent of the producer weight, a value considerably smaller than the Eniwetok value of 18.9 per cent. The dry weight of carnivores in both habitats rounded to the same value: 1.6 per cent of the producer crop which was algae at both places. The trophic structure of Silver Springs, (Odum (1957a) using producer weight as a basis, was 4.6 per cent herbivores and 1.5 per cent carnivores: figures very close to those of the middle section of Logan River.

SUMMARY AND CONCLUSIONS

1. Satisfactory chlorophyll extractions of encrusting algal communities were made by immersing entire rocks supporting the algae in acetone. Some algae were difficult to extract by merely soaking in acetone.
2. Chlorophyll was sampled on the middle section of Logan River by random selection of algae-bearing rocks at 18 stations. About 150 rocks were sampled. Stratification of the sampling was based on size classification of bottom material.
3. No significant difference existed between means of chlorophyll samples in fall and late winter and between the middle section above and below the Dugway.
4. Concrete "rocks" were found to be useful in measuring relative standing crops of chlorophyll.
5. The rate of dissolution of sodium chloride tablets was used as an index of rate of diffusion close to the algal communities.
6. Wide angle photographs of the celestial hemisphere made it possible to estimate the effect of shading on specific habitats for an entire year with 1 visit.
7. Chlorophyll based rates of photosynthesis were based on light and dark jar experiments with algae from Logan River and on other published rates.
8. The middle section of Logan River, the part of principal interest, flows over a bed of rubble and boulders with few areas of

fine sediments.

9. Due to a retentive watershed, the runoff of Logan River is gradual. Lowest water levels in late winter do not fall much below levels at the end of the runoff in summer. Turbidities exceeding 10 parts per million occur only at the beginning of the runoff over most of the river.

10. The middle section of Logan River is 18 miles long, has an average width of 36 feet and an average depth of 10 to 16 inches.

11. Current velocities 3 inches over the river bed range from 0.75 to 2.5 feet per second on the middle section during normal water levels.

12. Relative rates of diffusion varied considerably from point to point over the bed of most of the river. They were very uniform, however, at 1 station near the end of the river in the valley.

13. About 44 per cent of the possible hours of insolation fall on the middle section of Logan River. One valley station received about 65 per cent. Mountains and trees are the chief interceptors of insolation.

14. Ions in solution in Logan River are preponderantly bicarbonate, calcium, and magnesium.

15. Trout and whitefish are the preponderant top carnivores in Logan River. Sculpins are numerous but relatively unimportant on a weight basis.

16. The dominant herbivores are the larvae of diptera, ephemeroptera, trichoptera, and plecoptera.

17. The plant community is entirely one of algae with the exception of occasional bryophytes. Encrusting blue-greens, Vaucheria, Prasiola

mexicana, Palmella Myosurus, Cladophora, diatoms and Nostoc dominate.

18. A downstream change in quality and quantity of algae was interpreted as linear succession, but it was not without exception. Colonization of new surfaces followed a fairly definite order and took at least several months to produce a relatively stable community or one which was periodically extirpated by seasonal habitat changes.

19. The average quantity of chlorophyll per square meter of bottom of the middle section was 0.30 grams. Downstream supplementary stations supported 3 to 4 times as much chlorophyll as the middle section.

20. Chlorophyll based rates of photosynthesis were estimated to average near 1.0 gram of oxygen per gram of chlorophyll "a" per hour for 2 to 3 hour segments of the insolated day.

21. Gross primary production equal to about 0.6 kilogram per meter squared per year was measured on the middle section. Production in an impoundment and at supplementary stations on the lower river was 5 to 7 times this figure.

22. The annual net product of photosynthesis was estimated to be about 32,000 kilograms on the middle section. The average standing crop was about 22 per cent of annual net production.

23. Measurement of chlorophyll produced on 9 artificial "rocks" at each of 4 stations and of diffusion rates, insolation, turbidity, and water chemistry to which each rock was subjected was accomplished. No strong correlation was noted with any 1 of the factors measured and chlorophyll produced. Downstream increase in chlorophyll crop was postulated to be due to decrease in molar action, reduction of ice conditions, and possible increase in unmeasured, dissolved solids in trace amounts.

LITERATURE CITED

- Badcock, R. M. 1949. Studies in stream life in tributaries of the Welsh dee. *Jour. Anim. Ecol.* 18:193-208.
- Blum, J. L. 1956. The ecology of river algae. *The Bot. Rev.* 22: 291-341.
- Butcher, R. W. 1932. An apparatus for studying the growth of epiphytic algae with special reference to the River Tees. *Trans. North. Naturalists' Union* 1:1-15.
- Butcher, R. W. 1932. Studies in the ecology of rivers. II. The microflora of rivers with special reference to the algae on the river-bed. *Ann. Bot.* 46:813-861. Pls. 33, 34.
- Butcher, R. W. 1940. Studies in the ecology of rivers. IV. Observations on the growth and distribution of the sessile algae in the River Hull, Yorkshire. *Jour. Ecol.* 28:210-223.
- Butcher, R. W. 1945. Studies in the ecology of rivers. VI. Algal growth in certain highly calcareous streams. *Jour. Ecol.* 33:268-283.
- Butcher, R. W. 1947. Studies in the ecology of rivers. VII. The algae of organically enriched water. *Jour. Ecol.* 35:186-191.
- Clark, W. J. 1957. The drift algae of a mountain stream: Logan River. Unpub. Phd. Thesis, U.S.U. Lib., Logan, Utah.
- Davis, F. J. 1941. Surface loss of solar and sky radiation by inland lakes. *Trans. Wis. Acad. Sci. Arts Letters.* 33:83-93.
- Duxbury, A. C., and C. S. Yentsch. 1956. Plankton pigment nomographs. *Jour. Mar. Res.* 15:92-101.
- Edmondson, W. T. 1955. Factors affecting productivity in fertilized salt water. *Pap. Mar. Bio. & Oceanogr. Deep-sea Res. Suppl. to Vol.* 3:451-463.
- Edmondson, W. T. 1956. The relation of photosynthesis by phytoplankton to light in lakes. *Ecology* 37:161-174.
- Evans, G. C. 1956. An area survey method of investigating the distribution of light intensity in woodlands, with particular reference to sun flecks. *Jour. Ecol.* 44:391-428.

- Fleener, G. C. 1951. Life history of the cutthroat trout Salmo clarki Richardson, in Logan River, Utah. Trans. Amer. Fish. Soc. 81:235-248.
- Fritsch, F. E. 1929. The encrusting algal communities of certain fast-flowing streams. New Phytol. 28:165-196. Pl. 5.
- Fritsch, F. E. 1950. Phormidium incrustatum (Nag.) Gom., an important member of the lime-encrusted communities of flowing water. Biol. Jaarboek 17:27-39. Pl. 1, 2.
- Gessner, F. 1937. Untersuchungen uber assimilation and atmung submer-ser wasser pflanzen. Jb. Wiss Bot. 85:267-328.
- Hales, D. C. 1955. Evaluation of stream bottom fauna sampling techniques as used in the Logan River. Unpubl. M. S. Thesis, U.S.U. Lib., Logan, Utah.
- James, H. R., and E. A. Birge. 1938. A laboratory study of the absorption of light by lake waters. Trans. Wis. Acad. Sci. Arts Letters. 31:1-154.
- Jones, H., and J. R. Erichsen. 1949. A further ecological study of calcareous streams in the Black Mountain district of South Wales. Jour. Anim. Ecol. 18:142-159.
- Jones, H., and J. R. Erichsen. 1950. A further ecological study of the River Rheidol. Jour. Anim. Ecol. 19:159-174.
- Jones, H., and J. R. Erichsen. 1951. An ecological study of the River Towy. Jour. Anim. Ecol. 20:68-86.
- Kosminski, Z. 1938. Amount and distribution of the chlorophyll in some lakes of northeastern Wisconsin. Trans. Wis. Acad. Sci. Arts Letters. 31:411-438.
- Krauss, R. W. 1956. Photosynthesis in the algae. Indust. and Engineer. Chem. 48:1449-1458.
- Manning, W. M., C. Juday, and M. Wolf. 1938. Photosynthesis of aquatic plants at different depths in Trout Lake, Wisconsin. Trans. Wis. Acad. Sci. Arts Letters. 31:377-410.
- Manning, W. M., and R. E. Juday. 1941. The chlorophyll content and productivity of some lakes in northeastern Wisconsin. Trans. Wis. Acad. Sci Arts Letters. 33:363-393.
- Odum, H. T., and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr. 25:291-320.

- Odum, H. T., and R. C. Pinkerton. 1955. Times speed regulator: the optimum efficiency for maximum power output in physical and biological systems. *Amer. Scient.* 43:331-343.
- Odum, H. T. 1956. Primary production in flowing waters. *Limnol. and Oceanogr.* 1:102-117.
- Odum, H. T. 1957a. Trophic structure and productivity of Silver Springs, Florida. *Ecol. Monogr.* 27:55-112.
- Odum, H. T. 1957b. Primary production measurements in eleven Florida springs and a marine turtle-grass community. *Limnol. and Oceanogr.* 2:85-97.
- Ostle, B. 1954. Statistics in research. Ames, Iowa. The Iowa State College Press. 407 pp.
- Patrick, Ruth. 1949. A proposed biological measure of stream conditions based on a survey of the Conestoga Basin, Lancaster County, Pennsylvania. *Proc. Acad. Nat. Sci. Phila.* 101:277-344.
- Rabinowitch, E. I. 1945. Photosynthesis and related processes. Vol. I. New York: Interscience. 599 pp.
- Rabinowitch, E. I. 1951. Photosynthesis and related processes. Vol. II (1):603-1208. New York: Interscience.
- Rabinowitch, E. I. 1956. Photosynthesis and related processes. Vol. II (2):1210-2088. New York: Interscience.
- Reese, Mary J. 1937. The micro flora of the non-calcareous streams Rheidol and Melinder with special reference to water pollution from lead mines in Cardiganshire. *Jour. Ecol.* 25:385-407.
- Ruttner, F. 1954. Fundamentals of limnology. Univ. of Toronto Press. 242 pp.
- Ryther, J. H. 1956a. Photosynthesis in the ocean as a function of light intensity. *Limnol. and Oceanogr.* 1:61-70.
- Ryther, J. H. 1956b. The measurement of primary production. *Limnol. and Oceanogr.* 1:72-84.
- Sigler, W. F. 1951. The life history and management of the mountain whitefish Prosopium williamsoni (Girard) in Logan River, Utah. *Utah Agr. Exp. Sta. Bull.* 347. 21 pp.
- Snedecor, G. W. 1946. Statistical methods. Ames, Iowa. Iowa State College Press. 485 pp.
- Verduin, J. 1956. Primary production in lakes. *Limnol. and Oceanogr.* 1:85-91.

- Wassink, E. C. 1954. Mass culturing of algae in relation to the world energy situation. Pp. 247-270 in Autotrophic Micro-organisms. Cambridge. University Press.
- Weems, P. V. H. 1941. Line of position book. Weems System Publications. Annapolis, Md. 8 pp.
- Whitney, L. V. 1938. Continuous solar radiation measurements in Wisconsin lakes. Trans. Wis. Acad. Sci. Arts Letters. 31:175-200.
- Williams, J. S. 1948. Geology of the Paleozoic rocks, Logan quadrangle, Utah. Bull. Geol. Soc. Amer. No. 59:1121-1154.
- Zarbock, W. M. 1951. Life history of the Utah sculpin, Cottus bairdi semiscaber (Cope). Trans. Amer. Fish. Soc. 81:249-259.