A MULTISTAGE RECRUITMENT PROCESS IN LABORATORY FISH POPULATIONS: IMPLICATIONS FOR MODELS OF FISH POPULATION DYNAMICS[1]

DAVID G. HANKIN[2]

ABSTRACT

Laboratory studies have been previously used to examine fundamental aspects of fish population dynamics and may be explicitly structured to examine the stock-recruitment relation. Previous studies have shown that cycling of population numbers occurs in refuge-free environments, but provision of refuge areas allows maintenance of stable population numbers. Results of these studies may be adequately explained by simple stock-recruitment theory.

Laboratory experiments described here show that manipulation of refuge habitat quality can profoundly influence interactions among population components. Complex interactions among fry, juveniles, and adults created erratic pulses in numerical population growth. Numerical population dynamics could not be adequately explained by simple stock-recruitment theory.

Based on experimental observations, a multistage adult-juvenile stock-recruitment relation was developed and was found, through statistical analyses, to adequately describe observed numerical dynamics. The biological plausibility of complex multistage recruitment processes argues that expectations for empirical support of simple stock-recruitment theory may be unreasonable and inappropriate. The simple theory may often not be biologically appropriate and more complex models of numerical population dynamics may be required for biological realism and for meaningful data analysis. Whether collection of data necessary to allow use of such complex recruitment models is economically feasible and, if so, whether more complex models may prove of practical use for management of fish populations is at present unclear.

One poorly understood population process is the so-called stock-recruitment relation (Ricker 1954) describing the dependency of input of new individuals, R_t, on the density of adult parents some time previous, $S_{t-\tau}$. Although the theoretical basis of the stock-recruitment relation is well established (Ricker 1954; Beverton and Holt 1957) and recent study in theoretical ecology (May 1975; Oster 1975) has emphasized the impressive variety of population behaviors suggested by simple discrete-time models of the form $R_t = S_{t-\tau} \cdot G(S_{t-\tau})$, remarkably little empirical support for the theory exists. In part this reflects severe restrictions in data collection. In temperate populations, for example, only one observation of recruitment may be obtained annually and this observation is normally related not only to parent stock but also to fluctuating environmental conditions and mortality (from birth to recruitment) which may strongly influence the ultimate size of a recruited year class or cohort. The data collection process is exceedingly slow, and exogenous factors may confound the dependency of recruitment on parent stock.

Further, the theory itself is simplistic. Chief limitations are the requirements that feedback be exerted at only one point in time and that the responsible population component consists solely of adults. Alternative feedback control mechanisms could involve either juveniles or the adult stock at more than one point in time. For example, in largemouth bass, *Micropterus salmoides*, adults are in contact with developing larvae for only a short period of time during which adult-related density-dependent mortality might occur. Adults leave inshore nesting and nursery areas shortly after spawning, but yearling bass, produced by the adult stock a year previous, remain in inshore areas where they may prey extensively on younger juveniles (Ricker 1954). In Dungeness crab, *Cancer magister*, and other cannibalistic species, recruitment may depend not only on parent stock but also on adult densities when juveniles first enter the adult population and are extremely

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vulnerable (Butler 1961; Gotshall 1978). The behavior of mathematical models describing such multiple adult feedback mechanisms, termed "multistage" recruitment processes, has been recently investigated by McKelvey et al. (in press). Collection of data suitable for analysis of these more complex models would seem to pose difficulties far in excess of those required for the simple models. In such cases experimental laboratory studies may be more effective and more efficient than "field" investigations for providing insight into the fundamental problem of stock and recruitment.

Laboratory studies of stock and recruitment have many advantages over similar studies of natural wild populations. Strict environmental control (of food supply, temperature, dissolved oxygen, photoperiod, habitat dimension and type), elimination of sampling error through complete enumeration, and opportunity for unique behavioral observations in an aquatic environment are the most obvious. Less obvious but perhaps more significant advantages include the investigator's unrestricted manipulative control over population size and age structure, so that the chief modes of regulation are likely to be endogenous population mechanisms, causally density-dependent, and the opportunity for replication in quantity.

From the perspective of statistical analysis, the influence of exogenous, density-independent factors is reduced, observations may be collected over as wide a range of population states as desired, and (through replication) the inherent variability of the dynamic population processes themselves may be examined (Royama 1977).

Among fishes the study of laboratory populations has centered on a single species, the guppy, *Poecilia reticulata*. The characteristics of small size, rapid maturity, frequent and repeated reproduction, and a relatively short life span render the guppy an ideal subject for laboratory study of the stock-recruitment relation. Basic information has been gathered regarding reproduction (Felin 1935; Purser 1938; Turner 1937; Rosenthal 1952), fecundity (Felin 1935; Hester 1964), and growth (von Bertalanffy 1938), and there have been many, often long-term, studies of population behavior (Breder and Coates 1932; Shoemaker 1944; Silliman 1948, 1968; Silliman and Gutsell 1958; Laakso 1959; Warren 1973; Yamagishi 1976). While the focus of these studies has not been the stock-recruitment relation per se, it is often possible to

interpret observed population dynamics in part as a reflection of an overcompensatory function relating numerical population addition to densities of adult fish.

The guppy is a viviparous member of the family Poeciliidae and exhibits strong sexual dimorphism. The maximum weight for mature males is perhaps 0.2-0.4 g as compared with a maximum weight for females of perhaps 1-2 g. Sexual maturity is normally reached by both males and females at 12-16 wk at weights of 0.1-0.15 and 0.2-0.3 g. Average longevity under laboratory conditions might be 12-18 mo. Young are produced in discrete broods, ranging in size from 2 or 3 to 50, at roughly monthly intervals at 25° C. Brood size depends on female size and, as a result, the appropriate measure of adult reproductive potential is not the number of adults but, since fecundity is nearly proportional to female weight, the total adult female biomass. Males mate freely and indiscriminantly with available females, and sperm from a single mating may remain viable and produce successive broods for periods up to 6 mo (Winge 1937). Females are clearly the overwhelmingly important component of the adult stock.

At birth fry weigh 7-8 mg and, immediately after ejection by females, are extremely vulnerable to predation by adults. Cannibalism has been regarded as the primary feedback mechanism controlling population size (Breder and Coates 1932; Laakso 1959). Recent experiments have suggested that cannibalism is chiefly a function of contacts between individuals rather than of responses to limitations in food supply (Silliman 1968; Warren 1973).

Laboratory environments for guppy population study have differed significantly in two respects: food supply and provision of refuge areas. Food has been delivered at either fixed and limiting or "to excess" ration levels, and refuge areas have only rarely been provided. These studies have shown that total population biomass is strongly influenced by food supply (Silliman 1968), but numerical densities and dynamics are strongly affected by refuge area provision and only slightly influenced by food supply.

Cycles of abundance have been observed in all long-term studies where refuge areas have been absent (Breder and Coates 1932; Shoemaker 1944; Laakso 1959). Characteristics of abundance cycles (begun with small numbers of adults) include initial increases in numbers, reduction of such increases to near zero as adult predator density

becomes large, shift to an adult-dominated age structure, and reappearance of young individuals when adult density declines through mortality to levels at which fry survival once more occurs. In those few instances in which refuge habitats have been provided (Silliman 1948, 1968; Silliman and Gutsell 1958), the results have demonstrated that roughly stable populations, of greater numerical size, with finely graded age (or size) structure, may be maintained for apparently indefinite periods. Presumably, the stability of these populations reflects the decreased period of time during which fry are vulnerable to cannibalism.

In previous guppy population studies the weight of the mature female stock has not been recorded and hence it is impossible to attempt an adequate quantitative examination of stock-recruitment relations which may have been responsible for observed dynamics (e.g., Gulland 1962 based on previous studies). The experiments described on the following pages were specifically designed to allow quantitative assessment of the stock-recruitment relation. Refuge areas were provided and fry successfully entering these areas were considered as rough equals of recruited fish. Although females do not release broods synchronously (broods are delivered continuously with respect to the entire population), data were collected at discrete biweekly intervals. Net numerical change in a sampling interval could thus be related to adult reproductive potential and adult predator density at the beginning of an interval in a fashion analogous to that which might be attempted in analysis of the simple discrete-time models. A simple difference in refuge design (as compared with Silliman's earlier work) involving spacing between glass rods in a refuge fence, however, created unexpected patterns of numerical increase. These patterns were not anticipated and could not be explained on the basis of simple stock-recruitment theory. Analysis ultimately showed the presence of a complex mechanism involving both adult and immature population components, an adult-juvenile stock-recruitment relation.

METHODS AND MATERIALS

Experiments were performed in a 3 m × 3.7 m room insulated on three walls, including two outside walls, from floor to ceiling. A small electric floor heater maintained room temperature at approximately 22° C, about 3° C above ambient

winter temperature supplied by a propane heating unit in an adjoining room. An air-conditioner in the same adjoining room prevented summer temperatures from exceeding 26° C. Experimental aquaria were located along the three insulated walls.

Experimental Environments

Twelve aquaria, of dimensions 31 cm × 62 cm × 41 cm, each holding about 80 l of water, served as experimental units. Each aquarium was equipped with a 75 W thermostat-controlled aquarium heater, about 1 cm deep layer of 3-5 mm gravel, a large inside-type charcoal-glass wool filter, a full hood reflector with two 15 W showcase bulbs, a thermometer, and a refuge area (Figure 1). Refuge areas were enclosed by a fence consisting of two sheets of solid glass rods, 3 mm in diameter, spaced (initially) 5 mm apart on centers, fitted in Plexiglas[3] frames glued at right angles. The

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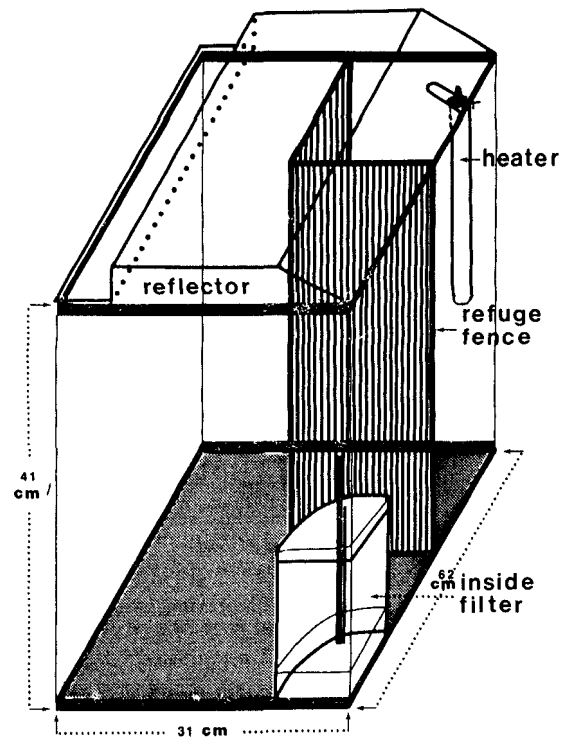

FIGURE 1.—Schematic of the experimental environments for guppies and southern platyfish.

fences partitioned off corners of aquaria, roughly 15 cm × 15 cm of aquaria bottoms, extended from aquaria bottoms to aquaria frames above the water level, and reserved about one-eighth of the total volume as refuge and nursery areas for fry. A 2 cm high Plexiglas frame surrounded both sides of a refuge fence base, preventing gravel from interfering with fence manipulation and allowing easy removal and replacement of the fence at population enumerations.

Light was provided for 12 h per day and was regulated by electric timers. To ensure standardized lighting conditions in all aquaria, the two 62 cm sides of an aquarium were covered with opaque polyethylene sheeting; of the two remaining sides, one abutted the wall and the other was left clear for observations of population behavior. Temperatures were maintained at approximately 25.5° C with a maximum recorded range in all aquaria over a 58-wk period of roughly 24°-28° C. Temperatures were monitored and recorded every 2 d. Air for filter units was supplied by small air pumps.

At weekly intervals filter units were cleaned, charcoal and glass wool replaced, and about 16 l of aquarium water and detritus were siphoned from each aquarium bottom and replaced with aged aerated water. A diatomaceous earth power filter was used weekly for 60-90 min periods per aquarium and helped maintain water quality.

Routine Experimental Manipulations

Feeding

Populations were fed accurately weighed amounts of food twice daily. Morning feedings consisted of dried food only (Tetramin brand Conditioning Food). Evening feedings consisted of thawed, rinsed, and drained adult brine shrimp, *Artemia salina*, and newly hatched *Artemia* nauplii. Nauplii were suspended in freshwater and pipetted directly into the refuge areas while dried food and adult brine shrimp were delivered to the main aquarium volume outside the refuge area.

Since no technical assistance was available to daily siphon uneaten food from aquaria, it was not possible to maintain a steady fixed ration level throughout the experimental period. Instead, rations of dried food and of adult brine shrimp were increased in increment steps as populations grew, maintaining a relatively constant ratio of food

supply to population biomass during initial stages of population growth. Food supply became fixed when populations had achieved about 50% of the apparent maximum biomass supported at the final fixed ration level. The increment steps prevented deterioration of water quality through decomposition of uneaten food and allowed for subsequent analysis of changes in population biomass as related to food supply. Exact ration levels and corresponding dates appear in the section on experimental design.

Marking

At triweekly intervals a fluorochrome, DCAF (2,4 bis (N,N' di/carboxymethyl/aminomethyl) fluorescein), was incorporated into the adult brine shrimp ration component. The DCAF-laden shrimp was fed twice daily for 3-d periods at ration levels corresponding to the normal adult brine shrimp feeding for the period. Dried food was not fed during marking intervals. Marking trials had indicated that circular fluorescent rings corresponding to time of injestion of DCAF were produced on the growing margin of guppy scales. Repeated marks could be produced by repeated administration at intervals exceeding 1 wk. Marking was designed to allow assessment of age structure at conclusion of the experiments from analysis of fluorescent marks on scales removed from fish. Scales were removed from samples of fish from all populations at week 36 and at week 58. Details of marking procedures may be found in Hankin (1978a).

Data Collection

At biweekly intervals complete enumeration of populations was performed. In early weeks (0-14) enumeration was staggered by 1 wk so that four populations and eight populations were enumerated on alternate weekends. In later weeks (14-58) all populations were enumerated in a 2-d interval at biweekly intervals.

All fish were removed from individual aquaria during enumerations and separated by size categories. Glass rod-Plexiglas grading devices, similar in design to refuge fences, were used to separate fish on the basis of "diameter" (or more correctly, maximum breadth). During weeks 0-36 six size categories were monitored, and two additional categories were included during weeks 36-58. A description of the size structure classifi-

cation achieved by the grading process and size category designations are contained in Table 1. These size category designations will be adopted throughout the paper for brevity.

After separation into size categories, numbers of males and females in each size category were recorded, and weights of males and females in size categories A_6, A_7, A_8 (weeks 0-36) and $A_{5.5}$, A_6, A_7, A_8 (weeks 36-58) were obtained separately. Weights of fry were not obtained due to dangers of handling mortality. Weights of remaining size categories were obtained without separation by sex as these groups contained nearly all immature fish. To determine weights, fish were placed in a small nylon net, blotted on paper towels until no further moisture was observed (about 1 min), and then transferred to a previously weighed plastic beaker containing about 40 ml of water. Weights of fish were determined as the difference between the previous weight and the weight obtained after addition of fish. Total population biomass was determined as the sum of all weight measurements for a given population but did not include weight of fry. An Ainsworth Model 10N analytical balance, accurate to three decimal places, was used for all weighings. Handling mortality was negligible. In 58 wk only five mortalities, all fish <2 mm in "diameter," were recorded as a direct result of biweekly manipulations at enumeration. Approximately 38,000 fish were handled during these enumerations.

All fish were also examined for external symptoms of disease at biweekly enumerations. Disease diagnosis and/or confirmation was performed at irregular intervals by Louis Leibovitz, Cornell University Veterinary School. Fish with obvious external disease symptoms (consistently diagnosed as chronic piscine tuberculosis) but otherwise apparently healthy were treated by a 20-min bath in Formalin (1:4,000). Severely afflicted fish near death were removed from populations and counted as mortalities. Numbers, weights, and sexes of fish showing symptoms and/or treated were recorded for each population at enumeration. Aquaria were examined daily for mortalities. Date of death, size category estimate, and sex were recorded for each observed mortality.

At termination (week 58) a sample of 41 gravid females ranging from 21 to 39 mm was selected from the populations. Each female was dissected and the number of embryos counted. Data collected was used to establish an overall relation between fecundity and female size for the experimental populations.

Experimental Design

The initial intent of population experiments was to examine dynamics of mixed species populations (guppies, *P. reticulata*, and southern platyfish, "platy," *Xiphophorous maculatus*) from the perspective of stock-recruitment theory. Due to excessive mortality among the southern platyfish and an apparent inability of their fry to successfully compete with guppy fry, the southern platyfish were removed from all populations at week 8 and experimental goals became limited to analysis of single species populations based on simple stock-recruitment theory. Numerical population growth of single species populations, however, was not anticipated on the basis of the simple theory. Numerical population growth often occurred as a series of discrete pulses of increase, followed by periods of roughly static population numbers. Behavioral observations and analyses of collected population data through week 36 indicated that the pulsing quality of numerical growth was probably caused by juvenile-fry interactions within refuge areas. Based on this hypothesis, experimental populations were manipulated and exposed to different treatments at week 36. Treatment consisted of alteration of original refuge area habitat quality and population growth under these new conditions was monitored through week 58 to test the juvenile-fry interaction hypothesis.

The experiments have been separated into two distinct phases based on the above-described ex-

TABLE 1.—Size-group classifications of guppies at enumerations during weeks 0-36 (Phase I) and weeks 36-58 (Phase II). Grader spacing is measured from center to center.

Weeks	Size-group designation	Grader spacing (mm)	Fish diameter range (mm)	Description
0-36	Fry	4	<1	Newly born fry
	J_4	4	1-2	All immature
	J_5	5	2-3	Immature males and females, mature males
	A_6	6	3-4	Largest mature males, small mature females
	A_7	7	4-5	Large mature females
	A_8	8	>5	Largest mature females
36-58	Fry	4	<1	Newly born fry
	$J_{4.0}$	4	1-1.5	All immature
	$J_{4.5}$	4.5	1.5-2	All immature
	$J_{5.0}$	5.0	2-2.5	Immature females, maturing males
	$A_{5.5}$	5.5	2.5-3	Maturing females, mature males
	A_6	6	3-4	Largest mature males, small mature females
	A_7	7	4-5	Large mature females
	A_8	8	>5	Largest mature females

perimental path. Weeks 0-36, which included original mixed species populations and subsequent unexpected behavior of single species populations, may be regarded as exploratory in nature and have been designated Phase I. The test of the juvenile-fry interaction hypothesis, during weeks 36-58, may be considered confirmatory in nature and has been designated Phase II. The logic of the experimental path is depicted in Figure 2. Experimental observations collected during Phase I were indeed responsible for the development of the juvenile-fry hypothesis tested during Phase II.
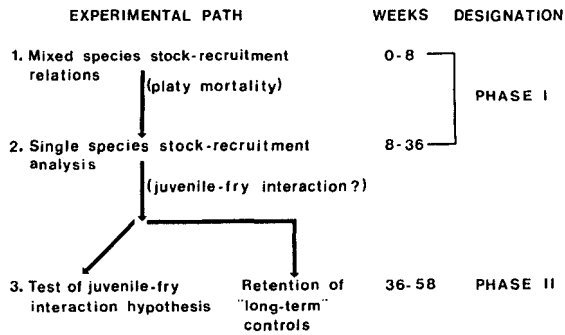

FIGURE 3.—Schematic of the laboratory facility showing blocking of experimental aquaria for guppy and southern platyfish populations.

FIGURE 2.—The experimental design for guppy and southern platyfish (platy) populations.

Phase 1 (Weeks 0-36)

WEEKS 0-8.—Twelve experimental aquaria were grouped into three blocks of four aquaria each and each block was assumed to have equal position effect (Figure 3). Blocks A and C contained replicate groups of four mixed species populations each. Block B had replicate single species guppy populations (aquaria 5 and 6) and platy populations (aquaria 7 and 8). A gold strain of guppies was used to allow visual separation of
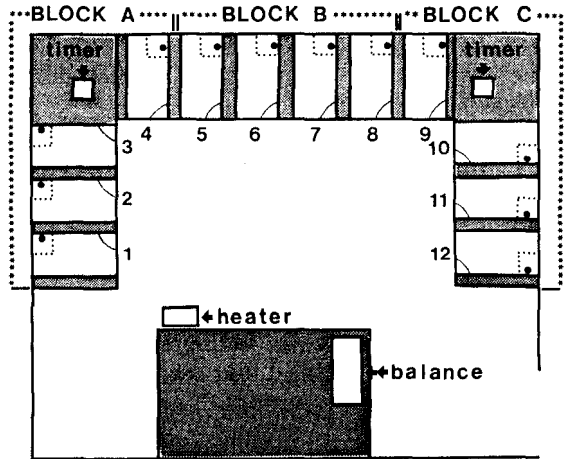
guppy and platy fry at birth, otherwise difficult with wild-type strains. Weights, sex, and numbers of each species initially stocked in aquaria are listed in Table 2. Estimated age of both guppies and platies at stocking was 14-18 wk.

All populations were fed rations containing approximately equal proportions of the food items with the exception of *Artemia* nauplii. All populations received a fixed daily ration of *Artemia* nauplii, 0.2 g. Total rations were increased in stepwise increments to keep the daily wet weight equivalent of rations at from 25 to 35% of total population biomass. Since growth of guppies appeared more rapid in mixed species populations, single species population rations were increased in rapid increments at the end of week 6. Food rations supplied to populations during the first 8 wk are in Table 3. At the end of week 8 all platies were removed from mixed species populations and

TABLE 2.—Stocking of guppies and southern platyfish at initiation of experiments, 5 June 1975. Weights (grams) in parentheses.

Block	Tank number	Guppies			Southern platyfish			Tank totals
		Female	Male	Total	Female	Male	Total	
A	1	5(2.540)	4(0.581)	9(3.121)	4(3.488)	4(2.188)	8(5.676)	17(8.797)
A	2	5(2.452)	4(0.599)	9(3.051)	4(3.668)	4(2.359)	8(6.027)	17(9.078)
A	3	5(2.548)	4(0.590)	9(3.138)	4(3.788)	4(1.861)	8(5.649)	17(8.787)
A	4	5(2.574)	4(0.664)	9(3.238)	4(3.455)	4(2.155)	8(5.610)	17(8.848)
B	5	5(2.639)	4(0.655)	9(3.294)				9(3.294)
B	6	5(2.746)	4(0.677)	9(3.423)				9(3.423)
B	7				4(4.038)	4(2.568)	8(6.606)	8(6.606)
B	8				4(4.176)	4(2.511)	8(6.687)	8(6.687)
C	9	5(2.521)	4(0.654)	9(3.175)	4(3.550)	4(2.152)	8(5.702)	17(8.877)
C	10	5(2.355)	4(0.542)	9(2.897)	4(3.553)	4(2.198)	8(5.751)	17(8.648)
C	11	5(2.288)	4(0.605)	9(2.893)	4(3.470)	4(2.161)	8(5.631)	17(8.524)
C	12	5(2.290)	4(0.675)	9(2.965)	4(3.762)	4(2.230)	8(5.992)	17(8.957)

TABLE 3.—Schedule of daily rations fed to guppy and southern platyfish populations during weeks 0-8. Total is expressed as a wet weight equivalent.[1]

Dates (1975)	Weeks	Dry food (g)	Artemia adults (g)	Artemia nauplii (g)	Total (g)
Mixed-species populations (populations 1-4, 9-12)					
2 June- 6 July	0-4	0.2	1.0	0.2	3.2
7 July - 3 Aug.	4-8	0.15	1.25	0.2	2.95
Single species populations					
Guppies (populations 5, 6)					
2 June -21 June	0-2	0.08	0.4	0.08	1.28
22 June- 6 July	2-4	0.08	0.4	0.2	1.4
7 July -20 July	4-6	0.06	0.6	0.2	1.4
21 July -22 July	—	0.08	0.8	0.2	1.8
23 July - 3 Aug.	6-8	0.10	1.0	0.2	2.2
Southern platyfish (populations 7, 8)					
2 June-21 June	0-2	0.15	0.75	0.15	2.4
22 June- 6 July	2-4	0.15	0.75	0.2	2.45
7 July - 3 Aug.	4-8	0.10	1.0	0.2	2.2

[1]To determine, multiply dry food ration by 10 and add all food types.

rations were reduced to equal ration levels in original single species guppy populations.

WEEKS 8-36.—Neither guppy population biomass nor numbers at week 8 differed significantly between original single species populations and mixed species populations so the 10 remaining populations were considered replicates during weeks 8-36. To eventually achieve population age structure which would be finely graded and to achieve equality in numbers of original females in all aquaria, the original females were gradually "phased out" by removal of one adult female from each population at weeks 11, 13, 15, and 17. Original females were easily separated from recently matured female progeny by their larger size. and were removed by selecting the smallest female first, in each population, to least affect population biomass. Food rations were increased in stepwise increments through week 22 after which time rations were fixed. A slight departure occurred during weeks 28-29 when dried food only was fed twice daily (Table 4).

TABLE 4.—Schedule of daily rations fed to guppy populations during weeks 8-36. Total is expressed as a wet weight equivalent.[1]

Dates (1975-76)	Weeks	Dry food (g)	Artemia adults (g)	Artemia nauplii (g)	Total (g)
3 Aug. -19 Aug.	8-10	0.10	1.0	0.20	2.2
20 Aug. -17 Sept.	10-14	0.13	1.3	0.20	2.8
17 Sept.-28 Oct.	14-20	0.15	1.5	0.20	3.2
29 Oct. -12 Nov.	20-22	0.18	1.8	0.20	3.8
13 Nov. -21 Dec.	22-28	0.20	2.0	0.20	4.2
22 Dec. -30 Dec.	28-29	[2]0.40	—	—	4.0
31 Dec. -15 Feb.	29-36	0.20	2.0	0.20	4.2

[1]To determine, multiply dry food by 10 and add all ration types.
[2]0.20 g fed twice daily. Three morning feedings were missed during this period.

Phase II (Weeks 36-58)

Three populations (5, 6, and 12) from the original 10 were selected at random to be long-term controls. Of the remaining seven populations, two pairs (1 and 2, 4 and 10) were mixed and divided to give three approximately comparable populations (for each mixed pair) of reduced numerical size and biomass. The remaining three populations were simply reduced in size to similar levels. Numbers of individuals in reduced populations ranged from 74 to 81, of which 42-49 were adults in size categories $\geq A_{5.5}$ (the largest adult male and smallest adult female size category, see Table 1). Total reduced population biomass ranged from 12 to 14 g, slightly less than one-half of apparent maximum population biomass.

The nine reduced populations produced in the above manner were assigned to three groups of three each for treatment. Treatment consisted of replacing original 5.0 mm spacing (on centers) refuge fences with refuge fences of 4.5, 5.0, or 5.5 mm spacing. Each group contained two populations of mixed population origin and one which had been reduced from a larger single population. Refuge areas were assigned to populations with the restriction that each of the three populations produced from a mixed pair must be assigned a different refuge fence spacing. A summary of manipulations at week 36 is presented in Table 5. Daily rations for Phase II are presented in Table 6.

RESULTS

Phase I

Weeks 0-8

The attempt to examine stock-recruitment relations in mixed species populations failed due to high platy mortality in certain aquaria and an apparent inability of platy fry to successfully compete with guppy fry for food. Relative competitive ability of platy and guppy fry was reflected in contrasting mean weights of platy juveniles in mixed and single species populations at the end of week 8. Mean weights of platy juveniles, all born during the first 2 wk of the experiments, were 0.0144 g in a mixed species population and 0.1037 g in a single species population at week 8. Guppy juveniles, also presumably born within the first 2 wk, had reached a mean weight of 0.0979 g by week 8 in the same mixed species population.

TABLE 5.—Manipulations of guppy populations at the end of Phase I (week 36) for test of refuge fence spacing treatment effect during Phase II (weeks 36-58).

Tank number	Refuge assignment (mm)	Origin
1	5.0	No. 1 and 2, mixed and reduced[1]
2	5.5	No. 1 and 2, mixed and reduced[1]
3	5.0	No. 3, reduced
4	4.5	No. 4 and 10, mixed and reduced[2]
5	5.0 —	"Long-term control" -------------------------------
6	5.0 —	"Long-term control" -------------------------------
7	4.5	No. 1 and 2, mixed and reduced[1]
8	5.5	No. 4 and 10, mixed and reduced[2]
9	4.5	No. 9, reduced
10	5.0	No. 4 and 10, mixed and reduced[1]
11	5.5	No. 11, reduced
12	5.0 —	"Long-term control" -------------------------------

[1] Plus eight fry from tank no. 3.
[2] Plus five fry and four $A_{5.5}$ (an adult male size category, refer to Table 1) males from tank no. 11.

TABLE 6.—Schedule of daily rations fed to treated guppy populations during Phase II (weeks 36-58). Total is expressed as a wet weight equivalent.[1]

Dates (1976)	Weeks	Dry food (g)	Artemia adults (g)	Artemia nauplii (g)	Total (g)
17 Feb.-28 Feb.	36-38	0.15	1.5	0.20	3.2
1 Mar.-15 Mar.	38-40	0.18	1.8	0.20	3.8
16 Mar.-18 Apr.	40-58	0.20	2.0	0.20	4.2

[1] To determine, multiply dry food by 10 and add all ration types.

Since both mixed and single species populations were fed at equal ration levels relative to total population biomass, it seems reasonable to infer a strong competitive advantage to guppy fry in securing food.

In contrast, the presence of platies apparently had little effect on guppy populations in mixed populations. Tests (Student's t) for differences in mean guppy population numbers and biomass between single species and mixed species populations at week 8 failed to reject, at the $\alpha = 0.05$ level, null hypotheses of equality in population numbers or biomass. After removal of platies, all guppy populations were treated as (equivalent) replicates.

Weeks 8-36

The 10 replicate guppy populations through week 36 showed a striking contrast between growth in numbers and growth in biomass. Biomass steadily increased in all populations and weights attained at each sampling period were nearly equal in all populations. Populations seemed near a common maximum supportable biomass by week 36. In contrast, numerical growth was highly variable and often occurred as discrete pulses of increase. Total population numbers

always varied greatly among populations and there was no indication of a common approach to an asymptotic or stable numerical population size (Table 7).

BIOMASS DYNAMICS.—In general, biomass growth in all guppy populations was typified by steady, nearly uniform, biweekly increments through the first 28 wk and by declining increments during weeks 28-36. Removals of individual females at weeks 11, 13, 15, and 17 and restriction of rations to dried food only during weeks 28-29 were clearly reflected in depressed biomass increments during these intervals of disturbance (Figure 4). At week 36 mean population biomass was 28.906 g and ranged from 26.291 to 30.717 g.

Using data for weeks 18-28 and 30-36 (periods during which neither removals nor atypical feedings occurred, and beyond the time when platies were also present in certain populations), maximum supportable biomass for each population was estimated by assuming a logistic biomass growth model. Application of the logistic model presumed that biomass growth was limited by the final fixed ration level reached at week 22. Maximum bio-
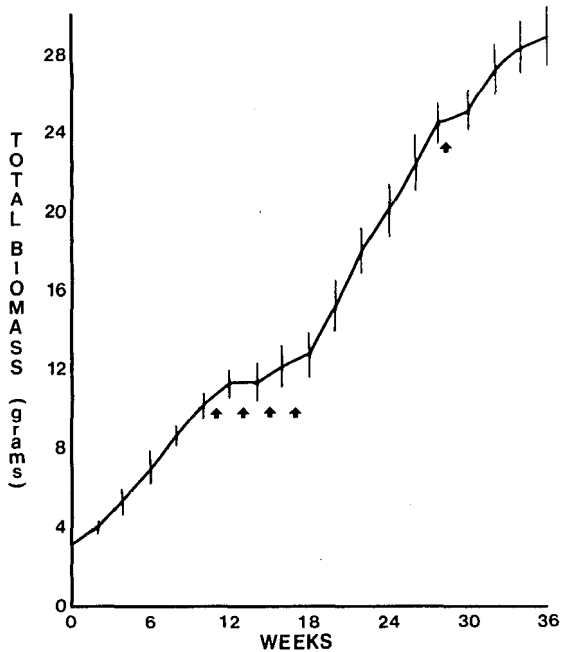

FIGURE 4.—Mean population biomass of guppies during Phase I. Removals of individual females at weeks 11, 13, 15, and 17 and restriction of ration to dried food only during weeks 28-29 are indicated by arrows. Vertical lines represent standard deviations.

TABLE 7.—Total population numbers and, in parentheses, total biomass in grams for single species (guppy) populations at week of enumeration during Phase I, weeks 0-36.

Week	Population number										Mean numbers (SD)	Mean biomass (SD)
	1	2	3	4	5	6	9	10	11	12		
0	9 (3.121)	9 (3.051)	9 (3.145)	9 (3.238)	9 (3.294)	9 (3.423)	9 (3.175)	9 (2.897)	9 (2.893)	9 (2.965)	9 (0)	3.120 (0.173)
1					9 (3.955)	34 (3.548)					21.5 (17.7)	3.752 (0.288)
2	29 (3.903)	43 (4.025)	37 (4.176)	31 (4.599)			38 (4.074)	39 (4.162)	40 (3.009)	12 (3.495)	33.6 (9.9)	3.930 (0.483)
3					38 (4.685)	33 (4.921)					35.5 (3.5)	4.803 (0.167)
4	53 (5.798)	57 (5.985)	39 (4.935)	50 (6.059)			35 (5.332)	64 (5.995)	32 (4.642)	28 (4.740)	44.8 (13.0)	5.436 (0.599)
5					43 (5.713)	63 (5.443)					53.0 (14.1)	5.573 (0.191)
6	72 (7.379)	75 (7.968)	39 (5.466)	58 (8.027)			48 (6.871)	61 (7.552)	33 (5.835)	34 (5.778)	52.5 (16.5)	6.860 (1.035)
7					41 (6.682)	61 (7.392)					51.0 (14.1)	7.037 (0.502)
8	91 (9.355)	97 (8.372)	38 (8.216)	69 (9.073)			47 (8.373)	59 (9.458)	33 (7.711)	54 (7.902)	61.0 (23.3)	8.558 (0.659)
9					39 (8.582)	61 (8.494)					50.0 (15.6)	8.538 (0.062)
10	108 (10.853)	93 (9.985)	39 (9.423)	83 (10.785)			48 (10.228)	60 (11.335)	32 (9.519)	78 (9.273)	67.6 (27.1)	10.173 (0.756)
11					40 (10.241)	63 (10.638)					51.5 (16.3)	10.440 (0.281)
12	136 (12.087)	103 (12.058)	38 (10.235)	89 (11.686)			46 (10.734)	58 (11.483)	62 (10.420)	76 (10.929)	76.0 (32.4)	11.205 (0.724)
13					38 (10.047)	59 (10.964)					48.5 (14.8)	10.506 (0.648)
14	158 (12.881)	100 (12.391)	61 (10.233)	88 (12.440)	36 (10.002)	58 (10.808)	46 (11.403)	66 (12.509)	85 (10.482)	100 (11.009)	79.8 (35.1)	11.416 (1.062)
16	181 (13.762)	106 (13.253)	77 (10.794)	85 (12.989)	36 (9.934)	66 (12.419)	43 (11.908)	74 (12.552)	89 (11.447)	105 (12.309)	86.2 (40.5)	12.137 (1.158)
18	190 (13.729)	113 (14.552)	92 (11.042)	83 (13.697)	40 (10.488)	92 (12.365)	51 (12.302)	67 (13.176)	84 (12.113)	104 (12.768)	91.6 (41.3)	12.623 (1.243)
20	190 (16.169)	112 (17.282)	98 (13.555)	81 (15.687)	64 (12.710)	111 (15.075)	82 (14.826)	78 (15.518)	86 (15.801)	103 (15.681)	100.5 (35.0)	15.230 (1.302)
22	192 (19.70)	112 (19.688)	100 (16.151)	78 (18.502)	73 (15.989)	107 (18.555)	95 (17.354)	92 (18.571)	87 (17.545)	101 (18.906)	103.7 (33.3)	18.097 (1.311)
24	189 (21.837)	113 (21.562)	98 (19.618)	95 (20.220)	76 (18.037)	104 (19.898)	98 (18.828)	97 (19.827)	85 (20.674)	103 (21.365)	105.8 (31.0)	20.187 (1.213)
26	191 (24.391)	112 (24.144)	99 (21.276)	127 (22.687)	75 (20.760)	102 (23.289)	96 (21.388)	125 (21.479)	85 (22.149)	102 (23.714)	111.4 (32.2)	22.528 (1.305)
28	200 (25.953)	111 (25.886)	95 (22.705)	149 (24.824)	75 (23.305)	102 (25.171)	103 (23.810)	130 (23.890)	85 (24.361)	104 (25.284)	115.4 (36.4)	24.519 (1.091)
30	197 (26.558)	112 (26.465)	107 (23.624)	142 (25.584)	83 (23.857)	102 (26.295)	101 (24.607)	139 (23.947)	138 (24.526)	132 (25.865)	125.3 (32.1)	25.133 (1.148)
32	194 (28.909)	110 (28.641)	128 (26.355)	151 (27.953)	91 (26.093)	168 (27.654)	101 (26.418)	135 (25.377)	152 (27.452)	160 (28.679)	139.0 (32.2)	27.350 (1.232)
34	191 (29.614)	118 (29.580)	162 (28.085)	143 (29.099)	98 (27.548)	171 (29.842)	98 (27.327)	149 (27.104)	178 (26.150)	173 (29.599)	148.1 (33.4)	28.395 (1.316)
36	186 (29.580)	114 (30.158)	178 (28.363)	156 (30.004)	112 (28.258)	197 (30.717)	119 (27.470)	144 (27.560)	186 (26.291)	169 (30.656)	156.1 (32.2)	28.906 (1.527)

mass for each population was estimated from the slope and intercept of a regression of the reciprocal of population biomass at week $t + 2$ against the reciprocal of biomass at week t as: maximum biomass $= \hat{B}_{max} = (1 - \text{slope})/\text{intercept}$. Estimates of maximum biomass ranged from 27.8 to 37.6 g (Table 8) with a mean estimate of 31.8 g.

The nearly uniform changes in total biomass throughout Phase I, despite widely divergent numerical growth patterns, implied that growth was strongly density-dependent. Density-dependence of growth was seen most dramatically in the mean weights of large adult females. Mean weights of adult females in size categories A_7 and A_8 were inversely related to mean population numbers during weeks 0-36 (Figure 5).

NUMERICAL DYNAMICS.—While the guppy populations appeared to approach a common maximum supportable biomass, no such commonality was evident in total population numbers. Numerically, populations grew in erratic and independent fashion with no clear indications of asymptotic behavior. Numerical growth was steadily positive in only a single population (population 1). In all other populations patterns of numerical increase were unanticipated and often consisted of discrete pulses of increase, followed by periods of static

TABLE 8.—Logistic growth method estimates of maximum biomass ($\hat{B}_{max}$ in grams) for Phase I guppy populations. Estimates exclude weight of fry and are based on data collected for weeks 18-28, and 30-36.

Population number	r^1	$\hat{B}_{max}$	Population number	r^1	$\hat{B}_{max}$
1	0.992	32.7	6	0.980	32.4
2	.997	33.4	9	.994	30.9
3	.993	32.0	10	.991	29.9
4	.995	37.6	11	.972	27.8
5	.993	30.6	12	.987	31.1

[1]Correlation coefficient for regression of 1/biomass$_{t+2}$ against 1/biomass$_t$.
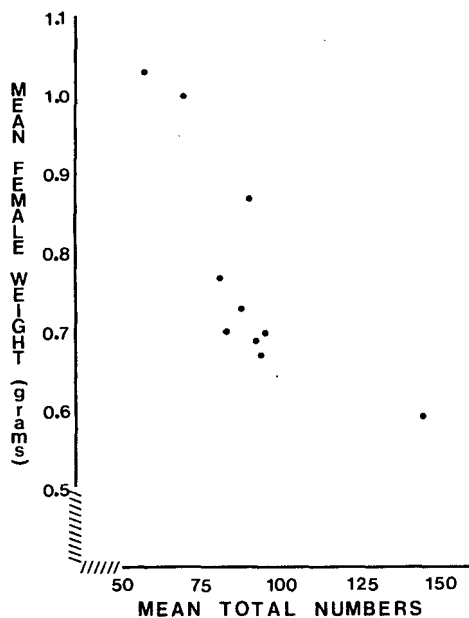
FIGURE 5.—Density-dependence of guppy growth illustrated by plot of mean female weight (in size categories $A_7 + A_8$) at week 36 against mean total numbers during weeks 0-36.

FIGURE 6.—Pulsing behavior of numerical population growth illustrated by guppy populations 3 (solid line) and 11 (dots).

population numbers, followed by further pulses of increase (Figure 6). No position effect was detected when mean total numbers in blocks A and C were compared by Student's t test.

The patterns of numerical increase exhibited by these populations were in striking contrast with the control (unexploited) populations maintained by Silliman and Gutsell (1958). Behavioral observations and examination of size structure data collected during Phase I indicated that the presence of juveniles in the J_4 size category somehow inhibited survival of newly born fry, presumably through some juvenile-fry interaction within the refuge area. Plots of estimated numbers of fry surviving to enumeration during a biweekly interval, corrected for observed mortalities (= ad-
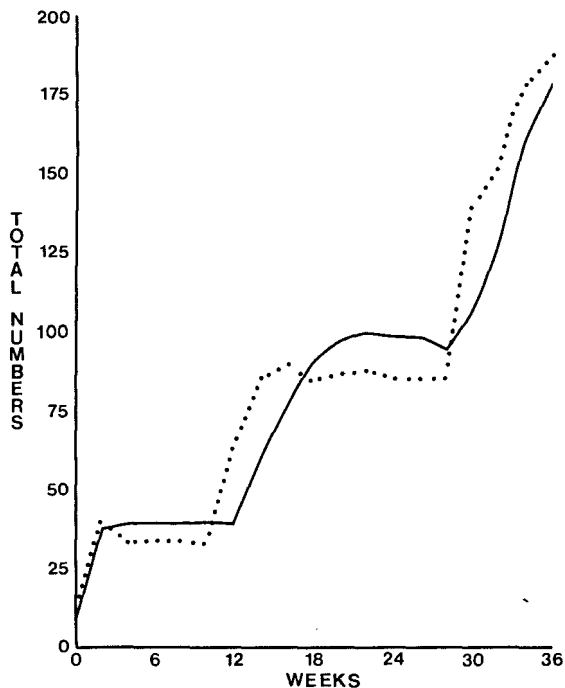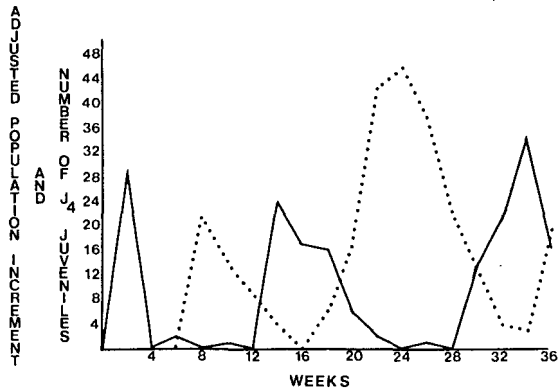
justed population increment), and numbers of J_4 juveniles present at the beginning of the interval, against time showed distinct offset peaks of abundance in many populations. The relations could be further improved by introducing a 2-wk time lag and plotting the number of J_4 juveniles at $t - 2$ wk and the adjusted population increment from t to $t + 2$ wk against time (Figure 7). The time lag improvement implied that only larger juveniles within the J_4 size category were responsible for inhibition of fry survival. Small J_4 juveniles at $t - 2$ wk would have become large J_4 juveniles (roughly equal to the $J_{4.5}$ size category monitored during Phase II) at time t.

Strong and statistically significant ($P < 0.05$) negative correlations between biweekly adjusted population increments and the natural logarithm of J_4 juveniles (+1) present 2 wk before the beginning of a sampling interval were found in 8 of 10 populations (Table 9). These negative correlations between numerical population growth and juvenile densities detected at several levels of adult stock density showed that numerical population growth, and thus the recruitment process, in these populations could not be a simple function of adult stock alone. Likely, interactions between newly

FIGURE 7.—Adjusted population increment (in t, $t + 2$) and number of J_4 guppy juveniles (at $t - 2$) plotted against week (at $t + 2$) in population 3. The plot incorporates a 2-wk time lag. Solid line is adjusted population increment. Dots show juvenile densities.

TABLE 9.—Linear correlation coefficients (r) between adjusted population increment ($API_{t, t+2}$) and natural logarithm of juvenile numbers [$\ln(J_{4_{t-2}} + 1)$] in Phase I guppy populations.

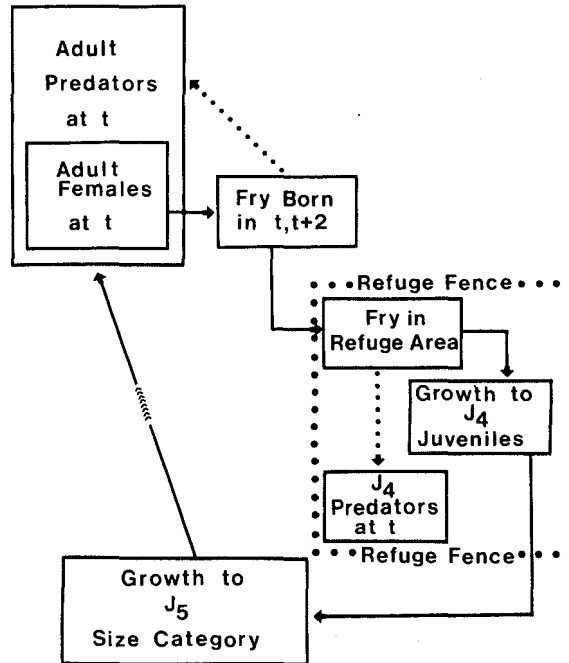| Population number	r	Population number	r
1	−0.5166*	6	−0.7704*
2	−.5919*	9	−.6042*
3	−.5215*	10	−.0487
4	−.7300*	11	−.6047*
5	−.6158*	12	−.3600

*$P \leqslant 0.05$.

FIGURE 8.—Diagram depicting the hypothesized numerical dynamics model for guppy populations. Solid lines and arrows indicate path from birth to survival as adult. Small dots and arrows depict paths leading to death through cannibalism by adults or juveniles.

born fry and immature juveniles had created a complicated population growth process involving both immature and adult population components as had been briefly mentioned by Ricker (1954).

A tentative conceptual model of numerical population dynamics was proposed and is depicted in Figure 8. Survival of newly born fry in a given experimental interval can be viewed as a two-step process. Fry born must first elude adult predators outside the refuge area. Fry which successfully elude adults and enter the refuge area are faced by predation, competition, or harrassment by large J_4 juveniles present in the refuge area. Pulses of numerical increase can easily be created if such a process occurs. Following the initial entrance of fry into the refuge area, growth of fry occurs. Once fry grow to the juvenile size at which interaction with newly born fry occurs, fry survival is inhibited so long as juveniles are smaller than the J_5 size category. Once reaching the J_5 size category, juveniles are transferred to the main aquarium environment at enumeration. The refuge area is once more free of juveniles, and fry successfully eluding adult predators and entering the refuge area are once more expected to survive.

Since the above explanation for the pulsing quality of numerical growth seen in many populations seemed a plausible hypothesis, alteration of the refuge fence design (by either increasing or decreasing spacing between glass rods) would likely increase or decrease the intensity and duration of juvenile-fry interactions within refuge areas. This hypothesis was examined in Phase II.

OTHER OBSERVATIONS.— Additional data collected during Phase I included examination of guppy scales for fluorescent marks and records of disease incidence. Examination of scales removed from fish at week 36 was disappointing. No scales showed more than five to seven marks while the maximum expected number of marks was nine. It is possible that at the final ration level individual fish did not receive sufficient food intake to produce detectable marks. Further research into the matter was not pursued, but marking was continued during Phase II so that experimental manipulations would remain constant. All guppy disease problems were chronic in nature, minor, and were consistently diagnosed as piscine tuber-

culosis. At no time did deaths due to disease approach epidemic levels in any population. Frequency of disease symptoms, deaths attributable to disease, etc., for each population may be found in Hankin (1978b).

Phase II (Weeks 36-58)

Long-Term Controls: Populations 5, 6, and 12

Total population biomass of control guppy populations during weeks 36-58 confirmed the earlier speculation that populations were near their maximum biomass by week 36. Net changes in total biomass from week 36 to week 58 were $+0.5$, $+0.1$, and $+0.9$ g in populations 5, 6, and 12. Minor asynchronous fluctuations in biomass occurred throughout Phase II in all control populations. Logistic-based estimates of maximum supportable biomass made at week 36 were 30.6, 32.4, and 31.1 g and agreed remarkably well with actual biomass levels at termination, 28.3, 30.7, and 30.7 g.

Control populations showed no signs of convergence in total population numbers nor of parallel fluctuations. Although total numbers in the three control populations differed greatly, total numbers and weights of reproductive females (size categories A_6-A_8) were similar. In populations 5, 6, and 12 there were 37, 36, and 42 such females at termination with corresponding total weights of 20.6, 17.6, and 20.0 g. Since fecundity is roughly proportional to female weight, the three populations had nearly equal reproductive potentials in spite of large differences in total numbers. Adult females accounted for from 57 to 72% of total population biomass. No uniformity in numerical or biomass densities was noted for adult males.

Treated Populations

BIOMASS DYNAMICS. — Total population biomass increased in all treated guppy populations during Phase II (Figure 9). At termination, mean population weights of the three treatment groups were not found significantly different in pairwise comparisons (Student's t tests). Since greatest differences in mean biomass among treatment groups occurred at week 58, there were probably no statistically significant differences in mean biomass throughout Phase II. Alteration of refuge fence spacing had no apparent effect on population biomass growth.
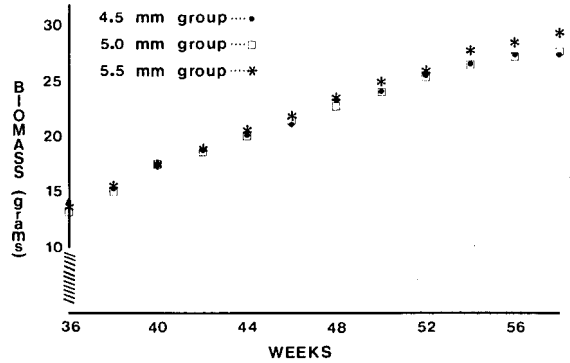

FIGURE 9.—Mean total biomass in treatment groups of guppies during Phase II.

Mean total weights of mature females (size categories A_6-A_8) differed significantly among treatment groups (Student's t tests). The mean percentage of total population biomass accounted for by adult females was consistently higher in the 5.5 mm group (71%) than in the 4.5 mm group (56%).

NUMERICAL DYNAMICS. — Although biomass growth was roughly equal for all treated guppy populations, treatment groups diverged rapidly in total numbers (Figure 10). Smallest population numbers were maintained in the 5.5 mm group, intermediate but highly variable numbers in the 5.0 mm group, and largest numbers in the 4.5 mm group. At termination mean total numbers in the 4.5, 5.0, and 5.5 mm treatment groups were 249, 160, and 128. Mean net additions during Phase II, in the same order, were 172, 86, and 47.
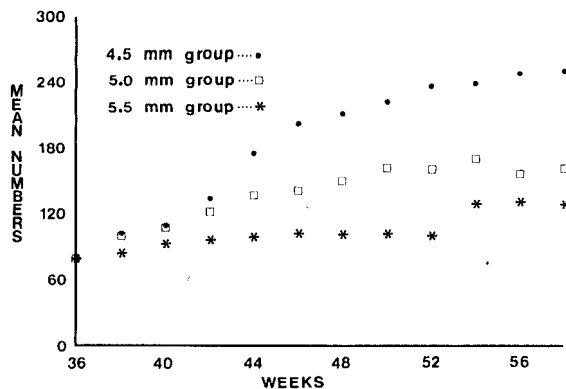

FIGURE 10.—Mean total numbers in treatment groups of guppies during Phase II.

Alteration of refuge fence spacing during Phase II was believed to have influenced both the intensity and duration of juvenile-fry interactions. Behavioral observations of a 5.0 mm refuge population provided a partial explanation of mechanisms involved. A female was observed delivering four fry and the subsequent immediate fate of the fry was followed. Two of the fry were pursued and consumed by two different adult females. Two other fry successfully entered a refuge area after vigorous pursuit by several males and females, including the female giving birth. Once within the refuge area the fry were chased and nipped by larger juveniles. Although the juvenile chase shortly ceased and the fry settled to the aquarium bottom apparently uninjured, alternative outcomes seemed possible. Fry could have been chased outside the refuge area where they would once more be vulnerable to adult predation or the juvenile contact could have resulted in death and perhaps cannibalism. The observations indicated that survival of newly born fry was determined in an extremely short period of time. From release to death or apparent survival in the refuge area never occupied more than perhaps 2 min. Since guppy fry are capable of rapid swimming within minutes after birth, it is unlikely that juvenile pursuit within the refuge area would be successful except during the first few minutes after birth.

The intensity and duration of juvenile-fry interactions, reflected in patterns and magnitude of numerical population growth among treatment groups, was measured and characterized (in parentheses see Table 10) in several ways:

1) by the number of biweekly intervals in which adjusted population increments were ≤ 0 ($\# PI \leq 0$);
2) by the length in biweekly intervals of the longest period without a positive population increment (Long. 0 PI);
3) by the median adjusted population increment (Med. PI);
4) by the median population numbers (Med. N);
5) by the total number of data observations with zero individuals per any size category ($\# 0/CAT$); and
6) by the mean percentage of population numbers in size categories $\geq J_{5.0}$ (% adult).

Measures 1) and 2) were designed to evaluate the prominence of pulsing. Intervals between successive pulses of increase should be greatest when

TABLE 10.—Comparison of measures of numerical population growth for treated guppy populations during Phase II. See text for explanation of column entries.

Treatment group	# PI≤0	Long. 0 PI	Med. PI	Med. N	# 0/CAT	% adult
4.5 mm:						
4	1	1	9	192	0	52
7	1	1	22	236	0	41
9	1	1	9	178	0	53
Mean	1	1	13.3	202	0	48.7
5.0 mm:						
1	2	2	21	196	0	47
3	4	1	8	146	0	64
10	4	2	1	83	6	87
Mean	3.3	1.7	10	141.7	2	66
5.5 mm:						
2	4	2	1	99	4	81
8	6	2	0	122	5	73
11	5	4	0	79	12	73
Mean	5	2.7	0.3	100	7	75.7

longest periods of juvenile presence occur within refuge areas. The 5.5 mm group should exhibit strong pulsing behavior while the 4.5 mm group should show little if any pulsing (Silliman and Gutsell 1958). Measures 3) and 4) were designed to evaluate effects of juvenile-fry interactions on population numbers. Although the duration of juvenile-fry interactions might not be reflected in total population size at any given time, it should be reflected in median population numbers and in median population increments during the experimental period. Measures 5) and 6) were designed to evaluate size structure smoothness and relative dominance by adults. The characteristic patterns of growth produced under different refuge environments should be reflected in the age structure of treated populations and, although less distinctly, in the size structure. The 4.5 mm group should have a finely graded size structure with juveniles nearly always present, while the 5.5 mm group should have a fluctuating size structure perhaps including distinct "size classes" corresponding to separate pulses of increase.

Comparison of these measures compiled for all treated populations showed clear separation for each measure between 4.5 mm and 5.5 mm groups. In no case was the 5.0 mm group clearly separated from the other groups, although means of all measures for the 5.0 mm group fell between means for 4.5 mm and 5.5 mm groups. Orders of means were in the directions expected on the basis of the juvenile-fry interaction hypothesis (Table 10).

The above comparisons do not, however, allow a "test" for differences in numerical population growth patterns among treatment groups, in part because the several measures are not independent of one another. Rather, comparison of these quan-

titative measures allows qualitative separation of treatment group behavior, illustrates the high variability in behavior within the 5.0 mm refuge fence group, and shows that measures of numerical dynamics generally conform to anticipated differences.

The larger variability in population behavior among the 5.0 mm treatment group was witnessed earlier among the original 10 replicate populations equipped with 5.0 mm refuge fence. Laakso (1959) speculated that the tendency toward cannibalism increased with age of guppies and it may be that at the $J_{4.5}$ stage such tendencies are first beginning to be expressed. The exact age or size at which they become fully expressed may be highly variable. An alternative possibility here would certainly include possible imperfections in refuge fence construction which might have allowed $J_{5.0}$ fish, which clearly exhibited antagonistic behaviors toward fry, to remain within 5.0 mm refuge areas beyond the size at which they should have been excluded.

SURVIVAL RATES.—Since the juvenile-fry interactions often created pulses of numerical increase in the guppy populations, there were frequent intervals in which there were no new individuals entering populations. Survival rates for most populations during Phase I and Phase II were estimated by comparing the numbers of fish present at the beginning of such an interval to numbers present at the beginning of the next biweekly interval during which new numerical growth was recorded. Survival rates for the 4.5 mm group and for certain 5.0 mm populations during Phase II could not be estimated due to the continuous nature of numerical increase. Estimates of survival rates for intervals >2 wk were converted to biweekly estimates assuming constant biweekly survival over the longer period. Mean biweekly survival rate estimates ranged from 0.972 to 0.995 during Phase I and from 0.953 to 0.984 during Phase II, averaging 0.984 and 0.970. These biweekly rates indicate roughly 50% annual survival, a reasonable figure for laboratory populations of guppies.

FECUNDITY.—Dissection of a wide size range of gravid guppy females at termination showed that numbers of embryos were linearly related to the cube of female length. Variability in embryo counts appeared to increase with female size (Figure 11). A linear regression of num-
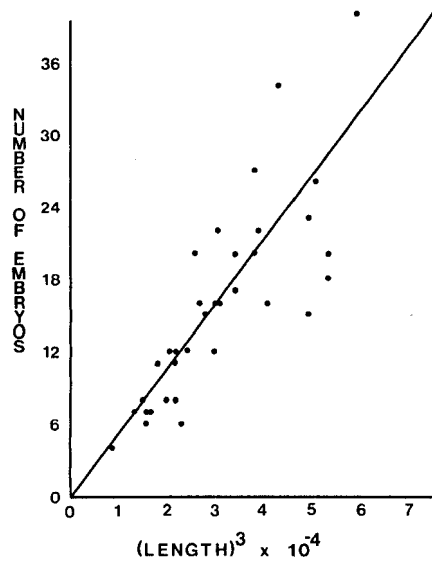

FIGURE 11.—Number of embryos plotted against the cube of female guppy length (standard length in millimeters). Regression line is forced through the origin.

bers of embryos against the cube of female length was forced through the origin and could be expressed as:

$$E = 5.328 \, (L^3 \times 10^{-4})$$

where E = number of embryos
L = standard length in millimeters.

The regression was forced through the origin to ease manipulation of the fecundity relation in further analyses and, over the majority of the size range, did not differ appreciably from a regression with intercept. The empirical relation obtained was similar to earlier results of Felin (1935) and Laakso (1959).

A mean condition factor (K in the formula weight = $K \cdot L^3$) for gravid and nongravid females in $A_{5.5}$ and larger size categories at weeks 36 and 58 was applied to the above relation to obtain an expression relating embryo counts to female weight in grams: $E = 22.347 \cdot$ female weight. In the following analyses the fecundity relation was assumed to have held constant throughout the 58-wk experimental period.

ANALYSIS: NUMERICAL DYNAMICS

Behavior of the treated guppy populations during Phase II generally supported the hypothesis of

juvenile-fry interactions and the proposed conceptual model. However, analysis to this point has implicitly assumed a constant input of newly born fry into the refuge areas, modified downward by the presence of interacting juveniles. Since fry were produced by reproductive females whose numbers. and weights increased greatly as populations grew, a complete analysis must clearly include a description of the female reproductive component. Additionally, the influence of adult predators outside the refuge area must be considered. In this section I develop a mathematical model of the dynamics of numerical population change and subject this model to statistical analyses.

Development of a Mathematical Model

Population reproductive potential increases with the weight and number of adult guppy females. The total reproductive potential, i.e., the maximum possible number of fry born in a given interval, in a population at the beginning of an interval can be computed from the fecundity relation and the total female weight as: reproductive potential = $22.347 \cdot \sum_{A_6}^{A_8}$ total weight females per size category. Total reproductive potential is not realized in any given interval since only some (variable) fraction of females will actually deliver broods. In order to obtain estimates of biweekly fry production, the probability that a female will deliver a brood during a 14-d experimental interval is needed.

The calculation of this probability requires: 1) the expected length of an interbrood interval (time from the last brood when the next brood is delivered), 2) an estimate of the gestation period or minimum time between broods, and 3) a frequency distribution for the interbrood interval. In guppies the interbrood interval is roughly 31 d (Breder and Coates 1932; Winge 1937; Rosenthal 1952), gestation period has been estimated at from 21 to 25 d (Winge 1937; Rosenthal 1952), and a rough frequency distribution may be constructed from the preceding studies. Using "renewal process" theory (Drake 1967), the probability that the waiting time Y until the next brood of an individual female is delivered will be ≤ 14 d (length of a sampling interval), when there is no knowledge of her exact stage in the brood cycle (as was the case for these populations), is denoted by $P(Y \leq 14 \text{ d})$. Letting T = interbrood interval, and s be a fixed

but random point in the brood cycle, then $T = s + y$; that is, the total length of the interbrood interval (T) is equal to the time since the last brood (s) plus the waiting time (y) until the next brood is delivered. Using a cumulative density function for the interbrood interval (T), which may be constructed from previous studies, one has (using standard notation):

$$P(T \leq t) = F_T(t).$$

Then $f_Y(y) \qquad = \dfrac{[1 - P(T \leq y)]}{E(T)}$

and $\quad P(Y \leq 14) = \displaystyle\int_0^{14} \dfrac{[1 - P(T \leq y)]}{E(T)} \, dy$

$$= 1/E(T) \cdot \int_0^{14} [1 - F_T(y)] \, dy \quad (1)$$

where $E(T)$ denotes expected value.

The probability of an interbrood interval of ≤ 14 d is 0 (gestation period estimates are at least 21 d) so Equation (1) may be reduced to: $P(Y \leq 14) = 14/E(T) = 14/31 \doteq 0.452$.

This probability may be applied to the estimated reproductive potential to obtain an estimate of the expected number of births in a 2-wk interval as: expected number of births $_{t,\,t+2} = 0.452 \cdot$ reproductive potential $_t$. Comparison of adjusted population increments $(\widehat{API})$ with expected number of births $(\widehat{EB})$ allows estimation of survival rates $(\hat{S})$ for fry born in a given interval as:

$$\hat{S}_{t,\,t+2} = API_{t,\,t+2}/\widehat{EB}_{t,\,t+2}.$$

Survival of newly born fry through a 2-wk interval depends on both predation by adults outside the refuge area and juvenile-fry interactions within the refuge area. Survival within the refuge area is conditioned upon the event "successful refuge entry," so one has:

$P(\text{survive to } t + 2) = P(A \text{ and } B) = P(A) \cdot P(B|A)$

where $P(A) \quad = P(\text{"successful refuge entry"})$
$P(B|A) = P(\text{survive within refuge area given } A \text{ has a successful outcome}).$

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Events A and B are related to densities of adults and juveniles, respectively, during a 2-wk interval.

By examination of only those sampling intervals for which the (initial) juvenile ($J_{4.5}$) density equals 0, one may separate the relation between adult density and fry survival from the complicating juvenile-fry interaction. For such intervals, neglecting natural mortality, survival within the refuge area should be approximately 1. That is, when $J_{4.5}$ density = 0: $P(A$ and $B) = P(A) = f$(adult density only). Biweekly fry survival rates were estimated as described above and plotted against numerical densities of fish in size categories $J_{5.0}$ through A_8 in 5.0 mm populations from Phase I and from long-term control populations during Phase II revealing a decreasing trend in survival rates with increasing predator density (Figure 12). Beyond 100 adults, estimated survival was close to zero. The trend appeared roughly exponential (one explanation is based on random encounters between predators and prey, see Ricker 1954), so a negative exponential model was used for further analysis:

$$P(A) = \exp[B_1 \cdot (\text{adult density})]; \ B_1 < 0.$$

Since adults were always present when juveniles were present in refuge areas, it was not possible to separate the effects of the juvenile-fry interaction from adult predation. By analogy, I also used the negative exponential model to describe the relation between juvenile numbers and refuge area fry survival rates, i.e.:

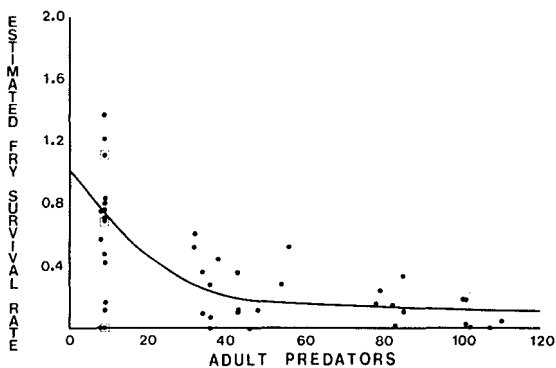$$P(B|A) = \exp[B_2 \cdot (J_{4.5} \text{ density})]; \ B_2 \leq 0.$$

FIGURE 12.—Relation between estimated guppy fry survival rates ($\hat{S}_{t, \ t + 2}$) and number of adult guppy predators (number $\geq J_{5.0}$ at t) when no $J_{4.5}$ juveniles were present at t. Line is drawn by eye. Squares represent multiple observations.

The full model appropriate for all sampling intervals is then:

P(survive to $t + 2$ given born in $t, t + 2$)

$$= \hat{S} = API/\widehat{EB} = \exp(B_1 X_1 + B_2 X_2)$$

where X_1 = number of adults in size categories $J_{5.0}$ and above at time t

X_2 = number of $J_{4.5}$ juveniles at t.

Statistical Analysis

Two techniques were used to fit the collected guppy population data to the proposed model developed above. Both techniques were based on the same assumed model although the model was expressed in different forms according to analysis technique:

$$\hat{S}_{t, t+2} = API_{t, t+2}/\widehat{EB}_{t, t+2}$$

$$= \exp(B_1 X_{1_t} + B_2 X_{2_t}), \text{ and} \qquad (2)$$

$$API_{t, t+2} = \widehat{EB}_{t, t+2} \cdot \exp(B_1 X_{1_t} + B_2 X_{2_t}). \ (3)$$

Multiple regressions, forced through the origin, were fit to a transformation of Equation (2) (adding 1 unit to API to avoid undefined natural logarithms)[4]:

$$\ln [(API_{t, t+2} + 1)/\widehat{EB}_{t, t+2}] = \hat{B}_1 X_{1_t} + \hat{B}_2 X_{2_t}.$$

Alternative estimates of B_1 and B_2, the "coefficients of predation" for adults and juveniles, were obtained by nonlinear least-squares regressions based on a Taylor series linearization of Equation (3) (Draper and Smith 1966). In this case one minimizes:

$$\sum (API_{t, t+2} - \widehat{API}_{t, t+2})^2 = \sum [API_{t, t+2}$$

$$- \widehat{EB}_{t, t+2} \cdot \exp(\hat{B}_1 X_{1_t} + \hat{B}_2 X_{2_t})]^2$$

to obtain the iterative solutions for B_1 and B_2. Iteration was continued for these estimates until the last estimate agreed with the previous estimate to six decimal places. All population data series were subjected to analysis by the same model. Note that the dependent variable for the

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[4]While an interaction term of the form $X_1 X_2$ might seem a logical addition to the above model, analyses failed to indicate that such an interaction was significantly involved in determining numerical dynamics of the populations.

multiple linear regressions is the natural logarithm of estimated survival rates, while for the nonlinear regressions it is actual observed population increments.

If the model were correct one would expect that statistical analyses should give:

1) estimates of the B_1 coefficient similar in all populations,
2) estimates of the B_2 coefficients which are:
   a) close to 0 in the 4.5 mm populations,
   b) some negative number in the 5.0 mm populations,
   c) some negative number larger in absolute value than in b) for 5.5 mm populations.

No juvenile interactions would be expected in the 4.5 mm treatment group and $J_{5.0}$ individuals contributing to predation in the 5.5 mm populations, but not included in X_2, would be expected to increase the B_2 coefficient. Numbers of $J_{4.5}$ individuals present at the beginning of intervals during Phase I were estimated from total numbers and weights recorded for the combined J_4 cate-

gory monitored during Phase I (see Hankin 1978b for details).

Results of multiple regression analyses of original and long-term 5.0 mm populations appear in Table 11 and of treated populations during Phase II in Table 12. Squared multiple correlation coefficients (r^2), when both adults and juveniles were included in regressions, ranged from 0.8003 to 0.9272 in Phase I populations indicating that about 80 to 90% of the uncorrected sums of squares of the natural logarithms of estimated fry survival rates could be explained by regression on adult and juvenile densities. Estimates of adult predation coefficients were similar for all populations, and estimates of juvenile predation coefficients differed in the expected order among treatment groups. Differences among juvenile predation coefficients were less striking than had been anticipated. Mean estimates of B_2 for 4.5, 5.0, and 5.5 mm treatment groups were -0.0280, -0.1009, and -0.1249.

Alternative estimates of B_1 and B_2, obtained by minimizing the squared deviations between actual and predicted biweekly adjusted popula-

TABLE 11.—Estimates of predation coefficients (B_1, B_2) and squared multiple correlation coefficients (r^2) for Phase I guppy populations. Based on multiple regression analysis of the hypothesized model: $\ln[(API + 1)/\widehat{EB}] = B_1 X_1 + B_2 X_2$. See text for explanation of model parameters.

Population number	Weeks	Fence (mm)	Adults and juveniles			Adults only		Juveniles only	
			B_1	B_2	r^2	B_1	r^2	B_2	r^2
1	0-36	5.0	−0.0471	+0.0055	0.9186	−0.0449	0.9185	−0.1029	0.8423
2	0-36	5.0	−.0426	−.0031	.9272	−.0429	.9272	−.1568	.3370
3	0-36	5.0	−.0202	−.1457	.8116	−.0397	.6298	−.2146	.7223
4	0-36	5.0	−.0322	−.0994	.9044	−.0448	.8406	−.2292	.6910
5	0-58	5.0	−.0316	−.1485	.8691	−.0512	.8099	−.3084	.7661
6	0-58	5.0	−.0221	−.1170	.9111	−.0416	.8580	−.2207	.8576
9	0-36	5.0	−.0472	−.0771	.8324	−.0589	.8080	−.2530	.6090
10	0-36	5.0	−.0317	−.1033	.8774	−.0480	.7954	−.2094	.7129
11	0-36	5.0	−.0335	−.1131	.8003	−.0456	.6664	−.1943	.5352
12	0-58	5.0	−.0257	−.0963	.8489	−.0347	.8140	−.2637	.6762

TABLE 12.—Estimates of predation coefficients (B_1, B_2) and squared multiple correlation coefficients (r^2) for treated guppy populations during Phase II. Based on multiple regression analysis of the hypothesized model: $\ln([API + 1]/\widehat{EB}) = B_1 X_1 + B_2 X_2$. See text for explanation of model parameters.

Population number	Weeks	Fence (mm)	Adults and juveniles			Adults only		Juveniles only	
			B_1	B_2	r^2	B_1	r^2	B_2	r^2
4	36-58	4.5	−0.0155	−0.0665	0.9005	−0.0328	0.8850	−0.1225	0.8888
7	36-58	4.5	−.0176	−.0253	.8529	−.0250	.8385	−.0755	.7852
9	36-58	4.5	−.0303	+.0079	.8867	−.0288	.8864	−.1340	.8047
Means: 4.5 mm group			−.0211	−.0280	.8800	−.0289	.8700	−.1107	.8262
1	36-58	5.0	−.0068	−.1228	.8744	−.0282	.8567	−.1608	.8727
3	36-58	5.0	−.0276	−.0682	.9211	−.0375	.9078	−.2258	.8352
10	36-58	5.0	−.0492	−.1117	.9501	−.0538	.9437	−.7307	.5749
Means: 5.0 mm group			−.0270	−.1009	.9152	−.0398	.9027	−.3724	.7609
2	36-58	5.5	−.0392	−.1433	.9599	−.0518	.9532	−.2274	.9078
8	36-58	5.5	−.0430	−.0417	.9550	−.0486	.9536	−.1732	.8999
11	36-58	5.5	−.0450	−.1896	.9114	−.0589	.8617	−.3131	.8057
Means: 5.5 mm group			−.0424	−.1249	.9421	−.0531	.9228	−.2546	.8711

tion increments, were strikingly different among treatment groups. Mean estimates of B_2 in 4.5 mm and 5.0 mm treatment groups were -0.0024 and -0.0857. Estimates for the three 5.5 mm populations were -0.0494, -0.1523, and "$-$. Large" (fails to converge to finite negative number), again indicating strong interaction by juveniles (Table 13). However, alternative fits of actual population increases against adult and juvenile densities could account for an average of only 59% of the variation in the uncorrected sums of squares of the adjusted population increment variable. Still, given initial population states at the beginning of intervals, the patterns of predicted increments exhibited pronounced pulses and generally behaved well relative to actual population histories (Figure 13).

FIGURE 13.—Sum of observed (solid line) and predicted (dots) population increments for guppy population 4 during Phase I.

TABLE 13.—Estimates of predation coefficients (B_1 and B_2) and squared multiple correlation coefficients (r^2) for all treated guppy populations for specified intervals. Based on iterative Taylor Series approximation analysis of the hypothesized model: $API = \widehat{EB} \times \exp(B_1 X_1 + B_2 X_2)$. Estimates which fail to converge ($-$.Large) are not included in means.

Population number	Weeks	Refuge (mm)	B_1	B_2	r^2
1	0-36	5.0	-0.0258	-0.0224	0.8286
2	0-36	5.0	$-.0340$	$-.0137$	.7364
3	0-36	5.0	$-.0172$	$-.1972$	.5295
4	0-36	5.0	$-.0223$	$-.1290$	.7867
5	0-58	5.0	$-.0636$	$-.4198$	.4000
6	0-58	5.0	$-.0184$	$-.1354$	.4997
9	0-36	5.0	$-.0509$	$-.0640$	.2900
10	0-36	5.0	$-.0346$	$-.0585$	.6453
11	0-36	5.0	$-.0195$	($-$.Large)	.7671
12	0-58	5.0	$-.0204$	$-.1137$	.4270
Means: Phase I and long-term controls—5.0 mm			$-.0307$	$-.1282$	.5461
4	36-58	4.5	$-.0267$	$-.0025$	.6519
7	36-58	4.5	$-.0181$	$-.0088$	.8022
9	36-58	4.5	$-.0284$	$+.0041$	.7512
Means: 4.5 mm group			$-.0244$	$-.0024$	.7351
1	36-58	5.0	$-.0120$	$-.0717$	.8459
3	36-58	5.0	$-.0286$	$-.0367$	.7236
10	36-58	5.0	$-.0484$	$-.1487$	.4371
Means: 5.0 mm group			$-.0297$	$-.0857$	.6689
2	36-58	5.5	$-.0367$	$-.1523$	.5103
8	36-58	5.5	$-.0355$	$-.0494$	.5890
11	36-58	5.5	$-.0246$	($-$.Large)	.6060
Means: 5.5 mm group			$-.0323$	$-.1009$	.5684

DISCUSSION

In no earlier population experiments with guppies have detailed analyses of numerical population growth been attempted. Analyses employed in this study were designed with two purposes in mind. Comparisons of numerical dynamics measures, while perhaps unsatisfying to those demanding rigorous statistical tests or parameter estimates, allowed qualitative distinctions to be drawn among treatment groups and
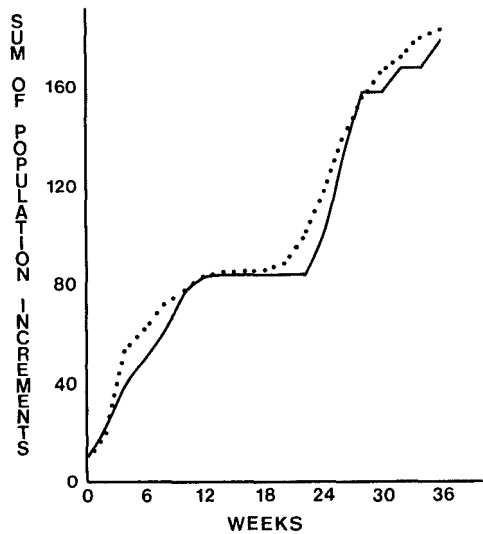
showed clear differences in the patterns and variability of numerical population growth. Least-squares regression techniques, while shedding no light on the qualitative features of numerical increase, allowed evaluation of the fit of the hypothesized numerical dynamics model to collected experimental data and also allowed estimation of adult and juvenile stock predation coefficients. That multiple regression analysis failed to indicate as striking differences in juvenile predation coefficients among treatment groups as did nonlinear least-squares regression illustrates a strong relation between analysis technique and analysis result. Clearly, parameter estimates based on linear fits of a survival equation are not comparable with those obtained by minimizing squared deviations between observed and predicted population increments, although the underlying numerical dynamics model and experimental data used are identical for both analyses. In the absence of detailed data specifying the true error component of the underlying model it is unclear which regression technique is appropriate. Regardless of such technical issues, all analyses support the hypothesis that alteration of refuge habitat quality may significantly change biological interactions among components of a population. This finding is compatible with earlier studies and also unifies the "conflicting" results of previous studies with and without refuge areas.

Analyses of these experimental populations show that there are two distinctly different components of experimental population growth and that these two components should be separated in mathematical treatments of population dynamics. Numerical growth in experimental populations is an extremely variable population phenomenon, only weakly predictable through convential models and statistical techniques. Total biomass growth is a relatively invariant population process, highly predictable, and nearly immediately responsive to slight disturbances in food supply. From a modeling perspective, these considerations imply that population biomass growth might be adequately described by a simple deterministic model, such as logistic growth, while description of numerical growth may require more complex and perhaps stochastic models.

Description of numerical dynamics is, of course, the province of stock-recruitment theory. Neglecting the issue of the extreme variability in numerical behavior of these populations for the moment, these experiments reveal at least two likely biological complications which may render simple stock-recruitment theory of limited practical application. The observed strong juvenile-fry interaction shows that recruitment may depend not only on parent adult stock but also on juvenile stock, perhaps at different times and in different places. Simple stock-recruitment theory clearly requires modification to account for such interactions. Also, density-dependence of growth may further compound the complexity of the recruitment process. While numerical change within sampling intervals may be adequately, although imperfectly, described by the model developed, eventual recruits, say in terms of adult females, are evidently not a simple fraction of numerical increase some fixed number of weeks previous. Models of recruitment in fish populations have not explicitly dealt with complications that might be introduced by the density-dependence of year-class growth, dependence that may occur after a year class has been established.

The probable general effects of a strong juvenile-fry interaction may be examined by making a few simplifying assumptions (none of which are more than only approximately met by guppies) and then to recast the experimental numerical dynamics model as a more general relation similar in form to the simple stock-recruitment model first proposed by Ricker (1954). These assumptions are: 1) The expected number of births is proportional to the number of reproductive females rather than to the biomass of females. 2) The number of reproductive females is proportional to the total number of adult predators. 3) The correlation between size and age is perfect and growth rates of individuals are density independent. Then, letting A = number of adult predators, J = number of interacting juveniles, and a, b_1, b_2 = constants, the experimental numerical dynamics model,

$$API = \widehat{EB} \cdot \exp(B_1 X_1 + B_2 X_2),$$

may be reexpressed as (using assumptions 1) and 2)):

$$API = a\, A \exp(b_1 A + b_2 J)$$

and if recruits are a constant fraction of numerical increase in a given period (using assumption 3)):

$$R = a'\, A \exp(b_1 A + b_2 J)$$

where a' = constant
R = "recruitment."

Three dimensions are required for visualization of a hypothetical stock-recuitment relation incorporating a juvenile-fry interaction. To examine such a relation, experimental estimates of b_1 (-0.031) and of b_2 (-0.160) were taken from the mean nonlinear estimates for 5.0 mm refuge fence populations. Based on ratios of expected number of births to numbers of adult predators, a rough estimate for a' was obtained (= 2) by assuming that recruitment was determined at the end of a sampling period. A plot of the adult-juvenile stock-recruitment relation thus produced is given in Figure 14.

There is a pronounced flattening of the recruitment surface with increasing juvenile density. At high juvenile density (15 on the graph), recruitment is low, nearly constant, and is essentially independent of adult stock. If such interactions occur within populations of fish simple plots of recruitment against adult stock would reveal little trend at high juvenile densities. At low juvenile densities, however, recruitment appears strongly related to adult stock in the classic dome-shaped manner. At low levels of adult stock recruitment may fluctuate considerably, independent of adult stock, as a response to high or low juvenile densities. In general the more intense the inhibition of fry survival rates by juveniles, the
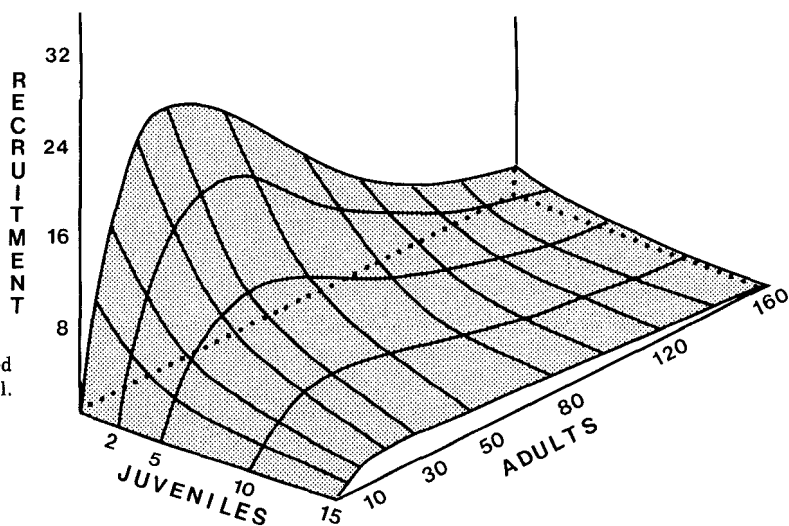
FIGURE 14.—Visualization of proposed adult-juvenile stock-recruitment model. See text for explanation.

more extreme would be the expected fluctuations in recruitment at the same adult stock densities. Variability in recruitment would be increased with a decrease in adult stock, as would be caused by fishing.

If, instead of juveniles of the same species, juveniles (or perhaps adults) of another species interact with fry (or larvae) in a similar manner, one may begin to imagine the complexity of possible "true" recruitment mechanisms in fish populations. Standard simple stock-recruitment relations may require more dependence of recruitment on adult stock alone than is justified. Intraspecific or interspecific interactions of the type observed in these experimental populations clearly create complex recruitment processes, incapable of even approximate description on the basis of adult stock alone. If recruitment theory is to be of practical significance in the management of fish populations, it seems that the numerical dynamics of given populations will have to be examined as unique biological phenomena, perhaps only rarely susceptible to standardized mathematical descriptions such as the Ricker stock-recruitment model.

One may, of course, deny the relevance of the above conclusions, derived from single species laboratory populations maintained under fixed food supply, for the modeling of natural populations. In particular, it may be questioned whether the extreme variability in numerical population growth observed in experimental populations does in fact also occur in natural populations. And it

may also be questioned whether natural populations actually exhibit such extreme response of individual growth rates to variations in population density. Several aspects of guppy life history and empirical observations from natural populations together argue that experimental variation in numerical population growth indeed has clear parallels in natural populations. The second issue, that concerning density dependence of growth, is less easily resolved.

The extreme variability in numerical population growth observed in these experimental populations arises primarily from small population size. This variation is inherent and depends on the guppy reproductive cycle. Since all statistical analyses were based on expectations of events, and since in small populations the discrepancy between actual outcomes of events and their expectations may be large, statistical analysis and prediction of numerical growth patterns were inherently weak. For example, fry survival rate estimates were based on the expected number of births in a 2-wk interval rather than on actual births which were unknown. At initiation of populations only five adult females were present. The initial "biweekly" sampling interval was 16 d so the probability of an individual female delivering a brood within the first interval was $16/31 = 0.516$. Since broods of females are delivered independently of one another, one may reasonably assume that the number of broods delivered in the first interval among five adult females was binomially distributed with parameters n (= 5) and

p (= 0.516). The mean of this distribution, $n \cdot p$, is the expected number of broods delivered in the first period, or: $5 \times 0.516 = 2.58$ broods.

Further, taking the mean initial weight of adult females to be 0.5 g, the fecundity relation predicts an expected brood size of 11.14 fry and a possible range of from 5 to perhaps 20/brood. Thus, the expected number of births (EB) is: 2.58 broods $\times$ 11.14 births/brood = 28.73 births = $n \cdot p \cdot u$ where: u = expected outcome of a success (i.e., expected number per brood). But the range of possible values for the random variable "number of births in a biweekly interval" was from 0 (0 broods $\times$ 5 births/brood) to 100 (5 broods $\times$ 20 births/brood) births. Assuming that perhaps 70% of the fry born in the first interval survived, since adult predator densities were very low, the collected statistic API could have had a range from 0 to about 70. Hence the estimated fry survival rates could have had a range of from 0 ($API/\widehat{EB}$ = 0/28.73), had no broods been delivered, to as high as 2.44 (70/28.73), if all five females delivered broods. Estimated fry survival rates at adult densities of eight or nine during the first 4 wk reflected this possible variation in actual numbers of broods delivered and number of births per brood and ranged from 0 to 1.38. Thus large variation among estimated fry survival rates at low adult densities is possible and unavoidable if the actual number of births is unknown.

In natural populations fluctuations in year-class strength, the natural analog to numerical experimental population increase, due to variation in early life survival, often range over two orders of magnitude (Forney 1976). While the primary causes behind such variations (often at the same or similar stock densities) seem to be usually environmental, unlike experimental populations under controlled conditions, this variation seems at least equal to that observed in these experiments. Guppy reproductive features, including small brood size, very high but variable fry survival, and high variability in timing of brood delivery, are replaced in most natural fish populations by high fecundity and extremely low and variable early life survival. Thus, although underlying causes differ markedly, observed fluctuations in numerical population growth of natural populations at least equal those observed in experimental populations.

The striking density dependence of growth observed in these populations may, however, repre-

sent an exaggeration of probable levels of growth response to density that may exist in natural populations. Many natural populations are probably not directly limited by their food supply, but rather by competing species, suitable habitat for all life stages, and/or harvest by man. Natural population biomass may in general fall below that which the underlying food supply could in theory support. Also, variation in food supply would make field observations of density-dependent growth less striking. Finally, empirical observations suggest that such intense growth depression with high population density is rarely a feature of commercial fish populations. Rather, observations of extreme stunting of fish size have been collected from simple single species populations in many respects analogous to the experimental populations. Stunting among high density pond and small lake populations of yellow perch, *Perca flavescens*, and eastern brook trout, *Salvelinus fontinalis*, is well known. Although extreme density dependence of growth does occur in natural populations, it seems unlikely for most exploited populations, especially when population biomass has been reduced to perhaps one-half of unexploited levels.

SUMMARY

The ultimate interest in laboratory study of the stock-recruitment process is to gain insight into this fundamental problem and to apply such insight to the study and modeling of natural populations. These experiments illustrate that the stock-recruitment process may involve more than a single adult stock-related feedback control and that more complex mechanisms may involve interactions among several stock components. While mathematical models of more complex stock-recruitment processes may be constructed, that such complex analytic models may be usefully applied in practice is far from clear. Two serious application problems exist and these problems seem inherent to analysis of stock-recruitment relations for any temperate species. The time frame and economic expense necessary to collect data suitable for statistical analysis of possible complex stock-recruitment models and the probably inherent variability of the recruitment process argue that if, indeed, such complex models are to be of practical use, major rethinking of analysis and data collection approaches is required.

Data collection during these experimental stud-

ies, which allowed eventual crude prediction of numerical population behavior, might be roughly analogous to the following field data collection: 1) Collecting data on at least adult stock, young-of-year, and yearling densities from 10 fish populations of the same species in similar environments for 18 yr each. 2) Restructuring refuge area habitats for six of the similar populations, perhaps by removing or increasing weed cover, dramatically reducing the size of all populations, and collecting appropriate data for an additional 11 yr. Few fishery investigators have the opportunity to carry out such an "experiment" in a field context. Instead, a single population may be studied, under fortunate circumstances, for perhaps one or two decades. Analogous replication is impossible. Since the investigator is (usually) not allowed to actively manipulate population age or size structure, but must instead maintain a passive observer role, data collected in a decade might cover only a small range of juvenile and/or adult stock sizes. Recruited year classes, exposed to perhaps violent fluctuations in environmental factors influencing early life survival, might rarely give any indications of a dependency of recruitment on adult or juvenile densities in previous years.

Faced with such constraints on data collection, there seem possible several constructive alternative responses. The general passive approach may be neither appropriate nor effective, and active (experimental) manipulation of populations, forcing collection of data not otherwise obtainable, may be required. This approach has been advocated by Walters and Hilborn (1976) although it clearly calls for major rethinking of the fishery biologist's role. Second, it is possible that year-class strength and adult and other stock components during past years may be estimated through data extraction techniques based on simple gross population measures, e.g., from total biomass harvested from commercial species (Walter and Hoagman 1975). Thus, rather than bemoaning the slow pace at which future observations may be gathered, one may consider past fishery data as an untapped reservoir of information suitable for analysis of the dynamics of recruitment. Statistical evaluation of relations among such extracted estimates does, however, raise serious analytic and philosophic issues. Finally, comparative study of year-class fluctuations among related species and fisheries holds far more promise for revealing biological mechanisms underlying recruitment than is indicated by published literature (Regier 1978).

Since there may be constructive responses to data collection problems, the probably inherent high variability of the stock-recruitment process causes the author greater concern. Although the impact of specific environmental factors may occasionally be separated from possible internal biological controls (Nelson et al. 1977) and allow reduction of unexplained variation in year-class strength, it seems unlikely that a single environmental variable regularly exerts significant impact on year-class strength. Thus, while apparent variation in year-class strength may be reduced under fortunate circumstances, either by accounting for environmental impacts or by considering all relevant stock components, it seems unlikely that collected data will ever fall neatly along some theoretical curve or surface. In general, expectations for statistical measures of goodness of fit for stock-recruitment relations are probably grossly unrealistic and poor fits should be expected. How one ought to evaluate empirical stock-recruitment fits, when the appropriate standard for comparison is probably not "100% of variation" or a correlation of 1, is not clear, although attention has already focused on optimal use of unreliable stock-recruitment parameter estimates (Walters 1975). The danger of presuming independence of recruitment and population stock components, however, seems far more severe than are errors of estimation and generally unsatisfying statistical analyses.

It is hoped that the results of these experiments and the demonstration of a complex multistage recruitment process will stimulate renewed interest in study of the possible biological determinants of recruitment. That simple stock-recruitment theory may often be biologically inappropriate seems clear. But whether more complex and more biologically realistic models of recruitment processes, with their further demands for data collection, will prove of practical use seems far from clear. In the author's view, at present, a wide gulf separates stock-recruitment theory from practice. More careful consideration of the practical use of this body of theory and more realistic expectations from its use are required if the theory is to achieve its proper role in fishery management.

ACKNOWLEDGMENTS

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