

INTERACTION OF FOOD LEVEL AND EXPLOITATION IN EXPERIMENTAL FISH POPULATIONS

By RALPH P. SILLIMAN, *Fishery Biologist*, BUREAU OF COMMERCIAL FISHERIES, BIOLOGICAL LABORATORY, SEATTLE, WASH. 98102

ABSTRACT

Nine populations of guppies (*Lebistes reticulatus*) were established in separate aquariums. Food supply was constant for groups of three populations in ratios of 0.5, 1.0, and 1.5 to a "standard" diet. Temperature, light, and space were constant and the same for all populations. After 28 weeks, populations had reached near-asymptotic levels, and mean numbers and weights for each group of three were in the same rank as their food levels.

Twenty-five percent, 33 percent, and 50 percent of the fish were removed per 3-week brood interval for each food-level group of three populations, thus providing

nine combinations. Continuation of exploitation at these rates led to relatively stable yields during weeks 59 to 72, after initial declines due to readjustment of populations. Yield curves for each food level revealed relation of yield to exploitation rate and biomass to be independent of amount of food consumed. Maximum yields occurred near the 0.33 (33 percent) exploitation rate for all food levels and represented about 25 percent of the food consumed. Results suggest that if commercially fished populations behave as the experimental ones did, management strategies may be applied independently of amount of food organisms available.

The purposes of laboratory fish-population experiments and their relation to other work in fishery dynamics have been set forth rather fully by Silliman (1948) and Silliman and Gutsell (1958). Briefly, the purposes are to provide experimental measurement of the effect of exploitation on stocks of fish, under as fully controlled environmental conditions as possible. The above authors also pointed out the advantages of the guppy (*Lebistes reticulatus*) as an experimental animal: rapid growth and reproductive rates, small size, and hardiness.

Food supply and exploitation rate must be among the most important factors that determine biomass and yield in exploited fish populations. The response of populations to exploitation is well known, as set forth in such works as Beverton and Holt (1957). The importance of food supply, although not as fully documented, is well recognized. For example, Zheltenkova (1961) adduced data indicating that a decreased supply of food reduced the rate of growth and catches of bream

in the Sea of Azov. She also reported a number of qualitative examples in another work (1958) that, although lacking numerical estimates of food amounts, tended to support the thesis that food supply is important in determining yield and rate of growth of several fishes in the U.S.S.R. These examples indicate not only the importance of food level at any given time but also the importance of the great fluctuations in this level that occur from one time to another.

Quantitative support for the idea that fluctuations in food supply would modify fluctuations in fish stocks resulting from other causes was provided early by Jensen (1928). His data on measured amounts of bottom food in certain Danish waters in the fall were significantly correlated with catches of plaice.

Because yield is related to both food supply and rate of exploitation, the interaction of these two is of obvious interest to the fishery manager. Might it be possible, for instance, to harvest a greater percentage of the stock when food supply and abundance are high than when they are low? The experiments described in this report were

carried out to throw light on this and similar questions, such as precisely how yields are related to exploitation at each food level. Answers were sought by investigating the effects at controlled exploitation and food level on population biomass and yield.

PLAN OF THE EXPERIMENT

Experimental tanks provided for three food levels and three rates of exploitation, a total of nine combinations. Because of limited facilities and personnel, replications were not made. The experience of Silliman and Gutsell (1958) helped to determine the specific food levels and exploitation rates to use. In each test the levels were chosen to bracket the ones that had provided the greatest yield in the previous experiments. Maximum yield for those experiments occurred when the populations were fed a standard diet and when 25 to 50 percent of the fishable stock was removed per 3-week period (the average interval between broods of a female guppy).

For the experiments reported here, food levels of 0.5, 1.0, and 1.5 times the "standard" diet were arbitrarily selected. An arbitrary selection of exploitation rates at 0.25, 0.33, and 0.50 per 3-week period was also made. The resulting nine combinations were assigned by lot to a row of nine experimental tanks, as follows: Tank A, diet 1.0, exploitation rate 0.25; B, 0.5, 0.25; C, 1.5, 0.50; D, 1.0, 0.50; E, 1.5, 0.25; F, 0.5, 0.33; G, 1.0, 0.33; H, 0.5, 0.50; I, 1.5, 0.33.

The plan of the experiment was simple: To start a population of guppies in each tank and allow all to grow until asymptotic size or a close approach to it had been attained. The populations were then exploited at the chosen rates, and this was continued until the yield from each tank became reasonably stable.

MATERIALS AND METHODS

The experiments were conducted from January 30, 1964, through June 17, 1965, at the former Biological Laboratory, Bureau of Commercial Fisheries, Washington, D.C.

FISH TANKS AND EQUIPMENT

Conventional glass-walled aquariums were used as experimental tanks (fig. 1). The water surface in each was 44 by 24 cm.; and the depth, 19 cm. (volume, 20 l.). Each was provided with a cotton-

charcoal filter (inside the tank) and an airstone. A pair of small pumps supplied air for both of these fixtures.

The available room illumination was used as a light source. It consisted of two banks of eight 40-watt fluorescent lamps (fig. 1). (Evidence to be presented later in the section "Changes During Exploitation" will support the assumption that differences in amounts of light received by different populations did not confound the interpretation of the experimental results.) All windows were covered, and lights were controlled by a time switch to be on each day from 6 a.m. to 6 p.m.

Refuges for the young fish were provided by fences placed in the left "front" (facing row of tanks with A to I from left to right as in fig. 1) corners of all tanks. Each fence consisted of glass rods supported by plastic rails. The rods were 21 cm. long and were placed vertically to form a fence 15 cm. long. The center of each glass rod (3 mm. in diameter) was 4.5 mm. from the center of the next rod, leaving spaces of 1.5 mm. between rods for the passage of the young fish. Fences were placed in tanks so as to enclose a 45° right triangular space in the corner of each.

A grader for separation of "fry" from "immature" sizes of fish consisted of a plastic box 20 cm. long with ends 10 cm. square. This box was open at the top, and the bottom was composed of plastic rods, 3 mm. in diameter, placed parallel to the longer axis of the box. Because centers of the rods were 5 mm. apart, 2-mm. spaces were left for grading the fish. All fish which would pass through the grader were classified as "fry"; immature fish which would not were classified as "immature."

EXPERIMENTAL DIET AND PROCEDURES

The diet I used was a standard one developed during previous experiments (Silliman and Gutsell, 1958). Food consisted of medium-grade dry tropical fish food, frozen *Daphnia*, and newly hatched *Artemia* nauplii. The dry food was a commercial product containing dried mosquito larvae, dried flies, dried *Daphnia*, fish-liver meal, beef meal, shrimp meal, salmon-egg meal, wheat-germ meal, fish-roe meal, clam meal, fish-bone meal, dried egg yolk, whole wheat meal, dehydrated kelp, dehydrated alfalfa-leaf meal, dehy-

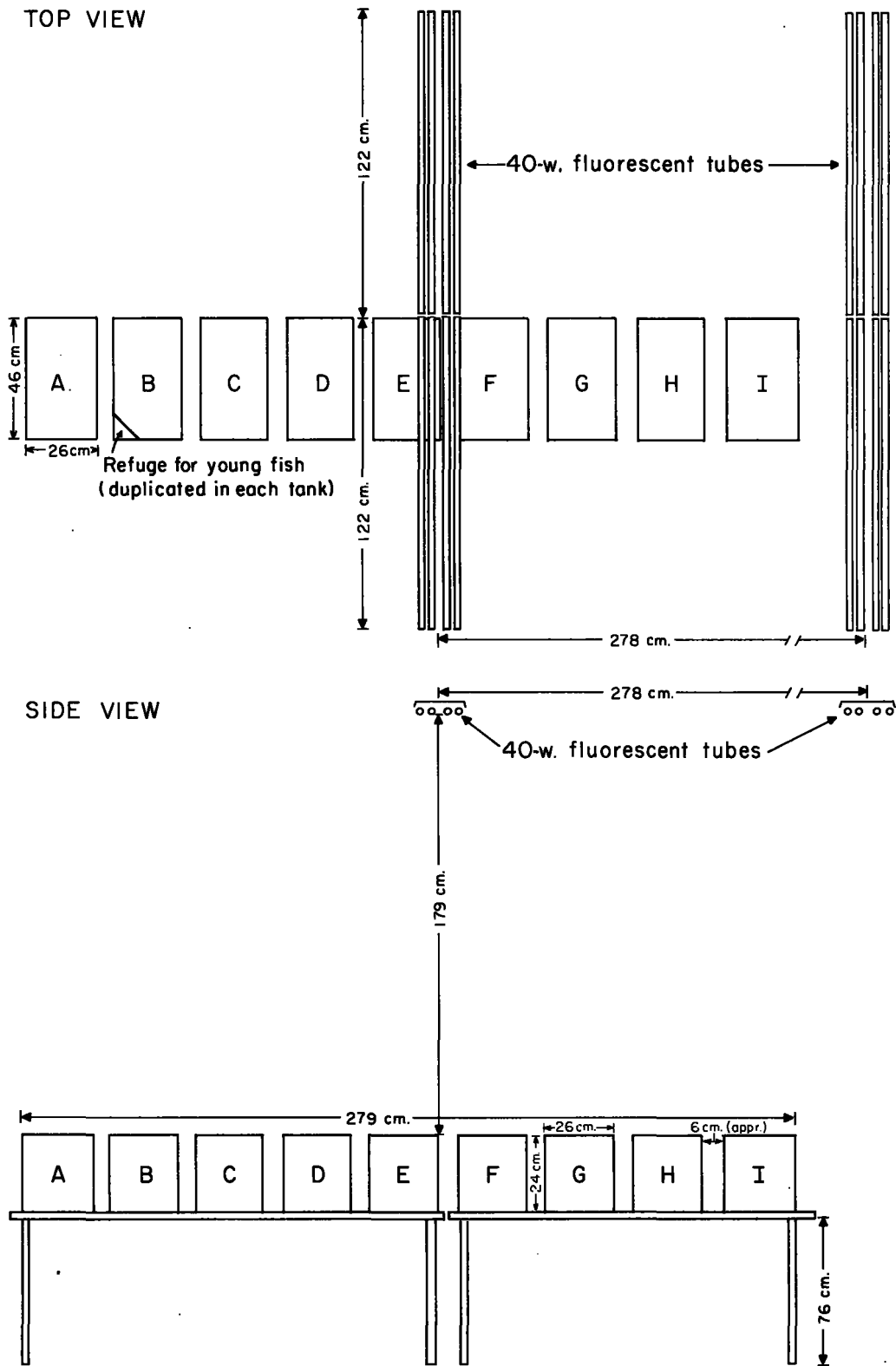


FIGURE 1.—General arrangement of tanks and orientation with respect to light fixtures. Door to room was located beyond end of light fixture in upper right corner, and was not visible to fish in tanks.

drated carrot, dehydrated lettuce, dehydrated spinach, and dehydrated water cress.

The following analysis was supplied by the maker:

Crude protein, minimum.....	40 percent
Crude fat, minimum.....	3 percent
Crude fibre, maximum.....	10 percent

Artemia nauplii were produced by placing the dry eggs in 750 ml. of salt water (one level tablespoonful per 750 ml.) and incubating them 2 days at about 24° C. Food was supplied to tanks according to the schedule in table 1. All of the daily food allotment was placed in the tanks at one time. During the early part of the experiment some food fell to the bottom of the tanks uneaten; it was siphoned out before the following day's feeding. When the populations had grown to pre-exploitation sizes, all food was consumed.

TABLE 1.—Schedule of food supplied to tanks receiving various diets. The "standard" diet is designated 1.0

Day of week	0.5 diet			1.0 diet			1.5 diet		
	Fro-zen Daph-nia	Ar-te-mia nau-plii ¹	Dry food	Fro-zen Daph-nia	Ar-te-mia nau-plii ¹	Dry food	Fro-zen Daph-nia	Ar-te-mia nau-plii ¹	Dry food
Sun.....	G.	G.	G.	G.	G.	G.	G.	G.	G.
Mon.....	0.5	0.2	0.05	1.0	0.4	0.10	1.5	0.6	0.15
Tues.....	.5	.2	.05	1.0	.4	.10	1.5	.6	.15
Wed.....	.5	.2	.05	1.0	.4	.10	1.5	.6	.15
Thurs.....	.5	.2	.05	1.0	.4	.10	1.5	.6	.15
Fri.....	.5	.2	.05	1.0	.4	.10	1.5	.6	.15
Sat.....	.2	.2	.05	.4	.4	.10	.6	.6	.15
Total.....	2.5	1.2	.35	5.0	2.4	.70	7.5	3.6	1.05

¹ This represents weight of eggs hatched. Actual weight of nauplii produced, for the "standard" diet was 0.125 mg. (Silliman and Gutsell, 1958). The determination was made by producing duplicate hatches of 0.4 g. of eggs; these hatches were then dried, weighed, and the average weight determined. No data were available to adjust for day-to-day variations in hatching success. The weight of nauplii represented such a small part of the total diet (about 1/100 of 1 percent) that variations would not significantly affect total food available.

The nine populations were started on January 30, 1964. (A list of dates for the numbered weeks of each experiment is given in table 2.) Stocks were from previously established aquariums and consisted of 432 guppies. I segregated the fish into males, females, and "juveniles," the latter including the categories "fry" and "immature" as defined above. All males were placed in a single container and then put into the nine tanks from A to I in succession, one fish at a time. I repeated this process until seven males were in each tank. I used a like process to put eight females in each tank. Similarly, 33 juveniles were placed in each tank, but they were introduced in groups of 10, 10, 10, and 3. Thus, each tank

contained 48 fish—7 males, 8 females, and 33 juveniles—chosen in a consistent manner from established aquarium stocks.

Populations were fished (exploited) at 3-week intervals, the approximate time between broods.¹ These rates bracketed the rate previously found to produce maximum yield (Silliman and Gutsell, 1958), which was about 0.33 per 3-week period. The "bracketing" rates were 0.25 and 0.50 per 3-week period. Fishing was done by removing each nth fish for fishing rate $\frac{1}{n}$ and was applied only to the "immature" and "adult" fish, excluding the "fry." "Adults" included all fish whose sex could be determined by external inspection; and "immatures", all others except the "fry" that passed through the grader described above.

Procedures were described in more detail by Silliman and Gutsell (1958), who also reported the technique of weekly counting and weighing the fish. This essentially consisted of counting fish individually and placing them on a strainer. From the strainer fish were transferred to a previously weighed container of water on a balance.

TABLE 2.—List of calendar weeks included in experiment

Week No.	Beginning		Week No.	Beginning	
	Year, month, and day			Year, month, and day	
0.....	1964 Jan.	26	37.....	1964 Oct.	11
1.....	Feb.	2	38.....		18
2.....		9	39.....		25
3.....		16	40.....	Nov.	1
4.....		23	41.....		8
5.....	Mar.	1	42.....		15
6.....		8	43.....		22
7.....		15	44.....		29
8.....		22	45.....	Dec.	6
9.....		29	46.....		13
10.....	Apr.	5	47.....		20
11.....		12	48.....		27
12.....		19			
13.....		26	49.....	1965 Jan.	3
14.....	May	3	50.....		10
15.....		10	51.....		17
16.....		17	52.....		24
17.....		24	53.....		31
18.....		31	54.....	Feb.	7
19.....	June	7	55.....		14
20.....		14	56.....		21
21.....		21	57.....		28
22.....		28	58.....	Mar.	7
23.....	July	5	59.....		14
24.....		12	60.....		21
25.....		19	61.....		28
26.....		26	62.....	Apr.	4
27.....	Aug.	2	63.....		11
28.....		9	64.....		18
29.....		16	65.....		25
30.....		23	66.....	May	2
31.....		30	67.....		9
32.....	Sept.	6	68.....		16
33.....		13	69.....		23
34.....		20	70.....		30
35.....		27	71.....	June	6
36.....	Oct.	4	72.....		13

¹ Each brood consists of 6 to 80 young, depending on the size of the female (Innes, 1945).

Total weight of fish, container, and water was determined, and the fish weight obtained by subtraction.

ENVIRONMENTAL CONDITIONS

Although temperature was controlled as closely as possible, there were some variations. These were examined in relation to possible effects on growth or survival. Oxygen determinations were also made, to ascertain if the levels were within those considered adequate for warm-water fishes.

TEMPERATURE

Room air temperature was controlled by a thermostatically regulated window heat pump, which could either heat or cool. Water temperature about 8 cm. below the surface of tanks A, E, and I (fig. 1) was recorded daily at about 8 a.m., noon, and 4 p.m. (Only one reading per day was taken on weekends.) The means indicated reasonably stable temperatures (table 3). No 30-day mean deviated more than 0.7° C. from the grand mean. The means for all three times of day gave some indication that tank A averaged higher than the others, but the greatest excess of A over either E or I was 0.5° C. Likewise, the means for all three tanks indicated that the 4 p.m. reading tended to be lower than the others, but again the greatest departure was 0.5° C. The means of "All 3 by All 3" revealed no consistent trend in temperatures during the experiment. The total range of individual temperature readings during the entire experiment was from 21.1° to 27.2° C.

TABLE 3.—Mean temperatures for tanks A, E, and I during three 30-day periods¹

Period	Temperature recording time	Mean temperature			
		Tank A	Tank E	Tank I	All 3 tanks
		°C.	°C.	°C.	°C.
Mar. 5- Apr. 21, 1964.....	8 a.m.	24.4	24.1	24.1	24.2
	Noon.....	24.5	24.4	24.3	24.4
	4 p.m.	23.9	24.0	24.1	24.0
	All 3 times....	24.3	24.2	24.2	24.2
Sept. 16- Nov. 2, 1964.....	8 a.m.	24.9	24.4	24.6	24.7
	Noon.....	24.4	24.6	24.5	24.7
	4 p.m.	24.8	24.1	24.3	24.3
	All 3 times....	24.8	24.3	24.6	24.6
Apr. 23- June 11, 1965.....	8 a.m.	24.6	24.3	24.3	24.3
	Noon.....	24.4	24.1	24.0	24.2
	4 p.m.	23.9	23.8	23.6	23.8
	All 3 times....	24.3	24.1	23.9	24.1
All 3 periods.....	All 3 times....				24.3

¹ The period means are based on 30 days in which three daily readings were taken in all three tanks. The period is not based on 30 consecutive days. The days that were excluded from the periods were ones in which fewer than three readings were made (these days usually were on weekends).

The rather small deviations just recorded suggest that temperature was fairly well controlled. Any effects on growth or survival must have been slight, and no further analysis of temperatures seems justified.

OXYGEN CONCENTRATION

Oxygen determinations were made for each tank during March 29 to April 14, 1965. Readings ranged from 4.54 to 5.58 p.p.m., all within or above the 3 to 5 p.p.m. that Lewis (1963) considered adequate for warm-water fishes.

Ozone was used in the tanks to control algae during weeks 56-72. This was supplied by a "Sander Ozonizer"² at the rate of 5 mg. per hour. Except for occasional treatments of individual tanks, the 5 mg. per hour was delivered to the main air supply, thus being divided among the nine tanks. Previous tests with fish not included in the experiments produced no mortalities when the entire 5 mg. per hour was supplied to a single 20-l. tank. No relation was noted between growth of algae and food supply or amount of light.

POPULATION CHANGES

For purposes of analysis, the experiment was arbitrarily divided into periods before (weeks 0-28), and after (weeks 29-72) exploitation began. Changes during the first period reflected increases in number and biomass resulting from reproduction and growth. Exploitation was responsible for the major changes in the second period, resulting in initial declines followed by relative stability in both population size and yield.

INITIAL GROWTH OF POPULATIONS

The stocks entered a period of growth in numbers and weight, each stock influenced by the amount of food supplied. Mean numbers and weights each week for the group of three tanks at each food level (tables 4 and 5, and fig. 2) clearly bring out the influence of food supply on growth. Total weights of the stocks were in the same rank as, but not exactly proportional to, amounts of food supplied. During weeks 21 to 28, mean weights for diet levels 0.5, 1.0, and 1.5 were 14.5, 26.0, and 36.6, respectively. These

² Trade names referred to in this publication do not imply endorsement of commercial products.

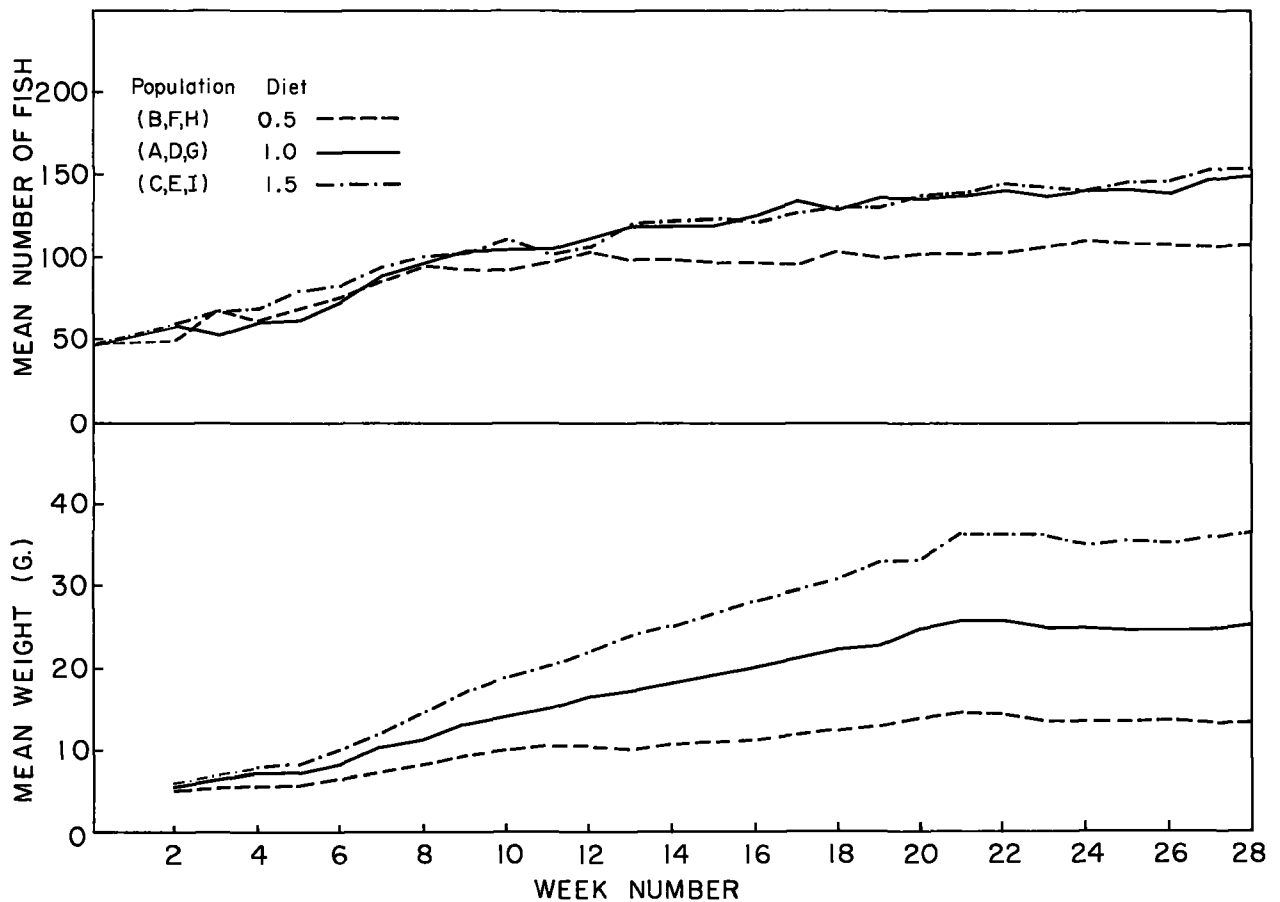


FIGURE 2.—Initial growth of populations. Data are means for the three populations at each diet level.

were in ratios 1.00:1.79:2.52 as compared with the 1:2:3 ratios of the diet levels.

Average numbers of fish fell even farther from the ratios of the diet levels than did the average weights. For weeks 21 to 28 they were 110, 145, and 149 in ratios 1.00:1.32:1.35. Comparison of these ratios with those for average weights indicated that the individual fish averaged larger at the higher diet levels. Weights of individual fish averaged 0.132, 0.179, and 0.246 g., respectively, in populations at diet levels 0.5, 1.0, and 1.5.

These results indicate that the greater biomass at the higher diet levels than at the lowest level was caused by both better survival and more rapid growth of individuals. Growth was the more important factor. The results indicate also some-

what less efficient food use at the higher diet levels than at the lowest, in the sense of the amount of biomass supported by a given amount of food. Thus, the 2.85 g. of food consumed per week (totals for *Daphnia* and dry food from table 1, plus 6 times $\frac{1}{2}$ of 0.000125 g. for *Artemia*), at the 0.5 diet level supported a biomass of 14.5 g., or 5.1 g. per gram of weekly consumption, whereas at the 1.5 diet level the comparable figures are 8.55 g., 36.6 g., and 4.3 g. This loss of efficiency may have been the result of crowding the larger biomass at the higher diet levels into the same amount of space as occupied by the biomass at the lowest diet level. Alternatively, it is possible that such efficiency may simply be a declining function of size in stabilized populations.

TABLE 4.—Weekly numbers of fish in each lettered tank during period of initial growth, first 28 weeks

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B	Tank F	Tank H	Tank mean	Tank A	Tank D	Tank G	Tank mean	Tank C	Tank E	Tank I	Tank mean
0.....	No. 48	No. 48	No. 48	No. 48	No. 48	No. 48	No. 48	No. 48	No. 48	No. 48	No. 48	No. 48
1.....	(¹) 52	(¹) 54	(¹) 45	-----	(¹) 60	(¹) 47	(¹) 70	-----	(¹)	(¹)	(¹)	-----
2.....	89	51	65	50	43	45	72	59	86	49	46	80
3.....	89	51	65	50	43	45	72	59	86	49	46	80
4.....	58	50	74	61	42	71	70	61	79	59	69	69
5.....	80	53	73	70	50	71	69	63	100	67	73	80
6.....	90	61	77	76	66	73	84	74	122	73	73	89
7.....	122	67	77	87	68	110	59	89	122	75	87	95
8.....	119	93	75	96	76	121	95	97	121	77	105	101
9.....	121	83	77	93	113	110	92	105	131	79	99	103
10.....	121	81	77	93	99	111	107	106	145	95	100	113
11.....	130	82	82	98	85	125	115	112	136	85	105	109
12.....	142	92	81	105	97	144	116	119	138	85	103	109
13.....	120	97	82	100	115	134	114	121	171	94	102	122
14.....	121	95	83	100	110	140	117	122	166	94	111	124
15.....	124	94	78	99	103	139	120	121	161	95	120	125
16.....	122	95	80	99	106	154	119	126	180	93	116	123
17.....	120	89	83	97	119	155	135	136	167	100	121	129
18.....	129	102	87	106	113	149	130	131	181	99	117	132
19.....	122	101	83	102	122	151	141	138	183	97	115	132
20.....	125	105	85	105	125	151	138	138	203	99	117	140
21.....	124	103	89	105	121	158	141	140	182	104	128	141
22.....	126	103	88	106	130	165	134	143	191	127	122	147
23.....	133	109	88	110	125	163	132	140	198	118	119	145
24.....	135	114	89	113	129	180	144	144	195	116	119	143
25.....	132	112	88	111	133	169	141	144	198	122	127	149
26.....	135	112	87	111	131	152	143	142	193	122	135	150
27.....	131	111	87	110	133	159	160	151	209	123	139	157
28.....	127	117	88	111	144	160	155	153	207	122	142	157

¹ Not counted.

TABLE 5.—Weekly weights of fish in each lettered tank and mean weight per diet during period of initial growth, first 28 weeks

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B	Tank F	Tank H	Tank mean	Tank A	Tank D	Tank G	Tank mean	Tank C	Tank E	Tank I	Tank mean
0.....	G. (1)	G. (1)	G. (1)	G. (1)	G. (1)	G. (1)	G. (1)	G. (1)	G. (1)	G. (1)	G. (1)	G. (1)
1.....	(¹)	(¹)	(¹)	(¹)	(¹)	(¹)	(¹)	(¹)	(¹)	(¹)	(¹)	(¹)
2.....	5.5	4.6	5.9	5.3	6.5	5.5	5.7	5.9	4.8	7.7	6.1	6.2
3.....	5.3	5.3	6.5	5.7	7.0	6.6	6.5	6.7	6.3	(²)	(²)	-----
4.....	5.6	5.8	6.5	6.0	8.2	7.1	7.6	7.6	7.8	8.7	7.8	8.1
5.....	5.3	6.4	6.2	6.0	7.3	7.1	8.8	7.7	9.3	8.3	8.4	8.7
6.....	6.3	7.6	7.0	7.0	7.8	8.6	10.0	8.8	11.0	10.0	10.3	10.4
7.....	6.7	8.9	7.7	7.8	9.5	10.5	12.5	10.8	13.5	12.3	12.2	12.7
8.....	8.3	9.3	8.5	8.7	11.3	11.4	12.0	11.6	16.2	14.5	14.2	15.0
9.....	8.7	11.0	9.8	9.8	13.0	13.5	13.7	13.4	18.6	17.1	16.4	17.4
10.....	9.6	10.9	10.4	10.3	13.6	15.0	14.8	14.5	20.0	19.0	18.8	19.3
11.....	10.0	12.3	10.4	10.9	15.2	16.2	15.8	15.7	21.7	20.5	19.9	20.7
12.....	10.4	11.2	10.9	10.8	16.6	16.8	17.5	17.0	24.2	22.9	21.0	22.7
13.....	10.9	10.4	10.9	10.7	17.3	17.6	18.3	17.7	25.8	24.2	22.9	24.3
14.....	11.4	10.6	11.8	11.3	18.2	18.6	18.9	18.6	26.3	25.8	24.8	25.6
15.....	12.1	11.4	11.5	11.7	19.4	19.9	19.7	19.7	27.9	27.0	26.6	27.1
16.....	12.2	11.8	11.8	11.9	20.4	20.4	21.0	20.6	29.7	29.2	27.5	28.8
17.....	12.6	12.2	12.2	12.3	21.6	21.2	22.3	21.7	31.6	30.2	28.3	30.0
18.....	13.7	12.8	12.4	13.0	23.0	22.5	23.4	23.0	33.3	31.8	29.2	31.4
19.....	12.7	13.1	15.2	13.7	22.8	23.2	24.1	23.4	33.8	32.7	33.3	33.3
20.....	15.6	14.5	14.0	14.7	25.6	24.4	26.4	25.5	35.6	33.6	32.2	33.8
21.....	17.3	14.2	14.4	15.3	26.0	26.5	27.4	26.6	38.2	39.4	33.3	37.0
22.....	16.0	14.3	14.9	15.1	26.4	25.8	26.9	26.4	40.5	37.0	33.3	36.9
23.....	14.6	14.4	13.9	14.3	25.8	24.9	26.3	25.7	40.8	37.6	32.5	37.0
24.....	14.4	14.2	13.9	14.2	25.5	25.5	26.6	25.9	38.2	35.9	33.0	35.7
25.....	14.3	14.6	13.7	14.2	25.4	24.4	26.3	25.4	40.0	35.7	32.9	36.2
26.....	15.2	14.5	14.1	14.6	27.2	(²)	26.6	-----	40.1	35.4	32.5	36.0
27.....	14.2	14.5	13.7	14.1	25.7	24.9	26.9	25.8	39.5	35.8	34.5	36.6
28.....	14.1	14.7	13.9	14.2	25.2	25.7	27.8	26.2	38.8	35.6	37.7	37.4

¹ Not weighed.

² No record.

³ Aberrant data discarded.

CHANGES DURING EXPLOITATION

It was desired to have the populations as stable as possible before the start of exploitation. Degree of stability was examined by studying the distribution of the individual populations with respect to the categories "fry," "immature," and "adult." For the 3 weeks immediately before the start of exploitation at each diet level, compositions according to these categories revealed fairly consistent patterns for the 0.5 and 1.0 levels (figs. 3 and 4), both between weeks and between

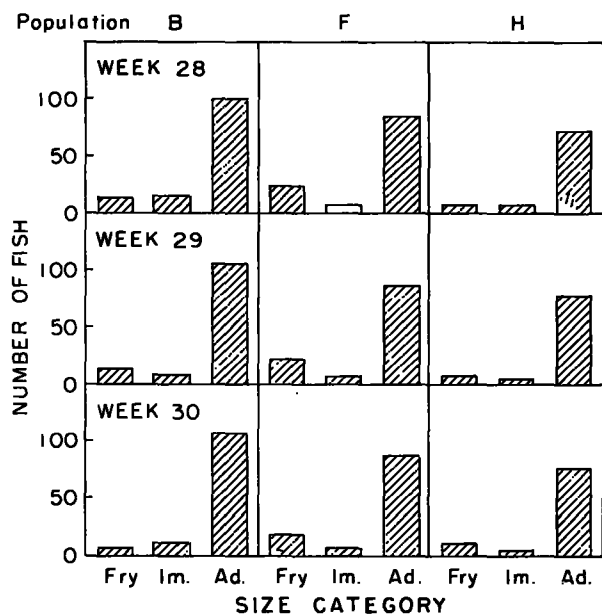


FIGURE 3.—Composition according to categories "fry," "immature," and "adult" (defined in section "Experimental diet and procedures") of populations at the 0.5 diet level, immediately before exploitation.

populations. (Weeks of removal were staggered to facilitate the laboratory routine. Thus, exploitation at the 0.5 level began a week after that at the 1.0 level.) The compositions are characteristic of mature populations at or near the asymptotic level—mostly adults that are rather stable in number and much smaller and somewhat more fluctuating numbers of juveniles.

Characteristics of the compositions were similar at the 1.5 level (fig. 5) except for the lack of consistency between populations. (Exploitation was delayed 4 weeks in the hope that this inconsistency might disappear.) Here the differences are marked

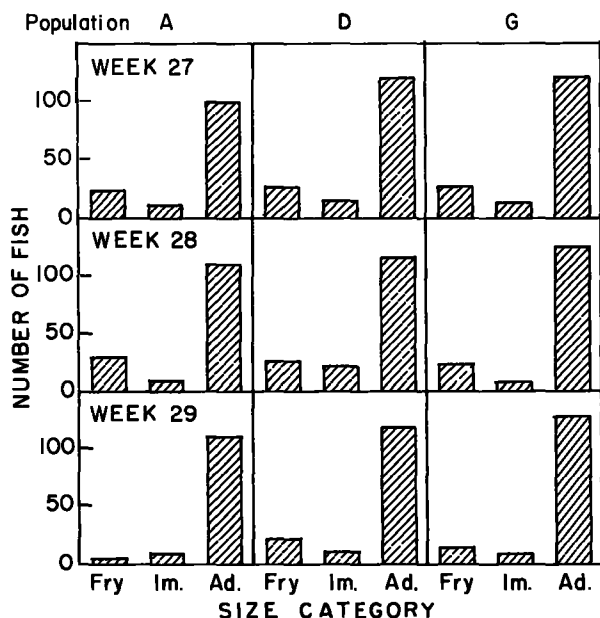


FIGURE 4.—Composition according to categories "fry," "immature," and "adult" (defined in section "Experimental diet and procedures") of populations at the 1.0 diet level, immediately before exploitation.

both in total number (as between C and E in week 34) and in percentage composition (as between C and I in week 32). These differences are surprising among populations held for more than 30 weeks under conditions of food supply, temperature, light, and space as nearly identical as possible. No ready explanation could be found among other conditions of the environment or among procedures of handling the fish. Probably genetic differences were not averaged out among the rather small numbers of adults (15) in the initial populations, in spite of the method of selection (section, "Initial growth of populations"). The differences may also have resulted from variations in gravidity among the eight adult females in each initial population. Support for some explanation related to the initial populations is found in the fact that C exceeded E and I in number and weight almost from the start of the experiment (weeks 2 to 28, table 3; weeks 5 to 20 and 22 to 28, table 4).

The differences among populations at the 1.5 diet level persisted, even though the start of exploitation was delayed 4 weeks beyond that for

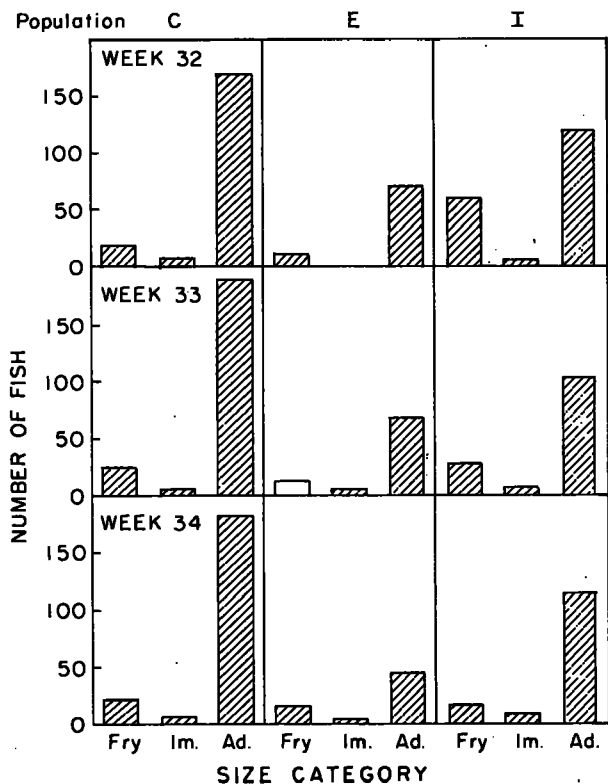


FIGURE 5.—Composition according to categories “fry,” “immature,” and “adult” (defined in section “Experimental diet and procedures”) of populations at the 1.5 diet level, immediately before exploitation.

the other six populations. I decided to proceed with exploitation of the 1.5 level group because of the substantial amount of time and effort already invested and the desire to have yields comparable with those for the other populations. This decision was supported by the fact that compositions were fairly stable within populations (fig. 5) even though discrepant between them.

Response of the populations to exploitation is indicated by the mean numbers and weights for each diet level (tables 6 to 9 and fig. 6). The saw-tooth pattern of reduction by removals and subsequent recovery is characteristic. As pointed out by Silliman and Gutsell (1958), this kind of variation reflects the resilience of natural populations as long as exploitation rates are not high enough to cause extinction.

As was also mentioned by Silliman and Gutsell, population weights are more stable than population numbers, since the latter are affected more by entrance and mortality of broods of fry. The weights reveal the typical decline in population size after the inception of exploitation, followed by near stability during the final weeks of the experiment. Although populations at all three diet levels decreased in biomass under exploitation, they maintained the preexploitation rank, which was the same as that of the diet levels.

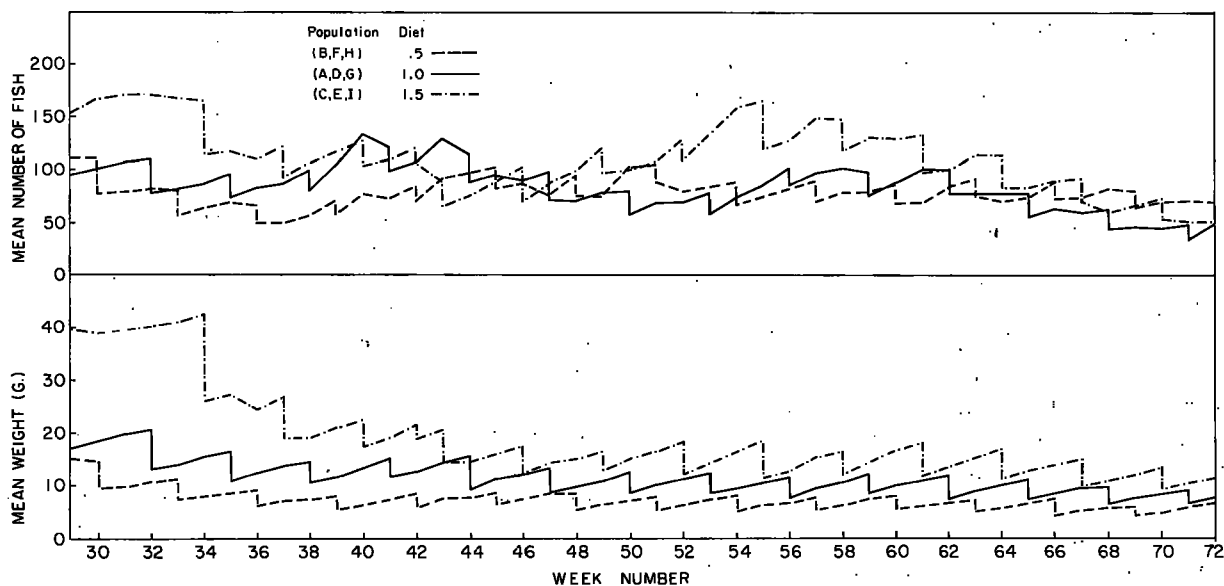


FIGURE 6.—Response of populations to exploitation. Data are means for each diet level.

TABLE 6.—Weekly numbers and food-level means for each tank during period of exploitation; postremoval numbers for removal weeks were obtained by subtracting numbers removed (table 7); exploitation rates are indicated in parentheses. Exploitation was started week 29 for 1.0 diet, week 30 for 0.5 diet, and week 34 for 1.5 diet

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B (0.25)	Tank F (0.33)	Tank H (0.50)	Tank mean	Tank A (0.25)	Tank D (0.50)	Tank G (0.33)	Tank mean	Tank C (0.50)	Tank E (0.25)	Tank I (0.33)	Tank mean
	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
29	127	118	91	112	122	158	148	143	204	126	133	154
30	127	114	93	111	104	90	110	101	217	141	141	166
31	101	80	52	78	105	104	110	106	217	143	150	170
32	97	83	67	82	119	93	119	110	200	126	184	170
33	100	87	54	80	96	52	91	80	221	142	138	167
34	90	65	34	63	99	62	93	85	211	158	141	170
35	98	72	36	69	95	71	123	96	131	109	111	117
36	82	69	46	66	73	79	95	82	133	69	124	109
37	70	50	27	49	75	77	106	86	146	74	142	121
38	73	62	34	56	90	74	133	99	107	94	118	106
39	93	72	45	70	107	71	134	104	129	109	111	116
40	82	62	83	76	92	134	172	133	135	122	121	126
41	85	59	72	72	98	131	131	120	114	112	100	109
42	92	97	60	83	82	94	143	106	136	118	106	120
43	106	97	70	91	115	113	157	128	89	97	77	88
44	114	99	71	95	94	101	149	115	68	65	91	75
45	126	110	66	101	80	104	100	95	70	83	112	88
46	107	91	60	86	82	101	85	89	73	92	139	101
47	110	63	51	75	91	108	91	97	77	45	137	86
48	106	122	53	94	69	76	61	69	73	60	160	98
49	87	100	38	75	67	88	75	77	75	112	174	120
50	88	131	85	101	71	89	76	79	39	105	154	99
51	94	135	84	104	101	53	52	69	29	98	193	107
52	71	104	63	79	88	51	67	69	57	130	198	128
53	70	109	69	83	101	50	81	77	76	145	175	132
54	70	125	65	87	109	26	87	74	86	172	220	159
55	63	118	42	74	116	39	101	85	88	159	247	165
56	70	117	55	81	150	52	102	101	106	58	216	127
57	80	121	65	89	148	49	95	97	128	81	234	148
58	74	116	43	78	141	55	107	101	119	78	242	146
59	75	111	47	78	141	56	98	98	108	87	192	139
60	109	105	46	87	139	44	81	88	107	80	196	128
61	90	88	25	68	135	44	122	100	110	95	194	133
62	86	104	62	84	150	49	94	98	63	85	152	100
63	115	107	51	91	120	33	77	77	66	129	148	114
64	97	81	33	70	120	36	74	77	68	126	149	114
65	103	86	33	74	109	31	39	76	39	105	103	82
66	108	88	69	88	85	20	78	62	54	110	102	89
67	97	76	49	74	93	26	60	60	59	112	106	92
68	121	76	49	82	92	28	65	62	32	82	67	80
69	118	74	47	80	68	19	50	46	33	81	85	66
70	118	64	28	70	68	18	47	44	33	94	93	73
71	107	78	29	71	79	21	44	48	20	65	68	51
72	102	74	31	69	77	11	58	49	26	63	66	52

YIELDS

Removals during the period of exploitation were comparable to the catches of commercial fisheries and provided information on stabilized yields. Data were analyzed both to determine when relative stability began and to measure the relation of yield to amount of food consumed.

COMPARATIVE YIELDS

Yields as well as population sizes were more stable in weights than in numbers; therefore, yields were studied in terms of weight. The course of yield for each population during the exploitation period (table 9 and fig. 7) included an initial period of decline as the populations adjusted themselves to removals. This decrease was followed by a period of relative stability beginning about week 49.

Even within the relatively stable period, yields showed considerable irregularity. This phenomenon resulted from variations in the response of

the populations to exploitation and from deviations of the percentages removed from the exact nominal exploitation rates. The latter deviations occurred because the removal rates were applied on the basis of numbers of fish rather than weights. Some of this random variability is averaged out in means of yields for three 14- or 15-week subperiods covering the entire period of exploitation (table 9 and fig. 8). These means again reflect the initial period of decline, followed by more stable yields.

The final period, including weeks 59 to 72, was one of fairly stable yield (fig. 7). Mean yields for this period (fig. 8) ranked the same according to exploitation rate for the 1.0 and 1.5 diets. Yields at the 0.5 diet were nearly identical. The period including weeks 59 to 72 fairly well fulfilled the planned objective of "a reasonably stable yield" (section, "Plan of the Experiment"), and data from it were used in the study of relation between food level and exploitation rates. Results from this period had the additional advantage of being

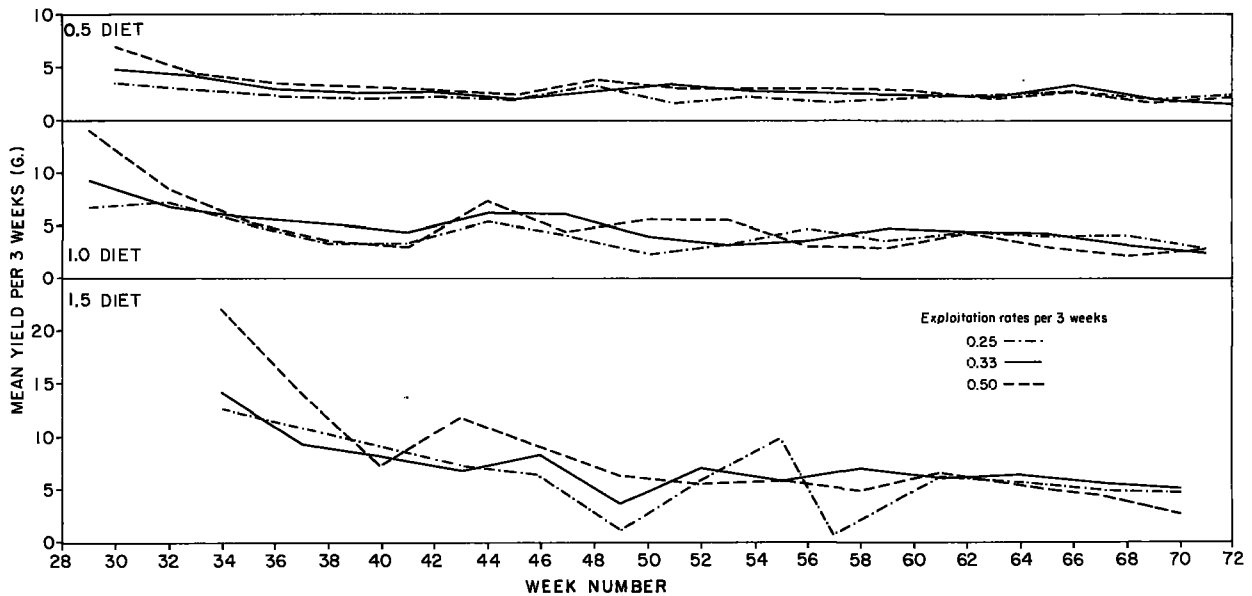


FIGURE 7.—Yield per three weeks of each population during period of exploitation.

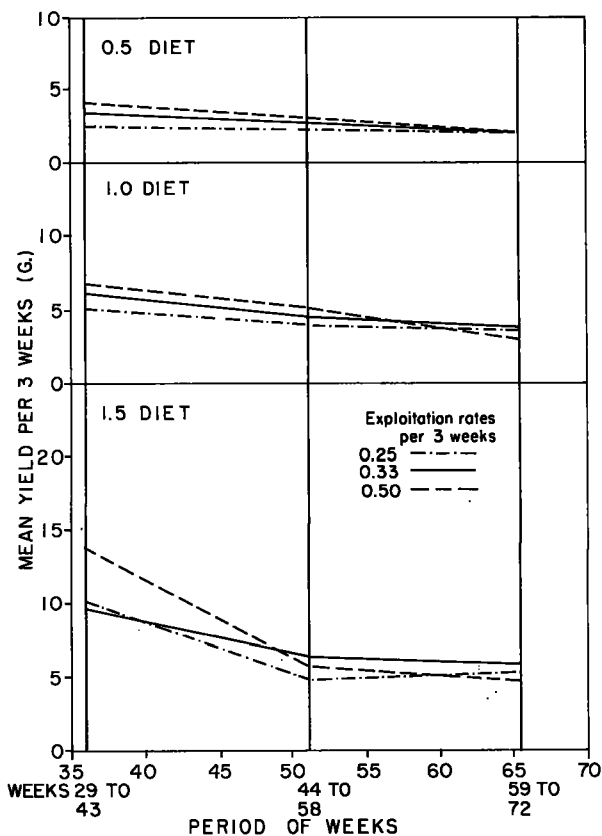


FIGURE 8.—Mean yields for three 14- or 15-week periods. Location of vertical lines along horizontal scale indicates center of each period.

free from the irregularities in removals and mortalities that occurred at the 1.5 diet level during weeks 37 to 57 (table 7, footnotes).

RELATION BETWEEN YIELD AND FOOD LEVEL

Data in the preceding section showed that yields at the 1.0 and 1.5 diets were related to exploitation rate, but that no such relation was detectable at the 0.5 diet. The available data may now be brought together in an attempt to answer such questions as that posed in the introduction: "Might it be possible, for instance, to harvest a greater percentage of the stock when food supply and abundance are high than when they are low?" It is instructive here to relate the yields to the average total weight or biomass of the populations (table 10). Because the populations were allowed to reach asymptotic size or a close approach to it, an additional point for each yield-biomass curve is available—that at zero rate of exploitation. If small deviations are charged to random variability, the appropriate curves (fig. 9) reveal a regular relation among exploitation rate, biomass, and yield at each diet level (curves fitted by inspection).

The curves suggested that the relation of yield to exploitation rate tends to be independent of diet level. Absolute yields were obviously dependent on amount of food available, but the greatest yield at each diet level occurred at or

TABLE 7.—Numbers removed (yields) for each diet and exploitation rate; exploitation rates are indicated in parentheses

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B (0.25)	Tank F (0.33)	Tank H (0.50)	Tank mean	Tank A (0.25)	Tank G (0.33)	Tank D (0.50)	Tank mean	Tank E (0.25)	Tank I (0.33)	Tank C (0.50)	Tank mean
	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
29					29	45	68	47				
30	20	31	41	33								
31												
32					23	35	40	33				
33	24	25	23	24								
34									29	43	95	56
35					19	25	24	23				
36	18	16	15	16					10	30	55	28
37												
38					16	23	24	21				
39	14	14	12	13								
40									10	30	41	24
41					14	24	27	22				
42	12	13	18	14					0	0	43	14
43									22	24	24	23
44					18	33	32	28				
45	18	16	26	20								
46									71	24	40	32
47					18	28	35	27				
48	15	21	21	19								
49									11	27	36	25
50					15	21	30	22				
51	17	21	15	18								
52									15	35	13	21
53					14	16	24	18				
54	17	20	23	20					72	43	24	46
55												
56					18	19	12	16				
57	13	24	23	20					15			
58										46	27	29
59					22	24	23	23				
60	14	23	21	19								
61									19	47	46	37
62					24	24	18	22				
63	14	22	11	16								
64									15	45	33	31
65					24	24	15	21				
66	14	19	17	17								
67									20	31	18	23
68					24	20	7	17				
69	14	18	15	16								
70									20	23	16	20
71					17	13	9	13				
72	15	14	16	15								

¹ Removals omitted because of accidental mortalities in week 36.
² Removals by error; added to week 43 removals in subsequent treatment.
³ Includes accidental mortality.
⁴ Omitted because of erroneous removals in week 43.
⁵ Accidental mortality considered to replace removals due in week 58.

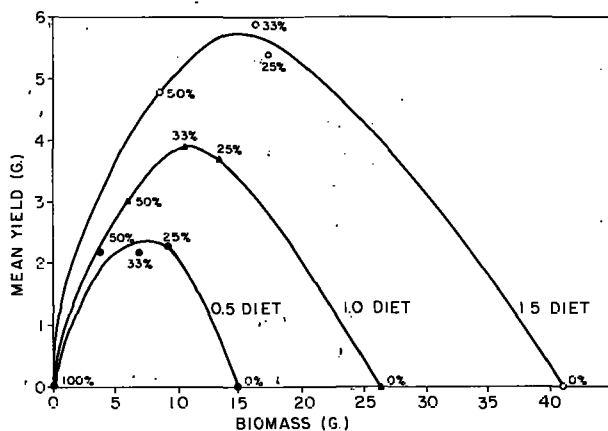


FIGURE 9.—Curves indicating relation of yield per 3-week brood interval to biomass and exploitation rate (indicated percentages) at each diet level. Points indicated for 0 percent exploitation rate are average population levels for the 3 weeks immediately before exploitation.

near the 0.33 exploitation rate (assuming that the different exploitation-yield relation at the 0.5 diet was due to random variation rather than a real difference in the relation). If the apparent independence of the exploitation-yield relation from food level reflects what happens in commercially fished populations, the finding is significant to fishery administration. Such independence would mean that the same management strategy might be applied when food organisms are scarce as when they are abundant.

From the viewpoint of the commercial fisherman, an exploited population is a machine for converting aquatic food to marketable fish flesh. It is of interest to see how efficiently our model of the machine operated at each food level. Maxima of the yield curves (fig. 9) indicate yields per 3 weeks of about 2.4, 3.9, and 5.8 g. at the 0.5, 1.0,

TABLE 8.—Weekly weights and food-level means for each tank during period of exploitation; postremoval weights for removal weeks were obtained by subtracting weights removed (table 9); exploitation rates are indicated in parentheses. Exploitation was started week 29 for 1.0 diet, week 30 for 0.5 diet and week 54 for 1.5 diet

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B (0.25)	Tank F (0.33)	Tank H (0.50)	Tank mean	Tank A (0.25)	Tank D (0.50)	Tank G (0.33)	Tank mean	Tank C (0.50)	Tank E (0.25)	Tank I (0.33)	Tank mean
29	14.2	15.3	17.5	15.7	26.1	26.8	28.4	27.1	45.2	37.5	35.9	39.5
30	14.6	15.5	14.7	14.9	19.9	14.9	20.2	18.3	42.2	38.1	37.4	39.2
31	11.5	10.1	8.2	9.9	21.0	16.9	21.5	19.8	(1)	41.0	37.6	39.0
32	11.9	11.3	8.9	10.7	22.0	17.4	22.6	20.7	42.2	39.5	39.0	40.2
33	12.1	12.0	9.4	11.2	15.6	10.1	16.6	14.1	43.7	40.8	38.6	41.0
34	9.6	8.3	5.9	7.9	17.2	11.7	18.0	15.6	45.7	42.7	39.1	42.5
35	10.3	9.0	6.8	8.7	17.6	13.2	19.2	16.7	23.6	30.8	27.7	27.4
36	10.9	9.4	7.3	9.2	14.0	9.0	14.8	12.6	25.8	19.8	28.4	24.7
37	8.7	8.1	4.9	7.2	15.3	10.1	16.0	13.8	30.0	20.5	30.6	27.0
38	9.4	7.9	5.1	7.5	15.8	11.3	17.0	14.7	14.3	21.5	21.9	19.2
39	9.7	8.5	6.1	8.1	12.8	9.2	13.2	11.7	16.3	23.4	23.4	21.0
40	7.8	7.0	4.5	6.4	14.2	11.0	14.7	13.3	17.2	25.4	25.4	22.7
41	8.7	7.8	5.5	7.3	16.0	12.6	16.7	15.1	12.6	26.0	19.0	19.2
42	10.2	8.6	6.8	8.5	13.8	10.5	14.5	12.9	15.7	28.3	21.3	21.8
43	8.6	7.1	7.2	7.6	15.3	12.5	15.2	14.3	9.5	30.4	22.4	20.8
44	8.6	8.2	6.5	7.8	16.5	13.8	16.8	15.7	7.5	17.1	18.7	14.4
45	10.1	9.3	7.2	8.9	12.9	8.6	12.2	11.2	9.6	18.5	20.2	16.1
46	9.1	8.2	6.1	7.8	13.6	9.6	13.7	12.3	12.2	19.8	21.3	17.8
47	9.8	9.3	6.6	8.6	15.0	11.6	14.3	13.6	14.2	14.1	15.0	14.4
48	10.1	9.1	7.1	8.8	11.6	8.3	9.8	9.9	14.6	14.6	16.1	15.1
49	7.6	7.3	4.2	6.4	12.5	9.0	11.2	10.9	16.2	15.7	18.2	16.7
50	8.5	8.1	5.3	7.3	14.0	10.7	13.0	12.6	12.2	16.9	16.6	15.2
51	9.3	9.3	5.6	8.1	13.3	6.8	10.3	10.1	11.3	19.0	19.5	16.6
52	8.4	6.9	3.7	6.3	14.0	8.0	11.5	11.2	12.5	21.3	21.5	18.4
53	9.0	7.9	4.6	7.2	15.8	9.2	12.8	12.6	8.5	17.7	17.1	14.4
54	9.7	8.8	5.7	8.1	12.2	4.8	11.1	9.4	10.2	19.6	19.6	16.5
55	7.9	6.9	4.3	6.4	13.2	5.9	12.9	10.7	12.3	22.3	21.6	18.7
56	8.5	7.5	4.4	6.8	15.2	6.6	13.6	11.8	7.5	13.5	17.3	12.8
57	9.4	8.4	5.9	7.9	12.2	5.0	11.3	9.5	9.6	16.0	20.6	15.4
58	8.6	6.9	3.6	6.4	13.1	6.4	12.0	10.5	11.3	16.1	22.0	16.5
59	10.3	7.9	4.7	7.6	14.9	7.7	14.3	12.3	8.4	18.0	16.6	14.3
60	10.8	8.1	5.6	8.2	13.1	6.5	10.6	10.1	10.9	30.0	18.9	16.6
61	9.2	6.5	3.6	6.4	14.7	7.6	11.7	11.3	12.6	21.6	20.7	18.3
62	9.5	7.2	4.4	7.0	15.8	8.5	12.1	12.1	8.2	17.5	16.3	14.0
63	10.3	7.9	4.3	7.5	12.1	5.5	9.6	9.1	10.6	18.3	16.6	15.2
64	8.8	6.4	2.9	6.0	13.5	6.7	10.7	10.3	12.3	19.5	20.1	17.3
65	9.6	7.5	3.8	7.0	14.5	8.2	11.2	11.3	8.6	15.6	14.7	13.0
66	10.3	8.0	4.5	7.6	11.6	5.7	8.6	8.6	8.4	17.3	16.5	14.1
67	8.2	6.0	2.6	5.6	13.0	6.4	10.0	9.8	9.5	18.2	18.0	15.2
68	8.8	6.2	3.2	6.1	13.7	6.0	10.9	10.2	5.6	14.8	13.5	11.3
69	8.8	7.0	3.8	6.5	11.6	4.3	8.2	8.0	6.6	16.0	14.6	12.4
70	7.8	5.5	2.5	5.3	12.5	4.9	8.8	8.7	8.0	18.3	15.7	14.0
71	8.2	6.6	4.0	6.3	13.1	5.3	10.4	9.6	5.9	14.6	12.6	11.0
72	9.7	6.9	4.6	7.1	11.6	3.1	9.2	8.0	6.4	15.7	13.6	11.9

¹ Aberrant datum discarded.

and 1.5 diet levels, respectively. Amounts of food consumed at these levels were 8.55, 17.10, and 25.65 g. per 3 weeks (sum of weekly totals for *Daphnia* and dry food plus 6 [0.000125 × diet ratio] for *Artemia*, all multiplied by 3, table 1); thus, conversion efficiencies were 0.28, 0.23, and 0.23. Again, the small difference at the 0.5 diet level probably is not significant. For practical purposes the conversions at all three diet levels are identical and are close to the 0.20 reported by Silliman and Gutsell (1958).

I conclude that efficiency of food conversion, as well as relation between exploitation rate and yield, is independent of amount of food available for the laboratory populations within the range of observation. Management strategies for commercially fished populations that behave in this manner can be applied with the expectation of the same conversion efficiency regardless of the abundance of available food organisms.

This finding seems to be contrary to that re-

ported under "Initial Growth of Populations." It is noteworthy, however, that the lesser efficiency at the two higher diet levels, mentioned there, occurred when the populations were stabilized at near asymptotic levels. Composition of such stabilized populations is different from that of exploited populations, and the growth reactions could well be different also.

The relation of food conversion efficiency to average size of individual fish can be examined by comparing the average weights with the food conversions for each of the nine populations during the exploitation period (weeks 59–72, data from tables 10 and 6, plus food amounts quoted above). L. M. Dickie (personal communication) has pointed out to me that if conversion efficiency be plotted as a regression on average body weight, there is a significant negative correlation (line is $E=0.317-0.667W$, where E is conversion efficiency as above, W is average body weight, and $r=-0.90$ and $P<0.01$). This determination sup-

TABLE 9.—Weights removed (yields) for each diet and exploitation rate; exploitation rates are indicated in parentheses

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B (0.25)	Tank F (0.33)	Tank H (0.50)	Tank mean	Tank A (0.25)	Tank G (0.33)	Tank D (0.50)	Tank mean	Tank E (0.25)	Tank I (0.33)	Tank C (0.50)	Tank mean
29	G.	G.	G.	G.	G.	G.	G.	G.	G.	G.	G.	G.
30	3.6	4.9	7.0	5.2	6.7	9.3	14.1	10.0				
31												
32					7.3	6.9	8.5	7.6				
33	2.9	4.2	4.5	3.9								
34									12.8	14.2	22.2	16.4
35					5.2	5.8	5.5	5.5				
36	2.3	2.9	3.0	2.9								
37									1.0	9.5	14.2	7.9
38					3.4	5.2	3.6	4.1				
39	2.1	2.6	3.2	2.6								
40									1.0	8.3	7.3	5.2
41					3.2	4.4	3.0	3.5				
42	2.3	2.7	2.9	2.6							8.4	
43									7.4	6.8	3.5	8.7
44					5.5	6.2	7.4	6.4				
45	1.9	2.0	2.4	2.1								
46									6.5	8.4	1.0	5.0
47					4.1	6.1	4.5	4.9				
48	3.4	2.8	3.8	3.3								
49									1.3	3.7	6.4	3.8
50					2.3	4.0	5.6	4.0				
51	1.6	3.4	3.1	2.7								
52									6.0	7.1	5.6	6.2
53					3.3	3.2	5.6	4.0				
54	2.4	2.7	3.0	2.7								
55									10.0	5.9	6.0	7.3
56					4.9	3.6	3.1	3.9				
57	1.7	2.6	3.0	2.4					1.8			
58										7.1	5.0	4.3
59					3.6	4.8	2.9	3.8				
60	2.2	2.1	2.8	2.4								
61									6.2	6.1	6.6	6.3
62					4.4	4.4	4.3	4.4				
63	2.3	2.2	1.9	2.1								
64									5.8	6.5	5.5	5.9
65					4.0	4.2	3.0	3.7				
66	2.7	3.3	2.7	2.9								
67									5.0	5.7	4.5	5.1
68					4.1	3.6	2.1	3.3				
69	1.8	2.0	1.6	1.8								
70									4.8	5.2	2.7	4.2
71					2.6	2.4	2.7	2.6				
72	2.4	1.5	2.2	2.0								
Mean												
29-43	2.6	3.5	4.2		5.2	6.3	6.9		10.1	9.7	13.9	
44-58	2.2	2.7	3.1		4.0	4.6	5.2		4.9	6.4	5.8	
59-72	2.3	2.2	2.2		3.7	3.9	3.0		5.4	5.9	4.8	

¹⁻⁵ Footnotes on Table 7.

TABLE 10.—Average biomass and yield per tank per 3 weeks for preexploitation asymptotic levels, and for levels during weeks 59 to 72. Exploitation rates are fractions removed per 3-week brood interval

Exploitation rate	0.5 diet		1.0 diet		1.5 diet	
	Biomass	Yield	Biomass	Yield	Biomass	Yield
0.00	G.	G.	G.	G.	G.	G.
0.25	14.9	0.0	26.4	0.0	141.2	0.0
0.33	9.3	3.3	13.3	3.7	17.5	5.4
0.50	7.0	2.2	10.5	3.9	16.3	5.9
0.50	3.9	2.2	6.2	3.0	8.7	4.8

¹ Taken as average of the weights for the three populations during the 3 weeks immediately preceding exploitation. Weeks were as follows: 0.5 diet, 28-30; 1.0 diet, 27-29; 1.5 diet, 32-34. Data from tables 5 and 8.

² Data from table 8.

³ Data from table 9.

ports the contention (Paloheimo and Dickie, 1965) that . . . "within a life-history stanza a given food abundance leads to a higher production of replaceable fish flesh if the producing population consists of the smaller more efficient fish than if it consists of the larger fish." He further pointed out that this regression line might be the population

counterpart of the "K-curve" which Paloheimo and Dickie developed for individual fish

$$(K_1 = \frac{\Delta W}{R \Delta t} = e^{-a-bR},$$

where W is body weight, R is rations, and a and b are empirical constants).

The fact that the "K-curve" is an exponential relation, whereas the guppy relation is linear, may stem from the wide range of sizes of individual fish in the guppy populations (about 10-40 mm. in length). It may also result from the chief method of population control among guppies—cannibalism. This behavior causes the food of the larger fish to pass through two or more trophic levels, with a consequent lowering of conversion efficiency. Obviously, such an effect would be the more pronounced the larger the average size of individual fish in the population, as long as smaller fish are present for prey, as was true for all populations during the exploitation period.

SUMMARY

1. Nine experimental populations of the guppy, *Lebistes reticulatus*, were established in 20-l. aquariums.

2. Groups of three populations selected by lot were fed at rates 0.5, 1.0, and 1.5 times the "standard" diet.

3. Amount of food, temperature, space, and light were held constant during the course of the experiment.

4. During weeks 21 to 28 of the experiment, mean weights of populations at the 0.5, 1.0, and 1.5 diet levels were 14.5, 26.0, and 36.6 g., respectively; mean numbers of fish were 110, 145, and 149.

5. The greater mass of the populations at the higher diet levels than at the lowest reflected faster growth more than better survival.

6. Exploitation of the populations in each diet level group of three was applied at rates of 0.25, 0.33, and 0.50 per 3-week reproductive period. There were, thus, nine diet-exploitation combinations. Exploitation was started during weeks 29 to 34, when the composition of the populations was reasonably stable, and continued to the end of the experiment during weeks 70 to 72.

7. Populations responded to exploitation with an initial drop in numbers and weight, followed by near stability in weight at new lower levels (numbers were less stable, owing to entrance and mortality [through cannibalism or otherwise] of broods of new-born fish).

8. Yields in weight during the final 14 weeks of the experiment were reasonably stable and were used in the study of the interaction between food level and exploitation.

9. Curves of yield as related to biomass and exploitation rate at each diet level showed that the relation of yield to exploitation rate was independent of diet level.

10. Yields were maximum near the 0.33 exploitation rate for all diet levels, and absolute amounts were 2.4, 3.9, and 5.8 g. per 3-week period for the 0.5, 1.0, and 1.5 diets, respectively.

11. The maximum yields represented conversion of about 25 percent of the food consumed, for all three diet levels.

12. Results suggest that, to the extent that commercially fished populations behave similarly to the laboratory populations, management strat-

egies may be applied regardless of abundance of food organisms.

ACKNOWLEDGMENTS

Most of the initial stock of guppies was donated from an aquarium maintained by Julius Rockwell, Jr. Part of the stock remained from experiments performed by Nancy Maynard. John Pricci, William Frazier, and Josephine Dickens fed and maintained the fish (all five of these people were members of the Bureau of Commercial Fisheries). L. M. Dickie and his staff of the Fisheries Research Board of Canada furnished useful suggestions which were followed in revising the manuscript.

LITERATURE CITED

- BEVERTON, RAYMOND J. H., and S. J. HOLT.
1957. On the dynamics of exploited fish populations. Great Britain Ministry of Agriculture, Fisheries, and Food; Fishery Investigations, Ser. 2, Vol. 19, 532 pp.
- INNES, WILLIAM T.
1945. Exotic aquarium fishes. Philadelphia, Innes Publ. Co., 507 pp.
- JENSEN, AAGE J. C.
1928. The relation between the size of the plaice stock and the quantity of "first-class plaice-food" in certain parts of the Limfjord. Rep. Danish Biol. Sta. 34(5): 87-98.
- LEWIS, WILLIAM M.
1963. Maintaining fishes for experimental and instructional purposes. So. Ill. Univ. Press, Carbondale, Ill., 100 pp.
- PALOHEIMO, JYRI E., and L. M. DICKIE.
1965. Food and growth of fishes. I. A growth curve derived from experimental data. J. Fish. Res. Bd. Canada 22(2): 521-542.
- SILLIMAN, RALPH P.
1948. Factors affecting population levels in *Lebistes reticulatus*. Copeia 1948 (1): 40-47.
- SILLIMAN, RALPH P., and J. S. GUTSELL.
1958. Experimental exploitation of fish populations. U.S. Fish Wildl. Serv., Fish. Bull. 58: 215-252.
- ZHELTKOVA, M. V.
1958. O vliyanii uslovii otkorma na populyatsiyu ryb (On the effect of feeding conditions on a fish population). Trudy Vses. Nauch.-Issled. Inst. Mors. Ryb. Khoz. Okean. (VNIRO) 34: 102-126. Fish. Res. Bd. Canada (St. Andrews N. B. Trans. Ser. 240).
1961. O bespechennost' pischei vida, populyatsii i piko lenni u ryb (The supply of food for a species, a population, or a year class of fish). Akad. Nauk S.S.S.R. Trudy Sovesh. Ikhtiol. Komm., No. 13, 82-93 (Trans. N.S. 2, Fish. Lab. Lowestoft, England, 1963, 17 pp.).