COMMUNITY PRODUCTIVITY AND ENERGY FLOW IN AN ENRICHED WARM-WATER STREAM

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Robin L. Vannote

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This is to certify that the

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ABSTRACT

COMMUNITY PRODUCTIVITY AND ENERGY FLOW IN AN ENRICHED WARM-WATER STREAM

by Robin L. Vannote

The productivity and energetics in the enrichment zone of a warm-water smallmouth bass stream were investigated. Biotic and abiotic energy losses were quantified in tracing the energy flow pattern from the primary trophic level, through the crayfish population, and ultimately to the smallmouth bass population.

The primary production was evaluated by diurnal oxygen curves, the harvest method for stream macrophytes, and predictor equations were developed relating periphyton production to stream temperature during periods of increasing or decreasing stream temperatures. The crayfish population was estimated by a marking-recapture technique and counts per unit enclosed area. Productivity of crayfish was estimated by computing average standing crop biomass and instantaneous rates of growth and mortality for separate size groups. The ecological status of the smallmouth bass population was studied by direct spawning observations, electrofishing, and collections utilizing rotenone. Bass productivity, based upon survivorship curves related to spawning density, was calculated using instantaneous rates of growth and mortality.

The annual gross and net primary productivity was estimated as 2.40 $\times 10^6$ and 1.42 $\times 10^6$ g cal m^{-2} yr^{-1} respectively. The net production of stream macrophytes was 4.95 $\times 10^5$ g cal m^{-2} yr^{-1}. The net production of

periphyton was 9.20×10^5 g cal m^{-2} yr^{-1}. Photosynthetic efficiencies, based on surface radiation within the photosynthetic range was 0.23% on an annual basis.

Crayfish was the staple item in the diet of smallmouth bass. Evaluated on a caloric energy basis or live weight biomass, crayfish was the dominant form of stream biota. The standing crop was estimated as 43 g m^{-2} (383 lbs $acre^{-1}$) with a caloric energy value of 33.7 k cal m^{-2}. Net crayfish productivity was 41.5 g m^{-2} yr^{-1} or 32.5 k cal m^{-2} yr^{-1}. Including community respiration, the total energy flux through the crayfish biota was 133.25 k cal m^{-2} yr^{-1}. The energy assimilated by crayfish represented 9.4% of the energy available at the primary level or 0.00527% of incident light energy.

Nesting density of smallmouth bass was 21 and 25 nests per linear stream mile during 1961 and 1962 respectively. The immediate postspawning stream conditions determined year class strength. The average standing crop of bass, as estimated by nesting density and survivorship curves based upon number of successful spawning attempts, was 14.9 kg ha^{-1} (12.1 lbs $acre^{-1}$). Smallmouth bass production was 13.6 kg ha^{-1} yr^{-1} or 1481 g cal m^{-2} yr^{-1} representing 0.00024% of incident light energy and 0.14% of net primary production.

Assuming crayfish were the only energy source available to the bass, harvesting efficiency was 14.6% of the annual crayfish production. Because of non-assimilated energy losses and energy diverted for body maintenance, 3.6% of crayfish production was used for biomass growth by bass.

The food base in the enriched stream was broad and rich. Factors limiting bass production were accelerated, artificial eutrophication of the stream and physical alteration of stream habitat by sedimentation of pools.

In the enriched stream, turbidity pulses, indiscriminate water flow regulation and low level industrial pollution produced fish kills of varying intensity during periods of strong diurnal oxygen pulses.

Summer diurnal oxygen pulses ranged from super saturation during afternoon peak photosynthetic activity to a low of 2.5 to 3.0 ppm three hours after sunset. Oxygen diffusion was the sole mechanism maintaining night oxygen level. It was concluded that further organic enrichment will depress night time oxygen levels to a critical level with regard to stream biota.

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By

ewis
Robin L. Vannote

A THESIS

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INTRODUCTION

The conversion of solar insolation into chemical energy is accomplished by the primary producers. The rate and efficiency of this conversion process largely determine the amount of energy available at the consumer level. Stream ecosystems are of an import-export type where the total community metabolism is regulated largely by the import of nutrients and organic matter. A large influx of organic matter stimulates community respiration, whereas a large import of inorganic, chemical nutrients promotes photosynthetic processes.

The Red Cedar River presents an ecosystem of complex interactions of photosynthesis, circulation, and total community respiration. These dynamic properties of the ecosystem vary seasonly in their intensity and certain components are either stimulated or depressed through man's activities. The inflow of organic matter, washed from the watershed during periods of runoff, increases the respiration compartment. The turbidity associated with the import of organic matter depresses photosynthetic activities. But the decrease in organic production may be greatly offset by the concurrent import of organic material. In either event, import of organic matter increases total community respiration. When the oxygen demand by the respiratory compartment exceeds the oxygen production by the producer community, the system becomes heterotrophic. Prolonged heterotrophy is maintained by an increase in organic import and frequently is accompanied by a shift in biota.

The import of mineralized nutrients into the stream favors the photosynthetic compartment. This compartment is more complex because modern effluents rarely contain only simple mineralized nutrients. Streams receive many complex chemical compounds included in the enrichment mixture. The actions or interactions of these components may inhibit the utilization of the nutrient portion. Furthermore, these antagonistic components contained in effluents may depress the photosynthetic processes and lower community efficiencies.

The fundamental object of this study was to investigate the factors governing and regulating the production of smallmouth bass in a representative, enriched warm-water stream. The method of attack has been to trace the principal energy flow patterns, quantifying biotic and abiotic energy losses, from the primary trophic level, through the major prey species (crayfish), and ultimately to the smallmouth bass.

The warm-water streams of Michigan are located primarily in the southern one-half of the lower peninsula and are in areas predominantly devoted to agriculture and resident developments. The stream economies are strongly influenced by land use. The major problem of the enriched warm-water streams, like many lakes, is that of accelerated, artificial eutrophication directly attributed to agricultural and domestic pollution aggravated by various levels of industrial pollution.

Statement of Fundamental Problems

More than 60% of the Red Cedar River watershed is devoted to crop production with corn predominating (Ash et al. 1958). About 20% of the watershed is wooded lands and idle fields. The basic nature of intensive, cash-crop agriculture leaves considerable portions of the watershed unprotected during seasons critical with regard to stream communities. After the midsummer wheat harvest, wheat stubble is turned under and land prepared for winter wheat planting. During the interim of field preparation and establishment of a binding protective turf, silt laden runoff generated by the fall rains produces a continuum of turbid stream pulses.

Similar turbidity pulses occur in the late spring while large sections of the watershed are placed into corn production. Continued cultivation of row crops throughout the summer aggravates the silt problem following each summer rain storm. The summer storm track across the lower peninsula of Michigan results in short, intense summer afternoon rain showers of limited areal extent. However, the intensity of these storms produces considerable runoff and stream turbidity.

The continual urban, residence encroachment on agricultural land is evident as surburban residence development expands outside of urban areas. Many of these expanding residential areas, attracted by the increased sales potential and evaluation, have followed the river courses. The encroachment of these developments has added an increased burden upon streams to assimilate community wastes and has accelerated the basic eutrophication problem of streams. Together, the increasing stream turbidities and nutrient enrichment are combined to alter the basic economy of the stream. The streams continually are progressing towards a complete heterotrophic status which if continued undoubtedly will produce a complete alteration of component biota.

The enriched, warm-water stream is shifting progressively from a autotrophic system augmented by the import-export economy of the watershed to one of primarily an import-export regime where large influxes of organic matter overshadow the producer capacity of the stream itself. Concurrently the large import of organic and inorganic material from the watershed suppresses the autotrophic community by light exclusion.

The above problems are all evident in the Red Cedar River. Five urban communities enrich the stream with treated and untreated domestic wastes. Industrial pollutants enter the stream from several small industrial plants.

The headwater of the stream receives wastes from a metal plating plant which either alone or in combination with domestic pollution severely limits or alters fish production in several miles of stream. The industrial pollution of a stream headwater is an extremely unfortunate situation and dictates constant surveillance especially during periods of critical low flow.

Within the past ten years, seven suburban resident developments have been located on land areas immediately adjacent to the Red Cedar River. These developments, each containing from 20 to over 100 homes, contribute to the enrichment of the stream. The resultant stream enrichment in itself is not detrimental to the community regime. However, accelerated autotrophic production greatly enlarges the natural metabolic oxygen demand. This, coupled with indiscriminate water flow regulation, low-level industrial pollution, and periodic turbidity pulses, produces severe diurnal oxygen pulses and results in fish kills of varying intensities.

It is these fundamental, basic problems of stream biodynamics that curtail the efficient utilization of a broad, enriched food base in the Red Cedar River. It is this situation, which until regulated by man, will prevent efficient conversion of the basic food supply into production of desirable game species.

In 1957, Tanner suggested the watershed approach to solving the increasing deterioration of the warm-water fishery and pointed directly to many conservation departments' apparent lack in gaining public support to include fishery interests in watershed management programs. The Michigan Department of Conservation has recognized the importance of watershed management for sustained yields of trout population in northern cold-water streams. However, the same programs have not, in most cases, been extended to the enriched, problem-streams supporting warm-water game fish.

The apparent neglect of the warm-water streams, in favor of the northern trout streams, results in part because of a lack of answers to questions such as: how much turbidity can we tolerate in a warm-water stream and how much stream enrichment can the rivers withstand before a complete shift to a heterotrophic regime?

I shall attempt to show that the enriched streams should not be dismissed as marginal sport fishing areas, but can be developed into sustained fisheries. I shall forward this thesis by stating that we can tolerate periodic turbidities of 100 ppm; we can tolerate inorganic enrichment to 75 ug 1^{-1} phosphorus; and we can tolerate summer temperatures to 30 C. But we can not tolerate in the presence of the above low level industrial pollution, sedimentation of stream pools, channel straightening, and a lack of adequate stream flow regulation. We can not tolerate an "industrial accident" or insecticidal contamination every five years, destroying in days the management efforts extended over years. And we can not tolerate organic enrichment beyond the immediate assimilation capacity of the stream.

It is my belief that integral watershed management concepts as outlined by Tanner (1957) and Langlois (1945) form a working solution to the problems of enriched, warm-water streams. Unless we can understand and solve the problems and make concrete recommendations for the management of the warm-water streams, we will not be ready to cope with identical problems as they progressively invade the marginal trout streams. It is likely, with the expanding industrial economy and population encroachment, that problems now existing in the warm-water streams will be extended to the northern streams long before the turn of the century.

STUDY AREA

The Red Cedar River drains an area of 472 square miles of south-central Michigan. Land use within the watershed is both agricultural and suburban-rural residence development. The stream originates as the outfalls of Pleasant and Cedar lakes in Livingston County. The river flows westward through five urban communities (Figure 1), Fowlerville, Webberville, Williamston, Okemos, and East Lansing, before entering the Grand River at Lansing, Michigan. The total stream length is about 50 miles. Stream gradient is 2.5 feet per mile.

The stream receives either domestic or industrial pollution or both as it passes each community. Williamston and East Lansing have both primary and secondary sewage treatment facilities. Effluents from the other communities enter the stream without treatment. Okemos and Okemos township recently were tied into the East Lansing treatment facilities, however the collection system was not operative during the study. The community of Fowlerville has approved plans for the construction of a lagoon type treatment facility for domestic wastes.

At present, the pollution accrual from Fowlerville constitutes the major pollution source above East Lansing. At this site, the stream receives domestic effluents in combination with metal plating plant wastes. In combination this pollution has created a septic stream zone. During low flow in summer months, the septic zone forms an effective barrier to fish migration. Downstream fish kills have been reported in recent years (PHS No 847, 1961) in the Fowlerville area.

Most of this study was conducted in a 2.2 mile stream reach (17.5 acres) located about 15 miles upstream from the mouth of the river. The

Figure 1. Drainage map of the Red Cedar River and principal tributaries showing the primary study area and comparative study sites.

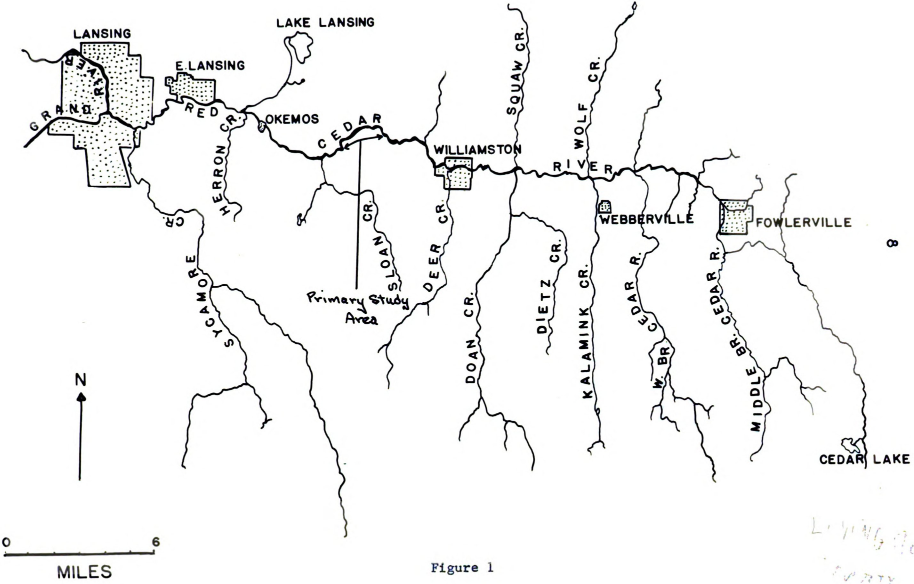

LANSING
GRAND RIVER
E. LANSING
LAKE LANSING
RED CEDAR RIVER
OKEMOS
HERRON CR.
SYCAMORE CR.
SLOAN CR.
Primary Study Area
DEER CR.
WILLIAMSTON
SQUAW CR.
DOAN CR.
DIETZ CR.
WOLF CR.
KALAMINK CR.
WEBBERVILLE
W. BR. CEDAR R.
FOWLERVILLE
MIDDLE BR. CEDAR R.
CEDAR LAKE
Livingston County
N
0
6
MILES

Figure 1

stream study area is located within the zone of stream enrichment with respect to the Williamston sewage treatment plant. This stream reach (Figure 2) was selected because it was known to contain a substantial population of smallmouth bass, *Micropterus dolomieui* Lacepede.

The population ecology and community productivity in this stream study area was then compared to that of other stream reaches. The stream bottom types in the study area are chiefly sand, gravel and cobbles in that order of abundance. Stream width is approximately 65 feet with a mean base flow depth of 18 inches. In recent years, aquatic macrophytes have been established extensively (50% of the area) throughout the study area.

Figure 2. The primary study area of the Red Cedar River.

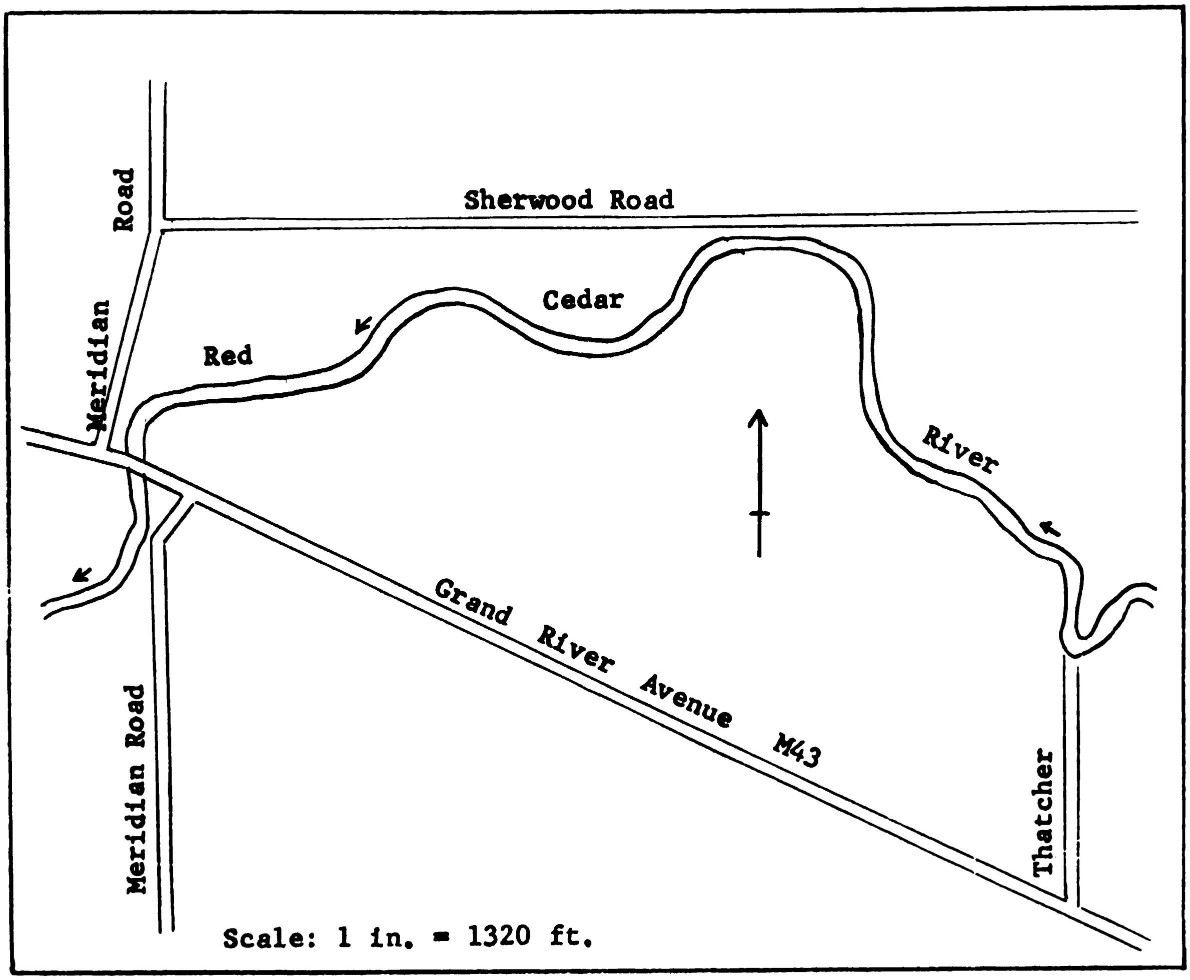

Sherwood Road
Meridian Road
Red
Cedar
River
Grand River Avenue M43
Meridian Road
Thatcher
Scale: 1 in. = 1320 ft.

Figure 2

METHODS

Primary Production

Aquatic Macrophytes

Aquatic macrophytes, primarily Vallisneria, were sampled twice during each of two growing seasons. The initial sampling period occurred midway in the growth phase. A second sampling series was obtained at the end of the growing season coincident with the estimated maximum standing crop. Aquatic macrophytes attained maximum density by late August or early September.

A sampling series consisted of 100 square-foot samples. The stream study area was divided into 100-foot strata, and ten strata were randomly selected for sampling. In each 100-foot stratum, the macrophyte crop was harvested from ten randomly selected plots. A sample consisted of all macrophytes attached to the enscribed substrate including root and rhizoidal systems. Harvested samples were field washed to remove sand, mud, and the larger invertebrates. The washing did not remove the periphyton film and its associated invertebrates. Washed samples were drained for a constant period prior to weighing on a Hanson dietetic balance. This measurement was recorded as wet weight.

During each sampling period representative samples of approximately 500 grams were placed in sealed polyethylene freezer bags. Later the percentage dry weight was determined gravimetrically after drying at 60 C.

Net productivity estimates were obtained by dividing the number of growing days into the average estimated standing crop over the entire study area. Productivity was estimated for the initial and terminal growth periods.

Diurnal Oxygen Curves

The primary production of the total community was measured by the upstream-downstream, diurnal oxygen curve method given by Odum (1956). Oxygen determinations of identical water masses, as identified by fluorescein dye, were made at stations 350 feet apart. When corrected for gas diffusion, the difference between upstream and downstream oxygen concentrations was a measure of net production. Gain or loss of oxygen across the air-water interface was assumed to be a function of diffusion and bubble formation. Oxygen loss due to bubble formation was estimated by suspending four inverted funnel traps at the water surface. The total trapping area was 277.4 cm^2. Gas was trapped by water displacement in graduated 10 cm^3 volumetric centrifuge tubes. Diffusion, using oxygen values corrected for temperature and barometric pressure, was estimated by the formula given by Odum (1956).

$$D = KS$$

where D = the diffusion rate per area ($g\ O_2\ m^{-2}\ hr^{-1}$)

K = the gas transfer coefficient at 0% saturation ($g\ O_2\ m^{-2}\ hr^{-1}$)

S = the saturation deficit between water and air

The gas transfer coefficient was calculated by the formula

$$K = \frac{z\ (q_m - q_e)}{S_m - S_e}$$

where z = the mean depth (m)

q_m = the rate of O_2 change in the morning ($g\ O_2\ m^{-3}\ hr^{-1}$)

q_e = the rate of O_2 change in the evening ($g\ O_2\ m^{-3}\ hr^{-1}$)

S_m = the predawn saturation deficit

S_e = the evening saturation deficit

Total community respiration was estimated by measuring the rate of oxygen change from 11:00 p.m. to 4:30 a.m. and correcting for inward diffusion (K) of atmospheric oxygen. Gross production was estimated by the addition of community respiration to the corrected net oxygen production. This method requires the assumption that respiration is constant during the 24-hour period. Brown (1953), using O^{18} found this assumption essentially true for Chlorella cultures in light and dark bottle experiments.

Total oxygen evolution was determined by measuring the area under a graphic plot and adding the loss due to bubble formation. All oxygen concentrations were determined by the Alsterberg modification of the Winkler procedure as given in "Standard Methods for the Examination of Water, Sewage, and Industrial Wastes" (APHA, AWWA, FSIWA, 1955).

Periphyton Production

Periphyton production data presented are those reported by Brehmer (1958), Grzenda (1960), and Rawstron (1961). While the raw data is not that of this writer, the interpretation is. The above workers exposed artificial substrates for varying periods, removed the accrued periphyton, and measured either absorbancy of extracted phytopigments or weight of accrued organic matter (see Grzenda and Brehmer 1960). This writer related the growth rates to average stream temperature and total available light during exposure periods. Predictor equations were calculated relating periphyton growth to seasonal periods of increasing and decreasing stream temperatures (photoperiods).

Crayfish

Population estimates of the river crayfish (Orconectes propinquus) were obtained by two methods. The methods were counts per unit enclosed area, and by a marking-recapture procedure. The sampling technique of the former method was in the exact manner described above for stream macrophytes.

Marking and recapture procedures were performed at night during peak crayfish activity. Collections were made from 10:00 p.m. to 2:00 a.m. Crayfish were blinded momentarily by a 12-volt lantern, captured by hand, and placed in a wash tub. After a two-hour collection period, crayfish were marked by clipping the margin of a telson. Shallow clipping prevented interception of the hemocoele. Marked crayfish were distributed uniformly throughout the collection area. The recapture census was made the following evening. In some cases two days elapsed before recapture was attempted. All crayfish captured during the census study were sexed, weighed on a Hanson dietetic balance, and measured for total carapace length.

Estimates of the crayfish population were calculated by use of Bailey's modification of the Petersen expression.

$$P = \frac{M\,(C + 1)}{R + 1}$$

where P = the number of crayfish

M = the number of marked crayfish

C = the catch taken for census

R = the number of recapture marks in the census sample

The assumptions underlying this method are discussed by Ricker (1958).

The Fish Population

Vital statistics of fish populations were obtained by seining, electrofishing, and poisoning. In addition, spawning activities of smallmouth bass were monitored to estimate size of the breeding population in various portions of the stream.

Electrofishing: Since 1958, annual studies of the fish population in the Red Cedar River have been undertaken using electrofishing gear. This writer has participated in these studies in all but the 1961 season. In detail, collection procedures varied each year, but in general the method involved the isolation of a stream segment (about 530 feet) with block nets and estimating the stock by a marking and recapture technique. In 1962, population estimates were made in one-half mile stream sections and block nets were not used.

A Homelite generator, rated at 230 volts and 10 amps, was used by a four- to five-member sampling crew. The generator, placed in a seven-foot pram, was grounded to a metal strip attached to the underside of the boat. Two positive electrodes were connected to the generator. Collected fish were held in liveboxes or wash tubs prior to measurement and marking. Fish length was recorded to the nearest millimeter. Weight was recorded on a Hanson dietetic or utility balance.

Experimental Poisoning: Two experimental sections of the Red Cedar River were treated with 5% rotenone (NoxFish) to obtain estimates of fish populations and to determine the efficiencies of other census methods. In each section previous knowledge of smallmouth bass spawning was available. The recovered bass stock yielded an index to the population structure which supported that spawning density. This bass population structure was then applied to other portions of the stream where only information concerning spawning density was available.

Prior to toxicant application, stream flow was measured with a Gurley current meter following techniques outlined by Grover and Harrington (1949). Application of rotenone to the stream was designed to give a concentration of 0.5% over a one-hour duration. A graphic plot was prepared (Figure 3) relating stream flow to the amount of rotenone required and the amount of potassium permanganate required to oxidize the rotenone.

The method of application varied between the two years. In 1961, rotenone concentrate (2.5 liters) was added directly to the stream from calibrated, 500-ml polyethelene, drip bottles. The drip bottles were attached to steel fence posts driven into the stream bottom. The experimental study area was isolated by upstream-downstream block nets. Immediately below the downstream net, four 12-quart pails, each containing four pounds of potassium permanganate crystals, were anchored in the stream.

The direct application of rotenone concentrate to the stream produced poor mixing within the study area. In addition, the potassium permanganate required constant agitation to dissolve at the desired rate. To circumvent the above deficiencies, the application procedure was modified the following year.

In 1962, the prescribed dosage of rotenone was first diluted with stream water in a 200-gallon water tank. The rotenone mixture was sprayed across a riffle immediately above the upstream block net. The spray pump was powered by a 1/4 hp Briggs and Stratton engine, and the unit was calibrated with a fluorescein tracer dye. Following the tracer dye downstream, areas of limited water circulation were delineated. These areas were then treated with additional rotenone solution to insure a complete kill.

The rotenone was oxidized with potassium permanganate bled into the stream at the downstream block net. Approximately 15 pounds of industrial grade potassium permanganate were dissolved in a 100-gallon water tank. This solution was gravity fed into a riffle portion of the stream. The flow of the oxidizer was regulated by a 3/4-inch gate valve installed at

Figure 3. Relationship between stream flow and the amount of rotenone and potassium permanganate required to treat a flowing water mass for one hour at 0.5%.

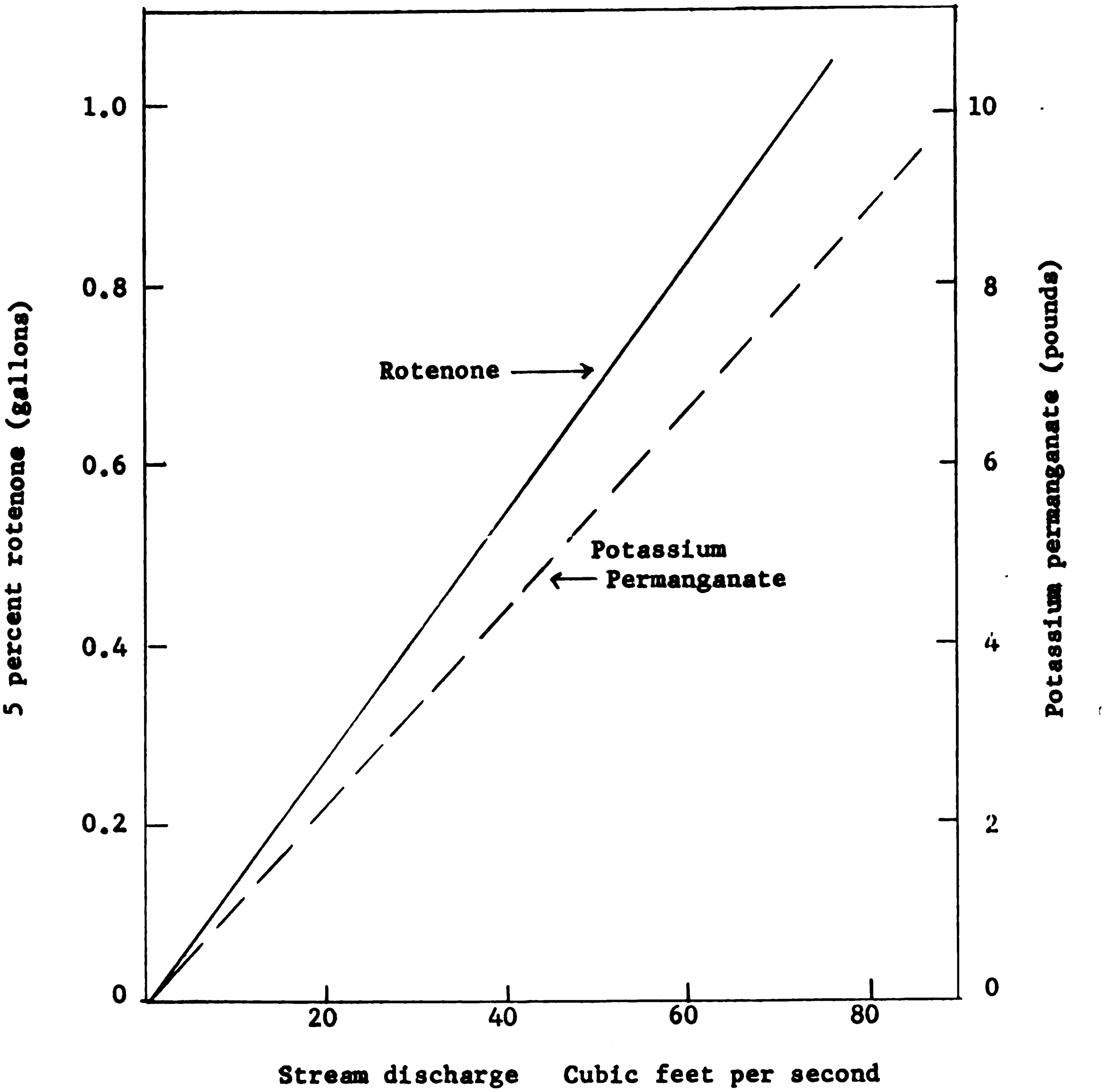

1.0
0.8
0.6
0.4
0.2
0
5 percent rotenone (gallons)
10
8
6
4
2
0
Potassium permanganate (pounds)
Rotenone
Potassium Permanganate
20
40
60
80
Stream discharge Cubic feet per second

Figure 3

the base of the tank. The theoretical dose of eight pounds of permanganate per gallon of rotenone (Ward, 1959) was increased fourfold. This increase was a precautionary measure in view of a large naturally occurring demand upon the oxidizer by stream deposits.

During the one-hour period when the toxicant was introduced into the stream, the downstream nets were tended constantly to remove fish. Additional crew members, at intermediate stations, recovered fish as they appeared. Post application pick-up was made by a crew working upstream recovering all fish including young-of-year. The area was covered five times working from the downstream to the upstream area. By working only in an upstream direction, the water remained clear. Following the last collection, the log jams were inspected and partially removed to locate trapped fish.

Collected fish were placed in wash tubs and removed to the laboratory and placed on ice. The following day the fish were processed for length, weight, and scale samples. In addition to fish collected within the study area, affected fish in downstream areas were collected. These fish were held separate from those collected in the experimental area.

<u>Smallmouth Bass Spawning Census</u>: Each spring, the nesting, spawning, and production of smallmouth bass fry was estimated in the 2.2 mile experimental section (Figure 2). In addition, comparative surveys of spawning activities were conducted in various other stream sections. The density of nesting in an area was considered an indirect index or census of the adult breeding population. Variations in breeding density and fry production were related to changes in water quality.

Inspection for spawning activities began when the minimum water temperature first reached 55 F and was continued until all fry emerged.

A few nests in the deeper pools that remained unseen, became evident upon emergence of the dark pigmented fry.

As each nest was located, its position was marked on maps prepared for each stream section. The nest position in the stream was established by spraying a white marker on an adjacent shore object. The following information was recorded for each nest:

1. Stage of development, e.g., eggs, fry, advanced fry.
2. Condition (fungus, clean, silted, abandoned).
3. Water depth, diameter, distance from shore, bottom material.
4. Current velocity four inches above nest.

In the final analysis, only those nests receiving a complement of eggs, whether successful or not, were considered for estimating the population of mature smallmouth bass.

Calorimetry

The caloric content of biological material was determined with a series 1300, Parr Oxygen Bomb Calorimeter. The procedures used were those outlined in "Oxygen Bomb Calorimetry and Combustion Methods" (Parr Instrument Company, 1960). For each material, a series of six or more one-gram samples were analyzed at 30 atm. oxygen. The resultant heat of combustion was monitored either with a mercury thermometer, a model MR Sargent X-Y recorder, or both. The calorimeter standardization (water equivalent) was not altered by the addition of the thermister cable.

Computations of the caloric value by the thermometer and heat rise curve traced by the X-Y recorder differed by less than 0.2 percent. This is within the reproducibility range for the instrument.

Prior to analysis, all samples were oven dried at 55 C, powdered, and compressed into pellets. Materials of low oil content did not pellet readily, or if compressed under extreme pressure, incomplete combustion resulted. This difficulty was circumvented by mixing the ground sample with distilled water to form a paste. Pellets of moistened material were firm yet porous after drying and ignition resulted in complete combustion.

The water equivalent of the calorimeter was determined using benzoic acid having a heat of combustion equal to 6318 calories per gram. Acid formed during the combustion process was determined titrametrically using 0.0725 N sodium carbonate (1 milliliter equals 1 calorie).

Stream Discharge and Velocity

Stream flow and velocity measurements were made utilizing equipment manufactured by the W. and L. E. Gurley Company. The models used were the Price pattern, pygmy current meter and a Type AA Price current meter.

THE ENVIRONMENT

Chemical

The seasonal aspects of nutrient transport and chemical quality of the Red Cedar River and tributary streams were reported by Vannote (1961). Here I will summarize reported results, and in some detail report subsequent findings related to the seasonal dynamics of phosphorus circulation in the stream. Phosphorus analyses were made by the author while working under a National Institutes of Health grant (Ball and Hayne - RG-5345-C3). Interpretation and analysis of the subsequent data were made while employed under the present fellowship grant.

The Red Cedar River is a highly buffered system having moderate seasonal variation in pH (7.5 - 8.4). Alkalinity and conductivity varied inversely with stream flow, i.e., high reading during seasons of base flow. Alkalinity was present as the bicarbonate ions. Methyl orange alkalinity varied between 160 and 330 mg l^{-1}. Conductivity corrected to 18 C varied between 330 μohms cm^{-1} during high stream stages to 620 μohms cm^{-1} at base flow.

Phosphorus

The seasonal dynamics of phosphorus circulation has received considerable attention both in marine and freshwater situations. A considerable literature has accumulated on seasonal phosphorus cycles in lakes. Hutchinson (1941) and Hutchinson and Bowen (1950) clarified the sedimentation, regeneration, and circulation of phosphorus in thermal, stratified lakes. Livingstone and Boykin (1962) demonstrated the phosphorus sorption capacity of pond muds and related phosphorus exchange to the total ionic activity of pond water.

Hayes, McCarter, Cameron, and Livingstone (1952), using isotope techniques, reported the phosphorus exchange equilibrium and circulation for a thermal, unstratified lake. Hayes and Coffin (1951) studied the same phenomenon in a dystrophic bog lake.

Phosphorus circulation in a marine estuary was characterized by Jeffries (1962). Estuary circulation was a function of tidal currents, river transport, and the seasonal dynamics of benthic and planktonic communities. Reid (1962), compiling data collected over a 30-year period, reported the phosphate circulation in the upper 100 m of the Pacific Ocean. The annual phosphorus cycle in coastal waters of the North Atlantic was quantified by Watt and Hayes (1963). These workers reported that phosphorus is in dynamic equilibrium with exchanges occurring between dissolved inorganic, particulate, and dissolved organic phosphorus pools.

Ball and Hooper (1963), using P^{32} combined in organic and inorganic carriers studied the phosphorus translocation through the biota of a cold-water trout stream. Detection of seasonal circulation of phosphorus in streams is complicated by pollution, seasonal flow variations, downstream transport, and the dynamics of the stream biota. Although many stream studies include routine phosphorus measurements, the circulation of this element in warm-water streams is largely unknown. This deficiency arises in part because of the seasonal aspects of many studies. Nutrient data frequently are related only to the production aspects of stream studies.

Below, I have related seasonal fluctuations of phosphorus to variation in stream flows in an attempt to clarify the dynamics of this element in streams. The seasonal circulation of phosphorus is reported for the following situations: 1) non-polluted streams, 2) polluted streams, and 3) the enrichment stream zone.

Non-polluted streams: The dynamics of phosphorus concentration as regulated by seasonal stream flow patterns is depicted in Figure 4 for a non-polluted, warm-water stream. The sampling station is located 200 meters downstream from the confluence of the East and South branches of the Red Cedar River. The stream above this station drains wooded and agricultural lands and receives no domestic pollutants. Agricultural pollution is minimal, if any.

Phosphorus concentration attained a seasonal maximum during the initial spring flood which accompanied the period of "ice-out." Line segment A in Figure 4 is an estimate of the phosphorus-discharge relationship during the spring high-water stage. During this period large amounts of autochthonous and allochthonous seston are flushed from the system and a positive correlation exists between phosphorus transport and stream flow (Vannote, 1961). As base flow conditions are approached, a reverse phenomenon occurs (line segment B). Phosphorus concentration, instead of decreasing with diminishing flow tends to increase. This increase, I have termed the phase of nutrient concentration.

I believe that biological mechanisms are responsible for the nutrient concentration phase, characteristic of this non-polluted stream area during the base flow recessional period. The increasing phase is coincident with the spring periphyton pulse. During the winter months and prior to spring floods, periphyton is quiescent, and phosphorus concentrations are minimal, about 20 ug l^{-1}. This phosphorus level is closely characteristic of ground water supply.

During the period of increasing biological activity, total phosphorus concentration increases due to a rapid rate of biological incorporation

Figure 4. The seasonal relationship between phosphorus concentrations and stream flow for a non-polluted warm-water stream.

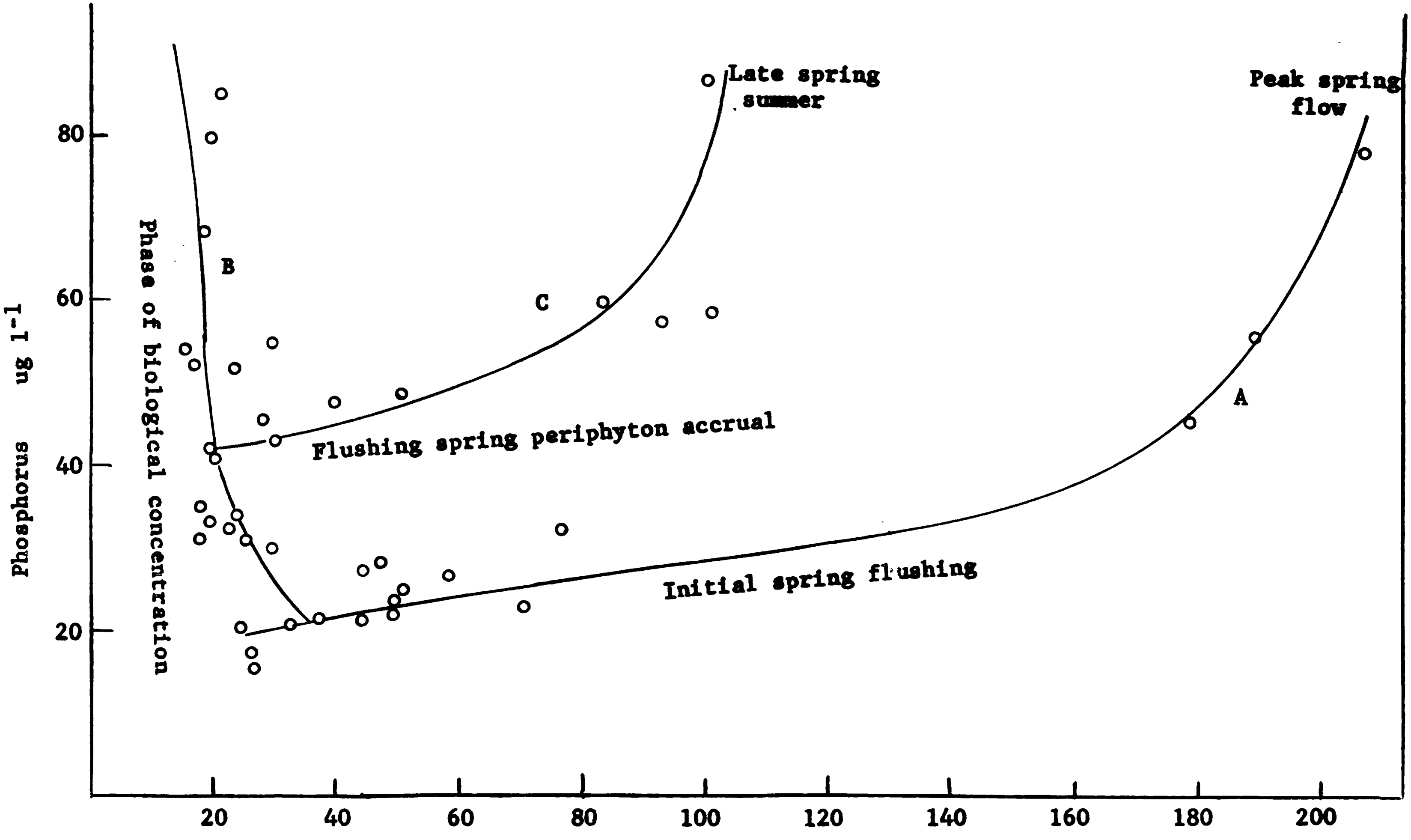

Phosphorus ug l-1
80
60
40
20
20
40
60
80
100
120
140
160
180
200
Stream Discharge cfs
Late spring
summer
Peak spring
flow
Phase of biological concentration
Flushing spring periphyton accrual
Initial spring flushing
A
B
C

Figure 4

and recycling of this nutrient. The peak, base flow phosphorus level is coincident with the maximum drift concentration of periphyton (diatoms). Hutchinson (1956) reported that phosphorus release from epilimnion bottom deposits by benthic organisms produced a similar phosphorus pulse in Linsley Pond. Hutchinson associated the phosphorus release with increased biological activity during the early summer months. Since the epilimnion portion of the pond, like a stream, is well oxygenated during this period, phosphorus release from bottom deposits would be restricted to biological activity, e.g., ingestion, excretion, and decomposition.

Dissolved phosphorus, like total, increased in concentration during the stream recessional stage. This phenomenon also may be explained biologically since stored phosphorus may break down and excess amounts be released during vigorous cell division (Strickland, 1960).

An important corollary to the nutrient concentration phase is the response to increased stream flow from late spring and early summer rains. Line C (Figure 4) relates the phosphorus response attributed to increased flow following a concentration phase. The phosphorus concentration increases with stream flow but at a much higher rate than observed during the initial spring flooding (line A). The higher phosphorus levels are attributed to the dislodging and downstream transport of the spring periphyton accrual.

During these seasonal phosphorus pulses, important amounts of phosphorus are removed from the system. The nutrient concentration phase is an important mechanism operating to retain vital stream nutrients. This is especially important to the regime of impoverished streams. It is through such concentrating mechanisms that essential elements are recycled and downstream losses are prevented from exceeding the upstream regeneration (Odum, 1957).

Figure 4 also indicates the importance of an adequate sampling program, one which includes all stream stages and seasonal differences.

Pollution Zone: The fluctuations in phosphorus levels with flow variations for a polluted stream, Lake Lansing Drain, is shown in Figure 5. This stream does not exhibit a seasonal phosphorus peak coincident with maximum discharge.

Maximum phosphorus levels occur during minimal flow periods. Increased stream flow dilutes the concentrated nutrient effluent as depicted by the estimated curve shown in Figure 5. The calculated, broken curve depicts a theoretical dilution curve established by assuming an initial base flow of 2.5 cfs manifested by a phosphorus concentration of 1000 ug 1^{-1}.

The theoretical curve assumes the dilutant is phosphorus free, and that stream sediments are not dislodged and suspended during flow increases. The estimated relationship (solid line) may follow the theoretical dilution curve rather closely at initial flow increases. At higher stream stages, however, the estimated curve most certainly departs from a strict dilution effect (theoretical curve). Departure is attributed to suspension of organic detrital deposits. In streams enriched to the level found in Lake Lansing Drain, a phosphorus response associated with peak flow periods is completely masked. Similarly, any response to a biological concentrating phase would be scarcely detectible.

Figure 5. The relationship between seasonal phosphorus levels and stream discharge in a polluted stream.

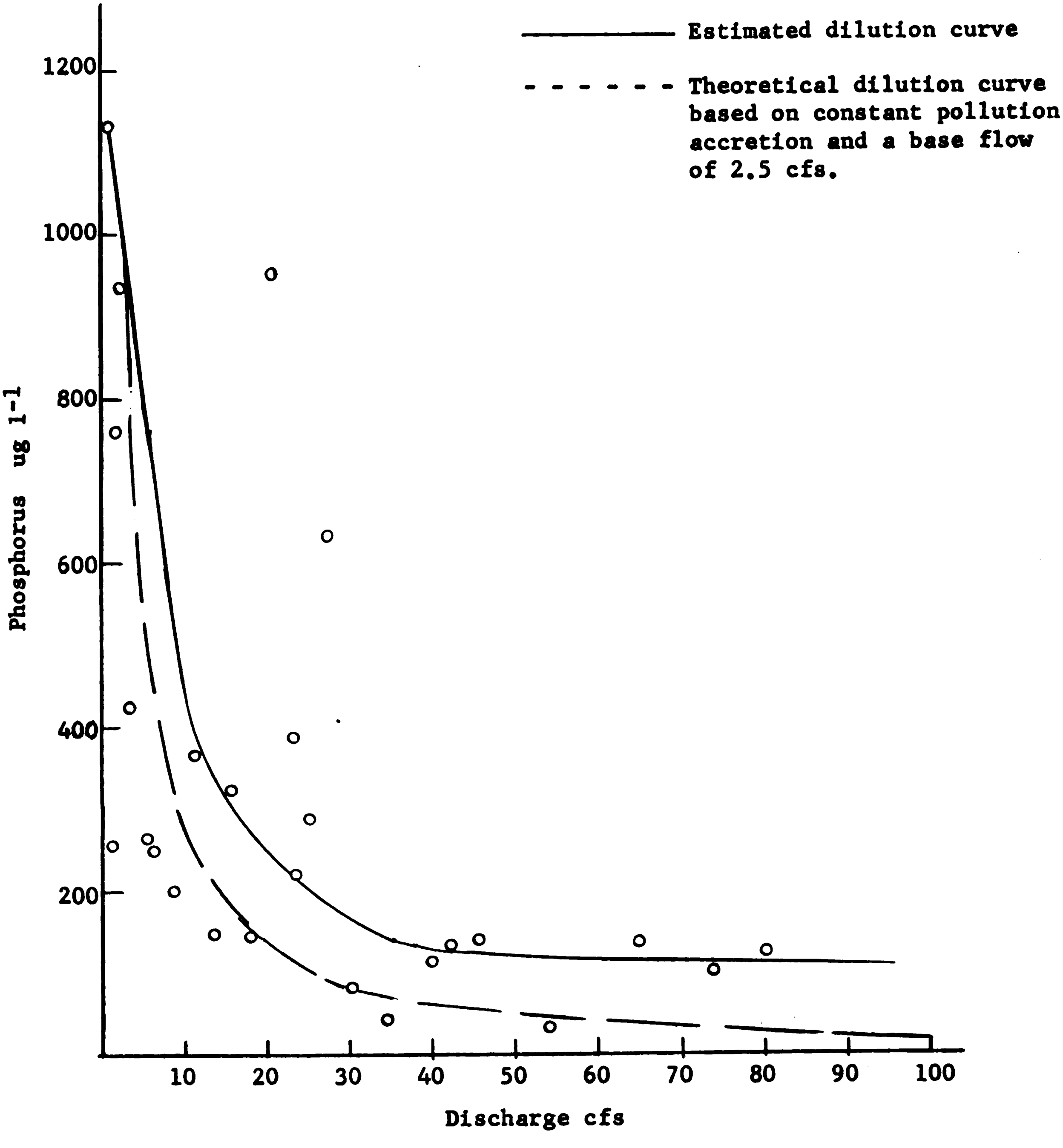

Estimated dilution curve
Theoretical dilution curve based on constant pollution accretion and a base flow of 2.5 cfs.
1200
1000
800
600
400
200
Phosphorus ug l-1
10
20
30
40
50
60
70
80
90
100
Discharge cfs

Figure 5

Enrichment zone: In the stream enrichment zone nutrients are present in luxury amounts in available forms. The community regime is autotrophic (at least most of the year) in contrast to the heterotrophic community in the pollution zone.

The nutrient quality of the stream at the Dobie Road station (river mile 9) is characteristic of the enrichment zone and the primary study area. Phosphorus data collected over a two-year period are plotted in Figure 6 as a function of stream discharge at sampling time. At this station phosphorus is abundant, rarely below 50 ug l^{-1}. The seasonal dynamics of this element with respect to stream flow may be described as a three-component system.

During periods of base flow (summer, late fall and winter), phosphorus levels moderate between 55 and 80 ug l^{-1}. During flow increases resulting from snow melt augmented by spring rains, phosphorus levels increase progressively with flow increases (line segment A) until a phosphorus peak is attained somewhat prior to peak discharge. Further flow increases (line segment B) are strictly dilutents bringing phosphorus concentration down to that level characteristic of base flow conditions. As the stream recedes from peak spring flow to summer base flow, nutrient levels remain rather uniform (line segment C).

The model described above is a function of stream storage, erosion, and transport augmented by contributions included in land runoff. At base flows phosphorus containing sediments accumulate in areas of limited circulation. Sediments are established by organic production in the stream and contributions from the watershed. Sedimentation occurs when vertical settling forces exceed horizontal downstream forces.

Figure 6. The seasonal phosphorus cycle in the zone of stream enrichment.

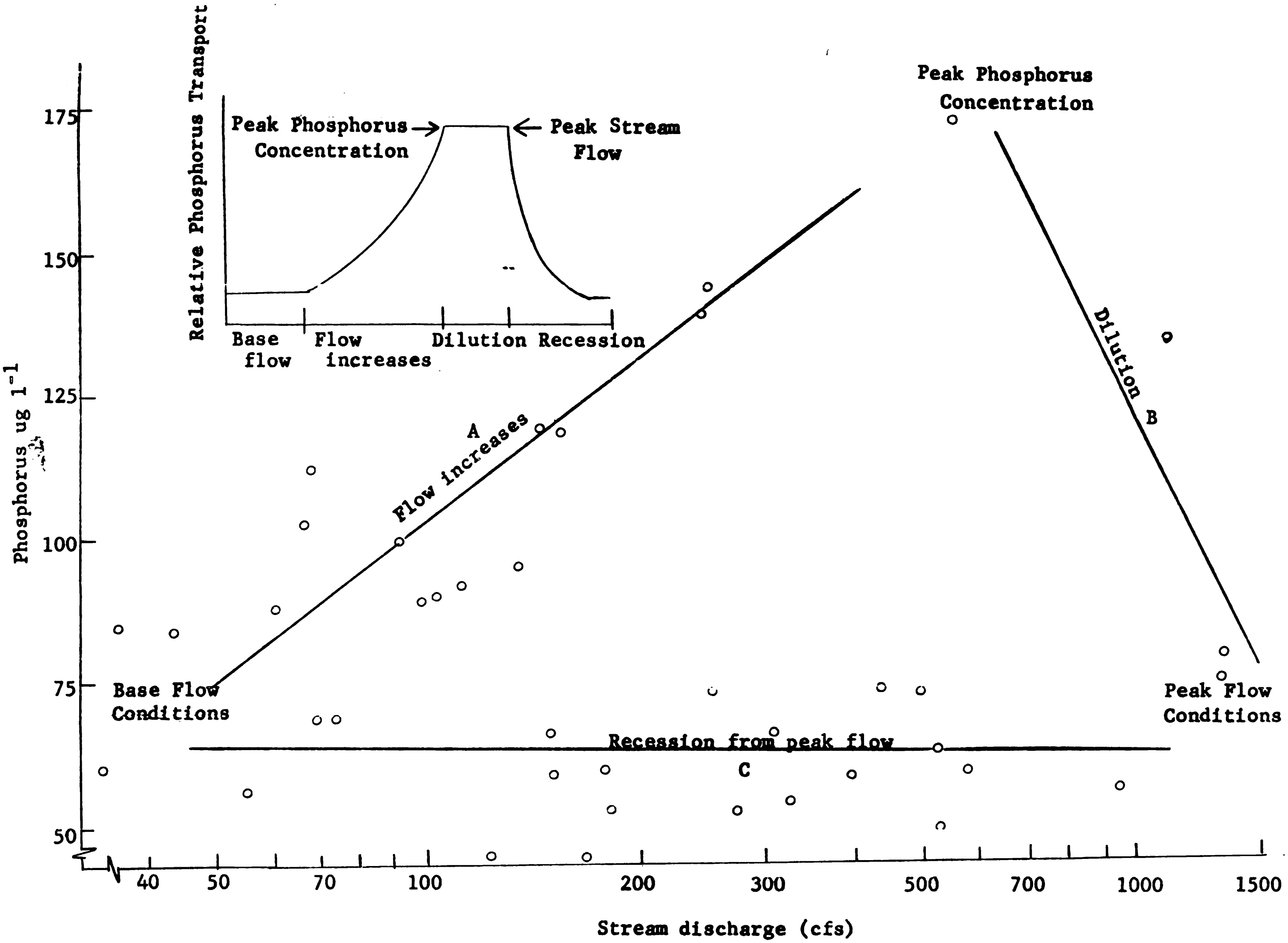

Relative Phosphorus Transport
Peak Phosphorus Concentration
Peak Stream Flow
Base flow
Flow increases
Dilution
Recession
Peak Phosphorus Concentration
Dilution
B
A
Flow increases
Base Flow Conditions
Peak Flow Conditions
Recession from peak flow
C
Phosphorus ug l-1
175
150
125
100
75
50
40
50
70
100
200
300
500
700
1000
1500
Stream discharge (cfs)

Figure 6

Suspension of sediments occurs in the spring when increased stream flow resuspends sediments. The phosphorus peak occurring prior to maximum flow indicates that an upper limit exists with respect to sediment erosion or exhaustion of phosphorus containing sediments. The dilution effect possibly results from the fact that a critical velocity is reached with respect to stream flow. Further increases in stream stage may result in little velocity increase because the stream crested and spilled over the banks.

The recessional stage from peak flow to base flow is characterized by a rather uniform phosphorus concentration. (A uniform nutrient level suggests that the exhaustion rate of stream deposits is directly proportional to stream flow.) During the recessional stage the relationship between phosphorus transport and stream flow would be linear. As base flows are approached, the sedimentation cycle would be initiated again.

Dissolved Oxygen

The oxygen concentration in the stream, a function of stream temperature, is regulated by autotrophic production, total community respiration, and surface exchange by diffusion. The direction and rate of diffusion is a function of percent saturation and water turbulence.

Severe diurnal oxygen pulses (Figure 7) occur in the Red Cedar River from July to September. The concentration of dissolved oxygen during this season is characteristically at a supersaturated level (8 to 11 ppm) during mid-afternoon peak autotrophic activity. About 3 to 4 hours after sunset, O_2 levels are depressed to 3.0 to 3.5 ppm by the large metabolic demand. The summer metabolic oxygen demand is about 2 g m^{-3} hr^{-1}. Predawn O_2 levels are maintained at 2.5 to 3.5 ppm. Diffusion is the sole

Figure 7. Diurnal oxygen curves for the study reach of the Red Cedar River during the 1961 summer.

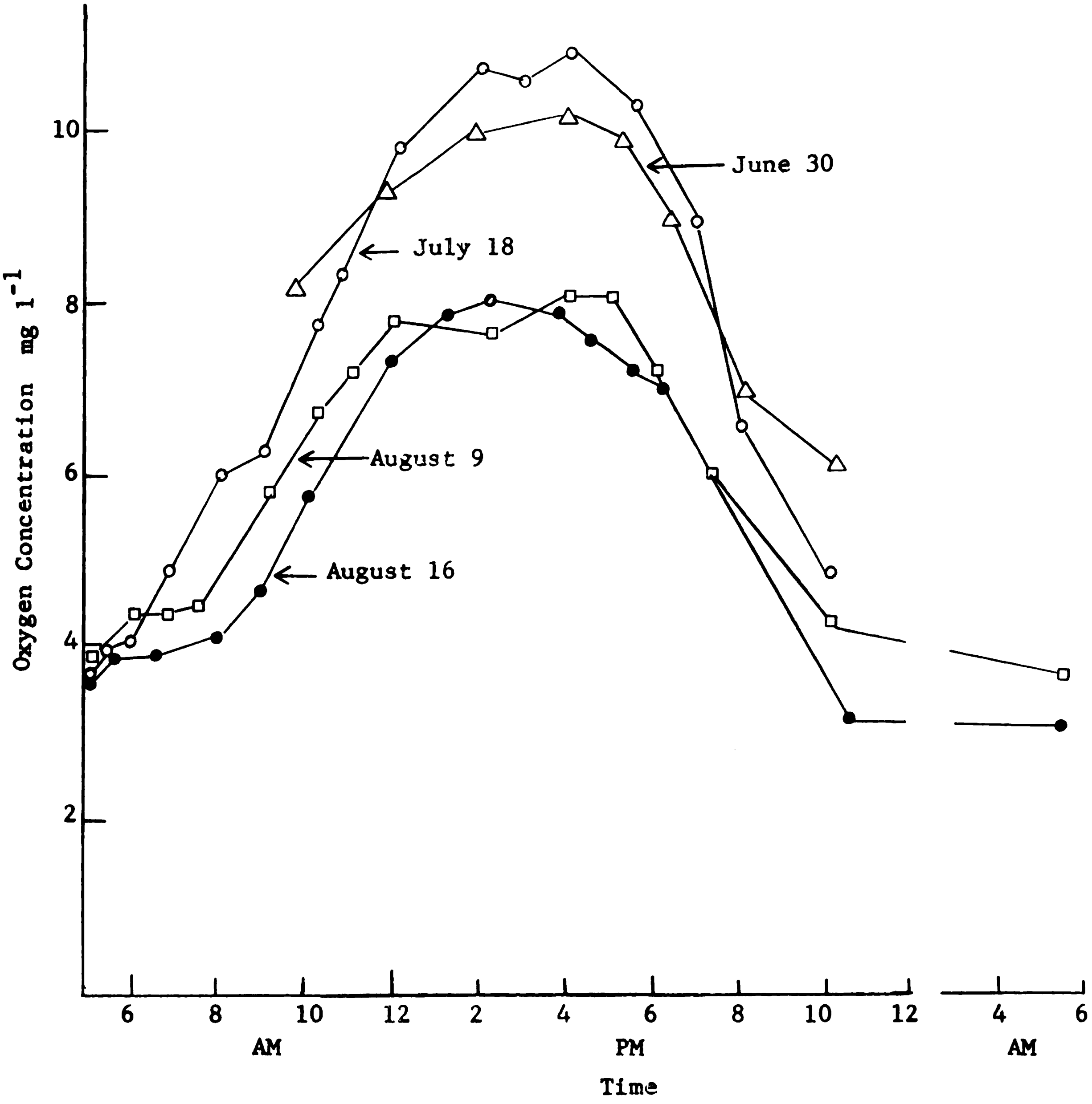

Oxygen Concentration mg l^{-1}
10
8
6
4
2
June 30
July 18
August 9
August 16
6
8
10
12
2
4
6
8
10
12
4
6
AM
PM
AM
Time

Figure 7

mechanism which prevents complete oxygen depletion during summer months. Any mechanisms, whether biotic or abiotic, lowering the diffusion rate or increasing the oxygen demand will correspondingly lower night oxygen levels.

The metabolic pulse of the Red Cedar River, as measured by diurnal oxygen curves, strongly suggests that further organic enrichment will depress night oxygen levels to a critical point. It is my belief that the Red Cedar River presently is receiving the maximum pollution load that it is capable of assimilating without a complete heterotrophic shift.

THE PRODUCTION

Primary Production

The primary production and energetics in the study reach was estimated by three techniques. Diurnal oxygen curves were developed to estimate community metabolism and gross primary production. The harvest method was employed to measure contributions by stream macrophytes. Predictor equations were developed relating periphyton production to stream temperature during seasons of increasing or decreasing photoperiods.

Diurnal Oxygen Curves

The diurnal, upstream-downstream oxygen technique developed by Odum (1956), was used to measure primary production of a 100 m stream reach. A dense bed of Vallisneria occupied about 50% of the substrate area. Diurnal oxygen measurements were made at about two week intervals during the 1961 summer. Community respiration and the gas transfer coefficient were calculated from nocturnal oxygen measurements.

The gas transfer coefficient varied from 0.45 to 2.0 g O_2 m^{-2} hr^{-1} at 0% saturation. Total community respiration was comparatively uniform (0.9 to 1.4 g O_2 m^{-3} hr^{-1}) throughout the summer months. Net production of macrophytes within the bed was determined twice during the summer by the harvest method. Net production was estimated from 30 square foot plots, selected randomly within the study area. Samples were taken 40 days and again 116 days after the initial growth period. Net macrophyte production and the 95% confidence limits for the mean estimates were 0.82 $\pm$ .46 g m^{-2} day^{-1} during the initial growth period and 0.31 g m^{-2} day^{-1} between the initial and final sampling period. The caloric energy of the macrophyte crop was 2893 cal g^{-1}.

The amount of oxygen produced may be converted to organic weight by conversion data given by Strickland (1960). In the photosynthetic process, assuming a photosynthetic quotient of 1.0, one mole of glucose is produced by the uptake of 6 moles of CO_2 and evolution of 6 moles of O_2. Plant communities rarely have a PQ $(\frac{+\Delta O_2}{-\Delta CO_2})$ equal to 1.0. Strickland (1960) recommends using a PQ = 1.2 unless a precise value is known.

On the basis of PQ = 1.2 and a photosynthetic product of carbohydrate (4000 cal g^{-1}), oxygen production is converted to calories by the following expression:

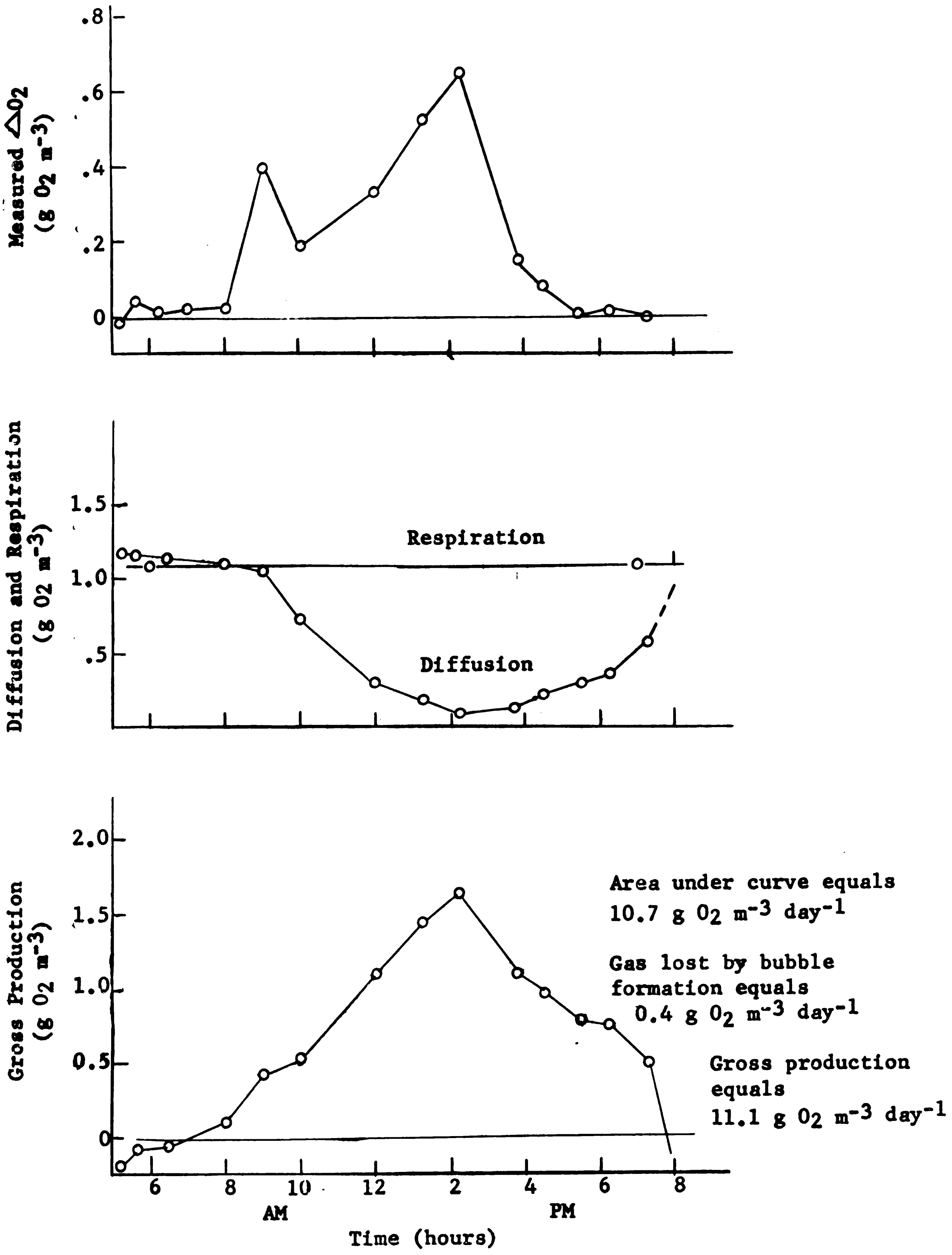
$$\text{g cal} = \text{g } O_2 \times \frac{1 \text{ mole}}{7.2 \text{ moles}} \times \frac{180 \text{ g}}{230 \text{ g}} \times 4000 \text{ cal}$$

Diurnal oxygen curves were found useful to estimate primary production in *Vallisneria* beds providing the gas diffusion coefficient remained constant throughout the 24-hour period. During two of the six trials, intense afternoon showers substantially altered the diffusion coefficient.

A representative curve and related data are given in Figure 8 for a favorable production estimate. Figure 9 presents a typical diurnal oxygen curve as modified by intense rain showers. The rainstorms effectively increased the oxygen diffusion resulting in an "apparent production" anomaly. McConnell (1963) experienced similar difficulties caused by wind generated surface ripples in ponds.

The formation of oxygen bubbles were not a serious problem in the *Vallisneria* beds. Oxygen bubbles rolled off the grass blades and rose to the surface where the gas could be trapped by inverted funnels. However, this was not the case with periphyton. Periphyton effectively held oxygen bubbles within the algal mat. Oxygen withheld as bubbles within the mat

Figure 8. Upstream-downstream diurnal oxygen curves generated by a densely stocked _Vallisneria_ bed. Curves relate oxygen change, respiration, diffusion, and gross production.



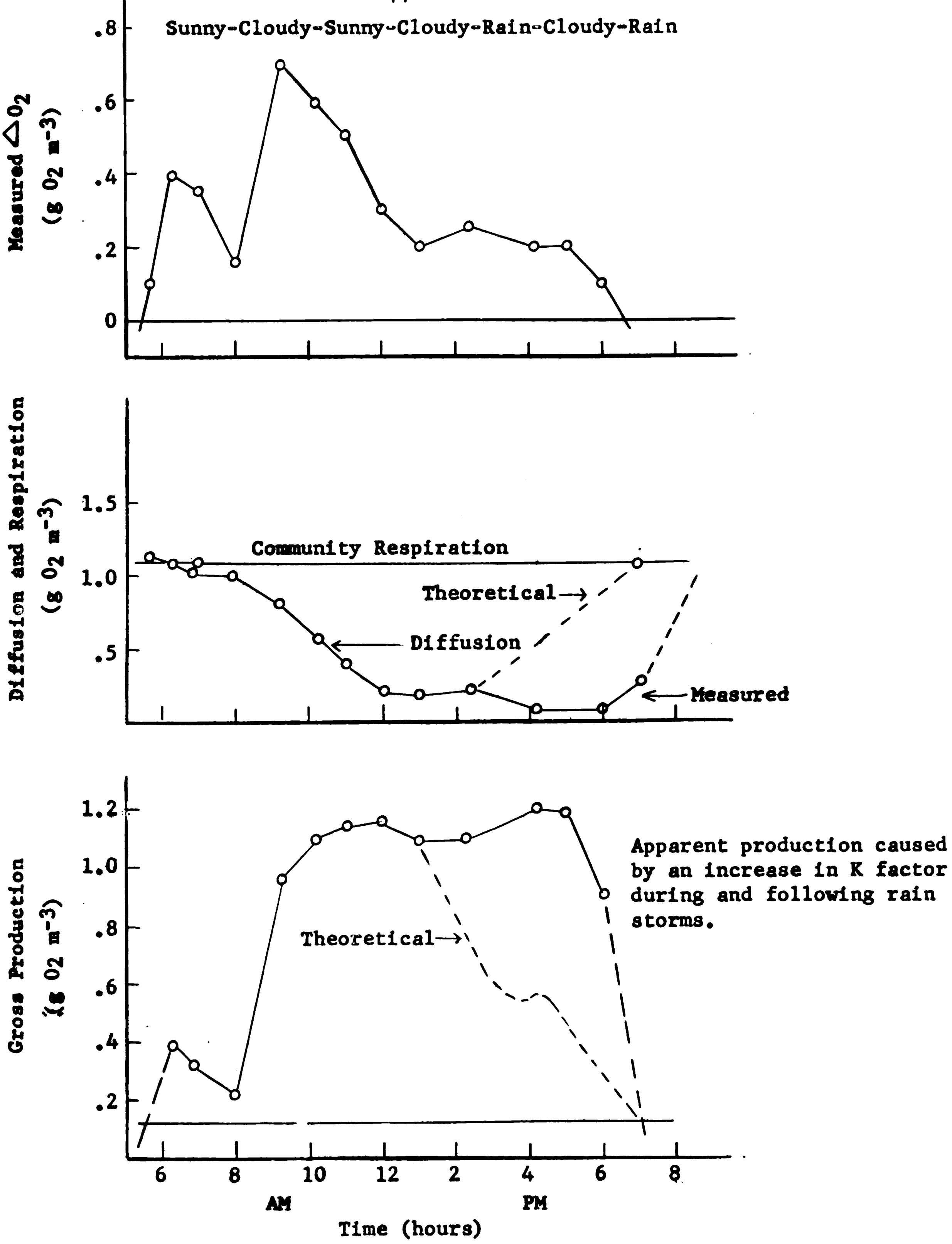
Area under curve equals $10.7\ g\ O_2\ m^{-3}\ day^{-1}$

Gas lost by bubble formation equals $0.4\ g\ O_2\ m^{-3}\ day^{-1}$

Gross production equals $11.1\ g\ O_2\ m^{-3}\ day^{-1}$

Figure 8

Figure 9. Upstream-downstream diurnal oxygen curve including the effects of afternoon rain showers.



Apparent production caused by an increase in K factor during and following rain storms.

Figure 9

would result in an underestimation of production. Bubble solution at night would lower respiration estimates and simultaneously cause an overestimation of inward gas diffusion.

The oxygen production data (g O_2 m^{-3} day^{-1}) were placed on an area basis (m^{-2}) by multiplying by average stream depth. The results of four successful oxygen curves are shown in Table 1 and are compared with a single station estimate by Grzenda (1960) for a periphyton community in the Red Cedar River.

The results of the oxygen data indicate a production decline throughout the summer. Total community respiration is variable and may increase towards mid-summer. The ratio of gross production to community respiration (P_g/R_c) clearly demonstrates an increasing heterotrophic shift. The P_g/R_c ratio decreases from 1.2 during June to 0.4 by mid-August. This indicated community respiration progressively exceeds autotrophic production from mid-July through August. Continued heterotrophic metabolism can be maintained only by organic import.

Heterotrophic conditions are characterized by strong diurnal oxygen pulses. Between mid-July and early September, strong diurnal oxygen pulses were observed in the stream. During this period oxygen concentration usually reached saturation values only at peak photosynthetic activity (mid-afternoon). By 11:00 p.m., oxygen concentration was commonly about 3.5 mg l^{-1}. Because of increased diffusion, predawn oxygen concentrations were maintained at 2.5 to 3.5 mg l^{-1}.

Bouck (1963) has demonstrated that fish subjected to diurnal oxygen pulses tend to regurgitate ingested food. Additional physiological responses to oxygen pulses were observed by significant shifts in blood protein fractions, surface to volume ratio of RBC, and hemoglobin concentration.

Table 1. Oxygen metabolism of a *Vallisneria*-Periphyton community in the Red Cedar River during the 1961 summer.

Date	Gross production $g\ O_2\ m^{-2}\ day^{-1}$	Community respiration $g\ O_2\ m^{-2}\ day^{-1}$	$\frac{P_g}{R_c}$	Maximum stream temp. C
30 June 1961	13.6	11.8	1.2	25
18 July 1961	10.0	10.8	0.9	24
9 Aug. 1961	7.8	16.8	0.5	24
16 Aug. 1961	5.5	13.0	0.4	23
April 1958[1]	1.8	0.6	3.0	--

[1] Grzenda (1960) single station estimate.

The seasonal oxygen metabolism of the Neuse River, a turbid, Piedmont-Costal stream in central North Carolina, was reported by Hoskin (1959). Hoskin found a constant excess of respiration over photosynthesis regardless of the season of the year. The heterotrophic metabolism of the Neuse River was attributed to an organic import greater than that produced by the autotrophic community. The P/R ratio of the Neuse River ranged from 0.2 to 0.7; production (0.29 to 9.8 g O_2 m^{-2} day^{-1}) was considerably lower than found in the enrichment zone of the Red Cedar River.

Odum, Burkholder and Rivera (1959) measured the oxygen metabolism of tropical, estuary communities, and reported production rates ranging from 11 to 44 g O_2 m^{-2} day^{-1}. Coral reefs were the most productive community; the gross production of a turtle grass community (Thalassia) varied from 8 to 15 g O_2 m^{-1} day^{-1}. The turtle grass community had production rates comparable to the Vallisneria community in the Red Cedar River.

Respiration by the autotrophic community may be estimated by reducing the gross production estimate by the magnitude of net macrophyte and periphyton growth increment. This calculation is made convenient by converting the data to energy terms. The essential data for estimating autotrophic respiration in the Red Cedar River are given in Table 2 for two sampling days.

The macrophyte production figures are daily averages and do not necessarily reflect the actual growth during the day oxygen measurements were recorded. Periphyton production was estimated using predictor equations based upon stream temperature (see page 63).

Autotrophic respiration was estimated by subtracting net production from gross production. The ratio of gross production to respiration gives

Table 2. Estimates of production and autotrophic respiration in a 100 meter section of the Red Cedar River.

	Production (kcal m^{-2} day^{-1})	
	June 30, 1961	August 16, 1961
Gross production (P_g)	41.34	17.16
Net production (P_n)		
Macrophytes	2.37	0.89
Periphyton	11.41	5.66
Respiration = P_g - P_n	27.56	10.61
R/P_g	67%	62%

the per cent gross energy transfer degraded to heat by metabolic activity. This ratio for the two summer estimates indicates that approximately 65% of gross energy transfer is degraded to heat. Odum (1959) reports that a mixed natural community uses 50% or more of the gross production for plant maintenance.

The gross and net productivity of an algal community, primarily *Plectonema Boryanum*, in an artificial stream was 2.76 and 0.98 k cal m^{-2} day^{-1}. (Kevern 1963). These production data indicate that approximately 64% of gross production in the artificial stream was degraded to heat by plant metabolism.

Aquatic Macrophytes

Vallisneria americana is the principal macrophyte found in the 2.2 mile study reach. Additional species, in order of abundance, include *Sagittaria*, *Elodea*, *Potamogeton*, and *Fontinalis*. The macrophyte community in the study reach consisted almost exclusively of *Vallisneria* and *Sagittaria*. The following discussion of macrophyte biomass and production applies principally to the two major forms.

Since 1957, the distribution and abundance of aquatic macrophytes has increased markedly in the Red Cedar River. Brehmer (1958) and Grzenda (1960) reported that periphyton was virtually the only primary producer in the stream during their study period (1955-1958). In 1958, I began water quality studies in the Red Cedar River. At this time macrophyte distribution was limited and confined to a few isolated beds. Since 1958 the distribution and abundance of stream macrophytes has become extensive particularly in zones of stream enrichment.

During the 1961 and 1962 seasons, approximately 50% of the experimental study reach was stocked with aquatic macrophytes. However, the stocking density during the 1962 season was three times greater than the previous season. Either Vallisneria or Sagittaria or both were found in each 100-foot study unit of the experimental reach. Only deeper pools and recent sand deposits lacked macrophytes. Stocking density was greatest in gravel runs and least in the sand-mud bottom pools.

The biomass of the macrophyte standing crop was measured by the harvest method twice during each of two growing seasons. Estimates of production by the harvest method yielded net accumulation of organic material (Penfound, 1956). During the growth phase, the macrophyte community is utilized only to a limited extent by consumer species. Therefore, net harvest is approximately equal to the total elaboration of organic material. Small amounts of Vallisneria are consumed by crayfish. Lesser but unknown amounts may be consumed passively by the fish population while foraging for aquatic insects. Ball (1948) and Gerking (1962) have discussed the occurrence of macrophytes in bluegills and suggested active feeding.

The average biomass and net production rate for each year is given in Table 3. The conversion of wet weight to dry weight was made by oven drying (60 C) representative samples. Dry weight varied from 4.8 to 5.5% of wet weight. The average conversion was expressed by

$$\text{g dry wt.} = \text{g wet wt.} \times 0.051 \pm 0.007$$

As the season progressed, the per cent dry weight increased. The change in per cent dry weight was attributed to progressive increases in the ratio of leaf to rooted plant portions and accrual of periphyton.

Table 3. Net primary production of stream macrophytes during the 1961 and 1962 growing season, as determined by the harvest method.

		Means ± 95 per cent confidence limits		
Harvest Date		Grams per sq. meter	Grams per sq. meter per day	Gram calories per sq. meter per day
26-27 June 1961 (40)[1]	Wet	545 ± 167	13.65 ± 4.22	
	Dry	28 ± 9	0.70 ± 0.21	2025 ± 608
11-12 Sept. 1961 (116)	Wet	925 ± 227	7.97 ± 1.96	
	Dry	47 ± 12	0.41 ± 0.10	1186 ± 289
16-17 July 1962 (71)	Wet	2591 ± 736	36.50 ± 10.37	
	Dry	132 ± 38	1.86 ± 0.53	5381 ± 1533
2-3 Sept. 1962 (119)	Wet	3194 ± 692	26.84 ± 5.82	
	Dry	163 ± 35	1.37 ± 0.30	3964 ± 868

---

[1] Number of growing days prior to harvest.

Unlike the periphyton community, macrophyte growth is seasonal (Figure 10). New growth appears in mid-May. The maximum production rate is attained by late June and rapidly diminishes. The total growing season is approximately 125 days. Vegetative growth is greatly reduced (0.3 g m^{-2} day^{-1}) by mid-August when plants begin seed production. In mid-September large segments of the crop detach from the rooted portion and drift downstream. By late September virtually the entire community has detached. Factors initiating the sudden and complete detachment of *Vallisneria* are unknown. Detachment occurs several weeks prior to leaf-fall.

At the end of the 1961 and 1962 growing season the average biomass and 95% confidence limits were estimated as 47 ± 12 and 163 ± 35 g m^{-2} respectively. These biomass estimates are equivalent to net production rates of 0.41 and 1.37 g m^{-2} day^{-1} dry weight. The 95% confidence limits for these estimates are approximately 25% of the mean. The broad confidence limits result in part from the discontinuous distribution. However, once a *Vallisneria* bed was encountered, the 95% confidence limits were reduced to about 15% of the mean estimate.

The macrophyte production rate in the Red Cedar River was considerably less than that reported by Knight, Ball, and Hooper (1962) for shallow Michigan ponds. Shallow ponds were reported to have a macrophyte production rate of 1.45 to 6.00 g m^{-2} day^{-1}. Odum (1957) reported a production rate of 7.40 g m^{-2} day^{-1} for Silver Springs.

The lower rates found in the Red Cedar River are attributed to the following: 1) production was calculated for the entire study area which was only 50% stocked, 2) the community may be expanding at an exponential rate and has not reached the maximum environmental carrying capacity.

Figure 10. Seasonal rates of production and biomass accumulation of the macrophyte population.

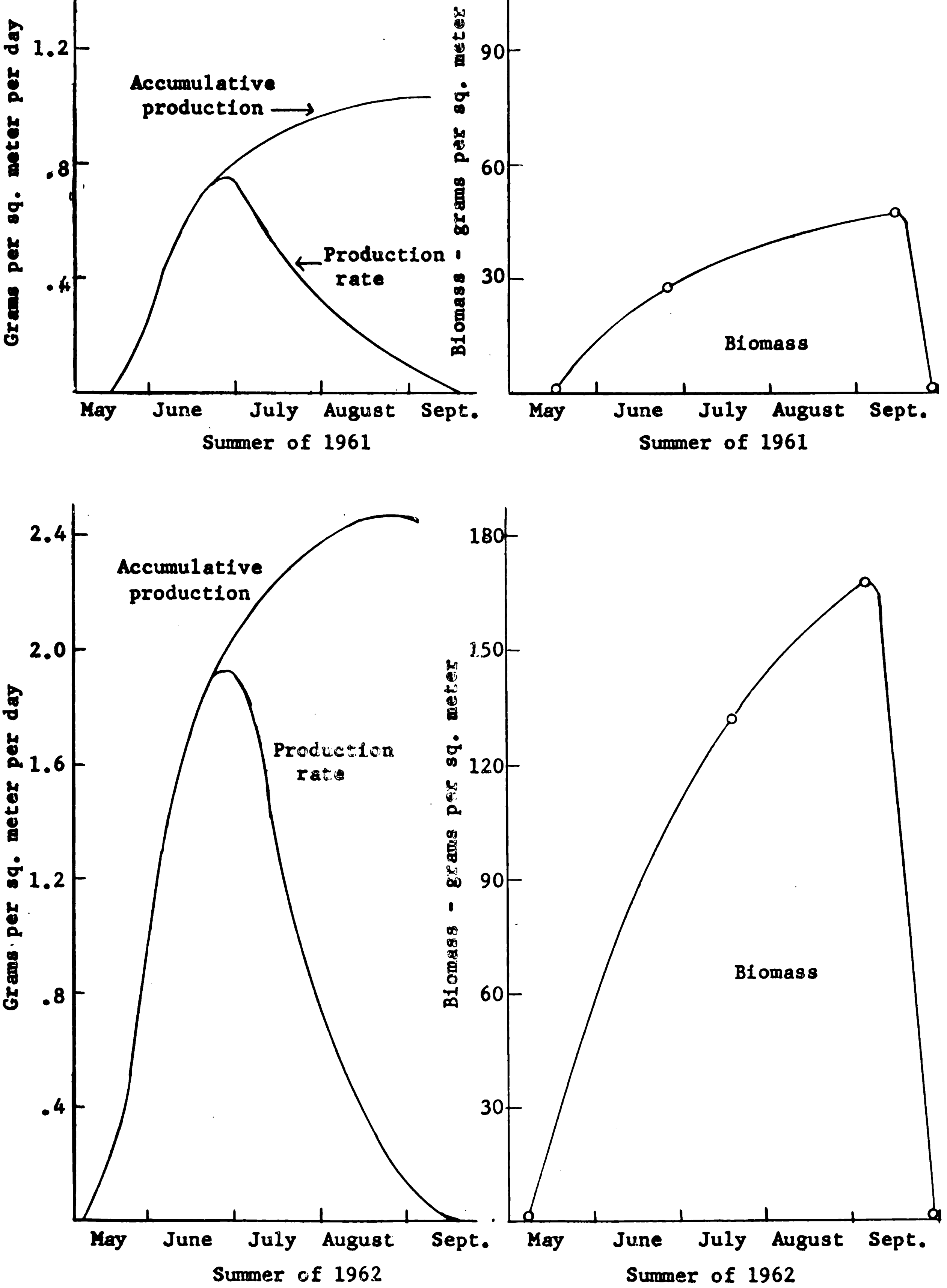

1.2
.8
.4
Grams per sq. meter per day
Accumulative production
Production rate
May
June
July
August
Sept.
Summer of 1961
90
60
30
Biomass - grams per sq. meter
Biomass
May
June
July
August
Sept.
Summer of 1961
2.4
2.0
1.6
1.2
.8
.4
Grams per sq. meter per day
Accumulative production
Production rate
May
June
July
August
Sept.
Summer of 1962
180
150
120
90
60
30
Biomass - grams per sq. meter
Biomass
May
June
July
August
Sept.
Summer of 1962

Figure 10

In the pond study by Knight, Ball, and Hooper (1962) stocking density varied from 75% to 95%. In addition, these workers reported that Chara was the dominant macrophyte. Chara is noted for incrustations of calcium carbonate, and this deposition may have contributed significantly to the harvest weight and apparent production rate.

There is some evidence that the macrophyte community in the Red Cedar River is expanding at a logarithmic rate. Speculation into the rate of population espansion is limited because quantitative data are available for only two growing seasons. If some validity can be attached to the observational records that macrophyte production prior to 1958 was confined to sparse isolated beds, we have some basis for speculation into the expansion rate. In Figure 11, I have plotted the average autumnal biomass for the 1961 and 1962 seasons and assumed a low level of macrophyte production in 1957. This graphic plot indicates that the current expansion rate may be exponential. Underestimating the 1957 biomass by a factor of ten to twenty would not alter substantially the hypothesis that the expansion is logarithmic in nature.

Assuming the community expansion behavior is consistent with the Pearl-Verhulst concept of logistic growth, the population is characterized by some maximum rate of growth (k_m). This maximum growth rate tends to be reduced proportionally as the population increases to some maximum population level (K) imposed by existing environmental conditions. For instantaneous rates, the logistic growth behavior may be described by the expression

$$k = k_m \left(1 - \frac{P}{K}\right)$$

where P equals the average population level accompanied by an instantaneous rate of growth k.

Figure 11. Estimated rate of macrophyte expansion in the Red Cedar River.

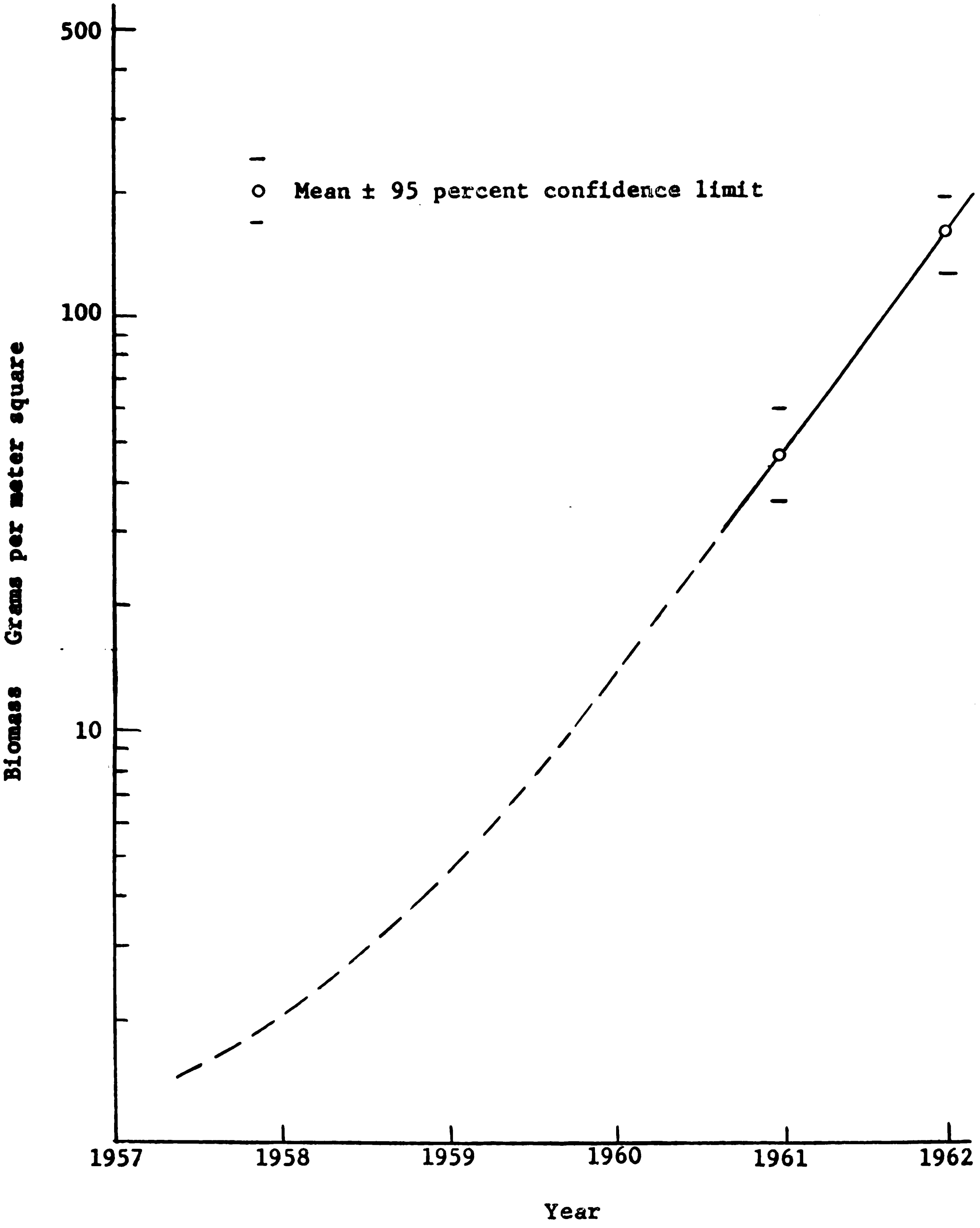

500
100
10
Biomass Grams per meter square
Mean ± 95 percent confidence limit
1957
1958
1959
1960
1961
1962
Year

Figure 11

For the Red Cedar River, the upper level (K) was estimated by measuring the average standing crop of a dense Vallisneria bed. The upper limit was estimated as 827 g m^{-2} dry weight. The annual instantaneous rate of population expansion (k) from 1961 to 1962 was 1.34 accompanied by an average macrophyte biomass (P) of 105 g m^{-2}. According to the above logistic equation

$$1.34 = k_m \left(1 - \frac{105}{827}\right)$$

or

$$k_m = 1.53$$

The calculated maximum growth rate may be compared to the actual population expansion rate to determine the relative phase of macrophyte expansion now existing in the Red Cedar River. This comparison requires the validity of several assumptions. These assumptions are: 1) population expansion follows, at least approximately, the logistic pattern, 2) the maximum average population density imposed by the environment is 827 g m^{-2}, and 3) the observational records of minimal macrophyte production prior to 1958 (less than 20 g m^{-2}) really existed.

Accepting the above assumptions, it is likely that the present instantaneous expansion rate of 1.34 is approaching or has passed the maximum growth rate of 1.53. The changes in environmental conditions which permitted the release and accelerated growth of stream macrophytes are not known. Some insight into the expansion may be gained by inspecting the efficiencies of the macrophyte population.

Efficiencies of Energy Transfer: Efficiencies for the growth or net increase of aquatic macrophytes are based upon the ratios of the energy content of the product to the incident radiation. The spontaneous transfer of energy from one form into another is always accompanied by an increase in entropy (second law of thermodynamics). Therefore, the ratio of energy of one level to another (L/L-1) must necessarily be less than 100%.

Rabinowitch (1951) estimates that plants fix photosynthetically about 1% of the total insolation. The average photosynthetic efficiency of the oceans is about 0.18% of the total radiation (Riley, 1944). A maximum phytoplankton efficiency of 0.3% was cited by Clarke (1946) for Georges Bank.

Odum (1959) and Clarke (1946) discuss the quantitative relationships of various trophic efficiencies commonly used to delineate energy transfer rates. Lindeman (1942) defines energy intake efficiencies as the ratio of energy intake at a given trophic level ($\lambda t/\lambda t\text{-}1$). For the primary producers, trophic efficiency is defined as the ratio of net production to incident radiation (P_n/L_t) or gross production to incident radiation (P_g/L_t) (Odum, 1959).

The energy content of the macrophyte crop in the Red Cedar River was determined by oxygen bomb calorimetry. The caloric value for _Vallisneria_ ranged from 2803 to 2993 calories per gram dry weight. The dry weight estimate of macrophyte production (Table 3) was converted to energy content by the following relationship:

$$\text{g cal} = \text{g dry weight} \times 2893 \pm 82$$

The calculated rates of daily energy fixation by the macrophytes in the Red Cedar River are given in Table 3 for the initial and terminal sampling periods. The rate of energy transfer was greater during the initial growth periods than for the entire growing season. This indicates that the population is expanding rapidly during the early growth stages and production rates decrease by midsummer. After mid-August most new growth occurred as seed production.

Records of solar insolation of the Michigan State University Pyrheliometer Station (expressed as the amount of solar energy received by a horizontal plane at the earth's surface) were obtained through the courtesy of Dr. E. H. Kidder, Department of Agricultural Engineering, Michigan State University. The radiation station operates an Eppley ten junction, pyrheliometer located on the Michigan State University Campus. The pyrheliometer station is located approximately three miles west of the study area.

With information on the energy content of the macrophyte crop and incident solar energy, P_n/L_t and P_g/L_t efficiencies were calculated for the macrophyte community. The energy conversion efficiencies are shown in Table 4 with the average daily insolation occurring during each period. The increased efficiencies during the 1962 season reflect the magnitude of population expansion. The reduction in efficiency within a growing season reflects a reduction in the turnover rate.

During the 1961 growing season, the P_n/L_t efficiency was 0.035% during the initial 40-day growing period and 0.023% on the basis of the entire season. In 1962 the efficiencies increased approximately threefold. Macrophyte production showed a net efficiency of 0.095% during the initial 71 days of growth and a net efficiency of 0.074% over the entire 1962 growing season.

The periphyton community in the Red Cedar River was reported by Grzenda (1960) to have a net efficiency ranging from 0.003 to 0.245%, with an annual mean efficiency of 0.07%. During a season comparative to the growing season for macrophytes, periphyton had an average P_n/L_t ratio of 0.073%. Unfortunately calorimetry equipment was not available during Grzenda's study. Grzenda calculated the energy in periphyton

Table 4. Conversion efficiencies of total solar radiation into the aquatic macrophyte crop.

Harvest date	Average insolation gram calories per sq. meter per day	Percent efficiency		Turnover rate percent
		P_n/L_t	P_g/L_t*	
26-27 June 1961	5.71 x 10^6	0.035	0.078	2.50
11-12 Sept. 1961	5.14 x 10^6	0.023	0.054	0.87
16-17 July 1962	5.65 x 10^6	0.095	0.225	1.41
2-3 Sept. 1962	5.36 x 10^6	0.074	0.175	0.84

* P_g estimated from P_n by respiration metabolism data reported by Odum (1957a).

from data reported by Juday (1940) for Lake Mendota. Subsequently, it was found that Grzenda's caloric value of 5900 cal g^{-1} was approximately 25% in excess. Periphyton (predominantly diatoms) was found to have a heat of combustion equal to 4420 cal g^{-1} ash free dry weight. Therefore Grzenda's efficiencies should be reduced by a factor of 0.26 to conform with actual caloric determinations. Kevern (1963) measured the caloric content of a blue-green algae cultured in an artificial stream as 4520 cal g^{-1}.

The P_n/L_t ratios for periphyton and macrophytes are approximately equal when calculated for the entire stream. However, periphyton is continuous in its distribution in the stream, and the macrophytes are discontinuous, presently about 50% stocked. The P_n/L_t ratio of a large, dense bed of Vallisneria, having a production rate of 11.20 g m^{-2} day^{-1} was 0.571%. The high energy transfer efficiency of Vallisneria may be a partial explanation for its rapid expansion rate.

The net efficiency ratio may be rearranged and stated

$$P_n = L_t \times \text{Efficiency}.$$

With equal light reaching the periphyton and macrophyte communities, it can be seen from the above expression that production depends upon plant efficiency. The efficiencies of an established Vallisneria bed are approximately eight times that of periphyton during comparable growth periods. The relatively high efficiency of Vallisneria may be a major factor promoting the rapid expansion rate evident in the Red Cedar River. The high efficiency may indicate that macrophytes are better competitors for essential nutrients during periods of critical shortages.

Periphyton Production

Primary production in the Red Cedar River is the summation of contribution by macrophyte and periphyton biota. In order to estimate the total primary energetics in the stream study reach, it was necessary to estimate the contribution by periphyton. The quantitative aspects of periphyton production have been studied by various workers prior to my study. Grzenda (1960) determined the annual production of periphyton at a single station (Dobie Road). Brehmer (1959) related annual periphyton production to the accrual, uptake, and regeneration of essential nutrients. Brehmer's sampling stations were stratified above and below the Williamston disposal plant.

Seasonal studies, of several months duration, were conducted by Peters (1959) and Rawstron (1961). Peters compared and found similar the periphyton taxa colonizing natural and artificial substrates. Rawstron clarified the relative productive differences in riffle and pool situations.

In view of the large amount of data available concerning periphyton production, I decided not to include routine periphyton studies. Instead, various relationships between environmental parameters and reported periphyton production were explored in an attempt to formulate predictor equations.

It was theorized that predictor equations could be established by equating production rates to some environmental factor multiplied by a constant. This in effect would adjust earlier estimates to conditions prevailing during my study.

Brehmer's (1959a) production data was reported as phytopigment units (AA × 10^3 dm^{-2} day^{-1}). The conversion of these data to organic weight was made by plotting the lower range of Grzenda's data relating organic weight to absolute absorbency. Since Brehmer's data were presented as daily production, the majority of the conversions would necessitate using the low range portion of Grzenda's data. The linear relationship of phytopigment absorbency to weight carried a negative intercept for the full range of data. An expression with a negative intercept was unacceptable for converting low production data. Therefore a curve was fitted to data in the range 0 to 30 mg and 0 to 0.25 AA units. This curve was then used to estimate organic weight from phytopigment data.

Subsequently, I found that in zones of stream enrichment a strong linear relationship existed between stream temperature and the $\log_{10}$ of periphyton production during periods of increasing or decreasing photoperiods. On the strength of highly significant correlation coefficients ($r_{xy} = 0.901$ and 0.986 for increasing and decreasing photoperiods respectively), regressions were calculated to describe the relationship between production and temperature.

The calculated regressions with the original data are shown in Figure 12 for Brehmer's Sherwood Road station. Temperature estimates were obtained from a continuous recording thermograph located at the Dobie Road station. Average temperature was calculated from the thermograph recordings during periods of substrate exposure.

In calculating the regression coefficients, two observations were excluded from consideration during the increasing photoperiod series (16 C - 0.039 g m^{-2} day^{-1} and 18.5 C - 0.038 g m^{-2} day^{-1}). I considered that these data (Figure 12) departed to an unnatural extent from the production rate immediately prior (0.94 g m^{-2} day^{-1}) and following (1.45 g m^{-2} day^{-1}) these observations. During this period, May 13 to 29, production was arrested at all stations in the enrichment zone indicating

Figure 12. The relationship between periphyton production and stream temperature for periods of increasing or decreasing photoperiods.

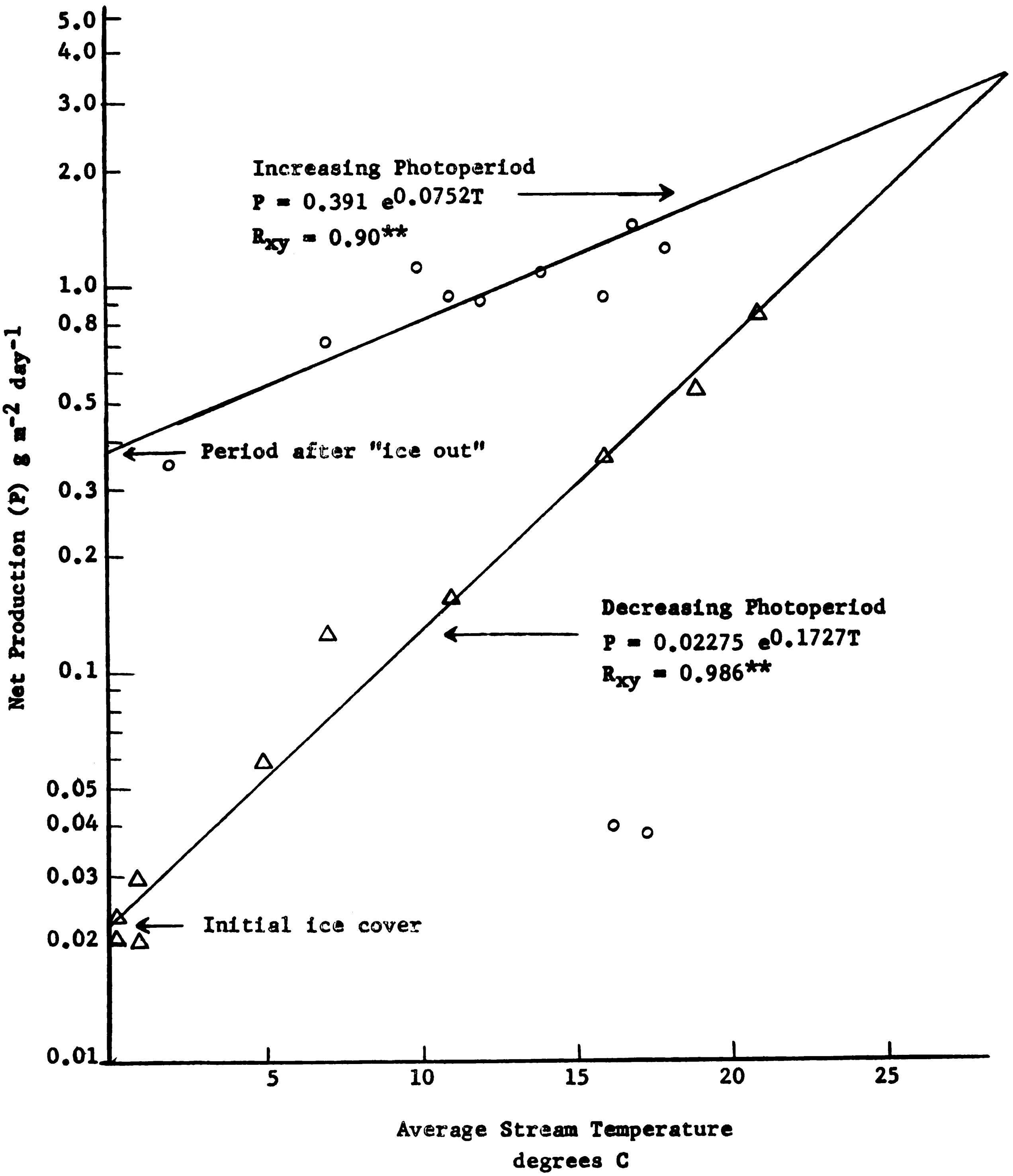

Net Production (P) g m^{-2} day^{-1}
5.0
4.0
3.0
2.0
1.0
0.8
0.5
0.3
0.2
0.1
0.05
0.04
0.03
0.02
0.01
5
10
15
20
25
Average Stream Temperature
degrees C
Increasing Photoperiod
$P = 0.391\ e^{0.0752T}$
$R_{xy} = 0.90^{**}$
Period after "ice out"
Decreasing Photoperiod
$P = 0.02275\ e^{0.1727T}$
$R_{xy} = 0.986^{**}$
Initial ice cover

Figure 12

that either a toxic arrestant or a depleted, essential nutrient inhibited production. The inclusion of these data into the regression coefficients, if in fact the causal factor(s) were not an annual occurrence, would alter substantially the usefulness of the predictor equation. The converse of the above statement, however, is also true.

The Sherwood Road station is located midway in my stream study reach, and production at this site was considered representative for the entire study area. At this station, periphyton production (P) in g m^{-2} day^{-1} may be estimated from stream temperature (T) in degrees centigrade by the following exponential expression:

Increasing Photoperiod: $P = 0.391\ e^{0.0752\ T}$

Decreasing Photoperiod: $P = 0.0228\ e^{0.1727\ T}$

The fact that separate predictor equations were required for periods of increasing and decreasing photoperiods predicate a different basic growth rate and temperature effect in the spring and fall.

Measurements of periphyton production were available for two additional stations within the zone of stream enrichment. These stations were located at Meridian Road (M43) and Dobie Road. A complete series of measurements were available for only the seasons of increasing photoperiod. At each station during increasing photoperiods, a highly significant correlation existed between stream temperature and the $\log_{10}$ of periphyton production (M43: $r_{xy} = 0.982$, df = 8; Dobie: $r_{xy} = 0.932$, df = 7). The predictor equations for estimating periphyton production (P) were calculated and expressed exponentially as:

M43: $P = 0.313\ e^{0.1169\ T}$

Dobie: $P = 0.136\ e^{0.1612\ T}$

The temperature and production data for the above two stations were combined and tested for heterogeneity by the analysis of covariance. The analysis revealed that neither the slopes nor the elevations of the regression lines were significantly different at the 5% level. The two stations were approximately five miles (8.05 km) apart, and the production measurements were made by different workers during the same season. This indicates that production, as estimated by artificial substrates, may not be dependent upon either the worker or the sampling site if water quality remains relatively unchanged.

The exponential relationship between periphyton production and temperature collapses in stream areas outside the enrichment or "clean water" zone. This apparent breakdown may be seen by inspecting Figure 13. The periphyton sampling stations are located at and below the Williamston sewage disposal plant. The terminal downstream station is located in the zone of stream enrichment as described above.

Several statements should be made and discussed pertaining to production dynamics in this stream area which receives community effluents. Statements: 1) Production at the zone of pollution, under cold-water conditions ($<$8 C) may be as great or greater than downstream recovery areas. 2) Production in pollution zones is depressed greatly at elevated water temperatures. 3) The use of artificial substrates for pollution monitoring is valid if the seasonal aspects of primary production are considered.

Referring to Figure 13 again, the reader can see that a false conclusion pertaining to water quality would be attained if autotrophic production was measured at stream temperatures below 8 C.

Figure 13. The interrelationships of periphyton production and stream temperature with distances from a point source of domestic pollution. Data are for seasons of increasing photoperiods.

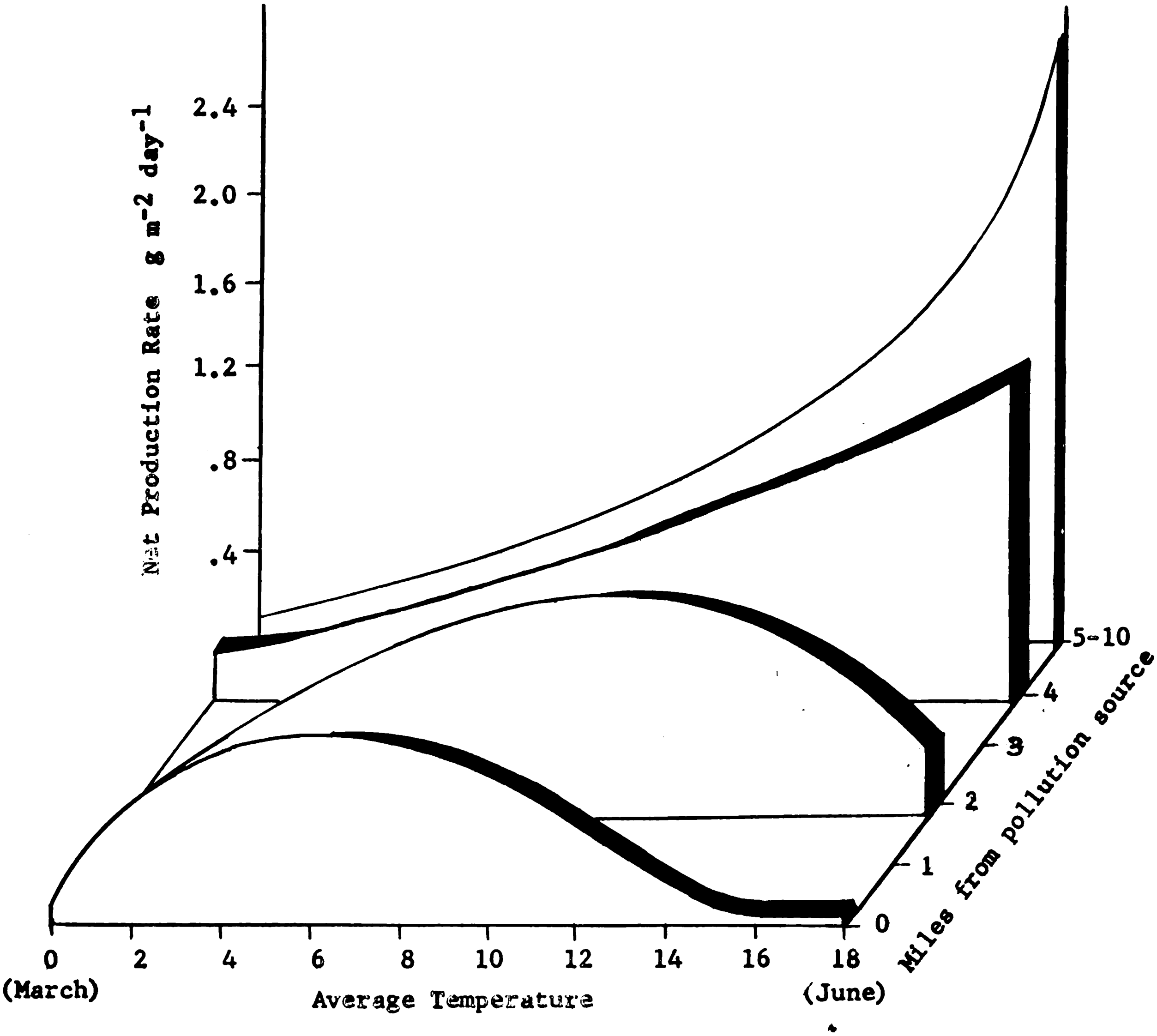

Net Production Rate g m-2 day-1
2.4
2.0
1.6
1.2
.8
.4
0
2
4
6
8
10
12
14
16
18
(March)
Average Temperature
(June)
0
1
2
3
4
5-10
Miles from pollution source

Figure 13

Suppression of periphyton production (predominantly diatoms) is coincident with maximum biological demand by consumer species. Since periphyton turnover is rapid, little opportunity exists for stream storage before periphyton becomes a component of stream drift. Therefore, to be available, periphyton must be produced continuously during periods of consumer demand. This is not the case in the zone of stream pollution. At the period of maximum consumer demand, periphyton production is suppressed at or below that level recorded under ice cover.

The biotic or abiotic mechanisms suppressing production may be temperature regulated. However, suppression may be caused by other factors strongly correlated with temperature increases, e.g., photoperiod, diminishing stream flow, lesser amounts of water available for effluent dilution, and heterotrophic competition.

At elevated stream temperatures, fungi and bacteria (Sphaerotilus, for one) may be serious competitors for available space. Under conditions favorable for both algae and bacteria growth, bacteria have a great advantage over algae because the former are not dependent upon light energy. Algae cultures, maintained at elevated temperatures, in presence of luxury nutrient concentrations, are particularly susceptable to bacteria contamination. Gotass et al. (1957) demonstrated that culture turbidity due to bacteria growth in algal cultures imposed a limit on energy conversion efficiencies. Algal yields from contaminated cultures are greatly reduced. The antagonistic effect of bacteria upon algae cultures has been attributed to nutrient depletion, clouding of culture media, and toxic metabolites.

Cooke (1959) has described the microorganisms found in trickling filter systems and reported the primary decomposers were bacteria and

fungi. Cooke cited the occurrence of eight species of hydrofungi attached to glass slides exposed in sewage effluents. Canter and Lund (1953) described the occurrence of several chytridiaceous fungi which are parasitic upon algae. In a literature review, Cooke (1954) indicated that the benthic bacterium, *Sphaerotilus natans*, is widespread in sewage and polluted water.

It is my belief that periphyton production in the vicinity of the Williamston disposal plant is suppressed at elevated summer temperatures because of direct competition of bacteria, fungi, or both. Under cold-water conditions (< 8 C) heterotrophic competition is not sufficient to suppress autotrophic production. Autotrophs are reported to be more dependent upon light than upon temperature (Steele, 1962). Bacteria production is temperature dependent with a Q_{10} very nearly equal to 2.0 (Moore, 1958).

The role of stream biota in stabilization and mineralization of domestic pollution is well known. Downstream areas from a point source of pollution commonly are divided into septic, recovery, and clean-water zones. These zones are not static, but shift either upstream or downstream depending upon the seasonal rates of assimilation. A common statement of the idea is that the septic zone is extended downstream during cold-water seasons and is reduced in extent during the warm-water seasons of high metabolic activity.

The converse of the above statement is evident in the Red Cedar River. Suppression of the autotrophic community is shifted progressively to downstream areas (Figure 13) with increasing stream temperature. When stream temperatures are less than 8 C, periphyton production is not depressed, and may in fact, exceed production in the clean-water zone. Apparently the deleterious effect of this effluent from the Williamston disposal plant is not directly toxic to periphyton. Instead, the reduction of periphyton production is probably a self limiting effect imposed by shifts in the associated community biota (heterotrophic competition).

The exponential relationships between stream temperature and periphyton production would fail if the pollution effect of the Williamston Disposal Plant were extended downstream to encompass the clean-water zone. The pollution zone would be expected to extend to additional downstream area if the demand upon the disposal plant exceeded its designed capacity. Withdrawal of upstream dilution water for irrigation would produce a similar effect.

Periphyton production in the study reach was estimated from the predictor equations established for the Sherwood Road station. The equations were used in the following manner:

From the time of "ice out" until June 30, the increasing photoperiod equation was used. The decreasing photoperiod equation was used for the remainder of the year. During periods of uniform temperature (moderate increases or decreases), an average stream temperature was interpolated from thermograph recordings. This average temperature was entered into the appropriate equation and the expression solved for an estimate of the average net production.

The estimated daily production for a uniform temperature series was entered in column four of Table 5. The product of the average production rate and duration of uniform temperature are shown in column five. The summation of column five equals the total net production by periphyton during the year.

Table 5. Estimates of periphyton production based upon water temperature during increasing and decreasing photoperiods.

Date 1961	Average temperature Degrees C	Number of days	Production[1] rate g m^{-2} day^{-1}	Total accumulation g m^{-2}
1/1 - 3/1	0.0	60	0.023	1.38
3/2 - 3/31	3.0	30	0.49	14.70
4/1 - 4/17	6.0	18	0.62	11.16
4/18 - 4/20	7.0	3	0.66	1.98
4/21 - 5/6	10.0	15	0.83	12.45
5/7 - 5/11	14.0	5	1.12	5.60
5/12 - 5/22	16.0	10	1.31	13.10
5/23 - 5/31	14.5	9	1.17	10.53
6/1 - 6/5	17.2	5	1.42	7.10
6/6 - 6/13	21.1	8	1.92	15.36
6/14 - 6/17	20.0	4	1.79	7.16
6/18 - 6/23	17.2	6	1.42	8.52
6/24 - 6/26	20.0	3	1.79	5.37
6/27 - 6/30	23.9	5	2.41	12.05
7/1 - 7/31	21.7	31	1.01	31.31
8/1 - 8/31	20.0	31	0.73	22.63
9/1 - 9/10	22.2	10	1.03	10.30
9/11 - 9/15	19.4	5	0.66	3.30
9/16 - 9/21	16.7	6	0.40	2.37
9/22 - 9/24	18.9	3	0.61	1.83
9/25 - 9/30	15.6	6	0.34	2.01
10/1 - 10/9	12.8	9	0.21	1.94
10/10 - 10/15	12.8	6	0.21	1.29
10/16 - 10/31	10.0	15	0.13	1.92
11/1 - 11/10	7.2	10	0.074	0.74
11/11 - 11/21	5.6	11	0.058	0.64
11/22 - 11/31	3.4	10	0.039	0.39
12/1 - 12/8	2.8	8	0.037	0.30
12/9 - 12/16	1.1	8	0.027	0.22
12/17 - 12/31	0.0	15	0.023	0.34
Totals		365		207.98

Average production rate = 0.57 g m^{-2} day^{-1}

[1] **Predictor equations:**

Increasing Photoperiod: $P = 0.391\ e^{0.0757\ T}$

Decreasing Photoperiod: $P = 0.02275\ e^{0.1727\ T}$

The average daily production in the experimental study area was 0.57 g m^{-2} day^{-1}. This estimate compares favorably with Grzenda's (1960) estimate of 0.56 g m^{-2} day^{-1} for his Dobie Road station. Both stations are in the clean-water, enrichment zone and are approximately 6.5 miles apart.

The comparison of the two independent estimates lands credibility to the use of predictor equations for estimating periphyton production in the Red Cedar River. A word of caution, however, should be interjected. Predictor equations were calculated only as an expedient method to estimate production. Their continued use requires community homeostasis. Homeostasis dictates not only an equilibrium between organisms and environment but also of those mechanisms which regulate the storage, recirculation and addition of vital nutrients.

Elevated production rates would be expected if factors now limiting production were removed or partially alleviated. Conversely, production rates may be depressed by increases in domestic, agricultural, or industrial pollution. The established predictor equations describe existing growing conditions. The equations have a significant, long range value for pollution evaluation. The exponential relationship between stream temperature and periphyton production lends itself well to statistical analysis, e.g., covariance. Appropriate statistical tests are available to determine significant changes in seasonal growth rates (slope), or the levels of production (intercepts).

The fact that periphyton production, in relation to stream temperature during either periods of increasing or decreasing photoperiods, can be described by a mathematical model is very satisfying in a science in which correlation with environmental factors proves so difficult. Rodhe

(1961) was successful in formulating a mathematical model to describe the integral assimilation of phytoplankton in relation to light and temperature.

It is equally discouraging to read statements in the literature such as written by Verduin (1959) in which he states: "Whenever one attempts to correlate metabolic rates under natural conditions with environmental factors which seem most likely to exert important influences (nutrient concentrations, temperature, light supply, etc.) one obtains a wide scatter similar, when presented graphically, to the pattern from a sawed-off shotgun (Verduin, 1954, Fig. 2, and 1956a, Fig. 5)."

When I first plotted periphyton production against temperature, I too was presented with a "shotgun" picture. However, when resolved into seasons of increasing or decreasing photoperiods, the relationships became apparent. Verduin's statement (1959) is unwarranted as it can only discourage student inquiry into the complex interrelationships of population dynamics.

Primary Energetics

Primary energetics in the Red Cedar River is the dynamic transfer and fixation of electromagnetic energy into a product available to the primary consumers. Electromagnetic energy is converted by the primary producers and stored as energy in chemical bonds. The transferred energy is utilized in part by the plants to maintain their metabolic processes. This portion of chemically fixed energy is called the "activity" of that level by MacFadyen (1948). The residual energy, temporarily stored as plant biomass, is available to the primary consumers. This portion of fixed energy is termed the productivity of that level by Allen (1951) and Ricker (1958) and net production by Clarke (1946) and Odum (1957). Gross production is the total energy transfer including that used for respiratory metabolism and biomass increment.

The residual energy form (net production) is of particular interest to ecologists because the magnitude of this energy compartment determines the ultimate productivity of consumer organisms.

The energy transfer by primary consumers in the Red Cedar River is the summation of contributions by the periphyton and macrophyte community. The annual rate of energy transfer by this segment of stream biota is shown in Figure 14 for the experimental study reach.

The total, annual solar energy, as recorded by an open field pyrheliometer, amounted to 12.38×10^8 g cal m^{-2} $year^1$. Of this amount, only 43% (0.3u to 0.7u) falls within the visual spectrum (Hand, 1946). Ultraviolet light amounts to 4% of total radiation. Infrared, with wave lengths larger than 0.7 u, comprises approximately 53% of the total insolation. Because infrared radiation is absorbed by cloud cover to varying degrees, approximately 50% of incident energy is considered within the photosynthetic range (Golley, 1960).

The amount of solar energy available at the substrate level (L_a) is a function of surface reflection, water depth, and absorbency by suspended material. A submarine photometer was used to measure subsurface illumination. The estimated available energy (9.26×10^7 g cal m^{-2} $year^{-1}$) is, at best, a rough approximation because photometer measurements were made in an unshaded portion of stream during summer months.

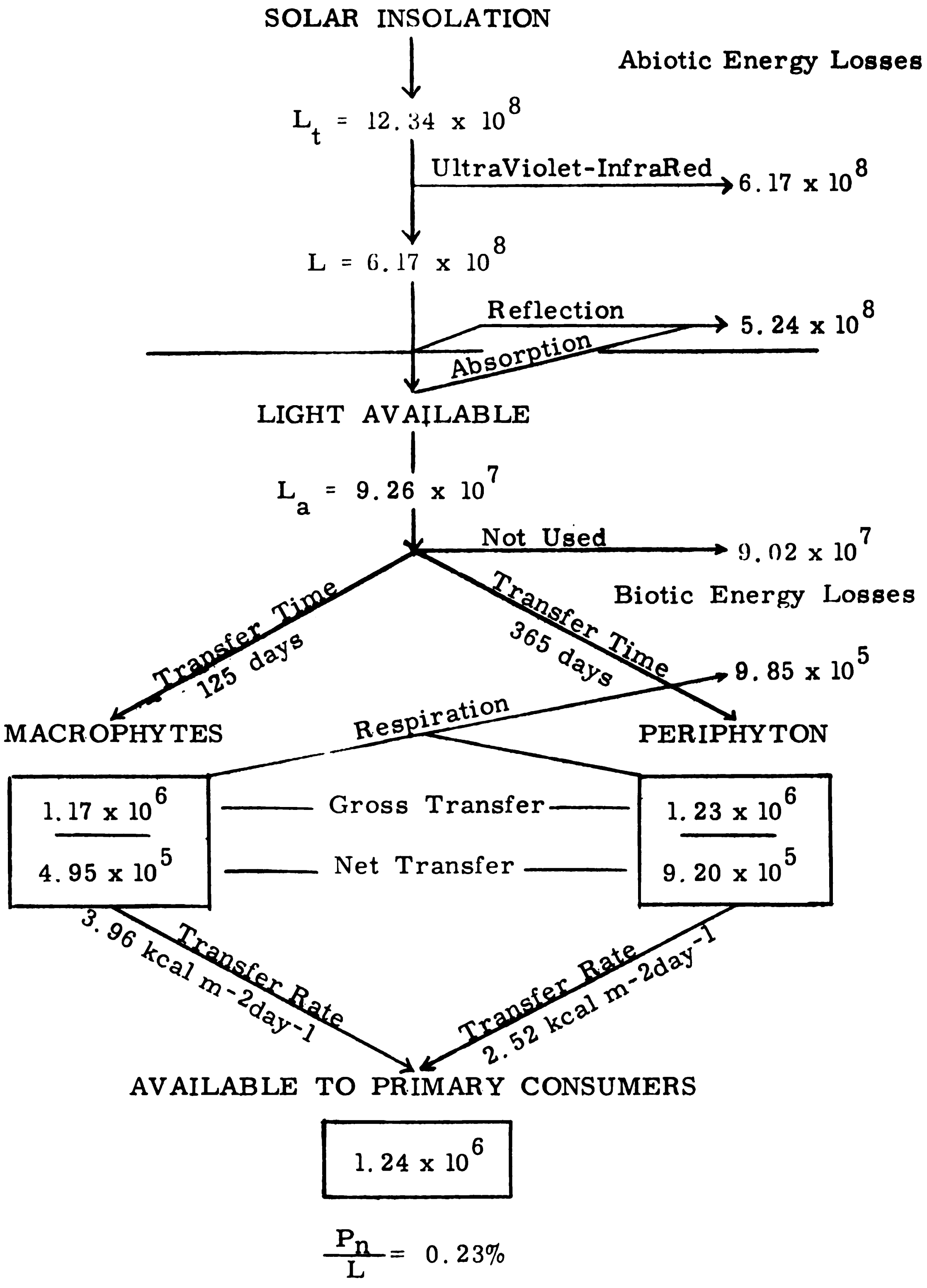
At base flow, approximately 36% of the surface illumination penetrates to the 50 cm depth, 14% to the 100 cm depth, and no illumination

Figure 14. Annual estimates of primary energetics in the experimental study reach of the Red Cedar River. All figures are gram calories per square meter per year. Solar insolation equals the total energy recorded by a pyrheliometer.

$L = g\ cal\ m^{-2}\ year^{-1}$ (0.3μ - 0.7μ range)

$L_a =$ available light at substrate level

$P_n =$ net production


SOLAR INSOLATION
Abiotic Energy Losses
$L_t = 12.34 \times 10^8$
UltraViolet-InfraRed
6.17×10^8
$L = 6.17 \times 10^8$
Reflection
5.24×10^8
Absorption
LIGHT AVAILABLE
$L_a = 9.26 \times 10^7$
Not Used
9.02×10^7
Biotic Energy Losses
Transfer Time 125 days
Transfer Time 365 days
9.85×10^5
Respiration
MACROPHYTES
PERIPHYTON
1.17×10^6
4.95×10^5
Gross Transfer
Net Transfer
1.23×10^6
9.20×10^5
Transfer Rate 3.96 kcal m-2day-1
Transfer Rate 2.52 kcal m-2day-1
AVAILABLE TO PRIMARY CONSUMERS
1.24×10^6
$\frac{P_n}{L} = 0.23\%$

was recorded below the 130 cm depth (turbidity 35 ppm). Available energy was calculated by assuming 30% transmission during base flow periods grading to 5% during the winter months. On the average, approximately 15% of surface illumination reached the substrate level.

The net energy transfer by primary producers was calculated as g cal m^{-2} $year^{-1}$. The calculations were made by multiplying the average annual production by the appropriate energy value. A summary of these estimates are:

Macrophytes: 1.37 g m^{-2} $day^{-1} \times 125$ days $\times 2893$ cal g^{-1} =
4.95×10^5 g cal m^{-2} $year^{-1}$

Periphyton: 0.57 g m^{-2} $day^{-1} \times 365$ days $\times 4420$ cal g^{-1} =
9.20×10^5 g cal m^{-2} $year^{-1}$.

Estimates of gross energy transfer (P_g) were made by obtaining respiration estimates from literature values. Grzenda (1960), citing Juday (1940), reported for periphyton that one-third of gross production was degraded into heat by respiration. Odum (1957), for a macrophyte community similar to that found in the Red Cedar River, estimated that 57.5% of gross production was lost to plant respiration. This value for macrophyte respiration is within the range predicted from diurnal oxygen curves.

On the basis of the above values for respiration, about 2.4×10^6 g cal m^{-2} of electromagnetic energy was transferred into chemical energy by the autotrophic community. Of this amount, 9.85×10^5 g cal (41%) was degraded into heat (respiration) and 1.42×10^6 g cal was incorporated into plant material (net production).

The net production of stream macrophytes during the 125-day growth season was 4.95×10^5 g cal m^{-2}. This production is equivalent to a net transfer rate of 3.96 k cal m^{-2} day^{-1}. Periphyton, produced in varying seasonal amounts, had an annual net production rate of 9.20×10^5 g cal m^{-2}, characterized by an average daily transfer rate of 2.52 k cal m^{-2}. During 1962, net macrophyte production was approximately 54% of periphyton production.

The ratio of transferred energy (P_n) to incident solar energy (L) is a measure of the ecosystem's ability to fix energy. The P_n/L ratio describes the efficiency of the system by including both biotic and abiotic energy losses. For the experimental study area, the P_n/L ratio was 0.23% in 1962.

A transitional, old field community located on a terrace adjacent to the Red Cedar River was reported to have a P_n/L ratio of 0.81% (Golley, 1960). Canada blue grass (Poa compressa) was the dominant vegetation on the river terrace. On the basis of available light during the growing season, the old field situation transferred 1.05% of the available light energy. Based upon available light, the P_n/L_a ratio of the Red Cedar River was 1.5%. The higher efficiency for the stream indicates that the stream biota are more efficient at using the available light.

Crayfish

The predator-prey relationship of a bass-crayfish association has been recognized by many workers including Tate (1949), Tester (1932) and Lambou (1961) among others. Although the importance of crayfish in the diet of smallmouth bass is recognized, crayfish production under active fish predation has received little attention. Literature concerning crayfish is limited largely to distribution patterns, life histories, and utilization as physiological test animals. Slack (1955) and more recently, Warren et al. (1960) reported seasonal standing crops of crayfish in small streams. However, no attempt was made by these workers to estimate crayfish production.

Crayfish are abundant in the Red Cedar River. As indicated by stomach analysis, crayfish constitute the major food source of smallmouth bass. Of 34 smallmouth bass, 6-18 inches in length, only one did not contain at least one crayfish. A large minnow population is used only to a limited extent by smallmouth bass. In many cases crayfish were the only items found in either the stomach or intestine. Inspection of the stomach contents of 117 rock bass, 3 inches and over, revealed that 77 fish (66%) had consumed recently at least one crayfish.

Two species of crayfish found in the Red Cedar River are the river crayfish, _Orconectes_ _propinquus_ and the mud crayfish _Orconectes_ _immunis_. The former is widely abundant throughout the stream. The mud crayfish is rather limited in distribution to the lower stream reaches where the pool bottom is mud or sand. _O_. _immunis_ leave the stream to construct burrows along the stream bank or in back-water slacks. _O_. _propinquus_ inhabits the rocky gravel portions of the stream and is dominant in the stream study reach.

_O_. _propinquus_ rarely leaves the stream, is active from late April until mid-October, and remains secluded under rocks during the winter. Copulation occurs in the spring, late summer, and fall. The females are in berry from mid-May to early June. The young hatch in early June and during the first summer remain secluded in marginal vegetation and under the periphyton mat. Unlike the adults, young-of-year crayfish are not active, nocturnal scavengers.

The number of age groups represented in a crayfish population may be inferred from a length-frequency graph. The seasonal changes in age structure of crayfish available to nocturnal collections are shown in Figure 15. In June three adult age groups are present. The adult population includes the yearlings (I), age-group II, and a relatively few large crayfish of age-group III. Group III crayfish are predominantly females, about 37 months in age, and die shortly after release of young. By mid-July only the young-of-year, and age-groups I and II remain.

This age structure conforms with that reported by Creaser (1934) for a similar crayfish population in the Huron River, a drainage adjacent to the Red Cedar River. In an Illinois stream, group II crayfish died in the fall (28 months) and none were reported to survive the third winter (Van Deventer, 1937). Tack (1940) reported a small proportion of O. immunis survived the third winter.

Trophic Status

The ecological niche of crayfish is unique in that crayfish transcent the primary trophic level, utilizing energy stored at various trophic levels. Crayfish are a link, secondary only to the primary producers, in channeling energy directly to smallmouth bass. Crayfish with varied food habits can not be assigned categorically to any one trophic level. Crayfish are primary consumers, primary carnivores, and decomposers.

The scavenger role of crayfish in recycling dead animal material directly back into the bass food chain is an important, highly efficient, ecological short circuit. Crayfish, by consuming dead fish, clams, or detritus, circumvent the decomposition, mineralization, and plant uptake cycles. This particular niche uniquely filled by crayfish should not be underestimated in a stream where decomposed material often is transported

Figure 15. Seasonal age structure of the adult, river crayfish, *Orconectes propinquus*, in the Red Cedar River.

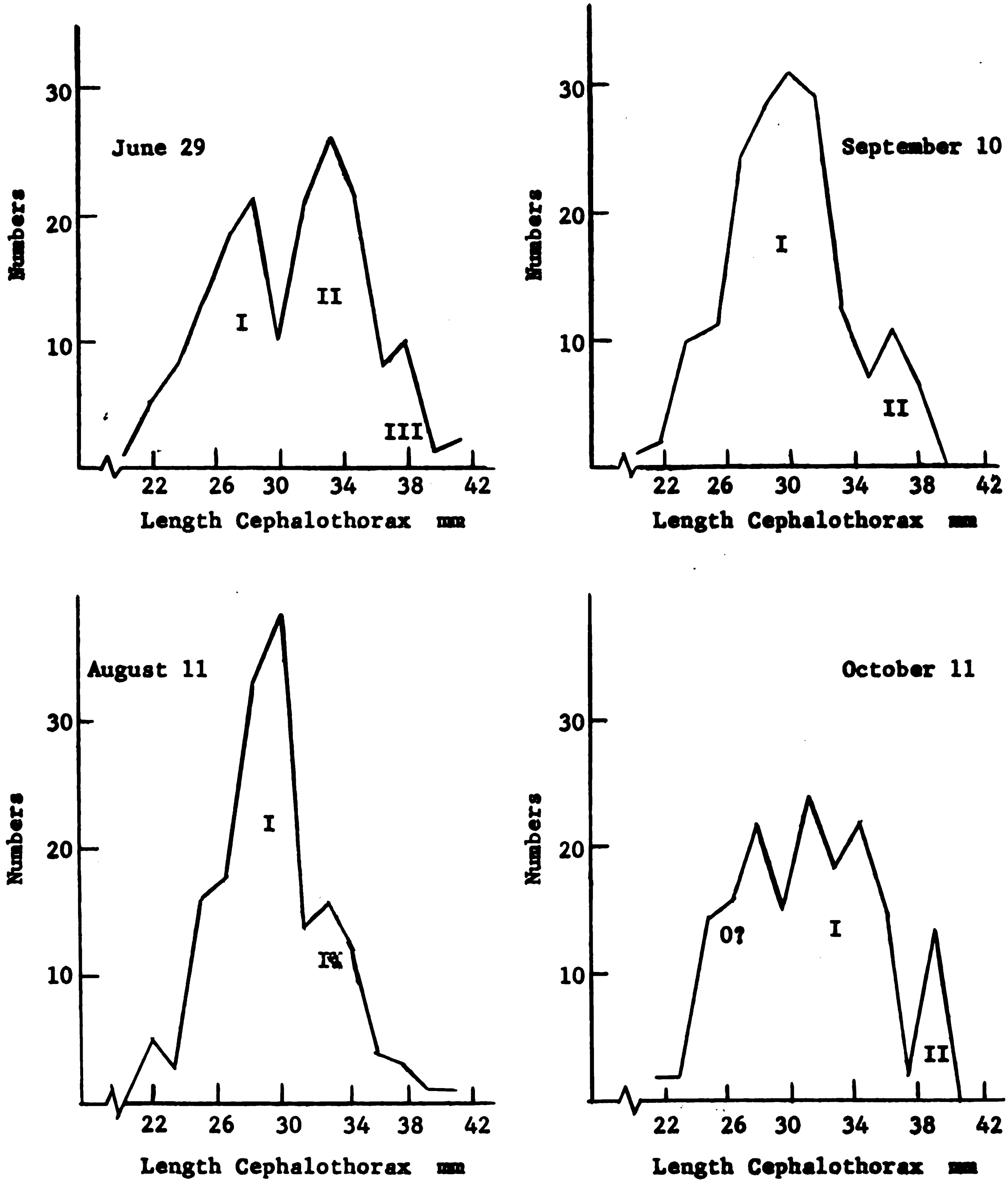

June 29
Numbers
30
20
10
I
II
III
22
26
30
34
38
42
Length Cephalothorax mm
September 10
Numbers
30
20
10
I
II
22
26
30
34
38
42
Length Cephalothorax mm
August 11
Numbers
30
20
10
I
II
22
26
30
34
38
42
Length Cephalothorax mm
October 11
Numbers
30
20
10
0?
I
II
22
26
30
34
38
42
Length Cephalothorax mm

Figure 15

to downstream areas. The short food chain from dead animal protein to crayfish protein to bass, a chain which excludes the primary level, may have ecological efficiencies to the order of 10%.

The trophic level is a functional concept and not one of species. Crayfish are polytrophic in that energy is derived from various community levels. In order to partition the energy flux (respiration + biomass increment) into proper trophic compartments, the food ingested by crayfish must be quantified.

Crayfish stomachs were collected periodically throughout the summer, preserved in 70% alcohol, and contents quantified under a dissecting microscope. Analyses of ingested food is complicated by the mandibular chewing and grinding in the gastric mill (diverticulum). The diverticulum is the site of mechanical grinding, enzyme secretion and active absorption (Prosser, 1952). Ingested food is homogenized by ossicles lining the stomach. Numerous quartz sand granules found in all crayfish stomachs probably aid in homogenization. Animal food frequently is recognized only by head capsules and body plates. Flesh of consumed clams and fish is not recognized and may be underestimated if stomach contents data are not combined with visual field records.

Approximately 40% of food ingested by young-of-year _O. propinquus_ was animal. The remainder was quantified as filamentous algae 30%, plant fragments 20%, and detritus 10%. The major animal food items of juvenile crayfish were midge larvae, mayfly nymphs, and scuds. In addition, skeleton portions of crayfish occurred in nearly half of inspected juvenile stomachs. It is not known if the crayfish remains are a result of cannibalism or simply consumption of exuviae following ecdysis.

I suspect, however, cannibalism is common among juvenile crayfish. This judgment is based on several factors; namely the high initial density (480 eggs produced per square meter), and a rapid succession of summer molts (every 12 days, Prosser, 1952) leaving many juvenile crayfish in a soft, vulnerable condition. A laboratory colony, maintained on a diet of cabbage, liver, and pelleted fish food, rapidly consumed newly molted crayfish. Warren (1960) also noted a high occurrence of apparent cannibalism among crayfish and estimated that the diet of young consisted of 60% animal material.

Recognizable food items in the stomachs of adult crayfish were largely vegetation and detritus. Adult crayfish did not have a large percentage of insects in stomach contents. Nocturnal scavenging by crayfish rapidly removed recently killed fish and clams. Following two fish kills of unknown cause and two experimental poisonings, available fish were consumed in several evenings. Extensive mortality of the pocketbook clam, _Lampsilis ventricosa,_ occurred during the 1961 and 1962 summers. Upon loss of muscle tone and subsequent opening of the shell, these clams were preyed upon by crayfish.

On the basis of stomach analysis, I estimated that the diet of adult crayfish consists of approximately 80% vegetation, 10% detritus and 10% animal material. These estimates suffer by the lack of an adequate method of evaluating homogenized animal tissue.

Bovbjerg (1952) reported that _O. propinquus_ is omivorous and a scavenger feeding primarily upon filamentous algae, other plant material and seeds. Animal items reported by Bovbjerg included mayfly nymphs, stone fly nymphs, midge, cranefly, and mosquito larvae. Stomach analysis of the crayfish, _O. immunis,_ led Tack (1940) to conclude that this species consumed 6% animal material, 83% plant fragments, and 11% detritus. In the trophic scheme for Silver Springs, Odum (1957) elected to place crayfish in the decomposer compartment with bacteria.

Growth

Crayfish growth is reflected by size increases following ecdysis. Adult crayfish molt once in late May and again towards the end of July. The spring molt of oviferous females is delayed until dispersion of young. Young-of-year crayfish molt throughout the summer, perhaps as often as every 12 days (Prosser, 1952).

Growth was measured as increases in average length of the cephalothorax. This measurement was converted to weight by the formula

$$\log W = -4.2851 + 3.5178 \log L$$

where W equals live weight in grams and L is the cephalothorax length in millimeters. The conversion formula was based upon approximately 1000 individual measurements ranging from 0.15 to 30 g. The cephalothorax length of O. propinquus is about 50% of total length.

The growth rate of individual crayfish is widely variable. By the end of the first growing season, juvenile crayfish vary from 0.5 to 2.5 grams. The size ranges become broader with increasing ages. The overlapping of age classes precludes using either length or weight as an age criterion. The variable growth rates may be genetically controlled (Van Deuenter, 1937) or may simply reflect a more variable spawning period than previously supposed.

The seasonal growth pattern for the average year classes is shown in Figure 16. During the first four months of life, O. propinquus grows about 13 mg day^{-1}. At the end of the first summer the average surviving individuals weigh 1.6 grams. Growth ceases during the winter and commences again with the spring molt. During the second summer, the growth rate is

Figure 16. Average growth rate of *O. propinquus* during the first three growing seasons.

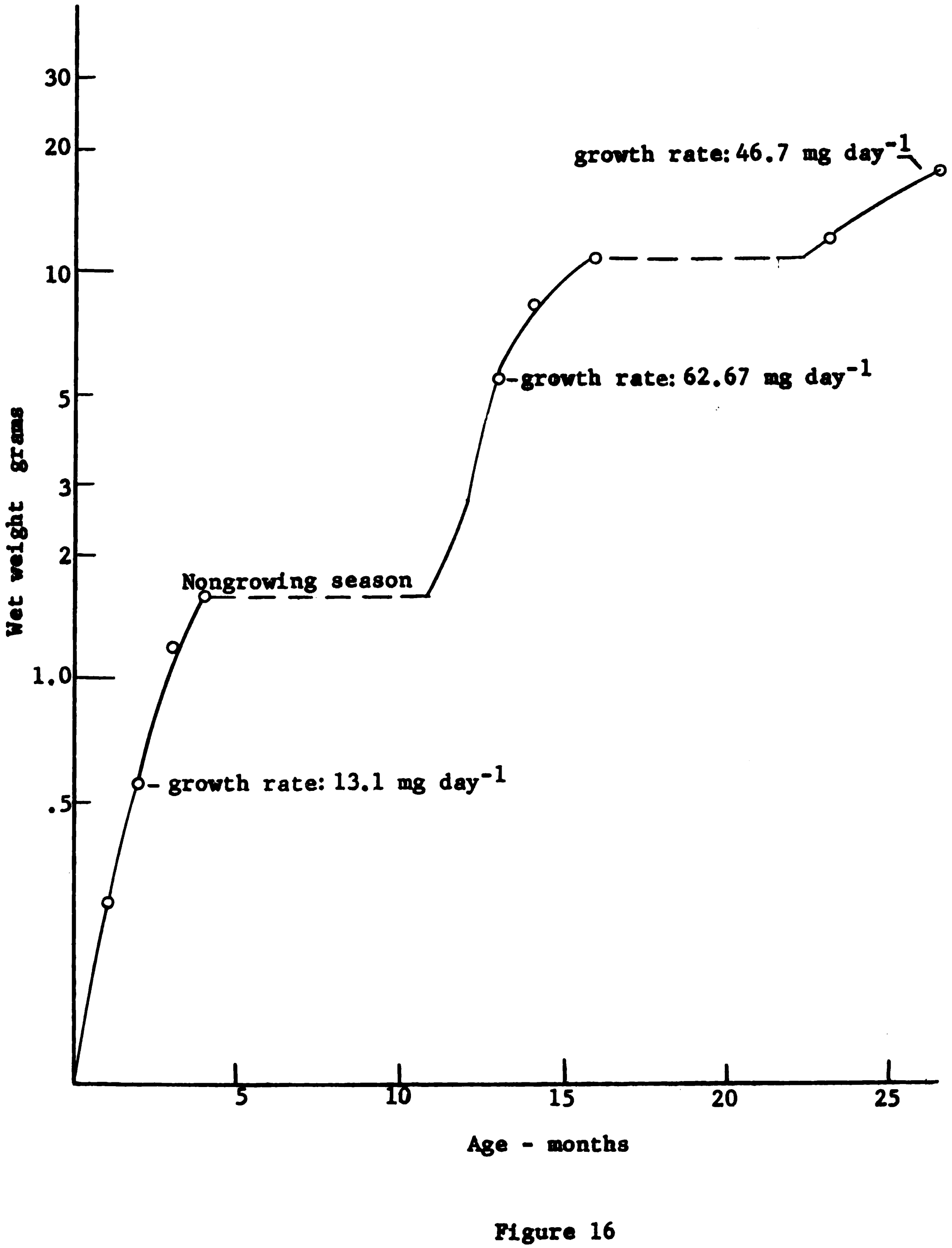

Wet weight grams
30
20
10
5
3
2
1.0
.5
5
10
15
20
25
Age - months
Nongrowing season
growth rate: 13.1 mg day^{-1}
growth rate: 62.67 mg day^{-1}
growth rate: 46.7 mg day^{-1}

Figure 16

maximal, about 63 mg day^{-1}. By September the yearlings average 11 grams although the range may be 5 to 20 grams. Growth during the third and last summer of life averages 47 mg day^{-1}, and the average individual weighs about 18 grams. Because of the variable growth rate some of the group II weigh as much as 30 grams at the end of the third summer. The females surviving the winter to spawn at 36 months of age probably do not molt again in the spring.

Reproductive Potential

The reproductive potential of *O. propinquus* was estimated by ovarian egg counts of individuals collected in the winter and early spring. A small proportion of young-of-year crayfish reached maturity during the first summer of life. Only individuals with a cephalothorax length greater than 21 mm (2.5 grams) contained eggs.

Egg production is a function of size, and the ability to produce eggs increases at a logarithmic rate with respect to size (Figure 17). Egg counts of females in berry were not made. Creaser (1934) enumerated eggs attached to the pleopods of oviferous *O. propinquus*. Creaser reported females 16 mm, 26 mm, and 34.5 mm in length, respectively carried 40, 175, and 250 eggs with very little egg mortality after attachment to the pleopods.

Ovarian egg counts as estimated from Figure 17 for individuals of corresponding size are 185 and 240 for the 26 and 34.5 mm crayfish, respectively. No individuals under 21 mm were found to contain eggs. The close agreement between ovarian egg count and eggs attached to pleopods indicate only a slight loss during the transfer process. Since Creaser reports minimal egg mortality during incubation, ovarian egg

Figure 17. The relationship between ovarian egg production and cephalothorax length of *Orconectes propinquus*.

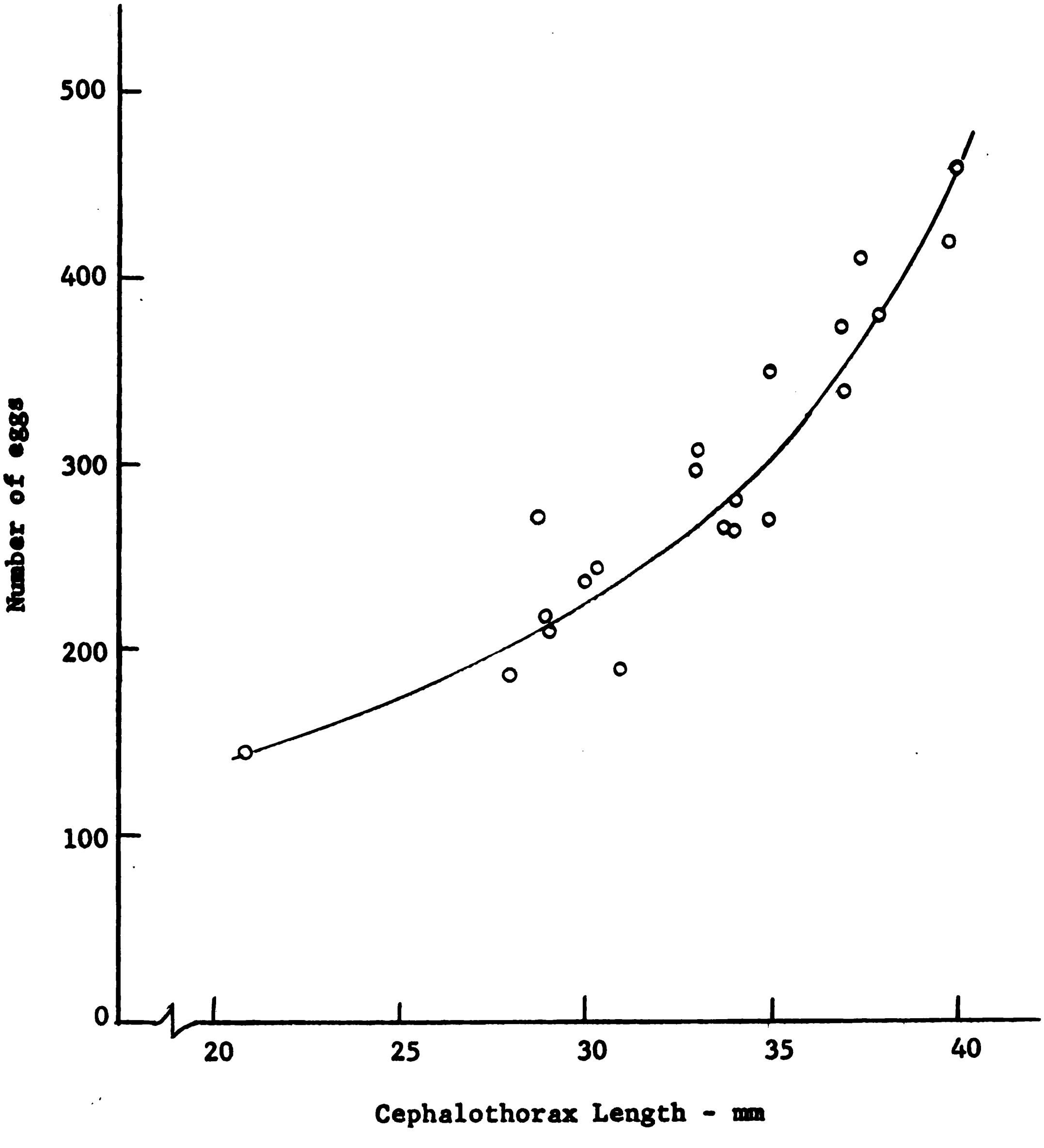

Number of eggs
500
400
300
200
100
0
20
25
30
35
40
Cephalothorax Length - mm

Figure 17

counts approximates the number of births. Tack (1940) also reported very little egg mortality during the incubation period for O. *immunis*.

Population Estimates

Population estimates of crayfish were obtained by a marking-recapture technique and counts per unit enclosed area. Young-of-year were not vulnerable to the marking-recapture census, and were estimated by a random plot technique using a Surber sampler. Attrition of young-of-year crayfish to the adult population occurred during late October immediately prior to winter seclusion. Population estimates were made on the basis of bottom types; separate estimates were obtained for sand-mud and gravel-cobble substrates.

Seasonal population estimates for the two substrate types are shown in Table 6. Adult crayfish were approximately 10 times more abundant on the gravel-cobble substrate than on the sand. The average population of adult crayfish was 0.63 and 5.58 individuals per square meter, respectively for the sand and gravel substrates. The preference for rocky substrates by O. *propinquus* confirms Bovbjerg's (1952) laboratory study relating migration to bottom types.

The substrate composition of the 2.2-mile study reach was estimated as 56% sand and finer materials and 44% gravel and coarser materials. Assuming the average population estimates are applicable to the entire study reach, the mean population density is 2.8 adult crayfish per square meter. Because of the low number of recaptures, the 95% confidence limits (Clopper and Pearson probability tables) are about 50% of the mean.

The August standing crop of juvenile crayfish was estimated by obtaining 25 random, square foot samples on each substrate type. The

Table 6. Population estimates of adult crayfish on various substrates as estimated by a marking-recapture technique. M = numbers marked; C = numbers in census trial; R = number of recaptures in census trial.

Bottom type	Marking date	M	×	C + 1	÷	R + 1	=	Population estimate	Sampling area $meter^2$	Number per $meter^2$
Sand	July 13	51		58		7		423	696.8	0.61
Sand	Aug. 20	59		62		11		333	511.0	0.65
Gravel-Cobble	June 29	100		165		9		1833	306.6	5.98
Gravel-Cobble	Aug. 11	165		174		17		1688	306.6	5.51
Gravel-Cobble	Sept. 10	150		137		13		1581	306.6	5.16
Gravel-Cobble	Oct. 11	150		93		8		1743	306.6	5.68

Study Area: 56% sand, mud, organic substrate.
44% gravel, cobble, rock substrate.

Mean population: 2.8 crayfish per $meter^2$.

average population density and 95% confidence limits were 16.36 ± 5.38 and 2.46 ± 1.04 per square meter for the gravel and sand substrates respectively. On the basis of per cent bottom composition, the average August standing crop of young-of-year crayfish was 8.86 per square meter.

Combining the average population estimates for adult and juvenile crayfish, the autumnal crayfish population in the study reach was 11.66 per square meter. Slack (1955) estimated the crayfish population of two Indiana streams and reported autumnal populations ranging from 23.2 to to 29.9 per square meter. Slack considered his estimates somewhat high due to a concentrating effect at low stream flow.

In addition to the marking-recapture census, population estimates of adult crayfish were obtained by counts per unit [illegible] area. The 2.2-mile study reach was subdivided into 100 foot units [illegible] ten randomly selected units were subsampled for crayfish. The population estimates and related capture data are shown in Table 7 for two sampling trials. Assuming the various substrates were sampled proportionately, the autumnal, adult population was 3.98 ± 1.39 m^{-2} or 12.84 m^{-2} including the young-of-year. The 95% confidence limits of the direct census method were approximately 30% of the mean estimate as compared to 50% of the mean for Petersen estimates.

Production

The primary objective of the crayfish study was to determine the production rate and to describe quantitatively the predator-prey relationship between smallmouth bass and crayfish. Calculation of crayfish production is complicated by the lack of an age determination mark. Length-frequency relationships are useful to ascertain age groups present (Figure 15), but are of little use in assigning an age to a particular individual.

Table 7. Density estimates of Orconectes propinquus in ten, randomly selected, 100-foot stream sections. Estimates do not include young-of-year.

June 26-27, 1961			September 11-12, 1961		
Number of samples ft^2	Number of crayfish	Area of sampling unit ft^2	Number of samples ft^2	Number of crayfish	Area of sampling unit ft^2
10	4	6000	10	6	6000
10	3	6500	10	2	6500
8	2	7500	10	0	7000
8	4	3300	10	3	7500
9	5	6800	10	0	7000
10	6	6500	10	6	6000
10	4	7600	10	5	6500
10	1	6500	10	2	9000
9	6	6500	10	6	6500
9	6	5700	10	5	6500
93	41	62900	100	37	68500

Population Estimates:	Square Foot	Square Meter
June 26-27, 1961	0.44 ± .14	4.75 ± 1.51
Sept. 11-12, 1961	0.37 ± .13	3.98 ± 1.39

To calculate the rate of crayfish production, the community structure on a weight basis was determined. The community structure was determined by combining data from several sources. During the seasonal, marking-recapture trials, crayfish in the 2.6 to 10.5 gram size groups were represented in sufficient numbers to describe adequately their relative abundance. To estimate the relative abundance of crayfish in the 10 to 30 gram weight groups, the descending data of four catch curves were plotted (Figure 18). The descending catch curve data suggests a rather stable distribution of weight classes, and more important, suggests that a probability may be assigned to a crayfish that describes its chances to attain a greater weight before death.

Combining the weight class estimates with descending catch curve data, the population structure of the crayfish community was computed. This structure is shown in Table 8 for a 306 m^2 gravel-cobble substrate in the experimental reach of the Red Cedar River. The young-of-year stock was estimated independently as 16.14 per square meter. This relative population structure, exclusive of the young-of-year, was applied to the crayfish population of the entire stream study reach where only the density of the stock was known.

From the population survivorship curve, based upon three adult age groups, it is possible to predict the change in numbers and simultaneous increase and decrease of the population biomass as a particular age class transcends its existence. From the time a year class is formed, crayfish increase in size, at the same time as they are reduced in numbers. The year class attains its maximum biomass when individual crayfish weigh about 6 grams (Figure 19). Population growth prior to attaining the 6

Figure 18. The descending data of four catch curves showing the estimated survivorship curve for *Orconectes propinquus*.

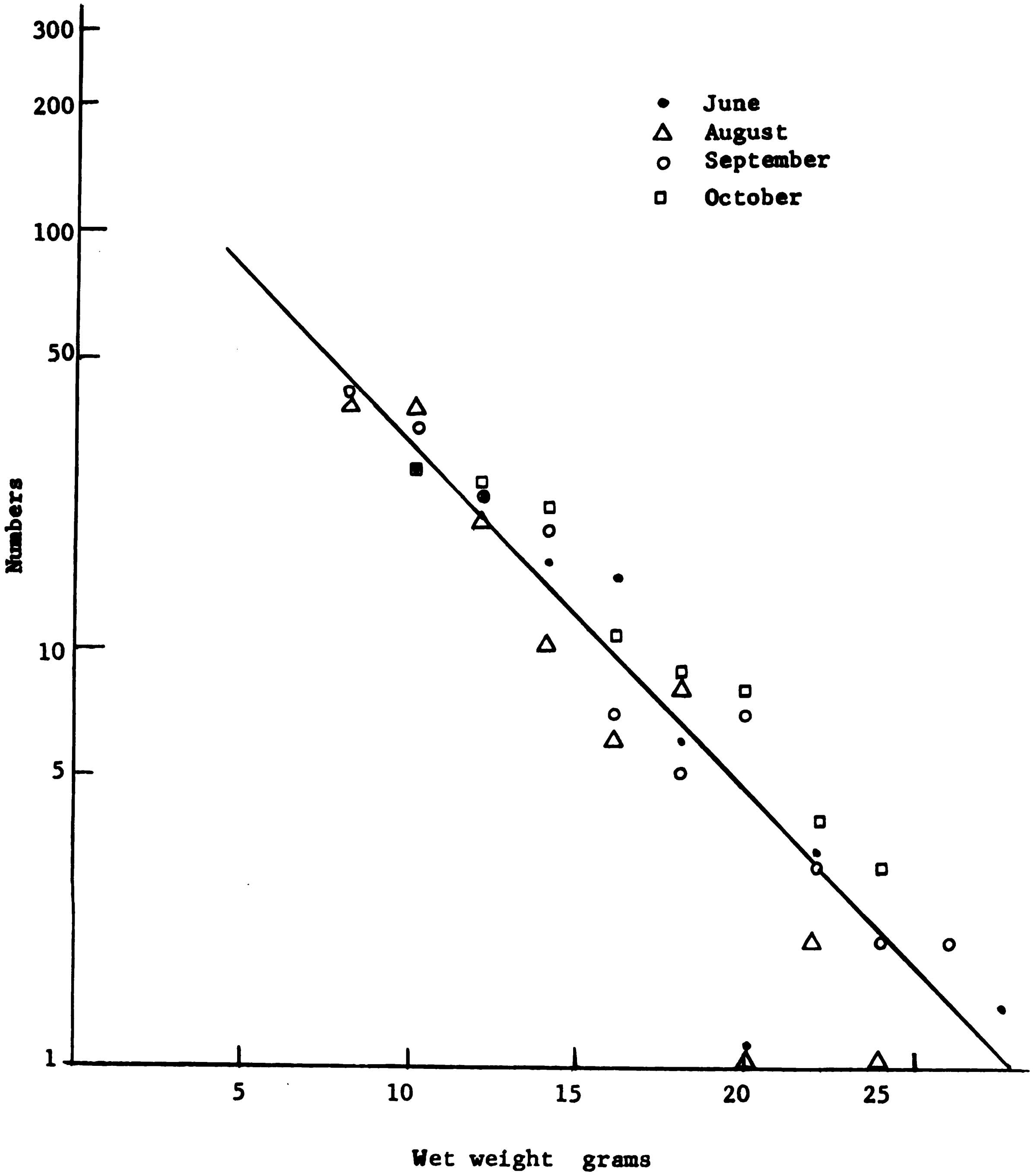

300
200
100
50
10
5
1
Numbers
● June
△ August
○ September
□ October
5
10
15
20
25
Wet weight grams

Figure 18

Table 8. The estimated population structure of an autumn crayfish population in a gravel-cobble portion of the Red Cedar River.

Gram weight class	Number of individuals	Gram biomass
Young-of-year	4950	2600
2.6 - 4.5	135	472
4.6 - 6.5	200	1100
6.6 - 8.5	240	1800
8.6 - 10.5	260	2470
10.6 - 12.5	225	2588
12.6 - 14.5	150	2025
14.6 - 16.5	70	1085
16.6 - 18.5	35	612
18.6 - 20.5	20	390
20.6 - 22.5	10	215
22.6 - 24.5	5	118
24.6 - 26.5	4	102
26.6 - 28.5	3	82
28.6 - 30.5	2	59
Totals	6309	15718

Figure 19. Theoretical change in standing crop biomass corresponding to a concurrent reduction in numbers of crayfish during the life of an age class.

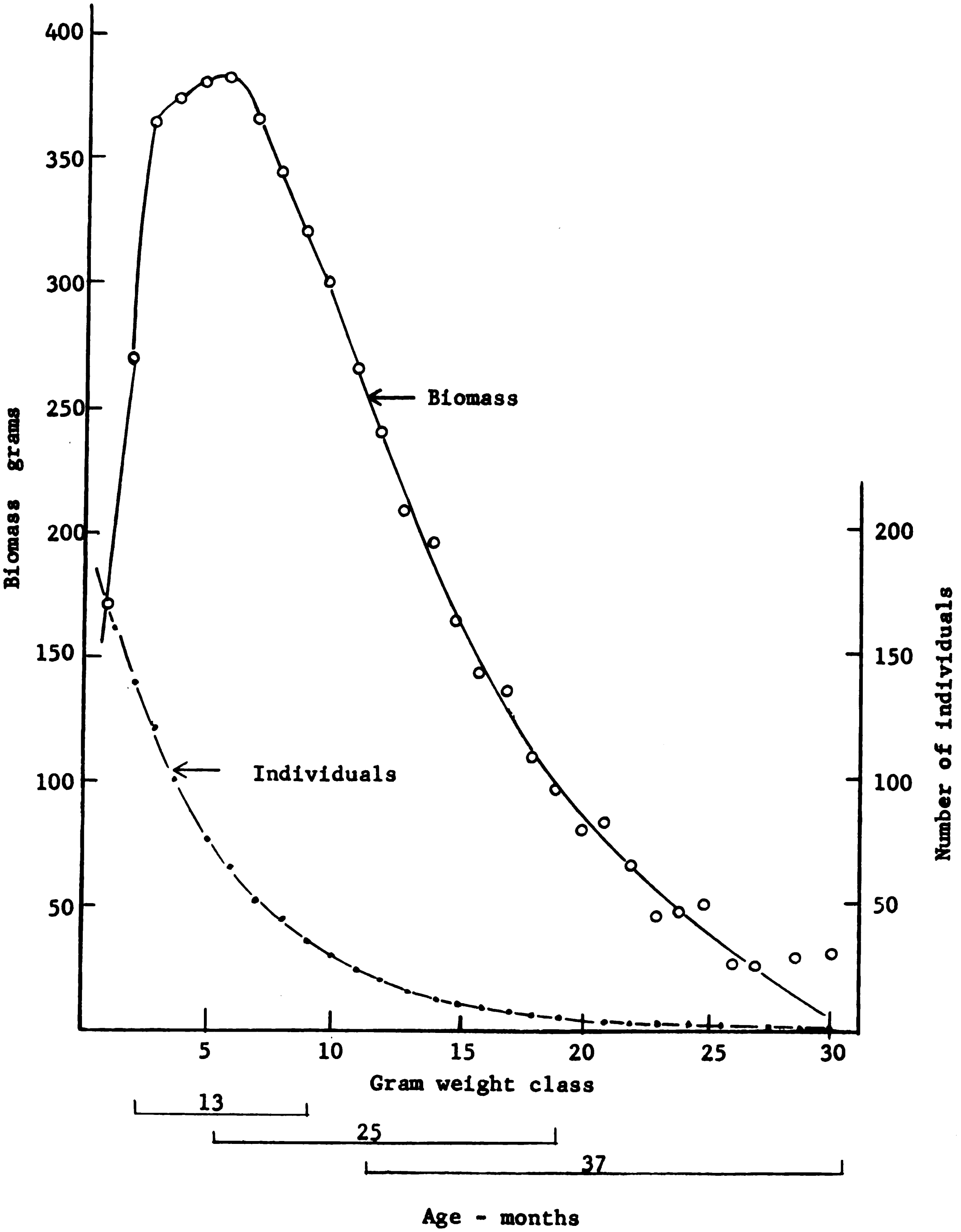

400
350
300
250
200
150
100
50
Biomass grams
Biomass
Individuals
200
150
100
50
Number of individuals
5
10
15
20
25
30
Gram weight class
13
25
37
Age - months

Figure 19

gram size exceeds the biomass loss due to mortality. After crayfish reach 6 grams, growth by surviving individuals progressively diminishes, and biomass loss due to mortality exceeds that growth accrued by survivors.

The six gram size class corresponds to Ricker's (1945) critical size for fish (instantaneous rate of growth = instantaneous rate of mortality). Harvest at the critical size gives maximum yield. In the Red Cedar River, yearling crayfish average six grams after the spring molt. It is after the spring molt that yearling crayfish become active nocturnal scavengers, and are particularly vulnerable to fish predation.

Crayfish production in the study reach was based upon an autumn, adult density of 3.98 m^{-2} and a young-of-year density equal to 8.86 m^{-2}. This population density was expanded to a hectar basis and partitioned into 2-gram size classes. The estimated number of crayfish in each size class is presented in column two of Table 9. The products of average weight and number of crayfish (group biomass) are entered in column three. The summation of column three is the autumnal crayfish biomass.

The net production rate is the amount of growth elaborated during a time interval regardless of whether all of it survives to the end of that time interval (Ivlev, 1945). This computation is made by multiplying the average biomass by the instantaneous rate of growth (k_i). The autumnal biomass is adjusted to the average biomass by determining the instantaneous rate of biomass growth (g_b) and calculating a "change factor" (Ricker 1958, Hayne and Ball 1956, and Gerking 1962).

The growth rate for individuals (k_i) was calculated on a daily basis using the average seasonal growth rates shown in Figure 16. The daily growth rates were multiplied by the length of the growing season (125 days) and the product entered in column 4 of Table 9. The individual

Table 9. Estimation of the annual crayfish production rate from group biomass and instantaneous rates of growth.

k_i = instantaneous rate of growth of the individuals;

g_b = instantaneous rate of growth of the biomass.

1	2	3	4	5	6	7	8	9	10
Gram Weight Class	Number ha^{-1}	Biomass kg ha^{-1}	k_i x t	g_b	$\frac{e^{g_b} - 1}{g_b}$	Average Biomass kg ha^{-1}	Production Rate kg ha^{-1} yr^{-1}	Ovarian Eggs	Total Ova ha^{-1}
Young-of-Year	88624	46.085	0.966	+1.035	1.75	80.648	77.906	-	-
2.6 - 4.5	3954	13.839	1.113	+0.345	1.19	16.468	18.329	160	316320
4.6 - 6.5	5857	32.214	1.113	+0.115	1.05	33.825	37.647	185	541680
6.6 - 8.5	7029	52.718	1.113	-0.115	0.96	50.609	56.329	215	725410
8.6 - 10.5	7614	72.333	1.113	-0.138	0.94	67.993	75.676	235	840830
10.6 - 12.5	6589	75.774	1.113	-0.160	0.91	68.954	76.746	260	779480
12.6 - 14.5	4393	59.306	0.598	-0.172	0.90	53.375	31.918	290	573330
14.6 - 16.5	2050	31.775	0.598	-0.172	0.90	28.598	17.102	325	299975
16.6 - 18.5	1025	17.938	0.598	-0.237	0.89	15.956	9.542	365	166440
18.6 - 20.5	586	11.427	0.598	-0.288	0.87	9.941	5.945	400	102000
20.6 - 22.5	293	6.230	0.598	-0.345	0.84	5.233	3.129	435	53070
22.6 - 24.5	146	3.431	0.598	-0.345	0.84	2.882	1.723	485	29585
24.6 - 26.5	117	2.983	0.598	-0.368	0.84	2.506	1.499	540	26460
26.6 - 28.5	88	2.420	0.598	-0.460	0.78	1.888	1.129	575	19550
28.6 - 30.5	59	1.740	0.598	-0.465	0.76	1.322	0.791	615	14145
Totals	128425	430.212				440.198	415.411		4488275

growth rates could not be partitioned into 2-gram size groups and the average growth rate for each age class was used. The objections to using the same growth rate for slow-growing individuals of an age group are somewhat counterbalanced by the large crayfish which grew at a rate greater than that described by the average growth rate. The proportion and direction of the error accumulated by using the average growth rate is not known.

The instantaneous rate of biomass growth (g_b) was calculated by 2-gram size classes and was computed as the natural logarithm of the surviving fractions as shown in Figure 19. The biomass growth rate increased to the critical size (6 grams) and then decreased. The instantaneous rates were entered in column 5 of Table 9, retaining the negative sign in event of a biomass decline. The weight change factors (column 6) were multiplied by the corresponding autumnal biomass estimates (column 3) and the product, equal to the average biomass, entered in column 7. Net production was computed by multiplying successively the entries of k_i and the average population biomass and entering the product in column 10. The summation of column 10 equaled the estimated production during the year.

The essential production data, extracted from the computational table, are summarized in Table 10. Crayfish production in the 2.2-mile study reach amounted to 41.5 g m^{-2} $year^{-1}$ or an amount about equal to the estimated standing crop (43 g m^{-2}). Young-of-year crayfish, representing approximately 10% of the standing crop, accounted for 20% of the annual production. Yearling crayfish contributed the largest fraction to the production rate.

Unfortunately comparative productivity estimates for crayfish were not found in literature. Many workers, however, have reported standing crop of crayfish occupying various habitats. Slack (1955) reported

Table 10. **Estimates of production rates and standing crop of crayfish, *Orconectes propinquus* in a 2.2-mile reach of the Red Cedar River. All weights are on a live weight basis.**

	Square meter	Acre
Number of Ova	448 m^{-2}	1.8×10^6 $acre^{-1}$
Number of Young-of-the-Year (August)	8.86 m^{-2}	3.6×10^4 $acre^{-1}$
Number of Adults (August)	3.98 m^{-2}	1.6×10^4 $acre^{-1}$
Standing Crop	43.0 g m^{-2}	383 lb $acre^{-1}$
Young-of-Year	4.6 g m^{-2}	41 lb $acre^{-1}$
Adults (I & II)	38.4 g m^{-2}	342 lb $acre^{-1}$
Net Production	41.5 g m^{-2} yr^{-1}	370 lb $acre^{-1}$ yr^{-1}
Young-of-Year	7.8 g m^{-2} yr^{-1}	70 lb $acre^{-1}$ yr^{-1}
Adults (I & II)	33.7 g m^{-2} yr^{-1}	300 lb $acre^{-1}$ yr^{-1}

autumnal crayfish biomass reaching a maximum of 217 lb acre^{-1} in Jacks Defeat Creek, a small Indiana stream. Tack (1941) found the standing crop of O. immunis in small ponds ranged from 46 to 255 lb acre^{-1}. Warren (1960) reported an adult standing crop of 250 lb acre^{-1} in the 3- to 5-foot wide Berry Creek. Lydell (1938) found upon draining a Michigan hatchery pond (Belmont No. 1) a crayfish biomass of 694 lb acre^{-1}, 689 lbs acre^{-1}, and 811 lb acre^{-1} in 1935, 1936, and 1937, respectively (Tack 1941).

The standing crop of crayfish in the Red Cedar River (383 lb acre^{-1}) is within the range reported by the above workers. Although no comparative productivity estimates are available, the minimum production rate may be estimated intuitively. In order to maintain the standing crop, the two-year-old crayfish, all of which die in the fall or following spring, must be replaced. If in fact there were no mortality of age-group II except that due to old age, a minimum production rate of 13.7 g m^{-2} yr^{-1} would be required to maintain the crayfish population structure at the present level (43 g m^{-2}).

The survival of crayfish during the first summer of life was estimated as about 2% of the potential egg production. Egg production by the adult population was estimated by summing the products of estimated surviving females and their innate capacity to produce eggs (Figure 17). The total egg production by size classes is shown in column 10 of Table 9. Yearling crayfish in the 8.6 to 10.5 gram size class have the greatest potential to produce young. On an area basis, approximately 450 eggs may be produced per square meter, however, mortality rapidly diminished the potential leaving by fall about nine juvenile crayfish per square meter.

Energetics

The energy flow through a trophic level or population equals the total assimilation at that level. Total assimilation equals the respiration plus the production of biomass. Above, I have discussed and estimated the production of crayfish biomass. In order to compute the gross production or total energy flux through the crayfish population, it is necessary to measure oxygen consumption by crayfish.

Oxygen consumption, by individual crayfish, was measured in a continuous flowing respirometer. A respiratory quotient (RQ) of 0.88 was assumed in the computations of metabolic rate. The crayfish diet was assumed to consist of 45% protein, 45% carbohydrate, and 10% fat. Metabolizing the above diet, an uptake of 1.0 liters of oxygen would produce 4.77 k cal.

The rate of oxygen consumption was extermely variable even among equal size crayfish. Metabolism rates varied from 0.08 to 0.27 ml O_2 g^{-1} hr^{-1} at 25 C. The variability was attributed in part to variation in exoskeleton thickness with respect to the molting cycle. The variation in oxygen consumption of a single individual prior, during, and after a molt is shown in Figure 20. The crayfish weighed approximately 12.5 grams and was within the respiratory chamber throughout the entire experiment. The exuviae was removed 15 minutes following ecdysis. The crayfish respiration increased sharply immediately prior to molting and continued to rise for two hours after molting. The respiration rate declined from 0.27 to 0.14 ml g^{-1} hr^{-1} during the next 12 hours. The crayfish was replaced in the respirometer 96 hours later, and after a 4-hour acclimatization period, oxygen consumption was 0.22 ml g^{-1} hr^{-1}.

Figure 20. Variations in the respiration metabolism of *Oconectes propinquus* during a molting cycle.

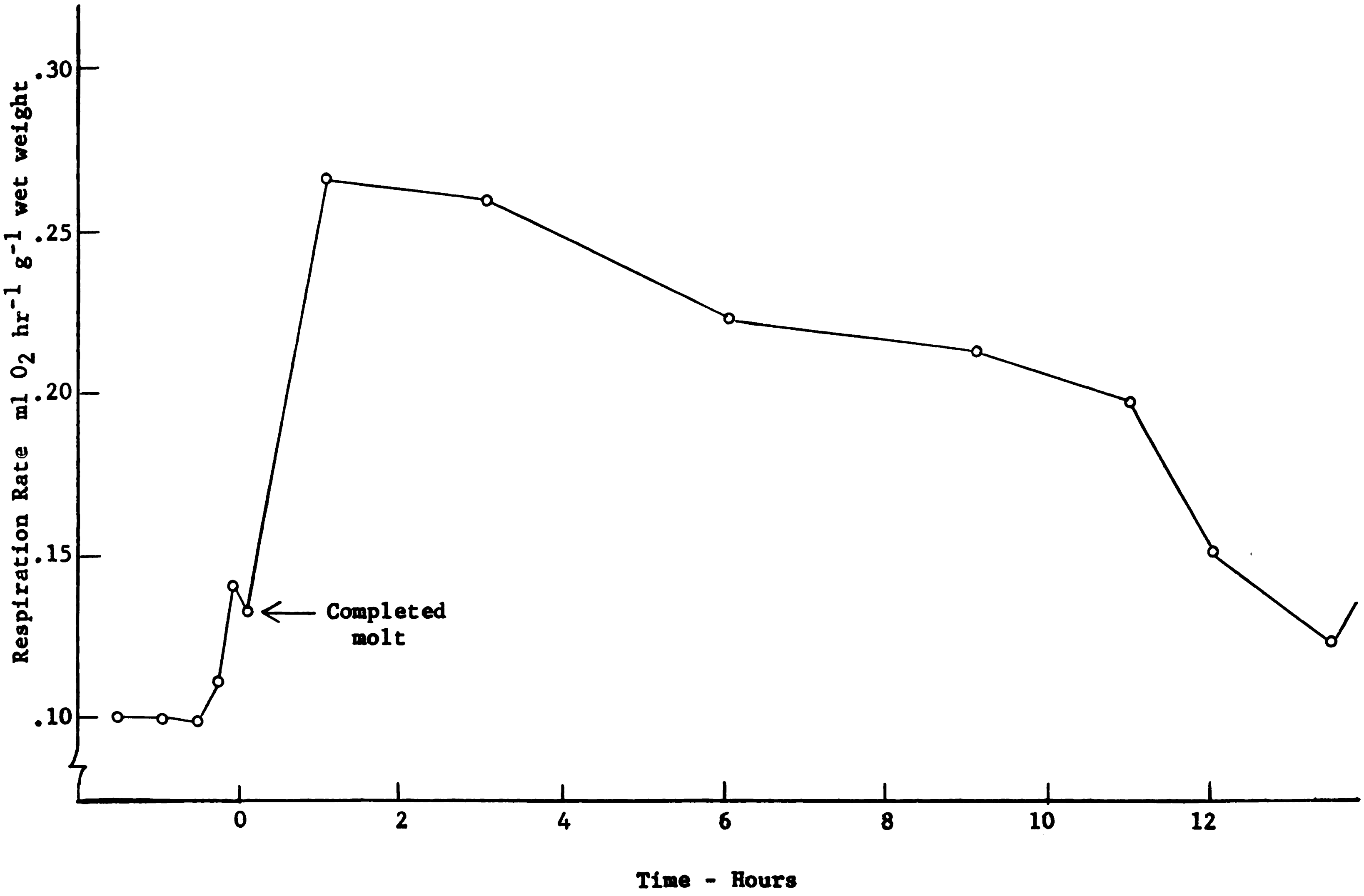

Respiration Rate ml O_2 hr^{-1} g^{-1} wet weight
.30
.25
.20
.15
.10
Completed molt
0
2
4
6
8
10
12
Time - Hours

Figure 20

In a mixed, natural population respiration rates are expected to be variable because of the molting cycle variation. To compute respiration for the crayfish population an average rate of 0.1 ml g^{-1} hr^{-1} was assumed. Respiration was calculated only for the 200-day activity period. Respiration during the winter hibernation period (November - April) was considered negligible. Therefore the respiratory rates may be low on two accounts; namely, failure to include molting differences and exclusion of the hibernation period.

Wolsky and Holmes (1933) reported an oxygen consumption rate of 0.07 ml g^{-1} hr^{-1} for the lentic crayfish *Astacus lepodactylus*. In 1934 Wolsky reported an average respiration rate of 0.10 ml g^{-1} hr^{-1} for the lotic crayfish *Astacus torrentium*. *Orconectes propinquus* taken from the Red Cedar River displayed similar respiration rates during the intermolt periods.

The respiration of the biomass of crayfish was estimated by multiplying the biomass, the time interval, and the respiration rate by the oxycaloric equivalent. A summary of these estimates are:

$$R = 43 \text{ g m}^{-2} \times 4800 \text{ hr} \times 0.0001 \text{ l g}^{-1} \text{ hr}^{-1} \times 4.77 \text{ k cal l}^{-1}$$

$$R = 100.74 \text{ k cal m}^{-2} \text{ yr}^{-1}$$

In order to compute the total energy flux through the crayfish population that energy utilized for biomass increment must be placed on a caloric level. This conversion also will permit an evaluation of energy conversion efficiency from the primary to the consumer level.

The caloric energy of crayfish was determined by oxygen bomb calorimetry. Crayfish were collected from the stream, oven dried (27% of wet weight), homogenized, and representative samples combusted at 30 atm oxygen. The mean and 95% confidence limits for estimating caloric energy from dry weight were expressed as

$$\text{g cal} = \text{g dry weight} \times 2901 \pm 84$$

Using the above conversion expression, the net production of crayfish (11.2 g m^{-2} yr^{-1} dry wt.), on a caloric energy basis, was 32.5 k cal m^{-2} yr^{-1}. Combining the respiration and productivity rates, the total energy flux through the crayfish population equaled 133.25 k cal m^{-2} yr^{-1} (R = 100.74, P = 32.51 k cal m^{-2} yr^{-1}). The energy dissipated by respiration metabolism was approximately three times that used for growth.

The energy assimilated by the crayfish population represents about 9.5% of the energy fixed at the primary level. The net production of crayfish represented slightly less than 3% of net primary production. Since crayfish derive some energy from levels other than the primary level, the above percentages do not actually represent trophic level efficiencies. It was estimated that crayfish derive approximately 80% of their energy from the primary level, therefore the trophic level efficiency of crayfish is about 7.5% of the net primary production.

The crayfish in the Red Cedar River represent only one component of the primary consumer level. In addition there are herbivore insects and fish which harvest a portion of the primary production. Nelson and Scott (1962) studied the bioenergetics of a turbid, Piedmont stream (Middle Oconee River) and reported a primary consumer efficiency of 2.18%. Teal (1957) and Odum (1957b) estimated that primary consumers in Root and Silver springs utilized 20.3% and 16.73% respectively of the energy fixed at the primary level. Lindeman (1942) for a cedar bog lake reported a primary consumer trophic level efficiency of 9.94%, and Dineen (1953), for a Minnesota Pond, reported a similar efficiency of 10.8%.

Smallmouth Bass

In 1956, Park, discussing the history and scope of population ecology, suggested that the most important goal of ecology is the basic understanding of community structure and energetic relationships. In this study, the presented food chain is culminated by the predator, smallmouth bass. The ecological status of smallmouth bass in the enriched, unstable stream environment was determined by studies of density, community structure, reproduction success, and productivity.

Stream Distribution of Smallmouth Bass

In addition to smallmouth bass, the sport fishery in the Red Cedar River is supported by rock bass and northern pike. Presently, the distribution of smallmouth bass is limited largely to the stream areas between East Lansing and Williamston (Figure 1). The ten-mile stream reach from the Williamston dam to the Community of Okemos supports the largest populations of smallmouth bass (10 to 20 lbs acre^{-1}). This stream reach is within the zone of stream enrichment with respect to the Williamston disposal plant.

The stream reach from Okemos to East Lansing supports a reproducing population of smallmouth bass, however, electrofishing records indicate a progressive deterioration of stock since 1958. A limited bass population exists in isolated stream areas above Fowlerville. At present, smallmouth bass are not found in the stream from Fowlerville downstream to about three miles below Webberville.

The 1958, 1959, and 1960 electrofishing surveys revealed successful bass reproduction in the Webberville area. In 1961 and 1962 no smallmouth bass spawning was observed in a one mile survey zone located three miles downstream from Webberville. In 1960 a fish kill occurred in downstream areas from Fowlerville. The absence of bass reproduction indicated that the 1960 fish kill extended at least to the Webberville area.

The 1962 electrofishing survey substantiated a population reduction indicated by the spawning survey. In the one-half mile zone below Webberville, the fish population was limited largely to yearling white suckers and northern pike, and no smallmouth bass were recovered in either the marking or census trial. It is believed that the white sucker and northern pike repopulated this area during the 1961 spawning run. The large pike probably remained in the area to feed upon the bumper crop of yearling suckers.

Population Estimates

Population estimates of smallmouth bass were made by electrofishing and stream poisoning with rotenone. In addition, the production of fry and an estimate of the adult breeding stock were obtained by nest counts during the spawning season. The 2.2-mile study reach was surveyed daily during the 1960, 1961, and 1962 spawning seasons. In addition, two, 1-mile stream segments were surveyed for comparative fry production. The comparative stream reaches included the zone three miles downstream from Webberville, as described above, and a zone located one mile upstream from the Michigan State University River Farm located in Okemos. Approximately one mile of stream could be surveyed each day.

Spawning Surveys: The most vulnerable period in the life history of fish exists from egg fertilization to early fingerling growth. It is during this postspawning period that environmental conditions determine year class strength. Cleary (1956) suggested that for smallmouth bass, a 45-day postspawning period is most critical with regard to fry survival. Cleary (1956), Surber (1942), Starrett (1951), and Allen (1951) among others have singled out stream stage as the major factor in determining year class strength. Webster (1945), Beeman (1924), and Watt (1959) have discussed postnesting temperature as imposing a limiting factor. Low temperatures after nesting prolong incubation and increase fungus infections.

In the Red Cedar River the stimulus to begin nest building appears to be temperature regulated, however, high stream discharges may deter spawning (Figure 21). In each of three seasons, spawning was delayed until stream flows were less than 200 cfs. This delay occurred in spite of earlier favorable temperatures. In all years except 1960, spawning began during a period of rapid temperature increases. The 1960 spawning season was delayed apparently by a period of high, moderately fluctuating stream discharge.

With few exceptions, bass nests were constructed in sheltered sites, commonly on the downstream side of a current obstruction. Nests usually were constructed within five feet of shore, in less than 30 inches of water, and on the stream side opposite a pool. In pools which traversed the entire stream width, nests were located at the downstream edge of the pool. Multiple nest construction was common particularly during periods of receding water levels. It was not uncommon for a male to construct two to three nests immediately adjacent to one another before selecting one.

The nest counts obtained in the primary study area and the comparative study zones are shown in Table 11. During the 1960 season, only the primary study reach was searched for spawning activity. Fifteen

Figure 21. The periods of maximum smallmouth bass spawning in relationship to stream discharge and minimum stream temperature during three spawning seasons in the Red Cedar River.

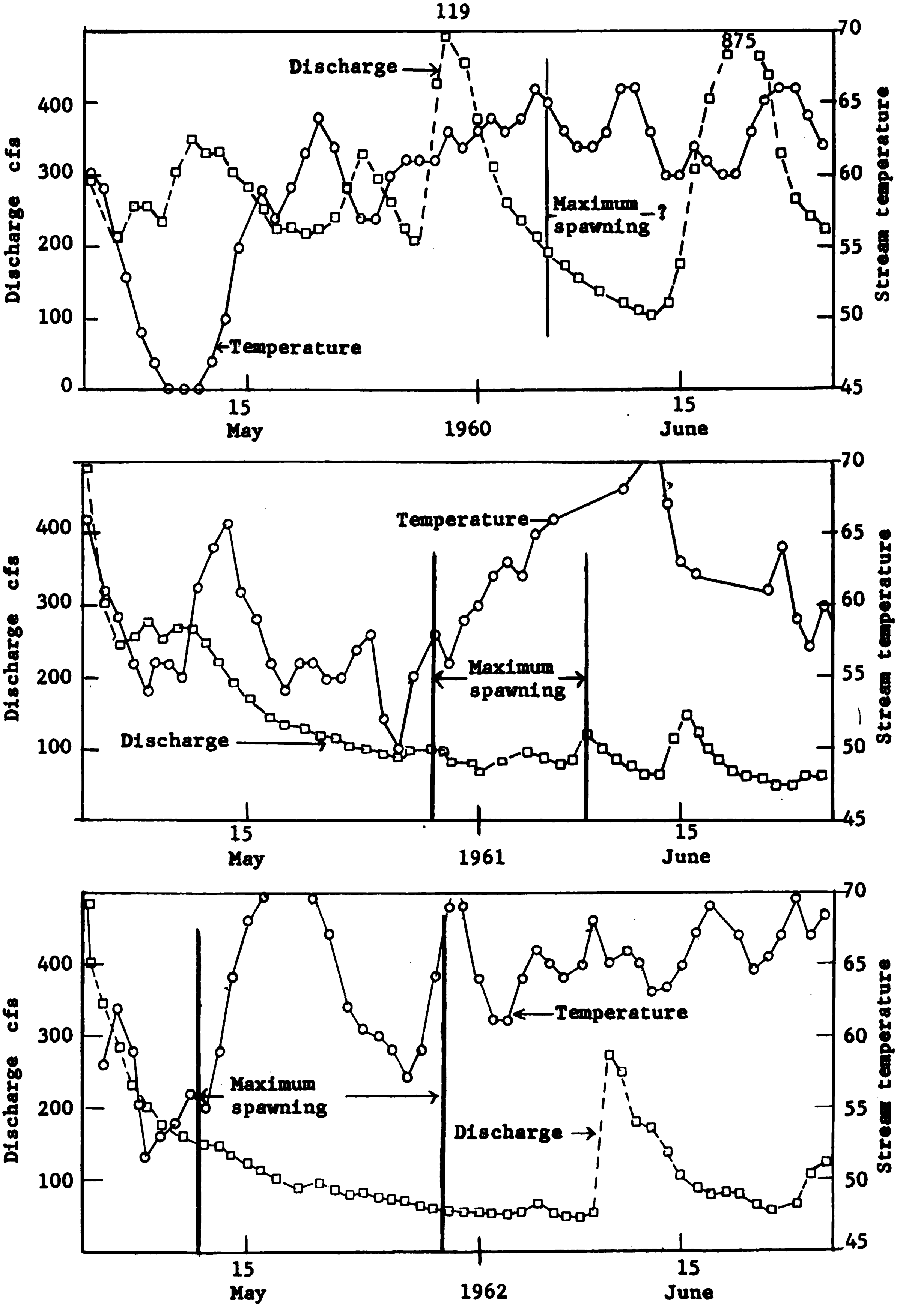

119
875
Discharge
Temperature
Maximum spawning ?
Discharge cfs
Stream temperature
0
100
200
300
400
45
50
55
60
65
70
15
May
1960
15
June
Temperature
Maximum spawning
Discharge
Discharge cfs
Stream temperature
100
200
300
400
15
May
1961
15
June
Temperature
Maximum spawning
Discharge
Discharge cfs
Stream temperature
100
200
300
400
15
May
1962
15
June

Figure 21

Table 11. Summary of smallmouth bass spawning in the Red Cedar River from 1960 to 1962.

Area	Stream length Miles	Nests with eggs	Nests with advanced fry	Estimated fry production[1]
Primary study area				
1960	2.2	15	2	6,000
1961	2.2	47	40	120,000
1962	2.2	54	48	144,000
Okemos area				
1961	1.0	--	12	36,000
1962	1.0	--	17	51,000
Webberville area				
1961 - 1962	1.0	--	0	0

[1] Computed on the basis of 3,000 fry per successful nest.

bass nests were located in 1960 prior to June 13. Any spawning after June 13 was obscured by high stream turbidity (120 ppm) and discharge (Figure 21). The stream remained turbid for the remainder of the month, and no additional spawning was observed. Judged solely on groups of "swim-up" fry, I estimated that two of the 15 nests succeeded in producing some fry.

In the 1961 and 1962 spawning seasons, water conditions were favorable throughout the entire spawning period. In the 2.2-mile study reach 47 nests received a complement of eggs during 1961 and 54 received eggs in 1962. Nest failure was 15% and 11% respectively during the 1961 and 1962 seasons, as compared to an estimated 85% mortality during the 1960 season when high water destroyed nesting attempts. The effects of differential mortality will be discussed in the section on community structure.

Nesting density in the experimental study area varied between 21 and 25 nests per mile of stream during the 1961 and 1962 seasons. This spawning density is approximately equivalent to one mature bass per 100 linear feet of stream. Of seven Iowa streams, Cleary (1956) reported average nesting densities of 15 to 29 bass nests per linear mile. A maximum spawning density of 53 nests per mile was reported for Iowa streams during favorable spawning years. Spawning density in the Little Miami River (Ohio) was reported to vary between 110 and 290 nests per mile (Brown, 1960), however, a low percentage (3% to 41%) were successful in producing fry.

In 1961 and 1962 high stream flow and turbidity were not contributing factors to nesting or fry mortality. The 11% to 15% failure of nests which received a complement of eggs was attributed to low water temperatures following early spawning attempts. Large bass invariably were the first spawners each year, and nesting attempts during the early favorable temperature periods were most vulnerable to subsequent low temperatures.

The presence or absence of the male bass appeared to have little effect upon nesting success during the incubation period. During daylight hours, smallmouth bass were never observed actively guarding a nest containing eggs. Prespawning nest defense was more pronounced than postspawning defense. After a nest received a complement of eggs, the male would maintain active patrol from an adjacent pool or cover, only swimming over the nest in event of potential predation. Failure of bass to spawn on favorable substrate was due to lack of residing cover.

Bass nests were clearly defined only for several days after spawning. During incubation, the male bass did not keep the nest or eggs free from silt. The accumulation of a fine layer of silt apparently had little effect upon success or failure of nesting attempts.

The apparent lack of nest guarding by smallmouth bass is not confined to the Red Cedar River. Webster (1953) noted similar habits by spawning smallmouth bass in feeder streams of Lake Cayuga. Cleary (1956) and Watt (1959) described the lack of nest guarding by smallmouth bass in Iowa streams. The earlier observations by Beeman (1924) and Reighard (1906) of strong nest guarding by smallmouth bass were based upon hatchery experiences. In hatchery ponds nest guarding may be more pronounced because of competition at the elevated stocking density.

Receding water levels in streams may be an important factor in contributing to a breakdown in nest guarding. Frequently nests are constructed adjacent to the shore bank to take advantage of shelter afforded by the stream bank and overhanging vegetation. Because of flow recession, nests frequently are covered by less than 12 inches of water during fry emergence. Shallow water and a lack of cover are major factors in deterring nest guarding by smallmouth bass in the Red Cedar River.

The sight of emerging fry stimulated the bass to guard the nest, however, bass usually patrolled at a distance of five to ten feet away. After the fry rise to the surface and spread out along the shore, the male bass lose the guarding stimulus. Male bass were never observed guiding fry into sheltered areas. The pattern of fry dispersal usually consisted of emergence to the surface and a gradual elongation of the school along the stream margin.

Bass fry feed at the surface upon Cladocera and copepods for about two weeks. After attaining a length of 14 to 16 mm, the fry begin feeding on the stream bottom insects. Chironomids, corixids, and baetids form the main diet at this time. By the end of June, the fry average 20 to 25 mm in length and the diet consists almost exclusively of midges and mayflies. By mid-July the fry average 40 mm and mayflies, particularly Baetidae and Heptageniidae, replace midges as the main food item. By October the fingerlings range from 5 to 9 cm and mayflies and scuds are the principal food items. One 8.7 cm fingerling contained a 3.5 cm Johnny darter in its stomach. Crayfish do not become an important food item until the second summer of life when yearling bass begin feeding upon the young-of-the-year crayfish.

Electrofishing and Poisoning: The fish stock in the 2.2-mile experimental study area was estimated as part of annual electrofishing programs conducted in various portions of the Red Cedar River. The 1962 population estimates of 11 species including smallmouth bass are given in Table 12 for the upper 0.5-mile reach of the experimental zone.

Table 12. Mark-recapture data and population estimates of fish in a 0.5-mile (3.9 acre) reach of the experimental study area.

Species	M	×	C	÷	R	=	Population* estimate
Smallmouth bass							
Young-of-year	67		84		4		1139
Age I and over	9		6		0		63
Rock bass	482		447		82		2627
Northern pike	4		1		0		8
White sucker	209		253		43		1230
Hog sucker	244		252		46		1337
Redhorse	323		87		10		2810
Spotted sucker	11		15		0		176
Bullhead	9		8		0		81
Pumpkinseed	3		2		0		9
Green sunfish	2		2		0		6
Carp	4		2		0		12
Totals	1367		1159		185		9498

M = numbers marked
C = total catch in census trial
R = number of recaptures in census trial

* Population estimated by Bailey's modification of the Petersen expression.

The marking census was completed in a 3-day period. The census trial required two days for completion.

In general, recaptures (marked fish) obtained during the census trial were sufficient to estimate adequately the rock bass and sucker populations. However, except for young-of-year, smallmouth bass were not recaptured in sufficient numbers to estimate the population structure. Smallmouth bass successively avoided capture by the direct current electrofishing gear, and marked smallmouth bass rarely were captured in the census trial. Bass apparently had ability to escape the margin of an approaching electrical field. If attracted into the field, the bass approached at high speeds and frequently were carried completely through the field.

Fajen (1959) experienced similar limitations of direct current electrofishing gear for obtaining population estimates of smallmouth bass in Missouri streams. In Ohio streams, alternating current gear was used successfully by Brown (1960) for population estimates of smallmouth bass.

Because electrofishing proved inadequate in sampling the bass population, stream segments of known nesting density were isolated by block nets and treated with rotenone. The population structure of smallmouth bass recovered from a poisoned zone was considered that required to support the observed spawning density. This age structure was then applied to the remainder of the 2.2-mile study area where only the spawning density was known.

The young-of-year smallmouth bass recovered in each poisoning operation was considered the recruitment from the nesting attempts in that area during that year. Furthermore the assumption that the poisoned zone offered no particular advantage or disadvantage as a nursery must be accepted. That is, the upstream and downstream areas are similar and emigration equals immigration. The same reasoning must also apply to the mature bass which produced the observed spawning.

On October 29, 1961, a 250-foot stream section containing one pool and supporting two successful nests in the spring, was isolated by block nets and treated with rotenone. During this poisoning attempt, the block nets failed due to accumulation of leaves and detritus. Because of the net failure, all efforts were diverted to capture smallmouth bass. Other fish species were not collected quantitatively.

In 1962 the poisoning treatment was completed on August 29 prior to leaf fall. A 530-foot stream section (0.59 acre), supporting three successful bass nests, was treated with rotenone. The block nets remained intact throughout the experiment and all fish species were collected. Prior to poisoning, the fish stock was estimated by the electrofishing gear using the marking and recapture procedures followed during the general fish survey. The subsequent poisoning established the efficiency of the electrofishing gear.

The results of the shocking trial are shown in Table 13. The smallmouth bass population was estimated at 47 of which 42 were young-of-the-year. No marked bass were recovered during the census run, and population estimates were made utilizing Bailey's modification of the Petersen expression. Two weeks prior to the electrofishing trial, the young-of-the-year bass population was estimated at 125 by using a minnow seine. The total number and biomass of fish recovered following the poisoning treatment are shown in Table 14. The recovered bass stock was 119 of which 96 were young-of-the-year.

The total fish stock recovered from the 0.59 acre poisoned section was 825 fish excluding minnows and darters. The total weight of

Table 13. Prepoisoning population estimates and related data for a 530-foot (0.59 acre) section of the Red Cedar River utilizing electrofishing gear.

Species	M	×	C+1	÷	R+1	=	Population estimate
Smallmouth bass							
Young-of-year	7		6		1		42
Age I and over	5		1		1		5
Rock bass	63		36		9		252
White sucker	45		37		8		208
Hog sucker	36		32		7		165
Redhorse	10+1		5		2		26
Spotted sucker	1		1		1		1
Bullhead	1		3		1		3
Pumpkinseed	1		1		1		1
Black crappie	1		1		1		1
Carp	1		1		1		1
Totals	172						705

Table 14. The numbers and weight of fish recovered from a 530-foot (0.59 acre) section of the Red Cedar River after poisoning with rotenone.

Group or species	Number	Total biomass		Pounds per acre	Percent total weight
		kg	pounds		
Minnows - Darters	--	21.213	46.7	78.9	40.5
Hog sucker	141	8.543	18.8	31.8	16.3
White sucker	194	6.186	13.6	23.0	11.8
Redhorse sucker	87	4.665	10.3	17.4	8.9
Spotted sucker	7	0.134	0.3	0.5	0.3
Bullhead	55	0.255	0.6	1.0	0.5
Carp	5	0.065	0.1	0.2	0.1
Rock bass	204	6.084	13.4	22.6	11.6
Smallmouth bass	119	4.988	11.0	18.6	9.5
Largemouth bass	1	0.190	0.4	0.7	0.4
Pumpkinseed	11	0.076	0.2	0.3	0.1
Black crappie	1	0.001	--	--	--
Totals	825[1]	52.400	115.4	195.0	100.0

[1] Total number does not include minnows and darters.

recovered fish was 52.5 kg (195 lbs acre^{-1}) of which minnows and darters comprised 40.5% or 21.2 kg. Four species of suckers had a combined weight of 19.5 kg or 37.3% of the total fish biomass. Game fish comprised approximately 20% of the total biomass. The biomass of rock bass, as in all stream areas sampled, exceeded that of smallmouth bass.

The age structure and biomass of the smallmouth bass population recovered from the two poisoned areas are summarized in Table 15. The failure of age-groups V to VII to appear in the collections is unfortunate, but does not reflect the absence of these age groups in the stream. Bass in the age-groups V-VII were recovered from pools downstream from the isolated experimental reaches. The absence of these larger fish indicates that pool size may limit an even distribution of all ages of bass in the stream.

The age structure was determined by expanding the recovery data shown in Table 15 to include recruitment from 10 nests. This was done for two reasons, namely to place each poisoning experiment on an equal number of nests and to elevate the data to include bass eight years of age. Bass growing in their ninth summer were the maximum age group represented in all collection methods.

To determine the average number of bass in each age class required to support 10 nests, a semilogarithmic survivorship curve was constructed (Figure 22) using the elevated age structure data. The number of bass in each age group was plotted against age at capture. To include age-groups V to VII a constant mortality rate was assumed. The data indicated that after the first year of life, mortality rates were essentially uniform (a constant proportion of each age class surviving).

Table 15. Recoveries of smallmouth bass after a rotenone treatment of two stream reaches in the experimental section of the Red Cedar River.

	October 29, 1961		August 30, 1962		Estimated population structure to support ten nests
Age class	Number of bass	Biomass grams	Number of bass	Biomass grams	
0	21[1]	90	96[2]	441	248.50
I	5	199	11	489	31.00
II	3	482	5	681	15.75
III	2	714	3	1177	10.10
IV	1	522	4	2016	6.60
V	0	--	0	--	4.20
VI	0	--	0	--	2.71
VII	0	--	0	--	1.75
VIII	1	1010	0	--	1.00
Totals	33	3017	119	4741	

[1] Recruitment from two successful nests (250 ft).

[2] Recruitment from three successful nests (530 ft).

Figure 22. Population structure of smallmouth bass in the Red Cedar River including recruitment from ten successful nests. Data included recoveries after two experimental poisonings and prepoisoning seine collections.

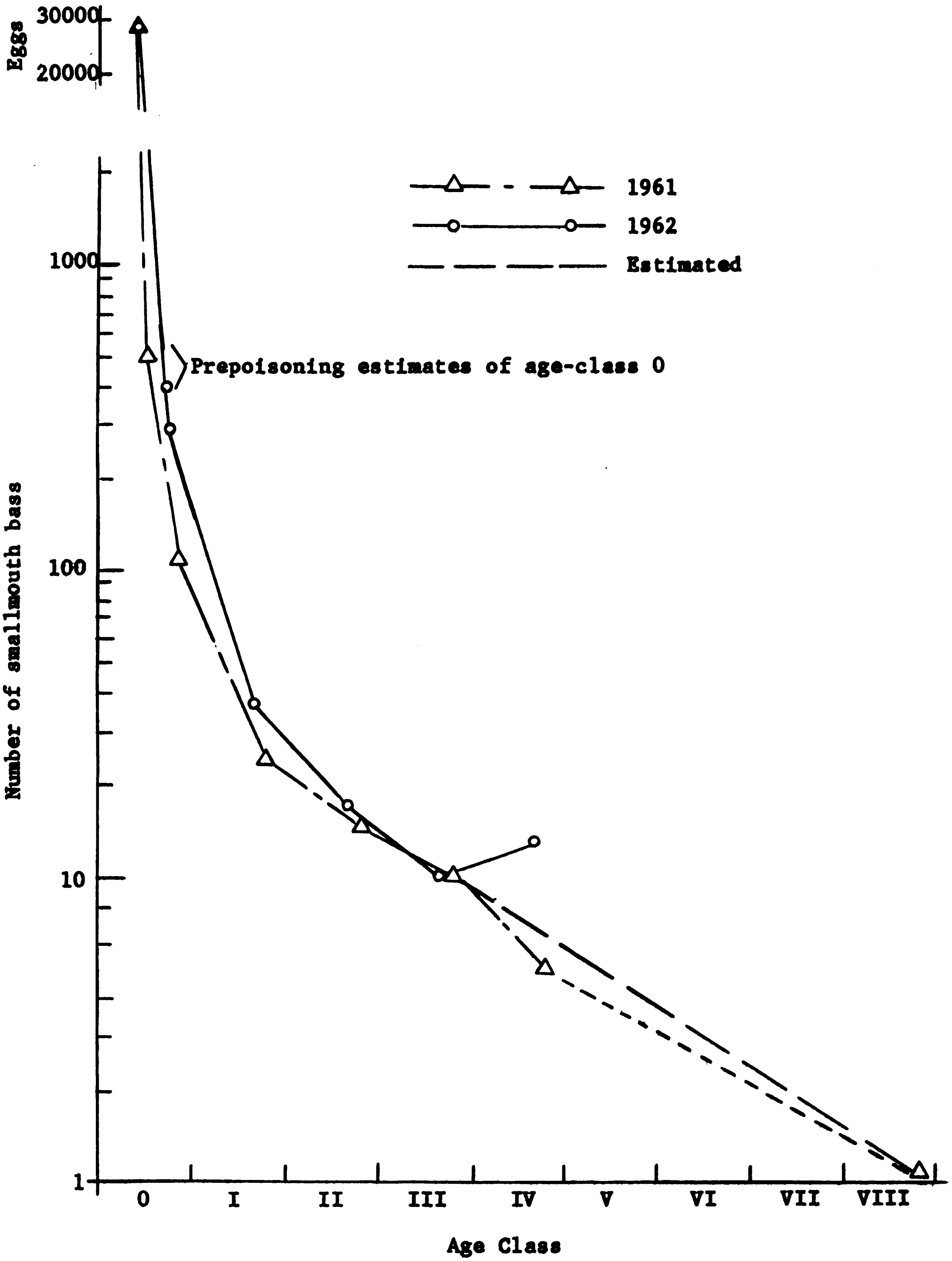

Eggs
30000
20000
1000
100
10
1
Number of smallmouth bass
1961
1962
Estimated
Prepoisoning estimates of age-class 0
0
I
II
III
IV
V
VI
VII
VIII
Age Class

Figure 22

McFadden (1961) and Ricker (1958) have discussed the various types of compensatory, density dependent and density independent mortality that operates on a fish population to reduce numbers to conform with environmental carrying capacity. For brook trout, McFadden found a stable recruitment of trout even when an extremely weak year class occurred. Stable recruitment was attributed to a variable density dependent mortality acting on the progeny during the early stages of life.

The estimated average population structure required under existing environmental conditions to support ten smallmouth bass nests is included in Table 15. The population structure was interpreted as the average of the two survivorship curves presented in Figure 22. The population structure is weak in the sense that age-groups V to VII were not represented in either poisoning collection, however, the age structure does have a firm anchor in that the number of nests in the 2.2-mile study zone is known with a fairly high degree of accuracy.

In interpreting the number of bass in each age group the fraction was retained rather than rounding off. This was done, because in computing the total fish stock in the 2.2-mile study zone, the estimated structure was expanded to include 54 nests. Assuming one-third of age-group III and all of the subsequent age groups reached maturity, the presented population structure would include 19.26 mature bass to support the ten nests. Assuming an even sex ratio, the number of adults approximates the minimum number required to produce ten nests.

Brown (1960) estimated that about 30% of age-group III bass in the Little Miami River reach maturity. Although the Miami River is several hundred miles south of Michigan and presumably has a longer growing season, the growth rates are comparable (Table 16).

Table 16. Comparison of lengths of smallmouth bass from various waters.

Water area	Number of fish	Total length (inches) at end of year							
		1	2	3	4	5	6	7	8
Red Cedar River Michigan	551	2.6	5.3	8.8	11.2	13.0	14.5	15.7	16.9
Lake Michigan Waugoshance Point[1]	1892	3.9	6.3	8.1	9.7	11.5	13.2	14.6	15.8
Massie Creek[2] Ohio	213	2.9	5.9	8.8	11.0	12.7	13.9	14.5	15.1
Little Saline Creek[3] Missouri	--	3.2	6.3	8.9	9.9	11.1	12.8	--	--
Potomac River[4] Maryland	--	3.9	7.6	9.6	11.2	13.2	14.7	--	--
Sandusky River[5] Ohio	125	3.4	6.7	9.2	11.9	14.3	15.0	--	--
Lake Erie[6] Western Basin	308	--	8.4	10.6	11.9	13.5	14.7	15.7	--
Lake Huron[7] South Bay	2566	--	--	9.0	10.2	11.4	12.6	13.8	14.8

[1] Latta 1957

[2] Brown 1960

[3] Fajen 1959

[4] Sanderson 1958

[5] Clark 1956

[6] Doan 1940

[7] Fraser 1955

Production Rate

To estimate fish production it is necessary to know the population structure, the individual growth rate, and the biomass growth rate. The biomass growth rate is an integral function of mortality and individual growth rates. Mortality rates are derived from the community structure. Therefore an error in computing the community structure would be reflected in the mortality rates. Individual growth rates are independent of the population structure since they are computed from measured weights at various ages.

The net production of smallmouth bass (in the Ivlev sense) was computed by adjusting the autumn biomass estimates to the average biomass and multiplying successively each age group biomass by the corresponding instantaneous rate of growth.

The autumnal biomass of smallmouth bass in the 2.2-mile (17.5-acre) experimental section of the Red Cedar River was calculated on the basis of the average nesting density during the 1961 and 1962 seasons (47 and 54 nests respectively). The observed nesting density was weighted by the estimated population structure required to support ten nests (Table 15). The number of bass in each age class was entered in column 2 of Table 17. The products of the age class frequency and the average individual weight were entered in column 4, the summation of which is equal to the autumnal biomass.

The autumnal biomass was adjusted to the average population biomass following, in detail, the procedures outlined by Ricker (1958) and recently used by Gerking (1962) to compute bluegill production. The following relationships express the principles involved in computing

Table 17. Estimation of the annual production rate of smallmouth bass in the 2.2-mile study reach of the Red Cedar River using group biomass and instantaneous rates of growth. k = instantaneous rate of growth of individuals; g = instantaneous rate of growth of the biomass; i = instantaneous rate of mortality.

Age	Population	Individual Weight g	Population Weight kg	k	i	g	$\frac{e^{gb} - 1}{g}$	Average Population Weight kg	Net Production Rate $kg\ yr^{-1}$
0	1267	3.9	3.6	4.78	4.40	+0.38	1.22	4.39	20.98
I	158	32	5.1	2.41	2.08	+0.33	1.18	6.02	14.5
II	80	130	10.4	1.40	0.68	+0.72	1.46	15.18	21.2
III	52	330	17.2	0.93	0.43	+0.50	1.30	22.36	21.0
IV	34	520	17.7	0.46	0.43	+0.03	1.02	18.05	8.3
V	21	705	14.8	0.30	0.48	-0.18	0.92	13.62	4.1
VI	14	915	12.8	0.26	0.48	-0.22	0.90	11.52	3.0
VII	9	1140	10.3	0.22	0.48	-0.26	0.88	9.06	2.0
VIII	5	1390	7.0	0.20	0.58	-0.38	0.83	5.81	1.2
Totals	1640		98.9					106.01	96.3

the weight change factor:

$k - i = g$, where k = the instantaneous rate of individual growth;
i = the instantaneous rate of mortality, and
g = the net instantaneous rate of increase in weight.

$e^g - 1$ = the fractional net increase in weight

$$\frac{e^g - 1}{g} \times \text{the observed weight} = \text{the average weight.}$$

Since each age group has its own characteristic growth and mortality rates, the above statistics must be computed separately for each age class.

The instantaneous rate of growth (k) of individuals was calculated on an annual basis expressed as the natural logarithm of the fractional weight gain as shown in Figure 23. The instantaneous rate of mortality (i) was calculated as the natural logarithm of the surviving fraction of individuals as interpreted from the survivorship curve (Figure 22). The weight change factor ($\frac{e^g - 1}{g}$) may be derived from the instantaneous rate by using any exponential table, or is conveniently tabled by Ricker (1958) for various combinations of k and i. The weight change factor multiplied by the autumnal population weight gives the average population weight. The annual net production is derived by multiplying the average population weight by successive entries of k.

The basic data required for the computation of net production of smallmouth bass in the 17.5-acre experimental stream reach are given in Table 17. A net production of 96.3 kg yr^{-1} was obtained by multiplying successively the entries of k and the average biomass and summing the products. On a unit area basis, the net production was 13.6 kg ha^{-1} yr^{-1} (12.1 lbs $acre^{-1}$). The average standing crop of smallmouth bass was 13.3 lbs $acre^{-1}$.

Figure 23. Growth in length and weight of smallmouth bass in the Red Cedar River.

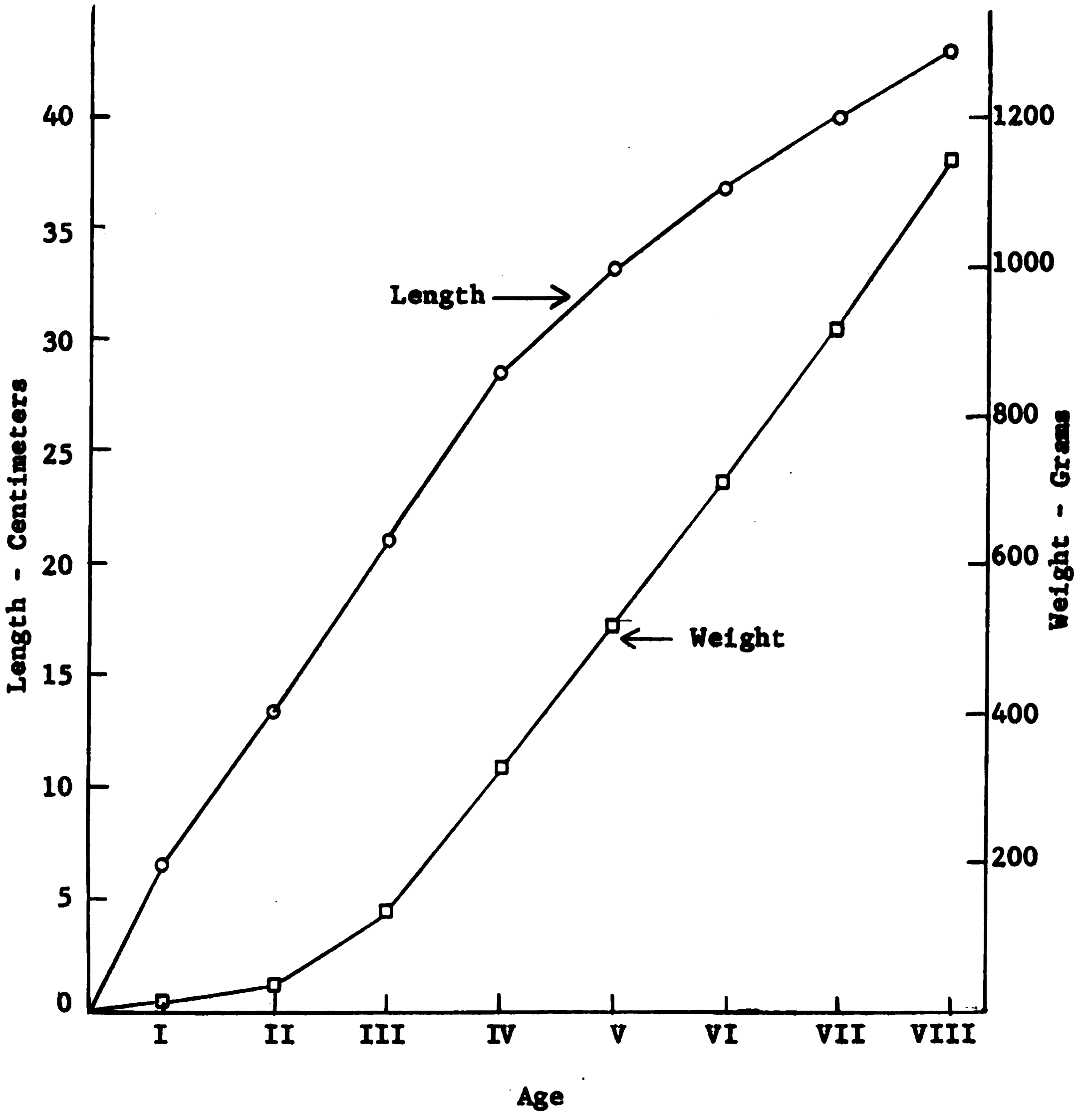

Length - Centimeters
0
5
10
15
20
25
30
35
40
Weight - Grams
200
400
600
800
1000
1200
Length
Weight
I
II
III
IV
V
VI
VII
VIII
Age

Figure 23

Energy Relationships

Bass production, to be comparable with production at other levels, must be converted to energy terms. This conversion will also facilitate a quantification of the predator-prey relationship between smallmouth bass and crayfish.

Bass production in the Red Cedar River was placed on an energy basis by determining the caloric content of whole fish. For calorimetry determination, bass were captured from the stream, the stomach contents removed, and live weight measured. The fish then were split and dried at 80 C until a constant weight was achieved. The dried bass were pulverized, pelleted, and combusted at 30 atm oxygen in a bomb calorimeter.

The relationship of live and dry weight to the caloric content of smallmouth bass was expressed as

$$\text{g cal} = \text{g wet wt.} \times 1089 \text{ cal}$$

$$\text{g cal} = \text{g dry wt.} \times 4743 \text{ cal}$$

The net production of bass in the study reach was 13.6 kg ha^{-1} yr^{-1} (12.1 lbs $acre^{-1}$). On a caloric energy basis, smallmouth bass production was 1481 g cal m^{-2} yr^{-1} (Table 18) representing 0.00024% of incident light energy in the photosynthetic range (0.3 μ to 0.7 μ). Approximately 0.14% of the energy fixed at the primary level by the periphyton and macrophyte crop is realized at the smallmouth bass level.

Hayne and Ball (1956) studied the energy relationships in two Michigan ponds containing three species of sunfish (*Lepomis*). Converting the reported total incident light energy to energy within the photosynthetic range, the production of sunfish in the ponds represented 0.0028% of incident light energy. On this basis, the efficiency of

Table 18. Production efficiencies at various community levels in the experimental section of the Red Cedar River.

Production level	Net production g cal m^{-2} yr^{-1}	Production efficiencies	
		$\frac{P_n}{P_{n-1}}$	$\frac{P_n}{L}$
Bass (P_2)	1,481	4.56%	0.00024%
Crayfish (P_1)	32,510	2.29%	0.00527%
Primary (P)	1,420,000	0.23%	0.23%
Light (L)	617,000,000	--	--

sunfish production was approximately 10 times that of smallmouth bass in the Red Cedar River. The higher efficiency for Lepomis reflects the fundamental differences in trophic status between sunfish and smallmouth bass. Bass after the first summer of life primarily are secondary consumers. Lepomis sp. are primary consumers feeding largely upon insects although plant material may make up 10% of the diet (Gerking, 1962).

Except for young-of-year, smallmouth bass in the Red Cedar River feed almost exclusively upon crayfish. A large minnow population (80 lbs acre^{-1}) is utilized only to a limited extent. The total fish biomass, as estimated by stream poisoning, amounted to 195 lbs acre^{-1}. The live weight biomass of crayfish was estimated at 383 lbs acre^{-1}, about twice that of the fish biomass. On an energy basis, the standing crop of crayfish represented 32.5 k cal m^{-2} whereas the total fish population, using the energy content of bass, represented 24.0 k cal m^{-2}. Judged solely on the dominant standing crop, evaluated on either a weight or energy basis, the experimental reach of the Red Cedar River would be classified as a crayfish stream.

The energy requirements for the production of smallmouth bass include that energy used in maintenance and the energy included in the production of new biomass. The energy requirements for growth and maintenance are characterized by food conversion efficiencies. Food conversion efficiency is the ratio of the weight of food consumed to the weight of biomass gain.

Using smallmouth bass taken from the Red Cedar River, Williams (1959) reported a median food conversion efficiency of 4.1 for bass fed on a diet of minnows. Lagler and Kruse (1953) fed minnows to smallmouth bass held in cages submerged in a Michigan pond and reported food conversion efficiencies ranging from 3.29 to 4.08. Ivlev (1945) stated that production of one gram live weight of fish required 4000 calories.

Converting Williams' (1959) growth efficiencies to a caloric basis, 4465 calories of food added 1089 calories (1 gram live weight) to the smallmouth bass. The 4465 calories of food required to add one gram of live weight to fish compares favorably to Ivlev's (1945) estimate of 4000 calories.

Assuming that on a caloric or organic weight basis, the food conversion efficiencies from minnows to bass as found by Williams are equally applicable to crayfish, we have some basis for determining the amount of crayfish required to produce the observed production of smallmouth bass. Bass, however, do not feed upon crayfish during the first year of life. It is during the second summer of life that crayfish become the staple item in the bass diet.

In the study zone the net production of smallmouth bass in age-groups I to VIII was 10.6 kg ha^{-1} yr^{-1}. On a caloric energy basis this production is equivalent to 1159 cal m^{-2} yr^{-1}. Using the caloric conversion efficiency derived from Williams' data, 4748 calories of crayfish would need to be consumed by bass from each square meter of stream bottom to achieve the observed production.

Crayfish production was estimated at 32510 g cal m^{-2} yr^{-1}. If crayfish were the only energy source available to smallmouth bass, the cropping efficiency by bass would equal 14.6% of the annual crayfish production. Because of nonassimilated energy losses and energy diversion for body maintenance, 3.6% of the crayfish production is used for biomass increases by bass.

The predator-prey relationship between bass and crayfish, based upon an average bass, is readily visualized. After the first two summers, the average weight gain by bass is nearly a constant 200 grams per year regardless of age (Figure 23). Again, assuming a 4.1 growth efficiency on a caloric basis, the growth by an individual smallmouth bass, equivalent to 2.18×10^5 g cal yr^{-1}, would require a diet containing 8.94×10^5 g cal yr^{-1}. Since crayfish production was estimated as 3.25×10^4 g cal m^{-2} yr^{-1}, the amount of crayfish produced on 25.5 m^{-2} would supply the annual energy requirements for one smallmouth bass, if the smallmouth bass could harvest 100% of the net crayfish production.

The caloric energy requirement would be filled by consuming 425 3-gram crayfish or 230 5-gram crayfish. These estimates must be considered minimal energy requirements because of the nature in which the food conversion efficiencies were derived. In all cases the food conversion efficiency was measured on fish held in cages or aquaria where movement was restricted. And perhaps more important, the fish were held at temperatures under which maximum enzymatic and absorption activity would be expected.

Assuming a 100% crayfish harvest by smallmouth bass is unrealistic. Rock bass are competitors for crayfish. Of 117 inspected rock bass, 66% had recently consumed at least one crayfish. The rock bass population in the primary study area during 1962, exclusive of young-of-the-year, has been estimated in excess of 40 lbs $acre^{-1}$ (Linton, ms). This standing crop of rock bass is approximately three times the biomass of smallmouth bass. On the basis of stomach analyses and standing crop of rock bass, I would estimate that the consumption of crayfish by rock bass is probably twice that harvested by smallmouth bass. Data to support this assumption are lacking principally because rock bass production has not been estimated.

If in fact rock bass competition for crayfish limited bass predation to 14.6% of the crayfish production, the average bass in excess of one year of age, would have a spacial requirement of 192 m^2 if crayfish were the only food source available. In the 7.1 hectar experimental area, there were approximately 400 smallmouth bass feeding principally upon crayfish. On the basis of 192 m^2 of stream bottom with its resultant available crayfish production of 8.93×10^5 g cal yr^{-1}, the bass population would require 7.6 hectars to supply its energy requirements. This area requirement is about 0.5 hectars larger than the primary study area.

The computation of spacial requirement of smallmouth bass would indicate that food supply limits bass production. This, however, is misleading on two accounts. It was assumed that crayfish are the only energy source available to smallmouth bass, and harvesting efficiency was 14.6%. A large minnow population (80 lbs $acre^{-1}$), although little used, is a large food reserve. It would be reasonable to suspect that before crayfish became a limiting factor, other energy sources would be exploited.

Summary

1. The ecological status of smallmouth bass in an enriched, warm-water stream was investigated. The method was to trace the principal energy flow patterns, quantifying biotic and abiotic energy losses, from the primary trophic level, through the major prey species (crayfish), ultimately to the smallmouth bass population.
2. The seasonal dynamics of the phosphorus cycle in warm-water streams was characterized by models based on seasonal stream flows and enrichment. Individual models were presented for nonenriched, polluted, and enrichment stream zones. The nonenriched stream zone was characterized by a biological concentration phase. In the pollution zone, flow increases were strictly dilutants, reducing phosphorus concentrations with increasing stream discharge. Phosphorus circulation in the enrichment zone was characterized by a three component model including an increasing, dilution, and recessional phase.
3. Primary productivity and energetics were estimated by three techniques. Diurnal oxygen curves were developed to measure community metabolism and gross primary productivity. The harvest method was employed to measure contributions by stream macrophytes. Predictor equations were developed relating periphyton production to stream temperature during seasons of increasing or decreasing photoperiods.
4. Annual gross and net primary productivity was estimated as 2.40×10^6 and 1.42×10^6 g cal m^{-2} yr^{-1} respectively. The net production of stream macrophytes was 4.95×10^5 g cal m^{-2} yr^{-1}. Net periphyton production, evaluated by predictor equations, was 9.20×10^5 g cal m^{-2} yr^{-1}.

5. Photosynthetic efficiencies, based on net production and surface radiation within the photosynthetic range, was 0.23% on an annual basis. The efficiency based on light available at the substrate level was 1.5%. During comparable growth periods, the photosynthetic efficiency of an established macrophyte bed was eight times that of periphyton.

6. The macrophytes in the stream have become extensively established only during the past five-year period. The present expansion rate may be exponential. Macrophytes occupied 50% of the stream bottom in the 2.2-mile study reach.

7. Crayfish (Orconectes propinquus) were the staple item in the diet of smallmouth bass. Evaluated on a caloric energy basis or live weight biomass, crayfish were the dominant community in the study zone. The standing crop of crayfish was estimated as 43 g m^{-2} (383 lbs $acre^{-1}$) with a caloric energy value of 33.7 k cal m^{-2}.

8. Productivity of crayfish, as estimated by instantaneous rates of growth and mortality, was 41.5 g m^{-2} yr^{-1} or 32.5 k cal m^{-2} yr^{-1}. By including community respiration, the total energy flux through the crayfish population was estimated to be 133.25 k cal m^{-2} yr^{-1}.

9. The energy assimilated by the crayfish population represented about 9.4% of the energy available at the primary level. The net production of crayfish was about 3% of net primary production and 0.00527% of incident light energy.

10. The immediate postspawning stream conditions are most critical with regard to survival of smallmouth bass fry. Initiation of nest building appears to be temperature regulated, however, high stream

stages deterred spawning. Nesting density of smallmouth bass was 21 and 25 nests per mile of stream during 1961 and 1962 respectively.

11. Direct-current electrofishing gear was not an effective collection device for smallmouth bass. The community structure of smallmouth bass was determined by two experimental poisonings using rotenone. Survivorship curves, based on the number of successful bass nests, were constructed from the rotenone recovery data.
12. The net production of smallmouth bass was estimated by multiplying successively each age group biomass by the corresponding instantaneous rate of growth. The net production was 13.6 kg ha^{-1} (12.1 lbs $acre^{-1}$) in the primary study area. The average standing crop of smallmouth bass was 13.3 lbs $acre^{-1}$.
13. On a caloric energy basis, bass production amounted to 1481 g cal m^{-2} yr^{-1} representing 0.00024% of incident light in the photosynthetic range. Approximately 0.14% of the available net primary production is realized at the bass level.
14. Assuming crayfish were the only energy source available to smallmouth bass, harvesting efficiency by bass would equal 14.6% of the annual crayfish production. Because of nonassimilated energy losses and energy diverted for body maintenance, 3.6% of the crayfish production is used for biomass increase by bass.

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