EXPERIMENTAL EXPLOITATION OF COMPETING FISH POPULATIONS

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ABSTRACT

Populations of the guppy, *Poecilia reticulata*, and the swordtail, *Xiphophorus maculatus* × *X. helleri*, were grown both independently and in competition under controlled conditions. Independent populations were permitted to grow for about a year and then successively exploited at two different rates for each species. In the control (unfished) pair of competing populations, both species grew for about 30 weeks, followed by decline and extinction of the swordtail and fluctuations in the guppy. Similar initial growth in the test pair was followed by exploitation of both species at various combinations of rates.

Measures of recruitment were available as weights of juveniles returned to adult tanks from separate nursery tanks. Data from fitted curves showed that guppy recruitment exceeded that of the swordtail under both independent and competing conditions. Depression of recruitment by competition was greater in the swordtail than in the guppy.

A mathematical model for competing populations consisted of a pair of differential equations including elements of the Volterra competition formulae and the Fox exponential surplus-yield model. By using the exploitation rates applied in the experiments, and constants from the independent populations, the model was applied to biomass data from the control pair of competing populations. Successive trials resulted in a reasonably good fit, and competition coefficients from this were used to fit data from the exploited test pair. Yield isopleths calculated from the fitted model showed that maximal yields were obtained when exploitation for the swordtail was lower than for the guppy, suggesting lower productivity in the swordtail. The maximum sustainable yield represented about 20% of food placed in tanks, and indicated at least as great efficiency from competing populations as from independent ones.

Results from the experiments clearly suggest that exploiting both members of a competing pair is preferable to exploiting either alone, provided fishing rates are adjusted in relation to the productivity of each species.

Classical studies of fishery dynamics, such as those discussed in the works of Beverton and Holt (1957) and Ricker (1958), deal mostly with single populations treated as if they existed independently. Fishery biologists have come to recognize, however, that in many situations the fish stock cannot be so treated (Larkin 1963; Murphy 1973). The exploited population of interest is interdependent with others (which may be either exploited or unexploited) through competitive or predator-prey relations. Any effect of exploitation on one stock may produce a reaction in another, resulting in readjustments in both populations, and invalidating the expected response to exploitation based on single-species dynamics.

A familiar example of an apparent competitive situation is contained in the population histories of the Pacific sardine, *Sardinops sagax*, and the northern anchovy, *Engraulis mordax*, off the coast of California. The sardine suffered a catastrophic decline in the mid-1940's, followed by an increase in the anchovy. An analog computer model of Silliman (1969a, b) demonstrated that at least part of the change in the anchovy population size could be simulated with data on the sardine population size and the differential equations of Volterra (1928). Murphy (1973) provided recent verification of the sardine-anchovy relation and suggested that similar relations may prevail in the Japanese and South African sardines.

Laboratory experiments on the exploitation of self-sustaining fish populations have been reported fairly extensively (Silliman and Gutsell 1958; Silliman 1968; Nagoshi et al. 1972). Experiments with competing populations have included such diverse organisms as yeast cells (Gause 1932); Protozoa (Gause 1934); *Daphnia* (Frank 1957); beetles (Park 1962); and warblers (MacArthur 1958). To the best of my knowledge, however, exploitation of competing laboratory fish populations has not previously been reported.

The purpose of the experiments reported below was to ascertain experimentally the reaction of two competing fish populations to exploitation.

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Within this general objective, it was desired to determine which combination of exploitation rates applied on the two species would provide the maximum sustainable yield. To approach this problem, test and control pairs of populations were established in aquariums and allowed to grow several months under controlled conditions. Various combinations of exploitation rates were then applied to the test pair to determine population interactions and total yields. A "base line" for evaluating the results was obtained by growing and exploiting each of the competing species independently.

APPARATUS AND PROCEDURES

Experimental Animals

A lengthy fund of experience (Silliman 1948, 1968; Silliman and Gutsell 1958) built up with the guppy, *Poecilia reticulata*, dictated this as one of the experimental fishes. For the other, it was desired to have a species that was similar to the guppy in size, reproduction, and feeding habit but readily distinguishable from it in a mixed population.

A fish that met these requirements fairly well was the red swordtail hybrid, *Xiphophorus maculatus* × *X. helleri*, which will be referred to simply as "swordtail." It is somewhat larger than the guppy, but lived in the same sized aquarium. It is a live-bearer, like the guppy, and will readily eat the foods commonly fed guppies. Its brilliant red color permits easy distinction in the adults, and even the newborn young are pink or orange and may be distinguished from newborn guppies. In both species, adult males can be distinguished from adult females by external inspection. Distinguishing male characters are the modified anal fin (gonopodium) and fin and body color in the guppy and the elongated lower caudal fin ("sword") in the swordtail.

Aquarium Tanks

Fish were grown in four conventional glass-walled aquariums, each with a water surface of 44 cm by 24 cm, a water depth of 19 cm, and a volume of 20 liters. Inside each tank was an air-stone and a fiber-charcoal filter. Tanks were placed in a row with their longer axes parallel, and lettered A, B, C, D from left to right.

Tanks A and C were for juvenile and adult fish together. They each had a refuge in the left front corner for the escape and subsequent removal of recently born fish, or "fry." This refuge was formed with a fence consisting of 21 cm by 3 mm glass rods placed 1.5 mm apart, enclosing a right isosceles triangular space of 15 cm hypotenuse.

Although guppies could survive and achieve population growth in the above-described tanks, preliminary experiments showed this not to be true for the swordtails. Tanks B and D were therefore provided as "nurseries" for the temporary relocation of newborn young from tanks A and C, respectively. The juveniles were placed back in tanks A and C when they had grown to such size that they would no longer pass through a sieve consisting of 3-mm plastic rods placed 2 mm apart, thus making them recruits to the fishable stock.

Food and Feeding

A diet previously developed for guppies (Silliman 1968) was fed to all fish (Table 1). The food *Artemia* nauplii, however, requires special mention. The original intention was to feed the fish in the nursery tanks one-half the amount fed those in the adult tanks. The weight of nauplii produced was mistakenly believed to be directly proportional to amount of *Artemia* eggs placed in the culture beakers and, therefore, one-half the amount of eggs placed in the beakers for the adult tanks was placed in those for the nursery tanks. Production tests (Table 2) based on duplicate hatchings produced under standard conditions, however, showed production not to be proportional to the amount of eggs. Amounts of eggs inserted were kept the same, nevertheless, on the chance that unhatched eggs were eaten (observed on one occasion).

Artemia nauplii provided so small a proportion (1/100%) of the total diet that the lack of proportion noted above would have no significant effect on total food intake. The small amount of living food provided by the nauplii was regarded in the same sense as vitamins in human nutrition: as something required in small amounts for good health, but not furnishing a significant proportion of total food intake by weight. It is pertinent to note that the smallest number of nauplii (1,500) indicated by any of the tests (Table 2) would provide over four nauplii per fish for the largest

TABLE 1.—Food placed in tanks, grams.

Dates included	3-wk periods	Day of week	Adult tanks Dry[1]	Frozen *Artemia*	*Artemia* nauplii	Total	Nursery tanks Dry[1]	Frozen *Artemia*	*Artemia* nauplii	Total
25 Oct. 1965	0-71	Sun.	0.1	—	—	0.1	0.05	—	—	0.05
to		Mon.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
6 Dec. 1969		Tues.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Wed.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Thurs.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Fri.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Sat.	0.1	—	(2)	0.1	0.05	—	(2)	0.05
		Total	0.7	5.0	—	5.7	0.35	2.5	—	2.85
7 Dec. 1969	71-124	Sun.	0.1	—	—	0.1	0.05	—	—	0.05
to		Mon.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
1 Jan. 1973		Tues.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Wed.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Thurs.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Fri. A.M.	0.1	1.0	(2)	1.1	0.05	0.5	(2)	0.55
		Fri. P.M.[3]	0.1	—	(2)	0.1	0.05	—	(2)	0.05
		Total	0.7	5.0	—	5.7	0.35	2.5	—	2.85

[1]Tropical fish food.
[2]Hatch from 0.4 g (adult) or 0.2 g (nursery) of eggs (Table 2). Silliman and Gutsell (1958) found that the hatch from 0.4 g of eggs weighed 0.125 mg. Test hatches of nauplii were not proportional in weight to the amount of eggs used (Table 2), and since the total weight would be only 1/100% of the diet, no weight is indicated in the table.
[3]This was combined with the Friday A.M. feeding in 35 out of 161 wk and with the Sunday feeding once.

TABLE 2.—*Artemia* production tests. All 48-h hatches at 24°C in 800 ml 3% salt water. Counts from 20 samples for each test. Samples were 0.3 ml, withdrawn by pipette from vigorously stirred cultures killed in 0.75% formaldehyde, and replaced.

Test dates	Source of eggs[1]	Wt of eggs (g)	Mean no. in samples Nauplii	Eggs[3]	Est. 1,000s in culture[2] Nauplii	Eggs[3]
1970:						
1/28-30	A	0.2	2.10	7.50	5.6	20.0
1/28-30	A	0.4	1.45	18.05	3.9	48.1
3/23-25	A	0.2	1.85	6.95	4.9	18.5
3/23-25	A	0.4	2.05	16.30	5.5	43.5
4/13-15	B	0.2	1.75	10.35	4.7	27.6
1971:						
5/ 3- 5	B	0.4	0.55	32.95	1.5	87.9
5/17-19	B	0.2	0.85	23.30	2.3	62.1
5/24-26	C	0.2	3.50	30.70	9.3	81.9
10/ 4- 6	C	0.2	3.65	33.40	9.7	89.1
11/29-12/1	C	0.2	2.75	34.30	7.3	91.5
1972:						
5/15-17	C	0.2	6.85	27.80	18.3	74.1
11/13-15	C	0.2	2.75	36.10	7.3	96.3

[1]All were commercial suppliers.
[2]Sample numbers times 800/0.3.
[3]Includes shells (from hatched eggs) and unhatched eggs.

number of fish recorded in any tank (343 guppies in tank C during the last week of 3-wk period 65).

Dry food was placed on the surface of the water and sank slowly if not eaten immediately (as occurred with large populations). Frozen food sank and was eaten as it thawed. *Artemia* nauplii were hatched in 800-ml glass beakers (Table 2). The entire water mass, including shells and unhatched eggs, was poured through a cloth filter which was rinsed with freshwater and then rinsed into the fish tanks.

Cleaning and Treatment

Detritus including uneaten food (none in large populations) was siphoned daily from the tanks onto a cloth filter and the siphoned water returned to the tanks. Once a week all the water was removed from the tanks and one-half the volume was replaced with tap water aged for 1 wk. At this time the tanks and their equipment were thoroughly cleaned, and the filter fiber and charcoal were replaced. Also, fish in the adult tanks were treated for 15 min in a 1:200 solution of a commercial aquarium disinfectant "Fungistop."[2]

Water Characteristics

Water temperature in tanks A and D (Tables 3, 4; Figure 1) was recorded daily (Saturday excluded during 3-wk periods 71-124). These end tanks were chosen to reveal any temperature gradient that might exist. Although there was a slight tendency for tank D to vary from tank A (Figure 1), the differences were mostly less than 1°C and are not believed to have significantly affected population growth. It will be shown in the section on oscillatory fluctuation that deviations of population size from the theoretical were not correlated with tank temperature.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 3.—Mean temperatures, °C, 3-wk periods, competing populations. Daily readings (21) to period 70, Sunday to Friday (18) from period[1] 72 on.

	Tank			Tank	
Period	A	D	Period	A	D
0	[2]24.2	[2]24.6	38	23.6	23.9
1	24.5	24.6	39	23.8	24.2
2	24.9	24.7	40	23.9	24.4
3	24.6	24.5	41	23.5	23.8
4	24.7	24.5	42	23.3	23.5
5	24.6	24.6	43	24.1	24.4
6	24.5	24.6	44	24.5	24.7
7	24.7	24.8	45	24.1	24.7
8	24.5	24.8	46	24.9	25.2
9	24.4	24.6	47	24.9	25.1
10	24.4	24.7	48	24.3	23.5
11	24.6	24.8	49	24.8	24.9
12	25.6	25.6	50	24.1	24.3
13	25.9	25.9	51	24.1	24.4
14	26.4	26.0	52	23.7	23.9
15	25.6	25.7	53	23.7	23.8
16	25.5	25.4	54	23.5	23.6
17	25.0	25.1	55	23.4	23.9
18	25.0	24.8	56	23.7	23.9
19	25.6	25.1	57	23.9	23.8
20	26.4	25.1	58	23.6	23.6
21	26.2	24.9	59	23.5	23.7
22	26.0	25.5	60	23.2	23.5
23	25.9	24.8	61	24.3	24.5
24	25.2	24.5	62	24.5	24.5
25	25.6	24.6	63	24.9	24.9
26	26.0	25.0	64	24.7	24.9
27	25.7	25.2	65	23.8	23.8
28	26.4	25.8	66	23.9	23.8
29	26.2	25.9	67	24.4	24.3
30	26.3	25.8	68	21.5	21.4
31	25.9	26.0	69	24.0	24.0
32	24.5	25.1	70	24.0	23.8
33	23.8	24.5	71	[1]23.9	[1]23.8
34	23.1	23.8	72	23.7	23.4
35	23.7	23.6	73	23.8	23.5
36	23.4	23.8	74	23.9	23.5
37	23.7	23.8	75	23.9	23.5

[1]One Friday and two Saturday readings missing, period 71.
[2]Based on 1 wk only.

TABLE 4.—Mean temperatures, °C, 3-wk periods, independent populations. Sunday to Friday readings (18).

	Tank			Tank	
Period	A	D	Period	A	D
79	24.6	24.1	102	24.5	24.3
80	23.5	23.2	103	24.7	24.2
81	25.0	24.5	104	24.5	23.6
82	24.7	24.3	105	24.4	23.6
83	24.4	24.2	106	24.3	23.5
84	24.5	24.5	107	24.1	23.8
85	24.3	24.3	108	24.2	23.8
86	23.9	23.7	109	24.3	23.9
87	24.2	23.8	110	24.4	23.9
88	24.2	23.6	111	24.3	23.8
89	24.6	23.9	112	24.5	23.9
90	24.6	23.9	113	24.6	23.9
91	24.6	24.2	114	24.6	23.9
92	24.5	23.8	115	24.1	23.5
93	24.5	23.9	116	25.8	25.2
94	24.6	23.7	117	25.6	24.9
95	24.2	24.0	118	25.4	24.7
96	24.3	23.9	119	24.9	24.1
97	24.2	23.6	120	24.5	23.6
98	24.4	24.2	121	24.7	23.6
99	25.6	25.4	122	24.1	22.9
100	25.7	25.4	123	24.5	23.3
101	24.7	24.5	124	[1]24.7	[1]24.2

[1]Last three readings missing.

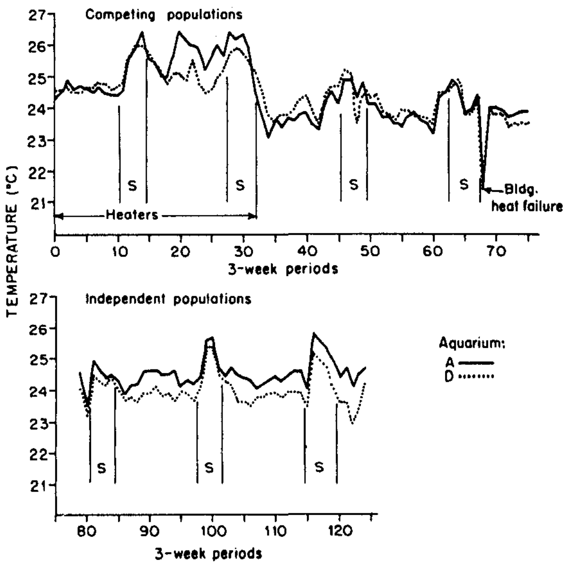

FIGURE 1.—Water temperatures (3-wk means). "S" indicates summer periods (approximately 20 June to 20 September).

Heaters were placed in tanks during periods 1-32 (Figure 1) but caused excessive temperature fluctuation and one instance of mortality from a nonfunctioning thermostat. During periods 33-174 the tank water was at room temperature. This was thermostatically controlled except that no cooling was available in the summer. Summer temperatures were thus somewhat higher than during the balance of the year (Figure 1), but the change was the same for all tanks.

Measurements of dissolved oxygen and carbon dioxide concentrations and pH were made at irregular intervals during the course of the experiment (Table 5). All O_2 readings were within or above the 3-5 ppm range considered satisfactory for warmwater fishes by Lewis (1963), and the CO_2 and pH readings were within the range he considered safe (CO_2<30 ppm., pH 5.0-9.0).

Light was provided from overhead fluorescent fixtures with standard tubes to period 11. After period 11, pink tinted tubes were used.

Handling, Enumeration, Exploitation, and Weighing

Areas behind the refuge fences described under "Aquarium Tanks" were inspected daily. If any newborn fish were found there or in other corners of the tanks, they were removed by netting or siphoning, counted, and placed in the nursery

TABLE 5.—Water condition on selected dates.

Dates		3-wk period	O_2, ppm. Tank A	O_2, ppm. Tank D	CO_2, ppm. Tank A	CO_2, ppm. Tank D	pH Tank A	pH Tank D
1968:								
Aug.	9	48	7.0	7.0	—	—	—	—
	16	48	6.0	—	—	—	—	—
	29	49	6.6	6.4	10	10	6.9	6.9
Sept.	6	49	6.2	6.8	—	—	—	—
	13	49	6.2	6.4	—	—	—	—
	20	50	6.4	6.4	10	10	—	—
	27	50	6.4	6.4	—	—	—	—
Oct.	4	50	6.4	6.4	—	—	—	—
	11	51	6.0	6.4	—	—	—	—
	18	51	6.4	6.8	—	—	—	—
	25	51	6.2	6.4	—	—	—	—
Nov.	8	52	6.0	6.6	—	—	—	—
	15	52	6.4	7.2	—	—	—	—
	28	53	6.4	7.0	—	—	—	—
Dec.	6	53	6.4	6.8	—	—	—	—
	13	54	6.4	6.6	—	—	—	—
	26	54	6.4	6.8	—	—	—	—
1969:								
Jan.	2	55	6.4	7.0	—	—	—	—
Sept.	17	67	6.6	6.6	10	10	8.0	8.0
Oct.	2	68	7.8	7.8	—	—	—	—
	9	68	7.4	8.2	—	—	—	—
	23	69	6.6	7.6	—	—	—	—
	30	69	6.2	7.6	—	—	—	—
Dec.	4	71	6.8	7.4	10	10	8.0	8.7
1971:								
Feb.	25-26	92	6.6	8.2	10	10	8.0	8.0
1972:								
Mar.	23	111	5.0	7.2	10	10	8.5	8.0

tanks. At the time of weekly cleaning, the water in the nursery tanks was poured through the sieve also described under Aquarium Tanks. Any fish remaining on the sieve were placed back in the adult tanks.

Fish were counted and weighed weekly during periods 0-71. During periods 71-124, this was done only at the approximate brood intervals of the fish, which were 3 wk for the guppy and 4 wk for the swordtail. Fish were counted simply by netting them from one container to another. Counts were categorized into "immature" (those whose sex could not be determined from external inspection), male, and female. Fry and juveniles were counted when moved between adult and nursery tanks. Dead fish found in tanks were recorded as mortalities.

Exploitation was done at the time of counting. To apply an exploitation rate of $1/n$, each nth fish was removed (n was always an integer). This was applied equally to juveniles and adults, but not at all to fish in the nursery tanks.

Population and catch weights were also determined at the time of counting. Fish were drained and placed in a previously weighed container of water. Total weight was measured and fish weight obtained by subtracting the tare.

COURSE OF POPULATIONS

Independent Populations

Although chronologically the competing populations preceded the independent populations, the more logical order of presentation is to deal with the independent populations first. This arrangement will be followed in the remainder of the report.

Separate populations of guppies and swordtails were started on 19 May 1970 (3-wk period No. 79). Each of these was permitted to grow for an initial period of about 1 yr (Figures 2, 3) before exploitation was begun. Even though complete equilibrium had not been reached, exploitation was started at 25% per brood interval (3 wk) for the guppy and 10% per interval (4 wk) for the swordtail. The lower rate for the swordtail was based on previous experience showing lower productivity for that species. Initial rates were maintained during weeks 289-334 for the guppy and 290-334 for the swordtail. Final rates were 33.3% for the guppy (weeks 337-373) and 16.7% for the swordtail (weeks 338-374). Responses were in accord with expectations for the guppy (Figure 2) and the early swordtail history, but there was an increase in both number and weight in the swordtail in the last five brood intervals (Figure 3). This anomaly will be discussed under "Oscillatory Fluctuation."

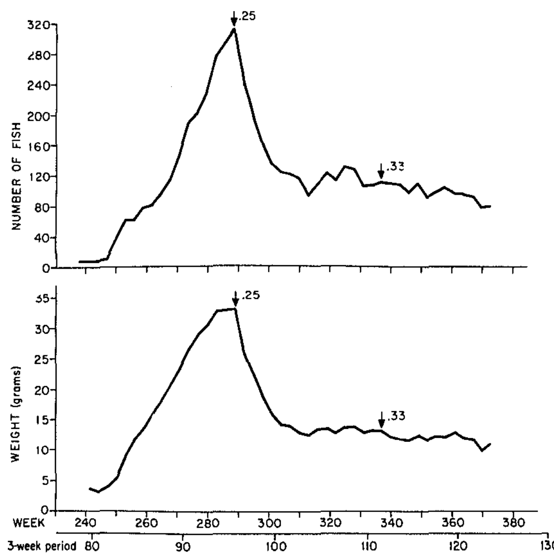

FIGURE 2.—Course of independent guppy population. Numbers indicate target exploitation rates.

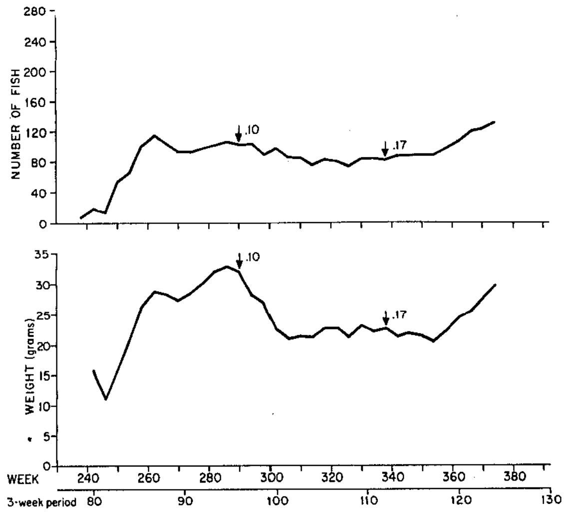

FIGURE 3.—Course of independent swordtail population. Numbers indicate target exploitation rates.

Competing Populations

The two mixed populations, each composed of both guppies and swordtails, were started 24 October 1965 (week 0). Three-week period 0 started with week 1, since weights were not recorded in week 0.

In the control (unexploited) pair of populations (Figure 4), both species grew for an initial period of about 30 wk. The swordtail population then began to decline and disappeared at week 129. This will be discussed in the section on competitive exclusion. Extinction of the swordtail was followed by a large oscillatory fluctuation in the guppy (about -39% to +26% of the asymptotic level), which will be discussed in the section on such fluctuations.

Initial growth in the test (exploited) pair was similar to that in the control pair (Figures 4, 5). Exploitation was started first on the swordtail

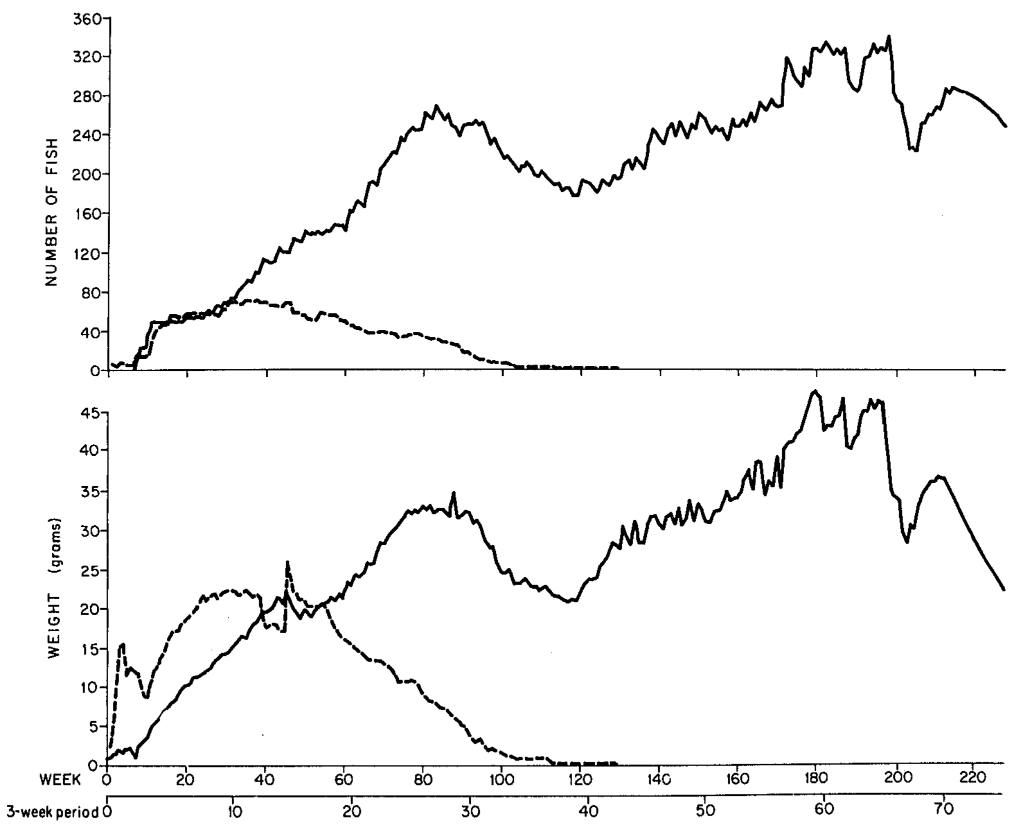

FIGURE 4.—Course of competing populations, control pair. Solid line, guppy; broken line, swordtail.

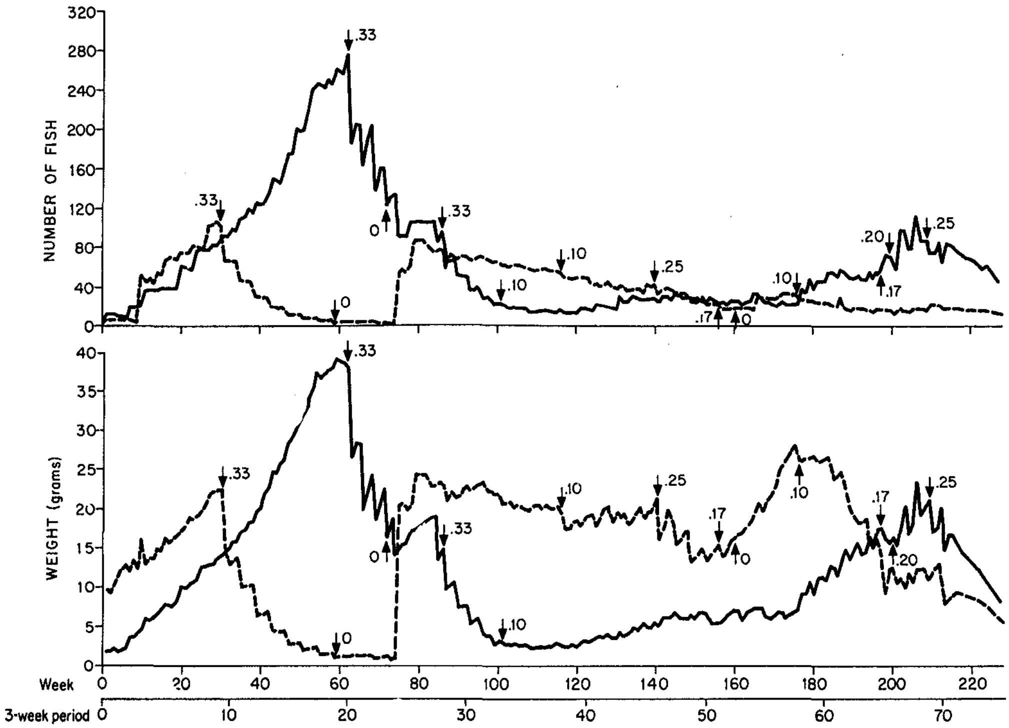

FIGURE 5.—Course of competing populations, test pair. Solid line, guppy; broken line, swordtail. Numbers indicate target exploitation rates.

(week 30), under the mistaken impression that the greater biomass then achieved by the swordtail indicated a greater productive capability. Exploitation produced a rapid decline in the swordtail to a low population level (Figure 5). Cessation of swordtail exploitation at week 59 and initiation of guppy exploitation at week 62 did not lead to recovery of the swordtail, in spite of a drastic decline in guppy abundance (Figure 5).

By week 74, it became apparent that the swordtail would require a lengthy period for recovery, even if guppy abundance were further reduced. To accelerate the study of exploitation, the populations were reconstructed during weeks 74-85, using fish from exploited populations that had been placed in a reserve tank. After reconstruction, the populations approximated fairly closely their number and weight at the time exploitation was started (compare week 85 with week 30 in Figure 5). Exploitation rates after week 85 were adjusted to keep both the guppy and swordtail at productive levels while trying as wide a range of pairs of exploitation rates as possible.

RECRUITMENT RELATIONS

Juvenile fish were counted both when removed from and returned to the adult tanks; it was thus possible to obtain a measure of recruitment. Numbers were converted to weights by use of factors (mean weights per fish) based on weighings of the juveniles: guppy, 0.0656 g based on 1,417 fish in 126 weighings spread over 199 wk; swordtail 0.0678 g, 337, 61, 196, respectively. At the beginning of the experiments, when few fish were in the nursery tanks, it was possible to distinguish individual groups of recruits by size, count them, and thereby estimate the "reproductive lag" from birth to recruitment. The lag was found to be approximately one brood interval (guppy, 3 wk; swordtail, 4 wk) for each species. In constructing the stock-recruitment relations, the recruitment for each brood interval was compared with the mean stock in the adult tanks during the preceding brood interval. During periods of exploitation, the catch was subtracted from the stock at the beginning of the interval.

Because of the great variability in the recruitment data, group means were used for both species. The basis of the grouping was an interval of 5 g (0.0-4.9, 5.0-9.9, etc.) in the adult tank stock weight. Data used in calculating recruitment curves were pairs consisting of the mean adult stock weight and mean recruit weight for each group.

The stock-recruitment data for the guppy (Figure 6) could be fitted by a Ricker (1958) curve of the type:

$$R_{N+1} = a\bar{S}_N \exp(-b\bar{S}_N),$$

where R_{N+1} is recruitment during brood interval $N+1$ and $\bar{S}_N$ is mean adult stock during brood interval N, both in grams. Fitting of the curves shown (Figure 6) was by least squares to the rectilinear logarithmic form of the relation:

$$\log_e R_{N+1}/\bar{S}_N = \log_e a - b\bar{S}_N.$$

Values of the constants are given in Table 6.

Data for the swordtail (Figure 7) did not conform well to the Ricker relation, as shown by the parabolic nature of the points for the competing stock, and were fitted better by a simple parabola:

$$R_{N+1} = a\bar{S}_N - b\bar{S}_N^2,$$

symbols as above. Curves shown (Figure 7) were fitted directly to the grouped data by least squares. Values of the constants are in Table 6.

Comparison of results for the two species (Figures 6, 7; Table 6) reveals both similarities and differences. Despite the different types of recruitment curves, there is the suggestion in both species that maximum recruitment occurs at intermediate rather than very high or very low adult stock levels, as has been observed for other species (Ricker 1958; Silliman 1969b). Also, recruitment for both species was depressed by competition. However, the depression was greater for the swordtail, as shown in the comparison of standardized recruitment (last column, Table 6). This is in keeping with the finding to be reported below that the guppy is more productive than the swordtail. This finding is also supported by the fact that guppy recruitment was greater than swordtail recruitment in both independent and competing situations (last column, Table 6).

Some additional information on recruitment was obtained from a study of count discrepancies. Because all additions to and removals from the adult tanks were recorded, it was possible to calculate an "expected" count (the previous count

TABLE 6.—Stock-recruitment data comparing populations of the two species with data from the relations: guppy, $R_{N+1} = a\bar{S}_N \exp(-b\bar{S}_N)$; swordtail, $R_{N+1} = a\bar{S}_N - b\bar{S}_N^2$.

Species and situation	No. of pairs of observations[1]	Constants, per brood interval a	Constants, per brood interval b	Recruitment at value of $\bar{S}_N$ for R_{max}, independent situation (g): Per brood interval[2]	Per week
Guppy:					
Independent	76	0.343	0.061	2.07	0.69
Competing	117	0.092	0.028	0.95	0.32
Swordtail:					
Independent	32	0.229	0.007	1.90	0.48
Competing	86	0.068	0.003	0.42	0.10
Total	311				

[1]In fitting curves, data were grouped by 5-g intervals of $\bar{S}_N$.
[2]Guppy, 3 wk; swordtail, 4 wk.

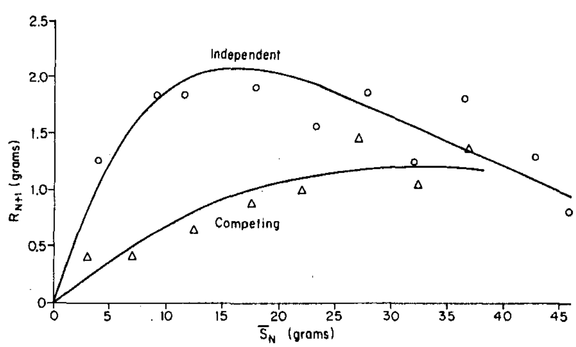

FIGURE 6.—Stock-recruitment relation for the guppy. Data grouped by 5-g intervals of $\bar{S}_N$. N is the number of the 3-wk brood interval.

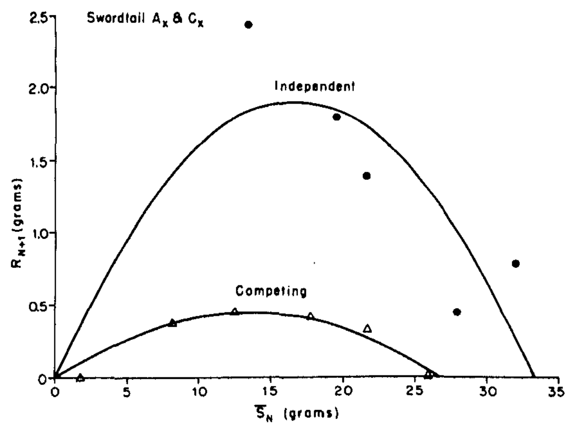

FIGURE 7.—Stock-recruitment relation for the swordtail. Data grouped by 5-g intervals of $\bar{S}_N$. N is the number of the 4-wk brood interval.

plus recruits and minus catch and deaths) to be compared with the actual counts made. Some of the observed discrepancies were no doubt due to unobserved deaths (dead fish eaten by others before seen) or to errors in counting. That some errors occurred is not surprising. Each expected-actual comparison involved as many as 17 separate counts. During each main count while exploiting the stocks the counter had to keep in mind the total number, the number caught, the state of maturity of each fish, and the sex of each mature fish.

The distribution of discrepancies for selected (to provide representative data) periods (Table 7)

TABLE 7.–Count discrepancies for selected periods: swordtail, April 1970 to June 1972; guppy, March 1970 to June 1972. Values represent "expected" number subtracted from the actual count.

Discrepancy	Swordtail	Guppy
−20	—	1
−12	—	1
−11	—	—
−10	3	1
−9	—	2
−8	2	1
−7	2	1
−6	1	1
−5	3	—
−4	3	2
−3	3	1
−2	1	3
−1	2	3
0	1	2
+1	1	3
+2	—	1
+4	—	1
+5	—	1
+6	—	3
+7	—	1
+8	—	2
+9	1	—
Total	23	31

shows that negative discrepancies (actual less than expected) exceed the positive for both swordtails and guppies. This no doubt arose from the unrecorded natural mortalities mentioned above. The two positive discrepancies for the swordtail probably represent counting errors. For the guppy, however, the fairly large proportion of positives exceeding three fish suggests that unrecorded recruitment occurred. Apparently some of the guppy "fry" escaped detection, even though a thorough search of the tanks was made. This phenomenon is in keeping with the observed greater hardiness of the guppy, and suggests that the superiority in recruitment for the guppy was even greater than indicated in the stock-recruitment relations reported above.

SIMULATION MODEL

Mathematical Derivation

Data of population weight reflect growth of individual fish as well as recruitment and mortality, and all of the analyses below will be in terms of weight. Development of the formulae requires a fairly extensive list of symbols, which are defined below.

P = Total population weight in grams.
t = Time from start, in 3-wk periods.
X = Fishing effort in arbitrary units.
q = Catchability coefficient.
F = Instantaneous rate of fishing mortality ($=qX$).
m = Three-week rate of fishing mortality.
G = Constant of the Gompertz growth curve.
k = Constant of the Gompertz growth curve and of the Fox (1970) population model.
c, h, j = Empirical constants.

Adding a term for the effect of fishing to the formulae of Volterra (1928) gives a pair of differential equations:

$$dP_1/dt = f(P_1) - f(P_2) - f(X_1), \qquad (1)$$
$$dP_2/dt = f(P_2) - f(P_1) - f(X_2). \qquad (2)$$

In these equations, the first term of the right hand side is for population growth; the second, for competition; and the third, for the effect of fishing. The development is exactly parallel for the two equations, and only that for Equation (1) will be outlined below.

For the growth term Volterra (1928) used $f(P_1) = j_1P_1 - h_1P_1^2$. This is the logistic growth curve, which requires symmetrical population growth. Growth for the guppy under fishing (equilibrium yield) was shown by Silliman and Gutsell (1958) and Silliman (1968) to be distinctly asymmetrical. The Gompertz (1825) curve, introduced as a population yield model by Fox (1970), is suitable for asymmetrical growth and will be shown in the section on determination of constants to be suitable for initial population growth in both the guppy and the swordtail. This is expressed:

$$P_t = P_0 \exp\left[G - G\exp(-kt)\right]. \qquad (3)$$

It can be shown by mathematical analysis of

Equation (3) that the limit $P_\infty = P_0 \exp(G)$, and by substituting this in Equation (3), differentiating and taking logs a growth term may be derived for Equation (1):

$$f(P_1) = P_1 k_1 (\log_e P_{1\infty} - \log_e P_1). \qquad (4)$$

For the competition term, Volterra (1928) used $f(P_2) = c_1 P_1 P_2$. Preliminary experimentation showed that this term was unsatisfactory for the guppy-swordtail experiments, since it was impossible to obtain even a reasonably good fit using it. I also experimented with $f(P_2) = c_1 (P_1 + P_2)$ on the theory that the sum of the populations, rather than their product, might be controlling, but it was equally unsatisfactory. The most suitable term proved to be simply:

$$f(P_2) = c_1 P_2. \qquad (5)$$

This term agrees with the reasonable idea that the competitive effect on one population is proportional to the size of the other.

For the fishing term I adopted from Fox (1970):

$$f(X_1) = q_1 X_1 P_1 = F_1 P_1. \qquad (6)$$

Substitution of Equations (4), (5), and (6) in Equation (1) provides the model for the first population:

$$dP_1/dt = P_1 k_1 (\log_e P_{1\infty} - \log_e P_1) - c_1 P_2 - F_1 P_1. \quad (7)$$

By exactly parallel derivation the model for the second population is:

$$dP_2/dt = P_2 k_2 (\log_e P_{2\infty} - \log_e P_2) - c_2 P_1 - F_2 P_2. \quad (8)$$

Thus the model for the competing populations represents a modification of the Fox (1970) exponential surplus-yield model, with the addition of a term for competition.

Determination of Constants

Growth data were obtained from the independent populations. Gompertz (1825) curves were fitted to the initial growth period for both species (Figures 8, 9), using the analog computer method of Silliman (1967). Asymptotic levels were 38.7 g for the guppy and 33.7 g for the swordtail. These values were used for the zero exploitation levels in fitting the Fox (1970) model. The zero points plus two other exploitation rates (relatively stable periods considered to be equilibrium points: guppy, weeks 316-334 and 355-373, Figure 2; swordtail, 322-334 and 342-354, Figure 3) gave three fitting points for each species (Figures 10,

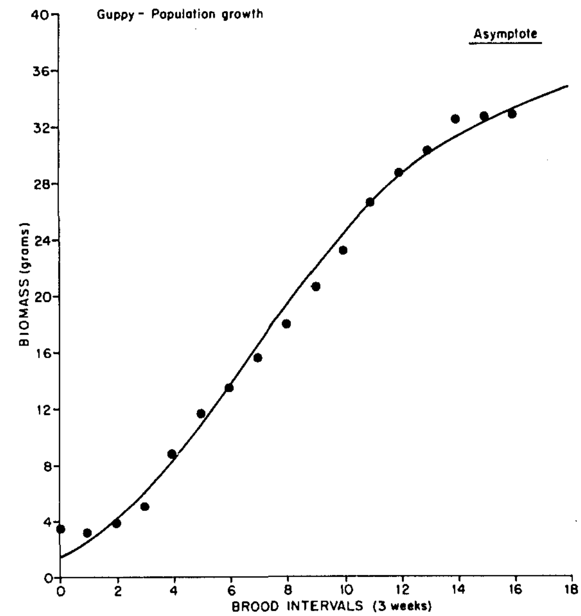

FIGURE 8.–Initial growth for the independent population of the guppy, with fitted Gompertz curve.

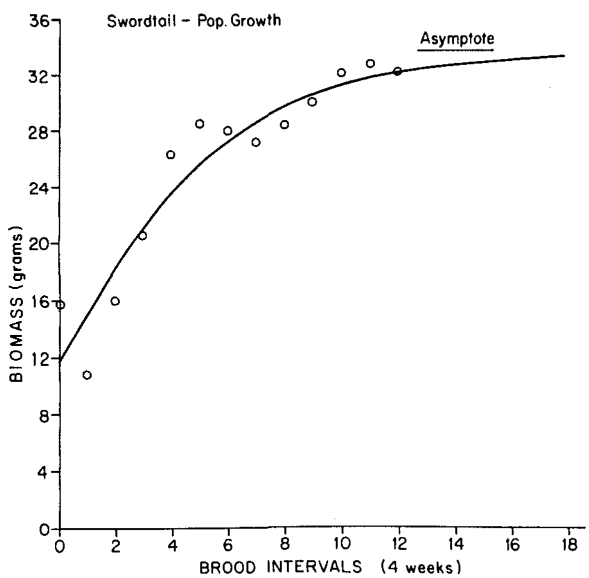

FIGURE 9.–Initial growth for the independent population of the swordtail, with fitted Gompertz curve.

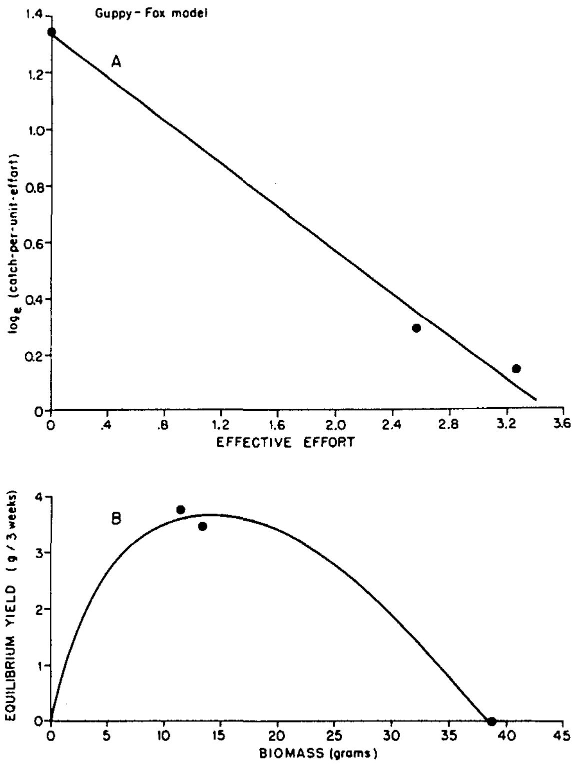

FIGURE 10.—Fox (1970) model fitted to yield data for the guppy. Exploitation rates are 0.000, 0.257, and 0.326 per 3-wk period (left-to-right in upper panel, reversed in lower panel).

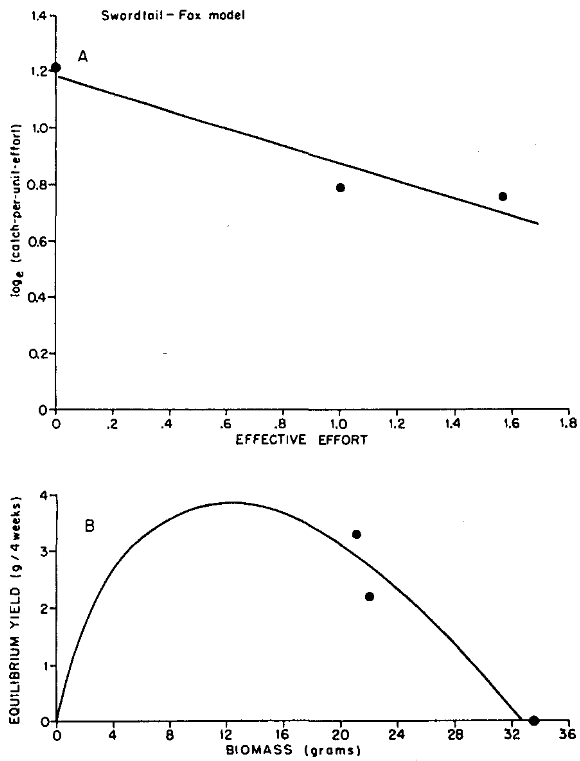

FIGURE 11.—Fox (1970) model fitted to yield data for the swordtail. Exploitation rates are 0.000, 0.100, and 0.157 per 4-wk period (left-to-right in upper panel, reversed in lower panel).

11). Effective exploitation rates shown varied slightly from the "target" rates because of lack of infinite divisibility of the populations and because of errors. The fitted Fox models yielded values of k of 0.260 per 3 wk and 0.321 per 4 wk for the guppy and swordtail, respectively. Comparable values for the Gompertz curves were 0.193 and 0.260. It was considered more appropriate to use the values from the Fox model because the analyses were based on that model. To place the swordtail on the same time scale as the guppy, the value of k was multiplied by ¾, or ¾(0.321) = 0.241.

Data of catch and biomass for the competing populations (Table 8) were used to calculate exploitation rates. Again the effective rates varied from the target rates as explained in the preceding paragraph. Also, it was again necessary to adjust the effective rates for the swordtail to the same time scale as the guppy. This was done by the formula $m = 1 - (1 - m')^{3/4}$, where m' is the unadjusted rate. Finally, for use in the differential equations, the 3-wk rates must be converted to instantaneous rates. The formula is: $F = -\log_e(1 - m)$, from Ricker (1958).

The use of instantaneous exploitation rates as employed herein assumes that P declines continuously, whereas the experimental technique was to remove all the fish at the beginning of the brood interval. It can readily be shown, however, that the reduction in population resulting from the application of m at the beginning of a period is exactly the same as the application of the equivalent F throughout the period, even if both are superimposed on a constant natural mortality.

A summary of all the constants used in applying Formulae (7) and (8) to biomass data from the competing populations is given in Table 9. Where both unadjusted and adjusted data are shown, the latter were the ones used.

Application of the Model

Using standard analog computer techniques (Ashley 1963) values of guppy and swordtail

TABLE 8.—Exploitation of competing populations. Rates are per brood interval: guppy, 3 wk; swordtail, 4 wk.

Week	Target rate	Effective rate	Biomass (g)	Catch (g)
	Guppy			
62	0.333	0.335	38.0	12.1
65			28.3	11.1
68			24.2	7.7
71			22.5	7.0
86	0.333	0.344	14.8	5.2
89			10.4	3.7
92			7.4	2.4
95			5.9	2.0
98			3.9	1.3
101	0.100	0.113	3.0	0.4
104			2.8	0.4
107			2.7	0.5
110			2.3	0.1
113			2.5	0.1
116			2.6	0.2
119			2.6	0.1
122			3.2	0.3
125			3.5	0.1
128			4.0	0.7
131			4.2	0.5
134			4.6	0.4
137			5.3	0.4
140			5.4	0.3
143			6.2	0.6
146			6.2	0.4
149			6.3	0.7
152			6.8	0.7
155			5.4	0.4
158			6.2	0.4
161			6.8	0.8
164			6.8	0.5
167			7.1	0.8
170			6.2	0.6
173			6.1	0.7
[1]175			6.7	2.0
179			10.3	1.2
182			11.0	1.0
185			12.2	1.1
188			14.5	1.5
191			15.5	3.4
194			16.2	1.8
197	0.200	0.223	17.5	6.4
200			16.3	2.5
203			20.2	3.6
206			23.1	4.7
209	0.250	0.259	21.0	5.3
212			19.9	5.1
215			16.6	4.5
218			14.1	3.6
221			12.4	3.5
224			10.6	2.8
227			8.3	1.9
		Swordtail		
30	0.333	0.346	22.3	8.0
34			13.5	3.9
38			10.2	4.0
42			6.7	2.6
46			4.3	1.5
50			2.8	0.8
54			2.2	0.8
58			1.5	0.4
116	0.100	0.112	19.0	2.6
120			18.2	2.4
124			19.1	1.3
128			20.2	2.5
132			19.2	2.3
136			20.1	1.9
140	0.250	0.254	21.2	5.9
144			18.8	4.9
148			16.9	4.5
152			15.0	3.0
156	0.100	0.112	15.2	1.7
176	0.100	0.088	26.2	1.2
180			26.6	1.2
184			26.5	1.5
188			22.0	2.2
192			18.0	4.0
[2]197			14.4	0.2
200			12.1	1.0
204			11.5	1.3
208			12.1	1.6
212			12.8	1.7
216			9.3	1.0
220			8.6	0.8
224			7.5	0.6
228			5.6	0.5

[1]Should have been 176.
[2]Should have been 196.

biomass were simultaneously generated using Formulae (7) and (8). A number of trials were made on data from the control populations (Table 10) to find the most suitable values of the competition coefficients c_1 and c_2. Values of $c_1 = 0.071$ (guppy) and $c_2 = 0.120$ (swordtail) produced curves (Figure 12) which fitted reasonably well except for the oscillatory variations to be discussed below.

TABLE 9.—Constants used in fitting simulation model to biomass data for competing populations.

Guppy: k_1 = 0.260 (3-wk), $P_{1\infty}$ = 38.2 g

Swordtail: k_2 = 0.321 (4-wk), k_2 = 0.241 (3-wk), $P_{2\infty}$ = 32.7 g

3-wk period	m_1 Target	m_1 Effective	F_1	3-wk period	m_2 Target	m_2 Effective	m_2 Adjusted	Adjusted F_2
20-23	0.333	0.335	0.408	9-19	0.333	0.346	0.273	0.319
28-32	0.333	0.344	0.422	38-45	0.100	0.112	0.085	0.088
33-64	0.100	0.113	0.120	46-50	0.250	0.254	0.197	0.219
65-68	0.200	0.223	0.252	51 only	0.100	0.112	0.085	0.088
69-75	0.250	0.259	0.300	58-75	0.100	0.088	0.067	0.069

TABLE 10.—Biomass levels, 3-wk means, control populations.

Period	Weight (g) Guppy	Weight (g) Swordtail	Period	Weight (g) Guppy	Weight (g) Swordtail
0	1.6	8.2	38	21.0	0.3
1	2.1	13.2	39	21.4	0.3
2	2.4	10.6	40	23.4	0.3
3	4.5	10.5	41	25.0	0.3
4	6.6	14.0	42	27.8	0.3
5	8.2	17.0	43	29.0	0.0
6	10.1	18.5	44	29.1	0.0
7	11.5	20.4	45	30.2	0.0
8	12.6	21.4	46	30.8	0.0
9	14.0	21.7	47	31.4	0.0
10	15.2	22.1	48	31.6	0.0
11	16.6	22.0	49	32.7	0.0
12	18.6	19.4	50	31.4	0.0
13	19.8	17.8	51	32.5	0.0
14	21.0	17.3	52	34.1	0.0
15	20.4	23.5	53	35.2	0.0
16	19.3	20.9	54	37.0	0.0
17	19.7	20.3	55	36.4	0.0
18	20.9	19.5	56	36.5	0.0
19	21.4	16.9	57	40.7	0.0
20	23.4	15.4	58	42.6	0.0
21	25.1	14.2	59	[1]47.3	0.0
22	27.3	13.4	60	44.1	0.0
23	29.1	12.8	61	43.9	0.0
24	30.8	11.1	62	42.4	0.0
25	32.3	10.8	63	42.7	0.0
26	32.6	9.4	64	45.5	0.0
27	32.7	8.0	65	44.4	0.0
28	32.2	7.2	66	34.4	0.0
29	32.7	5.7	67	29.7	0.0
30	32.0	4.0	68	32.5	0.0
31	30.1	3.0	69	35.8	0.0
32	27.1	2.0	70	36.7	0.0
33	24.8	1.5	71	[2]34.1	0.0
34	23.1	1.0	72	[2]30.9	0.0
35	23.3	0.9	73	[2]28.0	0.0
36	22.5	1.0	74	[2]25.5	0.0
37	21.9	0.6	75	[1,2]22.8	0.0

[1]Based on two observations.
[2]Based partly on interpolation.

TABLE 11.—Biomass levels, 3-wk means, test populations.

Period	Weight (g) Guppy	Weight (g) Swordtail	Period	Weight (g) Guppy	Weight (g) Swordtail
0	2.0	9.6	38	2.6	18.7
1	2.0	[1]12.6	39	2.5	17.9
2	3.8	13.0	40	3.1	18.4
3	5.6	14.2	41	3.4	18.5
4	6.8	14.3	42	3.7	19.5
5	7.6	16.0	43	3.8	19.2
6	9.4	17.2	44	4.4	18.5
7	10.6	18.9	45	4.9	19.5
8	12.6	20.5	46	5.2	18.9
9	13.4	22.3	47	6.2	18.6
10	15.1	13.4	48	6.3	15.9
11	16.6	11.1	49	6.1	14.5
12	18.7	8.9	50	6.6	14.0
13	21.5	6.6	51	5.4	14.5
14	25.0	4.3	52	6.1	14.7
15	27.9	3.1	53	6.5	16.5
16	30.8	2.5	54	6.8	18.3
17	35.4	2.1	55	6.8	20.6
18	37.1	1.5	56	6.2	22.7
19	38.5	1.2	57	6.4	[1]26.0
20	34.3	1.1	58	7.5	26.8
21	25.6	1.2	59	9.5	26.4
22	21.6	1.2	60	10.9	26.2
23	19.7	1.1	61	12.0	24.8
24	([2])	([2])	62	13.7	22.2
25	([2])	([2])	63	14.6	18.3
26	([2])	([2])	64	15.3	16.3
27	([2])	([2])	65	16.9	13.1
28	12.7	22.0	66	15.6	11.6
29	9.2	21.4	67	18.5	10.9
30	6.7	22.4	68	20.1	11.6
31	5.2	22.9	69	19.3	11.7
32	3.5	22.0	70	17.3	11.0
33	2.9	20.9	71	[3]16.3	[3]8.8
34	2.7	20.3	72	[3]14.2	[3]9.0
35	2.6	19.9	73	[3]12.4	[3]8.3
36	2.3	20.1	74	[3]10.5	[3]7.4
37	2.5	20.1	75	[3]8.7	[3]6.1

[1]Based on two observations.
[2]Reconstruction interval.
[3]Based partly on interpolation.

These values were used in applying Equations (7) and (8) to data from the exploited test populations (Table 11). Curves for the test populations (Figure 13) followed the general trend of the biomass levels, even though oscillatory deviations were great.

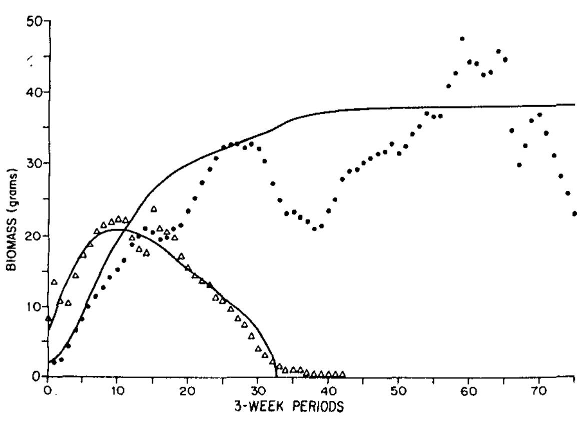

FIGURE 12.—Fitting of simulation model to control populations. *Dots are for guppy, triangles for swordtail. Solid lines are fitted curves.*

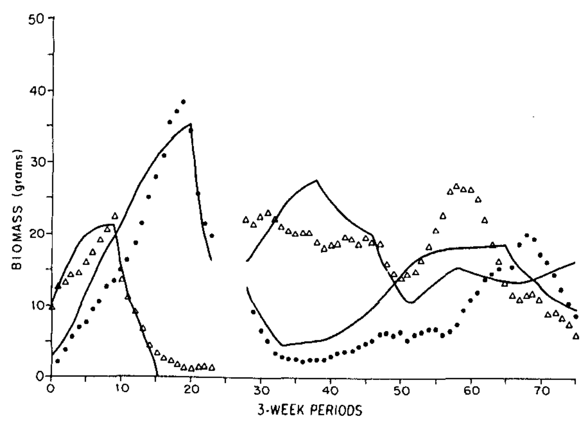

FIGURE 13.—Fitting of simulation model for test populations. *Dots are for guppy, triangles for swordtail. Solid lines are fitted curves.*

Oscillatory Fluctuations

The substantial oscillatory deviations evident in comparisons of observed and simulated biomass levels (Figures 12, 13) suggest the need for special study. Deviations can be evaluated more readily if they are plotted along a straight baseline (Tables 12, 13; Figure 14). Viewed in this manner, deviations appear at least roughly regular with respect to time. Also, they tend to be similar for control and test populations of the guppy for comparable periods. They did not, therefore, result solely from perturbations due to exploitation, although in the test populations deviations were somewhat greater post-exploitation than pre-exploitation.

Oscillations of the type described above seem to be basic to many populations. Walter (1973) points out that such a fluctuation occurred in Lake Michigan alewives. He developed delay-differential equations which are compatible with "an oscillatory sort of behavior centered about the equilibrium level." Although it would be of interest to apply such models to the guppy-swordtail data, it is unlikely that they would provide substantially different results insofar as the basic relations between exploitation and yield are concerned. It is with such relations that I am primarily concerned in this paper.

Since there were some fluctuations in water temperature (Figure 1) during the course of the experiments, it seemed possible that these might have caused all or part of the oscillatory population changes. To test this, a regression was erected for periods 33-75, when temperature fluctuations were fairly regular. The independent variable was water temperature, and the dependent variable was deviation of the control guppy population biomass from that predicted by the simulation model (Table 12, Figure 14). Results showed no significant correlation between biomass deviations and temperature (r = 0.087, P >0.1).

It is worthwhile in this discussion of oscillatory

TABLE 12.—Deviations of actual biomass from theoretical, on basis of fitted model, guppy.

Period	Deviation (g) Control	Test	Period	Deviation (g) Control	Test
0	−0.4	−1.0	38	−15.7	−2.7
1	−0.4	−1.8	39	−15.5	−2.9
2	−1.1	−1.5	40	−13.7	−2.6
3	−0.4	−1.5	41	−12.2	−2.8
4	−0.1	−2.3	42	−9.6	−3.0
5	−0.5	−3.7	43	−8.4	−3.5
6	−0.7	−4.1	44	−8.4	−3.6
7	−1.5	−5.2	45	−7.3	−3.9
8	−2.7	−5.1	46	−6.8	−4.5
9	−3.2	−6.0	47	−6.2	−4.6
10	−3.8	−6.2	48	−6.0	−5.5
11	−4.0	−6.6	49	−5.0	−6.9
12	−3.5	−6.5	50	−6.3	−7.6
13	−3.7	−5.7	51	−5.2	−9.9
14	−3.8	−3.9	52	−3.6	−10.1
15	−5.6	−2.6	53	−2.5	−10.4
16	−7.7	−1.0	54	−0.7	−10.6
17	−8.2	2.4	55	−1.3	−10.9
18	−7.7	3.1	56	−1.2	−11.7
19	−7.9	3.8	57	3.0	−11.6
20	−6.4	−1.0	58	4.9	−10.5
21	−5.2	0.0	59	9.6	−8.6
22	−3.5	1.6	60	6.4	−7.3
23	−2.1	3.4	61	6.2	−6.3
24	−0.9	([1])	62	4.7	−4.7
25	0.3	([1])	63	5.0	−3.9
26	0.3	([1])	64	7.8	−3.2
27	0.0	([1])	65	6.7	−1.7
28	−0.8	0.2	66	−3.4	−0.9
29	−0.7	−1.2	67	−8.1	3.2
30	−1.7	−1.9	68	−5.3	5.6
31	−4.1	−1.9	69	−2.0	5.6
32	−7.4	−2.3	70	−1.1	4.6
33	−10.2	−1.8	71	−3.7	4.6
34	−12.4	−2.0	72	−6.9	3.2
35	−12.6	−2.2	73	−9.8	2.0
36	−13.7	−2.7	74	−12.3	0.6
37	−14.6	−2.7	75	−15.0	−0.7

[1]Reconstruction interval.

TABLE 13.—Deviations of actual biomass from theoretical, on basis of fitted model, swordtail.

Period	Deviation (g) Control	Test	Period	Deviation (g) Control	Test
0	2.2	0.1	38	0.3	−8.8
1	4.5	0.3	39	0.3	−8.0
2	−0.8	−1.8	40	0.3	−6.2
3	−3.3	−2.6	41	0.3	−5.0
4	−1.9	−4.1	42	0.3	−3.1
5	−0.6	−3.7	43	0.0	−2.6
6	−0.4	−3.3	44	0.0	−2.7
7	0.5	−2.1	45	0.0	−1.0
8	0.9	−0.8	46	0.0	−0.9
9	0.9	1.0	47	0.0	1.3
10	1.3	−2.4	48	0.0	0.7
11	1.2	−0.8	49	0.0	1.1
12	−1.2	0.1	50	0.0	2.0
13	−2.4	0.2	51	0.0	3.8
14	−2.4	0.3	52	0.0	4.0
15	4.5	2.1	53	0.0	4.7
16	2.6	2.5	54	0.0	5.6
17	2.6	2.1	55	0.0	7.1
18	2.7	1.5	56	0.0	8.5
19	0.7	1.2	57	0.0	11.2
20	0.1	1.1	58	0.0	11.4
21	−0.4	1.2	59	0.0	11.2
22	−0.4	1.2	60	0.0	11.4
23	−0.2	1.1	61	0.0	10.3
24	−1.1	([1])	62	0.0	8.0
25	−0.6	([1])	63	0.0	4.5
26	−1.2	([1])	64	0.0	2.7
27	−1.7	([1])	65	0.0	−0.2
28	−1.6	5.8	66	0.0	−1.7
29	−2.0	4.1	67	0.0	−2.4
30	−2.5	3.6	68	0.0	−1.8
31	−2.0	2.4	69	0.0	−2.0
32	−1.1	0.2	70	0.0	−3.1
33	1.5	−2.3	71	0.0	−5.7
34	1.0	−4.2	72	0.0	−6.0
35	0.9	−5.6	73	0.0	−7.1
36	1.0	−6.3	74	0.0	−3.5
37	0.6	−6.9	75	0.0	−5.2

[1]Reconstruction interval.

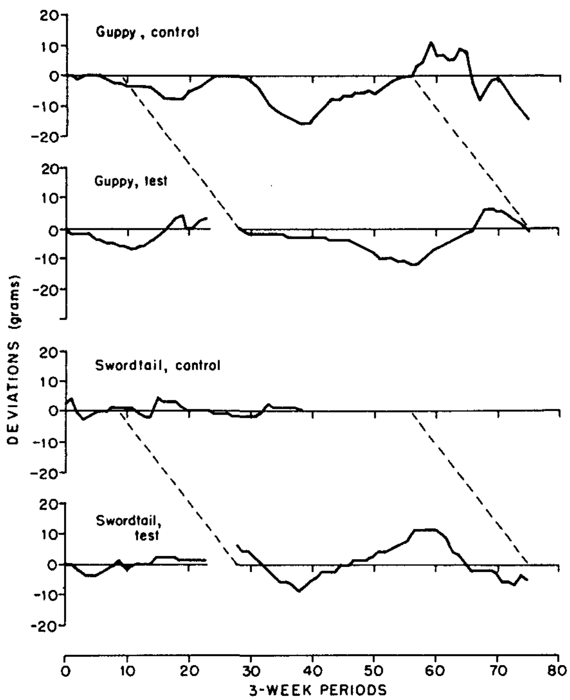

FIGURE 14.–Deviations from simulation model. Broken lines show lags for comparable portions of test and control populations.

fluctuations to consider the models fitted under independent and competing conditions. The former were based on equilibrium population conditions, whereas the latter recognized nonequilibrium conditions and used nonlinear differential equations capable of expressing continuous variation in population and yield under stable-limit cyclic variation. Conclusions for management may be different under the second type of formulation, nevertheless I feel that the conclusions drawn below are of value.

Finally, it is pertinent to discuss what seems likely to have been the start of an oscillatory fluctuation in the independent population of the swordtail. As mentioned under "Course of Populations," number and biomass increased during the final five brood intervals, contrary to what might be expected as a result of the 16.7% exploitation rate applied. The incipient oscillation may have been triggered by the low level of biomass reached just before it began, through overcompensation of the population. This level was lower than any that had been in effect since the initial growth of the population, and it may have moved the population toward the high recruitment rates shown in Figure 7.

CONCLUSIONS

Extinction of the swordtail population in the control pair (Figures 4, 12) as mentioned under "Course of Populations," is compatible with the theory of competitive exclusion first advanced by Gause (1934). He stated that where two populations are fully competing, one will have a slight advantage in growth or aggression and eventually displace the other. This occurrence illustrates one of the values of conducting population experiments over a sufficient period for natural phenomena to develop. The extinction of the swordtail could hardly have been anticipated during the first few months of the experiment, when growth of the swordtail actually outstripped that of the guppy. Gause's phenomenon of "mutual depression" (Gause and Witt 1935) also was exemplified in the experiments. Quantitative measures of this were provided by the coefficients of competition, c_1 and c_2, determined (by successive trials) for Formulae (7) and (8). These were 0.071 and 0.120 for the guppy and swordtail, respectively. These values show greater depression for the swordtail than for the guppy and, therefore, the superior competitive ability of the guppy. Growth advantage for the guppy was indicated by the values of k and P_∞ (Table 9), both of which were greater for the guppy.

My greatest interest in these experiments was to discover what combination of exploitation rates would produce the greatest sustainable yield for the two populations. This problem can be approached by calculating equilibrium yields for pairs of population sizes P_1 and P_2. At equilibrium, the left hand sizes of Equations (7) and (8) are equal to zero; with the constants already determined, F_1 and F_2 can be calculated for any pair of values P_1 and P_2. To obtain 3-wk yields, F_1 and F_2 were converted back to m_1 and m_2 by the formula $m = 1 - \exp(-F)$. Then total 3-wk yields, comparable to the yields actually obtained in the experiments (Table 8), represent the sum of m_1P_1 (guppy) and m_2P_2 (swordtail). Yields are directly comparable for the guppy, but values in Table 8 must be multiplied by three fourths for the swordtail.

I expressed the total yields $(m_1P_1 + m_2P_2)$ in the form of yield isopleths (Figure 15). Inspection of

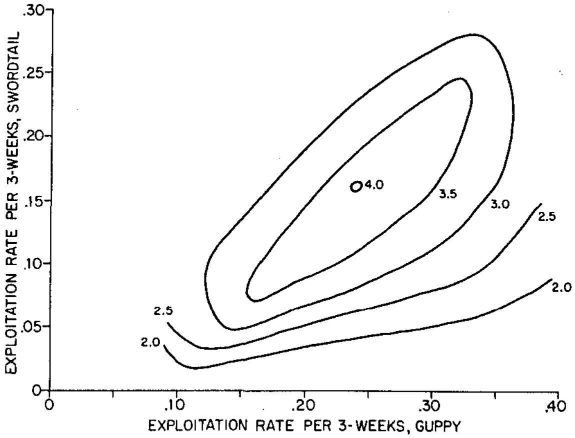

FIGURE 15.—Yield isopleths from data supplied by the simulation model. Numbers by isopleths indicate guppy yield plus swordtail yield per 3-wk period, in grams.

these isopleths reveals a ridge of high yields running roughly from $m_1 = 0.16$, $m_2 = 0.08$ to $m_1 = 0.33$, $m_2 = 0.24$. Thus, the optimal exploitation rate for the swordtail was always lower than that for the guppy, in agreement with the previously mentioned lower productive capacity of the swordtail. Also, moving from the high yield ridge toward either of the axes is moving toward lower yields. To the extent that they can be generalized, these two findings suggest that where two populations are competing, fishing both will produce greater sustainable catches than fishing either alone, provided that fishing rates are adjusted to the relative productivity of each species. The conclusion provides some support for the idea that excessive fishing of the sardine alone led to the catastrophic decline in catches in the California sardine-anchovy situation mentioned in the introduction. It is recognized that in many real fisheries, species are fished jointly by the same gear. In this case it is not possible to adjust the fishing rates separately, and results will be different (yields for a joint F will be less than for separate F's).

The maximum sustainable two-species yield, as indicated in Figure 15, is 4 g per 3-wk period, with $m_1 = 0.24$, $m_2 = 0.16$. It is of interest to see how efficiently food was used at these exploitation rates. Since juvenile fish were returned to the adult tanks from the nursery tanks, food placed in the latter must be included. During exploitation, all of the food in the adult tanks was eaten but not in the nurseries. Therefore the food consumed was between 1.0 and 1.5 times the adult amount, since food amounts for the nurseries were one-half those for the adult tanks. Three times the weekly totals of Table 1 gives 17.10 g for adult tanks only and 25.65 g for adult plus nursery tanks (weights of *Artemia* nauplii were negligible in data to two decimal places). The 4 g per 3-wk yield therefore represents food conversion efficiencies of between 0.16 and 0.23

The above efficiencies may be compared with those from the independent populations. The Fox (1970) models fitted as described under "Determination of Constants" provided estimated maximum 3-wk sustainable yields of 3.7 g for the guppy and 2.9 g for the swordtail (the latter converted from 4-wk to 3-wk basis). Food amounts were the same as for the competing populations and the comparable conversion efficiencies were 0.14 to 0.22 for the guppy and 0.11 to 0.17 for the swordtail. The range for the guppy is in reasonable agreement with the 0.20 reported by Silliman and Gutsell (1958) and 0.23 by Silliman (1968). That the guppy range is higher than the swordtail range is in keeping with other findings of superior guppy productivity reported above. Both ranges are below that for the competing populations. If significant, this difference suggests a slight gain in efficiency of the competing populations over either species growing alone.

Because the above conclusions have been derived from a mathematical model developed from the Volterra (1928) and Fox (1970) models, it is of value to refer to the work of Larkin (1963). He too used the Volterra equations as a point of departure. He applied his analyses only to hypothetical data, but his conclusions are nevertheless in general agreement with those given above. It is of interest to note his statement: "It is concluded that this formulation of interspecific competition together with variations should be applied to laboratory or natural situations to test its usefulness as a basis for prediction."

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