THE DYNAMICS OF FIVE ROCK BASS POPULATIONS IN A WARM-WATER STREAM

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This is to certify that the

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THE DYNAMICS OF FIVE ROCK BASS POPULATIONS
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Robert C Ball
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ABSTRACT

THE DYNAMICS OF FIVE ROCK BASS POPULATIONS
IN A WARM-WATER STREAM

by Kenneth J. Linton

The dynamics of five rock bass populations in the Red Cedar River were compared in order to determine their ability to maintain themselves by natural reproduction under the various environmental conditions. Fish were collected by an electrofishing technique and the age-classes and total populations were estimated by the Bailey modification of the Petersen method.

The age distributions differed in the five zones. Rapid declines occurred during the course of the study in two of the populations and a lesser decline occurred in another. One population remained relatively steady and the remaining one increased. The smallest variation in age distribution and the smallest proportion of older fish were observed in the increasing population.

The age-specific fecundity of the rock bass in the Red Cedar River was higher than in comparable studies. The number of eggs produced per female increased through age VI, then declined, although the low observation for age VII may have been due to chance. An estimate of sex ratio indicated that

the population consisted of 48.2% females, but the 95% confidence limits included 50%.

Overall survival of the immature stages was poorest in the zones in which a decline occurred and highest in the increasing population. No relationship was demonstrated between the numerical size of the parent stock and the immature survival. The smaller, declining populations had a larger proportion of older fish and showed a tendency to produce more eggs per female on the average due to the age-specific nature of the fecundity. The data suggested a trend toward a larger number of fish surviving to age III from larger cohorts of eggs.

The calculation of r, the intrinsic rate of natural increase, was adapted to the rock bass populations, expressed on an annual basis, and called r_a, the annual potential instantaneous rate of natural increase. It was calculated for three cohorts and two vertical age distributions for each of the five zones. The difference between the zones was statistically significant. The value of r_a was consistently negative in the two most polluted zones and was positive in every case in the least polluted zone. The associated mean generation times, T_g, were consistent and had a mean of about five years. The net reproduction rate, R_o, was less than unity for all of the estimates in the two polluted zones and greater than unity for all those in the least polluted zone.

Values of r, R_o, and T_g were compared with similar values for other organisms and were consistent with expectations. Variations in these values are discussed with respect to the environmental conditions and it is concluded that the success of the rock bass populations is impaired by the presence of pollutants.

The use of r_a is recommended in the management of important fisheries and in the evaluation of chronic low-level pollution.

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By

Kenneth Jack Linton

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INTRODUCTION

We are destroying our natural waters as a suitable environment for those organisms that we desire to maintain. The problem has been recognized for centuries, but ignored in the name of economy unless human lives were endangered. One of the reasons why this situation has persisted until very recent times is the lack of agreement as to what constitutes damage to the environment. Certain forms of gross damage are easily isolated and defined, such as accidental spillage of highly toxic industrial wastes. In these cases, provided that the toxic material does not persist in the environment, the damage is reparable by replacement of the organisms.

But it is extremely difficult to assess the effects of a low level of a complex mixture of pollutants such as we may often find in our natural waters. The bioassay, in which death is the criterion for harm and in which only a limited age span of the test organism is represented, is useless as a tool for the evaluation of such effects. It has been recognized for some time that the biota of an environment reflects the totality of pollutional influences. This is the basis for "indicator" organisms. Other approaches involve the measurement of specific physiological effects on the organisms, estimates of the standing crops of various species, or estimates of the production of the populations.

The approach taken here is to evaluate the status of the populations of an organism (the rock bass, *Ambloplites rupestris* (Rafinesque)) by means of an index as to the ability of the populations to maintain themselves through natural reproduction. If the environment created by the addition of low level pollutants is unsuitable for the continued maintenance of a natural population of the organism, then this index should reflect the effects of the pollutants.

Rock bass have been present in the Red Cedar River in sufficient numbers to provide potentially extensive sport fishing since at least the early part of this century. A series of personal interviews (Appendix C) with about twenty of the older residents of the drainage area indicated that these fish have been present in large numbers throughout nearly all of the river for most of that time. Yet a recent study (Linton and Ball, 1965) showed that in the early 1960's, the rock bass in certain parts of the stream declined sharply in numbers. But this decline did not occur over the entire watershed, so it is unlikely that climatological conditions during one or more spawning periods were strongly unfavorable and no evidence is available to show that some cataclysmic change had occurred in the environment. Therefore, it is believed that the cause of this population decline is one that has persisted over a period of several years and that, given the proper information and an appropriate index, it would have been possible to predict this decline prior to its occurrence.

If this impending decline or collapse of the population were reflected in the adjustment of the age structure of the populations, then the potential instantaneous rate of natural increase should have been consistently negative prior to the collapse and it should have been positive or near zero and fluctuating slightly in those populations which did not collapse and are not in immediate danger of collapsing. It should remain strongly positive in the expanding populations.

This procedure cannot result in a statement of the cause of the damage in itself, but it is a definite indication that damage has been or is being done to the collapsing populations.

It is the intent and purpose of this study to demonstrate that the potential instantaneous rate of natural increase does or does not reflect impending or occurring changes in the size of a population of fish in the natural environment.

DESCRIPTION OF THE RIVER

The Red Cedar River is a warm-water stream in south-central Michigan. It arises in Cedar Lake, Livingston County, and flows northwesterly through Ingham County, entering the Grand River within the city of Lansing. The river is about 50 miles long and drains a total area of about 472 square miles (Figure 1). In the upper drainage area, consisting largely of farm land, the channel has been extensively dredged and straightened. The lower portion of the river flows through some farm land and considerable urban areas, which contribute agricultural, domestic and industrial pollution. The stream ranges from 25 to 80 feet wide and the average gradient is about 2.4 ft/mile. The mean weekly 6:00 P.M. and 6:00 A.M. temperatures for the years of 1957 through 1964 are shown in Figures 2 and 3. The data indicate that the maximum summer temperatures may have increased over the period of this study. The monthly mean discharge for the years 1957 through 1964 is graphically represented in Figures 4 and 5. The discharge data were furnished by the United States Geological Survey, which maintains a recording station at the Farm Lane bridge.

The study section of the river extends from the Farm Lane bridge on the Michigan State University campus in East Lansing to the VanBuren Road bridge about one mile upstream from Fowlerville, comprising about 30 miles of the main stream (Figure 1). The arrows in Figure 1 indicate the physical features which delineate the five zones represented in this study. Since the Sycamore Creek drainage is not included here, the land area drained through the study section is about 355 square miles.

The study section was divided into five zones for this investigation. Zone I is that three and one-half mile portion of the stream from the Farm Lane bridge to Okemos Road. The water here is slow-moving and drops silt and detritus on the mud bottom. The river is influenced by the dam located about $\frac{1}{4}$ mile below the zone on the Michigan State University campus. The bottom at the upstream end of this zone is largely sand and rubble.

Zone II (eight and one-half miles long) consists of that part from the Okemos Road bridge to the Zimmer Road bridge below Williamston. It is the cleanest of the five zones, having a sand bottom in a large portion and gravel and boulders in most of the remaining portion. There are no urban areas in this part of the river except for the influence of Okemos at the extreme lower end. The number of riffle-pool combinations is higher in the part from the bridge at M-43 to Zimmer Road than in any other part of the river. Below M-43, the water is slower and deeper with fewer riffles.

Zone III extends from Zimmer Road bridge to the dam at Williamston, two and one-half miles upstream. The bottom

<u>Figure 1</u>. Map of the Red Cedar River showing location of zones (delineated by arrows) and intensive sampling stations.

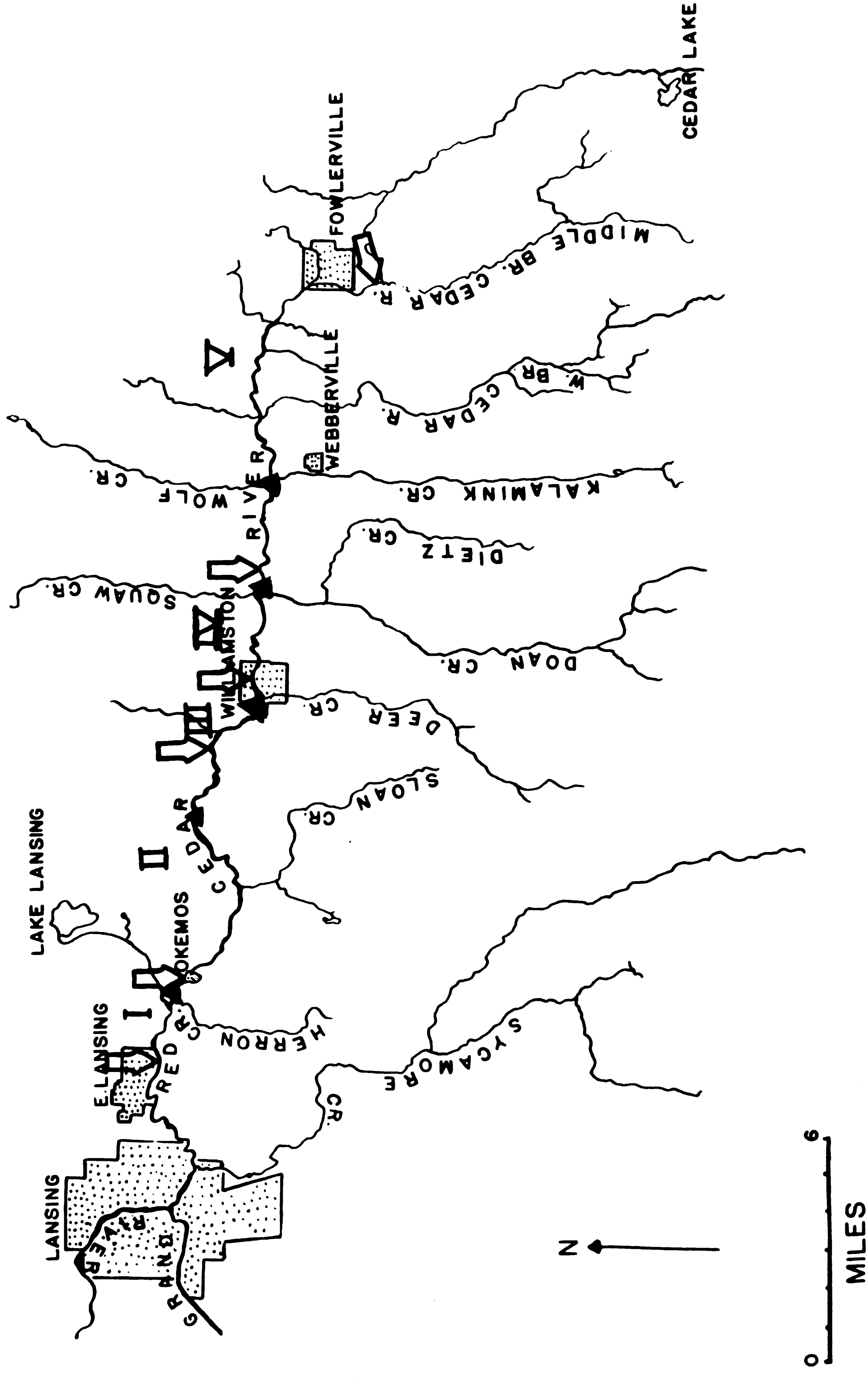
LANSING
GRAND RIVER
E. LANSING
RED CR.
HERRON CR.
LAKE LANSING
OKEMOS
I
II
III
IV
V
CEDAR RIVER
SLOAN CR.
DEER CR.
WILLIAMSTON
DOAN CR.
SQUAW CR.
DIETZ CR.
WOLF CR.
KALAMINK CR.
WEBBERVILLE
W. BR. CEDAR R.
FOWLERVILLE
MIDDLE BR. CEDAR R.
CEDAR LAKE
SYCAMORE CR.
N
0
6
MILES

Figure 2. Temperature* of the Red Cedar River in °F. as measured with a Taylor thermograph at the Michigan State University river farm at Okemos, Michigan, for the years 1957 through 1960. The upper curve represents the mean weekly temperature at 6:00 P.M. and the lower curve represents the mean weekly temperature at 6:00 A.M.

*Tabulated values in Appendix A.

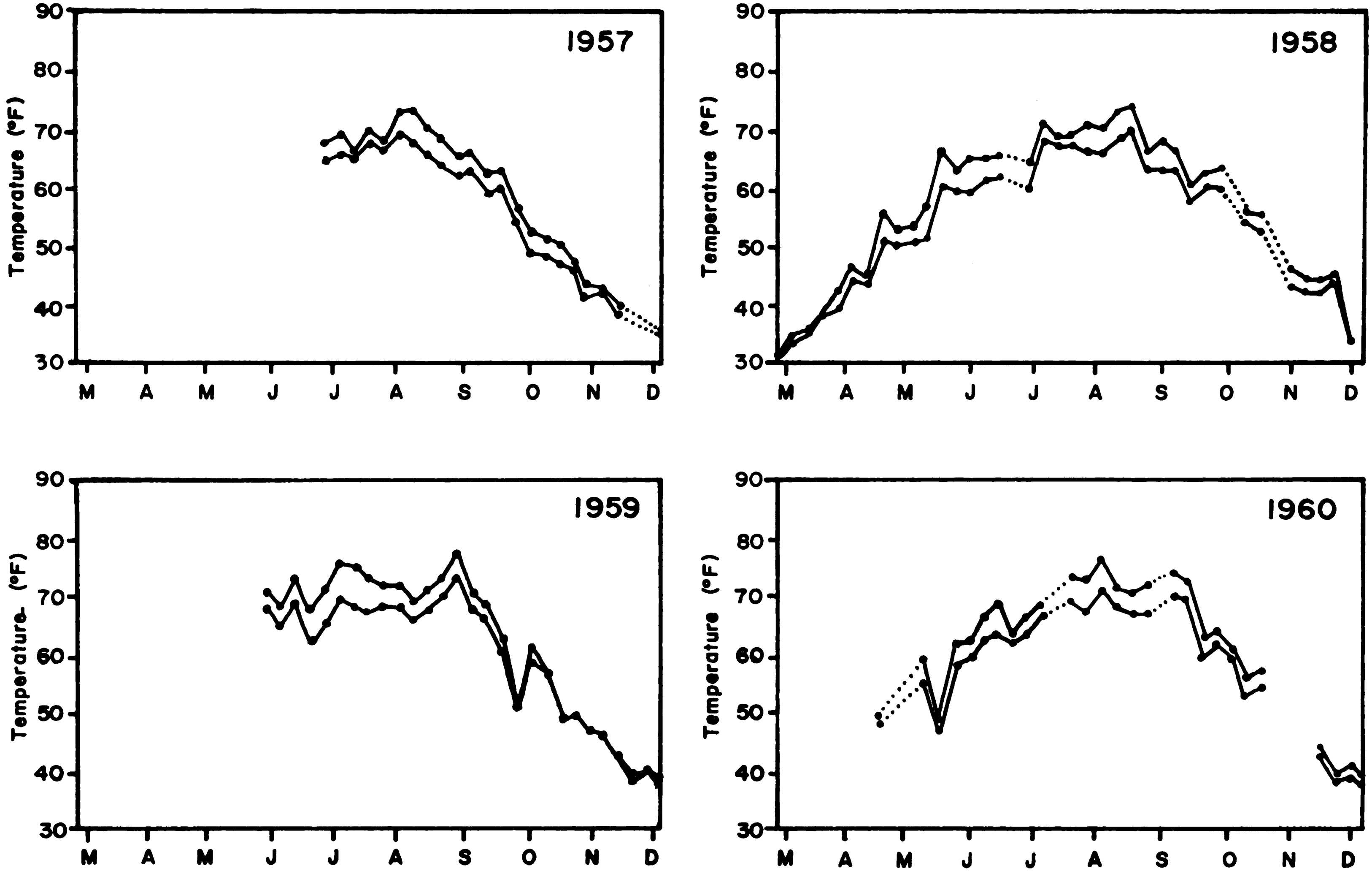
1957
1958
1959
1960
Temperature (°F)
90
80
70
60
50
40
30
M A M J J A S O N D

Figure 3. Temperature* of the Red Cedar River in $^{\circ}$F. as measured with a Taylor thermograph at the Michigan State University river farm at Okemos, Michigan, for the years 1961 through 1964. The upper curve represents the mean weekly temperature at 6:00 P.M. and the lower curve represents the mean weekly temperature at 6:00 A.M.

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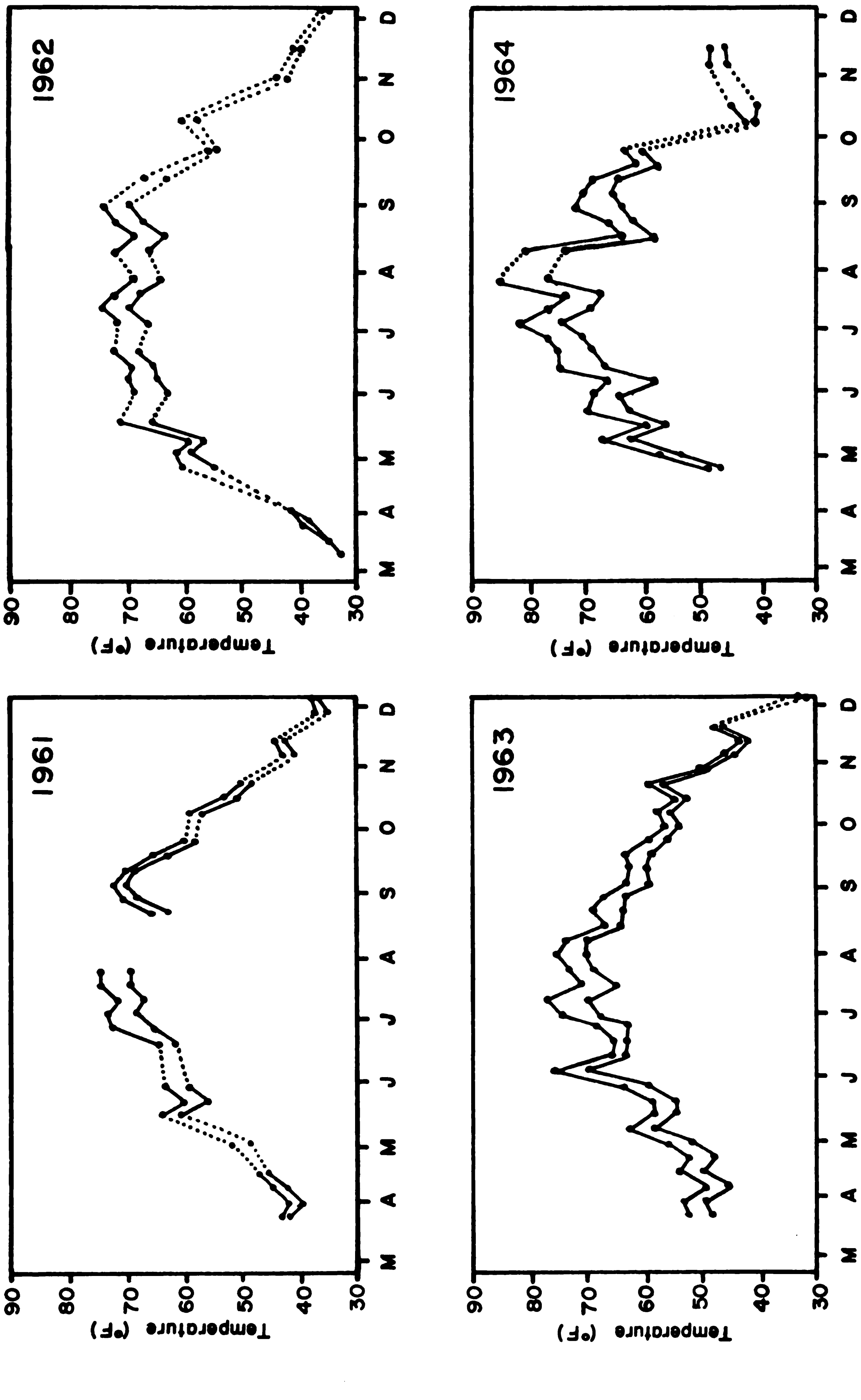
*Tabulated values in Appendix A.


1961
1962
1963
1964
Temperature (°F)
90
80
70
60
50
40
30
M A M J J A S O N D

<u>Figure 4</u>. Mean monthly discharge* of the Red Cedar River at Farm Lane bridge for the years 1957 through 1960 (data furnished by the United States Geological Survey Field Office, Lansing, Michigan).

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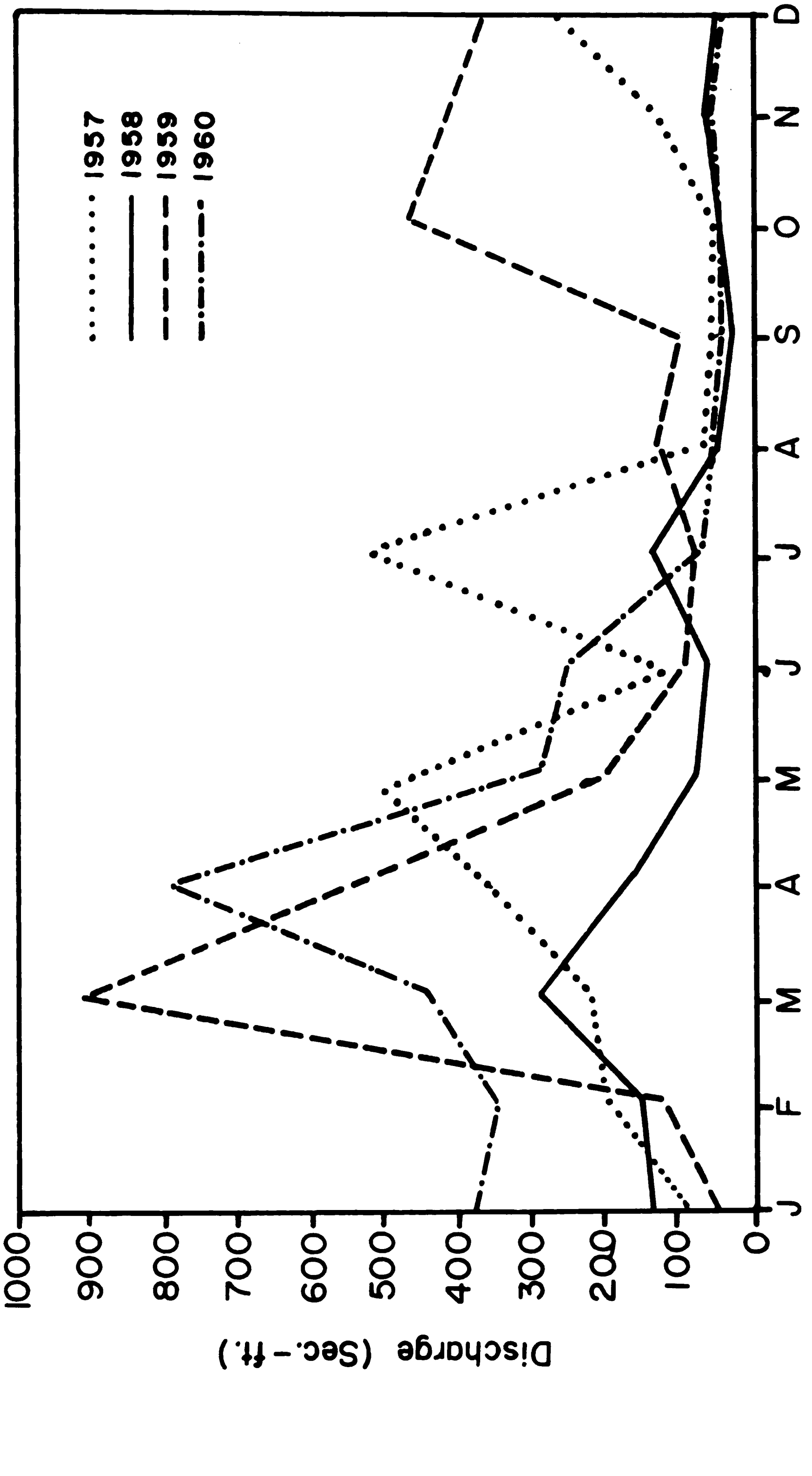
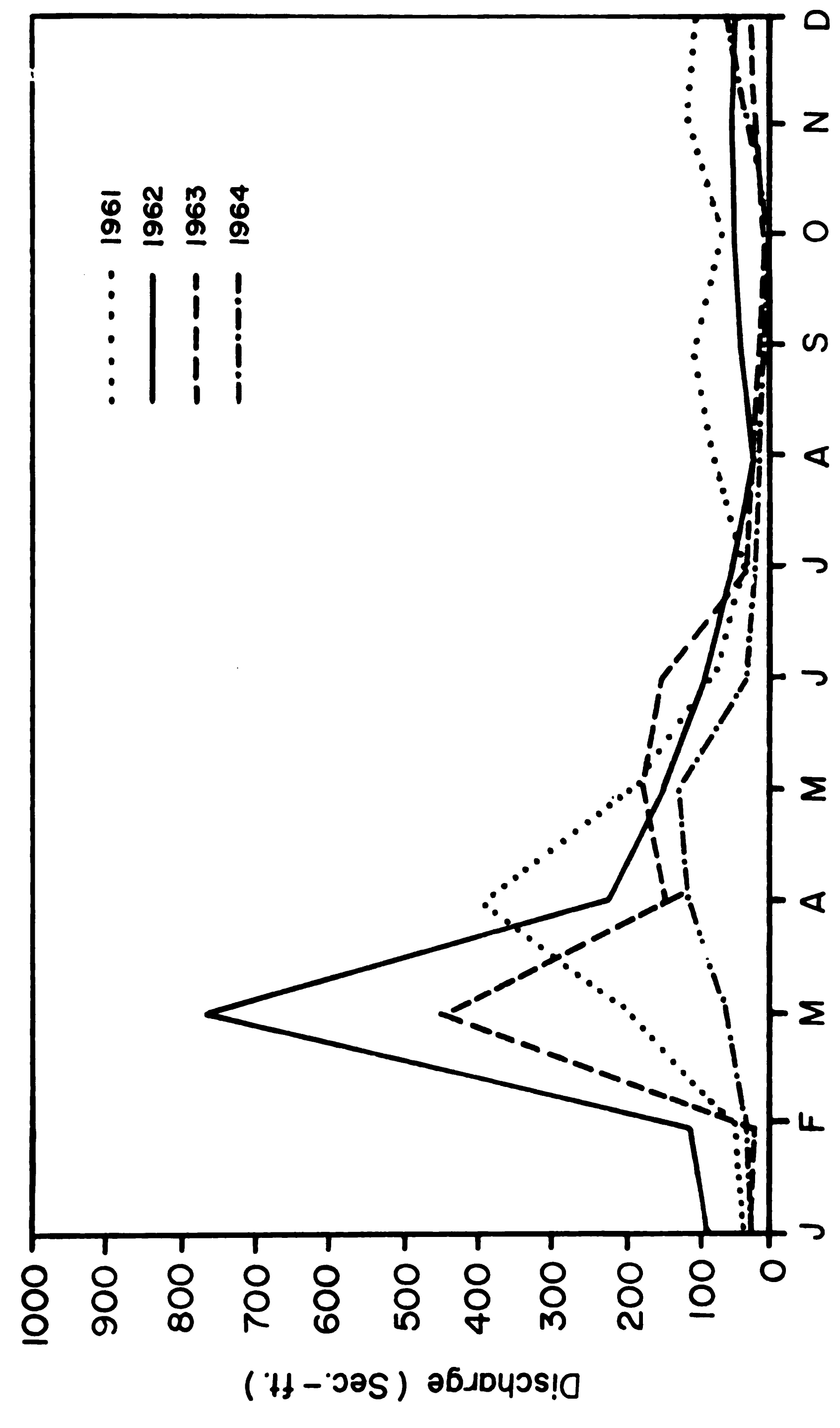
*Tabulated values in Appendix B.



1957
1958
1959
1960
Discharge (Sec.-ft.)
0
100
200
300
400
500
600
700
800
900
1000
Month
J
F
M
A
M
J
J
A
S
O
N
D

Figure 5. Mean monthly discharge* of the Red Cedar River at Farm Lane bridge for the years 1961 through 1964 (data furnished by the United States Geological Survey Field Office, Lansing, Michigan).

*Tabulated values in Appendix B.



Discharge (Sec. – ft.)
1000
900
800
700
600
500
400
300
200
100
0
J F M A M J J A S O N D
Month
1961
1962
1963
1964

varies from silt to sand and cobbles, with some detritus. It is strongly influenced by the Williamston sewage disposal plant. There are extensive beds of rooted higher aquatic plants immediately below the dam.

Zone IV includes the largest impoundment in the system and extends from the dam at Williamston to the bridge at Dietz Road. The reservoir proper comprises approximately half of the four-mile length, but its influence extends throughout the zone. The reservoir is confined to a narrow basin, but the flow is very slow. For the present study, the reservoir has been disregarded due to sampling problems and other considerations. Therefore, the results discussed refer only to the upstream portion of this zone. The mean width included in the calculations is also based only on this upstream portion. Further description of the impoundment may be found in Brehmer (1956).

Zone V represents the remaining 12 miles of the study section from the Dietz Road bridge to the bridge at VanBuren Road. It is influenced by the Webberville and Fowlerville urban areas. Probably the greatest influence is the industrial waste of the metal plating plant in Fowlerville. A large portion of this zone has been dredged and straightened and flows through farm land. The bottom is largely silt and mud. The depth and width of the dredged portions are quite uniform and the flow is slow.

The randomly selected half-mile zones used for the concentrated study of the rock bass populations in 1962 and 1964 are indicated by triangles in Figure 1. Selected physical features of the five intensive study areas are summarized in Table 1. The major macrophyte populations encountered throughout the five zones are *Valisneria* sp. and *Sagittaria* sp., although others may be locally abundant. For example, *Elodea* sp. is particularly abundant in parts of Zone III, fairly abundant in Zones I and V, and unimportant in Zones II and IV. More extensive treatments of the macrophytes of the Red Cedar River are found in a later section of this paper and in King (1964) and Vannote (1963).

Table 1. Physical features of the five intensive study stations in the Red Cedar River.

Zone	I	II	III	IV	V
Mean width (feet)	60.6	68.6	51.3	63.2	28.3
Mean depth (inches)	19.1	15.1	17.0	23.6	14.9
Total area (acres)	3.67	4.16	3.11	3.83	1.72
Bottom types* (percent)					
Silt	11.1	4.5	10.0	10.7	3.5
Boulders	1.5	6.2	5.9	0.3	1.0
Cobbles	4.0	23.2	13.4	0.7	2.3
Gravel	20.2	16.6	17.1	0.0	1.9
Sand and gravel	0.0	0.0	2.9	0.0	13.2
Sand	48.8	43.8	40.9	79.8	65.5
Detritus	14.4	5.7	9.8	8.6	12.7

*Approximately according to the Wentworth scale (Leet and Judson, 1958).

METHODS

Description of Physical Features

Selected physical features of the five intensive study areas were observed during the summer of 1962 while the river was at base flow.

A 100 foot steel tape was used to measure the half-mile reaches. At the end of each 100 foot interval, paint was sprayed on a convenient tree or structure on the bank and the width of the river was measured at that point. Depths were recorded for five points along a line perpendicular to the thread of the river, starting at the left bank: at 1/6 and at 1/3 of the distance to the right bank, in the middle of the river, and at 2/3 and at 5/6 of the distance to the right bank.

Subsequently, the crew started at the downstream end of the same reach and proceeded upstream, estimating the percentage of each bottom type in the categories listed for each 100 foot interval. The averages of the three estimates were recorded and summarized.

Macrophytes

In June and early July of 1964, approximately midway through their growing season, the aquatic macrophytes in each of the study zones were sampled by the harvest method.

Sample plot sites were located in the following manner. A table of random numbers was used to select ten 100 foot strata in each of the study reaches. For each stratum, 10 numbers were selected from the table of random numbers to represent distances from the lower end of the stratum. On arrival at the prearranged site, the width of the stream was measured. Again, from the table of random numbers, a number was selected to serve as a measurement from the right bank (facing upstream). This point then served as the upstream right-hand corner of the sample plot. The following possibilities were omitted from the plot selections: the extra 40 foot stratum at the upper end of the zone; the measurement "0" as a distance from the lower end of the stratum; and the last one foot of the width.

This method results in a bias toward selection of a sample plot lying in a narrow portion of the stream. The intensity of the bias is dependent on the uniformity of the width. Since the widths were quite uniform within a zone, this bias is not great in the present study.

The sample consisted of all macrophyte parts which were attached to roots or rhizoids in the sample plot and also included the roots and rhizoids.

Two pieces of equipment were used to obtain the samples. When the water was shallow enough to permit its use (91% of the samples), a rectangle composed of 1 inch boards enclosing a 1 square foot area was pressed into position on the river bottom. The plants were removed by hand and washed gently in the river water to remove silt and larger insects. This washing did not remove periphyton and associated small animals. The samples were drained for a constant period (30 seconds) and weighed immediately on a Hanson dietetic balance.

When the water was too deep to employ the square foot sampler (the remaining 9% of the samples), a Petersen dredge was used. The dredge sampled 0.83 square feet of the bottom. Appropriate corrections were made in the values.

Three representative samples of approximately 500 grams each were returned to the laboratory for determination of dry weight. These were subsequently dried to constant weight at approximately 55^{o}C.

The wet weights were converted to dry weight, the mean was calculated for each zone, and these stocks were converted to g/m^2. All the means were corrected to the estimated stock on July 4, 1964, the median collection date. The correction factor was obtained from the data of 16-17 July, 1962 reported by Vannote (1963) and consisted of the mean production per day expressed as a percentage of the standing crop on that date. The value used was 1.409% per day, which resulted in a maximum correction of 13.4% in the estimates reported above.

Rock Bass Populations

Population Estimates

The rock bass were collected prior to 1962 as part of a large limnological study of the Red Cedar River. Production of biomass was estimated for several components of the five stream communities (King, 1964; Linton and Ball, 1965). The rock bass collections in 1962 and 1964 were expanded expressly for the purpose of evaluating, from the standpoint of age structure and other factors, the changes in population density that were observed in the earlier study. The alteration of the methods in 1962 was largely a matter of increasing the size of the operations in order to secure an adequate sample for this type of analysis.

The rock bass population numbers were estimated by the Bailey modification of the Petersen method (Formula 3.7 in Ricker, 1958) using an electrofishing technique.

The fish were collected with a 220-volt Homelite direct-current generator which was mounted in an eight-foot wooden boat. The hand-held positive electrodes consisted of coiled copper tubing or straight copper pipe mounted on six-foot wooden handles and were opposed by a metal negative electrode plate on the bottom of the boat. The stunned fish were retrieved at the positive electrodes with dip nets having a one-fourth-inch mesh woven nylon bag or a graded mesh (one inch to one-eighth inch) cotton bag.

The stations were randomly selected within the limits of accessability. In 1959 through 1961, block nets were used to delineate the station during the estimation procedures. The stations ranged in length from 528 feet to 910 feet in 1959 and 1960. In 1961, all stations were 300 feet long. But in 1962 and 1964, the stations were 2640 feet long and no block nets were used.

In 1959 and 1960, the crew started at the downstream net and shocked upstream, fin-clipping all fish and releasing them at the approximate place of capture, recording only the number handled. On the second and subsequent runs, the fish were placed in a metal tub in the boat. About half-way through the station and again at the end, the fish were weighed and measured, scale samples were taken, and all the fish were released. In 1961, six live-boxes outfitted with nylon mesh bags were distributed through the station after the block nets were in place. The crew shocked upstream, putting all fish in the live-boxes. At the completion of a run, the fish were weighed and measured and scale samples were taken prior to releasing the fish. On subsequent runs, recaptures were recorded and released and the usual data were collected on the remainder of the fish.

In 1962 and 1964, the only changes employed were the following: use of a half-mile station instead of the smaller ones sampled previously; elimination of the block nets (unnecessary for this length of station); and estimation by age class as well as total population.

In view of the fact that both size-class and total estimates of the population numbers were obtained in 1962 and 1964, it was possible to investigate the relationship between the two types of estimates. It was believed that a consistent relationship probably existed between them. If true, it would be possible to obtain useful age-class estimates from the gross estimates made during previous years.

The procedures employed in the earlier sampling involved the determination of the ages of the rock bass comprising the census catch (fish collected on the second run). This yielded an observed distribution of the percentage of fish of each age which were handled in the census catch as well as the gross estimate of the total population numbers. The product of the proportion of the total number of fish handled which were of a given age and the total number of fish estimated to be in that area is an estimate of the number of fish of that age in that area. But it is known (Cooper and Lagler, 1956; Sullivan, 1956; Linton and Ball, 1965; et alia) that the electrofishing technique is biased toward capture of the larger fish. Therefore, the use of these percentages in a direct manner would yield erroneous and biased estimates of the potential instantaneous rate of natural increase. But if this bias was consistent and observable, it would be possible to construct a correction to the previous observations and make them useful.

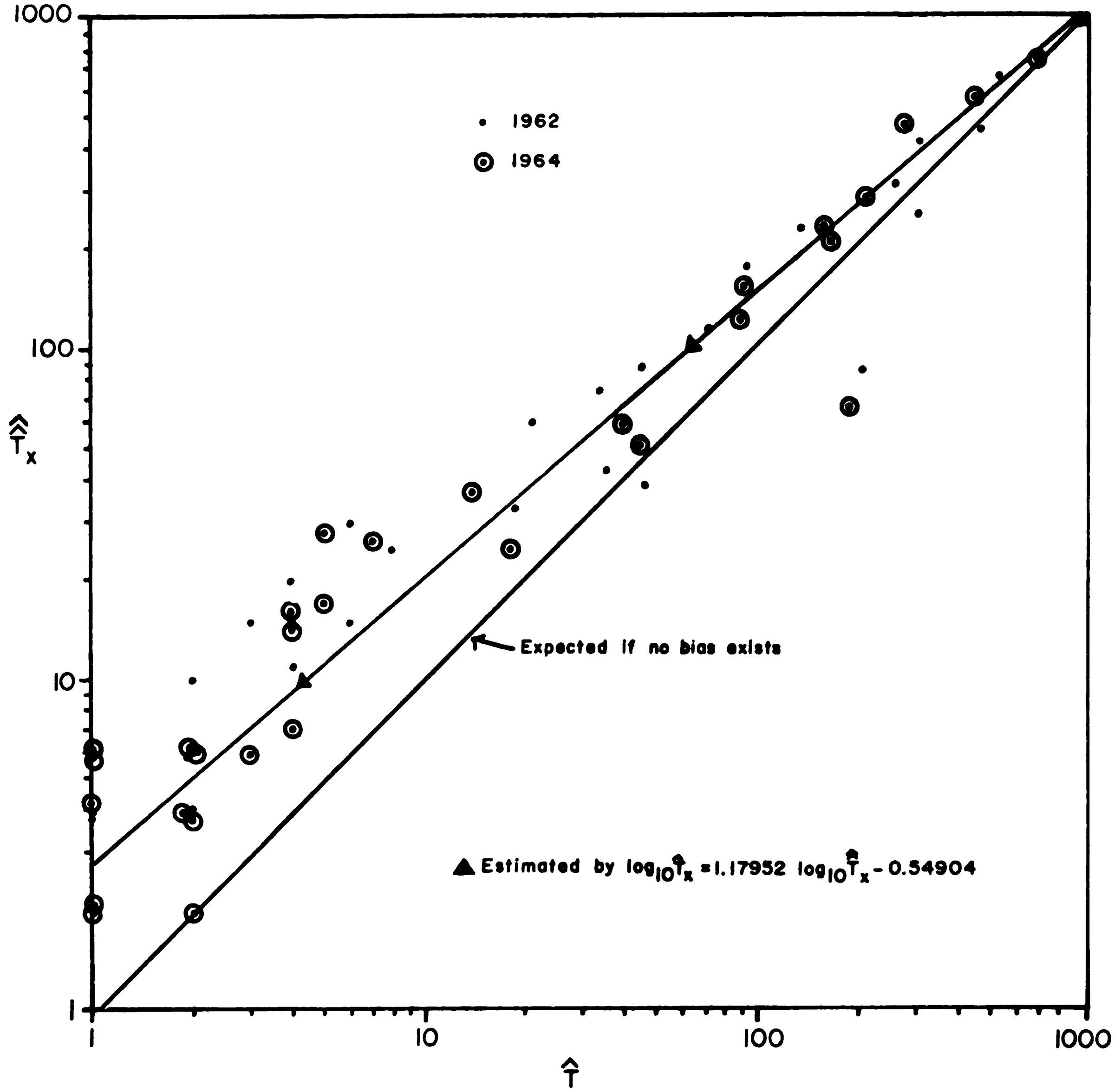
From the 1962 and 1964 gross population estimates, the observed percentages of each age in the census catch were used to estimate the total number of fish of each age ($\hat{\hat{T}}_x$) present in the population. These estimates were then compared (Figure 6) to the actual age-class estimates ($\hat{T}_x$) made from the unmodified data.

Two types of bias may be seen in this relationship: the vertical displacement of the observed line over the expected line; and the bias toward capture of the fish which occur in smaller numbers (the larger fish). The first of these is explained at least in part by the nature of the Bailey modification of the Petersen estimate. In both of the present types of estimates, the Bailey formula was used. It is:

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

It is preferred since it is a slightly lower estimate, whereas the Petersen formula, $T = MC/R$, tends to overestimate the population (Bailey, 1951; Chapman, 1951; Ricker, 1958). This is brought about by the fact that the inflation of the number of recaptures, R, is proportionately greater than the increase in the product of the number marked, M, and the number taken in the census catch, C. But in the gross population estimates in the present study, this correction appears only once. In the size-class estimates, $\hat{T}_x$, it appears once for each size-class. Thus, the sum of the size-class estimates will be smaller than the overall estimate, or the observations in Figure 6 will tend to be displaced above the expected values.

<u>Figure 6</u>. Estimates of the numbers of rock bass of various age-classes in the intensive study zones of the Red Cedar River based on gross Petersen estimates versus the corresponding actual age-class estimates.



1000
100
10
1
10
100
1000
$\hat{\hat{T}}_x$
$\hat{T}$
• 1962
⊙ 1964
Expected if no bias exists
▲ Estimated by $\log_{10}\hat{T}_x = 1.17952 \log_{10}\hat{\hat{T}}_x - 0.54904$

The bias toward capture of older fish is demonstrated in Figure 6 by comparing the vertical distance between the two lines (calculated and expected) expressed as a percentage of the value on the abscissa. For example, for X=2, the observed Y value is 150% greater than the expected Y value. For X = 200, the observed Y is only 33% greater. Since the older fish occur in smaller numbers, it may be seen that they constitute a disproportionately large segment of the number of fish handled in the estimation procedure.

From Figure 6, it was learned that the bias was indeed reasonably consistent and predictable. The equation for the least squares approximation to the relationship is:

$$\log_{10} \hat{T}_x = 1.17952 \log_{10} \hat{\hat{T}}_x - 0.54904$$

where $\hat{T}_x$ and $\hat{\hat{T}}_x$ are as indicated above. This equation was applied to correct the estimates of age-classes based on the gross estimates from 1959-61 and the observed ages of the rock bass in the corresponding census catches.

Fecundity

Two collections were made with hook and line in Zone II (June 13 and 15, 1966). Of the total of 189 fish collected, 70 gravid females were used for the fecundity study. Some of the females from the first day of collection were rendered unsuitable for the study by decomposition of the ovaries (these had been left overnight in 10% formalin). These were not included in the 70 fish used in this study. Immediately after collection, the fish taken on the second day were given an intraperitoneal injection of from 0.5 to 2.0 ml of 10% Formalin, which was a successful solution of the earlier problem.

In every case, the ovaries were removed and placed in tap water for at least ten minutes. They were then blotted on paper towels and weighed on a Mettler balance to the nearest 0.1 mg. Twenty samples were severed from the ovaries of fish of various ages, weighed to within the nearest 0.1 mg, and the eggs contained therein were counted. The samples counted contained from 95 to 926 eggs.

The weights of the ovaries were then multiplied by the mean number of eggs/gm to obtain the numbers of eggs/female. These were then separated according to age, and the mean number of eggs/female at each age was calculated. These values constituted the age-specific fecundity for the calculation of the potential instantaneous rate of natural increase.

Sex Ratio

The sample of 93 rock bass collected on June 15, 1966 was used to estimate the sex ratio in the populations. The sex of the individuals was determined by gross inspection of the gonads.

Survivorship

It is not necessary to know the shape of the survivorship curve for the juveniles of the population in order to calculate the potential instantaneous rate of natural increase (Birch, 1948), but it is necessary to know the overall survival from the egg stage to the reproductive age for the females. To obtain this information, it was necessary to estimate the number of eggs produced at a given time and the number of three-year-old females resulting from that cohort.

Observations were available on the numbers of rock bass in various age-classes in the five study zones for the years 1959 and 1961 (each three years prior to one of the years of intensive sampling for this study). Applying the results of the fecundity study, it was possible to estimate the numbers of eggs produced by the populations in 1959 and 1961. Since the sex ratio in the population was nearly unity, it was only necessary to divide the numbers of three-year-old females found in the intensive sampling years by half the numbers of eggs produced by the respective populations three years prior to the intensive sampling. This yielded two independent estimates of juvenile survival (or mortality) for each of the five zones, which could then be employed to calculate the total survivorship for the mature females. Immigration and emigration are considered as part of the mortality curve. The only remaining data necessary for this calculation are the numbers of females of each age observed in the populations. These data were obtained as described above.

Potential Instantaneous Rate of Natural Increase

The estimates of the potential instantaneous rates of natural increase for the various populations were computed as recommended by Birch (1948). The term used to describe this value was selected in preference to "intrinsic rate of natural increase" since the latter connotes a maximum value for the species considered. In every other respect, the two terms are synonymous and the calculations are identical. The calculation of r_a entails the solution of the following equation for r_a by trial and error:

$$\Sigma\, e^{-r_a x}\, l_x m_x = 1$$

where e is the base of the natural logarithms, r_a is the potential instantaneous rate of natural increase expressed as an annual rate, l_x is the survival of female offspring expressed as the ratio of the numbers of females alive at age x to the number of "female" eggs originally present in the cohort, m_x is the number of eggs produced by a female of age x, and x is the age expressed as the midpoint of the year. The values of the variables were obtained as described above under the appropriate headings.

The use of estimates of abundance for the various age-classes of female rock bass resulted in two possible abnormalities in the calculation of the survivorship column. First, it was possible to estimate that one year-class was absent, while an older year-class was present. Thus, it can result in the statement that the probability of being alive at age X+1 is greater than the probability of being alive at age X. Therefore, in the event that a zero occurred, it was replaced by the mean of the immediately preceding number and the immediately succeeding number. But since this only occurred in the older age groups, the effect on the value of "r_a" is negligible. Secondly, it is possible to estimate that an older year-class was present in larger numbers than a preceding year-class, even if the latter is present. This results in the same untenable position with respect to survivorship as stated above, but is handled in a slightly different manner. In this case, where X+1 exceeds X, but both are present, $((X+1) + X)/2$ was used to replace both of the values for the calculation of survivorship. It is to be expected that such "aberrant" relationships will arise in random sampling and it is believed that neither of these adjustments will lead to a less accurate value of r_a.

The initial computations were carried out on a desk calculator to provide a close, but minimum, value of r_a for each of the cases considered. The input data for the computer consisted of the ages, X, the $l_x m_x$ products, and the hand-calculated upper and lower approximations to r_a, which covered a span of 0.1 in length. The initial r_a with which the computer worked was a value to the nearest tenth such that the actual value of r_a would be reached if 0.001 were added to this value (and the $\Sigma e^{-rX} l_X m_X$ were recalculated) exactly

100 times. In fact, before the 100th computation was reached, the value of the sum would exceed unity. Thus, if a one is subtracted from the sum each time, a point is reached where this quantity, say Y, becomes negative. At this point, the computer was instructed to print out the last value of r_a (and Y) for which Y was positive as well as the first value of r_a (and Y) for which Y was negative. The value of r_a correct to the nearest 0.001 is then that value of r_a for which the associated value of Y is closest to zero. The program for these computations has been made available to the computer librarian on the Michigan State University campus. A sample of the final step of the calculations appears in Table 2.

Age Determinations

For all age determinations, scale samples were removed from the region of the tip of the compressed left pectoral fin. The samples were dried and impressions were made on small squares of acetate without heat, as recommended by S. H. Smith (1954). These impressions were projected at a magnification of about 22 diameters and the ages were determined by the number of annuli present. No growth rate information was obtained during this study. The growth rates of the rock bass in the five zones for the years 1958 through 1961 were reported by Linton (1964).

Table 2. Sample* calculation of the potential instantaneous rate of natural increase, r_a, for rock bass in the Red Cedar River.

For r_a = 0.159

Age (X)	rX	e^{-rX}	l_X	m_X	$\sum_x e^{-rX} l_X m_X$
3.5	0.5565	0.573	6.9720×10^{-4}	542	
4.5	0.7155	0.489	1.7557×10^{-4}	4876	
5.5	0.8745	0.417	0.6043×10^{-4}	6661	
6.5	1.0335	0.356	0.6043×10^{-4}	9174	
					1.00036300

For r_a = 0.160

Age (X)	rX	e^{-rX}	l_X	m_X	$\sum_x e^{-rX} l_X m_X$
3.5	0.5600	0.571	6.9720×10^{-4}	542	
4.5	0.7200	0.487	1.7557×10^{-4}	4876	
5.5	0.8800	0.415	0.6043×10^{-4}	6661	
6.5	1.0400	0.353	0.6043×10^{-4}	9174	
					0.99542688

*Example is for rock bass in Zone II, 1962 vertical estimate (based on simultaneous sampling over all age classes).

Net Reproduction Rate

The net reproduction rate was calculated for each cohort and each vertical estimate by the technique recommended by Birch (1948), which is:

$$R_0 = \Sigma\ l_x m_x$$

where R_0 is the net reproduction rate and l_x and m_x are as defined above (see page 31).

Mean Generation Length

The mean length of a generation, or, more properly, the mean age of a reproductive female, was estimated by the formula (Birch, 1948):

$$T = \frac{\log_e R_0}{r}$$

where T is the mean length of a generation, R_0 is the net reproduction rate, and r is the intrinsic rate of natural increase. In this case, r_a was used in place of r.

In the natural populations of rock bass in the Red Cedar River, it is probably not necessary to distinguish between mean generation length and mean age of a reproductive female, since it is unlikely that any of the fish present in the population are of post-reproductive age.

RESULTS

Fish Population Estimates

The total numbers of rock bass per mile of stream were estimated by the Petersen method. These estimates are presented in Table 3 according to the age of the fish and the year and zone where the estimates were made. The method used precluded reliable estimates of fish less than two years old. These tabled numbers represent "vertical" estimates of abundance, i.e., fish present in the station which were of the given age at the time of sampling. In the following discussions, these are to be distinguished from "horizontal" age distributions which result from estimating the number of survivors of a given cohort at successive intervals of time. In this study, the time intervals are one year.

Due to certain sources of bias inherent in the electrofishing technique, confidence intervals may not be assigned to the estimates. This same bias makes the estimates of numbers of age II fish questionable. Although this is of some importance in the population estimates, it does not influence the estimates of the potential instantaneous rates of natural increase. But certain features of the changing populations are evident in Table 3.

Table 3. Estimated numbers of rock bass per mile of stream by age, zone, and year of collection.

Zone	Age	Year 1959	1960	1961	1962	1964
I	II	2515	267	1220	8	556
	III	253	609	57	16	70
	IV	148	704	127	12	10
	V	14	129		4	2
	VI	14			4	2
	Total	2944	1709	1404	44	640
II	II	2142	863	1596	2530	2728
	III	430	283	178	1096	938
	IV	214	105	221	276	1422
	V	31	29	39	92	182
	VI		7		98	10
	VII					4
	Total	2817	1287	2034	4092	5284
III	II	338	244	468	530	438
	III	184	143	101	616	324
	IV	338	218	117	142	340
	V	114	85	28	38	180
	VI		6	9	8	36
	VII			4	4	4
	Total	974	696	727	1338	1322
IV	II	356	62	151	70	80
	III	81	62	29	186	28
	IV	184	62	0	6	14
	V		27	4	4	8
	VI			4	2	2
	VII				12	4
	VIII				2	
	Total	621	213	188	282	136
V	II	149	94		2	6
	III	66	135		64	4
	IV	47	13		24	8
	V	86	5		2	4
	VI	13	0		2	2
	VII		5		2	2
	VIII		5		2	
	Total	361	257	0	98	26

Note especially that drastic reductions occurred in the numbers of rock bass in zones I and V during the course of this study. By random happenstance, the estimate for zone V in 1961 was made near the upstream end of that zone shortly after a severe fish kill (Parker, 1961). But the population in the lower end of the zone was declining prior to the kill above and continued to decline throughout the course of this study. The numbers in zone IV were comparatively stable, but an overall decline occurred during these years. Zone III was apparently unaffected during this period or showed a slight increase in numbers. In zone II, the numbers increased considerably.

Of at least equal importance in this study is the numerical relationship of the young fish to the older members of the population (Table 4). The populations of zone II remained most consistent throughout the study with respect to age distribution as well as consistently showing the largest standing crop of rock bass, at least in numbers. This was also true of the biomass (Linton and Ball, 1965). A comparison of the remainder of the zones to zone II indicates that the age structures of the fish in the remaining zones showed a larger proportion of older fish. This would not be obvious in total population estimates or in biomass estimates, yet it is of extreme importance to the continued maintenance of the population.

Table 4. Estimated proportion of fish aged II or older which are at least age V. Data are for the rock bass in the Red Cedar River according to the zone and the year of collection.

Zone*	Year					Mean
	1959	1960	1961	1962	1964	
I	1%	8%	0%	18%	1%	5.6%
II	1	3	2	5	4	3.0
III	12	13	6	4	17	10.4
IV	0	13	5	7	10	7.0
V	27	6	**	8	31	18.0

* I Polluted
II Cleanest
III Receives sewage
IV Reservoir zone
V Polluted

** No observation

Fecundity

The fecundity of the rock bass was estimated by the gravimetric method. As stated above, it is necessary to obtain this information on an age-specific basis, but, as will become obvious in the calculation of the potential instantaneous rate of natural increase below, the first two or three years of maturity are of prime importance. When the intrinsic rate of natural increase is quite high, as in the case of invertebrates (Birch, 1948; Leslie and Park, 1949; Cooper, 1965; etc.), the first period or two of egg production will contribute an extremely large portion of the value of r. In the case of lower rates, such as are found in the vertebrates (Leslie and Ranson, 1940; Lotka, 1956; Leslie, 1945), the contribution of the first reproductive periods is relatively smaller, but still much greater than for the older segment of the population.

The estimates of the age-specific fecundity and the 95% confidence limits on the estimates are presented in Table 5. The total fecundity reported here is somewhat higher than that reported by Eddy and Surber (1947) of 5000 eggs/female, but in a random sample of mature females, with considerable weight placed on the younger fish, the figures are comparable. The figures for the present study are appreciably higher than those given by Vessel and Eddy (1941), who reported on the number of eggs by size-classes of the females. Their estimates ranged up to 11,000 eggs/female as compared with about

Table 5. Age-specific fecundity of the rock bass in the Red Cedar River.

Age	Mean estimated number of eggs/female	95% confidence limits	
		lower	upper
III	1,084	438	1,730
IV	9,753	7,773	11,733
V	13,321	9,573	17,069
VI	18,348	14,383	22,313
VII	15,017	7,027	23,007
VIII	10,150*		

*Estimated graphically from the curve for ages III through VII; no age VIII fish appeared in the sample for fecundity.

18,000 eggs/female for the six-year-old fish in the present study. The confidence limits on these estimates are wide, so there is insufficient evidence to indicate a real difference.

It has been reported (Allen, 1951; McFadden, 1961; Vessel and Eddy, 1941) that, in most fish, there is a strong positive relationship between the size of the female and the number of eggs produced per year. Table 5 does not offer strong evidence against those observations. Considering the confidence limits, such a relationship could easily be the case for the rock bass being studied. But, for the present purposes, it is desirable to use the best empirical evidence for the population being studied, so these means will be used in the calculations below. However, as will be shown, the differences are of little consequence in the calculation of the potential instantaneous rate of natural increase.

Sex Ratio

The sex ratio of the sample studied indicated that the population consisted of 48.2% females with 95% confidence limits based on the Clopper and Pearson "Confidence belts for proportions" (Dixon and Massey, 1957) of 0.37 and 0.60. Consequently, a sex ratio of unity was assumed. There was no indication that the sex ratio changes with age in the rock bass.

Survival of Immature Rock Bass

As indicated above, it is necessary to estimate the overall survival of the immature stages of the organism in order to compute r_a. It is not necessary to know the shape of the survival curve through this period for these computations, although this information is required for the calculation of the stable age distribution (Birch, 1948).

Two estimates of survival of the immature fish were computed for each of the zones, as well as the combined estimate of the rate. The latter is not a simple mean of the two estimates, but rather the estimate obtained when the sum of the number of survivors in each case is divided by the sum of the original complement of eggs. The estimates appear in Table 6.

The original complements of eggs were obtained by multiplying the numbers of females of each age by the appropriate fecundity figures. Since the most reliable estimates of the numbers of three-year-old female rock bass were obtained in 1962 and 1964 (these were not based on the correction factors), the egg complements were estimated for 1959 and 1961. But the estimate of no rock bass in zone V in 1961 precluded the possibility of making this survival estimate. In the computations below, the combined estimate for the appropriate zone was used in every case.

The survival of the immature rock bass in the Red Cedar River is obviously low. Of course, the mortality which leads

Table 6. Percent survival of rock bass from ovarian eggs to age III for each of the five intensive study zones in the Red Cedar River for the 1959 and 1961 cohorts.

Year	Zone*				
	I	II	III	IV	V
1959	0.0015%	0.0739%	0.0246%	0.0198%	0.0067%
1961	0.0108	0.0654	0.0351	0.0453	---
Combined	0.00497	0.06973	0.02739	0.02134	0.0067

* I Polluted
II Cleanest
III Receives sewage
IV Reservoir zone
V Polluted

to these figures has been operating over a period of three years. Although no comparable figures are available on rock bass, the survival of eggs of salmonids up to sac fry is usually over 90% (McFadden, 1961). In his Lawrence Creek brook trout, McFadden states that the initial high survival of the eggs is followed by a period of nine months during which about 98% of the cohort is lost to some form of mortality. However, it should be noted that salmonid eggs enjoy much more protection in the gravel of the redds than do the centrarchid eggs in their exposed nests. Particularly in warm-water streams, the instabilities of flow, temperature, turbidity, etc., would expose the eggs and sac fry to considerable mortality risks.

Slobodkin (1962) points out that most fish probably display a survivorship curve characterized by a large initial loss followed by a decreased, fairly constant percentage mortality. However, at least one exception to this type of curve has been reported for centrarchids. Jenkins (1955) reported that 13 pairs of adult black crappies yielding a potential of 590,000 eggs resulted in 136,000 yearlings. This implies a survival of 39% of the potential number of eggs. If the curve described by Slobodkin were applied here, it would be necessary to have some of the surviving crappies, if the subsequent survival was, say, 60%, living at the end of 25 years. This is unlikely. However, Jenkins' results are unusual and it is also true that this survival occurred while the population was recovering from a severe reduction in numbers.

The instantaneous mortality rate for adult rock bass in the Red Cedar River was calculated from an estimate of the survival rate based on the Robson-Chapman (1961) technique. It was used for the estimates of net production by Linton and Ball (1965). If the mortality of the immature rock bass in the Red Cedar River occurs over a period of three years and if the rate of mortality during the last two years of this period is assumed to be constant and equal to the adult instantaneous mortality rate, i_a, then a reasonable approximation to the curve suggested by Slobodkin should result. This should also be similar to that found for the Lawrence Creek brook trout (McFadden, 1961), for which the total survival for the first nine months from the egg stage was about two percent. In the present study, the overall immature survival for three years in zone II was estimated to be about 0.07% or, the annual instantaneous mortality rate, if constant, was 2.42291. Thus, if a three-year period is being considered,

$$N_t = N_O e^{-at}$$

where

$$a = i_o + i_1 + i_2$$

and i_o is the instantaneous mortality in the first year of life, i_1 that in the second year of life, etc. Now, if as stated above, the adult mortality is assumed to be constant and equal to the mortality rate for the last two years of the immature stage, then $i_1 = i_2 = i_a$. Then

$$a - 2i_a = i_o$$

The value of "a" associated with the total observed immature survival is 7.26872. Therefore, the instantaneous mortality rate for the first year of life of the rock bass would be 3.883, or the survival rate would be about 2%, which agrees closely with McFadden's results and with what is to be expected on the basis of Slobodkin's suggestion. Allen (1951) found the survival over the first six months of the 1940 cohort of brown trout in the Horokiwi Stream to average about 1.4% over his six stations reported and range from 0.4% to 2.3%.

In general, attempts (McFadden, 1961; Jenkins, 1955; Watt, 1959; Allen, 1951; Fry and Watt, 1957; Latta, 1965) to relate size of the egg complement to the number of offspring resulting at some later time have not been successful. McFadden (1961) was able to show a positive relationship between the number of eggs produced and the mortality from the egg stage to the fingerling stage. Which is another way of saying that, regardless of the number of offspring produced, only a certain, but ill-defined, number can survive. This was borne out in his comparison of the progeny per acre to egg production per acre. In this case, the numbers of progeny referred to the number of resulting nine-month-old fingerlings.

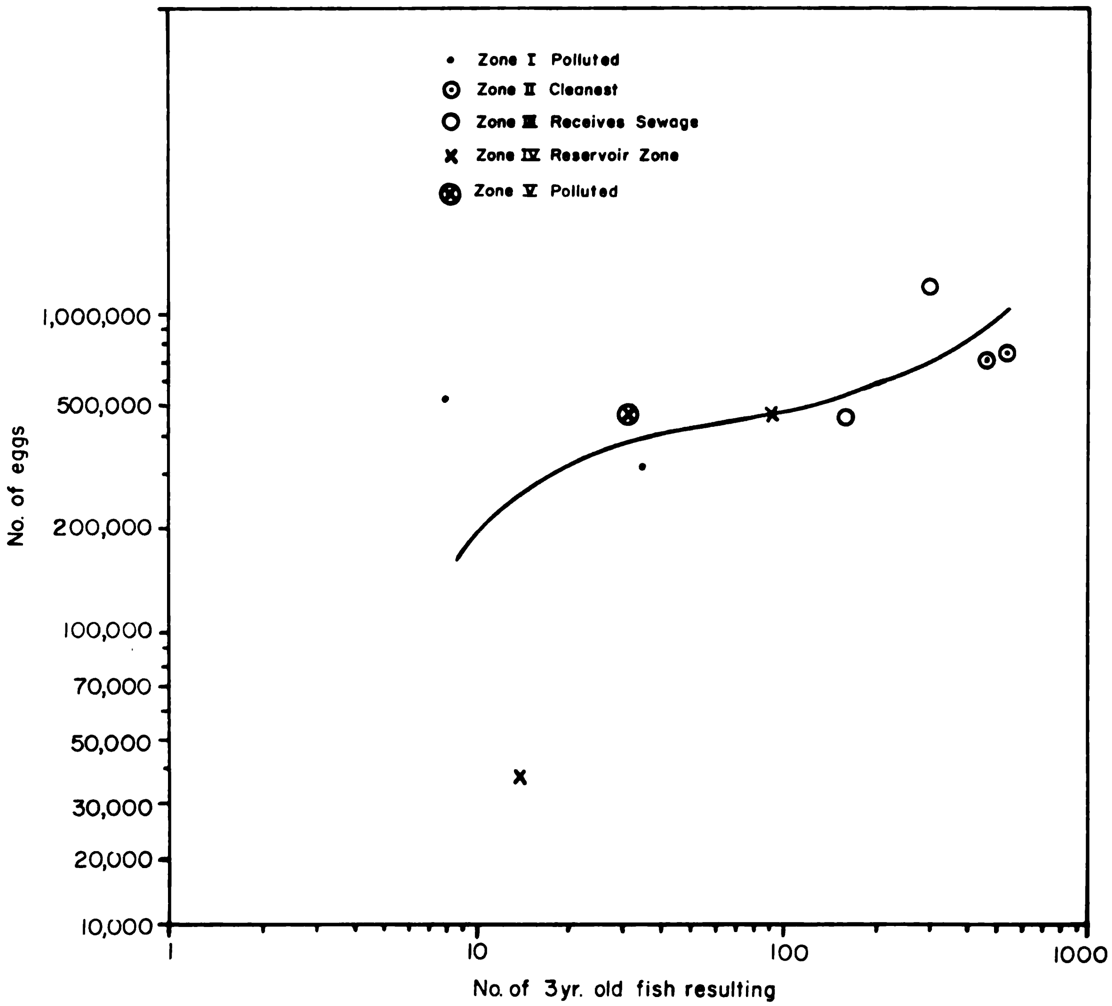
From about 20,000 eggs per acre to the largest number reported, the regression line was horizontal. Below this point, i.e., 20,000 per acre, there is reason to believe that some point exists less than which there is a positive relationship between the number of progeny and number of eggs, since the line must pass through the origin.

For the rock bass in the Red Cedar, an attempt to relate the original size of the parent stock (numbers per mile of stream) to the survival rate of the offspring to sexual maturity failed to demonstrate a recognizable relationship. The correlation coefficient, $r = +0.23$, was not significantly different from zero for nine independent pairs of observations.

The relationship between the initial number of eggs produced in the population and the resulting number of 3-year-old fish is expressed in Figure 7. There is a slight but variable positive relationship apparent in this figure. This indicates that if more eggs are produced, there is a trend toward the production of more fish of a mature age.

But of even more importance is the relatively small difference in the number of eggs produced regardless of the initial population size. That is, the numbers of eggs produced which are recorded in Figure 7 reflect the entire range of population sizes of the rock bass in the five zones in 1959 and 1961. This suggests that some regulatory device is in operation. If so, it is probably the following. As discussed above under "Fish population estimates," a characteristic of

Figure 7. The logarithmic relationship of the number of eggs produced by the rock bass populations in the Red Cedar River to the number of three-year-old fish resulting. The line was drawn by inspection.



• Zone I Polluted
Zone II Cleanest
Zone III Receives Sewage
Zone IV Reservoir Zone
Zone V Polluted
No. of eggs
1,000,000
500,000
200,000
100,000
70,000
50,000
30,000
20,000
10,000
1
10
100
1000
No. of 3yr. old fish resulting

those rock bass populations which have undergone a decline during this study is the relative preponderance of older fish. It is true that in the present study and in other studies, the older (or larger) fish produce many more eggs per individual. Thus, for the same population size, more eggs would be produced by the population which consisted of a higher proportion of old fish. Or, if the smaller of two populations had a larger proportion of older fish, it would be possible for the two populations to exhibit a similar total egg production.

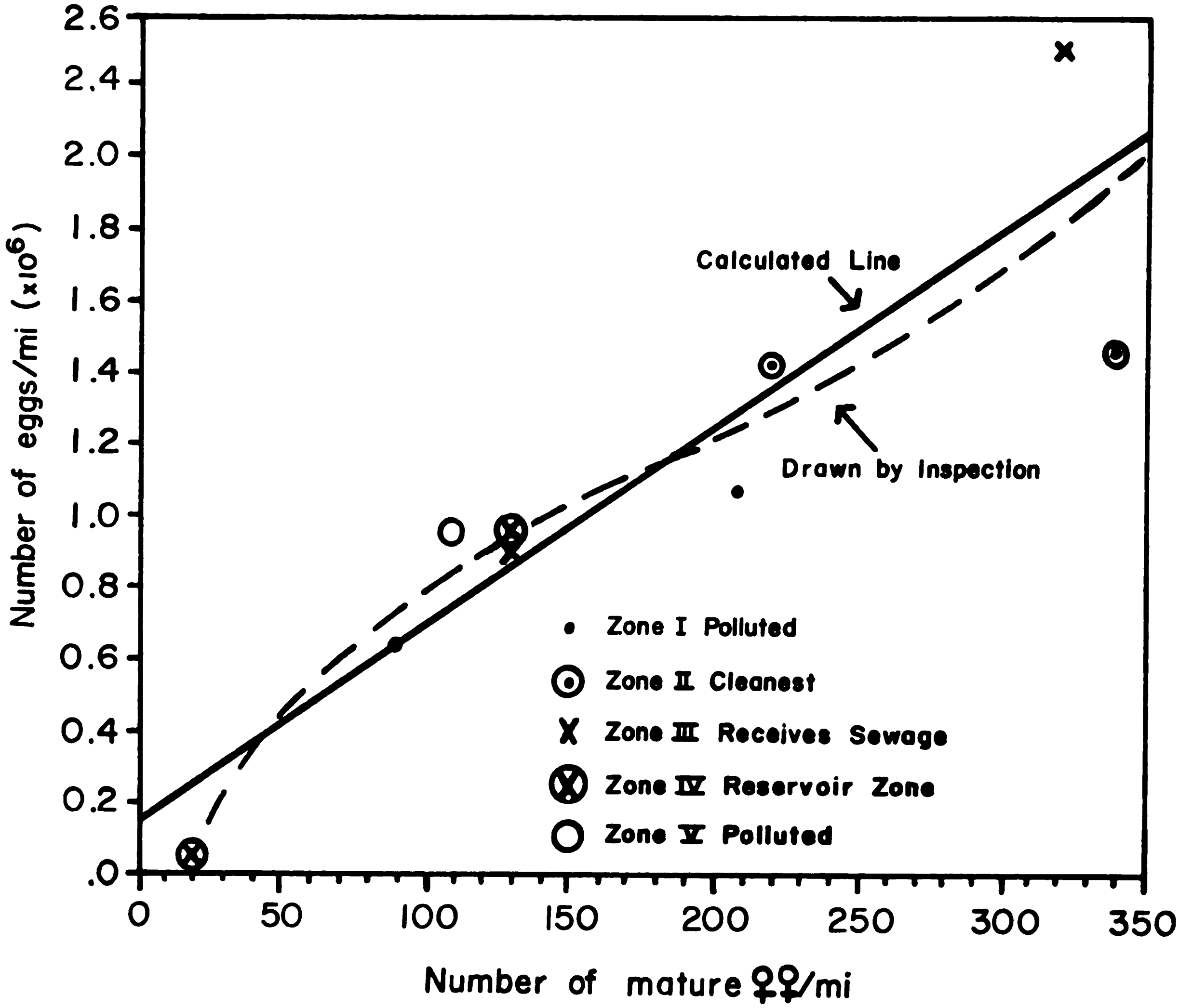
If this regulatory mechanism is operative in the present study, then the number of eggs produced per mile of stream by the five populations of rock bass should show a tendency to be similar in spite of variation in the number of mature females per mile. Figure 8 depicts this relationship for the rock bass populations in the Red Cedar River. The linear approximation (solid line) was calculated by the method of least squares, and the broken line was drawn by inspection.

The data suggest that the higher proportion of older fish in the smaller populations resulted in a tendency toward the production of the same number of eggs in spite of differences in the population sizes. But more extensive study is needed to adequately test and describe the phenomenon.

Potential Instantaneous Rates of Natural Increase

The potential instantaneous rate of natural increase was computed on an annual basis for the five populations of rock

Figure 8. The relationship between the total number of mature females per mile and the total number of eggs produced per mile for the rock bass in the Red Cedar River.


Calculated Line
Drawn by Inspection
Zone I Polluted
Zone II Cleanest
Zone III Receives Sewage
Zone IV Reservoir Zone
Zone V Polluted
Number of eggs/mi (x10^6)
Number of mature ♀♀/mi

bass in the Red Cedar River. For each of these five zones, three estimates were computed on the basis of the cohorts (1956, 1957, 1958) and two estimates were made from the vertical sampling in intensive study zones (1962 and 1964). In all cases, the age-specific fecundity, total immature mortality, and survivorship schedule for the adult females, as used in these calculations, consist of empirical observations of the rock bass populations in the Red Cedar River. The calculated values of r_a are found in Table 7.

We may now examine the effects of certain of the assumptions and observations made for the computation of r_a. For example, the schedule of fecundity could not be estimated each time the populations were estimated, since it requires killing the fish. Killing enough fish for these purposes would have a significant effect on the population. But it was noted above that the number of eggs per female is, in most studies, positively correlated with the size (or in this case, age) of the fish and continues to increase throughout the size range of the fish as the size of the fish increases. We may then look at the effect this would have on the calculations of r_a for the rock bass of the Red Cedar River. To investigate the effect of increased fecundity in the older age groups, which is strongest at a low value of r_a, we can recalculate r_a for the 1962 vertical estimate in zone V. This is among the lower values of r_a and is based on one of the more reliable population estimates (the correction factor

Table 7. Annual potential instantaneous rates of natural increase, r_a, for the rock bass in the five intensive study zones of the Red Cedar River for the cohorts of 1956, 1957, and 1958 and the vertical estimates for 1962 and 1964. (Units are numbers/head/year.)

Year	Type	Zone*				
		I	II	III	IV	V
1956	Cohort	-0.038	0.210	0.114	0.006	-0.468
1957	Cohort	-0.593	0.349	0.153	-0.120	-0.545
1958	Cohort	-0.400	0.347	0.207	-0.081	-0.197
1962	Vertical	-0.171	0.159	-0.104	-0.204	-0.288
1964	Vertical	-0.506	0.384	0.200	0.066	-0.045

* I Polluted
II Cleanest
III Receives sewage
IV Reservoir zone
V Polluted

was not used here). An alternate schedule of fecundity which results from extending that of the younger age groups linearly through the older age groups is 542; 4876; 6661; 9174; 11,000; 13,000 for ages III through VIII, respectively. These numbers represent the number of eggs per female, which are expected to give rise to females, or may be compared to 0.5 times the observations in Table 5. The value of r_a for the 1962 vertical estimate in zone V, which is reported below as -0.288, remains, with the alternate fecundity schedule, about -0.3. Thus, the effect of using the alternate fecundity schedule rather than the preferred empirical one is quite small.

Another possible source of error with regard to the fecundity schedule concerns the use of one schedule observed in zone II for the computation of r_a for all five zones. If a density-dependent mechanism for compensating for the reduced population in zone V were operating through the fecundity of the individual females, we might expect a larger number of eggs per female at a given age in zone V than in zone II. No empirical evidence is available to check this, but we may observe the effect it would have on r_a and compare this to the observed differences in r_a between the zones. For example, we might recalculate r_a for one of the estimates using twice the number of eggs per female. The differences in the values of r_a between zones II and I are of the order of about 0.5.

But such recalculation of r_a for the 1962 vertical estimate in zone II (using twice as many eggs) changes the value from 0.159 to 0.312, or a difference of about 0.15. Thus, even if twice as many eggs were produced by each female in the smaller populations, which seems to be extremely unlikely, there would be insufficient compensation to make up the observed differences in r_a. Yet it is still possible that some compensation could occur, which would tend to raise the values of zones I, IV, and V slightly.

We have already observed above that no such mechanism is operative through the juvenile mortality, since it is much higher (see Table 6) in those populations which are smaller. Thus, if there is any such effect, it is "depensatory."

The underlying distribution of r_a is obscure. But it is not likely to be normally distributed and perhaps not of the strength of an interval scale. The degree of dependence among the values for the five zones in each year (see "Methods" above), together with the immediately preceding considerations, suggests the Friedman analysis (Siegel, 1956) as an appropriate test. But it should be noted that there is a degree of dependence within the zones over the several years of the study in that a single estimate of the juvenile mortality was used for each zone. Although the juvenile mortality would be expected to vary from year to year, in the rock bass populations, only two estimates of this parameter were possible for each zone. The mean of these two estimates was used for the juvenile mortality in that zone for the calculation of the potential instantaneous rate of natural increase. Nevertheless, the observed differences may be cautiously interpreted as real differences in the populations in view of the low probability ($P < 0.01$) of chance deviations as great as these. No individual comparisons can be made with this test.

For comparative purposes, the value of r_a can be converted to the daily rate, say r_d, which is the commonly reported rate, by the simple expedient of dividing it by 365. This has been done for the rock base in the Red Cedar River and the values are assembled in Table 8. The observed values of r may be more readily compared with other values in the literature once the values of the net reproductive rate, R_o, and the mean generation time T_g, have been considered.

Net Reproduction Rate and the Mean Generation Time

The net reproduction rates, R_o, of the five ppopulations of rock bass in the Red Cedar River are arranged in Table 9 according to the zone, year, and type of estimate of r_a with which they are associated. The concept of net reproduction rate may be described as the ratio of the number of females in generation X + 1 to the number of females in generation X. Thus, the rate may be considered with respect to absolute time units only where the mean length of a generation, T_g, is known. The relationship of r, R_o, and T_g was outlined in

Table 8. Daily potential instantaneous rates of natural increase, r_d, for the rock bass in the five intensive study zones of the Red Cedar River for the cohorts of 1956, 1957, and 1958 and the vertical estimates for 1962 and 1964. (Units are numbers/head/day.)

Year	Type	Zone*				
		I	II	III	IV	V
1956	Cohort	-0.104×10^{-3}	0.575×10^{-3}	0.312×10^{-3}	0.016×10^{-3}	-1.282×10^{-3}
1957	Cohort	-1.625×10^{-3}	0.956×10^{-3}	0.419×10^{-3}	-0.329×10^{-3}	-1.493×10^{-3}
1958	Cohort	-1.096×10^{-3}	0.951×10^{-3}	0.567×10^{-3}	-0.222×10^{-3}	-0.540×10^{-3}
1962	Vertical	-0.468×10^{-3}	0.436×10^{-3}	-0.285×10^{-3}	-0.559×10^{-3}	-0.789×10^{-3}
1964	Vertical	-1.386×10^{-3}	1.052×10^{-3}	0.548×10^{-3}	0.181×10^{-3}	-0.123×10^{-3}

*
I Polluted
II Cleanest
III Receives sewage
IV Reservoir zone
V Polluted

Table 9. Net reproductive rate in numbers, R_0, for rock bass in the five intensive study zones of the Red Cedar River based on the cohorts of 1956, 1957, and 1958, and the vertical estimates of 1962 and 1964. (Units are numbers/head/generation.)

Year	Type	Zone*				
		I	II	III	IV	V
1956	Cohort	0.832	2.973	1.695	1.029	0.117
1957	Cohort	0.080	5.700	2.153	0.505	0.059
1958	Cohort	0.135	5.332	2.918	0.663	0.363
1962	Vertical	0.405	2.191	0.615	0.321	0.218
1964	Vertical	0.084	5.741	2.704	1.424	0.773

*
I Polluted
II Cleanest
III Receives sewage
IV Reservoir zone
V Polluted

"Methods" above. T_g is defined by this relationship.

The values of T_g associated with the net reproduction rates are presented in Table 10. If a comparison of the net reproduction rates is to be meaningful, it is necessary that the associated values of T_g be similar. Therefore, a Friedman analysis was done on the values in Table 11. The effect of zones was not significant ($P < 0.30$). Consequently, it was assumed that an overall mean was the best description of the mean generation time for rock bass in the Red Cedar River. This was found to be 5.029 years. Of course, if they are computed on the basis of the daily potential instantaneous rates of natural increase and the associated values of R_0 (which, incidentally, are not affected by the scale of r_a), the values of T_g and the mean of T_g are expressed in days. Thus, the mean becomes 1836 days, which simplifies the comparison of these statistics to those reported for other organisms.

R_0, T_g, and r_a

The maximum possible value of the potential instantaneous rate of natural increase, r_a, for a species is the "intrinsic rate of natural increase, r," for that species. This value was not determined in the present study and has not been determined in the past for the rock bass. But the closest approximation to that value would be the maximum observed value in the present study. Cooper (1965) and Hall (1964) indicated that natural populations of Hyalella and Daphnia, respectively,

Table 10. Mean generation length, T_g, of the rock bass in the Red Cedar River, calculated on the basis of the cohorts of 1956, 1957, and 1958 and the vertical estimates of 1962 and 1964. (Units are years.)

Year	Type	Zone*				
		I	II	III	IV	V
1956	Cohort	4.84	5.18	4.60	4.93	4.58
1957	Cohort	4.28	4.99	5.00	5.69	5.19
1958	Cohort	5.01	4.82	5.18	5.07	5.14
1962	Vertical	5.29	4.93	4.67	5.57	5.29
1964	Vertical	4.90	4.55	4.97	5.31	5.72

*
I Polluted
II Cleanest
III Receives sewage
IV Reservoir zone
V Polluted

were both turning over at about 60 to 70% of their maximum rate based on laboratory determinations of the intrinsic rate of natural increase. No comparable data are available on fish, but it is not unreasonable to assume that the rock bass in zone II are exhibiting a similar relationship.

F. E. Smith (1954) compiled the available data on the intrinsic rate of natural increase of various organisms up to the time of his publication and prepared a figure showing the relationship between r, R_O, and T (T_g in this paper) for each of the species. This permits the comparison of the present data on rock bass to the relative magnitude of these parameters for other species of organisms. Such a comparison places the rock bass among the other fairly long-lived vertebrates, which is to be expected if r_a is of the same order of magnitude as r. Thus, some slight credence is added to the observed values for rock bass.

Rock Bass and Their Environments In the Red Cedar River

Zone V

Generally speaking, this zone should be capable of sustaining a fairly large population of rock bass. Reference to Table 1 indicates that although the bottom is largely sand, there is a considerable amount of detritus, consisting mostly of fallen trees and branches, which provides adequate cover. Further cover for the developing fry is found in the extensive beds of macrophytes (Table 11) during the summer months.

Table 11. Standing crop of macrophytes in g dry wt./m^2 and percentage of area stocked by macrophytes in the five intensive study areas of the Red Cedar River on July 4, 1964.

Zone	I	II	III	IV	V
Dry weight standing crop (g/m^2)	58.61	109.04	38.42	2.77	82.88
Percent of area stocked	66	55	12	14	75

King (1964) ranks this as the highest of the five zones in total primary production (including the autotrophic aufwuchs) and second highest in the production of heterotrophic aufwuchs. So the food base is adequate for the maintenance of extensive fish populations if it is qualitatively adequate.

Yet Linton and Ball (1965) have shown that the total fish production in zone V is the lowest of the zones. The rock bass production is ranked as the second lowest. And in the present study, it ranks (along with zone I) as the lowest with respect to the potential instantaneous rate of natural increase of the rock bass populations. In fact, these values were consistently negative, which indicates that the rock bass population is incapable of sustaining itself with natural reproduction as long as the present environmental conditions are maintained. Thus, the present population is probably being supported in part by movement of fish into this area, perhaps from the tributaries or the upstream areas. However, reference to Tables 3 and 7 shows that this immigration is inadequate in zone V for maintaining the present population size. The population is rapidly decreasing to a critical level. Apparently, if the environmental conditions are not altered, the rock bass will either continue to decline until the "population" consists entirely of the fish moving into the area, or they will disappear entirely.

Of particular interest is the pattern of their decline. An inspection of Table 7 shows that the minimum value of r_a

is -0.545 for zone V. Since these are expressed on an annual basis, a table of natural logarithms shows us that the population could be declining (if the conditions were constant and the population parameters "tuned" to them) at a rate of about 42% per year. Of course, the conditions are not constant and the picture is further complicated by movement of some fish into and out of the area. But it is also obvious that, although no cataclysmic "fish kill" has occurred, the population is being lost. And this condition was reflected in the value of r_a at least as early as the 1956 cohort even though as late as 1959 and perhaps 1960, the population, as judged by its total biomass, did not appear to be in trouble. Thus, the "sublethal" conditions of stress in zone V are operating to reduce the population of rock bass in a fashion that would not be noticed in a casual pollution survey.

There are three likely causes of this decline in zone V. One of these is the runoff from the agricultural areas surrounding the stream, which is probably contributing variable concentrations of potentially lethal agricultural chemicals. Another possible cause is the sewage effluent from the small urban areas of Fowlerville and Webberville. But the most likely source of low levels of fish toxicants is the metal plating plant effluent from Fowlerville. Probably all three are affecting the fish populations to some extent.

Because the physical aspects of the environment in zone V are less suitable for rock bass than those in zone II, we can say with some certainty that the rock bass populations in zone V were not likely to have exceeded those found in zone II at the present time. If this is true, then the rate of decline of the rock bass in zone V indicates that either the source of the problem has existed for less than perhaps 15 years or that it has increased in severity within that time. It should be recalled that the personal interviews and other (admittedly scanty) records show that a substantial population of rock bass has existed here for at least several decades. Thus, it is unlikely that the domestic pollution alone is responsible for the decline, unless the community growth has been large in the last few years. And it has not in these two small communities. Therefore, it appears that an increased use of pesticides or the advent of the plating plant, or both, has been responsible for the decline.

The hypothesis that movement of fishes into an area of pollution is supporting the population there should be examined in more detail. At first glance, it may appear that this is an unlikely phenomenon, i.e., that the fish would tend to avoid this area. However, it should be recalled that one characteristic of the stream environment is its intrinsic instability. Strong seasonal changes occur with respect to temperature (Figures 2 and 3) and discharge (Figures 4 and 5). These even fluctuate considerably from day to day. For this reason, there are extensive times during the year when the area may not elicit an avoidance reaction in a wandering fish. On the contrary, with temporary alleviation of the deleterious concentrations of chemical constituents, a fish entering the area would find ample lebensraum. Even though the subsequent stress might prevent him from participating successfully in reproduction. Again, the usual form of bio-assay would fail to show any lethal environmental conditions.

Zone IV

This portion of the river is probably the least suitable for rock bass of all the five zones. Reference to Tables 1 and 11 shows that the bottom consists largely (about 80%) of sand and that the macrophytes and detritus fail to offer much cover for the fish. The river here is deeper than in the other zones and the flow rate is slower. King (1964) shows that the primary production is quite high, but the production of heterotrophic aufwuchs is low. He also shows that the in-organic sedimentation rate is exceptionally high, being a function of the flow rate, which is also reflected in the accumulation of silt reported in the present study (Table 1). All of which results from the fact that the zone is, for the most part, a reservoir backed up by the dam in Williamston (Figure 1).

The population reduction in this zone is less severe, started from a lower initial population, and is occurring at a slower rate than in zones I or V (Table 12). The latter, of course, would be expected if the cause is a polluting

Table 12. Standing crop of biomass (in lbs/acre) of rock bass in the Red Cedar River for zones I-V in the years 1959 through 1964.

Year	Zone*				
	I	II	III	IV	V
1959**	28	42	28	10	26
1960**	44	26	28	15	13
1961**	10	22	16	5	0
1962***	4	36	26	9	8
1963			No Observations		
1964***	19	65	40	4	2

* I Polluted
II Cleanest
III Receives sewage
IV Reservoir zone
V Polluted

** Linton and Ball (1965)

*** Present study

effluent near the upstream end of zone V. The total fish production was at an intermediate level up until 1961, at least, and was due largely to the presence of substantial numbers of white suckers and spotted suckers (Linton and Ball, 1965).

Zone III

This zone, according to Tables 1 and 11, appears to be rather good habitat for rock bass. There is extensive rocky bottom, considerable cover in the form of detritus, and, although this is not indicated in Table 11, there are large *Elodea* beds along part of the banks, which form excellent cover for the developing fry during the summer. Also, a short distance upstream are found heavy beds of *Valisneria* and *Saggitaria*. However, King (1964) reported that the total primary production is low on the average over the entire zone. The production of heterotrophic aufwuchs is excellent, being higher in this zone than in any of the other four. A very high production of the latter along with a low primary production seems incompatible, but is reasonable when one considers the effluent of the Williamston primary sewage treatment plant.

In addition to the usual instability of a stream, the discharge rate in zone III until a few years ago was also subject to the needs of the dam owner in the production of power for a private frozen food storage plant. The periodic flushing resulted in excessive siltation and inorganic sedimentation from the reservoir above. This was responsible in part for the low primary production rate, although the heterotrophic regime is mainly due to the allochthonous material from the sewage treatment plant.

In response to the abundant food supply, the total fish production in this zone exceeds that of any of the other zones (Linton and Ball, 1965). However, the rock bass production was of an intermediate magnitude, while the bulk of the production occurred in the northern hog suckers, white suckers, and redhorse. The total production of game fish was low. The value of r_a (Table 7) also reflected the status of the rock bass populations, being second only to the value for zone II, but appreciably lower.

Another factor should be considered in the study of any of the fish in zone III. Even a random movement of fishes around the lower end of the river would result in an accumulation of fish below the dam at Williamston, which provides an effective barrier to movement (the head is about 13 feet). Therefore, it should not be assumed that the high levels of the populations are maintained by natural reproduction alone. However, it is true that the food base is high and can sustain a large number of fish, even though the species composition is not a desirable one.

Zone II

This is the cleanest of the five zones with respect to pollution sources and is the most desirable habitat for rock bass in a physical sense. Nearly half the bottom is rocky (Table 1) and there is a profuse array of riffles and pools in the upper half of this zone. The macrophyte crop (Table 11) provides excellent cover during the summer, compensating for the rather sparse detritus cover. The gradient is quite high. This results, along with the higher discharge, in a low rate of inorganic sedimentation and relatively little silt deposition. Primary production is intermediate (King, 1964), as is heterotrophic aufwuchs production, and a large standing crop of crayfish (Vannote, 1963) provides a staple part of the diet for the rock bass.

This is the only zone which supports a large population of smallmouth bass. These together with the rock bass, contribute the largest centrarchid production to be found in the study section of the river. It is more than twice as great here as in the next lower zone. But the total fish production is lower here than in zone III. The northern hog sucker is present in fairly large numbers, although the total catostomid production is not high. From the standpoint of sport fishing, the species composition is most desirable in this zone.

The value of r_a for the rock bass in this zone is higher than for any other zone. It is consistently positive (Table 7) and shows that the population here is capable of maintaining itself and of expanding rapidly or providing a large, sustained surplus for harvesting. Table 12 shows that the standing crop of biomass was increasing up through 1964 and subsequent qualitative observations have shown that this increase has probably been maintained through 1966. The reason for this increase is not clear, although it may be tied to the rapid expansion of macrophyte stocks in this zone (King, 1964, and Vannote, 1963).

In general, the biota of this zone reflects, in addition to the physical conditions, the moderate enrichment of the chemical aspects of the environment. Presumably, if the enrichment is continued and, of greater importance, continues to increase, the biota will shift toward the preponderantly heterotrophic regime of zone III with most of the associated changes in community composition.

Zone I

On the basis of what is known about the environment in zone I, it would be expected that the fish production (including rock bass) would be quite high. The nutrient levels are high, as shown by the levels of total elementary phosphorus (Vannote, 1963) and there are riffles and pools in the upper end, although the high gradient is masked in the lower end by the presence of the dam below this zone. The discharge is high. Extensive cover for the rock bass and other fish is provided by the detritus and macrophyte stock. Reference to the discussion of zone III above would indicate that the production in the biota should respond to the strong enrichment from the sewage effluent (much of it raw) of the towns of

Okemos and East Lansing, including the Michigan State University campus.

But King (1964) states that both total primary production and heterotrophic aufwuchs production are the lowest here of any of the five zones. Linton and Ball (1965) state that total fish production is lower here than in any of the other zones except zone V. Up through 1961, the rock bass appeared to be mildly successful if judged on the basis of biomass. However, r_a for the rock bass was negative for some time prior to that, as it was in zone V. A similar precipitous drop in the biomass occurred in zone I in the subsequent years. An apparent recovery of the population occurred in 1964 (accompanied by a strongly negative r_a), but this appears to have been temporary and perhaps partly a fluke of the estimating procedure, since recent attempts to capture fish in this area indicate that the population has probably dropped to levels similar to those in 1962. It is possible that exceptionally good spawning conditions (for this area) occurred in 1962 or 1963, but it is likely that the increase in biomass resulted from the movement of larger fish into the zone, perhaps from zone II immediately upstream, and that these fish have now died or moved out again.

In general, the biota is failing to respond to the abundant nutrients and adequate physical characteristics. The reason is obscure, but it may be due to the cumulative effects of inhibiting factors, such as pesticides or other household products entering along with the sewage effluents. Or it may be that the nutrients themselves are present at levels that are toxic to various components of the biota. Again, the usual techniques of evaluating pollution have failed. A fish kill which occurred below this zone in the spring of 1965 was accompanied and followed by an extensive pollution survey, but the cause of even this sudden and obvious kill was not effectively pinpointed. Yet, the fish and other organisms in this part of the river are disappearing at a rate that is noticeable, except for infrequent and incomplete "fish kills," only through extensive and intensive study. A great deal more must be learned about the extent of effect and mode of operation of complex, low-level pollutants in the aquatic environment.

On The Use Of r_a In Fisheries Management

For a population, however small, the Ivlev production (Ivlev, 1945) is a positive quantity except in a few trivial cases. This is true in an intuitive sense as well as mathematical. That is, if the individuals are gaining any weight at all, even if there is no recruitment and all of the animals die a very short time, say dt, later, there has been some production. Only if whatever organisms were present at the beginning of this time were losing weight or remaining steady, and if recruitment were inadequate to compensate for this, would the Ivlev production be negative. It is the surplus net production we try to harvest in a fishery (Ricker, 1958). However, even from this standpoint, it is possible for the biomass to be increasing when the population is decreasing, or it is possible for the standing crop of biomass to remain high for some time after the potential instantaneous rate of natural increase in numbers, which is a measure of the ability of the population to maintain itself, has become negative. Thus, the value of r_a can be used to predict these declines before they occur. It is this characteristic which makes it potentially useful in the management of fisheries.

First, it should be noted that, if r_a is negative, we have no fishery resource to manage. We may then only manage the environment in order to restore the fishery. When r_a is positive, management may include direct operations on the fish populations in an effort to regulate and harvest the surplus. These methods and techniques have been discussed at great length by many authors (Ricker, 1958; Rousefell and Everhart, 1953; and many others) and need not be pursued further here. Rather, the interpretation and meaning of r_a should be explored.

We may look on r_a as an index of the "surplus numerical productivity" if the fecundity and mortality schedules remain constant and the age structure does not change. But these assumptions will probably never be met in practice. This is fortunate in fisheries management, because, were it not for these assumptions and the possibility that these schedules can be altered, such a discussion as this one would be entirely academic. That is, the population would grow or go to extinction regardless of our efforts. However, by manipulation of these quantities, either directly or indirectly through alteration of the environment, we may manipulate the future of the fish populations, or, to put it another way, we may manipulate r_a itself.

There are two major factors to consider in the manipulation of a fish population in order to maximize r_a. One of these is the fecundity schedule. An attempt to reduce the fecundity is obviously the wrong approach to increasing the fish population. We may neglect that possibility (unless we would like to eradicate a fish population). If, as indicated by Cooper (1965), natural populations respond under increased food by greater fecundity, then r_a could possibly be increased by reducing other forms of mortality in their food organisms. However, it may be recalled that most forms of fecundity alteration have a relatively small effect when compared with the differences observed in natural populations of rock bass (see the discussion under "Potential Instantaneous Rates of Natural Increase" above). It is probably true that a physiological maximum number of eggs can be produced by a fish of a given size. This suggests a way to increase fecundity; make the fish larger at a given age, which, alone, would have a relatively small effect on r_a. But recall that the first two or three periods of egg production account for the largest share of the value of r_a. Thus, if an increased size, or artificial stimulation of the gonads, would permit the fish to spawn first at an earlier age, a considerable increase in r_a would result (for a discussion of this, see Birch, 1948). This approach, if feasible, is probably the only means of appreciably increasing r_a through the fecundity schedule. As discussed above, altering the fecundity of the older members of the population has almost no effect on the magnitude of r_a.

Related to this phenomenon is the fact that alteration of the schedule of mortality of the older members of the population has a negligible effect on r_a. This, again, is fortunate in the management of fisheries, since it is the older (and hence larger) fish which are the desirable elements in most fisheries. In fact, the nearly complete removal of these older fish will probably have a rather small effect on the potential instantaneous rate of natural increase. This must be evaluated on the basis of individual species, since behavioral traits, such as older fish dominating spawning sites, would have an effect.

As pointed out above under the appropriate heading, the rates of mortality in the immature fish in most populations are large. It is here that the greatest reduction in r_a lies and, consequently, here where the greatest potential lies in the management of a fish population for maximum yield. It is also true that it is very difficult to work with this stage in the life of a fish. Indeed, it is extremely difficult to estimate their numbers, or, in some cases, even to locate them. These difficulties are reduced, however, in the case of anadromous salmonids. Weirs can be a very effective tool in estimating their numbers, growth rates, etc. For this reason, the uncovering of the sources and controls of mortality in the early life of fishes may be the most important and potentially most fruitful task in fisheries research today.

It is of interest to consider the prospects of the fish population with respect to time under various values of r_a. Quite obviously, if it is positive and large, the question is one of harvest. But if the value is negative, then we may ask how rapidly the decline will occur. Furthermore, we might ask how rapidly the population will go to extinction. Treating the latter question first, it should be stated that, mathematically, the population would never go to extinction, since a constant <u>proportion</u> of the population would be lost in each time interval. In a practical sense, when the last whole individual was lost, the condition would be met. For example, starting with a population of 1000 fish and a constant r_a of -0.5, we would experience a decrease of about 39% per year, or one individual would be left after 23.03 years. Presumably, this individual would die in the ensuing time period. However, it is also true that, with this r_a, we could expect to see the population size be only about 100 at the end of the first five years.

But this should not be too alarming. If the source of the excessive mortality is alleviated, or eliminated, it is true that most fish species are capable of restoring the original population in a relatively short period of time, even though the population becomes quite small before the recovery begins. The empirical data on the rock bass show that the potential instantaneous rate of natural increase is probably sensitive to an impending decline in the standing crop at least one mean generation time prior to the actual decline. In species such as the lake trout, which have a longer mean generation time, the biologist would have the warning in hand at least five years before any critical level of the population was reached. In view of the rates of decline shown above, he would likely have ten or more years before a critical population level was reached. Of course, the yield to the commercial fishery would be noticeably decreased sooner than this.

It is important to note that fluctuations in the value of r_a will occur for any species. It is also true that the variance of r_a is probably characteristically different for different species. Hence, an interpretation of observations of this statistic can be expected to improve if it is calculated on a continuing basis over a longer period of time for a given population.

The biologist should note that the horizontal life table, if based on similar observations of the numbers of fish in each age category, will yield more reliable results, since it is not necessary to assume a constant year class strength in the estimation of the mortality schedule.

Another important point to consider in the application of this statistic in practical fisheries management is that it is necessary to estimate the numbers of fish in the earliest reproductive age in order to get a valid estimate of r_a. But, in some well-managed fisheries, this age-class does not appear in the landed catch. Therefore, it will be necessary to maintain a continuing experimental fishery to follow changes in this portion of the age structure.

In view of the relatively little additional information required for its computation beyond what constitutes an average fish survey, it is proposed that the calculation of r_a be made a routine adjunct in the management of important fisheries.

Pollution Study Involving r_a

One aspect of nearly all fresh-water environments in this country is the presence of pollutants. Yet the evaluation of the effects of chronic low-level pollution on the biota is one of the most vexing problems facing the aquatic biologist today. Indeed, it is extremely difficult to show that such pollution has any damaging effect on the organisms.

"Damage to the organisms" can mean a number of different things. It may be said that an organism has been damaged when its physiological mechanisms have been upset to the extent that it is more vulnerable to its predators. Or perhaps when it is rendered more susceptible to diseases of various kinds. Or even when it is caused to suffer pain. But these interpretations are outside the scope of this paper. For the present purposes, "damage to the organisms" is intended to mean a reduction in the likelihood of maintenance of the populations regardless of the means by which it is effected. More specifically, the present interest is in the damage caused by man.

When toxic materials are released into an aquatic environment in sufficient concentration to kill all or a large proportion of the organisms present, the damage is obvious. It is not obvious when the addition of a pollutant (organic or inorganic, nutritious or toxic) shifts the likelihood of survival of a desirable population of organisms downward and that of an undesirable population upward. This may happen when the preferred food of a specific age-class of the desirable species is eliminated. Or when the normal spawning sites of a fish population are altered. Or any of a number of other possibilities.

Although it is rarely stated, the prevention or abatement of pollution is intended to maintain or create an environment which will support a desirable assemblage of organisms or to reduce or eliminate a public health hazard. If the environment we are creating or maintaining is suitable for the desired populations, then the populations should be able to sustain themselves by natural reproduction. Therefore, it seems entirely appropriate that our evaluation of the success of our pollution abatement or pollution prevention programs should include a measure of the ability of the populations to do just that. The potential instantaneous rate of natural increase, r_a, is an approach to the solution of this problem.

In order to properly apply and interpret the values of r_a, it will be necessary to establish the baseline characteristics of its mean and variance for the species concerned. This will entail the repeated calculation of r_a for populations which are living under conditions of little or no artificial stress, i.e., those which are occupying an environment in which they have been quite successful for an extended period of time and in which no new stress has been imposed in the recent past. It is essential that this process be carried out for each species which is to be employed.

Although this paper deals with the application of the method in the case of one fish species, it should be pointed out that not only can other fish species be employed, but many other taxa should serve as well. Fish are well-suited for this study since they are present in the same form the year around, spawn only once per year (most species), can be readily aged, and are large enough to handle easily. Furthermore, the methods for working with fish populations have been developed extensively. But it is true that fish do not live in all aquatic environments. As discussed above, the intrinsic rates of natural increase have been estimated for insects and microcrustaceans (see F. E. Smith, 1954) as well as vertebrates. But in general, one should consider the length of the life span of the organisms selected, since the effects of a short-term exposure will be reflected quickly in short-lived organisms, whereas the populations of longer-lived individuals will probably not display as large a natural variability. For example, a few days of relatively high turbidity will have an adverse effect on the primary producers in an aufwuchs community, which in turn may have a pronounced effect on the associated microfauna. Whereas the fish in the same environment may be relatively unaffected.

It should be recalled that a reduction in r_a is non-specific. It can reflect any sort of damage to the population. Hence, certain restrictions must be placed on its interpretation. It would not be possible to state on the basis of r_a alone that a specific component of a mixed pollutant (or mixture of pollutants from various sources) was responsible for the damage to the populations without further testing of the effects of the individual components. And it would not be possible to state that the poor reproductive capabilities of a population are due to a human activity unless it is known that the organisms can sustain themselves in that environment without that human activity. For example, the lack of a suitable physical environment may preclude a positive value for r_a even in the absence of human influence. But in a case where the organism is known to have been successful, the likelihood of a sudden change is small without some form of human interference. In this case, r_a should reflect the damage.

The value of r_a was discussed above with respect to the rock bass in a polluted warm-water stream. The calculation of r_a may also lead to a better understanding of the dynamics of the trout populations. Indeed, the smaller variance which is probably associated with the stability of the cold-water streams may make its interpretation easier. For the same reason, lake fish populations should be studied. Similarly, long-term studies should be initiated in order to determine the changes associated with natural eutrophication of our waters.

SUMMARY

The dynamics of five rock bass populations in a warm-water stream were investigated. Total and age-class estimates of population numbers were obtained in five sample series over a period of six years. Collections were made with an electrofishing technique and the populations were estimated by the Bailey modification of the Petersen method. The age-specific fecundity was estimated by the gravimetric method and the sex ratio was determined by gross inspection of the gonads.

Differences were noted in the age distributions of the rock bass populations in the five zones of the Red Cedar River. In two of the zones, rapid population declines occurred during the course of the study. The populations in both of these zones were characterized, prior to the decline, by larger proportions of older fish than that observed in an increasing population. The population remained relatively stable in one of the zones.

The fecundity of the rock bass was somewhat higher in the Red Cedar River than in comparable studies. The number of eggs produced per female increased with age at least through age VI, then declined, although wide confidence limits associated with the age VII fish indicate a possibility that the

decline is due to chance in the sampling. The population was estimated to consist of 48.2% females with 95% confidence limits of 0.37 to 0.60.

Survival of the immature rock bass from the ovarian egg cohort to age III varied widely between the zones. It was poorest in the zones in which a decline occurred and highest in the zone where the population was increasing, ranging from less than 0.005% to 0.07%. There was no relationship between the numerical size of the original parent stock and the survival of the offspring to age III, but the data suggested that a larger cohort of eggs led to a larger number of offspring three years later. The smaller populations which were declining, and which had a larger proportion of older fish, showed a tendency to produce more eggs per female on the average due to the age-specific nature of the fecundity schedule.

The potential instantaneous rate of natural increase, r_a, was calculated for the 1956, 1957, and 1958 cohorts and for the 1962 and 1964 vertical age distributions for each of the zones. A difference between the zones was demonstrated. In zones I and V, the most polluted areas of the river, r_a was consistently negative, indicating the cause of the decline probably existed for several years prior to the declines. The net reproduction rates, R_0, and mean generation times, T_g, were calculated for each of the estimates of r_a. The mean generation time was consistent and displayed a mean of about five years.

The net reproduction rate, R_o, was less than unity for all of the estimates in zones I and V, ranging from 0.1 to 0.8, and was positive in every case for zone II, the least polluted zone, ranging from 2.2 to 5.7. The values of r, R_o, and T_g for zone II were compared with similar estimates for other organisms and were found to be consistent with expectations. The values are discussed with respect to environmental observations and it is concluded that the differences in success of the rock bass populations can probably be attributed to pollutants.

The use of r_a is related to potential fisheries management applications and to possible application in the detection of chronic, low-level pollution. It is proposed that the calculation of r_a be made a routine adjunct to surveys in both fields.

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APPENDICES

APPENDIX A

Mean weekly temperature in ^{o}F of the Red Cedar River at 6:00 PM and 6:00 AM at the Michigan State University river farm, Okemos, Michigan, for the years 1957 through 1964.

Week of Year	1957 6:00 PM Temp.(°F)	1957 6:00 AM Temp.(°F)	1958 6:00 PM Temp.(°F)	1958 6:00 AM Temp.(°F)
9			31.0	31.0
10			34.6	33.6
11			35.9	35.1
12			38.5	38.0
13			42.3	39.7
14			46.6	44.4
15			45.1	43.7
16			56.7	51.3
17			53.2	50.3
18			53.9	50.3
19			56.6	51.9
20			66.1	60.6
21			63.9	59.3
22			65.1	59.3
23			65.6	61.1
24			66.0	62.9
25				
26	67.5	65.0	65.0	60.0
27	69.1	66.0	71.1	68.3
28	66.6	65.3	69.1	67.7
29	70.0	67.0	69.7	67.6
30	68.1	66.6	71.6	66.3
31	73.3	69.9	70.9	66.6
32	73.3	67.7	73.1	68.1
33	70.7	65.7	74.0	70.3
34	68.4	63.7	66.9	63.7
35	65.3	62.3	68.3	63.3
36	66.4	63.1	66.3	63.6
37	62.6	59.3	61.0	58.1
38	63.3	60.4	62.7	60.1
39	56.3	54.4	63.9	60.3
40	53.0	49.1		
41	51.4	48.9	56.0	54.4
42	50.3	47.7	55.4	52.4
43	47.7	46.6		
44	43.1	41.4	46.8	43.8
45	43.3	42.6	44.9	42.6
46	40.3	38.9	44.9	42.7
47			45.3	44.9
48			34.7	34.3
49	35.5	35.0		

	1959		1960	
Week of Year	6:00 PM Temp.(°F)	6:00 AM Temp.(°F)	6:00 PM Temp.(°F)	6:00 AM Temp.(°F)
9				
10				
11				
12				
13	39.4	38.6		
14				
15				
16			49.9	48.9
17				
18				
19	50.0	50.2	59.6	55.4
20	51.4	51.6	48.9	47.9
21			62.7	58.3
22	71.0	68.5	62.7	60.0
23	68.9	65.4	66.9	62.9
24	73.4	69.6	69.3	64.0
25	68.1	62.3	63.6	63.0
26	71.9	66.6	67.0	64.4
27	76.0	70.0	69.0	66.6
28	75.4	68.6		
29	73.7	67.9	73.3	69.7
30	72.9	68.7	73.4	68.0
31	72.9	68.9	76.4	71.4
32	69.9	66.9	72.1	68.1
33	71.7	68.0	71.1	67.1
34	73.6	70.7	72.4	67.9
35	77.4	73.9		
36	71.0	68.4	74.6	71.0
37	68.9	66.3	73.3	70.4
38	63.6	60.7	63.4	60.4
39	51.5	53.3	64.4	62.7
40	61.4	59.6	61.4	60.1
41	57.6	57.4	56.1	53.7
42	49.5	49.5	57.7	54.9
43	50.3	50.7		
44	47.7	47.7		
45	46.9	47.0		
46	43.0	43.1	44.7	43.7
47	39.5	38.5	40.1	39.0
48	40.6	40.6	41.7	39.3
49	38.3	37.8	39.3	38.6

Week of Year	1961 6:00 PM Temp.(°F)	1961 6:00 AM Temp.(°F)	1962 6:00 PM Temp.(°F)	1962 6:00 AM Temp.(°F)
9				
10				
11			33.0	33.0
12			35.3	35.1
13	42.5	41.5	40.0	39.4
14	42.0	39.4	42.0	42.0
15	44.7	42.1		
16	47.1	45.3	45.3	43.3
17			60.7	55.0
18	51.9	48.7	61.9	59.3
19			59.7	57.0
20	64.1	60.6	71.7	66.3
21	60.0	55.7		
22	63.6	59.1	69.0	63.9
23			69.9	65.0
24			69.7	65.6
25	64.3	61.5	72.6	68.4
26	72.6	65.6		
27	73.3	68.9	72.6	66.6
28	71.9	67.1	74.7	70.4
29	74.7	69.3	72.7	68.0
30	74.8	69.5	69.2	64.8
31				
32			72.6	66.8
33			69.6	64.6
34	66.0	63.6	72.9	67.9
35	71.0	68.7	74.3	70.0
36	72.7	70.6		
37	70.1	69.0	67.2	63.8
38	65.7	63.1		
39	60.0	58.3	55.8	54.4
40				
41	59.4	57.3	61.0	58.4
42	53.0	51.8		
43	50.3	49.1		
44			44.3	42.6
45	42.9	41.3		
46	44.1	43.1	41.3	40.0
47				
48	37.2	35.8		
49	38.0	37.4	36.1	35.3

Week of Year	1963 6:00 PM Temp.(^{o}F)	1963 6:00 AM Temp.(^{o}F)	1964 6:00 PM Temp.(^{o}F)	1964 6:00 AM Temp.(^{o}F)
9				
10			43.3	41.3
11				
12			47.4	43.3
13	52.5	48.5	50.6	47.0
14	53.7	50.0		
15	49.4	45.9	61.5	53.5
16	54.7	51.3	63.9	62.1
17	52.4	48.1	49.6	47.4
18	56.4	52.4	58.0	54.3
19	63.0	59.3	68.7	63.1
20	59.0	55.1	59.7	56.7
21	58.7	54.6	70.1	63.0
22	64.9	59.7	69.6	65.0
23	76.6	70.8	67.0	58.7
24	65.9	63.9	75.6	67.4
25	68.4	63.3	76.9	69.3
26	75.0	68.0	77.9	71.6
27	77.9	70.3	82.9	75.0
28	71.4	65.4	77.1	70.0
29	73.1	69.1	74.9	68.9
30	75.9	70.1	85.9	77.3
31	74.0	70.4		
32	74.7	69.3	81.1	74.7
33	67.1	64.3	64.5	59.0
34	69.3	64.1	67.3	62.6
35	67.4	63.7	72.3	64.7
36	63.3	59.9	71.6	66.1
37	63.0	60.0	69.5	65.6
38	63.3	59.7	61.7	58.7
39	59.7	56.7	64.0	61.1
40	56.7	54.7		
41	57.7	56.0	43.0	41.3
42	54.9	53.0	45.3	41.1
43	60.0	58.0		
44	50.1	49.9		
45	46.4	45.0	49.1	46.1
46	44.1	43.0	49.1	46.6
47	48.1	47.3		
48				
49	33.4	32.8		

APPENDIX B

Mean monthly discharge of the Red Cedar River at the Farm Lane bridge gauging station for the years 1957 through 1964 (data furnished by the United States Geological Survey Field Office, Lansing, Michigan).

	1957 (cfs)	1958 (cfs)	1959 (cfs)	1960 (cfs)
January	78.4	139.0	47.3	377.0
February	188.0	150.0	116.0	349.0
March	201.0	299.0	915.0	442.0
April	355.0	170.0	527.0	795.0
May	483.0	78.3	202.0	293.0
June	135.0	61.9	99.7	257.0
July	534.0	131.0	72.4	65.6
August	60.5	51.8	128.0	50.3
September	49.4	33.5	93.3	38.4
October	77.4	47.0	471.0	42.1
November	156.0	59.3	420.0	56.5
December	277.0	48.5	358.0	41.8

	1961 (cfs)	1962 (cfs)	1963 (cfs)	1964 (cfs)
January	34.9	86.6	31.8	31.4
February	57.8	110.0	31.2	34.6
March	192.0	763.0	451.0	65.3
April	380.0	218.0	140.0	114.0
May	195.0	165.0	177.0	122.0
June	75.2	90.2	148.0	36.8
July	37.1	53.4	31.9	21.4
August	72.3	28.2	20.7	20.9
September	95.0	41.6	18.5	16.7
October	66.1	48.6	15.9	17.8
November	102.0	50.6	21.2	32.9
December	109.0	42.1	20.5	46.0

Appendix C

Results of selected interviews with some earlier Red Cedar River fishermen concerning composition of sport catch. Interviews conducted by author in February and March of 1966.

Contributor*	Approximate time period	Type of fish							
		Carp	Suckers	Trout	Pike	Bass	Rock bass	"Sunfish"	Perch
a.	1900-1920		X		X		X	X	
b.	1906-1910		X		X				
c.	1914-1916			X					
d.	1920's	X							
e.	1930-1950	X			X	X	X	X	X
f.	1940-1945	X				X	X		

*a. Vern Hodge, Webberville, Mich. Fished occasionally, recalls that spearing was common.

b. Carl Glover, Fowlerville, Mich. Lived on West Branch of the Red Cedar River at that time, fished frequently using nets and "gunny sacks."

c. George Churchill, Lansing, Mich. Caught brook trout in Sycamore Creek, usually near Mount Hope Cemetery, and in Coon Creek.

d. Alex Dieterli, Fowlerville, Mich. Fished frequently, usually with spear, in vicinity of Fowlerville.

e. Amil (Tiny) Wallenmaier, Fowlerville, Mich. Fished at and above Fowlerville, sometimes with spear.

f. Robert Fortney, Sr., Paris, Mich. With Fish Division of the Michigan Department of Conversation at that time. Fished river for sport frequently, usually by casting. Recalls that rock bass were widespread and common in the river.