

TOTAL, PLANKTONIC AND BENTHIC
PHOTOSYNTHETIC PRODUCTION IN THE KANSAS RIVER

by

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A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

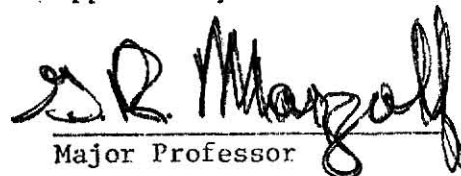
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—The river flower on towards its goal. Siddhartha saw the river hasten, made up of himself and his relatives and all the people he had ever seen. All the waves and water hastened, suffering, towards goals, many goals, to the waterfall, to the sea, to the current, to the ocean and all goals were reached and each one was succeeded by another. The water changed to vapor and rose, became rain and came down again, became spring, brook and river, changed anew, flowed anew. But the yearning voice had altered. It still echoed sorrowfully, searchingly, but other voices accompanied it, voices of pleasure and sorrow, good and evil voices, laughing and lamenting voices, hundreds of voices, thousands of voices.—

from Siddhartha
by Herman Hesse

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I would like to take this opportunity to thank those who gave their time to help me.

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A special thanks to Dr. Christopher Smith whose insistence on understanding everything in depth forced me to clarify and often rectify my ideas.

My greatest measure of appreciation to my major professor, who worked with rather than over me. In retrospect I would hesitate to claim any of the ideas on stream ecology as entirely my own. I would rather say that they evolved as the result of my interaction with my co-worker, teacher, and friend, Dr. G. R. Marzolf.

It is customary to thank one's wife for her patience and consideration. Certainly my wife Nancy had these attributes. But beyond that she was an equal partner in all phases of my thesis project, from carrying heavy sampling gear across sandbars to criticizing the manuscript. Without her help I could not have accomplished this work.

PREFACE

This study is a process oriented investigation of the photosynthetic producer communities in the Kansas River. The approach and character of the river establish this study as unique in the published literature (Blum, 1956; Hynes, 1974). This work is a reconnaissance effort in which specific hypotheses are generated, not tested.

A recent symposium on stream ecology developed the concept that lotic systems exist as a continuum (Hall et al., 1975). The physical characteristics and biota of stream systems vary from headwaters to the sea (figure 1) (Cummins, 1975). Streams are an integral part of the land they drain (Likens, 1975) and are sensitive to the same environmental parameters that define biome.

A continuum perspective of the Kansas River is indicated by figure 1. Figure 2 gives the geographical context. The Kansas River is sixth order, located in the Great Plains.

The Kansas River is formed by the confluence of the Republican and Smokey Hill Rivers near Junction City, Kansas (figure 2). Table 1 gives geomorphological data for the three rivers (taken from Baehr, 1954, and the U. S. G. S. Water Resources Division, 1968).

Table 1. Morphological and Flow Data.

River	Stream Gradient (m/km)	Meander Belt Avg. width (m)	Floodplain Avg. width (m)	Stream Avg. width (m)	Avg. Rate discharge (m ³ /s)
Kansas	0.36	2171.7	2955.6	114.3	62.5
Smoky Hill	0.40	1828.8	2209.6	45.3	46.7
Republican	0.46	1524.0	2290.3	76.2	19.3

Figure 1. Continuum model of lotic community characteristics and trophic character, from headwaters to the sea (modified from Cummins, 1975). The position of the Kansas River is noted.

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STREAM ORDER		<u>WIDTH</u>	<u>HEADWATERS</u>
1		0.5 meters	Allocthonous Input - Primarily Labile (Leaves - Sticks POM DOM) Total Canopy Cover Heterotrophic Processing
2		1-2 meters	
3		4-6 meters	Allocthonous Input - Labile & Refractory Partial Canopy Cover Autocthonous Input (Macrophytes Periphyton)
4		10 meters	Heterotrophy Dominates
5			Allocthonous Input - Refractory & Labile Minor Canopy Cover Autocthonous Input (Periphyton Plankton)
6		50-120 meters ← Kansas River	Heterotrophic During High Flow (Deep, Turbid)
7			Autotrophic During Low Flow (Shallow, Clear)
8			
9			
10			
11			Allocthonous Input - Primarily Refractory Zero Canopy Cover Autocthonous Input
12		700 meters	(Planktonic "reduced") Deep, Turbid Flow Heterotrophy Dominates

The substrate is primarily sand with frequent mud and gravel bars. The Kansas River receives domestic sewage, agricultural, and pastoral effluent. Typically the watershed is comprised of floodplain farm lands used for crop agriculture and well-managed prairie uplands which are unplowed and used for cattle grazing.

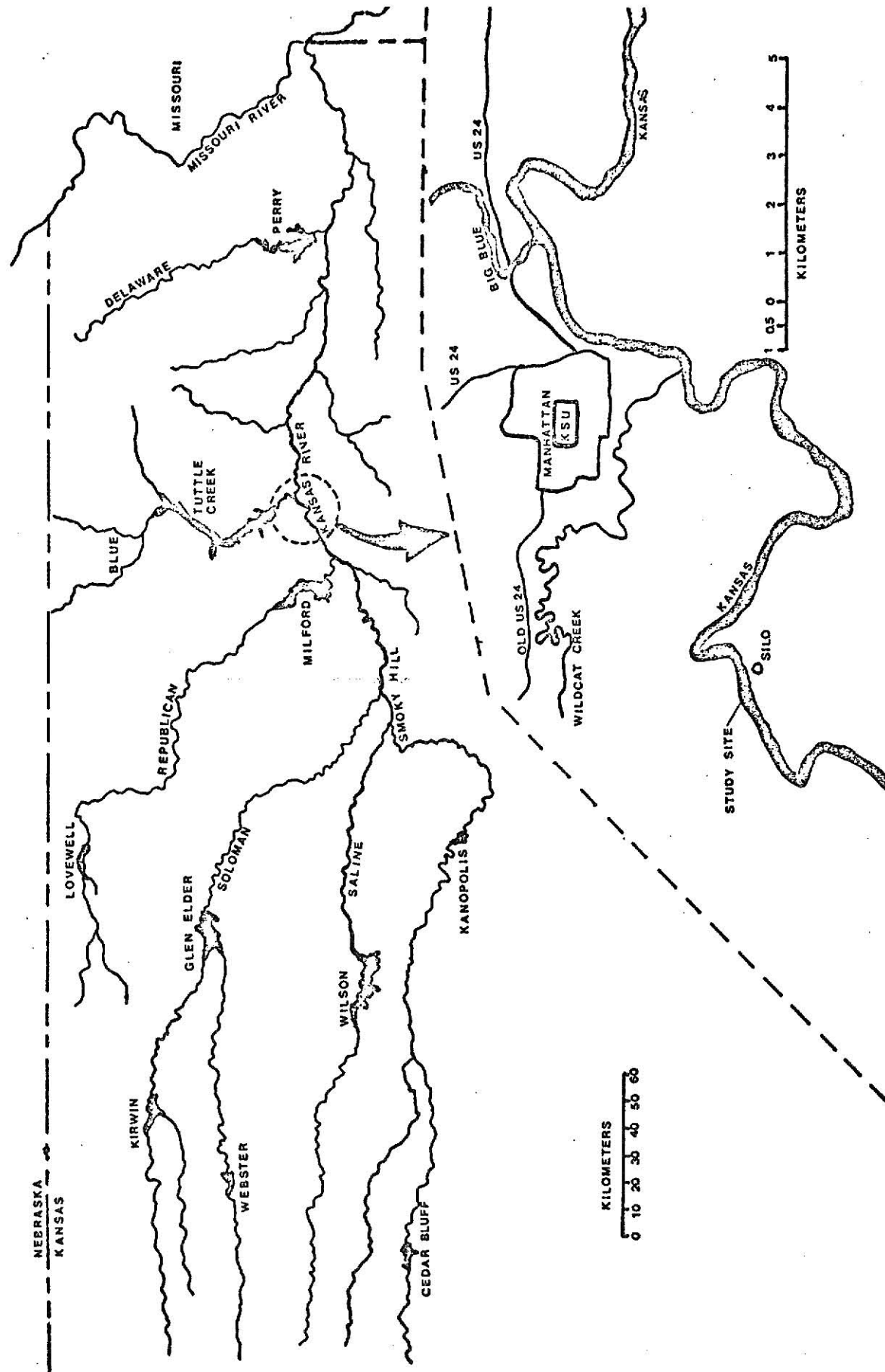
The study site was located about 5 kilometers southwest of Manhattan, Kansas and about 30 kilometers below the confluence of the Republican and Smokey Hill Rivers (figure 2). Access to the site was through the Kansas State Agricultural Experimental Station farms at Ashland Bottoms.

Fish characteristic of the Kansas River include channel catfish, drum, carpsucker, shovelnose sturgeon, and shortnose gar. Aquatic insects appear to be substrate limited by availability of snags, logjams, and man-made obstructions. Commonly found are Ephemeroptera (Heptageniidae), Tricoptera (Hydropsychidae), and Plecoptera (Isoperlidae). Backwater mudbars contain Oligochaete populations.

Flow patterns of the Kansas River are irregular, with a frequency that depends on the occurrence of floods and fluctuations in reservoir outflow. High levels of turbidity, reflecting agricultural runoff and resuspension of clay and silt deposits occur with high flow regimes. Increased turbidity decreases photosynthetic production by decreasing light penetration and increasing siltation (Ellis, 1936; Benson and Cowell, 1967; and Hynes, 1974). High rates of flow scour and flush the producer communities downstream (Leopold et al., 1964; Gumtow, 1955; Jackson et al., 1964).

Macrophytes are not present in the Kansas River. The photosynthetic producer community is composed of planktonic or benthic algae.

Figure 2. State and location of study area. Note the interruption of headwater-river continuum by reservoirs.



Potential sources of the plankton are tributaries, backwaters, reservoir impoundments, and the benthos (Blum, 1956; Hynes, 1974). Backwaters are both shallow and infrequent in the Kansas River. Tributaries are typically low order streams with insignificant rates of flow, or reservoir outlets. Planktonic densities in turbid Great Plains reservoirs are commonly low (Marzolf, 1971) and lake plankton is rapidly eliminated from streams (Chandler, 1937; Reef, 1939; Beach, 1960; Hartman and Himes, 1961; Neel, Nicholson, and Hirsh, 1963).

The species composition of planktonic algae is generally similar to that of the benthos (Hynes, 1974). Butcher (1932) found that numbers of benthic algae suspended in the open water reflect the quantity on the stream bed. Swanson and Bachman (1975) showed high positive correlation between wetted stream bed area and a chlorophyll index of plankton density. The character of the Kansas River substrate (sand and mud, Reimer, 1975) seemed likely to prevent accumulation of source episammic and epipellic communities by erosive scouring (Douglas, 1958a; Koboyasi, 1961). The origins and dynamics of stream plankton populations are a source of open questions.

Initial expectations were that stream turbidity and substrate instability would limit photosynthetic production in the Kansas River to low and perhaps immeasurably small levels.

A series of objectives were formulated. The thrust of these objectives was to measure and model the photosynthetic components of the Kansas River. The objectives were:

- 1) Develop or adapt methods suitable to estimating photosynthetic production in the Kansas River.
- 2) Estimate photosynthetic production rates of the benthic and

planktonic components of the Kansas River.

- 3) Identify physical parameters potentially important to each component.
- 4) Develop a model of lotic photosynthetic production for Kansas River type streams.
- 5) Identify physical parameters potentially important in the micro-distribution of the benthic primary producer community.

In order to facilitate the submission of a manuscript for review and publication, yet include the results of considerable methodological evaluation, I have adopted the following organizational format:

Objectives 1 through 4 are inter-related; they will be considered in part 1. The approach to objective 5 was distinctly different; it will be considered separately as part 2.

A detailed discussion of the methods of part 1 is contained in appendix I. These methods actually used will be listed without detail in the methods section of part 1.

PART 1

Introduction

The components of Kansas River photosynthetic production are benthic and planktonic. Total and planktonic production can be estimated directly; benthic production may then be estimated by difference.

The contribution of each component to total lotic production was estimated following a period of high turbid flow which presumably eroded and flushed out most of the producer populations. Also estimated were physical, chemical, and morphological parameters.

The development of the photosynthetic communities, as indexed by production rates, was regressed against the non-biotic parameters measured.

Systematic variation between production estimates and certain environmental parameters suggests a conceptual framework for viewing lotic primary production. This framework is generalized and presented as a model of lotic photosynthetic producer population dynamics.

Methods and Materials

Total photosynthetic production was estimated by analysis of the diurnal oxygen curve measured at a single point in the river (Odum, 1956; Owens, 1969). Corrections for diffusion utilize the aeration coefficient (f) calculated from morphometric data (Owens, 1964). A further discussion of the single station method and the aeration coefficient is contained in appendix I.

Oxygen measurements were made hourly with a Yellow Springs Instrument Model 54 oxygen meter. Company specifications list its accuracy as ± 0.1 ppm on the 0-10 ppm scale and ± 0.2 ppm on the 0-20 ppm scale.

Temperature was measured by a thermistor embedded in the oxygen meter probe. The accuracy of this thermometer as listed by the company specification is $\pm 0.7^\circ$ C.

Two meters were used during the 220 consecutive hours of field measurement. After recharging, the relief meter was recalibrated and checked against the relieved meter.

Barometric pressure was read in the field from a Taylor barometer that was calibrated against the standard elevation corrected barometer of the state meteorological service, Department of Physics, Kansas State University. Depth and width estimates were derived arithmetically from transects surveyed with metric tape and meter stick. Current velocities were estimated by timing the passage of a float along a measured distance (Robins and Crawford, 1954).

Hourly measurements were made on nine consecutive days beginning 13 September 1975 and ending 21 September 1975. Twenty-four hour intervals were monitored in the same fashion on 25-26 September 1975 and

11-12 October 1975.

The oxygen probe was placed in the main channel except on 25-26 September when both the main channel and a nearby riffle were sampled for the 24-hour period.

Isolation in $\text{gram-cal/cm}^2/\text{hr}$ was recorded by the Kansas State University Department of Physics meteorological station. The distance of the river site to the weather station is about 5 kilometers.

Nitrate-nitrite concentrations in mg/liter total nitrogen and orthophosphate concentrations in $\mu\text{g/liter}$ were estimated with techniques provided by the Hach Chemical Company, Ames, Iowa. Standard procedures were followed except that samples were centrifuged to remove suspended particulate materials.

Changes of oxygen concentration in light and dark bottles were used to estimate planktonic production. The production curve was estimated by attaching clear and foil-wrapped bottles to a rod fixed in the river bed. Depths selected for light and dark bottle incubation varied with existing turbidity and light conditions.

Streams are irregular in cross sectional profile and current velocity. Consequently the average cross sectional depth may not reflect the average depth experienced by the water and randomly suspended algae. Depth weighted for current velocity or weighted average depth (W.A.D.) is the average depth experienced by a random molecule of water or suspended algal cell (appendix I).

The planktonic production vs. depth curve was integrated to the depth intercept (entire curve) if the depth intercept was less than weighted average depth (W.A.D.). When the depth intercept exceeded

weighted average depth (W.A.D.) the planktonic production curve was integrated only to W.A.D. The area under the production vs. depth curve represents planktonic production ($\text{mg O}_2/\text{m}^2/\text{day}$).

Duplicate 300 ml. light and dark B.O.D. bottles were incubated from sunrise to sunset at each depth. The initial concentration of dissolved oxygen was established by fixing two bottles at dawn. Oxygen concentration was determined with the azide modification of the Winkler method (Standard Methods, 1971). Planktonic production vs. depth curves were integrated with a polar planimeter.

Benthic photosynthetic production was estimated by difference:

$$\text{Total Production} = \text{Phytoplankton Production} + \text{Benthic Production}$$

$$\text{Benthic Production} = \text{Total Production} - \text{Phytoplanktonic Production}$$

Trophogenic, as used in this paper, attributes measurable gross production to the noun it modifies. Trophogenic depth was estimated daily by vertical incubation of light and dark bottles, and is defined as the depth intercept of the production vs. depth curve.

Trophogenic area refers to the area of submersed substrate receiving sufficient light to be photosynthetically productive. Trophogenic area is estimated with morphometric data and trophogenic depth (figure 3).

A plankton density was indexed by assuming:

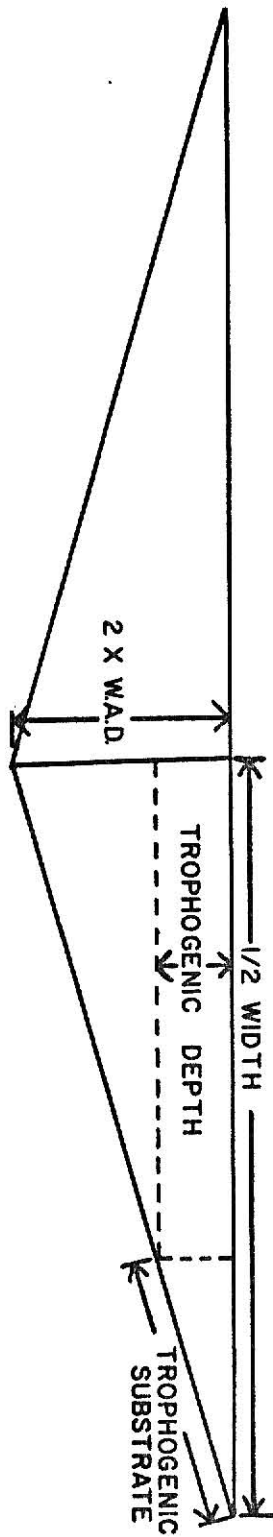
- 1) Benthic algae are limited by trophogenic area.
- 2) Lotic plankton derive 100% from the benthos.
- 3) Erosion of benthic algae is a linear function of trophogenic area.

Figure 3. The calculation procedures for trophogenic area and plankton density index from a triangular model of river cross section. Parameter values are averaged morphometric measurements and the depth to which measurable photosynthetic production occurs (trophogenic depth).

By similar triangles:

$$\frac{\text{Trophogenic depth (m)}}{\text{Trophogenic substrate (m)}} = \left[\frac{2 \times \text{W.A.D. (m)}}{\sqrt{(1/2 \text{ width})^2 + (2 \times \text{W.A.D.})^2}} \right]$$

$$\text{Trophogenic area (m}^2\text{/day)} = \text{Trophogenic substrate (m)} \times 2 \times \text{Current velocity (m/day)}$$



$$K_e - \text{Erosion constant (cells/m}^2\text{/day)}$$

$$\text{Plankton density index (cells/m}^3\text{/day)} = \left[\frac{\text{Trophogenic area (m}^2\text{/day)} \times K_e \text{ (cells/m}^2\text{/day)}}{\text{Volume (m}^3\text{/day)}} \right] \times \left[\frac{\text{Trophogenic depth (m)}}{2 \times \text{W.A.D. (m)}} \right]$$

Results

Production on September 20, 1975 ($\sim 6.480 \text{ g O}_2/\text{m}^2/\text{day}$) was more than five times that on September 13, 1975 ($\sim 1.138 \text{ g O}_2/\text{m}^2/\text{day}$) in spite of nearly equal isolation (294 and 261 gm-cal/cm^2 respectively) (figure 4). In general flow decreased, light was more abundant and penetrated to greater depth, production increased, and respiration decreased during the observation period. These and correlative data are presented in table 2.

The development of photosynthetic activity is illustrated by regression of total planktonic, and benthic production as linear functions of time (table 3). The correlation variable "time" integrates many interactions into a single variable. Time as a variable is useful in a descriptive but not an analytical sense.

Table 3. Correlation Coefficient r /observed level of significance α of selected parameters and the total, planktonic, and benthic production estimates.

Dependent Variable	Time (days)	Incident Light	Ortho- PO_4	$\text{NO}_2\text{-NO}_3$ N	Avg. $^\circ\text{C}$	Trophogenic Area	Plankton Density Index
Total production	r 0.8800 α 0.003	0.6600 0.0283	-0.7100 0.0136	-0.4400 0.1801	0.2700 0.4816	0.8600 0.0027	0.8200 0.0245
Planktonic production	r 0.9600 α 0.0001	0.4600 0.1534	-0.8700 0.0005	-0.6600 0.0245	0.3200 0.5569	0.8300 0.0011	0.9800 0.0001
Benthic production	r 0.7500 α 0.0419	0.7700 0.0058	-0.4100 0.2127	-0.0900 0.7850	-0.2200 0.4276	0.9200 0.0007	0.6400 0.0333

Time is very closely correlated with the generated parameter plankton density index ($r = 0.96$). Plankton density index is a variable calculated from the light regime and morphology of the river (figure 3). The regression of plankton production as a function of plankton density index has a correlation coefficient of 0.98 and observed level of signifi-

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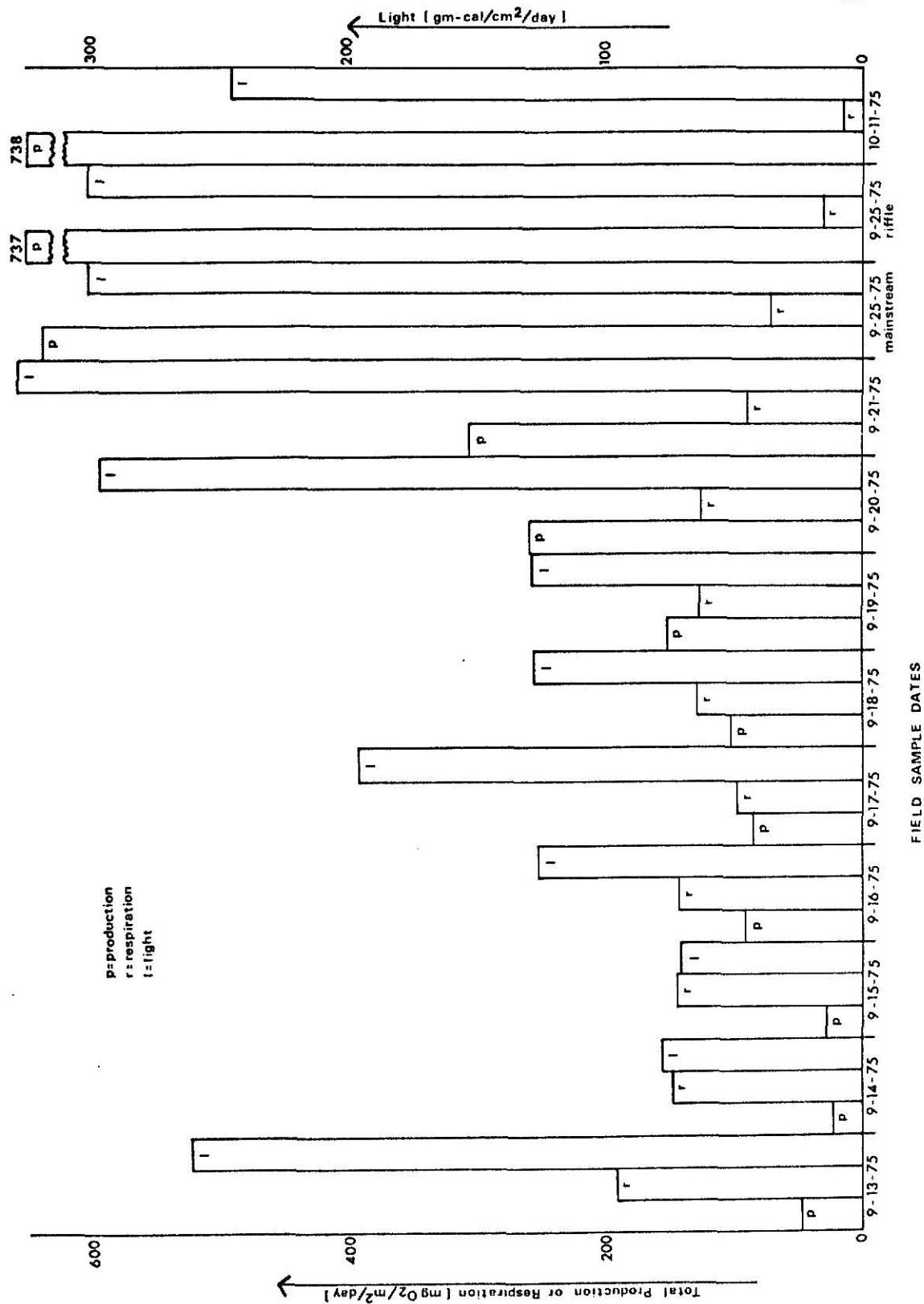
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Table 2. Production estimates, physical, chemical, morphological, and calculated parameter values for the dates sampled.

Date	Total Gross 1 Production ($\text{g O}_2/\text{m}^2/\text{day}$)	Total Gross Respiration ($\text{g O}_2/\text{m}^2/\text{day}$)	P/R ratio (total)	Planktonic Gross 1 Production ($\text{g O}_2/\text{m}^2/\text{day}$)	Benthic Gross 1 Production ($\text{g C}_2/\text{m}^2/\text{day}$)	Benthic/Planktonic Production Ratio	Tropho Depth* (cm)	Weighted Average Depth (cm)	Average Width (m)	Average Current Velocity (m/sec)
9/13/75	1.138	4.540	0.251	0.054	1.084	20.07	21.5	48.71	135.0	0.5003
9/14/75	0.567	3.552	0.160	0.036	0.531	14.75	21.0	48.41	132.5	0.5024
9/15/75	0.690	3.438	0.201	0.025	0.655	26.67	21.0	48.16	130.0	0.5089
9/16/75	2.016	3.421	0.589	0.064	1.952	30.50	20.5	47.85	131.0	0.5046
9/17/75	2.241	2.745	0.817	0.090	2.151	23.90	21.0	47.31	129.0	0.5103
9/18/75	2.445	3.111	0.786	0.107	2.338	21.85	22.5	47.38	127.0	0.5073
9/19/75	3.629	3.059	1.186	0.066	3.563	53.93	27.6	47.07	126.0	0.5062
9/20/75	6.480	3.510	1.846	0.101	6.379	63.16	27.0	46.85	124.0	0.5091
9/21/75	7.286	2.178	3.346	0.245	7.061	31.38	31.0	46.41	123.5	0.5014
9/25/75 (main)	13.449	0.734	18.323	0.523	12.926	24.72	62.0	45.70	120.0	0.5107
9/25/75 (trifle)	19.617	0.661	29.677	0.303	19.304	63.71	62.0	31.08	30.0	0.6150
10/11/75	11.552	0.312	37.002	0.212	9.431	4.45	79.5	34.87	83.5	0.4184
9/13/75	43.23	5.8357	1.1844	2.8426	261.00	0.51	0.61	17.50	5.3666	0.1000
9/14/75	43.41	5.7513	1.1608	2.7859	78.25	0.54	0.55	17.45	5.1756	0.0966
9/15/75	43.96	5.6427	1.1323	2.7175	70.90	0.62	0.70	15.25	5.1921	0.1000
9/16/75	43.60	5.7113	1.1387	2.7329	126.60	0.51	0.50	17.32	5.0941	0.0959
9/17/75	44.09	5.6878	1.1212	2.6909	154.00	0.45	0.60	18.45	5.2602	0.1041
9/18/75	43.83	5.5857	1.1033	2.6479	127.00	0.49	0.70	19.07	5.5078	0.1185
9/19/75	43.83	5.5108	1.0808	2.5939	137.90	0.49	0.65	17.26	5.7568	0.1335
9/20/75	43.90	5.434	1.0626	2.5502	294.70	0.49	0.65	17.73	6.5365	0.1773
9/21/75	43.32	5.4568	1.0552	2.5325	329.25	0.53	0.63	15.89	7.4159	0.2347
9/25/75 (main)	43.26	5.2948	1.0102	2.1245	301.30	0.46	0.65	13.75	14.6455	0.9815
9/25/75 (trifle)	53.14	1.5941	0.2064	0.4954	301.30	0.46	0.65	14.34	-----	-----
10/11/75	36.15	3.0187	0.4386	1.0526	245.10	0.22	0.31	16.55	14.2534	3.7046

* See text for explanation.

Figure 4. Total gross production, respiration and isolation estimates are given for each sample day.



cance $\hat{\alpha} < 0.0001$. Similarly benthic production is highly correlated with the generated parameter trophogenic area, $r = 0.92$ with $\hat{\alpha} < 0.007$ (table 3). Parameters generated from bioassay of the light regime and morphometric measures were the most useful in accounting for variation in production estimates (table 3).

The ratio of gross production to gross respiration (P/R ratio) may be used as an index to classify aquatic systems as heterotrophic (P/R < 1) or autotrophic (P/R > 1). The P/R ratio of the Kansas River was not constant but increased with time and ranged from 0.26 to 37.0 (table 2).

Ortho-phosphate concentration declined at a linear rate with time (table 2). The decline of ortho-phosphate coincided with increased rates of production (table 2). This inverse relationship was highly significant (table 3).

Total photosynthetic production in a riffle area exceeded that of the main channel by 46% (table 2). Photosynthetic production of riffle plankton was proportionally less than main channel plankton reflecting the smaller volume of riffle water per unit area (table 2). The entire riffle substrate was included in the photic zone on 25 September 1975 (table 2). Some unknown fraction of main stream substrate was not illuminated; and part of what was illuminated was only marginally productive. Thus the riffle benthic production estimate was substantially higher than the main stream benthic estimate on a per area basis (table 2).

Discussion

Photosynthetic production in the Kansas River is intermediate compared to production estimates of other lotic systems (table 4).

Table 4. Comparisons of Stream Production Rates.

Lotic System	Daily Production (g O ₂ /m ²)	Daily Respiration (g O ₂ /m ²)	P/R
Silver Springs (Odum)	18.60	17.50	1.06
Blue River (Duffer and Dorris)	20.00	14.00	1.42
Ivel River (Edwards and Owens)	10.90	9.50	1.14
Madison River (Wright and Mills)	4.80	1.60	3.00
Buffalo Creek (McDiffett, et al.)	5.62	2.16	2.60
Lost Creek (channelized)	4.64	2.34	1.98
Lost Creek (natural) (Gelroth, 1976)	0.82	1.23	0.66
Kansas River (just after flood, 13 September 1975)	1.14	4.54	0.26
Kansas River (11 October 1975)	11.55	0.31	37.00*
Kansas River (14 July 1974) (Taylor)	14.46	4.74	3.05

*See discussion relative to low production or respiration estimates.

Low rates of production in the Kansas River reflect the absence of macrophytes, the mobile character of the substrate, and the relatively

greater levels of turbidity. The wide range between minimum and maximum production rates (table 2) is an indication of the short-term variability of photosynthetic production and respiration in the Kansas River.

The variability between seasons or from year to year is not known for the Kansas River. Preliminary work from the summer of 1974 suggests that under optimum conditions production in the Kansas River is comparatively intermediate. The point to be taken from the production values presented in Tables 2 and 4 is that an important factor in production rate variation is short term events such as floods or reservoir release patterns. Rates of flow effectively determine the trophic nature of the Kansas River.

The P/R ratios on September 13, 1975 and October 11, 1975 are, respectively, the lowest and highest estimates contained in table 4. These estimates may represent a sensitivity limit of the method rather than any real phenomenon. When rates of respiration and production are exceeded by the rate of diffusion, any estimate of biological parameters is more likely to represent an artifact of the method rather than a true estimate. We feel confident of P/R ratios in the Kansas River only when production and respiration estimates exceed $0.08 \text{ g O}_2/\text{m}^2/\text{day}$ for estimates based on analysis of diurnal oxygen curves (Taylor, 1976).

It is encouraging that two methods of production estimation (total and planktonic), each with different assumptions, yield production estimates which are highly correlated to generated parameters (trophogenic area and plankton density index) (table 3). This is evidence for believing the assumptions are not incorrect or over simplified. However, no independent second estimates of total, planktonic, or benthic production are presently possible. Production estimates should be regarded as tentative until the validity and compatibility of the techniques can be

established.

The riffle vs. mainstream estimates of September 25, 1975 (table 2) illustrate the need for caution. Oxygen probes were placed virtually in line on a transect across the Kansas River. The riffle production estimate exceeded the mainstream estimate by 25%. Under the assumption of stream homogeneity these estimates should have been the same. The riffle estimate was higher because the substrate was relatively solid and entirely trophogenic. Riffle water and mainstream water were mixed at the downstream end of a sandbar island that separated them. Only mainstream estimates were utilized on all other days with the assumption that latitudinal variation would be integrated by mixing. We were unable to test this assumption.

The development of the producer populations is illustrated by the regression of total production as a function of time (table 3). Planktonic and benthic production also increase with time (table 3) but cannot be interpreted as easily.

Preliminary investigation suggests that reservoirs in Kansas are not a significant source of plankton in the Kansas River (Marzolf et al., 1975). The flow of low order minor tributaries is small relative to the Kansas (figure 2), and the photosynthetic component of low order streams is typically low (figure 1); indicating that these streams are insignificant contributors of plankton. The high correlation ($r = 0.96$) of the linear regression of planktonic production on time offers no hint of exponentiality as would be expected if the plankton were contributing to themselves by growth. The proposed source of plankton is eroded benthos. The low correlation ($r = 0.75$) between time and benthic production (table 3) may be understood by considering the bio-morphological structure of lotic systems.

The relation between production rate and biomass in streams differs from that in lakes. Any production estimate is a measure of the product of biomass (cells) times production rate per cell. In streams increases in biomass increase production rate, but increases in production rates do not necessarily increase biomass in any given reach. This is a result of benthic erosion and short residence times for the phytoplankton.

The transitory nature of the suspended algae effectively eliminates any consideration of space limitation to plankton. In contrast, the benthic algae are limited horizontally by the area of trophogenic substrate and vertically by erosion. This fundamental difference between the benthic and planktonic communities is important in understanding:

- 1) the relation of each producer component to the physical environment, and
- 2) the temporal changes in producer community ratios.

The high correlation between time in days and the plankton density index ($r = 0.96$) is offered as explanation for the high correlation between planktonic production and time. The relationship between time and plankton density index seems reasonable since incident light and trophogenic depth increased as production in river increased. The high coefficient of correlation must be regarded as fortuitous in this short term study because every time interval will not occur as a recovery period.

The close correlation between planktonic production and plankton density index ($r = 0.98$; $\alpha = 0.0001$) is strong evidence that:

- 1) stream plankton are only derived from the benthos, and
- 2) erosion of benthic algae is a function of trophogenic area.

The close correlation of benthic production ($r = 0.92$; $\alpha = 0.007$)

on trophogenic area relates to the primary assumption behind the calculation of trophogenic area; i.e. that colonization and saturation are immediate when stable substrate is available. A lag in colonization and saturation time could explain why the benthic production-trophogenic area correlation coefficient is less than that yielded by the planktonic production-planktonic density index regression. Alternatively epipellic and epipsammic algal communities in lotic systems may be more variable than the stream plankton. The cumulative variance of the total and planktonic estimates is manifest in the benthic production estimate. These hypothesis are neither mutually exclusive nor testable with the results presented.

Floods reduce the autotrophic community by erosion, increased turbidity (reduction in trophogenic depth), and subsequent siltation. Heterotrophic activity is increased by runoff import of allocthonous organic matter and terrestrial microbes. Respiration was highest early in this study, when high waters were receding (table 2). The change in production to respiration ratio (P/R) through time illustrates that recovery from a period of high turbid flow involves a trend towards autotrophy; i.e. increased production and decreased respiration.

The variable nature of the flow of this river makes it likely that classification as autotrophic or heterotrophic depends on when the measurement is made. The trophic nature of the Kansas River is perhaps best classified as variable. This result may have implications on the character of the consumer communities.

Nutrient concentrations (ortho-phosphate, nitrite-nitrate nitrogen) were well above limiting concentrations required for algal blooms (table 2). The negative correlation between ortho-phosphate and production

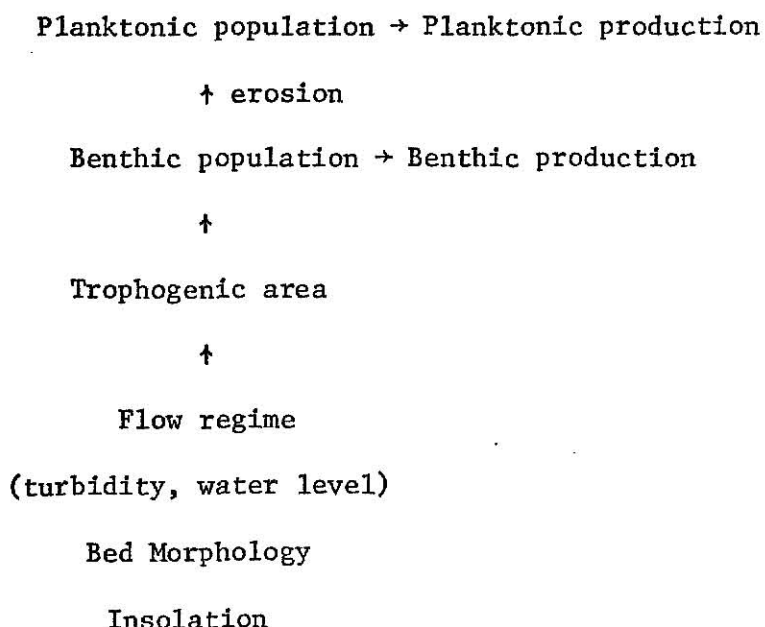
(table 3) may be interpreted as algal uptake, decreased runoff input, or fortuitous circumstance. Probably more important than the correlation is the fact that nutrient levels are so high in the Kansas River. These high nutrient levels probably reflect agricultural fertilization practices, feedlot drainage, and domestic effluents from Junction City and Fort Riley, Kansas.

Table 3 contains the remainder of the data as a correlation matrix. These data were reviewed and interpreted as less useful in understanding photosynthetic production than the variables already mentioned but are included here for completeness. No relationship contained in table 3 contradicts or offers evidence against any of the relationships or hypotheses expressed.

Population Dynamics: A Hypothetical Model

A structure has been erected for understanding the photosynthetic character of the Kansas River in terms of the physical environment.

In summary that structure is:



This structure is incomplete in that there is no consideration of population dynamics. Trophogenic area cannot be instantly saturated with benthic algae, and the rate of erosion is partially a function of benthic algal growth rate. Planktonic production has been estimated, yet planktonic reproduction was assumed to be zero.

The variable nature of flow and mobile character of substrates in great plains streams suggests that a common and perhaps pervading situation is the recovery (development) of photosynthetic activity, both benthic and planktonic. The situation modeled in this section is the development of photosynthetic producer populations under conditions of constant tur-

bidity, insolation, and flow (i.e. constant trophogenic area), following total erosion and export of the benthic and planktonic components. This model assumes:

- 1) Space (trophogenic area) limitation of the benthos,
- 2) No limitation of the plankton,
- 3) Plankton derive from the benthos by erosion,
- 4) Trophogenic area is constant,
- 5) Benthic and planktonic birth rates are constant, and
- 6) Zero mortality on both populations.

To begin the discussion the simplest case will be considered in which:

- 1) Only one diurnal interval (distance a water mass travels per unit time (t)) is considered,
- 2) The planktonic birth rate (b_o') = 0, and
- 3) The plankton are exported downstream and do not accumulate per unit volume of water.

Under these conditions all algae must derive from the benthos. Benthic mortality is assumed to be zero (6), thus the rate of erosion of benthic algae is analogous to benthic death rate and planktonic birth rate.

$$1) \frac{dd}{dt} = (d_o \cdot N(t))$$

$$\frac{dd}{dt} = \text{instantaneous death rate (erosion)}$$

$$d_o = \text{death (erosion) rate when } N = 0.$$

$$N(t) = \text{population size of the benthic algae at time } = t.$$

$$\frac{db}{dt} = \text{instantaneous birth rate (benthic) is assumed constant, no density dependence.}$$

$$= b_o$$

$$2) \frac{dN}{dt} = \left(\frac{db}{dt} - \frac{dd}{dt} \right) \cdot N(t)$$

$$\frac{dN}{dt} = \text{instantaneous rate of population change} \\ (\text{exponential growth model})$$

by substitution:

$$3) \quad \frac{dN}{dt} = (b_o - (d_o \cdot N_{(t)})) \cdot (N_{(t)})$$

Define K such that when $N_{(t)} = K$,

$$\frac{dN}{dt} = 0 \text{ (i.e. } K = \text{carrying capacity)}$$

At K:

$$4) \quad 0 = (b_o - d_o \cdot K) \cdot (K)$$

$$5) \quad d_o = b_o/K$$

by substitution equation 1 becomes:

$$6) \quad \frac{dN}{dt} = \left(\frac{b_o}{K} \right) \cdot (N_{(t)}) \\ = \frac{b_o \cdot (N_{(t)})}{K}$$

Therefore, equation 3 may be rewritten:

$$7) \quad \frac{dN}{dt} = \left(b_o - \frac{b_o \cdot (N_{(t)})}{K} \right) \cdot (N_{(t)}) \\ = b_o \cdot (N_{(t)}) \cdot \left(\frac{K - N_{(t)}}{K} \right)$$

(logistic growth model with $r = b_o$)

Population size of the benthic algae at time t is given by:

$$8) \quad N_{(t)} = \frac{K}{1 + e^{a-b_o t}}$$

a = constant of integration defining the position of the curve relative to the origin.

Population size of the planktonic or eroded algae is given by:

$$9) \quad \frac{dN_t}{dt} = \frac{b_o \cdot (N_{(t)}) \cdot (N_{(t)})}{K}$$

Note: Eroded (Planktonic) algae are assumed not to accumulate because they are exported downstream.

The ratio of benthic to planktonic population size and therefore benthic to planktonic production is given by:

$$\begin{aligned}
 10) \quad \frac{N(t)}{\frac{dd}{dt} \cdot (N(t))} &= \frac{N(t)}{\frac{b_o \cdot (N(t)) \cdot (N(t))}{K}} \\
 &= \frac{K}{b_o \cdot (N(t))} \\
 &= \frac{K}{b_o \cdot \left(\frac{K}{1 + e^{a-b_o t}} \right)} \\
 &= \frac{1 + e^{a-b_o t}}{b_o}
 \end{aligned}$$

However, for any given reach of real stream, plankton can accumulate in the sense that the water mass passing over that interval has previously passed over and eroded benthos from other upstream intervals. During the passage over these prior intervals planktonic reproduction may also contribute to the plankton.

Distance in a lotic system may be described by units of time if constant current velocity is assumed. Thus if the length of stream interval is defined as the distance a water mass travels in 24 hours (as it is for single station total production estimates); the amount of plankton (E_p) contributed by erosion from the benthic population at time = t from any interval is given by:

$$\begin{aligned}
 11) \quad (\text{Erosion Rate}_{(t)}) \cdot (\text{Benthic Population Size}_{(t)}) \\
 E_p = \frac{dd}{dt} \cdot (N(t)) = \frac{b_o \cdot (N(t)) \cdot (N(t))}{K}
 \end{aligned}$$

The contribution to the plankton by reproduction of the plankton (P_p) at time = t for a given interval X is given by:

$$12) P_p = b_o' (T_p \text{ at } (x-1) \text{ at } (t-1))$$

b_o' = planktonic birth rate

T_p = total plankton population

x = the distance from the stream interval sampled to the headwaters (reservoir) in 24 hr. time units (diurnal length)

The total plankton population at time = t for a given interval x is given by:

$$13) T_p(t) = E_p(t) + P_p(t)$$

$$14) = \frac{b_o (N(t)) \cdot (N(t))}{K} + (1 + b_o') \cdot (T_p \text{ at } (x-1) \text{ at } (t-1))$$

Plankton from erosion of benthos (E_p) accumulates per unit volume of water as a function of time, by the number of intervals eroded. Since the interval distance (x) has the same dimensions as time, plankton from erosion cannot accumulate beyond $t = x$ (except as erosion per interval (E_p) increases).

Planktonic contributions to the plankton at time = t and interval x are a function of the total planktonic population size at $(t-1)$ in interval $(x-1)$. The series of equations describing total planktonic population at time = t may be written:

		Total Plankton (T_p)	
$x = 4$	t	E_p	P_p
(for example)	1	E_{p1}	
	2	$E_{p2} + (1 + b_o') (E_{p1})$	
	3	$E_{p3} + (1 + b_o') (E_{p2} + (1 + b_o') (E_{p1}))$	
	4	$E_{p4} + (1 + b_o') (E_{p3} + (1 + b_o') (E_{p2} + (1 + b_o') (E_{p1})))$	
	5	$E_{p5} + (1 + b_o') (E_{p4} + (1 + b_o') (E_{p3} + (1 + b_o') (E_{p2})))$	
	6	$E_{p6} + (1 + b_o') (E_{p5} + (1 + b_o') (E_{p4} + (1 + b_o') (E_{p3})))$	
		or	
	1	E_{p1}	
	2	$E_{p2} + (1 + b_o') (E_{p1})$	
	3	$E_{p3} + (1 + b_o') (E_{p2}) + (1 + b_o')^2 (E_{p1})$	
	4	$E_{p4} + (1 + b_o') (E_{p3}) + (1 + b_o')^2 (E_{p2}) + (1 + b_o')^3 (E_{p1})$	
	5	$E_{p5} + (1 + b_o') (E_{p4}) + (1 + b_o')^2 (E_{p3}) + (1 + b_o')^3 (E_{p2})$	
	6	$E_{p6} + (1 + b_o') (E_{p5}) + (1 + b_o')^2 (E_{p4}) + (1 + b_o')^3 (E_{p3})$	

The generalized equation for the total plankton population (T_p) at any given interval (x) for any given time (t) is:

$$15) \quad T_{p(\text{at } x \text{ and } t)} = E_p(t) + (1 + b_o') E_{p(t-1)} + (1 + b_o')^2 E_{p(t-2)} + \dots + (1 + b_o')^{(x-1)} E_{p(t-x+1)}$$

The ratio of benthic to planktonic production (assuming production rate is proportional to population size) is given by:

$$16) \quad \frac{\text{Benthic}}{\text{Planktonic}} = \frac{N(t)}{T_p(\text{at } x \text{ and } t)}$$

$$17) \quad = \frac{K (1/1 + e^{a-b_o t})}{E_p(t) + (1 + b_o') E_{p(t-1)} + (1 + b_o')^2 E_{p(t-2)} + \dots + (1 + b_o')^{(x-1)} E_{p(t-x+1)}}$$

E_p may be written:

$$18) \quad E_p = \frac{b_o' (N(t)) \cdot (N(t))}{K}$$

$$19) \quad \text{From equation 8: } N(t) = \frac{K}{1 + e^{a-b_o t}}$$

20) Substituting for $N(t)$ in equation 18 gives:

$$E_p = b_o' \cdot \left(\frac{K}{1 + e^{a-b_o t}} \right) \cdot \left(\frac{K}{1 + e^{a-b_o t}} \right)$$

substitution and factoring gives:

$$\frac{\text{Benthic}}{\text{Planktonic}} =$$

$$\frac{K \left(\frac{1}{1 + e^{a-b_o t}} \right)}{b_o' K \left[\left(\frac{1}{1 + e^{a-b_o t}} \right)^2 + (1 + b_o') \left(\frac{1}{1 + e^{a-b_o(t-1)}} \right)^2 + (1 + b_o')^2 \left(\frac{1}{1 + e^{a-b_o(t-2)}} \right)^2 + \dots + (1 + b_o')^{(x-1)} \left(\frac{1}{1 + e^{a-b_o(t-x+1)}} \right)^2 \right]}$$

=

$$\frac{1}{b_o' (1 + e^{a-b_o t}) \left[\left(\frac{1}{1 + e^{a-b_o t}} \right)^2 + (1 + b_o') \left(\frac{1}{1 + e^{a-b_o(t-1)}} \right)^2 + (1 + b_o')^2 \left(\frac{1}{1 + e^{a-b_o(t-2)}} \right)^2 + \dots + (1 + b_o')^{(x-1)} \left(\frac{1}{1 + e^{a-b_o(t-x+1)}} \right)^2 \right]}$$

For purposes of comparison and graphical illustration, the following constants have been assigned values:

$$b_o = 0.75$$

$$K = 100$$

$$a = 4$$

The increase of benthic algae and subsequent erosive contributions to the plankton for a single interval over time are illustrated in figure 5. Near the benthic carrying capacity (K) the erosive contribution to the plankton is given by the benthic birth rate (b_o) times the standing crop ($\sim K$).

If the planktonic birth rate is zero (i.e. no planktonic contribution to the plankton), as it is for the generation of plankton density index, the plankton population density at interval $x = 4$ over time is given by figure 6. A family of curves for different values of b_o' over time is also given by figure 6.

Benthic to planktonic ratios over time are given for:

- 1) no accumulation,
- 2) accumulation but no planktonic contributions ($b_o' = 0$),
- 3) accumulation and planktonic contribution ($b_o' = 0.75$), and
- 4) interval $x = 4$

by figure 7.

This model predicts increased plankton densities downstream (i.e. larger interval number). At or near K (time = 99), the plankton population size versus interval number is plotted for:

- 1) accumulation but no planktonic contributions ($b = 0$), and
- 2) accumulation and planktonic contribution ($b = 0.2$; 0.75 ; and 1.0) (figure 8).

Figures 5 through 7 may be compared with the observed planktonic and benthic production curves (figure 9) and the observed benthic to planktonic ratio (figure 10). The same interval was sampled on every day; this study offers no data to compare with the accumulation per interval curves (figure 8).

The observed benthic production curve (figure 9) is essentially sigmoidal as predicted by the model. The observed planktonic production curve is also sigmoid, consistent with the model. The observed planktonic production curve asymptotes below the benthic production curve differing from all the model plankton curves that assume accumulation, regardless of birth rate. It is interesting that the observed plankton asymptote is smaller than the benthic asymptote. The interval number of the actual sample site is not known, but cannot be less than six or seven (figure 1, table 2). Even with zero plankton reproduction the planktonic asymptote should have been much larger than the benthic asymptote (figure 6). One explanation is a mortality associated with the plankton. The nature of this mortality is unknown, but high densities of net building caddis flies (filtering herbivores) have been observed, and turbulent flow can destroy algal cells (Hynes, 1974). Another explanation is that the production rate per cell of benthos may be greater than the production rate per cell of plankton. Comparing the two populations by production estimation may bias the comparison.

The observed benthic/planktonic production ratio curve (figure 10) compares favorably with those predicted by the model (figure 7) if the first few points are ignored. The extremely high ratios predicted by the model early in the recovery period reflect extremely low levels of plankton density. In a natural system such as the Kansas River, plankton

originating from tributaries, ponds, and reservoirs are especially likely to be washed in during an erosive event such as flood or large reservoir outflow (Hynes, 1974). Potentially it was plankton from these sources that depressed the benthic to planktonic ratio in the early recovery period. As riparian photosynthetic activity increased, these sources would become relatively and actually less.

The observed benthic, planktonic, and benthic/planktonic ratio curves are consistent with the model. Comparisons of model prediction curves with actual data should be regarded as tentative. The steady-state conditions under which the model curves were generated did not exist in the Kansas River from September 13, 1975 to October 11, 1975 (table 2). The curves of benthic and planktonic production versus time (figure 9) depend on a single estimate (October 11, 1975) for their sigmoidal shape. The observed relationships support but by no means verify the hypothetical population models.

Direct synthesis of the previously discussed environmental variables and the population model may offer the most realistic paradigm, and could easily be accomplished by slight modification of a few equations. However, such a synthesis could offer nothing new, but only reiterate what would be redundant arguments. The critical test of both the environmental and population hypothesis will require sustained and long term assessment of both benthic and planktonic population sizes, production rates, and mortality rates.

Figure 5. Benthic population size and eroded benthos per day for a single interval vs. time in days.

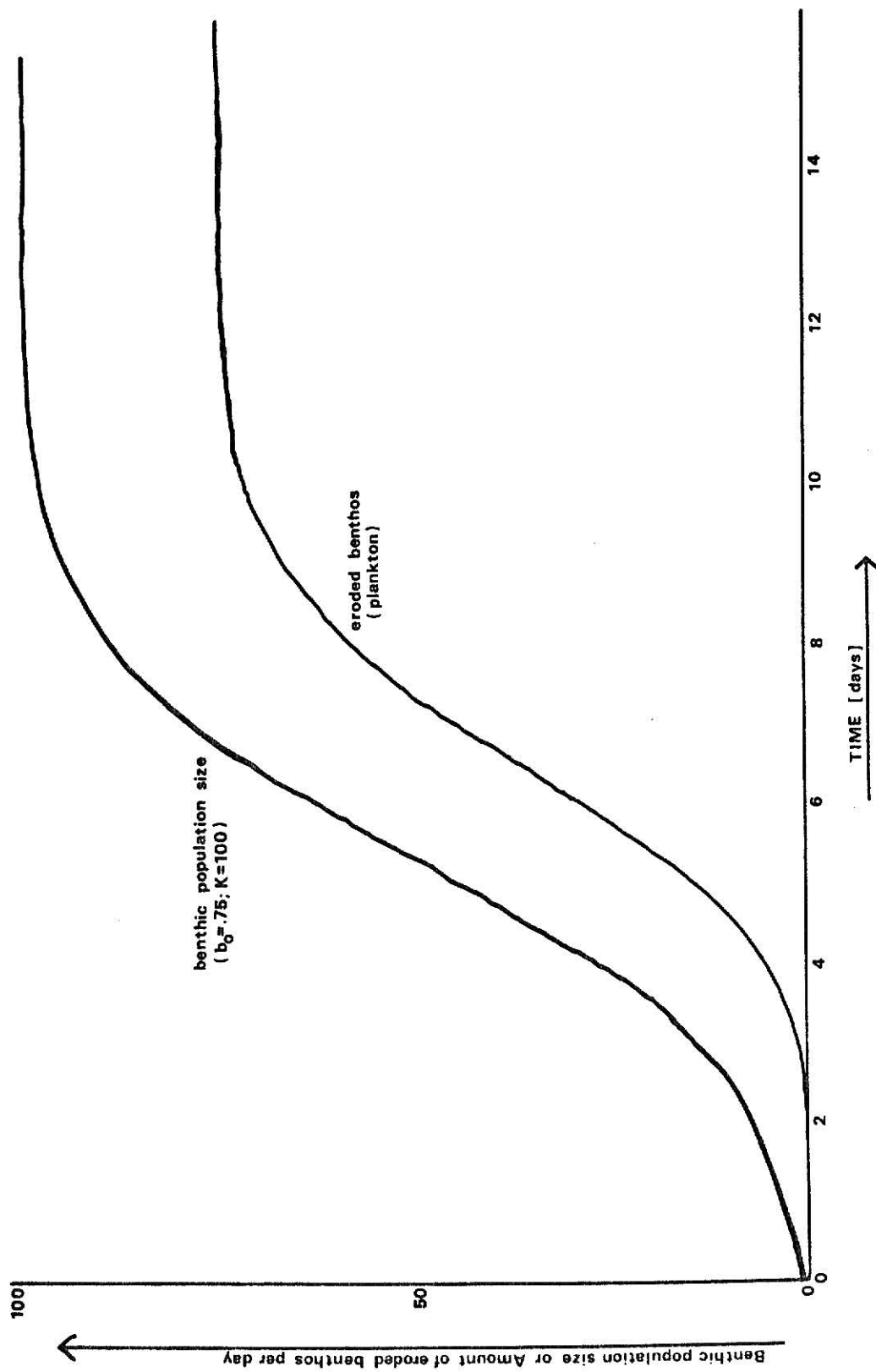


Figure 6. Planktonic (and benthic) population size for interval ($x = 4$) assuming no planktonic reproduction ($b_o' = 0$) and planktonic birth rates (b_o') of 0.75 and 1.0 vs. time in days.

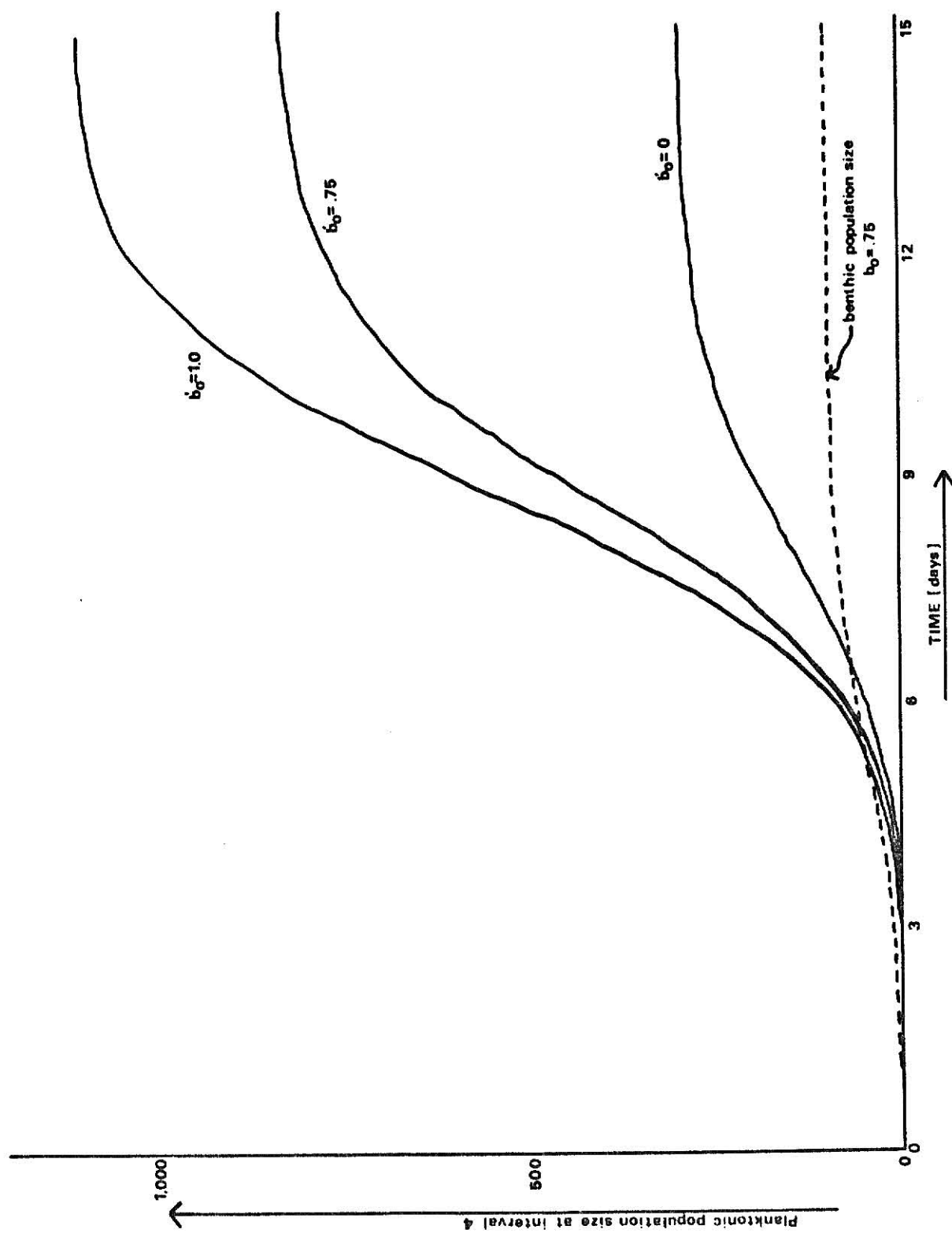


Figure 7. Benthic to planktonic population and/or production ratios for interval ($x = 4$) assuming:

- 1) no accumulation and no reproduction of plankton,
- 2) accumulation but no reproduction of plankton, and
- 3) accumulation and reproduction of plankton vs. time in days.

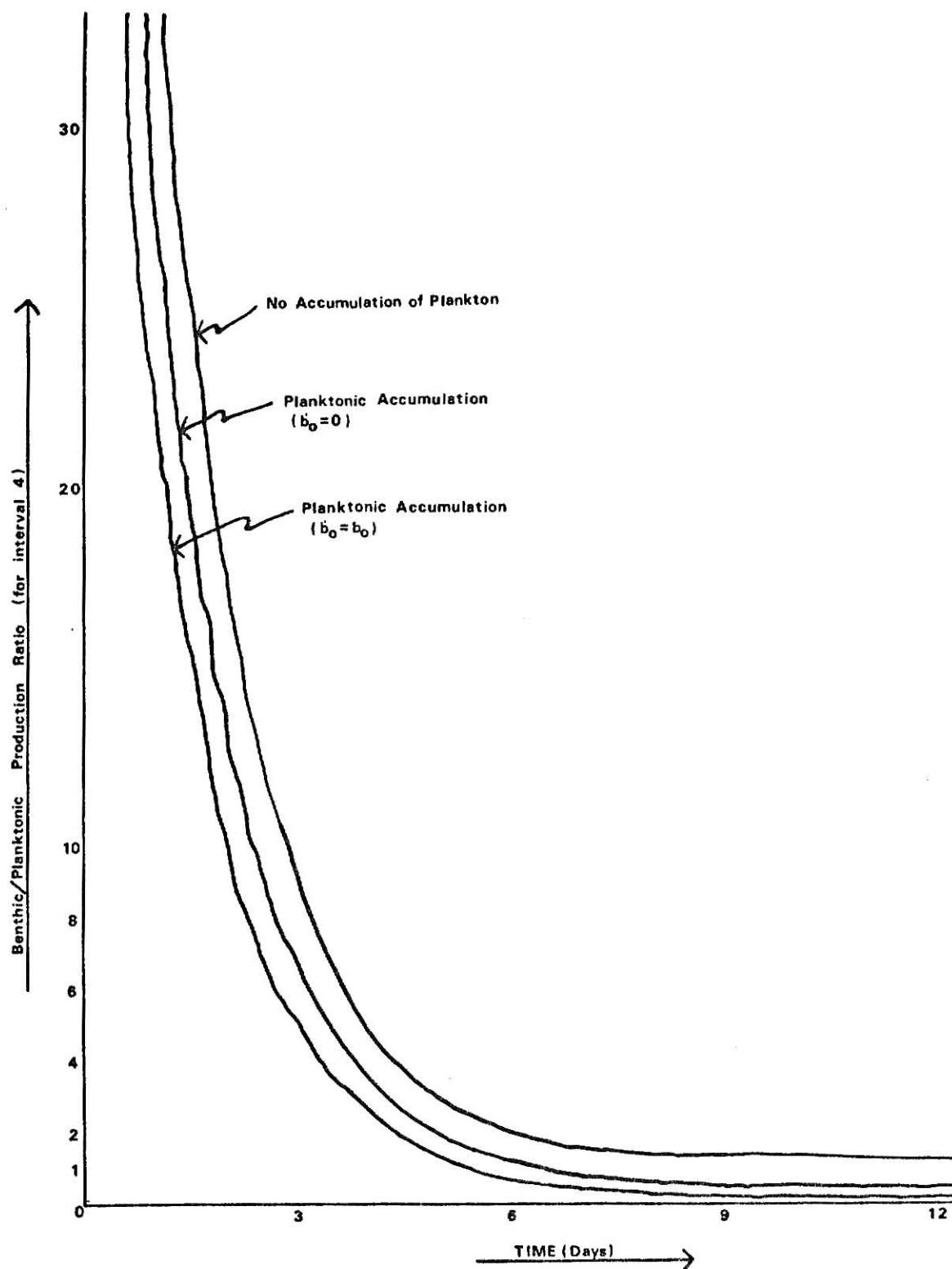


Figure 8. Population size of plankton (and benthos) vs. interval number for various birth rates (b_0) of the plankton at benthic population = K.

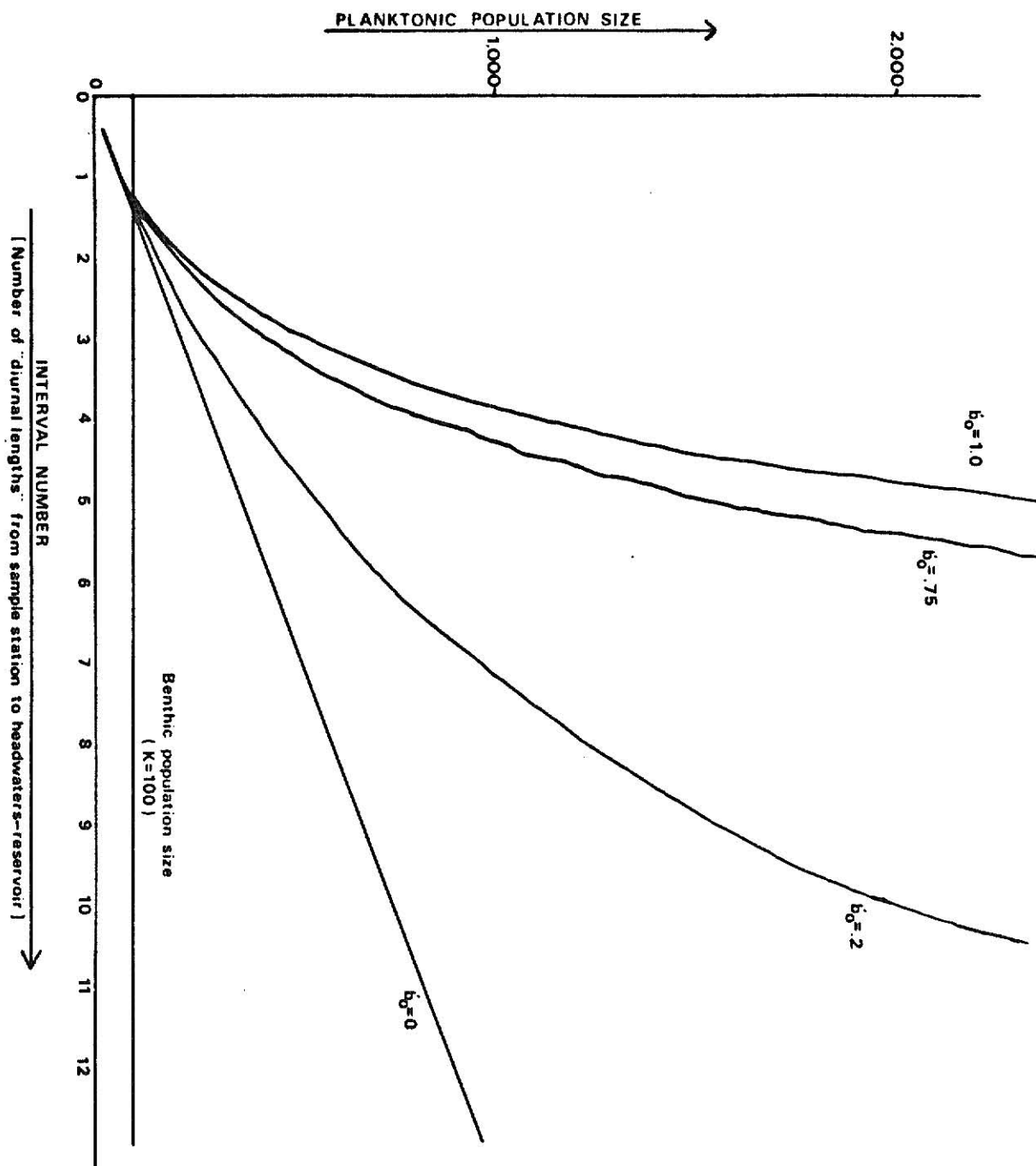


Figure 9. Observed benthic (X's) and planktonic (O's) production rates
vs. time in days from 9/12/75.

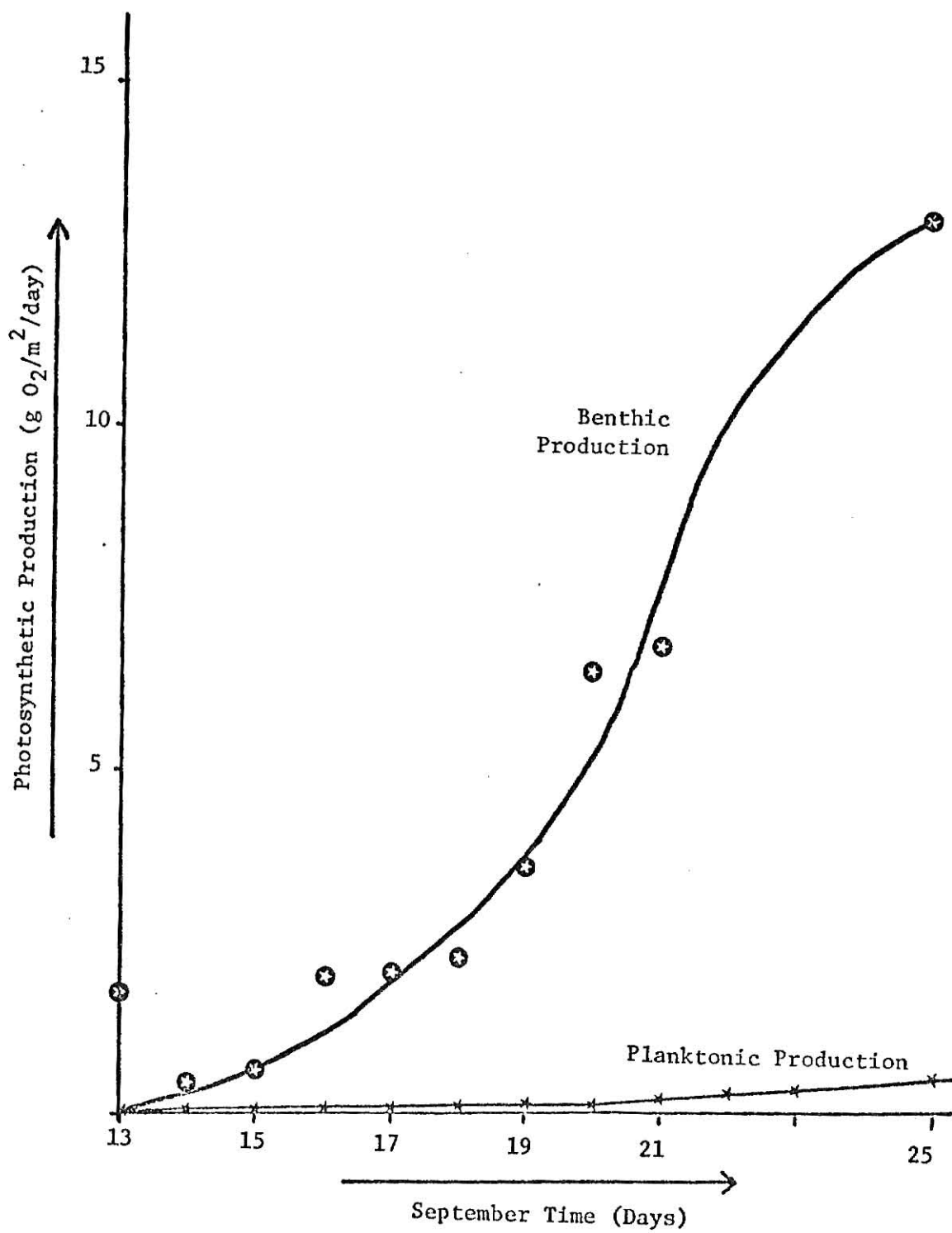
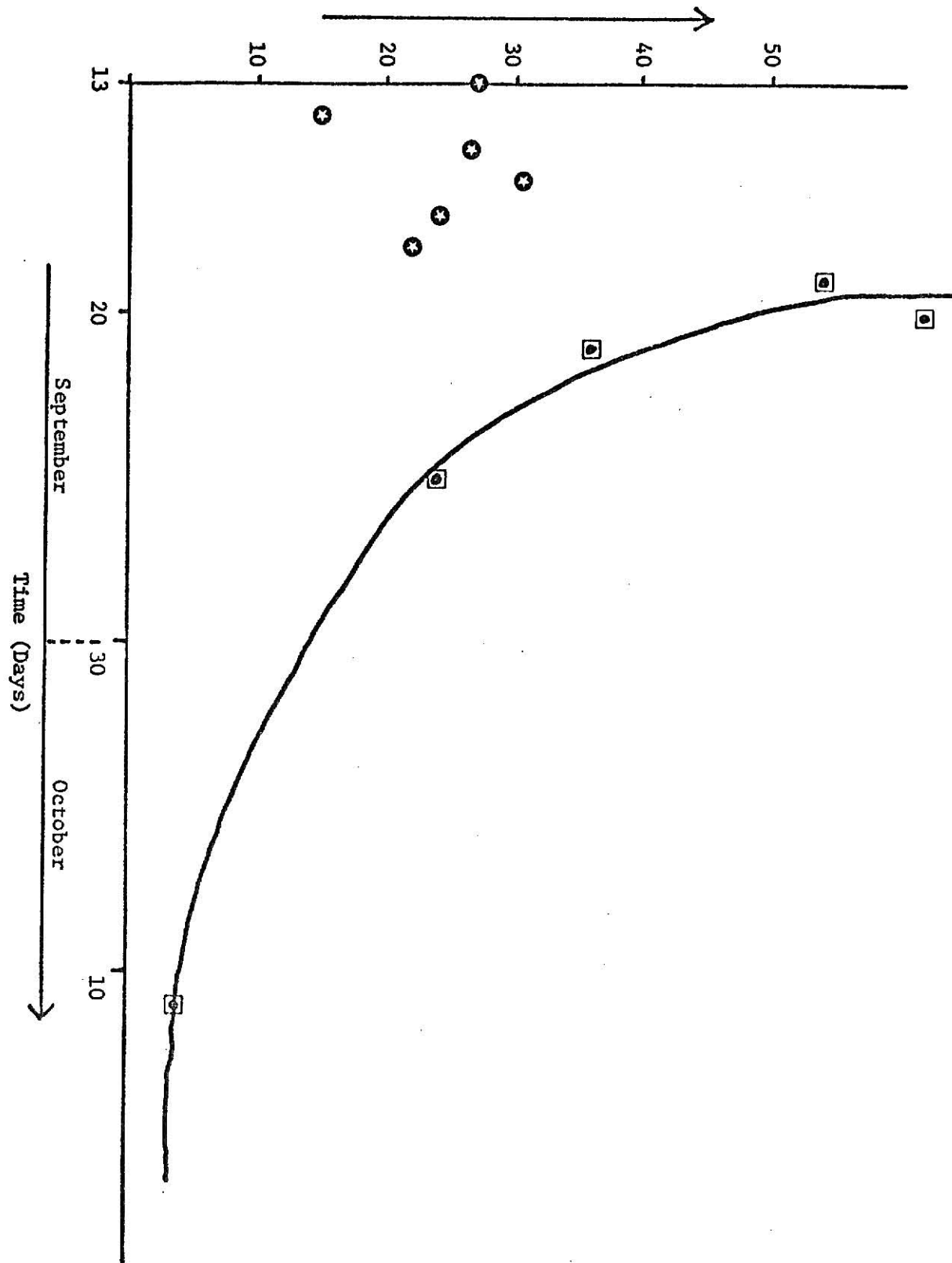


Figure 10. Observed benthic to planktonic production ratio vs. time in days from 9/12/75. See text for explanation of circle-star points early in the sample period.



Summary

The following characteristics of lotic production of medium order sandy substrate streams are suggested:

- 1) photosynthetic activity of the benthos and plankton,
and the trophic character of the river fluctuate according
to flow patterns,
- 2) the variable nature of flow patterns and high nutrient
concentrations make morphology and trophogenic regime
important in understanding photosynthetic production,
- 3) the benthic algal population at any interval is space limited
by trophogenic area and erosion,
- 4) the planktonic algal population originally derives by erosion
from the benthos,
- 5) the planktonic algal population at any interval is limited by:
 - i) the area and erosion rate of upstream benthos,
 - ii) the planktonic reproduction and mortality rate, and
 - iii) the downstream export rate,and
- 6) planktonic population densities increase downstream.

PART 2
PARAMETERS RELEVANT TO THE DISTRIBUTION OF
BENTHIC PHOTOSYNTHETIC PRODUCTION

Introduction

The importance of the benthos as a source of plankton and photosynthetic production is paramount in consideration of lotic primary productivity (Part 1). Benthic algae occur as "irregular mosaics on stream and river beds" (Hynes, 1974). The species composition of benthic algal communities has been found to be extremely variable both in space and time (Blum, 1960; Hynes, 1974). Habitat instability has been advanced as one explanation for the distribution patterns of benthic algae (Hynes, 1974). This effort is a preliminary examination of selected habitat parameters potentially important in the spatial variability of the benthic photosynthetic community.

Gross benthic photosynthetic production was indexed by inoculating light and dark bottles with cores of sediment. These experimental perturbations were conducted in conjunction with measurements of potentially controlling physical parameters in order to provide a data set for multiple regression analysis.

Core inoculation of light and dark bottles has not been established as a valid index or estimate of benthic photosynthetic production (Hynes, 1974). An experimental evaluation of core inoculation was conducted prior to the application of this technique to the benthic distribution problem. The results of this evaluation are given and discussed prior to the results and discussion of the actual study.

Materials and Methods

The dependent variable in the analysis is the index of gross benthic production in mg O_2 /liter. Gross benthic photosynthetic production for benthic algae of each sample site was indexed by inoculating two light and two dark bottles with a core taken from the substrate (Kobayasi, 1961). The corer was a glass tube with an inside diameter of 13 mm. The tube was calibrated in increments of about 2 cc.

Samples were taken by pushing the corer into the substrate to the 6 cc. mark. One finger was pushed down beside and under the corer. The core was removed with the finger covering the bottom, holding the core in the tube.

Inoculation was accomplished by inserting the end of the corer into the neck of the bottle and removing the covering finger. Inoculated bottles were filled, but not overflowed, at dawn, by siphon, from a carboy of river water.

Initial oxygen concentration was established by fixing two bottles at dawn. All other bottles were incubated just under the surface for a period of six hours, beginning at dawn. Two light and two dark bottles were not inoculated. These served as controls and estimated the phytoplankton contribution to inoculated bottle production.

The method of calculation for the benthic production index is:

[I] = initial $[O_2]$

[LI] = inoculated light bottle $[O_2]$

[DI] = inoculated dark bottle $[O_2]$

[LC] = control light bottle $[O_2]$ (no core added)

[LD] = control dark bottle $[O_2]$ (no core added)

$$\begin{aligned}
 & [LI] - [I] = \text{Net Production of Inoculated Bottles} \\
 & \quad \quad \quad \text{(benthic and planktonic)} \\
 & - [LC] - [I] = \text{Net Production of Control Bottles} \\
 & \quad \quad \quad \text{(planktonic)} \\
 \hline
 & [LI] - [LC] = \text{Net Production of Core} \\
 & \quad \quad \quad \text{(benthic)} \\
 \\
 & [I] - [DI] = \text{Gross Respiration of Inoculated Bottles} \\
 & \quad \quad \quad \text{(benthic, planktonic, chemical, and microbial)} \\
 & - [I] - [DC] = \text{Gross Respiration of Inoculated Bottles} \\
 & \quad \quad \quad \text{(planktonic)} \\
 \hline
 & [DC] - [DI] = \text{Gross Respiration of Core} \\
 & \quad \quad \quad \text{(benthic, chemical, and microbial)} \\
 \\
 & [LI] + [DI] - [LC] - [DC] = \text{Gross Production Estimate or Index} \\
 & \quad \quad \quad \text{(mg O}_2\text{/6 hour incubation period)}
 \end{aligned}$$

All concentrations represent two bottle averages expressed in mg O₂/liter/6 hour incubation period.

Two sample site locations per day were sampled in duplicate sets. One set of light and dark bottles was incubated at the surface. The other set was returned to the depth from which the core was taken.

The depth incubations were intended as a check on the effect of subjecting a "deep" sample to surface light intensities. It was postulated that actual production at depth could be estimated by decreasing the surface estimate in proportion to the decrease in production with depth given by the plankton production curve (Part 1) determined on that day:

$$\frac{\text{Planktonic production (surface)}}{\text{Planktonic production (depth)}} = \frac{\text{Benthic production (surface)}}{\text{Benthic production (depth)}}$$

Benthic production (depth) =

$$\frac{\text{Benthic production (surface)} \times \text{Planktonic production (depth)}}{\text{Planktonic production (surface)}}$$

All bottles were held in horizontal position by metal racks.

Sample sites were selected to maximize the variety and range of parameter combinations studied.

Parameters selected as potentially controlling or at least influential in benthic photosynthetic production may be divided into two categories. Those which affect benthic production at all sample sites simultaneously; i.e.: incident light, light extinction coefficient, phosphate concentration, nitrate concentration, and temperature. And those parameters which are site specific in their effect on production; i.e.: depth, available light, current velocity and substrate particle size. Parameters in the simultaneous class vary only from day to day. Site specific parameters in the local class vary with each observation. Methods of estimating all parameters except particle size are given in Part 1.

Sediment samples for particle size analysis were taken with the corer as described earlier. Two or three cores provided sufficient sample volume for sieve analysis. Samples were dried and sieved through mesh sizes coinciding with integer phi values between 8 and -7 (table 5).

Table 5. Grain-Size Scales for Sediments (after Folk, 1974).

Millimeters	Phi	Wentworth Size Class
256	8.0	Boulder
		Cobble
64	-6.0	
16	-4.0	
8	-3.0	Pebble
4	-2.0	
		Granule
2.0	-1.0	
1.0	0.0	Very coarse sand
		Coarse sand
0.50	1.0	
0.25	2.0	Medium sand
0.125	3.0	Fine sand
0.0625	4.0	Very fine sand
		Coarse silt

Table 5. (continued)

Millimeters	Phi	Wentworth Size Class
0.031	5.0	
0.0156	6.0	Medium silt
0.0078	7.0	Fine silt
0.0039	8.0	Very fine silt
Clay		

The relationship of particle size in millimeters to phi diameter is:

$$\phi = -\log_2 (\text{particle size (mm)}) \quad (\text{Krumbein, 1936})$$

Median phi was chosen to characterize the sediment. This measure was selected because it was the single measure that seemed likely to best describe the sediment.

Median phi (Med. ϕ) is the average of the phi categories multiplied by their respective weights and divided by the total weight (Inman, 1952):

$$\text{Med } \phi = \frac{\sum_{i=1}^8 \phi(i) \times \text{Weight}(i)}{\text{Total Weight}}$$

Least squares linear regression of parameter values on the benthic production index was done with a catalogued statistical program titled "Statistical Analysis System" available through IBM at the K.S.U. computer center.

Evaluation of Methods

Preliminary attempts to evaluate and validate the core inoculation approach to indexing benthic production took the form of hypothesis testing. Null hypothesis were formulated and a level of significance (α) = 0.05 chosen as critical. Non-parametric test statistics were used. The following null hypothesis were tested:

- 1) Ho: Benthic production index is independent of the number of cores inoculated,
 Ha: Benthic production index is directly proportional to the number of cores inoculated.
- 2) Ho: Benthic production index is directly proportional to the volume of core inoculated,
 Ha: Benthic production index is independent of the volume of the core added.
- 3) Ho: Benthic production index is directly proportional to nitrite-nitrate and ortho-phosphate concentrations,
 i.e. benthic production index response to inoculation is in part a nutrient enhancement phenomena,
 Ha: Nutrient enhancement is not an important component of benthic production index.
- 4) Ho: Benthic production index (depth) = Planktonic production

$$(\text{depth}) \times \frac{\text{Benthic production index (surface)}}{\text{Planktonic production (surface)}}$$
 Ha: Benthic production index (depth) = Planktonic production

$$(\text{depth}) \times \frac{\text{Benthic production index (surface)}}{\text{Planktonic production (surface)}}$$

Null hypothesis 1 was formulated to examine the question: Does addition of core samples actually increase the production index? The data set for this experiment was generated by triplicate sampling of an apparently homogenous area of benthic algae. Zero, one, two, three, four, and five 6 c.c. cores were triple replicated and incubated for about six hours. Volume and surface area sampled were held constant for each core.

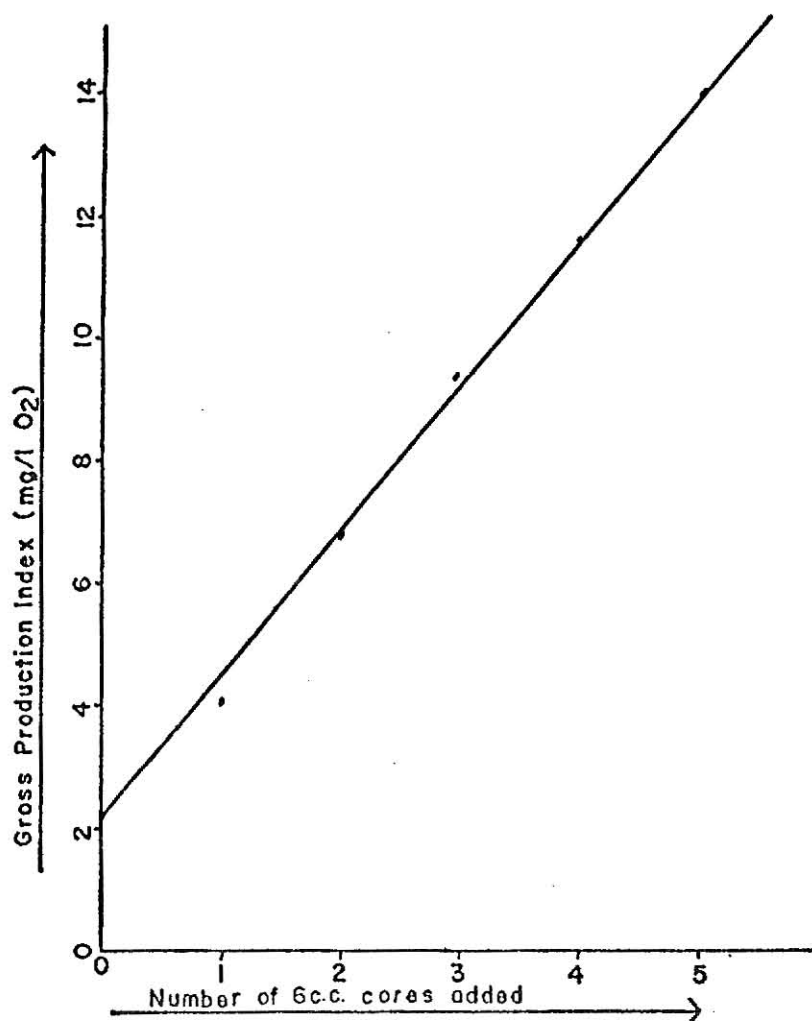
Least squares linear regression of numbers of core on gross production index yielded a correlation coefficient of 0.99 ($\hat{\alpha} < 0.01$) (figure 11). Null hypothesis 1 was rejected indicating a linear or sequential increase in gross production index with linear increase in number of core inoculated.

Null hypothesis 2 allows a test to determine whether volume or surface area of core determines the magnitude of benthic production index. Core volume may be varied by inserting the tube sampler deeper or shallower in the sediment. Core volumes of 0, 2, 4, 6, and 8 c.c. were sampled representing a range in depth of 0 to 4 centimeters. Three sediment types were sampled: mud, shallow water (< 10 cm.), sand, and deep water (> 40 cm.) sand. Initial oxygen concentration was established prior to 9 six hours of incubation period. Four samples for each core volume were incubated from each substrate type.

Table 6 presents the four bottle averages for each core volume from each substrate type. Each substrate type was analyzed independently with regard to null hypothesis 2. The null hypothesis was rejected in all the cases (Hotelling-Pabst test). This experiment is interpreted as indicating that volume of core, if greater than 2 c.c., is not critical to the gross production index.

The estimates of gross respiration are included in table 6 to illustrate

Figure 11. Gross production index values vs. number of constant
volume cores added.



a difference in substrate types. Respiration was substituted for production in null hypothesis 2. The modified null hypothesis is rejected for the mud substrate but not rejected for either of the sand substrate types.

Table 6. Substrate production and respiration index for increasing core volumes with core surface area held constant.

Station	Treatment (4 bottle avgs.)	Gross (mg O ₂ /liter)	Respiration (mg O ₂ /liter)
mud	2 c.c.	6.85	3.77
	4 c.c.	6.31	4.14
	6 c.c.	6.55	5.12
	8 c.c.	6.44	5.57
sand "shallow" 5 c.m.	2 c.c.	6.72	1.54
	4 c.c.	6.24	1.09
	6 c.c.	6.00	0.94
	8 c.c.	6.09	1.01
sand "deep" 1 m.	2 c.c.	5.90	0.93
	4 c.c.	5.53	1.14
	6 c.c.	6.38	1.57
	8 c.c.	5.97	1.35
control	no core	5.12	0.86

The results of null hypothesis 1 and null hypothesis 2 are interpreted as indicating that surface area of cores, rather than factors associated with underlying sediments affect the benthic production index.

The increase of respiration from mud substrate inoculates suggests that microbial population density and/or chemical oxidation demand are substantial. The relatively smaller particle size (greater surface area), higher concentrations of organic substances, and resulting anaerobic (reduced) environment of the mud are potentially the factors most important in the differential respiratory requirements of mud versus sand sub-

strate.

Inoculated dark bottles estimate algal, microbial, and chemical respiration in unknown ratios. Only gross production can be indexed by the oxygen concentration difference in light and dark bottle incubations.

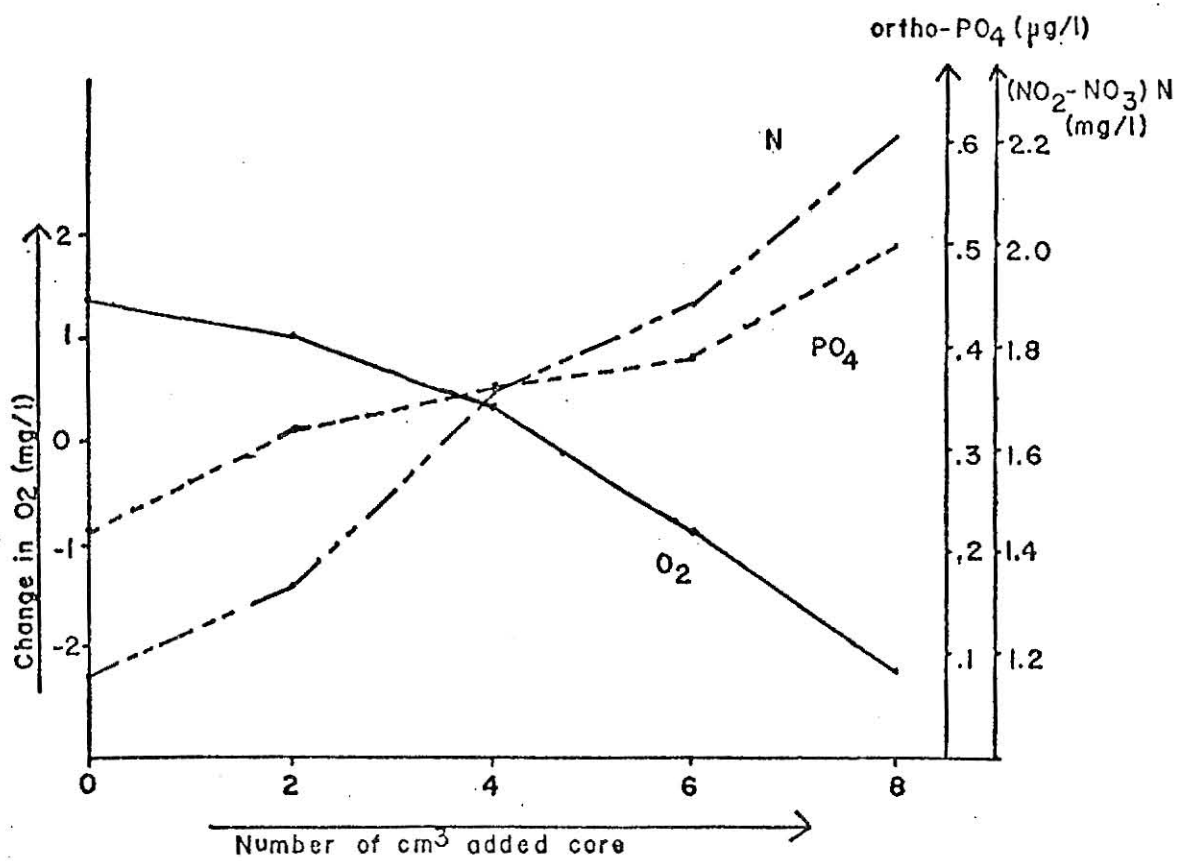
The possibility of a nutrient enhancement response caused by addition of reduced (soluble) nutrients from the core inoculate is suggested by the respiratory requirements of the mud substrate. Null hypothesis 3 examines this possibility. Light bottles containing viable river plankton were inoculated with 0, 2, 4, 6, and 8 c.c. of autoclaved mud core, and incubated for approximately six hours. Six replicates of each core volume were inoculated. Initial oxygen concentration was also estimated with six replicate samples. Concurrently concentrations of ortho-phosphate ($\mu\text{g/liter}$) and nitrite-nitrate nitrogen (mg/liter) were triplicate estimated before and after inoculation by a Hack Chemical Co. procedures.

Table 7 summarizes the data set. Figure 12 shows the relation between the change in oxygen concentration (left axis) and nutrient concentrations (right axis); each plotted as a function of autoclaved core added.

The elimination of microbial respiration and subsequent sequential decrease in oxygen concentration (figure 12 and table 7) indicates that chemical oxidation may be a substantial fraction of the oxygen consuming activity of mud core inoculate. Alternately, autoclaving may release dissolved organic matter and particulate organic matter which is more easily respired by river bacteria than that which is present in untreated cores or river water. It is also apparent that ortho-phosphate and nitrite-nitrate nitrogen are being added by core inoculation (figure 12).

It is not possible to independently examine either plankton production, microbial respiration, or chemical oxidation with this data set. The suggestion of nutrient enhancement remains an important criticism of

Figure 12. Change in O_2 , ortho- PO_4 , (NO_2 - NO_3) N concentrations (relative to initial concentration) vs. number of cm^3 (volume) of autoclaved core added. Increasing numbers of cm^3 added also indicated increased depth of core. Incubation time equals approximately six hours.



the core inoculation technique for indexing gross production; however, the effects of doubling nutrient concentrations already sufficient to support bloom conditions (table 7) are not likely to be manifest as drastic increases in algal production (Droop, 1973).

Table 7. Gross production index and nutrient concentrations for increasing inoculation volume of autoclaved mud core (six replicate averages).

	Control (no core added)	2 c.c.	4 c.c.	6 c.c.	8 c.c.
Change in $[O_2]$ (mg/l)	1.38	1.01	0.34	-0.93	-2.25
$[PO_4]$ (μ g/liter)	0.22	0.32	0.36	0.39	0.50
$[NO_2-NO_3 \text{ N}]$ (mg/liter)	1.16	1.33	1.72	1.88	2.21

The effect of subjecting a core taken at "depth" to surface light intensities was not known. At two stations, each sampling day, replicate cores were incubated. It was suggested (null hypothesis 4) that surface incubated cores could be corrected by comparison with the planktonic depth vs. production curve (from Part 1) of that day. Table 8 lists the observed (in situ) and expected (calculated) benthic production estimates. Chi square analysis resulted in the rejection of null hypothesis 4.

Under null hypothesis 4, the signs of the differences between calculated and measured values of the gross production index should have been 1/2 (+) and 1/2 (-). Based on the data contained in table 8, the null hypothesis is rejected. In situ estimates exceeded calculated or graphical estimates by an average of 0.61 mg/liter O_2 (table 8). This mean difference

had an associated standard deviation of 0.80. The large variance of the mean difference relative to the gross production index values caused the mean difference to be unacceptable as a correction factor.

Table 8. Calculated and measured values of the gross production index for the periods 13 September 1975 - 21 September 1975, 25 September 1975 and 11 October 1975.

Date	In Situ (measured)	Graphical (calculated)	(In Situ - Graphical)
9/13/75	1.90	1.60	0.30
	0.42	0.57	-0.15
9/14/75	-0.06	0.00	-0.06
	-0.24	0.00	-0.24
9/15/75	0.14	0.14	0.00
	3.38	1.43	1.95
9/16/75	0.60	0.43	0.17
	1.96	1.37	0.59
9/17/75	0.62	0.00	0.62
	0.04	0.00	0.04
9/18/75	0.42	0.00	0.42
	-0.08	0.00	-0.08
9/19/75	1.10	0.80	0.30
	0.08	0.00	0.08
9/20/75	0.80	0.00	0.80
	1.42	0.00	1.42
9/21/75	1.14	0.00	1.14
	0.04	0.00	0.04
9/25/75	2.26	0.76	1.50
	1.40	0.59	0.81
10/11/75	9.70	6.65	3.05
	8.46	7.75	0.71
			0.61 = mean
			0.80 = standard deviation
			0.17 = standard deviation from the mean

The effect of current as a physiological enricher by constant renewal of dissolved material gradients is well documented (Rutter, 1926; McIntyre, 1966a, b; Hynes, 1974). The effect of current is lost by enclosing the benthos in a bottle. Generating a gross production index by core inoculation and surface incubation of light and dark bottles imposes an artificiality that may distort the actual process being indexed. Numerous assumptions of the light and dark bottle technique are erroneous (Wetzel, 1976). Thorough discussion of the kinds and magnitudes of error in light and dark bottle methods is given by Strickland (1960), Vollenweider et al. (1969), and Strickland and Parsons (1972).

Null hypothesis 1, 2, and 4 were rejected. Insufficient data was collected to provide a test for null hypothesis 3. No independent estimate of benthic production was achieved to validate the inoculated light and dark bottle index. Core inoculation was not positively established as a method of indexing gross benthic production, but no result was inconsistent with that hypothesis. One should regard the benthic production index as a tenable if unproven assumption.

Results

Including all eight independent variables in a linear regression model resulted in an R^2 of only 0.4687, $\hat{\alpha} = 0.001$. Less than one half of the variation in benthic production index was accounted for by all the environmental variables measured. A model containing only time and depth as variables yields an R^2 of 0.4386, $\hat{\alpha} = 0.0001$. The next best two variable model contains time and current velocity ($R^2 = 0.3769$, $\hat{\alpha} = 0.0001$).

The correlation matrix for all variables is given by table 9. The correlation coefficients of the nutrient variables (ortho- PO_4 and NO_2 - NO_3 N) on benthic production index are exceeded only by the r associated with the variable time (table 9). The nutrient variables are closely correlated with time (table 9). Inclusion of the nutrient variables in regression models already containing the variable time increases the R^2 by only 0.004. Nutrient concentrations are above those required for bloom conditions (see Part 1 for discussion). The correlation between benthic production index and the nutrient variables is interpreted as a result of the time nutrient correlation and not the result of some causal relationship.

Table 9. Correlation coefficients (r) and observed levels of significance ($\hat{\alpha}$) for the correlation matrix of both benthic production index and associated environmental variables.

		Benthic Production Index (mg O ₂ /m ²)	Time (days)	Ortho-PO ₄ (μ g/l)	NO ₂ -NO ₃ N (mg/l)	Velocity (m/sec)	Temp. ° C	Isolation ² (gm-cal/cm ²)	Median ϕ
Benthic Prod. Index	r	1.0000	0.5423	-0.4699	-0.4478	0.2941	-0.2935	0.2473	0.0308
	$\hat{\alpha}$	0.0000	0.0001	0.0001	0.0001	0.0006	0.0006	0.0042	0.7259
Time	r	0.5423	1.0000	-0.9201	-0.7899	-0.0119	-0.3191	0.3647	-0.0834
	$\hat{\alpha}$	0.0001	0.0000	0.0001	0.0001	0.8920	0.0002	0.0001	0.3419
Ortho PO ₄	r	-0.4699	-0.9201	1.0000	0.8579	0.0099	0.3180	-0.2577	0.1054
	$\hat{\alpha}$	0.0001	0.0001	0.0000	0.0001	0.9099	0.7173	0.0029	0.2292
NO ₂ -NO ₃ N	r	-0.4478	-0.7899	0.8579	1.0000	0.495	0.0546	-0.0551	0.0810
	$\hat{\alpha}$	0.0001	0.0001	0.0001	0.0000	0.5726	0.5339	0.5300	0.3559
Velocity	r	0.2941	-0.1190	0.0099	0.0495	1.0000	0.0143	-0.0551	-0.3770
	$\hat{\alpha}$	0.0006	0.8920	-0.9099	0.5726	0.0000	0.8710	0.5300	0.0001
Temperature	r	-0.2935	-0.3191	0.0318	0.0546	0.0143	1.0000	-0.4332	0.0581
	$\hat{\alpha}$	0.0006	0.0002	0.7173	0.5339	0.8710	0.0000	0.0001	0.5082
Isolation	r	0.2473	0.3647	-0.2577	-0.0551	-0.0551	-0.4332	1.0000	-0.0577
	$\hat{\alpha}$	0.0042	0.0001	0.0029	0.5300	0.5300	0.0001	0.0000	0.5113
Med. ϕ	r	0.0308	-0.0834	0.1054	0.0810	0.3770	0.0581	-0.0577	1.0000
	$\hat{\alpha}$	0.7259	0.3419	0.2292	0.3559	0.0001	0.5082	0.5113	0.0000

Discussion

Time, depth, and current velocity are the variables most useful in accounting for variation in the benthic production index. The variable time is an index of many parameters affecting production. The general increase in benthic production with time reflects the development of a benthic flora after a period of high turbid flow. Sample sites were more likely to be productive and production was likely to be greater as this development progressed. Similarly shallow sites were more likely to have photosynthetic producer communities than deep sites. The negative correlation between current velocity and the benthic production index suggests that erosion is a significant factor in the production per area of the benthos.

Depth and current velocity are not independent of each other. The inverse correlation of these measures with the benthic production index is consistent with the general observation that highest benthic densities are found at the margins of the river channel.

Perhaps more important than the variation accounted for by the analysis of physical parameters is the variation left unexplained. One would expect epipellic and episammic algal communities to be highly variable in a turbulent stream such as the Kansas River. Chance may be as important as any combination of physical parameters in determining the state of a benthic algal population.

It is my somewhat subjective judgement that benthic algal distribution patterns are determined by the physical environment. I suspect that the precision of my measurement techniques was insufficient to resolve the microhabitat parameters. Further I feel that the core incubation technique has not been shown to provide a good index of benthic productivity. The core incubation technique should be verified by some independent measure of benthic production before this approach is continued.

APPENDIX 1

Methods and Discussion

A) Total Production Estimate.

Estimation of lotic production by monitoring diurnal concentrations of dissolved oxygen was first suggested by H. T. Odum in 1956. Dissolved oxygen concentrations are altered by three processes: photosynthetic production, aerobic respiration, and diffusion. The generalized equation relating these parameters is:

$$\pm \Delta O_2 = \text{Production} - \text{Respiration} \pm \text{Diffusion} \quad (1)$$

Photosynthetic production estimates in streams originally utilized two stations, one upstream and one downstream of the stream being observed. The working assumption is that a parcel of water travels between the two stations and experiences a change in dissolved oxygen concentration $[O_2]$ which reflects the biotic and physical processes which occurred during its passage. Water, at velocities typically found in nature does not travel as a single mass, rather it eddies and surges and is responsive to the vagaries of slope, bed morphology and wind. Attempts to correct for longitudinal mixing have been unsuccessful (Owens, Edwards, and Gibbs, 1964).

Single station estimates assume that "the incoming water has had the same diurnal history as the water preceding", i.e. "a second station would reveal a curve identical with that of the first station" (Odum, 1956). Obviously, a single estimate cannot characterize a stream from its headwaters to the sea.

The two methods are actually very similar. The single station method simply replaces the upstream station with the oxygen concentration one time unit earlier. Further calculations are identical. The two station estimate

applies only to the stream segment delineated by the two stations. To characterize a stream with a two station estimate renders it subject to the same criticism as the single station method.

Which method is best depends on field conditions encountered and what conclusions are to be drawn from the data. A riffle-pool stream would be difficult to characterize with the two station method. If both riffle and pool were included in the length examined, the assumption of laminar flow would be incorrect. If only a riffle were included, time from station to station would be so short that the changes in oxygen concentration might be immeasurable (Gelroth, 1976). Retention of water in pools renders them incompatible with the assumption of laminar flow. Larger river systems contain bars, riffles, and channels. Selection of the upstream and downstream stations identifies a unique segment of the river. Two station production estimates reflect the circumstances of a single segment and characterize a stream only to the extent that the segment represents actual conditions in the river. If the segment was characteristic of the stream, a single station estimate would yield identical results. The validity of the two station production estimate depends on the degree to which water travels downstream as a mass and the degree to which the segment identified represents the river.

The single station estimate is also inappropriate for riffle-pool streams. Samples are of water with different proportions of riffle-pool time. The distance water flows in one day (current velocity (km/hr) X 24 hrs/day) in small streams often extends beyond the headwater-convergence limits.

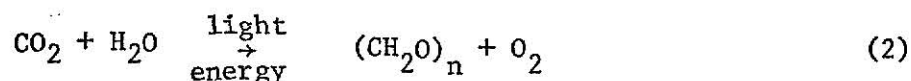
The single station technique seems most appropriate for large streams with daily flow distances over uniform stretches similar if not identical

with the sample station character. Oxygen concentration measurements are treated as random samples of the entire water mass, because of turbulent mixing. The single station method was chosen as best fitting the Kansas River situation.

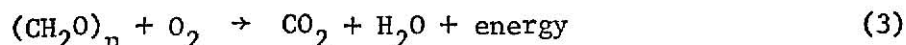
Five different approaches, each involving different assumptions, were used to estimate the components of equation 1. The impact of each approach was evaluated by modifying the single station calculation for each set of assumptions.

The following is an explanation of the assumptions and mathematics of the five single station calculations used to estimate total lotic production:

Generalized Photosynthetic Equation:



Generalized Respiratory Equation:



Photosynthetic production increases the dissolved oxygen concentration. Respiration causes a decrease in dissolved oxygen concentration. The relationship is expressed as:

$$\text{Net Production} = \text{Gross Production} - \text{Respiration}$$

(negative net production is not respiration)

A difficulty in estimating production by analysis of changes in dissolved oxygen concentration is, that gas in solution is constantly equilibrating to the pressure of atmospheric gas. Oxygen diffusion into or out of the water occurs at rates influenced by the partial pressure of dissolved oxygen compared to the partial pressure of atmospheric oxygen (saturation deficit), morphology of the stream bed as it influences turbulent mixing, and temperature. Oxygen concentration is assumed to be a

function of the biotic processes occurring in the stream and diffusion.

If the rate of diffusion is greater than the rate of biologically mediated oxygen change the biotic processes are masked. Rates of biological processes must exceed diffusion rates for the single station or double station method to generate a production and respiration estimate.

Gas exchange phenomena are not completely understood. Physical constants should be empirically determined. "Conflicting theories generate different relationships and exist in profusion" (Krenkel and Orlop, 1962).

Diffusion can be evaluated by observing aeration rates at night when photosynthetic production does not occur, then analyzing equation (4) with multiple regression procedures:

$$* \Delta [O_2] = R + f (S.D.) \quad (FR) \quad (4)$$

$$\Delta [O_2] = \text{mg/liter change in oxygen concentration per unit time (t)}$$

$$R = \text{respiration rate (mg/liter) per unit time}$$

$$f = \text{aeration coefficient (cm) per unit time}$$

$$S.D. = \text{saturation deficit (mg/liter)}$$

$$\Delta [O_2] = ([O_2]_{(t+1)} - [O_2]_{(t)}) \quad (5)$$

$$S.D. = (468/31.6 - \text{avg. temp.}) (B.P. \text{ avg.}/760) \quad (6)$$

(Montgomery, et al., 1964)

$$\text{Avg. Temp.} = \frac{(\text{Temperature } ^\circ \text{C.})_{(t+1)} + (\text{Temperature } ^\circ \text{C.})_{(t)}}{2} \quad (7)$$

$$B.P. \text{ Avg.} = \frac{(\text{Barometric pressure (mm Hg)})_{(t+1)} + (\text{Barometric pressure (mm Hg)})_{(t)}}{2} \quad (8)$$

$$t = \text{time units}$$

Equation 4 corresponds to the model:

$$Y = B_0 + B_1 X \quad (9)$$

A least squares-regression fit of night-time data yields an estimate of $f(B_r)$ and average respiration (B_o) (figure 13) (Brock, J., 1975). This method is coded FR (f from regression).

*It is important to have the data structure in mind when working through the calculations. Each hour is bracketed by measurements of oxygen concentration, barometric pressure, and temperature. Each hour is characterized by an average oxygen concentration, barometric pressure, temperature, and saturation values. Each hour has a O_2 value which is the difference between the bracketing values.

Another method of estimating "f" is given by Owens, et al. (1964).

Owens' method required stream flow, morphometric, and temperature measurements. The equation given for $f(20^\circ \text{ C.})$ is:

$$f_{(20^\circ \text{ C.})} = 50.8 U^{0.67} H^{-0.85} \quad (10)$$

f = aeration coefficient (cm/hr)

U = stream velocity (cm/hr)

H = average depth (cm)

The correction for temperature is given by Hart (1967):

$$f_{(T^\circ \text{ C.})} = f_{(20^\circ \text{ C.})} \times (1.0241) \quad (11)$$

Respiration is calculated as that portion of night time oxygen change not accounted for by diffusion. The hourly estimates of respiration are averaged for an estimate that is assumed constant, night and day. This method is coded FM (f from morphology).

Respiration varies with temperature. The nature of that variation is closely approximated by the Q_{10} equation (Guyton, 1954):

$$\log R_{(T_2)} = \log R_{(T_1)} + \log Q_{10} \frac{T - T_1}{10} \quad (12)$$

Q_{10} commonly has a value of about 2. The actual value of Q_{10} is known to vary, depending on the organisms involved and the temperature regime experienced (Yost, 1972).

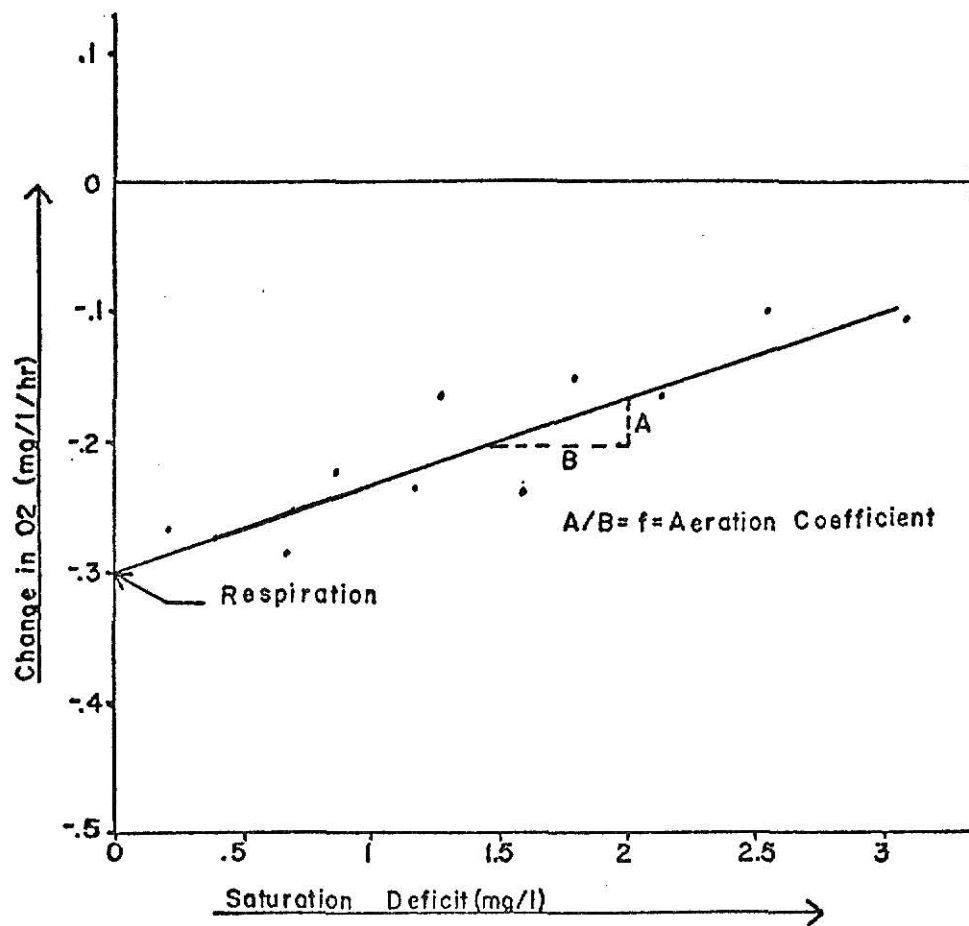
Figure 13. Graphical solution of respiration rate and the aeration coefficient (f). Input data are the night time estimates of ΔO_2 (mg/l)/hr and the saturation deficit (average) of each hour.

Notice that these parameters may also be calculated algebraically by least squares regression. The equation of the line corresponds to the model: $Y = B_0 + B_1 X_1$

B_0 = Respiration

B_1 = Aeration Coefficient

(from Brock, 1975).



Three corrections for temperature were attempted. The first method (FQ10A) was to take the regression fitted respiration estimate (B_0 in 9) and reference it to 20° C. using the average night time temperature:

$$\log R_{(\text{avg. temp.})} = \log R_{(20^\circ \text{ C.})} + \log \left(\frac{\text{Avg. Temp.} - 20}{10} \right) \quad (13)$$

$$\log R_{(20^\circ \text{ C.})} = \log R - \log \left(\frac{\text{Avg. Temp.} - 20}{10} \right) \quad (\text{FQ10A}) \quad (14)$$

The second correction (FQ10a) included hourly average temperature (Avg. Temp.) as a variable in the regression equation:

$$\begin{aligned} \Delta [O_2] &= R_{(20^\circ \text{ C.})} + f (\text{S.D.}) + R_{(20^\circ \text{ C.})} (0.1 * (\text{Avg. Temp.} - 20)) \\ &= (\text{error term}) + f (\text{S.D.}) + R_{(20^\circ \text{ C.})} (1 + 0.1 * (\text{Avg. Temp.} - 20)) \\ &\quad (\text{FQ102}) \end{aligned} \quad (15)$$

which corresponds to the expression:

$$Y = B_0 + B_1 X_1 + B_2 X_2 \quad (16)$$

In this model B_1 is an estimate of f and B_2 is an estimate of $R_{(20^\circ \text{ C.})}$. Q_{10} is assumed equal to 2.0.

The third attempt at correction (FQ10F), fit not only $R_{(20)}$ but also the Q_{10} value:

$$\begin{aligned} \Delta [O_2] &= R_{(20^\circ \text{ C.})} + f (\text{S.D.}) + R_{(20^\circ \text{ C.})} (Q_{10} * (\text{Avg. Temp.} - 20)) \\ &= R_{(20^\circ \text{ C.})} + f (\text{S.D.}) + (R_{(20^\circ \text{ C.})} * Q_{10}) (\text{Avg. Temp.} - 20) \\ &\quad (\text{FQ10F}) \end{aligned} \quad (17)$$

which corresponds to the model:

$$Y = B_0 + B_1 X + B_2 X \quad (18)$$

In this model B_0 is the estimate of $R_{(20^\circ \text{ C.})}$, B_1 is the estimate of f and $\left(\frac{10 B_2}{B_0} + 1 \right)$ is the estimate of Q_{10} .

Two temperature uncorrected estimates and three temperature corrected estimates are possible from the same data set. A PL/1 program was written which evaluates the data set all five ways and then plots production, respiration, and diffusion in $\text{mg O}_2/\text{m}^2$ for each. This program is documented and contained in appendix III.

Once the estimates of f , R , $R_{(20^\circ \text{ C.})}$, and Q_{10} are obtained diffusion and respiration for each hour are calculated:

$$D = f \text{ (S.D.)}$$

$$R_{(t^\circ)} = R_{(20^\circ \text{ C.})} + \log Q_{10} \frac{\text{Avg. Temp.} - 20}{10}$$

Production occurs only during day time intervals and is given by:

$$P = \Delta \text{ O}_2 + \text{Respiration} + \text{Diffusion} \quad (19)$$

Regretfully independent estimation of diffusion and total production was not possible. The criteria for judging the five methods were necessarily subjective. All the estimates were highly correlated and consequently were indistinguishable on the basis of correlation with physical parameters (from table 2).

The regression fitted models estimate respiration and the coefficient on the basis of measurements in the actual stream at the actual time of investigation. The morphological constants of Owens' aeration coefficient were calculated by log transformed regression fits of velocity and depth to directly measured diffusion rates in a wide variety of streams and rivers (Owens et al., 1964).

Night time values for rates of oxygen change number only one per hour with this data structure. Nine or ten points are used to fit the regression line which can use only night time values. Sampling error, especially when dissolved oxygen concentrations are near saturation, can result in incorrect and even nonsense values for fitted parameters. Also

oxygen continues to be evolved after sunset as photosynthetic organisms exhaust their cytochrome systems of free electrons. The duration and magnitude of this phenomenon is not considered in the regression fitted models.

The assumption of temperature moderated respiration (Q_{10} relationship) did not significantly alter the respiration estimate in any of the models. The range of temperatures was less than 6° C. on all of the days sampled. Further, assuming respiration constant throughout the night or fitting the intercept essentially estimates respiration for average night time temperature. Since water cools slowly during the night and warms slowly during the day, night time averages are commonly not much different from day time averages. The effort at temperature correction was not worthwhile.

Total production and total respiration estimates for each method are given in table 10. Table 11 gives daily values of the P/R ratio, f , the Q_{10} assumed or estimated, and the correlation coefficient associated with the models linear estimate of f , Q_{10} , and respiration (when appropriate). Large variation in day to day estimates of production, respiration, aeration coefficient, and Q_{10} values were the principle criteria for rejecting the regression method of estimation (table 11). As production increased, fitted estimates of the aeration coefficient and respiration became more consistent. This trend reflected a steeper gradient in dissolved oxygen change which made small sampling error less important.

Morphological constants give more consistent estimates of the aeration coefficient during periods of low production. Temperature corrections are probably unnecessary except in cases of drastic temperature fluctuations. If extensive work is to be done on a particular river or stream, it may be worthwhile to calculate a series of regression fitted aeration coefficients during periods of high productivity and simultaneously measure the appropriate morphological parameters. Thus a morphological

Table 10. Total gross production, respiration, and the mean values of each; for all five methods of calculation. (See text for abbreviation identification).

Date	Production mg O ₂ /m ²			Respiration mg O ₂ /m ²		
	FM	FR	FQ10A	FQ102	FQ10F	FQ10F
9/13/75	48.7	5.7	5.7	6.8	6.8	0.0
9/14/75	23.6	20.3	21.1	12.6	24.8	35.6
9/15/75	29.2	19.7	19.7	309.7	7.3	0.0
9/16/75	91.0	43.7	43.2	389.3	31.9	15.7
9/17/75	84.9	21.7	21.7	75.8	23.0	10.3
9/18/75	102.1	52.6	55.5	204.4	33.5	3.2
9/19/75	151.2	71.6	74.8	37.6	76.3	83.4
9/20/75	259.4	185.1	187.8	166.1	179.4	77.8
9/21/75	306.4	211.6	212.0	90.5	231.6	267.0
9/25/75 (main)	587.6	351.2	351.2	686.8	507.8	0.0
9/25/75 (riffle)	737.2	212.1	212.1	664.4	409.8	0.0
10/11/75	608.0	293.7	300.6	507.5	308.9	0.0
11/15/75	278.9	168.3	168.3	193.4	180.1	0.0
mean value	254.5	127.5	134.7	257.3	155.4	38.0

Table 11. Daily values of the P/R ratio, aeration coefficient (f), the Q10 (assumed or estimated) and the correlation coefficient associated with the models linear fit. (See text for abbreviation identification).

Date	P/R	f	Q10	r
9/13/75	0.2540	25.6964	---	----- FM
	1.3765 X 10 ¹ *	0.6179	---	0.048 FR
	1.3575 X 10 ¹ *	0.6179	2	0.050 FQ10A
	1.7326 X 10 ¹ *	0.1868	2	0.050 FQ102
	1.7628 X 10 ¹ *	0.2274	2.2958	0.050 FQ10F
9/14/75	0.1595	25.8907	---	----- FM
	0.6701	5.1495	---	0.091 FR
	0.6720	5.1495	2	0.092 FQ10A
	3.7309 X 10 ¹ *	3.8154	2	0.092 FQ102
	0.6973	3.7416	0.4150	0.092 FQ10F
9/15/75	0.2016	26.2461	---	----- FM
	23.1620	0.0000	---	0.086 FR
	23.3719	0.0000	2	0.300 FQ10A
	0.4866	12.2470	2	0.300 FQ102
	2.1500 X 10 ¹ *	11.2569	2.0000**	0.301 FQ10F
9/16/75	0.6385	26.2385	---	----- FM
	0.8386	4.8323	---	0.361 FR
	0.8307	4.3230	2	0.446 FQ10A
	0.5566	20.8258	2	0.446 FQ102
	2.0384	20.8429	33.3980	0.446 FQ10F
9/17/75	0.8625	26.6930	---	----- FM
	5.1388 X 10 ¹ *	0.0000	---	0.040 FR
	5.0809 X 10 ¹ *	0.0000	2	0.106 FQ10A
	0.6180	4.4122	2	0.106 FQ102
	2.2301	4.4006	13.3365	0.106 FQ10F
9/18/75	0.7876	26.5543	---	----- FM
	0.8937	7.1814	---	0.704 FR
	0.8954	7.1814	2	0.730 FQ10A
	0.6392	14.1610	2	0.730 FQ102
	10.4483	14.1715	62.5150	0.730 FQ10F
9/19/75	1.1863	26.6641	---	----- FM
	1.1082	7.0609	---	0.634 FR
	1.1018	7.0609	2	0.639 FQ10A
	1.0179 X 10 ¹ *	3.6585	2	0.639 FQ102
	0.9150	3.6544	2.0000**	0.639 FQ10F
9/20/75	2.0461	26.8378	---	----- FM
	1.7801	16.3469	---	0.708 FR
	1.7581	16.3469	2	0.709 FQ10A
	3.2371	17.5444	2	0.709 FQ102
	2.3066	17.5464	1.6894	0.709 FQ10F
9/21/75	3.3759	27.1715	---	----- FM
	2.2968	14.7876	---	0.936 FR
	2.2892	14.7876	2	0.967 FQ10A
	2.4479 X 10 ¹ *	5.4778	2	0.967 FQ102
	0.8645	5.4747	2.0000**	0.967 FQ10F
9/25/75 (main channel)	8.1443	27.4587	---	----- FM
	7.7490 X 10 ¹ *	14.5273	---	0.977 FR
	7.4939 X 10 ¹ *	14.5273	2	0.989 FQ10A
	2.1329	21.8364	2	0.989 FQ102
	1.5265 X 10 ¹ *	21.9169	2.0000**	0.989 FQ10F
9/25/75 (riffle)	4.9351 X 10 ¹ *	36.4332	---	----- FM
	1.4202 X 10 ¹ *	8.4223	---	0.866 FR
	1.3728 X 10 ¹ *	8.4223	2	0.895 FQ10A
	1.4485	18.2232	2	0.895 FQ102
	3.7033 X 10 ¹ *	18.2238	2.0000**	0.895 FQ10F
10/11/75	37.4172	30.2863	---	----- FM
	3.2212	10.4225	---	0.966 FR
	3.0619	10.4225	2	0.970 FQ10A
	1.4353	13.8450	2	0.970 FQ102
	4.6038 X 10 ¹ *	13.8437	2.0000**	0.970 FQ10F
11/15/75	3.106 X 10 ¹ *	31.1992	---	----- FM
	1.9251 X 10 ¹ *	13.1319	---	0.948 FR
	1.8649 X 10 ¹ *	13.1319	2	0.948 FQ10A
	7.2098	14.2495	2	0.948 FQ102
	1.2349 X 10 ¹ *	14.1982	0.6860	0.948 FQ10F

* These values reflect a respiration estimate less than 0, constrained to a positive value approaching zero, not a real P/R value.

** When estimated Q10 value was less than zero, Q10 was constrained to 2.0000.

aeration coefficient calculation could be generated for a particular system with data from that system. This morphological aeration coefficient could be used during periods of low productivity and the regression technique during high productivity.

Total production estimates referred to in Part 1 utilize an aeration coefficient calculated from Owens et al. (1964).

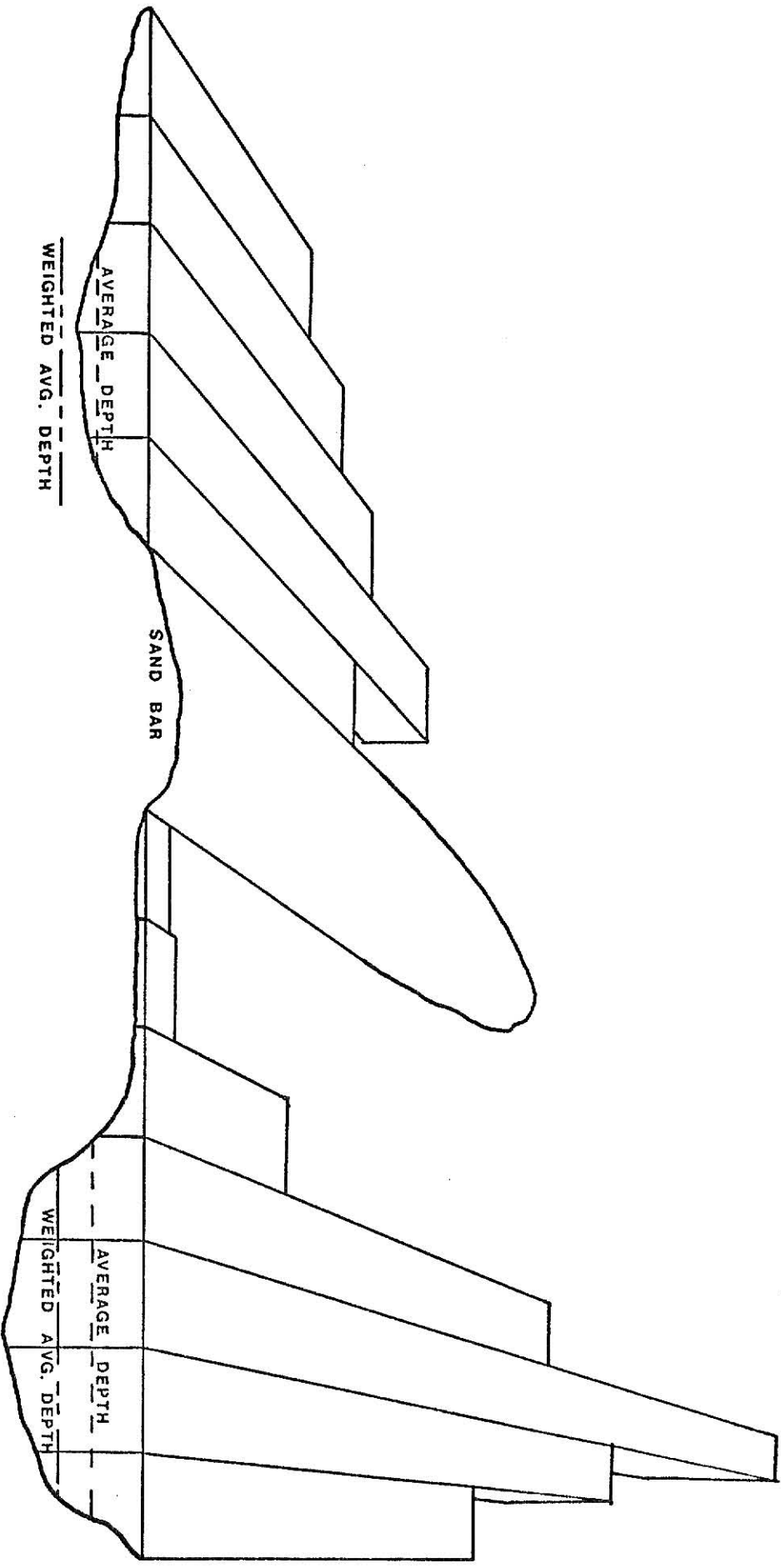
B) Planktonic Production Estimate.

Standard light and dark bottle techniques were used to estimate planktonic production. Incubation at depth of light and dark bottles is a standard method of phytoplankton production estimation (Standard Methods, 1971). This method is suited for lakes and oceans. Applying this technique to running waters requires special morphological considerations. It is necessary to construct a conceptual lake whose surface area equals the surface area experienced by the suspended algae but whose depth reflects the dynamic state of river volume.

Streams are irregular in cross sectional profile and current velocity. Consequently the average cross sectional depth may not reflect the average depth experienced by the water, and randomly suspended algae. Figure 14 illustrates a representative cross sectional profile, divided into equal intervals, with respective current velocities indicated for each interval. It is apparent that water passing through an interval per unit time is a function of both depth and current velocity (all intervals are of equal width). The depth of integration of the production curve must reflect the interaction of current velocity and bed morphology.

Transects were surveyed each day at several points. Each transect was comprised of 10 meter intervals. A representative depth and current velocity were estimated for each interval. The product of width, depth

Figure 14. A generalized cross section of river bed divided into equal width increments. Relative magnitude of current velocity and therefore volume of each increment is shown in perspective. The effect of weighting the depth of each increment by the current velocity of that increment when calculating "weighted average depth" vs. "average depth" is illustrated.



Cross-section of River Bed

and current velocity yields an estimate of flow for each interval. Summing the interval estimates of flow yielded an estimate of total flow for each transect. Summing the interval widths (10 m.) yields an estimate of transect widths. Summing the interval depths yields an average depth. Averaging flow, width, and depth for all the transects yields the parameter estimates for the day. Dividing flow by (width * depth) yields the daily estimate of current velocity.

The integration depth of the production curve can be calculated from the same data set. Each interval measurement of depth is weighted by the volume of water in that interval. The equations for calculating weighted average depth (W. A. D.) for one transect is the following:

$$\begin{aligned} \text{W. A. D.} &= \frac{\sum_{i=1}^n \text{Width} \cdot \text{Current Velocity}_{(i)} \cdot \text{Depth}_{(i)}}{\sum_{i=1}^n \text{Width}_{(i)} \cdot \text{Current Velocity}_{(i)}} \\ &= \frac{\sum_{i=1}^n \text{Current Velocity}_{(i)} \cdot \text{Depth}_{(i)}}{\sum_{i=1}^n \text{Current Velocity}_{(i)}} \end{aligned}$$

where n = total number of intervals in the transects.

The daily estimate of weighted average depth is the arithmetic average the transect estimates of that day. Diurnal length is the product of daily average current velocity (m/hr) times 24 hours/day.

The final dimensions of the conceptual lake are:

Length = Diurnal Length

Width = Average Width

Depth = Weighted Average Depth

The light and dark bottle production curve when integrated to weighted average depth gives production per area. The conceptual lake gives total

area. Total production = (production/area) * total area.

Note that if production per unit volume is calculated the volume calculation uses weighted average depth. Weighted depth serves not only to characterize the photic regime of the plankton but is also a real physical parameter of lotic systems.

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TOTAL, PLANKTONIC AND BENTHIC
PHOTOSYNTHETIC PRODUCTION IN THE KANSAS RIVER

by

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The Kansas River is a turbid, 5th or 6th order stream with a predominantly sandy substrate. The channel is shallow (braided at low flow). The instability of the sand substrate provides a highly dynamic environment for the establishment and growth of benthic algae; at times the photosynthesis of organic matter in the river occurs on the substrate and at times the cells break free and the synthesis takes place as they are drifting free in the current of the river. Both benthic and planktonic production rates can be substantial reflecting high nutrient levels in the river, yet under high flow regimes primary production is reduced.

Following a period of high turbid flow, total and planktonic production were estimated over a month long period, including 240 consecutive hours. Flow, nutrients, light, turbidity, temperature, oxygen and substrate character were monitored. Benthic production was estimated by difference from total production and planktonic production estimates.

The following characteristics of lotic production of medium order sandy substrate streams are suggested:

- 1) photosynthetic activity of the benthos and plankton, and the trophic character of the river are cyclic with a period that depends on flow pattern,
- 2) the variable nature of flow patterns and high nutrient concentrations make morphology and trophogenic regime important in understanding photosynthetic production,
- 3) the benthic algal population at any interval is space limited by trophogenic area and erosion,
- 4) the planktonic algal population originally derives by erosion from the benthos,
- 5) the planktonic algal population at any interval is limited by
 - i) the area and erosion rate of upstream benthos,
 - ii) the planktonic reproduction and mortality rate, and
 - iii) the downstream export rate, and
- 6) planktonic population densities increase downstream.

Concurrent with the production study, an effort was directed at revealing physical parameters important in the distribution of benthic photosynthetic production. Gross benthic photosynthetic production was indexed by inoculating light and dark bottles with cores of sediment. These experimental perturbations were conducted in conjunction with measurements of potentially controlling physical parameters in order to provide a data set for multiple regression analysis.

Depth (available light), time allowed for invasion, and current velocity (erosive force) were shown to be highly significant in explaining spatial variation in benthic production.