THE EFFECTS OF INTRASPECIFIC COMPETITION FOR FOOD ON REPRODUCTION IN THE GUPPY (POECILTA RETTICULATA) AND THE IMPLICATIONS FOR THE STOCK AND RECRUITMENT PROBLEM

## by

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## ABSTRACT

Laboratory experiments were conducted with female guppies to determine the effects of intraspecific competition for food on fecundity, fry size, and gestation period. Two groups of females which had been raised at different levels of intensity of competition were compared. Gestation period was significantly longer in the high competition group. The effects on fecundity and fry size were dependent on the size of the adult female. The largest females in the high competition group did not differ with respect to these parameters from individuals of the same size in the low competition treatment; the smaller females produced fewer but larger fry in each brood under high competition. The total weight of fry per brood produced by females of a given size was not different between treatments.

These results are discussed from the standpoint that the reproductive characteristics of the individuals of a population can be viewed as tactical components of a strategy whose objective is to maximize the present value of the number of surviving progeny produced by each individual in the course of its lifetime. The optimal distribution over time of energy devoted to reproductive ends and the optimal distribution at one point in time of a given amount of energy among many or few offspring are expected to vary among populations according to the particular age- and size-specific mortality rates faced by each population. Both magnitude and variability of mortality are important. It is suggested that by measuring the appropriate reproductive parameters
of the adult members of a population, it should be possible to make predictions about the shape and expected variability of the stock/recruit relationship.

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#### Abstract

Dr. Donald McPhail first suggested that I consider my problem from the point of view of $\underline{r}$ - and $K$ - selection. My understanding of the theory of reproductive strategy increased considerably as a result of conversations with Dr. Eric Charnov and Mr. Stephen Stearns.


In the final phases of the study, I received more than a little help from my friends. Ms. Valerie Best and Ms. Sharon Heizer typed the manuscript, and Ms. Stephanie Judy prepared several figures.

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## INTRODUCTION

One of the central problems of fishery biology is the nature of the relationship between the stock of spawning adults of a population and the strength of the recruit year-class which they produce. The problem can be resolved into two components, both of interest to the fishery manager:

1) What is the average number of recruits produced by a spawning stock of a given size? This relationship over a range of stock sizes defines the shape of the familiar stock-recruit curve and allows the manager to determine the optimal spawning stock size.
2) How much variation is to be expected about the average curve, and what are the specific causes of departures from the average? Variation in strength of year-classes produced by similar-sized spawning stocks is often very large in natural populations. The causes of the variation are usually very difficult to identify and quantify for reasons reviewed by Gulland (1965). If this question could be answered, it would be possible to predict the strength of recruiting year-classes some time before the actual time of recruitment, and therefore total stock sizes could be forecast.

The typical approach to estimation of the stock-recruit relationship has been to collect estimates of spawning stock size and resultant
recruitment for a series of years and to fit a curve to the data. Larkin (1973) has discussed the different types of curves which may be used. Curves described by Ricker (1954, 1958) and Beverton and Holt (1957) are the two types most often used in management; examples of these curves are shown in Figures 1 and 2. In both families of curves, recruitment increases with stock size at low population levels; the major difference between them is that at high stock levels the Ricker curve indicates an absolute drop in recruitment, whereas the Beverton and Holt curve approaches an asymptote. In both families of curves recruitment per unit stock reaches a maximum at intermediate stock sizes and decreases with further increases in spawning stock; thus both curves imply the existence of density-dependent processes regulating population size.

The viewpoint adopted in this study is that the stock/recruit curve for a population represents the result of all the interactions of the reproductive characteristics of the population with particular aspects of the environment. Reproductive characteristics of individual members of the population are assumed to have evolved by natural selection; the combination of reproductive traits shown by a given individual - age at first maturity, fecundity, reproductive lifespan, etc. - can be considered as tactics in a reproductive strategy whose objective is to maximize individual fitness. The hope is that from an understanding of these reproductive tactics in an evolutionary context will come an understanding of their population consequences - that is, the stock/recruitment relationship of the population. The observed year-to-year variation in recruitment indepent of stock density is assumed to


Figure 1. A family of Ricker stock-recruit curves. The general equation is $Z=W e^{a(l-w)}$. In curve $\underline{a}, a=0.667$; in $b$, $a=1.0$; in $c, a=2.678$. After Ricker (1958).


Figure 2. A family of Beverton and Holt stock/ recruit curves. The general equation is $R=\frac{1}{\alpha+\beta / E}$. After Beverton and Holt (1957)。
result from density-independent fluctuations in the relevant environmental variables; if this variability has been present in much the same form over evolutionary time, the reproductive tactics of the population should reflect some accommodation to it.

The experimental part of the present study deals with absolute fecundity and closely related variables. Bagenal(1973) has reviewed the possible relevance of fecundity to the stock and recruitment problem. He cites several field studies showing decreases in average absolute fecundity with increasing population density, namely Bagenal (1963b, 1965), Hodder (1963), Kipling and Frost (1969), Raitt (1968). Laboratory studies by Bagenal (1969a), Hester (1964), and Scott (1962) provide evidence that fecundity of individual females is positively related to nutritional level. The hypothesis which results from this is that observed reductions in fecundity at high population density result from reduced individual feeding level mediated by intraspecific competition; this hypothesis has been suggested several times in connection with the field studies cited above. Bagenal (1973) points out that the observed relationship between fecundity and population density is of the form necessary to produce the stock-recruitment curves of Beverton and Holt and of Ricker, although it is evident that other factors, such as compensatory mortality of eggs and larvae, can produce the same effect.

The objectives of this study, then, are the following:

1) to describe quantitatively the effects of intraspecific competition for food on fecundity and related reproductive parameters, and
2) to relate these findings to the stock and recruitment problem.

Herein competition is taken to mean the demand by two or more organisms for the same resource in excess of immediate supply; this definition is essentially that of Milne (1961). It is of interest to distinguish two different courses that competition may follow: "contest" and "scramble", in the terminology of Nicholson (1954). In contest competition, some of the competitors are able to satisfy completely their requirements for the scarce resources, while others secure little or none. In scramble competition, on the other hand, the available resource is divided more or less randomly among the competitors, and all receive less than their full requirements. The effect of competition, regardless of the course it takes, is to reduce consumption of the scarce resource (relative to full requirements) for some or all of the competitors.

When scarce food is the object of competition, at least some of the competitors will be forced to exist on reduced rations. This reduced energy input to an individual may be allocated among the conflicting intermal demands of maintenance, growth, and reproduction in different ways. Energy expenditure in all categories may be reduced, or expenditures
in one category may be maintained at a high level at the expense of the others. In this study attention is focussed on reproduction, but it is important to remember that reproduction is only one of several processes which may be affected by food shortage.

It would be extremely difficult to pursue the objectives set out-above in a natural fish population. The intensity of competition must depend on population density and the available supply of scarce resources; the identification of critical resources and measurement of available supply would be very involved. Furthermore, it is probable that fish fecundity at a given time is significantly influenced by events occurring from one to several reproductive seasons previously (Bowers and Holliday, 1961; Hester, 1964; Hodder, 1963; Kipling and Frost, 1969); therefore, it is desirable to know the history of a given individual over several reproductive seasons. Both of these problems are far more easily handled in the laboratory than in the field.

The guppy Poecilia reticulata (Peters) was chosen as the experimental animal for several reasons. Guppies are relatively easy to maintain in the laboratory and reproduce readily throughout the year. In addition, their short gestation period (about one month) makes it possible to collect a considerable amount of data on reproduction in a reasonable time.

In Poecilia fertilization is internal, and the embryos develop inside the ovary. The fry are released by the female at an advanced state of development; they can swim actively at birth and normally begin to feed soon after release.

The schedule of stages of oogenesis and embryonic development have been worked out for Poecilia reticulata by Stolk (1951). The ovary of a mature female normally contains oocytes and embryos of three discrete stages: (1) many small undifferentiated oocytes of less than 0.1 mm . diameter, (2) a smaller number of medium-sized oocytes up to 0.3 mm . diameter containing some yolk, (3) either a set of large yolky oocytes (or ova) or a similar number of developing embryos. If we take the day of parturition of one brood as day 0 and assume a constant brood period of 2.8 days, we may follow the development of the oocytes that will eventually constitute one brood. On day 0 some of the many small oocytes begin to differentiate and accumulate yolk. By day 28 these oocytes have become medium-sized oocytes as defined above; they join a pre-existing group of medium-sized oocytes, according to Stolk. Following the next parturition (day 56 in this model), some of the medium-sized oocytes lay down the bulk of their yolk supply very rapidly, maturing to large ova, and are fertilized. The resultant fry are borm on day 84.

On the basis of Stolk's work, it seems possible that, events occurring up to three brood periods before parturition may affect the numbers and sizes of fry produced. In an experimental study of the
effects of feeding on guppy reproduction, Hester (1964) found that brood size was significantly affected by feeding regime of the female during the two brood periods immediately preceding parturition. Hester was unable to rule out the possibility of three period effects.

If an individual guppy reduces the amount of energy dedicated to reproduction, one would expect some or all of the following effects:

1) a reduction in number of fry per brood,
2) a reduction in size of individual fry,
3) an increase in time between broods.

All of these potential effects are examined in this study.

The guppies used in this study were descendants of fish collected in August, 1967, in Trinidad, West Indies. The initial collection consisted of something over 100 adults and immatures taken by B. Seghers from the Tacarigua River about four kilometers northeast of its confluence with the Caroni. River. The fish were shipped by air to Vancouver, where the stock was maintained in aquaria in the laboratory of Dr . N.R. Liley at the University of British Columbia.

At the time of the initial collection the Tacarigua at the collecting site was three meters broad with a rather uniform depth of about .15 m . Current was measured at about $.4 \mathrm{~m} / \mathrm{sec}$., and the water was clear; however, after a rainstorm, the stream becomes turbid, and the flow may increase by an order of magnitude. Aside from an algal film on the stream bottom, there were no aquatic plants at the collecting site. Water temperature was not recorded in 1967, but at a similar site on the nearby Aripo River, temperature varied from 25.5 to $26.5^{\circ} \mathrm{C}$ in the summer of 1969. The cichlid Crenicichla alta and the characid Hoplias malabaricus, both of which prey on adult guppies, were present at the Tacarigua site. Other fishes present included the cichlid Aequidens pulcher, the characids Astyanex bimaculatus and Corynopoma risei, the loricariid Hypostomus robinii, and a pimelodid of the genus Rhamdia (Seghers, 1973, and pers. comm.).

From September, 1969, several hundred of the descendants of the original Tacarigua stock were maintained in the laboratory as a source of experimental animals. The fish were kept in 64 liter capacity glass aquari with floating plants, Ceratophyllum sp., for cover. Water temperatures were maintained at $26 \pm 1^{\circ} \mathrm{C}$ by the use of thermostatically controlled aquarium heaters. Aquaria were not exposed to natural light; the main illumination for the tanks was provided by 20 watt fluorescent lights about 35 cm . above the surface of the water. Lights were automatically controlled to maintain a constant day length of 14 hours throughout the study. All aquaria were filled with tap water to which was added one gram of rock salt per liter*; water lost by evaporation was replaced at frequent intervals with tap water. On a weekly basis 28 1. of water were removed from each tank and replaced with fresh tap water plus salt. Each tank was equipped with a glass wool and charcoal filter to circulate, aerate and filter the water.

The main food during most of the study was live Tubifex sp. (Oligochaeta); fish in stock tanks were fed once daily in amounts sufficient to maintain an almost continuous supply of live Tubifex on the tank bottom. This basic diet was supplemented with small quantities of Tetramin, a commercial dry fish iood. Departures from this basic diet will be discussed below.

Experiment 1: Measurement of Reproductive Parameters of Isolated Females Fed on Excess Tubifex

In August, 1970, 24 healthy mature females were selected from stock tanks as experimental animals. Fish were selected so as to
represent. equally all lengths of mature females present in the stock ${ }^{-}$ tanks ( $14-45 \mathrm{~mm}$. standard length). Individual females were isolated in glass jars of 1.95 1. capacity containing 1.3 1. of water with floating Ceratophylum as cover for fry. Jars were kept in $26^{\circ} \mathrm{C}$ water baths.

- The fish were fed once daily, six days a week with excess Tubifex. Each day before feeding, feces and food remaining from the previous day were siphoned from the jars, and the water was passed through a charcoal and glass wool filter and returned to the jar. At weekly intervals half the water in each jar was removed and replaced with tap water plus salt.

At lease once every 24 hours, jars were carefully examined for the possible presence of fry. Upon discovery, fry were removed from the jar, anaesthetized with MS-222, and measured to the nearest 0.1 mm . standard length under a compound microscope, using a technique adapted from Counts (1961).

After all fry had been released, the female was anaesthetized with MS-222 and measured to the nearest 0.1 mm . standard length with dial calipers. The female was then quickly blotted on a paper towel and placed in a pre-weighed beaker of water; the change in weight of the beaker plus fish was recorded to the nearest. 01 g . The female was then returned to her original jar, to which two males had been added. The males were removed after five days, during which time they were presumed to have inseminated the female (see Rosenthal, 1952).

## Experiment 2: Measurement of Ration of Dry Food

Experiment 1 provided descriptive information on reproduction of fish fed in excess; the next step was to measure the effects of reduced rations. In order to set up a treatment of reduced rations for fish of different sizes, it was necessary to establish a curve of full rations as a function of body size.
'Two separate attempts were made to measure guppies' actual consumption of Tubifex fed in excess. Neither experiment produced usable results; the main problems were the difficulty of accurately weighing the live Tubifex before feeding and of recovering all of the uneaten portion after feeding. To circumvent the difficulties of weighing live Tubifex, dry food (Tetramin) was used exclusively in ail experiments and in the stock tanks beginning in June, 1971.

In this and subsequent experiments a different system was used to isolate individual females in such a way as to minimize predation on fry and to provide improved circulation and filtration of water. Nylon mesh was attached to a plexiglass frame, using Pliobond glue or silicone aquarium sealant, to form 10 separate compartments, each measuring $10.2 \times 12.5 \times 27.8 \mathrm{~cm}$. Each framework was placed in a 64 l. capacity aquarium with a filter system as described above. The water level was maintained so that each individual compartment enclosed about 3.5 1. of water. Figure 3 is a schematic drawing of the apparatus. Each compartment which contained an adult female ( $A, C, D, G, I, J$ ) had fine mesh on three sides; even newborm guppies were too large to penetrate

b


Figure 3. Schematic drawing of the apparatus used in Experiments 2 and 3 to isolate experimental females. The outside dimensions are $20.4 \times 62.5 \times 27.8 \mathrm{~cm}$.
(a) Lateral view
(b) Top view. Solid lines indicate small mesh; broken lines indicate large mesh.
this mesh. The fourth side consisted of larger mesh through which fry but not adults could pass. Thus fry being pursued by their mothers were able to escape through the large mesh into the adjacent refuge compartment $(B, E, H)$. Each refuge compartment was divided diagonally by a fine mesh barrier in order to separate the fry of different females. Fry were observed to use the refuges in the intended manner.

Twenty experimental females were selected from stock tanks so as to give equal representation to all size classes present in the stock tanks ( $14-36 \mathrm{~mm}$ ) . The experimental animals were placed in the individual mesh compartments of the isolation apparatus. After a four day acclimation period, during which fish were fed and excess food was removed once daily, the experimental procedure was begun.

For four consecutive days a weighed quantity of dry food was placed in each compartment, and the fish were allowed to feed undisturbed for one hour. (A pilot study showed that virtually all feeding occurs in the first 15 minutes after food is presented, and that after an hour none of the fish studied showed any further interest in the remaining food.) At the end of the hour the amount of food remaining in each enclosure was recorded qualitatively ( 0 , trace, or + ), and any excess was removed. On the following day the amount of food offered was increased for fish which had consumed all or nearly all of the previous day's ration, and food was reduced for the others. In this manner, it was possible to bracket roughly the actual amount of food consumed in one feeding by an individual fish.

## Experiment 3: Measurement of Reproductive Parameters of Isolated Females at Full and Half Rations of Dry Food

In August, 1971, two groups of 10 healthy females were selected from the stock tanks for use in this experiment. Before the fish were actually selected, 10 values of standard length were picked which covered the range of sizes available in the tanks ( $14-28 \mathrm{~mm}$ ) . Fish from the stock tanks were then measured, and the first ones falling within 0.5 mm . of the predetermined lengths were assigned to full or half rations by the toss of a coin. Each selected fish was placed in the isolation compartment which had been previously designated at random for that specific length and ration. Thus fish were randomly assigned to food treatment and tank position, with the restriction that each treatment group contained the same range and distribution of sizes.

The isolated guppies were daily fed weighed quantities of Tetramin representing full or half rations for their particular weight. Feces and food from the previous day were removed prior to each feeding. Following each parturition, rations were adjusted to the appropriate percentage of post partum weight of the female ( $3.0 \%$ for high, $1.5 \%$ for low food treatment) in order to allow for weight changes due to growth during the experiment.

Tanks were checked at least once dailly for newborn fry, and when births occurred the same procedures were followed as described for Experiment 1. In addition, in this experiment after the standard
length of each fry had been measured, the entire brood was placed in a drying oven at $60^{\circ} \mathrm{C}$, and the dry weight of the brood as a whole was measured to the nearest 0.1 mg 。 after 48 hours, by which time the weights were constant.

RESULTS

In Experiments 1 and 3 mortality of experimental fish was high. The causes of the mortality are not known; possibly the restriction of normal activity imposed by the isolation chambers was somehow involved. Typically fish stopped feeding and remained inactive for a few days or a week before dying. Dead fish showed no external growths, lesions, or parasites, and post-mortem dissections revealed no internal abnormalities.

Because of the losses of experimental animals, both experiments were terminated earlier than anticipated. In Experiment 1, only three fish survived to day 50 ; of these, one died on day 60 , and the other two were alive on day 70, when the experiment was stopped. Experiment 3 was terminated on day 51 with four survivors. As discussed in the Introduction, it was anticipated that reproductive effects of nutrition would be apparent only after a time lag of up to three months. Thus, most, if not all, of the data on reproduction collected in the two experiments reflect feeding conditions in the stock tanks prior to the experiments themselves. This idea is supported by the results of Experiment 3, in which there are no significant differences between the high and low food treatments with respect to either numbers or sizes of fry produced.

## Experiment 1

It was anticipated that maternal size would have significant effects on both numbers and sizes of fry produced. Figure 4 shows
the relationship between the natural logarithm of number of fry in a brood and the standard length of the mother. the points all lie near a straight line with positive slope significantly different from zero ( $\mathrm{p}<.001$ ) .

Eighteen of the experimental females which died were dissected, and their ovaries were examined. Fifteen of these contained developing embryos, althouth in one case decomposition had progressed so far that it was impossible to count the embryos. Of the three females without embryos, one had produced a brood five days before dying, and the next batch of large oocytes had not yet been fertilized; in the other two cases there was no development of oocytes beyond the smallest, least differentiated stage. Figure 5 shows the regression of the natural logarithm of number of embryos on maternal length. The positive slope is significantly different from zero ( $p<.001$ ).

A comparison of the regressions of Figure 4 and Figure 5 may provide a measure of the extent of maternal camibalism, since the embryos counted by dissection had not, of course, been exposed to predation. The comparison was carried out by means of analysis of covariance. The hypothesis that the two regressions have a common slope was accepted at a low level of probability ( $\mathrm{p}=.08$ ). There was a nonsignificant tendency for the excess of embryos over fry actually born and recovered to be greater for smaller females than for larger ones; the largest females had about the same numbers of progeny in both cases (the regression lines intersect at a standard length of 39.7 mm .). The hypothesis that the elevation of the two regression lines is the same was rejected ( $p=.01$ );


Figure 4. The regression of the logarithm of numbers of fry per brood on maternal length. Experiment 1.


Figure 5. The regression of the logarithm of numbers of embryos obtained by dissection on maternal length. Experiment 1.
if the regressions are given the same slope, then for all lengths of females there were significantly more embryos than fry. This result suggests that the numbers of all broods actually born may have been reduced by cannibalism before the fry were removed and counted. However, the differential effect of maternal size is the opposite of what would be expected if predation were the cause of the difference. Sigrificant prematal mortality could also account for this effect. The data collected in Experiment 3 shed more light on this problem.

The relationship of length of fry to length of the mother is positive (Figure 6), but there is considerable variation of length of fry within broods. A straight line fit to the points has a positive slope significantly different from zero ( $\mathrm{p}<.001$ ), but accounts for only about one-fourth of the total sum of squares. Addition of higher order terms (up to quartic) to the regression equation does not significantly reduce the residual.

Two females produced two broods each, and two others produced three and four broods. Thus four individuals gave seven values of time between broods; the mean interval was 24.8 days (standard deviation:2.9; range:22-28 days).

## Experiment 2

After four days of experimental feeding, five fish had not eaten a significant amount on any day; these were all very inactive and were excluded from the analysis. Of the remaining 15 , three produced


Figure 6. The regression of fry length on maternal length. Experiment 1 . The regression line was calculated on the basis of the individual. lengths of 343 fry. For ciarity, only the mean length of each brood $\pm$ two standard errors has been plotted.
broods during the initial acclimation period; one of these died the day after giving birth. One male was added to each of the other two compartments in order to maintain a supply of fresh sperm for the reproductive study which was to follow; the data on feeding for these compartments were also excluded from the analysis.

The remaining twelve individuals all consumed all or nearly all of the food offered on at least one day. Where different amounts were eaten on different days, the higher value was used in the analysis. The solid line of Figure 7 shows the results of the regression analysis of weight of dry food eaten on live weight of female; the linear regression accounts for almost $98 \%$ of the total sum of squares. The Y-intercept of the line is at 0.62 mg . A regression line passing through the origin (broken line in Figure 7) fits the data almost as well; for convenience this second line was chosen as the basis for calculations of rations for Experiment 3.

Experiment 3
This experiment was designed to measure the effects of reduced rations on reproduction. It was intended that the experiment should last for three brood periods in order to allow for the possibility that brood size is determined early in the process of oogenesis. However, mortality of experimental fish was very high (half the fish died in the first 28 days), and the experiment was terminated on day 51 with four survivors.


Figure 7. The regression of daily consumption of dry food on wet weight of female. Experiment 20. Solid line: best linear fit ( $\mathrm{Y}=.6236+.0287 \mathrm{X}$ ). Broken line: best linear fit passing through origin ( $\mathrm{Y}=.02984 \mathrm{X}$ ).

In the course of the experiment, 11 different females produced 16 broods-meight broods in each treatment group.

Within each treatment group there is a significant positive regression of the natural logarithm of number of fry on maternal length; the hypothesis of zero slope was rejected in each treatment group (high food:p<.01; low food .05>p>.02). The two regressions are shown in Figure 8. The residual error about the regression line is significantly greater for low food than for high; this violates the assumptions of analysis of covariance, so statistical comparison of the two treatments was carried out as recommended by Snedecor (1956:97) by means of a t-test using 6 rather than 12 degrees of freedom. Hypotheses of equal slopes and equal intercepts were both accepted ( $p>.5$ ).

In Figure 9 fry size is plotted as a function of maternal size for each treatment group. Two broods from the high food group were born prematurely; fry from these broods had large yolk sacs which imposed an appreciable curve on the body, preventing accurate measurement. These two broods were excluded from this part of the analysis. For neither treatment is the slope of the regression line significantly different from zero. Possible differences in average size of fry between treatment were tested by means of a two-level nested analysis of variance (Table I). There were highly significant differences in average standard length of fry among broods within treatments ( $p<.005$ ), but the difference in average fry length between treatments was not significant in comparison (.25>p>.10).


Figure 8a. The regression of the logarithm of numbers of fry per brood on maternal length. Experiment 3 - high food treatment.


Figure 8b. The regression of the logarithm of numbers of fry per brood on maternal length. Experiment 3 - low food treatment.


Figure 9a. The regression of fry length on maternal length. Experiment 3 - high food treatment. The regression line was calculated on the basis of the individual lengths of 47 fry. The mean length of each brood $\pm$ two standard errors has been plotted.


Figure 9b. The regression of fry length on matemal length. Experiment 3 - Iow food treatment. The regression line was calculated on the basis of the individual lengths of 56 fry. The mean length of each brood $\pm$ two standard errors have been plotted.

TABLE I. Analysis of variance of standard length of fry- high food vs. low food

|  | Source of Variation | d. | SS | MS | F |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | Between treatments | 1 | . 879 | . 879 | $2.149(1,12)$ NS |
|  | Among broods within treatments | 12 | 4.912 | - 409 | 12.58(12,89) ** |
| - | Within broods; error | 89 | 2.890 | . 0325 |  |
|  | Total | 102 | 8.681 |  |  |

Comparison of Experiments 1 and 3
The failure of the fish of Experiment 3 to demonstrate significant differences in reproduction under different feeding regimes is not surprising in view of the response time-lags predictable on the basis of Turner's (1937) and Stolk's (1951) work on oogenesis and Hester's (1964) experiments on reproduction and nutrition. Most of the broods of Experiment 3 were born before the experimental treatment was expected to have taken effect. The data from this experiment probably result from conditions of life in the stock tanks prior to the experiment; the same is probably true for the fish of Experiment 1, although in this case the experimental feeding regime was the same as that of the stock tanks.

The fish of Experiment 1 were fed live Tubif'ex in excess, both in the stock tanks and in the experiment. For two months prior to the beginning of Experiment 3, fish in the stock tanks were fed exclusively on Tetramin given in a single daily feeding. I have no information on the relative nutritional value of Tubifex compared to Tetramin, but experienced aquarists are generally of the opinion that live food is better for fish than dry preparations. After introduction to the aquaria, uneater rubifex survived indefinitely on the bottom, and fish fed on them throughout the day. The dry food, on the other hand, was taken primarily from the surface or as it sank through the water column; uneaten flakes lying on the bottom were usually ignored. Thus the Tubifex-fed fish had the opportunity to feed at will throughout the day, whereas the dry food group effectively was restricted to less than one hour of feeding each day.

Maximum sizes attained by fish fed on Tubifex were considerably greater than those of fish raised on dry food. In selecting the experimental fish for Experiment 1, the largest female measured had a standard length of 45.2 mm . females larger than 30 mm . were common in all stock tanks. In setting up Experiment 3, on the other hand, the largest female encountered measured only 27.8 mm . This is an indication that growth and/or survival rates were lower when only dry food was provided.

Densities of fish in the stock tanks were not measured, but they were similar under both feeding regimes. Each 64 1. capacity stock tank contained approximately 100 to 150 adult guppies plus a similar but more variable number of fry and immatures.

It appears that the stock tank histories of the fish used in Experiments 1 and 3 are different enough that comparison of the results of the two experiments provides valid information on the central problems of this study. Unfortunately, densities and feeding regimes in stock tanks were not carefully controlled; however, the qualitative history of the fish of Experiment 1 was of good nutrition and low intensity of competition, whereas the fish of Experiment 3 experienced poorer nutrition and consequently more intense competition in the months preceding the experiment. On this basis the results of the two treatment groups of Experiment 3 have been pooled for comparison with Experiment 1.

In Figure 10 are reproduced the lines of best fit of the regressions of the natural logarithm of numbers of fry on maternal


Figure 10. Comparison of the regression lines of the logarithm of numbers of fry per brood on maternal length. Broken line: Experiment 1 (points are shown in Figure 4). Solid line: pooled data from Experiment 3 (points are shown in Figures 8a and 8b).
length for the two experimental groups; the points on which the lines are based are shown in Figures 4 and 8. Of course, only the section of the lines corresponding to females under 28 mm . is valid for comparative purposes, since no females above that size produced broods in Experiment 3. The data were compared by analysis of covariance, and the hypothesis that the two regressions were samples from populations having the same slope was rejected $(p=.05)$. The smaller females in Experiment 3 produced significantly fewer fry per brood than did females of the same size in Experiment 1. The lines intersect where maternal length is 26.9 mm. ; in other words, the largest females of the dry food group produced about the same numbers of fry per brood as females of corresponding size in the Tubifex group. This is the same sort of effect that appeared as a non-significant trend in Experiment 1, when numbers of embryos carried by fish of a given size were compared with numbers of fry actually born and recovered for counting.

Figure 11 shows the regression lines of fry lengths on maternal lengths for Experiment 1 and the pooled data for Experiment 3; the points are shown in Figures 6 and 9. The two regressions were compared by analysis of covariance, and the difference in the slopes was found to be highly significant ( $p=.004$ ). Again, in the size range of interest (maternal length 28 mm. ), the smaller females in the two groups show a substantial difference, while the larger ones perform about the same. The lines intersect at a maternal length of 26.6 mm . (almost identical to the point of intersection of the lines representing numbers per brood).


Figure 11. Comparison of the regression lines of fry length on maternal length. Broken line: Experiment 1 (points are shown in Figure 6). Solid line: pooled data from Experiment 3 (points are shown in Figures 9a and 9b).
and length of fry) are not sufficient to describe unambiguously the differences in reproductive response of the two experimental groups. It seems obvious that the smaller females responded differently under the different nutritional regimes, but it is not clear whether the total commitment of energy to reproduction by the small females in Experiment 3 actually decreased or was simply distributed among fewer and larger fry per brood. By the beginning of Experiment 3, it had become evident that the total weight of each brood should be measured in addition to the lengths of individual fry; accordingly, in Experiment 3 the dry weight of each brood as a whole was measured, as described above under Materials and Methods.

In order to obtain an estimate of the dry weights of broods produced in Experiment 1, the following technique was used. Assuming that dry weight of an individual fry is proportional to its length raised to some exponent, it follows that

$$
\begin{equation*}
D W_{\text {brood }}=a+b \Sigma\left(S L^{x}\right) \tag{1}
\end{equation*}
$$

where
DW brood is the dry weight of an entire brood,
( $\Sigma \underline{S L}^{\mathrm{X}}$ ) is the sum of the standard lengths of the fry making up the brood, individually raised to an exponent $\underline{x}$, and
$a$ and $b$ are the constants of a linear regression equation. Equation (1) was fit to the data of Experiment 3 using trial values of $x$ ranging from 0.1 to 10.0 . The residual sum of squares was minimal when x was 4.8 ; for this value of the exponent, the equation accounted for almost $97 \%$ of the observed variation in dry weight of broods (the fit to the points is shown in Figure 12). This equation


Figure 12. The regression of the dry weights of broods of Experiment 3 on $\sum\left(\mathrm{SL}^{4 \cdot 8}\right)$. See text for explanation.
was then used to calculate estimate of the dry weight of broods produced in Experiment 1 from the data on standard length of fry in those broods.

In Figure 13 are plotted the natural logarithms of brood dry weights as a function of maternal length for the two experimental groups: the positive slopes are obviously significant ( $\mathrm{p}<.001$ in both cases). When the two regressions are compared by analysis of covariance, the tendency for the smaller females of Experiment 3 to produce lighter broods than those of Experiment 1 is found not statistically significant; the hypothesis that the regressions have a common slope is accepted ( $p=12$ ). Additional variance may have been introduced into the data of Experiment 1 by the use of estimates rather than direct measurements of dry weight of broods; it is possible that this added error plus the small sample sizes have resulted in the erroneous acceptance of a false null hypothesis that the slopes are equal. In the same analysis the hypothesis that, given the regressions have a common slope, the elevation of the lines is not different, is also accepted ( $p=.42$ ).

Gadgil and Bossert (1970) suggest that reproductive effort, defined as the fraction of an organism's energy resources devoted to reproduction at a given time, be measured as the ratio of weight of sex products to total body weight. I have calculated the ratio of dry weight of each brood to the wet weight of the mother just after parturition; this index of reproductive effort should be nearly proportional to Gadgil and Bossert's measure.


Figure 13a. The regression of estimated brood dry weight on maternal length. Experinent 1.


Figure 13b. The regression of actual brood dry weight on maternal length. Experiment 3.- pooled data.

In both Experiment 1 and Experiment 3 the index of reproductive effort tended to increase as maternal length increased (Figure 14). Although there is a good deal of scatter about the regression lines shown in Figure 14, the positive slope of the line is significantly different from zero for Experiment 1 ( $p=.03$ ). In Experiment 3 the increase of reproductive effort with size is not significant ( $p=.18$ ). Comparison of the two sets of data by analysis of covariance showed that the two regressions were indistinguishable with respect to either slope ( $p=.99$ ) or elevation ( $p=.31$ ) of the lines of best fit.

In Experiment 3 five different fenales produced two broods each. The mean time between broods was 29.8 days (standard deviation: 2.95; range: 25-32 days). Although sample sizes are small, a comparison of these results with those of Experiment 1 (mean gestation period $=24.8$ days) leads to the conclusion that the mean time between broods was significantly smaller in Experiment 1 than in Experiment 3 ( $t=2.86,10$ d.f., $p<.02$ ).

Following is a brief summary of the conclusions from the comparison of the results of Experiment 1 with those of Experiment 3. Under conditions of relatively poor nutrition and, presumably, more intense competition, time between broods increases for all females of the sizes studied. The smaller females in an aquarium respond to deteriorating nutritional conditions by producing fewer but larger fry in each brood, while larger females are essentially unaffected. As


Figure 14a. The regression of index of reproductive effort
on maternal length. Experiment 1.


Figure 14b. The regression of index of reproductive effort on maternal length. Experiment 3 - pooled data.
accurately as can be determined from the present study, females of the same size produced about the same total weight of fry per brood under both nutritional regimes, but there is a suggestion that smaller females produced lighter broods under the poorer feeding regime.

## DISCUSSION

Svardson (1949) noted that, all other things being equal, natural selection should favor genotypes producing higher numbers of eggs, and so average fecundity within a population should increase with every generation. Since natural populations do not show this steady increase in fecundity over time, he reasoned that there must exist some selective pressure towards decreasing egg number and that observed fecundities must represent a compromise between opposing forces. Svardson suggested four selective forces which might operate to limit fecundity in fish; his discussion is summarized in the following paragraphs.

First, a fish must dedicate some energy to growth and maintenance in addition to reproduction. Increased energy devoted to growth and maintenance processes should increase the probability that an individual will survive until the next reproductive season. Also, since fish fecundity often increases with body size, energy put into growth during one time period may result in increased fecundity in subsequent spawnings. Thus in an evolutionary sense the advantages of increased fecundity at a given time may be counterbalanced by the future reproductive advantages likely to result from alternative uses of available energy.

Second, there may be a physiological strain involved in producing increasing numbers of eggs. This strain may directly reduce an individual's chance of surviving until the next reproductive season.

Third, for species which provide some form of parental care for their eggs and young, the limits on fecundity may be set not by the number of eggs which a female can produce but by the number of eggs or young which can be successfully cared for. The argument here follows that of Lack (1948) for birds.

- Finally, if there is a premium on large size of individual eggs, some compromise must be made between egg size and egg number, since, for a given input of energy to reproduction, any increase in energy per egg must reduce the total number of eggs produced. Svardson cited evidence from several sources to show that large eggs produce large larvae, which have an advantage over smaller individuals in intraspecific competition. Svardson's paper generates the hypothesis that fish populations whose larvae face intense intraspecific competition will produce fewer and larger eggs than populations of the same species for which intraspecific competition is a less important source of larval mortality; in these latter populations predation and unfavorable physical factors, which are assumed to act more or less independently of larval size, would be the important causes of larval deaths.


## Reproductive Strategy

Ideas similar to Svardson's have been developed in more general and detailed form in the recent literature on $\underline{Y}$ - and K - selection. MacArthur and Wilson (1967: 145-180) coined the terms in discussing optimal reproductive strategies in uncrowded and crowded environments. They argued that in an uncrowded environment with abundant resources, those genotypes will be favored which can utilize the most resources
and produce the largest numbers of progeny per unit time, maximizing $\underset{\text { r }}{ }$, the intrinsic rate of population increase of the logistic equation. 1 / Such individuals will be expected to predominate, for example, in a situation where climate is seasonally severe and a few survivors of the unfavorable season each year recolonize under conditions of abundant supply of resources. On the other hand in crowded environments with a relatively uniform and favorable climate, genotypes which can replace themselves at the lowest density of available resources (maximizing K , carrying capacity in logistic terminology) will be favored; these genotypes are termed K-strategists.

Pianka (1972) has summarized the development of the concepts of $\underline{r}$ - and K- selection. He states that $\underline{r}$ - strategies will evolve in populations which are usually maintained at low density relative to carrying capacity by a high rate of density-independent mortality. In such a situation resources will be abundant relative to the population's demand, and competition will be light, so each individual will have a high total income of energy. A high proportion of this energy income will be channeled into reproduction since alternative demands will be low: there is little benefit to be derived from energy devoted to gaining competitive advantage over conspecifics, and the high, often catastrophic, mortality makes it a better bet for an individual to

1/ The logistic equation defines a sigmoid curve of population growth over time. Its differential form is $\frac{d N}{d t}=r \mathbb{N}\left(\frac{K-N}{K}\right)$ where $\mathbb{N}=$ population size in numbers, $\underline{r}=$ intrinsic rate of population increase, and $\underline{K}$ = maximum attainable value of $N$, or carrying capacity. The equation was first derived by Verhulst (1838).
maximize present reproduction than to invest energy in growth, for example, in order to gamble on reproductive benefits in an uncertain future. Since the progeny will also face light competition but potentially high density-independent mortality, the optimal strategy for the parent is to minimize the amount of energy input per offspring so as to maximize the number of individuals produced. The net result is that r- selected populations will show rapid development, early maturity, high fecundity, and a tendency towards semelparity (a single reproductive period followed by death as in Onchorhynchus) ; individual offspring will be of "low quality" - small, without well-developed competitive or anitpredator mechanisms.

Pianka theorizes that high population density, with consequent increased intensity of competition and reduced resource availability, produces K- selection. Individual energy income is low, and a smaller proportion (relative to the $\underline{x}$ - selected case) is available for reproduction since more energy must be diverted to competitive ends. If the offspring will also encounter intense competition, more energy input per offspring is favored, and numbers per parent must be reduced. The reproductive consequences of K - selection should include slower development, greater competitive ability, lower resource requirements, delayed maturity, low fecundity, iteroparity (more than one reproductive attempt in a lifetime), and high quality offspring.

It is important to emphasize that natural selection always favors those genotypes which maximize $\underline{m}_{\text {s }}$ the birth rate minus the death
rate. The difference between $\underline{\underline{-}}$ - strategists and $\underline{K}$ - strategists lies in the response of this parameter to changes in population density, or more precisely, availability of resources. Figure 15, modified slightly from Gadgil and Bossert (1970: Fig. 1), illustrates the point. When population density is low and resources are abundant, the $\underline{\text { r- strategist will have }}$ a higher $\underline{m}$ as a result of its higher birth rate, since mortality under these conditions is presumably primarily density independent and affects r- strategists and K- strategists approximately equally。 However, the high birth rate of $\underline{m}$ strategists is achieved at the cost of "quality" of individuals; therefore, as population density rises and competition becomes more intense, the death rate of $\underline{\text { - }}$ strategists rises rapidly, and $\underline{m}$ is reduced accordingly. $K$ - strategists have low birth rates as a consequence of dedicating a significant proportion of their energy budget to non-reproductive activities, which act in one way or another to keep death rates relatively low even under conditions of high population density and low resource availability. Thus m for a K-strategist falls relatively slowly with increasing population density. Above some density (marked A in Figure 15) the output of surviving offspring is higher for the $\underline{K}-$ strategist than for the $\underline{\underline{-}}$ strategist. If population density (or resource availability) is consistently on the left side of $A_{\text {, }}$ then $\underline{r}$ - strategists will predominate in the population; K- strategists will be favored to the right of $A$. If conditions fluctuate to either side of $A$, one might predict that the population would be polymorphic for reproductive strategy or that some intermediate strategy would evolve. A third alternative would be the evolution of the ability to switch strategies according to conditions; this would seem particularly likely


Figure 15. The relationship between the instantaneous rate of population growth, $m$, and population density for $\underset{\sim}{x}$ strategists and K- strategists. See text for explanation. From Gadgil and Bossert (1970).
if the fluctuation showed a regular periodicity.

Pianka (1970) and Gadgil and Solbrig (1972) stress that ideal rand K- strategies represent the poles of a continuum. The latter workers state that the position of a population on this continuum relative to other closely related populations can be quantified according to the proportion of total energy income dedicated directly to reproduction. They suggest that one measure of this proportion is the total weight of offspring produced relative to weight of the parent. Gadgil and Solbrig emphasize that increased reproductive output does not by itself constitute evidence for strategy since increased availability of resources to a population, occasioned perhaps by a sudden catastrophic mortality, results in increased energy income for the survivors, which in turn can cause increased reproductive output without any change in the proportion. of total energy used for reproduction; they term this the population dynamic effect.

The literature on T - and K - selection so far discussed represents one approach to the problem of the evolution of life history characteristics. I find it an intuitively appealing introduction, but as so far stated, it needs some qualification. It is oversimple to think that all reproductive strategies can be placed somewhere along a one-dimensional continuum. This concept implies that life history characteristics such as age at first maturity, growth rate, and fecundity are so highly inter-dependent that they will always vary together in a predictable way in response to population density, resource availability, and mortality schedules.

In fact, the relationships are so complex that we should not be surprised to discover many populations displaying mixtures of "r-selected" and "K-selected" traits. Tinkle and Wilbur (1973) review several instances of occurrence of such "mixed strategies" - e.g. extremely high reproductive effort expended by populations whose adult density is quite stable and presumably near carrying capacity.

Such departures from what would be expected on the basis of $r-$ and K- selection arguments can best be understood if. we consider the basic objective of reproductive strategy. By definition natural selection favors those genotypes which make the greatest contribution to the gene pool of succeeding generations; it follows that the objective of reproductive strategy, as of any other evolving system, must be to maximize this contribution, or fitness.

Schaffer (1972) has shown that the quantity to be maximized is: $\underline{b}_{i}+\underline{p}_{i} \cdot\left[\frac{\underline{v}_{i}+2}{v_{0}}\right]$, where $\underline{\mathrm{b}}_{\mathrm{i}}$ is the number of progeny produced by a female at age $\underset{\underline{i}}{ }$ which survive to reproduce, and $p_{i}$ is the probability that the female will survive from age $\underline{i}$ to age $\underset{i}{ }+1$, and $\frac{\underline{v}_{i}+1}{\underline{v}_{0}}$ is Fisher's (1930) reproductive value for a female age $\underset{i}{+}$ l。 This last quantity is a device for expressing all expected future births to an individual in terms of their equivalent value in present births; the concept is analogous to that of present discounted value of future income in economics. Schaffer's formulation is deceptively simple; each term can be subdivided into several components, many of which are interrelated.

The term $\underline{b}_{i}$ is the absolute fecundity of an adult female at age i multiplied by the proportion of those eggs which survive to become reproducing adults. Fecundity is an increasing function of reproductive effort, the proportion of the organism's total energy income devoted to reproduction. Fecundity for a given reproductive effort is also likely to be an increasing function of parental size in organisms like fish, which continue to grow after reaching sexual maturity. Thus, fecundity at age $\underset{i}{ }$ can be a decreasing function of reproductive effort in previous seasons to the extent that growth has been reduced. Prereproductive survival of offspring is probably often a function of factors beyond the control of the adult (e.g. population density, resource availability, physical environmental factors); however, survival of young stages may in some cases be a function of egg or larval size, which in turn is negatively related to fecundity at any given level of reproductive effort.

The term $\underline{p}_{i}$ is the probability of adult survival from the present reproductive season to the next. It is likely to be a decreasing function of present reproductive effort. To the extent that adult survival is related to size, it may also be a function of reproductive effort in previous seasons. Additionally, it is likely to be age-specific.

The final term is Fisher's reproductive value. For an individual adult this is the expected production of surviving offspring in all future reproductive seasons, reduced by the probability of the adult's surviving to each season. All of this is further discounted according to the
population growth rate. If the population is increasing, then one surviving offspring in the present represents a higher proportion of the population than one produced in the future and is evolutionarily worth more; this is similar to the standard economic model wherein money which can begin earning interest now is worth more than the same amount to be received in the future. However, if the population is declining, it is as if there were a negative interest rate, and future reproduction is worth more than present.

In summary, a reproductive strategy is a combination of life history characteristics manifested by an organism which may be thought of as representing a set of tactical choices by the organism with respect to several interrelated variables. One group of these choices has to do with the magnitude and distribution of reproductive effort of the individual over its lifetime. Variables included in this group are ages of first maturity and onset of senescence, number of reproductive attempts in the lifetime (the choice of semelparity or iteroparity is included here), and energy tradeoffs among reproduction and other energy-consuming functions. The magnitude of the energy input to each individual egg or larva in a particular reproductive attempt represents a separate category of choice; for a given total energy input the organism must choose one of the infinite number of combinations of absolute fecundity and energy content of individual eggs or larvae; i.e. the same total energy can be distributed among many small young or a few large ones. Different combinations of choices (that is, different strategies) will result in different numbers of young which themselves survive to breed. Strategies which optimize the sum of present output plus the present value of future output will be favored by natural selection if they are heritable.

Species of the Family Poeciliidae have several characteristic Iife history features which must be considered in discussing their reproductive strategies. The shallow water areas they inhabit are often quite unstable over time, and population levels may fluctuate considerably. Generation time is typically short, varying from several weeks to a few months. Each adult female may produce several broods over a relatively Iong reproductive season. These features combine to make it very likely that successive generations, or even the same individual at different times, will face quite different sources and levels of mortality. Under such conditions the ability to make rapid adjustments of reproductive strategy to immediate and anticipated conditions should be of great selective value.

Aside from the purely descriptive information on guppy reproduction, the most interesting fact which emerges from my data is that under conditions of poorer mutrition and presumably more intense competition, the smaller females redistributed the same reproductive effort among fewer, larger fry (the same size as fry of larger females), while the larger females showed no change in strategy. This result prompts several questions for which I have hypothetical answers, most of which are testable.

What is the advantage to the smaller females of increased size of fry? When competition arnong fry is intense, larger fry may have a large enough survival advantage that, in spite of the reduction in
absolute fecundity, the fitness of the adult is increased by putting more energy into each individual offspring. This is essentially the same as Svardson's (1949) fourth hypothesis (see page 23). Magnuson (1962) found in a laboratory study that when competition for food was intense; larger juvenile medaka (Oryzias latipes) successfully dominated smaller ones and showed significantly faster growth. Bagenal (1969b) in a field experiment showed that brown trout (Salmo trutta) fry hatching from larger eggs had a higher survival rate than those from smaller eggs living in the same enclosures; he suggested that the mechanism producing this effect might have been that the larger fry were more effective at maintaining territories.

If the explanation of the first question is correct, then why did only the smaller females change strategy? One hypothesis is that reduction in rations acted as the signal for the change in strategy and that, as a result of contest-type competition, only the smaller females actually suffered reduced rations in the experiment. The difficulty with this hypothesis is that if the change of strategy is adaptive, and its effects are related to differential survival of fry of different sizes, then it is only the smaller females which are receiving the message about what conditions will be like for their fly. Since fry of both large and small females presumably face a similar competitive situation, the fitness of the larger females should be considerably reduced by their inability to read the environment and respond with a corresponding increase in size of fry. It is possible that the difference in response of large as opposed to small females is an artifact of the experimental
situation, in which food was localized in time and space, and where the population was spatially restricted in an environment offering little visual isolation among competitors: Magnuson (1962) found that both of these conditions increased the intensity of contest competition. Possibly under natural conditions competition is closer to the scramble type, and all sizes of adults are sufficiently affected by deteriorating conditions to receive the message and make the appropriate switch of strategy。

Why did reproductive effort not decline when the nutritional regime worsened? A simple hypothesis is that the level of reproductive effort is genetically fixed and cannot vary much except on an evolutionary time scale. Alternatively, it seems likely that when adult mortality is high and/or growth is slow, as in Experiment 3, there is little benefit to be gained by postponing reproductive effort until such time as probability of survival of fry might increase.

One of the major deficiencies of the present study is that I have only scanty information on the ecology of my experimental animals under natural conditions, where the characteristics under investigation evolved and presumably have adaptive value. I do have two pieces of information from Ben Seghers (personal communication) which seem relevant. First, although the Tacarigua River is relatively stable in comparison with other rivers of the area, it does undergo regular fluctuations in flow and related variables as a result of marked seasonal variations in rainfall. Second, predation on adult guppies by cichlids is probably relatively
intense. In an attempt to make up for the lack of field data on my own organisms, I will review in some detail field investigations on similar problems in related species.

## Field Studies on Peociliid Reproduction

J.D. McPhail (unpublished data) has made preliminary field and laboratory studies of reproduction of another small Peociliid, Neoheterandria tridentiger, in Panama; his results show some striking parallels with mine. He worked primarily with populations inhabiting small forest streams which dried up almost completely during the dry season. High wet season populations are reduced dramatically as the streams dry up; a very small proportion of these populations survives the dry period in isolated pools in deeper parts of the stream bed. When the rains come again, flash flooding causes a sudden expansion of available habitat, which the survivors recolonize. It seems probable that the onset of the wet season also brings about an increase in available food, which in these streams is mostly of terrestrial origin.

The changes in reproductive pattern through the year suggest that Neoheterandria populations switch strategy according to the season, although McPhail's data do not show directly that single individuals use different strategies at different times. Late in the dry season females in the isolated streambed pools suspend reproduction entirely. Early in the wet season females from the expanding populations produce relatively large numbers of small fry at approximately 10 day intervals (this specjes shows superfoetation, so the gestation period for an
individual brood is about 20 days during this season). Females taken from the dense populations of the late wet season and early dry season produce much smaller broods of large young at 15 day intervals. It looks as though these populations are using r-strategy when population density is low and K- strategy when the available habitat is relatively full.

McPhail also examined females from larger permanent streams in the same area. In most collections females tended towards the low fecundity/large fry end of the spectrum, as one would expect in a stable, benign environment. However, in some localities the females showed the $\underline{\underline{x}}$ - selected pattern (high fecundity and small fry); these populations all lived in localities where fish predators were abundant and adult mortality was probably high.

Krumholz (1948) studied the fecundity of populations of the Poeciliid Gambusia affinis in northern Illinois and southern Michigan, where they had been introduced for mosquito control. These populations, at the northern limit of the species' range, suffered high winter mortality followed by rapid increase to high densities during the spring and sumner months. During one reproductive season Krumholz made monthly collections of Gambusia from established populations in two ponds, one of which appeared to have low and the other moderate biological productivity. Early in the following spring he introduced mature virgin females and males to a very productive stock-watering pond; he made collections from this population throughout the summer. From the preserved collections Krumholz measured length frequencies, reproductive state of both sexes,
and numbers of embryos carried by gravid females. Unfortunately he made no measurements of size of young.

Females of two different life history types occurred in all of Krumholz' populations. Females born in mid to late summer grew to moderate size and overwintered as immatures; these females began to reproduce in early spring and produced three to five broods before dying, sometimes after a period of sterile senility in their second summer or autumn. The spring progeny of the over-wintered females showed rapid growth and matured at a much smaller size than did their mothers; they produced from one to three broods during late spring and summer and then died. Thus within the same population, females born in spring distributed their reproductive effort according to r-strategy, and females born in summer behaved like K - strategists; choice of strategy depended not on parentage but on season of birth.

In both life history types in all ponds fecundity at a given length decreased with each successive brood from a maximum at the first or second brood; another way of stating the same thing is that average fecundity for length showed a more or less steady decrease within a given pond as the season progressed. Comparisons among the three ponds showed that fish in the newly stocked, productive pond matured at a smaller size and produced more broods in the course of the season relative to the other ponds. For comparable life history types and times of year, average fecundity at a given length increased with moreasing pond productivity.

Krumholz attributed the decrease in fecundity over time to physiological changes associated with senescence in the females. However, his data do not rule out the possibility that decreasing fecundity (which may have been accompanied by an increase in size of individual fry) represented a switch in reproductive strategy in response to increasing population density and competition as the season advanced. It is suggestive that the drop in fecundity with time was most pronounced in the least fertile pond and that fecundity in the newly stocked, productive pond continued at a high level throughout the summer.

Krumholz (1963) reported the results of a study on Gambusia manni in two ponds in the Bahamas. The techniques were similar to those described for the previous study. In Daniels' Pond there were no aquatic predators; the pond at Calloo Mangrove was connected to the sea at high tide and contained several predatory marine species, including juvenile barracuda. Although he made no direct measurements of population densities, Krumholz felt that density was much higher in Daniel's Pond. The Daniels' Pond population contained a high proportion of large senile individuals, particularly in late summer and autumn at the end of the reproductive season; the maximum size observed at Calloo Mangrove was much smaller, and there was no evidence of senility. Krumholz reasoned that predators eliminated senescent Gambusia at Calloo Mangrove.

Krumholz concluded that growth was faster in the Daniel's Pond population due to presumed higher biological productivity of the pond. As indirect evidence for this hypothesis, he cited his observations that
both maximum size and size at first maturity were higher in Daniels' Pond. The plots of length frequencies for successive collections at Daniels' Pond show a clear advance of modal length frequencies from month to month, from which growth of individual cohorts can be estimated. The modal length frequencies for the Calloo Mangrove population are much less clear within any collection, and they vary erratically with time; possibly this is due to rapid changes in the age and size composition of the population due to high predation, but very rapid growth could have the same effect. Since the difference in predation mortality probably also accounts for the observed differences in maximum length between ponds, Krumholz' contention about differences in growth rates rests on the fact that the Calloo Mangrove fish mature at a smaller size. It has been shown for many species of fish that early maturity is often associated with fast growth; Svardson (1943) showed that fast-growing male guppies matured at an earlier age and smaller size than slower growers. In sum, on the basis of the limited evidence, it seems more likely that growth is more rapid at Calloo Mangrove.

The two populations showed marked differences in reproductive strategy. Calloo Mangrove females had higher average fecundity throughout the year in spite of being considerably smaller on the average than Daniels' Pond fish. In addition, peak reproduction, as measured by average fecundity and proportion of females which were gravid, started earlier in the year and continued longer at Calloo Mangrove.

In Figure 16 I have plotted fecundity against size of female for the two populations at three different times, which are representative of collections made during the early, middle, and late parts of the reproductive season. In all Calloo Mangrove collections fecundity increased exponentially with maternal length; the regression of fecundity on length for Daniels' Pond has zero slope early and late in the season, but-at the peak of the reproductive period the slope and height of the regression were quite similar to Calloo Mangrove. My explanation of the data is that the Calloo Mangrove population follows $r$ - strategy at all seasons due to high predation pressure, which keeps population density low, resource availability high, and competition low. The explanation of the Daniels' Pond data is more complicated and involves some speculation. I suggest that in January and July the population was resource-limited and was following K- strategy; the January population density was probably lower but so was biological productivity in the moderately seasonal Bahamas. In late January and early February a period of extremely low temperature caused heavy mortality in Daniels? Pond. The reduced population density, which coincided with seasonally increasing productivity of the pond, must have reduced the intensity of competition, and the population appears to have switched towards rstrategy for several months (February through May). In the absence of data one can only speculate that the increased fecundity in April was accompanied by a reduction in average size of fry and that in the early and late collections average size of fry was greater.


Figure 16. Average number of embryos carried by female Gambusia manni collected at two locations in the Bahamas at different seasons. Each point is an average of several individuals. Data from Krumholz (1963: Tables 15 and 17).

## Other Laboratory Studies of Fecundity and Nutrition

Hester (1964) investigated the effects of reduced rations on fecundity of a domestic strain of Poecilia reticulata. His results indicated that low rations during one brood period significantly reduced the numbers of fry in that brood and the one following. He observed no trend in size of fry with feeding level or maternal size, and there were no changes in length of the gestation period. The stock of guppies used by Hester was somewhat less fecund for length than my stock, and the fry he measured averaged much smaller than those in my study.

There are several discrepancies between Hester's results and those of the present study. Hester found that reduced rations affected large and small females similarly; this is probably due to the fact that his experimental fish were isolated in individual aquaria for the entire experiment. Thus there was no competition for food in Hester's experiments, whereas in my stock tanks larger individuals may have been able to garner a disproportionate share of food at the expense of the smaller fish. In the light of my results it is surprising that Hester reported no relation between size of fry and either ration or maternal size; however, it appears that he measured only 79 fry and that they were much more variable in length than those of my study. It is possible that with a larger sample he might have found a relationship between fry size and either ration or matemal size. With regard to gestation period I have no specific explanation of the constancy reported by Hester as opposed to the lengthening of the period under poor conditions which I observed. In general it should be emphasized that the two strains of Peocilia compared here have probably been under quite different selective regimes
for some time, and it would be unrealistic to expect them to respond in the same way even to identical situations.

Bagenal (1969a) reported on laboratory experiments on the relationship between feeding level and fecundity in Salmo trutta. In the first experiment fish were kept in two large tanks and fed on commercial dry-food - one tank at full rations and the other at half that level. At the end of eight months fecundities of the two groups of ripening fish were compared. Fish from the high food treatment had grown faster during the experiment, but when fecundities were adjusted for length there was no difference between the treatments. The slope of the regression of fecundity on length was significantly steeper in the low food group; the larger low food individuals were about as fecund as individuals of the same size in the high food treatment, but the smaller low food fish had very few eggs for their size. This is essentially the same situation that I observed in comparing my Experiments 1 and 3. Bagenal hypothesized that in the low food treatment the large individuals were securing a disproportionate share of the food; he set up a second set of experiments to explore this idea.

In his second experiments Bagenal set up four separate treatment groups of fish; two of these were fed at full and the other two at onethird rations. After five months of this regime growth depensation was evident in all tanks; to reduce the size range in each tank, the fish in the two tanks within each food level were sorted by size and reassigned to tanks so that each food level after the sorting consisted of one tank of larger fish and one of smaller ones. After four more months
the fish from the high food tanks were more fecund for their length than the low food fish, but this time there was no difference between treatments in the slope of fecundity on length.

In both sets of experiments Bagenal found that well-fed fish produced smaller eggs by dry weight than the food-deprived ones. Scott (1962) in a similar study on Salmo gairdneri found no difference in egg size by wet weight between food levels. Bagenal (1969a) pointed out that the water content of eggs increases as they mature, and that therefore the appropriate measure of egg size for comparative purposes is dry weight. Scott's well-fed fish were in a more advanced state of maturity than the starved ones; consequently, the similarity in wet weight between treatments suggests that the low-food fish had larger eggs in terms of dry weight.

## Studies on Exploited Marine Populations

Several field studies have documented year-to-year changes in fecundity within populations: Bagenal (1963b, 1965) for three species of flatfish in the Clyde Sea, Hodder (1963) for haddock (Melanogrammus aeglefinus) of the Grand Banks, and Raitt (1968) for Norway pout (Trisopterus esmarkii) in the North Sea. In all the above cases fecundity increases were apparently associated with either lowered population density or increases in available food per individual. In the absence of data on egg size or some other measure of quality it seems most probable that these cases represent Gadgil and Solbrig's (1972) population dynanic effect rather than any change in reproductive
strategy (i。e. change in magnitude or distribution of reproductive effort).

Bagenal (1966) gives a comprehensive review of his own and others' field studies on the fecundity of plaice (Pleuronectes platessa) throughout its range in the eastern North Atlantic and adjacent seas. Populations in different localities vary considerably in age composition and growth rate; since fecundity of plaice increases exponentially with length, different populations are compared in terms of the expected fecundity of a 37 cm . fish $\left(F_{37}\right)$, as calculated from the equation for the regression of fecundity on length for ${ }^{\circ}$ a given area. $F_{37}$ is lowest ( 84,000 eggs) in the Southern Bight of the North Sea; fecundity increases fairly evenly with distance in all directions from this area. Thus $F_{37}$ is high in the Bay of Biscay $(184,000)$, the west coast of Ireland $(153,000)$, and northem Norway (156,000). In two localities still farther away, Iceland and the Barents Sea, $F_{37}$ drops again (106,000 and 107,000 respectively). Fish from inside Trondheim Fjord in Norway and from the Baltic are much more fecund than those from other localities and do not fit the general pattern described above; in both cases; however, there is evidence from marking experiments and meristic studies to suggest that the populations involved are racially distinct from the other populations considered.

Bagenal (1966) postulates that over most of the area of plaice distribution, with the exception of Trondheim Fjord and the Baltic, there exists a single basic fecundity type and that differences in fecundity
are caused by local differences in food supply. In support of this hypothesis he notes that populations with high fecundity also tend to have the following characteristics:

1) low population density,
2) fast growth, and
3) high gutted weight at a given length.

It is consistent with the above analysis to say that most populations of plaice follow the same reproductive strategy and that variations in fecundity are due to the population dynamic effect.

In addition to his basic point about food supply, Bagenal (1966) notes that fecundity is higher in areas where the prevailing currents are likely to carry the planktonic plaice eggs and larvae far from suitable nursery grounds, and conversely, that low fecundity is associated with favorable currents. Bagenal points out that the survival value of high fecundity is obvious where mortality of young stages is likely to be high; however, the selective mechanism favoring lower fecundity under apparently better conditions is not immediately clear, since even under these circumstances more fecund individuals should on average make a larger contribution to the next generation. This is the same problem which Svardson confronted in 1949。

Bagenal considers Svardson's (1949) hypothesis that reduced. fecundity can result from selection for larger eggs, which produce larvae of greater competitive quality. Unfortunately, Bagenal's plaice samples were taken at different times of year in different localities, and therefore fish from different areas were at different stages of maturityo

Because of this, direct comparison of egg sizes among populations was not possible. He approached the question indirectly by comparing two populations on the basis of density of oven-dried eggs, which does not vary much within a population over a considerable range of developmental stages. He found that eggs from the more fecund population were also more dense; since all plaice eggs are positively buoyant, he reasoned that the denser eggs contained a higher proportion of fat. Bagenal considered that to be evidence against Svardson's hypothesis; however, it seems to me that Bagenal's point is irrelevant to the question of absolute size or energy content of an individual egg and that Svardson's hypothesis is still viable in this case.

There is another possible explanation of the variation in plaice fecundity reported by Bagenal. As Murphy (1968) and Schaffer (1972) have noted, if larval mortality varies appreciably from year to year, the fitness of an adult is increased if reproductive effort can be spread over more years, even at the cost of reduced fecundity in a given year. Data on annual variation in larval survival are not available for most of the plaice populations studied; however, it is possible to make a crude estimate of reproductive span in different populations from the age composition of different stocks. In Table II are assembled estimates of reproductive lifespan for most of the localities studied by Bagenal (1966), together with their respective $\mathrm{F}_{37}$ from his Table 2。 There is considerable uncertainty about the values for reproductive span, due to small sample sizes in many cases as well as to the fact that different populations are subject to different levels of fishing mortality, which

Table II. The calculated fecundity of female plaice 37 cm . in length ( $F_{37}$ ) and estimates of reproductive life span at different localities. Data on $F_{37}$ from Bagenal (1966). Other data from sources indicated.

| Locality | $F_{37}$ <br> (thousands) | Age <br> range | Reproductive <br> span (years) | Sample <br> size | Source <br> of data |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Barents Sea | 107 | V-XXII | 18 | $?$ | Wimpenny (1953) |
| S. Bight, N. Sea | 84 | I-XVII | 17 | 223 | Simpson (1959) |
| Flamborough Gd., N. Sea | 96 | II-XV | 14 | 33 | Simpson (1959) |
| Clyde Sea | 137 | III-X | 8 | 55 | Bagenal (1958) |
| Clyde Sea | 159 | II-XI | 10 | 156 | Bagenal (1963c) |
| Rye Bay | 127 | II-XVII | 16 | 84 | Bagenal (1960a) |
| Plymouth | 137 | III-X | 8 | 60 | Bagenal (1960a) |
| Wexford, So. Ireland | 139 | II-IV | 3 | 30 | Bagenal (1960b) |
| Schull, S. Ireland | 150 | II-IV | 3 | 9 | Bagenal (1960b) |
| Dingle, W. Ireland | 153 | II-VIII | 7 | 47 | Bagenal (1960b) |
| Galway, W。Ireland | 146 | II-V | 4 | 20 | Bagenal (1960b) |
| Kellybegs, W. Ireland | 132 | II-VII | 6 | 31 | Bagenal (1960b) |

Table II. The calculated fecundity of female plaice 37 cm . in length ( $\mathrm{F}_{37}$ ) and estimates of reproductive life span at different localities. Data on $F_{37}$ from Bagenal (1966). Other data from sources indicated. (continued)

| Locality | $F_{37}$ <br> (thousands) | Age <br> range | Reproductive <br> span (years) | Sample <br> size | Source <br> of data |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Arendal, S. Norway | 141 | III-XI | 9 | 12 | Bagenal (1962) |
| Bergen, W. Norway | 134 | IV-XV | 12 | 24 | Bagenal (1962) |
| Trondheim Coast | 150 | IV-IX | 6 | 11 | Bagenal (1962) |
| Troms申, N. Norway | 156 | IV-XVII | 14 | 37 | Bagenal (1962) |
| Bay of Biscay | 184 | II-VII | 6 | 47 | Bagenal (1963a) |
| Faxa Bay, Iceland | 106 | III-X | 8 | many | Taning (1929) |



Figure 17. The regression of fecundity of plaice from different areas on reproductive life span. The data are shown in Table TI.
reduces the age range of the exploited stock. My estimate of reproductive span is simply the difference in age between the youngest and the oldest observed mature female. The regression of $F_{37}$ on reproductive span (Figure 17) has a negative slope significantly different from zero ( $p=.01$ ) and accounts for $34 \%$ of the observed variation in fecundity among areas.

The herring (Clupea harengus) of the northeast Atlantic and adjacent seas, because of their long-standing economic importance, are one of the world's most thoroughly studied fish groups. Fecundity and reproduction in general have received considerable attention, due partly to the fact that the reproductive biology of different subgroups varies considerably and the differences have proved useful in identification of genetically separate stocks.

Parrish and Saville (1965) define three major sub-groups, which themselves can be further subdivided; here, I will term the major subgroups tribes and their further subdivisions stocks. The Oceanic Tribe (=Atlanto-Scandian) comprises stocks of large, long-lived herring which feed in the open Atlantic and spawn in winter and early spring in relatively deep water off Norway, Iceland, and the west coast of the British Isles. The Shelf Tribe are smaller and shorter-lived than the first group; they feed in the North Sea and over the continental shelf to the west of the British Isles. Different stocks of Shelf herring spawn from late summer to early winter on offshore banks throughout the feeding area; most stocks exhibit pronounced seasonal migration patterns within the
area. The Coastal Tribe live in the inshore waters of the Baltic and North Sea, where they spawm in spring in very shallow. water.

Table III is a summary of information on the reproductive biology of the three herring tribes; several striking trends are evident. Egg size varies quite regularly from group to group according to month of spawning (Figure 18); there is a smooth intergradation between the large eggs of the winter spawning Oceanic Tribe through the very small eggs spawned in late spring and summer by Baltic stocks of the Coastal Tribe. It is noteworthy that the trend holds between stocks within tribes and even within stocks: first-time spawners, which produce smaller eggs than older fish, spawn last in Norway (later in the spring), whereas in the southem North Sea recruits to the Downs Stock spawn before the rest of the population (earlier in the winter). In general, stocks laying large eggs are less fecund than those which produce smaller eggs (Figure 19).

Blaxter and Hempel (1963) raised herring larvae from different stocks in the laboratory in order to quantify some of the consequences of different egg sizes. They found that larger eggs produced larger larvae with a higher ratio of yolk weight to body weight at hatching. After hatching these larger larvae grew more rapidly to a larger maximum size than did larvae from smaller eggs. Larvae from large eggs also survived longer without food; such larvae in nature would have more time in which to locate their first food items.

Table III Reproductive parameters of Atlantic herring tribes. Data from Cushing (1967) unless otherwise noted.

| Tribe | Shelf | Shelf | Oceanic |
| :--- | :--- | :--- | :--- |
| Spawning time | Winter | Autumn | Spring |
|  |  |  |  |

1 Parrish and Saville (1965)


Figure 18. Average dry weight of ripe eggs of various stocks of clupea harengus of the northeast Atlantic plotted against month of spawning. From Hempel and Blaxter (1967)。


Figure 19. Fecundity-egg size diagram for some winter-spring and summerautumn spawning stocks of Glupea harengus. $F_{28}$ is the expected fecundity of a female 28 cm . in length. From Parrish and Saville (1965).

Within a stock fecundity increases exponentially with length of the spawning female (Baxter, 1959; many others). However, egg size does not vary in a given population with age or size of the spawner, except that first-time spawners tend to spawn smaller eggs than repeat spawners of the same stock (Hempel and Blaxter, 1967).

- The particular mix of fecundity and egg size adopted by a particular stock is seen by most workers as an adaptation to the ecological situation which the larvae most commonly encounter. High fecundity (and small egg size) is seen as an adaptive response to high predation rates on the larvae; large egg size (with concomitant lower fecundity) should increase the average number of surviving larvae per adult when low or uncertain food availability is the major difficulty facing the young (Hempel, 1965).

Cushing (1967) supported and extended the above point by examining the reproductive strategies of different herring stocks in relation to the planktonic production cycle, (timing, amplitude, and variability) in their respective nursery areas. Three autumn-spawning Shelf stocks and three spring-spawning Oceanic stocks all time their reproduction so that the period during which their larvae must begin to feed coincides with the average time of occurrence of the annual peak of phytoplankton abundance (which is taken as an indicator of abundance of the larval copepods eaten by young herring). Three winterspawning Shelf stocks, on the other hand, time their reproduction so that the larvae must begin feeding in mid-winter, when plankton abundance
is at its annual low point or is just beginning to increase towards a spring maximum. Other environmental factors considered by Cushing are summarized in Table IV; they are abundance of planktonic predators of herring larvae (medusae, ctenophores, chaetognaths) and variability in timing and amplitude of the production cycle (taken to be proportional to the depth of water in the nursery areas).

Two patterns emerge from Tables III and IV. First, the tradeoff between egg size and fecundity seems to be consistent with Hempel's. (1965) explanation: high predation favors increased fecundity at the expense of individual egg size, and low or highly variable food availability favors large egg size. Gushing's (1967) arguments can be extended to cover the problem of distribution of reproductive effort over the adult lifespan; reproductive effort expended in a single season - the ratio of gonad weight to body weight - decreases with increasing variability of the production cycle. As reproductive effort in a single season increases, reproductive span (here measured as the difference between the maximum observed age, $\mathrm{T}_{\max }$, and age at first maturity) decreases. These trends are further confirmed by consideration of the reproduction of the Baltic stocks of the Coastal Tribe (Parrish and Saville, 1965). These stocks spawn in very shallow water in spring and summer, and their larvae live in a situation of high food and high predation which is quite stable from year to year. Baltic herring represent the extreme cases of high fecundity, small eggs, high reproductive effort, and short reproductive span.

TABLE IV. Environment encountered by larval Atlantic herring. From Cushing (1967)

| Tribe <br> Spawning time | Shelf <br> winter | Shelf <br> autumn | Oceanic <br> spring |
| :--- | :--- | :--- | :--- |
| Average food <br> availability | low | high | high |
| Variation in <br> food avail- <br> ability | low | moderate | high |
| Abundance of <br> predators | low | high | low |

## Reproductive Strategy Theory and Stock/Recruitment

Cushing (1969, 1971, 1973) and Cushing and Harris (1973) have developed a new approach to the problem of the relation between spawing stock size and resultant recruitment. Using data from 31 different stocks Cushing plotted the recruitment per unit spawning stock against spawning stock on logarithmic axes. The slope of this regression he regarded as an index of density dependence, i.e. more negative values indicate a greater degree of density dependence. Cushing's index is related to the parameter a of Ricker's (1954, 1958) equation; increasing density dependence in Cushing's terms implies a larger value of $\underset{\text { a }}{ }$, which means that the peak of the dome of the Ricker curve is higher and occurs at a lower level of spawning stock. The novel aspect of Cushing's work is that he finds a linear relationship between his index of density dependence and the cube root of average fecundity of a given population. More fecund populations show more density dependence, have a more pronounced dome to the stock/recruitment curve, and can sustain themselves under heavier fishing pressure.

Cushing's work is open to criticism on several accountso First, all the stocks examined by him are under exploitation at different intensities, and therefore average stock sizes are differentially reduced from their virgin levels. If a given stock actually follows a dome-shaped stock/recruit curve, Cushing's technique will assign it a high index of density dependence when stock levels are high and a low index when stock is low; the calculated index is different according to whether most of the points lie on the ascending or descending limb of the stock/recruit
curve. This effect is illustrated in Cushing and Bridger (1966: Figure 21B) : two series of data for Norwegian herring, corresponding to different time periods and stock levels give very different values for the index of density dependence. A second criticism is that the data for individual stocks show a great deal of variation around the lines of best fit; it is clear that for many stocks the regression is not significant. Therefore, many of the derived indices of density dependence are of doubtful value. A third difficulty is that Cushing compares taxonomically and ecologically different groups of fishes on the single criterion of absolute fecundity without consideration of the effects of variables like body size and reproductive behavior on fecundity. If one considers two species of different body size whose eggs are approximately the same size, the same expenditure of reproductive effort will result in a higher fecundity for the larger species. Also, in interspecies comparisons fecundity tends to decrease as the amount of parental care for eggs and young increases.

When Cushing's work is viewed in the context of the theory of reproductive strategy discussed above, it is clear that he is considering only one of several variables of interest. In order to predict the response of a fish population to exploitation, one would want to consider agespecific reproductive effort, reproductive lifespan, age at first maturity and egg size, in addition to fecundity. However, in the absence of more comprehensive data, Cushing's conclusion is consistent with what would be predicted from considerations of reproductive strategy: that more fecund stocks will support a higher rate of fishing mortality. My reasoning
is that, all other things being equal, high fecundity indicates high reproductive effort, which should be accompanied by high levels of adult mortality, short reproductive span, early maturity, and relatively stable recruitment. A population with the above characteristics should be relatively insensitive to increased adult mortality due to fishing; in addition, high fecundity and early maturity mean that the population has a high capacity for increase and that under appropriate environmental conditions relatively small spawning stocks should be able to provide substantial numbers of recruits.

The picture as it stands is largely* qualitative and quite incomplete. However, the existing fisheries literature probably contains sufficient data for a more quantitative examination of the relations between reproductive strategy and the response of a fish population to harvesting. Such an approach might enable us to construct approximate stock and recruitment curves and to estimate sustainable yields on the basis of data collected during just one or a few seasons.

## CONCLUSIONS

1) The guppy population used in the present study, as well as natural Poeciliid populations investigated by other workers, appears to have evolved the ability to modify reproductive strategy in response to environmental conditions. Increasing intensity of competition for food appears to put a premium on large size of fry which brings about a decrease in fecundity, at least in the smaller females.
2) Measurement of the relevant reproductive parameters of the adult members of a natural population in just one or a few years should give insight into both the shape and the variability of the stock and recruitment relationship for that population. Among these relevant parameters are egg size, age at first maturity, reproductive lifespan, and reproductive effort at each spawning.

## SUMMARY

1) A central problem of fishery management is the determination of the relationship between the abundance of a stock of spawning adults and the resultant recruitment of young fish. It is of interest to determine both the shape of curve relating stock to recruitment and the year to year variation about the curve.
2) Theoretical stock/recruit curves imply the existence of density dependent population regulation; recruitment per unit stock is expected to decline at high stock densities.
3) A density dependent relationship between absolute fecundity and
population density has been demonstrated in many field and laboratory studies. It has been suggested that competition for food may be the mechanism producing the relationship.
4) The objectives of this study are to investigate the effects of competition for food on reproductive parameters - including size of fry and time between broods as well as fecundity - and to relate the findings to the stock and recruitment problem.
5) " Laboratory experiments were performed on guppies descended from natural stock collected in Trinidad, West Indies. Two series of data on reproduction were collected using female guppies selected from large stock tanks and maintained in isolation. The fish of the first series had been raised under conditions of relatively low intensity of competition for food; the second group of fish had experienced more intense competition. 6) In both series there was a significant positive regression of the logarithm of the number of fry per brood on matemal length. The slopes of the two regression lines were significantly different; the smaller females in the high competition group were less fecund than fish of the same size in the low competition treatment, but the larger females produced about the same numbers of fry in both treatments.
6) Under low competition the average size of fry increased significantly with maternal length, but when competition was more intense, the fry produced by the smaller females were larger, and all sizes of females produced fry as large as those of the largest females of the low competition treatment.
7) In both groups the weight of the entire brood increased significantly with maternal length; the regressions for the two groups were not different. Thus the smaller individuals of the high
competition group maintained the total weight of their broods but changed the distribution of weight among individual fry, producing smaller broods of larger fry.
8) The gestation period was significantly longer for females of the high competition group.
9) The set of reproductive characteristics manifested by an individual organism-amount and distribution over the organism's lifetime of energy devoted to reproduction, and distribution of energy among many or few gametes or progeny in a single reproductive attempt-mean be viewed as tactics which have evolved in concert as part of a reproductive strategy whose objective is to maximize the individual's genetic contribution to succeeding generations.
10) The ability to switch reproductive strategy in response to environmental conditions would seem to be of particular adaptive value to poeciliids, which typically have short generation times and life spans and often inhabit rather unstable environments. The guppy stock used in the present study clearly possesses some phenotypic flexibility for adjusting strategy to the environment; it is suggested that the reduction in fecundity and increase in size of individual fry produced by small females under intense competition would maximize the number of progeny surviving to reproduce under those conditions. Field studies by other investigators on related species in three other areas provide some evidence of similar switching of strategy.
11) The differential effect of ration on small and large females in this study is attributed to contest competition in which larger individuals were able to secure a disproportionate share of scarce food resources.
12) Other laboratory studies on guppies and trout (Salmo spp.) have also demonstrated a reduction in fecundity with reduced rations. In at least one case the reduction in fecundity was accompanied by an increase in egg size。
13) Several field studies have provided evidence of significant year to year variation in fecundity within exploited marine fish populations. In these cases fecundity appears to be inversely related to population density, and the effect may be mediated by competition for food.
14) An examination of data on geographical variation in fecundity of plaice (Pleuronectes platessa) reveals a significant tendency for fecundity to be inversely related to length of reproductive lifespan in different populations. It is suggested that populations whose larval mortality varies considerably from year to year tend to distribute reproductive effort over more years than populations for which larval survival is relatively constant.
15) A comparison of reproductive parameters of different stocks of herring (Clupea harengus) shows that winter and early spring spawners tend to produce relatively few and large eggs whereas summer-autumn spawners are more fecund and have smaller eggs. There is some evidence that both patterns represent adaptations to maximize the number of surviving larvae under the specific conditions which each spawning group faces. Large egg size (and low fecundity) is seen as an adaption to starvation as a major larval mortality source; small eggs and high fecundity occur in situations where predation is a major cause of larval deaths. The distribution of reproductive effort over the adult life span seems
to be related to the year to year variability in larval survival, as in plaice.
16) Cushing (1973) has demonstrated a rough relationship between the average fecundity of a fish population and the shape of its stock/recruit curve; more fecund species tend to follow curves having a more pronounced dome, which implies that these populations can sustain themselves under a higher rate of exploitation. I suggest that it should be possible to make more precise predictions about a population's stock/recruit curve by considering other reproductive parameters in addition to absolute fecundity--e.g. egg size, age at first maturity, and reproductive life span.

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Appendix Table I. Data from Experiment 1.

| Standard length of female (mm.) | Wet weight of female post partum (mg。) | Number of fry in brood | Mean standard length of fry within brood (mm.) | Standard deviation of fry lengths (mm.) | Estimated dry weight of brood (mg.) | Estimated index of reproductive effort |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 14.5 | 60 | 3 | 5.97 | . 21 | 2.26 | . 037 |
| 17.5 | 130 | 4 | 5.98 | . 26 | 3.03 | . 023 |
| 18.9 | 160 | 3 | 6.40 | 0.00 | 3.12 | . 019 |
| 22.5 | 310 | 9 | 6.37 | . 15 | 9.04 | . 029 |
| 22.4 | 260 | 4 | 6.05 | . 30 | 3.22 | . 012 |
| 25.2 | 400 | 16 | 6.36 | . 18 | 16.00 | . 040 |
| 25.3 | 330 | 12 | 6.38 | . 16 | 12.12 | . 036 |
| 26.7 | 430 | 21 | 6.50 | . 24 | 23.28 | . 054 |
| 27.1 | 500 | 25 | 6.47 | .30 | 27.42 | . 054. |
| 27.3 | 500 | 18 | 6.39 | . 25 | 18.54 | . 037 |
| 27.8 | 490 | 21 | 6.45 | . 22 | 22.51 | . 045 |
| 30.0 | 660 | 20 | 6.34 | . $20^{\circ}$ | 19.77 | . 029 |
| 30.5 |  | 9 |  |  |  |  |
| 31.7 | - 740 | 19 |  |  |  |  |
| 32.3 | 840 | 44 |  | . |  |  |
| 33.7 | 870 | 42 | 6.66 | . 30 | 40.07 | . 046 |
| 39.7 | 1650 | 39 | 6.54 | .21 | 44.54 | . 026 |
| 45.2 | 2470 | 175 | - 6.75 | . 38 | 177.59 | . 071 |

Appendix Table II. Numbers of embryos carried by females dying during Experiment 1.
15.5 ..... 8
22.5 ..... 8
$24 \cdot 4$ ..... 18
26.0 ..... 13
26.0 ..... 23
26.9 ..... 24
27.0 ..... 35
28.9 ..... 30
29.7 ..... 44
30.3 ..... 56
33.6 ..... 28
34.5 ..... 36
39.7 ..... 58
43.6 ..... 108

Appendix Table III. Data from Experiment 2.

Wet weight of female (mg.)
Weight of dry food consumed (mg.)
40
4
60
2

90
3
100
2
130
4
160
3
$200 \quad 9$
230 . 7
290 . 9
$740 \quad 22$
$780 \quad 23$
880 26

Appendix Table IV. Data from Experiment 3.


