Primary productivity of the Madison River in Yellowstone National Park, Wyoming
by Elston Herbert Todd

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Botany
Montana State University

Abstract:
An investigation of the downstream decrease in productivity of the Madison River in northwestern Yellowstone National Park was carried out in an effort to determine the correlation among primary,productivity, current velocity, water temperature, light, carbon dioxide concentration, time of day and reach of the river.

Seasonal, daily,and downstream variation in primary productivity over a 14-mile reach of the river was determined by harvesting the standing crop of macrophytes; measuring changes in carbon dioxide concentration; and determining chlorophyll concentration.

Statistical analysis using photosynthesis as the dependent variable and carbon dioxide concentration, light, water temperature, and current velocity as the independent variables, showed carbon dioxide concentration to have the highest partial correlation coefficient followed in decreasing order by temperature, light and velocity.

It was concluded that the downstream decrease in carbon dioxide concentration was of primary importance in accounting for the downstream decline in primary productivity of the river.

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ELSTON HERBERT TODD

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree

of

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Approved:

Head, Major Department

Chairman, Examining Committee

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ABSTRACT

An investigation of the downstream decrease in productivity of the Madison River in northwestern Yellowstone National Park was carried out in an effort to determine the correlation among primary productivity, current velocity, water temperature, light, carbon dioxide concentration, time of day and reach of the river.

Seasonal, daily and downstream variation in primary productivity over a 14-mile reach of the river was determined by harvesting the standing crop of macrophytes; measuring changes in carbon dioxide concentration; and determining chlorophyll concentration.

Statistical analysis using photosynthesis as the dependent variable and carbon dioxide concentration, light, water temperature, and current velocity as the independent variables, showed carbon dioxide concentration to have the highest partial correlation coefficient followed in decreasing order by temperature, light and velocity.

It was concluded that the downstream decrease in carbon dioxide concentration was of primary importance in accounting for the downstream decline in primary productivity of the river.

INTRODUCTION

Until recent years, investigations of primary production in bodies of water dealt almost exclusively with lakes, ponds and seas. With the possible exception of Butcher (1927, 1932a, 1932b, 1933, 1940, 1945, 1947, 1948), whose research pertained primarily to the ecology and taxonomy of English rivers, flowing waters were almost entirely ignored. Recently, however, methods were outlined (Odum, 1956) and demonstrated (Sargent and Austin, 1949, Odum and Odum, 1955, Odum, 1957a, Odum, 1957b) for the effective study of the metabolism of rivers, streams, and other moving masses of water. Since the publication of these exploratory works, there has been a significant increase in investigations of the biology of running water (Odum and Hoskin, 1957, Hoskin, 1959, McConnel and Sigler, 1959, Edwards and Owens, 1960, Owens and Edwards, 1961, Edwards and Owens, 1962, Owens and Edwards, 1962, Copeland and Duffer, 1964, Owens, Edwards and Gibbs, 1964, Kevern and Ball, 1965, Duffer and Doris, 1966).

The Madison River in northwestern Yellowstone National Park, Wyoming, offers an ideal opportunity for the study of an unpolluted stream in which there is a continual decrease in productivity from its headwaters to a point about 14 miles downstream.

The purpose of the present investigation was to determine quantitatively the primary productivity of the Madison River and to compare the measurements with standing crops of macrophytes and periphyton, light, temperature, carbon dioxide concentration, and current velocity utilizing three methods: (1) harvesting the standing crop of macrophytes, (2) measuring the changes of carbon dioxide concentration, and (3) determining chlorophyll concentration. The results are examined to determine what correlation exists among primary productivity, current velocity, water temperature, light, CO_2 concentration, time of day and reach of the river.

The present investigation is one of a group of investigations supported by Public Health Service Research Grant WP-00125 and Training Grant 5T1-WP-1 from the division of Water Supply and Pollution Control.

DESCRIPTION OF THE STUDY AREA

At an elevation of 2,080.6 m (6,826 ft) the Madison River is formed by the union of the Firehole and Gibbon Rivers which serve as the drainage of numerous hot springs and geysers in a northwestern portion of Yellowstone National Park. Allen and Day (1935) estimated that the total amount of thermal waters flowing into the Firehold River was 1.55 m^3/sec (54.92 ft^3/sec) and that thermal discharge into the Gibbon River amounted to 0.19 m^3/sec (6.85 ft^3/sec).

The Madison River flows in a westerly direction throughout the study area (Figure 1). For the first 9.7 km (6 mi) it passes through a deep canyon with cliffs and hills of welded tuff on its north and more rugged cliffs and talus slopes from the rhyolite flows of the Madison Plateau to its south. After the river leaves the canyon, it flows through an area of decomposed rhyolite and tuff.

The river bottom is variable, consisting of boulders, large to small cobble, coarse to fine gravel, sand and silt. These may be either cemented together or resting loosely on the bedrock material.

The width of the river ranges from about 25.9 m (85 ft) to about 67.1 m (220 ft) with an average of about 44.5 m (146 ft). The depth varies seasonally and at different loca-

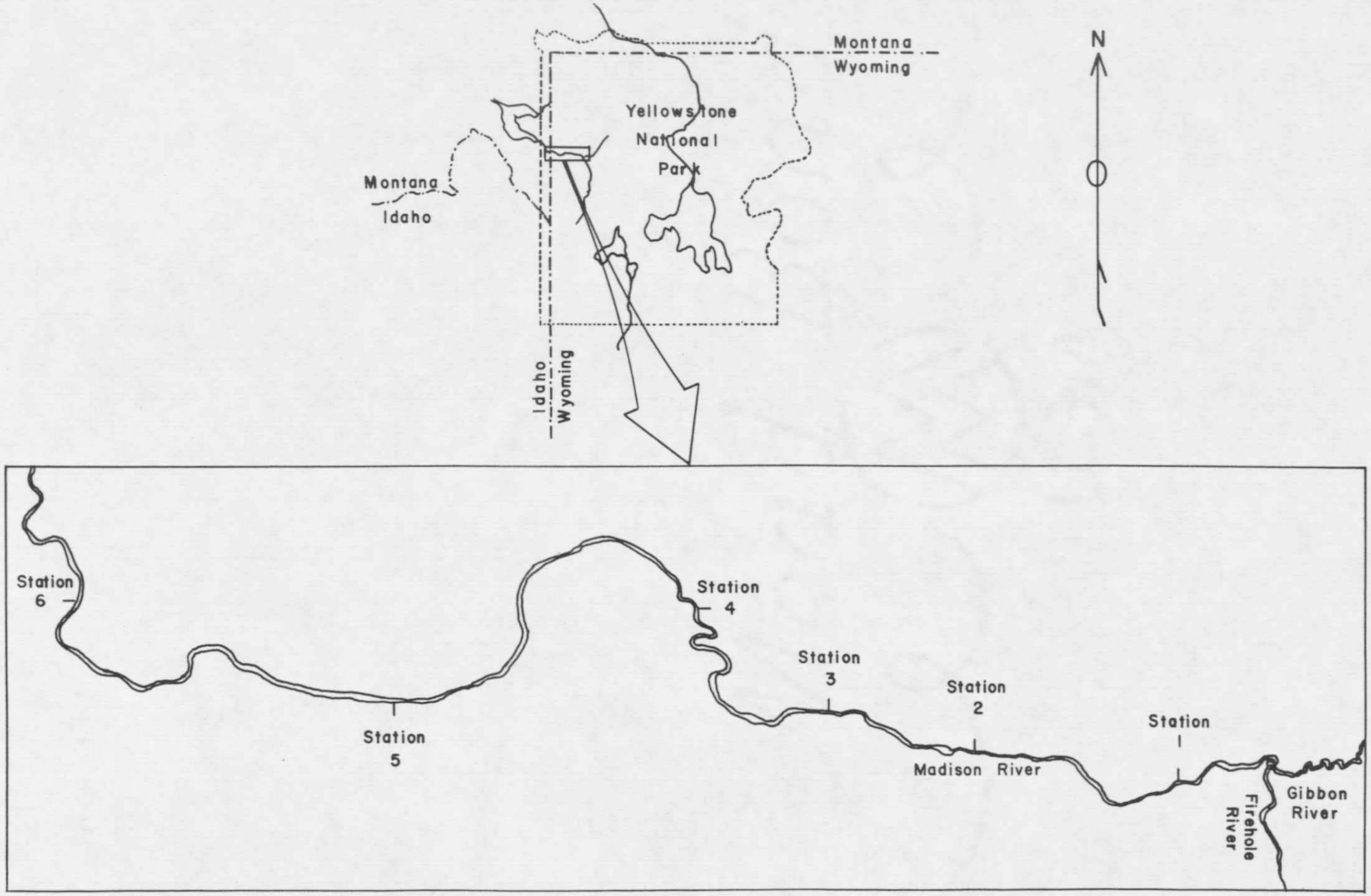

Figure 1: Map of Yellowstone National Park showing location of study area and stations.

tions within the study area. The depth at the most shallow point during dry weather is about 0.2 m (0.5 ft) while the deepest point during the period of greatest runoff is nearly 3.1 m (10 ft). Average depth is about 0.8 m (2.5 ft).

According to the Surface Water Records of Montana (1963-1964), the rate of discharge from the river normally fluctuates between a winter minimum of about 8.5 m^3/sec (300 ft^3/sec) and a spring maximum of about 43.9 m^3sec (1550 ft^3/sec). The extremes recorded are a maximum of 60.9 m^3/sec (2,150 ft^3/sec) on May 24, 1956, and an estimated minimum of 2.8 m^3/sec (100 ft^3/sec) on February 7, 1933. The average discharge over a forty-nine year period was 13.4 m^3/sec (473 ft^3/sec). Maximum discharge usually occurs during late May and early June, at which time the heaviest rainfall of the region coincides with the spring runoff from the heavy snows which cover this mountainous area.

Concentrations of various ions remain quite constant throughout the study area, but show seasonal variation. Chemically, the water is a sodium-bicarbonate-chloride type, with silica concentration remaining close to the saturation level of the water. Calcium and magnesium are present only in small amounts (Roeder, 1966).

Six stations were located on the stream, separating the river into five reaches. Station one was located at the National Park Service pullout designated, "Wild Animals at Home," 1.6 km (1 mi) from the confluence of the Firehole and Gibbon Rivers. At this station, long strands of aquatic macrophytes in dense stands covered about 85% of the substrate. Chara vulgaris was the most abundant plant, but there were conspicuous amounts of Potamogeton filiformis and P. strictifolius as well as Berula erecta. The plants grew from the silt, fine to coarse sand and fine gravel of the river bottom. Mixtures of coarse gravel and cobble up to about 7.6 cm (3 in) in diameter were exposed in scattered patches.

Station two was situated at a National Park Service pullout entitled, "Mt. Haynes," 3.3 km (2.04 mi) below station one. At this point, the vegetation was dense, but there was a smaller percent of the substrate covered by the plants than at station one. Chara and Potamogeton, the co-dominant genera at this station occurred on about 70% of the substrate, but there were large areas of exposed rubble.

Station three was established 2.6 km (1.60 mi) downstream from station two. At this location, the vegetation was less dense than at the preceding stations, but was still present in strands 0.6 to 0.9 m (2 to 3 ft) long. Chara vulgaris made up about 50% of the vegetative cover. The remainder consisted primarily of Sparganium chlorocarpum, Berula erecta and Glyceria borealis in about equal quantities. There were scattered boulders ranging in size from about 0.9 m (3 ft) to 1.8 m (6 ft) in diameter, but the major portion of the exposed river bottom was made up of coarse gravel and rubble.

Station four was situated about 9.1 m (10 yd) upstream from the 7 Mile Bridge, 3.3 km (2.03 mi) below station three. Less than 50% of the substrate of sand, gravel and cobble was covered by the vegetation. Chara vulgaris was the dominant macrophyte with Sparganium chlorocarpum and Myriophyllum exalbescens present in significant quantities.

Station five was located at the National Park Service pullout designated, "Riverside Soldier Station," 5.1 km (3.19 mi) below station four. The sparse vegetation consisted mainly of the mosses Hygroamblystegium fluviatile and Fissidens grandifrons with significant amounts of Chara vulgaris, Glyceria borealis and Berula erecta. The river bottom included sand, gravel, and small boulders and large slabs of exposed bedrock.

Station six was established at the old Riverside Ranger Station 5.1 km (3.16 mi) downstream from station five. About 90% of the river bottom supported no vegetation and consisted of unconsolidated cobble 7.6 to 15.2 cm (3 to 6 in) in diameter, small boulders 30.5 to 45.7 cm (12 to 18 in) in diameter, and a few scattered patches of coarse sand and fine gravel. The meager vegetation was dominated by the mosses, *Hygroamblystegium fluviatile* and *Fissidens grandifrons*, but *Myriophyllum exalbescens* and *Berula erecta* were conspicuous.

METHODS

Carbon Dioxide Concentration

Water samples were obtained from the six river stations at weekly intervals from May 15, to October 30, 1965. On each sampling date, collections were made every three hours at each station, commencing at 0600 hours and proceeding through 0600 hours the following day. All samples were collected in one-liter polypropylene plastic screw-cap bottles which were rinsed twice before being filled with the water sample.

Immediately upon return to the field laboratory, pH measurements were made with a Beckman Model 76 Expanded Scale pH meter. Alkalinity was determined for each set of samples at six hour intervals. The titrations were made on 100 ml of water with 0.1 N hydrochloric acid, using methyl orange as an indicator (Rutner, 1965).

Upon return to the laboratory at Bozeman, Montana, pH changes were correlated with carbon dioxide changes according to the method of Beyers *et al.* (1963).

A series of graphs was produced for each sampling date by first plotting the carbon dioxide concentration at station one as the ordinate against the time of collection as the abscissa. The carbon dioxide concentration of each successive station was displaced to the left by a time interval equivalent to the flow time from station one to the station whose data was being plotted.

By plotting the curves in this manner, the vertical distance between two curves corresponded to the carbon dioxide change during the time required to flow through the reach.

The change in carbon dioxide concentration per unit volume per minute from one station to the succeeding one downstream was determined by dividing the change in carbon dioxide concentration per unit volume by the flow time between stations. By multiplying this value by the average depth of the water between the two stations, the rates of change were converted to a unit area basis.

Concentration as parts per million (ppm) of free carbon dioxide for each collection time at each station was calculated by converting the milliequivalents per liter total alkalinity to parts per million alkalinity as HCO_3^- according to the equation derived by Rainwater and Thatcher (1960):

$$\text{ppm } CO_2 = 1.589 \times 10^6 \, [H+] \times \text{ppm alkalinity as } HCO_3^-$$

The concentration in ppm CO_2 was then converted to the equivalent molar concentration per cubic meter.

The exchange coefficient (k) between free carbon dioxide of the water and that of the atmosphere was computed by dividing the areal rate of change of carbon dioxide in a reach by the difference in concentration of free CO_2 between the water and atmosphere. The computation was made using only the measurements from the samples collected at 2100, 2400 and 0300 hours as pH curves indicated that respiratory rates were minimal at these times. The exchange coefficients calculated for these three sample periods were averaged to produce the values utilized in later calculations.

An exchange coefficient was not calculated for the reach between stations one and two in the above described manner because a few hundred yards above station one, a small hot spring discharged water greatly enriched with carbon dioxide into the river, thus distorting the measurements utilized in determining this parameter. Physical and biological characteristics of the reach between stations one and two and those between stations two and three were so similar that the exchange coefficient computed for the reach between stations two and three was also utilized for the reach between stations one and two.

The change in carbon dioxide due to biological factors was calculated by use of the equation:

$$R = C_c - k(C_f - C_a)$$

where C_c is the change in carbon dioxide concentration per unit area per minute, k is the CO_2 exchange coefficient, C_f is the concentration of free carbon dioxide in the river water, and C_a is the concentration of atmospheric carbon dioxide.

Hydrology and Morphometry

Discharge measurements were obtained from the rating table for the stream gaging station maintained by the U.S. Geological Survey near station six.

Flow times between consecutive stations were measured by introducing a few cubic centimeters of rhodamine-B dye into the main current at the upstream station. The passage of the mass of water into which the dye was introduced was detected fluorometrically at the succeeding downstream station by pumping water through a Turner Fluorometer, Model 110, equipped with a continuous flow cell and recorder. The time which elapsed between the introduction of the dye at the upstream station and the recorded passage of the peak dye concentration at the downstream station was considered to be the flow time between the two stations.

This procedure was repeated for several different river stages. Flow times were plotted against river stage and flow times for water levels intermediate to those measured were calculated from the graphs.

Current velocity was determined by dividing the flow times between stations into the distance separating the stations.

Areas of river reaches were measured by planimetry from aerial photographs.

Solar Radiation

Solar radiation was determined with a recording Eppley Pyroheliometer that was mounted on top of the laboratory at station six.

Temperature

While each sample was being collected, the temperature of the river water was measured with a standard laboratory thermometer.

Standing Crop of Macrophytes

The standing crop of macrophytes was measured periodically at all river stations from April 11, to November 1,

1964. The plants were harvested from a series of eight one-quarter-meter quadrats along a transect across the river and were placed while still moist in air-tight polyethylene plastic bags. The bags and their contents were refrigerated until the plants could be sorted according to species. Sorting was generally completed less than four days after the plants had been harvested.

After the plants were sorted, they were oven dried at a temperature of 105^{o} Centigrade, cooled to room temperature, then weighed on a triple beam balance.

The standing crop at all river stations as well as points intermediate to stations two and three, four and five, and five and six was measured using the same procedure on August 24-25, 1965, except that they were not sorted to species.

Chlorophyll Determination

Glass microscope slides were submerged in modified Catherwood Diatometers (Patrick et al., 1954) at all river stations from May 18, to October 24, 1965. Each slide remained in the water for a span of from two to four weeks before it was replaced by a new slide. Immediately upon removal from the diatometer, the slide was immersed in 30 ml of 90% acetone in an individual container and refrigerated.

Chlorophyll-a concentration of the extracts was determined according to the method of Richards with Thompson (1952). The spectrophotometric analyses were completed within twenty-four hours after the removal of the slides from the river.

RESULTS

Standing Crop of Macrophytes

Results of harvesting the macrophytic standing crops are recorded in Table I. The extremes and the means are expressed for the samples collected during the summer of 1964, whereas the weights shown for the summer of 1965 represent the collections of a single sampling period.

The mean weights for the stations in the 1964 samples indicate that there was a decrease in the standing crop of macrophytes downstream from station one. The 1965 samples from the stations did not show the downstream decrease so obviously, but it is easily noted in the means for the reaches. Furthermore, a correlation coefficient of -.9473 between samples of macrophytic standing crop and stations is significant to the 1% level of probability. With the exception of reach five, standing crops were much greater in 1965 than in 1964.

The floral composition of the community in 1964 also changed downstream as is shown in Table II. The dominant plants at the upper stations were _Chara_ and _Potamogeton_. At the lower stations, the mosses became dominant. _Berula_ and _Myriophyllum_ were minor components at all stations.

The seasonal variation in standing crops is evident in

Table I. Oven dry weights (gm/m^2) of macrophytic standing crops in the Madison River.

	1964 Samples			1965 Samples	
Station	Mean	Extremes	Mean for Reach	Station	Mean for Reach
1	360.8	212.0-564.7		811.3	
			310.5		849.2
2	260.1	238.2-299.4		887.1	
			232.6		517.1
2a				226.5	
3	205.0	113.9-304.3		437.8	
			165.6		449.9
4	126.1	80.4-202.5		461.9	
			117.4		238.5
4a				154.8	
5	108.7	56.1-236.2		98.8	
			81.5		59.7
5a				51.6	
6	54.2	14.0-115.6		28.7	
Average of Means	185.8			350.9	

Table II. Percent composition of macrophytic standing crop (1964).

Station	*Berula*	*Chara*	Mosses	*Myriophyllum*	*Potamogeton*	*Sparganium*	*Glyceria*
1	18.5	43.4	T	6.8	24.2	7.0	T
2	2.4	47.3	T	1.5	41.2	6.7	T
3	11.2	50.4	0.3	4.4	6.8	15.5	11.3
4	9.5	45.7	T	9.9	11.9	9.2	13.6
5	9.9	22.9	29.4	5.0	2.6	8.4	21.8
6	10.8	2.7	72.3	13.5	0.0	0.6	T

Table III. Averages of the values for stations five and six were used because samples were collected over the longest period from these stations. High water in May and June prevented sampling at the upper stations.

Table III. Oven dry weights (g/m^2) of macrophytes for various dates (1964).

May 9	June 26	July 27	Aug 3	Sept 16	Sept 22
45.2	42.6	55.3	110.1	167.3	124.1

The greatest growth occurred between July 27, and August 3, at which time there was a 99% increase.

Chlorophyll Determination

The average chlorophyll concentration at each station for the summer sampling period is shown in Figure 2. There was a significant decrease downstream from station one. The correlation coefficient between average chlorophyll concentration and stations was -.8360, which is significant to the 5% level of probability.

Seasonal fluctuations are protrayed in Figure 3, with maxima occurring in the latter part of July and the middle of October.

Figure 4 shows the rate of change of chlorophyll concen-

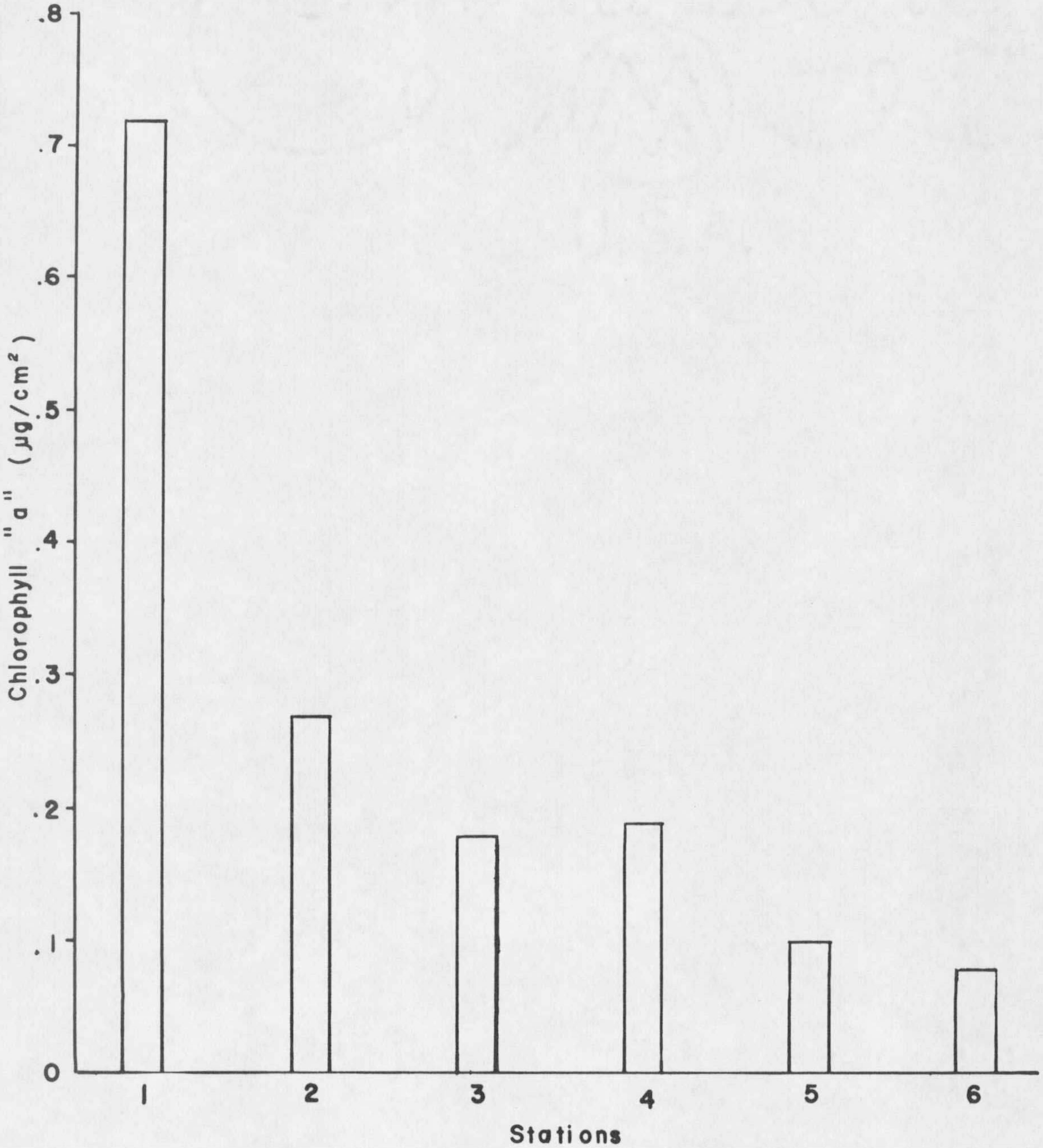

Figure 2: Average chlorophyll "a" concentration for each station during the summer sampling period (1965).

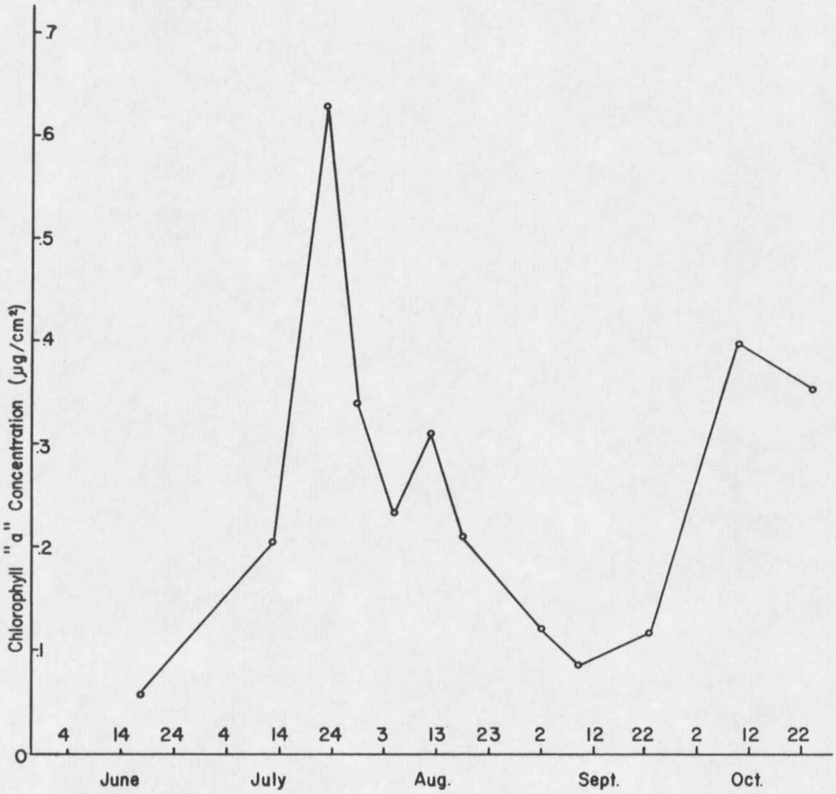

Figure 3: Seasonal fluctuation in chlorophyll "a". The concentration shown for each date is the average computed from the measurements for all stations at that collection time (1965).

tration in micrograms per square centimeter per day that the slides were in the water. Each point represents the average for slides collected from all stations on the indicated date.

Comparison of Figure 4 with Figure 3 reveals that the peak rate of change appeared on July 29, whereas the peak concentration occurred about a week earlier. The slides which were removed on July 23, had been in the water for a period of 35 days, while those removed on July 29, had been in the water for only 16 days. The September 9 minimum is present in both curves, so except for the displacement of the July peak, the two curves are similar.

pH and Alkalinity

Figure 5 is a series of pH curves showing changes which occurred during one sampling date at all stations during the twenty-four hour sampling period. The pH of station one was slightly greater than that at station two, otherwise there was a general increase downstream from station one. A daily cycle of changes is evident with the maxima usually occurring at 1500 hours and minima usually present at 0300 hours.

Figure 6 shows the relationship between total alkalinity and river depth at the gaging station during the summer

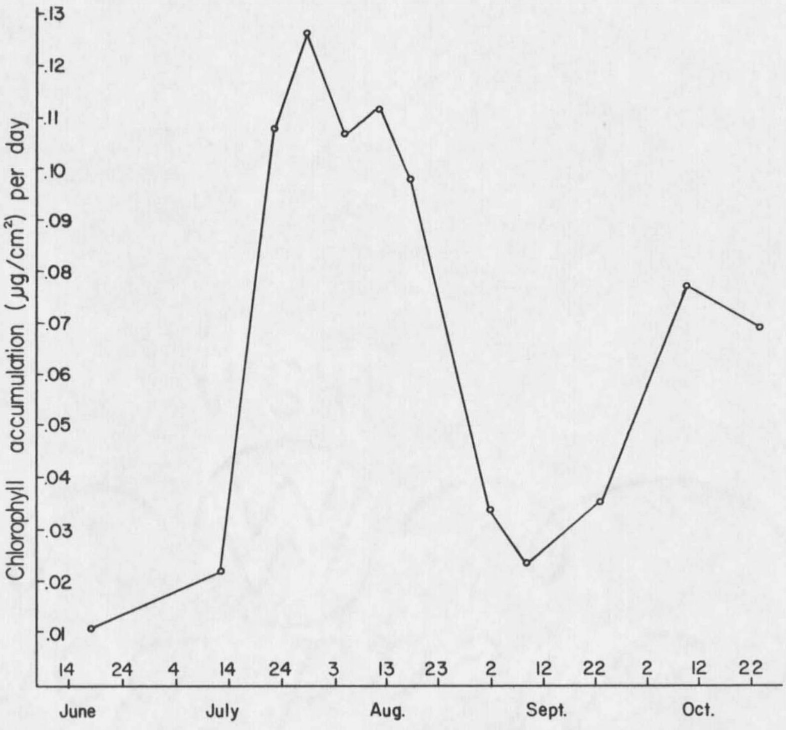

Figure 4: Rate of chlorophyll accumulation (μg/cm) per day on glass microscope slides in the Madison River (1965).

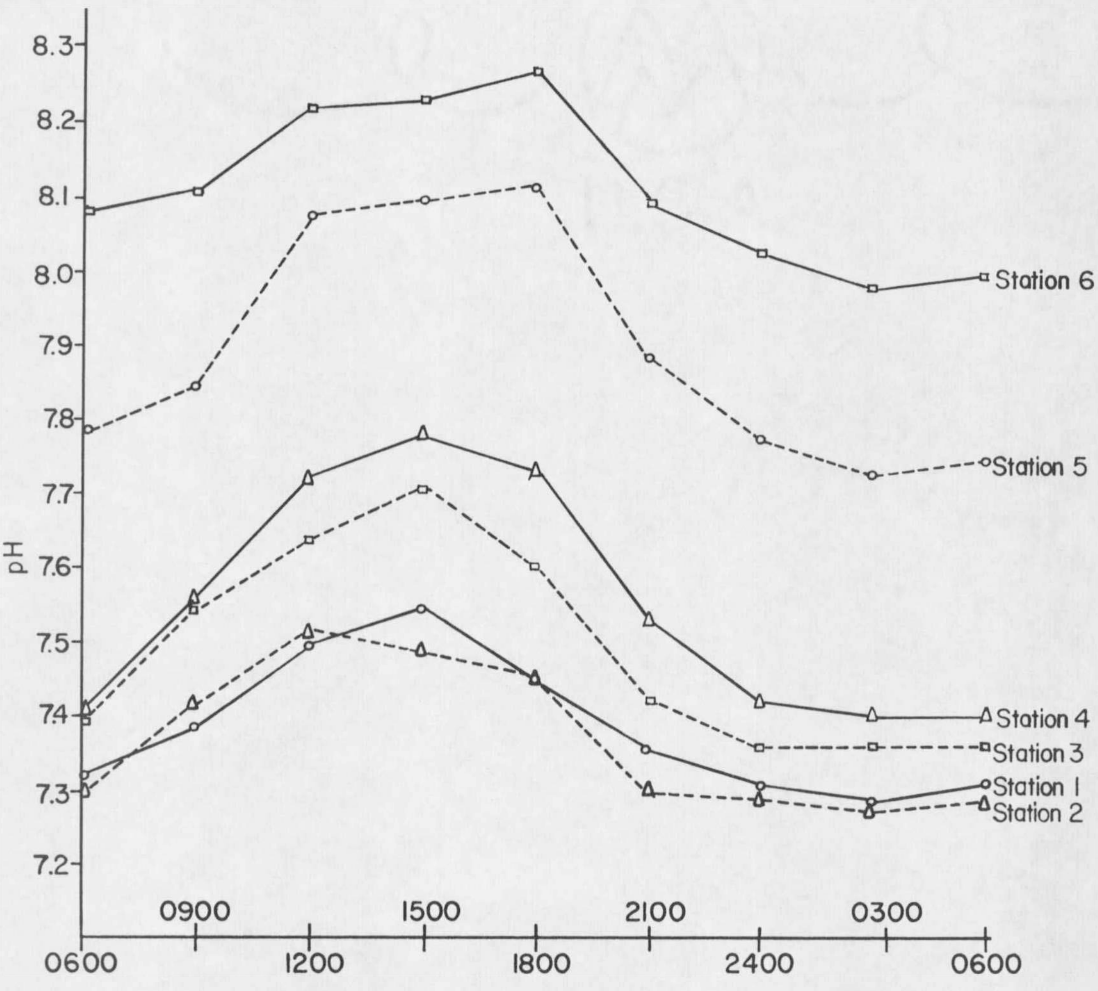

Figure 5: Examples of pH curves for all stations over a twenty-four hour period (July 14-15, 1965).

sampling period. The inverse relationship between alkalinity and river depth was apparently due to the dilution effect of surface runoff from snow melt. Maximum depth occurred on June 5, at which time the total alkalinity was minimal.

Each time the total alkalinity of the river water changed significantly, the relationship between pH change and total dissolved carbon dioxide was determined by titrating a sample with carbon dioxide saturated water as suggested by Beyers et al. (1963). An example of such a CO_2 - pH curve is shown in Figure 7. The CO_2 concentrations were computed from curves similar to Figure 7.

CO_2 Concentration

An example of total CO_2 concentrations is shown in Figure 8. The total CO_2 concentration at pH 8.4 was used as an arbitrary zero point for the calculations.

A significant decrease in total carbon dioxide concentration from the upper stations to those downstream is shown in Figure 8. There was also a daily periodicity with minima generally present between 1200 and 1500 hours and maxima usually occurring at 0300. At the pH ranges which occurred during the study period, the changes in total CO_2 corre-

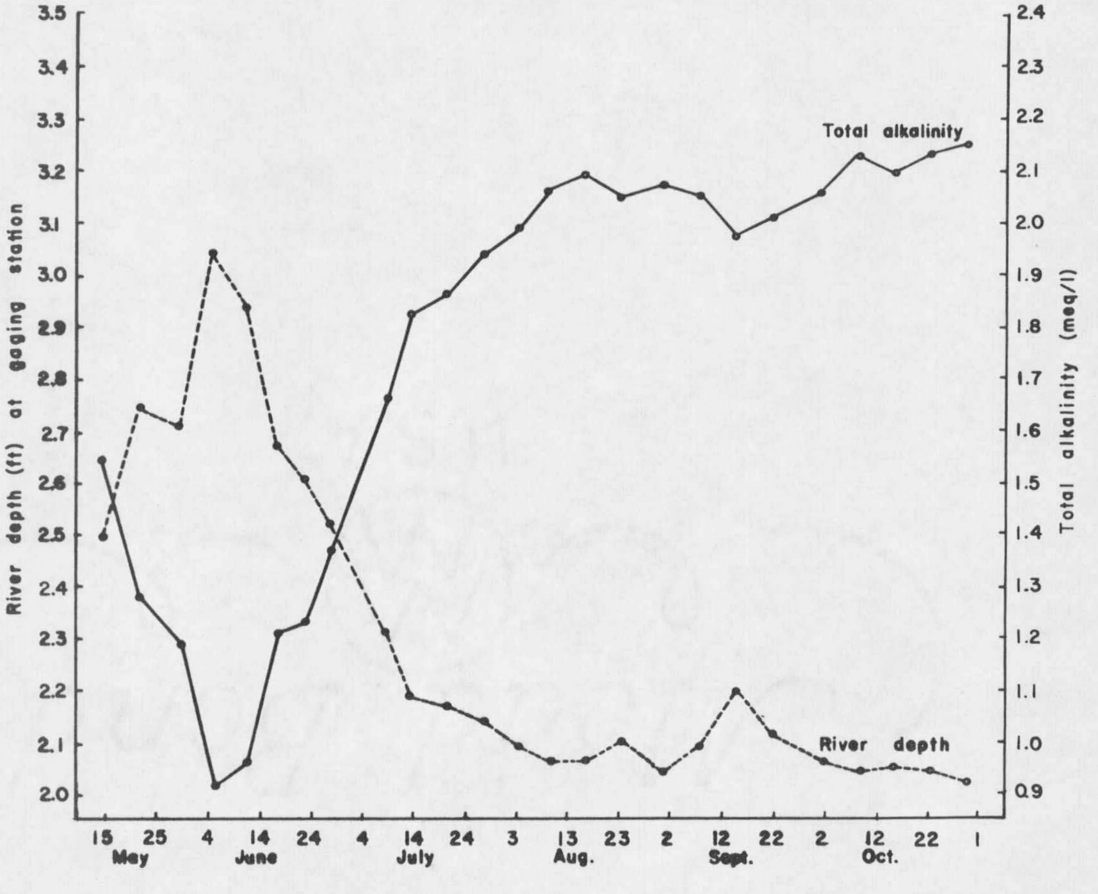

Figure 6: Weekly fluctuations in total alkalinity and river stage at the gaging station on the Madison River during the summer sampling period (1965).

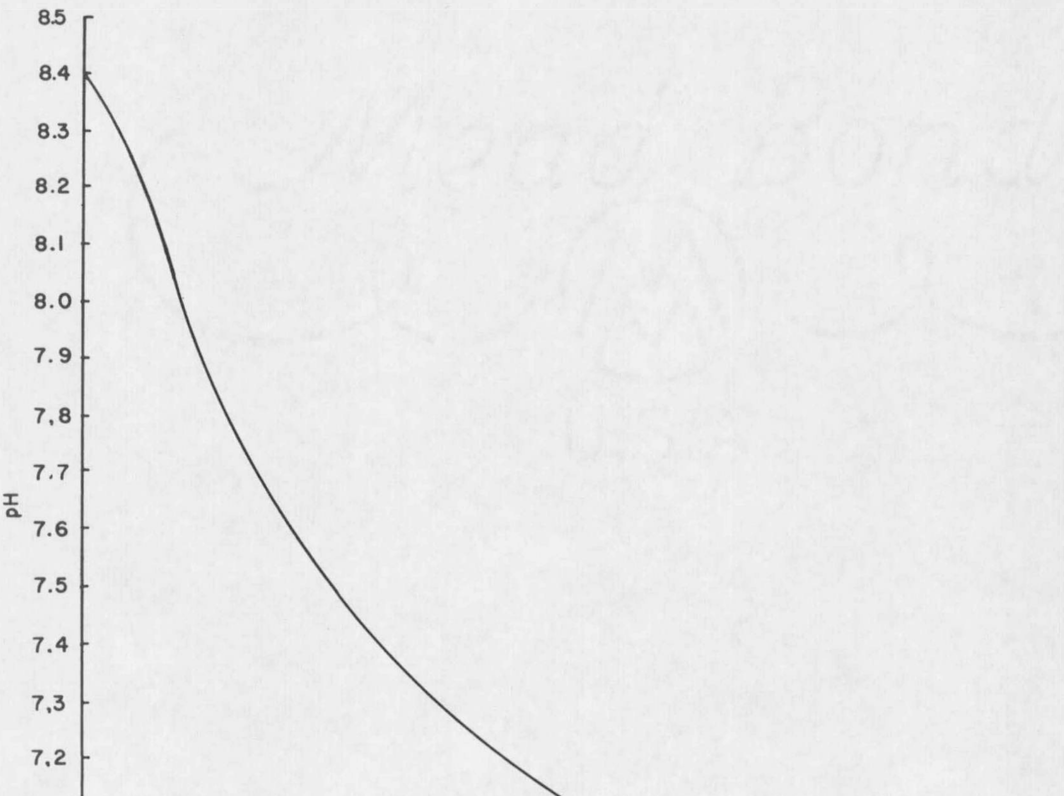

Figure 7: Example of curves produced by titrating a sample of Madison River water with carbon dioxide saturated distilled water.

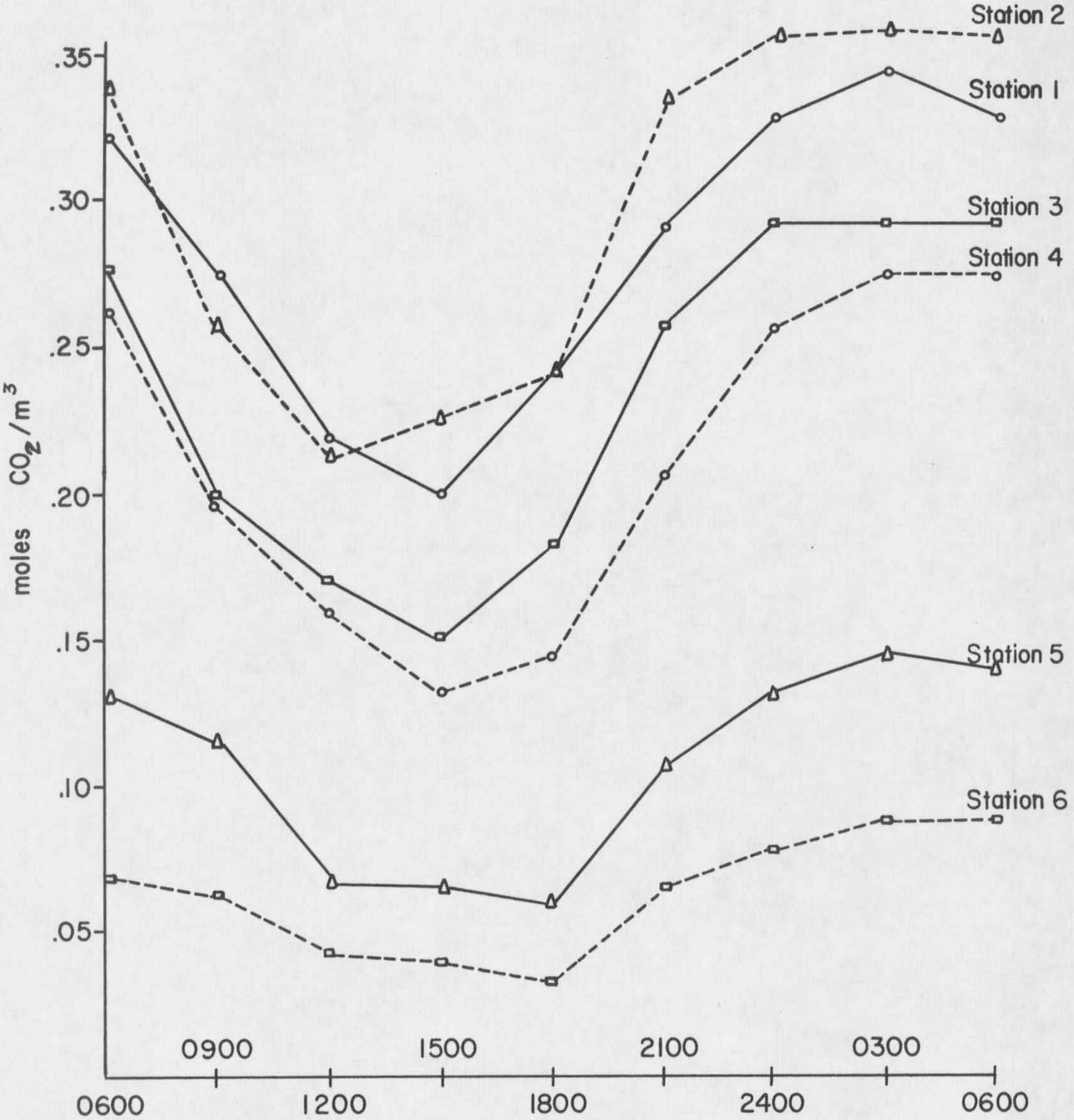

Figure 8: Example of curves showing the concentration of carbon dioxide at all stations during a twenty-four hour sampling period (July 14-15, 1965).

sponded to changes in free CO_2. This is evident if Figure 8 is compared to Figure 9, which portrays the free CO2 concentrations for the same period. A decrease in free CO_2 from the upper stations to the lower ones is apparent.

Changes in Total CO_2 Concentration

Figure 10 shows the rate of change in total carbon dioxide concentration due to biological factors for each of the reaches during a twenty-four hour period. Each point represents the average of all values measured over the entire summer collection period for the indicated time. It can be seen that the most rapid rates of utilization and production of CO_2 took place in the reach between stations one and two. A progressive downstream diminution is apparent with the lowest rates being exhibited in the reach from station five to station six.

Maximum rates of utilization of CO_2--indicating maximum photosynthetic rates--were achieved from 0900 to 1200 hours for all reaches except that between stations two and three, where it occurred during the interval between 1200 and 1500 hours.

There was a great deal of variation as to the time of

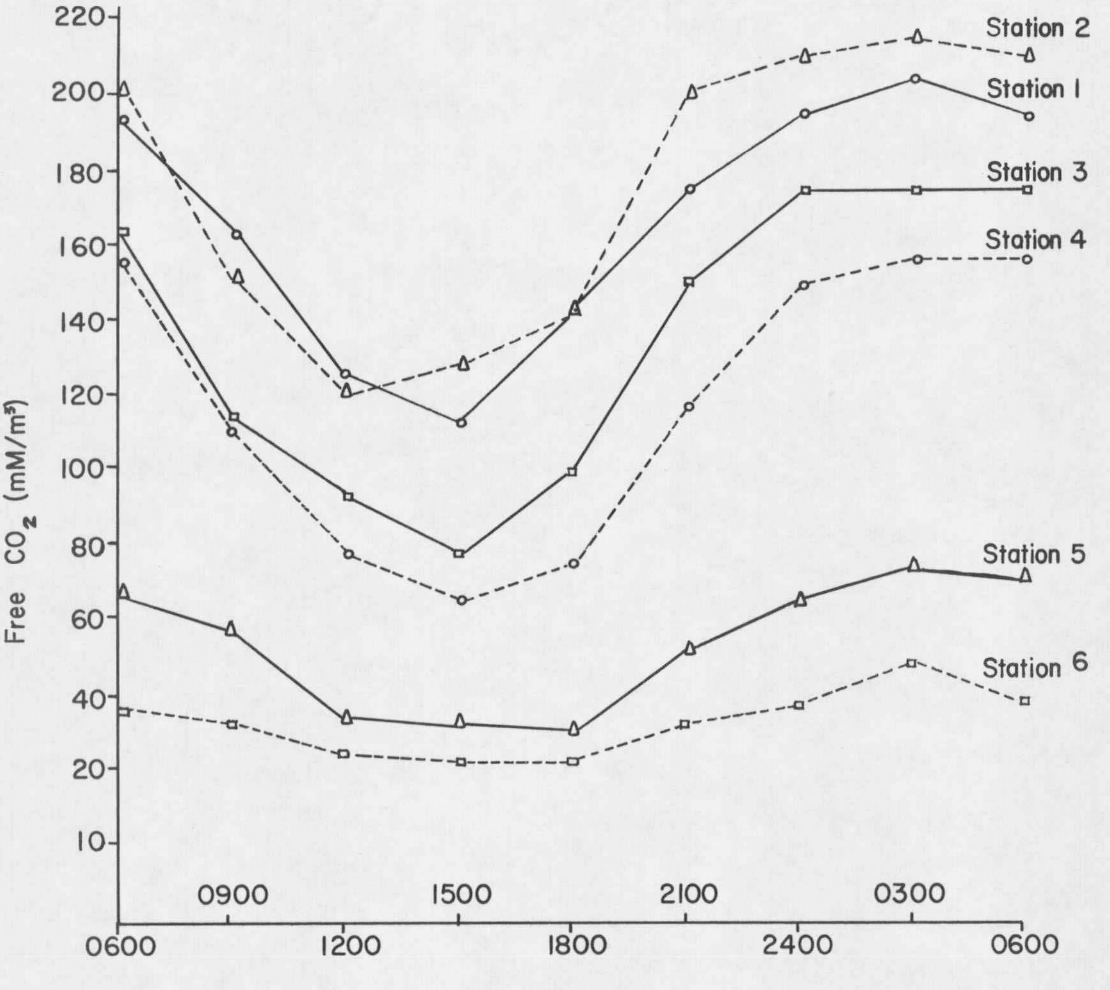

Figure 9: Example of curves showing the concentration of free carbon dioxide at all stations during a twenty-four hour sampling period (July 14-15, 1965).

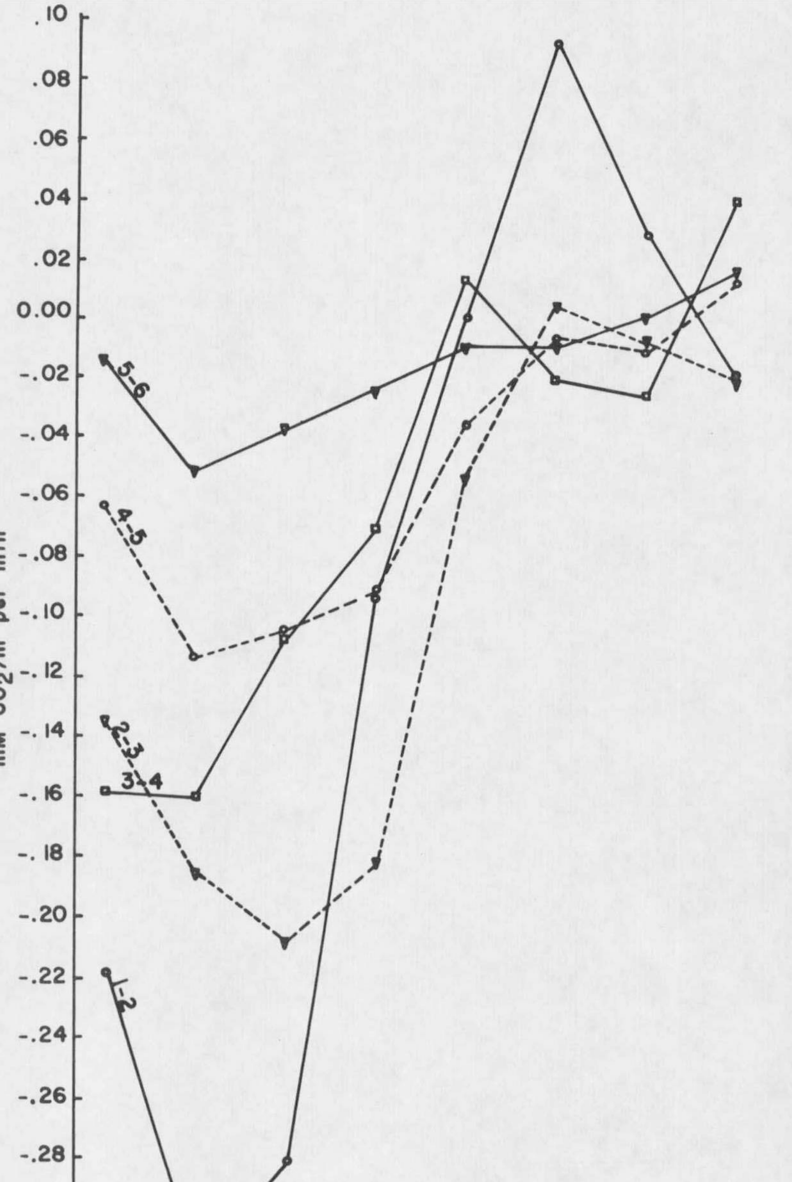

Figure 10: Average rates of change in carbon dioxide concentration due to biological factors in river reaches during a twenty-four hour period (1965).

maximum respiratory rates. The reach between stations one and two and that between two and three showed a peak between 2100 and 2400 hours. The peak respiration of the downstream reaches appeared to occur erratically, probably because of the inaccuracies of the method when small changes in CO_2 concentrations are involved.

The seasonal pattern of net photosynthesis is shown in Figure 11. The maximum rate occurred during the latter portion of June and the early part of July after which time there was a general downward trend toward the minimum achieved in late October during the latter part of the sampling period.

Light Intensity

Figure 12 shows the total light intensity between the hours of 0600 and 1800 for each sampling date through the summer. When Figures 11 and 12 are compared, it will be noted that photosynthesis was low on May 22 and June 5, whereas the light intensity was high. During the rest of the season, the highest photosynthetic rates were correlated with the highest light intensities and there was a gradual trend downward in photosynthesis correlated with de-

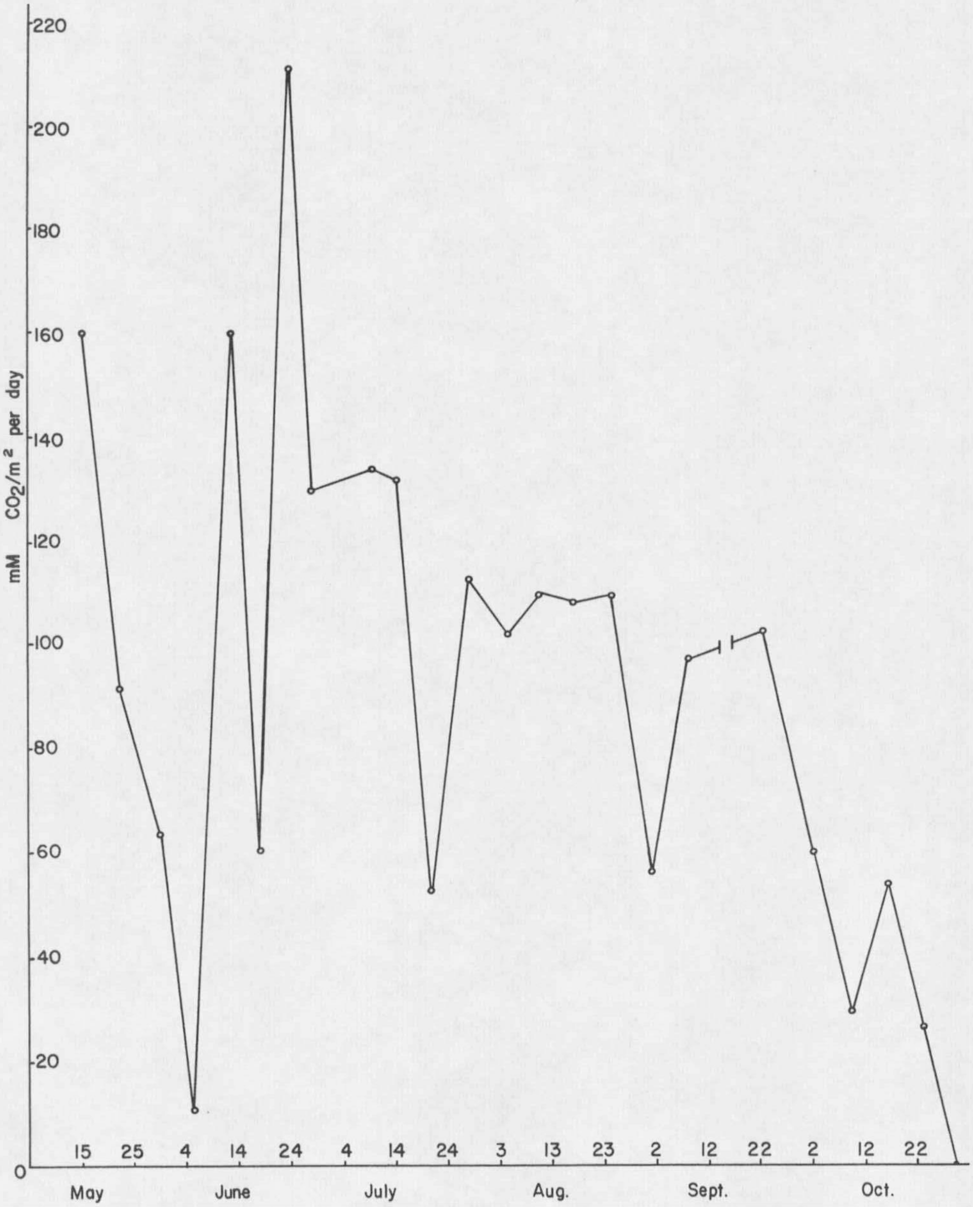

Figure 11: Average daily uptake of carbon dioxide for all stations over the entire summer sampling period on the Madison River (1965).

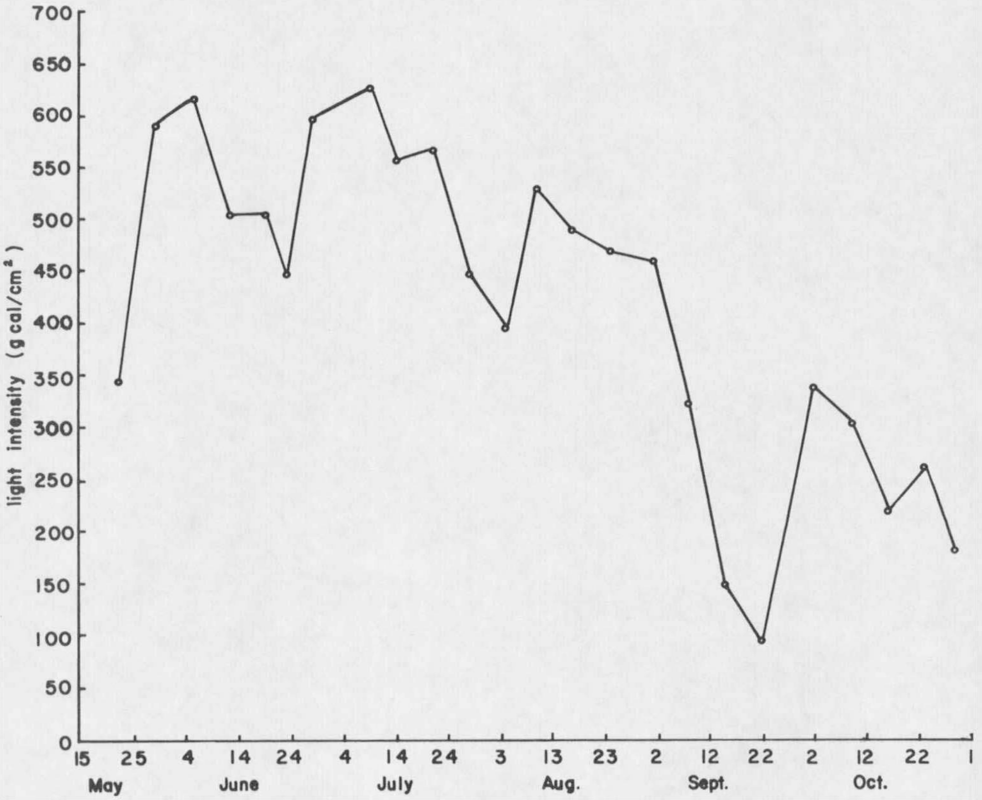

Figure 12: Light intensity (g cal/cm^2) per day from 0600 to 1800 hours for each sampling date throughout the summer sampling period (1965).

creasing light intensity.

Water Temperature

There was not a great deal of variation among the stations in their average daily water temperature as is shown in Figure 13. However, there was a general tendency for the downstream stations to become warmer than the upstream stations during warming trends and cooler during cooling conditions. This tendency can be noted in the warmer temperatures in spring and early summer, and the cooler temperatures in the fall at the lower stations.

Seasonally, there was a gradual warming trend toward the maximum which was attained in late July and early August, after which there was a more rapid cooling to the minimum that was reached during the latter part of the sampling period in October.

Current Velocity

Figure 14 shows the average current velocity for reaches between all stations for each sampling date throughout the summer sampling period. Changes occurred simultaneously in all reaches although there was a less abrupt change in the reach between stations two and three than the others. This

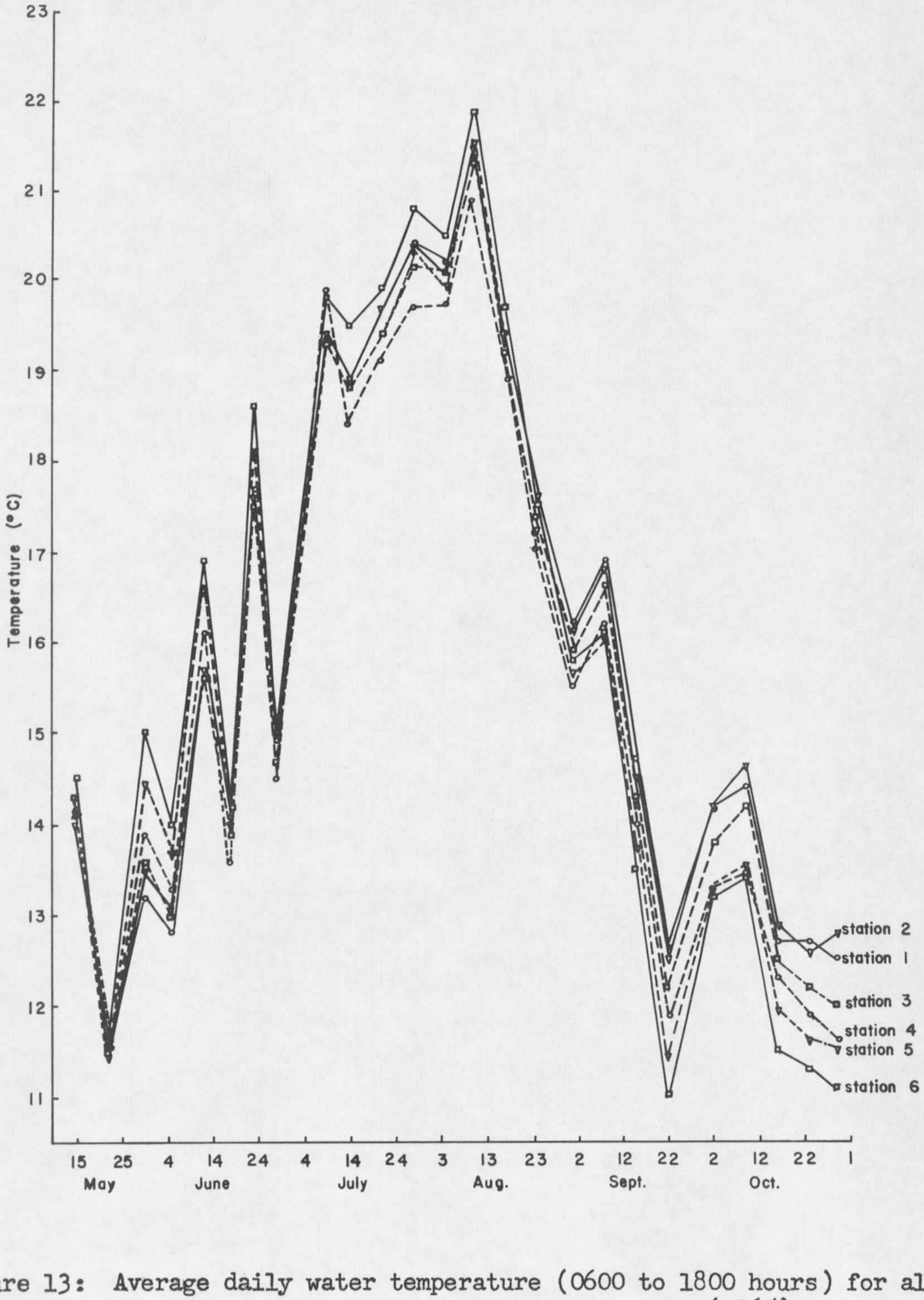

Figure 13: Average daily water temperature (0600 to 1800 hours) for all stations during the summer sampling period (1965).

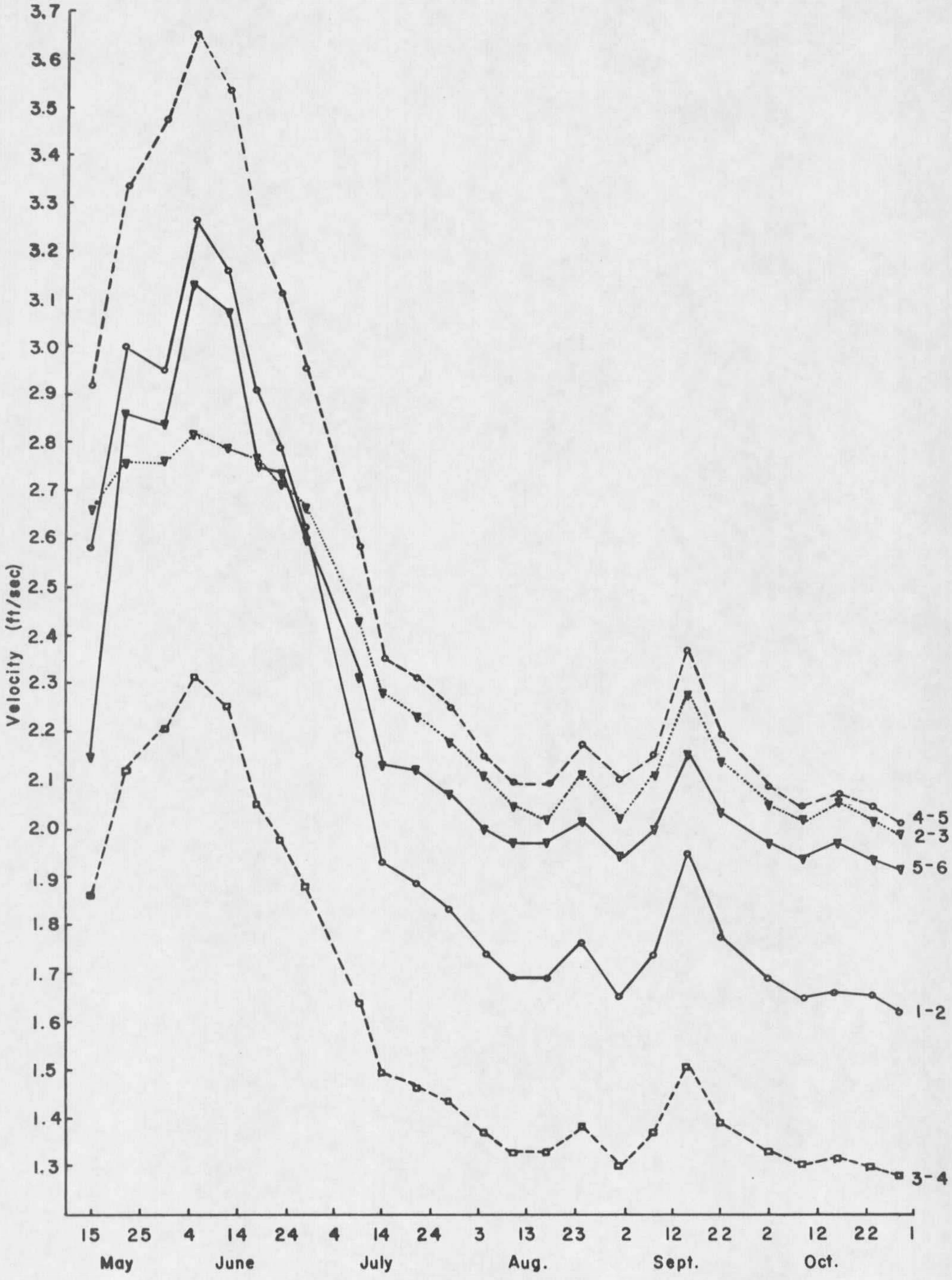

Figure 14: Average current velocity (ft/sec) for all reaches on each sampling date throughout the summer sampling period (1965).

was especially true during the period from mid-May to late June, at which time the maximum velocity was attained in all reaches.

During the spring runoff, when the maximum velocity occurred, the greatest average velocity was found in the reach separating stations four and five. This was followed in order of magnitude by reaches one to two, five to six, two to three and three to four. After the spring runoff, when the river reached its more stable summer level, the greatest average velocity was still found in the reach between stations four and five, but it was followed by reaches two to three, five to six, one to two and three to four.

Statistical Analysis of Data by Reach

A comparison was made of photosynthesis, carbon dioxide concentration, current velocity and temperature between reaches. The average values of these variables for each of the five reaches is given in Table IV.

A correlation coefficient of -.8202 (significant to the 0.1% level) was obtained between the downstream sequence of reaches and concentration of free carbon dioxide. The correlation coefficient of -0.4540 between reaches and photo-

Table IV. Average values of photosynthesis, carbon dioxide concentration, current velocity and temperature for the various reaches over the entire summer sampling period. (1965)

Reach	Photosynthesis moles/m^2/day	CO_2 Concentration moles/m^3	Current Velocity m/sec	Temperature °C
1	41.1	145.6	.65	16.0
2	32.1	131.6	.71	15.9
3	22.5	108.6	.52	15.7
4	16.5	78.7	.77	15.6
5	5.8	45.1	.69	15.8

synthesis was also significant to the 0.1% level. Correlation between reaches and current velocity (R=.1201) was found to be significant to the 1% level of probability. However, temperatures were not significantly different between the reaches.

The parallelism between photosynthesis, macrophyte standing crop, chlorophyll concentration, and free CO_2 concentration is portrayed in Figure 15.

Statistical Analysis of Pooled Data.

A study was carried out with an IBM 1620 Model II Disk Loaded Routine OMPREG. This program presents the means, standard deviation, variance and sum of the squares of each variable, the linear regression coefficients of the equation, the standard error of the regression coefficients, partial and multiple correlation coefficients, coefficients of determination, standard error of the estimate, _t_ value and F ratios.

Photosynthesis measurements were assumed to be a valid indicator of the primary productivity of the river and were taken as the dependent variable. Light, water temperature, current velocity and carbon dioxide concentration values

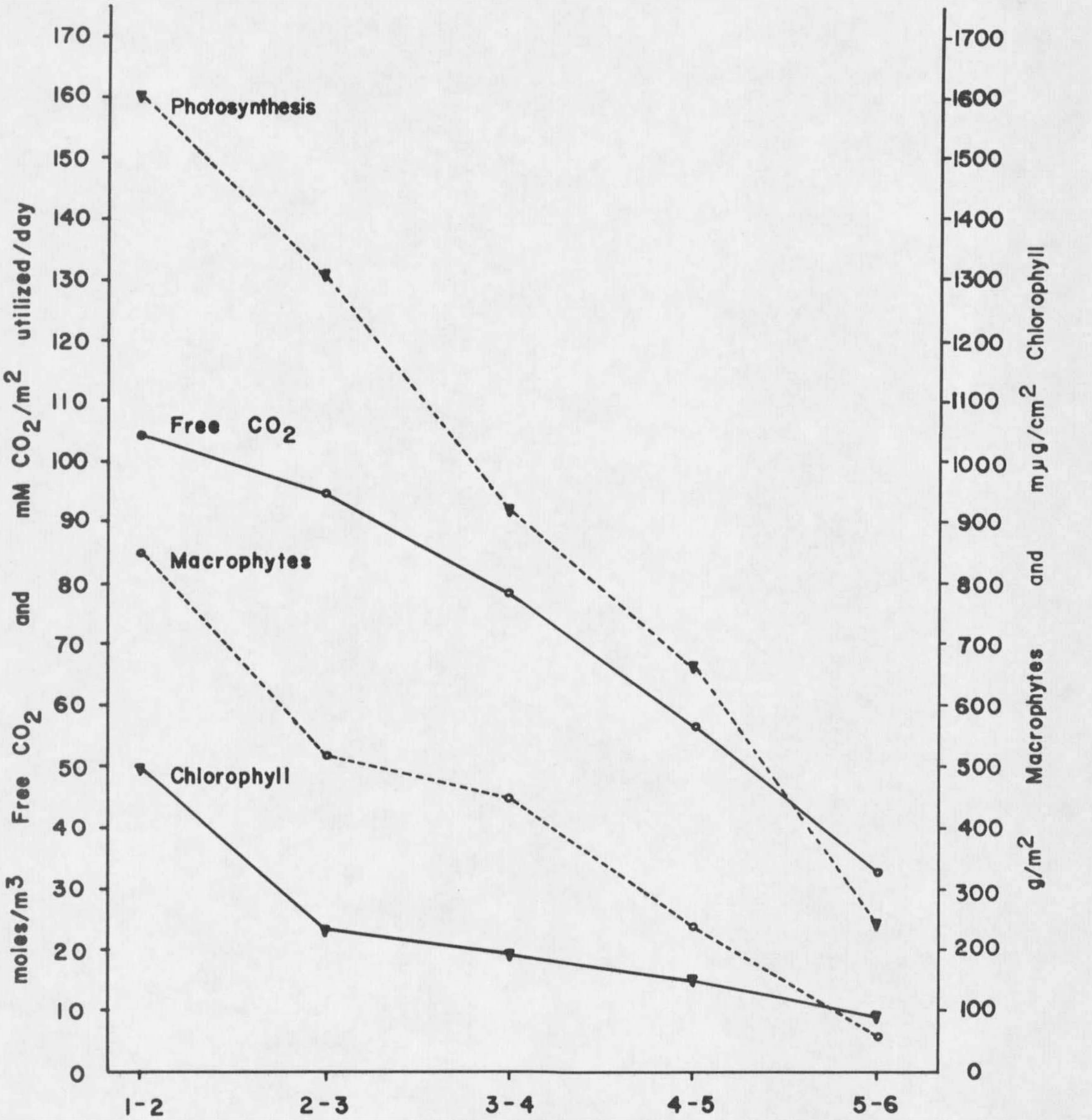

Figure 15: Comparison of free CO_2, photosynthesis, standing crop of macrophytes and chlorophyll concentration in the Madison River. Each point represents an average of the measurements over the entire summer sampling period for the designated reach (1965).

were used as independent variables. In this analysis all of the data for the entire study section were pooled without regard for differences between reaches.

Light intensity, which was measured by a single pyrheliometer located at station six, was considered as being the same for all stations. Doubtless, there was variation in the light over the 14 miles which separated station six from station one, but the difference was assumed to be negligible. Regressions were run, however, between the photosynthesis which occurred at a particular time of day and the light at the same time.

When a simple regression analysis was carried out using each independent variable individually, a correlation coefficient which was significant to the 0.1% level of probability was obtained for all factors except current velocity. The correlation coefficient for velocity was not significantly different from zero. By far the largest correlation coefficient was found for carbon dioxide concentration.

A multiple regression equation using each of the factors as separate independent variables gave a coefficient of determination of .2658 over the entire length of the river studied. This indicates that about 27% of the variation in the photosynthesis was associated with the variables used in the equation. Carbon dioxide concentration was found to have a much larger partial correlation coefficient than any of the other three factors (see Table V). It was followed in order by temperature, light and velocity. All except velocity were significant to the 0.1% level of probability. The partial correlation coefficient of velocity was not significantly different from zero.

Table VI portrays the constants of the multiple regression equation relating photosynthesis to light, water temperature, current velocity and CO_2 concentration. All $\underline{t}$ values except that for velocity indicate significance to the 0.1% level of probability. The $\underline{t}$ value for velocity shows no significant difference from zero.

In subsequent equations involving the entire length of the study area, when carbon dioxide occurred in combination with any of the other independent variables, its partial correlation coefficient was consistently larger than that of the others, and was in all cases significant to the 0.1% level of probability.