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Title: THE DYNAMICS OF EXPLOITED GUPPY POPULATIONS EXPOSED TO DIELDRIN

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Sixteen populations of guppies (Poecilia reticulata) were established in laboratory aquariums. Eight populations were exposed to dieldrin at a mean concentration of 0.525 ppb in the water and 2.11 ppm in the food, tubificid worms. Eight populations received control water and food. All populations were fed three grams of tubificid worms per day.

Exploitation rates of 0.60, 0.45, 0.30, and 0.15 were selected. Each rate was assigned to two control populations and two populations exposed to dieldrin. All fish except the young (less than nine millimeters) in each population were exploited at their designated rate according to a systematic exploitation schedule every 28 days. All populations were exploited fifteen times.

The number of fish in the exploited phase of populations exploited at 0.60 remained stable during most of the experiment. Populations exposed to dieldrin maintained a greater number of fish than control

populations through increased recruitment. Apparently, dieldrin reduced the cannibalistic behavior of adult guppies and allowed more young to survive to recruitment size. The biomass and yield in weight of control populations and populations exposed to dieldrin was similar. Increased recruitment in populations exposed to dieldrin was therefore compensated by reduced growth.

Reductions in recruitment resulting from increased cannibalism on young fish caused the number of fish in the exploited phase of populations exploited at 0.45, 0.30, and 0.15 to decline. Populations exposed to dieldrin maintained the same number of fish and followed the same trends as control populations. These populations maintained a high density of adult fish and intraspecific competition for food may have overcome the tendency of dieldrin to reduce cannibalistic behavior.

Although population number declined, the biomass and yield in weight of these populations remained stable. Reductions in recruitment had not yet caused a major decline in the number of adults and may have been compensated by increased fish growth. As population number declined, the average length and weight of the catch increased. Populations exploited at 0.45, 0.30, and 0.15 were apparently beginning to undergo periodic cycles.

Mean equilibrium yield in weight declined as exploitation rate was reduced. Yield in weight of each population was located on the descending limb of a surplus-yield curve.

Age, growth, production, and yield in weight of females in populations exploited at 0.60, 0.45, and 0.30 were determined from the length-frequency distributions of the catch. At each exploitation rate, during the younger age classes, when the production of a cohort of females was greater than its yield, the biomass of the cohort increased. During the older age classes, when yield became greater than production, the biomass of the cohort declined.

As exploitation rate increased, the mean individual weight of each age class and the relative growth rate of fish of a particular weight also increased. Increased growth enabled fish from high exploitation rates to maintain greater production and yield than fish from low exploitation rates.

The Dynamics of Exploited Guppy Populations Exposed to Dieldrin

by

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THE DYNAMICS OF EXPLOITED GUPPY POPULATIONS EXPOSED TO DIELDRIN

INTRODUCTION

The organochlorine insecticide dieldrin is ubiquitous in distribution in marine and freshwater environments. Effects of sublethal concentrations of dieldrin and other pesticides on survival, growth, and reproduction; uptake and elimination of pesticides; and pesticide levels in tissues of several species of organisms have been extensively studied and are summarized in reviews by Cope (1966), Moore (1967), and Nicholson (1967).

The presence of dieldrin in aquatic systems represents a potential hazard to economically important fish populations. Gathering information from natural populations for adequate understanding and assessment of the long-term impact of a toxicant on the complex relationships within fish populations is difficult. Fish populations maintained under controlled laboratory conditions can be useful in developing and examining concepts of population dynamics and determining the consequences of exposure to pesticides.

The ovoviviparous guppy (Poecilia reticulata) has been used successfully in the laboratory as a model of natural exploited fish populations (Silliman and Gutsell, 1958; Silliman, 1968). Guppies are well-suited for population studies because of their high reproductive potential, short life span, and tolerance to handling. Silliman and

Gutsell (1958) list several similarities and differences between laboratory guppy populations and natural exploited fisheries.

Guppies have also been used to examine sublethal effects of pesticides (Mount, 1962; Stock and Cope, 1969) and various other toxicants (Crandall and Goodnight, 1962). Roelofs (1971) found that 1.0 ppb and 2.5 ppb of dieldrin reduced the intrinsic rate of increase of guppies. This reduction resulted from delay in age at first reproduction and decrease in total number of offspring. A single, short, initial exposure to 0.05 ppm of dieldrin did not affect the reproduction of guppies over a twelve month period (Hubble and Reiff, 1967).

Cairns and Loos (1966) and Cairns, Foster, and Loos (1967) examined the effects of sublethal concentrations of dieldrin on unexploited guppy populations. Populations exposed to dieldrin developed greater numbers of fish than control populations over the initial months of the experiment. The authors concluded that dieldrin reduced cannibalism on young guppies by large adults and, thus, enhanced the survival of young fish. After six months, however, the number of fish in populations exposed to dieldrin declined to the level of control populations.

The feasibility of using guppies as models of natural populations and as test organisms in toxicity studies seems evident. With due constraint, aspects of the dynamics of guppy populations and their response to toxicants may be applied to natural fish populations.

The principle objectives of this investigation were twofold. First, the following aspects defining the dynamics of guppy populations fed a limited amount of food and subjected to different rates of exploitation were examined: 1) population number and yield in number, population biomass and yield in weight, and average length and weight of the catch; 2) female fecundity and reproduction; 3) growth, biomass, production, and yield of each age class of female guppies in the exploited phase of the fishery. Second, the impact of dieldrin on each of these aspects was assessed.

METHODS AND MATERIALS

Experimental Apparatus and Materials

Sixteen populations of guppies were established in laboratory aquariums. Eight populations were exposed to dieldrin and eight served as control populations.

Aquariums were constructed of plexiglas and each had a volume of 34.8 liters. The aquariums were covered with removable glass plates to prevent fish from escaping.

One hundred percent technical grade dieldrin was used in the experiment. Dieldrin contains not less than 85 percent of the insecticidally active compound HEOD. Dieldrin concentration, assayed by gas chromatography, is expressed as parts per billion of HEOD.

The pesticide dilution system was similar to the continuous flow dilution apparatus described by Chadwick et al. (1972). Filtered stream water was passed through a column of small gravel coated with dieldrin. The effluent from the column was then diluted to the appropriate concentration with control water. Water was introduced into all aquariums at a rate of 200 milliliters per minute. Continuous water flow assured maintenance of a constant concentration of dieldrin in the aquariums and rapid removal of waste products.

Fish accumulate dieldrin directly from water and also from food organisms. Dieldrin was therefore introduced into aquariums not

only through the water but also through the food, tubificid worms (Tubifex sp.), that had been previously exposed to dieldrin.

Dieldrin was introduced through the water at a mean concentration of 0.525 ppb of HEOD. Information gathered previously at our laboratory suggests that 0.5 ppb is the concentration that first affects the growth of newborn guppies. The 96-hour LC50 of newborn guppies from flowing water bioassay is 3.2 ppb. The 96-hour LC50 of mature female guppies weighing one gram is 23.6 ppb (Perry Anderson, personal communication).

Each population was fed a fixed ration of three grams of live tubificid worms per day. Worms fed to populations receiving dieldrin were held in 5.0 ppb of dieldrin for 24 hours prior to feeding. The worms accumulated 2.11 ppm of HEOD in their tissues.

Aquariums were provided with plants (Ceratophyllum demersum) as refuges for newborn guppies. Plants were placed in cylindrical, ungalvanized chicken-wire cages approximately ten centimeters in diameter and extending from the bottom of the aquarium to the water surface. As the plants grew, stems protruding through the wire were removed to keep the quantity of plants in each cage relatively constant. Three cages were placed in each aquarium. The cages were approximately 30 centimeters apart and arranged in a triangular pattern. Aquariums received 18 hours of illumination per day from flourescent lights placed 0.9 meters above the water surface.

Exploitation Procedures

Populations were separated into size groups for convenience during exploitation. Groups were also distinguished by sex and reproductive maturity. The size groups were young (less than 9 millimeters); immature (9 to 18.5 millimeters); young adult females (18.6 to 25.5 millimeters); adult females (longer than 25.6 millimeters); and adult males (possessing male coloration and gonopodium). At maturity, males begin to grow more slowly than females. Adult males are therefore considerably smaller than females of the same age.

Each population was established with 244 fish having the following size group distribution: 100 young, 80 immatures, 20 young adult females, 12 adult females, and 32 adult males. The initial biomass of the populations ranged from 21.927 to 24.665 grams.

Exploitation rates of 0.60, 0.45, 0.30, and 0.15 were selected. Each rate was assigned to two control populations and two populations exposed to dieldrin. Populations were exploited at their designated rate every 28 days. The date that a particular population was exploited was termed an exploitation point. The first exploitation point occurred 28 days after each population was established. Exploitation of each population at its designated rate was continued through fifteen exploitation points.

The method of exploitation was similar to that employed by Silliman and Gutsell (1958). A systematic exploitation schedule was developed for each exploitation rate. The schedule provided for the removal of a proportion of the population corresponding to the exploitation rate.

At an exploitation point, fish were removed from an aquarium and sorted into size groups. Each size group, except the young, was exploited at the rate assigned to the population. Fish from each size group were placed in an enamel pan and selected one by one. To avoid bias the largest fish was chosen first and selection was continued until the last, or smallest, fish was chosen. As the fish were selected, they were assigned successive positions in the number series of the exploitation schedule (Table 1). Fish assigned to certain fixed numbers in the series, designated exploitation numbers, were removed. All other fish were returned to the aquarium.

When the last number in the series was reached, the next fish selected was assigned the first number in the series. The procedure was continued until all fish in a particular size group were selected, assigned numbers in the series, and either removed or returned to the aquarium. The number assigned to the last fish in the size group was recorded and, at the next exploitation point, exploitation of that size group was begun with the next number in the series.

Table 1. Exploitation schedules for each exploitation rate. Exploitation numbers in each series were randomly chosen before the experiment was begun and remained unchanged throughout the experiment.

Exploitation Rate	Number Series	Total Number of Fish Removed in the Series	Exploitation Numbers
0.60	1-10	6	3, 5, 6, 7, 8, 9
0.45	1-20	9	4, 6, 7, 9, 10 11, 15, 18, 20
0.30	1-10	3	1, 3, 4
0.15	1-20	3	3, 5, 20

If, for example, at the 0.60 exploitation rate, the last fish in a size group was assigned number four, at the following exploitation point the first, or largest, fish selected would be assigned number five. This procedure ensures that the largest fish in the size group has an equal chance of being removed or remaining in the population.

Total weight and number of fish removed from a population and fish returned to the aquarium were measured. Length and weight of immatures, young adult females, and adult females removed from the population were recorded. Young adult females and adult females were cut open and the eggs counted. Each aquarium was examined daily for dead fish.

Determination of Age and Growth of Female Guppies from the Length-Frequency Distribution of the Catch

Direct determination of age and growth in guppy populations is very difficult. Since reproduction occurs continuously, guppy populations do not possess discrete age groups or year classes. Annuli do not appear on scales of guppies raised under constant laboratory conditions. In addition, because of their small size, marking guppies by standard methods is not feasible.

Therefore, an indirect method of age and growth determination was developed. The method, involving the use of the length-frequency distribution of the catch, is admittedly limited and embodies several assumptions which will be examined.

Since female guppies grow more rapidly and reach a larger size than male guppies after maturity, only age and growth of females was determined. The following terms will be used to describe the method of determining age and growth of females in exploited guppy populations from the length-frequency distribution of the catch:

1. Exploited phase of the fishery - Segment of the fish population 9 millimeters or larger at an exploitation point.
2. Cohort - All fish in a particular population that have entered the exploited phase of the fishery between the same two exploitation points. A population is composed of several cohorts at an exploitation point. The cohorts of the

population are distinguished by the particular exploitation points between which they entered the exploited phase.

3. Size class - Length range of females of the same cohort.
4. Age class - Group of female fish that have passed the same number of exploitation points. Age class indicates the number of times a cohort of females has been exploited and is, therefore, an index of age of the cohort in units of 28 days from the time the cohort entered the exploited phase.

Three major assumptions were made in determining age and growth from the length-frequency distribution of the catch. First, natural mortality in the exploited phase of the fishery was negligible. Second, at each exploitation rate, recruits enter the exploited phase between exploitation points at a constant rate. The number of recruits entering the exploited phase between exploitation points, or the number of fish in a cohort at recruitment, remained constant over all exploitation points from which the catch was used to determine age and growth. Third, fish of the same length grew at approximately the same rate.

Following the movement of a theoretical cohort of females through the exploited phase of a guppy fishery at equilibrium may be helpful in understanding the rationale for determining age and growth from the length-frequency distribution of the catch.

Between exploitation points, fish enter the exploited phase by reaching nine millimeters length. All fish that are nine millimeters or larger and first become exposed to exploitation at an exploitation point become identified as a particular cohort. During the period in which these fish first enter the exploited phase of the fishery, they are considered to be age class 0 since the fish have never been exposed to exploitation.

At an exploitation point, the cohort has N_O number of fish, is size class A and has mean individual length L_A. The number of fish in the cohort is reduced by exploitation from N_O to $N_O(1-c)$ where c is the exploitation rate. The number of fish removed from the cohort, or the catch, is $N_O c$. The yield of the cohort as age class 0 is therefore the catch at the first exploitation point.

Size class and mean individual length of the cohort can be determined from the length-frequency distribution of the catch (Figure 1). Because sampling was systematic, the number of fish of a given length in the catch is proportional to the number of fish of that length in the population. If natural mortality in the exploited phase is negligible and recruitment proceeds at a constant rate, the length-frequency distribution of the cohort and the catch from the cohort at the first exploitation point will be a rectangle with abscissal length equal to the

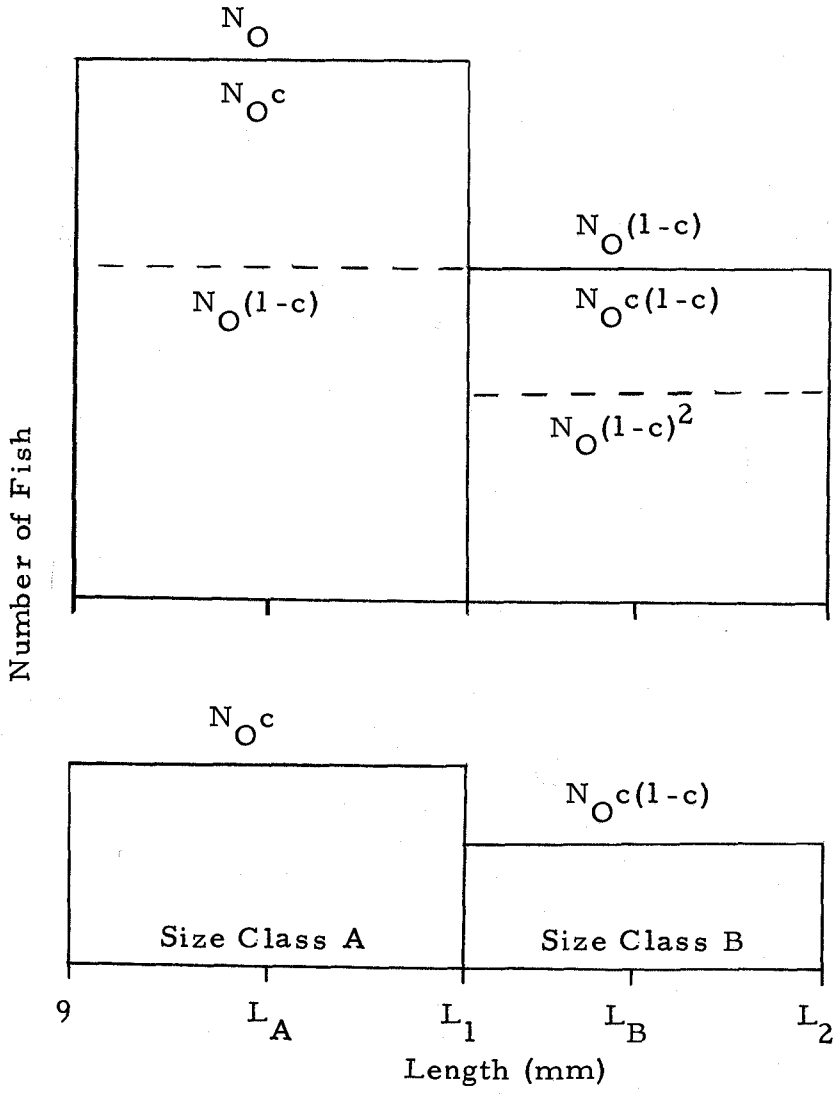

Figure 1. Theoretical length-frequency distribution of a cohort (upper figure) and the catch from the cohort (lower figure) at the first and second exploitation points. L_A is the mean individual length at the first exploitation point and L_B is the mean individual length at the second exploitation point. The number of fish in the cohort at the first exploitation point is N_O and c is the exploitation rate. Areas of each section of the rectangle are indicated within that section. Total area is indicated above the rectangle.

size class. The area of the cohort rectangle is N_o and the area of the catch rectangle is $N_o c$.

After exploitation the cohort is age class 1 since it has passed one exploitation point. The initial mean individual length of the cohort as age class 1 is L_A. During the following interval between exploitation points the size range of the cohort changes continually but the number, $N_o(1-c)$, remains constant. At the next exploitation point, the cohort is size class B and has mean individual length L_B. The number of fish in the cohort is reduced from $N_o(1-c)$ to $N_o(1-c)^2$. The yield of the cohort as age class 1, $N_o c(1-c)$, is the catch at the second exploitation point.

The length-frequency distribution of the cohort and the catch from the cohort at the second exploitation point is a rectangle with abscissal length equal to size class B. The area of the rectangle representing the cohort is $N_o(1-c)$ and the area of the rectangle representing the catch is $N_o c(1-c)$.

Production of the cohort is the total amount of tissue elaborated by the cohort between exploitation points, and is the product of relative growth rate and mean cohort biomass (Chapman, 1966). After converting mean individual length to weight by a length-weight relationship, the relative growth rate of the cohort as age class 1 can be expressed as $(W_B - W_A)/0.5(W_B + W_A)$ and the mean biomass as

$0.5\ N_O(1-c)(W_B+W_A)$. Production of the cohort as age class 1 is therefore $[(W_B-W_A)/0.5(W_B+W_A)]\ [0.5N_O(1-c)(W_B+W_A)]$ or $N_O(1-c)(W_B-W_A)$. Since natural mortality in the exploited phase is absent, $N_O(1-c)(W_B-W_A)$, or the difference between the final biomass and initial biomass of the cohort, represents cohort production between exploitation points. The yield in weight of the cohort as age class 1 is $N_O c(1-c)W_B$.

The cohort will continue to increase in mean individual length and suffer reduction in number at each exploitation point until the cohort disappears from the fishery, that is, until all the fish in the cohort are caught. The number of fish in a cohort that is age class p, where p, the numerical age class designation, represents the number of exploitation points the cohort has passed, is $N_O(1-c)^p$ and the catch from the cohort at the (p+1) exploitation point is $N_O c(1-c)^p$. The catch from the cohort over its lifetime is simply N_O, the number of fish in the cohort at the first exploitation point.

The length-frequency distribution described by the cohort over its lifetime consists of a series of rectangles each determined at an exploitation point and each with area $N_O(1-c)^p$ at the (p+1) exploitation point. The length-frequency distribution of the catch from the cohort is also a series of rectangles with each rectangle having area $N_O c(1-c)^p$.

At each exploitation rate, length-frequency distributions of the catch were constructed for control populations and for populations exposed to dieldrin. The length-frequency distribution of control populations at each exploitation rate included the combined catch from both control replicates from exploitation point seven through exploitation point fifteen, when the populations were in biomass equilibrium. Similarly, the length-frequency distribution of populations exposed to dieldrin at each exploitation rate included the combined catch of two replicates over the same exploitation points. Thus, an age class in the actual or composite length-frequency distributions, constructed from the catch from two replicates over nine exploitation points, was represented by the catch from 18 individual cohorts.

The actual length-frequency distributions of the catch were more irregular than the theoretical distributions, that is, age classes were not represented by perfect rectangles (Appendix 1). In general, however, the form of both distributions was similar. Therefore, the rationale developed for the theoretical distribution was applied to the actual length-frequency distributions of the catch to determine the number of fish in each age class and their size class and mean individual length.

To construct the length-frequency distributions, the number of female fish caught at each millimeter increment in length was plotted on blocked graph paper so that each block represented one fish. For

immature fish where sex could not be distinguished, a one to one sex ratio was assumed (the proportion of females in the populations ranged from 0.47 to 0.57). One-half of the immatures in the catch were randomly chosen as females and their lengths were plotted on the length-frequency distribution of the catch.

With the population at equilibrium, the catch from an individual cohort over its lifetime in the fishery, or the total area of the length-frequency distribution of the catch from the cohort is N_O, the number of fish in the cohort as age class 0. If the total area of the composite length-frequency distribution of the catch is N_O', then the area representing the catch from age class 0 is $N_O'c$.

The upper and lower length limits of the size class of age class 0 bound the area $N_O'c$. The lower length limit was defined as nine millimeters. The upper length limit was found by counting blocks at each millimeter length increment on the abscissa beginning at nine millimeters. The length of the $N_O'c$ block was the upper length limit of the size class of age class 0.

The upper length limit of the size class of age class 0 is the lower length limit of the size class of age class 1. The area representing age class 1 in the composite length-frequency distribution of the catch is $N_O'c(1-c)$. The upper length limit was found by counting blocks beginning at the lower length limit and determining the length of the $N_O'c(1-c)$ block.

In this manner, the size class of each age class present at each exploitation rate was determined. From the size class, mean individual length and weight were found.

Since an age class is represented by the catch from 18 individual cohorts, the average number of fish in a cohort of age class p is $(N_O'/18)(1-c)^p$. The average yield in number, or the catch, at the (p+1) exploitation point is $(N_O'/18)c(1-c)^p$. If W_P is the initial mean individual weight of the cohort as age class p and W_{P+1} is the final mean individual weight at the (p+1) exploitation point, the production of the cohort as age class p is $[(W_{P+1}-W_P)/0.5(W_{P+1}+W_P)]$ $[0.5(N_O'/18)(1-c)^p(W_{P+1}+W_P)]$. The average yield in weight of the cohort at the (p+1) exploitation point is $W_{P+1}(N_O'/18)c(1-c)^p$.

These values are taken to represent only approximations or indexes of the actual values of the parameters and are limited by the extent that the assumptions made in estimating the parameters are satisfied.

RESULTS AND INTERPRETATION

Population Number

The number of fish in the exploited phase of guppy populations varied considerably between exploitation points (Figure 2). Therefore, only major, long-term trends, over several exploitation points, toward increase or decrease in population number will be considered in detail.

At 0.60 exploitation rate, the number of fish in control populations declined through exploitation point six. Past exploitation point seven, no major trends toward increase or decrease in number were evident (Figure 2). The number of fish in populations exposed to dieldrin, while fluctuating more than the number of fish in control populations, showed no apparent long-term trends throughout the experiment.

At 0.45, 0.30, and 0.15 exploitation rates, control populations and populations exposed to dieldrin exhibited major declines in number of fish in the exploited phase. The number of fish in populations exploited at 0.45 and 0.30 declined slowly throughout the experiment. At 0.15 exploitation rate, however, decline in population number was delayed until exploitation point nine.

The decline in number of fish at these exploitation rates resulted from either an increase in natural mortality in the exploited phase or

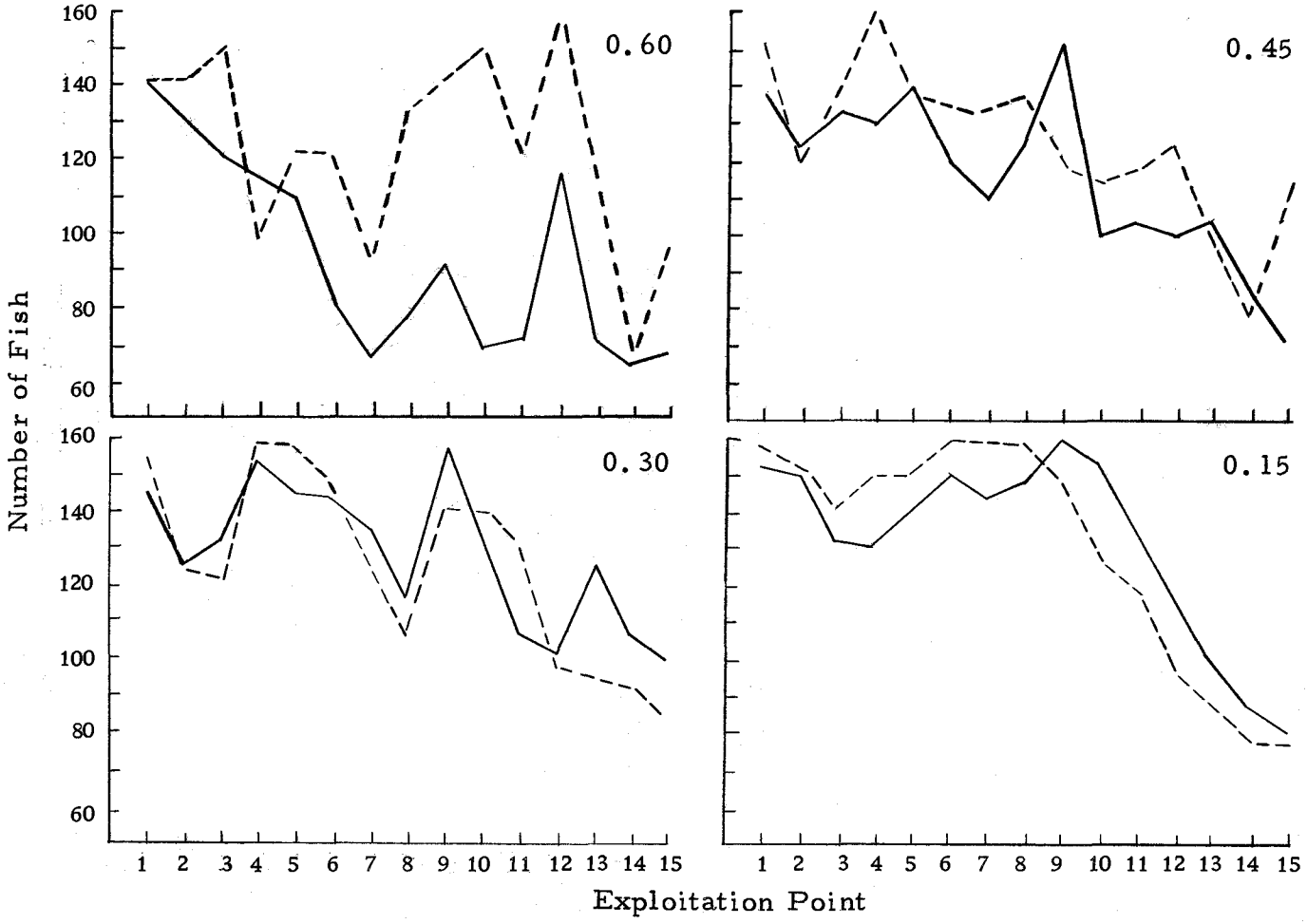

Figure 2. Number of fish in the exploited phase of the guppy fishery at each exploitation point. Exploitation rate is indicated in the upper right of each figure. At each exploitation rate, the solid line represents the average number of fish in two control populations and the broken line represents the average number of fish in two populations exposed to dieldrin.

a reduction in the number of recruits entering the exploited phase between exploitation points. Natural mortality will be considered first.

Aquariums were examined daily and very few dead fish were found. If the declines in population number resulted solely from natural mortality, many more dead fish would certainly have been observed in the aquariums. Although natural mortality in the exploited phase cannot be excluded, it is probably not as important as reduced recruitment in explaining declines in guppy population number.

Since a cohort of new recruits first appear in the exploited phase as members of the immature size group, recruitment can be monitored through changes in the number of immatures. Reductions in recruitment caused immediate decline in the density of immatures and total population density, but were not immediately apparent as a decline in the density of adult fish (Figure 3). Since some time is required for a cohort of recruits to become members of adult size groups, reduction in adult density was delayed. The density of adults began to decline slightly toward the end of the experiment, but the experiment was terminated before reduced recruitment was fully manifested as a major decline in adult density.

The time required for reductions in recruitment to appear as reductions in the number of adults depends upon fish growth rate. The effects of this time lag on biomass and yield in weight of

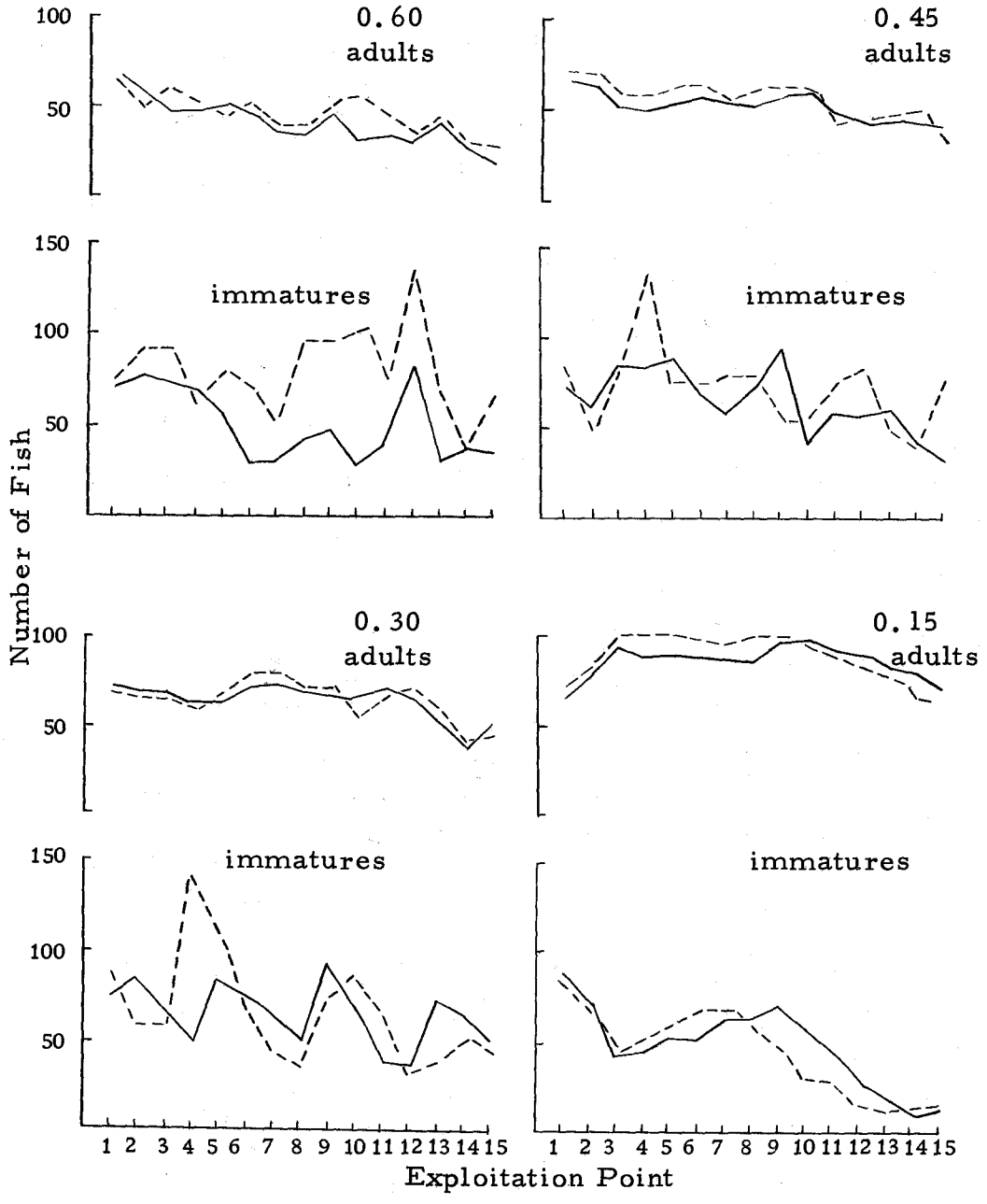

Figure 3. At each exploitation rate, number of adult fish (young adult females, adult males, adult females) and number of fish in the immature size group at each exploitation point. Exploitation rate is indicated in the upper right of each figure. At each exploitation rate, the solid line represents the average number of fish in two control populations and the broken line represents the average number of fish in two populations exposed to dieldrin.

populations undergoing continual reductions in recruitment will be discussed below.

Adults did not respond as quickly as immatures to reductions in recruitment, nor was adult density between exploitation points as variable as the density of immatures. A cohort of new recruits is generally exposed to exploitation several times as they pass through the immature size group and become adults. Apparently, as the cohorts increase in age, the variability, or magnitude of difference in number, between cohorts is reduced by successive exposures to exploitation.

Reductions in recruitment to the exploited phase of guppy populations resulted primarily from increased pre-recruit mortality of young, perhaps from cannibalism by adult guppies. Cannibalism is an effective means of population regulation in guppies held in aquariums (Breder and Coates, 1932; Silliman, 1948) and can be related to the density of adult fish (Rose, 1959).

In general, the density of adults increased as exploitation rate was reduced. Also, the mean weight of adult fish increased as population number declined (Figure 4). At the lower exploitation rates, large adults were plentiful enough to continually reduce the number of young surviving to recruitment size. Apparently, at 0.15 exploitation rate, a relatively longer period of time was required for a sufficient

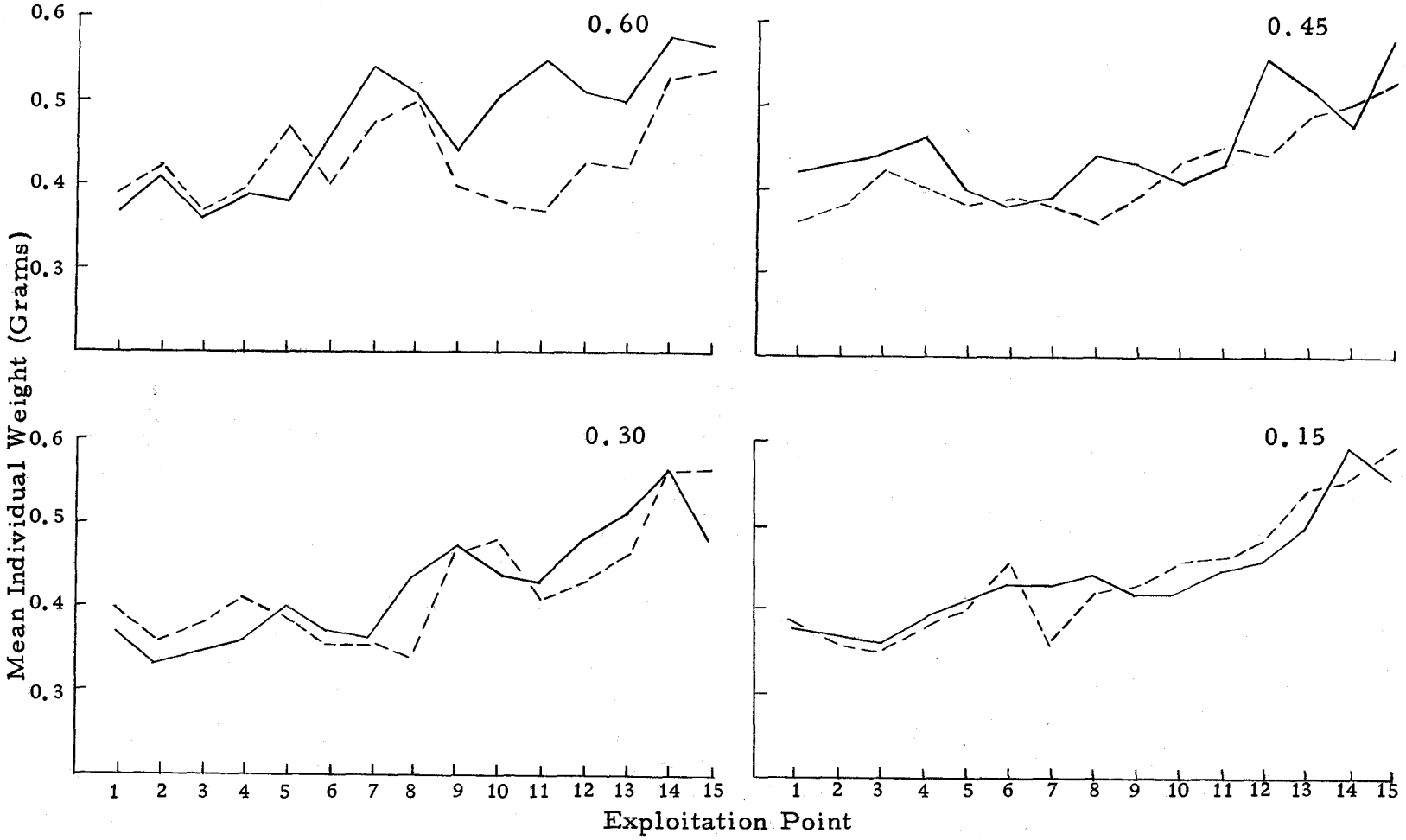

Figure 4. Mean individual weight of adult fish (adult males, young adult females, adult females) at each exploitation point. Exploitation rate is indicated in the upper right of each figure. At each exploitation rate, the solid line represents the average of two control populations and the broken line represents the average of two populations exposed to dieldrin.

number of large adults to develop and, thus, reductions in recruitment were delayed until exploitation point nine.

At 0.60 exploitation rate, the decline in number of fish in the exploited phase of control populations over the first six exploitation points may have resulted from increased cannibalism since the initial adult density in these populations was rather high. Continual exploitation at a high rate undoubtedly contributed to the reduction in both adult and immature density. After exploitation point seven, when adult density was kept low through exploitation, enough recruits were present to keep population number from declining.

At lower exploitation rates, continual reductions in recruitment prevented populations from reaching a stable equilibrium. Although all populations exploited at 0.60 remained stable during most of the experiment, populations exposed to dieldrin maintained a greater number of fish in the exploited phase than control populations (Figure 2).

Perhaps, at this exploitation rate, dieldrin reduced cannibalistic behavior of adult guppies and allowed more recruits to enter the exploited phase between exploitation points. Cairns and Loos (1966) and Cairns, Foster, and Loos (1967) suggested this explanation for the increase in population number of unexploited guppy populations exposed to dieldrin.

Reduction in cannibalistic behavior was not evident in populations exploited at 0.45, 0.30, and 0.15. At these exploitation rates, populations exposed to dieldrin maintained the same number of fish and followed the same trends as control populations.

The apparent differences between exploitation rates in cannibalistic behavior of guppies exposed to dieldrin may be related to the intensity of intraspecific competition for food or space among adults. Since all populations were fed the same amount of food, as exploitation rate declined, the density of adults and, thus, the intensity of intraspecific competition for food or space may have increased and overcome the tendency of dieldrin to reduce cannibalistic behavior.

Recruitment changes, though differing in origin, may have somewhat similar effects in exploited natural populations. The degree of similarity is, of course, restricted by inherent differences in species and by differences between controlled laboratory conditions and natural conditions.

Two aspects of the dynamics of guppy populations exploited at 0.60 are of interest. First, the effects of pesticide induced behavioral changes on the dynamics of populations can be examined. Second, as a result of the behavioral changes, differences and similarities in populations exploited at the same rate, but maintaining different levels of recruitment, can be considered.

The dynamics of guppy populations exploited at 0.45, 0.30, and 0.15 may be related to the dynamics of natural populations undergoing continual reductions in recruitment. The total impact of recruitment changes in natural populations is not immediate. As in guppy populations, some time may be required for reductions in recruitment to be manifested as changes in the number and biomass of fish in older age classes. The time required is dependent upon the number of age classes in the population, that is, upon the rates of exploitation and natural mortality; and upon the relative size of fish in each age class, or their growth rate.

Yield in Number

At each exploitation rate, yield in number followed the same general trends as the number of fish in the exploited phase of the population. Yield in number from populations exploited at 0.60 showed no major trends toward increase or decrease (Figure 5). Yield from populations exposed to dieldrin and exploited at 0.60 was greater than yield from control populations. At 0.45 and 0.30 exploitation rates, yield in number slowly declined following the decline in population number.

Yield in number began to decline at exploitation point nine in populations exploited at 0.15. Since exploitation rate was low, yield alone was not indicative of the large decline in population number that

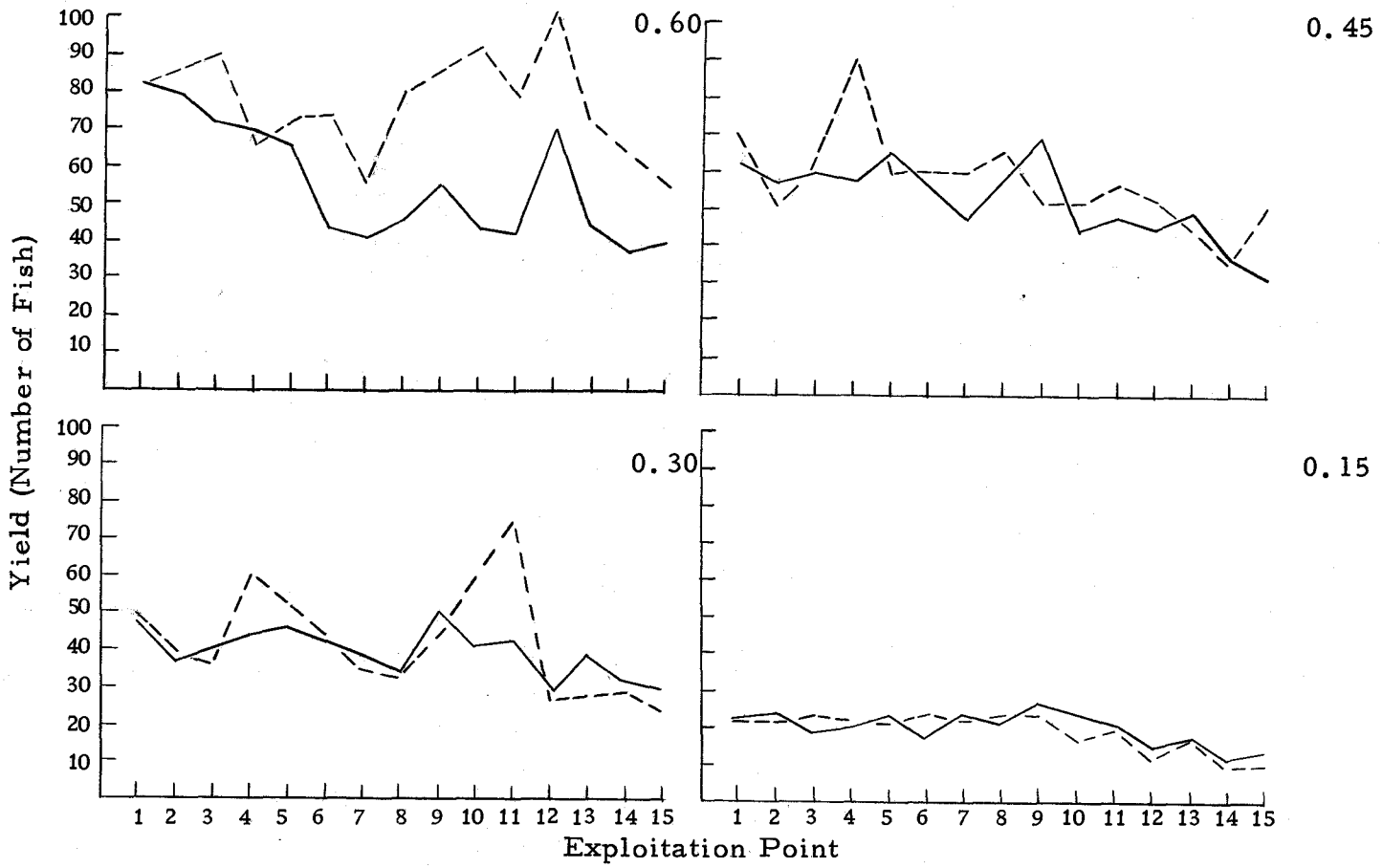

Figure 5. Yield at each exploitation point. Exploitation rate is indicated in upper right of each figure. At each exploitation point, the solid line represents the average yield of two control populations and the broken line represents the average yield of two populations exposed to dieldrin.

occurred after exploitation point nine. If the actual number of fish in the population was not known, information on amount of fishing effort or vulnerability of the stock would be necessary to correctly assess the magnitude of changes occurring in the population.

Population Biomass and Yield in Weight

At each exploitation rate, biomass of fish in the exploited phase of the fishery was more stable than number of fish in the exploited phase. Silliman and Gutsell (1958) and Silliman (1968) also observed that the number of fish in exploited guppy populations was not as stable as population biomass. After the onset of exploitation, some populations may have initially exhibited trends toward increase or decrease in biomass as the populations adjusted to exploitation (Figure 6). The biomass of populations exploited at 0.15, for example, increased over the first six exploitation points.

Past exploitation point seven, major trends toward increase or decrease in population biomass no longer occurred, and all populations were assumed to have reached biomass equilibrium. The mean equilibrium biomass of fish in the exploited phase declined as exploitation rate increased (Figure 7).

Catch per unit of effort in weight is commonly used as an index of the biomass of exploited fish stocks. In determining catch per unit

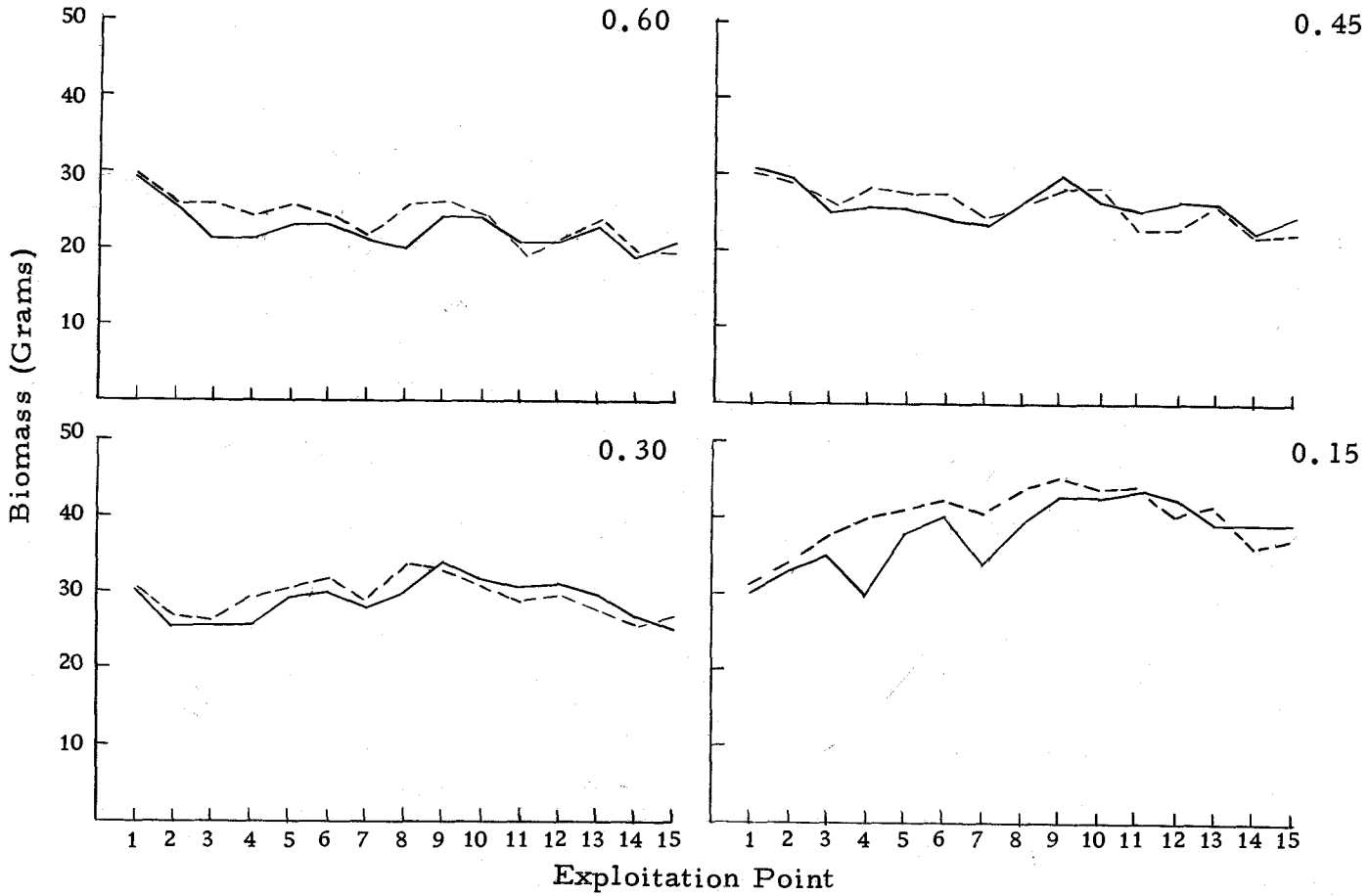

Figure 6. Biomass of fish in the exploited phase of the fishery at each exploitation point. Exploitation rate is indicated in the upper right of each figure. At each exploitation rate, the solid line represents the average biomass of two control populations and the broken line represents the average biomass of two populations exposed to dieldrin.

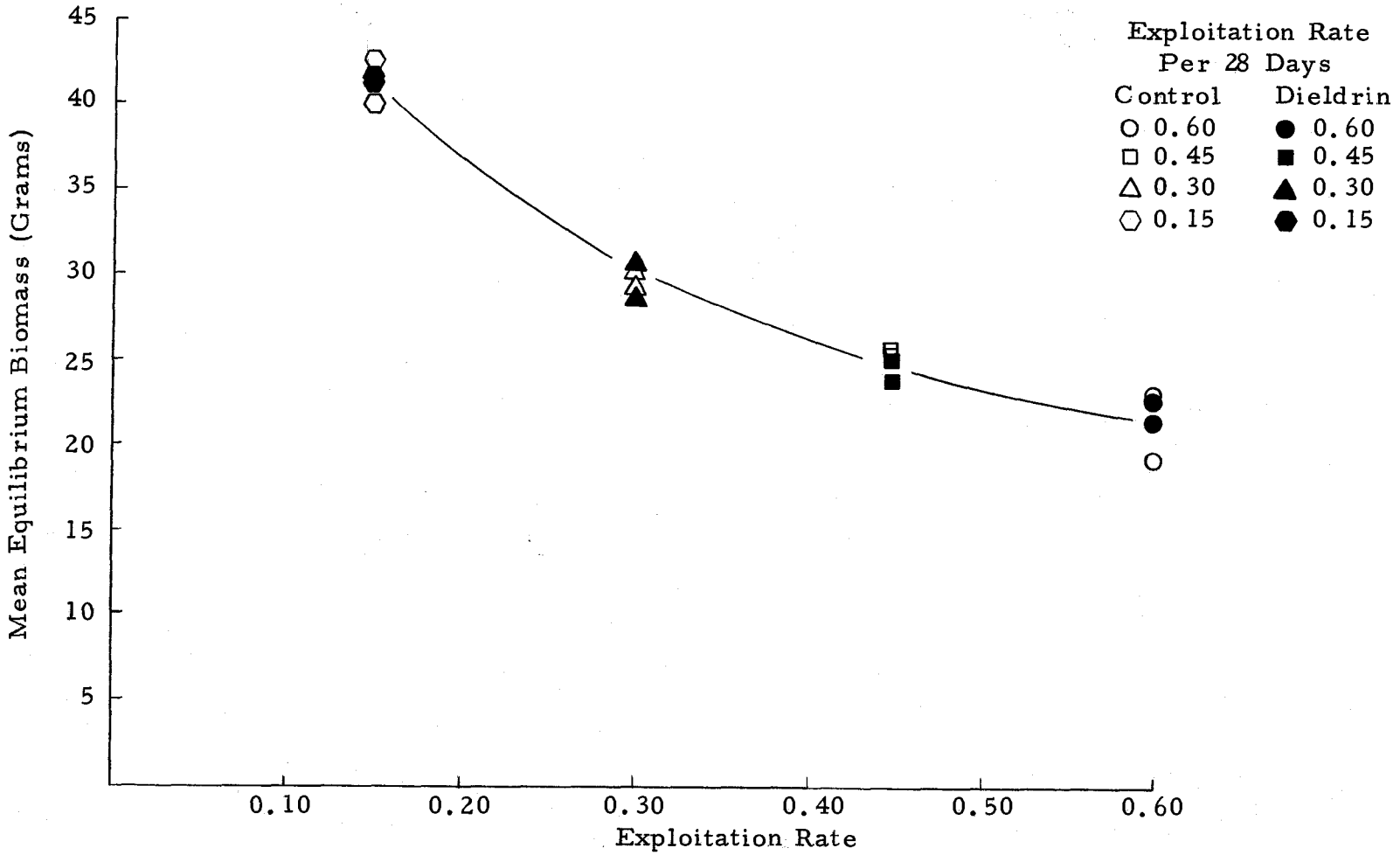

Figure 7. Relationship between mean equilibrium biomass of fish in the exploited phase and exploitation rate for control populations and populations exposed to dieldrin. Mean equilibrium biomass of fish in the exploited phase is the average biomass from exploitation point seven through exploitation point fifteen.

of effort in exploited guppy populations, Silliman and Gutsell (1958) assumed that percentage exploitation rate was proportional to amount of effort, and equated one unit of effort with each ten percent unit of exploitation.

In the present experiment, the method of Silliman and Gutsell was employed to determine the relationship between mean equilibrium catch per unit of effort and fishing effort. Thus, one unit of effort can be equated with 0.1 units of exploitation. Populations exploited at 0.60, 0.45, 0.30, and 0.15 were subjected to 6.0, 4.5, 3.0, and 1.5 units of effort, respectively. Mean equilibrium catch per unit of effort declined exponentially as fishing effort increased (Figure 8). A similar relationship between catch per unit of effort and fishing effort occurred for the exploited guppy populations of Silliman and Gutsell (Silliman, 1971).

Catch per unit of effort is exponentially related to fishing effort in the surplus-yield exploitation model of Fox (1970). Surplus-yield models relate yield to fishing effort or population biomass (catch per unit of effort), and are particularly useful in fisheries where only catch and fishing effort are known and determinations of age, growth, recruitment, and natural mortality are difficult to obtain (Fox, 1970; Silliman, 1971). The surplus-yield model of Fox generates an asymmetrical yield curve.

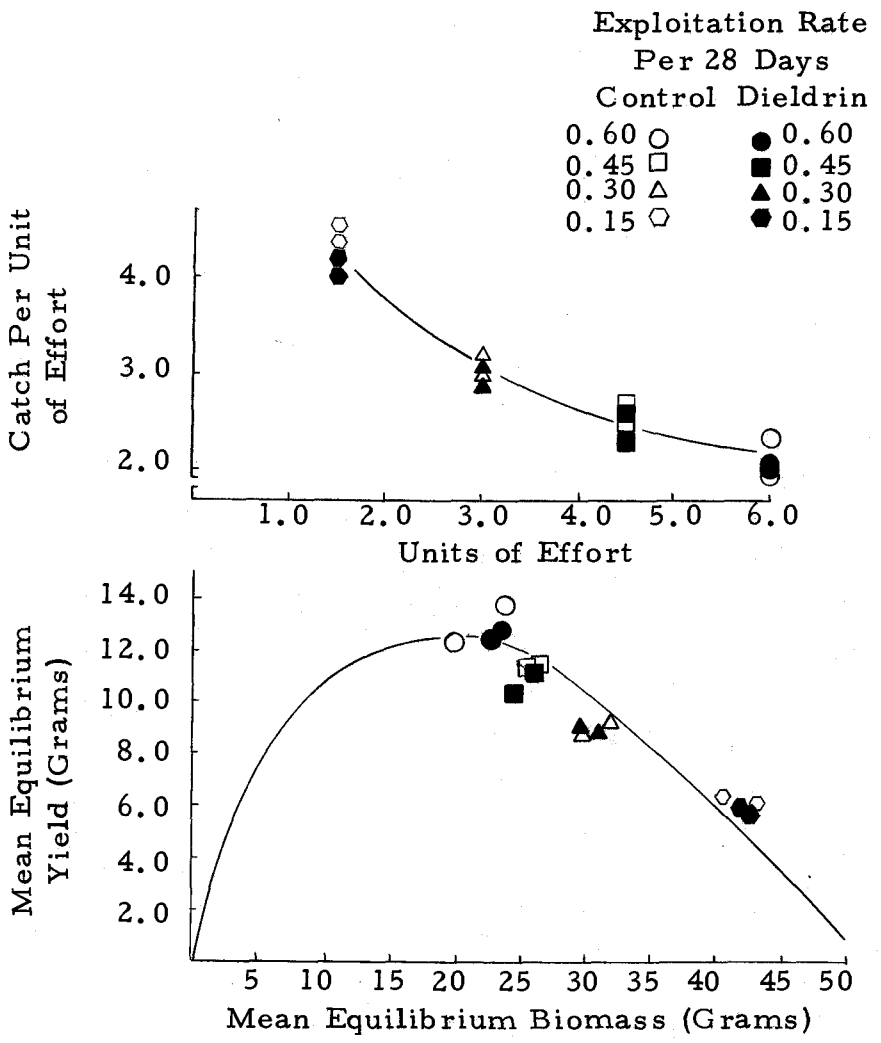

Figure 8. Relationship between catch per unit of effort and fishing effort (upper figure), and mean equilibrium yield and biomass of fish in the exploited phase of the guppy fishery (lower figure) for control populations and populations exposed to dieldrin. The curve in the lower figure was fit by the method of Fox.

The descending limb of the Fox model adequately describes the relationship between mean equilibrium biomass and yield of guppy populations exploited at 0.60, 0.45, 0.30, and 0.15 (Figure 8). The model predicts that maximum sustained yield would be obtained by an exploitation rate of 0.67. The populations were, therefore, underfished.

Since catch per unit of effort declines exponentially with increases in fishing effort, the Fox model implies that populations can withstand large increases in effort without becoming extinct. Fox (1970) states, however, that populations possessing asymmetrical yield curves such experimental guppy populations could be eliminated by increasing fishing effort "if the reproductive ability of the populations were overcome by fishing plus natural mortality." As discussed by Fox, the guppy populations of Silliman and Gutsell were eliminated by an exploitation rate of 75 percent.

In the present experiment, after 15 exploitation points, the exploitation rate of one control replicate, previously exploited at 0.60, was increased to 0.70, and the exploitation rate of another control replicate, previously at 0.45, was increased to 0.80. The population exploited at 0.70 became extinct at exploitation point 20, and the population exploited at 0.80 was eliminated at exploitation point 21.

Yield of guppy populations whose exploitation rate was increased to 0.70 and 0.80 declined as the populations approached extinction.

The number and size of reproducing adults was continually reduced by the higher exploitation rates. Reproduction and recruitment was, therefore, severely limited as the populations became composed primarily of a small number of immature and young adult fish.

The Fox model predicts that the biomass of populations exploited at 0.70 and 0.80 would be maintained at 17.8 grams and 15.4 grams, respectively. Thus, the ascending limb of the curve does not adequately describe changes in yield and biomass of guppy populations exploited at high rates.

In comparing biomass and number of fish in the exploited phase of guppy populations, two major differences are apparent. First, at the 0.60 exploitation rate, populations exposed to dieldrin maintained a greater number of fish in the exploited phase than control populations through increased recruitment. However, the mean biomass of populations exposed to dieldrin and control populations was similar. Second, the biomass of fish in the exploited phase of populations exploited at 0.45, 0.30, and 0.15 remained stable past exploitation point seven even though population number declined. Exploited guppy populations appear, at least for a period of time, to be able to maintain stable biomass while undergoing reductions in recruitment.

Perhaps the reasons for these differences can be best understood by first considering events occurring in the exploited phase that lead to changes in biomass. Silliman (1971), in discussing surplus-yield

models, points out that these models "equate growth rate (increase in biomass per year) to actual or potential annual equilibrium fishery yield at that size." Considered from this point of view, the biomass of fish in the exploited phase at an exploitation point depends upon the rate that biomass is removed from the exploited phase and the rate that biomass is replaced. If natural mortality in the exploited phase is negligible, biomass is removed as yield at the previous exploitation point. Biomass is replaced by the biomass of recruits (total weight of recruits when they are nine millimeters in length) and by the growth of fish in the exploited phase between exploitation points.

Since the weight of fish at recruitment is low (0.015 grams), the biomass of recruits makes only a minor contribution to replacement of fish biomass. The primary means of replacing biomass is by the growth of fish, including recruits, in the exploited phase, that is, by fish production. Therefore, with the population in biomass equilibrium, the yield and production of the population will be similar.

The biomass of guppy populations can now be examined within this conceptual framework. Populations exploited at 0.60 maintained the same equilibrium biomass and yield in weight even though the number of fish in populations exposed to dieldrin was greater than the number of fish in control populations. In order for these populations to maintain the same biomass and yield, the total growth of fish, or production of the populations, had to be similar. Total growth is

simply the sum of the growth of each fish in the exploited phase. Since all populations were fed the same size ration, food available per fish and therefore the growth of individual fish in populations exposed to dieldrin was less than in control populations. But populations exposed to dieldrin maintained a greater number of fish in the exploited phase than control populations, so that total fish growth, or total population production, was similar for all populations.

The biomass of recruits when they enter the exploited phase contribute to replacement of fish biomass that was removed as yield. Thus, decline in number of recruits entering the exploited phase of populations exploited at 0.45, 0.30, and 0.15 would lead to a decline in biomass and yield unless compensated for by increased growth rates of fish in the exploited phase. As recruit numbers declined, food that would have been consumed by these fish became available to other fish in the exploited phase. Therefore, at the lower exploitation rates, growth rates of fish in the exploited phase were higher than they would have been had recruits numbers not declined and relative food availability remained constant.

Nevertheless, growth rates, production, and yield were always greater at higher exploitation rates, where total numbers and biomasses of fish were generally lower and, in consequence, more food was available per fish and per unit biomass.

Average Length and Weight of the Catch

Average length and weight of the catch are relatively simple measurements to obtain and may be used as indexes of changes in size composition of a population resulting from exploitation. Since populations exploited at high rates have a greater proportion of smaller fish than populations exploited at low rates, the average length and weight of the catch is less. Silliman and Gutsell (1958) found that the average length of the catch from guppy populations declined as exploitation rate was increased. Average length and weight of the catch may also serve, with other parameters, as indicators of changes in recruitment.

The average length and weight of the catch from guppy populations exploited at 0.60, 0.45, 0.30, and 0.15 were compared to the number of fish in the exploited phase from exploitation point seven to exploitation point fifteen (Figures 9 and 10).

In guppy populations exploited at 0.60, the average length and weight of the catch from populations exposed to dieldrin was less than that from control populations. While populations exposed to dieldrin maintained a greater number of fish in the exploited phase than control populations, the fish were somewhat smaller. Since fish from all populations were exploited at the same rate and became vulnerable to exploitation at the same size, reduction in average length and weight

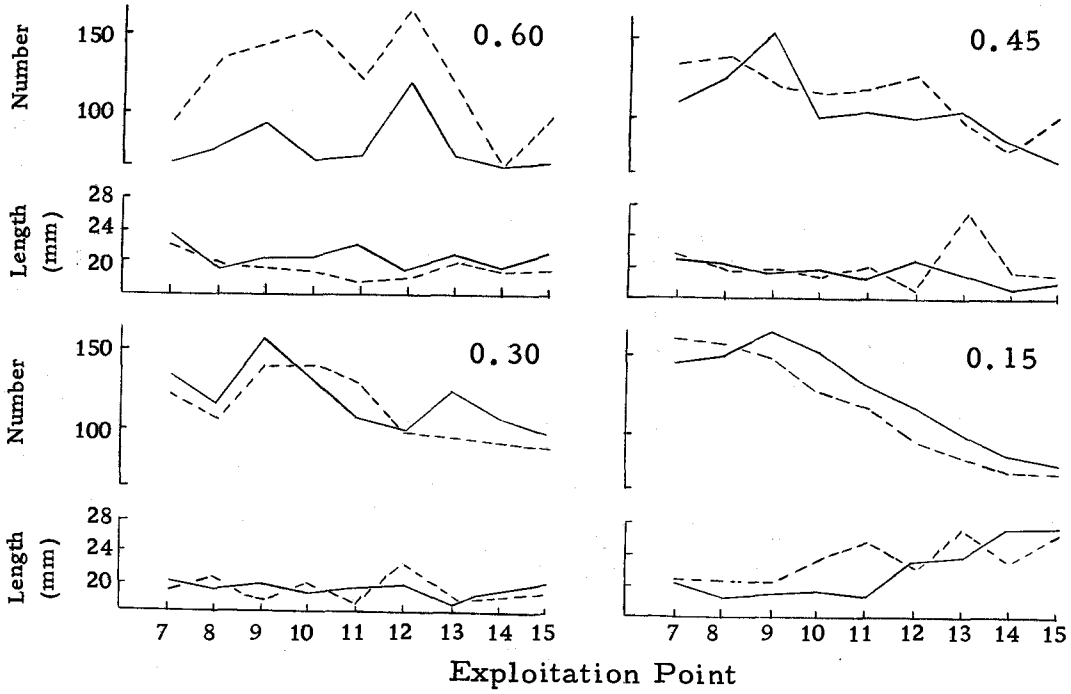

Figure 9. At each exploitation rate, number of fish in the exploited phase (upper figure) and average length of the catch (lower figure) from exploitation point seven through exploitation point fifteen. Exploitation rate is indicated in the upper right of each figure. At each exploitation rate, the solid line represents the average of two control populations and the broken line represents the average of two populations exposed to dieldrin.

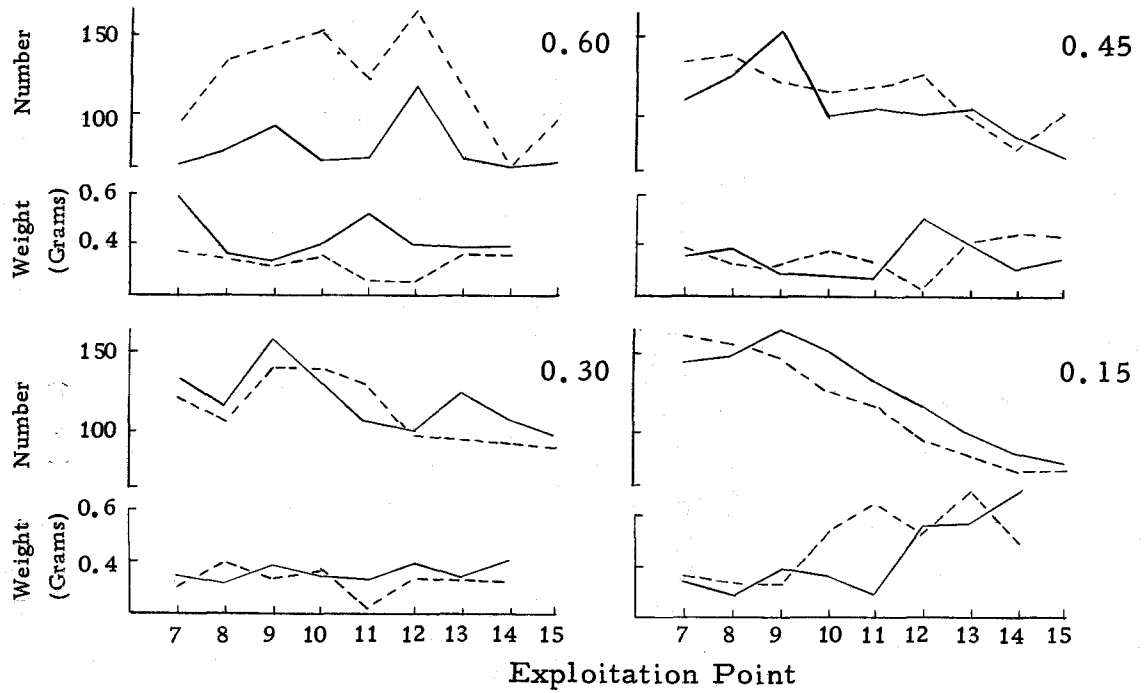

Figure 10. At each exploitation rate, number of fish in the exploited phase (upper figure) and average weight of the catch (lower figure) from exploitation point seven through exploitation point fifteen. Exploitation rate is indicated in the upper right of each figure. At each exploitation rate, the solid line represents the average of two control populations and the broken line represents the average of two populations exposed to dieldrin.

of the catch from populations exposed to dieldrin may have resulted from reduced fish growth.

Decline in number of fish in populations exploited at 0.45, 0.30, and 0.15 was related to reductions in recruitment, and was manifested primarily as a decline in the number of immature fish. Although the number of fish in the exploited phase of populations exploited at 0.45 and 0.30 declined, the average length and weight of the catch remained, for the most part, constant. Changes in the number of immature fish in the catch were apparently not large enough to significantly affect the average length and weight of the catch.

The effect of reduced recruitment on the size composition of guppy populations and, thus, on the average length and weight of the catch is clearly demonstrated in populations exploited at 0.15. Increases in the average length and weight of the catch, as the number of fish in the exploited phase declined, resulted from increases in the proportion of adults in the catch and, perhaps, compensatory increases in growth.

In general, the average length and weight of the catch from populations undergoing large reductions in recruitment may increase when reduced recruitment has not yet affected the number of fish in older age groups. Without information on fishing effort or vulnerability of age groups, such increases could be incorrectly interpreted as

resulting from reduction in either exploitation rate or vulnerability of the younger age groups.

Fecundity

The number of eggs produced by adult female guppies was dependent upon the length of the female and the rate of exploitation of the population (Figure 11). At each exploitation rate, the fecundity, F, of adult female guppies (greater than 25.6 millimeters) was related to their length, L, by the equation $F = aL^b$ (Bagenal, 1967). The fecundity of young adult females (18.6 to 25.5 millimeters) was independent of length and ranged from one to ten eggs. These eggs represent the first and, perhaps the second brood of the female.

The slope, b, of the length-fecundity relationship declined with increases in population biomass that resulted from lowering exploitation rate (Figure 12). Females from populations exploited at low rates produced fewer eggs than females of the same length from populations exploited at high rates. At each exploitation rate, the slope of the length-fecundity relationships of females from control populations and females from populations exposed to dieldrin were not significantly different ($P = 0.05$).

The decline in adult female fecundity with reduction in exploitation rate may be related to the amount of food available per fish. As previously mentioned, the density of adult fish increased as

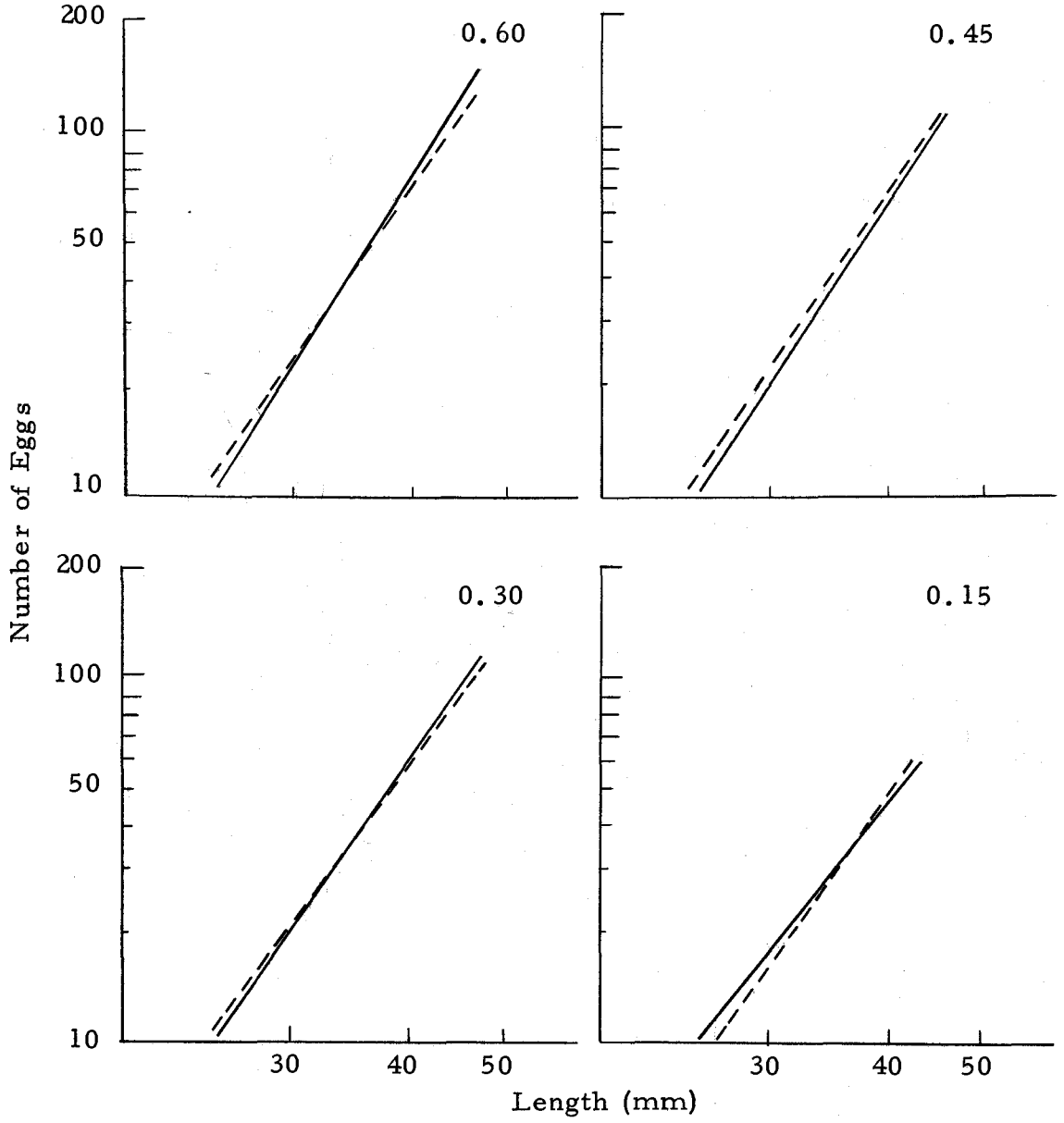

Figure 11. Relationship between number of eggs and length of adult female guppies from control populations and populations exposed to dieldrin at each exploitation rate. Exploitation rate is indicated in the upper right of each figure. At each exploitation rate, the solid line represents females from control populations and the broken line represents females from populations exposed to dieldrin.

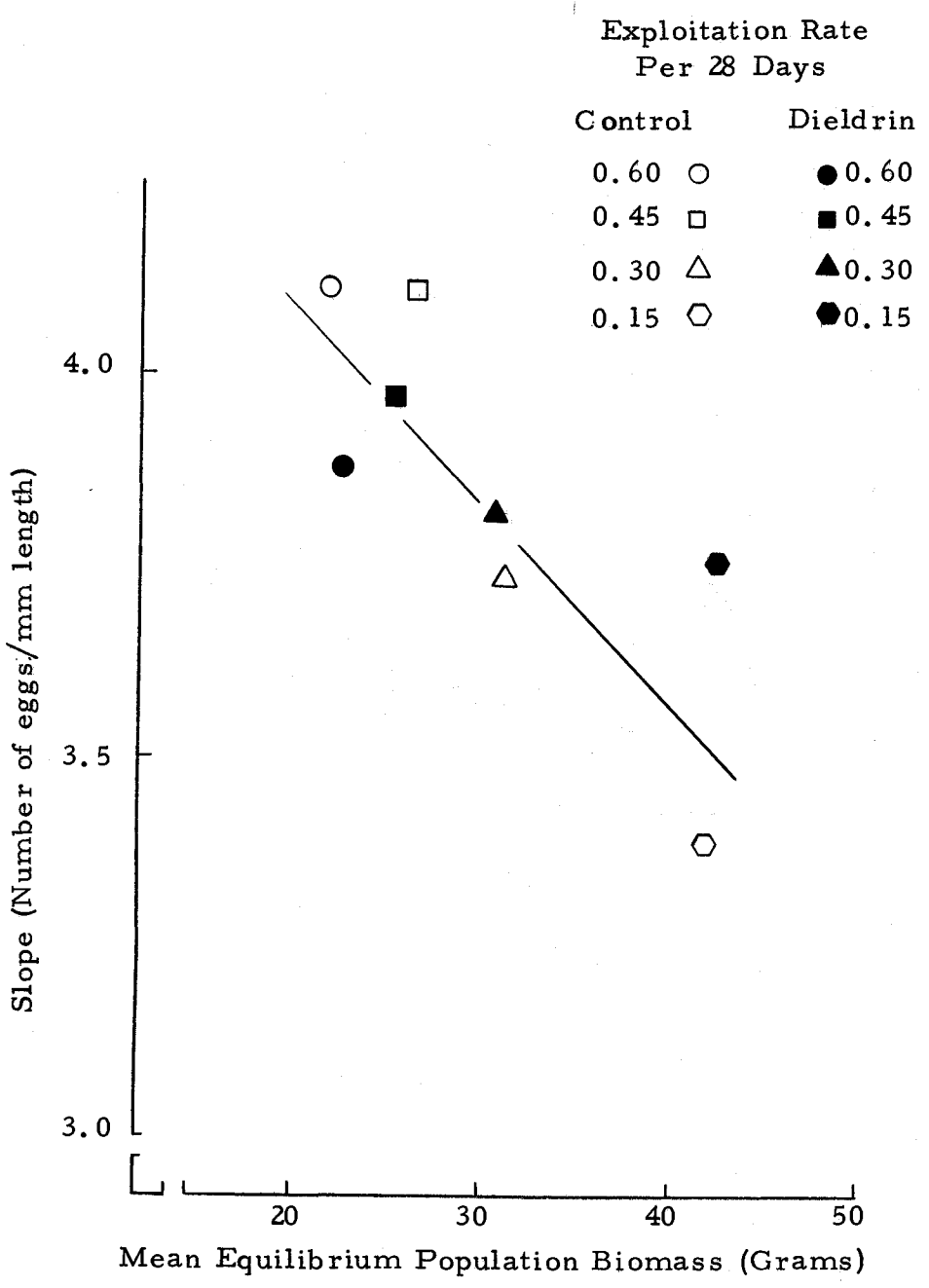

Figure 12. Relationship between adult female guppy fecundity, represented as the slope of the length-fecundity relationship, and mean equilibrium population biomass for control populations and populations exposed to dieldrin at each exploitation rate.

exploitation rate was lowered. The amount of food available per adult and, therefore, adult fecundity may have been greater at higher exploitation rates.

Hester (1964) found that the fecundity of female guppies could be reduced restricting the size of their ration. Scott (1962) showed that reduction in ration size delayed maturation and reduced fecundity of rainbow trout. Bagenal (1967) in his review of fish fecundity concluded that food supply has a definite effect on fecundity, but was uncertain about the importance of reduced fecundity in regulation of population size.

In guppy populations, reduced fecundity at lower exploitation rates was compensated by increased number of adult female fish. Total egg production and number of young produced were always sufficient to meet the potential recruitment needs of the exploited phase. Recruitment in guppy populations was regulated, through pre-recruit mortality, by the density of adult fish. Adult fish density, in turn, was dependent upon exploitation rate.

Growth, Biomass, Production, and Yield of Each Age Class

The parameters characterizing each age class of females in the exploited phase of populations exploited at 0.60, 0.45, and 0.30 are presented in Tables 2 through 4. Several assumptions were made

Table 2. Number of fish, yield in number, mean individual weight, biomass at the time of exploitation, production, and yield in weight of each age class of female guppies from populations exploited at 0.60, as determined from the length-frequency distribution of the catch from exploitation point seven through exploitation point fifteen.

Age Class	Number of Fish	Yield in Number	Mean Individual Weight (Grams)	Biomass (Grams)	Production (Grams)	Yield in Weight (Grams)
			Control Populations			
0	25.94	15.56	0.092	2.41	2.02	1.44
1	10.38	6.23	0.458	4.75	3.79	2.85
2	4.15	2.49	1.092	4.53	2.63	2.72
3	1.66	1.00	1.742	2.89	1.07	1.74
4	0.66	0.40	2.317	1.52	0.37	0.92
5	0.27	0.27	2.761	0.74	0.11	0.74
Total	43.06	25.95		16.84	9.99	10.41
Biomass of Recruits					0.39	
					10.38	
			Populations Exposed to Dieldrin			
0	37.89	22.73	0.049	1.86	1.28	1.11
1	15.16	9.09	0.248	3.76	3.02	2.25
2	6.06	3.64	0.631	3.82	2.32	2.29
3	2.42	1.45	1.086	2.62	1.09	1.57
4	0.97	0.58	1.724	1.67	0.61	1.00
5	0.39	0.39	2.286	0.89	0.21	0.89
Total	62.89	37.88		14.62	8.53	9.11
Biomass of Recruits					0.58	
					9.11	

Table 3. Number of fish, yield in number, mean individual weight, biomass at the time of exploitation, production, and yield in weight of each age class of female guppies from populations exploited at 0.45, as determined from the length-frequency distribution of the catch from exploitation point seven through exploitation point fifteen.

Age Class	Number of Fish	Yield in Number	Mean Individual Weight (Grams)	Biomass (Grams)	Production (Grams)	Yield in Weight (Grams)
			Control Populations			
0	24.89	11.20	0.053	1.34	0.97	0.60
1	13.69	6.16	0.210	2.87	2.14	1.29
2	7.53	3.39	0.508	3.82	2.24	1.72
3	4.14	1.86	0.924	3.82	1.72	1.71
4	2.28	1.02	1.292	2.94	0.83	1.31
5	1.25	0.56	1.624	2.03	0.41	0.90
6	0.69	0.31	1.957	1.35	0.22	0.60
7	0.38	0.17	2.321	0.88	0.13	0.39
8	0.21	0.21	2.569	0.53	0.05	0.53
Total	55.06	24.88		19.58	8.71	9.05
Biomass of Recruits					0.37	
					9.08	
			Populations Exposed to Dieldrin			
0	27.83	12.52	0.044	1.22	0.92	0.55
1	15.31	6.89	0.163	2.49	1.82	1.12
2	8.42	3.79	0.410	3.45	2.08	1.55
3	4.63	2.08	0.736	3.37	1.73	1.53
4	2.55	1.15	1.132	2.88	1.01	1.30
5	1.40	0.63	1.495	2.09	0.50	0.94
6	0.77	0.35	1.947	1.49	0.34	0.68
7	0.42	0.19	2.313	0.97	0.15	0.43
8	0.23	0.23	2.745	0.63	0.09	0.63
Total	61.56	27.83		18.18	8.64	8.73
Biomass of Recruits					0.30	
					8.94	

Table 4. Number of fish, yield in number, mean individual weight, biomass at the time of exploitation, production, and yield in weight of each age class of female guppies from populations exploited at 0.30, as determined from the length-frequency distribution of the catch from exploitation point seven through exploitation point fifteen.

Age Class	Number of Fish	Yield in Number	Mean Individual Weight (Grams)	Biomass (Grams)	Production (Grams)	Yield in Weight (Grams)
			Control Populations			
0	18.39	5.52	0.036	0.66	0.38	0.20
1	12.87	3.86	0.109	1.40	0.93	0.42
2	9.01	2.70	0.235	2.12	1.13	0.63
3	6.31	1.89	0.438	2.76	1.27	0.82
4	4.42	1.32	0.704	3.11	1.17	0.93
5	3.09	0.93	0.871	2.69	0.51	0.81
6	2.16	0.65	1.104	2.38	0.50	0.71
7	1.51	0.45	1.312	1.98	0.31	0.59
8	1.06	0.32	1.524	1.61	0.22	0.48
9	0.74	0.22	1.635	1.20	0.08	0.35
10	0.52	0.16	1.827	0.95	0.09	0.29
11	0.36	0.11	1.929	0.69	0.03	0.21
12	0.25	0.25	2.262	0.56	0.08	0.56
Total	60.69	18.38		22.11	6.70	7.00
Biomass of Recruits					0.28	
					6.98	
			Populations Exposed to Dieldrin			
0	16.39	4.49	0.031	0.52	0.26	0.14
1	11.47	3.44	0.112	1.28	0.92	0.38
2	8.03	2.41	0.298	2.39	1.42	0.71
3	5.62	1.69	0.502	2.82	1.14	0.84
4	3.94	1.18	0.754	2.97	0.99	0.89
5	2.75	0.83	0.966	2.65	0.58	0.80
6	1.93	0.58	1.153	2.22	0.35	0.66
7	1.35	0.41	1.282	1.73	0.17	0.52
8	0.94	0.28	1.453	1.36	0.16	0.40
9	0.66	0.20	1.614	1.06	0.10	0.32
10	0.46	0.14	1.812	0.83	0.09	0.25
11	0.32	0.10	1.860	0.59	0.01	0.18
12	0.23	0.23	1.860	0.42	0.00	0.40
Total	54.09	15.98		20.84	6.26	6.49
Biomass of Recruits					0.36	
					6.66	

in determining these parameters from the length-frequency distribution of the catch.

The first assumption, that natural mortality in the exploited phase was negligible, has been discussed previously. Losses to natural mortality in the exploited phase were probably minor. However, if natural mortality occurred at a constant rate during the lifetime of a cohort in the fishery, the actual values of the parameters at each age would be altered, but the changes in the parameters with age may not be greatly affected.

Exceptions to the second assumption, dealing with rates of recruitment seem most serious. At a particular exploitation rate, recruits were assumed to enter the exploited phase between exploitation points at a constant rate, and the total number of recruits that entered the exploited phase between exploitation points, that is, the number of fish in a cohort, was assumed to remain constant.

From exploitation point seven to exploitation point fifteen, when the length-frequency distribution of the catch was used to determine age and associated parameters, populations exploited at 0.45, 0.30, and 0.15 were undergoing reductions in recruitment. Thus, at these exploitation rates, the total number of recruits entering the exploited phase declined. Because the reductions were most severe in populations exploited at 0.15, age and growth of these populations were not determined. Age and growth of populations exploited at 0.45 and 0.30

were determined with the hope that systematic errors were not great, and that some comparison of parameters between exploitation rates could be made.

At a particular exploitation rate with the population in equilibrium, fish of the same length were assumed to grow at approximately the same rate. However, individual variations in growth rate among fish of the same length probably occurred. Thus, some fish, determined to belong to a particular age class by their position in the length-frequency distribution, may actually have been members of a different age class.

Indirect determinations of age and growth from the length-frequency distribution of the catch is perhaps justified as long as the limitations and assumptions of the method are realized. Examining some of the biological concepts that underlie surplus-yield models, such as the effects of density changes resulting from exploitation on growth, biomass, production, and yield of each age class, would be an arduous task in natural populations. Perhaps consideration of the impact of exploitation on these parameters in laboratory fish populations may best serve as a framework for questions and ideas regarding natural populations. The concepts that are developed in the following section, at least, seem logically sound and could, perhaps, be arrived at independent of experimentation by simply assuming that fish growth was dependent upon fish density.

The age class to which a cohort of female guppies belongs at an exploitation point is taken to indicate the number of times the cohort had been exploited prior to that exploitation point. The number of age classes is, therefore, an index of the length of life, in units of 28 days, of a composite cohort in the exploited phase. As exploitation rate increased, the number of age classes, or the length of life of a cohort, declined (Tables 2, 3, and 4).

Except for populations exposed to dieldrin and exploited at 0.60, the total number and biomass of fish in the exploited phase generally increased as exploitation rate declined. Since all populations were fed the same amount of food, increases in number and biomass of fish would reduce the amount of food available per fish and per gram of fish. Thus, guppy growth should be affected by density changes resulting from exploitation.

Three major aspects of the age class dynamics of exploited guppy populations will be considered. First, the growth of a cohort of female guppies will be examined. Second, changes in biomass, production, and yield of a composite cohort during its lifetime in the fishery will be considered. Third, differences in total biomass, production, and yield of female guppies between exploitation rates will be examined.

Relative growth rate is the commonly used expression for fish growth. The growth rate of an individual fish is generally considered

to be dependent upon its size rather than its age (Brody, 1945; Larkin, Terpenning, and Parker, 1957; Parker and Larkin, 1959). Thus, fish of the same age may grow at different rates if they are not the same size.

The impact of fish density on guppy growth becomes evident when the mean individual weight of an age class and the growth rate of fish of a particular weight are compared between exploitation rates. Female fish from high exploitation rates reached a particular weight at an earlier age than females from low exploitation rates. In addition, the relative growth rate of fish from high exploitation rates was greater than the growth rate of fish of the same weight from low exploitation rates (Figure 13).

Although growth rate is dependent upon weight, fish from different exploitation rates reached a particular weight at different ages. Therefore, fish of a particular age from a high exploitation rate may weigh more and, thus, have a lower growth rate than fish of the same age from a low exploitation rate. This is especially true of the older age classes of fish.

In guppy populations, fish density and food availability can be conceptualized as determining the general pattern of growth of a cohort during its lifetime in the fishery. High exploitation rates reduce fish density and, thus, increase food availability per fish and fish growth.

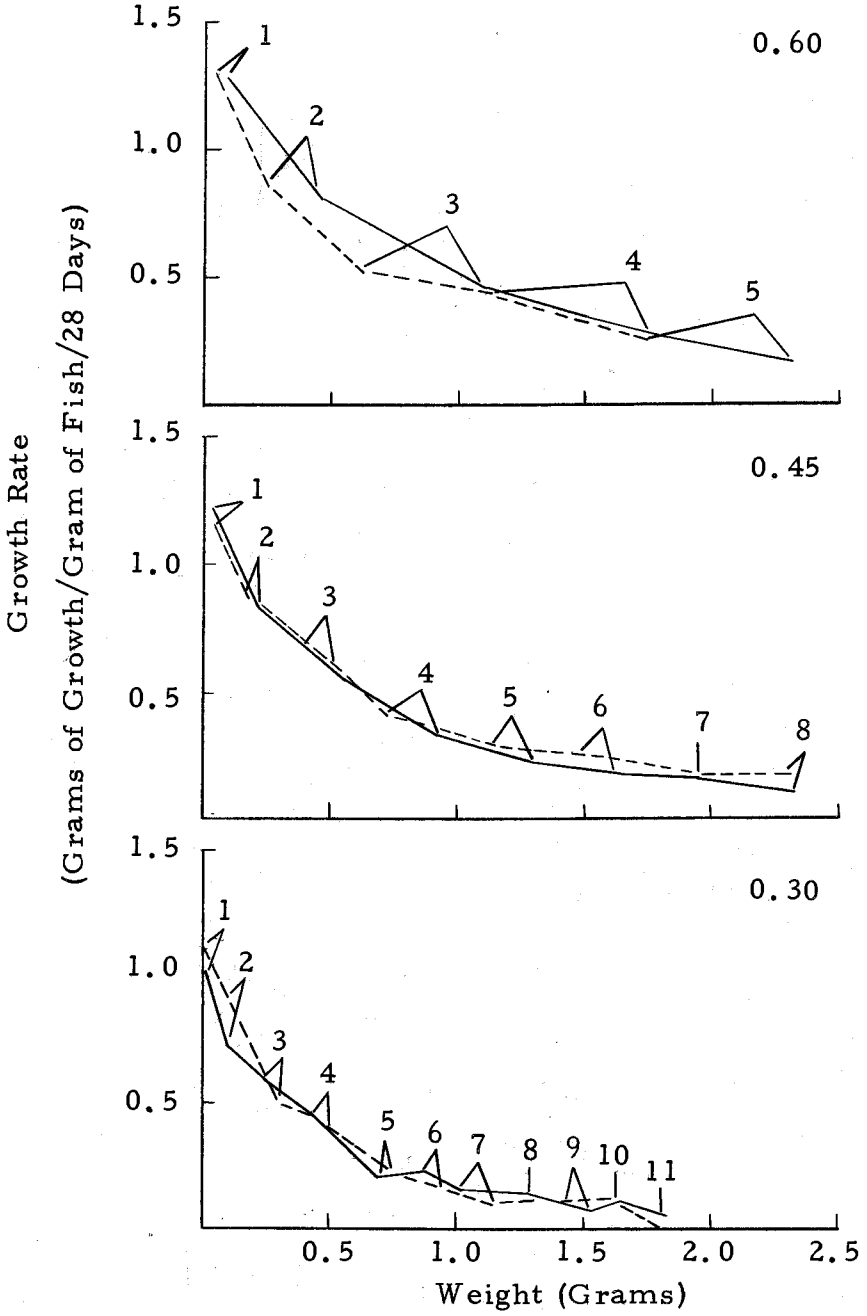

Figure 13. Relationship between relative growth rate and initial mean individual weight of female guppies from populations exploited at 0.60, 0.45, and 0.30. Exploitation rate is given in the upper right of each figure. At each exploitation rate, growth rate and initial mean individual weight of each age class is indicated. The solid lines represent control populations and the broken lines represent populations exposed to dieldrin.

If growth is considered in relation to age - a common procedure in fisheries - the impact of density changes on growth rate becomes more confusing.

A cohort during its lifetime in the exploited phase of a fishery in equilibrium establishes a specific pattern of growth determined by the density of the population. In addition, the cohort undergoes changes in biomass as it passes through each age class. Between exploitation points, production of the cohort leads to an increase in cohort biomass. At an exploitation point, cohort biomass is reduced by exploitation.

Thus, the relative magnitude of cohort production and yield determines whether the biomass of a cohort of a particular age at the time of exploitation is greater or less than its biomass at a previous age. Specifically, the biomass of the cohort as age class (n) at the time of exploitation will be greater or less than its biomass as age class (n-1) at the time of exploitation depending upon the difference between the production of the cohort as age class (n) and the yield of the cohort as age class (n-1). When the yield of the cohort as age class (n-1) is less than the production of the cohort as age class (n), the biomass of the cohort as age class (n) at the time of exploitation will be greater than its biomass as age class (n-1). Similarly, if the yield of the cohort as age class (n-1) is greater than the production of the cohort as age class (n), the biomass of the cohort as age class (n)

at the time of exploitation will be less than its biomass as age class (n-1).

Like growth rate, a specific pattern of change of cohort biomass at the time of exploitation is established as the cohort increases in age. At each exploitation rate, as the cohort moved through the younger age classes and was composed of small, fast-growing fish, production of the composite cohort was greater than yield, and the biomass of the cohort increased. As the composite cohort moved through the older age classes and was composed of relatively larger, slower growing fish, yield became greater than production and the biomass of the cohort declined.

In addition, the biomass of the cohort at the time of exploitation became maximum at age class (n) when the yield of the cohort as age class (n) first became greater than the production of the cohort as age class (n+1). Since yield was taken from the biomass at the time of exploitation, and all age classes were exploited at the same rate, yield was maximum when the biomass of the cohort was maximum.

Ricker and Foerster (1948) found a similar relationship between production, mortality, and biomass over a one year period for age 0 sockeye salmon. When production was greater than losses to mortality, the biomass of sockeye increased. Biomass reached a maximum when production equaled mortality, and then declined as mortality became greater than production.

Total equilibrium production and yield of female fish in the exploited phase declined as exploitation rate was reduced. At each exploitation rate, total production and yield is simply the sum of the production and the yield of all age classes of females (Tables 2, 3, and 4). Thus, differences in total production and yield of females between exploitation rates can be explained by examining the production and yield of a composite cohort as it passed through each age class.

Cohorts from low exploitation rates had a greater lifespan in the exploited phase and therefore could maintain production and yield for a longer period of time than cohorts from high exploitation rates. In addition, at low exploitation rates, as a cohort passed through the older age classes its growth rate, biomass, production, and yield became greater than the growth rate, biomass, production, and yield of cohorts of the same age from higher exploitation rates.

However, most of the production and yield of a cohort occurred as the cohort passed through the younger age classes. Increased growth rate, biomass, production, and yield of cohorts from high exploitation rates offset their reduced lifespan and enabled these populations to maintain greater production and yield than populations exploited at low rates.

At the 0.60 exploitation rate, both control populations and populations exposed to dieldrin had the same relative age distribution, that

is, the same proportion of fish in each age class. However, through increased recruitment, populations exposed to dieldrin were able to maintain a greater number of fish in the exploited phase than control populations.

Thus food available per fish and mean individual weight of fish of a particular age was greater in control populations than in populations exposed to dieldrin. The growth rate at a particular weight of fish from populations exposed to dieldrin was intermediate to control populations exploited at 0.60 and populations exploited at lower rates (Figure 13). This result may, at first, appear anamolous since populations exposed to dieldrin and exploited at 0.60 maintained a greater number of fish in the exploited phase than populations exploited at lower rates.

However, the biomass of populations exploited at 0.60 was less than the biomass of populations exploited at 0.45 and 0.30. Thus, food availability per gram of fish, or food available to fish of any particular weight, was greater in populations exploited at 0.60 resulting in greater growth.

At the 0.60 exploitation rate, control populations were able to attain a larger mean individual weight at each age and to maintain, in the younger age classes, greater biomass, production, and yield than populations exposed to dieldrin. However, the biomass, production,

and yield of the older age classes was greater in populations exposed to dieldrin.

The total biomass and yield of female guppies from control populations was somewhat greater than that of females from populations exposed to dieldrin. However, the biomass and yield of males was greater in populations exposed to dieldrin enabling these populations to maintain the same total biomass and yield of fish in the exploited phase as control populations.

DISCUSSION

Major fluctuations in catch resulting from changes in recruitment are typical of many fish stocks (Cushing, 1968). Often the cause of these fluctuations is unknown. Although recruitment changes in guppy populations may differ in origin and intensity of effect from natural populations, some useful similarities may exist.

Declines in the number of fish in the exploited phase of guppy populations exploited at 0.45, 0.30, and 0.15 were related to reduced recruitment. Reductions in recruitment resulted from increased pre-recruit mortality, primarily from cannibalism. Increased cannibalism was related to the development of a large number of adult fish. Thus, it seems that guppy populations exploited at 0.45, 0.30, and 0.15 were beginning to undergo periodic cycles similar to the unexploited guppy populations of Shoemaker (1947).

The number of fish in Shoemaker's populations increased when few large adults were present. After a few months, when the density of adults had increased, population number reached a peak and then began to decline. Shoemaker related the initial phase of the decline to reduction in young fish from cannibalism. Further decline was attributed to natural death of old adults. However, as the number of adult fish declined, more young were able to survive and population

number once again began to increase. Exploited guppy populations were apparently in the initial phase of decline since reduced recruitment and natural death had not yet seriously affected the number of adult fish.

While populations exploited at 0.45, 0.30, and 0.15 were beginning to cycle, no such trend was evident in populations exploited at 0.60. At this exploitation rate, the number of large adult fish was kept relatively small and, while cannibalism certainly occurred, recruitment and population number remained stable.

The tendency of periodic oscillations in population size to disappear as exploitation rate is increased was considered by Ricker (1954). A multiple age spawning population whose stock and recruitment curve begins to decline above the 45-degree line with slope greater than -1 will possess periodic oscillations when unexploited or exploited at low rates. These oscillations can be eliminated by increasing exploitation rate. As in guppy populations, the full impact of changes in recruitment are not immediate, and depend on the age of recruitment and maturity, and the number of age classes present in the population.

Ricker (1954) provides an example of a natural population, the Georges Bank haddock, whose response to exploitation was similar to that of guppies. The haddock stock performed periodic oscillations between 1912 and 1930 when the rate of exploitation was low. Increases

in exploitation rate between 1930 and 1943 eliminated population oscillations.

Herrington (1948) attributed the oscillations in the haddock stock to mortality of young from intraspecific competition with adults when adult density was high, and the time lag between changes in competition and resulting changes in recruitment.

Although the number of fish in the exploited phase of guppy populations exploited at 0.45, 0.30, and 0.15 declined, biomass and yield in weight remained stable past exploitation point seven. The potential loss of biomass from reduced recruitment was small when compared to total biomass and may have been compensated by increased growth of fish in the exploited phase.

Shoemaker (1947) found that as the population number of unexploited guppy populations declined, biomass increased at first and then remained stable up to a year after the initial decline in number began. He suggested that a stable biomass was maintained because growth equaled losses from natural deaths, including cannibalism. Eventually, however, population biomass began to decline as the death rate of old, large adults increased.

Thus, in guppy populations, reduction in recruitment biomass can, for a time, be compensated by increased growth. Reduction in population biomass and yield in weight will eventually occur when

reductions in recruitment biomass and natural deaths of old adult fish cannot be compensated by increased growth.

In natural populations, these effects may be transitory or may not occur depending on the ability of the populations to compensate for reductions in recruitment by increased growth. Such effects may also be obscured by changes in fishing effort or natural mortality. If the biomass and yield in weight of natural populations remained stable while undergoing continual long-term reductions in recruitment, and fishing effort and vulnerability remained constant, the number and biomass of young fish in the catch would decline and the average length and weight of the catch would increase.

A slightly different situation regarding recruitment was evident in populations exploited at 0.60. While the number of fish in the exploited phase of these populations remained relatively stable past exploitation point seven, populations exposed to dieldrin maintained a greater number of fish than control populations. Dieldrin apparently reduced cannibalistic behavior allowing more young to survive to recruitment size. Increased recruitment, however, was compensated by reduced growth, as evidenced by reduction in both mean individual weight of each age class and growth rate of females of a particular weight. Thus, populations exposed to dieldrin maintained the same biomass and yield in weight as control populations. Although the yield in weight of control populations and populations exposed to dieldrin

was similar, the average length and weight of the catch from the latter populations were reduced.

Apparent reduction in cannibalistic behavior was not evident in populations exploited at 0.45, 0.30, and 0.15. Because these populations maintained a high density of adult fish, intraspecific competition for food or space may have overcome the tendency of dieldrin to reduce cannibalistic behavior.

This hypothesis leads to an alternative interpretation of the data of Cairns, Foster, and Loos (1967). Their populations were begun with a small number of adult fish. All populations were fed the same amount of food. During the initial stages of population growth, populations exposed to dieldrin maintained a greater number of fish than control populations. The authors attribute this to reduced cannibalistic behavior. After six months, however, there was no difference in total number of fish in control populations and populations exposed to dieldrin. The authors postulate that the decline in number of fish in populations exposed to dieldrin resulted from a bacterial infection that was noticed in both control populations and populations exposed to dieldrin in the sixth month. Possibly, however, as the number of large fish in the populations increased, intraspecific competition for food or space overcame the tendency of dieldrin to reduce cannibalistic behavior and caused the sharp decline evident in the number of young fish and total population number.

Much of the preceding discussion was concerned with the regulation of growth by fish density. With the food supply of guppy populations kept constant and limited, strong density-dependent effects can be expected.

Apparently, the primary method of reducing intraspecific competition for food and space in guppy populations in aquariums is by reduction of recruitment through cannibalism. Competition for food and space and subsequent changes in growth may be reduced in natural populations through increased density-dependent mortality, increased forage range, utilization of alternate food sources and territoriality.

Beverton and Holt (1957) developed theoretical approaches for examining the effects of density changes on prey abundance, growth, and yield. They compared yield at different fishing intensities for populations where growth was not affected by density and for populations where growth declined with increases in density. At low fishing intensities, yield from populations with constant growth was greater than yield from populations with density-dependent growth. At high fishing intensities, yield was slightly greater in populations having density-dependent growth.

A similar comparison of the effects of density-dependent and constant growth on the yield of guppy populations exploited at different rates can be made. To determine yield of female guppies with growth independent of density, control populations exploited at 0.60 and 0.30

were assumed to maintain the number of recruits, age distribution, and yield in number characteristic of their exploitation rate, but possess the same mean individual weight at each age as populations exploited at 0.45. Under these conditions, yield of guppy populations exploited at 0.60 was reduced from 10.4 grams to 5.3 grams, and the yield of populations exploited at 0.30 was increased from 7.0 grams to 13.0 grams. Thus, a one hundred percent change in yield in guppy populations occurred when growth was assumed to be independent of fish density.

Perhaps changes in exploitation rate are similar to ecological thresholds (Larkin et al., 1957; Parker and Larkin, 1959) in fish populations where growth rate is dependent upon fish density. By altering fish density, exploitation provides new opportunities for growth. Thus, a cohort or year-class of fish during its lifetime in the fishery can be conceptualized as shifting its growth pattern in response to prolonged changes in exploitation rate.

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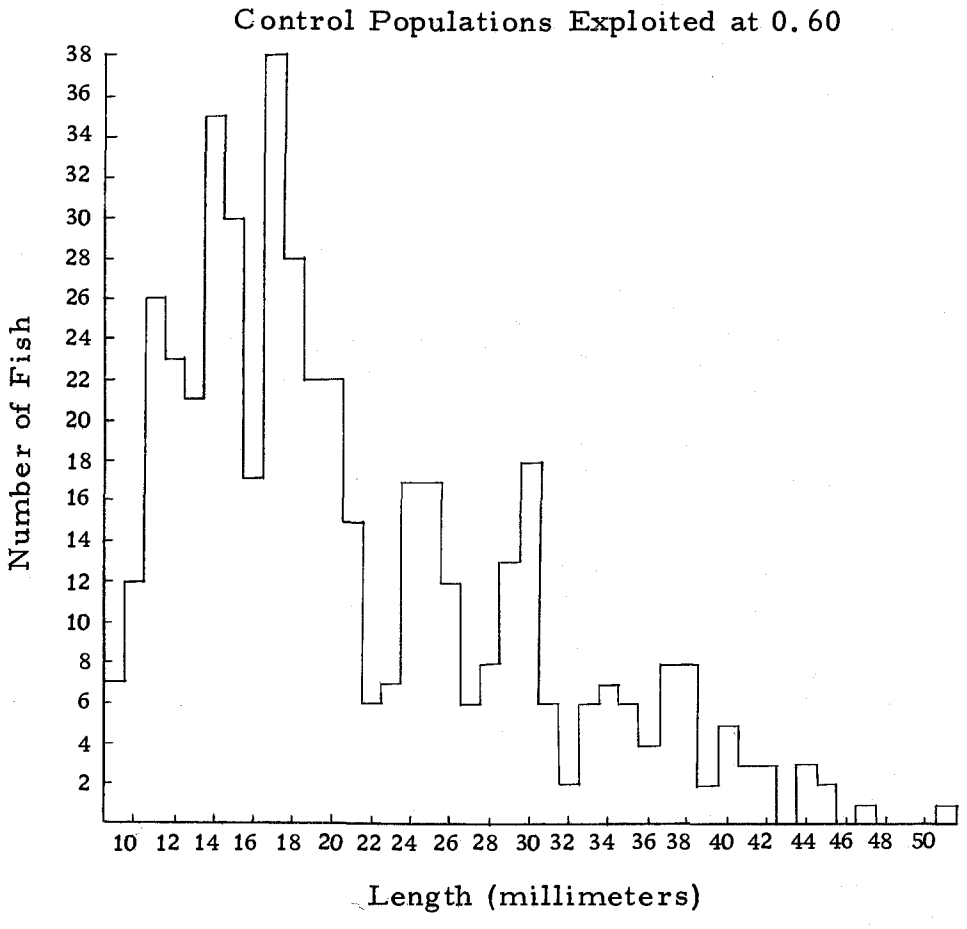
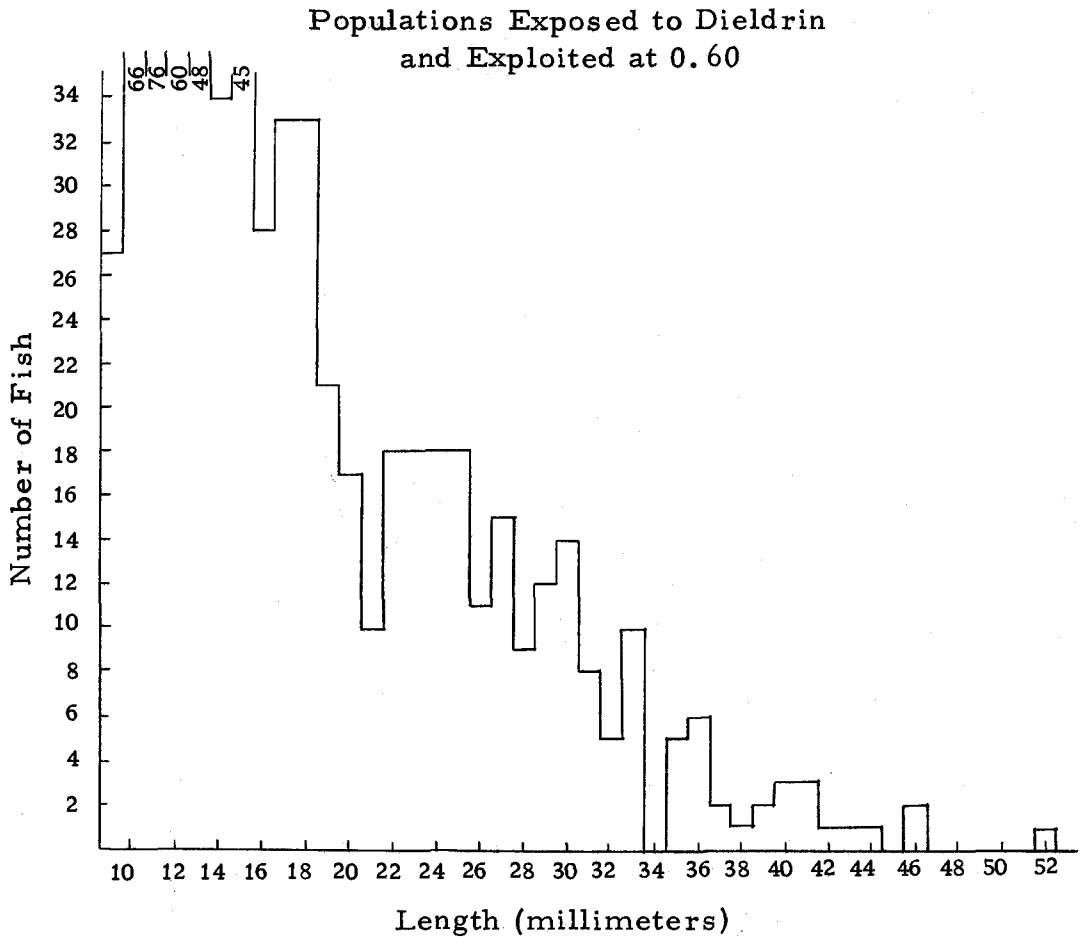
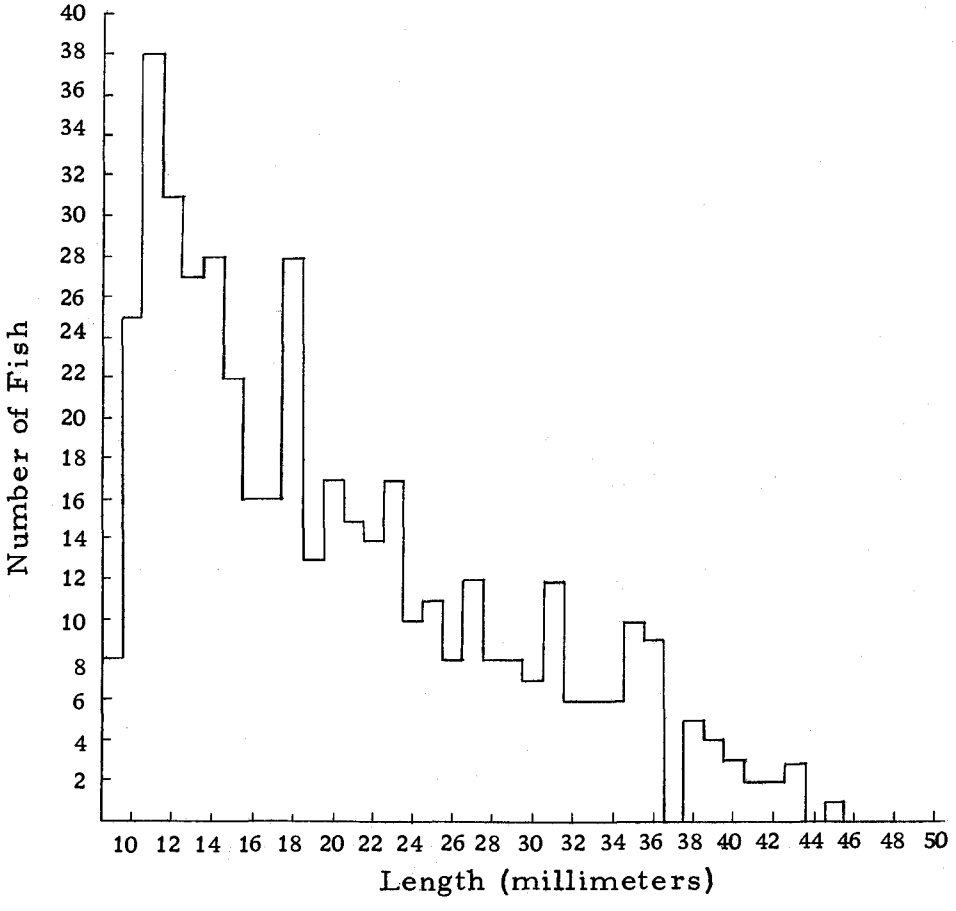
APPENDIX

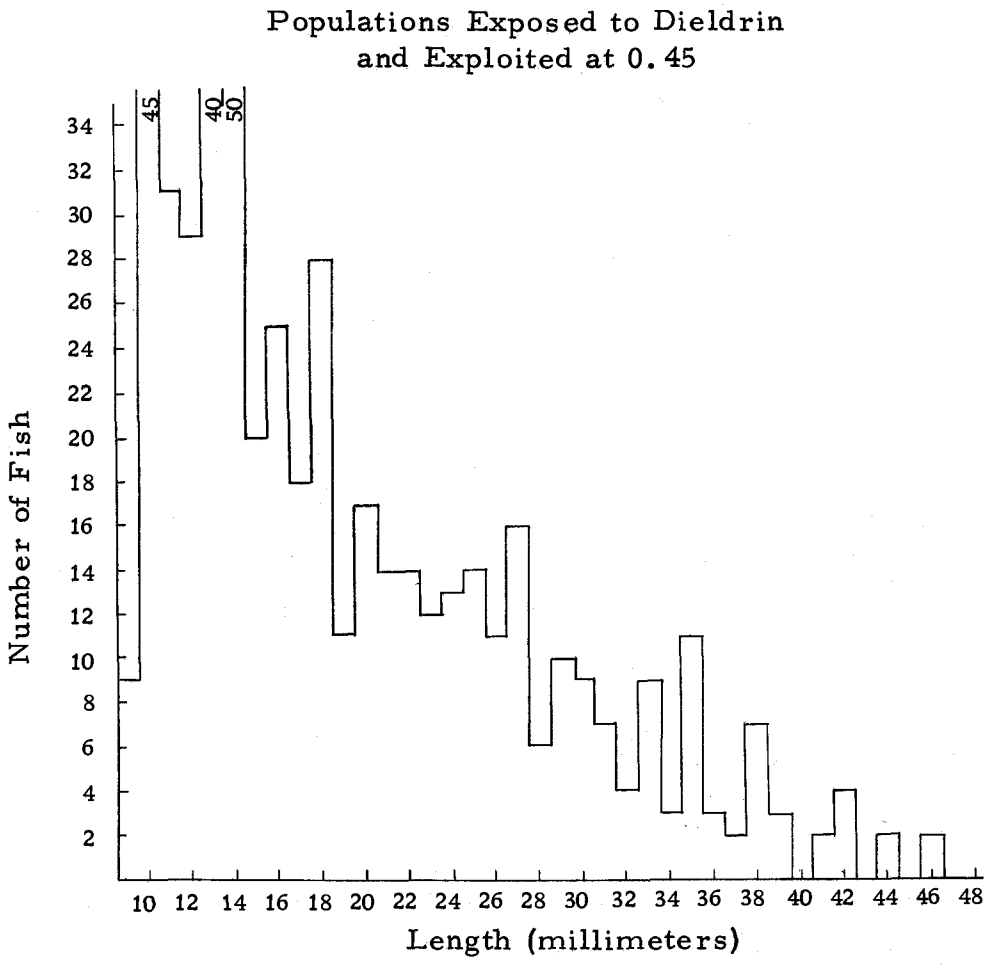
Appendix I. Length-frequency distributions of the catch of female guppies from control populations and populations exposed to dieldrin at each exploitation rate. Each length-frequency distribution was constructed from the catch from two replicates from exploitation point seven to exploitation point fifteen.




Populations Exposed to Dieldrin
and Exploited at 0.60
66
76
60
48
45
Number of Fish
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46 48 50 52
Length (millimeters)

Control Populations Exploited at 0.45




Populations Exposed to Dieldrin
and Exploited at 0.45
Number of Fish
Length (millimeters)
45
40
50
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
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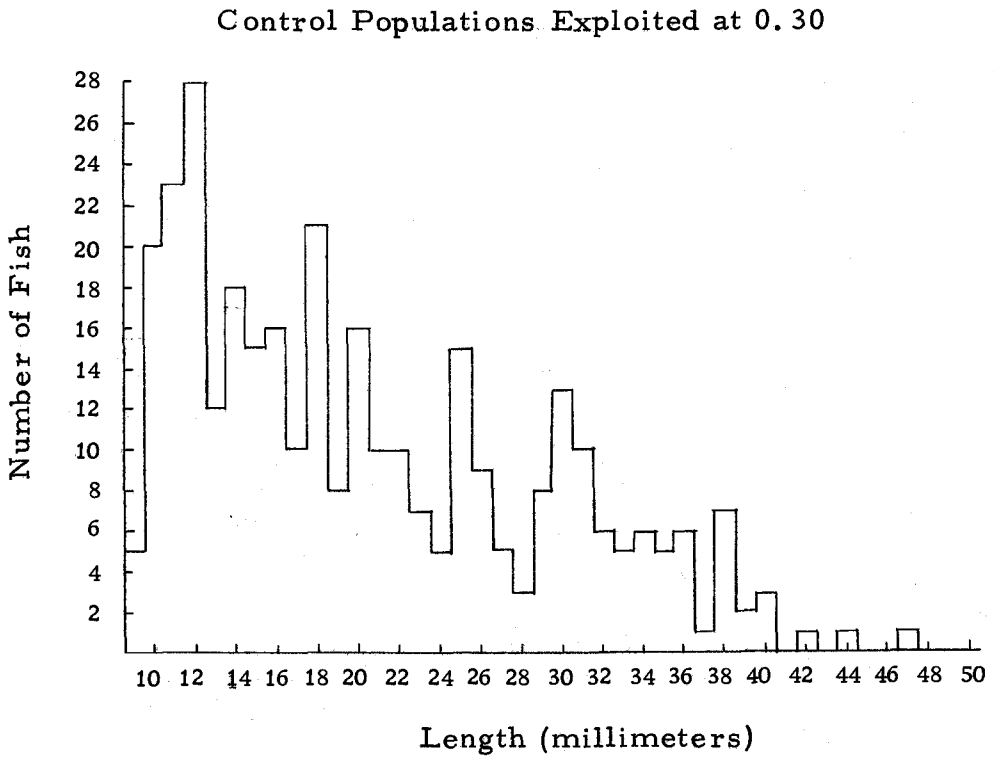
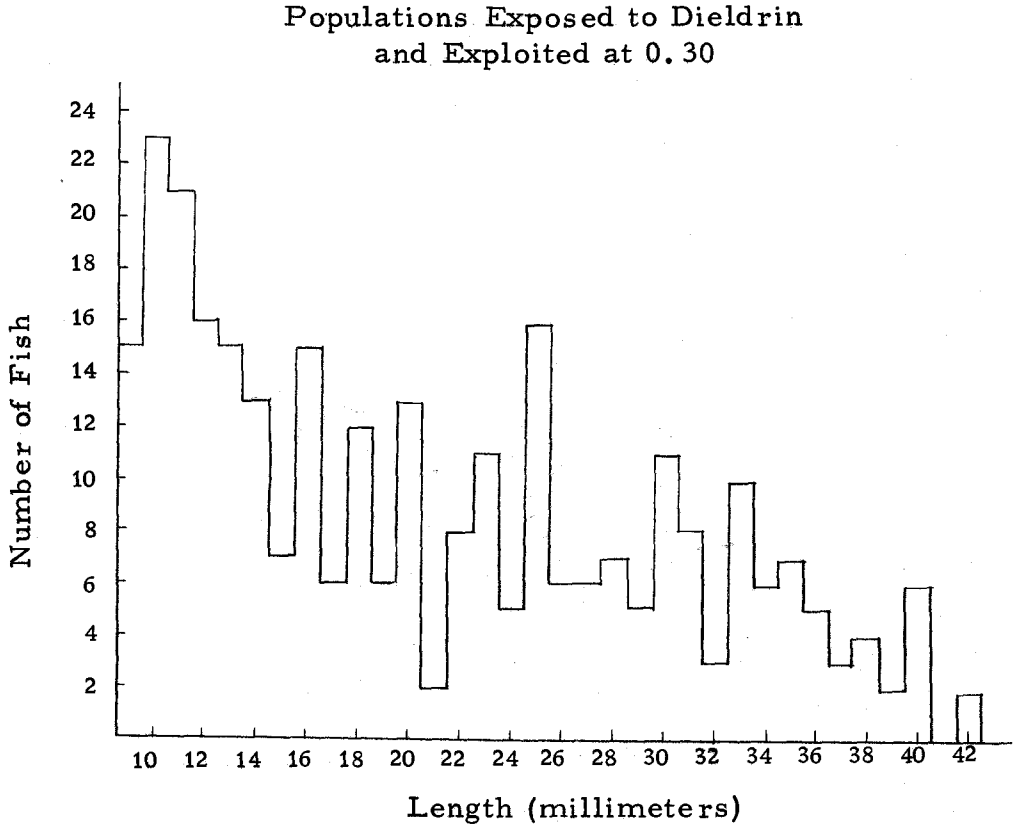

Control Populations Exploited at 0.30
Number of Fish
28
26
24
22
20
18
16
14
12
10
8
6
4
2
10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46 48 50
Length (millimeters)


Populations Exposed to Dieldrin
and Exploited at 0.30
Number of Fish
24
22
20
18
16
14
12
10
8
6
4
2
10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42
Length (millimeters)