Annual production by brook trout in Lawrence Creek during eleven successive years. No. 82 1974

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ANNUAL PRODUCTION BY BROOK TROUT IN LAWRENCE CREEK DURING ELEVEN SUCCESSIVE YEARS

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ABSTRACT

Annual production by the wild brook trout *(Salvelinus fontinalis)* population in Lawrence Creek, Wisconsin was estimated for 11 consecutive years (1960-70). Production annually by all age groups combined varied only 20 percent (436-526 kg) and averaged 478 kg (11.7 g/m^2). Much greater annual variations in annual production occurred within each of the age groups (119 percent range for age 0, 97 percent for age I, and 700 percent for age II) and in all four of the study sections (95 percent in Section A, 44 percent in Section B, 69 percent in Section C, and 176 percent in Section D).

Annual production was not dependent on the biomass of the population in April, when the 6-month period of most rapid growth began, but efficiency of annual production (P:B ratios) was significantly correlated with April biomass (r=-0.943**). Production was homeostatically regulated through compensatory adjustments in growth rates and survival rates of varying regulatory importance among age groups.

Within study sections, annual production was highest in Section A, the most upstream section, where it averaged 18.8 g/m^2, exceeded 20 g/m^2 during the last 4 years and reached a peak of 25.8 g/m^2 in 1969. High production in this section was attributed to physical alterations in the trout habitat resulting from a management program of "stream improvement" carried out in 1964 to increase pool area and streambank hiding cover for trout.

Despite the upward trend in production in developed Section A, streamwide production remained quite stable because of concurrent downward trends in production in Sections C & D. Comparison of annual production trends in improved Section A to annual production trends in the three unimproved sections revealed a high degree of intersectional dependence not previously realized from numerous analyses of standing stock data.

A simplistic production model was developed to tie together some of the compensatory adjustments in growth and survival among age groups 0-III that acted in synchrony each year to maintain production at a consistent level for the population as a whole.

This study of annual production and identification of some of the processes that regulate it provided insights into the dynamics of this brook trout population that no other population parameter provided. Such insights can be valuable additions to the storehouse of information that is needed to more effectively manage fish populations, whether that management is directed at optimizing production of fish for human consumption or improving the quality of sport fishing.

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CONTENTS

INTRODUCTION

Efforts by fishery biologists to assemble useful models of the dynamics of fish populations are analogous, I suggest, to the task of assembling an unusual puzzle—a puzzle having an unknown number of pieces, the shapes of which keep changing.

Some pieces of such a "population puzzle" may be relatively easy to acquire and have relatively constant shapes. Other pieces may also be easy to acquire but their places (functions) in the population puzzle are not apparent. Still others may be so difficult to obtain or so complex in shape that only approximate substitutes can be used. Finally, there will always be those missing pieces which cannot be found because no technology is available to collect them, or their absence is not even recognized. Hopefully, however, enough of the key pieces can be assembled to attain the fundamental objective of fishery science, the rational management of fish populations.

Few pieces of a fish population model provide as much biological insight as the one labelled "production," the total weight of body tissue produced by a population of fish during a given interval of time, including growth by fish that died during the time interval.

LeCren (1969) has stated that such a production estimate is probably "the best epitome of the population dynamics and environmental performance" of a species. This strong declaration is based on the fact that production represents the cumulative interaction (product) of two of the most important dynamic features of a fish population, namely, the number of fish and the rate at which they are growing or, occasionally, losing weight. Consequently, all environmental factors which influence either or both of these parameters also influence production. (An excellent diagrammatic summary of interrelationships between fish production and other components of an aquatic trophic system is illustrated in Appendix Figure 1 and is taken from LeCren 1972.)

Interest of fishery biologists in production has increased steadily during the past decade and two books about the methods and results of production studies have been published recently (Gerking 1967; Ricker 1968). Much of this interest, however, remains largely theoretical. Field studies of fish production are still few in number in comparison to studies of standing stocks or yields. Moreover, among the production studies of fish populations that have been published, two deficiencies in methodology are common. Production has usually been estimated for only one or two years, and among production studies of fish in lotic environments, only small portions of each stream or river have usually been studied. In those studies of short-term duration, it must be generally assumed by the investigator that all year classes in the population were initially of equal strength and were subsequently subject to similar rates of mortality and growth. Extrapolations of production based on sampling only a small portion of a body of water also constitute a potentially serious bias. Numerous studies of salmonid populations in streams, for example, have demonstrated great within-stream variability in population densities and growth rates—the two key components of production.

Yet, despite these inherent weaknesses, the resulting estimates of production have provided insights into the dynamics of fish populations that were not evident without them. And, hopefully, as the emphasis on production measurements continues to increase, weaknesses in sampling techniques will also become less frequent and production information will be more useful in making management decisions.

Both of the potentially serious biases were avoided in the study discussed in this paper. Population statistics of age structure, growth, and biomass of brook trout *(Salvelinus fontinalis)* were based on electrofishing collections throughout the 5.4 kilometers of Lawrence Creek three times yearly for 11 successive years. Additional age-specific growth data were also collected monthly in two 300-meter stretches of stream during 2 years.

Basic emphases in this paper are focused on annual increments of production by each age group in the population, total production by the population as a whole, and the population dynamics of the production process. These production estimates have been accumulated as part of other long-term studies at Lawrence Creek. Three of my published reports of these studies contain detailed information on production (Hunt 1966; Hunt 1969; and Hunt 1971). The 1966 paper focused on the dynamics of the production process itself based on monthly estimates for 60 consecutive months covering the lifespans of three year classes. Production was also related to angler harvest during the 60-month period. In the latter two papers, I used production information primarily as a tool to assist in evaluating responses of the brook trout population to habitat improvement.

Together, these three papers include estimates of annual production for 8 consecutive years (1960-67). I have attempted now in this paper to focus on some broader implications of these 8 annual estimates, previously considered in various shorter combinations of years, and I have added to the series 3 more years of unpublished production information.

The resulting series of eleven consecutive estimates of annual production is one of the longest and most reliable published records covering all age groups in a wild fish population. The series also spans lifetime production by eight generations of brook trout (the 1960-67 year classes) and for 5 of these year classes comparative data on total angler harvest will also be discussed.

METHODS

In two previous papers (Hunt 1966; Hunt 1969), I described in detail the field methods and calculation procedures used to determine annual production by each age group of brook trout in Lawrence Creek. Portions of those descriptions are partially reiterated here.

Production was calculated as the product of the average biomass and the instantaneous rate of growth (g) for each age group each month in each of four study sections. Average monthly biomass represented the arithmetic mean of biomass at the beginning and end of each month. Biomass at the beginning of the month represented the product of the number of trout of each age and the average weight of an individual fish of that age.

Population size at the beginning of each month (beyond the sixth month of life) was determined graphically by plotting straight line interpolations between three fixed "point estimates" representing standing stocks of trout present at the time of the annual early April, mid-June, and mid-September population estimates. Population estimate data, based on two electrofishing runs through the entire stream, were summarized by age group and inch-group within each of the four study sections. Sections ranged in length from 1.13 to 1.72 km, in average width from 4.33 to 10.06 m, and in area from 0.75 to 1.27 ha (Table 1). There were no artificial or natural barriers to prevent fish from moving freely throughout the stream.

Age structure calculations were based on frequency distributions of marked, known-age trout within each 2.5 mm (inch) group. As a part of each June population estimate, permanent marks were applied to all young-of-year trout captured on both electrofishing runs. Markings designated the year of hatching and section of capture. Unmarked young-of-year trout collected during September population estimates that had escaped capture in June were also marked. As a result of these biannual marking operations, at least 75 percent of the 1960-67 year classes consisted of marked individuals by the end of their tenth month of life. Electrofishing efficiencies on both marking and recapture runs were normally so high in Lawrence Creek that 95 percent confidence limits for population estimates usually differed by less than 5 percent from the point estimates for numbers of age I and age II trout present within each section, by less than 5 percent for the numbers of age 0 trout present in sections A and B, and by less than 10 percent for the numbers of age 0 trout present in sections C and D. Additional descriptions of the routine population estimate procedures used at Lawrence Creek have been published by McFadden (1961) and Hunt, Brynildson and McFadden (1962).

Age-specific growth data were collected monthly during 1963 and 1966. An electrofishing unit was used to collect monthly samples of trout from the same 300-meter stretches of Sections A and B. Length-weight data were taken in the field from marked, known-age trout only, sex was recorded when possible, and the trout were released. Age-specific mean lengths and weights were plotted on calendar paper for each month. Lengths and weights as of the first day of each month were read from straight line plots connecting sampling points within the month and length-weight estimates for the previous month.

Growth curves for 1963 were used as guides to derive growth curves for comparable age groups in 1961-62 when only three point estimates of growth were obtained annually (each April, June and September). The 1966 curves were similarily used to estimate monthly growth rates during 1964-70.

Estimates of population size and growth of age 0 brook trout required additional calculations for the first 5 months of life since this age group was not included in population estimates until June. Year class density at emergence was based on an estimate of egg production by the parent spawning stock and annual sampling of trout redds to determine success of embryonic development. The product of potential egg deposition and percentage of viable eggs or sac-fry provided an estimate of the number of fry emerging. Although a few fry are known to emerge as early as January 1 in Lawrence Creek, peak emergence is probably closer to February 1. This date was used as a standard in all production calculations each year. Consequently annual production for age group 0 represents the sum of only 11 monthly increments. Numbers of age 0 brook trout for the months of March, April, May, and June were estimated graphically by extending a subjective curved line backward from the fixed mid-September estimate, through the fixed mid-June estimate to the speculative estimate at emergence (Hunt 1966). Chapman (1965) relied upon approximately this same technique to estimate densities of coho salmon *(Oncarhynchus kisutch)* during their first few months of life.

Increments of growth in length and weight of age 0 brook trout during the February-June period were determined empirically from samples collected monthly during 1963 and 1966. Fry were collected with a hand-net or electric shocker and returned to the laboratory. A triple-beam balance was used to determine the aggregate weight (to nearest 0.1 g) of the live sample of

TABLE 1. *Physical characteristics of the four study sections of Lawrence Creek labelled A through D proceeding downstream*

Characteristics	Study Section A	B	C	D	Stream Total or Average
Length (in km)	1.72	1.38	1.19	1.13	5.42
Area (in hectares)	0.75	1.27	0.93	1.13	4.08
Average width (in m)	4.33	9.23	7.92	10.06	7.52

fry and an average weight was computed. Mean length (to nearest 0.2 cm) was based on measurements of individual fry. Between-year variations in monthly growth entered the calculations from May through December.

A computer program was employed to carry out final mathematical calculations of production. Basic data fed into the computer program included numbers of trout of each age present and their mean individual weights at the beginning of each month. Calculations followed the methods outlined by Ricker (1958). Final printout sheets contain monthly tabulations of instantaneous growth rates (g), instantaneous mortality rates (r), instantaneous rates of increase or decrease (k), biomass on the first of the month, average monthly biomass and the calculation of monthly production. Also included are the original entries of population size and mean individual weight by age group at the beginning of each time interval.

Computer programs were also used to derive a variety of simple linear correlation equations and a simple correlation matrix of 42 population and production variables.

Yield data for 1960-67 were gathered through a 100 percent compulsory creel census. Anglers could choose any study section, but permits were issued for only one section per trip. Anglers were required to return permits at the end of each trip and present catches for examination. Census data were accumulated on angling effort, fishing methods and catch for each study section. Length, weight, sex, and age data were recorded for all trout taken.

Fishing regulations varied during the 1960-67 seasons. During 1960, the minimum legal size limit was 22.9 cm (9 inches). During 1961-67, the size limit was 20.3 cm (8 inches). The daily bag limit was five trout all years, but during 1961-67, "fly fishing" was the only legal method in Sections C and D. Reduction of the size limit and the restriction on fishing methods in 1961 altered the total amount of fishing, the proportions of fishing effort in the various sections, and the number and age composition of the trout caught (Hunt 1970).

During the 1968-70 fishing seasons, no registration system or creel census operation was conducted. Fishing regulations reverted to normal statewide and more liberal rules—15.2 cm (6 inch) legal size limit and a daily bag limit of ten. I suspect, based on occasional car counts and conversations with anglers during 1968-70, that fishing effort and harvest were higher during these 3 years than at any time during 1960-67 when special restrictions applied to the Lawrence Creek fishery.

RESULTS

During the 11-year period, 1960-70, annual production by brook trout in Lawrence Creek varied from 436.8 kg to 526.2 kg (10.6-12.9 g/m^2). These extreme values differ by only 20 percent. Average production for the period was 478.1 kg annually, or approximately 12 g/m^2 (Table 2, Fig. 1).

Within the four study sections of Lawrence Creek, annual production was much more variable from year to year than for the stream as a whole (Fig. 2). Annual production (in kg/yr) during the 11-year period varied by 95 percent in Section A, by 44 percent in Section B, by 69 percent in Section C, and by 176 percent in Section D.

Production per unit area was greatest in Section A during 10 of 11 years, averaged 18.8 g/m^2 annually and reached a peak value of 25.8 g/m^2 in 1969. Annual production exceeded 20 g/m^2 in Section A during all 4 of the last 11 years of study (Table 2). In Section B, annual production remained more stable than in other sections and averaged 11.6 g/m^2, the second highest sectional average. In Sections C and D, annual production tended to decline during the last 5-6 years and averaged 10.6 and 8.2 g/m^2, respectively.

Within age groups, annual production was also more variable from year to year than was production for the stream as a whole (Fig. 3). Annual production varied by 119 percent among age 0 stocks, by 97 percent among age I stocks and 700 percent among age II stocks. On a unit area basis, annual production averaged 4.8, 5.0, 1.6, 0.3 and 0.1 g/m^2 for age 0 through IV+, respectively, for the

TABLE 2. *Annual production by brook trout in Lawrence Creek during 1960-70, summarized by study section*

	Production per Section								Stream Total	
	g/m^2/yr				kg/Section/yr					
Year	A	B	C	D	A	B	C	D	g/m^2/yr	kg/yr
1960	13.0	10.1	13.4	14.0	98.0	128.8	124.3	157.8	12.5	508.9
1961	17.2	13.5	10.2	8.0	128.8	171.9	95.3	90.3	11.9	486.3
1962	14.0	10.0	11.1	10.8	105.2	127.0	103.0	122.0	11.2	457.2
1963	16.5	12.0	12.9	11.5	123.8	152.4	119.8	130.2	12.9	526.2
1964	19.8	12.8	9.8	8.6	148.9	162.3	90.7	97.5	12.2	499.4
1965	19.5	9.8	11.0	5.4	147.0	125.2	102.5	61.2	10.6	435.9
1966	15.2	12.6	9.8	6.3	114.3	160.1	90.7	71.7	10.6	436.8
1967	21.7	9.4	10.9	6.7	161.0	119.8	101.2	75.2	11.2	457.2
1968	21.3	12.0	8.9	5.1	160.6	152.4	83.0	57.1	11.1	453.1
1969	25.8	12.0	7.9	6.6	191.0	152.4	73.5	74.3	12.0	491.2
1970	20.5	13.2	10.1	7.8	152.0	168.7	93.4	88.5	12.3	502.6
Avg.	18.8	11.6	10.6	8.2	139.3	147.4	98.0	93.4	11.7	478.1

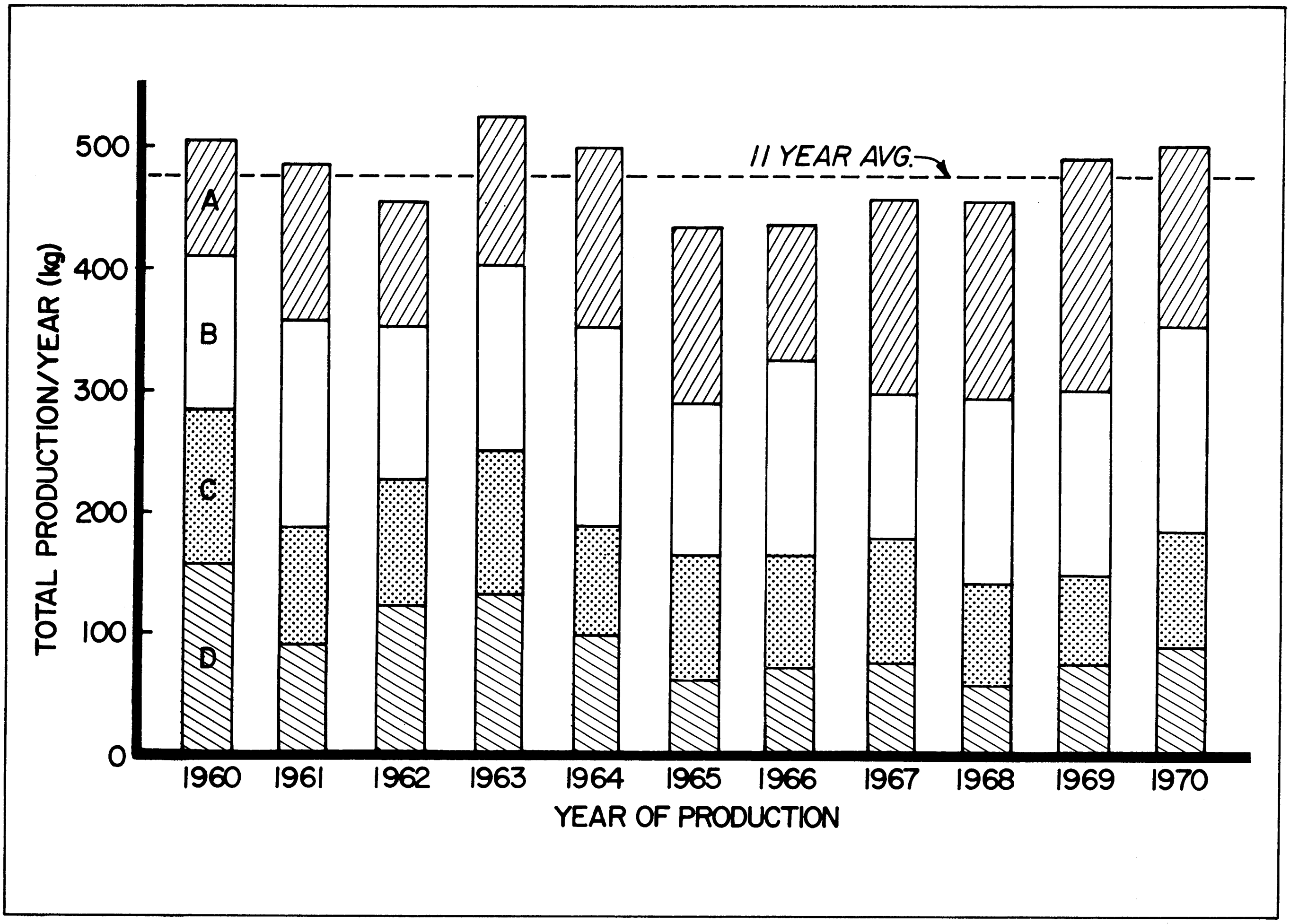


FIGURE 1. *Annual production by brook trout stocks in each of four study sections of Lawrence Creek during 1960-70, summarized in kilograms/section/year.*

entire stream (Table 3).

Age 0 stocks accounted for an average of 40.5 percent of annual production during the 11-year period and for the greatest production by any age group during 5 of 11 years. Age I stocks also accounted for the great proportion of annual production during 5 years and the greatest average contribution (43.1 percent) to annual production during the 11-year study period. In 1964, production by age 0 and age I stocks was similar (Table 4).

These two youngest age groups dominated production every year. A minimum of 74.0 percent, a maximum of 94.6 percent, and an average of 83.6 percent of annual production was contributed by age 0 and age I stocks

Annual production by age II trout (third year of life) was also substantial, especially during the last 9 years of the study. Age II production accounted for 21.2 percent of total production in 1967 and at least 15.0 percent of annual production during 5 of 11 years. During none of the years, however, was production by age II greater than production by age 0 or age I stocks.

In both absolute and proportionate terms, production by age III was greatest in 1968. During that year, age III production amounted to 0.6 g/m^2 and 5.1 percent of total production.

Annual production by age IV and older brook trout never exceeded 0.1 g/m^2 and always represented less than 1 percent of total production. For each gram of new body tissue produced annually by age IV trout, there was, on the average, 7 grams of new growth by age III, 36 grams by age II, 114 grams by age I, and 108 grams by age 0.

Among the eight year classes for which lifetime production estimates were derived, production varied from 372.4 kg (9.1 g/m^2) for the 1960 year class to 650.0 kg (15.9 g/m^2) for the 1961 year class (Table 5). These extreme values differ by nearly 75 percent as compared to only a 20 percent variation among the 11 estimates of annual production.

For all eight year classes, lifetime production averaged 470.8 kg (11.5 g/m^2), a value very similar (as it should be) to the 11-year average of 478.1 kg (11.7 g/m^2) of production measured on an annual basis. The 11-year values differ somewhat from the 8-year averages because portions of lifetime production by year classes other than the 1960-67 year classes are included in the 11-year series.

Age 0 stocks contributed 32.1 to 45.9 percent of lifetime production by the 1960-67 year classes. The 8-year average contribution was 40.8 percent (Table 6). Production by age I trout accounted for 37.0 to 46.0 percent of lifetime production and averaged 41.0 percent. An average of 81.8 percent of lifetime production occurred during the first two years of life of these eight generations of trout, and by the end of their third year of life, an average of 96.5 percent of lifetime production had been attained. Age 0 made the greatest contribution to lifetime production for four year classes and age I to the other four-year classes (Fig. 4).

For five of these eight year classes,

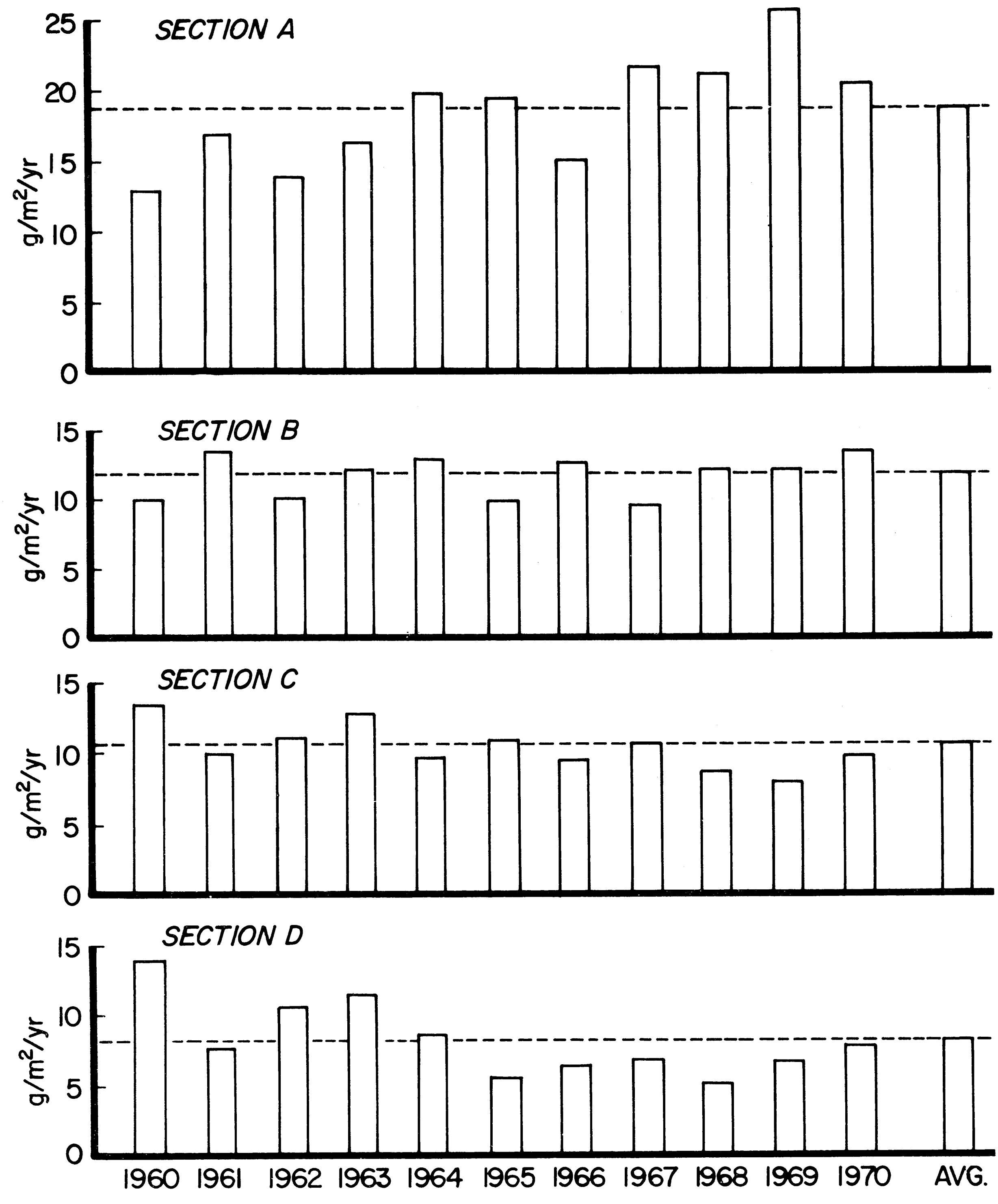


FIGURE 2. *Variations in annual production by brook trout stocks in each of the four study sections of Lawrence Creek during 1960-70, summarized in grams/m² /section/year.*

TABLE 3. *Annual production by brook trout in Lawrence Creek during 1960-70, summarized by age group*

Year	g/m²/yr						kg/Section/yr					
	0	I	II	III	IV+	Total	0	I	II	III	IV+	Total
1960	4.1	7.7	0.3	0.4	< 0.1	12.5	166.5	315.2	10.9	15.4	0.9	508.9
1961	6.8	3.9	1.1	< 0.1	0.1	11.9	279.9	159.7	45.8	0.4	0.5	486.3
1962	3.8	6.2	0.9	0.2	< 0.1	11.2	156.9	255.4	37.2	7.7	< 0.1	457.2
1963	6.4	4.0	2.2	0.2	< 0.1	12.9	262.2	163.7	89.8	8.2	2.3	526.2
1964	5.2	5.2	1.2	0.5	< 0.1	12.2	212.2	212.2	51.3	22.7	1.0	499.4
1965	4.3	4.2	1.9	0.2	< 0.1	10.6	174.6	171.9	80.3	6.8	2.3	435.9
1966	3.1	5.7	1.4	0.4	< 0.1	10.6	127.9	234.5	56.2	15.9	2.3	436.8
1967	3.8	4.5	2.4	0.5	< 0.1	11.2	155.1	183.3	97.1	20.9	0.8	457.2
1968	4.5	4.0	1.9	0.6	0.1	11.1	186.0	164.7	75.7	23.1	3.6	453.1
1969	4.7	5.3	1.6	0.3	0.1	12.0	193.2	215.5	68.9	10.4	3.2	491.2
1970	5.3	4.6	2.2	0.2	< 0.1	12.3	215.5	188.2	88.0	9.5	1.4	502.6
Avg.	4.8	5.0	1.6	0.3	< 0.1	11.7	193.7	205.9	64.0	12.7	1.8	478.1

TABLE 4. *Proportion of annual production accounted for by each age group of brook trout in Lawrence Creek during 11 successive years*

Year	Percent of Annual Production				
	0	I	II	III	IV+
1960	32.7	61.9	2.1	3.0	0.3
1961	57.6	32.8	9.4	0.1	0.1
1962	34.3	55.8	8.1	1.7	0.1
1963	49.8	31.1	17.1	1.6	0.4
1964	42.5	42.5	10.3	4.5	0.2
1965	40.1	39.4	18.4	1.6	0.5
1966	29.3	53.7	12.9	3.6	0.5
1967	33.9	40.1	21.2	4.6	0.2
1968	41.0	36.3	16.7	5.1	0.9
1969	39.3	43.8	14.0	2.1	0.8
1970	42.9	37.4	17.5	1.9	0.3
Avg.	40.5	43.1	13.4	2.7	0.3

TABLE 5. *Lifetime annual production by eight year classes of brook trout in Lawrence Creek*

Year Class	Annual Production (in g/m²)					Year Class Total (g/m²)	Year Class Total (kg)
	0	I	II	III	IV+		
1960	4.1	3.9	0.9	0.2	< 0.1	9.1	372.4
1961	6.8	6.2	2.2	0.5	< 0.1	15.9	650.0
1962	3.8	4.0	1.1	0.2	< 0.1	9.3	381.0
1963	6.4	5.2	1.9	0.4	< 0.1	14.0	571.5
1964	5.2	4.2	1.4	0.5	0.1	11.3	464.9
1965	4.3	5.7	2.4	0.6	0.1	13.0	532.5
1966	3.1	4.5	1.9	0.3	< 0.1	9.8	398.7
1967	3.8	4.0	1.6	0.2	< 0.1	9.9	399.2
Avg.	4.7	4.7	1.7	0.3	0.1	11.5	470.8
Percent of total	40.8	41.0	14.7	3.1	0.4	100.0	

TABLE 6. *Proportion of lifetime production accounted for by each age group in eight year classes of brook trout in Lawrence Creek*

Year Class	Percent of Lifetime Production				
	0	I	II	III	IV+
1960	44.7	42.9	10.0	2.2	0.2
1961	43.1	39.3	13.8	3.5	0.3
1962	41.2	43.0	13.5	1.8	0.5
1963	45.9	37.1	14.0	2.8	0.2
1964	45.7	37.0	12.1	4.5	0.7
1965	32.8	44.0	18.2	4.3	0.7
1966	32.1	46.0	19.0	2.6	0.3
1967	38.9	41.2	17.3	2.4	0.2
Avg.	40.8	41.0	14.7	3.1	0.4

TABLE 7. *Lifetime yield from five year classes of brook trout in Lawrence Creek*

Year Class	Yield (in kg by Age Group)				Total Lifetime Yield (kg)	Total Yield as % of Lifetime Prod.
	I	II	III	IV+		
1960	9.6	42.3	7.2	2.4	61.5	16.5
1961	7.7	65.6	19.3	5.7	98.3	15.1
1962	2.2	42.1	12.1	2.6	59.0	15.5
1963	4.0	49.3	19.7	3.2	76.2	13.3
1964	4.2	63.0	25.4	6.8*	99.4	21.4
Avg.	5.5	52.5	16.7	4.1	78.8	16.3

*Estimated on basis of 56% known exploitation of age IV in 1967 and known standing stock of 79 age IV+ trout in April 1968 having an average weight of 159 g.

lifetime yield estimates were also accumulated (Table 7). The weight of trout removed by anglers was equivalent to 13.3 to 21.4 percent of lifetime production and averaged 16.3 percent. No age 0 trout were cropped and 5 annual catches of age I trout weighed only 27.7 kg. This yield represented only 1.3 percent of the 2,184 kg of production by age 0 and I stocks during 1960-64.

Approximately two-thirds of the lifetime yield from the five year classes consisted of age II trout. Age II catches averaged 52.5 kg/yr, as compared to average yields of 5.5 kg/yr for age I, 16.7 kg/yr for age III, and 4.1 kg/yr for age IV+ (Table 7). By the end of the third year of life of trout in the 1960-64 year classes, 2,272 kg of growth had occurred, but only 290 kg (12.8 percent) had been removed by anglers.

Over the 8-year period for which yield data were gathered, annual catches varied nearly ten-fold (Fig. 5) and were equivalent to 2.4-26.4 percent of annual production (Table 8). Excluding the small harvest in 1960 when fishing regulations were more restrictive than those in effect during 1961-67, annual yields still varied by 248 percent and were equivalent to 10.0-26.4 percent of annual production.

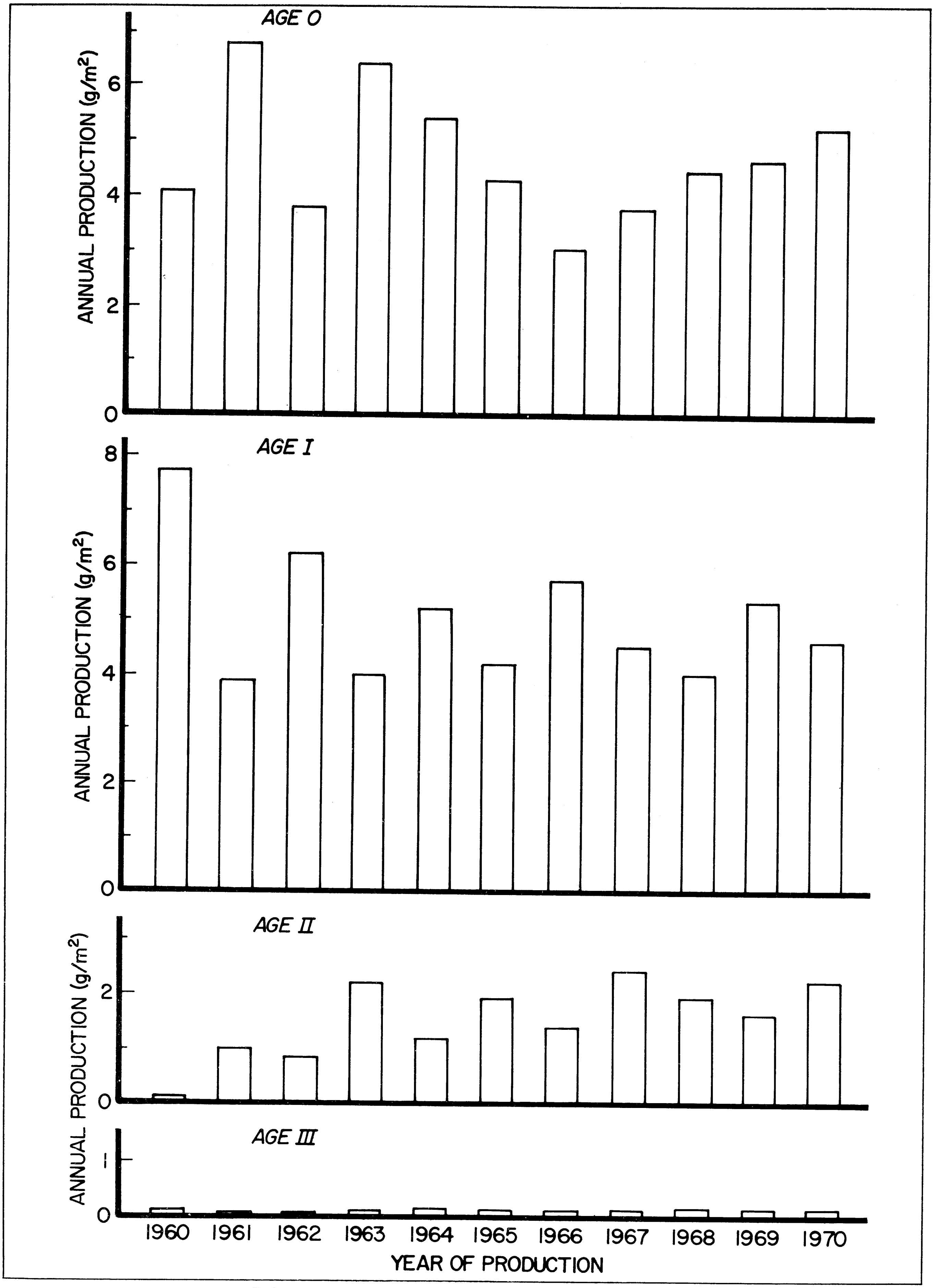


FIGURE 3. *Annual production by age groups 0-III stocks of brook trout in Lawrence Creek during 1960-70, expressed in grams/m^2/year.*

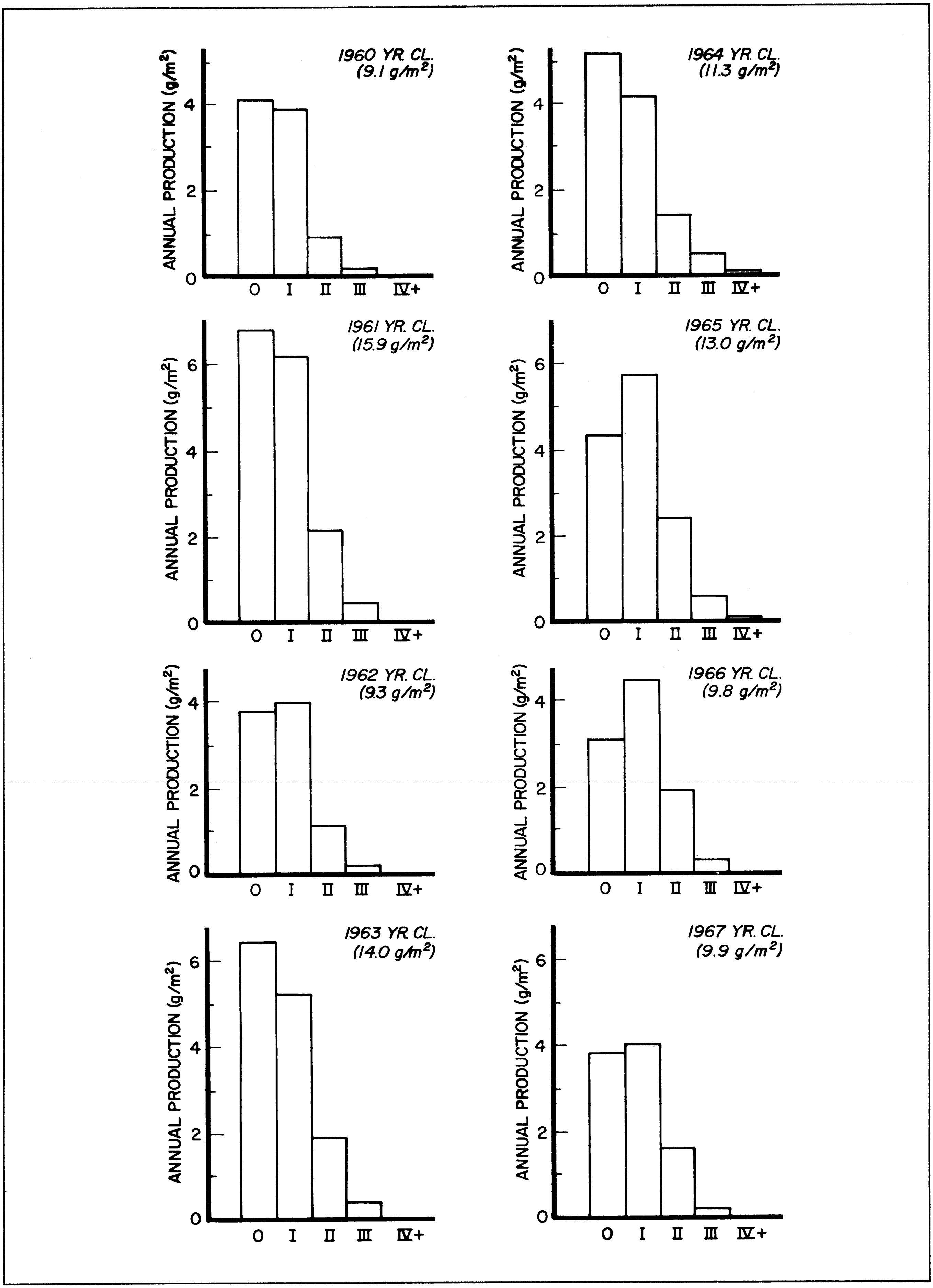


FIGURE 4. *Lifetime production by the 1960-67 year classes of brook trout in Lawrence Creek, expressed as grams/m²/year of life.*

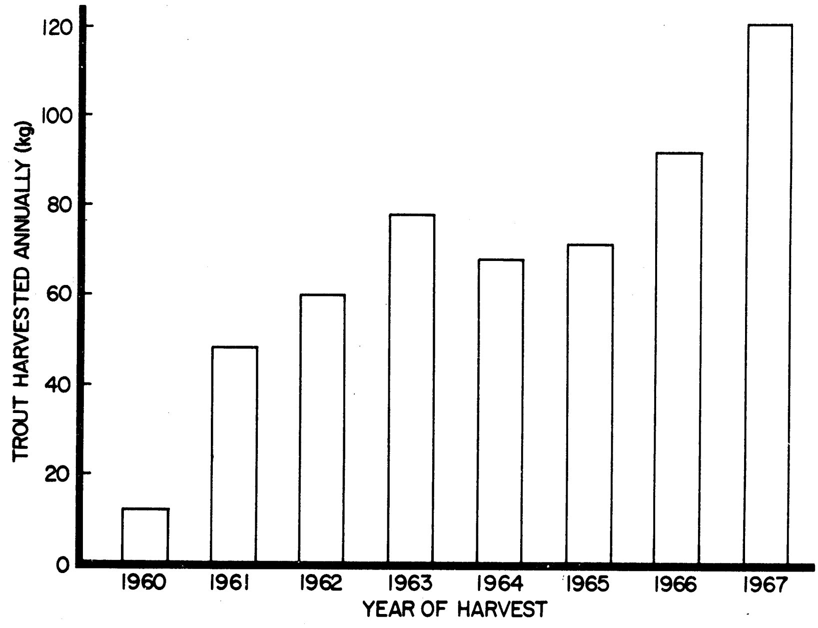


FIGURE 5. *Annual sport fishery yield of brook trout from Lawrence Creek during the 1960-67 fishing seasons.*

TABLE 8. *Sport fishery yield of brook trout from Lawrence Creek in relation to annual production during 1960-67**

Year	Annual Yield (in kg)	Annual Production (in kg)	Yield as a % of Annual Production
1960	12.2	508.9	2.4
1961	48.8	486.3	10.0
1962	59.6	457.2	13.0
1963	76.9	526.2	14.6
1964	67.8	499.4	13.6
1965	71.3	435.9	16.4
1966	92.3	436.8	21.1
1967	120.7	457.2	26.4

*The minimum legal size limit was 22.9 cm (9 inches) in 1960 and 20.3 cm (8 inches) for the 1961-67 fishing seasons. The daily bag limit was 5 all years, but during 1961-67 "fly-fishing" was the only legal method in sections C and D.

In Lawrence Creek, approximately 85 percent of annual production by brook trout occurs during the period from April 1 through September (Hunt 1966), the period during which our three electrofishing inventories of population age structure and biomass were made each year (Appendix Table 1). During 1960-70, standing stocks of brook trout in early April varied nearly three-fold (143-408 kg). Yet, despite such variation in stock biomass at the beginning of the main production period, 11 estimates of annual production differed only 20 percent. Clearly, annual production was poorly correlated with April biomass (Appendix Fig. 2). Similarly, long-term records of mid-summer or fall standing stocks, of sport fishery yields, or even of annual production within a given study section, failed to provide reasonable clues to the amazing consistency of annual production by the population as a whole. Annual estimates of production provided a perspective on the dynamics of this wild brook trout population that no other measured parameter provided.

POSSIBLE BIASES IN PRODUCTION CALCULATIONS

Egglishaw (1970) suggested that "infrequent sampling" of the Lawrence Creek population to obtain growth and numbers data could be an inherent bias contributing to the low variation in annual production estimates previously published (Hunt 1966). I do not think so.

From October 1 through the following March, growth of brook trout in Lawrence Creek is poor, especially among age I and older trout, as revealed by monthly collections of age-specific growth data during 1963 and 1966 (Hunt 1969). Poor growth, hence poor production, during the October-March period is primarily due to unfavorable water temperature regimes (Hunt 1966), reduction in feeding by adult trout during the spawning period (White 1967), and less active feeding by all age groups during the winter due to temperature-induced inactivity and poorer utilization of food consumed. Lack of potential food does not appear to be critical in Lawrence Creek (White 1967).

Although monthly increments of mortality were never estimated through field sampling for the October-March period (only total mortality for the entire period), lack of such empirical data should not seriously bias production estimates. Short-interval accuracy of numerical components in production equations for the October-March period would have been more critical if growth was also changing rapidly from month to month. However, such was not the case.

It is therefore doubtful that more than three field estimates of population structure would have greatly improved estimates of annual production, especially when these population inventories were made at the beginning, midway, and at the end of the 6-month period during which most annual growth occurs.

Concentration of growth and production in a period of one-half year or less is probably typical of most trout populations in freshwater environments (Allen 1969) and perhaps of most warmwater fish populations in temperate climates, too. A similar phenomenon was reported by Gerking (1962) in his study of production by a bluegill *(Lepomis macrochirus)* population in a lake in Indiana. Annual production was 91 kg/ha, nearly all of which occurred during the 5-month May-September period.

Inadequate sampling to obtain age-specific growth data and information on population numbers is certainly a recognized weakness in many production studies of wild fish populations. A more common, and often unrecognized weakness in methodologies of published production studies is that of sampling only a small portion of a lake or stream and extrapolating these sampling data to estimate production in the entire body of water. Each of the four study sections of Lawrence Creek is at least 1 km long. If the assumption had been made that annual production in any of those sections was representative of production in the entire stream, highly erroneous estimates for most years would have been derived. An extreme instance of this kind of extrapolation error would be one based on production in Section A during 1969. That year production was approximately 258 kg/ha. Multiplying this quantity by 10.1 ha yields a streamwide estimate of 2,580 kg of production, a value nearly five times greater than my estimate of 491 kg based on summing production estimates for the four study sections (Table 2). Production showed the least year-to-year variation in section B, a range of 44 percent, but even this spread is more than twice as great as the range in annual estimates for the stream as a whole.

INFLUENCES OF FISH MOVEMENTS AND HABITAT IMPROVEMENT ON PRODUCTION

Within sections, annual production tended to increase during the study period in Section A, remained fairly stable in Section B, and tended to decline in Sections C and D (Fig. 2). Nearly all of the spawning area in Lawrence Creek is located in Sections A and B and most of the deepest and largest pools are found in Sections C and D. Consequently, there is an upstream movement of adult trout to the spawning grounds in the autumn and a downstream movement of adult trout to the deeper pools during the winter, plus a predominantly downstream dispersal of age 0 trout from the spawning grounds throughout their first summer of life (McFadden 1961; Hunt 1965; Miller 1970). These intersectional movements associated with spawning, with search for more hospitable winter environments, and with dispersal of young-of-year influenced both the long-term production trends, especially in Sections A, C, and D, and the relatively stable streamwide production. Downstream movement from Section A of young and adult trout decreased after 1964 concomitant with completion of an intensive program of instream habitat development (see Table II in Chapman and Bjornn 1969). Thereafter, standing stocks of trout in Section A began to increase, especially the stocks of age I and older trout, and production also began an upward trend. During the last 4 years of this study (1967-70), annual production averaged 166 kg in Section A, or 46 percent more than the 4-year average for this section prior to habitat development. However, annual production was below average during 3 of the last 4 years in Section C and during all 4 years in Section D. Increased production in the uppermost section was counterbalanced by decreased production in the lower portion of stream.

These trends in production within sections could be interpreted to suggest that intensive habitat development in Section A was of little streamwide value. In other words, streamwide production was not increased; there were simply shifts in the relative sectional contributions. However, analyses of other trout population parameters and sport fishery yields and use indicate that such an assessment of the habitat development project is false. Standing stocks of legal-sized trout and the sport fishery were substantially enhanced. In this instance, at least, annual production was not the best indicator of the management value of trout habitat development. While it is not my intent in this paper to discuss the ecological implications of trout habitat development in detail (see Hunt 1969 and Hunt 1971), a brief summary of some of the major physical-biological interactions might be helpful in putting the sectional production trends in better perspective.

Physical alteration of the streambanks and channel of Section A was done primarily to increase pool area and overhanging streambank cover for trout, both of which were critical limiting factors on trout carrying capacity, especially during the winter period. Annual production of age 0 stocks stayed about the same, but it showed increasingly greater postdevelopment gains for successively older age groups—up approximately 17 percent for age I trout, 133 percent for age II, and 700 percent for age III during the first 3 years after development (Hunt 1971). These upward trends for age I and older stocks continued during the fourth through sixth years after development (Hunt, unpublished data) as more and more older-age trout accumulated, due primarily to increased rates of overwinter survival. As a consequence, more of the production that occurred during the first year or two of life was "tied up" in the standing stocks of age II and older trout rather than being "lost" through natural mortality each winter. And since age II+ stocks also dominated the sport fishery, more lifetime production by postdevelopment year classes ended up in anglers' creels. Substantially increased carryover each winter of young-of-year and yearling trout that chose to remain in developed Section A rather than moving out to downstream sections resulted in gradual stockpiling of older-age trout, more production by these older age groups, and better utilization of production by anglers. For the stream as a whole, total production probably was not benefited by developing only Section A, but concentration of more of the total production in this section and among the older age groups at the "expense" of production (but higher natural mortality) by age 0 and I stocks in Sections C and D resulted in much better human use of the potential of Lawrence Creek to grow 500 kg of trout flesh annually. During the 7-year period of 1961-67 for which streamwide production and yield data were available, yield was equivalent to more than 20 percent of annual production only during the last 2 years—21.2 percent in 1966 and 26.4 percent in 1967 (Table 8). Trout from Section A accounted for 40 percent of the 1966 catch and 30 percent of the 1967 harvest.

MECHANISMS OF POPULATION REGULATION OF PRODUCTION

Turning to the more relevant context of this paper, the processes of production itself, it is particularly striking that the trout population in Lawrence Creek appeared to function as a homeostatic unit on a streamwide basis. Somehow the level of production in any one section or age group was related to production that year in other sections and other age groups.

As indicated earlier, annual production at the population level was remarkably independent of trout biomass in April, the beginning of the period of major growth. However, "efficiency" of annual production was strongly density-dependent in relation to spring biomass (Appendix Fig. 3). This decrease in the rate of additional production with increasing biomass implies that there must have been compensatory adjustments in growth rates and/or survival rates within one or more of the dominant age groups.

Looking first at age 0 stocks, annual production appeared to be directly dependent on age 0 biomass (or number of "producing units"). Contrary to the relationship that existed at the population level, there was a significant positive correlation (r = 0.760*) between June biomass of age 0 stocks and age 0 annual production (Appendix Fig. 4). Annual production varied from approximately 3 to 6 kg per kg of June biomass, but the production:biomass ratios among these age 0 cohorts were not density dependent (Appendix Fig. 5). Neither summer growth (Appendix Fig. 6) nor summer survival (Appendix Fig. 7) of age 0 stocks was strongly influenced by their own density. All three of these relationships indicate that summer carrying capacity of Lawrence Creek for age 0 brook trout is apparently seldom attained.

The only detectable population parameter that may have regulated age 0 production was the density of age I trout. There was a significant negative correlation (r = -0.612*) between age 0 production and the mean number of age I trout present during the April-September period (Appendix Fig. 8). However, I was not able to validate the nature of the suppression interaction. Such likely possibilities as predation of age I trout on age 0 trout or suppression of growth of age 0 trout through competition for food or through behavioral dominance could not be demonstrated. Mean numbers of age I stocks had no statistically significant impact on summer growth or summer survival of age 0 stocks when tested separately, yet there was a strong correlation between age 0 production and age I abundance.

Among age I cohorts, annual production was positively related to age I biomass in the spring (Appendix Fig. 9), but efficiency of production declined with increasing biomass (Appendix Fig. 10). Approximately 1 to 2 kg of additional growth occurred for each kg of age I trout present at the beginning of the main period of growth. In this age group, declining efficiency of production was due in part to density-dependent changes in summer growth (Appendix Fig. 11) and summer survival (Appendix Fig. 12). Production by age I stocks was also influenced by density of age II trout in April (r = -0.644*), the mean number of age II trout present during the summer growing period (r = -0.612*), and most strongly by annual production of age II stocks (r =

-0.770**, Appendix Fig. 13). Production by age 0 stocks or density of age 0 stocks may have negatively influenced age I production too, but correlation factors were not significant at the 95 percent level (Appendix Table 1).

Age II stocks accounted for a maximum of 21 percent of annual production and 13 percent of the 11-year average. In this age group, as in age group I, the biomass of "producing units" present in April was a primary determinant of annual production ($r = 0.945^{**}$, Appendix Fig. 14). Similar to age I, the production efficiency by age II stocks was also inversely related to stock density ($r = 0.714^{**}$). Ratios of annual production to spring biomass fell within a rather narrow range of 0.4:1 to 0.8:1 despite a 10-fold difference in spring biomass (Appendix Fig. 15). Summer growth of age II stocks was slightly density dependent, but not significantly so (Appendix Fig. 16). Intra-age density did not appear to influence summer survival of age II stocks (Appendix Fig. 17).

INFLUENCE OF ANGLING ON PRODUCTION

A factor complicating analysis of age II production that was not an important influence on age 0 and age I production was removal of trout by anglers. No age 0 and less than 10 kg of age I trout were cropped annually during the 1961-67 seasons when a minimum legal size limit of 20 cm (8 inches) was in effect. The bulk of the catch each year consisted of two-year-olds, of which 38-90 kg were cropped annually (Appendix Table 2). The numbers of age II trout creeled during 1961-67 were equivalent to 26-40 percent of the April standing stocks as compared to removals of 1 percent or less of the April stocks of yearlings (Hunt 1970). Seasonal catches of 2-year-olds were highly dependent on the number of such trout present in the spring (Appendix Fig. 18).

Cropping of age III trout also undoubtedly reduced the amount of production by these stocks. At least 40 percent and an average of 50 percent of the 3-year-olds were harvested during the 1961-67 seasons. Harvest was positively correlated with preseason abundance of 3-year-olds (Appendix Fig. 18). Annual production by age III trout was positively correlated with April biomass of age III trout (Appendix Fig. 19), but unlike ages I and II trout, there was no relationship between efficiency of production and April biomass (Appendix Fig. 20). In this age group, intra-cohort density was never high enough to significantly influence summer growth ($r = -0.493$) or summer survival ($r = -0.134$). Within the correlation matrix of population variables tested, density or production of other age groups seemed to have no influences on production by the relatively sparse age III stocks (Appendix Table 1). Annual production by this age group appeared to be solely a function of the number of such trout present.

MAJOR PRODUCTION INTERACTIONS AMONG AGE GROUPS

In Appendix Figure 21, I have attempted to schematically summarize the inter-age and intra-age parameters of the production process just discussed for the four age groups that annually account for at least 99 percent of annual production. Production by age 0 was positively influenced by the number of such trout present (indicated by the + symbol on the closed loop), and there were no significant changes in summer growth or summer survival dependent on age 0 density. However, age 0 production was inversely related to age I density (hence the connecting arrow and negative sign between these two age groups). Age I production was positively correlated with age I density (+ sign on closed loop) but efficiency of production was compensatory (- sign on closed loop), e.g., summer growth and survival were both density-dependent. Age I production was also depressed by increased abundance (and production) of age II stocks, although the inter-age mechanism of suppression was not identified. Age II production was also density-dependent and efficiency of production declined as age II biomass increased. There was no detectable change in summer survival that could have caused the decrease in production efficiency with increased April biomass. The other component of production, growth rate, did not significantly decline in response to increased biomass either, but the slope of the regression line was negative. Production by age III stocks was highly dependent on age III density which never was high enough to depress growth or survival. Production by this age group seemed to be independent of other age groups.

During those years when the effect of fishing on production could be assessed, removal of trout by anglers was sufficiently high to limit production by age III stocks (hence the heavy arrow from "fishing mortality" to age III) and probably reduced production by age II stocks as well. Fishing had no impact on production by ages 0 and I stocks which annually accounted for 75 percent or more of total production.

Each year, then, as a result of these and other synchronous adjustments in numbers and growth rates of the various age groups, approximately 500 kg of trout tissue was consistently produced.

RELATIONS OF PRODUCTION INFORMATION TO IMPROVED FISHERY MANAGEMENT

The model I have diagrammed in Appendix Figure 21 is obviously a very incomplete summary of the processes that regulate and limit annual production in this trout population. Yet even such simplistic models can provide helpful perspectives on the rational management of fish populations, whether that management is directed at optimizing production of protein for human consumption or providing improved angling quality. For example, despite a wealth of long-term and accurate data on standing stocks and yields of trout, the degree of population homeostatis in Lawrence Creek was never realized until a series of annual estimates of production were evaluated. Such basic discoveries that annual production of a fish population is self-regulating and identification of some of the regulatory mechanism involved are highly important management facts. Rational intervention to beneficially manipulate a given fish population is dependent on knowing which processes to alter, how to alter them, the consequences of such alteration, and, even more basically, whether the population is even regulated at all by any internal factors.

The need for a holistic, streamwide approach in managing the trout population in Lawrence Creek is another principle given added emphasis as a result of this production study. It is more apparent than before that no one age group or stream section can be managed independently of other age groups and stream sections. Production studies such as this can help fishery managers to be more aware of such intricate relationships that exist in fish populations they oversee, and to understand more thoroughly how various management pressures might be applied with greater success, whatever the goal.

SPECULATIONS ABOUT FACTORS LIMITING PRODUCTION

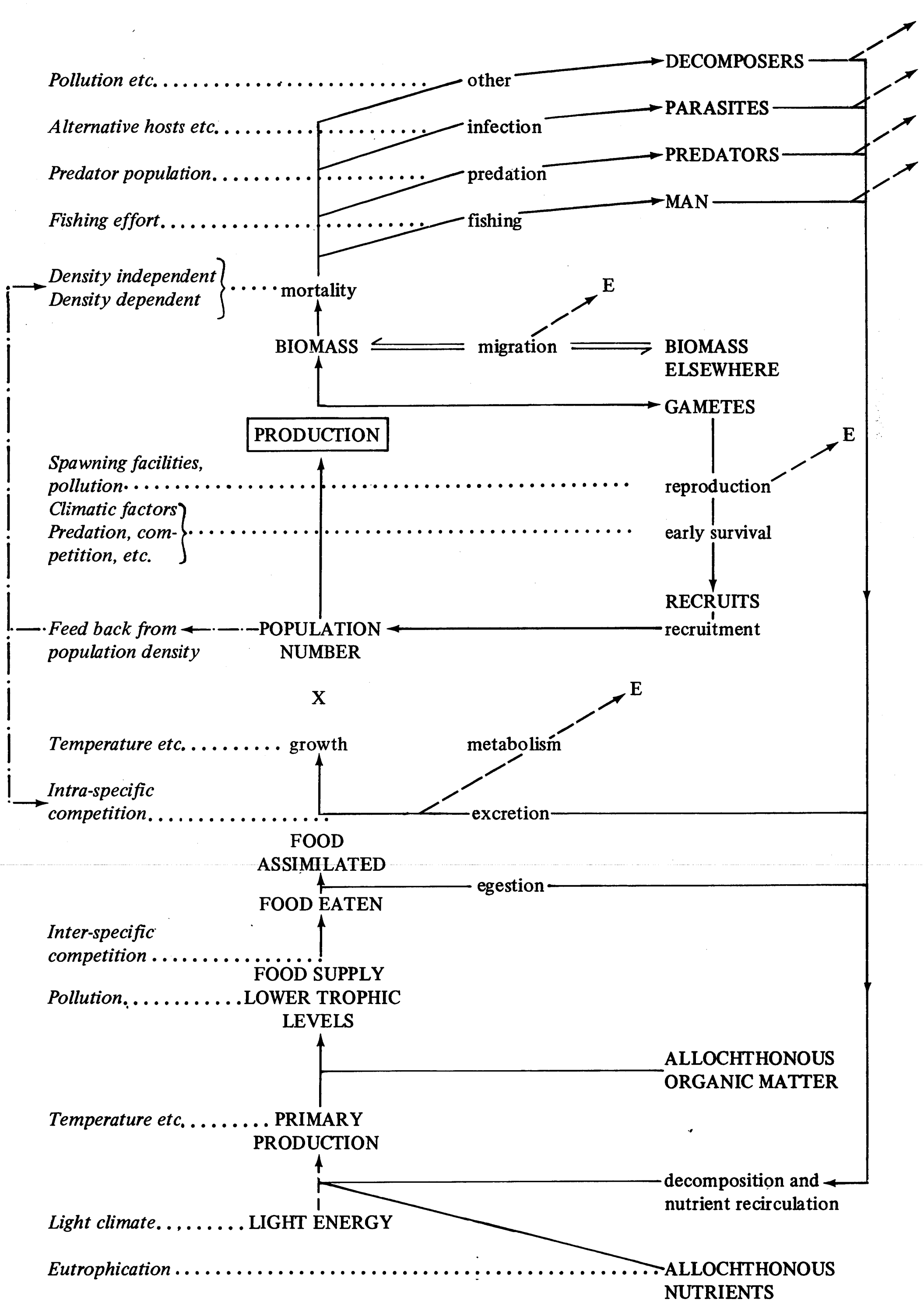
In this study, as in many ecological investigations, many "answers" are incomplete, many unresolved questions remain, many "pieces of the puzzle" are still missing. Annual production by brook trout in Lawrence Creek was shown to be surprisingly consistent and largely independent of the biomass of trout present at the beginning of the main period of annual growth. A few of the self-regulating processes were identified, especially compensatory adjustments in growth and survival that varied in importance according to age group. The population demonstrated great adaptability and resiliency in attaining a level of approximately 500 kg of production each year. But why this level? Of all the associated unanswered questions that could be raised, this is perhaps the most intriguing. What environmental components limited this brook trout population to this level of production, despite substantial variations in population size, age structure, and proportional distribution among the four study sections?

Allen (1969) suggested that because of the characteristic territorial behavior of salmonids, production in streams is commonly limited by the areas of "suitable" stream bed and the number of individual territories of various sizes that can be accommodated in this suitable area. Habitat development in Section A of Lawrence Creek reduced the absolute amount of stream bed by 51 percent, yet standing stocks and production of adult trout increased substantially, apparently in direct response to the amount of increase in pool area and streambank hiding cover (Hunt 1971). As Allen hypothesized and as my findings seem to substantiate, a distinction must be made between total streambed area and "suitable" or habitable area that trout will occupy. The former was substantially reduced by altering Section A, but the latter was apparently greatly increased.

Because of the interrelationships among stocks of trout in the four study sections, however, overall production in Lawrence Creek was little affected by altering only Section A. One obvious question this observation brings to mind is how much streamwide production might be increased if all sections were similarly developed? Would annual production increase to 2,000-3,000 kg or would some other limiting factor, such as the food supply or insufficient recruitment of young-of-year, prevent a streamwide response of this magnitude?

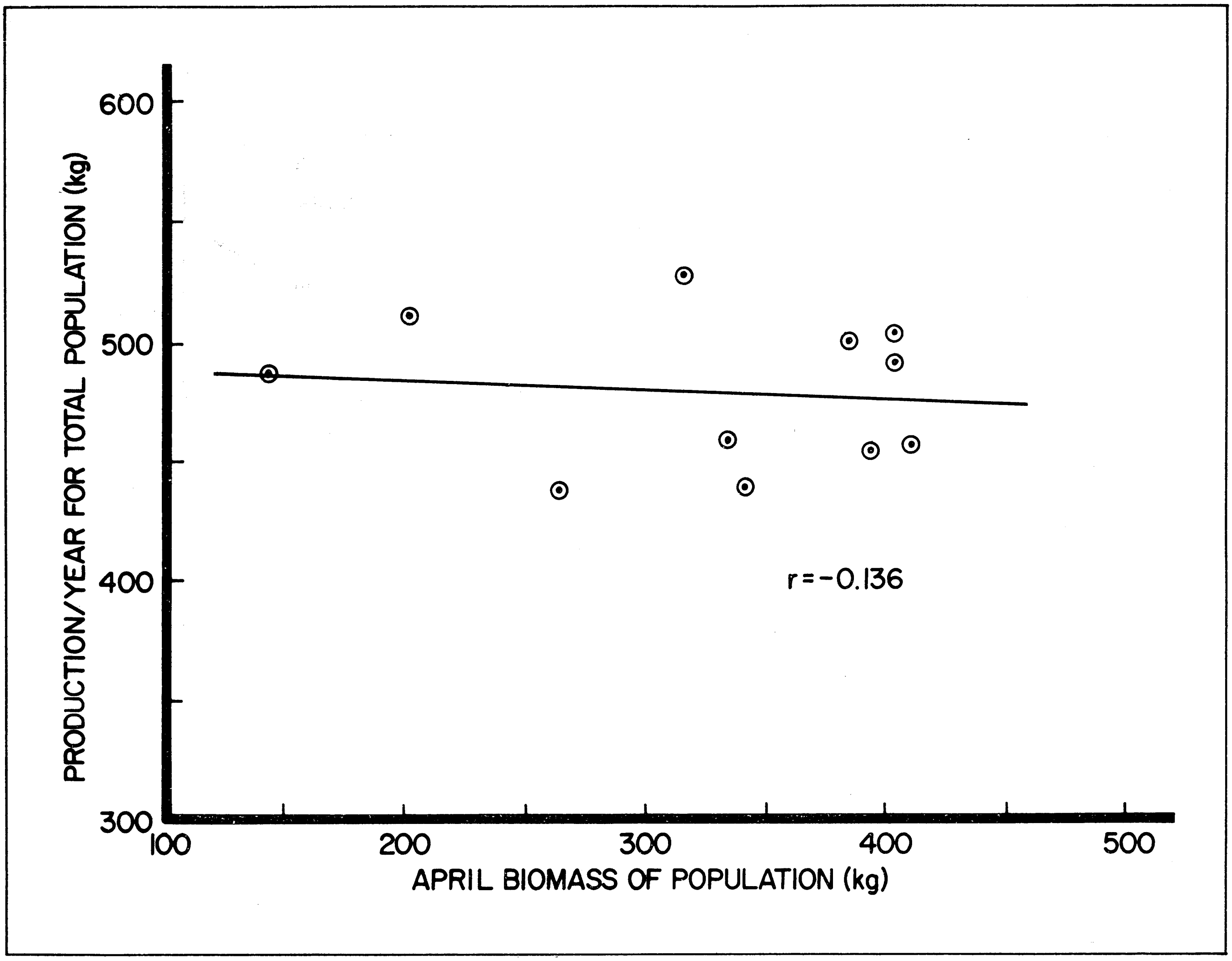
Based on the quality and quantity of production data accumulated on the population of brook trout in Lawrence Creek, plus the growing urgency to more effectively manage the fishery resources of the world, and the growing awareness of how production information can be used to do that job more effectively, I believe that Lawrence Creek constitutes a unique outdoor laboratory for conducting some of the most timely and useful research in fishery science today. Hopefully, this paper will serve as a stimulus to initiate more rigorous production research on this stream and also stimulate more fishery biologists to undertake production studies wherever they have opportunities to do so.

APPENDIX

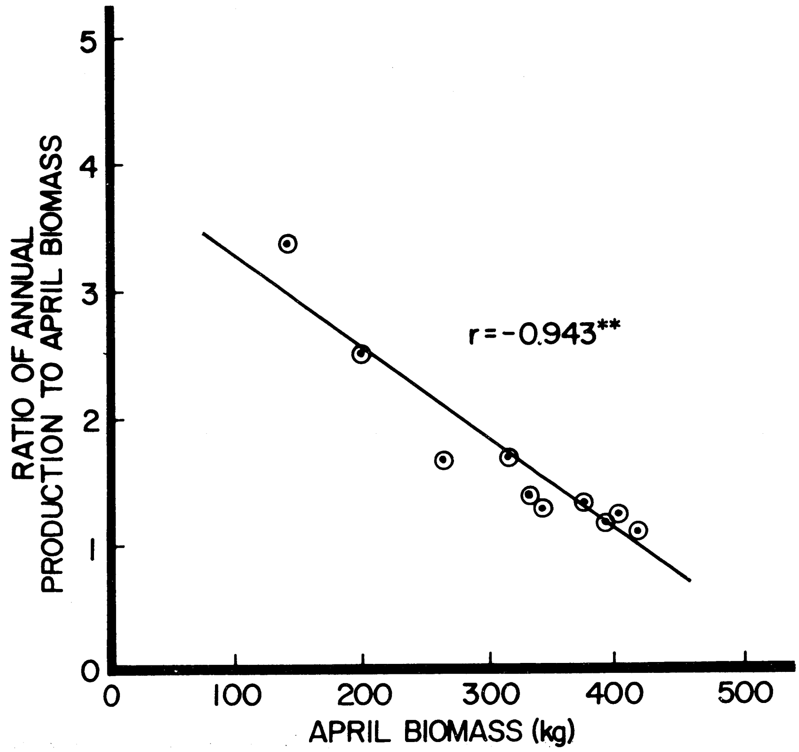


LEGEND: The items in capital letters are matter and/or energy and the flow between them is indicated by solid lines. The items in lower case letters are processes, while the items in italics (on the left hand side) are factors influencing these processes, their effects being shown by dotted lines. Energy (E) lost to the system is shown by oblique dashed lines. There is a loop to the right from PRODUCTION back to POPULATION NUMBER representing production and recruitment, and a second loop to the left indicating the special "feed-back" influence of population density, which is indicated by a dot-dash line.

APPENDIX FIGURE 1. *Diagrammatic representation of the interrelationships between production and other components in the part of the trophic system occupied by a fish population.*

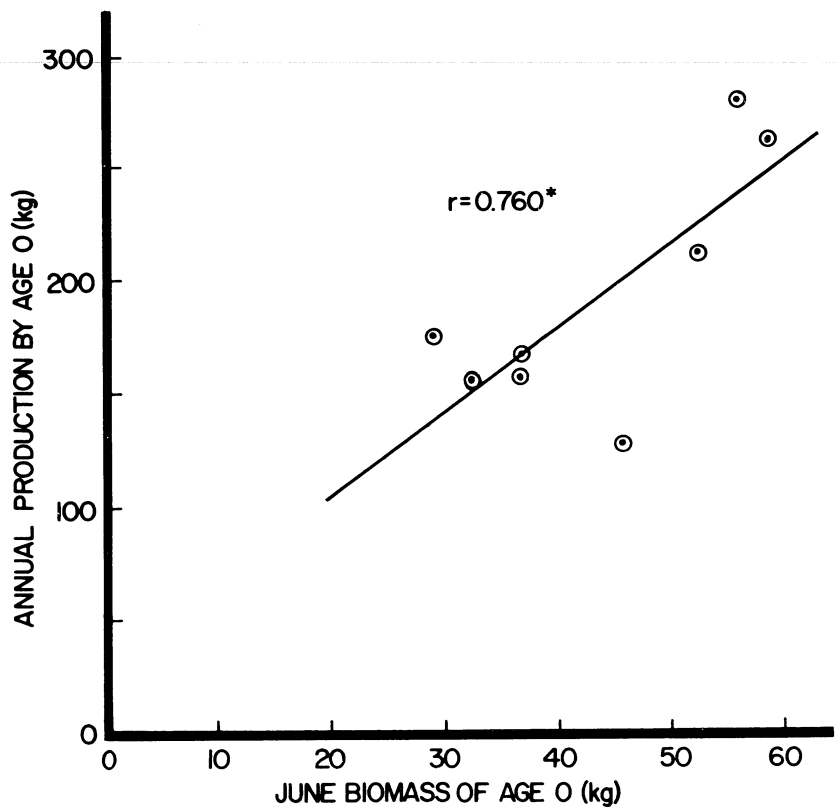


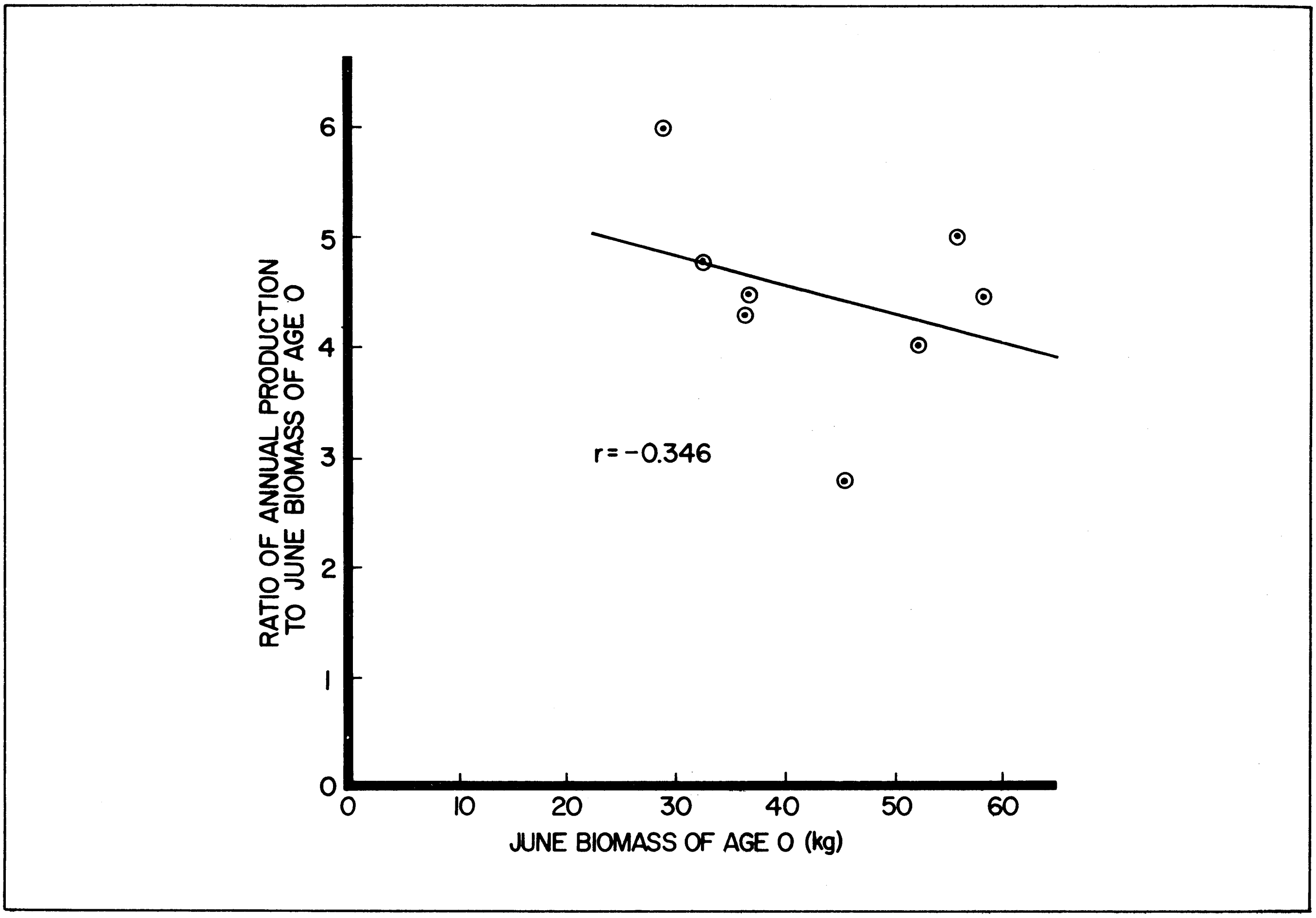
APPENDIX FIGURE 2. *Relation of annual production by the brook trout population in Lawrence Creek to population biomass in April.*



APPENDIX FIGURE 3. *Ratios of annual production to April biomass for the brook trout population in Lawrence Creek.*

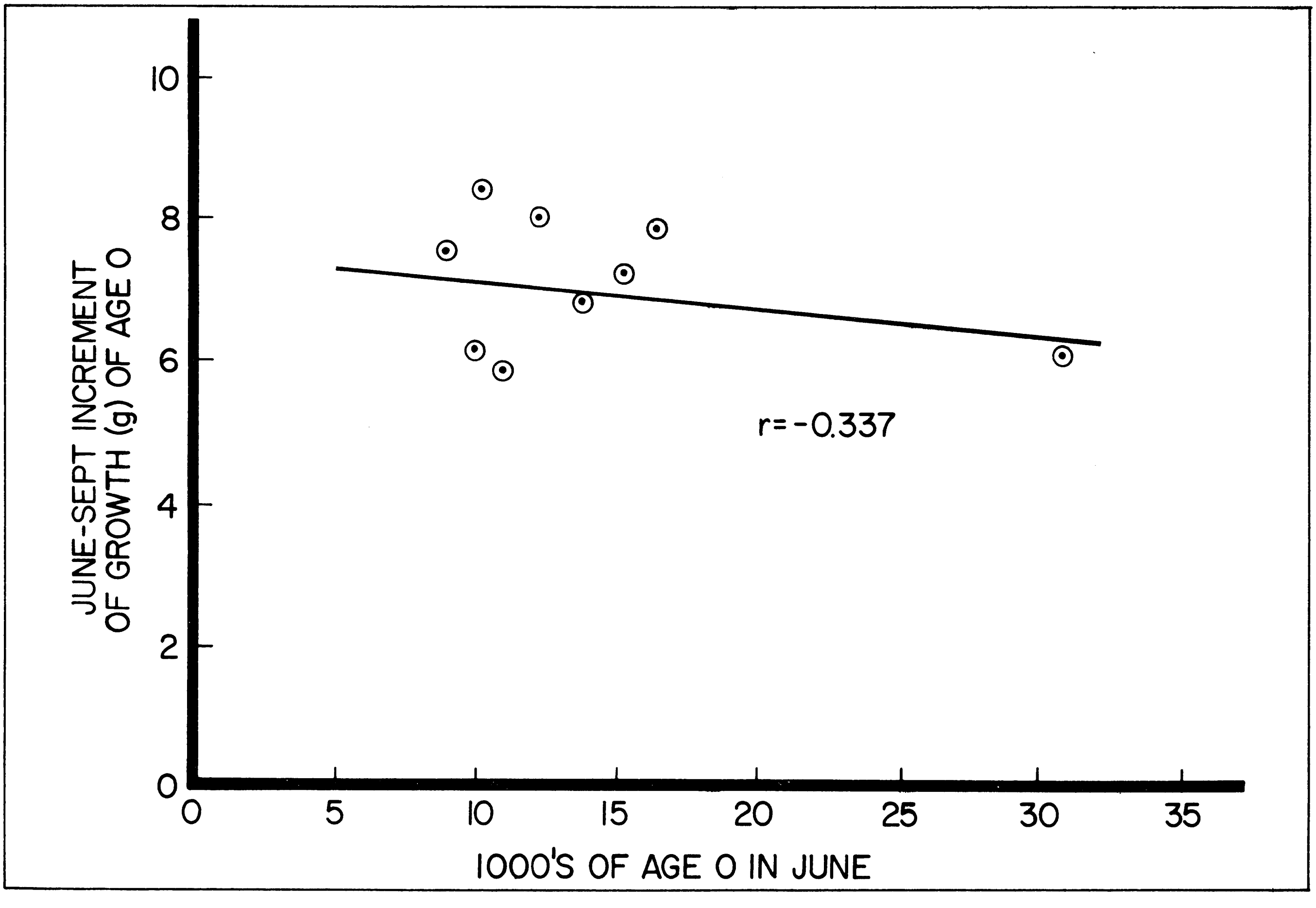
APPENDIX FIGURE 4. *Relation of annual production by age 0 stocks of brook trout in Lawrence Creek to biomass of age 0 stocks in June.*

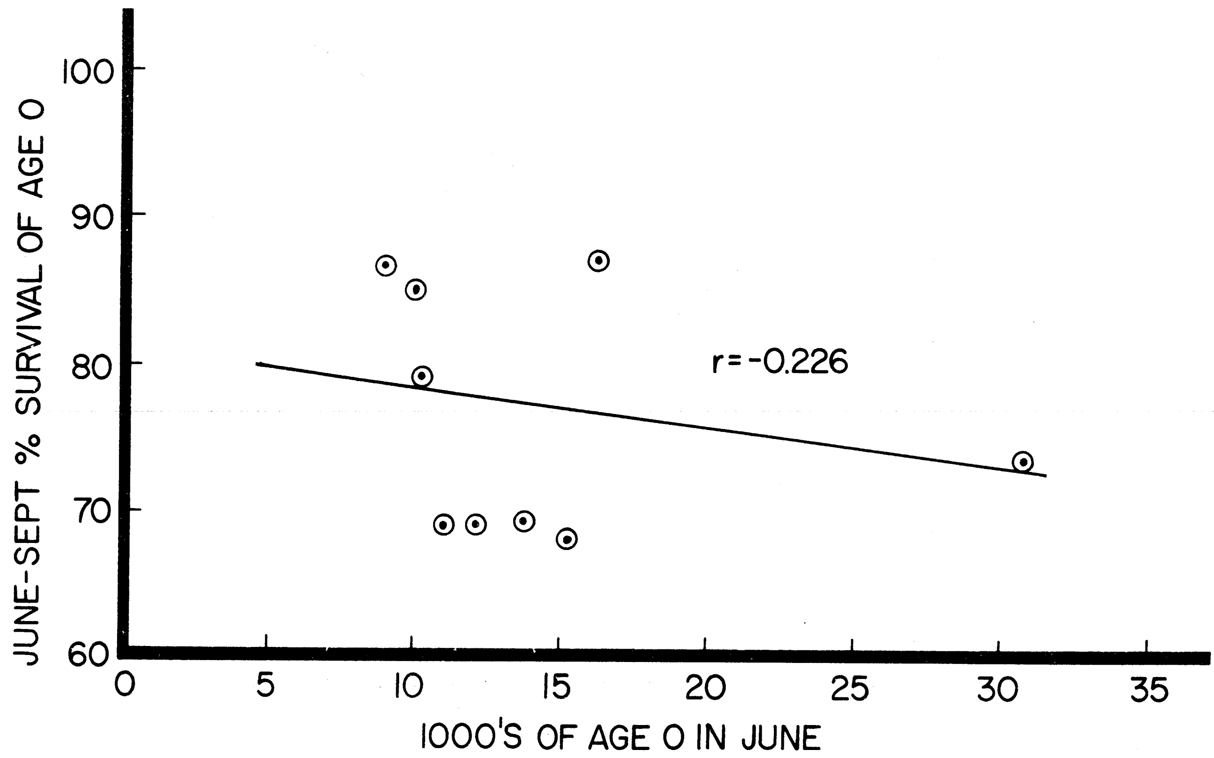




APPENDIX FIGURE 5. *Ratios of annual production to June biomass for age 0 stocks of brook trout in Lawrence Creek.*

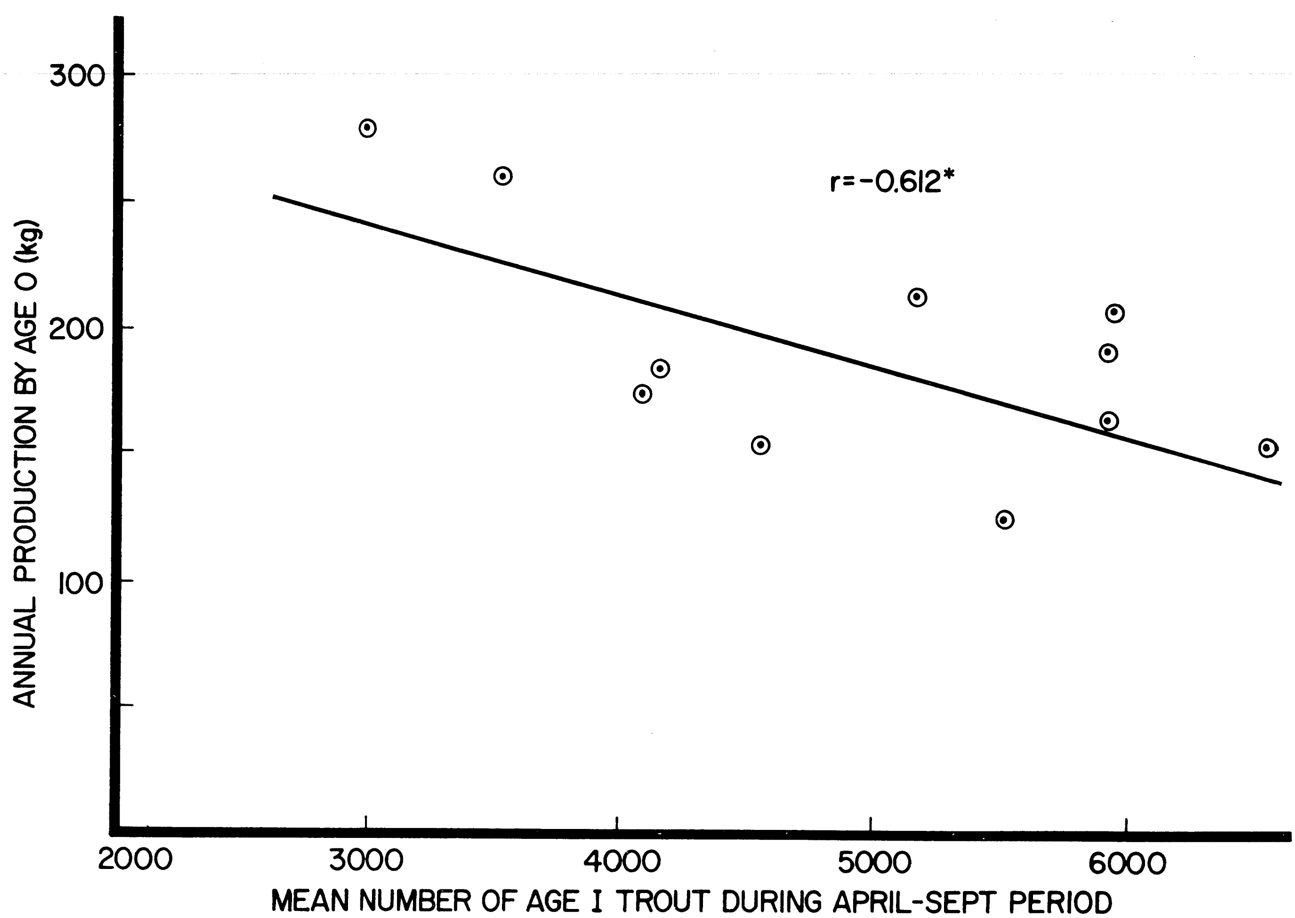
APPENDIX FIGURE 6. *Relation of summer growth of age 0 stocks of brook trout in Lawrence Creek to the number of age 0 brook trout present in June.*

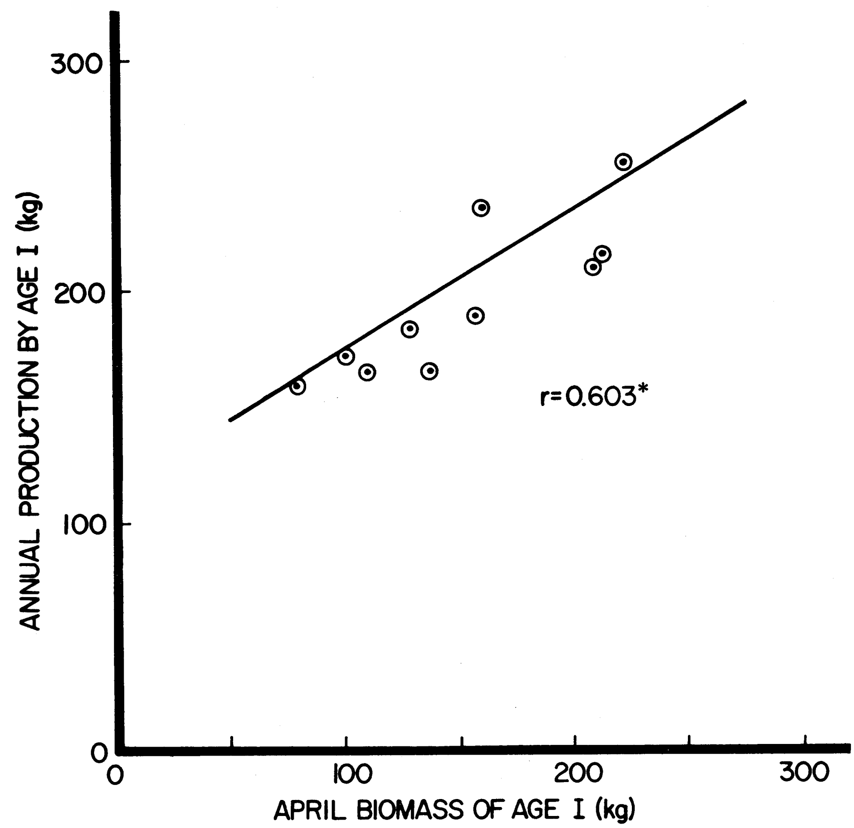




APPENDIX FIGURE 7. *Relation of summer survival of age 0 stocks of brook trout to the number of age 0 brook trout present in June in Lawrence Creek.*

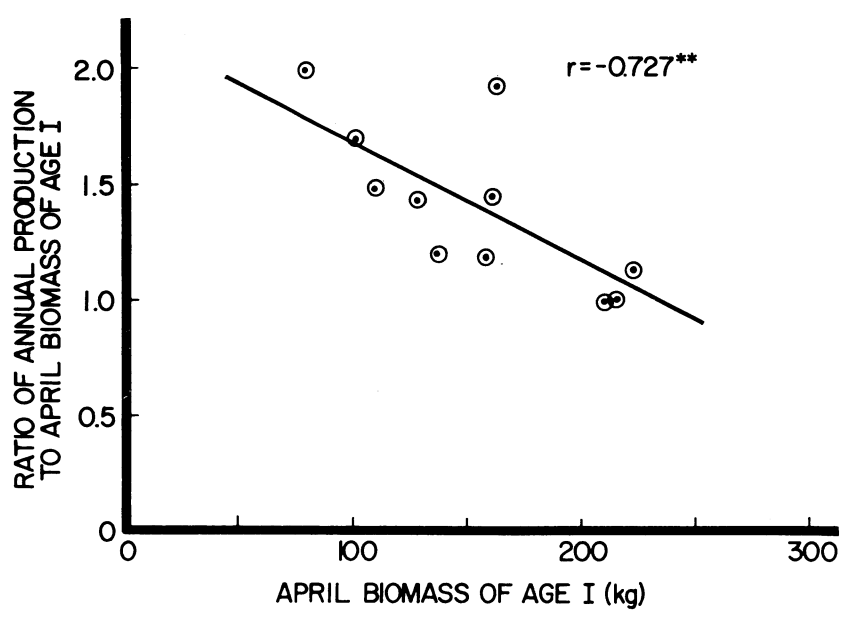
APPENDIX FIGURE 8. *Relation of annual production by age 0 brook trout to the mean number of age I brook trout present during the April-September period in Lawrence Creek.*

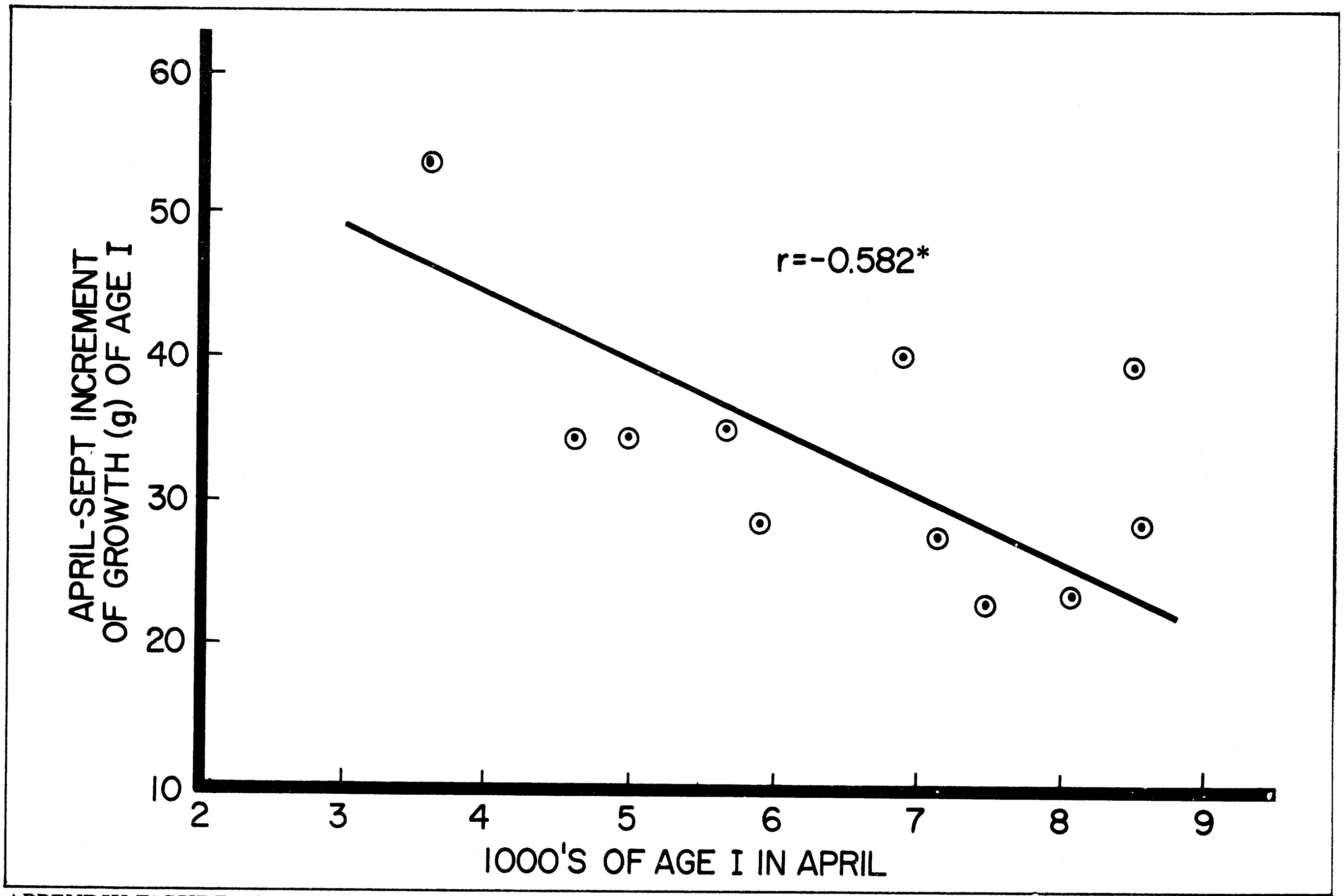




APPENDIX FIGURE 9. *Relation of annual production to April biomass for age I stocks of brook trout in Lawrence Creek.*

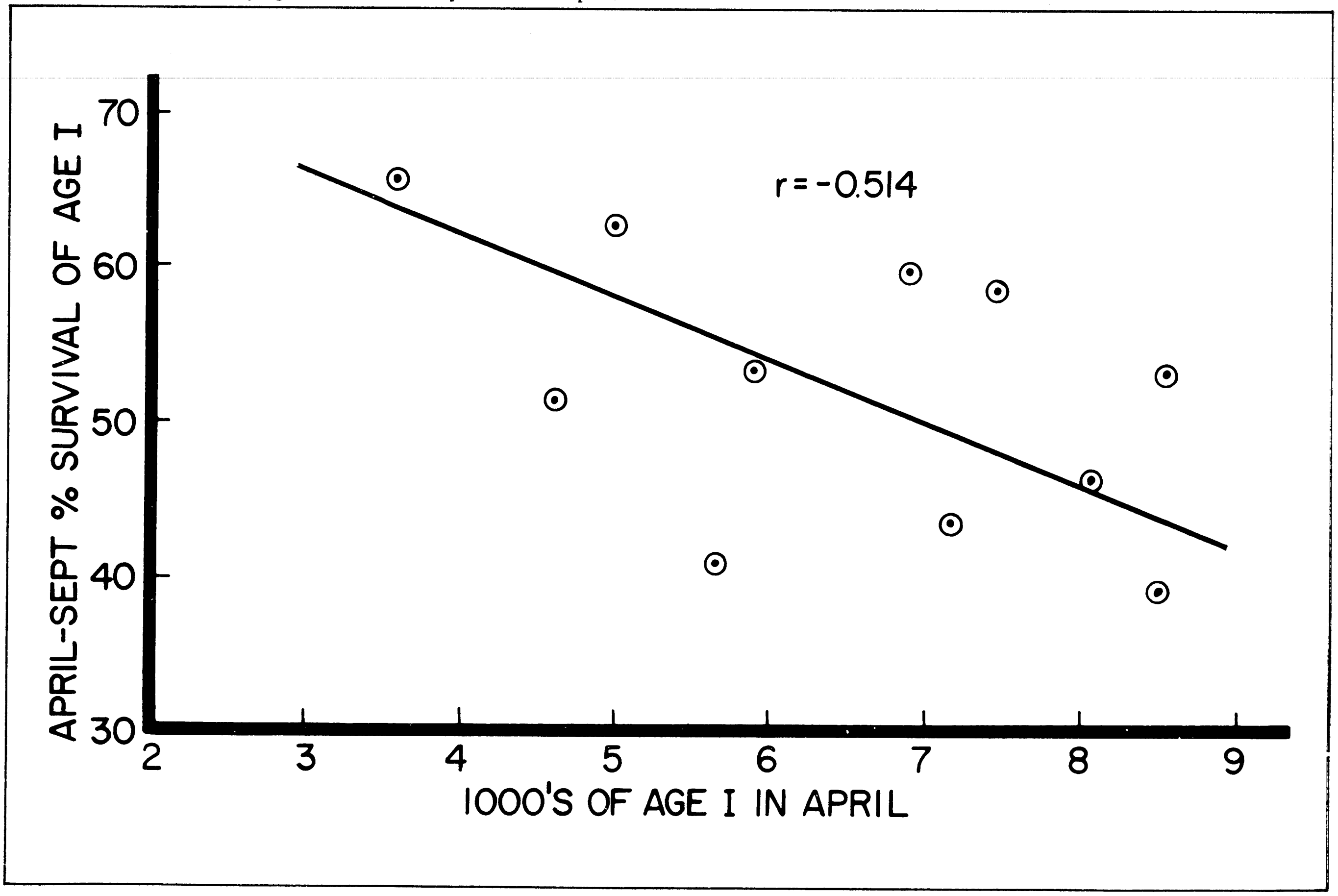
APPENDIX FIGURE 10. *Ratios of annual production to April biomass for age I stocks of brook trout in Lawrence Creek.*

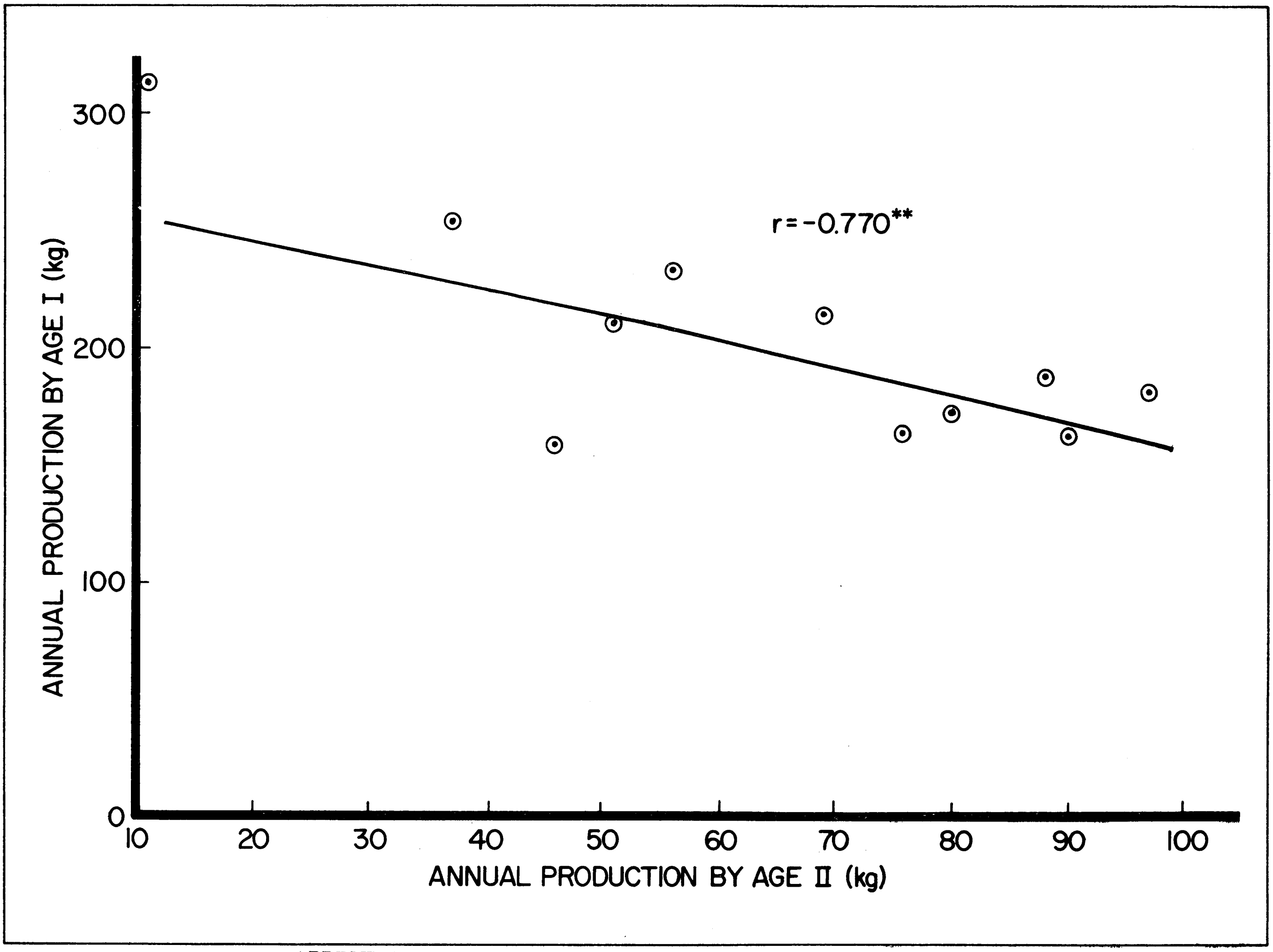




APPENDIX FIGURE 11. *Relation of summer growth of age I stocks of brook trout in Lawrence Creek to the number of age I brook trout present in April.*

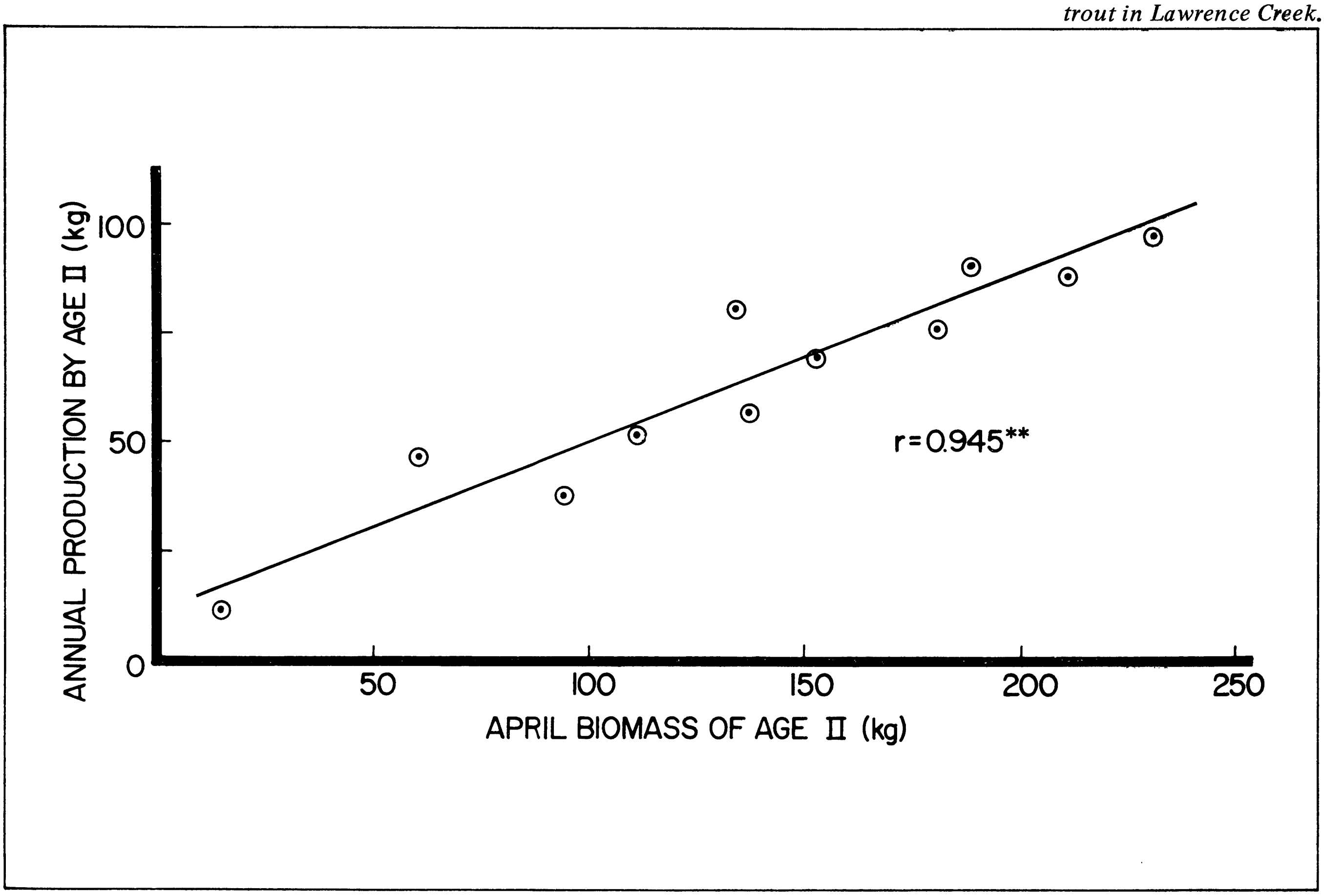
APPENDIX FIGURE 12. *Relation of summer survival of age I stocks of brook trout in Lawrence Creek to the number of age I brook trout present in April.*

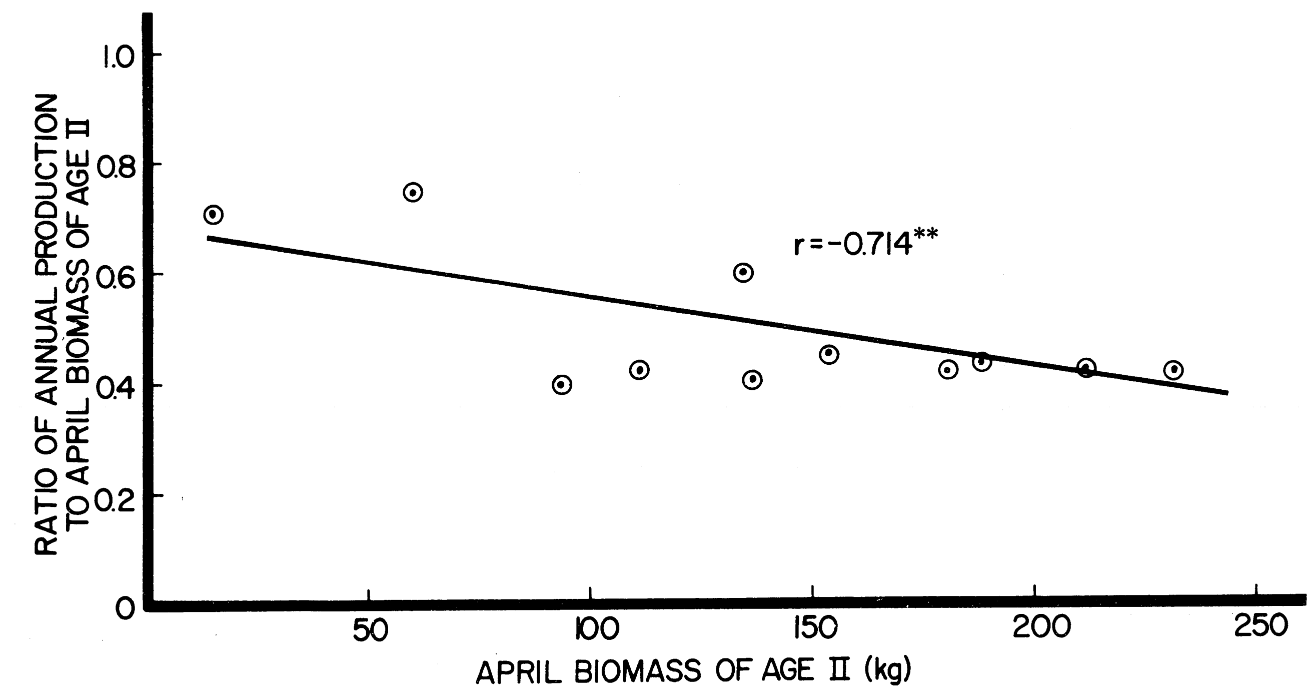




APPENDIX FIGURE 13. *Relation of annual production by age I stocks of brook trout to annual production by age II stocks of brook trout in Lawrence Creek.*

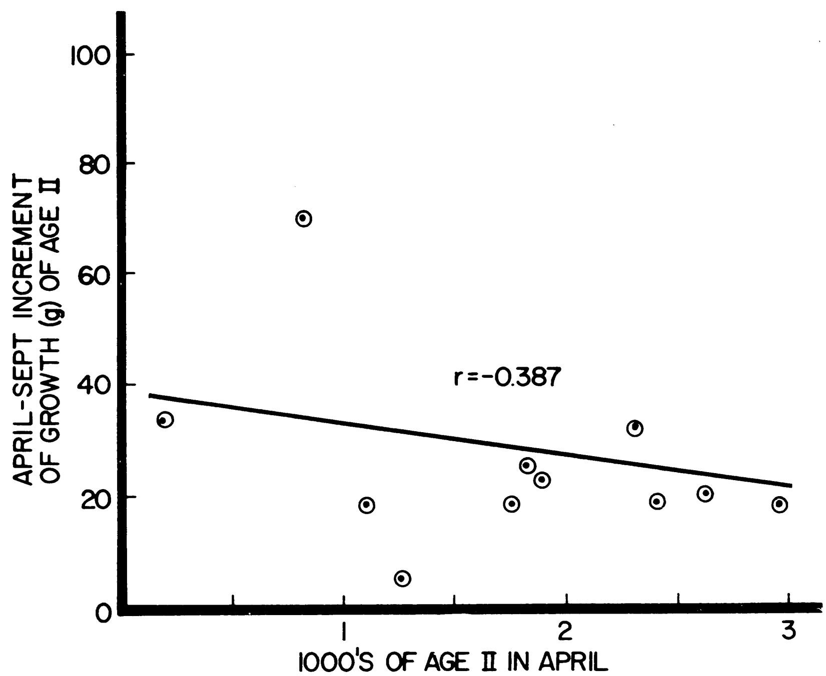
APPENDIX FIGURE 14. *Relation of annual production to April biomass for age II stocks of brook trout in Lawrence Creek.*

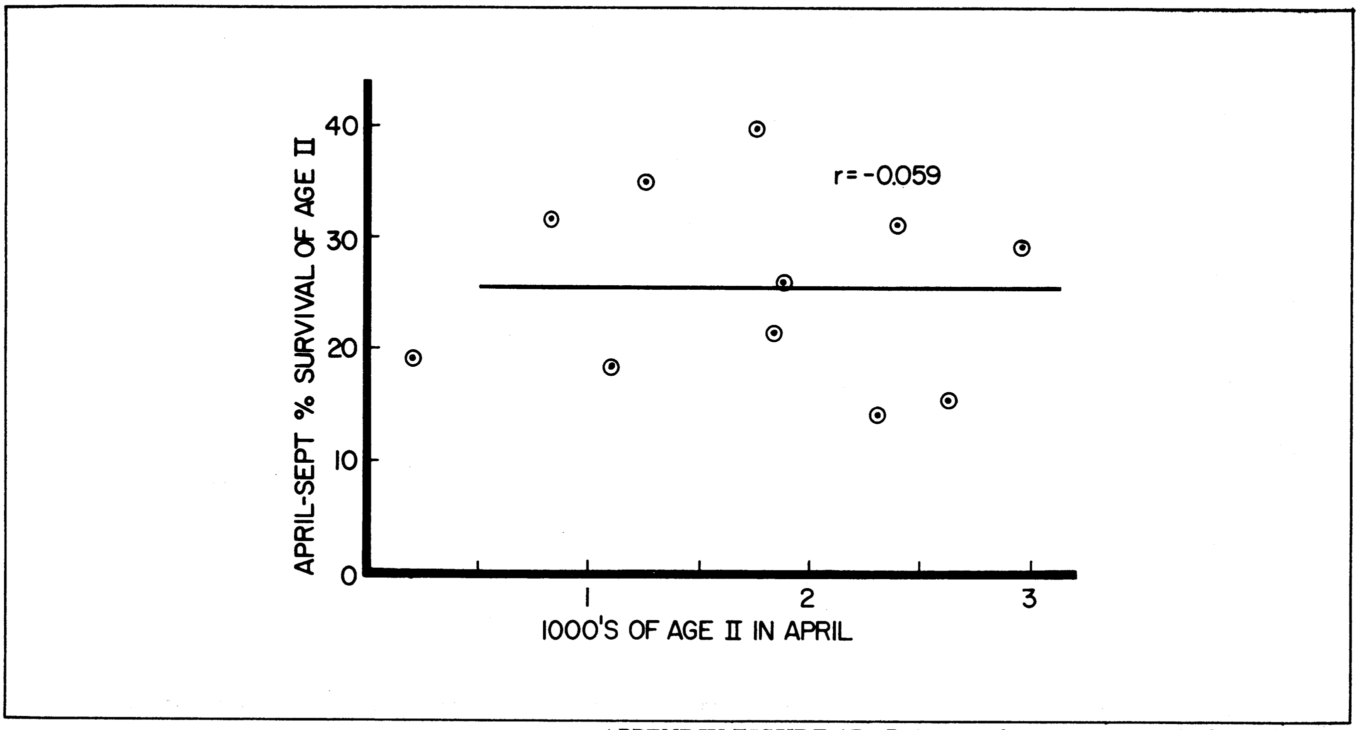




APPENDIX FIGURE 15. *Ratios of annual production to April biomass for age II stocks of brook trout in Lawrence Creek.*

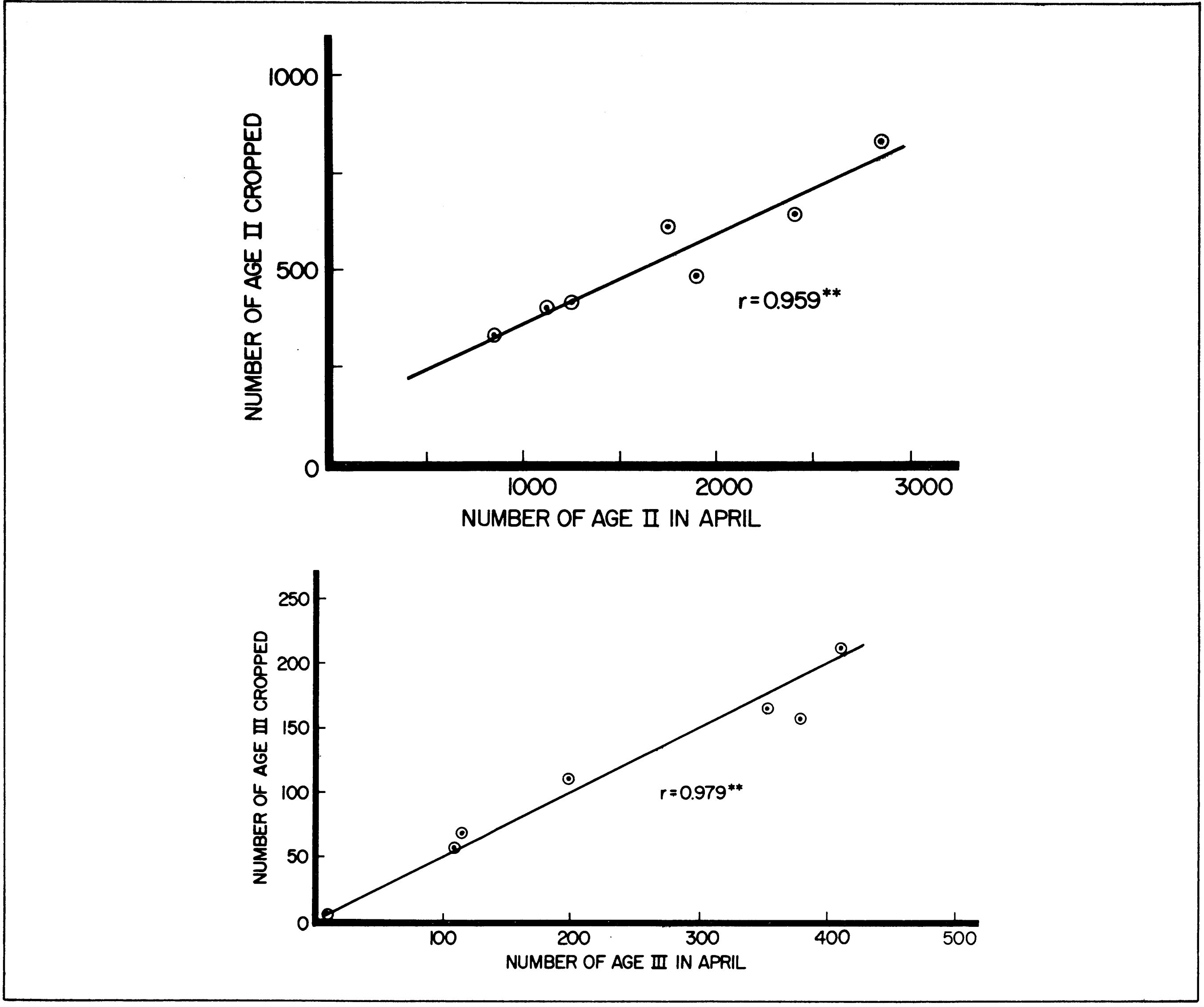
APPENDIX FIGURE 16. *Relation of summer growth of age II stocks of brook trout in Lawrence Creek to the number of age II brook trout present in April.*

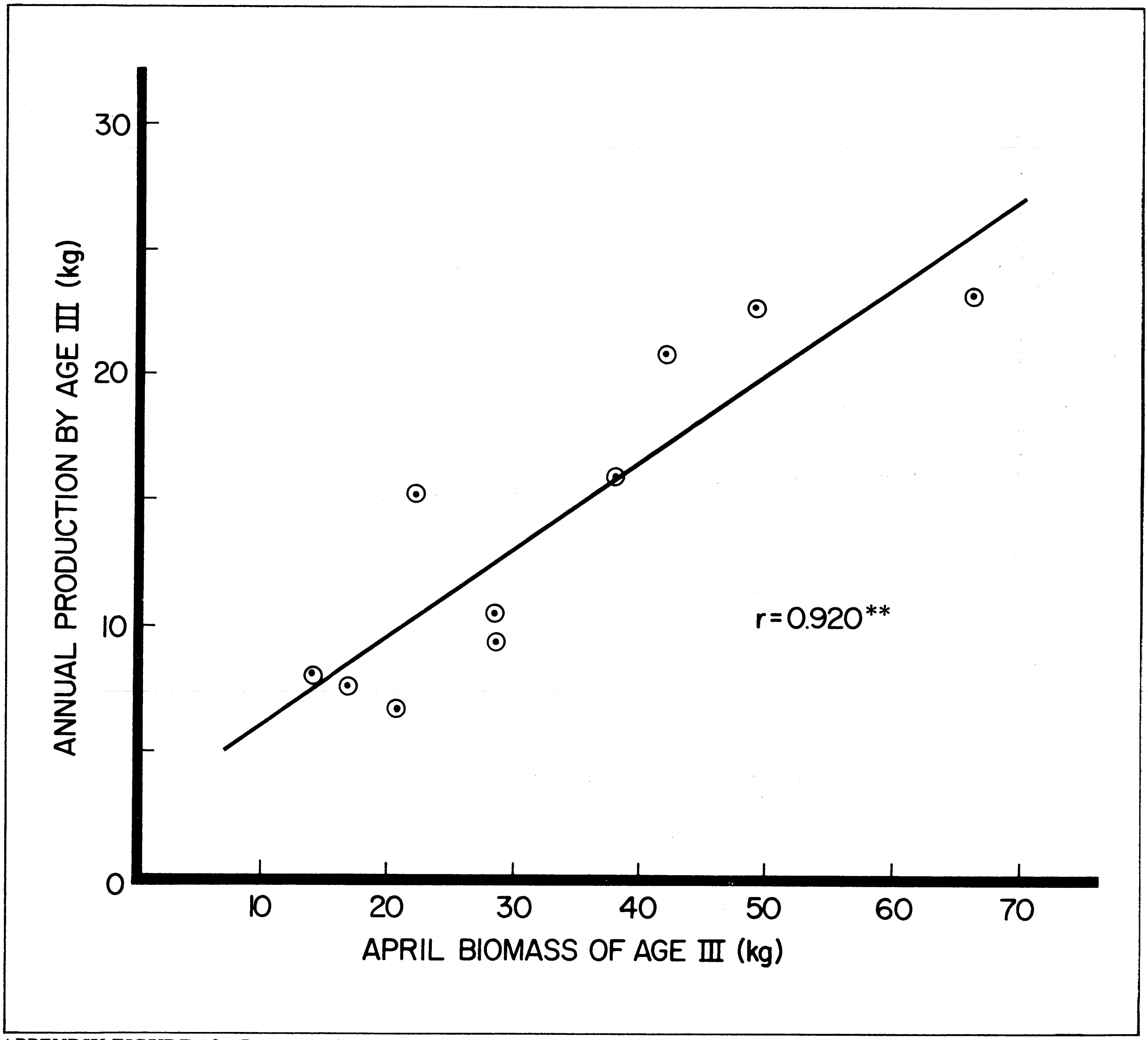




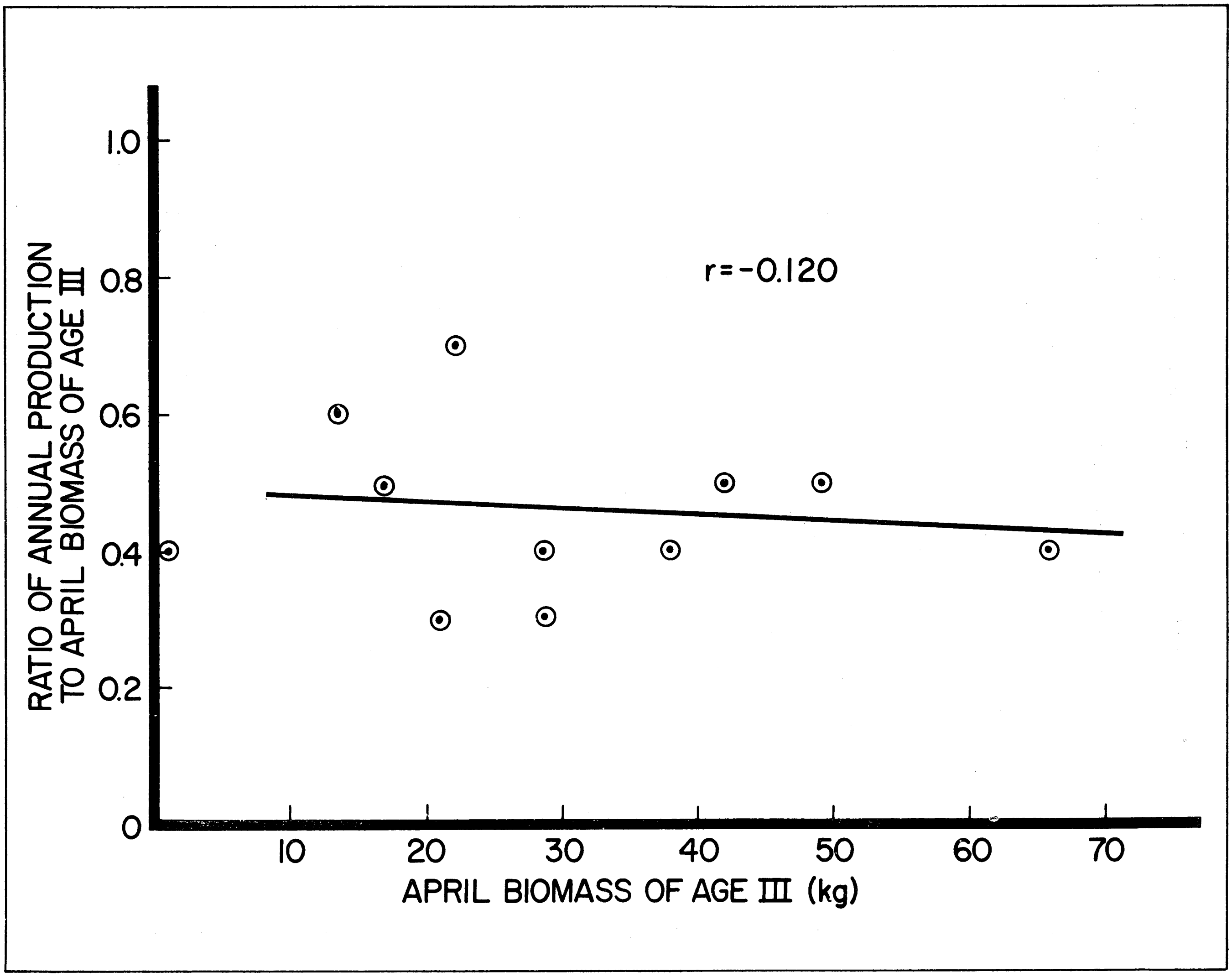
APPENDIX FIGURE 17. *Relation of summer survival of age II stocks of brook trout in Lawrence Creek to number of age II brook trout present in April.*

APPENDIX FIGURE 18. *Yields of age II and age III brook trout in relation to the numbers of age II and age III brook trout present in April in Lawrence Creek.*

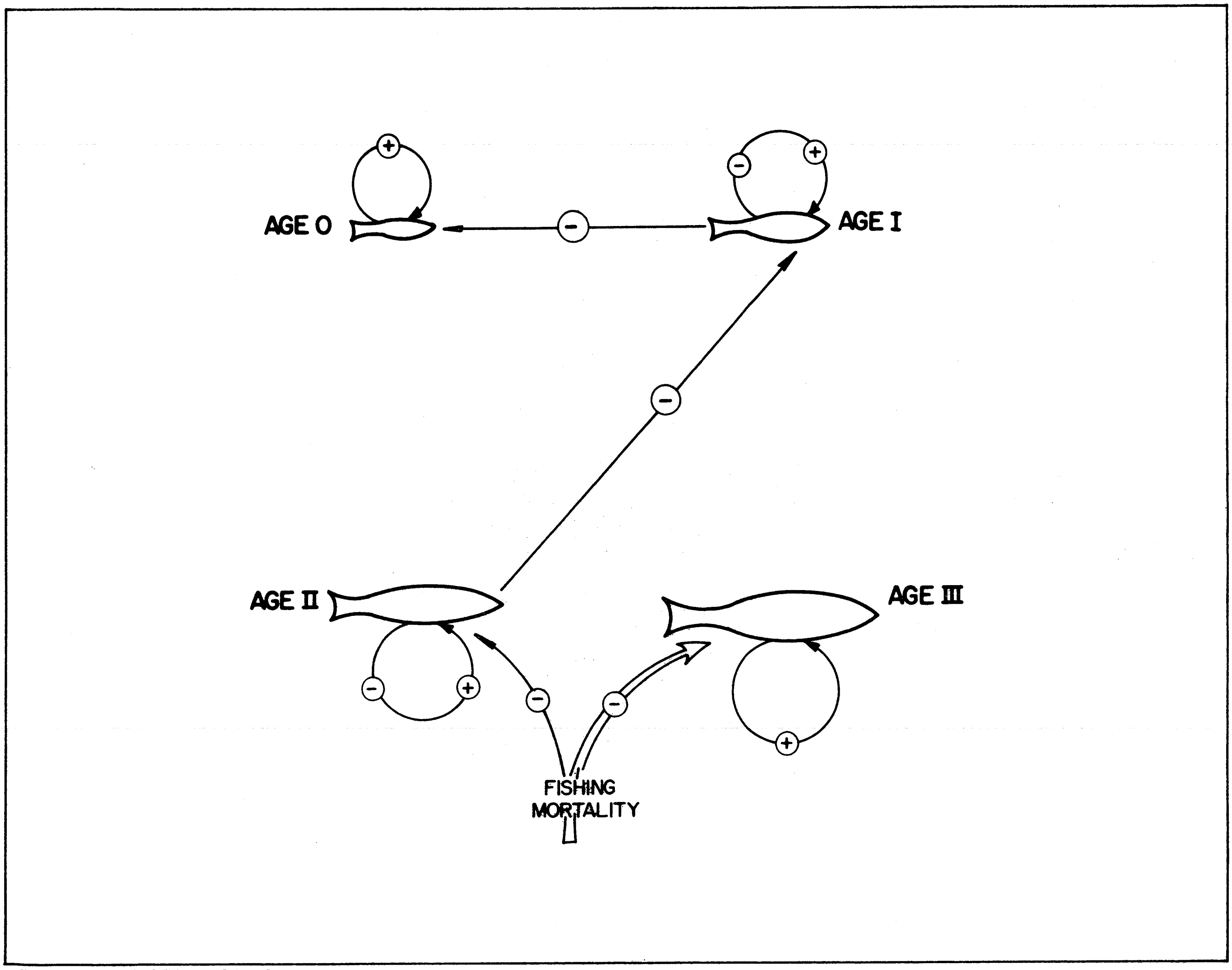




APPENDIX FIGURE 19. *Relation of annual production to April biomass for age III stocks of brook trout in Lawrence Creek.*



APPENDIX FIGURE 20. *Ratios of annual production to April biomass for age III stocks of brook trout in Lawrence Creek.*



APPENDIX FIGURE 21. *Schematic model of some inter-age group and intra-age group relationships that regulate annual production by the brook trout population in Lawrence Creek.*

APPENDIX TABLE 1. *Number and kilograms of brook trout in Lawrence Creek summarized by age group and time of year during 1960-70.*

	April										June	
	I		II		III		IV+		I-IV+		0	
Year	No.	Kg.	No.	Kg.	No.	Kg.	No.	Kg.	No.	Kg.	No.	Kg.
1960	8,510	163.4	210	15.3	197	22.1	2	1.0	8,919	201.8	10,017	37.1
1961	3,602	80.4	827	60.3	10	1.0	5	1.2	4,444	142.9	16,468	56.0
1962	8,567	223.5	1,113	93.8	107	16.8	1	0.2	9,788	334.3	11,051	36.7
1963	4,644	110.7	2,409	188.4	114	13.6	17	3.5	7,184	316.2	15,324	58.7
1964	7,489	212.1	1,269	111.0	380	49.0	20	4.4	9,158	376.5	13,964	52.5
1965	5,003	101.2	1,889	134.6	199	21.1	46	7.1	7,137	264.0	12,254	29.2
1966	6,915	161.4	1,764	137.7	355	38.1	29	5.3	9,063	342.5	10,316	45.8
1967	5,932	128.6	2,960	230.7	407	42.4	35	17.4	9,334	419.1	9,124	32.6
1968	5,696	136.7	2,320	180.6	559	66.1	79	11.7	8,654	395.1		
1969	8,046	214.2	1,834	153.1	205	28.5	39	7.9	10,124	403.7		
1970	7,180	158.2	2,635	211.1	223	28.6	30	5.8	10,068	403.7		

	September											
	0		I		II		III		IV+		0-IV+	
Year	No.	Kg.	No.	Kg.	No.	Kg.	No.	Kg.	No.	Kg.	No.	Kg.
1960	8,507	82.2	3,324	193.9	40	4.3	11	1.7	0	0	11,882	282.1
1961	14,313	156.3	2,360	179.0	261	37.6	3	0.7	0	0	16,937	373.6
1962	7,611	69.4	4,523	248.0	203	20.7	22	4.0	0	0	12,359	342.1
1963	10,367	114.4	2,388	138.2	750	72.5	37	5.6	5	1.6	13,547	332.3
1964	9,680	102.6	4,382	226.9	445	40.6	117	15.8	7	1.3	14,631	387.2
1965	8,452	88.8	3,138	175.5	487	46.2	60	6.8	6	1.2	12,143	318.5
1966	8,192	103.8	4,115	252.4	700	67.0	89	12.2	7	1.6	13,103	437.0
1967	7,895	87.3	3,162	164.5	866	82.4	128	15.6	15	2.5	12,066	352.3
1968	8,433	116.2	2,330	138.7	327	35.2	86	11.4	18	2.8	11,194	304.3
1969	10,039	126.6	3,728	184.1	390	41.6	48	7.2	15	3.3	14,220	362.8
1970	13,870	135.4	3,115	154.1	409	40.0	41	5.9	7	1.9	17,442	337.3

APPENDIX TABLE 2. *Annual yield of brook trout from Lawrence Creek during the 1961-67 fishing seasons*

	Yield in kg by Age Group				Total for Season
Year	I	II	III	IV+	(kg)
1961	9.6	37.9	0.6	0.7	48.8
1962	7.7	42.3	9.6	–	59.6
1963	2.2	65.6	7.2	1.9	76.9
1964	4.0	42.1	19.3	2.4	67.8
1965	4.2	49.3	12.1	5.7	71.3
1966	7.0	63.0	19.7	2.6	92.3
1967	2.5	89.6	25.4	3.2	120.7
Avg.	5.3	55.7	13.4	2.4	76.8

LITERATURE CITED

ALLEN, K. R.
1969. Limitations on production in salmonid populations in streams. Pages 3-18. *in* Symposium on salmon and trout in streams. T. G. Northcote (ed.). H. R. MacMillan Lectures in Fisheries, Univ. of British Col., Vancouver, Can.

CHAPMAN, D. W.
1965. Net production of juvenile coho salmon in three Oregon streams. Trans. Am. Fish. Soc. 94(1):40-42.

CHAPMAN, D. W. and T. C. BJORNN
1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153-176. *in* Symposium of salmon and trout in streams. T. G. Northcote (ed.). H. R. MacMillan Lectures in Fisheries, Univ. of British Col., Vancouver, Can.

EGGLISHAW, H. J.
1970. Production of salmon and trout in a stream in Scotland. J. Fish. Biol. 2:117-136.

GERKING, S. D.
1962. Production and food utilization in a population of bluegill sunfish. Ecol. Monogr. 32:31-78.

GERKING, S. D., ed.
1967. The biological basis of freshwater fish production. John Wiley and Sons, Inc., N. Y., N. Y. 495 pp.

HUNT, R. L.
1965. Dispersal of wild brook trout during their first summer of life. Trans. Am. Fish. Soc. 94(2):186-188.
1966. Production and angler harvest of wild brook trout in Lawrence Creek, Wisconsin. Wis. Conserv. Dep. Tech. Bull. No. 35. 52 pp.
1969. Effects of habitat alteration on production, standing crops and yield of brook trout in Lawrence Creek, Wisconsin. Pages 281-312. *in* Symposium on salmon and trout in streams. T. G. Northcote (ed.). H. R. MacMillan Lectures in Fisheries, Univ. of British Col., Vancouver, Can.
1970. A compendium of research on angling regulations for brook trout conducted at Lawrence Creek, Wisconsin. Wis. Dep. Nat. Resour. Res. Rep. No. 54. 37 pp.
1971. Responses of a brook trout population to habitat development in Lawrence Creek. Wis. Dep. Nat. Resour. Tech. Bull. No. 48. 35 pp.

HUNT, R. L., O. M. Brynildson and J. T. McFadden
1962. Effects of angling regulations on a wild brook trout fishery. Wis. Conserv. Dep. Tech. Bull. No. 26. 58 pp.

LECREN, E. D.
1969. Estimates of fish populations and production in small streams in England. Pages 269-280. *In* Symposium on salmon and trout in streams. T. G. Northcote (ed.). H. R. MacMillan Lectures in Fisheries, Univ. of British Col., Vancouver, Can.
1972. Fish production in freshwaters. Symp. Zool. Soc. London. No. 29. pp. 115-133.

MCFADDEN, J. T.
1961. A population study of the brook trout, *Salvelinus fontinalis.* Wildl. Monogr. No. 7. 73 pp.

MILLER, J. M.
1970. An analysis of the distribution of young-of-the-year brook trout, *Salvelinus fontinalis* (Mitchell), in Lawrence Creek, Wisconsin. Ph.D. Thesis. Univ. Wis., Madison. 118 pp.

RICKER, W. E.
1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 119. 300 pp.

RICKER, W. E., ed.
1968. Methods for assessment of fish production in fresh waters. Blackwell Sci. Publ., Oxford, Engl. 313 pp.

WHITE, D. A.
1967. Trophic dynamics of a wild brook trout stream. Ph.D. Thesis. Univ. Wis., Madison, 183 pp.

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