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EXPERIMENTAL EXPLOITATION OF FISH POPULATIONS

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ABSTRACT

Four laboratory populations of guppies were grown in small aquariums under controlled light, temperature, and food supply. Two of the populations were selected by lot as controls; the other two were used as experimental populations for application of various fishing pressures.

Successive application of fishing rates of 25, 10, 50, and 75 percent per triweekly period produced major changes in the experimental populations not duplicated in the controls. The general effect of exploitation was to produce a decrease in the size of the population, the amount of the decrease varying upward with the exploitation rate, until at the 75-percent rate the test populations were extinguished. Abundance and size composition of the stocks followed classical conceptions derived on theoretical grounds.

Equilibrium yield was found to be related to fishing rate in the manner of a humped curve, with maximal yield at fishing rates between 30 and 40 percent, when the populations were at approximately one-third their asymptotic weight. The yield of fish flesh at the maximum represented about one-fifth the weight of the food consumed.

The conventional fishery measures—catch, catch per unit of effort, and average fish length—were calculated and were found to yield a large amount of information about population size and results of changes in rate of exploitation.

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By RALPH P. SILLIMAN and JAMES S. GUTSELL, *Fishery Research Biologists*

In fishery investigations, interest centers about the catching rate, or rate of exploitation, since this rate is one, and often the only one of the factors affecting the fishery, which is under the control of man. Indeed, a large part of all fishery research has been directed toward the problem of finding the consequences of various fishing rates, and in particular of locating the rate which will provide the maximum sustained yield of fish for use as food. Most of the approaches to this problem have been ecological, consisting in the observation of the fish in their natural environment, and their reaction to changes in fishing and in environment. The well-known contributions of Baranov (1918), Russel (1931), Graham (1935), Thompson and Bell (1934), and Ricker (1948) use observations of this type, coupled with relatively simple mathematical models. Use of such observations is greatly complicated by the fact that population changes due to natural causes often mask those due to fishing.

More recently the maximum-yield problem has been approached through the technique of complex mathematical models, such as those developed by Beverton and Holt (1956). This approach, too, is difficult when the various recruitment, growth, and mortality rates affecting the populations not only vary but have their variations dependent on population characteristics. As noted by Schaefer (1943), "The problem is much more complex when the mortality or recruitment rates are not uniform, and leads, in general, to no simple solution."

The laboratory experiment as an approach to the maximum-yield problem has not to our knowledge been used previously for fish populations. For insects, the laboratory reactions of populations to removals have been studied by Nicholson (1954) and Watt (1955), using sheep blowflies and flour beetles, respectively. Although these experiments produced an abundance of useful information, it seems likely that the great differentiation of larval from adult insect forms caused the reactions to be somewhat different from those of fish populations, where in most exploited species the adult form is assumed at a very early age. An experiment utilizing two laboratory populations of the guppy, *Lebistes reticulatus*, was started by Silliman (1948) but was terminated before it had produced any results relating to exploitation.

The experiments reported herein represent a resumption of the work of Silliman (1948), who listed as reasons for choosing the guppy as an experimental animal, its small size, rapid reproductive and growth rates, and hardiness. Primary objectives of the work were to learn as much as possible about the reaction of fish populations to different rates of exploitation, to discover the relation between equilibrium yield and exploitation rate, and to establish principles of exploitation which would be applicable to commercially utilized fish populations. An additional objective was to find how many of the known facts regarding population changes would be revealed by the conventional measures of total catch, catch per unit of effort, and mean length of fish in the catch.

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PLAN OF THE EXPERIMENT

The experiment involved four aquarium tanks and their guppy populations, two of which were to be test populations exploited at selected rates and the other two of which were to serve as controls. The size of the aquariums, amount and type of food, etc., were based on previous experience of Silliman (1948). Experimental procedure was decided upon before work was begun, and consisted in starting the four populations at well below their asymptotic levels and allowing growth to asymptotic size before starting exploitation of the test populations (the plan was later changed to save time by starting exploitation at a population level somewhat below the asymptotic level). The two control populations (chosen by lot) were to be maintained under the same conditions as the test populations, with the exception of removals.

The intent was to make the experiment resemble as closely as possible a commercial fishery. For this reason the "fishing" was done in such a manner as to permit the escape of small fish, as occurs with net selection in an actual fishery. Also "refuges" were provided for newly born fish, comparable to the nursery grounds of many exploited populations. Removals were made triweekly, bearing the same relation in a time sense to the approximate 3-week guppy brood interval as does an annual fishing season to an annually spawning fish.

Finally, plans for exploitation included continuation of each selected fishing rate until equilibrium at that rate, or extinction of the populations, had occurred. In practice, the limitations of time required the interpretation of "equilibrium" to mean the lack of substantial changes in the magnitude and size composition of the catch and population, rather than the observation of the populations at each exploitation rate over a period long enough for the attainment of absolute equilibrium.

MAINTENANCE AND EXPLOITATION PROCEDURES AND EQUIPMENT

The four aquariums (designated *A*, *B*, *C*, and *D*) were placed in a concrete trough upon which was built a plywood box enclosing all units to form a lightproof enclosure. The box was painted a flat black inside and out. All heating and cooling apparatus, the bulbs of recording thermometers, and the aquariums were kept in a water bath approximately 9 cm. in depth. This water bath was constantly circulated by an electric stirrer and was covered with a layer of oil to reduce evaporation. The units were placed as shown on the accompanying diagram (fig. 1).

The aquariums were each 44 by 24 by 22.3 cm. and were filled with water to the depth of 17 cm. (volume of about 17 liters). A small electric air pump operated standard aquarium activated-charcoal filters (8 by 8 by 10 cm.) and stone aerators for each tank. In addition, each tank contained a refuge as a means of protection for the young fish; this was in the corner (fig. 1), closed in by a fence consisting of solid glass rods 3 mm. in diameter with 1.5-mm. spacing. Each aquarium was covered with a plastic screen to keep the fish from jumping out.

Once each week (usually on Friday) all populations were removed from the aquariums, and the water was filtered and the equipment cleaned. The water from each aquarium was filtered first through a silk cloth (20 standard mesh) and then through analytical filter paper. All units (filters, etc.) in the aquariums were thoroughly washed in running water. Two liters of water were replaced by an equal amount of new water each week.

At the time of cleaning the aquariums each population was separated in groups of mature males, mature females, immatures, and fry. Fry were distinguished from immatures by grading through a wire basket (2.5-mm. mesh). The males were classed as mature when the black spots on each side were prominent or when the typical male color was observed. The change from immature to adult females was determined by size and form.

After separation by sex and stage of maturity, all fish except the fry were weighed. Each population (or half of it if the amount was too large) was poured into a plastic household strainer 5 cm. in diameter with 1-mm. mesh (a plastic funnel 10 cm. high was used to keep the guppies from jumping out); the excess water from the strainer was removed by blotting the bottom on filter paper until practically no moisture showed on the paper; and the fish were then poured into a previously balanced pan holding about 75 ml. of water and were weighed on a torsion balance.

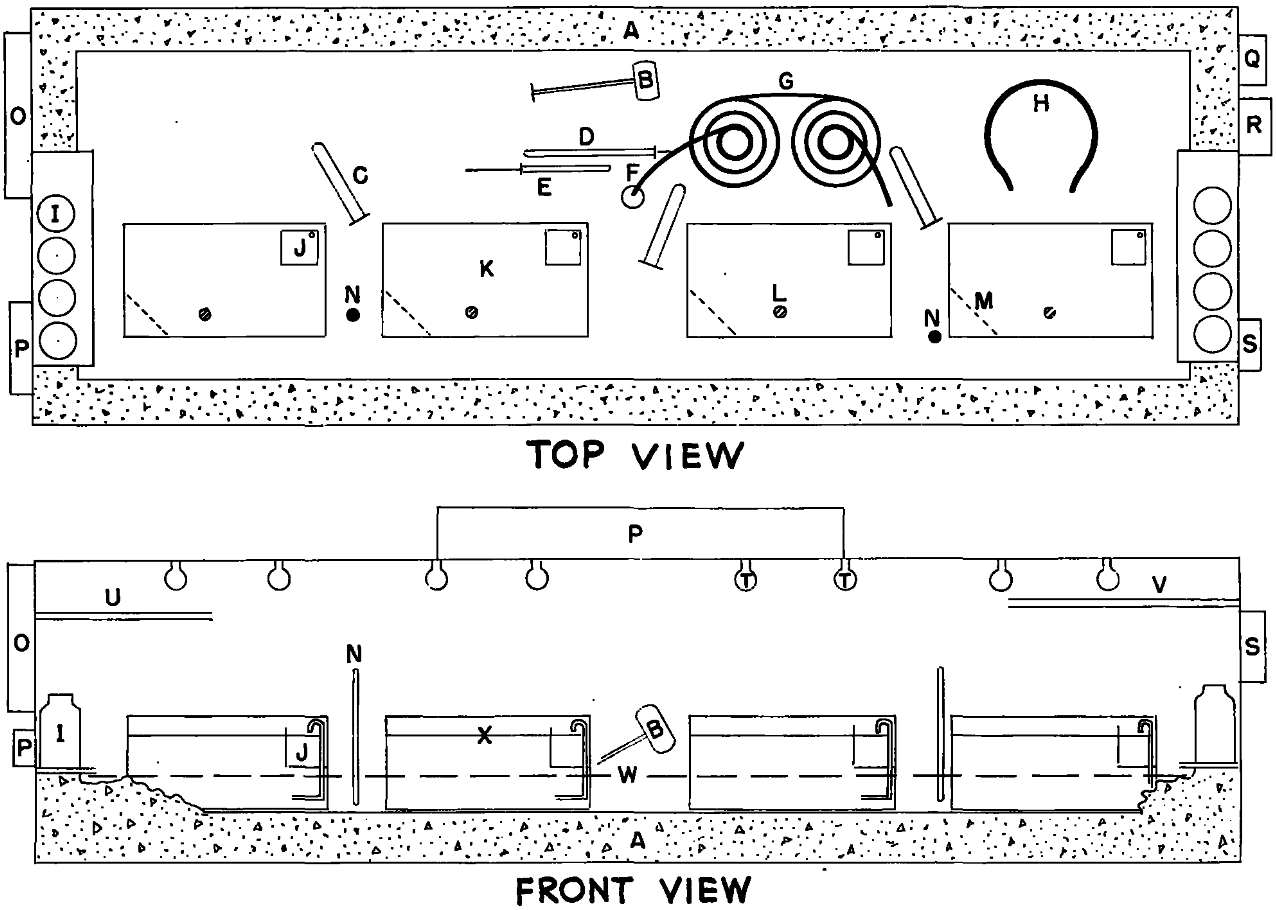

FIGURE 1.—Experimental apparatus: *A*, concrete tank with sides 4 inches thick; *B*, stirrer; *C*, submerged aquarium heater; *D*, bulb of thermoregulator; *E*, bulb of temperature recorder; *F*, outlet for cold-water coil; *G*, cold-water coils (water 54° C., continuous flow); *H*, heating unit; *I*, brine-shrimp (*Artemia*) hatching jars; *J*, filter (plastic containing activated charcoal); *K*, aquariums; *L*, aerators; *M*, refuges to harbor fry (1.5-mm. spacing); *N*, thermometers, laboratory glass; *O*, thermometer (7-day recording); *P*, air vent; *Q* and *R*, temperature control and switch; *S*, automatic time switch; *T*, lights (two 25-watt bulbs over each aquarium); *U*, cold-water inlet; *V*, air line; *W*, water-bath level; *X*, water line in aquariums.

When it was necessary to divide the population into two parts, the second half was drained and weighed with the first.

The cropping or removal of fish in the test populations was carried out at the end of each 3 weeks. Removals were made after the weighing, before the fish were returned to the aquariums. Fish were netted from a container one at a time, with removals corresponding to the exploitation rate being applied. Thus, at the 25-percent rate, each fourth fish was removed. To avoid bias, removals were started at successive croppings with fish No. 1, No. 2, No. 3, and No. 4, after which the cycle was repeated. The fry, having previously been separated from the rest of the populations, were not included in the removals. All fish removed were preserved in 5-percent formalin.

All four populations were fed frozen *Daphnia*, dry food, and brine shrimp (*Artemia*). The dry food was a standard commercial aquarium food, coarse grade. Two lots of this food were used, one for the first 99 weeks, the second for weeks 100 to 174. The second lot differed from the first only in the addition of aureomycin and vitamin B_{12}.

The Brine shrimp were prepared by placing one-fourth level teaspoon (approximately 1.2 ml.) of the eggs in 750 ml. of saline solution. This solution was prepared the previous day by putting one level tablespoon of common rock salt into each 750 ml. of water. The four individual hatching jars of shrimp eggs were kept at about 24° C. for

48 hours, after which time the hatched shrimp were syphoned off through a fine-mesh silk cloth and rinsed into the aquariums.

Near the end of the experiment, duplicate hatches of brine shrimp were produced for weighing to determine the amount being fed. Hatches of nauplii produced in the usual way were filtered from the salt water with several types of filters (bolting cloth; Gooch crucible with asbestos; sintered glass crucible, coarse; stainless-steel crucible, coarse). After being washed with distilled water to remove salt, the nauplii were placed in an oven at 60° C. for 10 to 12 hours, vacuum dried at 60° C. for 4 hours, and weighed. The average of the weighings was 0.125 mg.

Food was placed in each aquarium according to the following weekly schedule:

Day of week	*Amount per feeding of—* *Daphnia* (gram)	Brine shrimp (milligram)	Dry food (gram)
Sunday	-----	------	0. 1
Monday through Friday	1. 0	0. 125	. 1
Saturday	-----	. 125	. 1
Total amount per week	5. 0	0. 750	0. 7

Such minor variations from the above schedule as occurred were the same for all four aquariums.

A temperature regulator was installed in connection with electrical heaters (fig. 1) for the purpose of keeping the aquarium temperatures at 75° F. with a variation of ±2° F. This equipment did not function properly, however, and large variations in temperature occurred, as set forth later in the report. These variations were the same for all four aquariums, owing to the circulation of the water bath containing them.

Light was maintained practically constant by having the aquariums in a light-tight box, which was opened only during feeding, cleaning, or other need. The two 25-watt incandescent lamps above each aquarium were turned on 12 hours a day (6 a. m. to 6 p. m.) by means of an electrical time switch.

NARRATIVE OF EXPERIMENT

The first 5 weeks of experimentation were occupied with attempts to maintain populations of inferior stock, all of which died. During the sixth week new stock was obtained, and the populations grew satisfactorily. Thus the experiments reported herein started with week No. 6, May 6–12, 1951 (a list of week numbers is given in table 1). Two stocks were secured and were divided among the aquariums in such a way that aquariums A and C had stocks from one source and B and D from the other. Populations A and C were started with 5 males and 3 females each; populations B and D with 5 fish of each sex.

TABLE 1.—*List of week numbers used in table and graph designations*

Week No.	Beginning			Week No.	Beginning			Week No.	Beginning		
	Month	Day	Year		Month	Day	Year		Month	Day	Year
1	Apr.	1	1951	59	May	11	1952	117	June	21	1953
2		8		60		18		118		28	
3		15		61		25		119	July	5	
4		22		62	June	1		120		12	
5		29		63		8		121		19	
6	May	6		64		15		122		26	
7		13		65		22		123	Aug.	2	
8		20		66		29		124		9	
9		27		67	July	6		125		16	
10	June	3		68		13		126		23	
11		10		69		20		127		30	
12		17		70		27		128	Sep.	6	
13		24		71	Aug.	3		129		13	
14	July	1		72		10		130		20	
15		8		73		17		131		27	
16		15		74		24		132	Oct.	4	
17		22		75		31		133		11	
18		29		76	Sep.	7		134		18	
19	Aug.	5		77		14		135		25	
20		12		78		21		136	Nov.	1	
21		19		79		28		137		8	
22		26		80	Oct.	5		138		15	
23	Sep.	2		81		12		139		22	
24		9		82		19		140		29	
25		16		83		26		141	Dec.	6	
26		23		84	Nov.	2		142		13	
27		30		85		9		143		20	
28	Oct.	7		86		16		144		27	
29		14		87		23		135	Jan.	3	1954
30		21		88		30		146		10	
31		28		89	Dec.	7		147		17	
32	Nov.	4		90		14		148		24	
33		11		91		21		149		31	
34		18		92		28		150	Feb.	7	
35		25		93	Jan.	4	1953	151		14	
36	Dec.	2		94		11		152		21	
37		9		95		18		153		28	
38		16		96		25		154	Mar.	7	
39		23		97	Feb.	1		155		14	
40		30		98		8		156		21	
41	Jan.	6	1952	99		15		157		28	
42		13		100		22		158	Apr.	4	
43		20		101	Mar.	1		159		11	
44		27		102		8		160		18	
45	Feb.	3		103		15		161		25	
46		10		104		22		162	May	2	
47		17		105		29		163		9	
48		24		106	Apr.	5		164		16	
49	Mar.	2		107		12		165		23	
50		9		108		19		166		30	
51		16		109		26		167	June	6	
52		23		110	May	3		168		13	
53		30		111		10		169		20	
54	Apr.	6		112		17		170		27	
55		13		113		24		171	July	4	
56		20		114		31		172		11	
57		27		115	June	7		173		18	
58	May	4		116		14		174		25	

All four populations were allowed to grow without interference, under the conditions of food, light, temperature, and space as set forth above until week 40, when cropping of populations A and B was begun at the rate of 25 percent per 3-week period. Maintenance of populations C and

D was continued without change; thus *C* became the control for *A*, and *D* for *B*. The cropping of *A* and *B* was changed to 10 percent at week 79, to 50 percent at week 121, and finally to 75 percent at week 151.

Under the final high rate, populations *A* and *B* declined steadily until population *B* became extinct at week 170. The remaining three populations were maintained until week 174, when population *A* contained only one fish. At this time all three populations were killed, and the experiment therefore ended, the terminal date being July 31, 1954. Changes occurring in number and weight of the four populations during the experiment are portrayed in graphs, figures 2 and 3.

It is noteworthy that the two unexploited populations, after their initial growth, fluctuated about an asymptotic level and did not enter into a long-term decline. This is in contradistinction to the results of Shoemaker (1947) whose 13 laboratory populations of guppies began to decline sharply after the 75th week, reaching a final average weight after 137 weeks, about one-fifth the peak level. He concluded that such fluctuations in abundance were characteristic of populations containing a predator (adult) and prey

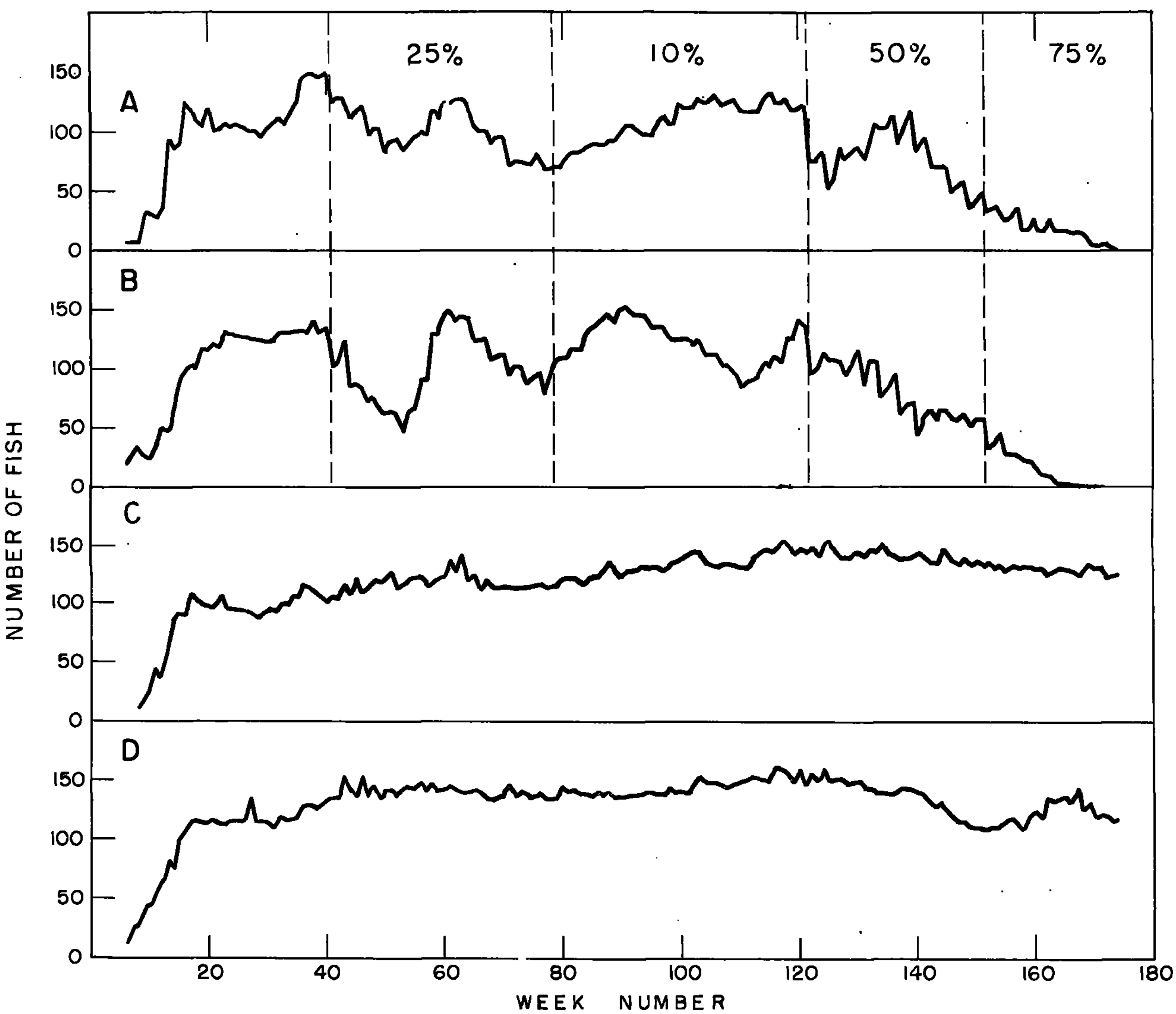

FIGURE 2.—Weekly population numbers during course of experiment. Percentages in upper two panels are triweekly exploitation rates.

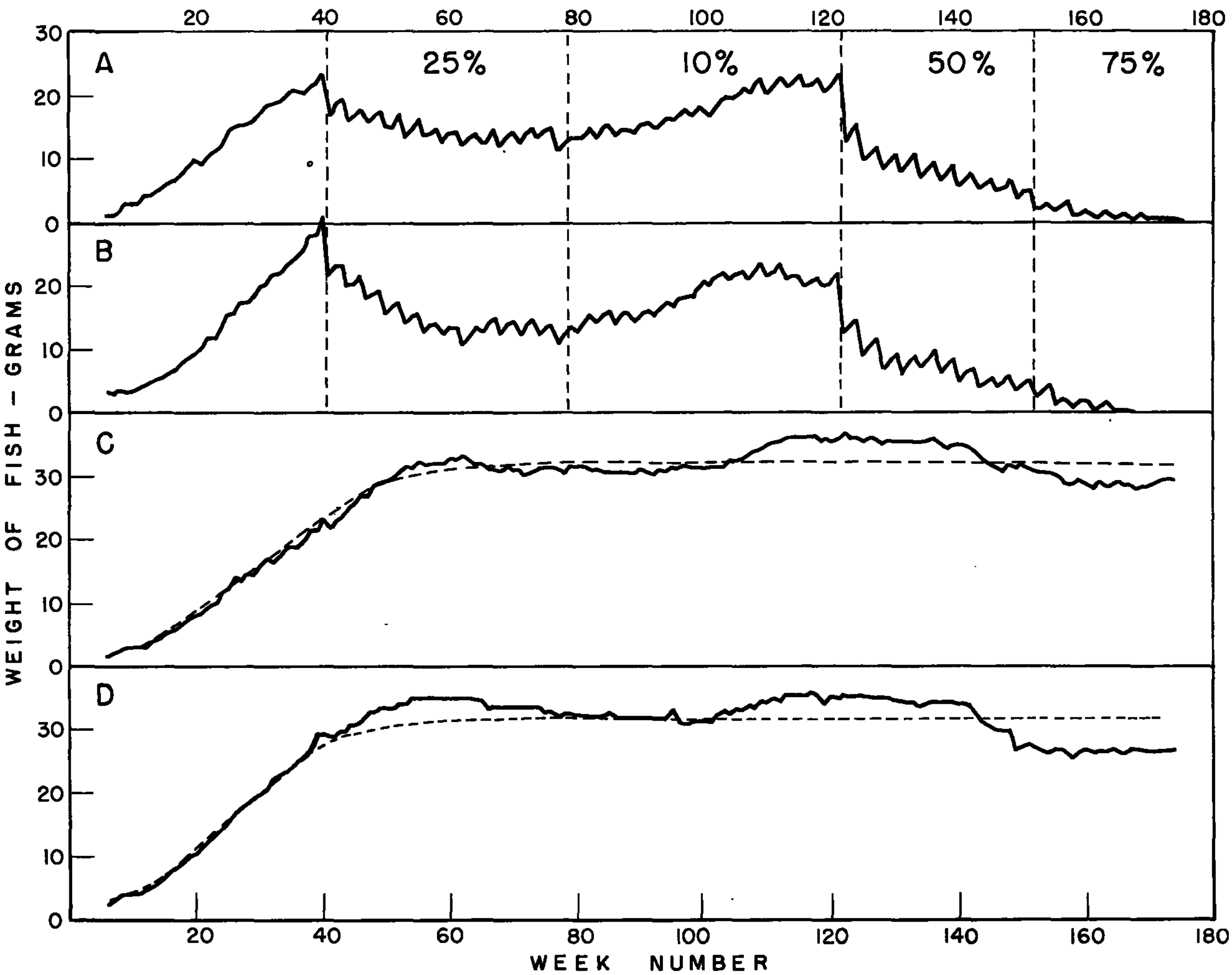

FIGURE 3.—Weekly population weights during course of experiment. Percentages in upper two panels are triweekly exploitation rates. Broken-line curves in lower two panels are logistic fits.

(juvenile) component, but certainly the experiments reported herein do not evidence fluctuations of the magnitude observed by Shoemaker. It seems possible that Shoemaker's fluctuations resulted from the method of feeding, in which an excess of food was offered at all times, and from the lack of special refuges for newborn fish. Such a situation could well lead to more unstable populations than one in which the amount of available food was fixed and refuges were available, as in the present experiments.

The number of generations of observation (44) required to obtain the information reported herein is impressive. This is equivalent to 44 years in an actual fishery even in the unlikely instance that variables other than fishing are controlled as fully as in the laboratory populations. It points up the lengthy observations needed as a reliable basis for management of commercial fisheries.

GROWTH OF POPULATIONS

Growth in weight (fig. 3) proved to be much more regular than growth in numbers (fig. 2). This undoubtedly resulted from the disturbance of numbers by the newly born broods of fry; because of their insignificant weight these broods disturbed total weight of the populations very little. Each of the four populations increased in weight almost without interruption until week 40, when cropping of populations *A* and *B* was begun. Growth of populations *C* and *D* continued until peaks were reached at weeks 62 and 58, respectively. During the remainder of the experiment the total weights fluctuated considerably but gave every indication of varying about a mean value, which would of course be the asymptotic population level.

Attempts were made to fit a number of types of growth curves, including the modified exponential (Sherman and Morrison, 1950), the Gompertz, and the logistic. Of these the logistic provided the most satisfactory fit to the observations. In making the fit, the asymptotic weight was taken as the mean for weeks 56 through 174: 32.1 grams for population *C* and 32.0 grams for population *D*. This correspondence, incidentally, seems remarkable for two populations with different genetic origins, and confirms the findings of other investigators (e. g., Spear and Glude, 1957) that within species environmental characteristics such as temperature and food supply can be more important than heredity as influences on growth. Constants of the curves were determined by the method of Spurr and Arnold (1948), fitting to the empirical weights for weeks 6 through 55. Deviations of the observational data from the fitted curves (fig. 3) indicated periodic fluctuations of about 65 weeks duration superimposed upon the basic growth pattern. These are similar for the two control populations, although the initial peak deviates more from the logistic curve in population *D* than in population *C*. The deviations are ascribable partly to changes in temperature, as will be discussed later.

CHANGES DURING EXPLOITATION

Changes in Number

The initial reaction to the imposition of a 25-percent triweekly exploitation rate to populations *A* and *B* was the expected decrease in total population numbers (tables 2 and 3, figs. 4 and 5). This decrease is contrasted with the continuing upward trend of the control populations *C* and *D*, clearly demonstrating that the decrease was the result of exploitation. In both *A* and *B* the decrease was composed of an immediate reduction in the accumulated stock of adults followed by an initial reduction in the number of juveniles. The space and food thus made available apparently caused an improved survival rate, resulting in a new influx of juveniles and a peak of population numbers at about week 60. A further adjustment between juveniles and adults then took place, resulting in a relatively stable ratio starting with week 73.

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Decreasing the exploitation rate to 10 percent caused the numbers of both adults and juveniles to increase in *A* and *B*. The history of the two populations after week 91 differs, however. In *A* the increase in adults continued throughout the 10-percent exploitation period, while the juveniles declined (presumably as the result of competition from the greater number of adults; cf. Park 1941) after week 100. In *B* the decline of juveniles started earlier (week 91) and was followed by a sharp increase beginning with week 109. Also, there was a decline in adult numbers after week 106. No firm hypothesis for these differences between *A* and *B* is offered, although they may result from genetic differences in reproductive rate and ability to secure food.

Changes under the 50-percent rate resemble those occurring under the 25-percent rate, the same initial decline in adults followed by an influx of juveniles being present. As anticipated, the final level for adults is much lower than under either the 10-percent or the 25-percent rate.

The 75-percent rate proved to be catastrophic for the test populations. Even though the amount of food and space per individual fish was great, this could not increase survival sufficiently to offset the loss of progeny resulting from the rapid reduction in mature adults. Both *A* and *B* proceeded steadily to extinction.

In general, the test populations demonstrated violent changes in population size and composition, coinciding with changes in exploitation rate, and not found in the control populations. It seems certain, therefore, that the changes did result from the experimental removal of fish at the stated rates.

The "natural deaths" (figs. 4 and 5) consist of dead fish found in the aquariums. Since most of the mortality occurs through cannibalism, these dead fish represent only a small fraction of the total mortality. However, it is of some interest that the rate of occurrence of dead fish increased during the latter part of the experiment in the two control populations, as the proportion of old fish became greater; apparently senility played some part in these deaths. In the test populations fish were cropped off so fast that there was no opportunity for an accumulation of older individuals.

The graphs of catch (figs. 4 and 5, center panels) verify some established principles of fishery ex-

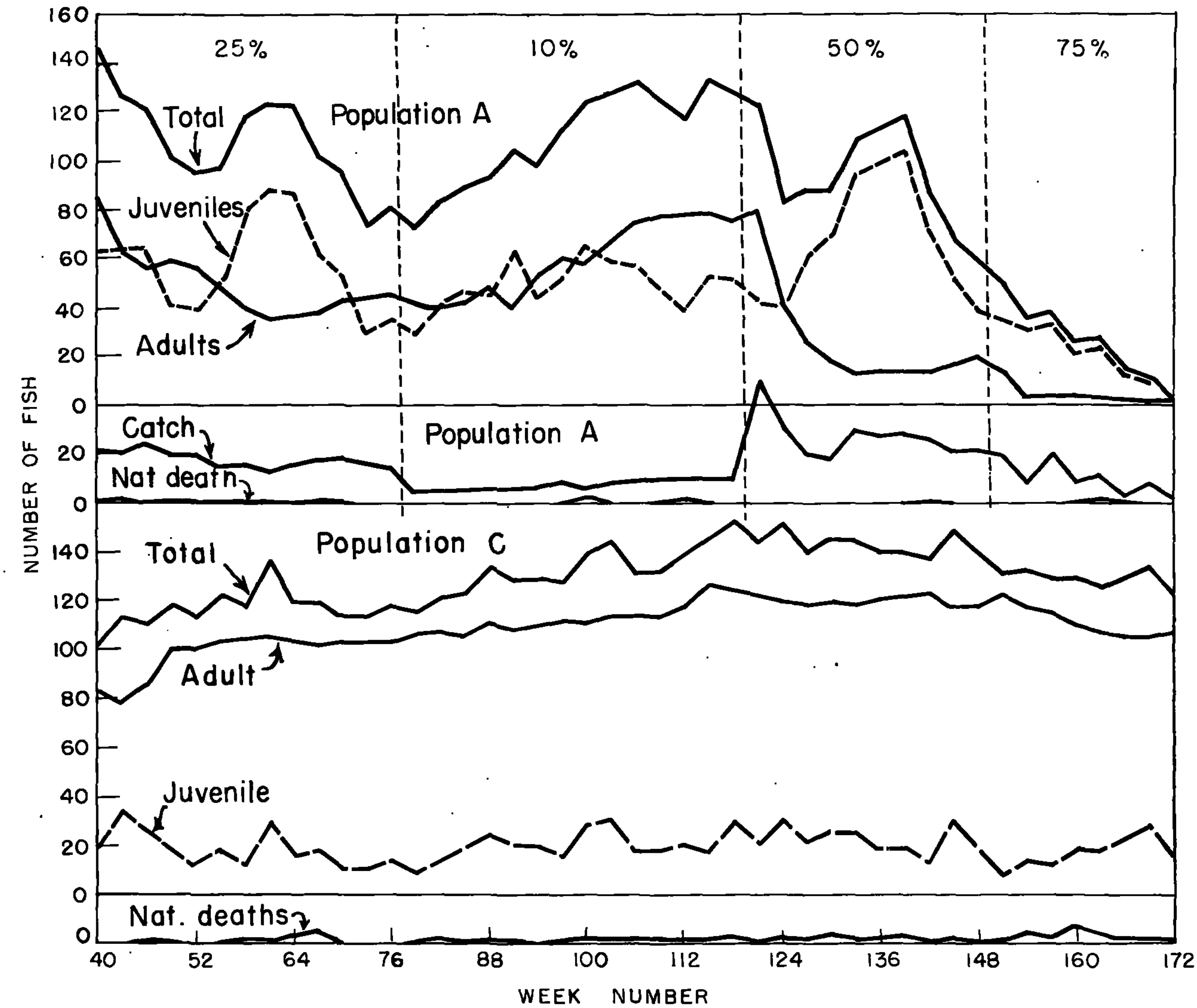

FIGURE 4.—Triweekly population, catch, and mortality numbers during exploitation period in populations A (test) and C (control).. Percentages in upper two panels are triweekly exploitation rates.

ploitation: (*a*) At such low levels of exploitation as 10 percent, the catch is stable but below what the stock is capable of producing; (*b*) increase of the rate from 10 percent to 50 percent produces a large temporary increase in catch, followed by a decrease and stabilization at a level lower than the initial, but higher than that at the 10-percent rate; (*c*) at the 75-percent rate both catch and stock decline steadily—this is true "overfishing."

Changes in Weight

As mentioned above, population weights are much less disturbed by the entrance and mortality of new broods of young fish, and therefore are less subject to violent fluctuations, than population numbers. For our purposes this is fortunate, for commercial-catch statistics are usually expressed in weights rather than in numbers of fish. The data on weights of the experimental populations (table 4, fig. 6), although less detailed than the data on numbers, are thus of particular interest for the examination of trends, and for comparison with commercial-fishery data. It is noteworthy that the weight curves (fig. 6) for comparable populations (A with B, C with D) correspond much more closely than the number curves (figs. 4 and 5). This lends support to the theory expressed above that the differences in the number

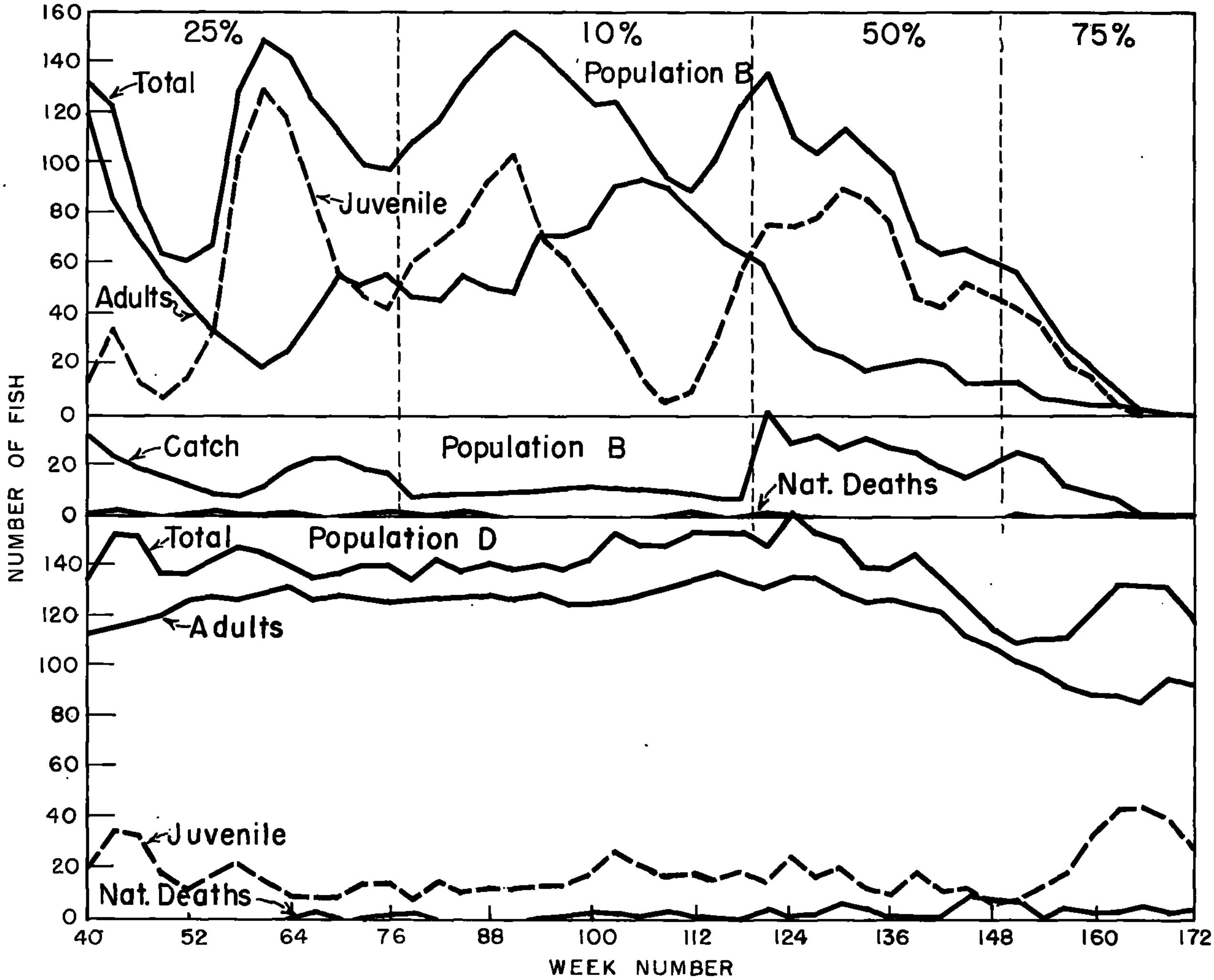

FIGURE 5.—Triweekly population, catch, and mortality numbers during exploitation period in populations *B* (test) and *D* (control). Percentages in upper two panels are triweekly exploitation rates.

curves for populations *A* and *B*, particularly during the 10-percent exploitation rate, may result from inherited differences in fecundity, which change the numbers substantially but the weights insignificantly.

It is instructive to compare the graphs of catch and total weight at the 50-percent rate with the graphs of "total landings" and "catch per skate" (a measure of total weight) in Thompson and Bell (1934, p. 37). Although Thompson and Bell's theoretical graphs were constructed with an assumed constant recruitment which obviously did not prevail in the guppy populations, the correspondence of the graphs is nevertheless remarkable. It shows that the experimental populations behaved as might be anticipated on the basis of a rather simple mathematical formulation. This was true even though the change in fishing rates ("number of skates") of the halibut example was such as to cause the final catch to be lower than the initial, whereas the reverse was true for the guppy experiment.

Changes in Sex Composition

Since the sex of mature fish could be readily determined by inspection, sex-composition data were available for the duration of the experiment. The percentage of males (table 5, fig. 7) indicates a marked tendency for a greater proportion of males in the exploited (*A* and *B*) populations as

TABLE 2.—*Triweekly data on population composition and catch under exploitation in test* (A) *and control* (C) *populations*

[Numbers listed are before removals at the indicated percentage rates. Categories "fry" and "immature" defined in text, section Maintenance and Exploitation Procedures and Equipment]

Exploitation rate and week No.	Population A									Population C							
	Juvenile			Adult			Grand total	Catch	Natural deaths	Juvenile			Adult			Grand total	Natural deaths
	Fry	Immature	Total	Male	Female	Total				Fry	Immature	Total	Male	Female	Total		
25 percent																	
40	[1]	[1]	64	47	38	85	149	22	1	[1]	[1]	19	37	46	83	102	0
43	[1]	[1]	64	36	27	63	127	21	2	[1]	[1]	35	34	45	79	114	0
46	21	45	66	35	21	56	122	25	0	[1]	[1]	25	39	47	86	111	1
49	18	24	42	38	21	59	101	20	1	9	9	18	43	57	100	118	0
52	16	23	39	33	23	56	95	20	1	4	9	13	44	57	101	114	0
55	39	9	48	28	21	49	97	15	1	11	8	19	47	57	104	123	0
58	53	25	78	21	19	40	118	16	1	7	6	13	47	58	105	118	2
61	69	20	89	18	17	35	124	13	0	24	7	31	48	58	106	137	0
64	61	26	87	20	16	36	123	16	0	13	3	16	45	59	104	120	4
67	29	35	64	21	17	38	102	18	2	14	4	18	46	56	102	120	6
70	20	33	53	24	19	43	96	19	0	5	6	11	48	56	104	115	1
73	8	21	29	27	18	45	74	16	0	4	7	11	47	56	103	114	0
76	23	12	35	22	24	46	81	15	0	7	7	14	48	56	104	118	0
10 percent																	
79	26	5	31	22	20	42	73	5	0	4	5	9	48	59	107	116	0
82	34	9	43	22	18	40	83	5	0	9	5	14	50	58	108	122	2
85	29	18	47	25	17	42	89	6	0	10	8	18	48	58	106	124	1
88	23	22	45	30	18	48	93	7	0	20	4	24	48	63	111	135	1
91	34	30	64	26	15	41	105	7	0	13	7	20	46	63	109	129	1
94	24	20	44	30	24	54	98	7	0	13	7	20	49	61	110	130	0
97	25	27	52	31	30	61	113	9	0	6	10	16	51	61	112	128	2
100	44	22	66	30	28	58	124	7	2	18	11	29	53	58	111	140	2
103	34	26	60	39	29	68	128	9	0	24	7	31	54	60	114	145	1
106	33	24	57	43	32	75	132	9	0	6	12	18	54	60	114	132	2
109	21	27	48	46	32	78	126	11	0	2	16	18	58	57	115	133	2
112	13	26	39	49	30	79	118	11	1	10	11	21	61	57	118	139	1
115	30	24	54	49	30	79	133	11	0	14	4	18	63	64	127	145	1
118	32	21	53	46	30	76	129	10	0	27	3	30	60	64	124	154	4
50 percent																	
121	26	17	43	47	33	80	123	49	0	14	8	22	58	54	122	144	1
124	20	19	39	19	24	43	82	31	0	24	7	31	58	63	121	152	3
127	47	15	62	10	16	26	88	21	0	11	10	21	54	65	119	140	3
130	50	21	71	5	13	18	89	19	0	17	9	26	56	64	120	146	5
133	48	47	95	5	8	13	108	30	0	15	11	26	55	64	119	145	2
136	58	42	100	8	6	14	114	28	0	5	14	19	55	66	121	140	2
139	61	44	105	7	7	14	119	29	0	8	11	19	58	64	122	141	3
142	33	41	74	7	7	14	88	27	1	6	8	14	60	64	124	138	0
145	26	25	51	9	9	18	69	22	0	25	7	32	57	61	118	150	2
148	14	25	39	12	9	21	60	23	0	13	7	20	57	62	119	139	1
75 percent																	
151	24	12	36	9	6	15	51	21	0	7	2	9	57	66	123	132	2
154	23	9	32	1	3	4	36	9	0	9	6	15	55	63	118	133	5
157	12	22	34	1	3	4	38	20	0	8	6	14	56	60	116	130	3
160	13	8	21	3	2	5	26	9	0	14	5	19	55	56	111	130	7
163	12	12	24	2	2	4	28	12	2	14	5	19	53	55	108	127	4
166	11	2	13	1	2	3	16	3	0	17	7	24	52	54	106	130	2
169	0	10	10	0	2	2	12	9	0	20	9	29	53	53	106	135	2
172	0	0	0	2	1	3	3	2	0	7	8	15	55	53	108	123	1

[1] Not listed separately; included in "total."

TABLE 3.—*Triweekly data on population composition and catch under exploitation in test* (B) *and control* (D) *populations*

[Numbers listed are before removals at the indicated percentage rates. Categories "fry" and "immature" defined in text, section Maintenance and Exploitation Procedures and Equipment]

Exploitation rate and week No.	Population B									Population D							
	Juvenile			Adult			Grand total	Catch	Natural deaths	Juvenile			Adult			Grand total	Natural deaths
	Fry	Immature	Total	Male	Female	Total				Fry	Immature	Total	Male	Female	Total		
25 percent																	
40	(1)	(1)	13	47	74	121	134	32	0	(1)	(1)	21	53	60	113	134	0
43	(1)	(1)	35	35	53	88	123	24	2	(1)	(1)	36	55	61	116	152	0
46	5	9	14	26	44	70	84	19	0	(1)	(1)	34	57	61	118	152	1
49	2	5	7	22	34	56	63	15	0	5	12	17	59	61	120	137	0
52	13	2	15	19	27	46	61	13	0	5	6	11	61	65	126	137	0
55	32	1	33	15	19	34	67	9	2	11	5	16	62	66	128	144	0
58	95	8	103	12	14	26	129	8	0	15	6	21	62	65	127	148	0
61	103	28	131	8	11	19	150	11	0	14	2	16	62	68	130	146	0
64	73	45	118	17	8	25	143	18	1	7	2	8	63	69	132	141	0
67	33	53	86	29	10	39	125	23	0	6	3	9	57	69	126	135	3
70	19	39	58	34	21	55	113	23	0	4	5	9	59	69	128	137	0
73	22	26	48	32	20	52	100	19	0	9	5	14	59	68	127	141	0
76	32	10	42	30	26	56	98	17	1	9	6	15	56	70	126	141	1
10 percent																	
79	45	17	62	25	22	47	109	7	0	1	7	8	55	72	127	135	1
82	45	26	71	25	21	46	117	8	0	8	7	15	56	72	128	143	0
85	43	34	77	31	25	56	133	9	1	4	6	10	56	72	128	138	0
88	54	40	94	28	23	51	145	9	0	5	7	12	57	72	129	141	0
91	58	46	104	29	20	49	153	10	0	6	6	12	56	71	127	139	1
94	41	32	73	45	27	72	145	10	0	6	7	13	57	71	128	141	0
97	24	39	63	45	27	72	135	11	0	7	7	14	55	70	125	139	2
100	2	46	48	47	29	76	124	12	0	8	9	17	52	73	125	142	3
103	13	21	34	54	37	91	125	11	0	15	12	27	54	72	126	153	2
106	9	8	17	53	41	94	111	10	0	10	11	21	55	73	128	149	1
109	3	2	5	50	41	91	96	10	0	7	10	17	55	77	132	149	4
112	8	1	9	46	35	81	90	9	1	13	6	19	56	79	135	154	0
115	30	0	30	42	30	72	102	7	0	9	7	16	56	81	137	153	1
118	56	3	59	37	28	65	124	7	0	12	7	19	56	79	135	154	0
50 percent																	
121	53	23	76	34	25	59	135	41	1	7	9	16	55	77	132	148	4
124	52	24	76	22	13	35	111	29	0	14	11	25	56	80	136	161	1
127	41	37	78	16	11	27	105	32	0	7	10	17	54	82	136	153	3
130	59	31	90	16	8	24	114	27	0	10	11	21	51	79	130	151	7
133	43	44	87	11	7	18	105	31	0	0	13	13	48	79	127	140	5
136	39	37	76	12	8	20	96	28	0	2	9	11	49	79	128	139	1
139	19	29	48	10	12	22	70	26	0	11	8	19	47	79	126	145	1
142	26	18	44	11	9	20	64	19	0	7	5	12	44	79	123	135	2
145	35	18	53	6	7	13	66	16	0	8	5	13	34	79	113	126	10
148	22	26	48	5	8	13	61	20	0	2	5	7	32	77	109	116	7
75 percent																	
151	24	20	44	9	5	14	58	26	1	5	3	8	30	72	102	110	9
154	13	24	37	4	3	7	44	23	0	10	3	13	29	70	99	112	1
157	11	10	21	3	3	6	27	12	1	17	2	19	25	68	93	112	5
160	7	9	16	3	1	4	20	9	1	30	4	34	24	66	90	124	3
163	0	5	5	2	2	4	9	7	2	31	13	44	25	64	89	133	4
166	0	0	0	1	1	2	2	1	0	29	16	45	26	61	87	132	6
169	0	0	0	1	0	1	1	1	0	22	19	41	27	63	90	131	3
172	0	0	0	0	0	0	0	0	0	10	17	27	30	64	94	121	4

[1] Not listed separately; included in "total."

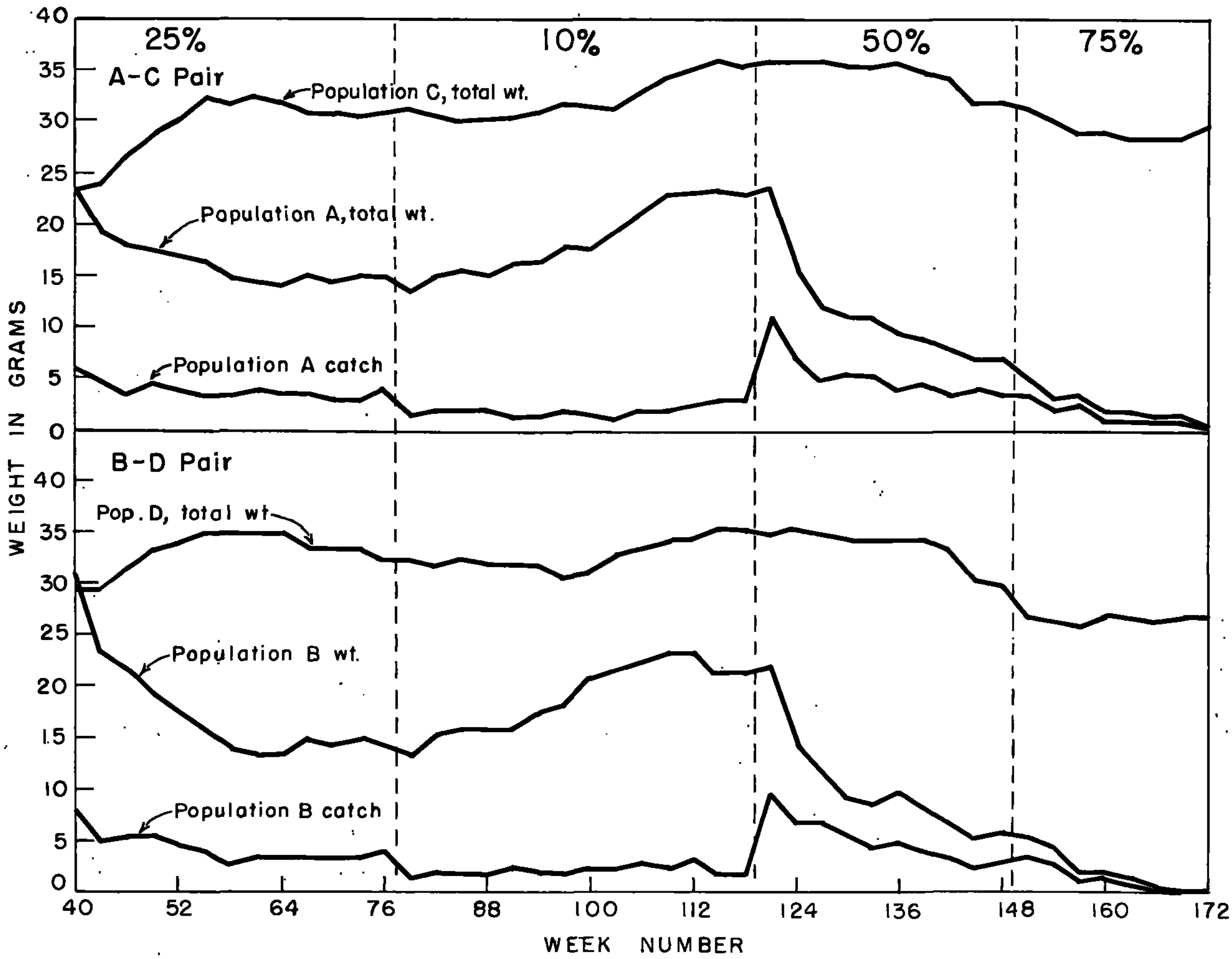

FIGURE 6.—Triweekly population and catch weights during exploitation period. Test populations (*A* and *B*) paneled with their respective controls (*C* and *D*). Percentages shown are triweekly exploitation rates.

compared with the controls (*C* and *D*). Because of the random method of selecting the fish for removals (described under Maintenance and Exploitation Procedures and Equipment) this could not have resulted from selective "fishing." Since it is possible to recognize males as mature at a somewhat earlier age than females, the apparent preponderance of males in the exploited populations may result merely from the younger average age in these populations as compared with the unexploited controls (figs. 4 and 5).

The control population *C* exhibited a strong tendency to stabilize at a 50–50 sex ratio, with only minor departures from this after week 97. In control population *D*, however, there was a decline in percentage of males with apparent stabilization at about 30 percent. This seems not to have affected the ability of the stock to maintain itself, since comparable (*C* and *D*) population sizes remained close to identity with respect both to numbers (fig. 2) and to weight (fig. 3).

The above findings are at variance with those of Breder and Coates (1932), who observed a stabilized sex composition of one-third males in three different laboratory populations of guppies. They attached considerable significance to this proportion, believing it to be characteristic of artificial populations of the species. In a later work, Breder and Coates (1936) found that the average proportion of males in the three populations after 4 years was still one-third, although this varied considerably from winter to

TABLE 4.—*Triweekly population and catch weights*

[In grams. Percentages listed are triweekly exploitation rates, and weights listed are before removals at these rates]

Rate and week No.	Population A		Population B		Population C	Population D
	Total weight	Catch weight	Total weight	Catch weight	Total weight	Total weight
25 percent						
40	23.3	6.0	30.8	8.0	23.3	29.3
43	19.7	4.9	23.5	5.0	24.0	29.6
46	18.0	3.7	22.0	5.6	26.8	31.5
49	17.6	4.4	19.6	5.6	29.1	33.4
52	16.9	4.1	17.5	4.5	30.5	34.0
55	16.3	3.5	16.0	4.0	32.3	35.2
58	15.1	3.5	14.2	3.1	31.8	35.2
61	14.7	3.8	13.6	3.5	32.3	35.0
64	14.0	3.3	13.3	3.5	32.2	35.0
67	14.8	3.3	14.8	3.7	30.9	33.4
70	14.7	2.8	14.7	3.6	31.1	33.5
73	15.0	3.0	14.8	3.4	30.6	33.3
76	14.9	3.9	14.1	3.8	31.0	32.6
10 percent						
79	13.3	1.4	13.3	1.5	31.5	32.5
82	14.9	2.1	15.6	1.9	31.1	32.2
85	15.5	1.9	16.2	1.9	30.6	32.3
88	15.0	2.0	16.1	2.1	30.5	32.2
91	16.1	1.7	16.2	2.3	30.7	31.9
94	16.6	1.5	17.5	2.2	30.9	32.1
97	18.0	1.9	18.6	1.9	31.8	31.2
100	17.5	1.7	20.9	2.3	31.6	31.5
103	19.4	1.2	22.0	2.4	31.6	32.8
106	21.2	2.0	22.6	2.8	32.8	33.4
109	23.0	2.0	23.6	2.7	34.5	34.6
112	23.2	2.6	23.7	3.3	35.4	34.7
115	23.5	2.9	21.4	1.9	35.8	35.7
118	22.9	3.0	21.5	2.2	35.3	35.6
50 percent						
121	23.5	11.2	21.9	10.2	35.9	35.0
124	15.3	7.0	14.9	7.0	35.8	35.7
127	11.9	5.2	12.1	6.8	36.0	35.2
130	11.2	5.7	9.4	5.3	35.5	34.4
133	11.1	5.6	9.2	4.3	35.4	34.3
136	9.6	4.2	10.0	4.8	35.9	34.5
139	9.0	4.3	8.5	4.2	34.9	34.3
142	8.1	3.5	6.9	3.5	34.4	33.5
145	7.2	3.9	5.4	2.6	31.9	30.6
148	7.0	3.5	6.2	2.8	31.8	29.9
75 percent						
151	5.2	3.4	5.3	3.7	31.5	26.9
154	3.0	2.1	4.5	2.9	30.3	26.5
157	3.3	2.4	2.0	1.2	29.2	26.2
160	1.9	1.2	2.2	1.7	29.0	26.8
163	1.8	1.2	1.3	1.1	28.5	26.7
166	1.3	.9	.5	.3	28.4	26.7
169	1.4	1.0	.2	.2	28.6	27.0
172	.6	.2	.0	.0	29.4	27.0

summer in accordance with the length of daylight. This seasonal variation was eliminated in the present experiments by the use of controlled artificial light, but the reason for the difference in average ratio between these populations and those of Breder and Coates, and for the difference between populations *C* and *D* of the present experiment, is obscure. Genetic differences seem to offer the most probable explanation.

Shoemaker (1947) found an apparent 50–50 sex ratio at birth in his laboratory populations of guppies, although the survival rate of males was considerably less than that of females, leading in a year to a population with about one-fifth males. Here again the source of this contrast with the present experiments is unknown.

TABLE 5.—*Percentage of male fish in mature portion of experimental populations during exploitation period*

Week No.	Percentage male for population				Week No.	Percentage male for population			
	A	*B*	*C*	*D*		*A*	*B*	*C*	*D*
40	55	39	44	47	109	59	55	50	42
43	57	40	43	47	112	62	57	52	41
46	62	37	45	48	115	62	58	50	41
49	64	39	43	49	118	60	57	48	41
52	59	41	44	48	121	59	58	48	42
55	57	44	45	48	124	44	63	48	41
58	52	46	45	49	127	38	59	45	40
61	51	42	45	48	130	28	67	47	39
64	56	68	43	48	133	38	61	46	38
67	55	74	45	45	136	57	60	45	48
70	56	62	46	46	139	50	45	48	37
73	60	62	46	46	142	50	55	48	36
76	48	54	46	44	145	50	46	48	30
79	52	53	45	43	148	57	38	48	29
82	55	54	46	44	151	60	64	46	29
85	60	55	45	44	154	25	57	47	29
88	62	55	43	44	157	25	50	48	27
91	63	59	42	44	160	60	75	50	27
94	56	62	45	44	163	50	50	49	28
97	51	62	46	44	166	33	50	49	30
100	52	62	48	42	169	0	100	50	30
103	57	59	47	43	172	67	0	51	32
106	57	56	47	43					

Change Due to Temperature

Malfunctioning of the thermostatic devices used in the experiment resulted in considerable variations in temperature of the water bath in which the aquariums were kept (table 6, fig. 8). Occasional violent fluctuations within the range 65°–91° F. were of short duration, but even the triweekly means were not constant.

TABLE 6.—*Triweekly mean and extreme water-bath temperatures (for week listed and previous two weeks)*

Week No.	Temperature ° F.			Week No.	Temperature ° F.		
	Minimum	Maximum	Mean		Minimum	Maximum	Mean
40	70.5	79.0	75.3	109	68.5	78.5	72.4
43	68.0	78.0	74.7	112	68.5	78.0	71.0
46	71.5	78.5	75.1	115	68.0	82.0	72.8
49	71.0	80.0	76.0	118	70.0	80.5	72.9
52	69.0	81.0	76.6	121	72.0	79.5	72.6
55	67.5	91.0	74.0	124	71.5	80.5	72.4
58	68.5	80.5	74.1	127	71.5	80.5	72.9
61	70.0	79.0	74.3	130	70.0	85.0	75.3
64	67.5	83.5	76.1	133	71.0	85.0	76.3
67	72.0	79.5	75.0	136	70.5	85.0	73.9
70	74.5	77.5	74.7	139	70.5	83.5	73.8
73	74.5	77.5	74.6	142	67.5	83.5	74.8
76	74.5	79.5	75.9	145	65.5	87.5	74.5
79	73.0	77.5	75.2	148	66.5	84.5	76.2
82	72.0	79.5	75.5	151	69.0	87.5	75.0
85	69.0	79.5	76.6	154	69.0	85.5	74.9
88	69.5	80.0	76.0	157	68.5	87.0	76.5
91	66.5	79.0	75.5	160	68.5	87.5	76.8
94	67.5	78.0	74.9	163	70.0	87.0	78.7
97	67.0	77.5	73.8	166	69.5	85.0	75.4
100	68.5	78.5	75.3	169	72.5	86.5	75.5
103	68.5	78.5	75.2	172	72.5	78.0	74.5
106	68.5	79.5	73.2				

To determine whether this temperature fluctuation had an effect on population size, the rectilinear correlation coefficients were calculated for the regression of population *C* and *D* mean weights on triweekly mean temperatures starting

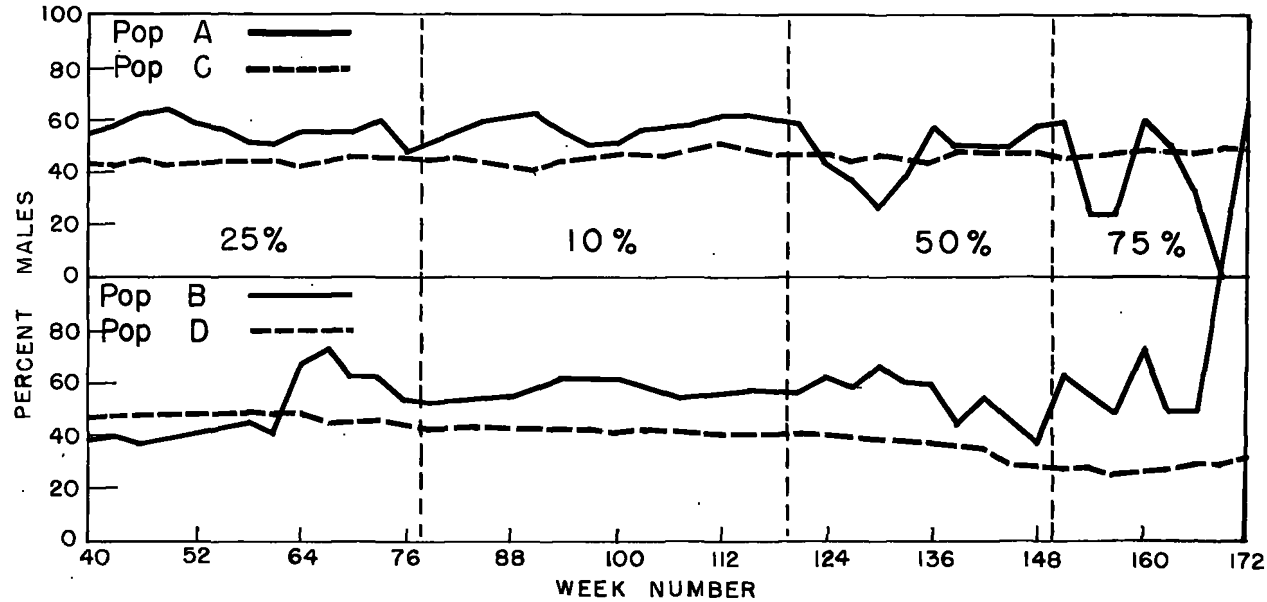

FIGURE 7.—Percentage of male fish in mature portion of experimental populations during the exploitation period. Percentages shown are triweekly exploitation rates.

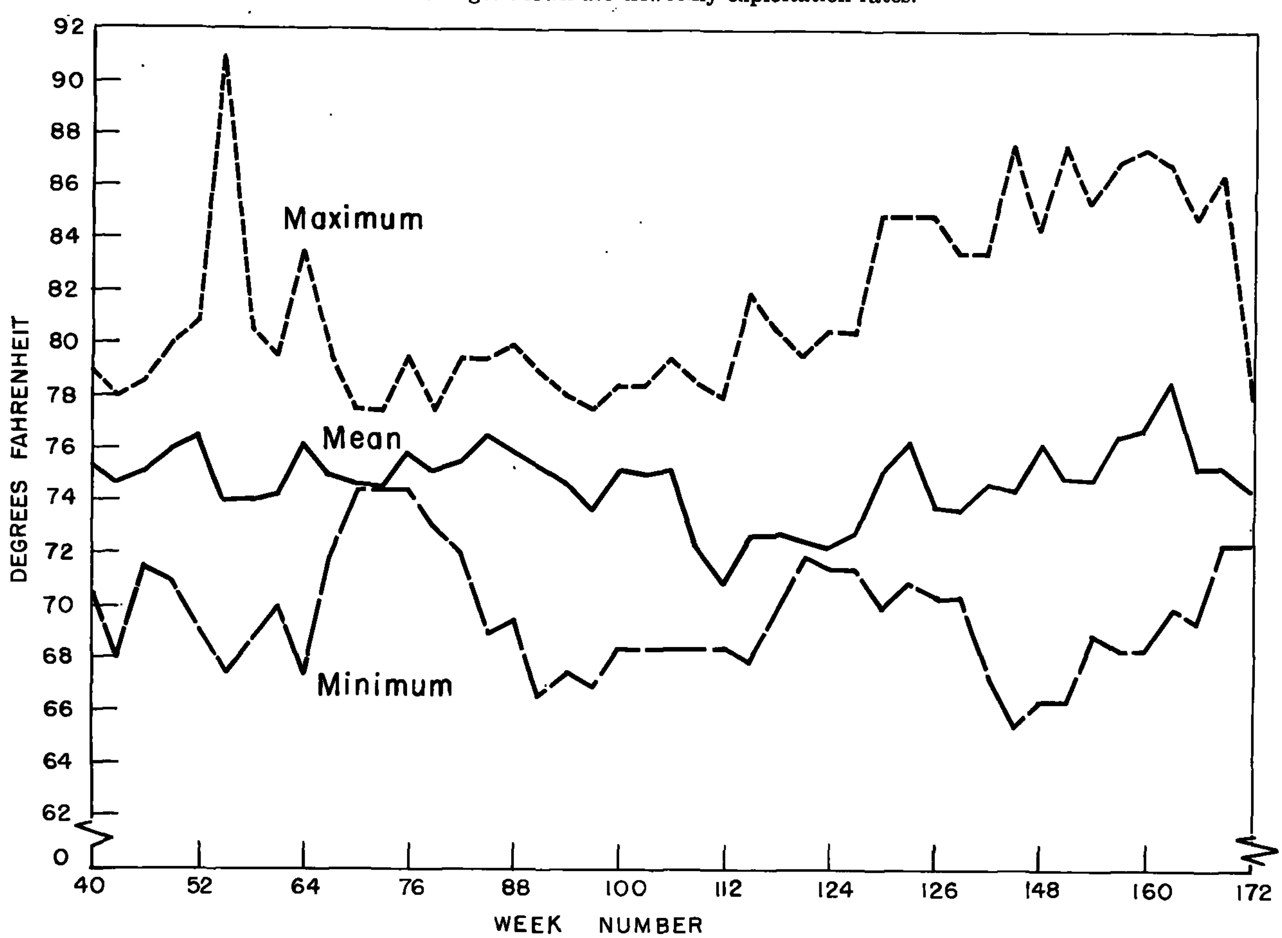

FIGURE 8.—Triweekly mean and extreme water-bath temperatures (for week listed and previous two weeks).

with week 40. The values, −0.5629 for C and —0.5316 for D, with values of P both less than .01, indicated a significant negative correlation of population size with temperature. Apparently continued temperatures much above 72° F. have an inhibiting effect on survival and growth (Gibson and Hirst, 1955, observed maximal growth of guppies in fresh water at 23° C. or 73° F.), reproductive rate, or some combination of these variables. A similar effect was observed by Shoemaker (1947), whose laboratory populations of guppies experienced a temperature range almost identical to that reported above. He suggested that reduced oxygen at the higher temperatures might be partially responsible.

The correlation between temperature and population size is rather mild, the squared coefficients indicating only about 30 percent of the fluctuations associated with temperature. The major portion of the periodic changes in size of the control populations must be ascribed to some factor as yet unknown. Similarity of the temperature correlations for the two populations does suggest that the electrically stirred water bath was efficient in maintaining uniform temperatures among all four aquariums.

EQUILIBRIUM YIELDS

Definition of Equilibrium

A rigorous definition of "equilibrium" in an exploited population would require that all vital rates, recruitment, growth, fishing mortality, natural mortality, be constant or fluctuate in a perfectly regular manner. In such a population the season-to-season age, size, and sex composition would be absolutely unvarying, and the yield would of course be constant. It is extremely unlikely that such a condition would ever obtain in any natural population, even if the fishing rates were held constant, for fluctuations would be imposed by changes in such aspects of the environment as food supply and temperature. Even under laboratory conditions it is hardly possible to control every known source of variation, and there are probably some that are unknown. Thus only by observations over a very long period of time could average values for the "equilibrium" constants be obtained.

In the present experiment it has been necessary to forego such long-term observations. Even as performed the work required over 3 years to observe the effects of 4 exploitation rates, with continuing and increasing risk of interruption by accidental experimental failure. It was felt that a close approximation to equilibrium conditions would obtain when a given exploitation rate had been maintained long enough so that there were no longer significant unidirectional changes in population composition. Observation of such a condition for a period of 6 weeks was the criterion for changing to another exploitation rate. Histograms (figs. 9 and 10) of the populations divided

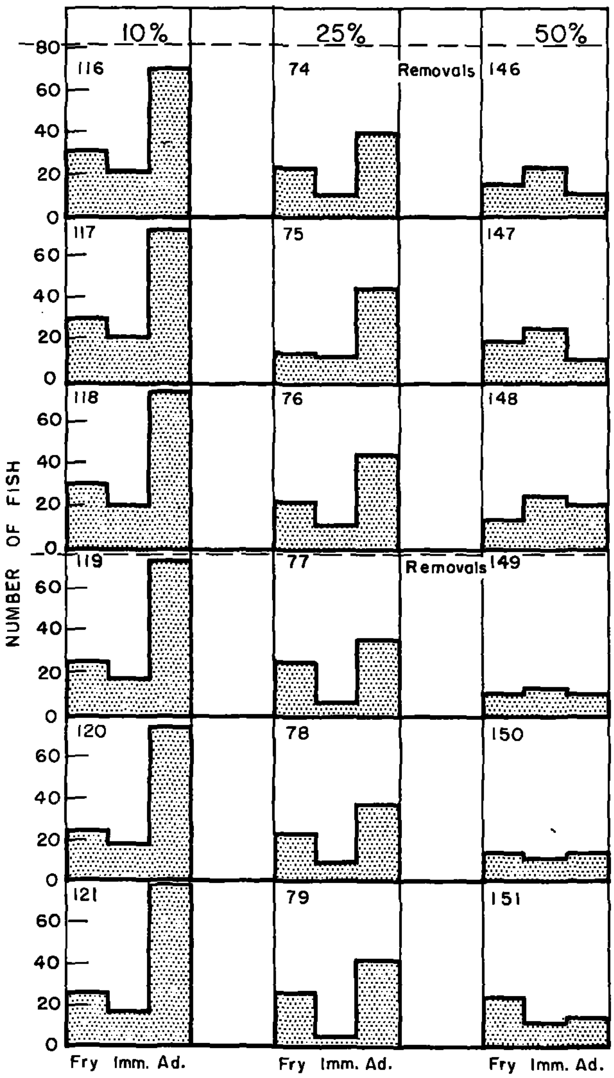

Figure 9.—Histograms of composition of population A during "equilibrium" period at each triweekly percentage exploitation rate. Week numbers given in each panel. "Removals" refers to cropping at point indicated by broken line.

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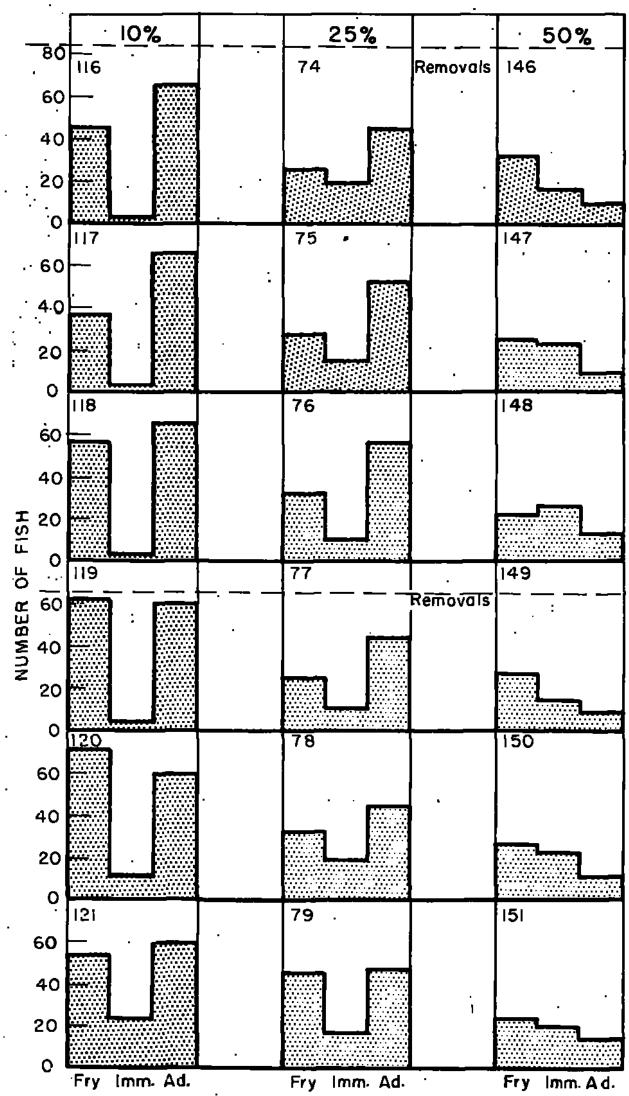

FIGURE 10.—Histograms of composition of population *B* during "equilibrium" period at each triweekly percentage exploitation rate. Week numbers given in each panel. "Removals" refers to cropping at point indicated by broken line.

into the categories "fry," "immature," and "adult" (as defined under Maintenance and Exploitation Procedures and Equipment) for the 6-weeks period preceding each change in exploitation rate indicate reasonable conformance to the criterion, but it is possible to question the establishment of equilibrium at the 50-percent rate. If, in fact, equilibrium did not exist at this level, the continued application of that rate would result in extinction just as occurred under the 75-percent rate. The presumed effects of this on the yield curves will be discussed below.

Whatever question may be raised as to the closeness of the approximation to equilibrium yields obtained by application of the "6-week" criterion, it remains true that the test of this or any analytical procedure lies in the consistency of the results. The reader may judge this for himself in the data presented below.

Relation Between Rate of Exploitation and Yield

Comparison of yields of the two test populations (fig. 11) shows that they are almost identical at each exploitation rate. Application of the *t* test indicates no significant difference (*P* approximately 0.2) and averaging of the yield data was therefore justified. The resulting mean yields (fig. 11) gave a more consistent representation of the relation between exploitation rate and yield than did the data for the individual populations.

The empirical relation between rate of exploitation and yield (table 7, fig. 12) is reminiscent of a parabola, but considerable experimentation did not reveal it to conform to any simple mathematical formula.[1] A difficulty arose in locating the second intersection with the *x* axis. Since the populations were extinguished at the 75-percent rate, it was known that yield there was zero. It is possible, however, that the point of zero yield might be reached anywhere between the 50- and the 75-percent rate. Thus the intersection has been bracketed but not located (and is so indicated in fig. 12).

By transforming percentage exploitation rates to instantaneous (Ricker 1948) rates (table 7, fig. 13) the yield curve derived herein may be com-

TABLE 7.—*Equilibrium yield, mean of populations A and B, as related to triweekly and instantaneous exploitation rates, and to population mass*

Exploitation rates		Population mass	Yield per 3 weeks
Triweekly (percent)	Instantaneous		
		Grams	*Grams*
10	0.11	21.5	2.50
25	.29	13.1	3.52
50	.69	5.0	3.20
75	1.39	0	0

[1] Dr. M. B. Schaefer has shown that if equilibrium yield be divided by instantaneous rate of exploitation, and this ratio plotted against instantaneous rate of exploitation, a relatively simple curve will result. Such a curve could be fitted by a polynomial, but for the purposes of this report the calculation does not seem justified. Extrapolation of a curve fitted by eye indicates population extinction at a weekly exploitation rate of about 59 percent.

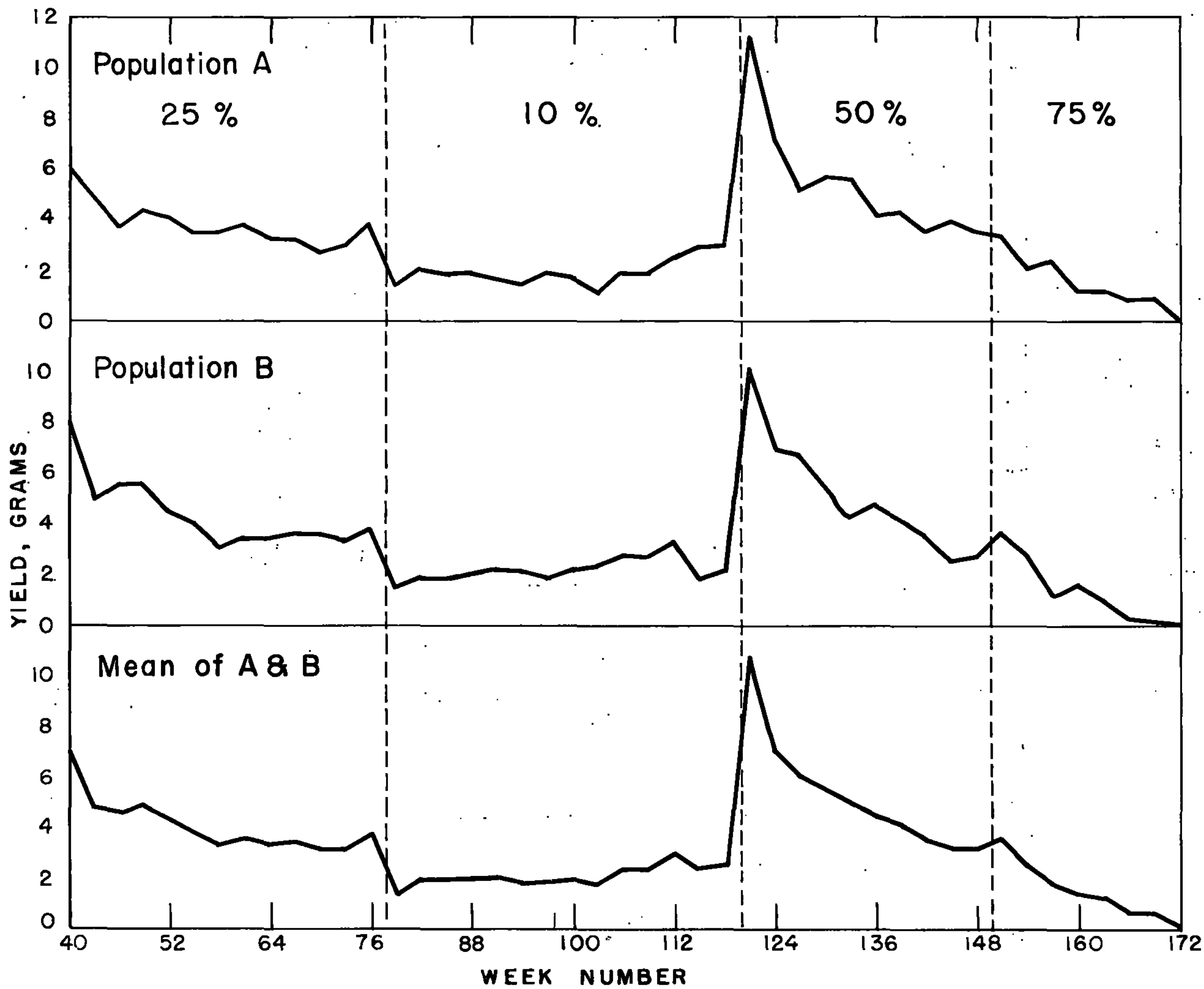

FIGURE 11.—Yield in weight of test populations under exploitation. Percentages in upper panel are triweekly exploitation rates.

pared with those of Beverton and Holt (1956, fig. IX: 22) which relate theoretical annual yield of North Sea haddock populations to the instantaneous fishing rate (F). In these curves, account has been taken of the dependence of both recruitment and growth on population density, making the mathematical models involved closely similar to natural populations. This similarity is validated by the close resemblance of Beverton and Holt's curve "s" to the guppy-yield curve, a resemblance the more remarkable when one considers the tremendous differences between the aquarium populations of guppies and the North Sea populations of haddock. We have here an example of the interplay of hypothesis and experiment characteristic of scientific research.

If yield is compared with mass of population (table 7, fig. 14) the results are comparable to the derivative form of the Verhulst-Pearl logistic, as discussed by Schaefer (1954). In this curve the second intersection of the x axis was taken to be the mean asymptotic level of the two control populations (C and D) under the assumption that this level would prevail in the test populations under zero exploitation. Comparison of the mass (weight) curves of the test and control populations (A with C, B with D, fig. 3) during the pre-exploitation period (weeks 6–10) lends support to this assumption.

It is obvious that the guppy curve does not conform to the logistic, since it departs from symmetry more than could be attributed to random

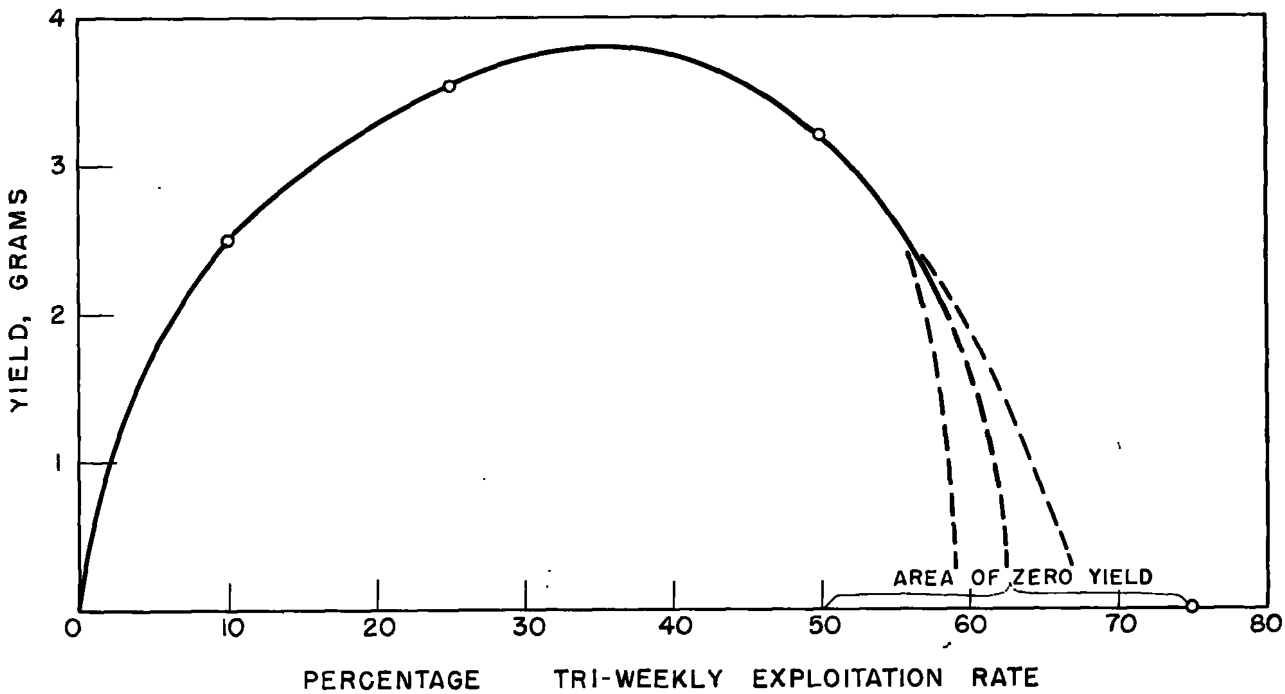

FIGURE 12.—Relation between triweekly rate of exploitation and the equilibrium yield in weight, mean of populations *A* and *B*.

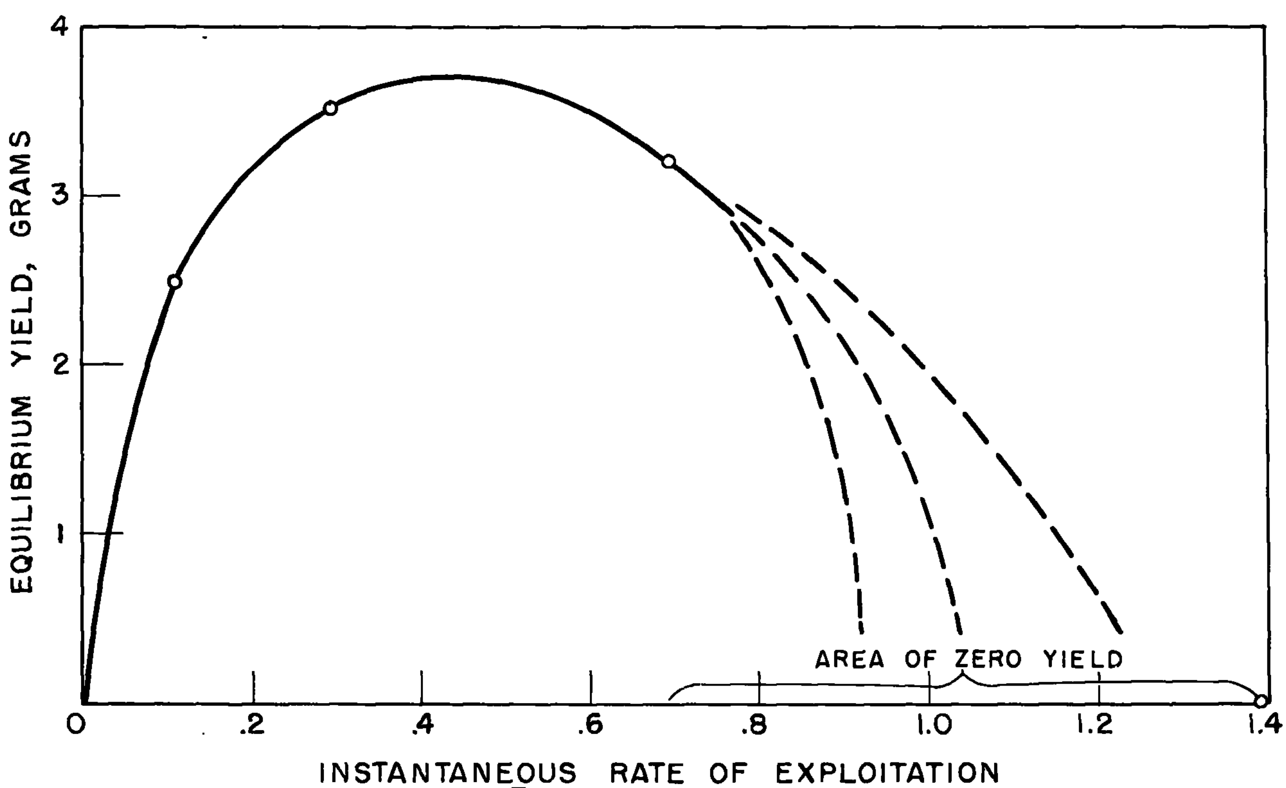

FIGURE 13.—Relation between instantaneous rate of exploitation and equilibrium yield, mean of populations *A* and *B*

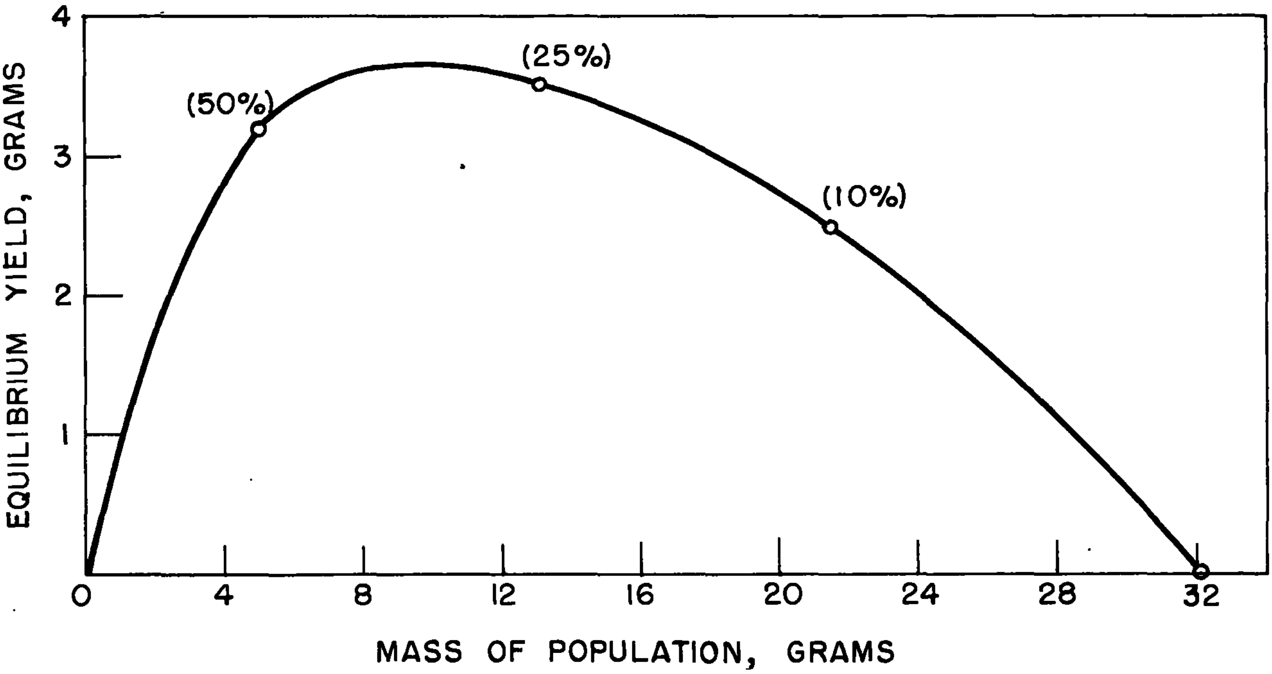

FIGURE 14.—Relation between mass of population and equilibrium yield, mean of populations *A* and *B*. Percentages in parentheses are triweekly exploitation rates.

variation or experimental error. It does, however, have enough features in common with the logistic to lend support to Schaefer's basic theory regarding the effect of changes in fishing intensity on fished stocks. He himself points out "that in at least some populations of fishes, the curve is actually somewhat asymmetrical."

It is pertinent to note here that the equilibrium-yield-on-mass curve of the population under exploitation, even if symmetrical, cannot be expected to conform to the derivative of the initial population-growth curve. The reason for this lies in the fact that the growing population has a different composition with respect to size, age, and maturity than the mature population under equilibrium conditions.

In general, all three of the treatments of the equilibrium-yield data discussed above have verified the contention of Sette (1943b) that "A population has its maximum increase when it is neither at its maximum, nor minimum, size, but when middling in size; and that is the level at which the most individuals can be regularly removed and still be fully replenished by the population's inherent tendency to grow." The empirical curves indicate that the maximum equilibrium yield for the guppy populations would occur at triweekly exploitation rates between 30 and 40 percent, with population mass at between 8 and 12 grams. If, as indicated above to be possible, 50 percent rather than 75 percent represents the real extinction rate, the maximum-yield findings would be the same although the curves would be more asymmetrical than shown here.

It is of interest to calculate the rate of food conversion at the maximum equilibrium yield. The maximum of the empirical yield curves depends somewhat on the subjective fitting by inspection, but the maximum observed yield was 3.5 grams per 3-week period. The amount of food consumed per such period (as detailed under Maintenance and Exploitation Procedures and Equipment) was 17.1 grams. The indicated efficiency of food conversion is thus 20 percent. Modern hatchery practice yields "conversion ratios" (pounds of food per pound of fish produced) of 2.35 to 4.95 for salmon (Burrows et al., 1952), equivalent to efficiencies of 42 and 20 percent, respectively. Data of Markus (1932) indicate an efficiency of 23 percent for largemouth bass. The results for the guppy populations are thus close to those recorded for other species.

Comparison of the efficiencies of food conversion at the three nonlethal exploitation rates indicates that exploitation rates in the range of 25 to 50 percent are most efficient, converting about 20 percent of the food consumed into available fish flesh. Efficiency for the 10-percent exploitation rate was only 15 percent.

INFORMATION FROM CONVENTIONAL MEASURES

Catch Per Unit of Effort

In most commercial-fishery investigations, direct data on population size are not available. Because knowledge of this statistic leads to calculation of rate of exploitation, and to observation of the effects of varying exploitation rates, it is highly desired by fishery administrators. In the experimental populations, therefore, it is of interest to see how closely the calculated catch per unit of effort reflects the known population sizes.

In calculating catch per unit, it was assumed that the amount of effort was directly proportional to the annual percentage exploitation rate applied, as would be true in a fishery where there were no competition between units of gear. Thus the 10-percent exploitation rate was equated to 1 unit of gear, 25 percent to 2.5 units, 50 percent to 5, and 75 percent to 7.5. Division of the known catches (table 4) by the assumed effort units completed the calculation. In this type of calculation catch per unit is by definition proportional to stock size, and would be exactly one-tenth the population weight, were the percentage exploitation rates applied on a weight basis. Since the rates were applied on the basis of numbers, some divergence between expected and actual weight caught per unit is possible.

The empirical curve of catch per unit of effort (table 8, fig. 15) shows that this measure does correspond to one-tenth the population weight, except during the period of the 10-percent exploitation rate, where there appears to have been a selection against the larger fish. In view of the method of selecting the fish for cropping, this is difficult to understand, and no explanation is offered. Nevertheless, the catch per unit of effort gives a good description of the major changes in population weight. In practical fisheries there are many sources of error in measuring both catch and effort, and the experiment can, of course, shed no light on these.

TABLE 8.—*Triweekly catch, effort, catch per unit of effort, and population size of exploited populations*

[Effort units explained in text]

Week No.	Effort (units)	Population *A*		Population *B*		Population *A+B*	
		Catch (grams)	Catch/unit (grams)	Catch (grams)	Catch/unit (grams)	Catch (grams)	Catch/unit (grams)
40	2.5	6.0	2.40	8.0	3.20	14.0	2.80
43	2.5	4.9	1.96	5.0	2.00	9.9	1.98
46	2.5	3.7	1.48	5.6	2.24	9.3	1.86
49	2.5	4.4	1.76	5.6	2.24	10.0	2.00
52	2.5	4.1	1.64	4.5	1.80	8.6	1.72
55	2.5	3.5	1.40	4.0	1.60	7.5	1.50
58	2.5	3.5	1.40	3.1	1.24	6.6	1.32
61	2.5	3.8	1.52	3.5	1.40	7.3	1.46
64	2.5	3.3	1.32	3.5	1.40	6.8	1.36
67	2.5	3.3	1.32	3.7	1.48	7.0	1.40
70	2.5	2.8	1.12	3.6	1.44	6.4	1.28
73	2.5	3.0	1.20	3.4	1.36	6.4	1.28
76	2.5	3.9	1.56	3.8	1.52	7.7	1.54
79	1.0	1.4	1.40	1.5	1.50	2.9	1.45
82	1.0	2.1	2.10	1.0	1.90	4.0	2.00
85	1.0	1.9	1.90	1.9	1.90	3.8	1.90
88	1.0	2.0	2.00	2.1	2.10	4.1	2.05
91	1.0	1.7	1.70	2.3	2.30	4.0	2.00
94	1.0	1.5	1.50	2.2	2.20	3.7	1.85
97	1.0	1.9	1.90	1.9	1.90	3.8	1.90
100	1.0	1.7	1.70	2.3	2.30	4.0	2.00
103	1.0	1.2	1.20	2.4	2.40	3.6	1.80
106	1.0	2.0	2.00	2.8	2.80	4.8	2.40
109	1.0	2.0	2.00	2.7	2.70	4.7	2.35
112	1.0	2.6	2.60	3.3	3.30	5.9	2.95
115	1.0	2.9	2.90	1.9	1.90	4.8	2.40
118	1.0	3.0	3.00	2.2	2.20	5.2	2.60
121	5.0	11.2	2.24	10.2	2.04	21.4	2.14
124	5.0	7.0	1.40	7.0	1.40	14.0	1.40
127	5.0	5.2	1.04	6.8	1.36	12.0	1.20
130	5.0	5.7	1.14	5.3	1.06	11.0	1.10
133	5.0	5.6	1.12	4.3	.86	9.9	.99
136	5.0	4.2	.84	4.8	.96	9.0	.90
139	5.0	4.3	.86	4.2	.84	8.5	.85
142	5.0	3.5	.70	3.5	.70	7.0	.70
145	5.0	3.9	.78	2.6	.52	6.5	.65
148	5.0	3.5	.70	2.8	.56	6.3	.63
151	7.5	3.4	.45	3.7	.49	7.1	.47
154	7.5	2.1	.28	2.9	.39	5.0	.33
157	7.5	2.4	.32	1.2	.16	3.6	.24
160	7.5	1.2	.16	1.7	.23	2.9	.19
163	7.5	1.2	.16	1.1	.15	2.3	.15
166	7.5	.9	.12	.3	.04	1.2	.08
169	7.5	1.0	.13	.2	.03	1.2	.08
172	7.5	.2	.03	0	0	.2	.01

Size Composition of the Catch

Because of the convenience with which fish sampled from the commercial catch can be measured, length composition of the catch is probably the second (next to catch per unit of effort) most common type of observation available to fishery biologists and administrators. Size-composition data have been widely used in fishery administration, and such data were gathered during the present experiment to determine the extent to which they reflect changes in population size and other population characteristics related to exploitation.

All fish removed during the cropping procedure were measured, and the length frequencies were compiled. The numbers of fish involved were too small to permit detailed analysis of the distributions, such as accurate location of modes or fitting of normal curves, but the mean lengths at each

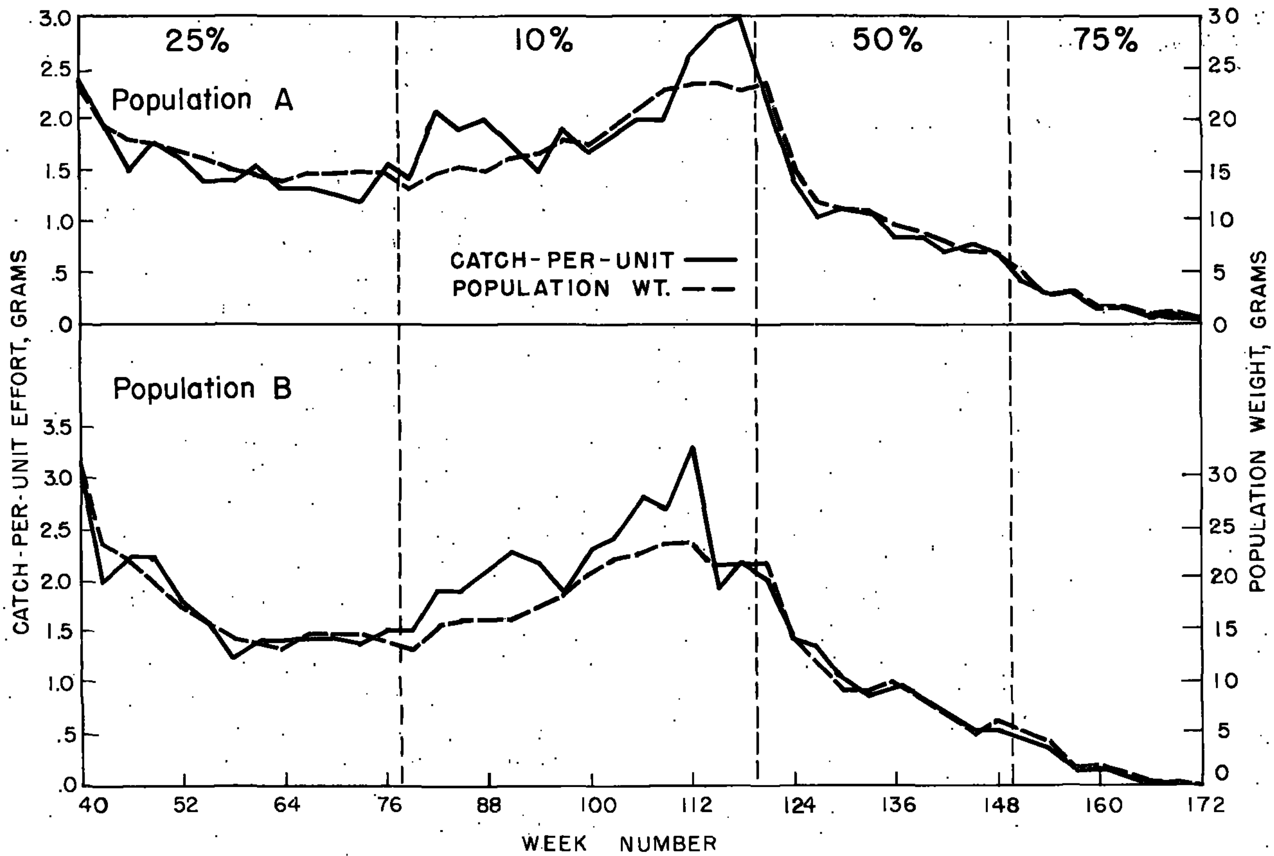

FIGURE 15.—Triweekly catch per unit of effort and population size of exploited populations. Percentages in top pane indicate triweekly exploitation rates.

cropping were calculated (table 9). With the exception of the last few weeks of the experiment, when numbers measured were too small (under 10 fish) to give reliable results, the changes in mean length (fig. 16) roughly paralleled those in population size (fig. 15). This is in accordance with expectation, since stocks that are "fished down" will normally consist of smaller fish than those that are at or near asymptotic abundance.

Catch, Catch Per Unit, and Size

A pertinent question is: "What could the intelligent fishery administrator have learned about the populations under exploitation, from a study of conventional fishery data?" In an attempt to answer this, the three series—catch, catch per unit of effort, and average length of individual fish in the catch—were brought together for examination (fig. 17). Data from the two exploited populations were combined in order to eliminate some of the variability not related to exploitation rates, inasmuch as previous comparisons had revealed the series for populations *A* and *B* to be similar in their essential features.

The start of a virgin fishery at the 25-percent exploitation rate was followed by the inevitable decline in both catch and catch per unit, reflecting a real decline in population size (fig. 15). After week 58, however, relative stability prevailed and indicated that the stocks could stand the drain of the fishery being imposed upon them. The decrease in catch at the 10-percent rate might have "been viewed with alarm" were not the catch per unit and average-length measures available. These, however, showed that the population was actually increasing in mass and in average size of individual fish. Data from the previous history of the fishery (25-percent rate) would indicate that the 10-percent exploitation rate did not utilize the full productivity of the stocks.

The sharp decline in catch, catch per unit, and average length after imposition of the 50-percent

TABLE 9.—*Number and mean length of fish cropped, by individual croppings, populations* A *and* B, *and mean of the two*

Week No.	Population *A*		Population *B*		Population *A* and *B*	
	No.	Mean length	No.	Mean length	No.	Mean length
		Mm.		*Mm.*		*Mm.*
40	22	28.5	32	27.6	54	28.0
43	21	26.3	24	25.9	45	26.6
46	25	23.6	19	28.3	44	25.7
49	20	25.4	15	31.3	35	28.0
52	20	24.5	13	28.7	33	26.2
55	15	26.3	9	32.2	24	28.5
58	16	24.3	8	30.1	24	26.3
61	13	27.5	11	27.0	24	27.3
64	16	24.1	18	24.0	34	24.1
67	18	23.2	23	22.4	41	22.8
70	19	23.0	23	23.1	42	23.1
73	16	24.3	19	25.0	35	24.6
76	15	26.0	17	26.2	32	26.2
79	5	28.0	7	24.8	12	26.2
82	5	30.8	8	26.8	13	28.4
85	6	27.4	9	26.0	15	26.6
88	7	26.1	8	27.0	15	26.6
91	7	25.0	10	25.9	17	25.5
94	7	25.8	10	26.0	17	25.9
97	9	26.0	11	24.3	20	25.1
100	7	26.8	12	25.0	19	25.7
103	9	22.0	11	26.6	20	25.0
106	9	25.7	10	27.6	19	26.7
109	11	24.0	10	28.1	21	26.0
112	11	25.6	9	30.5	20	27.8
115	11	27.2	7	27.2	18	27.3
118	10	28.1	7	28.8	17	28.4
121	49	26.4	41	25.9	90	26.3
124	31	25.5	29	25.5	60	25.5
127	21	25.3	32	24.1	53	24.6
130	19	23.7	27	23.7	46	23.8
133	30	23.3	31	22.0	61	22.7
136	27	22.2	30	23.9	57	23.1
139	29	22.1	26	23.0	55	22.6
142	27	22.3	19	24.1	46	23.1
145	22	23.2	16	21.8	38	22.7
148	23	22.3	20	21.1	43	21.8
151	21	23.1	26	22.1	47	22.6
154	9	22.7	23	20.8	32	21.4
157	20	20.9	12	20.6	32	20.8
160	9	20.7	9	23.6	18	22.2
163	11	19.5	7	22.8	18	20.8
166	3	26.0	1	25.0	4	25.8
169	9	21.3	1	24.0	10	21.6
172	2	22.5	0	0.0	2	22.5

rate most resembles the situations that have caused alarm among those concerned with real fisheries. Inspection of the equilibrium-yield curve (fig. 12) indicates that the 50-percent rate was indeed somewhat past the point of maximum return. If the history of the catch under the 25-percent rate were available, it would have become obvious at about week 142 that nothing was being gained by the additional fishing effort being put forth, and the fishery could have been cut back to an intermediate level in an attempt to secure a better yield at less cost. If the fishery had been started at the 50-percent level, the data would be difficult to interpret, but such a situation is unlikely among actual fisheries, which practically always start small and gradually increase. The value of obtaining as complete biological data as possible from the inception of a new fishery is sharply pointed up.

Finally, it is of interest to know whether the doom of the stocks at the 75-percent rate could have been foreseen. Certainly, if the previous history of the three measures were available, it would have become quickly apparent that the additional effort was not only depressing population size and average fish length, but was actually decreasing the catch. Under such circumstances, even the most optimistic fishing industry could probably be convinced of the need to retrench.

PRINCIPLES OF EXPLOITATION

Fishery biologists may think we presume a great deal when we venture to generalize for full-scale commercial fisheries from observations on our laboratory populations of guppies. True, the differences are immense between the vast, diffuse marine populations which form the object of most of our large fisheries, and the self-contained populations of guppies in their tiny laboratory tanks. They seem no greater, however, than the differences between laboratory populations of mice or guinea pigs and populations of human beings; the results of experimentation on the former have often been successfully applied to the latter, particularly in fields such as pathology, where experiments with human beings could not be carried out. With due caution, therefore, we offer certain applications of our findings to problems of commercial-fishery conservation. Before doing so, however, we may well enumerate the points of similarity and difference between our laboratory fish populations and the populations of marine fish upon which commercial fisheries depend.

It was set forth in describing the procedures and apparatus of the experiments that these were deliberately arranged to make them resemble as much as possible commercial fisheries. The following points of similarity to an idealized marine fishery may be listed:

1. The individual populations were fully interbreeding and self-reproducing.
2. There was a finite upper limit to population imposed by the food supply, which was held constant.
3. There was competition for food, both between individuals of the same size and between juveniles and adults.
4. Through cannibalism, the survival rates were dependent on population density.

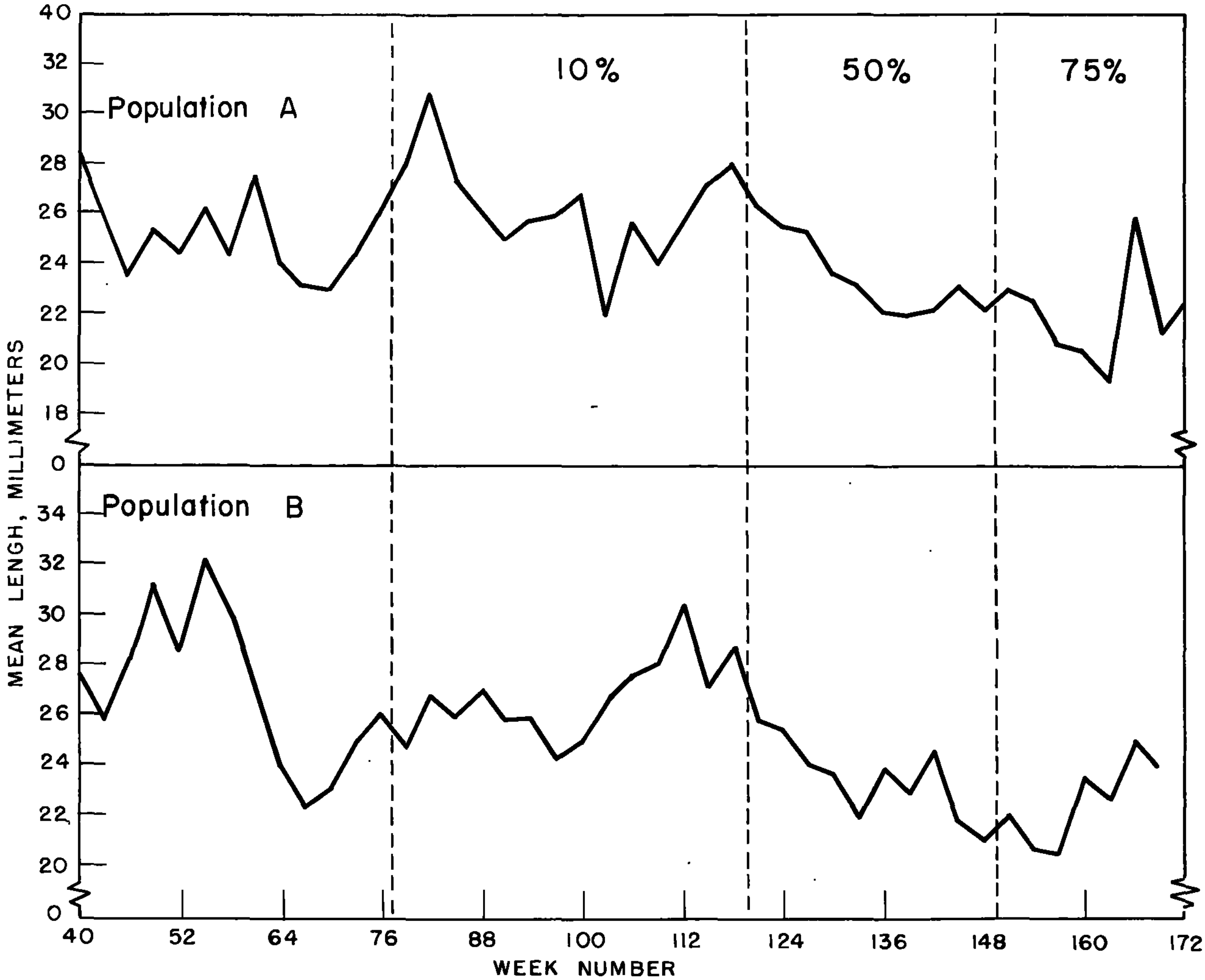

FIGURE 16.—Mean lengths of cropped fish under exploitation, by individual croppings. Percentages in top panel indicate triweekly exploitation rates.

5. The youngest juveniles were protected in a separate nursery area.

6. The "fishing" was done at intervals roughly equivalent to the reproductive period of the fish.

7. The "fishery" was selective, permitting the smallest juveniles to escape.

8. All catchable-sized fish were equally vulnerable to capture.

The chief differences (other than control of the environment) between laboratory and natural populations are:

1. The obvious differences in size and number of fish, and size of the environment.

2. The lack, in some cases, of an approach to infinite divisibility, such that a single fish may represent a substantial proportion of population size and number.

3. The low fecundity of the guppy as compared with most marine and anadromous fishes.

4. The lack of an independent population of predatory organisms such as preys on the stocks of many marine fishes.

5. Presence of an exploitation rate high enough to extinguish the population, which probably would not be economically feasible in most real fisheries.

The first category of differences is inherent in any small representation of a large thing, such as a ship model or a hydraulic model of a dam. Much research has been accomplished with such models.

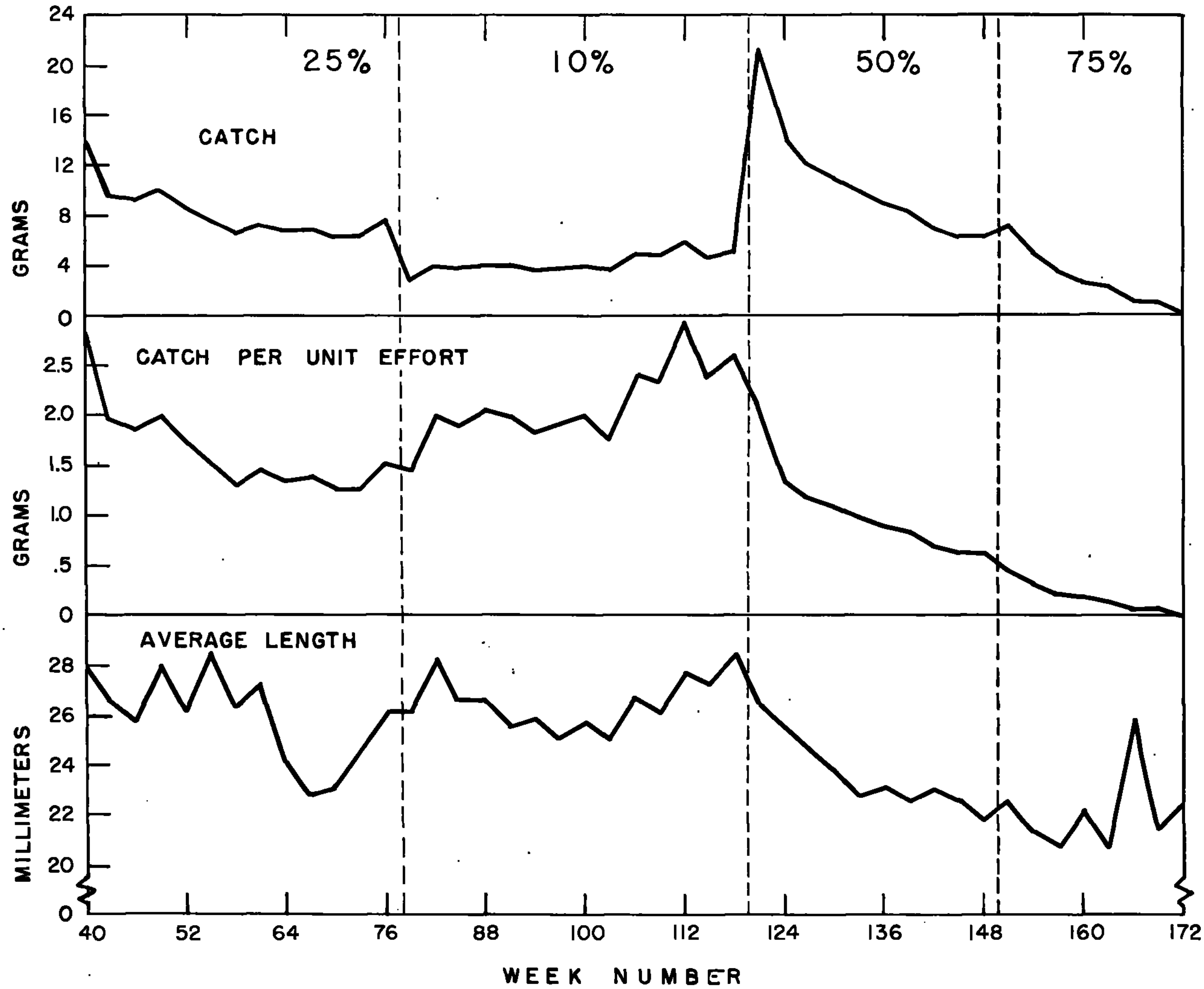

FIGURE 17.—Catch, catch per unit of effort, and average length for combined populations *A* and *B*. Percentages in top panel indicate triweekly exploitation rates.

however, and if the data are properly analyzed, valuable information is produced.

Lack of infinite divisibility presents difficulties chiefly in the roughness of data, such as the inconsistent average lengths obtained near the end of the experiments for the exploited populations. Inaccuracies resulting from this source should not be serious.

Low fecundity might be expected to present one of the most important sources of difficulty in applying the guppy results to commercial-fishery problems. Broods obtained from individual females by Silliman (1948) averaged about 20 fish each, as compared with the many thousands of eggs produced by marine species. Since the guppy is a live-bearer, however, the newborn young fish is a viable free-swimming organism, with considerably better chances of survival than the pelagic egg of marine species.

It would be difficult to say what larval size in marine fish is comparable in viability to the newborn guppy, but the tremendous mortalities suffered by marine pelagic eggs and larvae are notable. For instance, in the Pacific sardine, which is thought to lay 100,000 or more eggs per season, only about 100 larvae survive from 100,000 eggs after 40 days (Ahlstrom 1954); in the Atlantic mackerel, with a production of "several hundred thousand" eggs per season, only four 50-millimeter larvae survived from each 1 million eggs laid (Sette 1943a).[2] Thus the effective fecundity of the guppy in contributing to recruitment of the catchable stock may be as great as that of marine species. Indeed, the well-known inverse relation between egg number and degree of parental care (of which live-bearing is one form) may well provide just such an adjustment. A corollary implication of this relation is that the high fecundity and low survival rate of marine species probably make them much more inclined to violent fluctuations in recruitment (and thus abundance) than the guppy populations.

It is difficult to estimate the consequences of the absence of an independent predatory population. Certainly in marine fisheries the responses of populations to fishing pressures must be modified to some extent by the ever-present predation of larger fish, of sharks, or of seals and other marine mammals, as the case may be. In one manner of looking at the problem, this can be considered as another element of the controlled environment in the laboratory populations; the independent predation has been held constant at a value of zero.

One principle of exploitation, already established theoretically, has been verified by the present experiments: that even a low rate of exploitation causes some change in population size. Thus the equilibrium mass of the populations exploited at the 10-percent rate was about one-third less than the asymtotic mass of the unexploited control populations. It is demonstrated that a finding of simple reduction in population size, is not in itself a cause for alarm or retrenchment.

A second principle of exploitation is that fish populations up to a certain level of exploitation are resilient, responding to removals with increased survival and growth rates. This is brought out strikingly in the saw-tooth curves of population mass (fig. 2 and 3), each tooth representing the reduction due to removals, and the recovery therefrom. The effect of resiliency in restoring a population to a higher level of abundance after reduction in exploitation rates, is brought out by the increase in mass of both exploited populations to an equilibrium level about 50 percent greater than that prevailing under the 25-percent exploitation rate, after reduction of the rate to 10 percent. An instance of resilience in an actual marine-fish population was provided when stocks of North Sea trawl fish recovered significantly during the reduced fishing intensity of World War II (Margetts and Holt, 1948).

A principle complementary to that of resiliency is that if a population of the type considered here is continuously subjected to a rate of fishing greater than the maximum rate of replacement of which the population is capable (at a very low population level) it will continue to decline until extinction. Only about 20 reproductive periods were required to extinguish the guppy populations at the 75-percent exploitation rate, although it is true they had already been considerably reduced by application of the 50-percent rate. One needs to keep in mind here that many natural fish populations probably could stand fishing rates considerably in excess of 75 percent, and that in practical fisheries fishing usually becomes economically infeasible before the extinction rate is reached.

Perhaps the most important principle of exploitation is that there exists for each population, somewhere between zero and lethal exploitation rates, a rate of exploitation at which the maximum equilibrium yield will be produced. This is not a new idea, of course, but the laboratory experiments have provided verification and demonstration of it. Results reported above indicate that for laboratory populations under the controlled conditions imposed, with a constant supply of food, the maximum return is obtained under exploitation rates of 30 to 40 percent per reproductive period, when population mass is at about one-third its asymptotic level.

In commercial fisheries where the stocks might reasonably be expected to have reactions similar in some degree to those of the laboratory populations, and where catch and fishing effort are the only data available, the above findings may serve as a very rough guide to exploitation. If the population size is proportional to catch per unit of effort (Schaefer 1954) or can be derived from it (Ricker, 1940, 1944), fishing rates which reduce the size to not less than one-third to one-half its maximum value, when accompanied by an increase in catch, can tentatively be considered satisfactory pending estimation of the yield curve for the fishery in question; higher fishing rates should be

[2] The year class from which these data were obtained was a poor one, and the indicated survival rate probably below normal; the rate, however, does give an indication of the tremendous mortalities suffered in the marine environment.

permitted only with caution. It follows without saying that such a rough rule of thumb should be used only when supplementary biological data are lacking. Every effort should be made to obtain information on growth, survival, fishing, and reproductive rates, on fecundity, on age composition of the stock and age at maturity and on the relation of these variables to size of stock and conditions of the environment, so that management of the fishery can be placed on a solid scientific foundation.

In sum, the experimental populations have provided chiefly verification and demonstration of existing theories of exploitation rather than providing new ones. They have shown that the theoretical principles expounded by outstanding fishery biologists of recent decades are not simply the obscure results of abstruse mathematical formulations, but represent the visible, measurable reactions of living organisms to mortality imposed by man. If this report provides some illumination to those fishery biologists who are interested in the effect of exploitation on fish populations, and who think quantitatively but not necessarily mathematically, it will have served its purpose.

SUMMARY

1. Four laboratory populations of guppies were grown in small aquariums, under conditions of space, light, temperature, and food controlled as closely as possible.

2. Two of the populations were selected by lot for the exploitation tests; the other two were maintained without exploitation under identical conditions, as experimental controls.

3. Populations were maintained for a period of 168 weeks, during the last 128 of which the test populations were exploited.

4. Initial growth of the populations followed the logistic curve; asymptotic mass levels of about 32 grams were reached by the control populations in about 50 weeks.

5. Successive exploitation rates of 25, 10, 50, and 75 percent per reproductive period (3 weeks) were imposed on the two test populations.

6. Major changes in number during exploitation were similar for the two test populations. The 25-percent rate caused an initial decrease in the number of adults, followed by an increase in the number of juveniles. At the 10-percent rate there was an increase in the number of adults, followed by a decrease in the number of juveniles. Changes at the 50-percent rate were similar to those at the 25, but more extensive. At 75 percent there was rapid decline of both juveniles and adults to extinction.

7. Changes in weight resembled those in number, but fluctuations were less violent. The changes in weight of catch after the increase from 10- to 50-percent exploitation followed classical conceptions derived on theoretical grounds.

8. The proportion of males was greater in the test than in the control populations; the final apparent stabilization was at 50 percent for one control population and 30 percent for the other.

9. Comparison of control-population size with temperature fluctuations due to imperfect thermostatic control revealed a significant negative correlation accounting for about 30 percent of the fluctuations in population size.

10. Equilibrium yield, defined as the average yield during a period of 6 weeks without significant unidirectional changes in population composition, was related to fishing rate in a manner that indicated maximal yield at fishing rates between 30 and 40 percent, when the populations were at approximately one-third their asymptotic level.

11. The maximum actual yield realized represented the conversion into fish flesh of about 20 percent of the food consumed.

12. Examination of three conventional fishery measures, catch, catch per unit of effort, and average fish length, showed that these could yield a considerable amount of valuable information on population size and results of changes in rate of exploitation. Catch per unit closely, and average length roughly, followed changes in size of population.

13. The laboratory population experiments verified and demonstrated the following principles of exploitation:

a. Any exploitation of a population, however mild, reduces its abundance somewhat.

b. Below a certain level of exploitation fish populations are resilient, increasing their survival and/or growth rates to compensate for the fish removed.

c. It is possible, at least with some populations, to raise exploitation rates to the point at which they will cause extinction of the population.

d. Somewhere between no exploitation and excessive exploitation, there lies a level at which the maximum equilibrium yield can be obtained.

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APPENDIX

TABLES OF WEEKLY DATA AND LENGTH FREQUENCIES

TABLE A-1.—*Weekly population and removal numbers and weights, population A*

[Categories "fry" and "immature" defined in text, section Maintenance and Exploitation Procedures and Equipment.]

Week No.	Number before removals					Number natural deaths					Number removed	Weight, grams	
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total		Total	Removals
6			5	3	8							1.5	
7			5	3	8							1.6	
8			5	3	8							2.1	
9	([1])	25	5	3	33							2.9	
10	([1])	21	5	3	29							2.8	
11	([1])	20	5	3	28							3.6	
12	([1])	29	5	3	37		1			1		4.3	
13	([1])	88	5	3	96		2			2		4.6	
14	([1])	79	5	3	87		1			1		5.2	
15	([1])	83	5	3	91							6.0	
16	([1])	115	6	3	124		1			1		6.7	
17	([1])	110	6	3	119		3			3		7.1	
18	([1])	100	6	3	109							8.0	
19	([1])	93	10	3	106		2			2		9.3	
20	([1])	108	10	3	121							9.8	
21	([1])	89	10	2	101				1	1		9.7	
22	([1])	88	13	2	103		2			2		10.7	
23	([1])	92	13	2	107							11.5	
24	([1])	89	13	2	104							12.2	
25	([1])	70	33	2	105							14.3	
26	([1])	67	34	2	103		1			1		14.9	
27	([1])	64	35	2	101							15.4	
28	([1])	63	36	2	101							15.7	
29	([1])	59	35	2	96		1	1		2		16.2	
30	([1])	63	38	2	103							17.1	
31	([1])	63	40	4	107							18.7	
32	([1])	65	44	4	113							18.4	
33	([1])	59	45	4	108		1			1		19.0	
34	([1])	65	47	4	116							20.1	
35	([1])	75	47	5	127			1		1		20.9	
36	([1])	94	47	5	146							20.4	
37	([1])	66	49	35	150							20.5	
38	([1])	68	49	31	148							21.4	
39	([1])	60	49	38	147							22.1	
40	([1])	64	47	38	149			1		1	22	23.3	6.0
41	([1])	63	35	26	124				1	1		16.3	
42	([1])	·66	36	26	128				1	1		18.4	
43	([1])	64	36	27	127						21	19.7	4.9
44	([1])	67	27	19	113							15.9	
45	([1])	64	32	21	117							17.0	
46	21	45	35	21	122						25	18.0	3.7
47	17	32	30	18	97							15.8	
48	17	31	35	19	102							16.9	
49	18	24	38	21	101			1		[2] 1	20	17.6	4.4
50	13	18	31	21	83			1		1		14.9	
51	22	15	31	24	92							15.2	
52	16	23	33	23	95						20	16.9	4.1
53	24	14	26	21	85							13.7	
54	31	10	28	21	90			1		1		15.1	
55	39	9	28	21	97						15	16.3	3.5
56	40	21	19	20	100							14.0	
57	32	26	21	19	98				1	1		14.3	
58	53	25	21	19	118						16	15.1	3.5
59	60	20	13	17	110							12.8	
60	74	20	14	17	125							13.8	
61	69	20	18	17	124						13	14.7	3.8
62	80	19	16	12	127							12.3	
63	76	21	18	13	128							13.3	
64	61	26	20	16	123						16	14.0	3.3
65	38	40	14	12	104			1		1		12.4	
66	32	35	17	17	101							13.1	
67	29	35	21	17	102	1				1	18	14.8	3.3
68	26	25	21	17	89							12.4	
69	29	29	21	17	96							13.7	
70	20	33	24	19	96						19	14.7	2.8
71	15	25	18	13	71							12.9	
72	11	23	24	18	76							13.9	
73	8	21	27	18	74						16	15.0	3.0
74	23	10	19	21	73							13.3	
75	14	13	21	24	72							14.4	
76	23	12	22	24	81						15	14.9	3.9
77	26	6	19	18	69							11.5	
78	23	9	19	18	69							12.7	
79	26	5	22	20	73						5	13.3	1.4
80	26	7	19	17	72							13.3	
81	34	9	19	18	80							14.2	
82	34	9	22	18	83						5	14.9	2.1
83	32	11	23	16	82							13.6	
84	26	19	24	16	85							14.9	
85	29	18	25	17	89						6	15.5	1.9
86	31	20	23	15	89							14.2	
87	23	22	26	18	89							15.0	

See footnotes at end of table.

TABLE A-1.—*Weekly population and removal numbers and weights, population* A—Continued

Week No.	Number before removals					Number natural deaths					Number removed	Weight, grams	
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total		Total	Removals
88	23	22	30	18	93						7	15.0	2.0
89	26	20	25	21	92							14.7	
90	30	29	26	15	100							15.4	
91	34	30	26	15	105						7	16.1	1.7
92	29	27	26	24	106							14.8	
93	28	17	31	24	100							15.6	
94	24	20	30	24	98						7	16.6	1.5
95	21	20	30	26	97							16.3	
96	21	25	31	28	105							16.8	
97	25	27	31	30	113						9	18.0	1.9
98	30	24	26	27	107							17.2	
99	26	26	28	28	108			1		1		18.4	
100	44	22	30	28	124				1	1	7	17.5	1.7
101	31	25	35	30	121							17.1	
102	29	25	38	29	121							18.3	
103	34	26	39	29	128						9	19.4	1.2
104	36	19	38	31	124							19.4	
105	36	18	40	31	125							20.2	
106	33	24	43	32	132						9	21.2	2.0
107	24	22	45	32	123							20.5	
108	22	24	46	32	124							22.0	
109	21	27	46	32	126						11	23.0	2.0
110	24	22	45	28	119				1	1		20.5	
111	13	25	48	30	116							22.0	
112	13	26	49	30	118						11	23.2	2.6
113	19	29	44	26	118							21.6	
114	27	27	46	27	127							22.5	
115	30	24	49	30	133						11	23.5	2.9
116	32	22	44	27	125							21.6	
117	31	22	46	27	126							22.0	
118	32	21	46	30	129						10	22.9	3.0
119	26	18	43	32	119							21.1	
120	25	19	43	32	119							22.1	
121	26	17	47	33	123						49	23.5	11.2
122	27	7	19	21	74							12.9	
123	19	14	19	24	76							14.3	
124	20	19	19	24	82						31	15.3	7.0
125	18	8	10	16	52							10.0	
126	19	15	10	16	60							11.2	
127	47	15	10	16	88						21	11.9	6.2
128	51	10	4	12	77							8.3	
129	54	14	4	12	84							9.6	
130	50	21	5	13	89						19	11.2	5.7
131	30	35	3	8	76							8.2	
132	31	46	4	8	89							9.7	
133	48	47	5	8	108						30	11.1	5.6
134	58	36	3	4	101							7.1	
135	51	40	5	6	102							8.5	
136	58	42	8	6	114						28	9.6	4.2
137	51	24	5	7	87							6.9	
138	63	27	7	7	104							7.9	
139	61	44	7	7	119						29	9.0	4.3
140	39	39	2	5	85			1		1		6.2	
141	42	41	4	6	93							7.2	
142	33	41	7	7	88						27	8.1	3.5
143	40	20	6	4	70							5.7	
144	29	26	7	8	70							6.4	
145	26	25	9	9	69						22	7.2	3.9
146	15	23	6	5	49							5.1	
147	20	26	6	5	57							5.7	
148	14	25	12	9	60						23	7.0	3.5
149	11	13	6	4	34							4.2	
150	14	11	8	6	39							4.8	
151	24	12	9	6	51						21	5.2	3.4
152	25	4	1	3	33							2.0	
153	24	6	1	3	34							2.4	
154	23	9	1	3	36						9	3.0	2.1
155	7	16	1	2	26							2.0	
156	5	21	1	2	29							2.5	
157	12	22	1	3	38						20	3.3	2.4
158	12	5	0	1	18							1.1	
159	12	3	2	1	18							1.3	
160	13	8	3	2	26						9	1.9	1.2
161	9	6	1	1	17	1				1		1.1	
162	9	5	1	1	16		1			1		1.2	
163	12	12	2	2	28						12	1.8	1.2
164	11	3	1	1	16							.8	
165	11	2	1	2	16							1.1	
166	11	2	1	2	16						3	1.3	.9
167	3	8	0	2	13							.7	
168	3	8	0	2	13							1.2	
169	0	10	0	2	12						9	1.4	1.0
170	0	3	0	0	3							.4	
171	0	3	0	0	3							.5	
172	0	0	2	1	3						2	.6	.2
173	0	0	0	1	1							.3	
174	0	0	0	1	1							.4	

[1] Not listed separately; included in "immature".
[2] Includes one fish of unknown sex.

TABLE A–2.—*Weekly population and removal numbers and weights, population* B

[Categories "fry" and "immature" defined in text section, Maintenance and Exploitation Procedures and Equipment]

Week No.	Number before removals					Number natural deaths					Number removed	Weight, grams	
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total		Total	Removals
6	([1])	10	5	5	20		1			1		3.5	
7	([1])	19	5	4	28							2.9	
8	([1])	27	5	4	36		1			1		3.3	
9	([1])	19	5	3	27		1		1	2		3.3	
10	([1])	15	5	3	23							3.5	
11	([1])	30	5	3	38							3.8	
12	([1])	43	5	3	51							4.6	
13	([1])	40	5	3	48		1			1		4.8	
14	([1])	48	5	3	56		1			1		5.4	
15	([1])	74	6	3	83		2			2		6.0	
16	([1])	89	6	3	98		1			1		6.7	
17	([1])	94	6	3	103		3			3		7.2	
18	([1])	92	6	3	101							8.0	
19	([1])	108	6	3	117							9.0	
20	([1])	107	6	3	116							9.5	
21	([1])	112	6	3	121							10.3	
22	([1])	108	8	3	119							11.9	
23	([1])	120	8	3	131							12.2	
24	([1])	118	8	3	129							13.6	
25	([1])	112	13	3	128			1		1		15.9	
26	([1])	110	15	3	128		1	1		2		15.9	
27	([1])	102	20	3	125							17.6	
28	([1])	98	22	3	123							17.5	
29	([1])	98	22	3	123							18.5	
30	([1])	92	27	3	122							19.9	
31	([1])	93	27	3	123							20.5	
32	([1])	95	32	4	131							22.2	
33	([1])	92	35	3	130							21.9	
34	([1])	91	36	4	131							22.8	
35	([1])	87	40	4	131							24.2	
36	([1])	88	40	4	132							24.9	
37	([1])	51	42	38	131							26.2	
38	([1])	86	45	10	141							28.0	
39	([1])	34	45	51	130							27.8	
40	([1])	13	47	74	134						32	30.8	8.0
41	([1])	8	35	59	102							22.2	
42	([1])	17	35	54	106				2	2		23.6	
43	([1])	35	35	53	123						24	23.5	5.0
44	([1])	21	25	40	86							19.8	
45	([1])	20	25	42	87							20.7	
46	5	9	26	44	84						19	22.0	5.6
47	11	6	21	34	72							18.0	
48	17	5	22	34	78							18.8	
49	2	5	22	34	63						15	19.6	5.6
50	16	6	18	22	62							15.6	
51	16	2	18	28	64							16.8	
52	13	2	19	27	61						13	17.5	4.5
53	11	1	15	19	46							14.2	
54	28	1	15	19	63	2				2		15.3	
55	32	1	15	19	67						9	16.0	4.0
56	57	7	12	13	89							13.0	
57	58	7	12	13	90							14.0	
58	95	8	12	14	129						8	14.2	3.1
59	91	20	7	12	130							12.5	
60	99	28	8	11	146							13.6	
61	103	28	8	11	150						11	13.6	3.5
62	98	29	6	8	141			1		1		11.1	
63	84	43	10	7	144							12.5	
64	73	45	17	8	143						18	13.3	3.5
65	34	62	18	10	124							12.8	
66	37	53	24	10	124							13.8	
67	33	53	29	10	125						23	14.8	3.7
68	26	43	28	10	107							12.7	
69	28	43	30	10	111							14.0	
70	19	39	34	21	113						23	14.7	3.6
71	19	30	28	19	96							12.7	
72	24	30	29	19	102							13.8	
73	22	26	32	20	100						19	14.8	3.4
74	25	19	27	18	89							12.4	
75	27	15	27	25	94	1				1		13.7	
76	32	10	30	26	98						17	14.1	3.8
77	25	10	24	20	79							11.1	
78	32	18	24	20	94							12.4	
79	45	17	25	22	109						7	13.3	1.5
80	48	19	24	19	110							13.0	
81	45	19	25	21	110							14.2	
82	45	26	25	21	117						8	15.6	1.9
83	51	15	28	23	117							14.6	
84	41	32	30	25	128							15.6	
85	43	34	31	25	133					[2] 1	9	16.2	1.9
86	50	35	28	23	136							14.2	
87	50	42	28	22	142							15.3	
88	54	40	28	23	145						9	16.1	2.1
89	64	33	27	16	140							14.7	
90	59	45	29	18	151							15.3	
91	58	46	29	20	153						10	16.2	2.3
92	51	44	31	20	146							15.6	

See footnotes at end of table.

TABLE A-2.—*Weekly population and removal numbers and weights, population* B—Continued

Week No.	Number before removals					Number natural deaths					Number removed	Weight, grams	
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total		Total	Removals
93	56	33	37	20	146							16.3	
94	41	32	45	27	145						10	17.5	2.2
95	30	36	44	25	135							17.0	
96	26	38	44	26	134							17.9	
97	24	39	45	27	135						11	18.6	1.9
98	11	47	42	24	124							18.3	
99	2	48	46	28	124							20.0	
100	2	46	47	29	124						12	20.9	2.3
101	13	30	47	35	125							20.0	
102	7	27	50	35	119							21.3	
103	13	21	54	37	125						11	22.0	2.4
104	11	13	53	36	113							20.9	
105	9	13	53	36	111							21.8	
106	9	8	53	41	111						10	22.6	2.8
107	8	3	49	41	101							21.2	
108	10	3	49	41	103							22.3	
109	3	2	50	41	96						10	23.6	2.7
110	3	2	46	35	86							21.6	
111	6	1	46	35	88				1	1		22.6	
112	8	1	46	35	90						9	23.7	3.3
113	21	0	42	31	94							21.2	
114	32	0	42	30	104							21.3	
115	30	0	42	30	102						7	21.4	1.9
116	45	1	37	28	111							20.2	
117	36	3	37	28	104							21.1	
118	56	3	37	28	124						7	21.5	2.2
119	62	4	34	25	125							20.0	
120	71	11	34	25	141		1			1		20.7	
121	53	23	34	25	135						41	21.9	10.2
122	48	13	21	13	95							12.9	
123	47	20	22	13	102							14.1	
124	52	24	22	13	111						29	14.9	7.0
125	55	32	12	7	106							9.5	
126	50	31	15	11	107							11.0	
127	41	37	16	11	105						32	12.1	6.8
128	53	22	10	7	92							7.1	
129	55	28	11	8	102							7.9	
130	59	31	16	8	114						27	9.4	5.3
131	45	28	8	5	86							6.0	
132	62	29	9	6	106							7.4	
133	43	44	11	7	105						31	9.2	4.3
134	29	34	9	5	77							7.0	
135	29	38	9	8	84							8.7	
136	39	37	12	8	96						28	10.0	4.8
137	22	27	7	5	61							6.0	
138	26	30	8	5	69							7.1	
139	19	29	10	12	70						26	8.5	4.2
140	14	20	6	4	44							5.2	
141	27	19	7	6	59							6.3	
142	26	18	11	9	64						19	6.9	3.5
143	32	11	5	5	53							3.9	
144	40	14	5	7	66							4.6	
145	35	18	6	7	66						16	5.4	2.6
146	32	16	5	4	57							4.2	
147	25	23	5	4	57							5.0	
148	22	26	5	8	61						20	6.2	2.8
149	27	14	7	2	50							3.4	
150	26	22	8	3	59							4.5	
151	24	20	9	5	58		1			1	26	5.3	3.7
152	16	10	3	3	32							2.3	
153	8	23	3	3	37							3.3	
154	13	24	4	3	44						23	4.5	2.9
155	20	4	2	2	28							1.6	
156	18	5	3	2	28							1.9	
157	11	10	3	3	27				1	1	12	2.0	1.2
158	11	9	1	1	22							1.2	
159	7	12	1	1	21							1.8	
160	7	9	3	1	20		1			1	9	2.2	1.7
161	0	9	1	0	10	1				1		.7	
162	0	7	2	0	9		1			1		1.0	
163	0	5	2	2	9						7	1.3	1.1
164	0	2	0	0	2							.3	
165	0	2	0	0	2							.4	
166	0	0	1	1	2						1	.5	.3
167	0	0	1	0	1							.2	
168	0	0	1	0	1							.2	
169	0	0	1	0	1						1	.2	.2

[1] Not listed separately; included in "immature."
[2] Includes one fish of unknown sex.

TABLE A-3.—*Weekly population numbers and weights, population C*

[Categories "fry" and "immature" defined in text section Maintenance and Exploitation Procedures and Equipment]

Week No.	Number of fish					Number natural deaths					Weight, grams
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total	
6	(1)	1	5	3	9						1.5
7	(1)	4	5	4	13						2.1
8	(1)	1	5	4	10		1			1	2.7
9	(1)	10	5	4	19		2			2	3.2
10	(1)	18	5	4	27						3.1
11	(1)	36	5	3	44		9			9	3.0
12	(1)	28	5	3	36		1			1	3.2
13	(1)	51	5	3	59						4.0
14	(1)	76	5	3	84						4.4
15	(1)	83	5	3	91		1			1	4.9
16	(1)	81	5	4	90		1			1	5.6
17	(1)	101	5	3	109						6.2
18	(1)	94	4	3	101		1			1	6.3
19	(1)	92	4	3	99		1			1	7.4
20	(1)	90	4	3	97		2			2	8.0
21	(1)	91	4	3	98						8.5
22	(1)	97	7	3	107						9.4
23	(1)	85	8	3	96						9.9
24	(1)	83	9	3	95						11.5
25	(1)	75	16	3	94		2			2	12.3
26	(1)	75	16	3	94						13.8
27	(1)	68	19	3	90		1			1	13.5
28	(1)	63	22	3	88		1			1	14.6
29	(1)	67	21	3	91		1	1		2	14.3
30	(1)	68	24	3	95						15.3
31	(1)	65	25	3	93		1			1	16.9
32	(1)	67	29	3	99						16.7
33	(1)	61	34	3	98						17.5
34	(1)	66	35	5	106						18.7
35	(1)	68	32	5	105			1		1	18.9
36	(1)	75	33	6	114		1			1	19.2
37	(1)	45	36	32	113						19.9
38	(1)	52	35	22	109						21.5
39	(1)	28	36	42	106						21.5
40	(1)	19	37	46	102						23.3
41	(1)	23	37	46	106						21.9
42	(1)	24	35	45	104						22.8
43	(1)	35	34	45	114						24.0
44	(1)	30	35	44	109			1		1	24.9
45	(1)	38	36	47	121						26.0
46	(1)	25	39	47	111						26.8
47	10	19	40	47	116						27.0
48	16	14	41	49	120						28.7
49	9	9	43	57	118						29.1
50	12	11	42	57	122						29.3
51	18	10	43	57	128						29.7
52	4	9	44	57	114						30.5
53	5	12	44	57	118						31.4
54	9	9	46	57	121						31.4
55	11	8	47	57	123						32.3
56	11	9	47	57	124						31.6
57	2	6	47	60	115			1		1	32.0
58	7	6	47	58	118				1	1	31.8
59	10	6	47	58	121						31.9
60	11	7	47	58	123						32.3
61	24	7	48	58	137						32.3
62	14	7	48	58	127						33.0
63	28	6	49	58	141				1	1	32.6
64	13	3	45	59	120			3		3	32.2
65	13	6	45	60	124						32.0
66	6	3	46	58	113	1		1	2	4	31.0
67	14	4	46	56	120				2	2	30.9
68	5	7	46	56	114						30.8
69	6	6	46	56	114			1		1	31.3
70	5	6	48	56	115						31.1
71	5	5	47	56	113						31.1
72	6	4	48	56	114						30.0
73	4	7	47	56	114						30.6
74	8	3	48	56	115						30.8
75	8	5	48	56	117						31.1
76	7	7	48	56	118						31.0
77	4	5	47	58	114						30.8
78	1	7	48	58	114						30.7
79	4	5	48	59	116						31.5
80	9	2	50	60	121						31.4
81	8	4	50	59	121						31.4
82	9	5	50	58	122	1			1	2	31.1
83	6	4	49	58	117						31.0
84	10	4	48	58	120			1		1	30.3
85	10	8	48	58	124						30.6
86	12	5	47	61	126			1		1	30.5
87	14	5	48	61	128						30.3
88	20	4	48	63	135						30.5
89	11	5	48	63	127						30.4
90	5	9	47	61	122			1		1	31.2
91	13	7	46	63	129						30.7
92	12	7	47	61	127						30.4

See footnotes at end of table.

TABLE A-3.—*Weekly population numbers and weights, population* C—Continued

Week No.	Number of fish					Number natural deaths					Weight, grams
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total	
93	14	7	49	61	131						31.0
94	13	7	49	61	130						30.9
95	12	7	50	61	130						31.5
96	4	10	53	60	127				1	1	31.7
97	6	10	51	61	128			1		1	31.8
98	10	10	52	61	133						31.5
99	15	11	49	61	136			2		2	31.5
100	18	11	53	58	140						31.6
101	20	9	52	60	141						31.6
102	26	7	55	60	148						31.6
103	24	7	54	60	145			1		1	31.6
104	11	10	56	59	136					[2] 1	32.6
105	11	9	56	58	134				1	1	32.7
106	6	12	54	60	132						32.8
107	5	14	56	60	135				1	1	33.7
108	5	14	57	59	135				1	1	33.8
109	2	16	58	57	133						34.5
110	2	14	59	57	132						34.9
111	3	11	61	57	132			1		1	35.5
112	10	11	61	57	139						35.4
113	13	11	61	58	143						35.8
114	16	10	62	58	146	1				1	36.0
115	14	4	63	64	145						35.8
116	17	4	62	64	147						36.1
117	23	3	62	65	153			1		1	36.6
118	27	3	60	64	154			2	1	3	35.3
119	17	5	60	64	146						35.9
120	21	5	59	64	149			1		1	35.6
121	14	8	58	64	144						35.9
122	20	7	60	64	151						37.1
123	16	6	59	63	144				2	2	35.8
124	24	7	58	63	152			1		1	35.8
125	26	9	56	63	154			2		2	35.6
126	17	10	56	65	148						35.8
127	11	10	54	65	140			1		1	36.0
128	9	12	54	65	140			1	1	2	35.1
129	9	10	56	64	139				1	1	35.5
130	17	9	56	64	146			2		2	35.5
131	12	9	56	64	141						35.4
132	20	9	56	63	148				1	1	35.3
133	15	11	55	64	145			1		1	35.4
134	15	16	55	65	151			1		1	35.6
135	9	15	55	64	143				1	1	35.6
136	5	14	55	66	140						35.9
137	7	13	55	64	139			1	2	3	34.8
138	7	13	56	64	140						34.7
139	8	11	58	64	141						34.9
140	13	9	59	65	146						34.9
141	9	10	58	65	142						34.8
142	6	8	60	64	138						34.4
143	6	8	59	62	135			1		1	33.6
144	10	7	58	61	136						32.4
145	25	7	57	61	150			1		1	31.9
146	15	6	57	61	139				1	1	31.4
147	11	6	57	61	135						31.2
148	13	7	57	62	139						31.8
149	8	4	57	65	134						31.4
150	11	4	57	66	138						31.9
151	7	2	57	66	132				2	2	31.5
152	10	4	57	64	135				2	2	30.8
153	8	4	56	63	131			1	1	2	30.4
154	9	6	55	63	133			1		1	30.3
155	4	7	55	63	129						30.5
156	8	6	56	62	132				1	1	30.2
157	8	6	56	60	130				2	2	29.2
158	11	6	56	58	131				2	[2] 3	29.2
159	11	6	56	58	131				1	1	29.5
160	14	5	55	56	130			1	2	3	29.0
161	18	5	54	55	132		1		1	2	28.2
162	14	2	53	57	126						28.8
163	14	5	53	55	127				2	2	28.5
164	14	9	53	55	131						28.6
165	15	7	52	56	130			1		1	28.8
166	17	7	52	54	130				1	1	28.4
167	14	8	51	54	127			1		1	28.6
168	11	10	51	54	126				1	1	28.0
169	20	9	53	53	135						28.6
170	16	10	53	52	131					[2] 1	28.7
171	17	9	54	52	132						29.0
172	7	8	55	53	123						29.4
173	9	9	55	51	124				1	1	29.4
174	12	8	55	51	126						29.4

[1] Not listed separately; included in "immature."
[2] Includes one fish of unknown sex.

TABLE A-4.—*Weekly population numbers and weights, population* D

[Categories "fry" and "immature" defined in text section, Maintenance and Exploitation Procedures and Equipment]

Week No.	Number of fish					Number natural deaths					Weight (grams)
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total	
6	(1)	0	5	5	10						3.1
7	(1)	16	5	5	26		1			1	3.2
8	(1)	17	5	5	27						3.8
9	(1)	33	4	5	42						4.1
10	(1)	35	4	4	43						3.9
11	(1)	50	4	3	57		1		1	2	3.9
12	(1)	58	4	3	65						4.8
13	(1)	76	4	3	83						5.8
14	(1)	70	5	3	78						6.0
15	(1)	87	8	3	98						7.0
16	(1)	95	9	3	107						7.9
17	(1)	102	10	3	115						8.4
18	(1)	100	10	3	113						9.3
19	(1)	100	10	3	113		1			1	10.3
20	(1)	101	10	3	114						10.7
21	(1)	101	10	3	114						11.5
22	(1)	97	13	3	113						13.0
23	(1)	98	13	3	114						13.3
24	(1)	100	13	3	116						14.5
25	(1)	92	20	3	115						15.9
26	(1)	89	25	3	117						17.0
27	(1)	100	32	3	135						18.6
28	(1)	78	34	3	115						18.7
29	(1)	78	33	3	114			1		1	19.9
30	(1)	77	34	3	114						20.0
31	(1)	72	34	3	109		2			2	21.2
32	(1)	76	41	3	120						22.7
33	(1)	72	42	3	117		1			1	23.2
34	(1)	69	46	3	118						23.7
35	(1)	65	50	4	119						24.5
36	(1)	75	50	4	129						25.4
37	(1)	36	53	40	129						26.1
38	(1)	29	51	48	128						27.6
39	(1)	25	52	53	130						29.6
40	(1)	21	53	60	134						29.3
41	(1)	25	51	60	136						28.8
42	(1)	22	54	60	136						29.5
43	(1)	36	55	61	152						29.6
44	(1)	27	55	61	143						30.9
45	(1)	18	55	61	134	1				1	31.0
46	(1)	34	57	61	152						31.5
47	5	15	56	61	137						32.8
48	13	12	59	61	145						33.2
49	5	12	59	61	137						33.4
50	9	10	59	63	141						33.5
51	10	7	60	65	142						33.6
52	5	6	61	65	137						34.0
53	11	5	62	65	143						34.0
54	12	6	62	65	145						35.0
55	11	5	62	66	144						35.2
56	16	6	62	66	150						35.0
57	6	6	62	66	140						35.2
58	15	6	62	65	148						35.2
59	7	5	63	66	141						35.1
60	10	2	63	67	142						34.9
61	14	2	62	68	146						35.0
62	10	2	63	68	143						34.9
63	7	3	63	68	141						34.9
64	7	2	63	69	141						35.0
65	10	3	61	69	143						34.6
66	14	3	57	69	143			3		3	33.2
67	6	3	57	69	135						33.4
68	3	4	57	69	133						33.4
69	8	4	56	69	137						33.4
70	4	5	59	69	137						33.5
71	14	5	59	69	147						33.4
72	7	5	58	69	139						33.4
73	9	5	59	68	141						33.3
74	6	5	58	69	138						33.4
75	6	5	57	69	137						32.7
76	9	6	56	70	141			1		1	32.6
77	5	4	55	71	135			1		1	32.2
78	4	5	55	71	135						32.3
79	1	7	55	72	135						32.5
80	10	8	55	72	145						32.4
81	6	6	57	72	141						32.3
82	8	7	56	72	143						32.2
83	7	5	56	72	140						32.2
84	6	5	56	72	139						32.1
85	4	6	56	72	138						32.3
86	8	6	56	72	142						32.1
87	3	7	56	72	138						32.1
88	5	7	57	72	141						32.2
89	3	4	55	74	136			1		1	32.0
90	5	5	56	72	138						31.5
91	6	6	56	71	139						31.9
92	6	6	56	71	139						31.9

See footnotes at end of table.

TABLE A-4.—*Weekly population numbers and weights, population* D—Continued

Week No.	Number of fish					Number natural deaths					Weight (grams)
	Fry	Immature	Male	Female	Total	Fry	Immature	Male	Female	Total	
93	6	7	56	71	140						32.1
94	6	7	57	71	141						32.1
95	5	7	57	72	141						32.9
96	7	7	56	70	140				2	2	31.3
97	7	7	55	70	139						31.2
98	9	8	55	73	145						31.6
99	8	9	52	73	142			3		3	31.3
100	8	9	52	73	142						31.5
101	4	10	54	72	140				1	1	31.6
102	7	12	54	72	145	1				1	32.5
103	15	12	54	72	153						32.8
104	12	11	54	73	150						32.6
105	10	12	54	73	149						33.5
106	10	11	55	73	149			1		1	33.4
107	6	11	57	73	147				1	1	34.0
108	6	10	57	73	146			1		1	33.7
109	7	10	55	77	149			2		2	34.6
110	9	9	55	77	150						34.5
111	10	7	55	79	151						34.9
112	13	6	56	79	154						34.7
113	12	5	57	79	153						35.3
114	11	5	56	79	151			1		1	35.5
115	9	7	56	81	153						35.7
116	18	7	56	81	162						35.4
117	16	7	55	81	159						36.0
118	12	7	56	79	154						35.6
119	8	8	56	77	149				3	3	34.5
120	17	10	56	77	160						34.9
121	7	9	55	77	148			1		1	35.0
122	11	13	56	77	157						35.6
123	6	10	56	80	152			1		1	35.7
124	14	11	56	80	161						35.7
125	7	11	54	80	152			2		2	35.4
126	7	10	54	82	153						35.5
127	7	10	54	82	153			1		1	35.2
128	8	8	52	81	149			2	1	3	34.8
129	8	12	50	80	150			1	1	2	34.5
130	10	11	51	79	151				2	2	34.4
131	6	10	51	79	146				1	1	34.3
132	5	11	49	79	144			1	1	2	33.9
133	0	13	48	79	140			2		2	34.3
134	1	12	48	79	140					[2] 1	33.6
135	2	12	48	78	140						34.0
136	2	9	49	79	139						34.5
137	8	10	47	79	144			1		1	34.5
138	10	10	47	78	145						34.5
139	11	8	47	79	145						34.3
140	9	7	47	79	142						34.1
141	8	5	46	80	139						34.0
142	7	5	44	79	135		1		1	2	33.5
143	5	3	41	80	129			2	1	3	32.7
144	12	5	36	80	133			4		4	30.8
145	8	5	34	79	126			2	1	3	30.6
146	6	5	32	78	121			2	2	4	30.0
147	3	5	31	78	117			1	1	2	29.8
148	2	5	32	77	116				1	1	29.9
149	4	5	31	72	112				5	[2] 6	27.2
150	5	5	29	73	112			1		1	27.8
151	5	3	30	72	110				2	2	26.9
152	4	4	30	72	110						27.2
153	9	3	29	71	112				1	1	26.5
154	10	3	29	70	112						26.5
155	15	3	28	70	116			1		1	27.0
156	21	2	27	70	120			1	1	2	27.0
157	17	2	25	68	112			1	1	2	26.2
158	17	2	25	66	110			1	1	2	26.2
159	27	5	24	66	122					[2] 1	26.8
160	30	4	24	66	124						26.8
161	23	7	24	66	120			1		1	26.5
162	36	12	25	65	138			1	1	2	26.8
163	31	13	25	64	133				1	1	26.7
164	34	13	26	63	136			1		1	27.0
165	36	12	28	62	138				2	2	26.5
166	29	16	26	61	132			1	2	3	26.7
167	32	24	26	60	142				2	2	27.0
168	16	21	27	60	124						26.8
169	22	19	27	63	131		1			1	27.0
170	13	18	28	63	122				1	1	27.0
171	11	20	29	62	122			1	1	2	27.1
172	10	17	30	64	121			1		1	27.0
173	4	18	29	65	116				1	1	26.9
174	4	19	29	65	117						27.2

[1] Not listed separately; included in Immature.
[2] Includes one fish of unknown sex.

TABLE A-5.—*Temperature record, water bath, all populations*

[Data are for period from count time of previous week, taken as noon of count day, to count time at week listed, from thermograph records]

Week No.	Temperature			Week No.	Temperature			Week No.	Temperature		
	Average	Minimum	Maximum		Average	Minimum	Maximum		Average	Minimum	Maximum
6	74.8	72.5	77.0	63	77.2	72.0	79.5	120	73.1	72.0	79.5
7	75.5	73.5	77.5	64	77.4	67.5	83.5	121	72.4	72.0	73.5
8	74.1	73.0	77.5	65	75.6	72.0	79.5	122	72.4	72.0	73.0
9	75.0	72.5	77.0	66	74.9	73.0	79.0	123	72.3	72.0	72.5
10	75.8	71.5	79.0	67	74.6	74.0	77.0	124	72.5	71.5	80.5
11	75.2	73.5	76.5	68	74.7	74.5	77.5	125	73.0	71.5	80.5
12	75.1	73.0	76.6	69	74.7	74.5	75.0	126	72.2	71.5	79.5
13	77.8	74.5	79.0	70	74.7	74.5	75.0	127	73.5	71.5	75.5
14	77.4	75.0	78.5	71	74.4	74.5	76.0	128	75.4	72.0	84.0
15	76.8	73.0	79.0	72	74.8	74.5	77.5	129	75.0	70.0	83.0
16	78.5	76.5	80.5	73	74.7	74.5	77.0	130	75.6	70.0	85.0
17	77.2	75.5	80.0	74	75.7	74.5	78.5	131	77.0	72.0	84.0
18	78.8	76.0	80.0	75	75.2	74.5	78.5	132	76.9	71.5	85.0
19	75.3	72.0	76.0	76	76.9	74.5	79.5	133	74.9	71.0	82.0
20	78.6	75.0	80.0	77	75.4	74.5	77.5	134	76.5	71.0	85.0
21	79.3	77.0	81.5	78	75.3	74.0	77.0	135	73.5	70.5	82.0
22	76.3	74.0	79.0	79	75.0	73.0	76.5	136	71.6	70.5	76.5
23	78.2	76.0	81.0	80	75.2	73.0	79.5	137	73.9	70.5	83.0
24	76.8	74.0	81.0	81	75.4	72.0	79.0	138	76.3	70.5	83.5
25	76.6	74.0	80.0	82	75.9	72.0	79.0	139	71.3	70.5	77.0
26	75.6	73.0	78.5	83	75.8	71.0	79.5	140	72.3	71.0	77.5
27	74.6	73.0	76.5	84	77.8	73.5	79.5	141	76.2	67.5	83.5
28	75.4	73.5	78.5	85	76.1	69.0	78.5	142	75.9	70.5	83.5
29	74.6	73.5	75.5	86	74.5	69.5	78.5	143	73.8	69.5	83.0
30	74.8	73.0	76.0	87	76.6	70.0	80.0	144	77.6	72.5	87.5
31	75.2	74.0	76.5	88	77.0	71.5	79.0	145	72.0	65.5	78.0
32	74.1	72.5	75.5	89	76.3	67.5	79.0	146	76.7	72.5	82.5
33	76.9	72.0	79.5	90	74.3	66.5	77.5	147	78.1	70.0	84.5
34	75.5	72.0	78.5	91	75.9	68.5	78.0	148	73.8	66.5	83.0
35	75.2	72.0	80.0	92	74.9	67.5	78.0	149	76.1	68.0	86.0
36	73.8	71.5	77.0	93	75.4	69.0	77.0	150	73.6	66.5	84.5
37	76.2	73.0	78.5	94	74.4	68.0	77.0	151	75.2	69.0	87.5
38	73.6	70.5	74.5	95	74.3	67.5	77.5	152	73.8	70.0	82.0
39	77.2	71.5	79.0	96	73.4	67.0	76.0	153	75.2	69.5	85.5
40	75.2	72.0	78.0	97	73.7	67.5	76.0	154	75.6	69.0	83.5
41	73.0	68.0	76.5	98	75.2	68.5	77.5	155	74.2	71.5	84.0
42	75.2	72.5	77.5	99	75.4	69.0	77.5	156	77.3	71.5	87.0
43	75.8	73.5	78.0	100	75.4	69.0	78.5	157	77.9	68.5	85.0
44	74.8	72.5	77.5	101	74.7	68.5	78.5	158	77.4	69.0	87.5
45	76.2	73.0	78.5	102	76.2	69.0	78.5	159	77.0	70.5	86.0
46	74.4	71.5	77.0	103	74.6	68.5	78.5	160	75.9	68.5	84.0
47	73.8	71.0	75.5	104	74.6	68.5	79.5	161	77.8	70.5	87.0
48	77.3	73.5	80.0	105	72.5	68.5	77.0	162	77.4	70.0	85.5
49	76.8	74.0	78.0	106	72.6	68.5	78.0	163	80.8	71.5	84.5
50	77.4	74.0	79.5	107	71.8	68.5	78.0	164	78.0	69.5	85.0
51	77.7	74.0	79.5	108	73.1	68.5	78.5	165	74.8	70.0	82.0
52	74.7	69.0	81.0	109	72.2	68.5	78.0	166	73.5	70.0	81.0
53	72.6	68.0	77.0	110	70.2	68.5	77.5	167	75.1	72.5	83.0
54	74.4	67.5	79.0	111	70.4	68.5	77.5	168	75.6	72.5	86.5
55	74.9	68.0	91.0	112	72.5	70.5	78.0	169	75.9	73.0	83.5
56	72.7	68.5	78.5	113	72.2	70.0	78.5	170	74.5	73.0	76.5
57	74.4	69.0	79.5	114	73.7	68.0	82.0	171	74.3	72.5	78.0
58	75.1	69.0	80.5	115	72.5	68.5	80.5	172	74.7	72.5	78.0
59	75.3	72.0	79.5	116	75.2	70.0	80.5	173	73.8	72.5	78.5
60	74.3	70.0	79.0	117	71.2	70.0	73.5	174	74.0	72.5	76.5
61	73.3	70.5	76.0	118	72.3	72.0	72.5				
62	73.7	69.5	77.0	119	72.4	72.0	77.0				

TABLE A-6.—*Length frequencies (total length) of fish removed, population A*

Length, mm.	Number of fish for week No.—																						
	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100	103	106	109
11																								
12																								
13																								
14																								
15					1																			
16			1		1							1												
17					3													2						
18				2			1		2	1	2		1											1
19		1	2						1	6	2	1	1									1		
20		2	3	1			3		3	2	1		2				1	1	1			1	1	2
21		1	1	1				1		2	1	1	1			2	1					2		1
22	2	1	6	2	2	2	3	2		1	4	5	2				1	2		2	1	1		1
23	2	2	2	4	2	3	1	2	3		4	3	1	2			1		1	1	1		2	1
24	1	3	1	4	2	3	2	2	1	2	1	1			1	2				1	1		3	1
25	3	5	3		2	3	1	1	3	1	1	1			1				2	1	1	2		2
26	1		1	1	1												1		1	1				
27	1		2																	1	1	1		
28				1			1	1	1		1		1				1					1		
29	1	1		1	3		1				1									1				
30	2		1		1								2						1				1	
31	1						1			1			2	2									1	
32	3		1			3						1		1	1				1					1
33	4	2						1	1												1		1	
34		1										1			1						1			
35		1						1				1	1			1								1
36				1	1			1			1									1				
37	1			1														1						
38			1																					
39						1				1					1									
40										1						1		1						
41					1								1											
42						1	1																	
43									1								1							
44		1		1																				

Length, mm.	Number of fish for week No.—																					
	112	115	118	121	124	127	130	133	136	139	142	145	148	151	154	157	160	163	166	169	172	174
11	1																					
12																						
13																						
14																						
15						1	1								2		1					
16							1		1			1	1			1	2	1				
17					1		2		1	4		1	2	1	1	1	1	3				
18				1	3		1		5	4	1	4	1	2		2		3				
19		1		1	4	3	3	2	2	3	5	1	2	1	1	2	1			3		
20				1		1	2	7	1	3	5				1	6				3		
21	1			2	2	1	1	3	2	1	3	1	2	3		4		2		1		
22			1	6	3	1		8	3	4	1		4	4		1		1			1	
23	2	1		7	1	3	1	3	3	2	4	5	6	2	1		1				1	
24	1	2	1	5	2	1	1	2	1	2	2	1		3	1		2		1			
25	1	3		9	3	4	1	1	4	1	2	3	1	2		2			1			
26	1		2	3	1				3	2	1	2	1	1						1		
27		1	2	1	2						1		1									
28			1	1				1		1		1								1		1
29	1			1			1					1							1			
30	1			1		2					1							1				
31			1		1	1	1						2									
32				1	1	1		1														
33				1	3						1				1		1					
34	1		1	1			1							1								
35		2		1			1									1						
36	1		1		2									1								
37				3	1					1												
38		1																				
39				1	1	1		1							1							
40									1													
41										1												
42				1				1														
43				1		1																
44												1										

TABLE A-7.—*Length frequencies (total length) of fish removed, population* B

Length, mm.	Number of fish for week No.—																							
	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100	103	106	109
14																								
15										1														
16			1		1																			
17														1		1				1				
18			1						2		3								1					
19								1		3							1	1				1		
20							1	1	4	4	2		2						2		2			
21								1	2	5	3	2	1	2		1		1			1			
22			1					1	2	4	5	4	1		1	1		1		1	2			
23	1	3	1					3	3	2	2	3	1		1	1	1	1		1	2		3	1
24	4	4		2	2	1	1				3	3	1		1	1				4	2	3		1
25	5	3		1	3		1		1		1		2	1			1	2	2			1	1	2
26	3	1	5	1	1		1			1	2	1		1	2		1		1	1		2		
27	4	2		1				1	1	1		1	2			1				1		1	2	1
28	3	3				2					3	1						1		1			1	1
29	5	3					1		1	1			2	1	1		1	1	1	1				1
30	3	3				2					1	1	1	1			1		1		1		1	
31	3	2	1									1		1	1		1					1		2
32			4	1	1							1	1					1	1			1		
33			2	3	1											2								
34			2	2	1										1	1	1				1			
35				2	1													1	1			1	2	
36			1	1			1															1		
37					1	2		1																
38					1	2															1			1
39			1			1							1											
40								1	1		1													
41									1															
42							1																	
43	1							1		1														
44																								
45																								
46																								

Length, mm.	Number of fish for week No.—																					
	112	115	118	121	124	127	130	133	136	139	142	145	148	151	154	157	160	163	166	169	172	174
14								1														
15													3									
16				1		1						2			1							
17				3	1	2	1	5	1	2		3		1		3						
18				3	1	1	5	2			2		1		1	3						
19		1		3	3	3	1	1		3	1	1	6	3	6	1						
20	2			3	3	4	1	1	1	4	1	1	3	6	8		1	1				
21	1			2	3	4	4	1	10	3	3	1		3	4		4	2				
22			1		2	2	2	6	2	1	2	1		2				1				
23	1	1		1	2	3	4	4	4	2	2	1	2	7	1		1					
24	1	2	1	2	1	2	1	2	4	3	1	1	2			2	1			1		
25		2	1	4	3		2	4	2	1	1	2		1	1	2	1	2	1			
26	2		1	6	1	2	2	1	2	1			1	2		1		1				
27				1	1	2	1			2		2	1									
28					1	1				1	3											
29								2														
30				1	1	1				2	1											
31		1								1												
32	1										1											
33				1				1	3			1										
34	1		1	2	1																	
35	1		1	3																		
36			1		1	1					1			1								
37	1			2	1		1		1								1					
38	1			1	2								1									
39		1				1	1								1							
40																						
41				1		1																
42				1		1																
43					1																	
44																						
45																						
46							1															

TABLE A-8.—*Length frequencies (total length) of fish in control populations remaining at end of experiment*

Length, mm.	Number of fish for—		Length, mm.	Number of fish for—		Length, mm.	Number of fish for—	
	Population C	Population D		Population C	Population D		Population C	Population D
9	4	0	22	10	9	35	3	5
10	4	2	23	11	5	36	4	1
11	1	0	24	18	8	37	3	3
12	1	1	25	11	7	38	1	1
13	0	0	26	7	4	39	2	0
14	1	0	27	3	3	40	3	0
15	0	0	28	0	7	41	1	1
16	0	0	29	0	4	42	0	0
17	1	1	30	6	8	43	0	0
18	0	3	31	6	4	44	0	0
19	1	4	32	7	7	45	0	0
20	0	6	33	5	13	46	1	0
21	3	3	34	8	7			

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